Proceedings of the Linnean Society of New South Wales

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Proceedings of the Linnean Society of New South Wales

Issued 25th June, 1973

VOLUME 98
PART 1
No. 433

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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"

OFFICERS AND COUNCIL, 1973–74

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P. J. Stanbury, Ph.D.

Vice-Presidents
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N. G. Stephenson, M.Sc., Ph.D.; H. G. Cogger, M.Sc., Ph.D.

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B. D. Webby, M.Sc., Ph.D.
G. P. Whitley, F.R.Z.S.

Auditors
W. Sinclair and Company, Chartered Accountants

Linnean Macleay Lecturer in Microbiology, University of Sydney
K. Y. Cho, Ph.D.

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

ANNUAL GENERAL MEETING

28th MARCH 1973

The Ninety-eighth Annual General Meeting was held in the Society's Rooms, Science House, 157 Gloucester Street, Sydney, on Wednesday, 28th March 1973, at 7.30 p.m.

Dr. H. G. Cogger, President, occupied the chair.

The minutes of the Ninety-seventh Annual General Meeting (27th March 1972) were read and confirmed.

REPORT ON THE AFFAIRS OF THE SOCIETY FOR THE YEAR 1972

Publication

The Society's Proceedings for 1971, Part 4, was published on 17th April 1972, and for 1972, Parts 1, 2 and 3, on 22nd June, 11th October, 1972 and 8th January 1973.

The cost of publishing the Proceedings was as follows:

	$		$
Blockmaking (Illustrations)	1,046.23	Subscriptions ..	3,219.72
Printing	5,233.41	Miscellaneous Sales	704.48
Postage	170.91	Balance met from general funds ..	2,526.35
	6,450.55		6,450.55

	$
Net cost Proceedings	2,526.35
Net cost Reprints	88.04
Total net Publication Costs ..	$2,614.39

As recorded last year, in order to comply with Post Office regulations, a proportion of every member's subscription must be set aside specifically as a subscription to the Proceedings; Council decided that this should be $5.00 per annum. "Subscriptions" therefore include members and other subscribers, including the State Government, which purchases 100 volumes each year.

Membership

During the year 13 new members were admitted to the Society, six resigned, and two died. The numerical strength of the Society at 1st March, 1973, was: Ordinary Members, 265; Life Members, 29; Corresponding Members, 4; total, 298.

Monthly Meetings

Addresses were given at the April, July and October meetings; a symposium was held in June, a Field Day in September, and a Notes and Exhibits evening in November. Details of these may be found in the Abstract of Proceedings, Part 4, Volume 97 (1972).

Library

The re-cataloguing of all serials in accordance with rules followed in " Scientific Serials in Australian Libraries " (S.S.A.L.) has been completed. Amendments and additions to the library's holdings have been sent to S.S.A.L. (C.S.I.R.O.) to be incorporated in the next catalogue.

There has been a marked increase in requests for inter-library loans, and an average of about 30 per month have been fulfilled by supplying photocopies. In addition, a number of research students have consulted references in the library.

An invitation was issued to the Special Libraries Section of the Library Association of Australia to view the library, and hear something of its subject coverage, arrangement and services ; this resulted in a successful meeting on 30th October 1972, attended by about 50 members of the Association from all types of libraries. The address, given by the Society's Librarian, Mrs. C. McKay, was subsequently published in the Association journal.

During the coming year work will be concentrated on cataloguing the monographs which the library proposes to hold, namely works by Linnaeus and about Linnaeus, and the important collection of monographs issued by the British Museum.

It is hoped to begin the compilation of a cumulative index to the Proceedings of the last 50 years during the ensuing year.

Linnean Macleay Fellowship

Mrs. Lynette A. Moffat spent a further year as Linnean Macleay Fellow in the School of Biological Sciences. She resigned her Fellowship in January, 1973, to take up an appointment in the Faculty of Medicine, Sydney University.

During the year Mrs. Moffat was awarded her Ph.D. A paper entitled " The concept of primitiveness and its bearing on the phylogenetic classification of the Gekkota " was published in the Society's Proceedings in Part 4, Vol. 97 (1972).

Linnean Macleay Lectureship in Microbiology

Dr. K. Y. Cho, Linnean Macleay Lecturer in Microbiology, Sydney University, as from 1st January, 1969, reported as follows on his work for the year 1972 :

The main research work carried out this year is on the membrane biogenesis of *Azotobacter*. Growth of *Azotobacter* in the presence of spermine resulted in the accumulation of myelin-like structure. These structures were transformed into membrane after the removal of spermine. The utilization and not the accumulation was affected by inhibitors affecting macromolecular synthesis. It was suggested that these myelin-like structures may consist of phospholipid, an intermediate which may accumulate in the presence of a suitable inhibitor. An abstract of this work has been submitted for publication in Proceedings of the Australian Biochemical Society, May, 1973.

The identification of the unusual phospholipid of *Sarcina morrhuae* has been completed and a manuscript on this work has been accepted for publication in the *Australian Journal of Biological Sciences*, 1973.

Finance

The Honorary Treasurer presented the Balance Sheets and Income and Expenditure Accounts of the Society's four funds and commented on various aspects of the tabled documents.

Attention was drawn to the receipt during the year of an advance payment of $15,500 of the compensation monies due in respect of the resumption of Science House; this has been of considerable assistance in overcoming the problems of reconstruction with which the Society was faced.

In the General Account there was a deficit for the year of $7,875.15. Some $2,768 had been paid out of general funds for promotion expenses on behalf of the newly formed company which is to build and manage the proposed Science Centre, and it is anticipated that in due course this will be refunded to the Society by the company. A sum of $3,095 had been expended to enable the Society's library to continue to function as an active and effective scientific library in Sydney. The sum of $336 had been paid for illustrations for a forthcoming issue of the Proceedings that would normally have been charged during the coming year. The balance of the deficit, some $1,676, reflected the ever-increasing costs with which the Society is faced. However, it had been felt that the present was scarcely the time to curtail expenditure on scientific services, nor put the brake on activities aimed at providing for a new home and a field of profitable investment for our compensation monies.

The Linnean Society had agreed to undertake in its office the administration of Science House for a fee met jointly by the three owner bodies, and the General Account reflected this arrangement.

The Commonwealth Travel Grant was not part of the Society's own funds but was being held temporarily in the Society's bank account.

Interest from investments, and surplus income from the Fellowships Account were both a little higher. Income from Science House was lower than last year due to costs associated with its resumption.

The Bacteriology Account was in a satisfactory state and had attracted a small increase in interest.

The Fellowship Account was in a satisfactory state and had attracted a pleasing increase in interest. Out of the surplus income $266.66 had been transferred to accumulated funds and $4,458.85 transferred to the General Account.

The Scientific Research Fund had increased from $1,025 to $3,217.75 by donations and accumulation of interest.

The Honorary Treasurer reminded members that donations of $2.00 or over to the Scientific Research Fund were deductible from income tax. The fund offered a means whereby members and others could contribute according to their capacity to the endowment of the Society. Such funds were intended to support scientific work in the future, even as members and Fellows had benefited in the past from the foresight and generosity of the Society's distinguished founder and benefactor. The speed with which this fund could be put to practical use would depend on members' generosity, as well as upon the initially slow but ultimately spectacular benefits of compound interest.

Report on the Science Centre

The President then called on Professor N. G. Stephenson, Chairman of the Science Centre Planning Committee, to present his report.

Science House, erected by the Royal Society of N.S.W., the Linnean Society of N.S.W., and the Institution of Engineers, Australia, as a centre for learned societies, was resumed in 1970, and the total compensation offered and accepted amounts to $1·314 million dollars. The Linnean Society's share of this compensation money is $438,000, and payment to the former owners, including the Linnean Society, should be finalized this week.

As a consequence of these changes, a lease agreement had been negotiated with the Sydney Cove Redevelopment Authority, the new owners of Science House, for the continuing occupation and management of Science House by the Institution of Engineers, the Linnean Society and the Royal Society. The annual rent payable by Science House Management Committee to the Authority will be $26,000 ($500.00 per week); however, the rent paid by the Linnean Society for the space it occupies will not change ($3,560 per annum).

At a meeting of Science House Management Committee on 23rd August, 1972, the provision of management services for Science House on behalf of the Committee was discussed. These services have long been provided by the Institution of Engineers, and the Linnean Society, with the concurrence of its Secretary, Mrs. Inall, agreed to accept responsibility for the continuation of these services at a fee which the Society set at $2,400 per annum, this amount being subject to review.

The Linnean and Royal Societies of New South Wales have agreed to build a new Science Centre and to invest the monies received in compensation in this Centre as a joint venture. Up to the present, the steps taken towards this end have been guided by the Science Centre Planning Committee, consisting of representatives of both Societies. With the payment of compensation, the work of this Planning Committee will be taken over by a registered company, which will be known as Science Centre Pty. Ltd. and which will be jointly owned by the Linnean and Royal Societies.

The Board of Directors for this company has been appointed by the Linnean and Royal Societies, and consists of the following:

Linnean Society of N.S.W.:
- Professor D. J. Anderson.
- Dr. H. G. Cogger.
- Professor N. G. Stephenson.
- Dr. J. W. Vickery.

Royal Society of N.S.W.:
- Mr. E. K. Chaffer.
- Mr. J. W. Humphries.
- Mr. M. J. Puttock.
- Professor W. E. Smith.

Executive Secretary: Mrs. R. J. Inall.

Negotiations are proceeding for the purchase of land for the Science Centre, and it is hoped that an announcement regarding this can be made in the near future.

Project Managers

As soon as practicable, the Board of Directors will no doubt formalize the appointment of Jones, Lang, Wootton as project managers for the Science Centre. For some two years the firm has acted on behalf of the two Societies as Consultants. Its representatives have regularly attended meetings of the Science Centre Planning Committee and they have prepared feasibility studies on the various sites considered.

Financial Advisers

The Science Centre Planning Committee has appointed as Honorary Advisers Mr. H. McCredie, Secretary of the University of Sydney; Mr. J. Bragg, a partner of Cooper Bros. & Co., Chartered Accountants, Sydney; and Mr. J. Studdy, General Manager of Abbey Capital Property.

Architects

The Science Centre Planning Committee resolved at its last meeting to recommend to the Board of Directors of the new company that Jackson, Teece, Chesterman and Willis be appointed as Architects for the Science Centre Project.

Visit of the Director of the Commonwealth Foundation

Mr. J. Chadwick, Director of the Commonwealth Foundation, visited Sydney in February and was available for consultation on the 22nd. During this day the Science Centre Planning Committee had most useful discussions not only with Mr. Chadwick but also with representatives of Commonwealth Government departments. Mr. A. Griffith (Prime Minister's Department), Mr. D. Sturkey (Foreign Affairs, Aid Policy Section) and Mr. P. Free (Department of Science) came from Canberra for the day to meet Mr. Chadwick and members of the Committee.

A dinner in honour of Mr. and Mrs. Chadwick, held on the evening of 22nd February, was attended by Senator Lionel Murphy, Q.C., representing the Prime Minister, as well as by the Commonwealth Government and State Government representatives.

The meetings were followed up by Mrs. Inall, who made a short visit to Canberra subsequently for further discussions with Commonwealth representatives. The meetings in Sydney and Canberra were an unqualified success, as they enabled the Committee to meet informally the various authorities which we wish to involve to further this project. The Committee wishes to acknowledge the role Mrs. Inall has played in this respect. We have now, following advice received, applied to the Commonwealth Government for an annual grant, for three years in the first instance, to cover some of the administrative expenses in the establishment of the Science Centre.

Annual Elections

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

President: Dr. P. J. Stanbury.

Members of Council: Professor M. Hindmarsh, Dr. D. McAlpine, Dr. P. Myerscough, Dr. J. W. Vickery, Dr. B. D. Webby.

Auditor: W. Sinclair & Co.

The President, Dr. Cogger, explained that only five nominations were available for election to membership of Council as one of the nominees had resigned during the last month. As there were no provisions under the Act or Rules for dealing with such a situation, Council would fill this position as a casual vacancy at its next meeting as provided for under Rule 6 in the Act of Incorporation.

The Secretary announced with great regret that Dr. W. R. Browne had informed Council late last year that he would not be able to nominate for Council membership again due to personal circumstances. As a token of its appreciation, Council had appointed him Councillor Emeritus for the rest of his life.

The meeting passed a resolution expressing appreciation of Dr. Browne's long and devoted service to the Society.

President's Concluding Remarks

I regret that tonight I shall not be delivering a Presidential Address on the occasion of my retirement from the Presidency. Although I have a fairly recent precedent for this action, the Presidential Address is a tradition that I am sorry to see broken on any occasion. However, when I accepted the nomination for the Presidency a year ago I made it clear at the time that other commitments would almost certainly prevent me from preparing an Address.

Before handing over the reins to our new President, I want to discuss some of the prospects, as well as the problems, that are facing the Linnean Society in the immediate future. My purpose is the same tonight as in Council last week—to make those members present aware of the fact that this is their Society, and what it achieves will depend ultimately, as it always has in the past, on the participation and interest of its members. But there are new factors creeping into this relationship, most of which are a direct result of the rapidly increasing rate of change in the natural sciences, in our universities, and in social customs in general. We have to ask ourselves whether, and if so how, a learned society like ours can survive the onslaught of such varied and perhaps unrelated pressures as television, enormous student numbers in our universities, or public concern with major environmental issues, some of which are no doubt fashionable but are none the less of special importance to natural scientists. You may not know, for example, that your Council has laid down a deliberate policy of non-involvement in political issues. Some of you will doubtless agree with this stand, while others will not. I would like the scientific standing of the Linnean Society to be such as to have our views on major issues sought by scientific bodies and governments of all political persuasions.

Now there are, of course, areas where the Society has not had the resources to keep pace with changing values. Probably the best example would be the Linnean Macleay Fellowships. In times past the Macleay Fellowship was highly sought after and conferred very great honour and credit on an encumbent, while the stipend offered made it one of the more lucrative fellowships available. Fortunately, the honour and glory are still there, but the stipend is scarcely enough to support a graduate student lacking other resources. This is not the fault of the Society, but simply another instance of the effects of inflation.

Nevertheless, it may come as a surprise to most of you to know that the Linnean Society is probably the wealthiest scientific society in Australia. As you have already heard tonight from Professor Stephenson, we are about to embark with the Royal Society on a multi-million dollar scientific and commercial development, while our relationships with the Commonwealth and State Governments and with the Commonwealth Foundation leave no doubt that our Society is about to be drawn into major areas of scientific advice and planning which have not previously been the province of our Society.

But what is the society which is about to blossom on the local, and indeed the international scientific scene? How many people in the community at large know that it exists?

I have already mentioned that we are one of the wealthiest societies in this country, and there is no doubt that this is a major step in the right direction. We will soon be co-owners of a major scientific and commercial building in Sydney which will include a scientific library, lecture theatres, convention facilities, etc. I might add that Science House also has these facilities, but on a small scale. Anyway, these are the things we can regard as being on the Society's credit balance, as it were.

On the other hand, this rather wealthy Society has a relatively small membership and what must undoubtedly be the poorest member participation of any scientific society in Australia. As I said to Council last week, it has been my sorry and embarrassing duty on a number of occasions to welcome distinguished guest speakers to our meetings where they have addressed a dozen or fewer members. This is not only embarrassing to me, it is downright offensive to the speaker.

It seems to me, then, that the traditional meetings of the Linnean Society no longer work for a number of reasons. Most of us have commitments, which are perhaps no greater than those of our predecessors, but are unquestionably more complex logistically if not scientifically.

There have been vast changes in the complexity of the natural sciences which have resulted in higher and higher levels of specialization by natural scientists. I am very much a traditionalist myself, and the history of this Society and the historical basis of many of our activities give me real pleasure. However, I am bound to ask whether, if traditional actions and activities fail to elicit traditional responses, is it not time that these activities are re-examined. Can we afford the club-like atmosphere of the old Linnean Society if no one goes to the club any more? Your Council works hard and well on your behalf, but it is clear from attendance records that most Councillors feel that their duty stops short of having to attend regular monthly meetings.

I have just said that I am a traditionalist, but if there is one thing I have learned from a study of the Society's history it is that Sir William Macleay was not only a magnificent benefactor but also a man of extraordinary foresight and adaptability. I have absolutely no doubt in my mind that if he were alive today he would be right up front pressing us to change our traditional role, wherever necessary, to meet these changing conditions.

All I ask, then, is that all of you who have been interested enough in our Society to attend tonight should give serious thought to what you want out of the Society. How do you want to participate in it? Maybe you are happy with it as it is, but if you are not, then I urge you to get your views across to Council, either by letter or, preferably, by expressing those views in person to one or more Councillors.

Now, finally, I must say that I have been greatly honoured to serve as your President in this very exciting period of the Society's history, and it has given me a great deal of personal pleasure. To my colleagues on Council I am grateful for their help and tolerance; I can assure you that they have served you faithfully and well. However, I think we should all be especially grateful for the considerable time and effort expended on our behalf by Professor Stephenson, Dr. Vickery and Mrs. Inall.

And now I have very great pleasure in handing over the chair and the Presidency to Dr. Peter Stanbury. In view of the developments we have discussed tonight, Dr. Stanbury is taking on the Presidency at a very exacting and time-consuming stage in the Society's development. I wish him well and I have no doubt that the Society will be proud of his achievements.

A vote of thanks was moved to Dr. Cogger, the retiring President, by Mr. G. P. Whitley and carried by acclamation by the meeting.

LINNEAN SOCIETY OF NEW SOUTH WALES

GENERAL ACCOUNT

Balance Sheet as at 28th February 1973

1972 $		$	$
	Accumulated Funds—		
	Balance, 1st March 1972:		
	Amount Received from Sir William Macleay	40,000.00	
	Transfers from Income Account ..	7,563.65	
	Transfers from Contingencies Reserve	68,258.38	115,822.03
	Add Sydney Cove Redevelopment Authority Compensation Received ..		15,500.00
			131,322.03
	Less Deficiency for the Year		7,875.15
115,822	Balance, 28th February 1973		123,446.88
	Reserves—		
—	Science House Management	152.50	
1,143	Bookbinding	1,142.66	1,295.16
274	Sundry Creditors		—
—	Commonwealth Foundation Travel Grant ..		918.75
$117,239			$125,660.79

1972 $		$	$
	Fixed Assets—		
	Furniture, Fixtures and Fittings—At Cost	370.91	
	Less Depreciation Written Off ..	42.51	
323			328.40
	Office Machines—At Cost	1,306.13	
	Less Depreciation Written Off ..	296.73	
1,187			1,009 40
$1,510	Total Fixed Assets		1,337.80
	Investments—		
—	Deposit N.S.W. Permanent Building Society	5,000.87	
30,000	Commonwealth Loans—At Cost	30,000.00	
	Debentures—At Cost:		
39,700	Metropolitan Water, Sewerage and Drainage Board	39,700.00	
—	Mutual Acceptance Limited	5,000.00	
6,000	Sydney County Council	6,000.00	
30,470	Science House—At Cost (one-third Interest)	30,470.43	
4,750	Loan on Mortgage	4,750.00	
$110.920	Total Investments		120,921.30
	Current Assets—		
1,628	Sundry Debtors	612 95	
4	Cash on Hand	43.07	
3,177	Commercial Banking Company of Sydney Limited	2,745.67	
$4,809	Total Current Assets		3,401.69
$117,239			$125,660.79

AUDITORS' REPORT

We have audited the books and records of the Linnean Society of New South Wales for the year ended 28th February 1973, 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 1973, according to the explanation given to us and as disclosed by the books of the Society.

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

DATED at Sydney this nineteenth day of March 1973.

19th March 1973

Joyce W. Vickery,
Hon. Treasurer.

LINNEAN SOCIETY OF NEW SOUTH WALES

GENERAL ACCOUNT

Income and Expenditure Account for the Year Ended 28th February 1973

EXPENDITURE

1972 $		$
150	Audit Fees	250.00
343	Cleaning	442.00
129	Depreciation	206.33
1,053	General Expenses	733.90
875	Illustrations	1,046.23
64	Insurance	84.74
282	Library	138.09
250	Life Assurance Premium	250.00
93	Light and Power	98.11
702	Postages	641.21
3,380	Proceedings—Printing Costs	5,233.41
171	Professional Services	—
573	Printing and Stationery	526.15
167	Referees' Fees	95.00
219	Repairs and Maintenance	195.08
936	Reprints	923.72
15,005	Salaries and Honorarium	14,316.35
3,556	Science House Rent	3,556.00
232	Telephone	485.11
$28,180	Total Expenditure	$29,221.43

INCOME

1972 $		$	$
	Subscriptions:		
	Members'	470.00	
4,343	Proceedings	2,356.87	2,826.87
	Science House Management Reimbursement:		
	Salaries	672.50	
—	Management Fees	375.00	1,047.50
4,683	Interest Received		4,892.62
	Fellowships Account:		
3,893	Surplus Income for the Year Ended 28th February 1973		4,458.85
30	Rents Received		—
806	Reprints Sales		698.56
1,957	Sales		704.48
	Science House:		
7,215	Share of Surplus		6,717.40
22,927	Total Income		21,346.28
5,253	Deficiency for Year Transferred to Accumulated Funds		7,875.15
$28,180			$29,221.43

LINNEAN SOCIETY OF NEW SOUTH WALES

LINNEAN MACLEAY FELLOWSHIPS ACCOUNT

Balance Sheet as at 28th February 1973

1972 $		$	$
	Accumulated Funds—		
	Balance, 1st March 1972:		
	Amount Bequeathed by Sir William Macleay	70,000.00	
	Transfers from Income Account	52,539.64	
	Increase in Value of Assets	260.02	
			122,799.66
	Add:		
	Increase in Value of Assets	12.00	
	Transfer from Income and Expenditure Account	266.66	
			278.66
122,800			123,078.32
$122,800			$123,078.32

1972 $		$
	Fixed Assets—	
60,288	Commonwealth Loans—At Cost	59,500.00
	Debentures—At Cost:	
6,000	Electricity Commission of New South Wales	6,000.00
—	F.N.C.B. Waltons Corporation Limited	1,262.90
37,700	Metropolitan Water, Sewerage and Drainage Board	37,700.00
—	Mutual Acceptance Limited	800.00
1,800	Rural Bank of New South Wales	1,800.00
15,750	Loans on Mortgage	15,750.00
121,538		122,812.90
	Current Assets—	
1,262	Commercial Banking Company of Sydney Limited	265.42
$122,800		$123,078.32

Income and Expenditure Account for the Year Ended 28th February 1973

1972 $		$
2,933	Salary of Linnean Macleay Fellow	2,933.34
267	Transfer to Capital Account	266.66
3,893	Surplus for the Year transferred to General Account	4,458.85
$7,093		$7,658.85

1972 $		$
7,093	Interest Received	7,658.85
$7,093		$7,658.85

AUDITORS' REPORT

We have audited the books and records of the Linnean Society of New South Wales for the year ended 28th February 1973, 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 1973, according to the explanations given to us and as disclosed by the books of the Society.

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

DATED at Sydney this nineteenth day of March 1973.

Joyce W. Vickery,
Hon. Treasurer.

19th March 1973.

LINNEAN SOCIETY OF NEW SOUTH WALES

BACTERIOLOGY ACCOUNT

Balance Sheet as at 28th February 1973

1972 $		$	$	1972 $		$
	Accumulated Funds—				Investments—	
	Balance, 1st March 1972:			26,900	Commonwealth Loans—At Cost	26,900.00
	Amount Bequeathed by Sir William Macleay	24,000.00			Debentures:	
	Transfers from Income Account, etc.	13,227.41	37,227.41	1,800	Metropolitan Water, Sewerage and Drainage Board—At Cost	1,800.00
	Add Surplus for Year		364.34	8,000	Loan on Mortgage	8,000.00
				36,700		36,700.00
37,227	Balance, 28th February 1973		37,591.75		Current Assets—	
				527	Commercial Banking Company of Sydney Limited ..	891.75
$37,227			$37,591.75	$37,227		$37,591.75

Income and Expenditure Account for the Year Ended 28th February 1973

1972 $		$	1972 $		$
	University of Sydney:		1,902	Interest Received	2,214.34
1,850	Salary of Lecturer	1,850.00			
52	Surplus for the Year	364.34			
$1,902		$2,214.34	$1,902		$2,214.34

AUDITORS' REPORT

We have audited the books and records of the Linnean Society of New South Wales for the year ended 28th February 1973, 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 1973, according to the explanations given to us and as disclosed by the books of the Society.

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

DATED at Sydney this nineteenth day of March 1973.

Joyce W. Vickery,
Hon. Treasurer.

19th March 1973.

LINNEAN SOCIETY OF NEW SOUTH WALES

SCIENTIFIC RESEARCH FUND ACCOUNT

Balance Sheet as at 28th February 1973

1972 $		$	$	1972 $		$
	Accumulated Funds—				Investments—	
	Balance, 29th February 1972	1,025.00			Debentures—At Cost:	
	Interest Received	184.75		—	F.N.C.B.—Waltons Corporation Limited ..	1,021.00
	Donations Received	2,008.00		1,000	Loans on Mortgage	2,000.00
					Current Assets—	
1,025	Balance, 28th February 1973		3,217.75	25	Commercial Banking Company of Sydney Limited	196.75
$1,025			$3,217.75	$1,025		$3,217.75

AUDITORS' REPORT

We have audited the books and records of the Linnean Society of New South Wales for the year ended 28th February 1973, 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 1973, according to the explanations given to us and as disclosed by the books of the Society.

W. SINCLAIR & CO.,
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as amended.

DATED at Sydney this nineteenth day of March 1973.

JOYCE W. VICKERY,
Hon. Treasurer.

19th March 1973.

THE FIRST ZOEA LARVAE OF THE ESTUARINE CRABS *SESARMA ERYTHRODACTYLA* HESS, *HELOGRAPSUS HASWELLIANUS* (WHITELEGGE) AND *CHASMAGNATHUS LAEVIS* DANA (BRACHYURA, GRAPSIDAE, SESARMINAE)

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[Accepted for publication 20th September 1972]

Synopsis

In the vicinity of Sydney, N.S.W., *S. erythrodactyla* breeds from September to March, *H. haswellianus* from March to June, and *C. laevis* probably from October to February. A detailed description is given of the planktonic first-zoea larva of each species. When the larvae are classified in accordance with the key to the major groups of grapsid larvae given by Wear (1970), the results support Wear's view that the Sesarminae do not form a natural grouping on larval characters. The use of chromatophore patterns to identify larval species within the genus *Sesarma* is also discussed.

Introduction

Research on the rearing of larval Brachyura has been actively pursued in recent years and descriptions of second and later zoeal stages reared in the laboratory are now available for several species (*e.g.* Lebour, 1928 ; Costlow and Bookhout, 1960, 1962 ; Wear, 1967 ; Yang, 1971). There are also numerous descriptions of first zoea larvae of known parentage hatched from the egg in the laboratory. Yet of the 23 families, 217 genera and 643 species of Brachyura in Australian coastal waters (Griffin and Yaldwyn, 1967), the first zoea larvae of only two species have previously been described. These are *Mictyris longicarpus* Latreille, whose larvae were described by Cameron (1965) from crabs collected in Queensland, and *Leptograpsus variegatus* Fabricius, described by Wear (1970) from crabs collected in New Zealand waters. The present account is therefore the first to describe zoea larvae hatched in the laboratory from crabs collected intertidally in New South Wales.

The three species under investigation, *Sesarma erythrodactyla* Hess, *Helograpsus haswellianus* (Whitelegge) and *Chasmagnathus laevis* Dana, belong to the subfamily Sesarminae of the family Grapsidae. Wear (1970) pointed out a discrepancy between the adult and larval classification of the Sesarminae. On the basis of larval characters, the subfamily does not appear to represent a natural grouping. The results of the present study are discussed in relation to this problem. The taxonomic significance of the chromatophore pattern of the first zoea larva in the genus *Sesarma* is also discussed.

Materials and Methods

Sesarma erythrodactyla Hess, the red-fingered marsh crab, is a small estuarine crab whose adults vary in carapace width from about 10 mm to 17 mm. The species burrows in mangrove swamps, or lives in rocky crevices or under rocks on intertidal mudflats along the eastern Australian coast, from central Queensland to southern New South Wales. *Helograpsus haswellianus* (Whitelegge) is about the same size as *S. erythrodactyla* and lives under rocks on mudflats in sheltered estuaries from southern Queensland to Victoria and Tasmania, and to Spencer Gulf, South Australia. *Chasmagnathus laevis* Dana, a slightly larger species, also lives under rocks on mudflats along the New South Wales coast, but at a higher level on the shore than *S. erythrodactyla* and *H. haswellianus*, at or above the high tide level.

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The specimens used in this study were collected from Gymea Bay, Port Hacking, New South Wales, at monthly intervals from February to September, 1971. Ovigerous females were placed singly or in pairs in small plastic containers (diameter 17·5 cm) containing rocks and seaweed from the collection area and seawater, which was changed daily. Other mature males and females were placed in larger aquaria containing aerated seawater ; their habitat and feeding requirements were met in the same way as those of the ovigerous females. The ambient temperature was approximately 24° C.

The breeding cycles

The monthly collections provided data on the reproductive cycles of the three species.

In February and March, ovigerous females of *S. erythrodactyla* were numerous and three females laid eggs in the laboratory. From April to September no ovigerous females could be found. However, examination of the ovaries of females collected during this period showed that the ovaries were full of ripe oocytes in August. It therefore seemed likely that oviposition would begin in September or October. This implies a spring and summer breeding season of six to seven months, from September-October to March, and a non-breeding season of five to six months during the autumn and winter.

The females of *H. haswellianus* were found to carry eggs from March to June, 1971. The breeding season is thus confined to the autumn months and reaches a peak in May, when nearly every mature female observed was ovigerous.

In contrast, only two ovigerous females of *C. laevis* were obtained during the period of investigation. Both were collected in early February, indicating that February is the end of the breeding season of this species. The onset of the breeding season in *C. laevis* was not determined, but must be later than September, implying a relatively brief breeding season in the late spring and early summer (October to February).

Examination of the first zoea larval stage

For each species, the eggs were allowed to hatch in the laboratory and the first zoea larvae were studied in detail. Living larvae were observed in seawater, with methyl cellulose added to slow the movement of the larvae. Specimens required for dissection and whole mounts were fixed and preserved in 10% formalin in seawater, or were fixed in alcoholic Bouin's fluid and preserved in 80% alcohol. Dissections were performed in the preservative under the binocular microscope, using fine needles. Whole, fixed larvae were mounted in glycerine jelly by the following technique (Weesner, 1960). The larvae were transferred from 10% formalin to distilled water, and then to a solution of 20% glycerine in distilled water. The water was evaporated off in a 58° C oven for 20 minutes and the specimens, now in glycerine, were transferred to a drop of glycerine jelly at 40° C on a slide on a hot plate. The larvae were arranged in the correct position and covered with a coverslip. The preparation was then allowed to cool. When the jelly solidified it held the larva in place.

Drawings of the larvae were made with the aid of a drawing apparatus.

RESULTS

A complete description is given below of the first zoea larva of *Sesarma erythrodactyla*. Descriptions of the first zoea larvae of *Helograpsus haswellianus* and *Chasmagnathus laevis* are then given in a summarized form. For each species, characters are listed in proximal to distal order, unless otherwise stated. The measurements given are the average values obtained from 10 larvae.

The First Zoea Larva of Sesarma erythrodactyla *Hess*

After 20 days of incubation, the egg of *S. erythrodactyla* is 0·35 mm long and 0·29 mm across and the embryo is ready to hatch. Hatching is achieved by violent twitching movements of the abdomen, which tear the egg membranes. The abdomen emerges first, followed by the cephalothoracic region, whose maxillipeds also twitch strongly and rapidly. The larva hatches as a pre-zoea larva with a thin cuticle, lacking plumose processes. The pre-zoeal cuticle is soon shed and the larva emerges as the first zoea stage (Fig. 1). The larva is almost transparent, except for the large, heavily pigmented eyes and a number of black and dichromatic black to reddish-orange chromatophores.

The length of the larva, measured from the tip of the caudal fork to a point dorsal to the eyes, thence to the tip of the rostrum, is 1·21 mm.

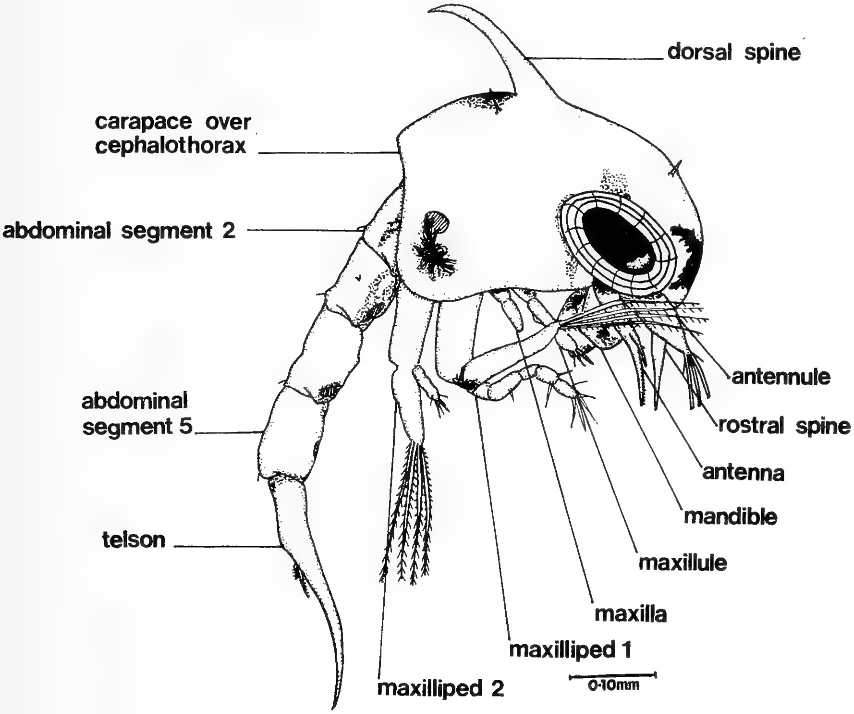

Fig. 1. The first zoea of *Sesarma erythrodactyla*, lateral view.

(i) *The cephalothorax*

The rostral spine of the cephalothorax is straight and is 0·13 mm long. The dorsal carapace spine, which is slightly curved posteriorly, is 0·15 mm long. The distance from the tip of the rostral spine to the tip of the dorsal spine is 0·60 mm. The posterior margins of the carapace are fringed with very fine, short hairs. The carapace also carries two dorsolateral setae just behind the dorsal carapace spine, and two anterolateral setae just above the eyes. The eyes are sessile and are large (0·16 mm in diameter) relative to the size of the larva.

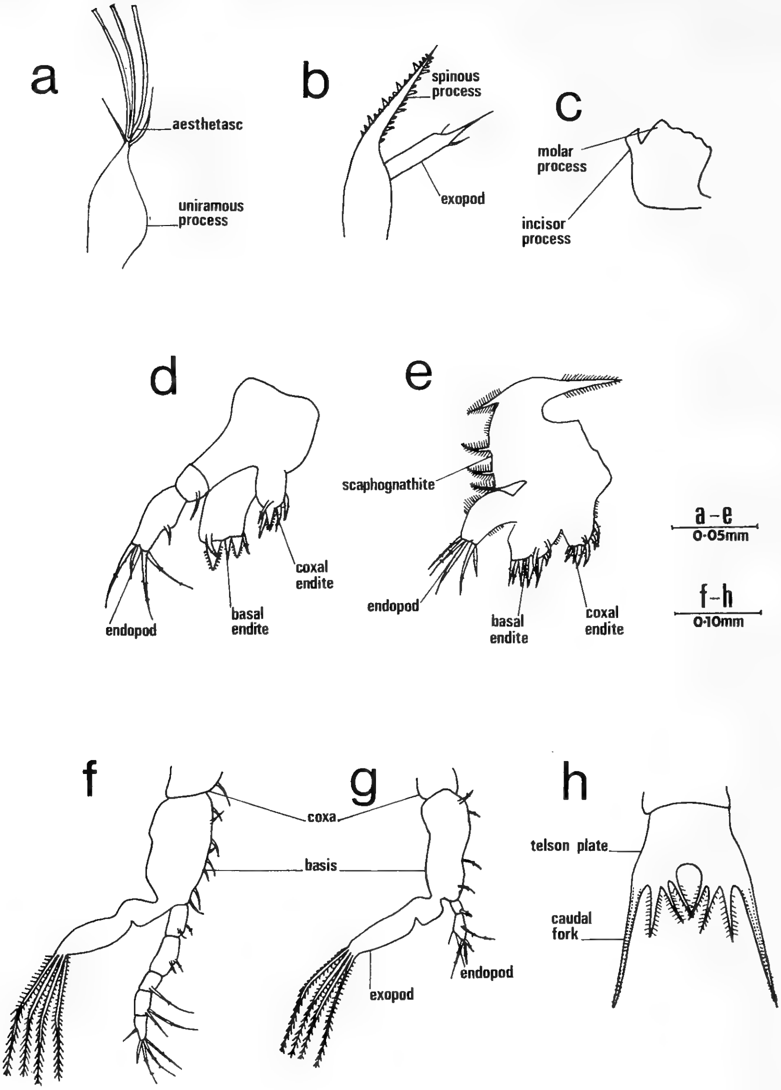

Fig. 2. The appendages and telson of the first zoea of *Sesarma erythrodactyla*. *a*, antennule ; *b*, antenna ; *c*, mandible ; *d*, maxillule ; *e*, maxilla ; *f*, maxilliped 1 ; *g*, maxilliped 2 ; *h*, telson, dorsal view.

(ii) *The cephalic appendages*

The five pairs of cephalic appendages are characterized by their segmentation and setation.

(*a*) *The antennule* (Fig. 2 (*a*)). The uniramous, unsegmented antennule is 0·09 mm long. It bears three long terminal aesthetascs of equal length (0·12 mm) and two shorter, terminal, non-plumose setae, each 0·04 mm long.

(*b*) *The antenna* (Fig. 2 (*b*)).The spinous process of the antenna is 0·14 mm long and bears a double row of 15 spines along its distal half. The third, sixth, ninth and twelfth spines are longer and stouter than the other spines.

The exopod is slightly more than half the length of the spinous process. One lateral seta and a small medial seta arise behind the pointed, spine-like tip of the exopod.

(*c*) *The mandible* (Fig. 2 (*c*)). The mandible is strongly toothed, with a ridged molar process and a small incisor process. It lacks a palp. The mandible is 0·95 mm across.

(*d*) *The maxillule* (Fig. 2 (*d*)). Both the coxal and basal endites of the maxillule bear five plumose setae ; on the coxal endite one of those setae is large, and on the basal endite two are large.

The endopod consists of three segments. The proximal segment is fused with the protopod and does not bear any setae. The medial segment is short and bears one non-plumose seta on its inner margin, about half way along its length. The long distal segment bears four terminal plumose setae and one subterminal non-plumose seta midway along the inner margin.

(*e*) *The maxilla* (Fig. 2 (*e*)). The coxal endite, the basal endite and the endopod of the maxilla are all bilobed and each lobe bears a number of marginal plumose setae. The medial and lateral lobes of the coxal endite possess five and three setae respectively. The medial and lateral lobes of the basal endite possess five and four setae, respectively. The inner margin of both endites are fringed with fine hairs.

The endopod forms two distal lobes of unequal size, separated by a shallow, terminal cleft. The larger lateral and smaller medial lobes give rise to three and two long, plumose setae, respectively. Both the outer and inner margins of the endopod are fringed with fine hairs.

The proximal tip of the scaphognathite is produced into a plumose spine, and four finely plumose setae are spaced along the outer and distal margins of the scaphognathite. Fine hairs fringe the portion of the scaphognathite between the two most proximal plumose setae.

(iii) *The thoracic appendages*

Like the cephalic appendages, the thoracic appendages are characterized by their segmentation and setation.

(*a*) *The first maxilliped* (Fig. 2 (*f*)). One sparsely plumose seta arises from the inner margin of the coxa of the first maxilliped. The basis, with a length of 0·15 mm, is about two and a half times as long as wide, and bears on its inner margin four pairs of short, non-plumose setae.

The endopod is 0·17 mm long. It bears a number of sparsely plumose setae. Proceeding in a proximal to distal direction, the ischium bears two short setae of about equal length on the inner margin, two-thirds of the way along its length ; the merus, which is about one and one-half times as long as the ischium, bears two short setae midway along the inner margin ; the carpus, about half the length of the ischium, bears one long inner distal seta ; the propodus, about three-quarters the length of the ischium, bears two long inner distal setae, and the dactylus, about the same length as the propodus, bears four long terminal setae and a very small unarmed seta midway along its outer margin.

The exopod, 0·16 mm long, is incompletely divided into two unequal segments. It is tipped with four long, biplumose, natatory setae, each 0·19 mm long.

(*b*) *The second maxilliped* (Fig. 2 (*g*)). The coxa of the second maxilliped is without setae. The basis, 0·14 mm long, bears four short, sparsely plumose setae along its inner margin.

The three-segmented endopod is 0·05 mm long. The first segment is without setae, the second bears one short, inner, distal, plumose seta, and the third segment bears a total of five setae : one long, plumose seta on the inner margin ; one short, smooth seta laterally ; and one long and two shorter plumose setae at the tip.

The exopod, 0·12 mm long, bears four long, terminal, biplumose, natatory setae, each 0·20 mm long.

(*c*) *The third maxilliped.* The third maxillipeds are rudimentary.

(*d*) *The pereiopods.* No pereiopods are present.

(*e*) *The gill buds.* No gill buds are present.

(iv) *The abdomen*

(*a*) *The abdominal segments.* The first, fourth and fifth abdominal segments are each 0·11 mm in length ; the second and third segments are shorter

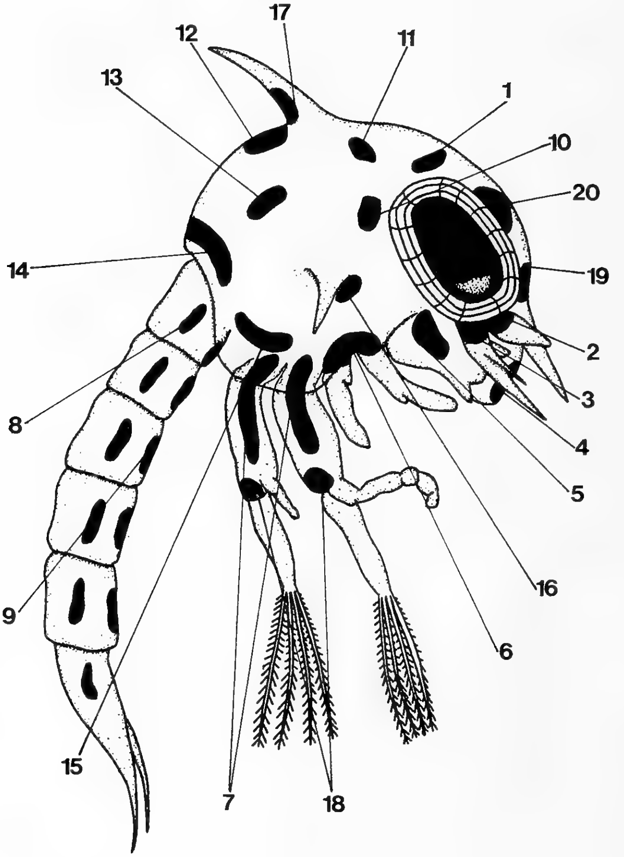

Fig. 3. The system of chromatophores of a first zoea larva, following Wear's 1968 modification of Aikawa's 1929 classification.

PRIMARY SYSTEM :

A. *Neural Group.* 1. Supracerebral 2. Antennular 3. Antennal 4. Labral 5. Mandibular 6. Maxillar 7. Maxillipedal 8. Lateral intestinal 9. Subintestinal.

B. *Visceral Group.* 10. Median gastric 11. Precardiac 12. Subcardiac 13. Postcardiac.

SECONDARY SYSTEM :

14. Posterior carapacial 15. Posteroventral carapacial 16. Lateral carapacial 17. Dorsal carapace spine 18. Maxillipedal 19. Optic 20. Median ocular centre.

(0·08 mm). The first segment bears no spines or setae. Segments two and three each carry a pair of dorso-lateral papillae. The papillae of segment two, which are directed forwards, are well developed, as in all brachyuran larvae. Those of segment three are very small and directed backwards. Segments two to five each possess short lateral expansions on their posterior margins and carry a pair of dorsal setae. Limb buds are absent.

(*b*) *The telson* (Fig. 2 (*h*)). The telson, including the caudal fork, is 0·23 mm long. The lateral cornua are long and slender; they are almost straight in dorsal view and only slightly curved dorsally in lateral view. Distally the cornua each bear two dorso-lateral rows of approximately 30 short fine hairs. The distance between the tips of the lateral cornua is 0·18 mm. The telson plate is 0·07 mm long, with a breadth of 0·12 mm at its posterior margin. The median cleft of the posterior margin is crescent-shaped and quite broad. On either side of the median cleft are three plumose setae, the middle seta of each side being shorter than the outer setae.

TABLE 1

Sesarma erythrodactyla. *Chromatophores of First Zoea Larva*

(+=chromatophore present; —=chromatophore absent)

PRIMARY SYSTEM		
A. *Neural Group*		
1. Supracerebral	—	
2. Antennular	+	Black
3. Antennal	+	Black
4. Labral	+	Black
5. Mandibular	+	Black
6. Maxillar	+	Black
7. Maxillipedal	+	First maxilliped only; black
8. Lateral intestinal	+	Segments 1 and 2; segment 1 coalesced with 13 below; dichromatic black to reddish-orange
9. Subintestinal	+	Segments 2–5; dichromatic black to reddish-orange
B. *Visceral Group*		
10. Median gastric	+	Dichromatic black to reddish-orange
11. Precardiac	—	
12. Subcardiac	+	Black
13. Postcardiac	+	Dichromatic black to reddish-orange; coalesced with 8 in abdominal segment 1
SECONDARY SYSTEM		
14. Posterior carapacial	—	
15. Postoventral carapacial	+	Dichromatic black to reddish-orange
16. Lateral carapacial	—	
17. Dorsal carapace spine	—	
18. Maxillipedal	+	First maxilliped only; black
19. Optic	+	Black
20. Median ocular centre	+	Black

(v) *The chromatophores*

The chromatophores of the first zoea of *S. erythrodactyla* are black or dichromatic black to reddish-orange in the living larva. Fixation and preservation of the larva causes a fading of the colours, and may eventually distort the original position of the chromatophores (Aikawa, 1933). The black chromatophores are the most stable but they, too, fade with time. Thus, although the chromatophores are constant inheritable characters of the zoeal (see Aikawa, 1929), they cannot be used for the identification of long preserved specimens. They may be used, with other identifying characters, to identify larvae which have not been preserved for long periods.

In 1929 Aikawa classified the zoeal chromatophores into two systems—a Primary System and a Secondary System. The Primary System, which is further subdivided into a Neural Group and a Visceral Group, contains profusely branched and segmentally arranged chromatophores. The Secondary System contains chromatophores which are numerous, sparsely branched and irregularly arranged. In 1968 Wear modified Aikawa's classification, by adding two new chromatophores to the Neural Group of the Primary System, and two new chromatophores to the Secondary System. Figure 3 is a diagram showing the position of the chromatophores. The numbering system used follows Wear's 1968 modification of Aikawa's classification.

The details of the chromatophores of the first zoea larva of *S. erythrodactyla* are listed in Table 1 in accordance with the scheme presented in Fig. 3. Observations on living larvae allowed the colour of the chromatophores to be accurately specified.

The First Zoea Larva of Helograpsus haswellianus (*Whitelegge*)

H. haswellianus hatches in the usual manner as a pre-zoea larva. After a short time the larva sheds this cuticle and becomes a first zoea. The first zoea larva of *H. haswellianus*, illustrated in Fig. 4 (*a*), has a total length of 1·49 mm. The important larval characteristics can be summarized as follows:

(i) *The Cephalothorax*

Rostral spine 0·15 mm long.
Dorsal carapace spine 0·15 mm long, strongly curved posteriorly from about one-fifth of the way along its length.
Length from tip of rostrum to tip of dorsal spine 0·53 mm.
Lateral carapace spines 0·09 mm long, directed slightly posteriorly and curved downwards.
Posterior margin of carapace fringed with short hairs, with seven to nine short stout spines ventrolaterally.
One pair of dorso-lateral setae just behind dorsal carapace spine.
Eyes sessile, 0·19 mm across.

(ii) *The cephalic appendages*

(*a*) *The antennule* (Fig. 5 (*a*))
Uniramous; 0·07 mm long.
Two long aesthetascs and one short seta terminally.

(*b*) *The antenna* (Fig. 5 (*b*))
Biramous.
Spinous process 0·14 mm long; bearing a double row of 12 spines along its distal length (spines 2, 4, 6 and 8 longer and stouter than remaining spines).
Exopod about two-thirds length of spinous process; one lateral seta and one very fine medial seta arising just below the spine-like tip.

(*c*) *The mandible* (Fig. 5 (*c*))
0·05 mm across.
Strongly toothed.
Well developed incisor and molar processes.

(*d*) *The maxillule* (Fig. 5 (*d*))
Coxal endite bearing five plumose setae.
Basal endite bearing five plumose setae, including one very long one.
Three segments of endopod bearing nil, one and five sparsely plumose setae, respectively.

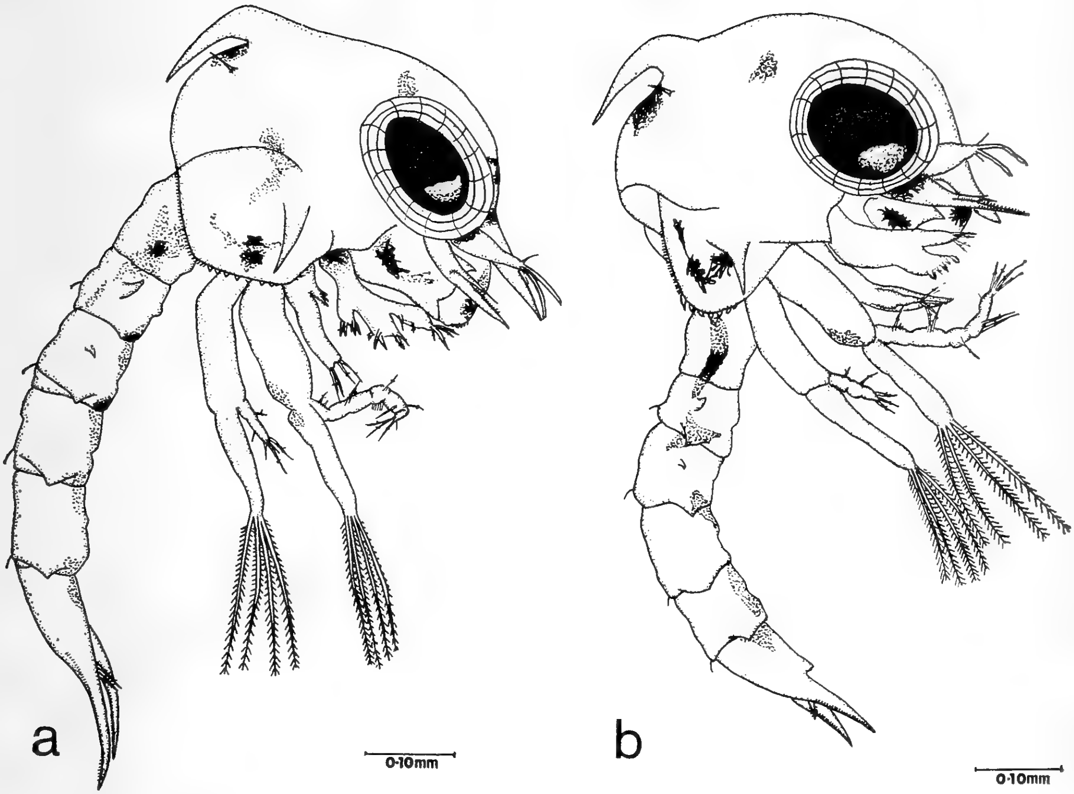

Fig. 4. The first zoea of: *a*, *Helograpsus haswellianus*, lateral view; *b*, *Chasmagnathus laevis*, lateral view.

(*e*) *The maxilla* (Fig. 5 (*e*))

Coxal endite bearing respectively four and three marginal plumose setae on the medial and lateral lobes.

Basal endite bearing respectively five and four marginal plumose setae on the medial and lateral lobes; inner margin fringed with fine hairs.

Medial and lateral lobes of endopod each bearing two terminal setae; outer and inner margins fringed with fine hairs.

Scaphognathite with proximal tip produced into plumose spine; four finely plumose setae spaced along the outer and distal margins.

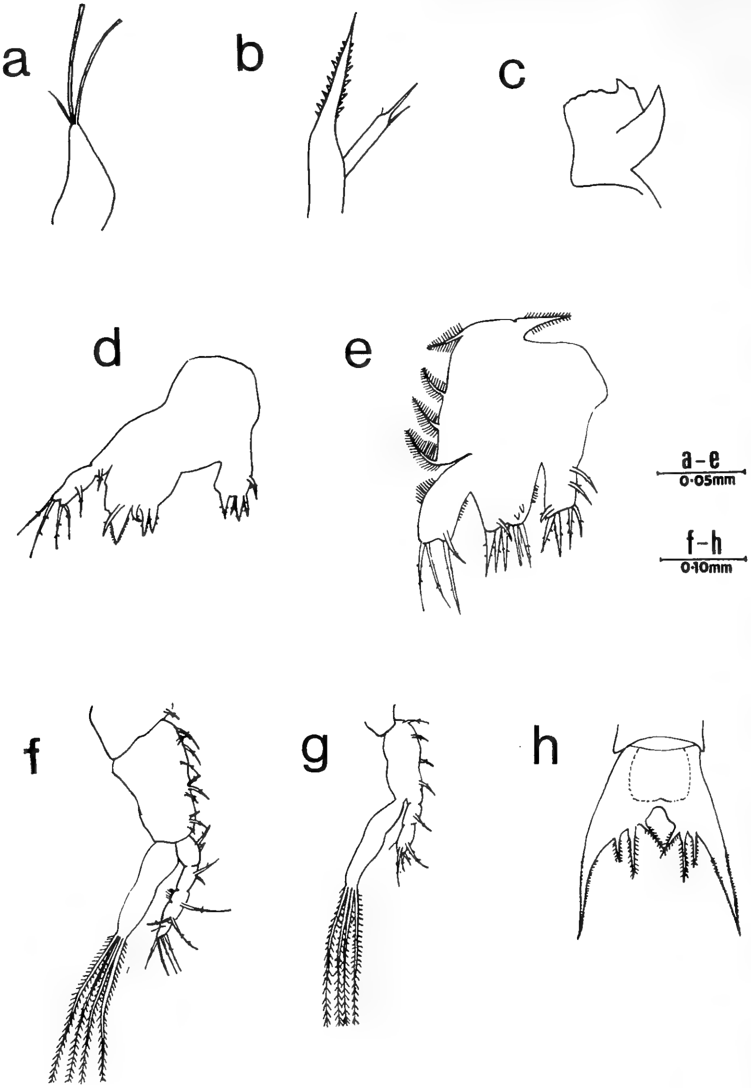

Fig. 5. The appendages and telson of the first zoea of *Helograpsus haswellianus*. *a*, antennule; *b*, antenna; *c*, mandible; *d*, maxillule; *e*, maxilla; *f*, maxilliped 1; *g*, maxilliped 2; ***h*, telson,** dorsal view.

(iii) *The thoracic appendages*

(*a*) *Maxilliped 1* (Fig. 5 (*f*)

Coxa bearing one sparsely plumose seta on inner margin.

Basis 0·15 mm long; bearing 10 sparsely plumose setae spaced along inner margin.

Endopod 0·18 mm long; five segments bearing respectively two, two, one, two and five sparsely plumose setae.

Exopod 0·14 mm long, bearing four biplumose, natatory setae terminally, each 0·20 mm long.

(*b*) *Maxilliped 2* (Fig. 5 (*g*))

Coxa bearing no setae.

Basis 0·15 mm long; bearing four sparsely plumose setae on inner margin.

Endopod 0·08 mm long; three segments bearing respectively nil, one and five setae; outer subterminal seta of third segment smooth and small, inner subterminal seta of third segment well developed. Remainder of endopod setae sparsely plumose.

Exopod 0·13 mm long; bearing four biplumose natatory setae terminally, each 0·20 mm long.

(*c*) *Maxilliped 3; Pereiopods; Gill buds*

All absent.

(iv) *The abdomen*

(*a*) *The abdominal segments*

Five segments each of about equal length (0·11 mm).

Segment 1 without spines or setae.

Segment 2 with a pair of forwardly directed dorso-lateral papillae.

Segment 3 with a pair of small, backwardly directed dorso-lateral papillae.

Segments 2–5 with posterior margins slightly expanded laterally; each bearing two dorsal setae.

Pleopod buds absent.

(*b*) *The telson* (Fig. 5 (*h*))

0·23 mm long.

Lateral cornua long, slender, curved slightly inwards and dorsally; 0·19 mm between tips; and bearing two dorso-lateral rows of fine hairs distally.

Telson plate 0·07 mm long, 0·14 mm broad at posterior margin; broad median cleft; three plumose setae on each side of cleft with inner seta of each side longest; distinct ventral protrusion of telson plate.

(v) *The chromatophores*

Since the description of the first zoea larva of *H. haswellianus* was made from preserved specimens, the precise details of the chromatophore pattern have not yet been obtained. The number and size of the dark black and brown chromatophores in the preserved larvae indicate that the living larvae are heavily pigmented.

The First Zoea Larva of Chasmagnathus laevis *Dana*

Although a large number of larvae was hatched from the eggs of two ovigerous females brought to the laboratory, most did not survive past the prezoea stage. However, a sufficient number moulted to enable the following summarized description of the first zoea larva of *C. laevis* to be prepared. The larva, which is illustrated in Fig. 4 (*b*), has a total length of 1·51 mm.

(i) *The cephalothorax*

Rostral spine 0·13 mm long, straight.

Dorsal carapace spine 0·16 mm long, strongly curved posteriorly from one-third of the way along its length.

Length from tip of rostrum to tip of dorsal spine, 0·50 mm.

Lateral carapace spines 0·06 mm long; directed somewhat posteriorly and curved downwards.

Posterior margin of carapace fringed with short hairs; with eight short, stout spines ventrolaterally.

One pair of dorsal setae just behind dorsal carapace spine.

Eyes sessile, 0·17 mm across.

(ii) *The cephalic appendages*

(*a*) *The antennule* (Fig. 6 (*a*))

Uniramous ; 0·10 mm long.

Two long aesthetascs of equal length and two short setae terminally.

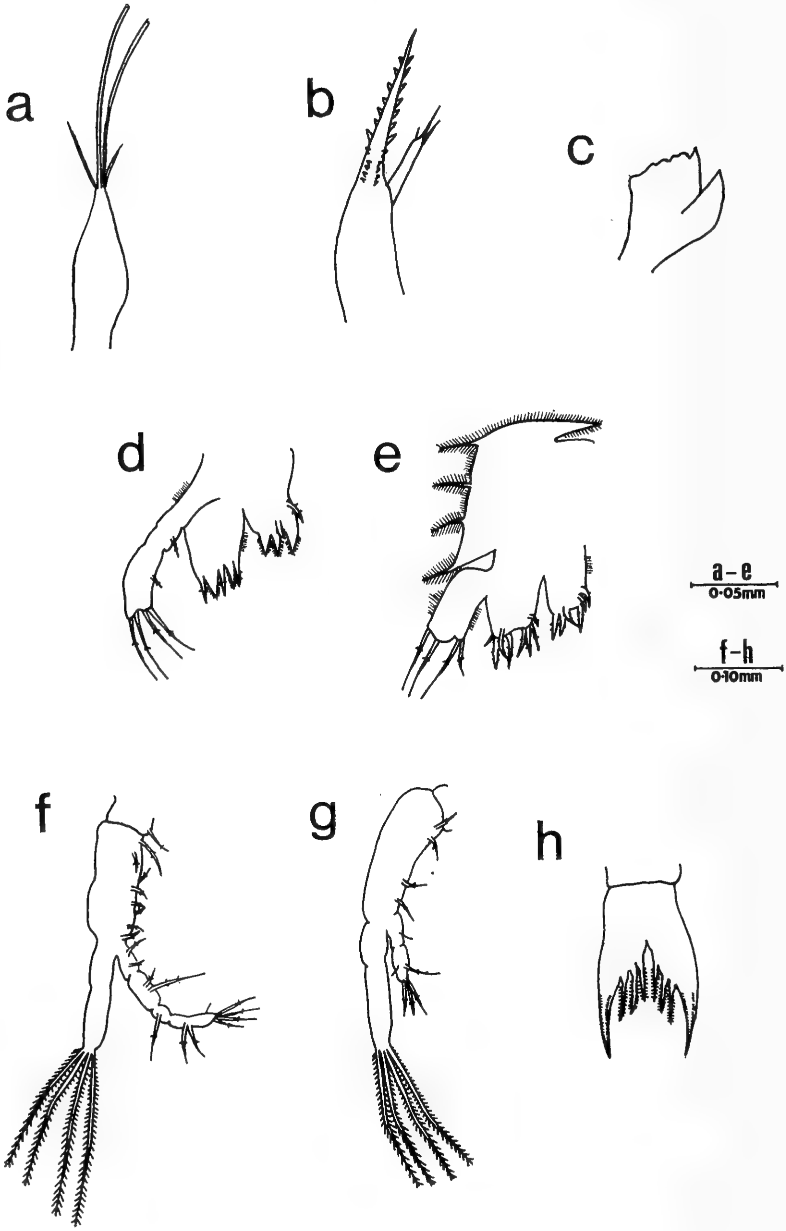

Fig. 6. The appendages and telson of the first zoea of *Chasmagnathus laevis*. *a*, **antennule** ; *b*, antenna ; *c*, mandible ; *d*, maxillule ; *e*, maxilla ; *f*, maxilliped 1 ; *g*, maxilliped 2 ; *h*, **telson,** dorsal view.

(*b*) *The antenna* (Fig. 6 (*b*))

Biramous.

Spinous process 0·19 mm long; bearing a double row of 12–13 spines distally (the eight most distal pairs of spines longer than the more proximal spines).

Exopod well developed, almost half length of spinous process; one lateral and one short, fine medial seta just below its spine-like tip.

(*c*) *The mandible* (Fig. 6 (*c*))

0·05 mm across.

Strongly toothed.

Well developed incisor process with three to four sharp teeth; ridged molar process.

(*d*) *The maxillule* (Fig. 6 (*d*))

Coxal endite bearing two large and three small plumose setae.

Basal endite bearing two large and three small plumose setae; inner margin fringed with fine hairs.

Endopod of three segments; proximal segment fused with protopod, bearing fine hairs laterally; medial segment bearing one smooth seta about midway along inner margin; distal segment bearing four terminal, sparsely plumose setae and one subterminal smooth seta, about midway along inner margin.

(*e*) *The maxilla* (Fig. 6 (*e*))

Coxal endite bilobed; bearing three plumose setae on each of its lobes; inner margin fringed with fine hairs.

Basal endite bilobed; bearing four plumose setae on each of its lobes.

Lateral and smaller medial lobe of endopod each bearing two terminal, sparsely plumose setae; outer and inner margins fringed with fine hairs.

Scaphognathite with proximal tip produced into a plumose spine; four finely plumose setae spaced along the outer and distal margins, which are otherwise fringed with fine hairs.

(iii) *The thoracic appendages*

(*a*) *Maxilliped 1* (Fig. 6 (*f*))

Coxa bearing one sparsely plumose seta on inner margin.

Basis 0·16 mm long; bearing eight sparsely plumose setae spaced along inner margin.

Endopod 0·16 mm long; five segments bearing, respectively, two, two, one, two and five sparsely plumose setae.

Exopod 0·16 mm long; bearing four long biplumose, natatory setae terminally, each 0·21 mm long.

(*b*) *Maxilliped 2* (Fig. 6 (*g*))

Coxa bearing no setae.

Basis 0·16 mm long; bearing four sparsely plumose setae on inner margin.

Endopod 0·08 mm long; three segments bearing respectively nil, one and five setae: seta of medial segment smooth and about midway along inner margin; outer subterminal seta of distal segment smooth, inner subterminal seta and terminal setae plumose.

Exopod 0·17 mm long; bearing four long, biplumose, natatory setae terminally, each 0·18 mm long.

(*c*) *Maxilliped 3; Pereiopods; Gill buds*

All absent.

(iv) *The abdomen*

(*a*) *The abdominal segments*

Segments 1, 3, 4 and 5 of about equal length (0·11 mm); segment 2 shorter (0·09 mm).

Segment 1 without spines or setae.

Segment 2 with a pair of well-developed dorso-lateral papillae directed forwards.

Segment 3 with a pair of small, backwardly-directed dorso-lateral papillae.

Segments 2–5 with posterior margins slightly expanded laterally; each bearing two dorsal setae.

Pleopod buds absent.

(*b*) *The telson* (Fig. 6 (*h*))

0·24 mm long.

Lateral cornua curved inwards and slightly curved dorsally; 0·12 mm between tips; each bearing two dorso-lateral rows of short hairs distally.

Telson plate rectangular, 0·08 mm long, 0·11 mm broad; indentation of posterior margin narrow; three plumose setae on each side of indentation; distinct ventral protrusion of telson plate.

(v) *The chromatophores*

Details of the chromatophores were not obtained for the first zoea of *C. laevis*, because only preserved specimens were available during the course of the present study.

DISCUSSION

The larval classification of the Sesarminae

In recent years Wear (1967, 1968*a*, 1968*b*, 1970) has made a detailed study of the classification of first zoea larvae of the Brachyura. His paper of 1970 discusses the classification of grapsid larvae in relation to the adult taxonomy of the Grapsidae and provides a key based on the larvae of 34 species from 17 of the 39 genera of grapsids. According to this key, there are discrepancies between the adult and larval classification of grapsids in the subfamilies Sesarminae and Varuninae. Within the Sesarminae, the first zoea larva in the genus *Sesarma* conforms to the following set of distinguishing characters:

> Lateral carapace spines absent; dorsal carapace spine short and stout; antennal spinous process small, exopod developed to about half length of spinous process; abdominal segments 3–5 without postero-lateral ridges; telson widely forked with cornua long and slender, lateral telson setae absent.

The first zoea larvae of the genera *Helograpsus* and *Chasmagnathus*, on the other hand, conform to a contrasting set of characters:

> Lateral carapace spines present; dorsal carapace spine usually long and slender; lateral carapace spines directed strongly downwards and inclined posteriorly, without hairs or tubercles; dorsal carapace spine curved; antennal exopod about half length of spinous process.

The characters of the first zoea larva of *Sesarma erythrodactyla* Hess, as described in the present study, agree with Wear's diagnosis in all respects except one. The first zoea of *S. erythrodactyla* has the postero-lateral margins of abdominal segments 3–5 expanded as small non-lobed ridges. This minor difference, however, does not prevent *S. erythrodactyla* from being classified with the other five species of *Sesarma* referred to in Wear's key.

Such postero-lateral expansions of the third to the fifth abdominal segments are consistent with published descriptions of the larvae of *S. cinereum* (Bosc.), *S. reticulatum* Say, *S. tetragonum* (Fabricius) and *S. ricordi* (H. Milne Edwards), in which the postero-lateral margins of the segments are variously described as terminating in a " deltoid tooth " (Hyman, 1924), " slightly rounded lateral spines which overlap the next segment " (Costlow and Bookhout, 1960), " minute spines " (Raja Bai, 1961), and " a short blunt point which overlaps the following segment " (Diaz and Ewald, 1968). It is only in the descriptions of the larvae of *Sesarma* sp. and *S. picta* de Haan by Aikawa (1929, 1937) and of *S. haematocheir* and *S. dehaani* by Yatsuzuka (1962) that the expansions of the postero-lateral margins of abdominal segments 3–5 are not recorded. Aikawa did not recognize the importance of the armature of the abdominal segments for classificatory purposes, and may have neglected such expansions if present, and Yatsuzuka refers to only a few major characteristics.

Similarly, the characters of the first zoea larvae of *Helograpsus haswellianus* (Whitelegge) and *Chasmagnathus laevis* Dana agree with Wear's diagnosis for the larvae of these genera. The present work therefore supports Wear's contention

TABLE 2

Chromatophores of the First Zoea Larvae of Six Species of the Genus Sesarma
(+=present; —=absent; 0=not determined)

	Sesarma Sp.	*S. picta*	*S. cinereum*	*S. reticulatum*	*S. tetragonum*	*S. erythrodactyla*
PRIMARY SYSTEM						
A. *Neural Group*						
1. Supracerebral ..	—	0	—	—	0	—
2. Antennular ..	—	—	—	+	+	+
3. Antennal ..	+	0	—	—	0	+
4. Labral	+	0	+	+	0	+
5. Mandibular ..	+	0	+	+	+	+
6. Maxillar ..	+	0	—	—	0	+
7. Maxillipedal—						
mxp 1 ..	—	0	+	—	—	+
mxp 2 ..	—	0	+	+	+	—
8. Lateral intestinal	+	+	+	+	+	+
9. Subintestinal ..	—	—	+	+	+	+
B. *Visceral Group*						
10. Median gastric ..	+	0	—	—	0	+
11. Precardiac ..	—	0	+	+	0	—
12. Subcardiac ..	+	0	—	+	+	+
13. Postcardiac ..	+	0	—	—	0	+
SECONDARY SYSTEM						
14. Posterior carapacial	—	—	—	—	0	—
15. Postoventral carapacial ..	+	0	—	+	0	+
16. Lateral carapacial	—	0	—	+	0	—
17. Dorsal carapace spine	—	0	—	—	—	—
18. Maxillipedal—						
mxp 1 ..	—	+	+	—*	+	+
mxp 2 ..	+	—	+*	+*	—	—
19. Optic	—	0	+	+	+	+
20. Median ocular centre	+	0	+	+	+	+

* From Aikawa (1929).

that the larval classification of the Sesarminae does not conform to the adult classification. The genus *Sesarma* falls into one larval category, the genera *Helograpsus* and *Chasmagnathus* into another.

Chromatophores and larval identification in the genus Sesarma

The chromatophore pattern of brachyuran larvae has been attributed diagnostic values at the generic and specific levels (Hyman, 1924; Aikawa, 1929, 1933), but few detailed studies of chromatophore pattern have been made. For the genus *Sesarma*, information on the chromatophore pattern of the first zoea larva is now available for six species (*S. erythrodactyla* Hess, this account; *S. tetragonum* (Fabricius); *S. reticulatum* Say; *S. cinereum* (Bosc.); *S. picta* de Haan; *S. sp.*; Aikawa, 1929, 1937; Costlow and Bookhout, 1960, 1962; Raja Bai, 1961). The details are summarized in Table 2. Despite the large gaps in some accounts, it seems probable that no two species have identical patterns of larval chromatophores. Since other species remain to be described, it cannot yet be asserted that the chromatophore pattern alone is sufficient to distinguish the larvae of species within a genus, but the possibility is worthy of further investigation. If the chromatophore pattern alone is not specific, it may be of value in conjunction with the setation of the appendages as a means of separating larval species.

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SEXUAL DIMORPHISM IN *HAPLOMITRIUM INTERMEDIUM*

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Synopsis

Sexual dimorphism in *Haplomitrium intermedium* G. K. Berrie has been investigated and confirmed and found to be correlated with a sex chromosome mechanism.

INTRODUCTION

The order Calobryales is known to be represented only by *Haplomitrium intermedium* G. K. Berrie in Australia. It was noted by Berrie (1962) that there is an apparent dimorphism between the female and male gametophytes; and later references to the genus (Schuster, 1967, 1971) suggest that other species have dimorphic gametophytes. Herein an attempt has been made to analyse the dimorphism in *H. intermedium.* It was done by (i) measurement of the morphological differences and (ii) a study of the cytology.

MORPHOLOGY

A random sample of the plants at the type locality was collected and maintained in the laboratory. From these plants, a further random sample of 25 female and 25 male plants was selected for quantitative measurement. In order to be certain (*a*) that the correct sex was selected, and (*b*) that there were no errors due to stage of maturity, only plants bearing terminal archegonia and antheridia, respectively, were selected. For each plant:

(i) Leaves. The top 10 leaves were dissected off serially from the tip and the following measurements taken: (*a*) *length* and (*b*) *width,* both measured at 40 times magnification. In analysing the results, it was noted that the measurements for leaf length and width fell into two populations. This was due to the larger " perianth " leaves surrounding the archegonia and antheridia. Hence, " perianth " leaves have been separated from the " lower " leaves for the analysis. (*c*) *Cell area* at the tip of each leaf. To do this, a square was inserted in the eyepiece of the microscope and the area of the resultant field of view measured. Then the number of complete and incomplete cells was scored and the mean cell area calculated by use of the formula

$$\frac{\text{Total area}}{\text{Number of complete cells} + \frac{1}{2}\text{ number of incomplete cells}} = \text{Mean cell area}$$

(ii) Stems. A transverse section of the stem was cut and the diameter measured at 100 times magnification. A further sample of 30 female and 30 male plants was taken for this measurement.

RESULTS

The means for the leaf and stem measurements were calculated and from these values an F test was carried out on each of stem diameter, cell area, leaf length (" perianth " and " lower "), leaf width (" perianth " and " lower ") and leaf length/width ratio (Table 1 (ii)), to test if the sample variances are

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TABLE 1

Measure under Analysis		Mean $\overline{X}$	Standard Deviation (SD)	Standard Error (SE)	(i) *t* Value	Prob. of Mean Independ.	(ii) *F* Value	Significance Level		Conclusion	
								5%	1%	(i)	(ii)
Stem diameter (mm) ..	♀ ♂	0·60 0·43	0·12 0·10	0·02 0·01	21·4	0·001	55·57	3·94	6·90	Significant difference	Significant difference
Cell area $x \times 10^2$ (sq μ)	♀ ♂	310·30 306·10	79·70 60·30	4·60 3·40	1·4	0·15	3·44	4·04	7·19	No significant difference	No significant difference
Leaf length, lower (mm)	♀ ♂	1·71 1·12	0·36 0·30	0·03 0·02	26·4	0·001	74·17	4·04	7·19	Significant difference	Significant difference
Leaf length, perianth (mm)	♀ ♂	2·22 1·23	0·48 0·29	0·04 0·03	37·5	0·001	161·89	4·04	7·19	Significant difference	Significant difference
Leaf width, lower (mm)	♀ ♂	1·16 0·78	0·45 0·32	0·04 0·02	34·7	0·001	30·46	4·04	7·19	Significant difference	Significant difference
Leaf width, perianth (mm)	♀ ♂	1·34 0·91	0·51 0·35	0·04 0·03	16·3	0·001	19·05	4·04	7·19	Significant difference	Significant difference
Leaf length/width, lower	♀ ♂	1·54 1·39	0·60 0·46	0·05 0·03	3·8	0·01	1·35	4·04	7·19	Significant difference	No significant difference
Leaf length/width perianth	♀ ♂	1·67 1·36	0·65 0·37	0·06 0·03	6·0	0·01	9·42	4·04	7·19	Significant difference	Significant difference

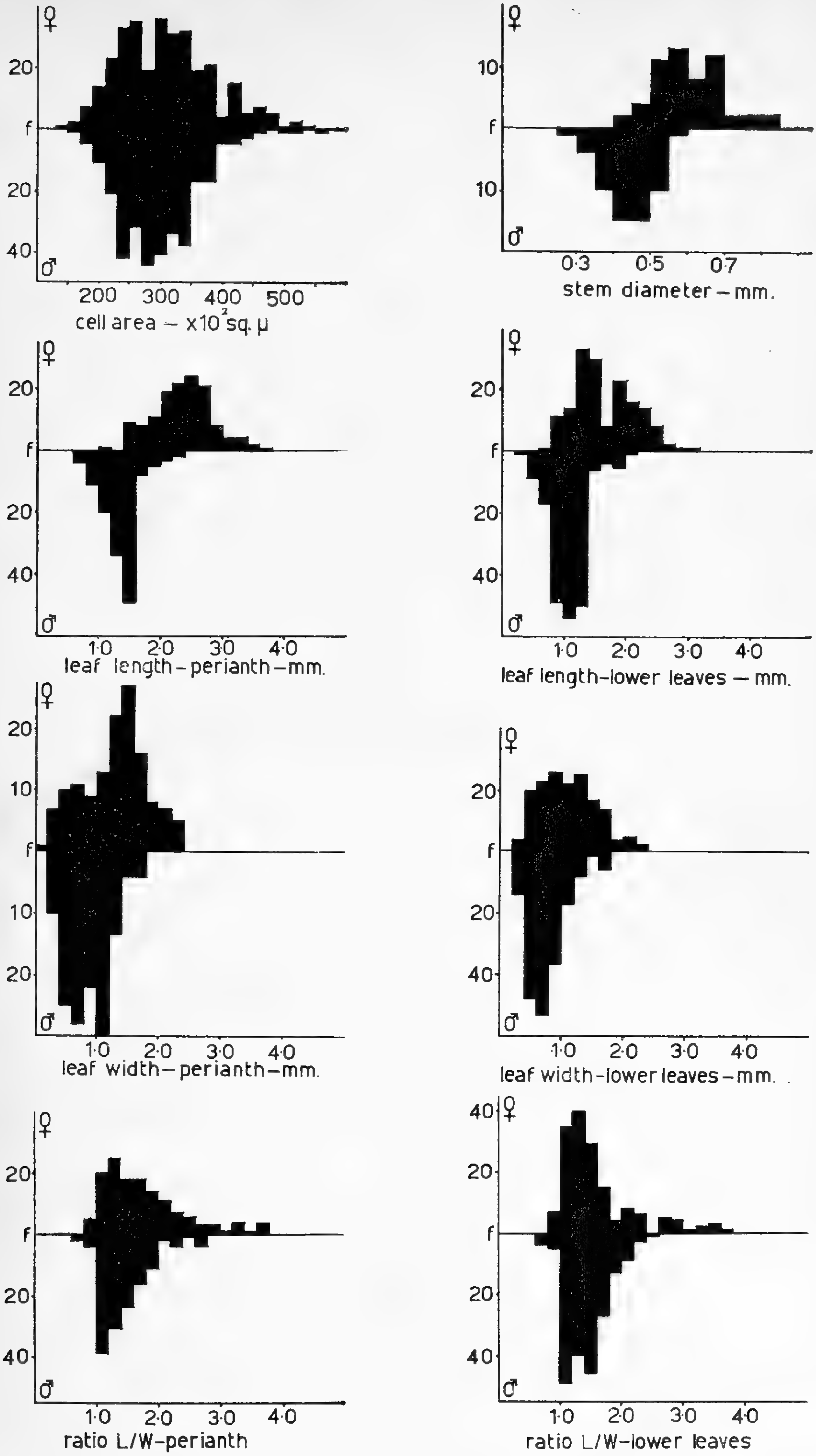

Fig. 1. Frequency distributions for characters analyse $d\bar{x}$=mean, sd=standard deviation, and se=standard error.

significantly different. In addition, the values for stem diameter, cell area, leaf length, leaf width and leaf length/width ratio for female and male plants have been presented in frequency distributions (Fig. 1). The *t* test was applied to these to test if the means for male and female characters are significantly different (Table 1 (i)).

INTERPRETATION

From Table 1, it can be seen that there are significant differences in the morphology of the female and male gametophytes of *Haplomitrium intermedium*. The female gametophytes have larger " perianth " and " lower " leaves, and have thicker stems than do the male gametophytes. However, it does appear that cell area and leaf length/width ratio are inherent properties of the species and are independent of sexual morphology.

CYTOLOGY

An attempt was made to investigate if the marked sexual dimorphism is reflected in the cytology.

Stolon tips, shoot tips and developing sporophytes were selected from material collected at the type locality and fixed in 3 : 1 Absolute Alcohol : Glacial Acetic Acid, for 12 hours at room temperature. These were transferred to Absolute Alcohol and stored at 0° C. Squash preparations were made and stained in Aceto-orcein (Darlington and LaCour, 1960). It was found to be necessary to macerate the gametophyte material. This was done by pretreating the tips in snail cytase for 45–60 minutes at room temperature.

From mitotic studies when comparing the female and male chromosome complements it was found that there is one chromosome which does not have an obvious homologue in the other's complement. This chromosome in the female complement displays positive heteropycnosis, having an heterochromatic knob at one end (Fig. 2). The odd chromosome in the male complement does not show any convincing evidence of heteropycnosis (Fig. 2). The chromosome No. 3 in the female complement is associated with nucleolar organization (NO). The nucleolar organizer is unconfirmed in the male complement. The longest chromosome (No. 1) and the shortest chromosome (No. 8) do not show any evidence of heteropycnosis in either complement, however they probably correspond to the M (macro-) and m (micro-) chromosome (Berrie, 1959).

In meiosis it was observed that Prophase I is not clear until late Diplotene. At Diakinesis there was found to be a mean of 18·9 chiasmata per cell and 2·1 chiasmata per bivalent. At Metaphase I the chiasmata are almost completely terminalized. However, it was noted that terminalization is completed earlier in one bivalent, and this bivalent tends therefore to enter Anaphase I precociously (Fig. 3). It was also observed that this bivalent is negatively heteropycnotic and has homologues of unequal length. This bivalent is obviously composed of the two unequal homologues observed in the mitotic karyotype studies. It seems reasonable to assume that this is a sex chromosome mechanism. The longer chromosome is always associated with the female complement and is the X chromosome, and the shorter chromosome is always associated with the male complement and is the Y chromosome. After Anaphase I, the chromosomes pass into a temporary interphase before starting a rapid second division. The final product of the division is two spores with $n=8+X$ and two spores with $n=8+Y$.

SUMMARY

From these studies, it can be seen that there is dimorphism between the female and male gametophytes of *Haplomitrium intermedium*. The male

Fig. 2. Chromosome karyotype interpretation. M=macrochromosome, m=microchromosome, NO=nucleolar organizer, X & Y=sex chromosomes.

gametophytes have thin stems, small leaves and a less marked perianth relative to the female gametophytes. Moreover, it can be seen that this dimorphism is associated with a sex chromosome mechanism.

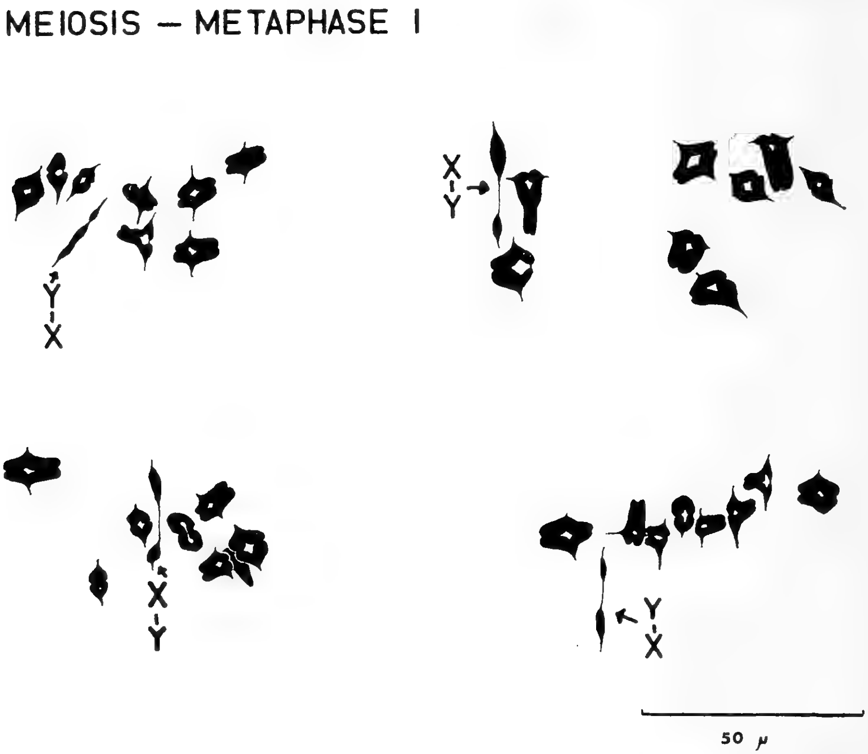

Fig. 3. Meiosis—metaphase 1. X–Y=sex chromosome bivalent.

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AN ANALYSIS OF THE CATCH BY TRAWLERS IN MORETON BAY (QLD.) DURING THE 1966–67 PRAWNING SEASON

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[Accepted for publication 20th September 1972]

Synopsis

A study of the trawling industry in Moreton Bay during the 1966–67 season suggests that the catch rate of prawns by trawl had not changed significantly since the early years of the industry. Neither was there evidence of a decline in the fishery in Moreton Bay for winter whiting (*Sillago maculata* Quoy and Gaimard), the only commercial fish taken regularly by trawl in large numbers.

Rates of capture of prawns and incidental fish were determined. The results, extrapolated to the activities of the prawning fleet in Moreton Bay, indicated a total seasonal catch of 1·8–2·1 million lb of prawns, and 1·6–1·9 million lb of incidental fish, including 0·17–0·20 million lb of winter whiting. An example of the catch composition of incidental fish caught during the sampling period is provided.

INTRODUCTION

The trawling industry in Moreton Bay began in 1950, when a four-fathom otter trawl was tested to ascertain the possibility of fish and prawn capture on a commercial basis by this method. In the following year about 40 boats were operating at the height of the season. Interestingly, a survey carried out at that time by the Department of Harbours and Marine led to the conclusion that " the operations of prawn trawlers are not detrimental to the stocks of immature food fishes ". The total prawn catch in Moreton Bay for the 1952–53 season was estimated at 300,000 lb, and in 1953–54 was 500,000 lb. By 1962 the total Queensland prawn catch was 4·4 million lb, over half of which was from Moreton Bay (Annual Reports of the Queensland Department of Harbours and Marine, 1950–62). The catch has fluctuated since to the 1966–67 season, when 1·8 million lb of prawns were received at Fish Board depots from both inside and outside the bay (Queensland Fish Board Report, 1967).

The number of trawlers operating in Moreton Bay varies seasonally. A total of 249 trawler licences were issued in the Brisbane district for the 1966–67 season. Of these, trawlers not licensed to work outside the bay numbered about 30, but most of the remainder trawled to a greater or lesser extent in Moreton Bay during the prawning season, September to February inclusive.

Since the Fish Board records do not distinguish between prawns taken inside Moreton Bay and those taken in grounds outside and adjacent to the bay, the quantity taken in neither area is known. Also, the quantity of incidental fish taken by the trawlers has not been previously determined. This study was carried out to ascertain the rate of catch of prawns and incidental fish and, by extrapolation of the data, to estimate their total seasonal quantities taken by the prawning fleet.

METHODS

Data used in this survey were obtained during October and November, 1966, and March, 1967, in the University of Queensland research vessel, a 37-foot trawler using an eight-fathom otter trawl with a 1·5 in mesh cod-end, towed at an estimated 2·5 knots. Most commercial trawlers operate at this speed.

Trawling was carried out at night with the commercial prawning fleet. Areas being worked changed frequently, depending on several factors, including

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weather, phases of the moon, tides, but was often simply a matter of follow the leader. If prawns were scarce in one area the fleet moved elsewhere such that no specific areas could be compared. However, by following the fleet a reasonable indication was obtained of their catches of fish and prawns.

It was assumed that all fish captured were killed by the trawling procedure. From observations, many are dead before the net is emptied on to the sorting tray, where they remain during the sorting process, which may take up to an hour. It was apparent that only isolated individuals survive the trawl and subsequent exposure.

For the estimation of total seasonal trawling time, the following parameters, derived chiefly by observations and discussions with fishermen, were used.

(*a*) Season. The bay season generally extended from September to February inclusive, although prawning continued at a significant level until the end of May, after which it was considered uneconomical to trawl. An influx of trawlers occurred during the period December to February inclusive, the " peak " of the season.

Table 1

Estimated and Actual Weights of Trial Trawls in Moreton Bay, September, 1966

No.	Estimated Weight (lb)	Actual Weight (lb)
1	24	21
2	16	18
3	3	4
4	11	10
5	16	18
6	20	23
7	31	36
8	20	23
9	9	9
10	25	28

(*b*) Number of boats. From September through November the average number of trawlers working the bay was normally 50; in the " peak " months it swelled to between 150 and 200, after which the number of vessels dropped to about 30, tailing off to the end of prawning in May.

(*c*) Time spent trawling. Allowing for times when the net is out of the water, the time spent trawling each night is 10 hours. Moreton Bay is open to trawling five nights a week, but the average weekly period worked appeared to be three and one-half nights, bad weather and maintenance accounting for the remaining time.

(*d*) Gear. The trawling gear in use in Moreton Bay is almost without exception the otter trawl; most nets are the legal minimum mesh size and maximum width of 1·5 in and eight fathoms, respectively. The average net width was taken to be seven fathoms to account for small trawlers not capable of towing the large nets.

From these parameters, a trawler may average 1,050 fathom-hours trawling each month.

In early samples both fish and prawns were weighed. However, trawler operators are usually adept at estimating the weight of a catch by its volume, and it was found in this case that the skipper of the research vessel was giving fairly reliable visual estimates of the weight of prawns in a basket and of fish on the sorting tray. Accuracy of his estimates was confirmed by a series of 10 trial hauls made under commercial prawning conditions. Table 1 shows the hauls which were first estimated and subsequently weighed by machine. A *t* test showed no significant difference between trial estimates and actual weights at the 0·05 level of probability.

Winter whiting, the only commercial fish species taken regularly in large numbers, and prawns were separated and weighed. Weights of the remaining incidental fish were visually estimated. Prawns were further divided into the two commonly used gradings made by professional prawners ; " large ", which includes large king (*Penaeus plebejus* Hess) and tiger (*Penaeus esculentus* Haswell) prawns, with which are sometimes found smaller quantities of the endeavour prawn (*Metapenaeus endeavouri* (Schmitt)), and " small " or " mixed bay prawns ", which include small individuals of the above species as well as other species, especially the greentail prawn (*Metapenaeus bennettae* Racek and Dall). More complex size and species groupings are sometimes made by fishermen to obtain the most economically valuable yield.

RESULTS

1. *Catch rates.* The catch rates of prawns and incidental fish during the sampling period are shown in Table 2, and those of whiting in Table 3. Results are expressed in terms of weight per hour per fathom of net, since these units have most relevance to bay prawning.

TABLE 2

Catches and Catch Rates of Fish and Prawns by Weight in Trawls in Moreton Bay during October and November, 1966, and March, 1967

Period	Total Trawl Duration (hr)	Total Weight (lb)	Weight/Hr/ Fathom
(*a*) *Incidental fish*			
October, 1966	28·6	348	1·53
November, 1966	27·8	419	1·89
March, 1967	7·0	149	2·66
(*b*) *Large grade prawns*			
October, 1966	28·6	367	2·0
November, 1966	27·8	296·5	1·66
March, 1967	7·0	71	1·58
(*c*) *Small grade prawns*			
October, 1966	28·6	119·5	0·57
November, 1966	27·8	85	0·38

TABLE 3

Catch Rate of Winter Whiting during the 1966–67 Sampling Period in Moreton Bay

Period	Weight/Hr/ Fathom (lb)
October, 1966	0·17
November, 1966	0·23
March, 1967	0·14

2. *Estimation of total seasonal prawn and incidental fish catch.* On the basis of the seasonal parameters described earlier, it was possible to estimate the total catches of the Moreton Bay prawning fleet in 1966–67. These estimates are contained in Table 4, where lower and upper values were obtained using a figure of 150 and 200 trawlers respectively, for the number of boats trawling at the height of the season, December through February. Estimates for the period September to February are based on the October and November, 1966,

samples, while those for the period March to May are based on the March, 1967, data. No data were obtained for the catch rate of small grade prawns in the latter samples and their catch rate was assumed similar to that during October-November.

TABLE 4

Lower and Upper Estimates of the Total Weights of Fish and Prawn Capture by Trawlers in Moreton Bay during the 1966–67 Prawning Season

Period	Estimated Weight (lb)	
	Lower	Upper
(*a*) *Incidental fish*		
September–February	1,356,000	1,626,000
March–May	267,300	
Total	1,623,300	1,893,300
(*b*) *Large grade prawns*		
September–February	1,274,600	1,528,400
March–May	131,300	
Total	1,405,900	1,659,700
(*c*) *Small grade prawns*		
September–February	333,600	400,600
March–May	45,400	
Total	379,000	446,000

3. *Analysis of the incidental fish catch.* Complete analysis of the fish catch was not attempted, but it was clear from earlier observations that only one commercial species, the winter whiting, was being taken by trawlers in constantly large numbers. From Tables 4 and 5 the whiting comprised approximately 10% by weight of the total incidental fish catch. The only other commercial fish species encountered in large numbers was the snapper (*Chrysophrys auratus* Bloch and Schneider), schools of which were sometimes trawled near reefs. Those taken in the net were always less than 4 in long.

TABLE 5

Lower and Upper Estimates of the Total Weight of Winter Whiting Catch by Trawlers in Moreton Bay during the 1966–67 Season

Period	Estimated Weight (lb)	
	Lower	Upper
September–February	158,200	189,700
March–May	13,500	
Total	171,700	203,200

Catches of other commercial species were generally in negligible quantity, including flathead (*Platycephalus* spp.), sole (*Achlyopa nigra* (Macleay) and *Paraplagusia guttata* (Macleay)) and golden pilchard (*Engraulis australis* (Shaw)). Isolated specimens of tailor (*Pomatomus saltator* (Linnaeus)), tusk fish (*Choerodon* spp.), sand whiting (*Sillago ciliata* McCoy) and mullet (*Mugil* spp.) were also taken during trawls in the present study.

The bulk of incidental fish, however, were non-commercial or " trash " fish species, usually less than 4 in in length, particularly cardinal fish, mainly

Apogon fasciatus fasciatus (Shaw) and less commonly *A. atripes* (Ogilby). These were the most frequently occurring species. But large numbers of silverbelly (*Gerres ovatus* (Gunther)), striped catfish (*Plotosus anguillaris* (Bloch)) and leatherjackets, mainly *Monacanthus oblongus* (Schlegel) and *M. oblongus otisensis* (Whitley), and rarely *M. chinensis* (Osbeck) were sometimes captured.

Species composition and quantities varied greatly from trawl to trawl of equal duration and an average or typical catch was not determined. However, a collection was made of all trawls on one night, 16th November, 1966, over an area of about five square miles east-south-east of Mud Island, in depths of from three to six fathoms. Trawling duration was 7 hours and 45 minutes. The catch composition is shown in Table 6. Species are arranged in order of numbers captured, and the percentage biomass of each is also given.

TABLE 6

Species Composition of 1,511 Fish Weighing 56 lb 9 oz Trawled in Moreton Bay on 16th November, 1966

Common Name	Species	No.	Percentage No.	Percentage Biomass
Cardinal fish	*Apogon* spp.	415	27·6	12·4
Striped catfish	*Plotosus anguillaris* (Bloch)	173	11·5	13·6
Squire*	*Chrysophrys auratus* (Bloch and Schneider)	173	11·5	6·1
Leatherjackets	*Monacanthus* spp.	140	9·3	5·2
Silverbelly	*Gerres ovatus* Gunther	73	4·8	7·4
Goatfish	*Upeneus tragula* Richardson	70	4·6	3·7
Flounder*	*Pseudorhombus* spp.	68	4·6	4·8
Bullrout	*Centropogon marmoratus* (Gunther)	60	4·0	1·2
Puttynose	*Polydactylus multiradiatus* (Gunther)	53	3·5	8·8
Golden pilchard*	*Engraulis australis* (White)	50	3·3	3·6
Winter whiting*	*Sillago maculata* Quoy and Gaimard	40	2·7	5·8
Smooth toad	*Spheroides* sp.	30	1·9	7·8
Sole*	*Cynoglossus* spp. and *Achlyopa nigra* (Macleay)	25	1·7	1·3
White pilchard	*Hyperlophus translucidus* McCulloch	22	1·4	<0·1
River perch	*Johnius australis* (Gunther)	21	1·4	6·3
Bullseye	*Priacanthus macracanthus* Cuvier and Valenciennes	17	1·1	3·7
Dragon fish	*Callionymus* and *Parapegasus* spp.	14	0·9	0·3
Grey catfish	*Euristhmus lepturus* (Gunther)	10	0·7	2·6
Grinner	*Saurida* spp.	8	0·6	1·4
Angler fish	*Antennarius striatus* (Shaw and Nodder)	8	0·6	0·4
Trumpeter	*Pelates quadrilineatus* (Bloch)	8	0·6	0·3
Sixpence	*Leiognathus moretoniensis* Ogilby	6	0·5	<0·1
Flathead*	*Platycephalus* spp.	5	0·3	0·8
Scorpionfish	Unidentified Scorpaenidae	4	0·3	<0·1
Tailor*	*Pomatomus saltator* (Linaeus)	3	0·2	<0·1
Shovelnose shark	*Aptychotrema banksii* (Muller and Henle)	1	<0·1	1·3
Weever	*Parapercis nebulosus* (Quoy and Gaimard)	1	<0·1	0·2
Yellow-tail pike	*Sphyraena obtusata* (Cuvier)	1	<0·1	0·2
Fantail herring	*Harengula* sp.	1	<0·1	0·1
Beardie	*Anacanthus barbatus* (Gray)	1	<0·1	0·1

* Denotes commercial species or genus which includes commercial species.

DISCUSSION

The 1967 report of the Queensland Fish Board gave a total quantity of prawns landed at Moreton Bay fish depots† from trawlers working inside and/or outside the bay, of 1,796,108 lb during the 1966–67 season. In addition to these

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† These depots are at Brisbane, Cleveland, Doboy Creek, Sandgate, Scarborough, and Wynnum (Fig. 1). A Southport depot, at which only trawlers operating outside Moreton Bay land prawns, is excluded.

depots, there is a privately owned processing company which accepts prawns from trawlers. In the 1966–67 season, a total of 277,434 lb of large king and tiger prawns and 235,388 lb of mixed bay prawns were landed there from trawlers working *inside* Moreton Bay. A further 400,000 lb of prawns from outside the bay were also landed there.

The grand total 1966–67 prawn catch for trawlers working out of depots other than Southport is thus 2·7 million lb. Moreton Bay prawns make up 55% of the total receivals of the private processing company, and if a similar proportionality is assumed for Fish Board landings, then approximately 1·5 million lb of prawns were taken from Moreton Bay in 1966–67.

This estimate is somewhat lower than the quantity estimated in the present investigation, 1·8–2·1 million lb. In this regard it is interesting to note that the Department of Harbours and Marine, in its 1967 Report, indicated that 1966–67 was one of the worst seasons on record. Reasons given included a depression in the general level of catches, an emigration of trawlers northward, especially to the new, rich grounds in the Gulf of Carpentaria, fewer trawlers from New South Wales moved into the bay, prevailing weather hampered fishing operations, and parts of the bay were closed to prawning for three months (September to November inclusive).

The applicability of empiric catch rates to the prawning fleet also depended on other factors which could not be evaluated, including differences in the efficiency of trawling gear and skill of individual operators.

Comparison can be made, however, with the level of catches in the early years of the fishery. Data are available for the average monthly catches of prawns in Moreton Bay by trawlers during 1952–53 and 1953–54 (Table 7).

TABLE 7

Average Monthly Landings of Prawns by Weight per Boat in the 1952–1953 and 1953–54 Prawning Seasons in Moreton Bay

(Source: Annual Report, Department of Harbours and Marine, Queensland, 1953 and 1954)

(*a*) 1952–53

1952		1953	
Month	Weight Prawns (lb)	Month	Weight Prawns (lb)
July	599	January	2,985
August	505	February	2,898
September	566	March	2,407
October	767	April	1,838
November	635	May	1,439
December	1,090	June	1,466

(*b*) 1953–54

1953		1954	
Month	Weight Prawns (lb)	Month	Weight Prawns (lb)
July	810	January	4,279
August	1,268	February	1,406
September	1,334	March	2,035
October	1,578	April	2,594
November	2,780	May	2,249
December	2,142	June	683

From Table 7, the average annual catch per boat was 17,195 lb in 1952–53 and 23,518 lb in 1953–54. From the present estimates, the average catch per boat for the nine-month season of 1966–67 was 20,586 lb. It seems likely, then, that the rate of prawn capture in the 1966–67 season was of the same order of magnitude as it was in the early phase of the industry. This suggests that the industry has not reached the state of over-fishing, as sometimes claimed by fishermen, especially if 1966–67 was considered a bad year for prawning.

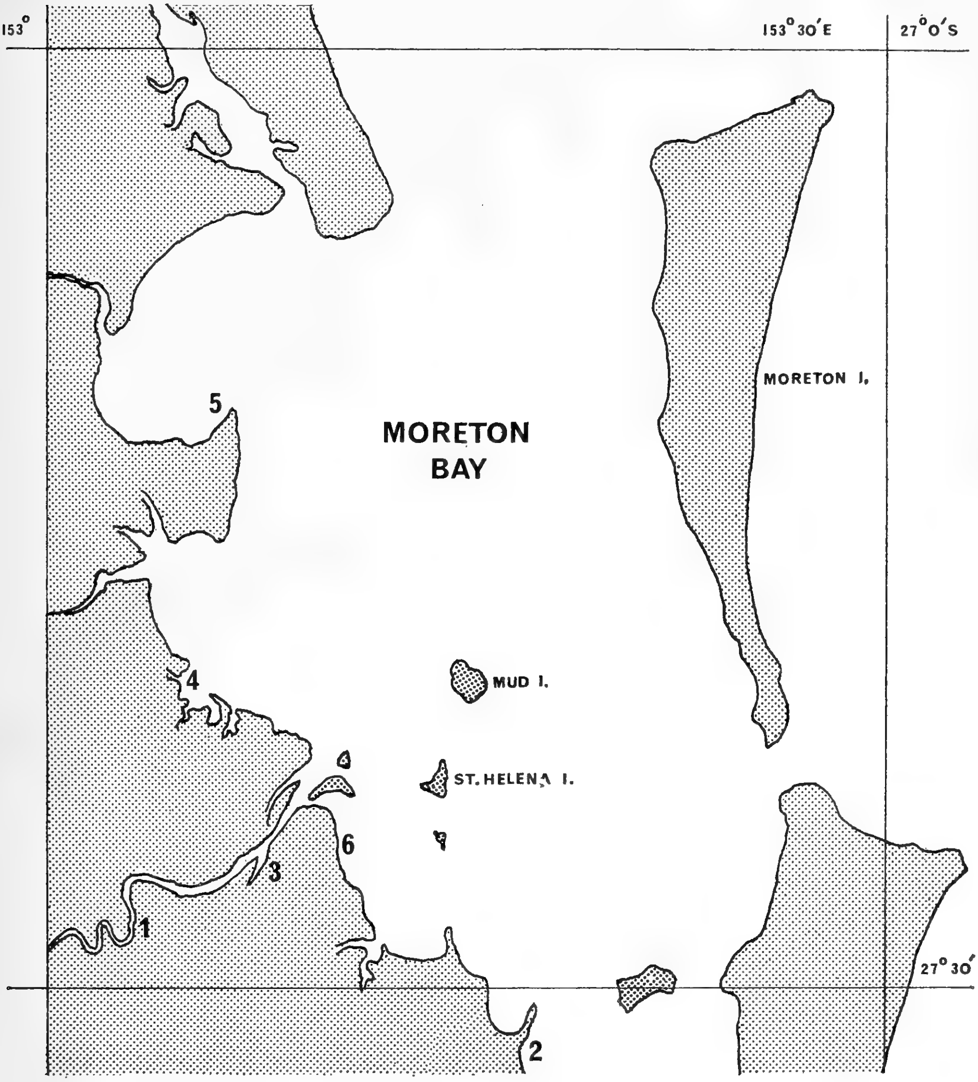

Fig. 1.—Moreton Bay, showing the locations of the Fish Board depots. 1—Brisbane; 2—Cleveland; 3—Doboy Creek; 4—Sandgate; 5—Scarborough; 6—Wynnum.

The incidental fish catch of Moreton Bay prawning has not been investigated in the past, but the ecological implications of the quantities involved, estimated at 1·6–1·9 million lb annually, certainly warrant further attention.

Winter whiting mortality due to trawling in Moreton Bay of an estimated 0·17–0·20 million lb annually, seems an alarming quantity, especially since the great majority of the fish are less than the legal size of capture of 8 in. On the other hand, this species reaches maturity at a somewhat smaller size, and appears to spawn several times each year (unpublished data).

There is no evidence of a decline in the winter whiting fishery in the bay. Individual catches by anglers of several hundred fish per day were not uncommon in 1966–67, and many anglers remembered similar catches over the 16 years that trawling had been carried out in Moreton Bay.

The commercial seine net fishery for whiting includes two species, winter whiting and sand whiting (*S. ciliata* McCoy). The latter species forms the greater part of the annual catch, although the actual proportions are unknown, since they are boxed together and no separate market records are kept. However, the fact that there is no sign of a decline in this fishery is further indirect evidence of the state of the whiting stocks in the bay.

ACKNOWLEDGEMENT

The untiring assistance of the trawler skipper, Mr. Les Wale, is gratefully acknowledged.

ANATOMY OF PETRIFIED RACHISES COLLECTED FROM THE JURASSIC OF AMARJOLA IN THE RAJMAHAL HILLS, INDIA

B. D. Sharma*

(Plate I)

(Communicated by J. F. Rigby)

[Accepted for publication 20th September 1972]

Synopsis

The anatomy of three different types of petrified rachises collected from the Amarjola fossiliferous locality is described. These include *Gleicheniorachis jurassica* gen. et sp. nov., *Cycadinorachis omegoides* gen. et sp. nov., as well as additional data concerning *Guptiorachis amarjolense* Sharma, 1971. Besides adding to our knowledge of the floral constitution at this locality, the present study also informs us about the manner of origin of pinna traces, and throws light on the interrelationship of different types of rachises. For the first time in a rachis, the *Cycas*-like, omega-shaped arrangement of bundles is described.

Introduction

Previously Sharma (1971) described the anatomy of a number of isolated rachises of ferns collected from the Amarjola fossiliferous locality in the Jurassic of the Rajmahal Hills, Bihar, India. Except for the two rachises, *Guptiorachis amarjolense* Sharma and *Osmundacaulis rajmahalense* (Gupta) Sharma, taxonomic positions of the rachises could not be decided and thus they were described as " rachis types ". The author made further collections of petrified rachises at Amarjola during 1971. The new collection includes mainly rachises of the bennettitalean frond genus *Ptilophyllum* Morris. Among the ferns, rachises of *Osmundacaulis* occur quite commonly. Besides these there are also a number of specimens of *Guptiorachis amarjolense* and *Gleicheniorachis jurassica* gen. et sp. nov. For the first time a petrified rachis possessing a number of concentric, mesarch bundles arranged in an omega-shaped structure was collected and is described here as *Cycadinorachis omegoides* gen. et sp. nov. Sections were prepared by grinding and polishing techniques and were mounted in Canada balsam.

Descriptions

Gleicheniorachis jurassica gen. et sp. nov.

Pl. I, Figs 1–4; Text-figs 1–6

Diagnosis: Rachis cylindrical or slightly flattened, 4·5–6·0 mm in diameter; hypodermis sclerenchymatous, 15–18 cells thick; ground tissue parenchymatous with a triangular sclerenchyma patch in the centre of rachis; stele C-shaped, free margins sharply incurving, surrounded by a continuous, regular layer of sclerotic cells. Xylem continuous, two–three cells thick, six–eight endarch protoxylem points. Pinna traces alternate, " extra-marginal type ".

Holotype: No. BGR. 1/Raj. A., Sharma Collection, University of Jodhpur.

Discussion: There are a number of specimens in the author's collection which range in diameter from 4·5–6·0 mm. Some are cylindrical, while others are slightly flattened with an adaxial depression (Text-fig. 2). The hypodermis is well developed in all specimens, it is 250–300μ thick. Ground tissue is mostly unpreserved, being replaced by some darkish substance. There is a characteristic triangular patch of sclerenchyma, 650–850 × 450–600μ in size, in the centre of the

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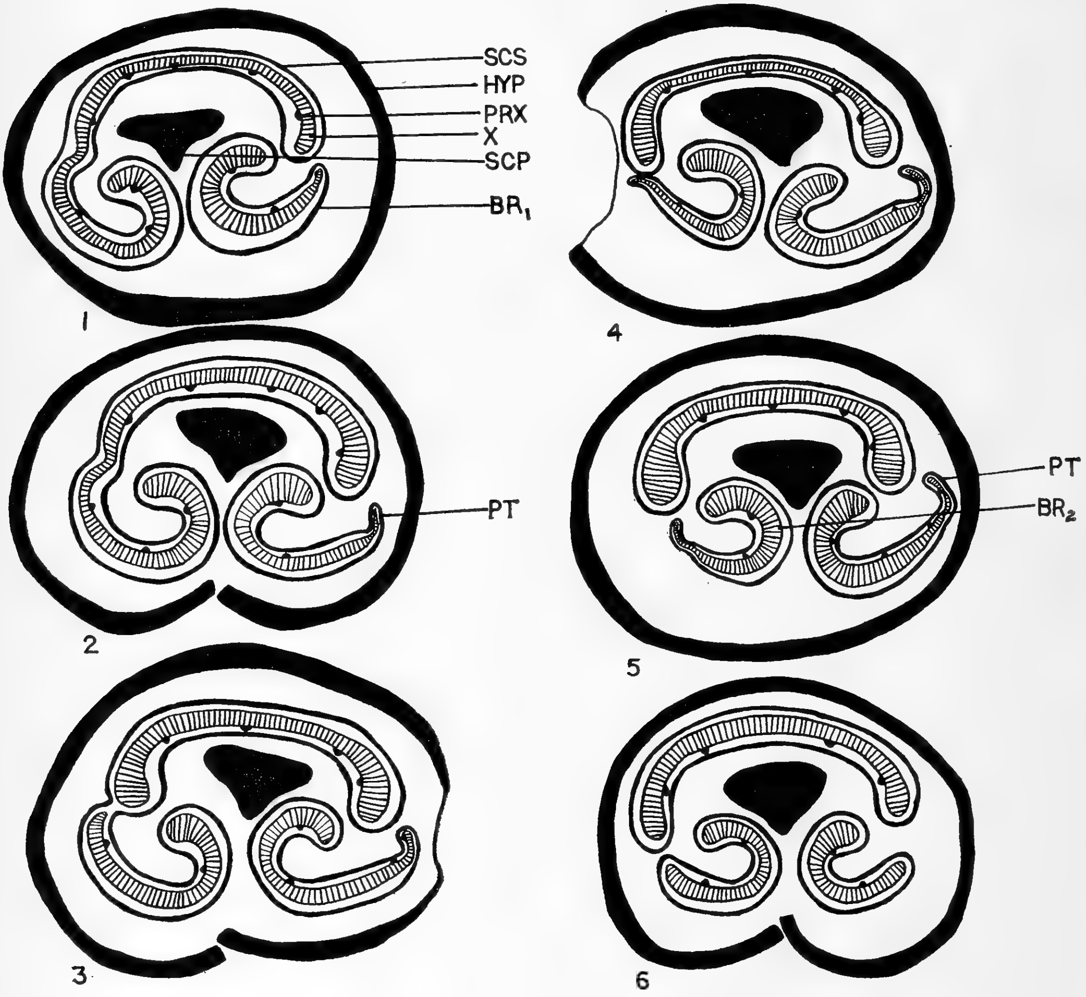
rachis. The large C-shaped stele, 3·0–3·5 × 1·5–2·0 mm in overall size, surrounds the patch. Metaxylem tracheids are hexagonal, 50–75 × 30–45μ in cross-section, while the protoxylem elements, which are situated at the endarch position in groups of 10–12 cells, are comparatively very narrow, ranging in diameter from 10μ to 15μ. Phloem, pericycle and endodermis are poorly preserved and their cellular structures cannot be studied easily.



Text-figs 1–6. *Gleicheniorachis jurassica* gen. et sp. nov. Serial transverse sections showing detachment of curved arms from the stele and formation of pinna traces, × 24. (SCS—sclerotic layer surrounding the stele; HYP—hypodermis; PRX—protoxylem; X—xylem; SCP—sclerenchyma patch; BR_1—first detached curved arm; BR_2—second detached curved arm; PT—initial pinna trace. All drawings are camera lucida sketches.)

A series of transverse sections (Text-figs 1–6) have been prepared from a number of rachises to study the mode of departure of pinna traces from the main stele. Initially, a curve or groove develops in the side arm of the C-shaped stele (Pl. I, Fig. 1; Text-fig. 1). This curve increases (Text-figs 2, 3) and ultimately the curved arm becomes detached from the main stele (Pl. I, Fig. 3; Text-fig. 4).

Then at the point of detachment in the curved arm, new cells are produced forming a small C-shaped structure (Pl. I, Fig. 4 ; Text-figs 4, 5) which is concave towards the centre of the rachis. This newly produced structure is the pinna trace initial. It consists of xylem having one or two endarch protoxylem points (Text-fig. 5), phloem, endodermis, as well as layers of sclerotic cells. At first all these tissues are continuous with those of the curved arm, but later, as a result of intrusion of sclerotic layers from both sides at the junction of the curved arm with the pinna trace initial, the latter is cut off and ultimately is detached from the parent stele to form a pinna trace. Tracheids of the pinna trace are comparatively narrower than those of the main stele. Pinna traces are produced successively in the two curved arms of the stele, showing thereby that the pinnae were either alternate or sub-alternate in this species. After cutting off of pinna traces (Text-fig. 6) the curved arms re-unite with the main stele, reforming the characteristic C-shaped stele of this genus.

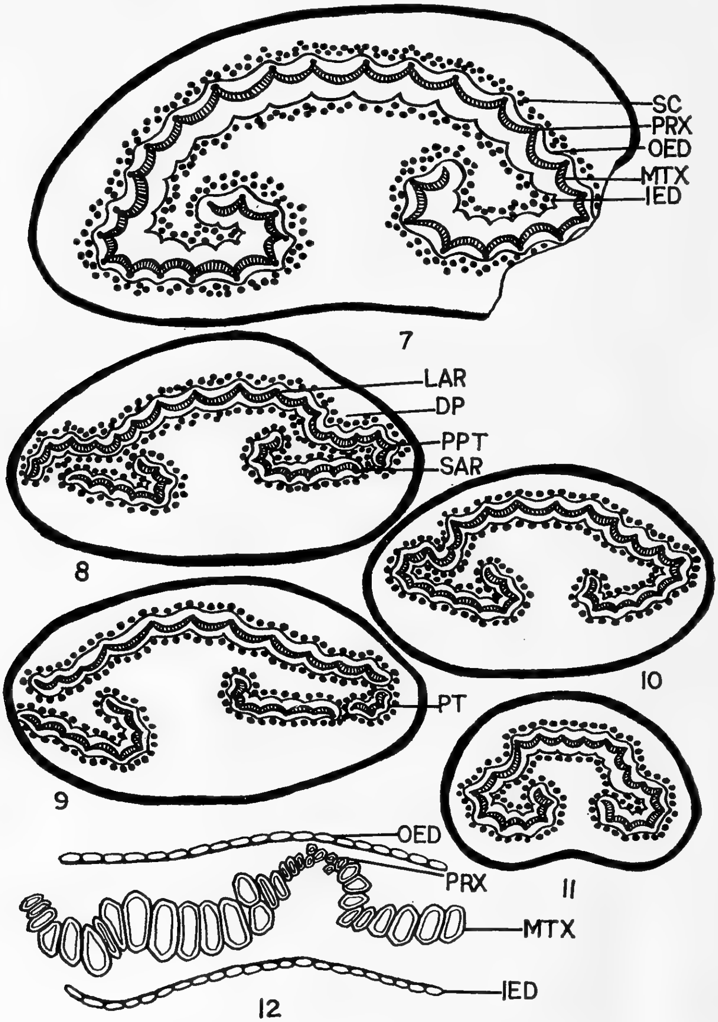
Comparison: The new genus shows a close resemblance to the living fern *Gleichenia*, which was also quite common during the Jurassic period in the Rajmahal Hills (Sharma, 1969*a*, 1971*a*). In *Gleichenia*, too, the stele is C-shaped with sharply incurving free arms enclosing a patch of sclerenchyma in the centre of the rachis ; protoxylem elements are endarch. The mode of pinna trace origin is more or less similar in *Gleichenia* and *Gleicheniorachis*, where it is of the " extra-marginal type " (Davie, 1914, 1916 ; Bower, 1923), however, they differ in details. In *Gleicheniorachis*, pinna traces are produced successively and from the detached portions of the curved arms of the stele, whereas in the living *Gleichenia* pinna traces are produced simultaneously from both sides of the main stele as a result of bulging from the side arms of the stele. Curved arms do not become detached from the main stele in the manner described above. Rachises of *Gleicheniorachis* can also be compared with the rachis of *Osmundacaulis rajmahalense* (Gupta) Sharma (1971) in the C-shaped structure of the stele, endarch positions of protoxylem points, and in the presence of a layer of sclerotic cells surrounding the stele. However, in the new genus this layer is continuous and quite regular, unlike the one found in *O. rajmahalense*, where it is more or less discontinuous and irregular in thickness. *Gleicheniorachis* can be further differentiated from *Osmundacaulis* by the presence of a triangular patch of sclerenchyma in the centre of the rachis and by a lesser number of, but well developed, protoxylem points. In *Osmundacaulis* a sclerenchyma patch is absent and protoxylem points are quite common in the stele.

Comparison of the new genus has also been made with living ferns possessing C-shaped steles and showing " extra-marginal types " of pinna trace origin. *Gleicheniorachis* differs from all these on the basis of its characteristic triangular patch of sclerenchyma, presence of a continuous layer of sclerotic cells surrounding the stele, and the alternating type of pinna trace origin.

Guptiorachis amarjolense Sharma

Text-figs 7–12

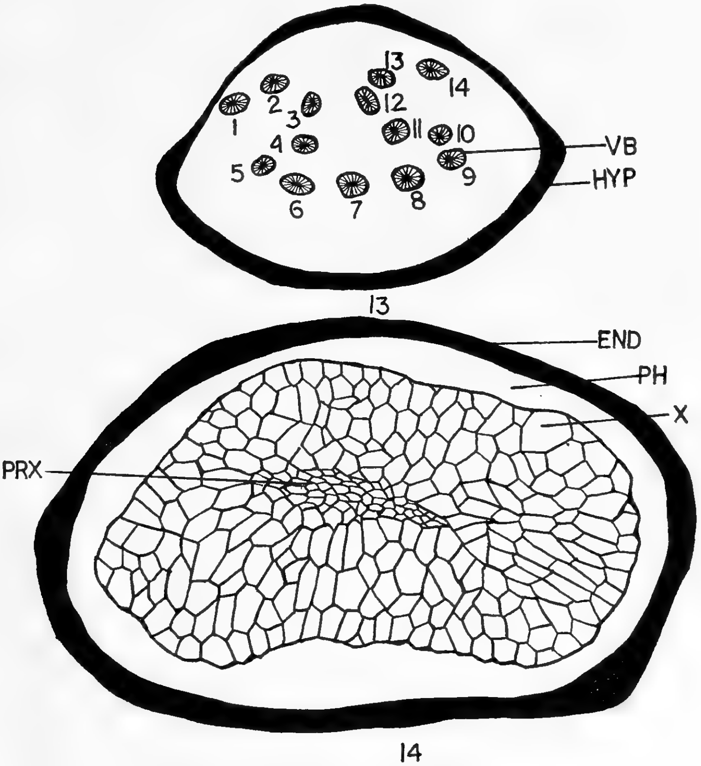
The previous description (Sharma, 1971) of this rachis was based on the circular cross section petiolar part of the frond, while in the present paper anatomy is described for the upper parts of the frond based on the study of a number of rachises of different diameters ranging from 2·5×2·0 to 8·0×5·0 mm. These rachises are flattened, with a central depression on the adaxial side. There is a hypodermis made up of four to five rows of thick-walled cells below the epidermis ; ground tissue is parenchymatous. The stele is typically C-shaped, consisting of a number of abaxially curved, saucer-shaped xylem plates (Text-fig. 7). Protoxylem elements are present at the junction of two adjacent xylem plates. Metaxylem tracheids are hexagonal and comparatively much wider than those of the protoxylem points (Text-fig. 12). Xylem plates are mostly one cell, but sometimes two cells thick. Tissues of phloem, pericycle and endodermis occur on either side of the xylem. Cells of the pericycle are not easily distinguished from cells of the phloem. The endodermis is one cell thick. Outside the endodermis on either side of the stele sclerotic cells are present forming a more or less continuous layer which is two to three cells thick in the basal part of the frond (Text-figs 7, 8). In thin rachises, the sclerotic layer becomes quite regular and two cells thick (Text-figs 9–11). In some transverse sections through



Text-figs 7–12. *Guptiorachis amarjolense* Sharma. 7–11, Transverse sections through rachises of various sizes showing shape and size of steles and mode of pinna traces origin, × 24. 12, Transverse section through a rachis showing a portion of stele. Exarch protoxylem point is produced at the junction of two adjacent xylem plates, × 72. (SC—sclerotic cells; PRX—protoxylem; OED—outer endodermis; MTX—metaxylem; IED—inner endodermis; LAR—long arm of stele; DP—depression in the arm; PPT—initial pinna trace; SAR—detached curved arm of stele; PT—pinna trace. All drawings are camera lucida sketches.)

thin rachises, it has been observed that no well-differentiated sclerotic layer is present on the inner side of the C-shaped stele, although it is quite clear on the outer side.

The present study also informs us about the manner of the vascular supply to the pinnae. Initially, grooves or depressions are produced on either side in the long arm of the stele (Text-figs 10, 11). Grooves increase in depth and ultimately the curved arms of the stele are detached simultaneously (Text-fig. 8), leaving a small portion of stele still attached with the long arm beyond the grooves. After some time even these portions beyond the grooves are also detached, and they act as pinna traces (Text-fig. 9). Thus in *Guptiorachis amarjolense*, also, the pinna trace origin is of the " extra-marginal type " similar to the one described above in *Gleicheniorachis jurassica*. Pinna traces are produced simultaneously on either side of the long arm and thus it may be presumed that the pinnae were borne either oppositely or sub-oppositely in the frond of the species. The pinna trace is a small, inwardly curved portion of the stele consisting of only two to three xylem plates (Text-fig. 9). The detached curved arms re-unite with the long arm, reforming the typical C-shaped stele of *Guptiorachis amarjolense*. The basic structure of the stele remains the same throughout the length of the leaf except that the number of xylem plates gradually



Text-figs 13–14. *Cycadinorachis omegoides* gen. et sp. nov. 13, Transverse section of rachis showing 14 concentric and mesarch bundles arranged in an omega-shaped structure, ×24. 14, Transverse section of rachis showing one of the bundles enlarged, ×300. (VB—vascular bundle; HYP—hypodermis; END—endodermis; PH—phloem; X—metaxylem; PRX—protoxylem. Both drawings are camera lucida sketches.)

decrease towards the distal end (Text-figs 9–11). In the petiolar part there are as many as 32 or more xylem plates in the stele (Sharma, 1971), whereas in thin rachises this figure may reduce to 20 (Text-fig. 11) or even less.

Cycadinorachis omegoides gen. et sp. nov.

Pl. I, Figs 5–7 ; Text-figs 13–14

Diagnosis: Rachis elliptical or cylindrical, 4–6 mm in diameter ; hypodermis sclerenchymatous, 0·5–0·6 mm thick ; ground tissue parenchymatous without mucilage canals ; vascular bundles 14, concentric, mesarch, arranged in an omega-shaped structure.

Holotype: No. BDC. 1/Raj. A., Sharma Collection, University of Jodhpur.

Discussion: There is a single specimen of this species in the author's collection ranging in thickness from 7×5 to 5×4 mm. A number of serial transverse sections have been prepared from the type specimen, of which slide No. BDC. 1a/Raj. A. (Pl. I, Fig. 5 ; Text-fig. 13) is the best preserved. The sclerenchymatous hypodermis is 10–12 cells thick. Ground tissue is made up of circular parenchymatous cells of different sizes (Pl. I, Fig. 6). Vascular bundles are arranged in an omega-shaped structure similar to that found in the living genus *Cycas*. Bundles are more or less circular, 500–550μ in cross section. All the tracheids of the metaxylem are similar and no distinction is present between centripetal and centrifugal xylems. Protoxylem tracheids are comparatively much narrower and occur in groups of 30–40 cells (Pl. I, Fig. 7 ; Text-fig. 14). In some of the vascular bundles protoxylem elements are not preserved, their place being either empty or filled in by some darkish substance (Pl. I, Fig. 6). Orientation of the protoxylem changes as the bundles pass into the side arms of the omega, where the protoxylem becomes nearer the upper side than the lower side of the bundle.

Comparison: The present material is closely comparable with the rachis of the living genus *Cycas* in the arrangement of the bundles which are placed in an omega-shaped structure ; orientation of the bundles also changes in the side arms of the omega. The structure of the bundles differs in *Cycadinorachis* from those of *Cycas*. In the latter, vascular bundles are diploxylic with a well-developed centripetal xylem and poorly represented centrifugal xylem lying adjacent to the phloem with the two xylems separated by parenchyma. In *Cycadinorachis* the vascular bundles are concentric and protostelic in nature and no distinction of centripetal and centrifugal xylem exists.

In the structure of vascular bundles *Cycadinorachis* can also be compared with a fern petiole possessing isolated meristeles. As in ferns, each meristele is provided with an endodermis, pericycle and phloem surrounding the central core of xylem, and protoxylem elements are situated at the mesarch positions. Unlike the ferns, there is a single, centarch protoxylem point in *Cycadinorachis*, whereas in the ferns there is more than one protoxylem point in a meristele, and these points lie near the periphery of the xylem. No known living or fossil ferns have the meristeles arranged in an omega-shaped structure.

DISCUSSION

The Amarjola fossiliferous locality has yielded in addition to ferns a large number of gymnospermous plants belonging to the groups Bennettitales, Cycads, Pentoxyleae and Coniferae (Sharma, 1967, 1969, 1971). Among the ferns, Osmundaceae is the most commonly occurring family, being found as rhizomes as well as petioles, while other ferns are known only from petioles or rachises as their rhizomes have still to be discovered. Studies on isolated petioles and rachises tell us not only about anatomical variations that exist, but also suggest

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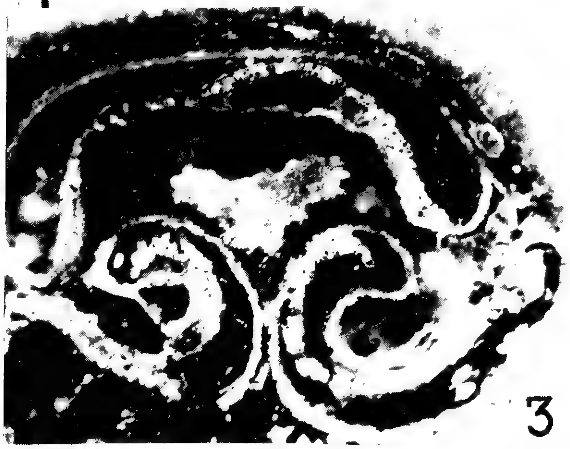

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phylogeny and inter-relationship. All the fern rachises described so far from Amarjola have an adaxially curved, C-shaped osmundaceous stele with protoxylem points situated mostly at the endarch position, and rarely mesarch or exarch. There is a similarity in the mode of pinna trace origin in the taxonomically described petioles and rachises, viz. *Guptiorachis amarjolense* Sharma (1971), *Osmundacaulis rajmahalense* (Gupta) Sharma (1971), and *Gleicheniorachis jurassica* gen. et sp. nov. All these species have the " extra-marginal type " of origin of pinna traces, which is considered as a more advanced feature than one in which pinna traces arise from the margins of the petiolar stele (Davie, 1914, 1916 ; Bower, 1923). The extra-marginal type of pinna trace origin also suggests that these fronds are of large size.

Discovery of *Cycadinorachis omegoides* gen. et sp. nov. shows not only that the omegoid arrangement of bundles, which is similar to the one found in the living genus *Cycas*, existed even during the Jurassic period, but also throws light on the relationship of the ferns with the cycads. Structure of bundles in *Cycadinorachis* is similar to the meristeles of ferns, while in their arrangement they are typically cycadean. The two petrified cycadean stems described so far from the Amarjola fossiliferous locality are *Sewardioxylon sahnii* Gupta (1960, 1971) and *Fascisvarioxylon mehtae* Jain (1964). Both these types of stems possess primitive anatomical structures and are devoid of mucilage canals (Sharma, 1971*b*). Maybe in the future some relationship will be established between *Cycadinorachis omegoides* and either of these two types of cycadean stems.

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EXPLANATION OF PLATE I

Figs 1–4. *Gleicheniorachis jurassica* gen. et sp. nov. showing various stages of detachment of curved arms and formation of initial pinna traces. × 20.

Fig. 5. *Cycadinorachis omegoides* gen. et sp. nov. showing 14 concentric, mesarch bundles arranged in an omega-shaped structure. × 20.

Fig. 6. Same, showing one of the rachis bundles and the surrounding cells of the ground tissue. × 60.

Fig. 7. Same, showing portion of the vascular bundle enlarged. Protoxylem elements lie in the centre and are surrounded by the tracheids of the metaxylem. × 200.

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VARIABILITY IN OAT STEM RUST IN EASTERN AUSTRALIA

N. H. Luig* and E. P. Baker*

[Accepted for publication 18th April 1973]

Synopsis

An unexpected degree of variability in *P. graminis* f. sp. *avenae* was revealed when isolates from eastern Australia were tested on the International Differential Set. Of the genes present in the differential set only *pg-8* provided a comprehensive protection against the pathogen.

Four grass stem rust cultures including one of *P. graminis lolii* were found to be related to oat stem rust. Certain selected genotypes from *Avena ludoviciana* and *A. fatua* were susceptible to all these cultures except to one of *P. graminis dactylidis*. Other single plant progenies from *A. ludoviciana* differentiated between the cultures.

INTRODUCTION

Although about two million acres are sown annually to oats in N.S.W., none of the currently recommended cultivars having resistance to oat stem rust, incited by *Puccinia graminis* Pers. f. sp. *avenae* Eriks. and E. Henn., were bred in Australia. The cultivar Garry introduced from Canada, carries two factors conditioning stem rust resistance but is susceptible to some field strains. Cultivar Saia, which belongs to the diploid sand oat species *Avena strigosa* Schreb., was introduced from Brazil and is grown for green feed production in Queensland and northern N.S.W. It is resistant to most strains of oat stem rust. Recently, breeding programmes have been initiated to incorporate stem rust resistance into commercial varieties, and the present studies were carried out to determine pathogenic variability in the oat stem rust fungus in eastern Australia.

REVIEW OF LITERATURE

In 1923 Stakman, Levine and Bailey differentiated oat stem rust races on three cultivars, and Bailey (1925) published an analytical key based on reactions on these genotypes: White Tartar (gene D=*Pg–1*), Richland (gene A=*Pg–2*) and Joanette Strain (gene E=*Pg–3*). For about thirty years oat stem rust investigators utilized these three monogenic varieties (or their equivalents) for identifying races. However, with the release of cultivars with the Hajira (or "Canadian") type of resistance (gene B=*Pg–4*) in North America, strains of stem rust virulent on plants with this resistance became widespread. Later, oat rust workers used two recessive genes to subdivide oat stem rust races. Green and Samborski (1962) used a line of Eagle^2 × C.I. 4023 with the gene F (*pg–8*) and Green (1965) reported that Santa Fe Selection C.I. 5844 with the gene H (*pg–9*) was useful as a differential variety. Earlier Stewart *et al.* (1956) had found a culture which attacked Saia, and since then this diploid has been used as a supplemental tester in North America. From 1957 cultures were designated on the basis of their behaviour on the original three testers and supplemental differentials, with alphabetical suffixes, often confusingly applied, were used. To overcome inherent difficulties associated with this procedure, Stewart and Roberts (1970) proposed the adoption of a standard international differential set comprising the above seven testers. "New race" numbers were assigned beginning with race 14, leaving races 1–13, described on the original three testers,

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* Department of Agricultural Botany, University of Sydney, Sydney, N.S.W., 2006.

unchanged. They also supplied an analytical key for these seven testers and presented the infection types of 97 new race numbers together with their virulence/avirulence indices. Recently genes for resistance other than those present in the above seven testers have been studied, *viz.*, *pg–11* (McKenzie and Martens, 1968), *pg–12* (Martens *et al.*, 1968) and *pg–13* (Roelfs and Rothman, 1971). The last gene has come into usage as a differential in the U.S.A., but the three genes have not been incorporated into the international set.

Waterhouse (1952) reviewed the work on oat stem rust variability in Australia until 1951. Using the three differentials White Tartar, Richland and Joanette Strain, he distinguished six physiologic races, *viz.*, 1, 2, 3, 6, 7 and 8. Of these, races 1 and 2, and 3 and 7, could be separated only at low temperatures on Joanette, and consequently, for rust survey purposes race 1 was grouped with race 2, and race 3 with race 7. The former were avirulent on plants with gene *Pg–1*, while races 3 and 7 attacked those with this gene.

During the years 1928 to 1938, 706 collections were tested, of which 85·7 per cent were race 1 and/or 2, 12·6 per cent were race 3 and/or 7, 0·4 per cent were race 8, which is virulent on plants with *Pg–2* and *Pg–3*, and 1·3 per cent belonged to race 6, which attacks all three genes *Pg–1*, *Pg–2* and *Pg–3*. This shows the prevalence of race 1 and/or 2 in the early years ; for example, during the first three seasons (1925–1927) only these types were recovered.

Of the 901 collections from all states of Australia and 30 collections from New Zealand studied by Waterhouse from 1939 to 1951, 57 per cent were identified as belonging to races 1 and/or 2. In each state they accounted for the majority of rust samples. Thirty-five per cent of the isolates proved to be race 3 and/or 7. and the remaining 8 per cent were race 8. Thus a significant shift towards virulence on *Pg–1* had taken place in the Australian oat stem rust flora during these two periods.

About 30 per cent (278) of the collections made by Waterhouse came from grasses, mainly *Avena fatua* L., *Lamarckia aurea* (L.) Moench., *Hordeum leporinum* Link., *Avena sterilis* L., *Dactylis glomerata* L. and *Amphibromus neesii* Steud. The percentages of the three abovementioned physiologic types based on these 278 isolates were 60, 34 and 6 respectively ; thus they did not significantly differ from collections made on commercial oats.

MATERIALS AND METHODS

Field collections of oat stem rust were tested annually during the last two seasons (1970–1971, 1971–1972) and a high proportion of samples from wild oats were included.

All isolates were observed on a set of 12 stocks which comprised : (1) seven differentials identical with the seven differential hosts used by Stewart and Roberts (1970) or substitutes carrying the same major gene, *viz.*, White Tartar 05* (*Pg–1*=gene D), Richland 08 (*Pg–2*=gene A), Joanette Strain R.L. 561 0617 (*Pg–3*=gene E), Rodney 0654 (*Pg–4*=gene B), Eagle^2 × C.I. 4023 0658 (*pg–8*=gene F), Santa Fe Reselection C.I. 5844–1 0661 (*pg–9*=gene H) and Saia C.I. 7010 0589 ; (2) two testers which possess the same major gene present in two varieties of group (1), *viz.*, Sevnothree C.I. 3251 0255 (*Pg–3*) and Rosen's Mutant C.I. 8159 0659 (*pg–9*) ; (3) two testers which combine major genes, *viz.*, Garry R.L. 1692 0605 (*Pg–2*, *Pg–4*) and Minn. A.G. 331 0615 (*Pg–1*, *Pg–2*) ; and (4) C.I. 3034 0660 which carries *Pg–1* and *pg–11*. Notes were recorded after 14 days on seedlings maintained at temperatures ranging from 15° C to 21° C. Infection types and nomenclature follow those of Stewart and Roberts (1970).

In addition to the field isolates, four cultures of grass stem rust, *viz.*, 69013 (*P. graminis* f. sp. *lolii* Guyot and Massenot), 69177 (tentatively designated

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* 0 numbers refer to the Sydney University Oat Accession Register.

TABLE 1
Infection Types Produced on Eight International Testers by 22 Strains of P. graminis avenae

Strain		Testers of Group 1							Supplementary Tester C.I. 3034	New Race No.*
Virulence Index	Accession Number	White Tartar	Richland	Joanette Strain	Rodney	Eagle^2 × C.I. 4023	Sante Fe Reselection	Saia	*Pg-1* *pg-11*	
		Pg-1	*Pg-2*	*Pg-3*	*Pg-4*	*pg-8*	*pg-9*	Undesig.		
0	71077	2	1+	;1‡	1	2	2	0;	2	1
0	70535	2	1+	X+	1	2	2	0;	2	5
1	70538	3+	1+	;1‡	1	2	2	0;	2	3, 49
1	71502	3+	1+	;1‡	2+	2	2	;	2	3
1, 11	R3	3+	1+	X+	1	2	2	0;	3+	
2	71577	2	3+	;1‡	1	2	2	0;1	2	11
2	BC3	2	3+	X+	1	2	2	0;	2	10
3	BC1	2	1+	3+	1	2	2	0;	2	2
1, 2	70388	3+	3+	;1‡	1	2	2	0;	2	
1, 3	BC2	3+	1+	3+	1	2	2	0;	2	7
1, 3, 11	R7	3+	1+	3+	1	2	2	X	3+	
1, 4	70553	3+	1+	X+	3+	2	2	0;	2	25
1, Sa	70590	3+	1+	X+	1	2	2	3+	2	
2, 3	70611	2	3+	3+	1	2	2	0;	2	8
2, 4	BC59	2	3+	X+	3+	2	2	0;	2	23
2, 9	R10	2	3+	X+	1	2	3	0;	2	82
3, 9	R2	2	1+	3+	1	2	3	X=	2	77
9, Sa	71394	2	1+	X+	1	2	3+	3+	2	
1, 2, 3	70497	3+	3+	3+	1	2	2	0;	2	6
2, 3, 4	70553	2	3+	3+	3+	2	3−	0;	2	22
2, 3, Sa	70590	2	3+	3+	1	2	3−	3+	2	
2, 3, 9, Sa	68001	2	3+	3+	1	2	3+	3+	2	

* According to Stewart and Roberts (1970).

P. graminis f. sp. *dactylidis* Guyot and Massenot), 69243 and 69968 which were found on *Deyeuxia quadriseta* Benth. and *Phalaris* sp., respectively were studied. All four cultures were described by Luig and Watson (1972).

EXPERIMENTAL RESULTS

(*a*) *Oat stem rust*

Using six testers with different single genes for resistance and Saia as proposed by Stewart and Roberts (1970), the Australian cultures can be differentiated into 22 strains on the basis of their reaction spectra (Table 1). Certain strains with the same virulence index were not considered identical. For instance, strain 1 (70538) and strain 1 (71502) are discriminated on the basis of their low and intermediate infection types respectively, on plants with *Pg–4*. Two of the strains are characterized by a virulent reaction on *pg–11* present in C.I. 3034.

TABLE 2
Percentages of Total Isolates of Oat Stem Rust Avirulent on Single Genes for Resistance in the Seasons 1970–1971 and 1971–1972

Gene	1970–71	1971–72
Pg–1	55·8	88·1
Pg–2	53·2	66·2
Pg–3	80·6	85·7
Pg–4	78·8	85·9
pg–8	100·0	100·0
pg–9	86·3	94·7
Saia	94·1	94·9

This degree of variability was unexpected as resistant cultivars carrying these genes have not been grown. Moreover, strains virulent on plants with these genes were quite widespread during the last two seasons 1970–1971 and 1971–1972 (Table 2). On the other hand acreages sown to the Canadian cultivar Garry and to Saia are too small to give the more virulent strains a definite advantage. By contrast little variation was encountered with wheat stem rust, *P. graminis* f. sp. *tritici* Eriks. and E. Henn., during the period 1929–1941 (Waterhouse, 1952) when the bulk of the inoculum in all Australian states comprised a single strain and nearly all wheat cultivars were susceptible.

No cultures virulent on plants with *pg–8* (gene F) were found, indicating that in Australia the gene present in C.I. 8111 $(\text{Eagle})^2 \times (\text{Hajira} \times \text{Joanette})$ is the best source of resistance among the genes present in the differentials.

On Joanette Strain (*Pg–3*), Rodney (*Pg–4*) and Saia, two resistant infection types were recorded (Table 1). It is possible that Saia possesses more than a single gene for resistance since Murphy *et al.* (1958) found two independent dominant genes for resistance in another *strigosa* variety, C.D. 3820. However, Rodney apparently possesses only a single gene for resistance. The variation on Rodney could be due to multiple alleles for virulence in the pathogen. Watson and Luig (1968) have described progressive increases in infection types on varieties with single genes for resistance in the case of wheat stem rust. On Joanette Strain clearly two levels of resistance were exhibited, and the variety Sevnothree which carries the same gene *Pg–3*, reacted similarly to all strains shown in Table 1. The resistant infection types on both varieties are very temperature-sensitive, high temperatures resulting in susceptibility.

Two of the strains listed in Table 1 produced susceptible infection types on the tester C.I. 3034 which possesses the genes *Pg–1* and *pg–11*. Since the bulk of the inoculum and the majority of the strains are avirulent on *Pg–1*, it is not possible to assess the extent of virulence on *pg–11* in the oat stem rust flora, but it seems certain that this partially recessive gene is of limited value for breeding. Resistance at the *pg–11* locus appears to be closely associated with yellow-green plant colour, but there is no close linkage between *pg–11* and the genes *Pg–2*, *Pg–3* and *Pg–4* (McKenzie and Martens, 1968). Thus *pg–11* could be combined with one or more of these factors.

A large proportion of the samples collected from wild oats and from other wild and cultivated grasses yielded more than one strain, including strains with several genes for virulence. This agrees with the findings of Roelfs and Rothman (1971), who reported that the patterns of the oat stem rust isolates in the U.S.A. differed according to the hosts from which the collections were made. They found that race 61 (7F) accounted for 2 per cent of the isolates obtained from commercial oats, but was identified in 29 and 18 per cent of the isolates examined from barley and wild grasses (mainly *A. fatua*) respectively. The fact that Waterhouse (1952) observed no differences in race patterns when collections made from cultivated and wild oats were compared may have been due to the few resistance genes used in the differential set at that time.

(*b*) *Related Grass Rusts*

When the four stem rust cultures which are pathogenic on grass species but which cannot attack cultivars of wheat, oats or rye (Luig and Watson, 1972) were inoculated on seedlings of 12 selected oat varieties, the resulting high infection types suggested that some of them must be considered closely related to *P. graminis avenae* (Table 3). However, the very low infection types produced by the cultures on the 12 differentials of the Australian oat stem rust set (Table 4), as compared to those induced by an avirulent strain of *P. graminis avenae*, indicate that they are different from oat stem rust.

TABLE 3

Infection Types Produced by a Strain of Oat Stem Rust and Four Grass Stem Rusts on 12 Selected Oat Varieties

Variety			Stem Rust Culture				
W Number	Varietal Name	Botanical Name	Strain 3 *P. gr. avenae*	69968	69243	69013 *P. gr. lolii*	69177 *P. gr. dactylidis*
09	Algerian	*A. sterilis*	3+	3=	1‡3=	0;1	0
026	Short Oat	*A. brevis*	3+	3+	3+	2+3	:1+
028	Wild Oat	*A. sterilis polystachya*	3+	;1	;1, 1‡	X–	0
033	Yarran	*A. sativa*	3, 3+	;	;1‡	;1, 2	0
054	Fulghum	*A. sativa*	3+	X, 2‡	2+3	0	0
0128	Bond	*A. sativa*	3+	;1‡	22+	23–	0
0132	Kendall	*A. sativa*	3+	$3^{c}3$	2‡3–	X	0
0175	Belar	*A. byzantina*	3+	X–, X	1‡, 23—	X–	0
0182	Glabrota	*A. strigosa*	3+	33+	33+	23–	2=2–
0202	C.I. 3498	*A. strigosa*	3+	2–2+	33+	2+3–	0;
0210	Bond × Iogold	*A. sativa*	2=2–	2–2	;1=	23–	0
0335	Erban	*A. sativa*	3+	2+3	2+3–	2	;1=

Luig and Watson (1972) suggested that two of the cultures, *viz.* 69243 and 69968, could be of hybrid origin. The high infection types produced by 69013 (*P. graminis lolii*) on the 12 selected oats, however, were unexpected, as this *forma specialis* was believed to be a true grass rust which had specialized on genotypes of *Lolium* sp. (Waterhouse, 1951). The fourth culture (69177) showed little virulence on all oat varieties tested, but it is highly pathogenic on most genotypes of *Dactylis glomerata*.

TABLE 4

Infection Types Produced by an Avirulent Strain of Oat Stem Rust and Four Grass Stem Rusts on the 12 Australian Oat Stem Rust Testers

	Genes Involved		*P. gr. avenae* 71622 Strain 0	Grass Stem Rusts			
	Alphab. Desig.	Pg Desig.		69968	69243	69013	69177
Richland 08	A	*Pg–2*	1+	;	;	;	0
Rodney 0654	B	*Pg–4*	1+	;1	0	0	0
White Tartar 05	D	*Pg–1*	2−	;	0	0	0
Jostrain 0617	E	*Pg–3*	1+	;1=	0;	0	0
Eagle^2 × C.I. 4023 0658	F	*pg–8*	2−	;1	;1	;1=	0
Santa Fe Reselection 0661	H	*pg–9*	X+	0;	0	0	0
Saia 0589	Undesig.	Undesig.	0;	3	X	2	0
Minnesota A.G.331 0615	A, D	*Pg1 Pg2*	1+	0	0	0;	0
Garry 0605	A, B	*Pg2 Pg4*	1+	0;	0	0	0
C.I. 3034 0660	A−	*Pg–1* *pg–11*	1+2−	;1	;1=	0	0
Rosen's Mutant 0659	H	*pg–9*	1+2	;1	;1=	0	0
Sevenothree 0255	E	*Pg–3*	1+	3	2+	0	0

(*c*) *Stem Rust on Wild Oats*

Waterhouse (1952) demonstrated that in Australia oat stem rust survives well on native and introduced grasses, and that species of wild oats are the most common hosts. The aim of the present work with wild oats, initiated by Professor I. A. Watson, was to detect a genotype susceptible to many strains of *P. graminis avenae* and related rusts. Such a genotype could then be utilized

(i) as a susceptible medium for somatic hybridization studies between these rusts,

(ii) as a susceptible parent in crosses with resistant genotypes to determine the genetic basis of resistance to the avirulent cultures used in this study, and

(iii) as a recurrent parent for transferring individual genes for resistance into a susceptible background. Such genes could comprise the recognized *Pg* series, and also genes for resistance to the avirulent cultures. Data from pathogenic studies, some of which are presented in Table 3, suggest that there exist, previously unrecognized, many genes for resistance to these cultures.

A large number of single plant progenies from common wild oats (*Avena fatua*) and winter wild oats (*A. ludoviciana* Durieu) were tested with the four grass rusts. All were resistant to culture 69177 and to strains of wheat stem rust and rye stem rust, *P. graminis* f. sp. *secalis* Eriks. and E. Henn., but with the other three rusts variability was apparent (Table 5).

TABLE 5

Infection Types Produced on Single Plant Progenies of Wild Oats by Cultures of P. graminis

Wild Oat Selection		Grass Rusts				*P. gr. avenae* Strain 1, 9
		69968	69243	69013	69177	
A. ludoviciana	A1	3+	3^c	3^c	0;	3+
,, ,,	B	3+	;	X+	0	3+
,, ,,	F	3+	3+	0;	0	3+
,, ,,	L	;1=	;1=	0;	0	3+
A. fatua	A	;1=	;	0	0	3+
,, ,,	WOA	3+	3+	3+	0	3+

Certain genotypes of *A. ludoviciana* (B and F) were resistant when tested with cultures 69243 and 69013, while giving susceptible reactions to 69968. Again, other genotypes of *A. ludoviciana* and *A. fatua* were susceptible or resistant to all four grass rusts. Since all wild oat seedlings exhibited susceptible infection types after inoculation with strains of oat stem rust, it is apparent that genotypes like Al and WOA can act as mutual hosts to *P. graminis avenae* and the three related grass rusts (Table 5) thus serving as a possible medium for somatic hybridization between these *formae speciales* of *P. graminis.*

DISCUSSION

Barberry bushes (*Berberis vulgaris* L.), on which the sexual stage of oat stem rust occurs, are rarely found in eastern Australia, and examination of occasional aeciospore formation has so far failed to indicate the presence of *P. graminis avenae* on barberry in Australia. In the U.S.A. it was found that the oat stem rust pattern in the vicinity of *B. vulgaris* was more variable and hence different from that obtained from regions where barberries are absent (Roelfs and Rothman, 1971).

Luig and Watson (1970) suggested that the introduction of wheat cultivars with several different single genes for resistance has been the major factor determining variability in the Australian wheat stem rust flora. The cultivation of commercial types with complex resistances resulted in a rapid increase of strains possessing several virulence genes. Most of the variability found in *P. graminis avenae* in eastern Australia cannot be explained by the presence of resistant cultivars. The acreages in N.S.W. sown to Burke and Laggan, both with the *Pg–2* gene (Upadhyaya and Baker, 1962), Lampton with *Pg–1*, and to Garry (genes *Pg–2* and *Pg–4*), are too small to have a significant effect on the prevalence of the more virulent strains. However, it appears certain that the cultivation of Saia in Queensland has favoured the survival of strains virulent on it.

Our studies have shown that the recessive gene *pg–8* derived from C.I. 4023 (Hajira × Joanette) and present in the oat stem rust differential C.I. 8111 provides an effective source of resistance to oat stem rust in eastern Australia. Since Joanette carries gene *Pg–3* only, gene *pg–8* (F) must have come from Hajira and could be identical with one of the linked genes Hj_1 or Hj_2 found by Upadhyaya and Baker (1960) in the Hajira derivative Garry.

Virulence on *pg–8* has been found to be dominant (Martens *et al.*, 1970), and it appears that mutations from the recessive to the dominant state in the corresponding gene for virulence on *pg–8* are rare in the Australian oat stem rust flora. On the other hand, in the United States a strain virulent on this gene was identified in 1962, and increased to 70 per cent of the isolates studied in 1963 (Stewart and Roberts, 1970). To achieve a broader basis for resistance, *pg–8* should be combined with another gene, *e.g. Pg–4*, *pg–9* or *Pg–3*. However, it cannot be easily combined with *Pg–1* or *Pg–2*, since all three genes are very closely linked (McKenzie and Green, 1965).

The other factors for resistance in the seven differentials appear to be of little value on their own if incorporated into an Australian cultivar (Table 2). The factor(s) in Saia would not give effective protection in Queensland and northern N.S.W. The gene *pg–9* is recessive and, therefore, more difficult to handle in a breeding programme, and it is ineffective against several strains. Of the four dominant genes, *Pg–4* probably is of the greatest value to the breeder when combined with other resistances (Table 1). Since it is not allelic with the other designated genes of the differential set, such a task should not be difficult.

Martens *et al.* (1970) studied the gene for gene relationships in the *Avena : P. graminis* host-pathogen system in Canada. Many rust strains were found to carry factors for virulence on genes for resistance never used in North America.

Strains homozygous recessive for the genes for virulence on *Pg–1*, *Pg–2* and *Pg–4* were widespread, probably due to the cultivation of varieties with these genes. Strains with the dominant genes for virulence on *pg–8* and *pg–9* accounted also for the bulk of inoculum in western and eastern Canada respectively. Virulence on *Pg–3*, apparently controlled by an extra-chromosomal component (Green, 1965), was predominant in the rust flora in both parts of Canada. In Australia, virulence on *Pg–3* and those controlled by the recessive genes corresponding to *Pg–1*, *Pg–2* and *Pg–4* were found to be more prevalent in the rust flora than virulence conditioned on *pg–8* and *pg–9* by two single dominant genes. In this instance there appears to be no linkage in the pathogen between recessive genes for virulence and recessive deleterious genes.

Luig and Watson (1972) stated that the grass species *Agropyron scabrum* Beauv. and *Hordeum leporinum* appear to be important sources of somatic hybrids between *P. graminis* f. sp. *tritici* and *P. graminis* f. sp. *secalis*. The present study dealing with single plant progenies of wild oats suggests that hybridization might occur between oat stem rust and related grass stem rusts including *P. graminis lolii* and *P. graminis dactylidis* on certain genotypes of *A. fatua* and *A. ludoviciana*. Likewise *Dactylis glomerata* and other cultivated and native grasses comprise genotypes which are susceptible to *P. graminis avenae*, *P. graminis lolii* and to three other cultures used in this study. If somatic hybridization occurs, subsequent selection on other species could result in the establishment of different types of *P. graminis*. It has been suggested that cultures 69968 and 69243 could have arisen as somatic hybrids involving *P. graminis avenae* as one parent (Luig and Watson, 1972).

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NEW RECORDS AND SPECIES OF *LAELAPS* AND ALLIED GENERA FROM AUSTRALASIA (ACARI: DERMANYSSIDAE)

ROBERT DOMROW*

(Plate II)

[Accepted for publication 18th April 1973]

Synopsis

Three species of *Laelaps* are described from " old endemic " Australian rodents (Muridae): *L. aella*, n. sp., from *Pseudomys gracilicaudatus*, *L. pammorphus*, n. sp., from *Zyzomys argurus* and *Z. woodwardi*, and *L. spatanges*, n. sp., from *P. hermannsburgensis* and *P. delicatulus*.

The first two, showing a full complement of 39 pairs of setae on the dorsal shield and relatively unmodified peritremes and genitoventral setae, are placed in the *nuttalli* species-group (hosts bush-rats &c.) rather than in the *finlaysoni* species-group (35 pairs of setae on dorsal shield; peritremes and anterior two pairs of genitoventral setae much abbreviated; hosts " old endemics ").

The hirsute third species, with 38 pairs of setae on the dorsal shield, is also readily separable from the *finlaysoni* species-group, and is placed in the newly-defined, monotypic *spatanges* species-group.

Within the *nuttalli* species-group, *L. assimilis*, normally a parasite of bush-rats (*Rattus fuscipes* and *R. lutreolus*), is noted from the " old endemic " *Mastacomys*, which occurs in intimate ecological connexion with *R. lutreolus*. This, however, is an example of host-specificity due to the gregariousness, rather than the phylogenetic relationships, of the hosts. One new host is listed for *L. mackerrasi*, and additional figures are given for *L. rothschildi* to facilitate comparison with *L. aella*. New locality records are given for *L. nuttalli* and *L. echidninus*.

L. hapaloti, the sole member of the *hapaloti* species-group (37 pairs of setae on dorsal shield, basal seta on coxa I spinose as in no other Australian species) is refigured and shown to be confined to " old endemic " hopping-mice of the genus *Notomys*, two species of which are listed as new hosts.

Australolaelaps rosamondae, n. sp., is figured and described from the swamp wallaby, *Wallabia bicolor* (Macropodidae), in Victoria. It shows the peritremes obsolescent as in the one known species (*A. mitchelli*) from Macropodinae, but coxa II carries an immense hook as in the two known species from Potoroinae: *A. greeni* and *A. validipes*.

New hosts and records are detailed for 20 species of 12 other dermanyssid genera (*Gymnolaelaps, Laelapsella, Mesolaelaps, Haemolaelaps, Neolaelaps, Domrownyssus, Eulaelaps, Raillieita, Bewsiella, Ornithonyssus, Rallinyssus,* and *Larinyssus*).

INTRODUCTION

Recent accessions have yielded the four new species of dermanyssid mites from Australian mammals described below. To facilitate their discussion, several new host-records for related parasites are also detailed. Infestations of captive, as distinct from wild, animals are noted.

The morphological terms used are largely those of Evans and Till (1965) and Lindquist and Evans (1965), while the hosts are listed after Ride (1970) and Leach [1958]. To avoid repetition, the illustrations (on which one division on the scales $=100\mu$) are generally arranged as follows (the few exceptions are obvious). The leading edge of the legs faces the top of the page, and the dorsal view is figured above the ventral. The capitula are drawn in ventral view, with the right palp shown dorsally.

Genus GYMNOLAELAPS Berlese

Gymnolaelaps Berlese, 1916, *Redia*, 12: 170. Type-species *Laelaps myrmecophilus* Berlese, 1892.

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Steyskal (1970) pointed out that only large lexicons give both the common Greek feminine noun λαιλαψ (a tempest), and the rare Latin masculine noun *Laelaps* (a dog in Ovid's *Metamorphoses*). Accordingly, the usage of classical acarologists varied, Michael preferring the feminine and Berlese the masculine (Tipton, 1960). However, among the species of *Laelaps* Koch is *L. festinus* Koch, a clear example of a Latin adjective in the masculine, and I therefore revert to this usage (see Art. 30 in Stoll *et al.*, 1964, and Domrow, 1963*a*).

Gymnolaelaps annectans Womersley

G. annectans Womersley, 1955, *Aust. J. Zool.*, 3 : 419.

Hypoaspis nidicorva Evans and Till, 1966, *Bull. Br. Mus. nat. Hist.*, 14 : 179. *New synonymy.*

New host-records.—One ♀ from dusky antechinus, *Antechinus swainsonii* (Waterhouse) (Marsupialia : Dasyuridae), Cradle Mountain, Tas., 20.iii.1963, R. H. Green.

Two ♀♀ from swamp antechinus, *A. minimus* (Geoffroy), Waratah, Tas., vi.1963, R.H.G.

Two ♀♀ from eastern swamp-rat, *Rattus lutreolus* (Gray) (Rodentia : Muridae), Mount Nebo, Qd, 12.xi.1964, E. H. Derrick.

Notes.—As the classification of the genera centred around *Hypoaspis* Canestrini " requires radical revision " (Evans and Till, 1966), no new combinations are proposed, either here or in *Haemolaelaps* Berlese.

Genus LAELAPSELLA Womersley

Laelapsella Womersley, 1955, *Aust. J. Zool.*, 3 : 416. Type-species *L. humi* Womersley, 1955.

Laelapsella humi Womersley

L. humi Womersley, 1955, *Aust. J. Zool.*, 3 : 417.

New host-records.—Seven ♀♀ from brush-tailed possum, *Trichosurus vulpecula* (Kerr) (Marsupialia : Phalangeridae), Pomonal, Vic., 31.iii.1968, J. H. Seebeck.

Four ♀♀ from southern bush-rat, *Rattus fuscipes* (Waterhouse), Loch Valley, Vic., iii.1963, R. M. Warneke. Three ♀♀ from *R. fuscipes*, Kangaroo Island, S.A., 11.ix.1967, S. H. Wheeler.

Two ♀♀ from Norway rat, *Rattus norvegicus* (Berkenhout), Hobart, Tas., 6.xi.1962, B. C. Mollison.

Twenty-three ♀♀ from broad-toothed rat, *Mastacomys fuscus* Thomas (Muridae), Dargo Road, Mount St. Bernard, Vic., 14.ii.1967, J.H.S.

Genus MESOLAELAPS Hirst

Mesolaelaps Hirst, 1926, *Proc. zool. Soc. Lond.*, 1926 : 840. Type-species *Laelaps* (*M.*) *anomalus* Hirst, 1926.

Mesolaelaps australiensis (Hirst)

L. (*M.*) *australiensis* Hirst, 1926, *Proc. zool. Soc. Lond.*, 1926 : 840.

New host-records.—Twelve ♀♀ from white-backed swallow, *Cheramoeca leucosterna* (Gould) (Passeriformes : Hirundinidae), Lake Victoria, between Ivanhoe and Broken Hill, N.S.W., 24.iv.1968, K. G. Simpson.

Three ♀♀ from Mitchell's hopping mouse, *Notomys mitchellii* (Ogilby) (Muridae), Pier Millan, between Ouyen and Sea Lake, Vic., 13.ii.1966, R.M.W.

Six ♀♀, *Rattus fuscipes*, Kangaroo Island, S.A., ii.1969 and 9.iii.1967, S.H.W.

Mesolaelaps bandicoota (Womersley)

Hypoaspis bandicoota Womersley, 1956, *J. Linn. Soc.*, 42 : 573.

New host-records.—One ♀ from quoll, *Dasyurus viverrinus* (Shaw) (Dasyuridae), Gladston, Tas., vii.1964, R.H.G.

Two ♀♀, *Rattus fuscipes*, Kangaroo Island, S.A., ii.1969 and 25.vi.1967, S.H.W.

Notes.—This specific name is best considered a noun in apposition to the generic name.

Mesolaelaps antipodianus (Hirst)

L. (*Heterolaelaps*) *antipodiana* Hirst, 1926 (*sic*), *Proc. zool. Soc. Lond.*, 1926 : 838.

New host-record.—Five ♀♀ from potoroo, *Potorous tridactylus* (Kerr) (Marsupialia : Macropodidae), near Pomonal, Vic., 17.vi.1964, R.M.W.

Notes.—This species and *Haemolaelaps marsupialis* (Berlese) normally parasitize various bandicoots (Marsupialia : Peramelidae), but these and potoroos are closely associated ecologically, at least in S.E. Queensland.

Mesolaelaps sminthopsis (Womersley)

L. (*L.*) *sminthopsis* Womersley, 1954, *Rec. S. Aust. Mus.*, 11 : 117.

New host-records.—Five ♀♀ and one nymph from nesting material of Leadbeater's possum, *Gymnobelideus leadbeateri* McCoy (Marsupialia : Petauridae), Loch Valley, Vic., 29.vii.1963, R.M.W.

Eight ♀♀ from common dunnart, *Sminthopsis murina* (Waterhouse) (Dasyuridae), Mount Clay, Vic., 26.vii.1968, J.H.S.

Notes.—This species is normally a parasite of various marsupial mice (Dasyuridae).

Genus HAEMOLAELAPS Berlese

Haemolaelaps Berlese, 1910, *Redia*, 6 : 261. Type-species *Laelaps* (*H.*) *marsupialis* Berlese, 1910.

Haemolaelaps casalis (Berlese)

Iphis casalis Berlese, 1887, *Acari, Myriapoda et Scorpiones hucusque in Italia reperta*, 38 : 8. Padua.

New host-record.—Nineteen ♀♀ and one deutonymph from uniform swiftlet, *Collocalia vanicorensis* (Quoy and Gaimard) (Apodiformes : Apodidae), Gatop, Finschhafen Subdistrict, N.G., x.1960, B. McMillan.

Haemolaelaps fahrenholzi (Berlese)

L. (*H.*) *fahrenholzi* Berlese, 1911, *Redia*, 7 : 432.

New host-record.—Two ♀♀ from fairy prion, *Pachyptila turtur* (Kuhl) (Procellariiformes : Procellariidae), Albatross Island, Tas., 24.i.1973, R.H.G.

Notes.—This cosmopolitan nidophile was most recently redescribed by Till (1963) and Evans and Till (1966). The present specimens show ratio length : breadth tarsus IV = 6, setae J_1 extending slightly beyond bases of J_2 (now lost), chelae 35μ long, coronal filaments uniformly long, margin of dorsal shield " double ", and pilus dentilis typical of *H. fahrenholzi.* They cannot, therefore, be identified with *H. pachyptilae* Zumpt and Till, 1956.

Haemolaelaps marsupialis (Berlese)

L. (*H.*) *marsupialis* Berlese, 1910, *Redia*, 6 : 261.

New host-record.—Two ♀♀ from *Potorous tridactylus*, near Pomonal, Vic., 17.vi.1964, R.M.W.

Notes.—See note on *Mesolaelaps antipodianus.*

Haemolaelaps flagellatus Womersley

H. flagellata Womersley, 1958 (*sic*), PROC. LINN. SOC. N.S.W., 82 : 300.

New host-record.—Five ♀♀ from echidna, *Tachyglossus aculeatus* (Shaw) (Monotremata : Tachyglossidae), Kelso, Tas., 17.ii.1961, B.C.M.

Notes.—The movable chela in this species is bidentate (apart from the tip).

Genus LAELAPS Koch

Laelaps Koch, 1836, *Deutschlands Crustaceen, Myriapoden und Arachniden*, 4: 19. Regensburg: Herrich-Schäffer. Type-species *L. hilaris* Koch, 1836.

Laelaps mackerrasi Domrow

L. mackerrasi Domrow, 1961, PROC. LINN. SOC. N.S.W., 86: 70.

New host-record.—Common on mottle-tailed Cape York rat, *Rattus leucopus* (Gray) (subspecies *cooktownensis* Tate), Dayman (Rocky) Point and Daintree Road, N of Mossman, Qd, vi.1970 and v.1971, R. Domrow and R. W. Campbell.

Laelaps nuttalli Hirst

L. nuttalli Hirst, 1915, *Bull. ent. Res.*, 6: 183.

New locality record.—Four ♀♀ from Pacific islands rat, *Rattus exulans* (Peale), Nouankao River, Eromanga, New Hebrides, 11.vii.1971, A. G. Marshall. Two ♀♀ and one ♂ from *R. exulans*, Tagabe, Vila, Efate, New Hebrides, 17.vii.1971, A.G.M. (The Royal Society and Percy Sladen Expedition to the New Hebrides, 1971).

Laelaps assimilis Womersley

L. assimilis Womersley, 1956, *J. Linn. Soc.*, 42: 557.

New host-records.—Several specimens from *Mastacomys fuscus*, Carlisle, Otway Ranges, Vic., 30.ix.1965, J.H.S. Numerous specimens from two *M. fuscus*, Penny's Saddle, Vic., 9.vi.1968, J.H.S. Numerous specimens from three *M. fuscus*, Kalorama, Vic., 20–23.ix.1968, J.H.S.

Five ♀♀ and four ♂♂, *Rattus fuscipes*, Kangaroo Island, S.A., ii.1969 and 9.iii.1967, S.H.W.

Notes.—This species is widespread on native species of *Rattus* Fischer, including *R. lutreolus* (see Domrow, 1965). The present records, however, are a case of host-specificity determined (at least initially) by the gregariousness, rather than the phylogenetic relationships, of the hosts, since *Mastacomys* Thomas, an " old endemic " (Ride, 1970), occupies the same habitat, and even the same runways, as *R. lutreolus*. Strandtmann (1958, 1959) noted the same phenomenon in dermanyssid nasal mites of birds: penguins and waders in marine environments harbour species of *Rhinonyssus* Trouessart distinct from those in ducks and grebes in fresh water.

Laelaps echidninus Berlese

L. (*Iphis*) *echidninus* Berlese, 1887, *Acari, Myriapoda et Scorpiones hucusque in Italia reperta*, 39: 1. Padua.

New locality record.—One ♀ from *Rattus exulans*, Tagabe, Vila, Efate, New Hebrides, 17.vii.1971, A.G.M. One ♀ from *R. exulans*, Narabut, New Hebrides, 23.x.1971, A.G.M. (RSPSE).

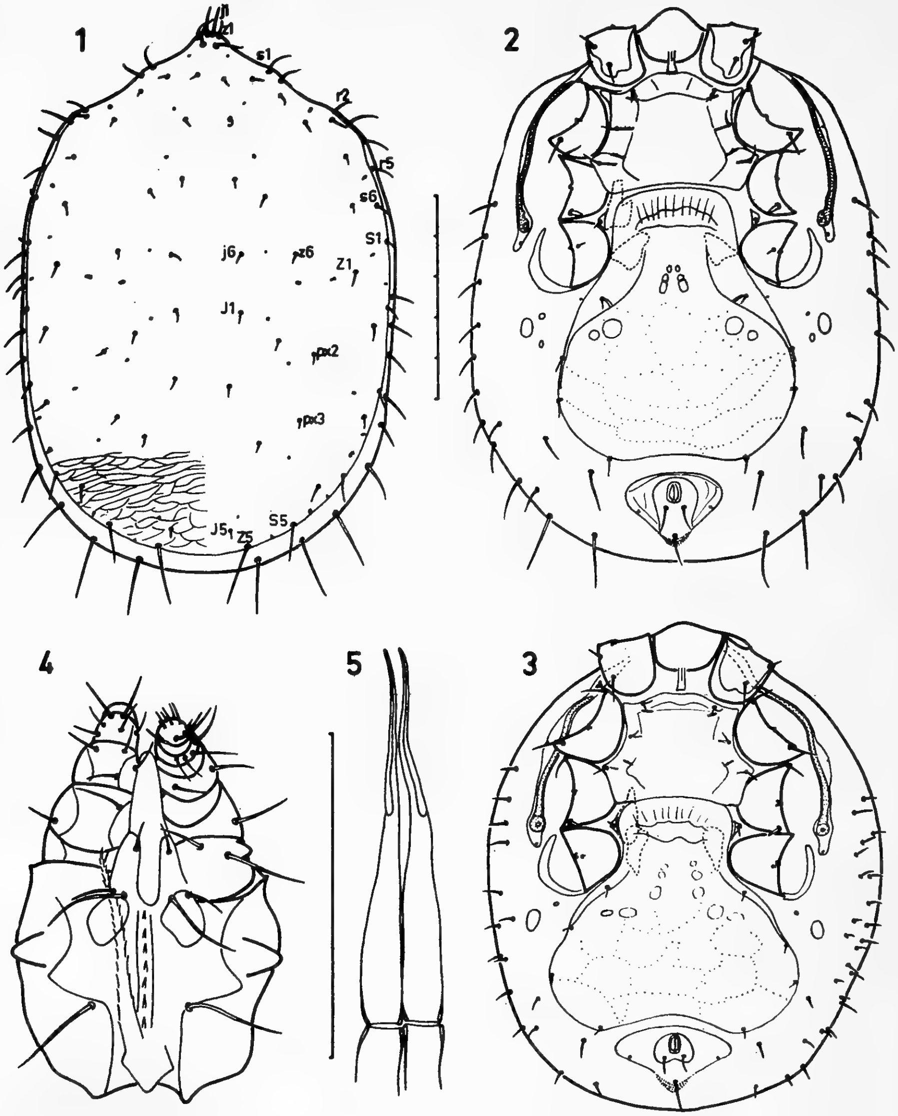
Laelaps aella, n. sp.

(Figs 1–2, 6–12)

Types.—Holotype ♀ and 20 paratype ♀♀ from eastern chestnut native-mouse, *Pseudomys gracilicaudatus* (Gould) (Muridae), Mt. Brockman, N.T., 25.vii.1971, J. H. Calaby. Deposited in Australian National Insect Collection, CSIRO, Canberra (13, including holotype) and QIMR (8).

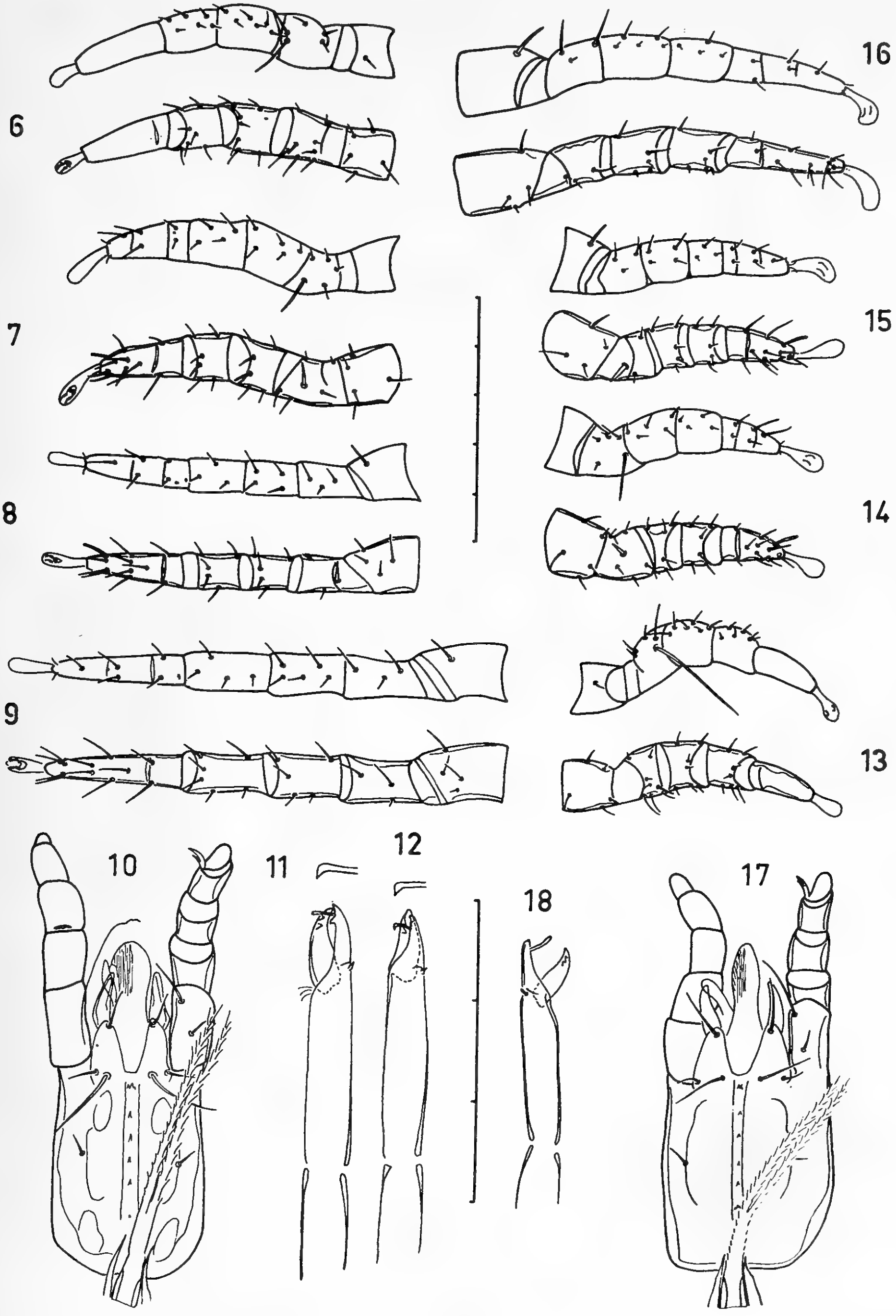
Female.—Capitulum with *c* falling short of deutosternum; *h*1–2 slightly, and *h*3 considerably, longer. Deutosternal groove with six rows of denticles, mostly single. Cornicles well-formed. Epistome diaphanous but extensive, reaching forward to middle of palpal genua; marbled discally at level of femora. Palpi (trochanter-tibia, and almost certainly tarsus) with setation called for by Evans and Till (1965) for dermanyssids in general; genu with *al*1 spatulate.

Claws bifid. Chelicerae fully formed. Fixed digit with two subterminal denticles and pilus dentilis (latter protruding externally, abruptly bent and foliate at tip); with setule and pore near base. Movable digit hyaline and straight internally, but bidentate externally to receive tip of fixed digit; corona present.

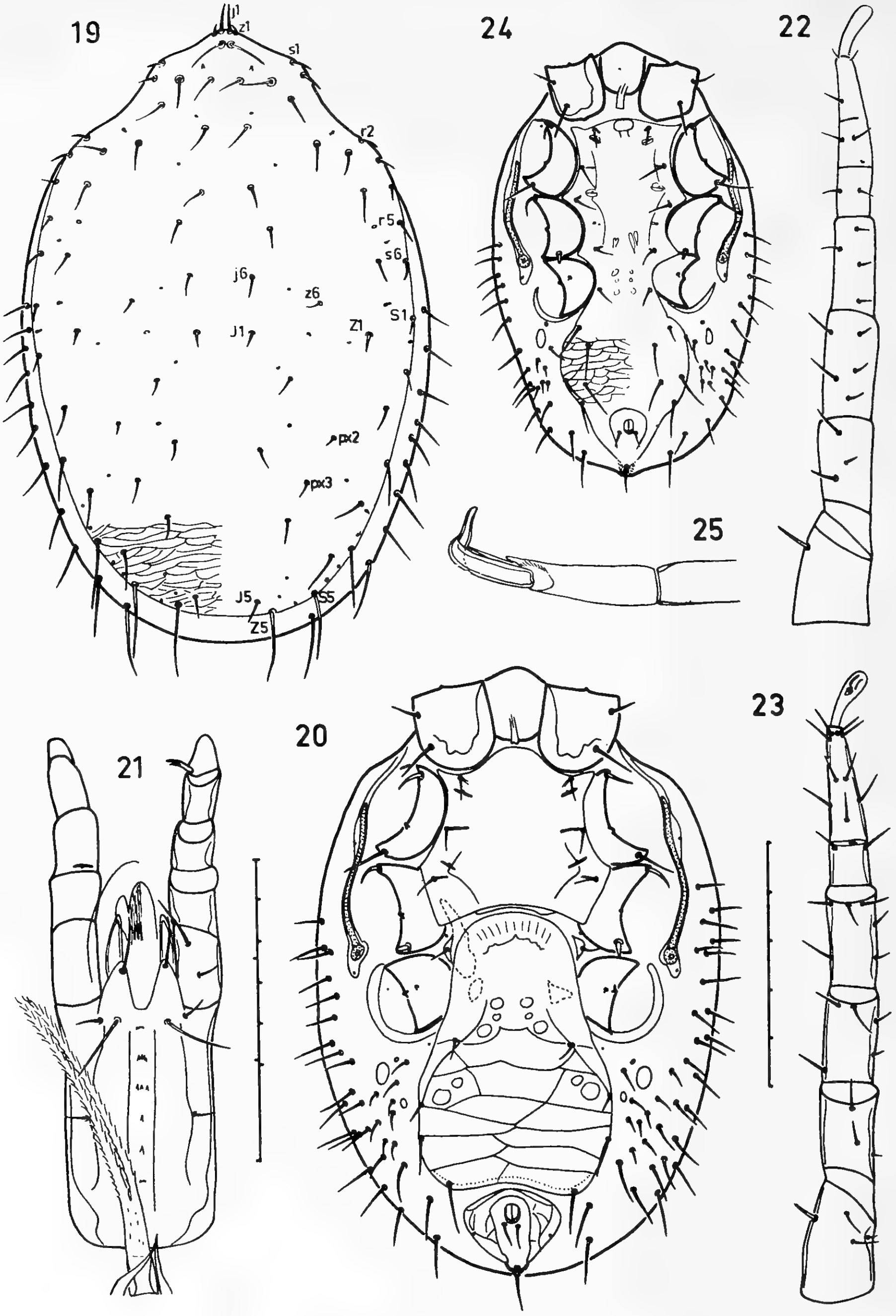


Figs 1–2. *Laelaps aella* ♀. 1, Dorsum of idiosoma. 2, Venter of idiosoma. Fig. 3. *L. rothschildi* ♀. Venter of idiosoma. Figs 4–5. *Australolaelaps rosamondae* ♀. 4, Capitulum. 5, Chelicerae in ventral view.

Idiosoma parallel-sided, rounded posteriorly, but angulate anteriorly; 1,280–1,370μ long normally, but only 1,260μ in freshly moulted specimen. Dorsal shield with similar outline; with transverse striations, paired muscle insertions, and pores (shield around pores immediately in front of *S*4 and *S*5 not weakened and transparent over large circular area). Setae in 39 pairs (vertical, subvertical, and humeral clusters rather more prominant than usual); short except for Z5. Little dorsal marginal cuticle free, with about 10 pairs of setae of increasing length posteriorly.



Figs 6–12. *Laelaps aella* ♀. 6–9, Legs I–IV. 10, Capitulum. 11–12, Left chelicera in lorsoexternal and dorsal view. Figs 13–18. *L. rothschildi* ♀. 13–16, Legs I–IV. 17, Capitulum. d8, Right chelicera in dorsoexternal view.



Figs 19–23. *Laelaps pammorphus* ♀ from *Zyzomys argurus*. 19, Dorsum of idiosoma. 20, Venter of idiosoma. 21, Capitulum. 22–23, Leg IV. Figs 24–25. *L. pammorphus* ♂ from *Z. argurus*. 24, Venter of idiosoma. 25, Right chelicera in ventral view.

Tritosternum narrow and undistinguished, reaching forward to *h*1; base flanked by two small, narrow, and diaphanous processes. Sternal shield wider than long, with anterior margin biconvex and posterior margin concave; internally denser around margins; surface virtually textureless. Six sternal setae very small, with canaliculus leading into body cavity from base of each; four sternal pores distinct, each with canaliculus. Endopodal shields only partially visible externally, but provided with larger apodemes extending under posterolateral corners of sternal shield; metasternal setae set on external portions; pores free in cuticle. Genitoventral shield roundly expanded behind coxae IV, slightly concave posteriorly to follow contour of anal shield; with distinct sigmoid lines isolating genital setae, and very weak, open pattern discally. Genital setae and three pairs of usurped ventral setae set on shield; all small and subequal. Genital pores minute, free in cuticle. Operculum rayed, supported by two genital apodemes. Anal shield slightly wider than long, striate and dense marginally; anus set in transparent central area, in front of all three subequal anal setae. Metapodal shields rounded, set outside two pairs of smaller plaques. Ventral cuticle with about 15 pairs of setae of increasing length posteriorly. Peritremes reaching forward to anterior margins of coxae II; borne on narrow shields fused vertically to dorsal shield and extended posteriorly, but not far enough to fuse with crescentic exopodal shields IV.

Legs with setation called for by Evans and Till (1965) for dermanyssids in general and for *L. echidninus* Berlese in particular (*i.e.*, one additional *pl* seta on genu IV, 2–5/1–2). Coxa III with *pv* spur-like. Trochanters I–II with *al*, and III–IV with *al* and *d*, strengthened, but always sharply pointed. Femora I–II with *pd*1 longer, II–III with *av* and *v*, respectively, very strong, but still sharply pointed (tip often broken off, particularly on II). Tarsi II–IV with *ad*1 and *pd*1 minute; II–III with *al*1 blunt. Tarsus I not examined. Coxa I without apodeme.

Male and immatures.—Unknown.

Notes.—*L. aella* is closely related to *L. rothschildi*, but differs in the decidedly less expanded contours of the genitoventral and anal shields. Further, the distinct transparent zone about the anus is open to the cribrum in the former, but entire in the latter.

The specific name is a Greek noun (ἄελλα, a stormy wind), and stands in apposition to the generic name. It was suggested by λαιλαψ (a dark, furious storm), but see note on *Gymnolaelaps*.

Laelaps rothschildi Hirst

(Figs 3, 13–18)

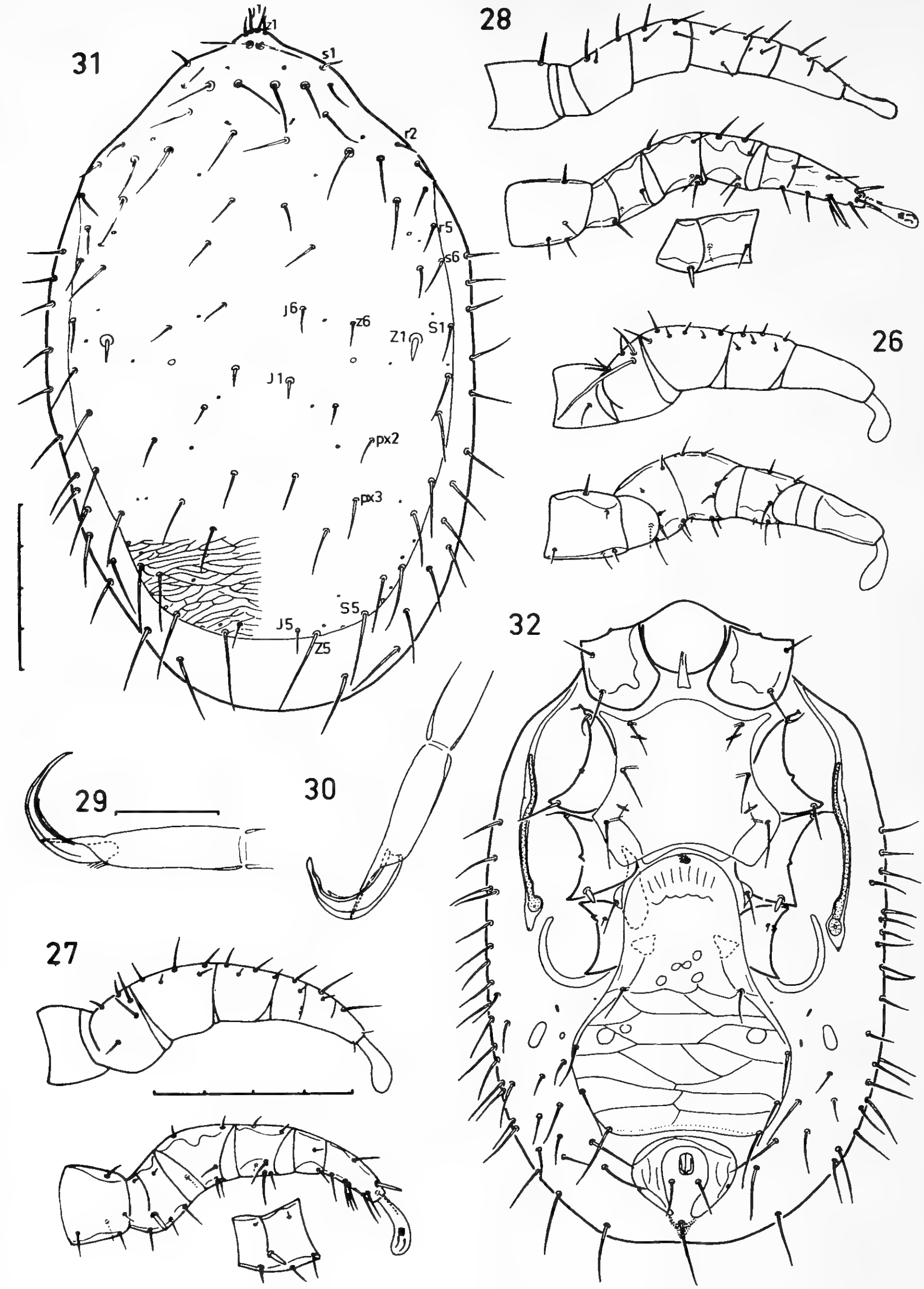
L. rothschildi Hirst, 1914, *Trans. zool. Soc. Lond.*, 20: 325.

Notes.—No new records of this common parasite of *Melomys* Thomas and *Uromys* Peters (Muridae) in New Guinea and coastal NE Australia are to hand. However, with increasing realization of the value of the setal formulae of the appendages, these have been figured for comparison with the similar *L. aella*. Additional references are Domrow and Smith (1956), Domrow (1958, in which the "large grey mouse" is undoubtedly an immature fawn-footed melomys, *M. cervinipes* (Gould)), and Domrow (1963*b*, in which the setation of the dorsal shield of the female is correctly figured). Domrow (1962, 1967) discusses gigantism, which occurs particularly in specimens from *Uromys*.

Laelaps pammorphus, n. sp.

(Figs 19–32)

Types.—Holotype ♀ and 10 paratype ♀♀ from common rock-rat, *Zyzomys argurus* (Thomas) (Muridae), Block Waterhole, Nicholson River, N.T., 29.viii.1967, B. Bolton and S. Parker. Deposited in ANIC. Allotype ♂ and 11 paratype ♀♀,



Figs 26–28. *Laelaps pammorphus* ♀ from *Z. argurus*. Legs I–III, with insets of femora II–III from specimen from *Z. woodwardi*. Figs 29–30. *L. pammorphus* ♂ from *Z. argurus*. Left chelicera in external and dorsoexternal views. Figs 31–32. *L. pammorphus* ♀ from *Z. woodwardi*. 31, Dorsum of idiosoma. 32, Venter of idiosoma.

Z. argurus, Border Waterhole, N.T. (NW of Camooweal, Qd), 31.viii.1967, A. Nicholls. Deposited in ANIC (allotype) and QIMR (remainder). Seventeen ♀♀ and nine ♂♂ (not types), *Z. argurus*, " Springvale ", N.T. (NW of Camooweal, Qd), 18–20.viii.1967, H. Dimpel, S.P., and A.N.

Five ♀♀ (not types) from Woodward's rock-rat, *Z. woodwardi* (Thomas), Mt. Brockman, N.T., 28.vii.1971, J.H.C.

Numerous specimens (not types) of both sexes, *Z. argurus* and *Z. woodwardi*, Nourlangie Rock, western Arnhem Land, 9.xi.1972, J.H.C.

Female.—Capitulum with *c* falling short of deutosternum ; *h*1–2 slightly, and *h*3 considerably, longer. Deutosternal groove with six rows of denticles, frequently multiple. Cornicles, epistome, palpi, and claws as in *L. aella*. Chelicerae as in *L. aella*, but pilus dentilis abruptly bent and foliate at tip.

Idiosoma oval, rounded posteriorly ; 1,480–1,590μ long normally, but only 1,410μ in freshly moulted specimens. Dorsal shield of similar outline ; with striations, muscle insertions, and pores (including shield around pores immediately in front of *S*4 and *S*5) as in *L. aella*. Setae in 39 pairs, rather short except posterolaterally ; some anterior *j* and *z* setae set in exaggerated alveoli ; *J*1 and *Z*1 slightly thickened. Narrow band of dorsal marginal cuticle free, with about 10 pairs of setae of increasing length posteriorly.

Tritosternum as in *L. aella*. Sternal shield subquadrate, with anterior margin strongly convex and posterior margin concave ; internally denser around margins ; surface virtually textureless. Six sternal setae very small, with canaliculus leading into body cavity from base of each ; four sternal pores distinct. Endopodal shields and metasternal complex as in *L. aella*. Genitoventral shield somewhat expanded and subquadrate behind coxae IV, slightly concave posteriorly as in *L. aella* ; with sigmoid lines isolating genital setae and transverse discal striae both distinct. Genital setae and three pairs of usurped ventral setae set on shield ; anterior two pairs barely half as long as posterior two pairs. Genital pores and operculum as in *L. aella*. Anal shield slightly longer than wide, striate and denser marginally ; anus set in transparent central area in front of two adanal setae rather smaller than postanal seta. Metapodal shields as in *L. aella*. Ventral cuticle with about 30 pairs of setae of increasing length marginally. Peritremes reaching forward only to middle of coxae II, otherwise as in *L. aella*.

Legs with setation called for by Evans and Till (1965) for dermanyssids in general and for *L. echidninus* in particular. Coxa III with *pv* spur-like. Trochanters I–II with *al*, and III–IV with *al* and *d* strengthened, but always sharply pointed. Femur I with *pd*1 considerably, and *ad*1 slightly, elongate ; II with *av* spur-like. Tarsi II–IV with *ad*1 and *pd*1 minute ; II–III with *al*1 blunt. Tarsus I not examined. Coxa I without apodeme.

Male.—Capitulum as in ♀. Fixed digit of chelicera tapering, very weak, and edentate. Movable digit almost entirely obliterated by strong spermatodactyl, which is abruptly bent dorsad at mid-length. Corona present.

Idiosoma 1,040–1,095μ long. Dorsum as in ♀, but only one specimen shows full complement of 39 pairs of setae on dorsal shield (*px*3 missing on one side of six specimens ; *px*3 missing on both sides of two specimens ; *px*3 missing on both sides, and *J*3 on one side, of one specimen).

Holoventral shield expanded behind coxae IV, with about five pairs of usurped ventral setae ; surface largely reticulate, but most strongly so on ventral area. Genital aperture normally placed. Venter otherwise as in ♀ ; cuticle with about 20 pairs of setae of increasing length marginally.

Legs as in ♀.

Immatures.—Unknown.

Notes.—The above description applies to specimens from *Z. argurus* (type-species of the subgenus *Zyzomys* Thomas). Those from *Z. woodwardi* (type-species of the subgenus *Laomys* Thomas) differ in degree in certain points (setae on dorsal shield longer, and *J*1 and *Z*1 stouter ; seta *v* on femur III spur-like ; pilus dentilis more amorphous), but are assigned to the same species.

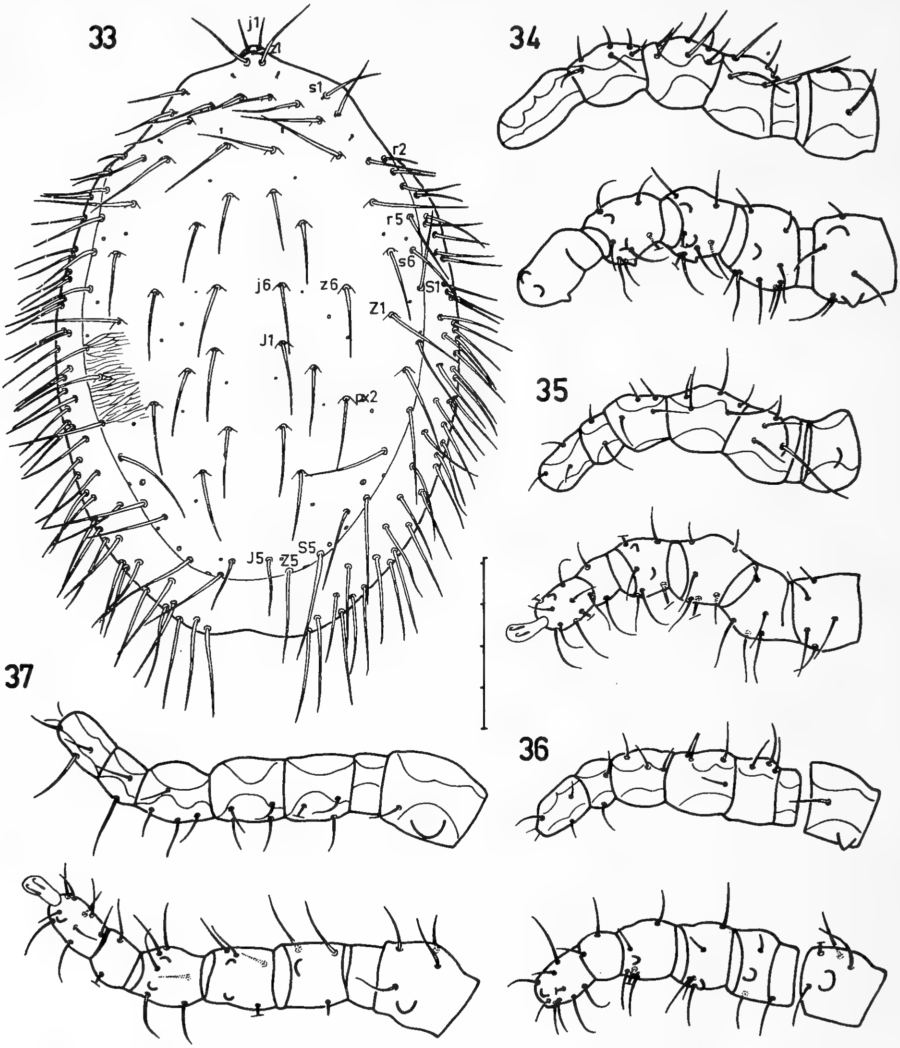


Fig. 33. *Laelaps spatanges* ♀ from *Pseudomys delicatulus*. Dorsum of idiosoma. Figs 34–37. *Australolaelaps rosamondae* ♀. Legs I–IV (seta *al* 2 on femur II and setae *ad* 1 and *pd* 1 on tarsus II neither detected nor necessarily absent).

This was written before I had seen the material from Nourlangie Rock noted above. The collector writes (*in. litt.*, 14.xii.1972) : " All . . . the . . . *Zyzomys* were collected on the same trapline at the same time. Extreme care was taken to avoid contamination and different equipment was used to process each species." The differences noted above can therefore be confirmed. They are, however, minor and best ascribed to physiologically induced intraspecific variation.

L. pammorphus, with 39 pairs of setae on the dorsal shield, runs to couplet 7 in Domrow's (1965) key, but females differ markedly from those of the two species included (*L. mackerrasi* and *L. southcotti* Domrow, 1958) by their enlarged sternal and genitoventral shields, and the spur-like seta *av* and *v* on femur II and III, respectively. Males in this genus are nondescript.

The specific name is a Greek adjective (παμμορφος, assuming all forms). It refers to the variability of the setae (particularly the short, stout *J*1 and *Z*1) on the dorsal shield.

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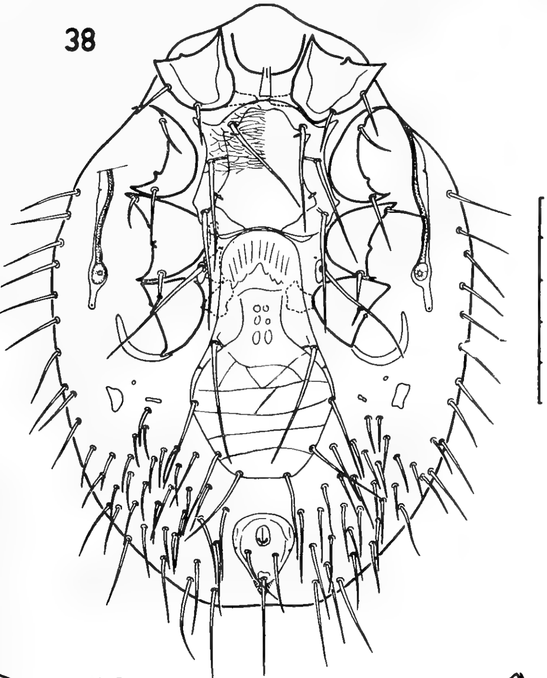

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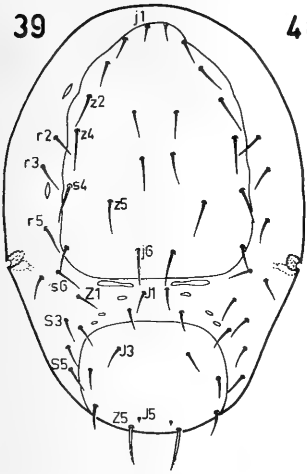

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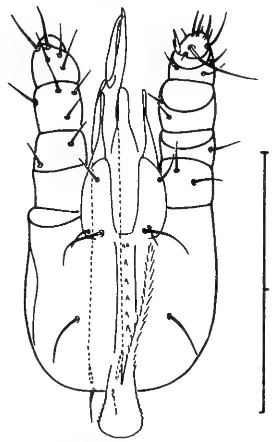

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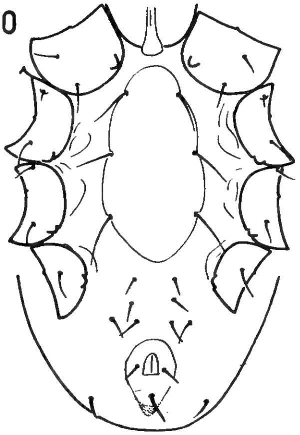


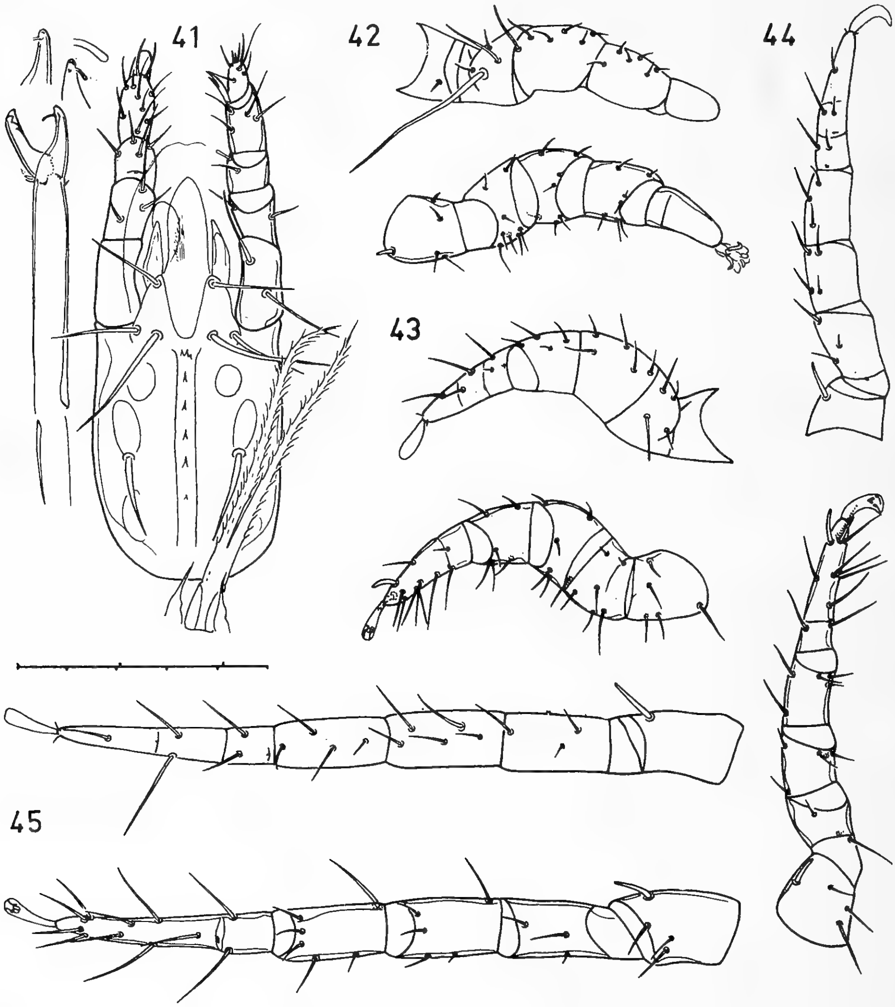
Fig. 38. *Laelaps spatanges* ♀ from *Pseudomys delicatulus*. Venter of idiosoma. Figs 39–40. *Australolaelaps mitchelli* protonymph from *Macropus rufogriseus*. 39, Dorsum of idiosoma. 40, Venter of idiosoma. Fig. 40*a*. *A. mitchelli* deutonymph from *M. rufogriseus*. Capitulum.

Laelaps spatanges, n. sp.

(Figs 33, 38, 41–45)

L. hapaloti Womersley, 1937, *Parasitology*, 29 : 532, *partim* (series from Basedow Range).

Types.—Holotype ♀ and three paratype ♀♀ from pebble mound mouse, *Pseudomys hermannsburgensis* (Waite), Yuendumu, N.T., 2–6.ix.1966, P. F. Aitken. Deposited in South Australian Museum, Adelaide. Two paratype ♀♀ from *P. hermannsburgensis*, Adelaide, S.A., 14.ii.1967, D. R. Smyth and C. M. Philpott (animals originally captured in northern S.A.—" was severe outbreak of this mite in laboratory "). Deposited in SAM.



Figs 41–45. *Laelaps spatanges* ♀ from *Pseudomys delicatulus*. 41, Capitulum, with insets of left chelicera in dorsoexternal view and tips of both fixed digits in ventral view. 42–45, Legs I–IV.

Two paratype ♀♀ from little native-mouse, *P. delicatulus* (Gould), Victoria, Port Essington, N.T., 9.vii.1965, J.H.C. Deposited in ANIC. Two paratype ♀♀ from *P. delicatulus*, Mt. Brockman, N.T., 25.vii.1971, J.H.C. Deposited in QIMR.

Five paratype ♀♀ (not three as stated by Womersley, 1956) from *Pseudomys* sp., Wallara North, Basedow Range, N.T., 1932, H. H. Finlayson. Deposited in SAM (3) and QIMR (2).

Female.—Capitulum with *c* rather shorter than interval between them; *h*1–2 of similar length, but weaker; *h*3 half as long again. Deutosternum, cornicles, epistome, palpi, and claws as in *L. aella*. Chelicerae slender, but fully formed; as in *L. aella*, but pilus dentilis short and slightly expanded at tip.

Idiosoma 1,275–1,435μ long, elongate-oval, slightly emarginate posteriorly in engorged specimens. Dorsal shield with similar outline (but always entire terminally) and narrowly transverse striations. Muscle insertions and pores (including shield around pores immediately in front of *S*4 and *S*5) as in *L. aella*. Setae in 38 pairs (lacking one pair of *px*; *J*4 doubled on right side of one specimen), long except for *z*1. Dorsal marginal cuticle quite extensive, with about 40 pairs of long setae.

Tritosternum as in *L. aella*. Sternal shield subquadrate, with anterior margin convex and posterior margin concave; internally denser around margins; with fine transverse reticulations over entire surface. Six sternal setae as long as shield, with canaliculus leading into body cavity from base of each; four sternal pores distinct. Endopodal shields and metasternal complex as in *L. aella*. Genitoventral shield subpentagonal behind coxae IV, with weak superficial markings as figured. Genital setae, attendant pores, and three pairs of usurped ventral setae set on shield. Operculum as in *L. aella*. Anal shield elongate, rounded anteriorly; slightly denser laterally and around base of very long postanal seta; adanal setae shorter, but still reaching well beyond cribrum. Metapodal shields irregular, set outside two pairs of smaller plaques. Ventral cuticle with about 45 pairs of setae of increasing length posteriorly. Peritremes as in *L. aella*.

Legs with setation called for by Evans and Till (1965) for dermanyssids in general and for *L. echidninus* in particular. Coxa III with *pv* spur-like. Trochanters I–II with *al* strengthened, but still pointed; I with *pv*2 spur-like; III–IV with *al* and *d* blunt. Seta *pd*1 on femur I considerably elongate, and slightly so on II; *ad*1 also slightly elongate on I. Genu I with *pd*3 slightly elongate. Tarsi II–IV with *ad*1 and *pd*1 minute; II–III with *al*1 and *av*1 blunt. Tarsus I not examined. Coxae I with transverse apodemes almost meeting just behind tritosternal base.

Male and immatures.—Unknown.

Notes.—The hirsute *L. spatanges* is the only Australian species of *Laelaps* to show one pair of intercalary (*px*) setae on the dorsal shield; all the others have, if not the usual two pairs, none.

The specific name is a Greek noun (σπαταγγης, a kind of sea-urchin), and stands in apposition to the generic name. It refers to the strong, outstanding setae of the idiosoma.

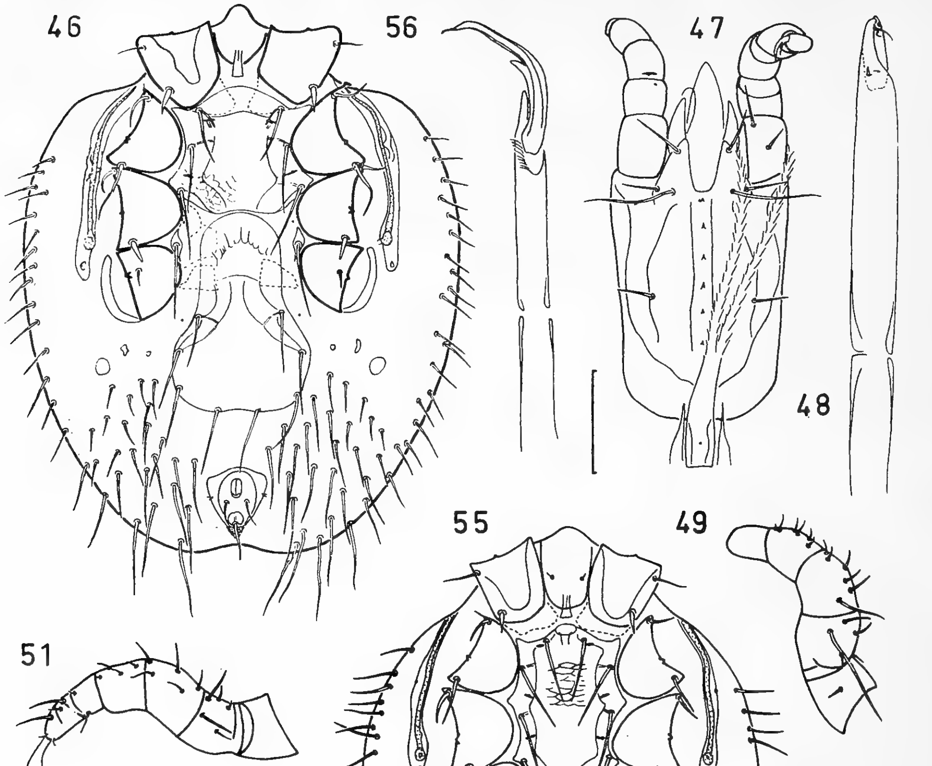
Laelaps hapaloti Hirst

(Plate II, Figs 46–56)

L. hapoloti Hirst, 1931 (*sic*), *Proc. zool. Soc. Lond.*, 1931: 563.

Material examined.—All previously recorded material was re-examined. Also 67 ♀♀, 21♂♂, and one deutonymph from *Notomys mitchellii*, Pier Millan, between Ouyen and Sea Lake, Vic., 13.ii.1966, R.M.W. One ♀ and one ♂ from *N. mitchellii*, Lameroo, S.A., 12.ix.1966, P.F.A. Three ♀♀ and two ♂♂ from *N. mitchellii*, Kyancutta, Eyre Peninsula, S.A., 15.xi.1971, C. Matthews. One ♀ from *N. mitchellii*, W of Lake Eyre, S.A., 1957, P. F. Lawson.

Five ♀♀ from spinifex hopping mouse, *N. alexis* Thomas, Turner's Well, Ernabella Range, S.A., 19.vii.1966. Three ♀♀ from *N. alexis* (subspecies *everardensis* Finlayson), H.H.F. Four ♀♀ and one ♂ from *N. alexis*, Sandringham Station, 35 miles NW of Bedourie, Qd, 16–19.vi.1968, Meredith Happold (*née* Stanley).



Figs 46–54. *Laelaps hapaloti* ♀ from *Notomys mitchellii*. 46, Venter of idiosoma. 47, Capitulum. 48, Right chelicera in dorsal view. 49–50, Leg I (tibia-tarsus foreshortened). 51–52, Legs II–III. 53–54, Leg IV. Figs 55–56. *L. hapaloti* ♂ from *N. mitchellii*. 55, Venter of idiosoma. 56, Left chelicera in ventral view.

Seventeen ♀♀ and two ♂♂ from fawn-coloured hopping mouse, *N. cervinus* (Gould), Sandringham Station, Qd, 13–19.vi.1968, M.H.

Two ♀♀ from *Notomys* sp., Ooldea, S.A., H.H.F. Nine ♀♀, one ♂, and one deutonymph from *Notomys* sp., three miles E of Birdsville, Qd, 1.viii.1957, P.F.L.

Five ♀♀ and one ♂ from " ? " Gould's wattled bat, *Chalinolobus gouldii* (Gray) (Chiroptera: Vespertilionidae), Adelaide, S.A., 9.v.1932, M. Francis. The locality, date, and collector may well be correct, but the supposed host is certainly not.

Notes.—Womersley (1937, 1956) provided additional data for this briefly described species, stating on both occasions that the type-series could not be found. The location of the series collected by Rau is unknown; it is not in the British Museum (Natural History), London, where some of Hirst's posthumous types are deposited (Hyatt, *in litt.*, 21.vii.1972—*Allothrombium wasseli* (*sic*), *Microtrombidium willungae*, *Spinturnix antipodianus* (*sic*), and *S. novaehollandiae*). But surely the series (eight ♀♀, three ♂♂) collected by Bellchambers is the second of the *two* mentioned by Hirst. Of these syntypes, I designate one ♀ as lectotype, see Arts 73 (*c*) and 74 (*a*).

Womersley also, on Finlayson's advice, suggested the true host was a hopping mouse (genus *Notomys* Lesson). According to Ride (1970) and Aitken (*in litt.*, 12.ix.1972), the only *Notomys* in SE South Australia is *N. mitchellii*, but the latter adds that the type-locality (Humbug Scrub, in dry sclerophyll forest in the Mount Lofty Ranges) is—and was—a most unlikely locality for any species of *Notomys*, and probably in error. Womersley and later Domrow (1965) recorded specimens from *N. mitchellii* at Murray Bridge and Kiamal, and the latter realized the host of his earlier series (1958) from a " marsupial mouse " at Soudan must have been in error. The two new hosts listed above confirm Finlayson. (The specimens from *Pseudomys* Gray, Basedow Range, placed in Hirst's species by Womersley are, in fact, a distinct new species described above.)

Domrow (1963*b*) showed that the setation of the dorsal shield of *L. hapaloti* was deficient, showing only 37, rather than the usual 39, pairs (supernumerary pairs *px*2–3 in the opisthonotal series lacking, see Costa, 1961). This is the pattern commonly seen—in the long series from *N. mitchellii* from Pier Millan, *z*6 are present in 50, represented only on one side in 28, and absent in 10, specimens. Similar variation occurs in the type-series, but the lectotype was chosen to show *z*6 (one ♂ further shows one *px* on the left side). The 10 documented specimens from *N. alexis* show *z*6, while the 19 from *N. cervinus* lack them. All, however, clearly belong to a single species diagnosed by host-preference and the spinose basal seta on coxa I.

Fresh illustrations are given for the venter of the idiosoma of both sexes, and the setal patterns on the capitulum and legs are shown not to diverge from those of *L. echidninus*.

Hirst's original spelling of the specific name (since he gave the alleged host-genus—*Hapalotis* Lichtenstein—correctly) is clearly a *lapsus*, and Womersley's tacit emendation was justified (Arts 32 and 33).

As noted above, all Australian rodents, both native and introduced—*Rattus rattus* (Linnaeus), *R. norvegicus*, *R. exulans*, and *Mus musculus*—are murids. They fall into four distinct groups of genera, but their relationships are not well understood (Ride, 1970):

(1) Bush-rats: *Rattus*.

(2) Water-rat: *Hydromys* Geoffroy; and false swamp-rat: *Xeromys* Thomas.

(3) A series of peculiarly Australian genera termed " old endemics "—tree-rats: *Mesembriomys* Palmer and *Conilurus* Ogilby; stick-nest rats: *Leporillus* Thomas; hopping-mice: *Notomys*; rock-rats: *Zyzomys*; broad-toothed rat: *Mastacomys*; and native-mice: *Pseudomys*.

(4) Mosaic-tailed rats: *Melomys* and *Uromys*.

A variety of species of *Laelaps* are now known from these rodents. The six typical members of the *nuttalli* species-group (39 pairs of setae on the dorsal shield; sternal and genitoventral shields unexpanded; genitoventral setae and peritremes unabbreviated) already published are divisible as follows (Domrow, 1965):

(*a*) Both setae on coxa I simple: *mackerrasi* and *southcotti* on various bush-rats and *Uromys*, respectively.

(*b*) Distal seta on coxa I spur-like: *breviseta* Domrow, *nuttalli* Hirst, and *assimilis* on various species of *Rattus*, *Melomys*, and *Uromys*.

(*c*) Both setae on coxa I spur-like: *wasselli* Domrow on *Hydromys*.

These species of *Laelaps* with the simplest features have therefore been recorded from all four host-groups noted above, except the " old endemics ". However, several series of *L. assimilis* (detailed above) have recently been taken from *Mastacomys*, which lives in close ecological association with, while being unrelated to, *R. lutreolus*.

There remain two species which, while largely resembling the *nuttalli* species-group, show expanded sternal and genitoventral shields. However, the lines (if any) dividing *Laelaps* and such annectant taxa as *Echinolaelaps* Ewing remain unclear (the latest statements are by Strandtmann and Mitchell, 1963; Strandtmann, 1963; Jameson, 1965; and Coffee and Retief, 1972), and the two species in question are retained in the *nuttalli* species-group. *L. rothschildi*, in fact, shows both setae on coxa I simple (Domrow, 1965, errs on this point), and is best considered in group (*a*). It is a species with characteristically short body setae, and peculiar to *Melomys* and *Uromys*. *L. echidninus* (the type-species of *Echinolaelaps*) fits in group (*b*) above, and occurs on various species of *Rattus*.

Four of the species of *Laelaps* previously recorded from " old endemics " form the distinct *finlaysoni* species-group (dorsal shield with only 35 pairs of setae; anterior two pairs of genitoventral setae and peritremes much abbreviated): *finlaysoni* Womersley on various species of *Pseudomys*, *albycia* Domrow on *P. fumeus* Brazenor, *calabyi* Domrow on *P. higginsi* (Trouessart), and *cybiala* Domrow on *Mastacomys*.

The fifth known species from " old endemics ", *L. hapaloti* from the curious *Notomys*, forms a third monotypic species-group unique in showing 37 pairs of setae on the dorsal shield and the basal seta on coxa I spinose.

The three new species described above from " old endemics " may now be commented upon. This will necessitate some erosion of my original species-group diagnoses (Domrow, 1965), but this seems preferable, with many of the hosts little understood taxonomically and unexamined for parasites, to any more radical treatment. Particularly to be avoided at this stage is the erection of additional genus-group taxa. *L. aella* is so closely similar to *L. rothschildi* that it must also be placed in the *nuttalli* species-group, despite the difference in host-preference. The former is from *Pseudomys gracilicaudatus*, while the latter is restricted to *Melomys* and *Uromys*.

L. pammorphus (from *Zyzomys*) also has a full complement of dorsal setae, but shows incipient shortening of the peritremes and anterior two pairs of genitoventral setae. However, the reduction in both characters is not as marked as in the *finlaysoni* species-group, and the species further lacks the transparent areas on the dorsal shield characteristic of that group, and noted below. It is therefore assigned rather to the *nuttalli* species-group.

The hirsute *L. spatanges*, like *L. hapaloti*, is a species apart, distinct in showing 38 pairs of setae on the dorsal shield. The *spatanges* species-group is therefore erected to include it; it and the *nuttalli* species-group lack the four enlarged transparent areas on the dorsal shield around the pores in front of setae *S*4 and *S*5 so characteristic of the *finlaysoni* and *hapaloti* species-groups. Its hosts (*P. delicatulus* and *P. hermannsburgensis*) are currently assigned to *Pseudomys s.l.*, but it should be noted that these two mouse-like forms were previously placed in *Leggadina* Thomas.

That relatively unmodified species of *Laelaps* are now known from the " old endemic " Australian rodents may indicate the latter are, in fact, but little modified members of the family Muridae despite their strict zoogeographical isolation. Further collecting aimed at the several still unsampled genera is necessary, and may throw light on the phylogeny both of these little-known hosts and their equally little-known parasites.

Genus NEOLAELAPS Hirst

Neolaelaps Hirst, 1926, *Proc. zool. Soc. Lond.*, 1926 : 836. Type-species *Liponyssus magnistigmatus* Vitzthum, 1918.

Neolaelaps spinosus (Berlese)

Leiognathus spinosus Berlese, 1910, *Redia*, 6 : 261.

New host-record.—Seven ♀♀ and one deutonymph (enclosing developing ♀) from flying fox, *Pteropus tonganus* Quoy and Gaimard (subspecies *geddiei* MacGillivray) (Chiroptera : Pteropodidae), Ipota, Eromanga, New Hebrides, 10.viii.1971. A. Agadjanian (RSPSE).

Genus DOMROWNYSSUS Evans and Till

Domrownyssus Evans and Till, 1966, *Bull. Br. Mus. nat. Hist.*, 14 : 121. Type-species *Pneumonyssus dentatus* Domrow, 1961.

Domrownyssus dentatus (Domrow)

P. dentatus Domrow, 1961, PROC. LINN. SOC. N.S.W., 86 : 73.

New host-record.—Four protonymphs from brown antechinus, *Antechinus stuartii* Macleay, Melbourne, Vic., 29.viii.1972, Rosamond Shepherd.

Notes.—The adults of this interesting species remain unknown.

Genus EULAELAPS Berlese

Eulaelaps Berlese, 1903, *Zool. Anz.*, 27 : 13. Type-species *Gamasus stabularis* Koch, 1839.

Eulaelaps stabularis (Koch)

G. stabularis Koch, 1839, *Deutschlands Crustaceen, Myriapoden und Arachniden*, 27 : 1. Regensburg : Herrich-Schäffer.

New Australian record.—Eight ♀♀ and four ♂♂ from introduced mouse, *Mus musculus* Linnaeus (Muridae), Hunting Ground, Tas., 8.ii.1964, T. O. Wolfe.

Notes.—This mite is a common parasite of small mammals in the Holarctic and Oriental Regions.

Genus RAILLIETIA Trouessart

Raillietia Trouessart, 1902, *C. r. Séanc. Soc. Biol.*, 54 : 1335. Type-species *Gamasus auris* Leidy, 1872.

Raillietia australis Domrow

R. australis Domrow, 1961, PROC. LINN. SOC. N.S.W., 86 : 75.

Material examined.—One ♀ from common wombat, *Vombatus ursinus* (Shaw) (Marsupialia : Vombatidae), near Taggerty, Vic., 26.vii.1971, R.S.

Notes.—This will confirm the original host-record.

Genus AUSTRALOLAELAPS Womersley

Australolaelaps Womersley, 1956, *J. Linn. Soc.*, 42 : 561. Type-species *A. mitchelli* Womersley, 1956.

Australolaelaps mitchelli Womersley
(Figs 39–40*a*, 59–60)

A. mitchelli Womersley, 1956, *J. Linn. Soc.*, 42 : 562.

New host-records.—Numerous specimens from red wallaby, *Macropus rufogriseus* (Desmarest) (Marsupialia: Macropodidae), Nile, Tas., vii.1972, B. L. Munday.

Four ♀♀ from swamp wallaby, *Wallabia bicolor* (Desmarest) (Macropodidae), Springhill, Daylesford, Vic., 1.iii.1972, R.S.

Deutonymph.—Basis capituli with *c* rather longer than half interval between them. Deutosternum with six denticles, mostly single. Hypostome with $h3 > h1 > h2$. Cornicles pale and elongate. Palpi with reduced setation, probably 2.3.6.8.9 (including two dorsodistal tibial rods). Claw bifid. Chelicerae slender, with fully formed edentate digits as in ♀; corona absent.

Idiosoma ovate, 330–380μ long. Dorsal shield lozenge-shaped, but somewhat truncate posteriorly; surface almost textureless, and margins retracted laterally except for four small humeral plaques, leaving 12 pairs of lateral setae (*s*1–3, *s*6, *r*2–3, 5, *S*1–5) free in cuticle. These setae plus 22 pairs (*px*2, in fact, is absent as often as present) on shield make up 34 pairs typical of adult ♀ (see notes on *A. rosamondae*, n. sp.). Marginal cuticle with about nine pairs of setae. Peritremes abbreviated.

Tritosternum with base minutely dentate laterally; laciniae reaching forward almost to *h*3, weakly barbed. Intercoxal shield elongate-oval, almost textureless, and with five pairs of setae of decreasing length posteriorly; pores not detected. Adjoining cuticle textured near insertions of coxae II–IV. Anal shield as in ♀. Ventral cuticle with about 22 pairs of setae, subequal except for one stronger subposterior pair.

Legs with same setation as in ♀, *i.e.*, with normal dermanyssid pattern detailed by Evans and Till (1965), except that femur II is unideficient dorsally, 2–4/3–1 (genu IV in ♀♀ from *Macropus dorsalis* (Gray) with additional *pl* seta, 2–5/1–2). Coxa II with anterior seta present, but small and set on tubercle. Distal segments of legs with more or less obvious indications of future (adult) hooklets in positions detailed by Womersley (1956).

Protonymph.—Capitulum essentially as in deutonymph. Palpi with reduced setation, probably 1.3.5.8.9 (including two dorsodistal tibial rods).

Idiosoma ovate 280–315μ long. Dorsal shield rounded anteriorly, sinuous laterally, and straight posteriorly; surface almost textureless; with 11 pairs of setae (*j*1–6, *z*2, 4–5, *S*4–5). Four pairs of mesonotal shieldlets present. Opisthonotal shield with five pairs of setae (*J*3, 5, *Z*3–5). Cuticle with 12 pairs of setae (*r*2–3, 5, *s*6, *J*1–2, *Z*1–2, *S*3–5, one extrascutal). Peritremes abbreviated.

Venter as in deutonymph except as follows: intercoxal shield with three pairs of subequal setae; cuticle with five pairs of setae.

Legs with normal dermanyssid setation detailed by Evans and Till (1965).

Australolaelaps rosamondae, n. sp.
(Figs 4–5, 34–37, 57–58)

Types.—Holotype ♀ (only known specimen) from *W. bicolor*, Springhill, Daylesford, Vic., 1.iii.1972, R.S. Deposited in ANIC.

Female.—Basis capituli stout, heavily sclerotized laterally and behind *h*2–3; with two strong ventrolateral bosses. Deutosternum with seven denticles in single file. Interval between *c* subequal to setae themselves; $h3 > h2 > h1$.

Cornicles not detected; hypostomal processes also diaphanous, extending forward to level of palpal tibiae. Epistome not detected. Palpi stout, with distal segments very short; trochanters armed with small ventrolateral boss. Setation reduced, probably 2.3.6.10.12 (including two dorsodistal tibial rods). Claws weak, apparently simple. Chelicerae retracted and details of distal quarter difficult to examine, but probably as figured, with very elongate digits.

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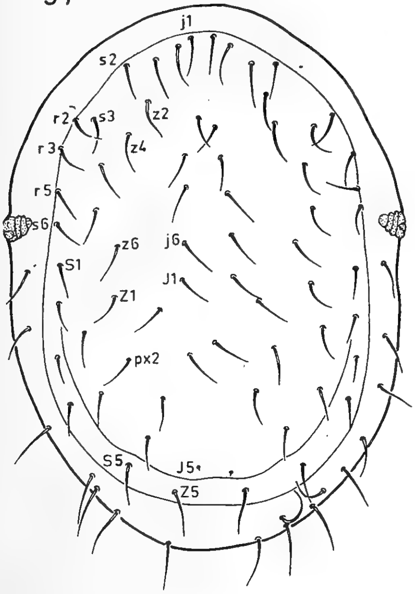

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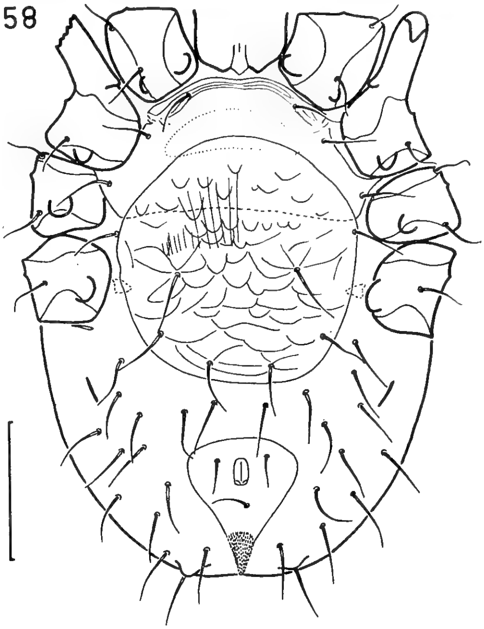

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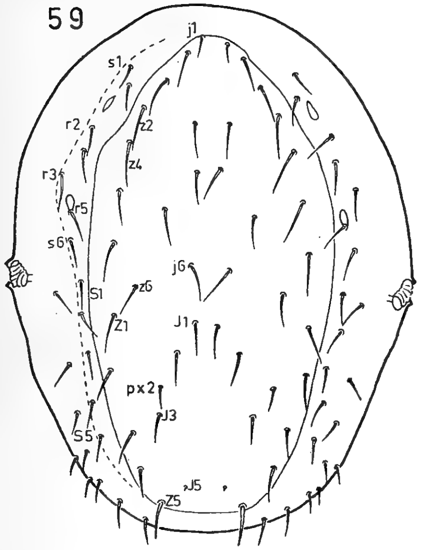

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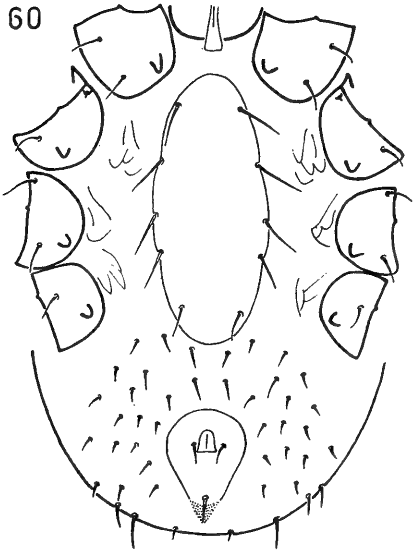

Figs 57–58. *Australolaelaps rosamondae* ♀. 57, Dorsum of idiosoma. 58, Venter of idiosoma. Figs 59–60. *A. mitchelli* deutonymph from *Macropus rufogriseus*. 59, Dorsum of idiosoma. 60, Venter of idiosoma.

Idiosoma small, 395μ long, 290μ wide when mounted. Dorsal shield parallel-sided, but broadly rounded anteriorly and posteriorly; with surface largely shagreened (paired muscle insertions present), but with posterolateral band weakly sclerotized, seemingly leaving setae *Z*5 and *S*3–5 free in cuticle. Paired pores not discernible. Setae on shield arranged in 34 pairs, subequal except for minute *J*5. Marginal cuticle bearing about 17 setae. Stigmata and peritremes entirely dorsal, with latter apparently complexly chambered and extended mesially rather than anteriorly.

Base of tritosternum roundly pointed posteriorly, but not strongly sclerotized as in some species of *Trichosurolaelaps* Womersley; laciniae weakly barbed, extending forward to *h*1. Sternal shield very broad, weakly sclerotized in general, but slightly denser discally; textureless except for few weak striations along biconvex anterior margin. Posterior margin shallowly concave; anterolateral cornua particularly weak, but posterolateral cornua distinct. Six sternal setae set on shield, but sternal pores not discernible. Metasternal complex represented only by two setae set in cuticle. Genital shield very broad, its surface (including broadly rounded and rayed operculum) marked with scale-like striae. Genital shield particularly, and two pairs of usurped ventral setae noticeably, set in from margin of shield. Pores accompanying genital setae not detected. Genital apodemes weak. Anal shield longer than broad, with rather straight anterior margin; almost textureless. Anus set well forward, its anterior margin level with bases of adanal setae; postanal seta of similar length, barely reaching distinct cribrum. Metapodal shields as such absent, but body wall indented behind line in this position. Exopodal shields represented only by merest remnant behind coxae IV. Opisthosoma with two small protuberances posteriorly and about 27 setae, of which four lie between genital and anal shields.

Legs sturdy, with short, well sclerotized segments. Setation as detailed by Evans and Till (1965) for dermanyssids in general, but seta *av* on coxa II obliterated by large ventrally-directed hook (which itself bears small basal boss), and femur II and genu IV unideficient dorsally (2–4/3–1 and 2–4/1–1). Only seta *pd*2 on femora-genua I–II distinctly longer than other setae. Coxae with distinct bosses arranged 2.1.1.1; II without anterodorsal process. Trochanters-tarsi I and III–IV and tibia-tarsus II each with one to three bosses or crotchets ventrally. Trochanters with single boss dorsally. Pulvillus I and III probably broken off rather than absent; II and IV inserted ventrally.

Notes.—The peculiarly Australian hirstionyssine genus *Australolaelaps* comprises three known species from macropodid marsupials. The recorded hosts of *A. mitchelli* are all wallabies and pademelons (Macropodinae): *Macropus dorsalis*, *M. eugenii* (Desmarest), and *Thylogale stigmatica* Gould, to which *M. rufogriseus* and *W. bicolor* were added above. The other two species are from rat-kangaroos (Potoroinae), *A. greeni* Domrow (1966*a*) being known only from *Bettongia gaimardi* (Desmarest) in Tasmania, while *A. validipes* (Domrow, 1955) is common on *Potorous tridactylus* (Kerr) and *P. apicalis* (Gould) in coastal SE Australia and Tasmania, respectively. Domrow (1966*a*) tabulated the comparative morphology of these species.

The very distinct fourth species described above is from the only species now retained in the genus *Wallabia* Trouessart (Macropodinae). It agrees with *A. mitchelli* from macropodines in showing obsolescent peritremes, but is at once separable by the heavy hooks on coxae II, a character shared with *A. greeni* and *A. validipes* from potoroines. It further differs from all three in showing bosses on the capitulum and in the arrangement of the 34 pairs of setae on the dorsal shield.

Unreduced species of such genera as *Laelaps* and *Haemolaelaps* show 39 pairs of setae on the dorsal shield (Costa, 1961), comprising 22 pairs in a podonotal, and 17 pairs in an opisthonotal, series. As the patterns in *Australolaelaps* are much reduced, it may be useful to analyse the deficiencies along the lines of a recent treatment of the closely related genus *Trichosurolaelaps* by Domrow (1972).

The least reduced podonotal pattern (19 pairs, *i.e.*, *z*1, *z*3, and *r*4 missing) occurs in both sexes of *A. mitchelli* and the ♂ of *A. validipes*. The ♀ of *A. rosamondae* (♂ unknown) and both sexes of *A. greeni* show 18 pairs, further lacking *s*1. The ♀ of *A. validipes* shows 17 pairs, further lacking *j*2.

The least reduced opisthonotal pattern (16 pairs, *i.e.*, *px*3 missing) occurs in the ♀ of *A. rosamondae* (♂ unknown). Both sexes of *A. greeni* show 15 pairs, further lacking *px*2, though the ♀ of *A. mitchelli*, which also shows 15 pairs,* lacks *J*4 rather than *px*2. The ♂ of *A. mitchelli* shows 14 pairs, lacking both *px*2 and *J*4. Both sexes of *A. validipes* show 13 pairs, further lacking *S*3.

Thus a similarity in the total counts of setae on the dorsal shield in two species may be superficial, reflecting a deficiency in the podonotal series in the one, but in the opisthonotal in the other.

The new taxon is dedicated to its collector, the specific name being a Latin noun in the genitive case.

Genus BEWSIELLA Domrow

Bewsiella Domrow, 1958, PROC. LINN. SOC. N.S.W., 82 : 352. Type-species *B. fledermaus* Domrow, 1958.

Bewsiella fledermaus Domrow

B. fledermaus Domrow, 1958, PROC. LINN. SOC. N.S.W., 82 : 353.

New host-record.—Many specimens from above tail of fawn horseshoe bat, *Hipposideros galeritus* Cantor (subspecies *cervinus* Gould) (Chiroptera : Hipposideridae), Montmartre Cave, Vila, Efate, New Hebrides, 29.vi.1971, A.G.M. (RSPSE).

Genus ORNITHONYSSUS Sambon

Ornithonyssus Sambon, 1928, *Ann. trop. Med. Parasit.*, 22 : 105. Type-species *Dermanyssus sylviarum* Canestrini and Fanzago, 1877.

Ornithonyssus bacoti (Hirst)

Leiognathus bacoti Hirst, 1913, *Bull. ent. Res.*, 4 : 122.

One ♀ from sugar glider, *Petaurus breviceps* Waterhouse (Marsupialia : Petauridae), Vermont, Vic., 31.v.1962, R.M.W.*

Laboratory infestation of eastern pigmy possum, *Cercartetus nanus* (Desmarest) (Marsupialia : Burramyidae), Melbourne, Vic., n.d., R.M.W. (animals originally captured in Victoria).

One ♀ from tuan, *Phascogale tapoatafa* (Meyer) (Dasyuridae), Lauriston, Vic., 8.ii.1964, R.M.W.*

One ♀, two ♂♂, and two protonymphs from *Antechinus stuartii*, The Grampians, Vic., 20.vii.1963, R.M.W.*

Laboratory infestation of dibbler, *Antechinus apicalis* (Gray), Canberra, A.C.T., 11.v.1967, Patricia Woolley (animals originally captured at Cheyne Beach, W.A.).

Laboratory infestation of guinea-pig, *Cavia porcellus* (Linnaeus) (Rodentia : Caviidae), Kila Kila, Papua, 4.x.1968, N. Talbot.

Six ♀♀ and two protonymphs from *Rattus fuscipes*, Buchan, Vic., 13.iv.1962, R.M.W.* Two ♀♀ from *R. fuscipes*, Heathmere, Vic., 23.xi.1962, R.M.W.*

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* Domrow's (1966*a*) total count of 35 pairs for the female of *A. mitchelli* is true of the many specimens in which the second marginal seta shown behind the left stigma by Womersley (1956) *is* on the shield. However, other specimens show this seta free in the cuticle, and much more convincingly arranged *Z* and *S* series. It is therefore now considered an extrascutal seta.

Laboratory infestation of *Rattus lutreolus*, The Grampians, Vic., 28.xi.1962, R.M.W. ; two ♀♀ from *R. lutreolus*, Bridgewater Lake, Vic., 21.xi.1962, R.M.W.*

Natural infestation of long-haired rat, *Rattus villosissimus* (Waite), Brunette Downs, N.T., n.d., J. L. Carstairs.

Two ♀♀ from *Notomys mitchellii*, Pier Millan, between Ouyen and Sea Lake, Vic., 13.ii.1966, R.M.W.*

Six ♀♀ and four protonymphs from smokey mouse, *Pseudomys fumeus* Brazenor, The Grampians, Vic., 5.vi.1963, R.M.W.*

Notes.—This is the tropical rat mite, and I am grateful to Mr. R. M. Warneke for advice that those records marked * are " probably laboratory infestations ".

Ornithonyssus sylviarum (Canestrini and Fanzago)

D. sylviarum Canestrini and Fanzago, 1877, *Atti Ist. Veneto*, 5 : 124.

New Australian record.—Economic infestation of domestic fowl, *Gallus gallus* (Linnaeus) (Galliformes : Phasianidae), Parkville, Vic., x.1969, H. E. Harrigan and J. H. Arundel.

New host-records.—Many specimens from dusky wood-swallow, *Artamus cyanopterus* (Latham) (Passeriformes : Artamidae), Canberra, A.C.T., 5.i.1966, I. C. R. Rowley.

Five ♀♀, one ♂, and 12 protonymphs from fairy martin, *Hylochelidon ariel* (Gould) (Passeriformes : Hirundinidae), Salter's Spring, S.A., 12.xi.1966, M. Smyth.

Many specimens from laughing kookaburra, *Dacelo gigas* (Boddaert) (Coraciiformes : Alcedinidae), Evandale, Tas., 29.vi.1967, R.H.G.

Many specimens from nest of little grassbird, *Megalurus gramineus* (Gould) (Passeriformes : Sylviidae), Launceston, Tas., 15.x.1966, R.H.G.

Notes.—See Domrow (1966*b*) for other records of this introduced pest-species on native birds.

Genus RALLINYSSUS Strandtmann

Rallinyssus Strandtmann, 1948, *J. Parasit.*, 34 : 512. Type-species *R. caudistigmus* Strandtmann, 1948.

Rallinyssus gallinulae Fain

R. gallinulae Fain, 1960, *Bull. Annls Soc. r. ent. Belg.*, 96 : 295.

New host-record.—One ♀ from Lewin water-rail, *Rallus pectoralis* Temminck (Gruiformes : Rallidae), Myrtle Park, Tas., 23.iv.1971, R.H.G.

Rallinyssus congolensis Fain

R. congolensis Fain, 1956, *Revue Zool. Bot. afr.*, 53 : 396.

New Australian record.—One ♀ from spotless crake, *Porzana tabuensis* (Gmelin) (Rallidae), Flinders Island, Tas., 5.v.1972, R.H.G.

Notes.—Previously recorded from this host in the Philippines (Wilson, 1967 ; Domrow, 1969).

Genus LARINYSSUS Strandtmann

Larinyssus Strandtmann, 1948, *J. Parasit.*, 34 : 507. Type-species *L. orbicularis* Strandtmann, 1948.

Larinyssus orbicularis Strandtmann

L. orbicularis Strandtmann, 1948, *J. Parasit.*, 34 : 507.

New host-record.—Five ♀♀ from nasal cavities of silver gull, *Larus novaehollandiae* Stephens (Charadriiformes : Laridae), Lake Martin, near Cressy, Vic., viii.1973, T. O'Brien.

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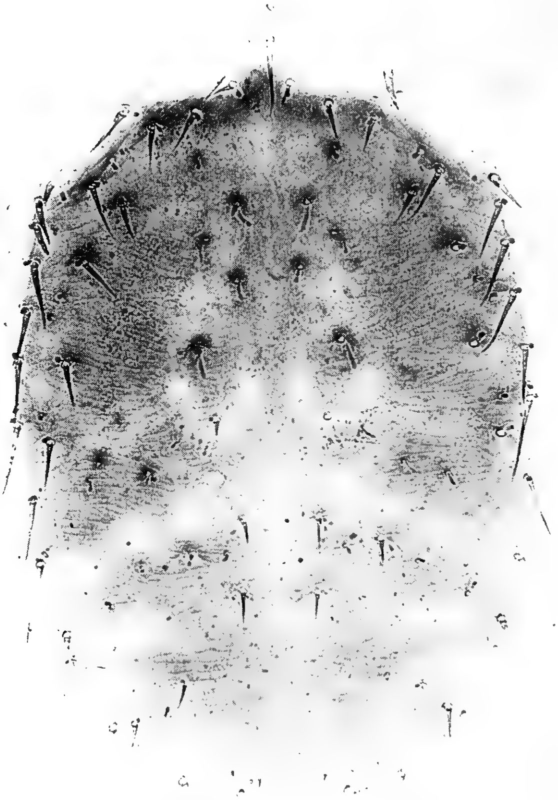
I am grateful to the many zoologists named above for making time in the field to collect parasites, and to Misses Leanne Jackson, Jenny Kübler, and Robyn Wilson for their assistance.



Laelaps hapaloti ♀ from *Notomys mitchellii*. Dorsal shield (995µ long) showing extensive transparent areas surrounding pores immediately in front of setae *S*4 and *S*5. This specimen lacks setae *z*6.

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A NEW SPECIES OF *OSMUNDACAULIS* FROM THE JURASSIC OF QUEENSLAND

R. E. GOULD*

(Communicated by J. F. RIGBY)

(Plates III-V)

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Synopsis

A new species of petrified osmundaceous stem, *Osmundacaulis hoskingii* sp. nov., is described from the Jurassic Injune Creek Beds of the Surat Basin, Queensland. Distinguishing features include : a dissected siphonostele with internal and external endodermis, leaf gap sclerenchyma, and numerous, deep, narrow xylem strands ; the petiole bases exhibit a crenate mass of sclerenchyma lining the adaxial bay of the vascular trace and numerous scattered sclerenchyma strands in the inner cortex and stipules. These stems represent the earliest known appearance of the " *O. skidegatensis* group ". The species contains two varieties, *O. hoskingii* var. *hoskingii* and *O. hoskingii* var. *tabulatus* var. nov. ; the latter is characterized by the presence of unusual tabulae-like structures in the pith.

INTRODUCTION

Jurassic strata in Queensland have yielded numerous specimens of fossil osmundaceous stems, and some of these have been reported by Kidston and Gwynne-Vaughan (1914), Dunstan (1920), Sahni (1920), Edwards (1933), and Hill, Playford, and Woods (1966). Almost all have been referred to the species *Osmundacaulis dunlopi* (Kidston and Gwynne-Vaughan) Miller 1967 or *O. gibbiana* (Kidston and Gwynne-Vaughan) Miller 1967, which were originally described from the Jurassic of New Zealand (Kidston and Gwynne-Vaughan, 1907). The new species described here, *O. hoskingii* sp. nov., is based on several silicified specimens collected from the Injune Creek Beds on " Mt. Organ " Station in the Surat Basin west of Wandoan (Text-fig. 1), and is divided into two varieties, *O. hoskingii* var. *hoskingii* and *O. hoskingii* var. *tabulatus* var. nov. The Injune Creek Beds are of Middle Jurassic age, although they possibly extend into the Upper Jurassic ; the stratigraphy has been discussed elsewhere (Gould, 1968). Specimens are housed in the Department of Geology and Mineralogy, University of Queensland (UQ).

SYSTEMATIC PALAEOBOTANY

Division PTEROPHYTA

Order FILICALES

Family OSMUNDACEAE

Genus OSMUNDACAULIS Miller, 1967

Type species : Osmundites skidegatensis Penhallow, 1902 (Miller, 1967).

Original diagnosis : Structurally preserved rhizomes, roots, and (or) leaf bases of plants resembling species of *Leptopteris*, *Osmunda*, or *Todea*, but which cannot be assigned to any one of these genera. Stems containing a pith ; xylem cylinder dissected by leaf gaps ; leaf traces oblong or adaxially curved in transverse section ; xylem strand of root diarch (Miller, 1967, p. 146).

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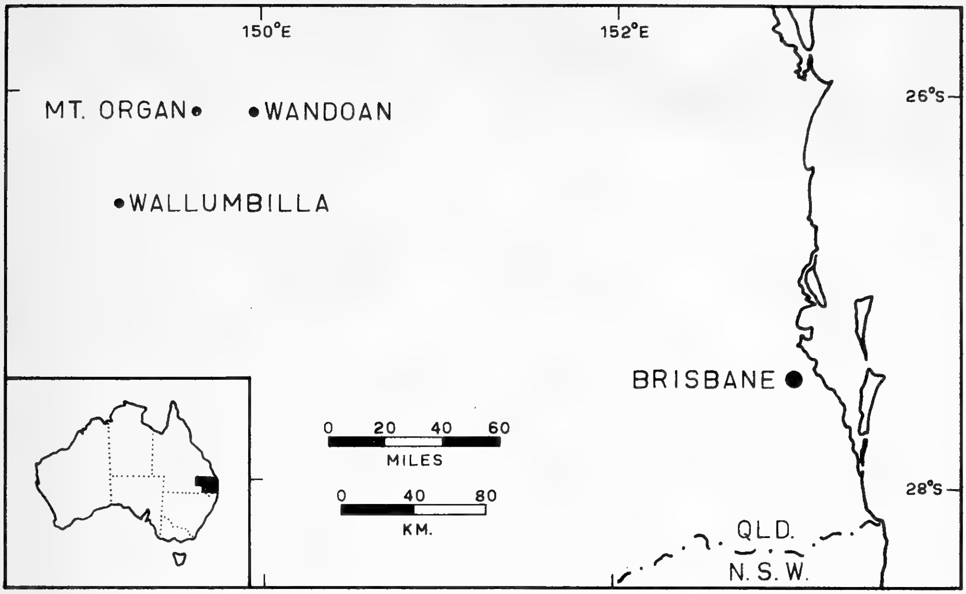


Text-fig. 1. Locality map.

Discussion : The organ genus *Osmundacaulis* was instituted for fossil axes which exhibit the general features of trunks and rhizomes of living Osmundaceae, but cannot be classified in any extant genus " for one or more of the following reasons :

(1) Lack of preservation of sufficient diagnostic detail,
(2) the presence of structural features that are not characteristic of living species, and
(3) the combination of features of Recent genera in such a way that assignment to one of them cannot be made " (Miller, 1967).

Osmundites Unger, 1854, was illegitimate because of Jaeger's (1827) prior use of the name for misidentified cycadophyte foliage ; in any case Unger's type species, *Asterochlaena schemnicensis* Pettko, 1849, actually belongs to *Osmunda* (Miller, 1967). A very complete survey of the fossil Osmundaceae has recently been presented by Miller (1971).

Living osmundaceous genera have been distinguished on morphology of sterile and fertile fronds ; recognition of species has also depended on various aspects of frond morphology (Hewitson, 1962). However, it has been found that genera can be recognized on anatomical details of the stem and stele, and the arrangement of sclerenchyma in the petiole bases (Hewitson, 1962 ; Miller, 1967, 1971). The structure and disposition of sclerenchyma in the petioles is the only character which is reliable for purposes of species recognition (Kidston and Gwynne-Vaughan, 1907 ; Hewitson, 1962 ; Miller, 1967, 1971), and thus studies of fossil axes can be undertaken with some confidence.

In the following descriptions the number of gaps appearing in a transverse section of the xylem cylinder is given, and this is equal to the number of " bundles " as defined by Hewitson (1962, p. 80). The term " radial strand " is used here for any group of stelar xylem tracheids with a prominent radial dimension when seen in transverse section, regardless of whether the group is connected to adjacent strands or not. By investigation of extant examples, Miller (1971) has shown that the rhizomatous or arborescent habit of the stem is reflected by the direction of growth of the roots, and hence the growth habit of fossil axes can be determined. In rhizomatous specimens the roots permeate outwards through the mantle of leaf bases and most are cut longitudinally by a transverse section of the axis ; in arborescent forms the roots grow down through the mantle and most are cut transversely by a cross-section of the trunk.

Osmundacaulis hoskingii sp. nov.

(Plate III, Figs 1, 2 ; Plate IV, Figs 1–8 ; Plate V, Figs 1–6 ;
Text-figs 2A–D, 3A–I)

Holotype : UQF53534 ; figured in Plate III, Fig. 2 ; Plate IV, Fig. 2 ; Text-fig. 2A.

Type locality : " Mt. Organ " Station, via Wandoan, Queensland (Roma 4-mile Military Sheet c. 250756) ; Injune Creek Beds.

Diagnosis : Arborescent and rhizomatous axes of *Osmundacaulis* with stems 8–30 mm wide, surrounded by adhering leaf bases and adventitious roots. Stele a dissected siphonostele, 6–20 mm in diameter ; endodermis internal and external, connected through leaf gaps, with 2–10 such gaps in a transverse section ; pith of parenchyma with scattered strands of sclerenchyma ; xylem ring 1–5 mm wide, composed of 35–70 radial strands, with 14–20 gaps ; each radial metaxylem strand 20–64 tracheids deep with tangential width of 2–12 tracheids ; metaxylem tracheids 14–110μ in diameter (rarely up to 150μ) with 1–3 vertical series of regular scalariform pits on each wall ; leaf gaps immediate, usually containing sclerenchyma. Inner cortex parenchymatous, sometimes with scattered strands of sclerenchyma ; outer cortex sclerenchymatous. Leaf trace with two endarch protoxylem groups which bifurcate at base of petiole or higher ; adaxial ends of C-shaped trace strongly incurved and commonly merged together in outer cortex of stem and basal part of petiole ; sclerenchyma from leaf gap may be continuous along trace, or develop within adaxial bay of trace in outer cortex of stem and in base of petiole. Petioles stipulate, arising at 5°–30° to stem ; cataphylls occasionally present ; single mass of sclerenchyma lining adaxial concavity of C-shaped petiolar strand, upwards appearing crenate in transverse section ; inner cortex parenchymatous, usually with scattered strands of sclerenchyma ; sclerotic ring round or oval, homogeneous ; stipules parenchymatous with scattered sclerenchyma strands increasing in number and size upwards. Adventitious root traces arise in pairs from leaf trace below, or where, latter separates from stele ; each root trace surrounded by a parenchymatous inner and sclerotic outer cortex where it enters inner cortex of stem.

Derivation of name : The plant is named after Mr. and Mrs. I. Hosking and sons (" Mt. Organ " Station, via Wandoan), who collected, and kindly presented to the author, many of the specimens used in this study.

Discussion : Osmundacaulis hoskingii is characterized by a dissected siphonostele with leaf gap sclerenchyma and deep, narrow, xylem strands ; the fusion of the incurved ends of the leaf trace in the stem and basal part of petiole ; and the distribution of sclerenchyma in the petioles (Text-fig. 2B, D). The species conforms with Miller's (1967, 1971) " *O. skidegatensis* group ", and represents the earliest appearance of this type in the fossil record.

The new species contains two distinct varieties, the type variety *O. hoskingii* var. *hoskingii*, and *O. hoskingii* var. *tabulatus* ; these are described and discussed in the following pages.

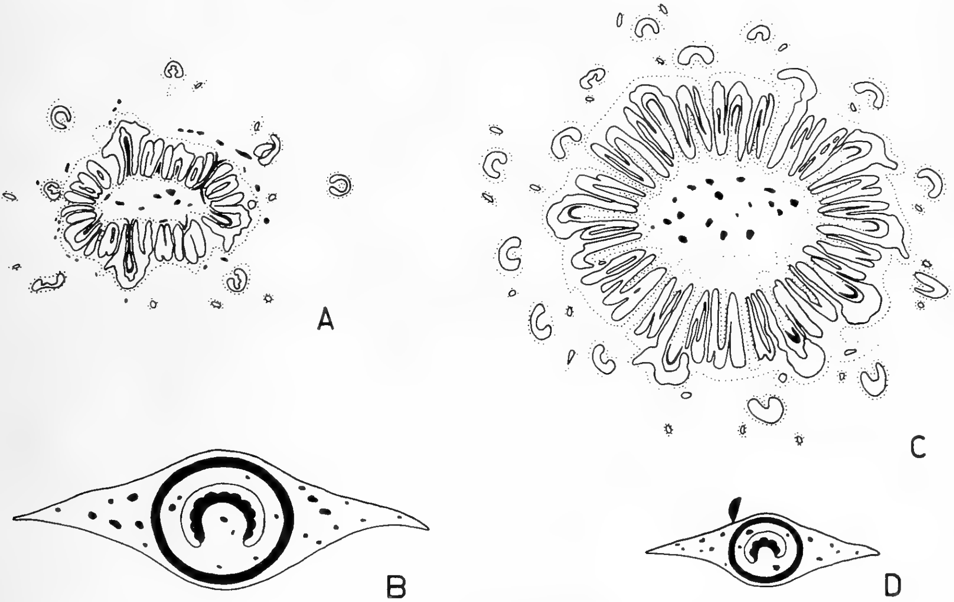
Osmundacaulis hoskingii sp. nov. var. *hoskingii*

(Plate III, Figs 1, 2 ; Plate IV, Figs 1–8 ; Plate V, Fig. 1;
Text-figs. 2A, B, 3A–I)

Varietal type : UQF53534 (holotype of species).

Diagnosis : Osmundacaulis hoskingii axes up to 20 cm in diameter ; stems 8–20 mm wide, usually arborescent. Stele about 6–12 mm in diameter ; internal and external endodermis connected through 2–10 complete leaf gaps in a transverse section ; pith 4–9 mm by 1–5 mm, parenchymatous, with scattered strands of sclerenchyma ; xylem ring 1–3 mm wide, composed of 35–48 radial strands with 14–20 gaps, each strand 20–56 tracheids thick with tangential width of 2–12 tracheids. Inner cortex 0·3–3 mm wide, parenchymatous, sometimes with scattered sclerenchyma strands, containing 3–13 leaf traces in any one given transverse section. Outer cortex fibrous, narrow, sinuous, 0·1–1·7 mm wide, containing 3–7 leaf traces in a transverse section. Petioles arise at 5°–15° to stem ; cataphylls occasionally present ; at outside of mantle petiole bases show crenate mass of sclerenchyma lining adaxial bay of vascular trace and numerous scattered sclerenchyma strands in inner cortex and stipules.

Further description and discussion : General.—The variety is described from six specimens which are round or slightly oval in cross-section, with lengths of up to 13 cm although both ends are broken across. Each specimen contains a central stem composed of a pith, vascular ring, inner cortex, and a narrow sclerotic outer cortex ; this is surrounded by a closely adhering mantle of petiole bases and adventitious roots (Plate III, Figs 1, 2).



Text-fig. 2. All ×3·4. A, B, *Osmundacaulis hoskingii* sp. nov. var. *hoskingii*. A, cross-section of stele, UQF53534 (holotype) ; B, transverse section of petiole. C, D, *Osmundacaulis hoskingii* sp. nov. var. *tabulatus* var. nov. ; C, transverse section of stele, UQF53539 (varietal type) ; D, transverse section of petiole. Sclerenchyma black ; in cross-sections of steles endodermis shown by a dotted line, sclerenchyma of outer cortex not shown.

Stele.—A cross-section of the stele is shown in Text-fig. 2A. Endodermal tissue consists of one layer of cells with well-developed Casparian strips ; in longitudinal section the walls are finely waved (*cf.* Esau, 1953, fig. 17.2C). Protoxylem tracheids are 10–20μ in diameter with walls 1–6μ thick ; metaxylem tracheids have diameters of 14–96μ (rarely up to 150μ) and wall thicknesses of 2·5–14μ. Details of cells between the xylem and the endodermis are mostly not preserved. A porose layer of phloem is developed on the abaxial side of the xylem ring, and thin-walled, somewhat disorganized cells occur between the internal endodermis and the adaxial ends of the radial metaxylem strands.

Leaf traces.—The xylem of the leaf trace usually separates from the stem xylem with two endarch protoxylem groups ; in a few cases there are one or three groups (Plate IV, Fig. 8). However, unlike the condition in *Plenasium* Presl, 1836, where the leaf trace also exhibits two proximal protoxylem groups and separates from two adjacent crozier-shaped metaxylem strands (see Hewitson, 1962; Chandler, 1965; Miller, 1967, 1971), each trace in *O. hoskingii* var. *hoskingii* is associated with only one original metaxylem strand of the stem which is divided into two strands by the leaf gap. Text-figure 3 shows the sequence as would be seen in an ascending series of transverse sections; some details are also shown in Plate IV, Figs 5–8. The leaf trace is strongly arched within the stem and extreme base of the petiole, and the incurved ends of the trace commonly fuse together, showing in section a circle of endodermis, with the accompanying sclerenchyma and inner cortex, within the oval trace (Plate IV, Fig. 1). The trace opens out again into the normal C-shape in the petiole. Total number of leaf traces in a transverse section of the whole cortex of the stem is 7–19.

Petioles.—The leaf bases consist of a vascular trace, inner cortex, sclerotic ring, and a pair of lateral stipules (Plate IV, Fig. 4; Text-fig. 2B); except for the stipules, which arise with the petiole, the tissues are continuous with the corresponding zones of the stem. The bases range from 2·5–4 mm wide, tip to tip, where they leave the stem, to 15–34 mm wide at the outside of the mantle. Cataphylls appear to be present in two specimens, but they are not regularly arranged.

The xylem of the petiolar trace contains metaxylem tracheids that are 23–95μ (occasionally up to 140μ) in diameter; the xylem trace is 1–6 (mostly 1–4) tracheids thick. Two or three protoxylem groups project on the adaxial side of the trace at the very base of the petiole, and 6–21 groups occur at the outside of the mantle. In some cases, although the vascular trace retains its adaxially curved C-shape, the xylem may be divided into two or three strands.

The xylem trace is usually surrounded by a parenchymatous sheath, phloem, pericycle, and endodermis. In some cases there is a greater development of phloem on the abaxial side of the trace, and in a few petioles of one specimen there is an abnormal development of pericycle with large cells up to 140μ by 70μ. The endodermis is one or two cells thick, often dark in colour, and shows distinct Casparian strips.

The concavity of the C-shaped vascular trace is lined with a single mass of sclerenchyma; this exhibits a distinctly crenate appearance in transverse section as the abaxial side closely parallels the adaxial side of the xylem trace, and the sclerotic mass is indented opposite the projecting protoxylem groups (Plate IV, Fig. 2). Walls of the fibres nearest the endodermis usually have reticulate thickening.

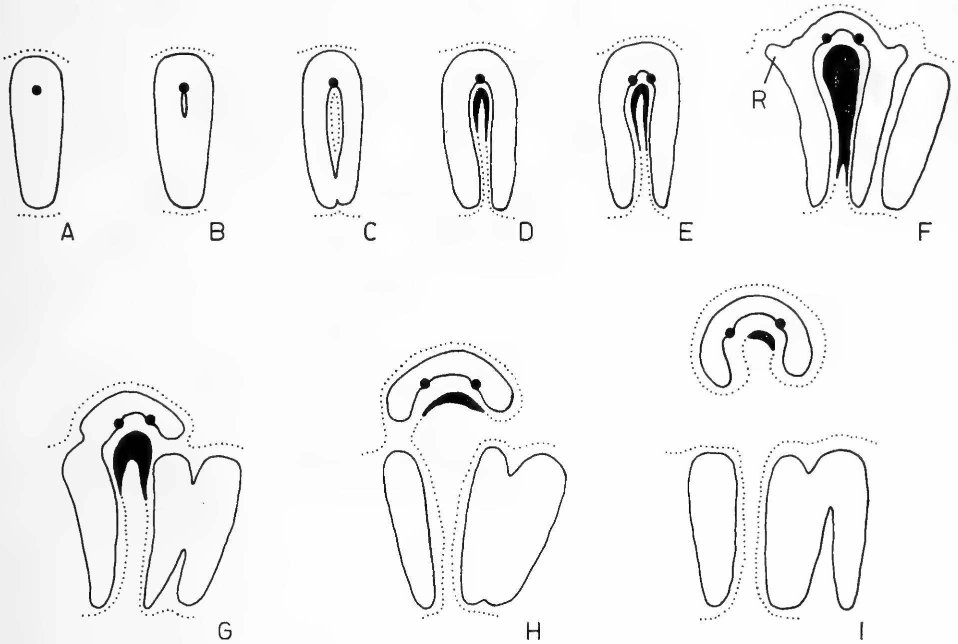
The inner cortex of the petiole base consists of polygonal parenchyma cells, generally with scattered strands of sclerenchyma fibres which increase in number upwards. Sometimes the strands occur throughout the tissue right from the inner cortex of the stem, while in other cases the strands are not developed, the inner cortex being parenchymatous throughout.

The sclerotic rings are round to oval in cross-section, measuring 1·5–2·3 mm in diameter near the stem and 3–11 mm at the outside of the mantle; thickness of the ring varies from 0·13–0·5 mm near the point of attachment to the stem to 0·2–0·6 mm further out. There is a slight increase in fibre diameter from the outside to the inside of the ring, which is otherwise homogeneous.

The stipules consist of polygonal parenchyma cells with strands of sclerenchyma. Some radially elongated parenchyma cells, arranged perpendicularly to the surface of the petiole, may occur on the abaxial side of the sclerotic ring. One or two sclerenchyma strands are usually present in the base of the stipules, and these increase to over 30 at the periphery of the mantle; sometimes, however, the stipules are parenchymatous where they arise from the stem, and the sclerenchyma strands develop higher up.

Roots.—The adventitious roots are 0·5–2·5 mm in diameter. Within the mantle the majority are cut transversely by a transverse section of the axis, indicating that the plant was probably arborescent; in a cross-section of one specimen, however, the roots are seen in longitudinal section.

Foreign intrusions.—Some of the specimens contain foreign axes consisting of a star-shaped xylem trace and a parenchymatous cortex; these axes commonly displace the parenchymatous tissue of the pith and inner cortex of the stem and petioles (*e.g.* Plate IV, Fig. 3). A somewhat similar axis has displaced the stem in the holotype of *O. kidstoni* (Stopes) Miller, 1967, which is from probably Lower Cretaceous strata near Wallumbilla (Stopes, 1921; Posthumus, 1924).



Text-fig. 3. A–I, stylized series of ascending transverse sections showing separation of leaf trace from a strand of stelar xylem and formation of leaf gap in *Osmundacaulis hoskingii* sp. nov. var. *hoskingii*. Internal endodermis commonly does not appear within xylem strand as shown in C; development of leaf gap sclerenchyma also varies. Sclerenchyma black; endodermis dotted line; protoxylem large black dots; R, root trace.

Comparison.—The new variety can be closely compared with two rather ill-preserved forms described by Schelpe (1955, 1956) from the Lower Cretaceous (Neocomian) Uitenhage Series of South Africa, *O. natalensis* (Schelpe) Miller, 1967, and *O. atherstonei* (Schelpe) Miller, 1967. *Osmundacaulis natalensis* is very similar to *O. hoskingii* var. *hoskingii* in many respects, including the stele and leaf traces (see Schelpe, 1955, pp. 653–654, fig. 1), but the petioles at the outside of the mantle only show a crenate mass of sclerenchyma within the adaxial bay of the vascular trace, with no sclerenchyma strands in the inner cortex or stipules (Schelpe, 1955, p. 655, fig. 4). Detailed comparison with *O. atherstonei* is not possible because of poor preservation.

Osmundacaulis hoskingii sp. nov. var. *tabulatus* var. nov.

(Plate V, Figs 2–6; Text-fig. 2C, D)

Varietal type: UQF53539; figured in Plate V, Figs 2–4; Text-fig. 2C.

Type locality: " Mt. Organ " Station, via Wandoan, Queensland; Injune Creek Beds.

Diagnosis: Rhizomatous axes of *O. hoskingii* with stems 18–30 mm wide. Stele 12–20 mm in diameter with 3–6 complete leaf gaps in a transverse section; pith 4–10 mm wide, interrupted by regularly spaced, broadly conical (height 2–3·5 mm), distally directed tabulae-like structures consisting of layers of thin-walled, rounded, polygonal, and irregular elongated cells; tabulate structures 0·7–1·5 mm thick, bounded by an endodermis usually connected to the internal endodermis of the stele; xylem ring 2·5–5 mm wide, composed of 53–70 radial strands, with 16–19 gaps, each strand 43–64 tracheids deep, and 2–11 tracheids wide tangentially. Inner cortex 1·5–3·2 mm wide, containing 12–20 leaf traces in a given transverse section. Sclerotic outer cortex irregular, 0·8–3 mm wide, containing 11–26 leaf traces in a transverse section. Petioles at the outside of mantle with crenate mass of sclerenchyma lining adaxial bay of vascular trace, and scattered strands of sclerenchyma throughout inner cortex and stipules.

Derivation of name: The varietal epithet derives from the presence of the tabulae-like structures in the pith.

Further description and discussion: General.—The variety is based on two incomplete specimens with radii of 3·5 cm and 3·8 cm, and lengths of 6 cm and 7 cm. Both specimens were probably rhizomatous. The type consists of a single central stem surrounded by a mantle of adhering leaf bases and adventitious roots (Plate v, Figs 2–4). The other specimen (UQF53540) contains three stems surrounded by a mantle (Plate v, Figs 5, 6); although, from their relative orientations, two of the stems would appear to arise from the third, their steles are not connected, those of the two subordinate stems being corroded where they touch the central one.

Stele.—The stele is similar to that in *O. hoskingii* var. *hoskingii*, although leaf gap sclerenchyma is not developed to such a marked extent (Text-fig. 2C). The pith consists of parenchyma and scattered strands of sclerenchyma, although the latter are not always present. The parenchyma cells are equidimensional, rounded to polygonal, and arranged more or less in vertical rows.

The pith is interrupted at intervals of 3–7·5 mm by transverse, broadly conical tabulae-like structures with the apices directed distally (Plate v, Figs 4, 6). The "tabulae" are 0·7–1·5 mm thick, and the vertical height of the cone from apex to base is 2–3·5 mm. The structures contain round, equidimensional polygonal, elongate, and irregular, thin-walled cells measuring 30–164μ in diameter, or 70–270μ by 18–140μ; when seen in a longitudinal section of the stem, the smaller, more equidimensional cells tend to be at the upper and lower surfaces of the cone, with the elongate, irregular and twisted cells confined to the median layer. The large, irregularly arranged cells are somewhat similar to some of the phloem on the abaxial side of the xylem ring. The "tabulae" are bounded by a line of endodermal cells, continuous with the internal endodermis of the stele. Cells of the pith adjacent to the "tabulae" are often larger than those of the rest of the pith, measuring 65–280μ by 55–95μ, with the long axes arranged perpendicularly to the "tabulae"; this tissue appears to be the result of meristematic activity. Some "tabulae" are incomplete in that the apex is lacking; also some may not be connected to the stele all round, thus appearing detached in a longitudinal section of the stem.

Protoxylem tracheids are 12–35μ in diameter with walls 1·5–7μ thick. Metaxylem tracheids are 27–140μ (mostly 40–110μ) in diameter; walls are 3·5–27μ thick. The xylem strands are surrounded on all sides by a parenchyma xylem sheath 3–16 cells thick. Phloem cells occur outside the xylem sheath on the abaxial side of the xylem cylinder, with their best development in the wedges between the external lobes of the xylem. A well-developed porose layer is present. Some of the cells are very similar to those in the median layer of the tabulae. Outside the phloem is a layer of crushed cells, possibly representing protophloem. The pericycle is normally 1–3 cells thick ; in some places, however, the xylem sheath and phloem are crushed and there is an abnormal development of large, linearly and radially arranged, pericycle cells, which is somewhat suggestive of meristematic activity.

The endodermis is 1–3 cells thick and Casparian strips are sometimes visible.

Leaf traces.—Leaf traces depart from the stele in the same manner as those in *O. hoskingii* var. *hoskingii*, and the incurved ends of the trace usually fuse together within the stem and proximal end of the petiole base. The leaf trace separates from the stele with two endarch protoxylem groups which bifurcate after the trace enters the petiole ; at the outside of the mantle there are 4–6 endarch protoxylem groups in the petiolar trace. Twenty-five to 44 leaf traces occur in any transverse section of the whole cortex of the stem.

Petioles.—The petiole bases are similar to those of *O. hoskingii* var. *hoskingii* although somewhat smaller (Text-fig. 2D), measuring 4–5 mm tip to tip where they arise, and 10–14 mm wide at the outside of the mantle. In specimen UQF53540 the leaf bases are disorganized and not well developed, but the structure is still discernible. Metaxylem tracheids of the petiolar trace are 40–96μ in diameter ; the xylem arch may break up into two or three segments as in *O. hoskingii* var. *hoskingii.* The xylem is surrounded by a xylem sheath, phloem, pericycle, and dark stained endodermal cells ; the phloem is mainly developed on the abaxial side of the trace. The round sclerotic rings are 1·7–2·5 mm in diameter near the stem and 1·2–5 mm further out ; thickness of the rings varies from 0·1 mm to 0·3 mm, and there is a slight increase in fibre diameter towards the inner cortex of the petiole.

Roots.—Diarch adventitious root traces arise in pairs from the stele in association with leaf traces. The roots are 0·5–1·5 mm in diameter, and they permeate through the mantle so that most are seen in longitudinal section in a transverse section of the axis. Roots are also found in the pith of the stem (Plate v, Figs 3, 4). In one of the specimens the roots form a mat outside the mantle of petiole bases.

Comparison.—The tabulate structures in the pith are characteristic of *O. hoskingii* var. *tabulatus* (*cf.* Plate v, Fig. 1, and Figs 4, 6). The structures have no known counterpart in the modern representatives of the family, and their function in the fossil is not apparent. The axes of *O. hoskingii* var. *tabulatus* are rhizomatous, while those of *O. hoskingii* var. *hoskingii* are usually arborescent, and the development of the "tabulae" may be linked with the rhizomatous condition. The stem and stele of the variety *tabulatus* are larger, the cortex thicker, and the petioles smaller and less well developed than those of the variety *hoskingii.*

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EXPLANATION OF PLATES

PLATE III

Figs 1, 2. *Osmundacaulis hoskingii* sp. nov. var. *hoskingii*; transverse sections. 1, UQF53535, from " Mt. Organ " Station; ×1·6. 2, UQF53534, holotype, from " Mt. Organ " Station; ×2·2. (Transmitted light.)

PLATE IV

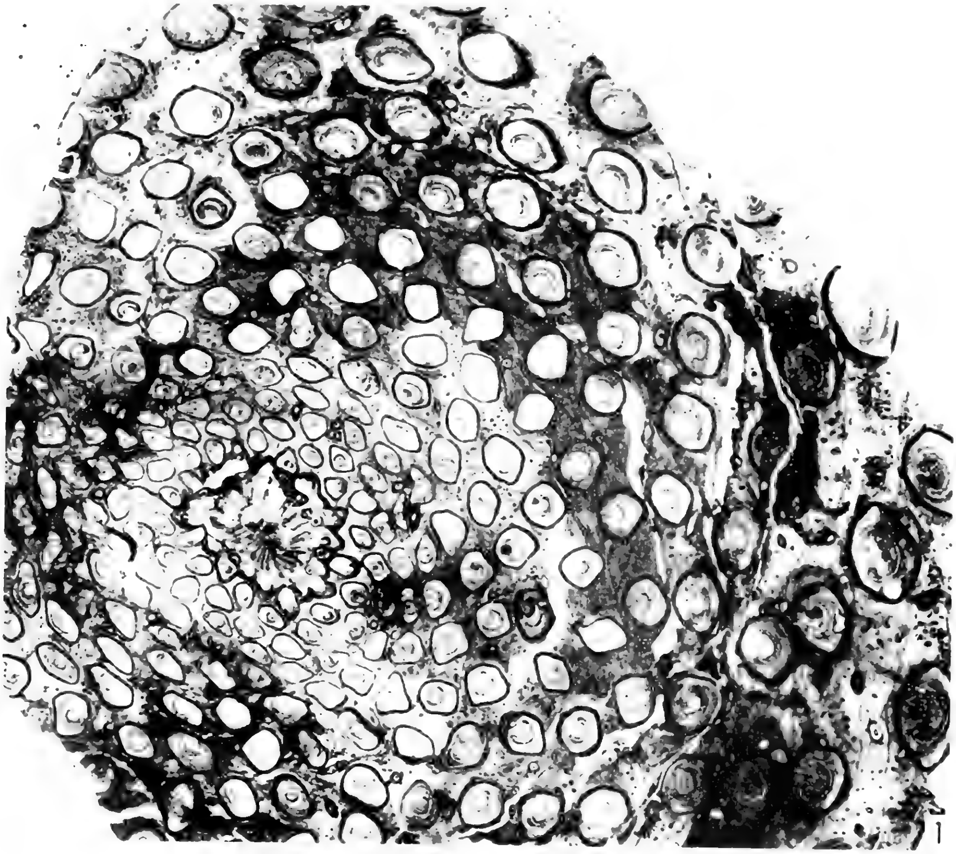
Figs 1–8. *Osmundacaulis hoskingii* sp. nov. var. *hoskingii*. 1, Transverse section of vascular trace of petiole close to stem, showing the incurved ends and the isolated circle of endodermis and sclerenchyma in the adaxial bay; UQF53535; ×33. 2, Transverse section of petiole in mantle, showing crenate mass of sclerenchyma lining adaxial bay of vascular strand; UQF53534, holotype; ×9. 3, Transverse section of stem and inner layers of petiole bases; pith intruded by foreign axes; UQF59498, from " Mt. Organ " Station; ×4. 4, Transverse section of petiole bases; UQF53535; ×3·5. 5–8, UQF59498; transverse sections of xylem ring showing departure of leaf trace; cortex of foreign axis in lower right of Fig. 6; the occurrence of three, instead of two, adaxial protoxylem groups on the departing leaf trace in Fig. 8 is atypical; Fig. 5, ×22; Figs 6–8, ×20. (Figs 1–3, 5–8, transmitted light; Fig. 4, transmitted and reflected light.)

PLATE V

All Figures ×2

Fig. 1. *Osmundacaulis hoskingii* sp. nov. var. *hoskingii*. Longitudinal section of stem and adhering petiole bases; UQF53535.

Figs 2–6. *Osmundacaulis hoskingii* sp. nov. var. *tabulatus* var. nov. 2–4, Varietal type, UQF53539, from " Mt. Organ " Station. 2, 3, Transverse sections; the section in Fig. 3 contains a root in the pith. 4, Longitudinal section showing the tabulate structures in the pith; note root in cross-section within pith at lower left. 5, 6, UQF53540, from " Mt. Organ " Station. 5, Transverse section showing external mantle of roots. 6, Longitudinal section; note tabulae-like structures in the pith.



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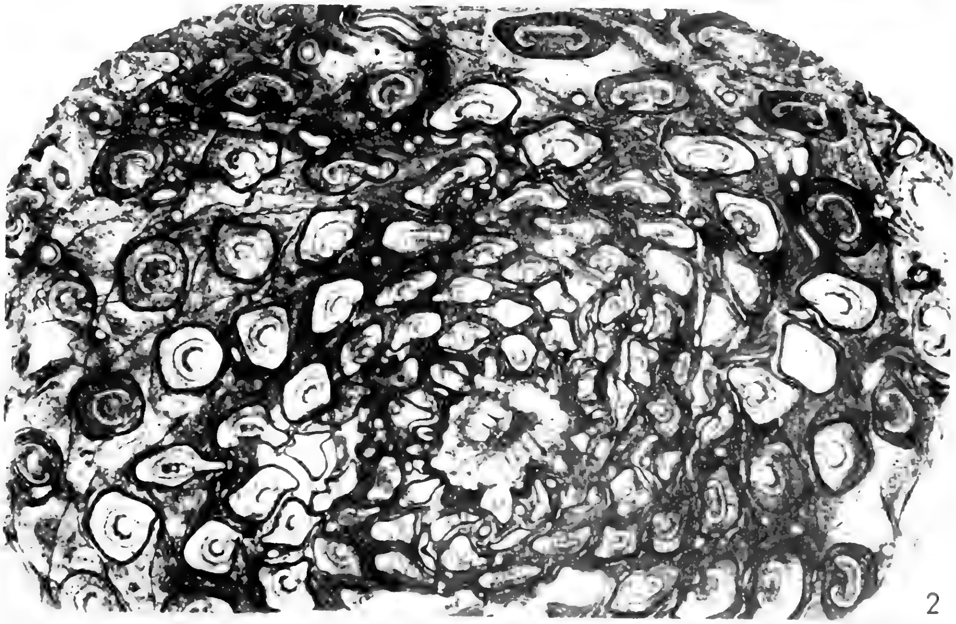

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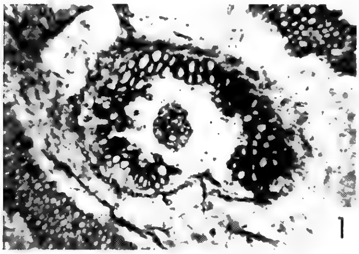
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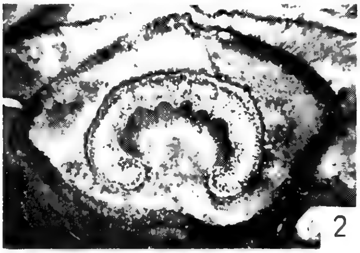
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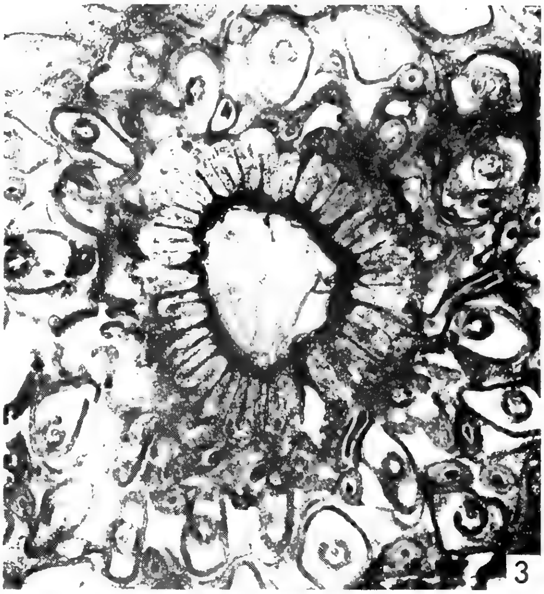
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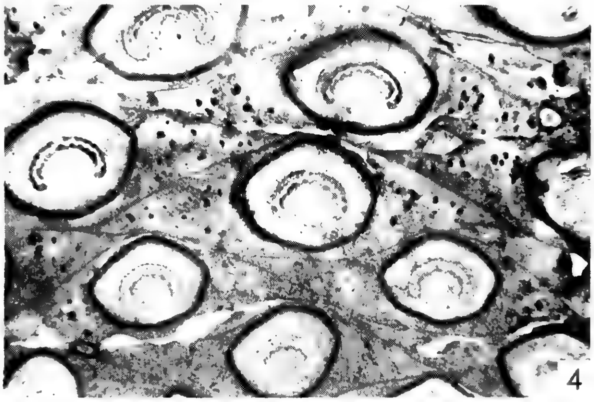
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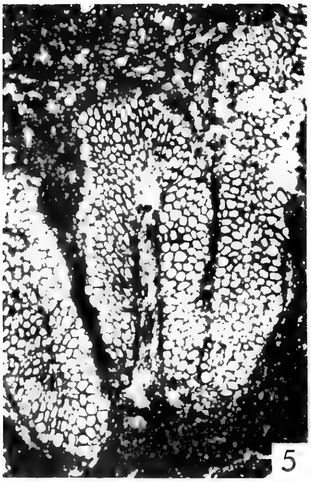
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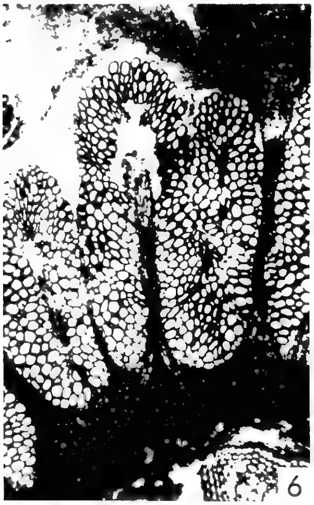
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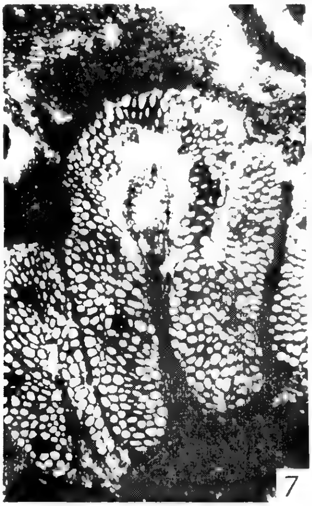
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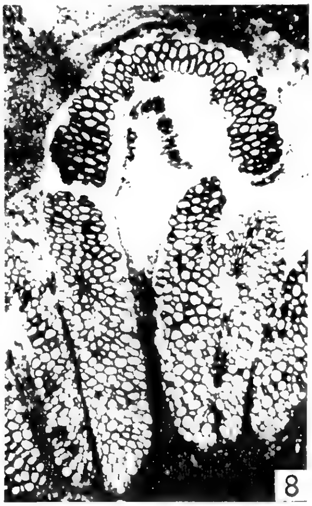
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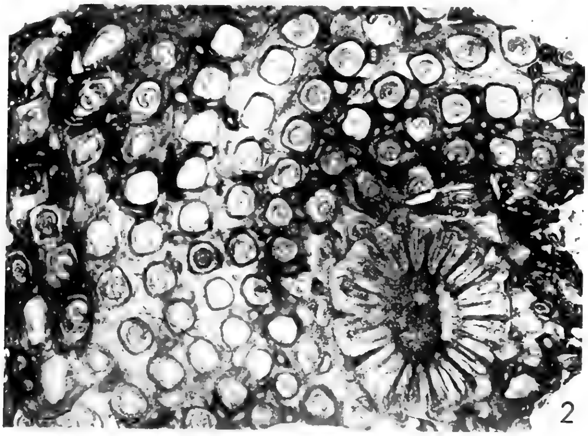
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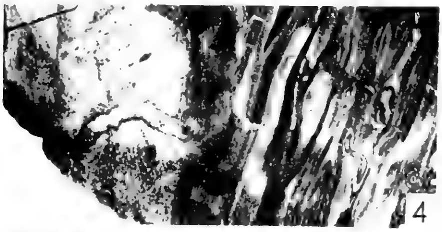
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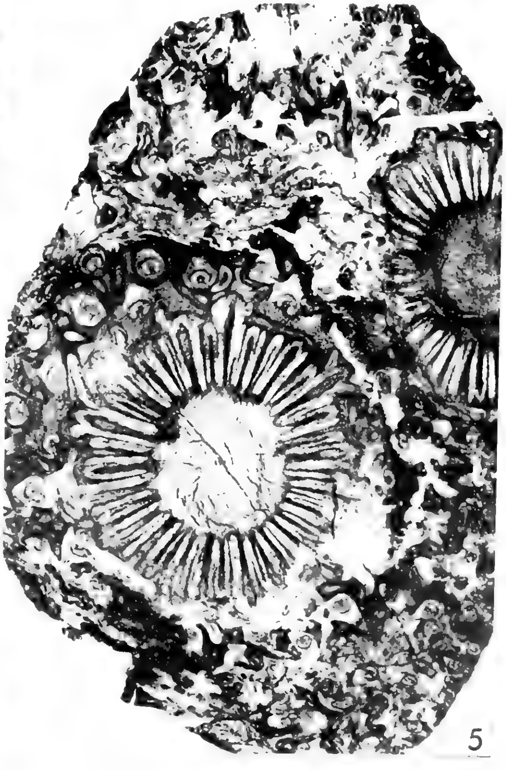
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NOTES ON THE ECOLOGY, ZOOGEOGRAPHY, AND COLORATION OF THE GOBIESOCID CLINGFISHES, *LEPADICHTHYS CARITUS* BRIGGS AND *DIADEMICHTHYS LINEATUS* (SAUVAGE)

GERALD R. ALLEN[1] AND WALTER A. STARCK II[2]

(Communicated by GILBERT P. WHITLEY)

[Accepted for publication 18th April 1973]

Synopsis

The commensal association between *Lepadichthys caritus* Briggs and comasterid crinoids is reported and notes are included on the live coloration. The species was originally described from a single specimen collected at the Seychelles Islands, Indian Ocean. It is recorded in the present paper from Palau, New Guinea, and the Great Barrier Reef. Observations are also included on the ecology of *Diademichthys lineatus,* a gobiesocid which sometimes associates with sea urchins of the genus *Diadema.*

Briggs (1969) described *Lepadichthys caritus* from three specimens, 15·5 to 22·8 mm standard length, collected at the Seychelles Islands during the International Indian Ocean Expedition programme in 1964. The description did not include information on habitat or live coloration.

While diving along the edge of Malakal Channel in the Palau Group, western Caroline Islands, in February, 1972, the junior author sighted a small blackish fish hovering among the arms of a comasterid crinoid. Later we collected seven of these fish (6·9 to 23·1 mm SL), which agree with Briggs' description of *L. caritus,* by gathering up approximately 20 crinoids, depositing them in a bucket of sea water, adding a small amount of quinaldine (a fish anaesthetic), and shaking out the fishes. The crinoids were taken from relatively shallow water (approximately 2 to 4 m) along the edge of Malakal Channel. They were generally attached to coral outcrops which projected several metres from the bottom. Currents of 2 to 3 knots, which are associated with the changing tides, are characteristic of the area.

Briggs gave the alcohol coloration of his specimens as " perfectly pale and translucent with no evidence of pigmentation ". The live colours of the specimens we collected in Palau were as follows : head and body jet black except for three yellow longitudinal lines, about pupil width or less ; one on dorsal midline, from snout to vicinity of dorsal fin origin ; other two on each side of body, from snout, through upper part of eye, along upper portion of side to caudal fin ; mid-portion of caudal fin dusky blackish ; remainder of fin translucent with yellow-orange tinge ; dorsal, anal, and pectoral fins likewise translucent with yellow-orange tinge.

The clingfish from Palau discussed by Bayer and Rofen (1957) is most certainly the same species. Briggs (personal communication) stated that a formal description of the fish was never published, but a drawing of the specimen sent by Rofen agreed with the clingfish which was described later by Briggs as *L. caritus.* The live coloration reported by Bayer and Rofen is similar to our Palau material except there is no mention of a yellow stripe on the dorsal midline.

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The general colour pattern of *L. caritus* is similar to that of *L. lineatus* which Briggs (1966) described from the Red Sea. However, *lineatus* has two additional pairs of lines on the lower half of the body on a background of reddish-brown. This species was observed by Fishelson (in Briggs, 1966) as a commensal with the Red Sea crinoid, *Capillaster multiradiata.* Briggs (1969) remarked that *L. lineatus* is most closely related to *L. caritus*, a conclusion which our observations substantiate.

During May, 1972, the junior author observed and collected two individuals of *L. caritus* (17·2 and 27·2 mm SL) at a depth of 10 m living commensally with a bright yellow crinoid at Madang, New Guinea. The coloration of these fish was yellow, which served as an effective camouflage. The Palau specimens also blended in effectively with their crinoid host, which was largely blackish with yellow tips on the pinnules. Fish from both localities assumed a reddish coloration (except for the yellow lines) immediately after immersion in formalin while still alive. The Palau fish underwent a similar change while under the influence of quinaldine, but the normal coloration was restored as soon as the effects of the drug had vanished. After several months of preservation in alcohol, the Madang specimens agree with the colour description given by Briggs.

Two additional specimens (7·5 and 7·8 mm SL) were collected in November, 1972, by the senior author in 14 m depth at Opal Reef, Great Barrier Reef, off Port Douglas, Queensland. The fish were associated with a himerometrid crinoid (*Himerometra robustipinna* Carpenter) and were identical in live coloration to the Palau specimens.

The specimens from Palau, New Guinea, and the Great Barrier Reef, which have been deposited at the Australian Museum in Sydney, represent a substantial increase in the known geographic range of *L. caritus*, which was previously recorded only from the Seychelles, Indian Ocean. A similar increase in geographic range was recently reported for *L. bolini*, which, prior to Briggs' (1969) Seychelles record, was known on the basis of a single specimen collected at the New Hebrides. It is likely that several of the nine known species of *Lepadichthys* will ultimately prove to have relatively widespread Indo-West Pacific distributions, but because of their small size and inconspicuous habits they remain largely uncollected.

At Madang we observed about a dozen individuals of *Diademichthys lineatus* (Sauvage). Pfaff (1942) reported that this small clingfish associated with sea urchins of the genus *Diadema.* However, only one of the fish we sighted was with *Diadema*, in spite of the abundance of the latter. The fish were usually observed hovering horizontally over small patches of coral of the genus *Acropora.* This unusual, long-snouted clingfish was generally jet black with translucent fins and several narrow white lines positioned as follows : mid-dorsal line from tip of snout to about dorsal fin origin ; pair of lines on side from snout, passing through upper portion of eye and continuing along middle of sides to region slightly ahead of caudal base ; mid-ventral line from pelvic disc to origin of anal fin. *D. lineatus* is widespread in the Indo-West Pacific region.

The gobiesocids, *Lepadichthys caritus* and *L. lineatus* are the only fishes which are known to form a commensal association with crinoids, although Bruce (1971) reported a number of pontoniid shrimps from crinoid hosts. The crinoids offer concealment from predators which is further enhanced by the camouflage coloration of the fishes. Perhaps the fishes also take advantage of the favourable position of the crinoids (i.e., high above the bottom, exposed to currents) in procuring planktonic food which could be eaten directly from the current or after it became entangled in the " sticky " crinoid appendages. The transparent sea whip goby *Cottogobius yongei* Davis and Cohen (1969) forms a similar association with the antipatharian, *Cirrhipathes.*

Diademichthys lineatus is a more mobile clingfish and may range several metres away from its host coral head or *Diadema*, which is used primarily as a sanctuary when danger threatens, and possibly as a nocturnal retreat. Allen (1972) discussed similar, although closer, relationships between apogonid fishes and the crown-of-thorns starfish, *Acanthaster*, and urchins of the genus *Diadema*. Whitley (1950) reported the presence of sea urchin tube feet among the stomach contents of *Diademichthys*. Hence, these clingfish may sometimes obtain nourishment from their hosts.

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THE PSILOPSOCIDAE (PSOCOPTERA) OF NEW GUINEA

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[Accepted for publication 21st March 1973]

Synopsis

Two new species of *Psilopsocus* from New Guinea are described, additional information on *Ps. nigricornis* Enderlein, the type species, is given, and a key to the known species is provided.

Enderlein (1903) erected the genus *Psilopsocus* for *Ps. nigricornis* from New Guinea. Mockford (1961) described *Ps. nebulosus* from the Philippines, and Smithers (1963) described *Ps. mimulus* from Australia, at the same time recording the family from South Africa on the basis of nymphal material only of an undescribed species.

This paper is a contribution to the study of the Psocoptera of the Melanesian Arc; in it are described two further species of *Psilopsocus* from New Guinea, additional information is given on *Ps. nigricornis*, and a key to the five known species is included.

Psilopsocus pulchripennis sp.n.

Male

Coloration (in alcohol). Head dull ivory with brown markings. Median epicranial suture very dark brown. Vertex with a narrow brown band adjacent to the inner margins of the compound eyes and on either side of the epicranial suture, which broadens posteriorly to cover the back of the head. This gives the impression that the top of the head is brown with two narrow anteriorly converging ivory bands running parallel with inner margins of the compound eyes and a little mesad of them. Frons ivory with a dark brown spot between the anterior ocellus and the epistomial suture. Postclypeus ivory with nine dark brown stripes which do not converge anteriorly but run *parallel to one another* throughout their length from the epistomial suture to the anterior margin of the postclypeus. Anteclypeus very dark brown in the middle of the posterior half, elsewhere colourless. Labrum dark brown with a median colourless area near the anterior margin. Genae pale with a dark brown spot above mandibular attachment. Scape and pedicel very pale brown; flagellar segments black. Eyes black. Ocellar tubercle black. Maxillary palp with basal and second segments pale brown; third and distal segments black. Dorsum of mesothorax brown, paler adjacent to sutures. Fore and middle legs with femora and tibiae pale brown, the latter with a very dark brown apical band; tarsi very dark brown. Femur of hind leg almost colourless with dark brown band at the distal quarter; remainder of hind leg pale except for the dark brown middle and distal tarsal segments. Fore wing (Fig. 5) with reddish brown pterostigma. Membrane marked in shades of grey-brown. Veins yellowish brown to dark brown except for cu_2 and the basal half of cu_{1a}, which are colourless. Hind wing hyaline, tinged with grey brown in the distal half, more densely so near apex, and near hind margin. Veins dark brown except for colourless cu_2. Abdomen pale, irregularly banded in shades of reddish brown; apical structures very dark brown.

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Morphology. Length of body: 3·3 mm. Median epicranial suture very well defined, anterior arms less so. Vertex smoothly rounded with a very fine, short, sparse pubescence. Frons, postclypeus, labrum and genae similarly pubescent. Lengths of flagellar segments: f_1: 1·0 mm; f_2: 1·0 mm. Scape and pedicel much thicker than the long slender flagellar segments which bear long, fine setae. Eyes large, inner margins above diverging strongly behind; reaching a little above vertex and a little behind the head. IO/D: 0·55; PO: 0·88. Ocelli fairly large. Measurements of hind leg: F: 0·75 mm. T: 1·5 mm; t_1: 0·45 mm; t_2: 0·075 mm; t_3: 0·1 mm; rt: 6:1:1·3; ct: 18, 1, 1. Fore wing length: 4·5 mm; fore wing width: 1·6 mm. Pterostigma of fore wing (Fig. 5) with well marked hind angle with an extremely short spur vein. Veins *rs* and *m* meeting in a point; m_1 meets wing margin at apex; apex of areola postica more than halfway from hind margin to *m*. Vein cu_{1a} arises well basad of point where cu_{1b} reaches margin. Hind wing length: 3·5 mm; hind wing width: 1·2 mm. Hind wing with *rs* and *m* fused for a fairly long length. Vein *m* curves after separation from *rs* to run almost parallel with costal margin. Epiproct (Fig. 6) well sclerotized, with sinuous hind margin; a row of four small setae occurs near hind margin; two similar setae lie basad of the end setae of the row. Paraproct (Fig. 7) with broad, blunt-ended dorsally-directed process and a posterior, narrow, ventrally-directed, blunt rod. Hypandrium simple, sclerotized, rounded behind with the posterior and lateral edges upturned to form a bowl in which lies the phallosome; lightly setose. Phallosome (Fig. 4) in the form of a simple sclerotized ring of varying thickness, open anteriorly with little sclerotization of the penial bulb.

Material Examined

New Guinea: 1 ♂ (holotype), Kassem Pass, 1.ix.1970 (C.N.S. and I.W.B.T.). The holotype will be deposited in the Australian Museum.

Discussion

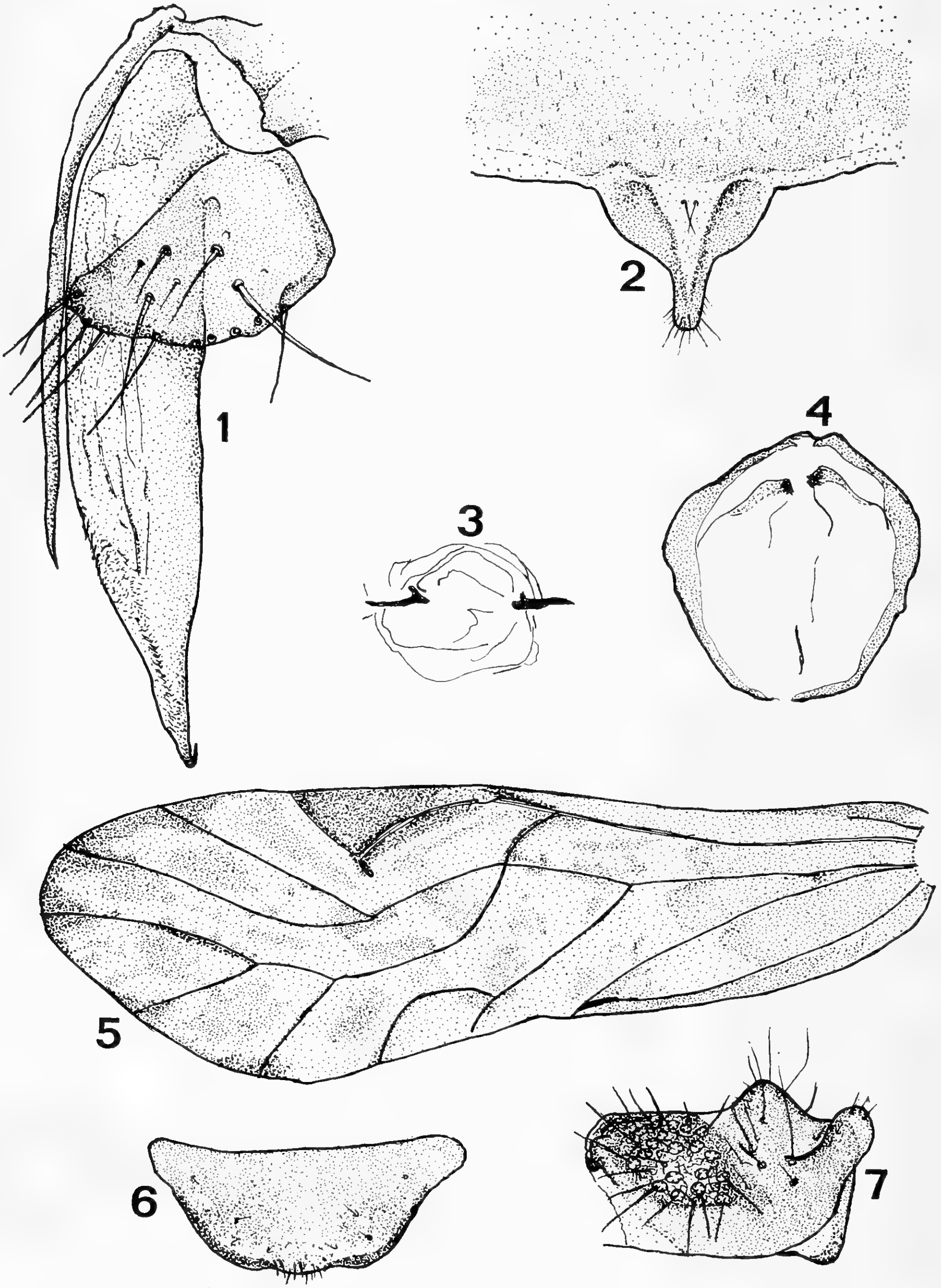
Ps. pulchripennis differs from other species of the genus in that cells M_1, M_2 and M_3 of the fore wing are centrally darker than they are nearer the veins and the paraproct is of distinctive shape. The female is unknown.

Psilopsocus marmoratus sp.n.

Male

Coloration (in alcohol). Head ivory with brown markings. Median epicranial suture pale. Vertex ivory with a brown band along inner margin of eye and a similar band, broadening posteriorly, on either side of median epicranial suture. Frons ivory with a V-shaped mark anterior to median ocellus, the arms of the V reaching the epistomial suture and passing on either side of a small median dark brown spot. Postclypeus with *parallel* brown stripes. Anteclypeus dark brown posteriorly, colourless anteriorly. Labrum dark brown, colourless in middle near distal margin. Genae ivory with a brown mark immediately below insertions of antennae. Scape and pedicel pale, flagellar segments black. Ocellar tubercle black. Basal and second segment of maxillary palp pale, remaining segments very dark brown. Dorsum of mesothorax brown, pale adjacent to sutures. Femora brown; tibiae pale brown, middle and distal tarsal segments a little darker. Fore wings (Fig. 8) patterned in shades of grey-brown; pterostigma reddish brown. Veins brown except for $m+cu$, cu_2 and basal half of cu_{1a}. Hind wings hyaline, faintly tinged with grey near anterior margin. Veins brown except for pale cu_2. Abdomen pale, marked irregularly in reddish brown. Terminal structures dark brown.

Morphology. Length of body: 2·6 mm. Median epicranial suture distinct; anterior arms less so. Head with short, fine, sparse pubescence. Lengths of flagellar segments: f_1: 0·7 mm; f_2: 0·7 mm. Scape and pedicel short and stout; flagellar segments long and slender; bearing long fine setae. Eyes fairly large but not reaching level of vertex when viewed from the side nor extending behind head when seen from above; inner margins strongly diverging



Figs 1–3. *Psilopsocus nigricornis* End. 1, ♀ gonapophyses. 2, ♀ subgenital plate. 3, ♀ sclerotizations of 9th sternite. Figs 4–6. *Ps. pulchripennis* sp. n. 4, ♂ phallosome. 5, ♂ fore wing. 6, ♂ epiproct. 7, ♂ paraproct.

behind. IO/D : 1·1 ; PO : 0·9. Ocelli large. Measurements of hind leg : F : 0·55 mm ; T : 1·05 mm ; t_1 : 0·35 mm ; t_2 : 0·05 mm ; t_3 : 0·075 mm ; rt : 7 : 1 : 1·5 ; ct : 16, 1, 1. Fore wing length : 3·2 mm ; fore wing width : 1·2 mm. Pterostigma with sharp hind angle and spur vein extending almost halfway from pterostigma to *rs*. Apex of pterostigma more than halfway from wing margin to *m*. Vein m_1 meets wing margin at wing apex. Hind wing length : 2·4 mm ; hind wing width : 0·8 mm. Hind wing with *rs* and *m* fused for a fairly long length. Epiproct (Fig. 12). Paraproct (Fig. 10) with a broad, blunt-ended dorsally-directed process. Phallosome very similar to that of *Psilopsocus pulchripennis* (Fig. 4).

Female

Coloration (in alcohol). As in male but a little darker with hyaline areas of wing near margin a little more extensive.

Morphology. Length of body : 2·8 mm. Lengths of flagellar segments : f_1 : 0·8 mm ; f_2 : 0·8 mm. Eyes smaller than in male also not reaching level of vertex. IO/D : 1·0 ; PO : 0·75. Ocelli large. Measurements of hind leg : F : 0·57 mm ; T : 1·1 mm ; t_1 : 0·32 mm ; t_2 : 0·05 mm ; t_3 : 0·075 mm; rt : 6·4 : 1 : 1·5 ; ct : 13, 1, 1. Fore wing length 3·5 mm ; fore wing width : 1·2 mm. Venation as in male. Hind wing length : 2·7 mm ; hind wing width : 0·9 mm. Epiproct simple, sclerotized, with a few strong setae in distal half and a few small setae in basal half. Middle section of hind margin a little more strongly sclerotized than elsewhere. Subgenital plate (Fig. 11). Gonapophyses (Fig. 9) with slender ventral valve ; dorsal valve broad-based narrowing suddenly to slender, pointed, distal half ; external valve ovoid. Sclerotizations around entrance to spermatheca shown in Fig. 13.

Material Examined

New Guinea : 1 ♂ (holotype), McAdam Park, near Wau, 5.ix.1970. (C.N.S. and I.W.B.T.) ; 1 ♀ (allotype), Mt. Missim, near Wau, 1,500 m, 7.ix.1970. (C.N.S. and I.W.B.T.) ; 1 ♂ (paratype), Gauka, S of Minj, 1,660 m, 22.viii.1970. (C.N.S. and I.W.B.T.). Holotype, allotype and paratype in Australian Museum.

The paratype male is much paler than the other specimens and was probably collected soon after moulting.

Discussion

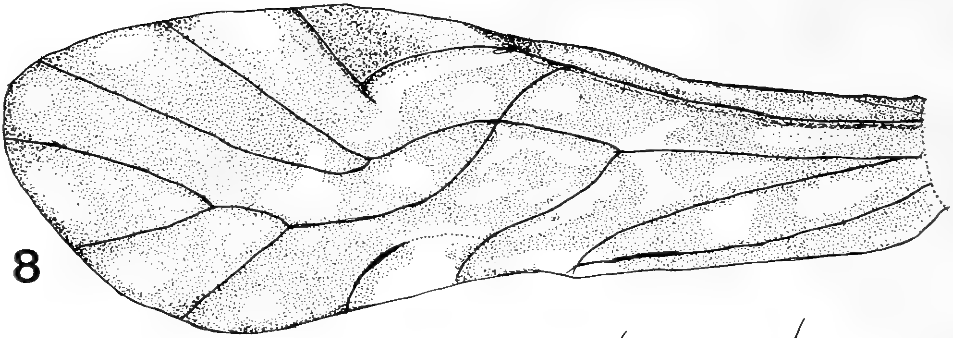
Ps. marmoratus differs from other species of the genus, except *Ps. nigricornis*, in having the distal cells of the fore wing with a well-defined hyaline area at or near the wing margin. The female differs from that of *Ps. nigricornis* in the form of the dorsal valve of the gonapophyses (*cf.* Figs 1 and 9). The dorsal valve in *Ps. nigricornis* is characteristically recurved (Fig. 1).

Psilopsocus nigricornis Enderlein

The female now available permits expansion of the original description by illustration of the subgenital plate (Fig. 2), the gonapophyses (Fig. 1) and the sclerotizations round the entrance to the spermatheca (Fig. 3). The male remains unknown. Enderlein (1903, pl. xiv, fig. 74) gives an illustration of the wings.

Material Examined

New Guinea : 1 ♀, Bainyik, 12.xii.1963. (D. K. McAlpine.)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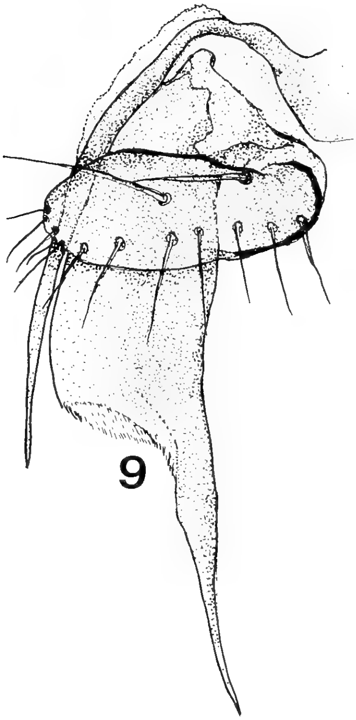
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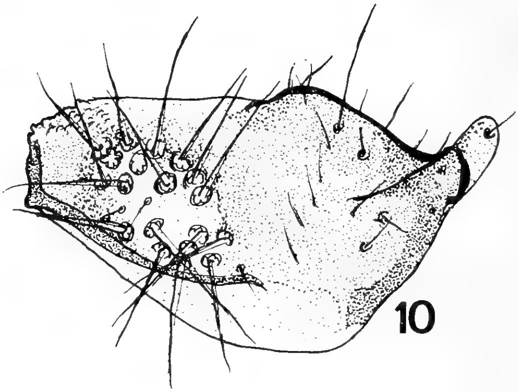
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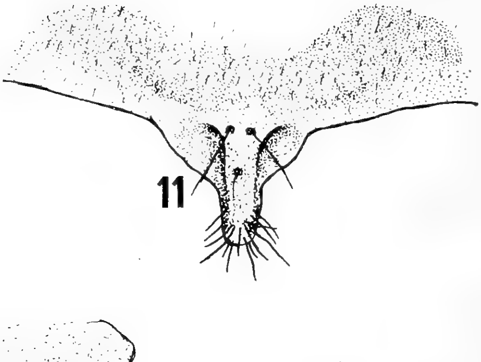
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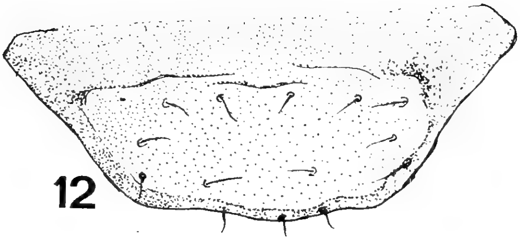
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Figs 8–13. *Psilopsocus marmoratus* sp. n. 8, ♂ fore wing. 9, ♀ gonapophyses. 10, ♂ paraproct. 11, ♀ subgenital plate. 12, ♂ epiproct. 13, ♀ sclerotizations of 9th sternite.

KEY TO THE SPECIES OF *Psilopsocus*

1. Fore wing with clearly defined, hyaline areas at or near wing margin in cells M_1 and M_2.... 2
   Fore wing without such clearly defined hyaline areas.................................. 3
2. Cell M_2 with a hyaline spot proximally and another near the wing margin....*marmoratus* sp. n.
   Cell M_2 with hyaline spot near wing margin only......................*nigricornis* Enderlein
3. Colour in distal half of cell R_5 and in cells M_1 and M_2 uniform, not mottled..*nebulosus* Mockford
   Colour pattern in distal half of cell R_5 and cells M_1 and M_2 mottled.................... 4
4. Vein cu_{1b} half as long as cu_{1a}......................................*mimulus* Smithers
   Vein cu_{1b} much less than half as long as cu_{1a}..........................*pulchripennis* sp. n.

In addition to the wing characters used in the above key, perusal of the descriptions in this and the papers referred to will reveal many differences of detail between species in wing pattern, phallosomes, subgenital plates and gonapophyses. In particular, the form of the dorsal valves of the gonapophyses and the proportions of the subgenital plates are useful characters in females. In males, there are differences in the degree and form of the sclerotizations of the penial bulb, slight though these are in this genus. *Ps. pulchripennis* and *Ps. marmoratus* have, however, very similar phallosomes. *Ps. mimulus* has a very distinctive areola postica owing to the branching of cu_1 being much nearer the wing base than in any other species.

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RESISTANCE TO RUST (*UROMYCES APPENDICULATUS*) IN BEANS (*PHASEOLUS VULGARIS*)

Barbara Ballantyne*

[Accepted for publication 20th June 1973]

Synopsis

The field reactions of 158 lines of beans to natural infection by rust were assessed in trials at Rydalmere, New South Wales, during the autumn of 1970 and of 1971. Many of the bush green and red kidney beans were only slightly affected and the results suggest that some of them have race non-specific resistance to rust. This is supported by field observations on their behaviour in New South Wales and by comparison of results of this trial with overseas reports. The pole beans and most dry beans showed either a high level of specific resistance or were severely rusted, and there was no evidence for non-specific resistance in these groups. Breeding of beans with stable resistance to rust in both temperate and tropical areas is discussed and the value of an International Bean Rust Nursery to such programmes is considered.

Introduction

Rust (*Uromyces appendiculatus* (Pers.) Unger) is widespread on beans (*Phaseolus vulgaris* L.) throughout the world (Guyot, 1957), but is most severe in the tropical and sub-tropical areas such as Mexico (Crispin and Dongo, 1962), Brazil (Shands *et al.*, 1964), Venezuela (Diaz Polanco and Renaud Casanova, 1966), Costa Rica (Christen and Echandi, 1967) and East Africa (Howland and Macartney, 1966 ; Leakey, 1971).

Many races of the fungus have been reported (Table 1). The relationships between the races in the different countries are not clear, although some workers (Crispin and Dongo, 1962 ; Netto, Athow and Vieira, 1969 ; Leakey, 1971) have reported that the races in their countries differ from those in the U.S.A. Harter and Zaumeyer (1941) designated seven differentials, but these have been inadequate in many situations. The additional differentials used have generally been restricted to one country only and have not been readily available.

Table 1

Reported Races of Bean Rust

Country	Number of Races	Reference
United States of America, mainland	35	Harter and Zaumeyer, 1941 Fisher, 1952 Sappenfield, 1954 Zaumeyer, 1960 Hikida, 1961 Goode, 1961 McMillan, 1972
United States of America, Hawaii	2	Parris and Matsuura, 1941
Mexico	31	Crispin and Dongo, 1962
Brazil, Minas Gerais	26	Netto, Athow and Vieira, 1969
Brazil, Rio Grand do Sol	16	Augustin *et al.*, 1972
Costa Rica	11	Christen and Echandi, 1967
East Africa	8	Howland and Macartney, 1966 Leakey, 1971
Australia	3	Waterhouse, 1953
	8	Johnson, personal communication
New Zealand	3 or 4	Yen and Brien, 1960
The Netherlands	2	Hubbeling, 1957

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TABLE 2

Bean Cultivars Bred for Race Specific Resistance to Rust

Cultivar	Reference	Area	Remarks
POLE BEANS			
Hawaiian Wonder . .	Frazier and Hendrix, 1949	Hawaii	
Westralia.	Cass Smith *et al.*, 1951	Western Australia	Grown only to a limited extent
Mangere Pole	Yen *et al.*, 1962	New Zealand	Westralia was the source of rust resistance
Dade	Conover *et al.*, 1962	Florida	Affected by a new race of rust (McMillan, 1972)
Polaris	McMillan, 1972	,,	Dade was the source of rust resistance. Affected by a new race of rust
BUSH BEANS			
Redlands Greenleaf B . .	Groszmann, 1963	Queensland	Affected by new races of rust (Anon., 1971)
Redlands Pioneer . .	,,	,,	,, ,, ,, ,,
Redlands Greenleaf C . .	Anon., 1971	,,	Affected by a new race of rust (Anon., 1971)
NAVY BEANS			
Burnia	Groszmann and Gallagher, 1966	Queensland	Affected by new races of rust (Gallagher, 1972)
Kerman	,, ,, ,, ,,	,,	,, ,, ,, ,, ,,
Gallaroy	Gallagher, 1968	,,	,, ,, ,, ,, ,,
NB1-S1	Anon., 1963; Gottl, personal communication	New South Wales	Affected by a new race of rust (Johnson, personal communication)
NB2-S2	,, ,, ,,	,,	,, ,, ,, ,, ,, ,,
NB3-S3	,, ,, ,,	,,	,, ,, ,, ,, ,, ,,
PINTO BEANS			
Pinto 5	Zaumeyer and Harter, 1946	Colorado	Agronomically unsuitable
Pinto 14	,, ,, ,,	,,	,, ,,
Scout	Wood, personal communication	,,	,, ,,
Luna	Quinones, 1963	New Mexico	
GREAT NORTHERN BEANS			
Great Northern US 1140	Zaumeyer *et al.*, 1960	Montana	A leading cultivar, which has maintained its rust resistance in the U.S.A. However, Nebr 67–117, Tara, and some plants of Jules, the resistance of which is apparently derived from 1140 (Coyne and Schuster, 1970) are affected by a new race of rust in Queensland

Various cultivars bred for a high level of resistance to specific races of rust have been rendered susceptible later by the appearance of new rust races. Many are listed in Table 2. The large numbers of races and the frequent appearance of new ones capable of affecting cultivars with race-specific resistance indicate that investigation of race non-specific or horizontal resistance could be valuable (Van der Plank, 1963).

Differences occur in the frequency and severity of infection of susceptible lines, particularly in relation to latitude. Dry beans in the Great Northern, Navy, Pinto and Red Mexican groups and the pole beans are more commonly affected by rust than most bush, Horticultural and Red Kidney types. In addition the Great Northern, Pinto, Red Mexican and pole beans are more severely affected by rust in a range of geographical areas and race situations than the bush, Horticultural and Red Kidney types. Some examples are in Table 3. Outside the tropical and sub-tropical areas rust generally causes losses only in these commonly and severely affected types. Exceptions to this are rare and are also included in Table 3.

In New South Wales rust causes occasional losses in green bean crops grown in northern coastal areas and in some dry bean crops, particularly those grown in more humid areas or planted late in summer (Anon, 1972). For many years considerable differences in rust severity have been noted among susceptible cultivars in trials and commercial crops. Some dry beans in the Navy, Great Northern, Pinto and Red Mexican groups and the pole cultivar " Blue Lake " and several bush cultivars derived from it were severely affected, whereas the green bean cultivars in widespread commercial use were slightly affected.

To investigate these differences trials were conducted with a range of dry and fleshy podded beans. These included cultivars in commercial use in New South Wales for several years and recently introduced lines from Europe and the U.S.A.

Materials and Methods

The trials were conducted in the autumns of 1970 and 1971 at Rydalmere (34° latitude), near Sydney, where natural rust infection occurs each year. In 1971, 109 lines were sown on 14th and 15th January and in 1971, 129 lines were sown on 25th and 26th January with 25 seeds per plot and two plots for each line. The plots were not randomized. Cultivars known to be severely affected by rust were interspersed through the planting and used as buffer rows around the trials.

Rating was carried out when most of the pods were filled but still firm and green. The categories used were as follows:

Immune: no rust sori present.

Highly resistant: no rust sori present until late in the trial, when very small pustules occurred.

Slightly rusted: few to many leaves affected; pustules small, inconspicuous and without a yellow band; some larger pustules surrounded by a yellow band occurred, but usually only on young leaves inside the bush.

Moderately rusted: many leaves affected, pustules usually larger than in the slightly rusted class and sometimes with a yellow band.

Severely rusted: all or most of leaves affected; most of the pustules large and surrounded by a yellow band; premature defoliation of some cultivars.

Race determinations were carried out on six specimens from the 1970 trial. Collections from the 1971 trial were lost because of refrigeration failure. Urediniospores from single pustules were inoculated with a scalpel on to the damp lower surfaces of bean leaves one-third expanded. The spores were spread over the leaf surfaces with the thumb and first finger. Hands were washed between

TABLE 3

Rust Severity on Bean Cultivars in Various Countries Arranged According to Latitude

Latitude	Area	Reference	Type or Cultivar	Severity
5° N–12° S	East Africa	Leakey, 1971	Navy	Severe
			Many stringless cvs.	Severe
5° N–5° S	Kenya	Anon., 1960	Navy	Severe
19–20° N	Hawaii, U.S.A.	Frazier *et al.*, 1948	Pole	Severe
25–31° N	Florida, U.S.A.	Townsend and Tisdale, 1936	Pole (Kentucky Wonder)	Severe in annual outbreaks
			Bush green beans	Normally little infection. Severe in 1936
23° N	Hong Kong	Anon., 1969	Pole	Severe
32° S	Environs of Perth, Western Australia	Cass Smith *et al.*, 1951	Pole including Kentucky Wonder and Black Creaseback	Very susceptible in annual outbreaks
			Dwarf beans	Less severely affected than pole beans
32·5° N	Chula Vista, California, U.S.A.	Harter, Andrus and Zaumeyer, 1935	Great Northern, Navy, Pink, Pinto, Red Mexican types, one strain Kentucky Wonder	Very susceptible in annual outbreaks
			White Kidney, Red Kidney, Yellow Eye, Cranberry types and a wide range of green and wax beans	Slightly affected
26–37° N	Texas, U.S.A.	Larsh, 1943	Pinto	Very severe in occasional outbreak
33–36·5° N	Arkansas, U.S.A.	Goode, 1961	Bush snap	Severe in 1959 and 1960
37–39° N	Virginia, U.S.A.	Fromme and Wingard, 1918	Navy, Pink, Pinto types, Kentucky Wonder and Creaseback	Severe in annual outbreaks
			One Navy and one marrow type	Moderate
			White Kidney, Red Kidney, Yellow Eye and horticultural types and many green and wax podded beans	Little or no infection
37–39° N	Eastern Virginia, U.S.A.	Cook, 1936	Bush green beans, mainly Bountiful	Normally little infection. Severe in 1936
37–40° N	Maryland, U.S.A.	Zaumeyer, personal communication	Bush green	Moderate to severe in some crops in autumn once in 3–5 years
37–41° N	Colorado, U.S.A.	Zaumeyer and Harter, 1946	Pinto	Severe in some seasons
39–41° N	New Jersey, U.S.A.	Haenseler, 1936	Bush green	Normally little infection. Severe in 1936
41–45° N	New York State, U.S.A.	Burkholder, 1957	Kentucky Wonder	Very susceptible
			Michelite	Affected late in some seasons
			Red Kidney, White Kidney, Yellow Eye types, Perry Marrow and Black Turtle Soup	Not affected
		Zaumeyer, 1960	Blue Lake	Severe in one outbreak
			Bush green	Not affected

TABLE 3—*Continued*
Rust Severity on Bean Cultivars in Various Countries Arranged According to Latitude—Continued

Latitude	Area	Reference	Type or Cultivar	Severity
42–43° N	Massachusetts, U.S.A.	Boyd, 1936	Bush green	Normally little infection. Severe in 1936
	Maine, U.S.A.	Morse, 1918	Kentucky Wonder, Creaseback and Pinto, pink and small white types	Severe
			Red Kidney and horticultural types	No infection
41–45° N	Wyoming, U.S.A.	Zaumeyer, 1946	Great Northern and Tennessee Greenpod	Severe in rare outbreak
			Other beans	No infection
45–49° N	Montana, U.S.A.	Zaumeyer, 1946	Great Northern	Severe in rare outbreak
42–49° N	Idaho, U.S.A.	Anderson, 1941	Great Northern	Severe in rare outbreak
			Kentucky Wonder	Prevalent in 1941
45° N	Olivia, Minnesota, U.S.A.	Ballantyne, unpublished data	Pink, Pinto U.I. 111 and 114 and Red Mexican U.I. 36	Severe
			Sanilac, Seafarer, Seaway, Gratiot	Moderate
			Michigan Improved Cranberry	Very slight
			Taylor Cranberry, Yellow Eye, Black Turtle Soup and Red Kidney types	No infection
46–49° N	Washington State, U.S.A.	Huber, 1936	Blue Lake and Kentucky Wonder	Severe in rare outbreak
49° N	Canada	Conners, 1954	Blue Lake and Kentucky Wonder	Severe
		Conners and Savile, 1948	Michelite and Blue Pod (navy)	Severe
51–54° N	The Netherlands	Hubbeling, 1957	Red Mexican, U.I. 34, Great Northern, Early Blue Lake, many other pole green beans and certain bush green European cultivars	Very susceptible

inoculations. The plants were held in humidity chambers for 36 hours and then on greenhouse benches, where temperatures fluctuated between 11–18° C minimum and 25–30° C maximum. Readings were taken 14 days after inoculation. Three plants of each of three indicator cultivars, Epicure, Golden Gate Wax and Redlands Greenleaf B, from the rust differential series of Johnson (personal communication) were used for each specimen.

RESULTS AND DISCUSSION

In the 1970 trial, rust infection was first seen on 14th February and spread rapidly and uniformly through both replicates of a particular line. In 1971 rust was first seen on 22nd February and spread less rapidly and less uniformly.

Three of the collections from the 1970 trial were determined as race A (from cvs Brown Beauty, Pinto U.I. 111 and South Australian Climber) and three were race B (from cvs Alturas, Apollo and Redlands Greenleaf B) according to the classification of Johnson (personal communication).

The reactions to rust are given in detail in Table 4 and are summarized in Table 5. The cultivar Jules contained some plants that were highly resistant and others that were severely rusted. Five lines differed in severity of infection in both replicates between the 1970 and 1971 trials. Four later-maturing lines, Idelight, X Ida 266–2 and 266–3, were more severely affected in 1970. Weather conditions in 1971 were apparently less favourable for rust development prior to maturity of Caralto and more favourable prior to the maturity of other late maturing lines. Disease ratings did not differ between replicates in the 1970 trial, but were different for replicates of 10 lines in the 1971 trial. These differences indicate that each line should be tested for at least two seasons. This would expose the lines to a wider range of environmental conditions and possibly to other races of the fungus.

In these trials severe infection occurred on susceptible lines of pole green, Great Northern, Navy, Pinto, Red Mexican and some European beans and slight infection occurred on many other bush green beans and Red Kidney types as reported in other areas of the world. This suggests that some of the lines which were classed as slightly affected in these trials may have non-specific resistance to rust.

The green bean cultivars widely grown for many years in coastal areas and exposed to many races of rust are normally only slightly affected, but under seasonal conditions favourable for infection and development of rust, they are moderately or severely affected. They also give a susceptible reaction in greenhouse tests (Ballantyne, unpublished data). These include the fresh market cultivars Brown Beauty, College Pride, Hawkesbury Wonder, Tweed Wonder and Windsor Longpod and the processing cultivars Gallatin 50 and Tendercrop. Brown Beauty, Hawkesbury Wonder and Tweed Wonder showed specific resistance to the two races of rust first recorded in Australia, but this was overcome by one new race which appeared in 1948 (Anon, 1949 ; Waterhouse, 1954) and others which were recorded subsequently (Johnson, personal communication). Further testing is necessary to define more closely the resistance of other lines which were classified as slightly rusted in these trials but have been less widely grown.

All lines bred or selected in eastern Australia for fresh market production were slightly affected except for Redlands Greenleaf C, where race-specific resistance is indicated by its susceptibility to a race of rust recently recorded in Queensland (Anon, 1971).

The processing beans bred in the U.S.A. are generally either Tendercrop types or bush " Blue Lake " types (Zaumeyer, 1972). The Tendercrop types, for example Apollo, Canyon, Cascade, Gallatin 50 and White Seeded Tendercrop,

TABLE 4

Field Reactions of Beans to Rust at Rydalmere, New South Wales, 1970 and 1971

Reaction	Green and Wax Podded Beans			Dry Beans	
	Bush		Pole	Bush	Trailing
Immune	*Fresh market* (Australian) Redlands Greenleaf C^{ab}		*Fresh market* (Australian) Westralia^{ab}	*Navy or Small White* (Australian) NB1–S1^{b} NB2–S2^{b} NB3–S3^{b}	*Miscellaneous* Black Turtle Soup^{b}
Highly resistant . .				*Navy or Small White* (Australian) Gallaroy^{ab}	*Great Northern* (U.S.A.) Jules^{b} (some plants only) Nebr 67–117^{b} Tara^{b}
Slightly rusted . .	*Greenpodded for processing* (Australian) Burnley Conquest^{b} *Greenpodded for processing* (U.S.A.) Apollo^{ab} Canyon^{ab} Cascade^{b} Catskill^{b} Custer^{ab} Gallatin 50^{ab} Idachief^{a} Idagem^{a} *Idelight^{a} Jackpot^{ab} Lakette^{a} Lake Superior^{b} Niagara 773^{b} Picker^{b} Rodeo^{a}	8C–8^{ab} *Greenpodded for fresh market* (Australian) Brown Beauty^{ab} College Pride^{a} Hawkesbury Wonder^{a} Redlands Autumn-crop^{ab} Redlands Belle^{ab} Redlands Greenleaf^{ab} Redlands Pioneer^{ab} St. Andrews^{a} Tweed Wonder^{ab} Windsor Longpod^{ab} 66–526^{a} 86–2B–4–2^{b} 86–6–2–1^{b} 92–2–2^{b} 92–2–12^{b} 92–4–3^{b} 1C–3–B–B–6^{b}		*Red Kidney* (U.S.A.) California Dark Red Kidney^{b} Charlevoix^{ab} Manitou^{b} Redkote^{b} Royal Red^{b} *Miscellaneous* (Europe) Goudkorell^{b}	*Miscellaneous* Borlotto^{ab} (Europe) Perry Marrow^{b} (U.S.A.)

TABLE 4—*Continued*

Field Reactions of Beans to Rust at Rydalmere, New South Wales, 1970 and 1971—Continued

Reaction	Green and Wax Podded Beans		Dry Beans	
	Bush	Pole	Bush	Trailing
	Salem[b] Seminole[ab] Tendercrop[ab] Tendergreen[b] White Seeded Tendercrop[b] Wondergreen[a] Greenpod 492[a] ,, 1137[a] ,, 1139[a] H 70–7–4[b] H 72–1–3-2[a] H 77–4–1–1[b] H 84–3C[b] H 85-1-3[b] H 86–1–1–1[b] H 86-1-2–1[b] Nebr. 67–101[a] X Ida 25,[ab] 69–3,[ab] 92–6[ab] *266–2,[a] *266–3[a] 266–5[a] and 276–1[ab] 11 X Ida 83 sister lines to Canyon[ab] XP–B–3[a] *Greenpodded for fresh market* (U.S.A.) Harvester[a] Spartan Arrow[a] *Greenpodded* (European) Colana[b] Cordon[b] Elan[b] Fin de Mont Clar[a] Flits[b] Gloire d'aubagne[a] Imuna[a] Jolanda[b] Multima supra[b] *Wax podded for processing* (U.S.A.) Midas[b] Moongold Wax[b] Valgold[ab] *Miscellaneous* 63-2032[a]			
One replicate slightly rusted, other moderately rusted	*Greenpodded for processing* (U.S.A.) Bush Blue Lake 274[b] Idachief[b] Idagem[b] Lake Erie[b] Orbit[b] *Greenpodded* (European) Amanda[b] Coram[b]			

TABLE 4—*Continued*

Field Reactions of Beans to Rust at Rydalmere, New South Wales, 1970 and 1971—Continued

Reaction	Green and Wax Podded Beans			Dry Beans	
	Bush		Pole	Bush	Trailing
	Maestro[b] H 85–1–1 -1[b] X Ida 92–1,[b] *266- 2,[b] *266–3[b]				
Moderately rusted	*Greenpodded for processing* (U.S.A.) Alturas[ab] *Idelight[b] *X Ida 92–1[a] *266–4,[a] *265–5[b] *280–1,[a] 283 ·1[ab]	*Greenpodded* (European) Caralto[b] Carlos Favorit[a] Duplex[a] Enfant de Mont Calme[a] Fin de Bagnols[ab] Fin de Fin[a] Fin de Villeneuve[ab] Master[a] Triomphe de Farcy[ab]			
One replicate moderately rusted, other severely rusted	*Greenpodded for processing* (Australian) *Bland[b] *Leeton[b] *Turon[b] *Yanco[b] *Greenpodded for processing* (U.S.A.) Olympia[b]	*Greenpodded* (European) *Prelude[b] *Widusa[b]		*Navy and Small White* *Sanilac[b]	
Severely rusted ..	*Greenpodded for processing* (Australian) *Bland[a] *Leeton[a]	*Greenpodded* (European) Cantate *Caralto[a] Centrum	Blue Lake[ab] South Australian Climber	*Navy and Small White* (U.S.A.) *Sanilac[a] Seafarer[ab]	*Navy and Small White* (U.S.A.) Michelite[a]

TABLE 4—*Continued*

Field Reactions of Beans to Rust at Rydalmere, New South Wales, 1970 and 1971—Continued

Reaction	Green and Wax Podded Beans			Dry Beans	
	Bush		Pole	Bush	Trailing
	*Turon[a] *Yanco[a] *Greenpodded for processing* (U.S.A.) OSU 58,[ab], 190,[ab] 949[ab] X Ida 266-4,[b] 280–1[b]	Corene[a] Lotus[a] Mignon[ab] *Prelude[a] Simplo[ab] *Widusa[a]		Seaway[ab] *Miscellaneous* (Canadian) Limelight[b] *Miscellaneous* (European) Cannellino A[ab]	*Great Northern* (U.S.A.) GN U.I. 15,[a] 31,[a] 59[ab] and 123[ab] Jules (except a few plants) *Pinto* (U.S.A.) Pinto U.I. 111,[a] 114[ab] *Red Mexican* (U.S.A.) RM U.I. 3,[a] 34,[a] 36,[ab] 37[a] *Miscellaneous* (European) Cannellino B[b]

[a]=1970 trial.
[b]=1971 trial.
* indicates lines which gave differing results in the two trials.

TABLE 5
Summary of Rust Reactions of Groups of Beans at Rydalmere, New South Wales

Type	Resistant		Susceptible		
	Immune	Highly Resistant	Slightly Affected	Moderately Affected	Severely Affected
POLE GREEN	+	..	..	..	+
BUSH GREEN :					
Fresh market types (bred in Australia and U.S.A.)	+	..	++ +++	..	..
Tendercrop types	..	..	++ +++	..	..
Bush Blue Lake types	..	..	++	+	+++
Other green beans bred in U.S.A.	..	..	++ +++	++	+
European types	..	..	+++	+++	+++
BUSH WAX	..	..	++	..	..
DRY EDIBLE :					
Navy and Small White types	++	+	..	..	++
Great Northern types	..	++	..	..	++
Red Mexican types	..	..	..	..	++
Pinto types	..	..	..	..	+
Red Kidney types	..	..	++	..	..

+=1– 2 lines.
++=3– 5 lines.
+++=6–12 lines.

++=11–16 lines.
++

++=17–30 lines.
+++

were all slightly affected. Cultivars with " Blue Lake " parentage but without typical " Blue Lake " pods were moderately or slightly affected. Examples are Bush Blue Lake 274, Lakette, Lake Erie and Lake Shasta.

There is no indication of non-specific resistance in (i) the three pole green beans grown in these trials and the bush " Blue Lake " types with pod quality similar to that of the pole " Blue Lake ", such as OSU 58, 190 and 949. Specific resistance may be present in Westralia. (ii) The Great Northern, Navy, Pinto and Red Mexican types included in these trials. The author is currently surveying the resistance of a wide range of lines within these groups. Race-specific resistance in Gallaroy, Jules (some plants), Tara, NB1–S1, NB2–S2, NB3–S3 and Nebr. 67–117 is demonstrated by their susceptibility to a race of rust recently recorded in Queensland (Gallagher, 1972 ; Gallagher and Johnson, personal communication). Specific resistance may also occur in Black Turtle Soup.

Attention has been drawn to the narrow genetic base and vulnerability to disease of the main groups of beans bred in the U.S.A. (Adams, 1972 ; Zaumeyer, 1972) and grown in that country and elsewhere.

The dry beans in the Great Northern, Navy, Pinto and Red Mexican groups, pole beans and some bush green beans of the bush " Blue Lake " and European types are very vulnerable to damage by rust. Incorporation of non-specific resistance into such lines would greatly increase the areas in which they can be satisfactorily grown for green beans, seed beans or both.

The results of these trials and reports in the literature suggest that non-specific resistance may limit the severity of bean rust in many areas, particularly at latitudes of more than 32°. The degree of non-specific resistance shown by some lines in these trials as well as in commercial crops is adequate where conditions are sub-optimal but is inadequate where conditions are optimal for infection and development of rust. In the temperate regions at higher latitudes, beans are normally grown for only three to four months of the year, so inoculum build up is slower ; plants are grown with relatively short nights and thus short periods of dew and of high humidity.

Non-specific resistance is likely to be inadequate in some tropical areas where beans are grown for many months of the year, allowing extensive build up of inoculum. Longer nights and more frequent rains result in longer periods of dew and high humidity.

In most breeding programmes producing cultivars for the temperate regions in latitudes in excess of 32°, the level of non-specific resistance shown in some of the bush green and Red Kidney beans would be sufficient. This could be achieved by including lines which show evidence of non-specific resistance and by avoiding those known to be severely affected by rust. The progeny should be screened in an area or areas where a wide range of races is present and where there is clear separation of susceptible lines into classes differing in severity, as in the trials reported here. This would permit the elimination of severely rusted lines and the selection of slightly rusted lines which may have non-specific resistance. Such practices have produced green bean cultivars (Anon, 1964 ; 1965 ; 1967) with such resistance under eastern Australian conditions.

In other breeding programmes such as those for most tropical areas, adequate resistance may not be achieved by these procedures. The information available in the literature does not indicate which is the best approach to producing cultivars with the necessary degree of permanent resistance to rust in a range of locations. The information required may be obtained by distributing material showing resistance to a range of races of rust in particular areas to other countries for assessment of rust reaction. Such International Bean Rust Nurseries could expose material to a wider range of races and indicate material worthy of further investigation. Both genetic and pathological studies should be made under field and greenhouse conditions. Races present within the nurseries should be determined using an augmented set of differentials. It is envisaged that the results would be useful in three main areas.

1. (*a*) Lines with low coefficients of infection may be detected. The studies of Rajaram and Luig (1972) with four entries from the International Spring Wheat Rust Nursery that showed very low average coefficients of infection revealed several genes for specific resistance within each line. This supports the theory that the more genes for resistance that are present in a particular host the less likely it is to be made susceptible by variation in the pathogen (Watson, 1970).

(*b*) If no entries with low average coefficients of infection were detected lines showing specific resistance to particular races could be investigated to determine

(i) the genotype of the resistant lines by testing the progeny of crosses between resistant and susceptible lines with many races of rust ;

(ii) the genetic nature of the resistance by intercrossing between the resistant lines and testing with many races.

Results from this may indicate which genes could be combined to give lines with low average coefficients of infection.

2. The material showing non-specific resistance could be investigated using a range of races to determine the components of this resistance. While there are

many factors (Hooker, 1967) which could be studied, the greenhouse work of Fromme and Wingard (1921) on size and density of pustules and my field experience suggest the following tests are particularly relevant.

(i) Length of dew period required for infection ; lines requiring a long dew or moist period would be retained for use as parents.
(ii) Efficiency of penetration ; lines with the lowest rate of pustule development per unit spore load would be retained.
(iii) Changes in resistance as the host ages ; lines which are unable to develop full-sized pustules at an early stage of maturity relative to the seedling stage would be retained.
(iv) Length of incubation ; lines slow to develop sporing pustules would be retained.
(v) Pustule size ; lines which produced smaller pustules with a range of races would be retained.

Hybridization of the lines showing the highest levels of these components of resistance and testing of the progeny as outlined above may permit the improvement of non-specific resistance.

3. In selection of a site for a central testing station with a wide range of races and a climate optimum for rust development.

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TWO NEW PARASITIC MITES (ACARI: SARCOPTIDAE AND ATOPOMELIDAE) FROM TASMANIAN MARSUPIALS

ALEX FAIN* AND ROBERT DOMROW†

[Accepted for publication 23rd May 1973]

Synopsis

Tasmanian marsupials harbour the two mite parasites figured and described: *Diabolicoptes sarcophilus*, n. g., n. sp. (Sarcoptidae), from the Tasmanian devil, *Sarcophilus harrisii* (Boitard) (Dasyuridae), and *Petrogalochirus macropus*, n. sp. (Atopomelidae), from the red wallaby, *Macropus rufogriseus* (Desmarest) (Macropodidae). Diabolicoptinae, n. subfam., is erected for the former because it differs markedly in tibiotarsal structure from the two known sarcoptid subfamilies (Sarcoptinae and Notoedrinae).

Interesting Australian mites continue to come to hand, and this note will describe two new sarcoptiform (astigmatic) species from Tasmanian marsupials. The first was taken in association with a Tasmanian devil; it belongs to a new sarcoptid genus, which, since it presents an unusual combination of characters and does not correspond with either known sarcoptid subfamily, is placed in a new subfamily. The second is a listrophoroid from the widespread red wallaby. Relevant current papers are Fain (1968, 1972) and Fain and Domrow (1973).

Family SARCOPTIDAE Murray

Within the Acaridiae, the presence of either spines (modified setae) or sclerotized processes on the tarsi is a character useful in separating the families of mange- and skin-mites of mammals and birds. In the Sarcoptidae (and the allied Teinocoptidae), the tarsi in both sexes always bear several spines, but lack recurved processes; in the other families (*e.g.*, Psoroptidae, Knemidokoptidae and Epidermoptidae), the reverse is true, there being at least one well-developed sclerotized process on the tarsi, while spines are only exceptionally present.

The new genus described below presents aberrant characters and does not fit exactly into any of these families. Its most curious character seems to be the strong sexual dimorphism in the structure of the tarsi. In the female and immatures, the tarsi lack spines and carry only normal setae and strong, recurved sclerotized processes. In the male, all tarsi bear one or two strong spines and one to three rather weakly developed sclerotized processes.

In other characters, the new genus resembles more the family Sarcoptidae: Body rounded, with cuticle completely striate and without shields. Propodosomal shield absent. Setae v_i present. Gnathosomal base rather long, but nearly completely obscured dorsally by prolongation of body (tegmen). Chelicerae short. Legs short and conical, but normally formed, I being narrower than II. Tarsi I–II with sucker carried on long stalk, but III–IV without suckers. Tarsi III–IV of female and nymph, and III in male and larva, with three long setae. Vulva transverse, without epigynium. Male without adanal suckers.

We therefore think the new genus should be placed in a new subfamily of the family Sarcoptidae. The two subfamilies already recognized may be defined:

Subfamily Sarcoptinae Murray: Tibiae-tarsi III–IV fused in both sexes. Tarsi I–II and tibiotarsi III with two spines in both sexes. Tibiotarsus IV with two spines in female and one spine in male. Sclerotized processes on tarsi absent in both sexes. Type-genus *Sarcoptes* Latreille.

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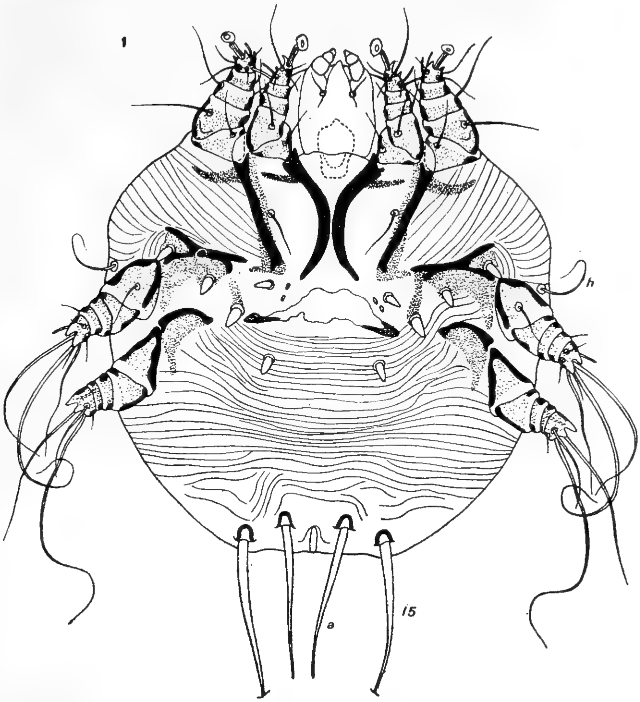


Fig. 1. *Diabolicoptes sarcophilus* female. Venter.

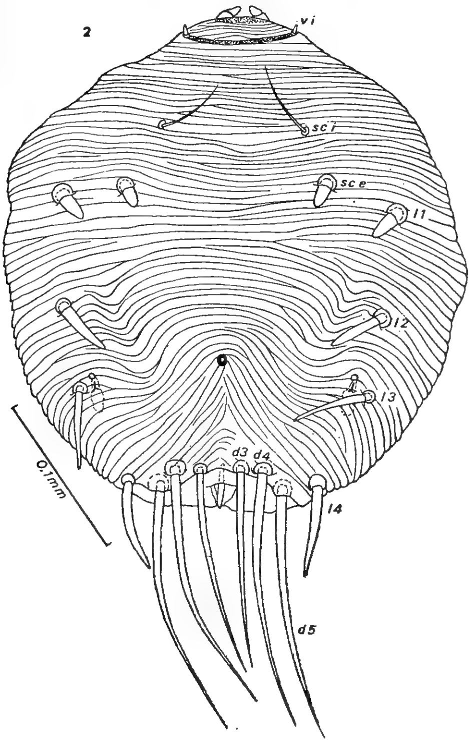


Fig. 2. *Diabolicoptes sarcophilus* female. Dorsum.

Subfamily Notoedrinae Fain: Tibiae-tarsi III–IV as in Sarcoptinae, but tarsus IV free in male. Tarsi I–II with four, and tibiotarsus III with two to five, spines in both sexes. Tibiotarsus IV with two to four spines in female. Tarsus IV with one to two spines in male. Sclerotized processes on tarsi absent in both sexes. Type-genus *Notoedres* Railliet.

The new taxon at this level is

Subfamily DIABOLICOPTINAE, n. subfam.

Definition.—All tarsi free in both sexes. Tarsi I–II with two, and III–IV with three, sclerotized processes in female and nymph, but without spines. Tarsi I–IV with one or two spines and one to three sclerotized processes in male. Type-genus *Diabolicoptes*, n. g. (masculine).

Genus DIABOLICOPTES, n. g.

Definition.—Epimera I contiguous in female, but fused in midline to form Y in male. Adults with anus ventroterminal and genital suckers vestigial. Female with bursa copulatrix opening dorsally. Male with small aedeagus situated at level of epimera III, and without adanal suckers. Adults and nymphs with following idiosomal chaetotaxy: v_i, sc_i, sc_e, h, sh, d_{3-5}, l_{1-5}, a, g_a, g_m, g_p, cx_I and cx_{III} (some of these setae are modified into strong spines; the posterior setae d_{3-5}, a, and l_5 are long to very long, maximum 165μ, and situated along the posterior border of the idiosoma). Solenidiotaxy: tarsi 2.1.0.0; tibiae 1.1.1.1; genua 1.1.0.0. Type-species *Diabolicoptes sarcophilus*, n. sp.

Diabolicoptes sarcophilus, n. sp.

(Figs 1–20)

Types.—Holotype and three paratype females, allotype and one paratype male, two paratype nymphs, and one paratype larva, all extracted from faeces of a Tasmanian devil, *Sarcophilus harrisii* (Boitard) (Marsupialia: Dasyuridae), Launceston, Tas., 17.xi.1972, J. H. Arundel. Holotype, allotype and one paratype female, nymph and larva in Australian National Insect Collection, C.S.I.R.O., Canberra; remainder in P.L.I.T.M.

These mites are probably skin parasites, and their presence in faeces would then be due to the host's biting itself. It is also possible that the mites originated from the host's food (mutton, rabbit, guinea-pig—it was held in captivity for 10 weeks).

Female.—See Figs 1–2, 5–12. Holotype 305μ long (including gnathosoma), 270μ wide. Longest setae on posterior border of idiosoma 150μ long. Gnathosomal base longer than wide, more or less parallel-sided. All tarsi with normal setae (7.7.6.5); tarsi I–II with two curved and pointed, and III–IV with three conical, sclerotized processes.

Male.—See Figs 3–4, 13–20. Allotype 276μ long, 258μ wide. Gnathosomal base trapezoidal, wider anteriorly. Tarsus I with five simple setae, one strong, recurved spine apically, and two sclerotized processes. Tarsi II–III with four simple setae, two strong spines, and one (tarsus II) or three (tarsus III) sclerotized processes. Tarsus IV with three simple setae, one strong spine, and three sclerotized processes.

Nymph.—Length 310μ, width 270μ. Closely resembling adult female, but vulva absent.

Larva.—Length 234μ, width 210μ. Idiosomal chaetotaxy as in adult, but d_{3-5}, l_4, a, and genital setae absent. Tarsi I–III with 7.7.6 simple setae and 2.1.3 sclerotized processes.

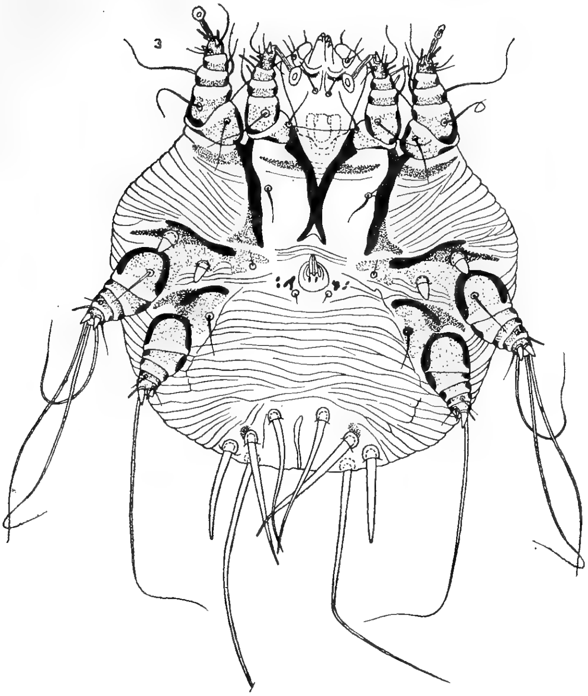


Fig. 3. *Diabolicoptes sarcophilus* male. Venter.

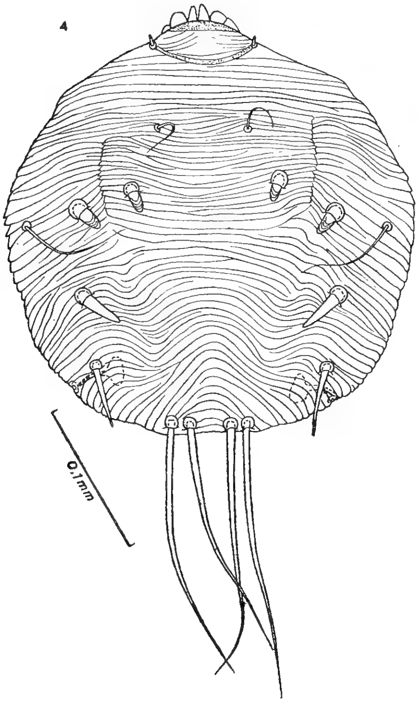


Fig. 4. *Diabolicoptes sarcophilus* male. Dorsum.

Family Atopomelidae Gunther
Genus Petrogalochirus Fain

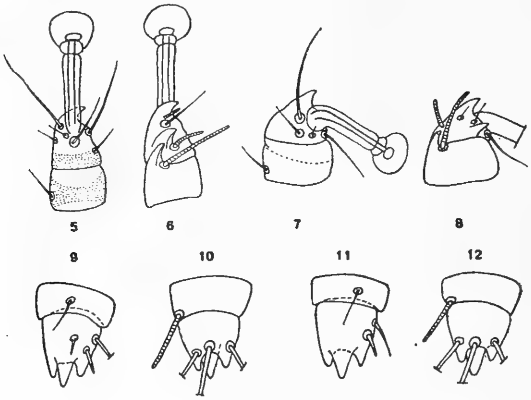
Petrogalochirus Fain, 1970, *Bull. Annls Soc. r. ent. Belg.*, 106 : 278. Type-species *P. tasmaniensis* Fain, 1970, *ibid.*

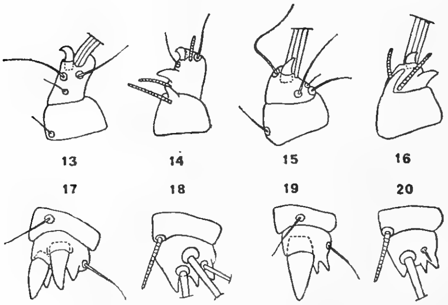
The genus *Petrogalochirus* to date contains two parasites of Australian marsupials : *P. tasmaniensis* was described from the brush-tailed rock-wallaby, *Petrogale penicillata* (Griffith) (Macropodidae), in Tasmania, while *P. dycei* (Domrow, 1960) was taken on the brush-tailed possum, *Trichosurus vulpecula* (Kerr) (Phalangeridae), in the Australian Capital Territory.

The new species described below is immediately distinguishable from the known species by showing, in the female, a well developed, sclerotized shield on the posterior part of the dorsum. This shield is completely lacking in the other two species.

Petrogalochirus macropus, n. sp.
(Figs 21–22)

Types.—Holotype and one paratype female, and one paratype tritonymph from the red wallaby, *Macropus rufogriseus* (Desmarest) (Marsupialia : Macropodidae), Nile, Tas., vii.1972, B. L. Munday. Holotype and paratype tritonymph in A.N.I.C. ; paratype female in P.L.I.T.M.





Figs 5–12. *Diabolicoptes sarcophilus* female. Ventral (or ventrolateral) and dorsal (or dosolateral) views of tibiae-tarsi I–IV.

Figs 13–20. *Diabolicoptes sarcophilus* male. Ventral (or ventrolateral) and dorsal (or dorsolateral) views of tibiae-tarsi I–IV.

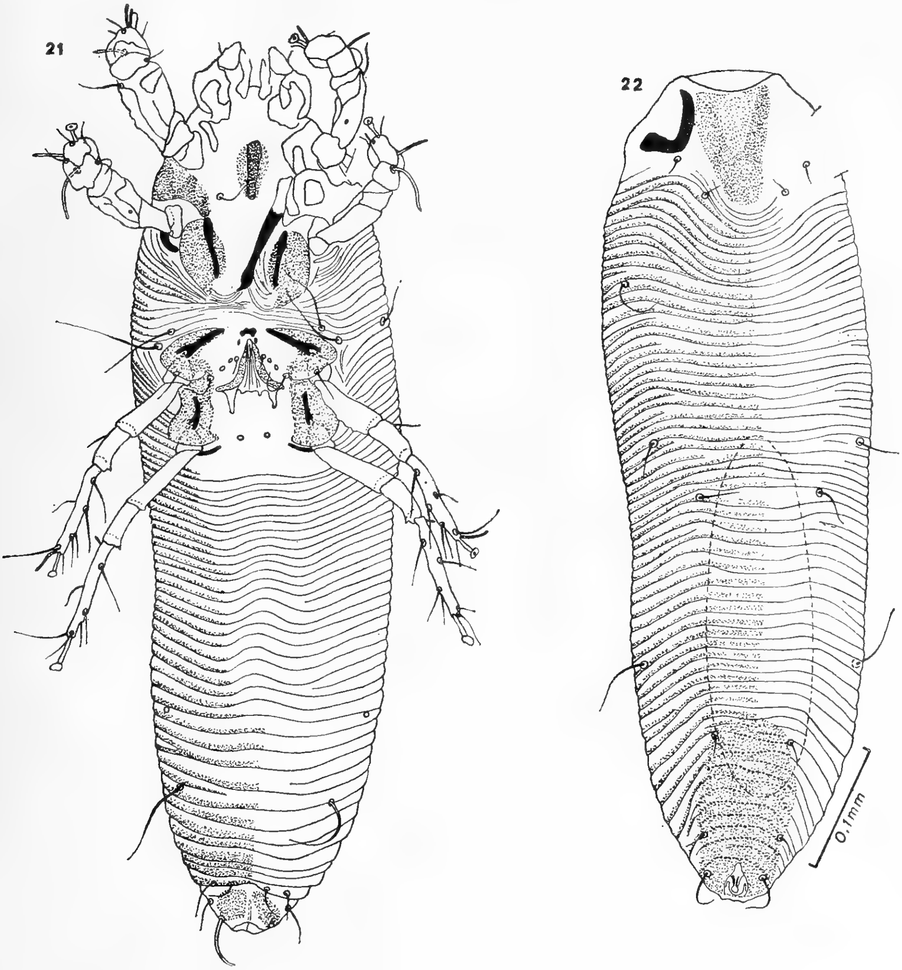
Female.—See Figs 21–22. Holotype 630μ long (including gnathosoma), 188μ maximum width. Propodosomal (prescapular) shield longer than wide; postscapular shield absent. Cuticle behind shield regularly striate and soft, except on posterior part of dorsum, which is covered by strongly sclerotized and striate shield 130μ long and 72μ wide. Holotype contains elongate egg (255μ × 75μ); bursa copulatrix only partially visible. Paratype non-ovigerous, bursa very long, with basal extremity situated at level of coxa III. Genital papilla situated dorsally in posterior part of opisthosomal shield. Venter of opisthosoma striate. All legs with pedunculate sucker. Posterior legs very thin, with elongate femora and tibiotarsi.

Male.—Unknown.

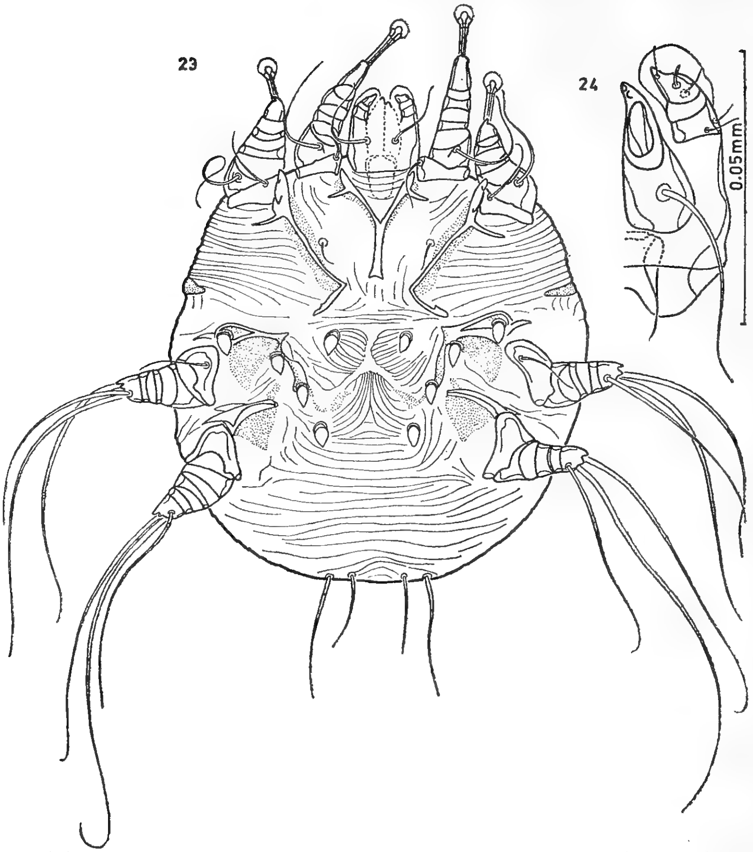
Tritonymph.—Length 585μ. Very similar to female, but vulva and opisthosomal shield absent.

Larva.—Unknown.

Nomenclature.—As generic names are nouns by definition, see Art. 11 (f), both specific names proposed in this paper are also nouns. They stand in apposition to the generic names, and refer less to any morphological or ecological peculiarity than to the hosts involved.



Figs 21–22. *Petrogalochirus macropus* female. Venter and dorsum.



Figs 23–24. *Diabolicoptes phascogale* female. Venter, with details of gnathosoma in ventral view.

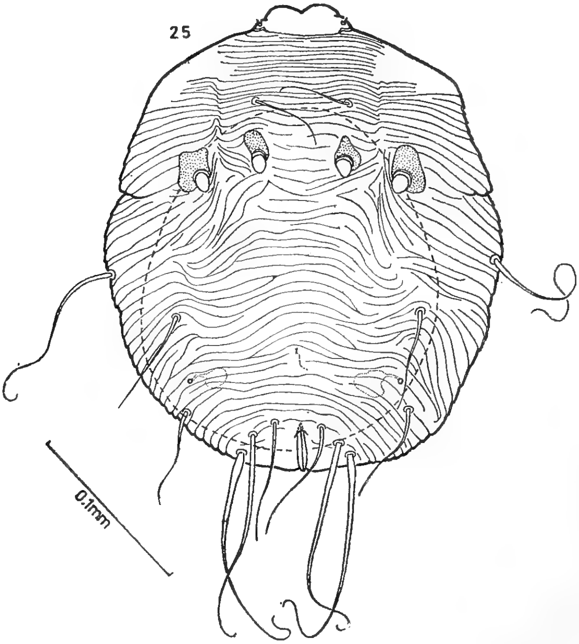
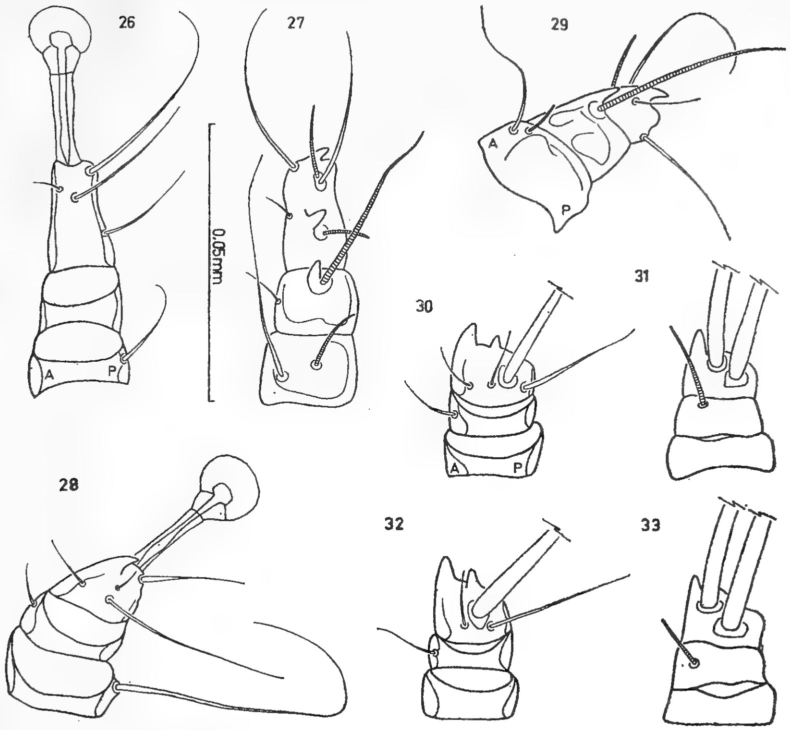


Fig. 25. *Diabolicoptes phascogale* female. Dorsum.



Figs 26–33. *Diabolicoptes phascogale* female. Ventral and dorsal views of genua-tarsi I–IV (II somewhat foreshortened).

ACKNOWLEDGEMENTS

Printing of the illustrations was subsidized by the World Health Organization, Geneva, as part of its support of the W.H.O. Regional Reference Centre for Arboviruses at this Institute.

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ADDENDUM

Diabolicoptes phascogale, n. sp.
(Figs 23–33)

Diagnosis.—*D. phascogale* is separable from *D. sarcophilus* on several counts : (i) *idiosomal seta* l_4 *absent*, and only sc_e and l_1 hypertrophied (these latter set on distinct shieldlets) ; (ii) *epimera I fused to form perfect Y* ; (iii) epimera II each with two retrorse hooklets ; and (iv) tarsus I decidedly longer than II–IV.

Types.—Holotype female and one paratype female from tuan, *Phascogale tapoatafa* (Meyer) (Dasyuridae), Christmas Hills, near Melbourne, Vic., viii.1973, T. Ealey. Holotype in A.N.I.C. ; paratype in Q.I.M.R.

Female.—See Figs 23–33. Idosoma (including gnathosoma and undifferentiated ovum) 285μ long, 225μ wide. Most dorsal setae slenderly tapering, to 145μ long. *Genital suckers not detected.* Opening of bursa copulatrix a minute slit. *Anus dorsoterminal.* Gnathosoma sarcoptid. Chaetotaxy, solenidiotaxy, and processes on legs typical.

Notes.—The specific name is formed according to the paragraph on nomenclature in the text proper.

The characters italicized necessitate minor modification to the generic definition.

ON SOME FRUCTIFICATIONS OF THE GLOSSOPTERIDALES FROM THE UPPER PERMIAN OF N.S.W.

W. B. K. HOLMES*

[Accepted for publication 23rd May 1973]

(Plates VI-VIII)

Synopsis

Fructifications referable to the Glossopteridales are described from the Upper Permian of New South Wales. They include *Austroglossa walkomii* gen. et sp. nov., a female gymnospermous fructification attached to a *Glossopteris conspicua* Feist. leaf; male fructifications, *Eretmonia cooyalensis* sp. nov., *Isodictyopteridium costatum* sp. nov. and *Dictyopteridium sporiferum* Feist. ex Zeiller. An unusual leaf type is noted.

INTRODUCTION

The material to be described was mostly collected by the author from a small quarry at Kane's Flat, near Cooyal, 29 km north-east of Mudgee, New South Wales, at latitude 32° 28′ S, longitude 149° 51′ E.

The slabs of shale covered with impressions of fossil leaves have been used to a limited extent as ornamental stone for interior decoration in new buildings.

The fossil bed is approximately 2 m thick. A coarse sandstone at the base of the bed contains impressions of many plant stems up to 25 cm in diameter. Above the plant stems is a hard blue-grey siltstone with few fossils. This grades up to a fine grey laminated shale which is packed with countless leaves of a number of *Glossopteris* form species. *Glossopteris conspicua* Feist. and *G. damudica* Feist. are the most common types with lesser numbers of *G. communis* Feist., *G. browniana* Brongn., *G.* (?) *mitchelli* Walkom, *G. angustifolia* Brongn. and other indeterminate glossopterid and gangamopteroid forms being present. Plants belonging to other classes are very rare. Species noted are *Phyllotheca australis* Brongn., *Stellotheca robusta* (Feist.) Surange and Prakesh, *Noeggerathiopsis* sp., *Sphenopteris lobifolia* Morris and *Sphenopteris polymorpha* Feist., including fertile fronds of the last-named species. Two thin coal seams overlie this bed.

GEOLOGICAL HORIZON

The above locality is in the Illawarra Coal Measures at the north-western edge of the Western Coalfield. The Permian and Triassic sediments in this area are almost horizontal and are unconformable with the Lower Palaeozoic basement (Dulhunty and Packham, 1962). An outcrop of the basement rocks occurs on the road leading to the quarry at approximately 45 m below the level of the quarry. The basal conglomerates of the Triassic Narrabeen Series cap the hill 55 m above the quarry. This places the locality just below the middle of the Permian sequence of the area.

Dulhunty (in Packham, 1969, p. 387) states that the coal measures in this area are regarded as equivalent to at least the upper sections of the Newcastle Coal Measures, which are Upper Permian.

The flora from this horizon can be correlated with the flora of the Baralaba Coal Measures and Blackwater Group of the Bowen Basin of Queensland (Rigby, 1972*b*), and the Raniganj Stage of the Damuda Division of Bihar, India.

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* Hampden Hall, Kempsey, N.S.W.

SYSTEMATIC BOTANY

Division. Spermatophyta. Sub-division. Gymnospermae.
Class. Pteridospermae. Order. Glossopteridales.

Genus AUSTROGLOSSA gen. nov.

Diagnosis

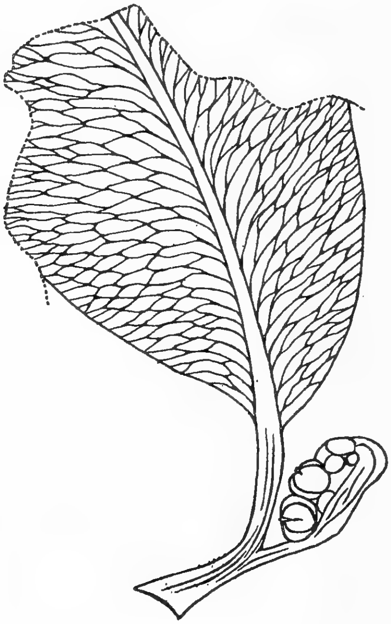
A female fructification of a cluster of platyspermic seeds on a pedicel adnately attached to the petiole of a *Glossopteris* leaf.

Type species *Austroglossa walkomii* sp. nov.

Text-fig. 1; Plate VI, fig. 1; Plate VII, figs 2, 3

Diagnosis

A female fructification of platyspermic seeds of the *Cordaicarpus* type; borne in a cluster on a pedicel adnately attached to the petiole of a leaf resembling in external form and venation *Glossopteris conspicua* Feist. Seeds not encased in a cupule or otherwise covered.



Text-fig. 1. *Austroglossa walkomii* gen. et sp. nov. Holotype. Specimen F55027. Natural size.

Description

Leaf type. The fertile leaves are variable in size and shape and are similar to sterile leaves with the same venation. The leaves are simple, petiolate, broad-ovate to narrow elliptic with obtuse or broadly acute apex. Length ranges from 7 cm to 15 cm and the width from 2 cm to 5 cm. The petiole is 1·5 cm to 2 cm in length and 2 mm to 3 mm in width and is usually marked with conspicuous parallel striations which continue through the length of the midrib. The leaf-base broadens to approximately 6 mm where it has abscissed from the main stem. The secondary veins emerge from the midrib at an angle of 20° to 30° and reach the margin at an angle of 45° to 80°. In specimens with very coarse mesh the secondary veins are not persistent from the midrib to the margin but branch and fuse with adjacent veins to form open meshes which decrease in length towards the margin. The number of secondary veins at the margin varies from 8 to 20 per 10 mm and is usually double the number leaving the midrib.

Female fructification. The fructification is a cluster of platyspermic seeds of the *Cordaicarpus* type borne on a pedicel. The pedicel is from 2 mm to 10 mm in length and approximately 1 mm in width ; adnately attached to the petiole midway between the leaf base and the lamina. In some specimens the pedicel is conjoined to the petiole so that the cluster of seeds appears to be attached to the base of the midrib. This is probably due to the pedicel being at right angles to the plane of the lamina at time of fossilization.

As many as 20 seeds are present in immature clusters, but on the majority of mature clusters only 6 to 10 seeds remain. The numerous single seeds found at this locality are very constant in size and shape, thus indicating that the seeds only became detached on reaching maturity.

The cluster is not enclosed in a cupule and the seeds have no covering or protective scales.

Seeds. The mature seeds are preserved as flattened discs 4 mm in diameter. A sarcotesta or wing 1 mm in width surrounds the nucellus except at the apex and base. A narrow acute projection 1 mm or more in length enters the apex of the nucellus as a result of sediment having entered the micropyle. On some seeds this projection continues as a fine ridge to the base.

The seeds are attached directly to a spindle-shaped receptacle, and on some specimens there is a suggestion of a spiral arrangement. Detached seeds bear a small scar at the emarginate base.

Occasional seeds have some carbonaceous material remaining in the nucellus, but maceration with nitric acid and potassium chlorate followed by an alkali has failed to reveal any details of structure or enclosed pollen grains.

Holotype. Specimen F55027. The Australian Museum, Sydney.
Paratypes. F51835 (collected by E. McCarthy) and F55029.
Locality. Kane's Flat, Cooyal, New South Wales.
Horizon. Illawarra Coal Measures, Upper Permian.

A Male Fructification

Specimen F55028 in the Australian Museum Fossil Collection has impressions of two *Glossopteris conspicua* Feist. type leaves with attached male fructifications. The leaf illustrated in Plate VII, fig. 6, has a cluster of sporangia borne on a pedicel attached to the petiole in a similar manner to the female fructification *Austroglossa walkomii*. The cluster of sporangia is oval, approximately 15 mm long and 8 mm wide. Numerous elliptical sacs 2 mm ×1 mm are attached to the axis at an angle of approximately 45°. Unfortunately no organic material is preserved to verify the male nature of this organ. However, I believe it will prove to be the male counterpart of *Austroglossa walkomii.*

Comparisons

Plumstead (1958*a*) described the female fructification *Pluma longicaulus* Plumstead as " looking like a bunch of rounded objects each 4 mm in size, lying slightly below the level of a dark oval patch 3 cm ×2 cm. The whole surface of this patch—round objects as well as intervening spaces—is covered by dark strengthening tissue, suggesting that the rounded seeds (?) were encased or covered. There is no sign of the axis on which they grew." The male fructification of *Pluma longicaulis* Plumstead and of a detached species, *P. thompsonii* Plumstead, have long arched axes from which hang a fringe of objects reminiscent of pollen sacs.

The *Cordaicarpus* type seeds of *Austroglossa walkomii* form a cluster on a spindle-shaped receptacle. At no stage of development of the seeds is there any indication that the cluster or individual seeds had any protective covering. The details of the male fructification attached to similar leaves to those of *A. walkomii* are not well enough known, but the compact oval cluster of sporangial sacs is in contrast to the feather-like appearance of the *Pluma* spp. It is possible that a relationship of family rank exists between the two genera, *Austroglossa* and *Pluma*, but proof of this must await discovery of better preserved specimens of both genera.

Rigby (1972*a*, p. 113) likens a specimen of *Arberia minasica* White to the male of *Pluma longicaulis* Plumstead, but I consider a relationship between these two fructifications to be extremely remote.

The form genus *Cordaicarpus* was proposed by Geinitz for platyspermic seeds, ovate or ovate-cordate in shape, with a cordate or round base and a narrow wing. The name, with its inference of Cordaitean relationship, is misleading. The choice between *Samaropsis* Goeppert and *Cordaicarpus* Geinitz depends only on the breadth of the wing (Seward, 1917, p. 354).

Many species of detached seeds have been described from the Upper Palaeozoic rocks of Gondwanaland (Walkom, 1921, 1928, 1935; Pant, 1958; Pant and Nautiyal, 1960; Maithy, 1964). Many of these have been associated with *Glossopteris* leaves, but none resembles the present seeds. A seed described by Arber (1902, p. 20) as *Cardiocarpus* sp. is similar in shape but much larger than the seeds of *Austroglossa walkomii.*

Discussion

Surange and Shrivastava (1957, pp. 47–49) drew attention to fructifications having been described as borne on certain species of *Glossopteris.* They pointed out the need to establish the true identity of the leaf on the basis of cuticular study, otherwise, as Shrivastava's work has shown (Shrivastava, 1957), the identification of a fructification-bearing leaf, based on external features alone, may be wrong to start with and consequently lead to wrong conclusions regarding the definition of the plant represented by these organs.

In shape and venation, the coarse-meshed form of the holotype of *Austroglossa walkomii* agrees with the illustrations of leaves of *Glossopteris conspicua* Feist. in Feistmantel (1881, Pl. 28A); Walkom (1928, text fig. 7); White (1966, Pl. B, fig. 2, and Pl. C, fig. 1); and Rigby (1972*b*, text fig. E and Pl. 1, fig. 6). Specimens referred to *Glossopteris conspicua* Feist. figured by Arber (1905*b*) and Du Toit (1927) appear to be different. The narrower leaf and finer venation of the paratype shown in Plate VII, fig. 3, resembles a leaf of *Glossopteris browniana* Brongn. figured by Arber (1905*b*, Pl. III, fig. 1).

Shrivastava's studies of cuticles (Shrivastava, 1957) demonstrate clearly the artificiality of the *Glossopteris* genus where species have been described with only their macro-characteristics being known. Shrivastava (1957, pp. 12–13) states "... a comparison of the fronds of *Glossopteris conspicua* Feist. and *Glossopteris formosa* Feist. shows that they differ externally only in their size, otherwise the form and venation is similar in both species ... the differences between their cuticles are not only sufficient to separate them specifically but also to warrant their inclusion in separate groups, perhaps of generic rank."

A leaf figured by Shrivastava (1957, Pl. I, fig. 3) was found to have an identical cuticle to specimens of *Glossopteris browniana* Brongn., yet on external characteristics Shrivastava suspected that it belonged to a different species. The external form of that particular leaf is very similar to some of the leaves to which the present fructifications are attached.

The possibilities are that *Austroglossa walkomii* could belong to *Glossopteris conspicua* Feist., *G. formosa* Feist. or *G. browniana* Brongn., and the correct identity of the leaf cannot be established until its cuticle is known.

Dr. E. P. Plumstead has examined the photographs illustrating this paper and has identified the leaf of the holotype as *Glossopteris conspicua* Feist. and suggested that the specific epithet *conspicua* should be used for this fructification. Dr. Plumstead thought the illustrated paratype (Plate VII, fig. 3) may be a different fructification and that the leaf might be *Glossopteris browniana* Brongn. However, at the Cooyal locality I have collected a series of leaves (some with fructifications attached) which grade from one form to the other. The difference in appearance of the seeds of this paratype is due to their immaturity. At this stage of development the seeds are more spherical in shape and are preserved in all orientations, whereas the mature seeds are always preserved in the one plane due to the seeds being flatter and the wing more developed. Seeds of both types are to be seen on the paratype specimen F51835. On one bedding plane there are numerous detached clusters of immature seeds, probably the result of storm damage.

Leaves identified on their macro-characteristics as *Glossopteris conspicua* Feist. have been recorded in South Africa from the Middle Ecca Beds at Vereeniging in Transvaal (Plumstead, 1952, 1958*a*), from the Upper Karoo Beds (Du Toit, 1927), and from the Orange River Colony (Arber, 1905). The bisexual fructification, *Scutum draperium* Plumstead, which is attached to the Vereeniging leaves, must be placed in a different family from the genus *Austroglossa*.

To avoid possible confusion at a later date when details of the cuticle of *Austroglossa walkomii* become known, I have not chosen a specific name alluding to a leaf type, but have named the fructification for Dr. A. B. Walkom, who was one of the first palaeobotanists to recognize that *Glossopteris* leaves belonged to seed plants.

Genus ERETMONIA Du Toit, 1932

Type species. *Eretmonia natalensis* Du Toit, 1932.

Generic diagnosis. As amended by Surange and Maheshwari (1970). Male fructifications, fertile leaves stalked, lamina thick, expanded, of various shapes, orbicular or roundly triangular, apex acute or rounded, lamina surface showing faint to distinct dichotomizing veins ; two sporangial clusters, one on either side of leaf stalk.

Eretmonia cooyalensis sp nov.

Text-fig. 2 ; Plate VIII, figs 8, 9

Diagnosis

Male fructification ; fertile leaf stalked, lamina linear, venation dichotomous. Sporangia borne in two clusters, one on either side of leaf stalk. Each cluster comprised of approximately 12 sporangia arranged in a single whorl.

Description

Leaf lamina linear, 17 mm long × 3 mm wide ; texture thin ; no midrib. Three veins enter the leaf lamina from faint striations on the petiole. The veins fork once or twice and continue more or less parallel to each other to the leaf apex. No cross connections can be seen. Petiole 13 mm in length, tapering in width from 1·5 mm at the leaf base to 1 mm at the base of the lamina. Two distinct ridges run from near the base of the petiole to just below the lamina, where they diverge to become pedicels to which are attached the terminal clusters of sporangia. Pedicels 4 mm long × 0·25 mm wide. Approximately 12 sporangia arranged radially or spherically in a single cluster on each pedicel. Sporangia oval, 2·5 mm × 1·5 mm, pointed at each end and marked with faint longitudinal striations.

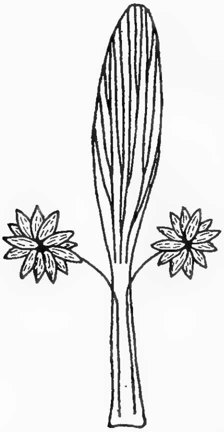
Holotype. Specimen F55031. The Australian Museum, Sydney, N.S.W.
Locality. Kane's Flat, Cooyal, N.S.W.
Horizon. Illawarra Coal Measures, Upper Permian.

Comparisons

Eretmonia natalensis Du Toit is a stalked leaf with a spathulate lamina. The distal end of the lamina was described as having a spoon-like depression in which Du Toit thought the sporangia may have been attached. His figured specimens (Du Toit, 1932, figs 10 and 11) show the sporangia disarranged at the side of the lamina. Surange and Maheshwari (1970) thought the spoon-like depressions were due to an act of preservation and they amended the generic diagnosis of *Eretmonia* Du Toit to contain a number of modified fertile leaves from the Raniganj Stage of India. No spoon-like depression is present on the Indian specimens or on the lamina of *Eretmonia cooyalensis.*

E. cooyalensis differs from the three species from India described by Surange and Maheshwari (*E. utkalensis*, *E. hinjradaensis* and *E. karanpurensis*) in having the sporangia in a single whorl to form the cluster on each pedicel. The sporangia on the three Indian species are arranged in several whorls in each cluster. They also differ in the shapes of their laminae.

Glossotheca utkalensis Surange and Maheshwari, a fertile leaf with several clusters of sporangia on a single pedicel, has a linear lamina similar to the lamina of *Eretmonia cooyalensis.*



Text-fig. 2. *Eretmonia cooyalensis* sp. nov. Reconstruction of holotype. Specimen F55031. ×2.

Discussion

Eretmonia cooyalensis is described from only one specimen and its counterpart. It is preserved as an impression and is complete except for the top left portion of the lamina. The cluster of sporangia on the right-hand pedicel is disarranged.

This new species is placed provisionally in the genus *Eretmonia* Du Toit. It certainly belongs to the same genus as the three species from India. I suspect that Du Toit's specimens were similar to the fertile male scale leaves of *Glossopteris angustifolia* Brongn. described as *Lidgettonia australis* White (White, 1963, p. 392; Pl. XXII, fig. 1). A revision of this group of fructifications is desirable.

Detached sporangia associated with the *Glossopteris* flora were first recorded by Arber (1905*a*), who believed they were attached to scale leaves. Walkom (1928, Pl. XXXVI, fig. 4) illustrated a group of detached clusters of sporangia. Du Toit (1932) showed groups of sporangia in close association with a modified leaf. Sen (1955) found that similar sporangial sacs contained pollen grains of the *Pityosporites* type. Surange and Maheshwari (1970) described three new species of *Eretmonia* and a new genus *Glossotheca* which demonstrated how these sporangia were attached to modified leaves. This type of sporangium belongs to the form genus *Arberiella* Pant and Nautiyal (1960). Because of their constant association with *Glossopteris* leaves, the *Eretmonia* and *Glossotheca* genera are placed in the Glossopteridales.

Detached sporangia and groups of sporangia occur sparingly at this locality. They resemble the sporangia attached to *Eretmonia cooyalensis* sp. nov. A detached intact cluster is illustrated in Plate VIII, fig. 10.

Genus DICTYOPTERIDIUM Feist. ex Zeiller, 1902

Type species. *Dictyopteridium sporiferum* Fiest. ex Zeiller, 1902.

Dictyopteridium sporiferum Feist. ex Zeiller

(Plate VIII, fig. 14)

Three impressions of detached pitted laminae from the Cooyal locality are referred to this form species.

Description

Male fructifications ; laminae elliptical, 35 mm to 60 mm in length, 10 mm to 15 mm in width; apex obtuse to broad-acute. The figured specimen, Plate VIII, fig. 14, has a short broad pedicel 2 mm long × 3 mm wide, but this feature is not present on the other two specimens. No visible venation. Oval pits 1 mm × 0·5 mm scattered irregularly over whole surface of lamina. Number of pits approximately 24 per 5 mm square. In those specimens where counterparts have been found, the surface of the counterpart is tuberculate instead of pitted.

Comparisons

Zeiller (1902, Pl. IV, fig. 8) shows a specimen from the South Rewah Basin which has the same arrangement of pits but is more elongated than the Cooyal specimens.

Feistmantel (1881) figured several specimens of this species from the Raniganj and Barakar Groups, some of which are said to have a reticulate venation and some have tubercles of a larger size along the margins. His specimen on Plate XXIIIA, fig. 14, is closest to the present material.

The outer covering of the fructification *Plumsteadia microsacca* Rigby as shown on the holotype of that species (Rigby, 1971, fig. 2*a*) appears to be a similar type of organ to the present specimens. White (1963, p. 395) suggested that *Dictyopteridium sporiferum* may represent the male half of this fructification, which is borne on leaves referred to *Glossopteris communis* Feist. This type of leaf is present in very limited numbers at the Cooyal locality.

Discussion

Rigby (1972*b*) gave a summary of all known specimens described as " *Dictyopteridium sporiferum* ". Several different species seem to have been included under this name. The exact nature of these organs is not known due to the rarity of specimens and their poor state of preservation. I believe that they are the sporangiate organ of one type of plant bearing *Glossopteris* leaves, and I agree with Plumstead (1958*a*, p. 71) and White (1966, p. 51) that they should be included in the Glossopteridales.

Genus ISODICTYOPTERIDIUM Rigby, 1972*b*

Type species. *Isodictyopteridium walkomi* Rigby, 1972*b*.

Generic diagnosis

Linear lanceolate organ bearing numerous irregularly arranged, widely spaced, circular tubercles, superimposed on a fine longitudinal, occasional anastomosing venation that arches towards the margin and passes without interruption into the scalloped margin that surrounds the broadly pedicellate organ. Affinities unknown.

Isodictyopteridium costatum sp. nov.
(Plate VIII, figs 11, 12, 13)

Diagnosis

Organ of *Isodictyopteridium* type and having a prominent midrib from the base to the apex of the lamina.

Description

Male fructification (?); single detached oblong-linear lamina or several laminae radiating from a common point. Length 33 mm to 45 mm, width 8 mm to 10 mm. Midrib prominent, 1 mm or more in width, tapering slightly from base to apex. No visible venation. A smooth or undulate marginal thickening or wing surrounds the lamina. Circular or oval pits approximately 0·5 mm across are scattered irregularly over surface of midrib and adjacent areas but not on the marginal wing. From 10 to 20 pits occur in an area of 5 mm square.

Holotype. Specimen F55033. The Australian Museum, Sydney, N.S.W.
Paratype. Specimen F55034.
Locality. Kane's Flat, Cooyal, N.S.W.
Horizon. Illawarra Coal Measures, Upper Permian.

Comparisons

Neither *Isodictyopteridium walkomii* Rigby nor any of the specimens referred to *Dictyopteridium sporiferum* Feist. ex Zeiller possess a midrib. Except for this feature, *Isodictyopteridium costatum* may be compared with *I. walkomii* Rigby and the following specimens of *Dictyopteridium sporiferum* which have a marginal wing or border bare of pits or tubercles: White (1963, Pl. XXIV, fig. 12), Maheshwari (1965, Pl. 1, fig. 12) and White (1966, Pl. D, fig. 1). Another specimen figured by White (1966, Pl. D, fig. 2) has a bare margin, but the pits appear to be more closely spaced.

Discussion

No venation is visible on either the holotype or the paratype specimens, but this is probably due to the nature of the preservation. The two halves of these fossils are negative images of each other, *i.e.* one part shows pits, the counterpart shows corresponding tubercles. The illustration of the holotype shows the pitted face, and that of the paratype is of the tuberculate side.

Although the actual point of attachment of the three laminae on the paratype is missing, it is highly unlikely that this radial arrangement is accidental. Specimens arranged in this manner could not possibly represent the male half of a *Cistella*-type fructification as suggested by White (1963, p. 395).

In view of the rarity of these fructifications, it is noteworthy that two of the comparable specimens quoted above (Maheshwari, 1965; Rigby, 1972*b*) show two laminae in close proximity on the one slab.

I believe that these are male fructifications, probably belonging to a *Glossopteris*-type plant, and are modified leaves arranged in a similar manner to the clusters of sterile leaves of *Glossopteris* as described by Etheridge Jnr (1894) and Plumstead (1958*b*).

Genus GLOSSOPTERIS Brongn., 1822

Type species. *Glossopteris browniana* Brongn., in part, 1822.

Glossopteris sp.

(Plate VII, fig. 7)

A number of specimens of an unusual form of *Glossopteris* leaf have been collected at the Cooyal locality.

Description

Leaves simple, variable in size, 4 cm to 8 cm in length, 2 cm to 3 cm in width. Lamina lobed at the base, occasionally without lobes when lamina is shortly decurrent on petiole. Leaf margin irregular, slightly scalloped and undulate, rarely entire. Petiole 10 mm to 15 mm in length, 4 mm to 8 mm in width; continuing into the leaf as a very broad midrib which tapers to the apex. Secondary veins in lower part of leaf leave the midrib at 70°–90° continuing in a straight or slightly arched course to the margin. At the base of the lamina the veins tend to recurve into the lobes; in the upper part of the leaf the veins leave the midrib at an increasingly acute angle. Secondary veins 15 to 20 per 10 mm form long and narrow parallel meshes. The whole surface of the petiole and the lower part of the midrib is covered with small rounded pits 0·2 mm to 0·5 mm in diameter.

Discussion

The leaves are variable in size and shape but the venation and pitting on the stout petiole and lower part of the midrib are constant features. The venation is similar to that of *Glossopteris ampla* Dana.

The pitting on the petiole and midrib may be the result of collapse of tissues during preservation. A remote possibility is that these were fertile leaves and the pits contained sporangia or pollen sacs. Dr. R. E. Gould has suggested that these leaves may have commenced growth as fertile organs, but due to a metabolic upset they failed to become fertile and resulted in this aberrant form.

At fossil localities where large numbers of *Glossopteris* leaves are preserved, an occasional leaf of most species may be found with the lamina having an acutely lobed base. The lobing appears to be the result of the decurrent portion of the lamina tearing away from the lower part of the midrib at some stage during the growth of the leaf.

Glossopteris cordata Dana and a species from the Illawarra Coal Measures, *G. nephroedicus* Etheridge Jnr, have auriculate lower portions of their laminae. Du Toit (1932) listed *G. nephroedicus* as a synonym of *G. cordata*. He illustrated four specimens of *G. cordata* Dana. The venation is very open and coarse and is stated to be like *G. ampla* Dana or even *G. retifera* Feist. However, leaves which are referred to *G. ampla* Dana have fine elongated parallel meshes (see Walkom, 1922, Pl. 3, fig. 17; Rigby, 1966, Pl. 34, figs 41, 42).

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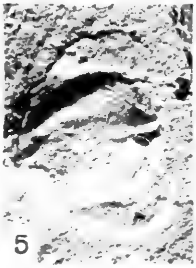

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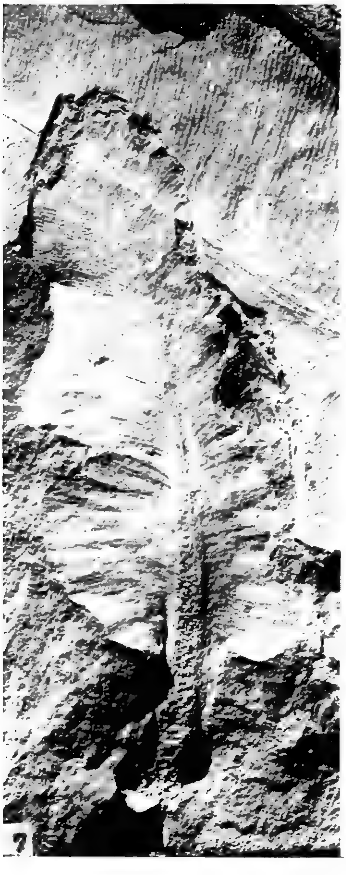

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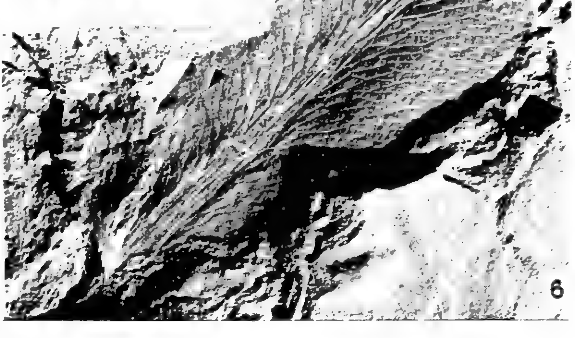

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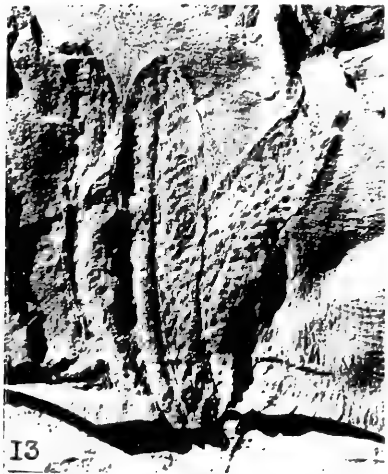
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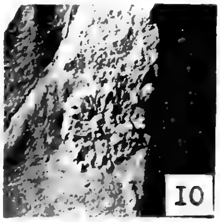
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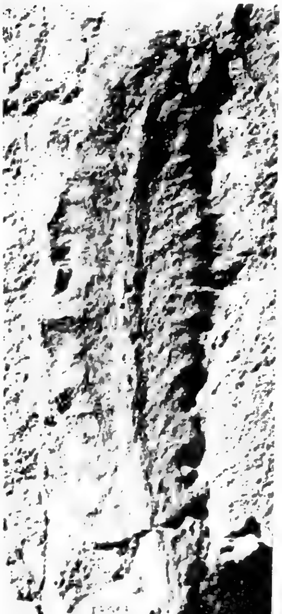
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EXPLANATION OF PLATES

All illustrations are approximately natural size except where otherwise stated. The numbers shown are the registered numbers of the specimens in the Fossil Collection of the Australian Museum, Sydney, N.S.W.

PLATE VI

Fig. 1. *Austroglossa walkomii* gen. et sp. nov. Holotype. F55027. ×2.

PLATE VII

Fig. 2. *Austroglossa walkomii* gen. et sp. nov. Holotype. F55027.

Fig. 3. *Austroglossa walkomii* gen. et sp. nov. A leaf with an attached cluster of immature seeds. Paratype. F55029.

Fig. 4. A detached mature seed of *A. walkomii*. F55030A. ×4.

Fig. 5. A detached mature seed of *A. walkomii*. F55030B. ×4.

Fig. 6. A cluster of sporangia attached to a *Glossopteris conspicua* Feist. type leaf. F55028. ×1·25.

Fig. 7. *Glossopteris* sp. An unusual leaf.

PLATE VIII

Fig. 8. *Eretmonia cooyalensis* sp. nov. Holotype. F55031. ×3.

Fig. 9. *Eretmonia cooyalensis* sp. nov. Holotype. F55031.

Fig. 10. A detached cluster of sporangia. F55032.

Fig. 11. *Isodictyopteridium costatum* sp. nov. Holotype. F55033. ×3.

Fig. 12. *Isodictyopteridium costatum* sp. nov. Holotype. F55033.

Fig. 13. *Isodictyopteridium costatum* sp. nov. Three fertile laminae radiating from a common point. Paratype. F55034.

Fig. 14. *Dictyopteridium sporiferum* Feist. ex Zeiller. Six detached seeds of *Austroglossa walkomii* gen. et sp. nov. are scattered in the top right quarter. F55035.

THE DEVELOPMENT AND ADULT STRUCTURE OF THE VERTEBRAL COLUMN IN *LEIOPELMA* (AMPHIBIA: ANURA)

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[Accepted for publication 20th June 1973]

(Plates IX-XII)

Synopsis

The development of the vertebral column in an anuran with notochordal amphicoelous vertebrae, namely the rare, endemic New Zealand frog, *Leiopelma*, is described for the first time, and a detailed description is given of its internal morphology in adult stages. Long-standing claims that the persistent notochord and the absence of ball-and-socket joints in the vertebral column are primitive character-states in the Anura are upheld, contrary to a recent claim (Inger, 1967) that the ectochordal state of the vertebrae of *Leiopelma* has evolved secondarily as a result of neoteny from the holochordal condition found in most other frogs. All the so-called transverse processes of the vertebrae are pleurapophyses because discrete ribs are present during developmental stages, and the forked ribs of the third or fourth vertebrae enclose the anterior lymph hearts. The urostyle of *L. archeyi* develops from the first four pairs of postsacral neurapophyses and the ventral region of the perichordal tube of the first five postsacral vertebrae which undergoes squamous cell hyperplasia and subsequent metaplasia into hyaline cartilage to form the hypochord. Factors contributing to the evolution of the short presacral column and long pelvic girdle in anurans are also discussed.

Although it has been customary to place *Leiopelma* and the North American genus *Ascaphus* in the same family, differences in their vertebral morphology as well as a number of other characters strongly support Kuhn's (1967) suggestion that these two genera are not closely related. As *Leiopelma* and *Ascaphus* possess a number of character-states which are generally considered primitive in frogs, it would appear that they are both relics of ancient but otherwise independent groups within the Anura.

INTRODUCTION

Only two genera of living frogs, *Ascaphus* Stejneger, 1899 from North America and *Leiopelma* Fitzinger, 1861 from New Zealand, are known to possess notochordal amphicoelous vertebrae in adult stages. In other anurans the notochord is discontinuous if not entirely absent from the adult vertebral column and the joints between adjacent centra are synovial joints which may be procoelous, opisthocoelous or amphicoelous in shape, the last-named having a free intervertebral disc. Various aspects of vertebral structure and development in anurans with synovial intercentral joints have been described by many authors, including Cope (1866), Gadow (1897, 1901, 1933), Ridewood (1897), Schauinsland (1906), Beddard (1907), Nicholls (1916), Gillies and Peberdy (1917), de Gaay Fortman (1918), Noble (1922, 1924, 1931), Mookerjee (1931), Ramaswami (1933), Zaharesco (1935), Mookerjee and Das (1939), Al-Hussaini (1941), Hodler (1949*a*, 1949*b*), Smit (1953), Stokely and List (1955) and de Silva (1956). Much of the earlier work on anuran vertebrae has been reviewed by Remane (1936), Devillers (1954) and Griffiths (1959*a*, 1963).

The only investigations concerned specifically with the vertebrae of ascaphids appear to be Ritland's (1955) account of the external and internal morphology of the adult vertebral column of *Ascaphus*, van Dijk's (1960) discussion of the number of vertebrae contributing to the urostyle in this genus and E. M.

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Stephenson's (1952, 1960) descriptions of the external features of the vertebrae of the three species of *Leiopelma*. There appears to be no detailed account, however, of the internal morphology of the adult vertebral column in *Leiopelma* or of vertebral development in either of these two genera.

The present investigation of the internal morphology and ontogenetic development of the vertebral column of *Leiopelma* has been undertaken in order to ascertain the extent to which it resembles the column of *Ascaphus* as described by Ritland (1955), and to determine if possible whether the ectochordal centra (*sensu* Griffiths, 1963) and uninterrupted notochord of adult stages are persistent ancestral conditions as believed by Noble (1924, 1931), E. M. Stephenson (1952), Griffiths (1963), Kluge and Farris (1969), Spinar (1972) and others or secondarily derived from the holochordal condition as postulated by Inger (1967).

MATERIAL AND METHODS

Twelve specimens of developing *Leiopelma archeyi* were available for investigation in the form of transverse, longitudinal or approximately horizontal serial sections cut at 10 or 12μ and stained in van Gieson's stain, Masson's Trichome or Heidenhain's Azan. As this material had already been sectioned, it was not possible to stage the embryos by reference to tables of development such as Shumway's (1940) table for *Rana pipiens* or Nieuwkoop and Faber's (1956) table for *Xenopus laevis*. They were therefore given the arbitrary stage numbers 2 to 9 to indicate increasing age. Stages 2 to 5 were intracapsular embryos, Stage 6 was hatching, while Stages 7, 8 and 9 were tailed froglets fixed one, two and three weeks after hatching respectively.

Five serially sectioned specimens of developing *Leiopelma hochstetteri* were also available, all cut transversely at 10μ. They had been used in the experiments described by N. G. Stephenson (1955) and their ages with respect to hatching were unknown. As the youngest specimen of *L. hochstetteri* was clearly less advanced in its development than the youngest specimen of *L. archeyi*, it was called Stage 1, while two other specimens which appeared overall to be about the same age as the oldest *L. archeyi* were regarded as Stage 9H. These specimens were stained in Mallory's Triple Stain.

The adult material examined included a specimen of *L. archeyi*, male, snout-vent length 27 mm, and a specimen of *L. hochstetteri*, male, snout-vent length 34 mm. The vertebral columns of these two animals were serially sectioned horizontally at 10μ and 12μ respectively and stained in Mallory's Triple Stain and Masson's Trichrome.

Selected sections through developing and adult vertebrae were photographed using a Zeiss Photomicroscope II, while the vertebrae of *L. archeyi*, Stages 4, 6, 7, 8 and 9, are also illustrated by contour reconstructions using the method described by Pusey (1939). The magnification of all illustrations is shown by the accompanying horizontal or vertical line.

VERTEBRAL DEVELOPMENT

Leiopelma archeyi

Stage 2, T.S. (Pl. IX). The notochord is almost uniform in cross-sectional area throughout the trunk and is more dorsoventrally depressed anteriorly than posteriorly. There appears to be only one elastic notochordal sheath, contrary to Mookerjee's (1931) contention that a two-layered sheath is universal in the Anura, and the notochordal tissue itself is diffuse and vacuolated, the layer of cells underlying the notochordal sheath being the notochordal epithelium.

The relationships of the posterior region of the skull and the most anterior vertebra or atlas are not clear owing to the diffuse nature of the sclerotogenous mesenchyme in this region. Further posteriorly the neurapophyses are forming between consecutive spinal nerve ganglia. The more anterior neurapophyses are cartilaginous while the more posterior elements are still procartilaginous. Each neurapophysis is dorsolaterally situated on the notochord, extending laterally to meet the myotome and dorsally as far as the ventral margins of the adjacent ganglia. Further dorsally beside each ganglion is an aggregation of mesenchymatous cells which are connected to the dorsal extremity of the neurapophysis, while the region dorsal to the ganglion between the spinal cord and the myotome is filled with loose mesenchyme. The surface of the notochord between and beneath the bases of the neurapophyses is invested by a thin layer of squamous cells which forms the perichordal tube.

Situated distally to the myotomes adjacent to the third vertebra are large vessels, the anterior lymph hearts, which at this stage are widely separated from the developing axial skeleton.

Stage 3, T.S. (Pl. IX, X). The notochord is oval and depressed in cross-section from the *basis cranii* to the tenth vertebra, gradually increasing in size posteriorly so that its cross-sectional area in the tenth vertebra is approximately four times that in atlas. Posterior to the tenth vertebra the notochord becomes cylindrical and even larger, so that its cross-sectional area in the anterior tail is approximately eight times that in atlas.

Fourteen pairs of neurapophyses are present. Their cartilaginous bases extend for a short distance anteriorly and posteriorly along the lateral surfaces of the perichordal tube in the anterior trunk and along its dorsolateral surfaces further posteriorly. The arch pedicels of the first twelve vertebrae are slender, subcylindrical structures curving around the spinal cord, and the procartilaginous apices of each pair of neurapophyses are widely separated from one another above the spinal cord. The arch pedicels of the thirteenth and fourteenth vertebrae extend only a short distance above the notochord to terminate laterally to the spinal cord. Cells from the dorsal extremities of the myotomes are contributing to the apices of the neurapophyses. A short distance below the apex of each neurapophysis of the second to the ninth vertebrae there are procartilaginous processes extending a short distance anteriorly and posteriorly from the arch. Only the posterior processes are present on the atlas and both pairs of processes are absent from the tenth and following vertebrae. These processes represent the developing zygapophyses and only those of the first three vertebrae are joined together by procartilage at this stage, those of the more posterior vertebrae being connected by diffuse bands of mesenchyme.

On the neurapophyses of the second to the tenth vertebrae there is a laterally directed transverse process whose apex is mesenchymatous. On some vertebrae, particularly the second, third, seventh and tenth, the unchondrified material is clearly a separate element from the transverse process and is therefore a rib, those of the third vertebra lying against the mesial surfaces of the anterior lymph hearts. Both transverse processes and ribs are lacking on atlas and vertebrae eleven to fourteen.

The perichordal tube of the first ten vertebrae has increased in thickness to become a sheath of squamous cells several cells thick, and is slightly thicker ventrally than dorsally to the notochord. Further posteriorly the outer limits of the perichordal tube are ill-defined, at first laterally then also ventrally to the notochord. In the regions between consecutive vertebrae the notochord is enclosed only by the perichordal tube, but between the atlantal neural arch and the occipital arch of the skull there are also strong cartilaginous connections attached to the lateral surfaces of the perichordal tube.

Occupying much of the space between consecutive neurapophyses at the level of the transverse processes are the ganglia of the spinal nerves. The only spinal nerve lacking a ganglion is the first, which lies between the atlantal arch and the skull and consists of the ventral root only. At this stage the ganglia of nerves two to fourteen vary little in size, while those of the more posterior nerves gradually become smaller. The origins of the dorsal and ventral roots in the spinal cord are in almost the same transverse plane as the ganglia, and the spinal nerves pass ventrally on either side of the notochord.

Stage 4, late intracapsular embryo, L.S. (Fig. 1, Pl. x). The apices of the neurapophyses of the first ten vertebrae lie close together but have not fused, while those of the eleventh vertebra are still widely separated from one another. The arch pedicels are slender and subcylindrical and are orientated vertically to the notochord when seen in side view. The atlantal neural arch is the largest in the column and, dorsally to the spinal cord, is widely separated from the skull. The regional variation in the size of the neural arches and the notochord is illustrated in Fig. 1.

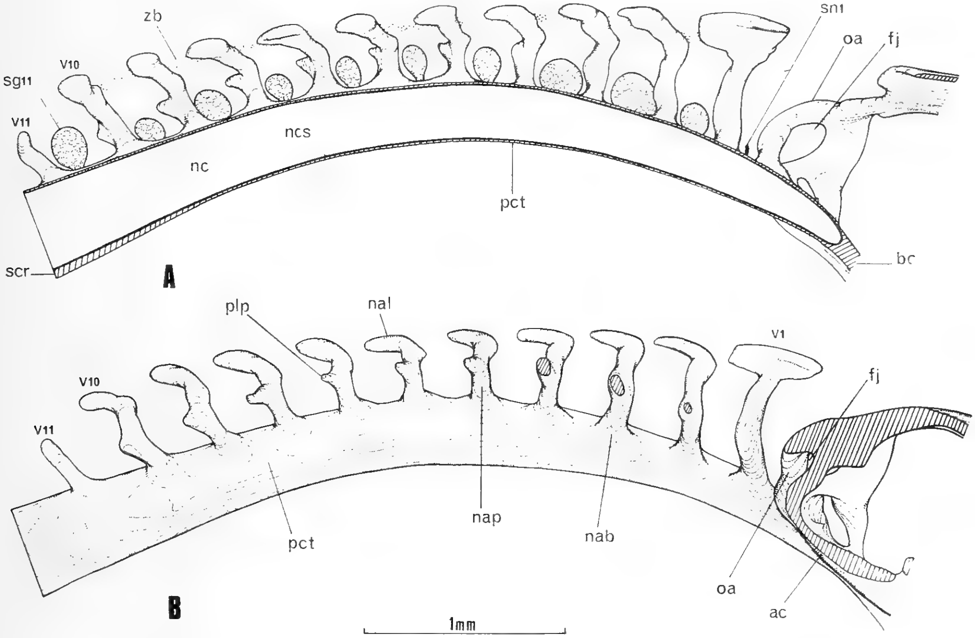

Fig. 1. Contour reconstructions of vertebrae 1–11 in a late intracapsular embryo (Stage 4) of *Leiopelma archeyi*. Posterior region of chondrocranium reconstructed in part. A. Medial view of half vertebral column showing relationship of procartilaginous zygapophyseal bars and spinal nerve ganglia to neural arches. B. Lateral view of vertebral column showing relationship of neural arches to perichordal tube. Ganglia and zygapophyseal bars omitted. *ac*, auditory capsule; *bc*, basis cranii; *fj, foramen jugulare*; *nab*, base of neural arch; *nal*, lamina of neural arch; *nap*, neural arch pedicel; *nc*, notochord; *ncs*, notochordal sheath; *oa*, occipital arch; *pct*, perichordal tube; *plp*, pleurapophysis; *scr*, subchordal rod; *sg11*, ganglion of 11th spinal nerve; *sn1*, 1st spinal nerve; *V1, V10, V11*, 1st, 10th and 11th vertebrae; *zb*, procartilaginous zygapophyseal bars.

All the neural arches as far back as the tenth vertebra are joined together by bands of procartilage lying dorsolaterally to the spinal cord and representing the zygapophyses. The zygapophyseal joints have not yet appeared, but the position of the atlanto-occipital joint is shown by a layer of younger cartilage which extends laterally and posteriorly from the surface of the notochord between the bases of the atlantal neural arch and the occipital region of the chondrocranium.

Regional variation has occurred in the sizes of the spinal nerve ganglia, the largest being those of nerves three, four and eleven, and the smallest those of nerves seven and eight.

The ventral part of the perichordal tube is of uniform thickness from the chondrocranium to the ninth vertebra but, from the tenth to the thirteenth vertebra its thickness ventrally to the notochord has increased owing to squamous cell hyperplasia.

Stage 5, later intracapsular embryo, T.S. and oblique H.S. (Pl. x). The notochord still has its greatest cross-sectional area in the anterior tail, in the twelfth and thirteenth vertebrae where it is almost circular in section. It gradually becomes smaller and more depressed in the more anterior vertebrae and posterior skull but further anteriorly in the *basis cranii* it is compressed slightly to become subcircular again in section. Posterior to the thirteenth vertebra the notochord tapers gradually to the end of the tail.

A sheath of squamous cells comprising the perichordal tube now invests the notochord throughout the vertebral column. It has chondrified by the deposition of matrix similar to that in the neural arches. In the specimen sectioned transversely the increase in thickness of the ventral part of the perichordal tube begins towards the posterior end of the tenth vertebra and reaches its maximum in the twelfth vertebra. In the thirteenth vertebra the thickness of the perichordal tube is reduced laterally to the notochord as well as ventrally so that the notochord of the fourteenth vertebra is invested by a uniformly thin sheath of squamous cells.

Fourteen pairs of neurapophyses are present, the first ten of which are fused together mid-dorsally. In contrast to the arch pedicels which are subcylindrical, the dorsal laminae of the arches are broader plates of cartilage which form a partial roof over the neural canal. The cartilaginous arch bases of the first nine vertebrae lie laterally to the notochord from which they are separated by the perichordal tube, and consecutive arch bases almost meet one another so that the intervertebral region is very short. In the tenth and following vertebrae the arches lie dorsolaterally to the notochord and the distance between consecutive arches increases. In this region, unlike the more anterior trunk, there is cartilaginous continuity between consecutive arch bases in the form of a band of cartilage attached to the dorsolateral surface of the perichordal tube. These tracts of cartilage extend posteriorly from the fourteenth pair of neurapophyses, varying slightly in thickness at irregular intervals. They are present as far back as the eighteenth pair of spinal nerves (Pl. x (F)), after which they diminish and disappear.

In the specimen sectioned transversely, only the second, third, fourth, tenth and eleventh vertebrae have clearly defined ribs, those of the second, third and fourth vertebrae being at least partly chondrified while those of the tenth and eleventh are mesenchymatous. There is no fusion in this specimen between the ribs of adjacent vertebrae.

In the specimen sectioned horizontally there are clearly defined ribs attached to the apices of the transverse processes of the third to the eleventh vertebrae inclusive. Those of the third, fourth and fifth vertebrae are cartilaginous, the right rib of the eighth vertebra is cartilaginous proximally and procartilaginous distally, while the remaining ribs consist entirely of procartilage. The right rib of the third vertebra is deeply notched to enclose the anterior lymph heart and is separate from the rib of the fourth vertebra. On the left side of the body the ribs of the third and fourth vertebrae are fused together and the combined rib encloses the lymph heart. In the posterior region of the body the largest rib elements are those of the tenth vertebra, suggesting that this is to be the sacral vertebra. At this stage, however, the ilia of the pelvic girdle are still widely separated from the vertebral column (Pl. x (F)).

Stage 6, at hatching, T.S. and L.S. (Figs 2, 3; Pl. xi). In the specimen sectioned transversely the cross-sectional area of the notochord gradually increases from front to back, reaching its maximum in the ninth, tenth and eleventh vertebrae, and there appears to be little change in its cross-sectional area in the following two vertebrae. The notochord is laterally compressed to a small degree within the *basis cranii*, becoming circular in cross-section in the first three vertebrae. In the following eight vertebrae it is slightly depressed dorsoventrally while that of the more posterior tail is squarish in outline. In the specimen which was sectioned longitudinally, the notochord gradually increases in size from its anterior extremity just behind the hypophysis to the level of the fourteenth vertebra.

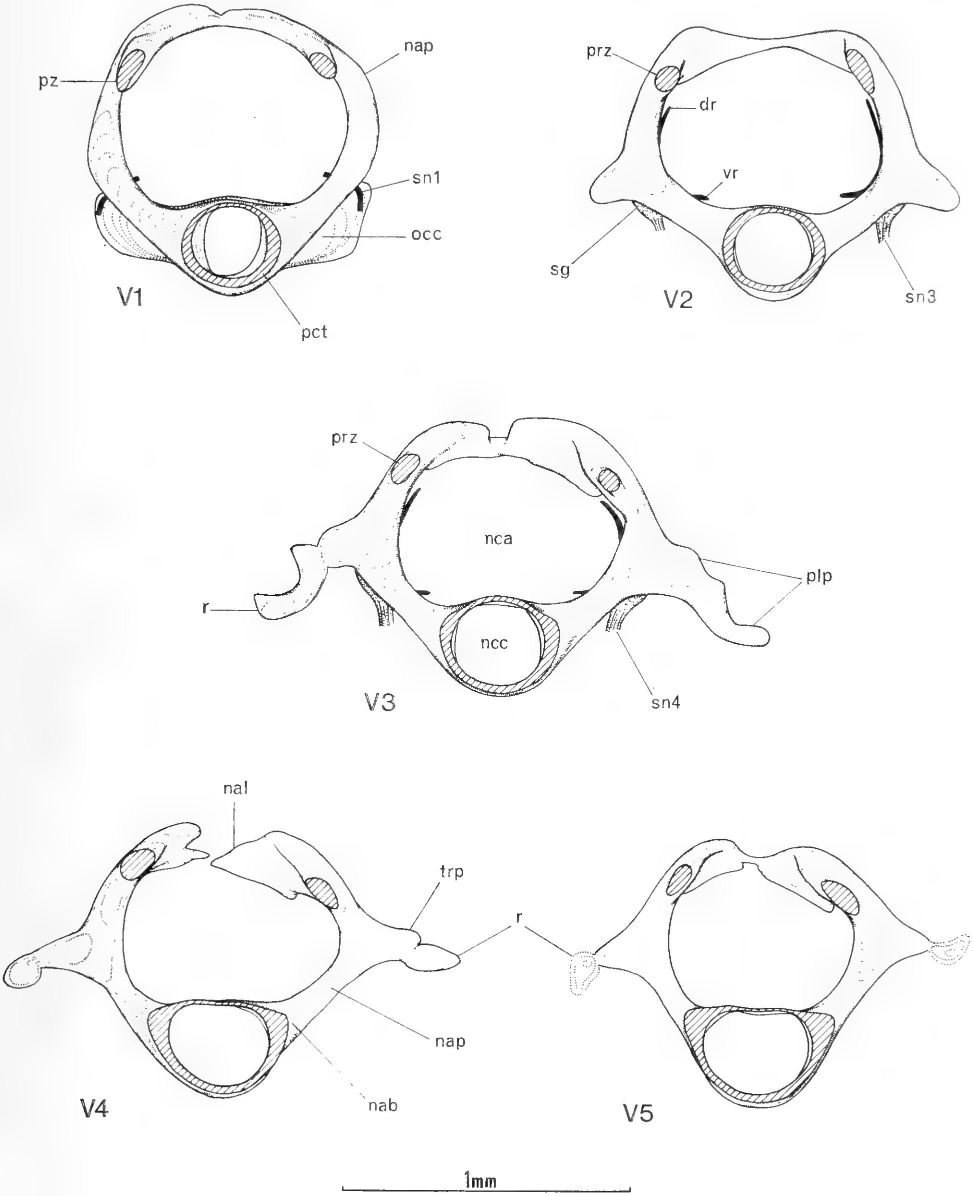

Fig. 2. Contour reconstructions of vertebrae 1–5 of *L. archeyi* at hatching (Stage 6). First vertebra from posterior aspect, vertebrae 2–5 in anterior view. The procartilaginous ribs of the 5th vertebra are shown in coarse stipple. *dr*, dorsal root of spinal nerve ; *nab*, base of neural arch ; *nal*, lamina of neural arch ; *nap*, neural arch pedicel ; *nca*, neural canal ; *ncc*, notochordal canal ; *occ*, occipital condyle ; *pct*, perichordal tube ; *plp*, pleurapophysis ; *prz*, prezygapophysis ; *pz*, postzygapophysis ; *r*, rib ; *sg*, spinal nerve ganglion ; *sn1–4*, spinal nerves 1–4 ; *trp*, transverse process ; *vr*, ventral root of spinal nerve.

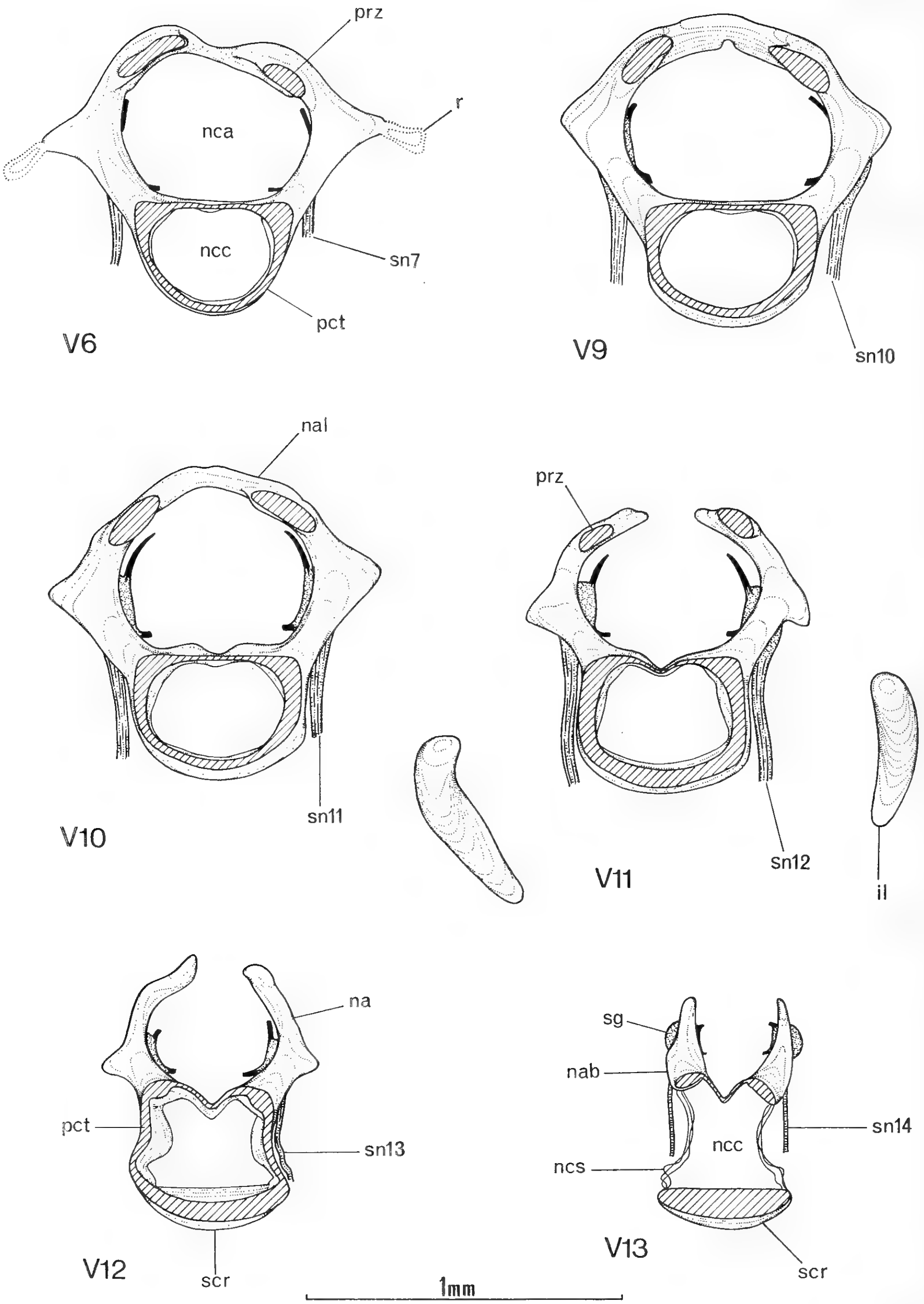

Fig. 3. Contour reconstructions from anterior aspect of the 6th vertebra and vertebrae 9–13 of *L. archeyi* at hatching (Stage 6). The procartilaginous ribs of the 6th vertebra are shown in coarse stipple. The mesenchymatous ribs of vertebrae 9–13 were too indistinct in outline for reconstruction. *il*, ilium ; *na*, neural arch ; *nab*, base of neural arch ; *nal*, lamina of neural arch ; *nca*, neural canal ; *ncc*, notochordal canal ; *ncs*, notochordal sheath ; *pct*, perichordal tube ; *prz*, prezygapophysis ; *r*, rib ; *scr*, subchordal rod ; *sg*, ganglion of spinal nerve ; *sn7–14*, spinal nerves 7–14.

The perichordal tube of the first ten vertebrae of both specimens is of uniform thickness along the vertebral column and is slightly thicker ventrally than it is dorsally to the notochord. The ventral thickening of the perichordal tube which begins at the posterior end of the tenth vertebra and reaches its maximum in the thirteenth vertebra is increased at this stage by the metaplasia of chondrified squamous cells into hyaline cartilage in which the cells are subspherical and the matrix more abundant. This subchordal rod of cartilage occupies the full width of the notochord and is chondrified as far as the posterior end of the thirteenth vertebra. The dorsal and lateral regions of the perichordal tube which lie between the arch bases and the subchordal rod of the thirteenth vertebra are thin and membranous. In the fourteenth vertebra the subchordal rod also becomes membranous and diffuse and disappears towards the posterior end of this vertebra.

In the specimen sectioned transversely, fourteen pairs of neurapophyses are present. Except for the fourth, and the eleventh to the fourteenth pairs, they are fused together dorsally to the spinal cord for a short distance near the posterior end of the arch. The arch bases of the first four vertebrae are attached laterally to the perichordal tube while those further posteriorly are more dorsolaterally placed with respect to the notochord. The tracts of cartilage extending back from the arch bases of the fourteenth vertebra disappear a short distance behind the vent at approximately the level of the sixteenth pair of spinal nerves so that the notochord in the remainder of the regressing tail is surrounded by a thin membranous perichordal tube. In the longitudinally sectioned specimen, none of the fourteen pairs of neurapophyses had fused together.

Transverse processes occur on all vertebrae with the exception of the atlas and the fourteenth vertebra, and in many cases have clearly defined rib elements attached to them. The ribs of the third vertebra are cartilaginous and are curved so that they lie against the mesial and ventral surfaces of the anterior lymph hearts, while those of the tenth vertebra are represented by condensations of mesenchyme attached to the transverse processes. At this stage the ilia are growing anteriorly and dorsally towards the vertebral column. Although the anterior ends of the ilia are level with the eleventh vertebra at this stage, the greater size of the tenth vertebra and its ribs than the eleventh vertebra and its ribs suggests that the former is the sacral vertebra. This is supported by the fact that the anterior ends of the ilia are procartilaginous and evidently in a state of rapid elongation.

The spatial relationships of the components of the spinal nerves with one another and the adjacent vertebrae are the same as in earlier stages : the dorsal and ventral nerve roots, the ganglia and the spinal nerves passing ventrally beside the vertebrae all lie in approximately the same transverse plane, and the ganglia lie in approximately the same horizontal plane as the transverse processes.

Stage 7, one week after hatching, T.S. and L.S. (Fig. 4). Although the two specimens representing this stage hatched and were fixed at the same time, the longitudinally sectioned specimen is more advanced in its vertebral development than the one sectioned transversely. As they also differ in other respects, they are described separately.

In the specimen sectioned transversely the notochord gradually increases in size posteriorly as far as the fifteenth vertebra. It is slightly compressed in the *basis cranii* and the first three vertebrae, is slightly depressed in the remaining vertebrae, and is somewhat irregular in cross-sectional outline. The perichordal tube is slightly thinner dorsally to the notochord than it is ventrally, while its lateral surfaces are covered by the cartilage of the neural arch bases except for a narrow region between adjacent vertebrae. The ventral thickening of the perichordal tube to form the subchordal rod begins in the tenth vertebra, has partly changed into hyaline cartilage in the twelfth to the fourteenth vertebrae, and disappears in the region of the fifteenth vertebra between the fifteenth and sixteenth pairs of spinal nerves.

Fifteen pairs of neurapophyses are present in this specimen, the more anterior eleven of which are fused together mid-dorsally. The neurapophyses of the twelfth vertebra lie close together above the spinal cord without fusing while those of the thirteenth, fourteenth and fifteenth vertebrae consist of the arch pedicels only, and these diminish in size posteriorly. Joint cavities are forming in the cartilaginous zygapophyseal bars connecting the first three vertebrae, those connecting the third to the eleventh vertebrae being undivided although the position of the joint is clearly defined. Posterior to the eleventh vertebra there are no zygapophyseal connections between consecutive neural arches.

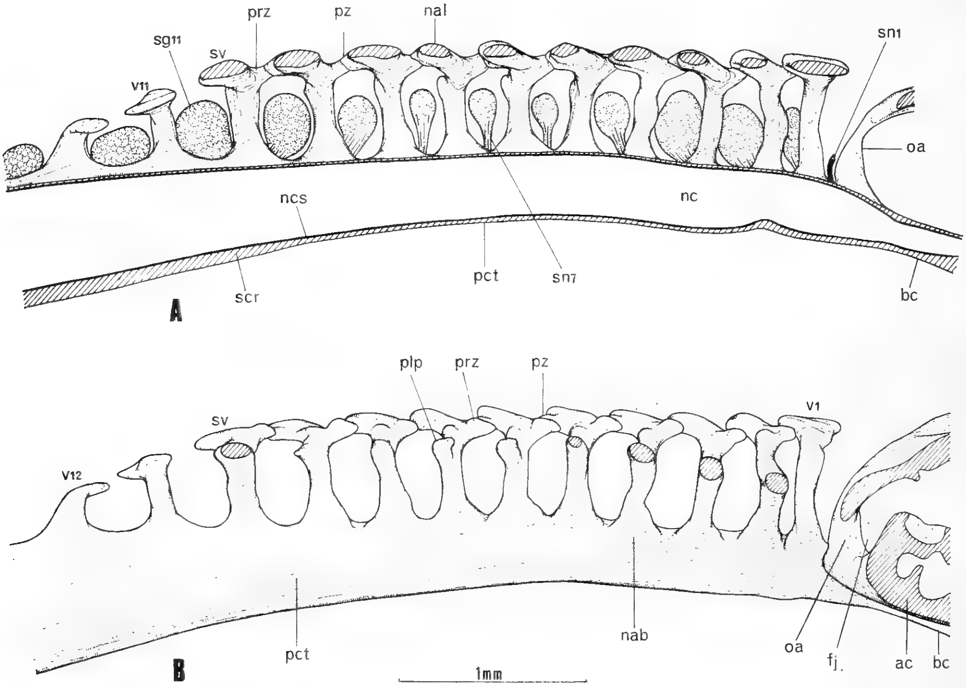

Fig. 4. Contour reconstructions of vertebrae 1–12 of *L. archeyi* one week after hatching (Stage 7). Posterior region of chondrocranium reconstructed in part. A. Medial view of half vertebral column showing relationship of neural arches to one another and to ganglia of spinal nerves. B. Lateral view of vertebral column showing relationship of neural arches to one another and to perichordal tube. Ganglia omitted. *ac*, auditory capsule ; *bc*, basis cranii ; *fj*, *foramen jugulare* ; *nab*, base of neural arch ; *nal*, lamina of neural arch ; *nc*, notochord ; *ncs*, notochordal sheath ; *oa*, occipital arch ; *pct*, perichordal tube ; *plp*, pleurapophysis ; *prz*, prezygapophysis ; *pz*, postzygapophysis ; *scr*, subchordal rod ; *sg11*, ganglion of 11th spinal nerve ; *sn1*, *sn7*, 1st and 7th spinal nerves ; *sv*, sacral vertebra ; *V1*, *V11*, *V12*, 1st, 11th and 12th vertebrae.

Transverse processes are present on all vertebrae except the atlas and the last three in the column. Cartilaginous ribs are attached to the transverse processes of the third, fourth and fifth vertebrae, those of the fourth vertebra instead of the third as is usual in *Leiopelma* being deeply notched to enclose the anterior lymph hearts. The ribs associated with the sixth, seventh and twelfth vertebrae are procartilaginous or mesenchymatous while the remaining vertebrae lack separate rib elements. The pleurapophyses of the eleventh vertebra are connected to the ilia of the pelvic girdle by broad bands of connective tissue, thus demonstrating that the eleventh vertebra is the sacral vertebra in this specimen instead of the tenth as is usual in *Leiopelma* (E. M. Stephenson, 1952, 1960).

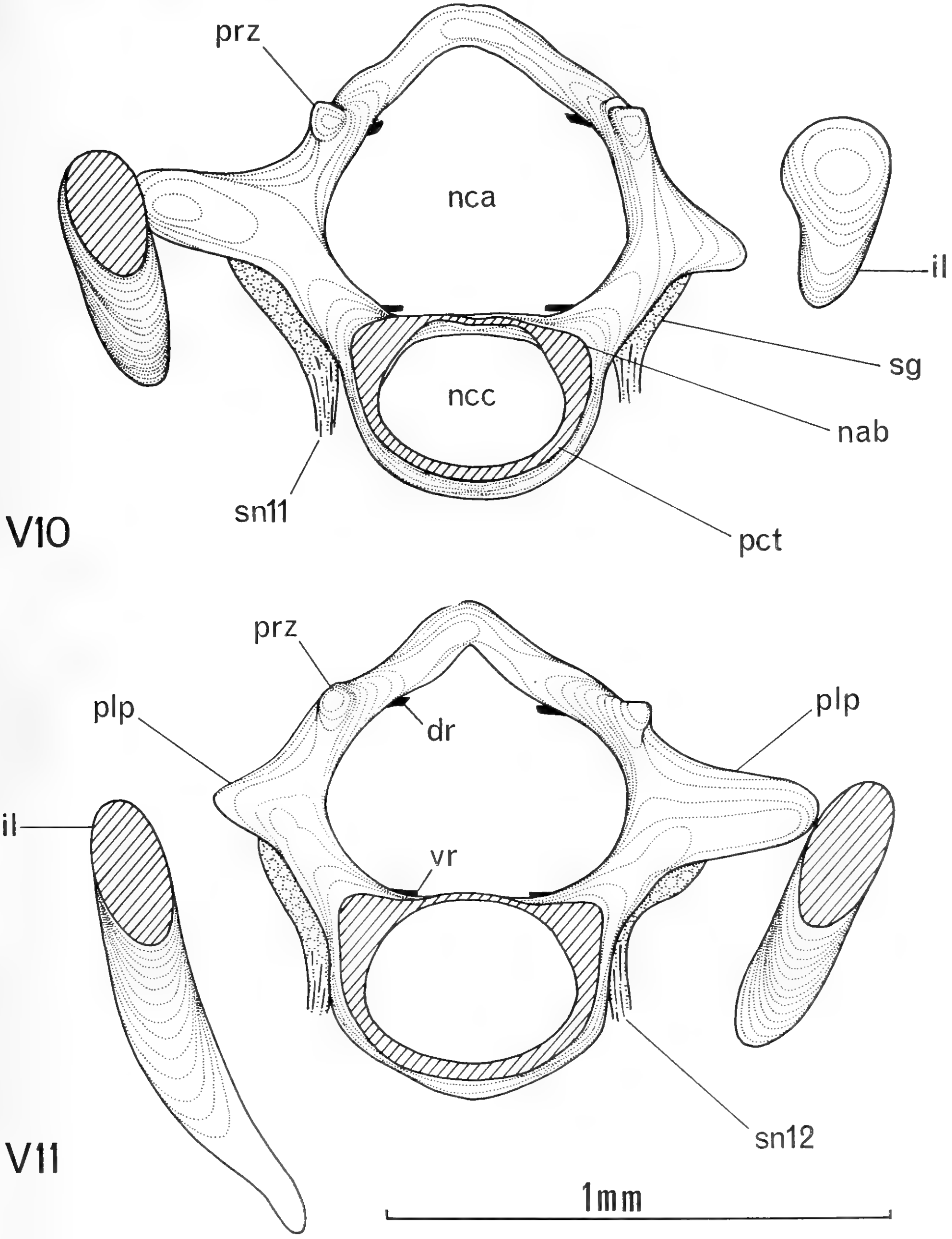

Fig. 5. Anomalous sacrum comprising the 10th and 11th vertebrae in a specimen of *L. archeyi* two weeks after hatching (Stage 8). Contour reconstructions from anterior aspect. *dr*, dorsal root of spinal nerve ; *il*, ilium ; *nab*, base of neural arch ; *nca*, neural canal ; *ncc*, notochordal canal ; *pct*, perichordal tube ; *plp*, pleurapophysis ; *prz*, prezygapophysis ; *sg*, ganglion of spinal nerve ; *sn11*, *sn12*, 11th and 12th spinal nerves ; *vr*, ventral root of spinal nerve.

A synovial cavity has begun to form in the posterolateral regions of the atlanto-occipital joint, the more medial region of the joint on either side of the continuous notochord remaining undivided.

In the specimen which was sectioned longitudinally, the tenth vertebra is the sacral vertebra, a total of fourteen pairs of neurapophyses are present, the first ten of which are fused together mid-dorsally, and the ribs of the third vertebra are notched to enclose the anterior lymph hearts. The somewhat more advanced

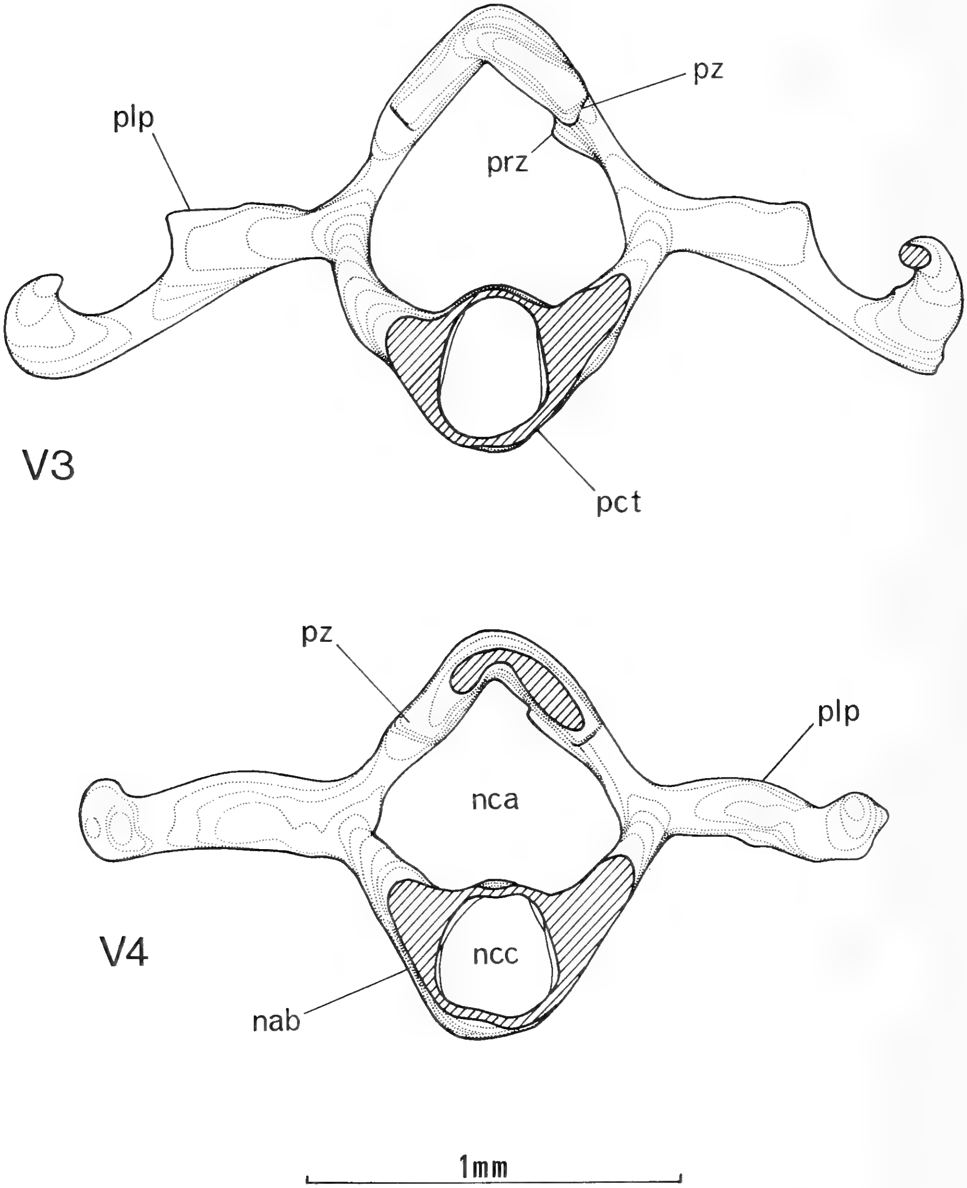

Fig. 6. Third and fourth vertebrae of *L. archeyi* three weeks after hatching (Stage 9). Contour reconstructions from posterior aspect. *nab*, base of neural arch ; *nca*, neural canal ; *ncc*, notochordal canal ; *pct*, perichordal tube ; *plp*, pleurapophysis ; *prz*, prezygapophysis ; *pz*, postzygapophysis.

state of vertebral development in this specimen is shown by the presence of joint cavities in all the zygapophyseal bars connecting the first ten vertebrae, there being no zygapophyseal connections between the more posterior neural arches, the somewhat greater extent of the synovial cavity in the atlanto-occipital joint, and the onset of perichondral ossification of the vertebrae. Ossification begins on the neural arches at the level of the transverse processes but does not extend to the ends of these processes or to the bases or the laminae of the arches.

Stage 8, two weeks after hatching, T.S. (Fig. 5). Perichondral ossification of the vertebrae is more advanced than in Stage 7, extending further down the neural arches towards their bases and further dorsally onto the arch laminae. The synovial cavities between the zygapophyses are more extensive with the postzygapophyses overlying the prezygapophyses of the following vertebrae. The neurapophyses of the eleventh vertebra as well as those of the more anterior vertebrae are fused together mid-dorsally.

Of the two specimens at this stage which were available for investigation, one had fourteen and the other fifteen pairs of neurapophyses. In the latter, the sacrum is anomalous in that the right transverse process of the tenth vertebra and the left process of the eleventh vertebra support the pelvic girdle (Fig. 5). In the former the sacrum appears to consist of only the tenth vertebra but, unlike the latter in which the transverse processes supporting the girdle are in contact with the ilia, the transverse processes and ilia of this specimen are widely separated from one another. It would thus appear that this specimen is also anomalous in that development of the sacrum has been retarded relative to the rest of the column.

Stage 9, three weeks after hatching, T.S. (Figs 6, 7 ; Pls XI, XII). There are fourteen pairs of neurapophyses of which the first twelve are fused together mid-dorsally, the thirteenth are widely separated dorsally to the spinal cord and the fourteenth consist of low arch pedicels. Further posteriorly the bars of cartilage lying along the dorsolateral surfaces of the perichordal tube are irregularly thickened and end just behind the sixteenth pair of spinal nerves. At this stage there is cartilaginous continuity between all the neural arch bases on each side of the body as a result of fusion between consecutive arches on the dorsolateral surface of the perichordal tube. The perichordal tube itself has the same configuration in the presacral region as it did in Stage 7.

The notochord is slightly compressed from side to side in the *basis cranii*, the nine presacral vertebrae and the anterior end of the tenth or sacral vertebra, increasing gradually in cross-sectional area from front to back. Within the posterior end of the sacral vertebra the cross-sectional area of the notochord is suddenly reduced to less than half its value at the anterior end of the vertebra as a result of centripetal growth of the neural arch bases and subchordal rod. Maximum constriction of the notochord occurs in the twelfth vertebra behind which it gradually expands to become only slightly smaller at the end of the subchordal rod than in the anterior end of the sacral vertebra. Within this region of notochordal constriction the appearance of the notochordal sheath and notochordal tissue also change, the sheath being corrugated and thickened due to constriction, and the notochordal tissue more dense due to an accumulation of non-cellular material. In the presacral vertebrae and in the tail posterior to the end of the subchordal rod, the notochord and its sheath appear the same histologically as at the onset of vertebral development.

The subchordal rod is now composed entirely of hyaline cartilage and gradually narrows from the posterior end of the sacral vertebra to its posterior end just behind the vent, at the level of the sixteenth pair of spinal nerves.

In the eleventh and twelfth vertebrae the subchordal rod has fused on either side of the notochord to the ventral surfaces of the neural arch bases while the arch bases of the thirteenth and fourteenth vertebrae and the following bars of

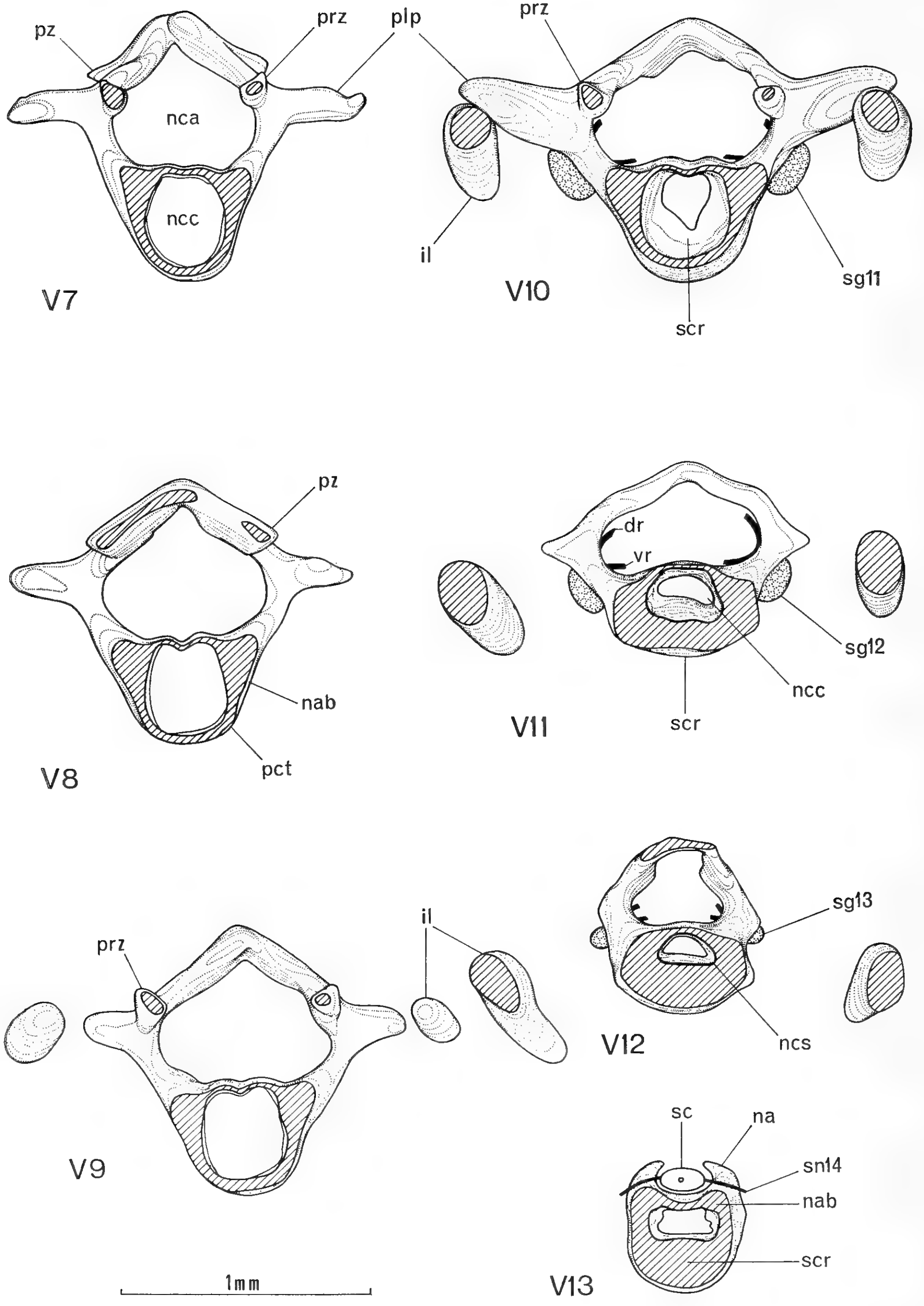

Fig. 7. Contour reconstructions of vertebrae 7–13 in *L. archeyi* three weeks after hatching (Stage 9). 8th and 13th vertebrae in posterior view, remainder from anterior aspect. *dr*, dorsal root of spinal nerve ; *il*, ilium ; *na*, neural arch ; *nab*, base of neural arch ; *nca*, neural canal ; *ncc*, notochordal canal ; *ncs*, notochordal sheath ; *pct*, perichordal tube ; *plp*, pleurapophysis ; *prz*, prezygapophysis ; *pz*, postzygapophysis ; *sc*, spinal cord ; *scr*, subchordal rod ; *sg11–13*, ganglia of spinal nerves 11–13 ; *sn14*, 14th spinal nerve ; *vr*, ventral root of spinal nerve.

cartilage are still separated from one another and the subchordal rod by the perichordal tube. In the region of the tail posterior to the end of the subchordal rod the perichordal tube is of almost uniform thickness around the notochord and is apparently fibrous in nature.

Synovial joints are present between the postzygapophyses of the first to the ninth vertebrae and the prezygapophyses of the second to the tenth vertebrae, posterior to which there are no zygapophyses. Their articular surfaces are flat in end view and are inclined upwards and outwards from the midline at an angle of approximately 45° to the horizontal. The synovial joint between atlas and the occipital condyles is not yet complete and is traversed by the unconstricted notochord.

There are no discrete rib elements present at this stage owing to their fusion to the transverse processes of the vertebrae. As discrete ribs have been found at some stage of development in association with all vertebrae bearing transverse processes, the latter are more correctly described as pleurapophyses. The pleurapophyses of the third vertebra are deeply notched to enclose the anterior lymph hearts which are covered dorsally by the cartilaginous suprascapulae of the pectoral girdle. The pleurapophyses of the tenth or sacral vertebra lie dorsally to the ilia of the pelvic girdle, to which they are attached by ligaments. The ilia extend anteriorly beyond this point to reach the level of the pleurapophyses of the ninth vertebra but are not joined to them.

The spinal ganglia are more ventral in position at this stage, lying between the pedicels of the neural arches below the level of the pleurapophyses. The relative positions of the dorsal and ventral nerve roots, the ganglia and the spinal nerve trunks are also changing in different parts of the body. The result is that the nerve roots, particularly towards the sacrum, come to lie some distance anteriorly to the ganglia to which they belong. The relationship of the nerves to the vertebrae is described below in the section on adult stages. Sixteen pairs of spinal nerves are present at this stage, the most posterior of which lie laterally to the posterior end of the subchordal rod.

Leiopelma hochstetteri

Stage 1, T.S. In this specimen, the youngest of all the available specimens of *Leiopelma*, the spinal cord is flanked dorsolaterally by the neural crest and laterally by the somites which have not yet begun to differentiate into myotomes and sclerotomes. The notochord lying between the spinal cord and the subnotochord has a single sheath and the same histological characteristics as in *L. archeyi*.

Stage 9H, T.S. Of the two oldest available specimens of *L. hochstetteri*, one was sectioned completely and the other only as far back as the anterior end of the eighth vertebra. These two specimens are a little more advanced than the oldest available specimen of *L. archeyi* (Stage 9) with respect to perichondral ossification in that the layer of bone on the neural arches is somewhat thicker and extends further dorsally towards the apices and further ventrally towards the bases of the neurapophyses. The transverse processes have also ossified as far as their junction with the associated ribs.

In some other respects, vertebral development in these specimens of *L. hochstetteri* is less advanced than in *L. archeyi* Stage 9. In the partially sectioned specimen the first four pairs of neurapophyses are unfused while in the other specimen, which has thirteen pairs of neurapophyses in all, the apices of the first ten pairs lie close together above the spinal cord but remain unfused. The eleventh, twelfth and thirteenth pairs of arches are more widely separated mid-dorsally. Ribs are still detectable as distinct elements from the transverse processes of the vertebrae, those of the third and fourth vertebrae being cartilaginous and fused to the transverse processes. The more posterior ribs are

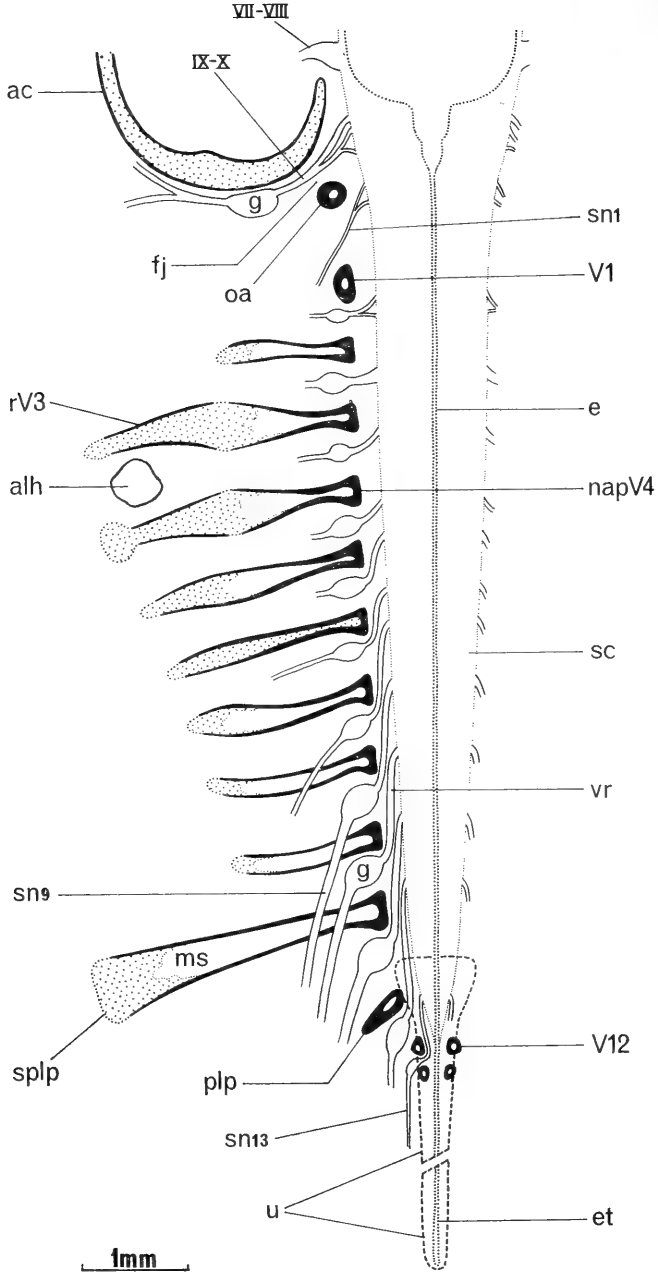

Fig. 8. Composite horizontal section of vertebral column and posterior skull of adult *L. archeyi* in ventral view, showing relationship of spinal nerves, ganglia and ventral nerve roots to spinal cord, neural arches and urostyle. As the urostyle lies ventrally to the ependymal tube, its position is indicated by a heavy broken line. Only the anterior and posterior ends of the urostyle are shown. Diagrammatic, scale approximate. *ac*, auditory capsule; *alh*, anterior lymph heart; *e*, ependyma; *et*, ependymal tube; *fj*, *foramen jugulare*; *g*, ganglion; *ms*, marrow space; *napV4*, neural arch pedicel of 4th vertebra; *oa*, occipital arch; *plp*, pleurapophysis; *rV3*, rib of 3rd vertebra; *sc*, spinal cord; *sn1*, *sn9*, *sn13*, 1st, 9th and 13th spinal nerves; *splp*, sacral pleurapophysis; *u*, urostyle; *V1*, *V12*, 1st and 12th vertebrae; *vr*, ventral nerve root: *VII–X*, cranial nerves. Bone, solid black; cartilage, coarse stipple.

procartilaginous or mesenchymatous, including the ribs of the tenth vertebra, which appears by virtue of its size to be the sacral vertebra although it is still widely separated from the ilia of the pelvic girdle. There is slight constriction of the notochord within the eleventh and twelfth vertebrae but its histological appearance remains unchanged. The subchordal rod consists of hyaline cartilage for the greater part of its length but it has not yet fused to the bases of the post-sacral neural arches.

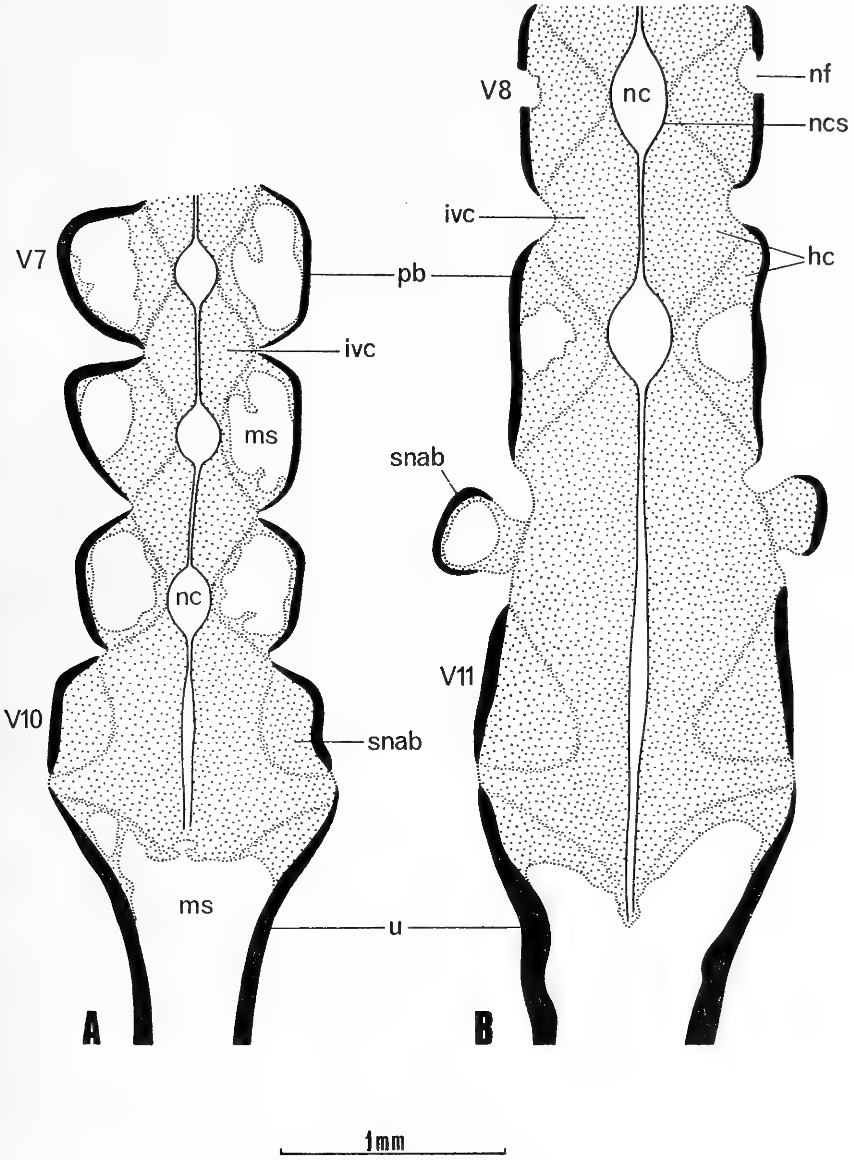

Fig. 9. Posterior vertebrae and anterior end of urostyle of adult *Leiopelma* in horizontal section showing the structure of the sacral vertebra and the relationships between the notochord, the bases of the neural arches and the intervertebral cartilage. A. *L. archeyi*, ♂, snout-vent length 27 mm. B. *L. hochstetteri*, ♂, snout-vent length 34 mm. *hc*, hyaline cartilage; *ivc*, intervertebral cartilage; *ms*, marrow space; *nc*, notochord; *ncs*, notochordal sheath; *nf*, nutritive foramen; *pb*, perichondral bone; *snab*, base of sacral neural arch; *u*, urostyle; *V7–V11*, 7th to 11th vertebrae.

With respect to the joints developing between atlas and the occipital condyles and between the zygapophyses of consecutive vertebrae, these two specimens of *L. hochstetteri* are comparable with the Stage 9 specimen of *L. archeyi*.

ADULT VERTEBRAL COLUMN

L. archeyi, H.S. (Figs 8, 9; Pl. XII). Thirteen pairs of neurapophyses are present in this specimen, of which the first nine are presacral, the tenth is sacral, and the eleventh, twelfth and thirteenth are fused to the anterior dorsal surface of the urostyle. The first eleven pairs of arches are fused together mid-dorsally and, with the exception of the sacral vertebra, the perichondral bone of the arch laminae is fused as well as the inner core of hyaline cartilage. The neural arch of the sacral vertebra remains unossified mid-dorsally. The arches of the twelfth and thirteenth vertebrae are separate mid-dorsally but fused together on either side of the neural canal dorsally and ventrally to the thirteenth pair of spinal nerves. The arches of the first ten vertebrae articulate by means of zygapophyses and are also connected by strong sheets of collaginous connective tissue. A similar connective tissue sheet joins the atlantal arch to the occipital arch of the skull but there is no zygapophyseal connection between these two arches which are widely separated from one another. Zygapophyses are also absent posterior to the sacrum. The tenth and eleventh arches are widely separated and the eleventh, twelfth and thirteenth arches are considerably smaller than those of the more anterior vertebrae.

With the exception of atlas and the twelfth and thirteenth vertebrae, all the neural arches bear pleurapophyses, those of the presacral and sacral vertebrae being ossified perichondrally for the greater part of their length and cartilaginous at their distal extremities. Most of them have also undergone endochondral ossification but the marrow spaces do not extend as far distally as the layer of perichondral bone so that the ends of the processes retain a core of hyaline cartilage. In those pleurapophyses with a suture in the perichondral bone between the rib element and the transverse process, namely those of the third and fourth vertebrae, the marrow cavities do not extend out beyond the level of the sutures. In each case, endochondral ossification of the pleurapophyses appears to have progressed outwards from the neural arch rather than originating from separate ossification centres within the pleurapophyses. The pleurapophyses of the eleventh vertebra are much smaller than those of the more anterior vertebrae and consist almost entirely of perichondral bone.

From the occiput to the twelfth vertebra the neural canal enclosed by the neural arches contains the spinal cord, which tapers gradually posteriorly as it gives off successive spinal nerves of which there are thirteen pairs in all. The spinal cord itself does not extend further posteriorly than the twelfth vertebra, but its investing membranes and the lining of the spinal canal or ependyma continue back between the thirteenth pair of neurapophyses and along the dorsal surface of the urostyle to its posterior extremity. The most anterior spinal nerve on each side has neither ganglion nor dorsal root, but its ventral root is in two parts lying close together, one behind the other. The following twelve pairs of nerves have dorsal and ventral roots as well as ganglia although the ventral roots of the second pair resemble those of the first in having two components arising from the spinal cord. The roots and ganglia of the third pair of nerves lie in approximately the same transverse plane, but further posteriorly the distance between the origins of the nerve roots in the spinal cord and the ganglia to which they belong becomes greatly increased. Maximum displacement is found in the case of the eleventh nerve, whose ganglion lies between the tenth and eleventh vertebrae and whose roots leave the spinal cord anteriorly to the ninth vertebra.

The bodies of the presacral and sacral vertebrae, often referred to as centra, are largely cartilaginous, the only bone present being the perichondral and endochondral bone of the neural arch bases, which extend almost to the ventral surface of the column, and the thin layer of perichondral bone covering the dorsal and ventral surfaces of the vertebral bodies. All the cartilage within and between consecutive vertebrae is hyaline cartilage, the perichordal tube of chondrified squamous cells present in developmental stages having disappeared. From the arrangement of the cartilage cells and matrix within the vertebrae, which is more clearly seen in the specimen of *L. hochstetteri* than in this specimen of *L. archeyi*, it is evident that much of the cartilage of the presacral vertebral bodies belongs to the bases of the neurapophyses. The cartilage between adjacent vertebrae appears to have arisen as a result of hyperplasia of the perichordal tube in the ends of adjacent vertebral bodies which has become hyaline like the arch bases. Unlike the neural arch bases, however, whose growth has not constricted the notochord to any extent, growth of the cartilage in the ends of the vertebrae has constricted the notochord to a slender thread.

The notochord, together with its sheath, is still continuous from the posterior region of the *basis cranii* to the anterior end of the urostyle ventral to the eleventh pair of neurapophyses. It is continuous through the atlanto-occipital joint, lying very close to the ventral surface of the joint, and contains fibrous cartilage in the base of the skull, the joint region and the anterior end of atlas. In the middle of atlas, as in the following eight vertebrae, it is unconstricted and extends almost to the dorsal and ventral surfaces of each vertebral body. In these vertebrae it has essentially the same histological appearance as in earlier stages. In the sacral vertebra the notochord is constricted to a considerable extent and has changed histologically to appear fibrous and non-cellular. In this form and with little further constriction the notochord passes back into the anterior end of the urostyle, but it terminates here owing to the presence of the adjacent marrow space. No vestige of the notochord remains further posteriorly ; the urostyle has ossified perichondrally and endochondrally for almost its entire length, the single cavity within it being a marrow space in endochondral bone, not the notochordal canal. The only parts of the urostyle which are still cartilaginous are the most anterior portion of the urostyle where it joins the body of the sacral vertebra and its most posterior extremity where it still appears to be growing.

L. hochstetteri, H.S. (Fig. 9 ; Pl. XII). Of the thirteen neural arches present in this specimen the tenth is sacral, the eleventh belongs to an additional post-sacral vertebra, and the twelfth and thirteenth are fused to the anterior end of the urostyle. Zygapophyseal joints connect the first to the eleventh arches, there being no zygapophyseal connections between the atlantal arch and the occipital arch of the skull or between the arches posterior to the eleventh vertebra. The two halves of the first twelve arches are joined together mid-dorsally by hyaline cartilage which, except for that of the tenth vertebra, is enclosed in a thin layer of perichondral bone, while the two halves of the thirteenth arch are separate from one another.

Pleurapophyses are borne by the second to the twelfth vertebrae inclusively, those of the presacral and sacral vertebrae possessing cartilaginous distal portions which, except for those of the ninth vertebra, are fused to their transverse processes. The distal cartilaginous rib elements of the ninth vertebra are connected to their transverse processes by ligaments. The bases of the pleurapophyses contain marrow spaces continuous with those in the neural arches but in the pleurapophyses of the third and fourth vertebrae which have sutures in their perichondral bone, the marrow spaces do not extend into the ribs. The pleurapophyses of the eleventh and twelfth vertebrae are ossified to the tip.

As in *L. archeyi*, there are thirteen pairs of spinal nerves, of which only the first pair lacks dorsal roots and ganglia. The relationship of the nerves to their roots and ganglia and to the spinal cord, and the transition from spinal cord to ependymal tube in the region of the twelfth neural arch are also similar in the two specimens.

Except for the sacral and immediately postsacral regions, the relationships of the neural arch bases to the intervertebral cartilage and the internal structure of the vertebral bodies including the conformation of the notochord are the same in *L. hochstetteri* as in *L. archeyi.* The similarities and differences between these two frogs in the structure of their posterior presacral, sacral and postsacral vertebrae are illustrated in Fig. 9. The body of the sacral vertebra in both cases consists in part of the bases of the neural arches but, unlike the presacral vertebrae, the mesial surfaces of the arch cartilages do not lie close to the surface of the notochordal sheath. These elements are separated from one another by a region of cartilage which is hyaline like that of the arch bases but which appears, like the hyaline intervertebral cartilage, to have formed as a result of metaplasia and hyperplasia of the perichordal tube. Like the intervertebral cartilage also, and unlike the cartilages of the arch bases, the cartilaginous core of the sacral vertebra has strongly constricted the notochord within it. In *L. archeyi* the bases of the sacral neural arches contribute to the body of the vertebra, but in *L. hochstetteri* the arches are separate from the dorsal regions of the vertebral body, and further ventrally where they join the latter they project laterally from the surface of the column. In both frogs the sacral neural arches are smaller in horizontal section than those of the presacral vertebrae, and are proportionally much smaller in *L. hochstetteri* than in *L. archeyi.*

DISCUSSION

From the foregoing description of the development and adult structure of the vertebral column of *Leiopelma archeyi* and *L. hochstetteri* as well as from E. M. Stephenson's (1952, 1960) accounts of the external morphology of the vertebrae of all three species of *Leiopelma*, it is evident that individual variation in vertebral characteristics is not uncommon. Embryos of the same age may be at somewhat different stages of vertebral development as shown by the closure or otherwise of the neurapophyses, the proximity of the ilia of the pelvic girdle to the vertebral column and the extent of perichondral ossification while the structure of the column can also vary in the number of presacral vertebrae (nine or ten), the number of vertebrae modified to support the ilia and the number of postsacral vertebrae which are free or are incorporated into the anterior end of the urostyle. Variation also occurs in the ribs of the more anterior vertebrae in that those of the third, fourth or both may be forked, and fusion can occur between these ribs on either side of the body. As this range of variability was observed in the comparatively few specimens available for the present investigation, it is often difficult to be certain which embryonic and adult features are characteristic of species and which are due to individual variation. Also some developmental stages were not represented, notably the early intracapsular stage between Stages 1 and 2 exhibiting the sclerotomic precursors of the vertebrae, and sub-adult stages more than three weeks old. Consequently it was not possible to determine the cellular density of the sclerotomes or the presence or absence of a sclerocoel (see Wake, 1970). Nor was it possible to observe the onset of endochondral ossification in the neural arches, or ossification of the perichordal tube as illustrated in *L. hochstetteri* by E. M. Stephenson (1960), or later stages in the formation of the cranio-vertebral joint and urostyle, which apparently occur after the completion of metamorphosis. Despite these limitations, however, it is possible to compare the adult vertebral columns of *Leiopelma* and *Ascaphus* with one another and with non-ascaphid anurans as well as a number of features of vertebral development in *Leiopelma* and non-ascaphids.

Vertebral Column of Adult Leiopelma *and* Ascaphus

Leiopelma and *Ascaphus* are unique among living anurans in that they retain an uninterrupted notochord and lack synovial joints between the bodies of adjacent vertebrae throughout life (E. M. Stephenson, 1952, 1960 ; Ritland, 1955). Although some other frogs such as *Rana temporaria* retain these characteristics for some two years after metamorphosis, synovial cavities form during the third year and the notochord is subsequently entirely lost from the ends of the vertebrae (Mookerjee, 1931). In Griffiths' (1963) terminology, the vertebrae of *Leiopelma* and *Ascaphus* are ectochordal in that the fully formed vertebral body is a hollow bony cylinder enclosing the persistent notochord while the vertebrae of *Rana* are holochordal because the notochord is ultimately resorbed so that the body of the vertebra becomes a solid cylinder of bone. The term amphicoelous has also been used to describe the vertebrae of *Ascaphus* and *Leiopelma* but its accuracy has been questioned by E. M. Stephenson (1952, 1960) and Ritland (1955) on the grounds that the vertebrae of these frogs are structurally very different from the notochordal amphicoelous vertebrae of some other vertebrates.

In *Leiopelma* the bodies of adult presacral vertebrae consist of the perichordal tube together with the bases of the neural arches which cover its lateral surfaces. Although Ritland (1955) described the laterally situated endochondrally ossified regions of the vertebral bodies in *Ascaphus* as centra, a comparison between his illustrations of the vertebrae in end view with his horizontal sections shows that these ossified regions are the arch bases as in *Leiopelma.* In both genera the notochord is moniliform in shape and its extreme constriction between consecutive vertebrae results from hyperplasia of the perichordal tube in this region to form the intervertebral cartilage. Although the mid-vertebral regions of the notochord appear unconstricted, a comparison between the width of the notochord in the eighth and ninth vertebrae of a tailed froglet of *L. archeyi* three weeks after hatching (Fig. 7) and that in a sexually mature specimen (Fig. 9) shows that some mid-vertebral constriction occurs as well.

Despite the overall similarity between *Leiopelma* and *Ascaphus* in the internal morphology of their presacral vertebrae, there are also differences between them. The neural arch bases of *Ascaphus* (Ritland, 1955, Fig. 3, Pl. 1) contain considerably more endochondral bone than those of *Leiopelma* (Fig. 9) including *L. hochstetteri* which, according to E. M. Stephenson (1960), has the most heavily ossified skeleton of all three species of *Leiopelma.* The notochord, on the other hand, is more strongly constricted intervertebrally in *Leiopelma* than in *Ascaphus* and differs histologically in the two genera. In *Leiopelma* the notochord is fibrous only where it is strongly constricted between consecutive vertebrae, the tissue within the unconstricted mid-vertebral portions consisting of vacuolated notochordal cells, but in *Ascaphus* the fibrous cord is continuous throughout the vertebral column, forming a fibrous core through the middle of the vacuolated notochordal tissue in the centre of each vertebra.

Primitiveness of Ectochordy and Continuous Notochord

Until recently it was generally accepted that the ectochordal centra and continuous notochord in *Ascaphus* and *Leiopelma* are ancestral conditions retained in living forms (Noble, 1924, 1931 ; E. M. Stephenson, 1952 ; Griffiths, 1963 ; Kluge and Farris, 1969 ; Spinar, 1972). Inger (1967), however, postulated that ectochordal centra have been secondarily derived from the holochordal condition as a result of neoteny. He pointed out the reduced ossification of the skeleton in some species of ascaphids, namely of *Leiopelma* as described by E. M. Stephenson (1960), and considered the holochordal condition to be primitive because most lepospondylous amphibians had holochordal vertebrae. According to Inger, the only evidence for the primitive nature of ectochordy is its appearance as an early ontogenetic state in many frogs.

Contrary to Inger's (1967) contention, the available evidence points to the primitiveness within the Anura of the notochordal state of the vertebrae of *Leiopelma* and *Ascaphus*. The sequence in which organs appear during the ontogeny of an animal does not constitute evidence for the early or late appearance of these organs during the animal's evolutionary history as organs which are known to have arisen relatively late in phylogeny often appear early in ontogeny and *vice versa* (de Beer, 1958). The state of the vertebrae of the Lepospondyli is also irrelevant as the Anura are generally considered to have evolved from labyrinthodonts, either independently or together with the Urodela and Apoda (see Romer, 1968). A current view is that all three orders of living amphibians evolved from labyrinthodonts belonging to the Dissorophoidea (Bolt, 1969).

Within the Amphibia as a whole, persistence of an uninterrupted notochord in the adult vertebral column is more primitive than its partial or complete absence because an uninterrupted notochord was inherited by labyrinthodonts from their rhipidistian ancestors (Romer, 1966). In any smaller group within the Amphibia such as the Anura, the presence of an uninterrupted notochord in adult stages may be this original amphibian character-state retained in living forms, or it may have arisen secondarily as a result of neoteny, especially as heterochrony appears to be widespread among frogs (E. M. Stephenson, 1960, 1961 ; N. G. Stephenson, 1965 ; Jacobson, 1968).

Pre-anuran fossils do not resolve this point because only one extinct amphibian is known which is structurally intermediate between Palaeozoic tailed amphibians and the Anura, namely *Triadobatrachus massinoti*. Contrary to the opinion of most authors, including Piveteau (1937, 1955) and Watson (1940), who considered *T. massinoti* to have been adult, Griffiths (1956, 1963) claimed that it was an immature animal comparable to living frogs during metamorphosis. There is also uncertainty as to the structure of its vertebrae. According to Piveteau (1937) they are cylindrical, amphicoelous, with a medial constriction, and separated from one another by a lens of cartilage. Griffiths (1963) re-examined the specimen and described its vertebral column as a chain of bony, spool-shaped centra, pierced by a persistent notochord, and without any evident emargination on either their anterior or posterior borders. The difference between these two descriptions concerns the continuity or otherwise of the notochord throughout the column and the nature of the material between consecutive vertebrae. From Piveteau's (1937, 1955) photographs of the fossil, it is clear that ball and socket joints are not present between consecutive vertebrae and that the ends of the vertebral bodies, particularly those lying between the ilia of the pelvic girdle, contain conical plugs of matrix (see also Hecht, 1962). Whether this matrix has replaced notochordal tissue or cartilage is unknown. From Piveteau's photographs it is impossible to decide whether the vertebrae of *T. massinoti* were solid, holochordal elements joined together by imperforate lenses of intervertebral cartilage, or whether they were hollow and ectochordal with the notochord strongly constricted between the vertebrae by the intervertebral cartilage as in *Ascaphus* and *Leiopelma* or unconstricted as in some apodans and urodeles (see Mookerjee, 1930 ; Hilton, 1948 ; Lawson, 1966 ; Wake, 1970).

Even if the structure of the vertebrae of *T. massinoti* could be determined with certainty, its bearing on the vertebral morphology of living frogs is questionable. In the first place, although *T. massinoti* is structurally intermediate in many of its skeletal characteristics between Palaeozoic amphibians and the Anura, it was not necessarily ancestral to the Anura (*cf.* the relationship between the Jurassic Ardeosauridae and the Recent Gekkonidae—Moffat, 1972).

Therefore it cannot be assumed that the various types of vertebrae found in living frogs have necessarily evolved from that found in *Triadobatrachus*. In the second place, if Griffiths' (1956, 1963) contention that *T. massinoti* was an immature animal is correct, it cannot be assumed that the condition of its vertebrae is primitive in the Anura, although this may be the case. It is the state of the vertebrae in the adult animal which shows the stage reached by this animal in the evolution of vertebral structure in the group to which the animal belongs. In any case, as the amount of bone in the skeleton of *T. massinoti* is comparable to that in adult anurans rather than metamorphosing stages where the skeleton is still largely cartilaginous (see Parker, 1881), it would appear that *Triadobatrachus* was in fact an adult animal representing an early stage in the evolution of the Anura.

Fossil frogs belonging to the genus *Notobatrachus* from the Jurassic of Patagonia (Reig, 1957) provide some evidence for the primitiveness of notochordal vertebrae in the Anura. According to Reig, the vertebrae of *Notobatrachus* have the same form as those of *Leiopelma* and *Ascaphus* ; he described biconcave centra and unossified intercentra (*i.e.* intervertebral cartilages), while his figures 6 and 7 show the presence of a slender notochordal canal in the ends of the vertebrae. Although it cannot be assumed that *Notobatrachus* was directly ancestral to any group of living frogs, including *Leiopelma* and *Ascaphus*, with which some authors consider it to be confamilial (*e.g.* Griffiths, 1963), the existence of a persistent notochord in its vertebrae and the absence of ball and socket articulations between them demonstrate that the type of vertebral construction found in *Leiopelma* and *Ascaphus* is not a recently acquired condition but existed in the earliest known members of the Anura.

Although the structure of the vertebrae in adult *Leiopelma* and *Ascaphus* bears a superficial resemblance to that found in immature stages of other living frogs with holochordal vertebrae such as *Bufo melanosticus* and *Rana temporaria*, the differences between them are significant (see also Ritland, 1955). In metamorphosing *B. melanosticus* and *R. temporaria* only 9 mm and 12 mm respectively in total length the ball and socket joint between the vertebrae has already begun to develop, the notochord consists only of notochordal tissue and is of uniform width in horizontal sections except for the narrow region between the vertebrae, where it is constricted by the ring of intervertebral cartilage (Mookerjee, 1931, Pl. 15, fig. 8 ; Pl. 16, fig. 12). In adult *Ascaphus* and *Leiopelma* there is no sign of an incipient joint within the intervertebral cartilage, the constricted portions of the notochord are fibrous and its relatively unconstricted portions occur only in the centres of the vertebrae. Therefore the state of the vertebrae in adult *Ascaphus* and *Leiopelma* is not the same state as that found in juvenile *Bufo* and *Rana* and consequently cannot be considered neotenic compared with the adult condition in the last-named genera.

In some families of frogs, such as the Australian Leptodactylidae, the procoelous holochordal vertebrae do not develop by the invasion of an arc of connective tissue into the intervertebral cartilage as in *Bufo* and *Rana* (Mookerjee, 1931) but by the fusion of a free intervertebral disc to the posterior end of the preceding vertebra (N. G. Stephenson, 1965). Stephenson maintained that within the Leptodactylidae heterochronous changes have been responsible for many of the morphological differences used to distinguish genera and species and that all stages are found in adult leptodactylids from the completely free intervertebral disc condition to the completely fused procoelous state found in *Cyclorana australis*. A similar range of structure was described by N. G. Stephenson (1965) in other parts of the leptodactylid skeleton. For example, the skull of adult *Glauertia russelli* is similar in structure to that of juvenile *C. australis* in that it is largely cartilaginous and the bony elements are small. delicate structures which in many cases are widely separated from one another, whereas the skull of adult *C. australis* is heavily ossified with extensive surface sculpturing and many elements are broad plates of bone with extensive sutures between them. If adult *Leiopelma* and *Ascaphus* were neotenic compared with other frogs such as *Rana temporaria* in the way that *Glauertia russelli* is neotenic compared with *Cyclorana australis*, one would expect this to be evident in their cranial morphology. In fact, the amount of bone in the skull of *Leiopelma hochstetteri* (E. M. Stephenson, 1951, fig. 16) and *Ascaphus truei* (Noble, 1931, fig. 81) is of approximately the same order as that found in *R. temporaria* (Marshall, 1951, figs 7, 8).

Although it is possible that the presence of an uninterrupted notochord and the absence of ball and socket joints in the vertebral columns of *Leiopelma* and *Ascaphus* could have resulted from some form of heterochrony other than overall neoteny (see de Beer, 1958), the similarity between *L. archeyi* and *L. hochstetteri* in the states of these characters despite heterochronous changes in other parts of the skeleton (see E. M. Stephenson, 1960) suggests that the internal morphology of the vertebral column of *Leiopelma* is not affected by heterochrony. Furthermore, although the vertebrae of *Ascaphus* as illustrated by Ritland (1955) are more heavily ossified than those of *Leiopelma*, constriction of the notochord is no greater than in *Leiopelma*.

From the foregoing discussion it would appear that the presence of an uninterrupted notochord and the absence of ball-and-socket joints in the vertebral columns of *Leiopelma* and *Ascaphus* are not secondarily derived conditions resulting from neoteny as postulated by Inger (1967) but ancestral conditions which have been retained in living forms and which are therefore primitive character-states within the Anura. Whether the type of vertebra found in these two genera could have been ancestral to all other types of anuran vertebrae, however, has yet to be established. The principal ontogenetic changes required to derive the type of holochordal vertebrae found in *Bufo* and *Rana* (see Mookerjee, 1931) are the invasion of the intervertebral cartilage by an arc of connective tissue to form the ball-and-socket joints and more extensive ossification to obliterate the notochord within the vertebra. Atrophy of the notochord and ventral portions of the perichordal tube, including the presacral subchordal cartilage in *Xenopus* (Mookerjee, 1931; Smit, 1953) produces the stegochordal condition (Griffiths, 1959*b*, 1963). From Mookerjee's (1931) account and the present description of vertebral development in *Leiopelma*, it is clear that the critical stages in ontogeny which determine the adult state of the vertebrae in these frogs occur during or immediately after metamorphosis, even in frogs like *Rana temporaria* which take several more years to complete development. It is not possible to comment here on the possible course of evolution of the holochordal procoelous vertebrae of the Leptodactylidae because, although it is known that the condyles of the vertebrae are formed by the fusion of free intervertebral discs (N. G. Stephenson, 1965), other aspects of the ontogeny of leptodactylid vertebrae are unknown. According to Griffiths (1959*b*, 1963), the free disc condition in the Megophryinae and some members of the Criniinae is not the developmental precursor of procoelous or opisthocoelous vertebrae but is the end product of a particular type of vertebral development.

Two other aspects of vertebral development and adult structure in *Leiopelma* require further discussion, namely the occurrence of ribs and the construction of the sacrum and urostyle.

Ribs

The presence of ribs in association with the third and fourth vertebrae of *Ascaphus* and *Leiopelma* has long been recognized (Noble, 1931; E. M. Stephenson, 1952, 1960; Ritland, 1955) but the laterally directed processes without sutures borne by other vertebrae are usually described as transverse processes or diapophyses, thus implying that they consist entirely of outgrowths from the neural arches. From the present study it is clear that all these processes including those of the sacral vertebra, whether or not they possess a suture in adult stages, are formed in part from tissue originating outside the vertebra and are therefore pleurapophyses (see Cligny, 1899*a*, 1899*b* ; Hoffstetter, 1939 ; Smit, 1953). N. G. Stephenson (1965) pointed out that the terminal cartilaginous epiphyses of the pleurapophyses which are found in leptodactylids as well as many other frogs including *Ascaphus* and *Leiopelma* presumably represent the cartilaginous sternal (*i.e.* distal) portions of the ribs of other tetrapods.

According to Piveteau (1937), the forked ribs of the third vertebra in *Ascaphus* and *Discoglossus* enclose the anterior lymph hearts. Ritland (1955) disagreed with Piveteau and claimed that the large ribs of the third and fourth vertebrae, one pair of which may be forked, provide origins for muscles inserting on the scapula and suprascapula of the pectoral girdle. In *Leiopelma* the forked ribs also have muscles attached to them but they are also closely associated from early stages with thin-walled vessels which are usually empty of cellular material but sometimes contain erythrocytes. These vessels are evidently the anterior lymph hearts described by Piveteau (1937) and the occasional presence of erythrocytes in them is explained by the ability of lymph vessels to return extravasated erythrocytes to the blood vascular system (Le Gros Clark, 1965). In early embryos the dorsal components of the pectoral girdle are widely separated from the ribs and lymph hearts but by the third week after hatching. *i.e.* during metamorphosis, the suprascapula has grown over the ends of the pleurapophyses so that each lymph heart is enclosed in a channel whose floor and inner wall are formed by the two rami of the pleurapophysis and whose roof is the suprascapula (Plate XI (J)).

Development of Urostyle

The urostyle of adult anurans represents the proximal region of the postsacral (caudal) axial skeleton after atrophy of the embryonic or larval tail during metamorphosis. Its structure and development in a variety of frogs have been described by many authors including Ridewood (1897), Gadow (1897), Schauinsland (1906), Mookerjee (1931), Mookerjee and Das (1939), Hodler (1949*b*), E. M. Stephenson (1952), Smit (1953), Stokely and List (1955), van Dijk (1960) and Griffiths (1963), many of whom have given comprehensive reviews of the previous literature. The main points of disagreement regarding the structure of the urostyle concern the number of vertebral elements contributing to its formation and their relationship with the hypochord. Both these points can be clarified with respect to *Leiopelma*, bearing in mind that the situation in other frogs, particularly those with stegochordal presacral vertebrae, is not necessarily the same.

In the past there were basically three opinions regarding the construction of the urostyle. According to Gadow (1897, 1933) and Romer (1945, 1962, 1966), the urostyle results from the fusion of as many as 12 vertebrae, while Noble (1931) and Shumway (1942) maintained that it is formed by the fusion of three longitudinal, unsegmented strips of cartilage. The third school of thought now appears to be correct, that the urostyle of anurans consists in part of an unsegmented rod which lies ventrally to the notochord and which eventually fuses with several anterior postsacral neural arches (Mookerjee, 1931 ; MacBride, 1932 ; Mookerjee and Das, 1939 ; Smit, 1953 ; Stokely and List, 1955 ; Griffiths, 1963).

In developing *Leiopelma archeyi* the ventral component of the urostyle is a rod of cartilage formed from the ventral part of the postsacral perichordal tube which has increased in thickness due to hyperplasia of the chondrified squamous cells comprising it and their subsequent metaplasia into hyaline cartilage. It occupies the full width of the notochord and, towards the end of metamorphosis, fuses with the bases of the postsacral neural arches and the tracts of cartilage connecting them. The ventral component of the urostyle of *Ascaphus* is formed in the same way as a rod of cartilage within the perichordal tube (Eaton, 1959). In the trunk of *Xenopus laevis* tadpoles there is also a subchordal rod of cartilage which forms from the ventral region of the perichordal tube, but it is resorbed together with the notochord during metamorphosis (Ridewood, 1897 ; Mookerjee, 1931 ; Smit, 1953).

The question arising here is whether the subchordal rod of cartilage in the postsacral region of *Leiopelma* and *Ascaphus* should be described as a hypochord. According to Mookerjee (1931), the rod of cartilage in the trunk of *Xenopus* is not homologous with the hypochord in the tail because the latter is not part of the perichordal tube but a separate structure fused to its ventral surface. A separate hypochord has been described in a number of other anurans and, according to Mookerjee and Das (1939), its relationship with the perichordal tube varies in different species. In *Rana afghana*, *Microhlya rubra*, *Rhacophorus maculatus* and *Xenopus laevis* there lies between the membranous ventral portion of the perichordal tube and the cartilaginous hypochord a continuous band of hyaline cartilage which subsequently degenerates, together with the notochord when the hypochord fuses with the postsacral neural arches and the dorsal region of the perichordal tube to form the urostyle. According to Mookerjee and Das (1939), the band of hyaline cartilage is absent in other anurans such as *Bombinator igneus* so that the hypochord rests directly on the membranous perichordal tube while in others again such as *Rana temporaria* and *Bufo melanosticus* the entire perichordal tube in the region of the urostyle chondrifies but remains distinct from the hypochord even when subsequent ossification of the urostyle is well advanced (Mookerjee, 1931, Pl. 15, Fig. 10 ; Mookerjee and Das, 1939, Fig. 12B). The separate identity of the hypochord in the pelobatid *Megophrys major* is particularly clear because metamorphosing stages of this frog have approximately 17 ossified caudal vertebrae of which the most anterior four are attached to the dorsal surface of the cartilaginous hypochord (Griffiths, 1956, 1963).

Although the separate identity of the hypochord is usually established from its manner of origin during ontogeny, this seems to be as variable as the later relationship of the hypochord with the overlying perichordal tube. From the works of Mookerjee (1931) and Smit (1953) it appears that the hypochord of *Rana temporaria*, *Bufo melanosticus*, *Bombinator igneus* and *Xenopus laevis* originates as a longitudinal condensation in the subvertebral mesenchyme which subsequently chondrifies. Stokely and List (1955) described the hypochord in *Pseudacris nigrita* during metamorphosis as an ossified rod-like process but concluded that the exact origin of the hypochord during ontogeny has yet to be determined. Griffiths (1963) described the hypochord of *Megophrys major* as a posterior, ventral outgrowth of the first postsacral intervertebral body and implied that it arises in this manner in all anurans. Despite this diversity of opinion and the diversity it suggests regarding the origin of the hypochord in different members of the Anura, it would appear that the separate hypochord in many species has no counterpart in *Leiopelma* and *Ascaphus* whose subchordal rod of cartilage is part of the perichordal tube. Nevertheless the subchordal rod of *Leiopelma* and *Ascaphus* may be considered homologous with the hypochord of other anurans since they are both rods of cartilage which lie ventrally to the postsacral notochord and constitute the ventral component of the urostyle. According to Szarski (1962), organs which have the same structure and the same location in relation to neighbouring organs are homologous, although they may develop in very different ways.

The number of postsacral vertebral segments involved in the formation of the urostyle has also been debated, largely because discrete caudal vertebrae are rarely found in anurans. To date, *Megophrys major* described by Griffiths (1956, 1963) appears to be the only exception in that metamorphosing stages have approximately 17 ossified caudal vertebrae, of which the first four contribute to the urostyle. In embryonic and recently hatched *Leiopelma archeyi* there are usually fourteen pairs of neurapophyses in all, less often fifteen. As the tenth pair is usually sacral and the specimens with fifteen pairs had the eleventh vertebra modified to support the pelvic girdle, it would appear that four pairs of postsacral neurapophyses are normally present during developmental stages. In the adult specimen of *L. archeyi* examined, only three pairs of postsacral neurapophyses were present, which suggests that the tiny fourth pair belonging to the fourteenth vertebra had been indistinguishably incorporated into the urostyle. E. M. Stephenson (1952) maintained that no more than three postsacral vertebrae are normally found in developing *L. hochstetteri*, while her illustration of a common condition of the anterior urostyle of adults (1952, Fig. 2) shows only two postsacral arches. Three pairs of postsacral neurapophyses were present in the adult *L. hochstetteri* examined here, but this specimen was atypical in possessing a free postsacral vertebra. In these circumstances it would appear that *L. archeyi* normally has one more neural arch on the anterior end of the urostyle than *L. hochstetteri* and that in both species the most posterior arch is indistinguishable in adults.

In view of the small size of the most posterior pair of neurapophyses, the number of arches recognizable during developmental stages of *Leiopelma* may not represent the total number of vertebral segments incorporated into the urostyle. The total number of segments can be determined, however, from the relationship between the subchordal rod of hyaline cartilage and the spinal nerves. In late intracapsular and hatching stages of *L. archeyi* the anterior and posterior limits of the rod are ill-defined but, by three weeks after hatching, at a stage comparable to late metamorphosis in other frogs, it terminates abruptly just behind the vent. As the specimen at this stage examined here had a total of fourteen neural arches, the tenth of which was sacral, and the subchordal rod began immediately behind the sacral vertebra and terminated in the region of the sixteenth pair of spinal nerves, it is evident that the most anterior five postsacral vertebrae formed the urostyle and that the fifth of them lacked a neural arch. The dorsal components of this vertebra are the posterior extensions of the tracts of cartilage situated dorsolaterally to the notochord and connecting the bases of the more anterior postsacral arches. Whether the urostyle of *L. hochstetteri* also comprises five vertebrae could not be determined from the material available.

According to van Dijk (1960), the eleventh, twelfth, thirteenth and possibly the anterior half of the fourteenth vertebrae contribute to the formation of the urostyle in *Ascaphus*. van Dijk based this conclusion on the relationships of the coccygeal lymph hearts and the origin on the urostyle of the *pyriformis* muscle in an adult specimen and a larva with well developed hind limbs. He also claimed that Ritland's (1955) identification of a thirteenth spinal nerve in *Ascaphus* suggests the participation of the eleventh, twelfth and thirteenth vertebrae in its urostyle. From this investigation of *Leiopelma* it is seen that the number of spinal nerves associated with the anterior end of the urostyle in fully metamorphosed frogs can show the minimum number of vertebrae present but gives no indication of the total number involved. In embryonic *L. archeyi* the spinal cord and its associated nerves are present throughout the tail but in adults all but the most anterior three postsacral nerves have been resorbed and the spinal cord posterior to the last of the persistent nerves, *i.e.* the thirteenth, is reduced to a slender ependymal tube extending along the dorsal surface of the urostyle to its posterior extremity. As each spinal nerve lies anterior to the vertebra of the same number, the presence of the thirteenth spinal nerve in adult *L. archeyi* gives no indication that the fourteenth and fifteenth vertebrae are present in the urostyle.

van Dijk (1960) commented on the extreme elongation of the urostyle in *Ascaphus* behind the thirteenth spinal nerve and concluded that the thirteenth vertebra extends almost as far as the position at which the fifteenth should lie due to posterior movement of both the ischiopubic region of the pelvic girdle and the posterior end of the urostyle relative to the sacrum. Similar elongation of the urostyle also occurs in *Leiopelma archeyi* but in this case it applies to the fifteenth vertebra. In the specimen three weeks after hatching which was sectioned transversely at 10μ, it was calculated that all five urostylar vertebrae were the same length, *i.e.* 0·27 mm. It was also calculated that the presacral column in this specimen measured 2·62 mm and was therefore almost twice as long as the urostyle. As the urostyle of the adult *L. archeyi* sectioned horizontally was the same length as the presacral colum,, *i.e.* 6·8 mm, it is clear that the urostyle has not only increased in length by almost 5·5 mm to become five times its original length but has also grown much more rapidly than the presacral column. As the proportions of the anterior end of the urostyle in postmetamorphic *Lieopelma* do not seem to alter with age (see E. M. Stephenson, 1960, Fig. 3), most of the elongation of the urostyle takes place at its posterior end in the region of the fifteenth vertebra. Moreover, the presence of cartilage at the posterior end of the urostyle of adult *Leoipelma* shows that its growth may continue after sexual maturity.

Evolution of Anuran Pelvis

According to van Dijk (1960), the backward migration of the end of the urostyle and the ischiopubic region of the pelvic girdle rather than a forward migration of the sacro-iliac articulation accounts for much of the forward slope of the ilia in *Ascaphus* and therefore a primitively vertical pelvic girdle would have articulated with a sacrum not more than two vertebrae further back than at present. From the ontogenetic development of the pelvis and sacrum in *Leiopelma*, it is clear that backward migration of the posterior parts of the pelvis and urostyle in postmetamorphic stages accounts for the disproportionately long pelvic girdle in adult frogs compared with non-anuran amphibians, living and extinct (see Smith, 1927; Hilton, 1945–47; Wake, 1963; Romer, 1966), but plays no part in determining the position of the sacrum. This is determined during metamorphosis, before the posterior end of the urostyle is clearly defined, by the growth of the ilia towards the vertebral column, the sacral vertebra being the one whose pleurapophyses are induced to enlarge by the proximity of the anterior ends of the ilia (Ridewood, 1897). The growth of the ilia in an antero-dorsal direction is demonstrated by the movement of their anterior extremities from a position below and behind the pleurapophyses of the eleventh vertebra in hatching stages (Fig. 3) to a position slightly above and in front of the pleurapophyses of the ninth vertebra three weeks after hatching, the tenth vertebra by this stage having become the sacrum (Fig. 7). As the acetabula are situated ventrally to the thirteenth vertebra in both these stages, the posterior migration of the ischiopubic region characteristic of later stages has not yet begun, so that the increase so far in the length of the ilia is due entirely to the growth of their anterior ends in an antero-dorsal direction.

Slight changes in the rate and direction of growth of the ilia and of the more posterior pleurapophyses of the vertebral column during this period could account to a large extent for the different positions of the sacrum in anurans and the different numbers of vertebrae comprising it. Another factor which may alter the position of the sacrum is a shift of the entire pelvic girdle anteriorly or posteriorly along the body as indicated by the position of the acetabulum during early metamorphosis. Developmental changes of this nature can not only explain the variability of the presacral and sacral regions within species (see Ridewood, 1897) but can also account for the different numbers of presacral and sacral vertebrae which are typical of different species, and which vary between the nine presacrals and one sacral normally found in *Ascaphus* and *Leiopelma* (E. M. Stephenson, 1952 ; Ritland, 1955) to the six presacrals and three sacrals of the brachycephalid *Oreophrynella quelchii* (Noble, 1931). Although occasional specimens of *Leiopelma*, *Ascaphus* and some other frogs such as *Xenopus* have one more than the number of presacral vertebrae typical of the species concerned (Hodler, 1949*b* ; E. M. Stephenson, 1952 ; Ritland, 1955), it is generally agreed that the overall evolutionary trend in the Anura is towards further shortening of the presacral column as a result of forward migration of the sacro-iliac articulation (Gadow, 1901 ; Green, 1931 ; Ramaswami, 1933 ; Ritland, 1955).

Although anterior migration of the sacro-iliac articulation in the Anura can result from an anterior shift in the position of the pelvic girdle and/or anterior growth of the ilia, it is apparent that only the first of these alternatives could have led to reduction of the presacral column in the ancestors of the Anura. Among the Palaeozoic rhachitomous labyrinthodonts belonging to the Dissorophoidea, which are currently considered to contain the ancestors of the three living amphibian orders (Bolt, 1969), the number of presacral vertebrae varied between eighteen and twenty-six and the pelvic girdle had the robust, plate-like construction and the vertical ilium characteristic of early amphibians (Watson, 1940 ; Gregory, 1950 ; Carroll, 1964 ; Bolt, 1969). As relative changes in the rate of elongation of a vertical ilium would not alter its position on the vertebral column, variation in the number of presacral vertebrae in the Dissorophoidea must have resulted from shifts in the position of the entire girdle. The pelvic girdle of the Triassic pre-anuran *Triadobatrachus massinoti* is structurally intermediate between those of the Dissorophoidea and the Anura in that approximately six caudal vertebrae are present instead of a urostyle, the acetabula lie below the eighteenth vertebra, the fifteenth and possibly the sixteenth vertebrae are sacral and the ilia, although directed anteriorly, are shorter and stouter than those of adult frogs (see Piveteau, 1937 ; Hecht, 1962). Although it is not certain whether *T. massinoti* was a sexually mature adult or a metamorphosing juvenile, it is evident from the relative positions of the sacral ribs, the anterior ends of the ilia, the caudal vertebrae and the acetabula that posterior migration of the ischio-pubic region has not taken place and that the position of the sacrum has been determined little if at all by anterior growth of the ilia.

The sacral vertebra of living anurans varies considerably in external form, not only in the nature of its articulations with the presacral vertebra and the urostyle (see Griffiths, 1963) but also in the shape of its pleurapophyses, which may be of almost uniform width throughout their length as in *Rana* (Noble, 1931 ; Ramaswami, 1933), or slightly expanded as in *Leiopelma* and *Ascaphus* (E. M. Stephenson, 1952, 1960 ; Ritland, 1955) or broadly expanded distally as in other anurans including *Scaphiopus* and *Xenopus* (Noble, 1931). According to E. M. Stephenson (1952, 1960) the sacral vertebra of *Leiopelma* appears to be unique in the Anura because the bony neural arches are joined together dorsally and ventrally by cartilage and the vertebra as a whole is narrower from front to back than the presacral vertebrae. The sacral vertebra of *Ascaphus* as described by Ritland (1955) is fully ossified and of normal size comparable to that of *Discoglossus*. In horizontal section the sacral vertebra of *Ascaphus* (Ritland, 1955, Fig. 3A) resembles the presacral vertebrae in that the mesial surfaces of the neural arch bases lie close to the surface of the unconstricted notochord, whereas horizontal sections of *Leiopelma* (Fig. 9) show the arch bases to be widely separated from the surface of the notochord which has become greatly constricted by hyperplasia of the perichordal tube within the vertebra. Whether the marked difference seen here between the sacral vertebrae of *L. archeyi* and *L. hochstetteri* is of normal occurrence could not be determined from the material available but, of these two specimens, the sacral vertebra of *L. archeyi* more closely resembles the presacral vertebrae in the size of the arch bases and their relationship to the perichordal tube than does the sacral vertebra of *L. hochstetteri*.

From E. M. Stephenson's (1952, 1960) descriptions and illustrations of the sacral vertebra in *Leiopelma*, its failure to fuse ventrally appears to be due to the absence of a centre of ossification between the arch bases like those of the more anterior vertebrae. However, the atlas also lacks a mid-ventral centre of ossification (E. M. Stephenson, 1960, Fig. 3), yet this vertebra becomes enclosed in bone in later stages, apparently due to ventral growth and subsequent fusion of the bone of the neural arches. As the sacral vertebra fails to ossify dorsally and ventrally even in comparatively aged specimens in which the mid-dorsal cartilage has calcified (E. M. Stephenson, 1960), it would appear that the persistence of cartilage mid-dorsally and mid-ventrally in this vertebra has not resulted simply from delayed development of the vertebra but has instead been selected for because of its functional significance. It probably serves as a shock-absorber to reduce jarring of the axial skeleton during saltorial locomotion, especially as the ligamentous connection between the ilia and the sacral pleurapophyses appears to be a firm one (E. M. Stephenson, 1952). According to Ridewood (1897), a close connection between the ilia and sacrum such as that found in " the frog " (presumably *Rana* sp.) is rare in anurans, the majority of which have considerable mobility of the ilia relative to the sacrum, especially those genera with broadly expanded sacral pleurapophyses. In terrestrial anurans, mobile sacro-iliac articulations would act as shock-absorbers, but in some aquatic forms such as *Pipa* and *Xenopus* the extreme mobility of these joints is an adaptation to allow rapid elongation of the body to dilate the pharynx for the rapid engulfment of food (Willem, 1939).

Relationship between Leiopelma *and* Ascaphus

The vertebral morphology of *Ascaphus* and *Leiopelma* is not indicative of close relationship between them. Although the persistence of a continuous notochord in adult stages and the absence of synovial joints between the bodies of consecutive vertebrae are character-states found only in these two genera of anurans, they have been shown already to be character-states inherited from the ancestors of the Anura and could therefore have persisted independently in distantly related genera. Although the moniliform configuration of the notochord is similar in *Ascaphus* and *Leiopelma*, it results from greater constriction between vertebrae than within them due to centripetal growth of the intervertebral cartilage, and centripetal growth of the intervertebral cartilage also occurs in other anurans which acquire synovial intervertebral joints such as *Rana temporaria* (Mookerjee, 1931). Other vertebral characteristics, on the other hand, such as the continuous fibrous core of the notochord in *Ascaphus* and the structure of the sacral vertebra in *Leiopelma*, as well as other differences between the two genera reported by Noble (1931), E. M. Stephenson (1951), N. G. Stephenson (1951*b*), Stephenson, Robinson and Stephenson (1972) and Robinson, Stephenson and Stephenson (1973) strongly suggest that *Ascaphus* and *Leiopelma* are not sufficiently closely related to be placed in the same family (see Kuhn, 1967 ; Fawcett and Smith, 1971).

In view of the number of character-states shared by *Ascaphus* and *Leiopelma* which appear to be primitive states in anurans generally (Howes, 1888 ; Noble, 1931 ; de Villiers, 1934*a*, 1934*b* ; Pussey, 1943 ; E. M. and N. G. Stephenson, 1947 ; N. G. Stephenson, 1951*b*, 1965 ; Szarski, 1951 ; E. M. Stephenson, 1951, 1952, 1955, 1960 ; Ritland, 1955 ; Griffiths, 1963), it would appear that these two genera are both relics of ancient but otherwise independent groups within the Anura. Further support for this contention is provided by the presence of additional primitive character-states in one genus or the other, such as the well-developed abdominal ribs of *Leiopelma*, traces of which also appear in the discoglossid *Bombina* but which are absent from *Ascaphus* (Noble, 1931; E. M. Stephenson, 1952, 1960).

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EXPLANATION OF PLATES

Abbreviations : *a*, atlas ; *alh*, anterior lymph heart ; *cart*, cartilage ; *fc*, fibrous cartilage ; *g*, ganglion of 13th spinal nerve ; *il*, ilium ; *ivc*, intervertebral cartilage ; *my*, myotome ; *ms*, marrow space ; *n*, *na*, neurapophysis or neural arch ; *nab*, base of neural arch ; *nal*, lamina of neural arch ; *nc*, notochord ; *ncs*, notochordal sheath ; *occ*, occipital condyle ; *pb*, perichondral bone ; *pct*, perichordal tube ; *plp*, pleurapophysis ; *prz*, prezygapophysis ; *pz*, postzygapophysis ; *r*, rib ; *sc*, spinal cord ; *scp*, suprascapula ; *scr*, subchordal rod ; *sg*, spinal nerve ganglion ; *sg9*, *sg11*, *sg16*, *sg18*, ganglia of 9th, 11th, 16th and 18th spinal nerves ; *sn13*, 13th spinal nerve ; *snab*, base of sacral neural arch ; *splp*, sacral pleurapophysis ; *trp*, transverse process ; *u*, urostyle ; *V5*, *V9*, 5th and 9th vertebrae ; *zb*, zygapophyseal bar.

Plate ix

Vertebrae of intracapsular embryos of *Leiopelma archeyi* in transverse section. A. Mid-trunk vertebra of a Stage 2 embryo. Van Gieson. B.–G. Stage 3 embryo. Azan. B. Region between bases of atlantal neurapophyses and occipital region of chondrocranium. C. Posterior region of neural arch base of second vertebra showing its relationship to the perichordal tube and the notochord. D. Third vertebra showing relationship between neurapophysis, mesenchymatous rib and anterior lymph heart. E. Seventh vertebra with mesenchymatous rib. F. Intervertebral region between eighth and ninth vertebrae. Note mesenchymatous zygapophyseal bar. G. Eleventh vertebra. The single arrow in E and G indicates cells migrating from the dorsal extremity of the myotome to the dorsal region of the neurapophysis.

Plate x

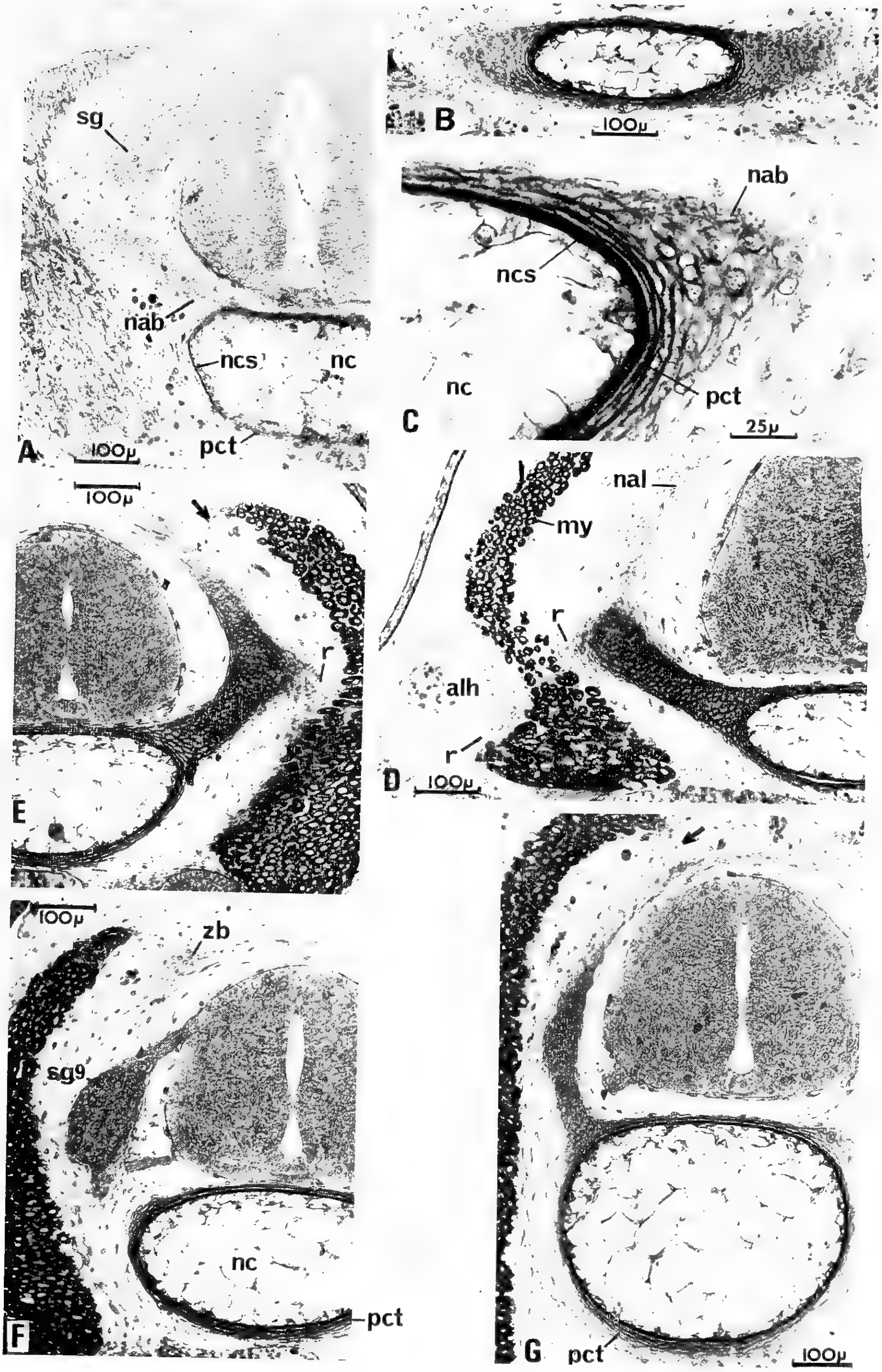
Axial skeleton of late intracapsular embryos of *Leiopelma archeyi*. A and B, Stage 4, L. S. Azan. A. Developing atlanto-occipital joint. B. Procartilaginous zygapophyseal bar between fourth and fifth vertebrae. C.–F. Stage 5. C. Tenth vertebra with mesenchymatous rib. T. S. Azan. Migration of cells from dorsal extremity of myotome to neurapophysis is indicated by the double arrow. D. Eleventh vertebra with mesenchymatous rib and mid-ventral hyperplasia of perichordal tube. T. S. Azan. E. Cartilaginous zygapophyseal bar between fifth and sixth vertebrae. Oblique H. S. Masson. F. Posterior trunk and anterior tail. Note tract of cartilage, *cart*, along dorsolateral surface of notochord. Oblique H. S. Masson. The single arrow in A, B and E points anteriorly.

Plate xi

Vertebrae of *Leiopelma archeyi* at hatching (Stage 6) and three weeks after hatching (Stage 9) in transverse section. Azan. A.–F. Stage 6. A. Cartilaginous rib of third vertebra showing its relationship to the transverse process of the neural arch and the anterior lymph heart. B. Cartilaginous rib and transverse process of fourth vertebra. C. Mesenchymatous rib of eleventh vertebra. D. Twelfth vertebra with mesenchymatous rib and subchordal rod. E. Thirteenth vertebra with mesenchymatous rib and subchordal rod. F. Oblique T.S. of fourteenth vertebra showing maximum height of neural arch on the left and the tract of cartilage joining the bases of the neural arches on the right. Limits of perichordal tube are ill-defined. G.–L. Stage 9. G. Developing atlanto-occipital joint. H. Developing zygapophyseal joint between third and fourth vertebrae. J. Anterior lymph heart lying between pleurapophysis of third vertebra and suprascapula. K. Pleurapophysis of sixth vertebra showing rib fused to transverse process. L. Ligamentous connection between sacral pleurapophysis and ilium. All figures are to the same scale shown at bottom of plate.

Plate xii

Urostylar region of *Leiopelma archeyi* three weeks after hatching (Stage 9) and vertebrae of adult *Leiopelma*. A.–E. Developing urostyle in *L. archeyi*, Stage 9. T.S. Azan. A. Eleventh vertebra showing fusion of subchordal rod to neural arch bases and constriction of notochord. B. Thirteenth vertebra. C. Subchordal rod and tracts of cartilage on dorsolateral surfaces of notochord posterior to 14th pair of spinal nerves. D. Posterior end of subchordal rod immediately anterior to 16th pair of spinal nerves. E. Axial skeleton of tail immediately posterior to end of subchordal rod and 16th pair of spinal nerves. F.–J. Vertebrae of adult *Leiopelma*. H.S. F. Atlanto-occipital joint of *L. hochstetteri*, showing fibrous cartilage in the notochordal canal in the anterior end of atlas and the posterior region of the *basis cranii*. Masson. G. Mid-trunk vertebrae of *L. hochstetteri*. Masson. Only the right side of the column is shown. H. Mid-vertebral and intervertebral regions of the notochord in the trunk of *L. archeyi*. Mallory. J. Posterior trunk vertebrae, sacral vertebra and anterior urostyle of *L. archeyi*. Mallory. The arrow accompanying figures F.–J. points anteriorly.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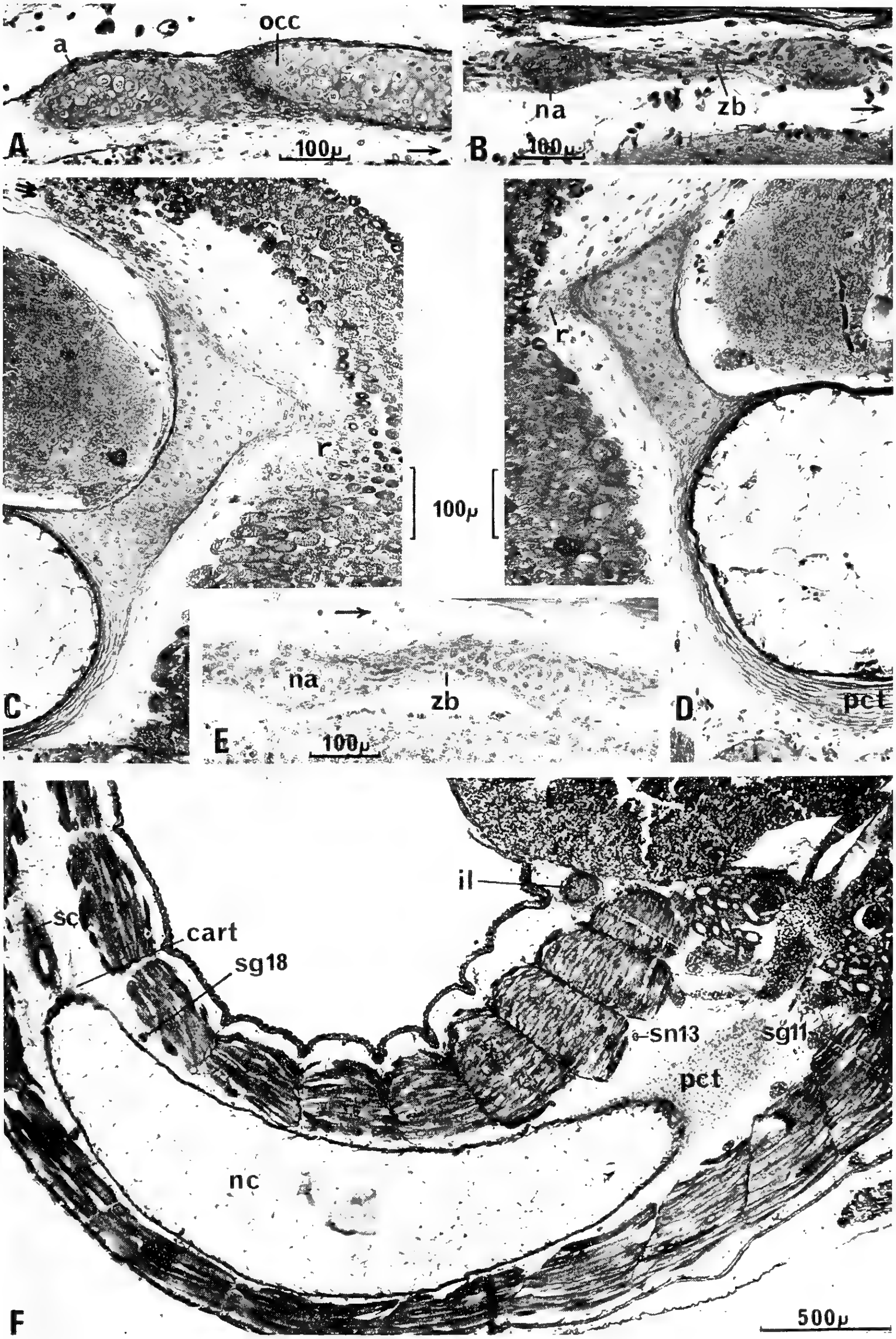
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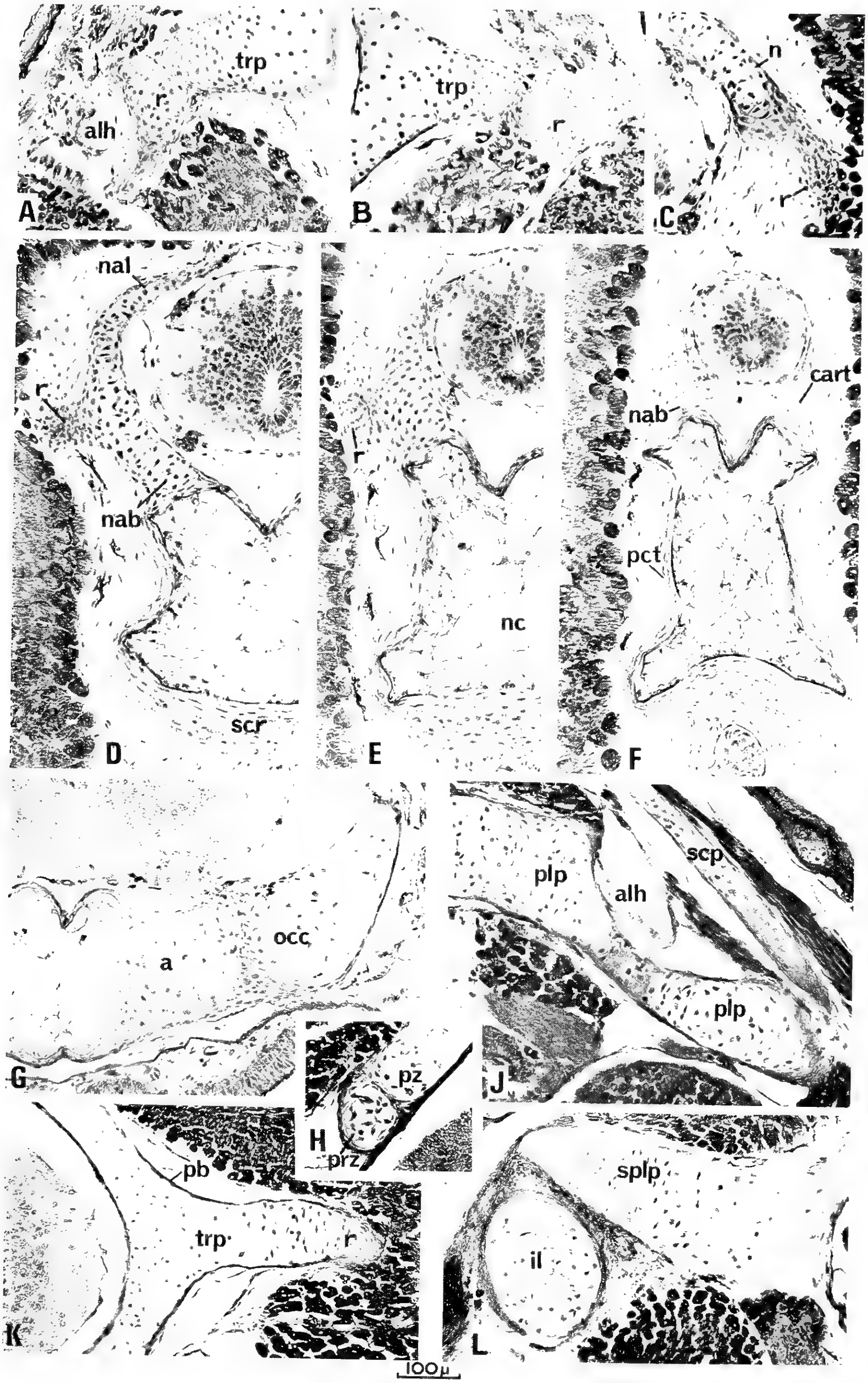
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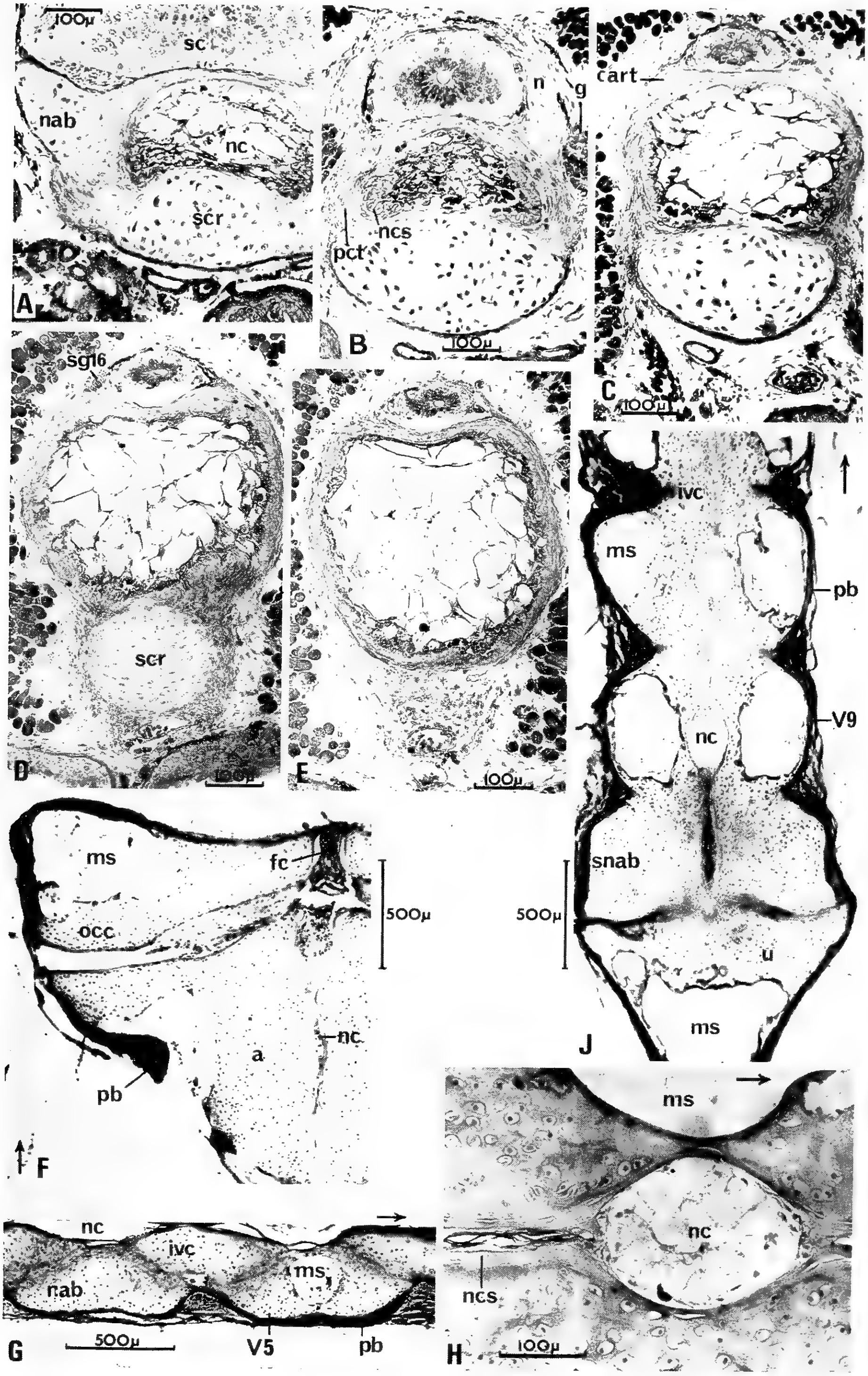
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POLYCHAETA OF WALLIS LAKE, NEW SOUTH WALES

PATRICIA HUTCHINGS*

[Accepted for publication 19th September 1973]

Synopsis

A systematic account of the polychaete fauna of Wallis Lake, New South Wales, is given. Five new species are described belonging to the genera, *Haploscoloplos, Barantolla, Euclymene, Lysilla* and *Rhinothelepus*, the latter being a new genus.

INTRODUCTION

The Polychaeta described in this paper were collected during an ecological survey of Wallis Lake, conducted by the Zoology Department of University of New South Wales.

Wallis Lake is a salt-water coastal lagoon on the central coast of New South Wales. The lake is approximately 12 miles long and 3 miles across at its widest point. The maximum depth of water is 16 feet. The lake is continually open to the sea at its northern end at Forster. Two small creeks flow into the northern part of the lake, which carry large amounts of fresh water after periods of prolonged rain.

All the polychaetes were collected from the eastern shores of the lake during December 1970, using a Smith-McIntyre grab. Thirty-two species of polychaetes were found, of which six are new species, and one of these is placed in a new genus. Five of these new species are described in this paper. Of the remaining species, four are new records for Australia and four have been described to genus only. Type material has been deposited in the Australian Museum (AM), British Museum (Natural History) (BM) and the Smithsonian Institution (USNM). The remainder of the collection has been deposited in the Australian Museum, apart from a small reference collection given to the Zoology Department, University of New South Wales.

The benthic communities and detailed descriptions of the habitats are being described by O'Gower, Dixon and Hutchings (in preparation), but a brief description of habitats and locality are given below (see Fig. 1).

STATIONS

Nine sites in Wallis Lake were selected, and at each site 50 replicate samples were collected.

1– 50	Sand-Booti Booti.
51–100	Mixed weed bed of marine angiosperms, opposite Yahoo Island.
101–150	Sand, just south of above.
151–200	Mainly sandy mud clay. Sparse *Halophila* (marine angiosperm), Charlotte Bay.
201–250	Just inshore of above, very thick weed and clayey mud, Charlotte Bay.
251–300	Sand, south of Godwin Island and opposite Wallis Island.
301–350	*Posidonia* Beds (marine angiosperm), just west of above.
351–400	*Zostera* Beds (marine angiosperm), just west of above.
401–450	Sand, fast flowing, just west of stations 301–350.

It may seem surprising that such a relatively small area as Wallis Lake should yield six new species, one of which is placed in a new genus and four new records for Australia; but polychaetes have been neglected in Australia. The majority of Australian polychaete records are based upon work done at the

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* The Australian Museum.

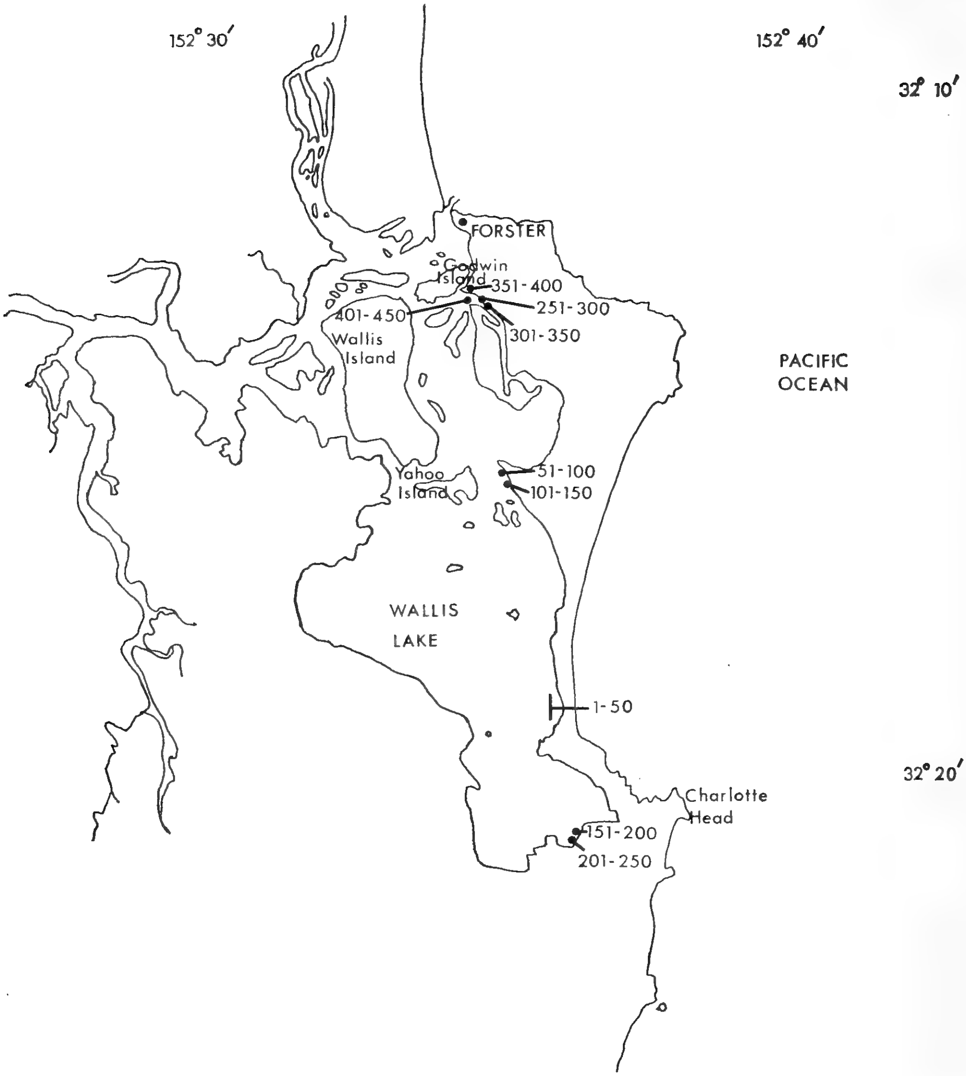

Fig. 1. Wallis Lake showing station numbers.

beginning of this century by Haswell, Benham, Augener and Fauvel and more recently by Rullier (1965) and Knox and Cameron (1971). For this reason there are many undescribed species of polychaetes in Australia, and the geographical distribution of described species is poorly known.

This is the first of a series of papers which will describe the polychaete fauna of estuaries and coastal lagoons on the eastern coast of Australia.

Systematic Account

The nomenclature is that of Hartman (1959*a*, 1965) except for the sub-genus *Hediste*, where Pettibone (1963) has been followed. Synonymies have been given only when they refer to Australian records.

SPECIES LIST

POLYNOIDAE	*Eunoe etheridgei* Benham
SIGALIONIDAE	*Sthenelais boa* (Johnston)
PHYLLODOCIDAE	*Eulalia* sp.
	Phyllodoce duplex McIntosh
NEREIDAE	*Australonereis ehlersi* (Augener)
	Ceratonereis mirabilis Kinberg
	Nereis (*Hediste*) *diversicolor* O. F. Müller
	Platynereis dumerilii antipoda Hartman
NEPHTYIDAE	*Nephtys australiensis* Fauchald
	Nephtys n. sp.
GLYCERIDAE	*Glycera americana* Leidy
EUNICIDAE	*Marphysa sanguinea* Montagu
LUMBRINERIDAE	*Lumbrineris latreilli* Audouin and Milne Edwards
ARABELLIDAE	*Arabella* sp.
SPIONIDAE	*Prionospio malmgreni* Claparède
	Scolelepis sp.
CIRRATULIDAE	*Cirriformia tentaculata* Montagu
ORBINIIDAE	*Haploscoloplos simplex* n. sp.
OPHELIIDAE	*Armandia intermedia* Fauvel
SCALIBREGMIDAE	*Hyboscolex longiseta* Schmarda
CAPITELLIDAE	*Barantolla lepte* n. sp.
	Notomastus hemipodus Hartman
	Scyphoproctus djiboutiensis Gravier
ARENICOLIDAE	*Arenicola bombayensis* Kewalramani *et al.*
MALDANIDAE	*Euclymene trinalis* n. sp.
OWENIIDAE	*Owenia fusiformis* della Chiaje
TEREBELLIDAE	*Lysilla apheles* n. sp.
	Lysilla pacifica Hessle
	Streblosoma amboinense Caullery
	Rhinothelepus lobatus n. g., n. sp.
	Pista sp.
SABELLIDAE	*Branchiomma cingulata* (Grube)

Family POLYNOIDAE Malmgren, 1867

Genus EUNOE Malmgren, 1865

Eunoe etheridgei Benham, 1915

Harmothoe (*Eunoa*) *etheridgei* Benham, 1915 : 197–200, figs 43–51.

Stations

351–400, two specimens.

Remarks

This species has not been recorded since Benham (1915) described it from off Gabo Island, Victoria, in 200 fathoms. The Wallis Lake specimens agree well with the description given by Benham. The median and lateral antennae are darkly pigmented. The elytra are covered in small greyish black spots, with some black conical tubercles scattered along the posterior margins. The elytral margins are heavily fringed with papilla.

Previously known distribution

Off Gabo Island, Victoria, Australia, in 200 fathoms.

Family SIGALIONIDAE Malmgren, 1867

Genus STHENELAIS Kinberg, 1855

Sthenelais boa (Johnston, 1839)

Sigalion boa Johnston, 1839 : 439.
Sthenelais boa.—Fauvel, 1923 : 110, fig. 41*a*-1 ; Day, 1967 : 109, fig. 1.20 f-1.

Stations

351–400, several specimens.

Remarks

This species has been recorded from Moreton Bay, Queensland, by Rullier (1965).

Previously known distribution

Atlantic from Scotland ; English Channel ; North Carolina, U.S.A. ; south to Senegal ; Mediterranean ; and S. Africa.

Family PHYLLODOCIDAE Williams, 1852

Genus EULALIA Savigny, 1817

Eulalia sp.

Stations

151–200.

Remarks

A small anterior fragment, which cannot be positively identified to species.

Genus PHYLLODOCE Savigny, 1818

Phyllodoce duplex McIntosh, 1885

Phyllodoce duplex McIntosh, 1885 : 167–168, pl. 27, fig. 8, pl. 32, fig. 9, pl. 15*a*, fig. 1 ; Augener, 1913 : 126.

Stations

401–450, one specimen.

Remarks

One specimen with a partially everted proboscis. Central discs of brown pigment between each segment.

Previously known distribution

Twofold Bay, New South Wales, in 150 fathoms ; and Port Phillip Bay, Victoria, Australia.

Family NEREIDAE Johnston, 1865

Genus AUSTRALONEREIS Hartman, 1954

Australonereis ehlersi (Augener, 1913)

Nereis (*Leonnates*) *ehlersi* Augener, 1913 : 142–145, pl. 3, fig. 53, text-fig. 12*a-c*.
Leonnates ehlersi.—Monro, 1938 : 618-628, figs 7–13.
Leptonereis ehlersi.—Monro, 1938 : 618-628, figs 7–13.
Australonereis ehlersi.—Hartman, 1954 : 19–23, figs 1–6.

Stations

1–50, 101–150, 251–300 ; 13, eight and seven specimens respectively.

Remarks

This species is commonly found in sandy muddy habitats in estuarine or lagoon situations. It lives in a limp sandy tube.

Previously known distribution

Western Australia ; Victoria ; and New South Wales ; and the author has also found it in Hervey Bay, Queensland, Australia.

Genus CERATONEREIS Kinberg, 1866

Ceratonereis mirabilis Kinberg, 1866

Ceratonereis mirabilis Kinberg, 1866 : 170 ; Day, 1967 : 324, fig. 14.10*a-g*.

Stations

301–350, 351–400, many specimens.

Remarks

This species appears to be widespread throughout Australia and has been recorded from *Zostera* beds, intertidally in sand, in mussel clumps and offshore in 30–40 fathoms.

Previously known distribution

Brazil ; Gulf of Mexico ; Red Sea ; Indo-West Pacific to Japan ; Solomon Islands ; and Australia.

Genus NEREIS Linnaeus, 1758

Nereis (*Hediste*) *diversicolor* O. F. Müller, 1776

Nereis diversicolor.—Fauvel, 1923 : 344, fig. 133*a-f*.
Nereis (*Hediste*) *diversicolor* Pettibone, 1963 : 174–179, fig. 44*g-h*.
Neanthes diversicolor Hartman, 1960 : 35.

Stations

1–50, 101–150, 201–250, 251–300, numerous specimens.

Description

This species is characterized by the presence of one or two simple falcigers, in the supra acicular neuropodial lobe of posterior segments. These setae are formed by the complete fusion of the end piece to the shaft of the falciger. All the notopodial setae are spinigerous. The arrangement of the paragnaths is as follows : I—0–9, II and IV—arched group, III—transverse mass of 2–3 irregular rows, V—0, VI—1–9, VII–VIII—wide scattered band of 1–2 irregular rows.

Remarks

Hartman (1960) placed this species in the genus *Neanthes* as the notosetae consist only of spinigers, and conical paragnaths are usually present on all areas of the proboscis. *N. diversicolor* is very similar morphologically to *N. japonica* Izuka and *N. limnicola* Johnson. These species can only be distinguished by their reproductive habit and the morphology of the sexually mature animals. Hartman (1959*b*, 1960) has suggested that all these species should be referred to *N. diversicolor.* Pettibone (1963) considers the three species to be valid and has suggested that they are placed in a separate subgenus *Hediste* to denote their close relationship. All these species are characterized by the simple falcigers. Unfortunately none of the specimens from Wallis Lake were sexually mature, so at this stage they are referred to *N. diversicolor*.

It seems likely that *Neanthes uncinula* Russell, described from the *Zostera* beds of Moreton Bay, Queensland (Russell, 1962), and which Rullier (1965) subsequently described from the same locality, may be synonymous with *N. diversicolor* or a member of this species complex. It differs from *N. diversicolor* in that paragnaths are absent from VI whereas *N. diversicolor* has 1–9 paragnaths on VI. But this problem cannot be resolved until a sexually mature individual of *N. uncinula* and its reproductive biology are described.

In Europe, *N. diversicolor* is common intertidally, in brackish or estuarine conditions, in mud, or muddy sand. It is often associated with weed beds. Similar conditions are present in Wallis Lake. *N. diversicolor* has not previously been recorded from the southern hemisphere.

Previously known distribution

Greenland; Iceland; Norway to English Channel; North Sea; Baltic; Mediterranean; Adriatic; Gulf of St. Lawrence to Massachusetts, U.S.A.; and Puerto Rico (?).

Genus PLATYNEREIS Kinberg, 1866

Platynereis dumerilii antipoda Hartman, 1954

Nereis (*Platynereis*) *australis*.—Augener, 1913: 182–184; 1923: 35–39. Not *Heteronereis australis* Schmarda, 1861.

Platynereis dumerilii antipoda Hartman, 1954: 35–36, figs 33–37.

Stations

201–250, one specimen.

Remarks

This species agrees well with the description given by Hartman (1954). *P. dumerilii antipoda* has only been described from Australia, whereas the nominate subspecies *P. dumerilii dumerilii* is cosmopolitan in temperate and tropical waters.

Previously known distribution

N.W. Tasmania; St. Vincent Gulf and Pennington Bay, South Australia; and Sydney, New South Wales.

Family NEPHTYIDAE Grube, 1850

Genus NEPHTYS Cuvier, 1817

Nephtys australiensis Fauchald, 1965

Nephtys australiensis Fauchald, 1965: 334–335, figs 1–2.

Stations

51–100, 101–150, 151–200, 201–250, 251–300, 351–400; one, 13, 28, four, many, six specimens respectively.

Remarks

This species is commonly distributed throughout weed beds and muddy sand flats in New South Wales, and the author has recorded it from Hervey Bay, Queensland.

Previously known distribution

South Australia and New South Wales, Australia.

Genus NEPHTYS Cuvier, 1817
Nephtys n. sp.

Stations

401–450, numerous specimens.

Remarks

This is a new species which is being described by Hannelora Paxton (1974), therefore no further comment is made here except to record its presence in Wallis Lake.

Family GLYCERIDAE Grube, 1850
Genus GLYCERA Savigny, 1818
Glycera americana Leidy, 1855

Glycera americana Leidy, 1855 : 147–148, pl. 11, figs 49–50 ; Augener, 1922 : 29–35 ; 1927 : 196 ; Knox, 1960 : 221–223, figs 1–3.

Stations

251–300, one specimen.

Description

The gills begin on the XVI–XVII segment and continue to near the posterior end. They arise from the posterior side of the parapodia. Each gill is a ramose structure borne on a short basal stem.

Previously known distribution

East coast of America from New England to Brazil ; west coast of America from Canada to Peru ; New Zealand ; South Australia, Victoria, Queensland, and New South Wales in Australia.

Family EUNICIDAE Savigny, 1818
Genus MARPHYSA Quatrefages, 1865
Marphysa sanguinea (Montagu, 1815)

Nereis sanguinea Montagu, 1815 : 20.

Marphysa sanguinea.—Fauvel, 1923 : 408, fig. 161*a-h* ; Day, 1967 : 396, figs 17.5*u-y*.

Marphysa furcellata Crossland, 1903 : 141, pl. 15, figs 13–14 ; Augener, 1913 : 281.

Stations

301–350, 351–400, three specimens.

Remarks

Commonly found in weed beds of *Zostera* or *Posidonia* in New South Wales.

Previously known distribution

N. Atlantic ; English Channel ; Mediterranean ; Senegal ; North Carolina, U.S.A., to the Gulf of Mexico ; Southern California ; Japan ; New Zealand ; Western Australia, Moreton Bay and the Great Barrier Reef, Queensland, Australia.

Family LUMBRINERIDAE Malmgren, 1867
Genus LUMBRINERIS Blainville, 1828
Lumbrineris latreilli Audouin and Milne Edwards, 1833

Lumbrineris latreilli Audouin and Milne Edwards, 1833 : 242, pl. 12, figs 13–15 ; Day, 1967 : 438, figs 17.16*p-t*.

Lumbriconereis latreilli.—Fauvel, 1923 : 431, fig. 171*m-r*.

Stations

51–100, one specimen.

Remarks

The specimen fits the description given by Day well except that the blade of the compound hooks present in the anterior parapodia appears slightly shorter. This species has previously been recorded from Australia in Port Phillip Bay, Victoria, by Knox and Cameron (1971).

Previously known distribution

Cosmopolitan in temperate and tropical seas.

Family ARABELLIDAE Hartman, 1944

Genus ARABELLA Grube, 1850

Arabella sp.

Stations

251–300, one fragment.

Remarks

A small posterior fragment.

Family SPIONIDAE Grube, 1850

Genus PRIONOSPIO Malmgren, 1867

Prionospio malmgreni Claparède, 1870

Prionospio malmgreni Claparède, 1870 : 73 ; Day, 1967 : 492–493, fig. 18.9*a-c* ; Hartman, 1969 : 161, figs 1–4.

Stations

51–100, 151–200, 201–250, 251–300, 301–350, 351–400 ; several specimens collected at each locality.

Remarks

P. malmgreni is distinguished by the presence of a prominent transverse membranous ridge which unites the lamellae of setiger 7. Less conspicuous ridges are present on the next few segments. Pluridentate hooded hooks appear in the neuropodia from setiger 14 and in the notopodia after setiger 40.

Previously known distribution

Atlantic from North Carolina, U.S.A. ; North Sea ; Mediterranean ; South California ; Japan ; and Solomon Islands.

Genus SCOLELEPIS Blainville, 1828

Scolelepis sp.

Stations

251–300, 351–400.

Remarks

A few anterior fragments were found which could not be positively identified. The neuropodial setae are long hooded hooks with two teeth above the main fang. The notopodial setae are very narrow winged capillaries. Some of the fragments are full of large oocytes.

Family CIRRATULIDAE Carus, 1863

Genus Cirriformia Hartman, 1936

Cirriformia tentaculata (Montagu, 1808)

Terebella tentaculata Montagu, 1808 : 110.
Audouinia tentaculata.—Fauvel, 1927 : 91, fig. 32*a-g*.
Cirriformia tentaculata.—Day, 1967 : 515, fig. 20 : 4*a-d*.

Stations

251–300, 301–350, 351–400 ; few specimens.

Previously known distribution

North Sea ; English Channel ; W. Africa ; S. Africa ; Indian Ocean ; Japan ; New Caledonia ; New Zealand ; and Port Phillip Bay, Victoria, Australia.

Family ORBINIIDAE Hartman, 1942

Genus Haploscoloplos Monro, 1933

Haploscoloplos simplex n. sp.

(Fig. 2A-D)

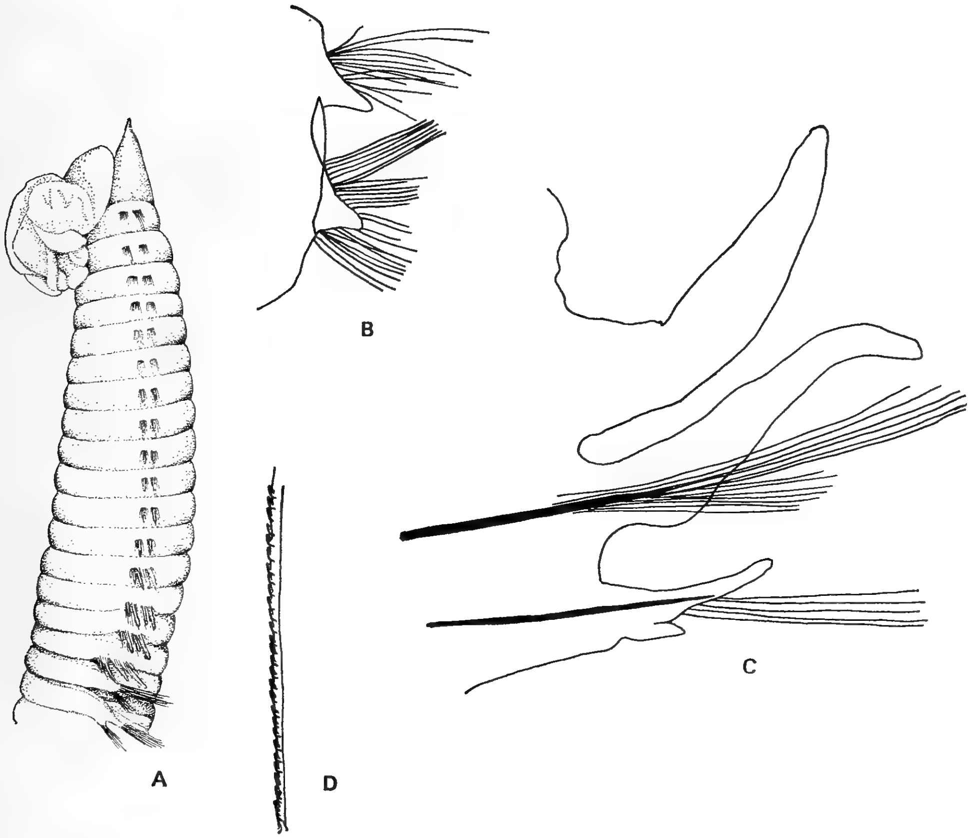

Fig. 2. *Haploscoloplos simplex*. A, Anterior lateral view. B, Early thoracic parapodium. C, Abdominal parapodium. D, Side view of part of notopodial seta.

Holotype (AM. W.5246) complete specimen 6·5 cm in length, 2 mm wide. Paratypes (AM. W.5002, W.5004, W.5005), eight, four and 11 specimens respectively (BM. ZB.1973: 1) (USNM. 49487).

All material collected from Stations 401–450, which is a sandy habitat.

Description

Preserved specimens white. Transition from thorax to abdomen is at setigerous segments 16–18. Branchiae are present from the 12th segment onwards. The thoracic branchiae are small, but the abdominal ones are well developed simple cylindrical filaments. The prostomium is a tapered cone. Faded eye spots are arranged in two oval patches at the base of the prostomium.

In the thorax the notopodial postsetal lobe is a small elongated lobe which gradually increases in size towards the posterior thorax, but it never exceeds one-third of the length of the setae. The thoracic neuropodial postsetal lobe is present from the 9th setiger and is a simple narrow triangular lobe. No interramal cirri or stomach papillae are present on the thorax or abdomen. The thoracic neurosetae consist of two types, (1) long distally pointed spinous setae, which when viewed side on have a toothed appearance, and (2) 10–15 simple acicular type setae with a slightly bent tip. The bases of these setae appear to be split, and they are slightly more chitinized than the spinous setae.

In the abdomen the branchiae are well developed simple cylindrical filaments with tapered tips. The postsetal abdominal notopodial lobe is a simple narrow leaf-shaped lobe and is the same length as the notosetae. The corresponding neuropodial lobe is smaller than the notopodial lobe and is split unequally just below the tip. The dorsal part is well developed, whereas the ventral part is much smaller. The abdominal neuropodia are supported by a single yellow aciculum. All the abdominal setae are spinous, no furcate setae are present. The posterior ventral margins of the segments have slightly thickened glandular edges.

Remarks

Haploscoloplos simplex can be distinguished from *H. bifurcatus* Hartman, which has been recorded from New South Wales and South Australia, by the absence of divided thoracic neuropodial postsetal lobes. The only other species of this genus recorded from Australia is *H. kerguelensis* (McIntosh), which differs from *H. simplex* in that the transition from thorax to abdomen occurs between segments 9–11, and thoracic branchiae are absent. *H. simplex* can be distinguished from all other species of this genus except *H. panamensis* Monro by the presence of simple branchiae and the segment on which they begin and also the segments at which the transition from thorax to abdomen occurs. *Haploscoloplos panamensis* closely resembles *H. simplex* but differs in that the posterior thoracic neuropodial postsetal lobe is divided and that furcate setae are present.

Family OPHELIIDAE Malmgren, 1867

Genus ARMANDIA Filippi, 1861

Armandia intermedia Fauvel, 1902

Armandia intermedia Fauvel, 1902: 86, figs 29–30; Day, 1957: 104.

Armandia lanceolata Willey, 1905: 288, pl. 5, fig. 120; Augener, 1914: 33.

Stations

201–250, three specimens.

Remarks

This species has previously been recorded from Australia as *A. lanceolata*, which Day (1957) synonymized with *A. intermedia*.

Previously known distribution

Red Sea; Ceylon; Japan; New Caledonia; Solomon Islands; N.W. Australia; Low Isles, Queensland, and Port Phillip Bay, Victoria, Australia.

Family SCALIBREGMIDAE Malmgren, 1867
Genus HYBOSCOLEX Schmarda, 1861
Hyboscolex longiseta Schmarda, 1861

Hyboscolex longiseta Schmarda, 1861: 54, pl. 27, fig. 211; Day, 1967: 588–589, fig. 27.2*a-d*.
Lipobranchius capensis Willey, 1904: 266, pl. 14, fig. 14, pl. 15, figs 23–24.

Stations

301–350, 351–400; six specimens.

Remarks

This is the first record of this family from Australia, although this species has been recorded from New Zealand. The specimens from Wallis Lake are 10–15 mm long with a prominent T-shaped prostomium. The eyes are completely hidden by the peristomial fold.

Previously known distribution

Natal, S. Africa; S.W. Africa; New Zealand; and Solomon Islands.

Family CAPITELLIDAE Grube, 1862
Genus BARANTOLLA Southern, 1921
Barantolla lepte n. sp.
(Fig. 3A-D)

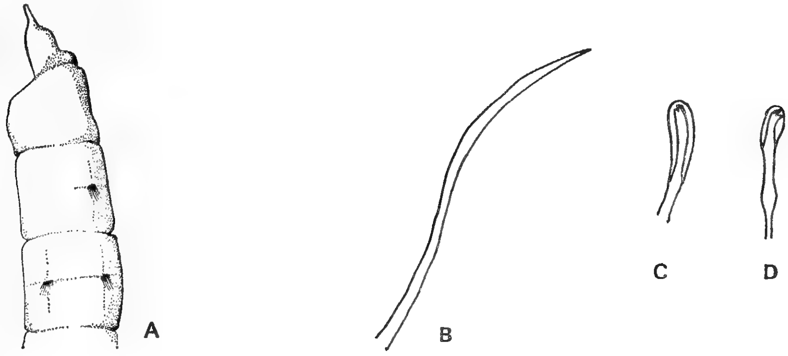

Fig. 3. *Barantolla lepte.* A, Anterior lateral view. B, Thoracic capillary seta. C, Thoracic hooded hook. D, Abdominal hooded hook.

Holotype (AM. W.5407) Station 1–50, incomplete specimen, 45 mm long, 1 mm wide with 65 abdominal segments.

Paratypes (AM. W.5413) Station 1–50, five specimens; (AM. W.5414) Station 1–50, 55 specimens; (AM. W.5415) Station 101–150, 55 specimens; (AM. W.5408) Station 151–200, 220 specimens; (AM. W.5416) Station 151–200, 35 specimens; (AM. W.5412) Station 151–200, 15 specimens; (AM. W.5411) Station 201–250, five specimens; (AM. W.5409) Station 251–300, 42 specimens; (AM. W.5410) Station 351–400, 13 specimens; (BM. ZB.1973: 4) Station 256, 10 specimens; (USNM. 49489) Station 252, 10 specimens.

This species is found in a wide range of habitats from sand, mud and weed beds.

Description

Small thread-like worms, encased in a fine mucous sandy tube. There are no visible branchiae. The thorax consists of 11 setigerous segments and the abdomen of numerous segments. The pygidium is a heart-shaped lobe without appendages. The prostomium is a pointed cone with a slightly bulbous tip. On either side of the base of the prostomium is a slanting patch of 10–15 subepidermal eye spots.

The first thoracic segment is apodous and is twice the length of the first setigerous segment, which has only a fascicle of notosetae. The setae of thoracic segments 2–7 are narrow winged capillaries. The remaining thoracic segments 8–12 have long-handled hooded hooks in both the neuro- and notopodia. There are no mixed fascicles of capillary setae and hooks. The formula of the thoracic setae may be expressed as follows:

$$\text{First thoracic segment} + \frac{6s+5h}{0+5s+5h}$$

where s refers to capillary setae and h to hooded hooks.

Segments 8–12 are slightly longer than the preceding ones and are slightly bi-annulate. The transition from the thorax to the abdomen is well marked as abdominal setae are borne on raised glandular tori. Both fascicles of notosetae are borne on the same torus, whereas the fascicles of neurosetae are on separate tori. These glandular tori give the abdominal segments a slightly capanuliform shape. All the abdominal setae are short-hooded hooks. The abdominal epidermis is marked by a series of narrow rings.

Remarks

Barantolla lepte is placed in the genus *Barantolla* as it has 12 thoracic segments, of which 11 are setigerous. The notosetae of the first six setigerous segments are capillary setae, and the remaining thoracic notosetae are hooded hooks. Only two other species of this genus have been described—*B. sculpta* Southern and *B. americana* Hartman. *B. lepte* can be distinguished from *B. sculpta* by the absence of abdominal segments with a membranous collar from which parapodial lobes and branchiae arise. *B. sculpta* has only been recorded from brackish pools near Salt Lake, Calcutta, India. The other described species, *B. americana*, differs from *B. lepte* in that the first eight thoracic neuropodia have capillary setae, where in *B. lepte* only the first five have capillary setae. The formulae for the thoracic setae of *B. americana* may be expressed as follows:

$$\text{First thoracic segment} + \frac{6s+1\ \text{mixed}+4h}{8h+3h}$$

More recently Hartman (1971) has described some specimens as "*Barantolla* near *americana*" from abyssal depths of 2,000–3,753 m, off southern California. These specimens have capillary setae in the first six thoracic, neuropodia and therefore they can also be distinguished from *B. lepte*. The formulae for the thoracic setae of "*B.* near *americana*" may be expressed as follows:

$$\text{First thoracic segment} + \frac{6s+1\ \text{mixed}+4h}{6s+5h}$$

Genus NOTOMASTUS Sars, 1851

Notomastus (*Clistomastus*) *hemipodus* Hartman, 1947

Notomastus (*Clistomastus*) *hemipodus* Hartman, 1947: 424, fig. 48; 1969: 393, figs 1–5.

Stations

1–50, 51–100, 101–150, 151–200, 201–250, 251–300, 301–350, 351–400; numerous specimens.

Description

Dark red in colour when alive, and often encased in a mucous tube with some sand grains adhering. Epithelium of anterior thoracic segments aereolated. Prostomium, depressed and conical, with two small patches of eye spots, almost hidden by the transverse nuchal slits. Peristomium a simple ring with no setae. Eleven thoracic setigerous segments, of which the first lacks neurosetae. All thoracic setae are capillaries. Numerous abdominal segments with no visible branchiae. Abdominal setae are long-handled hooks ; a crescent of 5–6 small teeth above the main fang. Small glandular patches around the abdominal podia. Nephridial apertures present on the ventral side of the neuropodia.

Remarks

This species has only previously been recorded intertidally from Beaufort, N. Carolina, and from 97 m in Newport Canyon on the west coast of America.

Previously known distribution

Beaufort, N. Carolina, and Newport Canyon, U.S.A.

Genus SCYPHOPROCTUS Gravier, 1904

Scyphoproctus djiboutiensis Gravier, 1904

Scyphoproctus djiboutiensis Gravier, 1904 : 557–561, figs 1–7 ; Fauvel, 1953 : 373, fig. 194*a-b* ; Day, 1967 : 604–605.

Stations

351–400 ; four specimens.

Description

This species has 12 thoracic setigers with capillary setae in both rami. Numerous abdominal thin-walled segments, with no gills present. The final abdominal segments are fused to the pygidium to form an anal plate. The plate slants posteriorly and is flattened dorsally and on its margins there are 10–12 groups of notopodial spines.

Remarks

This species has not been previously recorded from Australia.

Previously known distribution

Tropical Indian Ocean from Gulf of Aden ; Ceylon ; and Mozambique.

Family ARENICOLIDAE Johnston, 1846

Genus ARENICOLA Lamarck, 1801

Arenicola bombayensis Kewalramani, Wagh and Ranade, 1959

Arenicola cristata.—Ashworth, 1911 : 21–24 ; 1912 : 105–111, fig. 45 ; Augener, 1914 : 42. Not *Arenicola cristata* Stimpson, 1856.

Arenicola bombayensis Kewalramani, Wagh and Ranade, 1959 : 109 ; Wells, 1962 : 347–348, pl. 2–3.

Stations

201–250 ; several specimens.

Description

These worms were kindly identified by Professor G. P. Wells.

This species is characterized by 17 setigers, of which setigers VII to XVII are branchiferous. In life the stout pinnate gills are olive green in colour. There are seven pairs of nephridia which open on setigers V to XI.

Remarks

This species was first described from an intertidal mud flat near Bombay in 1959 by Kewalramani *et al.* In 1911 Ashworth described a variant of *A. cristata* from Barrow Island, N.W. Australia, and Augener (1914) confirmed this identification. Since then Wells (1962) has re-examined the specimens and referred them to *A. bombayensis*. The material from Wallis Lake represents the only other record of this species from Australia.

Previously known distribution

Bombay, India; and Barrow Island, N.W. Australia.

Family MALDANIDAE Malmgren, 1867

Genus EUCLYMENE Verrill, 1900

Euclymene trinalis n. sp.

(Fig. 4A-F)

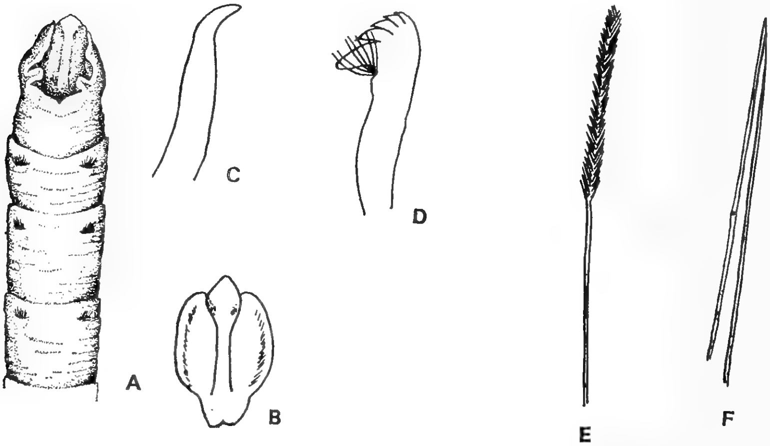

Fig. 4. *Euclymene trinalis*. A, Anterior end. B, Cephalic plate. C, Modified neuroseta from 3rd setiger. D, Neuroseta from posterior segments. E, F, notosetae.

Holotype (AM. W.5224). Station 251–300, complete specimen 6·5 cm in length and 2 mm wide at anterior end.

Paratype (AM. W.5227). Station 151–200, complete specimen 4·5 cm in length and 1 mm wide at anterior end.

Fragments of this species were also found at Stations 151–200 and 251–300. All specimens were living in sand or sandy mud habitats.

Description

Lives in firm sandy tubes. Reddish brown in colour. Small pointed prostomium. The cephalic plate is oval with small lateral indentations. The posterior margins of the plate are smooth with a small notch mid-posteriorly. Nuchal folds straight, and seven-eighths the length of the cephalic plate. A few ocelli present at the top of the nuchal folds, but they are more numerous on the anterior lateral sides of the cephalic rim and on the prostomium.

Body with 19 setigers and two achaetous preanal segments. First preanal segment slightly longer than second. Prominent pygidial ring. Anal funnel with 27–29 approximately equal triangular lobes plus one very much longer lobe. The tips of the lobe are tinged with bluish black pigment. The anus is sunk in the centre of the anal funnel surrounded by numerous radii. First five setigerous segments are approximately the same length, the segments then increase in length until segment 7, this length being maintained until the final two setigerous segments, which are shorter. The first five setigerous segments have a narrow collar which makes the segments appear slightly bell-shaped. The epidermis of the head is deeply aereolated. The last five setigerous segments are tinged with bluish green pigment and the epidermis is marked with numerous narrow rings. A narrow ventral longitudinal glandular strip is present on posterior segments.

Neurosetae of first three setigerous segments are simple smooth tipped acicular setae. The holotype and paratype show variation in the numbers of these acicular neurosetae and the number is not necessarily constant for a segment. The holotype has four, two, one on one side and one, one, three on the other side. The paratype has one, two, one and one, one, two respectively. The size of the acicular setae is not constant and where only a single one is present this tends to be very much larger than when four are present. Other fragments of this species found at the same stations exhibit similar variation. The remaining neurosetae have four teeth above the main fang with a well developed tendon. The rows of neurosetae are surrounded by patches of glandular tissue. On the posterior segments the neurosetae are on well marked raised glandular ridges which are joined dorsally by a thin strip of glandular material. Notosetae are of two kinds: (1) simple narrow bladed capillary setae with fine pointed tips, and (2) capillary setae with the posterior third finely barbed.

Remarks

Within the genus *Euclymene*, variation in the number of setigers and acicular setae is fairly common, but variation in the number of acicular setae within a segment has not been reported previously. Several species of *Euclymene* have 19 pairs of setigers, but they differ from *E. trinalis* in having one or three preanal segments, *E. tropica* (Monro) and *E. watsoni* (Gravier), *E. collaris* (Claparède) and *E. lombricoides* (Quatrefages) respectively. *E. trinalis* has a similar number of setigers and preanal segments to *E. papillata* Berkeley and Berkeley and *E. auklandica* Augener but differs in that the acicular setae are smooth tipped, lacking any signs of vestigial hooks.

E. glandularis (Day) appears to be the most closely related species to *E. trinalis*, but *E. glandularis* has a crenulated posterior margin of the cephalic plate and the neurosetae have 5–6 teeth above the main fang, whereas *E. trinalis* has a smooth posterior margin to the cephalic plate and the neurosetae have only four teeth above the main fang.

Family OWENIIDAE Rioja, 1917
Genus Owenia delle Chiaje, 1844
Owenia fusiformis delle Chiaje, 1844

Owenia fusiformis.—Day, 1967: 649–651, fig. 31.1*e-j*.

Stations

51–100, 201–250; two specimens.

Remarks

Rullier (1965) recorded *O. fusiformis* from Moreton Bay, Queensland, and synonymized it with *Ammochares tenuis* Haswell. Haswell (1883) records that *A. tenuis* is exceedingly common in Port Jackson, Sydney, but unfortunately the type specimen cannot be found and is presumed lost. As the author has found *O. fusiformis* throughout the Sydney area, it seems likely that Rullier is correct in synonomizing *A. tenuis* with *O. fusiformis*.

Previously known distribution

Cosmopolitan.

Family TEREBELLIDAE Malmgren, 1867

Genus Lysilla Malmgren, 1866

Lysilla apheles n. sp.

(Fig. 5A)

Holotype (AM. W.5239). Station 190 incomplete specimen, 10 thoracic setigers and approximately 12 abdominal segments 15 mm in length, and diameter of anterior end 2·5 mm.

Paratypes (AM. W.5237, W.5239). Stations 184 and 155 respectively. Both lack posterior abdomen and have 10 and 20 abdominal segments respectively. (BM. ZB.1973 : 2). Station 189.

All material from a sandy mud clay substrate with sparse *Halophila*, a marine angiosperm.

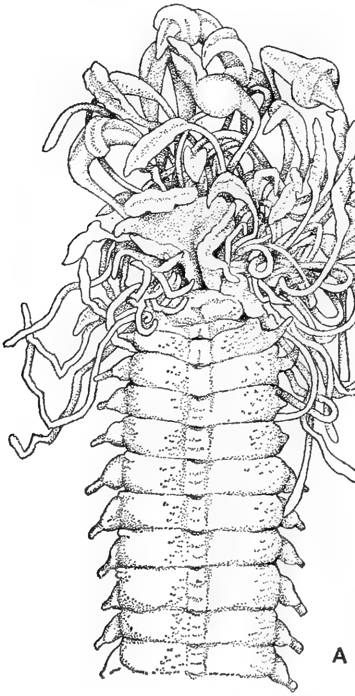

Fig. 5. *Lysilla apheles*. A, Ventral view of anterior end

Description

Short fat swollen body which is dark pink in colour, with crimson pink tentacles. Head with an anterior tongue-like upper lip, above which there is a broad trefoil frilly tentacular lobe which bears numerous tentacles. Three kinds of tentacles are present, small simple cylindrical filaments at the base of the tentacular lobe, larger grooved tentacles and a few tentacles in which the posterior part is spatulate. No eye spots or gills are present. Ten thoracic setigers and no abdominal setigers. The notosetae are simple smooth capillary setae. The extreme tips of these setae are finely serrated. The bundles of notosetae are enclosed in a setal sac. Neurosetae are completely absent.

Nephridial papillae are present on all setigerous segments but they are best developed on the middle setigerous segments. The papillae emerge from the bases of the setal sacs on the ventral side. The papillae are best developed on the holotype and least developed on paratype BM. ZB.1973-2 ; this probably reflects differences in the state of maturity of the specimens. Distinct narrow ventral groove running along the body. The entire ventral surface of the body is glandular and covered in small warts.

Remarks

This species is referred to the genus *Lysilla* as it lacks gills, neurosetae and abdominal notosetae. *L. apheles* differs from *L. pacifica* Hessle, which is also present in Wallis Lake, in that the notosetae are smooth winged capillaries and not barbed as in *L. pacifica.* Of the remaining described species of *Lysilla* only *L. loveni* Malmgren and *L. pambanensis* Fauvel have smooth winged capillary setae, but they have six and 13–18 pairs of setigers respectively, whereas *L. apheles* has 10 pairs of thoracic notosetae.

Lysilla pacifica Hessle, 1917

Lysilla pacifica Hessle, 1917 : 232–233, fig. 66 ; Imajima and Hartman, 1964 : 348.

Lysilla ubianensis Caullery, 1944 : 197, fig. 156*a-e* ; Day, 1967 : 721, fig. 36.3*i-j*. A new synonym.

Stations

51–100, 151–200, 301–350, 351–400 ; several specimens.

Remarks

Lysilla ubianensis, which Caullery (1944) described from Indonesia and which has subsequently been recorded from S. Africa and the Solomon Islands (Day, 1957, 1967 ; Gibbs, 1971), is synonymized with *L. pacifica* Hessle. In Hessle's description of *L. pacifica* he records finding two specimens with 12 pairs of barbed winged notosetae and one with nine pairs of notosetae. Similarly, in Wallis Lake some specimens have nine pairs while others have 12 pairs. However, one specimen has 11 pairs of notosetae, and this is also considered to be *L. pacifica* as Imajima and Hartman (1964) state that this species may have between nine and 12 pairs of notosetae. Two other specimens have 13 pairs of barbed notosetae, but apart from the extra pair of setae they fit the description of *L. pacifica.* No other species of *Lysilla* has 13 pairs of barbed notosetae.

Many of the specimens are full of eggs and the nephridiopores which are present on all setigerous segments are well developed on many specimens.

Previously known distribution

Indonesia ; S. Africa ; Japan.

Genus STREBLOSOMA M. Sars, 1872

Streblosoma amboinense Caullery, 1944

Streblosoma amboinense Caullery, 1944 : 180–181, fig. 144*a-d*.

Stations 201–250 ; five specimens.

Description

Three pairs of gills on segments 2–4 consisting of 10–12 simple filaments each arising separately from the body wall. The gill filaments are dark green in freshly preserved specimens. Notosetae begin on the first branchiferous segment and extend for 28–29 segments. Two kinds of notosetae are present: long narrow winged capillaries which have faintly striated edges, and short winged capillaries with smooth edges and finely pointed tips. The uncini begin on the fourth setigerous segment (segment 5) and are borne on low uncigerous ridges on the abdomen. The avicular uncini are similar to those shown by Caullery, but even within an individual there is some variation in the shape of the uncini. Nephridial papillae are present on setigers 2, 3 and 4.

Previously known distribution

Indonesia.

Rhinothelepus n. g.

The genus *Rhinothelepus* placed in the subfamily Thelepinae is characterized by an elongated tentacular lobe and by numerous simple gill filaments present on segments 2 and 3. Smooth tipped notosetae begin on segment 3 and continue for 15 segments. Uncini begin on setiger 6 and continue on to the abdomen. The uncini are short based with a subterminal dorsal button. No lateral lobes are present.

Type species.—*Rhinothelepus lobatus.*

Rhinothelepus lobatus n. g., n. sp.

(Fig. 6A-B)

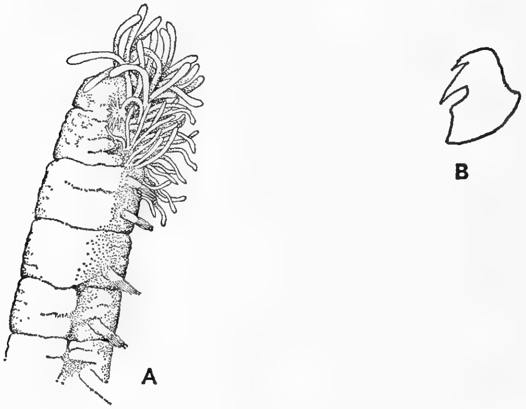

Fig. 6. *Rhinothelepus lobatus.* A, Lateral view of anterior end. B, Thoracic uncini.

Holotype (AM. W.5234). Station 380, incomplete specimen, 15 thoracic setigers and seven abdominal segments, 26 mm in length and 4 mm in diameter at anterior end.

Paratypes (AM. W.5228) Station 158, (AM. W.5229) Station 355, (AM. W.5230) Station 400, (AM. W.5231) Station 360, (AM. W.5233) Station 375, (AM. W.5234) Station 380, (AM. W.5235) Station 355, (AM. W.5236) Station 370, (BM. ZB.1973 : 3) Station 374, (USNM. 49488) Station 370.

All the material collected either from sandy-mud clay or from *Zostera* beds.

Description

Lives in fine sandy mucus tubes. Tentacular lobe extended to form a U-shaped tongue-like projection which is bent back dorsally. Margins of the tentacular lobe are convoluted and bear numerous grooved tentacles. The tentacular lobe is glandular and the inner walls are strongly ridged. At the ventral base of the lobe are groups of small fine tentacles. Eye spots present.

Numerous simple gill filaments present on segments 2 and 3. The gills are arranged in two discrete groups separated by a distinct median gap. No lateral lobes on anterior segments; or distinct ventral pads. From about the tenth setigerous segment onwards a narrow ventral glandular strip present. Notosetae begin on segment 3 (second branchiferous) and continue for 15 segments. The setae are smooth tipped narrow winged capillaries. The avicular uncini begin on the sixth setigerous (segment 8) and continue on to the abdomen. As no completely intact specimens have been found, it is not known if the uncini continue to the pygidium. The abdominal uncini are borne on narrow long rectangular pinnules and are arranged in single rows throughout. The uncini are short based with a subterminal dorsal button on a deep prow. Prominent nephridial papillae are present on setigers 4 and 5.

Remarks

This species clearly belongs to the subfamily Thelepinae as it has simple cylindrical gill filaments, smooth tipped notosetae and because of the shape of the uncini. The specimens from Wallis Lake closely resemble *Telothelepus capensis* Day in having an elongated tentacular lobe, but they differ as to the segment on which the uncini begin. The segment on which the neuro- and notosetae begin is a very important generic character in genera, belonging to the subfamily Thelepinae. For this reason a new genus, *Rhinothelepus*, has been created, for no other genus in this subfamily has neurosetae beginning an segment 8.

Genus PISTA Malmgren, 1866

Pista sp.

Stations

201–250; one incomplete specimen.

Remarks

A small anterior fragment with two pairs of tufted whorls of gills. The uncini of segments 5 and 6 have posteriorly elongated bases. This is probably an undescribed species but in view of the condition of the specimen it is not being described.

Family SABELLIDAE Malmgren, 1867

Genus BRANCHIOMMA Kölliker, 1858

Branchiomma cingulata (Grube, 1870)

Sabella (*Dasychone*) *cingulata* Grube, 1870: 67–68.

Dasychone cingulata.—Augener, 1914: 213.

Branchiomma cingulata.—Imajima and Hartman, 1964: 335.

Stations

201–250; a single specimen.

Remarks

The radioles are transversely striped with alternate bands of purple and reddish brown.

Previously known distribution

Victoria, New South Wales, Western Australia; Japan; Indo-Pacific; Fiji; and Solomon Islands.

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THE GEOLOGY OF THE REGAN'S CREEK AREA, NEAR CARGO, CENTRAL NEW SOUTH WALES

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Synopsis

Oldest rocks in the area are extensively altered andesites, basalts and volcanic conglomerates, sandstones and siltstones of the pre-Upper Gisbornian Cargo Andesite. The overlying Regan's Creek Limestone (? Upper Gisbornian-? Lower Eastonian) is subdivided into three members. The lowest, Ashton Member, consists of thinly-bedded limestones with calcareous sandstones and siltstones, the middle, Red East Member, comprises massive limestones, and the topmost, Checkers Member, contains thinly and massively bedded limestones. The Regan's Creek Limestone is overlain by the Malongulli Formation, comprising black calcareous siltstones and limestone lenses, and is regarded as Upper Eastonian in age.

The Ordovician succession is separated from the Upper Devonian sequence to the east by the Columbine Mountain Fault. The Upper Devonian Catombal Group is represented in the area by the upper beds of the " Columbine Sandstone " and the overlying Canangle Subgroup. This latter unit is subdivided into a lower, dominantly conglomeratic, Carlton Formation, and upper, mainly silty, Warree Creek Beds. The Catombal Group succession of the area is regarded as dominantly fluviatile in origin. Intrusive bodies of Post-Ordovician age include a large gabbro and small basalt and monzonite. Basalts of probable Tertiary age occur as hill-cappings in the north-east part of the area.

INTRODUCTION

The area studied is situated approximately 3·3 km south-east of Cargo, 42 km south-west of Orange in central New South Wales (see Fig. 1). The region is in an area of north-south trending " thrusts " faults on the western margin of the tectonic unit, the Molong Rise (Packham, 1960).

The first detailed study of the locality was by Stevens (1947, unpubl.), who included the western half of the area in a survey of the Cowra-Canowindra-Cargo-Toogong district. The portion relative to the Regan's Creek area was published in 1950, and a more accurate age determination of the Ordovician sequence was given by Stevens in 1957. Walker (1958, unpubl.) studied the Upper Devonian sequence as part of a survey of the Upper Devonian of the Cargo region. Aspects of the fauna of the Regan's Creek Limestone have been described by Hill (1957), Phillips-Ross (1961), Webby (1969, 1971*a*) and Webby and Semeniuk (1971), while a trilobite from the Malongulli Formation was described by Webby, Moors and McLean (1970).

CARGO ANDESITE

The oldest formation in the area studied was defined by Stevens (1950) as the Cargo Andesite Series, taking its name from the main area of outcrop around the village of Cargo. It has been described also by Ryall (1965) from the Canowindra region to the west, and by Semeniuk (1970) from the Bowan Park area to the north. Dips of the formation are generally to the east in the Regan's Creek area, but folding has been intense in places, especially in the region south of the Canangles Road, where it is intruded by a large gabbroic body. Outcrop is generally poor and contacts between members of the sequence are rarely exposed.

Petrography

The lithology of the Cargo Andesite in the region examined is extremely variable and extensive alteration of almost all the rocks makes identification of many, especially the volcanics, extremely difficult. Of these volcanics,

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pyroxene andesite is the most common type, and when relatively fresh, exhibits andesine laths generally up to 2 mm in length, sometimes forming glomeroporphyritic aggregates, with interstitial, pale green augite. However, alteration is generally strong, with albite, epidote, prehnite, sphene, carbonate, chlorite, quartz, pumpellyite and celadonite the most common secondary minerals developed. In particular, the plagioclase is very rarely preserved in its unaltered state. Some probable basalts, containing labradorite, are also represented in the sequence. The volcanic rocks are frequently amygdaloidal, the amygdules generally being filled by quartz, chlorite and carbonate. Stevens (1950), Ryall (1965) and Semeniuk (1970) have recorded hornblende andesites in the Cargo Andesite, but these have not been observed in the Regan's Creek area.

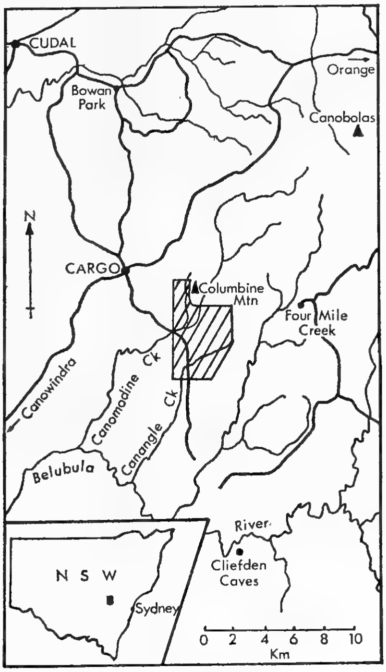

Fig. 1. Locality map.

Coarse conglomerates are common, consisting of generally well-rounded fragments of a variety of volcanic rocks, mainly of basalt-andesite composition and showing marked similarities to the volcanic rocks occurring elsewhere in the andesite sequence. Also present are pebbles of fine-grained red-brown volcanic sandstones and siltstones containing abundant detrital feldspars and rock fragments. The pebbles generally range in size from 1–3 cm and the amount of matrix in these rocks varies greatly. The matrix, where present, is commonly very fine probable albite, quartz, chlorite and carbonate and there is often chlorite and carbonate cement. The conglomerates occur abundantly below the northern area of outcrop of the Regan's Creek Limestone and on the western margin of the central and southern areas of the limestone, usually forming strike ridges.

Associated with these coarse conglomerates are lenses of fine brown volcanic sandstones and siltstones, commonly exhibiting well-defined bedding. They typically show angular feldspars (albite) comprising about 25% of the rock, in an almost cryptocrystalline matrix of clay materials, albite, quartz and chlorite. Carbonate and chlorite alteration is common, especially in the volcanic rock fragments (average 0·075–0·1 mm) and iron-oxide staining is abundant. Apatite and epidote occur rarely.

A major lense of massive, strongly recrystallized limestone is present in the andesite sequence (see Fig. 2). It is uncertain, however, whether it is truly part of the succession or merely a sliver of the overlying Regan's Creek Limestone dragged down by faulting.

Correlation and Age

The Cargo Andesite appears very similar petrographically to the Walli Andesite (Stevens, 1952) in the Cliefden Caves area about 16 km to the south (see Fig. 1) and the Mount Pleasant Andesite (Smith, 1966) to the east of the latter, particularly with regard to the descriptions of the Walli Andesite by Smith (1966, 1968). Stevens (1951, 1952) has correlated these units with the Cargo Andesite. Packham (1969) has suggested that these andesitic sequences are of Lower-Middle Ordovician age (Darriwillian or older). No fossils have been found in the Cargo Andesite of the Regan's Creek area or elsewhere and no accurate age determinations can be made. However, the base of the overlying Regan's Creek Limestone is probably no younger than Upper Gisbornian and hence the age of the Cargo Andesite can be considered here as at least pre-Upper Gisbornian (see also Semeniuk, 1970).

Environment of Deposition

It has been generally thought that deposition of the Ordovician andesitic sequences of central N.S.W. occurred under marine conditions (Stevens, 1954 ; Smith, 1966, 1968). This is based mainly on the evidence of pillow lavas in the Cliefden area (Stevens, 1957 ; Smith, 1966), limestone lenses in parts of the andesitic sequences, and the occurrence of limestones overlying the andesites (Ryall, 1965 ; Smith, 1966). It is thus likely that much of the deposition was marine. However, in the area examined here no pillow lavas have been confirmed and the limestone body is of uncertain origin. The abundance of conglomeratic detritus with generally rounded pebbles in the upper parts of the succession represented in this area suggests that only shallow water conditions prevailed during the closing uplift of the older andesitic sequence. This would then have provided a source rock for the volcanic detritus in the highest parts of the sequence, considered here, and would imply considerable breaks in accumulation of the Cargo andesite.

REGAN'S CREEK LIMESTONE

The presence of a small limestone body in the Regan's Creek area was recorded by Andrews and Morrison (1915) and Carne and Jones (1919), but it was not discussed in any detail until the work of Stevens (1950). At that stage it was referred to simply as " the limestones near the Canangles Road " and considered to be of Silurian age. Stevens (1957) proposed the name " Regan's Creek Limestone " for this limestone and, on the basis of tentatively identified corals, proposed a late Middle or early Upper Ordovician age for the formation.

The Regan's Creek Limestone occurs in three separate areas of outcrop. North of the Canangles Road, it is present in a broad, truncated synclinal structure plunging to the north-west at about 30°. To the south-west of the road a second area of outcrop occurs with a general easterly dip of 40°. To the south of this area is a third belt of limestone probably overturned to the west and bounded by the Columbine Mountain Fault to the east and possibly another fault on its western margin. In the following discussion these areas are referred to as Areas 1, 2 and 3 respectively (ref. Fig. 2).

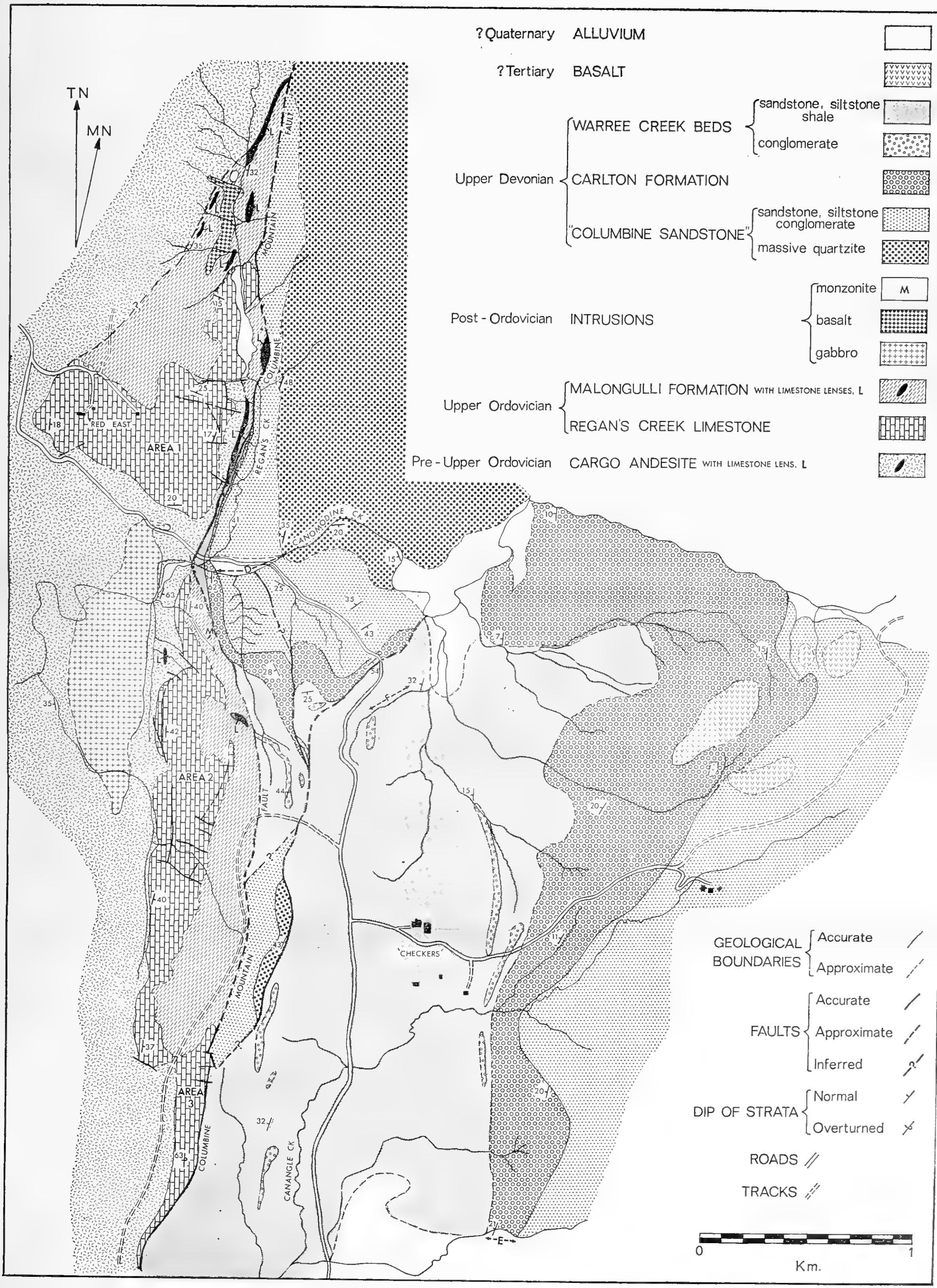

Fig. 2. Geology of the Regan's Creek area. For subdivision of the Regan's Creek Limestone, see Figs. 3, 4.

Three distinct members within the Regan's Creek Limestone were mapped, the Ashton, the Red East and the Checkers Members, in ascending stratigraphic order. The Ashton Member typically consists of lithic sandstones, siltstones and marls with some massive limestones. The Red East Member comprises massive grey limestones, while the Checkers Member contains thinly bedded yellow, pink and grey limestones, together with massive grey limestone beds. The Checkers Member could be subdivided into four further sub-units. The Regan's Creek Limestone attains a thickness of at least 158 m, although the full succession is not present in any one complete section.

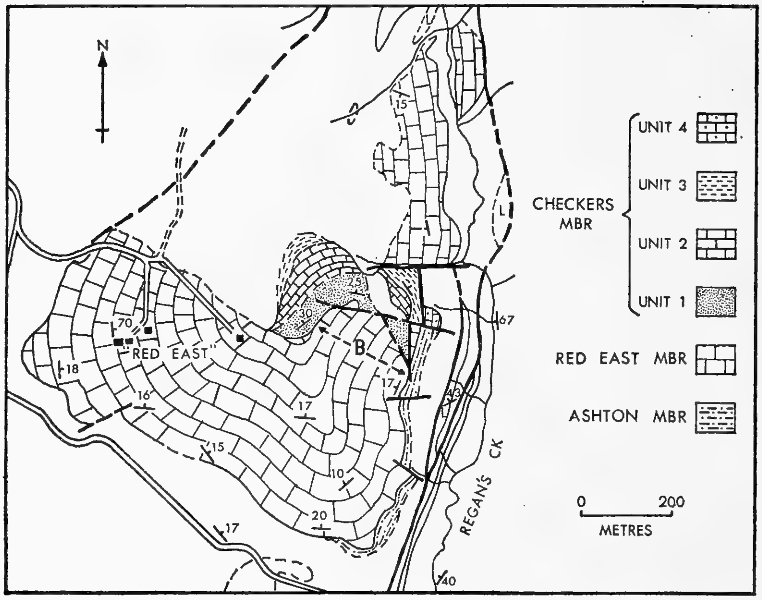

Fig. 3. Subdivision of the Regan's Creek Limestone. Area 1.

The limestone overlies the Cargo Andesite but the actual contact is not exposed. The presence of abundant basic-intermediate volcanic detritus in the lower beds of the Ashton Member (see below) suggests derivation from the Cargo Andesite and a probable time break between the two formations. Also, the fact that the Ashton Member is not always represented at the base of the limestone sequence suggests a disconformable relationship may be present. Strike and dip of strata in the andesite sequence are generally similar to those of the overlying limestones although there is some discordance in the south of the area. The upper contact with the Malongulli Formation is also problematical as this contact is not exposed anywhere in the area.

Ashton Member

This unit occurs only in the south-eastern part of the limestone outcrop of Area 1, dipping westerly, and in the northern part of Area 2 dipping to the east (Figs 3, 4 (A)). The type section was taken in Area 2 at the best exposure (Fig. 4 (A), section A). The total thickness of the member at this locality is 41 m (Fig. 5 (A)) and, while outcrop is not sufficient to accurately measure the unit in Area 1, a similar thickness appears likely there. Bedding varies in thickness from about 1 cm in the finer sediments to about 15–30 cm in the more massive limestones.

Petrography. The sequence consists of yellow, brown and red lithic, calcareous sandstones and siltstones, with occasional red and grey limestone beds which become more abundant upward, where the sequence passes conformably into the massive limestones of the Red East Member.

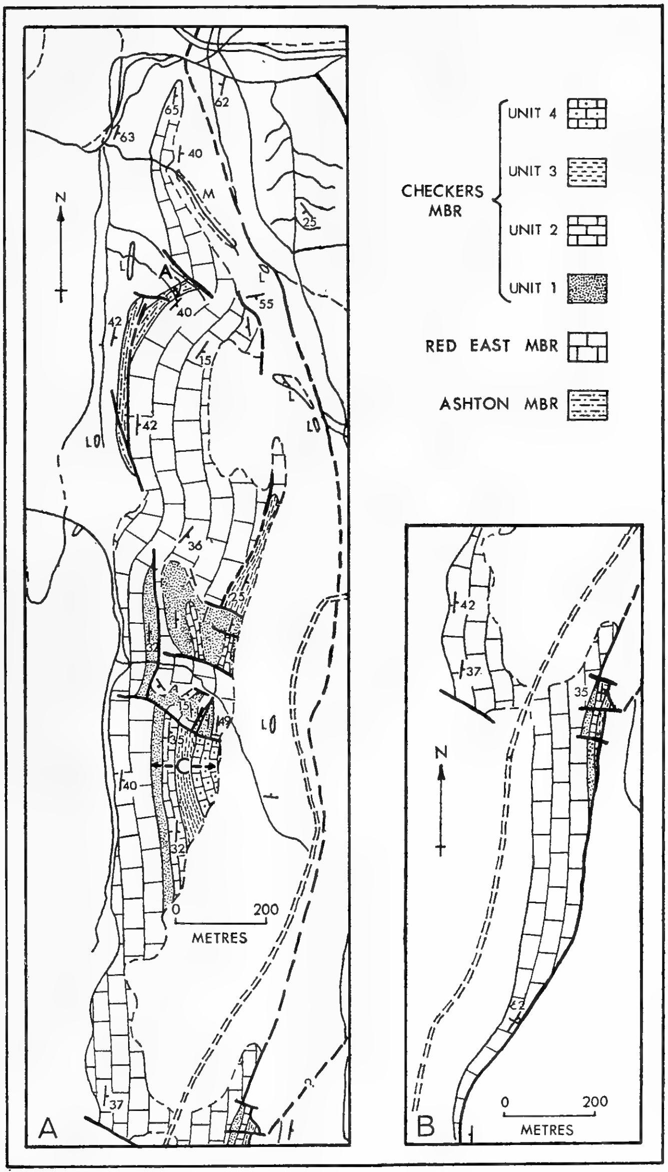

Fig. 4. Subdivision of the Regan's Creek Limestone. A. Area 2. B. Area 3.

Typically, the lithic sandstone shows poor sorting and fair to poor rounding of rock fragments and quartz grains. The latter generally range in size up to about 1 mm, with an average of 0·25 mm. Volcanic rock fragments are heavily altered, with chlorite, feldspars, quartz and opaque minerals dominant and biotite may be present. Other fragments consist of metaquartzites and fine volcanic sandstones and siltstones, with quartz and chlorite dominant. Matrix consists of fine quartz and probable clay minerals (" sericite " is also common). Hematite and limonite form abundant cements, but calcite, often lustre-mottled, is dominant. Fragmentary skeletal debris may also be present.

The limestone beds commonly have a micrite or microspar content, with grainsize ranging from almost cryptocrystalline to about 0·05 mm. Skeletal fragments (? *Lichenaria*, shell fragments in greatest abundance) and intraclasts of micrite occur rarely. Algal encrustation of skeletal material together with algal lumps are common locally.

Fauna. Stromatoporoids *Labechiella regularis* (Yabe and Sugiama), and *Cystistroma donnellii* Etheridge are abundant low in the sequence (Horizon " a " in Fig. 5 (A)), as is the tabulate coral *Nyctopora stevensi* Hill. ? *Lichenaria* occurs rarely as fragments in the middle of the sequence. The brachiopod ? *Rhynchotrema* sp. occurs abundantly in two horizons (" b ", " d ", Fig. 5 (A)) in the middle of the sequence and the large brachiopod, cf. *Eodinobolus* sp., is present in a bed also near the middle of the succession (Horizon " c ", Fig. 5 (A)).

Red East Member

This unit comprises the bulk of the outcrop of the Regan's Creek Limestone, consisting of massively outcropping grey limestone, rarely showing bedding planes, and its structure is basically that mentioned above for the Regan's Creek Limestone as a whole.

A complete section through the Red East Member is not obtainable, but the best continuous exposure of the succession through the limestone occurs in the vicinity of " Red East " on the eastern side of the outcrop (Fig. 3, section B) and is illustrated in Fig. 5 (B). The greatest single thickness that can be measured is in Area 2, where at least 57 m are represented and the unit is more fossiliferous here than at " Red East ". The base of the member was taken as the first massive pink-grey limestone with siliceous nodules and the stromatoporoid *Cystostroma.* Bedding is poorly defined in this unit—in the lower part it is on the scale of 5–30 cm, but higher in the member it is generally of the order of 30–60 cm.

Petrography. The lithology of this unit is extremely consistent, with grey-black limestone consisting of fine, granular, microspar carbonate (common size 0·025–0·04 mm). In some cases the rocks can be seen to contain very fine micritic pellets in a microspar granular aggregate. Burrows of *Chondrites*-type are common in this unit, the burrows generally being filled with slightly coarser carbonate grains than the host rock. Where skeletal material is more abundant, ? intraclasts containing skeletal fragments in a microspar matrix may be seen.

Siliceous nodules, typically parallel to bedding planes, occur abundantly in this unit. They consist of microcrystalline silica and chalcedony.

Fauna. Fossils are generally sparsely represented in the Red East Member, with rare local grouping of forms. They are typically very strongly silicified.

The stromatoporoid *Cystostroma cliefdenense* Webby occurs abundantly in all areas of outcrop of this member. A specimen from the Red East Member is illustrated by Webby (1969, Pp. 117, fig. 5). The cylindrical labechiid *Alleynodictyon nicholsoni* Webby is represented near the top of the unit in Area 2, and material from this locality has been described and illustrated by Webby (1969, Pl. 122, figs 1, 2 ; 1971*a*, Pl. 5, figs 4, 5). *Labechia variabilis* Yabe and Sugiyama is commonly represented immediately below the Checkers Member in Area 2. A specimen from this locality has been illustrated by Webby (1969, Pl. 121, fig. 1). The tabulate corals *Heliolites digitalis* Hill and *Propora bowanensis* Hill are common in all areas of outcrop, the former being more abundant in the upper part of the member. *Tetradium cribriforme* (Etheridge) occurs sparsely in all areas of outcrop, while *Aulopora* sp. is quite common in Area 2. The only rugosan

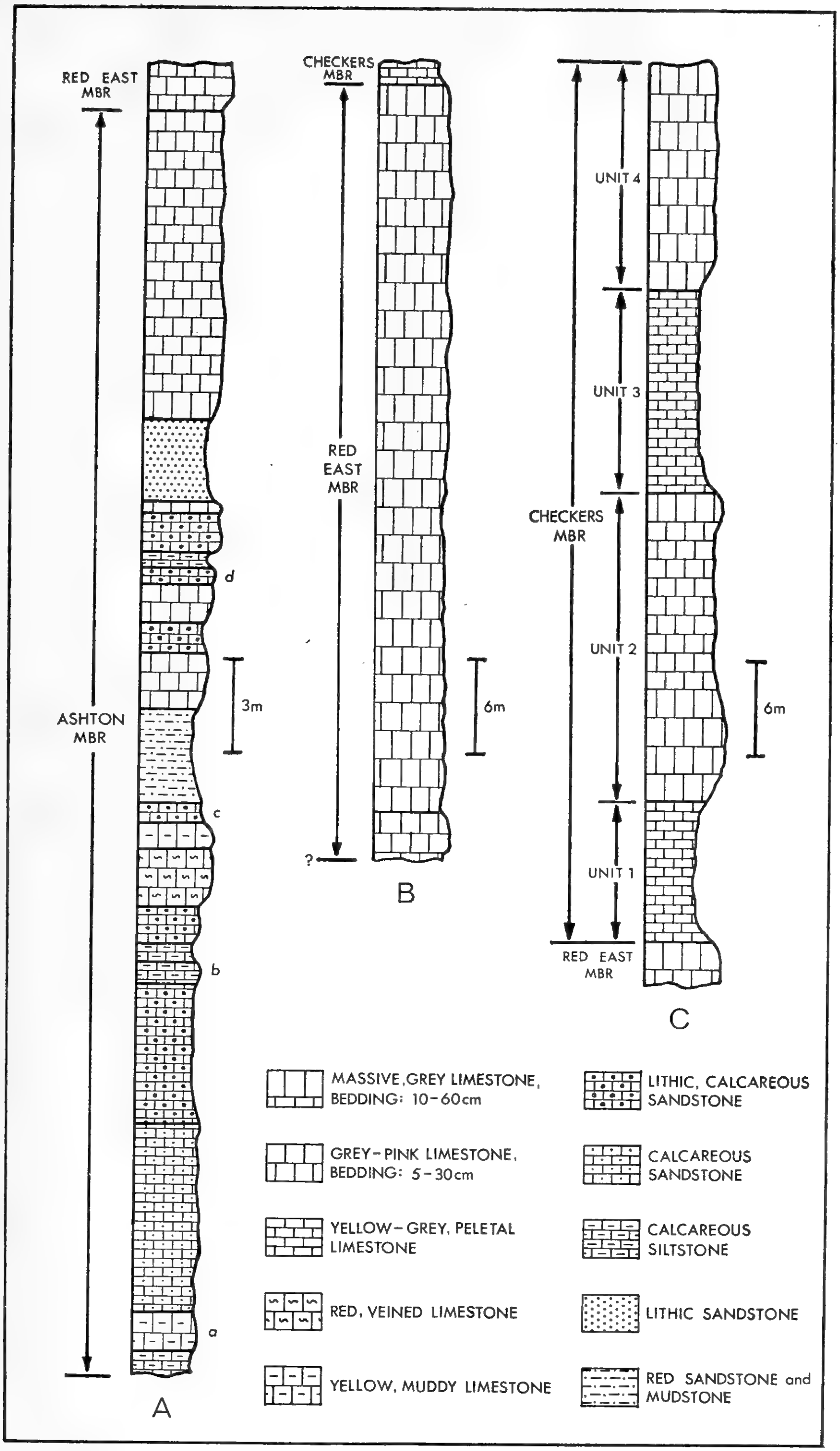

Fig. 5. Stratigraphic sections of the Regan's Creek Limestone. A. Ashton Member, Area 2. B. Red East Member, Area 1. C. Checkers Member, Area 2. For full section localities, see text.

collected is *Hillophyllum priscum* Webby, which occurs rarely throughout the member. Brachiopods *? Doleroides* sp. and cf. *Eodinobolus* sp. are represented in Areas 1 and 2, the former being found in the upper parts of the sequence and the latter common in the lower horizons. Gastropods *Lophospira* sp. and *? Raphistomina* sp. are common locally in the higher beds of the member in Areas 1 and 2 and algal encrustations are common throughout.

Checkers Member

This member is found in all three areas of outcrop of the Regan's Creek Limestone, apparently conformably overlying the Red East Member. It is overlain with uncertain relations by the Malongulli Formation (see below). On the basis of lithology, and to some extent fauna, the member has been subdivided into four units. The lowest (Unit 1) consists of grey and yellow thinly-bedded limestone. Unit 2 contains massive grey limestone, Unit 3 again consists of yellow thinly-bedded limestones, and Unit 4 is a massive, grey limestone similar to Unit 2. Near " Red East ", Units 1, 2 and 3 are found, while to the south all four units occur. The fact that the same sequence of beds is found in the Checkers Member throughout the limestone outcrop indicates that there are not merely two units repeated by a strike fault, and there is also generally a more abundant fauna in Unit 3 than Unit 1. As in the case of the Ashton Member at the base of the sequence, the Checkers Member is not always found overlying the Red East Member throughout the area of outcrop of the Regan's Creek Limestone, due to faulting and probably simply to lack of development.

The small-scale complexities in the structure of the Regan's Creek Limestone are best illustrated by the Checkers Member. In Area 1 the basic structure of the member is an anticline on the eastern margin of the main syncline of the Red East Member, plunging to the north at about 25°. The relationships to the north and east of this area of outcrop of the Checkers Member are complicated by numerous cross and strike faults, the larger examples of which are shown in Fig. 3. The basic structure in Area 2 is even more complex, where in the central part of the outcrop strike and cross faulting, together with tight folding about north-south axes, cut out development of some of the units (Fig. 4 (A)). In the southern part of Area 2 a simple easterly dipping sequence occurs with full development of the Checkers Member. In Area 3, only a small, cross-faulted sequence of the member is present. It is likely that the Columbine Mountain Fault occurs along the eastern margin of the limestone in this area, although there is no outcrop of any beds adjacent to the most easterly exposure of the Checkers Member. Overturning of the limestone sequence in Area 3 is indicated by the reversal in the lithological succession with the presence of fossils in their growth positions in the Checkers Member.

The type section for the member (Fig. 4 (A), section C) is of total thickness 60 m (Fig. 5 (C)). At the section locality the four sub-divisions of the member have thicknesses as follows : Unit 1, 13 m ; Unit 2, 20 m ; Unit 3, 13 m ; Unit 4, 14 m. The top of Unit 4 was taken as the highest outcrop of limestone, but the actual contact with the overlying Malongulli Formation is not exposed.

The yellow limestones of Units 1 and 3 show typical bedding thicknesses of 5–15 cm, while the massive grey limestones of Units 2 and 4 have bedding generally on a scale of 5–60 cm.

Petrography. The thinly-bedded limestones of Units 1 and 3 are characterized by an abundance of brown pellets, usually well sorted, averaging 0·25 mm and with algal circumcrusts. They are apparently composed of microcrystalline carbonate. Skeletal debris is particularly abundant in the form of shell fragments, Bryozoa, pelmatozoan fragments and corals, and these also show algal encrustation. All this material is generally widely separated in interstitial micrite and microspar. In some beds coarser sparrudites may occur, containing poorly sorted pellets and intraclasts, with coarse skeletal debris. Coarse interstitial calcite ranging in size up to 1 mm is suggestive of an original sparry calcite cement.

Typical grey limestones from Units 2 and 4 show almost cryptocrystalline, equant grains of carbonate, often forming aggregates approximately 0·2 mm in size and occurring in a " matrix " of clear microspar of average size 0·02 mm. Pellets and intraclasts of peletal material may be represented. Skeletal fragments are relatively rare in these units, but where present they are frequently encrusted with algae. Many of these pellets consist of algal debris.

Fauna. The Checkers Member contains the most abundant fauna in the Regan's Creek Limestone, and is most prolific in Units 1 and 3. The fauna identified are listed below, with abundances abbreviated as c—common and r—rare.

	Unit			
	1	2	3	4
Stromatoporoidea :				
Ecclimadictyon amzassensis (Khalfina)	c		?	
Cystostroma cliefdenense Webby		c	r	
? *Pseudostylodictyon* sp.	r			
Tabulata :				
Heliolites cf. *digitalis* Hill	c	c	c	r
Propora bowanensis Hill	c	r	c	
Propora sp.	c	r	c	
Tetradium cribriforme (Etheridge)	c		r	r
Tetradium sp.	r			
Eofletcheria gracilis Hill			c	
Eofletcheria cf. *irregularis* Hill			r	
Nyctopora stevensi Hill			r	
? *Aulopora* sp.			r	
? *Lichenaria* sp.			r	
? *Coccoseris* sp.	r		r	
Rugosa :				
Palaeophyllum proliferum Webby	?		r	
? *Hillophyllum* sp.	r		r	
Brachiopoda :				
cf. *Leptellina* sp.	c		c	
? *Ptychopleurella* sp.	r		r	
? *Zygospira* sp.	c		r	
? *Sowerbyites* sp.			r	
Bryozoa :				
Stictopora sp.	c		c	
? *Batastoma* sp.	r		r	
Conodonts :				
Belodina compressa (Branson and Mehl)	c		c	
Belodina sp.	r			
Eobelodina fornicala (Stauffer)	r			
Panderodus cf. *feulneri* (Glenister)	c			
Panderodus cf. *gracilis* (Branson and Mehl)	c			
Phragmodus sp.	c			
Bryantodina sp.	c			
Ozarkodina sp.	r			
? *Dichognathus* sp.	r			
? *Cordylodus* sp.	r			
? *Drepanodus* sp.	r			
Gastropoda :				
Lophospira sp.	r	r	r	
Miscellaneous :				
Pelmatozoan ossicles	c		c	
Trace fossil " *Chondrites* "	c	r	c	
Dasycladacean algae	r		r	
Algal encrustations	c	c	c	c

Several elements of this fauna have been previously described. Hill (1957) described and figured *Propora bowanensis* (Pl. IV, figs 21, 22*a*), *Eofletcheria gracilis* (Pl. IV, fig. 22*b*), ? *Lichenaria* sp. (Pl. IV, fig. 24) from the Regan's Creek Limestone. However, the horizon within the limestone from which these specimens were obtained was not recorded. It is likely that it was either in the Checkers Member or high in the Red East Member. *Palaeoporites* has not been obtained from any other sampling. A specimen of *Tetradium* sp. was illustrated by Webby and Semeniuk (1971, Pl. XXI, fig. 6) and representatives of *Palaeophyllum proliferum* from the Checkers Member were listed by Webby (1972*b*, p. 152) as paratypes of that species. Phillips-Ross (1961, Pl. 23, figs 3, 4) described " *Stictopora* sp. B " from the " base of the Regan's Creek Limestone ", but this was probably from the Checkers Member.

Comparisons with other Ordovician limestones in central N.S.W.

Webby (1969, 1973) has proposed a succession of stromatoporoid and coral faunal groups (Fauna I, II, III) in the Upper Ordovician of central N.S.W. and suggested that Faunas I and II are represented in the Regan's Creek Limestone.

Fauna I: At Regan's Creek, this fauna is characterized by the stromatoporoids *Labechiella regularis* and *Cystistroma donnellii* of the Ashton Member, these forms occurring also in the lower part of the Cliefden Caves Limestone and Reedy Creek Limestone (Webby, 1969, 1973). A ? Lower or Upper Gisbornian age was suggested for this fauna by Webby (1969).

Fauna II: The abundant fauna in the upper part of the Red East Member and throughout the Checkers Member is characteristic of Fauna II. The stromatoporoids *Cystostroma cliefdenense*, *Labechia variabilis* and *Ecclimadictyon amzassensis* are all diagnostic of Fauna II in the upper part of the Cliefden Caves Limestone (Webby, 1969, 1973). The tabulate corals *Heliolites digitalis* and *Aulopora* sp. in both the Cliefden Caves Limestone and Quondong Formation of the Bowan Park Group and *Propora bowanensis* in the Quondong Formation (Semeniuk, 1970; Webby, 1973) are diagnostic Fauna II representatives found also in the upper part of the Regan's Creek Limestone. The rugosan *Palaeophyllum proliferum* is one of the characteristic elements of Fauna II in the Cliefden Caves Limestone, Quondong Formation and the Checkers Member of the Regan's Creek Limestone. Webby (1969) proposed an Upper Gisbornian or Lower Eastonian age for Fauna II. Hence in common with the Cliefden Caves Limestone a ? Upper Gisbornian to ? Lower Eastonian age may be assigned to the Regan's Creek Limestone. Distribution of other faunal elements of the Regan's Creek Limestone in Ordovician limestones of central N.S.W. are mentioned by Webby (1973).

MALONGULLI FORMATION

This unit was defined by Stevens (1952) in the Cliefden Caves district to consist of " impure siliceous limestones with some tuffs, shales and limestone breccias ". In the Regan's Creek area, Stevens (1950) described black banded shales and cherts occurring in two small, fault-bounded inliers as " the oldest rocks in the Cargo district ", being of Upper Ordovician age on the evidence of the graptolite fauna. He later (1954, unpubl.) tentatively included these rocks in the Malongulli Formation. On the basis of marked similarities in lithology, some aspects of the fauna and the underlying limestone formation, they should definitely be included in that formation.

Rocks of the Malongulli Formation occur in three isolated localities in the area studied (Fig. 2). In the most northerly area of outcrop it overlies the

Regan's Creek Limestone and has a general north-westerly dip, averaging 35°. A second outcrop of the formation occurs in a sliver bounded by limestone of uncertain stratigraphic position to the west and by the Columbine Mountain Fault to the east. It has an average dip of 40° to the west in this locality (Figs 2, 3). Further south, on the eastern margin of the central area of outcrop of the Regan's Creek Limestone, there occurs a third outcrop of the Malongulli Formation, which was mapped by both Stevens (1950) and Walker (1958, unpubl.) as belonging to the Upper Devonian succession. It has a generally easterly dip of 40°.

Bedding in the formation varies in thickness from about 0·5 mm up to several centimetres. Very small-scale slumping and load casts may be seen occasionally in interlayered calcareous and siliceous bands.

Stratigraphic relationships with the underlying Regan's Creek Limestone cannot be determined since the contact is not exposed, being obscured by slumping of Malongulli material over the limestone. However, bedding attitudes indicate the boundary is faulted in several places. The upper limit of the formation is faulted in all cases either against the Cargo Andesite in the north-west or along the Columbine Mountain Fault against the Catombal Group in all other localities. In the Cliefden Caves area the Malongulli Formation is conformable with the Cliefden Caves Limestone (Stevens, 1952) and grades into the overlying Angullong Tuff at its upper contact. It is estimated that up to 80 m of sediment is represented in the formation in the Regan's Creek area, although the total original amount is unknown due to the faulting. In the Cliefden Caves area the formation reaches 462 m in thickness (Moors, 1966, unpubl.).

Small-scale open folding is characteristic, with folds having general north-south trending axes and diameters of about 1 m common. Numerous drag-folds are associated with movements on small-scale faults.

The Columbine Mountain Fault is well exposed in Regan's Creek, where the Malongulli Formation is thrust over the Upper Devonian "Columbine Sandstone". The fault plane dips to the west at about 50°, i.e. it is a high-angle reverse fault.

Petrography

Lithologically, the formation is dominated by indurated, laminated, grey-black calcareous siltstones and fine sandstones which characteristically weather to a light brown friable state. There is typically prominent banding of isotropic brown material (? iron-stained chalcedony) wrapping detrital grains. Carbonate occurs as ragged grains, usually separated in microcrystalline silica, occasional quartz grains and opaque material. The banded appearance of the rock is due to the relative proportions of brown, isotropic material and carbonate grains. Average grainsize ranges from 0·04 mm to 0·25 mm. Circular and strongly elongate quartz grains probably represent altered sponge spicules. The limestone lenses near the base of the formation show great lithological similarities to the more carbonate-rich bands of the normal siltstones, whereas the black siltstones developed higher in the formation (as in Regan's Creek) appear very similar to the layers containing abundant sponge spicules, carbonate and quartz grains wrapped by isotropic brown material occurring in the laminated rocks. Coarser more silica-rich sandstones occur in the higher parts of the formation.

Fauna

The Malongulli Formation in the Regan's Creek area contains graptolites, trilobites, conodonts, brachiopods and sponge spicules. In black, calcareous siltstones in Regan's Creek (Fig. 2) the graptolites *Orthograptus* cf. *calcaratus* Lapworth, *Dicellograptus* sp. and *Climacograptus* sp. are represented. However, the most varied fauna was found in the leached siltstones in the southern part of the area (Fig. 2). This includes the graptolites *Dicranograptus* cf. *kirki* Ruedemann, *Orthograptus* cf. *calcaratus* and *Orthograptus* sp. together with the trilobite *Encrinuraspis optimus* Webby, Moors and McLean and fragments of a trinucleid. Two fragments of *E. optimus* from the Regan's Creek area were figured by Webby, Moors and McLean (1970, Pl. 126, figs 8, 9). The brachiopods *Sowerbyella* sp. and fragments of lingulids also occur. A small conodont fauna was obtained from the limestone lenses and more calcareous siltstones of this locality and determined as follows: *Belodina compressa* (Branson and Mehl), *Panderodus* cf. *gracilis* (Branson and Mehl), *Ozarkodina* sp., *? Distacodus* sp., *? Panderodus* sp., *? Drepanodus* sp. and *? Prionidina* sp.

The fauna from the Regan's Creek area listed by Sherrard (1954) as *Orthograptus apiculatus* (Elles and Wood), *Retiograptus geinitzianus* Hall and *Dicellograptus* sp. was included by Sherrard (1954, 1962) in her zone of *Nemagraptus pertenuis*, of Lower Gisbornian to Middle Eastonian age. Revision of these forms and others in the Cliefden Caves district by Moors (1970) has led him to include the assemblage in the zone of *Dicranograptus hians* of Upper Eastonian age. Comparisons of the forms recognized here with those described by Moors from the Malongulli Formation at Cliefden suggests the Regan's Creek assemblage may also be assigned to the *D. hians* zone and thus an Upper Eastonian age is likely for the formation at Regan's Creek. *Encrinuraspis optimus* is represented also in the Malongulli Formation at Cliefden Caves.

CATOMBAL GROUP

Nomenclature

Upper Devonian rocks of the Cargo district have been generally compared with those further north in the Molong-Wellington region and the first nomenclature given to this suite of rocks was for those in the latter area. Matheson (1931) described the Devonian sequence in the Catombal Range north of Molong as belonging to a Lower to Middle Devonian " Transition Series " and an Upper Devonian " Catombal Series ". Basnett and Colditz (1945) later included both these " series " in a " Catombal Series " of Upper Devonian age. Joplin *et al.* (1952) then proposed the name " Catombal Formation " for the Upper Devonian rocks of the Molong-Wellington region. Walker (1958, unpubl.) elevated Joplin's " Catombal Formation " to group status and applied this name to the Upper Devonian strata of the Cargo district. Conolly (1963) accepted the term " Catombal Group " and used it for the Upper Devonian sequence in the Molong-Wellington region, considering the lithologies of that area were essentially the same as those of the Cargo region.

Catombal Group in the Cargo Area

Süssmilch (1906) described the Devonian conglomerates, sandstones and shales of the Gap and Oaky Creeks area, north-east of Cargo. Stevens (1950) divided the Devonian succession east of Cargo into a " Lower Series " of green shales occurring in an anticline north of the Black Mountain (north of Cargo) and an " Upper Series " of quartzites and shales in Columbine Mountain and the Black Rock Range east of Cargo. Shales and conglomerates of Lower Carboniferous age were considered to overlie the Upper Devonian " Upper Series ". Stevens and Packham (1953) defined the " Black Rock Sandstone " to include the " Upper Series " of Stevens (1950) in the Black Rock Range of the Four

TABLE 1

Nomenclature Applied to the Catombal Group of the Cargo Region

Stevens, 1950	Stevens and Packham, 1954	Stevens, 1954 (unpubl.)			Walker, 1958 (unpubl.), Conolly, 1963	Conolly *in* Packham, 1969	This paper
Lower Carboniferous conglomerates and mudstones		Canangle Formation	Catombal Group	Canangle S/G	Warree Creek Shale	Warree Creek Shale	Warree Creek Beds
					Carlton Conglomerate	Carlton Conglomerate	Carlton Formation
Upper Devonian 'Upper Series'	Black Rock Sandstone	Black Rock Sandstone		Black Rock S/G	Columbine Sandstone	Macquarie Park Sandstone	"Columbine Sandstone"
					Paling Yard Formation	Paling Yard Formation	"Paling Yard Formation"

Mile Creek region, to the east of the Regan's Creek area. It was stated as unformably overlying the Bull's Camp Rhyolite (Stevens and Packham, 1953) of ? Lower-Middle Devonian area. Stevens (1954, unpubl.) adopted the term " Canangle Formation " for these " Lower Carboniferous " rocks (1950). His " Lower Series " (1950) was grouped with the Wallace Shale (Stevens and Packham, 1953) and the " Upper Series " (1950) was referred to the Black Rock Sandstone of Stevens and Packham (1953).

Walker (1958, unpubl.) defined the Black Rock Subgroup to include the Black Rock Sandstone and the Canangle Subgroup to replace the Canangle Formation. Walker suggested subdivision of the Black Rock Subgroup of the Cargo area into a lower " Paling Yard Formation ", with conglomerates, sandstones and shales, and an overlying " Columbine Sandstone " comprising sandstones and shales. The Canangle Subgroup was subdivided into the " Carlton Conglomerate " with coarse conglomerates and an overlying " Warree Creek Shale " with green siltstones and shales. An Upper Devonian age was suggested by the entire sequence. Conolly (*in* Packham, 1969) substituted the term " Macquarie Park Sandstone " for the " Columbine Sandstone " in the Cargo area, the former being defined only in the Molong-Wellington region (Conolly, 1963). The relationships of the Cargo and Molong-Wellington belts of the Catombal Group are discussed below.

In the Regan's Creek area, only the upper part of the " Columbine Sandstone " is present, together with the overlying " Carlton Conglomerate " and " Warree Creek Shale ". The latter two units are here formally defined and described as the Carlton Formation and Warree Creek Beds. Table 1 summarizes the history of nomenclature of the Catombal Group of the Cargo area. In the area studied, the Catombal Group occurs in two major structural elements : an anticline plunging to the south of Columbine Mountain in the western part of the area, and a broad syncline in Checkers valley. A major fault separates these two regions, truncating the structures (see Fig. 2).

" *Columbine Sandstone* "

As mentioned above, only the upper parts of this " formation " are represented in the area studied, and hence the informal terminology of Walker (1958) is retained here for convenience. The type section of the " Columbine Sandstone " proposed by Walker (1958) was measured in Canangle Creek to the south of the present area and was considered to be 277 m thick. In the best exposure of the sequence in the Regan's Creek area (Canomodine Creek, Fig. 2, section D), approximately 28 m of massive pink quartzite is overlain by about 185 m of red siltstones, shales, minor quartzitic sandstones, green siltstones, nodular calcareous beds and conglomerates near the top. The exact thickness of the higher part of the sequence cannot be determined owing to faults and lack of outcrop, but the succession at this locality is summarized in the stratigraphic column of Fig. 6. A fault-bounded area of outcrop of this unit occurs further to the south (Fig. 2) and the top of the upper siltstone succession is represented along the eastern margin of the area studied. It is possible that when the Catombal Group of the entire Cargo area is restudied it may be possible to subdivide the " Columbine Sandstone " into two formations, corresponding to the lower quartzite and upper sandstone-siltstone sequences. There is not sufficient unfaulted exposure in the Regan's Creek area, however, for such subdivision to be attempted with confidence.

Petrography. The quartzitic sandstones of the " Columbine Sandstone " form a very distinctive lithology and are generally very uniform in texture and composition. They consist of hard, almost saccharoidal quartzite, pale pink in colour commonly, especially in the quartzitic sequence of the lower part of the

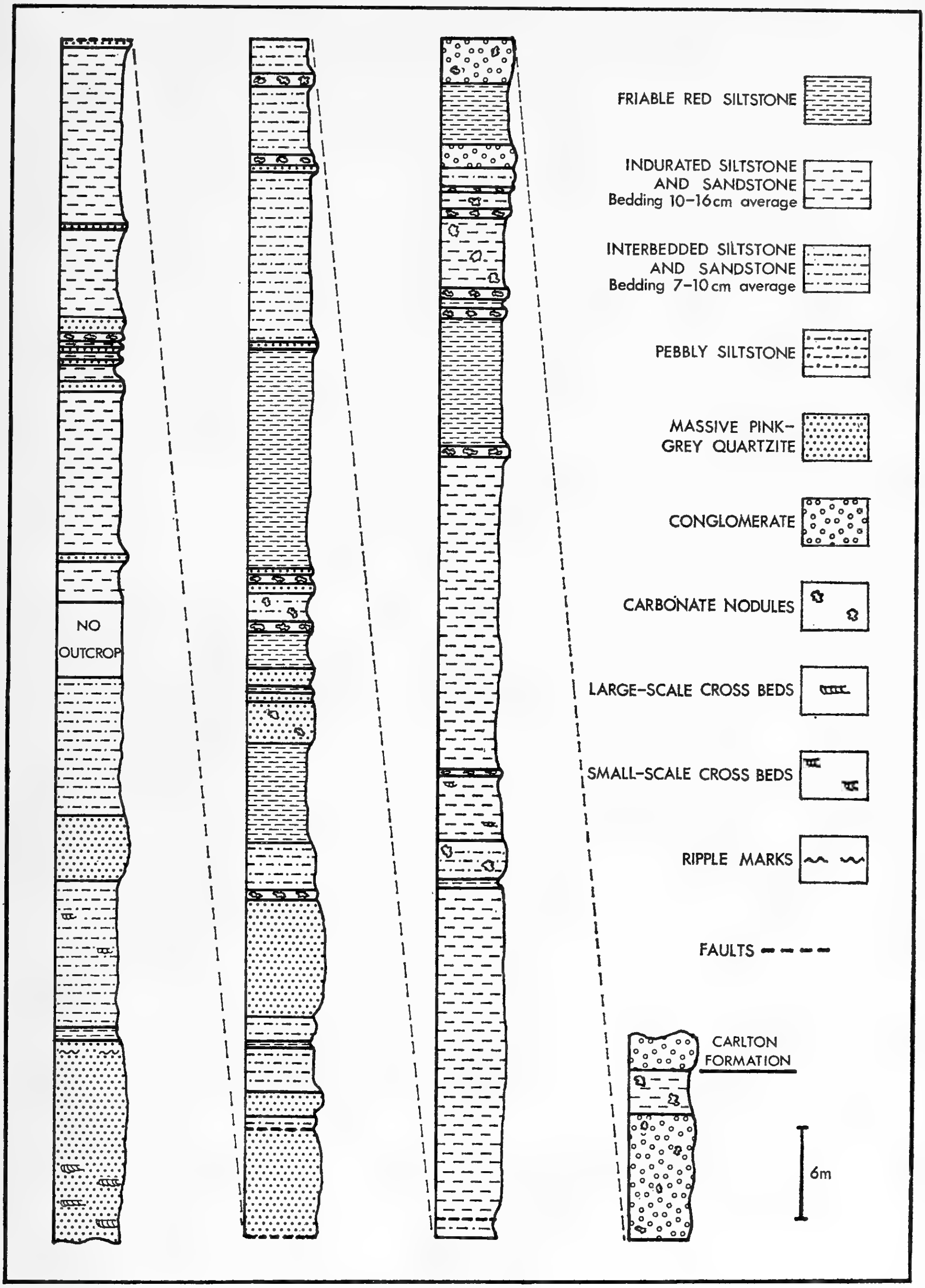

Fig. 6. Stratigraphic section, upper beds of the "Columbine Sandstone", Canomodine Creek.

" Columbine Sandstone ", but also white, pale green and red. They are dominantly comprised of moderately to well-sorted and well-rounded quartz, average grainsize 0·25–0·5 mm. Green biotite and white mica occur rarely as detrital grains. Rock fragments commonly make up less than 5% of the rock and appear to be dominantly sedimentary in origin, with fine-grained, hematite and limonite-stained quartzose siltstones and very fine-grained quartzite. Some fragments consist of cryptocrystalline limonite-stained material and are possibly of volcanic origin. The rock fragments generally show better rounding than the detrital quartz grains, but comparable size. Heavy minerals include rare tourmaline and zircon. Interstitial " matrix " material is very minor and comprises very fine-grained quartz, white micas and ? clay. Cement is dominantly very fine granular red iron oxide and quartz overgrowths occur rarely.

Typical siltstones from the upper siltstone sequence of the " Columbine Sandstone " show well sorted and rounded quartz grains of average size 0·05 mm. Micas include green-brown biotite and white micas, represented more abundantly than in the quartzites. Red iron oxide is abundant in the red siltstones as extremely fine granules, although it apparently only rarely forms a cement. It is generally lacking in the green siltstone beds. " Matrix " material consists of an almost cryptocrystalline aggregate of fine quartz and probable clays with fine-grained " sericite " and green chlorite.

The calcareous beds occur as lenticular bodies, usually 15–90 cm thick, and may disappear laterally over a distance of about 1 m. They normally have the appearance of light grey nodules, of diameter about 2 cm, set in a matrix of fine red silt, and occur abundantly throughout the upper siltstone sequence of the " Columbine Sandstone ". A representative coarse carbonate bed in Canomodine Creek illustrates the characteristics of this lithology. It contains large, subangular to subrounded, poorly sorted quartz grains ranging in size up to 2·5 mm. Sedimentary rock fragments and polycrystalline quartz fragments are common. Many siltstone and fine sandstone pebbles show abundant replacement of matrix material by carbonate. In some cases all that remains of a rock fragment is an aggregate of well-sorted quartz grains entirely enclosed in a calcite cement. Red iron oxide is an abundant cement in the siltstone fragments. The commonest " rock fragment " now consists of fine, cloudy granular carbonate with rare quartz grains. Remobilization of the carbonate is indicated by its filling of fractures in quartz grains. The extent to which carbonate is represented in these lenses is very variable, ranging from large aggregates to minor amounts of cement, and contacts between carbonate lenses and the enclosing siltstones are typically gradational. Some discussion of the possible origin of these beds is made below.

The conglomerate beds occurring near the top of the sequence are petrographically similar to those in the overlying Carlton Formation and are discussed below.

Sedimentary Features. The massive quartzitic sandstones of the lower part of the " Columbine Sandstone " show bedding on the scale of 15–60 cm. The overlying siltstones and fine-grained sandstones show finer bedding, usually on a scale of 2 cm or less.

Both small- and large-scale cross beds occur in the massive quartzites, while small-scale sets (less than 5 cm thickness) are abundant in the overlying lithologies. The large-scale sets are solitary or rarely grouped, with average thickness of each set of about 15–30 cm. Their lower bounding surface is usually planar and non-erosional. The small-scale sets are generally similar in appearance, but with average thickness of about 5 mm, commonly occurring as grouped sets and sometimes showing erosional contacts between the sets.

Ripple marks occur rarely, being generally small-scale current ripples (wave length up to about 8 cm). Linguloid ripples occur sparsely in red siltstones near the top of the lower quartzite sequence.

Rare, minor penecontemporaneous bedding slumps may be associated with collapse of ripple fronts in small-scale cross-bedded siltstones.

Scouring and channel formation are commonly shown. Preserved channel structure (often filled with carbonate " nodule " detritus, fine sandstones and siltstones) are represented in the upper siltstone sequence. Mud cracks occur sparsely in the finer sediments.

Carlton Formation

As mentioned above, the " Carlton Conglomerate " of Walker (1958, unpubl.) is here formally defined as the Carlton Formation. The type sequence was taken in the south-eastern corner of the area (Fig. 2, section E), where a well-exposed conformable succession occurs on the eastern limb of the Checkers valley syncline. At this locality massive red-brown conglomerates overlie red, friable conglomerates, pebbly sandstones and siltstones of the upper " Columbine Sandstone ". The conglomerates decrease in abundance through the sequence, becoming interbedded with green and brown pebbly sandstones and siltstones until the formation passes conformably into green, pebbly sandstones and minor conglomerate lenses of the Warree Creek Beds. This upper contact cannot always be mapped with certainty, but was taken as the approximate boundary between continuous, massive conglomerates (with interbedded siltstones) and siltstones with discontinuous, lenticular conglomerate beds. In the type section the formation reaches a thickness of 66 m (see Fig. 7, A) but in Canomodine Creek on the western limb of the Columbine Mountain anticline (Fig. 2) only 21 m are represented. This thinning of the formation to the west suggested to Walker (1958) that the upper parts of the " Carlton Conglomerate " and lower beds of the " Warree Creek Shale " may be time-equivalent. This proposal is also suggested by the thick, massive conglomerate unit in the north-eastern part of the area (Fig. 2), which, by its abundance of coarse conglomerate, would be included in the Carlton Formation, but is stratigraphically equivalent to a thick, green sandy and silty sequence to the south. This latter sequence by its lack of conglomerates, would be included in the Warree Creek Beds. It is evident, therefore, that the two members of the Canangle Subgroup are in part facies-equivalent to each other. However, it is felt that as broad, mappable units they can be usefully distinguished and obviously represent two distinct environments of deposition.

Plant fragments occur abundantly in the green sandstones and siltstones, usually strongly oxidized with limonite replacement. Both leaf and stem fragments are represented. Some better preserved material was found in the siltstones of the Warree Creek Beds and is discussed below.

Petrography. The conglomerates are extremely constant in composition, consisting of well-rounded, elongated pebbles of fine quartzitic sandstones very similar to the sandstone of the " Columbine Sandstone ". The pebbles have a common size of 5–10 cm with rarer representatives 15–18 cm in length. Limestone pebbles occur in the Canomodine Creek section and milky quartz fragments are rare throughout the formation. Sorting of the pebbles is generally poor and sphericity is low. Matrix is not abundant, being composed of poorly sorted quartz grains up to about 1 mm commonly and with moderate rounding. Hematite occurs commonly as cement in the matrix, together with quartz overgrowths. Calcite may be abundant locally as cement. Carbonate lenses similar to those of the " Columbine Sandstone " are present and the indurated

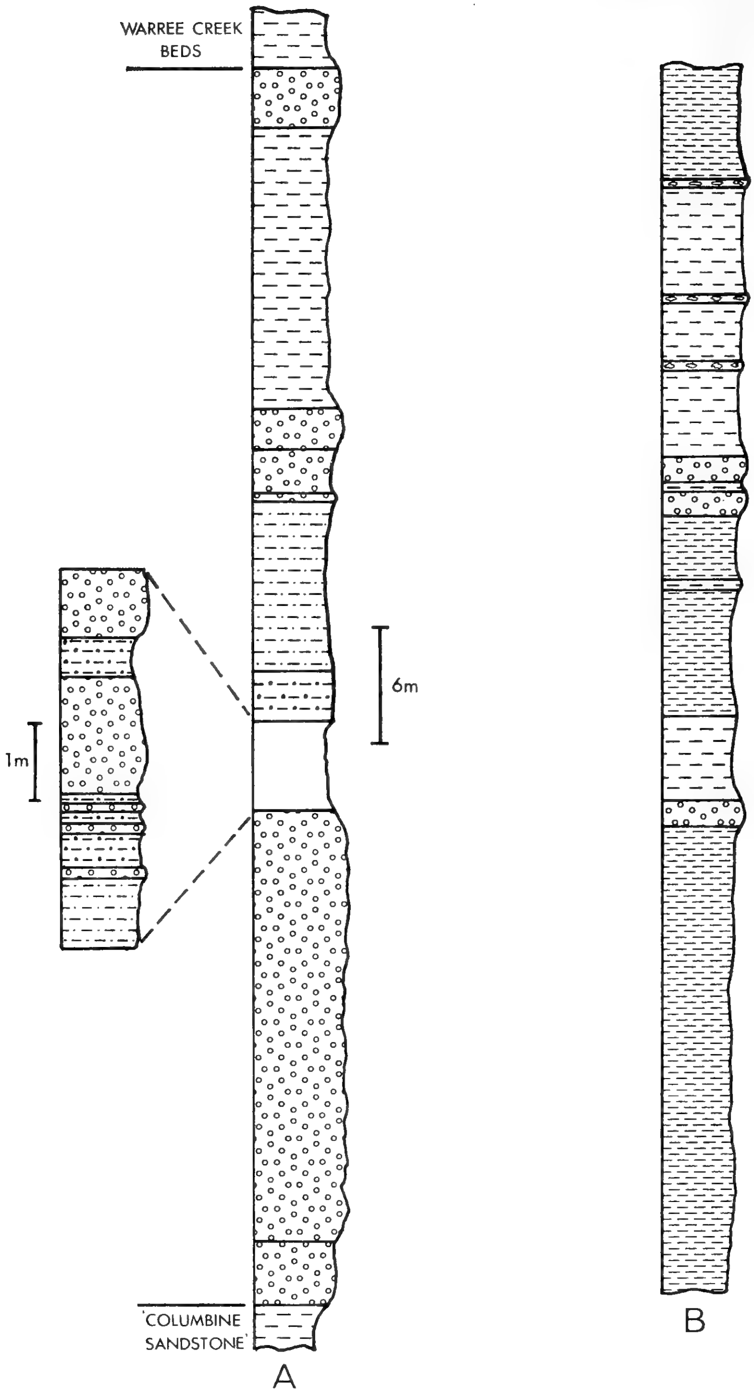

Fig. 7. Stratigraphic sections of Canangle Subgroup. A. Type section of the Carlton Formation. B. Representative sequence, middle part of Warree Creek Beds. For section localities, see text. Legend as in Fig. 6.

fine green sandstones and siltstones interbedded with the conglomerates in the higher parts of the formation are comparable to those of the Warree Creek Beds and are discussed below.

Sedimentary Features. Bedding in the Carlton Formation ranges from 60–180 cm in thickness, but bedding planes are usually very poorly defined. In the indurated siltstones and sandstones, bedding is commonly on a scale of 15 cm or less. The base of a massive conglomerate unit is marked by scouring of the underlying siltstones and fine sandstones and pebbles in the conglomerates generally show random orientation, rarely being aligned.

Warree Creek Beds

The upper member of the Canangle Subgroup is here defined as the Warree Creek Beds, conformably overlying, and possibly partly equivalent to, the Carlton Formation. The top of the succession is not defined, no higher formation having been observed.

Lack of suitable continuous exposure of the formation, owing to alluvium cover and general sparsity of outcrop away from the creeks, makes accurate measurement of the thickness of the unit impossible. However, it is estimated that at least 125–185 m are present in the syncline of the Checkers valley. A thickness of 35 m could be measured overlying the Carlton Formation in Canomodine Creek (Fig. 2), but the sequence here is disrupted by the Columbine Mountain Fault. A section representative of the middle part of the unit is shown in Fig. 7, B (section F, Fig. 2). The general sequence of the Warree Creek Beds consists of coarse, lenticular conglomerates with green sandstones and siltstones at the base followed by a considerable thickness of green and red friable shales, and finally conglomerate lenses and green sandstones near the top.

Fragmentary plant remains occur abundantly in the green siltstones, with fronds, probably of the genera *Archaeipteris* or *Rhacopteris* common. Adamson and Trueman (1962) reported plant fossils in grey siltstones of the " Canangle Formation ", south of Canangle Creek and north-west of the " Needles " (the gorge cut by the Belubula River in the Black Rock Subgroup). These forms included *Rhacopteris inaequilaterata* Göpp. and *Archaeopteris wilkinsoni* Feist. and were considered to be Lower Carboniferous, the age suggested by Stevens (1950, 1954) for the " Canangle Formation ". However, Warris (1964) also found representatives of *Leptophloem* in green shales of the " Canangle Formation " to the south-east of the Regan's Creek area and suggested an Upper Devonian age for the formation. Walker (1958) had previously included the entire Catombal Group in the Upper Devonian. As *Archaeopteris* is represented also in the Upper Devonian, there is no evidence in the present area to extend the Canangle Subgroup into the Lower Carboniferous.

Petrography. The brown and green conglomerates are lithologically very similar to those of the underlying Carlton Formation. They contain quartz sandstone pebbles 12–15 cm in length as a framework. Where sand-size detritus becomes more abundant towards the top of a conglomerate lens, the pebbles cease to form a framework, becoming sparse and usually finer (3 or 4 mm). The matrix, then, is dominant and consists of fine green sandstones, typical of the indurated green lithologies in the remainder of the sequence.

The finer-grained beds comprising the bulk of the succession are generally similar in composition, varying only in the proportion of coarser detritus that has been mixed with the finer fraction. This finer fraction typically consists of a very fine sand or coarse silt-size quartz moderately sorted, and showing abundant limonite staining of most grains. Coarser sand-size detritus is often mixed with this finer fraction, together with coarse quartz grains and rock fragments. These larger quartz grains may be well-sorted, with average size of about 1 mm. Rock fragments are often of polycrystalline quartz.

Sedimentary Features. The bedding features of this member are generally similar to those of the underlying formation with regard to the coarser lithologies. In many conglomerate-bearing outcrops a scoured surface is overlain by coarse conglomerate, which grades upward with decrease in pebble content into pebbly sandstones and siltstones, and finally red and green friable shales. This general sequence may range over as much as 20 m vertically, but outcrop is insufficient for detailed measurement. In many cases the coarse pebbly beds are lacking and an individual outcrop may only show fine sandstones overlain by shales. These graded sequences appear to be generally very lenticular in nature. Very small-scale cross-bedding (sets of less than 1 cm) occurs extremely rarely in the fine sandstones and siltstones. Irregular oscillation ripple marks are present sparsely in the finer lithologies.

Provenance and Environment of Deposition

In the " Columbine Sandstone ", presence of derived quartz overgrowths on some detrital grains suggests a sedimentary source rock and the great predominance of sedimentary rock fragments over volcanic and metamorphic material supports such an origin. A probable original plutonic source for much of the quartz may be inferred from their general lack of inclusion. There is insufficient evidence to suggest a source direction for the small amount of " Columbine Sandstone " in the area studied.

Calcareous nodule beds common in the upper part of the " Columbine Sandstone " (and rare in the Carlton Formation and Warree Creek Beds) show great similarities to deposits from the Old Red Sandstone of the Welsh Borderland and south Wales. Allen (1960) termed these deposits cornstones and recognized two types : concretionary cornstones and conglomeratic cornstones. It seems both types may be represented in the area studied here. Similarities between the concretionary cornstones and the Columbine nodular beds include the following :

(*a*) They occur in wedging units, up to 1·5 m thick (generally less in the Regan's Creek area).

(*b*) The units often begin with small, knotted, irregular concretions of argillaceous limestone embedded in massive siltstones.

(*c*) The concretions contain rare to abundant quartz of silt to fine sand grade, with a small amount of mica.

(*d*) Enclosing siltstones grade gradually into concretions as patches of calcite increase gradually in size and abundance.

These similarities hold for carbonate bodies that are apparently *in situ.* However, it is evident that others occur as channel-filling and may represent reworking and accumulation in old stream channels of *in situ* formed nodules of the type mentioned above. In that case they would be related to the conglomeratic cornstones, which according to Allen (1960) are merely " intraformational conglomerates ", probably derived from concretionary cornstones. According to Allen (1960), the concretionary cornstones were formed by " simultaneous mechanical deposition of silt, clay and precipitated carbonates in evaporating bodies of water, cut off from major supplies of clastic detritus ".

It is possible also that the carbonate material represents derivation from a limestone rock (i.e. the carbonate is detrital). Post-depositional reworking by intrastratal solution may then have formed the calcareous cement for this limestone and associated terrigenous detritus.

Hence it is possible that some calcareous nodular bodies may have formed by precipitation of carbonate *in situ*, while many others represent derivation, either from a limestone or at least a calcareous, nodular soil (? caliche) with mixed abundant terrigenous detritus. In all cases it is apparent that post-depositional carbonate mobilization and accumulation as cement has occurred.

The " Columbine Sandstone " was interpreted by Walker (1958) as being essentially marine, on the basis of brachiopods in the area north of Cargo. J. Davis (pers. comm., 1973) has restudied the Upper Devonian sequence of this area and reports definite marine strata (quartzites and green shales with brachiopods) at the base of the " Columbine Sandstone " and that in the remainder of the quartzite sequence there is no sedimentological evidence for any change in environment. In the higher parts of the succession (upper " Columbine Sandstone " and Carlton Formation) of that area it appears likely there is change to non-marine conditions. In the Regan's Creek area there is no evidence for marine conditions in the upper beds of the " Columbine Sandstone " and a non-marine environment is suggested by the channel scours filled with carbonate material and the common occurrence of rootlet fragments, some in growth position.

The abundance of sedimentary rock fragments in the Carlton Formation is indicative of derivation from a quartzose sandstone and siltstone terrain, comprising rocks probably similar to those of the " Columbine Sandstone ". A minor amount of material has apparently been derived from volcanic, meta-quartzite and limestone sources.

At the base of the Carlton Formation a large influx of coarse, gravel detritus is indicated, continuing the trend of the upper beds of the " Columbine Sandstone " and a fluviatile regime is likely. Characteristic features of this formation such as poor sorting and stratification, chaotic arrangement of pebbles and alternation of fine sediment and gravel were considered by Allen (1965) as characteristic of braided streams, possibly in an alluvial fan environment.

The lithological similarities between the Warree Creek Beds and Carlton Formation suggest similar source rock, a sandstone type, as evidenced by the conglomerate pebbles.

The probably mainly rapid deposition of the Carlton Formation gradually subsided during the early stages of accumulation of the Warree Creek Beds, with only occasional channels still depositing conglomerates. Mixing of coarser material with the fine sands and silts of the higher parts of the sequence may indicate periodic small floods of coarse detritus. The predominant green colour of the sediments suggests mainly reducing conditions and possible stream channel deposition predominating for the coarser deposits. The red coloration is mainly confined to finer, friable shales and these may represent alluvial-flat accumulation under oxidizing condition, a situation similar to that envisaged by Friend (1965) for the Old Red Sandstone of Spitsbergen.

Comparisons of the Catombal Group of the Molong-Wellington and Cargo Regions

In the Molong-Wellington area, Conolly (1963) proposed subdivision of the Black Rock Subgroup into the Paling Yards Formation, Brymedura Sandstone and Macquarie Park Sandstone, in ascending stratigraphic order. The Paling Yard Formation is only thinly developed near Molong and apparently lenses out to the north. It lacks the conglomerates of the type area north-east of Cargo (Conolly, 1963) and Webby (1972*a*) has suggested that the formation in the Molong-Wellington region may in fact belong to the underlying Garra Formation. The coarse sandstones of the Brymedura Sandstone were suggested by Conolly (1963) and Webby (1972*a*) to be equivalent to the conglomerate lenses of the Paling Yard Formation north-east of Cargo. Walker (*in* Conolly, 1963) suggested that south of Molong the Paling Yard Formation, Brymedura Sandstone and " Columbine Sandstone " were represented. Detailed mapping of this latter area may well show that the Brymedura Sandstone is in fact a facies-equivalent of the Paling Yard Formation to the south.

The Canangle Subgroup of the Molong-Wellington region was divided by Conolly (1963) into a lower Kurrool Formation and upper Curra Creek Conglomerate. The Kurrool Formation was considered a transitional horizon between the white quartzites of the Macquarie Park Sandstone and the coarse conglomerates of the Curra Creek Conglomerate, being dominantly red siltstones and sandstones (Conolly, 1963). As such, it may occupy the position of the upper sandstone-siltstone sequence of the " Columbine Sandstone " of the Regan's Creek area, between the pink-grey quartzites of the lower " Columbine Sandstone " and the conglomerates of the Carlton Formation, or at least overlap this part of the succession.

Hence it would appear that the original subgroup divisions of Walker (1958) for the Catombal Group of the Cargo area may not be directly applicable to the Molong-Wellington region, since it is possible that the Kurrool Formation may may be partly equivalent to the top of the " Columbine Sandstone ". The Curra Creek Conglomerate probably mainly corresponds to the Carlton Formation and Warree Creek Beds, thus being the major equivalent of the Canangle Subgroup in the Molong-Wellington belt. Suggested correlation within the Catombal Group is summarized in Table 2.

TABLE 2

Tentative Correlation of Members of the Catombal Group

	CARGO	MOLONG-WELLINGTON
Canangle Subgroup	Warree Creek Beds	Curra Creek Conglomerate
	- - - - - - - - - - - - - -	
		—— ? - - - - - - - - - ? - - - -
	Carlton Formation	
		Kurrool Formation
Black Rock Subgroup	" Columbine Sandstone "	— — ? — — ? — — — — — — —
		Macquarie Park Sandstone
	" Paling Yard Formation "	Brymedura Sandstone ? Paling Yard Formation

INTRUSIVE BODIES

Gabbro

The largest intrusive in the area is a fine-grained gabbro, outcropping from the Canangles Road for about 1·5 km to the south. It was previously mapped as a dolerite (Stevens, 1950), extending only as far south as Canomodine Creek. It is a distinctive grey-green rock with abundant cream feldspar laths ranging up to about 4 mm in length. The only compositional variations observed were a decrease in grainsize (not always apparent) adjacent to its contact with the Cargo Andesite. The contact is best exposed in Canomodine Creek, where there are apophyses of gabbro into conglomerates of the Cargo Andesite. Inclusions of the conglomerates in the intrusive body here extend over about 60 cm and the chilled margin ranges only over about 1·8 m from the contact. The intrusive nature of the body is confirmed by its disruptive effects on bedding in the country rock at other localities. No contact metamorphic effects in the Cargo Andesite were observed.

Fresh specimens of the gabbro typically show interlocking labradorite laths of average size 1–2 mm in an intergranular texture with ragged grains of pale green, weakly pleochroic augite (average size 1 mm). Pale green chlorite and fine-grained opaques also occur, together with carbonate and clay alteration of the feldspar. The pyroxene appears mainly unaltered. Near the contact with the Cargo Andesite, grainsize decreases to an average 0·5 mm. In places, alteration of the gabbro has been intense and the dominant secondary minerals present include epidote, quartz, chlorite, carbonate and albite. Fresh plagioclase is rare in these heavily altered specimens. The zeolite clinoptilolite occurs as pink, platy crystals in joint filling.

Basalt

A basaltic body occurs intruding the Malongulli Formation in and to the west of Regan's Creek in the north-western part of the area. It was mapped as " porphyrite " by Stevens (1950) and contains cream feldspar laths, often aligned, in a grey-green aphanitic groundmass. The feldspar is rarely fresh, being usually altered to " saussurite ", clay minerals, carbonate and dominant albite, but where relatively fresh, a labradorite composition may be seen. Pale green, euhedral augite occurs and the groundmass is composed of an intergranular aggregate of feldspar laths, granular augite and opaques. Minor amounts of secondary epidote and chlorite are present, the chlorite occasionally occurring as alteration along the augite cleavages. The groundmass feldspar now appears to be dominantly albite.

Monzonite

A small intrusive body occurs probably as a dyke in the Malongulli Formation in a creek bed near the northern end of Area 2 of the Regan's Creek Limestone (Figs. 2, 4 (A)) and has not been previously mapped in this area. It is typically highly weathered and its outcrop extent cannot be determined accurately. In rare, relatively fresh specimens the rock shows a meshwork of interlocking pink feldspars in a dark green groundmass. In thin section it has a monzonitic fabric of interlocking laths of potassic feldspar (up to about 4 mm in length) and andesine. The potassic feldspar constitutes a little over half of the total feldspar. There is extensive alteration of the feldspar to " sericite ", clay minerals and carbonate. Brown biotite, almost completely replaced by pale green, bladed chlorite along cleavages, occurs as ragged grains. Chlorite also occurs abundantly with chalcedony.

All the intrusives occur in Ordovician strata, but no younger formations overlie them, so no definite age other than post-Ordovician can be proposed for them.

BASALT OF ? TERTIARY AGE

Post-Devonian basalts occur on five hills, unconformably overlying the Carlton Formation and " Columbine Sandstone " of the Catombal Group in the north-eastern corner of the area studied (Fig. 2). They were mapped as one outcrop by Walker (1958). The present thickness of basalt is estimated to vary from 4·6 m in the smallest capping to about 30·8 m in the largest. Irregularities in the pre-basalt topography are indicated by a variation of up to 27·7 m in the elevation of the approximate position of the base of each basalt capping.

The basalt is a black to dark grey, mainly aphanitic rock with rare phenocrysts of plagioclase (up to 2 or 3 mm in length). It may be rarely scoriaceous. There is some variation in composition since fine-grained biotite and olivine occur in the largest area of outcrop, while clinopyroxene is more abundant in xenolith-bearing basalts at the two northern outcrop areas. Typical basalts from the southern area of outcrop contain porphyritic labradorite, usually with abundant opaques and colourless, probable pyroxene; some grains also contain inclusions of a more calcic plagioclase. Resorption features and normal zoning are commonly shown. Olivine and red-brown biotite grains (up to about 0·5 mm) occur rarely. Groundmass consists of a fine-grained intergranular aggregate of plagioclase laths, with granular clinopyroxene and abundant opaques. Probable xenocrysts include diopside, plagioclase and opaques. Fine quartz sandstone xenoliths may be present near the base of the basalt. Some of the quartz grains are pale brown to yellow in colour and nearly isotropic, suggesting possible partial fusion of the silica during incorporation of the rock fragments into the magma. A characteristic feature is the occurrence of a broad, brown, isotropic glassy corona around the xenoliths, typically with clustered aggregates of colourless, prismatic clinopyroxene granules growing with their long axes perpendicular to the xenolith margins. Such features reflect rapid chilling of the magma around the xenolith body.

The exact age of the basalt is unknown. However, Tertiary (Miocene) plants and diatoms are associated with olivine and titanaugite-bearing basalts immediately to the north on the Upper Devonian rocks of the Gap Creek area (J. Davis, pers. comm., 1973). Hence a comparable age is likely for the basalts in the Regan's Creek area.

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POLLEN ANALYSIS OF A BURIED ORGANIC DEPOSIT ON THE BACKSHORE AT FINGAL BAY, PORT STEPHENS, NEW SOUTH WALES

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[Accepted for publication 19th September 1973]

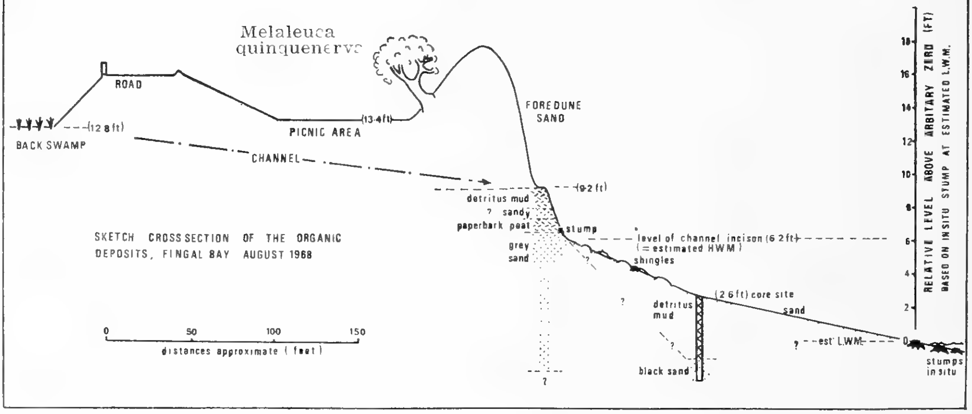
Synopsis

A pollen analysis of relict organic deposits above and below present high tide level at Fingal Bay beach (Central Coast, N.S.W.) is reported. The vegetational changes recorded appear to show the effect of a rising post-glacial sea-level on plant communities occupying coastal Pleistocene sand dunes through rising watertable levels and alterations in dune topography. Pollen curves reflect the destruction of local and seaward dune *Eucalyptus-Angophora* forest and establishment of the ti-tree/paperbark swamp more characteristic of the present-day beach hinterland.

Introduction

Organic sediments, similar to those being deposited in the beach-ridge swales, dune depressions and fresh-water barrier lagoons so characteristic of the southeastern coast of Australia, are occasionally exposed on present-day beaches. Pollen analyses of such " peats " have been described for Dee Why, N.S.W. (Martin, 1971), and for Wilson's Promontory, Victoria (Hope, 1969). In this paper a pollen analysis of samples taken from the vertically disjunct organic strata in the eroded foredune and foreshore of Fingal Bay is described. This deposit extends discontinuously from *ca* 0·9 m above estimated mean high water† to at least 2·4 m below estimated H.W.M. (*ca* 0·7 m below estimated low water) (Fig. 1). As well as the obvious connection of this deposit with sea level changes and coastal regression—stumps occur *in situ* at and just below low tide level—the site is of interest as it is situated midway between the extensive Pleistocene-Recent parallel beach-ridge systems of the Newcastle Bight Embayment and Myall Lakes described by Thom (1965) (Fig. 2). As such, Fingal Bay has probably undergone analogous changes in its sedimentological

FIG. 1



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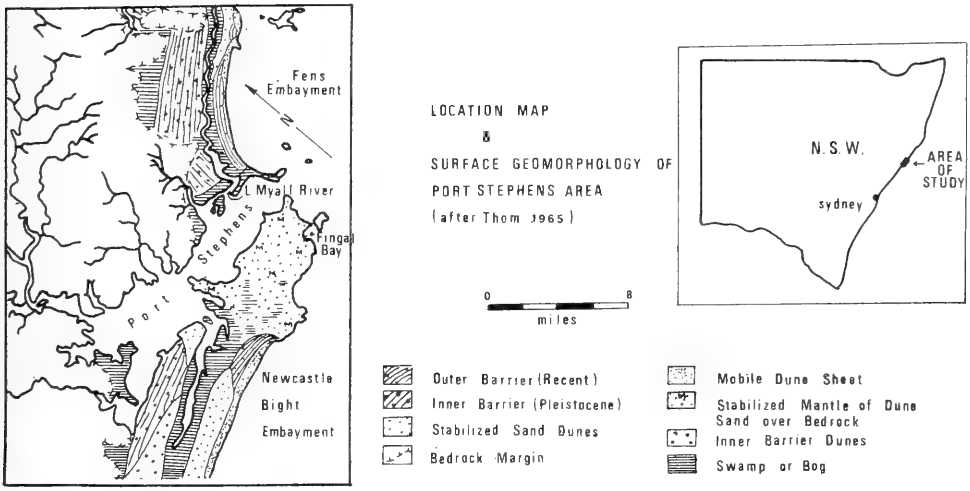
† Based on the depth of incision into the beach sediments by a small artificial channel entering the beach near the deposit. The tidal range at Fingal Bay is 1·5 m (4·9 ft).

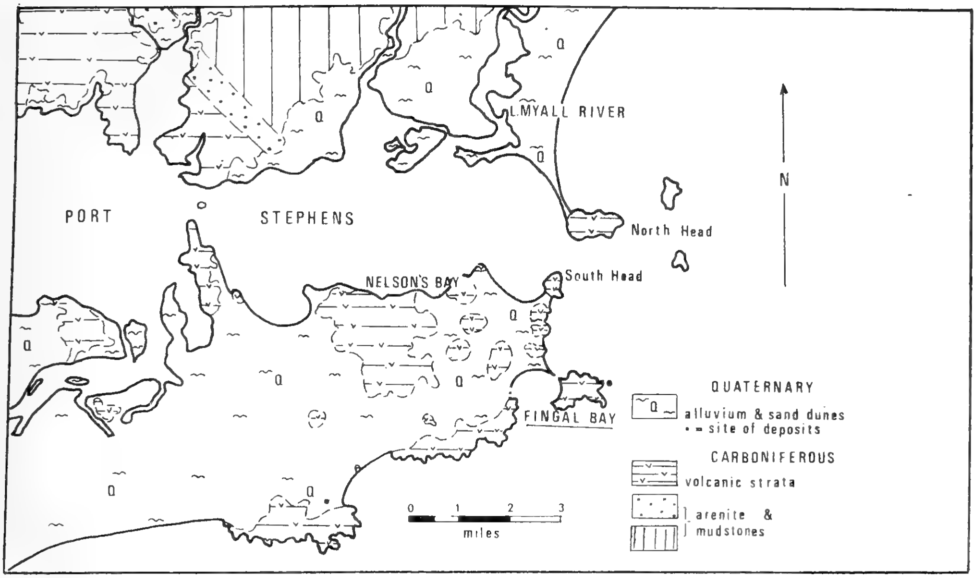
regime during fluctuations in sea level. Much of the Holocene geomorphological and vegetational history preserved in these landforms is increasingly under threat of loss by beach mining and beach resort development.

FIG. 2



LOCATION MAP & SURFACE GEOMORPHOLOGY OF PORT STEPHENS AREA (after Thom 1965)

FIG. 3



GEOLOGY OF PORT STEPHENS (after Engel 1962)

PRESENT TOPOGRAPHY AND VEGETATION

Fingal Bay (Fig. 3), situated on the central coast of N.S.W., consists of a shallow embayment approximately 1 km across at the " mouth " and apparently eroded out of a sand mass connecting isolated outcrops of volcanic rocks. The hinterland consists of a stabilized sand mantle over the igneous bed rock ; again peaks of volcanic rock up to 244 m (800 ft) dominate the relatively subdued dune-swale landscape (Engels, 1962). It is probable the sands are of both Pleistocene and Holocene deposition. Fresh-water swamps in dune depressions occur up to 6 m (20 ft) above mean sea level, with dune ridges up to 1·5 m (5 ft) above the swale. Beach-ridge and dune habitats, depending on shelter and the period elapsed since the last serious phase of dune mobility, support communities of *Eucalyptus pilularis-E. gummifera-Angophora lanceolata* dune forest (the climax association on deep stable sands), *Banksia serratifolia-Angophora* woodland, *Banksia-Leptospermum* dune thicket, or *Leptospermum-Acacia* dune scrub (behind the foredune). With fire-caused destruction of dominants, a variety of Leguminosae, Proteaceae, Myrtaceae and Epacridaceae species form locally extensive areas of disclimax dune scrub (Pidgeon, 1943). The plant associations found locally have been described by Osborn and Robertson (1939) and Pidgeon (1943); these predominantly are successions on wind-blown sands and beach-ridges and include the important *Melaleuca quinquenervia* and *Casuarina glauca* associations in fresh water and brackish-subsaline aquatic environments. Recent ecological studies in the Myall Lakes area are outlined by Carolin (1971). Rocky coastal exposures support *Casuarina* and Epacridaceae-Proteaceae heathland. Volcanic outcrops support more mesophytic vegetation, either mixed *Eucalyptus* spp. forest with scattered *Casuarina torulosa* and an undergrowth of *Pomaderris*, *Acacia*, *Monotoca*, *Dillwynia*—species also found in dry heath—or subtropical rainforest of Indo-Malaysian species. This often extends along wet gullies into the eucalypt forest. *Drimys* and *Podocarpus* may be present (Osborn and Robertson, 1939). An estuarine environment exists within Port Stephens. Tolerance of diverse ecological conditions produces anomalous occurrences of species within the area.

Lithology and Age of Deposit

(Fig. 1)

At present the organic strata are best exposed during winter retrogression of the beach. They outcrop beside a small artificial channel draining a back-swamp near the southern end of Fingal Bay, a site adjacent to the beachside picnic area on the northern limits of the township. Three " peat " horizons can be recognized, the upper two exposed in the partially destroyed foredune, the third below an overlay of shingles on the foreshore. From the top, a detritus mud layer *ca* 20 cm thick and truncated by sands of the present foredune at 0·9 m (3 ft) above the estimated H.W.M. is underlain sequentially by *ca* 20 cm of grey sand, then a second organic stratum of paperbark peat *ca* 25 cm thick. This contains wood fragments and is underlain by grey, sometimes peaty, sand to at least estimated L.W.M. The peat horizons are presently exposed some 9–12 m (30–40 ft) horizontally along the beach. A stump is visible in the base of the peat (per. comm. Dr. A. R. H. Martin, Sydney University, 1972). The foreshore deposit consists of *ca* 1·5 m (4·6 ft) of coarse to fine detrital muds extending into at least 0·6 m of black sand. Stumps seemingly rooted in this organic deposit are exposed through the shingle and at low water level. Vertical relationships between the organic strata and estimated H.W.M. were surveyed by dumpy levelling but the stratigraphic relationship remains uncertain. Progradation of the beach since 1968 and development of Fingal Bay as a resort renders this impractical. Compression of the upper peat beds by the sand overburden is evident. Three samples submitted for carbon-14 dating have been described by Thom *et al.* (1969):

(*a*) Peat from surface of top detrital mud stratum, approximately 0·9 m above estimated H.W.M.—3150 ± 115 C-14 years B.P. (0–2157).

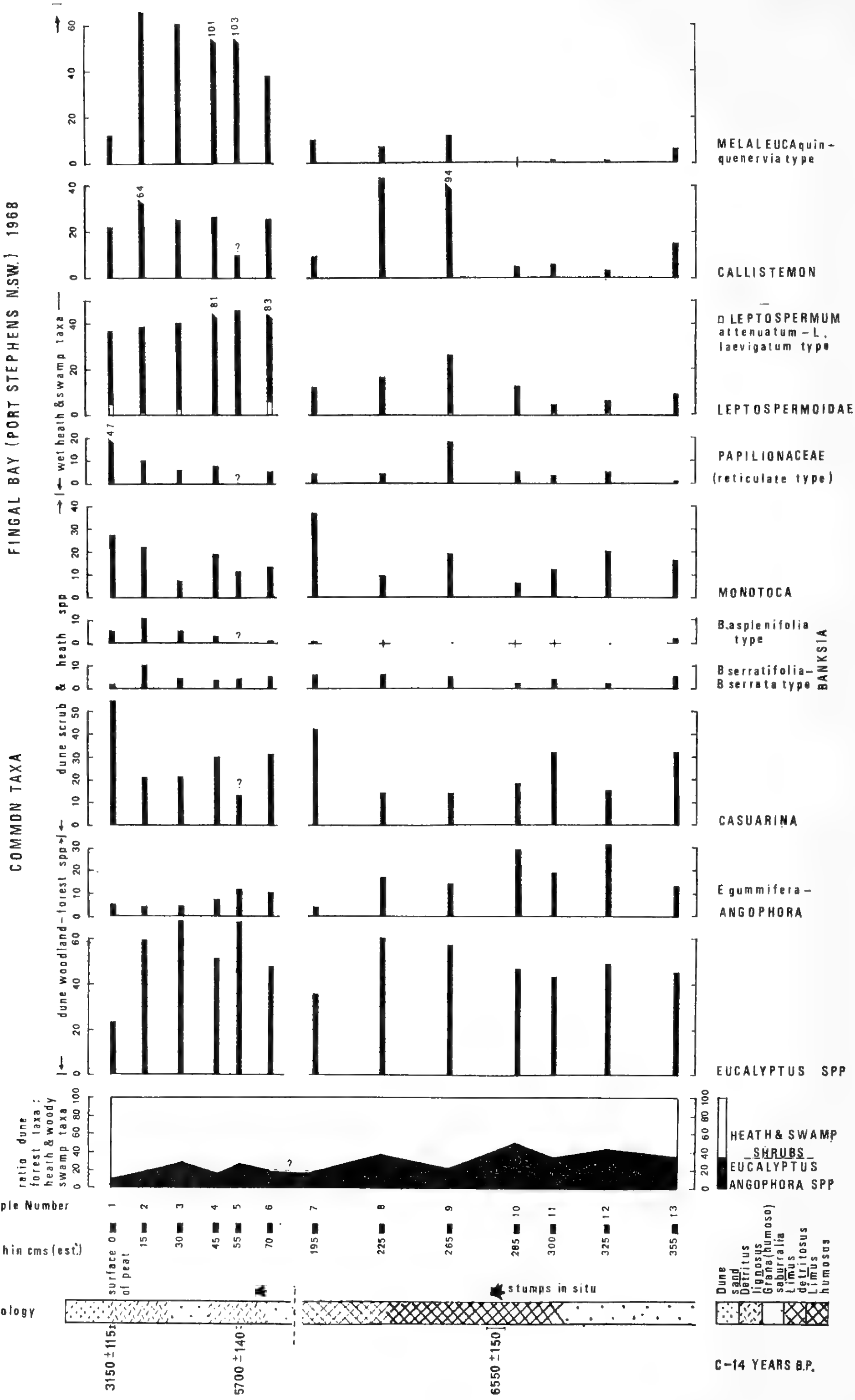
(*b*) Melaleuca stump, imbedded in the paperbark peat *ca* 0·4 m above estimated H.W.M.—5700 ± 140 C-14 years B.P. (0–2158).

(*c*) Stump (? " Melaleuca ") *ca* 1·8 m below estimated H.W.M. (approximating to L.W.M.)—6550±150 C-14 years B.P.

Samples for pollen analysis collected by Dr. A. R. H. Martin in 1966 and 1968 were processed using the sieve technique proposed by Churchill (1957) and standard chemical procedures outlined in Faegri and Iversen (1964). Pollen counts of whole mounts—up to 2,500 grains—were made along with estimates of the absolute pollen content of the samples using the weighing procedures of Jørgensen (1967). The frequency of occurrence of all pollens and spores was expressed as a percentage of the arboreal dune forest taxa pollen total (including *Casuarina* and the long-distance transported pollen component). This pollen sum hopefully minimizes irregular fluctuations in the pollen curves caused by the limited pollen dispersal of most Proteaceae, Epacridaceae and Leguminosae genera and local over-emphasis of the pollen of many Myrtaceae genera tolerant of waterlogged conditions.

Studies of modern pollen rains in Australia, essential for an objective interpretation of fossil pollen spectra, have been mainly confined to studies in connection with allergies and then in urban areas, e.g. Derrick (1966). Recent work at Wilson's Promontory, Victoria, by Hope (1969) used fixed long-term pollen traps to characterize various plant communities, from salt marshes to tall forest, in terms of their local pollen spectra and the degree to which a pollen type is represented at (i) sites where the plant source is present, and (ii) in terms of regional representation at other, non-local, sites (where the pollen source is absent). These data support the subjective " weightings " used in the interpretation of fossil pollen spectra from the Fingal Bay site and the pollen sum used to calculate such curves. Different plant communities at Wilson's Promontory were found to produce distinctive pollen spectra dominated by pollen produced by the local " dominant " (i.e. plant species forming the tallest stratum present) and " sub-dominant " species, the latter often having a significant contribution to pollen spectra of woodland and forest. In terms of local representation, the percentage of a pollen type approximated percentage total cover of the plant only for Myrtaceae, Casuarinaceae and Fagaceae species. The conclusions of Churchill (1968) regarding long-distance wind dispersal of *Eucalyptus* pollen were supported: this pollen type, together with the prolifically produced and widely dispersed pollens of *Casuarina*, *Nothofagus* and Gymospermae, and to a lesser extent that of *Pomaderris*, *Drimys*, *Acacia*, *Bursaria*, *Coprosma-Opercularia*-type, Compositae and *Cyathea*, constitute the major fraction of the regional pollen rain (and long-distance transported pollen). Of the sedges, herbs and monocots, only the pollens of Chenopodiaceae, Plantaginaceae and to a lesser extent of Compositae and Gramineae form an important constituent of the regional pollen rain. Proteaceae, Epacridaceae (*Monotoca* may be a significant exception) and Leguminosae pollens are badly under-represented even at sites where species in these families are locally abundant. Extra-local transport of these pollen types is likely to occur only *via* insects or wind-blown flower fragments. Pollen of *Juncus* apparently does not survive extractive procedures. The pollen spectrum of a *Juncus maritimus* salt marsh forms the one exception to plant communities dominated by pollen from the " dominant " species. Pollen productivity of local " dominant " species and community structure (heath, thicket, woodland, etc.), especially density of vegetation, were found to significantly influence the levels of " dominants' " pollens and non-local pollens recorded; the representation of non-local pollens in open communities being approximately double that encountered in dense thicket. This variable " filtering " effect on pollen from more distant sources by littoral plant communities, similar to that described by Tauber (1965), may conceivably affect the pollen spectrum as much as a change in (pollen) representation or frequency of " dominant " plants. The consequent difficulties of interpreting fossil pollen

Fig 4



The frequency of occurrence of all pollen and spores is expressed as a percentage of the total arboreal duneforest taxa including Casuarina & long distance transported taxa spectra are compounded by the necessary inclusion within the one pollen taxon of several species having divergent ecological niches. *Casuarina glauca* (often near salt-water estuaries and paperbark swamps) and *C. torulosa* (wet to dry sclerophyll forest, often on hillslopes) are examples.

Most pollen curves for Fingal Bay, calculated on the total number of pollens of types widely dispersed as a regional pollen rain, may consequently be assumed generally to reflect changes in local plant associations. The majority of plants whose pollen was encountered in fact grow in the area at present or inhabit niches conceivably existent in the past. A high pollen percentage, following the local *v.* regional representation characteristics of pollen taxa, as discussed above, is assumed to reflect either an abundance of the source plant in the local environs (aquatics, ferns, and sedges in particular) or *in situ* growth of that plant in the deposit (especially woody shrubs). Arboreal dune forest taxa can be assumed to be less liable to parochial fluctuations in their pollen record, as can the Chenopodiaceae, and hence some regional significance can be attached to low and absent pollen records.

Peat formation in coastal swamps may be rapid ; 3·6 m accumulated at Cotters Lake (Wilson's Promontory, Victoria) in *ca* 4,000 years, with the top 90 cm accumulating since European settlement (Hope, 1969). It is accordingly hoped that the widely separated samples necessary in this study are in fact sufficient to portray local trends.

Results of Pollen Analysis

Pollen curves presented in Figs 4, 5 and 6 show two major vegetational zones, based on the predominance (i.e. establishment) of woody taxa characteristic of communities behind present-day beaches. Zone 1—dominated by dune forest taxa of presumed general rather than local occurrence. These can occur inland on dunes away from the present coast. Zone II—dominated by local pollen taxa derived from coastal ti-tree and paperbark swamps. To facilitate discussion the zones have been further divided. To avoid repetitive text, it is emphasized that the plant community *descriptions* given for each subdivision of the zones, particularly local conditions prevailing at the time of deposition of the relevant sample, should be read as *interpretations* made from the pollen curves for that sample ; the transposition from pollen percentages to abundance of the corresponding plant taxon and its distance from the depositional site, etc., being made subjectively, using qualifications based on modern pollen rain data. Except when stated otherwise, the pollen data are not being directly described *per se.*

Zone I

(*a*) Sample 13. *Shallow freshwater dune lake conditions* supporting abundant Cyperaceae and *Triglochin*, possibly *Phragmites*, and the algae *Tetrahedron* and *Chara*, and bordered by *Callistemon* and *Banksia* (*asplenifolia-type*) on wet sands, with *Monotoca*, *Banksia* (*serratifolia-type*) and *Eucalyptus* on drier sites. Low pollen percentages of dune scrub taxa, and a relatively high Gramineae count, suggest relatively open conditions with *Eucalyptus-Angophora* dune forest and *Casuarina* woodland in the vicinity. Very low occurrence of salt-tolerant taxa, e.g. Chenopodiaceae, indicate the absence of any local marine environment. Overall the evidence suggests a perched dune lake surrounded by well-developed dune forest with little understorey, on deep stable sands.

(*b*) Samples 12 and 11. *Progressive infilling of the freshwater lake* by sand, thereby effectively lowering the watertable level below ground level to allow considerable pollen humification and invasion of the site by *Persoonia*, *Acacia*, *? Astrotricha*-type and Leguminosae taxa. A general surround of *Eucalyptus-Angophora* forest with *Monotoca*, *Leucopogon* and other Epacridaceae, and *Dillwynia* is indicated. Charcoal in Sample 11 suggests fire as the cause of the

Fig 5

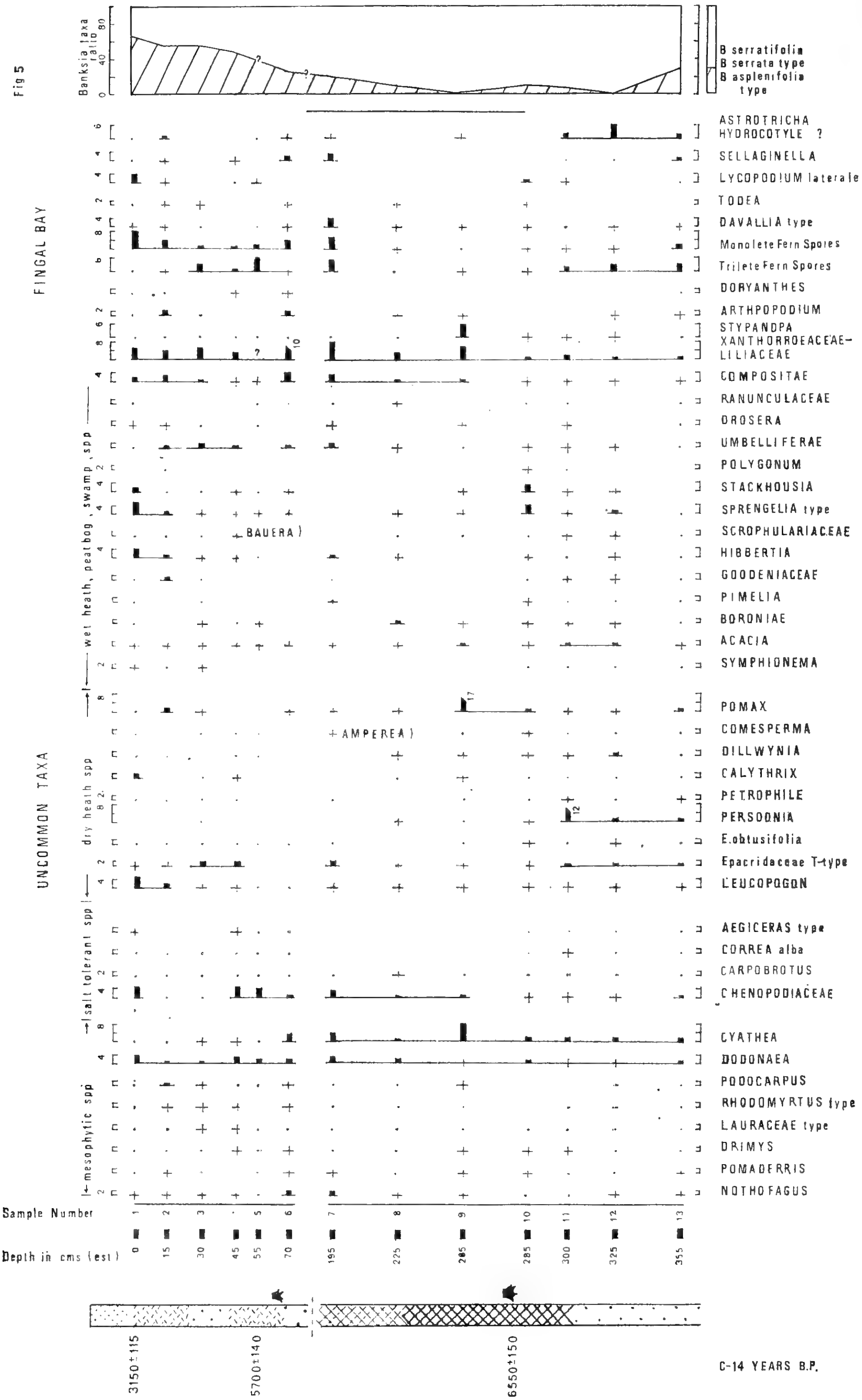
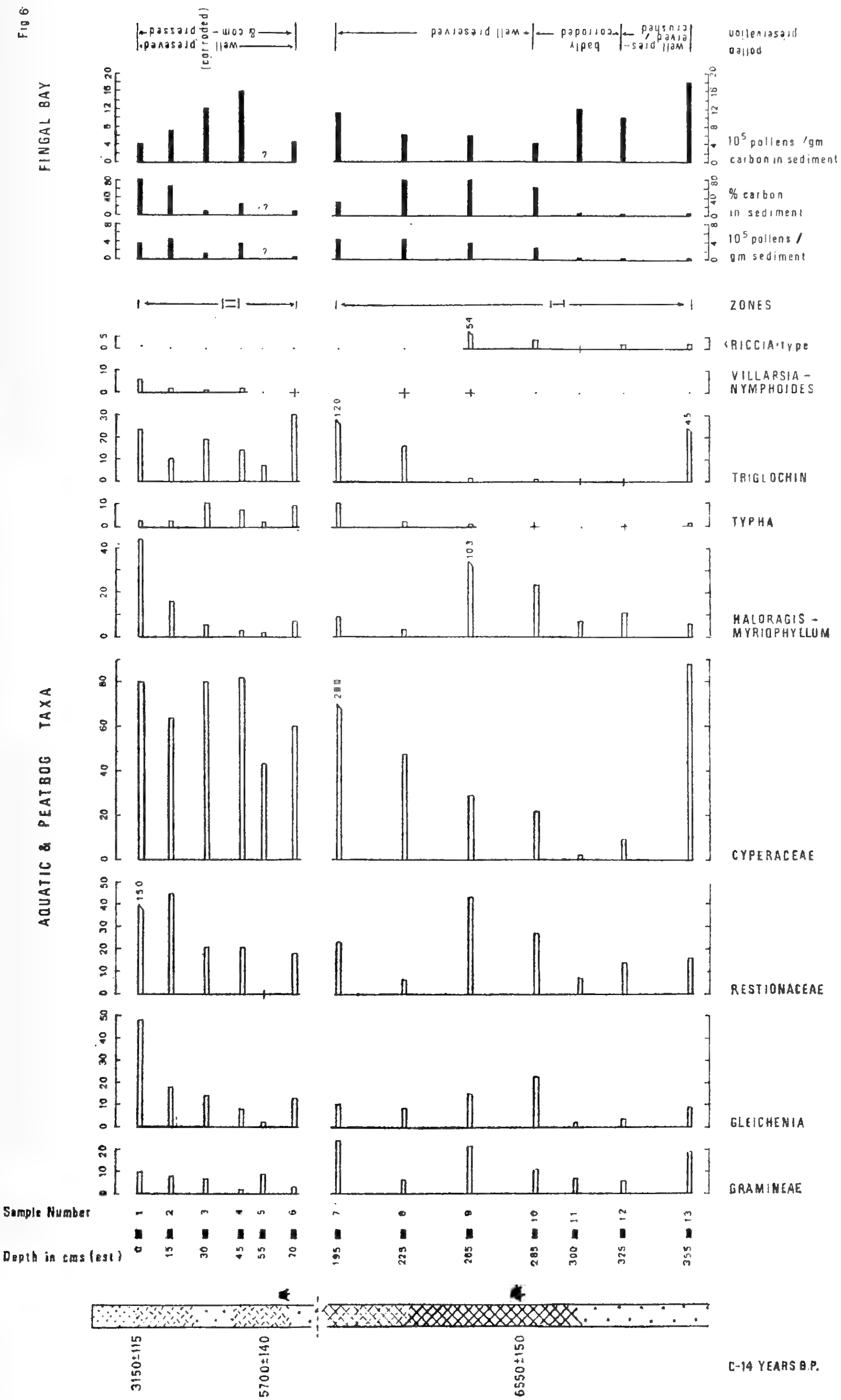

Banksia taxa ratio
0
40
80
B serratifolia
B serrata type
B asplenifolia type
FINGAL BAY
ASTROTRICHA
HYDROCOTYLE ?
SELLAGINELLA
LYCOPODIUM laterale
TODEA
DAVALLIA type
Monolete Fern Spores
Trilete Fern Spores
DORYANTHES
ARTHPOPODIUM
STYPANDPA
XANTHORROEACEAE-LILIACEAE
10
COMPOSITAE
RANUNCULACEAE
DROSERA
UMBELLIFERAE
POLYGONUM
STACKHOUSIA
SPRENGELIA type
SCROPHULARIACEAE
BAUERA
HIBBERTIA
GOODENIACEAE
PIMELIA
BORONIAE
ACACIA
SYMPHIONEMA
wet heath, peatbog, swamp, spp
17
POMAX
AMPEREA
COMESPERMA
DILLWYNIA
CALYTHRIX
PETROPHILE
12
PERSOONIA
E.obtusifolia
Epacridaceae T-type
LEUCOPOGON
dry heath spp
UNCOMMON TAXA
AEGICERAS type
CORREA alba
CARPOBROTUS
CHENOPODIACEAE
salt tolerant spp
CYATHEA
DODONAEA
PODOCARPUS
RHODOMYRTUS type
LAURACEAE type
DRIMYS
POMADERRIS
NOTHOFAGUS
mesophytic spp
Sample Number
1
2
3
4
5
6
7
8
9
10
11
12
13
Depth in cms (est)
0
15
30
45
55
70
195
225
265
285
300
325
355
3150±115
5700±140
6550±150
C-14 YEARS B.P.

Fig 6


FINGAL BAY
AQUATIC & PEATBOG TAXA
well preserved
& com - preserved
(corroded)
well preserved
badly corroded
well pres- / erved / crushed
pollen preservation
10^5 pollens /gm carbon in sediment
% carbon in sediment
10^5 pollens / gm sediment
ZONES
I
II
'RICCIA'-type
VILLARSIA - NYMPHOIDES
TRIGLOCHIN
TYPHA
HALORAGIS - MYRIOPHYLLUM
CYPERACEAE
RESTIONACEAE
GLEICHENIA
GRAMINEAE
54
120
45
103
288
150
Sample Number
1 2 3 4 5 6 7 8 9 10 11 12 13
Depth in cms (est)
0 15 30 45 55 70 195 225 265 285 300 325 355
3150±115
5700±140
6550±150
C-14 YEARS B.P.

sand movements. Organic matter, however, continued to accumulate, possibly as part of a soil.

(*c*) Samples 10 and 9. *Formation of a sedge peat bog under a rising watertable.* Local development of a *Gleichenia*-Restionaceae bog, associated probably with a rise in the local watertable, was paralleled by small increases in Leptospermoidae genera, *Melaleuca quinquenervia* and a significant decline in *Angophora* and *Eucalyptus gummifera.* Gramineae, of limited occurrence in dune forest and dense dune scrub, also increased. Trends suggest decline of the *Eucalyptus-Angophora* dune forest and its replacement by *Eucalyptus* dune woodland, a development that is favoured by partial subduing of deep stable sand dune relief. Slight development—possibly at a considerable distance from the depositional site—of the ti-tree/paperbark swamp and dune scrub communities characteristic of the present beach hinterland environment is weakly defined by the pollen record. Locally, bog development outstripped the local watertable heightening, the bog being invaded by woody shrubs *Callistemon* and Leguminosae (*cf Viminaria*) as well as *Pomax* and *Haloragis.* In the absence of a significant percentage of *Triglochin* pollen, the abundant "*Riccia*"-type spores indicate exposure of a moist mud surface.

(*d*) Samples 8 and 7. *Re-establishment of a Cyperaceae-Triglochin swamp.* Pollen records including the alga *Tehrahedron* imply a gradually rising water level submerging the *Gleichenia*-Restionaceae bog, i.e. a reversal in the spontaneous development within such a community. Local elimination of Leguminosae, *Callistemon*, *Haloragis* and *Riccia*, is apparent, concurrent with an increased record of pollen from heathland taxa, Epacridaceae spp., *Monotoca*, *Banksia asplenifolia*-type, *Hibbertia*, Xanthorrhoeaceae-Liliaceae-type, Pteridophyta and *Selaginella* taxa with relatively little *Callistemon.* An extensive freshwater swamp with distant heath and still remote paperbark and ti-tree communities is suggested. Complete elimination of the *Angophora-Eucalyptus gummifera* component and much of the other *Eucalyptus* stands, together with an increasing sand content in the peat, point to further destruction of the dune relief. Of interest are the relatively high percentages of *Casuarina*, Gramineae, *Typha* and Chenopodiaceae pollen. A brackish water hydrosere of *Potamogeton*, *Myriophyllum*, *Phragmites* (Gramineae), Cyperaceae, *Typha* and *Ruppia*, fringed by *Casuarina glauca* and *Melaleuca quinquenervia* is described by Osborn and Robertson (1939), Pidgeon (1943) for the Myall Lakes environs. Identification of brackish water conditions at 195 cm seems improbable in the absence of definite indicators of a brackish water community, e.g. *Ruppia* and pollen definitely assignable to *Potamogeton* or *Myriophyllum.* The percentages of Chenopodiaceae pollen recorded are far below that believed to indicate saline or estuarine conditions (Hope, 1969). Artefactual heightening of the *Monotoca* and *Casuarina* pollen taxa (both readily dispersed) would be expected with a decreased *Eucalyptus* pollen influx. However, increased proximity of the Fingal Bay site to the sea seems probable. Erosian under present-day sea levels has truncated this detrital mud deposit at this point (Sample 7) *ca* 1 m below the estimated H.M.W. An increased sand content in Samples 6 and 7 could indicate a partial burial of the foreshore deposit by sand movements prior to *ca* 5800 C-14 years B.P. with later phases of orgonic deposition (Zone II) occuring in depressions in such a sand mantle between *ca* 5800 and 3150 C-14 years B.P. A palaeosol exposed in the present foredune represents the only evidence for a still more recent period of dune surface.

Zone II

Pollen spectra of Samples 6 to 1 are dominated by pollen taxa derived from plant communities characteristic of the hinterland close to present-day beaches. Lowered percentages in Sample 5 are probably due to the unavoidably low pollen total counted. Two trends in local vegetation are revealed : (i) the development and subsequent decline of a *Melaleuca quinquenervia* swamp with watertable levels sufficiently, if periodically, high to continuously support aquatic flora including Cyperaceae, *Triglochin* and *Villarsia* (a community common around the fringes of the Myall Lakes and in the swales of the low " inner " parallel dune ridge system) ; (ii) significant declines in Leptospermoidae pollen taxa representing dune scrub and ti-tree swamp vegetation common behind the foredune. Less locally, *Angophora-Eucalyptus* forest (partially re-established in the interval between Samples 7 and 6 ?) was finally eliminated in the area by 3150 C-14 years B.P., it being possibly replaced by a *Casuarina* woodland or *Banksia* dune scrub. A generally subdued sand mantle relief is implied.

(*a*) Samples 6 to 4. *Development of a paperbark swamp* of *Melaleuca quinquenervia* supporting sedges, *Triglochin*, and *Villarsia* probably with hummocks of Restionaceae spp. and *Gleichenia*. *Callistemon*, dense stands of Leptospermoidae taxa, *Casuarina*, heathland elements including Xanthorrhoeaceae-Liliaceae, Umbelliferae and *Banksia* spp. are indicated locally, with *Eucalyptus* and *Monotoca* on drier sands. *Typha* (?) and Chenopodiaceae pollen percentages indicate some proximity to the sea.

(*b*) Sample 3. *Deposition of a sand horizon* indicating a hiatus of unknown duration in the organic sedimentation. Coincident with this phase of sand mobility, local pollen spectra indicate a partial elimination of the *Melaleuca quinquenervia* and Leptospermoidae communities relative to the previous phase. Established *Melaleuca* can survive partial burial—an example grows through the Fingal Bay picnic ground infill—and it is likely the decline in pollen representation reflects a more general disturbance of dune vegetation. *Angophora-Eucalyptus gummifera* further declined, Chenopodiaceae pollen was lacking—the former possibly producing an artefactual increase in the *Eucalyptus* pollen percentage. Watertable levels periodically above ground level are indicated by the dual evidence of corroded pollen and significant occurrences of aquatic species *Triglochin*, *Villarsia* and *Typha*.

(*c*) Samples 2 and 1. *Replacement of the paperbark swamp by a sedge peat bog.* During formation of a *Gleichenia*-Restionaceae peat bog—though with water levels periodically sufficient to support occasional Cyperaceae, *Triglochin* and *Villarsia*—dune species that had been established locally through the disturbances recorded in Sample 3 became replaced by plants able to tolerate bog conditions. The accumulation of organic detritus may have been responsible for the virtual disappearance of *Melaleuca quinquenervia* as suggested by Osborn and Robertson (1939). *Banksia*-Leptospermoidae dune thicket (common behind present-day beach foredunes), and *Callistemon*, *Pomax* (rare) on moist sands gave way to peat bog taxa, Leguminosae (probably *Viminaria*), *Sprengelia*, and other epacrids, *Haloragis*, *Lycopodium* and pteridophytes. Drier situations supported *Calythrix*, *Leucopogon*, *Monotoca* and *Symphionema*. Nearby dune *Eucalyptus* stands virtually disappeared, accentuating the record of *Casuarina* pollen (wind dispersed). Ecologically ambiguous pollen taxa (i.e. those containing morphologically indistinguishable pollen derived from taxa with divergent ecological niches ; e.g. *Stackhousia* spp., coastal dunes to open forest, *Hibbertia* spp., sand dunes to dry sclerophyll forest, Compositae spp., lake margins, paperbark swamp, wet to dry heath and wet to dry sclerophyll forest) became more abundant as did Chenopodiaceae pollen. This latter pollen taxon possibly reflects, establishment of salt marsh-estuarine conditions in Port Stephens. Burial of the deposit coincides with the attainment of present-day sea levels in the Holocene marine transgression as postulated by Shepard (Bird, 1968). It is suggested that Zone II reflects destruction or modification of near-beach plant communities by fluctuations in local watertable levels and loss of dune shelter as the sea approached its present level. The local paperbark swamp of the sheltered dune hollows changed to the Banksia-Leptospermoidae thickets found behind the foredune, then to boggy conditions surrounded by dunes generally lacking in arboreal taxa. These changes, a reversal of normal vegetational successions on stable sand dunes, probably were due to lowering and destruction of the seaward dune barrier.

DISCUSSION

The majority of pollens found originate from plants common in the general area today. There is considerable difficulty in interpreting some important pollen taxa ecologically, e.g. *Casuarina*, *Eucalyptus*, Gramineae, and most pollen fluctuations must be assumed to represent local vegetational changes only. The *Angophora-Eucalyptus gummifera* component may be an exception. Ecological studies in sand dune environments have indicated the importance of the watertable level on the distributions of plant associations and the feedback interaction of these communities in constructing and preserving dune relief (Bird, 1968; Carolin, 1971). Vegetational fluctuations at Fingal Bay reflect two opposing trends, (i) natural successions of plant communities progressively stabilizing and ameliorating the free-draining mobile sand environment, and (ii) disturbances of and retrogression in these plant communities by fire, watertable level fluctuations, etc., tending to produce land-surface instability. Adjustments to a changed edaphic environment have been seen in many pollen taxa. The close connection between vegetation and sand topography, however, makes some insight into the local geomorphological history possible.

(*a*) There is no definite vegetational evidence for local saline or subsaline conditions. The sediment types agree well with the organic muds, silts and peats associated with freshwater depressions in the Myall Lakes area and contrast with the shelly clays common to salt marshes and estuaries in the same area (Thom, 1965). The Fingal Bay deposits must therefore have accumulated behind a seaward sand barrier eroded away since *ca* 3000 C-14 years B.P. Vegetational evidence suggests this barrier was once both extensive and high (possibly stranded Pleistocene dunes). Coastal regression of the N.S.W. coastal sand barriers has been postulated south of Macleay (Hails, 1964) and at Dee Why (Martin, 1971).

(*b*) Prior to *ca* 6000 C-14 years B.P. significant stands of *Eucalyptus-Angophora* dune dorest existed in the general area, this being followed by almost total elimination of the *Eucalyptus gummifera-Angophora* component by *ca* 5800 C-14 years B.P. A possible partial re-establishment around *ca* 5700 C-14 years B.P. was followed by virtual disappearance at *ca* 3000 C-14 years B.P. Progressive destruction of deep stable sand dunes (and forest) seaward of the present bay under a rising sea level is a probable cause. The overall decline in *Eucalyptus* pollen relative to other woody taxa supports this conclusion.

(*c*) Periodic phases of sand dune instability are recorded, these often correlated with declines in *Eucalyptus*, *Angophora* and/or *Casuarina*, between 6550 and 3150 C-14 years B.P. Evolution of the present dune topography has obviously been locally cyclic in terms of land surface stability and instability. Within phases of local sand dune stability, aquatic plant taxa record a fluctuating watertable level. Perched watertables are common in the area at present—the back swamp at Fingal Bay is 1·8 m above the est. H.W.M. Pollen curves imply the watertable level changed from being " perched " (a function of climate and drainage) to one increasingly controlled by sea level after *ca* 5700 C-14 years B.P., e.g. the *Banksia asplenifolia*/*B. serratifolia* ratio—sympatric species whose respective intercompetitive abilities are related to the local moisture regime (Y. Siddiqui, in Carolin, 1971)—suggest increasingly moist local conditions. Vegetational history at Fingal Bay appears best explained as adjustments to changes in the physical environment of a coastal hinterland during and dominated by the post-glacial sea level rise. Climatic changes are consequently obscured, and it is unlikely that such sites will prove useful in palaeoclimatic studies.

(*d*) The period covered by the Fingal Bay deposits overlaps with the " Older Peron " to " Younger Peron " higher sea levels proposed by Fairbridge (1961). Of special interest is the vegetation record of Sample 5 dated at 5700±140 C-14 years B.P. and coinciding with the " Older Peron " level. Although lowering of the peat stratum by compaction undoubtedly has occurred under the sand overburden, it appears difficult to explain the existence of a *Melaleuca quinquenervia*-Leptospermoidae freshwater swamp community within 1 m of the present estimated H.W.M. under a sea level approximately 2 m higher. Freshwater flooding of a depression protected behind a sand barrier during such a higher sea level cannot be substantiated by the low *Trigochin* and Cyperaceae pollen percentages. By the same reasoning, conditions postulated for Sample 7 may reflect such a flooding and hence a sea level locally somewhat higher than that proposed by Shepard (1963), between 6500 and 5700 C-14 years B.P. It is suggested, therefore, that there is no evidence for higher than modern sea levels during the Holocene period represented at Fingal Bay.

Single grains of *Nothofagus moorei*-type, reaching 2% in Samples 6 and 7, indicate long distance transport (presumably from Barrington Tops) is of continuous, if limited, occurrence. Similarly, *Cyathea* spores occasionally occurred in unexpectedly high numbers. Overall, records of pollen derived from the mesophytic plant associations appeared more frequently in Zone II: possibly reflecting increasingly oceanic climates on formerly non-coastal situations.

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HOMOLOGIES OF AMPHIBIAN VERTEBRAE

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Synopsis

A number of long-standing uncertainties regarding the homologies of amphibian vertebrae are clarified. Although the centra of all tetrapods are basically similar because of their intersegmental location, those of different groups may be homologous either with the pleurocentra of labyrinthodonts or with their intercentra or with a combination of both types of element. Moreover, the states of centra which resemble one another with respect to their osseous components may not be strictly homologous because of differences in their unossified components. Homologous states of the centrum may be primitive or advanced within a group.

INTRODUCTION

The question of homology between the vertebrae of living amphibians and those of amniotes is a subject which has been debated for many years and still awaits solution, despite Devillers' (1954) and Williams' (1959) rejection of the theory and nomenclature of Gadow (1897, 1933) concerning the evolution of tetrapod vertebrae. Although Wake (1970) considered this problem at some length, referring in particular to work published since Williams' (1959) paper, several points merit further discussion.

Wake (1970) agreed with Williams (1959) that the vertebrae of living amphibians are homologous with those of amniotes because they alternate with the primary segments of the body, but he questioned Williams' conclusion from this that the amphibian centrum is a pleurocentrum like that of amniotes. The intersegmental position of the vertebrae in all terrestrial vertebrates is shown by the origins of the myocommata and, in amniotes, also by the recombination of half sclerotomes from adjacent segments early in vertebral development. The absence of a sclerocoel in all three orders of living amphibians and the paucity of sclerotomic tissue in anurans and urodeles (Wake, 1970) show that amphibians differ from amniotes in the early stages of vertebral development but do not affect the homologies of the adult vertebrae (see Szarski, 1962). Before considering the possible homology of the centrum of living amphibians with the intercentrum or pleurocentra of labyrinthodonts, however, it is necessary to clarify several points regarding homology and to consider what is described as the centrum in different groups of tetrapods.

THE CONCEPT OF HOMOLOGY

A clear understanding of homology and the so-called laws of evolution is essential to any discussion of the phylogenetic significance of the characteristics of organisms. Although these topics have been discussed at length by numerous authors, including Etkin and Livingston (1947), Zangerl (1948), Remane (1956), de Beer (1958), Rensch (1959), Simpson (1961), Szarski (1962), Gans (1969) and Kluge (1971), so that the limitations of the laws of evolution are now generally recognized, there is still an element of vagueness associated with the concept of homology. This vagueness stems largely from a failure by some authors (e.g. Zangerl, 1948; Abercrombie *et al.*, 1951; Kluge, 1971) to distinguish between at least two of the three basic components of the concept, namely the definition of homology, the criteria used to detect it and its application in biological reasoning.

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It is often stated or implied (e.g. by Kluge, 1971) that Darwin in his *Origin of Species* was responsible for the so-called evolutionary definition of homology. According to Szarski (1962), this definition states that those characters are called homologous which give evidence of the common ancestry of their bearers. In fact, Darwin (1859, p. 434) was quite clearly applying Owen's (1843) definition which states that *an homologous organ or homologue is the same organ in different animals under every variety of form and function.* Where Darwin differed from Owen was in ascribing the presence of the same organ in different animals to a relationship by descent instead of by Divine Creation.

The criteria used for the recognition of homologues were listed by Etkin and Livingston (1947), Remane (1956) and Szarski (1962), the principal criteria being mutual location in different organisms, particular structure, and connection by intermediate states of the organ. In some instances, the third of the principal criteria, as well as the accessory criteria listed by Szarski (1962), presuppose that the phylogenetic relationships of the organisms concerned are already known. According to Zangerl (1948), however, the identification of homologues serves only one purpose : it provides a method for the determination of phylogenetic relationships. Gans (1969) commented on the apparently circular reasoning involved in this situation and concluded that a phylogenetic criterion for homology may be applied as long as the phylogeny being used is not one that is derived from the particular characteristic studied. According to Gans (1969), an established phylogeny is tested each time a new character is found which can be subjected to analysis.

Furthermore, an homologous state of an organ occurring in a number of organisms is not necessarily primitive in the taxon to which the organisms belong. For example, the notochordal amphicoelous state of the centrum in *Sphenodon* and most geckos is homologous because of particular structure (Werner, 1971) and is a primitive state within the Gekkota (Moffat, 1972, 1973). The procoelous state of the centrum in other geckos and the Pygopodidae is also homologous according to the criteria of particular structure and connection by intermediates, but this state is an advanced state within the Gekkota which has evolved on at least five separate occasions in parallel (Moffat, 1972, 1973). De Beer (1958) described homology of the latter type as latent homology, since parallel evolution of the same advanced state may be regarded as evidence of genetic affinity, even though the state itself was not present in the common ancestor. Latent homology is evidently of widespread occurrence in the Gekkota, since the advanced state of many characters is morphologically the same state in all members of the Gekkota which possess it (Moffat, 1973), and is probably of widespread occurrence in other organisms as well.

THE CENTRUM

The components of the vertebrae of living tetrapods are identified in embryonic or juvenile animals because in most adult vertebrae they have either been resorbed or are indistinguishably fused together. The innermost component of the developing vertebral column is the notochord whose homology in different groups is evident from its position in the body and its histological characteristics (see Szarski, 1962). The perichordal tube is homologous for the same reasons, as it is a sheath of squamous cells enclosing the notochord (see Wake, 1970 ; Werner, 1971 ; Moffat, 1972, 1974). In most amniotes, each neurapophysis of the cartilaginous vertebra is connected by a neurocentral suture to another element which in turn rests on the perichordal tube, and the ventral part of the vertebra lying between the two neurocentral sutures is described as the vertebral body or centrum.

Although most authors agree by implication if not by direct statement that the perichordal tube or primary centrum (see Werner, 1971) is homologous in different groups of tetrapods (e.g. Mookerjee, 1936 ; Williams, 1959 ; Wake, 1970 ; Werner, 1971), opinion differs regarding the identity in amniotes of the region of the vertebra lying between the perichordal tube and the so-called neurocentral suture, i.e. the secondary centrum. According to Howes and Swinnerton (1901) and Ganguly and Mitra (1958) this region in *Sphenodon* and geckos respectively is a lateral outgrowth from the perichordal tube, and Mookerjee (1936) and Williams (1959) considered this to be so in all amniotes. Goette (1897), Schauinsland (1906) and Werner (1971), on the other hand, described the secondary centrum of various amniotes including geckos and *Sphenodon* as the base of the neural arch which acquires a suture after it has been laid down as a single element resting on the perichordal tube.

The cartilaginous vertebrae in developmental stages of many living amphibians have no sutures comparable to the neurocentral sutures of reptiles and mammals and in this respect they resemble the cartilaginous vertebrae of one other group of amniotes, namely birds. The neural arches at this stage of development in birds and most amphibians rest on the perichordal tube or, in some urodeles, directly on the notochordal sheath (Marcus and Blume, 1926 ; Piiper, 1928 ; Mookerjee, 1930, 1931, 1936 ; Mookerjee and Das, 1939 ; Williams, 1959 ; Wake, 1970 ; Moffat, 1972, 1974). During subsequent ossification of the vertebra, separate endochondral ossification centres occur adjacent to the notochord as well as in the neural arches of all amniotes including birds, while perichondral bone forms a midventral centre on the vertebra which is separate from the perichondral bone of the arches (Williams, 1959 ; Romanoff, 1960 ; Werner, 1971). Because of its manner of ossification, the vertebral body or centrum of birds as well as reptiles and mammals is considered to be a combination of primary and secondary centra.

In amphibians the patterns of perichondral and endochondral ossification are highly variable. In general, however, the centrum is thought to consist only of the primary centrum or perichordal tube and the bone resulting from its partial or complete perichondral and/or endochondral ossification, together with any bone which may be formed from endochondral ossification of cartilage within the notochordal canal (see Griffiths, 1963 ; Wake, 1970). From Wake's account it would appear that secondary centra which can be identified as distinct bodies of cartilage or endochondral bone are absent from living amphibians.

As stated above, the purpose of determining whether the part of the vertebra called the centrum is the same part and therefore homologous in different groups of living tetrapods is to assist in the determination of their phylogenetic relationships. One method of determining whether superficially different organs are homologous is by the existence of intermediate states of that organ either in living forms or in fossils. As the only parts of vertebrae which are preserved as fossils are the ossified components and nothing can be known regarding their membranous or cartilaginous precursors in ontogenetic development, the only practicable method of comparing the components of living and fossil vertebrae is by reference to bony elements which are separated from one another by sutures.

The homology of vertebral sutures is relatively easy to establish. The neurocentral sutures of living amniotes are homologous with those of labyrinthodonts according to Szarski's (1962) criterion of mutual location. They occupy the same position on the vertebra, lying between the dorsal elements which roof the neural canal and the ventral elements which enclose or replace the notochord. This homology is also evident from the existence of sutures in the same position in fossil tetrapods which are intermediate between Palaeozoic labyrinthodonts and living amniotes. The elements lying dorsally to the sutures are the neuropaphyses, while the ventral elements in each vertebral segment, irrespective of the number present in a particular animal, constitute the centrum (see also Panchen, 1963, 1967). The absence of neurocentral sutures from many living amphibians, presumably from all stages of their development (Wake, 1970), does not mean that the regions of the vertebra which are homologous with the neuropaphyses and centra of labyrinthodonts are also absent, but it does prevent their identification.

Wake (1970) claimed that the report by Williams (1959) of a neurocentral suture in young specimens of *Leiopelma hochstetteri* is the only recorded instance of such a feature in living amphibians. Although it is clear from an earlier investigation by the present author (Moffat, 1972, 1974) that the cartilaginous vertebrae of *L. hochstetteri* and *L. archeyi* (*op. cit.*, Pls 1–3) have no neurocentral sutures comparable to those found in amniotes such as gekkonid lizards (see Werner, 1971, Figs 31, 35), even after the onset of perichondral ossification of the neural arches, E. M. Stephenson's (1960) Fig. 3*d* of a young postmetamorphic specimen of *L. hochstetteri* shows quite clearly that neurocentral sutures are present in later stages. Each vertebra in this specimen, except for the atlas and the sacral vertebra, had a midventral centre of ossification which was widely separated from the bone of the neurapophyses. The notable difference between the neurocentral sutures of geckos and *Leiopelma* is that the former are present in the cartilage of the vertebra, appearing soon after the onset of chondrification (Werner, 1971, Fig. 23), and persist after the rest of the vertebra has ossified (*op. cit.*, Figs 37, 38), whereas the neurocentral sutures of *Leiopelma* are superficial and their appearance coincides with the appearance of the central ossification centre at a stage when ossification of the arches is comparatively well advanced. As separate midventral ossification centres, in this case paired, have also been described in *Xenopus laevis* (Bernasconi, 1951), while Mookerjee (1931, Pl. 16, fig. 14) recorded a neurocentral suture in the cartilage as well as the perichondral bone of a trunk vertebra of *Bufo melanosticus* about two years old, it would appear that neurocentral sutures may not be uncommon in anuran vertebrae although the time of their appearance varies. Therefore the vertebrae of some anurans, like those of amniotes, can be shown to consist of a ventral centrum and dorsal neuropaphyses because these elements are separated by sutures at some stage during development.

Homologies of Amphibian Centra

The question whether the centrum of living amphibians is a pleurocentrum like that of amniotes as claimed by Williams (1959) or an intercentrum as postulated by Estes (1965) cannot be determined at the present time because the evolutionary history of the modern orders is too poorly known from fossils (Wake, 1970). There appears to be no doubt, however, that the Amphibia evolved from crossopterygian fishes belonging to the Rhipidistia and that the Reptilia, the forerunners of all other amniotes, evolved from amphibians (Szarski, 1962 ; Romer, 1966, 1968 ; Carroll, 1969*a*, 1969*b*). As the earliest amphibians such as *Pholidogaster* and the Rhipidistia had protorhachitomous vertebrae in which the elements lying ventrally to the neural arches were intercentra and pleurocentra (Romer, 1947, 1964, 1966, 1968 ; Westoll, 1970), it is reasonable to accept that the vertebrae of all other amphibians and those of amniotes evolved originally from vertebrae of this type. In contrast to amniotes, whose centrum is clearly a pleurocentrum because intermediate states are found in fossils as well as some living reptiles, the single centrum of living amphibians could be a pleurocentrum which lacks ossified intercentra as in most amniotes, or an intercentrum which lacks ossified pleurocentra as in Palaeozoic stereospondylous labyrinthodonts, or a combination of both these elements.

Estes (1965) accepted the possibility that the centrum of living amphibians might be an intercentrum and explained the apparent anomaly of an intersegmental intercentrum in terms of its movement during development from an original midsegmental position in embryos to an intersegmental position in adults. As no such movement has even been recorded in descriptions of amphibian vertebral development, Estes' reasoning would lead to the conclusion that amphibian centra are pleurocentra.

Another explanation for the existence of intersegmental intercentra, which does not depend on embryological evidence whose admissibility is questionable (see Szarski, 1962), was offered by Panchen (1963, 1967) in an attempt to determine in labyrinthodonts the positions of the myocommata and hence the intersegmental boundaries whose theoretical positions were functionally unsatisfactory if one accepted Williams' (1959) contention that the labyrinthodont pleurocentrum is homologous with the amniote centrum and the intercentrum with the amniote intervertebral disc. Panchen suggested that the entire centrum of labyrinthodonts is homologous with the centrum of amniotes, the oblique division between the pleurocentra and intercentrum of rhachitomes moving posterodorsally in the temnospondyl line leading to stereospondyls whose centra are intercentra, and anteroventrally in the anthracosaurian line leading to seymouriamorphs and reptiles whose centra are predominantly if not entirely pleurocentra. In the ancestors of living amphibians, the oblique division could have moved in either direction, or it may have been lost entirely as a result of fusion between the intercentrum and pleurocentra. If, as Bolt (1969) has suggested, all living amphibian orders evolved from labyrinthodonts belonging to the Dissorophoidea in which the main component of the centrum was a pleurocentrum, it could be that the Lissamphibian centrum is mainly if not entirely a pleurocentrum like that of amniotes after all.

It has usually been accepted that similarity in the shape of a single centrum signifies the same type of centrum in various groups of vertebrates. For example, the centra of various fishes, *Leiopelma* and *Ascaphus*, various urodeles, apodans and fossil reptiles, *Sphenodon* and most geckos have all been described as amphicoelous because in all of these vertebrates the centra are biconcave (Goodrich, 1930 ; Noble, 1931 ; Robinson, 1962, 1967 ; Romer, 1956). In the case of many fossil forms, e.g. Triassic squamates (Kuhn, 1952 ; Peyer and Kuhn-Schnyder, 1955 ; Colbert, 1966), it is impossible to determine from the literature whether the centra were solid structures or whether they enclosed a continuous notochord. Among the living forms listed above, the vertebrae are described as amphicoelous because the osseous centra have a deep conical depression in each end and enclose a persistent notochord, but the state of the centrum is not the same state in all these forms because the notochord may be strongly constricted between consecutive vertebrae by the intervertebral cartilage as in some urodeles, *Ascaphus* and *Leiopelma*, or unconstricted as in many fishes, *Sphenodon* and most geckos (see also McBride, 1932 ; E. M. Stephenson, 1952, 1960 ; Ritland, 1955). There are also different types of procoely in amphibians and reptiles. In the Anura the condyle is formed from the intervertebral cartilage, either *in situ* or as a separate element which becomes fused to the centrum in front of it (Mookerjee, 1931 ; Griffiths, 1963 ; N. G. Stephenson, 1965), while the condyle in the Gekkota, if not in all reptiles, is a posterior outgrowth of the centrum itself (Holder, 1960 ; Werner, 1971 ; Moffat, 1972).

Within the Anura, it would appear that the stegochordal state of the centra described by Griffiths (1963) in the Pipidae, Pelobatidae and Discoglossidae is the same state, i.e. homologous, because the centra in these families are dorsoventrally flattened elements lying dorsally to the degenerated notochord. Similarly, the holochordal state of the centra of most other frogs also appears to be homologous since Griffiths described these centra as solid cylinders of bone.

Anuran ectochordy, however, takes at least two forms. According to Griffiths (1963) the ectochordal centra of the Ascaphidae and Rhinophrynidae are hollow cylinders of bone enclosing a persistent notochord, and ectochordy represents an intermediate stage in the development of holochordy. This may be true of the Rhinophrynidae if fully developed centra in this family have the same structure as immature stages of holochordal centra such as those of *Rana temporaria* and *Bufo melanosticus* (Mookerjee, 1931) in which the notochord consists only of notochordal tissue and is of uniform width in horizontal section except for the narrow region between consecutive centre where it is constricted by the intervertebral cartilage. The ectochordy of *Leiopelma* and *Ascaphus* differs from that of immature *R. temporaria* and *B. melanosticus* in that the constricted regions of the notochord are fibrous and its comparatively unconstricted portions are restricted to the middle of each centrum (Ritland, 1955; Moffat, 1972, 1974).

From the foregoing discussion, it is evident that the same organ in different organisms, in this case the vertebral centrum in living tetrapods, can have more than one type of homology. Also the terms used to describe similar states of centra such as their shape may apply to the osseous centrum but take no account of differences in the morphology of their soft parts. Even when it can be shown that the state of a skeletal element is homologous in different organisms because of the particular structure of its ossified and unossified components, this state may be primitive or advanced in the taxon concerned. In these circumstances, recognition that an organ or a state of that organ is homologous in different organisms is insufficient in itself for determining the phylogenetic relationships of the organisms concerned. The particular nature of the homology and its primitive or advanced nature within the taxon concerned must also be recognized, and require much detailed study for their elucidation.

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THE ONTOGENY, MORPHOLOGY, TAXONOMY AND DISTRIBUTION OF THE MILIOLID FORAMINIFERAN *QUINQUELOCULINA PHILIPPINENSIS* CUSHMAN, 1921

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(Plate XIII)

Synopsis

The ontogeny, morphology, taxonomy and distribution of the miliolid foraminiferan *Quinqueloculina philippinensis* Cushman (1921) is discussed with special reference to North Queensland. The synonymy of this species tentatively includes *Q. punctata* d'Orbigny (1826) (*nom. nud.*), *Q. affinis* d'Orbigny (1826) (*nom. nud.*), *Q. affinis* Fornasini (1902) (a junior homonym of *Q. affinis* Costa, 1856), *Q. punctata* Fornasini (1905) (a junior homonym of *Q. punctata* Reuss, 1853), *Miliolina auberiana semireticulata* Heron-Allen and Earland (1924), *Q. thalmanni* Vroman (1936), *Q. pseudoreticulata* Parr (1941), *Q. reticulata elongata* LeRoy (1941*b*) (a junior homonym of *Q. sarmatica elongata* Karrer, 1887), *Q. ornata* Narchi (1965) and *Q. reticulata* of numerous authors (*non* d'Orbigny, 1826). This large synonymy results from prior workers neglecting the variation of individual species, overlooking previously described species and employing unnecessarily subjective methods in subdividing species.

INTRODUCTION

Quinqueloculina philippinensis Cushman (1921) is a very common shallow water, subtropical to tropical, Indopacific foraminiferal species. It is a species which has been consistently misunderstood in the literature by numerous authors since its establishment fifty years ago, probably due to its wide range of variation. This study has been undertaken to clarify the variation and affinities of *Q. philippinensis*.

Historical Summary

Quinqueloculina punctata d'Orbigny (1826) (*nom. nud.*) and *Q. affinis* d'Orbigny (1826) (*nom. nud.*) were established to include miliolids with reticulate ornamentation and a carinate periphery. The former differs from the latter only in possessing an apertural neck. These species were afforded nomenclatural validity by Fornasini (1902, 1905), who regarded them as synonymous. However, both names are preoccupied, the former is a junior homonym of *Q. affinis* Costa (1856) and the latter a junior homonym of *Q. punctata* Reuss (1853).

Triloculina reticulata is another species with reticulate ornament described by d'Orbigny (1826), who diagnosed it as differing from *Q. affinis* in having only three chambers, rather than five, showing on the exterior.

Schlumberger (1893, fig. 25) showed by means of an axial cross-section that *T. reticulata* is quinqueloculine. Brady (1884) considered *T. reticulata* to be the common tropical and subtropical dentate form with reticulate ornament and many authors have appeared to have followed Brady's concept of this species, including Chapman (1900), Goddard and Jensen (1907), Cushman (1917, 1918, 1921 in part), Heron-Allen and Earland (1924 in part), Hofker (1933), Bermúdez (1935), LeRoy (1941*a*, 1941*b*, 1964), Germeraad (1946), Asano (1951), Barker (1960 in part) and Chiji and Lopez (1968). However, Parr (1941) recognized that Brady's *M. reticulata* was more globular and evolute than *T. reticulata* of d'Orbigny and segregated it as a new species, *Q. pseudoreticulata*.

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Miliolina kerimbatica Heron-Allen and Earland (1915) was erected to include taxa similar to *Triloculina linneiana* d'Orbigny (in Sagra, 1839), which is a large, elongate, ribbed species, and *Q. reticulata* but differing in " the deeply channelled grooves, with their prominent and flat-topped dividing ridges, arranged in strongly contorted and almost reticulated patterns on the shell-surface " (*loc. cit.*, p. 575). Pictorially they show this species to be very variable, not only in ornament but also in test length/test width ratios and in apertural neck length. Cushman, (1921) referred this species to Quinqueloculina and described two new varieties *Q. kerimbatica* var. *reticulostriata* characterized by a ribbed periphery and reticulate ornament on chamber sides, and *Q. kerimbatica* var. *philippinensis* characterized by reticulate ornament on the periphery and smooth chamber sides. Both varieties possess a phialine lip and are distinct from *Q. kerimbatica* in ornament. *Miliolina kerimbatica* (s.s.) and its two varieties have been subsequently referred to *Triloculina* (Cushman, Todd and Post, 1954 ; Graham and Militante, 1959). Hofker (1968) showed Cushman's varieties to have quinqueloculine chamber arrangement with the chamber floor covered by wall extensions which he considered as diagnostic of *Quinqueloculina* (*Miliola*). Hofker regarded *Q. kerimbatica philippinensis* as the microspheric form of *Q. kerimbatica reticulostriata* and both as synonymous with *Miliolina kerimbatica* (s.s.). Previously, Hofker (1964) had considered *Q. kerimbatica* to be a junior synonym of *Q. tricarinata* d'Orbigny (=*Miliola tricarinata* of Hofker).

The literature records numerous other species with partially reticulate ornamentation. *Miliolina auberiana semireticulata* Heron-Allen and Earland (1924) was given to differ from *Quinqueloculina kerimbatica philippinensis* in having a sharp periphery.

The quaternary species *Q. thalmanni* Vroman (in Boomgaart and Vroman, 1936) was described to include specimens differing from *Q. reticulata* (Brady, *non* d'Orbigny) in that the neck is ornamented with parallel furrows. Vroman considered it to be affiliated to *Q. reticulata*, *Q. kerimbatica* and *Q. reticulostriata*. *Q. reticulata elongata* LeRoy (1941*b*) (a junior homonym of *Q. sarmatica* Karrer var. *elongata* Karrer, 1877) was erected to include specimens which differ from *Q. reticulata* (Brady, *non* d'Orbigny) in being more elongate. Lloyd (1966) considered *Q. reticulata elongata* to lie within the limits of variation of *Q. pseudoreticulata* Parr. *Q. ornata* Narchi (1965) is similar to *Q. reticulata* in ornament, but given to differ in " the ornamentation of the chambers, the simple tooth and the small size " (*loc. cit.*, p. 10).

Materials and Methods

In addition to reviewing the available literature, this report is based on faunas recovered from some one hundred and seventy stations between the Capricorn Is. Group and Port Douglas on the continental shelf of North Queensland, Australia. Samples (prefixed " S ") are curated in the Geology Department, James Cook University of North Queensland.

Each sample was split until a portion contained approximately three hundred specimens (ranging to ±250) and this was completely picked. Specimens of *Quinqueloculina philippinensis* were counted and their number proportional to the specimen count for all foraminifera calculated for each sample. The resulting percentages from samples between Palm Is., Cape Bowling Green and the Great Barrier Reef are plotted on Text-fig. 12 (station number locations are as in Ponder, 1972).

Methods of test dissection, and thin section preparation are outlined in Ponder (1972).

Systematic Description

Order FORAMINIFERIDA Eichwald, 1830
Suborder MILIOLINA Delage and Hérouard, 1896
Family MILIOLIDAE Ehrenberg, 1839
Genus Quinqueloculina d'Orbigny, 1826
Quinqueloculina philippinensis Cushman, 1921
(Pl. xiii, Figs 1–31 ; Text-figs 1–10)

Quinqueloculina punctata d'Orbigny, 1826 : 302 (*nom. nud.*) ; Fornasini, 1905 : 13 (*non Q. punctata* Reuss, 1853).

Quinqueloculina affinis d'Orbigny, 1826 : 302 (*nom. nud.*) ; Fornasini, 1902 : 23 (*non Q. affinis* Costa, 1856 : 329).

Miliolina pulchella (d'Orbigny) ; Brady, 1884 (part pl. 3, fig. 10) : 174.

Miliolina reticulata (d'Orbigny) ; Brady, 1884 : 178 ; Flint, 1899 (part) : 301 ; Chapman, 1900 : 175 ; Goddard and Jensen, 1907 : 297 ; Heron-Allen and Earland, 1924 : 608.

Quinqueloculina reticulata (d'Orbigny) ; Cushman, 1917 (part pl. 16, figs 1, 3) : 55 ; 1918 : 290 ; 1921 : 434 ; Hofker, 1933 : 95 ; Bermúdez, 1935 : 160 ; LeRoy, 1941*a* : 22 ; 1941*b* : 71 ; 1964 : F19 ; Germeraad, 1946 : 63 ; Asano, 1951 : 6 ; Barker, 1960 : 18 ; Chiji and Lopez, 1968 : 110.

Quinqueloculina kerimbatica (Heron-Allen and Earland) var. *philippinensis* Cushman, 1921 : 438 ; 1924 : 61 ; Frerichs, 1970 : 146.

Miliolina auberiana semireticulata Heron-Allen and Earland, 1924 : 607.

Quinqueloculina cf. *kerimbatica* (Heron-Allen and Earland) var. *philippinensis* Cushman ; Cushman, 1922 : 68 ; Bermúdez, 1935 : 159.

Quinqueloculina kerimbatica (Heron-Allen and Earland) ; Keijzer, 1935 : 113.

Quinqueloculina thalmanni Vroman, in Boomgaart and Vroman, 1936 : 422.

Quinqueloculina pseudoreticulata Parr, 1941 : 305 ; Collins, 1958 : 361 ; Barker, 1960 : 18 ; Lloyd, 1966 : 88 ; Albani, 1968 : 98 ; 1970 : 73.

Quinqueloculina reticulata (d'Orbigny) var. *elongata* LeRoy, 1941*b* : 71 (*non Q. sarmatica* Karrer var. *elongata* Karrer, 1877).

Quinqueloculina sp. Graham and Militante, 1959 : 49.

Triloculina kerimbatica (Heron-Allen and Earland) var. *philippinensis* (Cushman) ; Graham and Militante, 1959 (part pl. 8, figs 1–3) ; Resig, 1969 : 88.

Triloculina kerimbatica (Heron-Allen and Earland) var. *reticulostriata* (Cushman) ; Graham and Militante, 1959 : 55.

" Young miliolidae " Barker, 1960 (part pl. 3, fig. 10) : 6.

Quinqueloculina sp. cf. *Q. philippinensis* Cushman ; Seiglie, 1965 : 71.

Quinqueloculina sp. aff. *Q. reticulostriata* Cushman ; Seiglie, 1965 : 71.

Quinqueloculina ornata Narchi, 1965 : 10.

Quinqueloculina (*Miliola*) *kerimbatica* (Heron-Allen and Earland) ; Hofker, 1968 : 18.

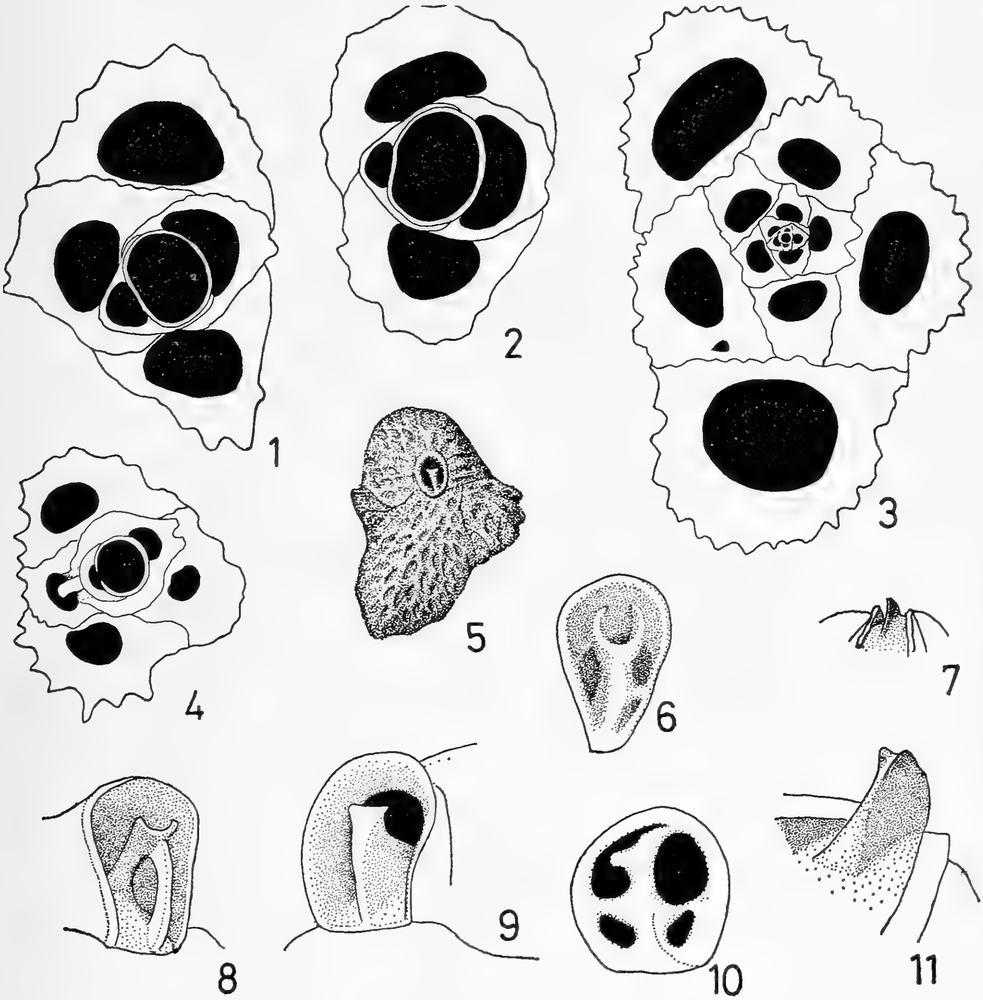
Type specimen : United States National Museum Catalogue number, 1350.

Type locality : Albatross station D5159, Sulu Archipelago, Tawi Twai Group at a depth of eighteen metres.

Material studied : Nine hundred and fifty specimens, two axial cross-sections and ten specimens cut along the axial plane.

Diagnosis : Test quinqueloculine, usually large, subcircular to oval. Wall thick, with wall extensions usually covering chamber floors. Ornamentation reticulate, costate or lacking. Apertural end of chamber constricted and with phialine lip ; apertural apparatus an imperforate, simple tooth bifid only at the tip.

Description: Test usually large, subcircular to oval in side view, irregularly oval to irregular lensoid in apertural view, with shape most regular in juvenile megalospheric tests. Periphery rounded to carinate, sometimes squarely truncate in adults (Pl. XIII, Fig. 4) but typically so in juvenile microspheric tests (Pl. XIII, Figs 26, 27). Sutures distinct, slightly indented or flush with the general contour of the test. Third to last and earlier chambers do not protrude distinctly from the test periphery. The apertural end of the ultimate chamber occasionally protrudes from the general test profile forming a neck of variable development (Pl. XIII, Figs 2, 19, 22, 23, 26). Test wall thick and increases in thickness with increasing test size. Ornamentation usually reticulate, may



Text-figs 1–11. Figs 1–7, 9–11. *Quinqueloculina philippensis* Cushman, 1921: 1–4, axial cross sections; 1, 2, 4, megalospheric; 3, microspheric; 1, 2, F7998, S900, ×90; 3, F7996, S346, ×50; 4, F7997, S195, ×100; 5, apertural view of Pl. XIII. Fig. 4. F7698, S163, ×40; 6, 10, apertures subdivided by teeth, F7998, S900, ×80; 7, 11, final chamber dissected to show primary tooth, F7998, S900, ×80; 9, aperture showing flaring lip and primary tooth, F7701, S899, ×80; 8, *Quinqueloculina kerimbatica* Heron-Allen and Earland, 1915, showing the perforated primary tooth, F7999, S943, ×80.

approach a costate condition (Pl. xiii, Figs 4, 11, 12, 17, 28) or become very irregular (Pl. xiii, Figs 3, 7, 8). Reticulation may be coarse (Pl. xiii, Figs 3, 5, 14, 16, 17, 24) or fine (Pl. xiii, Figs 10, 15, 18, 19) restricted to the chamber periphery (Pl. xiii, Figs 26, 27, 29) or cover the entire test (Pl. xiii, Figs 5, 6, 15, 16, 21, 24) or be absent over large areas of the test (Pl. xiii, Figs 14, 17, 19, 22, 23). The apertural neck may be costate (Pl. xiii, Fig. 23) or smooth (Pl. xiii, Fig. 19). Proloculus ovoid ; in microspheric tests 0·02 mm in diameter and in megalospheric tests 0·15–0·20 mm in diameter. Detueroconch a semicircular tube from half a whorl to a whorl in length, with the chamber walls extending over the proloculus. Other chambers are a half a whorl in length though the ultimate chamber may, very occasionally, be less (Pl. xiii, Figs 1, 2). Cross-sections show chambers to be internally semicircular, externally semicircular, subquadrate or subtriangular. Apertural end of chamber constricted and with a variously developed apertural phialine lip (Text-fig. 9). The number of chambers showing on the test exterior varies from four to five in adults and juvenile microspheric tests, but may be as few as two in juvenile megalospheric tests where three or four are typical. Chamber wall extensions cover the chamber floor in tests greater than approximately 0·25 mm in length. Chamber arrangement is quinqueloculine (Text-figs 1–4). Aperture semicircular early in ontogeny, progressing to a broad keyhole shape when large and is nearly circular when supported on an apertural neck. Apertural apparatus is a simple imperforate tooth, bifid at the tip in large specimens (Text-figs 6, 7, 9, 11).

Occasionally aberrant specimens have secondary teeth joining the primary tooth with the apertural wall (Text-figs 6, 10). Tooth size generally related to aperture size.

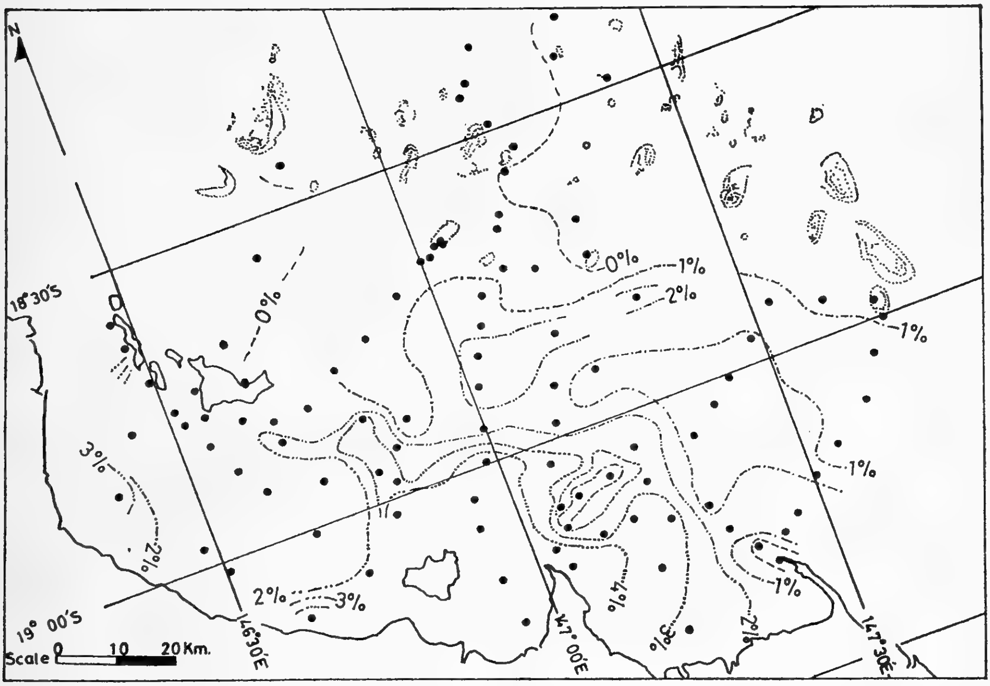
Test dimensions: Length from 0·14 mm to 1·5 mm, width from 0·12 mm to 1·00 mm. Thickness from 0·10 mm to 0·8 mm.

Remarks: The limits of variation in *Quinqueloculina philippinensis* are difficult to define. Particularly variable features include ornament, the nature of the chamber periphery and the development of an apertural neck. As the test increases in size, the chamber periphery changes from squarely truncate to more rounded or carinate, the tooth becomes bifid, and the ornament becomes less restricted.

Microspheric and megalospheric tests are externally indistinguishable when adult. However, in smaller specimens microspheric tests usually have five bluntly truncate chambers showing on the exterior of the test (Pl. xiii, Figs 26, 27), while juvenile megalospheric tests are more regular in apertural view and generally have less than five chambers showing on the exterior (Pl. xiii, Figs 25, 29, 30, 31). These differences arise because megalospheric tests are more involute than microspheric forms and often have less than five post-deuteroconch chambers.

Quinqueloculina philippinensis has been variously referred to *Quinqueloculina* (s.s.), *Q.* (*Miliola*), *Miliolina* and *Triloculina*. It is unequivocally a *Quinqueloculina* by virtue of successive chamber planes, being 144° apart and its possession of an apertural tooth. The type species of *Miliolina* Williamson (1858), *Triloculina laevigata* d'Orbigny, also has both of these features (see Schlumberger, 1893). Loeblich and Tappan (1964) regarded *Miliolina* as synonymous with *Triloculina* but this cannot be the case as successive chamber planes are 120° apart in *Triloculina*. *Miliolina* must be regarded as a junior synonym of *Quinqueloculina*.

Hofker (1968) considered *Q. kerimbatica philippinensis* to be a member of *Q.* (*Miliola*) on the basis that wall extensions cover the chamber floor. This feature is not definitive of *Q.* (*Miliola*) because it is sometimes shown by the type species of *Quinqueloculina* (s.s.) *Serpula seminulum* Linné (see Schlumberger, 1893, fig. 16). *Miliola* is a distinct genus, the type species, *M. saxorum* Lamarck, is rendered distinct from *Quinqueloculina* in possessing a trematophore (see Loeblich and Tappan, 1964, fig. 357, 2*c*). The apertural apparatus of *Q. philippinensis* is a simple tooth, except for an insignificant number of aberrant forms which possess a coarsely subdivided multiple aperture (trematophore) (Text-figs 6, 10). In this study only two such forms were found among nine hundred and fifty specimens examined and their coarse trematophores are quite distinct from the finely perforate trematophores of *M. saxorum.* It is concluded that *Q. philippinensis* is best regarded as a member of *Quinqueloculina.*



Text-fig. 12. Distribution of *Quinqueloculina philippensis* Cushman (1921) off Townsville. Contours represent abundance of the species calculated as a percentage of specimens comprising the total fauna.

Quinqueloculina affinis Fornasini (1902), *Q. punctata* Fornasini (1905), *Miliolina auberiana semireticulata* Heron-Allen Earland (1924), *Q. thalmanni* Vroman (1936), *Q. pseudoreticulata* Parr (1941), *Q. reticulata* var. *elongata* LeRoy (1941) and *Q. ornata* Narchi (1965) all fall within the range of variation of North Queensland *Q. philippinensis* Cushman and are here regarded as junior synonyms. They all have a similar test shape, quinqueloculine chamber arrangement, a phialine lip and a simple tooth which may be bifid at the tip. *Q. affinis* Fornasini with a well developed reticulate ornament and *Q. auberiana semireticulata* with a poorly developed reticulate ornament are both carinate morphs of *Q. philippinensis* which lack an apertural neck (Pl. XIII, Figs 17, 20). *Q. punctata* Fornasini is a less common morph of *Q. philippinensis* with well developed reticulate ornamentation, carinate periphery and a well developed apertural neck (Pl. XIII, Fig. 19).

The type of *Q. thalmanni* is probably megalospheric. It is a less common morph of *Q. philippinensis* with a rounded periphery, poorly developed reticulate ornamentation on an apertural neck possessing oblique costae. *Q. pseudoreticulata* and *Q. reticulata elongata* are typical large *Q. philippinenses* with a rounded periphery, well developed reticulate ornament and lacking an apertural neck (Pl. XIII, Figs 21, 24). *Q. ornata* is a juvenile microspheric form of *Q. philippinensis* with reticulate ornament neck restricted to the subacute periphery and a short apertural neck (Pl. XIII, Fig. 26).

Q. philippinensis Cushman (1921) is not a subspecies of *Miliolina kerimbatica* Heron-Allen and Earland (1915). Members of both species occur in North Queensland faunas and there is no gradation between them. *M. kerimbatica* differs in having a longer test, a narrower aperture and a large perforated tooth (Text-fig. 8).

Text-fig. 13. World distribution of *Quinqueloculina philippensis.*

Q. philippinensis is neither a subspecies of, nor synonymous with *Q. kerimbatica reticulostriata* Cushman (1921) as both species are present at each type locality (see Cushman, 1921). *Q. kerimbatica reticulostriata* differs in possessing a more elongate test, peripheral ribs and sand grains embedded in the sutures between chambers. These differences are not due to *Q. philippinensis* being a microspheric morph of *Q. reticulostriata* as suggested by Hofker (1968), as Cushman (1921, Pl. 89, fig. 2) clearly shows a megalospheric representative of *Q. philippinensis* with only one chamber after the deuteroconch. In North Queensland megalospheric *Q. philippensis* comprise the numerically dominant generation and megalospheric specimens are morphologically quite distinct from *Q. kerimbatica reticulostriata.*

Many authors have confused *Quinqueloculina reticulata* (d'Orbigny) with *Q. philippinensis.* These two species are distinct even though both have quinqueloculine chamber arrangement and reticulate ornamentation. *Q. reticulata* has a larger test length/test width ratio. Large specimens show a smoothly biconvex outline in apertural view, possesses a longer, narrower aperture with a longer tooth, and chamber wall extensions do not cover the chamber floor (Schlumberger, 1893, fig. 25). *Triloculina carinata* d'Orbigny (1839) is similarly distinguished from *Q. philippinensis* (Hofker, 1964).

Q. maculata (Egger, 1893) differs from *Q. philippinensis* only in having more protruding rounded chambers as seen in aperture view.

Distribution: In the portion of the North Queensland continental shelf studied in this project, *Q. philippinensis* shows considerable variety in abundance (Text-fig. 12). It is consistently common ($>3\%$ of the total population) in a zone from Cape Cleveland to the north of Magnetic Island. Sandy sediments in this area provide a favoured environment and in one such sample *Q. philippinensis* made up nearly 20% of the total population. In the remaining area its distribution is fairly random, ranging from 0–3%. It is very rare or absent in littoral environments and in depths greater than thirty fathoms.

Although *Q. philippinensis* shows a large variation in morphology in all samples where it is abundant, specimens with fine reticulations (Pl. XIII, Figs 10, 15, 18, 19) are confined to Great Barrier Reef littoral samples.

Distribution data based on the synonymy above are plotted in Text-fig. 13.

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EXPLANATION OF PLATE XIII

Figs 1–31. *Quinqueloculina philippensis* Cushman, 1921, side view showing variation in external morphology. 1–18, 20, ×24; 19, 21–31, ×43; 1–3, 7, 9, 11, F7706, S195; 4, F7704, S440; 5, 8, 13, 16, F7698, S193; 6, 12, F7707, S332; 10, 15, 18, 30, F7700, S343; 14, 20, F7705, S175; 17, F7701, S899; 19, F7696, S943; 21–24, F7699, S163; 25, F7703, S323; 26, 31, F7697, S896; 27, F7702, S894; 28, 29, F7708, S893.


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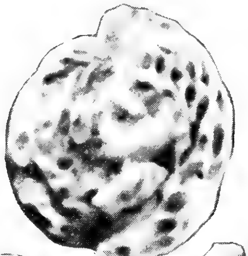
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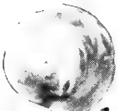
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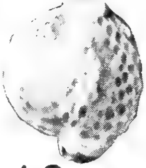
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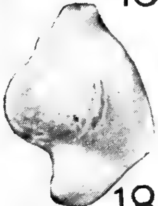
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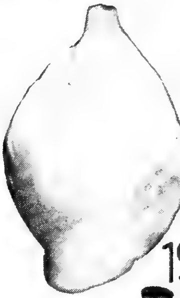
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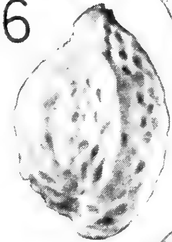
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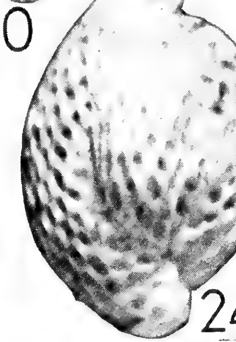
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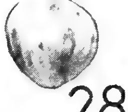
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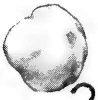
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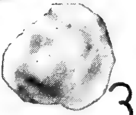
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ABSTRACT OF PROCEEDINGS

ORDINARY GENERAL MEETING

28th March 1973

Held in the Society' oms, 157 Gloucester Street, Sydney.

Dr. P. J. Stanbury in the Chair.

Minutes of the last Ordinary General Meeting (29th November 1972) were taken as read and confirmed.

Papers read (by title only, with an opportunity for discussion at the next Ordinary General Meeting) :

Notes on some Ascidians from Port Jackson, Botany Bay and Port Hacking, N.S.W. By P. Kott.

Mangrove Swamp and Salt Marsh Communities in southern Australia. By M. Kratochvil, N. J. Hannon and L. D. Clarke.

Microbiology of an Ashbed. By M. A. Renbuss, G. A. Chilvers and L. D. Pryor.

Announcement :

The Chairman announced that as Anzac Day fell on the usual monthly meeting date of the Society, the April meeting would be held on the 2nd May instead.

Address :

An address was given by Dr. P. G. Valder, School of Biological Sciences, University of Sydney, entitled " Japanese Gardens ".

ORDINARY GENERAL MEETING

25th April 1973

Held in the Society's Rooms, 157 Gloucester Street, Sydney.

Dr. P. J. Stanbury in the chair.

Minutes of the last Ordinary General Meeting (28th March 1973) were taken as read and confirmed.

Papers read (by title only) :

The first zoea larvae of the estuarine crabs *Sesarma erythrodactyla* Hess, *Helograpsus haswellianus* (Whitelegge) and *Chasmagnathus laevis* Dana (Brachyura, Grapsidae, Sesarminae). By P. A. Green and D. T. Anderson.

Sexual Dimorphism in *Haplomitrium intermedium*. By H. J. Hewson.

The concept of primitiveness and its bearing on the phylogenetic classification of the Gekkota. By L. A. Moffat.

Address :

An address was given by Dr. G. J. Caughley, School of Biological Sciences, University of Sydney, entitled " The ecology of large mammals ".

ORDINARY GENERAL MEETING

27th June 1973

Held in the Society's Rooms, 157 Gloucester Street, Sydney.

Dr. P. J. Stanbury in the chair.

Minutes of the last Ordinary General Meeting (25th April 1973) were taken as read and confirmed.

Papers read (by title only):

An analysis of the catch by trawlers in Moreton Bay (Qld.) during the 1966–67 prawning season. By J. L. Maclean.

Anatomy of petrified Rachises collected from the Jurassic of Amarjola in the Rajmahal Hills, India. By B. D. Sharma.

Announcements:

Two booklets were tabled illustrating cruising expeditions.

A letter from Monash University with a request for specimens, seeds and information regarding banksia to help with the production of a new book, was tabled.

Address:

An address was given by Professor G. Seddon, School of History and Philosophy of Science, University of New South Wales, entitled " A Cooks tour of the Swan Coastal Plain ".

ORDINARY GENERAL MEETING

25th July 1973

Held in the Society's Rooms, 157 Gloucester Street, Sydney.

Minutes of the last Ordinary General Meeting (27th June 1973) were taken as read and confirmed.

Papers read (by title only):

Notes on the ecology, zoogeography, and coloration of the Gobiesocid Clingfishes, *Lepadichthys caritus* Briggs and *Diademichthys lineatus* (Sauvage). By G. R. Allen and W. A. Starck II.

A new species of *Osmundacaulis* from the Jurassic of Queensland. By R. E. Gould.

The Psilopsocidae (Psocoptera) of New Guinea. By C. N. Smithers and I. W. B. Thornton.

Announcement:

The Chairman brought to the attention of members a new series of films on ABC television entitled " Wild Australia " ; the ABC had indicated that it would welcome comments on these from members of the Society.

Exhibit:

Mr. G. P. Whitley submitted biographical notes on Captain Thomas Stackhouse, R.N. (1832–1886), a founder of the Linnean Society of New South Wales. Stackhouse was born in England and served in the Royal Navy in various parts of the world, first as Mate in 1850, promoted to Lieutenant in 1853 and entitled to wear medals, Commander 1863 and retired April 1, 1870, and was promoted to Captain 1878. He was Secretary of the Australian Club, Sydney, about 1873–75 and a co-founder of the Linnean Society of New South Wales in 1874. He went on dredging excursions in Sydney Harbour with Sir William Macleay and was associated with the scientists of H.M.S. "*Challenger*". He was elected a Trustee of the Australian Museum on 1st July 1875 and was a member of the Royal Society of New South Wales until 1878. He does not appear to have published any papers but was interested in the botany and coleoptera of New England, where he lived in his later years. He died at Maclean, New South Wales, on 24th September 1886 and was buried in the Church of England cemetery there. No portrait of him has been traced. (Acknowledgements are gratefully made to the Maclean District Historical Society and to the Australian Club, Australian Museum, Library of New South Wales, Mitchell Library, Registrar-General's Department and the Royal Society of New South Wales, Sydney, for assistance.)

Mr. Whitley also exhibited (by permission of the Director of the Australian Museum) a portrait of Captain Arthur Alexander Walton Onslow, R.N., from the Museum archives. Captain Onslow (1833–1882) was one of the first councillors and an early Secretary of the Linnean Society of New South Wales, and took part in Macleay's *Chevert* expedition. Mennell's *Dictionary of Australasian Biography* (1892 : 355) dealt with his life.

In view of the approaching centenary of the Linnean Society of New South Wales, it may be appropriate to note that the Australian Museum archives contain portraits of several of our early officials and members, for example, H. G. Alleyne, J. C. Cox, Sir William Macarthur (our first Vice-President), the Macleays, George Masters, E. P. Ramsay and Professor W. J. Stephens.

Address :

An address was given by Professor G. M. Philip, Department of Geology and Geophysics, University of Sydney, entitled "Sexual dimorphism among echinoids".

ORDINARY GENERAL MEETING

25th September 1973

Held in the Society's Rooms, 157 Gloucester Street, Sydney.

Dr. P. J. Stanbury in the chair.

Minutes of the last Ordinary General Meeting (25th July 1973) were taken as read and confirmed.

Papers read (by title only) :

New records and species of *Laelaps* and allied genera from Australasia (Acari : Dermanyssidae). By R. Domrow.

The development and adult structure of the vertebral column in *Leiopelma* (Amphibia : Anura). By L. A. Moffat.

Paper read :

Variability in oat stem rust in eastern Australia. By N. H. Luig and E. P. Baker.

Announcements :

The Chairman brought to the attention of members the Commonwealth Public Inquiry into the National Estate ; the chairman of this committee, the Hon. Mr. Justice R. M. Hope, would be the guest speaker at the Annual Dinner of the Nature Conservation Council of New South Wales, on the 13th October 1973.

It was also announced that the Society's annual Field Day would be held on the 21st October at the Royal National Park.

Address :

An address was given by Professor J. J. Veevers, Macquarie University, entitled " Deep Sea drilling off Western Australia ".

FIELD DAY

A Field Excursion was held on the 21st October 1973 to coincide with a month of activities organized by the Opera House Committee to celebrate the opening of theSydney Opera House. The excursion was arranged to the Royal National Park where local and overseas visitors were shown how to identify Australian flora and fauna by members of the Society.

ORDINARY GENERAL MEETING

28th November 1973

Held in the Society's Rooms, 157 Gloucester Street, Sydney.

Minutes of the last Ordinary General Meeting were taken as read and confirmed.

Papers read (by title only) :

Resistance to Rust (*Uromyces appendiculatus*) in beans (*Phaseolus vulgaris*). By B. Ballantyne.

Two new parasitic mites (Acari : Sarcoptidae and Atopomelidae) from Tasmanian marsupials. By A. Fain and R. Domrow.

On some fructifications of the Glossopteridales from the Upper Permian of New South Wales. By W. B. K. Holmes.

NOTES AND EXHIBITS

Mr. G. P. Whitley exhibited a letter from Alfred Russel Wallace, dated 2nd October 1892, to Charles Hedley (by courtesy of the Australian Museum, in whose archives it reposes).

Wallace was born one hundred and fifty years ago and his theory of evolution by means of natural selection was announced in July 1858, simultaneously with Darwin's, before the Linnean Society of London. In the library of that Society, incidentally, there is a manuscript list of Australian birds, by Wallace.

Charles Hedley (1862–1926) was for many years conchologist at the Australian Museum and was particularly interested in the implications of the distribution of the Pacific land-snail, *Placostylus.*

The full text of the letter is as follows :

Parkstone, Dorset.
Octr. 2nd. 1892

Dear Sir,

Thanks for your letter & enclosure on *Placostylus*. I cannot accept your conclusions drawn from the distribution of *one* genus—& without any full knowledge either of its past history or modes of dispersal—as at all certain. I have *not* asserted, as you say, an absolute land-connection between Australia and New Zealand, but only a very much closer approach. But even a connection at such a *remote epoch* as I suggest (early Tertiary or Cretaceous) might have been, & probably was *before* the genus *Placostylus* came into existence ! Your omission of all reference to this essential point of *date of origin* of the genus, vitiates all your arguments as against *my views*. The existence of land-shells, rather abundantly, in *all* oceanic islands shows that they have some means of dispersal *independent of land-connection*, or even of near approach ; hence no arguments from present distribution of land-shells can prove land-connection.

It is each specialist *assuming* that land-connection is necessary to explain the distribution of his special group, that has caused such apparent contradictions in geographical distribution, and rendered it impossible to arrive at any sound conclusions as to the past changes of the earth.

I have endeavoured to show the fallacy of such assumptions both in my " Geog. Dist. of Animals " & in my " Island Life "; and you are only drawing conclusions similar to those which I have again & again shown to be invalid. In my chapter on the " Flora of N. Zealand " I have fully shown the tropical & Melanesian element in the N.Z. flora, and the chapters on " The Azores " and " Bermuda " as well as those on the " Galapagos " and " St. Helena ", show how impossible it is to draw valid conclusions as to *land-connections* from similarity in land-molluscs.

Yours very truly
Alfred R. Wallace—

C. Hedley Esq.

Professor T. G. Vallance exhibited the Linnean Society's copy of Edward Daniel Clarke : *A Syllabus of Lectures in Mineralogy* (8vo, Cambridge, 1807). Part of our inheritance from the Macleay family, this particular copy of a rare book belonged to William Sharp Macleay, F.R.S. (1792–1865), and bears his signature with the inscription *Trin* : *Coll* : *Cant.* and the date 1816. In that year Macleay, already a B.A., attended Clarke's lectures. He was clearly an attentive student. The book exhibited was interleaved throughout with blank sheets and these are largely covered with Macleay's miniscule script ; additional annotations appear on many pages of the printed text. A few notes represent later additions to the manuscript. Some, in fact, can be dated as post-1839, the year Macleay came to Sydney, indicating that he retained an interest in mineralogy, but the greatest number belong to the year 1816. The whole of this manuscript of roughly 100,000 words has now been transcribed and considerable progress has been made in identifying the sources of Clarke's information as reported by Macleay. As no other detailed account of Clarke's course appears to have survived the record has unique interest. It is hoped eventually to publish the transcript with critical commentary.

E. D. Clarke (1769–1822) was appointed Professor of Mineralogy at Cambridge in 1808 and held the Chair, the first in any English-speaking university, until his death just over 150 years ago. His successor, incidentally, was J. S. Henslow, the mentor and friend of Charles Darwin. Clarke came to mineralogy by way of a classical education and extensive travel. For some twelve years he travelled throughout Europe and visited Russia, the Middle East and Egypt, indulging his taste for antiquities and natural history. His published account of the travels fills six quarto volumes (1810–1823). On the way back to England he spent some months of 1802 in Paris, taking the opportunity to attend lectures by such masters as Fourcroy in Chemistry and Haüy in Mineralogy. Although these influences were crucial to his subsequent career, it was as traveller and collector of antiquities that Clarke was hailed on his return home. Cambridge rewarded him for his donations with its LL.D. His old college, Jesus, appointed him senior tutor in 1805 and in March 1807 Clarke began the first of what became an annual series of lectures in mineralogy.

So attractive were these lectures that late in the following year the University made Clarke Professor of Mineralogy. Macleay's notes demonstrate Clarke's diligence and thoroughness as a teacher. Most mineral species were illustrated by samples from Clarke's collection, many, along with his store of anecdotes, gathered in the course of his travels. Clarke had acquired some skill as an analytical chemist but relied heavily in his lectures on the published work of others, notably Klaproth and Vauquelin. His information was a blend of ancient and modern. Pliny and other authors of antiquity are called upon often ; of contemporary sources the most heavily used appear to have been Robert Jameson's *System of Mineralogy* (3 vols., Edinburgh, 1804–1808) and René Haüy's *Traité de Mineralogie* (4 vols. + atlas, Paris, 1801). Clarke, indeed, seems to have done much to propagate Haüy's concepts at a time when British mineralogy was under strong German influence.

Few items of Australasian interest appear in Macleay's notes. Under the item *jade* we have a remark about a prince of New Zealand taking to New Holland an axe with a head of jade. Another weapon with a head of trap (=? greenstone), given by the prince to Governor King, but then in Clarke's collection, was shown to the class. Botany Bay " Diamonds " or " Topaz " (=quartz) also rate a comment ; they appear to have become commonly available in Britain during 1814. Clarke has other references to New Holland in later editions (1818, 1820) of the printed Syllabus. Among his students of this later period was William Branwhite Clarke, known to some as the " Father of Australian Geology ".

In addition to the Macleay copy of the Syllabus, several letters of mineralogical interest by or referring to E. D. Clarke (including one from C. I. La Trobe, father of the La Trobe remembered in Melbourne) as well as others of Clarke's published works were exhibited and discussed.

Mrs. R. J. Inall, Secretary, exhibited two books from the Society's rare book collection. *Anatomy of Plants* by N. Grew (Rawlins, 1682), and *Historie of Foure-Footed Beastes* by Edward Topsell (London, Laggard, 1607).

LIST OF MEMBERS

(31st December, 1973)

Ordinary Members

(An asterisk (*) denotes Life Member)

1973 Allen, Gerald Robert, B.A., Ph.D., Australian Museum, P.O. Box A285, Sydney South, N.S.W., 2000.
1940 *Allman, Stuart Leo, B.Sc.Agr., M.Sc., 99 Cumberland Avenue, Collaroy, N.S.W., 2097.
1965 Anderson, Derek John, Ph.D., School of Botany, University of N.S.W., P.O. Box 1, Kensington, N.S.W., 2033.
1959 Anderson, Professor Donald Thomas, B.Sc., Ph.D., D.Sc., School of Biological Sciences, Department of Zoology, Sydney University, 2006.
1964 Anderson, Mrs. Jennifer Mercianna Elizabeth, B.Sc.Agr., 24 Watson Street, Bondi, N.S.W., 2026.
1965 Andrew, Mrs. Phillipa Audrey, M.Sc. (*née* Croucher), 10 Black Street, Watsonia, Victoria, 3087.
1963 Ardley, John Henry, B.Sc. (N.Z.), F.R.E.S., Wellcome Australasia Ltd., P.O. Box 108, Concord, N.S.W., 2137.
1927 *Armstrong, Jack Walter Trench, " Cullingera ", Nyngan, N.S.W., 2825.
1972 Armstrong, James Andrew, B.Sc.Agr., Royal Botanic Gardens, Sydney, N.S.W., 2000.
1952 Ashton, David Hungerford, B.Sc., Ph.D., 92 Warrigal Road, Surrey Hills, Victoria, 3127.
1912 Aurousseau, Marcel, M.C., B.Sc. (Hons.), D.Litt. (Hon.), F.R.G.S., F.A.H.A., 229 Woodland Street, Balgowlah, N.S.W., 2093.

1961 Bain, Miss Joan Maud, M.Sc., Ph.D., 10/1 Spencer Road, Killara, N.S.W., 2071.
1949 Baker, Professor Eldred Percy, B.Sc.Agr., Ph.D., Department of Agricultural Botany, Sydney University, N.S.W., 2006.
1962 Ballantyne, Miss Barbara Jean, B.Sc.Agr., N.S.W. Department of Agriculture, Private Mail Bag No. 10, Rydalmere, N.S.W., 2116.
1959 Bamber, Richard Kenneth, F.S.T.C., M.Sc., F.Inst.Wood Sci., 113 Lucinda Avenue South, Wahroonga, N.S.W., 2076.
1972 Barkas, John Pallister, B.Sc., 20 Medusa Street, Mosman, N.S.W., 2088.
1955 Barlow, Bryan Alwyn, B.Sc., Ph.D., School of Biological Sciences, The Flinders University, Bedford Park, South Australia, 5042.
1965 Basden, Ralph, M.Ed., B.Sc. (Lond.), F.R.A.C.I., A.S.T.C., 183 Parkway Avenue, Hamilton, N.S.W., 2303.
1954 Baur, George Norton, B.Sc., B.Sc.For., Dip.For., 3 Mary Street, Beecroft, N.S.W., 2119.
1935 *Beadle, Professor Noel Charles William, D.Sc., University of New England, Armidale, N.S.W., 2350.
1940 Beattie, Joan Marion, D.Sc. (*née* Crockford), 2 Grace Avenue, Beecroft, N.S.W., 2119.
1964 Bedford, Geoffrey Owen, B.Sc., Koronivia Research Station, Nausori, Fiji.
1952 Bennett, Miss Isobel Ida, Hon.M.Sc., 69 Carabella Street, Kirribilli, N.S.W., 2061.
1972 Benson, Douglas Howard, B.Sc., Royal Botanic Gardens, Sydney, N.S.W., 2000.
1964 Bertus, Anthony Lawrence, B.Sc., Biology Branch, N.S.W. Department of Agriculture, Private Mail Bag, No. 10, Rydalmere, N.S.W., 2116.
1948 Besly, Miss Mary Ann Catherine, B.A., School of Biological Sciences, Department of Zoology, Sydney University, 2006.
1961 Bishop, James Arthur, Department of Genetics, The University of Liverpool, Liverpool 3, England.
1964 Blackmore, John Allan Philip, LL.B. (Syd. Univ.), 25 Holden Street, Ashfield, N.S.W., 2131.
1968 Blaxell, Donald Frederick, D.D.A., B.Sc., Royal Botanic Gardens, Sydney, 2000.
1960 Bourke, Terrence Victor, B.Sc.Agr., Department of Agriculture, Stock and Fisheries, Popondetta, Papua.
1973 Bower, Colin Charles, B.Sc., Department of Zoology, Sydney University, 2006.
1967 Boyd, Robert Alexander, B.Sc., Department of Botany, University of New England, Armidale, N.S.W., 2350.
1946 Brett, Robert Gordon Lindsay, B.Sc., 48 Main Road, Lindisfarne, Tasmania, 7015.
1960 Brewer, Ilma Mary, D.Sc., 13 Wentworth Road, Vaucluse, N.S.W., 2030.
1955 Briggs, Miss Barbara Gillian, Ph.D., National Herbarium of N.S.W., Royal Botanic Gardens, Sydney, 2000.
1972 Brown, Kenneth R., B.Sc., School of Zoology, University of N.S.W., Kensington, N.S.W., 2033.
1924 Browne, Ida Alison, D.Sc. (*née* Brown), 363 Edgecliff Road, Edgecliff, N.S.W., 2027.
1911 Browne, William Rowan, D.Sc., F.A.A., 363 Edgecliff Road, Edgecliff, N.S.W., 2027.
1949 Burden, John Henry, 1 Havilah Street, Chatswood, N.S.W., 2067.

1931 *Burges, Professor Norman Alan, M.Sc., Ph.D., Vice-Chancellor, The New University of Ulster, Coleraine, County Londonderry, Northern Ireland.
1968 Burns, James, A.A.S.A., 127 Plateau Road, Avalon Beach, N.S.W., 2107.
1970 Byrnes, Norman Brice, B.Sc., Dip.Ed., 14 Bowline Street, Jamboree Heights, Queensland, 4074.

1960 Cady, Leo Isaac, P.O. Box 88, Kiama, N.S.W., 2533.
1959 Campbell, Keith George, D.F.C., B.Sc.For., Dip.For., M.Sc., 17 Third Avenue, Epping, N.S.W., 2121.
1927 Campbell, Thomas Graham, 30 Froggatt Street, Turner, A.C.T., 2601.
1968 Canning, Miss Estelle Margaret, B.Sc. (Melb.), 50 Swan Street, Wangaratta, Victoria, 3677.
1934 *Carey, Professor Samuel Warren, D.Sc., Geology Department, University of Tasmania, Hobart, Tasmania, 7000.
1949 Carne, Phillip Broughton, B.Agr.Sci. (Melb.), Ph.D. (London), D.I.C., Division of Entomology, C.S.I.R.O., P.O. Box 1700, Canberra City, A.C.T., 2601.
1956 Carolin, Professor Roger Charles, B.Sc., A.R.C.S., Ph.D., School of Biological Sciences, Department of Botany, Sydney University, 2006.
1957 Casimir, Max, B.Sc.Agr., Biological and Chemical Research Institute, N.S.W. Department of Agriculture, Private Mail Bag, No. 10, Rydalmere, N.S.W., 2116.
1936 *Chadwick, Clarence Earl, B.Sc., Biological and Chemical Research Institute, N.S.W., Department of Agriculture, Private Mail Bag No. 10, Rydalmere, N.S.W., 2116.
1956 Chambers, Professor Thomas Carrick, M.Sc. (N.Z.), Ph.D., Botany School, University of Melbourne, Parkville, Victoria, 3052.
1973 Chapman, Arthur David, B.Sc., C.S.I.R.O., Division of Plant Industry, Herbarium Australiense, P.O. Box 1600, Canberra City, A.C.T., 2601.
1959 Chippendale, George McCartney, B.Sc., 4 Raoul Place, Lyons, A.C.T., 2606.
1971 Cho, Kai Yip, B.Sc., Ph.D., Department of Microbiology, University of Sydney, N.S.W., 2006.
1932 *Churchward, John Gordon, B.Sc.Agr., Ph.D., "Erlangga", Glen Shian Lane, Mount Eliza, Victoria, 3930.
1946 Clark, Laurance Ross, M.Sc., C.S.I.R.O., Division of Entomology, P.O. Box 1700, Canberra City, A.C.T., 2601.
1956 Cogger, Harold George, M.Sc., Ph.D., Australian Museum, P.O. Box A285, Sydney South, N.S.W., 2000.
1956 Common, Ian Francis Bell, M.A., D.Sc.Agr., C.S.I.R.O., Division of Entomology, P.O. Box 1700, Canberra City, A.C.T., 2601.
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III–IV. *Osmundacaulis hoskingii* sp. nov. var. *hoskingii.*
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