Proceedings of the Linnean Society of New South Wales

VOLUME 97

No. 429-432

CONTENTS OF PROCEEDINGS, VOLUME 97

PART 1 (No. 429)

(Issued 22nd June, 1972)

CONTENTS

Page

Annual General Meeting :

PART 2 (No. 430)

(Issued 11th October, 1972)

CONTENTS

PART 3 (No. 431)

(*Issued 8th January, 1973*)

CONTENTS

PART 4 (No. 432)

(*Issued 30th April, 1973*)

CONTENTS

Proceedings of the Linnean Society of New South Wales

Issued 22nd June, 1972

VOLUME 97
PART I
No. 429

Registered for posting as a periodical—Category A.

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, 1972–73

President
H. G. Cogger, M.Sc., Ph.D.

Vice-Presidents
L. A. S. Johnson, D.Sc.; T. G. Vallance, B.Sc., Ph.D.;
N. G. Stephenson, M.Sc., Ph.D.; R. C. Carolin, B.Sc., Ph.D., A.R.C.S.

Honorary Treasurer
Joyce W. Vickery, M.B.E., D.Sc., F.L.S.

Secretary
Mrs. Ruth J. Inall

Council

D. J. Anderson, Ph.D.
D. T. Anderson, D.Sc.
R. K. Bamber, F.S.T.C.
Barbara G. Briggs, Ph.D.
W. R. Browne, D.Sc., F.A.A.
R. C. Carolin, B.Sc., Ph.D., A.R.C.S.
H. G. Cogger, M.Sc., Ph.D.
Mary M. Hindmarsh, B.Sc., Ph.D.
L. A. S. Johnson, D.Sc.
Elizabeth C. Pope, M.Sc., C.M.Z.S.
P. J. Stanbury, Ph.D.
N. G. Stephenson, M.Sc., Ph.D.
F. H. Talbot, M.Sc., Ph.D., F.L.S.
E. LeG. Troughton, F.R.Z.S.
P. G. Valder, B.Sc.Agr., Ph.D.
T. G. Vallance, B.Sc., Ph.D.
Joyce W. Vickery, M.B.E., D.Sc., F.L.S.
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.

Linnean Macleay Fellow of the Society as from 1st July, 1971
Mrs. Lynette Anne Moffat, B.Sc.Hons.

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

ANNUAL GENERAL MEETING

29th March 1972

The Ninety-seventh Annual General Meeting was held in the Society's Rooms, Science House, 157 Gloucester Street, Sydney, on Wednesday, 29th March 1972, at 7.30 p.m.

Dr. L. A. S. Johnson, President, occupied the chair.

The minutes of the Ninety-sixth Annual General Meeting (31st March 1971) were read and confirmed.

Report on the Affairs of the Society for the Year 1971

Publication

The Society's Proceedings for 1970, Part 3, was published on the 31st March 1971, and for 1971, Parts 1, 2 and 3, on the 17th June, 15th September and 10th December 1971.

Donations totalling $250.00 were made during the year towards the cost of publication, which was as follows:

	$		$
Block-making	874.92	Donation	250.00
Printing	3,629.60	Subscriptions	3,822.36
Postage	228.38	Balance met by Society	600.54
	$4,732.90		$4,732.90

	$
Net cost Proceedings	655.54
Net cost Reprints	286.52
Total net Publication Costs	$942.06

The accounts have been set out in detail this year so as to show the true net cost. 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 11 new members were admitted to the Society, three resigned, and four were removed from the list of members. The numerical strength of the Society at 1st March 1972, was: Ordinary Members, 267: Life Members, 26; Corresponding Members, 3; total, 296.

Professor Sir Rutherford Robertson, K.B.E., C.M.G., F.A.A., F.R.S., was honoured by the Queen in the 1972 New Year's Honours List with a knighthood.

Monthly Meetings

Addresses were given at the June and July meetings, and a Symposium was held at the October meeting; a Field Day excursion took the place of the

Ordinary Monthly Meeting in September, while Notes and Exhibits were a feature of the November meeting.

Details of these may be found in the Abstracts of Proceedings in Part 4, Vol. 96 (1971).

Library

During the year it was decided to retain the library, and a part-time librarian was appointed. In order to make additional space available, most of the monographs have been sent to Fisher Library, Sydney University, on permanent loan; a suitable book-plate will be inserted in each volume by the University, indicating that it is from the Linnean Society's collection.

The serials have been re-shelved into alphabetical order as in the Scientific Serials catalogue; we hold 1,595 serials, of which 565 are current. A new catalogue is now in preparation, and it is hoped that when this is complete it will be possible to circulate a list of our holdings to interested libraries.

Subsequently, it is proposed to catalogue those monographs, mainly from the British Museum, still remaining in the Society's library.

Linnean Macleay Fellowship

Dr. A. Anne Warren (*née* Howie) completed her Fellowship in the Department of Geology, University of Melbourne. A paper entitled "A Brachiopod Labyrinthodont from the Lower Trias of Queensland", based on her research during the year, was published in Vol. 96, Part 4 (1971).

Mrs. Lynnette A. Moffat was appointed Linnean Macleay Fellow in the School of Biological Sciences, Sydney University, for one year as from the 1st July 1971. Her topic of research is the relationship of amphibians and reptiles, using recently developed methods such as cytotaxonomy and serology.

Linnean Macleay Lectureship in Microbiology

Dr. K. Y. Cho, Linnean Macleay Lecturer in Microbiology, University of Sydney, as from 1st January 1969, reported as follows on his work for the year to December, 1971:

"Work has been completed on the investigation of aspects of the internal organization of *Escherichia coli* by electron microscope studies of auxotrophs defective in envelope synthesis. Spermine treatment of a diaminopimelic acid-requiring strain under conditions of diaminopimelic acid starvation (thereby blocking cell envelope synthesis) resulted in the detection of a polar organelle. This organelle is connected to the plasma membrane and consists of ribosomes in association with a structure in interlocking electron dense and light components. It is proposed that this structure is an apparatus for the synthesis and assembly of protein and phospholipid components of the cell envelope, including the organization of cell division. If some of the electron-light components represent nucleic acid, then this organelle may also be involved in the replication and transfer of DNA. This is the first organelle other than membrane invagunations that has been discovered in *Escherichia coli* or any prokaryote.

"The work has been accepted for publication in the *Australian Journal of Biological Science.*

"Other work under investigation includes the isolation of phospholipid requiring auxotroph of Azotobacter for the study of membrane biogenesis, and the effect of spermine on Azotobacter."

Finance

The balance sheets were presented by the Honorary Treasurer, who pointed out that during the year the Society had been faced with unusually heavy expenditure, some of it of a non-recurrent nature, which had resulted in a deficiency of $5,253.07 in the General Account.

This had been due:

(*a*) To the general inflationary increase in costs and services of all kinds;

(*b*) to the general increase in rates of salaries, which the Society is obliged to meet in order to obtain and keep suitable staff;

(*c*) to the retirement of our previous Assistant Secretary and obligation to provide long service leave and an appropriate pension;

(*d*) to the reorganization of our record and accounting systems and general office procedures, necessitating also the purchase of some new office equipment.

(*e*) to the reorganization of the library, which involved the part-time employment of a trained librarian and an assistant.

The costs of the last mentioned will be covered in part by monies received under the compensation claim from the Sydney Cove Re-development Authority.

The accounts have been presented in a slightly different form this year, on the recommendation of our Auditor, in order to bring them more closely into line with modern business practice.

The Bacteriology and Fellowships Accounts remain in a satisfactory condition.

A new account has been opened, styled the Linnean Society of N.S.W. Scientific Research Fund. Monetary donations of $2.00 or over to this fund are exempt from income tax. Its funds can be used only for scientific research, but permission to capitalize donations to it and allow it to accumulate has been obtained. The Honorary Treasurer drew the particular attention of members to this fund and its taxation benefits and expressed the hope that, as and when they were able, they might contribute to it as a means of stimulating scientific research in the future in the tradition established by Sir William Macleay and continued thereafter by the Society.

Report on Science Centre

With support from the N.S.W. State Government in the nature of a Crown grant of what has become an increasingly valuable block of land, the Linnean and Royal Societies, together with the Institution of Engineers, were able to build Science House in 1930. Since then this building, on the corner of Gloucester and Essex Streets, has provided in Sydney a Science Centre with lecture hall, meeting room facilities, libraries and accommodation not only for the owner bodies, but also for tenants of the building and other scientific and educational groups, and often on a regular basis.

The resumption of Science House in December 1970 led the Linnean and Royal Societies to request the Government of New South Wales to provide, as it had done in 1930, a new site for these Societies to re-house themselves. The Societies have resolved to accept responsibility for the building of a new Science Centre much as they had in the building of Science House some 40 years ago. It is expected that part of the new Centre will provide accommodation and shared general facilities for professional and scientific organizations under favourable terms, while another part of the Centre will provide office space at commercial letting rates. The New South Wales Government, no doubt mindful of the history and contribution of both Societies within this State, has considered our request sympathetically, has encouraged us in our efforts, and has indicated that it will give as much support as possible to our scheme.

Following the approval given by both the Linnean and Royal Societies for the building of a Science Centre, a Planning Committee was appointed, with representatives from both Societies. This committee has met regularly during the last year and has kept pace with the requirements, stage by stage, in the broad initial planning and in the clarification of the position of both Societies in relation to the project. Progress towards the establishment of a Science Centre may be summarized under the following headings.

Compensation

Science House provided for the Linnean and Royal Societies not only a home but also a source of income. The compensation which is being claimed from the Sydney Cove Redevelopment Authority, the new owners of Science House following the resumption, is substantial. It is not yet known what the final amount will be, but this information should be available before long. It is the intention of both Societies to invest the compensation money, excluding the amount paid in respect to claims for disturbance, in the new Science Centre. Until the exact figure for compensation is known, and until the cost of erecting a building on a particular site has been calculated, it will not be possible to say how much additional finance will be required. However, the compensation money for the two Societies should provide enough cash in hand. An application has been made to the Sydney Cove Redevelopment Authority for advances to the two Societies on this compensation money, and we have been advised that cheques will be available subsequent to clearance from the Valuer-General's Office. In short, the resumption of Science House will inevitably remove from the Societies their owned-home and source of income. The Societies, conscious of their long history and anticipated long future, have resolved to invest compensation money in such a way as to provide another owned-home and source of income. To do this, they are working jointly, knowing well that they will build a better Science Centre to fulfil their future needs if they combine their resources rather than act separately.

Site and Tenure

Two sites in the eastern Rocks Area, as well as other suitable sites, are under consideration. At a meeting with representatives of the two Societies on 9th March 1972, the Minister of Cultural Activities undertook to investigate the possibility of special concessions in the event of a site being chosen in the Rocks redevelopment area, where land leases may ordinarily be of rather limited duration. In the event of the Science Centre being erected in a suitable area, the Government would be prepared to undertake to rent a specified area of the income-providing office space of the Centre.

Property Consultants and Legal Advisers

Messrs. Jones, Lang, Wootton, property consultants to Science House and valuers for compensation purposes, were appointed by the two Societies to be Property Consultants for the Science Centre project. As property consultants, they will be responsible for a wide range of services which in the initial stages involve (*a*) general consultancy work leading to the establishment of a viable basis for development ; (*b*) negotiations in respect to a suitable parcel of land and the right to develop it to an agreed floor space ratio and for agreed uses ; (*c*) negotiations for finance for the project. Later they will be involved in the co-ordination and direction of the development project, the leasing of the space created within the development surplus to the requirements of the Science Centre itself, and possibly the management of the completed development.

Messrs. Stephen, Jacques & Stephen, Legal Advisers to Science House, have been appointed by the two Societies as legal advisers for the Science Centre project.

Act of Incorporation

The Act of Incorporation of the Linnean Society of New South Wales dates back to 1884, and under this Act, which has not been so far revised, the Linnean Society is far more restricted in its possible investments and hence sources of income than is the Royal Society of New South Wales ; it is also restricted in various other ways, even in respect to the Fellowships it offers. With the approval of its members, the Linnean Society is now in the process of amending its Act of Incorporation. The matter is at this stage in the hands of the Parliamentary Draughtsman and the Minister of Cultural Activities has offered his assistance in bringing forward an Enabling Act.

Science Centre Company

In order for the Linnean and Royal Societies to operate a Science Centre appropriately, it will be necessary for the Societies jointly to form a company. Preparation of a draft Memorandum and Articles of Association has been completed, and such a company could be established at short notice.

Progress Reports

In response to an early questionnaire, a considerable number of scientific and professional organizations expressed an interest in the possibility of accommodation in the proposed Science Centre. These bodies are being advised from time to time of the stage reached in the project. A first progress report has been prepared and circulated.

Government Approval of the Plan

It is clear that the Government of New South Wales approves of our action in proceeding towards the establishment of a Science Centre. The Minister of Cultural Activities, the Director of the Sydney Cove Redevelopment Authority, Treasury officials and members of the Public Service Board have all given generously of their time and have made offers of help. It is realized by the two Societies, as also by the Government, that if the compensation payment reaches the level anticipated by the Societies the financing of the new Centre could proceed independently of the Government. However, if a new building on a new site is to be a Science Centre in the real sense and is to provide low-cost facilities for other societies, then tangible assistance at least by way of concessions or guarantees will be required from the Government. We have been invited to discuss this matter further with the Minister of Cultural Activities at a later date.

During the coming year it is hoped to see the finalizing of the financial aspects of the project, the appointment of an architect, and the completion of the architect's brief outlining of the concept of the proposed Centre.

Presidential Address

The President then gave the Presidential Address, " Evolution and Classification in *Eucalyptus* ".

Annual Elections

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

President : Dr. H. G. Cogger.

Members of Council : Professor Donald T. Anderson, Professor Derek Anderson, Dr. L. A. S. Johnson, Dr. P. J. Stanbury, Professor N. G. Stephenson, Dr. F. H. Talbot.

Auditor : W. Sinclair & Co.

The Chairman announced with great regret that Dr. A. B. Walkom had informed Council 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 for Dr. Walkom's long and devoted service to the Society.

The Chairman then installed Dr. H. G. Cogger as President.

A vote of thanks to the retiring President, Dr. L. A. S. Johnson, was moved by Dr. Vickery and carried by acclamation.

LINNEAN SOCIETY OF NEW SOUTH WALES

GENERAL ACCOUNT

Balance Sheet as at 29th February 1972

1971 $		$	$
	<u>Accumulated Funds—</u>		
	Balance, 1st March 1971:		
	Amount Received from Sir William Macleay	40,000.00	
	Transfers from Income Account ..	13,816.72	53,816.72
	Add Transfer from Contingencies Reserve..		68,258.38
			122,075.10
	Less:		
	Adjustment—Science House	1,000.00	
	Deficiency for the Year	5,253.07	6,253.07
53,817	Balance, 29th February 1972		115,822.03
	<u>Reserves—</u>		
68,344	Contingencies		—
1,153	Bookbinding		1,142.66
—	Sundry Creditors		274.60
$123,314			$117,239.29

1971 $		$	$
	<u>Fixed Assets—</u>		
	Furniture, Fixtures and Fittings—At Cost	337.11	
	Less Depreciation written off	14.30	
—			322.81
	Office Machines—At Cost	1,306.13	
	Less Depreciation written off	118.61	
—			1,187.52
—	Total Fixed Assets		1,510.33
	<u>Investments—</u>		
30,097	Commonwealth Loans—At Cost	30,000.00	
	Debentures—At Cost:		
39,689	Metropolitan Water, Sewerage and Drainage Board	39,700.00	
6,000	Sydney County Council	6,000.00	
31,470	Science House—At Cost (One-third Interest)	30,470.43	
4,750	Loan on Mortgage	4,750.00	
112,006	Total Investments		110,920.43
	<u>Current Assets—</u>		
—	Sundry Debtors	1,627.65	
40	Cash on Hand	3.59	
11,268	Commercial Banking Company of Sydney Limited	3,177.29	
11,308	Total Current Assets		4,808.53
$123,314			$117,239.29

LINNEAN SOCIETY OF NEW SOUTH WALES

GENERAL ACCOUNT

Income and Expenditure Account for the Year Ended 29th February 1972

EXPENDITURE

1971 $		$
105	Audit Fees	150.00
151	Cleaning	342.90
—	Depreciation	32.91
443	General Expenses	1,049.65
754	Illustrations	874.92
35	Insurance	64.07
249	Library	281.99
—	Life Assurance Premium	250.00
23	Light and Power	92.95
288	Postages	701.55
5,042	Proceedings—Printing Costs	3,379.60
57	Proof Reading	—
—	Professional Services	171.00
323	Printing and Stationery	572.84
55	Referees' Fees	167.00
197	Repairs and Maintenance	218.60
841	Reprints	936.32
233	Sir William Macleay Lecture	—
5,952	Salaries and Honorarium	15,005.45
3,556	Science House Rent	3,556.00
60	Telephone	232.32
18,364	Total Expenditure	28,180.07
3,147	Surplus for the Year	—
$21,511		$28,180.07

INCOME

1971 $		$	$
	Subscriptions:		
	Members	520.00	
	Proceedings	3,822.36	
1,672			4,342.36
1,000	Contributions		—
4,514	Interest Received		4,683.12
	Fellowships Account:		
37,23	Surplus Income for the Year Ended 29th February 1972		3,893.43
800	Grant—N.S.W. Government		—
29	Rents Received		29.50
585	Reprints Sales		806.40
	Sir William Macleay Lecture:		
52	Dinner Receipts		—
1,920	Sales		1,957.05
	Science House:		
7,216	Share of Surplus		7,215.14
21,511	Total Income		22,927.00
—	Deficiency for Year transferred to Accumulated Funds		5,253.07
$21,511			$28,180.07

AUDITORS' REPORT.

We have audited the books and records of the Linnean Society of New South Wales for the year ended 29th February 1972, 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 29th February 1972, 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 seventh day of March, 1972.

Joyce W. Vickery,
Hon. Treasurer.

7th March 1972.

LINNEAN SOCIETY OF NEW SOUTH WALES

LINNEAN MACLEAY FELLOWSHIPS ACCOUNT

Balance Sheet as at 29th February 1972

1971 $		$	$
	Accumulated Funds—		
	Balance, 1st March 1971:		
	Amount Bequeathed by Sir William Macleay	70,000.00	
	Transfers from Income Account ..	52,272.98	122,272.98
	Add:		
	Increase in Value of Investments		260.02
	Transfer from Income and Expenditure Account		266.66
122,273	Balance, 29th February 1972		122,799.66
$122,273			$122,799.66

1971 $		$
	Fixed Assets—	
59,886	Commonwealth Loans—At Cost	60,288.00
	Debentures—At Cost:	
6,000	Electricity Commission of New South Wales ..	6,000.00
37,897	Metropolitan Water, Sewerage and Drainage Board ..	37,700.00
1,745	Rural Bank of New South Wales	1,800.00
15,750	Loans on Mortgage	15,750.00
121,278		121,538.00
	Current Assets—	
995	Commercial Banking Company of Sydney Limited ..	1,261.66
$122,273		$122,799.66

Income and Expenditure Account for the Year Ended 29th February 1972

1971 $		$
2,400	Salary of Linnean Macleay Fellow	2,933.26
800	Transfer to Capital Account	266.66
3,723	Surplus for the Year transferred to General Account	3,893.43
$6,923		$7,093.35

1971 $		$
6,923	Interest Received	7,093.35
$6,923		$7,093.35

AUDITORS' REPORT.

We have audited the books and records of the Linnean Society of New South Wales for the year ended 29th February 1972, 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 29th February 1972, 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 seventh day of March, 1972.

Joyce W. Vickery,
Hon. Treasurer.

7th March 1972.

LINNEAN SOCIETY OF NEW SOUTH WALES

BACTERIOLOGY ACCOUNT

Balance Sheet as at 29th February 1972

1971 $		$	$
	Accumulated Funds—		
	Balance, 1st March 1971:		
	Amount Bequeathed by Sir William Macleay	24,000.00	
	Transfers from Income Account	13,244.22	
	Research Fund Transfer	20.00	
			37,264.22
	Add Surplus for the Year		52.09
			37,316.31
	Less Net Increase in Value of Investments		88.90
37,264	Balance, 29th February 1972		37,227.41
$37,264			$37,227.41

1971 $		$
	Investments—	
30,636	Commonwealth Loans—At Cost	26,900.00
	Debentures:	
	Metropolitan Water, Sewerage and Drainage Board—	
1,800	At Cost	1,800.00
3,400	Loan on Mortgage	8,000.00
35,836		36,700.00
	Current Assets—	
1,428	Commercial Banking Company of Sydney Limited	527.41
$37,264		$37,227.41

Income and Expenditure Account for the Year Ended 29th February 1972

1971 $		$
	University of Sydney:	
1,950	Salary of Lecturer	1,850.00
—	Surplus for the Year	52.09
$1,950		$1,902.09

1971 $		$
1,943	Interest Received	1,902.09
7	Deficiency	—
$1,950		$1,902.09

AUDITORS' REPORT.

We have audited the books and records of the Linnean Society of New South Wales for the year ended 29th February 1972, 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 29th February 1972, 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 seventh day of March, 1972,

Joyce W. Vickery.
Hon. Treasurer,

7th March 1972,

LINNEAN SOCIETY OF NEW SOUTH WALES

SCIENTIFIC RESEARCH FUND ACCOUNT

Balance Sheet as at 29th February 1972

Accumulated Funds—	$	Investments—	$
Transfer from Bacteriology Fund	20.00	Loan on Mortgage	1,000.00
Donations Received	1,005.00	Current Assets—	
		Commercial Banking Company of Sydney Ltd.	25.00
Balance, 29th February 1972	1,025.00		
	$1,025.00		$1,025.00

AUDITORS' REPORT.

We have audited the books and records of the Linnean Society of New South Wales for the year ended 29th February 1972, 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 29th February 1972 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 seventh day of March, 1972.

Joyce W. Vickery,
Hon. Treasurer.

7th March 1972.

PRESIDENTIAL ADDRESS

EVOLUTION AND CLASSIFICATION IN *EUCALYPTUS*

L. A. S. Johnson
National Herbarium of New South Wales, Royal Botanic Gardens, Sydney

[Delivered 29th March 1972]

Synopsis

Following general discussion of some principles of classification, some probable evolutionary trends in *Eucalyptus* are discussed, especially in relation to the recent classification of Pryor and Johnson (1971). Particular stress is laid on the multiple trends and varied final conditions in the calyx and corolla, which are more or less opercular, and in the inflorescence. Characters of anthers, ovules and seeds, cotyledons, hairs, oil glands and ducts, and associated insects are also reviewed as expressed in the eight subgenera recognized (including *Angophora*). Suggestions are made as to the phylogenetic connections of some subgenera and sections, and some problems of relationship are indicated within the eucalypts and between them and other Myrtaceae, which may respond to further detailed investigation and critical synthetic and analytical evaluation. A few changes in the Pryor and Johnson scheme are made or suggested.

> " Our reasonings grasp at straws for premises and float on gossamers for deductions."
> A. N. Whitehead, *Adventures of Ideas* (1933).

On Classification

Four years ago (Johnson, 1968) I expatiated from this chair on the philosophy, methodology, problems, and especially the limitations of taxonomy in general. I concluded that no optimal classification was definable, much less attainable, whether on a phenetic or a phyletic basis, but that " none the less, the elucidation of phylogeny can still proceed, and our unperfectable classifications can still be improved by reducing inconsistency until uncertainty or instability renders further change unprofitable ". No group of Australian plants has had so many investigators as the so-called genus *Eucalyptus*, yet such is its complexity and so many the gaps in our knowledge that its classification is still manifestly improvable, and its detailed phylogeny still not elucidated.

Recently my colleague Lindsay Pryor and I have published, in skeletal form, a new scheme of classification of the eucalypts (Pryor and Johnson, 1971). In deriving this scheme and in our own current revision of it, we have had to consider characters from as many fields as possible, and to evaluate them as to evolutionary significance. As I hope to have shown in 1968, a truly theory-free classification of organisms is an impossibility, although one may certainly develop classifications for which there is no defined theoretical foundation and in which the underlying theoretical assumptions are confused and frequently unconscious.

If the distortions due to these assumptions are so multifarious and chaotic as to be evenly spread, constituting " white noise ", and if this background " noise " is not too great, some meaningful set of signals may be extracted from a phenetic analysis based on many characters. It is then up to us to interpret, in some scientifically or pragmatically profitable way, the results of the analysis. For this purpose, the " results " should not be taken as merely one particular hierarchical classification as represented by the dendrogram produced by a particular strategy. Whenever we proceed from the data to a dendrogram we lose information, and many topologically as well as metrically different dendrograms (and thus formal classifications) can be produced from a given set of data, merely by quite defensible manipulation of the strategies employed, as Lance and Williams (1967 ; Williams, unpub. 1971) have very clearly shown.

If, then, we wish to make effective use of phenetic analysis to generate hypotheses (i.e. for " interpretation " of taxonomic data) we shall need to consider *various* dendrograms and also to check back frequently to the characters themselves. Such hypotheses may relate to the prediction of properties (including genetic and physiological behaviour) of taxa and individuals. A " general " classification is supposed to be widely useful for such prediction, and we may claim that the Pryor and Johnson system of 1971 (which I shall designate PJ_1 for convenience hereafter) meets this criterion better than any other yet available for *Eucalyptus*, although it is bound to be seriously in error at certain points, some of which are already apparent (see below). Predictivity may be improved in this case also by going beyond the generalized summary given by the classification to the particular data from the individual taxa concerned. I should say here that PJ_1 is not based on a numerical analysis, is explicitly not a neo-Adansonian system which claims to give characters " equal weight " (a will-o'-the-wisp notion at best), and is not theory-free. Nevertheless, it is phenetically based to a considerable degree, and the foregoing remarks on broadly-based phenetic classifications are applicable to taxonomic work of this kind and not only to taximetric studies.

Another kind of hypothesis is the phylogenetic, which may be said to imply retrospective prediction ; that is, it predicts what we may hope to find out, in the future, about the past—and thus " explain " the present ! Since we accept, as indeed most pure pheneticists do, that the characters of organisms which are important to them, and to us, are determined largely by their evolutionary history, we inevitably become involved in partial circularity of argument if we base our classifications themselves to some degree on phylogenetic considerations and interpretations. The building of such partially phylogenetic classifications involves some positive feedback from conclusions to argument, and hence incurs stern disapproval from those who seem to think that scientific investigation and interpretation should depend on simple elementary logic. This is an oversimplification and the use of phyletic reasoning in classification, provided that it is subjected to checks and balances, has been defended by various authors (for discussion and further references see Johnson, 1968, 1970 ; Hull, 1967 ; Ghiselin, 1969).

It is also possible to develop more or less defensible models for the derivation by numerical methods of cladistic reconstructions, which may or may not then be used for classification.

We have not used taximetrics of either kind in *Eucalyptus*, because the detailed accumulation of numerical data, species by species, has not been possible on a sufficiently reliable basis. Recent studies by ourselves and others, notably D. J. and S. G. M. Carr (for references see Pryor and Johnson, 1971), all serve to show how much morphological misinterpretation (that is, false homology) there has been in eucalypt descriptions up to the present. I would hope that within the next decade it will indeed be feasible to carry out taximetric analysis both by variable-strategy phenetic techniques and by the use of phyletic (cladistic and perhaps patristic) models, and that these studies will employ accurately expressed and interpreted data. Such work may enable us (i) to add to the general usefulness of our classification which will, however, always remain a compromise, (ii) to compare the character associations themselves more effectively in relation, say, to their adaptive significance, and (iii) to reconstruct more plausibly the phylogenetic history.

In the meantime we have PJ_1, already developing towards PJ_2.* What does it summarize for us in the evolutionary history of the eucalypts and what questions for future investigation does it help to define ? (We shall not here discuss its practical usefulness, important as that is.)

---

* A step in this development is the publication of new taxa and formalization of changes of status foreshadowed in PJ_1, by Johnson and Blaxell (in press, *a* and *b*).

THE CLASSIFICATION ADOPTED

PJ_1 recognizes eight main groups within the eucalypts, which are displayed in Figs 1, 4 and 5 and Table 1. We have arrived at these by agglomeration of similar species and division according to apparent major gaps in the continuity of character variation. They correspond in general to fertility groups. No case is known of successful interbreeding, even to F_1 stage, between any of these groups, although interbreeding is common within groups, and particularly within sections. Fertile intersectional hybrids are also known in a number of cases, but none involve the sections EA, EF, SB, SS, SD or SW. (Hereafter I shall use the code designations of sections and lower taxa, an integral part of PJ_1. The coding for each subgenus is the same as the initial letter of its name.)

TABLE 1

Distributional Synopsis of Eucalyptus *Classification* (PJ_1)

Regions: Q=Queensland, N=New South Wales, V=Victoria, T=Tasmania, S=South Australia, W=southern half of Western Australia, south of 26° S, K=northern half of Western Australia, Y=Northern Territory, M=Malesia (incl. New Guinea). Modal or near-modal values are italicized. For "No. of subseries" a non-subdivided series is counted as one subseries. The columns are additive, the rows are not so because of overlapping distributions (e.g. W and K together total 191 species). Taking superspecies and subspecies levels respectively (rather than species) as units, the totals for the genus would be 316 (superspp.) and 531 (subspp.).

SUBGENUS Section	No. of Series	(No. of Subser.)	Code	Distribution (No. of spp.)									Total Species
				Q	N	V	T	S	W	K	Y	M	
ANGOPHORA			A										[7]
Liberia	1	(4)	AA	5	*7*	1	—	—	—	—	—	—	7
BLAKELLA			B										[9]
Lemuria	1	(1)	BA	*6*	1	—	—	—	—	*6*	*6*	2	9
CORYMBIA			C										[33]
Rufaria	4	(6)	CA	11	5	1	—	2	5	*15*	*14*	2	25
Ochraria	3	(3)	CC	*7*	3	1	—	—	—	—	—	—	8
EUDESMIA			E										[15]
Quadraria	2	(5)	EA	2	—	—	—	2	*9*	4	4	—	10
Apicaria	2	(3)	EF	*4*	1	—	—	—	—	*3*	2	—	5
GAUBAEA			G										[2]
Curtisaria	1	(1)	GA	*2*	—	—	—	—	—	—	—	—	2
IDIOGENES			I										[1]
Gympiaria	1	(1)	IA	*1*	—	—	—	—	—	—	—	—	1
MONOCALYPTUS (=EUCALYPTUS *s. str.*)			M										[91]
Renantheria	9	(26)	MA	15	*64*	23	11	7	14	—	—	—	91
SYMPHOMYRTUS			S										[285]
Equatoria	2	(2)	SB	*2*	—	—	—	—	—	1	1	1	4
(incl. *Howittaria*)			(SS)										
Tingleria	1	(1)	SD	—	—	—	—	—	*1*	—	—	—	1
Transversaria	2	(5)	SE	*10*	*11*	2	—	1	1	—	—	—	14
Bisectaria	18	(23)	SI	4	8	5	—	16	*85*	8?	7	—	93
Dumaria	4	(6)	SL	—	2	2	—	8	*28*	1	—	—	31
Exsertaria	3	(8)	SN	*17*	*15*	5	—	2	2	11	8	3	30
(incl. *Umbrawarria*)			(SQ)										
Maidenaria	2	(11)	SP	9	*35*	24	13	3	—	—	—	—	46
Adnataria	11	(17)	SU	*40*	33	16	—	13	4	9	10	—	65
Sebaria	1	(1)	SW	*1*	*1*	—	—	—	—	—	—	—	1
Total species				136	*186*	80	24	54	149	58	52	8	443

It will be seen that we have included *Angophora* among the eight major groups which we have ranked as subgenera. *Angophora* has traditionally been kept apart generically from *Eucalyptus*. We are not at this stage reducing *Angophora* formally to subgeneric rank, with the consequent new nomenclatural combinations necessary under the International Code of Botanical Nomenclature, but I am myself refraining from this solely to avoid possible reverse changes if all or most of the subgenera are later accorded full generic rank. There are likely to be quite good reasons for the latter step, but certainly not for the over-simplified two-genus proposal of the Carrs, in which "*Eucalyptus*" (*sensu* Carr et Carr) would comprise *Eudesmia*, *Gaubaea*, *Idiogenes* and *Monocalyptus* of PJ_1, while our remaining subgenera (except *Angophora*) would constitute "*Symphyomyrtus*" (*sensu* Carr et Carr). An inspection of Figs 4 and 5 and our suggested groupings in Fig. 1 will make clear the basis for rejecting this (see also Pryor and Johnson, 1971, pp. 16–19).

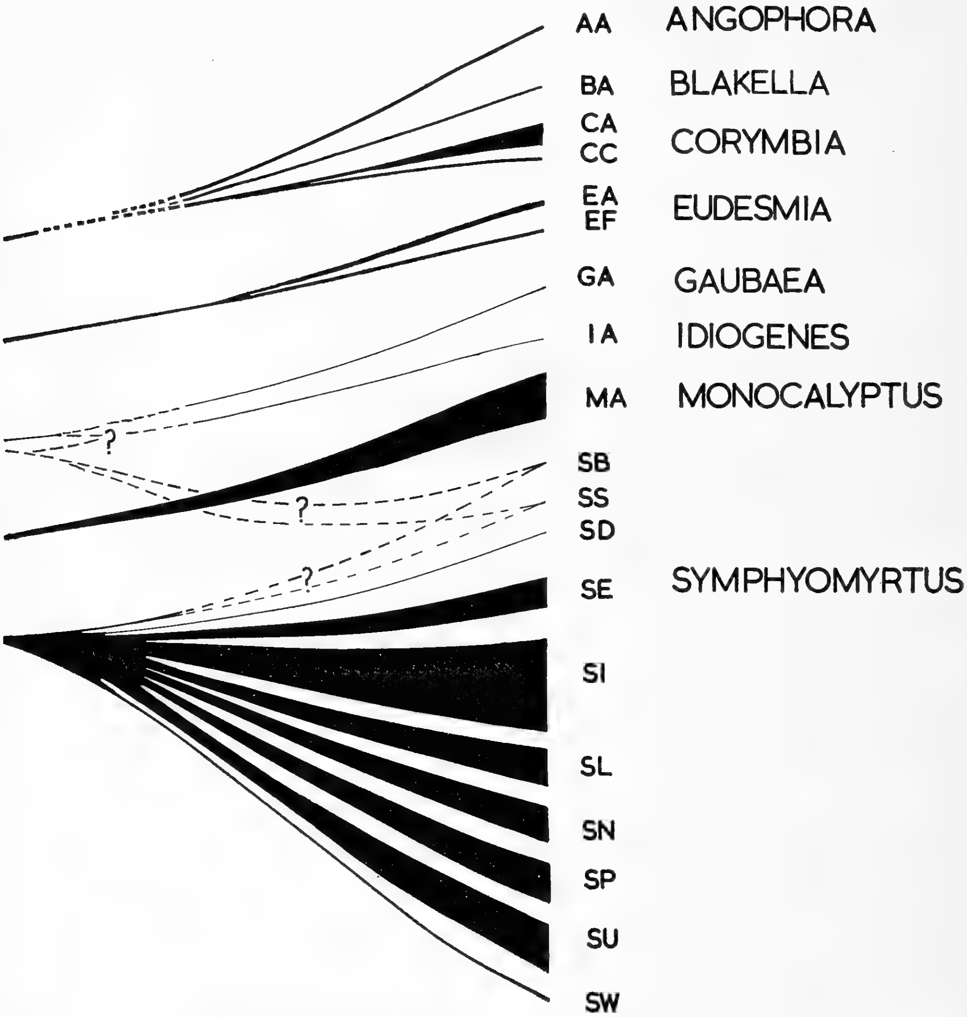


Fig. 1. Suggested general phylogeny of eucalypt subgenera and sections. Widths of branch-ends are in order of, but not proportional to, number of species. Sections designated by their two-letter codes of PJ_1 scheme.

Division of *Eucalyptus* would certainly cause considerable inconvenience, even dismay, amongst those who care little about the relationships, particularly since more than half of the species (including those best known overseas) would fall into *Symphyomyrtus* (*sensu* PJ_1). I consider that the change should not be made until we have a rather better-developed picture of the relationships of the subtribe Eucalyptinae (*Eucalyptus* incl. *Angophora*) with the various groups hitherto referred to the heterogeneous subtribe Metrosiderinae and with other Leptospermoideae.

EVOLUTIONARY TRENDS

Eucalyptus in the traditional circumscription has been characterized chiefly by the operculate flower, and thus distinguished from *Angophora*. [The presence of floral opercula of various kinds in other clearly less closely related Myrtaceae such as *Eucalyptopsis* (perhaps somewhat related), *Acicalyptus*, *Cleistocalyx*, *Piliocalyx* and *Calyptranthes* is obviously due to convergence and is not relevant here except as indicating a certain " prospective adaptation " to this development in the family.] It is clear from comparison of inflorescences, anthers, cotyledons, oil ducts in the pith and elsewhere, leaf-venation, bristle-glands, trichomes, wood anatomy, and the occurrence of pathogens (e.g. *Ramularia*, Walker and Bertus, 1971), some of which are displayed in Fig. 4, that *Corymbia* and *Blakella* are more closely related to *Angophora* than to other subgenera of *Eucalyptus*. I think it virtually certain that these three had a common ancestral stock after their divergence from the other subgenera, as indicated in Fig. 1. Both 4-merous and 5-merous flowers occur in *Angophora* and to convert an *Angophora* into a *Corymbia* requires little more than " operculization " by concrescence of sepal and petal primordia into rings shortly after their initiation, combined with some modification of flowering and fruiting hypanthia and of trichomes. Even in *Angophora* the petals are broad-based and possess thick triangular median regions which are effectively valvate in the bud (though the thinner margins are imbricate). Formation of an operculum from such a flower-structure seems a more likely phylogenetic event than in most Myrtaceae, where the petals have a narrow basal " claw " and are thin-textured throughout. *Arillastrum*, which may be significant in this regard, will be discussed later.

Thus we are led to consider the possible or probable trends in the evolution of various organs or other attributes of eucalypts, and of their association in the several groups. I can deal with these only in summary fashion; further discussion and most relevant references will be found in Pryor and Johnson (1971), and it is assumed that the general morphology of eucalypts is familiar. The opercular structures and the inflorescence are at present perhaps best known, but have been much misunderstood until recently. The trends in these are complex and will be treated first and most fully.

(1) *Opercular Structures.* The range of these is illustrated in Figs 4 and 5. Pryor and Knox (1971) give an account of their development in various groups. One or both perianth whorls are opercular due to formation of a ring meristem, except in *Angophora* and presumably in ancestral forms. In all cases, however separate primordia are present at the initial stages and the separate tips into which these develop are often more or less discernible even in mature buds. Both calyx and corolla are normally tetramerous, each with two decussate pairs of tips, but fives are most common in *Angophora* and may be found in occasional flowers of some species of other subgenera (e.g. in *Gaubaea* and in SUNCC *E. porosa* of *Symphyomyrtus*), while in *Monocalyptus* there is only a single (calycine) whorl with usually only two initial primordia present. It is perhaps conceivable that the opercular condition of the corolla is monophyletic. However, I think this very unlikely in view of the lack of resemblance in other characters between the angophoroid group (subgenera A, B, C) and others, as well as other distinctive

features amongst some of the latter as discussed below. The calycine operculum (where it occurs) *cannot* be monophyletic. Opercular conditions can be classified into the following types (*italicized* letters refer in a complex but mnemonic way to operculum-types; PJ_1 code symbols are in roman):

Type *A*: *Calyx* of free persistent sepals; *corolla* of 5→4 free broad-based petals: Generalized ancestors, also *Angophora.*

Type *E*(*A*)*G*: *Calyx* of free persistent sepals (often small due to early cessation of growth); *corolla* (initially 4-tipped) opercular: *Eudesmia* section EA *Quadraria* (most species, see below): *Gaubaea.* [These derived* *independently* from *early* generalized ancestors of type *A*, not from *Angophora.*]

Type *E*(*F*): *Calyx* of free tips in very early bud but basal meristematic rings of calyx and corolla becoming united early in development, so that the sepal tips (often becoming extremely obscure) are carried high on the operculum of *calyx and corolla*: *Eudesmia* section EF *Apicaria*, also in various intermediate conditions from Type *E*(*A*)*G* in subseries EAAB, EAAC. [Derived from (EA line of) Type *E*(*A*)*G*.] Understanding of the operculum in the species of EF, EAAB, EAAC has come only recently, independently through the investigations of Carr and Carr, Johnson, and Pryor and Knox.

Type *IS*(*B*): *Calyx* of free deciduous sepals pushed off at an early stage by enlargement of the opercular *corolla*: *Idiogenes*, *Symphyomyrtus* sections SB *Equatoria* and SS *Howittaria* (which as discussed below should probably be included in SB), also (probably by secondary phylogenetic reduction and loss of ring-meristem stage of calyx) in some species of section SI *Bisectaria* and again in section SW *Sebaria.* [Derived in I and SB–SS from Type *A* as in early ancestral forms or possibly through a Type *E*(*A*)*G* stage as in *Gaubaea*; probably derived from Type *SBC*(*C*) in SI. In SW it is less likely that the calyx was ever truly opercular.]

Type *SBC*(*C*): *Calyx* opercular, shed before anthesis (sometimes very early), leaving a scar detectable by a break in the cuticle at the rim of the hypanthium in older buds; *corolla* opercular: *Blakella*, *Corymbia* section CC *Ochraria*, most of *Symphyomyrtus* [sections SD *Tingleria*, SE *Transversaria*, most of SI *Bisectaria*, SL *Dumaria*, SN *Exsertaria* (which must include the so-called section SQ *Umbrawarria* of PJ_1), SP *Maidenaria*, most of SU *Adnataria*]. [Derived separately (i) in B and CC from Type *C*(*A*)*S*(*U*) by ontogenetically earlier cessation of growth and abscission of the calycine operculum, (ii) in S from an early ancestral Type *A* condition, but probably not from the *C*(*A*)*S*(*U*) or *IS*(*B*) Types as at present represented.]

Type *C*(*A*)*S*(*U*): *Calyx* opercular and shedding at anthesis with the opercular *corolla*, to which it is more or less intimately appressed [but, unlike *E*(*F*), without primordial fusion between the whorls] to form an apparently single operculum, thus no calyx scar is present before anthesis: *Corymbia* section CA *Rufaria*, *Symphyomyrtus* section SU *Adnataria* in part (series SUJ, SUL, SUN, SUX). [Derived separately, (i) in CA probably direct from an angophoroid Type *A* ancestor, (ii) in SU *on several distinct occasions* from Type *SBC*(*C*) by continued growth of the calycine ring-meristem and delayed abscission (in some species such as SUNAA *E. argophloia* and SUNCC *E. porosa* the calycine operculum may abscind just before the corolline).]

Type *M*: *Calyx* opercular, with usually only two tip primordia; *corolla* completely lacking even as primordia: *Monocalyptus.* [Derived probably separately from other lines at an early epoch, though doubtless through unknown stages from an early Type *A* ancestor; we can only guess at the stage at which

---

* *Derivation* will usually denote phylogenetic change in what follows, while *development* will refer to ontogeny or organogeny, unless the context clearly indicates otherwise.

the corolla was lost—perhaps it was before operculization of the calyx.] The operculum of *Monocalyptus* (≡ section MA *Renantheria*) has been misinterpreted in the past but its nature has recently been established by Pryor and Knox (1971); it is very strong evidence against the hypothesis of Carr and Carr (which a decade ago I also tended in part to favour) of a close affinity between *Eudesmia, Gaubaea, Idiogenes*, and *Monocalyptus* (of PJ_1), and their consequent grouping as "*Eucalyptus*" *sensu* Carr et Carr.

(2) *Inflorescence.* (*a*) *Unit Inflorescence.* The basic inflorescence in the Myrtaceae appears to be thyrsoid, with dichasial branching as one would expect

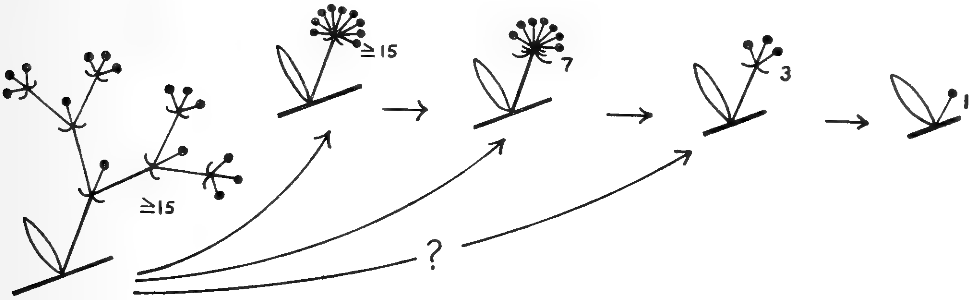


Fig. 2. Derivation of eucalypt umbellasters (unit inflorescences) from an indefinite dichasium. For further explanation see text.

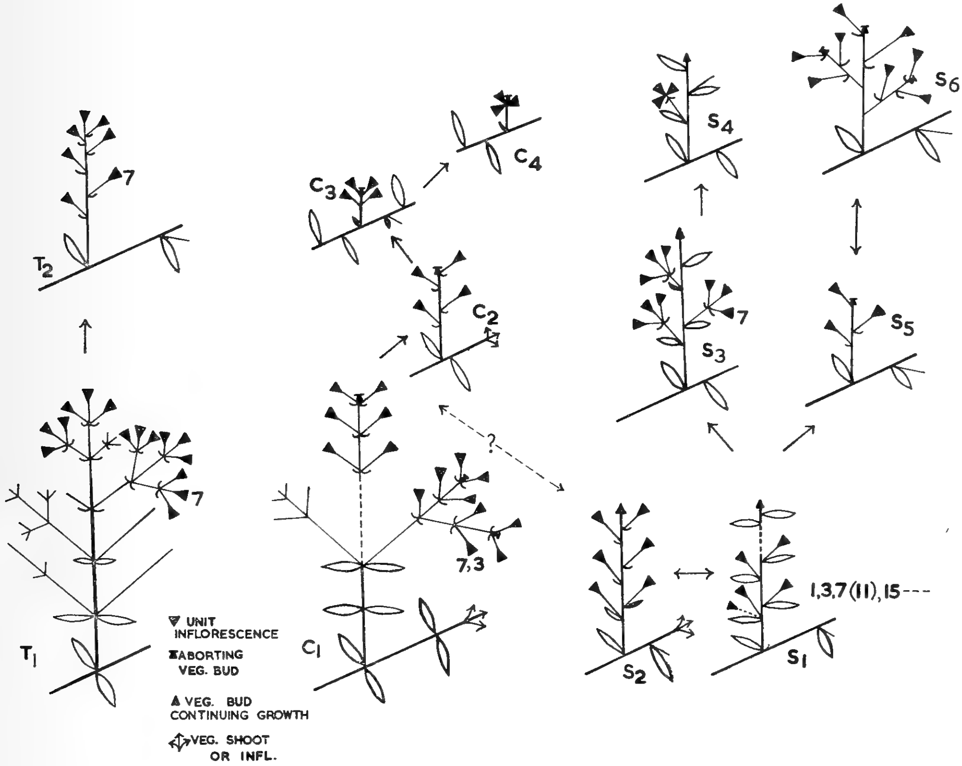


Fig. 3. Conflorescence types of eucalypts, and their suggested derivations. For further explanation see text.

in a family with primarily opposite and decussate phyllotaxy. If we were to take type T_1 of Fig. 3, but suppose the branches to end in individual flowers instead of unit inflorescences, it would correspond in general pattern with such a dichasial thyrse. More or less unreduced inflorescences of this type may be found in many Myrtoideae and in some Leptospermoideae (particularly Metrosiderinae *sens. lat.*), and by a comparative approach one can see how even the highly reduced inflorescences of such genera as *Callistemon* and *Leptospermum*, in their several ways, are derived from dichasial thyrses.

Eucalypt inflorescences are usually described as consisting of " umbels ", but (see Pryor and Johnson, 1971, pp. 2–4 and refs. therein) the basic unit inflorescence is clearly a condensed dichasium, which is itself of course derivable from a thyrse simply by termination of each axis in a flower after the *first* node. The number of flowers (f) in a dichasium is given by $f=2^n-1$, where n is the order of branching attained. Figure 2 illustrates diagrammatically the derivation of the umbelliform cymelets (" unit inflorescences ") from a dichasium (each plane of branching is actually orthogonal to the previous, but the whole is shown in two dimensions in the figure).

I shall coin the term *umbellaster** for such a unit (Latin *umbella*+*-aster*, suffix connoting " sham ", as in " poetaster ", etc.). Umbellasters may contain the full dichasial branching of the various orders, thus differing from a normal dichasium only in the non-elongation of all internodes except the first (peduncle) and the last (pedicel) and sometimes in the partial or complete suppression of bracts of higher orders (the first pair is always present, though deciduous and sometimes fused into a calyptra). Thus for $n=1$, 2, 3, 4, 5 we should have umbellasters with 1, 3, 7, 15, 31 flowers. However, as Carr and Carr (1959) have pointed out, due to crowding and suppression in the umbellaster bud, branching may be monochasial at higher orders, and a familiar case is the 11-flowered umbellaster in which only one flower of each pair is produced at the final branching. Even where the flower number of 15 is found it may be due to two stages of monochasial branching from a dichasium of 7, rather than representing a fourth-order dichasium.

Possibly the umbellaster condition was separately derived more than once from uncondensed dichasia, and indeed umbelliform inflorescences occur occasionally in other Myrtaceae, e.g. some species of *Backhousia*. The most common flower number is 7, with 3 also frequent; phylogenetic reduction in number, sometimes associated with increase in flower- and fruit-size, seems to have been common, but increase to numbers above 15 is also quite likely. Carr and Carr (*l.c.*) object to Pryor's earlier reference to the single axillary flower of some species as " the ultimate stage of reduction from an indefinite dichasial cyme . . . " because of their emphasis on ontogeny, and say that " even from the point of view of phylogeny, Pryor's statement would be misleading ". Pryor's statement *was* made from the point of view of phylogeny (informed by ontogeny), as is my present comment, and if one looks widely at the Myrtaceae it is evident that it is not misleading. The cited paper reports very valuable developmental studies but, in its account (and inferences therefrom) of an aberrant individual of SNEEP *E. camaldulensis* as if it represented a characteristic condition for the species, as well as in its suggestion that the three-flowered umbellaster is primitive even for such groups as *Corymbia*, it shows how ontogeny without a broad comparative and phylogenetically oriented background can be misleading indeed.

There are tendencies to certain flower numbers in some of the sections, and more particularly in some series and subseries, but in general the number in the

---

* This term is explicitly intended to include conditions in which the flowers are sessile. Carr and Carr (1959), like some others whom they cite, extend the term *umbel* to cover the fundamentally different, sympodial umbellaster, but nevertheless exclude the trivial variants in which the pedicels do not elongate.

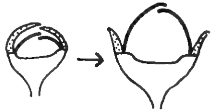
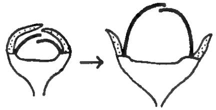
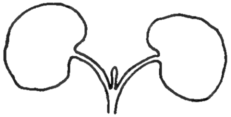
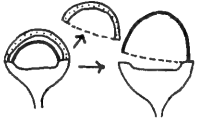
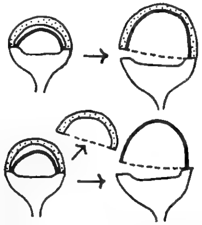
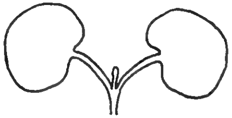
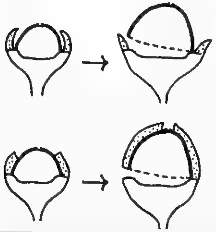
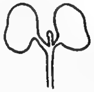
umbellaster seems to be a fairly flexible character evolutionarily, though it is often constant at the species or subspecies level, and especially so in individuals [contrary to the report of variation in SPIAC *E. kitsoniana* by Carr and Carr, *l.c.*, which our evidence does not confirm as the usual condition even in that species]. Various developments of bracts are found, and also the interpolation of an intranode to produce a " stepped " 4+3 umbellaster (as in some species of SU *Adnataria*). Carr and Carr (*l.c.*) may be consulted for descriptions of these, but with caution as to the interpretations. In certain species the apparent " umbels " described by earlier authors are in fact compounds of several umbellasters (see below).

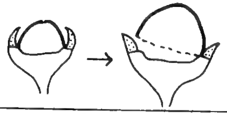
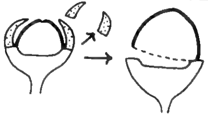
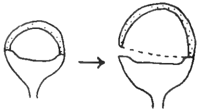
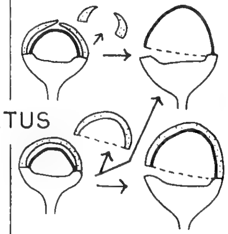
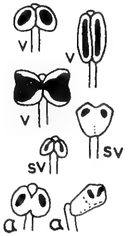
(*b*) *Conflorescence.* As a purist (or pedant ?), I use *conflorescence* in preference to the Graeco-Latin mongrel " synflorescence " (as used by Troll, 1964, and others) to cover shoots or shoot-systems bearing a number of " unit inflorescences ". In many plants one cannot define unit inflorescence and conflorescence in any clearly exclusive way, but this is not a difficulty in *Eucalyptus* if one examines the structures concerned carefully and comparatively.

Figure 3 illustrates broadly the patterns and probable or possible phylogenetic trends in eucalypt conflorescences. The unit inflorescence shown in these diagrams is an umbellaster, and the numerals placed near some of these indicate the most usual flower number in the types concerned. The column " Inflor." in Figs 4 and 5 gives the conflorescence types characteristic of the subgenera (sections are also indicated in *Symphyomyrtus*).

I shall discuss the main trends briefly ; it is to be understood that some of the phylogenetic derivations probably occurred more than once. The diagrams are generalized, and further variations, which may be adaptively important, are found in the number of internodes and development of intranodes (between the two opposed members of a leaf- or bract-pair, leading to a quasi-alternate but still decussate phyllotaxy). Variations occur also in the position of the umbellasters or sometimes conflorescences on a year's shoot growth (*basitonic, mesotonic, acrotonic* from proximal to distal) as discussed by Carr and Carr (1959). These are partly correlated with the various conditions illustrated but, unless leading to a conflorescence of obviously different appearance, are not separately shown in Fig. 3. Duration of bud development also varies, sometimes extending over two years with a marked diapause ; clearly, this is also of adaptive significance in relation to climate.

Type T (" terminal ") conflorescences may well represent a very early separate line from the remainder. In these the main and all other axes terminate in an umbellaster and thus in a flower ; hence the conflorescence is truly a terminal type. The expanded subtype T_1 characterizes the small tropical sections SB *Equatoria* (including the well-known SBA:A *E. deglupta* of eastern Malesia) and SS *Howittaria* (which in PJ_2 may well be included in *Equatoria*). In PJ_1 we have referred these to *Symphyomyrtus* but perhaps they represent a separate phylad as indicated in Fig. 1. The reduced subtype T_2 is found in *Idiogenes* which consists of that notorious bone of contention IAA:A *E. cloëziana*. So far as I have checked, truly terminal conflorescences occur in no other section, although in some species of *Eudesmia* conflorescences of subtypes S_3 and S_4 (see below) may possibly be primitively and not secondarily terminal as I have tentatively suggested. Subtype S_3 structurally resembles a shoot bearing a series of reduced T_2's but, on the general resemblance of species bearing this subtype, I would regard S_3 as a secondary development of S_1. *Idiogenes* (=section IA *Gympiaria*) differs in ovule and seed type from *Symphyomyrtus* whereas *Equatoria* and *Howittaria* do not appear to do so ; thus their mutual affinity is not to be too readily assumed. As mentioned earlier, however, there is a correspondence in operculum type between the three groups with type T conflorescences.

SUBGENUS	FLOWER BUD: YOUNG, ANTHESIS	ANTHER	COTYLEDONS	INFLOR.	OVULE	HAIRS	BRISTLE GLANDS	PITH DUCTS, GLANDS	PSYLLID
[GENERALIZED ANCESTOR]			?	DICHASIAL THYRSE		a?			
ANGOPHORA				C_1	h	a(≥2)	+	D, G	
BLAKELLA				C_2, C_3, C_4	h	r(B),–	+	±D, G	
CORYMBIA				C_1 C_2	h	a(1),–	+	D, G	
EUDESMIA				S_1, S_3, S_4	h	r(E)	–	–, G	G, –

SUBGENUS	FLOWER BUD: YOUNG, ANTHESIS	ANTHER	COTYLEDONS	INFLOR.	OVULE	HAIRS	BRISTLE GLANDS	PITH DUCTS, GLANDS	PSYLLID
GAUBAEA				C_1, C_3	a	–	–	–	–
IDIOGENES				T_2	a	–	–	–	–
MONOCALYPTUS				S_1	a	r(M), –	–	–	S
SYMPHYOMYRTUS				T_1 (SB, SS) S_1 (SE, SI, SL SN, SP, SU) S_2 (SD) S_3 (SNI) S_5 (SU, SW) S_6 (SU)	h	–	–	–, ±G	G, –

Figs 4 and 5. Occurrence of certain features in eucalypt subgenera and sections. "Inflor." column gives conflorescence types as in Fig. 3. "Psyllid" column refers to *Glycaspis* subgenera only (G=subg. *Glycaspis*, S=subg. *Synglycaspis*); other genera of Psyllidae are also found on eucalypts. For further explanation see text.

Type C (" corymbioid ") conflorescences are characteristic of the *Angophora-Blakella-Corymbia* trio, though also found in the quite different *Gaubaea*. Superficially resembling type T, the C_1 subtype especially is often described as terminal and such conflorescences often do in fact mark the end of growth of their shoots. However, all of type C differ fundamentally from type T in that the main and branch axes do not end in umbellasters but in small, aborting, vegetative buds or tips. In the more reduced (derived) subtypes C_2, C_3, C_4 the conflorescence is usually or always borne laterally on a leafy shoot, as seen in series CCC *Maculatae* (the " Spotted Gums "), and in the more reduced *Blakella*. In the latter case the bracts subtending the umbellasters may be lacking, and in some species (e.g. BAA:D *E. grandifolia*) the umbellasters are sessile in a cluster which is itself umbelliform but includes a tiny abortive vegetative tip. Such cluster-like conflorescences were confused with umbellasters (themselves not then understood) and described as " umbels " by Blakely and earlier authors. Blake (1953), who first apprehended the coherence and limits of this group (his *Clavigerae*, a name also used for the single series BAA in PJ_1), appreciated the compound nature but did not make clear the equivalence with the *Corymbia* conflorescence.

Type S (" simple ", despite some secondary derivatives !) conflorescences are the most common (Figs 4, 5) and are characteristic of *Eudesmia*, *Monocalyptus*, and *Symphyomyrtus* (excepting SB and SS). Some of the variants are virtually identical in pattern with variants of type C, with which they share the fundamentally " non-terminal " condition. However, type S (except in a few probably derived cases such as EAADE *E. gamophylla* in *Eudesmia*, and many of section SU *Adnataria* in *Symphyomyrtus*) is distinguished by continued growth of the vegetative tip either during or after flower-bud development, and by the evidently basic condition of simple umbellasters borne in the axils of foliage leaves.

This basic S_1 pattern may well have arisen more than once, probably by reduction from ancestors with simple lateral dichasia in the leaf axils. It is universal in the very well-defined *Monocalyptus*, where it has undergone little secondary change (though the umbellasters themselves range from 3- to >30-flowered) ; it is the most usual condition in *Eudesmia* (umbellasters most commonly 3-flowered but in some species 7- or many-flowered) : it is very widespread in *Symphyomyrtus* (umbellasters very often with 7, quite often with 3 or 11, less frequently with 1 or >15 flowers). Superposed twin umbellasters may be found in some axils, for instance not uncommonly in section SI *Bisectaria* ; these do not show any common rhachis or secondary bracts (so far as I know) and are probably a phylogenetically secondary development associated with the presence of supernumerary axillary buds.

The S_2 condition of the curious " Yellow Tingle ", SDA:A *E. guilfoylei* (the sole species of section SD *Tingleria*) is fairly clearly due simply to reduction of subtending leaves to a bract-like state. Its continuing growth shows it to be basically distinct from the superficially similar " racemes of umbels " of, say, IAA:A *E. cloëziana* (type T_2) and to a lesser degree from the conflorescence of SWA:A *E. microcorys* (type S_5, elongated). *Eudesmia*, as mentioned, shows some odd conditions and the apparent " umbels " in, for example, EAACM *E. jucunda* or EAADA *E. gongylocarpa* are probably clusters of umbellasters of type S_4—but they need further investigation.

In *Symphyomyrtus*, subtype S_3 occurs only once, in SNI:A *E. michaeliana*. This rather perplexing species seems to be closest in leaf-venation, seeds, etc., to the " Red Gums " of section SN *Exsertaria* and its peculiar axillary triads of umbellasters are here tentatively interpreted as a secondary expansion of the S_1 condition by an interpolated dichasial branching. A study of inflorescences in hybrids, if they can be made, may help to elucidate this. *E. michaeliana* needs more study morphologically, chemically, and by breeding experiments to determine whether our hypothesis as to its position is justified. It does not seem to have much in common with SB *Equatoria* and SS *Howittaria* to support any suggestion that its three-umbellaster groups are reduced T-type conflorescences.

In section SU *Adnataria*, the " true Boxes and Ironbarks ", sub-type S_1 is found as well as conditions transitional to, and fully characteristic of, sub-types S_5 and S_6. These are the " terminal, paniculate inflorescences " of the older describers of the species concerned. The condition like T_1 and C_1, yields a massing of flowers towards the ends of the branches and doubtless has adaptive significance. Its derivation from S_1 is clear, as is that of section SU from the basic stock of *Symphyomyrtus*. The " Tallow-wood ", SWA : A *E. microcorys* (constituting section SW *Sebaria*) has a similar inflorescence but is an isolated species whose links with the rest of *Symphyomyrtus* are still obscure.

The remaining features to be mentioned require, or allow, only a briefer treatment. References are given only when they are not covered in Pryor and Johnson (1971) or otherwise need special mention.

(3) *Androecium.* (*a*) *Anthers.* Figures 4 and 5 summarize the anther types, which are more fully illustrated by Blakely (1934, 1965). The attachment of the filament to the connective is not shown, but the primitive dorsal attachment and versatile condition is indicated by the letter " v ", and is retained in all groups except some sections of *Symphyomyrtus*. Here more basal attachment and the semi-versatile condition are associated with the series SIX *Calycogonae* (left anther of " sv " pair in Fig. 5) and SIZ *Foecundae* (right anther of " sv " pair) of section SI *Bisectaria*, while completely adnate anthers with more or less pore-like openings are characteristic of section SU *Adnataria*. The usual (" porantheroid ") condition in the latter is as in the left-hand of the " a " pair, but in the three series SUT *Polyanthemae*, SUV *Paniculatae*, and SUX *Melliodorae* the so-called " terminales-type " anther (right-hand of the " a " pair) is found. No breeding barrier exists between species with these two anther types, and the division on anthers cuts across that on persistence of calycine operculum [see above under operculum-type *C*(*A*)*S*(*U*)]. Hence until more information is available on other characters we cannot say whether the anther or the operculum condition (or both) arose more than once.

The generalized " macrantherous ", versatile anthers with long, separate dehiscence-slits are variously shortened in some series but these variants are not separately shown. Small anthers with short, somewhat divergent loculi (top left of *Symphyomytus* group) are found in SB and SS, the *Equatoria-Howittaria* group, which may need to be excluded from *Symphyomyrtus*. A unique, specialized anther type (bottom " v " of *Symphyomyrtus* group) characterizes the single species of SD *Tingleria*. The " renantherous " type with the loculi confluent at the top was once thought to be a defining character for the " *Renantherae* ". From these the sections SB and SW have now been removed, and it has been shown that the bulk of the " *Renantherae* " belong together with a few species (series MAA *Preissianae*) which exhibit the primitive " macrantherous " anther type, and also with some intermediates (series MAB *Diversifoliae*) in *Monocalyptus* (in which PJ_1 recognizes only a single large section MA *Renantheria*). Thus the renantherous anther type is of later origin than the separation of the *Monocalyptus* line.

(*b*) *Other androecial features.* Other features of the androecium are also useful in classification and of evolutionary interest but can only be mentioned. They include (i) the so-called *staminophore* (*androphore* would be a happier term) or staminal ring, (ii) the grouping of stamens into four clusters evident in many *Eudesmia* species and occasionally elsewhere, e.g. in SW *Sebaria*, (iii) the development or otherwise of oil-glands in the filaments [a nice series is shown, for instance, from MAA *Preissianae* (abundant, large glands) through MAB

Diversifoliae (few, small glands) to other series of *Monocalyptus* (without glands)], (iv) the more or less staminodial condition of the outer stamens in certain groups, e.g. EAAD *Odontocarpinae*, SIX *Calycogonae*, SUJ *Ochrophloiae*, SUV *Paniculatae*, and SUX *Melliodorae*, a feature which has clearly had multiple origins, (v) various conditions in the flexure of filaments, which are inflexed in young buds even if straight in mature buds with long opercula such as those of SICB *Cornutinae*, and in the apposition of anthers to the disc* (e.g. in SL *Dumaria*).

The detailed study of pollen by electron microscopy may yield information of classificatory and possibly phylogenetic value. Pollen-morphological examination with the light microscope has not been very helpful in *Eucalyptus*.

(4) *Gynoecium and Associated Features.* (*a*) *Ovary, style, etc.* No discussion of these features is yet possible which would be of much taxonomic or phylogenetic significance, except as treated under (*b*). We may look hopefully to others currently studying the development and morphology to bring forth some illuminating discoveries in this field.

(*b*) *Ovule and seed.* Arrangement of ovules and ovulodes on the placenta has been studied by Carr and Carr (1962, 1963) and may prove to have considerable value in elucidating phylogenetic relations within *Eucalyptus*, and also between particular groups of *Eucalyptus* and other genera, as mentioned below under the discussion of possible polyphylesis. I have not yet examined placentation and ovule arrangement extensively and cannot comment upon them in detail.

Two basic ovule types, the *anatropous* and the *hemitropous*, are found in the eucalypts (Gauba and Pryor, refs. in Pryor and Johnson, 1971) and are associated with certain seed characters, especially the presence of a raphe in the anatropous type, as one would expect. These and other seed characters, notably the varying degree of development of the inner epidermis of the outer integument as a crystal epithelium, cannot be elaborated here. They strongly support the PJ_1 scheme, especially in the complete separation of *Gaubaea* from *Eudesmia*, the inclusion of EFC *Miniatae* in *Eudesmia*, the affinity of *Angophora*, *Blakella*, and *Corymbia*, and the marked difference between those three and both *Eudesmia* and *Gaubaea*. Sectional groupings within *Symphyomyrtus* are also supported by seed characters but these need more study. Ovule and seed types appear to associate *Idiogenes* with *Gaubaea* rather than with SB *Equatoria* and SS *Howittaria*, although *Idiogenes* resembles these latter in its T-type conflorescence and Type *IS*(*B*) operculum. Further comparisons may tell us in which of these characters convergence must be invoked.

Figures 4 and 5 show only the anatropous-hemitropous distinction ; the anatropous is most general in Myrtaceae but campylotropous or hemitropous ovules do occur elsewhere in the family, for instance in *Arillastrum* (Dawson, 1970, and see below). Most interestingly, the seeds of GAA : A *E. curtisii* are extremely similar externally and anatomically to those of *Tristania conferta*. *Tristania* as currently recognized is a heterogeneous group and should probably be split into three genera. Clearly, the resemblances and differences between *Gaubaea* (and other subgenera) and the components of *Tristania* and their allies will need much deeper investigation. It is of course not necessarily the case that either all the hemitropous or all the anatropous subgenera belong together phylogenetically.

(*c*) *Fruit* (*including fruiting hypanthium*). Features of the fruits are of course used a great deal in distinguishing and circumscribing the species and subspecies of *Eucalyptus*, and many of these features run through series, sections, or even subgenera. It is easy, for instance, to recognize an *Angophora*, a *Blakella*,

---

* Carr and Carr prefer to term this the nectary ; it is nevertheless a floral disc in the general sense in which that term is employed in taxonomic description.

or a *Corymbia* by its fruit and, on a lower level, the fruits of *Monocalyptus* series MAH *Capitellatae* (the " true Stringybarks ") are all patently variations on a theme, as are those of *Symphyomyrtus* series SIC *Cornutae* or SIT *Oleosae*. It has not as yet been so easy to describe or define the whole congeries of characters which hold the major groups together, or to discern trends which may be phylogenetically interpreted.

(5) *Cotyledons.* These will not be discussed in detail. Some idea of the types characteristic of the subgenera is given in Figures 4 and 5. The angophoroid group A, B, C clearly hangs together and so do the sections of *Symphyomyrtus* with their emarginate (bilobed) cotyledons (though the dubiously included SB and SS need to be checked). The right-hand figure for *Symphyomyrtus* shows the " bisected ", Y-shaped cotyledons characteristic of the large section SI *Bisectaria* for which other positively uniting characters are still being sought, though the process of taxonomic agglomerative clustering (on a non-numerical basis at present) tends to associate the various series of this section. Y-shaped cotyledons occur also in SLUBA *E. dundasii*, which on other features appears to belong to section SL *Dumaria*, a group which seems to have radiated in parallel with *Bisectaria* but has retained the broader, bilobed cotyledons of the rest of *Symphyomyrtus*. The description by Carr and Carr of certain small outgrowths as cotyledonary stipules is open to further study and interpretation. Stipules are not a general feature of Myrtaceae.

(6) *Emergences.* (*a*) *Trichomes* ("*hairs*"). Hairs are found on various organs, most often juvenile shoots and leaves but also sometimes on adult shoots and even inflorescences and hypanthia. They need detailed anatomical study and their significance cannot be fully assessed.

Type " a " (Figs 4, 5) comprises " angophoroid " hairs arising singly from undifferentiated parts of the epidermis. They are either uniseriately several-celled as in *Angophora*, or single-celled and very short as in *Corymbia*. I have not found hairs of this type in *Blakella*.

Type " r " comprises radiating uniseriate hairs which arise in clusters from more or less raised oil glands. Three sub-types are recognizable at sight but not yet accurately described or analysed; I suspect that they have arisen independently in the course of phylogeny. They are found as follows: (i) subtype " r(B) " (blunt-ended, 1- or 2-celled, rather thin-walled hairs, often almost erect, on prominent glands or bristle-glands) in some species of *Blakella*, e.g. BAA : H *E. gilbertensis*. (ii) Subtype " r(E) " (blunt-ended, of rather thin-walled cells, on slightly prominent or flat glands) on juvenile shoots of all species of *Eudesmia*. (iii) Subtype " r(M) " (acute-ended, of rather thick-walled cells, on prominent glands) on juvenile shoots of all species of series MAH *Capitellatae* (these are the so-called " stellate hairs " of the Stringybarks) and of an undescribed species from south-eastern New South Wales (discovered after publication of PJ_1) which may require the establishment of a new series or subseries in *Monocalyptus*. Somewhat papilliferous raised glands are found on a few species (e.g. MAKCA *E. regnans*) of series MAK *Obliquae*, and these may be regarded as morphologically transitional between the " r(M) " condition and the hairless state of most of *Monocalyptus*. Hairs are reported from a few species of *Symphyomyrtus*; the report by Maiden for SUABB *E. leptophleba* is false and evidently due to mixture of material, that for SICBE *E. lehmannii* is based on blunt several-celled papillae on the surfaces of glands. Significantly, hairs are absent in *Gaubaea* and *Idiogenes*, which were referred to *Eudesmia* (as "*Eudesmieae*") by Carr and Carr as recently as 1970 (see Pryor and Johnson, 1971 for discussion). Trichomes closely resembling the various eucalypt types do not seem to occur in other genera of the Myrtaceae, but simple hairs of rather different types are quite common in many genera.

(*b*) *Bristle-glands.* These (Figs 4, 5) are characteristic of the angophoroid trio *Angophora*, *Blakella*, and *Corymbia*, and are essentially elongated protruding oil glands, with a multicellular wall. In *Blakella* they are very thin and may superficially resemble simple trichomes, which has led to misdescription of species of this group. Some degree of elongation of raised oil glands occurs in other species and in young seedlings of MAKAA *E. obliqua*, for instance, these are quite bristle-like, though doubtless representing a parallel or convergent development. *E. obliqua* is quite unlike the angophoroids in other respects.

(7) *Oil Ducts and Glands in the Pith.* These are described by Carr and Carr (refs. in Pryor and Johnson, 1971) and are distributed as shown in Figs 4 and 5 (information partly from Carr and Carr, partly new observation). Once again the angophoroid A, B, C are linked, by the possession of oil ducts in the pith. Presence or absence of glands may be a fairly regular feature in some sections or series (e.g. most of the first half of the series of SI in the PJ_1 arrangement have pith glands, whereas SIP–SIZ inclusive lack them ; most of SL have pith glands ; SE, SN and SP lack them) but in other cases there is considerable variation even within series (as in those of SU). They are absent altogether from *Gaubaea*, *Idiogenes*, *Monocalyptus*, and SB *Equatoria* and SS *Howittaria*. In SP *Maidenaria* oil glands are reported in the secondary bark of older trees of most species but not quite all ; this feature appears to be peculiar to the section.

It is difficult to interpret these conditions in terms of trends (or adaptations) but they do aid in a polythetic classification. It should be remembered that oil glands are almost always present in the primary cortex and in leaves and some floral parts.

(8) *Chemical Features.* (References will be found in Pryor and Johnson, 1971, and in works cited therein).

(*a*) *Terpenes and other essential oil constituents.* This is a classical field in eucalypt chemotaxonomy, and indeed the work of R. T. Baker and H. G. Smith and their successors is classical in chemotaxonomy generally. The patterns tend to support PJ_1 but caution is necessary in interpretation, due to the possibility of switches in metabolic pathways which may be determined by quite simple genetic changes, and not necessarily very rigidly stabilized by selection so far as the oil constituent end-products are concerned. Information is hoped for soon on such critical groups as *Gaubaea*, *Idiogenes*, SB *Equatoria* and SS *Howittaria*.

(*b*) *Polyphenols.* The information in this field, due chiefly to the work of Hillis, has been presented according to Blakely's classification, and in a few critical cases is based on material of doubtful identification. I hope chemists will review it in relation to PJ_1 to see what light is shed thereby, and that they may be able also to interpret the significance of occurrences more clearly in the light of increased knowledge of biochemical pathways. At present I can only say that PJ_1 appears to be supported in general, especially in relation to the delimitation of *Monocalyptus* which contains (though not invariably) the distinctive substance renantherin.

(*c*) *Leaf waxes* (*chemistry and shape of cuticular deposits*). As pointed out by Pryor and Johnson (1971) this has proved a disappointing field, despite the thorough studies by Hallam and Chambers. Although there is a general fit to the broad classification of PJ_1, there is evidence of much parallelism, and the shapes revealed in the electron-micrographs seem often to be associated simply with glaucous *versus* non-glaucous conditions as seen with the naked eye, different types being found in obviously closely related species which are often within a single superspecies.

(*d*) *As reflected by host-insect associations.* This field has not been at all thoroughly surveyed but the large, lerp-forming genus *Glycaspis* (Hemiptera: Psyllidae) has been intensively studied taxonomically by Moore, and its associations are interesting at the subgenus level. No *Glycaspis* at all is known from *Angophora*,* *Blakella* or *Corymbia*, although one subgenus, *Boreioglycaspis*, is found on *Melaleuca*, which is only rather remotely related to any eucalypt. *Gaubaea* and *Idiogenes* are insufficiently examined but no *Glycaspis* is recorded from those subgenera either. The type subgenus *Glycaspis* occurs widely on *Symphyomyrtus* (no information from SB–SS, SD, and no record from SW although this has been searched) and on a few species of *Eudesmia* (both EA and EF) as well as, oddly enough, on *Tristania conferta* (which does *not* seem to be related to these eucalypt groups—see above). On the other hand the numerous species of subgenus *Synglycaspis* are confined to *Monocalyptus*. At sectional and lower levels in the eucalypts the occurrences of *Glycaspis* species seem to me to have much less taxonomic significance, and I would certainly not agree with Moore's suggestions that eucalypt-*Glycaspis* associations throw doubt on eucalypt relationships which are firmly established on other grounds. One can hardly do this when one finds the same *Glycaspis* species on species of SI and SU (e.g. *G. repentina*) or even of EA and SN (on both of which *G. onychis* occurs).

One could go on to discuss other features, e.g. wood and bark anatomy, leaf venation patterns, fungal pathogen susceptibility (such as the association of *Phytophthora cinnamomi* and *Monocalyptus*, or *Ramularia* and the angophoroids), epidermal anatomy (a possibly promising field in which work has begun by scanning electron microscope techniques by the Carr group and others). But this would not add much to the picture at this stage. Neither would the scanty fossil evidence, which provides no detailed background of the phylogenetic history. Chromosome numbers are depressingly constant (see Pryor and Johnson, 1971).

DISTRIBUTION OF GROUPS AND CHANGES IN THE CLASSIFICATION

Distributions of the subgenera and sections are of interest and are shown in a general way in Table 1. It would perhaps be better to use phytogeographic divisions rather than States, but to do so would have involved difficulties of compilation.

Table 1 is compiled to recognize some small changes from PJ_1; we know a little more about some distributions, and with further study have altered our views on a few species and subspecies. Apart from the species mentioned above under " Trichomes ", the most interesting specific case concerns *E. pachycalyx*, referred with doubt in PJ_1 to the synonymy of SNABAA *E. alba* [ssp. *alba*], in the absence of the Type specimen (apparently lost while on loan some twenty years ago) or any other material. *E. pachycalyx* has now been rediscovered and, having examined twigs, leaves, buds, flowers, fruits, seeds and cotyledons, I am convinced that it belongs in section SI *Bisectaria*. I here assign it the code SIQ:E, placing it in series SIQ *Squamosae*, although it differs in bark type and other details from SIQ:A *E. squamosa*, the other strictly eastern member of *Bisectaria* [SIR:E *E. bakeri* is merely the eastern vicariant of the central and western SIR:A *E. jutsonii* s. lat.]. It is most remarkable to find a true *Bisectaria* in north-eastern Queensland, adding to the mystery of why this species and *E. squamosa* should have reached the humid east. In other series of *Bisectaria* only eremaean species appear to have crossed the continent. Likewise, why did *Bisectaria* radiate and flourish so exceedingly in the west while its *Squamosae* representatives (which are hardly primitive in the section) barely hang on in the east?

Another change from PJ_1 is the elimination of section SQ *Umbrawarria*. I am now convinced that its sole species, *E. umbrawarrensis*, is closely related to

---

* Except one very doubtful record of subgenus *Glycaspis* on BAA:A *E. tessellaris*.

SNABG *E. brevifolia*, and assign it the new coding SNABI. Further, " SLI:G *E. comitae-vallis* " is in fact, so far as the Type specimen is concerned, a probable hybrid : SLI:I *E. concinna* × SLUAA *E. ovularis* (syn. *E. cylindrocarpa*, not the undescribed SLUAC to which the name " *E. ovularis* " has been misapplied in Western Australia). *E. brachycorys* is not, then, a subspecies of " SLI:G " but appears to be a member of series SLU *Dundasianae* subseries SLUA *Ovularinae*, and I here assign it to the coding SLUAK (Mr. M. I. H. Brooker, pers. comm., suggested this affinity for *E. brachycorys*, and I agree with it).

A question for the future will be to determine whether there are general adaptive tendencies in the several sections and subgenera which are linked to their present distributions and the climates and conditions of their geographic origins, if those can be determined.

Are the Eucalypts Polyphyletic ?

Elevation of some or all of the subgenera to generic status would be obligatory, at least in my view, if we were to become convinced that their phyletic relationships lay more closely with other genera of the Myrtaceae than with each other. I suspect that this may in fact be so.

It is possible, as we have seen, that *Gaubaea* is related to *Tristania*, while *Angophora-Blakella-Corymbia* may well be more closely related to *Arillastrum* (*Spermolepis*), a very interesting New Caledonian genus studied by Dawson (1970). Dawson has shown that *Arillastrum* should not be placed in Metrosiderinae if that subtribe is reasonably restricted in its content and circumscription. Unlike the *Metrosideros* alliance, *Arillastrum* has stamens (some staminodial) in many whorls, ovulodes as well as normal ovules and these arranged in a definite pattern, campylotropous ovules (not very different from the " hemitropous " type of some eucalypts), a crystal layer in the seed-coat, and broad reflexed cotyledons. The petals are not as broad-based as in *Angophora* but are less clawed than in many Myrtaceae and have a median thickened area. I emphatically do not suggest that *Arillastrum* is to be regarded as representing any kind of ancestor of any group of eucalypts ; nevertheless it shares a number of characters with several of the " hemitropous " set of eucalypt subgenera, although it differs variously from all of them. Dawson has pointed out that *Tristania* (s. lat.), and *Xanthostemon* also, should be separated from the *Metrosideros* group, although they have retained the anatropous ovule condition. *Eucalyptopsis*, which resembles eucalypts in seeds, cotyledons, and of course in having an operculum, may also be related to some of the eucalypt lines.

Correlation of the results of Dawson's continuing work with that of students of " *Eucalyptus* " (I dare now to put it in quotes !) should be of the greatest interest to the phyletic taxonomist and to the phytogeographer. We must, I think, seek the origins of the eucalypt lines near the very roots of subfamily divergence in the Myrtaceae, although I would not support the suggestion of Pilipenko (1962) that " *Eucalyptus* " is derived from " *Eugenia* " (itself a heterogeneous assemblage) ! If the eucalypts are indeed polyphyletic in this broad (subtribal) sense, then they present an even more remarkable example of parallel and convergent evolution, presumably in response to environmental selection, than has been thought.

Conclusion

I have discussed with varying degrees of sketchiness some of the observed characters and the apparent trends in them, in relation to the PJ_1 classification. Naturally I consider that they support this classification, within the general limitations of classifications as discussed at the beginning of this address. If I did not, then I should change the classification, and have indeed suggested some possible changes for checking. The suggestion of polyphylesis from rather widely separate origins is, I suppose, the most radical and far-reaching, but it calls for more substantial evidence before incorporation into the formal system. Uncertainty at this level does not vitiate the detailed system at lower levels.

Space is lacking here to recapitulate the various and complex hypotheses involved ; they are implicit in PJ_1, to some extent in Fig. 1, and in the foregoing discussion—and they can be dragged into the light by those who will, I hope, help to investigate them.

As a gratuity to those critics who regard speculation as a scientific sin, I refer them to the quotation from A. N. Whitehead which is the ironic text for this address. I am not very attracted by formalism and rigidity in science (though I am grateful that there are some who are) and would venture that even in the Queen of the Sciences mathematicians of insight and wide-ranging interest would agree that somewhat imprecise visualization of things as a whole, and gathering of many threads of thought and fact, can be as profitable as the equally necessary punctilious following-through of detail. In this small field of eucalyptology, such a two-pronged approach should also be productive. We have generated some hypotheses—it is for the next few years to show how good or bad they are.

ACKNOWLEDGEMENTS

I thank Professor L. D. Pryor, Mr. D. F. Blaxell, and Mr. M. I. H. Brooker for providing information ; Dr. Barbara G. Briggs read and constructively criticized the manuscript, and I am also grateful to her as well as to Mrs. Jennifer Walsh for assistance with the figures.

References

BLAKE, S. T., 1953.—Studies on northern Australian species of *Eucalyptus*. *Aust. J. Bot.*, 1 : 185–352.

BLAKELY, W. F., 1934.—" A Key to the Eucalypts." 1st ed. (The Worker Trustees, Sydney.)

————, 1965.—" A Key to the Eucalypts." 3rd ed. (Commonwealth of Australia Forestry and Timber Bureau, Canberra.)

CARR, D. J., and CARR, STELLA G. M., 1959.—Developmental morphology of the floral organs of *Eucalyptus*. I. The inflorescence. *Aust. J. Bot.*, 7 : 109–141.

————, and ————, 1962.—Natural groups within the genus *Eucalyptus*. *In* " The Evolution of Living Organisms." (Symposium.) (Royal Society of Victoria, Melbourne.)

CARR, STELLA G. M., and CARR, D. J., 1963.—The taxonomic position of certain eucalypts. *Proc. Roy. Soc. Vict.*, 77 : 207–216.

DAWSON, J. W., 1970.—Pacific capsular Myrtaceae. I. Reproductive morphology of *Arillastrum gummiferum* Panch. ex Baillon (New Caledonia). *Blumea*, 18 : 431–440.

GHISELIN, M. T., 1969.—The principles and concepts of systematic biology. *In* " Systematic Biology ", 45–55. (National Academy of Sciences, Washington.)

HULL, D. L., 1967.—Certainty and circularity in evolutionary taxonomy. *Evolution*, 21 : 174–189.

JOHNSON, L. A. S., 1968.—Rainbow's end : the quest for an optimal taxonomy. (Presidential address.) PROC. LINN. SOC. N.S.W., 93 : 8–45.

————, 1970.—Rainbow's end : the quest for an optimal taxonomy. *Syst. Zool.*, 19 : 203–239. (Reprint of Johnson, 1968, with addendum.)

————, and BLAXELL, D. F., in press *a*.—New taxa and combinations in *Eucalyptus*—I. *Contrib. N.S.W. natn. Herb.*, 4 (No. 5).

————, and ————, in press *b*.—New taxa and combinations in *Eucalyptus*—II. *Contrib. N.S.W. natn. Herb.*, 4 (No. 6).

LANCE, G. N., and WILLIAMS, W. T., 1967.—A general theory of classificatory sorting strategies. I. Hierarchical systems. *Computer J.*, 9 : 373–380.

PILIPENKO, F. S., 1962.—Proiskhozhdenie i ėvoliutsiia roda ėvkalipt. (The origin and evolution of the genus *Eucalyptus*). *Bot. Zhurn.*, 47 : 188–201.

PRYOR, L. D., and JOHNSON, L. A. S., 1971.—" A Classification of the Eucalypts." (Australian National University, Canberra.)

————, and KNOX, R. B., 1971.—Operculum development and evolution in eucalypts. *Aust. J. Bot.*, 19 : 143–172.

TROLL, W., 1964.—" Die Infloreszenzen ", 2, pt. 1. (Fischer, Stuttgart.)

WALKER, J., and BERTUS, A. L., 1971.—Shoot blight of *Eucalyptus* spp. caused by an undescribed species of *Ramularia*. PROC. LINN. SOC. N.S.W., 96 : 108–115.

WILLIAMS, W. T., unpub. 1971.—Principles of clustering. (MS.)

Note : For other authors mentioned in the text without dates the references (sometimes numerous) will be found in Pryor and Johnson, 1971.

A BROODING ECHINOID FROM TASMANIA

ALAN J. DARTNALL
The Tasmanian Museum, Hobart, Tasmania

[Accepted for publication 15th September 1971]

Synopsis

A brooding species of echinoid which belongs to the genus *Pachycentrotus* is described. It is of interest because only one other non-cidaroid, regular urchin is known to brood its young. The species is also endemic to the Maugean marine fauna of south-eastern Tasmania.

INTRODUCTION

The sea urchin genus *Pachycentrotus* was erected by H. L. Clark (1912) to accommodate *Sphaerechinus australiae* A. Agassiz. The genus is restricted to the waters of south and south-eastern Australia and, hitherto, was considered to contain only the one species. A further species considered to belong to the genus is described below.

Family STRONGYLOCENTROTIDAE

Genus *Pachycentrotus* H. L. Clark, 1912

Pachycentrotus bajulus sp. nov.

Description of Holotype

A small echinoid with a slightly depressed test; *hd.* =33 mm., *vd.* =21 mm. The diameter of the apical system is 10·6% *hd.* and the diameter of the peristome is 30% *hd.* Viewed from above the test looks like a rounded pentagon because the ambulacral areas are slightly inflated and project beyond the level of the interambulacra.

There are 22–23 plates in each column of the ambulacra. Each plate carries a large, centrally placed primary tubercle which increases in size from the apical system to about the eighteenth plate and then becomes smaller as the ambulacra approach the peristome. Two other tubercles are distinct features of the ambulacral plates (Fig. 1 (*b*)). Firstly, one tubercle is set on the lateral apex of the ambulacral edge of the plate, and secondly, a tubercle is situated beside and below the large primary tubercle and between that tubercle and the poriferous area of the plate. Other small tubercles are present on the ambulacral plates, two or three being present on the plates near the apical system and about sixteen on the largest ambulacral plates. Most of the ambulacral plates are perforated by four pairs of pores arranged in an arc of three pore-pairs on the outside edge with the extra pair placed towards and below the primary tubercle of each plate. Towards the periproct and peristome only three pairs of pores are present, two at the edge and one inset. On preliminary examination it appears that the pore-pairs are arranged in arcs of three or four because the inner pair of pores of the preceding plate is aligned with the outer pore-pairs of the following plate.

There are 18–19 plates in each column of the interambulacra. Each interambulacral plate carries a large primary tubercle towards the lower edge of the plate (Fig. 1 (*a*)). The arrangement of smaller primary and secondary tubercles is also shown in the figure. The tubercles on the test are all smooth and imperforate.

The apical system of the holotype is illustrated in Fig. 2. The genital and ocular plates each carry a large primary tubercle similar to those found on the ambulacral and interambulacral plates. Ocular plates II and III are exsert,

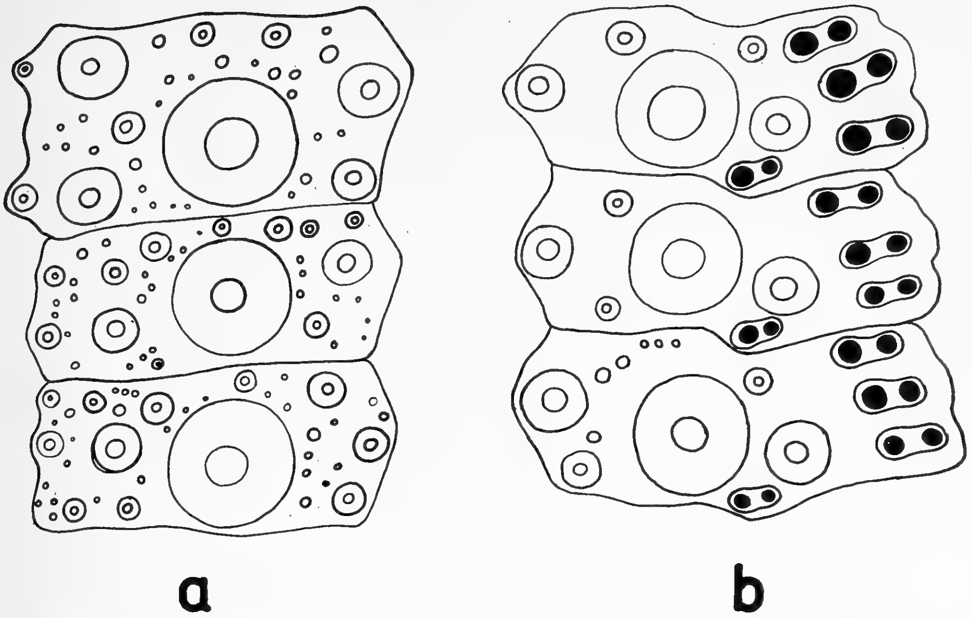


Fig. 1. *Pachycentrotus bajulus* sp. nov. (*a*) Interambulacral plates 6–8 from apical system. (*b*) Ambulacral plates 6–8 from apical system.

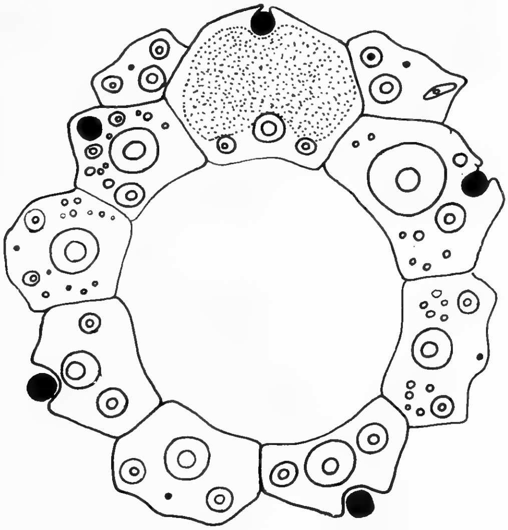


Fig. 2. *Pachycentrotus bajulus* sp. nov. Genital and ocular plates.

the remainder insert. The madreporite occupies most of genital plate II and is inflated, projecting above the level of the other ocular plates. In the holotype the periproctal plates are lost. About a dozen, irregularly arranged, imbricate plates are present in a denuded specimen of 20 mm. *hd*. The anus is situated to one side of the periproct.

The peristomial membrane carries numerous small slightly imbricating plates and ten ovoid, perforate plates for passage of the buccal tube feet. Small open gill slits are present at the perimeter of the peristome.

The primary spines are about 6 mm. in length, possess a milled ring at the base, and are longitudinally ridged. Most are about twice as broad above the milled ring as at the tip and commence to taper about halfway along the spine. Some of the primary spines are slightly expanded at the tip. The secondary spines are about 2 mm. in length, are slightly thorny along the longitudinal ridges, and are more club-shaped than the primary spines. Large globiferous pedicellariae are common. Tridentate, ophiocephalous and two kinds of triphyllous pedicellariae are also present (see Fig. 3).

Colour. The interambulacral plates and the imperforate parts of the ambulacral plates are pale green. The colour is most intense around the apical system and fades away until, close to the peristome, the test is the off-white colour common to the poriferous areas. The madreporite is buff coloured. The primary spines are variously banded with dull violet-brown and green and the tips of the spines are white.

Type locality. Darlington Beach, Maria Island, off the east coast of Tasmania. Latitude 42° 44′ S. Longitude 149° 05′ E.

Holotype. A dried, partially denuded specimen from the type locality. Taken at low tide under rocks, 15.iv.1968. Coll. A. J. Dartnall, Tasmanian Museum Reg. No. H603.

Paratypes. One dried specimen with 17 young amongst the spines of the test (Tasmanian Museum Reg. No. H604), four spirit specimens (T.M. Reg. No. H605), and three spirit specimens (Australian Museum Reg. No. J7801). All taken from under stones at low tide. February, 1948, Eaglehawk Neck, S.E. Tasmania. Coll. V. V. Hickman.

One dry specimen from Eaglehawk Neck, Tasmania, 27.i.1928, coll. W. Irwin Smith (Australian Museum Reg. No. J6393).

Three spirit-preserved specimens from under stones at low tide, Adventure Bay, Bruny Island, S.E. Tasmania ; 6–15.i.1937, coll. V. V. Hickman (National Museum of Victoria Reg. No. H155).

Etymology. The specific name is derived from the Latin masculine noun *bajulus*, meaning porter, in reference to the brooding habit of the animal.

Affinities. *Pachycentrotus bajulus* is most clearly related to *Pachycentrotus australiae* (Agassiz). I have not seen any specimens from Tasmania which I would refer to *P. australiae*. One of the Tasmanian specimens described by H. L. Clark (1938, p. 404) is certainly *P. bajulus* (this is paratype J6393), but I have not seen the remainder of the series. Comparative comments here rest on the information in the literature and two specimens of *P. australiae* from the collections of the South Australian Museum.

P. bajulus is a smaller animal than *P. australiae*, maximum recorded *hd.* being 33 mm. and 38 mm. respectively. The gill clefts are deeper in *P. australiae* and the pair of curved processes which extend from the epiphyses of Aristotle's lantern and retain the tooth, are longer and more pointed in *P. bajulus*. The interambulacral plates of *P. australiae* carry more spines than those of the new species and the large, primary boss characteristic of *P. bajulus* is not present in that species. The globiferous pedicellariae of *P. bajulus* have deeper shoulders with more acute corners than those of *P. australiae* and the palms of the triphyllous pedicellariae are more expanded in the new species.

Remarks. *Pachycentrotus bajulus* is the only non-cidaroid, regular urchin from Australia known to brood its young. The only other echinoid in this category is *Hypsiechinus coronatus* (family Temnopleuridae), which is limited to the far northern North Atlantic (Hyman, 1955). In *H. coronatus* the young are

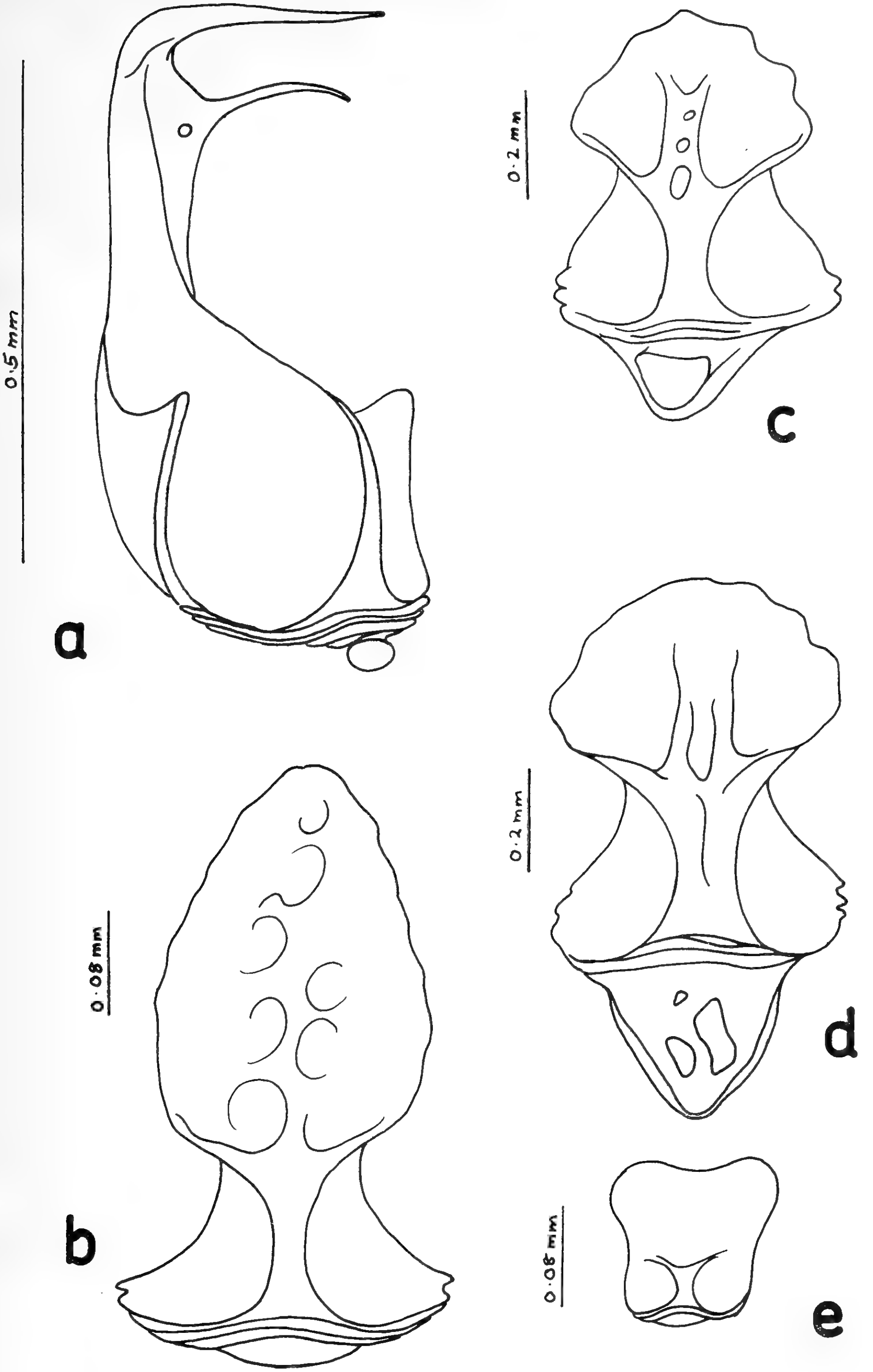


Fig. 3. *Pachycentrotus bajulus* sp. nov. (*a*) Jaw of globiferous pedicellaria. (*b*) Jaw of tridentate pedicellaria. (*c*) Jaw of small triphyllous pedicellaria. (*d*) Jaw of large triphyllous pedicellaria. (*e*) Jaw of ophiocephalous pedicellaria.

brooded around the plates of the periproct. In *P. bajulus* the young ride scattered amongst the spines over the whole test. There is no marsupium or preferred brooding area. The holotype carried 12 young, ranging from 1·5 mm. to 5·5 mm. *hd.*, when it was collected. Paratype H604 carries 17 young ranging from 1–3 mm. *hd.* (illustrated in *Australian Natural History*, in press).

In a zoogeographical context the new species is also of great interest because it shows some parallels with the distributional and reproductive phenomena already reported in some sea stars from Tasmania (Dartnall, 1970). In this case *P. australiae* is replaced by *P. bajulus* in south-eastern Tasmania. The reproductive cycles of both species are unknown, though *P. australiae* is said to have small eggs and, probably, pelagic larvae (Mortensen, 1943). However, reproductive isolation of the two species may be inferred. *P. bajulus*, so far as is known, is restricted to south-eastern Tasmania and is a further example of the endemic fraction of the Maugean fauna which characterizes the area (see Bennett and Pope, 1960, and Dartnall, in press).

It is of interest to note here that recent work has shown that a chiton, *Ischnochiton mayi*, with a similar S.E. Tasmanian distribution, is also a brooding form (E. Turner, personal communication). The occurrence of brooding animals in the shallow water fauna of the south of Tasmania when non-brooding closely related species are found in warmer, more northern waters may make it possible to elucidate some of the factors which make brooding and viviparity advantageous in a habitat. Also, in any consideration of the effects of pollution on the marine fauna of the area it must be emphasized that replacement of this part of the fauna from adjacent areas will be slow (Chia, 1970) or, if modification of the habitat is extensive, nearly impossible.

ACKNOWLEDGEMENTS

I thank Emeritus Professor V. V. Hickman for his generous donation of material.

References

BENNETT, I., and POPE, C. E., 1960.—Intertidal zonation of the exposed rocky shores of Tasmania and its relationship with the rest of Australia. *Aust. J. Mar. Freshw. Res.*, 11 : 182.

CLARK, H. L., 1912.—Hawaiian and other Pacific echini. *Mem. Mus. Comp. Zool.*, 34 : 205.

————, 1938.—Echinoderms from Australia. *Mem. Mus. Comp. Zool.*, 55.

CHIA, F. S., 1970.—Reproduction of Arctic marine invertebrates. *Marine Pollution Bulletin*, 1 (N.S.), 5 : 78–79.

DARTNALL, A. J., 1970.—The Asterinid sea stars of Tasmania. *Proc. Roy. Soc. Tasm.*, 104 : 73.

————, in press.—Littoral Biogeography, in *Biogeography and Ecology in Tasmania*. W. Williams ed. Monographie Biologicae, Junk, The Hague.

HYMAN, L. H., 1955.—*The Invertebrates.* Vol. IV, *Echinodermata.* McGraw-Hill, New York.

MORTENSEN, Th., 1943.—*Monograph of the Echinoidea III (3). Camarodonta II. Echinidae, Strongylocentrotidae* etc. Reitzel, Copenhagen.

THE OCCURRENCE OF ROOT NODULES IN THE GINKGOALES, TAXALES, AND CONIFERALES

A. G. Khan* and P. G. Valder
School of Biological Sciences, The University of Sydney

(Plate I)

[Accepted for publication 17th November 1971]

Synopsis

The roots of 57 species of the Ginkgoales, Taxales, and Coniferales were examined for the presence of nodules of the *Podocarpus*-type and for the occurrence of mycorrhizal associations. Of the conifers, those placed in the Araucariaceae, Podocarpaceae, and Sciadopityaceae all bore nodules, whereas species of the Cupressaceae, Pinaceae, and Taxodiaceae did not. No nodules were observed on *Gingko biloba* or *Taxus baccata*.

Vesicular-arbuscular mycorrhizas were of general occurrence amongst the plants examined except for the members of the Pinaceae, which bore the ectotrophic type.

Introduction

Records of the occurrence of root nodules amongst the Ginkgoales, Taxales and Coniferales have been tabulated by Allen and Allen (1965) and a fuller report of the occurrence of structures variously described as exostoses, mamelons, tubercles, and nodules is given in Table 1. However, apart from the records for *Podocarpus* spp. by numerous authors, for *Dacrydium franklinii*, *Microcachrys tetragona*, *Phyllocladus trichomanoides* and *Saxegothaea conspicua* by Sprat (1912), for *Pherosphaera hookeriana* (*Microstrobus niphophilus*) and *P. fitzgeraldii* (*M. fitzgeraldii*) by Saxton (1930*a*, 1930*b*) and for species of *Agathis*, *Dacrydium*, and *Phyllocladus* by Baylis *et al.* (1963), no evidence has been reported which indicates that the structures described differ in any way from short roots.

Table 1

Records of the Presence of Nodules Amongst the Coniferales

Family, Genus and Species	Literature Citations
Araucariaceae	
Agathis australis	Cockayne, 1921; Yeates, 1924; Bieleski, 1959; Baylis *et al.*, 1963; Morrison and English, 1967.
A. robusta	Janse, 1897 (as *Dammara robusta*).
A. vitiensis	Allen and Allen, 1965.
Araucaria spp.	Hooker, 1854.
A. angustifolia	Daugherty, 1963.
A. heterophylla	Janse, 1897; Yeates, 1924 (both as *A. excelsa*).
Cupressaceae	
Cupressus sp.	Hooker, 1854.
C. sempervirens	Janse, 1897 (as *C. fastigiata*).
Libocedrus bidwillii	Yeates, 1924.
Sabina chinensis	Janse, 1897 (as *Juniperus chinensis*).
Thuja sp. (*Platycladus ?*)	Hooker, 1854.
Podocarpaceae	
Acmopyle pancheri	Sahni (1920).
Dacrydium sp.	Hooker (1854).

---

* Present address: University of Panjab, New Campus, Lahore, West Pakistan.

TABLE 1—*Continued*

Records of the Presence of Nodules Amongst the Coniferales—Continued

Family, Genus and Species	Literature Citations
PODOCARPACEAE—*Continued*	
D. bidwillii	Yeates, ex Allen and Allen, 1965.
D. biforme	Yeates, 1924 ; Baylis *et al.*, 1963.
D. colensoi	Yeates, 1924.
D. cupressinum	Yeates, ex Allen and Allen, 1965 ; Baylis *et al.*, 1963.
D. intermedium	Yeates, ex Allen and Allen, 1965 ; Baylis *et al.*, 1963.
D. franklinii	Sprat, 1912.
D. kirkii	Yeates, ex Allen and Allen, 1965.
D. laxifolium	Yeates, ex Allen and Allen, 1965.
Microcachrys tetragona	Sprat, 1912.
Microstrobos fitzgeraldii	Saxton, 1930*a*, 1930*b* (as *Pherosphaera fitzgeraldii*).
M. niphophilus	Saxton, 1930*a*, 1930*b* (as *Pherosphaera hookeriana*).
Phyllocladus sp.	Hooker, 1854.
P. alpinus	Baylis *et al.*, 1963.
P. glaucus	Yeates, ex Allen and Allen, 1965.
P. trichomanoides	Sprat, 1912.
Podocarpus spp.	Hooker, 1854 ; von Tubeuf, 1896, according to Nobbe and Hiltner, 1899 ; Bond, 1959.
P. acutifolius	Yeates, ex Allen and Allen, 1965.
P. blumei	Becking, 1965.
P. dacrydioides	Hooker, 1865 ; Petri, 1903 ; Yeates, 1924 ; Baylis *et al.*, 1963.
P. elatus	Petri, 1903 ; McLuckie, 1923.
P. elongatus	Petri, 1903 ; Sprat, 1912 ; Phillips, 1932 (both as *P. elongatus* and *P. thunbergii* var. *angustifolia*).
P. falcatus	Phillips, 1932.
P. ferrugineus	Yeates, 1924 ; Baylis *et al.*, 1963.
P. gracilior	Parker, 1932.
P. hallii	Yeates, 1924 ; Baylis *et al.*, 1963.
P. henkelii	Phillips, 1932.
P. imbricatus	Janse, 1897 (as *P. cupressinus*).
P. latifolius	Saxton, 1930 (as *P. thunbergii*) ; Phillips, 1932 ; Bond, 1967.
P. macrophyllus	Nobbe and Hiltner, 1899 ; Shibata, 1902 ; Petri, 1903 ; Schaede, 1943 (all as *P. chinensis*) ; Petri, 1903.
P. macrophyllus var. *maki*	Becking, 1965.
P. nagi	von Tubeuf, 1896, according to Nobbe and Hiltner, 1899 ; Shibata, 1902 (both as *P. nageia*) ; Becking, 1965.
P. neriifolius	van Tiegham, 1970, according to Becking, 1965 ; von Tubeuf, 1896, according to Shibata, 1902 ; Egle and Munding, 1951 ; Becking, 1965.
P. nivalis	Yeates, ex Allen and Allen, 1965 ; Bond, 1967.
P. nubigenus	Schaede, 1943.
P. "*prostrata*" (no such name known)	Yeates, ex Allen and Allen, 1965.
P. rospigliosii	Furman, 1964 ; Becking, 1965.
P. salignus	Sprat, 1912 ; Bottomley, 1913 (both as *P. chilina*).
P. spicatus	Yeates, 1924 ; Baylis *et al.*, 1963.
P. spinulosus	McLuckie, 1923.
P. totara	Sprat, 1912 ; Yeates, 1924 ; Baylis *et al.*, 1963.
P. "*variegatus*" (a cultivar ?)	Ferreira dos Santos, 1947, ex Allen and Allen, 1965.
P. wallichianus	Petri, 1903 (as *P. latifolia* Wall.).
Saxegothaea conspicua	Sprat, 1912.
TAXODIACEAE	
Cunninghamia sp.	Hooker, 1854.
Taxodium sp.	Hooker, 1854. According to Hooker, the elder de Candolle had earlier noted exostoses on *T. distichum* (*Theorie Elementaire*, Ed. 2, p. 356).
SCIADOPITYACEAE	
Sciadopitys verticillata	Uemura, 1964.

Allen and Allen (1965) found no nodules on *Ginkgo biloba* and, although they recorded Hiltner (1903) as having reported their occurrence, no evidence of this could be found in his paper. Similarly, it was not found that Yeates (1924) had recorded nodules on *Araucaria cunninghamii*.

Uemura (1964) appears to be the only person to have reported nodules on *Sciadopitys verticillata*, stating that they closely resembled those of *Podocarpus macrophyllus* but were smaller and appeared as " narrow ellipsoides ". He gave no detail of their structure but reported that Noelle (1910) and Laing (1923) had found them to be mycorrhizal. These authors, however, recorded the presence of endotrophic mycorrhizas but made no mention of nodules.

Daugherty (1963) saw beaded roots on the fossil *Araucariorhiza joae* and suggested that the bulb-like expansions at the tips might possibly be incipient nodules. Such an occurrence, however, has not been observed in living conifers and it seems probable that he was observing beaded roots at the commencement of a new growth cycle.

It has now been shown that the nodules of *Podocarpus* spp. develop as normal features of the roots, are not dependent on any microorganisms for their development, and differ markedly from short roots, being fully differentiated structures with no root cap or apical meristem and with an endodermis surrounding and overarching the vascular strand (Khan, 1967). Hence, in view of the uncertainty concerning the nature of many of the structures described as exostoses, mamelons, tubercles, and nodules for other members of the Coniferales and for members of the Ginkgoales and Taxales, the survey reported below was carried out.

Plants were obtained from a variety of sources in New South Wales, their root systems examined for the presence of nodule-like structures, and sections made to observe their anatomy.

RESULTS AND DISCUSSION

The results of this survey are set out in Table 2. All species of the Araucariaceae, Podocarpaceae and Sciadopityaceae examined bore nodules analogous to those described for *Podocarpus* spp., bore short roots as well, produced beaded roots as a result of metacutization and subsequent regrowth, and contained a vesicular-arbuscular endophyte in the cortices of both the nodules and young roots.

TABLE 2

A Record of Nodules, Mycorrhizas and Beaded Rootlets Observed on Species of the Ginkgoales, Taxales and Coniferales

(+ = present, — = absent, V = vesicular-arbuscular, E = ectotrophic)

Order, Family, Genus, Species	Nodules	Beaded Rootlets	Mycorrhiza
GINKGOALES			
GINKGOACEAE			
Gingko biloba L.	—	+	+V
TAXALES			
TAXACEAE			
Taxus baccata L.	—	+	+V
CONIFERALES			
ARAUCARIACEAE			
Agathis australis Salisbury	+	+	+V
A. dammara (Lambert) L. C. Richard ..	+	+	+V
A. moorei (Lindley) Masters	+	+	+V
A. robusta (C. Moore) F. M. Bailey ..	+	+	+V
A. vitiensis (Seeman) Drake..	+	+	+V
Araucaria araucana (Molina) K. Koch ..	+	+	+V
A. cunninghamii Aiton ex D. Don.. ..	+	+	+V
A. heterophylla (Salisbury) Franco	+	+	+V
A. columnaris (Forster f.) Hooker ..	+	+	+V

TABLE 2

A Record of Nodules, Mycorrhizas and Beaded Rootlets Observed on Species of the Ginkgoales, Taxales and Coniferales

(+ = present, — = absent, V = vesicular-arbuscular, E = ectotrophic)

Order, Family, Genus, Species	Nodules	Beaded Rootlets	Mycorrhiza
CUPRESSACEAE			
Austrocedrus chilensis (D. Don) Florin et Boutelje	—	—	—
Callitris muelleri (Parl.) F. Mueller	—	—	+V
C. columellaris F. Mueller	—	—	+V
C. rhomboidea R.Br. ex A. et L. C. Richard	—	—	+V
Chamaecyparis obtusa (Sieb. et Zucc.) Endl.	—	+	+V
Cupressus arizonica Greene	—	+	+V
C. funebris Endl.	—	+	+V
C. glabra Sudworth	—	+	+V
C. sempervirens L.	—	+	+V
C. torulosa D. Don	—	+	+V
Fokienia hodginsii (Dunn) Henry et Thomas	—	+	+V
Juniperus communis L.	—	+	+V
Libocedrus plumosa (D. Don) Sargent	—	+	+V
Platycladus orientalis (L.) Franco	—	—	+V
Thujopsis dolabrata (L.f.) Sieb. et Zucc.	—	—	—
Tetraclinus articulata (Vahl) Masters	—	—	+V
Widdringtonia whytei Rendle	—	—	+V
PINACEAE			
Abies nordmanniana (Steven) Spach	—	+	+E
Cedrus deodara Loudon	—	—	+E
Keteleeria davidiana (Bertrand) Beissner	—	+	+E
Larix kaempferi (Lambert) Carriere	—	+	+E
Picea abies (L.) Karsten	—	+	+E
Pinus radiata D. Don	—	+	+E
P. wallichiana A. B. Jackson	—	+	+E
Pseudotsuga menziesii (Mirbel) Franco	—	—	+E
Tsuga canadensis (L.) Carriere	—	—	+E
PODOCARPACEAE			
Dacrydium franklinii Hooker f.	+	+	+V
Microstrobos fitzgeraldii (F. Mueller) Garden et Johnson	+	+	+V
Phyllocladus hypophyllus Hooker f.	+	+	+V
P. trichomanoides D. Don	+	+	+V
Podocarpus brassii Pilger	+	+	+V
P. compactus Wasscher	+	+	+V
P. elatus R.Br. ex Endl.	+	+	+V
P. falcatus (Thunberg) R.Br.	+	+	+V
P. ladei F. M. Bailey	+	+	+V
P. latifolius (Thunberg) R.Br.	+	+	+V
P. lawrencei Hooker f.	+	+	+V
P. macrophyllus (Thunberg) D. Don	+	+	+V
P. spinulosus (Sm.) R.Br. ex Mirbel	+	+	+V
TAXODIACEAE			
Cryptomeria japonica (L.f.) D. Don	—	+	+V
Cunninghamia lanceolata (Lambert) Hooker	—	+	+V
Glyptostrobus pensilis (Staunton ex D. Don) K. Koch	—	—	+V
Metasequoia glyptostroboides Hu et Cheng	—	—	+V
Sequoia sempervirens (Lamb.) Endl.	—	—	+V
Sequoiadendron giganteum (Lindl.) Bucholz	—	—	+V
Taxodium distichum (L.) L. C. Richard	—	—	+V
T. mucronatum Tenore	—	—	+V
SCIADOPITYACEAE			
Sciadopitys verticillata (Thunberg) Sieb. et Zucc.	+	+	+V

All members of the Podocarpaceae examined bore numerous nodules, of more or less uniform size within a species and usually in two opposite rows, giving the roots a most distinctive appearance (Pl. I, Fig. *a*). The size of the nodules varied according to the species, the smallest (0·3–0·5 mm. diameter) being those of *Microstrobus fitzgeraldii*, those of *Phyllocladus hypophyllus*, *P. trichomanoides* and *Dacrydium franklinii* being medium sized (0·5–0·9 mm.), and those of *Podocarpus* spp. being the largest (0·8–1·5 mm.). As observed by Sprat (1912) and Baylis *et al.* (1963), the vascular strand in species with small nodules is very rudimentary, but in *Podocarpus* spp. it is sufficiently developed to show a diarch structure. Unfortunately, material of *Microcachrys* and *Acmopyle* was not obtained, as it would be particularly interesting to confirm the occurrence of nodules in these genera. The only record for *Acmopyle* is that for *Acmopyle pancheri* by Sahni (1920). He reported that the roots of this plant bore tubercles but gave no details of their structure, and his only illustration was of a longitudinal section of what he claimed to be a tubercle regenerating and becoming a root. This illustration shows no evidence of the structure peculiar to the nodules of other genera of the Podocarpaceae.

In the Araucariaceae the roots of all species of *Agathis* and *Araucaria* examined bore nodules analogous to those occurring in *Podocarpus*, although they were more elongated and arranged in a much less regular fashion (Pl. I, Fig. *b*). The root systems of these plants, therefore, presented a much less characteristic appearance than those of members of the Podocarpaceae. Only in *Araucaria araucana* was anything approaching the regular arrangement occurring in *Podocarpus* seen. However, although the nodules in *Agathis* and *Araucaria* were elongated and less regularly arranged, they were structurally analogous to those of *Podocarpus*, being fully differentiated, lacking a root cap and apical meristem and having a vascular strand completely overarched by the endodermis (Pl. I, Fig. *c*). Like the nodules of members of the Podocarpaceae, they exhibited regeneration from cells of the pericycle, and it seems reasonable to suppose that they occur throughout the Araucariaceae.

The only other plant on which such nodules were found was *Sciadopitys verticillata* (Pl. I, Fig. *d*), the single representative of the family Sciadopityaceae. Here again the nodules were elongated, variable in size, and arranged irregularly. These nodules, too, exhibited regeneration from the pericycle.

All members of the Pinaceae examined were involved in mycorrhizal associations of the ectotrophic type and had short roots, each with an apical meristem, open-ended endodermis, and root cap. Several of them had developed beaded rootlets as well.

In *Ginkgo biloba*, *Taxus baccata*, and all members of the Cupressaceae and Taxodiaceae examined, the long roots bore short lateral roots only and, with the exception of *Austrocedrus chilensis* and *Thujopsis dolabrata*, contained vesicular-arbuscular endophytes. Many of them were exhibiting beaded rootlets as well, and it may well be that these occur also in those species for which they were not recorded in this survey, just as *A. chilensis* and *T. dolabrata* would be expected to be mycorrhizal under other circumstances.

The root systems of many of these plants, with their short roots and beaded rootlets, bore a striking resemblance to those of members of the Araucariaceae. Thus it is not surprising that authors should have reported the presence of nodules on their root systems and even, as was done by Janse (1897), on angiosperms such as *Acer* spp., which have root systems very similar in appearance.

As a result of the present survey, then, a clear pattern has emerged with regard to the occurrence of nodules and mycorrhizas amongst the Ginkgoales, Taxales and Coniferales. Nodules of the *Podocarpus*-type have been found only in the Araucariaceae, Podocarpaceae and Sciadopityaceae, and vesicular-arbuscular mycorrhizas seem to be of general occurrence in all families except the Pinaceae, the members of which form the ectotrophic type. It must be emphasized, however, that most of the plants examined were growing in cultivation far from their natural habitats and only a selection of species was examined. Thus there may well be exceptions to the generalization stated above. As far as mycorrhizas are concerned, it may yet be shown that some species can form more than one type. Such an occurrence, for instance, is reported by Filer (1969), who records, amongst other observations, that *Quercus phellos* and *Populus deltoides* have mostly ectotrophic, frequently ectendotrophic, and sometmies endotrophic mycorrhizas.

The taxonomic significance of the occurrence of nodules has been mentioned by Sprat (1912), who discusses the affinities of the Podocarpaceae and Araucariaceae, noting that they have much the same geographical distribution. Both she and Saxton (1930*b*) regard the universal occurrence of nodules to be a factor lending weight to the grouping of genera in the Podocarpaceae.

The occurrence of nodules in *Sciadopitys* is also a factor strengthening the separation of this monotypic genus from the Taxodiaceae and its placement in a family of its own. This Japanese plant occurs within the distribution of *Podocarpus* and, according to Dallimore and Jackson (1966), Greguss places it in the Podocarpaceae on the basis of the similarities in wood structure. In the present study it was also observed that when the short roots became dormant the tips underwent the same type of metacutization as that observed in *Podocarpus*.

It is unfortunate that the word " nodule " should have been applied at all to structures produced laterally on the root systems of conifers and their relatives, since it suggests analogies with the nodules of legumes and plants such as *Casuarina* spp. Had they been given a different name to begin with, it is doubtful whether confusion would ever have arisen in the literature concerning their function and mode of origin. Much work still remains, however, before it can be decided whether or not their function differs in any way from that of other roots with vesicular-arbuscular endophytes.

ACKNOWLEDGEMENTS

The writers particularly wish to thank Mr. J. Fairburn for taking the photographs, members of the National Herbarium of N.S.W. for checking the names of all the plants examined, and Dr. I. V. Newman for his advice and assistance.

References

ALLEN, E. K., and ALLEN, O. N., 1965.—Nonleguminous plant symbiosis. *Proc. 25th a. Biol. Colloq., Ore. St. Coll.*, Gilmour, C. M., and Allen, O. N., eds. Oregon State University Press, Corvallis, pp. 77–106.

BAYLISS, G. T. S., MCNABB, R. F. R., and MORRISON, T. M., 1963.—The mycorrhizal nodules of *Podocarpus*. *Trans. Br. mycol. Soc.*, 46 : 378–384.

BECKING, J. H., 1965.—Nitrogen fixation and mycorrhiza in *Podocarpus* root nodules. *Pl. Soil*, 23 : 213–226.

BIELESKI, R. L., 1959.—Factors affecting growth and distribution of the kauri (*Agathis australis* Salisb.). *Aust. J. Bot.*, 7 : 252–294.

BOND, G., 1959.—The incidence and importance of biological fixation of nitrogen. *Advmt Sci., Lond.*, 15 : 382–386.

————, 1967.—Fixation of nitrogen by higher plants other than legumes. *A. Rev. Pl. Physiol.*, 18 : 107–126.

BOTTOMLEY, W. B., 1913.—The root nodules of the Podocarpaceae. *Rep. Br. Ass. Advmt Sci.*, 82 : 679.

COCKAYNE, L., 1921.—*The Vegetation of New Zealand.* Leipzig.

DALLIMORE, W., and JACKSON, A. B., 1966.—*A Handbook of the Coniferae and Ginkgoaceae*, 4th ed., revised by S. G. Harrison. Edward Arnold, London.

DAUGHERTY, L. H., 1963.—Triassic roots from the Petrified Forest National Park. *Am. J. Bot.*, 50 : 802–805.

EGLE, K., and MUNDING, H., 1951.—Uber den gehalt an Haminkopen in den Wurzelknollchen von Nicht-Leguminosen. *Naturwissenschaften*, 38 : 548–549.

FILER, T. H., Jr., 1969.—Mycorrhizae in twenty southern bottomland hardwoods. Abs. Papers, XI Internat. bot. Congr., p. 59.

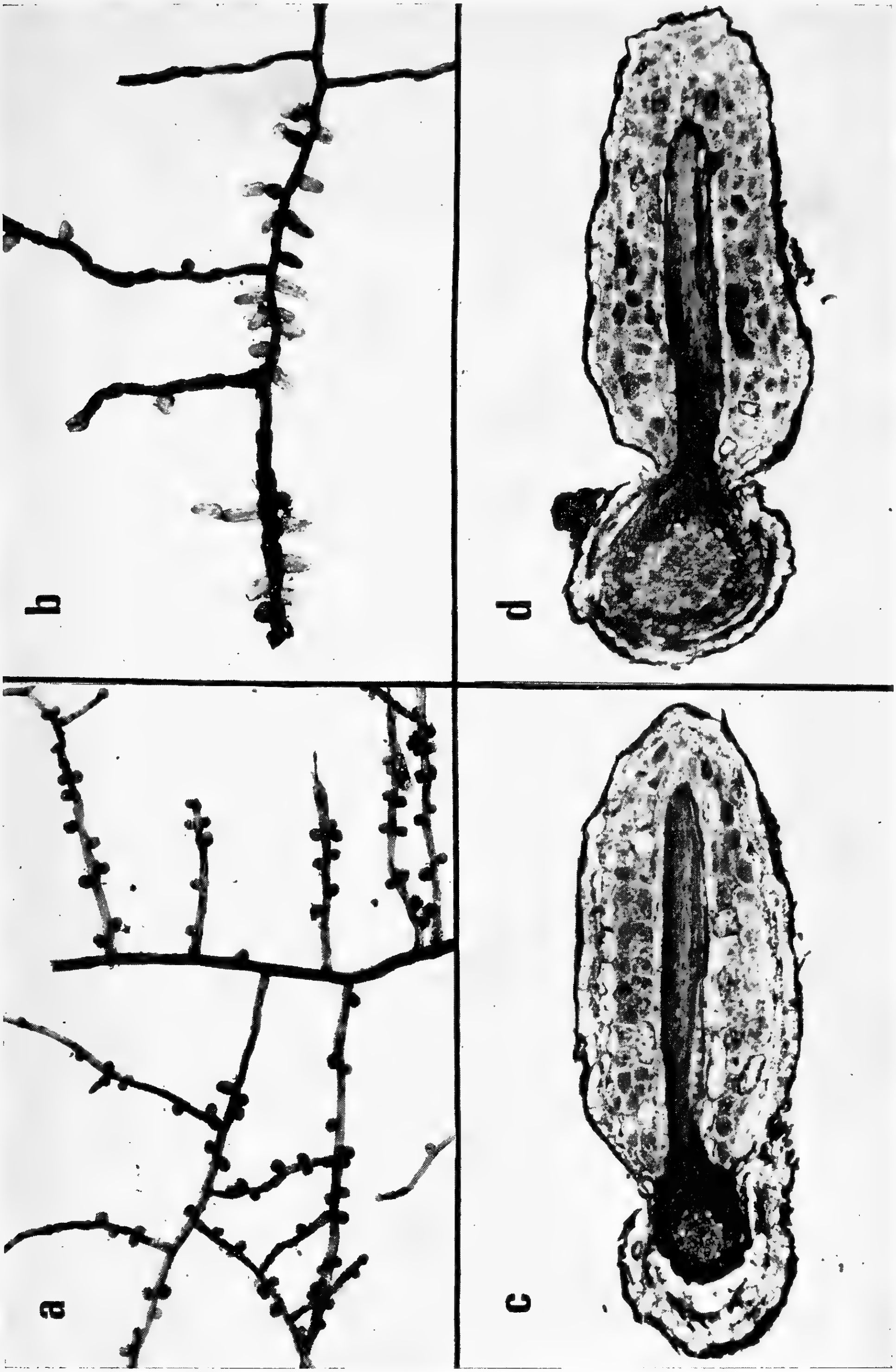


PLATE I

(*a*) Root of *Podocarpus spinulosus* showing nodules. × 1½.
(*b*) Root of *Araucaria cunninghamii* showing nodules and beaded rootlets. × 1½.
(*c*) Longitudinal section of nodule of *A. cunninghamii*, showing endodermis enclosing the vascular system and absence of root cap and apical meristem. × 24.
(*d*) Longitudinal section of nodule of *Sciadopitys verticillata*. × 24.

FURMAN, T. E., 1964.—Mycorrhizal nodules of *Podocarpus*. Abs. in *Bull. ecol. Soc. Am.*, 45 : 151.

HILTNER, L., 1903.—Beitrage zur Mykorrhizafrage. I. Uber die biologische und physiologische Bedeutung den endotropen Mykorrhiza. *Naturw. Z. Forst-u. -Landw.*, 1 : 9–25.

HOOKER, J. D., 1854.—On some remarkable spherical exostoses developed on the roots of various species of Coniferae. *Proc. Linn. Soc. Lond.*, 2 : 335–336.

JANSE, J. M., 1897.—Les endophytes radicaux de quelques plantes javanaises. *Annls Jard. bot. Buitenz.*, 14 : 53–201.

KHAN, A. G., 1967.—Podocarpus root nodules in sterile culture. *Nature, Lond.*, 215 : 1170.

MCLUCKIE, J., 1923.—Studies in symbiosis. III. Contribution to the morphology and physiology of the root nodules of *Podocarpus spinulosa* and *P. elata*. PROC. LINN. SOC. N.S.W., 48 : 82–93.

MORRISON, T. M., and ENGLISH, D. A., 1967.—The significance of mycorrhizal nodules of *Agathis australis*. *New Phytol.*, 66 : 245–250.

NOBBE, F., and HILTNER, L., 1899.—Die endotrophe Mykorrhiza von *Podocarpus* und ihre physiologische Bedeutung. *Landwn VersStnen*, 51 : 241–245.

NOELLE, W., 1910.—Studien zur vergleichenden Anatomie und Morphologie der Koniferenwurzeln mit Rucksichtauf die Systematik. *Bot. Ztg*, 68 : 169–266.

PARKER, R. N., 1932.—*Casuarina* root nodules. *Indian Forester*, 58 : 362–364.

PETRI, L., 1903.—Ricerche sul significato morfologico e fisiologico dei prosporidi (sporangioli di Janse) nelle micorize endotrophiche. *Nuovo G. bot. ital.*, 10 : 541–562.

PHILLIPS, J., 1932.—Root nodules of *Podocarpus*. *Ecology*, 13 : 189–195.

SAHNI, B., 1920.—On the structure and affinities of *Acmopyle pancheri* Pilger. *Phil. Trans. R. Soc.*, 210 : 253–310.

SAXTON, W. T., 1930*a*.—The root nodules of Podocarpaceae. *S. Afr. J. Sci.*, 27 : 323–325.

————, 1930*b*.—Notes on conifers. VII. *Pherosphaera hookeriana* Archer. *Ann. Bot.*, N.S., 44 : 957–963.

SCHAEDE, R., 1943.—Die Symbiose in den Wurzelknollchen der Podocarpeen. *Planta*, 33 : 703–720.

SHIBATA, K., 1902.—Cytologische studien uber die endotrophen Mykorrhizen. *Jb. wiss. Bot.*, 37 : 643–684.

SPRAT, E. R., 1912.—The formation and physiological significance of root nodules in the Podocarpineae. *Ann. Bot.*, N.S., 26 : 801–814.

UEMURA, S., 1964.—Isolation and properties of microorganisms from root nodules of nonleguminous plants. *Bull. Govt Forest Exp. Stn Meguro*, 167 : 59–91.

YEATES, J. S., 1924.—The root nodules of New Zealand pines. *N.Z. Jl. Sci. Technol.*, 7 : 121–124.

TYPE SPECIMENS IN THE MACLEAY MUSEUM, UNIVERSITY OF SYDNEY

VI. MOLLUSCS

W. F. Ponder
The Australian Museum, Sydney

AND

P. J. Stanbury
The Macleay Museum, University of Sydney

[Accepted for publication 15th September 1971]

Synopsis

The molluscan type specimens, comprising 112 species, which belong to the Macleay Museum are listed in systematic order. These types are now housed on permanent loan in the Australian Museum, Sydney.

Introduction

The Macleay Museum at the University of Sydney contains a comprehensive zoological collection including a number of type specimens. Lists of types of insects (Hahn, 1962), fish (Stanbury, 1968), reptiles (Goldman, Hill and Stanbury, 1969), birds (Stanbury, 1969*a*), mammals (Stanbury, 1969*b*) and decapod crustaceans (Griffin and Stanbury, 1970) have been published.

This paper lists the types of 112 mollusc species. Most of these types were collected on Sir William Macleay's expedition to the coast of New Guinea in the *Chevert* (for details of this voyage see Macmillan, 1956). Several molluscan types that should be located in the Macleay Museum were not found during the present search for type specimens and it seems likely that they are permanently lost. Only those specimens actually found are included in the list.

Specimens have been taken to be types if the specimen agrees precisely with the original description and the locality is one of those originally stated. The type specimens appearing in the following list are now on permanent loan to the Australian Museum, Sydney.

The Macleay Museum also contains the remainder of the *Chevert* gastropod material on which Brazier reported. The bivalves have not been worked on, and are still housed in the Macleay Museum. The gastropods are of special value because for a number of the species they are the only specimens which have been recorded from Australia.

All the specimens in the Macleay Museum were stored dry, in cardboard trays, with or without transparent glass lids. In almost all instances the labels are handwritten and the handwriting is that of Masters, the first Curator of the Macleay Museum. None of the specimens has been previously registered.

The Type List

The list of types is arranged in systematic order. Modern generic locations are indicated where these have been changed since the original description. Most of the species were described by Brazier (1872, 1875, 1876, 1877, 1878, 1879, 1881), who did not accompany his descriptions with illustrations. Consequently, an indication is given, where possible, of the source of a figure of each species. Hedley (1891, 1901) figured some of Brazier's type specimens. In some cases it has been possible to identify positively the figured specimen, and this has been selected as a lectotype. This action is taken because Hedley's excellent figures are generally used for Brazier's species, so that giving the specimens on which they are based lectotype status will tie them permanently to Brazier's names.

Registered numbers prefixed by " A " refer to Macleay Museum numbers. Those prefixed by " C " refer to Australian Museum numbers.

ACKNOWLEDGEMENTS

We are grateful to Mr. P. H. Colman, and Mrs. K. Cole and Miss Jeannine Kemple for their technical assistance in compiling this list. Dr. A. W. B. Powell of Auckland, New Zealand, checked the generic allocations of the species of the family Turridae.

Name under which Described, Reference	Locality, Number of Specimens, Designation	Register Number, Modern Generic Name if Changed, Known Synonym, Other Notes
Puncturella galerita Hedley, 1902*a* : 703, fig. 26.	Darnley Island, Torres Strait 7 (syntypes)	A 160
Clanculus granosus Brazier, 1877*j* : 43. Fig'd Hedley, 1901*a* : 128, pl. 17, fig. 30.	Barnard Is., No. 3, N.E. coast of Australia 2 (syntypes)	A 75
Thalotia maculata Brazier, 1877*j* : 44. Fig'd Pilsbry, 1889 : 417, pl. 67, fig. 78.	Cape York, N. Australia 2 (syntypes)	A 150
	Katow, New Guinea 1 (syntype)	A 150 i
	Warrior Reef, Torres Strait 6 (syntypes)	A 150 ii
	Darnley Is., Torres Strait 7 (syntypes)	A 150 iii
Stomatella ornata Brazier, 1877*k* : 47. Ref. Hedley, 1901*a* : 128.	Barnard Islands, No. 3, N.E. coast of Australia (4 syntypes)	Syn. of *Stomatella stellata* Souverbie, 1863 A 148
Neritina (*Neripteron*) *marmorata* Brazier, 1877*i* : 22.	Katow River, New Guinea 3 (syntypes)	A 126
Helicina maino Brazier, 1876*a* : 112.	Katow, New Guinea 1 (holotype)	A 37 *Sphaeroconia*
Helicina macleayi Brazier, 1876*a* : 112.	Barnard Islands, No. 3, N.E. Australia 40 (syntypes)	A 103 *Ceratopoma*
Helicina (*Trochatella*) *sophiae* Brazier, 1875*c* : 4.	Treasury Island, Solomons Archipelago 3 (syntypes)	A 104
Helicina coxeni Brazier, 1876*a* : 111.	Yule Island, New Guinea 22 (syntypes)	A 22, A 46 *Sphaeroconia*
Pupina crossei Brazier, 1876*a* : 110–111. Fig'd Hedley, 1902*b* : 20, pl. 3, fig. 38.	Palm Island, N.E. Australia 3 (syntypes)	A 136 *Signepupina* (*Parpupina*)
Pupina nitida Brazier, 1876*c* : 136. Fig'd Cox, 1868 : 100, pl. 16, figs 6*a*, *b*. Hedley, 1902*b* : 20, pl. 3, fig. 37.	Barrow Island, N.E. Australia 23 (syntypes)	Syn. of *Pupina bilinguis* Pfeiffer, 1851 A 138 *Signepupina*
Pupina macleayi Brazier, 1875*a* : 5.	Endeavour River, Qld 18 (syntypes)	Syn. of *Pupina pettardi* Crosse, 1874 A 137 *Ambipupina*
Pupinella crossei Brazier, 1876*a* : 111. Fig'd Tapparone-Canefri, 1883 : 267, pl. 10, figs 18–19	Yule Island, New Guinea 35 (syntypes)	A 21, A 44 *Helaposa*
Pupina angasi Brazier, 1875 : 5. Fig'd Smith, 1889 : 204, pl. 13, figs 3–4 (as *Pupinella louisiadensis* Smith = *angasi* Brazier)	" New Guinea " = Rossel Island, Louisiade Islands 3 (syntypes)	A 163 *Scaeopupina*

Cyclophorus (*Ditropis*) *beddomei* Brazier, 1877*n* : 122. nom. nov. pro *Cyclophorus macleayi* Brazier, 1876*a* : 113. Fig'd Hedley, 1902*a* : 706, pl. 34, figs 15–17.	Cape York, N. Australia 20+ (syntypes)	A 87 *Ditropisena*
Vivipara alisoni Brazier, 1879 : 221.	Diamantina River, Qld 2 (syntypes)	A 164 *Notopala*
Bithinia hyalina Brazier, 1875*c* : 9.	Eastern Creek, N.S.W. 6 (syntypes)	Syn. of *Gabbia australis* Tryon, 1865 A 69
Rissoina teres Brazier, 1877*g* : 367. Fig'd Hedley, 1901*a* : 127, pl. 17, fig. 27 (chosen as lectotype).	Bet Island, Torres Strait 2 (paralectotypes)	A 146
	Katow, New Guinea 3 (lectotype and paralectotypes)	A 146 i
	Mud Bay, Cape York, Qld 2 (paralectotypes)	A 146 ii
	Warrior Reef, Torres Strait 1 (paralectotype)	A 146 iii *Rissoina* (*Phosinella*)
Rissoina inconspicua Brazier, 1877*g* : 368. Fig'd Hedley, 1901*a* : 128, pl. 17, fig. 29.	Sue Island, Torres Strait 2 (syntypes)	A 143 *Schwartziella* Dungeness Island specimens missing
Rissoina efficata Brazier, 1877*g* : 366. Fig'd Hedley, 1901*a* : 127, pl. 17, fig. 26 (chosen as lectotype).	Barnard Islands, No. 3, N.E. Australia 5 (lectotype and paralectotypes)	A 142 *Rissoina* (*Moerchiella*)
Rissoina inermis Brazier, 1877*g* : 367. Fig'd Hedley, 1901*a* : 127, pl. 17, fig. 28 (chosen as lectotype).	Darnley Island, Torres Strait 6 (lectotype and paralectotypes)	A 144 *Rissoina* (*Zymalata*)
Rissoina pulchella Brazier, 1877*g* : 367. Fig'd Laseron, 1956 : 393, fig. 13.	Barnard Island, No. 3, N.E. Australia 10 (syntypes)	A 145 i
	Home Islands, off Cape Grenville, N. Australia 1 (syntype)	A 145
Rissoina cardinalis Brazier, 1877*g* : 368. Ref. Hedley, 1901 : 127. Fig'd Laseron, 1956 : 395, figs 16, 17.	Cape Grenville, North Australia 2 (syntypes)	A 141
	Cape York, N.E. Australia 4 (syntypes)	A 141 i
	Katow, New Guinea 25 (syntypes)	A 141 ii
Cerithium bicanaliferum Brazier, 1877*f* : 317. Fig'd Hedley, 1901*a* : 127, pl. 17, fig. 25 (chosen as lectotype).	Darnley Island, Torres Strait 8 (lectotype and paralectotypes)	A 72
Cerithium abbreviatum Brazier, 1877*f* : 316. Fig'd Hedley, 1901*a* : 126, pl. 17, fig. 24 (chosen as lectotype).	Katow, New Guinea 2 (lectotype and paralectotype)	A 71 *Ataxocerithium*
Cerithium elegantissimum Hedley, 1899 : 436, fig. 24. nom nov. pro *Cerithium minimum* Brazier, 1877*f* : 317. (non *C. minimum* Hutton, 1873).	Darnley Island, Torres Strait 10 (syntypes)	A 73
	Bet Island, Torres Strait 1 (syntype)	A 73 i

Name under which Described, Reference	Locality, Number of Specimens, Designation	Register Number, Modern Generic Name if Changed, Known Synonym, Other Notes
Trichotropis gracilenta Brazier, 1877*f*: 313. Fig'd Hedley, 1901*a*: 126, pl. 17, fig. 23.	Darnley Island, Torres Strait 1 (holotype)	A 156
Trichotropis tricarinata Brazier, 1877*f*: 312. Fig'd Hedley, 1901*a*: 126, pl. 17, fig. 22 (chosen as lectotype).	Bet Island, Torres Strait 1 (lectotype Katow, New Guinea 2 (paralectotypes)	Syn. of *Turbo separatista* Dillwyn, 1817 A 157 A 157 i *Lippistes*
Eulima nitens Brazier, 1877*e*: 285. Fig'd Hedley, 1901*a*: 125, pl. 17, fig. 21.	Darnley Island, Torres Strait 1 (holotype)	A 101
Eulima amabilis Brazier, 1877*e*: 285.	Darnley Island, Torres Strait 1 (holotype)	A 100
Uber labyrintheum Hedley, 1924: 156, pl. 22, fig. 6.	Darnley Island, Torres Strait 2 (paratypes)	A 159 (=Brazier's (1877*c*: 239) record of *Natica deiodosa* Reeve) *Polinices*
Epidromus bednalli Brazier, 1875*c*: 6. Fig'd Macpherson and Gabriel, 1962: 158, fig. 190 (p. 157).	Guichen Bay, South Australia 1 (syntype)	A 99 *Ratifusus* Does not agree with the dimensions given in the original description
Tritonium (*Epidromus*) *angasi* Brazier, 1877*a*: 174.	Darnley Island, Torres Strait 2 (syntypes)	Syn. of *Nivitriton antiquatus* (Hinds, 1844) A 158 Hedley (1901*a*: 123) reported these shells as missing Sue Island specimens missing
Columbella (*Amycla*) *pudica* Brazier, 1877*c*: 231–232. Fig'd Hedley, 1901*a*: 124, pl. 16, fig. 10.	Darnley Island, Torres Strait 40+ (syntypes)	A 84 *Pyrene*
Columbella inscripta Brazier, 1877*c*: 230. Fig'd Hedley, 1901*a*: 124, pl. 16, fig. 8.	Darnley Island, Torres Strait 1 (syntype) Katow, New Guinea 23 (syntypes) Warrior Reef, W. side, Torres Strait 1 (syntype) Cape York, Qld 2 (syntypes)	Syn. of *C. moleculina* Duclos, 1835 A 82 iii A 82, A 82 iv A 165 A 82 ii *Nitidella* Percy Island specimens missing
Murex eximius Brazier, 1877*a*: 170.	Darnley Island, Torres Strait 1 (holotype)	Syn. of *Murex rectirostris* Sowerby, 1834 A 124
Murex confusa Brazier, 1877*a*: 172. Fig'd Hedley, 1901*a*: 123, pl. 16, fig. 4.	Darnley Island, Torres Strait 1 (holotype)	A 125 *Favartia*

Melatoma dampieria Hedley, 1922: 250, pl. 45, fig. 41 (chosen as lectotype).	Sharks Bay, Western Australia 3 (lectotype and paralectotypes)	A 122 *Inquisitor*
Drillia spaldingi Brazier, 1876*d*: 153–154. Fig'd Hedley, 1901*a*: 122, pl. 16, fig. 1. (Specimen from Long Island figured. This specimen not noted in the original list of localities.)	Bet Island, Torres Strait 1 (syntype) Darnley Island, Torres Strait 6 (syntypes)	A 98 A 98 i *Inquisitor*
Drillia mastersi Brazier, 1876*d*: 153. Fig'd Hedley, 1908: 487, pl. 8, fig. 8.	Warrior Island, Torres Strait 2 (syntypes)	Syn. of *Pleurotoma* (*Drillia*) *essingtonensis* Smith, 1888 A 97 *Inquisitor*
Clathurella macleayi Brazier, 1876*d*: 157. Fig'd Hedley, 1901*a*: 122, pl. 16, fig. 2.	Cape York, N.E. Australia 3 (syntypes) Bet Island, Torres Strait 2 (syntypes) Princess Charlotte Bay, N.E. Australia 2 (syntypes) Cape Grenville, N. Australia 5 (syntypes) Darnley Island, Torres Strait 14 (syntypes) Katow, New Guinea 13 (syntypes)	A 169 i A 169 ii A 169 iv A 169 iii A 169 v A 169 vi *Iredalea*
Daphnella cheverti Hedley, 1922: 327, pl. 53, fig. 161.	Darnley Island, Torres Strait 1 (holotype)	A 166 (Identified as *Daphnella pluricarinata* Reeve, 1845, by Brazier, 1876*d*: 159)
Clathurella tricolor Brazier, 1876*d*: 158. Fig'd Hedley, 1901*a*: 122, pl. 16, fig. 3.	Palm Island, Qld 3 (syntypes)	A 79 *Leinardia nigrocincta tricolor* (Brazier)
Clathurella darnleyi Brazier, 1876*d*: 154. Fig'd Tryon, 1884: 256, pl. 1, fig. 73. Hedley, 1922: 310, pl. 51, fig. 134.	Darnley Island, Torres Strait 51 (syntypes)	A 76 *Pseudorhaphitoma*
Clathurella barnardi Brazier, 1876*d*: 157. Fig'd Hedley, 1922: 345, pl. 55, fig. 178.	Barnard Islands, No. 3, Torres Strait 1 (syntype) Palm Island, Torres Strait 4 (syntypes)	A 132 A 168 *Pseudodaphnella*
Daphnella cestrum Hedley, 1922: 327, pl. 53, fig. 160.	Darnley Island, Torres Strait 4 (holotype and paratypes)	A 170 *Daphnella* Identified by Brazier (1876*d*: 155) as *Clathurella debilis* Hinds, 1844
Clathurella ramsayi Brazier, 1876*d*: 157. Fig'd Hedley, 1922: 350, pl. 56, fig. 188.	Katow, New Guinea 1 (holotype)	A 78 *Pseudodaphnella*
Syrnola pulchra Brazier, 1877*d*: 261. Fig'd Hedley, 1901*a*: 125, pl. 16, fig. 20 (chosen as lectotype).	Darnley Island, Torres Strait 1 (lectotype) Cape York, N. Australia 1 (paralectotype)	A 149 A 149 i

Name under which Described, Reference	Locality, Number of Specimens, Designation	Register Number, Modern Generic Name if Changed, Known Synonym, Other Notes
Turbonilla confusa Brazier, 1877*d* : 258–259. Fig'd Laseron, 1959 : 238, fig. 166.	Darnley Island, Torres Strait 1 (holotype)	A 4 *Pyrgiscus*
Turbonilla cheverti Hedley, 1901*a* : 124, pl. 16, fig. 13 nom. nov. pro *T. exima* Brazier, 1877*d* : 257 (non A. Adams, 1860).	Percy Islands, No. 2, N.E. Australia 1 (holotype)	A 2 *Pyrgiscilla*
Turbonilla darnleyensis Brazier, 1877*d* : 257. Fig'd Hedley, 1901*a* : 124, pl. 16, fig. 12 (chosen as lectotype).	Darnley Island, Torres Strait 6 (lectotype and paralectotypes)	A 7 *Chemnitzia*
Turbonilla aplini Brazier, 1877*d* : 258. Fig'd Hedley, 1901*a* : 125, pl. 16, fig. 14 (chosen as lectotype).	Katow, New Guinea 3 (lectotype and paralectotypes)	A 8 *Exesilla*
Odostomia compta Brazier, 1877*d* : 260. Fig'd Hedley, 1901*a* : 125, pl. 16, fig. 16 (chosen as lectotype).	Darnley Island, Torres Strait 11 (lectotype and paralectotypes)	A 129
Odostomia parvula Brazier, 1877*d* : 260. Fig'd Hedley, 1901*a* : 125, pl. 16, fig. 19.	Darnley Island, Torres Strait 4 (syntypes)	Syn. of *O. compta* Brazier, 1877 A 130
Odostomia polita Brazier, 1877*d* : 260. Fig'd Hedley, 1901*a* : 125, pl. 17, fig. 18.	Darnley Island, Torres Strait 1 (holotype)	Syn. of *O. compta* Brazier, 1877 A 131
Odostomia affinis Brazier, 1877*d* : 259. Fig'd Hedley, 1901*a* : 125, pl. 16, fig. 17.	Cape York, N. Australia 3 (syntypes)	A 127 Darnley Island specimens missing
Odostomia clara Brazier, 1877*d* : 259. Fig'd Hedley, 1901*a* : 125, pl. 16, fig. 15 (chosen as lectotype).	Darnley Island, Torres Strait 3 (lectotype and paralectotypes)	A 128
Ringicula abyssicola Brazier, 1877*m* : 78–79. Fig'd Hedley, 1901 : 129, pl. 17, fig. 37 (chosen as lectotype).	Darnley Island, Torres Strait 2 (lectotype and paralectotype)	A 140
Scaphander multistriata Brazier, 1877*m* : 84. Fig'd Hedley, 1900 : 510, pl. 26, fig. 12. (Figured specimen not located.)	Darnley Island, Torres Strait 1 (syntype)	A 147
Haminea decora Brazier, 1877*m* : 83–84. Fig'd Hedley, 1901*a* : 130, pl. 17, fig. 38 (chosen as lectotype).	Albany Passage, Cape York 3 (lectotype and paralectotypes) Cape Grenville, N. Australia 1 (paralectotype)	A 102 i A 102
Atys darnleyensis Brazier, 1877*m* : 85. Fig'd Hedley, 1901*a* : 130, pl. 17, fig. 39 (chosen as lectotype).	Darnley Island, Torres Strait 50 + (lectotype and paralectotypes)	A 65

Atys cheverti Brazier, 1877*m*: 85–86. Fig'd Hedley, 1901*a*: 130, pl. 17, fig. 40.	Darnley Island, Torres Strait 70+ (syntypes)	A 64
	Cape Grenville, N. Australia 1 (syntype)	A 64 i
Atys densa Brazier, 1877*m*: 86.	Darnley Island, Torres Strait 1 (holotype)	A 66
Atys pulchra Brazier, 1877*m*: 86.	Darnley Island, Torres Strait 23 (syntypes)	A 68 *Cylichna*
Mnestia granosa Brazier, 1877*m*: 81.	Darnley Island, Torres Strait 14 (syntypes)	A 123 *Cylichna*
Atys duboisa Brazier, 1877*m*: 86–87.	Darnley Island, Torres Strait 64 (syntypes)	A 67 *Cylichna*
Cylichna brazieri Pilsbry, 1893: 315. nom. nov. pro *Cylichna minuta* Brazier, 1877*m*: 80–81 (non *C. minuta* H. Adams, 1872).	Darnley Island, Torres Strait 1 (syntype)	Syn. of *Utriculus amphizostus* Watson, 1886 A 88 *Retusa*
Peplimnea caurina Iredale, 1943: 213.	Lennard River, N.W. Australia 50 (syntypes)	C. 79556
Diplommatina gowllandi Brazier, 1875*a*: 31; 1875*b*: 670, pl. 83, figs. 19–21.	Fitzroy Island, N.E. Australia 8 (paratypes)	A 161 *Eclogarinia* Holotype in British Museum
Tornatellina eucharis Brazier, 1876*a*: 110. Fig'd Hedley, 1902*a*: 705, pl. 34, fig. 12.	Barnard Island, No. 3, N.E. Australia 2 (syntypes)	A 151 *Elasmias*
Tornatellina terrestris Brazier, 1876*a*: 109.	Yule Island, New Guinea 4 (syntypes)	A 155 *Elasmias*
Tornatellina mastersi Brazier, 1876*a*: 108. Fig'd Hedley, 1902*a*: 705, pl. 34, figs. 13–14.	Darnley Island, Torres Strait 14 (syntypes)	A 153 *Lamellidea* (*Tornatellinops*)
Tornatellina grenvillei Brazier, 1876*a*: 109.	Home Islands, N.E. Australia 18 (syntypes) Albany Island, Cape York, Qld 10 (syntypes)	Syn. of *Tornatellina mastersi* Brazier, 1876 A 152 A 152 i
Pupa (*Vertigo*) *rossiteri* Brazier, 1875*d*: 18–19.	Lake Macquarie, N.S.W. 4 (syntypes)	A 135 *Gastrocopta* (*Australbinula*)
Pupa (*Vertigo*) *macleayi* Brazier, 1876*a*: 110. Fig'd Hedley, 1902*b*: 19, pl. 3, fig. 39.	Bet Island, Torres Strait 31 (syntypes)	A 134
	Nepean Island, N. Qld 3 (syntypes)	A 134 i
	Warrior Island, Torres Strait 3 (syntypes)	A 134 ii *Gastrocopta* (*Australbinula*) Sue Island and Dungeness Island specimens are missing

Name under which Described, Reference	Locality, Number of Specimens, Designation	Register Number, Modern Generic Name if Changed, Known Synonym, Other Notes
Themapupa dirupta Iredale, 1939: 11, pl. 1, fig. 8.	Barrier-Napier Range, N.W. Australia 3 (holotype and paratypes)	(C. 64897, 64896 respectively)
Bulimus macleayi Brazier, 1876*a*: 108. Fig'd Hedley, 1894: 387, pl. 26, fig. 8, 22–23.	Yule Island, New Guinea 2 (syntypes)	A 54 *Amimopina*
Helix (*Ochthephila*) *dalbertisi* Brazier, 1876*a*: 104. Fig'd Hedley, 1891: 79, pl. 10, fig. 11 (chosen as lectotype).	Yule Island, New Guinea 2 (lectotype and paratype)	A 33 *Paratrochus*
Helix (*Conulus*) *porti* Brazier, 1876*a*: 104.	Albany Island, N. Australia 1 (holotype)	A 110 *Pupisoma* (*Imputegla*)
Helix (*Thalassia*) *gayndahensis* Brazier, 1875*c*: 2. Fig'd Hedley, 1901*c*: 16, pl. 2, figs. 17–19.	Gayndah, Qld 4 (syntypes)	A 119 *Delinitesta*
Helix (*Conulus*) *grenvillei* Brazier, 1876*a*: 104. Fig'd Hedley, 1902*b*: 21, pl. 3, fig. 46.	Home Islands, off Cape Grenville, N.E. Australia 1 (holotype)	A 108 *Queridomus*
Helix (*Patula*) *spaldingi* Brazier, 1876*a*: 103. Fig'd Hedley, 1902*a*: 705, pl. 34, figs. 9–11.	Cape York, Qld 5 (syntypes)	A 115
	Bet Island, Torres Strait 23 (syntypes)	A 115 i
	Sue Island, Torres Strait 18 (syntypes)	A 115 ii
	Coconut Island, Torres Strait 10 (syntypes)	A 115 iii
	Warrior Island, Torres Strait 1 (syntype)	A 115 iv *Torresiropa*
Helix antelata Cox, 1870: 83–84. Fig'd Solem, 1959: 96, pl. 33, figs. 4–6.	Aneiteum, New Hebrides 8 (paratypes or topotypes ?)	Syn. of *Liardetia samoensis* (Mousson, 1865) A 51
Helix (*Thalassia*) *annulus* Brazier, 1876*a*: 100. Fig'd Hedley, 1891: 78, pl. 10, fig. 10.	Katow River, New Guinea 19 (syntypes)	A 16, A 43
	Dungeness Island, Torres Strait 1 (syntype ?)	A 171 *Nitor* (*Pravonitor*)
Westracystis tentus Iredale, 1939: 44, pl. 3, fig. 14.	Barrier Range, N.W. Australia 11 (syntypes)	C. 64901
Helix (*Thalassia*) *sappho* Brazier, 1876*a*: 100.	Yule Island, New Guinea 12 (syntypes)	A 172 *Expocystis*
Helix (*Conulus*) *starkei* Brazier, 1876*a*: 103. Fig'd Hedley, 1891: 75, pl. 9, fig. 5.	Yule Island, New Guinea 1 (holotype)	A 112 *Serostena*

Helix (Conulus) maino Brazier, 1876*a* : 101. Fig'd Hedley, 1891 : 75, pl. 9, fig. 6.	Yule Island, New Guinea 15 (syntypes)	A 45 *Durgellina*
Helix (Conulus) reedei Brazier, 1876*a* : 101–102. Fig'd Hedley, 1902*b* : 20, pl. 3, fig. 45.	Darnley Island, Torres Strait 21 (syntypes)	A 111 *Sodaleta*
Helix (Conulus) darnleyensis Brazier, 1876*a* : 102. Fig'd Hedley, 1902*b* : 21, pl. 3, fig. 43.	Darnley Island, Torres Strait 2 (syntypes)	A 107 *Sodaleta*
Helix (Conulus) barnardensis Brazier, 1876*a* : 102. Fig'd Hedley, 1902*b* : 21, pl. 3, fig. 44.	Barnard Island, No. 3, N.E. Australia 1 (holotype)	A 106 *Sodaleta*
Helix (Conulus) nepeanensis Brazier, 1876*a* : 102. Fig'd Hedley, 1902*b* : 20, pl. 3, figs 40–42.	Nepean Island, Torres Strait 6 (syntypes) Coconut Island, Torres Strait 7 (syntypes)	A 109 i A 109 *Sodaleta*
Helix (Discus) lomonti Brazier, 1876*a* : 101. Fig'd Tapparone-Canefri, 1883 : 91, pl. 2, figs 5–7 (shell), pl. 6, fig. 2, pl. 8, fig. 3, pl. 9, fig. 4 (anatomy).	Yule Island, New Guinea 23 (syntypes)	A 56, A 20 *Geodiscus*
Bulimus rossiteri Brazier, 1881 : 586.	Nehone Bay, N.W. New Caledonia 1 (paratype)	A 160 *Placostylus* Holotype in Acad. Nat. Sci., Philadelphia
Bulimus (Eumecostylus) macfarlandi Brazier, 1875*c* : 4.	Solomons Archipelago 2 (syntypes)	A 70 *Placostylus*
Helix (Zonites) gawleri Brazier, 1872 : 618. Fig'd Kobelt, 1903 : 37, pl. 7, figs 12–14.	Mount Lofty Ranges, South Australia 1 (paratype ?)	A 173 *Strangesta*
Helix (Rhytida) jamesi Brazier, 1876*a* : 99.	Palm Island, N. Qld 4 (paratypes)	Syn. of *Murphitella franklandiensis* (Forbes, 1851)
Helix (Rhytida) beddomei Brazier, 1876*a* : 98–99.	Albany Island, Cape York, Qld 10 (syntypes)	A 116 *Murphitella*
Torresitrachia monticola Iredale, 1939 : 48, pl. 3, fig. 13.	Barrier (Napier) Range, N.W. Australia 2 (paratypes)	C. 79563
Westraltrachia alterna Iredale, 1939 : 51, pl. 3, fig. 17.	Barrier Range, N.W. Australia 1 (holotype)	C. 64888
Westraltrachia incerta Iredale, 1939 : 51, pl. 3, fig. 16.	Barrier Range, N.W. Australia 1 (holotype)	C. 64886
Helix (Hadra) derbyi Cox, 1892 : 566, pl. 20, figs 4–5.	Barrier Range, N.W. Australia 3 (syntypes)	C. 64883
Rhagada construa Iredale, 1939 : 60, pl. 4, fig. 3.	Oscar Range, N.W. Australia 54 (holotype and paratypes)	C. 64851 (holotype) C. 79564 (paratypes)

Name under which Described, Reference	Locality, Number of Specimens, Designation	Register Number, Modern Generic Name if Changed, Known Synonym, Other Notes
Rhagada mimika Iredale, 1939 : 61, pl. 4, fig. 4.	Napier Range, N.W. Australia 3 (holotype and paratypes)	C. 64851 (holotype) C. 79565 (paratypes)
Rhagada sutra Iredale, 1939 : 61, pl. 4, fig. 9.	Napier Range, N.W. Australia 18 (holotype and paratypes)	C. 64858 (holotype) C. 79566 (paratypes)
Helix (*Hadra*) *oscarensis* Cox, 1892 : 565, pl. 20, figs 6–7.	Oscar Range, N.W. Australia 8 (syntypes)	(C. 64908, C. 64909)
Rhagada oscarensis perca Iredale, 1939 : 63.	Oscar Range, N.W. Australia 24 (holotype and paratypes)	C. 64882 (holotype) C. 79035 (paratypes)
Amplirhagada terma Iredale, 1939 : 67, pl. 5, fig. 8.	Barrier Range, N.W. Australia (holotype)	C. 79034
Helix (*Hadra*) *cookensis* Brazier, 1875*d* : 17.	Cooktown, N. Qld (error=Brooke Island, Rockingham Bay, N. Qld) 4 (syntypes)	A 174 *Varohadra*
Helix nicomede Brazier, 1878*d* : 79, pl. 8, fig. 6.	Cardwell, N. Qld 2 (paratypes)	A 175 *Spurlingia*
Helix (*Hadra*) *palmensis* Brazier, 1876*a* : 105. Fig'd Fulton, 1904 : 7, pl. 1, figs 5–6.	Palm Island, New Guinea 2 (syntypes) Great North Palm Island, N.E. Australia 2 (syntypes)	A 113 A 113 i *Gnarosophia*
Geotrochus elisus Hedley, 1891 : 86, pl. 11, figs 24–25.	British New Guinea 4 (syntypes)	A 61 *Claudettea* (*Claudena*)
Helix (*Geotrochus*) *siculus* Brazier, 1876*a* : 106–107. Fig'd Tapparone-Canefri, 1883 : 144, pl. 3, fig. 15, pl. 6, fig. 6 (as *meditata* Tapparone-Canefri=*siculus* Brazier (Iredale, 1941 : 75)).	Katow River, New Guinea 2 (holotype and paratype)	A 50, A 55 *Canefriula*
Helix (*Geotrochus*) *brazierae* Brazier, 1876*a* : 107. Fig'd Tapparone-Canefri, 1883 : 152, pl. 4, fig. 2, pl. 5, fig. 2, pl. 7, fig. 1, pl. 8, figs 7, 13.	Yule Island, New Guinea 22 (syntypes)	A 58 i, A 58, A 25 *Canefriula*
Helix (*Geotrochus*) *yulensis* Brazier, 1876*a* : 105. Fig'd Tapparone-Canefri, 1883 : 123, pl. 3, fig. 2, pl. 6, fig. 1, pl. 8, fig. 11.	Yule Island, New Guinea 60+ (lectotype and paralectotypes)	A 23, A 26, A 59 (lectotype C. 62382) *Rhynchotrochus* Lectotype chosen by Clench and Turner, 1966 : 69, pl. 18, figs 14–16
Helix (*Geotrochus*) *strabo* Brazier, 1876*a* : 106. Fig'd Tapparone-Canefri, 1883 : 126, pl. 3, figs 1–3, pl. 6, fig. 3.	Katow River, New Guinea 3 (lectotype and paralectotypes)	A 57 (lectotype C. 62381) *Rhynchotrochus* Lectotype chosen by Clench and Turner, 1966 : 68, pl. 19, figs 6–8

Helix (*Geotrochus*) *zeno* Brazier, 1876*a* : 107–108. Fig'd Hedley, 1891 : 88, pl. 11, fig. 27.	Hall Sound, New Guinea 2 (lectotype and paralectotype)	A 62 *Letitia* (*Saccoletitia*) Lectotype chosen by Clench and Turner, 1968 : 43, pl. 5, figs 5–6
Lortiella froggatti Iredale, 1934 : 71, pl. 5, fig. 5, pl. 6, fig. 5.	Lennard River, N.W. Australia 29 (paratypes)	A 40 Holotype (C. 61862) and paratypes (C.61683) in Aust. Museum
Austriella sordida Tenison-Woods, 1881 : 82–83, figs 10–11.	Port Denison, Qld 4 (syntypes)	A 63
Rhyssoplax excellens Iredale and Hull, 1926 : 181, pl. 19, figs 22, 27, 40.	Darnley Island, Torres Strait 1 (holotype)	A 139 Previously identified as *Chiton pulcherrimus* Sowerby Brazier, 1877*m* : 75
Dentalium duodecemcostatum Brazier, 1877*l* : 56. Fig'd Hedley, 1901*a* : 128, pl. 17, fig. 31.	Darnley Island, Torres Strait 1 (holotype)	A 91
Dentalium robustum Brazier, 1877*l* : 56. Fig'd Hedley, 1901*a* : 128, pl. 17, fig. 32 (chosen as lectotype).	Katow, New Guinea 5 (lectotype and paralectotypes)	A 95
Dentalium annulosum Brazier, 1877*l* : 58. Fig'd Hedley, 1901*a* : 129, pl. 17, fig. 36 (chosen as lectotype).	Princess Charlotte Bay, N.E. Australia 4 (lectotype and paralectotype)	A 89 =*anulosum* Brazier err. (corrected Hedley, 1901)
Dentalium cheverti Sharp and Pilsbry, 1897 : 9. nom. nov. pro *Dentalium septemcostatum* Brazier, 1877*l* : 57 (non *D. septemcostatum* Ahlich, 1859). Fig'd Hedley, 1901*a* : 129, pl. 17, fig. 34 (chosen as lectotype).	Evans Bay, Cape York, Qld 4 (lectotype and paralectotypes)	A 96
Dentalium decemcostatum Brazier, 1877*l* : 55.	Katow, New Guinea 2 (syntypes)	A 90
Dentalium katowense Brazier, 1877*l* : 56. Fig'd Hedley, 1901*a* : 129, pl. 17, fig. 33.	Katow, New Guinea 1 (holotype)	A 92
Dentalium quadricostatum Brazier, 1877*l* : 58. Fig'd Hedley, 1901*a* : 129, pl. 17, fig. 35.	York Island, Torres Strait 1 (syntype) Katow, New Guinea 11 (syntypes) Princess Charlotte Bay, N.E. Australia 14 (syntypes)	A 94 A 94 i A 94 ii
Dentalium laeve Brazier, 1877*l* : 59. Fig'd Hedley, 1900 : 499, pl. 26, figs 8–10 (chosen as lectotype).	Darnley Island, Torres Strait 1 (lectotype) 100+ (paralectotypes) York Island, Torres Strait 25 (paralectotypes) Princess Charlotte Bay, N.E. Australia 7 (paralectotypes) Cape Grenville, N. Australia 1 (paralectotype)	C. 7525 A 93 A 93 i A 93 ii A 93 iii *Cadulus*

References

Brazier, J. W., 1872.—Descriptions of six new species of land-shells from Australia, and Lord Howe's Island. *Proc. Zool. Soc.* (*Lond.*), 1872 : 617–619.

————, 1875*a*.—Descriptions of eleven new species of terrestrial and marine shells, from north-east Australia. *Trans. Roy. Soc. N.S.W.*, 1874 : 29–33 (issued separately, dated 1874).

————, 1875*b*.—Descriptions of eleven new species of terrestrial and marine shells from north-east Australia. *Proc. Zool. Soc.* (*Lond.*), 1874 : 668–672.

————, 1875*c*.—Description of fourteen new species of shells from Australia and the Solomon Islands. Proc. Linn. Soc. N.S.W., 1 : 1–9.

————, 1875*d*.—Descriptions of eight species of Australian and Tasmanian land and fresh water shells. Proc. Linn. Soc. N.S.W., 1 : 17–20.

————, 1876*a*.—Descriptions of thirty-five new species of land shells from New Guinea, Australia, and islands in Torres Straits, collected during the Chevert Expedition. Proc. Linn. Soc. N.S.W., 1 : 98–113.

————, 1876*b*.—List of land shells collected during the Chevert Expedition. Proc. Linn. Soc. N.S.W., 1 : 117–133.

————, 1876*c*.—Description of a new *Pupina* collected during the Chevert Expedition. Proc. Linn. Soc. N.S.W., 1 : 136–137.

————, 1876*d*.—A list of the Pleurotomidae collected during the Chevert Expedition, with the description of the new species. Proc. Linn. Soc. N.S.W., 1 : 151–162.

————, 1877*a*.—List of marine shells, with descriptions of the new species collected during the Chevert Expedition. Proc. Linn. Soc. N.S.W., 1 : 169–181.

————, 1877*b*.—Shells collected during the Chevert Expedition. Proc. Linn. Soc. N.S.W., 1 : 199–215.

————, 1877*c*.—Shells collected during the Chevert Expedition. Proc. Linn. Soc. N.S.W., 1 : 224–240.

————, 1877*d*.—Shells collected during the Chevert Expedition, with descriptions of the new species. Proc. Linn. Soc. N.S.W., 1 : 249–261.

————, 1877*e*.—Continuation of the Mollusca of the Chevert Expedition, with new species. Proc. Linn. Soc. N.S.W., 1 : 283–301.

————, 1877*f*.—Shells collected during the Chevert Expedition. Proc. Linn. Soc. N.S.W., 1 : 311–321.

————, 1877*g*.—Continuation of the Mollusca of the Chevert Expedition. Proc. Linn. Soc. N.S.W., 1 : 362–368.

————, 1877*h*.—Continuation of the Mollusca of the Chevert Expedition. Proc. Linn. Soc. N.S.W., 2 : 1–6.

————, 1877*i*.—Continuation of the Mollusca collected during the Chevert Expedition. Proc. Linn. Soc. N.S.W., 2 : 20–25.

————, 1877*j*.—Continuation of the Mollusca collected during the Chevert Expedition. Proc. Linn. Soc. N.S.W., 2 : 41–46.

————, 1877*k*.—Continuation of the Mollusca collected during the Chevert Expedition. Proc. Linn. Soc. N.S.W., 2 : 46–53.

————, 1877*l*.—Continuation of the Mollusca collected during the Chevert Expedition. Proc. Linn. Soc. N.S.W., 2 : 55–60.

————, 1877*m*.—Continuation of the Mollusca collected during the Chevert Expedition. Proc. Linn. Soc. N.S.W., 2 : 74–89.

————, 1877*n*.—Description of two new species of *Helix*, from New Guinea and the Louisiade Islands. Proc. Linn. Soc. N.S.W., 2 : 120–122.

————, 1878*a*.—Continuation of the Mollusca collected during the Chevert Expedition. Proc. Linn. Soc. N.S.W., 2 : 128–135.

————, 1878*b*.—Mollusca of the Chevert Expedition. Proc. Linn. Soc. N.S.W., 2 : 143–145.

————, 1878*c*.—Continuation of the Mollusca of the Chevert Expedition. Proc. Linn. Soc. N.S.W., 2 : 368–369.

————, 1878*d*.—Descriptions of seven new species of terrestrial and marine shells from Australia. Proc. Linn. Soc. N.S.W., 3 : 77–81.

————, 1878*e*.—Mollusca of the Chevert Expedition. Proc. Linn. Soc. N.S.W., 3 : 155.

————, 1879.—Description of a new species of *Vivipara*. Proc. Linn. Soc. N.S.W., 3 : 221–222.

————, 1881.—Description of a new *Bulimus* from New Caledonia. Proc. Linn. Soc. N.S.W., 6 : 586–587.

Clench, W. J., and Turner, R. D., 1966.—Monograph of the genus *Rhynchotrochus* (Papuininae : Camaenidae). *J. Malac. Soc. Aust.*, 1 (9) : 59–87.

————, 1968.—Monograph of the genus *Letitia* (Papuininae : Camaenidae). *J. Malac. Soc. Aust.*, 1 (11) : 32–49.

Cox, J. C., 1868.—*A Monograph of Australian Land Shells.* William Maddock, Sydney, 111 pp.

————, 1870.—Descriptions of seventeen new species of land shells from the South-Sea Islands, in the cabinet of Mr. John Brazier, of Sydney. *Proc. Zool. Soc.* (*Lond.*), 1870 : 81–85.

————, 1892.—Descriptions of some new species of pulmonate Mollusca from Australia and the Solomon Islands. Proc. Linn. Soc. N.S.W., (n.s.), 6 : 565–570.

FULTON, H., 1904.—A critical list of the *Sphaerospira* section of *Thersites*. *J. Malac.*, 11 : 2–11.

GOLDMAN, J., HILL, L., and STANBURY, P. J., 1969.—Type specimens in the Macleay Museum, University of Sydney. 11. Amphibians and reptiles. PROC. LINN. SOC. N.S.W., 93 : 427–438.

GRIFFIN, D., and STANBURY, P. J., 1970.—Type specimens in the Macleay Museum, University of Sydney. V. Decapod crustaceans. PROC. LINN. SOC. N.S.W., 95 : 122–131.

HAHN, E., 1962.—*A List of the Designated Type Specimens in the Macleay Museum, Insecta.* Duplicated book, Macleay Museum, 184 pp.

HEDLEY, C., 1891.—The land molluscan fauna of British New Guinea. PROC. LINN. SOC. N.S.W., (2), 6 : 67–116.

————, 1899. The Mollusca of Funafuti. Part 1. Gasteropoda. *Aust. Mus. Mem.*, 3 : 395–488.

————, 1900.—Studies on Australian Mollusca. Part 2. PROC. LINN. SOC. N.S.W., 25 : 495–513.

————, 1901*a*.—A revision of the types of the marine shells of the " Chevert " Expedition. *Rec. Aust. Mus.*, 4 : 121–130.

————, 1901*b*.—Studies on Australian Mollusca. Part 3. PROC. LINN. SOC. N.S.W., 25 : 721–732.

————, 1901*c*.—Studies on Australian Mollusca. Part 4. PROC. LINN. SOC. N.S.W., 25 : 16–25.

————, 1902*a*.—Studies on Australian Mollusca. Part 5. PROC. LINN. SOC. N.S.W., 26 : 700–708.

————, 1902*b*.—Studies on Australian Mollusca. Part 6. PROC. LINN. SOC. N.S.W., 27 : 7–29.

————, 1908.—Studies on Australian Mollusca. Part 10. PROC. LINN. SOC. N.S.W., 33 : 456–489.

————, 1922.—A revision of the Australian Turridae. *Rec. Aust. Mus.*, 13 : 213–359.

————, 1924.—Some naticoids from Queensland. *Rec. Aust. Mus.*, 14 : 154–162.

IREDALE, T., 1934.—The freshwater mussels of Australia. *Aust. Zool.*, 8 : 57–78.

————, 1939.—A review of the land Mollusca of Western Australia. *J. Roy. Soc. W.A.*, 25 : 1–88.

————, 1941.—A basic list of the land Mollusca of Papua. *Aust. Zool.*, 10 : 51–94.

————, 1943.—A basic list of the fresh water Mollusca of Australia. *Aust. Zool.*, 10 : 188–230.

IREDALE, T., and HULL, A. F. B., 1926.—A monograph of the Australian loricates. Part 6. *Aust. Zool.*, 4 : 164–185.

KOBELT, W., 1903.—*Agnatha Systematisches Conchylien-Cabinet von Martini und Chemnitz*, ed. Kuster, Bd. 1, Abth. 12B, 362 pp.

LASERON, C. F., 1956.—The families Rissoinidae and Rissoidae (Mollusca) from the Solanderian and Dampierian Zoogeographical Provinces. *Aust. J. Mar. Freshw. Res.*, 7 : 384–484.

————, 1959.—The family Pyramidellidae (Mollusca) from northern Australia. *Aust. J. Mar. Freshw. Res.*, 10 : 177–267.

MACMILLAN, D. S., 1956.—*A Squatter Went to Sea.* Currawong Publishing Co., Sydney. 165 pp.

MACPHERSON, J. H., and GABRIEL, C. J., 1962.—*Marine Molluscs of Victoria.* Melbourne Univ. Press. 475 pp.

PILSBRY, H. A., 1889.—Trochidae, Stomatiidae, Pleurotomariidae, Haliotidae. *Manual of Conchology*, 11, 519 pp.

————, 1893.—Acanthochitidae, Cryptoplacidae and appendix. Tectibranchiata. *Manual of Conchology*, 15, 436 pp.

SHARP, B., and PILSBRY, H. A., 1897.—Scaphopoda. *Manual of Conchology*, 17, 348 pp.

SMITH, E. A., 1889.—On the land-and-freshwater-shells of the Louisiade Archipelago. *Ann. Mag. Nat. Hist.*, Ser. 6, 4 : 199–209.

SOLEM, A., 1959.—Systematics and zoogeography of the land and freshwater Mollusca of the New Hebrides. *Fieldiana : Zool.*, 43 : 1–359.

STANBURY, P. J., 1968.—Type specimens in the Macleay Museum, University of Sydney. I. Fishes. PROC. LINN. SOC. N.S.W., 93 : 203–210.

————, 1969*a*.—Type specimens in the Macleay Museum, University of Sydney. III. Birds PROC. LINN. SOC. N.S.W., 93 : 458–461.

————, 1969*b*.—Type specimens in the Macleay Museum, University of Sydney. IV. Mammals. PROC. LINN. SOC. N.S.W., 93 : 462–463.

TAPPARONE-CANEFRI, C., 1883.—Fauna malacologica della Nuova Guinea e delle isole adiacenti. *Ann. Mus. Civ. Storia Nat., Genova*, 19 : 1–313.

TENISON-WOODS, J. E., 1881.—On some new marine Mollusca. *Trans. Roy. Soc. Vict.*, 17 : 80–83.

TRYON, G. W., 1884.—Conidae, Pleurotomidae. *Manual of Conchology*, 6, 413 pp.

GENETIC BASES FOR RESISTANCE IN TWO COMMON WHEAT CULTIVARS TO STEM RUST STRAINS OF UNUSUAL AVIRULENCE[1]

A. K. SANGHI[2] AND E. P. BAKER

[Accepted for publication 17th November 1971]

Synopsis

The genetic basis for resistance in two cultivars, Pusa and Mona, of common wheat (*Triticum aestivum* L.) to certain avirulent strains of stem rust was investigated. These cultivars are susceptible to field strains of wheat stem rust (*Puccinia graminis* var. *tritici* Eriks. and Henn.). The stem rust strains employed comprised rye stem rust (*P. graminis* var. *secalis* Eriks. and Henn.) and strains classified as wheat stem rust but possessing unusual genes for avirulence. These latter strains included sexual and somatic hybrids between wheat and rye stem rusts. Pusa and Mona were shown to possess four and three genes, respectively. From the segregation patterns in hybrids between the parents and pathological tests on lines carrying single genes conditioning resistance two genes were found to be common to each cultivar. One was identified as *Sr18* previously described and shown to be present in varieties throughout the world. A total of five distinct genes was identified in these cultivars. Observations on the behaviour of lines possessing isolated genes with that of the parents indicated that additive gene action was involved in conditioning the hypersensitive parental infection types.

INTRODUCTION

Cultivars of common wheat (*Triticum aestivum* L. em. Thell.) are in general resistant to rye stem rust (*Puccinia graminis* var. *secalis* Eriks. and Henn.) but comparatively little is known about the genetic basis of such resistance or of its relationship to that conditioning resistance to wheat stem rust (*P. graminis* var. *tritici* Eriks. and Henn.). However, since certain wheat genotypes are at least moderately susceptible to particular collections of rye stem rust some progress has been made in analyses of these aspects. Further, firstly sexual hybrids (Johnson, 1949) and asexual hybrids (Watson and Luig, 1959; Bridgmon and Wilcoxon, 1959) between wheat and rye stem rusts have been produced in the laboratory. Normally such hybrids are intermediate in pathogenic characteristics between the parental cultures and are frequently avirulent on wheat genotypes recognized as susceptible to field strains of wheat stem rust. Secondly, certain exceptional strains classified as *forma specialis* or variety *tritici* of *P. graminis* from pathogenic attributes on various diagnostic hosts are likewise avirulent on some wheat genotypes normally susceptible to wheat stem rust strains. These two groups of rust strains are considered to possess unusual genes for avirulence.

In the present study the genetic bases for resistance in the wheat cultivars Pusa and Mona to a culture of rye stem rust and to cultures of wheat stem rust with unusual genes for avirulence were investigated. These two cultivars are recognized as lacking resistance genes to all isolates of *P. graminis* var. *tritici* collected in the field on wheat.

REVIEW OF LITERATURE

The host-pathogen relationships of genes for avirulence in certain strains of rust identical with, or closely related to, those used in the current studies have

---

[1] Adapted from part of a Ph.D. thesis submitted to the University of Sydney by the senior author. The financial assistance of the Wheat Industry Research Committee of New South Wales and the University of Sydney is gratefully acknowledged.

[2] Present address: Agricultural Experiment Station, University of Udaipur, Udaipur, India.

been studied in a number of investigations. Loegering and Powers (1962) inoculated 20 common wheat genotypes with 108 F_2 cultures from a cross between culture 111–55A (race 111) and culture 36–55A (race 36) of *P. graminis* var. *tritici* and concluded that eight independent genes for pathogenicity were involved. Berg *et al.* (1963) studied the genetic basis for resistance to culture 111–55A in crosses between Little Club (susceptible) and Marquis and Kota (resistant), respectively. They reported that three dominant genes conditioned resistance in each resistant variety. Sheen and Snyder (1964), employing Marquis chromosome substitution lines in a Chinese Spring background, located one gene on chromosome 2A and a second gene on chromosome 3B in Marquis conferring resistance against race 111. The same authors (Sheen and Snyder, 1965), using Kenya 338 chromosome substitution lines, found that seven substitution lines differed from the susceptible Chinese Spring background in conditioning perceptible resistance to a culture of race 111. Rondon *et al.* (1966) found two and three independent genes in P.I. 94701 and Reliance, respectively, operative against race 111. Sears *et al.* (1957) reported a gene for resistance to a culture of race 111 on chromosome 7A of Chinese Spring and Thatcher. Williams and Gough (1965) reported four genes, of which three were identified as *Sr7*, *Sr13* and *Sr14*, respectively, in Khapli operative against race 111. Gough and Williams (1963) reported that three incompletely dominant genes in each of the cultivars Acme and Mindum (both *T. turgidum* L.) conditioned resistance to culture 111–SS2.

The investigations of Luig and Watson (1965) showed that Eureka (*T. aestivum*) possessed two independent genes, one *Sr6* operative against rust strains 103–H–2 and 111–E–2, and the other *SrE1* operative against 103–H–2 ; *Sr6* is also known to condition resistance to certain field strains of *P. graminis* var. *tritici*. The same authors explained the resistance of Gabo to strains 103–H–2 and 111–E–2 on the basis of a single gene, which they designated *SrG2*. A second gene *SrG3* in this cultivar controlled resistance to culture A20 of *P. graminis* var. *secalis*. They reported also that Charter possessed these two genes. Baker *et al.* (1970) located *SrG2*, which was redesignated as *Sr18* in the sequence of gene symbols used to catalogue stem rust resistance genes in wheat, on chromosome 7D and concluded that the gene was present in a number of wheat cultivars throughout the world. Sanghi and Luig (1971) found it necessary to invoke five genes to explain the pattern in inheritance of resistance exhibited by Mentana to cultures identical with those employed in the current investigations. The gene *Sr8*, effective against certain field strains of wheat stem rust, also operated against all six cultures utilized. Four genes were considered to be present in Yalta ; the gene *Sr11*, known to condition resistance to many field wheat stem rust strains, operated against only two of the cultures.

MATERIALS AND METHODS

A short description of each of the cultivars is as follows :

Pusa W801 (W numbers refer to the Sydney University Wheat Accession Register) is an Indian selection from local collections. The spikes are apically tipped and the grains white, vitreous and plump.

Mona W1168 is a selection made in Australia from a cross Plowman's No. 3 × Canberra. The spikes are apically tipped and grains white.

Morocco W1103 is of unknown pedigree. The spikes are fully awned with pubescent glumes. The grains are pale red in colour.

Purple Straw W1816 is of unknown pedigree. The spikes are lax, apically tip awned with glabrous glumes. The grains are pale red in colour.

W2691 is a line developed at Sydney University specifically for susceptibility to *P. graminis* var. *secalis* and to strains of *P. graminis* var. *tritici* with unusual genes for avirulence. It originated from an F_2 plant of the cross Little Club × (Gabo^3 × Charter).

All five cultivars are fully susceptible to Australian field strains of stem rust collected on wheat.

The nomenclature of the wheat stem rust strains employed follows that adopted by Watson and Luig (1963, 1966). The six stem rust strains used in inheritance studies were described in detail by Sanghi and Luig (1971) and originally by Watson and Luig (1959), Luig and Watson (1965) and Baker *et al.* (1970). The origin and characteristics of each strain are hence only here briefly described.

> Accession 57241 is a field culture of *P. graminis* var. *secalis.*
>
> Cultures 103–H–2 (58–L–1) and M–10b (58–L–2) originated as somatic hybrids between stem rust strain NR–2 (*P. graminis* var. *tritici*) and 57241.
>
> Culture 111–E–2 (56–L–1) is a strain of *P. graminis* var. *tritici* to which few wheat cultivars are susceptible. It could have arisen from a cross between *P. graminis* var. *tritici* and *P. graminis* var. *secalis* (Luig and Watson, 1965).
>
> Culture H–42 (64–L–1) is a sexual hybrid between *P. graminis* var. *tritici* strain 111–E–2 and *P. graminis* var. *secalis* culture H–34 and combines to some extent the pathogenic range of both parents. It is virulent on Black Winter rye. Morocco and W2691 are among the few wheat cultivars which are susceptible to H–42. It does not correspond to any race of wheat stem rust described by Stakman *et al.* (1962) from its infection types on the standard differential set.
>
> Culture 71–0 (63666) was collected on *Agropyron scabrum* L. in Queensland in 1963. It is a strain of wheat stem rust non-pathogenic on wheat genotypes commonly susceptible in the field.

Pots of seedlings were inoculated with a suspension of uredospores in " Mobil Sol 100 ", a low viscosity light paraffin oil, used as a spore carrier. A " Desaga Spray Can " was used to apply the oil-rust suspension. Artificial moisture, in the form of a suspended fog, was created in a glasshouse for 12–15 hours during incubation. After inoculation the pots were placed on benches in well-lit glasshouses maintained at temperatures of 70±5° F. Notes on rust infection types were taken 12–14 days after inoculation. Seedling infection types were based on the scale proposed by Stakman *et al.* (1962).

TABLE 1

Infection Types Exhibited by Seedlings of Pusa, Mona, Susceptible Wheat Cultivars and F_1 Plants Inoculated with Six Strains of Stem Rust

Wheat Cultivar or Hybrid	Rust Strain					
	57241	103–H–2	M10–b	111–E–2	H–42	71–0
Pusa W801	0;	0;	;1 – 2=	0;	0;	;1 – 2=
Mona W1168	2≡2=	;	2=n	;	;	2n
W2691	2‡3c	3+	2‡3c	3+	3+	2n
Morocco W1103	;2≡	2–	3+	3	3	2
Purple Straw W1816	;2–	2=	3+	;2≡2=	;2≡	3+
W2691 × Pusa	0;	0;	2	0;	0;	2
Pusa × W2691	0;	0;	2	0;	0;	2
Morocco × Pusa	0;	0;	2+	0;	0;	2=
Pusa × Morocco	0;	0;	2+	0;	0;	2=
Purple Straw × Pusa	0;	0;	2+	0;	0;	2+
Pusa × Purple Straw	0;	0;	2+	0;	0;	2+
W2691 × Mona	2+	;2≡	3n	;	;	3n
Mona × W2691	2+	;2≡	3n	;	;	3n
Morocco × Mona	;	;2≡	3n	;	;	2 – n
Mona × Morocco	;	;2≡	3n	;	;	2 – n
Purple Straw × Mona	;2=	;	3n	;	;	3n
Mona × Purple Straw	;2=	;	3n	;	;	3n

The genetic analyses of the resistant parents were based on results from the F_1, F_2, F_3 and F_4 generations of crosses with a susceptible parent. In the case of cultures 103–H–2, 111–E–2, H–42 and 57241, the susceptible parent was W2691. Morocco was employed for M10–b and Purple Straw in the case of 71–0 since W2691 exhibited only moderately susceptible (" 2‡3c ") infection types to these rust cultures.

EXPERIMENTAL RESULTS

The infection types exhibited by parental and F_1 seedlings to the six rust cultures are set out in Table 1.

PUSA W801

The resistant infection type (" 0; ") of Pusa was dominant in F_1 tests with cultures 103–H–2, 111–E–2, H–42 and 57241. In tests with cultures M10–b and 71–0, in which Morocco and Purple Straw were used as susceptible parents, the F_1 seedling infection types indicated partial dominance of the Pusa reaction.

Inheritance of Resistance to Cultures 103–H–2, 111–E–2 and H–42

The F_2 population of the cross W2691 × Pusa was derived from 11 F_1 plants. The progenies of different plants were, in general, tested with culture 103–H–2, 111–E–2 or H–42. In certain instances the same plant progeny was tested with more than one culture. The data are presented in Table 2. In a total of 2,386 seedlings, 41 were susceptible and the results suggested the presence of three independent genes conditioning resistance in Pusa to each of the three cultures. Infection types ranged from " 0; ", " ; ", " 2≡ " (classified as highly resistant), " 1+ ", " 2= ", " 2 – 2 " (resistant—moderately resistant) to " 3 ", " 3+ " (susceptible). The data from different families were homogeneous ($P = 0 \cdot 50$–$0 \cdot 30$). The segregation pattern further suggested that each gene conditioned a different, but resistant, infection type.

TABLE 2

Number of F_2 Seedlings in Different Infection Type Classes in the Cross W2691 × Pusa Tested with Three Stem Rust Cultures

Rust Culture	Infection Types HR 0;,;,2≡	Infection Types R – MR ;1+,2=,2–2	Infection Types S 3,3+	Total	χ^2 63 : 1 HR+R–MR : S	P Value
103–H–2 ..	612	53	11	676	0·018	0·90–0·80
111–E–2 ..	878	116	19	1013	0·646	0·50–0·30
H–42	629	57	11	697	0·001	0·98–0·95
Total ..	2119	226	41	2386	0·377	0·70–0·50

HR = highly resistant ; R – MR = resistant to moderately resistant ; S = susceptible.

The breeding behaviour of 239 F_2 plants to culture 103–H–2, presented in Table 3, conformed statistically to an expected ratio of 37 homozygous resistant : 26 segregating : 1 homozygous susceptible line and supported the hypothesis proposed from F_2 results. Of the 86 segregating lines, 59 segregated in a ratio approximating 63 resistant : 1 susceptible or 15 resistant : 1 susceptible seedling. A population of 50 seedlings in each F_3 line is needed to distinguish a 3 : 1 from a 15 : 1 segregation ratio at $P > 0 \cdot 95$. In practically all cases the number in each line exceeded 50, and these two segregation classes could thus be distinguished. However, a population of 235 individuals is needed to distinguish a 15 : 1 from a 63 : 1 segregation ratio. Hence these classes were not separated in the analysis because seedling numbers were insufficient to determine into which class certain segregating lines should have been placed.

The number of such lines approximated the expected 20/64 of the F_3 populations. Seedlings in 27 lines segregated in a 3 resistant : 1 susceptible ratio ; of these, 12 segregated for 3 " 2= " : 1 " 3+ ", 8 for 3 " ;1+ " : 1 " 3+ " and 7 for 3 " 2,2+ " : 1 " 3+ " infection type. The number of lines in each group approximated the expected 2/64 of the population. These results confirmed that Pusa possesses three genes which condition " 2= ", " ;1+ " and " 2 " infection types, respectively, for resistance to culture 103–H–2. The first two genes are dominant, whilst that conditioning a " 2 " infection type is incompletely dominant, since heterozygous genotypes showed " 2+ " infection types.

TABLE 3

Behaviour of F_3 Lines of the Cross W2691×Pusa Tested with Culture 103–H–2

F_3 Classification	Infection Types or Reactions	Number of Lines		Ratio Expected
		Observed	Expected	
Homozygous resistant	0;,2≡,2=,;1+,2	151	138·17	37
Segregating	63R:1S or 15R:1S	59	74·69	20
Segregating	3(2=) : 1(3,3+)	12	7·47	2
Segregating	3(;1+) : 1(3,3+)	8	4·47	2
Segregating	3(2,2+) : 1(3,3+)	7	7·47	2
Homozygous susceptible	3,3+	2	3·73	1
Total	—	239	239·00	64

$\chi^2_5=8\cdot104$; $P=0\cdot20–0\cdot10$.

For an expected 37 resistant : 26 segregating : 1 susceptible ratio, $\chi^2=3\cdot265$; $P=0\cdot20–0\cdot10$.
R = resistant.

The results of F_3 tests with cultures 111–E–2 and H–42, presented in Tables 4 and 5, respectively, showed a similar pattern of segregation indicating the presence of three independent genes in Pusa for resistance to these cultures. The genetic relationship between genes operative against the three cultures was studied when the same 239 F_3 lines were inoculated separately with cultures 103–H–2 and 111–E–2. In like manner 104 F_3 lines were employed in correlated tests involving cultures 103–H–2 and H–42. A P value of $<0\cdot001$ was obtained in each case from chi-square tests for independent behaviour of F_3 lines. Four

TABLE 4

Behaviour of F_3 Lines of the Cross W2691×Pusa Tested with Culture 111–E–2

F_3 Classification	Infection Types or Reactions	Number of Lines		Ratio Expected
		Observed	Expected	
Homozygous resistant	0;,;2≡,2=,;1+2	147	138·17	37
Segregating	63R:1S or 15R:1S	63	74·69	20
Segregating	3(;2≡2=) : 1(3,3+)	12	7·47	2
Segregating	3(;1+) : 1(3,3+)	8	7·47	2
Segregating	3(2,2+) : 1(3,3+)	7	7·47	2
Homozygous susceptible	3,3+	2	3·73	1
Total	—	239	239·00	64

$\chi^2_5=6\cdot638$; $P=0\cdot30–0\cdot20$.

For an expected 37 resistant : 26 segregating : 1 susceptible ratio, $\chi^2=1\cdot888$; $P=0\cdot50–0\cdot30$.

lines segregating against culture 111–E–2 were homozygous resistant to cultures 102–H–2 and two lines segregating in tests with H–42 were homozygous resistant when tested with 103–H–2. This discrepancy was probably due to misclassification of lines with smaller seedling numbers. The high correlation observed suggested that the three genes conditioning resistance to each of the cultures 103–H–2, 111–E–2 and H–42, respectively, were identical.

TABLE 5

Behaviour of F_3 Lines of the Cross W2691×Pusa Tested with Culture H–42

F_3 Classification	Infection Types or Reactions	Number of Lines		Ratio Expected
		Observed	Expected	
Homozygous resistant ..	0;,;2≡,2=,;1+,2	208	196·56	37
Segregating	63R:1S or 15R:1S	91	106·25	20
Segregating	3(;2≡) : 1(3,3+)	16	10·63	2
Segregating	3(;1+) : 1(3,3+)	12	10·63	2
Segregating	3(2,2+) : 1(3,3+)	9	10·63	2
Homozygous susceptible	3,3+	4	5·31	1
Total	—	340	340·01	64

$\chi^2_5=6\cdot324$; P=0·30–0·20.

For an expected 37 resistant : 26 segregating : 1 susceptible ratio, $\chi^2=1\cdot212$; P=0·70–0·50.

Inheritance of Resistance to Culture 57241 of Rye Stem Rust

The F_2 generation of the cross W2691×Pusa consisted of 577 seedlings derived from three F_1 plants. A chi-square test for heterogeneity indicated that the data from different families were homogeneous (P=0·70–0·50) and the results from the families were therefore combined. In a total of 577 seedlings, 530 were highly resistant (" 0 ", " 1 ", " 2≡ " infection types), 37 were resistant (" ;1+2 ", " 2= ", " 2– " infection types), and 10 were moderately susceptible (" 2+3c " infection types). These data conformed to a segregation ratio of 63 resistant : 1 moderately susceptible seedling and suggested the presence of three independent genes in Pusa conditioning resistance to this culture. Tests involving 228 F_3 lines (Table 6) confirmed the hypothesis proposed on the basis of F_2 tests.

According to the hypothesis 37/64 would be homozygous resistant, 26/64 segregating and 1/64 homozygous for moderate susceptibility. Among the

TABLE 6

Behaviour of F_3 Lines of the Cross W2691×Pusa Tested with Culture 57241

F_3 Classification	Infection Types or Reactions	Number of Lines		Ratio Expected
		Observed	Expected	
Homozygous resistant ..	0;,;,2≡,;1+:12–,2	134	131·81	37
Segregating	63R:1MS or 15R:1MS	78	71·25	20
Segregating	3(;1+) : 1(2‡3c)	6	7·13	2
Segregating	3 (2–,2+) : 1(2‡3c)	7	7·13	2
Segregating	3(;12–,X–) : 1(2‡3c)	4	7·13	2
Homozygous moderately susceptible	2‡3c	2	3·56	1
Total	—	228	228·01	64

MS=moderately susceptible.

$\chi^2_5=2\cdot459$; P=0·80–0·70.

For an expected 37 resistant : 26 segregating : 1 susceptible ratio, $\chi^2=0\cdot726$; P=0·70–·050.

segregating lines 20/64 would segregate for 63 resistant : 1 moderately susceptible or 15 resistant : 1 moderately susceptible and 6/64 for 3 resistant : 1 moderately susceptible seedling. In the latter category three groups of infection types were distinguished in populations derived from 17 F_2 plants. These groups were characterized by " ;1+ ", " 2− " and " 12− " seedling infection types, respectively, on homozygous genotypes. When tested statistically the number of lines observed in each of these categories did not deviate significantly from the number expected. The F_3 data, when grouped, conformed to a ratio of 37 homozygous resistant : 26 segregating : 1 homozygous for moderate susceptibility and indicated the presence of three independent genes conditioning resistance to culture 57241.

To study the genetic relationship between genes for resistance in Pusa to cultures 103–H–2, 111–E–2, H–42 and 57241, 79 resistant and four susceptible lines from the cross W2691 × Pusa, of which the reactions to cultures 103–H–2, 111–E–2 and H–42 were known, were selected and inoculated with 57241. Homozygous resistant lines with " ;1+ " and " 2 " infection types to 103–H–2, 111–E–2 and H–42 were also homozygous resistant to 57241 and exhibited similar infection types. One homozygous line showing " 2= " to 103–H–2, " 2≡2= " to 111–E–2 and " ;2≡ " infection types to H–42 exhibited " 2‡3c " infection types to 57241, whilst two lines homozygous susceptible to 103–H–2, 111–E–2 and H–42 gave " ;12− " infection types to 57241. These results indicated that the gene conditioning a " 2= " to 103–H–2, a " ;2≡2= " to 111–E–2 and a " ;2≡ " infection type to H–42 is not operative against 57241 and that the gene conditioning a " ;12− " infection type to 57421 is ineffective against cultures 103–H–2, 111–E–2 and H–42. This infers that Pusa has a fourth gene for resistance. The dominant gene giving a " 2= " to 103–H–2, " ;2≡2= " to 111–E–2 and a " ;2≡ " infection type to H–42 is inoperative against 57241. The second and third genes condition " ;1+ " and " 2 " infection types, respectively, against all four cultures ; the second behaves in a dominant manner, whilst the third is partially dominant and when heterozygous conditions a " 2+ " infection type with all four cultures. The fourth gene conditions a " ;12− " infection type and operates against 57241 alone. This gene is partially dominant and when heterozygous conditions an " X− " infection type. These four genes are designated provisionally *SrPs1*, *SrPs2*, *SrPs3* and *SrPs4*, respectively.

The first gene does not operate against culture 57241, the fourth does not operate against cultures 103–H–2, 111–E–2 and H–42, while the second and third operate against all four cultures.

Inheritance of Resistance to Culture M10–b

The results of F_2 seedling tests in the cross Morocco (susceptible) × Pusa (resistant) indicated the presence of two independent genes for resistance in Pusa to this culture. In a total of 660 F_2 seedlings derived from three F_1 plants, 612 were resistant to moderately resistant (" ;12= "–" 2+ " infection types) and 48 were susceptible (" 3,3+ " infection types). This number conformed to a 15 resistant : 1 susceptible seedling ratio ($P = 0 \cdot 30–0 \cdot 20$). The results (Table 7) of the progeny tests of F_2 plants agreed with the ratio of 7 homozygous resistant : 8 segregating : 1 homozygous susceptible F_3 line expected on this hypothesis. Further evidence for the presence of two genes was obtained from progeny tests of F_2 plants of the cross Purple Straw × Pusa. Purple Straw, susceptible to culture M10–b in crosses with Pusa, also gave a two-gene segregation pattern in F_3 (Table 7). Individual F_3 lines segregating monofactorially gave a 1 resistant : 2 intermediate : 1 susceptible rather than a 3 resistant : 1 susceptible seedling segregation ratio, indicating that both genes for resistance in Pusa against culture M10–b are partially, rather than completely, dominant.

Inheritance of Resistance to Culture 71–0

The F_2 populations from reciprocal crosses between Purple Straw and Pusa totalled 468 plants derived from five F_1 plants. A chi-square test on combined data for a 15 resistant : 1 susceptible seedling ratio gave a P value of 0·30–0·20. This indicated the presence of two independent genes in Pusa operative against 71–0. This was confirmed in F_3 tests. The breeding behaviour of F_2 plant progenies agreed with an expected ratio of 7 homozygous resistant : 8 segregating : 1 homozygous susceptible F_3 line.

Fifty-one F_3 lines from the cross Purple Straw × Pusa were studied to investigate the relationship between genes operative against cultures M10–b and 71–0. An identical breeding behaviour was obtained, indicating that the same genes operate against both cultures.

TABLE 7

Behaviour of F_3 Lines of the Crosses Morocco × Pusa and Purple Straw × Pusa Tested with Cultures M10–b and 71–0

Cross	Rust Culture	R	Seg	S	Total	χ^2 7 : 8 : 1	P Value
Morocco × Pusa	M10–b	30	37	5	72	0·156	0·95–0·90
Purple Straw × Pusa	M10–b	18	28	5	51	2·109	0·50–0·30
Purple Straw × Pusa	71–0	18	28	5	51	2·109	0·50–0·30
Total ..	—	66	93	15	174	3·325	0·20–0·10

Seg = segregating.

Isolation of Genes

Fifty-seven F_4 lines from the cross W2691 × Pusa were tested to study the relationship between the genes operative against the six rust cultures. These F_4 lines were derived from eight F_3 lines segregating monogenically for 3 ("2="):1 ("3+"), 3 (";1+"):1 ("3+") and 3 ("2"):1 ("3+") infection types, respectively, and two F_3 lines homozygous susceptible when tested with culture 103–H–2. Seedlings of separate sowings of each line were tested with each of the six cultures simultaneously in the same glasshouse. The results supported the hypothesis that each selected F_3 line carried a single gene for resistance and confirmed that the two susceptible lines were homozygous for susceptibility to culture 103–H–2 ; F_4 lines homozygous for resistance to culture 103–H–2 due to the gene *SrPs1* (conditioning a "2=" infection type) were homozygous resistant to cultures 111–E–2 and H–42 (";2≡2=" and ";2≡" infection types, respectively) but were homozygous for moderate susceptibility to cultures 57241, M10–b and 71–0. These results indicated that *SrPs1* is ineffective against the latter three cultures and that moderate susceptibility in these lines is due to the W2691 genotype. Lines homozygous for resistance to culture 103–H–2 due to the gene *SrPs2* (conditioning a ";1+" infection type) were homozygous for resistance to cultures 111–E–2, H–42 and 57241 but homozygous for moderate susceptibility to cultures M–10b and 71–0. Lines homozygous for resistance to culture 103–H–2 due to *SrPs3* (conditioning a "2" infection type) were homozygous resistant to all six cultures.

Two F_4 lines, which were homozygous susceptible to cultures 103–H–2, 111–E–2 and H–42, were resistant to cultures 57241, M10–b and 71–0 and exhibited ";12–" infection types to these cultures. These tests indicated that these lines did not carry any of the abovementioned genes and that resistance was apparently due to the fourth gene *SrPs4*.

SrPs3, one of the two genes operating against cultures M–10b and 71–0, operates against all cultures used and *SrPs4*, the second gene operating against cultures M10–b and 71–0, provides resistance against culture 57241 but not cultures 103–H–2, 111–E–2 and H–42.

The results obtained from the genetic analysis of Pusa indicated that it possesses a total of four genes for resistance to the six stem rust cultures utilized.

The infection types on seedlings of selected F_4 lines with different homozygous genotypes for resistance are presented in Table 8.

TABLE 8

Seedling Infection Types Exhibited by Parents and Selected F_4 Lines of the Cross W2691×Pusa Tested with Six Stem Rust Cultures

Pedigree	Rust Culture						Effective Gene(s)
	103–H–2	111–E–2	H–42	57241	M10–b	71–0	
II65.62.2.87.4 . .	2=	;2=2=	;2=	2‡3c	2‡3c	2‡3c	*SrPs1*
II65.62.2.34.4 . .	;1+	;1+	;1+	;1+	2‡3c	2‡3c	*SrPs2*
II65.62.2.133.1	2	2	2	2–	2	2	*SrPs3*
II65.62.2.104.1 . .	3	3	3	;12–	;12–	;12–	*SrPs4*
Pusa	0;	0;	0;	0;	;1–2=	;1–2=	*SrPs1 SrPs2* *SrPs3 SrPs4*
W2691	3+	3+	3+	2‡3c	2‡3c	2‡3c	—

MONA W1168

The resistant infection type of Mona was dominant in the case of cultures 103–H–2, 111–E–2 and H–42 but incompletely dominant with cultures 57241, M10–b and 71–0 in F_1 seedling tests (Table 1).

Inheritance of Resistance to Cultures 103–H–2, 111–E–2 and H–42

When tested with cultures 103–H–2, 111–E–2 and H–42 the F_2 populations segregated into a ratio of 63 resistant : 1 susceptible seedling (Table 9). Thus the action of three independent genes for resistance in each case was inferred and this hypothesis was confirmed in F_3 tests.

TABLE 9

Number of F_2 Seedlings in Different Infection Type Classes in the Cross W2691×Mona Tested with Three Stem Rust Cultures

Cross	Rust Culture	Infection Types			Total	χ^2 63 : 1 HR–R +R:S	P Value
		HR–R ;2=,2=2=	R 2–,2	S 3,3+			
W2691×Mona	103–H–2	546	60	14	620	1·950	0·20–0·10
	111–E–2	1084	38	16	1138	0·181	0·70–0·50
	H–42	1083	50	10	1143	3·513	0·50–0·10
	Total	2713	148	40	2901	0·636	0·50–0·30

The breeding behaviour of progenies of F_2 plants agreed with the expected ratio of 37 homozygous resistant : 26 segregating : 1 susceptible F_3 line when tested with each of the three cultures. Two hundred and thirty-four F_3 lines were tested with culture 103–H–2 (Table 10). On the basis of the hypothesis proposed, 37/64 of the lines would be homozygous resistant, 20/64 would segregate in a ratio of 63 resistant : 1 susceptible or 15 resistant : 1 susceptible, 6/64 would segregate in a ratio of 3 resistant : 1 susceptible seedling and 1/64 would be homozygous susceptible. When tested statistically the number of lines observed in each of these categories did not deviate significantly from that expected.

TABLE 10

Behaviour of F_3 Lines of the Cross W2691×Mona Tested with Culture 103–H–2

F_3 Classification	Infection Types	Number of Lines		Ratio Expected
		Observed	Expected	
Homozygous resistant	;,2≡,2=,2	144	135·28	37
Segregating	63R:1S or 15R:1S	62	73·12	20
Segregating	3(2=1) : 1(3,3+)	16	14·62	4
Segregating	3(2,2+) : 1(3,3+)	6	7·31	2
Homozygous susceptible	3,3+	6	3·67	1
Total	—	234	234·00	64

$\chi^2_4=4\cdot122$; $P=0\cdot50$–$0\cdot30$.

For an expected 37 resistant : 26 segregating : 1 susceptible ratio, $\chi^2=2\cdot885$; $P=0\cdot30$–$0\cdot20$.

A total of 291 F_3 lines was tested with culture 111–E–2 (Table 11). Five were homozygous for “ 3,3+ ” infection types. This proportion of susceptible lines (approximately 1/64 of the population) supported the hypothesis that Mona possesses three independent genes for resistance. This was indicated further by the occurrence of 33 lines (approximately 6/64 of the population) which segregated in a 3 resistant : 1 susceptible seedling ratio. Occasionally within this group, individual progenies segregated in a 1 (“ 2 ”) : 2 (“ 2+ ”) : 1 (“ 3 ” infection types) seedling ratio. The range of infection types among resistant segregants thus indicated incomplete dominance of one gene.

TABLE 11

Behaviour of F_3 Lines of the Cross W2691×Mona Tested with Culture 111–E–2

F_3 Classification	Infection Types or Reactions	Number of Lines		Ratio Expected
		Observed	Expected	
Homozygous resistant	;,2≡,2=,2−2	185	168·23	37
Segregating	63R:1S or 15R:1S	68	90·94	20
Segregating	3(;2≡2=) : 1(3,3+)	8	9·09	2
Segregating	3(2=n) : 1(3,3+)	13	9·09	2
Segregating	3(2,2+) : 1(3,3+)	12	9·09	2
Homozygous susceptible	3,3+	5	4·55	1
Total	—	291	290·99	64

$\chi^2_5=10\cdot201$; $P=0\cdot10$–$0\cdot05$.

For an expected 37 resistant : 26 segregating : 1 susceptible ratio, $\chi^2=4\cdot222$; P=0–20·0–10.

Three groups of resistant infection types were exhibited among lines segregating 3 resistant : 1 susceptible seedling. The number of lines comprising each group was close to 2/64 of the F_3 populations tested. These groups were characterized by “ ;2≡2= ”, “ 2=n ” and “ 2 ” resistant infection types, respectively. As in the case of Pusa crosses, no attempt was made to discriminate between lines segregating 63 resistant : 1 susceptible or 15 resistant : 1 susceptible seedling. The proportion of lines in this combined segregating class approximated the expected 20/64.

Results from tests of 152 F_3 lines with culture H–42 (Table 12) were similar to those described for culture 111–E–2. Three lines were homozygous for

" 3,3 + " infection types. The number of lines in each category which segregated for 3 resistant : 1 susceptible seedling was close to that expected for a three independent gene segregation.

TABLE 12

Behaviour of F$_3$ Lines of the Cross W2691 × Mona Tested with Culture H–42

F$_3$ Classification	Infection Types or Reactions	Number of Lines		Ratio Expected
		Observed	Expected	
Homozygous resistant	;,2≡,2=,2−,2	93	87·88	37
Segregating	63R:1S or 15R:1S	40	47·50	20
Segregating	3(;2≡) : 1(3,3+)	7	4·75	2
Segregating	3(2=n) : 1(3,3+)	4	4·75	2
Segregating	3(2,2+) : 1(3,3+)	5	4·75	2
Homozygous susceptible	3,3+	3	2·38	1
Total	—	152	152·01	64

$\chi^2_5=3\cdot600$; P=0·70–0·50.

For an expected 37 resistant : 26 segregating : 1 susceptible ratio, $\chi^2=0\cdot999$; P=0·70–0·50.

One hundred and fifty-two F$_3$ lines from the cross W2691 × Mona were used to study the relationship between genes conferring resistance to cultures 103–H–2, 111–E–2 and H–42. A high positive correlation was observed for behaviour of F$_3$ lines to the three cultures indicating that the same genes were operative against cultures 103–H–2, 111–E–2 and H–42. These factors are designated tentatively *SrMn1* conditioning a " 2= " infection type to 103–H–2, a " 2≡2= " infection type to 111–E–2 and a " ;2≡ " infection type to H–42, *SrMn2* conditioning a " 2=n " infection type and *SrMn3* conditioning a " 2 " infection type to all three cultures.

Inheritance of Resistance to Culture 57241 of Rye Stem Rust

A total of 573 F$_2$ seedlings derived from three F$_1$ plants was tested with culture 57241. The plants in each family segregated into three groups of infection types, " 2≡2= ", " 2—2 " and " 2‡3c ", respectively. The chi-square for heterogeneity indicated that segregation in the individual families was similar (P=0·80–0·70) and the data from all families were therefore combined. The F$_2$ data, which conformed to a segregation ratio of 13 resistant (" 2≡2= ", " 2—2 ") : 3 moderately susceptible (" 2‡3c " infection types) seedlings (P=0·80–0·70), indicated the presence of an incompletely dominant and a recessive gene for resistance in Mona to this culture. Tests in F$_3$ confirmed the hypothesis proposed and progenies of F$_2$ plants conformed statistically to a ratio of 7 homozygous resistant : 8 segregating : 1 line homozygous for moderate susceptibility ; of the 181 lines tested, 69 were homozygous resistant, 99 segregated and 13 were homozygous susceptible. There was no apparent difference in results from reciprocal crosses.

One hundred and nine F$_3$ lines from the cross W2691 × Mona were tested to study the relationship between genes operative against cultures 103–H–2 and 57241. Seedlings of separate sowings of each line were tested with each of the two cultures simultaneously in the same glasshouse and the results are presented in Table 13. A P value of <0·001 was obtained for a chi-square test for independent behaviour of F$_3$ lines to the two rust cultures. These results indicated that at least one gene is effective against both cultures. Of the 109 lines tested, 65 were homozygous resistant (" ;2≡ "–" 2 " infection types) to culture 103–H–2 and 56 to culture 57241. Of the 65 lines homozygous resistant to culture 103–H–2, 45 were homozygous resistant, 10 segregated and 1 was homozygous for moderate susceptibility (" 2‡3c " infection types) in tests with 57241. The line moderately susceptible to culture 57241 exhibited " 2≡ " infection types to 103–H–2 indicating that it possessed *SrMn1*, which is therefore not operative against 57241. The behaviour of lines carrying the second gene designated *SrMn2*, which gave a " 2=n " infection type to both cultures, indicated that this gene was recessive in tests with 57241 but dominant in the case of 103–H–2. The lines carrying the third gene designated *SrMn3* exhibited " 2 " infection types to both cultures. This gene behaved in a partially dominant fashion conditioning a " 2+ " infection type when heterozygous. These results indicated that the two genes giving resistance to culture 57241 also operate against 103–H–2.

TABLE 13

Behaviour of F_3 Lines of the Cross W2691 × Mona Tested with Cultures 103–H–2 and 57241

Behaviour to Culture 103–H–2	Behaviour to Culture 57241			Total
	Resistant	Segregating	Moderately Susceptible	
Resistant	45	19	1	65
Segregating . .	11	29	2	42
Susceptible . .	—	1	1	2
Total . .	56	49	4	109

For independence, $\chi^2_2=36\cdot856$; $P=<0\cdot001$.

Inheritance of Resistance to Culture M10–b

Four hundred and forty-seven F_2 generation seedlings tested with culture M10–b segregated into two infection type classes—" 2=n "–" 3n " (375 seedlings) and " 3,3+ " (72 seedlings). These numbers of plants in the two classes gave a satisfactory fit to a ratio of 13 resistant : 3 susceptible ($P=0\cdot20–0\cdot10$), indicating the presence of two independent genes for resistance in Mona, one dominant and the other recessive. This hypothesis was confirmed in F_3 tests (Table 14). A P value of 0·80–0·70 was obtained for an expected ratio of 7 homozygous resistant : 8 segregating : 1 homozygous susceptible line in the cross between Mona and Morocco. Evidence for the action of one incompletely dominant and one recessive gene was further obtained from progeny tests of F_3 lines of the cross Purple Straw × Mona tested with M10–b. A P value of 0·30–0·20 was obtained for an expected ratio of 7 homozygous resistant : 8 segregating : 1 homozygous susceptible line.

TABLE 14

Behaviour of F_3 Lines of the Cross Mona × Morocco Tested with Culture M10–b and Purple Straw × Mona Tested with Cultures M10–b and 71–0

Cross	Rust Culture	R	Seg	S	Total	Ratio Expected	χ^2	P Value
Mona × Morocco . .	M10–b	36	46	4	86	7 : 8 : 1	0·631	0·80–0·70
Purple Straw × Mona	M10–b	27	44	7	78	7 : 8 : 1	3·055	0·30–0·20
Purple Straw × Mona	71–0	16	39	23	78	1 : 2 : 1	1·256	0·70–0·50

Inheritance of Resistance to Culture 71–0

Four hundred and nine F_2 plants tested with culture 71–0 were derived from three F_1 plants. A chi-square test for heterogeneity indicated that the data from different families were homogeneous (P=0·70–0·50) and the data were combined. Based on infection types, the plants were classified into two groups in an observed ratio of 300 with " 2–3n " and 109 with " 3,3+ " infection types. The observed segregation was an acceptable fit to a 3 resistant : 1 susceptible seedling ratio. These results were therefore best explained on the basis of a single gene difference for infection type. This hypothesis was confirmed in F_3 tests (Table 14). Seventy-eight F_3 lines segregated in 1 homozygous resistant : 2 segregating : 1 homozygous susceptible seedling ratio.

These 78 F_3 lines were used in studying the relationship between genes conditioning resistance to cultures M10–b and 71–0. The data, presented in Table 15, showed a P value of $<0 \cdot 001$ for a test of independent behaviour, and indicated that genes in common were involved in the two cases. Twenty-seven lines were resistant to culture M10–b and 16 to 71–0. Five lines, which were resistant to culture M10–b (exhibiting " 2= " infection types), were susceptible to culture 71–0 but no line susceptible to M10–b was resistant to 71–0. Among the 44 lines segregating to culture M10–b, 11 were susceptible but none was homozygous resistant to 71–0. These results indicated that the genes conditioning " 2 " infection types to M10–b and 71–0 are identical and that the gene conditioning a " 2=n " infection type to M10–b did not operate against culture 71–0.

TABLE 15

Correlated Behaviour of Seedlings of F_3 Lines of the Cross Purple Straw × Mona Tested with Cultures M10–b and 71–0

Behaviour to Culture 71–0	Behaviour to Culture M10–b			Total
	Resistant	Segregating	Susceptible	
Resistant	16	—	—	16
Segregating . .	6	33	—	39
Susceptible . .	5	11	7	23
Total . .	27	44	7	78

For independence, $\chi^2_2=57 \cdot 603$; P value$=<0 \cdot 001$.

Isolation of Genes

Thirty-two F_4 lines from the cross W2691 × Mona were tested to study the relationship between the genes operative against the six rust cultures. These F_4 lines were derived from six lines segregating monogenically for " 2= ", " 2–n " and " 2,2+ " infection types, respectively, when tested with culture H–42. Seedlings of separate sowings of each line were tested with each of the six cultures simultaneously in the same glasshouse. The results supported the hypothesis that each selected F_3 line carried a single gene for resistance to culture H–42 ; F_4 lines homozygous for resistance to culture H–42 carrying *SrMn1* (" ;2= " infection type) were also homozygous for resistance to 103–H–2 and 111–E–2 but homozygous for moderate susceptibility to cultures 57241, M10–b and 71–0. These tests inferred that the gene *SrMn1* is not operative against the latter three cultures and that the moderate susceptibility observed was due to the W2691 genotype which exhibits a " 2‡3c " infection type to these cultures. Each F_4 line homozygous resistant to culture H–42 due to the action of *SrMn2* (" 2=n " infection type) were also homozygous resistant to cultures 103–H–2. 111–E–2, 57241 and M10–b but were homozygous for moderate susceptibility to culture 71–0. This gene behaved in a dominant manner with 103–H–2, 111–E–2 and H–42 but was recessive with cultures 57241 and M10–b.

Lines homozygous in F_4 for resistance to culture H–42 due to the presence of *SrMn3* (" 2 " infection type) were homozygous resistant to all cultures.

Tests with the six rust cultures thus revealed that Mona has three genes conditioning resistance to the cultures employed. The seedling infection types of selected F_4 lines with different homozygous genotypes for resistance are presented in Table 16.

TABLE 16

Seedling Infection Types Exhibited by Parents and Selected F_4 Lines of the Cross W2691 × Mona Tested with Six Stem Rust Cultures

Pedigree	Rust Culture						Effective Gene(s)
	103–H–2	111–E–2	H–42	57241	M10–b	71–0	
II65.66.7.25.1	2=	;2≡2=	;2≡	2‡3c	2‡3c	2‡3c	*SrMn1*
II65.66.7.53.3	2=n	2=n	2=n	2=n	2=n	2‡3c	*SrMn2*
II65.66.7.133.1 ..	2	2	2	2–	2	2n	*SrMn3*
Mona	;2≡	;	;	2≡2=	2=n	2n	*SrMn1* *SrMn2* *SrMn3*
W2691	3+	3+	3+	2‡3c	2‡3c	2‡3c	—

DISCUSSION

A number of genes in hexaploid wheat specifically conditioning resistance to cultures of *P. graminis* var. *tritici* possessing unusual genes for avirulence, *P. graminis* var. *secalis* and sexual or somatic hybrids between these *formae speciales* were revealed in the present study. A total of five genes in this category was found in two cultivars, neither of which is known to possess resistance to Australian field strains of wheat stem rust. The cultivar Pusa was shown to possess four, and Mona three, genes, respectively, conditioning resistance.

On the bases of information from both genetical and pathological tests the genes *SrPs1* and *SrMn1*, on the one hand, and *SrPs3* and *SrMn3*, on the other, are allelic. Evidence in this connection was based on the absence of segregation in F_2 and F_3 generations in crosses between the parental genotypes (Sanghi, 1968).

The gene *SrPs1* is the same as reported by Luig and Watson (1965) in Gabo and Charter, Williams *et al.* (1966) in Marquis and Reliance, Sears *et al.* (1957) in Hope, Sanghi (1968) and Baker *et al.* (1970) in Purple Straw and Mentana. Kaveh *et al.* (1968) found that the gene designated *Mq'A* in Marquis was allelic, or very closely linked, with a gene for rust resistance on chromosome 1D of Hope.

By aneuploid analysis Anderson and Williams (1968) placed *Mq.A* in Marquis and *Rl.A* in Reliance on chromosome 1D. Baker *et al.* (1970) designated their gene *Sr18* and located it on chromosome 1D by aneuploid analysis. They also concluded that *Sr18* is widespread in wheat cultivars. Because of the presence of this gene in various unrelated cultivars, it is difficult to trace its origin.

No relationship between *SrPs2*, *SrPs3*, *SrPs4* and *SrMn2* and other previously reported genes could be established. A study of segregation in crosses between lines carrying isolated genes for resistance in an appropriate common background is needed to establish genetic relationships in such instances.

The gene *SrMn2* in Mona was dominant in tests with cultures 103–H–2, 111–E–2 and H–42, but recessive to cultures 57241 and M10–b. The phenomenon of reversal of dominance of resistance to rust has been reported by Knott and Anderson (1956), who noted that the gene *Sr6* was dominant to race 56 but recessive in the case of 15B.

Despite the presence of multigenic systems in both parents conditioning resistance to the specific rust cultures employed, it was possible to isolate singly the host genes involved. Observations on the behaviour of lines of this type in comparison with the parental reactions afford opportunities for studying the nature of gene interaction in conditioning rust infection types. Additive gene action was indicated in the present instance. For example, the hypersensitive " 0; " infection type exhibited by Pusa to culture 103–H–2 was due to the additive effects of genes *SrPs1*, *SrPs2* and *SrPs3*, which individually condition " 2= ", " ;1+ " and " 2 " infection types, respectively.

SUMMARY

The genetic basis for resistance to certain stem rust strains possessing unusual genes for avirulence was studied in two wheat parents Pusa and Mona, susceptible to field strains of wheat stem rust. These rusts included two cultures of wheat stem rust, one (race 71–0) collected on *Agropyron scabrum* in the field and the other (race 111–E–2) presumably originating from barberry infection. In addition one culture of rye stem rust (culture 57241) and certain sexual (culture H–42) or somatic hybrids (cultures 103–H–2 and M10–b) between wheat and rye stem rusts were employed.

Tests involving F_1, F_2, F_3 and F_4 generations from the crosses of Pusa and Mona (resistant) with susceptible parents indicated that the resistance in the case of the former was conditioned by four genes and in the case of the latter by three genes. The relationship between certain of these genes was established. From the segregation patterns in hybrids between the parents and pathological tests on isolated lines carrying single genes conditioning resistance *SrPs1* (Pusa) and *SrMn1* (Mona), on the one hand, and *SrPs3* and *SrMn3*, on the other, were allelic. A total of five genes in both parents were identified.

The genes *SrPs1* and *SrMn1* were considered to be idential with *Sr18*, previously described and shown to be present in varieties throughout the world.

References

ANDERSON, M. K., and WILLIAMS, N. D., 1968.—Aneuploid analysis of genes for stem rust resistance derived from Marquis and Reliance wheat. *Agron. Abstr.*, 1968 : 2.

BAKER, E. P., SANGHI, A. K., MCINTOSH, R. A., and LUIG, N. H., 1970.—Cytogenetical studies in wheat. III. Studies of a gene conditioning resistance to stem rust strains with unusual genes for avirulence. *Aust. J. biol. Sci.*, 23 : 369–375.

BERG, L. A., GOUGH, F. J., and WILLIAMS, N. D., 1963.—Inheritance of stem rust resistance in two wheat varieties Marquis and Kota. *Phytopathology*, 53 : 904–908.

BRIDGMON, G. H., and WILCOXON, R. D., 1959.—New races from mixtures of urediospores of varieties of *Puccinia graminis*. *Phytopathology*, 49 : 428–429.

GOUGH, F. J., and WILLIAMS, N. D., 1963.—Inheritance of stem rust reaction in two durum varieties Acme and Mindum. *Phytopathology*, 53 : 295–299.

JOHNSON, T., 1949.—Intervarietal crosses in *Puccinia graminis*. *Can. J. Research* (C), 27 : 45–65.

KAVEH, H., WILLIAMS, N. D., and GOUGH, F. J., 1968.—Allelic and linkage relations among genes for reaction to wheat stem rust. *Agron. Abstr.*, 1968 : 12.

KNOTT, D. R., and ANDERSON, R. G., 1956.—The inheritance of rust resistance. I. The inheritance of rust resistance in ten varieties of common wheat. *Can. J. agr. Sci.*, 36 : 174–195.

LOEGERING, W. Q., and POWERS, H., Jr., 1962.—Inheritance of pathogenicity in a cross of physiological races 111 and 36 of *Puccinia graminis* f. sp. *tritici*. *Phytopathology*, 52 : 547–554.

LUIG, N. H., and WATSON, I. A., 1965.—Studies on the genetic nature of resistance to *Puccinia graminis* var. *tritici* in six varieties of common wheat. PROC. LINN. SOC. N.S.W., 90 : 299–327.

RONDON, M. R., GOUGH, F. J., and WILLIAMS, N. D., 1966.—Inheritance of stem rust resistance in *Triticum aestivum* ssp. *vulgare* " Reliance " and P.I. 94707 of *Triticum durum*. *Crop Sci.*, 6 : 177–179.

SANGHI, A. K., 1968.—Studies on the genetic nature of resistance in common wheat to strains of stem rust possessing unusual genes for avirulence. Ph.D. thesis, Univ. of Sydney.

SANGHI, A. K., and LUIG, N. H., 1971.—Resistance in wheat to *formae speciales tritici* and *secalis* of *Puccinia graminis*. *Can. J. Genet. Cytol.* (in press).

SEARS, E. R., LOEGERING, W. Q., and RODENHISER, H. A., 1957.—Identification of chromosomes carrying genes for stem rust resistance in four varieties of wheat. *Agron. J.*, 49 : 208–212.

SHEEN, S. J., and SNYDER, L. A., 1964.—Studies on the inheritance of resistance to six stem rust cultures using chromosome substitution lines of a Marquis wheat selection. *Can. J. Genet. Cytol.*, 6 : 74–82.

————, 1965.—Studies on the inheritance of resistance to six stem rust cultures using chromosome substitution lines of Kenya wheat. *Can. J. Genet. Cytol.*, 7 : 374–387.

STAKMAN, E. C., STEWART, D. M., and LOEGERING, W. Q., 1962.—Identification of physiological races of *Puccinia graminis tritici.* United States Department of Agriculture. Agriculture Research Service. Bull. *E 617* (revised 1962), pp. 53.

WATSON, I. A., and LUIG, N. H., 1959.—Somatic hybridization between *Puccinia graminis* var. *tritici* and *Puccinia graminis* var. *secalis*. PROC. LINN. SOC. N.S.W., 84 : 207–208.

————, 1963.—The classification of *Puccinia graminis* var. *tritici* in relation to breeding resistant wheats. PROC. LINN. SOC. N.S.W., 88 : 235–258.

————, 1966.—Sr 15—a new gene for use in the classification of *Puccinia graminis* var. *tritici*. *Euphytica*, 15 : 239–250.

WILLIAMS, N. D., and GOUGH, F. J., 1965.—Inheritance of stem rust reaction in Khapli emmer cross. *Crop Sci.*, 5 : 145–147.

WILLIAMS, N. D., GOUGH, F. J., and RONDON, M. R., 1966.—Interaction of pathogenicity genes in *Puccinia graminis* f. sp. *tritici* and reaction genes in *Triticum aestivum* ssp. *vulgare* " Marquis " and " Reliance ". *Crop Sci.*, 6 : 245–248.

EVISCERATION AND REGENERATION IN *THYONE OKENI* (BELL, 1884)

D. J. TRACEY*
School of Biological Sciences, University of Sydney, Sydney, N.S.W., Australia

[Accepted for publication 17th November 1971]

Synopsis

The normal anatomy and histology of *Thyone okeni* was examined in order to compare normal and regenerated tissue. The anatomy was typical of the Dendrochirota, and not significantly different from that of *Thyone briareus.*

The process of auto-evisceration is described, and some explanations of the functional significance of the process are discussed. A new explanation based on nitrogen excretion is considered.

Regeneration of new viscera is described, and the mode of regeneration compared with that in other holothurians. The regenerated gut was found to be formed by a proliferation along the whole free edge of the mesentery. The time taken for complete regeneration is greater than six weeks and about four times as slow as in *Thyone briareus.* A model of the process of regeneration is proposed, in the context of recent ideas on development.

INTRODUCTION

Some holothurians will eviscerate themselves in response to noxious stimuli or change of season. Regeneration of the viscera following auto-evisceration has been studied in the aspidochirotes *Stichopus* (Bertolini, 1930 ; Dawbin, 1949) and *Holothuria* (Bertolini, 1932 ; Kille, 1936) and in the dendrochirote *Thyone briareus.* Several workers have studied evisceration and regeneration in this species (Pearse, 1909 ; Scott, 1914), and Kille (1935) gave a comprehensive picture of its morphological changes during regeneration.

In the aspidochirotes, even closely related genera show quite different modes of regeneration and so in the work to be described, the process of regeneration was followed in a species of dendrochirote not previously examined, in order to establish whether it followed a course of regeneration similar to that described for *Thyone briareus* by Kille (1935).

MATERIALS AND METHODS

MATERIAL

Occurrence. Thyone okeni (Bell, 1884) occurs in about 16 feet of water off Bottle and Glass rocks, Port Jackson, N.S.W. Each animal is invested with a coat of large pieces of shell and gravel and clings to the underside of mussel clumps with its tube feet.

Classification. This animal was classified according to the artificial key given by Clark (1946). Spicules were prepared by macerating the whole body wall in hot 10% KOH, and were then dehydrated and mounted. They are completely unornamented spines (Fig. 1 (B)), few in number and quite atypical for holothurians in general, and indicate *Thyone okeni* Bell—of which only three specimens have been previously reported (Bell, 1884 ; Clark, 1921). In fact Clark found no spicules apart from the tables in the tube feet (Fig. 1 (A)).

---

* Present address : Department of Biological Sciences, Stanford University, Stanford, California 94305, U.S.A.

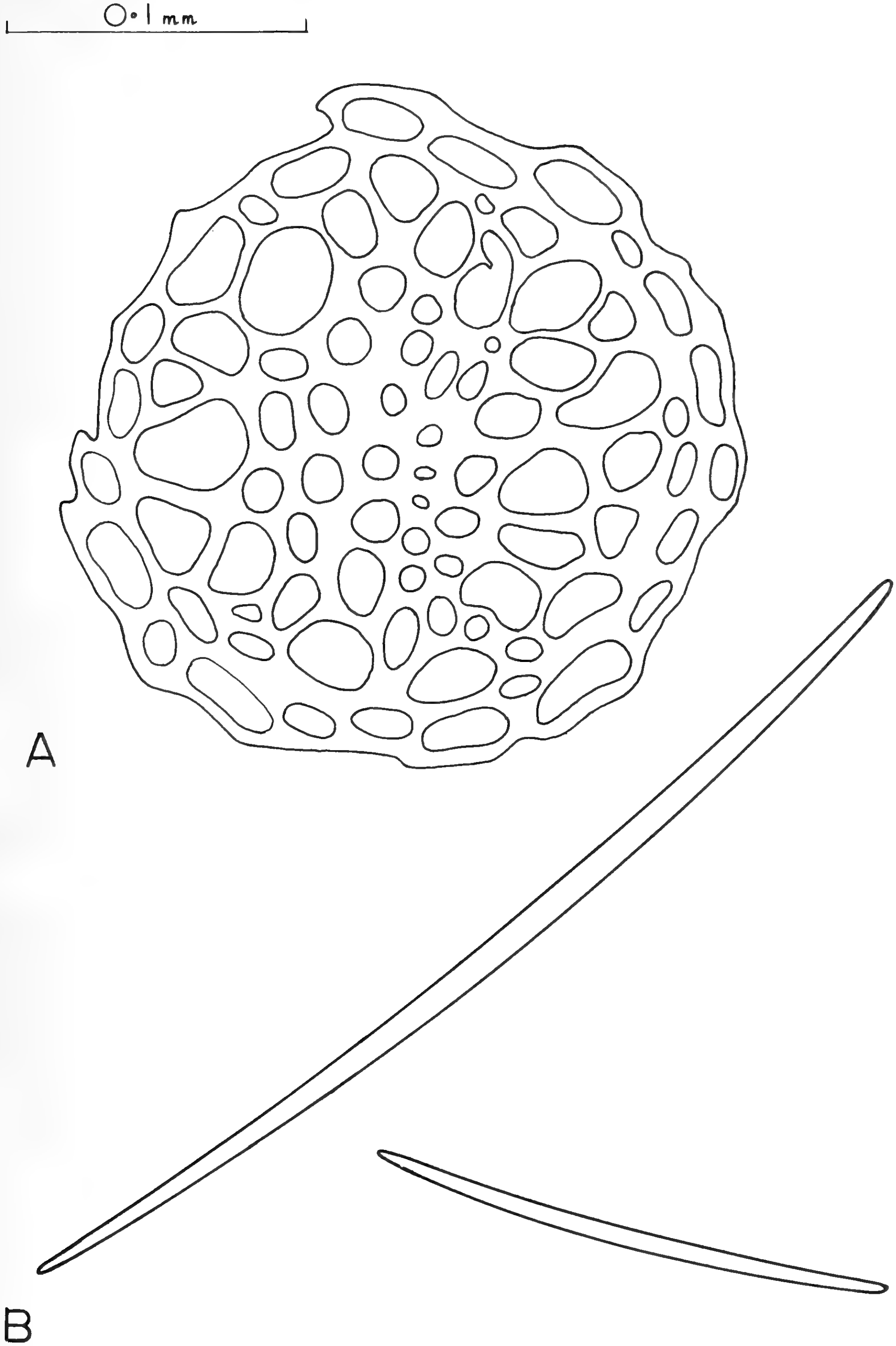


Fig. 1. *Thyone okeni.* (A) Table from tube foot. (B) Spicule from body wall.

Experimental Procedures

Some 30 animals were collected and kept in large aquaria, in which the water was kept circulating for aeration at the surface. The sea water was filtered and changed every two days for the duration of the experiment. The water temperature was constant at 19 ± 1° C.

Two methods of evisceration were tried—ammoniated sea water (Kille, 1935) and injection of distilled water (Dawbin, 1949). For the study on regeneration, 16 animals were induced to eviscerate by injection of about 0·3 ml. distilled water per gramme wet weight. Wet weight is quite variable in each animal, but the amount of water used is not critical. In every case the lantern, gut, and as much gonad as possible was eviscerated ; this was ensured by washing the animals through with extra water. The animals were kept for periods of up to eight weeks, during which six (37%) died and were discarded. Histolysis and decomposition is very rapid after death.

Every week one or two of the animals were narcotized by gradual addition of $MgSO_4$ to 100 ml. of surrounding sea water. They were then killed by dissection and immersion in Bouin's fixative. Specimens were left for a week in Bouin's for adequate fixation and some decalcification.

Every animal was displayed, examined and drawn under the dissecting microscope, and three transverse slives of tissue taken for histological examination. One was taken in the area of the developing lantern, one in the region of the small intestine, and one showing the large intestine.

About 100 serial sections were taken from the first slice, while 40 sections were taken at selected intervals through the second and third slices. Sections were 8μ thick and ordering was retained throughout. All sections were stained with Lillie's modification of the triple Masson stain.

Results

Normal Anatomy (Fig. 2)

The normal anatomy of *Thyone okeni* differs little from that of *Thyone briareus*, but the features important in regeneration will be outlined. The animal is brown and about 50 mm. long, and tube feet are scattered profusely and uniformly over the whole body, so that the ambulacra can hardly be distinguished.

The aquapharyngeal bulb is about 20 mm. long, and is supported by retractors whose insertion is nearly as far back as the middle of the body. The genital tubules are numerous, slender and long, and inserted behind the middle of the body. There is a single polian vesicle and madreporite.

The course of the gut is typical for holothurians. From the pharynx, the descending small intestine leads down the edge of the dorsal mesentery to the posterior of the body cavity, where it recurves forwards and becomes the ascending small intestine, supported by the left mesentery. Before it reaches the anterior of the animal, it turns once again to become the large intestine, supported by the ventral mesentery and leading into the cloaca. There are altogether six regions of the alimentary canal, distinguishable morphologically and histologically (Nace, 1966). These are the pharynx (inside the lantern), then a short oesophagus, a muscular stomach, a long and coiled small intestine forming the bulk of the gut, the rectum which is a dark brown expansion in contrast to the prevailing light orange, and finally the pulsatile cloaca. The relative lengths of these regions can be seen in Fig. 2.

Transverse sections of the gut show a lining epithelium, an inner connective tissue layer, a muscle layer, an outer connective tissue layer and coelomic epithelium. The layers differ in their proportions and somewhat in their staining along the gut, and there is a cuticle lining the stomach. The rectum carries large numbers of brown globules in the inner connective tissue layer and lining epithelium.

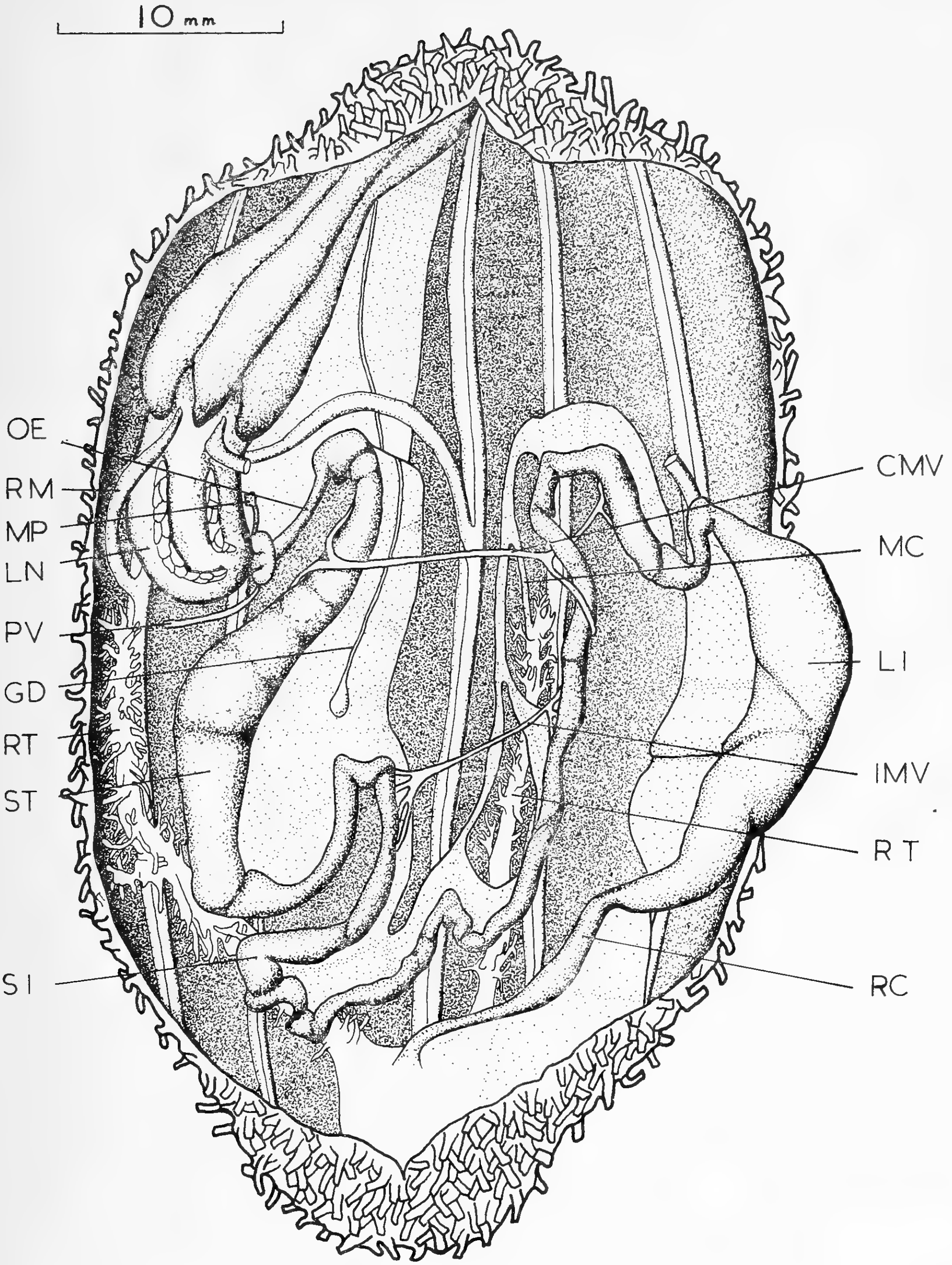


Fig. 2. *Thyone okeni*—normal anatomy. OE=oesophagus, RM=retractor muscle, MP=madreporite, LN=lantern, PV=polian vesicle, GD=gonoduct, RT=respiratory tree, ST=stomach, SI=small intestine, CMV=contra mesenterial cross blood vessel, MC=cord of mesentery supporting left respiratory tree, LI=large intestine, IMV=ipsi mesenterial cross blood vessel, RC=rectum.

The cloaca bears two respiratory trees which continue to function after evisceration. The only other significant structure in the body cavity is the gonad tuft—this is a large mass, purple in the female and light brown in the male, which may fill half the body cavity.

EVISCERATION

Kille's ammonia treatment did not succeed in inducing evisceration. Injection with distilled water was effective in every case, although there was wide variation in sensitivity. The time lapse between injection of water into the body cavity and the start of evisceration varied between 0 and 20 min. with an average of about 5 min.

After this time, contraction of the body wall raises the coelomic fluid pressure until the tentacles are everted. Further contraction distends the proximal thin-walled part of the introvert. This bursts and coelomic fluid rushes out carrying with it the base of the lantern. Meanwhile the retractor muscles have broken, and the tentacle crown becomes further separated from the rest of the body. The gut is extruded, still enclosing some mesentery and the hemal plexus in its loops. Lastly, variable amounts of gonad are expelled, and the lantern and tentacular crown become completely detached. Eventually the circular muscles around the hole contract and close off the body cavity.

The animal has now lost all means of feeding or digestion, and the associated blood system, as well as the central nervous and water vascular systems. It is left with the body wall, the cloaca and respiratory trees and most of the mesentery.

REGENERATION

Lantern. The lantern is a complex structure, and because the series of specimens was limited and rather variable, the process of regeneration could not be reconstructed as completely as Kille did with *Thyone briareus.* However, general features of the process were the same in both species. At first a connective tissue platelet heals over the site of the wound, and this supports the lantern rudiment, which is a flattened disc penetrated by the edge of the dorsal mesentery. At two weeks the longitudinal water canals have grown forward and unite to form a water vascular ring with a diameter of about 1 mm. The lantern is still wider than long, but by four weeks it has extended and differentiated until it is 3·5 mm. long and 1 mm. wide. At six weeks (Fig. 3 (D)), the lantern is 8 mm. long and 3 mm. wide and differentiation is complete, even to the polian vesicle and the madreporite with its stone canal.

Meanwhile, the longitudinal muscles have grown forward with the underlying water canals towards the introvert. At this point the inner part of the longitudinal muscle constricts and eventually pinches off to form a separate strand. This strand is still connected with the longitudinal muscle by a temporary mesentery, continuous with connective tissue which can be seen in sections to extend between the inside and outside of each longitudinal muscle.

As time goes on, the new retractor muscle extends its origin posteriorly and the supporting mesentery disappears, until at six weeks the retractor muscles are distinguishable from the normal only in their slenderness and more posterior/anterior origin.

Regeneration of Gut. The two main features of gut regeneration are the development of a new gut from the proliferating mesentery edge, and changes in the distribution of the mesentery which at first reduce the length of the free edge and then gradually return it to its original length.

Initially the width of the mesentery in the posterior elbow is about 4 mm. and the length of the free edge is 145 mm. By two weeks the mesentery width has increased greatly in the posterior (15 mm.) and anterior elbows in such a way

Fig. 3. *Thyone okeni*—stages in the regeneration of the gut from mesentery edge. (A) 7 days. (B) 14 days. (C) 21 days. (4) 42 days after evisceration.

that the free edge of the mesentery has been reduced in length (50 mm.). The course of the gut is now virtually straight from the anterior connective tissue platelet to the intact cloaca. At this stage, the new gut is visible under the dissecting microscope as a distinct thickening (*c.* 0·1 mm.). This thickening consists of a bead of connective tissue enclosed by epithelium continuous with that of the mesentery (Fig. 4 (A)). The gut rudiment varies in thickness along the

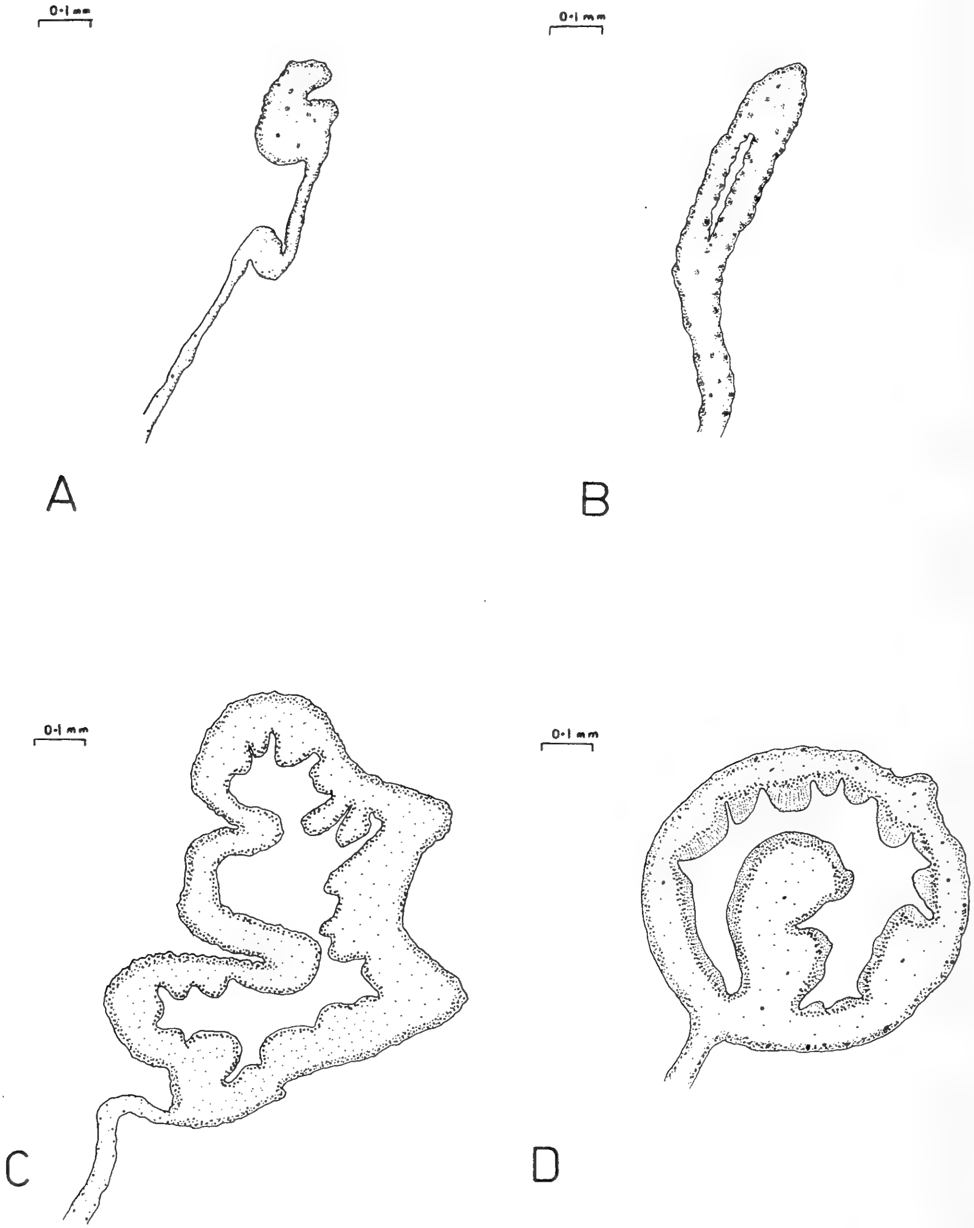


Fig. 4. *Thyone okeni*. TS of regenerating rectum. (A) 7 days. (B) 14 days. (C) 28 days. (D) 42 days.

mesentery edge, and is more marked at positions corresponding with the stomach and the rectum (Fig. 3). At these points an isolated lumen has already begun to form as a simple channel in the connective tissue. Anterior and posterior to these lumina, the gut rudiment is still solid.

By three weeks (Fig. 3 (C)) the gut is thicker (up to 0·7 mm.) and has now begun to lengthen (65 mm.) and even to coil. The stomach and rectum are even more pronounced, and a lining epithelium has begun to develop in those isolated lengths of gut where the lumen is already present. At the same time, the width of the mesentery decreases at the posterior (9 mm.) and anterior elbows, so that the gut is once more longer than the animal. However, the timing of this process is quite variable.

By six weeks (Fig. 3 (D)) the gut has become more uniform as the small intestine thickens up (0·7 mm.). Although the adult thickness (1·0 mm.) and length have not yet been restored, histological differentiation is complete, and the gut has the characteristic layers of lining epithelium, muscular layers of circular and longitudinal fibres, a thin outer layer of connective tissue, and the coelomic epithelium (Fig. 4 (D)). The gut is now an almost perfect miniature of that of the intact animal, but there is no evidence that feeding has resumed.

Regeneration of Gonad Tubules, and Other Changes. Variable amounts of gonad may remain after evisceration. These gonad tubules appear to shrivel and degenerate and perhaps undergo resorption. Meanwhile, new tubules are regenerating from the gonadial base, and these reach a length of about 3 mm. at six weeks.

No regeneration of haemal cross vessels was found, as it had been in *Thyone briareus* and *Stichopus mollis*. This is probably because elongation of the gut did not proceed far enough in 42 days for a haemal plexus to be established in the posterior elbow of the gut—whereas beginnings of a haemal plexus were present in *Thyone briareus* at 14 days. However, at six weeks both ipsi- and contra-mesenterial blood vessels have begun to develop, and would probably give rise to a haemal plexus at a later stage.

This emphasizes that the time scale of regeneration was quite different in the two species. Thus *Thyone briareus* regenerated about four times as fast as *Thyone okeni*. Unfortunately, Kille does not state the temperature at which his animals regenerated, but since his experiments were carried out at Woods Hole it was unlikely to have been higher than 19° C., at which *Thyone okeni* regenerated.

An incidental change during regeneration is a reduction in extent of the respiratory trees soon after evisceration, and this is accompanied by an extension of the podial ampullae. However, by three weeks after evisceration this effect is no longer noticeable.

Discussion

Evisceration

The process of evisceration was similar to that in *Thyone briareus* except that it was more variable, and gonads were often expelled. The two species share this similarity with *Phyllophorus* (Domantay, 1931)—and in general. evisceration probably involves loss of the gut and the lantern with its tentacular crown in all the Dendrochirota except the Psolidae. This mode of evisceration contrasts with that of the Aspidochirota such as *Stichopus* (Dawbin, 1949), *Holothuria* (Kille, 1936) and *Actinopyga* (Mosher, 1956), in which contraction of the body wall causes rupture of the cloaca. Through this rupture the gut and often the respiratory trees are expelled, but the lantern stays intact.

The adaptive advantage of evisceration, if any, is still obscure. It has been proposed that it acts to confuse or distract predators (Domantay, 1931), but no important predators of holothurians are known, and evisceration occurs too long after mechanical disturbance for it to be of any use (Dawbin, 1949).

It has also been proposed that without its viscera an animal would have a lower metabolic rate and be better able to survive adverse conditions such as lack of oxygen (Pearse, 1909). However, lack of oxygen would not be a problem for littoral animals, which often survive without their respiratory trees. Consequent regeneration could easily require more energy than might be saved by evisceration.

Dawbin therefore proposed that evisceration was due entirely to structural weakness breaking under strain. These structural weaknesses occur at well-defined positions—for example, the membranous base of the tentacles or the walls of the cloaca and at each end of the gut.

Now the fact that some holothurians eviscerate seasonally (Bertolini, 1932*a* ; Mosher, 1965 ; Swan, 1961), and that such a complex process as evisceration and consequent regeneration occurs in many species of holothurians with a constant course and often high survival rate, argues that the process has some adaptive advantage. It seems that evisceration, when not caused by mechanical trauma, is due to accumulation of excretory products in the water rather than to lack of oxygen (Dawbin, 1949).

Perhaps evisceration serves as a radical means of excretion. Some waste is certainly disposed of by amoebocytes which are themselves excreted via the gut or respiratory trees. However, it may be that some insoluble excretory product accumulates in the wall of the rectum until it reaches an intolerable level, whereupon the only means of removing it is to eviscerate the gut.

This would explain why excretory products such as ammonia in the sea water are so effective in stimulating evisceration. The numerous brown globules in the wall of the rectum of an uneviscerated animal may be accumulations of such excretory products. They have not been found in the regenerating rectum.

Hyman (1955) notes that " Schreiber has reported the partial destruction and regeneration of coelomic epithelium of the rete network in the removal of the secretion spherules from the rete into the haemal system by the amoebocytes ". This makes such a radical mechanism of excretion as removal of the gut a little less improbable.

Although the majority of the aspidochirotes and dendrochirotes seem to be able to eviscerate, *Stichopus regalis* is one of the few species in which eviscerated specimens have been found in nature, and this argues against evisceration as a means of excretion.

REGENERATION

Regeneration follows a similar course in *Thyone okeni* and in *Thyone briareus.* The only points of difference are the temporary mesenteries supporting new retractor muscles and the much longer time scale in the former. Both species of *Thyone* share this mode of regeneration with the aspidochirote *Stichopus mollis* (Dawbin, 1949) in that the gut is regenerated by a thickening along the whole free edge of the mesentery.

However, in *Holothuria* (Kille, 1936) regeneration of the gut follows quite a different pattern. The cloaca and the oesophagus each send out a hollow tubular outgrowth along the torn edge of the mesentery, and these meet to form a simplified digestive tract which later differentiates fully.

In the wider context of echinoderms in general, the first process involved in regeneration is the closing over of the wound by a coagulum of coelomocytes or by the body wall if it is flexible enough. There is, then, a distinction between somatic and visceral regeneration. Somatic regeneration seems to be governed by outgrowth from remnants of the water vascular system and its accompanying nerve tracts. Visceral regeneration has only been studied seriously in holothurians and has already been discussed.

Regeneration is a special case of development and has been interpreted in this way by application of Child's gradient field theory. However, ideas on morphogenesis have changed considerably over the last decade and models of differentiation have become at the same time more sophisticated and more operational.

I think that a model for the process of regeneration which can be applied to holothurians is one based on removal of an inhibitor for differentiation produced by the eviscerated parts. Thus in the intact animal, the presence of the fully developed viscera inhibits further growth and differentiation, but when the animal eviscerates, the undetermined cells of the mesentery edge and analogous parts are released from inhibition and immediately proliferate. Any system capable of regenerating could then be regarded as showing an equilibrium between an innate tendency to grow and differentiate, and an inhibition of such growth by a substance produced by differentiated tissue.

In conclusion, it seems that holothurian tissue could be very suitable for tissue culture. In this work, holothurian tissue has survived for up to three months in a sea water medium with no external nutrition. Holothurians might then prove a useful tool in the study of the induction and control mechanisms of development.

ACKNOWLEDGEMENTS

I should like to acknowledge help from Isobel Bennett, Ken Welton, John Merrick and Ken Sanderson, who obtained specimens for me ; and in particular from Dr. W. H. Dawbin, whose help and advice were invaluable.

References

BELL, F. J., 1884.—*Rept. zool. coll. Indo Pacific Ocean, Voyage of H.M.S. " Alert ", 1881–1882.*

BERTOLINI, F., 1930.—Rigenerazione dell' apparato digirente nelle *Stichopus regalis. Publ. Staz. Zool., Napoli,* 10 : 439.

————, 1932*a*.—L'autotomia dell' apparato digirente e la sua rigenerazione nella Oloturie, come fenomena spontaneo e normale. *Rend. R. Acc. Lincei* (Cl. Sc. fis. mat. and nat.) S. 6, 15 : 893.

————, 1932*b*.—Rigenerazione dell' apparato digirente nelle Holothuria. *Publ. Staz. Zool., Napoli,* 12 : 432.

BOOLOOTIAN, R. A., 1966.—*Physiology of Echinodermata.* New York : Wiley.

BONNER, J. T., 1965.—*The Molecular Biology of Development.* Oxford : Clarendon Press.

CLARK, H. L., 1921.—*Echinoderm Fauna of Torres Straits.* (Carnegie Inst. Wash. Pub. 214, p. 205.)

————, 1946.—*Echinoderm Fauna of Australia.* (Carnegie Inst. Wash. Pub. 566, p. 203.)

DAKIN, W. J., 1952.—*Australian Seashores.* Sydney : Angus & Robertson.

DAWBIN, W. H., 1949.—Autoevisceration and the regeneration of viscera in the Holothurian *Stichopus mollis* (Hutton). *Trans. Roy. Soc. N.Z.,* 77 : 497.

DOMANTAY, J. S., 1931.—Autotomy in Holothurians. *Univ. Philippines Nat. and Applied Sci. Bull.,* 1 (4) : 389.

HYMAN, L., 1955.—*The Invertebrates. IV. Echinodermata.* New York, McGraw-Hill.

KILLE, F. R., 1935.—Regeneration in *Thyone briareus* Lesueur following induced autotomy. *Biol. Bull.,* 69 : 82.

————, 1936.—Regeneration in Holothurians. *Yearbk. Carnegie Inst. Wash.,* 35 : 85.

MOSHER, C., 1956.—Observations on evisceration and visceral regeneration in the sea cucumber, *Actinopyga agassizi* Selenka. *Zoologica N.Y.,* 41 : 17.

————, 1965.—Notes on the natural evisceration of the sea cucumber *Actinopyga agassizi* Selenka. *Bull. Mar. Sci.,* 15 : 255.

NACE, A. G., 1966.—Histology of anterior digestive tract of *Thyone briareus. Amer. Zool.,* 6 (4) : 615.

PEARSE, A. S., 1909.—Autotomy in Holothurians. *Biol. Bull.,* 18 : 42.

SCOTT, J. W., 1914.—Regeneration, variation and correlation in *Thyone. Amer. Nat.,* 48 : 280.

SWAN, E. F., 1961.—Seasonal evisceration in the sea cucumber, *Parastichopus californicus. Science,* 133 : 1078.

TRINKAUS, J. P., 1965.—Mechanisms of morphogenetic movements. *In* " Organogenesis ". (Eds. De Haan, R. L., and Ursprung, H. Holt, Rinehart & Winston, N.Y.).

A NEW SPECIES OF HYLID FROG FROM NEW SOUTH WALES

Michael J. Tyler
South Australian Museum, North Terrace, Adelaide, S.A.

and

Angus A. Martin and Graeme F. Watson
Department of Zoology, University of Melbourne, Parkville, Vic.

(Plate II)

[Accepted for publication 17th November 1971]

Synopsis

A new species of *Litoria* from central coastal New South Wales is described. Its variation and affinities are examined and it is considered to be most closely related to *L. citropa* (Tschudi).

Introduction

The anuran fauna of New South Wales has received considerable attention and has been demonstrated to be a rich and diverse assemblage. Cogger (1960) recorded 45 species of frogs from the State, and Moore (1961) recognized 43.

In recent years further studies have modified and increased the content, and have affected the nomenclature of Moore's checklist of species: Littlejohn and Martin (1964) restored *Crinia victoriana* Boulenger to specific status and reported its occurrence in the extreme south-east of the state; Littlejohn (1965) resurrected *Hyla verreauxi* (Dumeril) from the synonymy of *H. ewingi* Dumeril and Bibron and found both species in New South Wales; Straughan and Main (1966) reported *Crinia darlingtoni* Loveridge from the north-eastern border of the State; Straughan (1968) described two new species of *Mixophyes* Günther; Straughan (1969) elevated *Hyla bicolor glauerti* Copland to specific status; and Tyler (1971) resurrected *Litoria* Tschudi to accommodate the Australian species formerly referred to *Hyla* Laurenti.

In January, 1970, two of us (Martin and Watson) collected representatives of an undescribed species of *Litoria* near Byabarra, approximately 190 miles north-north-east of Sydney. Additional representatives of this species have been found subsequently by other collectors at adjacent localities. In our description of the new species we follow the methods and terminology of Tyler (1968). The abbreviations used in the text are: E–N/IN=eye to naris distance/internarial span; HL/HW=head length/head width; HL/S–V=head length/snout to vent length; TL/S–V=tibia length/snout to vent length.

Litoria brevipalmata n. sp.

Holotype. South Australian Museum No. R.11236. An adult male collected at Ourimbah Creek, about five miles north-west of Gosford, New South Wales, by F. Parker, on 29th January, 1971.

Definition. A moderate-sized species (males 41·0 mm.; females 45·2–47·4 mm.) characterized by short hind limbs (TL/S–V ratio 0·409–0·459), unwebbed fingers and greatly reduced webbing between the toes. The dorsal surface of the head, body and limbs are immaculate, pale brown; there is a continuous, broad, black stripe extending from the post-orbital margin to the axilla, bordered inferiorly by a narrow, white labial stripe.

Description of holotype. The head is smoothly rounded and slightly longer than broad (HL/HW 1·128). In relation to the body size the head is moderate, its length being approximately one-third of the snout to vent length (HL/S–V 0·324). The snout is not prominent and does not project conspicuously beyond the anterior limit of the mandible ; it is evenly rounded viewed both from above and in profile. The nostrils are dorsolateral in position and considerably closer to the tip of the snout than to the eye. The distance between the eye and the naris is greater than the internarial span (E–N/IN 1·267). The canthus rostralis is straight but not sharply defined ; the loreal region is gently sloping. The eye is large ; its diameter is considerably greater than the eye to naris distance.

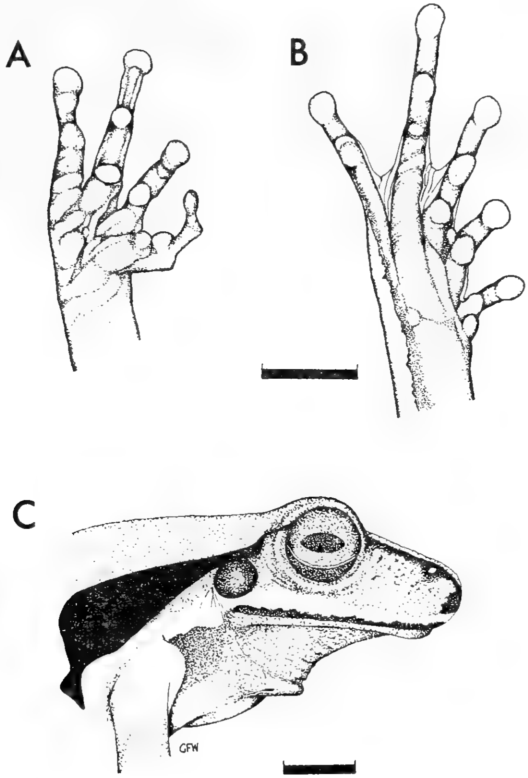


Fig. 1. *Litoria brevipalmata* new species, paratype female, M.U.Z.D. No. 13/70. (A) Palmar surface of hand. (B) Plantar surface of foot. (C) Lateral view of head. The bars represent 5 mm.

The tympanum is large and prominent, its diameter two-thirds of the eye diameter, and separated from the eye by a distance equal to about half the eye diameter. The upper margin of the tympanum is hidden beneath the supratympanic fold. The vomerine teeth are in two small series on prominent elevations directly between the choanae. The tongue is circular and almost completely adherent to the floor of the mouth.

The fingers are long, slender, unwebbed and without lateral fringes (Fig. 1 (A)). The sequence of decreasing length is 3>4>2>1. When the digits are extended the thumb is inclined at right angles to the fourth finger. Terminal discs are small, the diameter of that of the third finger being about one and one-half times the width of the penultimate phalanx.

The hind limbs are short; the TL/S–V ratio is 0·459. Toes in decreasing order of length are 4>5>3>2>1. The webbing between the toes is greatly reduced, reaching the base of the penultimate phalanx of each toe except the fourth (Fig. 1 (B)). The toes have slender lateral fringes. There is a prominent oval inner and a very poorly defined and rounded outer metatarsal tubercle.

The dorsal surfaces of the head, body and limbs are entirely smooth, and the limbs lack dermal appendages. There is a prominent supratympanic fold extending from the eye to a position above the insertion of the arm. The ventral mandibular margin, the abdomen and the ventral surfaces of the thighs are granular, the granules progressively decreasing in size, but increasing in prominence, posteriorly. The skin of the submandibular and pectoral regions is smooth and distended as a result of inflation of the vocal sac. Nuptial pads are glandular.

The dorsal surfaces are a very pale, uniform brown, on which there is black stippling, so sparsely distributed as to be hardly visible. From the tip of the snout to the post-axillary region there is a black stripe, narrowest on each side of the eye and expanding behind the tympanum into a large black patch. A white stripe on the labial border expands posteriorly to form a white patch about the insertion of the arm. The striking contrast thus created is further emphasized by a black margin to the white stripe (Fig. 1 (C)). The posterior surfaces of the thighs, the axilla and the sides of the body bear black variegations and circular black spots on a pale grey background. The ventral surfaces of the body and limbs are a dull cream colour.

In life the dorsum was the colour of milk chocolate, and the groins, posterior surfaces of the thighs, and the axillary regions were very pale green.

Dimensions: snout to vent length 41·0 mm.; tibia length 18·8 mm.; head length 15·0 mm.; head width 13·3 mm.; eye to naris distance 3·8 mm.; internarial span 3·0 mm.; eye diameter 4·6 mm.; tympanum diameter 3·0 mm.

Variation. There are three paratypes: Australian Museum No. R.30835, an adult male collected at Ourimbah Creek Road, 2 miles west of Ourimbah on 13th March, 1971, by J. Barker; University of Melbourne, Department of Zoology (M.U.Z.D.) No. 13/70, an adult female collected 2·5 miles north-east of Byabarra (near Wauchope), N.S.W., on 28th January, 1970, by A. A. Martin and G. F. Watson; and M.U.Z.D. No. 190/70, an adult female collected 4 miles west of Ourimbah, N.S.W., on 29th January, 1970, by Martin and Watson.

The male paratype has the same snout to vent length as the holotype; the females measure 45·2 and 47·4 mm. respectively. In their proportions there is close agreement with those of the holotype, the ranges of the ratios used here to express such proportions being: E–N/IN 1·258–1·433; HL/HW 1·078–1·092; HL/S–V 0·336–0·349; TL/S–V 0·409–0·429. In life and in preservation colouration conforms closely to that of the holotype. Plate II shows a living female paratype.

Ovarian eggs in a gravid female in the series (M.U.Z.D. No. 13/70) are pigmented and have a diameter of about 1·4 mm.

Comparison with other species. The combination of external morphological characters by which we have defined *L. brevipalmata* is such that the species can readily be distinguished from all other species of *Litoria*. However, the nature of the combination is so unusual that the phylogenetic relationships to other species are difficult to establish.

There are a number of species of hylid frogs in New South Wales which possess elongate, unwebbed fingers with rather small terminal discs: *L. aurea* (Lesson), *L. booroolongensis* (Moore), *L. freycineti* Tschudi, *L. latopalmata* Günther, *L. lesueuri* (Dumeril and Bibron), and *L. nasuta* (Gray). They have been compared in such detail by Moore (1961) that we list here only a few of the salient characters distinguishing them from *L. brevipalmata*. *Litoria aurea* is considerably larger (up to twice the size of *L. brevipalmata*), with extensively webbed toes; *L. booroolongensis* is comparable in size but has longer hind limbs and webbing which reaches the discs of all toes. *Litoria freycineti* and *L. nasuta* are slender, elongate species with long hind limbs, long toes, and dermal ridges on the back; interdigital webbing is reduced but still far more extensive than in *L. brevipalmata*. *Litoria latopalmata* is usually grey in preservative and also has long hind limbs and more extensively webbed toes.

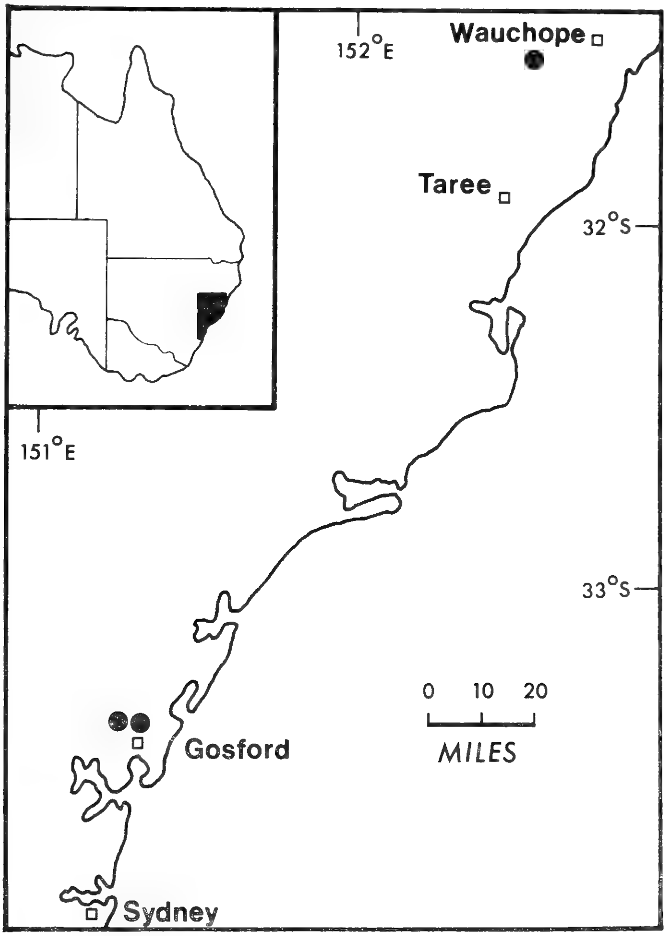


Fig. 2. Known geographic distribution of *Litoria brevipalmata*. The area involved is shown in black in the inset.

Despite a number of obvious morphological differences, *L. brevipalmata* may be most closely related to *L. citropa* (Tschudi), which has a similarly proportioned hand and foot and a broad post-ocular stripe reaching, and usually extending beyond, the post-axillary region. *Litoria citropa* is most readily distinguished by its larger size (females measuring up to 64 mm. in length). In addition *L. citropa* possesses a submandibular dermal gland which, when well developed, is visible as a broad glandular area adjacent to the lingual margin of the mandibles.

Field notes. The specimens collected near Byabarra and Ourimbah in 1970 were found hopping across roads on warm rainy nights. Other species of *Litoria* calling near Byabarra were *L. caerulea* (White), *L. dentata* (Keferstein), *L. glauerti*, *L. gracilenta* (Peters), *L. latopalmata* and *L. peroni* (Tschudi). With the exception of *L. gracilenta*, the same species were calling at Ourimbah, together with *L. chloris* (Boulenger), *L. freycineti*, *L. phyllochroa* (Günther) and *L. verreauxi*.

Distribution. *L. brevipalmata* is known only from the type series from the Ourimbah and Byabarra areas (Fig. 2). We presume that further collecting will reveal that *L. brevipalmata* occurs between, and perhaps beyond, the currently known localities.

ACKNOWLEDGEMENTS

We are indebted to Dr. H. G. Cogger of the Australian Museum for the loan of a specimen here referred to the new species; to the University of Melbourne for travelling expenses; and to Dr. W. G. Inglis of the South Australian Museum for criticism of the manuscript.

References

COGGER, H. G., 1960.—*The Frogs of New South Wales.* Australian Museum, Sydney. 38 pp.

LITTLEJOHN, M. J., 1965.—Premating isolation in the *Hyla ewingi* complex (Anura: Hylidae). *Evolution*, 19 (2): 234–243.

——— and MARTIN, A. A., 1964.—The *Crinia laevis* complex (Anura: Leptodactylidae) in southeastern Australia. *Aust. J. Zool.*, 12 (1): 70–83.

MOORE, J. A., 1961.—The frogs of eastern New South Wales. *Bull. Amer. Mus. Nat. Hist.*, 121: 149–386.

STRAUGHAN, I. R., 1968.—A taxonomic review of the genus *Mixophyes* (Anura, Leptodactylidae). PROC. LINN. SOC. N.S.W., 93 (1): 52–59.

———, 1969.—The *Hyla bicolor* complex (Anura, Hylidae) in north Queensland. *Proc. Roy. Soc. Qld.*, 80 (5): 43–54.

——— and MAIN, A. R., 1966.—Speciation and polymorphism in the genus *Crinia* Tschudi (Anura, Leptodactylidae) in Queensland. *Proc. Roy. Soc. Qld.*, 78 (2): 11–28.

TYLER, M. J., 1968.—Papuan hylid frogs of the genus *Hyla*. *Zool. Verh., Leiden*, (96): 1–203.

———, 1971.—The phylogenetic significance of vocal sac structure in hylid frogs. *Univ. Kansas Publ. Mus. Nat. Hist.*, 19 (4): 319–360.

Living female specimen of *Litoria brevipalmata* (paratype, M.U.Z.D. No. 13/70).

A FELLODISTOMID CERCARIA FROM *MYTILUS PLANULATUS*

J. C. Walker
School of Public Health and Tropical Medicine,
Sydney University

[Accepted for publication 15th September 1971]

Synopsis

The large furcocercous cercaria of a fellodistomid trematode is reported from the mussel, *Mytilus planulatus,* in New South Wales. Apart from its size, this cercaria is unusual in having an almost fully developed reproductive system and in the possession of intestinal caeca of unequal length. These and other details of morphology differentiate this cercaria from others previously recorded from this family. The larva is described and named *Cercaria praecox* n. sp.

Introduction

In Sydney Harbour and on the south coast of New South Wales the mussel, *Mytilus planulatus* Lamarck, 1819 is occasionally infected with the larval stages of a fellodistomoid trematode. The visceral mass and gonad of infected mussels are packed with sac-like sporocysts, usually bright orange, in which develop large furcocercous cercariae. This infection of mussels is rare in Sydney Harbour, only four of more than one thousand *Mytilus* examined over two years being infected, and the cercariae have been found in only one of four areas sampled so far. This is at " The Spit " in Middle Harbour. A low rate of infection in mussels collected near Bateman's Bay on the New South Wales south coast has been reported by Dr. M. J. Howell (personal communication). These larvae have been found before, as wholemounts of sporocysts and cercariae labelled " Fork Tailed Cercaria, *Mytilus* sp., Sydney Harbour, 1932 ", are in the Parasitology Museum, School of Public Health and Tropical Medicine, Sydney. No other details of this earlier collection are known, and as there is no published description, the larva is described here and named *Cercaria praecox* n. sp., with reference to its advanced state of gonad development.

Materials and Methods

The description is based on sporocysts and cercariae dissected from mussels and examined both alive in seawater and as wholemounts fixed with hot 70% alcohol then stained with Gower's carmine, and on serial sections cut at 9μm. from infected host tissue. Twenty-seven larvae, selected for their advanced state of development, were measured, and all measurements are, unless stated otherwise, from living cercariae flattened under a coverslip and are in millimetres. The values stated in the text are the minimum and maximum obtained for each character measured.

Description

Distome, non-ocellate, furcocercous cercaria developing in simple sporocysts in the visceral mass and gonad of *Mytilus planulatus.* Sporocysts bright orange, cercariae white. Body of cercaria aspinose, contractile, varying from elongate to globose. Body length of specimens measured unflattened; extended 1·90–2·10, contracted 0·20–1·0; body width, extended 0·19–0·20, contracted 0·40–0·70. Oral sucker wider than long, 0·25–0·60 × 0·24–0·41; ventral sucker at centre of body, circular, 0·15–0·28 diameter. Mouth terminal; no prepharynx; pharnyx large, length 0·14–0·30, width 0·14–0·24; oesophagus extending past ventral sucker ; caeca thick walled with blind ends, that of the right side extending to the end of the body, that of the left side half way only.

Groups of gland cells in region of oral sucker, beside pharynx, and in lateral fields and centre of body behind ventral sucker. Details of ducts not determined.

Reproductive system well developed. Testes ventral, just posterolateral to ventral sucker ; oval, 0·09–0·18 × 0·50–0·13 ; cirrus sac 0·21–0·42 × 0·10–0·14, containing bipartite seminal vesicle, unspined cirrus and prostatic cells ; situated

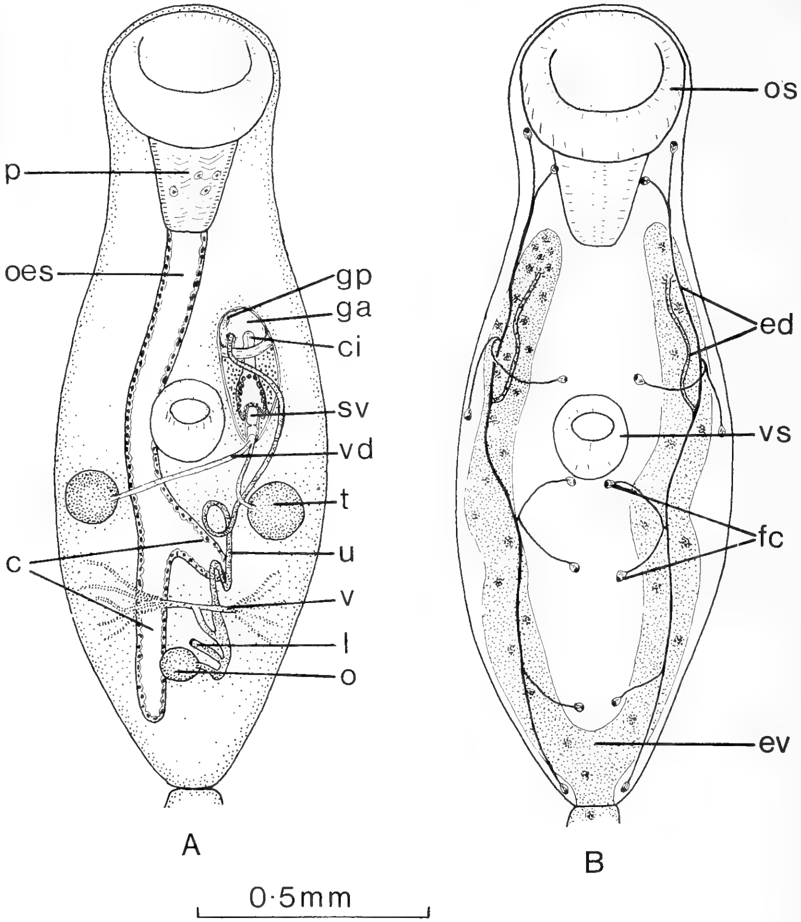


Fig. 1. *Cercaria praecox* n. sp. (A) Body of cercaria, ventral view showing intestine and reproductive system. Specimen flattened under a coverslip resulting in displacement of organs such as cirrus sac, which is normally vertical. (B) Body of cercaria, ventral view showing excretory system.

Abbreviations for Text-figures

c—caeca.
ci—cirrus.
ed—excretory duct.
ev—excretory vesicle.
fc—flame cell.
ga—genital atrium.
gp—genital pore.
l—laurer's canal.
o—ovary.
oes—oesophagus.
os—oral sucker.
p—pharynx.
sv—seminal vesicle.
t—testis.
u—uterus.
v—primordium of vitelline glands.
vd—vas deferens.
vs—ventral sucker.

slightly to left of and anterior to ventral sucker, bending ventrally to open into genital atrium from above. Ovary posterior to testes and just anterior to excretory vesicle, entire, circular to oval, 0·08–0·18×0·04–0·13. Laurer's canal present, short, opening on dorsal surface near ovary. Uterus with several coils in post-testicular area, extending anteriorly to open ventrally into genital atrium. Primordia of vitelline glands in lateral fields at level of ovary, with a racemose pattern of collecting ducts.

Excretory vesicle thin walled, lyre-shaped, with long arms ; protonephridium stenostomate ; recurrent tubule ciliated, extending back to region of ventral sucker, where it receives an anterior and a posterior collecting tubule, each of which is joined to two groups of two flame cells. The excretory formula is, therefore, $2[(2+2)+(2+2)]$. A muscular sphincter opens into a single caudal tubule extending from the excretory vesicle to the furcae, where it divides ; excretory pores at tips of furcae. Excretory vesicle and tail of some older specimens filled with refractile concretions.

Tail length to fork in unflattened specimens 1·33–3·30, width 0·13–0·16 ; furcal length 0·79–1·60.

Sporocysts simple, sac-like ; broader posteriorly, narrowing to anterior tip, where birth pore is situated. Length of largest specimens after fixation and staining 3·0.

Host : *Mytilus planulatus* Lamarck, 1819.

Localities : Sydney Harbour and the south coast of N.S.W.

Type Material : School of Public Health and Tropical Medicine, Sydney. Reg. No. MN1663.

Discussion

Holliman (1961), in a checklist of known marine cercariae, mentioned 20 species of fork-tailed fellodistomid cercariae, and in the same article described four new species, thus bringing the total number known at that time to 24.

Nineteen of these larvae are ascribable to the Dichotoma group of cercariae, minute larvae with spinose bodies and short intestinal caeca which rarely extend past the ventral sucker, considered by Cable (1953) to be larvae of the Gymnophallinae. The adults of this group lack a cirrus sac and have compact vitellaria situated in the mid-line, near to the ventral sucker. The genital pore is also median. *Cercaria praecox* n.sp. differs in each of these characteristics, and presumably the adult form of this larva is distinct from the adults of the Gymnophallinae.

The cercaria of *Fellodistomum felis* Nicoll, 1909, which develops in the bivalve *Nucula tenuis* (Montagu), differs from *C. praecox* in being smaller (cercarial body 0·59×0·36), in having a short oesophagus and caeca of equal length, and in not reaching the same stage of gonad development in the molluscan host. Whilst the vitelline follicles of most of the Fellodistominae, including *F. felis*, are anterior to the ventral sucker, in *C. praecox* two groups of cells which are presumably the primordia of the vitellaria are situated in the lateral fields at the level of the ovary, which is posterior. Little change in the position of organs is likely during growth to the adult, as the larva is already very advanced in development.

Three other furcocercous larvae, *C. haswelli* Dollfus, 1927, *C. kenti* Dollfus, 1927, and *C. mathiasi* Dubois, Baer and Euzet, 1952, possess the characters of the genus *Tergestia* Stossich, namely 13 muscular lobes arranged in a circle, incomplete ventrally, around the oral sucker, and six paired cuticular folds on the sides of the forebody. The tails of these cercariae are dilated proximally, forming an organ considered to be a pneumatophore (Angel, 1960). *C. praecox* lacks all these characters and differs also from the larvae of *Tergestia* in having intestinal caeca of unequal length and in the arrangement of the gonads.

The cercaria of the genus *Haplocladus* described by Rees (1947) is similar to *C. praecox* in a number of respects, particularly the excretory system, but has an unbranched intestine and testes placed in tandem, lateral to the excretory bladder near the posterior end of the body.

Four subfamilies of the Fellodistomidae were recognized by Cable (1953). These were: Fellodistominae Nicoll, 1909; Gymnophallinae Odhner, 1905; Haplocladinae Odhner, 1911; and Tandanicolinae Johnston, 1927. Dollfus (1947) maintained, and Yamaguti (1953) accepted this view, that *Monascus* Loos, 1907 has priority over *Haplocladus* Odhner, 1911 and that the correct subfamily name is Monascinae.

Cable (1954) stated that the primitive condition in the Fellodistomidae is furcocercous, but that this has been altered along several lines. Thus cercariae related phylogenetically may differ greatly in the development and morphology of the tail. Expression of relationship between fellodistomid cercariae should, consequently, be based on the morphology of the body and on knowledge ot life histories. *C. praecox* n. sp. is more representative of the Monascinae than of any other of the subfamilies of the Fellodistomidae. The intestine, with its long oesophagus and unequal length caeca placed behind the ventral sucker, could be considered an intermediate stage between a form with equal length caeca and *Monascus* with an unbranched intestine. Although the flame cell pattern of the Fellodistomidae is variable and the same pattern may be found in quite different genera, the formula of *C. praecox* $2[(2+2)+(2+2)]$, is found in three genera of the Monascinae: *Monascus*, *Tergestia*, and *Proctoeces*.

Though it is similar to the Monascinae, *C. praecox* is clearly not congeneric with any of the members of that subfamily, and further clarification of its taxonomic position depends on the finding of other stages in the life cycle. Several fellodistomid life cycles are known, and these may provide guidelines in the search for the adult of *C. praecox*.

Metacercariae of *Proctoeces* are known to be progenetic in their molluscan second intermediate hosts (Stunkard and Uzmann, 1959; Dollfus, 1964), and are probably able to dispense with the definitive host, a fish, though the abnormal host conditions result in frequent loss of fertility. *C. praecox* reaches an advanced stage of gametogeny in the molluscan host, spermatids being present in the testes of large cercariae, and requires only to pass through the stages of egg-shell formation and vitellogenesis, and oviposition to reach sexual maturity, and it may possibly have a life cycle similar to that described by Stunkard and Uzmann (1959) for *Proctoeces maculatus*. However, such a large, inactive larva as *C. praecox* would more probably be ingested by either a second intermediate host or the definitive host. No cercariae have been seen to leave the infected mussels in the laboratory and those larvae released by dissection have shown no tendency to swim, but instead sink to the bottom, where they lie, contracting and expanding the body and coiling and uncoiling the tail (Fig. 2). In the dissected mussels, cercariae and sporocysts were carried by ciliary currents and ejected, and this would presumably happen to cercariae emerging from sporocysts under natural conditions, though larvae of some Gymnophallinae are known to develop as unencysted metacercariae between the mantle and shell of bivalves (Holliman, 1961). Cercariae which emerged from or were ejected from mussels would sink to the bottom or into the mass of weed and sponges lower down on the wharf piles where infected mussels have been found. In this situation detritus feeders such as crabs or ophiuroids would be likely second intermediate hosts. Chubrik (1952) described the life cycle of *Fellodistomum felis* in which an ophiuroid, *Ophiura sarsi* Lutken, acts as second intermediate host. The ophiuroid is eaten by a fish and the adult fluke develops in the gall-bladder and bile ducts. Bottom-feeding fish which eat invertebrates could possibly be the definitive host of *C. praecox*. Similarly, fish, such as Toados (Ovoididae) and Porcupine-fish (Diodontidae), which eat mussels, could also be the definitive host of this cercaria.

Stunkard and Uzmann (1959) suggested that fish acquire infection with species of *Proctoeces*, which are progenetic in bivalves, by eating the infected molluscs. This situation could lead to false host records for some trematodes, as a fish examined soon after ingesting an infected mussel would contain apparently mature adult flukes in its intestine.

It is probable that the adult of *C. praecox* n. sp., when found, will bear close relationship to the Monascinae, possibly constituting a new genus in that subfamily.

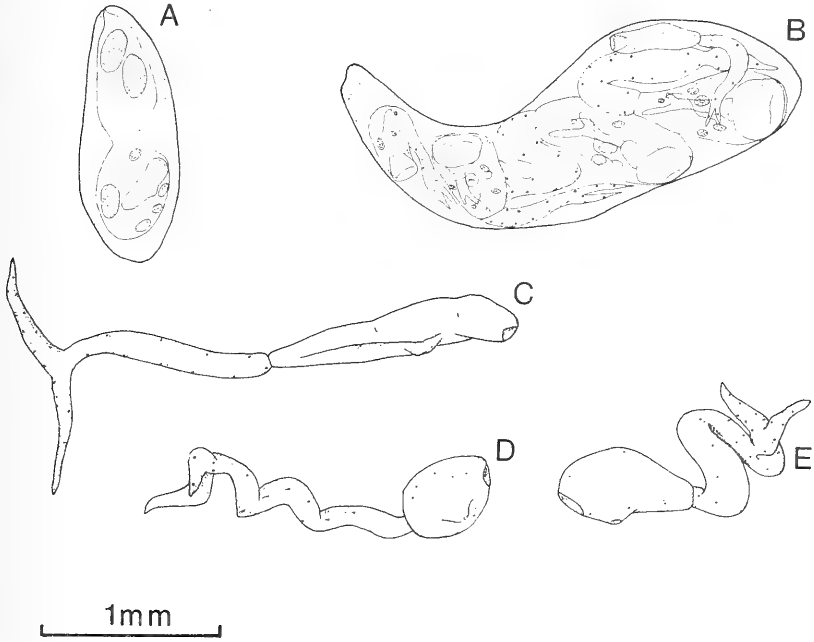


Fig. 2. *Cercaria praecox* n.sp. (A) Young sporocyst containing germ balls and developing cercaria. (B) Mature sporocyst containing mature and developing cercariae. (C) Cercaria in extended position. (D), (E) Cercariae with bodies contracted and tails coiled.

ACKNOWLEDGEMENTS

I wish to thank Dr. M. J. Howell of the Department of Zoology, Australian National University, for providing serial sections of material collected on the south coast; Professor B. McMillan of the School of Public Health and Tropical Medicine, Sydney University, and Dr. D. T. Anderson of the Zoology Department, Sydney University, for comments on the manuscript. This publication is made with the permission of the Commonwealth Director-General of Health, Canberra, A.C.T.

References

ANGEL, L. M., 1960.—*Cercaria haswelli* Dollfus 1927; a reexamination of Haswell's material, with discussion of the genus *Tergestia*. *Libro Homenaje al Doctor Eduardo Caballero y C., Mexico*, 1960: 75–86.

CABLE, R. M., 1953.—The life cycle of *Parvatrema borinqueñae* gen. et sp. nov. (Trematoda: Digenea) and the systematic position of the subfamily Gymnophallinae. *J. Parasit.*, 39: 408–421.

————, 1954.—A new marine cercaria from the Woods Hole region and its bearing on the interpretation of larval types in the Fellodistomatidae (Trematoda: Digenea). *Biol. Bull.*, 106 (1): 15–20.

CHUBRIK, H. K., 1952.—Larval development stages of the trematode *Fellodistomum felis* Nicoll 1909 found in invertebrates of the Berring Sea. *Zool. Zhur.* (*SSSR*), 31: 653–658.

Dollfus, R. P., 1947.—Sur *Monascus filiformis* (Rudolphi, 1819) A. Loos, 1907, trématode de l'intestin de *Cepola rubescens* (L.) en Méditerranée. *Ann. Parasitol.*, 22 : 319–323.

————, 1964.—Metacercaria : *Proctoeces progeneticus* (Trematoda Digenea) chez une *Gibbula* (Gastropoda Prosobranchiata) de la côte atlantique du Maroc. *Ann. Parasitol.*, 39 : 755–774.

Holliman, R. B., 1961.—Larval trematodes from the Apalachee Bay area, Florida, with a check-list of known marine cercariae arranged in a key to their superfamilies. *Tulane Studies in Zoology*, 9 (1) : 2–74.

Rees, W. J., 1947.—A cercaria of the genus *Haplocladus* from *Nucula nucleus* (L.). *Jour. Mar. Biol. Assoc. United Kingdom*, 26 : 602–604.

Stunkard, H. W., and Uzmann, J. R., 1959.—The life cycle of the digenetic trematode, *Proctoeces maculatus* (Loos, 1901) Odhner, 1911, Syn *P. subtenuis* Linton, 1907) Hanson, 1950, and description of *Cercaria adranocerca* n. sp. *Bioll. Bull. Woods Hole*, 116 : 184–193.

Yamaguti, S., 1958.—*Systema Helminthum.* Vol. 1, Parts 1 and 2. The Digenetic Trematodes of Vertebrates. Interscience Publishers, Inc., New York, 1575 pp.

The *Proceedings of the Linnean Society of New South Wales* contain original papers relative to "the Science of Natural History in all its branches", and reports of business transacted at the meetings of the Society.

NOTES AND INSTRUCTIONS FOR AUTHORS

Original papers may be submitted for consideration for publication in the Society's Proceedings. Submission of a manuscript must imply that the contents are original and have not been published previously in the same, similar, or abbreviated form, and that no similar paper is being or will be submitted for publication elsewhere until it has been either (*a*) not accepted for publication by the Society or (*b*) withdrawn by the author.

Papers submitted should embody the results of a significant piece of work. Interim reports, serialized studies and student theses should not be submitted.

Papers are accepted for publication (or otherwise) by the Council of the Society after taking into consideration advice received from at least one referee. The decision of Council is final.

Once accepted for publication a paper becomes the property of the Society, and copyright is vested in the Society. Reproduction of the author's synopsis in abstracting journals is authorized.

A paper may be withdrawn by the author at any time prior to acceptance.

Papers may be submitted by members or non-members of the Society but a paper submitted by a non-member must be communicated by a member of the Society, and will not ordinarily be considered for acceptance before July in each calendar year.

SUBMISSION OF MANUSCRIPTS

Manuscripts should be forwarded to the Secretary, The Linnean Society of New South Wales, 157 Gloucester Street, Sydney, N.S.W. 2000.

Text and illustrations must be submitted in duplicate. The illustrations may be duplicated by any acceptable clear method and the duplicate set need not necessarily be identical in size with the originals. The author should retain a third copy for checking proofs. If a paper is not accepted for publication, the original copy of the typescript and illustrations will be returned to the author, but the duplicate copy may be retained by the Society.

Owing to the ever growing costs of publication, authors are requested to write their papers clearly and concisely and exercise all reasonable economy in the number and form of illustrations and tables.

Grants towards the cost of publication should be secured wherever possible from the author's own institution or elsewhere; contributions from authors, especially non-member authors, may be requested at Council's discretion, particularly in the case of lengthy papers, or those with numerous illustrations or tables.

Manuscripts must be submitted in final, fully corrected form. Authors may be liable for the cost of proof corrections (if allowed) if the number of alterations and corrections is considerable. Authors are urged to submit their paper to a colleague for constructive criticism prior to final typing and submission for publication.

MANUSCRIPTS

Papers should be typewritten, double spacing throughout, on one side of quarto or foolscap paper, with at least one-inch margins all round. The desired position of all text-figures, maps and tables may be indicated in the margin. All pages should be numbered serially and securely fastened together. Papers should conform to the following general layout as far as practicable or appropriate:

(*a*) *Title.*—The title should be concise but informative. The name(s) of the author(s) and the name of the institution where the work was carried out should follow the title. The name of a new taxon of plants or animals should not be included in the title. A short title appropriate for the running heading of subsequent pages may be suggested. The title, etc., should be on a *separate page* at the commencement of the typescript.

(*b*) *Synopsis.*—A concise abstract (without abbreviations), preferably consisting of not more than about 200 words, should be supplied on a *separate sheet* and in *triplicate*. It should be complete in itself and indicate the scope of the work. It will be printed below the title of the paper and in the Society's Abstract of Proceedings; it will be available for reprinting by abstracting journals.

(*c*) *Table of Contents.*—This should give the complete hierarchy of headings and sub-headings used in the subject-matter of the paper. It should be supplied on a *separate sheet* for guidance of the editor and will not ordinarily be printed.

(*d*) *Introduction*, followed by the *Subject Matter* of the paper. Papers may be divided into sections described by short headings.

(*e*) *Discussion, Conclusions or Summary* (if necessary).—This should summarize the conclusions reached rather than be a précis of the paper as a whole (cf. Synopsis).

(*f*) *Acknowledgements*, if any.

(*g*) *References.*—The author, who is alone responsible for their accuracy, should carefully check all references against the text, to ensure especially that:

(i) The spelling of authors' names is consistent, and the dates, volume numbers and page numbers are correct.

(ii) All authors quoted in the text are included in the list of references.

References should be cited in the text by the author's name and date, e.g., Bullough (1939) or (Bullough, 1939) according to context, and listed alphabetically under References thus:

Bullough, W. S., 1939—A Study of the Reproductive Cycle of the Minnow in Relation to the Environment. *Proc. zool. Soc. Lond.*, 109, A: 79-108.

If more than one reference by the same author(s) published in the same year is cited, use a, b, etc., after the year in both text and list, e.g., Bullough (1939 a).

Titles of books must be given in full together with the place of publication, name of publisher and indication of edition if other than the first.

Latin names of plants and animals (genera, species and their subdivisions) should be underlined to indicate italics. An initial capital letter must be used for Latin names of orders, families and similar names, but these should not be underlined.

Abbreviations.—Only standard abbreviations should be used; authors should refer to the British Standard 1991: Part 1, 1967. Recommendations for Letter Symbols, Signs and Abbreviations. The abbreviations of names of periodicals should conform to those in the World List of Scientific Periodicals.

Footnotes should be avoided as far as possible.

Codes of Nomenclature.—The Botanical and Zoological Codes of Nomenclature must be strictly followed. If a new taxon is described, the institution in which the type material is deposited must be indicated.

Language.—Papers in languages other than English are unlikely to be accepted for publication. Foreign authors are urged to seek assistance, if necessary, in rendering the paper in fluent English prior to submission.

Measurements must be expressed in the metric system as far as practicable, and exclusively in scientific description.

Illustrations and Tables

The maximum dimensions available for either text-figures or plates are 20 x 12.5 cm.

Black and white drawings and diagrams for text-figures should be in Indian ink on smooth white card such as Bristol board the lines cleanly drawn, and due attention paid to the consequences of reduction. Graphs should similarly be in Indian ink on white card, or on faint blue-lined co-ordinate paper. Maps should be in Indian ink on white card or tracing linen; if the latter the linen should not be folded. Maps should be of a size and scale that can be conveniently reduced to the size of a single page.

It is desirable that all black and white illustrations should be drawn 1½-2 times the size that they will appear in print.

Photographs for half-tone plates should be the size required for final reproduction or slightly larger, printed on glossy paper, of good contrast and best quality. A number of small photographs can be arranged to form one plate.

Illustrations for colour reproduction cannot be accepted unless the author meets the difference in cost between black and white and colour reproduction.

Illustrations of all kinds should bear the author's name and the number of each, lightly pencilled on the back, and their required orientation clearly indicated.

Legends for illustrations should be typed on separate sheets at the end of the manuscript. Great care should be taken in stating magnifications of illustrations, making it clear whether numbers quoted refer to before or after reduction.

Tables.—Tables should be numbered consecutively and referred to specifically in the text by number. Each table, together with a heading descriptive of its contents, should be submitted on a separate sheet. Elaborate tables should be avoided.

General

Proofs.—A set of galley proofs will be forwarded to the author who should correct and return them promptly to the Secretary.

Reprints.—Twenty-five reprints are supplied free to authors who are members of the Society. Additional reprints may be ordered at the authors' expense, if desired. No free reprints are supplied to non-members who may, however, order the number required at their own expense. Orders for reprints should be placed with the Secretary immediately after the paper has been accepted for publication. Orders received after the paper has been printed may not be accepted.

Joint Authorship.—In the case of papers by more than one author, one of them must accept responsibility for all correspondence with the Society regarding the paper.

AUSTRALASIAN MEDICAL PUBLISHING CO. LTD.
71-79 ARUNDEL ST., GLEBE, SYDNEY, N.S.W., 2037

Copies of the PROCEEDINGS OF THE LINNEAN SOCIETY OF NEW SOUTH WALES (with the exception of a few Volumes and Parts) may be purchased from the Society, Science House, 157 Gloucester Street, Sydney, N.S.W., 2000.

Current charges for the PROCEEDINGS are:

Volumes—$16.00 each for 1st Series (Volumes 1–10); $11.00 each for 2nd Series (Volumes 11–20) and all subsequent volumes.

Parts—$5.00 each for all back parts; $4.00 each for current Parts. For volumes of 5 or 6 Parts, $1.00 each for first and last Parts.

Prices do not include postage.

Subscription to the PROCEEDINGS—$11.00 per volume, plus 80c postage—$11.80.

All prices are in Australian currency.

These charges may be revised from time to time, and inquiries should be addressed to The Secretary, Linnean Society of New South Wales, Science House, 157 Gloucester Street, Sydney, N.S.W., 2000, Australia.

The Society's PROCEEDINGS are printed and published for the Society by the Australasian Medical Publishing Co., Ltd., 71–79 Arundel Street, Glebe, N.S.W., 2037.

Proceedings, Volume 97, Part 1, 1972

CONTENTS

Page

Annual General Meeting :

Proceedings of the Linnean Society of New South Wales

Issued 11th October, 1972

VOLUME 97
PART 2
No. 430

Registered for posting as a periodical—Category A.

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, 1972–73

President
H. G. Cogger, M.Sc., Ph.D.

Vice-Presidents
L. A. S. Johnson, D.Sc.; T. G. Vallance, B.Sc., Ph.D.;
N. G. Stephenson, M.Sc., Ph.D.; R. C. Carolin, B.Sc., Ph.D., A.R.C.S.

Honorary Treasurer
Joyce W. Vickery, M.B.E., D.Sc., F.L.S.

Secretary
Mrs. Ruth J. Inall

Council

D. J. Anderson, Ph.D.
D. T. Anderson, D.Sc.
R. K. Bamber, F.S.T.C.
Barbara G. Briggs, Ph.D.
W. R. Browne, D.Sc., F.A.A.
R. C. Carolin, B.Sc., Ph.D., A.R.C.S.
H. G. Cogger, M.Sc., Ph.D.
Mary M. Hindmarsh, B.Sc., Ph.D.
L. A. S. Johnson, D.Sc.
Elizabeth C. Pope, M.Sc., C.M.Z.S.
P. J. Stanbury, Ph.D.
N. G. Stephenson, M.Sc., Ph.D.
F. H. Talbot, M.Sc., Ph.D., F.L.S.
E. LeG. Troughton, F.R.Z.S.
P. G. Valder, B.Sc.Agr., Ph.D.
T. G. Vallance, B.Sc., Ph.D.
Joyce W. Vickery, M.B.E., D.Sc., F.L.S.
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.

Linnean Macleay Fellow of the Society as from 1st July, 1971
Mrs. Lynette Anne Moffat, B.Sc.Hons.

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

A SERIES OF OLIGOSACCHARIDES, OCCURRING IN THE HONEYDEW OF INSECTS, BASED ON TURANOSE

RALPH BASDEN
Department of Chemistry, University of Newcastle, N.S.W.

[Accepted for publication 15th December 1971]

Synopsis

A series of oligosaccharides, occurring in the honeydew of various insects, is described. Each oligosaccharide yields, on hydrolysis, the disaccharide turanose and a second fragment consisting of from one to five glucopyranose units. These oligosaccharides have been found to occur in the honeydew of sap-sucking insects of several different Families.

The parent sugar, turanose, and two members of the series are already known. This paper names and describes two new members of the series, cryptose, a pentasaccharide, and lasiose, a hexasaccharide, and foreshadows a still higher member.

The honeydew excreted by several sap-sucking insects is a syrup containing a number of sugars, the composition of which differs very markedly from that of the sap ingested by the insect. The sugars in the sap of several eucalypts have been reported (Basden, 1965) as consisting of approximately 10% raffinose, 80% sucrose and 10% of a mixture of glucose and fructose. The honeydew of the insects feeding on the sap of these eucalypts contains about 10% sucrose, 10% raffinose and the remainder consists of sugars of high molecular weight.

The present investigation commenced with the examination of the honeydew of *Eriococcus coriaceus* Mask. (Basden, 1967). It was shown that the honeydew contained several sugars which were not present in the sap, nor indeed had been previously reported as occurring in nature. These sugars have been found subsequently to occur in the honeydew of several insects and of different Families as shown in Table 1.

TABLE 1
Insects, the Honeydew of which Contains the Sugars Described in this Paper

Insect	Family
Siphonophora rosae Linn.	*Aphididae*
A mealy bug	*Coccidae*
Cryptes baccatus Mask.	*Coccidae*
Eriococcus coriaceus Mask.	*Coccidae*
Eucalyptolyma maidenii Frogg.	*Psyllidae*
Cardiaspina densitexta Taylor	*Psyllidae*
Lasiopsylla striatus Frogg.	*Psyllidae*

Two of the sugars, turanose and laminaribiose, had been prepared in the laboratory but had not been isolated as such from a natural source. Another sugar, eriose, had not been previously reported at all. Since the above paper was published two further oligosaccharides have been identified. One, for which the name cryptose is proposed, is a pentasaccharide and the other, lasiose, is a hexasaccharide. There is evidence of the occurrence of a still higher oligosaccharide, but it is in such small amount that its separation and examination at present are impracticable.

These two oligosaccharides, cryptose and lasiose, as well as eriose and melezitose, which have been previously described, are all easily hydrolysed and all yield the disaccharide turanose as one of the products, the other fragment of the molecule being, as shown in Table 2, either glucose or one of the 3-D-glucopyranosides, each being one glucopyranosyl unit larger than its predecessor in the group. The identity of the turanose, glucose, laminaribiose and laminaritriose have been proved by comparison with authentic specimens of the respective sugars. As no authentic laminaritetraose has been available, the identity of this sugar has been assumed on the following grounds :

(1) From analogy with laminaribiose and laminaritriose in the series.
(2) It gives the characteristic colour of the laminarin sugars on treatment with aniline-diphenylamine phosphate reagent.
(3) It occupies the typical position of a tetrasaccharide on the chromatogram.
(4) Its molecular weight is that of a tetrasaccharide.

TABLE 2

The Sugars of the Turanose Series

Sugar	Structure	Structure Determined by	Products of Hydrolysis
Turanose ..	O–D–Gp(1→3)Fru.f	Hudson 1944	
Melezitose ..	O–D–Gp(1→3)Fru.f(2→1) O–D–Gp	Hehre 1953	Turanose, glucose
Eriose ..	O–D–Gp(1→3)Fru.f(2→1) O–D–Gp(3→1)O–D–Gp	Basden 1967	Turanose, laminaribiose
Cryptose ..	O–D–Gp(1→3)Fru.f(2→1) O–D–Gp(3→1)O–D–Gp(3→1) O–D–Gp		Turanose, laminaritriose
Lasiose ..	O–D–Gp(1→3)Fru.f(2→1) O–D–Gp(3→1)O–D–Gp(3→1) O–D–Gp(3→1)O–D–Gp		Turanose, laminaritetraose

The symbols Gp and Fru.f represent glucopyranose and fructofuranose respectively and are the symbols prescribed in The Handbook for Chemical Society Authors 1960.

When more of the material has been accumulated, the composition will be verified.

The classical method of separation of sugars from a mixture by percolation through a column of Celite and charcoal, using increasing strengths of aqueous ethanol as eluent has been found impracticable due to the small differences in mobility of several of the components of the honeydew.

The sugars were satisfactorily separated by paper chromatography, sometimes repeated three times. Experimental details are given later in this paper.

Sufficient of only one of the sugars, cryptose, has been obtained to enable its physical properties to be determined. Specimens of eriose and lasiose are being collected as opportunity occurs and will be examined when sufficient of both has been collected.

Cryptose. $C_{30}H_{52}O_{26}$

This sugar, named from *Cryptes baccatus* Mask., in which it occurs, crystallizes from a concentrated aqueous solution as fine needles generally associated in rosettes. These crystals are soluble in water, pyridine and slightly in methanol. They are insoluble in ethanol. They have a faintly sweet taste. Cryptose does not reduce Fehling's solution. Its melting point is 160° C. and its $[\alpha]_D^{25}$ +110·7 (C=4).

Cryptose is separated from the other sugars of *Eriococcus* honeydew by paper chromatography. A streak of honeydew solution is made on Whatman's no. 3 chromatograph paper and this is treated as a descending chromatogram at room temperature. The solvent found most efficient was butanol : acetone : water, 3 : 4 : 1. It was run for 48 hours, the paper dried, and the area occupied by cryptose was located, removed and extracted with water in a Soxhlet extractor. The solution was decolourized with charcoal and then evaporated to a syrup. It is important to use charcoal which has had any residual acidity neutralized as cryptose readily hydrolyses in an acid medium. On standing several days at room temperature, the sugar crystallized from the syrup as rosettes of fine colourless needles.

Cryptose has been proved to be a pentasaccharide by the determination of its molecular weight. Using a Metrolab Model 302 Vapour pressure Osmometer, the molecular weight was found to be 820 (calculated 828). On a paper chromatogram using butanol : acetone : water, 3 : 4 : 1 as solvent at room temperature cryptose was found to have a motility $R_G = 0 \cdot 19$ and on development with aniline-diphenylamine phosphate it yielded a mauve stain classified as Victorian mauve B.C.C. 297 of the British Colour Council Dictionary of Colours. This colour must be observed as soon as it is formed as it quickly darkens on exposure.

Lasiose. $C_{36}H_{62}O_{31}$

This sugar, named from *Lasiopsylla striatus* Frogg. in the honeydew of which it occurs, was separated from the crude *Eriococcus* honeydew in a manner similar to that employed for cryptose. From the intensity of colour and the size of the stain on a paper chromatogram it is estimated that lasiose comprises less than 10% of the total sugar content of the honeydew. Lasiose is readily hydrolysed by dilute acid, yielding turanose and another sugar which has been assumed to be laminaritetraose. Insufficient lasiose has been obtained to permit an examination of its physical properties other than to observe that it crystallizes in (apparently) monoclinic plates. These are soluble in water, in pyridine, and slightly soluble in methanol. They are insoluble in ethanol. On a paper chromatogram at room temperature and with butanol : acetone : water, 3 : 4 : 1 solvent it has a R_G 0·01 and yields a Victorian mauve stain with the aniline-diphenylamine reagent. It is of interest to note that the honeydew of every insect examined contains, in addition to the series of sugars named above, about 10% raffinose. This is approximately the proportion present in the original sap and seems to indicate that the raffinose passes through the alimentary system of the insect unchanged and that the oligosaccharides of the turanose series are derived from sucrose. No indication has yet been obtained as to the manner in which sucrose is broken down and the fragments recombined to form the complex oligosaccharides.

The hydrolysis of all the sugars in this turanose series was effected by heating a fragment of the sugar or a drop of its solution with 0·05 M sulphuric acid at 100° C. for five minutes. The solution was neutralized with barium carbonate, separated from the precipitate on a centrifuge, and the supernatant solution evaporated and chromatographed on Whatman's no. 1 paper using authentic samples of turanose, laminaribiose and laminaritriose as controls. The location of the various sugars on the chromatogram was determined by dipping the dried chromatogram in aniline-diphenylamine reagent as prescribed by Bailey and Bourne (1960) and comparing the colours and positions of the standards with those of the sugars under test.

References

Bailey, R. W., and Bourne, E. J., 1960.—Colour reactions given by sugars and diphenylamine-aniline sprays on paper chromatograms. *J. Chrom.*, 4 : 206.

Basden, R., 1965.—The occurrence and composition of manna in *Eucalyptus* and *Angophora*. Proc. Linn. Soc. N.S.W., 90 : 152.

————, 1967.—The occurrence and composition of the sugars in the honeydew of *Eriococcus coriaceus* Mask. Proc. Linn. Soc. N.S.W., 92 : 222.

Hudson, C. S., 1944.—Turanose. *J. Org. Chem.*, 9 : 117.

Hehre, E. J., 1953.—Melezitose. *Adv. in Carbohydrate Chemistry*, 8 : 277. Academic Press Inc., N.Y.

GREY BILLY AND ITS ASSOCIATES IN EASTERN AUSTRALIA

W. R. Browne

[Accepted for publication 16th February 1972]

Synopsis

As a geological term " grey billy " was first used by David in 1887 to denote the quartzitic rock formed by the silicification of Tertiary sands and gravels under basalt, but its meaning has since been extended by some workers to include the siliceous duricrust. It is contended that to avoid confusion the name should be applied as originally defined.

The silicified rock is often ferruginous and may be variously coloured. It is found usually on the floors of old valleys, under basalt of older Tertiary (pre-Pliocene) age; in frequent association with it are white (leached) bedded Tertiary clays, and leaching of the bedrock is not uncommon. Bedrock may be locally silicified. It is considered that the alterations—both silicification and leaching—have been effected by solutions related to the basalt, and that where the basalt has been entirely removed by erosion, the existence of any of the alterations indicates its former presence. Thus the grey billy association may be important in regard to palaeogeography.

Illustrative examples are described from various parts of New South Wales, particularly the Monaro country of the Southern Highlands, and the work of previous observers is reviewed. Brief mention is also made of the distribution of grey billy in the other States of eastern Australia.

INTRODUCTION

During the last century there have been occasional references, whose frequency has increased of late years, in the geological literature of the States of eastern Australia to sub-basaltic quartzites—Tertiary river- or lake-deposits that have suffered alteration through contact with superincumbent flows of basalt. The present paper is in part an attempt—by no means complete or exhaustive—to bring together and review references to described occurrences, and in part a record of my own observations made in the course of field-work over many years, particularly in the Southern Highlands of New South Wales.

My gratitude is due to Dr. J. A. Dulhunty, Prof. A. H. Voisey, Dr. F. W. Booker and Mr. D. G. Moye for kindly showing me relevant geology in the Goulburn River valley, parts of New England and the Central Highlands and the Adaminaby area respectively. My introduction to some of the occurrences in the Lower Hunter valley I owe to the late Sir Harold Raggatt, at the time an officer of the N.S.W. Geological Survey. Another member of that Survey, the late Mr. A. C. Lloyd, guided me to places of interest in the neighbourhood of Dubbo and elsewhere. Lastly I am much indebted to my wife for collaboration in the field, transport and discussion; without her help much of the work could not have been done. For direction to outcrops of importance I have made considerable use of the excellent reports and reconnaissance geological maps of parts of the Southern Highlands made by members of the Geological Survey of N.S.W., and published in the 1950's. The topographical maps of the Adaminaby, Berridale and Dalgety areas made by the Snowy Mountains Hydroelectric Authority, of which copies were kindly made available to me, have proved extremely useful.

HISTORICAL

Silicified sub-basaltic deposits probably came under notice first in Victoria because much of the alluvial gold there occurred in what were known as " deep leads "—deposits of Miocene age or older that had been sealed down and preserved by flows of basalt. Hardening of the upper parts of the beds through siliceous cementation resulted in continuing protection after the disappearance of the basalt through erosion, and incidentally provided an obstacle to their economic exploitation. Other beds proved to be stanniferous in Queensland and New South Wales and for many years were significant producers ; now, however, they are chiefly of historic interest.

Mr. T. W. E. (afterwards Sir Edgeworth) David (1887*a*, 1887*b*), then on the staff of the Geological Survey of N.S.W., described from the Vegetable Creek (Emmaville) tin-leads of New England a hard, siliceous rock underlying basalt as " grey billy ", the name by which it was known to the local miners. So far as I am aware, this was the first definition of the term in geological literature, though the rock had already been referred to in earlier reports, and David himself had used the name without explanation in the Legend of a geological map (1884). It seems to have been originally applied to bouldery masses of quartzitic rock which were probably for the most part formed by disintegration and weathering *in situ* of sheets of the material, but David also referred to " irregular-shaped lumps of hard rock 2 to 3 feet in longest diameter " through which current-bedding of the surrounding loose drift could often be traced ; he suggested that these " concretions " were formed by segregation of silica in the uncompacted deposits. The sub-basaltic quartzite was called " flinty quartzite " by Brown (1926) and " contact quartzite " by Craft (1931*a*).

In his interesting book on opal the late F. G. Leechman (1961), himself a Cornishman, stated that " billy " is a corruption of " bully ", a common Cornish term for " a big, round stone " ; since many of the original tin-miners in New England came from Cornwall, this is without doubt the correct explanation of the word, the adjective being obviously an allusion to the prevailing colour of the rock.

B. Dunstan (1900, 1902*a*) of the Geological Survey of Queensland, who had received his geological training in New South Wales, gave the name " billy " to rounded siliceous boulders appearing in river-alluvium in the Clermont area, and later to similar boulders associated with alluvial sapphires in the neighbouring Anakie field (1902*b*). Perusal of his reports suggests that he was referring to two similar-appearing rock-types with very different origins, some apparently of sub-basaltic type, others disintegrated siliceous duricrust (Woolnough, 1927). According to Whitehouse (1940, p. 4), after it had been shown that some quartzitic rocks were due to metamorphism by Tertiary basalt Dunstan suggested a similar origin for the duricrustal quartzites of western Queensland ; Whitehouse also (p. 13) states that the name " billy " has been used in Queensland for the two types of quartzitic rock indifferently. Discoveries of precious opal in association with duricrust popularized the use of " billy " for duricrustal quartzite in Queensland, and this usage spread to New South Wales (cf. Kenny, 1934 ; Whiting and Relph, 1961 ; Branagan, 1969) though it appears not to have reached South Australia, the other opal State.

To denote siliceous surface-crusts of uncertain origin found in South Africa Lamplugh (1907) coined the word " silcrete ". These crusts appear to be somewhat analogous to certain surface-quartzites of western Queensland. The term was first applied to Australian duricrustal quartzite by Williamson (1957), but, unfortunately, its meaning has been by some writers (e.g. Vallance, 1969, p. 525) extended to include the sub-basaltic rock. Others, like Voisey (1942*a*, 1942*b*) and the authors of the Geological Survey reports on the Snowy Mts., Adamson, Hall and Lloyd (1954, 1955, 1956) employ the term " grey billy " exclusively in describing the sub-basaltic deposits ; while Chalmers (1967) equates " grey billy " and " silcrete " and deprecates the use of the former for silicified sub-basaltic deposits. Since the formations in question are genetically different, but each in its own way is significant in regard to the Kainozoic history of Australia, it is desirable for the avoiding of confusion that a clear distinction be drawn between them by strict use of appropriate designations. Some of the rather heterogeneous quartzites so widespread in the interior of the continent are possibly to be grouped with silcrete, but the name " grey billy " clearly has priority, and should be used, for the sub-basaltic rocks which are the subject of this note.

General Description of Grey Billy

Though originally denoting large rounded boulders, the name is now applied more particularly to the layers or sheets of silicified sand and/or gravel often occurring beneath terrestrial Tertiary basalt-flows and as a designation for specimens of this material. A specific colour is not implied by the name any more than it is by " greywacke ", but certainly by far the commonest colour is pale grey, though it may be pink, cream, yellow, yellow-brown, dark red, dark brown, bluish, black or white. For the most part the original materials have been valley-floor and perhaps lake-shore deposits, but where there has been valley-in-valley structure silicified terrace-deposits resting upon bedrock may be seen at levels well above that of the innermost valley-floor. Raggatt (Browne and Raggatt, 1935 ; Raggatt, 1939) described such from Trunkey in the Central Highlands.

Probably most grey billy occurs in old river-valleys, but where the basalt was poured out on a plateau-surface the regolith covering it may show silicification. Cotton (1910) described from Elsmore and other places in western New England outcrops of silicified granite debris, chiefly of coarse angular quartz-grains with large lumps of stanniferous reef-quartz scattered through it ; and Voisey (1942) has recorded fossil granite soils converted into grey billy in the Uralla area. In the Central Highlands some 9 miles east of Crookwell on the plateau-surface about 3,000 feet ASL grey billy has been noted consisting of angular fragments up to 9 inches long of granitic material embedded in a matrix of coarse, angular quartz-grains.

Plant-remains have occasionally been found in grey billy. The well-known occurrence in the township of Dalton in the Yass district (Sussmilch, 1937) contains abundant distinct plant-impressions, the original material having possibly been carbonized by heat and later etched out by weathering. Fragments of charcoal, silicified roots and stems of a fossil angiosperm have been reported from grey billy near Ulladulla on the South Coast (Brown, 1926) and hollow casts of plant-stems from silicified soil 10 miles north of Armidale (Voisey, 1942*b*) ; the material containing them may have been silicified clay rather than sand. David (1887*b*) and Curran (1891) found blocks of silicified wood in the grey billy of Emmaville and of Bald Hills (Mt. Panorama) near Bathurst respectively. Plant-remains, however, are perhaps more common in the unaltered beds beneath the grey billy.

The layer of grey billy may be up to 8 or 10 or even 15 feet thick but may thin out laterally and is often succeeded downwards quite sharply by uncompacted gravel, sand, clay or other material.

Where the basalt has been eroded away and the deposit beneath it revealed, the grey billy may weather into angular blocks of about 6 or 8 inches edge which are strewn over the ground where the basalt has been. More commonly, however, the silicified layer tends to be undermined and cracked, and eventually to break off in isolated large blocks or tabular masses with rounded and generally smooth, dimpled surfaces and a lustre varying from subvitreous to dull according to grainsize and degree of cementation. These masses may in time become partially buried in the loose gravels originally beneath them or in others of a later generation, and no obvious evidence of a continuous sheet may exist, but the size, shape and abundance of the blocks or slabs will serve as a proof that they are virtually *in situ* ; in certain instances a train of isolated boulders may be traced to the mass whence they were derived.

If silicification has been incomplete or unevenly distributed differential weathering makes the rock irregularly cavernous; individual sand-grains are etched out, particularly where the cement is in part ferruginous, and if the rock has been gravelly pebbles may be completely weathered out.

TEXTURE AND COMPOSITION

The sandy grey billy has very variable grainsize; it may be exceedingly fine-grained and compact, almost glassy and with a smooth fracture and greasy or oily lustre, but is more usually medium-grained or coarse and gritty with subordinate matrix, saccharoidal texture and uneven fracture. Another type consists of little glassy quartz-grains and tiny rock chips sporadically distributed through an irresolvable or felsitic matrix; it has a stony or porcellanous appearance and an almost conchoidal fracture. Much of the Hunter valley material is of this type (Raggatt, 1939). Some types composed entirely of exceedingly fine irresolvable material may be silicified clay or soil. Silicification appears to have been the result of deposition from solution, producing cementation and metasomatism. Where a rudaceous layer is interbedded individual pebbles may be replaced by silica with retention of original structures such as bedding (Browne, 1964). Many pebbles are of white vein-quartz which has been immune from metasomatism, but their boundaries against the matrix are occasionally blurred by secondary outgrowths (Murray, 1887; Dunstan, 1900*b*). In the coarse sandy type outgrowths in optical continuity may give the grains a hexagonal outline perceptible by the naked eye. Commonly massive, the rock may show bedding or layering, through the inclusion of pebbles, and is occasionally cross-bedded. Very rarely it may be intersected by quartz-veinlets.

Little is known of the microscopic petrography of grey billy. David considered the cementing material of the Emmaville grey billy to be chalcedony. Specimens of the Ulladulla rock (Brown, 1926) consist of allothigenic quartz in a cryptocrystalline matrix and contain more than 98% of silica. Compact types from Tallong (Waterhouse and Browne, 1930) show common opal both as a matrix and as paper-thin veinlets associated with chalcedony, but in other types quartz is the sole siliceous constituent. Some specimens are composed of discrete angular quartz-grains with corroded edges in a microcrystalline matrix. Williamson (1957) briefly described samples from various parts of New South Wales and Victoria and made the interesting discovery of clusters of minute rutile prisms associated with authigenic quartz in samples from Tallong; the titanium, he suggested, might have "entered into solution from the overlying basalts". Analysed samples of the Tallong and other New South Wales rocks yielded Williamson silica-percentages by weight between 97 and 99, with very small percentages of other constituents, iron oxides reaching a maximum of 2·18 and TiO_2 of 1·27.

In the grey billy of New England alluvial gold and stream-tin were found, sometimes in quantities sufficient to warrant extraction, and it is likely that topaz, sapphire, garnet, zircon and other detrital minerals are present, as they are in the unconsolidated gravels and sands.

SELECTIVE ALTERATION

Not everywhere, even in the same valley, is the contact between basalt and underlying sediments marked by grey billy; indeed, in some instances there is little or no sign of alteration. Two basalt-flows may be separated by a layer of dark red-brown bole, a partially consolidated substance that adheres to the tongue, really a soil derived from the lower flow and altered by the upper. At Tallong at a spot where basalt has rested directly on fine-grained Permian sandstone, this is prismatized and somewhat hardened but otherwise apparently unaltered. To the left of the road between Yarrangobilly Caves and the village of Yarrangobilly, some 12 miles north of Kiandra, are four thin flows of basalt with small thicknesses of interflow and subflow sediments; those beneath the upper flows are uncemented grits, but the lowest flow is underlain by grey billy resting on bedrock of partly silicified limestone. The reason for this selectivity is not clear.

Relation to Basalt

David stressed the situation of the Emmaville grey billy at the contact between basalt and gravels, and other workers have done likewise. Most of the outcrops I have seen are either in evident contact with overlying basalt or are traceable laterally with little or no interruption into material that does underlie basalt, so that the relation to the volcanic rock is abundantly clear. In other instances the grey billy is separated by a few miles from the nearest basalt outcrop, but generally the distribution of basalt remnants great or small indicates sufficiently their former continuity across the intervening space. These relations are well exemplified in the Shoalhaven country, for which Craft's (1931*a*, 1931*b*, 1931*c*, 1932*a*, 1932*b*) maps and descriptions make quite evident the close relation of his "contact-quartzites" to Tertiary basalt-flows; a particularly clear instance is exposed near Badgery's Lookdown at Tallong. Even where no basalt is known to occur for miles around, the physical characters of the rock itself and its relation to its environment are usually sufficient for identification.

The suggestion is occasionally made that even where there is actual contact the relation of billy to basalt is purely adventitious, that it is the remnant of a pre-basaltic crust of unspecified antecedents that has had the good fortune to be preserved in a hollow under basalt; its occasional long distance from known basalt outcrops is considered to support this hypothesis. To those holding such views the classic advice "Go and see" cannot be improved upon. He would indeed be a very timid or very obstinate fellow who could retain any vestige of doubt of a causal relation after extended examination of the field-evidences—the oft-repeated close and intimate association of grey billy and basalt, the silicification of screes and soils and terrace-deposits as well as valley-floor sediments in the vicinity of basalt-flows, the silicification of interflow deposits and the association of both basalt and grey billy with underlying leached beds, as noted below.

Associated Sub-basaltic Deposits

In natural exposures or in artificial excavations like quarries and road-cuttings it is sometimes possible to get partial or complete sections through grey billy and the deposits beneath it down to their base and into bedrock. Where the original material was gravel or boulders the silicified layer may be underlain by loose gravels. But the valley may have been very mature and its deposits may have included flood-plain silts, or it may have for some reason expanded locally into a lake with clayey and fine sandy sediments showing bedding, lamination, cross-bedding and contemporaneous washouts, perhaps with occasional layers of peat or lignite. The clay is commonly white, cream or pink, and is locally known as pipeclay; it may be associated with grey billy or may directly underlie basalt. So far as I know it has always been tacitly regarded as a normal transported deposit. It is true, of course, that white clay may, in association with carbonaceous beds or in certain climatic and/or topographical environments, such as those characteristic of the far North Coast of New South Wales, result from the decomposition *in situ* of basalt and other rocks, and that this material may be eroded, transported and deposited in still waters. But the close and common association of the clays here referred to with basalt suggests very strongly that they are related to it and have been leached after deposition, probably by magmatic waters. It would appear that leaching may be selective and diminishes at depth in the deposits. Occasional lenses or layers of very fine white and even running sands are found amid the clay, and the clayey matrix of compacted gravel beds is apt to be leached.

Sub-basaltic white clays are almost ubiquitous in association with the Tertiary basalts of this State. David found them at Emmaville, locally prismatized in contact with basalt, and they have been noted in various parts of the Central Highlands. Craft reported white clays and sands from the Shoalhaven country and they are very common, either under grey billy or directly under basalt, in other parts of the Southern Highlands, as in the Cooma-Adaminaby-Berridale-Dalgety area and at Bombala (Relph, 1969). In my experience the beds do not as a rule exceed 25 feet in thickness, but from the succession given by Gill and Sharp (1957, pp. 29–30) it would appear that at Kiandra leaching has persisted, somewhat selectively, through a depth of about 80 feet from the base of the basalt. One circumstance, the significance of which has not been satisfactorily explained, is the frequency with which at the base of the sub-basaltic column white clay is found resting on leached bedrock and overlain by gravelly or sandy deposits.

Limonitic material under lava-flows has been noted in a few places, as in the Comboyne plateau on the middle North Coast, where it appears as a finely laminated bed about 8 inches thick possibly deposited rhythmically, or seasonally, as a cement to detrital sands or gravels ; in such circumstances it is explicable as having been precipitated from springs on the bed of a pre-basalt lake or river. But quite frequently the siliceous grey billy is coloured a dark brown, apparently through deposition of thin films of iron hydroxide, and indeed in certain places this seems to be the sole cementing material. Its time-relation to the silicification has not been investigated, but its close association with the grey billy suggests contemporaneity.

Carbonaceous beds close to the basalt-contact may be changed into a coaly substance—a case of simple heat-metamorphism ; such an occurrence was briefly referred to by Dulhunty (1946) from Cottage Creek some 16 miles south of Cooma. Diatomaceous earth deposits may be locally converted into common opal, as at Bunyan near Cooma and Wyralla and Tintenbar on the Richmond River (Morrison, 1920).

A comparatively rare associate of grey billy is travertine or kunkar. David (1887*b*) and Cotton (1910) both reported it with basalt and grey billy from a number of places in New England, and an occurrence from Rock Flat near Cooma is mentioned below. It is not clear whether the travertine is related to the grey billy or whether the association is purely fortuitous. Though travertine is deposited from hot springs in volcanic regions, the similar substance *kunkar* is known to result sometimes from the weathering and decomposition of basalt, forming discrete nodules or continuous sheets in basaltic soil.

BEDROCK ALTERATION

Leaching has not been confined to the sub-basaltic sediments but has also quite frequently affected bedrock to a depth of several feet, producing white clay (pipeclay). Slates, particularly where highly jointed and steeply dipping, seem to be very susceptible to attack by percolating waters, but biotite-granite on which basalt has been outpoured has been reduced to an incoherent and barely recognizable mass of white clay and sand. Leaching of slates, which has been studied chiefly in the Central and Southern Highlands, appears to be in some way selective, leached being side by side with quite unleached sections of the bedrock, possibly as the result of varying permeability.

On the other hand certain phenomena suggest selective sub-basaltic silicification of bedrock. Of the examples observed the most interesting is that of Rock Flat, 2,900 feet ASL, 9 miles from Cooma on the road to

Nimmitabel ; this occurs in the broad valley of Rock Flat Creek, formerly basalt-filled but now locally eroded down to bedrock. Unfortunately, the silicified outcrops have been much mutilated by quarrying, but originally there were a larger and a smaller mass rising from the alluvium of the creek along a roughly meridional line. At the northern end of the smaller is a bubbling " soda-spring " and from the creek-bank near by a chalybeate spring issues (cf. Pittman, 1901) ; these, with other small springs now extinct, have been responsible for a terrace or platform of ferruginous travertine a few feet above the creek (Browne, 1914). The larger siliceous outcrop shows lamination dipping steeply, and quarrying revealed pockets of loose quartz-sand amid the solid rock well below the surface, suggesting a shaly sandstone that had been imperfectly silicified and later disintegrated by percolating surface-water. The smaller outcrop is massive, but intersected by a cemented breccia of angular quartzite blocks resembling closely the fault-breccias found in some Palaeozoic limestones. In one of the masses ripple-marking was noted. The rock is typically opaque white, very pure, fine and even-grained, and the internal evidence and general environment suggest that the outcrops are remnants of sandstone, shale and perhaps limestone that had protruded from the pre-basalt valley and had been metasomatically altered by a basalt-flow. A few hundred yards away to the west a belt of Silurian quartzite that emerges from beneath the cover of Tertiary basalt and crosses the railway line obliquely near Rock Flat siding is locally converted into what appears to be chalcedonic silica. Craft (1931*b*, p. 251) has noted the local conversion of Palaeozoic sandstone into glassy " contact-quartzite " under Tertiary basalt at Windellama in the Shoalhaven country.

In a different catagory is a mass of vein-quartz standing in the midst of grey billy at Kings Plains near Blayney, apparently a resistant Palaeozoic relic around which pre-basalt Tertiary sediments were deposited. A similar occurrence has been described by McRoberts (1948) from Bombala.

SOURCE OF THE SOLUTIONS

There can be little doubt that the solutions responsible for the changes in the original deposits were somehow connected with the basalts, but the nature of the connexion is a matter of speculation. For grey billy the problem was briefly discussed by Waterhouse and Browne (1930) and by Williamson (1957). The geochemistry of the process of alteration is beyond the scope of this note, but attention may be drawn to the following considerations :

1. The great majority of the basalts concerned are of alkaline type and many of them show signs of deuteric alteration involving late-magmatic solutions. In particular, in the Southern Highlands they are known to include examples of " sunburnt basalt " (Lafeber, 1956), notable for its content of analcime and other zeolitic minerals and likely to be accompanied by alkaline solutions ;
2. Sub-basaltic silicification and leaching are not constant or universal, but selective ;
3. Any explanation must account both for grey billy, in which alteration has been essentially constructive or additive, and for leaching, in which it is destructive or subtractive.

ORDER OF DEPOSITION

The common appearance of terracing or trap-featuring in the Tertiary basalts indicates that there has been repeated outpouring of flows with a time-interval between them sufficient to permit consolidation of the rock, weathering and soil-formation on a given flow or even the deposition on it of gravels, sands or finer alluvia. That the time-interval has not always been regular is suggested by the fact that the thickness of interflow sediments is very variable.

From the alternation of flows and alluvial deposits in a valley the natural inference is that the valley was repeatedly shallowed and the valley-floor raised, perhaps with ponding of the stream by a basalt barrier, until the valley was completely filled. Obviously the higher deposits and flows are the younger.

Occasionally, however, one finds evidence of what seems to have been valley-in-valley structure, where alluvial deposits appear on bedrock terraces or shoulders on the valley-sides at one or more levels well above its floor, and all the deposits have been buried beneath basalt. It may be difficult to determine the sequence of events in such circumstances. There may have been true valley-in-valley structure with remnants of earlier alluvium on the upper valley-floor and a succession of basalt-flows may have buried both the earlier and the later deposits ; in this case the highest alluvium is the oldest and the higher basalt the youngest. On the other hand, an appearance of terraces and terrace-deposits may have come about if, during an interval in the normal filling of the valley by successive flows, there was erosional encroachment on the valley walls, with later deposition on the newly excavated bench before the next flow. In this event both the highest basalt and the highest alluvium are the youngest.

The orderly succession of events may, of course, have been interrupted by tectonic movements or by the formation, at some stage, of twin-streams (Browne and Raggatt, 1935).

Geological Age of Grey Billy and its Associates

In general it may be said that the Tertiary basalts in eastern Australia with which the altered sub-basaltic sediments are connected form part of the erosion-surface of the Miocene peneplain, occupy exhumed valleys sunk below its surface, or, more rarely, are perched on monadnocks upon it. Recent isotopic datings—certainly not numerous as yet—suggest that the volcanic activity spanned a time-range from Lower Eocene to Miocene (Dulhunty and McDougall, 1966 ; McDougall and Wilkinson, 1967 ; Webb *et al.*, 1967 ; Wellman *et al.*, 1969) in New South Wales and south-eastern Queensland, the majority of the samples so far tested being Lower Miocene or Oligocene. This period of extrusion corresponds approximately with that postulated for the Older basalts of Victoria, and in these notes is for convenience designated earlier Tertiary. For eastern Victoria Murray (1887) noted that silicified Tertiary alluvium is connected with the Older basalts, and Gill (1942) reported it from under Older basalt at Lilydale. On the other hand a detailed account of the Kainozoic sediments associated with the Newer basalts of western Victoria by Gill (1964) makes no mention of silicified deposits, and a similar significant silence is noticed in Murray's account of the Newer basalts. Many years ago Dr. D. E. Thomas, former Government Geologist of Victoria, told me that in his experience silicification of sub-basaltic sediments is known only in connexion with Older basalts. The only apparent exception is at Mt. Macedon where Skeats and Summers (1912) stated that sands and gravels under Tertiary trachytes and Newer basalt are locally changed to quartzite.

During a short visit to the country some 50 miles east and north-east of Hughenden in northern Queensland I had an opportunity of examining flat-topped and slightly dissected plateaux covered with what are probably Newer (late Pliocene and Quaternary) basalts (*cf.* Maitland, 1898). Though occasional subflow and interflow deposits were noted I saw no signs of sub-basaltic silicification or leaching. This negative evidence, of course, may or may not be significant.

It has generally been assumed that extrusion of the basalts followed closely on deposition of the sediments (Andrews, 1914, pp. 519–520 ; Sussmilch, 1937 ; Voisey, 1957 ; Gill and Sharp, 1957). This, indeed, might well be inferred from the common occurrence of interflow deposits, the occasional presence of amygdaloidal phases at the base of the basalt, the corrugation or crumpling of apparently still plastic clays by the " push " of advancing lava and the local leaching of sediments, which would be accomplished more readily in relatively loose and permeable than in compacted deposits. Unfortunately, discrepancies have been found between age-determinations of beds and basalt made by different methods. For example, the plant-bearing beds at Armidale (Voisey, 1957) were on palynological grounds thought to be Eocene or early Oligocene, but by isotopic dating (McDougall and Wilkinson, 1967) the basalt covering them is late Lower Miocene (21 m.y.). If one is to regard both methods of determination as reliable, then, to reconcile the conflicting dates one must assume that an interval of 10 m.y. or more separated deposition and burial of the beds. Such an explanation is rendered somewhat less improbable by Slade's discovery, quoted by Voisey, that the Armidale beds had been dissected to a depth of 200 feet before extrusion of the basalt.

In a somewhat different category is the diatomaceous earth at Bugaldi in the Warrumbungle Mts. area, which contains skeletons of the fossil fish *Maccullochella macquariensis* (Murray Cod); these Hills (1946) considered to be not older than Pliocene, but the olivine-basalt on top of the beds is apparently equivalent to that which has been dated (Dulhunty and McDougall, 1966) as Upper Miocene. At Bunyan near Cooma, where an identical skeleton was found, the enclosing diatomaceous earth is older than the basalt hard by, which itself is older than the Miocene peneplain.

It would be interesting to compare a K/Ar dating of the basalt at Kiandra with the age of the underlying lignite, determined on its pollen-content as Upper Eocene or Lower Oligocene (Gill and Sharp, 1957); and an isotopic age for the basalt in the Redbank Plains beds of the Brisbane-Ipswich area in Queensland (Jones, 1926) with that based on the fauna of the associated sediments—probably Eocene or Oligocene (Hills, 1934).

Post-Basaltic Deposits

Though not necessarily related directly to the sub-basaltic beds, certain post-basalt deposits are not uncommonly found in close proximity to them. Erosion induced or accelerated by the late Miocene (?) Macleay uplift (Browne, 1967) caused older Tertiary basalt-filled valleys to be exhumed in many instances down to approximately their pre-basalt bed-level, exposing their original sediments, often silicified; these were then broken up and redistributed among the deposits of a later period. Many very mature upland valleys and valley-plains of the plateau areas of New South Wales as we see them now are demonstrably post-basalt and pre-Kosciusko uplift and may reasonably be referred to an earlier Pliocene stillstand that followed the Macleay uplift; a closer look will show that many if not all of them are really re-excavated pre-basalt valleys and contain relics of their original alluvial deposits. Where these have been gravels or sands that have remained uncemented, differentiation between the old and the new may be difficult or impossible, but where a layer of grey billy was formed this was in many instances undermined and broken into fragments which became more or less rounded and waterworn and incorporated as cobbles or boulders in the Pliocene deposits. These may also contain pebbles of basalt and redistributed material from loose pre-basalt deposits. The size, abundance and degree of rounding of the grey billy boulders may provide a rough guide to the distance of transport from their original situation and they may even be traceable laterally into almost undisturbed remnants of silicified rock *in situ*. These relations of pre-basalt and post-basalt deposits are well exemplified along the Upper Murrumbidgee near Adaminaby, the Shoalhaven down to Tallong and the Lower Hunter, as noted below.

Due to erosion since the long Pliocene stillstand some of the post-basalt accumulations have suffered dissection, so that remnants of them are " perched " with respect to a later valley floor. However, gravels and boulder-deposits in these upland valleys are being added to at the present day as, for example, where the still eroding tributaries of a main mature valley debouch on to its floor. Such accumulations, in the form of fan-deposits containing in some instances cobbles and boulders of grey billy, are to be seen in tributaries of the Snowy system in the Berridale-Dalgety area.

The great uplifts of the Kosciusko epoch induced considerable rejuvenation of the earlier Pliocene rivers, from the coast far into the highlands on the east, and from the hinge of uplift on the west, so that both pre-basalt and earlier-Pliocene deposits are now high above existing river beds in the rejuvenated sections as, for example, in the Lower Shoalhaven and in many Upper Macleay tributaries.

The Vanished Basalt

Tertiary basalt attains quite considerable thicknesses in the Eastern Highlands of New South Wales. Probably the thickest pile is that forming the Liverpool Range just north of the Goulburn River, which measures upwards of 2,500 feet. At Point Lookout, 50 miles east of Armidale, the basalt is 1,500 feet thick (Andrews, 1904) and that of the Mt. Royal Range probably exceeds 1,000 feet. In the Southern Highlands 15 miles south of Cooma Hudson's Peak is 4,042 feet ASL, and from its top to the neighbouring Rock Flat Creek there is a thickness of about 1,100 feet of basalt, while at The Three Brothers 10 miles south of Cooma the basalt is more than 800 feet thick. Elsewhere the flows have been reduced to remnants less than 100 feet thick, may be represented only by thin spreads of boulders, or may have disappeared completely. An inspection of the State Geological Map or of larger-scale maps of regions in the Eastern Highlands belt reinforces the impression gained from field study that the basalt-cover was formerly of very much greater vertical and lateral extent. If account is taken of the relics of grey billy and/or its associates cropping out far from any basalt, and of basaltic dykes of probable Tertiary age, the area is materially increased.

Removal of large volumes of basalt without leaving a trace is not altogether surprising. The rock-mass carries within itself the elements of its own destruction, since the deuteric alteration to which it is so subject causes the parts affected to decompose readily in the belt of weathering. The " sunburnt basalt ", not uncommon in the Cooma-Dalgety-Kiandra area and recognizable by its hackly fracture, is prone to disintegration at the surface into small angular and pisolite-like fragments which are readily transported (they have accumulated abundantly, for instance, around Maffra Lake and elsewhere), and the layers of palagonitic material amid the basalt are subject to chemical breakdown. Moreover, the volcanic mass, especially in valleys, often consists of a series of relatively thin flows, each perhaps 20 or 30 feet thick, in some instances columnar, and separated by interflow soils or sediments which, besides being liable to erosion, may act as channels for groundwater. For these and other reasons decay, disintegration and removal of basalt is apt to be comparatively rapid.

Duricrust and the Grey Billy Association

In general grey billy and its associates are easily recognized, particularly where Tertiary basalt is in an appropriate position near by, but there may be circumstances in which uncertainty arises.

The lateritic duricrust profile consists typically of three main elements (Whitehouse, 1940), in descending order the ferruginous or lateritic, the mottled, and the pallid or kaolinic zone. In western Queensland Whitehouse found a discontinuous or lenticular siliceous layer to be occasionally present, perhaps most commonly in the mottled zone. Except for the siliceous layer the succession, so far as is known, holds with a varying degree of completeness for the Eastern Highlands belt of New South Wales but, mainly beyond the Darling River, a siliceous zone appears at the top, followed downwards by a soft pallid zone. Woolnough (1927) seems to have equated this siliceous zone to the laterite of eastern Australia, but at the time he wrote very little was known about laterite in the east—although David (1887*b*, 1889) had already reported and described laterite from Emmaville—and very little interest was taken in it or its genesis. Investigations made since Woolnough wrote (e.g. Kenny, 1934 ; Wöpfner, 1960, 1961) have cast doubt on the correlation, and shown that the so-called siliceous zone is rather more complex than he envisaged and may include components of more than one geological age and origin. Moreover, lateritic and lateritoid materials have become known which lie in broad upland valleys of probable earlier-Pliocene age and are therefore younger than the duricrust.

In New South Wales a distinction can generally be made between the duricrust profile and the grey billy association. The former rests on the Miocene peneplain surface, some of it, indeed, derived from the basalt of which that surface is partly composed. On the other hand, grey billy and its associates are broadly contemporaneous with or somewhat older than the basalts and crop out on top of the volcanic rock only where the overlying flow responsible for the alteration has vanished through erosion ; they commonly bear no close relation to the Miocene peneplain surface, occurring as a rule either in valleys cut into it or on monadnocks above it.

Where, as often happens, parts of the duricrust profile or of the sub-basaltic succession are missing distinction may be difficult. There may be similarities in appearance and weathering pattern between sandy grey billy and the siliceous duricrust of the far west and north-west of the State, but for the former the not uncommon association of pebbly layers, the pebbles usually well sorted, well rounded and obviously alluvial, should provide a fairly reliable criterion of origin. The mottled zone of the duricrust has no counterpart in the grey billy association, but leached sub-basaltic clay, whether derived from contemporaneous alluvium or from bedrock, may easily be mistaken for the pallid zone of the duricrust, particularly where the top part is iron-stained, simulating a mottled zone. In such circumstances the relation to the Miocene peneplain surface and the general topographical and lithological surroundings may help to resolve the difficulty. For instance, the deposit of finely-laminated white clay underlain by white sand near Dalton in the Yass-Gunning area is not far from the grey billy in a wide upland valley at Dalton village, and the hills a few miles away are capped with Tertiary basalt (Morrison and Raggatt, 1928, p. 218 ; Sussmilch, 1937 ; Joklik, 1950). Again, the transported white clay described by Morrison and Raggatt (1928, p. 219) from Home Rule near Gulgong, more than 14 feet thick and buried under 45 feet of quartz-gravel and sandy alluvium, is in an area of Tertiary deep leads overlain by basalt largely covered by surface-alluvium. Both these deposits are more likely to be of sub-basaltic than of duricrustal origin.

It is true that remnants of a grey billy association and of duricrust, both *in situ*, may be quite close together, as in the Emmaville and Inverell districts of New England and on the Shoalhaven Plain, and that for individual outcrops distinction may be far from easy ; however, if basalt is present, the spatial relation of the doubtful outcrop to it, if determinable, should be conclusive. Of course, in rare instances erosion and river transport may have brought about a mingling of grey billy boulders and disintegrated siliceous duricrust, as appears to have happened at Clermont and Anakie in Queensland (Dunstan, 1900, 1902), in which case distinction by field methods may be quite impossible.

Very little laboratory research appears to have been done on the siliceous zone of the duricrust, apart from that by Williamson (1957). It might be possible to establish mineralogical criteria to supplement the results of field study in distinguishing between it and grey billy; for example, one might expect chalcedony and/or common opal to play a prominent part in the cementing material of duricrustal quartzite in contrast to the predominant role of authigenic quartz in grey billy. White clay from the pallid zone of a siliceous duricrust has yielded 30% of free silica, expressed largely as opaline cement and replacement of felspar in an originally arkosic rock; but it is doubtful if any reliable mineralogical or chemical distinction is possible between the sub-basaltic clay of the Eastern Highlands belt and the pallid-zone clay of the lateritic duricrust, which is the type prevalent in the same belt.

The Grey Billy Association in New South Wales

General

Grey billy and some of its associates are widely distributed in the Eastern Highlands belt of this State. They are known from Bombala on the south (McRoberts, 1948) to Emmaville on the north (David, 1887) and from Ulladulla and Narooma on the east (Brown, 1926; Hall, 1969, p. 555) to Condobolin and Cargelligo (Raggatt, 1938) on the west. In conjunction with relics of Tertiary basalt they help to throw light on Kainozoic palaeogeography and on topographical history. Apart from mention made above, it is proposed to illustrate this thesis by giving notes on specific examples and considering some of their implications. Most attention is devoted to the Monaro country of the Southern Highlands, with which I am familiar and which has been mapped by the State Geological Survey and by myself. It is covered on a scale of 1 : 100,000 by Commonwealth Military Topographic Sheets 8725 (Cooma), 8625 (Berridale), 8626 (Tantangara) and 8624 (Numbla), and is included in less detail in the General Map of the Snowy Mountains Area (1 : 250,000) published by the Snowy Mountains Hydroelectric Authority, on which Fig. 1 is based. Geological maps accompany the appropriate Geological Survey reports, but on them no distinction is made between earlier and later Tertiary rocks. Other areas mentioned herein I have studied in much less detail. Where possible the occurrences are grouped according to the river-systems with which they are associated. Altitudes are based on reduced aneroid readings and are approximate.

Eucumbene-Snowy Basin

Kiandra.—Andrews (1901) noted white clays with interbedded lignites directly under basalt at New Chum Hill, and elsewhere found scattered large blocks of grey billy derived from an adjacent sub-basaltic source. These are within the walls of the wide Eucumbene valley near its head, and perhaps 200 feet above its present floor at Kiandra. Other basalt-capped outcrops of grey billy south and south-west of Kiandra within the Tumut River valley (Hall and Lloyd, 1954) belong to the Murrumbidgee system.

Adaminaby Plateau.—This is crossed from NW to SE by the Main Divide and its western part is drained by Eucumbene tributaries (Fig. 1). Adamson (1955) found several small patches of basalt on the valley walls and floor of Fryingpan and Buckenderra Creeks (now both incorporated in Lake Eucumbene reservoir up to 3,800 feet ASL) at altitudes ranging from 3,800 to 4,000 feet, and the western wall of Buckenderra valley is a ridge rising to 4,400 feet, capped with basalt 300 feet thick. In a few places this rests on alluvium, the highest known at 4,120 feet, near the northern end of the ridge. No sign of alteration has been noted, but Pipeclay Creek, basalt-filled near its source at 4,200 feet, is suggestively named.

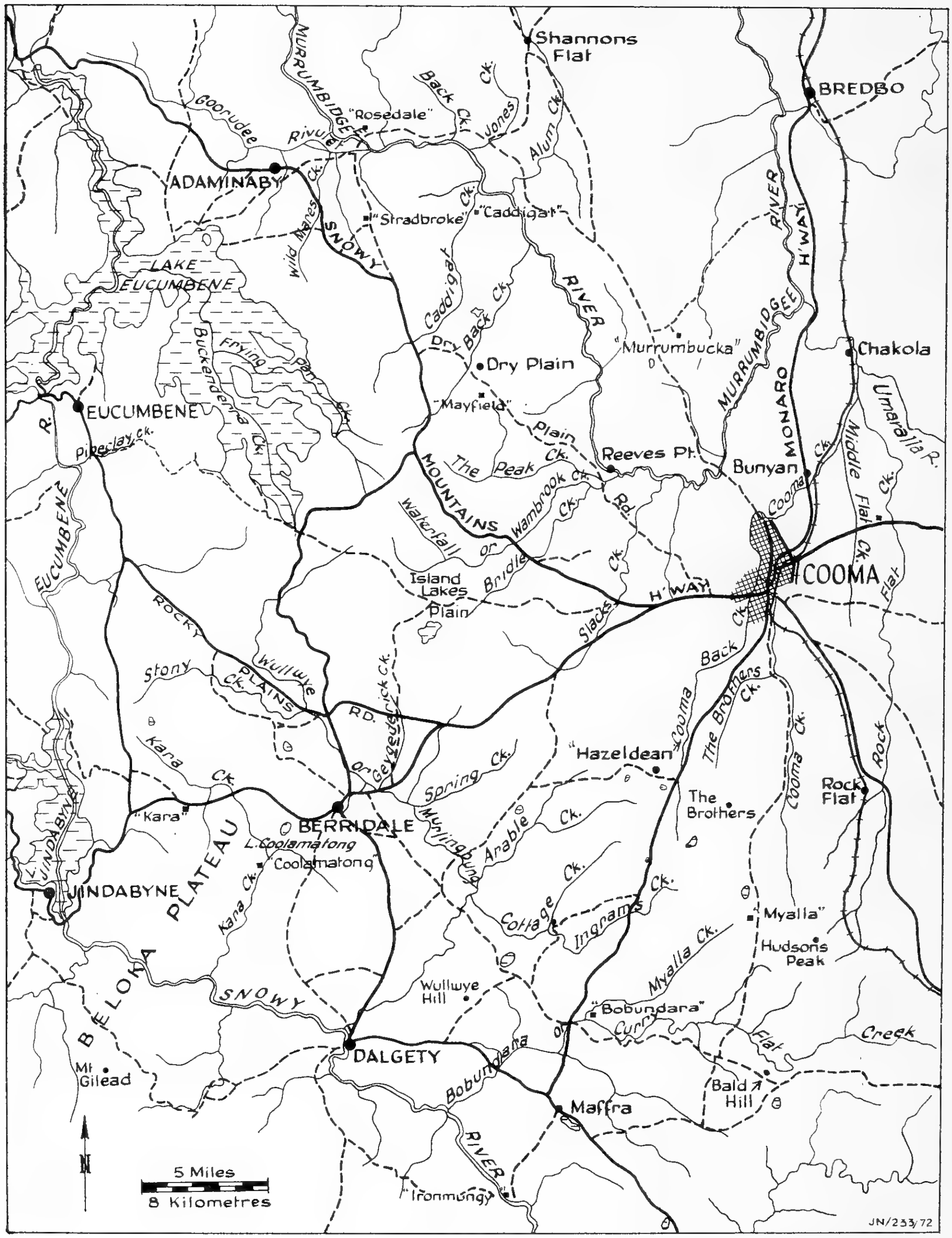

Shannons Flat
BREDBO
Goorudee Rivulet
MURRUMBIDGEE
"Rosedale"
Back Ck.
Ck.
Jones
Alum Ck.
ADAMINABY
Ck.
Wild Mares
SNOWY
"Stradbroke"
"Caddigat"
Ck.
RIVER
RIVER
H'WAY
LAKE EUCUMBENE
Caddigat
Back Ck.
Dry
Dry Plain
"Murrumbucka"
MURRUMBIDGEE
MONARO
Chakola
Buckenderra
Frying Pan Ck.
EUCUMBENE
R.
Piperlay Ck.
"Mayfield"
Plain Ck.
The Peak Ck.
Reeves Pt.
Bunyan
Ck.
Umaralla R.
Middle Flat Ck.
Ck.
MOUNTAINS
Wambrook Ck.
Ck.
Rd.
Cooma
COOMA
EUCUMBENE
Waterfall
or
Bridle
Island Lakes Plain
Slacks Ck.
H'WAY
Flat
ROCKY
Stony
Wullwye
PLAINS
Ck.
RD.
Back Ck.
The Brothers Ck.
Cooma
Cooma Ck.
Kara
Ck.
Gegedzerick Ck.
or
Spring Ck.
"Hazeldean"
The Brothers
Rock
Rock Flat
"Kara"
BERRIDALE
L. Coolamatong
Coolamatong
Murlingbung
Arable
Ck.
JINDABYNE
PLATEAU
JINDABYNE
Kara Ck.
Cottage Ck.
Ingrams Ck.
"Myalla"
Hudsons Peak
Myalla Ck.
BELOKA
SNOWY
Wullwye Hill
"Bobundara"
Curry Flat
Creek
Mt Gilead
DALGETY
Bobundara
Maffra
Bald Hill
RIVER
"Ironmungy"
N
5 Miles
8 Kilometres
JN/233/72

Fig. 1.

The plateau is bounded on the SW by a creek which rises near the junction of the Jindabyne-Eucumbene and Rocky Plains roads and is a tributary of Stony Creek. On the left wall of its wide valley near its head is a long bank or ridge of gravels with an apparent thickness of 50 feet. Amid the gravels are rounded boulders of grey billy and vein-quartz up to 2 feet. On the top of the deposit near its NW end a patch of pebbly grey billy *in situ* some 20 feet by 9 feet was found, and traces of white clay were noticed on the road under the gravels. It seems that an earlier Tertiary deposit was superficially silicified under basalt and during the earlier-Pliocene exhumation was largely broken up and redistributed. It is probably significant that the gravel bank is collinear with a basalt-capped ridge 3½ miles to the SE separating Wullwye Creek from its tributary, Stony Creek. These two streams and their tributaries are locally bordered by gravel banks 30 or 40 feet above the present channels, and near their junction and debouchment on to the lowland north of Berridale a boulder-bed of brown quartzite appears at about 3,050 feet ASL, 150 feet above Stony Creek on its right bank, and terrace-gravels containing basalt and quartzite pebbles are seen at about 160 and 60 feet respectively above Wullwye Creek; these may all be related to post-basalt differential uplift of the plateau.

Jindabyne Area.—A deposit, first noted by David on a field-trip in 1900, 7 miles from Berridale along the Jindabyne road where it is joined by the Hilltop track, nearly opposite Kara homestead, appears to be entirely sub-basaltic in character. A flat-topped hill, rising to about 100 feet above the floor of the upland valley traversed by the road, forms part of a ridge separating the east-flowing Kara Creek from a tributary, and is crowned with 30 feet of gravels. These, now much disturbed and reduced by quarrying, cover an area 470 yards by 380 yards, consist mainly of quartzite and chert, and are overlain by disrupted masses of grey billy up to 6 feet in diameter and 18 inches thick, obviously *in situ*. The base of the gravel is iron-cemented to a thickness of 18 inches. Basalt is absent.

At Jindabyne, a little north of the junction of the Kosciusko and Dalgety roads there was, before the filling of the Jindabyne reservoir, quite an extensive deposit of bedded white clay to be seen at 2,950 feet within the valley of Widows Creek. It was at least 20 feet thick, with an overburden of red soil, and may have been sub-basaltic. The nearest known basalt outcrops are six miles away, one on the Dalgety road resting on granite, the other at Jillamatong Hill, where a basalt cap overlies quartz grit and, I understand, white clay. These are all within the Jindabyne trough.

Some 8 miles south of Jindabyne the basalt-crowned monadnock of Mt. Gilead rises above the Beloka plateau to a little over 4,200 feet ASL. On the northern side Tertiary sediments under 130 feet of basalt have been changed to grey billy.

Berridale-Dalgety Area.—In the undulating country fronting the Beloka plateau and watered by south-flowing tributaries of the Snowy grey billy and its associates are prominent along Wullwye and Bobundara creeks and their affluents. The road from Cooma to Berridale at between 6 and 8 miles out traverses a number of very flat headwater branches of Spring Creek whose floors are strewn with small angular blocks of disintegrated grey billy, evidently related to remnants of basalt hard by; where the Rocky Plains road takes off at 6 miles out of Berridale the rock is massive. From one of these valleys I have (1964) described grey billy surrounding a small lake, and more recently I have noted, some half mile south of the lake, an expanse of sandy grey billy, just above the floodplain, perhaps 200 yards square and broken into great slabs up to 15 feet in diameter and 5 feet thick, tilted at small angles in every direction. A little farther down bedded white clay of unknown thickness is exposed in shallow pits in the floodplain; clearly its erosion has caused undermining and collapse of the grey billy. Not improbably the little lake was formed by a similar collapse.

Closer to Berridale near the junction of Geygederick Creek and Wullwye Creek at 2,820 feet ASL grey billy is seen amid projecting outcrops of quartz-diorite, and varying in texture from pebbly through sandy to a very fine-grained glassy type with smooth fracture; to this outcrop my attention was kindly directed by Dr. A. B. Costin, C.S.I.R.O., Canberra. Some 1½ miles NNW of Berridale white bedded clay and leached bedrock slates are visible near basalt outcrops and overlain by post-basalt gravels, and near Wullwye Creek is a little basalt knoll amid alluvium and capped with gravels including a boulder of grey billy.

The Berridale-Bobundara road runs SE along the broad, flat valley of Wullwye Creek covered by remains of the basalt flows that once filled it, together with grey billy, sandy, gritty and pebbly, siliceous and ferruginous, in places cavernous through imperfect cementation. A very extensive outcrop is seen 4 miles out of Berridale, more than 600 yards wide and apparently up to 10 feet thick. It underlies 150 or 200 feet of basalt and rests on terraced basalt, which descends almost to creek level. Post-basalt gravels also border this stretch of Wullwye Creek at intervals, 20 feet above its present level. Three miles from Berridale on the same road granite bedrock is bleached and crumbles to a loose sandy clay under an old basalt-filled valley.

An interesting section is displayed along the track that takes off from the Bobundara road at 14 miles south from Cooma, traverses the plateau diagonally for 2 miles and then descends to the floor of Cottage Creek, dropping 500 feet in 2½ miles. The plateau, 3,400 feet ASL, is composed of Tertiary basalt (30 feet) resting on Ordovician slates and quartzites. At the beginning of the descent, at about 3,300 feet, are what may be terrace gravels. At 3,100 feet a remnant of an old erosion-terrace or valley-floor with relics of grey billy on it is crossed. On the left of this a quarry-face in a sloping bank reveals dipping leached Ordovician slates and quartzites, with silicified gravels and boulder-screes of old quartzite. A little farther on a steep tributary creek crossing the track exposes cemented quartz-gravels on bedded white clay at 2,950 feet. Beyond this at 50 feet higher is an extensive flat or terrace on which a remnant of basalt 30 feet thick overlies ferruginous shale, cemented gravels and silicified rubble resting on a bedrock of leached slates. The track continues down to the creek, passing "Cottage Creek" homestead (2,820 feet), and crosses Ingram's Creek, which comes in from the east and joins Cottage Creek a little way downstream. Hereabouts may be seen silicified Ordovician quartzites and leached slates in the creek bed, and great disrupted blocks of pebbly grey billy traversed by quartz-veinlets on the bank of Ingram's Creek 40 feet above the creek and overlain by basalt. Cottage Creek makes a sharp bend to the right and after a meandering course of 5 miles or more joins Wullwye Creek at 2,620 feet. Just below the junction, and partly obscured by a landslide, basalt overlies grey billy, white clay (15 feet or more) and peat. The grey billy may be traced down Wullwye Creek for about half a mile, where it forms a terrace at 30 feet, with 20 feet of loose Pliocene (?) gravels on top. The drainage-area of Cottage Creek and its tributaries is about 2 miles wide and the evidence suggests the exhumation of an early-Tertiary valley, which had been gradually filled with basalt of a total thickness of at least 750 feet. During pauses in the extrusion sedimentation took place, and valley widening through encroachment on and erosion of the eastern wall of the valley.

The components of Bobundara Creek come mainly from the east, and there are indications that its valley and those of its tributaries were filled with basalt and interflow sediments through a vertical range of about 1,100 feet. Much of that at the higher levels was subsequently eroded away, but there are still relics of basalt along the sides and on the floors of the valleys, with outcrops of interflow and subflow sediments. Grey billy, bedded white clay, bole and leached slate bedrock have been noted in various places. Terraced basalt appears on the southern slope of Bald Hill up to at least 3,250 feet ASL, and 200 feet lower great blocks of grey billy, containing what appear to be fragments of vein-quartz, crop out. Bole and vitrified soil (?) underlie basalt at 2,900 feet on the road 1¼ miles SE of Maffra.

An unnamed tributary flowing south beside the Bobundara road 17 miles south of Cooma shows a good section in a road-cutting on its right bank. At 30 feet above the creek and 3,050 feet ASL is a prominent outcrop of pebbly grey billy with very little matrix, 4 or 5 feet thick, with thin interbedded lenses of fine, white siliceous material, probably silicified soil, containing casts of plant rootlets. The grey billy slabs rest apparently on loose gravel and are tilted; the bedrock slates are leached and the silicified sediments are overlain by about 300 feet of basalt forming the surface of the plateau. The succession is exposed for 60 yards or more on the roadside and remnants of loose white quartz terrace-gravels continue down the creek for another 2 miles. Other outcrops of grey billy are seen near the mouth of Myalla Creek, which enters the main creek near "Bobundara". Here Bobundara Creek, flowing on basalt at 2,600 feet, turns SW; and 400 feet up on its right bank, a mile E of Wullwye Hill, is a large expanse of laminated white clay overlain by 6 or 8 feet of sandy grey billy. This has evidently been covered by basalt, of which patches still survive on the granite plateau surface.

Two miles to the south an instructive succession is revealed in road cuttings where the Dalgety-Maffra road descends through 400 feet in 2 miles to cross Bobundara Creek at 2,500 feet. No less than eight flows of basalt, ranging from 5 to 100 feet in thickness, alternate with beds of white clay (one of them 25 feet thick), lignite and grey billy. The first two have been superficially crumpled or corrugated by the push of advancing lava, and the lignite or peat seems to have experienced some heat alteration. At the top of the sequence is an apparent thickness of 150 feet of a massive breccia, chiefly of tight-packed boulders of argillaceous quartzite and slate, the latter as well as the matrix of the rock being leached. A 10-foot bed of white clay with lenses of very fine, white sand is interstratified with the breccia and is locally current-bedded. The whole mass has a downhill slope of about 10°, as if tilted by faulting. But for the presence of the clay the breccia might be taken for a kind of scree; as it is, its interpretation is still to seek. A small remnant of basalt on top of it gives a clue to the leaching of the breccia and bedrock slate. At the surface, with the removal of the white-clay matrix the breccia weathers to a brownish ferruginous rubble. Much of the basalt is very decomposed and the granite basement that crops out near the river has been locally converted into loose, iron-stained sandy clay.

Two miles WSW of Berridale lies Lake Coolamatong, perched on a low, flat valley-divide 2,950 feet ASL. It is bordered by siliceous and ferruginous grey billy and has an overflow WSW into Kara Creek, which has descended steeply from the Beloka plateau to follow the base of its eastern scarp to the Snowy. Siliceous grey billy, gritty and pebbly, appears at 2,900 feet half a mile SW of the lake on the track to "Coolamatong" and half a mile farther on forms a terrace up to 2,880 feet, lying on leached slate bedrock at 60 feet above creek level. Farther down on the left bank short, steep tributaries flow over ferruginous and siliceous grey billy from nearly 3,100 feet ASL to 2,850 feet.

On the right bank behind "Coolamatong" homestead are terrace-accumulations of subangular pebbles and cobbles of slate, quartzite and grey billy up to 100 feet above the creek, and these continue north for about a mile along the scarp-foot; they are not improbably Lower Pliocene, but near the base the rubble is silicified, and may be pre-basaltic. Silicified bedrock crops out here and across the creek at 600 yards south of the lake.

Along the Snowy at Dalgety (*cf.* Relph and Wynn, 1960) no sub-basaltic deposits have been noted, but at 100 feet above it on both sides are early Pliocene (?) high-level gravels. However, some 12 miles downstream on the right bank of the river at 100 feet up and 500 yards away from it, there is very coarse, gritty grey billy, with ill-defined pebble-bands, chiefly of milky quartz. The rock is disintegrating into rounded blocks up to 9 feet long, which bestrew the slope over a vertical interval of 50 or 60 feet, but the true thickness is probably not more than 10 feet. Though dimpled and cellular like that of normal grey billy, the surface is rough and the rock does not ring under the hammer.

On the opposite side of the river beside the road from Maffra to " Ironmungy " homestead is a knoll capped with grey billy about 3 feet thick resting on loose gravels, rounded boulders of it mingling with the gravels on the slopes; the total thickness may be about 50 feet. As the knoll is about 100 feet above the river and 400 yards away, it would appear that the earlier-Tertiary ancestor of the Snowy was much bigger than the present stream. A few miles south grey billy crops out under basalt along Lambing Creek, a Snowy tributary.

Murrumbidgee Basin (Fig. 1)

Adaminaby Area.—The eastern half of the Adaminaby plateau as well as the country north of it is drained by the Upper Murrumbidgee and its tributaries. From the north come Jones Creek and Alum Creek. Where the former is crossed by the Rosedale-Murrumbucka road there is a considerable expanse of grey billy *in situ*, most of it pebbly, its top at 3,260 feet ASL, or 60 feet above the creek; it continues down creek for at least 600 yards. Alum Creek is crossed by the road 3 miles farther on but has been rejuvenated here to a level well below its pre-basalt one; there are, however, high-level gravels (? Pliocene) at 80 feet above it. Some miles upstream, where the Cooma-Shannons Flat road follows it closely, Alum Creek occupies a wide, flat swampy valley in which pebbly grey billy crops out a little above creek-level at intervals beside the road from 3 miles S of Shannons Flat school to three quarters of a mile beyond it. There is at least one small patch of basalt on ferruginous grey billy at 3,600 feet.

The country around Adaminaby is traversed by tributaries of the Murrumbidgee. A little north of the township Goorudee Rivulet flows east to join the river a quarter of a mile below Rosedale bridge. Where the Yaouk road from Adaminaby crosses it at about 3,280 feet ASL sandy grey billy, cavernous and disintegrating into large blocks, crops out 20 feet above the swampy valley floor. Other outcrops at a higher level have not been examined.

A mile east of Adaminaby a road takes off to the SW from the Snowy Mountains Highway. Half a mile along it a little craggy outcrop of cemented gravel overlies bedded white clay 20 feet thick resting on leached slate bedrock at 3,390 feet, 25 feet above the swampy valley of Happy Valley Creek. At 1¼ miles further on, at 3,550–3,600 feet, the road crosses an exposure of siliceous and ferruginous grey billy at least 100 yards wide. This obviously pre-basalt deposit is roughly 150 feet above those beside Happy Valley Creek.

Some 3½ miles east of Adaminaby on the road leading to Rosedale bridge (where the Murrumbidgee flows at 3,190 feet) and 1½ miles SW of the bridge a prominent vertical outcrop of silicified Ordovician quartzite is exposed at 3,210 feet as a faulted mass flanked on either side by leached slates. The outcrop continues southwards as the crest of a steeply-sloping ridge and is traceable for 1½ miles to an altitude of 3,470 feet ASL. The silicified rock is typically white, closely resembling that from Rock Flat described above. It is thought that silicification and bleaching were related to a former basalt-flow that occupied the Murrumbidgee valley almost down to its present floor level; such a suggestion is in harmony with the evidence of grey billy and white clay deposits but little above the valley floors of Goorudee Rivulet, Happy Valley Creek, Jones Creek and other tributaries in their lower reaches.

The country traversed by the Snowy Mountains Highway for 5 miles south from Adaminaby abounds in exposures of grey billy and its associates, of which sections are visible on and near the road itself and along side-tracks. The highest exposure occurs at 3,600 feet ASL some 500 yards south of the track to " Stradbroke " ; here grey billy with angular chips of black silicified slate is underlain by white clay and has a distinct slope down from the road. Extensive outcrops may be seen along the " Stradbroke " track east and the old Adaminaby track west of the Highway, where the base of the grey billy, resting on white clay, descends to 3,450 feet. The total east-west width disclosed exceeds 2 miles but diminishes considerably northwards. Nearer Adaminaby where the highway crosses Wild Mares Creek at 3,330 feet an extensive remnant of pebbly grey billy 40 feet up the right bank of the creek has been broken, apparently through undermining, into great slabs, one of them 18 feet by 18 feet, another 20 feet by 9 feet, and none more than 4 feet thick. Most are tilted, and the underlying white clay is traceable for a quarter of a mile down the creek, whilst leached bedrock is exposed beside the highway for more than 150 yards west of the creek.

Bedded white clay may also be seen at intervals along the highway in road cuttings and eroded valley flats. It is particularly well displayed in two cuttings each 10 or 12 feet high, one 400 yards north of the " Stradbroke " turn-off at 3,540 feet, the other three-quarters of a mile farther north at 3,450 feet. In the latter the well-laminated sandy clay containing obscure plant remains is truncated at its northern end by a contemporaneous washout wherein white clay is interlaminated with narrow bands of quartz-granules and mica-flakes. Some 300 yards south, in a flat tributary valley west of the highway, at about 20 feet lower than the cutting, tilted cavernous grey billy rests upon white clay.

Leached slate bedrock is seen in some places, as noted above. Of particular interest is an exposure on the highway between the more northerly white-clay cutting and the Wild Mares Creek bridge. This is visible for about a quarter of a mile at an altitude ranging from 3,400 to 3,450 feet ; the low watershed of Wild Mares Creek and Stradbroke Creek is traversed by the highway for 1½ miles, and this is the only stretch of it that is not composed entirely of Kainozoic deposits.

Even if allowance is made for the effect of the northerly slope of the valley floors, it is hard to explain the varying altitude of grey billy along the highway, particularly as compared with that of the white clay in adjacent outcrops. It may be due in part to the breaking up, tilting and lowering of the hard crust through undermining, by removal of subjacent clay as the result of erosion, a suggestion originally made to me by Mr. Moye ; another possible explanation is faulting, of which, however, no traces have been seen.

On the road that runs south from Rosedale bridge to join the Snowy Mountains Highway grey billy and leached slate are seen up to an altitude of 3,450 feet and grey billy appears also in the valley of a creek just east of the road.

Internal evidence makes it clear that though the nearest basalt outcrop is 2½ miles away to the east, the altered sediments described above and the valleys in which they lie antedate the lava outpourings and were once themselves covered with basalt.

Post-basaltic deposits are not uncommon, locally obscuring the earlier-Tertiary beds. They overlie the cemented gravels on the Happy Valley road and on the road from Adaminaby to the Rosedale bridge at 3,350 feet, where they are seen to consist of boulders and gravels including waterworn grey billy. They appear to form much of the surface in Adaminaby and its immediate vicinity and in the country drained by Wild Mares Creek and Stradbroke Creek. Here they partially cover the grey billy and white clay, forming flat-topped, somewhat dissected banks, up to at least 50 feet thick, of subangular boulders and pebbles of brown quartzite, hard black slate and grey billy in a matrix of transported red clay. In the two road-cuttings in white clay mentioned above they lie unconformably on the clay, and near the base include layers containing, *inter alia*, slabs of iron-cemented grey billy. These deposits, lying on the floors of mature upland valleys, are thought to be probably earlier-Pliocene.

Certain boulder-beds (Adamson, 1955) along the left bank of Wild Mares valley look like scree-deposits. They are composed of angular and subangular boulders up to 4 feet long, mainly of quartzite and iron-hardened slate, derived from the somewhat steep walls of the valley and embedded in soil. Obviously post-basaltic, they may be of Pliocene or even Quaternary age.

A few miles to the SE deposits of an ancestral Caddigat Creek may be studied on the Dry Plain road, a mile east of its intersection with the Snowy Mountains Highway, on top of a low, flat ridge at 3,800 feet ASL. This forms the watershed between Caddigat Creek and Back Creek, both here occupying old-mature upland valleys at about 100 feet lower. Cemented gravels and interbedded white clays to a total thickness of perhaps 20 feet lie upon leached bedrock slates. Locally the gravels are iron-cemented, but elsewhere their clayey matrix is bleached, and along the track running NNE from the Dry Plain road occasional fragments of grey billy may be seen amid black basaltic soil. A few miles north, where the Tertiary deposits cross to the west of Caddigat Creek, sections of them are revealed through deepening of the creek, and they spread out for about a mile on a low, gently-sloping plain at 3,600 feet. Near " Caddigat " homestead they descend to 3,450 feet ASL, but beyond it the creek and its tributaries are deeply entrenched, and I have not examined them. In addition to siliceous grey billy there are, especially in the northern part of the area, iron-cemented grits and coarse sands etched out by weathering into a maze of anastomosing tiny ridges, apparently because of rhythmical cementation. Some of the siliceous grey billy is made up largely of rounded pebbles and occasional large blocks of vein-quartz in a matrix of coarse gritty quartz-grains. Basalt, fairly extensive in the south, is reduced in the north to scattered patches, many in visible or virtual contact with the sediments.

A few post-basalt accumulations have been noted. On the Snowy Mountains Highway 350 yards north of the Dry Plain road junction is a section of 15 feet of cobbles of old rocks, rounded and subangular, with a few lenses of sand, on the floor of a Caddigat tributary. The land-surface west of " Caddigat " homestead is strewn with large blocks of Ordovician quartzite, vein-quartz and grey billy, due to flood distribution possibly in Recent time, and a creek bed nearby is choked with boulders of siliceous grey billy. These deposits extend for more than a mile west of the homestead.

The highest altered sub-basaltic deposit I have observed is at " Mayfield ", three-quarters of a mile west of the " Glenbernie " turn-off on the Dry Plain road, 4 miles south of its junction with the Snowy Mountains Highway. It is an interflow deposit of bedded white clay, possibly 10 feet thick, with its top at 3,980 feet ASL, and is overlain by perhaps 100 feet of basalt. At " Elanora ", half a mile to the north, it emerges from under the basalt and apparently forms part of the section visible along the Dry Plain road just north of the " Glenbernie " turn-off ; this may be 40 or 50 feet thick, and includes, under the clay, a thin bed of gravel and a 2-foot layer of peat resting on or against leached bedrock. The whole succession seems to be a remnant of sediments deposited on the valley floor of an ancestral Back Creek. Indeed, 1½ miles to the NE basalt on the ridge at 4,000 feet extends down to the floor of Back Creek valley at 3,600 feet and continues west on to the top of the flat ridge that bears the sub-basaltic

Caddigat gravels. The evidence suggests at least two episodes of lava extrusion separated by crustal uplift and erosion.

Dry Plain road continues SE down along the sloping comb of a ridge to near the Murrumbidgee at Reeves Point, descending 1,400 feet in 6 miles. Many years ago Mr. F. A. Craft kindly told me of sub-basaltic deposits visible on the road. The upper, at between 3,500 and 3,600 feet ASL, consists of ferruginous gravel overlain by possibly 50 feet of bedded white clay ; the other at about 3,280 feet is a much less conspicuous bed, perhaps 10 feet thick, of loose well-rounded pebbles of quartzite and vein-quartz. Both deposits lie on leached slate bedrock and are overlain by basalt. The full significance is not at the moment apparent.

On its way to Cooma the road crosses The Peak Creek, a Murrumbidgee tributary, on basalt at 2,600 feet, and on both sides of the river where it turns east basalt appears at but little above its present level. Also within its valley there are post-basalt gravels at 100 feet above the river ; these may be contemporaneous with some of those shown on Adamson's map as bordering the Murrumbidgee further north.

The Country around Cooma.—Two meridional belts of basalt, each up to more than a mile wide, pass about 8 and 10 miles respectively to the west of Cooma, but little alteration seems to have accompanied their extrusion. The only notable example is to be seen at 3,300 feet ASL one-quarter to one-half mile west of the Snowy Mountains Highway where it crosses the summit of a ridge separating Slacks Creek from Bridle Creek. The succession has been much confused by quarrying operations, but a small outcrop of pebbly grey billy about 10 feet thick is visible in one place, and elsewhere a few feet of ferruginous grit and gravel, both apparently resting on loose gravels of unknown thickness. A little white clay shows at one point and bedrock of quartzite and slate traversed by quartz-veins seems to have been locally silicified. The creeks are 400 and 300 feet respectively below the summit of the ridge, and patches of basalt that once filled their broad valleys are to be seen almost to the top of the ridge. The outcrop of grey billy is 30 or 40 feet higher than the nearest basalt outcrop, but it is difficult to determine which is the younger. Certain it is, however, that a pre-basalt river once flowed at a considerable height above the present creeks ; it may have been the common ancestor of both.

The deposits on the Island Lake Plain road depicted as Tertiary on Hall's (1955) map are scree-like or rubbly accumulations chiefly of brown Ordovician quartzite, angular to subangular, mantling outcrops of weathered Tertiary basalt. They may have been partly stratified by water-action and are Pliocene or younger.

Leached slate bedrock under basalt is seen on the Snowy Mountains Highway where it descends the right bank of Bridle Creek valley on the Adaminaby road about 8 miles out from Cooma, and on the Cooma-Dry Plain road where it leaves the plateau at 3,000 feet and drops down steeply into a youthful tributary of Bridle Creek.

Much of the country south and east of Cooma is basalt-covered and many tributaries of the Murrumbidgee clearly had a pre-basalt existence. For instance, the bed of Cooma Back Creek, where it is crossed by the Bobundara road 9 miles south of Cooma, is 10 feet below basalt-covered grey billy, and 5 miles to the north at " Woodstock " gate and for 500 yards south of it there are uncemented white gravels underlain by white clay at 2,850 feet, which a little distance south disappear under basalt. A mile to the east and at 150 feet lower disintegrating sandy and gravelly grey billy with white clay crops out in the valley of The Brothers Creek, a tributary of Cooma Creek, as sub-basaltic and interflow deposits, and continue across the Myalla road on to the floor of Cooma Creek valley. Occasional outcrops of grey billy appear further up the valley, and interflow beds of white clay further south along the Myalla road. In the basalt country south of Cooma grey billy has been noted on the west-east track from " Hazeldean " homestead to the Bobundara road and interflow white clay on the Nimmitabel road near Rock Flat.

Post-basalt gravels and cobbles of redistributed grey billy have been observed in Cooma beside the railway half a mile south of the railway station at about 20 feet above Cooma Creek.

The country north and north-east of Cooma is undulating, consisting of low submeridional ridges of old rocks, rising to upwards of 2,700 feet ASL, separating wide, shallow valleys and in places crowned with remnants of Tertiary basalt which extend down into the valleys ; the latter also contain pre-basaltic and post-basaltic sediments. These features are well seen on either side of the road from Cooma to Numeralla for its first 10 miles. From the western bounding ridge of Middle Flat valley basalt extends down the side of the valley, and at a mile north of the road a deposit of diatomaceous earth is partially surrounded by basalt and locally hardened and converted into common opal. Farther north Silurian dacitic crystal tuff is changed to white clay studded with tiny quartz grains. Cobbles and boulders of redistributed pebbly grey billy appear on an old flood-plain 40 feet above the creek channel, which is cut in leached quartzites and slates. The next ridge, separating Middle Flat from Rock Flat (Tolbar) Creek valley, is capped by a small outlier of basalt at least 100 feet thick a quarter of a mile north of the road. Some 50 feet below it is a layer of siliceous grey billy *in situ* but breaking up into rounded slabs 10 or 12 feet in diameter by 2 feet thick, poorly cemented, cavernous, and strewing the ground with weathered-out pebbles. Polygonal surface-cracking of the slabs is common, and they are tilted in all directions. Between basalt and grey billy the section is obscured by a veneer of post-basalt (earlier-Pliocene ?) gravels, cobbles and boulders of vein-quartz, black slate, brown quartzite and basalt, which covers the slope for some distance north and south. On the road these gravels, which extend for nearly a mile east to Tolbar Creek and through a vertical range of 50 or 60 feet, lie on white clay possibly 15 feet thick with the bedding emphasized by thin laminae of limonite. This may be stratigraphically below the grey billy described above ; it appears to underlie basalt and to rest partly on a thin basalt flow and partly upon bedrock. It contains obscure plant remains and is gently flexed with a low easterly dip. Locally, bedrock slate has been leached and limestone and crystal tuff replaced by limonite. Across Tolbar Creek (2,485 feet) the road keeps on its easterly course on a high-level flood-plain about 100 feet above a tributary creek for a mile, and then rises toward the eastern wall of the valley. At 2,750 feet a cutting reveals 8 feet of waterworn cobbles sitting unconformably upon about 20 feet of white clay passing down into ferruginous sands, which rest on leached bedrock slates and quartzites. The clay with its thin limonitic laminae closely resembles that on the western side of Tolbar Creek but is 200 feet higher. It is considered to be pre-basaltic and the overlying cobbles, consisting of white quartz, brown quartzite and grey billy (?), are thought to be post-basaltic. Another 2 miles and the road reaches its highest elevation of more than 3,000 feet, where it traverses the face of a north-sloping ridge, the watershed between the Umaralla River and its tributary Tolbar Creek. Here it skirts the base of a Tertiary basaltic outlier that rises southward more than 200 feet to the flat summit of the ridge. There appear to be three flows of basalt, the topmost being 110 feet and each of the others less than 30 feet thick. On the top of the ridge, immediately south of the basalt outcrop and at a slightly higher level are scattered fragments of grey billy and ferruginous shale, possibly relics of deposits under a flow now vanished. Beneath the topmost flow are 70 to 80 feet of coarse quartz-grits, fine gravel, plant-bearing shales and, at the base, quartzitic boulder-beds. The middle flow seems to be underlain by white clays with corrugated or rucked-up surface, ferruginous shales and iron-cemented gravels, whilst the lowest flow rests on semi-consolidated gravels. In several places where contact with the Tertiary rocks is exposed the bedrock of Ordovician phyllites is leached. The lowest basalt has been traced in a direction N 18° E (true) for 480 yards along a flat spur on the Umaralla side of the watershed. There are also signs of basalt and sub-basaltic deposits on the western side of the ridge 400 feet above Tolbar Creek.

The basalt so abundant south of Cooma dwindles and disappears to the north. Some 3 miles out along the Monaro highway a few large boulders of grey billy may be seen in the basalt country, and at $1\frac{1}{2}$ miles north of Governors Hill and 130 feet above the Umaralla River is a solid outcrop of pebbly grey billy at 2,460 feet ASL. East of Governors Hill within the wide valley of Cooma Creek grey billy has been noted at about 2,450 feet, and basalt overlying grey billy has been observed 2 miles to the north and at approximately the same level within the valley of a small creek flowing north to the Umaralla River ; it is mantled by high-level gravels, which also rise in places above the flood-plain of the river and its tributaries to 2,470 feet or more. Beside the railway line at three-quarters of a mile south of Chakola Siding at the very edge of the Umaralla River is a small patch of basalt at about 2,400 feet. These are the most northerly outcrops of basaltic lava and sub-basaltic sediments known to me in this stretch of country.

Country North of Cooma.—Downstream of its confluence with the Umaralla River the Murrumbidgee is bordered by many remnants of terrace-gravels at altitudes up to 240 feet above the present river (Browne, 1944), extending at least as far north as Michelago ; the presence of occasional cobbles of basalt and grey billy among them indicates a post-basalt age. However, on the highway some 3 miles south of Bredbo a couple of cuttings reveal sections through white, bedded clays not less than 25 feet thick, truncated by beds of river gravel at least 30 feet thick ; these are in a shallow valley at about 2,400 feet, or 100 feet above the river, which is about half a mile to the west with a gravel-crowned ridge at 2,540 feet in between. The gravels, lying unconformably on the clay, consist of black, hardened chiastolite slate, quartzite, silicified rhyolite, grey billy in large boulders and acid gneissic granite such as is got *in situ* on the left bank of the river. Its presence suggests that the gravels mark the bed of an early Pliocene (?) ancestor of the river which had also been occupied by its earlier-Tertiary progenitor.

If the patch of silicified breccia on felsite $1\frac{1}{4}$ miles to the north and at about the same altitude is accepted as of sub-basaltic origin, and account is taken of the basalt dykes which have been noted at intervals from Bredbo to a few miles north of Michelago, we may with some justification assume that earlier-Tertiary basalt formerly extended for some 45 miles north of Cooma in the Cooma-Canberra corridor. Details of the geology of the 25 miles of country thence to Canberra I have not studied.

Summary of Inferences

From the information presented above regarding the areas examined the following generalizations emerge :

(1) The earlier Tertiary drainage-pattern was in many places very similar to that of the present day.

(2) The earlier Tertiary topography was gradually buried under basalt over a considerable time-interval to a depth of at least 1,200 feet above some of the valley-floors.

(3) Later, possibly in early Pliocene time, prolonged erosion removed much of the basalt and to a large extent restored the landscape to its pre-basalt condition but left some evidences of its previous presence, particularly in the river-valleys.

(4) Later again, but still in the Pliocene, erosion was succeeded by deposition in the exhumed valleys and the deposits were in their turn somewhat dissected.

(5) The arterial rivers—Eucumbene, Snowy, Murrumbidgee and Umaralla—participated in these happenings, but subsequent erosion has removed the evidences more thoroughly than in their tributaries.

Canberra-Lake George Area

Evidences of Tertiary volcanic activity in Canberra and the adjacent country are very scanty. Öpik and Noakes (1954) both make mention of the " Fyshwick Gravels ", which the former (1953) regarded as Permian (?) fluvio-glacial deposits, but which as later examination has shown are clearly remnants of grey billy. They were exposed in a small, shallow quarry in the industrial suburb of Fyshwick, but, unfortunately, all traces of them are now buried beneath buildings and industrial rubbish. They occurred on a low ridge sloping north to the Molonglo River and about 50 feet above it. As revealed in the quarry, a large rounded and dimpled block of typical grey billy was surrounded by and partially embedded in stratified quartz-gravel, and 150 yards to the north-west were the remains of a sheet of grey billy *in situ* in process of disruption, the biggest slab being 9 feet by 2 feet by 1½ feet ; there were some loose gravels around them, and the fact that the grey billy was devoid of pebbles suggests that the gravels may be of later age, possibly early Pliocene. Other outcrops of unconsolidated gravel scattered about the city (e.g. near St. John's Church on the north side of the valley) have been thought to belong to the same group (Legge, 1937).

Taylor (1907*b*) recorded that shafts sunk through the gravels and boulder-beds on the western wall of the Lake George depression disclosed the presence of underlying white clays ; he also noted white clays on the floor of the lake, and a quartzitic rock later identified by Garretty (1937) as grey billy. Some 5 miles south of Bungendore between the road and the Captains Flat railway line is a great expanse of leached Ordovician slate, of whose existence I learnt through the courtesy of Dr. and Mrs. F. H. Morley of Canberra. It forms part of the floor of the wide valley-plain in which farther south the Molonglo River flows. The leached slate extends over, perhaps, 100 acres or more and is said to be 30 or 40 feet thick.

Farther south the western wall of the wide Molonglo valley is bordered for several miles by remnants of a terrace above the flood-plain. At a spot on the Queanbeyan-Captains Flat road about 13 miles south from Bungendore one of these is capped by quartz-gravel, sand and clay, all iron-impregnated, and resembling some of the altered sub-basaltic deposits of the Monaro country described above. The nearest known Tertiary basalt (Garretty, 1937) is a small patch 10 miles east of Lake George and 2 miles south of Tarago.

It is tempting to speculate that basalt once filled the lowland corridor running north from Cooma to Canberra and Queanbeyan and that it spread down along the Molonglo valley to Lake George and the country east of it.

Shoalhaven Basin

In his admirable series of studies of the physiography of the Shoalhaven River valley Craft (1931*a*, 1931*b*, 1931*c*, 1932*a*, 1932*b*) lays considerable stress on the role of Tertiary basalts and their associated " contact quartzites ". An important physiographic feature recognized by him is the Shoalhaven Plain, an extensive undulating surface sloping gently north at between 2,400 and 2,000 feet ASL, bounded east and west by higher land and forming the flat-floored very mature valleys wherein the river and its tributaries flow. It is traceable from the headwaters to below the great right-angled bend at Tallong. Basalt remnants crop out upon it here and there, some of considerable size, as at Nerriga and downstream from Tallong to Caoura. As well as white clays and sands with some peat, abundant outcrops of grey billy and ferruginous conglomerate are scattered over the surface, many of them bordering the river and its tributaries. Some are in close relation to basalt (Craft, 1931*a*, pp. 111, 118–119 and Pl. VI) and are evidently *in situ* ; these may pass down into uncemented sands or gravels or may rest directly on leached bedrock. Others are incorporated as subangular blocks and rounded pebbles and boulders in later rudaceous accumulations ; they have evidently been broken up and the fragments redistributed by river-action following the almost complete removal of the basalt. On the road from Braidwood to Nowra, part of which traverses the Shoalhaven Plain obliquely, three outcrops of grey billy and a few small patches of basalt and of unsilicified gravels are crossed in a distance of 20 miles.

In the upper parts of the basin the Shoalhaven Plain has had channels incised in it to a depth of 300 or 400 feet ; farther down there has been later rejuvenation with the excavation of deep gorges, so that at Tallong, 40 miles from the coast, the Shoalhaven Plain is 1,600 feet above the present stream.

The history of the evolution of the present river system seems to have in general paralleled that of the Snowy and Murrumbidgee, but can be carried a little farther. An ancestral Shoalhaven with tributaries existed in earlier-Tertiary time and was later filled with basalt, which caused alteration of the pre-basalt sediments. Following the Miocene peneplanation the Macleay uplift resulted in re-excavation of the valleys to a little below the pre-basalt level and in their expansion to form the Shoalhaven Plain. Most of the basalt vanished and much of the sub-basaltic material was broken up and redistributed. Later there was moderate regional uplift and entrenchment of the main streams for a few hundred feet, and lastly, in closing Pliocene time, the Kosciusko uplifts initiated the vigorous erosion and rejuvenation that is still proceeding.

The sequence of events is well illustrated within a relatively small area around Tallong where the river turns east and makes for the coast.

South Coast

The outcrops of grey billy described from the neighbourhood of Milton and Moruya (Brown, 1926) are up to 80 feet above sea-level and 15 feet thick, and in a few places are in visible contact with overlying basalt. Both sandy and pebbly types are present and in one deposit common opal was recognized. Joint-blocks of the rock were found to have crumbly white sandstone or loose sand at the core, as if silicification had been incomplete. Some of the basalt is unaccompanied by grey billy and in a few places it rests on white clay.

Farther south both basalt and Tertiary gravels are locally prominent. Some gravels and sands are younger than the basalt, as at Broulee Island north of Moruya, some are not in visible relation to basalt and others are clearly subbasaltic, but only at Brow Lake north of Narooma are they known to be silicified. Leached bedrock near Coila Lake may be related to basalt close by.

Macquarie Basin

The Macquarie River flows north and west from the Main Divide of eastern Australia to join the Darling ; it has two chief headwater components, Campbells River and Fish River. The country drained by these was evidently once covered with Tertiary basalt, which now appears as isolated masses great and small, mostly valley-fillings that very probably belonged to more than one phase of earlier Tertiary volcanicity. Some remnants straddle the Main Divide at more than 4,000 feet and in many places the flows are underlain by sediments. Five miles ENE of Oberon Nunans Hill, rising to an altitude of 3,750 feet ASL, adjacent to a tributary of Fish River, is capped by 125 feet of basalt resting on iron-cemented quartz-gravel, and around Oberon at more than 3,600 feet basalt fills broad, mature valleys overlying river-deposits of quartz-gravel and boulders with a thickness of as much as 40 feet ; locally, these deposits have been silicified and/or iron-cemented. Fifteen miles west of Oberon at 3,250 feet ASL, the road to Rockley crosses the flat-topped ridge forming the watershed between Campbells River and its tributary Sewells Creek. It is capped by 150 feet of basalt in two flows separated and underlain by sediments which are in places silicified. Sewells Creek is nearly 500 and Campbells River 700 feet below the top of the ridge, and it seems that the two streams are descendants of an ancestral river that in pre-basalt time flowed where the watershed is today, a condition that has also been described for other rivers in this State (Browne and Raggatt, 1935). South-west of Rockley pebbly grey billy has been noted at 2,850 feet ASL, some 70 feet above Peppers Creek, and a few miles north of the township, where the road to Bathurst traverses the broad valley of Fostars Creek, grey billy and iron-cemented alluvium crop out where the present valley-floor coincides approximately with the pre-basalt one.

Upstream of Bathurst Campbells River and Fish River unite to form the Macquarie, which traverses a widely expanded undulating lowland cut in granite and forming the Bathurst Plains. Relics of pre-basaltic valleys in the shape of basalt outcrops and altered sediments rise above the general level forming an arc roughly concentric with a wide curve in the present river (Curran, 1891 ; Ross, 1898). Along the road from Rockley the first evidence of former valley-filling basalt is seen on a hill half a mile south of Georges Plains and 8 miles south of Bathurst. This rises to about 2,400 feet ASL and 130 feet above the wide, alluviated and terraced valley of Vale Creek, a tributary of the Macquarie. The hill is crowned with siliceous conglomeratic grey billy in process of disintegration and the fluvial deposit may be 50 feet thick.

The most considerable mass of basalt forms the level-topped capping of Mt. Panorama ridge on the southern outskirts of Bathurst, more than half a mile long and rising to 2,878 feet ASL, or about 750 feet above the river. It is apparently 100 to 150 feet thick and rests upon alluvial deposits that include quartz-gravels, sand and clay and granite rubble. Locally the sands and gravels have been converted into grey billy, some of which, incorporating numerous fragments of white quartz, may easily be mistaken for broken-up vein-quartz. A few feet of white sand and sandy clay were reported from immediately under the basalt on the eastern side of the ridge. The thickness of the deposits where measured is about 20 feet, but may exceed this elsewhere.

Small outliers of basalt appear, mostly to the north-west of the Mt. Panorama mass, the most conspicuous being that at Mt. Pleasant, underlain by 40 feet of uncemented quartz-gravel. The top of the deposits at Georges Plains and Mt. Pleasant is at 2,400 and 2,360 feet respectively, whereas on Mt. Panorama it is at about 2,720 to 2,770 feet ; the difference in altitude may be explained by supposing that the higher beds were laid down in an earlier channel of the ancestral river.

At lower levels in the surrounding country are accumulations of alluvial gravels evidently much younger than those just described and probably, in part at least, of Lower Pliocene age (Curran, 1891).

Downstream from Bathurst the Macquarie valley and that of its tributary Bell River contain remnants of basalt (Harper, 1909 ; Colditz, 1942). Some of the flows rest on alluvial deposits but, so far as I know, no grey billy has been reported. At Dubbo the valley is very wide and alluviated and the country is gently undulating. Tertiary basalt appears on both sides of the river (Curran, 1885), lying directly on Jurassic strata or on Tertiary alluvium. A quarry but little above present river-level revealed a deposit 15 or 20 feet thick of small, white gravel with bands of ferruginous material, whose top surface is locally capped with amygdaloidal basalt. Elsewhere layers of Jurassic sandstone and shale overlain by patches of basalt are iron-impregnated at the surface but bleached white lower down, and Curran recorded basalt lying on a few feet of white clay.

On the Peak Hill road some 2½ miles out of Dubbo is a ridge of iron-impregnated gravels with odd boulders up to 2 feet in diameter ; the age of these deposits is not known, but their alteration is conceivably related to the former presence of Tertiary basalt.

Other Localities in the Central Highlands

Elsewhere in the Central Highlands belt evidences of alteration of alluvial deposits by Tertiary basalt have been noted as, for example, in the Trunkey (Arthur) area some 30 miles SSW of Bathurst, where Raggatt (Browne and Raggatt, 1935) found sub-basaltic " drift " locally converted into siliceous grey billy and forming terrace deposits at 50 feet above present creek-level.

The Tertiary basalts of the Mittagong Range between Mittagong and Robertson are in places underlain by ferruginous gravels (Taylor and Mawson, 1904). An extensive deposit of white clay, fine quartz-gravel, ferruginous gravel and grey billy revealed by a quarry on the Moss Vale-Nowra railway near Burrawang, 8 miles east of Moss Vale, is clearly related to adjacent olivine-basalt, whilst on the Hume Highway 4 miles north of Berrima and 3 miles west of Bowral a fine example of leached Triassic shale in direct contact with Tertiary basalt is seen in a new cutting. The basalt is much deuterized.

In the Orange district at Spring Hill, Millthorpe and elsewhere white clays under basalt have been noted. In the vicinity of the village of Neville, 15 miles south of Blayney, I found grey billy by the roadside, and on the Cudgegong road some 12 miles from Mudgee an accumulation of grey billy boulders up to 18 inches in diameter at 40 or 50 feet above the level of the present Cudgegong River. In each of the last two instances the grey billy has evidently been redistributed by river action, though not borne very far ; its presence suggests the exhumation of an earlier Tertiary valley and a former filling of basalt where now there is none.

Palaeozoic bedrock slates converted into white clay immediately under Tertiary basalt have been observed at Kings Plains, 7 miles east of Blayney, and at a point a few miles west of Taralga near Crookwell, and it seems likely that some of the white kaolinic clays in the Mudgee district and elsewhere (Morrison and Raggatt, 1928, p. 217) are altered sub-basaltic bedrock.

Lower Hunter Valley

Raggatt (1939) examined occurrences of grey billy along the Lower Hunter River and ascribed their formation to the influence of Tertiary basalt now vanished. I have been able to supplement and extend his observations and to show that the deposits are quite widely distributed along the river. A number of them were noted by David (1907) and are marked as High-Level Gravels on the geological map accompanying his Memoir. Actually, as is indeed implicit in Raggatt's description, they belong to two separate epochs of deposition.

In addition to those noted by Raggatt on the Denman-Muswellbrook road and at Jerrys Plains and Abbey Green near Singleton, remnants, some of them considerable, have been examined at 200–250 feet ASL on the left bank of the river between Singleton and Glendon, on the right bank 1½ and 2 miles SSW of Glendon, and at Lower Belford. Farther downstream they have been noted at Dalwood north of the Luskintyre bridge near Lochinvar, and at Gosforth (Browne, 1927). The most easterly occurrence examined is on the right bank 3 miles due north of West Maitland near the site of the former Melville bridge. A detailed search would, doubtless, reveal other occurrences.

The original grey billy is mostly in large blocks 3 feet and more in length, often stoutly tabular with rounded edges; one block at Gosforth measured 6½ feet by 4 feet by 3 feet. This material is obviously *in situ* or virtually so; at Abbey Green it is seen in process of disruption along joint-planes. Some of it is silicified sand, some silicified gravel with well-rounded pebbles up to 2 or 3 inches and small chips of chert. The deposits are usually in the form of low hills or ridges between 100 and 130 feet above the river.

In close association with the grey billy *in situ* there is an abundance of loose, well-rounded material ranging in size from large boulders to fine gravel. In certain places, as at Abbey Green, South Belford and Belford church, this is dominantly of grey billy but it usually includes recognizable Carboniferous lavas—rhyolite and toscanite, some apparently silicified—with silicified wood (Permian ?), black chert and red jasper. At Jerrys Plains there are pebbles of hard, ferruginous shale and sandstone; in the Denman road occurrence well-rounded pebbles of fresh olivine basalt are conspicuous. These accumulations are doubtless in part composed of redistributed pre-basaltic material but in part they are obviously post-basaltic. At Dalwood and near Melville bridge only redistributed grey billy was observed, and the pebbles and cobbles are smaller than those higher upstream.

The deposits have been to some extent used for road-metal, and in consequence small concentrations of rounded grey billy are apt to be found at subnormal or supranormal altitudes on quarry tracks or even on public roads; for instance, several large boulders on the roadside on the Branxton-Stanhope road beyond the Elderslie bridge at 200 feet above the river are apparently discarded road material.

The loose gravels and boulders are at approximately the same level as the grey billy *in situ*, but at Jerrys Plains and elsewhere have accumulated up to at least 15 feet above the latter; farther down the river they seem to extend below them. Thickness of the deposits is hard to determine because of the tendency to soil-creep; that at Gosforth appears to be about 20 feet thick.

The terrace-deposits of grey billy and later gravels are, very roughly, 200 to 300 feet below the general level of the valley-plain in which the Lower Hunter is incised and a little over 100 feet above the present river level. They appear to follow approximately the meanderings of the river, though some of the more tortuous of these, winding as they do over siltic flood-plains, are plainly of more recent origin. It would seem that in earlier Tertiary time the floor of the meandering valley was but little above its present elevation, that its deposits were buried under basalt-flows, and that it rose little if at all during the subsequent Tertiary uplifts.

Basalt crowns the highlands at the source of the Upper Hunter and its tributaries, and the Liverpool Range basalts extend as far south as the latitude of Muswellbrook and to within 4 or 5 miles of the main river; but the undulating country, in which the Lower Hunter is incised, is now, so far as is known, devoid of Tertiary basalt. Its removal during early Pliocene time was probably complete, partly because of the feeble response of the area to the forces of uplift and partly, as pointed out long ago by Taylor (1907*a*), because of the poor erosional resistance of the Permian beds in which the valley is largely excavated. It is pertinent to note that Dulhunty (1938) has mapped considerable remnants of Tertiary basalt in the valley of the Goulburn River, the chief tributary of the Lower Hunter, covering about one-third of its basin, and has reported the presence of grey billy at numerous places between its head and its junction with the Hunter at about 100 feet above the present valley floor.

Sussmilch (1940) rejected Raggatt's explanation of the grey billy as the result of alteration by basalt-flows, and equated it with siliceous duricrust such as appears in the far west of the State. His arguments were forced and unrealistic even in the light of what was known of duricrust at the time, and particularly so in view of the virtual certainty that the Lower Hunter grey billy is the equivalent of the silicified sub-basaltic deposits in the Goulburn River valley.

Northern Highlands (*New England*)

In New England Tertiary basalt covers a very much larger area than in any other division of the State and the sub-basaltic " drifts " have received considerable attention in the past because of their content of economic minerals. The deep leads in the north-west at Emmaville were reported on by David (1884, 1887*a*, 1887*b*), and those in the Inverell area by Carne (1911) and Cotton (1910), all of whom commented on the presence of grey billy as the result of silicification of sub-basaltic alluvium. In some instances an existing creek flows directly above its early Tertiary ancestor which, now hidden beneath basalt, may lie several hundred feet below the present surface; or, again, the " deep lead " capped by basalt may crown the ridge forming the watershed between two parallel creeks. In Emmaville and to the west and north-west of it, where the Vegetable Creek lead and its branches were mined for stream-tin, there are many evidences of their presence in the shape of white clay, grey billy and patches of basalt.

The road from Inverell north to Ashford passes over basalt for much of the way, the " drift " underlying which in some places, as at Bukkulla, 21 miles from Inverell, is of fine iron-impregnated gravel. On the 3-mile descent of 600 feet from the lateritized plateau on the south to the Macintyre River at Inverell one may note a number of grey billy outcrops at different levels resting on granite bedrock and underlying basalt, evidently terrace-deposits.

From Glen Innes south to the vicinity of Armidale the Main Divide is composed mostly of Tertiary basalt, in places resting on alluvium. Some present-day valleys, like that of Beardy River, are clearly older than the basalt, which may form a considerable filling with an upper surface lower than the old granitic valley-walls. Other old rivers have been laterally displaced by basalt, and some of the basalt-capped spurs branching from the Main Divide have sub-basaltic deposits exposed on their flanks as, for example, some 5 miles along the road from Ben Lomond to Wandsworth, where grey billy underlies basalt at an altitude of about 4,075 feet ASL. Voisey (1942*b*) has mapped this and other occurrences of sub-basaltic deposits in southern New England and noted the frequency of grey billy among them; and (1942*a*) has used grey billy as an aid in determining approximately the pre-basalt topography in the neighbourhood of the Main Divide between Glen Innes and Walcha.

David (1887*a*) reported on the country forming the Rocky River and Uralla goldfield. It seems that the earlier Tertiary basalt that covered the old valley deposits was reduced to scattered flat-topped remnants at between 3,500 and 3,600 feet by the early Pliocene ancestor of Rocky River; this formed a wide valley-plain at about 200 feet lower, laying bare the pre-basalt auriferous deep-leads and revealing grey billy in several places. David found that the local miners used the term " white billy " to describe a very hard, dense rock cropping out around the margins of basalt sheets or laid bare by erosion, in places acting as a resistant covering to auriferous sands, and elsewhere forming a breccia. It contains some kaolin and is perhaps a silicified clay.

Many years ago on a rapid motor-trip from Walcha, along the Oxley Highway to Tia and thence to Nowendoc across a west-east spur of the Main Divide at 4,300 feet, much Tertiary basalt was encountered particularly at the higher levels, where it was at least 300 feet thick. The pre-basalt surface must have been of considerable relief, bedrock of phyllite and schist invaded by gneissic granite being in places at altitudes of nearly 4,100 feet ASL, and locally overtopping the basalt nearby. The basalt seemed to rest mostly on bedrock but occasionally on alluvial deposits 30 or 40 feet thick. Grey billy was noted on the Oxley Highway six miles east of Walcha at 3,300 feet and at a point 21 miles north of Nowendoc at about 3,900 feet ASL, associated with basalt and resting on schists. Some of the metamorphic bedrock was locally silicified, the alteration being possibly related to the basalt eruptions.

On the western slopes of the New England plateau a few miles north of Barraba the east-west Nandewar Range is formed of Tertiary basalt-flows overlying a deposit of diatomaceous earth and with interflow beds of leached sand and clay.

In various parts of New England there are accumulations of uncemented gravels in upland valleys as, for example, a few miles east of Armidale on the road to Hillgrove and near the Oxley Highway some 13 miles from Walcha along the Apsley River just above the Apsley Falls. These deposits are probably post-basalt and are above the limits of rejuvenation caused by the Kosciusko uplift ; they are provisionally regarded as earlier-Pliocene.

On the west, some 15 miles north of Narrabri on the way to Killarney Gap in the Nandewar Mts., the road traverses a wide boulder-fan of which redistributed grey billy is a prominent constituent ; with it are boulders, increasing in size towards their source, of teschenite, basalt and trachyte brought down by creeks from the heights of the volcanic Nandewar Mts., and probably still accumulating.

Grey Billy in Other States

So far as I know, the grey billy association is found only in the four eastern States.

According to Murray (1887) Tertiary sands and gravels, in many instances silicified, are commonly associated with the Older basalts of Victoria, particularly in the east ; some of these form the summits of plateaux and plateau-remnants rising to 5,000 feet ASL, e.g. the Dargo and Bogong High Plains, Mt. Useful, etc., while others are at medium elevations around the flanks of the main highlands at Glen Maggie, Tanjil, Russell Creek and elsewhere in Gippsland. More recently Gill (1942) has described from the Lilydale district silicified sands and gravels, whitish clays and lignites underlying the Older basalts.

From south-eastern Queensland in the mature Brisbane River valley between Brisbane and Ipswich Jones (1926) has described and illustrated blocks of quartzite up to 15 feet long enclosing many angular fragments of siliceous rock. The blocks are embedded and partially buried in uncemented heteropsephitic gravels and boulder-beds which Jones included in his Redbank Series, though Whitehouse later (1940) queried the placement.

Under the guidance of the late Professor W. H. Bryan, I had an opportunity of examining the principal occurrence at Sherwood close to the meandering Oxley Creek, a tributary of the Brisbane River. A remnant of the basalt contemporaneous in the Redbank Series crops out a mile away, and field examination leads one to conclude with some confidence that the quartzite blocks are relics of a sheet of grey billy related to basalt, which has been locally eroded away. Exposure of the sheet and its disruption and redistribution by river action, probably in early Pliocene time, were followed by partial burial in river detritus.

Jones also records limestones of the Redbank Series in Queen's Park, Ipswich, which are believed to have been partially silicified by overlying basalt ; Tertiary limestone some 16 miles south of Ipswich has been similarly altered.

Richards (1916, p. 115) found deposits of diatomaceous earth interbedded among the Tertiary basalt flows of south-eastern Queensland, and I have had the opportunity of seeing one of these beds, between Canungra and Beechmont, now partially converted into common opal, apparently under the influence of the overlying basalt flow. Skeats (1914) described common opal from beds associated with Tertiary basalt at Tweed Heads on the New South Wales border.

In the valley of the Logan River east of Beaudesert the late Mr. L. C. Ball, then Chief Government Geologist of Queensland, showed me blocks, up to 2 feet thick and 6 feet in diameter, of grey billy virtually *in situ* some 20 feet above the present river, apparently related to a former valley-filling basalt of which remnants are visible on the adjacent plateau. This basalt is probably Lower Miocene, like that of Beechmont and Toowoomba (Webb *et al.*, 1967).

The grey billy in the Clermont-Anakie area described by Dunstan and mentioned above, is related to basalt whose geological age is uncertain, but whose mode of occurrence and relation to the topography suggest an earlier-Tertiary rather than a Pliocene age.

Morgan (1968) has reported flows of basalt from the Cooktown area and listed " billy " among the Kainozoic deposits, but gives no indication of its relation to the basalts.

From the West Coast of Tasmania 5 miles east of Granville Harbour, Waterhouse (1914) described a succession of horizontally-bedded fluviatile quartz-conglomerates, grits and sandstones, at least 100 feet thick, containing detrital tourmaline and topaz and chips of silicified wood, and partially overlain by Tertiary basalt. Locally unconsolidated, they have been in places cemented by silica (quartz and chalcedony), thought to have resulted from decomposition of the basalt. Waterhouse's careful description leaves no doubt that the silicified rock is grey billy. No precise dating of the basalt has been made, but from physiographic considerations it may be older Tertiary.

References

Adamson, C. L., 1955.—Geology of Snowy Mountains. Prog. Rept. 4, Adaminaby. *A. Rept. Dept. Mines, N.S.W.*, (1951): 78–84.

Andrews, E. C., 1901.—Kiandra Lead. *Geol. Surv. N.S.W., Min. Res.*, 10.

————, 1904.—New England plateau—Physiography. *Rec. Geol. Surv. N.S.W.*, 7 (4): 281–300.

————, 1914.—Tertiary and post-Tertiary history of N.S.W. *Brit. Assn. Adv. Sci. Handbook, N.S.W.*, 518–526.

Branagan, D. F., 1969.—Cainozoic rocks outside the Murray Basin. *J. Geol. Soc. Aust.*, 16 (1): 544.

Brown, Ida A., 1926.—Tertiary formations on the South Coast of N.S.W. *J. Proc. Roy. Soc. N.S.W.*, 59: 387–399.

Browne, W. R., 1914.—Geology of the Cooma District, Part 1. *J. Proc. Roy. Soc. N.S.W.*, 47: 172–222.

————, 1927.—Geology of the Gosforth District, Pt. 1. *J. Proc. Roy. Soc. N.S.W.*, 60: 213–277.

————, 1944.—Geology of the Cooma District, Part 2. *J. Proc. Roy. Soc. N.S.W.*, 77: 156–172.

————, 1964.—Grey Billy and Tor topography in Monaro. Proc. Linn. Soc. N.S.W., 89: 322–325.

————, 1967.—Geomorphology of the Kosciusko Block. Proc. Linn. Soc. N.S.W., 92: 117–144.

————, and Raggatt, H. G., 1935.—Buried rivers in Eastern Australia. *Austr. Geographer*, 2: 24–30.

Carne, J. E., 1911.—The tin-mining industry in N.S.W. *Geol. Surv. N.S.W., Min. Res.*, 14.

Chalmers, R. O., 1967.—*Australian Rocks, Minerals and Gemstones.* Sydney, Angus and Robertson.

Colditz, M. Joyce, 1942.—Physiography of the Wellington District. *J. Proc. Roy. Soc. N.S.W.*, 76: 235.

Cotton, L. A., 1910.—The tin deposits of New England, Pt. 1. Proc. Linn. Soc. N.S.W., 34: 733–781.

Craft, F. A., 1931.—Physiography of the Shoalhaven Valley. Proc. Linn. Soc. N.S.W., 56: (*a*) 99–132; (*b*) 243–260; (*c*) 412–430.

————, 1932.—Physiography of the Shoalhaven Valley. Proc. Linn. Soc. N.S.W., 57: (*a*) 197–212; (*b*) 245–260.

Curran, J. M., 1891.—Geology and petrography of Bathurst. Proc. Linn. Soc. N.S.W., 6 (Second Series): 173–234.

————, 1885.—The geology of Dubbo. Proc. Linn. Soc. N.S.W., 10 (First Series): 170–185.

David, T. W. E., 1884.—Prog. Report on Vegetable Creek leads (with map). *A. Rept. Dept. Mines N.S.W.* (1883): 153–158.

————, 1887*a*.—Reports on Vegetable Creek, Uralla and Rocky River goldfields. *A. Rept. Dept. Mines N.S.W.*, (1886).

————, 1887*b*.—The Vegetable Creek tin-mining field. *Mem. Geol. Surv. N.S.W.*, (*Geol.*), I.

————, 1889.—Origin of laterite in New England. *Aust. Assoc. Adv. Sci.*, I (1888): 233–241.

————, 1907.—Geology of the Hunter River coal-measures (with maps and sections). *Mem. Geol. Surv. N.S.W.*, *Geology*, 4.

Dulhunty, J. A., 1938.—Stratigraphy and physiography of the Goulburn River District. *J. Proc. Roy. Soc. N.S.W.*, 71: 297–317.

————, 1946.—Physical changes accompanying the drying of some Australian lignites. *J. Proc. Roy. Soc. N.S.W.*, 80: 22–27.

————, and McDougall, I., 1966.—K/Ar dating of basalts in the Coonabarabran-Gunnedah District. *Aust. J. Sci.*, 38: 393–394.

Dunstan, B., 1900.—The Permo-Carboniferous coal-measures of Clermont. *Geol. Surv. Qld. Pub.* 148.

————, 1902*a*.—The Clermont goldfield. *Geol. Surv. Qld. Pub.* 176.

————, 1902*b*.—The sapphire fields of Anakie. *Geol. Surv. Qld. Pub.* 172.

Garretty, M. D., 1936.—Introductory account of the geology and petrology of the Lake George District. Proc. Linn. Soc. N.S.W., 61: 186–207.

————, 1937.—Notes on the physiography of the Lake George region. *J. Proc. Roy. Soc. N.S.W.*, 70: 285–293.

Gill, E. D., 1942.—Tertiary sub-basaltic deposits of the Lilydale District, Victoria. *Proc. Roy. Soc. Vict.*, 54: 245–255.

————, 1964.—Rocks contiguous with the basaltic cuirass of western Victoria. *Proc. Roy. Soc. Vict.*, 77: 332–355.

————, and Sharp, K. R., 1957.—The Tertiary rocks of the Snowy Mts. *J. Geol. Soc. Austr.*, 4: 21–40.

Hall, L. R., 1956.—Geology of Snowy Mountains, Progress Rept. 5, Berridale. *A. Rept. Dept. Mines, N.S.W.*, (1952): 132–134.

————, and Lloyd, J. C., 1954.—Geology of the Snowy Mts., Progress Rept. 1, Toolong. *A. Rept. Dept. Mines N.S.W.*, (1950): 96–104.

Harper, L. F., 1909.—Physiography of the N.E. watershed of the Macquarie River. *Rec. Geol. Surv. N.S.W.*, 8: 321.

Hills, E. S., 1934.—Tertiary fresh-water fishes from southern Queensland. *Mem. Qld. Mus.*, 10 (4): 157–174.

————, 1946.—Fossil Murray cod from diatomaceous earths in N.S.W. *Rec. Aust. Mus.*, 21: 380–382.

Joklik, G. F., 1950.—Dalton-Gunning area. *J. Proc. Roy. Soc. N.S.W.*, 84: 17–27.

Jones, L. J., 1940.—Gulgong goldfield. *Geol. Surv. N.S.W.*, *Miner. Res.*, 38.

Jones, O. A., 1926.—Tertiary deposits of the Moreton District, S.E. Queensland. *Proc. Roy. Soc. Qld.*, 38: 23–46.

Kenny, E. J., 1934.—West Darling District. *Geol. Surv. N.S.W.*, *Miner. Res.*, 36.

Lafeber, D., 1956.—Columnar jointing and intracolumnar differentiation in basaltic rocks. *Verh. K. ned. geol. mijnb. Genoot.*, 16: 241–251.

Lamplugh, G. W., 1907.—Geology of the Zambesi Basin. *Quart. J. Geol. Soc., Lond.*, 63: 162–216.

Leechman, G. F., 1961.—*The Opal Book*. Sydney: Ure Smith.

Legge, J. G., 1937.—Physiography and geology of the F.C.T. *Rept. Aust. Assn. Adv. Sci.*, 23: 84–88.

McDougall, I., and Wilkinson, J. F. G., 1967.—K/Ar dates on some Cainozoic volcanic rocks from north-eastern N.S.W. *J. Geol. Soc. Aust.*, 14: 225–233.

McRoberts, Helen M., 1948.—General geology of the Bombala District, N.S.W. *J. Proc. Roy. Soc. N.S.W.*, 81: 248–266.

Maitland, A. G., 1898.—Delimitation of the artesian water area north of Hughenden, Qld. *Qld. Geol. Surv. Pub.* 121.

Morgan, W. R., 1968.—The geology and petrology of Cainozoic basaltic rocks in the Cooktown area. *J. Geol. Soc. Aust.*, 15: 65–78.

Morrison, M., 1920.—Tintenbar opal field, N.S.W. *A. Rept. Dept. Mines, N.S.W.*, (1919): 173.

————, and Raggatt, H. G., 1928.—In *The Mineral Industry of N.S.W.* N.S.W. Mines Dept.

Murray, R. F., 1887.—*Geology and Physical Geography of Victoria.* Melbourne: Govt. Printer.

Öpik, A. A., 1953.—Geology of Canberra City District. *Bull. Bur. Miner. Res. Aust.*, 32.

————, and Noakes, L. C., 1954.—In White, H. L. (Ed.). Canberra: A Nation's Capital. *A.N.Z.A.A.S. Handbook*, 115–152.

Pittman, E. F., 1901.—*Mineral Resources of N.S.W.* Sydney: Govt. Printer.

Raggatt, H. G., 1939.—Silicified terrace sands (Grey Billy) in the Hunter Valley. *J. Proc. Roy. Soc. N.S.W.*, 72: 318–324.

Relph, R. E., 1969.—Cainozoic rocks of N.S.W. *J. Geol. Soc. Aust.*, 16 (1): 551.

————, and Wynn, D. W., 1960.—Geology of the Snowy Mts. *Prog. Rept.* 14, Jillamatong. *N.S.W. Mines Dept. Tech. Rept.* 5, (1957): 126–129.

Richards, H. C., 1916.—The volcanic rocks of S.E. Queensland. *Proc. Roy. Soc. Qld.*, 27: 105–204.

Ross, W. J. Clunies, 1898.—The basalts of Bathurst. *J. Proc. Roy. Soc. N.S.W.*, 31: 296–313.

Skeats, E. W., 1914.—Plant-bearing common black opal from Tweed Heads. *Proc. Roy. Soc. Qld.*, 26: 18–22.

————, and Summers, H. S., 1912.—The geology and petrology of Mt. Macedon. *Bull. Geol. Surv. Vict.*, 24.

Sussmilch, C. A., 1937.—Geological history of the Cainozoic in N.S.W. Proc. Linn. Soc. N.S.W., 62: viii-xxxiii.

————, 1940.—Geomorphology of the Hunter River District. Proc. Linn. Soc. N.S.W., 65: 301–322.

Taylor, T. G., 1907*a*.—Correlation of contour, climate and coal. Proc. Linn. Soc. N.S.W., 31: 517–529.

————, 1907*b*.—The Lake George Senkungsfeld. Proc. Linn. Soc. N.S.W., 32: 325–345.

————, and Mawson, D., 1903.—The geology of Mittagong. *J. Proc. Roy. Soc. N.S.W.*, 37: 306–350.

Vallance, T. G., 1969.—Mesozoic and Cainozoic igneous rocks of N.S.W. *J. Geol. Soc. Aust.*, 16 (1): 525.

Voisey, A. H., 1942*a*.—The Tertiary land surface of southern New England. *J. Proc. Roy. Soc. N.S.W.*, 76: 82–85.

————, 1942*b*.—The geology of the County of Sandon, N.S.W. Proc. Linn. Soc. N.S.W., 67: 288–293.

————, 1957.—Erosion surfaces around Armidale. *J. Proc. Roy. Soc. N.S.W.*, 90: 128–133.

Waterhouse, L. L., 1914.—Reconnaissance of the North Heemskirk tinfield. *Tasm. Dept. of Mines Geol. Surv. Rept.* No. 6, 13–16.

————, and Browne, W. R., 1930.—Quartzite (Grey Billy) with opal and chalcedony at Tallong. *J. Proc. Roy. Soc. N.S.W.*, 63: 140–154.

Webb, A. W., Stevens, N. C., and McDougall, I., 1967.—Isotopic age-determinations of Tertiary volcanic rocks of south-eastern Queensland. *Proc. Roy. Soc. Qld.*, 79: 79–92.

Wellman, P., McElhinny, M. W., and McDougall, I., 1969.—On the Polar-wandering path for Australia during the Cainozoic. *Geophys. J. Roy. Astron. Soc.*, 18: 371–395.

Whitehouse, F. W., 1940.—Studies in the late geological history of Queensland: (1) The laterite soils of western Queensland. *Univ. of Qld. Papers, Geol. Dept.*, n.s. 2: 2–22.

Whiting, J. W., and Relph, R. E., 1961.—Occurrence of opal at Lightning Ridge and Grawin. *Tech. Rept. Dept. Mines, N.S.W.*, 6: 7–21.

Williamson, W. O., 1957.—Silicified sedimentary rocks in Australia. *Amer. J. Sci.*, 255: 23–39.

Woolnough, W. G., 1927.—Chemical criteria of peneplanation. *J. Proc. Roy. Soc. N.S.W.*, 61: 17–53.

Wöpfner, H., 1960.—Some structural developments in the Great Artesian Basin. *Trans. Roy. Soc. S. Aust.*, 83: 179–194.

————, 1961.—Occurrence of a shallow ground-water horizon in N.E. South Australia. *Trans. Roy. Soc. S. Aust.*, 85: 13–19.

A NEW GENUS BASED ON THE SEVEN–BANDED *RICHARDSONIANUS DAWBINI* RICHARDSON 1969 (HIRUDINOIDEA: RICHARDSONIANIDAE)[1]

LAURENCE R. RICHARDSON[2]

[Accepted for publication 15th December 1971]

Synopsis

The new genus has the vaginal duct proportionally longer than in the g. *Bassianobdella*. Hibernation is recorded, as also predation on *Goddardobdella elegans* with evidence for predation on other invertebrates. Mass aggregation of *G. elegans* is described.

The type species for the new genus is an aquatic jawed sanguivore, the median regions of the reproductive systems formed each on a posteriorly directed primary loop, bimyomeric and mesomorphic; the vagina with a relatively long vaginal duct; etc.; the general morphology of the median regions resembling those in *Richardsonianus australis*. Essentially on this basis, *dawbini* was assigned to the g. *Richardsonianus* and recognized from the pattern as a new species (Richardson, 1969*a*). The vagina in *dawbini* is U-shaped with subequal limbs, and this was interpreted at that time as an immature form similar to the folded immature vagina known to me in *Hirudo medicinalis* and *Goddardobdella elegans*, both of which lack a vaginal duct.

Subsequently (Richardson, 1970), a U-shaped vagina was found in a 7-banded leech from Victoria. This species has a very short, atypical vaginal duct, leading me to recognize the U-shaped vagina as developed on the posterior portions and around the elbow of the primary loop, and as such, a distinctive morphological form which is associated in 7-banded leeches with elongate cylindrical ejaculatory bulbs, a combination not seen in other leeches. The g. *Bassianobdella* was provided for 7-banded leeches with the short atypical vaginal duct, and individual species have now been described from Victoria (Richardson, 1970), Tasmania (1971), New South Wales (1972*a*), and a possible fourth, undescribed, species for Kangaroo Island, South Australia. It was indicated (1970) that a separate and new genus was required for 7-banded leeches of the Torresian.

It seemed possible (1970) that the combination of elongate cylindrical ejaculatory bulbs and a U-shaped vagina might lead to a division of the Richardsonianidae into subfamilies. This has become doubtful. Elongate cylindrical ejaculatory bulbs are now known in *Quantenobdella howensis* of Lord Howe Island (Richardson, 1972*b*) and *Habeobdella stagni* of south-western Western Australia (1972*c*), both of these having a typical long vaginal duct, the vagina restricted to the posterior portion of the recurrent limb of the primary loop, and a 5-banded pattern.

Hirudo novemstriata Grube 1867 is based on specimens from Rockhampton, Queensland, and known only in Grube's accounts. It is described as having nine longitudinal dorsal dark bands, the median wider than the paired bands which are narrow and of equal width; the bands separated by eight narrow light stripes; the stripes commencing at the 10th annulus, etc. (Richardson, 1969*b*). In preserved specimens of *dawbini*, the marginal light stripes show in dorsal view, these with the three pairs of narrow stripes give a total of eight stripes; the wide band of the paramedian fields, diminish so that the medial half is paler than

---

[1] A study assisted by a grant from the Nuffield Foundation.

[2] 4 Bacon St., Grafton, N.S.W.

the lateral half, and the two appear each as a dark band, narrow, and of the width of the other paired bands, giving eight narrow bands and a wider median band, a total of nine. Grube describes the margins as continuous with the venter, the paired stripes commencing in somite viii. On these two points, *novemstriata* differs from *dawbini*, otherwise it seems most probable that *novemstriata* is a 7-banded leech.

Dr. A. Soos, the Hungarian Museum of Natural History, has examined the Grube collection, now housed in the Zoologische Museum, Humboldt-Universitat zu Berlin. He informs me there are no specimens in the collection labelled as *Hirudo novemstriata.*

Kaiyabdella gen. nov.

Derivation: Kaiya (Aborigine), to bite; bdella, a leech. f.

Richardsonianidae; ix to xxiv complete 5-annulate (total 16); xxv, 4-annulate; somital sense organs, small; jaws, small, located in open recesses; teeth, about 50, small, narrowly spaced; no salivary gland papillae; dorsal salivary glands, sparse, with poorly formed right and left columns of aggregated ducts; radial muscles, an obvious system; mouth and lumen of pharynx, narrow, the lumen tapering; pharynx with six internal muscular ridges as a dorsolateral and ventrolateral pairs, each pair joining to enter a jaw, none ending independently on the margin of the entrance to the pharynx; pharynx terminating anteriorly in ix, with the compartments in xi to xviii each with a pair of small lobed secondary anterior caeca and a larger pair of simple primary caeca at the median level, the latter increasing in size posteriorly and from xv extending into the following somite; xix, postcaeca originate from the anterior level in the somite and extend to xxv/xxvi; the compartment in xix reduced in diameter behind the postcaeca, narrowly tubular to xix/xx and joining terminally to the intestine; intestine, tubular, tapering posteriorly to join terminally to the rectum; genital pores, xi b_5/b_6 and xii b_5/b_6; 10 pairs of simple saccular testes; anterior regions of paired male ducts with the epididymis in the adjacent halves of xii and xiii, posterior to the elongate cylindrical ejaculatory bulbs in the adjacent halves of xi and xii; median regions, bimyomeric, mesomorphic; penis sheath, reflecting in xii b_2; oviducts, very short; common oviduct, long; vagina caecate, cylindrical, folded on itself at xiii/xiv or in xiv as subequal recurrent and procurrent limbs; vaginal duct longer than the procurrent limb of the vagina; vagina and duct, ventral to the crop. Pattern, striped. Aquatic. Sanguivorous. Australian region.

Type species: Richardsonianus dawbini Richardson 1969 (Richardson, 1969*a*, p. 128).

The following description is based on specimens from Alumy Creek, Grafton, N.S.W., the type locality, and others from waters on the Clarence River flood plain.

General Form

In life, a strongly muscular leech of moderate size, capable of moderate extension. At rest, elongate, tapering subcylindrical anteriorly, somewhat depressed posteriorly with obtusely rounded margins; the posterior sucker, large, and only slightly less than the maximum width of the body. Extended, subcylindrical. An elegant capable swimmer, the posterior two-thirds of the body flattened, the margins not sharply keeled posteriorly.

Preserved, extended, anteriorly subcylindrical, gradually widening from the small anterior sucker to be slightly depressed along the nephric region, narrowing obtusely in the postnephric region to form a wide base for the posterior sucker.

In life, a specimen 35·0 mm. long at rest, was 12·0 mm. long in maximum contraction; 45·0 mm. in full extension.

Preserved, extended specimens taken in December, range in length from 45·0 mm. to 82·0 mm. In a specimen 50·0 mm. long, the anterior sucker is 2·0 mm. wide ; the width at v/vi, 2·5 mm., increasing behind this to 3·75 mm. at 10·0 mm. from the anterior end, with a depth of 1·75 mm. ; the width increasing gradually posteriorly to a maximum of 4·0 mm. at xxii (50·0mm.from the anterior end) and the depth, 2·0 mm. along this region ; narrowing behind xxv to the basis (2·0 mm. wide) of the posterior sucker which is a little wider (3·75 mm.) than long, and has about 32 muscular rays on the ventral surface.

Colour

In life, generally brownish, dark brown to greyish brown, with a black median band, and three pairs of dark brown bands ; the bands separated by narrow golden to golden yellow contrast stripes ; a dusky yellow marginal stripe separates the dorsum from the dusky greenish yellow to ashen grey venter which is irregularly maculate with dark black to greyish black patches. The dorsum of the posterior sucker, uniformly dark brown excepting the pale margin.

Preserved, the general colour diminishes to a pale greyish brown ; the median band, to dark greyish black ; the paired bands, to be greyish, excepting the lateral half of the inner paired bands is distinctly darker than the medial half ; the stripes, to pale cream or dusky white ; the venter, dark grey.

Pattern. Fig. 1, A, B, F

The median band is continuous, excepting in an occasional specimen in which it may be interrupted at intervals for a length of about an annulus. The median band varies slightly in width. In the majority, it fills the median field and extends to include the line of paramedian somital sense organs which may be within the band, in contact with the margin of the band, or immediately lateral to the margin of the band and in the inner paired stripe, recognizably closer to the medial edge of the stripe.

The narrow inner and middle paired stripes occupy the medial and lateral portions of the paramedian fields which are completed by the wide inner paired bands.

The narrow middle and outer paired bands extend along the lines of the intermediate and supramarginal sense organs, very briefly into the adjacent fields, and are separated by the narrow outer paired stripe of the intermediate fields.

The marginal stripes include the marginal sense organs, occupy the marginal field (supramarginal+submarginal), extend from xxvi a_1a_2/a_3 anteriorly to form a narrow contrast edge on the velum and this includes the preocular paramedians of somite i.

The ocular arch is entirely within the background colour which is complete between the margins across ii and iii, and complete across xxvii.

The narrow inner paired stripes of the paramedian fields extend from iii/iv to xxvi/xxvii and are continuous ; the narrow middle paired stripes, lateral in the paramedian field, extends from just in v or v/vi to xxv/xxvi, and may be either continuous or broken briefly anteriorly for about the length of an annulus ; the two stripes totalling less than half of the width of the field which is completed by the wide inner paired band defined between them, the width of this band increasing as the body widens so that it occupies always the greater part of the field, and is the widest band.

The outer paired stripes occupy the greater part of the intermediate fields, are continuous from vi a_2/a_3 to xxv/xxvi, or just into xxvi, and divide the middle and outer paired bands between these limits.

The venter is dark, paler than the dorsum, sharply separated from the marginal stripes ; maculate, the maculae of the length of an annulus or shorter,

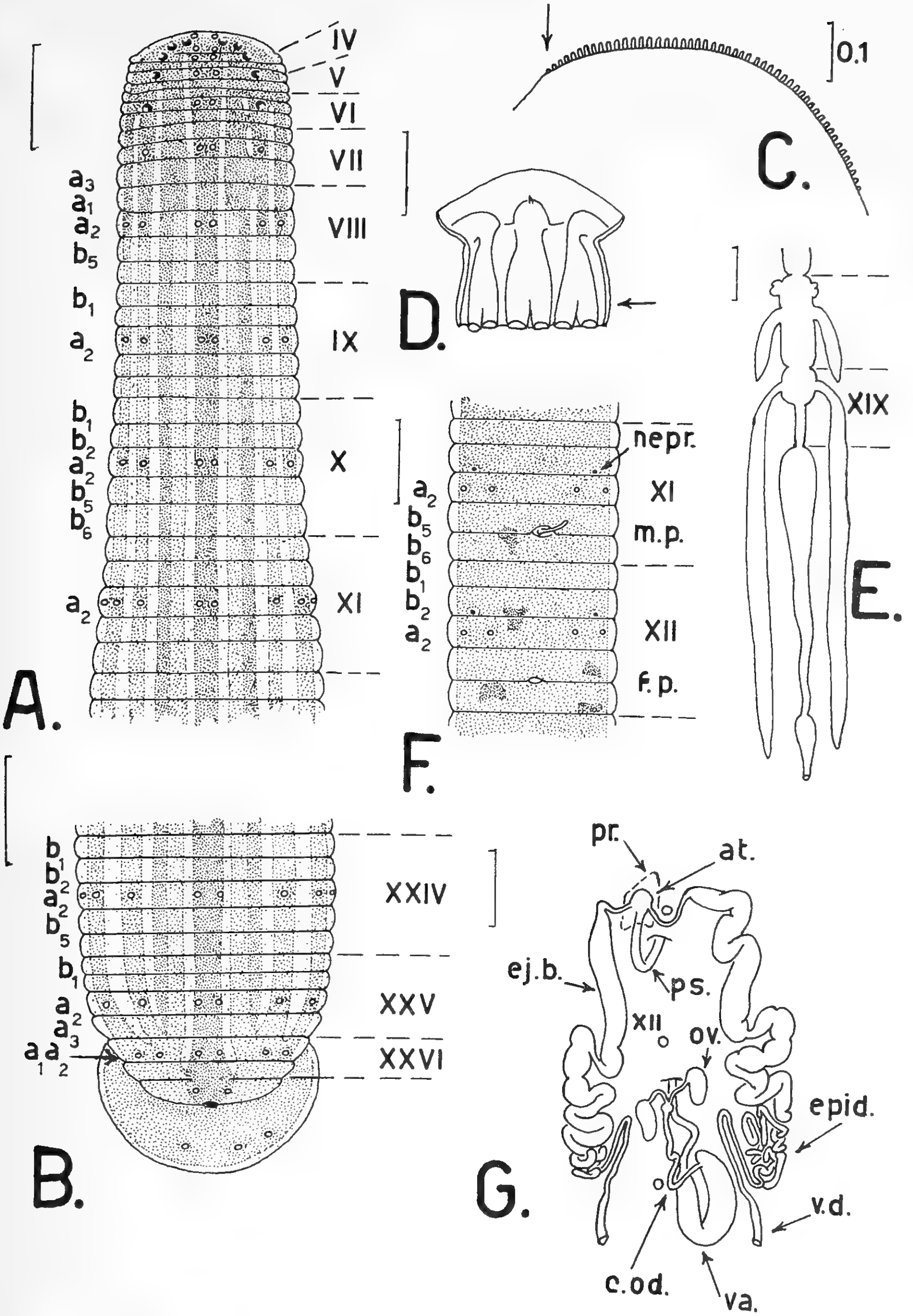


Fig. 1. *Kaiyabdella dawbini* (Richardson 1969). A. Dorsal aspect, somites i to xi, and B. xxiv to xxvii, showing annulation and pattern. C. Right ventrolateral jaw and dentition, arrow indicates medial end. D. Pharynx opened along mid-ventral line to show internal muscular ridges; jaws; arrow indicates mid-point in the length of the pharynx. E. Compartments and caecation of crop in xviii and xix, postcaeca; intestine. F. Ventral aspect, somites xi and xii; pattern; genital pores, etc. G. Anterior region of male paired ducts; male median region; and female reproductive system, the female median region displaced so that the dorsal aspect of the vagina is at the right.

Somites and somital ganglia indicated by Roman figures; intersomital levels, by broken lines; annuli, "a_2", etc.; somital ganglia shown at relative size.

at., atrium; c.od., common oviduct; ej.b., ejaculatory bulb; epid., epididymis; f.p., female pore; m.p., male pore; nepr., nephropore; ov., ovary; pr., prostate; ps., penis sheath; va., vagina; v.d., vas deferens.

Scales, 2·0 mm, excepting C., 0·1 mm.

irregular in form, often squarish to rectangular, varying from one to three to five in a somite, few in the pregenital region, increasingly more numerous posteriorly, with the venter closely maculated from xx to xxv.

Annulation. Fig. 1, A, B, F

Somital sense organs obvious in small round white patches on the dorsum and venter as transverse and longitudinal series, only marginals detectable with difficulty. Secondary sensillae obvious as white points, one or two in the median field, four or five in each paramedian field, one or two in each intermediate field, back to vii/viii, and behind this many annuli carry a very fine transverse white line in place of individual spaced sensillae. Nephropores, obvious, each in a small white patch, elevated on low papillae in some specimens, and situated just medial to the line of the ventral intermediate sense organs. Intersomital and interannular furrows, equivalent, no general indication of couplets or triplets of annuli, nor of somital limits as such. Annuli in moderately extended specimens often divided into narrow longitudinal rectangles by fine lines, but nowhere morphologically areolate.

Somite i is indicated by a pair of distinct well-formed paramedian sense organs immediately anterior to the first pair of eyes in the paramedian line in ii ; somite iii carries the second pair of eyes and a distinct pair of paramedian sense organs ; iii/iv, extending across the median and paramedian fields, incompletely separates iii from iv, but is indicated by a short length on the margin which defines the anterior edge of the dorsolateral lobe of the sucker ; somite iv, incomplete 2-annulate, a_1a_2 with the third pair of eyes and obvious paramedians $>a_3$, a_1a_2/a_3 sometimes weak in the intermediate field, incises the dorsolateral lobe of the margin of the sucker, and this lobe strongly defined posteriorly by iv/v ; v, 2-annulate above, a_1a_2 with the fourth eyes $=a_3$, a_1a_2/a_3 reaches to the marginal sense organs so that a_1a_2 forms the upper portion of the lateral margin of the sucker and uniannulate v completes this and the ventral margin ; vi, 3-annulate above, $a_1<a_2<a_3$, the fifth pair of eyes small and often obscure in a_2, the furrow a_1/a_2 reaching to the submarginals and vi 2-annulate below this with $a_1a_2>a_3$; vii, 3-annulate above and below, $a_1<a_2<a_3$; vii $a_3=$viii a_1 ; viii, 4-annulate, $a_1>a_2=b_5>b_6$, the first pair of nephropores on a_1 ; ix to xxiv, 5-annulate (total 16) ; ix, $b_1<b_2<a_2>b_5<b_6$; x, $b_1<b_2=a_2=b_5>b_6$; xi, $b_1<b_2=a_2<b_5>b_6$; xii, $b_1=b_2<a_2=b_5=b_6$; xiii to xxii, with the annuli closely equal, $b_1=b_2=a_2=b_5=b_6$; xxiii, $b_1=b_2<a_2>b_5=b_6$, as also xxiv but with $b_5>b_6$, the last nephropores on xxiv b_2 ; xxv, 4-annulate $b_1=b_2<a_2<a_3$, and xxv a_3 the last annulus complete across the venter ; xxvi, 2-annulate, $a_1a_2>a_3$, the somital sense organs posterior in a_1a_2 ; the furrow xxvi/xxvii, incomplete in the median field ; xxvii, uniannulate, with the anus at the posterior margin.

Some paramedians and intermediates show on the dorsum of the posterior sucker.

Alimentary Tract. Fig. 1, C, D, E

The jaws are housed in open recesses ; small, low convex in profile and about 0·5 mm. high at the median end ; the dental margin, low convex, about 0·6 mm. long ; teeth, about 50, narrowly conical, tapering to a point, narrowly spaced, minute, the tallest near the medial end, about 0·02 mm. high, and the height diminishing very gradually along the row.

There are no salivary gland papillae.

The entrance to the pharynx is small, no wider than the base of the dorsomedian jaw ; pharynx, suspended by an obvious system of extrinsic radial muscles extending back into x ; pharynx, rather thin-walled, the lumen restricted, tapering ; three pairs of internal muscular ridges, dorsomedian and ventrolaterals, each pair fusing at about the middle of the length of the pharynx into a single ridge which enters the appropriate jaw ; no ridges ending independently on the margin of the entrance to the pharynx.

Salivary glands, relatively sparse ; the dorsal glands not divided obviously into compact masses, the ducts partially aggregated but not forming strongly developed columns.

The pharynx terminates in the middle of ix, followed by a short simple compartment ; in x, a full compartment of the crop with a pair of small, simple caeca in the anterior position ; in xi, and posteriorly, secondary small simple anterior caeca (lacking in some specimens) and simple longer primary caeca in the median position which are increasingly longer from xiii extending posteriorly in the paramedian chamber into the anterior portion of the following somite ; nowhere an indication of secondary posterior caeca. In xix, the postcaeca emerge from the lateral aspects of the anterior portion of the compartment and extend into xxv ; the posterior portion of the compartment in xix reduced abruptly behind the postcaeca to be narrowly tubular, thin-walled, and connects terminally to the intestine at xix/xx, opening through a small internal papilla which includes a sphincter.

The intestine, broadly tubular initially, lacking compartmentation, tapers progressively to join terminally to the rectum at xxiii/xxiv ; rectum, wider than the terminal portion of the intestine, tapers to end at the anus.

Reproductive System. Fig. 1, F, G

Epididymis posterior to the ejaculatory bulb, the relationship, linear ; ejaculatory bulbs, elongate, cylindrical ; median regions, bimyomeric, mesomorphic, formed on posteriorly directed primary loops ; vagina, caecate, U-shape with subequal limbs, and a long vaginal duct.

Genital pores, xi b_5/b_6 and xii b_5/b_6.

Testes, 10 pairs in the median longitudinal chamber, the first at xiii/xiv, the last at xxii/xxiii, saccular, each connecting by a short vas efferens to the vasa deferentia in the paramedian chambers ; growth of the epididymis posteriorly in the anterior half of xiii results in a reflection of the vas deferens posteriorly from xii/xiii into the anterior half of xiii as a simple secondary loop ; epididymis, a closely coiling single mass in the contiguous halves of xii and xiii, continuing anteriorly from this as a wider thin-walled tubular portion with much of the appearance of a sperm duct and folded on itself in an S-form in the posterior half of xii ; this portion reduces abruptly into a very narrowly tubular connection to the ventral end of the ejaculatory bulb at or posterior to the level of ganglion xii ; ejaculatory bulb muscular, tubular, elongate, of the length of a somite, almost straight or folded vertically on itself, reducing abruptly to continue as the narrow, muscular, short, ejaculatory ducts which extend ventrally and then medially to the atrium.

The male atrium lies just anterior to ganglion xi ; the muscular, opalescent penis sheath, elongated in a primary loop reflecting at xi/xii ; the recurrent limb longer than the procurrent limb.

Ovaries, simple saccular, small, located in the posterior half of xii, briefly posterior to the anterior end of the vaginal duct ; oviducts, short, each no longer than an ovary, join at xii/xiii into a distinct atrium.

Female median region formed in the median chamber on a posteriorly directed primary loop reflecting at xiii/xiv ; common oviduct, thin-walled with a relatively large lumen, elongate, occupies the anterior portion of the recurrent limb, the vaginal duct the equivalent portion of the procurrent limb, the two of a similar length and intimately associated along the length of the vaginal duct, the common oviduct departing the vaginal duct to loop anteriorly briefly in a secondary loop to join subterminally to the vagina ; vaginal caecum, short, small; vagina U-shape, extending as a single continuous chamber along the posterior portion of the recurrent limb, around the elbow, and along the posterior portion of the procurrent limb, of the primary loop, and tapering briefly in joining the vaginal duct; vaginal duct, strongly muscular with a reduced lumen, loosely folded on itself or tortuous, but always distinctly longer than either limb of the vagina; vagina and duct always ventral to the crop.

Prostate glands, an elongate pyriform compact mass enclosing the atrium (partially in some), and tapering briefly along the penis sheath; albumin glands, thick, uniform ensheathment of the full length of the common oviduct.

General Behaviour, Distribution, etc.

Kaiyabdella dawbini is a firm-bodied muscular leech which readily escapes between the fingers of the tightly clenched hand. It is an elegant swimmer, occasionally to be seen swimming quite slowly close to the bottom, and capable of swimming short distances, 5 to 10 feet at a relatively fast speed—in the order of a foot a second. Generally, it is secretive, to be found beneath logs and stones, hidden in crevices and in the submerged axils of bulrush, etc., and must be searched for.

It is known from the coastal flood-plain of the Clarence River and adjacent systems in north-eastern New South Wales. I have not found it on the plateau or tablelands. It occurs in lowland streams, ponds, long-established dams, mostly small waters with a soft river silt bottom, rich with and even choked by submerged and emergent aquatic vegetation; but it is also present in Lakes Hiawatha and Minnie Water, both small shallow lakes inside the coastal dunes, firm bottomed, with only a sparse spaced emergent vegetation.

Out of water, placed on its back on a firm surface, *dawbini* does not right itself in the usual manner, a torsion of the anterior end of the body, attachment of the anterior sucker, and the body then rolled over progressively from the anterior end until righted; but flexes the body ventrally, raising both ends. It then flexes the body dorsally, arching it on the surface, and by rapid repetition of these two actions, suddenly rights the body.

K. dawbini is commonly associated with *Goddardobdella elegans*, with the latter as the more abundant species, e.g. 40 *dawbini* and 154 *elegans* in a collection made on two days at Alumy Creek, Grafton, N.S.W. This is paralleled in my experience of *Bassianobdella fusca*. A thorough search of 300 yards along a tributary of the Macquarie yielded two specimens of *fusca* and six specimens of *Richardsonianus* sp., with the latter a readily collected species elsewhere in this system (Richardson, 1972*a*).

Both *dawbini* and *elegans* are essentially secretive, with *elegans* the more rapidly reactive sanguivore. When the collector enters a water, *elegans* will appear within five minutes; *dawbini*, rarely in less than 10 minutes and most commonly long after all *elegans* in the vicinity have been collected. *B. fusca* did not appear until after all four *R.* sp. in the pool had been taken. Bosisto (1859) may possibly have experienced a similar slower response from *B. victoriae* than the rapidly aggressive attack of *R. australis*, paralleling the long-known difference in behaviour in the case of the monostichodont true horse-leech of Europe and the medicinal leech, and on this basis referred to *B. victoriae* as a horse-leech.

K. dawbini has not been recorded in the field from late May through to September, with one exception. Two fully grown individuals were found in mid-August, 1970, deep in a crevice in a short reef of soft rock in shallow water at Lake Hiawatha. With them, also small glossiphoniform leeches. All were lethargic. None reacted to handling. None made any attempt to escape in the water. The *dawbini* were quiescent in the hand. They appeared dormant and hibernating. These leeches were taken in the late afternoon. With full sun all day, the temperature of the waters in the shallows was 18·5° C.

Predation by K. dawbini. Fig. 2

Macrophagous erpobdellid and haemopid leeches are known predators which attack and ingest other leeches. Predation of sanguivores on other leeches is only briefly reported in the literature so far as I have seen.

Pinto (1923) refers to *Limnobdella* (now *Oxyptychus*) *brasiliensis* as cannibalistic, and as sucking blood from the crop of other leeches. Blair (1927) in an account of *Hirudo medicinalis* in England, states that he has " one actual instance of a leech fullfed, being bitten by another ". Keegan *et al.* (1969) refer to " *Hirudo* " *nipponia* as eventually killing leeches of other speeches, as attacking engorged individuals of its own species, and show (Fig. 19) many *nipponia*, a small species, attached to a large sanguivore, *Hirudinaria manillensis*.

Fig. 2. The 7-banded *Kaiyabdella dawbini* (Richardson 1969) attached to *Goddardobdella elegans* (Grube 1867) in the typical feeding posture which can be maintained for up to twelve hours.

Kaiyabdella dawbini takes vertebrate blood meals. It attacks unfed individuals of the aquatic jawed sanguivore *Goddardobdella elegans*, and takes a meal from these. In a jar, *dawbini* readily attaches to an earthworm, to a large grass grub, and remains attached for periods up to twelve hours. The crops of engorged *dawbini* taken at Lake Hiawatha contained a transparent clear, faintly bluish tinged, soft gel in which there were a few minute white bodies, each with many short coarse radiating spine-like processes, and more sparsely, a few small brownish oil globules. Colour, etc., were suggestive of crustacean haemolymph concentrated by water extraction.

The indications are that *dawbini* attacks and feeds from other suitable invertebrates, in addition to attacking vertebrates.

A collection from Alumy Creek, Grafton, on 14th November, 1967, included 36 *K. dawbini* and 131 *G. elegans* which were all placed in a large jar with water. When seen about an hour later, many of the leeches were on the sides of the jar above the water level. These were all *elegans*. Leeches in the water were swimming rapidly and erratically, with some as pairs on the bottom or sides of the jar appearing to be in copula. The pairs were recognized as a *K. dawbini* with a *G. elegans*, both with the posterior sucker attached to the glass, the *dawbini* partly folded across the *elegans*, extended along its side, and attached by the anterior sucker to the venter of the *elegans* just anterior to the level of the clitellum.

G. elegans removed from the jar were found to have from one to 20 and more wounds, some trifid as typical of the jawed sanguivorous incision, others as round holes each about 1·5 mm. in diameter, both types extending through the body wall. Such wounds were on all parts of the body, even on the margin and interior of the anterior sucker, but none on the posterior sucker. In some cases, fragments of botryoidal tissue, portions of a lateral longitudinal vessel, of epididymis, etc. protruded through the wound ; but none were seen as though cut into or perforated.

Five *G. elegans* were placed in water in a jar. When these had become quiet and settled on the glass, two *K. dawbini* were introduced into the water. Without contact with the *dawbini* or other obvious reason for reaction, the *elegans* began moving quickly and then swimming rapidly and erratically, with one moving up above the water level. The *dawbini* pursued the swimming *elegans*, soon attaching each by its anterior sucker to an *elegans*, trailing briefly with it, and the *elegans* ceasing to swim, the pair sank to the bottom of the jar.

Both attach the posterior sucker to the jar, the *dawbini* attaching and re-attaching its posterior sucker until this is finally placed just anterior to the posterior sucker and close to the body of the *elegans*.

There is then a considerable struggle during which the *dawbini* changes the position of the anterior sucker. Most commonly in this and other trials the struggle terminated with the posterior end of the body of the *dawbini* extending across the posterior portion of the *elegans* ; then lengthwise along the side of the *elegans* and progressively beneath it along the clitellar region ; and the anterior sucker of the *dawbini* attached to the venter of the posterior portion of the preclitellar region of the *elegans*.

In this manner, the anterior sucker of the *elegans* is prevented from reaching the solid surface, and the *elegans* is entirely immobilized. The manner in which the *dawbini* secures the *elegans* is suggestive of a modification and deviation of copulatory behaviour.

In various trials, the pair remained stationary in the one place and in the one posture for ten to twelve hours, and some few longer before separating.

The released *elegans* is not firm bodied. It appears flabby, shrunken, with some regions showing partial collapse, and there are small clouds of coagulated mucus. Leeches in this condition are sluggish in behaviour, swim feebly, survive some few hours, and die. *K. dawbini* were not seen to attack a leech enfeebled in this manner.

Following release of the *elegans*, the crop of the *dawbini* is only partially distended. It contains a thin pale whitish milky fluid rich with many small clear colourless oil droplets. This has been seen also in the crop of *dawbini* taken in the field in March and April.

Rapid attack and sustained attachment are shown also when a large earthworm is supplied to *dawbini*. The *dawbini* becomes immediately restless, commences swimming within 15 seconds, and attaches by the anterior sucker anterior to the clitellum within 45 seconds. The *dawbini* partially wraps around the worm, and attaches the posterior sucker to the jar. The two remain in this manner and without change in position for twelve and a half hours, or even more.

Following attachment of the anterior sucker to the worm, the worm struggles actively for some three minutes. It then slowly extends, becomes quiescent, intestinal peristalsis ceases, and it becomes unresponsive to the touch, with no reaction to stroking or gripping lightly with the forceps, all as though the worm was anaesthetized or in severe shock. An hour later, with the leech still attached, the worm is fully responsive to stimuli, and intestinal peristalsis is normal.

K. dawbini as readily attaches to large grass grubs.

Mass Aggregation of Goddardobdella elegans

Mass aggregations occur with the appearance in the open of a large number of active individuals of a single essentially secretive species of aquatic leech. It is an occasional and temporary event extending over two or three days, with the number of individuals greatly in excess of the normal population of the locality where the aggregation develops. It is associated with upstream mass movement or migration.

A localized population increase occurs with some species in the mating season. The individuals continue to be secretive, and accordingly I have referred to it previously as reproductive swarming since it differs in this way from mass aggregation which is not correlated with reproduction. Dr. M. Howell, the Australian National University, has described to me behaviour by *Vivabdella arcana* similar to reproductive swarming.

Mass aggregation has been reported for some macrophagous haemopids and erpobdellids in North America (Richardson, 1942 ; Sawyer, 1970). Sawyer found aggregation of *Erpobdella punctata* associated with an abundant availability of an aquatic annelid ; but there was no correlation with food supply in mass aggregations which I studied in the Province of Quebec. Mass aggregations of *Percymoorensis marmoratis* were possibly migratory. Aggregation activity could be followed upstream for two or three days with a population of this large leech of five to 10 individuals to a square yard of the bottom. The size of the aggregations diminished after the third day. The late Professor J. Percy Moore wrote me he had seen behaviour of this kind in Himalayan streams.

In the present case, a class of school pupils collected 23 *G. elegans* and four *K. dawbini* from Alumy Creek, Grafton, in a short interval of time on the 10th of November, 1967. A second collection from the same vicinity on the 14th of November contained 133 *elegans* and 36 *dawbini*.

Individuals of *G. elegans* were active and obvious among the sparse rooted aquatic vegetation in the shallow marginal waters to a depth of one foot, with one *elegans* to the square foot.

None were to be seen in this manner in the creek on the 15th of November, or later. The population reduced to about the usual level, i.e. in the order of one individual to 15 to 20 square feet.

Features here common to mass aggregation as known to me previously are : initially, small numbers of *elegans* active in the open ; a sharp rise to peak numbers greatly above the normal population ; a sudden total disappearance of active *elegans* in the open ; with this, a drop to the normal population level ; no correlation with any change in the availability of food.

The mass aggregation was found near the head of the creek, indicating the probability of an upstream migration, as seen in other cases.

The activity of the *K. dawbini* in the open at the time of the mass aggregation can be reasonably correlated with predation on the readily available *G. elegans* ; but the number of *dawbini* favour some measure of upstream movement for this species also.

ACKNOWLEDGEMENTS

I am much indebted to Miss E. Pope, the Australian Museum, Sydney, and Dr. J. C. Yaldwyn, now of the Dominion Museum, Wellington, for help in many ways in the initial stages of this and related studies ; to Mr. P. Strong and his pupils in the Grafton High School for the large collection of the two species at Alumy Creek ; to the Librarian, the University of New England, for assistance with literature ; and Professor Marvin C. Meyer, the University of Maine, for help with difficult literature.

References

BLAIR, W. N., 1927.—Notes on *Hirudo medicinalis*, the medicinal leech, as a British species. *Proc. Zool. Soc. Lond.*, 1927 : 999–1002.

BOSISTO, J., 1859.—Art. 3. On the *Hirudo australis*. *Trans. phil. inst. Victoria*, 3 : 18–22.

KEEGAN, H. L., TOSHIOKA, S., and SUSUKI, H., 1969.—Blood sucking Asian leeches of families Hirudidae and Haemadipsidae. Spec. Rept. 406th Med. Lab. U.S. Army Medical Command, Japan, 1.vi, 1–130.

PINTO, C., 1923.—Ensaio monographico dos Hyrudineòs. *Rev. Mus. Paulista.*, 13 : 5–266.

RICHARDSON, L. R., 1942.—Observations on the migratory behaviour of leeches. *Can. Field-Naturalist*, 51 : 67–70.

————, 1969*a*.—A contribution to the systematics of the hirudinid leeches with description of new families, genera and species. *Acta Zool. Hung.*, 15 (1–2) : 97–149.

————, 1969*b*.—The rediscovery of *Hirudo elegans* Grube 1867. *Mem. Queensland Mus.*, 15 (3) : 191–203.

————, 1970.—*Bassianobdella victoriae* gen. et sp. nov. (Hirudinoidea : Richardsonianidae). *Mem. natl. Mus. Victoria*, 31 : 41–49.

————, 1971.—*Bassianobdella ingrami* sp. nov. from Tasmania. *Pap. Proc. Roy. Soc. Tasmania*, 106 : 113–118.

————, 1972*a*.—*Bassianobdella fusca* sp. nov. (Hirudinoidea : Richardsonianidae) with an initial demonstration of systematic values in the lengths of annuli in the mid-nephric somites. *Rec. Australian Mus.*, 28 (8) : 129–139.

————, 1972*b*.—*Quantenobdella howensis* Richardson 1969 of Lord Howe Island, with a brief comment on dispersal by passive transport (Hirudinoidea : Richardsonianidae). *Mem. natl. Mus. Victoria*, 33 : 65–72.

————, 1972*c*.—*Habeobdella stagni*, a new genus and species from South Western Australia (Hirudinoidea : Richardsonianidae). *J. Roy. Soc. Western Australia*, 54 (2) : 47–52.

SAWYER, R. T., 1970.—Observations on the natural history and behaviour of *Erpobdella punctata* (Leidy) (Annelida : Hirudinea). *Amer. Midl. Naturalist*, 83 (1) : 65–80.

FOSSIL *MANGINULA*-LIKE FUNGI AND THEIR CLASSIFICATION

D. R. SELKIRK
School of Biological Sciences, University of Sydney

(Plates III-VII)

[Accepted for publication 16th February 1972]

Synopsis

Four new species of *Manginula*-like fungi are described from Lower Miocene deposits in New South Wales. Fossil material with ascospores is regarded as belonging to *Vizella* Sacc. and a form-genus *Entopeltacites* is created for fossil material in which spores are not known. New combinations in *Vizella* and *Entopeltacites* are proposed for previously described fossil material.

INTRODUCTION

Dilcher (1965) and Lange (1969) described fossil fungi showing affinities to the modern genus *Manginula* Arnaud, 1918. Several very similar forms occur on fossil leaves in Tertiary sub-basaltic sediments from Homeward Bound Claim, New Chum Hill, to the north-west of Kiandra township, New South Wales, Australia (lat. 35° 47′ S., long. 148° 29′ E.). The lowest lignite exposed in this locality contains large numbers of well-preserved leaves, apparently belonging to a member of the Myrtaceae. The leaves bear abundant epiphyllous fungi referable to the Meliolaceae, Asterinaceae and Trichopeltaceae as well as a number of microthyriaceous forms. Similar fungi occur on leaves of ? Lauraceae in the sediment.

Cookson (1947) described three species of fossil microthyriaceous fungi from New Chum Hill and regarded the sediments as Oligocene-Miocene. Gill and Sharp (1957) assigned an Eocene-Early Oligocene age to the sediments on palaeobotanical evidence and regarded the basalts and underlying sediments as penecontemporaneous. Radiometric age determinations of basalts from the area indicate that they are Lower Miocene (P. Wellman, pers. comm.) and the sediments are thus likely to be Lower Miocene.

Preparation of fossil fungi

Blocks of lignite were collected, stored in plastic bags until required, and then air-dried at room temperature for two weeks. Small blocks were placed in acetone for 30 minutes, broken into smaller pieces, drained of excess acetone and immersed in water. Leaves were dissected from the lignite, washed, and stored in 50% glycerine. Leaves were examined for fungi under a dissecting microscope and cuticular preparations made using nitric acid and 5% potassium hydroxide. Macerated cuticles were washed thoroughly in water and mounted in balsam or glycerine jelly. Some specimens were stained in a saturated alcoholic solution of methylene blue. Dilcher (1965) found that treatment of his fossil material with alkali alone was sufficient to give good cuticular and fungal preparations. Preparation of material from Kiandra required variation of maceration techniques depending on the fungi present. Delicate epiphyllous forms were badly bleached by acid, while fungi with large dark perithecia (such as Asterinaceae) often required acid treatment for up to 10 minutes before perithecial and hyphal structure became clear. Prolonged treatment with alkali alone did not clear these perithecia.

Statistical analysis of cell length measurements in *Vizella discontinua* (described below) indicates that there is no significant difference in measurements obtained from material treated with alkali alone or with acid and alkali.

DESCRIPTION OF SPECIMENS

All fossil specimens from Kiandra described are lodged in the Herbarium, New South Wales Department of Agriculture, Rydalmere, N.S.W. (cited in text as DAR). All measurements of cell size in fossil material are given in the following form :

minimum–(mean ; standard deviation ; number of measurements)–maximum. Measurements are based on camera lucida drawings at ×1750.

Order DOTHIORALES

Family Entopeltaceae

(1) *Vizella* Saccardo (sensu Hughes, 1953)

Synonym : *Shortensis* Dilcher, Palaeontographica 116B, 29, 1965.

(*a*) *Vizella memorabilis* (Dilcher) Selkirk, comb. nov.

Basionym : *Shortensis memorabilis* Dilcher, Palaeontographica 116B, 30, 1965.
Lectotype : Dilcher's slide L.f.60, Peabody Natural History Museum, Yale University, Palaeontographica 116B, 1965, Pl. 17, figs 135–137 ; Pl. 20, figs 157–159 ; Pl. 21, figs 160–161.

(*b*) *Vizella discontinua* Selkirk, sp. nov.

Pl. III, figs 1–7 ; Pl. IV, figs 1–4

Fossil fungi. Colonies up to 5 mm. diameter. Mycelium intracuticular, composed of alternating long and short cells ; long cells colourless, 13–(23·5 ; 5·1 ; 50)–37μ long, short cells brown, 4–(6·0 ; 0·9 ; 150)–10μ long×4–(5·5 ; 0·9 ; 150)–8μ wide, square to rectangular. Main hyphae dichotomously or pseudodichotomously branched at an acute angle ; lateral branches opposite (occasionally alternate), arising from long cells only, rarely dichotomously branched, at 90° to main hyphae. Perithecia intracuticular, 85–125μ diameter when mature, outer wall pseudoparenchymatous, ostiolate. Ostiole *ca.* 20μ diameter, not surrounded by specialized cells. Ascospores ovate-elliptical, 9–(12·1 ; 1·2 ; 91)–15μ long×3–(5·2 ; 0·6 ; 91)–6μ wide, 1-septate, composed of a large cell 7–(9·3 ; 0·9 ; 91)–11μ long×3–(5·2 ; 0·6 ; 91)–6μ wide and a small cell 2–(2·9 ; 0·9 ; 91)–4μ long×2–(2·8 ; 0·4 ; 91)–4μ wide. Hyaline band *ca.* 1·5μ wide present in large cell.

Holotype : DAR 17207 (slide), cuticle of ? myrtaceous leaf, Kiandra, N.S.W., Lower Miocene, Pl. III, fig. 7.

Remarks

In the centre of some colonies the long cells are the same colour as short cells with distinct, bulging lateral walls (Pl. III, fig. 4). Only a few long cells are involved and away from the centre of a colony long cells are colourless with thin lateral walls. Differences between long cells in the centre of a colony and those towards the periphery are possibly developmental. All colonies must have originated from spores on the surface of the cuticle, and the first few cells of the colony may be on the surface of the cuticle or at least not so deeply immersed in the cuticle as later formed cells. The extra thickening of the initial cells may represent adaptation to resist desiccation, later formed cells, more deeply embedded in the cuticle, having thinner walls.

Lateral branches are frequently borne on small thickened projections of lateral walls of long cells, often constricted at the base (Pl. III, fig. 5). The first cell of a lateral branch may be either a short or long cell and both types may occur when two lateral branches are given off from the same long cell. Some lateral branches are associated with fructifications and form part of the fruiting body. No specimens show the development of a fruiting body from cells of the dichotomous system as recorded in *Vizella memorabilis* (Dilcher, 1965). Most lateral branches are not associated with fructifications, but themselves bear laterals, until lateral branches of the third and fourth orders produce an anastomosing network. Ultimate laterals do not show regular division into short and long cells, but are colourless hyphae up to 4μ wide with incomplete cross-septa at irregular intervals (Pl. III, fig. 2).

In some colonies small pores occur irregularly along the hyphae, often surrounded by a pronounced thickened rim (Pl. III, fig. 3). More than one pore may be present in a single long cell. Most pores are in the lower face of the hyphae, but some occur in the upper face, the thickened rim not being so pronounced as in pores on the lower surface. No signs of haustoria penetrating the cuticle have been seen, and the presence of pores in the upper surface of hyphae makes it doubtful whether they have any parasitic function.

The mature perithecium is strongly arched away from the surface of the leaf, the wall one layer thick (Pl. IV, fig. 4). A number of stages in development of fruiting bodies are present. The earliest recognizable stage is an irregular grouping of what appear to be cross-septa in colourless hyphae (Pl. IV, fig. 3). In later stages the walls of the cells become thicker and more evident and the fructification becomes dark (Pl. IV, figs 1, 2).

Ascospores are often fractured along the hyaline band, which may indicate that the walls are thinner in this position. Ascospores are usually clumped in groups within the perithecium and are arranged radially with the small cell to the outside. Similar positioning of spores occurs in *Vizella memorabilis* (Dilcher, 1965) and is a reflection of positioning of ascospores in the ascus in modern *Vizella* spp. (Pl. IV, fig. 9). No stages in spore germination have been observed, nor are there any indications of a germ pore as in *Vizella memorabilis* and other *Vizella* spp.

(2) Form-genus *Entopeltacites* gen. nov.

Generitype: *Entopeltacites osbornii* (Lange) Selkirk, comb. nov.
Fossil fungal colonies. Mycelium with general characteristics of *Vizella* Sacc. or *Manginula* Arnaud; epicuticular or intracuticular. Fructification pseudoparenchymatous, ostiolate or not. Spore characters unknown or uncertain.

(*a*) *Entopeltacites osbornii* (Lange) Selkirk, comb. nov.

Basionym: *Manginula osbornii* Lange, Aust. J. Bot., 17, 568, figs. 1–9, 1969.
Occurrence: Eocene, South Maslin Sands, South Australia.

(*b*) *Entopeltacites maegdefravii* (Lange) Selkirk, comb. nov.

Basionym: *Manginula maegdefravii* Lange, Aust. J. Bot., 17, 568, figs 10–15, 1969.

Occurrence: Eocene, South Maslin Sands, South Australia.

(*c*) *Entopeltacites attenuatus* Selkirk, sp. nov.

Pl. VII, figs 1–4

Colonies up to 5 mm. across, intracuticular. Hyphae dark, dichotomously branched, bearing lateral branches which are themselves dichotomously branched, angle of branching 50–60°. Lateral branches opposite or alternate. Ultimate lateral branches forming anastomosing network. Hyphal cells 2–(11·3; 5·3; 120)–24μ long × 1–(1·7; 0·4; 100)–3μ wide; cross-septa with distinct pore, thicker than the lateral walls. Fructifications ostiolate, wall pseudoparenchymatous, dark. Spore characters uncertain.

Holotype: DAR 17248 (slide), upper cuticle, leaf of ? Lauraceae, Kiandra, N.S.W., Lower Miocene, Pl. IX, figs 1–3.

Remarks

Hyphae extend widely over the leaf, appearing as fine lines on the cuticle (Pl. VII, fig. 1). In central areas of colonies hyphae are dark brown, but become paler towards the edges of colonies and are often almost colourless, the cross-septa being the only visible portion of the hypha. Lateral branches are often borne on a short projection of the lateral wall of a cell, ending in a thick cross-septum. Smaller lateral branches often have short dark cells scattered along the hypha, joined by a number of short or long colourless cells. There is no regularity in the arrangement of dark or light short cells and long cells. Hyphae are covered by an extremely thin layer of cuticle, and in some parts the upper wall of hyphae is level with the surface of the cuticle or even slightly raised above it.

The fructification wall is strongly arched away from the surface of the leaf. In the centre of many fructifications there is a distinct ostiole, apparently formed by breakdown of a number of central cells. No modified cells surround the ostiole. Ostioles are up to 6μ diameter. Fructifications are up to 65μ diameter, but the small number present makes it inadvisable to include fructification diameter in the diagnosis.

In the centre of many colonies there appear to be remnants of the spore which gave rise to them (Pl. VII, fig. 4). The small cell extending laterally from the hypha may represent the small cell of a 2-celled ascospore as in *Vizella memorabilis* and *V. discontinua*. The hyphal cell beneath this small cell would then represent the large cell of the ascospore which has given rise to hyphae in two directions. No spores have been seen in or in association with fructifications and the exact nature of the spore-like structures is questionable. Further specimens may show them to be 2-celled ascospores.

(*d*) *Entopeltacites irregularis* Selkirk, sp. nov.

Pl. VI, figs 1–3

Colonies intracuticular. Hyphae pale brown to hyaline, cross-septa distinct, irregularly branched at 90° forming close anastomosing network (occasional dichotomies occur); cells 2–(6·6; 3·4; 110)–14μ long × 1·5–(2·4; 0·5; 70)–3·5μ wide. Fructification pseudoparenchymatous. Spore characters unknown.

Holotype: DAR 17213 (slide), upper surface leaf of ? Lauraceae, Kiandra, N.S.W.; Lower Miocene, Pl. VI, figs 1–3.

Remarks

The mycelium of this species is very indistinct. Cross-septa are prominent, and most of the mycelium is colourless (Pl. VIII, fig. 2). Alternating long and short cells occur in parts of all colonies, but the character is not constant. In many areas, hyphae appear to follow cuticular flanges of epidermal cell walls (Pl. VI, fig. 1). Fructifications and hyphae are covered by a very thin cuticle layer but in some places hyphae are on the cuticle surface.

Numbers of small (14–40μ diameter) fructifications are present. They are pseudoparenchymatous and appear to have developed in the same manner as in *Vizella discontinua*. The earliest recognizable stages consist of an irregular grouping of thickened walls which resemble mycelial cross-septa. Larger fructifications are darker.

(*e*) *Entopeltacites cooksoniae* Selkirk, sp. nov.

Pl. V, figs 1–3

Colonies up to 1·5 mm. across, intracuticular. Hyphae forming anastomosing network, main hyphae dichotomously branched bearing lateral branches which may themselves be dichotomously branched. Hyphae brown in centre of colony becoming irregularly brown and hyaline in lateral branches and towards the periphery. Hyphal cells 3–(6·7 ; 2·1 ; 207)–15μ long × 4–(5·6 ; 1·0 ; 192)–8μ wide, square to rectangular, occasionally cuneate, cross-septa markedly thicker than lateral walls. Lateral stigmopodium-like structures present, mainly confined to centre of colonies. Fructification pseudoparenchymatous ; wall dark. Spore characters unknown.

Holotype: DAR 17258 (slide), cuticle of unidentified leaf, Kiandra, N.S.W., Lower Miocene, Pl. v, figs 1–3. The species is named in honour of Dr. Isobel Cookson.

Remarks

The mycelium of this species is very distinctive. The main dichotomous hyphae bear frequent lateral branches (Pl. v, fig. 1). Hyphae in the centre of most colonies are thinner than those towards the periphery. In lateral branches the lateral walls of hyaline cells are thin, often apparently lacking altogether. Lateral walls of brown cells are distinct, but markedly thinner than the cross-septa. At the ends of branches hyphae are usually hyaline and cross-septa are the only parts visible. Some cells are divided by a longitudinal septum.

Lateral outgrowths from the hyphae are common in the centre of colonies. These resemble stigmopodia present in *Manginula perseae* and *Vizella memorabilis*. There is no evidence, however, of a pore or penetration peg penetrating the cuticle and the outgrowths may not be true stigmopodia. The stigmopodium-like outgrowths are up to 10μ long × 5μ wide, irregular in shape and brown to hyaline. Their walls are often indistinct, and are apparently lacking at the apex of many specimens. Some outgrowths appear to be simple evaginations of the hyphal cell wall (Pl. v, fig. 2). In others there is a distinct wall between the hyphal cell and the outgrowth. In one specimen outgrowths from two hyphal cells form a loop over an intervening hyphal cell. Small 2- or 3-celled lateral branches are common. The basal cells of these branches often resemble the stigmopodium-like outgrowths, which possibly represent either modified or abortive lateral branches.

Hyphae and fructifications are covered by about 2·5μ of cuticle. Only a few relatively intact fructifications are present. Most lack almost all the upper wall which has broken away leaving only the margins. The upper wall is dark, composed of irregular cells (Pl. v, fig. 3). The apical portion of all fructifications is damaged and I have been unable to decide whether an ostiole is present or not. Fructifications seen are 100–110μ diameter. A number of young stages are recognizable showing the typical irregular arrangement of cross-septa in hyaline hyphae described above in *Vizella discontinua*. One fructification in which the outer wall is mostly lacking has faint indications of a basal layer with irregular cross-septa.

PROBLEMS IN CLASSIFICATION OF FOSSIL ENTOPELTACEAE

The fossil fungi from Kiandra appear to represent a group of closely related species. They are placed in different genera on the basis of preservation or otherwise of spores. Similar fungi have been described from Eocene deposits in Tennessee (Dilcher, 1965) and South Australia (Lange, 1969). All the fossil species have very similar fructifications and hyphae, and strongly resemble the modern *Manginula perseae* described by Arnaud (1918). Spores are present in only two fossil species : *Shortensis memorabilis* Dilcher and *Vizella discontinua* described above.

Although the fossil species are very similar, their classification into genera is somewhat confusing. 2-celled ascospores present in fossil specimens led Dilcher (1965) to establish the genus *Shortensis* for perfect stages of *Manginula*.

Lange (1969) held Arnaud's (1918) description of *Manginula* as an imperfect form to be incorrect. He theorized that the unicellular pycnidiospores figured by Arnaud for *Manginula perseae* were in fact ascospores in which one cell had disintegrated leaving an apparently unicellular spore, and concluded that *Manginula* is a perfect form. He described a modern species with 2-celled ascospores and two fossil forms without spores as species of *Manginula* and regarded *Shortensis* Dilcher as a synonym of *Manginula*.

Hughes (1953) regarded *Vizella* as containing perfect stages of *Manginula*. In his description of *Vizella hendrickxii* Hughes stated that " pycnidia of *V. hendrickxii* very probably may be referred to as the *Manginula* state ".

Ascospores of some *Vizella* spp. are similar to those described by Dilcher (1965) in *Shortensis*, Lange (1969) in *Manginula eichleri* and in *Vizella discontinua* from Kiandra.

The 2-celled spores of some *Vizella* spp. are not always described as such. Spores of *V. bingervilliana* are " unicellulaires, munies à la base d'un très court appendice hyalin " (Moreau and Moreau, 1951). Figures accompanying this description show spores very similar to those of *V. gustaviae* which has 2-celled spores with a large upper cell and a small basal cell (Batista and Ciferri, 1957), Hughes (1953) regarded *V. bingervilliana* as probably synonymous with *V. gomphispora*, which he described as having ascospores " composed of a large upper cell usually with a basal appendage ", a situation which also occurs in *V. hendrickxii*. Hughes does not discuss the nature of this " appendage ".

The type specimen of *Vizella hendrickxii* (Hansf.) Hughes (Herb, IMI 47458) has ascospores in which the large dark cell has a small cell-like hyaline appendage (Pl. IV, fig. 8). Specimens of a form apparently belonging to *Vizella* on leaves of *Acmena smithii* from Somersby Falls, near Gosford, N.S.W., have spores of the same type. Sections through asci show the appendage as basal and containing definite cytoplasm (Pl. IV, fig. 9). The " appendage " described in many species of *Vizella* is almost certainly such a small basal cell and I regard all reports of such appendages as referring to a 2-celled spore.

Hughes (1953) commented that " the presence or absence of a basal appendage is not considered to be a good generic character ", and pointed out that in the type collection of *Vizella conferta* (the type species of the genus) ascospores may have appendages or lack them. Lange (1969) noted that the small cell of ascospores of *Manginula eichleri* Lange often disintegrates, leaving a spore closely resembling the unicellular pycnidiospores of *Manginula perseae*. Hughes (1953) mentioned that the basal cell of ascospores of *Vizella hendrickxii* is very difficult to see, and that in the original description of the species the spores had been described as 1-celled. On the basis of the occasional breakdown of the basal cell of such ascospores, Lange (1969) concluded that Arnaud (1918) had interpreted 2-celled ascospores with missing basal cells as unicellular pycnidiospores in his description of *Manginula perseae*.

In the absence of re-examination of type material of *M. perseae*, Arnaud's description is not disproved. Lange's postulation conflicts with descriptions of similar pycnidiospores to those described for *Manginula perseae* in *Manginula leucospermi* (Batista, Peres and Maia, 1963) and their presence in related genera. Only re-examination of type material of all species of *Manginula* and determination of the mode of development of spores would allow a decision that they are ascospores not pycnidiospores.

Until a revision of modern material is carried out I have regarded fossil material with 2-celled ascospores as *Vizella* spp. (including *Shortensis*). The genus *Manginula* is retained for pycnidial forms, and fossil material lacking spores is placed in a form-genus, *Entopeltacites*. Specimens described as *Manginula eichleri* by Lange (1969) have spores similar to those of *Shortensis*

Dilcher and *Vizella discontinua* and most probably represent a species of *Vizella*, possibly previously described.

Hyphae of *Vizella*, *Manginula* and *Entopeltacites* are fairly characteristic. Most modern species have pale brown to hyaline hyphae with cross-septa very much thicker and darker than the lateral walls. In species with hyaline hyphae cross-septa are the only parts of hyphae visible. This is also the case in ultimate branches of species with more deeply coloured hyphae. Fossil species show the same characters. Table 1 shows hyphal structure of some modern and all fossil species.

TABLE 1

Mycelial Characters in Vizella, Manginula *and* Entopeltacites

	Branching Pattern	Long Cell/ Short Cell Alternation	Stigmopodia
Vizella psychotriae (Batista *et al.*, 1960)	Irregular	Absent	—
Vizella crescentiae (Batista *et al.*, 1960) ..	Irregular	Absent	—
Vizella splendida (Batista *et al.*, 1960) ..	At 45° (dichotomous) ?	Absent	—
Vizella hendrickxii	Dichotomous	Regular	—
Vizella memorabilis (Dilcher, 1965) ..	Dichotomous	Absent	+
Vizella discontinua	Dichotomous	Regular	—
Manginula perseae (Arnaud, 1918) ..	Dichotomous	Regular	+
Manginula leucospermi (Batista, Peres and Maia, 1963)	Not stated	Absent	+
Manginula eichleri (Lange, 1969)	Dichotomous	Absent	—
Entopeltacites osbornii (Lange, 1969).. ..	Dichotomous	Present but variable	—
Entopeltacites maegdefravii (Lange, 1969) ..	Dichotomous/ pseudo-dichotomous	Occasional	—
Entopeltacites attenuatus	Dichotomous	Absent	—
Entopeltacites cooksoniae	Dichotomous	Absent	+
Entopeltacites irregularis	Irregular	Occasional	—

Hyphae of *Vizella discontinua* closely resemble those of *V. hendrickxii* (Pl. IV, fig. 7) and *Manginula perseae*. In both *Vizella discontinua* and *Manginula perseae* short cells are darker than the long cells. Colour differences between cells in fossil hyphae should be accepted as significant with caution. Colour in some cells could be due to retention of oxidized material in thicker-walled cells after maceration. Marked colour differences between cells occur in *Vizella discontinua* and *Entopeltacites cooksoniae*. In some modern *Vizella* spp. dark cells may occur in otherwise colourless hyphae and the feature is very pronounced in *Manginula perseae*. Since colour differences between hyphal cells occur in modern species of the group to which fossil forms are believed to belong, such differences in fossil material can probably be fairly safely regarded as reflecting the state in the fossils as living organisms.

Lange (1969) commented that *Manginula* " is most unlikely to be subcuticular ", even though Arnaud's (1918) figures show a thin layer of cuticle over the hyphae. It can be difficult to determine whether hyphae are epicuticular or subcuticular, particularly if cuticular preparations are seen in surface view. Dilcher (1965) described hyphae of *Vizella memorabilis* as epicuticular. Specimens of *V. memorabilis* kindly sent to me by Dilcher show the hyphae covered by a thin layer of cuticle. The cuticle layer is visible in both sectional and surface views and consists almost entirely of cuticular striations (Pl. IV, figs 5, 6). Some parts of the hyphae appear to be level with the cuticle surface and are not crossed by striae. A fructification in the same specimen has a definite layer of cuticle covering those sections of the wall which remain. Hyphae and fructifications of *Vizella discontinua* and *Entopeltacites cooksoniae* are covered by a 2–4μ thick layer of cuticle. Other fossil species from Kiandra have a very thin layer covering them. Most modern *Vizella* spp. are subcuticular, as is *Manginula leucospermi*. *Vizella bingervilliana* is described as having a superficial mycelium, but perithecia are subcuticular (Moreau and Moreau, 1951).

It seems that modern and fossil species form a group in which the mycelium is either on or just below the surface of the cuticle. Where hyphae are embedded in the cuticle the term " intracuticular " may be preferable to " subcuticular ".

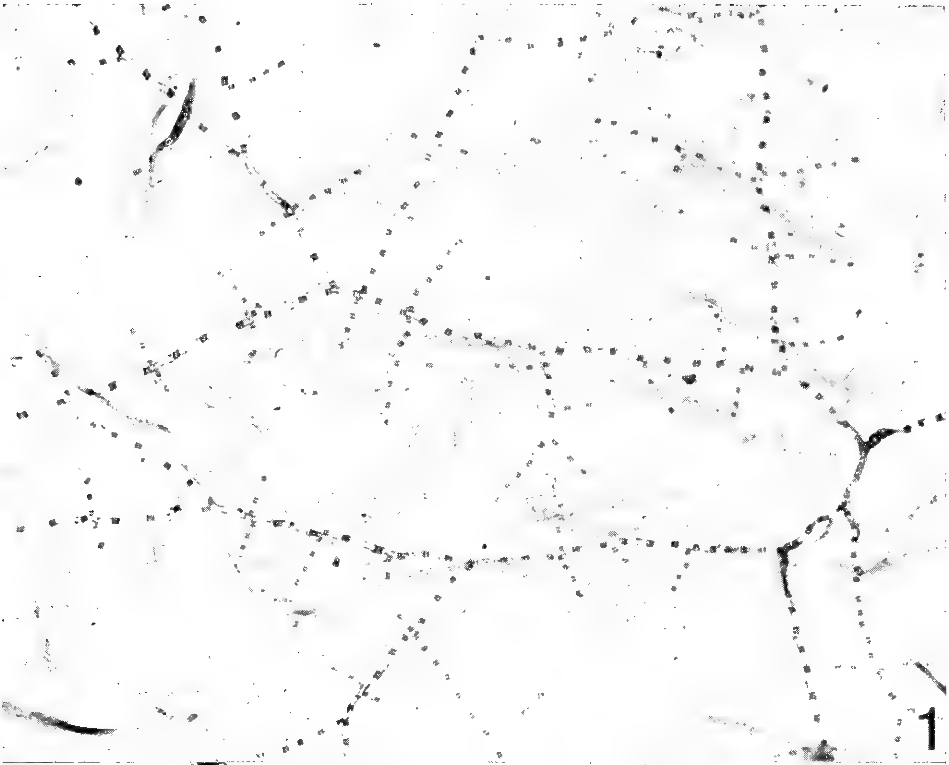
Mention should also be made of the genus *Entopeltis* in connection with classification of the fossil species. Hughes (1953) regarded *Entopeltis* as a synonym of *Vizella*, but the two are treated as separate by Von Arx and Müller (1954), who regarded them as separable on the structure of the outer wall of the perithecium. *Vizella* has a multi-layered wall ; *Entopeltis* a single layered wall.

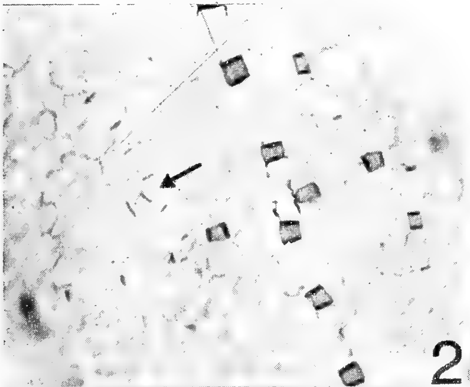
If this division of the genera is accepted the fossil species appear to be closer to *Entopeltis* than *Vizella*. Transverse sections of perithecia of *Vizella discontinua* show a single layer of cells with no indication that deeper layers have broken away (Pl. IV, fig. 4). Careful focussing does not reveal any deeper layers in the wall when intact perithecia are examined in surface view. Insufficient material of the three species of *Entopeltacites* was available to allow sectioning, but no deeper layers are detectable in the walls of these. Thus the fossil forms could be placed in *Entopeltis*, which has hyphae similar to *Vizella*.

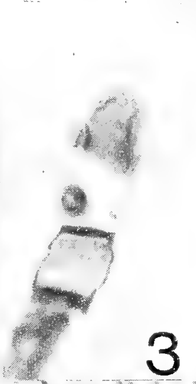
The problem of classifying fossil material is really one of the taxonomy of modern forms. A critical revision of morphology and taxonomy of modern forms described as *Vizella*, *Entopeltis* and *Manginula* would be necessary before a final decision as to the best classification of the fossil forms could be made. Until such a revision is made I have thought it best to emphasize the apparently close relationship by including well-preserved fossil material in the modern genus. A number of modern forms (apparently undescribed) were collected from various localities in N.S.W. during the present study. Collections were made from localities in subtropical rainforest, temperate rainforest (on *Nothofagus*) and in moist gullies in dry sclerophyll forest. Modern and fossil members of the group seem to indicate moist conditions, but until much more is known about their distribution ecological extrapolation based on them should be very cautious.

ACKNOWLEDGEMENTS

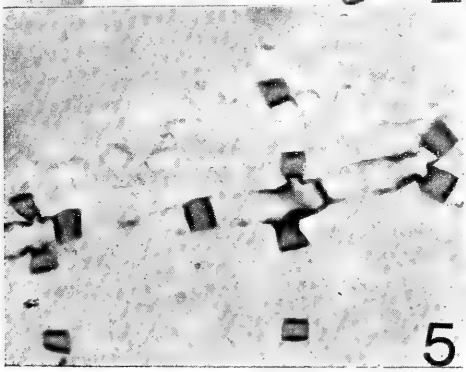
I wish to thank the former Kosciusko State Park Trust for permission to collect the fossil material ; Dr. D. L. Dilcher for providing material of *Vizella memorabilis* ; Dr. R. T. Lange, for the loan of type material of fossil species ; the Director, Commonwealth Mycological Institute, for loan of type material of *Vizella hendrickxii* ; Mr. J. Walker for loan of material from Department of Agriculture Herbarium.

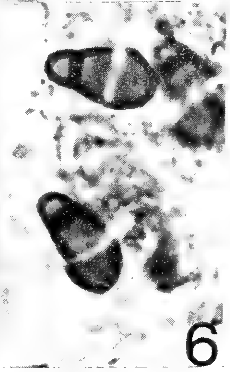

1


2

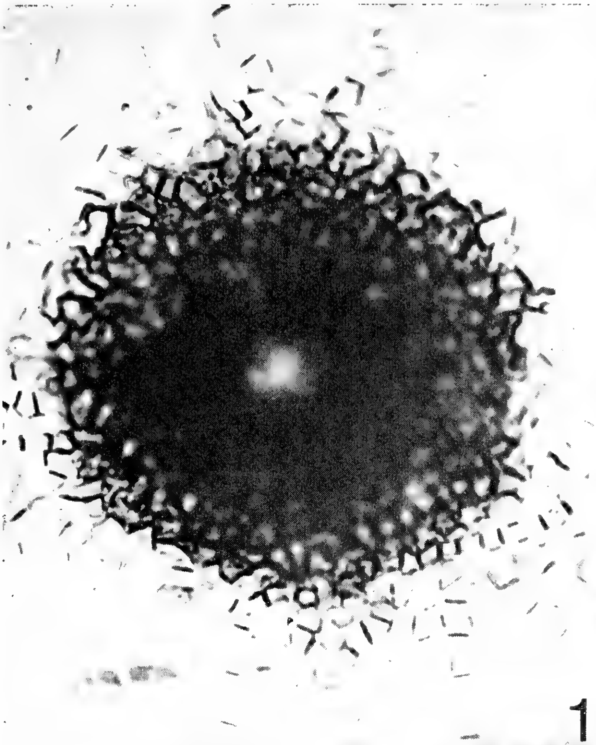

3

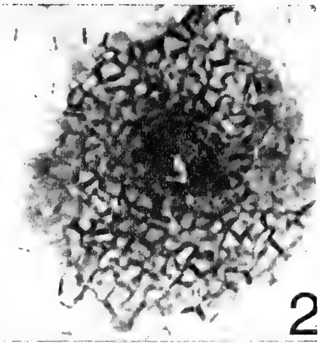

4

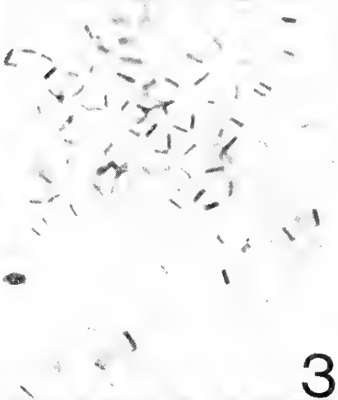

5

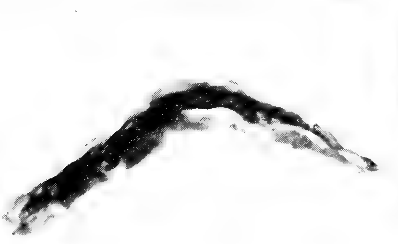

6

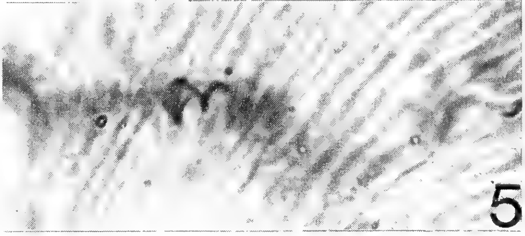

7

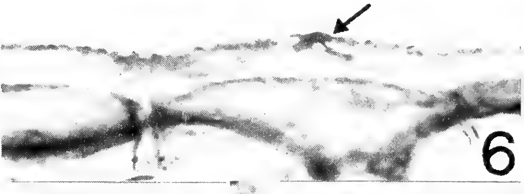

1

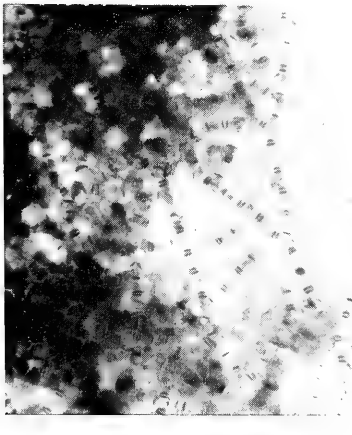

2

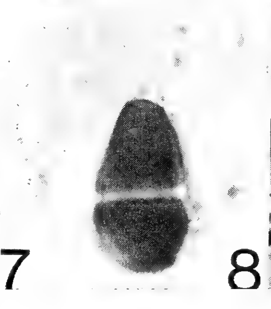

3

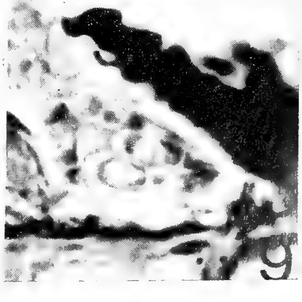

4

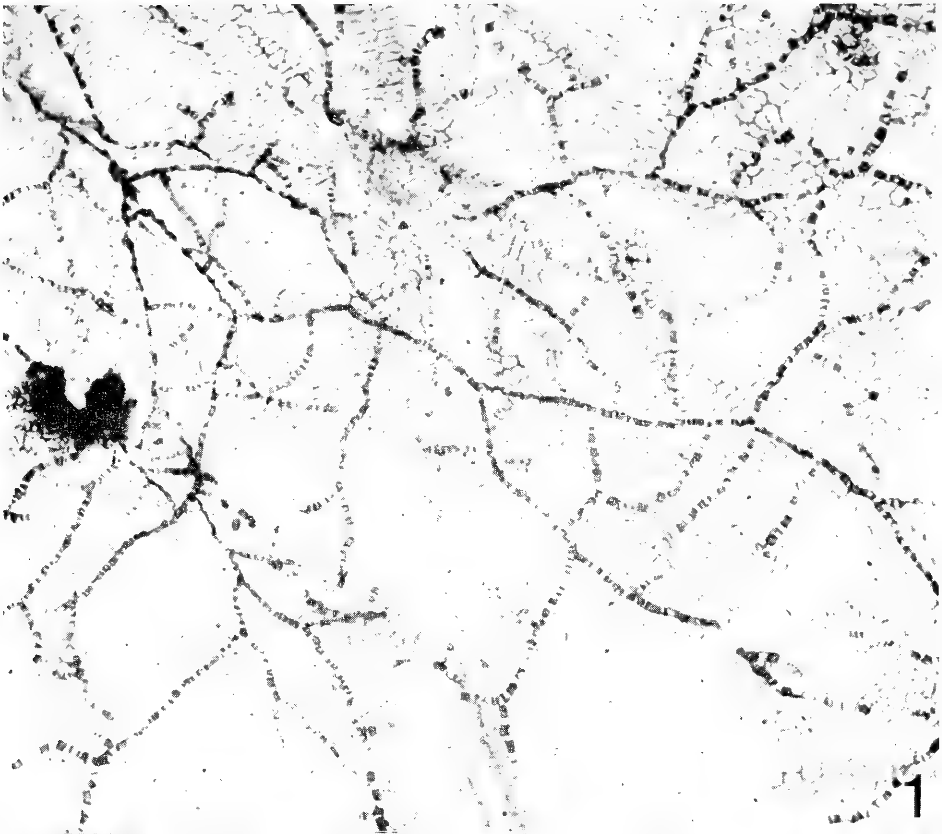

5


6

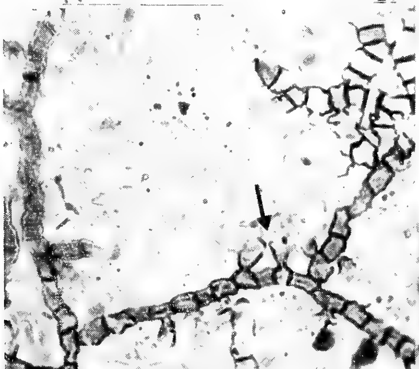

7


8

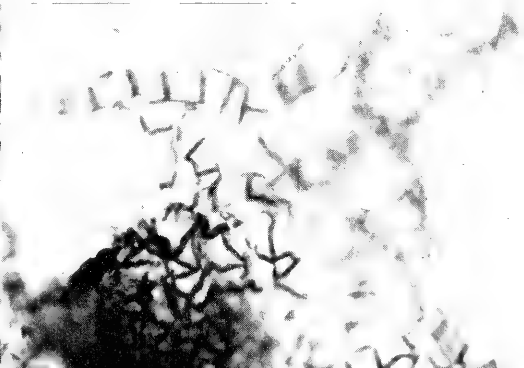

9



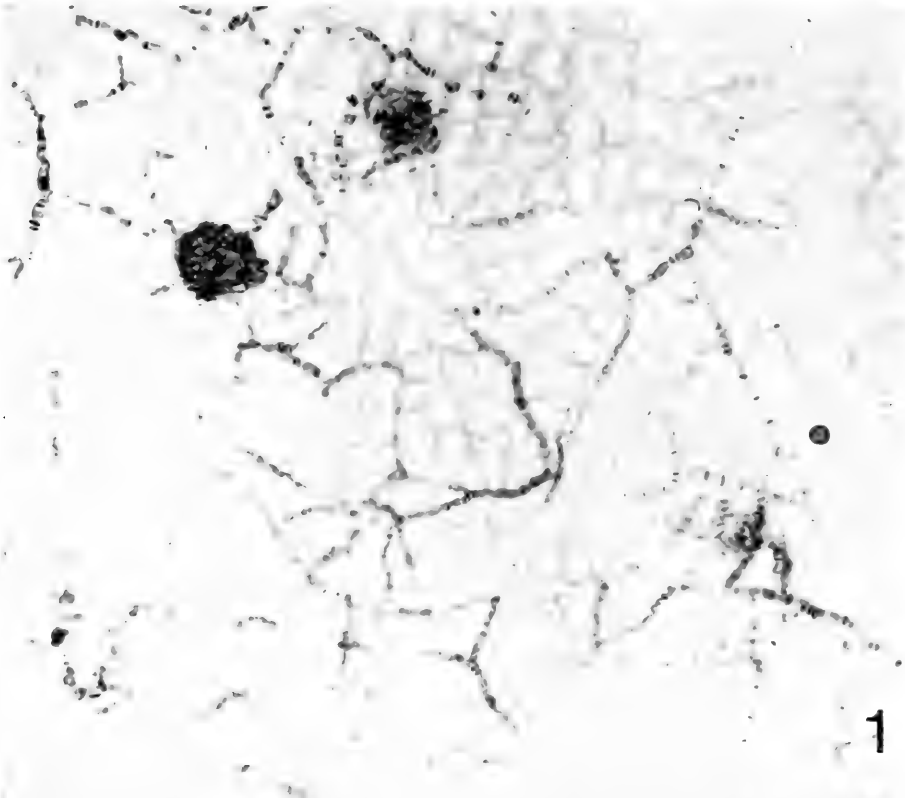
1



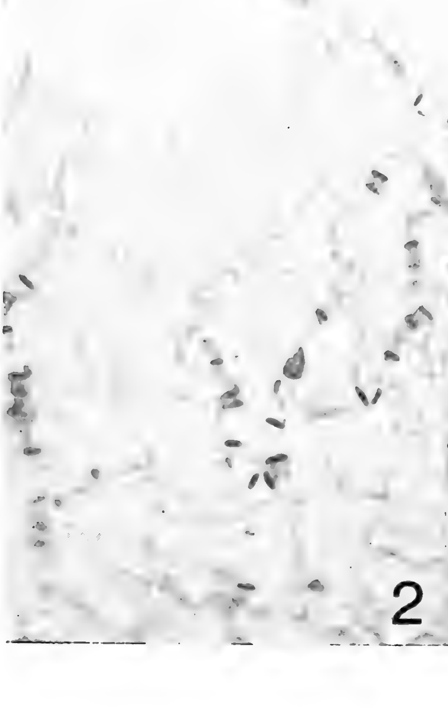
2



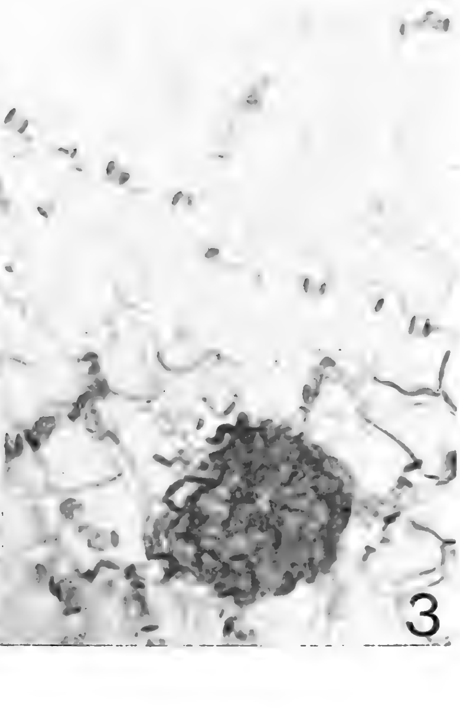
3



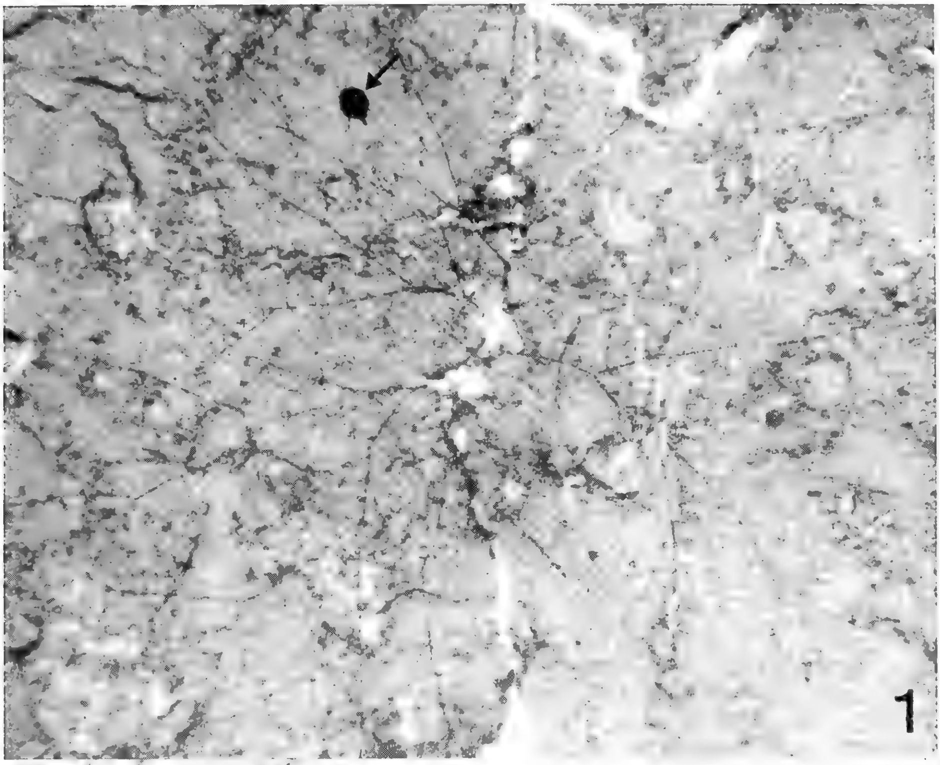
1



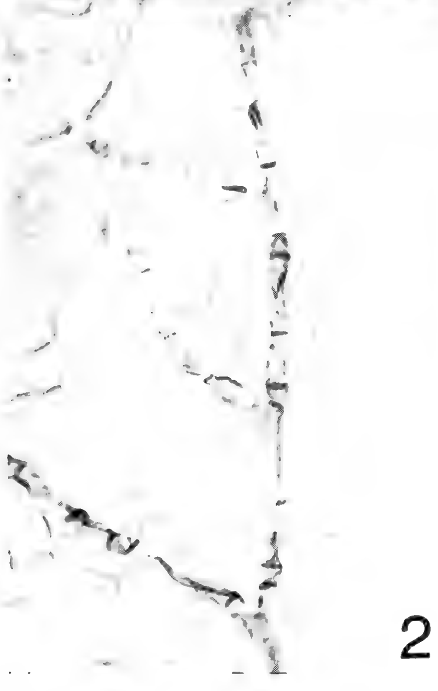
2



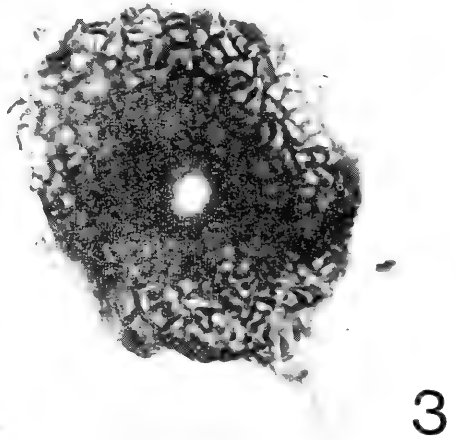
3



1



2



3

4

References

Arnaud, G., 1918.—Les Astérinées. *Annls. Éc. Natn. Agric. Montpellier Nlle Série* 16 : 1-288.

Arx, J. A. von, and Müller, E., 1954.—Die Gattungen der amerosporen Pyrenomyceten. *Beitr. Kryptog Flora Schweiz.*, 11 (1) : 1-434.

Batista, A. C., and Ciferri, R., 1957.—Contribução ao estudo dos Ascomicetos Pernambucanos. *Sydowia*, Beih. 1 : 325.

Batista, A. C., Peres, G. E. P., Bezerra, J. L., and Maia, H. da Silva, 1960.—Revisão de alguns fungos Stigmateaceae. *Nova Hedwigia*, 2 : 476-483.

Batista, A. C., Peres, G. E. P., and Maia, H. da Silva, 1963.—Dois novos fungos da familia Manginulaceae. *Inst. Micol. Univ. Recife Publ.*, 223 : 1-9.

Cookson, I. C., 1947.—Fossil fungi from Tertiary deposits in the Southern Hemisphere. Part I. Proc. Linn. Soc. N.S.W., 72 : 207-214.

Dilcher, D. L., 1965.—Epiphyllous fungi from deposits in Western Tennessee, U.S.A. *Palaeontographica*, Abt. B, 116 : 1-54.

Gill, E. D., and Sharp, K. R., 1957.—The Tertiary rocks of the Snowy Mountains, Eastern Australia. *J. Geol. Soc. Aust.*, 4 : 21-40.

Hughes, S. J., 1953.—Fungi from the Gold Coast. II. *Mycol. Pap.*, 50 : 1-104.

Lange, R. T., 1969.—Recent and fossil epiphyllous fungi of the *Manginula-Shortensis* group. *Aust. J. Bot.*, 17 : 565-574.

Moreau, C., and Moreau, M., 1951.—Pyrénomycètes du Caféier en Côte d'Ivoire. *Revue Mycol. Suppl. colon.*, 16 (1) : 12-80.

EXPLANATION OF PLATES

Plate III

Figs 1-7. *Vizella discontinua* Selkirk sp. nov., New Chum Hill, Kiandra, N.S.W., Lower Miocene. 1, DAR 17206, × 100, portion of colony showing hyphal branching. 2, DAR 17206, × 375, showing cross-septa in ultimate lateral hyphal branches (arrow). 3, DAR 17203, × 1250, pore in lower face of long cell. 4, DAR 17205, × 300, hyphae in centre of colony showing thick walled long cells. 5, DAR 17206, × 440, detail hypha showing origin of lateral branches and a dichotomy. 6, DAR 17247, × 1200, ascospores. 7, DAR 17207, holotype, × 1200, ascospores in perithecium.

Plate IV

Figs 1-4. *Vizella discontinua* sp. nov. 1, DAR 17205, × 545, mature fructification. 2, DAR 17205, × 545, young fructification. 3, DAR 17205, × 545, early stage of fructification development. 4, DAR 17263, × 610, section through cuticle and fructification wall.

Figs 5-6. *Vizella memorabilis* (Dilcher) Selkirk comb. nov. 5, × 1200, surface view of cuticle showing cuticular striations overlying hypha. 6, × 1200, section showing hypha within cuticle.

Figs 7-8. *Vizella hendrickxii* (Hansf.) Hughes, Herb. IMI 47458. 7, × 95, portion of colony. Note alternation of long and short cells and dichotomous branching. 8, × 1500, ascospore.

Fig. 9. *Vizella* sp. on leaves of *Acmena smithii*, Somersby Falls, near Gosford, N.S.W. Section through perithecium showing 2-celled ascospores in ascus, × 900.

Plate V

Figs 1-3. DAR 17258, holotype, *Entopeltacites cooksoniae* Selkirk, sp. nov., New Chum Hill, Kiandra, N.S.W., Lower Miocene. 1, × 150, portion of colony showing hyphal branching. Note irregular arrangement of dark and hyaline cells in lateral branches. 2, × 470, hyphae showing stigmopodia (arrows). 3, × 650, portion of fructification.

Plate VI

Figs 1-3. DAR 17213, holotype, *Entopeltacites irregularis* Selkirk sp. nov., New Chum Hill, Kiandra, N.S.W., Lower Miocene. 1, × 390, colonies with fructifications. Note tendency of hyphae to follow epidermal cell walls. 2, × 730, detail hyphae. 3, × 730, small fructification.

Plate VII

Figs 1-4. *Entopeltacites attenuatus* Selkirk sp. nov., New Chum Hill, Kiandra, N.S.W., Lower Miocene. 1, DAR 17248, holotype, × 60, colony with fructification (arrow). 2, DAR 17248, holotype, × 785, hyphae. 3, DAR 17248, holotype, × 785, fructification. 4, DAR 17265, × 1500, possible germinated spore.

THE RUGOSE CORAL *PALAEOPHYLLUM* BILLINGS FROM THE ORDOVICIAN OF CENTRAL NEW SOUTH WALES

B. D. Webby
Department of Geology and Geophysics, University of Sydney

(Plates VIII, IX)

[Accepted for publication 16th February 1972]

Synopsis

Three new species of *Palaeophyllum* are described from Ordovician limestones of central New South Wales. They range through horizons of broadly Eastonian to Lower Bolindian age. Two distinct types of budding are well displayed—in the species from the upper part of the Cliefden Caves Limestone, axial and parricidal, and in the species from the top of the Malachi's Hill Beds, peripheral and non-parricidal.

INTRODUCTION

The first species of *Palaeophyllum* to make its appearance in the Ordovician successions of central New South Wales is *P. proliferum* sp. nov. It occurs in the upper part of the Cliefden Caves Limestone and the upper part of the Regan's Creek Limestone, and in the middle part of the Bowan Park Limestone (now referred to the Quondong Formation of the Bowan Park Group by Semeniuk, 1970). These occurrences belong to Fauna II of Webby (1969), and seem to represent a Lower Eastonian or Upper Gisbornian ? age. Associated with *P. proliferum* in the upper part of the Cliefden Caves Limestone and the Quondong Formation are two species of *Hillophyllum* (Webby, 1971). *Palaeophyllum*, though probably not the same species, has been noted by Webby (1969, p. 642) as occurring in Ordovician limestone near Gunningbland, in association with *Streptelasma*, *Plasmoporella inflata* Hill and *Cliefdenella etheridgei* Webby.

A second species, *P. crassum* sp. nov., comes from the upper part of the Cargo Creek Limestone. It is associated with *Quepora calamus* Webby and Semeniuk and streptelasmatids, underlying the main fossiliferous bands containing massive *Favistina* and favositids. Another species of *Palaeophyllum* occurs in the upper part of the Ballingoole Formation of the Bowan Park Group and, though poorly preserved, yet another in the upper part of the Canomodine Limestone. All these occurrences seem to belong to Fauna III, and to be of Upper Eastonian age.

The Bowan Park Group is succeeded by the Malachi's Hill Beds (Semeniuk, 1970). Towards the top of the formation locally derived limestone pebbles contain an abundant coral fauna including *P. macrocaule* sp. nov., *Favistina*, *Catenipora* and many favositids. Succeeding massive limestones yield a similar fauna which shows little sign of reworking. The graptolites in the lower part of the Malachi's Hill Beds have suggested to Semeniuk an age near the Eastonian/Bolindian boundary or Lower Bolindian, which implies that the overlying coral fauna may have a Bolindian age. It possibly represents the youngest Ordovician coral assemblage in central New South Wales, and constitutes a fourth biostratigraphic assemblage (Fauna IV) typified by abundant favositids, *Favistina*-like forms and the first appearance of *Catenipora*. *Calapoecia*, recorded from an isolated limestone lens near Boree Creek, west of Bowan Park (Stevens, 1956), may also come from this stratigraphic level.

Strusz (1960, 1961) described a species of *Palaeophyllum* from limestone beds at the top of the Oakdale Formation in the Oakdale Anticline of the Mumbil area, near Wellington. He referred it to *P. rugosum* Billings, and considered it to belong to a topmost Ordovician or Lower Silurian horizon. The species is associated with *Tryplasma lonsdalei* Etheridge, *T. derrengullenense ?* Etheridge and *Nipponophyllum* aff. *giganteum* Sugiyama. A second species, *Palaeophyllum* sp. nov. ?, is reported by Strusz from the base of the overlying Narragal Limestone (late Llandoverian-Wenlockian). Packham (1968, p. 154), however, has noted that these basal beds of the Narragal Limestone are separated from the main body of the limestone by a thin succession of acid-intermediate volcanics, and either form the uppermost part of the Oakdale Formation or consist of another unit resting on the Oakdale. Packham (1969, p. 103) has viewed the coral fauna of the Oakdale Formation with its *Palaeophyllum*, *Syringopora* and genera related to *Halysites* as apparently of late Eastonian-Bolindian age. He (1969, p. 83) has observed a similar limestone 15 miles south of Strusz's area containing halysitids, *Multisolenia* sp., *Heliolites daintreei* Nicholson and Etheridge and *Syringopora* sp., and underlying shales with an Eastonian graptolite assemblage.

In contrast, Ivanovskij (1965) has regarded the rugose element of Strusz's Oakdale fauna as characteristic of the late Llandoverian or even transitional Llandoverian-Wenlockian, and Webby and Semeniuk (1969, p. 357) have favoured a Lower Silurian rather than an Upper Ordovician age because of the much greater generic and specific diversity of the halysitids than in typical Ordovician occurrences. Apart from the occurrence of *Palaeophyllum*, there is little in common between the Oakdale coral fauna and the confirmed Ordovician coral faunas of New South Wales. But then there is also a remarkable lack of similarity between the rugose element of the Oakdale fauna and the Lower Silurian faunas of the Bridge Creek Limestone, Quarry Creek Limestone and Rosyth Limestone being studied by R. A. McLean (pers. comm.).

The presence of an " advanced " dissepimented rugosan like *Nipponophyllum* and species of *Tryplasma* (*sensu stricto*) clearly indicates that the Oakdale coral fauna is no older than Ashgillian (i.e., Upper Bolindian). It is either younger than the coral fauna at the top of the Malachi's Hill Beds and older than the Bridge Creek Limestone (possibly Upper Bolindian) or, alternatively, younger than the Bridge Creek, Quarry Creek and Rosyth Limestones and older than the Narragal and Borenore Limestones (about late Llandoverian or transitional Llandoverian-Wenlockian, as Ivanovskij has already advocated). It is difficult to reconcile Packham's occurrence of *Multisolenia* underlying an Eastonian graptolite horizon when the genus has not been confirmed in the large bodies of Ordovician (mainly Eastonian) limestone of the region.

In addition to the occurrences in central New South Wales, *Palaeophyllum* has been recorded from the Trelawney Beds of northern New South Wales (Philip, 1966), and from near the top of the Gordon Limestone in the Florentine valley of Tasmania (Banks, 1965).

Catalogue numbers of specimens in the University of Sydney palaeontological collections have the prefix SUP.

Systematic Descriptions

Suborder Columnariina Rominger 1876

Family Stuariidae Milne-Edwards and Haime 1850

Genus *Palaeophyllum* Billings 1858

Type species. *P. rugosum* Billings 1858.

Discussion. Dorothy Hill (1961) has redescribed the type material of *P. rugosum*, and has given a revised diagnosis of the genus. From present observations, the genus exhibits more than one type of budding, and therefore the statement " peripheral, non-parricidal increase " should be omitted from the diagnosis. In *P. gracile* Flower 1961 and *P. proliferum* sp. nov., axial, parricidal budding is represented, and in *P. rugosum* Strusz 1961, *non* Billings 1858, peripheral, quadripartite, parricidal budding. *P. aggregatum* (Nicholson and Etheridge, 1878), judging from Wang's (1948, p. 102, text-fig. 3*b*) illustration, and a thin section in the Sedgwick Museum (SM.A. 7544*c*), Cambridge, shows tripartite and quadripartite, parricidal increase. Also, apparently lateral, non-parricidal division is exhibited by *P. humei* Sinclair 1961 and possibly in the type species, *P. rugosum* Billings 1858 (Hill, 1961, p. 2).

Ivanovskij (1969) has recently lumped all the known species of *Palaeophyllum* into three species—*P. thomi* (Hall, 1857), *P. fasciculum* (Kutorga, 1837) and *P. lebediensis* (Čerepnina, 1960), the first two each having an additional variant, *P. thomi* var. *cateniforme* Flower 1961 and *P. fasciculum* var. *halysitoides* Troedsson 1928, respectively. The species are distinguished by the nature of septa and tabulae. *P. thomi* has rudimentary minor septa and updomed tabulae with axial sag, and *P. fasciculum* has well-developed minor septa and updomed tabulae with a flat axial zone. *P. lebediensis* has long major septa—usually longer than in the other two species—almost always reaching the axis, well-developed minor septa, updomed tabulae, sometimes with axial depression, and numerous tabellae. The species are very broadly conceived and would be much better regarded as species groups. Indeed, they appear to have some value in such a broad grouping. The *P. thomi* group is a cosmopolitan Middle-Upper Ordovician group, the *P. fasciculum* group, a cosmopolitan Upper Ordovician-Lower Silurian group, and the *P. lebediensis* group, a geographically restricted Upper Ordovician group. Of the New South Wales species, *P. proliferum* and probably *P. crassum* belong to the *P. thomi* group, and *P. macrocaule*, to the *P. lebediensis* group. This latter occurrence extends the range of the *P. lebediensis* group from the Siberian Platform, Gornaja Šorija and Gornyj Altai to central New South Wales. *P. rugosum* Strusz 1961, *non* Billings 1858, which differs from the type species in exhibiting peripheral, quadripartite, parricidal budding, in having slightly longer minor septa and typically flat to updomed axial portions of tabulae, seems to belong to the *P. fasciculum* group.

Palaeophyllum proliferum sp. nov.

Plate VIII, figs 1–11

Material. One unsilicified specimen (SUP 43231) comes from the upper part of the Cliefden Caves Limestone, Trilobite Hill, and another (SUP 43230), from the same horizon at the Island. Silicified material comprises six specimens (SUP 43243–45, 43271–73) from the upper part of the Cliefden Caves Limestone, Licking Hole Creek, eight specimens (SUP 29136, 43246–48, 43267–70) from the Quondong Formation, Quondong, and three specimens (SUP 28150–52) from the upper part of the Regan's Creek Limestone. Holotype is SUP 43231 ; other numbered specimens designated paratypes.

Description. The large phaceloid corallum of the holotype is up to 220 mm. across and 150 mm. high. Within the corallum there are small patches of fused (cerioid) corallites and areas showing a cateniform character. Smaller colonies, especially the silicified specimens, are more strictly dendroid. Fine, transverse growth lines, and relatively narrow, shallow, vertical septal grooves and broad, gently raised interseptal ridges are exhibited on external surfaces of some silicified specimens (SUP 29136, 43244). Frequent budding of individual corallites in both larger and smaller coralla is observed. Up to five buds may develop at a particular level (Pl. VIII, fig. 11), but more often two, three or four (Pl. VIII, figs 1, 3, 5–6, 8). Increase is predominantly axial and parricidal, though in a few transverse sections there is also a suggestion of lateral budding (Pl. VIII, fig. 5). Possible rejuvenescence is seen in one corallite (SUP 43243). The calice is moderately deep, steep sided and has a floor which is gently updomed, with a relatively broad, axial depression, to flat. Individual corallites vary in size from 1·5 to 6 mm. in diameter, usually ranging from 2·5 to 5 mm. (on average 3·6–3·9 mm.). Long major septa and very short minor septa are developed, the latter only now and then seen to extend beyond the peripheral stereozone. The major septa most frequently extend to near the axis without touching, leaving an axial space of about 1 mm. But they exhibit considerable variability, sometimes meeting at the axis, and occasionally being quite short and rudimentary. The number of major septa range from 12 to 22, usually 15 to 19 (on average 16–17). The peripheral stereozone is of varying thickness, from 0·1 to 0·6 mm., usually 0·2–0·3 mm., and formed from dilatated peripheral ends of septa and intervening fibrous tissue. The stereozone of a particular corallite usually retains a constant thickness, but, in longitudinal section of the calice, is seen to gradually taper from the calical floor to the top of the calical wall. A number of corallites, especially those in contact, show irregularities in shape, sometimes including prominent attenuations of the corallite wall around adjacent corallites (Pl. VIII, fig. 5). A few corallites exhibit transverse processes, up to 2·5 mm. long, which are suggestive of rudimentary connecting processes. Altogether there seems to be a remarkable degree of plasticity in size and shape of the corallites of this species, and most active budding.

Tabulae are updomed, with prominent axial depression, to flat, spaced from 6 to 10 in 5 mm. vertically. They are mainly complete, but there are also a few incomplete tabulae (tabellae) usually near or associated with a division. Tabulae become irregular and incomplete, even absent altogether, in areas of active increase. The width of the axial depression is from 1·0 to 1·5 mm.

Remarks. The species of *Palaeophyllum* from Ordovician limestone near Gunningbland (Webby, 1969, p. 642), previously thought to possibly be conspecific with *P. proliferum*, is now regarded as distinct. Specimens (SUP 43261–63) of the Gunningbland species have similar dimensions, but differ in having more widely spaced corallites and much less prominent budding.

P. proliferum appears to have closest affinities to *P. thomi* (Hall, 1857) from the " Richmond formation " of El Paso, Texas, and the Aleman Formation of the Montoya Group, New Mexico (Hill, 1959; Flower, 1961). However, *P. proliferum* exhibits more variability in the size and shape of the corallites and different budding. Also, in *P. proliferum*, a corallite of 5 mm. diameter has on average 19–21 major septa, whereas in *P. thomi* a corallite of the same dimensions has 21–23 major septa.

Palaeophyllum crassum sp. nov.

Plate IX, figs 1–3

Material. Holotype (SUP 43237) from tributary on the south-east side of Canomodine Creek, in the upper part of the Cargo Creek Limestone.

Description. The corallum is dendroid-phaceloid, more than 85 mm. across and 25 mm. high. Corallites are mainly from 6 to 12 mm. in diameter (on average 8–9 mm.). Septa are of two orders, the major usually extending to 0·5–1·2 mm. of the axis, and seem to form, with the downturned tabulae, an aulos-like structure, from 1 to 3 mm. across. The minor septa vary from barely protruding beyond the septal stereozone to extending about 1 mm. in from the margin of the stereozone. The total number of septa is from 44 to 54 (on average 48–50). The peripheral stereozone ranges from 0·5 to 1·1 mm. (usually 0·7–0·8 mm.) thick, and seems to be formed from thickening of septa at their bases with intervening fibrous tissue. Long, slightly wavy, major septa are developed, which thin markedly just inside stereozone, and then taper more gradually towards inner ends.

There is a tendency for the development of well differentiated axial and peripheral regions, the axial region occupying about one-fifth to one-third of the total corallite diameter. Tabulae are mainly complete, gently arched across broad peripheral region with slight downturn at peripheral edge, and more sharply flexed across U-shaped axial depression. Occasional incomplete tabulae occur, and are usually restricted to peripheral areas and margins of the axial depression. Tabulae are spaced from 7 to 10 in 5 mm. vertically, with slightly more in peripheral regions (9–11) than in axial areas (7–9), due to the additional incomplete tabulae in peripheral areas. Many of the complete and incomplete tabulae meet or almost join in the downward flexure at the margin of the axial depression, forming, together with the inner ends of the major septa, the aulos-like structure.

Remarks. A poorly preserved species of *Palaeophyllum* from the upper part of the Canomodine Limestone, on the south bank of the Belubula River, east of Cranky Rock, compares with *P. crassum* but, as the specimen (SUP 43264) shows, it has much longer minor septa. A different species occurs in the upper part of the Ballingoole Formation, Bowan Park Group, at Malachi's Hill. As seen in the specimen (SUP 29131), it may be distinguished from *P. crassum* in having less prominent minor septa, and updomed, mainly complete tabulae, more or less flat in the axial region and steeply inclined peripherally.

Possibly, *P. crassum* bears the closest relationships with the type species, *P. rugosum* Billings 1858, from a Black River or lowermost Trenton horizon at Lake St. John, Little Discharge, Canada (Hill, 1959, 1961). However, the New South Wales species is slightly larger, with a thicker stereozone, it has relatively more septa, and a more prominent axial, aulos-like structure involving the major septa and tabulae.

Palaeophyllum macrocaule sp. nov.

Plate IX, figs 4–10

Material. Six specimens (SUP 43233–36, 43274–75) from limestone and one specimen (SUP 29130) from underlying breccias at the top of the Malachi's Hill Beds, north-east of Malachi's Hill. Holotype is SUP 43236 ; other numbered specimens designated paratypes.

Description. The corallum is phaceloid, up to 170 mm. across and 185 mm. high. Peripheral, non-parricidal budding well represented (Pl. IX, figs 6, 8), usually one bud at a time, but in one specimen (SUP 43274), two peripheral buds developed in adjacent quadrants of the corallite. The calice appears to be steep sided and moderately deep, with an updomed floor. Corallites are variable in size, from 2·5 to 7·0 mm. in diameter (on average 4·5 mm.). The septa are differentiated into major and minor, the major commonly extending to near the axis, but may reach the axis or, on the other hand, may barely extend beyond one-half the distance to the axis. In some corallites, especially those with larger diameters and major septa reduced in length, one septum, possibly the cardinal, may be elongated to form an axial, columella-like structure (Pl. IX, figs 5, 9). These blade-like axial structures are not consistently aligned in one direction within an individual corallum, perhaps implying that they do not consistently form from the same (cardinal ?) septum unless, during growth, there is some rotation of individual corallites. This long septum tends to be more dilatated in the axial region than in the periaxial region, and occasionally it appears to be fused with the opposite septum. Sometimes, because of thinning in the periaxial region, it almost appears as an isolated element. The total number of septa is from 28 to 46 (on average 38–40). Major and minor septa are much dilatated in the peripheral zone. They taper rapidly just inside the peripheral stereozone, and then more gradually towards their inner ends. The stereozone is formed from the thickening of peripheral edges of septa and possibly intervening fibrous tissue. In specimens exhibiting smaller corallites, the peripheral stereozone is usually 0·2–0·4 mm. thick, in larger corallites, 0·5–0·6 mm. thick. The minor septa are of variable length, typically nearly one-half the length of the major.

Tabulae are close spaced, having a gently to steeply updomed form. Both complete and incomplete tabulae are represented. In one corallite of the holotype, some 45 mm. high, the tabulae exhibit variation from very gently convex to highly domed forms, these latter sometimes exhibiting a shallow, narrow, axial depression, 1·0 to 1·5 mm. wide, and narrow peripheral troughs (Pl. IX, fig. 4). In another specimen (SUP 29130), the tall domes change to low domal and flat (even slightly sagging) forms. Incomplete tabulae are commonly developed and may be situated axially or peripherally. They are usually of variable size. From 8 to 13 tabulae are spaced in 5 mm. vertically (on average 10–11 in 5 mm.).

Remarks. Although in the material studied it seems possible to recognize larger and smaller varieties, graphical representation of plots of corallite diameter and number of septa shows a fairly even spread of values and no pronounced twofold concentration. The thicker peripheral stereozone (0·5–0·6 mm.) and columella-like axial structure may have developed to strengthen the colonies with larger corallites.

A specimen (SUP 43232) of the species of *Palaeophyllum* from the Trelawney Beds of northern New South Wales compares with *P. macrocaule*, having corallites with a similar diameter and septal number, but with very short minor septa, barely protruding beyond the peripheral zone, major septa usually almost meeting at the axis without an axial structure, and flatter tabulae, especially in peripheral regions, and slightly wider spacing (9–10 in 5 mm. vertically).

Ivanovskij's (1969) *P.* ex gr. *lebediensis* from the Upper Ordovician (Ashgillian) of the Siberian Platform bears a number of basic differences from the type material of *P. lebediensis* described by Čerepnina (1960) from the Upper Ordovician of Gornyj Altai and Gornaja Šorija. Čerepnina described *P. lebediensis* as having a corallite diameter of 10–18 mm., septa of two orders, the major numbering from 35 to 47 (though in her figured specimens of larger corallites, from 9–11 mm. in diameter, I have only counted 31–33 major septa), and tabulae spaced 5–6 in 5 mm. vertically. On the other hand, Ivanovskij (1969, pl. 10, fig. 2*a*-*b*) depicted a form from the Siberian Platform having corallites of 5·5–7·0 mm. diameter, 21–23 major septa, minor septa barely showing, and tabulae much more closely spaced (9–12 in 5 mm.), including many incomplete elements. This form seems to be a quite distinct species, though it should be retained in the *P. lebediensis* species group. It bears very close resemblances to *P. macrocaule*, differing only in lacking the columella-like axial element and in having less well developed minor septa.

ACKNOWLEDGEMENT

The author has been assisted by funds from the Australian Research Grants Committee and a Sydney University Research Grant.

References

BANKS, M. R., 1965.—East, Central, North-west and West Tasmania. *In* Smith, E. M., and Williams, E. (Eds.), *Geological Excursions for the Australian and New Zealand Association for the Advancement of Science.* 38th Congress, 16–20 August 1965. Pp. 35–44. Dept. Mines Tasm., Hobart.

BILLINGS, E., 1858.—Report for the year 1857. *Geol. Surv. Canada, Rept. Prog., 1857.*, pp. 147–192.

Čerepnina, S. K., 1960.—Podklass Tetracoralla (Rugosa). *In* Khalfin, L. L. (Ed.), Biostratigrafija paleozoja Sajano-Altajskoj Gornoj oblasti. Tom I, Nižnij Paleozoj. *Tr. sib. naučno-issled. Inst. Geol. Geofiz. miner. Syr.*, 19 : 387–393.

Flower, R. H., 1961.—Part I. Montoya and related colonial corals. *Mem. Bur. Min. Res. New Mexico*, 7 : 1–97.

Hall, J., 1857.—Geology and Palaeontology of the Boundary. *In* Emory, W. H., *United States and Mexican Boundary Survey Report*, 1 (2), pp. 101–140, 167–174, pl. 20. Washington.

Hill, D., 1959.—Some Ordovician corals from New Mexico, Arizona, and Texas. *Bull. Bur. Min. Res. New Mexico*, 64 : 1–25.

————, 1961.—On the Ordovician corals *Palaeophyllum rugosum* Billings and *Nyctopora billingsii* Nicholson. *Geol. Surv., Canada, Bull.*, 80 : 1–7.

Ivanovskij, A. B., 1965.—Stratigrafičeskij i paleobiogeografičeskij obzor rugoz ordovika i silura. *Inst. Geol. Geofiz. Sib. Otd. AN. SSSR.*, pp. 1–119.

————, 1969.—Korally semejstv Tryplasmatidae i Cyathophylloididae (Rugozy). *Inst. Geol. Geofiz. Sib. Otd. AN. SSSR.*, pp. 1–112.

Kutorga, S., 1837.—*Zweiter Beitrag zur Geognosie und Paläontologie Dorpat's und seiner nächsten Umgebungen*, pp. 1–51. St. Petersburg.

Nicholson, H. A., and Etheridge, R., 1878.—A monograph of the Silurian fossils of the Girvan district in Ayrshire. Vol. I, Fasc. I, pp. 1–135. Edinburgh and London.

Packham, G. H., 1968.—The Lower and Middle Palaeozoic stratigraphy and sedimentary tectonics of the Sofala-Hill End-Euchareena region, N.S.W. Proc. Linn. Soc. N.S.W., 93 : 111–163.

————, 1969.—Ordovician system. The geology of New South Wales. *J. geol. Soc. Aust.*, 16 : 76–103.

Philip, G. M., 1966.—The occurrence and paleogeographic significance of Ordovician strata in Northern New South Wales. *Aust. J. Sci.*, 29 : 112–113.

Semeniuk, V., 1970.—The Lower-Middle Palaeozoic stratigraphy of the Bowan Park area, Central-Western New South Wales. *J. Proc. Roy. Soc. N.S.W.*, 103 : 15–30.

Sinclair, G. W., 1961.—Notes on some Ordovician corals. *Geol. Surv. Canada, Bull.*, 80 : 9–18.

Stevens, N. C., 1956.—Further notes on the Ordovician formations of Central Western New South Wales. *J. Proc. Roy. Soc. N.S.W.*, 90 : 44–50.

Strusz, D. L., 1960.—The geology of the parish of Mumbil, near Wellington, N.S.W. *J. Proc. Roy. Soc. N.S.W.*, 93 : 127–136.

————, 1961.—Lower Palaeozoic corals from New South Wales. *Palaeontology*, 4 : 334–361.

Troedsson, G. T., 1928.—On the Middle and Upper Ordovician faunas of northern Greenland, Part II. *Meddel. om Grønland*, 72, 198 pp.

Wang, H. C., 1948.—Notes on some rugose corals in the Gray collection, from Girvan, Scotland. *Geol. Mag.*, 85 : 97–106.

Webby, B. D., 1969.—Ordovician stromatoporoids from New South Wales. *Palaeontology*, 12 : 637–662.

————, 1971.—The new Ordovician genus *Hillophyllum* and the early history of rugose corals with acanthine septa. *Lethaea*, 4 : 153–168.

———— and Semeniuk, V., 1969.—Ordovician halysitid corals from New South Wales. *Lethaea*, 2 : 345–360.

EXPLANATION OF PLATES

Plate viii

Figs 1–11. *Palaeophyllum proliferum* sp. nov. 1–5, SUP 43231, holotype, upper part of the Cliefden Caves Limestone, Trilobite Hill. 1, transverse section, × 3, showing bipartite and tripartite parricidal increase. 2, longitudinal section, × 3, exhibiting axial, parricidal division. Note variability of the tabulae, including irregular, incomplete forms in areas of active budding. 3, transverse section, × 4, showing bipartite and quadripartite mode of budding. 4, longitudinal section, × 4, showing typical form of tabulae. 5, transverse section, × 4, illustrating bipartite and tripartite, parricidal increase, and irregular, attenuated shape of some corallites in contact. 6–9, silicified specimens, paratypes, from Quondong Formation, Quondong. 6, SUP 43246, × 2, oblique view showing budding with " daughter " corallites not occupying entirely all the space of the original " mother " corallite. 7, SUP 43247, × 2, side view of branching colony. 8–9, SUP 43248, top and side views of specimen showing quadripartite division. Note the four " daughter " corallites do not occupy entirely the space of the former " mother " corallite. 8, × 3. 9, × 2. 10–11, silicified specimens, paratypes, from upper part of Cliefden Caves Limestone, Licking Hole Creek, × 2. 10, oblique view of a colony encrusted by a heliolitid coral. 11, oblique-side view of dendroid colony. Note the branch at the right produces five buds.


1


2

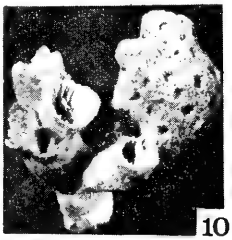

3

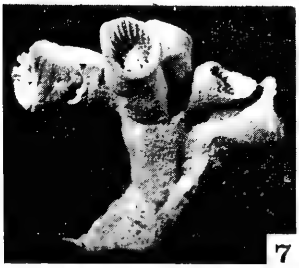

4

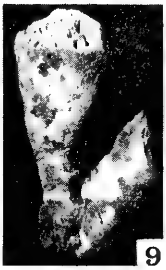

5


6

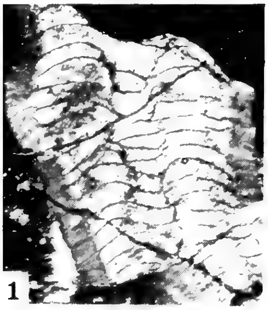

8


10


7

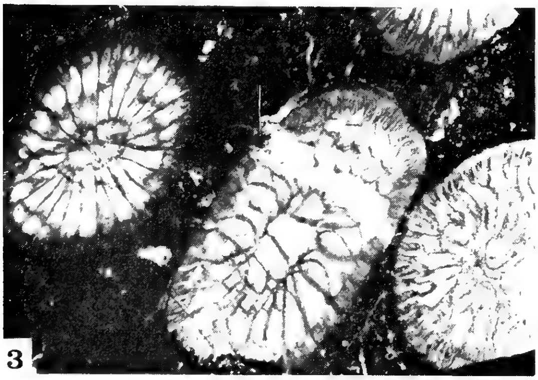

9

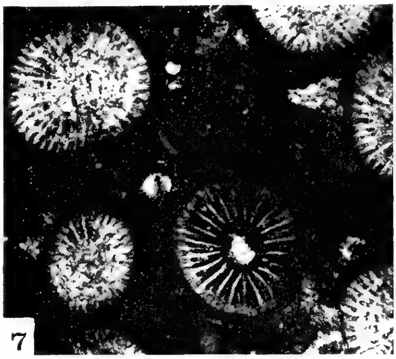

11


1


2

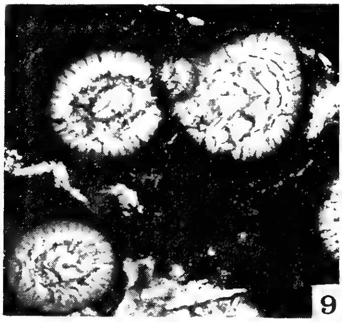

4

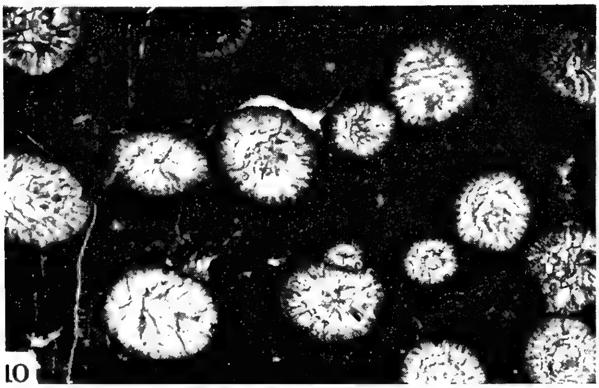

3


7


8


5


9


10

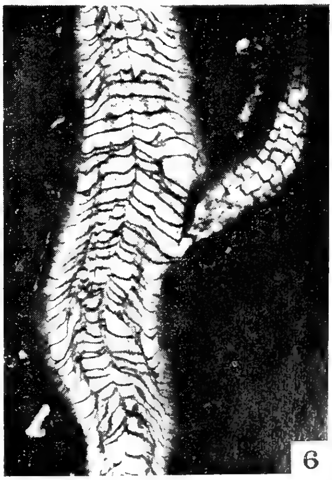

6

PLATE IX

Figs 1–3. *Palaeophyllum crassum* sp. nov., SUP 43237, holotype, from the upper part of the Cargo Creek Limestone, south-east of Canomodine Creek. 1, longitudinal section, ×4. 2, transverse and longitudinal section, ×3. 3, transverse section, ×3. Note the centrally situated corallite is intersected slightly obliquely, and shows the aulos-like structure clearly.

Figs 4–10. *Palaeophyllum macrocaule* sp. nov. 4–6, SUP 43236, holotype. 4, longitudinal section, ×3. 5, transverse section, ×4, showing axial, columella-like structures in relatively large corallites. 6, longitudinal section, ×3, exhibiting peripheral, non-parricidal budding. 7, SUP 43235, paratype, ×4, transverse section showing colony with relatively smaller corallites. Note well-defined major and minor septa. 8, SUP 43275, paratype, ×3, longitudinal section showing peripheral, non-parricidal increase. 9, SUP 29130, paratype, ×3, transverse section showing corallite with a peripheral bud. 10, SUP 43233, paratype, ×3, transverse section exhibiting typical form of corallum, with a peripheral bud off one corallite. Figs 4–8, 10 are from the limestone at the top of the Malachi's Hill Beds, north-east of Malachi's Hill. Fig. 9 is from the breccias just beneath the limestone.

The *Proceedings of the Linnean Society of New South Wales* contain original papers relative to "the Science of Natural History in all its branches", and reports of business transacted at the meetings of the Society.

NOTES AND INSTRUCTIONS FOR AUTHORS

Original papers may be submitted for consideration for publication in the Society's Proceedings. Submission of a manuscript must imply that the contents are original and have not been published previously in the same, similar, or abbreviated form, and that no similar paper is being or will be submitted for publication elsewhere until it has been either (*a*) not accepted for publication by the Society or (*b*) withdrawn by the author.

Papers submitted should embody the results of a significant piece of work. Interim reports, serialized studies and student theses should not be submitted.

Papers are accepted for publication (or otherwise) by the Council of the Society after taking into consideration advice received from at least one referee. The decision of Council is final.

Once accepted for publication a paper becomes the property of the Society, and copyright is vested in the Society. Reproduction of the author's synopsis in abstracting journals is authorized.

A paper may be withdrawn by the author at any time prior to acceptance.

Papers may be submitted by members or non-members of the Society but a paper submitted by a non-member must be communicated by a member of the Society, and will not ordinarily be considered for acceptance before July in each calendar year.

SUBMISSION OF MANUSCRIPTS

Manuscripts should be forwarded to the Secretary, The Linnean Society of New South Wales, 157 Gloucester Street, Sydney, N.S.W. 2000.

Text and illustrations must be submitted in duplicate. The illustrations may be duplicated by any acceptable clear method and the duplicate set need not necessarily be identical in size with the originals. The author should retain a third copy for checking proofs. If a paper is not accepted for publication, the original copy of the typescript and illustrations will be returned to the author, but the duplicate copy may be retained by the Society.

Owing to the ever growing costs of publication, authors are requested to write their papers clearly and concisely and exercise all reasonable economy in the number and form of illustrations and tables.

Grants towards the cost of publication should be secured wherever possible from the author's own institution or elsewhere; contributions from authors, especially non-member authors, may be requested at Council's discretion, particularly in the case of lengthy papers, or those with numerous illustrations or tables.

Manuscripts must be submitted in final, fully corrected form. Authors may be liable for the cost of proof corrections (if allowed) if the number of alterations and corrections is considerable. Authors are urged to submit their paper to a colleague for constructive criticism prior to final typing and submission for publication.

MANUSCRIPTS

Papers should be typewritten, double spacing throughout, on one side of quarto or foolscap paper, with at least one-inch margins all round. The desired position of all text-figures, maps and tables may be indicated in the margin. All pages should be numbered serially and securely fastened together. Papers should conform to the following general layout as far as practicable or appropriate:

(*a*) *Title.*—The title should be concise but informative. The name(s) of the author(s) and the name of the institution where the work was carried out should follow the title. The name of a new taxon of plants or animals should not be included in the title. A short title appropriate for the running heading of subsequent pages may be suggested. The title, etc., should be on a *separate page* at the commencement of the typescript.

(*b*) *Synopsis.*—A concise abstract (without abbreviations), preferably consisting of not more than about 200 words, should be supplied on a *separate sheet* and in *triplicate.* It should be complete in itself and indicate the scope of the work. It will be printed below the title of the paper and in the Society's Abstract of Proceedings; it will be available for reprinting by abstracting journals.

(*c*) *Table of Contents.*—This should give the complete hierarchy of headings and sub-headings used in the subject-matter of the paper. It should be supplied on a *separate sheet* for guidance of the editor and will not ordinarily be printed.

(*d*) *Introduction*, followed by the *Subject Matter* of the paper. Papers may be divided into sections described by short headings.

(*e*) *Discussion, Conclusions or Summary* (if necessary).—This should summarize the conclusions reached rather than be a précis of the paper as a whole (cf. Synopsis).

(*f*) *Acknowledgements*, if any.

(*g*) *References.*—The author, who is alone responsible for their accuracy, should carefully check all references against the text, to ensure especially that:

(i) The spelling of authors' names is consistent, and the dates, volume numbers and page numbers are correct.

(ii) All authors quoted in the text are included in the list of references.

References should be cited in the text by the author's name and date, e.g., Bullough (1939) or (Bullough, 1939) according to context, and listed alphabetically under References thus:

Bullough, W. S., 1939—A Study of the Reproductive Cycle of the Minnow in Relation to the Environment. *Proc. zool. Soc. Lond.*, 109, A: 79-108.

If more than one reference by the same author(s) published in the same year is cited, use a, b, etc., after the year in both text and list, e.g., Bullough (1939 a).

Titles of books must be given in full together with the place of publication, name of publisher and indication of edition if other than the first.

Latin names of plants and animals (genera, species and their subdivisions) should be underlined to indicate italics. An initial capital letter must be used for Latin names of orders, families and similar names, but these should not be underlined.

Abbreviations.—Only standard abbreviations should be used; authors should refer to the British Standard 1991: Part 1, 1967. Recommendations for Letter Symbols, Signs and Abbreviations. The abbreviations of names of periodicals should conform to those in the World List of Scientific Periodicals.

Footnotes should be avoided as far as possible.

Codes of Nomenclature.—The Botanical and Zoological Codes of Nomenclature must be strictly followed. If a new taxon is described, the institution in which the type material is deposited must be indicated.

Language.—Papers in languages other than English are unlikely to be accepted for publication. Foreign authors are urged to seek assistance, if necessary, in rendering the paper in fluent English prior to submission.

Measurements must be expressed in the metric system as far as practicable, and exclusively in scientific description.

Illustrations and Tables

The maximum dimensions available for either text-figures or plates are 20 x 12.5 cm.

Black and white drawings and diagrams for text-figures should be in Indian ink on smooth white card such as Bristol board the lines cleanly drawn, and due attention paid to the consequences of reduction. Graphs should similarly be in Indian ink on white card, or on faint blue-lined co-ordinate paper. Maps should be in Indian ink on white card or tracing linen; if the latter the linen should not be folded. Maps should be of a size and scale that can be conveniently reduced to the size of a single page.

It is desirable that all black and white illustrations should be drawn 1½-2 times the size that they will appear in print.

Photographs for half-tone plates should be the size required for final reproduction or slightly larger, printed on glossy paper, of good contrast and best quality. A number of small photographs can be arranged to form one plate.

Illustrations for colour reproduction cannot be accepted unless the author meets the difference in cost between black and white and colour reproduction.

Illustrations of all kinds should bear the author's name and the number of each, lightly pencilled on the back, and their required orientation clearly indicated.

Legends for illustrations should be typed on separate sheets at the end of the manuscript. Great care should be taken in stating magnifications of illustrations, making it clear whether numbers quoted refer to before or after reduction.

Tables.—Tables should be numbered consecutively and referred to specifically in the text by number. Each table, together with a heading descriptive of its contents, should be submitted on a separate sheet. Elaborate tables should be avoided.

General

Proofs.—A set of galley proofs will be forwarded to the author who should correct and return them promptly to the Secretary.

Reprints.—Twenty-five reprints are supplied free to authors who are members of the Society. Additional reprints may be ordered at the authors' expense, if desired. No free reprints are supplied to non-members who may, however, order the number required at their own expense. Orders for reprints should be placed with the Secretary immediately after the paper has been accepted for publication. Orders received after the paper has been printed may not be accepted.

Joint Authorship.—In the case of papers by more than one author, one of them must accept responsibility for all correspondence with the Society regarding the paper.

AUSTRALASIAN MEDICAL PUBLISHING CO. LTD.
71-79 ARUNDEL ST., GLEBE, N.S.W., 2037

Copies of the PROCEEDINGS OF THE LINNEAN SOCIETY OF NEW SOUTH WALES (with the exception of a few Volumes and Parts) may be purchased from the Society, Science House, 157 Gloucester Street, Sydney, N.S.W., 2000.

Current charges for the PROCEEDINGS are:

Volumes—$16.00 each for 1st Series (Volumes 1–10); $11.00 each for 2nd Series (Volumes 11–20) and all subsequent volumes.

Parts—$5.00 each for all back parts; $4.00 each for current Parts. For volumes of 5 or 6 Parts, $1.00 each for first and last Parts.

Prices do not include postage.

Subscription to the PROCEEDINGS—$11.00 per volume, plus 80c postage—$11.80.

All prices are in Australian currency.

These charges may be revised from time to time, and inquiries should be addressed to The Secretary, Linnean Society of New South Wales, Science House, 157 Gloucester Street, Sydney, N.S.W., 2000, Australia.

The Society's PROCEEDINGS are printed and published for the Society by the Australasian Medical Publishing Co., Ltd., 71–79 Arundel Street, Glebe, N.S.W., 2037.

Proceedings, Volume 97, Part 2, 1972

CONTENTS

Proceedings of the Linnean Society of New South Wales

Issued 8th January, 1973

VOLUME 97
PART 3
No. 431

Registered for posting as a periodical—Category A.

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, 1972–73

President
H. G. Cogger, M.Sc., Ph.D.

Vice-Presidents
L. A. S. Johnson, D.Sc.; T. G. Vallance, B.Sc., Ph.D.;
N. G. Stephenson, M.Sc., Ph.D.; R. C. Carolin, B.Sc., Ph.D., A.R.C.S.

Honorary Treasurer
Joyce W. Vickery, M.B.E., D.Sc., F.L.S.

Secretary
Mrs. Ruth J. Inall

Council

D. J. Anderson, Ph.D.
D. T. Anderson, D.Sc.
R. K. Bamber, F.S.T.C.
Barbara G. Briggs, Ph.D.
W. R. Browne, D.Sc., F.A.A.
R. C. Carolin, B.Sc., Ph.D., A.R.C.S.
H. G. Cogger, M.Sc., Ph.D.
Mary M. Hindmarsh, B.Sc., Ph.D.
L. A. S. Johnson, D.Sc.
Elizabeth C. Pope, M.Sc., C.M.Z.S.
P. J. Stanbury, Ph.D.
N. G. Stephenson, M.Sc., Ph.D.
F. H. Talbot, M.Sc., Ph.D., F.L.S.
E. LeG. Troughton, F.R.Z.S.
P. G. Valder, B.Sc.Agr., Ph.D.
T. G. Vallance, B.Sc., Ph.D.
Joyce W. Vickery, M.B.E., D.Sc., F.L.S.
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.

Linnean Macleay Fellow of the Society as from 1st July, 1971
Mrs. Lynette Anne Moffat, B.Sc.Hons.

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

TWO NEW FUR-MITES (ACARI: ATOPOMELIDAE) FROM AN AUSTRALIAN TIGER CAT (MARSUPIALIA: DASYURIDAE)

Alex Fain* and Robert Domrow†

[Accepted for publication 22nd March 1972]

Synopsis

Dasyurochirus (*D.*) *major*, n. sp. and *Labidopygus australiensis*, n. g., n. sp. (Atopomelidae) are described from a tiger cat, *Dasyurus maculatus* (Kerr) (Dasyuridae).

The listrophoroid mites of Australia and New Guinea have been studied by several authors, notably Gunther, Womersley, and Domrow. A recent revision of the group by Fain (1972) included 63 species in 22 genera.

In this supplementary note, we describe two new species from the same individual tiger cat, one belonging to *Dasyurochirus* Fain, the other representing a new genus. The taxonomic nomenclature is that adopted by Fain (1963).

Genus Dasyurochirus Fain

Dasyurochirus Fain, 1970, *Bull. Annls Soc. r. ent. Belg.*, 106: 277. Type-species *D. biscutatus* Fain, 1970, *ibid.*

Dasyurochirus (*Dasyurochirus*) *major*, n.sp.
(Figs 1–3)

Diagnosis.—This species, known only from the male, differs from *D.* (*D.*) *leprosus* Fain, 1971, in the following points:

1. The body is larger.
2. The postscapular shields comprise transverse bands 4–6μ long and 60–65μ wide, in front of which the postscapular region is not punctate, but in part scaly.
3. The small, clear adanal discs are distinctly larger.
4. The penis is smaller.
5. The sclerotized fork fused to epimera III in front of the genitalia is distinctly longer.
6. The two subapical ventral setae on tibiotarsi III are modified and unequal.

Types.—Holotype male (only known specimen) found attached to fine hair skirting stem of scrotum of tiger cat, *Dasyurus maculatus* (Kerr) (Marsupialia: Dasyuridae), Eccleston, N.S.W., 20.vii.1971, M. D. Murray. In Australian National Insect Collection, C.S.I.R.O., Canberra.

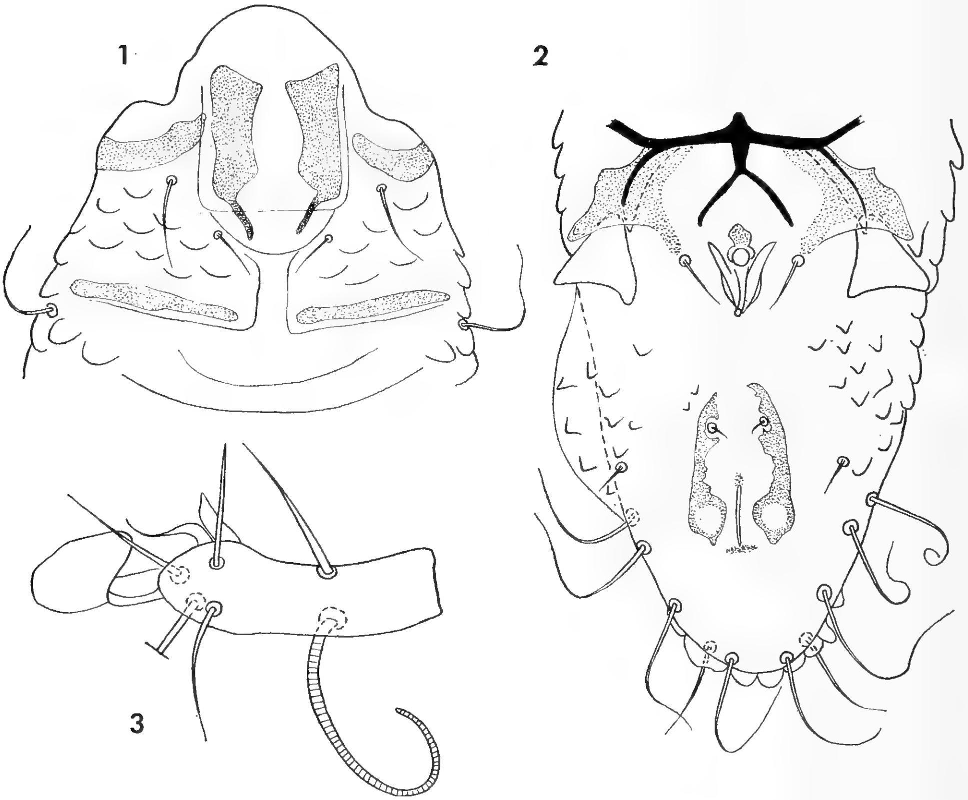
Male.—Idiosoma (including gnathosoma) 435μ long, 164μ wide (maximum). Similar to *D. leprosus*, except as noted above.

---

* Prince Leopold Institute of Tropical Medicine, Antwerp.
† Queensland Institute of Medical Research, Brisbane.

Genus Labidopygus, n. g.

Diagnosis.—This genus is known only from the male and immatures. In the male, the cuticle is largely striate, except for the anterior and posterior regions of the dorsum occupied by punctate shields, and in the central portion of the venter. The prescapular shield is single and oval, and not accompanied by postscapular shield(s). All legs terminate in a sucker, except I, which carry only a short stump, a mere remnant of the ambulacra. Adanal suckers two, small, but well developed. On each side, external to adanal suckers, is a strongly sclerotized, cylindroconical process, directly anteriorly and carrying fine, transverse ridges. These organs serve to clasp the nymph during copulation. Legs IV slightly stronger than III. Tibiotarsi III–IV with two and one strong ventral spine(s), respectively; solenidia set in basal third of segment.



Figs 1–3. *Dasyurochirus major* male. 1, Anterior portion of dorsum. 2, Posterior portion of venter. 3, Tibiotarsus III.

Labidopygus is separable from all other known Australian atopomelid genera by the presence (in the male) of two small, but normally formed, adanal suckers, and two copulatory processes. In the males of other known genera of the region, the adanal suckers are either completely lacking, or modified and (apparently) non-functional (Fain, 1972).

Type-species *L. australiensis* Fain and Domrow.

Labidopygus australiensis, n. sp.

(Figs 4–5)

Types.—Holotype male, five paratype males, and several immatures with same collection data as *D. major*. Holotype and two paratype males in A.N.I.C.; one paratype in P.L.I.T.M.; two paratypes in Queensland Museum.

4

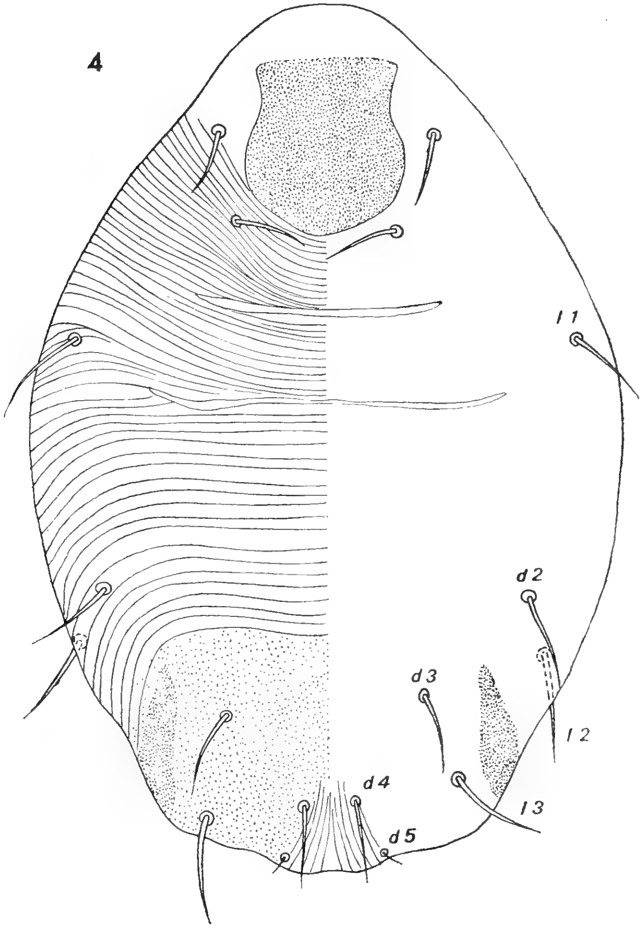


Fig. 4. *Labidopygus australiensis* male. Dorsum.

Male.—Idiosoma (including gnathosoma) 255μ long, 153μ wide (maximum) in holotype; ovoid. Prescapular shield ovate, more or less in form of shield with rounded sides. Hysterosomal shield wider than long, reinforced laterally by more strongly sclerotized areas. Remainder of dorsum transversely striate. Striate grooves of coxae I–II narrow; coxae II with strong triangular process posterolaterally. Epimera III and IV fused medially to form two strong, independent arcs. Penis small, situated at level of coxae IV. Anus ventral, flanked by adanal suckers and copulatory processes detailed above. Dorsal setae moderately long and strong (20–30μ); d_2 set far to side; l_5 120μ long; a_e and a_3 lacking.

5

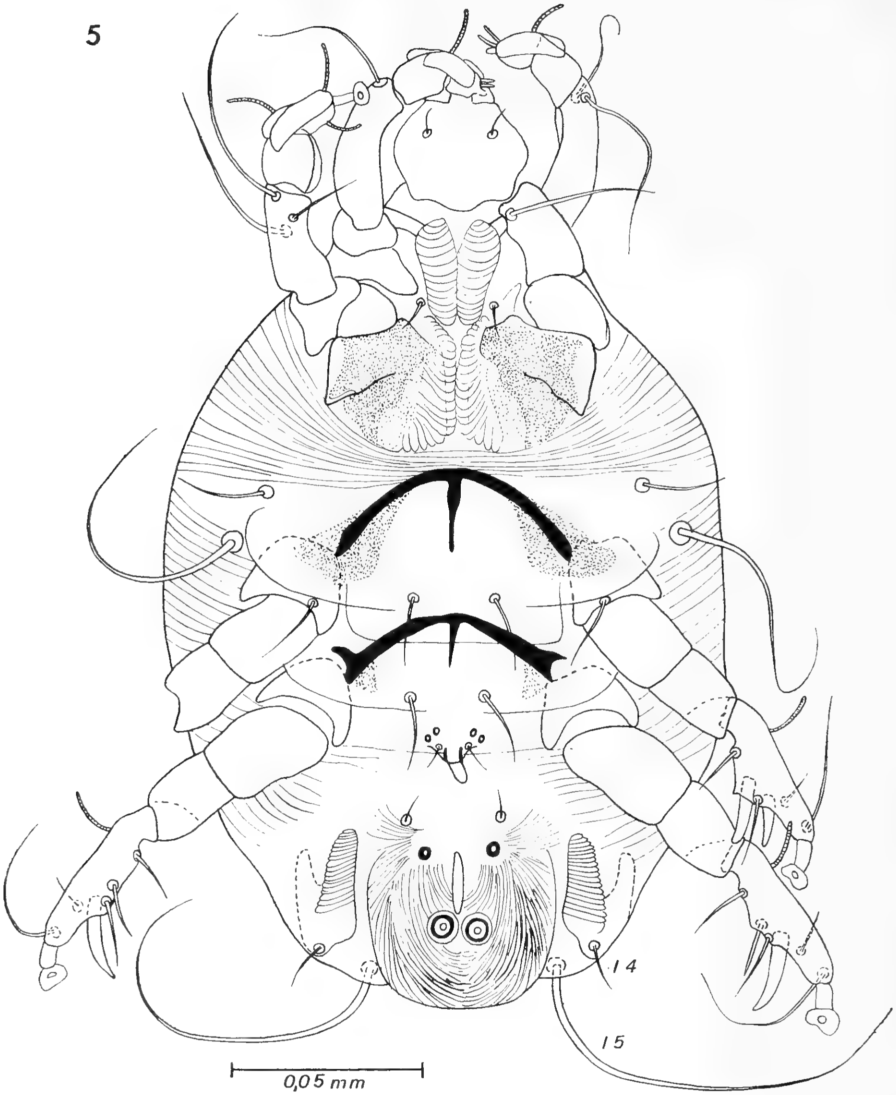


Fig. 5. *Labidopygus australiensis* male. Venter.

ACKNOWLEDGEMENTS

We are grateful to Mr. A. L. Dyce, McMaster Laboratory, C.S.I.R.O., Glebe, for the chance to study these interesting specimens.

References

FAIN, A., 1963.—Les acariens producteurs de gale chez les lémuriens et les singes avec une étude des Psoroptidae (Sarcoptiformes). *Bull. Inst. r. Sci. nat. Belg.*, 39 : 1–125.

————, 1971.—Notes sur quelques Atopomelidae de la région australienne (Acarina : Listrophoroidea). *Revue Zool. Bot. afr.*, 83 : 238–242.

————, 1972.—Les listrophoridés d'Australie et de Nouvelle-Guinée (Acarina : Sarcoptiformes). *Bull. Inst. r. Sci. nat. Belg.*, 48 : 1–196.

FOUR NEW COPEPODS (CRUSTACEA: HARPACTICOIDA, CANUELLIDAE) SIMULTANEOUSLY OCCURRING WITH *DIOGENES SENEX* (CRUSTACEA: PAGURIDEA) NEAR SYDNEY

R. Hamond

[Accepted for publication 21st June 1972]

Synopsis

Sunaristes tranteri nov. sp. is described and compared with the other four undoubted species of this genus, all of which are associated with hermit-crabs. In north-west Europe the only species is the type of the genus, *S. paguri* Hesse; *Pagurus cuanensis* and *Diogenes pugilator* are recorded for the first time as hosts for this species in this area, where the usual host is *P. bernhardus* (the record of *P. prideauxi* as a host for *S. paguri* in British waters is shown to be doubtful). It is shown that variously poorly described canuellids, placed from time to time in *Sunaristes*, are ineligible for generic placement in the basis of existing descriptions; however, the five species here referred to *Sunaristes* form an extremely close-knit group.

Brianola sydneyensis, *B. pori* and *B. elegans* nov. spp. are described; the setal formulae of all six known species of *Brianola* are compared. The taxonomic differences between corresponding swimming-feet in different species are most marked in the first pair of swimming-feet, less so in the second pair, and least of all in the third and fourth pairs. *B. reichi* (Por) is the most aberrant species, but is best left in *Brianola* pending a major revision of the family.

Keys are given to the accepted species of both these genera.

Introduction

The family Canuellidae (for diagnosis see Lang, 1948) comprises harpacticoid copepods of moderate to large size, occurring intertidally or in small depths among benthos. None have yet been recorded in Australian territorial waters, although the "Siboga" took *Canuella curticaudata* off the Aru Islands and *Sunaristes paguri* off New Guinea (Scott, 1909, but see below). The nearest other records of canuellids are from Ceylon (Thompson and Scott, 1903), Mozambique (Wells, 1967), Madagascar (Humes and Ho, 1969), and the Red Sea (Por, 1967); records outside the Indo-West Pacific area are summarized by Lang (1948) and Bodin (1967, list only).

Material and Methods

The four new species described below were collected in two localities, both in the coastal suburbs of metropolitan Sydney.

(1) In Narrabeen Lagoon (approximately 33° 43′ S., 151° 17′ E.), among weeds at the water's edge on 4.x.1969; a single female (the holotype) of *Brianola pori* nov. sp. As far as I can ascertain (see Acknowledgements) no pagurid has ever been found in this lagoon.

(2) In the swimming pool of the C.S.I.R.O. Division of Fisheries and Oceanography (approximately 34° 04′ 30″ S., 151° 08′ 53″ E.). The pool empties directly into Gunnamatta Bay during low tide (although the drainpipe can be

---

* Author's present address: Scaldbeck, Morston, Holt, Norfolk, U.K.

shut off to keep the pool full to any desired level for as long as needed), and is filled during high tide by a centrifugal pump whose inlet is under the boat jetty, just below ELWST and about 20 m. from the pool. The pool is about 30 m. long, 13 m. wide and 3 m. deep, rectangular in shape, and can be filled to the brim; the common Sydney rock-oyster (*Crassostrea commercialis* Roughley and Iredale) is found on the concrete walls, and various small fish (up to about 12 cm. in length) and invertebrates live on the limestone bottom. One of the most conspicuous invertebrates is the small hermit-crab *Diogenes senex* Heller, inhabiting empty shells almost exclusively of the gastropod *Pyrazus ebeninus* Bruguière, although a small percentage live in shells of *Bellastraea* sp. or *Austrocochlea* sp.; no other species of hermit-crab has yet been found in the pool. The following two samples of *D. senex* in their shells were soaked overnight in formalinized seawater, which was then filtered through plankton gauze of pore size 0·3 mm., and were then rinsed with several lots of tapwater, which was also filtered through the same gauze, the filtrate being examined under the binocular microscope.

(*a*) About 200 *D. senex*, collected on 20.xi.1970, yielded 6, 1, 5, 2 *Sunaristes tranteri* nov. sp. (*i.e.* six females of which one was ovigerous, five males, and two copepodites whose sex was not determined; *cf.* Hamond, 1971*a*, 1971*b*), as well as harpacticoids of other families (preserved) and other organisms such as small polychaetes (discarded).

(*b*) About 1,000 *D. senex*, collected on 28.ii.1971, yielded 5, 3, 9, 24 *S. tranteri*, 20, 11, 30, 33 *Brianola pori* nov. sp., 9, 3, 9, 105 *Brianola sydneyensis* nov. sp., and 13, 2, 12, 0 *Brianola elegans* nov. sp., as well as many other harpacticoids (preserved), hydroid polyps apparently rubbed off the *Pyrazus* shells (*Hydractinia* sp. and ? *Campalecium* sp., both preserved), and other invertebrates as before (discarded).

The copepods were dissected and mounted as previously (Hamond, 1969, 1971*b*); the terminology employed and all abbreviations are those in normal use by workers on harpacticoids. Special attention was paid to making drawings of uncompressed entire animals from various aspects, in order to record the somitic ornamentation as exactly as possible; it was also found that the male antennule of *Sunaristes* could not be drawn satisfactorily except in the uncompressed state (Figs 9–11). All figures of females are from the holotypes, and of males from the allotypes, unless otherwise indicated; dissected paratypes are labelled 1, 2, 3, . . . for females and A, B, C, . . . for males, undissected paratypes being without individual designations. Type specimens have been deposited in the Australian Museum, Sydney, under the following registration numbers:

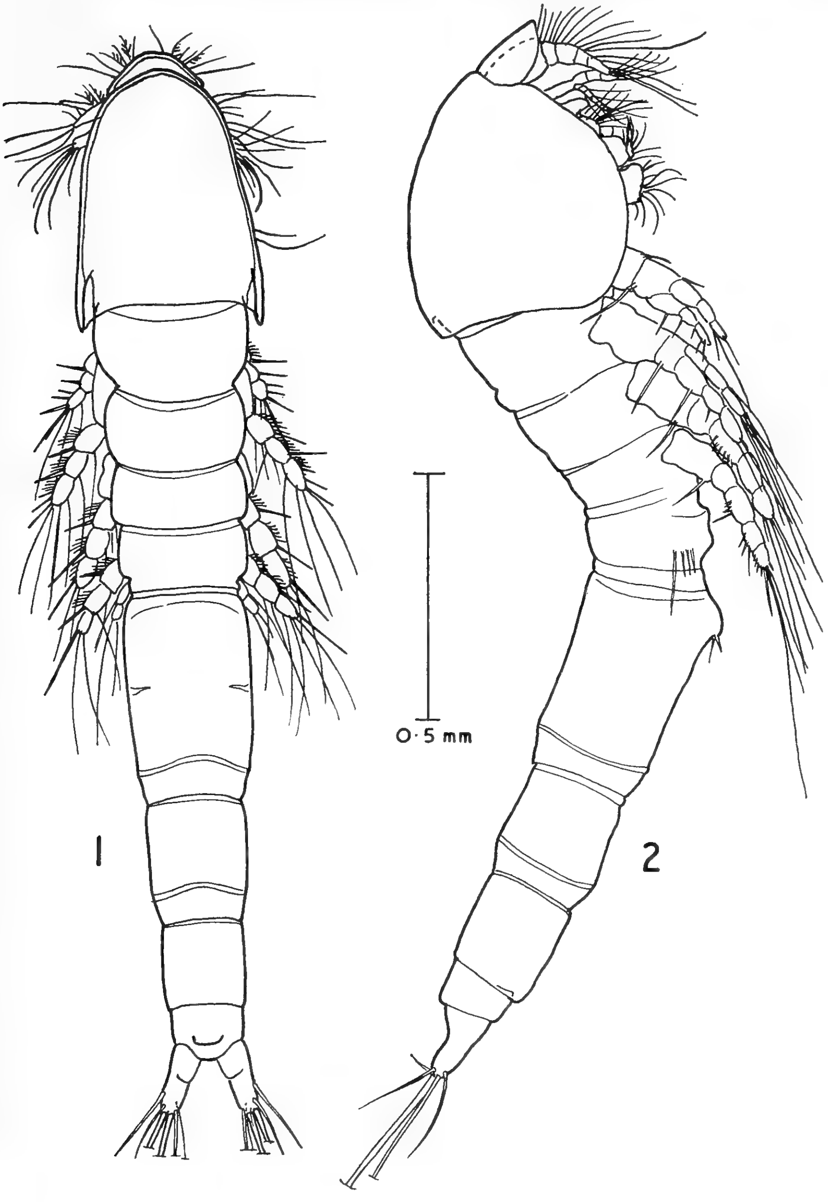
P.18678	*Brianola elegans*, nov. sp.	Holotype, female.
P.18679	*B. elegans*	Allotype, male.
P.18680	*B. sydneyensis*, nov. sp.	Holotype, female.
P.18681	*B. sydneyensis*	Allotype, male.
P.18682	*B. pori*, nov. sp.	Holotype, female.
P.18683	*B. pori*	Allotype, male.
P.18684	*Sunaristes tranteri*, nov. sp.	Holotype, female.
P.18685	*S. tranteri*	Allotype, male.

All the paratypes are being kept in my own collection for comparison with canuellids to be found in future.

Sunaristes tranteri nov. sp.

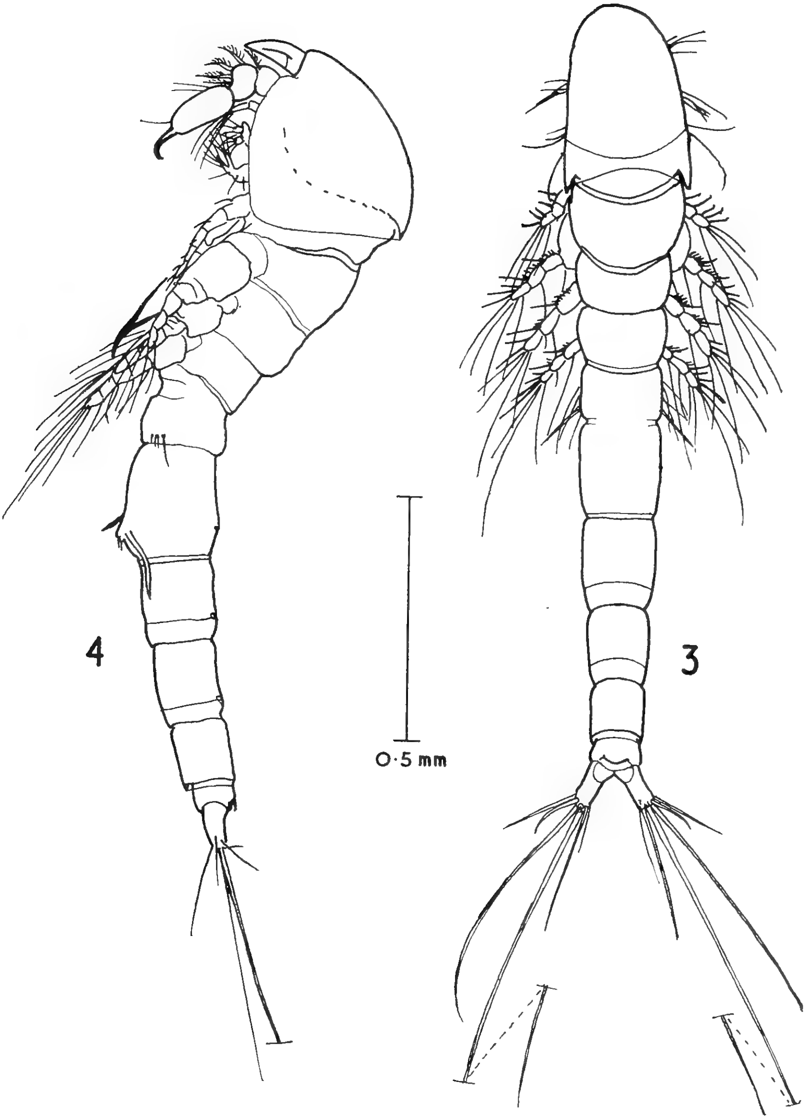
(Figs 1–21)

Female (*holotype*). Length 2·3 mm., measured in side view round the curves, along the axis of each section of the body. Body long and slender, with a high, vaulted prosome which is somewhat compressed laterally (Figs 1, 2).



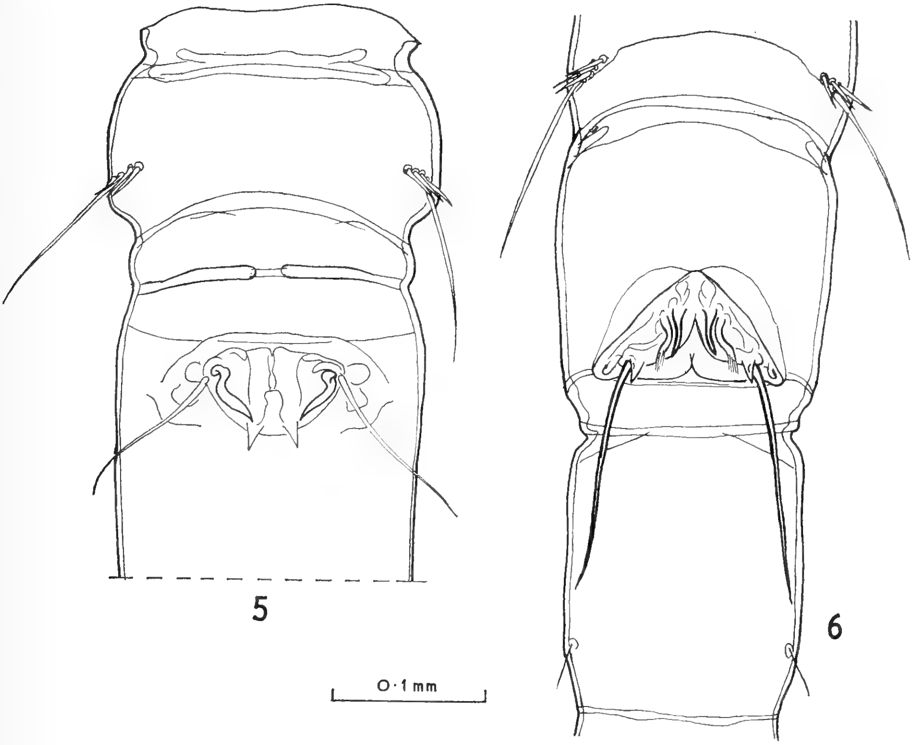
Figs 1, 2.

Rostrum directed downward (Fig. 2), short and broadly rounded (Fig. 8). The rear margin of each abdominal somite bears a few sensillae, but there is no other somitic ornamentation anywhere. Abdominal somites longer than broad (except



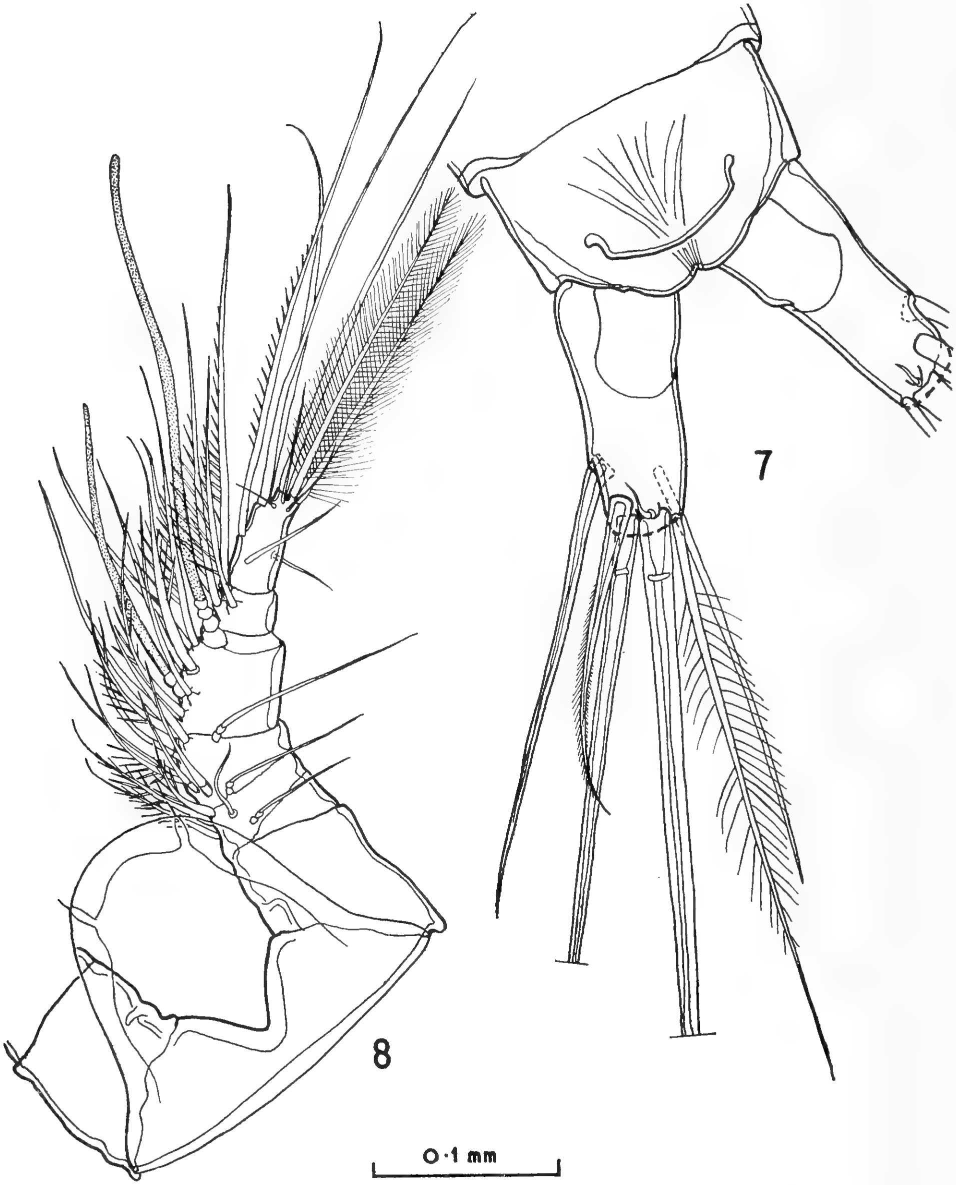
Figs 3, 4.

the anal somite) and cylindrical, separated by conically tapering intersomitic membranes; genital double-somite not divided, genital area as in Fig. 5. Operculum shallowly curved, with a smooth edge. Furcal rami slightly divergent (Fig. 7), the inner wall of each ramus distinctly shorter than the outer. Each ramus bears seven setae (Fig. 7); the two longest are each minutely serrated along the middle third of their outer edges, but are smooth otherwise.



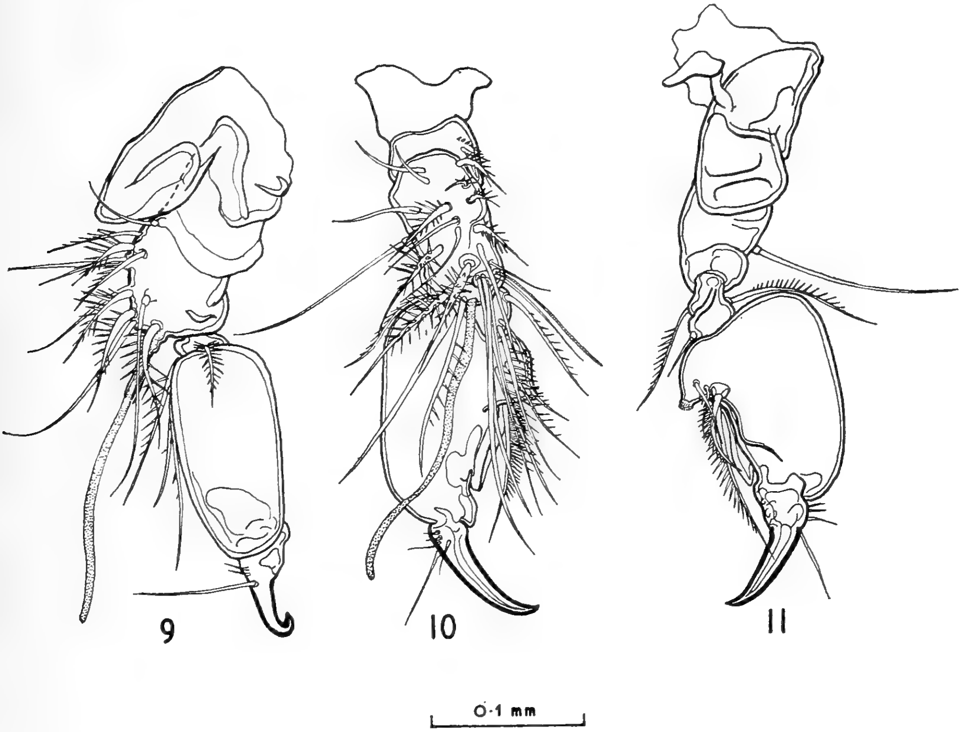
Figs 5, 6.

Antennule (Fig. 8) short and stout, with six indistinct segments, of which the third bears two aesthetascs (the distal of which is much the longest); all the segments except the basal segment carry numerous setae. Antenna (Fig. 12) with one lateral, two lateral and two terminolateral, and six terminal, setae respectively on the three endopod segments; each of the seven exopod segments bears an inner seta, and the distal segment also bears two terminal setae. The basis of the mandibular palp (Fig. 13) has two inner setae and one arising between the rami; the three exopod segments each bear an inner seta and the distal segment also has two terminal setae, while the two endopod segments carry three inner and eight terminal setae respectively.



Figs 7, 8.

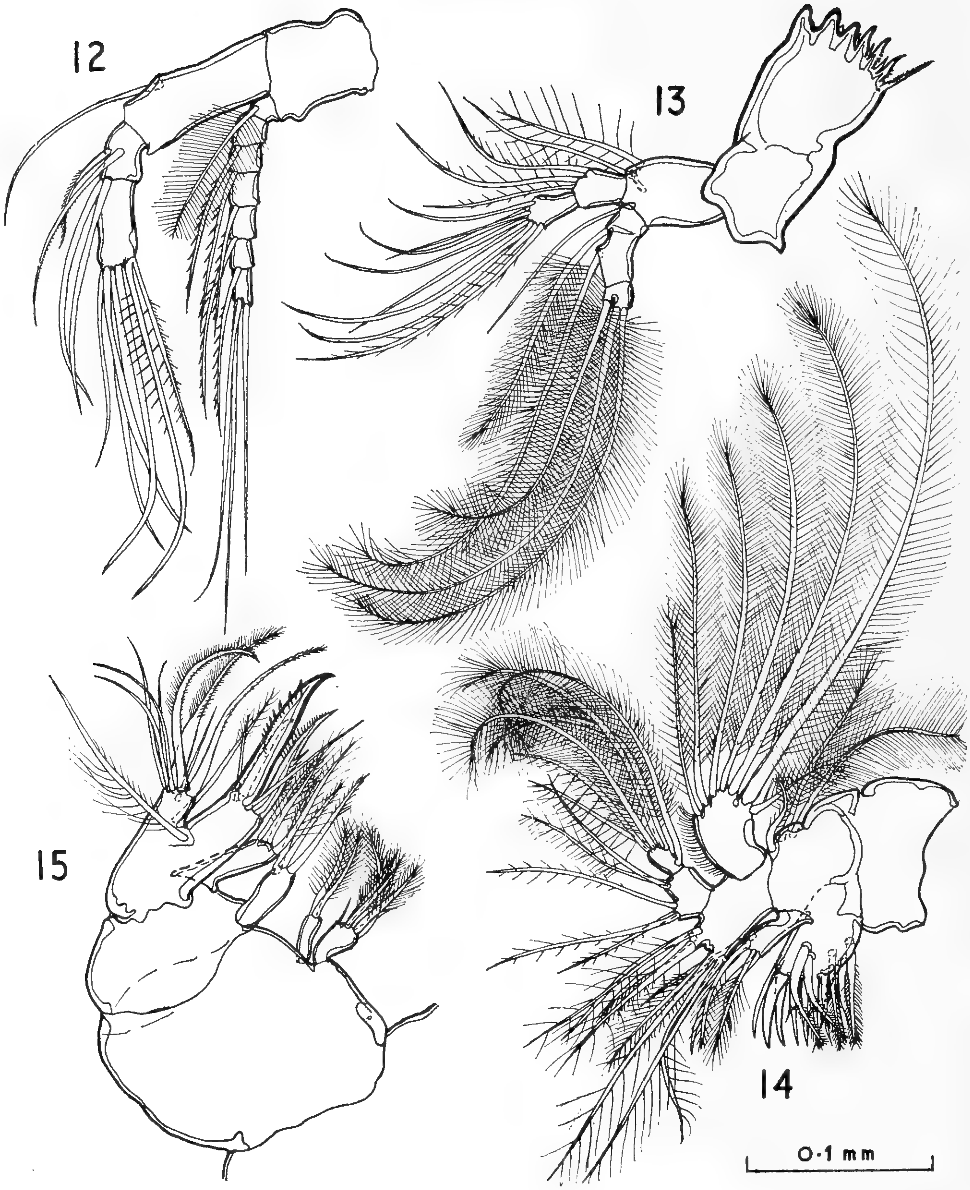
Precoxal arthrite of maxillule (Fig. 14) with a total of ten teeth, smooth setae, and plumose setae (these structures appear to intergrade) along its cutting edge, as well as three palmar setae (two frontal and one abfrontal), all of which are sparsely set with coarse short pinnules. Coxa with three epipodal setae (see below, variability), four setae on the arthrite, and one at the origin of the basis ; basis with four + four inner setae ; the two endopod segments bear five and six setae respectively, and the single exopod segment has seven setae which increase regularly in length from the first (innermost) to the sixth, the seventh being very small.



Figs 9–11.

Maxilla (Fig. 15) with two precoxal endites, bearing five and two setae respectively ; two coxal endites with three setae each ; and a well-developed basal endite prolonged into a heavily built thorn with a row of denticles along its distal margin. Round the base of this thorn are the insertions of two slightly curved spines (smaller copies of the thorn) and two straight slender setae which may or may not be sparsely pinnate near their ends. The endopod is not clearly separated from the basis, nor its segments from one another ; it bears a total of nine setae (of which one is very easily overlooked, being slender and hidden among the others) and the basis has a seta near the insertion of the endopod.

Maxillipede (Fig. 16) with fused coxa and precoxa, but with distinct basis and endopod. The setae are arranged as follows : precoxa, 1 ; coxa, 2 + 4 + 3 ; basis, 2 ; endopod, 11.

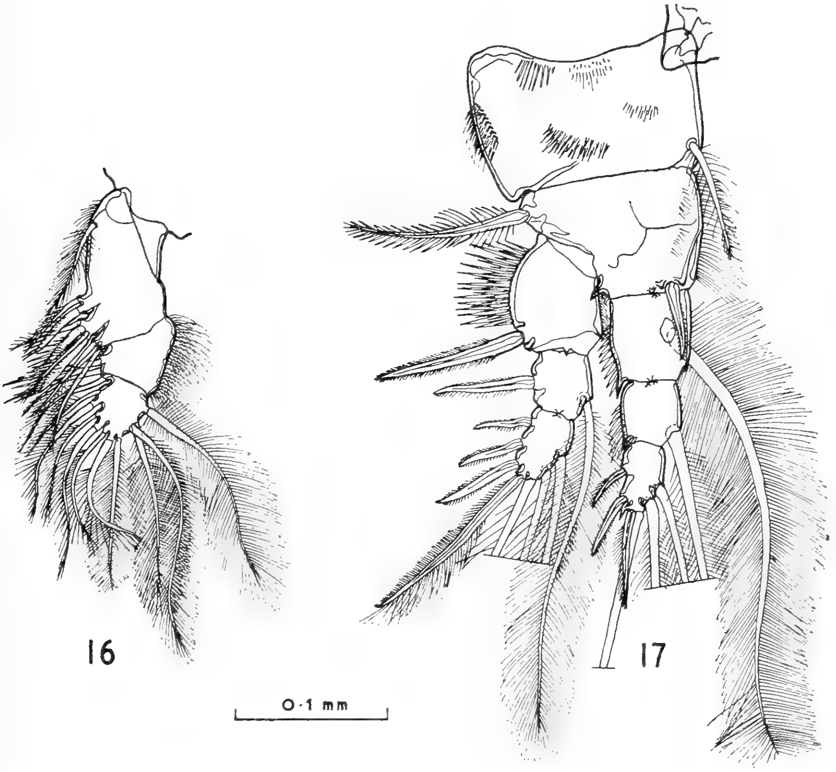


Figs 12–15.

All rami of swimming legs have three segments each ; the endopod is longer than the exopod in P1 and P2, about equally long in P3, and much shorter and slimmer in P4. The inner seta of the first endopod segment in P4 is slightly longer than the entire endopod. Setal formula (*cf.* Por. 1967, p. 109) :

P1 (Fig. 17)		P2 (Fig. 18)		P3 (Fig. 20)		P4 (Fig. 21)	
exp	enp	exp	enp	exp	enp	exp	enp
0.1.7	1.1.6	0.1.7	1.1.5	0.1.5	1.1.3	0.1.4	1.0.3

exactly as in *S. paguri* Hesse (Sars, 1911 ; Humes and Ho, 1969 ; Codreanu and Mack-Fira, 1961 ; own observations) ; the formula 1.1.4, 0.1.3, given by Por (1967, p. 109) for P4 of *S. paguri* is clearly erroneous.



Figs 16, 17.

On every segment of both rami of the swimming legs a comb of spines is either present (+) or absent (–) on the outer surface (as in Humes and Ho, 1969, table II) ; Table 1 of the present paper consists of Humes and Ho's table II together with my own observations.

TABLE 1

Spinulation of Sunaristes *spp.* (*as in Humes and Ho, 1969, table II*)

R=right, L=left, foot of the same pair, of a specimen examined by me; L is left blank except where it differs from R. Variants are placed in brackets

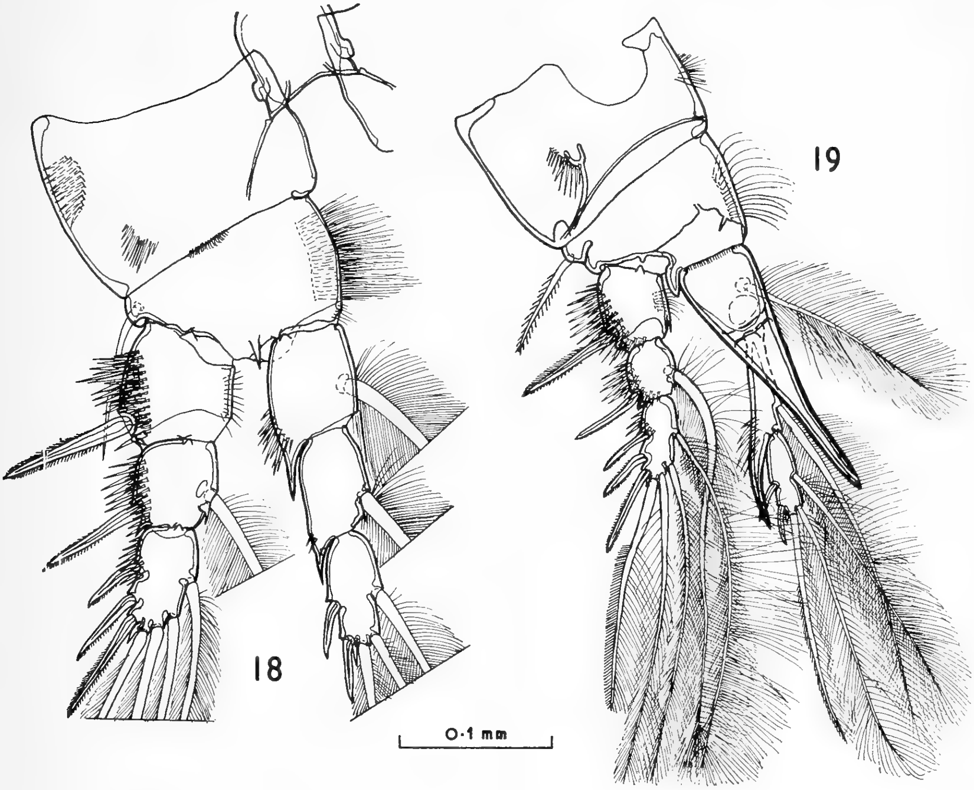
	P1		P2		P3		P4	
	exp	enp	exp	enp	exp	enp	exp	enp
				Females				
S. paguri	+−−	++−	++−	−−−	++−	−−−	++−	−−−
Sunaristes sp. from Auckland.. ..	+−−	++−	+++	+−−	+++	−−−	+++	−−−
S. inaequalis	+−−	++−	+++	++−	+++	−+−	+++	−++ (−+−)
S. tranteri :								
Holotype :				Few				
R	+−−	++−	+++	++−	+++	++−	+++	+−−
L	..	..	..	..	..	..	..	−+−
Paratype 1 :								
R	+−−	++−	+++	+−−	+++	+−−	+++	+−−
L	..	..	..	..	..	..	..	++−
Paratype 2 :								
R	+−−	++−	+++	+−−	+++	++−	+++	−−−
L	(Abnormal)		..	..	..	..	..	..
S. dardani	+−−	++−	+++	++−	+++	−+−	++−	−− (−+)
				Males				
S. paguri :								
Humes and Ho ..	+−−	++−	++−	−+−	++−	++− (−+−) (−−−)	++−	−+− (++−)
Own material :								
R	+−−	++−	++−	−+−	++−	++−	++−	+−−
L	..	..	..	..	..	..	..	++−
S. tranteri :								
Allotype, L and R	+−−	++−	+++	−+−	+++	++−	+++	++−
Paratype A, L and R	+−−	++−	+++	−+−	+++	++−	+++	++−
S. inaequalis	+−−	++−	+++	−+−	+++	+++	+++	−++
S. dardani	+−−	++−	+++	−+−	+++	−+−	++−	−− (−+)

P5 (Fig. 5) consisting of a minute thickening of the chitinous rear margin of the fifth pediger, bearing four setae of approximately equal thickness, of which the outermost is long, the other three all being very short.

Male (*allotype*). Length 1·9 mm., measured as in the female (Figs 3, 4). Very like the female but shorter, and slimmer in proportion to its length; also distinguishable from the female at sight by the dark brown sclerotization of the hooks (*a*) on the end of the antennule (Figs 9–11), (*b*) on the end of the first endopod segment of P2 (Fig. 19), and (*c*) of the coupling apparatus on the genital area (Fig. 6); all these sclerotized hooks are also visible in Fig. 4.

Variability. The holotype, the allotype, and three paratypes (2♀, 1♂) have been dissected; the following variations were found:

(*a*) The third (smallest and most distal) epipodal seta in Fig. 14 was not found on the other maxillule of the holotype, nor on either maxillule of any other dissected specimen.



Figs 18, 19.

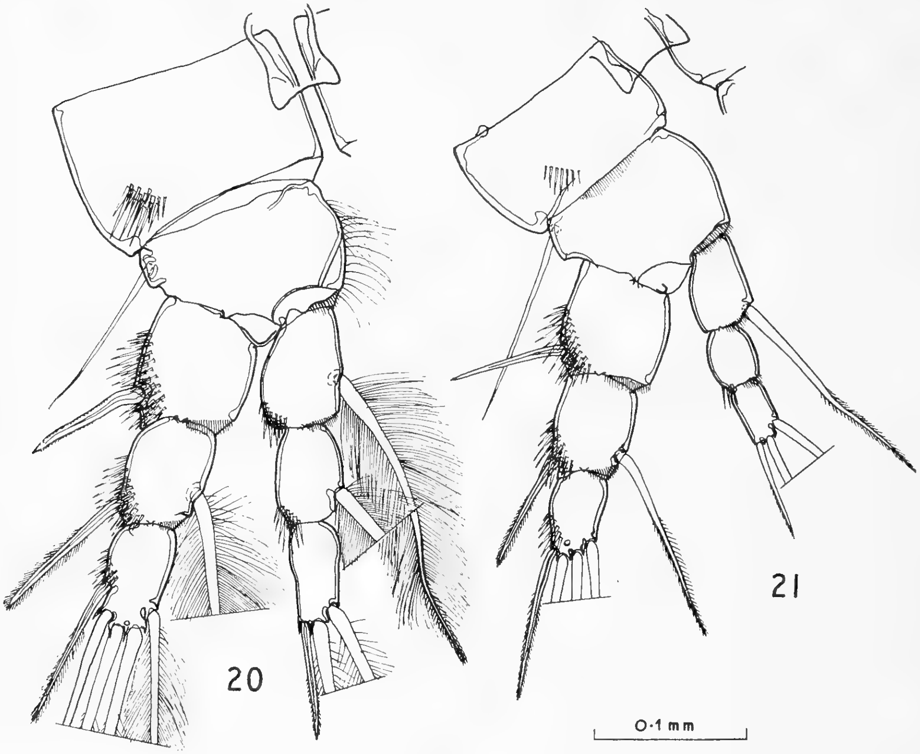
(*b*) The number of setae on the coxal arthrite is very hard to see, because setae lie over one another; however, in the holotype and in paratype A there appeared to be four on one maxillule and five on the other, whereas the other dissected specimens each had five setae on both maxillules.

(*c*) The seta arising between the rami from the mandibular basis is lacking on both mandibles of paratype 1, but is present on both mandibles of all the other dissected specimens.

(*d*) The antennal exopod is normal in all the dissected specimens except that, on one side only of paratype 2, it consists of only one segment with a lateral and two terminal setae.

(*e*) For variability in the spinulation, see Table 1.

Remarks. This species (named in honour of my colleague, the Australian planktologist and copepodologist D. J. Tranter) is so close to *S. paguri* that a redescription of the latter does not seem to be warranted at present (see Codreanu and Mack-Fira, 1961; Humes and Ho, 1969). The type-locality for *S. paguri* is the harbour at Brest, France ("la rade de Brest"—R. Bourdon, in litt.), from which it would be highly desirable to collect further specimens since the type material (Hesse, 1867) appears to be lost. However, specimens of *S. paguri* from Roscoff, kindly sent by Dr. Bourdon (see below), agreed entirely with *S. tranteri* except for:



Figs 20, 21.

(1) the spinulation (Table 1); in this respect the Roscoff specimens agreed exactly with material from Holland (Humes and Ho, 1969) and the single female from near Oslo studied by Sars (1911). Unfortunately, Codreanu and Mack-Fira give no details of the spinulation of their material (but see below);

(2) the ratio, in the female, of the total length of the fourth endopod to the length of the inner seta on the first segment thereof. In another species, *S. inaequalis* Humes and Ho, this seta is longer than this endopod in the male (Humes and Ho, fig. 42), but is shown as shorter than the endopod in the female (Humes and Ho, fig. 38), although in their text these authors explicitly state that this seta is shorter than this endopod in both sexes of *S. inaequalis*.

KEYS TO THE SPECIES OF *Sunaristes*

Four named species, *S. paguri* Hesse 1867, *S. dardani* Humes and Ho 1969, *S. inaequalis* Humes and Ho 1969, and *S. tranteri* nov. sp., are defined well enough to make it quite certain that they belong to this genus. A fifth species comprises at present a dissected and an undissected female kindly sent by Dr. Maureen Lewis (*née* Barclay) from the harbour at Auckland, New Zealand, where they were associated with *Pagurus novaezealandiae* Filhol ; although they cannot be identified with any of the other species, it would be inadvisable to describe them until more specimens (including males) are available. The five species may be separated as follows (*cf.* Humes and Ho, 1969, table 1) :

Key to females

1. P4 enp with two segments.................................*dardani*
P4 enp with three segments.................................2

2. P2–P4, exp 3 without spinules (P3 enp 1 also without spinules ;
P4, ratio of enp 1 inner seta : total enp = 3 : 2)..................*paguri*
P2–P4, exp 3 with spinules.................................3

3. P3 enp 1 with spinules (P4, enp 1 inner seta : total enp = 7 : 6)....*tranteri*
P3 enp 1 without spinules.................................4

4. P2–P4, enp 2 without spinules ; P4, enp 1 inner seta : total enp = 3 : 2
.... the Auckland species
P2–P4, enp 2 with spinules; P4, enp 1 inner seta: total enp = 3: 4..*inaequalis*

Key to males

1. P4 enp with two segments.................................*dardani*
P4 enp with three segments.................................2

2. P2–P4, exp 3 without spinules ....*paguri*
P2–P4, exp 3 with spinules.................................3

3. P3 enp 3 without spinules ; P4 enp 1 with spinules ....*tranteri*
P3 enp 3 with spinules ; P4 enp 1 without spinules............*inaequalis*

NOTE ON *Sunaristes paguri*

At the moment this appears to be the only valid European species of the genus (see note below on *S. bulbosus*), of which it is the type ; it extends from Norway to the Black Sea (Lang, 1948 ; Sars, 1911 ; Codreanu and Mack-Fira, 1961 ; Humes and Ho, 1969), and in north-west Europe has hitherto always been found with *Pagurus bernhardus*, which is by far the most abundant pagurid in that area in shallow water. Norman and Scott (1906, p. 130) summarized their own and other records of *S. paguri* as " always in washings from the shells inhabited by the common hermit-crab (*Pagurus prideauxi*) " ; as far as my experience goes, the term " common " has never been applied in British waters to any hermit-crab other than *P. bernhardus*, and it appears therefore that Norman and Scott's record of *prideauxi* (accepted by Codreanu and Mack-Fira) is a slip of the pen. However, Dr. Bourdon's specimens of *S. paguri* were taken with *P. cuanensis* at a depth of 30 m. on the dredging-ground Paradis, near Roscoff, in shells of *Turritella communis*, and intertidally at Saint-Efflam with *Diogenes pugilator* ; these are the first indisputable records of hosts other than *P. bernhardus* in north-west Europe, although in the Mediterranean *S. paguri* has several species of host (Codreanu and Mack-Fira). I can find no record that anyone has deliberately examined a large number of any British species of hermit-crab other than *P. bernhardus*, for *S. paguri* ; this is surprising, because some British pagurids are locally abundant offshore (Pike and Williamson, 1959).

As recently indicated (Hamond, 1971*a*), *S. paguri* has not been found on the coast of Norfolk, even though *P. bernhardus* is abundant there ; this may have been, however, because the two collections made with a view to securing it were both in the first week of August, and were therefore just too late for the mass death of the adults which follows immediately after the breeding season (Codreanu and Mack-Fira). If it is genuinely absent from Norfolk waters, its presence under very similar conditions on the coast of Holland (*cf.* Humes and Ho, 1969) must be due to recruitment from the English Channel.

NOTES ON OTHER SPECIES OF *Sunaristes* SENS. LAT.

The literature on the canuellids is full of instances where species have been transferred to *Sunaristes* for a longer or shorter period, as if this name was a sort of repository for any large species bearing a vague resemblance to *S. paguri*. The result has been a state of the greatest possible confusion, due almost entirely to insufficient descriptions and figures ; for instance, Thompson and Scott (1903) succeeded in squeezing the descriptions of three allegedly new species (*S. inopinata*, *S. longipes* and *S. curticaudata*) on to a single page (their p. 256, and a short passage at the top of p. 257) and all the figures on to a single plate (their Plate III, figs 1–17) ; there is not a single drawing of a mouth-part, or of somitic ornamentation, or of the animal in dorsal view, while of the 17 figures only one is of a male (their fig. 7). It is hardly surprising that at least one character which was accepted as a generic criterion by Lang (1948), namely the degree to which the first pediger is fused with the prosome, has been shown to vary within a single species (*S. paguri*) by Codreanu and Mack-Fira (1961) ; in these circumstances a revision of the family in depth, though urgently required, is simply not possible, although the outline revision by Por (1967) contains some useful concepts.

Thompson and Scott's *curticaudata* is probably indeterminable ; however, Scott's opinion (1909) that the alleged *Canuella curticaudata* taken by the " Siboga " is identical with the former, is clearly mistaken (Sewell, 1940). On the other hand, the " Siboga " species is possibly identical with *Sunaristes bulbosus* Por (1964) ; the corresponding figures show a very close resemblance. Sewell was himself mistaken in assuming that his own *Canuella scotti* was identical with the " Siboga " species ; the former lacks an inner seta on P1 enp 1 (present in the latter) but has a peculiar small inner seta on P1 enp 3 (not shown in the admittedly rudimentary figures either of Scott (1909) or of Por (1964)). Pending adequate redescription, I suggest the following synonymy :

A. *Sunaristes curticaudatus* Thompson and Scott (1903). No synonyms.
B. *Sunaristes bulbosus* Por (1964), syn. *Canuella curticaudata* Scott (1909).
C. *Canuella scotti* Sewell (1940). No synonyms.

These are all Indo-Pacific species, and all, especially *S. bulbosus*, are therefore likely to occur in Australian waters. None of them can be placed in a given genus with certainty, and they are therefore left in the genera to which they were originally assigned, purely for convenience.

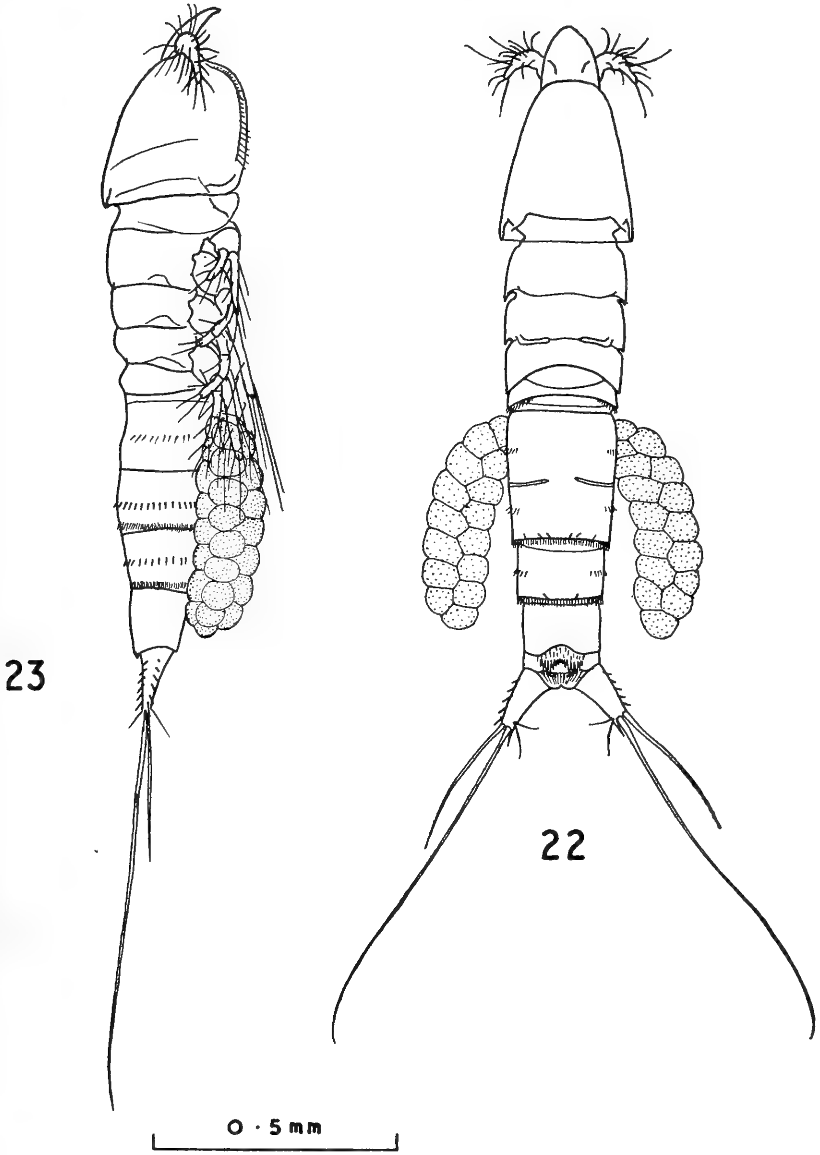
The finds of alleged *S. paguri* in New Guinea (Scott, 1909) and Ceylon (Thompson and Scott, 1903), regarded as doubtful by Humes and Ho, are almost certainly of some other species, perhaps *S. tranteri* or an indeterminable canuellid. They are probably not of *S. bulbosus*, which shows two characters that appear to exclude it from *Sunaristes* as defined here :

(1) The type of sexual dimorphism found in P2 (Por, 1964, figs 19 and 21) appears to be different ; and
(2) the rami of P4 each have a very short middle segment and a very long distal segment, the junction between them being sharply angulate (Por, 1964, fig. 20 ; *cf.* Scott, 1909, pl. LXIV, fig. 4), very different from P4 of *Sunaristes* spp. as understood here.

Brianola sydneyensis nov. sp.

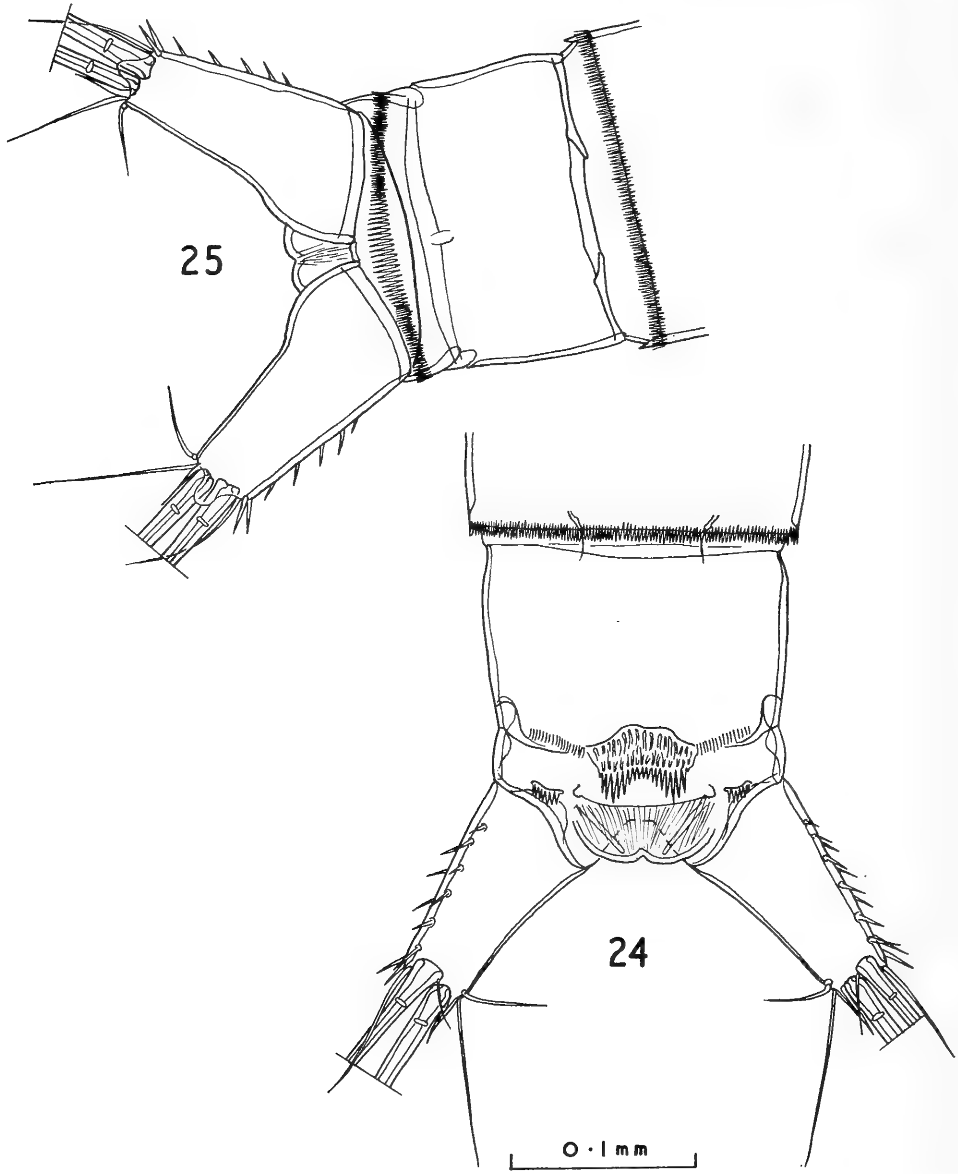
(Figs 22–40)

Female (*holotype*). Length 1·43 mm.; body without a noticeable " waist ", the prosome conically tapering, and the abdomen with rectangular somites all of which are broader than long (counting the genital double-somite as two separate somites for this purpose only) (Figs 22, 23). Rostrum large, bell-shaped (Figs 22, 31).



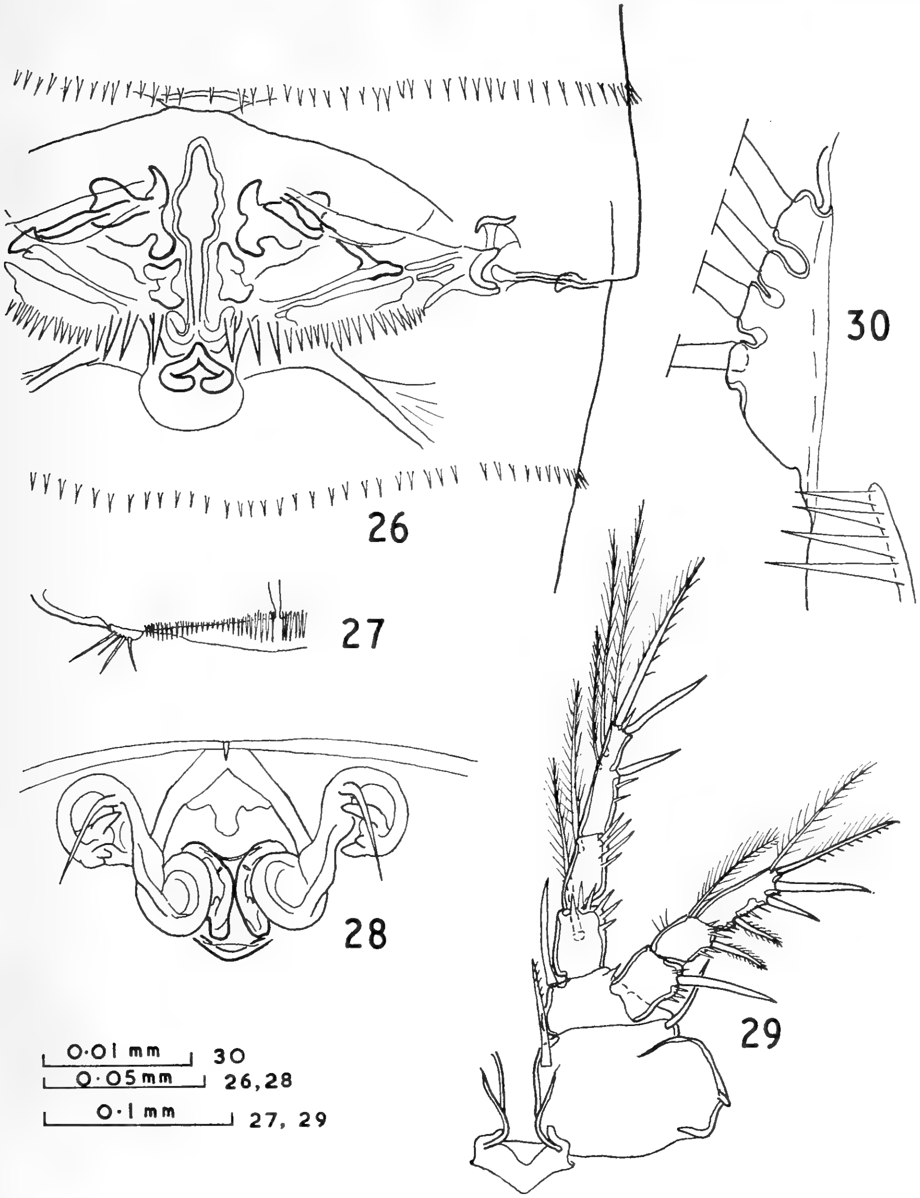
Figs 22, 23.

The genital double-somite has a lateral comb of spinules on each of its halves, and there is a similar comb on the somite behind it; this somite, and the rear half of the genital double-somite, each have a fringe of spinules completely circling the body and forming the rear margin of the somite, and a similar rear-marginal fringe is present ventrally to the operculum (Fig. 25). The operculum itself (Fig. 24) is smooth-edged and almost straight, but immediately anterior to it is a median pseudoperculum whose dorsal surface is cut into grooves parallel to the long axis, and whose rear margin is drawn out into a comb of long sharp



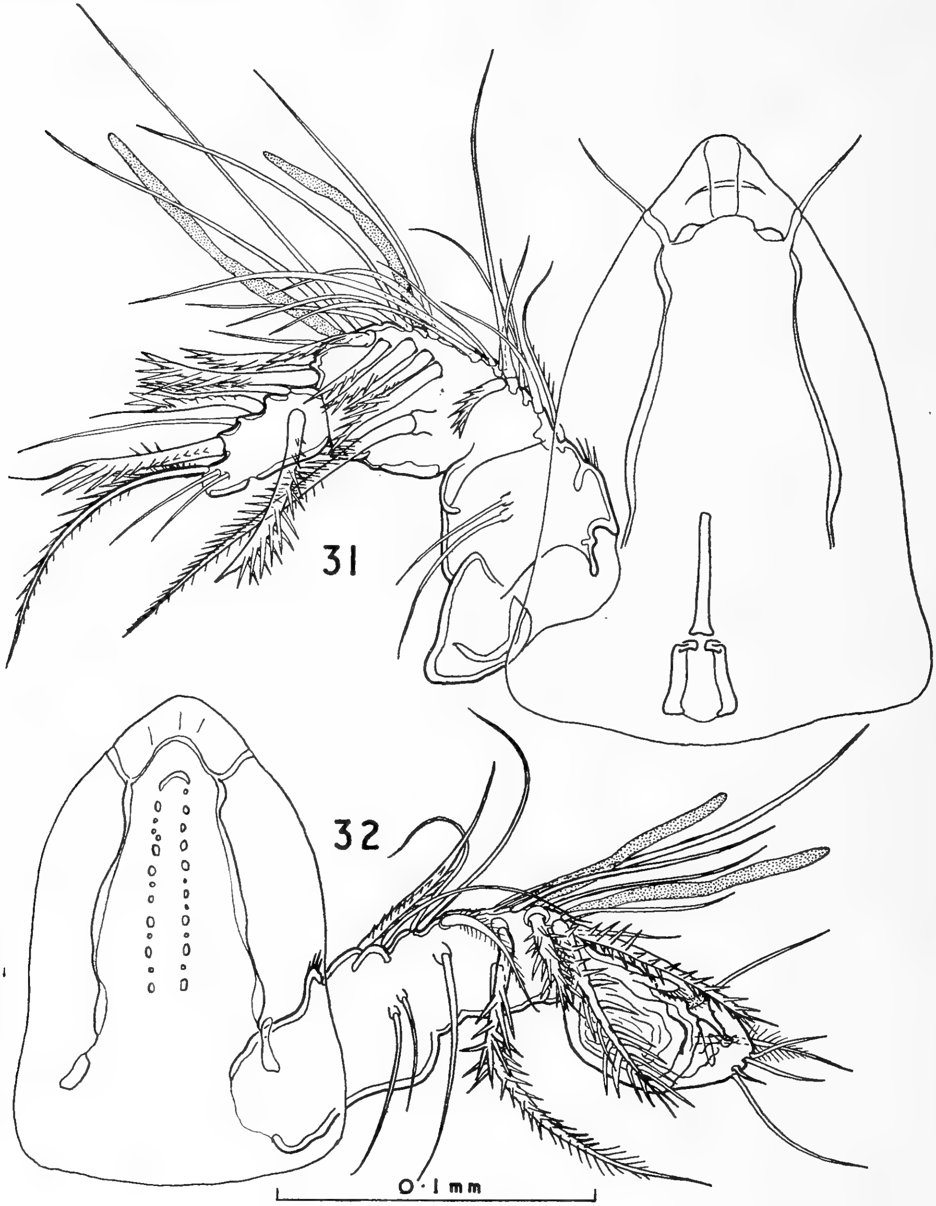
Figs 24, 25.

teeth ; these teeth are shortest in the middle and longer towards the ends of the comb. Lateral to the pseudoperculum is a row of tiny spinules, and lateral to the operculum is a short row of about six sharp and thick-walled teeth. Furcal rami short, broad, and divergent at about 80°, both margins curving inwards but the inner more so than the outer, which has pairs of sharp spinules spaced along it. The surface of the ramus is thickly covered with fine pointed spines, flattened rather like the scales of a butterfly's wing, which are very difficult to see *in situ* but are easily detached ; they appear to be present also in *B. stebleri* (*cf.* Monard,



Figs 26–30.

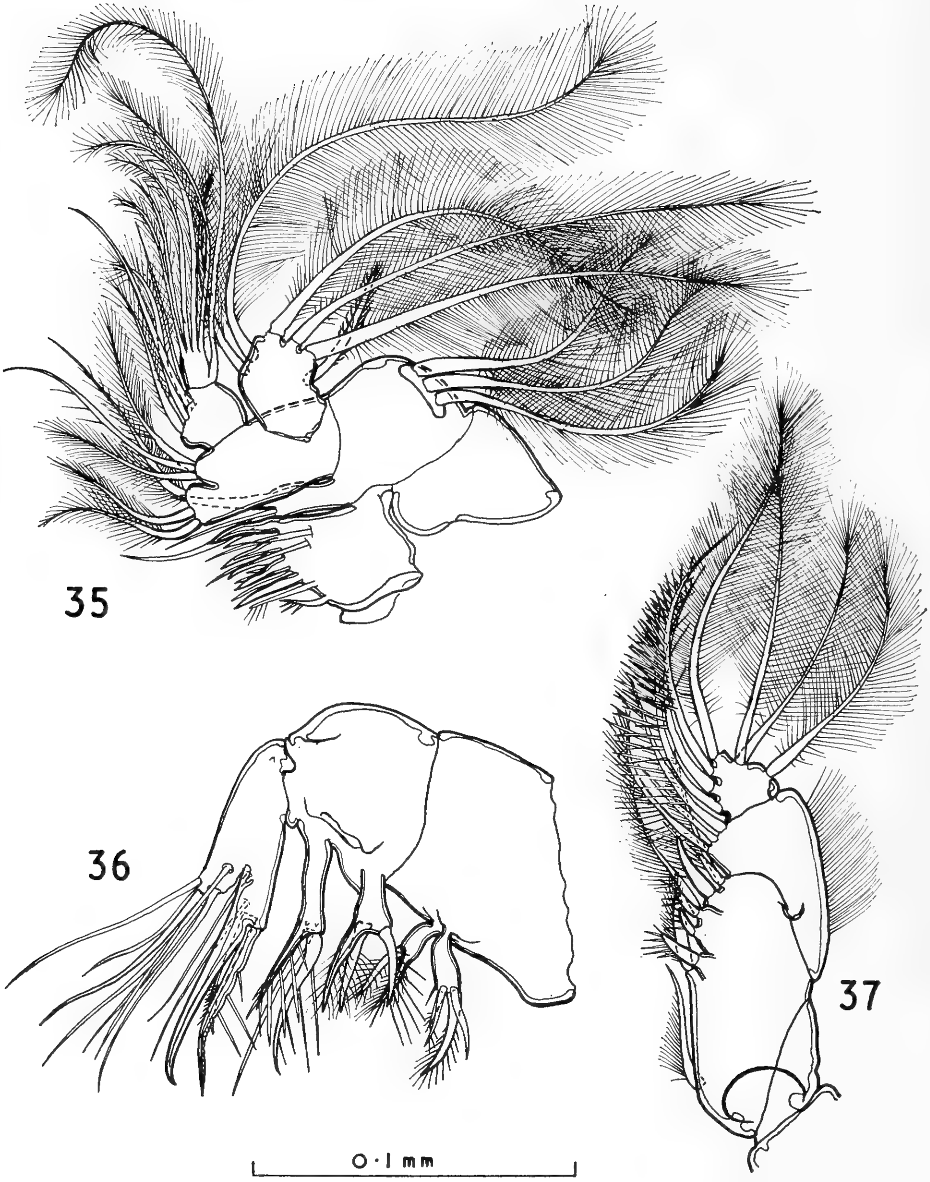
1937, p. 21, " formations en triangle allongé "), and are about the same size and shape as the outer marginal spines of the furcal ramus. Ventrally, the tip of the ramus is drawn out into a rounded projection (Fig. 25), and there is a slender thorn-like projection on the adaxial side of the tip ; there are two large furcal setae and four smaller ones. Genital field (Fig. 26) with a curved comb of spines, which are largest in the midline and become progressively smaller towards either side.



Figs 31, 32.

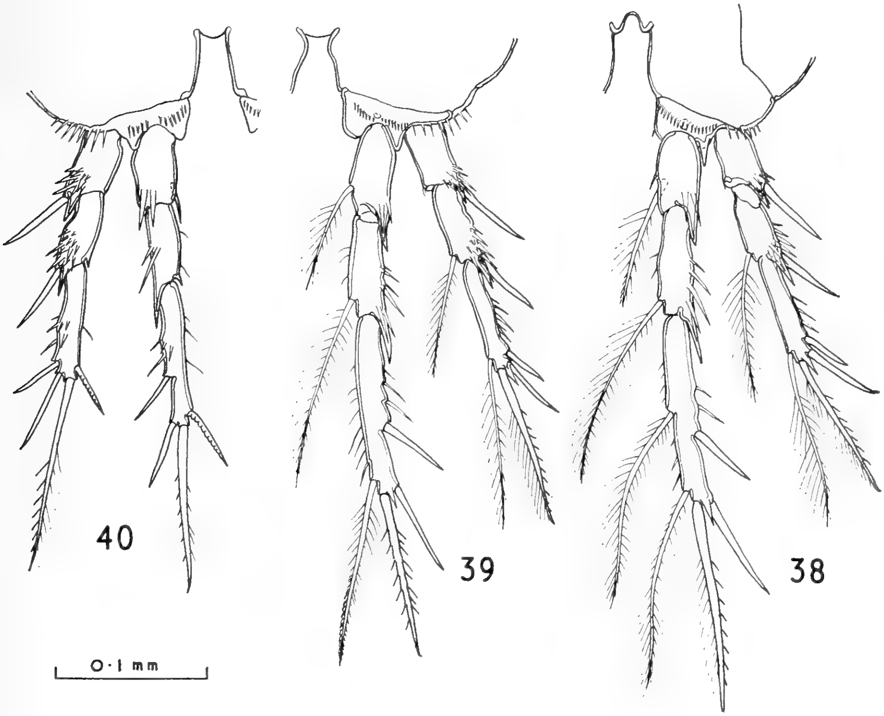
Antennule (Fig. 31) indistinctly segmented (four or five segments), with two aesthetascs on the leading edge of the penultimate segment, and with numerous setae of which the dorsalmost tend to be more heavily built, and provided with more lateral spines, than the others. Antenna (Fig. 33) with four segments, of which the basal carries a six-segmented exopod. Mandible (Fig. 34) with a two-segmented exopod bearing two and four setae, and a one-segmented endopod bearing 11 setae; the basis has two inner setae. Maxillule (Fig. 35) with three epipodal setae on the coxa, two groups of three setae each on the

Figs 33, 34.



Figs 35–37.

basis, six setae on the single exopod segment, and four and five setae respectively on the two endopod segments. Maxilla (Fig. 36) with two precoxal and two coxal endites; the endopod carries seven setae, and is not distinct from the basis, which is prolonged into a long hooked thorn surrounded by two stout and two slender setae. Maxillipede (Fig. 37) with its four components distinct from one another; the precoxa bears one, the coxa two+three+three, the basis three, and the endopod seven setae, shaped and ornamented as shown. All rami of swimming feet with three segments each, the endopod always longer than the exopod; setal formula:



Figs 38–40.

P1 (Fig. 29)		P2 (Fig. 38)		P3 (Fig. 39)		P4 (Fig. 40)	
exp	enp	exp	enp	enp	exp	exp	enp
0.1.5	1.1.6	0.1.4	1.1.5	0.1.4	1.1.4	0.0.4	1.0.4

P5 (Fig. 27, and on a larger scale in Fig. 30) of the usual canuellid form, with four setae.

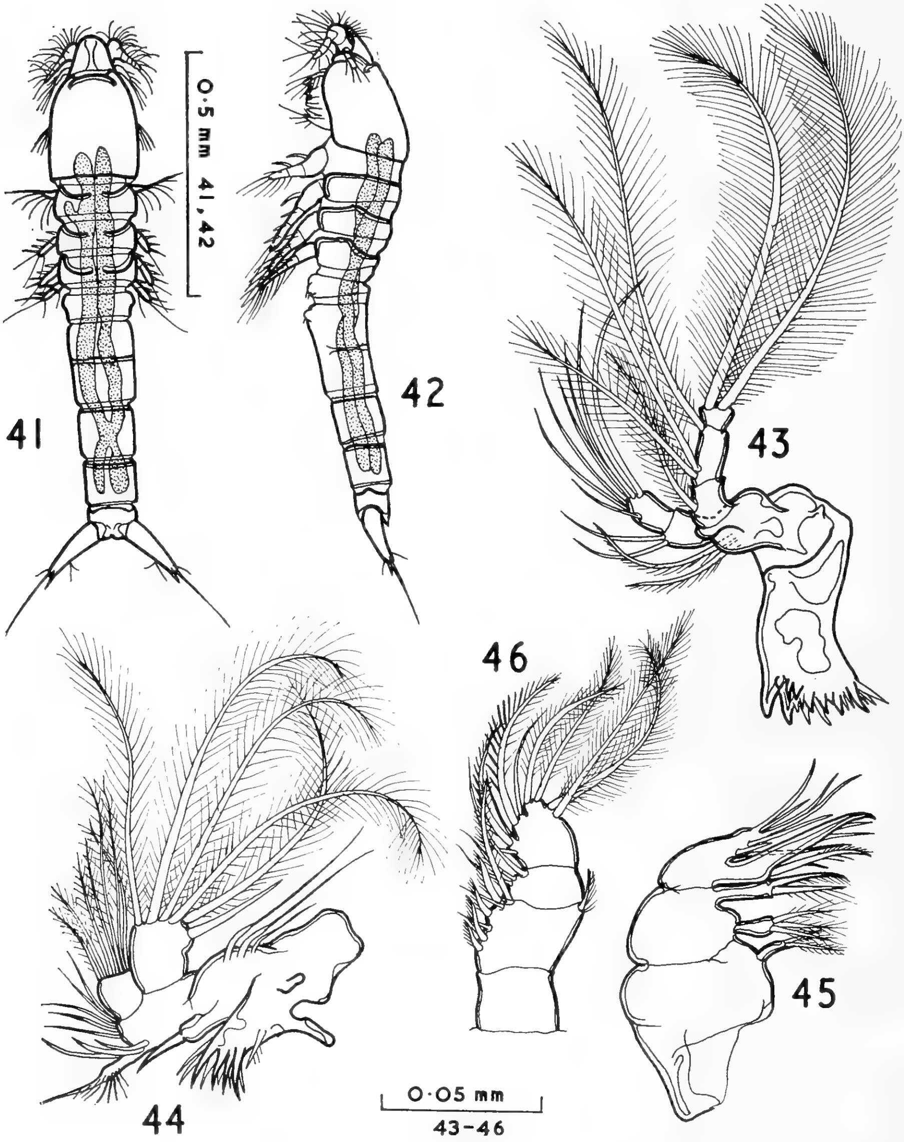
Male (*allotype*). Length 1·38 mm., similar to the female except for the antennule (Fig. 32), the genital field (Fig. 28), and in being slightly slimmer in the middle third of the body. No sexual dimorphism in the swimming legs.

Variability. None observed, among three females and two males dissected.

Brianola pori nov. sp.

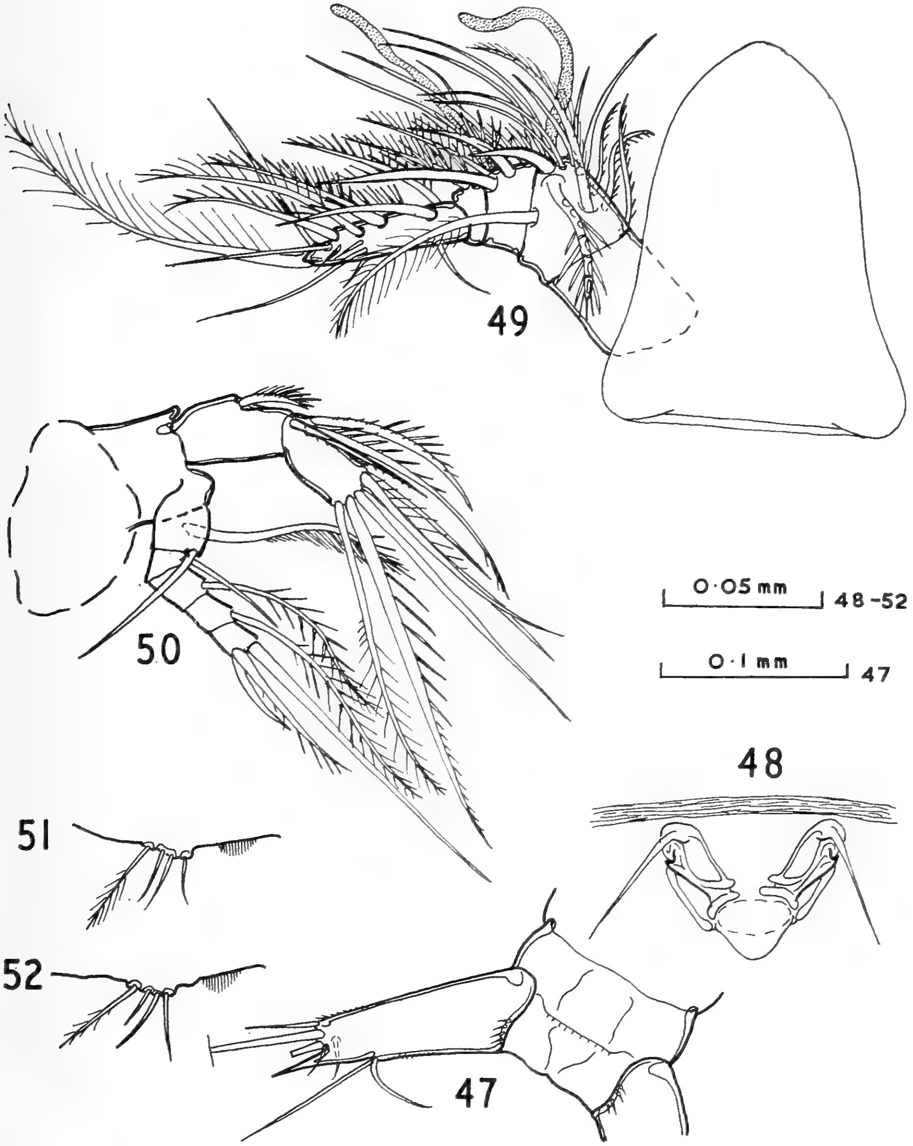
(Figs 41–60)

Female (*holotype*). Length 1·1 mm. Rostrum bell-shaped (Fig. 49); prosome (Fig. 41) in dorsal view distinctly parallel-sided with a broadly rounded front, and noticeably wider than the rest of the body, which is slender and very slightly tapering. Genital double-somite divided dorsally and laterally, but not ventrally (Figs 41, 42); genital area as in Fig. 48. There is no spiny pre-operculum; the operculum (Fig. 47) has a straight edge with angulate corners,



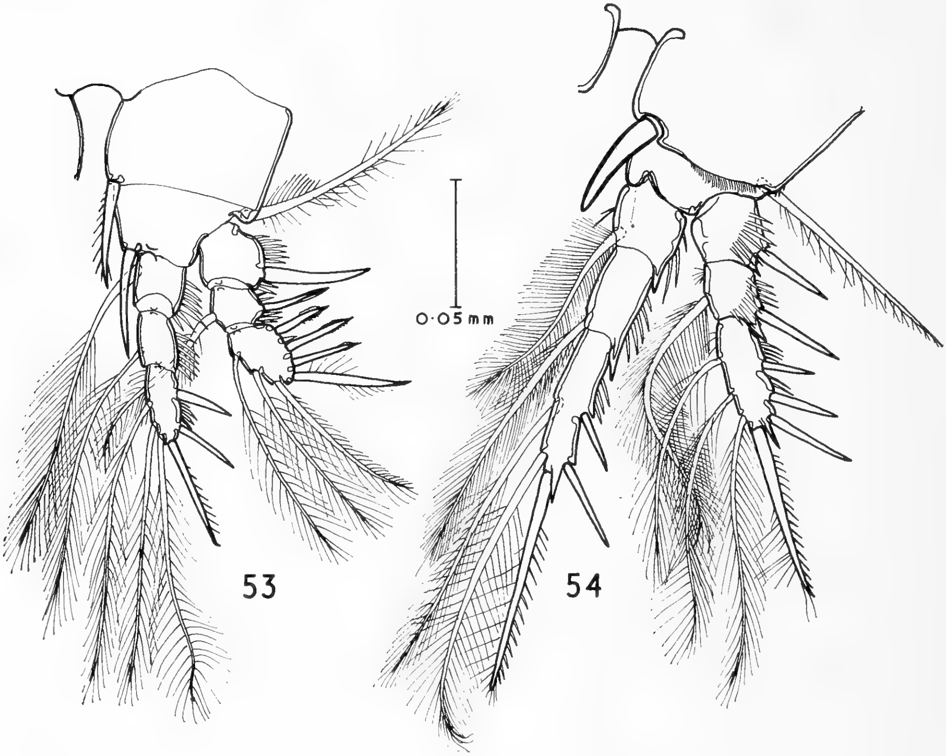
Figs 41–46.

and with a few very small blunt marginal teeth; it is very transparent and difficult to see. Furcal rami diverging at somewhat more than a right angle; each furcal ramus is long and tapering, almost straight, and produced apically into a long sharp thorn on the inner side; there is no ventral apical projection.



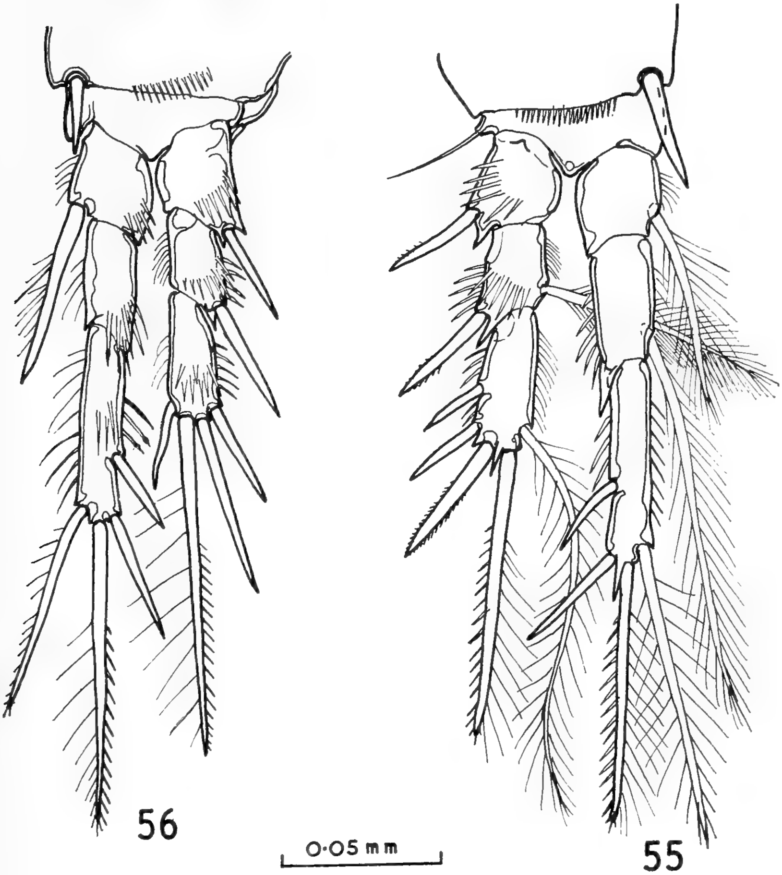
Figs 47–52.

A pair of smooth setae arise at about two-thirds of the length of the inner edge, at the base of which there is also a row of four or five large spinules (Fig. 47); terminally there are two large setae (of which the inner is broken off on both sides) and three small ones (dorsal, ventral, and exterolateral). There is no sign of " butterfly-scales ", but there is a row or band of tiny spines along the outer and the inner edges. There is a ventral fringe of needle-like spinules running right across the body on the rear margin of the genital double-somite (rear half only), of the somite behind it (but not of the somite behind that), and of the very short anal (=opercular) somite ; otherwise, there is no somitic ornamentation anywhere on the body.



Figs 53, 54.

Antennule (Fig. 49) with five segments, of which the second and the third each bear an aesthetase ; the terminal segment is very long. Antenna (Fig. 50) with a large exopod whose terminal segment bears three setae ; the two basal segments appear to be fused, since there are only five altogether. The two segments of the endopod are about equally long. Mandible (Fig. 43) with a three-segmented endopod whose segments bear one, three and two setae, and a two-segmented exopod with two and six setae ; there are also two setae arising together from between the rami. I was unable to obtain a preparation in which the rami of the mandibular palp were not twisted around each other. Maxillule (Fig. 44) ; pre-coxal arthrite with a total of about 10 spines and setae on the biting edge ; coxa with a spine on the arthrite and with three epipodal setae ; basis with a large inner seta (whose thickened base is covered with setules), and with three smooth inner setae, two on one face and one on the other face ; rami each of one segment, exopod with six and endopod with seven setae. Maxilla (Fig. 45) with one precoxal endite and two coxal endites ; basis prolonged internally into a heavy hooked spine with a thick spinous seta arising laterally from its base ; endopod not distinct from basis, and bearing a total of seven setae. Maxillipede (Fig. 46) with its four components (as in *B. sydneyensis*) distinct, bearing nought, seven, three and nine setae respectively ; the precoxa is unusual in lacking a seta and in the junction between it and the coxa being straight instead of at a steep angle.



Figs 55, 56

All four swimming feet with both rami composed of three segments ; setal formula as follows :

P1 (Fig. 53)		P2 (Fig. 54)		P3 (Fig. 55)		P4 (Fig. 56)	
exp	enp	exp	enp	exp	enp	exp	enp
0.1.7	1.1.6	0.1.7	1.1.5	0.1.5	1.1.4	0.0.4	1.0.4

The swimming endopods are all longer than their respective exopods. An inner spine is present on the coxa of each swimming foot, but that of P2 is much larger than any of the others ; there is an inner spine on the basis of P1 only. P5 (Figs 51, 52) consisting of four setae, of which the abaxial is sparsely plumose.

Male (*allotype*). In general very like the female, from which it differs only in being slightly slimmer (Fig. 57) and smaller (length 0·83 mm.), in the usual modification of the antennule (Fig. 58), and in the reduction in size and in ornamentation of many of the setae of P3 (Fig. 59 ; *cf.* Fig. 55, ♀) and P4 (Fig. 60 ; *cf.* Fig. 56, ♀).

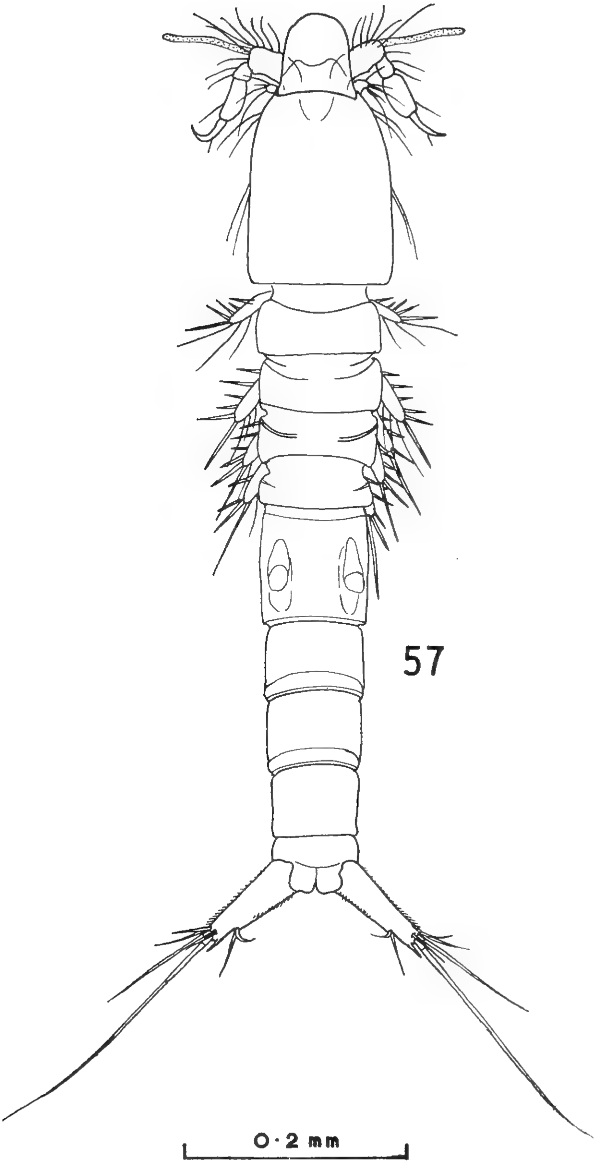
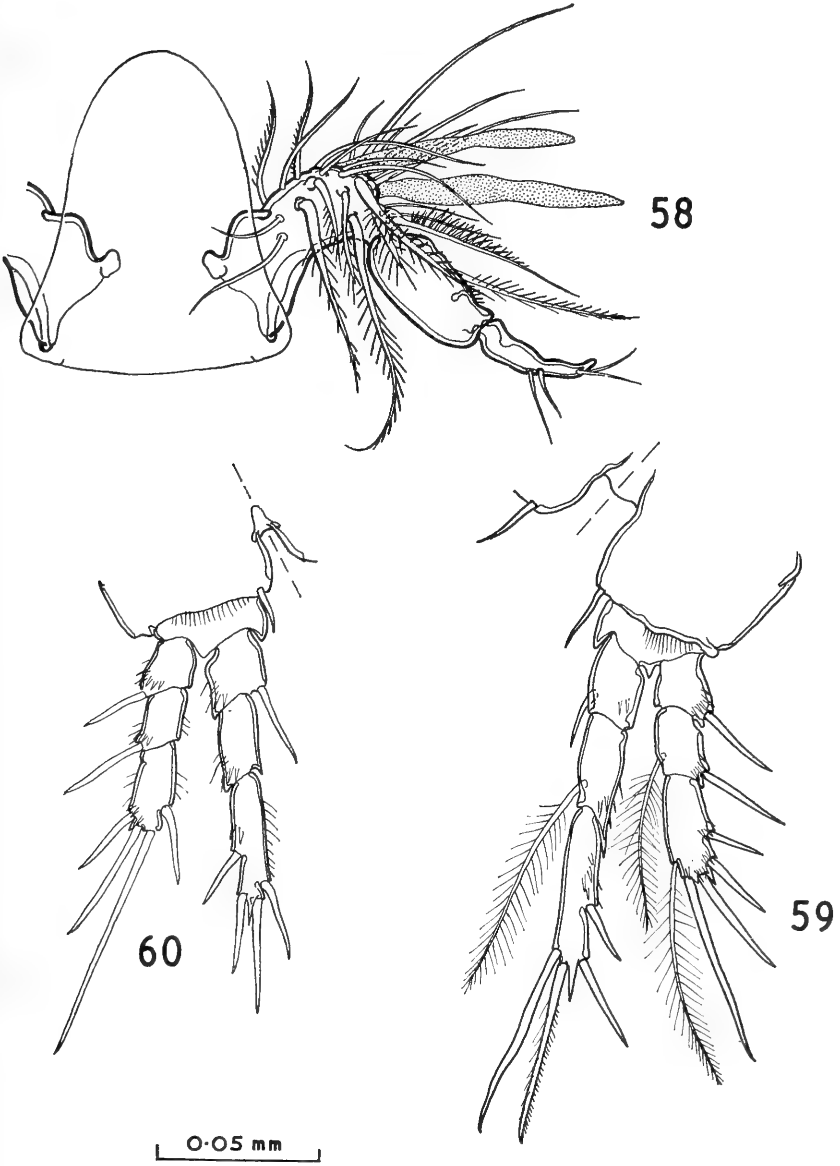


Fig. 57.

Variability. None observed among three females and two males dissected.

I have pleasure in naming this species after Dr. F. D. Por, Hebrew University, Jerusalem, distinguished for his work on harpacticoids.

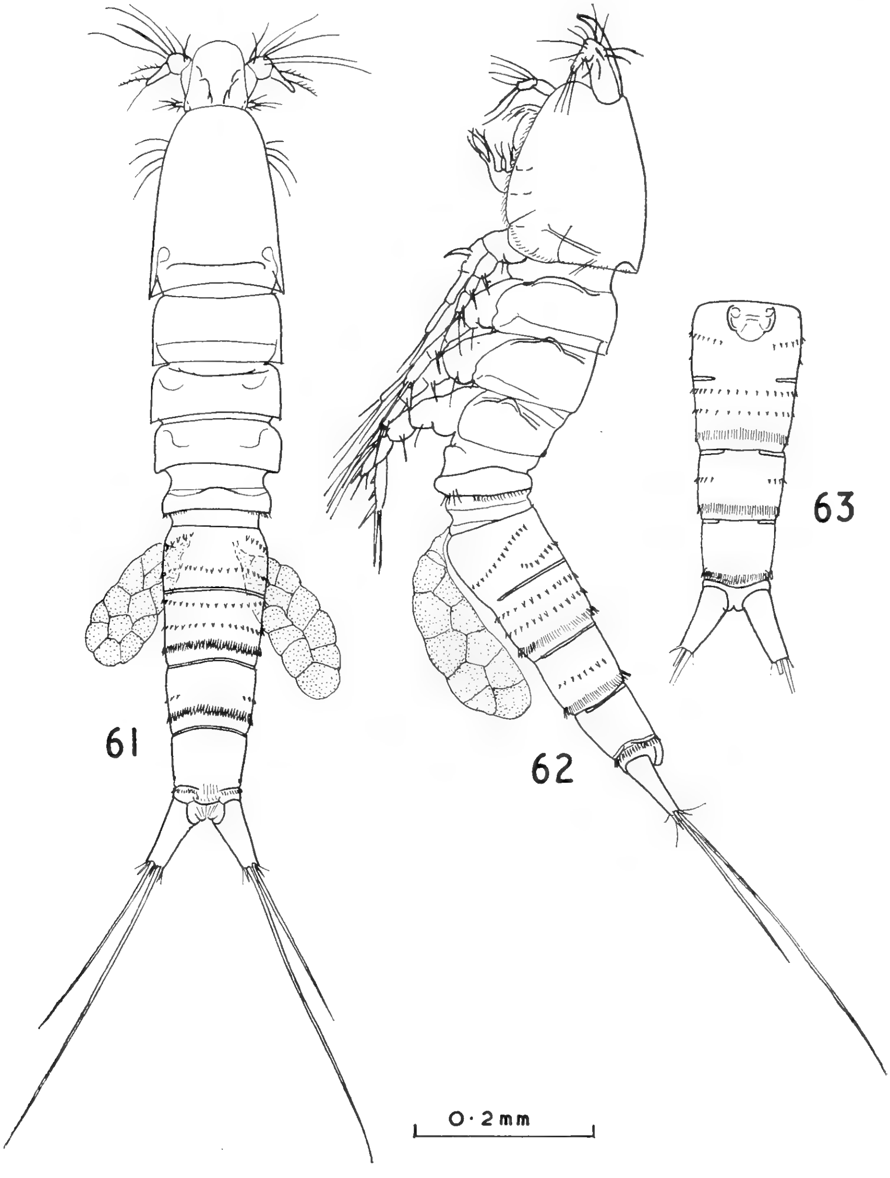


Figs 58–60.

Brianola elegans nov. sp.

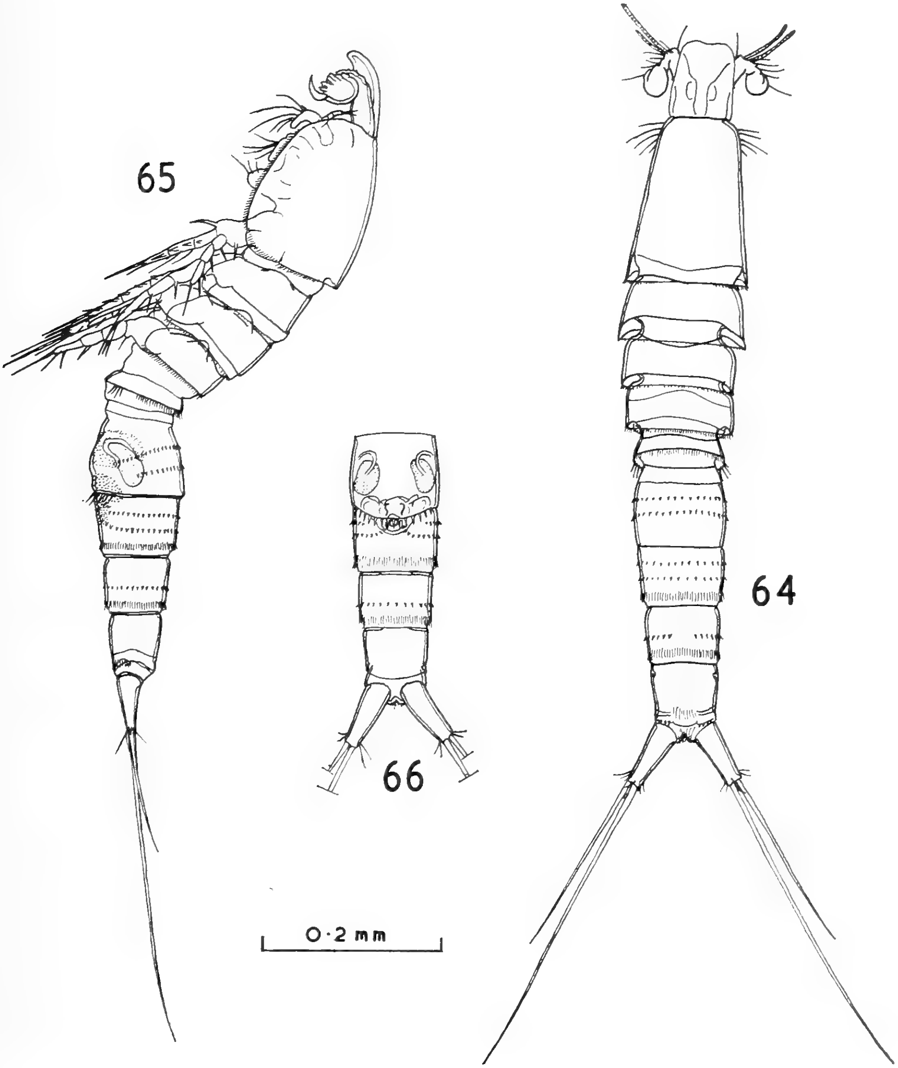
(Figs 61–83)

Female (*holotype*). Length 0·97 mm.; in dorsal view (Fig. 61) the thorax is parallel-sided, and from it the prosome tapers forwards and the abdomen towards the furca. Rostrum (Fig. 72) less pointed than in *B. pori* or *B. sydneyensis.* The ventral and rear margins of the prosomal shield have a single row of short setules running along them (Fig. 62); the lower rear corner of the



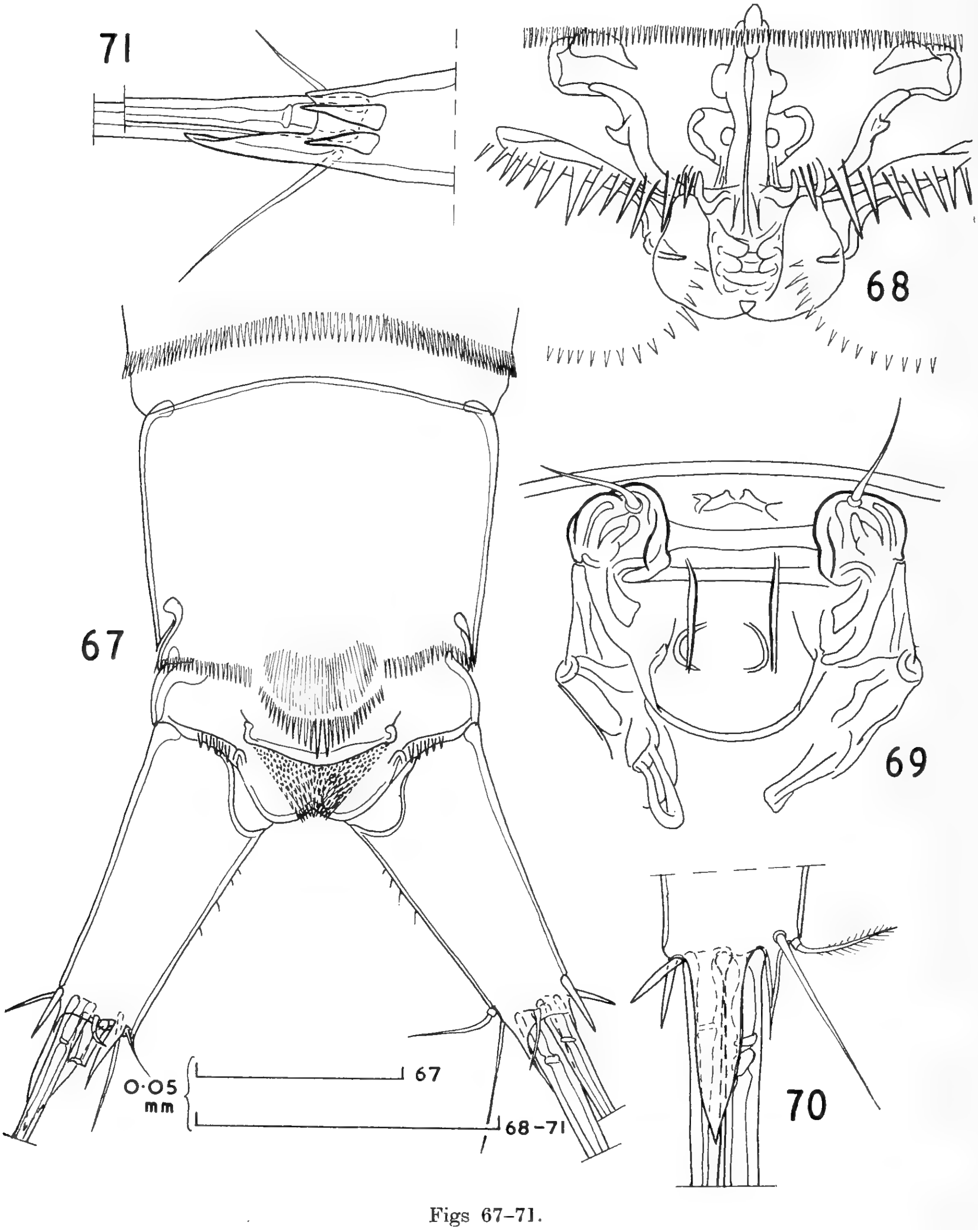
Figs 61–63.

shield is separated from the ventral and rear margins, in each case by a thin pleat-like groove in the integument (as if the chitin had been lightly scored with a sharp blade). Along the ventral margin the setules are recurved and are set upon the very edge itself; on the lower rear corner the setules leave the edge in order to follow a shorter path across the corner, and regain the edge on reaching



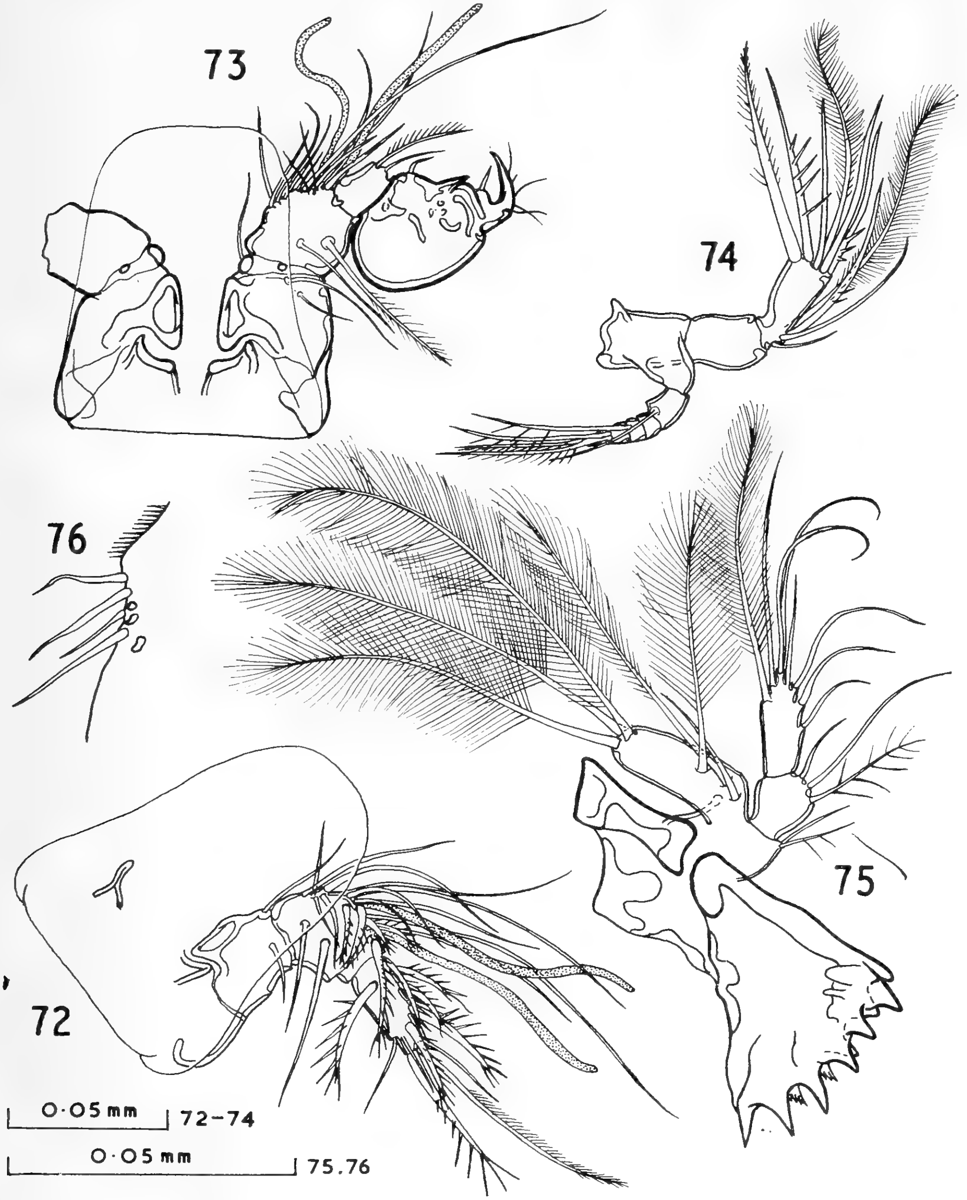
Figs 64–66.

the rear margin, upon which the setules point directly towards the tail. Of the pedigers only the fifth has any ornamentation, consisting of a lateral comb ot spinules on the rear margin; this comb begins some way above P5 and does not extend more than a short way on to the dorsal surface. The genital double-somite is divided on all sides except ventrally; on the front half there is a comb of small widely spaced denticles running from just behind the genital area (Fig. 63; detail, Fig. 69) to the dorsolateral surface (curving forwards as it does so), and behind it another comb running across the dorsal surface and extending a short way on to the lateral surface. The rear half has two such combs, and a rear-marginal fringe of spinules; all three encircle the body without interruption,



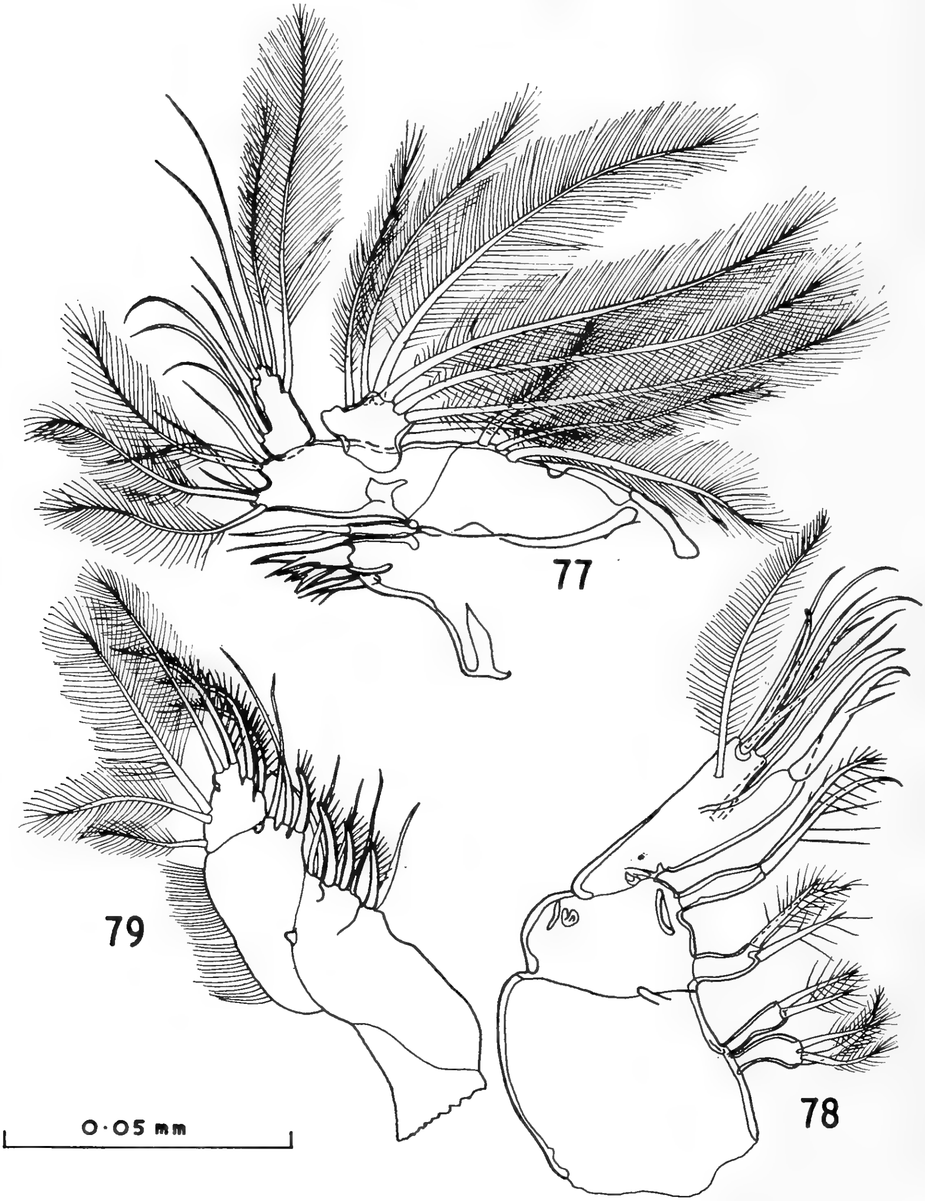
Figs 67–71.

as does the rear-marginal fringe on the somite behind the genital double-somite. This latter somite has only a small lateral comb of denticles, and the somite behind it has no denticles at all, but has a rear-marginal fringe which is incomplete dorsally owing to the presence of the spiny pseudoperculum (Fig. 67), which



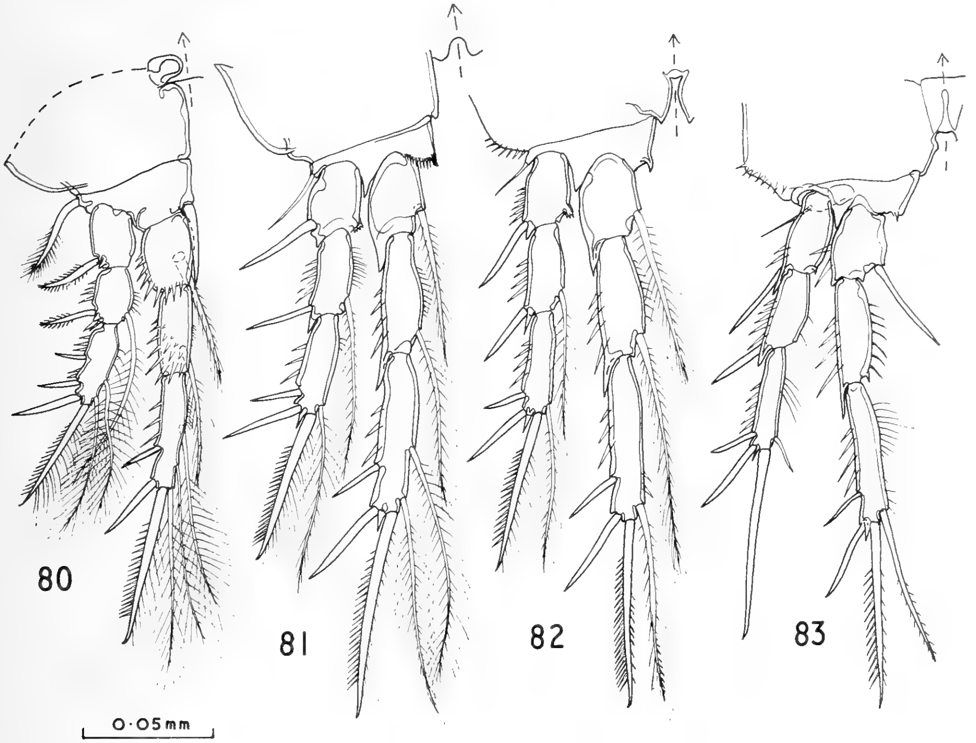
Figs 72–76.

differs at first glance from that of *B. sydneyensis* (Fig. 24) in that the teeth are longest in the middle from which they decrease regularly towards either side. The operculum has a rounded apex, and straight sides ending in bluntly angulate corners ; immediately below and behind it, the integument is covered with tiny chitinous warts which are small and round nearest the operculum, but become progressively longer and more like setules going away from it. A similar area of roughened integument below and behind the operculum is found elsewhere among harpacticoids only in the diosaccid genus *Robertgurneya* (Lang, 1948, 1965; own observations).



Figs 77–79.

The furca diverges at about 70°, and each ramus is almost straight; it tapers less than in either *B. pori* or *B. sydneyensis*. The two inner setae are subterminal, and the apex is drawn out into both an inner sharp thorn (Fig. 70) and a long and strong (but very transparent) tongue-like ventral projection. There is a small dorsal seta, and the two outer setae have become flattened spines, broadest in lateral view (Fig. 71) but narrow when seen from above (Fig. 67) or from below (Fig. 70). There are also two large terminal setae, as usual. A few small spinules are present on the inner margin only of the ramus ; " butterfly-scales " could not be seen in the holotype, although present on all the other specimens.



Figs 80–83.

Antennule (Fig. 72) with five segments of which the third and the fourth each bear an aesthetasc. Antenna (Fig. 74) with a large exopod, whose first free segment has a distinct outer thorn ; there are six segments altogether, and the basal segment (not clearly marked off from the basis) is remarkably broad at the base. The two endopod segments are about equal in length. Mandible (Fig. 75) with a single-segmented exopod, bearing three inner and three terminal setae, and a two-segmented endopod whose segments bear three and seven setae respectively ; there are also two inner setae on the basis. The teeth of the cutting edge are most heavily sclerotized on the outer part of the edge.

Maxillule (Fig. 77) with about seven teeth on the cutting edge of the precoxal arthrite ; the precoxa, coxa, and basis are not very clearly separated. The coxa has three epipodal setae and an arthrite with two setae ; the basis is very long and narrow, with two terminal groups of four and three setae respectively ; the exopod is pentagonal, with seven setae of which the outermost is short and heavily barbed ; the endopod has three inner and six terminal setae. Each ramus is one-segmented. Maxilla (Fig. 78) with two precoxal and two coxal endites ; the endopod is not separated from the basis, and bears a total of seven terminal setae, as well as one on its outer surface ; there is also a seta arising from between the endopod and the basis, but on the far side (its proximal part is shown dashed in Fig. 78). Maxillipede (Fig. 79) consisting of the usual four components, which are all clearly distinct, the coxa being separated on either side by very steeply sloping sutures. The setation of the four components is as follows : precoxa, nil ; coxa, two + four + two ; basis, three ; endopod, seven.

All rami of swimming feet with three segments, the endopod in each case distinctly longer than the exopod. Setal formula :

P1 (Fig. 80)		P2 (Fig. 81)		P3 (Fig. 82)		P4 (Fig. 83)	
exp	enp	exp	enp	exp	enp	exp	enp
0.1.6	1.1.6	0.1.4	1.1.5	0.1.4	1.1.4	0.0.4	1.0.4

An inner spine is present on the basis of P1 only, and not on any of the coxae of the swimming feet. The basis of each of the other legs has a small hook-like thorn in place of the inner spine ; the lower inner corner of the first exopod segment is unarmed in P1, has a very small hook in P4, and is produced into a small serrated chitinous comb in P2 and P3. The outer basal seta is partly tucked in behind the first exopod segment in P4, but is mounted in full view in the other feet ; in P1 it is transformed into a stout, almost spiniform, seta which is delicately bipinnate. P5 (Fig. 76) with four smooth setae.

Male (*allotype*). Very like the female but slightly smaller (Figs 64–66) ; length 0·80 mm. Rostrum almost trapezoidal, especially when squashed flat (Fig. 73) ; prosome tapering more markedly than in female, owing to its sides being straight instead of slightly convex. The margin of the prosome shield bears a curved row of setules as in the female ; the rear margins of pedigers 2 and 3 have tiny blunt setules, and those of pedigers 4 and 5 a fringe of longer setules, both dorsally and laterally. The abdominal segments bear the same combs of spinules as in the female, but here the rear comb on the rear half of the genital double-somite curves sharply in towards the genital area (Fig. 66 ; detail, Fig. 68), and the comb on the somite behind it encircles the body except for a small dorsal gap (Fig. 64). The antennule (Fig. 73) is modified in the usual way.

Variability. None observed among three females and two males dissected.

REMARKS ON THE SPECIES OF *Brianola*

The only species known to Lang (1948, p. 166) was the type of the genus, *B. stebleri* Monard (1926, as *Brianella* preocc., replaced by *Brianola* nom. nov. in Monard, 1927, p. 145), known only from females. Por (1964) described certain features of the male of *B. stebleri*, and a new species *Canuella reichi* which was later (Por, 1967) transferred to *Brianola* ; in the latter paper he also described *Brianola exigua.* All these three species are now known from both sexes, but none has been figured completely in regard to such features as the structure of the furcal apex, or the exact pattern of somitic ornamentation, or the relationship between operculum and pseudoperculum. The following conclusions may, however, be drawn.

(1) *B. reichi*, although included in the following key, should perhaps be removed from this genus, since it differs from the remaining species in several characters (Por, 1964, pp. 60–61) in which the other species agree among themselves. However, at the moment it is quite impossible to suggest any other genus as appropriate for *reichi*.

(2) *B. exigua* presents two doubtful features :

(*a*) The swimming-feet of cannuellids bear, on the margins of their segments, and of many other copepods, more or less pointed projections which I have called thorns (Hamond, 1968, top of p. 46) and which are integral with the somite bearing them, as distinct from appendices (spines and setae taken together) which have an articulated base and are thus distinct from the somite bearing them, although set into some kind of scar or socket on or near the somite margin. Spines and setae, although often distinct, are connected by many intermediates, and in some harpacticoids (of which the cannuellids are a good example) the appendices round the end of a ramus could equally well be described either as spines or as setae. In drawings, appendices always have a line of demarcation at the base, whereas this is never so with thorns. Por's description and figure of the apex of the terminal endopod segment of P4 in *B. exigua* conflict with one another; his drawing (1967, fig. 47) shows a thorn and four appendices (giving a formula of 004.104, exactly as in all other species of the genus—see Table 2 of the present paper), whereas his text gives a formula of 004.105.

(*b*) The apparent absence of an inner seta on P1 exp 2 may also be due, either to it having been broken off and the attachment-scar having been overlooked (being very difficult to see), or to genuine absence in Por's material due to abnormality.

With regard both to *reichi* and *exigua*, Por's findings have been accepted at face value in couplet 2 of the following key, but I have also allowed *exigua* to come up in couplet 3 in case either of my conjectures is confirmed. The key applies to both sexes.

Provisional Key to the species of Brianola

1. P2 exp 3 with 7 setae; P3 exp 3 with 5 setae; hardly any somitic ornamentation .... *B. pori*
   P2 exp 3 with 4 setae; P3 exp 3 with 4 setae; a significant amount of somitic ornamentation 2
2. P1 exp 2 with no inner seta; P4 enp 3 with 5 setae.......... *B. exigua*
   P1 exp 2 with an inner seta; P4 enp 3 with 4 setae 3
3. Limb-segments bear totals of spines and setae, as indicated:

P1 exp 3	P1 enp 3	P2 enp 3	
4	5	4	..........*B. reichi*
4	6	4	..........*B. exigua*
5	4	5	..........*B. stebleri*
5	6	5	......*B. sydneyensis*
6	6	5	.........*B. elegans*

When using this key, it is always desirable to confirm the initial determination by inspection of other characters, such as the shape of the body in dorsal view, the pseudoperculum, the somitic ornamentation, and the appearance of the furcal ramus.

Discussion

The current opinion (Por, 1967, p. 104) that the family Canuellidae is centred within the largely unexplored and faunistically inexhaustible Indo-West Pacific realm, is certainly borne out by the present findings; when one remembers that no less than four species of the family, all of them new, were found simultaneously with the same population of hermit-crabs (the previous record being two such species simultaneously; Humes and Ho, 1969), in collections along an infinitesimal fraction of the long Australian coastline, the potential wealth of species remaining to be discovered needs no emphasis. This being so, the need to describe every new species in as detailed and careful a way as possible becomes more imperative than ever, especially considering what a homogeneous family the canuellids are, and how little some of the alleged species appear to differ morphologically from one another. *Sunaristes* seems to be a natural genus when restricted to the five species in the keys on p. 177, but a formal generic diagnosis is not feasible at present owing to the large number of insufficiently known species, any of which might turn out to belong to this genus, but none of which should be positively admitted to it until they have been thoroughly redescribed and refigured. On the other hand, *Brianola* is a dumping-ground rather than a genus (although its members have many points in common); in the present state of our knowledge, to transfer species to or from it would only increase the prevailing confusion.

By analogy with *S. paguri*, the association between *S. tranteri* and *Diogenes senex* is probably a very close one; however, this may well not be true of any of the new species of *Brianola* because the holotype of *B. pori* was found in a place from which no pagurids have been recorded (see Material and Methods), and because other species of this genus appear to be free-living. I have not yet had either the chance to examine other species of pagurid in the Sydney area or the time to go through my numerous samples of Sydney harpacticoids in a search for canuellids; however, from observations while sorting these samples, it seems that canuellids are much scarcer than certain other families.

ACKNOWLEDGEMENTS

I am most grateful to Dr. D. J. G. Griffin (Australian Museum, Sydney) for identifying *Diogenes senex*, and to him, to Miss Isobel Bennett (formerly of the University of Sydney) and to Dr. R. J. MacIntyre (University of New South Wales), for information about the lack of pagurids in Narrabeen Lagoon; also to Dr. W. Ponder (Australian Museum, Sydney) for the authorships of the names *Pyrazus ebeninus* and *Crassostrea commercialis*, and to the Chief of the Division of Fisheries and Oceanography, C.S.I.R.O., Cronulla, for the loan of phase-contrast equipment.

ADDENDUM

Since the above was written, Humes (1971) has found *Sunaristes dardani* in the Pacific; the variations in spinulation recorded by him have been omitted from Table 1, and do not affect the key in the present paper.

TABLE 2

Setal Formulae of Brianola *spp.*

	P1		P2		P3		P4	
	exp	enp	exp	enp	exp	enp	exp	enp
stebleri	0.1.5	1.1.4	0.1.4	1.1.5	0.1.4	1.1.4	0.0.4	1.0.4
reichi	0.1.4	1.1.5	0.1.4	1.1.4	0.1.4	1.1.4	0.0.4	1.0.4
exigua	0.0.4	1.1.6	0.1.4	1.1.4	0.1.4	1.1.4	0.0.4	1.0.5
sydneyensis	0.1.5	1.1.6	0.1.4	1.1.5	0.1.4	1.1.4	0.0.4	1.0.4
pori	0.1.7	1.1.6	0.1.7	1.1.5	0.1.5	1.1.4	0.0.4	1.0.4
elegans	0.1.6	1.1.6	0.1.4	1.1.5	0.1.4	1.1.4	0.0.4	1.0.4

References

BODIN, P., 1967.—Catalogue des nouveaux copépodes harpacticoides marins. *Mem. Mus. Nat. Hist. nat. Paris*, A, 50 (1): 1–76.

CODREANU, R., and MACK-FIRA, V., 1961.—Sur un copépode, *Sunaristes paguri* Hesse 1867, et un Polychète, *Polydora ciliata* (Johnston) 1838, associés au Pagure *Diogenes pugilator* (Roux) dans la Mer Noire et la Méditerranée. La notion de cryptotropisme. *Rapp. Comm. int. Explor. Sci. Mer Medit.*, 16: 471–494.

HAMOND, R., 1968.—Some marine copepods (Misophrioida, Cyclopoida, and Notodelphyoida) from Norfolk, Great Britain. *Crustaceana*, suppl. 1 (Studies on Copepoda): 37–60.

————, 1969.—Methods of studying the copepods. *J. Quekett micr. Club*, 31 : 137–149.

————, 1971*a*.—The leptostracan, euphausiid, stomatopod, and decapod Crustacea of Norfolk. *Trans. Norfolk Norwich Natur. Soc.*, 22 (2) : 90–112.

————, 1971*b*.—The Australian species of *Mesochra* (Copepoda, Harpacticoida) with a comprehensive key to the genus. *Aust. J. Zool.* (Suppl.), 7 : 1–32.

HESSE, M., 1867.—Observations sur des Crustacés rares ou nouveaux des côtes de France. *Ann. Sci. nat.*, 5 (Zool. Palaeontol.) (7) : 199–216. (Not seen.)

HUMES, A. G. (1971).—*Sunaristes* (Copepoda, Harpacticoida) associated with hermit crabs at Eniwetok Atoll. *Pacific Science*, 25 (4) : 529–532.

———— and Ho, J. S., 1969.—The genus *Sunaristes* (Copepoda, Harpacticoida) associated with hermit-crabs in the Western Indian Ocean. *Crustaceana*, 17 (1) : 1–18.

LANG, K., 1948.—*Monographie der Harpacticiden.* Stockholm, Nordiska Bokhandeln.

————, 1965.—Copepoda Harpacticoidea from the Californian Pacific coast. *K. Svensk. Vetensk.-Akad. Handl.*, Ser. 4, 10 (2) : 1–560.

MONARD, A., 1926.—Note sur la faune des harpacticoides marins de Cette. *Arch. Zool. exp. gen.* 65, notes et revue, 2 : 39–54.

————, 1927.—Synopsis universalis generum harpacticoidarum. *Zool. Jahrb., Syst.*, 54 : 139–176.

————, 1937. Les harpacticoides marins de la région d'Alger et de Castiglione. *Bull. Trav. Stn. Aquicult. Peche Castiglione 1935*, 2 : 9–93.

NORMAN, A. M., and SCOTT, T., 1906.—*The Crustacea of Devon and Cornwall.* London.

PIKE, R. B., and WILLIAMSON, D. I., 1959.—Observations on the distribution and breeding of British hermit crabs and the stone crab (Crustacea : Diogenidae, Peguridae, and Lithodidae). *Proc. zool. Soc. Lond.*, 132 : 551–567.

POR, F. D., 1964.—A study of the Levantine and Pontic Harpacticoida (Crustacea, Copepoda). *Zool. Verh. Leiden*, 64 : 1–128.

————, 1967.—Level bottom Harpacticoida (Crustacea, Copepoda) from Elat (Red Sea), part 1. *Israel J. Zool.*, 16 : 101–165.

SARS, G. O., 1911.—*An Account of the Crustacea of Norway, 5. Harpacticoida.* Bergen Museum, Bergen, Norway.

SCOTT, A., 1909.—The Copepoda of the Siboga Expedition. I. Free-swimming, littoral, and semi-parasitic Copepoda. *Siboga Exped. Monogr.*, 29a : 1–323.

SEWELL, R. B. S., 1940.—Copepoda Harpacticoida. *Sci. Rep. John Murray Exped.*, 7 (2) : 117–382.

THOMPSON, I. C., and SCOTT, A., 1903.—Report on the Copepoda collected by Professor Herdman, at Ceylon, in 1902. *Rep. Govt. Ceylon Pearl Oyster Fish. Gulf of Manaar*, 1 (suppl. Rep. 7) : 227–307.

WELLS, J. B. J., 1967.—The littoral Copepoda (Crustacea) of Inhaca Island, Mozambique. *Trans. R. Soc. Edinburgh*, 67 (7) : 189–358.

A NEW PERMIAN AND UPPER CARBONIFEROUS (?) SUCCESSION NEAR WOODSREEF, N.S.W., AND ITS BEARING ON THE PALAEOGEOGRAPHY OF WESTERN NEW ENGLAND

Ilfryn Price*

[Accepted for publication 21st June 1972]

Synopsis

A fossiliferous Permian arenite (Ironbark Creek Arenite) occurs immediately west of the Peel Fault near Woodsreef. This overlies, with apparent conformity, a sequence containing both volcanic derived sediments (typical of the Carboniferous rocks of the region) and conglomerates similar to those in other Permian units in the Peel Fault Zone. It is suggested that this is a new Upper Carboniferous/Lower Permian sequence (Crow Mountain Creek beds). These two new units help confirm McKelvey and Gutsche's (1969) model for the Lower Permian palaeogeography of Western New England involving a tectonic high east of the Peel Fault. They provide more tentative support for Campbell's (1969) suggestion of a similar feature in the Upper Carboniferous. The development of a non-volcanic tectonic high east of the Peel Fault began before volcanic activity in the region had ceased and prior to the only folding episode in the area.

Introduction

It is nearly sixty years since W. N. Benson (1913) first demonstrated the importance of the tectonic boundary marked by the " Great Serpentinite Belt of N.S.W.". This boundary, now recognized as the Peel Fault, separates the eugeosynclinal " Central Complex " of the New England Geosyncline from the more gently deformed and broadly miogeosynclinal " Western Belt of Folds and Thrusts " (Voisey, 1959).

During 1970 the author undertook a detailed examination of some 80 km² of this terrain in the vicinity of the village of Woodsreef, some 17 km east of Barraba, a town 540 km north-west of Sydney. Evidence from this study, particularly from Upper Palaeozoic sediments west of the Peel Fault, provides a basis for examining aspects of the palaeogeography of western New England. This discussion is confined to the successions either side of the serpentinite body (Fig. 1) which obscures the Peel Fault around Woodsreef. These comprise an eastern succession of radiolarian jaspers, basic lavas and argillites and a western succession of conglomerates, arenites and mudstones.

Benson (1913) included the eastern succession in his Woolomin Series. Proud and Osborne (1952) considered the same rocks belonged to Benson's overlying Tamworth Series, but advanced no evidence for their revised interpretation. Lithologically, the eastern succession appears to belong to the Woolomin Beds (Crook, 1961*a*), within which identical associations are now placed elsewhere along the Peel Fault. Palaeontological data from the Woolomin Beds are limited to a few Silurian fossils (Lusk, 1963 ; R. L. Hall, pers. comm., 1970). The age of these rocks exposed around Woodsreef remains uncertain, but is most probably similar.

Correlation of the western succession with the stratigraphy of the central and western zones of the Western Belt of Folds and Thrusts is not so straightforward due to the relative structural complexity close to the Peel Fault together with the lack of palaeontological control and significant marker horizons. Benson (1913) allocated the sequence to his Lower Carboniferous " Burindi Series ", whilst Proud and Osborne (1952) preferred to refer the bulk of it to Benson's underlying " Barraba Series ". They restricted the Burindi Series to a narrow fault-bounded strip immediately adjacent to the Peel Fault. No such distinction was recognized by Leslie (1963), who placed all these rocks in the Lower Carboniferous Namoi Formation, bringing the stratigraphic nomenclature into line with that now in use farther west.

---

* Sedgwick Museum, Downing St., Cambridge CB2 3EQ, England.

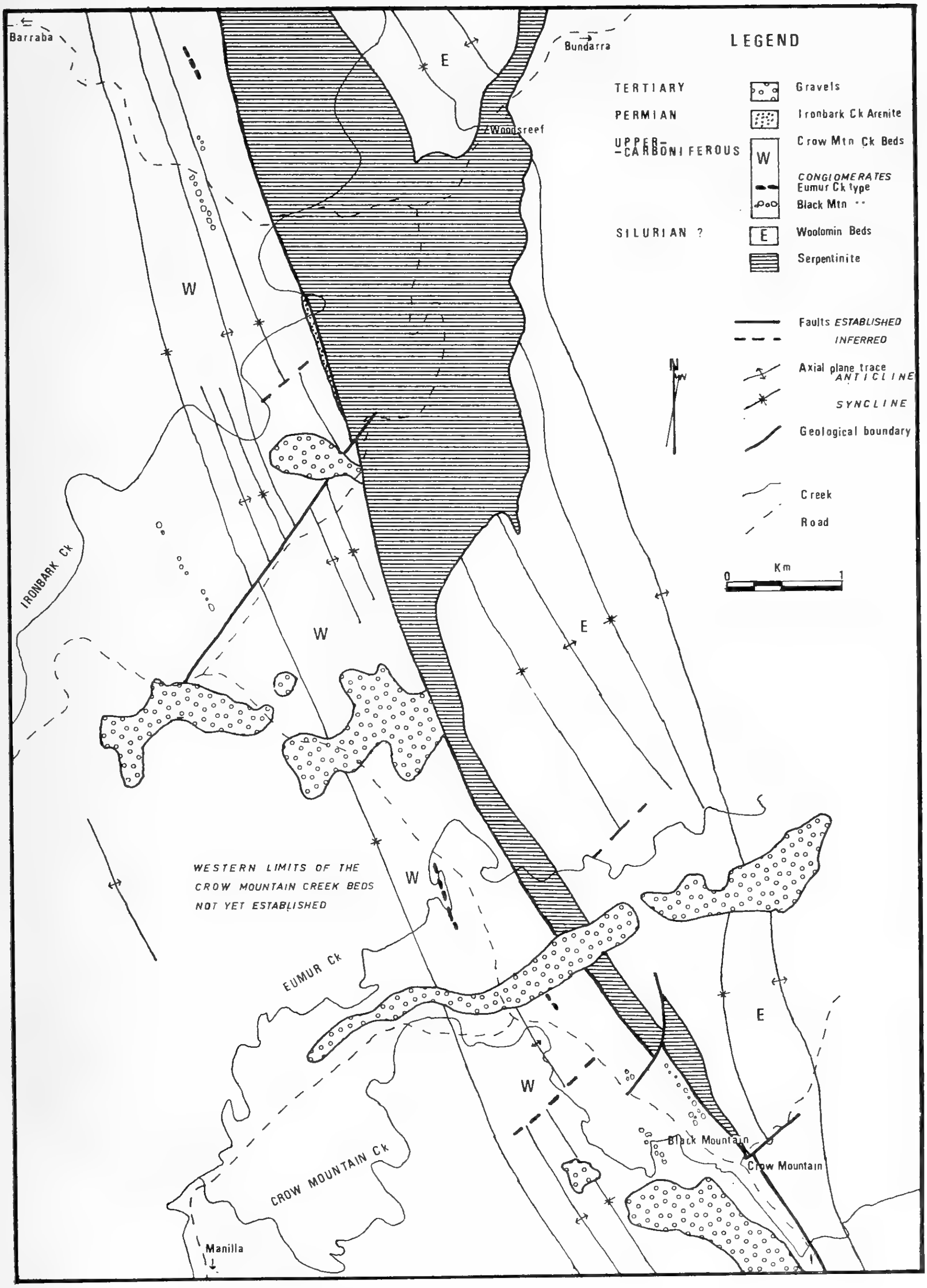


Fig. 1. Geological map of the Woodsreef area.

Further revision is justified. A new fossiliferous Permian arenite is described below. It is proposed that this be called the "*Ironbark Creek Arenite*". The remainder of the western succession cannot easily be correlated with known stratigraphic units in the region. In view of the uncertainty as to their exact age, all these rocks have been placed in a new unit, the "*Crow Mountain Creek beds*". This is suggested merely as an informal unit owing to the lack of a type section or an exact age for the rocks included therein.

STRATIGRAPHY OF THE WESTERN SUCCESSION

(1) *The Ironbark Creek Arenite*

The type section of this new unit is located on the southern bank of Ironbark Creek 0·8 km downstream of the bridge on the Barraba-Woodsreef road (U.N.E. Fossil Locality L891). Four spiriferids identified to date from the type locality (F10594–F10609 U.N.E. Fossil Catalogue) are:

Pseudosyrinx sp. nov.;
Sulciplica cf. stutchburii (Etheridge, 1892);
Trigonotreta cf. stokesi (Koenig, 1825);
Ingelarella ? ovata Campbell, 1961.

All these identifications were based on descriptions provided by Armstrong (1969). His time ranges suggest a Sakmarian or perhaps Lower Artinskian age for the fauna. In addition Dr. B. Runnegar (pers. comm., 1971) identified *Deltopecten* sp. from the type locality and suggested the fauna correlated with Dickins' (1968) Allandale fauna.

The new name is suggested for the arenite in which these fossils are found. It is tectonically overlain by serpentinite, whilst its lower limit is taken as the top of underlying mudstones. The Ironbark Creek Arenite becomes the third established occurrence of Permian sediments from the Peel Fault Zone. Others are:

(i) The Andersons Flat Beds (Crook, 1961*b*) near Nundle;
(ii) Unnamed fossiliferous Permian sediments north-east of Attunga (Hall, 1963).

The Ironbark Creek Arenite is probably a chronostratigraphic equivalent of the second of these two units (Runnegar, pers. comm., 1971).

Also, Johnston (1968) described Upper Carboniferous or Lower Permian rocks overlying fossiliferous Namoi Formation near Cobbadah, 20 km north of Woodsreef along the Peel Fault, but no reliable age has yet been obtained.

(2) *The Crow Mountain Creek Beds*

This informal name is proposed in order to simplify discussion of the palaeogeographic implications of the rocks in question. In this section reasons are outlined for not correlating these rocks with the known succession of the region.

Apart from rare worm burrows and crinoid ossicles, the only fossils found in the Crow Mountain Creek beds are a single rugose coral and a brachiopod fragment, both from a small limestone lens at the ford on the road into Black Mountain Homestead. These could not be positively identified but both Drs. B. Runnegar and J. Roberts suggested that they had a Carboniferous rather than a Devonian or Permian aspect.

Later in this paper two petrographic types of conglomerate in the Crow Mountain Creek beds will be described. One type contains abundant clasts of radiolarian jasper, a feature of Permian sediments along the Peel Fault (McKelvey and Gutsche, 1969). With the exception of these conglomerates the terrigenous sediments are all volcanogenic and resemble known Lower Carboniferous marine sediments in the Western Belt of Folds and Thrusts. The second conglomerate type has a volcanic clastal assemblage very similar to that found in the Middle (Upper ?) Carboniferous Rocky Creek Conglomerate, a terrestrial unit occurring farther west. Continuous exposure across beds of the jasper-bearing conglomerates shows that they are conformable with and not faulted into the volcanic-derived rocks.

The Ironbark Creek Arenite overlies mudstone of the Crow Mountain Creek beds with apparent conformity and no evidence of shearing along the contact. Whilst the fossiliferous unit might be a fault sliver in the Peel Fault Zone, there is no direct evidence of this, and at present it appears that the Permian arenite has a conformable association with mudstones of the type found throughout the Crow Mountain Creek beds.

Thus the western succession (excluding the Ironbark Creek Arenite) has affinities with both the Carboniferous and Permian of the surrounding region. Rocks of both ages may be present. The petrographic similarities with the Rocky Creek Conglomerate and the apparent conformity with the Ironbark Creek Arenite suggest that rocks of Upper Carboniferous age exist in the Woodsreef area. Furthermore, it appears that the jasper-bearing conglomerates are older than their petrographic equivalents in the Permian sediments along the Peel Fault to the south.

There is sufficient evidence to say that these rocks do not belong in the Namoi Formation as suggested by Leslie (1963). Deformation prevents the definition of a type section, and increases the difficulty in erecting a formal stratigraphic unit. Further work should establish the extent of the Crow Mountain Creek beds. At present their western contact with older sediments is thought to coincide approximately with a fold axis about 1·6 km west of the Peel Fault (Fig. 1). Jasper-bearing conglomerates have not been found west of this line. The fold axis may be faulted since it also marks a change in the intensity of folding. A representative section of the Crow Mountain Creek beds may be seen along Crow Mountain Creek between Crow Mountain and this fold axis.

GENERAL PETROGRAPHY

(1) *Introduction*

The Woolomin Beds comprise a sequence of jaspers, basic lavas and argillites. Very low-grade metamorphism has affected the sequence, leading to extensive recrystallization of the jaspers and, in suitable lithologies, the development of chlorites, white micas, albite, epidote, prehnite and pumpellyite. Radiolaria are rarely visible in the jaspers but they are abundant in less recrystallized specimens taken from xenoliths in the serpentinite.

Mudstones form the bulk (50–60%) of the Crow Mountain Creek beds. For present purposes they are unimportant and only the palaeogeographically significant arenites and conglomerates will be discussed here. The small limestone lens mentioned in the preceding section is the only limestone known in the unit to date. Two petrographic varieties of conglomerate, also recognizable in hand specimen, are found in the Crow Mountain Creek beds. They have been designated as types in order to describe and contrast them conveniently. Before so doing it must be emphasized that neither type is thought of as representing a particular stratigraphic marker and no correlation can be made between individual beds of either type.

(2) *Conglomerates of the Black Mountain type*

Type locality: In Crow Mountain Creek 75 m below the ford on the road to Black Mountain Homestead.

Lithology: Medium- to coarse-grained polymictic orthoconglomerates with well rounded clasts in a silty or arenaceous matrix of distinctly different grainsize.

Principal constituents of clasts: Andesitic volcanics and granodiorites.

Occurrence: As lenses throughout the area (Fig. 1), but more frequent in the south. These lenses are usually isolated within mudstones but in one instance the conglomerates form the basal bed to a massive arenite.

Discussion: The most extensive exposure occurs at the type locality, where a conglomerate lens has a maximum thickness of 12 m and a range in clast diameter from 10 to 50 cm. Many clasts are ellipsoidal, but no preferred orientation of their long axes could be recognized. The only indicator of palaeocurrent directions in these conglomerates is the northward decrease in abundance and clast size, suggesting a source in a very generally southerly direction.

Most clasts belong to an assemblage of andesitic lavas and ash-flow tuffs. Tonalites and granodiorites are common. The latter exhibit occasional granophyric intergrowths. They also have up to 1% of disseminated chalcopyrite. Less common clasts are fine-grained protoquartzites (in the sense of Pettijohn, 1957). These are distinctive due to their accessory constituents—zircon, muscovite, magnetite and plagioclase. Petrologically and texturally, they are very similar to quartzite clasts from the Rocky Creek Conglomerate described by Yeates (1970). This latter unit also has igneous clasts closely resembling those of the Black Mountain type conglomerates.

(3) *Conglomerates of the Eumur Creek type*

Type locality: In Eumur Creek 250 m west of the Barraba-Crow Mountain road.

Lithology: Fine- to medium-grained polymictic orthoconglomerates with subrounded irregularly shaped clasts and no sorting between clasts and matrix.

Principal constituents of clasts: Radiolarian jaspers and basic lavas.

Occurrence: As narrow beds at three widely separated localities (Fig. 1) with two beds at one locality and one at each of the others.

Discussion: As before, it is the type locality of these conglomerates which provides the most extensive exposure. Two beds of conglomerate outcrop, each about 2 m thick. These are separated by 1 m of mudstone. Both beds can be traced over a strike length of some 400 m, giving them a tabular or blanket form in contrast to the more lensoidal shape of the Black Mountain type conglomerates.

The only noticeable difference between jasper clasts in these conglomerates and the jaspers of the Woolomin Beds is the recrystallization and assumed destruction of Radiolaria in the latter. Basic lavas in clasts are texturally and petrologically similar to lavas east of the Peel Fault but have not been metamorphosed. Other materials in clasts are mudstones (including banded varieties), siltstones and rare intermediate lavas. One oolitic limestone fragment was noted in a specimen from the type locality.

The conglomerates are all poorly sorted with a range in grainsize from silt grade material to a maximum diameter of 2 cm. The coarsest clasts are found at the type locality. Graded bedding is visible in the most southerly occurrence.

In the section at the type locality arenites, striking parallel to the conglomerate bed, crop out a few metres above and below them. Eumur Creek cuts the type horizon of the conglomerates in two places (Fig. 1). The same relationship with the arenites may be seen in both outcrops, indicating conformable interbedding of the conglomerates with the arenites.

(4) *Arenites in the Crow Mountain Creek beds*

Two varieties are recognizable in outcrop. These are, firstly, thinly interbedded arenites in mudstones, and secondly, thick massive arenites. Individual beds of the first variety range from 1 to 20 cm in thickness, whilst the massive arenite beds are usually at least 10 m thick. Interbedding with arenites occurs over varying thicknesses of mudstones. These beds often show graded bedding and typical turbidite sole markings. Intraformational mudstone detritus is a less common feature of the massive arenites.

The rocks range from tuffs (waterlain and normally redeposited) through feldspathic arenites with a detrital pyroclastic or lithic volcanic component to volcanic derived lithic arenites. A greater abundance of pyroclastic material, principally devitrified glass and shards, is a feature of the interbedded arenites which are invariably the more tuffaceous of the two groups. Although still derived from a volcanic terrain, the massive arenites have a much greater lithic contribution. Pumice and volcanic glass fragments are the commonest lithic components, but fine-grained intermediate lavas, quartzites, mudstones, granophyric fragments and occasional carbonates are also present. There is a large variation in the relative abundance of feldspar and lithic material, whilst the quartz content is uniformly low. No arenaceous equivalent of the Eumur Creek conglomerates has been found. Burial metamorphic assemblages are absent.

(5) *The Ironbark Creek Arenite*

This is a massive unit much thicker (40 m maximum) than similar lithologies in the Crow Mountain Creek beds. Two other mesoscopic features distinguish it from the latter, namely:

(i) Abundant fossils mainly single brachiopod valves;
(ii) Dispersed, well-rounded clasts with a flattened ellipsoidal shape. Some have one flattened face, giving a hemi-ellipsoidal shape but with a smoothed and rounded edge.

Both these features are more prominent in the centre of the bed. At the type locality this central zone also contains a 15 cm bryozoan horizon.

The Ironbark Creek Arenite is a lithic labile arenite with a low feldspathic content. Quartz is more abundant than feldspar. The lithic contribution is not dominated by volcanic material, nor does the quartz appear to be of volcanic origin. Fine quartzose sediments are the principal lithic components, but they contain no radiolarian tests. Metaquartzite, mudstones and rare intermediate and basic lavas and ash flow tuffs complete the lithic assemblage.

PROVENANCE AND SEDIMENTATION OF THE WESTERN SUCCESSION

Arenites in the Crow Mountain Creek beds indicate an environment in which arenaceous volcanogenic debris periodically supplemented the prevailing mudstone sedimentation. Redeposited pyroclastic material, as evidenced by the arenites interbedded with mudstones, is the more common manifestation of this interruption. Graded bedding in, and cut-and-fill structures at the base of the thin arenite beds suggest they are turbidites (*cf.* Kuenen, 1964). Mass movement of poorly consolidated pyroclastic debris would be aided by the steep gradients and tectonic instability of an active volcanic terrain. The massive arenite beds are believed to represent the erosion of the better consolidated parts of such a terrain. Thus arenaceous sediments in the Crow Mountain Creek beds are interpreted as indicating the existence of a volcanic distributive province.

In contrast to the arenites, the conglomerates show two very different source areas; one chiefly volcanic and the other dominated by sedimentary rocks. Furthermore, material from each of these sources underwent very different sedimentation processes, a conclusion borne out by the textural differences between the two conglomerates.

The Black Mountain type conglomerates were probably derived from the same volcanic distributive province as the arenites with the inclusion of a subvolcanic plutonic component. Accommodating fine-grained protoquartzites into any model for a volcanic distributive province is difficult. As was mentioned above, identical clasts occur in the Rocky Creek Conglomerate to the west. It may be that the Black Mountain type conglomerates were reworked from this piedmont deposit. Without directional indicators it seems reasonable to assume that this volcanic province lay to the west since this is the direction suggested by all the vectorial evidence available for volcanic derived sediments in the Western Belt of Folds and Thrusts (McKelvey, pers. comm., 1970).

The Eumur Creek type conglomerates, in addition to their singular provenance, present a peculiar sedimentation problem. They are restricted in occurrence and are not associated with petrographically similar sands. Moreover, they are interbedded with volcanic derived arenites, indicating the close juxtaposition in time of two very different source areas. The poor sorting and low clastal sphericity of these conglomerates imply rapid transport from a nearby source area with only a limited period of deposition.

The only petrographically compatible source for the Eumur Creek type conglomerates is to the east from the Woolomin Beds. This implies a tectonic high east of the present line of the Peel Fault. This need not have formed a continuous land mass ; indeed, the limited extent of the conglomerates suggests it was discontinuous and only intermittently exposed to erosion. Such a situation also helps to explain the absence of arenaceous sediment derived from the same source area. Brief rapid erosion of a nearby terrain need not have yielded any detritus other than the poorly sorted material found in the Eumur Creek type conglomerates.

The dispersed ovoid clasts in the Ironbark Creek arenites must be explained. No local or regional evidence supports a glacial rafting hypothesis. Organic rafting explains neither their shape nor frequency. A more tenable hypothesis is that this unit represents an extremely shallow water sedimentary environment with the extraneous pebbles introduced by tidal currents. Smoothing of one face on some pebbles does not seem impossible in such a situation. Thus the Ironbark Creek Arenite is envisaged as indicating either a littoral or a near shore shoaling facies. Biogenic debris supports this hypothesis.

It is hard to link the petrography of the Ironbark Creek Arenite with either of the distributive provinces established for the Crow Mountain Creek beds. Elements of both are present in the rock. However, in a broad sense its predominantly sedimentary/metamorphic provenance links the arenite to the eastern distributive province.

Worm tracks in the mudstones, occasional crinoid ossicles in the arenites and the turbidite features of many of them show that the Crow Mountain Creek beds are marine. It is impossible to estimate the order of depth of the water in which they were deposited, but it is clear that the mudstone/arenite sediments represent deeper water sedimentation than the Ironbark Creek Arenite. A comparison of these two units indicates a shallowing of the sedimentary basin. This presumably accompanied the growth of the high to the east so that littoral conditions prevailed on its periphery.

The Woodsreef Area in a Regional Palaeogeographic Framework

Recently, two palaeogeographic reconstructions of Western New England have been proposed (Fig. 2) by Campbell (1969) for the Carboniferous and McKelvey and Gutsche (1969) for the Lower Permian. In Campbell's model for the Upper Carboniferous much of Central New England is occupied by an emergent tectonic high which he termed the " New England Arch ". A rather similar feature was suggested by McKelvey and Gutsche. They show a broad tectonic land between the Peel Fault and a line from Ashford through Inverell to Armidale. Permian sediments in New England are only known from either side of this block. The foregoing discussion confirms the existence of such an uplifted land area.

During this study the Upper Carboniferous or Permian sediments at Cobbadah (Johnston, 1968) were re-examined. They comprise a thick unit of arenites and conglomerates overlying fossiliferous Lower Carboniferous rocks with apparent conformity and show the supracrustal provenance characteristic of the Permian sediments along the Peel Fault. Orthoconglomerates are identical to the Eumur Creek type conglomerates and to the known Lower Permian conglomerates farther south at Attunga (Hall, 1963) which McKelvey and Gutsche used in their palaeogeographic model.

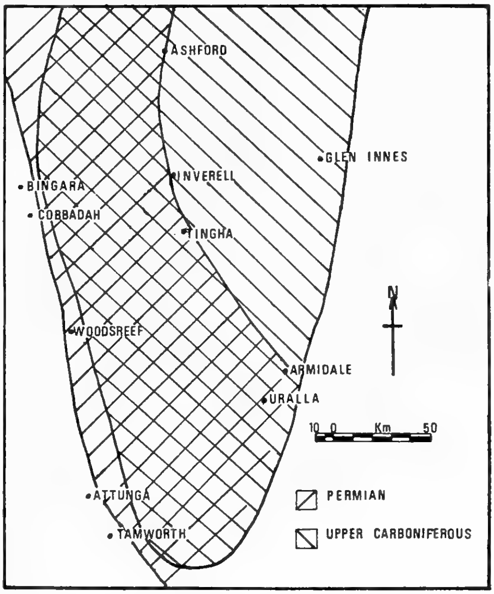


Fig. 2. The approximate locations of the Upper Carboniferous and Lower Permian land masses in New England suggested respectively by Campbell (1969) and McKelvey and Gutsche (1969).

Whilst the Eumur Creek type conglomerates and those at Cobbadah fit this model, the former are definitely older than the Ironbark Creek Arenite, and they are part of a succession in which the bulk of the clastic sediments have a volcanic provenance. Thus the New England Arch must have been initiated before volcanogenic sedimentation (presumably from the west) had finished. It seems likely that, east of Woodsreef at least, a land mass was intermittently exposed as early as the Upper Carboniferous. This may mark the first appearance of such a block prior to its more extensive development in the Lower Permian.

If the rocks at Cobbadah derived from the east are in fact Upper Carboniferous, as seems probable by the absence of palaeontological evidence, then it would imply the more extensive development northwards of the New England Arch. Farther south at Attunga the first known indication of this structure is in the Lower Permian, at which time a shallow water environment existed at Woodsreef and perhaps marine sedimentation had finished around Cobbadah.

Until palaeontological proof of the age of the Crow Mountain Creek beds or the similar rocks near Cobbadah is forthcoming, it cannot be said that they definitely confirm Campbell's model for the New England Arch. However, they do not negate his suggestions and it seems very probable that the New England

Arch was active in the Upper Carboniferous, at least north of the latitude of Woodsreef.

Folding west of the Peel Fault must postdate the Ironbark Creek Arenite, which is affected by the one deformation recognizable in the area. Thus the tectonic boundary now marked by the fault must have been an important palaeogeographic division well before the onset of folding and probably of faulting in the area. The eastern boundary of the Lower Permian land mass in Western New England must have been close to the Peel Fault, and the development of the adjacent tectonic high probably started as early as the Upper Carboniferous, before volcanic activity farther west had completely ceased.

ACKNOWLEDGEMENTS

This work was begun whilst the author was a student at the University of New England and completed at the University of Sydney with the support of a University Research Grant.

Dr. B. C. McKelvey's advice and criticism was greatly appreciated, as was that of Dr. B. Webby in revising the manuscript. Dr. B. Runnegar's help with the palaeontology is acknowledged with thanks, and Dr. H. J. Harrington, Mr. E. Leitch and Mr. G. McLung are likewise thanked for their suggestions in discussions on the area.

References

ARMSTRONG, J. D., 1969.—Permian Spiriferida of eastern Australia. Unpublished Ph.D. thesis, Uni. of Qld.

BENSON, W. N., 1913.—Geology and palaeontology of the great serpentinite belt of New South Wales. (i) Introduction. PROC. LINN. SOC. N.S.W., 38 : 662–724.

CAMPBELL, K. S. W., 1961.—New species of the Permian Spiriferids *Ingelarella* and *Notospirifer* from Queensland and their stratigraphical implications. *Palaeontographica A.*, 117 : 150–192.

————, 1969.—New England region, Carboniferous system, palaeogeography. *J. Geol. Soc. Aust.*, 16 (1) : 258–261.

CROOK, K. A. W., 1961*a*.—Stratigraphy of the Tamworth Group (Lower and Middle Devonian), Tamworth-Nundle district, N.S.W. *J. Proc. Roy. Soc. N.S.W.*, 94 : 173–188.

————, 1961*b*.—Post Carboniferous stratigraphy of the Tamworth-Nundle district, N.S.W. *J. Proc. Roy. Soc. N.S.W.*, 94 : 209–213.

DICKINS, J. M., 1968.—Correlation of the Permian of the Hunter Valley, N.S.W., and the Bowen Basin, Queensland. *Bull. Bur. Miner. Res. Geol. Geop. Aus.*, 80.

ETHERIDGE, R., 1892.—(In Jack, R. L., and Etheridge, R.) *The Geology and Palaeontology of Queensland and New Guinea.*

HALL, R. L., 1963.—The geology of an area northeast of Attunga, N.S.W. Unpublished B.Sc.(Hons.) thesis, U.N.E.

JOHNSTON, D. A., 1968.—The geology of the Halls Creek-Oaky Creek district, south of Bingara, N.S.W. Unpublished B.Sc.(Hons.) thesis, U.N.E.

KOENIG, G., 1825.—*Icones Fossilium Sectiles.* London.

KUENEN, P. H., 1964.—Deep-sea sands and ancient turbidites. (In *Developments in Sedimentology.* 3. *Turbidites.*) Elsevier, Amsterdam, 3–33.

LESLIE, R. B., 1963.—Geology of the Tamworth Trough area, N.S.W. Unpublished report, Frome-Broken Hill Co. Pty. Ltd., 6000–G–20.

LUSK, J., 1963.—Copper ores and their distribution in western New England. Unpublished M.Sc. thesis, U.N.E.

MCKELVEY, B. C., and GUTSCHE, N. W., 1969.—The geology of some Permian sequences on the New England Tablelands, N.S.W. *Spec. Publ. Geol. Soc. Aust.*, 2 : 13–20.

PETTIJOHN, F. J., 1957.—*Sedimentary Rocks.* (2nd Ed.) Harper and Row, New York.

PROUD, J. S., and OSBORNE, G. D., 1952.—Stress environment in the genesis of chrysotile with special reference to the occurrence at Woodsreef, near Barraba, N.S.W. *Econ. Geol.*, 47 : 3–23.

VOISEY, A. H., 1959.—Tectonic evolution of northeastern N.S.W., Australia. *J. Proc. Roy. Soc. N.S.W.*, 92 : 191–203.

YEATES, A. N., 1970.—The Gravesend Sequence. Unpublished B.Sc.(Hons.) thesis, U.N.E.

STUDIES IN THE ECOLOGY OF COASTAL HEATH IN NEW SOUTH WALES

I. Vegetation Structure

M. Y. Siddiqi,* R. C. Carolin* and D. J. Anderson†

[Accepted for publication 21st June 1972]

Synopsis

The structure of coastal heath has been studied at Mourawaring Point, New South Wales, using the DIVINF Classification programme of Lance and Williams (1968). Three main vegetation groups have been recognized in the area, based on divisions of an edaphic catenary sequence: (*a*) sand heath, (*b*) ground-water heath, and (*c*) peaty swamp. The sand heath may be divided into two groups, which are related to the depth of underlying water table: the " dry " sand heath (*Banksia serratifolia-Hypolaena fastigiata* group) and the " wet " sand heath (*Banksia ericifolia-Casuarina distyla-Hakea teretifolia-Schoenus brevifolius* group). The ground-water heath may be divided into a further three groups, based on the depth and nutrient status of the accompanying soils: the *Banksia ericifolia-Casuarina distyla-Hakea teretifolia-Cyathochaete diandra* group, the *Casuarina distyla-Themeda australis-Eragrostis* sp. group, and the *Casuarina nana-Banksia integrifolia-Westringia fruticosa* group. The peaty swamp is characterized as a *Baeckea imbricata-Juncus* sp. group.

Introduction

In any investigation of the distribution of a single species, or a group of species, a primary concern of an ecologist is to understand the whole system of which they form a part; autecological studies alone remain incomplete until they are integrated into the synecology of the community (*cf.* Anderson, 1960). But various autecological data cannot be integrated to provide a synthetic picture of plant communities except in a strictly subjective sense (see Anderson, 1963). Although various quantitative methods are currently available for examining the composite structure of plant communities, however, it must be emphasized that such synecological studies alone remain unsatisfactory, since studies on so large a scale are likely to raise more questions than they can answer.

The present paper deals with an analysis of macrostructure of a heath located at Mourawaring Point on the central coast of New South Wales. This study has been supplemented by investigations of the microdistribution of the most abundant heath species together with related experimental work which will be reported in subsequent papers.

Numerous quantitative techniques are now available for examining the composite and gross structure of plant communities. These techniques are based on one of two basic concepts underlying the description of vegetation: classification and ordination (see Curtis and McIntosh, 1951; Bray and Curtis, 1957; Williams and Lambert, 1959, 1960, 1961; Lambert and Williams, 1962, 1966; Anderson, 1965; Williams, Lambert and Lance, 1966; McIntosh, 1967; Greig-Smith *et al.*, 1967, etc.). For the present analysis, there are good reasons to select a classification procedure for the preliminary analysis of heterogeneity (Siddiqi, 1971), and of the classification procedures available, the technique of divisive information analysis (Lance and Williams, 1968) has been preferred.

Description of the Area

Situated within Bouddi State Park, about 10 miles north-east of Gosford, New South Wales, Mourawaring Point is a headland which faces the sea. The area comprises two opposing slopes, separated by a narrow gully. A creek runs

---

* Botany Building, School of Biological Sciences, University of Sydney, Sydney, N.S.W., 2006.

† School of Botany, University of New South Wales, Sydney, N.S.W.

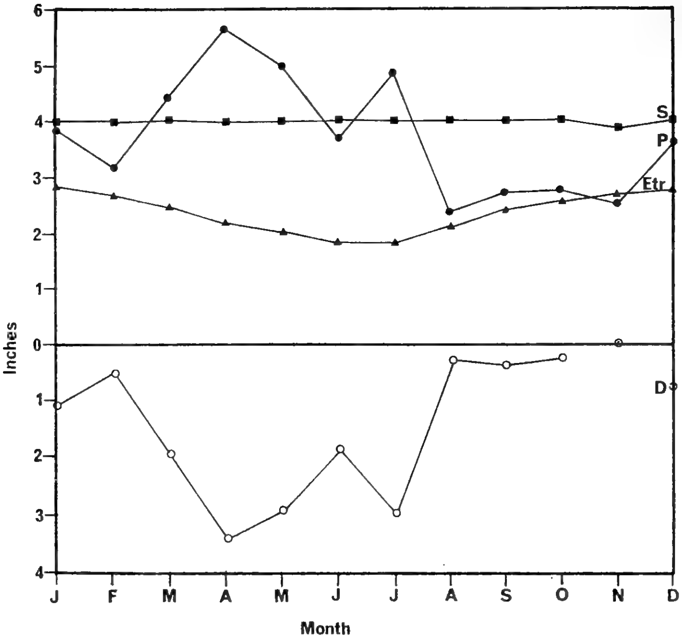


Fig. 1. Moisture budget of Sydney, calculated from climatic averages for thirty years (see text). Four inches are taken as the hypothetical maximum water storing capacity of soil.
S=Storage : P=Precipitation : Etr=Evapotranspiration : D=Drainage

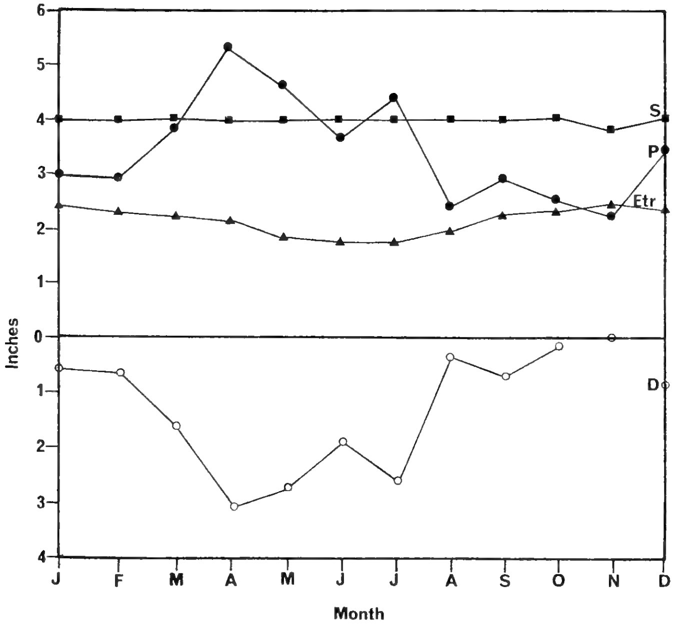


Fig. 2. Moisture budget of Newcastle, calculated from climatic averages for thirty years (see text). Four inches are taken as the hypothetical maximum water storing capacity of soil.
Symbols as in Fig. 1.

at the bottom of the gully and supports a typical swamp vegetation in its environs. The general topography of the area is shown in Fig. 3.

The east-facing slope has a deep sandy belt, surrounded by soils of higher clay content on either side. The transition between soil types is very sharp and is reflected in the equally sharp demarcation between the dominant vegetation types (see Fig. 4). The west-facing slope consists entirely of shallow clayey soil with iron-stones near the surface, with the exception of a narrow sandy belt at the top. The soils are derived from the shales and sandstone of the Gosford formation of the Narrabeen group within the Triassic series (see McElroy, 1957).

Fig. 3. Topographic map of the study area, showing location of sampling grids (light broken lines) and the distribution of the final groups (heavy broken lines) in relation to height contours. (Contour intervals in metres: large Roman numerals refer to Final Groups as shown in Fig. 5.)

Climatically, the area is situated in a moderately high rainfall belt along the east coast of Australia (mean rainfall = 47″). Figures 1 and 2 show the mean monthly precipitation and the moisture budgets for Sydney (*c.* 40 miles south) and Newcastle (*c.* 40 miles north), respectively the nearest meteorological stations available. The moisture budgets have been calculated according to Prescott, Collins and Shirpurkar (1952). The moisture index (Im) of Thornthwaite (1948) was calculated as +58 for Sydney and +62 for Newcastle. According to these indices the climate of Sydney would be described as B–2 humid (upper limit) and that of Newcastle as B–3 humid (lower limit).

The vegetation can be described as a typical heath (see, *e.g.*, Wood and Williams, 1960), with *Banksia serratifolia* as the most prominent shrub on the deep sandy ridge and *B. ericifolia*, *Hakea teretifolia* and *Casuarina distyla* the most prominent species on the clayey and sandy soils towards the gully. A typical swamp vegetation, dominated by *Baeckea imbricata* and *Juncus* sp., is present surrounding the creek on peaty water-logged soil.

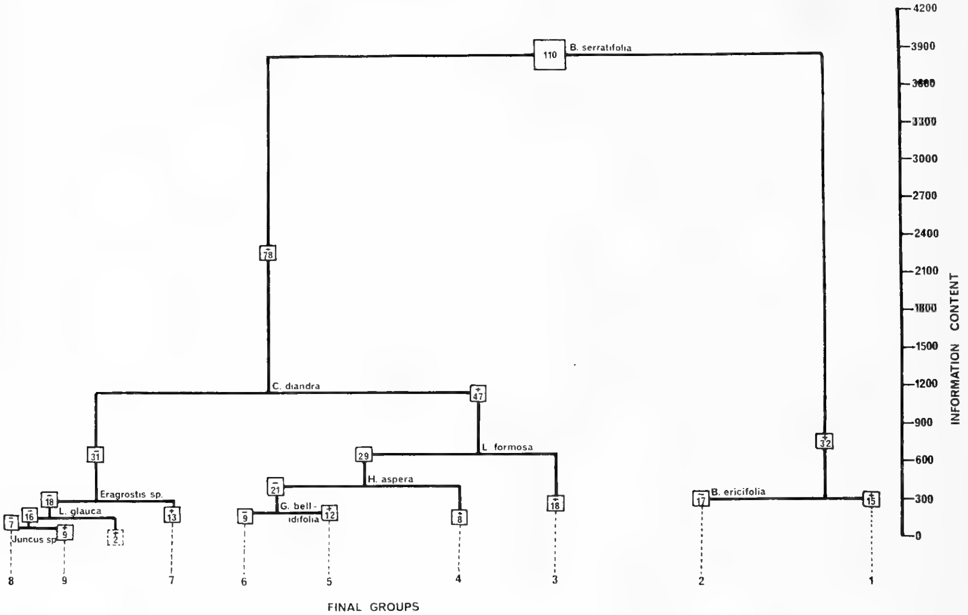


Fig. 4. The hierarchical species/site classification, obtained by the information analysis. The final groups are indicated by numbers which are used in the text.

METHODS

The entire area supporting a low heath vegetation at Mourawaring Point was sampled by a method of restricted randomization to obtain qualitative data for all the species present. Eleven grids, each 2,500 sq. m. in area, were initially located and presence or absence of species recorded for 10 randomly placed (5 × 5) m. quadrats within each grid, thus making data from a total of 110 primary sites available for analysis. Three random soil samples were collected in each site by means of a 6″ diameter auger; these samples were pooled to give a representative sample for each site. Both vegetation and soils were sampled in March, 1968.

A total of 106 species were encountered over the sampled area. Since many of these occurred so infrequently, it was decided to limit the analysis to those species which were present in five or more quadrats, a total of 72 species. The program " DIVINF " used in the present analysis is available at the C.S.I.R.O. Division of Computing Research, Canberra, A.C.T.

The soil samples were air-dried. The moisture factors (defined as air dry weight × 100/oven dry weight—Metson, 1956) were determined and subsequently the samples were analysed for pH, exchangeable Na, K, Ca, Mg, P, and total N.

The area has been topographically surveyed and the grids are mapped in relation to the contour intervals in Fig. 3.

Results

The results of the hierarchical monothetic species/site classification are shown in Fig. 4.

As programmed, 20 final groups have been obtained. It is apparent from Fig. 4 that the bulk of information content is carried by the first division, based on *Banksia serratifolia*. It would perhaps be appropriate to designate the two groups thus obtained as major groups, the group (+) *B. serratifolia* as major group I and the group (—) *B. serratifolia* as major group II.

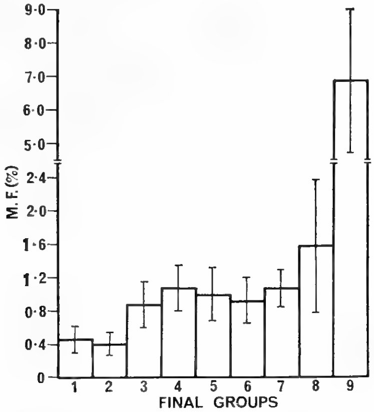


Fig. 5. Mean values of moisture factor (M.F.) of the final groups. 95% confidence limits are also indicated.

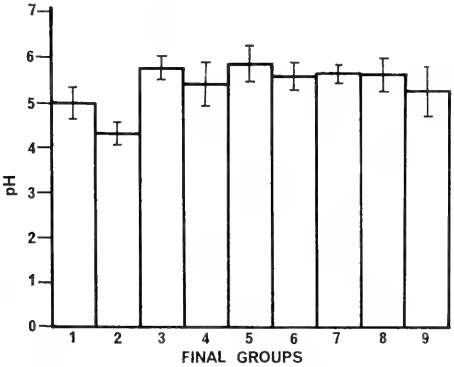


Fig. 6. Mean values of pH of the final groups. 95% confidence limits are also indicated.

An initial problem in the treatment of data is to select the hierarchical level below which the divisions can be considered insignificant. One approach to this problem is the objective one of using a significance test (twice the information fall may be taken as a conservative estimate of χ^2 see Webb *et al.*, 1967), thereby discarding all the divisions below that level. Alternatively, it is possible to be entirely subjective and accept all those groups which are explicable in ecological terms. The problem with the application of an entirely objective approach is that sometimes the divisions at a lower hierarchical level are ecologically more important than indicated statistically, and potentially valuable information may be lost by discarding these divisions. (This problem may arise as a result of great unevenness in the number of species in different groups, as has been observed in the present case, *e.g.* final groups 8 and 9). In the present instance, therefore, these groups below the formal level of significance (300 I.C.), which appear from field experience to be ecologically significant, have been accepted.

Using this criterion, nine groups are obtained. The distribution of these groups in the field is shown in Fig. 3.

The mean values of the soil variables calculated for the nine site groups are compared in Figs 5–12.

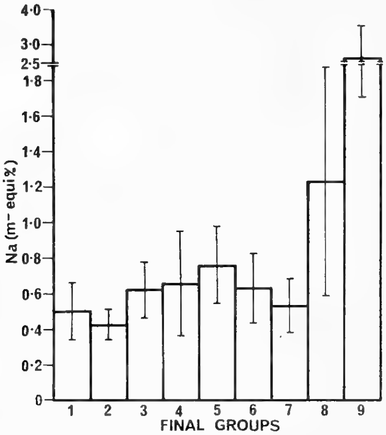


Fig. 7. Mean values of exchangeable sodium (Na), expressed as milliequivalent percentage of oven-dry soil, of the final groups. 95% confidence limits are also indicated.

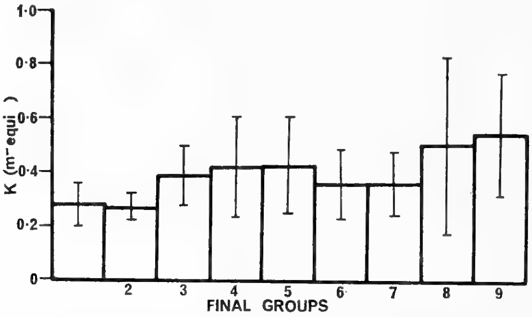


Fig. 8. Mean values of exchangeable potassium (K), expressed as milliequivalent percentage of oven-dry soil, of the final groups. 95% confidence limits are also indicated.

Unfortunately, a complete fire history is not available for the area. The only information available from non-authenticated sources is that the area was completely burnt 12–15 years prior to the date of collection of data in this study, followed by one or two small-scale, localized fires, the last being 3–4 years prior to collection of data (*c.* 1964). The pattern produced by the last burn can still be seen ; the tall, dense scrub of *Banksia ericifolia*, *Casuarina distyla* and *Hakea teretifolia* in the gully represents the site left unburnt in this last fire.

A comparison of the soil analyses indicates that the first division, based on *B. serratifolia*, distinguishes the vegetation into the major groups on the basis of the physical soil structure. Major group I, (+) *B. serratifolia*, is confined to those sites with an entirely sandy soil profile. The two final groups recognized within this major group represent a wetter situation (group 1, (+) *Banksia* *ericifolia*) with a shallower water table (*c.* 90–150 cm.) and higher pH ; and a drier situation (group 2, (—) *B. ericifolia*) with a very deep water table (considerably deeper than 180 cm.—the exact extent was not determined, but it seems to be below the level where it may be important for root growth) and more acid in reaction. The nutrient status of soils from the two groups is strikingly similar except for Na, which is relatively higher in the group 1 soils (Figs 5–12).

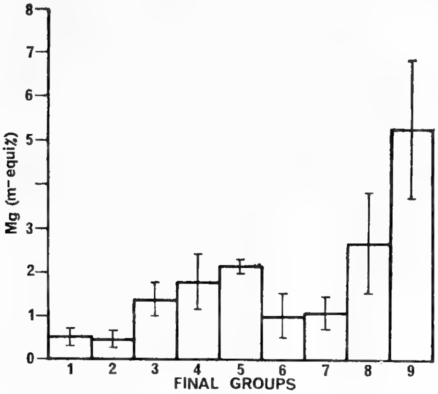


Fig. 9. Mean values of exchangeable magnesium (Mg), expressed as milliequivalent percentage of oven-dry soil, of the final groups. 95% confidence limits are also indicated.

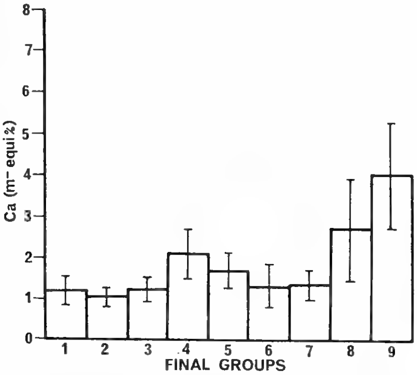


Fig. 10. Mean values of exchangeable calcium (Ca), expressed as milliequivalent percentage of oven-dry soil, of the final groups. 95% confidence limits are also indicated.

Major group II includes seven final groups (3–9). The first division within this major group is based on *Cyathochaete diandra*, which differentiates a habitat with a shallow horizon of sandy loam, a shallow or deep horizon of clayey loam over a relatively impermeable clay layer, (+) *C. diandra* section, from a (—) *C. diandra* section which contains three varied habitats : (*a*) a steep slope with little or no sandy top soil, a thin loamy horizon over a thin clay layer (with exposed rock faces at some sites), bordering on swamp on one edge ; (*b*) a clayey ridge with relatively well developed loamy and clayey horizons, extending to the opposing edge of the swamp ; and (*c*) the peaty swamp.

The next division in the (+) *C. diandra* section is based on *Lambertia formosa*. The sub-section (+) *L. formosa* (group 3) consists of sites located on the west-facing slope, with a shallow loamy horizon on clay with iron-stones on the surface.

The sub-section (—) *L. formosa* consists of two distinct habitats: (*a*) with a deep loamy horizon, and (*b*) with a shallow loamy horizon, which are distinguished in the next division of this sub-section, based on *Hibbertia aspera*. Group 4 ((+) *H. aspera*) represents the sites with a fairly prominent, deep loamy horizon over relatively impermeable clay, whereas the (—) *H. aspera* part of the division represents the sites with a shallow loamy horizon. The subsequent division of this part is based on *Goodenia bellidifolia*, group 5 ((+) *G. bellidifolia*) represents the slopes and parts of the gully which were burnt in the previous fire; whereas group 6 ((—) *G. bellidifolia*) represents that part of the gully which has not been burnt for the last 12–15 years and which supports a tall, dense scrub of *Banksia ericifolia*, *Casuarina distyla* and *Hakea teretifolia*. Although the soils of groups 5 and 6 are more or less similar in their profiles, the soils of group 5 show an increase in the mean nutrient status.

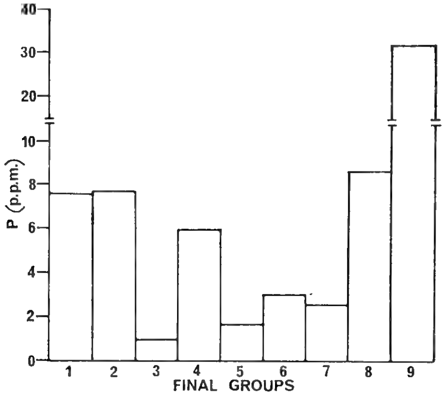


Fig. 11. Mean values of exchangeable phosphorus (P), expressed as parts per million (p.p.m.), of the final groups. Confidence limits are not calculated since in some final groups only few degrees of freedom were available (see text).

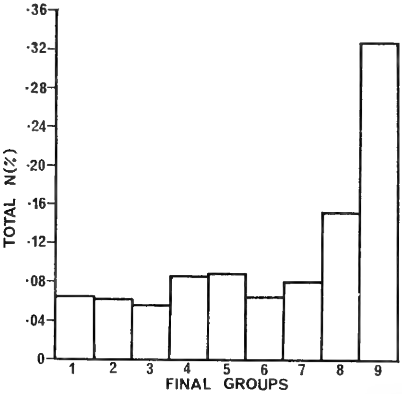


Fig. 12. Mean values of total nitrogen (N), expressed as percentage of oven-dry soil, of the final groups. Confidence limits are not calculated since in some final groups only few degrees of freedom were available (see text).

The next division in the *C. diandra* section is on *Eragrostis* sp. Group 7 ((+) *Eragrostis* sp.) consists of sites with a truncated profile, with a shallow clayey layer, bordering on the swamp on one edge. The section (—) *Eragrostis* sp. shows a lower level of heterogeneity on the hierarchical level, but ecologically it is still very heterogeneous, including both swampy and non-swampy sites. The next division in this section is on *Lomandra glauca*, the (+) *L. glauca* group separating the two sites on the west-facing slope with loose yellow sand, from (−) *L. glauca* section with the remaining non-swampy sites bordering on the swamp and the swampy sites. The division in this section, based on *Juncus* sp., separates the non-swampy sites, group 8 ((+) *Juncus* sp.). Group 8 is still somewhat heterogeneous, consisting of three sites on the nutritionally richer clayey ridge on the southern side of the swamp and four sites on the northern and eastern banks of the swamp whose nutrient values are comparable to the mean values of groups 3–7.

Exchangeable phosphorus and total nitrogen were determined for a batch of 44 samples, four from each grid. The mean values of P-content for the final groups are plotted in Fig. 11. This shows a relatively high P-content for groups 1 and 2 soils (7–9 p.p.m.) on the sandy sites as compared to most of the ground-water heath sites, excluding the swamp and the sites bordering on it. Within the loamy and clayey sites the values are relatively higher (5–7 p.p.m.) on the sites with well developed top soil (group 4) and decrease to a minimum of *ca.* 1 p.p.m. on the sites where the top soil is shallow (group 3, *ca.* 1–2 p.p.m.; group 5, 1–2 p.p.m.; group 6, 2–3 p.p.m.; group 7, 2–5 p.p.m.; group 8, 2–5 p.p.m. on the northern and eastern boundaries and 16 p.p.m. on the southern clayey ridge). The swampy sites show a relatively high P-content, *ca.* 40 p.p.m., which is probably due in part to the dissolution of organic matter.

The mean values of total nitrogen for the final groups are compared in Fig. 12. This figure shows a degree of uniformity among the soils of all the groups, except for the soils of groups 8 and 9, which show a relatively high N-content (0·152% and 0·329% respectively) than the rest (0·057–0·088%). However, Hannon (1956) has reported very low values for nitrate nitrogen for similar soils, the highest being 2 p.p.m. in surface layer of a swamp, with the ammoniacal nitrogen usually in the range of 1–2 p.p.m.

The characteristic vegetation types of the final groups are summarized in Appendix 1, together with the notes on the relationship of species within the two major groups. The terms characteristic vegetation type and characteristic species are used in a very general sense to define the species which occur in all or nearly all the quadrats (sites) of a particular group.

DISCUSSION

The two major groups obtained from the first division based on *Banksia serratifolia* broadly correspond to the ecosystems recognized by Groves (1964) and Groves and Specht (1965) within the Victorian heath formation, on a sub-formation level, *viz.* " sand heath " (major group I) and " ground-water heath " (major group II). By contrast with the results of Groves (1964) and Groves and Specht (1965), however, a clear-cut floristic and structural differentiation between the two ecosystems is indicated in the present case. In sand heath, *B. serratifolia* is dominant on the deep sandy ridge where the water table is very deep (group 2), whereas in the gully, where the water table is shallow, *B. ericifolia*, *Casuarina distyla* and *Hakea teretifolia* become dominant (similar to the ground-water heath). However, in both the situations more than 50% of the characteristic species are those which occur exclusively in the sand heath, the proportion being greater (70%) in group 2 than group 1 (52%). On the other hand, major group II (except the swamp and the sites bordering on it) is dominated by *B. ericifolia*, *C. distyla* and *H. teretifolia*, and *c.* 30% of the characteristic species are those which occur exclusively in major group II.

The exclusive occurrence of these species in any one situation within a small area presents an intriguing problem. Although the sand heath sites and the ground-water heath sites differ in their nutrient status, the difference is relatively slight among many sites. It is difficult to imagine that so small a difference would produce such a sharp zonation among so large a number of species. Groves (1964) and Groves and Specht (1965) have attributed the difference in the growth curves of their heath ecosystems to the drying out of the top soil in the ground-water heath during the summer dry periods. At Mourawaring Point, however, the rainfall is high and scattered through the year. An examination of the moisture budget (see Figs 1 and 2) indicates that no severe water deficiency is experienced throughout the course of most years. Another important factor operating in the present area is the variation in water table, but this variation does not serve to explain the delimitation of these species since the depth of water table in the gully in sand heath is about the same as at most of the ground-water heath sites, although it seems to affect the overall structure of the community due to the taller growth of the shrub species *B. ericifolia*, *C. distyla* and *H. teretifolia* in this habitat.

Under these climatic conditions, the aeration of the top soil may be expected to be very different between the sandy sites and the ground-water heath sites. Flocker *et al.* (1959) and Pearson (1966) have suggested that in moist compact soils inadequate aeration is the most important factor in controlling root growth. The heathland species, with the bulk of their root system within the top few inches of soil (*cf.* Specht and Rayson (1957*b*); Botany Department, Sydney University (unpublished data from Myall Lakes); Clarke (1967)) are therefore likely to be affected by this aeration factor to a considerable extent. Thus, since the depth of the water table is similar in the wet sand heath and most of the ground-water heath, it seems reasonable to suggest that the physical soil structure through its control of aeration is probably the most important determinant in the delimitation of the exclusive sand heath species. Another important factor which requires consideration is competition, especially in a case of such a sharp zonation among a large number of species within a small area. It may well be that these species are capable of growing in the ground-water heath, but that their competitive ability is greatly reduced under poor aeration that they are eliminated by the more aggressive species of this habitat. Similarly, the converse may be true for the exclusive ground-water heath species. Loach (1964), Sheikh (1969*a*, 1969*b*, 1970) and Sheikh and Rutter (1969) have studied English wet heath vegetation in relation to aeration, and suggest that the exclusion of *Erica tetralix* from well-aerated soils is mainly due to competition with *Molinia*, a very aggressive species in this habitat. Bannister (1964) has also demonstrated the operation of an interspecific competition factor, operating between individuals of *Calluna* and *Erica*, which results in the eventual elimination of the latter.

The difference in the structure and composition of the " wet " sand heath (sand heath in the gully where the water table is shallow) and the " dry " sand heath (sand heath at the deep sandy ridge with deep water table) may be attributed either to a (seasonally) high water table, or competition, or a combination of both. That is, the absence in dry sand heath of such species as *Banksia ericifolia*, *B. aspleniifolia*, *Casuarina distyla* and *Hakea teretifolia* (which are dominant in the " wet " sand heath) may be attributed either to a relatively low water availability due to a deep water table or to their inability to compete with the species which are more aggressive at the sites with a deep water table and well-aerated top soil, or to a combination of both. Conversely, their occurrence in the " wet " sand heath in a dominant role may be attributed to an increased water availability due to shallower water table or to a much reduced intensity of competition with the otherwise aggressive species of sand heath, *e.g. B. serratifolia*. The reduction in density of *B. serratifolia* in " wet " sand heath is evident from a casual examination of the area. Rutter (1955) has similarly shown a clear relationship of vegetation with water table in samples of British wet heaths and suggests that although the water table depth may have important direct effects, some of the changes in abundance of a particular species may be due largely to changes in the competitive power of its associates.

Within the ground-water heath, the general structure of vegetation seems to be rather similar (except the swamp and the sites bordering on it) with most of the characteristic species being common in all the groups. The dominant species in all these groups (except group 7) are *Banksia ericifolia*, *Casuarina distyla* and *Hakea teretifolia*. Group 6 marks the 12–15 years old fire line, the area which supports mature, tall, dense scrub of the three dominant species. This area is species-poor (*c.* 15 species/25 sq. m.) in comparison to the groups 3–5 (*c.* 20 species/25 sq. m.), which contain the seedlings of the three dominant species with no tall storey and represent an area which was burnt 3–4 years prior to collection of data. Group 6, among its 10 characteristic species contains only low herbaceous species apart from the three dominants, whereas groups 3–5 have few other richly represented shrubs among their 15–20 characteristic species. It seems likely that this differentiation within the ground-water heath is primarily due to an open canopy as a result of fire and the composition of vegetation in these groups would perhaps be similar as a result of elimination of photophilic species which seem to have relatively narrow tolerance ranges. In general, the nutrient status of soils of these groups is similar except that phosphorus is relatively higher in group 4 soils and magnesium and calcium are slightly higher in groups 4 and 5 soils, than the rest.

The occurrence of *Lambertia formosa* only on the group 3 sites (situated on the west-facing slope) is associated both with aspect and the presence of iron-stones near the soil surface. The association of *L. formosa* with iron-stones has also been noticed on slopes of other than west-aspect.

Group 4 represents sites found on the east-facing slope which exhibit a well-defined deep loamy horizon, with a relatively impermeable clay layer at a depth of more than 90 cm. The generally improved nutrient status (especially phosphorus) of the soils of this group is associated with deep loamy horizon, in which a relatively large biomass of roots are found, compared to the sites where the impermeable clay layer is closer to the surface. Following a fire, the decay of these dead roots results in a gradual release of nutrients, particularly phosphorus (Groves (1964) and Jeffrey (1964, 1967) have shown that the roots of *Banksia ornata* and *B. serrata*, especially the proteoid roots, store large amounts of phosphorus). The species which occur exclusively in this group are *Banksia spinulosa*, *Hibbertia aspera*, *Scaevola ramosissima* and *Lasiopetalum ferrugineum*. Their exclusive occurrence in this area may be attributed either to an improved nutrient status (particularly of phosphorus) or to a deeper water table as compared to the other sites of the ground-water heath.

Group 5 is very similar to group 6 in the development of soil profiles and associated nutrient status, except for magnesium, which is relatively high in the soils of this group. The segregation of this group from group 6 seems to be due to the introduction and propagation of photophilic species in the absence of a tall storey, *e.g. Banksia aspleniifolia*, *Goodenia bellidifolia*, etc.

Soils of group 7 sites are shallow, with a truncated profile overlying the rock bed. There is some evidence of top soil erosion, which may be due in part to wind since this area lies at the mouth of a " wind-funnel ". This subjection to frequent wind cut may account for the abundance of low-grown shallow-rooted species in these sites.

Group 8 includes three sites on the north-facing clayey ridge which have a markedly higher nutrient status in comparison to all other non-swampy sites. These sites contain *Banksia integrifolia* and *Casuarina nana*, which occur here exclusively. There is no obvious explanation available for such an increase in soil nutrients except that this area is a nesting place for sea birds, being close to the sea and *Casuarina nana* bushes providing adequate shelter. The remaining sites in this group lie at the boundary of swamp and are nutritionally similar to the other ground-water heath sites.

Group 9 consists entirely of the swampy sites which remain waterlogged throughout the year. This area is dominated by tall *Baeckea imbricata* bushes.

Thus, it seems that fire regimes, physical structure of soil (aeration), depth of water table and, to a lesser extent, nutrient status of soil are the main determinants of the large-scale mosaic of vegetation (site groups). It may be pointed out, however, that these hypotheses regarding the relationship of various species with the environmental factors, and with each other, require substantiation from analysis of their small-scale distribution as related to edaphic factors and experimental evidence. This will be presented in subsequent communications.

ACKNOWLEDGEMENTS

The authors wish to thank Dr. P. J. Myerscough for his helpful suggestions and criticism. The work was carried out as part of a Ph.D. thesis while one of us (M.Y.S.) was receiving a University of Sydney Post Graduate Research Studentship, which is gratefully acknowledged. We also wish to thank the National Parks and Wildlife Service of N.S.W. for permitting us to make use of the Bouddi State Park.

References

ANDERSON, D. J. (1960).—A comparison of some upland plant communities with particular reference to their structure. Ph.D. thesis, University of Wales.

———, 1963.—The structure of some upland plant communities in Caernarvonshire. III. The continuum analysis. *J. Ecol.*, 51 : 403–414.

———, 1965.—Classification and ordination in vegetation science : controversy over a non-existent problem ? *J. Ecol.*, 53 : 521–526.

BANNISTER, P., 1964.—The water relations of certain heath plants with reference to their ecological amplitude. III. Experimental studies : General conclusions. *J. Ecol.*, 52 : 499–509.

BRAY, J. R., and CURTIS, J. T., 1957.—An ordination of the upland forest communities of Southern Wisconsin. *Ecol. Monogr.*, 27 : 325–349.

CLARKE, C. D., 1967.—The relationship between water table level and distribution of *Banksia spp.* in the Myall Lakes region. B.Sc.(Hons.) thesis, University of Sydney.

CURTIS, J. T., and MCINTOSH, R. P., 1951.—An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology*, 32 : 476–496.

FLOCKER, W. J., VOMOCIL, J. A., and HOWARD, F. D., 1959.—Some growth responses of tomatoes to soil compaction. *Soil Sci. Soc. Amer. Proc.*, 23 : 188–191.

GREIG-SMITH, P., AUSTIN, M. P., and WHITMORE, T. C., 1967.—The application of quantitative methods of vegetation survey. I. Association-analysis and principal component ordination of rain forest. *J. Ecol.*, 55 : 483–503.

GROVES, R. H., 1964.—Experimental studies on heath vegetation. Ph.D. thesis, University of Melbourne.

———, and SPECHT, R. L., 1965.—Growth of heath vegetation. I. Annual growth curves of two heath ecosystems in Australia. *Aust. J. Bot.*, 13 : 261–280.

LAMBERT, J. M., and WILLIAMS, W. T., 1962.—Multivariate methods in plant ecology. IV. Nodal analysis. *J. Ecol.*, 50 : 775–802.

———, 1966.—Multivariate methods in plant ecology. VI. Comparison of information-analysis and association-analysis. *J. Ecol.*, 54 : 635–664.

LANCE, G. N., and WILLIAMS, W. T., 1968.—Note on a new information-statistic classificatory program. *Comp. J.*, 11 : 195.

LOACH, K., 1964.—Inter-relations between soil nutrients and vegetation in wet heaths. Ph.D. thesis, University of London. Cited by Sheikh, K. H., 1969*a*, in *J. Ecol.*, 57 : 89–101.

MCELROY, C. T., 1957.—Sydney-4-mile Geological Series Explanatory Notes No. 6. *Bur. Min. Resour.*

MCINTOSH, R. P., 1967.—The continuum concept of vegetation. *Bot. Rev.*, 33 : 130–187.

METSON, A. J., 1956.—Methods of chemical analysis for soil survey samples. New Zealand D.S.I.R.

PEARSON, R. W., 1966.—Soil environment and root development. In Plant Environment and Efficient Water Use (Ed. R. H. Pierre *et al.*) (Amer. Soc. Agr. and Soil Sci. Soc. Amer.—Publishers.)

PRESCOTT, J. A., COLLINS, J. A., and SHIRPURKAR, G. R., 1952.—The comparative climatology of Australia and Argentina. *Geog. Rev.*, 42 : 118–133.

Rutter, A. J., 1955.—The composition of wet heath vegetation in relation to the water table. *J. Ecol.*, 43 : 507–543.

Sheikh, K. H., 1969*a*.—The effects of competition and nutrition on the interrelations of some wet-heath plants. *J. Ecol.*, 57 : 89–101.

————, 1969*b*.—The responses of *Molinia caerulea* and *Erica tetralix* to soil aeration and related factors. II. Gas concentration in soil air and soil water. *J. Ecol.*, 57 : 727–736.

————, 1970.—The responses of *Molinia caerulea* and *Erica tetralix* to soil aeration and related factors. III. Effects of different gas concentrations on growth in solution culture : And general conclusions. *J. Ecol.*, 58 : 141–154.

————, and Rutter, A. J., 1969.—The responses of *Molinia caerulea* and *Erica tetralix* to soil aeration and related factors. I. Root distribution in relation to soil porosity. *J. Ecol.*, 57 : 713–726.

Siddiqi, M. Y., 1971.—An ecological analysis of coastal heath in New South Wales. Ph.D. thesis, University of Sydney.

Specht, R. L., and Rayson, P., 1957*b*.—Dark Island heath (Ninety-Mile Plain, South Australia). III. The root systems. *Aust. J. Bot.*, 5 : 103–114.

Thornthwaite, C. W., 1948.—An approach toward a rational classification of climate. *Geog. Rev.*, 38 : 55–94.

Webb, L. J., Tracey, J. G., Williams, W. T., and Lance, G. N., 1967.—Studies in the numerical analysis of complex rain-forest communities. I. Comparison of methods applicable to site/species data. *J. Ecol.*, 55 : 171–191.

Whittaker, R. H., 1962.—Classification of natural communities. *Bot. Rev.*, 28 : 1–239.

Williams, W. T., and Lambert, J. M., 1959.—Multivariate methods in plant ecology. I. Association analysis in plant communities. *J. Ecol.*, 47 : 83–101.

————, 1960.—Multivariate methods in plant ecology. II. The use of an electronic digital computer for association analysis. *J. Ecol.*, 48 : 689–710.

————, 1961.—Multivariate methods in plant ecology. III. Inverse association analysis. *J. Ecol.*, 49 : 717–729.

Williams, W. T., Lambert, J. M., and Lance, G. N., 1966.—Multivariate methods in plant ecology. V. Similarity analyses and information-analysis. *J. Ecol.*, 54 : 427–445.

Wood, J. G., and Williams, R. J., 1960. *Vegetation. In the Australian Environment.* (C.S.I.R.O. Aust., Melbourne.)

APPENDIX I

CHARACTERISTIC VEGETATION TYPES OF THE FINAL GROUPS

* indicates presence exclusively in that major group.

** indicates the presence of the species in both the major groups.

The numbers in parentheses indicate the groups which contain that particular species, within the major group.

Authorities for the binomials as in Beadle, Evans and Carolin, " Flora of the Sydney Region " Reeds (in press).

MAJOR GROUP I

GROUP 1. (+) BANKSIA ERICIFOLIA

Lomandra glauca	**	(1 and 2)
Hypolaena fastigiata	*	(1 and 2)
Schoenus brevifolius	**	(1)
Casuarina distyla	**	(1 and 2)
Hakea teretifolia	**	(1 and 2)
Banksia aspleniifolia	**	(1 and 2)
Banksia serratifolia	*	(1 and 2)
Banksia ericifolia	**	(1)
Acacia suaveolens	*	(1 and 2)
Bossiaea ensata	*	(1 and 2)
Aotus ericoides	*	(1 and 2)
Eriostemon lanceolatus	*	(1 and 2)
Hibbertia obtusifolia	*	(1 and 2)
Hibbertia fasciculata	*	(1 and 2)
Haloragis teucrioides	**	(1 and 2)
Pimelia linifolia	**	(1 and 2)
Actinotus helianthi	**	(1)
Platysace linearifolia	*	(1 and 2)
Dampiera stricta	**	(1 and 2)

GROUP 2. (—) BANKSIA ERICIFOLIA

Lomandra glauca	**	(2 and 1)
Lomandra micrantha	**	(2)
Hypolaena fastigiata	*	(2 and 1)
Anisopogon avenaceus	*	(2)
Banksia serratifolia	*	(2 and 1)
Acacia ulicifolia	*	(2)
Acacia suaveolens	*	(2 and 1)
Bossiaea ensata	*	(2 and 1)
Aotus ericoides	*	(2 and 1)
Eriostemon lanceolatus	*	(2 and 1)
Hibbertia obtusifolia	*	(2 and 1)
Hibbertia fasciculata	*	(2 and 1)
Haloragis teucrioides	**	(2 and 1)
Pimelia linifolia	**	(2 and 1)
Platysace linearifolia	*	(2 and 1)
Dampiera stricta	**	(2 and 1)

MAJOR GROUP II

GROUP 3. (+) LAMBERTIA FORMOSA

Lomandra glauca	**	(3, 5)
Cyathochaete diandra	**	(3, 4, 5, 6)
Schoenus brevifolius	**	(3, 5)
Casuarina distyla	**	(3, 4, 5, 6, 7)
Petrophile fucifolia	**	(3)
Hakea teretifolia	**	(3, 4, 5, 6)
Lambertia formosa	*	(3)
Banksia ericifolia	**	(3, 4, 5, 6)
Acacia myrtifolia	*	(3, 4, 5, 6)
Callistemon citrinus	**	(3, 6)
Pimelia linifolia	**	(3, 4, 7)
Actinotus helianthi	**	(3)
Leucopogon esquamatus	**	(3, 5)
Epacris pulchella	**	(3, 5, 6)
Goodenia bellidifolia	*	(3, 5)

GROUP 4. (+) HIBBERTIA ASPERA

Machaerina teretifolia	*	(4)
Cyathochaete diandra	**	(4, 3, 5, 6)
Casuarina distyla	**	(4, 3, 5, 6, 7)
Hakea teretifolia	**	(4, 3, 5, 6)
Banksia aspleniifolia	**	(4, 5)
Banksia ericifolia	**	(4, 3, 5, 6)
Banksia spinulosa	*	(4)
Acacia myrtifolia	*	(4, 3, 5, 6)
Hibbertia aspera	*	(4)
Haloragis teucrioides	**	(4, 5, 6, 7)
Leptospermum flavescens	**	(4)
Pimelia linifolia	**	(4, 3, 7)
Scaevola ramosissima	*	(4)
Lasiopetalum ferrugineum	*	(4)

GROUP 5. (+) GOODENIA BELLIDIFOLIA

Selaginella uliginosa	**	(5)
Lomandra glauca	**	(5, 3)
Cyathochaete diandra	**	(5, 3, 4, 6)
Schoenus brevifolius	**	(5, 3)
Lepidosperma limicola	*	(5, 6)
Themeda australis	*	(5, 7)
Casuarina distyla	**	(5, 3, 4, 6, 7)
Hakea teretifolia	**	(5, 3, 4, 6)
Banksia aspleniifolia	**	(5, 4)
Banksia ericifolia	**	(5, 3, 4, 6)
Acacia myrtifolia	*	(5, 3, 4, 6)
Mirbelia rubiifolia	*	(5, 6)
Haloragis teucrioides	**	(5, 4, 6, 7)
Leucopogon esquamatus	**	(5, 3)
Epacris pulchella	**	(5, 3, 6)
Goodenia bellidifolia	*	(5, 3)

GROUP 6. (—) GOODENIA BELLIDIFOLIA

Cyathochaete diandra	**	(6, 3, 4, 5)
Lepidosperma limicola	*	(6, 5)
Casuarina distyla	**	(6, 3, 4, 5, 7)
Hakea teretifolia	**	(6, 3, 4, 5)
Banksia ericifolia	**	(6, 3, 4, 5)
Acacia myrtifolia	*	(6, 5)
Mirbelia rubiifolia	*	(6, 5)
Haloragis teucrioides	**	(6, 4, 5, 7)
Callistemon citrinus	**	(6, 3)
Epacris pulchella	**	(6, 3, 5)

GROUP 7. (+) ERAGROSTIS SP.

Themeda australis	*	(7, 8)
Eragrostis sp.	*	(7)
Casuarina distyla	**	(7, 3, 4, 5, 6)
Haloragis teucrioides	**	(7, 4, 5, 6)
Pimelia linifolia	**	(7, 3, 4)
Operculia aspera	*	(7)
Rulingia hermaniifolia	*	(7)

(*Hakea teretifolia* and *Banksia ericifolia* are also present, but less frequently.)

GROUP 8. (—) JUNCUS SP.

Lomandra longifolia	**	(8)
Themeda australis	*	(8, 7)
Westringia fruticosa	*	(8)

(No species is represented in all the sites of the group.)

GROUP 9. (+) JUNCUS SP.

Juncus sp.	*	(9)
Baeckea imbricata	*	(9)
Hydrocotyle bonariensis	*	(9)
Lobelia alata	*	(9)

SIR WILLIAM MACLEAY MEMORIAL LECTURE, 1972

ENERGY FLOWS IN THE BIOSPHERE—THE IMPACT OF MAN

R. O. SLATYER*

For this address I have chosen to talk about the way in which energy underlies the workings of the biosphere, the workings of natural ecosystems, and the workings of human societies. Although the subject matter will lead me out of biology at some stages, I think it is apparent to most people that the impact of man on the biosphere is directly related to the product of his numbers multiplied by the effects of each individual. In turn, I believe that the impact of each person is closely related to the degree to which his own metabolic energy is supplemented by external energy sources. One can get some idea of human dependence on such energy sources by visualizing what would happen if supplies of energy were stopped. The relative impact of such an occurrence on a primitive compared with modern society reflects the additional degree to which technologically advanced cultures are dependent on external energy.

I hope Sir William Macleay would have approved of this topic. In looking back over past Macleay lectures, I have noted that it has been fashionable for lecturers to attempt to justify their choice of topic in terms of Sir William's interests and activities. His stimulus to biology in Australia was so great that this has not been too difficult to achieve, even if occasionally lecturers may have embellished that part of his record closest to their own interests. For my lecture, therefore, I think I should remind you that Sir William was, first and foremost, a natural historian, with a reverence for the workings of natural systems and their component organisms. Also, he undoubtedly pictured science and society as being closely interwoven in human affairs. My speculation is that, had he been alive today, he would have been in the front rank of activities concerning the rational use of the biosphere, by man, in perpetuity. Perhaps I might even assume that he would have regarded human use of energy as being of key importance in this context, and that he would have been active in seeking to restrain its growth and ensure its more efficient utilization.

GLOBAL ENERGY EXCHANGES

The planet earth, although 93 million miles from the sun, is bathed by a flow of radiant energy which has hardly changed since life itself began. This flux, the solar constant, has a value of about $2 \cdot 0$ cal. cm.$^{-2}$ min.$^{-1}$. For the planet as a whole it represents $1 \cdot 5 \times 10^{18}$ kWh. per year, a truly tremendous amount of energy.

About a third of this energy is reflected directly back to space, mainly from clouds, and smaller amounts are absorbed and scattered diffusely by various atmospheric components, including molecular constituents and dust particulates. Consequently, an average of not much more than half the total finally reaches the earth's surface, but the fraction varies widely, with time of day, cloudiness, season, latitude and elevation, and, more recently, with areas of greatest human activity.

Of the amount reaching the earth, various amounts again are directly reflected back to space. For the earth as a whole, the fraction averages about 10%; but it also varies, from as little as 5% for clear deep water, to higher than 80% for fresh snow. Most terrestrial surfaces reflect between 20% and 40%. The

---

* Department of Environmental Biology, Research School of Biological Sciences, Australian National University, P.O. Box 475, Canberra City, A.C.T., 2601.

remainder is absorbed by the surface (soil, water, ice, vegetation, buildings, etc.). A very small fraction, which I will consider in more detail below, is stored as chemical energy by means of photosynthesis.

As well as this inward flux of solar energy towards the surface, the surface re-emits thermal radiation. Since every body radiates energy at a rate proportional to the fourth power of its absolute temperature, thermal radiation is continually exchanged between the surface and the atmosphere, and from the planet, as a whole, to space. Over a 24-hour period the net inward and outward radiation fluxes are generally closely balanced, but heating and cooling trends which may continue for a few days, or seasonally, reflect cumulative in-balances. These exchanges are summarized in Table 1.

TABLE 1
Energy Exchanges of the Planet Earth

1. Total reaching the planet	100%
(*a*) Absorbed by stratosphere	6%
(*b*) Absorbed by troposphere	8%
(*c*) Reflected by clouds	33%
(*d*) Reflected by surface	10%
(*e*) Absorbed by surface	43%
2. Total re-emitted from the planet	100%
(*a*) Reflected from short-wave flux	43%
(*b*) Emitted long-wave flux	57%
(1) Net from surface	11%
(2) Net from troposphere	40%
(3) Net from stratosphere	6%

Source of data: Van Wijk (1963).

At any point on the earth's surface the observed temperatures reflect the result of these radiation fluxes and of horizontal re-distributions of energy. When radiation inflow is reduced by solar inclination, as in winter and at high latitudes, less energy is available, and temperatures tend to fall. When skies are clear and dry, rapid energy inflow by day and outflow by night lead to wide daily temperature variations. When skies are cloudy or smoggy less energy reaches the surface, but energy outflow is also slowed, leading to cooler days but warmer nights.

These global energy exchanges, combined with the rotation of the earth, provide the basic energy for the global atmospheric and ocean circulation. Although the direct energy exchanges usually represent the greatest influences on local weather and climate, major re-distributions of energy occur in the circulatory patterns—as cold winds on otherwise sunny summer days testify. The gulf stream of the North Atlantic is an impressive example of major climatic modification (in western Europe) caused by energy originally absorbed in tropical oceans.

So solar energy is clearly of fundamental importance to the global environment, and the present patterns of weather and climate reflect a delicate balance between the inflows, outflows and redistributions.

ENERGY FLOW IN BIOLOGICAL SYSTEMS

Solar energy flows into living systems through photosynthesis. The fraction of energy which is captured by green plants is tiny, being only about a tenth of 1% of that reaching the earth's surface, but there are good reasons for it being so low. In the first place, only about 45% of the energy received is in the visible part of the electro-magnetic spectrum and so is available for photosynthesis. Secondly, the maximum biochemical efficiency of photosynthesis is about 25%

of the energy absorbed. So these two factors combined set an upper limit of about 11% overall energy conversion.

However, metabolism also requires energy and, in general, 25–50% of the energy utilized in photosynthesis itself is required for metabolism of the photosynthesizing plants. Taking an average of 40%, this reduces the upper limit for energy capture to about 7%.

When one looks around for ecosystems which have figures for net photosynthetic energy uptake of this magnitude, they are lacking. For short periods some reports exist of values as high as 4–5%, but for periods of a year the highest yielding ecosystems do not appear to capture more than about 1·5%.

This is because it is unusual to have ecosystems in which, on a continuous basis, every quantum of incident radiation strikes a chloroplast, and in which there are no restraints on photosynthesis other than radiation. On average only a relatively small fraction of the radiant flux actually strikes a chloroplast, and adverse temperature, water status, nutrients or other factors reduce the biochemical efficiency of the photosynthetic process itself. If realistic figures of 10% and 15% are taken for each of these latter two parameters, it can be seen that the figure of 7% total conversion is finally reduced to about 0·1%. These figures are summarized in Table 2.

TABLE 2
Solar Radiation and Photosynthesis

	%
1. Fraction of solar radiation which is photosynthetically active	45
2. Maximum biochemical efficiency of photosynthetic energy capture (percentage of (1))	25
3. Respiratory metabolism by photosynthetic organisms (percentage of (2))	40
4. Solar radiation which actually strikes a chloroplast (percentage of (1))	15
5. Effect on adverse temperature, nutrient level or water status (percentage of (2))	15
6. Overall fraction (product of (1) × (2) × (100 − (3)) × (4) × (5))	0·1

Source of data:
Item 1. Monteith, 1965.
2. Slatyer, 1970.
3. de Wit *et al.*, 1970; McCree, 1970.
4, 5. Personal estimates.

While this final fraction is small, the amount of energy it represents is still very large—a total of $5 \cdot 2 \times 10^{14}$ kWh. (Fogg, 1968); see also Leith (1963), SCEP (1971)). It is this amount of energy on which all other life depends.

It is not appropriate in this address to deal with ecosystem structure and function in a comprehensive manner, but there are several aspects concerning energy utilization which I would like to draw to your attention.

In the first place, a primary feature of most natural ecosystems is that they tend towards self-regulation. Solar energy is absorbed by the chlorophyll-containing organisms to provide, through photosynthesis, the basic energy input. This energy then flows through the ecosystem in the metabolism of the consumer and decomposer organisms, and is progressively dissipated as heat. Associated with this flow of energy is a cycling of nutrients through the food chain with the decomposer organisms returning nutrients to the soil in a form that enables their reabsorption by the green plants. Thus the ecosystem as a whole tends to be balanced and self-contained.

Only where energy or nutrients are added to, or removed from, the ecosystem does it move out of energy and nutrient balance. Only when all biological activity is prevented does energy flow stop. The organic residues which accumulate in bogs or in deep waters, and which have become fossil fuels, represent energy removed from the biosphere and stored in an abiotic environment.

Secondly, in most ecosystems the photosynthesizing organisms, or surfaces, are usually spread fairly uniformly in space, but the consumer organisms may be clumped in their distribution or even migratory. Uniform spatial distribution of the producers permits maximum interception of radiant energy. The presence of colonies of consumer means that, within an ecosystem, there are local centres where energy consumption exceeds energy production. Foraging by the animals, or energy flow to the colony, as for example in the flow of water across a coral reef or through an estuary, is then required to supply energy to the sites of consumption. When migratory animals are involved, however, or when long distance energy dispersal mechanisms—such as ocean currents—are operative, the scale of an ecosystem needs to be regional or even planetary. Clearly, most local definitions indicate a lack of complete nutrient cycling and energy balance within such ecosystems, with some nutrients and energy being imported or exported.

Thirdly, the amount of photosynthesis which can go on in an ecosystem sets an upper limit on the energy which can flow through it, and hence on its potential productivity. So potentially the most productive ecosystems should be those in warm, high radiation, environments where water supply and nutrient levels are not limiting photosynthesis. The actual productivity—change of biomass with time—however, is strongly influenced by the successional status of an ecosystem.

In the early stages of succession, when total biomass is low, the amount of energy needed to maintain the existing biomass is relatively small, so a relatively high fraction of the energy stored in photosynthesis can be channelled into increasing biomass. Consequently, productivity is high. As succession proceeds, however, more and more energy is required for maintenance of the existing biomass, less is available for creating new biomass, so productivity falls. Finally, productivity can reach zero, even in the most favourable environments.

As a result, the most productive environments often tend to be those which show pronounced fluctuations between favourable and unfavourable conditions. Environmental severity during the unfavourable periods tends to limit biomass, so that productivity can be high during favourable periods. These ecosystems lend themselves to harvest—the removal of biomass beyond the ecosystem—by migratory animals and by man.

Fourthly, species diversity in an ecosystem tends to increase with ecological succession, and to reach maximum levels in environments where the fewest constraints on photosynthesis or energy flow exist. Of course, in some successionally mature systems, such as mature, temperate forests, reduced space and energy flow can lead to reduced diversity, but the generalization still appears to be valid.

So the most diverse ecosystems are those such as tropical forests, or coral reefs and their associated waters, and the least diverse those in which major environmental constraints operate.

It follows that when major perturbation of an ecosystem—by, say, fire or drought—occurs, the ecosystem is not only set back to an early successional stage but there will tend to be a rapid infilling of the environmental niches so created, by the organisms available. Here again the implications to management of agricultural systems are clear.

In summary, then, we see that natural ecosystems are powered by solar energy through photosynthesis, that there is a tendency for their energy storage and species diversity to increase with succession. This process can proceed furthest in those environments in which there is continuous and rapid energy inflow. As environmental conditions become less favourable for energy inflow, the limits are set at lower levels.

Any factor which reduces biomass tends to destabilize the ecosystem. However, the reduction tends to shift the system into a more productive stage. Productivity is greatest in the early successional stages, since photosynthesis is maximal as soon as the photosynthetic surface reaches its optimal value for a particular environment, and this stage is reached while total biomass is still relatively low.

Let us look at how man interacts with his ecosystems and with the biosphere.

Energy Flow in Human Systems

Energy flows through human populations in two main forms. In the first place man needs food energy for metabolism just as does any other animal. Secondly, he has learned to utilize energy other than that provided by his own metabolism, and has been able to harness it both to the manipulation of natural ecosystems to increase his food producing ability, and to the myriad of other activities which occur in his social systems.

Until the recent development of nuclear energy sources, and with the exception of gravitational energy, man has been totally dependent on solar energy, acting through photosynthesis, for both these sources of energy—food being obtained from the products of contemporary photosynthesis, in the form of living organisms; and non-metabolic energy coming from fossil fuels and organic residues.

The first men had no sources of supplementary energy. As hunter-gatherers, the role they played in the ecosystems they occupied was little different to that of other omnivorous mammals. They preyed on, and were preyed on by, other animals. They gathered plant foods when and where they were available. They did not remove energy or matter from their ecosystems, they did not attempt to manage them, and their nomadic life style meant that their activities were widely distributed. Consequently, they were, in all respects, creatures of their natural systems.

Gradually, however, their hunting and gathering skills increased, with the use of crude tools and the development of various management strategies. These procedures represented energy input by man into ecosystems in order to maintain stability. Thus we see an important theorem emerging—to influence the structure and function of an ecological system requires energy. Initially, this energy was simply the metabolic energy of man himself. It served to increase his food supply and provide protection against predators. In consequence, his numbers rose, so that new management strategies had to be devised to increase food supply further.

In this way, agriculture began and man's foot was placed squarely on the food supply-population growth treadmill. As each management strategy led to increased production, population itself increased so the degree of dependence on the managed systems increased further and new strategies had to be devised. Even at this early stage in the cultural evolution of human beings it was apparent (in retrospect !) that there was no solution to that problem other than stabilizing human population numbers.

Furthermore, additional energy was required for each new strategy, since each required a greater modification of the natural ecosystems and their maintenance in intrinsically unstable, but relatively productive, early successional stages of low diversity.

The first forms of non-human energy were probably domesticated draft and transport animals and the use of water power and fire. Apart from the energy needed to create and maintain water retention and reticulation structures, water power was renewable, but draft animals themselves required food and their herding required human energy expenditure. Energy from the combustion of wood and other organic material also was used for cooking, heating, and the construction of tools and artifacts.

As agriculture became established, human settlements moved from a tribal nomadic mode to a village colony mode, involving the transportation of food from the fields to the village for consumption. The mounds that are used, by archaeologists, to locate and date ancient cultures reflect the accumulation of organic debris as well as of building materials—and indicate that food and body wastes were often not fully recycled back to the fields. In situations where recycling was effective, some human-animal power agricultural systems appear to have reached quite a high level of ecological stability. Yields per acre were low, however, and the nutrient requirements were balanced by weathering plus nutrients from human and animal wastes.

Linked with the increasing use of non-human energy was a greater efficiency per person in agriculture, so that more human energy was available for activities other than obtaining food. In this way cultural and social evolution was able to proceed, and increasing amounts of non-human energy were progressively channelled into the production, distribution and consumption of an increasing variety of biologically non-essential goods and services.

In modern agriculture this trend has continued. Now only a few per cent of the population is directly involved in food production, the direct and indirect energy inputs have increased dramatically with the use of mechanical and chemical methods of crop production and protection, and of elaborate transportation and marketing arrangements, and the degree to which nutrients are recycled from centres of consumption to centres of production has decreased further.

Looked at in an ecological context, man's agricultural strategy has been to remove environmental constraints on photosynthesis—particularly by the addition of water and nutrients where these have been limiting, and to push his ecosystems back to early successional stages, generally by cultivation. This device has also accelerated nutrient flow from organic residues to plant nutrients, but at the cost of reducing the total store of nutrients in biological circulation. In addition, he has attempted to short-circuit the natural food chains by suppressing the activity of species other than those he wishes to encourage.

In general, seasonal environments in which the active season is highly favourable to biological activity have lent themselves most readily to modification by man. By introducing species able to utilize the favourable season effectively, it has been relatively easy to harvest the production so induced and the unfavourable season has assisted in the control of predatory and parasitic species.

Environments favourable to year-round biological activity have tended to be difficult to manage because of the continued presence of predatory and parasitic species in great diversity. (Harvest of top carnivores, such as fish or game, from such systems provides an exception in this respect.) Biologically unfavourable environments have tended to have such severe environmental restraints on productivity that they could not sustain a yield for man, except where the restraints are removed, as in irrigated desert regions. In such ecosystems, however, problems of soil physical and chemical changes under human modification have tended to reduce their productive potential in many instances.

Compared with natural systems, therefore, biomass and diversity are reduced, productivity increased, a harvest is removed and the harvested materials transported to centres of consumption concentrated in towns and cities. Recycling of nutrients is replaced by direct and continuous additions. Productivity and stability are only maintained in these systems by major direct and indirect inputs of energy.

Modern, energy based agriculture is very efficient when measured in terms of productivity per person, even though it involves serious modification of natural ecosystem structure and function. In the same way, productivity of the other goods and services used by human populations tends to increase in efficiency as more and more non-metabolic energy is utilized.

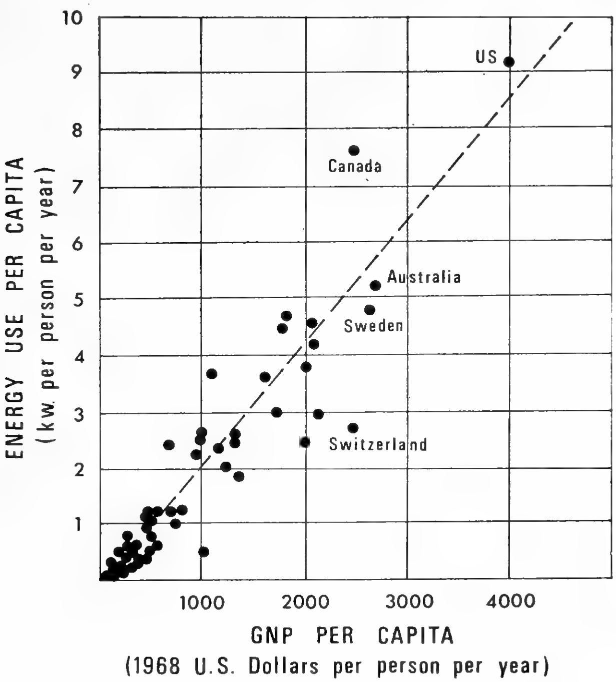


Fig. 1. Relationship between energy use per capita and GNP. (From Meadows *et al.* (1971), plus Australian data from Kirov (1971) and the Commonwealth of Australia Yearbook (1971).)

The Impact of Human Use of Energy

Let us now turn to look at the overall energetics of human societies, and examine the likely effects of the increasing tendency to use more and more energy per person.

In the first place, it is important to recognize how closely human activity is linked to energy consumption. This is impressively depicted in Fig. 1, where GNP is plotted against energy consumption for those countries of the world for which data are available. Although GNP is regarded more and more as a poor indicator of human welfare, it is a good indicator of human activity. It is easy to see how energy consumption underlies this activity.

In Table 3 some of the background to this pattern of energy consumption is revealed. Firstly, it can be seen that the normal rate of human metabolism is about 100 watts—the energy we use being comparable to a normal sized incandescent light bulb. The average figure for total energy use by man is 21 times as great: 2·1 Kw. So, on average, man brings 21 times more energy to bear in his cultures than is available from his own musclepower.

When this average is broken down, the disparities between different groups of countries is revealed. The average Australian now uses power at the rate of 5·2 kW., the average American at 9·3 kW., whereas the average person in developing countries uses only 0·2 kW. So while the Australian citizen commands 52 times as much energy as he needs for metabolism, the ratio for developing countries is only 2 : 1.

TABLE 3

Per Capita Rate of Energy Use by Man

	kW
1. Metabolic energy use by man	0·1
2. Total energy use by man :	
A. Average for world population	2·1
B. Australia	5·2
C. United States	9·3
D. Developing countries	0·2

Source of data :
Item 1. Converted from Table 4, Item 6.
2A. Converted from Table 4, Item 4.
2B. Kirov, 1971.
2C. SMIC, 1971.
2D. UN Statistical Papers, World Energy Supplies.

Supplementary information, on an annual basis, is given in Table 4 as total amounts in kWh. The values for the total solar flux, for the solar energy absorbed by the earth's surface, and for global photosynthesis, all referred to earlier, are tabulated, as is the annual figure for man's metabolic needs. The new figures give values for the total energy now used by man, and its projected value in the year 2000.

TABLE 4

Basic Global Energy Statistics

(Annual amounts)

1. Total extraterrestrial solar flux	$1 \cdot 5 \times 10^{18}$ kWh.
2. Solar energy absorbed by earth's surface	$6 \cdot 5 \times 10^{17}$ kWh.
3. Total photosynthesis	$5 \cdot 2 \times 10^{14}$ kWh.
4. Total energy now used by man (1970)	$7 \cdot 0 \times 10^{13}$ kWh.
5. Estimated total energy required by man (2000)	$3 \cdot 5 \times 10^{14}$ kWh.
6. Metabolic energy used by man (1972)	$3 \cdot 9 \times 10^{12}$ kWh.

Source of data :
Item 1. Slatyer, 1970.
2. Van Wijk, 1963 ; Slatyer, 1970.
3. Fogg, 1968.
4, 5. SMIC, 1971.
6. Assuming world population of $3 \cdot 7 \times 10^9$ people and average ingestion rate of 2,500 kilo calories per day.

It is these latter figures, in comparison with those for global photosynthesis, that are the most revealing for biologists. For it can be seen that the present human population is using an amount of energy which is rapidly approaching the level of global photosynthesis. Furthermore, at the present rate of increase in total energy use the world's people will use an amount approximately equivalent to global photosynthesis shortly after the year 2000. This means that, in terms of total energy flow, one species, *Homo sapiens*, out of all the species of animals and plants on this planet, is now approaching that of all other organisms combined. Looked at in this manner, it is not surprising that the impact of man is becoming biospheric rather than local or regional in scale.

The question that confronts us is whether or not this rate of energy consumption, of human activity, is likely to affect the functioning of biosphere, or is likely to affect those aspects of the human environment which are just as essential to our well-being as is an adequate supply of food. This latter subject warrants more than an address on its own, so I cannot explore it, despite its interest and importance. Let us instead concentrate on the direct effects of energy consumption and their implications.

The present levels of energy use, though disturbing, are not as disturbing as the problems of continued growth. Global energy consumption is growing exponentially at an average rate of about 5·5% per year, providing a doubling time of 12–13 years (SMIC, 1971). In Australia the rate is about 6% per year, with a doubling time of 11–12 years (Kirov, 1971). The implications of doubling times are well known to biologists, but are not well appreciated by the public at large. With reference to energy use, a doubling time of 13 years means that, if the rate of increase has been constant up until the present, there will be as much energy consumed in the next 13 years as the total amount already consumed. Since, in fact, growth rates have been increasing, there will be more energy consumed in the next 13 years than in the whole history of man. And in the subsequent 13 years there will be twice as much again.

Most forms of power generation and use result in the production of waste substances and all result in the production of heat. The direct effect of waste products on the environment can only be eliminated if the substances themselves are not discharged or are discharged at rates that do not disturb ecological balance. While this is possible in the case of material wastes (even if it may be very difficult for other reasons), in the case of heat it is physically impossible. The laws of thermodynamics mean that, ultimately, a heat output equivalent to the energy content of the fuel being used must be produced, unless the thermal energy is stored as some form of chemical energy.

So heat production remains as one problem which cannot be avoided, and it is important to try to put it in perspective. At the present time, waste heat is causing problems on a local scale and is beginning to cause problems on a regional scale. Already, for example, very large quantities of fresh water runoff in the U.S. are utilized for cooling purposes ; by 2000 it is estimated that about one-third of the total runoff will be so utilized (Clark, 1969). Already " heat islands " are occurring around major urban-industrial complexes, causing measurable changes in local weather conditions. In the Los Angeles basin, energy consumption is already equal to 6% of the solar energy received. In the year 2000 it is predicted that it will be equal to 18% (SCEP, 1970). In the entire Boston-Washington megalopolis, of 30,000 km.^{2}, at the same time, the heat injection will be equivalent to about 50% of the solar radiation received in winter and 15% in summer (Landsberg, 1970). Under certain synoptic conditions mean temperature increases of up to 11° C. for such regions by the year 2000 have been predicted (Porter *et al.*, 1971).

Even on a global scale, effects may soon be detectable. Recent calculations (Porter *et al.*, 1971) suggest that, in terms of heat production alone, and assuming that the extra heat is dissipated by an increase in surface temperature which, in turn, increases the rate of long wave radiation, mean surface temperature will rise by 0·6° C. by 2000 and 1·2° C. by the year 2020. While the phenomenon is more complicated than their model suggests, the example illustrates the magnitude of the problems that human energy use is generating.

The degree to which heat production can affect climate depends largely on whether regional, and ultimately global, energy balances are changed. While heat from energy consumption may exercise a significant influence on the energy balance, therefore, the degree to which it does so will depend not only on its absolute amount but also on the degree to which the other energy balance components change. For example, land clearing and construction can affect the albedo of the earth's surface. Dust and other atmospheric emissions can affect the transmission of both short and long wave radiation through the atmosphere, both directly and indirectly through inducing changes in cloudiness. In this way the planetary albedo itself can be changed, as well as surface and surface and atmospheric temperature. When it is realized that, as a broad generalization, a 1% change in the global energy balance is likely to result in a mean temperature change of the order of 1° C. (Ehrlich and Ehrlich, 1972), it is not difficult to see that significant temperature changes could arise.

At this stage these interactions are not well understood, but there does seem to be general agreement among scientists on three aspects. Firstly, that any significant change in the energy balance is likely to have an effect on climate ; secondly, that even a 1% change could be significant in this respect ; and thirdly, that quite small effects on climate could have serious effects on food production.

Increasing the Efficiency of Energy Use

Developed nations are clearly dependent on high levels of energy utilization for a continuation of a technology based society. Developing nations appear to aspire to this life style and hence to these levels of energy use.

In consequence, the challenge for the future seems to be to produce and use energy as efficiently as possible, and with the least possible ecological disturbance.

There seem to be substantial opportunities for making progress along these lines. In the first place the environmental impact of different energy sources varies widely. There are three major types of energy source—natural, renewable sources (including water and wind, geothermal sources, and solar energy) ; fossil sources (comprising coal, natural gas, and petroleum) ; and nuclear sources.

Table 5
Energy Sources

Source	World[1] 1966	Australia[2] 1970	World[1] 2000
	%	%	%
Fossil fuels :			
Solid	40	47	15
Liquid	36	49	32
Gas	17	1·8	27
	93	98	74
Nuclear	0·2	—	22
Natural	6·5	2·0	5·0
	100	100	100

Source of data :
[1] Hartley, 1969.
[2] Kirov, 1971.

Table 5 shows the relative fractions of each at present being utilized, and projected for the year 2000. As a generalization it can probably be said that combustion of fossil fuels has the greatest adverse ecological effects, and natural sources the least. Therefore, a clear challenge exists to reverse the present order.

Fossil fuels are environmentally bad because they are responsible for most of the atmospheric pollution emanating from urban and industrial centres and transportation systems due to emissions of oxides of carbon, sulphur and nitrogen and other compounds. Furthermore, the fuels themselves constitute precious raw materials for technology and even for food. To burn them simply for energy release is a profligate form of resource utilization, particularly when reserves are only adequate for a few decades.

Nuclear fuels are relatively clean by comparison, but there are the problems of radioactive waste disposal, and the thermal efficiency of nuclear plants is lower than that of fossil plants, so there is a greater amount of heat liberated per unit of useful energy produced—even before the energy is used in its final applications.

Natural, renewable, sources are generally regarded as " clean " energy sources in that there is no mining of raw fuel materials, no refining and transportation of materials, and there are no waste products in power generation. However, only gravitational water power and solar energy represent major energy sources, and there is a finite limit of the amount of hydro-electric power that can be generated (*cf.* Table 5).

Apart from progress in nuclear power technology, which is proceeding at a rapid pace in many centres, this analysis leaves solar energy as a major power source which remains virtually undeveloped at the present time. Although major technological developments in energy capture, energy storage and long distance energy transmission are required, the attraction of solar energy is that it is a clean source in the sense of waste product emission during power generation, and its use would minimize the overall heat budget problems of the biosphere, since energy already reaching the earth's surface would be used. Although the albedo of the collecting surfaces might differ from that of the surrounding terrain, and the long wave emissions from the surface would be suppressed, the heat so absorbed would balance the heat liberated in ultimate use, so the global energy exchange would be virtually unaffected. Consequently, it seems to me that a major programme on solar energy utilization is warranted, even though heat production at points of energy use would cause local and regional energy imbalance in just the same way as with other energy sources. In fact, since energy would be absorbed at the sites of solar power stations, and liberated at the points of use, local and regional imbalances would be accentuated. The climate control systems are not yet sufficiently well understood to say whether this would be better or worse than heat injection alone, but with global balance being achieved. (A more detailed description of these energy sources can be found elsewhere (see, for example, Slatyer, 1972).)

In terms of efficient energy use there also appear to be steps which can be taken to improve efficiency. In agriculture, the increased use of ecological principles could reduce direct and indirect energy needs in cultivation, nutrition, pest and disease control and many other facets. In industry, the development of a recycling technology could substantially reduce the energy now needed to obtain and process raw materials. Better insulation in structures would substantially reduce the energy needed for heating and air-conditioning. In transportation systems we see inefficient energy utilization everywhere.

So it seems as though there is scope for increasing the efficiency of energy production and use, and in reducing its environmental impact, even though the problems will not reach a steady state situation until human population and the demands of each person also level out.

The overriding question which remains unanswered is whether or not the people of the world are prepared to move away from the type of life-style so characteristic of Western countries, based on economic growth and consumerism, with all that entails in the sense of endless production and consumption and planned obsolescence. It is in that socio-economic environment where population growth, and growth of personal needs, continues unchecked. I do not advocate a return to the noble savage ; on the contrary, I think that the development of an ecologically acceptable technology is as great a challenge as man has yet faced. But clearly there are limits to growth, and energy use underlies most of them.

ACKNOWLEDGEMENT

Ms. Sally Stephens collected much of the data on which this lecture is based.

References

CLARK, J. R., 1969.—Thermal pollution and aquatic life. *Scientific American*, 220 : 19–27.
COMMONWEALTH OF AUSTRALIA, 1971.—*Yearbook 1971.* (Commonwealth Printer, Canberra.)
EHRLICH, R. R., and EHRLICH, A., 1972.—*Population, Resources, Environment.* (Freeman and Company, San Francisco, 2nd Edition.)
FOGG, G. E., 1968.—*Photosynthesis.* English Universities Press, London.
HARTLEY, H., 1969.—The future of world energy. *New Scientist*, 44 : 3–5.
KIROV, N. Y., 1971.—Fuels and energy in Australia. *Search*, 2 : 298–305.
LANDSBERG, H. E., 1970.—Man-made climatic changes. *Science*, 170 : 1265–1274.
LEITH, H., 1963.—The role of vegetation in the carbon dioxide content of the atmosphere. *J. Geophys. Res.*, 68 : 3887–3898.
MCCREE, K. J., 1970.—An equation for the rate of respiration of white clover plants grown under controlled conditions. In *Prediction and Measurement of Photosynthetic Activity.* (Centre for Agricultural Publishing and Documentation, Wageningen.)
MEADOWS, D. H., MEADOWS, D. L., RANDERS, J., and BEHRENS, W. W., 1972.—*The Limits of Growth.* (Universe Books, New York.)
MONTEITH, J. L., 1965.—Radiation and crops. *Experimental Agric.*, 1 : 244–251.
PORTER, W. A., HAGLER, M. O., and KRISTIANSEN, M., 1972.—Global temperature effects of the use of fusion energy and the fusion torch. *IEEE Trends in Nuclear Science*, NS, 18 : 31-36.
SCEP, 1970.—*Man's Impact on the Global Environment.* (M.I.T. Press, Cambridge.)
SLATYER, R. O., 1970.—Water and energy—Cornerstones of productivity. *J. Aust. Inst. Agric. Science*, 2 : 8.
————, 1972.—Environmental problems arising from human use of energy. Report 4 : 27–35. Australian Academy of Science, Science and Industry Forum, Canberra.
SMIC, 1971.—*Inadvertent Climate Modification.* (M.I.T. Press, Cambridge.)
WIJK, W. R. van, 1963.—*Physics of Plant Environment.* (North Holland Publishing Co., Amsterdam.)
WIT, C. T. de, BROUWER, R., and PENNING de VRIES, F. W. T., 1970.—In *Prediction and Measurement of Photosynthetic Activity.* (Centre for Agricultural Publishing and Documentation, Wageningen.)

The *Proceedings of the Linnean Society of New South Wales* contain original papers relative to "the Science of Natural History in all its branches", and reports of business transacted at the meetings of the Society.

NOTES AND INSTRUCTIONS FOR AUTHORS

Original papers may be submitted for consideration for publication in the Society's Proceedings. Submission of a manuscript must imply that the contents are original and have not been published previously in the same, similar, or abbreviated form, and that no similar paper is being or will be submitted for publication elsewhere until it has been either (*a*) not accepted for publication by the Society or (*b*) withdrawn by the author.

Papers submitted should embody the results of a significant piece of work. Interim reports, serialized studies and student theses should not be submitted.

Papers are accepted for publication (or otherwise) by the Council of the Society after taking into consideration advice received from at least one referee. The decision of Council is final.

Once accepted for publication a paper becomes the property of the Society, and copyright is vested in the Society. Reproduction of the author's synopsis in abstracting journals is authorized.

A paper may be withdrawn by the author at any time prior to acceptance.

Papers may be submitted by members or non-members of the Society but a paper submitted by a non-member must be communicated by a member of the Society, and will not ordinarily be considered for acceptance before July in each calendar year.

SUBMISSION OF MANUSCRIPTS

Manuscripts should be forwarded to the Secretary, The Linnean Society of New South Wales, 157 Gloucester Street, Sydney, N.S.W. 2000.

Text and illustrations must be submitted in duplicate. The illustrations may be duplicated by any acceptable clear method and the duplicate set need not necessarily be identical in size with the originals. The author should retain a third copy for checking proofs. If a paper is not accepted for publication, the original copy of the typescript and illustrations will be returned to the author, but the duplicate copy may be retained by the Society.

Owing to the ever growing costs of publication, authors are requested to write their papers clearly and concisely and exercise all reasonable economy in the number and form of illustrations and tables.

Grants towards the cost of publication should be secured wherever possible from the author's own institution or elsewhere; contributions from authors, especially non-member authors, may be requested at Council's discretion, particularly in the case of lengthy papers, or those with numerous illustrations or tables.

Manuscripts must be submitted in final, fully corrected form. Authors may be liable for the cost of proof corrections (if allowed) if the number of alterations and corrections is considerable. Authors are urged to submit their paper to a colleague for constructive criticism prior to final typing and submission for publication.

MANUSCRIPTS

Papers should be typewritten, double spacing throughout, on one side of quarto or foolscap paper, with at least one-inch margins all round. The desired position of all text-figures, maps and tables may be indicated in the margin. All pages should be numbered serially and securely fastened together. Papers should conform to the following general layout as far as practicable or appropriate:

(*a*) *Title.*—The title should be concise but informative. The name(s) of the author(s) and the name of the institution where the work was carried out should follow the title. The name of a new taxon of plants or animals should not be included in the title. A short title appropriate for the running heading of subsequent pages may be suggested. The title, etc., should be on a *separate page* at the commencement of the typescript.

(*b*) *Synopsis.*—A concise abstract (without abbreviations), preferably consisting of not more than about 200 words, should be supplied on a *separate sheet* and in *triplicate.* It should be complete in itself and indicate the scope of the work. It will be printed below the title of the paper and in the Society's Abstract of Proceedings; it will be available for reprinting by abstracting journals.

(*c*) *Table of Contents.*—This should give the complete hierarchy of headings and sub-headings used in the subject-matter of the paper. It should be supplied on a *separate sheet* for guidance of the editor and will not ordinarily be printed.

(*d*) *Introduction*, followed by the *Subject Matter* of the paper. Papers may be divided into sections described by short headings.

(*e*) *Discussion, Conclusions or Summary* (if necessary).—This should summarize the conclusions reached rather than be a précis of the paper as a whole (cf. Synopsis).

(*f*) *Acknowledgements*, if any.

(*g*) *References.*—The author, who is alone responsible for their accuracy, should carefully check all references against the text, to ensure especially that:

(i) The spelling of authors' names is consistent, and the dates, volume numbers and page numbers are correct.

(ii) All authors quoted in the text are included in the list of references.

References should be cited in the text by the author's name and date, e.g., Bullough (1939) or (Bullough, 1939) according to context, and listed alphabetically under References thus:

Bullough, W. S., 1939—A Study of the Reproductive Cycle of the Minnow in Relation to the Environment. *Proc. zool. Soc. Lond.*, 109, A: 79-108.

If more than one reference by the same author(s) published in the same year is cited, use a, b, etc., after the year in both text and list, e.g., Bullough (1939 a).

Titles of books must be given in full together with the place of publication, name of publisher and indication of edition if other than the first.

Latin names of plants and animals (genera, species and their subdivisions) should be underlined to indicate italics. An initial capital letter must be used for Latin names of orders, families and similar names, but these should not be underlined.

Abbreviations.—Only standard abbreviations should be used; authors should refer to the British Standard 1991: Part 1, 1967. Recommendations for Letter Symbols, Signs and Abbreviations. The abbreviations of names of periodicals should conform to those in the World List of Scientific Periodicals.

Footnotes should be avoided as far as possible.

Codes of Nomenclature.—The Botanical and Zoological Codes of Nomenclature must be strictly followed. If a new taxon is described, the institution in which the type material is deposited must be indicated.

Language.—Papers in languages other than English are unlikely to be accepted for publication. Foreign authors are urged to seek assistance, if necessary, in rendering the paper in fluent English prior to submission.

Measurements must be expressed in the metric system as far as practicable, and exclusively in scientific description.

ILLUSTRATIONS AND TABLES

The maximum dimensions available for either text-figures or plates are 20 x 12.5 cm.

Black and white drawings and diagrams for text-figures should be in Indian ink on smooth white card such as Bristol board the lines cleanly drawn, and due attention paid to the consequences of reduction. Graphs should similarly be in Indian ink on white card, or on faint blue-lined co-ordinate paper. Maps should be in Indian ink on white card or tracing linen; if the latter the linen should not be folded. Maps should be of a size and scale that can be conveniently reduced to the size of a single page.

It is desirable that all black and white illustrations should be drawn 1½-2 times the size that they will appear in print.

Photographs for half-tone plates should be the size required for final reproduction or slightly larger, printed on glossy paper, of good contrast and best quality. A number of small photographs can be arranged to form one plate.

Illustrations for colour reproduction cannot be accepted unless the author meets the difference in cost between black and white and colour reproduction.

Illustrations of all kinds should bear the author's name and the number of each, lightly pencilled on the back, and their required orientation clearly indicated.

Legends for illustrations should be typed on separate sheets at the end of the manuscript. Great care should be taken in stating magnifications of illustrations, making it clear whether numbers quoted refer to before or after reduction.

Tables.—Tables should be numbered consecutively and referred to specifically in the text by number. Each table, together with a heading descriptive of its contents, should be submitted on a separate sheet. Elaborate tables should be avoided.

GENERAL

Proofs.—A set of galley proofs will be forwarded to the author who should correct and return them promptly to the Secretary.

Reprints.—Twenty-five reprints are supplied free to authors who are members of the Society. Additional reprints may be ordered at the authors' expense, if desired. No free reprints are supplied to non-members who may, however, order the number required at their own expense. Orders for reprints should be placed with the Secretary immediately after the paper has been accepted for publication. Orders received after the paper has been printed may not be accepted.

Joint Authorship.—In the case of papers by more than one author, one of them must accept responsibility for all correspondence with the Society regarding the paper.

AUSTRALASIAN MEDICAL PUBLISHING CO. LTD.
71-79 ARUNDEL ST., GLEBE, N.S.W., 2037

Copies of the PROCEEDINGS OF THE LINNEAN SOCIETY OF NEW SOUTH WALES (with the exception of a few Volumes and Parts) may be purchased from the Society, Science House, 157 Gloucester Street, Sydney, N.S.W., 2000.

Current charges for the PROCEEDINGS are:

Volumes—$16.00 each for 1st Series (Volumes 1–10); $11.00 each for 2nd Series (Volumes 11–20) and all subsequent volumes.

Parts—$5.00 each for all back parts; $4.00 each for current Parts. For volumes of 5 or 6 Parts, $1.00 each for first and last Parts.

Prices do not include postage.

Subscription to the PROCEEDINGS—$11.00 per volume, plus 80c postage—$11.80.

All prices are in Australian currency.

These charges may be revised from time to time, and inquiries should be addressed to The Secretary, Linnean Society of New South Wales, Science House, 157 Gloucester Street, Sydney, N.S.W., 2000, Australia.

The Society's PROCEEDINGS are printed and published for the Society by the Australasian Medical Publishing Co., Ltd., 71–79 Arundel Street, Glebe, N.S.W., 2037.

Proceedings, Volume 97, Part 3, 1972

CONTENTS

Proceedings of the Linnean Society of New South Wales

Issued 30th April, 1973

VOLUME 97
PART 4
No. 432

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, 1972–73

President
H. G. Cogger, M.Sc., Ph.D.

Vice-Presidents
L. A. S. Johnson, D.Sc. ; T. G. Vallance, B.Sc., Ph.D. ;
N. G. Stephenson, M.Sc., Ph.D. ; R. C. Carolin, B.Sc., Ph.D., A.R.C.S.

Honorary Treasurer
Joyce W. Vickery, M.B.E., D.Sc., F.L.S.

Secretary
Mrs. Ruth J. Inall

Council

D. J. Anderson, Ph.D.
D. T. Anderson, D.Sc.
R. K. Bamber, F.S.T.C.
Barbara G. Briggs, Ph.D.
W. R. Browne, D.Sc., F.A.A.
R. C. Carolin, B.Sc., Ph.D., A.R.C.S.
H. G. Cogger, M.Sc., Ph.D.
Mary M. Hindmarsh, B.Sc., Ph.D.
L. A. S. Johnson, D.Sc.
Elizabeth C. Pope, M.Sc., C.M.Z.S.
P. J. Stanbury, Ph.D.
N. G. Stephenson, M.Sc., Ph.D.
F. H. Talbot, M.Sc., Ph.D., F.L.S.
E. LeG. Troughton, F.R.Z.S.
P. G. Valder, B.Sc.Agr., Ph.D.
T. G. Vallance, B.Sc., Ph.D.
Joyce W. Vickery, M.B.E., D.Sc., F.L.S.
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.

Linnean Macleay Fellow of the Society as from 1st July, 1971
Mrs. Lynette Anne Moffat, B.Sc.Hons.

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

NOTES ON SOME ASCIDIANS FROM PORT JACKSON, BOTANY BAY AND PORT HACKING, NEW SOUTH WALES

PATRICIA KOTT*

[Accepted for publication 20th September 1972]

Synopsis

Twenty-eight species of Ascidiacea from N.S.W. are discussed. The collections are from the sea bed and from rocky vertical and horizontal faces at sublittoral locations. The species associated with these diverse environments are discussed.

A new species of *Aplidium* and a new monotypic genus in the subfamily Styelinae are described. *Adagnesia opaca* Kott, a free living species previously thought endemic to Moreton Bay, is recorded from Port Hacking.

INTRODUCTION

Several small collections of the class Ascidiacea from bays in the central New South Wales coast are reported on. These have been taken from subtidal depths by bottom sampler and by hand (skin diving). Extensive field notes and colour transparencies of the living specimens have enabled a comparison of preserved and living material to be made. Field notes on habitat are also available, and the characteristics that apparently determine the association of species with certain substrates and current conditions are discussed.

SYSTEMATICS

Podoclavella meridionalis Herdman

Podoclavella meridionalis Herdman, 1891 : 603. Kott, 1957 : 91 and synonymy.

Records : North-western Australia and eastern Australia.

New Records : Off Cronulla.

Description : Solitary club-shaped individuals, 5 cm tall, 0·5 cm wide at the free end, tapering to a more leathery stalk occupying the lower half of the body. Elsewhere the test is gelatinous and semi-transparent. The zooid occupies the upper half of individual, while the posterior abdominal extension of the zooids extends into the stalk. The atrial aperture is terminal and the branchial aperture antero-ventral. The test on the dorsal side of the branchial aperture is thickened and closes down over the aperture, which when open is directed downwards towards the substrate. Some of the 25 oblique muscle fibres on the thorax extend from the atrial siphon and some from the branchial siphon but most extend from the ventral border posteriorly and dorsally and fade out on the abdomen. There are 30 rows of about 70 regular oval stigmata in each row. The branchial tentacles are arranged in four circles, with the largest tentacles in the posterior row. The thorax is about half the length of the abdomen. The voluminous stomach is collapsed into irregular folds and is present in the middle third of the abdomen. Few embryos at an early stage of development are present in the posterior corner of the thorax.

Ecological notes : The present specimens were taken from horizontal rock surfaces on the sea bed, at 25 to 30 m, where there is little water movement except when the seas are rough. They were present in a density of about 5 to 6 per square metre.

---

* Zoology Department, University of Queensland, St. Lucia.

cone, in which the zooids open all around the surface in circular to oval or elongate systems. The posterior abdomina extend down the length of the colony toward the base. The zooids are crowded together in circular to long double row systems. The zooids are of the usual form with a wide atrial aperture which has the anterior rim produced into a lip. There are four rows of about eight stigmata crossed by parastigmatic vessels. There are eight distinct stomach folds. There is a well-developed posterior abdominal stolon. A gastro-intestinal connective extends between the stomach and the rectum.

Taxonomy: *Distaplia dubia* (Oka) (see Tokioka, 1953) and *D. vallii* Herdman (see Van Name, 1918) both have parastigmatic vessels and internal stomach folds. The present species is distinguished by the eight distinct internal longitudinal stomach folds and the smaller number of stigmata in each row.

Polycitor giganteum (Herdman)

Polyclinum giganteum Herdman, 1899: 79. Kott, 1972*a*: 9, and synonymy.

Records: From Rottnest Island, Western Australia, and around the southern coast of Australia to Port Jackson. *New Records:* Bare Island, Congwang Bay, near Bare Island, Botany Bay off Cronulla, Port Hacking.

Description: The colonies are usually large and rounded but are sometimes separated into several lobes. The rounded head narrows into a sandy sometimes expanded basal portion by which the colony is anchored to the substrate. The test is firm and semi-transparent and the zooids open around the upper surface of the colony. There are rounded swellings on the surface over the anterior end of each zooid. Zooids extend down into the basal part of the colony. They are large and 6 mm long when contracted. The thorax represents about one-fifth the total length of the zooid. Both the branchial and atrial apertures are anterior and their borders are conspicuously marked off into six lobes. There are about 15 strong longitudinal muscle bands running along both sides of the abdomen, and almost enclosing it, except dorsally where the intestine is not covered by longitudinal muscle bands. There are from 10 to 16 rows of about 20 stigmata and long pointed dorsal languets in the branchial sac. The stomach is present in the posterior half of the abdomen and has four distinct folds.

Large specimens have one to three larvae present in the peribranchial cavity at one time, but of these there is usually only one at all well developed and they are not necessarily fertile. The larvae are large, about 1·2 mm long with fairly short tail wound only half the distance round the body of the larva which conform in all ways with previous descriptions.

Ecological notes: The colonies are semi-transparent in life as well as in preservative. However, in the living material two colour phases have been identified, viz. a white phase and an orange phase, and both are taken together. The orange pigmentation is in the body wall especially around the atrial siphon, and in the larvae. The orange phase appears to occur when the zooids are expanded and near to the surface of the colony or when the thoraces are distended with larvae. When zooids are contracted deep into the colony the orange colour is not apparent and the white phase is represented.

As with other gelatinous species, *P. giganteum* appears to favour vertical or near vertical faces and locations where there is little water movement so that firm attachments can be effected and there is no risk of their being dislodged.

Eudistoma pyriforme (Herdman)

(Figs 3, 4)

Psammaplidium pyriforme Herdman, 1886: 419. *Eudistoma pyriforme;* Kott, 1972*a*: 9, and synonymy.

Records: St. Vincent Gulf, Great Barrier Reef, W. Pacific, Madagascar. *New Records:* Off Cronulla.

Description: The colonies are sandy and vary in shape, from long and pillar-like, with a rounded expansion basally, or basally divided up into branches; or, pillow-shaped basally with a shallow platform-like extension on the upper surface. The zooids open on the upper surface of the colonies on which the test forms slight rounded swellings over the anterior end of each zooid. Zooids are arranged in a single circle around the perimeter of the narrow pillar-like colonies, with the atrial openings toward the centre of each circle. In the wider colonies there may be more than a single circle of zooids. Zooids are up to 0·5 cm long. They have strong longitudinal muscle bands on the thorax forming an almost continuous coat; externally there are well separated thin bands of circular muscle. Distinct circular sphincter muscles are developed on both siphons. There are three rows of branchial tentacles most numerous in the anterior row. These rows of tentacles occupy a large part of the branchial siphon. There are three rows of stigmata with about 18 stigmata in each row. There are 12 longitudinal thoracic muscle bands which in some zooids appear to spread out to form an almost continuous coat. The abdomen is about three times the length of the thorax in the contracted specimens. The oesophagus is very long and the rounded stomach is present in the posterior third of the abdomen. Both the intestine and the proximal part of the rectum are bent into S-shaped curves. There are two developing eggs in the oviduct. The proximal part of the rectum is coiled into an elaborate S-shape, although the portion of the descending limb of the gut loop posterior to the stomach is only slightly curved. There is a single mature embryo in the peribranchial cavity and a large developing embryo in the distal part of the oviduct. The embryos appear to develop as they pass up the oviduct, as is characteristic of this genus.

Taxonomy: The shape of the present colonies is different from that previously described for the species, as more usually there are a large number of circles of zooids opening all over the surface of a large rounded colony. The zooids are, however, identical with those previously described for *E. pyriforme*, especially in regard to the thoracic musculature and the gut loop. Kott (1972*a*) has indicated the problems associated with the identification of species in this genus.

Ritterella proliferus (Oka)

Distoma proliferum Oka, 1933: 436. *Polycitor proliferus;* Tokioka, 1953: 204, and synonymy. *Ritterella dispar;* Kott, 1957: 102; 1963: 78.

Records: From Arrawarra (New South Wales) to Hervey Bay (Queensland); Taiwan; Japan. *New Records:* Botany Bay, near Bare Island.

Description: The colonies consist of a more or less top-shaped head, narrowing to a slightly expanded base from which more than one lobe may arise. Zooids open on the flat upper surface of the colony and the test is raised over the anterior end of the zooids. The colonies are pale greenish colour in preservative. The test is semi-transparent, naked and gelatinous. Both apertures open separately on the surface. The branchial aperture is on a very short siphon with its margin divided into six rounded lobes. The atrial aperture is on a fairly long siphon extending from the antero-dorsal corner of the thorax. The thorax is about the same length as the abdomen. The posterior abdomen is of varying lengths from a short pointed extension of the abdomen to a longer structure in which the gonads are bunched. There are 19 fine irregular folds on the stomach and a posterior stomach present in the gut loop.

Taxonomy: Kott (1969) has pointed out that this species previously described as *Polycitor* is in fact a species of the genus *Ritterella*, and this is confirmed by the structure of the present zooids.

Ritterella herdmania Kott

Ritterella herdmania Kott, 1957 : 102. 1972*a* : 11, and synonymy. *Psammaplidium pedunculatum ;* Herdman, 1899 : 88.

Records : South-Western Australia, St. Vincent Gulf, Westernport, Port Phillip Bay, Newport, Port Jackson. *New Records :* Little Turriel Point, Port Hacking.

Description : The specimens conform to previous descriptions of this species (see Kott, 1972*a*), except that there are only about six stigmata in each row instead of the usual 12 stigmata previously reported. This is probably because the colonies are young.

Ecological notes : The species disappears during the summer and is just starting to re-grow at the end of April. It reaches a peak in late winter and the zooids are actively budding from the basal stolon in specimens from Little Turriel Point taken in August 1966.

Aplidium directum n. sp.

(Fig. 5)

Type location : Off Cronulla (Coll. J. MacIntyre). 90 m (17.vi.65) ; 140 m (16.vi.65).

Holotype : Australian Museum registration no. Y1110.

Paratype : Australian Museum registration no. Y111.

Description : The colonies are small, flat-topped cylindrical lobes sometimes rising from a common base. The test is very sandy throughout. There is a common cloacal aperture in the centre of the free end of each colony. Zooids are arranged around the periphery of the flat top and open into a central common cloacal opening. The zooids are very delicate. There are 12 very fine longitudinal muscle bands extending in a single band along either side of the posterior abdomen. There is a single atrial lip from the body wall anterior to the atrial opening, which is on a short siphon opposite the first row of stigmata. There are 10 to 12 stigmata in each of 10 rows. The stomach is small and has five distinct folds. There is a rounded posterior stomach. The posterior abdomen is about the same length as the abdomen but the thorax is slightly longer. Colonies are about 1·5 cm high. The test is raised into slight swellings over each zooid and the central common cloacal apertures are prominent.

Taxonomy : These small upright cylindrical colonies are reminiscent of *Aplidium stewartense* (Millar ; see Kott, 1969), *Aplidium cottrelli* (Brewin, 1957), and *Aplidium novaezealandae* Brewin, 1952, which are all sandy, flat-topped species with the zooids in circular systems opening on to the upper flat top of the colony. *Aplidium directum* is distinguished from all these species by the presence of an atrial siphon and the origin of the atrial lip from the body wall anterior to the atrial opening. The Antarctic *Aplidium stewartense* occupies a similar habitat, on the sea bed, as the present species.

Aplidium flavolineatum (Sluiter)

Amaroucium flavolineatum Sluiter, 1898 : 30. *Aplidium flavolineatum ;* Kott, 1963 : 105, and synonymy.

Records : Rottnest Island (Western Australia), South Australia, Victoria, Tasmania, Wreck Bay and Port Jackson (New South Wales) ; South Africa.

New Records : Little Turriel Point, Port Hacking.

Description : The living colonies have orange zooids in a semi-transparent test. In preservative the zooids are white, in a jelly-like matrix.

The colonies are investing. More than 1 cm thick in the centre but decreasing to about 0·5 cm around the borders. The surface of the test is raised into minute lobes accommodating the branchial lobes. There are common cloacal apertures randomly distributed over the surface. The zooids are crowded in the colony and are vertical at the surface but the posterior abdomen curves in the basal half of the test so that the posterior abdomina lie parallel to the surface in the basal half of the test. There are 15 longitudinal muscles on the thorax. The branchial sac has nine rows of about 12 stigmata. The anterior border of the atrial aperture is produced into three large leaf-like languets. The stomach is large and voluminous with about 30 folds. Testis lobes are arranged in two rows in the posterior abdomen.

Taxonomy: This species is distinguished by its jelly-like transparent common test and investing form, and the large number of stomach folds. The recorded distribution of the species in South Africa and around the south coast of Australia is similar to that indicated for other species (see Kott, 1971, 1972*a*).

Trididemnum cerebriforme Hartmeyer

Trididemnum cerebriforme Hartmeyer, 1913: 139. Kott, 1963: 275, and synonymy.

Records: South and West Africa, south-western and South Australia, New South Wales, Queensland.

New Records: Little Turriel Point, Port Hacking.

Description: Colony has the usual grey brain-like appearance, is hemispherical, and the surface is divided into complicated convolutions and is deeply " infolded ". The secondary common cloacal canals are at the oesophageal level of the zooids and the primary cloacal canals extend posterior to the zooids. The zooids are darkly pigmented around the anterior part of the thorax. The branchial aperture is large and the atrial aperture posteriorly directed. There are three rows of oval stigmata. Larvae are present in the colony and are of the usual form described for this species. They are 0·6 mm long.

Didemnum augusti Michaelsen

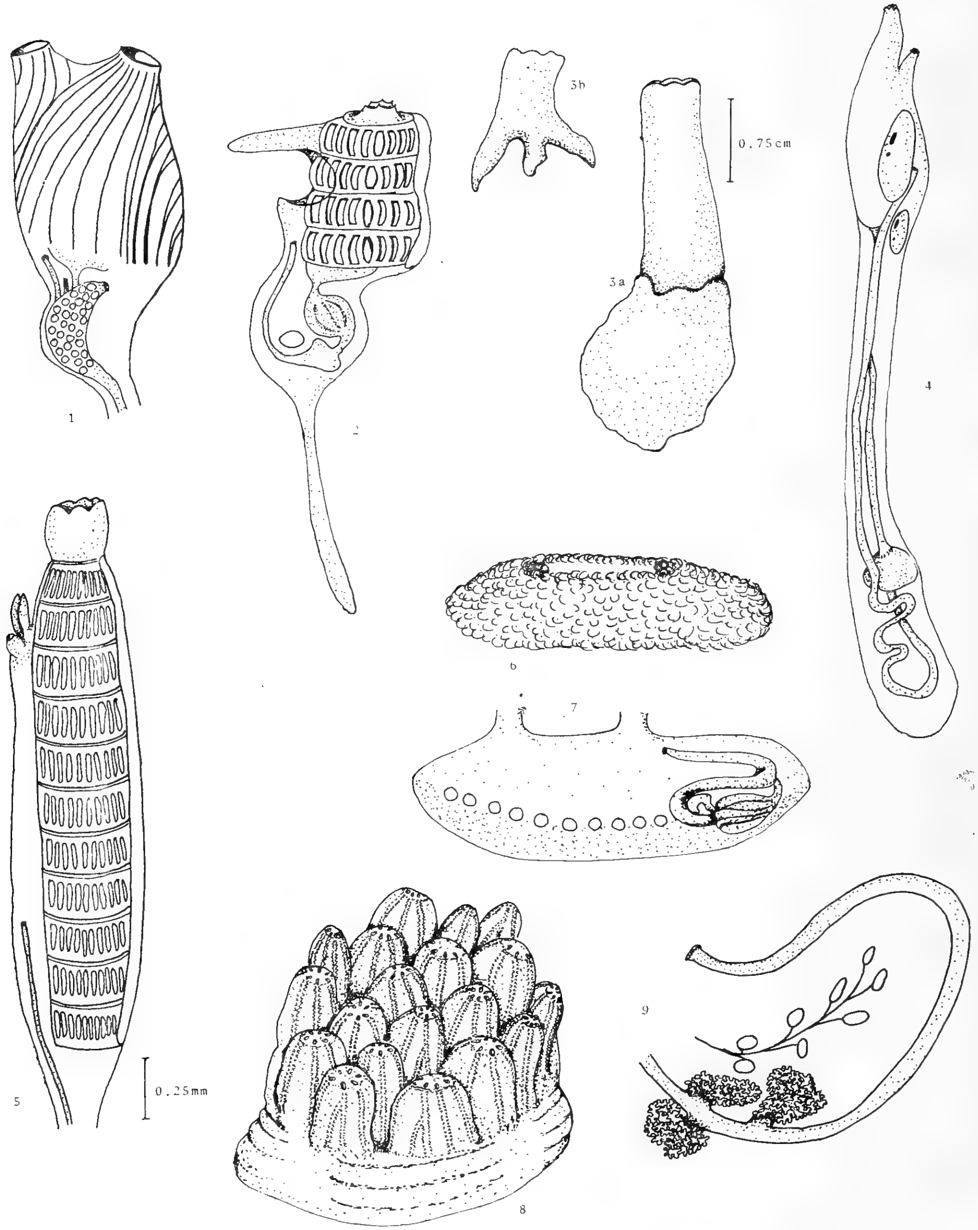
Didemnum augusti Michaelsen, 1920: 39. Kott, 1962: 323, and synonymy.

Records: St. Vincent Gulf (South Australia), Westernport (Victoria), Port Jackson (New South Wales). *New Records:* Little Turriel Point, Port Hacking.

Description: The zooids are pinkish. The colonies form investing sheets with the surface marked off into rounded areas by depressions corresponding to the course of the deep primary cloacal canals which extend the whole length of the zooids. The secondary cloacal canals are thoracic. The spicules are large, and stellate and dense throughout. Both the surface and basal layers of test are thin although the zooids are embedded in solid columns of test and open into the common cloacal canals which surround these. Zooids do not cross the cloacal spaces in their own separate thoracic sheath. The spicules are 0·02–0·04 mm in diameter and have eight conical rays in optical cross section. They are dense throughout the test. There are eight and a half coils of the vas deferens around a single undivided testis follicle. The test along either side of the atrial opening is thickened in a position corresponding to the usual lateral organ.

Taxonomy: The cauliflower-like appearance on the surface of this colony is characteristic of the species, in which the ventral surface of the zooid is embedded in solid pillars of test, between thin layers of basal and surface test. In the region of the primary canals the thin surface test is, in preserved specimens, depressed to form a furrow in the surface.

The species does resemble *Didemnum maculatum* (Nott) (see Kott, 1971) from New Zealand and the east coast of Australia but it is distinguished from that species by the thin basal layer of test.



Figs 1–9. 1, *Podoclavella australis:* Thorax muscles removed from posterior end to show swelling of distal portion of oviduct. 2, *Distaplia distomoides:* Zooid. 3, 4, *Eudistoma pyriforme:* 3, Colony; 4, Zooid. 5, *Aplidium directum:* Thorax. 6, 7, *Monoandrocarpa plana:* 6, Individual; 7, Individual removed from test viewed from left side. 8, *Botrylloides magnicoecum:* Colony. 9, *Pyura cancellata:* gut loop with liver lobes and gonad.

Didemnum moseleyi (Herdman)

Leptoclinum moseleyi Herdman, 1886 : 272. *Didemnum moseleyi ;* Kott, 1972*a* : 19, and synonymy.

Records : From the Pacific and Indo-Malayan region ; in Australia from Rottnest Island (Western Australia) across the southern coast to the Great Barrier Reef (Queensland). *New Records :* Little Turriel Point, Port Hacking.

Description : The colonies are greyish pink in preservative. They are irregularly lobed and investing seaweed. The spicules become less dense below the surface layer of test, and the pinkish colour of the colony is caused by the zooids showing through the spicules. Spicules outline the branchial lobes in the surface and are minute and stellate 0·02–0·03mm in diameter. There are eight and a half coils of the vas deferens around an undivided testis follicle. Larvae are present in these colonies and are of the usual form (see Kott, 1962). The surface of the test is sometimes raised into small spicule-filled pointed papillae. In one colony the surface is raised into rounded lobe swellings and ridges which correspond to irregularities in the surface to which they are attached (in this case a hydroid). Thoraces cross the common cloacal spaces in independent test sheaths, although they are sometimes joined in rows. The thoraces of the zooids are minute with four to six stigmata in each row. The spicules also occasionally fill the branchial lobes. The spicules are stellate with six to eight points in optical transverse section.

Taxonomy : This is a commonly found species of *Didemnum* and is characterized by the size and shape of the spicules, the common cloacal system, the small zooids and large number of vas deferens coils.

Didemnum lambitum (Sluiter)

Didemnoides lambitum Sluiter, 1900 : 18. *Didemnum lambitum ;* Kott, 1962 : 317, and synonymy ; 1972*a* : 18.

Records : South Australia, New South Wales and New Zealand. *New Records :* Little Turriel Point, Port Hacking.

Description : The colonies are described by the collector as " candle-grease ascidians ", and the living specimens are fleshy pink (or pale yellow) in colour. The colonies are branched finger-like lobes with terminal common cloacal apertures. The primary cloacal cavities are posterior abdominal surrounding a central core of solid gelatinous test. Spicules are present throughout the test. There are eight coils of the vas deferens around a single undivided testis lobe. Larvae of the usual form are present in the colonies.

Leptoclinides rufus (Sluiter)

Polysyncraton rufum Sluiter, 1909 : 72. *Leptoclinides rufus ;* Kott, 1972*a* : 16, and synonymy.

Records : South Australia, Victoria, Tasmania, New South Wales, Queensland and New Zealand. *New Records :* Little Turriel Point, investing a specimen of *Microcosmus australis* which was attached subtidally to a rock wall.

Description : The living specimen has been described as having " tawny colourings ". The spicules are sparse throughout the test and are accumulated especially around the common cloacal canals. The zooids are embedded in the common test and open into the cloacal canals by a posteriorly directed atrial aperture. There are six and a half coils of the vas deferens around five testis lobes.

This appears to be a young colony of this species and the common cloacal systems are not specially well developed, although the thoraces of the zooids tend to extend into the roof of the cloacal canals.

Phallusia depressiuscula (Heller)

Ascidia depressiuscula Heller, 1878 : 5. *Phallusia depressiuscula ;* Kott, 1966 : 293, and synonymy.

Records : The species has a wide recorded distribution from all around the Australian coast, the Pacific and the Indo-Malayan region. *New Records :* Bare Island, Botany Bay ; Little Turriel Point, Port Hacking.

Description : Living specimens are yellow-greyish to brownish. In some specimens there are black pigment spots in the surface test, especially on the anterior part of the individual. In the centre of each pigment accumulation there are irregular swellings of the terminal ampullae of the test vessels. In those parts of the test where there are no black spots the test vessels subdivide into terminal ampullae evenly distributed over the surface. Specimens up to 15 cm long and 10 cm deep in the posterior third of the body have been taken. They are fixed by the ventral part of the posterior third of the body or by part of the left side. The prebranchial area is very shallow. The simple branchial tentacles are closely placed. The accessory openings from the neural gland are mostly to the left of the dorsal lamina although some open into the right peribranchial cavity. The dorsal lamina is ribbed. There are curved pointed papillae on the internal longitudinal vessels at their junction with the transverse vessels. Accessory papillae are also present from each side of the base of the papillae.

Adagnesia opaca Kott

Adagnesia opaca Kott, 1963*a* : 75 ; 1972*b* : 238.

Records : Moreton Bay, Queensland (type locality). *New Records :* Off Cronulla.

Description : A portion only of a single individual was taken. It is recognized by the sandy test, extended anteriorly to cover the branchial aperture from the right side and to cover the atrial aperture from the left side. The portion of the branchial sac is typical of the species with pointed dorsal languets and numerous bifid papillae each more or less corresponding to a pair of spiral infundibulae.

Taxonomy : This unusual monotypic genus has not been recorded previously outside its type locality in Moreton Bay.

Monoandrocarpa new genus

Small solitary individuals ; branchial folds present ; polycarps in a single row on each side of the body, each consisting of a sac-like ovary with a single testis follicle.

Type species : Monoandrocarpa plana n. sp.

Monoandrocarpa plana new genus, new species

(Figs 6, 7)

Type locality : Off Cronulla 16.vi.65. Coll. J. MacIntyre 160 m.

Holotype : Australian Museum registration no. Y852.

Paratypes : (three specimens) Australian Museum registration no. Y853.

Further Records : Off Cronulla 180 m.

Individuals are elliptical and dorso-ventrally flattened. The surface test is produced into long hairs around the meridian of the body to which sand and shell particles adhere. There is a longitudinal area on the upper (dorsal) surface, which is free of sand. Both branchial and atrial apertures are contained in this upper sand-free area separated from one another by an interval equal to about half the length of the body. Specimens are solitary and up to 1·5 cm long including the sandy coat. The dorsal lamina extends along the middle of the upper surface, and the endostyle along the middle of the ventral surface. There are four branchial folds on each side of the body with internal longitudinal vessels arranged as follows:

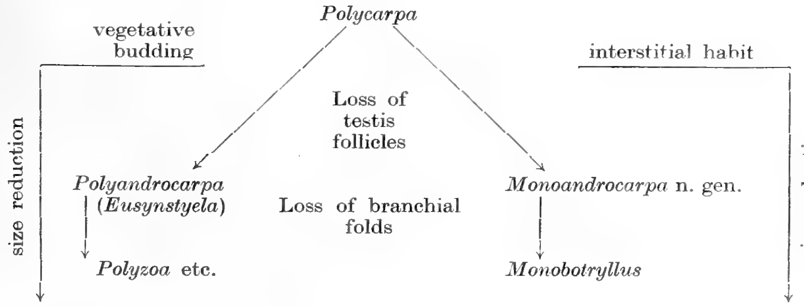
DL 0(6) 0(4) 0(8) 0(5) 0E

with about five oval stigmata in each mesh. There is some variation in the size of the folds and any one may be larger than the others. The gut forms a short rounded loop. The stomach is short and extends anteriorly on the under side of the branchial sac: and the wall is thrown into 12 longitudinal folds. There is a fairly long curved pyloric caecum enclosed in the pole of the gut loop. The descending limb of the gut loop extends posteriorly above the branchial sac and the rectum extends anteriorly along the mid dorsal line to terminate at the base of the atrial opening in an anus bordered by minute finger-like lobes. The gonads are rounded polycarps arranged in a row along the meridian of each side of the body, opposite the fourth (and most ventral) branchial fold. There are 10 to 13 gonads on the left side of the body, and up to 16 on the right. Each gonad consists of a single testis follicle, beneath a rounded sac-like ovary. The single vas deferens extends around the anterior aspect of the ovary to open on the mesial side of the female duct.

Taxonomy: This interstitial species is similar to *Polycarpa incubita* Sluiter, 1904, in both the shape and size of the individuals, although Sluiter's species does not have hairs produced from the test. *Polycarpa incubita* also has a row of polycarps on each side of the body although they are unusual, with the duct rising from the centre of a conical gonad. Unfortunately the testis follicles have not been described.

The present genus has close affinities with *Polyandrocarpa* (subfamily Polyzoinae family Styelidae), in which there is a similar reduction in the number of polycarps to a single row and a reduction in the number of testis follicles in each to two (in *Eusynstyela*, subgenus) and a single testis follicle in each gonad in *P.* (*Eusynstyela*) *monotestis* Tokioka, 1953. In *Polyandrocarpa*, however, it is vegetative budding that has resulted in zooids of reduced size, and colonies are formed. The present genus is most closely related to *Monobotryllus* Oka, 1915, a small solitary genus of the Styelinae in which there are similar rows of polycarps with a single testis follicle in each. *Monobotryllus*, however, has a flat branchial sac without folds.

The present genus, therefore, apparently belongs with the Styelinae, in which vegetative budding does not occur. Its size may be associated with its interstitial habit, which is shared with other genera of the Styelinae, but from which it is distinguished by the maintenance of branchial folds, the presence of numerous polycarps in a row on each side of the body, and the presence of a single testis follicle in each gonad. The phylogenetic relations of the genus are shown in the following diagram:



Stolonica australis Michaelsen

Stolonica australis Michaelsen, 1927 : 202 ; Kott, 1972*a* : 28, and synonymy. *Records :* South-western Australia to Tasmania. *New Records :* Little Turriel Point (on ascidian attached to rock wall subtidally).

Description : The individuals are stalked and sandy. There are two folds on each side of the body with about two internal longitudinal vessels between the folds. The gut loop is short and the stomach has the usual distinct glandular folds and a curved caecum. Gonads are present around the ventral border on either side of the endostyle. The present specimens have the curved caecum and are stalked, in contrast to the closely related *Amphicarpa diptycta.*

Botrylloides magnicoecum Hartmeyer

(Fig. 8)

Botrylloides nigrum var. *magnicoecum* Hartmeyer, 1912 : 271. Kott, 1972*a* : 30, and synonymy.

Records : (See Kott, 1972). *New Records :* Little Turriel Point, Port Hacking ; Bare Island, Botany Bay ; Fairlight, near Manly (N.S.W.).

Description : The living specimens are orange, although in preservative they may be dark grey to purple. The pigment cells are present, especially in the atrial lip and round the branchial aperture and along both sides of the endostyle. The colonies consist of rounded to cucumber-shaped lobes rising from a common base. Each lobe has a terminal common cloacal cavity with an aperture at the apex of the lobe which expands widely in the living colonies to expose the terminal openings of the common cloacal canals. There are about six longitudinal cloacal canals around each lobe and these may anastomose with one another or branch along their length. The common cloacal canals are surrounded on each side by a row of zooids. When the colony is contracted the free end of the lobes appears pointed. However, when the terminal aperture is widely expanded the tips of the lobes are flattened. There is some sand incorporated into the basal common test, which is otherwise gelatinous and semi-transparent. There are 15 rows of stigmata. The stomach is short and rounded and there is a long pyloric caecum curved in the pole of the gut loop.

Ecological notes : The appearance of living specimens of this species is very sharply in contrast to the preserved specimens, both in regard to colour and to the shape of the colony. In preservative the dark purple collapsed lobes bear no resemblance whatsoever to the upright and pointed orange whitish lobes of the living specimen. The characteristic longitudinal common cloacal canals extending along the side of the lobes are especially conspicuous in the living specimens.

Taxonomy : The present specimens differ from those previously described in that the subdivision of the colonies into separate lobes does not extend down into the basal zooid-free common test and the lobes are consequently sessile rather than stalked.

Botrylloides nigrum Herdman

Botrylloides nigrum Herdman, 1886 : 50. Kott, 1972*a* : 30, and synonymy.

Records : See Kott, 1972. *New Records :* Bare Island, Botany Bay.

Description : The living specimens are bright orange, pale beige or light green. Investing colonies are formed that are rather irregular, and in which the borders grow out into lobes. The preserved specimens are purple brown. Zooids are present in long double row systems. In younger colonies there are some circular systems. There are 12 rows of about 14 stigmata. The stomach is expanded at the cardiac end and narrows toward the pyloric end ; it is longer than its diameter. The stomach caecum is only barely distinguishable. Eggs are present in a pouch evaginated from the posterior part of the body and there is a postero-dorsal cluster of testis follicles. The collector has described specimens as including attached portions of a lighter (orange) colour. These are in fact actively growing lobes of the colony.

Taxonomy : This species is of characteristically irregular investing form. The zooids, vertical to the outer surface, are arranged in the usual long, double row systems, which together with the barely distinguishable stomach caecum distinguish the species. The zooids are smaller than those of *Botrylloides magnicoecum* and the pigment cells are fairly evenly distributed through body wall of the zooid. The zooids occupy almost the whole thickness of the test, which also tends to distinguish the species from *B. magnicoecum*, in which there is very often a central or basal core of common test into which the zooids have not penetrated.

Botrylloides leachi (Savigny)

Botryllus leachii Savigny, 1810 : 7. *Botrylloides leachi ;* Kott, 1972*a* : 29, and synonymy.

Records : See Kott (1972*a*). *New Records :* Little Turriel Point, Port Hacking.

Description : The colonies are the usual stalked and rather flattened tongue-like lobes. The zooids are in circular systems opening into depressions along the outer surface of the lobes. In the preserved specimens the test is transparent and the zooids are a pale colour. There are no zooids in the stalk. The stomach is longer than its diameter and is not as much reduced in diameter at the pyloric end as in *B. nigrum.* There is a very short pyloric sphincter. There are eight rows of stigmata, three internal longitudinal vessels and two to four stigmata in each mesh. The testis follicles are present above the gut loop on the left and level with the gut loop on the right.

Taxonomy : This species is easily distinguished by the firmness of the test and the rows of circular to oval systems of zooids along the side of the tongue-like lobes. These develop by subdivision of parent systems as each is increased in length by the addition of zooids to the system. In some cases systems can be seen partially subdivided.

Cnemidocarpa etheridgii (Herdman)

Styela etheridgii Herdman, 1899 : 38; Kott, 1972*a* : 31, and synonymy.

Records : Cockburn Sound (Western Australia) to d'Entrecasteaux Channel (Tasmania) and Moreton Bay (Queensland). *New Records :* Off Cronulla.

Description : A single specimen only is available. It is rounded and spherical with a hard sand-ingrained test. The apertures are close together on the upper surface. The surface test is round and uneven, especially around the sessile apertures. The internal longitudinal vessels are arranged as follows :

E 3(6) 2(18) 3(13) 2(15).

There are eight stigmata in each mesh. The gut forms a deeply curved fairly narrow loop ; the stomach is pleated internally but these are not evident on the outer wall of the stomach. The dorsal tubercle has a simple opening directed anteriorly. The anal border is divided into a number of rounded lobes. There are five long gonads on the right side of the body, although none was apparent on the left. The body musculature is very strong. The long gonads consist of double rows of testis follicles beneath and slightly invaginated into the ovarian tubes. There are small upright endocarps in the gut loop and between the gonads.

Styela plicata (Lesueur)

Ascidia plicata Lesueur, 1823: 5. *Styela plicata;* Kott, 1952: 216, and synonymy.

Records: (See Kott, 1952.) *New Records:* Audley, upper Port Hacking (below the weir).

Description: The specimens are of the usual form.

Ecological notes: Audley is on an arm of Port Hacking well up into the National Park. The water here is at least seasonally quite brackish, and it is surprising that a species should occur so far away from the open sea. It has been noted, however, that *Styela plicata* does quite often extend some distance into estuaries and it has previously been recorded from Freshwater Bay in the Swan River estuary and therefore appears to tolerate brackish conditions better than most species of Ascidiacea.

Polycarpa tinctor (Quoy and Gaimard)

Ascidia tinctor Quoy and Gaimard, 1934: 608. *Polycarpa tinctor;* Kott, 1964: 134, and synonymy; 1972*b*: 242.

Records: North-western Australia, Queensland, New South Wales. *New Records:* Off Cronulla (10–20 m, 50 m, 140 m coll. J. MacIntyre).

Description: The body is of the usual oval laterally flattened form. The test is rigid and both apertures are fairly close together anteriorly. The test is impregnated with sand and is very hard and rigid. The branchial sac has very narrow folds with up to 14 internal longitudinal vessels crowded on them. There is a wide interval between the folds with two to three internal longitudinal vessels. The dorsal tubercle is in a deep peritubercular area and has a simple longitudinal slit. The gut forms a simple arc; the short stomach has internal longitudinal glandular folds. There is a row of oval polycarps around the anterior border of the body on both sides of the endostyle. The polycarps have the usual double row of testis follicles beneath the shorter ovary.

Pyura cancellata Brewin

(Fig. 9)

Pyura cancellata Brewin, 1946: 121. Kott, 1971: 61, and synonymy. *Pyura carnea* Brewin, 1948: 134.

Records: Lakes Entrance, Portland (Victoria); North Island, South Island, Chatham Island, Stewart Island (New Zealand). *New Records:* Off Cronulla.

Description · The specimens are spherical and sandy and the apertures appear to be sessile. However, they are supported on short siphons that are obscured by the heavy coating of sand, embedded in and enclosed by anastomosing hairs from the surface test to form an outside sandy coat around the individuals. When the siphons are extended they protrude nakedly through the sandy coat, but when they are contracted the sand appears to completely cover the apertures. The body wall is thin, transparent and closely adherent to the test. There is a deep velum developed at the base of the branchial and atrial siphons that leaves a horizontal slit-like opening. There are strong longitudinal and circular muscles on the siphons and on the siphonal vela. The dorsal tubercle is small, with a circular opening with out-turned horns. Longitudinal vessels are arranged as follows:

DL 2(15) 2(18) 1(18) 2(18) 2(16) 2(12) 2(12) 1(2) 3.

The stigmata are oval and there are 2–3 in meshes between the folds. The present specimens are about 2·5 cm in diameter. The gut forms a wide open slightly curved loop. The anal border is divided into about 12 deeply separated lobes. The gonads are polycarp-like sacs along either side of a central duct.

Taxonomy: These specimens are identical with those previously described for this species and also resemble very closely *P. tunica* Kott, 1969, from the Antarctic. The siphonal vela, which are conspicuous in the present specimens, have also been described for the New Zealand specimens.

Herdmania momus (Savigny)

Cynthia momus Savigny, 1816 : 143. *Herdmania momus ;* Kott, 1972*a* : 41, and synonymy.

Records: (See Kott, 1972*a*). *New Records:* Off Cronulla.

Notes on Habitat

Off Cronulla the sea-bed is sandy from 10–50 m and the bottom has tidal ripples on the surface. From 50–90 m sediments grade to the fine grey mud which comprises the substrate at greater depths, although at 140 m there is some coarse sand (J. MacIntyre, pers. comm.). The deposition of fine silt and absence of ripple marks below 50 m indicate that currents are reduced. The occurrence of free living *Polycarpa tinctor* is associated with the sandy substrate at 10–50 m, and at 140 m. *Adagnesia opaca* is also associated with the coarse sediments at 140 m. Rooted aplousobranch species *Aplidium directum* and *Eudistoma pyriforme*, together with free-living species *Pyura cancellata* and *Monoandrocarpa plana*, are associated with the muddy substrate and reduced current flow at 90 m and at greater depths. At these depths there are no investing species, although large fixed species *Herdmania momus* and *Cnemidocarpa etheridgii* are present attached to rocks and shell fragments at the deeper stations where current flow is minimal. Of these species *Polycarpa tinctor*, *Aplidium directum* and *Eudistoma pyriforme* are known to be viviparous, and *Monoandrocarpa plana* and *Adagnesia opaca* probably are since the length and orientation of the gonoducts respectively favour such a habit.

On horizontal, rocky substrates off Cronulla at depths of 25–30 m, where tidal currents and surge are likely, there are stalked aplousobranch species *Podoclavella meridionalis* and *Sycozoa pedunculata*. However, from 2–16 m in Port Hacking on vertical and horizontal rock faces where tidal currents are strong there are more species of investing habit (Didemnidae, Botryllinae) and larger colonies and individuals which effect firm attachment where there are rocky surfaces (*Polycitor giganteum*, *Phallusia depressiuscula*).

Station Lists

Off Boat Harbour, south of Cronulla (coll. Underwater Research Group, N.S.W.).
    25 m, attached to flat rocks :
        Podoclavella meridionalis.

Off Cronulla (coll. Underwater Research Group, N.S.W.).
    30 m, on horizontal rock sea-bed :
        Podoclavella meridionalis.
    dredged ; ? depth :
        Sycozoa pedunculata.

Off Cronulla (coll. J. MacIntyre, 1965, 1966).
    10–50 m :
        Polycarpa tinctor.
    60 m :
        Polycitor giganteum.
    90 m :
        Aplidium directum n.sp.

Off Cronulla (coll. J. MacIntyre, 1965, 1966).—*Continued.*

140 m :
Eudistoma pyriforme
Aplidium directum n.sp.
Polycarpa tinctor
Herdmania momus
Adagnesia opaca (fragment).

160 m :
Pyura cancellata
Eudistoma pyriforme
Herdmania momus.

180 m :
Monoandrocarpa plana
Cnemidocarpa etheridgii
Pyura cancellata
Eudistoma pyriforme
Aplidium directum
Monoandrocarpa plana.

Little Turriel Point, Port Hacking (coll. Underwater Research Group, N.S.W., C. Lawler).
16 m, on vertical rock faces and horizontal rock surfaces. Calm water, strong tidal flow :
Sycozoa cerebriformis (large numbers in irregular patches)
Ritterella herdmania (dense patches in winter)
Botrylloides leachi.
subtidal, attached to other benthic organisms on vertical rock wall :
Podoclavella australis
Sycozoa cerebriformis
Didemnum patulum
Didemnum moseleyi
Leptoclinides rufus
Aplidium flavolineatum.
12 m, on rock face :
Botrylloides magnicoecus.
16 m, on debris on bottom little water movement except tidal current :
Ritterella herdmania
Aplidium flavolineatum (five to six colonies/sq. m).
9–16 m, on rock walls, ceilings of caves :
Didemnum lambitum.
? depth, on vertical rock face :
Phallusia depressuiscula.
? depth, attached to benthos on bottom :
Trididemnum cerebriforme.

Audley, upper Port Hacking (coll. Underwater Research Group, N.S.W.).
below weir :
Styela plicata.

Bare Island, Botany Bay (coll. Underwater Research Group, N.S.W., C. Lawler).
2–3 m, on rock :
Botrylloides nigrum.
9 m, on rock :
Polycitor giganteum.
12 m, on rock, vertical faces little water movement :
Polycitor giganteum
Phallusia depressiuscula.

Near Bare Island (coll. Underwater Research Group, N.S.W., C. Lawler).
Ritterella proliferus.

Congwang Bay, near Bare Island (coll. Underwater Research Group, N.S.W., C. Lawler).
9 m, along rocky almost vertical cliff, little water movement :
Polycitor giganteum (in patches, not common).

Fairlight, near Manly (coll. Underwater Research Group, N.S.W., C. Lawler).
6 m, on vertical rock faces, little water movement :
Botrylloides magnicoecum (not common).

References

BREWIN, BERYL I., 1948. Ascidians of the Hauraki Gulf, Part I. *Trans. R. Soc. N.Z.*, 77 (1) : 115–138.

————, 1952. Ascidians of New Zealand. Part VII. Ascidians from Otago coastal waters. Part II. *Trans. R. Soc. N.Z.*, 79 (3–4) : 425–458.

————, 1957. Ascidians of N.Z. Part X. Ascidians from north Auckland. *Trans. R. Soc. N.Z.*, 84 (3) : 577–580.

HARTMEYER, R., 1912.—Die ascidien der deutschen tiefsee Expedition. *Wiss. Ergebn. dt. Tiefsee-Exped.* "*Valdivia*", 16 (3) : 223–392.

————, 1913.—Tunicata. (*In :* L. Schultze, Zool. u. anthrop. Ergebnissee Forschungsreise in Sudafrika. Bd 5, Lft 2.) *Denkschr. med.-maturw. Ges. Jena*, 17 : 125–144.

HELLER, C., 1878.—Beitrage zur nähern kenntniss der tunicaten. *Sber. Akad. Wiss. Wien.*, 77 (1) : 2–28, +pls.

HERDMAN, W. A., 1886.—Report on Tunicata collected during voyage of H.M.S. "Challenger" during years 1873–76. Pt. II. Ascidiae compositae. *Zool. Chall. Exp.*, 14 (38) : 1–425.

————, 1891.—A revised classification of the Tunicata, with definitions of the orders, sub-orders, families, sub-families and genera, and analytical keys to the species. *J. Linn. Soc.*, 23 : 558–625.

————, 1899.—Descriptive catalogue of the Tunicata in the Australian Museum. Australian Museum, Sydney. Catalogue 17 : 1–139.

KOTT, PATRICIA, 1952.—The ascidians of Australia. I. Stolidobranchiata and Phlebobranchiata. *Aust. J. mar. Freshw. Res.*, 3 (3) : 206–333.

————, 1957.—The ascidians of Australia. II. Aplousobranchiata Lahille ; Clavelinidae Forbes and Hanly and Polyclinidae Verrill. *Aust. J. mar. Freshw. Res.*, 8 (1) : 64–110.

————, 1962.—The ascidians of Australia. III. Aplousobranchiata Lahille : Didemnidae Giard. *Aust. J. mar. Freshw. Res.*, 13 (3) : 265–334.

————, 1963.—The ascidians of Australia. IV. Aplousobranchiata Lahille ; Polyclinidae Verrill (continued). *Aust. J. mar. Freshw. Res.*, 14 (1) : 70–118.

————, 1963*a*.—*Adagnesia opaca* gen. nov., sp. nov. A remarkable Ascidian of the Family Agnesiidae from Moreton Bay, Queensland. *Pap. Dep. Zool. Univ. Qd.*, 2 (3) : 75–79.

————, 1966.—Ascidians of north Australia. *Pap. Dep. Zool. Univ. Qd.*, 2 (15) : 279–304.

————, 1969.—Antarctic Ascidiacea. A monographic account of the known species based on specimens collected under U.S. Government auspices 1947 to 1963. *Antarct. Res. Ser.* 13 : i–xv, 1–239, fig. 1–242, pl. 1–3, map, tables 19.

————, 1971.—Antarctic Ascidiacea. II. Collections made south of 40° south latitude 1963/67, principally by the U.S.N.S. Eltanin. *Antarct. Res. Ser.*, Biology, 16 (4) : i–iii, 1–60.

————, 1972*a*.—Ascidians of South Australia. I. Spencer Gulf, St. Vincent Gulf and Encounter Bay. *Trans. R. Soc. S.A.*, 96 (1) : 1–58.

————, 1972*b*.—Some Sublittoral Ascidians in Moreton Bay and their seasonal occurrence. *Mem. Qd. Mus.*, 6 (2) : 233–260.

LESUEUR, C. A., 1823.—Description of several new species of *Ascidia*. *J. Acad. Nat. Sci. Philad.*, 3 : 2–8.

MICHAELSEN, W., 1920.—Die krikobranchen ascidien des westlichen Indischen ozeans : Didemniden. *Jb. hamb. wiss. Anst.*, 37 : 1–74.

————, 1927.—Einige neue westaustralische ptychobranchiate ascidien. *Zool. Anz.*, 71 : 193–203.

MILLAR, R. H., 1963.—Australian ascidians in the British Museum (Natural History). *Proc. zool. Soc. Lond.*, 141 (4) : 689–746.

OKA, A., 1915.—Report upon the tunicata in the collection of the Indian Museum. *Mem. Ind. Mus.*, VI : 1–33.

————, 1933.—Ein Fall von kolonialknospung bei einer Synascidie. *Proc. Imp. Acad.*, Vol. IX, no. 8, 436–438. Text fig. 1.

QUOY, J., and GAIMARD, P., 1834. — Voyages de découvertes de l'Astrolabe 1826–29. "Mollusques." *Zoologie*, 3 : 559–626 ; 4 : 304–306.

SAVIGNY, J. C., 1810 (?).—Tableau systématique des ascidies, tant simple que composées. Paris, p. 7.

SLUITER, C. P., 1898.—Beiträge zur kenntniss dei fauna von Sudafrica II Tunicaten. *Zool. Jb.* (Systematik), 11 : 1–64.

————, 1900.—Tunicaten aus dem Stillen Ocean. *Zool. Jb.* (Systematik), 13 : 1–35.

————, 1909.—Die tunicaten der Siboga Expedition. Pt. 2. Die merosomen ascidien. *Siboga Exped.*, 56B : 1–112.

TOKIOKA, T., 1953.—Ascidians of Sagami Bay (Iwanami Shoten), Tokyo 1953, 1–315.

VAN NAME, W. G., 1918.—Ascidians from the Philippines and adjacent waters. *Bull. U.S. natn. Mus.*, 100 (1) : 49–174.

PLURELLIDAE, A NEW PHLEBOBRANCHIATE FAMILY OF THE ASCIDIACEA

PATRICIA KOTT*

[Accepted for publication 20th September 1972]

Synopsis

A new colonial phlebobranchiate species from Investigator Strait, South Australia, is described and assigned to a new genus for which a new family, Plurellidae, is erected. The species shares certain convergent characteristics with *Pyrosoma* (Thaliacea) but these are not regarded as phylogenetically significant.

INTRODUCTION

Species of the aberrant family Perophoridae were previously regarded as the only colonial forms in the enterogonid order Phlebobranchia. The new species described below, although morphologically related to *Ascidia spp.*, reproduces vegetatively and forms large colonial aggregates. It has been assigned to a new genus for which a new family Plurellidae, is erected. The family is distinguished from Perophoridae in many ways and the colonial habit shared by the two families does not indicate a phylogenetic affinity and does not clarify the problematical affinities of that family (Berrill, 1950).

Family PLURELLIDAE new family

Type genus: *Plurella* n. gen.

Branchial sac with internal longitudinal vessels supporting secondary papillae at their junction with transverse and parastigmatic vessels; stigmata rectangular, not coiled; dorsal lamina a plain edged membrane; gut on left of branchial sac; gonads not present in the gut loop; zooids reproduce vegetatively to form large colonial aggregates.

Genus PLURELLA n.g.

Type species: *Plurella elongata* n. sp.

Dorsal gland opens into the peribranchial cavity by many simple openings; several sac-like ovaries open by separate ducts.

PLURELLA ELONGATA n.sp.

Type location: Investigator Strait, Coll. J. Watson.

Holotype: Station Y. 18. Low flat reef, 101 ft; National Museum of Victoria registration number: H164.

Paratypes: Station Y. 19. Low flat reef, 106 ft; National Museum of Victoria registration numbers: H165, 166 (attached to roots of *Halocynthia hispida*).

Description: Large hemispherical colonies comprising aggregates of elongate zooids adhering to one another along their length. The longest zooids extend across the base of the colony and, as new zooids are added, in parallel to the colony, it increases in diameter and height. There is some irregularity in the parallel arrangement of zooids as they curve to match the form already established. Each zooid is completely surrounded by a thin layer of test impregnated with sand and, for most of its length, is loosely adherent to adjacent zooids. Posteriorly,

---

* Zoology Department, University of Queensland, St. Lucia.

at the base of the endostyle there is a circular area of very thin test which is free of sand, and it is possibly here that budding occurs. The body wall in the region of the gonads is very closely adherent to the test, and here the colony is more compact so that the surface area occupied by the atrial openings of the zooids is less than that occupied by the anterior ends of the zooids, which are free for about 0·5 cm of their length.

Zooids are up to 4·0 cm long with wide branchial apertures anteriorly and atrial apertures posteriorly. Both apertures are surrounded by very weak circular muscles. They are wide open and of almost the same diameter as the siphons. There are about 12 pointed lobes on the margin of the branchial aperture and six on the margin of the atrial aperture. The branchial siphon is a long, delicate tube, without conspicuous musculature except for the very delicate circular muscles around the aperture. It is about one-quarter of the length of the branchial sac and is delimited basally by a ring of about 40 simple branchial tentacles. There is a wide flat prebranchial area. The body musculature is confined to broad strong transverse bands on the right side of the thorax. To the left of the dorsal lamina there are about seven small oval areas, equidistant down the length of the branchial sac, where rays of very short fine muscle fibres extend from the body wall into the branchial sac. There is only a very small peritubercular V with a minute dorsal tubercle with a simple opening. The dorsal ganglion is about three-quarters of the distance down the branchial sac and the neural gland is slightly anterior and to the left of the ganglion. The neural gland opens into the peribranchial cavity by numerous simple openings along the length of its duct between the gland and the prebranchial peritubercular area. The branchial sac is long and only slightly wider than the branchial siphon. There is a single simple fold to the left of the dorsal lamina.

There are about 50 very fine internal longitudinal vessels on each side of the branchial sac with rounded secondary papillae where they cross the transverse and occasional parastigmatic vessels. There are two to three oval stigmata in each mesh. The oesophagus, from the postero-dorsal corner of the thorax, is short and opens into a rounded, smooth-walled stomach. The gut loop is simple and open with the intestine extending anteriorly and curving dorsally into a short posteriorly directed rectum which opens by a two-lipped anus into the base of a posteriorly directed atrial siphon from the posterior part of the dorsal border of the zooid. The gut is covered with excretory cells.

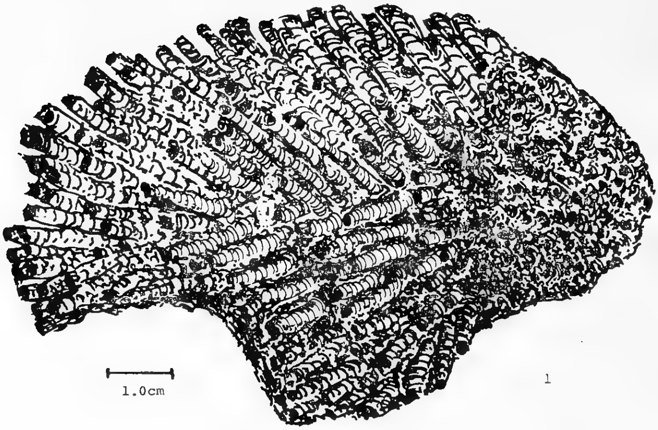
The heart extends obliquely across the right side of the posterior end of the branchial sac.

There is a long compact slightly lobed clump of testis follicles in the mid-line posterior to the branchial sac. Two to three fine ducts extend anteriorly more or less in the mid-dorsal line and then across the posterior border of the base of the atrial siphon from the right. Here each male duct expands into a rounded seminal vesicle which is associated with a sac-like ovary. Each ovary and seminal vesicle opens immediately into the base of the atrial siphon. The gonads and their ducts are embedded in the transparent body wall which, in this region, is firmly associated with the test.

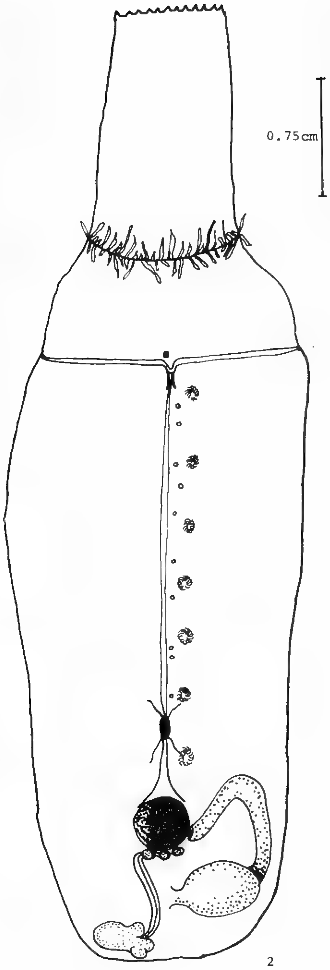
The atrial siphon is as long, although not as wide as the branchial siphon, and is equally delicate and without conspicuous musculature except for the very fine circular bands surrounding the apertures which in the specimens examined are always wide open.

PHYLOGENY

The branchial sac and dorsal lamina, and the confinement of body musculature to the right side of the body demonstrate affinities with *Ascidia spp.*, while the separate openings of the neural gland were previously thought to be exclusive to *Phallusia*. The species is, therefore, regarded as belonging



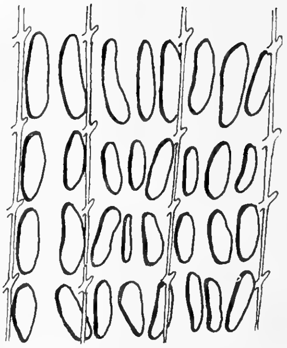
1

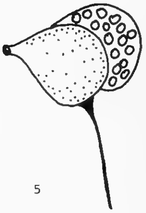


2

3

4





5

to the suborder Phlebobranchia. However, the budding process appears to involve the ectoderm and mesoderm from the body wall posterior to the branchial sac and does not appear to be identical with the process in Perophoridae (the only phlebobranch family in which budding was previously known), where new zooids form from a basal vascular stolon.

The species demonstrates convergent evolution with certain species of colonial Styelidae. In particular, the unusual form of the colony with branchial and atrial openings at opposite ends has been observed in a new species of *Polyandrocarpa* from Victoria (Kott, in press), in which the dorsal gland and ganglion are similarly posterior in association with the posterior position of the atrial apertures and the elongate zooids.

The unusual gonads and short oviducts of the present species are also similar to those found in certain genera of the Styelidae, where testis and ovary are often separated and where the gonads are separated into several parts served by separate ducts.

It is the position of the gonads, posterior to the branchial sac and at the edge of the atrial aperture that has drawn attention to other similarities in the form of zooid and colony of *Pyrosoma* (order Pyrosomida in the sub-class Thaliacea). The wide open branchial and atrial apertures with the pointed lobes lining the apertures, the posteriorly directed atrial opening from the posterior end of the body, and the site for bud formation are all similar to the condition found in *Pyrosoma*. However, although it is tempting to explore the probable ascidian origin for *Pyrosoma* (see Neumann, 1935 ; Berrill, 1950) through an ancestor it shares with the present species, the similarities are more likely to be due to convergence ; and to have resulted from the style of colony in both, where the progressive addition of new zooids has forced the atrial aperture to the posterior end of the body and has favoured the development of long siphons to gain access to the surface through the crowded zooids. This contention is supported by the presence of an ascidiid dorsal lamina in Plurellidae while the Pyrosomidae retain the primitive dorsal languets of the Cionidae.

The family Plurellidae, therefore, must be considered phylogenetically related to the Ascididae, from which it has evolved by the development of a process of vegetative reproduction, a reduction in zooid size, the development of colonies, and the specialization of the gonads.

Acknowledgements

Acknowledgement is made to Mr. S. Shepherd, Department of Fisheries and Fauna Conservation, South Australia, and Mrs. J. Watson, National Museum of Victoria, who collected the material in the Investigator Strait, South Australia.

References

Neumann, G., 1909–35.—Thaliacea in Kukenthal and Krumbach. *Handb. der Zoologie*, 5 (2) : 226–323.

Berrill, N. J., 1950.—The Tunicata. *Roy. Soc. Publs.*, 133 : i–iii, 1–354.

Kott, Patricia (in press).—The Ascidians of Westernport and adjacent localities. *Mem. Natn. Mus. Victoria.*

Figs 1–5. 1, Colony. 2, Zooid opened along ventral surface and branchial sac removed to show branchial tentacles, neural gland openings, small circular muscle areas connecting body wall and branchial sac, gut loop and gonads. 3, Individual removed from test from left side. 4, Portion of branchial sac. 5, Seminal vesicle and flask-shaped ovary.

MANGROVE SWAMP AND SALT MARSH COMMUNITIES IN SOUTHERN AUSTRALIA

M. KRATOCHVIL,* NOLA J. HANNON* AND LESLEY D. CLARKE*

(Plate x)

[Accepted for publication 23rd August 1972]

Synopsis

Vegetation maps of three areas close to Sydney indicate the diversity of the associations of the mangrove and salt marsh species and of their distributions with respect to the source of tidal flow. The floristics of this district and its major environmental characteristics are compared with those of localities in the other southern States of Australia.

NOMENCLATURE

Arthrocnemum australasicum (Moq.) Moss is not correctly applied to the plant thus named herein and throughout the series of related papers. For the present, it is probably best referred to as *Salicornia quinqueflora* Bunge ex Ungern-Sternberg, but this group is in need of revision (L. Johnson, pers. comm.).

Cladium junceum has now been transferred to the genus *Baumea* and is correctly cited as *B. juncea* (R.Br.) Palla.

INTRODUCTION

The rate of urban extension throughout southern Australia threatens maritime communities with severe disturbance, if not extinction. Many stands have already been eliminated, particularly within the past 30 years. Pollution is now prevalent in the majority of the remaining stands and yet our knowledge of these ecosystems, which are of particular interest, is very incomplete. Chapman's (1960) monograph clearly indicates the dearth of information for Australia where, as in other areas of the world, intertidal situations sheltered from wave action support mangrove and/or salt marsh communities.

However, such apparently cosmopolitan habitats do not support plant communities that are identical or even similar, despite the universal dominating influence of saline tidal flow in these situations. At least two major variants of these community types can be distinguished within the immediate vicinity of Sydney. Comparison of the floristics of these salt marsh communities with those even in Victoria and South Australia reveals marked differences. In addition, the limited comparisons that can be made of the performances of the same species in different areas of Australia suggest considerable intra-specific variation; for example, in *Avicennia marina* (Forsk.) Vierh. var. *resinifera* (Forst. f.) Bakh., McNae (1966) records that in northern Queensland its seedlings require high light intensity and are killed by shade or mud cover; also that adults occur in situations where the salinity of the soil water is 9%. Beard (1967) has located a stand of *Avicennia* in north-western Australia completely isolated from the sea, situated 25 miles inland, which is presumed to be a relic from the last recession of the sea level thought to have occurred at least 2,500 years ago. Presumably *Avicennia* seedlings have satisfactorily established in this highly atypical habitat. Both of these reports contrast sharply with the environmental requirements for survival of *Avicennia marina* seedlings collected in the Sydney district (Clarke and Hannon, 1970). In a few isolated areas in the Sydney district, such as in South West Arm of Port Hacking, mature *Avicennia* individuals of only 1 m

---

* Botany School, University of New South Wales.

height occur in situations where at high tide the shoot system is completely submerged. Long, finger-like projections hang downwards from the stems and are exposed to the air at low tide. McNae (1966) points out that *Avicennia marina* occurs further south and in cooler temperatures in Australia than in Africa and Sauer (1965) notes that since it grows under a great climatic range all round Australia, its sparse geographic pattern presumably reflects unfavourable edaphic and exposure conditions.

It is apparent that the need for study of these areas is urgent and that all available information should be placed on record so that at the least, detailed descriptions of these communities may be preserved. The purpose of this paper is to record vegetation maps that were prepared in 1965, in the course of studies of these communities in the Sydney district, and also limited observations that have been made in similar habitats in several areas of southern Australia.

I. Vegetation Maps of Communities in the Sydney District

Localities

The areas that are described here are located as follows:

(i) Woolooware Bay: the most southern arm of Botany Bay, 17·6 km due south of Sydney. The north-eastern shore communities in this arm have been studied in the greatest detail (Clarke and Hannon, 1967, 1969, 1970, 1971). (Military Map Sheet $\frac{\text{South } 1\cdot 56}{\text{N.I.NE.NW}}$ Zone 8; Port Hacking. 1 Mile Series. Grid Reference 155970). The communities cover approximately 60 hectares.

(ii) Bonnie Vale: within the Royal National Park, 25·6 km due south of Sydney: near Bonnie Vale, along the eastern shore of Cabbage Tree Creek which empties into Port Hacking. (Military Map Sheet $\frac{\text{South } 1\cdot 56}{\text{N.I.NE.NW}}$ Zone 8; Port Hacking. 1 Mile Series. Grid Reference 118878.) Approximately one-third of the area has been mapped.

(iii) Within Ku-ring-gai Chase, 20·8 km due north of Sydney: near Terrey Hills along the western edge of a tributary of Smith's Creek. (Military Map No. 417—Zone 8; Broken Bay. 1 Mile Series. Revised edition. Grid Reference 221394.) Approximately one-fifth of the area has been mapped.

Method

The communities at Woolooware Bay have been demarcated from aerial photography, but very much more detailed mapping was done in the other two areas. The method that was used in preparing these maps is as follows: A base line along an appropriate compass bearing was marked by posts located at 30·8 m intervals. A position which could be readily located by reference to a permanent external marker was selected as one end of the base line and the direction of the line was determined by consideration of its visibility from many points within the area to be mapped. A grid of areas of 30·8×30·8 m was outlined by placing transects at right angles to the base line. The boundaries of each floristically distinct area and the position of the conspicuous isolated individuals were measured with reference to the grid axes on 31 m length tapes and were mapped on graph paper using a scale of 2·54 cm = 15·4 m.

Description of the Vegetation

The maps and the details of the location of the marker pegs are given in Figs 1, 2 and 3 and show the present spatial relationships of the prominent species of these communities. The descriptions of the communities which have been recognized and used as mapping units are presented with the maps.

Fig. 1. Vegetation distribution at Woolooware Bay.

The area at Woolooware Bay displays narrow ecotones between the zones that cannot be accurately detected on the aerial photograph nor indicated on the map at this scale. This serves to indicate that the zones are very sharply demarcated and that the Woolooware Bay area contrasts in this respect with both of the other areas. In the maps of these latter areas, it is possible that small patches of herbaceous species amongst the *Juncus* may not have been detected owing to the marked intermingling of the species and the great differences in height of the components of these communities. Furthermore, in certain positions the borders of some of the communities can be delimited only subjectively and have been indicated by a dotted line.

Discussion

These are the first records of the communities at Woolooware Bay and at Smith's Creek, but a generalized map of all the Cabbage Tree Creek area was prepared by Collins (1921). Collins' map distinguished only three communities and was prepared without a compass (pers. comm.). In addition, no reference point was given and thus it is not possible to orient the 1921 map accurately to allow comparison with the present distribution of the species. A survey of Smith's Creek has since been made by Steenson and Barratt (1970).

The patterning of the species at Woolooware Bay is similar to the simple zonation described by earlier workers (*e.g.* Pidgeon, 1940) for this type of habitat. The intricacy of the pattern at the other areas has not previously been studied. At Woolooware Bay and other areas where the species are arranged similarly, extensive areas of sediments have accumulated in sheltered parts of large rivers and bays. In contrast, the other localities are of relatively small size and are situated at the base of steep slopes in young valleys, from which the creek flow has been restricted (see Plate x, Fig. 1). Consequently, the soil material derived as a result of natural erosion has accumulated and caused the development of these low-lying areas of impeded drainage.

The maps indicate that although most species are found in both areas, the species groupings at Bonnie Vale and Smith's Creek have little in common with one another or with sharply zoned mangrove and salt marsh communities. The results of a detailed examination of the relationship between species distribution and microtopography at Woolooware Bay and Bonnie Vale have already been reported (Clarke and Hannon, 1969).

The Bonnie Vale area (shown in Fig. 2) differs strikingly from the more usual species patterns in the following respects :

(i) *Avicennia* penetrates a long way inland from the Creek, some plants occurring in positions that are rarely (if ever) flooded by the tide. Some individuals are very large (7·6 m tall ; 46 cm D.B.H.). Some show unusual features such as pneumatophore-like structures of 5–9 cm length projecting downwards from the trunks of the trees at distances from 2 to 6 m above ground level. Many *Avicennia* are unhealthy and large numbers of the " dwarf " form occur. Contrary to Hamilton's (1919) interpretation, these " dwarf " forms are thought to develop in areas of increased salinity.

(ii) *Aegiceras* is very abundant. The tallest individuals that have been found in Sydney (4 m) occur in an unmapped area in a dense thicket along a drainage channel, but located at quite a distance from the Creek. A very large number of small dead trees occur closer to the Creek (refer to map). Collins (1921) reported the burial of mangroves by sand in this area, and progressive elevation of the area caused by drift sand has probably led to a marked increase in salinity in this area. This may explain the death of some of the *Aegiceras*.

(iii) *Arthrocnemum* is sparse and unhealthy, except in more elevated positions, such as under *Casuarina* trees.

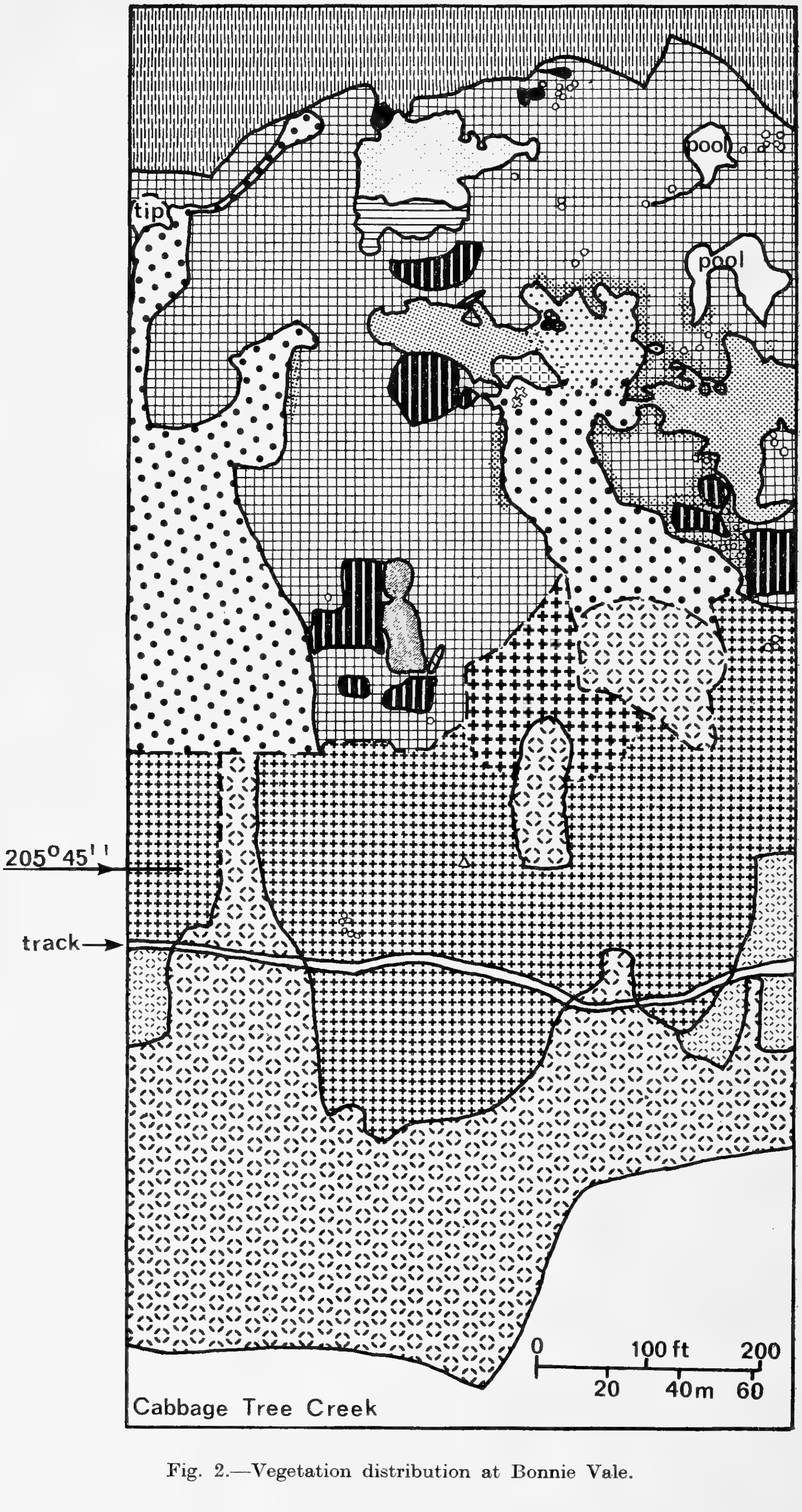
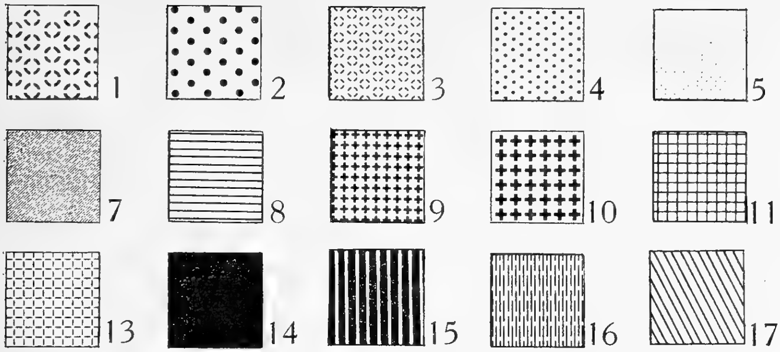


Fig. 2.—Vegetation distribution at Bonnie Vale.



Key to Fig. 2

Description of Community

1. A pure stand of *Avicennia*,* generally healthy with well developed pneumatophores. Few trees are in excess of 5 m in height and D.B.H. 20 cm ; they are mostly about 2 m in height. The tallest trees are unhealthy.

2. This complex occurs along creek beds, and contains *Avicennia* (varying from 15 cm " dwarf " shrubs to trees 8 m high and D.B.H. 46 cm), *Aegiceras* (30–152 cm high) and *Arthrocnemum* with occasional patches of *Sporobolus* or *Samolus*. The *Avicennia* tends to occur at the centre of the creek-bed, and the *Aegiceras* and *Arthrocnemum* nearer the edge. In some cases *Arthrocnemum* occurs amongst *Avicennia* pneumatophores (but not where these are dense) and it is always sparse. Many of the *Avicennia*, especially the taller plants, are unhealthy, and the majority of the *Aegiceras* appear moribund, although some of the very small plants (30 cm) are healthy. The most landward mangroves are " outliers " which can be flooded by tide only rarely, if ever. However, they are exceptionally tall, and quite healthy. There are numerous bare patches.

3. This complex consists of dead *Aegiceras* and sporadic clumps of *Sporobolus*, and shows marked evidence of sand encroachment.

4. This community contains *Arthrocnemum* and *Sporobolus*, rarely in association, the latter genus being largely confined to the edges and elevated positions. Small *Aegiceras*, " dwarf " *Avicennia* and very sparse patches of *Samolus* may occur among the herbs.

5. This is a pure mat of *Arthrocnemum*, which is sparse and straggling and contains many bare patches.

6. A mixture of *Arthrocnemum* and *Sporobolus*, the latter being shorter than when associated with *Juncus*.

7. As above, but *Sporobolus* mostly occurs at the edges or in more elevated positions. Sparse *Samolus* is also present.

8. An *Arthrocnemum-Samolus* community with scattered clumps of *Juncus* and *Sporobolus*. In some spots, *Sporobolus* is not associated with *Juncus*.

9. This complex is very difficult to map successfully, as it contains all species except *Casuarina*, and the relative density of the components is very variable. It consists of stunted but healthy *Avicennia* scrub and most unhealthy *Aegiceras*, the latter predominating (death appears to be due to deposit of sand). In patches among the scrub occur *Arthrocnemum*, *Samolus* and *Sporobolus*, either together, or separately, and generally sparse. Thin patches of *Juncus* and *Sporobolus* also occur amongst the mangrove scrub, and there are many bare patches.

10. As above, but the clumps of *Juncus* are much larger, forming a thick sward in places, so that *Juncus* is the dominant species rather than mangrove.

11. This is a thick sward of *Juncus*, which is everywhere accompanied by tall *Sporobolus*.

12. As above, but scattered *Aegiceras* occurs at the perimeters.

13. As above, but containing more *Aegiceras* and less *Juncus*.

14. A mat of pure *Sporobolus*.

15. A stand of mature *Casuarina* with a dense understory of *Juncus* and *Sporobolus* and in some cases a few individual *Arthrocnemum*. The *Casuarina* average 6 m in height, but some individuals reach 9 m. The D.B.H. varies from 8 cm to 23 cm. None of the clumps is really dense, and dead trees are associated with most of the clumps. In a few cases young trees of adventitious origin occur at the edge of the stands.

16. This consists of tall, healthy *Casuarina* forming a border of varying width and merging into a community (dominated by *Livistona australis* and *Angophora costata*) at the base of a sandstone hill.

○ Isolated *Casuarina* tree.

× Isolated *Avicennia* tree.

△ 182·88 m marker peg on baseline.

17. This is a small group of young *Casuarina* (61–76 cm high) produced as adventitious outgrowths from trees in a nearby stand.

---

* All species names as in Clarke and Hannon (1967).

(iv) *Sporobolus* and *Juncus* occur at the seaward edge of the swamp, often abutting on to the mangroves. *Juncus* has a very extensive distribution in this area.

(v) *Casuarina* is stunted and mostly occurs in isolated clumps in slightly elevated positions throughout the marsh. Dead *Casuarina* stumps are found in areas now covered by *Juncus*, *Arthrocnemum* and, to a lesser extent, mangrove.

Cabbage Tree Creek enters the Port Hacking River about 0·8 km downstream to the north from the salt marsh area and at low tide sand spits almost completely sever the Creek from the River. Presumably this influences the amount of tidal inundation that occurs. The construction, in 1956, of a bridge across the Creek at the northern end of the marsh still further restricts the entry and exit of tidal water in the marsh area.

The diverse and unusual species associations are the outstanding features of the Smith's Creek area, as shown in Fig. 3. The *Casuarina* stands in this locality are quite unique due to the marked erosion of the areas they have occupied. Intersecting creeks have exposed part of the root systems, in some places to the extent that the trees have a very distinctly leaning habit (see Plate x, Fig. 2). Because of erosion and deposition amongst these stands, *Casuarina* occurs in a wide variety of very unusual species combinations, *e.g.*, *Arthrocnemum-Triglochin-Casuarina-Aegiceras* form a community. Many dead *Casuarina* stumps occur, but no seedlings can be found. Adventitious propagation of shoots from lateral roots is very common (see Plate x, Fig. 3).

The differences in species groupings in these two localities are attributed, at least in part, to differences in tidal flow, accretion and erosion in these areas. Salinity may also be involved due to microtopographic differences (Clarke and Hannon, 1969).

Bonnie Vale and Smith's Creek have been selected since they are the only localities in this district where mangrove swamps and salt marshes occur within sanctuaries. Road building on the catchment areas above these sites provide a serious potential danger. Since it is intended that the areas will always be preserved in their natural state, the possibility therefore exists for future examination and detection of changes within these communities.

Long-term observations of areas are the most satisfactory means of determining whether a plant community has reached equilibrium with its environment. This would be of particular interest in these situations since it has been customary to attribute seral status to the communities occurring on tidal mud flats. Clarke and Hannon (in prep.) have not accepted this view for these communities in the Sydney district.

It appears that active accretion of sand has occurred and is continuing to occur at Bonnie Vale, whereas at Smith's Creek both vigorous erosion in certain parts of the area and deposition of material in other parts is apparent. These features at Smith's Creek are illustrated in Plate x, Figs 2 and 4. Changes may therefore be expected to occur with reasonable rapidity and can be examined in light of the predictions of Clarke and Hannon (in prep.). The rate of sediment accretion in any area is entirely dependent on local conditions and may therefore vary widely in different situations. However, the studies made by Chapman (1959) and Ranwell (1964) in British salt marshes where *Spartina* occurs indicate that the rates of accretion are such as to cause marked changes in vegetation pattern in periods of only 12–25 years, and even less in some instances (Boorman, 1971).

In contrast, the chances of preservation of the Woolooware Bay area are remote—it is likely that all the extensive areas of mud flats will be destroyed in the near future. Denudation of quadrats in the ecotones at Woolooware Bay was followed by re-establishment of vegetation similar to the original cover, even though after three years the quadrats could still be readily distinguished from the adjacent undisturbed areas (Clarke and Hannon, in prep.). Regeneration of the same cover indicates that the present zonation is reflecting an equilibrium with the prevailing conditions.

II. Community Variation in Southern Australia

The observations that have been made in other areas are summarized in Table 1 to show the many differences that occur in these communities. It is apparent that many features concerning the distribution pattern of these species are not understood. The differences between the communities at Bunbury and the other Western Australian areas examined suggest that comparative studies of these communities would be particularly interesting.

Arthrocnemum arbuscula, *A. halocnemoides* and *Atriplex* sp. that occur in the South Australian maritime communities are also found inland from the coast in non-tidal areas on clay soils of high salt content, and with halite crystals on the soil surface, as well as at intervals across the Nullarbor Plain and as far west as Norseman in Western Australia. At Eucla, they occur on the lee side of calcareous maritime sand dunes and *A. arbuscula* usually is the dominant species fringing the salt lakes between Norseman and Esperance. It is apparent that these species are not only salt-tolerant, but also capable of existing under more xeric conditions than those prevailing in the maritime communities.

The wide variety of soil types on which these communities occur is of interest, particularly since in Chapman's (1960) classification of salt marshes the northern European and western Atlantic groups are subdivided on the basis of soil types. It appears that edaphic conditions are relatively unimportant in these Australian communities, at least in comparison to tidal influence, and the inland occurrences of *Avicennia* (Beard, 1967) and *Arthrocnemum* species indicate that even tides are not an essential, even though a usual component of the environment of these species.

General Discussion

Comparison of these communities with those in similar habitats in other parts of the world shows differences and indicates that the variation occurring in Australia is not atypical. While *Distichlis* occurs from latitudes just south of Sydney in South Australia, Victoria and Tasmania, it appears to be absent from Western Australia as in New South Wales. Extensive development of grasses is a feature of the majority of Northern Hemisphere marshes. In addition, the zonal pattern of phanerogam distribution is a near-universal feature of salt marsh vegetation and is the chief reason for the seral interpretation that has generally been attributed to their component communities.

Furthermore, the Sydney district is one of the few localities in which well-developed examples of mangrove swamps and salt marsh communities occur in close association. In northern Australia, mangrove swamps dominate the maritime areas, but further south fewer species of mangroves can establish themselves successfully and salt marshes develop behind a frontal zone of *Avicennia* and *Aegiceras*. Still further south, mangroves are completely replaced by salt marshes. A similar situation is found in Florida and between the north and south islands of New Zealand (Chapman, 1960). Clarke and Hannon (in prep.) have proposed that in the Sydney district the mangrove and salt marsh flora grow in conjunction, but not as a succession as was originally suggested by Pidgeon (1940). In addition, no evidence has been obtained for the Sydney district that mangrove species are prograding the shoreline. However, McNae's (1966) descriptions of the relative positions occupied by seedlings and adults of

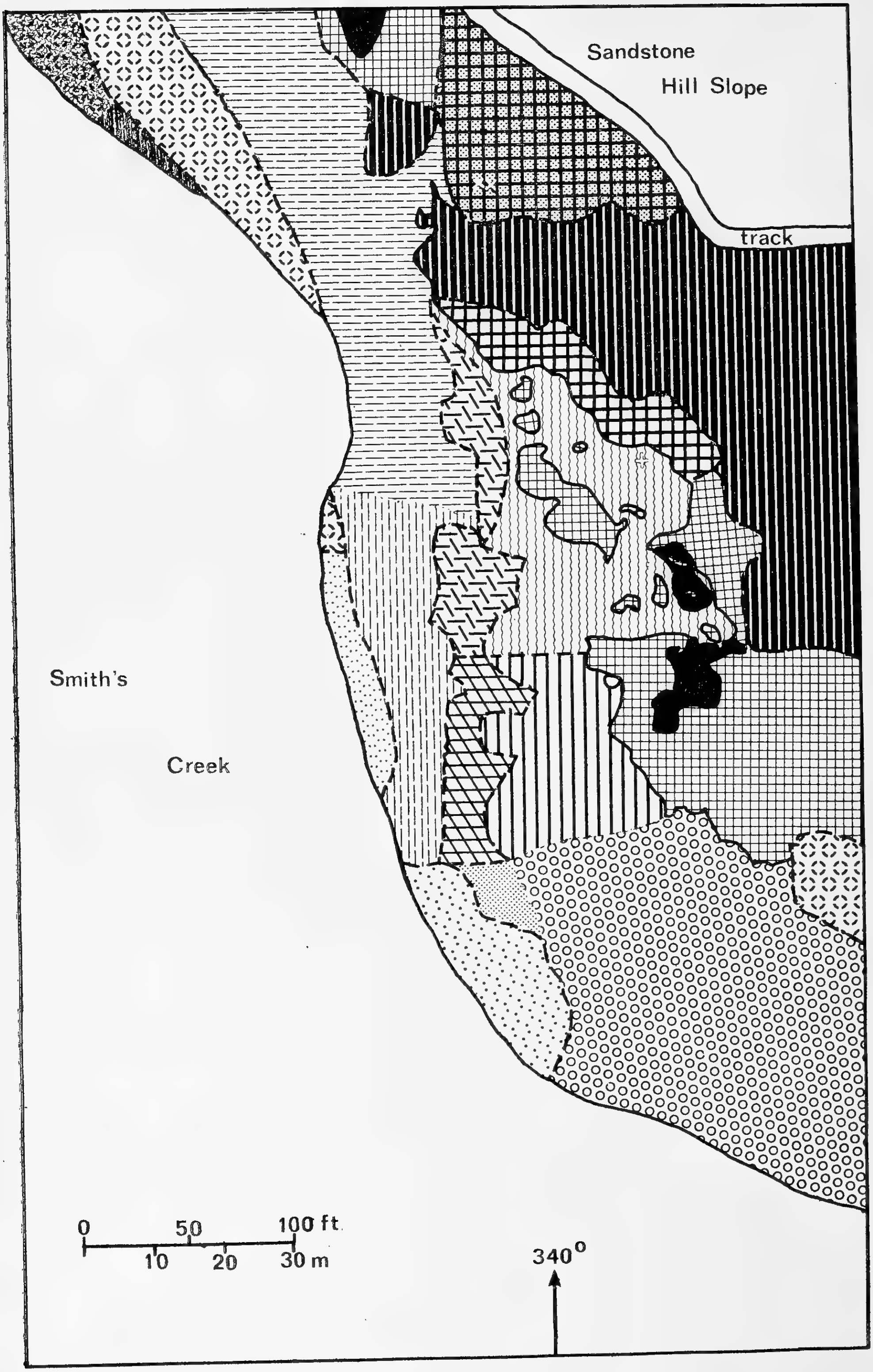
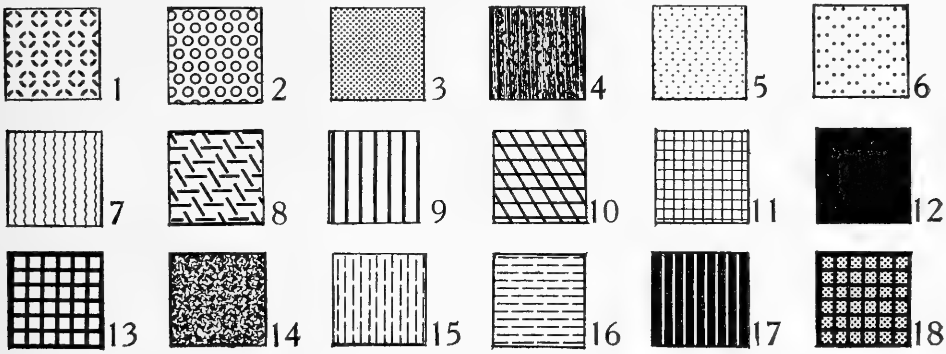


Fig. 3. Vegetation distribution at Smith's Creek.

Avicennia marina in Queensland and the relative stability of the rooting medium in these positions support the view that in that area *Avicennia* is effective in trapping silt, which is the role typically attributed to mangroves.

It is obvious that stands of these tide-affected communities should be preserved in many areas to perpetuate the considerable ecological and genotypic variation that occurs, even between geographically close localities within Australia as well as for the features that distinguish them from their counterparts in many areas of the world.



KEY TO FIG. 3

1. A community of *Avicennia* averaging about 5 m in height, although some individuals reach 8 m. It is bordered by *Aegiceras* up to 1·5 m high.

2. A very mixed community containing (1) a poorly demarcated patch of *Casuarina* (up to 5–6 m high and D.B.H. 10 cm), with occasional patches of *Arthrocnemum* beneath it. There is evidence of both erosion and deposition in this area. Most of the *Casuarina* are adventitious in origin; (2) a few "dwarf" *Avicennia*; (3) numerous scattered *Aegiceras* ranging from seedlings to trees 1·7 m high; (4) patches of *Samolus* and *Triglochin* of variable density.

3. A mat of *Samolus* and *Triglochin* (largely separate), with a few scattered *Aegiceras*.

4. A mat in which *Samolus* mingles with a *Sporobolus* sward.

5. A *Sporobolus* community with *Aegiceras* scattered throughout.

6. As above, but very few *Aegiceras* occur.

7. A patchy *Arthrocnemum* and *Triglochin* community (the two genera occurring both separately and together) with scattered *Aegiceras* up to 1·5 m high.

8. As above, but *Casuarina* is also present.

9. An *Arthrocnemum-Triglochin* community, as described above. Neither *Aegiceras* nor *Casuarina* is present.

10. An *Arthrocnemum-Triglochin* community as described above, containing *Casuarina* but not *Aegiceras*.

11. A *Juncus* community associated with sporadic patches of *Sporobolus*.

12. Pure *Sporobolus*.

13. A *Cladium-Sporobolus* community.

14. *Casuarina* with *Sporobolus* understory.

15. *Casuarina* with *Cladium-Sporobolus* understory, *Sporobolus* dominant.

16. *Casuarina* with *Cladium-Sporobolus* understory, *Cladium* dominant.

17. A *Casuarina* community with a *Juncus* understory, and sporadic patches of *Sporobolus* occur among the *Juncus*. The *Casuarina* reach a maximum of 9–12 m and a D.B.H. of 8–13 cm.

18. A *Cladium-Sporobolus-Phragmites* community.

× Isolated *Avicennia* tree.

+ Isolated *Aegiceras* bush.

References

BEARD, J. S., 1967.—An Inland Occurrence of Mangrove. *West. Aust. Nat.*, 10: 112–115.

BOORMAN, L. A., 1971.—Studies in Salt Marsh Ecology with special reference to the Genus *Limonium*. *J. Ecol.*, 59: 103–120.

CHAPMAN, V. J., 1959.—Studies in Salt Marsh Ecology. IX. Changes in Salt Marsh Vegetation at Scolt Head Island. *J. Ecol.*, 47: 619–639.

————, 1960.—*Salt Marshes and Salt Deserts of the World.* Leonard Hill Ltd., London. 392 pp.

CLARKE, LESLEY D., and HANNON, NOLA J., 1967.—The Mangrove Swamps and Salt Marsh Communities of the Sydney District. I. Vegetation, Soils and Climate. *J. Ecol.*, 55: 753–771.

————, 1969.—The Mangrove Swamps and Salt Marsh Communities of the Sydney District. II. The Holocoenotic Complex with particular reference to Physiography. *J. Ecol.*, 57: 213–234.

————, 1970.—The Mangrove Swamps and Salt Marsh Communities of the Sydney District. III. Plant Growth in relation to Salinity and Waterlogging. *J. Ecol.*, 58: 351–369.

————, 1971.—The Mangrove Swamps and Salt Marsh Communities of the Sydney District. IV. The Significance of Species Interaction. *J. Ecol.*, 59: 535–553.

COLLINS, MARJORIE I., 1921.—On the Mangrove and Salt Marsh Vegetation near Sydney, N.S.W., with special reference to Cabbage Tree Creek, Port Hacking. PROC. LINN. SOC. N.S.W., 46: 376–392.

CURTIS, W., and SOMERVILLE, J., 1947.—Boomer Marsh—a preliminary Botanical and Historical Survey. *Proc. Roy. Soc. Tas.*, 151–157.

HAMILTON, A. A., 1919.—An Ecological Study of the Salt Marsh Vegetation of the Port Jackson District. PROC. LINN. SOC. N.S.W., 44: 463–513.

MCARTHUR, W. M., 1957.—The Plant Ecology of Garden Is. in relation to the Neighbouring Islands and Adjacent Mainland. *J. Roy. Soc. W.A.*, 40: 46–64.

MCNAE, W., 1966.—Mangroves in Eastern and Southern Australia. *Aust. J. Bot.*, 14: 67–104.

PIDGEON, ILMA M., 1940.—The Ecology of the Central Coastal Area of New South Wales. III. Types of Primary Succession. PROC. LINN. SOC. N.S.W., 65: 221–249.

RANWELL, D. S., 1964*a*.—*Spartina* Salt Marshes in Southern England. II. Rate and Seasonal Pattern of Sediment Accretion. *J. Ecol.*, 52: 79–94.

————, 1964*b*.—*Spartina* Salt Marshes in Southern England. III. Rates of Establishment, Succession and Nutrient Supply at Bridgwater Bay, Somerset. *J. Ecol.*, 52: 95–105.

SAUER, J. D., 1965.—Geographic Reconnaissance of Western Australian Seashore Vegetation. *Aust. J. Bot.*, 13: 39–69.

STEENSON, J., and BARRATT, T., 1970.—Field Survey of Saline Mud Flats, Smith's Creek, Ku-ring-gai Chase. *J. Nat. Pks.*, Sept., 11–14.

WOOD, J. G., 1937.—Vegetation of South Australia. Handbook of Flora and Fauna of S.A. Govt. Printer, Adelaide.

EXPLANATION OF PLATE X

Fig. 1. Salt marsh developed at base of sandstone hill. Salt marsh genera present are *Juncus* (background), *Aegiceras* on a mat of *Samolus*, *Casuarina* (right middle ground), patches of *Sporobolus* (foreground) interspersed with deposits of sand.

Fig. 2.—Erosion in mature *Casuarina* stand at Smith's Creek. White dowel sticks are for measurement of accretion rate.

Fig. 3. Adventitious development of *Casuarina*. Note mangrove adjacent to *Casuarina*, on the left side.

Fig. 4. Deposition of sand at Smith's Creek. Note mounds covered by *Arthrocnemum*, and large numbers of dead *Casuarina* stumps.

LOCATION OF THE EXTERNAL REFERENCE MARKERS

Bonnie Vale

1. Zero on the base line is marked by the steel peg at 8·08 m from the fire hydrant (at 213°), located at approximately 158·50 m from the concrete block supporting the eastern end of the bridge spanning Cabbage Tree Creek.

2. A steel peg is located at 182·88 m from zero along the base line (205° 45′).

3. A painted triangle is marked on a prominent sandstone boulder on the hillslope above the marsh at a bearing of 115° 45′ from the 192·33 m point on the base line.

Smith's Creek

1. Zero on the base line is marked by a painted vertical groove of 59 cm length on a sandstone boulder. This boulder is on the northern side of the track at 0·24 km east from the base of the hill. It is opposite the first extensive patch of *Arthrocnemum* in the marsh.

2. A steel peg is located at 30·5 m from zero along the base line (160°).

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

TABLE 1

A Comparison of the Mangrove and Salt Marsh Communities in Several Areas of Southern Australia

	Sydney, N.S.W.	Northern N.S.W.—Gosford to Coff's Harbour*	Victoria†	Hobart, Tasmania	South Australia	South-Western Australia
Soil parent material	Triassic Sandstone	Quaternary Alluvial deposits	Primary Quaternary Sands and Clay Silts.	Mudstone — occasional Dolerite	Tertiary Limestone	Quaternary Limestone
Soil texture ..	Sand	Sand	Sandy clay to clayey or silty sand, overlain in *Arthrocnemum* zone by fibrous peat layer of 5–15 cm depth	Clay loam	Heavy clay	Sandy loam—light clay
Yearly mean max temp (C)‡ ..	21·7	—	19·8	16·7	22·8	23·1
Yearly mean min temp (C)‡ ..	13·4	—	10·0	8·3	11·8	13·1
Mean yearly rainfall (cm)‡ ..	113·79	—	65·76	63·58	53·57	91·41
Highest recorded annual rainfall (cm)‡	219·28	—	96·62	110·21	78·61	133·78
Lowest recorded annual rainfall (cm)‡	58·45	—	39·65	39·17	28·75	50·80
GENUS or SPECIES						
Avicennia marina var. *resinifera*	Abundant, trees and shrubs	As for Sydney	*Western Port* — dense thicket 2–4 m tall with smaller forms more widely spaced on landward and seaward margins Many seedlings throughout zone, which varies from 9 to 367 m width, but which is generally 46–55 m wide. On the northern and western inner shores and islands and on the sheltered areas of French Island and Philip Island *Port Phillip Bay*—localized occurrences along western shore *Corner Inlet*—scattered bushes, 61–91 cm tall at several localities	Absent	Abundant, healthy shrubs *Pt. Adelaide* — dense thicket 5 m tall, few seedlings, except at edges, pneumatophores up to 61 cm tall *Pt. Gawler* — occasional trees, up to 6 m; dark scaly bark; healthy dense shrubs; "dwarf" forms (away from water's edge) *Pt. Wakefield*—few stunted shrubs up to 3 m high; restricted to water's edge; few pneumatophores *Spencer's Gulf* — shrubs up to 2 m at Pt. Pirie and Pt. Augusta, absent elsewhere *Ceduna*—few straggling shrubs 1·2 m tall	*Bunbury*—diseased shrubs up to 5 m *Mandurah*—absent *Perth, Swan River*—absent
Aegiceras corniculatum	Relatively few by comparison with *Avicennia*	More abundant than in Sydney	Absent	Absent	Absent	Absent
Arthrocnemum australasicum	Abundant	Less abundant than in Sydney	Abundant, mingling with landward fringe of mangroves and extending to *Melaleuca* zone; sparse where *A. arbuscula* is prominent	Abundant, pure stand at water's edge	Occurs only at Pt. Augusta and Ceduna immediately landward to and sharply zoned from the mangroves	*Bunbury*—abundant *Mandurah, Perth, Swan River*—less abundant than in Sydney
Arthrocnemum arbuscula (R.Br.) Moq.	Absent	Absent	*Western Port* — commonly occurs as dense sward 1·5–2·4 m tall in well drained situations and as scattered individuals 15 cm–1 m tall with dense *A. australasicum* and *Samolus* in more waterlogged areas; does not extend as far seaward as *A. australasicum*; sharply zoned from *Stipa*	Abundant	Abundant, 2 m tall at Pt. Wakefield, sharply zoned from mangroves; landward from *A. australasicum* at Pt. Augusta and Ceduna	*Bunbury*—absent *Mandurah, Perth, Swan River*—less abundant than in South Australia

---

* At Erina, near Gosford, the vegetation is similar to that at Woolooware Bay.

† Information for Victoria has been supplied by Dr. D. H. Ashton, Botany School, University of Melbourne, Victoria. Dr. Ashton also notes that *Hemichroa pentandra* R.Br., *Statice australis* Spreng. and *Samolus repens* are common in Victorian marshes associated with *Arthrocnemum* sp. and that a bare zone commonly separates *Arthrocnemum* sp. from the *Stipa* zone.

‡ The climatic data are based on records collected over the period 1911–1940 in the capital city of each State.

§ This species requires revision.

TABLE 1—*Continued*

A Comparison of the Mangrove and Salt Marsh Communities in Several Areas of South Australia—Continued

	Sydney, N.S.W.	Northern N.S.W.—Gosford to Coff's Harbour*	Victoria†	Hobart, Tasmania	South Australia	South-Western Australia
Arthrocnemum halocnemoides Mees	Absent	Absent	Locally common, usually landward of *A. arbuscula*, where both species occur	Present	Abundant, sharply zoned from *A. arbuscula* at Pt. Augusta and Ceduna	*Bunbury*—absent *Mandurah, Perth, Swan River*—less abundant than in South Australia
Atriplex	*A. patula* L. occurs, but is very uncommon	Absent (?)	*A. paludosa* R.Br. is locally common in some parts of Western Port, where it is more prominent than in other localities; occurs landward to *A. arbuscula* in more elevated positions	Absent	*A. paludosa* and *A. stipitata* Benth. abundant in more elevated positions. Recorded by Wood (1937) as components of drier communities	*A. paludosa* recorded by McArthur (1957)
Triglochin	*T. striata* fairly common	Less abundant than in Sydney	*T. striata* scattered throughout *A. australasicum*, *A. arbuscula* and *A. halocnemoides*	Uncommon. *T. striata* recorded by Curtis and Somerville (1947)	Absent	*Bunbury*—absent *Mandurah* — *T. mucronata* R.Br. fairly common, forming carpet under *Casuarina*
Suaeda	*S. australis*—sporadic, uncommon	Absent (?)	*S. maritima* L.—scattered individuals occur from landward edge of mangroves to *Stipa*, or bare zone in front of *Stipa*	*S. maritima*§ uncommon. Recorded by Curtis and Somerville (1947)	Absent	*S. australis* — uncommon except at Bunbury
Sporobolus virginicus	Abundant	Less abundant than in Sydney, directly landward to mangroves	Rare	Absent (?)	Recorded by Wood (1937) as component of wetter areas, but now apparently cleared	Uncommon except at Bunbury
Juncus maritimus var. *australiensis*	Abundant	Abundant, occurs landward of either mangroves or *Sporobolus*	Uncommon *Western Port, Port Phillip*—occurs with *Stipa* (which appears to be its equivalent in Victoria) and *Cladium filum*,§ or as scattered clumps amongst *A. arbuscula* and *A. halocnemoides*	Uncommon, recorded by Curtis and Somerville (1947)	Recorded by Wood (1937) in wetter areas, but now apparently cleared	Less abundant than in Sydney, except at Bunbury
Cladium	*C. junceum* uncommon	Absent (?)	*C. filum*§ R.Br. uncommon *Western Port, Port Phillip* — occurs in association with *Stipa*	*C. filum*§ uncommon. Recorded by Curtis and Somerville (1947)	*C. junceum* and *C. filum*§ recorded by Wood (1937) in wetter areas now apparently cleared	Absent
Distichlis	Absent	Absent	*D. disticophylla* (Labill.) Fassett *Western Port, Corner Inlet* — abundance variable; may be associated with *A. australasicum* or with *Stipa*, *Cladium* and *Juncus*	*D. disticophylla* abundant, dominating the grass-rush-sedge community	*D. spicata* (L.) Greene recorded by Wood (1937) in wetter areas now apparently cleared	Absent
Casuarina	*C. glauca* abundant	*C. glauca* abundant	Absent *Melaleuca ericifolia* Smith thickets are the local equivalent of this zone	Absent	*C. stricta* Ait. recorded by Wood (1937) as climax on coast, where rainfall exceeds 51 cm; now apparently cleared	*C. glauca* — less abundant than in Sydney

---

* At Erina, near Gosford, the vegetation is similar to that at Woolooware Bay.

† Information for Victoria has been supplied by Dr. D. H. Ashton, Botany School, University of Melbourne, Victoria. Dr. Ashton also notes that *Hemichroa pentandra* R.Br., *Statice australis* Spreng. and *Samolus repens* are common in Victorian marshes associated with *Arthrocnemum* sp. and that a bare zone commonly separates *Arthrocnemum* sp. from the *Stipa* zone.

‡ The climatic data are based on records collected over the period 1911–1940 in the capital city of each State.

§ This species requires revision.

Sokal and Sneath, 1963; Camin and Sokal, 1965; Crovello, 1967; Kluge and Farris, 1969). These new data and techniques will no doubt contribute greatly to the development of phylogenetic classifications provided that they are not expected to replace the older data and methods but are used instead in conjunction with morphological data and long-standing basic principles of evolutionary deduction.

The most comprehensive enquiry into the phylogenetic relationships of the Gekkota in recent years was Kluge's (1967*a*) " Higher Taxonomic Categories of Gekkonid Lizards and their Evolution ", which involved the examination of 18 characters, 16 of which were morphological, in 82 genera of geckos. As some of the characters used by Kluge are still too poorly known in geckos generally to be used to determine their interrelationships, and some of his methods and conclusions require re-examination, it is necessary to review his paper in some detail. Before doing so, however, the meanings of the terms classification, taxonomy, phylogeny and primitive must be clearly recognized.

According to Simpson (1961), zoological classification is defined as the ordering of animals into groups (or sets) on the basis of their relationships, that is, of associations by contiguity, similarity, or both, and taxonomy is the theoretical study of classification, including its bases, principles, procedures and rules. Thus the subjects of classification are organisms and the subjects of taxonomy are classifications. Both classification and taxonomy are also used to express the end results of these processes (Sokal and Sneath, 1963). Phylogeny, on the other hand, is defined as evolutionary history (Abercrombie, Hickman and Johnson, 1951).

The relationship between phylogeny and classification has been discussed at length by many authors, including Simpson (1945, 1961), Blackwelder (1967) and Mayr (1969). Blackwelder pointed out that evolution has given rise to the organisms being classified, that the sequence of forms which give rise to a particular species represents the phylogeny of that species, and that some of the characteristics of the organisms have resulted from phylogeny because they have been inherited from an ancestor which possessed the same characteristics. He emphasized, however, that phylogeny can never be known but can only be inferred from the degrees of similarity between organisms and for this reason cannot be regarded as a basis of classification. But classification, like the detection of phylogenetic relationships, is based on the degrees of similarity between organisms. Provided that the similarities used in classification are due to common ancestry, the classification will be consistent with the evolutionary history of the organisms concerned, if only in the sense that it expresses their interrelationships in very general terms. As classification is essentially a tool " to provide a convenient, practical means by which zoologists may know what they are talking about and others may find out " (Simpson, 1945), it should be as stable as possible despite increasing knowledge about the organisms classified. A classification intended to be consistent with phylogenetic relationships will be most stable if the similarities on which it is based are the result of descent from a common ancestor, and for the recognition of such similarities a clear understanding of the nature of primitiveness is essential.

THE CONCEPT OF PRIMITIVENESS

The different aspects of primitiveness are frequently confused (see Sporne, 1956; Cain and Harrison, 1960; Simpson, 1961; Sokal and Sneath, 1963). In the first place, primitiveness is always relative: a characteristic of an organism or the organism itself may be primitive in one lineage or taxon but not necessarily primitive in another. (A taxon as used here was defined by Simpson (1961) as a group of organisms recognized as a formal unit at any level of a hierarchic classification.) For example, those organs which are in a primitive state with respect to the Gekkonidae may not be primitive with respect to the Squamata, and primitive geckos may not be primitive squamates.

Simpson (1961) defined the usage of the terms primitive and specialized (=advanced, *sensu* Kluge, 1967*a*) with respect to the characteristics of taxa, lineages and phylogenies as follows: Within a taxon, the characteristics (=character-states, *sensu* Kluge, 1967*a*) of the common ancestry are primitive and others are more or less specialized in proportion to their departure from the ancestral condition. Within a single lineage, characteristics occurring earlier are more or less primitive and those appearing later more or less specialized in proportion to their times of appearance. Within a phylogeny (which is divided into taxa and consists of branching lineages) characteristics of any one common stem are more primitive than different characteristics of its descendant branches ; within single branches they are more primitive or more specialized in accordance with earlier or later appearance ; and between branches they are more primitive or more specialized in accordance with less or more departure from the stem condition.

In practice, as an extant taxon comprises the living representatives of one or more lineages, a character-state is considered to be primitive if it is either the ancestral state retained in the living forms, in which case it is the original state of the character within the taxon, or is less modified from this ancestral state (*i.e.* less advanced or specialized) than other states of the character within the taxon. The distinction between primitive (=original) and primitive (=less advanced) character-states is important, not only for establishing the phylogenetic relationships of the taxon *inter se*, but also for determining its relationship to other taxa.

The concept of primitiveness as applied to organisms is open to several interpretations (see Sokal and Sneath, 1963) and is therefore meaningless unless the terms of reference are clearly specified. One interpretation is that an organism is more primitive than other organisms within the same taxon when it more closely resembles their ancestral stock with respect to the states of particular characters, which is another way of saying that these characters are in a more primitive state in this organism than in other members of the taxon (*vide supra*). An organism is also considered to be primitive if it possesses more primitive character-states than any other organism within the same taxon and therefore bears a greater overall resemblance to the ancestral stock than other members of the taxon. This is the usual connotation of primitiveness when groups of organisms are described as primitive without any qualification of the term, *e.g.* primitive geckos, primitive squamates. Although such a group may represent an ancient lineage with the taxon, *i.e.* one which arose at an early stage in the history of the taxon, it does not follow that this lineage is ancestral to other members of the taxon as it may have arisen with other character-states which are not primitive in the taxon as a whole.

The bearing of these different aspects of primitiveness on the phylogenetic relationships of geckos was not adequately taken into account by Kluge (1967*a*), whose method of classifying the Gekkonidae *inter se* was based on quantitative phyletics (or numerical cladistics), the branch of numerical taxonomy in which quantitative methods are used to infer phylogenetic relationships among living organisms whose ancestry cannot be determined from the fossil record (Camin and Sokal, 1965 ; Kluge and Farris, 1969). As various aspects of numerical taxonomy, including phyletics (or cladistics), have been described and criticized by many authors including Cain and Harrison (1960), Sokal and Sneath (1963), Mayr (1964, 1965), Camin and Sokal (1965), Watson, Williams and Lance (1966), Blackwelder (1967), Inger (1967), El-Gazzar, Watson, Williams and Lance (1968), Kluge and Farris (1969) and Colless (1971), only Kluge's (1967*a*) methods and conclusions regarding the classification of geckos need to be considered here.

CRITERIA FOR THE DETERMINATION OF PRIMITIVE CHARACTER-STATES

The data considered by Kluge (1967*a*) to show the primitiveness of character-states were grouped by him into four categories, or criteria of primitiveness. His First Criterion for regarding a character-state as primitive in living geckos is its similarity to the state of the character in fossil forms presumed to be related to the ancestors of the modern group. His other three criteria which are those used in quantitative phyletics allow the primitiveness of a character-state to be determined in the absence of fossil evidence (see Wagner, 1961 ; Kluge and Farris, 1969), by comparing living geckos with other living squamates and with one another. On the basis of the Rule of Parsimony (see Camin and Sokal, 1965 ; Kluge and Farris, 1969), whereby it is assumed that the more widely a character-state occurs among related taxa, the less likely it is due to multiple parallel evolution (Kluge, 1967*a*), a character-state was considered by Kluge (*op. cit.*) to be primitive in the Gekkonidae if it is universal or frequent in other squamate families or subfamilies (Second Criterion of Primitiveness) or in the Gekkonidae themselves (Third Criterion). According to the Fourth Criterion, those character-states which are confined to the Gekkonidae and occur in those geckos with the largest number of primitive features as determined by one or more of the first three criteria are also considered to be primitive.

The fossil forms cited by Kluge (1967*a*) in connection with his first criterion of primitiveness were not the ancestors of squamates in general or of the Gekkonoidea in particular (the Gekkonoidea being all geckos, living and extinct), but were instead a single family of Upper Jurassic lizards, the Ardeosauridae, which are currently placed within the Gekkonoidea (Hoffstetter, 1964). By the late Jurassic, most of the larger suprafamilial groups of living lizards, namely the Scincomorpha, Anguimorpha and Iguania as well as the Gekkonoidea, were already strongly differentiated (Hoffstetter, 1953, 1967) and there had previously been considerable radiation of highly specialized squamates during the Triassic (Kuhn-Schnyder, 1954 ; Robinson, 1962 ; Hoffstetter, 1962 ; Colbert, 1966 ; Tarlo, 1967, 1968). In view of the evident diversity of squamates during the Triassic and Jurassic and the fortuity of fossilization, it cannot be assumed that the Ardeosauridae were the only geckos in existence during the Upper Jurassic and therefore directly ancestral to the living Gekkonidae (*cf.* Kluge, 1967*a*, pp. 35, 51). Nor can it be assumed that they were necessarily more primitive than other geckos, living or extinct, in their structural characteristics including the procoelous state of their vertebrae (*op. cit.*, pp. 35, 36). On the contrary, as the genus *Bavarisaurus* (Fam. Bavarisauridae—Hoffstetter, 1964) from the same horizon as the Ardeosauridae was probably also a gekkonoid (Hoffstetter and Gasc, 1969) yet differed from the Ardeosauridae in various structural features including the apparent amphicoely of their vertebrae (Hoffstetter, 1964), it is not improbable that both of these families were in some respects advanced groups of geckos despite their early appearance in the history of the Gekkonoidea.

In order to determine from the fossil record which character-states are primitive in a modern group of lizards it is necessary to refer, not only to fossil members of this group which may have had a mixture of primitive and advanced character-states like modern members, but also to earlier groups of reptiles containing the ancestors of the lacertilian group under investigation. Although the immediate squamate ancestors of the Gekkonoidea are not yet known, it is now accepted that the ancestors of the Squamata (and Rhynchocephalia) were members of the Eosuchia, which in turn evolved from cotylosaurs (Romer, 1966, 1968). A character-state which occurred in any one of these ancestral groups and was directly inherited by the Gekkonidae is automatically a primitive character-state within the Gekkonidae, irrespective of whether it was a primitive or advanced condition within a particular ancestral group and irrespective of the number of living forms which still retain it. Such a character-state is not merely similar to those occurring in fossil forms (Kluge, 1967*a*, p. 15—first criterion of primitiveness) but is exactly the same character-state as one of those occurring in an ancestral group, and is primitive in the Gekkonidae because it is the original state of the character from which all other states within this family have evolved. Moreover, this primitive (=original) character-state in geckos can also be the primitive (=original) state of the character in other reptiles arising from the same ancestral group.

Wilson (1965) and Inger (1967) used the term unique to describe a character-state which has arisen only once in phylogeny and which has never been temporarily reversed in any of the lineages possessing it, and maintained that unique character-states, provided that they can be identified, serve as extremely reliable indicators of phylogenetic relationships. It is important to realize that a unique character-state is not necessarily primitive in a particular taxon: the primitive or advanced nature of a unique state depends on the stage in the evolutionary history of the taxon at which the state appeared. Provided that this unique state arose prior to the origin of the taxon, however, it is automatically primitive within this taxon.

In view of the fragmentary fossil record of early squamates, it is not possible to tell whether a character-state which apparently arose for the first time in these forms appeared only once and is therefore unique or appeared several times in parallel. The greater the antiquity of a character-state, however, the greater is the probability that it is in fact unique. For example, a character-state which was present in the earliest reptiles, was inherited by eosuchians and later by the earliest known squamates and rhynchocephalians and is also present in geckos is almost certainly unique and is therefore of considerable importance in establishing the phylogenetic relationships of the Gekkonidae, not only *inter se*, but with other lizards as well. Camp (1923) also stressed the importance of character-states of great antiquity (or high palaeotelic value) because they reveal relationships which might otherwise be obscured by a high degree of specialization in the states of other characters.

For the recognition of unique character-states among living organisms whose ancestry cannot be determined from the fossil record, Inger (1967) put forward four criteria. The first and fourth of these, which referred respectively to the absence of obvious selective differences between the states of a character and to unusual developmental patterns, were rejected by Kluge and Farris (1969) on the grounds that they are not sufficiently objective. Inger's second and third criteria referred respectively to the occurrence of the state in many taxa of the group being studied and to the low variability of the state within these taxa. From these criteria it is clear that Inger was attempting to establish, not the uniqueness of character-states, which is absolute, but their relative primitiveness within a particular taxon (*cf.* the criteria used in quantitative phyletics for determining the primitiveness of character-states—Kluge and Farris, 1969). In practice, however, the term unique can be used, not in its strict, absolute sense, but in a relative sense to describe a character-state which has arisen only once within a particular taxon. Such a unique advanced state within that taxon will be a primitive state in all smaller groups possessing it within the taxon concerned.

The determination of the primitiveness of character-states in living organisms from a comparison of these organisms with one another is based on the following assumption: if the same character-state occurs in two or more species or groups of species (genera, families, etc.) of living organisms it is assumed to have been inherited from a common ancestor unless there is evidence to show that it has arisen independently in these taxa as a result of parallel evolution. This assumption is the basis of all systems of classification intended to be consistent with phylogenetic relationships among living organisms whose ancestors cannot be observed directly, either as living forms or fossils, and is the principle of Parsimony (see Camin and Sokal, 1965; Kluge and Farris, 1969) on which Kluge's second and third criteria of primitiveness were based. It does not deny the existence or minimize the importance of parallel evolution as suggested by Inger (1967) but is instead the only practicable method for detecting parallelisms which, according to Rensch (1959), are very common evolutionary phenomena and which may be caused by similar hereditary factors including parallel mutation and/or by parallel selection acting on homologous or analogous characters.

Kluge's (1967*a*) explanation of the Rule of Parsimony, that the more widely a character-state occurs in related taxa the less likely it is due to multiple parallel evolution, and therefore his second and third criteria of primitiveness, lose sight of a well-known evolutionary phenomenon: the extent to which a character-state is widespread in a present-day taxon depends, not only on the stage in the evolutionary history of the taxon at which the state appeared, but also on the rate of evolution and extinction in the lineage possessing this state compared with other lineages with other states (see Mayr, 1955). Thus character-states which occur in comparatively few members of a taxon may nevertheless be primitive. Conversely, an advanced character-state may be of widespread occurrence within the taxon, especially if it arose soon after the appearance of the taxon and is therefore almost as ancient within this taxon as the primitive state from which it evolved. Although this advanced state is primitive compared with other more advanced states within the taxon, it does not follow that all states of the character which are found in fewer members of the taxon than this state have necessarily evolved from it as assumed in quantitative phyletics. Because of this assumption, a character-state can be primitive according to the second of Kluge's criteria and advanced according to the third or *vice versa*. Obviously at least one of these criteria must be giving an incorrect assessment of primitiveness.

The validity of Kluge's (1967*a*) fourth criterion of primitiveness is even more dubious. In the first place, as its terms of reference are conclusions based on one or more of the first three criteria, any errors inherent in these criteria or arising from their application will automatically invalidate conclusions based on the fourth criterion. Moreover, although it may be true that the probability of a character-state's being primitive increases very rapidly with the increase in the number of primitive character-states with which it is correlated (Sporne, 1954; Kluge, 1967*a*, p. 15), one cannot assume that the state concerned *is* primitive and therefore a valid indicator of phylogenetic relationships. Unless the primitiveness of a character-state as determined by this criterion can be supported by other evidence, *e.g.* from the fossil record, the character concerned should not be chosen as a basis for evolutionary classification.

In order to determine which of several states of a character is the most primitive, it is necessary to consider all the available evidence. As the evidence varies with different characters depending on their antiquity, their presence in fossils and their distribution among living forms, no predetermined formula such as that used in quantitative phyletics can be relied upon to give a true assessment of primitiveness. On the contrary, it is necessary to analyse each character separately in the light of the evidence which specifically applies to it. Also, an assessment of primitiveness which is based on a comparison of living organisms is not necessarily less significant than another based on fossil evidence (*cf.* Kluge, 1967*a*, p. 15). For example, the primitiveness of eyelids in the Squamata is virtually indisputable since the squamate brille or spectacle consists of modified eyelids and the evolutionary sequence from eyelids to brille can still be seen in some lacertids and scincids; the movable " eyelids " of some forms with a brille are modified extrabrillar fringes (Bellairs and Boyd, 1947; Bellairs, 1948).

Finally, when ordering genera into larger taxa according to the occurrence of various character-states, their occurrence should be described by reference to these genera and not to the taxa to be erected. Kluge (1967*a*) deliberately described the distribution of character-states in subfamilies of geckos which he subsequently defined on the basis of this distribution for simplicity's sake, rather than repeat the numerous generic names for each character-state under discussion (*op. cit.*, p. 8), the only genera cited in connection with each character being those with the less common state. The presentation of data only in this form limits their re-examination by other workers, especially as there is a discrepancy between Kluge's Table 1 and his Appendix 1 in the numbers of genera placed in the Diplodactylinae and the Gekkoninae. It is also conducive to circular argument, an obvious example being as follows : character-states are primitive within the Gekkonidae because they occur in the more primitive geckos, particularly the Eublepharinae (*op. cit.*, pp. 19, 33), yet these geckos are considered to be the most primitive because they possess the greatest number of primitive character-states (*op. cit.*, pp. 21, 45). Clearly, any phylogenetic classification based on such reasoning requires re-examination.

Despite the foregoing criticisms of Kluge's (1967*a*) methods, and of his conclusions regarding the primitiveness of some character-states (see Appendix), his four subfamilies of geckos appear on the whole to be natural assemblages in that the members of each group appear to be more closely related to one another than to the members of any other group. The Eublepharinae and Sphaerodactylinae are generally accepted as natural assemblages (Boulenger, 1885 ; Underwood, 1954 ; Vanzolini, 1968*a*, 1968*b*), while subsequent work by Kluge (1967*b*) and the occurrence of the triangular process on the pleurapophyses of the second sacral vertebra (*vide infra*) support Kluge's (1967*a*) contention that the Gekkoninae and Diplodactylinae are also natural groups within the Gekkonidae. The reason why these four subfamilies appear to be natural assemblages is that Kluge (1967*a*, p. 41) grouped his 82 genera of geckos on the basis of the greatest number of shared or unshared character-states and the least number of parallelisms. That is, he classified the Gekkonidae according to the degrees of similarity or dissimilarity among them on the understanding that the more closely two forms resemble one another, the more closely they are related by descent. For such a classification a correct assessment of the primitiveness within the Gekkonidae of the character-states employed is not essential.

A correct assessment of the primitive or advanced nature of character-states within the Gekkonidae is most essential, however, in order to establish that the four subfamilies are indeed natural assemblages and to determine their phylogenetic relationships with one another and with other squamates. Although it is not possible here with the data available to verify the generic composition of each subfamily, it is possible to demonstrate that Kluge's (1967*a*) conclusions regarding the evolutionary history of the subfamilies are unacceptable. Kluge summarized his views as follow : The Diplodactylinae appear to have been derived directly from the most primitive subfamily, the Eublepharinae, whereas the Gekkoninae probably evolved from a considerably more advanced form. According to Kluge, the gekkonid subfamily Sphaerodactylinae is the most advanced, and it appears to have been derived from the evolutionary stock that gave rise to the Gekkoninae.

In the following reassessment of the phylogenetic relationships of the four subfamilies of geckos, two other families are considered as well, namely the Pygopodidae and the Xantusiidae. The Pygopodidae are the closest living relatives of the Gekkonidae as shown by the fact that they have many morphological features in common (McDowell and Bogert, 1954 ; Underwood, 1957 ; Stephenson, 1961), some of which are advanced character-states within the Squamata which are shared by no other living lizard. Such a state is the extreme development of the lip of the cochlear limbus of the inner ear (Shute and Bellairs, 1953). The position of the Xantusiidae, on the other hand, is much less certain although some authors such as McDowell and Bogert (1954), Hoffstetter (1962) and Savage (1963) have suggested that this family should also be included with the Gekkonidae and Pygopodidae in the Infraorder Gekkota.

EVOLUTION OF THE GEKKONIDAE AND PYGOPODIDAE

Fourteen of the characters used by Kluge (1967*a*) in his classification of the Gekkonidae are also used here to determine the evolutionary history of the Gekkota (*i.e.* the Gekkonidae and Pygopodidae). The states of these characters which are claimed here to be primitive in the Gekkonidae (see Appendix) are also primitive in the Gekkota because they are ancestral states retained in living forms. Only three other characters are sufficiently well known to be used to determine gekkotan inter-relationships, namely the *rectus superficialis* muscle, limbs and the triangular processes on the pleurapophyses of the second sacral vertebra. According to Camp (1923), pygopods have the *rectus superficialis* whereas geckos do not. As this muscle is present in crocodiles, *Sphenodon* and many squamates including all limbless forms in which it is essential for locomotion, its absence from other squamates is regarded as a secondary condition (Camp, 1923; Underwood, 1957). Thus, within the Gekkota, the presence of this muscle in the Pygopodidae is more primitive than its absence from the Gekkonidae. Although Camp (1923) named only seven genera of geckos as lacking the *rectus superficialis*, he considered it to be absent from all geckos. In view of the extreme thinness of the ventral body wall in these lizards through which the viscera are often clearly visible (*e.g.* Carr, 1964, pp. 138–139), it is evident that the ventral abdominal musculature is greatly reduced. In contrast, the ventral body wall of pygopods is opaque and relatively thick (personal observation) and the *rectus superficialis*, according to Camp (1923), forms a broad ribbon on each side of the mid-line. In these circumstances Camp's contention that the *rectus superficialis* is absent from geckos generally is accepted as correct.

The presence of limbs is more primitive than their partial or complete absence because four well developed limbs were present in the ancestors of the Squamata. The triangular processes on the pleurapophyses of the second sacral vertebra as described by Holder (1960) and Cogger (1964) are found in members of the Eublepharinae, Gekkoninae and Sphaerodactylinae but not in pygopods or, as far as is known, in the Diplodactylinae. According to Holder (1960), these processes are found in the gekkonine genera *Heteronota* (=*Heteronotia*—see Wermuth, 1965), *Peropus* (=*Gehyra*—see Mitchell, 1965; Wermuth, 1965), *Phyllodactylus*, *Hemidactylus*, *Gekko*, *Lepidodactylus*, *Aristelliger* and *Afroedura* and in the sphaerodactyline genera *Sphaerodactylus* and *Gonatodes* but were absent from all the diplodactyline genera she examined. They are also present in the gekkonines *Stenodactylus*, *Tropiocolotes*, *Ptyodactylus* and *Tarentola* (El-Toubi and Khalil, 1950, 1955) and in the eublepharine *Coleonyx* (Kluge, 1962). As sacral pleurapophyseal processes are also found in various living non-gekkotan lizards (Hoffstetter and Gasc, 1969) as well as some Triassic squamates (Peyer and Kuhn-Schnyder, 1955) and Jurassic rhynchocephalians (Hoffstetter, 1955; Cocude-Michel, 1963), their presence is considered here to be a primitive character-state within the Gekkota.

The occurrence in the Pygopodidae and the four subfamilies of geckos of the primitive states of these 17 characters within the Gekkota is shown in Table 2. Table 1 shows the occurrence of these states in the different genera of pygopods as this information is scattered in the literature. From Table 2, two facts about the Gekkota are obvious, namely that few characteristics clearly distinguish one group of gekkotans from another and that parallel evolution has occurred many times. The presence of the *rectus superficialis* and the absence of walking legs distinguish the Pygopodidae from the Gekkonidae while the presence of eyelids, by definition, distinguishes the Eublepharinae from all other members of the Gekkota. The only other character-states which appear to be confined to particular groups of gekkotans are the presence of the sacral pleurapophyseal processes in the Eublepharinae, Gekkoninae and Sphaerodactylinae and the absence of these processes from the Diplodactylinae and Pygopodidae. Unfortunately, however, the state of this character could not be determined in all genera of geckos so that the possibility remains that some members of the Eublepharinae, Gekkoninae and Sphaerodactylinae may also lack sacral pleurapophyseal processes.

Whether or not the Diplodactylinae prove to be distinguishable from all other geckos by their lack of sacral pleurapophyseal processes, this subfamily appears to be distinct from the Gekkoninae because, apart from the sacral processes, the Gekkoninae have three primitive and five advanced character-states which are absent from the Diplodactylinae and the Diplodactylinae have two primitive states which are absent from the Gekkoninae. The Diplodactylinae also appear to be distinct from the Sphaerodactylinae because, apart from the sacral processes, the Sphaerodactylinae have one primitive and four advanced states which are not shared by the Diplodactylinae and the Diplodactylinae have four primitive and one advanced states which are absent from the Sphaero-

Table 1

As the occurrence of primitive gekkotan character-states in the Pygopodidae had to be ascertained from a number of different sources (*cf.* Kluge, 1967*a*, *re* the occurrence of these states in the Gekkonidae), these data are given in Table 1.

The presence or absence of these character-states in the five genera of pygopods whose internal morphology is known (*i.e.* excluding *Ophidiocephalus*) was for the most part ascertained from the works of Camp (1923), Kinghorn (1926), McDowell and Bogert (1954), Underwood (1957), and Stephenson (1961). Data not given in these papers, namely the number of scleral ossicles in *Delma* and *Pletholax*, the state of the post-cloacal bones in *Delma, Aprasia* and *Pletholax*, the states of the second visceral arch and the splenial and angular bones in *Pletholax* and the shape of the vertebral centra and sacral pleurapophyses in all five genera, were obtained from personal examination of alizarin transparencies.

Although Camp (1923) described the presence of the *rectus superficialis* muscle only in *Pygopus* and *Lialis*, he pointed out that the presence of this muscle is essential for the locomotion of limbless lizards, so that its presence in the other three genera may be taken for granted. The fact that it has not been described in these genera is shown by the symbol " 0 ". The " + " and " — " symbols denote respectively the known presence or absence of the primitive state of a character in each genus.

Table 1

Occurrence of Primitive Gekkotan Character-states in the Pygopodidae

Character-state	*Pygopus*	*Delma*	*Lialis*	*Aprasia*	*Pletholax*
Eyelids	—	—	—	—	—
Four limbs	—	—	—	—	—
Rectus superficialis muscle..	+	0	+	0	0
Sacral pleurapophyseal processes	—	—	—	—	—
Postcloacal bones	+	+	+	+	—
Approximately 14 scleral ossicles	+ (15)	+ (16)	+ (14)	+ (14)	+ (14)
Paired premaxillae in adults	—	—	—	—	—
Paired nasals in adults ..	+	+	+	—*	+
Paired frontals in adults ..	—	—	—	—	+
Paired parietals in adults ..	+	+	—	+	+
Squamosal	+	+	+	+	+
Supratemporal	—	—	—	—	—
Splenial	+	+	+	—	+
Angular	—	—	—	—	—
Continuous hyoid arch ..	+	+	+	0†	0†
Continuous 2nd visceral arch	—	—	—	0†	—
Amphicoely‡..	—	—	—	—	—

[*] Partially fused at least (Stephenson, 1961).

[†] Not known because specimens were damaged in this region.

[‡] Adult pygopod vertebral centra are procoelous with a persistent notochord and have non-synovial joints between them like procoelous geckos (Holder, 1960; Moffat, 1972).

dactylinae. In contrast, the distribution of character-states shown in Table 2 does not distinguish between the Gekkoninae and Sphaerodactylinae. As all eight primitive character-states and 11 of the 12 advanced states found in the Sphaerodactylinae also occur in the Gekkoninae and the only advanced state not found in the Gekkoninae, namely the discontinuous hyoid arch, occurs in only one of the five sphaerodactyline genera, there is no justification for regarding the Sphaerodactylinae as a separate subfamily from the Gekkoninae on the basis of the data in Table 2. The evidence for the validity of the Sphaerodactylinae as a separate subfamily involves characters such as the scalation of the digits, the superciliary scales and folds, sexual dichromatism, sexual dimorphism in ventral pholidosis, the morphology of the inner ear and adult body size (see Vanzolini, 1968*b*) but too little is known of the occurrence of different states of these characters in geckos generally for a clear distinction to be drawn between the Sphaerodactylinae and Gekkoninae. Indeed, one of the genera placed by Kluge (1967*a*) in the Gekkoninae, namely *Pristurus*, may belong instead to the Sphaerodactylinae.

According to Kluge himself (*op. cit.*, p. 33), there are many similarities between *Pristurus* and the Sphaerodactylinae which include diurnal or shade activity, sexual dichromatism, the presence of " eyelids " (*i.e.* superciliary folds or extrabrillar fringes—see Bellairs and Boyd, 1947), simple undilated digits as in *Gonatodes*, small adult size and the absence of preanal organs. As Kluge considered that the splenial had not been lost in parallel by *Pristurus* and the Sphaerodactylinae, he clearly regarded these two groups as closely related. A close relationship between the Neotropical Sphaerodactylinae and *Pristurus* of north-east Africa and south-west Asia (see Romer, 1956, p. 542) is not surprising since some groups of endemic New World gekkonine genera are more closely related to Old World gekkonines than they are to one another (Kluge, 1967*a* ; Vanzolini, 1968*b*). However, if *Pristurus* has more characteristics in common with the Sphaerodactylinae than the Gekkoninae and if the available evidence suggests that these similarities have not arisen in parallel, this genus must be transferred to the Sphaerodactylinae even though such a change would extend the geographical distribution of the Sphaerodactylinae to include north-east Africa and south-west Asia and would also suggest that this subfamily arose in the Old World rather than in Neotropical America as is generally believed to be the case (see Werner, 1961 ; Vanzolini, 1968*b*). For the present purpose, however, namely the determination of evolutionary relationships between subfamilies of geckos and pygopods, *Pristurus* is retained in the Gekkoninae even though it is clearly recognized that this genus and possibly others may be transferred from one subfamily to another, and that the character-states used by Kluge (1967*a*) to define gekkonid subfamilies may be augmented or changed in the light of further knowledge.

TABLE 2

With the exception of the states of the premaxillae in the Diplodactylinae and of the *rectus superficialis* muscle and sacral pleurapophyseal processes in geckos generally, the occurrence in the four subfamilies of geckos of the primitive character-states listed in Table 2 was determined from Kluge (1967*a*). Data regarding the premaxillae in the Diplodactylinae were obtained from Kluge (1967*b*) and the occurrence of the *rectus superficialis* and sacral pleurapophyseal processes in the Gekkota is discussed in the text. The occurrence of all 17 primitive states in the various genera of pygopods is given in Table 1.

The total number of genera given for each subfamily of geckos was taken from Kluge's (1967*a*) Table 1 showing the numbers of scleral ossicles found in the different genera, not from his Appendix I listing the material from which all osteological data were obtained and which listed 13 diplodactyline and 51 gekkonine genera. As Kluge cited individual genera and species in his text only in connection with the less common states of characters in each subfamily, it is possible that the numbers of genera listed here in Table 2 as having the more common conditions may not always be correct.

The headings " P " and " A " refer respectively to the presence or absence of the primitive state of each character, while the numerals refer to the number of genera in each group which possess or lack this state. The symbol " 0 " means that the presence or the absence of a primitive character-state has not been reported to occur in a group ; where all the genera in a group have not been described with respect to a character-state (as indicated by ¶) it is possible that some of the undescribed genera may possess or lack the state concerned. With respect to the occurrence of paired premaxillae in adult eublepharines, the symbols " P " and " A " are used instead of numerals to show that the primitive state is present in some and absent from other genera in this group. As Kluge (1967*a*) was concerned with the state of the premaxillae at hatching, the distribution of the paired condition in adults could not be determined numerically.

Although the absence of the primitive state of a character implies the presence of an advanced state of that character, no attempt is made here to indicate the number of times advanced states may have arisen within a group (*cf.* Kluge, 1967*a*, Table 2).

TABLE 2

Occurrence of Primitive Gekkotan Character-states in the Gekkota

Primitive Character-state	Pygopodidae Five genera		Eublepharinae Five genera		Gekkoninae 58 genera		Diplodactylinae 14 genera		Sphaerodactylinae Five genera	
	P	A	P	A	P	A	P	A	P	A
Eyelids	0	5	5	0	0	58	0	14	0	5
Four limbs	0	5	5	0	58	0	14	0	5	0
Rectus superficialis muscle ..	5	0	0	5	0	58	0	14	0	5
Sacral pleurapophyseal processes¶	0	5	1	0	12	0	0	9	2	0
Postcloacal bones¶	4	1	5	0	45	7	14	0	0	5
c. 14 scleral ossicles per eye ..	5	0	1*	4	56	2*	0	14	5	0
Paired premaxillae in adults¶	0	5	P	A	0	58	5	9‖	0	5
Paired nasals in adults ..	4	1	5	0	43	15*	14	0	5	0
Paired frontals in adults¶ ..	1	4	0	5	6*	51	0	14	0	5
Paired parietals in adults	4	1	0	5	57‡	1	14	0	5‡	0
Squamosal	5	0	5	0	55	3*	14	0	4	1
Supratemporal	0	5	3*	2	0	58	0	14	0	5
Splenial	4	1	5	0	56	2	14	0	0	5
Angular	0	5	4	1*	1	57	0	14	0	5
Continuous hyoid arch¶ ..	3	0	5	0	58	0	14	0	4	1
Continuous 2nd visceral arch¶	0	4	1	4	0	58	1†	13	0	5
Amphicoely	0	5	0	5	57	1	9	5§	1	4

* Primitive character-state is present in some species and absent from other species of at least one of these genera.

† As Stephenson and Stephenson (1956) described the 2nd visceral arch of *Naultinus* as uninterrupted, whereas Kluge (1967*a*) described it as interrupted, there would appear to be intrageneric variation in *Naultinus* with respect to this character.

‡ Parietals paired at sexual maturity although fusion may occur later in some genera.

§ According to Kluge (1967*a*), *Phyllurus*, *Carpodactylus*, *Crenadactylus*, *Diplodactylus* and *Oedura* all show a tendency toward procoely. All the representatives of these genera examined by Holder (1960), however, were described as amphicoelous with the exception of one species of *Phyllurus*, *P. milii*, which had notochordal procoelous vertebrae. Subsequent re-examination of this material has confirmed these findings except for *Carphodactylus laevis* which was found to have centra which are very slightly convex posteriorly (Moffat, 1972). In these circumstances, it would appear that intrageneric variation with respect to the shape of the centrum may be widespread in the Diplodactylinae.

¶ Presence or absence of primitive character-state not known for all genera of geckos and/or pygopods.

‖ Fusion of premaxillae may be partial or complete, the variation in some cases being intrageneric (Kluge, 1967*b*).

The second fact about the Gekkota which is self-evident in Table 2, namely that parallel evolution has been of widespread occurrence in their evolution, is clearly demonstrated by the coexistence of the primitive state and an advanced state of 11 of the 17 characters in at least two groups within the Gekkota. As the advanced state of each character (*e.g.* the absence or fused state of bony elements and procoely of the vertebral centrum) is morphologically the same state in all groups in which it occurs, even when it has arisen in parallel in two or more groups, it may also have arisen in parallel in two or more groups where it is not accompanied by the primitive state. It is for the purpose of detecting parallelisms of the latter type that as many characters as possible should be used in the determination of phylogenetic relationships. However, if an advanced character-state can be shown to have arisen only once within the Gekkota so that it is unique within this group, it is as important as the primitive state of the character for determining gekkotan relationships *inter se* although it has no bearing on relationships between the Gekkota and non-gekkotan lizards. As all groups within the Gekkota possessing such a unique advanced state must have inherited it from the same source, it follows that this state of the character is more primitive than any other state in the groups possessing it although it is an advanced state in the Gekkota as a whole. The distribution of character-states which are primitive in the Gekkota can eliminate some evolutionary sequences such as the evolution of non-eublepharine geckos from the Eublepharinae (*vide infra*) but, unless it can eliminate all but one sequence, the distribution of unique advanced states is also required to show that a particular sequence is correct. As none of the advanced states of the 17 characters used here can be shown to be unique and the distribution of primitive states as shown in Table 2 permits more than one sequence consistent with these data, the relationships of geckos and pygopods cannot be determined precisely.

As all the character-states listed in Table 2 are primitive in the Gekkota because they are ancestral states retained in living forms, it follows that all of these states must have been present in the immediate common ancestor of geckos and pygopods. Three of these primitive states, namely the continuous hyoid arch, the squamosal and paired nasals, are of no help in determining relationships within the Gekkota because they occur in all four subfamilies of geckos as well as in pygopods. The distribution of the other 14 primitive states among the five groups of living Gekkota is summarized in Figs 1A and 1B which show the two most parsimonious phylogenies of the Gekkota (*sensu* Kluge and Farris, 1969) which are consistent with the available data.

As the Sphaerodactylinae cannot be distinguished from the Gekkoninae using the data in Table 2 the former group is omitted temporarily from the following discussion. From the distribution of primitive character-states in the other four groups, it is clear that none of these groups in its present form could have been ancestral to any other because each group retains at least one primitive state which is not present in any other group. For example, as the Gekkoninae and Diplodactylinae retain primitive character-states such as paired parietals and amphicoelous vertebrae which are absent from the Eublepharinae, neither the Gekkoninae nor the Diplodactylinae could have evolved from the Eublepharinae (*cf.* Kluge, 1967*a*). Nor could the Gekkoninae have evolved from the Diplodactylinae as the latter lack sacral pleurapophyseal processes, the primitive number of scleral ossicles, paired frontals and the angular, all of which occur in at least some members of the Gekkoninae. The possibility of direct evolutionary sequences between any other two of these four groups can be ruled out in a similar manner, by reference to the appropriate primitive character-states.

The distribution of primitive character-states in the Eublepharinae, Diplodactylinae, Gekkoninae and Pygopodidae does not rule out the possibility that each of these groups may have arisen independently from the same ancestral stock, especially as many advanced states in the Gekkota are known to have evolved in parallel. If these four groups did arise independently, all of their advanced character-states must have arisen in parallel, including the loss of the *rectus superficialis* muscle and the transformation of eyelids into a brille. The *rectus superficialis* would have been lost on at least three separate occasions, once in each group of geckos, while the brille would have appeared at least three times, once each in the Gekkoninae, Diplodactylinae and Pygopodidae. To accept such a phylogeny, however, would be to ignore one of the basic tenets of evolutionary deduction, namely the principle of parsimony whereby the same character-state occurring in two or more groups of organisms is assumed to have been inherited from a common ancestor unless there is evidence to the contrary In view of the widespread occurrence of parallel evolution in the Gekkota, the principle of parsimony is applied here only to those characters whose advanced states do not appear to have arisen in parallel within this group, namely the *rectus superficialis* and the eye-covering (see Table 2). Nor is there any suggestion that the loss of the primitive states of these characters and their replacement by advanced states is correlated with body form. The brille occurs in geckos and pygopods and the *rectus superficialis* is retained in many tetrapod non-gekkotan lizards as well as in limbless forms. However, from the distribution of the primitive and advanced states of these two characters in the Eublepharinae, Diplodactylinae, Gekkoninae and Pygopodidae, it is clearly impossible for the advanced states of both characters to have arisen only once within the Gekkota.

If the *rectus superficialis* was lost only once so that its absence is a unique state within the Gekkota, it follows that the Gekkonidae arose from a common stem distinct from the Pygopodidae and that eyelids must have been lost on at least two occasions, once in non-eublepharinae geckos and again in pygopods (Fig. 1A). On the other hand, if true eyelids were lost and the brille acquired only once within the Gekkota, it follows that non-eublepharine geckos and pygopods must have evolved from a common stem distinct from the Eublepharinae and that the *rectus superficialis* was lost independently in eublepharine and non-eublepharine geckos (Fig. 1B). In the absence of data on characters other than those used here, the only way to choose between these alternative evolutionary sequences would be to establish that either the absence of the *rectus superficialis* or the presence of the brille is a unique state within the Gekkota.

Among lizards in general, the *rectus superficialis* is present in some families and absent from the others and, within the family Agamidae, is present or absent in different genera (Camp, 1923; Underwood, 1957) so that this muscle has clearly been lost several times within the Lacertilia. As it also shows considerable variability in its development (Maurer, 1896, 1898; Camp, 1923), there would appear to be no restriction on its loss on more than one occasion within the Gekkota.

The loss of true eyelids has also occurred several times in the Lacertilia as shown by their absence from several families apart from the Gekkonidae and Pygopodidae and by the existence of a morphological series from eyelids to brille in some lacertids and scincs (Walls, 1942; Bellairs and Boyd, 1947; Bellairs, 1969). In all snakes, too, the eyelids have evolved into a brille (Walls, 1942; Bellairs and Boyd, 1947; Bellairs, 1948, 1969). Although the brilles of geckos and pygopods do not appear to resemble one another more closely than those of other lizards in their morphological characteristics (Bellairs and Boyd, 1947; Underwood, 1957), geckos and pygopods do share another characteristic associated with the eye which does not appear to have been described in any other lizards and is absent from snakes (Cogger, 1967). This characteristic is the practice of wiping the eye with the broad, fleshy tongue which has been described or illustrated in geckos and pygopods by Smith (1952), Mitchell (1958), McPhee (1959), Worrell (1963), Bustard (1963, 1965, 1970), Carr (1964) and Cogger (1967) and it is no doubt of considerable advantage to pygopods and non-eublepharine geckos which lack eyelids and a nictitating membrane to keep the eyes free from dust, especially as vision is a major sense in the Gekkota, many of which are most active in dim light (Underwood, 1970).

It was thought at first that if this eye-licking behaviour could be shown to exist only in those gekkotans possessing a brille, it could reasonably be regarded

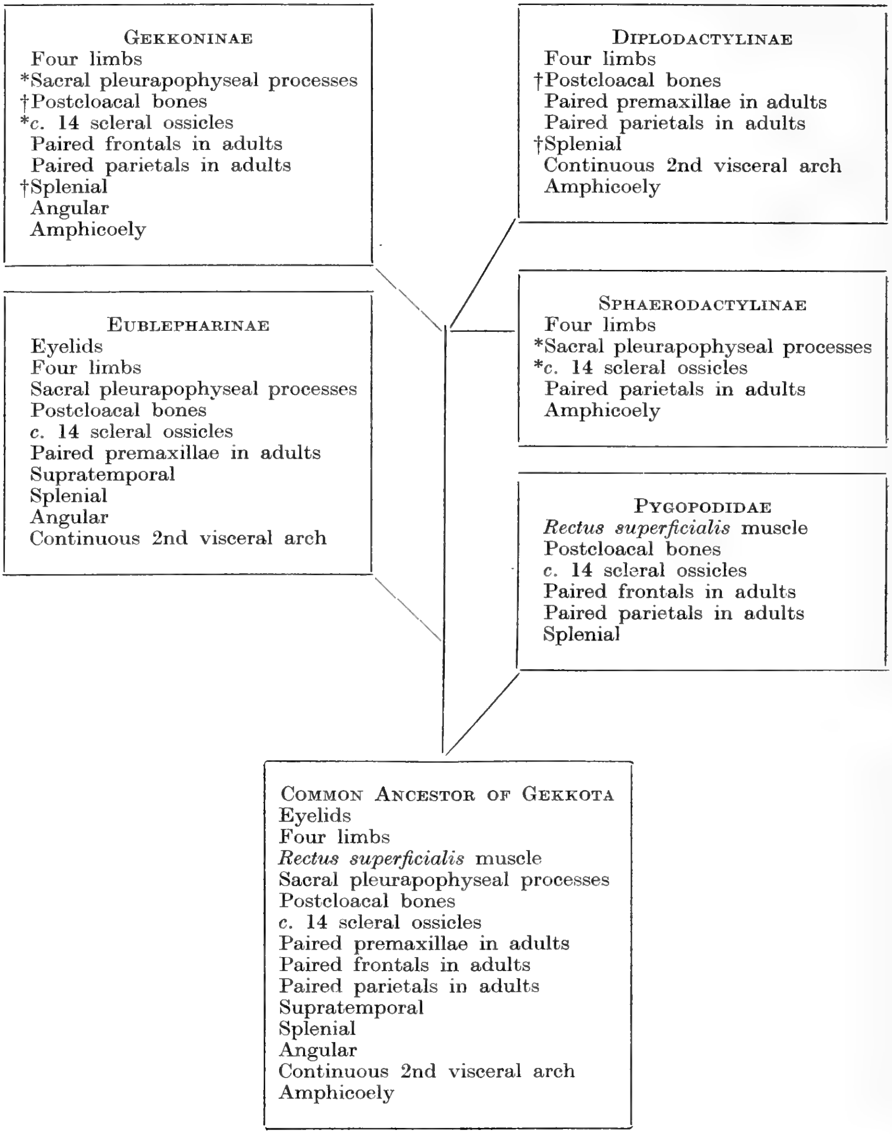


Fig. 1A.

FIGURE 1

Diagrammatic representations of the two possible phylogenies of the Gekkota based on the data in Table 2 and consistent with the principle of parsimony, giving the order in which the five groups of living gekkotans could have diverged from one another. The primitive character-states listed for each group are those states which are absent from at least one of these groups. No attempt is made to show the relative advancement of these five groups (*cf.* Kluge, 1967*a*) or to indicate either the relative or the absolute periods of time involved in their evolution.

Fig. 1A—All geckos are shown arising from a common stock in which the *rectus superficialis* had been lost, in which case the eyelids evolved into a brille independently in the Pygopodidae and non-eublepharine geckos.

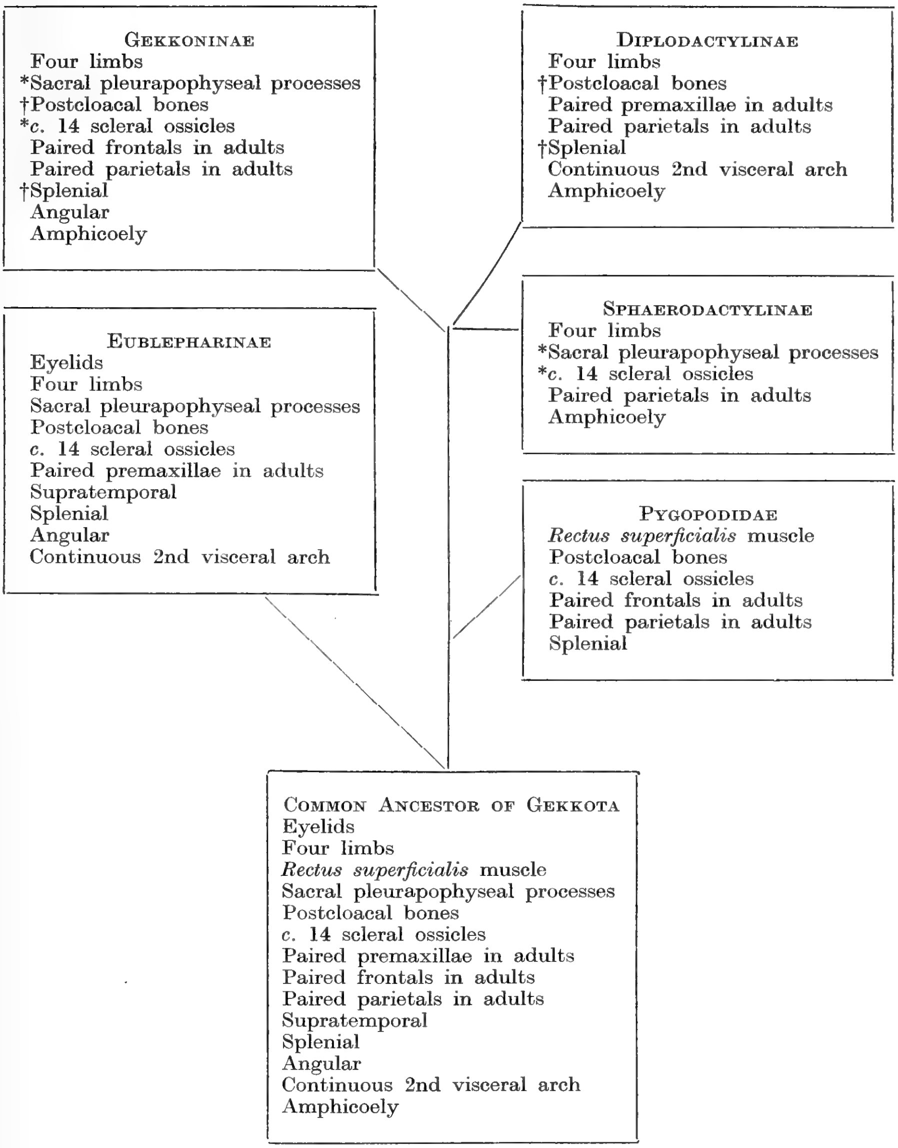


Fig. 1B.

Fig. 1B—The non-eublepharine geckos and pygopods are shown arising from a common stock in which the eyelids had evolved into a brille. In this case the *rectus superficialis* was lost independently in the Eublepharinae and non-eublepharine geckos.

* Primitive character-state present in the Sphaerodactylinae and Gekkoninae but not in the Diplodactylinae.

† Primitive character-state present in the Diplodactylinae and Gekkoninae but not in the Sphaerodactylinae.

as having evolved in association with the brille. In these circumstances it would be most improbable that both the brille and eye-licking behaviour could have evolved on more than one occasion within the Gekkota, so that the brille could be regarded as a unique as well as an advanced state within this group. This argument breaks down, however, when it is recognized that eublepharine geckos can also lick their eyes. Bustard (1963, 1965) reported the occurrence of eye-licking in *Coleonyx variegatus* and it has also been elicited in *Eublepharis macularius* in conditions simulating a dust storm (Maderson, 1971). Therefore it is clear that the ability to pass the tongue high up the side of the head and over the eyes must have existed in the Gekkota prior to the appearance of the brille.

From the foregoing discussion, it is evident that neither the brille nor the absence of the *rectus superficialis* muscle can be described from the information available as a unique character-state within the Gekkota. Therefore, on the basis of the distribution of primitive character-states within the Gekkota, the two alternative relationships between geckos and pygopods as shown in Figs 1A and 1B appear equally probable. The more conservative of these alternatives, that the Eublepharinae and non-eublepharine geckos arose from a common stem distinct from the Pygopodidae (Fig. 1A), is accepted provisionally because it does not require any alteration to the existing classification of the Gekkota. The alternative evolutionary sequence as illustrated by Fig. 1B in which the non-eublepharine geckos are shown to be more closely related to the Pygopodidae than to the Eublepharinae would necessitate the elevation of the Eublepharinae to familial status and the restriction of the family Gekkonidae to include only the Diplodactylinae, Gekkoninae and Sphaerodactylinae and such a change in classification is not justified by the present state of knowledge of gekkotan relationships. Further knowledge regarding the distribution of primitive and advanced states of other characters which are as yet poorly known in gekkotans generally, such as the visual cells and accessory structures of the eye (see Underwood, 1970), the inner ear and glandular scales (see Vanzolini, 1968*b*) as well as cytological, biochemical and serological characters may demonstrate conclusively which, if either, of these evolutionary sequences is correct.

It is now relevant to consider the inter-relationships of the non-eublepharine geckos, including the Sphaerodactylinae. It has already been shown that the Diplodactylinae could not have evolved from the Gekkoninae in their present form or *vice versa* because each of these groups retains primitive character-states which are not present in the other. For the same reason, neither the Gekkoninae nor the Diplodactylinae could have evolved from the Sphaerodactylinae, nor could the Sphaerodactylinae have evolved from the Diplodactylinae. Although the Sphaerodactylinae cannot be distinguished from the Gekkoninae using the data in Table 2 and would therefore appear to have evolved from the Gekkoninae as they exist today, Vanzolini (1968*b*) pointed out that sphaerodactyline geckos have undergone mosaic evolution with respect to other characters which show relationships within this group and regarded the Sphaerodactylinae as an old group of geckos which branched off the general gekkonid stock at a stage no longer represented by any living species. Therefore none of the existing sub-families of non-eublepharine geckos can be considered ancestral to any other.

From the distribution of primitive character-states as summarized in Figs 1A and 1B, it is seen that one of three evolutionary sequences could have given rise to the Gekkoninae, Diplodactylinae and Sphaerodactylinae. The three groups may have arisen independently from the ancestral non-eublepharine stock, or the Gekkoninae and Sphaerodactylinae may have evolved from a common stock (with sacral pleurapophyseal processes and *c.* 14 scleral ossicles) distinct from the Diplodactylinae in which these processes were lost and the ossicle number increased, or the Gekkoninae and Diplodactylinae may have evolved from a common stock (with post-cloacal bones and splenial) distinct from the Sphaerodactylinae which lost these bones. It is most improbable that the Diplodactylinae and Sphaerodactylinae evolved from a common stock distinct from the Gekkoninae because none of the character-states listed in Table 2 occurs only in these two groups and they are both comparatively small groups which are very different in other morphological characteristics (see Kluge, 1967*a*, 1967*b* ; Vanzolini, 1968*b*) and which are restricted and widely separated in their geographical distribution (*vide infra*). Although the second of these alternative evolutionary sequences appears at first to be the most probable because the Sphaerodactylinae and Gekkoninae share more primitive and advanced character-states than any other two non-eublepharine subfamilies, this sequence can be confirmed only by establishing that a unique advanced gekkotan character-state occurs only in these two groups. As no advanced gekkotan character-state is known to fulfil these requirements, it is also possible that the Diplodactylinae, Gekkoninae and Sphaerodactylinae evolved independently from the same ancestral stock.

From the distribution of character-states as shown in Table 2, it is seen that the Gekkoninae have more primitive states (12) and more advanced states (14) than either the Diplodactylinae (with 10 primitive and 10 advanced states) or the Sphaerodactylinae (with 8 primitive and 12 advanced states). Therefore, of these three subfamilies, the Gekkoninae are not only the most variable but are also closest to the ancestral non-eublepharine stock because they retain the greatest number of primitive character-states. The Gekkoninae are also by far the largest group numerically (58 genera) and the most widespread, occurring on islands and continents throughout the world between the 50° latitudes (Kluge, 1967*a*) while the Diplodactylinae comprise 14 genera restricted to the Australasian region and the Sphaerodactylinae currently consist of only five genera restricted to Neotropical America (Kluge, *op. cit.*, 1967*b* ; Vanzolini, 1968*b*). Although the Diplodactylinae and Sphaerodactylinae are small groups compared with the Gekkoninae, their restricted distribution suggests that they are not the living representatives of formerly larger, more widespread groups (*cf.* the Eublepharinae—Boulenger, 1885 ; Kluge, 1967*a*) but have instead undergone the major part of their evolution in the regions where they are found today.

The evolutionary history of the Diplodactylinae, Gekkoninae and Sphaerodactylinae which best explains the distribution of character-states in these three groups, as well as their differences in size and geographical distribution, is as follows : the ancestral stock of the existing non-eublepharine geckos radiated throughout most of the world in tropical and temperate regions, replacing most of the Eublepharinae whose present discontinuous world-wide distribution indicates the former existence of a large and widespread group. In the process of radiating into a wide variety of habitats around the world, different groups of non-eublepharine geckos retained and lost different combinations of primitive character-states and acquired different combinations of advanced states. In or near Australasia, one of these groups became sufficiently distinct from other non-eublepharine geckos to be classified today as a separate group, the Diplodactylinae. On the other side of the world, in northern Africa or Neotropical America, another group with a different combination of primitive and advanced states evolved into the existing Sphaerodactylinae. The groups of non-eublepharine geckos which remained after the appearance of the Diplodactylinae and Sphaerodactylinae, and which have not become sufficiently distinct from one another to be placed in separate taxa, were the earliest members of the Gekkoninae.

This evolutionary history of the Diplodactylinae, Gekkoninae and Sphaerodactylinae is believed to be correct because it offers a satisfactory explanation for the known data concerning these groups. It explains why the Gekkoninae are the most widespread geographically and the most numerous in terms of genera. It accounts for the fact that the Gekkoninae are at the same time the most variable among themselves and the most similar to ancestral forms with respect to the distribution of character-states. It explains the obviously widespread occurrence of parallel evolution in these three subfamilies (see Table 2) and the absence of advanced character-states which are universally present in two groups and absent from the third and which might therefore be unique states among non-eublepharine geckos (*cf.* the absence of the *rectus superficialis* and the presence of the brille with respect to gecko-pygopod relationships). Moreover, if the Sphaerodactylinae and Diplodactylinae evolved from two different groups within a widespread and variable ancestral stock, it is not necessary to establish the relative antiquity of these two subfamilies. Whether they arose at the same time or at different times in geological history does not affect the interrelationships of living non-eublepharine geckos and for this reason the three subfamilies are shown in Figs 1A and 1B arising from the same point. The subfamily Gekkoninae, on the other hand, is only as old as the more recent of the other two subfamilies, since this group represents all the non-eublepharine geckos which remained after the divergence of the Diplodactylinae and Sphaerodactylinae.

Affinities of the Xantusiidae

It remains now to consider whether the Xantusiidae can be included with geckos and pygopods in the Infra-order Gekkota as proposed by McDowell and Bogert (1954), Hoffstetter (1962) and Savage (1963). Although no final statement regarding xantusiid relationships can be given here as it requires a detailed comparison between the Xantusiidae and all other living lizards, it is relevant to consider the circumstances which would justify transferring the Xantusiidae from the Scincomorpha to the Gekkota and to discuss the extent to which xantusiids, geckos and pygopods resemble one another.

The tetrapod Gekkonidae and the limbless Pygopodidae are placed together in the Gekkota, not only because they have many more character-states which are not apparently correlated with body form in common with one another than with any other group of lizards, including the extreme development of the cochlear limbus which is found only in these two families (Shute and Bellairs, 1953), but also because none of the character-states shared by either of these families and non-gekkotan lizards (*e.g.* imbricate scales in pygopods and most non-gekkotan families) suggests relationship with a particular non-gekkotan group. Having established that the Gekkonidae and Pygopodidae resemble one another so closely that they may be considered to have arisen from a common ancestral stock which was shared by no other group of living lizards, it is then possible to determine the course of evolution within the Gekkota from the distribution of character-states which are primitive in the Gekkota and of others which may be unique and advanced within this group.

If the Xantusiidae are to be placed in the Gekkota as well, it is necessary to show that this family has more character-states in common with either the Gekkonidae or the Pygopodidae than with any other family in the Infra-order Scincomorpha, *i.e.* the Teiidae, Scincidae, Lacertidae or Cordylidae (=Zonuridae) with which the Xantusiidae are classified at present (Romer, 1956; Bellairs, 1969). The presence in the Xantusiidae and either the Gekkonidae or the Pygopodidae of character-states which are primitive (=original) in the Squamata as a whole is not in itself indicative of close relationship as such states have been inherited from the ancestors of all living lizards. On the other hand, the presence only in these families of one character-state which is unique as well as advanced within the Squamata would establish beyond question that these three families are more closely related to one another than to any other living lizards. In practice, however, it is often difficult to determine whether one state of a character (*e.g.* of the preanal pores, postcranial endolymphatic apparatus and vocalization in geckos) is more primitive than another and it is rarely possible to establish conclusively that a character-state is unique as well as advanced in a particular group of lizards (*e.g.* the brille in geckos and pygopods). It is for these practical reasons that two groups are considered to be closely related to one another if they have many character-states in common, in the hope that at least one of these states is advanced in squamates generally and has not arisen in parallel in the two groups.

The data used in the following discussion of the distribution of character-states in the Xantusiidae and the Gekkota as currently defined have been compiled from the works of Camp (1923), Bellairs and Boyd (1947, 1950), Shute and Bellairs (1953), McDowell and Bogert (1954), Romer (1956), Stephenson and Stephenson (1956), Underwood (1957, 1970), Stephenson (1961), Kluge (1962, 1967*a*, 1967*b*), Savage (1963), Hoffstetter and Gasc (1969) as well as from the present author's study of the vertebral morphology of these lizards (Holder, 1960; Moffat, 1972). Three character-states have been considered erroneously to be characteristic of the Xantusiidae and geckos, namely the production of only two eggs at ovulation and the absence of the pineal (or parietal) foramen and the angular bone in the lower jaw (McDowell and Bogert, 1954). It is now known that the Xantusiidae produce from one to nine offspring at a time and possess both the pineal foramen and the angular bone (Savage, 1963) and that the angular bone is also present in some geckos (Kluge, 1962, 1967*a*).

Character-states which are shared by the Xantusiidae and the Gekkota and which, in some cases, have been regarded as evidence of their close relationship fall into three categories : character-states which are primitive in the Squamata, those which are advanced in the Squamata and those whose primitive or advanced nature is uncertain. The occurrence of 33 primitive character-states in these lizards is shown in Table 3, in which the data concerning the Eublepharinae and non-eublepharine geckos are given separately because of the possibility that the latter group may be more closely related to the Pygopodidae than to the Eublepharinae.

With the exception of the post-cloacal bones (*vide infra*), all the character-states listed in Table 2 as primitive in the Gekkota are also primitive in the Squamata because they were inherited from the ancestors of the Squamata. Of the additional character-states listed in Table 3, the majority are primitive in the Squamata because they also occurred in fossil groups containing the ancestors of the Squamata (see Romer, 1956). Non-synovial joints between adjacent vertebral centra, which occur in xantusiids and pygopods as well as in geckos as described by Holder (1960), are considered to be more primitive than the synovial intercentral joints of other lizards because the former are characteristic of the notochordal amphicoelous vertebrae of geckos and *Sphenodon* and were undoubtedly present in the earliest fossil reptiles as well. Direct communication between the duct of Jacobson's organ and the choanal groove in the superficial palate is considered to be more primitive than the absence of such communication because the former condition is also found in *Sphenodon* and the latter condition in other squamates arises from the former during ontogeny (Bellairs and Boyd, 1950). The broad, flat tongue with no more than a slight terminal notch found in xantusiids, geckos and pygopods is also considered to be primitive compared with the deeply forked tongues of some other lizards (Bellairs, 1969), especially as the tongue of *Sphenodon* is also broad, flat and undivided (personal observation).

Of the 33 primitive squamate character-states listed in Table 3, 28 occur in geckos (25 in the Eublepharinae and 25 in non-eublepharine geckos), 19 in pygopods and 23 in the Xantusiidae. Although the Xantusiidae more closely resemble ancestral lizards than do pygopods because they retain a greater number of these primitive character-states, this does not mean that they are more closely related than pygopods to geckos which, of these three groups of lizards, are most similar to the ancestral stock. Of the 19 primitive states in the Pygopodidae, only the *rectus superficialis* is not also found in geckos. Of the 23 primitive states in the Xantusiidae, five are absent from geckos and, of the 28 primitive states present in geckos, 10 are absent from the Xantusiidae. Although the distribution of primitive character-states suggests that geckos and pygopods diverged from one another at a later stage in evolutionary history than the Xantusiidae diverged from their common ancestor, it is necessary to consider other

TABLE 3

The presence of the primitive state of a character within a group, whether or not other members of the group have an advanced state of the same character, is shown by the symbol " + ". The symbol " — " denotes the absence of a primitive state from all members of a group while the " A " symbol indicates that the primitive state is known to be absent from some members of a group but may be present in others.

TABLE 3

Occurrence of Primitive Squamate Character-states in Geckos, Pygopods and Xantusiids

Character-state	Euble-pharinae	Non-eublepharine geckos	Pygopodidae	Xantusiidae
Paired premaxillae in adults	+	+	—	—
Paired nasals in adults	+	+	+	+
Paired frontals in adults	—	+	+	+
Paired parietals in adults	—	+	+	+
Paired vomers in adults	+	+	+	—
Ectopterygoid (=transpalatine)	+	+	+	+
Lachrymal bone	+	A	—	+†
c. 14 scleral ossicles	+	+	+	+
Jugal	+	+	+	+
Palaeochoanate bony palate	+	+	+	+
Pineal foramen	—	—	—	+
Supratemporal	+	—	—	+
Squamosal	+	+	+	+
Upper temporal arch	—	—	—	+
Postorbital arch	—	—	—	+
Arterial foramen in stapes	+	+	—	A
Eyelids	+	—	—	—
Duct of Jacobson's organ in direct communication with choanal groove	+	+	+	—
Splenial	+	+	+	—
Angular	+	+	—	+
Tongue, broad, undivided	+	+	+	+
Uninterrupted hyoid arch	+	+	+	+
Uninterrupted 2nd visceral arch	+	+	A	—
Sacral pleurapophyseal processes	+	+	—	A
Autotomy	+	+	+	+
*Amphicoely	—	+	—	—
*Notochordal centra in adults	+	+	+	A
*Non-synovial joints between adjacent centra	+	+	+	+
*Complete series of intercentra	+	+	+	+
Centra squarish in ventral outline	+	+	+	+
Zygapophyseal joint between atlas and axis	—	—	—	+
Rectus superficialis muscle	—	—	+	+
Four limbs	+	+	—	+
Total number of primitive character-states in each group	25	25	19	23

* Character-state not found in other lizards.

† Partly fused to prefrontal (Savage, 1963).

character-states which are not primitive in squamates in order to determine their inter-relationships. The fact that the Xantusiidae and the Gekkota resemble one another in their vertebral structure is not indicative of close relationship (*cf.* Hoffstetter, 1962; McDowell and Bogert, 1954) because, although these lizards are the only living forms known to possess non-synovial intercentral joints and a complete series of intercentra, these primitive states could have been retained independently in two groups more closely related to other lizards than to one another.

A number of character-states which are known to be advanced in the Squamata also occur in xantusiids, gekkonids and pygopodids such as a brille, a single premaxilla, absence of the splenial bone, a discontinuous second visceral arch and procoelous vertebrae. Although each of these advanced states appears to be present in all members of the Xantusiidae (Savage, 1963), none of them is a unique state which arose once in the common ancestor of the Xantusiidae and the Gekkota because, in each case, the corresponding primitive state exists in the Gekkota. Nor is it possible for the Xantusiidae to have inherited these advanced states from the Gekkota because the Xantusiidae retain primitive character-states which are absent from all living gekkotans (see Table 3). A similar argument applies to advanced character-states which are universally present in the Gekkota but co-exist with the primitive state in the Xantusiidae (*e.g.* the absence of the pineal foramen). It is therefore evident that advanced character-states which occur in the Xantusiidae and the Gekkota, and whose corresponding primitive states exist in either of these groups, must have evolved in parallel.

Character-states whose primitive or advanced nature in the Squamata has not yet been demonstrated and which are known to occur only in the Xantusiidae and the Gekkota include the distinctive morphology of the base of the braincase and the presence of post-cloacal bones (McDowell and Bogert, 1954; Underwood, 1957). Underwood (1957), however, considered the absence of post-cloacal sacs (with which the post-cloacal bones are intimately associated) to be a secondary condition in lizards generally, *i.e.* that the presence of these structures is primitive in the Squamata, because the development of a special organ and its later disappearance are bound to influence associated organ systems such as nerves, muscles and blood-vessels.

From the foregoing discussion of character-states which are shared by the Xantusiidae and the Gekkota, it is evident that no conclusions can be drawn regarding xantusiid affinities from these character-states alone. Other character-states, however, which occur in only one of these two groups and which, in some cases, can be shown to be advanced states in the Squamata as a whole, do give some evidence regarding the relationships of the Xantusiidae. For example, the extreme development of the lip of the cochlear limbus of the inner ear, which is considered to be an advanced condition in squamates, is found only in geckos and pygopods, there being no limbic lip in the family Xantusiidae, which is generally regarded as having affinities with the Gekkonidae (Shute and Bellairs, 1953). According to Miller (1966), the cochlear duct anatomy of xantusiids shows this group to be closely related to the Scincidae but with enough differences to merit their separate familial status. Baird (1970) described the internal ear of *Xantusia* as basically like that of scincs and maintained that the scincid and gekkonid conditions have both departed significantly from the typical lacertilian condition as found, for example, in the Teiidae. The superficial palate of the Xantusiidae, in which the ectochoanal cartilages are so greatly enlarged that they overlap in the mid-line, is advanced compared with the superficial palates of most lizards including geckos, pygopods, lacertids, teiids and scincs in which each ectochoanal cartilage passes backwards and ventrally between the vomer and the palatal process of the maxilla and supports the choanal fold (Bellairs and Boyd, 1950). The Xantusiidae are also advanced compared with some other lizards with an upper temporal arch in that the upper temporal fenestra is closed by the juxtaposition of the postorbitofrontal and squamosal bones with the parietal, and in this respect resemble the Cordylidae (Romer, 1956 ; Savage, 1963). According to Etheridge (1967), the caudal vertebrae of the Xantusiidae are structurally intermediate between those of scincs and lacertids.

In short, as the presence in the Xantusiidae and the Gekkota of primitive squamate character-states is not in itself indicative of relationship and as all the known advanced states shared by these two groups have arisen in parallel, there are no grounds at present for transferring the Xantusiidae to the Gekkota as proposed by McDowell and Bogert (1954), Hofstetter (1962) and Savage (1963). On the contrary, the resemblance between the Xantusiidae and various families in the Scincomorpha with respect to other advanced squamate character-states suggests that the Xantusiidae are rightly placed in the Scincomorpha. As pointed out earlier, however, the final answer to this question must await a detailed comparison between the Xantusiidae and non-gekkotan lizards.

Acknowledgements

This paper was prepared for publication during the author's tenure of a Linnean Macleay Fellowship in Zoology from the Linnean Society of New South Wales. Grateful acknowledgement is also accorded to Professor N. G. Stephenson for his constructive criticism of the manuscript and to Professor L. C. Birch for making available facilities in the School of Biological Sciences, University of Sydney.

References

Abercrombie, M., Hickman, C. J., and Johnson, M. L., 1951.—*A Dictionary of Biology*. Harmondsworth, Middlesex : Penguin.

Baird, I. L., 1970.—The anatomy of the reptilian ear. *In : Biology of the Reptilia*, 2 : 193–275. Edited by C. Gans and T. S. Parsons. London : Academic Press.

Bellairs, A. d'A., 1948.—The eyelids and spectacle in geckos. *Proc. zool. Soc. Lond.*, 118 : 420–425.

————, 1969.—*The Life of Reptiles.* Vols. 1 and 2. London : Weidenfeld & Nicolson.

————, and Boyd, J. D., 1947.—The lachrymal apparatus in lizards and snakes. I—The brille, the orbital glands, lachrymal canaliculi and origin of the lachrymal duct. *Proc. zool. Soc. Lond.*, 117 : 81–108.

————, 1950.—The lachrymal apparatus in lizards and snakes. II—The anterior part of the lachrymal duct and its relationship with the palate and with the nasal and vomero-nasal organs. *Proc. zool. Soc. Lond.*, 120 : 269–310.

Blackwelder, R. E., 1967.—*Taxonomy. A Text and Reference Book.* New York : Wiley & Sons.

Boulenger, G. A., 1885.—*Catalogue of the Lizards in the British Museum* (*Natural History*). Vol. 1. 2nd Edition. London : British Museum.

————, 1887.—*Catalogue of the Lizards in the British Museum* (*Natural History*). Vol. 3. 2nd Edition. London : British Museum.

Brock, G. T., 1932.—Some developmental stages in the skulls of the geckos, *Lygodactylus capensis* and *Pachydactylus maculosa*, and their bearing on certain important problems in lacertilian craniology. *S. Afr. J. Sci.*, 29 : 508–532.

Bustard, H. R., 1963.—Gecko behavioural trait : Tongue wiping spectacle. *Herpetologica*, 19 : 217–218.

————, 1965.—Observations on Australian geckos. *Herpetologica*, 21 : 294–302.

————, 1970.—*Australian Lizards.* Sydney : Collins.

Cain, A. J., and Harrison, G. A., 1960.—Phyletic weighting. *Proc. zool. Soc. Lond.*, 135 : 1–31.

Camin, J. H., and Sokal, R. R., 1965.—A method for deducing branching sequences in phylogeny. *Evolution*, 19 : 311–326.

Camp, C. L., 1923.—Classification of the lizards. *Bull. Am. Mus. nat. Hist.*, 48 : 289–481.

Carr, A., 1964.—*The Reptiles.* Time-Life International (Nederland) N.V.

Carroll, R. L., 1969.—Problems of the origin of reptiles. *Biol. Rev.*, 44 : 393–432.

Chrapliwy, P. S., Smith, H. M., and Grant, C., 1961.—Systematic status of the geckonid lizard genera *Gehyra*, *Peropus*, *Hoplodactylus* and *Naultinus*. *Herpetologica*, 17 : 5–12.

Cocude-Michel, M., 1963.—Les rhynchocéphales et les sauriens des calcaires lithographiques (Jurassique supérieur) d'Europe occidentale. *Nouv. Archs. Mus. Hist. nat. Lyon*, 7 : 1–187.

Cogger, H. G., 1964.—The comparative osteology and systematic status of the gekkonid genera *Afroedura* Loveridge and *Oedura* Gray. Proc. Linn. Soc. N.S.W., 89 : 364–372.

————, 1967.—*Australian Reptiles in Colour.* Sydney : Reed.

COLBERT, E. H., 1966.—A gliding reptile from the Triassic of New Jersey. *Am. Mus. Novit.*, (2246): 1–23.

COLE, C. J., 1970.—Karyotypes and evolution of the *spinosus* group of lizards in the genus *Sceloporus*. *Am. Mus. Novit.*, (2431): 1–47.

————, 1971*a*.—Karyotypes of the five monotypic species groups of lizards in the genus *Sceloporus*. *Am. Mus. Novit.*, (2450): 1–17.

————, 1971*b*.—Karyotypes and relationships of the *pyrocephalus* group of lizards in the genus *Sceloporus*. *Herpetologica*, 27: 1–8.

COLLESS, D. H., 1971.—" Phenetic ", " phylogenetic " and " weighting ". *Syst. Zool.*, 20: 73–76.

CROVELLO, T. J., 1967.—Problems in the use of electronic data processing in biological collections. *Taxon*, 16: 481–494.

DE BEER, G. R., 1958.—*Embryos and Ancestors.* 3rd Edition. Oxford: Clarendon Press.

EL-GAZZAR, A., WATSON, L., WILLIAMS, W. T., and LANCE, G. N., 1968.—The taxonomy of *Salvia*: a test of two radically different numerical methods. *J. Linn. Soc.* (*Bot.*), 60: 237–250.

EL-TOUBI, M. R., and KHALIL, A., 1950.—Caudal ribs in geckos. *Nature, Lond.*, 166: 1120.

————, 1955.—The post-cranial osteology of Egyptian geckos. *Bull. Inst. Désert*, 5: 99–136.

ETHERIDGE, R., 1967.—Lizard caudal vertebrae. *Copeia*, 1967: 699–721.

FOX, R. C., and BOWMAN, M. C., 1966.—Osteology and relationships of *Captorhinus aguti* (Cope) (Reptilia: Captorhinomorpha). *Paleont. Contr. Univ. Kans.* (*Vertebrata*), Art. 11: 1–79.

GOODRICH, E. S., 1930.—*Studies on the Structure and Development of Vertebrates.* First Edition, reprinted 1958 in 2 vols. New York: Dover.

GORMAN, G. C., HUEY, R. B., and WILLIAMS, E. E., 1969.—Cytotaxonomic studies on some unusual iguanid lizards assigned to the genera *Chamaeleolis*, *Polychrus*, *Polychroides* and *Phenacosaurus*, with behavioral notes. *Breviora*, (316): 1–17.

————, WILSON, A. C., and NAKANISHI, M., 1971.—A biochemical approach towards the study of reptilian phylogeny: Evolution of serum albumin and lactic dehydrogenase. *Syst. Zool.*, 20: 167–185.

GUGG, W., 1939.—Der Skleralring der plagiotremen Reptilien. *Zool. Jb.* (*Anat.*), 65: 339–416.

HOFFSTETTER, R., 1953.—Les sauriens anté-crétacés. *Bull. Mus. natn. Hist. nat. Paris.*, sér. 2, 25: 345–352.

————, 1955.—Rhynchocéphalia. *In: Traité de Paléontologie*, Vol. 5, Amphibiens, Reptiles et Oiseaux, pp. 556–576. Edited by J. Piveteau. Paris: Masson.

————, 1962.—Revue des récentes acquisitions concernant l'histoire et la systématique des squamates. *Colloques int. Cent. natn. Rech. Scient.*, 104: 243–278.

————, 1964.—Les sauria du Jurassique supérieur et spécialement les Gekkota de Bavière et de Mandchourie. *Senckenberg. biol.*, 45: 281–324.

————, 1967.—Coup d'oeil sur les sauriens (=lacertiliens) des couches de Purbeck (Jurassique supérieur d'Angleterre). *Colloques int. Cent. natn. Rech. scient.*, (163): 349–371.

————, and GASC, J.-P., 1969.—Vertebrae and ribs of modern reptiles. *In: Biology of the Reptilia*, Vol. 1, pp. 201–310. Edited by C. Gans, A. d'A. Bellairs and T. S. Parsons. London: Academic Press.

HOLDER, L. A., 1960.—The comparative morphology of the axial skeleton in the Australian Gekkonidae. *J. Linn. Soc.* (*Zool.*), 44: 300–335.

HOWES, G. B., and SWINNERTON, H. H., 1901.—On the development of the skeleton of the tuatara, *Sphenodon punctatus*: with remarks on the egg, on the hatching, and on the hatched young. *Trans. zool. Soc. Lond.*, 16: 1–86.

INGER, R. F., 1967.—The development of a phylogeny of frogs. *Evolution*, 21: 369–384.

KINGHORN, J. R., 1926.—A brief review of the family Pygopodidae. *Rec. Aust. Mus.*, 15: 40–64.

KLUGE, A. G., 1962.—Comparative osteology of the eublepharid lizard genus *Coleonyx* Gray. *J. Morph.*, 110: 299–332.

————, 1967*a*.—Higher taxonomic categories of gekkonid lizards and their evolution. *Bull. Am. Mus. nat. Hist.*, 135: 1–59.

————, 1967*b*.—Systematics, phylogeny, and zoogeography of the lizard genus *Diplodactylus* Gray (Gekkonidae). *Aust. J. Zool.*, 15: 1007–1108.

————, and FARRIS, J. S., 1969.—Quantitative phyletics and the evolution of anurans. *Syst. Zool.*, 18: 1–32.

KUHN-SCHNYDER, E., 1954.—The origin of lizards. *Endeavour*, 13: 213–219.

LEONE, C. A. (Ed.), 1964.—*Taxonomic Biochemistry and Serology.* New York: Ronald Press.

McDOWELL, S. B., and BOGERT, C. M., 1954.—The systematic position of *Lanthanotus* and the affinities of the anguinomorphan lizards. *Bull. Am. Mus. nat. Hist.*, 105: 1–142.

McPHEE, D. R., 1959.—*Snakes and Lizards of Australia.* Brisbane: Jacaranda Press.

MADERSON, P. F. A., 1971.—Personal communication.

————, and CHIU, K. W., 1970.—Epidermal glands in gekkonid lizards: evolution and phylogeny. *Herpetologica*, 26: 233–238.

MAURER, F., 1896.—Die ventrale Rumpfmuskulatur einiger Reptilien. Eine vergleichend-anatomische Untersuchung. *In: Festschrift zum siebenzigsten Geburtstages von Carl Gegenbaur*, Vol. 1, pp. 183–256. Leipzig.

———, 1898.—Die Entwicklung der ventralen Rumpfmuskulatur bei Reptilien. *Morph. Jb.*, 26 : 1–60.

Mayr, E., 1964.—The new systematics. *In : Taxonomic Biochemistry and Serology*, pp. 13–32. Edited by C. A. Leone. New York : Ronald Press.

———, 1965.—Classification and phylogeny. *American Zoologist*, 5 : 165–174.

———, 1969.—*Principles of Systematic Zoology.* New York : McGraw-Hill.

Miller, M. R., 1966.—The cochlear duct of lizards. *Proc. Calif. Acad. Sci.*, Ser. 4, 33 : 255–359.

Mitchell, F. J., 1958.—Adaptive convergence in Australian reptiles. *Aust. Mus. Mag.*, 12 : 314–317.

———, 1965.—Australian geckos assigned to the genus *Gehyra* Gray (Reptilia, Gekkonidae). *Senckenberg. biol.*, 46 : 287–319.

Moffat, L. A., 1972.—The phylogenetic significance of notochordal centra in amphibians and reptiles : A comparative study of vertebral morphology and development in *Leiopelma* (Amphibia : Anura) and the Gekkota (Reptilia : Lacertilia). Ph.D. thesis in Zoology, University of Sydney, Australia.

Myers, G. S., 1961.—The New Zealand lizard names *Naultinus* and *Hoplodactylus. Herpetologica*, 17 : 169–172.

Noble, G. K., and Klingel, G. C., 1932.—The reptiles of Great Inagua Island, British West Indies. *Am. Mus. Novit.*, (549) : 1–25.

Pennock, L. A., Tinkle, D. W., and Shaw, M. W., 1968.—Chromosome number in the lizard genus *Uta* (Family Iguanidae). *Chromosoma*, 24 : 467–476.

Peyer, B., and Kuhn-Schnyder, E., 1955.—Squamates du Trias. *In : Traité de Paléontologie*, Vol. 5, Amphibiens, Reptiles et Oiseaux, pp. 578–605. Edited by J. Piveteau. Paris : Masson.

Rensch, B., 1959.—*Evolution Above the Species Level.* London : Methuen.

Ritland, R. M., 1955.—Studies on the postcranial morphology of *Ascaphus truei.* I—Skeleton and spinal nerves. *J. Morph.*, 97 : 119–178.

Robinson, P. L., 1962.—Gliding lizards from the Upper Keuper of Great Britain. *Proc. geol. Soc.*, (1601) : 137–146.

Romer, A. S., 1956.—*Osteology of the Reptiles.* Chicago : University Press.

———, 1966.—*Vertebrate Paleontology.* 3rd Edition. Chicago : University Press.

———, 1968.—*Notes and Comments on Vertebrate Paleontology.* Chicago : University Press.

Ruth, E. S., 1918.—A study of the calcium glands in the common Philippine house lizard. *Philipp. J. Sci.* (*B, Trop. Med.*), 13 : 311–317.

Savage, J. M., 1963.—Studies on the lizard family Xantusiidae. IV—The genera. *Contr. Sci.*, (71) : 3–38.

Shute, C. C. D., and Bellairs, A. d'A., 1953.—The cochlear apparatus of Geckonidae and Pygopodidae and its bearing on the affinities of these groups of lizards. *Proc. zool. Soc. Lond.*, 123 : 695–709.

Simpson, G. G., 1945.—The principles of classification and a classification of mammals. *Bull. Am. Mus. nat. Hist.*, 85 : i–xvi, 1–350.

———, 1961.—*Principles of Animal Taxonomy.* New York : Columbia University Press.

Smith, H. M., 1952.—A behavioral analog of brillar eyelids in spectacled geckos. *Herpetologica*, 8 : 95–96.

Smith, M. A., 1933.—Remarks on some Old World geckoes. *Rec. Indian Mus.*, 35 : 9–19.

———, 1935.—*The Fauna of British India, including Ceylon and Burma. Reptilia and Amphibia.* Vol. 2, Sauria, pp. 1–440. Edited by R. B. S. Sewell. London : Taylor & Francis.

———, 1939.—Evolutionary changes in the eye coverings of certain lizards. *Proc. Linn. Soc. Lond.*, 151st Session, pp. 190–191.

Sokal, R. R., and Sneath, P. H. A., 1963.—*Principles of Numerical Taxonomy.* San Francisco : Freeman.

Sporne, K. R., 1954.—Statistics and the evolution of dicotyledons. *Evolution*, 8 : 55–64.

———, 1956.—The phylogenetic classification of the angiosperms. *Biol. Rev.*, 31 : 1–29.

Stephenson, N. G., 1960.—The comparative osteology of Australian geckos and its bearing on their morphological status. *J. Linn. Soc.* (*Zool.*), 44 : 278–299.

———, 1961.—The comparative morphology of the head skeleton, girdles and hind limbs in the Pygopodidae. *J. Linn. Soc.* (*Zool.*), 44 : 627–644.

———, and Stephenson, E. M., 1956.—The osteology of the New Zealand Geckos and its bearing on their morphological status. *Trans. R. Soc. N.Z.*, 84 : 341–358.

Szarski, H., 1962.—The origin of the Amphibia. *Q. Rev. Biol.*, 37 : 189–241.

Tarlo, L. B. H., 1967.—Triassic reptiles from the shores of Tethys. Systematics Assoc. Publ. No. 7, Aspects of Tethyan Biogeography, pp. 103–109. Edited by C. G. Adams and D. V. Ager.

———, 1968.—An outline classification of the Squamata. *Br. J. Herpet.*, 4 : 32–35.

Taylor, E. H., and Leonard, A. B., 1956.—Concerning the relationship of certain neotropical gekkonid lizard genera, with comments on the microscopical structure of their glandular scales. *Kans. Univ. Sci. Bull.*, 38 : 1019–1029.

Tinkle, D. W., Wilbur, H. M., and Tilley, S. G., 1970.—Evolutionary strategies in lizard reproduction. *Evolution*, 24 : 55–74.

Underwood, G., 1954.—On the classification and evolution of geckos. *Proc. zool. Soc. Lond.*, 124 : 469–492.

————, 1957.—On lizards of the family Pygopodidae. A contribution to the morphology and phylogeny of the Squamata. *J. Morph.*, 100 : 207–268.

————, 1970.—The Eye. *In : Biology of the Reptilia*, Vol. 2, pp. 1–97. Edited by C. Gans and T. S. Parsons. London : Academic Press.

Vanzolini, P. E., 1968*a*.—Lagartos Brasileiros da familia Gekkonidae (Sauria). *Arq. Zool. S. Paulo*, 17 : 1–84.

————, 1968*b*.—Geography of the South American Gekkonidae (Sauria). *Arq. Zool. S. Paulo*, 17 : 85–112.

Vaughn, P. P., 1955.—The Permian reptile *Araeoscelis* restudied. *Bull. Mus. comp. Zool. Harv.*, 113 : 305–467.

Wagner, W. H., Jr., 1961.—Problems in the classification of ferns. *In : Recent Advances in Botany.* From Lectures and Symposia presented to the IX International Botanical Congress, Montreal, 1959, Vol. 1, Sect. 9 : 841–844. Toronto : University Press.

Walls, G. L., 1942.—The vertebrate eye and its adaptive radiation. *Bull. Cranbrook Inst. Sci.*, (19) : i–xiv, 1–785. Bloomfield Hills, Michigan : Cranbrook Press.

Watson, L., Williams, W. T., and Lance, G. N., 1966.—Angiosperm taxonomy : a comparative study of some novel numerical techniques. *J. Linn. Soc.* (*Bot.*), 59 : 491–501.

Wermuth, H., 1965.—Liste der rezenten Amphibien und Reptilien : Gekkonidae, Pygopodidae, Xantusiidae. *In : Das Tierreich*, Lief. 80, pp. 1–246. Berlin : Walter de Gruyter.

Werner, Y. L., 1956.—Chromosome numbers of some male geckos (Reptilia : Gekkonoidea). *Bull. Res. Coun. Israel*, 5B : 319.

————, 1961.—Remarks on the evolution of geckos (Reptilia : Gekkonoidea). *Bull. Res. Coun. Israel*, 9B : 198–199.

————, 1971.—The ontogenic development of the vertebrae in some gekkonoid lizards. *J. Morph.*, 133 : 41–92.

Whiteside, B., 1922.—The development of the *saccus endolymphaticus* in *Rana temporaria* Linné. *Am. J. Anat.*, 30 : 231–266.

Wilson, E. O., 1965.—A consistency test for phylogenies based on contemporaneous species. *Syst. Zool.*, 14 : 214–220.

Worrell, E., 1963.—*Reptiles of Australia.* Sydney : Angus & Robertson.

Appendix

As Kluge's (1967*a*) data regarding the occurrence of character-states in the Gekkonidae are also used by the present author to deduce a phylogeny of geckos which differs from that proposed by Kluge, it is necessary to reconsider his characters and the character-states he regarded as primitive within this group. The following four characters were rejected in the present investigation because they are still too poorly known to be used in the phylogenetic classification of geckos.

Vocal ability and Number of eggs laid (=clutch size)—Kluge's decisions regarding the primitive and advanced states of these characters were based on cursory observations and his 4th Criterion of Primitiveness. Tinkle, Wilbur and Tilley (1970) claimed that the reproductive strategies of eight families of non-gekkotan lizards bear no relation to their taxonomic arrangement, and that clutch size is positively correlated with snout-vent length at maturity. As the Sphaerodactylinae are small geckos and the genus *Lepidoblepharis* contains the smallest of all known Recent lizards (Vanzolini, 1968*b*), the laying of one egg by sphaerodactylines and the laying of two by other geckos (Kluge, 1967*a*) would appear to have no phylogenetic significance.

Escutcheon scales—Kluge's (1967*a*) contention that escutcheon scales have evolved from preanal organs in geckos, based on his 4th Criterion of Primitiveness, contradicts the earlier opinions of Noble and Klingel (1932) and Taylor and Leonard (1956) that the reverse is true in these and other lizards, while Maderson and Chiu (1970) postulated that glandular scales and preanal organs have evolved independently from unspecialized epidermis. Maderson and Chiu (1970) also pointed out that macroscopically similar epidermal glands in geckos may represent parallel adaptive trends involving different parts of the epidermis and that great care should therefore be exercised in using glandular structures in systematic investigations.

POSTCRANIAL ENDOLYMPHATIC APPARATUS—Calcareous material is produced by the endolymphatic apparatus of all classes of vertebrates (Whiteside, 1922) and calcified postcranial endolymphatic sacs occur in some iguanids and the Xantusiidae as well as many geckos (Camp, 1923). Some evidence exists that calcified sacs occur only in females (Kluge, 1967*a*, Pl. 5, figs 2, 3) and that their calcification is seasonal and associated with eggshell formation (Ruth, 1918). As nothing is known of the detailed structure of the endolymphatic apparatus in geckos or of the existence of uncalcified postcranial sacs in geckos which lack calcified sacs (Kluge, 1967*a*), the primitive or advanced nature of the latter within the Gekkonidae cannot be determined.

The following 14 characters are used in the present investigation but the states of the frontal and parietal bones of the skull, the number of scleral ossicles and form of the vertebral centrum which are considered here to be primitive among geckos were regarded by Kluge (1967*a*) as advanced.

SKULL ROOFING BONES: PREMAXILLAE, NASALS, FRONTALS, PARIETALS—The paired condition should be regarded as the primitive (=original) state of these bones in the Squamata because they were paired in cotylosaurs, eosuchians and other early lepidosaurs and are also paired in some living lizards (Romer, 1956; Robinson, 1962). However, from the variation seen in living geckos in the occurrence of the paired and fused states of the different skull roofing bones and the variation in the stage of ontogeny at which fusion occurs (see Brock, 1932; Stephenson, 1960; Kluge, 1967*a*, 1967*b*), it is clear that heterochrony (de Beer, 1958) has contributed to the cranial evolution of geckos. Neoteny in the broad sense, which is only one of eight possible types of heterochrony as recognized by de Beer, has also been an important factor in gekkonid evolution (Stephenson and Stephenson, 1956; Stephenson, 1960, 1961). Therefore the paired state of any of the skull roofing bones in living geckos may represent a persistent ancestral condition in some forms and a secondarily derived condition in others. For the sake of parsimony, however, it should be regarded as primitive, irrespective of the number of genera possessing it, unless there is evidence to show that it has arisen secondarily.

NUMBER OF SCLERAL OSSICLES PER EYE—Although Kluge (1967*a*) regarded an ossicle count in the low- to mid-twenties as primitive in geckos, it is clear from his own data and discussion, as well as from the presence of 14 scleral ossicles in eosuchians (Underwood, 1970), that the primitive number is 14 or therabouts. According to Gugg (1939), the number of scleral ossicles in living squamates and *Sphenodon* shows little variation about 14, but he did not examine any of the indigenous Australian geckos placed by Kluge (1967*a*) in the Diplodactylinae. There are 14 or 15 ossicles per eye in pygopods (Underwood, 1957) and in the Xantusiidae (Savage, 1963), and 13–17 (usually 14) in Kluge's Group I of the Gekkoninae and 12–15 (usually 14) in his sphaerodactyline genera, while some members of the eublepharine genus *Coleonyx* are also listed as having 14 scleral ossicles. The higher number of ossicles found in other eublepharines (15–25), Group II of the Gekkoninae (15–28) and the Diplodactylinae (21–40) show considerably more inter- and intra-generic variation and should be regarded as advanced conditions.

FORM OF THE VERTEBRAL CENTRUM—Contrary to the opinion of Kluge (1967*a*), all the available evidence points to the primitiveness in geckos of the amphicoelous state of the centrum. As this evidence is presented in detail elsewhere (Moffat, 1972) and is intended for publication in due course, it will suffice here to summarize the main points. Notochordal amphicoelous centra were characteristic of the earliest reptiles or Cotylosauria (Vaughn, 1955; Fox and Bowman, 1966; Romer, 1966; Carroll, 1969), and also occurred in the pelycosaurian ancestors of the mammal-like reptiles and in ichthyosaurs as well as in the Eosuchia which contained the ancestors of other lepidosaurs and the Archosauria (Romer, 1956). This type of centrum is thus the original state of the centrum in reptiles and was inherited from the Eosuchia by the Rhynchocephalia, including the relatively unspecialized and conservative Sphenodontidae, of which *Sphenodon* is the only living representative (Romer, 1966 ; Hoffstetter and Gasc, 1969). As the notochordal amphicoelous centra of geckos are strikingly similar to those of *Sphenodon* in their soft anatomy as well as their bony components (see Howes and Swinnerton, 1901 ; Werner, 1971), especially when they are compared with the notochordal amphicoelous centra of some living amphibians (see Goodrich, 1930, fig. 58 ; Ritland, 1955), there can be little reasonable doubt that the Gekkonidae as well as *Sphenodon* have inherited their notochordal amphicoely from their distant cotylosaurian ancestors. Therefore the procoely of the Eublepharinae, as well as that of some non-eublepharine geckos, is an advanced gekkonid character-state.

ANGULAR, SPLENIAL, SQUAMOSAL AND SUPRATEMPORAL BONES—As these bones were present in presquamate groups of reptiles (Romer, 1956) their presence is more primitive than their absence in living geckos because the same structural elements do not reappear once they have been lost in phylogeny (Szarski, 1962). A single temporal bone has usually been identified as the supratemporal (see Stephenson, 1961) but it has also been called a tabular (McDowell and Bogert, 1954) or a squamosal (Underwood, 1957 ; Kluge, 1962). According to Romer (1956, p. 116) the position of this element relative to the parietal precludes it from being a tabular. As a comparative embryological study is required to determine whether the single temporal bone of non-eublepharine geckos is a supratemporal, or a squamosal as in some members of the Eublepharinae, Kluge's (1967*a*) contention that it is always the squamosal is provisionally accepted.

HYOID AND SECOND BRANCHIAL ARCHES—As the hyobranchial skeleton of reptiles, which serves for the attachment of throat and tongue muscles, represents part of the gill-bearing visceral skeleton of fishes (Romer, 1956), the most primitive condition of this apparatus in any group of reptiles is that which most closely approaches the piscine condition. Therefore three complete branchial arches are primitive character-states in lizards and reduction of the hyoid and second branchial arches are advanced conditions (Camp, 1923 ; Romer, 1956 ; Stephenson and Stephenson, 1956 ; Kluge, 1967*a*). Kluge's contention that three complete arches in the Gekkonidae are found only in *Coleonyx* and not also in *Naultinus* as described by Stephenson and Stephenson (1956) may stem from the recent confusion over the nomenclature of New Zealand geckos (see Chrapliwy, Smith and Grant, 1961 ; Myers, 1961), although Kluge himself used the more generally accepted names used by Smith (1933) and Wermuth (1965). It is also possible that the second visceral arch is continuous in some *Naultinus* and interrupted in others.

EYE COVERING—Bellairs and Boyd (1947) and Bellairs (1948) considered the possibility that the eyelids found in some geckos have evolved from extra-brillar fringes with loss of the brille or spectacle (Smith, 1935, 1939) and concluded that the reverse has occurred : that a brille has evolved independently in snakes and in several families of lizards including the Gekkonidae as a result of fusion of the primordia of the true eyelids.

POST-CLOACAL BONES—These elements occur in association with post-cloacal sacs in pygopods and xantusiids as well as in geckos (McDowell and Bogert, 1954 ; Underwood, 1954, 1957). According to Kluge (1967*a*) post-cloacal sacs occur in geckos of both sexes but the bones occur only in males. Post-cloacal bones are also present in male but not female pygopods (personal observation), the only exception being *Pletholax*, which had conspicuous testes but no post-cloacal bones. Therefore the presence of these bones in geckos is considered to be more primitive than their absence.

MICROBIOLOGY OF AN ASHBED

MAIJA A. RENBUŠS,*† G. A. CHILVERS† AND L. D. PRYOR†

[Accepted for publication 19th July 1972]

(Plate XI)

Synopsis

The dilution plate technique was used to evaluate changes in the microbial population of an "ashbed" soil produced by burning a logpile on the soil surface. After burning, bacteria rapidly recolonized the soil and shortly their numbers exceeded those in the unheated control soil population. Actinomycetes and fungi recolonized the soil more slowly. The early bacterial and fungal recolonizers were shown to include many types not detected in the control soil. Approximately one year was required for this distinctive "ashbed" microflora to revert to "normal". This time period correlated reasonably well with the time period during which such soil remained stimulatory to plant growth. A causal relationship is postulated.

INTRODUCTION

Forest plantations in Australia are often established in areas covered by low-yielding native forest. After removing any merchantable trees, the remainder may be bulldozed into windrows and burnt. Species of *Pinus* and *Eucalyptus* planted into the "ashbed" soil under burnt windrows usually grow very much faster than those planted into the adjacent unburnt soil. This growth response is referred to locally as the "ashbed effect" and the size discrepancy between ashbed and the other trees persists for many years, especially on poorer soils. Plate XI is an aerial photograph showing the effect in a 15-year-old stand of *Pinus radiata* growing at Dunn's Pinch in the Australian Capital Territory. Several studies of the phenomenon have been published (Forest Department, Western Australia, 1957; Hatch, 1960; Applequist, 1960; Pryor, 1963; Humphreys and Lambert, 1965; Cromer and Vines, 1966), but the immediate cause of this growth response has not been identified.

The present situation may be summed up briefly as follows: Liberal application of wood ash to unheated soil gives, at best, only a mild growth stimulus, but if soil is heated in a dry oven above 100° C it will support growth comparable to that on an ashbed (Griffith, 1946; Pryor, 1963). This suggests that the ashbed is just a special instance of a heat treated soil, and so can be related to the plant growth responses described by earlier workers such as Frank (1888) for steam heated soil and Pickering (1908) for dry heated soil. Pryor (1963) found that luxury doses of artificial fertilizers containing both nitrogen and phosphorus will also simulate the ashbed effect. Clearly, an ashbed (or other heated-soil) grown plant is better nourished than one grown on the same soil left unheated, but the underlying causes remain obscure. Arbuckle (1953) and Applequist (1960) demonstrated an increase in available phosphorus as a result of heat treating the soil, but no one has reported an increase in inorganic nitrogen. A general change in form of nitrogen from nitrate to ammonia has been widely reported (*e.g.* Kelly and McGeorge, 1913; Tam and Clark, 1943) but the evidence suggests that there may be a net reduction in total inorganic nitrogen, so the answer is unlikely to be resolved in terms of simple arithmetical changes in the absolute quantity of plant nutrients within the soil.

---

† Botany Department, School of General Studies, Australian National University, Canberra, Australia.

* Now Maija A. Carty.

Two other forms of soil treatment are known to give similar, though perhaps less dramatic, growth responses to heating. These are gas fumigation (*e.g.* Tam and Clark, 1943) and gamma irradiation (*e.g.* Bowen and Rovira, 1961*a*). It seems reasonable to conclude that the sterilizing effect upon soil organisms, which is the immediate and common result of all these diverse treatments, is causally linked with the subsequent plant growth response. This is not to deny that in ashbed soils there are additional factors operating such as the release of inorganic phosphorus from the mineral fraction or the addition of cations in the ash, but these would seem to be contributory only.

The following study was made to evaluate the degree of sterilization and the resulting major changes in the microbial population of an ashbed. The only relevant information available is by Wright and Tarrant (1957), who reported that after logging and burning there was an increase in total numbers of bacteria and actinomycetes together with a decrease in the relative abundance of actinomycetes. No records of changes in the fungal population have been found and in particular there is no indication of how long such alterations in the population persist. In this study, continuous estimations of bacterial, actinomycete and fungal numbers were made during the 15 months following a burn. In addition, some qualitative comparisons were made of fungal and bacterial populations between ashbed and control soils. Simultaneous data were collected on plant growth responses.

MATERIALS AND METHODS

Preparation of the ashbed

A small area of rather poor, fine-sandy loam was selected near the edge of the Australian National University campus and cultivated thoroughly to mix the surface soil. It was then raked smooth and subdivided into four 5 × 5 ft blocks. Eucalypt logs were carefully stacked to a height of 5 ft in the form of a single pile straddling and overlapping two of the blocks. The adjacent control blocks were covered with reflective material to protect them from radiant heat and the woodpile then set alight. Temperatures under the centre of the fire were recorded continuously at various depths by means of buried thermocouples wired back to a metering unit. At the conclusion of the fire, the unburnt woody residues were raked off the ashbed and all four blocks were delineated by a 5 × 5 ft square of 6 in mesh reinforcing iron, subdividing each block into 100 smaller squares for sampling purposes. Two days after the fire, the plots were spray-irrigated to initiate biological activity in the dry ashbed plot.

Quantitative evaluation of soil micro-organisms

(i) Sampling soil—To minimize disturbance of the experimental plots, the following method of sampling was adopted after preliminary trials had shown it capable of giving reproducible results. From each block, 10 of the mesh subdivisions were selected by use of a table of random numbers. A soil sample was collected from each of these subdivisions by pushing a 2 cm diameter metal tube 8 cm into the soil and the soil core knocked out into a sterile tube for transport to the laboratory. The cores were broken up and 2 g of soil subsampled from each one. The 10 subsamples were then bulked to give a 20 g sample for the block. The residual soil was also bulked and the mean moisture content determined.

(ii) Estimating microbial numbers.—The dilution plate method was used since it produces the maximum amount of quantitative data and at the same time provides colonies of micro-organisms for qualitative evaluation. The 20 g bulked soil sample was dispersed by shaking in 200 ml of sterile water and a tenfold dilution series prepared. From appropriate dilutions, sets of five replicate plates were prepared for bacterial and actinomycete counts and 10 plates for fungi. Bacteria and actinomycetes were isolated in a modification of Thornton's Standardized Medium (Thornton, 1922) containing mineral salts, glucose (1·0 g/l.) and " Difco Neopeptone " (0·5 g/l.), with a pH of 7·0. Fungi were isolated in a similarly based medium containing more glucose and " Neopeptone " (10 and 5 g/l.), with 30 mg/l. of rose bengal and streptomycin to inhibit bacterial growth, with a pH of 5·5.

Qualitative evaluation of soil micro-organisms

(i) Fungi.—Fungal colonies were identified by direct microscopic examination. Where a colony could not readily be keyed down to species level, subcultures were number coded and kept for subsequent comparative purposes.

(ii) Bacteria.—Bacteria are not amenable to such direct treatment and a continuous comparison could not be made. The ten-week sample was evaluated as follows : One plate from each of the blocks was selected to contain approximately 50 bacterial colonies which were subcultured on to slopes. When grown, each streak was dispersed in sterile solution to produce a liquid inoculum which was poured over an agar plate. After a minute this inoculum was poured off and the plate allowed to dry for half an hour. An " Oxoid Multodisk " with eight tips containing various standard antibiotic samples was placed in the centre of each plate. After four days' incubation at 25° C, the zone of inhibition around each antibiotic tip was recorded. The pattern of response to the eight antibiotics is constant under such standardized conditions and was used as a method of " typing " or " finger-printing " the isolates.

Evaluation of plant growth response

To confirm that this particular soil could respond with an " ashbed effect ", an ashbed plot and a control plot were each planted with nine eucalypt seedlings previously grown to about 30 cm height in pots of peat moss. No nutrients had been added to these seedlings for the previous month so that little or no nutrients were added to the soil in transplanting. The heights of these trees were recorded at frequent intervals. Soil samples were also collected from various depths, potted and planted with smaller seedlings for a glasshouse experiment.

To obtain data on the rate of decline of the stimulatory properties of this soil when treated, it was necessary to substitute a controlled heat treatment for ashbedding. Samples of the same soil were collected at monthly intervals and heated in an oven to 150° C for three hours. Half of this soil was placed in pots and subjected to a weekly watering. The rest was stored dry. All samples were inoculated with unheated soil at the rate of 5 g per pot. After five months, all pots were given several heavy waterings, then planted with 5 cm high eucalypt seedlings. Twelve replicates were provided for each treatment and the pots were randomized at weekly intervals during the growth period of nine weeks. At the end of this period all plants were carefully washed clean of soil and dry weights determined.

RESULTS

The sterilizing effect of the fire

Figure 1 shows the maximum temperature attained at different depths in the soil during the course of the fire. All depths sustained a temperature of at least 100° C for more than six hours. Temperatures at depths down to 15 cm were clearly lethal to all life forms and all vegetative cells could be expected to die down to 20 cm, the lowest depth to which temperature probes were placed.

Microbial assays performed on single soil cores taken before and immediately after the fire showed that the soil was apparently sterilized down to 25 cm depth.

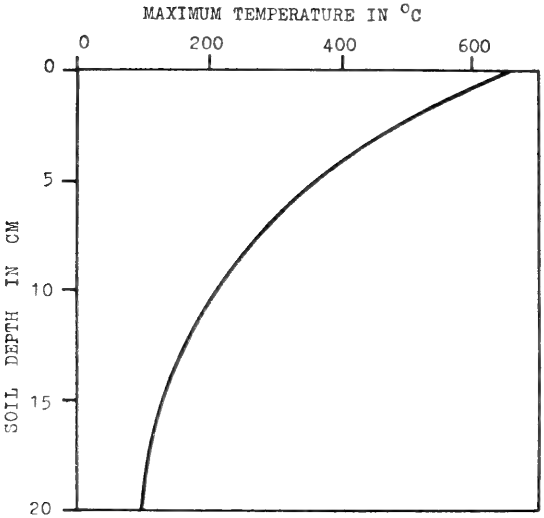


Fig. 1.—Profile of temperature maxima attained under log fire set to produce an experimental ashbed.

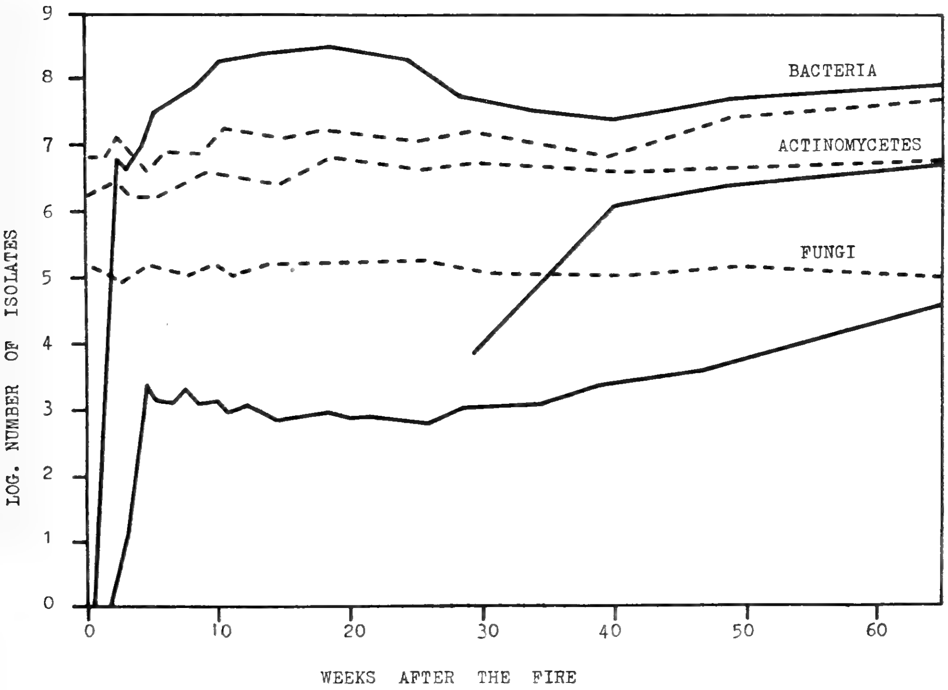


Fig. 2. Changes in the mean number of microbial colonies isolated from ashbed and control soils with time. Solid graph lines refer to the ashbed soil and broken lines to the control soil population.

Quantitative changes in the soil microbial population

Figure 2 shows the progressive changes in numbers of bacteria, actinomycetes and fungi respectively. The eucalypt planted and unplanted plots (both ashbed and control) gave similar populations at all times so that the presence of plants appears to have little relevance to the general soil population even during the recolonization phase. The planted and unplanted plots were consequently treated as replicates for microbial estimations in order to economize on assays. Microbial populations in the control soil showed very little variation throughout the sampling period. In the ashbed soil, the most dramatic change occurred in bacterial numbers which had returned to their original level within one week and within a month exceeded it tenfold. Bacterial numbers continued to rise to a peak after 18 weeks then declined slowly toward normal. Forty-eight weeks after the fire they were not significantly different from the control populations. Actinomycetes were the slowest group to reappear in the ashbed (first record 29 weeks after the fire) but then increased rapidly to approach the control population by 48 weeks. Fungi reappeared within three weeks, increasing in numbers rapidly at first, but after six weeks the population growth was checked until the following spring. It was still rising slowly 66 weeks after the fire, at which time numbers had still not quite returned to normal. This check in the fungal recolonization process was the only effect that coincided with seasonal changes, unless the slow return of the actinomycetes was brought about by the low winter temperature.

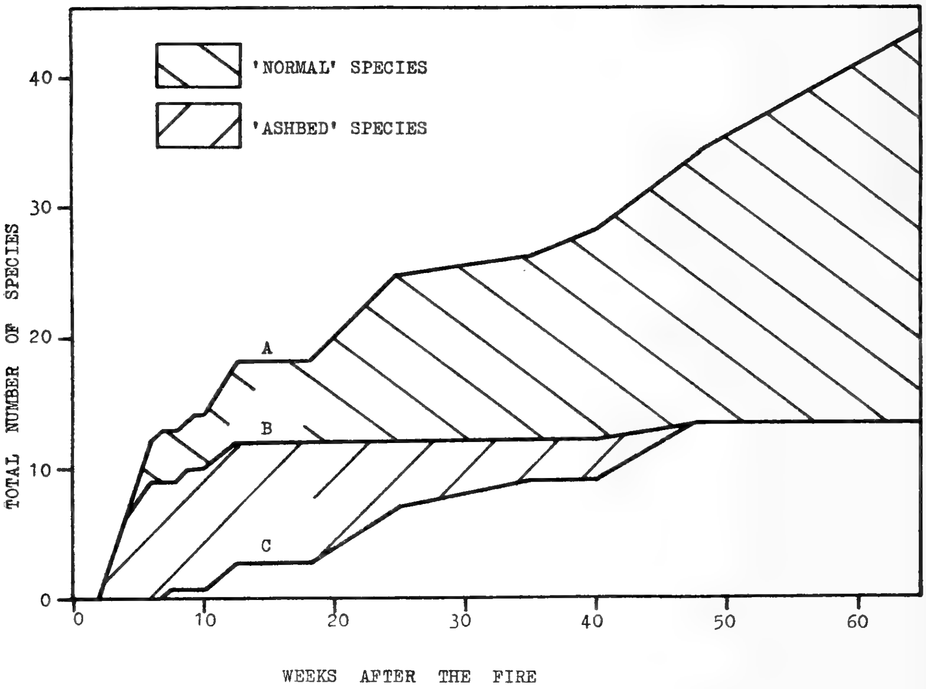


Fig. 3. Recolonization of the ashbed soil by fungi. A, Cumulative total of all species isolated. B, Cumulative total of species peculiar to the ashbed. C, Cumulative total of specie which disappeared from the isolation plates during the study.

Qualitative changes in the microbial populations

(i) Actinomycetes.—The complete absence of actinomycetes from ashbed dilution plates during the first six months was the most prominent qualitative difference between the microbial populations of ashbed and control soils. Because actinomycetes were estimated on the same plates as bacteria, it would not have been possible to detect them until they attained one-thousandth of the bacterial population ; so that they were probably building up slowly for some time before their first recording on the twenty-ninth week.

Some prominent actinomycetes were selected from the control soil and inoculated on to sterile eucalypts grown in sand culture by the method of Bowen and Rovira (1961*b*). No significant effects on plant growth were produced by these inoculations.

(ii) Fungi.—A total of 33 species of fungus was isolated from the control soil dilution plates. These appeared with remarkable constancy in both planted and unplanted plots throughout the experiment. This " normal " population provided a standard against which changes in the ashbed population could be continuously calibrated.

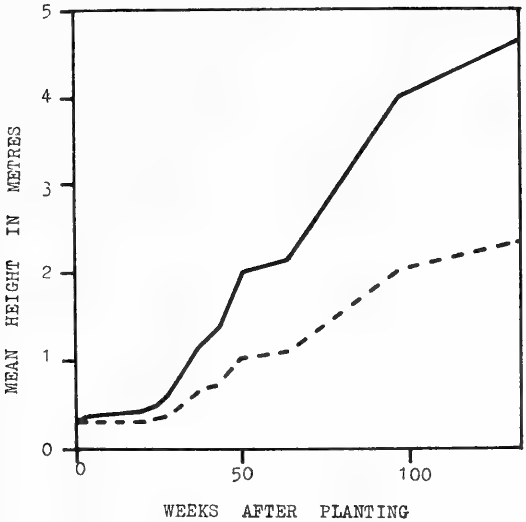


Fig. 4. Mean growth curves of eucalypts planted into ashbed and adjacent control soil. The solid graph line refers to the ashbed trees and the broken line to control trees.

Figure 3 shows the change in species composition during the recolonizing process. The first colonizers were never recorded in the control soil. Species typical of the control population soon appeared, however, and progressively replaced the " ashbed " species so that 48 weeks after recolonization commenced none of the latter could be detected. After 66 weeks all but three of the " control " species had returned to the soil.

(iii) Bacteria.—Ten weeks after the burn, when bacterial numbers were at a peak, antibiotic typing of bacterial isolates gave the following results : 55% of the isolates from the ashbed were shared by both plots and 72% of the isolates from control soil were also common to both plots, showing overall a reasonably good coincidence between replicates of the same population. When the ashbed and control plots were compared, however, only 26% of the isolates were common to both, indicating that the ashbed population was substantially different in composition from the control soil population. The ashbed isolates in general differed in having greater resistance to antibiotics.

Plant growth response in the ashbed

The growth of eucalypt trees on ashbed and control plots was recorded over a period of three years (Fig. 4). At the end of this time the ashbed grown trees were approximately double the height of the controls.

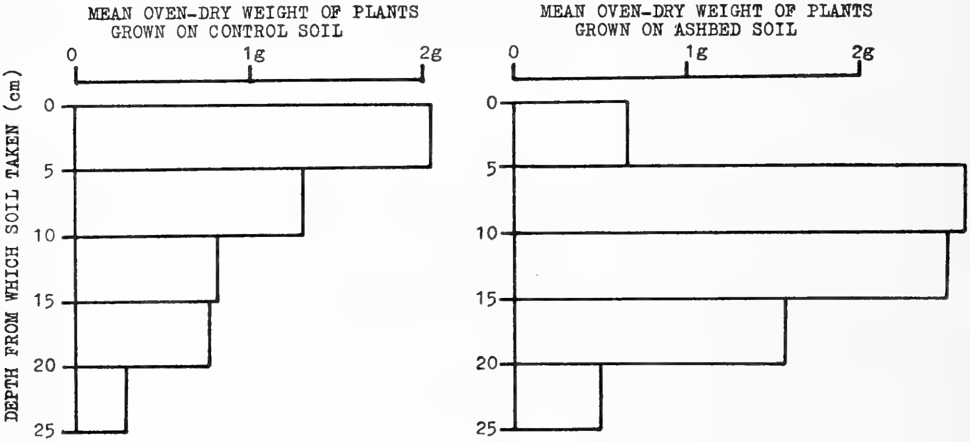


Fig. 5. Comparison of four-month-old eucalypt seedlings grown in pots upon different layers of soil taken from ashbed and adjacent control sites. Each histogram represents the mean of eight replicates.

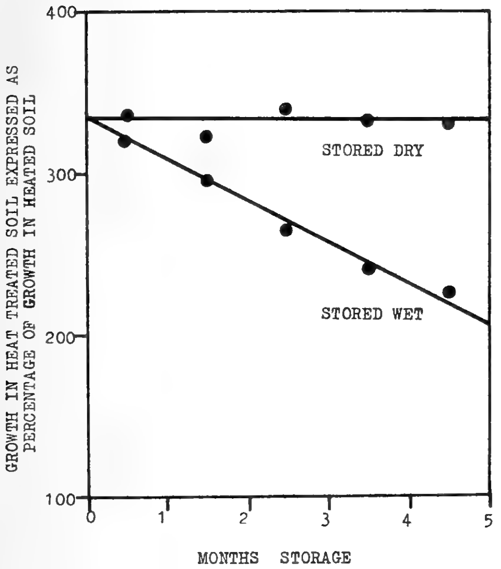
Figure 5 shows the growth of eucalypt seedlings planted into pots of ashbed and control soil recovered from different depths immediately after the burn. The topmost layer of ashbed soil, which contained ash from the fire and was the only one to show an increase in pH, was inhibitory to plant growth when compared with the control. All other layers of ashbed soil showed improved growth over the control, the greatest relative stimulation occurring in the 10–15 cm depth. The microbial samples taken earlier combine inhibitory soil from the topmost layer with stimulatory soil from the second layer.

Soil from a position close to the ashbed site, which was dry heated in an oven to 150° C to simulate the original burn (a comparison of Figs 1 and 5 indicates that this is close to the optimum), gave an enhanced growth response similar to that for ashbed soil. To obtain some estimate of the rate at which the soil stimulatory properties decayed, further dry heated samples were prepared and then stored for different periods. Figure 6 showed that heated soil, when stored dry, retained its stimulatory power unaltered over the storage period. Soil stored wet exhibited a linear decline in potency, of which half had been dissipated in five months. Extrapolation of this result suggests that after 10 months the soil would no longer stimulate additional plant growth.

It is worthy of note that ashbed and heated-soil grown plants all had very well developed fine root systems. Indeed, between different experiments a close linear correlation was obtained between oven-dry weight of the test plants and the number of fine root tips counted.

DISCUSSION

Although an " ashbed effect " may be registered in plant growth differences for as long as 10 years after the initial burn, it is clear that the " ashbed-factors " which generate this effect need not be nearly as persistent. Some idea of their period of operation may be gained from an analysis of growth curves of affected and control plants. The most complete data on ashbed growth response has been collected by Humphreys and Lambert (1965) and their cumulative height curves of *Pinus radiata* grown at Sunny Corner, N.S.W., on ashbeds and adjacent unaffected soils are of special interest. Ashbed trees outgrew the controls, acquiring a substantial height advantage that was maintained for more than 10 years. However, when their graphs are compared along the " age " axis it is apparent that for trees above 4 ft in height the growth curves of both ashbed and control trees are nearly identical in shape and differ significantly only by their separation in time. In effect, the ashbed trees apparently acquired a " time lead " of approximately 15 months over the controls during the first few years of growth. Points read off from Humphreys and Lambert's graphs have been used to calculate the curve in Fig. 7, which shows that the time lead of the ashbed trees was acquired in a non-linear manner, rapidly at first, then tailing off asymptotically. It is concluded from this that the factors which are responsible for the growth stimulus in ashbed soils are mainly active within the first year's growing period. The present small ashbed experiment did not provide tree growth data suitable for such an analysis. However, the alternative approach to the problem (Fig. 6) suggested a survival time for ashbed factors of a similar order to the above. Interestingly, though, the first approach suggests that the ashbed factors influence the plant growth logarithmically while the second method implies a linear rate of decay of these factors.



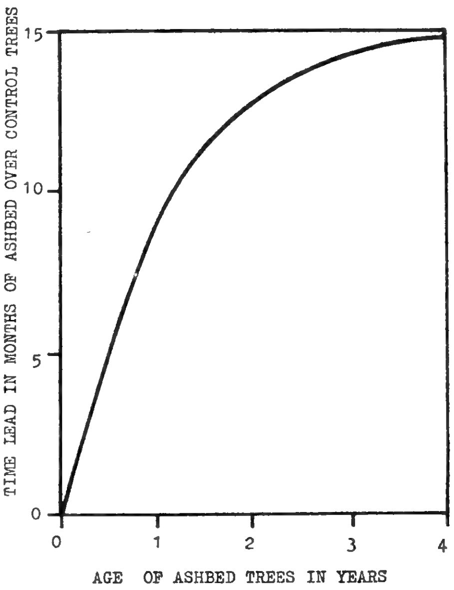


Fig. 6. Growth response of nine-week-old eucalypt seedlings raised in heat-treated soil which has been stored for varying lengths of time.

Fig. 7. Cumulative time lead of ashbed trees over control trees. Calculated from *P. radiata* height data of Humphreys and Lambert (1965).

The short survival time imputed for the main ashbed factors from the above considerations makes even more attractive the introductory argument that the ashbed effect owes much to the sterilizing event. In particular, the general coincidence between the duration of the distinctive ashbed microflora and these factors (of the order one year) suggests a causal relationship. This would probably repay more detailed investigation, especially in relation to microbiological changes in the rhizosphere region. Conceivably, such a change in the microflora could result in a period of reduced competition with roots for plant nutrients, or perhaps there is less direct antagonism towards the plant. Present knowledge does not permit a decision between this hypothesis and the alternative interpretation that the plant growth and the distinctive microflora are parallel symptoms of other underlying changes in the physical or chemical composition of the soil.

ACKNOWLEDGEMENTS

Our thanks are due to Mr. W. Roberts of the Forestry Research Institute, Canberra, for recording soil temperatures during the burn.

This work was carried out while one of us (M.A.R.) held an A.N.U. Research Scholarship.

References

APPLEQUIST, M. B. (1960).—Effects of cleared-and-burned hardwood slash on growth of planted loblolly pine in Livingston Parish, Louisiana. *J. For.*, 58 : 899.

ARBUCKLE, R. H. (1953).—Phosphate—Change in availability in soils with temperature. N.Z.D.S.I.R. Soil Bureau Bulletin (n.s.), 8 : 51.

BOWEN, G. D., and ROVIRA, A. D. (1961*a*).—Plant growth in irradiated soils. *Nature*, 191 : 936.

BOWEN, G. D., and ROVIRA, A. D. (1961*b*).—The effects of micro-organisms on plant growth. I. Development of roots and root hairs in sand and agar. *Plant and Soil*, 15 : 166.

CROMER, R. N., and VINES, R. G. (1966).—Soil temperatures under a burning windrow. *Aust. For. Res.*, 2A.

FOREST DEPARTMENT, W.A. (1957).—" Ashbed Effect." Rep. For. Dept. W. Aust., 1956–7, p. 22.

FRANK, A. B. (1888).—Über den Einfluss welchen das sterilisieren des Erdbodens auf die Pflanzen-Entwickelung ausübt. *Ber. Deut. Bot. Gesell.*, 6 : 87. Cited by Kopeloff and Coleman (1917).

GRIFFITH, A. L. (1946).—The effects of burning on the soil as a preliminary to artificial regeneration. Indian Forest Bull. No. 130. Dehra Dun.

HATCH, A. B. (1960).—Ashbed effects in Western Australia forest soils. *W.A. For. Dept. Bull.* No. 64.

HUMPHREYS, F. R., and LAMBERT, M. J. (1965).—An examination of a forest site which has been exhibiting the ashbed effect. *Aust. J. Soil Res.*, 3 : 81.

KELLY, W. P., and MCGEORGE, W. (1913).—The effect of heat on Hawaiian soils. Hawaii Agric. Exp. Sta. Bull. No. 30.

PICKERING, S. U. (1908).—Studies on germination and plant growth. *Jour. Agr. Sci.*, 2 : 411.

PRYOR, L. D. (1963).—Ashbed growth response as a key to plantation establishment. *Australian Forestry*, 27 : 48.

TAM, R. K., and CLARK, H. E. (1943).—The effect of chloropicrin and other soil disinfectants on the nitrogen nutrition of the pineapple plant. *Soil Sci.*, 56 : 245.

THORNTON, H. G. (1922).—On the development of a standardised agar medium for counting soil bacteria with especial regard to the repression of spreading colonies. *Ann. Appl. Biol.*, 9 : 241.

WRIGHT, E., and TARRANT, R. F. (1957).—Microbiological soil properties after logging and slash-burning. *Pacific Northwest For. Exp. Sta. Note* No. 157 : 5.

Aerial view of 15-year-old *P. radiata* exhibiting the "ashbed effect" at Dunn's Pinch, A.C.T. Arrows indicate position of ashbeds.

ABSTRACT OF PROCEEDINGS

Ordinary General Meeting

29th March 1972

Held in the Society's Rooms, 157 Gloucester Street, Sydney.

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

Minutes of the last Ordinary General Meeting (24th November 1971) and Special General Meeting (24th November 1971) were taken as read and confirmed.

Papers read (by title only, with an opportunity for discussion at the next Ordinary General Meeting):

A brooding Echinoid from Tasmania. By A. J. Dartnall.

Type Specimens in the Macleay Museum, University of Sydney. VI. Molluscs. By W. F. Ponder and P. J. Stanbury.

A new species of hylid frog from New South Wales. By M. J. Tyler, A. A. Martin and G. F. Watson.

Announcement:

It was announced that Council was prepared to receive applications for the Linnean Macleay Fellowship, tenable for one year from the 1st July 1972, from qualified candidates. Each applicant must be a member of this Society and be a graduate in Science or Agricultural Science of the University of Sydney. Applications must be lodged with the Secretary of the Society, who would supply further details and information.

Ordinary General Meeting

26th April 1972

Held in the Society's Rooms, 157 Gloucester Street, Sydney.

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

Minutes of the last Ordinary General Meeting (29th March 1972) were taken as read and confirmed.

An opportunity for discussion was given for papers taken as read at the March Ordinary General Meeting:

A brooding Echinoid from Tasmania. By A. J. Dartnall.

Type specimens in the Macleay Museum, University of Sydney. VI. Molluscs. By W. F. Ponder and P. J. Stanbury.

A new species of hylid frog from New South Wales. By M. J. Tyler, A. A. Martin and G. F. Watson.

Papers read (by title only):

The occurrence of root nodules in the Ginkgoales, Taxales and Conferales. By A. G. Khan and P. G. Valder.

The genetic bases for resistance in the common wheat cultivars Pusa and Mona to rye stem rust and other stem rust strains possessing unusual genes for avirulence. By A. K. Sanghi and E. P. Baker.

Evisceration and regeneration in *Thyone okeni* (Bell, 1884).

A fellodistomid Cercaria from *Mytilus planulatus*. By J. C. Walker.

Announcements:

The Nature Conservation Council of N.S.W. announced of Festival of Nature Films to be held during Earth Week, 18th–22nd September.

The Associated Portland Cement Manufacturers (Australia) Ltd. announced that their Annual General Meeting would be held on the 28th April 1972; the Colong/Bungonia issue, of interest to conservationists, would be discussed.

Address:

An address was given by Dr. A. J. Underwood, Department of Zoology, Sydney University, entitled " A New Look at Intertidal Zonation of Snails ".

ORDINARY GENERAL MEETING

28th June 1972

Held in the Society's Rooms, 157 Gloucester Street, Sydney.

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

Minutes of the last Ordinary General Meeting (26th April 1972) were taken as read and confirmed.

Papers read (by title only):

A series of oligosaccharides, occurring in the honeydew of insects, based on turanose. By R. Basden.

Grey Billy and its associates in eastern Australia. By W. R. Browne.

A new genus based on the seven-banded *Richardsonianus dawbini* Richardson 1969 (Hirudinoidea: Richardsonianidae). By L. R. Richardson.

Announcement:

The President announced that the General Monthly Meeting of the Royal Society of N.S.W. would be on Wednesday, 5th July 1972, at 7.45 p.m. An address on " Livestock Disease Control " would be given by Mr. R. A. Hall, Chief, Division of Animal Husbandry.

Programme:

The President turned the chair over to Professor R. C. Carolin, who introduced a symposium on " Sub-Urban Planning ". The participants were Mr. I. Sim, Planning Officer for the State Planning Authority of N.S.W.; Mr. A. Rappaport, Senior Lecturer in Architecture, University of Sydney; and Mr. A. A. Strom, Advisor in Conservation, Department of Education, N.S.W.

ORDINARY GENERAL MEETING

26th July 1972

Held in the Society's Rooms, 157 Gloucester Street, Sydney.

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

Minutes of the last Ordinary General Meeting (28th June 1972) were taken as read and confirmed.

Papers read (by title only):

Fossil *Manginula*-like fungi and their classification. By D. R. Selkirk.

The Rugose Coral *Palaeophyllum* Billings from the Ordovician of Central New South Wales. By R. D. Webby.

Announcements :

It has come to the Society's attention that Mr. Marcel Aurousseau, a member since 1912, has received the following distinctions : the Victoria Medal of the Royal Geographical Society for 1969 ; the Honorary Fellow of the Australian Academy of the Humanities for 1972.

At the General Monthly Meeting of the Royal Society of N.S.W. on Wednesday, the 2nd August 1972, an address on " Congenital Anomalies " was given by Dr. William G. McBride, C.B.E., M.D., F.R.C.O.G.

The Royal Society of N.S.W. also announced that nominations for the Edgeworth David Medal, 1972 should be submitted not later than the 30th October 1972.

Programme :

An address entitled " Small Mammals on Coastal-Heaths in N.S.W. " was given by Mr. Heimo Posamentier of the Australian Museum.

Macleay Memorial Lecture

The Sir William Macleay Memorial Lecture for 1972, entitled " Ecology and Society ", was given by Professor R. O. Slatyer on 16th August, at 8.00 p.m. It was held in the Central Lecture Block of the University of New South Wales as part of the A.N.Z.A.A.S. Congress.

Field Day

A Field Excursion was held on the 24th September 1972 to Jibbon Beach. This is a small bar between two small rocky headlands at the mouth of Port Hacking facing north towards Bate Bay. The bar has impounded a small lagoon which contains some interesting marsh plants and animals. The bar itself is vegetated with Tea-tree and is one of the most southerly locations for *Ipomoea brasiliensis* — tropical strand creeper. At this time of the year many of the heathland plants are in flower and attract many birds. At the eastern end of the beach are some aboriginal rock carvings and middens.

Ordinary Monthly Meeting

25th October 1972

Held in the Society's Rooms, 157 Gloucester Street, Sydney.

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

Minutes of the last Ordinary General Meeting (26th July 1972) were taken as read and confirmed.

Papers read (by title only) :

1. Two new fur-mites (Acari : Atopomelidae) from the Australian tiger cat (Marsupialia : Dasyuridae). By R. Domrow and A. Fain.
2. Ecology of Coastal Heath-Vegetation Structure. By M. Y. Siddiqi, R. C. Carolin and D. J. Anderson.

Announcement :

The Chairman announced that the monthly meeting in November would be a Notes and Exhibits evening, and asked members to let the Secretary know if they had a contribution to make to the programme.

Address:

An address entitled " The Flora of the New Hebrides and its relationship " was given by Dr. W. L. Chew of the Royal Botanic Garden, Sydney.

ORDINARY MONTHLY MEETING

29th November 1972

Held in the Society's Rooms, 157 Gloucester Street, Sydney.

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

Papers read (by title only):

Four new Copepods (Crustacea: Harpacticoidea, Canuellidae) simultaneously occurring with *Diogenes senex* (Crustacea: Paguridae) near Sydney. By R. Hamond.

A new Permian and Upper Carboniferous (?) succession near Woodsreef, N.S.W., and its bearing on the palaeogeography of Western New England. By I. Price.

NOTES AND EXHIBITS

Dr. I. V. Newman exhibited a selection of colour slides illustrating ecocide in Vietnam, which, with an explanation, were selected from a lecture entitled " Ecocide in Indochina ' given by Dr. E. W. Pfeiffer, a zoologist of the University of Montana, in April 1972. The lecture was issued by the World Without War Council of Eugene, Oregon, U.S.A. The Association for International Cooperation and Disarmament (N.S.W.) made the material available to us. Dr. Pfeiffer had made four trips to Indochina, with facilitation and aerial transport from the U.S. Department of Defense.

The slides exhibited three types of land cover in normal state: Mountain forest and pasture, rice farming in the Delta, and shifting cultivation in hilly country. Ecocidal features shown by the slides resulted from three types of weapon: (1) Herbicides spread by aeroplane—Agent orange (24D plus 245T) for defoliation and Agent blue (Cacodylic acid) for desiccation of rice. Half the mangrove forests of the southern zone of Vietnam have been destroyed; and the destruction of general forest represents that Zone's supply of board timber for 30 years. (2) Rome ploughs (giant bulldozers) denuded great areas of forest. (3) Conventional bombing: this is largely by B–52s. A slide shows about 200 craters ($1\frac{1}{2}$ plane loads) each 9–13 m across and 3–5 m deep. Areas were shown impossible to farm, either from the concentration of craters of these bombs, or from the concentration of duds of other types of bombs, rockets, and grenades, which made work too hazardous. Water in the innumerable craters greatly increased the incidence of mosquito-borne diseases. One slide showed the top of a wooded ridge blasted clear by a " daisy-cutter " bomb to prepare a helipad. This bomb clears an area the size of a football field, blowing away tree trunks of 1 m diameter, killing animal life at 1,000 m by concussion, and causing haemorrhage in humans at 1,600 m. Dr. Pfeiffer's inquiries about this bomb show the difficulty of getting sure information. The Air Force said, " We never drop it if humans are known to be present " (even N.L.F.) . . . " we always . . . drop propaganda to get everybody out . . . for a radius of 1,500 m. We never use it against people." The Military Assistance Command Science Advisor and U.S. Embassy people all said it was used against troops regularly—two or three per week in summer 1971. The briefing Colonel said they were not announced like the B–52s because " they have such a devastating effect, we don't like to give them much publicity ".

Dr. C. N. Smithers discussed the migrations of Wanderer butterflies in Australia.

Since 1963 a study of population movements of Australian butterflies, especially Wanderers (*Danaus plexippus* (L.)), has been under way. Data have been collected through a force of voluntary cooperators who have marked and released specimens and reported migratory flights.

The movements of the Wanderer have turned out to be very different from what they are in its native North America. The exhibit will show their Australian movements and explain some of the techniques used.

Mrs. J. De Nardi exhibited six species of *Atriplex*, " Salt Bush ", from the family Chenopodiaceae, including new records, extensions of range, and recent collections of species not sighted for many years in N.S.W.

A series of three good seasons, winter 1970, summer 1970–71 and winter 1971, in far western New South Wales, resulted in a prolific growth of vegetation. Summer rains produced good growth of annuals and perennials benefited from the winter rains. The botanists at the National Herbarium of New South Wales took advantage of this sequence of good seasons, undertaking extensive field work in the area. Collections of the families Compositae, Gramineae, Chenopodiaceae and Papilionaceae, which are prominent in this flora, included several interesting records.

Professor T. G. Vallance exhibited a sample of Devonian limestone metamorphosed as an inclusion in a Tertiary (?) plug of fine-grained analcime-rich olivine basalt in the valley of Mullamuddy Creek, 15 km south-east of Mudgee, N.S.W. The limestone xenolith has been converted to a hydrogrossular-calcite-xonotlite rock. This is believed to be the first report of the mineral xonotlite ($Ca_6Si_6O_{17}(OH)_2$) from New South Wales and, probably, Australia. Fine fibrous xonotlite occurs here in white to pale pink patches and veinlets ; its identity has been confirmed by X-ray and optical study. The associated hydrogarnet has the cell edge *a* 12·13Å and is near hibschite ($Ca_3Al_2Si_2O_8(OH)_4$) in composition.

The two silicate phases mentioned are stable at relatively low temperatures and only in the presence of high concentrations of H_2O. Their formation must have resulted from extreme watery dilution of CO_2 in the vapour phase generated during metamorphic decarbonation. Interstitial analcime in the basalt suggests the intrusive magma was distinctly hydrous. Again, as the plug appears not to have been deeply eroded, groundwater may have supplemented magmatic water in the hydrous metamorphism of the limestone blocks. A more detailed account will be published later.

Dr. A. R. H. Martin showed a pollen diagram from Club Lake, Kosciusko. This diagram from believed deltaic sediments of a small stream, entering the head of Club Lake (alt. *ca.* 1,890 m), is shown by C_{14} dating to cover the period 7000 to 1500 B.P.

The chief features are a general increase in *Eucalyptus* and a decrease in grass pollen during this period. At the present stage of enquiry it is considered unwise to try to interpret this as a rise in tree line. An interesting feature of the diagram is the very low prominence of certain local floristic components such as *Podocarpus*, and the regular occurrence of a long-distant element, such as Chenopodiceae. This component is derived mainly from the west, as would be expected from the pattern of predominant winds.

An apparent downward fluctuation in *Eucalyptus* frequency about 2000 B.P. (if real) may perhaps be correlated with a climatic fluctuation about this time during which solifluction terraces formed at high altitudes on exposed sites.

LIST OF MEMBERS

(31st December, 1972)

ORDINARY MEMBERS

(An asterisk (*) denotes Life Member)

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, Donald Thomas, B.Sc., Ph.D., 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., Cooper (Australia) Ltd., P.O. Box 12 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.), 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, 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.
1971 Beard, John Stanley, M.A., B.Sc., D.Phil., Director, Royal Botanic Gardens, Sydney, N.S.W., 2000.
1940 Beattie, Joan Marion, D.Sc. (*née* Crockford), 2 Grace Avenue, Beecroft, N.S.W., 2119.
1964 Bedford, Geoffrey Owen, B.Sc., c/- 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.
1941 Blake, Stanley Thatcher, D.Sc. (Q'ld.), 1110 Waterworks Road, The Gap, Queensland, 4061.
1968 Blaxell, Donald Frederick, D.D.A., B.Sc., Royal Botanic Gardens, Sydney, 2000.
1960 Bourke, Terrence Victor, B.Sc.Agr., c/- Department of Agriculture, Stock and Fisheries, Popondetta, Papua.
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 Botany, 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., Box 2227, G.P.O., Darwin, Northern Territory, 5794, Australia.

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, Canberra, 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.
1959 Chippendale, George McCartney, B.Sc., Australian Botanical Liaison Officer, Royal Botanic Gardens, Kew, Richmond, Surrey, England.
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/- C.S.I.R.O., Division of Entomology, P.O. Box 1700, Canberra City, A.C.T., 2601.
1901 Cleland, Professor Sir John Burton, M.D., Ch.M., C.B.E., 1 Dashwood Road, Beaumont, Adelaide, South Australia, 5066.
1966 Clough, Barry Francis, B.Sc.Agr.
1956 Cogger, Harold George, M.Sc., Ph.D., Australian Museum, P.O. Box A285, Sydney South, N.S.W., 2000.
1946 Colless, Donald Henry, Ph.D. (Univ. of Malaya), c/- Division of Entomology, C.S.I.R.O., P.O. Box 1700, Canberra City, A.C.T., 2601.
1956 Common, Ian Francis Bell, M.A., M.Sc.Agr., C.S.I.R.O., Division of Entomology, P.O. Box 1700, Canberra City, A.C.T., 2601.
1969 Conacher, Robert Davy, LL.B., 15 Terrigal Avenue, Turramurra, N.S.W., 2074.
1968 Cook, Mrs. Margaret Lee (*née* Debenham), B.Sc., 42 Hunter Street, Strathfield, N.S.W., 2135.
1950 Crawford, Lindsay Dinham, B.Sc., c/- Victorian Plant Research Institute, Department of Agriculture, Burnley Gardens, Melbourne, Victoria, 3000.
1957 Crook, Keith Alan Waterhouse, M.Sc., Ph.D. (New England), Department of Geology, Australian National University, G.P.O. Box 197, Canberra, A.C.T., 2601.

1960 Dart, Peter John, B.Sc.Agr., Ph.D., Soil Microbiology Department, Rothamsted Experimental Station, Harpenden, Herts., England.
1968 Dartnall, Alan John, B.Sc., Tasmanian Museum, Box 1164M, G.P.O., Hobart, Tasmania, 7001.
1972 Das, Dr. Jagadish, M.B., B.S., 48 Fitzroy Street, Burwood, N.S.W., 2134.
1957 Davies, Stephen John James Frank, B.A. (Cantab.), Ph.D., C.S.I.R.O., Private Bag, Nedlands, Western Australia, 6009.
1945 Davis, Professor Gwenda Louise, Ph.D., B.Sc., Faculty of Science, University of New England, Armidale, N.S.W., 2350.
1967 De Nardi, Mrs. Jan Christina, B.Sc. (Q'ld.) (*née* Morrow), 42 William Street, Paddington, N.S.W., 2021.
1971 Disney, Henry John de Suffren, M.A., The Australian Museum, College Street, Sydney, 2000.
1953 Dobrotworsky, Nikolai V., M.Sc., Ph.D., Department of Zoology, University of Melbourne, Parkville, Victoria, 3052.
1954 Domrow, Robert, B.A., B.Sc., Queensland Institute of Medical Research, Herston Road, Herston, Queensland, 4006.
1946 Durie, Peter Harold, M.Sc., C.S.I.R.O., Veterinary Parasitology Laboratory, Yeerongpilly, Queensland, 4105.
1952 Dyce, Alan Lindsay, B.Sc.Agr., 48 Queen's Road, Asquith, N.S.W., 2078.

1953 Edwards, Dare William, B.Sc.Agr., Forestry Commission of N.S.W., Division of Wood Technology, 96 Harrington Street, Sydney, 2000.
1967 Edwards, Edward John, B.A., B.Sc., Dip.Ed., 38 Shirlow Avenue, Faulconbridge, N.S.W., 2776.
1947 Endean, Robert, M.Sc., Ph.D., Department of Zoology, University of Queensland, St. Lucia, Queensland, 4067.
1930 English, Miss Kathleen Mary Isabel, B.Sc., 6/168 Norton Street, Leichhardt, N.S.W., 2040.
1957 Evans, Miss Gretchen Pamela, M.Sc., 27 Frederick Street, Taringa, Queensland, 4066.

1964 Facer, Richard Andrew, Department of Geology, Wollongong University College, Wollongong, N.S.W., 2500.
1955 *Fairey, Kenneth David, Box 1176, G.P.O., Sydney, 2001.
1957 Filewood, Lionel Winston Charles, c/- Department of Agriculture, Stock and Fisheries, Konedobu, Papua.
1969 Flood, Peter Gerard, B.Sc.(Hons.), Department of Geology, University of Queensland, St. Lucia, Queensland, 4067.
1930 Fraser, Miss Lilian Ross, D.Sc., 1 Laurence Street, Pennant Hills, N.S.W., 2120.
1970 Freeman, Brian Warwick, B.Sc., Brain Research Unit, Department of Physiology, Sydney University, Sydney, 2006.
1972 Frodin, David Gammon, Ph.D., F.L.S., Department of Biology, University of Papua, New Guinea, Box 1144, P.O., Boroko, T.P.N.G.

1935 *Garretty, Michaen Duhan, D.Sc., Box 763, G.P.O. Melbourne, Victoria, 3001.
1971 Gerretson-Cornell, Luciano, 8/38 Judd Street, Cronulla, N.S.W., 2230.
1972 Gibbs, Alwyn Francis, B.Agr.Sc.(Hons.), M.Agr.Sc., Ph.D., Mitchell College, Bathurst, N.S.W., 2795.
1969 Goodfellow, David Ralph, 3 Tobruk Avenue, Carlingford, N.S.W., 2118.
1944 Greenwood, William Frederick Neville, 11 Wentworth Avenue, Waitara, N.S.W., 2077.
1972 Griffin, Desmond J. G., M.Sc., Ph.D., The Australian Museum, P.O. Box A285, Sydney South, N.S.W., 2000.
1946 *Griffiths, Mrs. Mabel, B.Sc. (*née* Crust), 54 Delmar Parade, Dee Why, N.S.W., 2099.
1936 Griffiths, Mervyn Edward, D.Sc., Wildlife Survey Section, C.S.I.R.O., P.O. Box 84, Lyneham, A.C.T., 2602.
1972 Grigg, Gordon Clifford, Ph.D., Zoology Department, University of Sydney, 2006.
1939 *Gunther, Carl Ernest Mitchelmore, M.B., B.S., D.T.M., D.T.M. & H. (England), M.B.E., 29 Flaumont Avenue, Lane Cove, N.S.W., 2066.

1959 Hadlington, Phillip Walter, B.Sc.Agr., 129 Condamine Street, Balgowlah, N.S.W., 2093.
1971 Hamond, Richard, B.Sc., Ph.D., C.S.I.R.O., Box 21, Cronulla, N.S.W., 2230.
1952 Hannon, Miss Nola Jean, B.Sc., Ph.D., 22 Leeder Avenue, Penshurst, N.S.W., 2222.
1964 Harden, Mrs. Gwenneth Jean, M.Sc. (*née* Hindmarsh), Kellys Plains Road, Armidale, N.S.W., 2350.
1967 Hardwick, Reginald Leslie, B.Sc., Parklands, 12c/1 Evelyn Avenue, Concord, N.S.W., 2137.
1968 Hayden, Mrs. Elizabeth Jean, B.Sc. (Melb.), 17 Malara Street, Waramanga, A.C.T., 2611.
1958 Hennelly, John Patten Forde, B.Sc., Highs Road, West Pennant Hills, N.S.W., 2120.
1951 Hewitt, Bernard Robert, B.A. (Q'ld.), B.Sc. (Syd.), M.Sc., (N.S.W.), A.R.A.C.I., Pegawai Pertanian, Bandar Seri Begawan, Negri Brunei.
1963 Hewson, Miss Helen Joan, B.Sc.(Hons.), Ph.D., Department of Botany, School of General Studies, Australian National University, P.O. Box 4, Canberra, A.C.T., 2600.
1964 Higginson, Francis Ross, B.Sc.Agr.(Hons.), Ph.D., Soil Conservation Service of N.S.W., Box 4293, G.P.O., Sydney, 2001.
1938 Hill, Professor Dorothy, Ph.D., D.Sc., F.A.A., F.R.S., Department of Geology and Mineralogy, University of Queensland, St. Lucia, Queensland, 4067.
1943 *Hindmarsh, Professor Mary Maclean, B.Sc., Ph.D., 4 Recreation Avenue, Roseville, N.S.W., 2069.
1967 Holland, Ray James Thurstan, M.A. (Syd.), M.A.C.E., c/- Sydney Grammar School, College Street, Sydney, 2000.
1953 *Hotchkiss, Professor Arland Tillotson, M.S., Ph.D. (Cornell), Department of Biology, University of Louisville, Louisville, Kentucky, 40208, U.S.A.
1956 *Hotchkiss, Mrs. Doreen Elizabeth, Ph.D., B.A., M.A. (*née* Maxwell), 2440 Longest Avenue, Louisville, Kentucky, 40208, U.S.A.
1967 Hoult, Errol Hubert, B.Sc.(Hons.), Department of Agronomy, University of New England, Armidale, N.S.W., 2350.
1942 Humphrey, George Frederick, M.Sc., Ph.D., C.S.I.R.O. Building No. A12, Sydney University, N.S.W., 2006.
1970 Hunt, Glenn Stuart, B.Sc., Dip.Ed., School of Zoology, University of New South Wales, P.O. Box 1, Kensington, N.S.W., 2033.

1960 Ingram, Cyril Keith, B.A., B.Ec., " La Mancha ", Mt. Tomah, via Bilpin, N.S.W., 2758.

1957 Jackes, Mrs. Betsy Rivers, B.Sc., Ph.D. (Univ. Chicago) (*née* Paterson), 5 Ashton Street, Vincent, Queensland, 4814.
1963 Jacobs, Miss Janice Lorraine, B.Sc., School of Biological Sciences, Department of Botany, Building A12, Sydney University, 2006.
1966 Jacobs, Surrey Wilfred Laurence, Royal Botanic Gardens, Sydney, N.S.W., 2000.
1960 James, Sidney Herbert, M.Sc., 54 Holmfirth Street, Mt. Lawley, Western Australia, 6050.
1969 Jamieson, Barrie Gillean Molyneux, B.Sc., Ph.D. (Bristol), Zoology Department, University of Queensland, St. Lucia, Queensland, 4067.
1964 Jancey, Robert Christopher, M.Sc., Ph.D., c/- Department of Botany, University of Western Ontario, London, Ontario, Canada.
1963 Jefferies, Mrs. Lesly Joan, 18 Derby Street, Camberwell, Victoria, 3124.
1960 Jenkins, Thomas Benjamin Huw, Ph.D., Department of Geology and Geophysics, Sydney University, 2006.
1947 Johnson, Lawrence Alexander Sidney, B.Sc., D.Sc., c/- National Herbarium, Royal Botanic Gardens, Sydney, 2000.
1960 Jolly, Violet Hilary, M.Sc.. Ph.D., 2 Hauraki Road, Takapuna, Auckland 9, New Zealand.
1958 Jones, Edwin Llewelyn, B.A., P.O. Box 196, Leeton, N.S.W., 2705.
1971 Jones, Mrs. Valerie, National Herbarium, Royal Botanic Gardens, Sydney, N.S.W., 2000.
1930 Joplin, Miss Germaine Anne, B.A., Ph.D., D.Sc., Department of Geophysics, Australian National University, Canberra, A.C.T., 2600.
1972 Joseph, Miss Adela Helen, 29 Dudley Street, Pagewood, N.S.W., 2035.
1960 Judd, Howard Kenniwell, Minnamurra Falls Forest Reserve, Box 14, P.O., Jamberoo, N.S.W., 2533.

1949 Keast, James Allen, M.Sc., M.A., Ph.D. (Harvard), Professor of Biology, Department of Biology, Queen's University, Kingston, Ontario, Canada.
1951 Kerr, Harland Benson, B.Sc.Agr., Ph.D., Summer Institute of Linguistics, P.O. Ukarumpa, E.H.D., Territory of New Guinea.
1937 Kesteven, Geoffrey Leighton, D.Sc., The Project Leader, Fisheries Research Station, C.S.I.R.O., P.O. Box 5, Deception Bay, Queensland, 4508.
1957 Kindred, Miss Berenice May, B.Sc., Basel Institute for Immunology, Grenzacjerstrasse 487, Basel, Switzerland.

1971 Lander, Nicholas Sea, B.Sc., National Herbarium, Royal Botanic Gardens, Sydney, 2000.
1956 Langdon, Raymond Forbes Newton, M.Agr.Sc., Ph.D., Department of Botany, University of Queensland, St. Lucia, Queensland, 4067.
1964 Lanyon, Miss Joyce Winifred, B.Sc., Dip.Ed., 1/20 Clanalpine Street, Eastwood, N.S.W., 2122.
1932 Lawson, Albert Augustus, " Rego House ", 23–25 Foster Street, Sydney, 2000.
1934 Lee, Mrs. Alma Theodora, M.Sc. (*née* Melvaine), Manor Road, Hornsby, N.S.W., 2077.
1936 Lee, Professor David Joseph, B.Sc., School of Public Health and Tropical Medicine, Sydney University, 2006.
1965 Lewis, Mrs. Alison Kay, B.Sc.(Hons.), Dip.Ed. (*née* Dandie), Flat 1, Albert Road, Strathfield, 2135.
1964 Littlejohn, Murray John, B.Sc., Ph.D. (W.A.), Department of Zoology, University of Melbourne, Parkville, Victoria, 3052.
1943 Lothian, Thomas Robert Noel, Botanic Gardens, Adelaide, South Australia, 5000.
1961 Love, Lesley Dorothy, Ph.D. (*née* Clarke), 46 Vancouver Avenue, Toongabbie, N.S.W., 2146.
1966 Lovedee, Miss Lois Jacqueline, B.Sc. (A.N.U.), 11 Dundilla Road, French's Forest, N.S.W., 2086.
1957 Luig, Norbert Harold, Ph.D., c/- Faculty of Agriculture, Sydney University, 2006.
1958 Lyne, Arthur Gordon, B.Sc., Ph.D., Division of Animal Physiology, C.S.I.R.O., P.O. Box 239, Blacktown, N.S.W., 2148.

1951 Macdonald, Colin Lewis, 7 Watford Close, North Epping, N.S.W., 2121.
1968 MacInnes, Mrs. Christine D. (*née* Clarke), B.Sc.(Hons.), 71 Macaulay Road, Stanmore, 2048.
1948 Macintosh, Professor Neil William George, M.B., B.S., Department of Anatomy, Sydney University, 2006.
1922 Mackerras, Ian Murray, M.B., Ch.M., B.Sc., C.S.I.R.O., Division of Entomology, P.O. Box 1700, Canberra City, A.C.T., 2601.
1971 Maclean, John Leslie, B.Sc.(Hons.), M.Sc., c/- D.A.S.F. Fisheries Research Station, Kanudi, via Konedobu, T.P.N.G.
1931 *Mair, Herbert Knowles Charles, B.Sc., 111 Deepwater Road, Castle Cove, N.S.W., 2069.

1948 Marks, Miss Elizabeth Nesta, M.Sc., Ph.D., Department of Entomology, University of Queensland, Brisbane, Queensland, 4067.
1966 Martin, Angus Anderson, B.Sc.(Hons.), Rand, Department of Zoology, University of Melbourne, Parkville, Victoria, 3052.
1957 Martin, Anthony Richard Henry, M.A., Ph.D., School of Biological Sciences, Department of Botany, Sydney University, 2006.
1971 Martin, Helene Alice, Ph.D., School of Biological Sciences, School of Botany, University of New South Wales, P.O. Box 1, Kensington, N.S.W., 2033.
1953 Martin, Mrs. Hilda Ruth Brownell, B.Sc. (*née* Simons), c/- Mrs. H. F. Simons, 43 Spencer Road, Killara, N.S.W., 2071.
1964 Martin, Peter Marcus, M.Sc.Agr., Dip.Ed., School of Biological Sciences, Botany Building A12, Department of Botany, Sydney University, 2006.
1966 Mather, Mrs. Patricia (*née* Kott), M.Sc., Ph.D. (W.A. and Q'ld.), Department of Zoology, University of Queensland, St. Lucia, Queensland, 4067.
1951 McAlpine, David Kendray, M.Sc., Ph.D., Australian Museum, P.O. Box A285, Sydney South, N.S.W., 2000.
1957 *McCusker, Miss Alison, M.Sc., Botany Department, University College, Box 9184, Dar es Salaam, Tanzania.
1954 McDonald, Miss Patricia M., B.Sc., Dip.Ed., 33 Holdsworth Street, Neutral Bay, N.S.W., 2089.
1956 McGarity, John William, M.Sc.Agr., Ph.D., Agronomy Department, School of Rural Science, University of New England, Armidale, N.S.W., 2350.
1965 McGillivray, Donald John, B.Sc.For. (Syd.), Dip.For. (Canb.), P.O. Box 107, Castle Hill, N.S.W., 2174.
1948 McKee, Hugh Shaw, B.A., D.Phil. (Oxon.), Service des Eaux et Forêts, B.P. 285, Noumea, New Caledonia.
1957 McKenna, Nigel Reece, Department of Education, Konedobu, Papua.
1944 Mercer, Professor Frank Verdun, B.Sc., Ph.D. (Camb.), School of Biological Sciences, Macquarie University, North Ryde, N.S.W., 2113.
1947 Messmer, Mrs. Pearl Ray, " Wychwood ", 11 Kuring-gai Avenue, Turramurra, N.S.W., 2074.
1952 *Meyer, George Rex, B.Sc., Dip.Ed., B.A., M.Ed., Centre for Advancement of Teaching, Macquarie University, North Ryde, N.S.W., 2113.
1949 *Miller, Allen Horace, B.Sc., Dip.Ed., School of Teacher Education, Canberra College of Advanced Education, P.O. Box 381, Canberra City, A.C.T., 2601.
1948 Millerd, Miss Alison Adèle, Ph.D., C.S.I.R.O., Division of Plant Industry, P.O. Box 1600, Canberra City, A.C.T., 2601.
1947 Millett, Mervyn Richard Oke, B.A., " Beeyung ", 72 McNicol Road, Tecoma, Victoria, 3160.
1965 Milward, Norman Edward, B.Sc.(Hons.), M.Sc., Zoology Department, James Cook University of North Queensland, P.O. Box 999, Townsville, Queensland, 4810.
1972 Mitchell, G. S., 24 Keswick Avenue, Castle Hill, N.S.W., 2154.
1956 *Moffat, Mrs. Lynette Anne, B.Sc., Ph.D. (*née* Holder), 48 Rutledge Street, Eastwood, N.S.W., 2122.
1963 Moore, Barry Philip, B.Sc., Ph.D., D.Phil., C.S.I.R.O., Division of Entomology, P.O. Box 1700, Canberra City, A.C.T., 2601.
1960 Moore, Raymond Milton, D.Sc.Agr., c/- Woodland Ecology Unit, C.S.I.R.O., P.O. Box 1666, Canberra City, A.C.T., 2601.
1955 Morgan, Mrs. Eva, M.Sc., 5317 Borland Road, Los Angeles, California, 90032, U.S.A.
1970 Moulds, Maxwell Sidney, 14 Chisholm Street, Greenwich, N.S.W., 2065.
1955 Muirhead, Warren Alexander, B.Sc.Agr., C.S.I.R.O., Irrigation Research Station, Private Mail Bag, Griffith, N.S.W., 2680.
1931 Myerscough, Dr. Peter J., School of Biological Sciences, Botany Building A12, Sydney University, 2006.

1947 Nashar, Professor Beryl, B.Sc., Ph.D., Dip.Ed. (*née* Scott), 43 Princeton Avenue, Adamstown Heights, N.S.W., 2289.
1925 Newman, Ivor Vickery, M.Sc., Ph.D., F.R.M.S., F.L.S., 1 Stuart Street, Wahroonga, N.S.W., 2076.
1967 Nicholls, Anthony Oldham, B.Sc., c/- Woodland Ecology Unit, C.S.I.R.O., P.O. Box 1666, Canberra City, A.C.T., 2601.
1935 *Noble, Norman Scott, D.Sc.Agr., M.Sc., D.I.C., Unit 21, 1 Lauderdale Avenue, Fairlight, N.S.W., 2094.
1920 Noble, Robert Jackson, B.Sc.Agr., Ph.D., 32A Middle Harbour Road, Lindfield, N.S.W., 2070.
1970 Nuzum, Miss Caroline Evelyn, Mountain Lagoon Road, Bilpin, N.S.W., 2758.

1948 O'Farrell, Professor Antony Frederick Louis, A.R.C.Sc., B.Sc., F.R.E.S., Department of Zoology, University of New England, Armidale, N.S.W., 2350.

1950 O'Gower, Professor Alan Kenneth, M.Sc., Ph.D., 20 Gaerloch Avenue, Bondi, N.S.W., 2026.
1927 Osborn, Professor Theodore George Bentley, D.Sc., F.L.S.
1950 Oxenford, Reginald Augustus, B.Sc., 10 Greaves Street, Grafton, N.S.W., 2460.

1952 Packham, Gordon Howard, B.Sc., Ph.D., Box 90, P.O., Northbridge, N.S.W., 2063.
1940 *Pasfield, Gordon, B.Sc.Agr., 8 McDonald Crescent, Strathfield, N.S.W., 2135.
1972 Paxton, John R., Ph.D., The Australian Museum, College Street, Sydney, N.S.W., 2000.
1962 Payne, William Herbert, A.S.T.C., A.M.I.E.Aust., M.A.P.E., 250 Picnic Point Road, Picnic Point, N.S.W., 2213.
1957 Peacock, William James, B.Sc., Ph.D., C.S.I.R.O., Division of Plant Industry, P.O. Box 1600, Canberra City, A.C.T., 2601.
1964 Pedder, Alan Edwin Hardy, M.A. (Cantab.), Ph.D., Institute of Sedimentary and Petroleum Geology, 3303 33rd Street, N.W. Calgary 44, Alberta, Canada.
1922 Perkins, Frederick Athol, B.Sc.Agr., 93 Bellevue Terrace, Clayfield, Queensland, 4011.
1962 Philip, Graeme Maxwell, M.Sc. (Melb.), Ph.D. (Cantab.), F.G.S., Department of Geology and Geophysics, The University of Sydney, Sydney, N.S.W., 2006.
1947 Phillips, Miss Marie Elizabeth, M.Sc., Ph.D., Parks and Gardens Section, Department of the Interior, Canberra, A.C.T., 2600.
1969 Phippard, John Harry, B.Pharm., 5/594A Blaxland Road, Eastwood, N.S.W., 2122.
1969 Pickard, John, B.Sc.Agr., National Herbarium of N.S.W., Royal Botanic Gardens, Sydney, 2000.
1935 Pope, Miss Elizabeth Carington, M.Sc., C.M.Z.S., 8 Loorana Street, East Roseville, N.S.W., 2069.
1938 Pryor, Professor Lindsay Dixon, M.Sc., Dip.For., Department of Botany, School of General Studies, Australian National University, Box 197, P.O., City, Canberra, A.C.T., 2601.
1967 Pulley, Mrs. Jean May, B.Sc.Agr., Dip.Ed., 12 Clisby Close, Cook, A.C.T., 2614.

1969 Quinn, Christopher John, B.Sc.(Hons.), Ph.D., Department of Botany, School of Biological Sciences, University of New South Wales, P.O. Box 1, Kensington, N.S.W., 2033.

1960 Racek, Albrecht Adalbert, Dr.rer.nat. (Brno, Czechoslovakia), School of Biological Sciences, Department of Zoology, Sydney University, 2006.
1962 Rade, Janis, M.Sc., Flat 28A, 601 St. Kilda Road, Melbourne, Victoria, 3000.
1951 Ralph, Professor Bernhard John Frederick, B.Sc., Ph.D. (Liverpool), A.A.C.I., School of Biological Sciences, University of New South Wales, P.O. Box 1, Kensington, N.S.W., 2033.
1952 Ramsay, Mrs. Helen Patricia, M.Sc., Ph.D., School of Biological Sciences, University of New South Wales, P.O. Box 1, Kensington, N.S.W., 2033.
1953 Reye, Eric James, M.B., B.S. (Univ. Q'ld.), Entomology Department, University of Queensland, St. Lucia, Queensland, 4067.
1957 Reynolds, Miss Judith Louise, Ph.D., 118 Homer Street, Earlwood, N.S.W., 2206.
1961 Richards, Miss Aola Mary, M.Sc.(Hons.), Ph.D. (N.Z.), School of Biological Sciences, University of New South Wales, P.O. Box 1, Kensington, N.S.W., 2033.
1968 Richards, Bryant Neville, B.Sc.For., Ph.D. (Q'ld.), 21 College Avenue, Armidale, N.S.W., 2350.
1964 Richardson, Barry John, 12 Bowden Street, Parramatta North, N.S.W., 2150.
1967 Richardson, Laurence Robert, M.Sc., Ph.D., F.R.S.N.Z., 4 Bacon Street, Grafton, N.S.W., 2460.
1946 Riek, Edgar Frederick, B.Sc., Division of Entomology, C.S.I.R.O., P.O. Box 1700, Canberra City, A.C.T., 2601.
1958 Rigby, John Francis, B.Sc., Geological Survey of Queensland, 2 Edward Street, Brisbane, Queensland, 4000.
1972 Ritchie, Alexander, B.Sc., Ph.D., 173c Kissing Point Road, Turramurra, N.S.W., 2074.
1932 *Robertson, Sir Rutherford Ness, C.M.G., F.R.S., B.Sc., Ph.D., F.A.A., Master, University House, Australian National University, Box 4, Canberra, A.C.T., 2600.
1967 Rodd, Anthony Norman, Royal Botanic Gardens, Sydney, 2000.
1970 Ruello, Nick Vincent, B.Sc., 1 Terrell Avenue, Wahroonga, N.S.W., 2076.

1960 Salkilld, Barry William, Dip.Soc.Stud. (Univ. Syd.), 71 Beresford Road, Thornleigh, N.S.W., 2120.
1962 Sands, Miss Valerie Elizabeth, M.Sc., Ph.D., P.O. Box 3066, Sherwood, Whangarei, New Zealand.
1970 Satchell, Professor Geoffrey Harold, B.Sc.(Hons.) (Lond.), Ph.D. (Leeds), Department of Zoology, University of Otago, P.O. Box 56, Dunedin, N.Z.
1919 *Scammell, George Vance, B.Sc., 7 David Street, Clifton Gardens, N.S.W., 2088.
1965 Selkirk, David Robert, School of Biological Sciences, Carslaw Building F07, Sydney University, 2006.

1961 Selwood, Mrs. Lynne, B.Sc., Ph.D. (*née* Bedford), c/- E. C. Abernethy, 28 Butler Street, Inverell, N.S.W., 2360.
1950 *Sharp, Kenneth Raeburn, B.Sc., Eng. Geology, S.M.H.E.A., Cooma, N.S.W., 2630.
1948 Shaw, Miss Dorothy Edith, M.Sc.Agr., Ph.D., Department of Agriculture, Stock and Fisheries, Port Moresby, Papua-New Guinea.
1930 Sherrard, Mrs. Kathleen Margaret, M.Sc., 43 Robertson Road, Centennial Park, Sydney, 2021.
1947 Shipp, Erik, Ph.D., 24 Goodrich Avenue, Kingsford, N.S.W., 2032.
1959 Simons, John Ronald, M.Sc., Ph.D., 242 Kissing Point Road, Turramurra, N.S.W., 2074.
1955 Slack-Smith, Richard J., c/- P.D.P., Rua Fonte da Saudade 280, 2c–20, Rio de Janeiro, Brazil.
1953 Smith, Eugene Thomas, 22 Talmage Street, Sunshine, Victoria, 3020.
1971 Smithers, Courtenay Neville, Ph.D., Australian Museum, College Street, Sydney, 2000.
1943 Smith-White, Professor Spencer, D.Sc.Agr., F.A.A., School of Biological Sciences, Botany Building A12, Sydney University, Sydney, N.S.W., 2006.
1967 South, Stanley A., B.Sc. Address unknown.
1945 Southcott, Ronald Vernon, D.Sc., M.D., D.T.M. & H., F.A.C.M.A., 2 Taylors Road, Mitcham, South Australia, 5062.
1937 Spencer, Mrs. Dora Margaret, M.Sc. (*née* Cumpston), No. 1, George Street, Tenterfield, N.S.W., 2372.
1960 Staff, Ian Allen, B.Sc., Dip.Ed., Ph.D., Department of Botany, School of Biological Sciences, La Trobe University, Bundoora, Victoria, 3083.
1968 Stanbury, Peter John, Ph.D., The Macleay Museum, School of Biological Sciences, Sydney University, 2006.
1932 Stead, Mrs. Thistle Yolette, B.Sc. (*née* Harris), 14 Pacific Street, Watson's Bay, N.S.W., 2030.
1956 Stephenson, Professor Neville George, M.Sc. (N.Z.), Ph.D. (Lond.), School of Biological Sciences, Department of Zoology, Sydney University, 2006.
1965 Straughan, Mrs. Isdale Margaret, B.Sc., Ph.D., Allan Hancock Foundation, University of Southern California, University Park, Los Angeles, California, 90007, U.S.A.
1952 Sullivan, George Emmerson, M.Sc. (N.Z.), Ph.D., Department of Histology and Embryology, Sydney University, 2006.
1962 *Swinbourne, Robert Frederick George, 4 Leeds Avenue, Northfield, South Australia, 5085.

1965 Talbot, Frank Hamilton, M.Sc., Ph.D., F.L.S., Australian Museum, P.O. Box A285, Sydney South, N.S.W., 2000.
1940 Taylor, Keith Lind, B.Sc.Agr., c/- C.S.I.R.O., Division of Entomology, Stowell Avenue, Hobart, Tasmania, 7000.
1950 Tchan, Professor Yao-tseng, Dr., es Sciences (Paris), Department of Microbiology, Sydney University, 2006.
1950 Thompson, Mrs. Joy, B.Sc.Agr. (*née* Garden), 10 Alexander Avenue, Mosman, N.S.W., 2088.
1956 Thomson, James Miln, D.Sc. (W.A.), Department of Zoology, University of Queensland, St. Lucia, Queensland, 4067.
1960 Thorne, Alan Gordon, B.A., Department of Pre-History, School of Pacific Studies, Australian National University, Box 4, Canberra, A.C.T., 2600.
1949 Thorp, Mrs. Dorothy Aubourne, B.Sc. (Lond.), Ph.D., " Sylvan Close ", Mt. Wilson, N.S.W., 2740.
1944 Thorpe, Ellis William Ray, B.Sc., University of New England, Armidale, N.S.W., 2350.
1968 Timms, Brian Victor, B.Sc.(Hons.), Zoology Department, Monash University, P.O. Box 92, Clayton, Victoria, 3168.
1943 Tindale, Miss Mary Douglas, D.Sc., 60 Spruson Street, Neutral Bay, N.S.W., 2089.
1971 Tracey, David, B.Sc.(Hons.), Department of Biological Sciences, Stanford University, Stanford, California, 94305, U.S.A.
1921 *Troughton, Ellis Le Geyt, C.M.Z.S., F.R.Z.S., c/- Australian Museum, P.O. Box A285, Sydney South, N.S.W., 2000.
1965 Tucker, Richard, B.V.Sc., Dr.Vet.M., Veterinary School, Department of Veterinary Anatomy, University of Queensland, St. Lucia, Queensland, 4067.

1952 Valder, Peter George, B.Sc.Agr., Ph.D. (Camb.), School of Biological Sciences, A12, Department of Botany, Sydney University, 2006.
1949 Vallance, Professor Thomas George, B.Sc., Ph.D., Department of Geology and Geophysics, Sydney University, 2006.
1917 Veitch, Robert, B.Sc., F.R.E.S., 24 Sefton Avenue, Clayfield, Queensland, 4011.
1930 Vickery, Miss Joyce Winifred, M.B.E., D.Sc., Royal Botanic Gardens, Sydney, 2000.
1940 Vincent, Professor James Matthew, D.Sc.Agr., Dip.Bact., Department of Microbiology, School of Biological Sciences, University of New South Wales, P.O. Box 1, Kensington, N.S.W., 2033.

1972 Virgona, Christopher Terence Francis, B.Sc. (N.S.W.), 5 Burton Street, Mosman, N.S.W. 2088.
1934 *Voisey, Professor Alan Heywood, D.Sc., 9 Milton Street, Carlingford, N.S.W., 2118.

1961 Walker, Donald, B.Sc., M.A., Ph.D., F.L.S., 18 Cobby Street, Campbell, Canberra, A.C.T., 2601.
1952 Walker, John, B.Sc.Agr., Biological and Chemical Research Institute, N.S.W. Department of Agriculture, Private Mail Bag No. 10, Rydalmere, N.S.W., 2116.
1970 Walker, John Charles, B.Sc., (Gen. Science), School of Public Health and Tropical Medicine, Sydney University, N.S.W., 2006.
1909 Walkom, Arthur Bache, D.Sc., 5/521 Pacific Highway, Killara, N.S.W., 2071.
1946 Wallace, Murray McCadam Hay, B.Sc., C.S.I.R.O., W.A. Regional Laboratory, Nedlands, Western Australia, 6009.
1947 Ward, Mrs. Judith, B.Sc., 16 Mortimer Avenue, New Town, Hobart, Tasmania, 7008.
1969 Warren, Dr. Alison Anne, B.Sc., Ph.D. (Cantab.) (*née* Howie), Department of Geology, University of Melbourne, Parkville, Victoria, 3052.
1966 Wass, Robin Edgar, B.Sc.(Hons.) (Q'ld.), Ph.D., Department of Geology and Geophysics, Sydney University, 2006.
1936 Waterhouse, Douglas Frew, C.M.G., D.Sc., F.R.S., C.S.I.R.O., P.O. Box 1700, Canberra City, A.C.T., 2601.
1947 *Waterhouse, John Teast, B.Sc., School of Biological Sciences, University of New South Wales, P.O. Box 1, Kensington, N.S.W., 2033.
1941 Watson, Professor Irvine Armstrong, Ph.D., B.Sc.Agr., Faculty of Agriculture, Sydney University, 2006.
1964 Webb, Mrs. Marie Valma, B.Sc., 30 Talfourd Street, Glebe, N.S.W., 2037.
1963 Webby, Barry Deane, Ph.D., M.Sc., Department of Geology and Geophysics, Sydney University, 2006.
1946 Wharton, Ronald Harry, M.Sc., Ph.D., Division of Entomology, C.S.I.R.O., Long Pocket Laboratories, Indooroopilly, Queensland, 4068.
1926 *Whitley, Gilbert Percy, F.R.Z.S., Australian Museum, P.O. Box A285, Sydney South, N.S.W., 2000.
1954 Williams, John Beaumont, B.Sc., Botany Department, University of New England, Armidale, N.S.W., 2350.
1954 Williams, Mrs. Mary Beth, B.Sc. (*née* Macdonald), P.O. Box 330, Armidale, N.S.W., 2350.
1960 Williams, Neville John, B.Sc., A.A.E.C. Research Establishment, Private Mail Bag, Sutherland, N.S.W., 2232.
1952 Williams, Owen Benson, M.Agr.Sc. (Melbourne), c/- C.S.I.R.O., Division of Animal Physiology, Box 239, Blacktown, N.S.W., 2148.
1950 Willis, Jack Lehane, M.Sc., A.A.C.I., 26 Inverallan Avenue, Pymble, N.S.W., 2073.
1972 Wilson, Peter Gordon, B.Sc. (Hons.), 12 Arthur Street, Dee Why, N.S.W., 2099.
1947 Winkworth, Robert Ernest, Rangelands Research Unit, C.S.I.R.O., P.O. Box 109, Canberra City, A.C.T., 2601.
1968 Wood, Alec Edward, B.Sc.Agr., Ph.D., 25 George Street, Bexley, N.S.W., 2207.
1965 Woodward, Thomas Emmanuel, M.Sc. (N.Z.), Ph.D. (Lond.), D.I.C., Department of Entomology, University of Queensland, St. Lucia, Queensland, 4067.
1964 Wright, Anthony James Taperell, B.Sc., Department of Geology, Wollongong University College, Wollongong, N.S.W., 2500.

1964 Yaldwyn, John Cameron, Ph.D. (N.Z.), M.Sc., Dominion Museum, Private Bag, Wellington, New Zealand.
1965 Young, Graham Rhys, 8 Spark Street, Earlwood, N.S.W., 2206.

Corresponding Members

1959 Burgess, Rev. Colin, 2 Hamilton Row, Yarralumla, A.C.T., 2600.
1949 Jensen, Hans Laurits, D.Sc.Agr. (Copenhagen), State Laboratory of Plant Culture, Department of Bacteriology, Lyngby, Denmark.
1958 Moore, Kenneth Milton, Cutrock Road, Lisarow, N.S.W., 2251.

LIST OF PLATES

PROCEEDINGS 1972

LIST OF NEW SPECIES

VOL. 97

New Family

	Page
Plurellidae	258

New Genera

	Page		Page
Entopeltacites	143	*Monoandrocarpa*	250
Kaiyabdella	131	*Plurella*	258
Labidopygus	162		

New Combinations

memorabilis (*Vizella*)	142	maegdefravii (*Entopeltacites*) ..	143
osbornii (*Entopeltacites*) ..	143	dawbini (*Kaiyabdella*) ..	136

New Species

attenuatus (*Entopeltacites*) ..	143	elegans (*Brianola*)	192
australiensis (*Labidopygus*) ..	163	elongata (*Plurella*)	258
bajulus (*Pachycentrotus*) ..	30	irregularis (*Entopeltacites*) ..	144
brevipalmata (*Litoria*) ..	83	macrocaule (*Palaeophyllum*) ..	154
cooksoniae (*Entopeltacites*) ..	144	plana (*Monoandrocarpa*) ..	250
crassum (*Palaeophyllum*) ..	153	pori (*Brianola*)	186
dasyurochirus major (*Dasyurochirus*)	161	praecox (*Cercaria*)	87
		proliferum (*Palaeophyllum*) ..	152
directum (*Aplidium*)	246	sydneyensis (*Brianola*) ..	179
discontinua (*Vizella*)	142	tranteri (*Sunaristes*)	157

Index

1973

Copies of the PROCEEDINGS OF THE LINNEAN SOCIETY OF NEW SOUTH WALES (with the exception of a few Volumes and Parts) may be purchased from the Society, Science House, 157 Gloucester Street, Sydney, N.S.W., 2000.

Current charges for the PROCEEDINGS are:

Volumes—$16.00 each for 1st Series (Volumes 1–10); $11.00 each for 2nd Series (Volumes 11–20) and all subsequent volumes.

Parts—$5.00 each for all back parts; $4.00 each for current Parts. For volumes of 5 or 6 Parts, $1.00 each for first and last Parts.

Prices do not include postage.

Subscription to the PROCEEDINGS—$11.00 per volume, plus 80c postage—$11.80.

All prices are in Australian currency.

These charges may be revised from time to time, and inquiries should be addressed to The Secretary, Linnean Society of New South Wales, Science House, 157 Gloucester Street, Sydney, N.S.W., 2000, Australia.

The Society's PROCEEDINGS are printed and published for the Society by the Australasian Medical Publishing Co., Ltd., 71–79 Arundel Street, Glebe, N.S.W., 2037.

Proceedings, Volume 97, Part 4, 1972

CONTENTS