Proceedings of the Linnean Society of New South Wales

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(Issued 10th March, 1969)

(Sir William Macleay Memorial Lecture and Papers read June–July, 1968)

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PART 3 (No. 418)

(Issued 18th July, 1969)

(Papers read September–November, 1968)

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ANNUAL GENERAL MEETING

27th March, 1968

The Ninety-third Annual General Meeting was held in the Society's Rooms, Science House, 157 Gloucester Street, Sydney, on Wednesday, 27th March, 1968, at 7.30 p.m.

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

The minutes of the Ninety-second Annual General Meeting (29th March, 1967) were read and confirmed.

Report on the Affairs of the Society for the Year

The Society's Proceedings for 1967, Vol. 92, Parts 1 and 2 were published on 11th September and 22nd December, 1967, respectively.

During the year 12 new members were admitted to the Society, three died, three resigned and three were removed from the list of members. The numerical strength of the Society at 1st March, 1968, was: Ordinary Members, 275; Life Members, 31; Corresponding Member, 1; total, 307.

It is regretted that the deaths of the following members have to be reported: Miss Margery Olwyn Levy, B.Sc., Dip.Ed., died suddenly at Katoomba, N.S.W., on 2nd April, 1967. She had been a member of the Society since 29th April, 1964; Dr. Edward Gordon Haig Manchester, M.B., B.S., who was elected to membership of the Society on 29th March, 1967, died suddenly in Sydney on 24th September, 1967; Professor Patrick Desmond Fitzgerald Murray, M.A., D.Sc., died suddenly on a voyage to England on 18th May, 1967 (see page 3 for obituary notice); Mr. David Sutherland North of Lindfield, N.S.W., who had been a member of the Society since 1912, died on 20th August, 1967.

Papers read at Ordinary General Meetings totalled 27. Lecturettes were given at the following meetings: July, Geological Aspects of the Great Barrier Reef, by Professor W. G. H. Maxwell; October, Some Observations on the Status of Rainforest, by Mr. G. N. Baur. The address of the immediate Past President, Professor R. C. Carolin, entitled "The Concept of the Inflorescence in the Order Campanulales" was discussed at the June meeting. At the April meeting a symposium entitled "Marine Sciences of the Central Coast of New South Wales—Recent Researches" was held under the leadership of Miss Elizabeth C. Pope. A symposium was held at the September meeting under the leadership of Dr. D. T. Anderson on "Some Recent Studies on Intertidal Animals". Interesting notes and exhibits were given at the April, September and November meetings. We are grateful to all who contributed in these various ways to the interest of the meetings. No meetings were held in May or August.

Library accessions from scientific institutions and societies on the exchange list amounted to 1,965 compared with 2,199 and 2,016 for the years 1966 and 1965. The total number of borrowings of books and periodicals from the library by members and institutions for the year was 222. Members and others continued to consult publications in the Society's rooms, and books and periodicals were made available for photographic copying. The following requests for exchange of publications were acceded to during the year: the

Proceedings for: Folia Histochemica et Cytochemica (publication of the Polish Histochemical and Cytochemical Society), Krakow, Poland; Annuaire, Faculte de Biologie (University de Sofia, Sofia, Bulgaria); Atti (Societa Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano, Milan, Italy; Botanical Reprints (instead of Proceedings) to Institute of Ecological Botany, University of Uppsala, Uppsala, Sweden, in exchange for Acta Phytogeographica Suecica; Abstract of Proceedings to Science of Science Foundation Library, University of Sussex, Brighton, Sussex, England. The disposal by purchase and gift of certain periodicals and duplicates in the library has made available considerable much-needed space, and it is proposed during the coming year to re-arrange the library to provide adequate space for currently received exchanges. The library itself has been greatly improved by the installation of fluorescent lighting, a water service, sink, hot-water heater and cupboard and a platform ladder for convenience.

The net return to the Society from Science House was $2,724.81 for the year.

A plaster plaque of Rev. R. Collie, which has been in the possession of the Society for a number of years, was repaired by the Art Section of the Australian Museum and is in the Society's rooms.

The Rules of the Society have been revised as from 29th November, 1967, and reprinted, the date of issue being 31st January, 1968.

The Society has assisted in matters affecting the conservation of Dee Why Lagoon, Norfolk Island and Colong Caves, and has also supported the Australian Conservation Foundation and the Nature Conservation Council of New South Wales.

Dr. W. J. Peacock, conjointly with Dr. D. M. Green has been awarded the Edgeworth David Medal by the Royal Society of New South Wales. Dr. Peacock has been a member of the Society since 1957 and was Linnean Macleay Fellow of the Society in Botany during 1961 and 1962.

Linnean Macleay Fellowship

In November, 1967, Miss Alison K. Dandie, B.Sc. (Hons.) was re-appointed to a Linnean Macleay Fellowship in Botany for one year from 1st January, 1968. Miss Dandie has continued her research on the part played by vesicular-arbuscular mycorrhiza in crop and pasture plants in New South Wales. Particular emphasis was placed on attempts to find a reliable means of obtaining such mycorrhiza in test plants. Attempts to germinate *Endogone*-type spores in culture have been begun, using various methods. *Endogone*-type spores isolated from a number of different soils from Castle Hill were compared, and found to differ only slightly in their dimensions and gross morphology, the differences between soils being no greater than those within soils.

Linnean Macleay Lectureship in Microbiology

Dr. Y. T. Tchan, Reader in Agricultural Microbiology and Linnean Macleay Lecturer in Microbiology, University of Sydney, reported on his work for the year ending 31st December, 1967, as follows: At the beginning of this year he was in Taiwan as Leverhulme Fellow. His stay there was chiefly engaged in lecturing to different universities. A total of over 100 lecturing hours were delivered. A number of scientific discussions and seminars were given at several research centres. On his return to Sydney his activities were mainly concerned with teaching and administration. However, some research progress was made. A paper will be read in the coming

Australian Conference on Electron Microscopy. Another paper on the importance of systematics of Azotobacteriaceae in the study of its ecology will be published in the 9th International Congress of Soil Science in 1968.

Presidential Address

Rainbow's End: the Quest for an Optimal Taxonomy

The aims and justification of taxonomy are discussed, followed by an examination of the foundations of ordination and classification. The Adansonian or phenetic philosophy is critically examined and it is concluded that its claims of objectivity and precision are ill-founded, since subjective or arbitrary choices and definitions are necessary concerning acceptable or relevant attributes, homologies and correspondences, measures and commensurabilities of attributes, and measures of similarity. Phylogeny, represented topologically as a temporal branching sequence, is held to be the nearest approach to a firm basis of reference in nature for biological classification. The charge that phylogenetic reconstruction involves viciously circular reasoning is discussed and rejected, though some positive feedback is admitted.

The theory and application of numerical taxonomy are discussed in general and the potential value of numerical phyletics is stressed. The possibility of using DNA base matching as a solid foundation is briefly examined. It is shown that, while phenetic classifications are infinitely variable, topological phyletic reconstructions do not themselves supply the kind of taxonomy that is usually demanded, since they do not adequately express significant evolutionary change of the kind expressed as "grades". No optimal classification can be defined, but improvement is possible up to a point of inherent instability.

While the underlying facts and processes can be scientifically studied as part of taxonomy, classification itself remains largely a disciplined art, which is not convertible to an exact science by any form of arbitrary quantification. The necessity for compromise and continued synthesis is stressed. The suggested replacement of Linnean hierarchy by "numericlature" is mentioned but held to be premature and to have serious disadvantages. Mathematical concepts are discussed wherever relevant to the foundations of the subject. (For full text see pages 8 *et seq.*)

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

President: Professor T. G. Vallance, B.Sc., Ph.D.

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

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

The Chairman then installed Professor T. G. Vallance as President.

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

OBITUARY NOTICE

Patrick Desmond Fitzgerald Murray

Professor Murray, who died on 18th May, 1967, had been a member of the Society from 1922 to 1929 and from 1949 to 1966. He was born in London on 18th June, 1900, the son of Sir Hubert Murray, Lieutenant Governor of Papua (1908-1940). Educated at St. Ignatius College, Sydney, he proceeded to the University of Sydney, where he graduated B.Sc., with First Class Honours in Zoology and Botany, and gained the John Coutts Scholarship for distinction in Science, and a University Medal in 1922. Subsequent to graduation he spent two years working at Oxford University under Professor Goodrich and Julian Huxley, and in conjunction with Huxley, studied the effects of grafting certain tissues on to the membranes of the embryonic chick, the results being given in a series of papers, three of which were published in the Proceedings.

On returning to Sydney he was appointed to a Linnean Macleay Fellowship of the Society in Zoology from 13th April, 1924, and held this Fellowship until 1926. In 1926 he gained a Doctor of Science Degree of the University of Sydney. After three years of demonstrating and lecturing in the Department of Zoology at the University of Sydney he was awarded a Rockefeller Fellowship at the Universities of Freiburg and Cambridge. In 1939 he was appointed a London University Reader in Biology and Comparative Anatomy at St. Bartholomew's Hospital Medical School and Head of the Department of Biology in the College.

In 1949 he was appointed to the Challis Chair of Zoology in the University of Sydney, which he held until 1960, when he accepted a Readership in the Department of Zoology of the University of New England. The two positions he held in London and Sydney were ones of considerable academic responsibility, the duties of which he discharged conscientiously and with distinction. Research was with him an absorbing interest and he published many papers. Amongst other honours he was elected a Foundation Fellow of the Australian Academy of Science.

He was interested in the affairs of the Linnean Society and was a member of Council for five years (1950-1954). As an approachable and friendly man, always ready to discuss matters of interest, he was held in the highest respect by those who came to know him.

The sympathy of members of the Society are extended to his widow.

LIABILITIES.	$	$
Accumulated Funds—		
Amount received from Sir William Macleay during his lifetime	28,000.00	
Further sum bequeathed by his will	12,000.00	
		40,000.00
Contingencies Reserve		47,344.13
Current Liabilities—		
Bookbinding Account	1,691.16	
Income Account	20,117.10	
Suspense	16.43	
		21,824.69
		$109,168.82

ASSETS.	$	$
Fixed Assets—		
Commonwealth Loans, at Cost	30,097.00	
Debentures:		
Metropolitan Water, Sewerage and Drainage Board, at Cost	33,688.75	
Sydney County Council	6,000.00	
Science House (one-third), at Cost	30,470.43	
		100,256.18
Current Assets—		
Cash in Hand	40.00	
Commercial Banking Company of Sydney, Ltd.	8,872.64	
		8,912.64
		$109,168.82

INCOME ACCOUNT. Year Ended 29th February, 1968.

	$	$	$
To Honorarium and Salary		4,137.88	
,, Printing Proceedings		3,137.60	
,, Reprints		517.30	
,, Illustrations		648.26	
,, Insurance		31.78	
,, Postage	372.91		
,, Petty Cash	109.88		
		482.79	
,, Expenses:			
,, Audit	33.60		
,, Printing and Stationery	293.62		
,, Printing Rules	199.00		
,, Expenses	112.98		
,, Library Lighting	368.20		
,, Installing Sink and Heater	145.50		
,, Freight and Packing	160.84		
,, Cleaning	156.40		
,, Furniture	94.50		
		1,564.64	
,, Library	246.59	246.59	
,, Science House Rent	2,413.00	2,413.00	
Expenditure for Year			13,179.84
Balance to 1968–69			20,117.10
			$33,296.94

	$	$	$
By Balance from 1966–67			14,752.61
,, Subscriptions:			
1967–68	1,617.00		
Arrears	78.40		
Advance	28.00		
		1,723.40	
,, Interest		3,688.89	
,, Science House		5,537.81	
,, Rent		47.50	
,, Sales		2,168.75	
,, N.S.W. Government Grant		800.00	
,, Fellowships Account (surplus income at 29th February, 1968, transferred)		2,991.34	
,, Sale of Reprints		776.64	
,, Library: Sale of Surplus Periodicals		810.00	
Receipts for Year			18,544.33
			$33,296.94

4th March, 1968.

A. B. Walkom,
Hon. Treasurer.

AUDITOR'S REPORT TO MEMBERS.

I have examined the books of account and vouchers of the Linnean Society of New South Wales for the year ended 29th February, 1968, and certify that the above Balance Sheet and accompanying Income Account are correct, and in accordance therewith, and in my opinion present the true state of the Society's affairs at 29th February, 1968, as shown by the books. Certificates of the investments have been inspected.

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

Sydney, 11th March, 1968.

LINNEAN SOCIETY OF NEW SOUTH WALES.

LINNEAN MACLEAY FELLOWSHIPS ACCOUNT.

Balance Sheet at 29th February, 1968.

LIABILITIES.	$
Accumulated Funds—	
Amount bequeathed by Sir William Macleay	70,000.00
Surplus Income Capitalized	50,939.66
	$120,939.66

ASSETS.	$	$
Fixed Assets—		
Commonwealth Loans, at Cost	60,885.50	
Debentures:		
Metropolitan Water, Sewerage and Drainage Board, at Cost	38,596.98	
Rural Bank of N.S.W., at Cost	4,345.50	
State Electricity Commission	5,000.00	
Loan on Mortgage	12,070.00	
		120,897.98
Current Assets—		
Commercial Banking Company of Sydney, Ltd. ..		41.68
		$120,939.66

INCOME ACCOUNT. Year Ended 29th February, 1968.

	$
To Salary of Linnean Macleay Fellow	3,200.00
,, Balance, being Surplus Income transferred to General Account ..	2,991.34
	$6,191.34

	$
By Interest	6,191.34
	$6,191.34

A. B. Walkom,
Hon. Treasurer.

4th March, 1968.

AUDITOR'S REPORT TO MEMBERS.

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

Sydney, 11th March, 1968.

LINNEAN SOCIETY OF NEW SOUTH WALES.

BACTERIOLOGY ACCOUNT.

Balance Sheet at 29th February, 1968.

LIABILITIES.	$	$	ASSETS.	$	$
Accumulated Funds—			Fixed Assets—		
Amount bequeathed by Sir William Macleay ..	24,000.00		Commonwealth Loans, at Cost	30,636.25	
Accumulated Income Capitalized	12,620.00		Debentures:		
Research Fund	20.00		Metropolitan Water, Sewerage and Drainage Board, at Cost	1,600.00	
		36,640.00	Loan on Mortgage	4,400.00	
Current Liability—					36,636.25
Income Account at 29th February, 1968		566.65	Current Assets—		
			Commercial Banking Company of Sydney, Ltd. ..		570.40
		$37,206.65			$37,206.65

INCOME ACCOUNT. Year Ended 29th February, 1968.

	$		$
To University of Sydney (towards salary of Lecturer)	1,900.00	By Balance from 1966–67	548.79
,, Balance to 1968–69	566.65	,, Interest	1,917.86
	$2,466.65		$2,466.65

AUDITOR'S REPORT TO MEMBERS.

I have examined the books of account and vouchers of the Linnean Society of New South Wales for the year ended 29th February, 1968, and certify that the above Balance Sheet and accompanying Income Account are correct, and in accordance therewith, and in my opinion present the true state of the Society's affairs at 29th February, 1968, as shown by the books. Certificates of the investments have been inspected.

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

Sydney, 11th March, 1968.

A. B. Walkom,
Hon. Treasurer.

4th March, 1968.

PRESIDENTIAL ADDRESS

RAINBOW'S END: THE QUEST FOR AN OPTIMAL TAXONOMY

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

[Delivered 27th March, 1968]

Synopsis

The aims and justification of taxonomy are discussed, followed by an examination of the foundations of ordination and classification. The Adansonian or phenetic philosophy is critically examined and it is concluded that its claims of objectivity and precision are ill-founded, since subjective or arbitrary choices and definitions are necessary concerning acceptable or relevant attributes, homologies and correspondences, measures and commensurabilities of attributes, and measures of similarity. Phylogeny, represented topologically as a temporal branching sequence, is held to be the nearest approach to a firm basis of reference in nature for biological classification. The charge that phylogenetic reconstruction involves viciously circular reasoning is discussed and rejected, though some positive feedback is admitted.

The theory and application of numerical taxonomy are discussed in general and the potential value of numerical phyletics is stressed. The possibility of using DNA base matching as a solid foundation is briefly examined. It is shown that, while phenetic classifications are infinitely variable, topological phyletic reconstructions do not themselves supply the kind of taxonomy that is usually demanded, since they do not adequately express significant evolutionary changes in patterns of organisation. No optimal classification can be defined, but improvement is possible up to a point of inherent instability.

While the underlying facts and processes can be scientifically studied as part of systematics, classification itself remains largely a disclipined art, which is not convertible to an exact science by any form of arbitrary quantification. The necessity for compromise and continued synthesis is stressed. The suggested replacement of the Linnaean hierarchy by "numericlature" is mentioned but held to be premature and to have serious disadvantages. Mathematical concepts are discussed wherever relevant to the foundations of the subject.

> "He said 'I hunt for haddocks' eyes
> Among the heather bright,
> And work them into waistcoat-buttons
> In the silent night . . .' "
>
> LEWIS CARROLL (1871)—
> "Through the Looking-Glass, and What Alice Found There."

The "aged, aged man" would seem to have made two misjudgements: he sought unnecessary and rather unsuitable materials for his purpose, and then looked in a most unlikely place for them. Is the search by some taxonomists for the one "correct" classification of organisms equally futile and misguided? Before we can answer this question we shall need to look rather closely at some of the foundations of taxonomy.

The history of taxonomy and of taxonomic attitudes and methods has been reviewed in detail often enough. A presidential address gives one licence to wander at large over a field of interest. That is what I propose to do, examining certain relevant aspects or opinions, and offering comments and animadversions upon them, in the hope of discovering or deciding what taxonomy can or should hope to achieve. I shall use the terms "taxonomy" and "systematics" as roughly equivalent, with a tendency towards the principles-*versus*-practice distinction made by some American authors (e.g., Simpson, 1961). Except in passing, I shall mean by taxonomy the classification of organisms and not, as is fashionable today, of automobile components, criminals, Latin texts (Griffith, 1967), or heraldic beasts. In order to achieve reasonable precision, I shall have occasion at times to use some of the elementary language and concepts, but little of the notation, of certain aspects of mathematics, in particular of set theory and higher geometry.

The Status and Justification of Taxonomy

Taxonomists are often heard to complain that other biologists accord them insufficient respect, that universities pay little attention to taxonomy, and so forth—in fact that they are kept in subjection in a scientific peck order in which biology itself ranks none too high, molecular biology apart (for the obvious reason that molecular biologists are asking simpler, and in a sense genuinely more fundamental, questions which can be answered—sometimes—even by physical scientists). I shall now risk the wrath of my colleagues and assert that, although there is indeed some cause for these complaints, not a few non-initiates pay the taxonomic priesthood more respect than we perhaps merit. The historico-nomenclatural system, which is probably much less justified and immutable than systematists are wont to claim, burdens taxonomy with an enormous deadweight of out-dated and sometimes very bad work, professional and amateur, old and new. In any other non-historical discipline such publications would lapse into the obscurity they deserve.

Although systematics continues to attract more than its fair share of unshakable conservatives and legalists, much of its accumulated dross must eventually be swept away. If it is not, we may find that traditional systematics has been by-passed, whether we like it or not. I say this as one who has rather punctiliously followed the rules of nomenclature, though with increasing impatience—not at the existence of rules, but at the stultifying consequences of those we have.

Despite these criticisms, much systematic work of the past is in fact not out-dated—just as Pythagoras's theorem is as valid today as ever, or, less absolutely, as Newton's mechanics is all that we need to cope with those many familiar problems where the scale is such that the answers given by quantum mechanics and relativity theory would not differ, at the order of accuracy required, from the Newtonian answers. Also, following a becalmment in the doldrums during the first forty years of this century, systematics was able to recruit more workers possessing sound scientific training and some idea of the complexity and dynamics of the populations from which their specimens are drawn. Taxonomic research improved markedly as a result.

As we all know, this revirescence was associated with the progress of cytogenetic and evolutionary theory, and in its early days it first found full expression in the symposium "The New Systematics" (ed. Huxley, 1940). Much earlier, the Darwinian revolution had imbued many taxonomists (chiefly those whose education was not completed before the establishment of evolutionary thinking!) with the notion that if the phylogeny of a group could be successfully reconstructed, the taxonomic problems concerning it would be solved. Whether or not classification was thereby improved, some life certainly came into the subject for a few decades. Other systematists toiled on, sorting and shuffling, without much theoretical interest at all and, when favoured by nature with clear-cut situations, some among them produced classifications which continue to satisfy most users. There are groups in which nobody cares except the specialists themselves. Sometimes the technicality, obscurity, and dullness of the specialists' esoteric works have helped to bring about and preserve this state of blessed isolation.

In general, whether good or bad, theoretically disposed or otherwise, taxonomists themselves, like other scientists and scholars, find their own activities self-justifying because they bring some degree of intellectual satisfaction. This is doubtless the chief motivation for most of us, whatever rationalizations we offer about usefulness when called upon to show why society should support us. Nevertheless, society does support us, niggardly though we claim this support to be. Why? Partly because, from sheer inertia, the dispensers of funds will usually keep a going concern alive, but also, as any worker in a systematic service organization can testify, because there is a genuine call, from science and industry as well as many other activities of man, for the services of the namer and classifier.

The Need to Classify

None of us can communicate, or even live, unless we sort or classify the phenomena of our experience; further, we need in some way to label the classes or sets to which we assign these phenomena (for an introduction to the mathematical theory of sets see, for example, Room and Mack, 1966, and for an application to taxonomy see Buck and Hull, 1966). Often we know that someone else, the specialist classifier, is more efficient at this task than we are, and so we avail ourselves of his services. Having classified and named (labelled) a phenomenon or group of phenomena, we can ascertain further information about it and can talk about it. We may even, naïvely, consider that we know what it is. How often an inquirer asks, "What is this organism?" and, on being told "*Melania alba*", considers himself somehow wiser than before. Anthropologists know well the supposed power conferred by knowledge of a name.

The role of taxonomy in education is emphasized by Davis and Heywood (1963), who say that it "remains the principal agency through which the student may gain acquaintance with the diversity of organisms, the patterns of variation in the living world and . . . the evolutionary mechanisms which have brought these patterns about. The taxonomic approach is a focal point for students of biology and enables them to fit together into a framework of ideas a mass of otherwise unco-ordinated facts".

The classificatory nature of the whole of science is sometimes stressed. Many of my generation will remember from their schooldays a textbook of chemistry by Sherwood Taylor (1939), which begins with the words: "Natural science is the process of systematically arranging and classifying man's knowledge of the world about him." Perhaps this only partially defines the nature of science, but the search for more inclusive and if possible more simply and generally describable classes, of relations as well as things, is an important factor in arriving at the general but precise "laws" (as they are so inappropriately called) which science seeks.

The Question of Optimality

So much for the need for some sort of taxonomy. A chain of questions then arises: Are some classifications better than others? If so, when does the improvement (assuming that we have some means of assessing it) justify changing an existing system—or, how are we to choose between co-existing systems? If improvement is possible, then is there, logically, a *best* classification (practically attainable or not) to which we can try to approximate? Finally, if there is an optimal classification, what is its basis?

As soon as we attempt to answer these questions, or even to define the terms used in them, we find ourselves faced with many more questions. In any field where definitions are required we are led into an infinite regress; so we must agree to take certain things for granted—to set up starting points, as it were. In the more rigid contexts of logic or mathematics one starts with certain postulates, but even in the expression of these one must perforce use certain terms and syntactic relationships of undefined meaning. For example, in modern mathematics, the concept of "point" is usually left undefined; likewise, logical links such as "it follows that" must be accepted more or less intuitively (Courant and Robbins, 1961).

Much has been written on the philosophical bases of classification, including biological classification. While this literature is academically interesting and has important implications for essentially simple (but not always easy!) domains of inquiry such as mathematics, its application to essentially vague (i.e., very highly complex) domains such as biological taxonomy seems to be of little practical assistance. Most practising systematists continue their studies without worrying about philosophical foundations and it appears that, in their own work, many philosophically minded authors proceed in much the same way as other competent systematists. In contrast, evolutionary theory has noticeably influenced the methods, approach, results, and particularly the interpretations, of those systematic workers who are strongly aware of the genetical and evolutionary background and implications of their work, whether they call themselves "biosystematists" or eschew such labels.

THE PHILOSOPHY OF PHENETICISM

Despite this lack of practical effect, the modern philosophical school of taxonomy, foremost among whose early spokesmen were the botanist J. S. L. Gilmour (e.g., Gilmour, 1940), now at Cambridge, and (somewhat later) the Oxford zoologist A. J. Cain (e.g., Cain and Harrison, 1958; Cain, 1959), has had an increasing appeal over the past thirty years to theoretically minded taxonomists (especially those educated in certain universities). The background to this way of thought is the "operational" approach of logical positivism, a more far-reaching anti-metaphysical philosophy than empiricism but, like empiricism, of obvious appeal to the scientific mind (Britton, 1958, and references therein and in Gilmour and Walters, 1964, and Carolin, 1967).* It has culminated in the so-called Adansonian, neo-Adansonian, or phenetic credo which, perhaps by historical accident, is now so closely associated with what is labelled numerical taxonomy (Sneath and Sokal, 1962) or taximetrics (Rogers, 1963). The strong influence of the phenetic viewpoint is exemplified

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* To define my own philosophical standpoint, I should perhaps say that, while preferring logical positivism to metaphysical philosophies, I find it entirely reasonable to believe in the material reality of the universe—material, of course, in the sense that, despite the Uncertainty Principle, we can learn a great deal about the behaviour of "matter-energy" at various levels of aggregation and organization, and that the fundamentals (though not always the details) of this behaviour are independent of the existence of ourselves or other observers. As to the place of purpose and particularly of life in this physical world, I can see no justification for any form of supernaturalism, mysticism, transcendentalism, or neo-vitalism, nor can I see anything inconsistent with physics in the fact that, in the sense of information theory but not of physical thermodynamics, organisms increase negentropy while they grow as individuals or populations. Life is the state of possessing mechanisms for self-perpetuation, replication, and (in a sense) occasional increase of the organization of systems of physical components; that is the only way in which it is "different". Explicitly or not, these views are probably shared by most biologists. Neo-vitalism today seems often to arise, curiously enough, among physicists (e.g., Wigner, reviewed by Pais, 1967).

in the generally well-balanced and comprehensive modern textbook of angiosperm taxonomy by Davis and Heywood (1963), where its merits are accepted as almost self-evident.

Strictly, *Adansonianism* advocates multi-attribute classification, grouping on the basis of many equally weighted attributes drawn from many parts of the organism, and refusing to attach greater weight *a priori* to certain "essential" characters. Michel Adanson's approach (Lawrence, 1963), in the context of the eighteenth-century Enlightenment, represented a deliberate break from the blend of debased Platono-Aristotelian philosophy and theology which constituted mediaeval Scholasticism. Although it was abandoned by progressive philosophers, Scholasticism continued to obfuscate some scientists' thought long after the Middle Ages and its outward forms, at least, were preserved in the concepts of "genera", "species", "characters", and "differentiae", as well as in the doctrine of divine special creation, accepted by Linnaeus and other orthodox taxonomists of his day (see also Hull, 1965). In practice, many good systematists were partial Adansonians long before the term came into its present vogue. Phylogeny, as we understand it, was a concept unknown to Adanson, though he was no divine-creationist, but modern *pheneticism* not only purports to be stringently Adansonian but also emphatically rejects the use of phylogenetic considerations in reaching taxonomic conclusions (that is to say, in arriving at particular classifications). However, its proponents are mostly careful to state that they do not reject subsequent or independent phylogenetic interpretation, or "speculation" as many prefer to put it. Most pheneticists also reject taxonomic use of the "biological species concept" developed, with variations, in numerous publications by Dobzhansky, Huxley, Mayr, Stebbins, and others, and strongly advocated in rather purist terms by Áskell Löve (e.g., Dobzhansky, 1951; Huxley, 1942; Mayr, 1939, 1957*a*, 1957*b*, 1963; Stebbins, 1950; Löve, 1964).

Since many evolutionary taxonomists and biosystematists have thought that pheneticism unjustifiably neglects the important gains in understanding contributed by their approach to biology, a spate of discussions has ensued, some of them strongly polemical, in which various issues have been debated and frequently confused. Traditional taxonomists have joined in with more pragmatic arguments and from fear of displacement or interference by technical innovations which, perhaps often rightly, they regard as unnecessary. On the whole the pheneticists have spoken more loudly and with the confidence of revolutionaries who sense that the *Zeitgeist* is on their side. In the course of a decade the numerical pheneticists have come to hold the centre of the stage. Such successes are at times due to salesmanship rather than scientific merit, and we shall do well to look critically at the foundations of phenetics. Time and performance, of course, will provide the acid tests.

I shall defer most of the discussion of numerical techniques in taxonomy until we have dealt with the more general subject of systematizing the objects of our experience.

THE NATURE OF ORDINATION

As several authors (e.g., Williams, 1967) have recently reminded us, an orderly arrangement of objects, or more usually of the symbols representing them, need not be a classification; we may settle for an *ordination*, that is, we may assign relative positions to objects according to their states with respect to a set of their "attributes", a separate dimension being necessary for each attribute. This procedure establishes an "attribute-space" (usually abstract), in which the objects are represented by points or sometimes regions. Obviously, to be meaningful in the ordination, each of these attributes must be represented by at least two states in the set of objects under consideration; in other words, they are "pluri-state attributes".* An example of the simplest non-trivial case would be the ordering in one dimension of, say, men according to their measurements (states) of the attribute *height*, or of events according to *sequence in time* (unless relativistic considerations are negligible the latter case requires specification of a frame of reference). Two or more objects may occupy the same position in the attribute-space. They are then indistinguishable with respect to the attributes concerned, but we may still regard them as distinct entities by reference to other attributes.

Ordination *does* involve some implicit classification, as we shall see. Consider a set of objects each possessing what we may call "elementary attributes". For the moment we may define the latter as any properties we can and wish to specify, for example six-leggedness, a length of four millimetres, or orange colour. Before we can assign positions to the objects in any ordination we must establish working homologies between them. This implies setting up one-to-one (pluri-unique) correspondences, over the object set, between some of the elementary attributes of the objects. The result may be more or less reasonable according to the circumstances. It is reasonable to establish a correspondence between the surface areas of a moss leaf, a cycad leaf, and a lycopod leaf if we are interested in photosynthetic capacity—it is scarcely reasonable if our interest is in phylogeny, since most botanists regard these leaves as evolutionarily non-homologous. The establishment of a correspondence ranging over the object set, whether reasonable or not, is tantamount to a classification of the attributes: we have assigned a certain one of the elementary attributes of each object to a class. From the property by which we define this class we derive a pluri-state attribute applicable to all members of the object set; the elementary attributes then become the individual "states".

The property "measurable length" is here regarded as an abstraction from the set of actual measurable lengths; the very definition of this set implies a classification of these elementary attributes on the basis of a property common to them all (the property of being a *length*). We could look at this relation in other ways: for instance, we might regard the possession of a particular length as dependent on having length at all; again, the particular lengths are attributes of the individual objects while length is a property of all the objects.† It is unfortunate that the term "attribute" (or "character") is used in the literature at these different levels. In what follows it will be necessary to use it in both senses but either the context or some qualifying term should make the particular application clear.

It has been assumed in the preceding that for a single object the "states" should be mutually exclusive—ordinarily a leaf cannot have more than one measurement of length (at any instant). When the actual observations are made upon *parts* of the objects under ordination (or classification) the state may be expressed by some suitable statistic, for example, the mean leaf-length or the largest observed leaf-length (the object here being a plant, a

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* I shall use the prefixes "pluri-" and "multi-" to signify respectively "more than one" and "more than two" (or "more than three" for dimensionality).

† When appropriate, the zero state must be included in the range of the pluri-state attribute. Here length, even if sometimes zero, is considered to be a property of all the objects if a comparison on the basis of length is meaningful. Thus, for a snake, it is reasonable to treat the length (zero) of the external limbs as a comparable attribute to the non-zero lengths of such organs in other reptiles; on the other hand for an amphioxus, say, the concept of a measure of length, zero or not, of limbs is inapplicable. In the latter case, if comparing with other chordates, the two-state attribute "presence or absence of limbs" might be appropriate.

population, or a leaf over an extended time). Although this procedure will simplify the ordination, it will result in loss of information. Alternatively, the objects (being composite with respect to the attribute or attributes concerned) may be represented in the attribute-space not as single points but as regions, which may overlap. For complete specification we then require an evaluable density function. For any one attribute (dimension) this may or may not be easily expressed. If the distribution of variation is Normal, we need to specify only (estimates of) the mean and the standard deviation (or the variance); if it is non-Normal but follows some other regular pattern it may also be expressed in terms of the distribution function and a small number of parameters. Sometimes a logarithmic or other non-linear scaling transformation may yield such a simple distribution. However, frequency (= density) distributions of variation may be quite irregular, or plurimodal, or discontinuous (e.g., flowers 4-merous 21%, 5-merous 79%). Moreover, since more than one attribute is usually involved, the *covariation* within the composite object also becomes important. Thus, the pluridimensional density functions may be very complex indeed, and the extent to which they should be simplified for composite objects (e.g., species or higher taxa) will be a matter of judgement and practicability in each case.

Serious difficulties are introduced into the dimensional representation if some (pluri-state) attributes depend for their expression on the existence of certain states of others, and are therefore not uniformly relevant over the whole set of objects. These circumstances result in the attribute-space being inhomogeneous as to dimensionality (see also Reynolds, 1965). In numerical taxonomy this is a practical problem which has usually been somewhat unsatisfactorily avoided by various shifts and devices such as redefinition of attributes, or by weighting methods (Kendrick, 1965) which most numerical pheneticists frown upon (see Long, 1966, for a facile dismissal and misunderstanding of the serious dependence problem raised by Kendrick).

Still other problems arise when "states" which it seems reasonable to group into a single "attribute" do not admit of an unequivocal measure by which they may be arranged serially, for example, variants of a chemical constituent which differ in replacement-groups. A representation which preserved the symmetry of such cases, and in which they could be combined with serial (or two-state) cases would call for a space wherein some attributes were expressible in terms of linear co-ordinates and some in terms of higher-order symmetrical (e.g., triangular, tetrahedral, etc.) co-ordinates. This of course implies dimensions within dimensions and enters realms of complexity which, though perhaps beyond practical handling and certainly introducing anisotropic properties into the spaces concerned, should not be glibly passed over, since they *are* inherent in the general problem of ordination. Anticipating matters to be discussed later, in numerical *classification*, which is not necessarily subject to the same practical restrictions as to the spaces implied in the models used, Lance and Williams (1967*c*) have devised an information-statistic computer strategy to deal with mixed data including non-exclusive, non-serial,* multi-state attributes. Still more recently, Wallace and Boulton (1968) have developed another mixed-data strategy.

Although ordination implies assignment of relative position, it is not essential for it to be metric; no particular fixed measure is obligatory. The relation expressed by saying that, in a one-dimensional linear (in the sense of non-closed) space, B lies *between* A and C does not require either that we

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* "Non-serial" seems preferable in this context to "disordered", as used by Lance and Williams.

know just how far B is distant from A and C, or that it has any fixed position, or indeed that a measure of distance has any meaning at all. Here three distinct points will define an ordering, without any specification of direction in the space. If a direction is assigned, two points A and B are sufficient to define an ordination. Further, ordination remains mathematically meaningful, though difficult to handle, if (in each or any of the dimensions) the arrangement is cyclic (then, however, we should require a minimum of four points in the non-directional non-metric case, three in the directional non-metric) or in some other way not simply linear. Moreover, no concept of a continuum is necessarily required; there may be only discrete positions. Thus, the abstract space in which we represent an ordination may differ from our everyday concept of physical space in one or more of five ways:

(1) it may be finite,
(2) it may be more than three-dimensional,
(3) it may be non-Euclidean,
(4) it may be non-metric,*
(5) it may be discontinuous.

It must, however, be a topological space. In loose terms: however we may deform our representation by variation of scales in any direction, the ordination must not be altered. In any but the simplest cases it is no easy matter to elucidate and explain the topological and metrical properties of the infinite variety of definable spaces; *this is no reason to assume*, as is often done, *that simple spatial models are particularly appropriate to taxonomic ordination*. (For an introduction to some abstract spaces see, e.g., Sawyer, 1955, and Courant and Robbins, 1961; there are many more advanced texts, for instance that of Kelley cited by Williams and Dale, 1965).

Non-mathematicians are conditioned to believe that there is something "natural" about Euclidean space and the Euclidean metric (the latter means, roughly, that if we set up rectangular, similarly-scaled, Cartesian co-ordinates in an n-dimensional space then the distance between any two points P and Q is given by the Pythagorean function

$$d(P,Q)=[\sum_{i=1}^{n}(x_{iP}-x_{iQ})^2]^{\frac{1}{2}},$$

where x_{iP}, x_{iQ} are the co-ordinates of P, Q respectively in the ith dimension. This is an extension to n dimensions of the familiar theorem of Pythagoras that the length of the hypotenuse of a right triangle is the square root of the sum of the squared lengths of the two orthogonal sides. (Oblique co-ordinate axes may also be set up in a Euclidean space, and are used with the Mahalanobis "generalized distance" measure (Sokal, 1965; Menitskiĭ, 1966) though Kendall (1957) and Williams and Dale (1965) have challenged the validity of the procedure in respect of this particular statistic.) However, from what we may know of cartography and navigation most of us will admit that something rather different is involved in the geometry of the surface of a sphere. We customarily think of a sphere as an object in three-dimensional linear (Euclidean) space. Mathematically, however, its surface geometry can be considered in complete isolation as a closed, curved, two-dimensional space which we can, if we wish, *embed* in a three-dimensional Euclidean space. We shall probably also have heard that representation of space-time in the General Theory of Relativity calls for a particular four-dimensional case of a strange collection called Riemannian spaces, which

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* Conditions exist in which there is not a complete absence of metrical properties; semi-metric, quasi-metric, and disjoint metric spaces all arise in numerical taxonomy (Williams and Dale, 1965).

constitute a more general class of curved spaces. These notions of naturalness arise in the ordering of our spatial experience of the physical world, but we are accustomed also to graphical representation of non-spatial quantities in co-ordinate systems in what appear to be Euclidean spaces. Actually, such representations often do not imply, or allow, any concept of inter-point distance involving more than one co-ordinate, and there is then in fact no implication of a Euclidean (Pythagorean) metric. As an extension from such representations, the concept of abstract Euclidean spaces of more than three dimensions has become familiar, as has the correspondence (isomorphism) of algebra and geometry, first clarified by Descartes, which freed geometry of the need for pictorial representability.

Euclidean metrics are implicit in most of the models used in classical statistics, including such probabilistic techniques of multivariate statistics as principal component analysis, factor analysis, and canonical analysis, which depend on the method of least squares (e.g., Kendall, 1950, 1957; Seal, 1964). Because of these familiarities and the convenient pre-existence of statistical techniques, some authors on taximetrics (e.g., Sokal, 1961, 1965; Sokal and Sneath, 1963; Goodall, 1964; Jancey, 1966) have shown a strong preference for Euclidean models. Sokal (1961, p. 73) and Boyce (1964) speak (nonsensically in the context of comparison of attribute sets) of the Pythagorean measure as "true distance" when contrasting it with the "mean character distance" (M.C.D.), used by Cain and Harrison (1958). The M.C.D. in fact defines what may be called a lattice metric—the distance function here is

$$d(P,Q)=\sum_{i=1}^{n} | x_{iP}-x_{iQ} |$$

$\left(\text{ignoring the M.C.D.'s scaling factor } \frac{1}{n}\right)$ which means that the shortest distance between two points is, in general, "around the corners", as for a rook's moves in chess ($n=2$) or an ant travelling along the bars of a children's "jungle-gym" ($n=3$). Such a lattice-metric space can be embedded in a Euclidean space; it differs from the latter in that, given a basis of rational numbers, no concept of algebraic irrational numbers is needed to express distances within it, nor are there any smooth curves or transcendental irrationals like π. Unlike those of a Euclidean space, lattice-space distances are not invariant under rotation of axes, indeed in general (with a rational-number basis) the "fixed" points themselves will "disappear" under such rotation. These details are not relevant to practical taximetrics but are mentioned to illustrate that some of the mathematical properties which we take for granted in the Euclidean metric can change drastically with a very simple change of metric. Lance and Williams (1967*c*) refer to this lattice metric as the "Manhattan metric" and point out that it is the first-order case of a general class (Minkowski metrics), the Euclidean metric being the second-order case.

The infinite-order case is of interest since it is the "chess-king's metric" in which

$$d(P,Q)=| x_{iP}-x_{iQ} |_{\max},$$

that is, the distance is simply the value of the greatest single co-ordinate difference between the points.

There is no *a priori* reason why such a metric, or indeed many others, should yield a less "realistic" measure of "distance" (or its complement, similarity) between sets of attribute-states. Nevertheless, even the mathematically sophisticated Williams and Dale (1965) favoured Euclidean systems, on grounds of statistical convenience and "pictorial" representability (which fails in any case due to the distortions and indeed the semi-metric property of projective mappings of higher-dimensional spaces on to their lower-dimensional subspaces, i.e., originally distinct points may not be distinct in the mapping). Jancey (1965) suggests that the intuitive concept of similarity in terms of real spatial relationships renders the Euclidean metric worthy of retention. If this merely reinforces preconceptions, its value seems doubtful and, as Macnaughton-Smith (1965) says, "this 'visualizable' quality is by no means a necessity, and one would wish to use the most appropriate function regardless of whether it was visualizable". More recent papers on taximetrics (e.g., Lance and Williams, 1967*c*) show less attachment to Euclidean representations.

For particular purposes, ordination procedures may be more efficient than classifications in that they need not involve us in loss of information, nor do they set up so many "artificial" distinctions or segmentations of gradual transitions. Their usefulness will naturally depend on the appropriateness to our purposes of the attributes chosen, and on the measure adopted for assigning position in each dimension. Incommensurability in the various dimensions is a problem only if we are interested in such concepts as similarity over a multiplicity of attributes or "distance" between objects (points or regions) in the attribute-space. Perhaps, if our mental apparatus were differently organized, multidimensional ordination would meet most of our requirements for the organization, retrieval and comparison of information. This is a question for those studying the design of logical and quasi-mental machines.

The Nature of Classification

As it happens, our minds cannot cope with multidimensional systems and we need to classify, even though we lose information and introduce distortions and artificialities in the process.

In dealing with the chain of questions posed earlier, it will be useful to refer frequently to one of the most definitive statements of the "philosophical" attitude, a contribution by Gilmour and Walters (1964) entitled "Philosophy and Classification". I should make it clear that, although I shall offer some severe criticisms of the purely phenetic approach, a good deal of what Gilmour and Walters have to say is not in dispute and that they are aware of some of the unresolvable aspects of the problems raised.

It has been repeatedly stressed, especially by Gilmour and his followers, that the values of classifications should be assessed according to the range of their purposes. We need not here discuss classifications of narrowly-defined purpose, although many of the problems associated with more general classifications may arise, *in parvo*, in the special cases also.

Biological taxonomy is expected to produce classifications of broad utility; Gilmour and Walters have termed these *general-purpose classifications*. More essentialistic taxonomists have aimed to produce so-called "natural" classifications which, it is claimed, would in part meet the requirements of a general-purpose classification but would also, as it were, reflect some more fundamental truth about nature. As Gilmour and Walters point out, there are philosophical objections to the term "natural" (and its opposite, "artificial") in this usage. They say: "the view that there are such 'natural kinds', differing in some 'fundamental' way from other, 'artificial' methods of classifying the same objects, is very difficult to sustain; a more useful way of looking at the situation is that these so-called '[natural] kinds' are classes showing [a] high degree of correlation of attributes, differing only in degree from other classes with a less high correlation". (The second part of this statement raises difficulties, discussion of which is deferred.) Later, they outline eight principles which they suggest should be applied to biological classification. Since these represent, in summary, an influential attitude, I shall quote them in full as a framework for critical comment.

> "(1) The term 'classification' is used by philosophers to describe the act, conscious or unconscious, of grouping objects into classes because of certain attributes they have in common."

Comment: We may have difficulty in defining "objects" and "attributes" but the definition will serve. Here, and in what follows, these authors use "attributes" to include what I have called "elementary attributes" rather than "pluri-state attributes". I shall follow their usage while it remains relevant.

> "(2) Classification, used in this sense, is man's basic method of dealing with the multiplicity of individual objects in the world around him."

Comment: Whilst the statement is true enough, its restriction to "man" is unnecessary and symptomatic of an anthropocentric viewpoint which pervades philosophy. Other animals classify, so do some machines; certainly any highly intelligent being would do so (though, as I have said, some might be less compulsive classifiers than ourselves). The process of classification does not depend on the existence of man. It does, I suppose, depend on the existence of an *agent* of some kind—"*classifico ergo sum!*"—but we may be led into unprofitable by-ways if we pursue this further.

> "(3) Since classification is a product of man's need to deal with his environment, the actual classifications that he makes are determined by his desires and purposes in relation to that environment."

> "(4) The suitability of any particular classification can only be judged in relation to the purpose for which that classification was made."

Comment: This is not necessarily so; a classification made for one purpose may suit another very well. It should be judged in relation to the purpose for which it is *required*.

> "(5) Two types of classification can be distinguished, with every gradation between them: 'general-purpose' classifications and 'special-purpose' classifications."

> "(6) General-purpose classifications consist of classes containing objects with a large number of attributes in common, thus making them useful for a wide range of purposes; special-purpose classifications consist of classes containing objects with only a few attributes in common, and hence serve a more limited range of purposes."

Comment: In a "common-sense" way, we doubtless all think that we can see what is meant here. However, the concept of "number of attributes in common", or more sophisticated measures of similarity, lies at the heart of the phenetic (Adansonian) approach, and of the mathematical methods which have been developed on the basis of this approach. Therefore we must examine this statement more critically. There are several hidden variables here, and unless we can somehow define, measure, and control them, the statement simply will not do as a basis for the precise, "objective" approach to taxonomy which many pheneticists state to be their aim.

First, we must consider the domain from which the attributes are to be chosen. Every "object", a term which may be extended to cover any physical or conceptual object of discourse or thought, has an infinitude of attributes. That is to say, the object itself does not set any bound beyond which we can say "no further attributes exist"; this conclusion is not affected by the practical limitations of our thought. (We can ignore such playthings of paradox-fanciers as "the concept which has no attributes".) A little reflection will show, for instance, that any object bears various relationships, tenuous as they may be, to every other physical object or collection of objects in the universe, at every point on the world-line of every particle in space-time. There are likewise relationships to the past and future states of the object itself, and indeed to innumerable abstract concepts. Perhaps this sounds extreme, but it is an inescapable conclusion from any general concept of an attribute, and there is no *a priori* reason to stop at any particular point in our search for further attributes. It may be objected that relations to other objects are not *intrinsic* attributes of the object under consideration. Reflection will show that *all* describable characteristics are relations to other objects or concepts; we simply cannot speak meaningfully about the properties of a thing in itself, Plato or Whitehead notwithstanding. Likewise, it is of no practical help to adopt a holistic standpoint and claim that everything is part of one great integrated whole and that the individual objects and their attributes are mental abstractions from this whole—this can only lead one to say "everything is as it is" and to resign from the game. *Second*, the considerations just stated will show also that the attributes themselves are infinitely divisible. Our concept of "elementary attributes" implies no atomicity. *Third*, there can exist no absolute measure of similarity (i.e., matching correspondence) between non-identical sets of attributes which are infinite, unbounded, and unconstrained.

Infinity is no simple subject, but we are now trapped into considering some consequences of invoking it. We find that measures of matching can in fact exist between certain infinite sets. Let us consider, for instance, the set of all positive integers A: {1, 2, 3, 4, . . .} and the set of odd positive integers B: {1, 3, 5, 7, . . .} , and regard the elements of these sets as our selected elementary attributes of two "objects" which being here equivalent to the sets described, we may also label A and B. Let us then first take these elements in the order given and, by an act of classification, group them in pairs (1,1), (2, 3), ... as "states" of a set G of pluri-state attributes which we shall call {I, II, III, IV, . . .}. We could define the "possible" states of the members of G in various ways; one way would be: the "states" of I comprise the presence of 1 or 2 or 3 or . . . . . . in the first position, likewise for II in the second position, and so on. This would permit the comparison of a whole class of sets similar to A and B. Each of the sets A, B, G is infinite but, in the language of the Cantorian theory of transfinite numbers, denumerable (Courant and Robbins, 1961; Dantzig, 1962).

If we compare all the attributes, or any ordered sample of them, and write 1 for a match, 0 for a non-match, we have the correspondence:

G:	I	II	III	IV	. . . . . .
A:	1	2	3	4	. . . . . .
B:	1	3	5	7	. . . . . .

giving the matching sequence: 1 0 0 0 . . . . . ., that is, a simple matching coefficient (Sokal and Sneath, 1963), if we start from 1, of

$$S_{AB}=\frac{\text{matches}}{\text{matches}+\text{non-matches}}=\frac{1}{n},$$

where n is the number of attributes being measured. Obviously, as n tends to infinity, S_{AB} tends to zero. If we start elsewhere we have $S_{AB}=0$ in any case. This is not very helpful but, with what follows, it illustrates the point that it is not only the attributes used, but also the way in which they are grouped and arranged, which affects the results.

If we now look at these sets in another way (one of an infinity of ways) and take as our set H of two-state attributes {i, ii, iii, iv, . . .} the presence or absence (anywhere in A or B) of the numbers 1, 2, 3, 4, ... (this is in effect establishing a new set B′ from the union of B with the set { absence of 2, absence of 4, ... }), we have the correspondence:

$$\begin{array}{llllll} \mathrm{H:} & \mathrm{i} & \mathrm{ii} & \mathrm{iii} & \mathrm{iv} & \ldots\ldots \\ \mathrm{A:} & 1 & 2 & 3 & 4 & \ldots\ldots \\ \mathrm{B}': & 1 & - & 3 & - & \ldots\ldots \end{array}$$

Then, by taking the whole or any ordered sample, we have, scoring for matches as before, 1 0 1 0 1 ...... if we start with an odd number, or 0 1 0 1 0 ...... if we start with an even number, giving $S_{AB'} = \frac{1}{2}$ for any ordered sample of an even number of attributes from H and $S_{AB'} \to \frac{1}{2}$ (as the sample size increases) for any ordered sample of an odd number of attributes from H. We can indeed say that $S_{AB'} = \frac{1}{2}$ for the comparison (made in this particular way) of the two infinite sets of elementary attributes. Moreover, we can say that statistically the most probable estimate of $S_{AB'}$ from any random sample from H is also $\frac{1}{2}$,* and can in fact evaluate the probability of obtaining this or any other result for a sample of any given size. We have, in fact, for our defined sets and procedure, a parameter $S_{AB'}$ and a probability distribution for sampling error.

The infinite sets A, B, and B′, just discussed, are in fact (if considered as linearly ordered sets) bounded in one direction and not in the other, but it would not affect the argument if we took the sets of all integers and of all odd integers (positive, zero, and negative), which are not bounded in either direction. What is more, we may calculate the matches between pluri-dimensionally ordered sets, such as the two-dimensional arrays:

$$\mathrm{C:} \left\{ \begin{array}{cccccccc} 1 & 2 & 1 & 3 & 1 & 4 & \cdot & \cdot \\ 2 & 1 & 3 & 1 & 4 & 1 & \cdot & \cdot \\ 3 & 4 & 3 & 5 & 3 & 6 & \cdot & \cdot \\ 4 & 3 & 5 & 3 & 6 & 3 & \cdot & \cdot \\ 5 & 6 & 5 & 7 & 5 & 8 & \cdot & \cdot \\ 6 & 5 & 7 & 5 & 8 & 5 & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \end{array} \right\} \text{ and } \mathrm{D:} \left\{ \begin{array}{cccccccc} 2 & 2 & 3 & 3 & 4 & 4 & \cdot & \cdot \\ 1 & 2 & 1 & 3 & 1 & 4 & \cdot & \cdot \\ 4 & 4 & 5 & 5 & 6 & 6 & \cdot & \cdot \\ 3 & 4 & 3 & 5 & 3 & 6 & \cdot & \cdot \\ 6 & 6 & 7 & 7 & 8 & 8 & \cdot & \cdot \\ 5 & 6 & 5 & 7 & 5 & 8 & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \end{array} \right\},$$

giving the "obvious" matching coefficient of $S_{CD} = \frac{1}{4}$, though by considering other attributes derived from these sets (e.g., presence or absence of a prime number in a given position) other similarities would be obtained. Such comparable arrays may be bounded or unbounded in any direction, provided that they are conformable or can be rendered conformable. If there is no "natural" bound, one must of course choose appropriate or arbitrary starting points for a matching procedure.

Thus, on such a model, having set up a particular correspondence and using any particular measure of similarity, there *does* exist an actual parametric value of similarity over these infinite sets which we may hope to estimate in various ways. Why, then, do I say that in the general case of all attributes, no such parameter exists—in other words, that no meaning can be attached to the concept of such a parametric value? The reason is that

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* Strictly, for odd-numbered samples the *two* most probable values are those two of the possible values nearest on either side of $\frac{1}{2}$, and these converge on $\frac{1}{2}$ as the sample size increases.

our examples possessed underlying ("built-in", if we like) regularities or patterns which pervaded each of two conformable sets and that, furthermore, we could find a simple and pervading relationship between these two patterns themselves, even though the sets were infinite. We had, in fact, a set-up case with several constraints. In the all-attributes case, no such pervading regularity can exist, since there are no constraints to prevent us bringing in any number of other infinite sets of attributes (elementary or pluri-state) to swamp into infinitesimal proportions any regularity existing among some of the attributes. As a further complication, describable attributes may be dependent upon the existence of other attributes, for example blood pigments cannot be compared as between a bloodless animal and one with blood. This is one aspect of the "no-comparison" problem familiar in the taximetric literature, and I have alluded to it in the discussion of ordination.

It is abundantly clear that, because of such fundamental difficulties, any recourse to an all-attributes concept or to "true" or overall similarity leads us into a hopeless morass. We can, of course, though not without problems, arrive at numerical answers purporting to indicate degrees of similarity (or "distance") if we restrict ourselves to finite sets of attributes or to samples from infinite sets of certain restricted types, as we have seen. This involves subjective decisions, as to:

(i) the set of objects considered usefully comparable;
(ii) the domain of attributes which we consider relevant to our interest in the objects;
(iii) the "fineness" with which we analyse the features into elementary attributes (≡ states);
(iv) the establishment of equivalences or homologies between parts of the objects under comparison; and the consequent grouping of the elementary attributes into two- or multi-state sets, thus specifying what we usually term "the attributes" or "the characters" ("multi-state" here includes "continuously-varying");
(v) the method and intensity of sampling of the objects;
(vi) the method and intensity of sampling of the acceptable sets of "relevant" attributes;
(vii) the quantitative or qualitative measures to be used in expressing the "states" of each attribute (involving an often arbitrary assignment of working commensurability)*;
(viii) the measure of similarity (or distance) to be adopted.

Only some of these are susceptible to a more or less quantitative approach; in those cases statistical or other mathematical principles and techniques will sometimes assist in the judgement but subjective, though not always arbitrary or uninformed, decisions as to appropriateness or usefulness are needed all along the line. I shall mention later some useful bases for such judgements but, as an initial restriction, we may reasonably confine our attention to *attributes which show a degree of stability or regularity in the individual objects over the time-range in which we are interested.* Such a restriction must itself be arbitrary; furthermore, since it does not in itself

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* Williams and Dale (1965) have recognized "the highly autocratic nature" of the convention that attributes are dimensionless ("dimension" is used here as in dimension theory of physics, not in a spatial sense) and that quantities representing different attributes are jointly available for arithmetical manipulation. "Standardization" to unit variance, or in some other way, may add some reasonableness to the commensurability assumption but does not remove the difficulty; the particular scaling thus derived depends in any case on the constitution of the chosen sample of objects.

introduce sufficient constraint to prevent the swamping of overall regularities by additional attributes, *there is still no parametric value of similarity.*

The concept of a "general" classification has been criticized also by Edwards and Cavalli-Sforza (1964), while some authors (e.g. Olson, 1964) have explicitly but unjustifiably assumed that there exists a finite set of "meaningful" characters.

To resume the enumeration of Gilmour and Walters' principles:

> (7) "General-purpose classifications can be made only when the objects concerned are influenced by a powerful factor, which causes a number of their attributes to be highly correlated in their occurrence; in the absence of such a factor, only special-purpose classifications can be made."

Comment: It will be best to avoid discussion of causality; we have perhaps already ventured too far into the philosophical chamber of horrors! In discussing the previous principle I stressed the importance of pervading regularity or pattern (terms which are free of the causative or the particular mathematical connotations of "factor"). We need to know not only something of the patterns but also the range of their pervasiveness and the extent of their relevance to our particular concerns. High correlation (or any other measure of covariation) of occurrence of attributes (i.e., of "states"), which Gilmour and Walters consider to be the *sine qua non* for a general classification, is meaningful only over a restricted domain, as we have seen, and is therefore dependent on our interest and purpose. If we attempt a "general" classification, for example, of the object set:

> {Mao Tse-tung, a peanut, the Sphinx, an electron, a litre of alcohol, the star Achernar} ,

we shall find it very unsatisfying *because we cannot define the field of our interest* or readily choose attribute sets showing regularities. Such sets *could* be found among the infinity of attributes, but would appear to us to be absurdly chosen.

The question is whether one can choose such a domain pervaded by a regularity which, firstly, is perceivable by us, and secondly, seems meaningful and useful to us. For a set of miscellaneous everyday objects there are various ways of selecting a set of *many* pluri-state attributes which would show a high correlation of their states. For instance, the selection could be such that a classification derived from a randomly chosen subset of the original attribute set would have a high probability of grouping the objects according to their geographical origin, which would then be the "factor" or regularity determining the high correlation. Our immediate response is, "But this is a special-purpose classification, and the attributes were specially selected." This is true, but when we select (and we *do* select) the acceptable attributes to be drawn upon in making a "general" taxonomic classification we also unconsciously choose a particular set of attributes specially reflecting a "factor" which is strongly linked to our (selected) interests.

In biological taxonomy, many regularities are discernible among the attributes which we customarily consider useful for classification, of interest to other branches of biology, or of practical importance. The reasons for these qualities and for the regularities are themselves closely though complexly related, and this is the nub of the matter. Evolutionary processes, selection and adaptation, population structure and dynamics, and the genetic mechanism itself in its grosser aspects as well as in its physico-chemical basis and its organization for the storage, replication, transfer, and implementation of instructive information—all these, intricately interwoven as they are, are closely associated with those perceivable (phenetic) characteristics of organisms which concern us. How this bears on our original questions concerning optimal classification will be discussed after dealing with a few remaining points.

> "(8) A distinction can be made between typological and definitional methods of making a classification. In the former, which is exemplified in the semantic development of the words used in everyday language, no one or more attributes are necessarily possessed by *all* the objects in a particular class, but rather, these objects show a 'family resemblance' to an imaginary 'type-representative' of the class. The definitional method, on the other hand, involves a conscious laying-down of certain attributes that an object *must* possess in order to belong to a particular class. Each method is appropriate to a particular type of purpose."

Comment: Provided that we define the attributes and attribute-sets, this is a valid methodological distinction. The use of "typological" here may be misleading, however, since it suggests the essentialistic concept of an archetype or *Bauplan* which has been effectively criticized, for example, by Simpson (1961) and Hull (1965). It will suffice to quote with approval Simpson's dicta that "Typological theory is linked with philosophical idealism [i.e. essentialism. L.J.] which on pragmatic grounds (if no other!) must be excluded from modern science" and that "such metaphysical beliefs . . . have no heuristic value". This is not to deny the usefulness of a sort of "working" Type concept derived as an ordering of our experience and used for the purpose of orientation of further experience (Carolin, 1967). Such a concept must be subject to any necessary revision in the light of new data or of reconsideration, and need have neither essentialistic nor phylogenetic implications. (This has no present connection whatever with the system of nomenclatural "types" which are now merely formal reference points for the names of taxa.) The first of the two methods distinguished by Gilmour and Walters may be redefined to exclude any notion of a "type-representative" and then becomes in effect the *polythetic* method (Sokal and Sneath, 1963; Williams and Dale, 1965) used either intuitively or numerically in most biological systematics today. The second is similar to the *monothetic* method employed by some "old-fashioned" systematists in placing their taxa, and used generally in keys and some other post-classification procedures for discrimination and assignment, as well as in ecological, non-biological and *ad hoc* classifications. Monothetic classifications are by nature arbitrary or suitable only for special purposes, and will not henceforth concern us.

Apart from these "Principles", several other statements of Gilmour and Walters are pertinent as expressions of the phenetic school's viewpoint. They will serve as convenient pegs (not, I hope, as a gallows!) upon which to hang some observations. Gilmour and Walters refer disapprovingly to "the impression that taxonomic work has an aim of its own, apart from the aims of biological science as a whole, and that, if this aim could be fully accomplished, it would result in a single, perfect, ideal classification of living things", and proceed to uphold "the view that neither affinity nor phylogenetic relationship can be regarded as valid aims for taxonomy and that they have been adopted because of a lack of appreciation by biologists of one of the basic principles of classification enunciated by philosophers—namely the principle that it should serve some extraneous purpose."

We may grant that the quest for a single, perfect classification is beset with difficulties, some of which are inherently insoluble. But what do the words "should" and "extraneous" mean in this passage? We have seen that classifications can only be judged in relation to some set of requirements (not necessarily an *aim* of the maker of the classification) but the expression of phylogeny is as valid as any other requirement, even if it cannot be perfectly fulfilled. Biological classifications are useful precisely because of circumstances inextricable from those involved in evolution in general and the phylogeny of the groups concerned in particular. Hence one cannot speak of "extraneous" purpose as if this must exclude phylogenetic expression.

The authors proceed: "This lack of appreciation has left, so to speak, a vacuum which was filled, in pre-Darwinian times by the semi-theological concept of affinity, and later by the *equally vague* [My emphasis. L.J.] concept of phylogenetic relationship."

I am at a loss to understand how even a philosopher, much less two biologists, could make this astonishing statement! Phylogenetic (cladistic) relationship, though not metrically expressible in any unequivocal way, is (potentially) topologically representable with little ambiguity, at least above the level of the coenospecies. We may not *know* the details of phylogeny but (unless we reject biological evolution) we must accept that they *exist uniquely* in space and time, and therefore form a concrete basis for concepts of phylogenetic relationship, however defined. In contrast, the notion of "affinity" is subject to unlimited variation and any claim for a firm basis for it must be metaphysical. The province of metaphysics appears to be to pose and seek to answer questions which are either practically or inherently unanswerable. If the former become practically answerable then that part of the subject moves into the realm of natural science. The latter have no place in science—or perhaps in any useful inquiry—except as a warning.

Gilmour and Walters then suggest that the purpose of taxonomy should be to make a "broad map of the diversity of living things which, by taking account of as wide a range of attributes as possible, will serve the needs of as many as possible of those concerned with animals and plants"; they regard phylogeny as the "factor" making such a general-purpose classification possible.

This procedure provides no definable basis for agreement or for testing whether a classification should be changed or not, except that these authors would "regard stability of nomenclature as a very important factor in deciding whether or not to alter the rank of a taxon". Now, under the present system formal changes merely of *rank* (as distinct from transfer from one group to another) are not called for by changes of *position* on the topological map of inferred phylogeny (some palaeontological cases apart) and in fact usually arise from re-evaluation of the importance of phenetic differences, so that it is hard to see how the phenetic philosophy itself affects this situation! From their next remark that "where new knowledge renders an existing classification clearly absurd, changes must be made, but we suggest that such cases should be comparatively few", it is clear that, just like phyleticists, Gilmour and Walters cannot stomach classifications which are manifestly inconsistent with the inferred phylogeny or at least with the inferred genetic constitution. In a later paper, Walters (1965) expresses an even more extreme pragmatism; one may share his impatience with nomenclatural formalities and quibbles, but these are not a product of phyleticism.

The virtue of arbitrarily imposed stability of any unsatisfactory system is not apparent, though frivolous changes should be avoided. Systematics as a humble servant supplying changeless tags for gardeners, agriculturists, foresters, or physiologists would contribute little of interest to biology. Caution, criticism, and common sense play useful roles in science but conservatism for its own sake is inimical to it. If taxonomy were to have only the uninspiring goals set up for it by Gilmour and Walters it might as well be abandoned to any rude mechanicals who cared to gather voluminous data for a computer. Understanding of nature would not be its purpose and any value it might have for biological theory would be incidental.

THE VICIOUS CIRCLE

Another philosophical defence of phenetics rests on the assertion that to allow phylogenetic conclusions (speculations, hypotheses) to influence taxonomic conclusions involves us in circular reasoning and is therefore inadmissible. This view is forcefully expressed by Sokal and Sneath (1963) and accepted by Williams and Dale (1965). Many practising systematists (e.g., Carolin, 1967) now defend it in theory, but nevertheless appear to be influenced by phylogenetic thinking in their actual work.

It is true that there are some recursive loops in the phyletic taxonomist's reasoning. This applies equally to morphological interpretation and description, in particular to the problem of homology. Attempts to develop "logical", non-phylogenetic definitions of homology (e.g., Mason, 1957; Carolin, 1967) are doomed to failure, being open to the same criticisms as phenetic taxonomy.* Indeed homology needs no separate treatment since comparative morphology implies taxonomy and *vice versa*. The need for very careful interpretation of morphological homology on a basis of evolutionary likelihood is illustrated by the highly modified and cryptic structures of many animals and plants, for instance the "bulrush" or "cat-tail" genus *Typha* (Briggs and Johnson, 1968) as considered in relation to other groups of monocotyledons. No phenetic comparison could be of much value here unless the relevant homologies were for the most part correctly worked out beforehand. The comparative survey by Hamann (1961) of the families of the "Farinosae", though most comprehensive and thoughtful, includes a numerical phenetic study of which we cannot confidently accept the results, because of serious doubt as to the homology of many of the features compared. Here, as often in broad surveys, the data have been drawn partly from various published descriptions, which may be very misleading. Throckmorton (1965) points out that phenetic parallelism may be equivalent to genotypic homology, that is, similar conditions which appear to arise independently may be due to separate "assembling" of elements of a common pre-existing genotype.

We have seen that there is a hidden circularity in any definition of a "general classification" and a hidden infinite regress in every aspect of phenetics. The Infinite Regress and the Vicious Circle or ultimate tautology are the two most inescapable hard facts of philosophy, mathematics, and science—at bottom we must come upon one or the other. They have been encountered by every critical child who has asked, "If God [or whatever agent or process one wishes to substitute] made the Universe, then who made God?" In any case, what is before or after, backwards or forwards, on a cosmic (or ultra-cosmic) scale? Such ancient questions are ultimately

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* Key (1967) attempts to define *operational homology* thus: "Feature a_1 of organism A is said to be *homologous* with feature b_1 of organism B if comparison of a_1 and b_1 with each other, rather than with any third feature, is a necessary condition for minimising the overall difference between A and B". Despite its spuriously precise formulation, such a definition is itself thoroughly non-operational except in finite cases, for the reasons already given. When discussing set-correspondences, I have used the term "working homologies" simply for such correspondences of features (of objects of any kind) as we may take, possibly on very complex and subtle grounds, to be a reasonable basis for further steps in the comparative procedure. The "operational homology" concept discussed at length by Sokal and Sneath (1963) boils down to much the same thing; it is only vaguely operational, in the sense of having some empirical consequences which can be checked (Hull, 1967).

unanswerable, though they may be pushed back somewhat along the regress, but they may help us to dispense with some unnecessary non-answers to non-questions.

The partial circularity inherent in the phylogenetic approach is not reducible to a *petitio principi* as is the simple vicious circle of logic. It is not just saying tautologically that conclusion B follows from premise A when we have already used B in formulating A (as, for instance, "a classification produced by a good taxonomist is good", having defined a good taxonomist as "one who always produces good classifications"). Nor is it arguing in an epistemological circle (Hull, 1967), that is, purporting to show that B is true because of A when we can only know that A is true if we know that B is true (as, for instance, "a newly discovered mammal from Africa is a placental mammal because all African mammals are placentals").

Rather, we are accepting a degree of positive feedback in what is not a chain but an anastomosing plexus of reasoning and evidence. The premises and reasoning used in arriving at a representation of a (hopefully) deduced phylogeny are highly complex, as are the conclusions (see, for example, the attempted reconstructions of the phylogeny of Dipsacaceae by Ehrendorfer, 1964*a*, 1964*b*, and of Proteaceae by Johnson and Briggs, 1963; also Thorne, 1963). There is no hope of making them fully explicit, but to deny them validity on that ground would be to deny validity to all but the simplest reasoned conclusions in science or life. Many pheneticists take the view that, in the absence of a "time-machine" (Carolin, 1967), palaeontological data provide the only information of direct phylogenetic significance that can be validly fed into a taxonomic system. But most of us do, after all, believe that the processes of evolution are pretty well understood. Most phylogenetically inclined taxonomists and general evolutionists consider that the existing corpus of evidence justifies the use of evolutionary principles to make sense of the diversity of Recent as well as fossil organisms. This involves a great deal of argument by analogy and extrapolation, but so does most of science. How many of us *know* from direct evidence that we consist of neutrons, protons, and electrons, or even that we have chromosomes? But we believe it because we have convincing evidence of consistency in the physical world. In the course of describing and analysing the phylogenist's, and in fact the common scientific, method of successive approximation, Hull (1965, 1967) presents powerful philosophical arguments for a similar rejection of the charge that phyletics is based on viciously circular reasoning, in either the logical or epistemological sense.

It is a commonplace that, outside mathematics, most scientific hypotheses and theories are inductively derived, though we aim to reduce the number of such hypotheses to a minimum and to use them as postulates for a deductive superstructure. They are testable by predictive value, self-consistency, and consistency with extraneous evidence. Operationism requires a hypothesis to be potentially falsifiable, that is, subject to tests which *could show* it to be false. If we exclude phylogenetic interpretation, phenetic "general" classifications of organisms are scarcely hypotheses at all*; they are subject merely to practical evaluation by their predictivity within the field of our interest. Phyletic classifications (which of course use phenetic techniques as *part* of their method of derivation) may certainly be equally effectively judged

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* This is admitted by Williams and Dale (1965), though we may accept their suggestion that non-probabilistic numerical classifications in other fields have value as hypothesis-generating systems. While they allow that phylogenetic hypotheses may be generated, these authors tend to dismiss them on the ground of their alleged untestability.

on predictivity; they also embody biological hypotheses (though the classification as such may not fully *express* them), which are subject to many checks of self-consistency and extrinsic consistency—though such checks are not necessarily easily expressed in quantitative terms. It has been claimed (e.g., by Birch and Ehrlich, 1967*a*) that these embodied hypotheses, and indeed synthetic evolutionary theory generally, are not falsifiable. This is due to the unsophisticated assumption that a useful hypothesis must be a sufficiently simple and definable proposition to be falsifiable in the same way as the statements: "all swans are white" (known to be false) and "the equation $x^n+y^n=z^n$ has no solutions where x, y, z, and n are integers and $n > 2$" (the celebrated "Last Theorem" of Fermat, which is not a deductively proved theorem at all but has not been shown to be false). Phylogenetic hypotheses are susceptible of demonstration that they are very likely to be untrue, and this is indeed the only disprovability we can hope for in a good deal of science. We can achieve a considerable and reasonably convincing understanding of nature in such ways, and can apply a great deal of criticism to our evidence, arguments, and conclusions. Mackerras (1964), in a cogent defence of the phylogenetic method, says that "to make a preliminary arrangement on general resemblance (as is often done), test its components for phylogenetic concordance or discordance, and then base a classification on the results of those tests, is not circular reasoning in any sense of the words."

Birch and Ehrlich (1967*b*) say, "We *do not* need to consider the unknown history of the organisms . . . in order to classify them . . . Phylogenetic history . . . is not pertinent to most of the uses of classification. Astronomers do not have to know the histories of sidereal bodies, nor physicists of atomic particles in order to do valid scientific work with them." These authors claim precision for phenetic methodology and are opposed to "mixtures" of phenetics and phyletics in classificatory procedures. An outrageous stab on their part is to accuse the evolutionist Ernst Mayr of Platonism; to interpret Mayr's insistence on the "reality" (i.e., reasonable definability) and importance of the species in evolutionary theory as a form of Platonic essentialism is a gross distortion indeed. Birch and Ehrlich's quoted statement is partly true; we certainly *can* classify without reference to phylogeny (Linnaeus did it!) and, for the reasons already given, such classifications may work quite well. This is in itself *no* reason at all to reject consideration of phylogeny, which is one important aspect of the evolutionary process that underlies the workability of our classifications. Astronomers *do*, of course, consider the histories of stars and may modify their classifications accordingly. The case of [sub]atomic particles is simpler and not really comparable; nevertheless elucidation of underlying regularities and the possible transformations of particles is highly pertinent to our mental systematization of them. Improved classification in these cases does in fact involve positive feedback (i.e., a "mixed" procedure).

For the reconstruction of phylogenies we can use evidence of many kinds which is not just derived from the patterns of phenetic diversity we observe in the organisms under study. Cytogenetic data, for example, have a special relevance beyond mere matching of attributes of the chromosomes or of the genetic systems. The contribution of comparative biochemistry, especially where its adaptational significance is evident or where biosynthetic pathways indicate probable directions of change (e.g., Scora, 1967), frequently goes beyond mere phenetic comparison. Quite often there is a fossil record of considerable value. In particular, probable directions in the evolution of organ-systems can be deduced from ontogenetic, ecological, adaptational, and historical evidence and comparisons. Examples are legion and can be found in works on evolutionary theory and in many publications presenting critically argued reconstructions, as in the case of the Proteaceae, already cited. A single example will suffice: floral adaptations for pollination by long-tongued insects or by birds cannot have occurred in geological periods before such animals existed. Any phenetic classification which grouped organisms in a manner inconsistent with such a fact (taking all other relevant information into account) would not be acceptable as even roughly consistent with phylogeny, and there is no reason why we should be asked to accept it simply because of claims of repeatability, objectivity, precision, or stability. Repeatability is not dependent on the phenetic approach and the claimed objectivity and precision are superficial. Stability has been mentioned already and later will be discussed further.

In summary, such philosophical considerations as we have reviewed, far from invalidating the phyletic approach to taxonomy, may be turned against the pheneticists themselves.

Taximetrics*. I. Numerical Phenetics

Evaluation and methods

We have discussed at length the foundations of phenetics. Only brief mention can be made of the techniques of numerical taxonomy and their applicability. These are being used, often on rather trivial problems, by increasing numbers of taxonomists who often seem to accept very uncritically the philosophical foundations and the mathematical models which they explicitly or implicitly embody. The worth of the results seems usually to be measured against what the taxonomist has done, or would have done, without the techniques—an amusing test, to say the least. Mathematical methods of ordination and classification seem to have thrown very little new light on the taxonomic problems of "difficult" groups, despite their usefulness in ecology or in non-biological fields where there is no obviously prime source of regularity comparable with phylogeny and the genetic constitution of organisms.

It is true that Watson *et al.* (1966, 1967) have produced a slightly better classification of the Epacridaceae and a considerably better one of the Ericaceae than those previously existing (not necessarily "accepted" as they put it)—but the latter were almost a century old and based on less complete data and, in the case of Drude's less satisfactory classification, on an analytic or monothetic approach. From the data, it seems to me that many good modern taxonomists should have been able to effect equal improvement by adequate study and phylogenetic consideration. Indeed, by careful study and reasoning, Watson had already cleared up most of the problems, though the computer analysis suggested some placings for doubtful genera. In the more difficult case of the Basidiomycetes, reported by Kendrick and Weresub (1966), "Adansonian" computer analyses gave thoroughly unsatisfactory results as compared with a reasoned phylogenetic approach. It would be difficult to explain these away by criticism of the mathematical models or

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* The forms "taxometrics" and "taxonometrics" are also in current use. "Taximetrics" is etymologically the best-formed since the first root is the Greek τάξις, τάξεως (or Ionic τάξιος)—"an arranging", of which the combining form in Greek compounds was ταξι-(Liddell and Scott, 1864). The word "taxonomy" is badly formed (cf. the French "taxinomie") but is now firmly established by usage. One may hope that "taximetrics", as used by Rogers (1963), will prevail, or perhaps it is not yet too late to substitute the simpler "taximetry", with the ending on the model of "geometry", "trigonometry", "biometry", "anthropometry", etc. Further development of the first of these examples could lead to the delightful consequence of numerical taxonomists' being called "taximeters".

techniques employed; the source of trouble seems to have been evolutionary convergence. In a group of *Solanum* species and hybrids, Heiser *et al.* (1965) found that the results of a phenetic numerical analysis were less satisfactory than those of a "subjective" study when checked with the considerable biosystematic information.

A recent *coup d'œuil* over the grass family, using a probabilistic mixed-data method (Clifford and Goodall, 1967), seems only to confirm the well-established features of modern non-numerical classifications and to indicate that the "difficult" cases actually are so. Its sampling basis of one species per tribe would certainly satisfy neither traditional taxonomists nor phyleticists. The authors claim it as an "advantage" that "such a limited sampling eliminates all the intra-taxon variability", which hardly engenders confidence in their appreciation of the significance of nature's complexity. In their study of difficult species-complexes in *Cassia*, Irwin and Rogers (1967), using the graph-theory model of Wirth *et al.* (1966), seem to be reasonably well satisfied with the results. The taxa are too closely related to show clear phylogenetic patterns, but little biosystematic information is available. The taximetric clustering procedure seems at least to have promoted the authors' confidence.

A notable exponent of numerical methods recently remarked to me that, given suitable data and an appropriate program, "the computer can produce a better classification than a poor taxonomist". But then, so can a good taxonomist—and, being in possession of much extraneous information and reasoning power which are not in the storage unit or the programmed strategy of the computer, he can often do so with much less tedious recording of data. Might it not be more economical to employ a few more good taxonomists? This ought to be possible out of a world population of 3×10^9.

The literature provides ample illustrations of considerably divergent classifications of the same material, *from the same data*, produced by various strategies of numerical taxonomy (Boyce, 1964; Olson, 1964; Katz and Torres, 1965; Minkoff, 1965; Rohlf and Sokal, 1965; Sheals, 1965; Kendrick and Weresub, 1966; Lance and Williams, 1966*a*; Sokal and Michener, 1967; 't Mannetje, 1967). Varying the attribute sampling gives somewhat different results again; so does changed scoring, whether it implies altered attribute definitions or grouping, changes in measure, or all of these. It is true that different methods sometimes yield reasonably concordant results for the major divisions of a group but in these circumstances the taxonomist is seldom in doubt in any case. If, after a careful investigation, a taxonomist remains in doubt as to the classification of particular groups, it is usually due to intrinsic complexities, past or present, in evolutionary situations. Lack of well-defined clustering and especially of nested groupings is inherent in such situations; consequently the different characteristics of the various taximetric strategies will result in lack of consistency. These instabilities arise from the fundamental difficulties discussed earlier; they cannot be regarded simply as functions of a signal : noise ratio (Lange *et al.*, 1965) (though this may vary with the method), since the signal itself is to some extent what we define it to be.

The theoreticians of numerical taxonomy have enjoyed themselves immensely over the past decade (though not without developing several schools with scant respect for each other!). The mushrooming literature is quite fascinating and new developments tumble after each other. Anyone who is prepared to learn quite a deal of matrix algebra, some classical mathematical statistics, some advanced geometry, a little set theory, perhaps a little information theory and graph theory, and some computer technique, and who has access to a good computer and enjoys mathematics (as he must if he gets this far!) will probably find the development of new taximetric methods much more rewarding, more up-to-date, more "general", and hence more prestigious than merely classifying plants or animals or working out their phylogenies. Unlike the taxonomic questions themselves, the methodological questions which the taximetric mathematician sets himself are mostly so definite and so answerable—yet hunting for the answers is difficult enough to be interesting:

Does a certain distance function define a metric, semi-metric, quasi-metric, or non-metric space? Is it monotonic (varying throughout in the same direction) as object-groups are successively fused? What are the properties of the Canberra metric as a variant of the Manhattan metric? What are the relative advantages of divisive and agglomerative strategies? (One can do a little classifying of the strategies themselves—without using the computer, so that there is some intellectual satisfaction in it.) What are the properties and advantages of hierarchical (nested) systems as opposed to overlapping, clustering (clumping) systems? To what extent are particular agglomerative sorting strategies space-distorting? Can dimension-reducing ordination techniques such as principal component analysis and factor analysis be used efficiently as a basis for extracting a classification from an ordination? What are the virtues of rotation of axes in a factor analysis to yield "simple structure"? What do the "factors" of factor analysis mean? (Not so easy to answer.) Are certain matrices always positive semi-definite (symmetric with all eigenvalues non-negative)? Are certain functions algebraically tractable? Do annoying singularities occur? Are probabilistic models really applicable or desirable? Can predictivity be usefully measured? What are the virtues of combining R- and Q-analysis, and what are the appropriate techniques? (As now agreed both by Sokal and Sneath (1963) and Williams and Dale (1965), these terms refer to matrices: the elements of a Q-matrix are measures of comparison of objects (individuals) while those of an R-matrix are measures of association of attributes.) How effective are heuristic "hill-climbing" strategies (Rubin, 1967) which search for optimal structure by systematic trial? How large a data matrix can particular computers handle for particular programs and how much computer time does an analysis take? Are programs easily modifiable? What methods can handle mixed data, and how validly? Should attribute scores be standardized to unit variance, or in some other way? Are double-negative matches to be included? What *is* negative in any case? (Suppression of a character may well be the derived condition within our frame of reference; to assign greater importance to "presence" than "absence" is a decidedly subjective judgement.) Is the information-statistic the best basis for agglomerative strategies?

Some of these questions are discussed in an enlightening paper by Williams and Dale (1965). Although these authors make the usual, partially invalid, pheneticist assumptions, their mathematical discussion is most helpful and pertinent. However, reference to various subsequent papers is necessary (e.g., Bonner, 1964, 1965; Macnaughton-Smith, 1965; Hall, 1965, 1967 *a*, 1967*b*; Davidson and Dunn, 1966; Goodall, 1966; Gower, 1966; Jancey, 1966; Menitskiĭ, 1966; Wirth *et al.*, 1966; Lance and Williams, 1966*a*, 1966*b*, 1967*a*, 1967*b*, 1967*c*; Davidson, 1967; Estabrook, 1967; Orloci, 1967; Rubin, 1967; Crovello, 1968; Wallace and Boulton, 1968), and indeed any attempt to be comprehensive in this field is obsolescent before it reaches the printer. The well-known text of Sokal and Sneath (1963), which was welcomed by non-initiates as the Bible of the subject, though still important, has already taken on the archaic flavour of an Old Testament, both as to foundations and as to the range and evaluation of mathematical methods and models.

Are phenetic numerical methods, then, of value in practical systematics? I think they can be, especially now that computers can process high-order matrices (approaching 200 "objects", or even more) and that mixed-data programs have been developed to deal with two-state, multi-state, and infinite-state (continuously-varying) quantities in the same matrix (Lance and Williams, 1967*c*; Wallace and Boulton, 1968). Our ordinary intuitive processes begin to lose efficiency with problems of this magnitude, especially when a comparable number of attributes is used. The computer's elucidation of "structure" in the data may be useful to us in *suggesting* an appropriate classification, even though we are aware of the numerous subjective and arbitrary decisions implied in the choice of data and of mathematical models.

I do not believe, however, that we should accept any such classification as the last word or as indicating that answers exist to the chain of questions posed early in this address. Ordinarily one can attempt to evaluate such a classification by evolutionary considerations and can modify it accordingly if necessary—there is no need to stand in awe of its "objectivity". If this is not feasible, one can accept it as possibly better than one could do by intuitive methods. *Having accepted a finite set of relevant attributes* (not necessarily all *used* in the analysis), one may judge classifications as to *predictivity within that set* by means of the probabilistic utility function of Goodall, who, in an interesting paper (Goodall, 1966), outlines some of the constraints which are necessary before any probabilistic technique can be validly used.

Warburton (1967) suggests that the purpose of classification should be to maximize "the probability that statements known to be true of two organisms are true of all members of the smallest taxon to which they both belong. It should not be impossible to develop tests for this property to objectively decide which of several rival classifications is best." Any such test, of course, would depend on definition of a finite set of "statements". If we agree to that, Warburton's criterion could provide a useful pragmatic test within a frame of reference, but because of this arbitrary aspect it answers no general question about *the* best classification.

No good reason exists why any particular horizontal cuts across phenograms* should be accepted as meaningful "phenon levels" (Sneath and Sokal 1962; Sokal and Rohlf, 1962; Sokal and Sneath, 1963) upon which to erect our formal taxonomy. All claims for phenetic "standards" of rank collapse on analysis, including those reiterated in the rather brash paper in which Sokal and Sneath (1966) set out their recipes for a great leap forward to "efficiency in taxonomy".

Although a number of earlier authors had proposed numerical methods for taxonomic classification, it is interesting that one of the influential streams in the modern period is associated with the work of P. H. A. Sneath (for references see Sokal and Sneath, 1963) on the classification of bacteria, a group in which phylogenetic interpretation has been unsatisfactory and equivocal. Another vigorous stream, associated with W. T. Williams and his collaborators, began in the field of ecology and has close associations with workers in such areas as criminology (Macnaughton-Smith, 1965), industry, and business, in all of which classification has been and must

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* Phenograms are phenetic dendrograms purporting to show similarity by a tree-like diagram of nested subsets of the objects—not merely topologically but scaled according to the particular measure used.

surely remain an *ad hoc* or arbitrary matter (however "objective" we may cause it to appear by making the subjective decisions *before* beginning the calculations).

Generally experienced systematists, young or old, who employ taximetric methods usually seem to make excuses for them: "Well, the computer analysis didn't do any better than (or as well as) I could, but it wasn't a bad job and perhaps it gave me an odd idea here and there" would sum these up. Despite substantial response arising from genuine interest as well as from bandwaggoning, the showing after ten years' hard selling is not at all impressive so far as improved practical classification or biological understanding are concerned. The onus must surely be increasingly on the numerical pheneticists to give reasons, other than its meretricious glitter, why we should buy their product except with considerable reserve. Fashion, spurious objectivity, and competition for financial grants (Rollins, 1965) are not very scientific reasons. Neither is fear of being included by such determinedly iconoclastic zealots as Paul Ehrlich (1965)† in the class: { "members of the old school" who "would still like to see a pinch of phylogenetic speculation mixed into their basic data (presumably for sentimental reasons)" and who "will continue to promote this confusion for some time to come"} —and thus excluded from the class: { "those who wish to look forward"} , regarded by Ehrlich (objectively, no doubt) as non-overlapping with the former class. There is a familiar ring to this: "He who disagrees with me is a reactionary."

Our only certain scientific pay-off from phenetic taximetric methods is that, having gathered a lot of data, we shall therefore be less likely to overlook features of evolutionary or practical significance. Often the game may not be worth the candle.

Relation to genetic basis

Sneath and Sokal (1962) introduced the concept of the "matches asymptote", hypothesizing (Sokal and Sneath, 1963) that "the similarity between two operational taxonomic units is some parametric proportion of character matches which we are estimating with a sample of characters" and that "as the number of characters sampled increases, the value of the similarity coefficient becomes more stable". The meaningless of a parametric value in the all-attributes case has been demonstrated but it may still seem reasonable to consider that, given a suitable measure of similarity, such a parameter exists for the "matches in the nucleotide sequence of the DNA of the genotype". If that is so, then, over the attributes ordinarily regarded as important, the confidence band for an estimate of this parameter will narrow as the sample size increases. In that there *is* a certain regularity, related to the genetic information, over the attributes we are likely to consider, some such convergence is indeed to be expected. The existence of a numerically definite asymptote will of course depend on the acceptance of a *particular* finite attribute set defined by enumeration of its elements, but it is doubtless correct to say, in an imprecise way, that the larger the sample of attributes the better our comparisons will tend to be in reflecting the similarities of the genotypes. However, even if we knew the entire nucleotide sequences over a set of organisms we should still have to make many decisions on matching procedure. (We can hardly speak of comparing "genes"—the gene is no longer a useful operational unit at the level of molecular genetics.) We certainly could not set up pluri-unique correspondences of DNA base

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† More recently (Ehrlich and Ehrlich, 1967), this author has realised that numerical phenetics is inherently indeterminate in its results,—and appears to have adopted a nihilistic attitude to taxonomic improvement in general.

sequences over the whole genotype of organisms which were at all diverse or differed in karyotype (see Ehrlich, 1964, and Reynolds, 1965, for possible further difficulties). Taking the step up to the comparison of proteins will not remove this difficulty, though such comparisons as can be made in this field will provide information at least as useful as that from other attributes.

Related to, but not identical with, the "matches-asymptote" hypothesis is the "non-specificity hypothesis" (Sneath and Sokal, 1962; Sokal and Sneath, 1963) which assumes that "there are no distinct large *classes* of genes affecting exclusively one class of characters such as morphological, physiological or ethological, or affecting special regions of the organism". This suffers from the same fundamental difficulties of definition and testing as other phenetic concepts but, so far as the phenetic tests may be accepted as valid, it appears often not to hold very well (e.g., Rohlf, 1965; Thornton and Wong, 1967). Indeed, the lack of correspondence of groupings derived from different sets of data (say, from internal anatomy and external morphology, or from larval and adult stages) is a problem in phyletic as well as in phenetic taxonomy, but at least the phyletic approach to its resolution should be more intelligent and subtle than crude lumping of the data or results. An alternative, of course, is to take the view of Ehrlich (1964, 1965) that "phylogenetic speculation is fun, but seems to have little scientific purpose" and hence to regard all classifications as special, so that "one wishing to make predictions about the distribution and ecology of larval mosquitoes would presumably do better to work with a taxonomy based only on characters of the larvae".

Phylogeny cannot be perfectly elucidated, and it is inherently complex and reticulate at those levels of grouping at which interbreeding among groups still occurs. Nevertheless its unique existence provides the nearest thing to a solid base for general taxonomy.

Taximetrics. II. Numerical Phyletics

Conditioned as they have become by reiterated assertions to believe that operationist philosophy demands that taxonomy must be purely phenetic, only a few of the theoreticians of taximetrics have shown interest in developing mathematical models and corresponding numerical techniques for the elucidation of phylogeny. One can set up plausible, though clearly oversimplified, models of phylogenetic processes, just as one can for genetic systems. Some at least of these models are reasonably tractable mathematically, as are the rather idealized models of population genetics which have often proved fruitful in suggesting hypotheses and in testing for consistency.

The "advancement index" of Sporne (1948, 1954, 1956, 1960) was an early attempt to assess evolutionary advancement. Sporne's approach was different from later methods discussed here, but is of limited applicability, for the reasons given by Davis and Heywood (1963, p. 39). The concept of a statistically measured overall "advancement" is both too indefinitely based to have much statistical validity and too generalized for effective reconstruction of phylogenies.

A simple phylogenetic consistency test, based on the postulate of unidirectional change in individual characters, was developed by Wilson (1965). This field of study has been termed *cladistics* by Camin and Sokal (1965) who, having formulated a set of assumptions regarding evolutionary sequences, developed a computer strategy based on the principle of parsimony. Its aim was to construct *cladograms* (phyletic dendrograms) representing an evolutionary minimum-path branching pattern for the set of OTU's under consideration. The method was checked against the palaeontologically well-documented phylogeny of horses and also for a group of imaginary organisms ("Caminalcules") which had been independently generated using the phylogenetic principles enunciated. This important pioneering work has naturally appealed to those phyleticists who do not wish to turn their backs altogether on numerical methods, but has been virtually ignored by many pheneticists. Camin and Sokal themselves continue to prefer a phenetic basis for classification "until an operational system combining cladistics and phenetics can be established"; since any such system *must* be arbitrary, from the nature of the phenetic component, I cannot see how this aim can be achieved with the "objectivity" which Camin and Sokal desire.

Cavalli-Sforza and Edwards (1967) have discussed, in considerably greater depth and detail, some mathematical models and estimation procedures for phylogenetic analysis. Their intention, only partially fulfilled, was to use maximum-likelihood methods to estimate the form and proportions of "the most probable tree uniting the presently living populations". Their "branching random walk" model assumes that evolutionary changes leading to divergences in genetic constitution are, at the level concerned, essentially stochastic, summarized as "random genetic drift and variable selection". One could disagree with these assumptions, and it is clear from the authors' very honest discussion that many arbitrary decisions have to be made as to the nature of the spaces and metrics implied by the models and by the methods of estimation. Tests of the method in cases where there is good fossil and other evidence for a particular phylogeny should be interesting. Cavalli-Sforza and Edwards dismiss Camin and Sokal's paper with the observation that the latter authors' assumption "that evolution *proceeds* according to some minimum principle" cannot justify the use of a "method of minimum evolution", though Cavalli-Sforza and Edwards do not deny the possible usefulness of such methods.

Working with amino acid sequences of cytochrome *c* from an assortment of vertebrates, two insects, and three fungi, Fitch and Margoliash (1967) have used a numerical method of phylogenetic analysis on the basis of "mutation distance", that is, the minimal number of nucleotides which must be altered in order to convert the coding for one cytochrome to that for another. This is an excellent paper, but I cannot resist quoting the metaphorical gem that if "one wishes to test a tree which differs only in the order in which the chicken, duck, and penguin are joined, the only legs in need of recalculation are those five descending to these birds from the avian apex". The mental picture which this conjures up is slightly less surrealistic if we note that Fitch and Margoliash's trees grow upside-down and have legs instead of branches!

Silvestri and Hill (1964) stress the value of the *patristic* approach (i.e., genetic comparison) in microbiological systematics, since there are few reliable data for cladistic hypotheses in that field. However, Silvestri (1964) also points out that phenetic differentiation may be outstripped by DNA evolution because of the degeneracy of the genetic code.

Further development of numerical phyletics is certain and seems to have considerable promise, but inasmuch as the methods *are* numerical they impose their inbuilt metric properties on a situation for which topological "reality" is more or less inherent, but "distance", if defined on essentially phenetic grounds, is dependent on our point of view. "Mutation distance" will usually be determinable only in respect of a few loci, and therefore inadequately sampled, but it does perhaps represent the nearest thing to a "natural" *metric* basis for biological taxonomy.

Quality and Quantity in Mathematics

The urge to quantify is upon all biology and the social sciences. Undoubtedly it has already brought considerable benefits, but we should not forget that science is *not* the process of measuring natural phenomena; that is merely a technique of science. Very largely the aim of science is to discern qualitative differences, that is, to simplify and reduce the number of quantities which it is necessary to specify. For instance, in particle physics today the algebraic theory of *groups* (this term has here no connection with "groups", i.e., classes or sets, in classification) has been successfully applied to the ordering and prediction of quantum phenomena, as indeed it was applied earlier to symmetry relations in such fields as crystallography. The essence of the algebraic concept of a group is not quantity but *structure*: a particular set of relations between elements, the latter usually being *operations* in the particular class of relations which satisfy the group concept. This principle is expressed with greater generality in the concept of *isomorphism: the matching of sets of relations*, not quantities. It is these qualitative aspects with which much of modern algebra is concerned (e.g., Maxwell, 1965; Hollingsworth, 1967). The same is true of much advanced geometry, especially the non-metric geometry of position (mostly abstract and expressed in a notation allied to that of set theory): topology, or *analysis situs* as it was once called.

We should not be bewitched by number, in particular by the continuum (for basic concepts and some enlightening philosophical discussion, see Dantzig, 1962). We shall probably never be able to express or apprehend complex situations in their precise quantitative detail. Over the centuries, beginning with the natural numbers 1, 2, 3, ..., we have had to extend our concept of quantity to embrace zero, directed (positive and negative) numbers, rational fractions, algebraic and transcendental irrationals, complex numbers, and various kinds of hypercomplex numbers, such as quaternions, vectors, and matrices. To cope with *change* and with infinite processes, the differential and integral calculus was necessary. Further, to deal precisely with matters as uncomplicated (as compared, say, with those of biology) as the specification of simple events and relations in space-time, mathematicians have combined vectors, matrices, and calculus into the formidable subject of tensor analysis— and this in cases where there are no difficulties of multiple incommensurability. *We have no hope of extending this kind of precise quantitative mathematics* to describe the biological situations encountered in taxonomy. Mathematics is hard, paradoxically, because its subject matter is simple—and the subject has thus been able to progress a long way.

Statistics, largely based on probability theory, has been developed to cope with circumstances, in physics as well as in less simple fields, where we are concerned with large numbers of events which display a degree of disorder, that is, lack of individual specifiability (except where individual observation is feasible). Statistics requires certain assumptions, as we have seen, which are often not justified in systems of incommensurables. May we not be well advised to avoid putting all our money on Quantity? Qualitative assessment (which, as we have seen, does *not* exclude mathematical concepts) may be a surer winner in heavy going. To be sure, we can often extract qualitative structure, or qualitative generalizations, from quantitative data and, when we can, we should doubtless do so.

Cladistic Spaces

We can also very often perceive qualitative structure, and subject our interpretation to empirical tests, by qualitative means. Quantitative expression of a situation, or a quantitative check, is of no greater value unless the assumptions underlying it are justified. We now know that often they are not. In the words of Hull (1965), an author whom all the devotees of numerical objectivity (*and* all phyleticists!) should read, "talk of taxonomic space, like talk of gene pools, is strictly metaphorical. . . . Taxonomic space . . . is an amorphous continuum with no intrinsic metric; there is nothing about taxonomic space to indicate how long to make the unit of measurement or at what point to begin measuring once the unit is chosen". To this we may add that the dimensionality of taxonomic space, even in the sense of phyletic space, is arbitrary and the space is not isotropic (similar in properties in all directions).* There is a time dimension which is metrizable for our purposes by the ordinary physical criteria. The remaining dimensions will depend on our model or mental construct of the space. Two main phyletic cases arise: (I) We can say that there are n dimensions (including time) where n is the number of recognized "ends" (individuals, species, OTU's or whatever our smallest unit of taxonomic division is taken to be). This will be a pure "cladon-space", and any cladistic tree within it can be mapped without loss of information on to a two-dimensional space to form a conventional dendrogram, *provided* that we are not concerned with any measure of distance or indeed with any ordering except on the time co-ordinate. In this case it is *only the order of branching* which counts. (II) We can admit $p+1$ dimensions (including time) where p is the number of attributes taken into account. This class of phyletic-phenetic space, which is merely an attribute-space with a time dimension added, is the basis of Cavalli-Sforza and Edwards's primary model; it has some metric properties but need not be fully metric in the sense of Williams and Dale (1965). A tree in it cannot be mapped on to a two-dimensional space without considerable loss of information. Two- or three-dimensional representations such as those advocated by Sporne (1956), among many others, though useful as illustrations, cannot hope to be very accurate in representing either phenetic or evolutionary distance, according to whatever measure we adopt.

Whether or not we agree on some arbitrary working commensurability over the dimensions representing attributes (or some such measure as Fitch and Margoliash's "mutation distance"), in both space classes (I) and (II) time is incommensurable with the other dimensions. We cannot legitimately combine time and the other forms of "distance" into any general distance measure. This is in fact the strength of the time-oriented standpoint; the time-sequence is potentially determinable and often practically inferable. Thus, the only unequivocal dendrograms are topological cladograms which are *qualitative* in nature, except that if we do have palaeontological evidence of actual times of branchings these cladograms become unequivocally metric as to the time axis only.

Cladistics and Classification

Assuming that we have arrived by reasonable inference at a cladistic tree, does this then at last lead us to an optimal *classification*? It certainly does not lead us to an *ordination* of the objects at any time level (more strictly, in any hyperplane normal to the time axis), unless we accept a particular attribute-space as in case (II) just described. But we may consider the possibilities of effective classification without ordination.

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* Edwards and Cavalli-Sforza (1964, Cavalli-Sforza and Edwards, 1967) specifically *define* an isotropic "evolutionary space-time" but this isotropicity is achieved by a transformation which, as they say, "is a reflection of the genetic assumptions which are being made, and these will be peculiar to each case".

Often, by reference to the time sequence of branching, we may refer the objects to a nested (hierarchical) system of sets. However, if we are working wholly or partly below the level of effective genetic isolation, the tree is a banyan, anastomosing in its lower levels at least. The sets will then intersect in a complex manner and in this case there is certainly *no* unique hierarchy. This is one reason why the "biological" species concepts are important in taxonomic theory and practice, however difficult to define they may be in some groups of organisms (see Simpson, 1961, for an elaboration of this matter, and Hull, 1964, 1965, for an illuminating philosophical discussion). In these reticulate cases, which are usually below and about the "species" level in the conventional system, but may include somewhat higher levels if allopolyploidy has occurred, *only subjective or arbitrary classification is possible—there is no one "right answer"*, though some classifications are certainly worse than others. Numerical methods cannot alter this, though they may aid in evaluation of data and obviate the possibility of grossly subjective (that is, "unreasonable") judgements.

For many years I have worked with the large genus (or group of genera) *Eucalyptus*, which presents a maze of anastomosing situations of this kind, though not including alloploidy. It has long been clear to me that no single "best" classification, phenetic or "biological", is possible in such genera. It would be a wasted effort to aim at one, and it is a fond hope indeed that some numerical analysis or other is going to "solve" the classification problem. Nevertheless, it is not wasted effort to attempt to understand the group or to describe as well as we can the situations which exist within it, in terms of phenetic variation, ecological relations, breeding behaviour, and so forth. As Harlan Lewis (1957) has said, "it may be easier to determine why the group is difficult than to decide the most appropriate taxonomic disposition".

This is where the biosystematic way of thought has the advantage over the formalism of the pure pheneticist. Biosystematics, even when not highly experimental, is attempting to understand and describe an aspect of nature in dynamic terms. This need by no means always, or even usually, be pushed to the level of a detailed analysis of population dynamics; we can infer a great deal from many other cases where detailed studies have been made. We need to see the forest as well as the trees, *and* some of the trees as well as the forest, but not always at the same time or place.

Formal taxonomy at the specific level cannot always aim at perfection, though there are in fact many perfectly straightforward cases where no dispute at all is likely to arise as to the correct grouping—nature often does present us with comforting discreteness at a particular time level, hence the not inconsiderable success of traditional systematics. In the difficult cases, we can frequently improve the formal classification up to a certain point by removing the grosser inconsistencies between formal treatment and our biological understanding, although possibly replacing them with lesser inconsistencies elsewhere. When we reach the stage where there is no gain in consistency (this is itself not unequivocally measurable; see Hull, 1964), we may as well describe the situation, and stop. Whatever theorists may suppose, practising systematists are well aware that there are vast fields in which much more effective work can be done before reaching the point where *inherent* instability becomes limiting. Instabilities arising out of ignorance or sheer wrong-headedness are, or were, common enough, but we need not judge any subject by its incompetents. The improvement may sometimes be made with the aid of numerical methods, but is often quite feasible without them. Whether it is always worthwhile, by any method, is another question. Ehrlich (1964, 1965) thinks not; he may be right, but this is a highly subjective judgement, like many pronouncements of the objectivists. Certainly some more consideration of priorities in taxonomy, as suggested by Ehrlich, should increase the efficiency of the subject as an aid to understanding. This is quite apart from economic priorities, which are already well recognized.

Returning to a level above coenospecies and above alloploid formation, where the cladograms are free of loops, the problems are again discussed by Simpson (1961) and by Hull (1964, 1965). They are at two levels: phylogenetic interpretation and formal treatment. We shall here assume that our interpretation is as good as we can get it—how, then, do we group, and how do we rank?

Since lineages are continuous in time (up to the point of extinction), classification *along* the time axis must be largely arbitrary, although the rate of evolutionary change is by no means constant (see, e.g., Simpson, 1953) and some authors (e.g., Takhtajan, 1953) have described evolutionary change as chain-like rather than line-like. I cannot deal here with the difficulties peculiar to the classification of allochronous forms. They are of much less practical importance than those concerning contemporary organisms and may be safely left to the palaeontologists. The text-book of Simpson (1961) and the references given therein cover the subject adequately. Phyletic numerical analysis may doubtless sometimes prove helpful in this field for the elucidation of phylogeny and the quantitative study of anagenetic change, but any purely phenetic analysis across different time levels is inappropriate for general classification. Tuomikoski (1967) gives a useful discussion of palæontological classification over all time levels but appears not to perceive the virtual impossibility of a satisfactory solution.

Amongst organisms at any one time level, it may at first seem obvious that, if we have deduced the topological structure of a divaricating tree and expressed it as a cladogram, we then have a hierarchy laid out before us. The nested groupings would then present no problem though assignment of rank would seem to have no non-arbitrary objective basis.

Unfortunately the situation is not so simple. Hull (1964) gives an admirable discussion of the difficulty of fitting the traditional Linnaean hierarchy (indeed any hierarchy) to the phylogenetic background, and the reasons why Simpson's criterion of consistency can be only imperfectly applied. There are two main sources of difficulty:

(1) The definiteness of a topological cladogram depends not only on our knowledge, which may be quite inadequate to indicate the *exact* sequence of branching, but also on the taxonomic *unit* of the cladogram. Any questions of monophyly will depend upon the unit adopted and here we encounter some circularity in the definition of categories, if monophyly is taken as a criterion (as it is by Simpson, 1961, and many other phyletic taxonomists). A stem of a cladogram may be simple if we *define* it as being of generic cross-section, as it were, at all points, but if we dissect it into species strands we may find quite a network.

(2) Providing our representation of time and populations is sufficiently coarse-grained, we may be able to say that species diverged at such-and-such a level but it is not so easy with higher categories. This is fundamentally because we insist on recognizing these categories by the "level of organization" or "broad adaptive patterns" of the organisms we refer to them, as well as by inferred monophyly (e.g., Simpson, 1953, 1961). This familiar double function of the taxonomic categories was neatly expressed by Huxley (1958) when he coined the terms *grade* and *clade*, now widely adopted. The corresponding terms (due to Rensch, 1960) for processes of differentiation

are *anagenesis* (evolutionary "advance") and *cladogenesis* (evolutionary separation), with the addition of *stasigenesis* (evolutionary stasis).

To illustrate this double requirement, the familiar example will serve: The reptiles, mammals, and birds represent three grades, but cladistically the last two are simply branches (clades, ignoring some parallelism in the case of the mammals) of equal status to other branches still treated as reptiles. In set-theoretic terms, the set: { all vertebrates whose ancestors attained the reptilian level of organization } includes two (now) pretty clearly defined non-intersecting *proper subsets*: { mammals } and { birds } , which we do *not* now call "reptiles", together with the residue (the complement of the union of { mammals } and { birds }) which we *do* call reptiles but are jointly defined (within the original set) only by the fact that they are not mammals or birds.

Ehrlich (1964) has said that "a system based on phylogenetic relationships will not necessarily represent degree of phenetic differentiation". Restricting "phenetic differentiation" to what we regard as adaptationally and practically important, this is quite true.

Now, in such cases the traditional hierarchy is *not conformable* with the cladistic hierarchy, and the situation recurs throughout the living world. It may be argued that the classification actually used is essentially phenetic. So, in a sense, it is, but the choice of attributes used and the actual assignment of individual taxa take evolutionary (but not only cladistic) considerations very much into account.

Evolution, indeed, is *not* summed up merely in the topology of a phyletic tree. Phenetic differences of many kinds (underlain by the genetic information and the systems for its exchange, suppression, modification, and so forth) are the very stuff on which selection works. As I have said earlier, because we are part of the world in which selection operates and because what is a practical matter for selection is often a practical matter for us, we are also concerned with such phenetic characteristics, and a purely cladistic classification will not meet our needs. Nor will a patristic system.

Thus we are presented with a dilemma: If we choose to classify purely phenetically (this *need* not be hierarchic—overlapping clusters or simply ordination are systematizations, though psychologically unsatisfying to most of us) then we have no firm basis and are ignoring phylogeny, which *does* interest us. If we choose to classify purely cladistically (assuming that we have enough information) then we fail to display phenetic aspects of nature which are highly important in the evolutionary process, to the organisms themselves, and to ourselves.

The customary attempted solution of the evolutionary taxonomist is a compromise. Its general rationale is given by Simpson (1961). It has been followed, inevitably with varying degrees of imperfection, by many taxonomists, sometimes avowedly (e.g., Johnson, 1959, pp. 76–77), sometimes implicitly, and sometimes even when accompanied by disavowal.

Such a procedure is obviously not very logical and its defence may present many problems. It is offensive to those who dislike compromise and demand a clear codification of all procedures (e.g., Sokal and Camin, 1965). But it serves our purpose very well, and we should think very hard before we abandon it. For an anology we may look to language. Natural languages are complex, not very logical systems, full of redundancies and overlaps. Ordinary language will not do for mathematics or even for the discussion of semantics itself, so we invent special symbolic languages and meta-languages. Nevertheless, most of us have not yet found it necessary, feasible, or desirable to discard common language even in scientific communication. With some modifications and supplementation, it serves us better than any substitute yet thought of, *because it suits our psychology* (which is far from simply logical and linear) and because it links us with the knowledge of the past.

If, for similar reasons, we retain the broad framework of Linnaean hierarchical taxonomy (though we may see fit to do away with some of its more uselessly archaic features), we must face the fact that *no optimal taxonomy exists.* We could discard Linnaean taxonomy for one of the innumerable phenetic systems (there is no optimality there, as we have seen), or we could use a purely cladistic system which could then (in theory) be optimized, down to a certain level, as to the nesting of sets but not as to ranking. As Hull (1964) has shown, this latter would result in a "prohibitively complex and asymmetrical classification", which would not meet our requirements as we see them at present.

Recognizing and accepting the procedures which man has followed in intuitive classification, Davidson (1967) suggests a radical departure from the formal models employed by other taximetrists, whether phenetic or phyletic. He recommends that mathematics should be used to construct a cybernetic model congruent with the "classification program used by man since time immemorial". His efforts will be worth watching.

One of the logicians' objections to the usual formal hierarchy has been the recognition of categories which may contain only one member of next lower rank, for example, unispecific ("monotypic") genera. This objection arises from a particular set-theoretic treatment under which the existence of such categories leads to what has been called Gregg's Paradox. This paradox, like most others, is a consequence of the logical system adopted. Under the more reasonable method of definition of taxon-names (in the sense of logic) used in a logical analysis of the Linnaean hierarchy by Buck and Hull (1966), the paradox vanishes. We can thus rest easy with a long-established feature of systematics which is certainly meaningful to most biologists.

The continual "improvement" of classifications (on whatever basis) leads at present to some instability in names, which certain biologists and others appear to find most vexatious (this is quite apart from formal changes due to newly discovered nomenclatural priorities, and so forth). Systematists themselves often do not mind these changes, at least in groups with which they are familiar, since they feel that the new nomenclature expresses the "cleaning-up" which has been achieved. Nevertheless, the instabilities do cause confusion. Various authors have suggested that there should be a fixed nomenclature, perhaps using single-word names for species, separate from classification. Some (e.g., Michener, 1963; Sokal and Camin, 1965) sugggest the use of code *numbers.* Hull (1966) proposes the adoption of Michener's fixed numbers supplemented by a system of "phylogenetic numericlature" with adjustable "positional numbers" to indicate current views on phylogenetic arrangement. Perhaps some such system will eventually come, but at present it seems premature. The mnemonic value of words, and of binomials in particular, remains, despite challenges, and a great deal of information in the literature would become difficult of access if the present system were discarded. Similar views are expressed by Randal and Scott (1967), who point out the usefulness of natural-language input to data-processing machines, and also the greater detectability of errors by the eye when words are used. Parkes (1967) gives a similar qualified defence of traditional nomenclature, but we retain it chiefly, I think, *faute de mieux.*

CONCLUSION

So, neither phyletics nor phenetics will lead us to the optimal classification, the crock of gold, because it is not there. 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. Above all, taxonomists can set themselves the task, as more and more of them do, of describing the situations they perceive, giving reasons for their judgements, and suggesting lines of inquiry. The investigation of phenetic and "biological" characteristics of organisms and of their evolution is the scientific part of taxonomy. Classification itself remains an art, but a disciplined and respectable art whose aim is to serve science, not to express the personality of its exponents.

The classificatory component of taxonomy cannot itself be made into a science by ill-founded philosophy or essentially arbitrary numerical procedures and taxonomists would be well advised to treat "philosophical" pheneticism as unjustified in its claims and unproductive in practice. They will surely find numerical techniques useful, particularly on the big problems, and especially if the taximetrists can free themselves of their pheneticist dogmas. Taxonomists may remember, however, that many other techniques and tools, new and old, are at their disposal, including the subtlety of the human intellect and its power of perceiving *Gestalt* and of bringing information and theoretical reasoning of all kinds to bear on a problem.

If systematics is made into a sterile exercise, a purely pragmatic service, or a playground for technicians, I would advise intelligent young biologists to steer well clear of it. On the other hand it can be, as I have found it, a stimulating and rewarding (though *inherently inexact*) branch of science, *with its dash of art, like most other stimulating branches of science, including mathematics itself*. To conclude with the words of that wise and wide-ranging taxonomist, Lincoln Constance (1964), taxonomy in its widest sense, which goes far beyond the formulation of classifications, remains "an unending synthesis".

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My colleague Dr. Barbara Briggs, by her helpful criticism, has prevented this journey through the mists of theory and philosophy from being even more disordered and discursive than it is; I am most grateful to her. My wife has patiently typed illegible and tortuous manuscript, and borne with long discussions; I am equally grateful to her. I wish to thank also (and to ask tolerance for the cut-and-thrust of debate from) my friends Dr. W. T. (Bill) Williams and Dr. Paul Ehrlich whose stimulating and provocative, but also constructive, words and works have partly brought about the present assessment of trends in taxonomy, with much of which I naturally do not expect them to agree!

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THE RHAPHIDOPHORIDAE (ORTHOPTERA) OF AUSTRALIA
PART 7. *PALLIDOTETTIX*, A NEW GENUS FROM THE NULLARBOR PLAIN, SOUTH-WESTERN AUSTRALIA

Aola M. Richards
Department of Zoology, University of New South Wales, Sydney

[Read 27th March, 1968]

Synopsis

A new genus *Pallidotettix* is erected, and the new species *Pallidotettix nullarborensis*, n. sp. is described from limestone caves on the Nullarbor Plain in south-western Australia.

Introduction

The Nullarbor Plain is an area of Tertiary limestone about 75,000 square miles in extent, situated in south-western Australia. It extends from Ooldea and Colona on the east to Balladonia and Point Culver on the west, a distance of about 500 miles. To the north it is bounded by the Great Victoria Desert and to the south by the Great Australian Bight.

From 1957 onwards, a number of speleological expeditions have explored many of the caves which occur throughout the southern part of the Plain, and most of the material in this paper is based on the Rhaphidophoridae collected on these trips. These insects have been collected from at least 24 of the known caves, and observed in another three caves. Their distribution ranges from White Wells Cave, (N 14)* in the far east, to Gecko Cave (N 51) at the farthest western extremity of the limestone and as far north as Lynch Cave near the Transcontinental Railway (Text-fig. 1). Examination of these specimens has shown them to belong to a single species which is described here and placed in the new genus *Pallidotettix*, n.g. as *Pallidotettix nullarborensis*, n. sp. The species appears to be confined to the limits of the Nullarbor limestone.

P. nullarborensis is the palest Australian rhaphidophorid so far examined by the author. Sexual dimorphism is not strongly developed. It is absent from body size, antennae and number of linear spines on the hind femora. It is present in leg length, although not as pronounced as in some species of other genera. *P. nullarborensis* is one of the larger of the Australian Rhaphidophoridae. An adult male may reach a length of up to 17 cm. from the tip of its antennae to its hind tarsi. It is of comparable size to *Novotettix naracoortensis* Richards, but females are somewhat larger.

Pallidotettix does not show any close affinities with other Australian rhaphidophorid genera so far studied. The structure of the external genital plates in both sexes is quite distinctive.

Genus Pallidotettix, n. g.

Body sparsely clothed with short setae. Legs long and slender. Antennae very long and tapering, almost touching at their bases; scape about three times as large as pedicel, which is narrower than scape, but broader than

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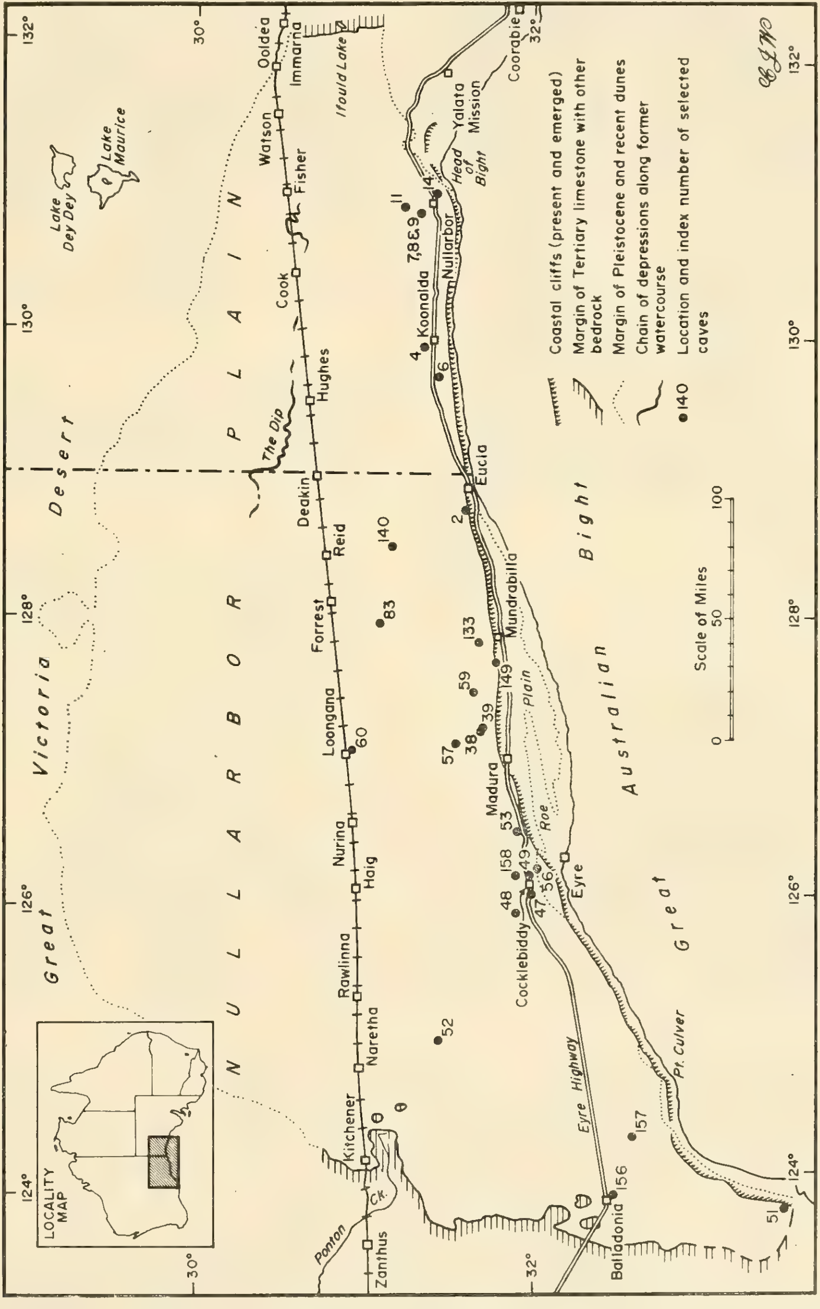
* The Nullarbor caves and dolines have been indexed by the Australian Speleological Federation, and the numbers are prefixed by the letter N. This system is used throughout this paper.

other segments; from fourth segment onwards segments subequal in length, although steadily decreasing in size; all segments thickly clothed with short setae. A single anterior, median ocellus only. Fastigium rising very abruptly, convex, grooved medianly and longitudinally. Fore coxae unarmed. All femora sulcate ventrally. Apical spines on femora, tibiae, first and second



Text-figure 1.—Map of the Nullarbor Plain showing approximate boundary of the Nullarbor Limestone, and the locations of the caves from which *Pallidotettix nullarborensis* has been collected.

proximal segments of hind tarsi constant in number. Fore femur bears two apical spines beneath, one prolateral and one retrolateral; fore tibiae bears four apical spines, one above and one beneath both prolaterally and retrolaterally; fore tarsus unarmed. Middle femur bears two apical spines beneath, one prolateral and one retrolateral; middle tibia bears four apical spines, one above and one beneath, both prolaterally and retrolaterally; middle tarsus unarmed. Hind femur bears two apical spines beneath, one prolateral and one retrolateral; hind tibia bears a pair of long apical spurs above, a pair of subapical spines above, a pair of shorter apical spurs beneath and a pair of subapical spines beneath, one from each pair being prolateral and the other retrolateral; two proximal segments of hind tarsus each bears two apical spines above, one prolateral and one retrolateral; other two segments unarmed. Subgenital plate of female trilobed distally and slightly keeled. Subgenital plate of male wider than long, distal margin emarginate and medianly produced into a small lobe.

Type species for the genus: PALLIDOTETTIX NULLARBORENSIS, n. sp.

PALLIDOTETTIX NULLARBORENSIS, n. sp.

(Text-fig. 2, Figs 1–6)

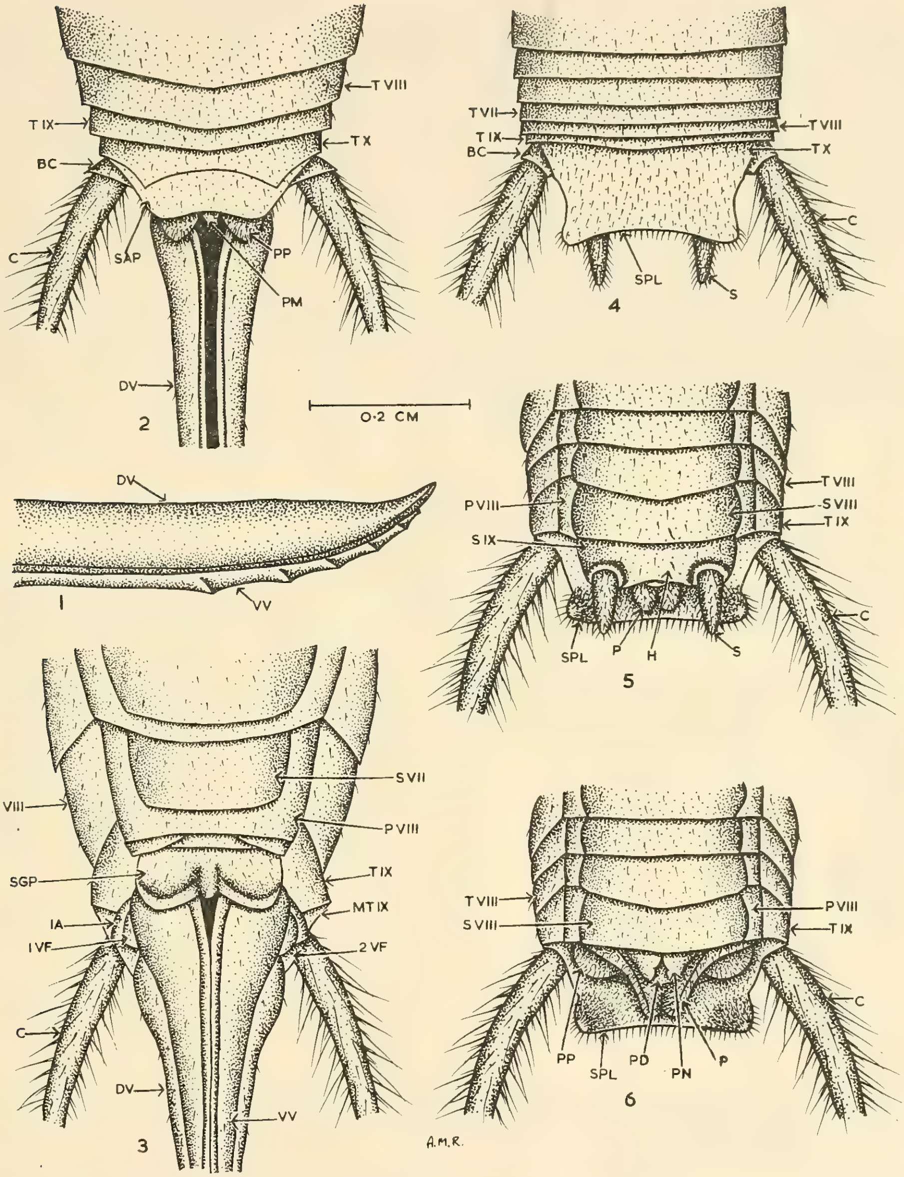
Colour.—Basic colour ochreous, with pronotum, mesonotum, metanotum and abdominal terga irregularly mottled with light brown; fore and middle femora and tibiae of all legs ochreous, hind femora ochreous with transverse light brown bands; tarsi ochreous; antennae ochreous; ovipositor light reddish-brown.

Body.—Length up to 16 mm. Body sparsely clothed with setae. Ovipositor 0·8 length of body; ventral valves armed distally with six teeth, gradually decreasing in size towards apex (Fig. 1). Antennae broken. Fastigium longer than high with base touching scapes of antennae. Maxillary palps with third and fourth segments subequal in length.

Antennae.—As in generic description. Third segment on dorsal aspect 2·25 as long as pedicel in female, and 1·75 as long in male; on ventral aspect 1·25 as long as pedicel in female, 1·1 as long in male. Sexual dimorphism absent. No spines on flagella of male or female.

Legs.—Fore and middle legs subequal in length, with hind leg 1·5 length of fore and middle legs. Sexual dimorphism slightly developed, fore, middle, and hind legs of female being 0·9 as long as male. Hind femora, all tibiae and proximal two segments of hind tarsi armed with variable numbers of linear spines (Table 1). No spines occur on fore or middle femora and tarsi. Apical spines constant in number as in generic description. Ratio of length of legs to length of body: Fore leg, male 3·3:1; female 2·5:1. Middle leg, male 3·1:1; female 2·4:1. Hind leg, male 4·8:1; female 3·7:1.

Genitalia. FEMALE: Suranal plate, Fig. 2 (SAP), concave laterally, distal margin emarginate and clothed with setae; rest of plate sparsely clothed with setae. Subgenital plate, Fig. 3 (SGP), 2·8 wider than long, distal margin trilobed, two lateral lobes rounded and thickened along margins, median lobe shorter and smaller than two lateral lobes and forming a keel two thirds length of plate; whole plate almost glabrous. MALE: Suranal plate, Fig. 4 (SPL), concave laterally, distal margin slightly emarginate with two latero-distal lobes; distal margin clothed with short setae, whole plate thickly clothed with setae, lateral lobes thickly clothed with setae on ventral surface of plate (Figs 5, 6). Subgenital plate, Fig. 5 (H), 3·8 wider than long, convex laterally; distal margin slightly emarginate, and medianly produced into a small lobe; whole plate sparsely clothed with



Text-figure 2.—*Pallidotettix nullarborensis*, n. sp. 1, Distal portion of ovipositor showing teeth on ventral valve; 2, Female genitalia, dorsal view; 3, Female genitalia, ventral view; 4, Male genitalia, dorsal view; 5, Male genitalia, ventral view; 6, Male genitalia, ventral view, subgenital plate removed to expose structures beneath.

INDEX TO TEXT-FIGURE 2

BC, basal segment of cercus; C, cercus; DV, dorsal valve; H, subgenital plate, male; IA, intersegmental apodeme; MT IX, membrane of tergite IX; P, paramere; P VIII, pleurite VIII; PD, pseudosternite; PM, perianal membrane; PN, penis; S, stylus; S VII, S VIII, S IX—sternite VII, VIII, IX; SAP, suranal plate, female; SGP, subgenital plate, female; SPL, suranal plate, male; T VII, T VIII, T IX, T X—tergite VII, VIII, IX, X; 1 VF, first valvifer; 2 VF, second valvifer; VV, ventral valve.

setae. Two styli, Fig. 5 (S), broad, conical, thickly clothed with short setae, length of styli being 1·6 length of sternite IX (S IX). Parameres, Fig. 6 (P), elongate with rounded apex, subequal in width to length, thickly clothed with long and short setae. Pseudosternite, Fig. 6 (PD), twice as wide as long, with rounded apex. Penis, Fig. 6 (PN), two-lobed, each lobe subequal in width to length. Paraprocts, Fig. 6 (PP), twice as long as wide, partially hidden between suranal plate and parameres, clothed with setae.

Distribution.—Limestone caves on Nullarbor Plain, stretching from White Wells Cave, South Australia, to Gecko Cave, Western Australia.

Gecko Cave (N 51), 15 miles east of Mt. Ragged, south of Balladonia, W.A. (type locality), coll. D. C. Lowry 27/6/65; Lynch Cave (N 60), two miles south-east of Loongana, W.A., coll. D. C. Lowry 12/5/66, A. M. Richards 3/2/68; Pannikin Plain Cave (N 49), W.A., coll. D. C. Lowry 27/12/65; Tommy Graham's Cave (N 56), near Madura Pass, W.A., coll. D. C. Lowry 11/12/65; Horseshoe Cave (N 59), W.A., coll. D. C. Lowry 7/5/66; Blowhole (N 52), 32 miles south-west of Rawlinna, W.A., coll. D. C. Lowry 1/12/65; Moonera Tank Cave (N 53), W.A., coll. D. C. Lowry 14/5/66; Murra-el-elevyn Cave (N 47), W.A., coll. I. D. Wood 3/1/64, P. F. Aitken 3/1/64, E. Hamilton-Smith 28/12/64 and 17/1/65, D. C. Lowry 27/4/66, A. M. Richards 31/1/68; Cocklebiddy Cave (N 48), W.A., coll. P. F. Aitken 3/1/65, D. C. Lowry 12/1/66, A. Baynes 24/3/67; Unnamed Cave (N 57), 20 miles from Madura Pass, W.A., coll. D. C. Lowry 11/12/65; Unnamed Cave (N 140), W.A., coll. D. C. Lowry 14/9/66; Unnamed Cave (N 149), W.A., coll. D. C. Lowry 21/9/66; Old Homestead Cave (N 83), W.A., coll D. C. Lowry 2/9/66; Snake Pit Cave (133), Mundrabilla Station, W.A., coll. A. Baynes 27/3/67; Walpet Cave (N 38), W.A., coll. P. F. Aitken January, 1964; Joe's Cave (N 39), W.A., coll. P. F. Aitken January, 1964; Weebubbie Cave (N 2), W.A., coll. P. F. Aitken 3/1/60, G. S. Hunt 29/12/65; Murrawijinie No. 1 Cave (N 7), Nullarbor Station, S.A., coll. A. M. Richards 25/1/68; Murrawijinie No. 2 Cave (N 8), Nullarbor Station, S.A., coll. A. M.

TABLE 1

Variability in number of linear spines on the legs of Pallidotettix nullarborensis, *n.sp.*

		Mean		Number Specimens		Standard Deviation		Range	
		L	R	L	R	L	R	L	R
Fore tibia	Pro.	4·0	3·9	25	25	0·3	0·4	3– 5	3– 5
Inf.	Retro.	4·0	3·9	25	25	0·2	0·3	3– 4	3– 4
Mid tibia	Pro.	3·6	3·6	25	25	0·5	0·5	3– 4	3– 4
Inf.	Retro.	3·6	3·7	25	25	0·5	0·5	3– 4	3– 4
Hind femur	Pro.	11·3	12·7	25	22	3·2	3·7	6–17	7–17
Inf.	Retro.	14·6	15·6	25	22	6·3	4·5	7–35	8–26
Hind tibia	Pro.	40·9	41·4	25	21	6·8	6·0	33–60	31–57
Sup.	Retro.	43·6	43·7	25	21	5·8	7·1	34–58	33–65
Hind tarsus	Pro.	3·9	3·8	25	20	1·1	1·0	2– 6	2– 6
1 Sup.	Retro.	3·8	3·8	25	20	1·0	0·9	2– 6	2– 6
Hind tarsus	Pro.	1·1	1·2	25	20	0·5	0·4	0– 2	1– 2
2 Sup.	Retro.	1·0	1·0	25	20	0·4	0·3	0– 2	0– 2

INDEX TO TABLE 1

L., left leg; Inf., inferior; Pro., prolateral; R., right leg; Retro., retrolateral; Sup., superior.

Richards 25/1/68; Murrawijinie No. 3 Cave (N 9), Nullarbor Station, S.A., coll. C. Warner February, 1957, A. M. Richards 26/1/68; Koonalda Cave (N 4), S.A., coll. P. F. Aitken 7/1/59; A. Gallus January, 1968; White Wells Cave (N 14), S.A., coll. P. F. Aitken 12/1/60; Koomooloobookka Cave (N 6), Koonalda, S.A. coll. C. Warner February, 1957; New Cave (N 11), S.A., coll. N. Mollet January, 1955; Caves, Nullarbor, S.A., coll. J. Madden January, 1957; Cave, Nullarbor, S.A., coll. K. Renwick January, 1957; Cave, Nullarbor, coll. unknown January, 1952. Also observed by D. C. Lowry during 1966 in Unnamed Cave (N 156) near Balladonia, W.A., in Unnamed Cave (N 157) south-east of Balladonia, W.A.; and in Unnamed Cave (N 158) near Cocklebiddy, W.A.

Types.—Holotype male, allotype female, two paratypes, one male and one female, in National Insect Collection, C.S.I.R.O., Canberra. Two paratypes, one male and one female, in Western Australian Museum Collection, Perth; paratype, one female, in South Australian Museum Collection, Adelaide.

Material examined.—Fourteen adults, 120 nymphs.

Acknowledgments

I wish to thank all the people who have helped in the collection of specimens from various caves across the Nullarbor Plain. In particular I should like to thank Mr. D. C. Lowry, Geological Survey, Perth and his wife for sending me specimens from the western part of the Plain. I am also indebted to Dr. W. P. Crowcroft, Director of the South Australian Museum, Adelaide, for the loan of material for study. I am grateful to Mr. J. N. Jennings, Australian National University, Canberra for permission to reproduce his map of the Nullarbor Plain, and to Mr. D. C. Lowry for plotting on it the exact location of the caves. Finally, I wish to thank Mr. C. J. Wilkinson, Geography Department, University of New South Wales, for drawing the map.

A TAXONOMIC REVIEW OF THE GENUS *MIXOPHYES*, (ANURA, LEPTODACTYLIDAE)

I. R. Straughan
Department of Zoology, University College of Townsville, Townsville, Queensland

(Plates I–II)

[Read 27th March, 1968]

Synopsis

Two species of *Mixophyes* Günther are described and the two subspecies already defined are elevated to species.

Introduction

Moore (1961, p. 165) suggested that *Mixophyes* from northern New South Wales might fall into two species—one from mountain streams and the other from large coastal rivers. Analysis of additional material of *Mixophyes* collected by the author from northern New South Wales and southern Queensland shows that three easily distinguishable morphological types, each with a distinct call, are recognisable. Also the geographically isolated *Mixophyes* from northern Queensland is distinct in morphology and call from any of the southern forms. These four species are described in this paper.

Material and Methods

All the material listed by locality (tabulated north to south) was collected by the author from breeding congresses during summers from 1960 to 1967 inclusive. This material is lodged with the Queensland Museum, Brisbane. All material in the Australian Museum (Sydney) collections was examined. Specimens examined by Moore (*op. cit.*) in the American Museum of Natural History were not seen. Synonymies include the original reference, reference to Parker (1940) who gives complete synonymies to that date, and all subsequent references. The descriptions follow the pattern suggested by Moore (*op. cit.*, p. 155). Length of inner metatarsal tubercle was measured along its long axis, and length of first toe from its tip to its junction with inner metatarsal tubercle. A key to all the known species of *Mixophyes* is provided.

Mixophyes fasciolatus Günther

(Pl. I, Fig. 1)

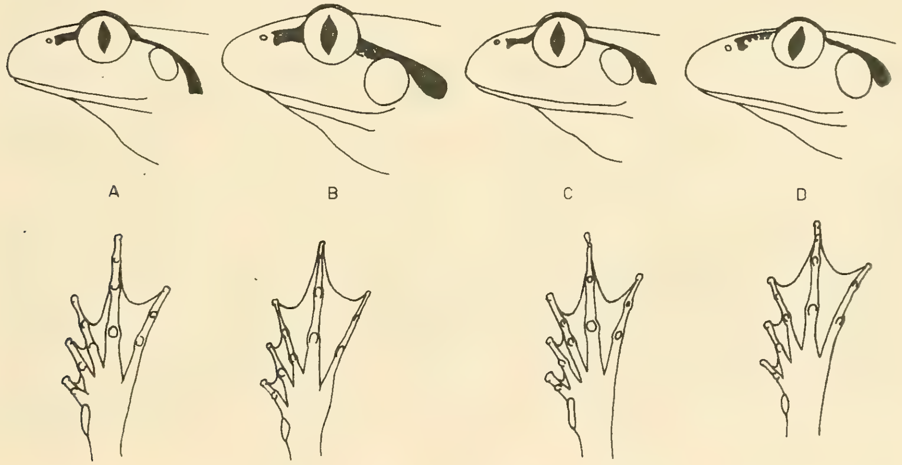
Mixophyes fasciolatus Günther, 1864, p. 46, pl. 7, fig. 1. *Mixophyes fasciolatus* Günther, Slevin, 1955, p. 359 [part.]; Moore, 1961, p. 162, fig. 1 [part.]. *Mixophyes fasciolatus fasciolatus* Günther, Parker, 1940, with complete synonymy (delete Fletcher, 1892, p. 18).

Type locality: Clarence River, N.S.W. Topotypic material 3 ♂♂, 1 ♀, collected two miles east of Grafton, Clarence River, 17-III-1963.

Diagnosis: Species of *Mixophyes* are distinguishable from all other Australian frogs by pupil vertical when constricted; vomerine teeth in front of choanae; round tongue, only 1/4 to 1/5 free behind; distinct tympanum; limbs with dark cross bars; and feet with well developed web.

Mixophyes fasciolatus is distinguished from its congeners by web to distal sub-articular tubercle on outer margin of third toe; three joints of fourth toe free of web; inner metatarsal tubercle as long as first toe; dark cross bars on limbs narrower than intervening light; lateral zone of dark spots dividing dark dorsal and white ventral surfaces; outer metacarpal tubercle well developed; tympanum oval, long axis tilted towards eye.

Description: Large (60–80 mm., snout-vent length) with long barred legs. Dorsal surface smooth to finely granular; tan to pale grey marked with darker blotches: characteristically a dark mid-dorsal band present, commencing as interorbital Y or T continuing posteriorly with irregular margins. Band may be broken into less regular blotches, in extreme cases leaving only interorbital bar and oblique elongate patches scattered over remainder. Junction of dark dorsal and pale ventral surfaces marked by series of irregular dark lateral spots between arm and groin. Distinct black head stripe from behind nostril, through eye, above tympanum, curving round its upper margin, ending at level of lower margin and separated from it by width of stripe (Fig. 1c). Triangular patch in front of nostril with base along upper lip and apex at nostril. Dorsal surfaces of limbs with dark cross bands not as wide as intervening pale. Bands widening on margins of limbs to form dark and light saw tooth pattern, breaking up irregularly on posterior surface of thigh producing rough marble pattern. Ventral surface, including limbs, white, smooth except for area around vent. Base of triangular expansion of dark limb bars visible from below. Chin and throat dusted with dark. Tympanum distinct, oval, long axis tilted towards eye from vertical (Fig 1c). Fingers unwebbed, in order of length 3 > 4 = 1 > 2. Elongate well-developed inner, and smaller well-developed oval, outer metacarpal tubercle. Webbing between toes strong. First toe free of web to proximal sub-articular tubercle, as is second on inner edge. On outer edge of second, fringe of web to dilated tip. Web only to proximal sub-articular tubercle of third on inner edge and



Text-fig. 1. General head profiles and hind feet of *Mixophyes*, spp., showing head stripes, shape of snout, position of tympanum, extent of webbing, and size of inner metatarsal shovel. a.—*M. balbus*, b.—*M. iteratus*, c.—*M. fasciolatus*, d.—*M. schevilli.*

to distal on outer edge. Three joints of fourth free. Fifth webbed to tip, but web reaching only to level of distal sub-articular tubercle at lowest point between fourth and fifth (Fig. 1c). No outer metatarsal tubercle but well-developed, shovelshaped, inner metatarsal tubercle as long as first toe. Sub-articular tubercles oval moderately developed (Fig. 1c). Vomerine teeth platelike, directed towards each other from anterior margin of choanae to midline between choanae, nearly touching.

Material examined: *Queensland*: Mount Cooroy 2 ♂♂; Jimna Range 5 ♂♂; Nanango 3 ♂♂; Kumbia 2 ♂♂; Yarraman State Forest 3 ♂♂; Yarraman 7 ♂♂; Bunya Mountains 17 ♂♂, 3 ♀♀; Blackbutt 4 ♂♂; Maleny 12 ♂♂, 7 ♀♀; Upper Brisbane River 6 ♂♂; Chevellum 4 ♂♂; Woodford 3 ♂♂; D'Aguilar 2 ♂♂; Mount Mee 14 ♂♂, 11 ♀♀; Ravensbourne National Park 1 ♂; Mount Glorious-Mount Nebo 107 ♂♂, 42 ♀♀; Samford 5 ♂♂; Withcott 4 ♂♂; Lake Manchester 7 ♂♂, 2 ♀♀; Gold Creek Road 4 ♂♂; Ma Ma Creek 1 ♀; Mount Tambourine 18 ♂♂, 3 ♀♀; Cunningham's Gap 21 ♂♂, 4 ♀♀; Nerang River 3 ♂♂; Spicer's Gap 1 ♂; Beechmont 1 ♀; Springbrook 11 ♂♂; Binna Burra 4 ♂♂; Christmas Creek 14 ♂♂; Coomera Gorge 1 ♂; Currumbin Creek 7 ♂♂, 1 ♀; Queen Mary's Falls National Park 14 ♂♂, 3 ♀♀; Mount Lindsay 2 ♂♂. *New South Wales*: Chillingham 5 ♂♂, 1 ♀; North Arm Tweed River near Murwillumbah 31 ♂♂, 12 ♀♀; Island in Tweed River 2 ♂♂; Woodenbong 3 ♂♂; Tweed River, Mount Warning 6 ♂♂; Richmond River (4 miles north of Kyogle) 1 ♂; Ulong 2 ♂♂; Upper Clarence River 7 ♂♂; Richmond River (south of Kyogle) 4 ♂♂; Grafton 3 ♂♂, 1 ♀; Point Lookout, New England National Park 51 ♂♂. *Australian Museum*: 6791 ♂, Clarence River (N.S.W.); 6794 ♂, Pine Mountain (Qd.); R.4247 ♂, Warrell Creek, Nambucca (N.S.W.; R.5090 ♂, Richmond River (N.S.W.); R.5872 ♂, R.5873 ♂, R.5876 ♂, R.5877 ♂, Nambucca River (N.S.W.); R.6265 ♂, R.6287 ♂, R.6289 ♂, R.6291 ♂, Gurravembi, Nambucca River (N.S.W.); R.6499 Juvenile, Avoca, via Gosford (N.S.W.); R.7463 ♂, Dunoon, Richmond River (N.S.W.); R.8472, Juvenile, Avoca, via Gosford (N.S.W.); R.8937 ♂, R.8939 ♂, Mount Tambourine (Qd); R.10456 ♂, Dorrigo Scrub (N.S.W.); R.10506 ♂, Wyong (N.S.W.); R.12081, Juvenile, Palmdale, Wyong (N.S.W.); R.12645 ♂, R.12646 ♂, R.12647 ♂, R.12649 ♂, R.12650 ♂, R.12651 ♂, R.12653 ♂, R.12654 ♂, R.12655 ♂, R.12656 ♂, Lowana, Dorrigo (N.S.W.); R.13543 ♂, Old Koreelah (N.S.W.); R. 15127 ♂, R.16945 ♂, R.17698 ♂, Bunya Mountains (Qd.); R.16922, Juvenile, Mount Glorious (Qd.); R.20498, Juvenile, Guineacor Caves, Wombeyan Caves (N.S.W.).

Distribution: Along and east of the Great Dividing Range from Bundaberg (Qd.) in the north to Gosford and Wombeyan Caves (N.S.W.) in the south.

MIXOPHYES ITERATUS, sp. nov.

(Pl. I, Fig. 2)

Mixophyes fasciolatus Günther; Fletcher, 1892, p. 18; Slevin, 1955, p. 359 [part.]; Moore, 1961, p. 163 [part.].

Type locality: Tweed River, Mount Warning, N.S.W.

Holotype: Australian Museum Reg. No. R.25929, ♂, collected 23-XII-1963.

Paratypes: 1 ♀ Australian Museum; 1 ♂, 1 ♀ Queensland Museum, collected same time and place as holotype.

Diagnosis: Distinguishable from frogs of other genera by the six features listed for *M. fasciolatus*, and from its congeners by web to tip of first, third, and fifth toes; two joints of fourth toe free of web; inner metatarsal tubercle strongly developed but relatively short—half as long as first toe; dark cross bars on limbs as wide as intervening light; tympanum almost round, long axis vertical; skin very granular on back and legs; and pointed snout.

Description: Extremely large for Australian frogs (80–115 mm. snout-vent), strongly developed hind legs and webbed feet, resembling *Rana*.

Holotypes: Back finely granular, dark olive to black almost obscuring typical *Mixophyes* dorsal patterning. Dark head stripe broad, almost same width throughout except above tympanum, where it narrows to thin line on edge of supra-tympanic fold (Fig. 1b). Broad lateral band of spots tending to irregular mottling between arm and groin. Dark cross bars on dorsal surface of limbs as wide as intervening olive, not expanded on margins. On posterior surface of thighs, cross bars coalese forming uniform dark background with few distinct yellow spots of diameter approximately equal to width of cross bars. Ventral surface smooth, white on belly limbs. Fine darker dusting on chin. Tympanum distinct, almost round, long axis vertical. Sharp supra-tympanic fold (Fig. 1b). Fingers without web, arranged in order of length: 3 > 4 > 1 > 2. Inner metacarpal tubercle, oval, well developed. Outer almost flat on palm. Nuptial pad on first finger only thin strip along inner edge. Toes fully webbed, reaching tip of first, second, and third toes on outer margins and tip of fifth. On inner edges of second and third to proximal and distal sub-articular tubercles, respectively. Only two joints of fourth toe free of web, narrow fringe to tip on outer margin (Fig. 1b). Inner metatarsal tubercle without well-developed shovel edge, length equal to half of first toe (measured from tip to its junction with tubercle). Sub-articular tubercles elongate, flattened. No outer metatarsal tubercle. Vomerine teeth in slightly oblique transverse series, almost meeting in midline, almost entirely in front of choanae.

Snout-vent length 80·5 mm.

Variation: Three paratypes and other specimens examined vary little from holotype. Females larger than males (> 100 mm.), skin with texture of coarse sandpaper. Dorsal colour from pale olive to dark bottle green.

Material examined: *Queensland*: Kumbia 1 ♂; Bunya Mountains 3 ♂♂, 1 ♀; Cunningham's Gap 5 ♂♂; Queen Mary's Falls National Park 2 ♂♂, 2 ♀♀; Mount Lindsay 2 ♂♂, 1 ♀. *New South Wales*: Upper Richmond River (6 miles north of Kyogle), 7 ♂♂, 1 ♀; Tweed River, Mount Warning, 4 ♂♂, 2 ♀. *Australian Museum*: R.7493 ♀, R.7494 ♀, Dunoon, Richmond River (N.S.W.); R.7550 ♂, Dorrigo (N.S.W.); R.12308 ♀, Mullumbimby (N.S.W.); R.12642 ♂, R.12643 ♀, R.12644 ♀, Lowana, Dorrigo (N.S.W.); R.16762 ♀, Coolmangar, via Lismore (N.S.W.); R.16946 ♂, Mullumbimby (N.S.W.); R.19038 ♀, R.19039 ♀, R.19040 ♀, R.19041 ♂, R.19042 ♂, Wallaby Creek, Urbenville (N.S.W.); R.25877 ♀, Ourimah (N.S.W.).

Distribution: Bunya Mountains and along the Queensland-New South Wales border east of Stanthorpe, south to the Dorrigo Plateau, N.S.W.

MIXOPHYES BALBUS, sp. nov.

(Pl. II, Fig. 1)

Mixophyes fasciolatus Günther, Moore, 1961, p. 162.

Type locality: Point Lookout, New England National Park, N.S.W., between 4,250 and 4,750 feet altitude.

Holotype: ♂ Australian Museum Reg. No. R.25922 collected 15-X-1965.

Paratypes: 10 ♂♂, 3 ♀♀ collected same time and place as holotype, by I. R. Straughan and A. R. Main (Australian Museum and Queensland Museum).

Diagnosis: Distinguished from other Australian frogs by six features listed for *M. fasciolatus*; and from other *Mixophyes* species by web extending only to distal sub-articular tubercle of third toe on outer margin, three joints of fourth toe free of web; inner metatarsal tubercle well-developed shovel, equal in length to first toe; cross bars on dorsal surface of limbs narrow, not distinct over whole surface, without distinct triangular bands on margins of limbs; dorsal surface diffuses laterally to merge with white ventral, without sharp change marked by narrow zone of dark dots; males with well-developed nuptial pads on metacarpal, first and second fingers; and oval tympanum, long axis directed obliquely towards eye.

Description: Large frogs (60–80 mm. snout-vent length) with strong limbs poorly marked by dark cross bars.

Holotype: Dorsal surface yellowish grey (grey in alcohol) diffusing gradually into white ventral. Lateral surface not marked with dark spots. Dark markings of typical *Mixophyes* pattern—interorbital T extending posteriorly as broad mid-dorsal stripe of irregular outline; few scattered irregular dark patches on remainder of back. Dark head stripe, bold between nostril and eye, thin line above tympanum (Fig. 1a). Triangular patch in front of nostril, not as dark as head stripe, with well marked edge. Bars on dorsal surface of limbs narrower than intervening light, not distinct over whole surface, broadening terminally, but not forming distinct triangles on margins of limbs. Extremities of dark limb bars not visible from below. Posterior surface of thigh diffusely speckled with dark. Ventral surface of body and limbs white, hands and feet darker, chin dusted with darker. Tympanum distinct, dorsal margin obscured in head stripe and supratympanic fold, oval, long axis directed towards eye (Fig. 1a). Fingers without web, stouter than in other species of *Mixophyes,* in order of length $3 > 4 > 1 = 2$. Inner metacarpal tubercle elongate, strongly developed; outer oval and equally developed. Dark horny nuptial pad covering dorsal surface of first finger except for distal phalanx; separate round pad on inner surface of inner metacarpus and tubercle; and thin strip dorsally on inner edge of second finger. Toes webbed to: sub-articular tubercle of first, proximal sub-articular tubercle of second and third on inner margins, tip and distal sub-articular tubercle on outer margins of second and third respectively, and tip of fifth. Three joints of fourth toe free of web, narrow fringe along outer edge to tip (Fig. 1a). Inner metatarsal tubercle strongly shovel-shaped, basal length approximately equal to length of first toe (measured from tip of toe to junction with tubercle). No outer metatarsal tubercle. Sub-articular tubercles variably developed. Vomerine teeth typical of *Mixophyes*—transverse plates in front of choanae almost joining in midline, directed slightly backwards towards midline.

Snout-vent length = 75·0 mm.

Variation: Webbing consistent on both sexes. Females without nuptial pads, more slender fingers. First, second, and fourth fingers almost equal in length, not always in same order as type (any order possible). Dorsal pattern with similar variation to other species of *Mixophyes*—less regular dark markings. Spots of dark in groin and behind arm in some females, not marking a zone of sharp transition from dark dorsal to white ventral colouring.

Material examined: *New South Wales*: Point Lookout, altitude 4,500 to 4,750 feet, 14 ♂♂, 5 ♀♀, 16-X-1965; Point Lookout, ca. 4,250 feet, 27 ♂♂ (21 sympatric with *M. fasciolatus*), 19-II-1966. *Australian Museum*: R.7479 ♂, Kurrajong Heights (N.S.W.); R.7567, Juvenile, Illawarra (N.S.W.); R.7587 ♂, Burrawang (N.S.W.); R.8328 ♂, Mount Wilson (N.S.W.); R.8455 ♂, Moss Vale District (N.S.W.); R.9218 ♂, Williams River, Dorrigo (N.S.W.); R.10063 ♂, Blackheath (N.S.W.); R.12547 ♂, Mount Irvine (N.S.W.); R.12567

♂, Mount Wilson (N.S.W.) ; R.12633 ♂, R.12648 ♂, R.12652 ♂, Lowana, Dorrigo (N.S.W.) ; R.12788 ♂, R.12789 ♀, Mount Irvine (N.S.W. ; R.17086 ♂ ,R.17087 ♀, R.17131 ♀, Dorrigo (N.S.W.) ; R.17097 ♂, R.17581 ♂, Point Lookout, via Ebor (N.S.W.) ; R.17671, Juvenile, Linden, Blue Mountains (N.S.W.) ; R.18555 ♀, Barrington Tops (N.S.W.) ; R.19178 ♂, R.19179 ♂, R.19180 ♀, Royal National Park, Sydney (N.S.W.) ; R.19257 ♂, 15 miles SE Moss Vale (N.S.W.) ; R.19430 ♂, Mount Wilson (N.S.W.) ; R.24493 ♂, R.24494 ♂, R.24495 ♂, R.24496 ♂, R.24497 ♂, R.24498 ♂, Falconbridge (N.S.W.).

Distribution: East of the Great Dividing Range from the Dorrigo Plateau south to Illawarra

Mixophyes schevilli Loveridge, new combination

(Pl. II, Fig. 2)

Mixophyes fasciolatus schevilli Loveridge, 1933, p. 56; Parker, 1940, p. 15.

Type locality: Millaa Millaa; Lake Barrine, 4,000 feet Bellender Ker Range, North Queensland.

Topotypic material: Millaa Millaa, 1 ♂, 2 ♀♀, collected 11-II-1963; Lake Barrine, 1 ♀ collected 11-XII-1964.

Diagnosis: Distinguished from other genera by six features listed for *M. fasciolatus* and from other species in the genus by toes strongly webbed with only two joints of fourth toe free of web, web to tip of third toe on outer edge; basal length of inner metatarsal tubercle only approximately half length of first toe; smooth skin, yellow-brown to red colour; cross bars on limbs narrow, alternating with fine dark lines, passing completely round forelimb, tibia, and foot; back of thigh with dark diffuse broad horizontal band formed from coalesing of cross bars, without pale spots; and oval tympanum, long axis tilted towards eye from vertical.

Description: Large raniform frogs (60–90 mm. snout-vent). Dorsal surface smooth, yellow-brown, tan, or darker brown with red tinge, back pattern typical *Mixophyes*—dark interorbital T or Y continuing backwards as irregular broad mid-dorsal stripe and irregular scattered blotches over remainder. Dark head stripe with continuous black upper margin, broken on lower margin between nostril and eye (Fig. 1d). Triangular patch in front of nostril edged in black, otherwise paler. Dorsal surface of limbs with distinct dark cross bars alternating with finer dark lines. Bars narrower than intervening background, continuous across ventral surface round forelimb, tibia, and foot. On thigh, bars coalese and posteriorly form a diffuse dark horizontal band, not marked by paler spots. A few scattered lateral dark spots. Ventral surface of body and thighs white, smooth except immediately adjacent to vent. Throat white, chin dusted with black. Tympanum oval, long axis tilted from vertical towards eye (Fig. 1d). Fingers not webbed, in order of length $3 > 4 > 1 > 2$. Inner metacarpal tubercle elongate to oval well developed; outer oval, barely raised from palm. Toes webbed to: just beyond sub-articular tubercle of first, tip of second and third on outer margins, proximal sub-articular tubercle and slightly beyond on inner margin of second and third respectively, and tip of fifth. At most, two joints of fourth toe free of web (Fig. 1d). Inner metatarsal tubercle shovel-shaped, without well developed edge, length approximately half length of first toe from tip of toe to junction with tubercle. Sub-articular tubercles oval, flattened. No outer metatarsal tubercle. Vomerine teeth oblique transverse plates directed from front margin of choanae to midline between choanae.

Material examined: *Queensland*: Mount Finigan (Cooktown) larvae only; Black Mountain (20 miles north of Kuranda), 2 ♂♂, 3 ♀♀; 7 miles west of Atherton, ca. 4,000 feet, 2 ♂♂, 1 ♀, 23 Juveniles; Mount Hipipamee, 1 ♂, 1 ♀; Lake Eacham, 1 ♂, 1 ♀; Lake Barrine, 1 ♀; Malanda, 1 ♂; Millaa Millaa, 1 ♂, 2 ♀♀; Tchupala Falls, Palmerston National Park, 2 ♂♂, 2 Juveniles. *Australian Museum*: R.266 ♂, 20 miles inland of Cairns (Qd.); R.770 ♂, R.4693 Juvenile, Cairns District (Qd.); R.17017 ♂, Dinner Creek, near Cairns (Qd.).

Distribution: Atherton Tablelands and coastal ranges of north Queensland from Mount Finigan (near Cooktown) south to the Johnstone River.

Key to all known species of MIXOPHYES

1. Toes webbed to tip of third toe on outer margin; only two joints of fourth toe free of web. Basal length of inner metatarsal tubercle half length of first toe (measured from tip of toe to its junction with metatarsal tubercle) .... 2.
Toes not webbed beyond distal sub-articular tubercle of third toe on outer margin; three joints of fourth toe free of web, except for a fringe along outer margin. Inner metatarsal tubercle equal in length to first toe .... 3.

2. Dark cross bars on limbs as broad as intervening light, coalescing on posterior surface of thigh to form uniform dark background with scattered pale blotches .... *Mixophyes iteratus.*
Dark cross bars on limbs narrower than intervening light, coalescing on posterior surface of thigh to form diffuse dark speckled, horizontal band .... *Mixophyes schevilli.*

3. Dark cross bars on limbs sharp, well defined; widening on the margins into dark triangles, the bases of which are obvious from below ..... *Mixophyes fasciolatus.*
Dark cross bars not sharply defined, with few irregular marginal expansions which are not visible from below .... *Mixophyes balbus.*

DISCUSSION

Mixophyes fasciolatus Günther as redefined here, is synonymous with *M. fasciolatus fasciolatus* Günther, defined by Loveridge (1933, p. 55) and followed by Parker (1940, p. 13) who gives a complete synonymy, in which only one reference does not now refer to this species, i.e., Fletcher (1892, p. 18) referring to specimens with fully webbed toes from the Tweed River, N.S.W. Slevin (1955) referred three specimens from Ulong, Richmond River, N.S.W., two with fully webbed toes, to *M. fasciolatus*. Moore (1961) found specimens from Lowana, Mullumbimby, and Dunoon (all in northern N.S.W.) as well as the specimens of Fletcher (1892) and Slevin (1955) were webbed to the extent considered as diagnostic of *M. fasciolatus schevilli* Loveridge. As this sub-species was erected for northern Queensland forms and *M. fasciolatus* for southern Queensland-northern N.S.W. forms, Moore (*op. cit.*) believed that, because the two forms occurred in sympatry, sub-species could not be recognised. He suggested that two species might be involved: a highland rapids species with "mountain brook" tadpoles and a coastal stream species with more extensive webbing and probably with unspecialised larvae. These "fully webbed" specimens have been transferred to the new species *M. iteratus*.

Specimens of *M. balbus* recorded in the literature under *M. fasciolatus* are listed under Australian Museum numbers for *M. balbus* and may be cross referenced to Moore's list (p. 164). Moore (*op. cit.*, p. 163) refers tadpoles, found at 5,000 feet at Point Lookout, N.S.W. to *M. fasciolatus*, but as this is the type locality for *M. balbus*, and *M. fasciolatus* is known only at lower altitudes, this reference is more likely to be to *M. balbus*.

M. fasciolatus is sympatric with *M. iteratus* and *M. balbus* in different parts of its range and exhibits no integrading with either. *M. balbus* and *M. iteratus* occur sympatricly at several localities where no intergrades have

Fig. 1. *Mixophyes fasciolatus.*

Fig. 2. *Mixophyes iteratus.*

Fig. 1. *Mixophyes balbus.*

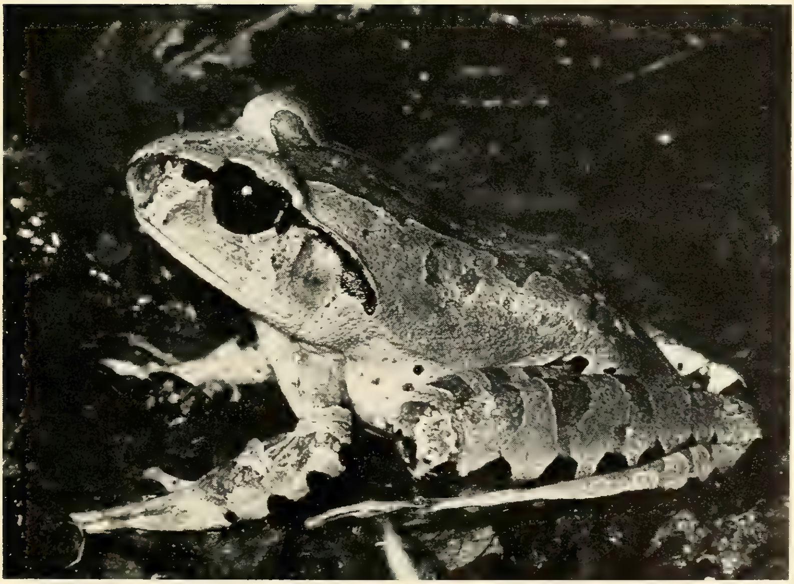


Fig. 2. *Mixophyes schevilli.*

been collected. *M. schevilli* is restricted in distribution and is geographically isolated, but exhibits greater differences in morphology from the other species of *Mixophyes*, than is found between these species. Straughan (1966) showed that each of these species has a distinct mating call and found no intergrading in areas of sympatry of the three southern species. Also the call of *M. schevilli* reflects the degree of difference from the southern species shown by morphology. Parker (1940, p. 15) gives a complete synonymy for *M. schevilli*.

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EXPLANATIONS OF PLATES I–II

PLATE I

Fig. 1. *Mixophyes fasciolatus* (natural size). Dark dorsal and limb patterns obscured by the overall darkness of this highly hydrated specimen. Dark sawtooth pattern on margins of limbs and lateral series of dark spots obvious.

Fig. 2. *Mixophyes iteratus*, sp. nov. (½ × natural size). ♀ Paratype Qd. Mus. showing fully webbed feet, wide cross bars on limbs and granular skin.

PLATE II

Fig. 1. *Mixophyes balbus*, sp. nov. (natural size). Holotype Aust. Mus. Reg. No. R.25922 showing two joints of third toe free of web; diffuse limb bars with irregular expansions at margins, absence of lateral series of dark spots, and nuptial pads on first and second toes.

Fig. 2. *Mixophyes schevilli* (natural size). Showing irregular cross bars narrowing to and alternating with thin dark lines.

THE SECRETORY CAPACITY OF THE STOMACH OF THE WOMBAT (*VOMBATUS HIRSUTUS*) AND THE CARDIOGASTRIC GLAND

G. W. Milton,* D. J. Hingson† and E. P. George‡
(*Communicated by Dr. Mervyn Griffiths*)

[Read 27th March, 1968]

Synopsis

The secretory capacity of the stomach of the wombat (*Vombatus hirsutus*), and of the cardiogastric gland of this animal has been studied.

It was found that the secretory power of this stomach resembles that of man and animals commonly used in gastric research. The concentrations of ions in gastric juice generally fitted the Hollander two-component theory of gastric secretion. A close correlation between the concentration of pepsin and of K^+ was demonstrated. The electrophoretic pattern of the gastric juice of the wombat resembled that obtained from the gastric juice of man. The maximum secretory capacity of the stomach of this animal was lower than that of man. It was found that a considerable increase in the gastric output could be obtained by augmenting the effects of histamine stimulation by injections of insulin.

INTRODUCTION

In three mammals, the wombat (*Vombatus hirsutus*), the koala "bear" (*Phascolarctos cinereus*) and the North American beaver (*Castor canadensis*) there exists on the lesser curvature of the stomach a highly specialised area of secreting cells, known as the cardiogastric gland (Home, 1808; Johnstone, 1898; Mackenzie, 1918; Milton, 1962). The anatomy of this gland has been studied in the beaver (Smith *et al.*, 1911; Nasset, 1953) and in detail in the wombat (Hingson and Milton, 1967). In the latter animal the gland consists of about 20 infoldings of the gastric epithelium with the muscularis mucosae and submucosa. Each of the gland pits opens into the lumen of the stomach through a separate ostium. The pits are lined with thickened gastric epithelium which contains innumerable gastric glands. The cells in these gastric glands are of the usual type found in the lining of a carnivorous mammalian stomach. The chief and parietal cells are particularly prolific and the gland tubules appear to possess a good blood supply from the left gastric artery. A separate branch of the vagus nerve enters the gland from the parietal surface. The remainder of the stomach in the wombat has a lining similar to that of other mammals, the antrum is well defined and consists of non-acid secreting epithelium. There is also a small band of non-acid secreting epithelium close to the oesophageal opening. The body of the stomach is lined with glands similar to other animals. The glands here consist of surface mucus cells, mucus cells at the neck of the gland, chief and parietal cells and an occasional argentaffin cell.

Each of the animals possessing a cardiogastric gland is a herbivore. The precise diet of the wombat is not fully known, but it probably consists of roots and grasses that are found near its burrow. Both the wombat and the

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* Department of Surgery, University of Sydney, Sydney.

† Research Student, Johns Hopkins University, Baltimore, U.S.A.

‡ School of Physics, University of New South Wales, Sydney.

koala are large marsupial animals and are therefore widely separated in evolution from contemporary mammals such as the beaver.

The object of the present paper is to report a study of the secretory function of the wombat stomach and of the cardiogastric gland. We have also investigated the ionic relationships in the gastric juice of this animal to ascertain if they are in agreement with the Hollander two-component theory of gastric secretion (Hollander, 1932).

Material and Methods

Nine adult healthy wombats weighing between 13–25 kg. were used in these experiments. The animals were fasted for 18–24 hours and anaesthetised with nitrous oxide and oxygen mixture administered through a face mask. As soon as anaesthesia had been induced a fine intravenous catheter was inserted into one femoral vein and passed into the inferior vena cava. The catheter was attached to a three-way tap and through it a connection made to a syringe containing dilute pentothal sodium (1 gm./60 ml.). Anaesthesia was maintained by occasional injection of 1–3 ml. of this solution. Throughout all experiments the animal was given a continuous infusion of histamine acid phosphate (2·2 μg. base/kg. body wt./min.) administered by a slow infusion pump. In several experiments once a steady baseline of secretion had been established booster doses of histamine were administered (0·5 mgm./kg.) subcutaneously. After some hours of histamine the animals were given a subcutaneous injection of soluble insulin (50 units).

The experiments were divided into two groups. In Group 1 the secretion from the whole stomach excluding the antrum was studied. An intragastric tube was passed through the mouth and its position checked by opening the abdomen. A tight ligature was then passed around the antral region just distal to the end of the tube, thereby excluding the antral secretion from the rest of the stomach. In Group 2 the stomach was opened along the anterior surface and a suction tube passed through the mouth and fixed over the openings of the cardiogastric gland by sewing the tip of the tube to the lesser curve just beyond the gland. The gland area was then excluded from the remainder of the stomach by sewing together the anterior and posterior gastric surfaces across the tube with an atraumatic stitch. In this way a pouch was made which consisted largely of the cardiogastric gland. A second tube was placed in the remainder of the stomach through the gastrotomy opening and brought out through the anterior abdominal wall. The tubes used to aspirate the gland area and the stomach were double lumened, the smaller lumen being an air inflow to prevent excessive suction. When the tubes were in place the caudal end of the table was raised eight inches to prevent the saliva from trickling into the stomach and to facilitate aspiration.

At the conclusion of the experiment the position of the tubes was checked and also the patency of the septum between the cardiogastric gland and the body of the stomach.

The samples of gastric juice were collected under ice and the collecting cylinder changed half-hourly. After insulin injections the collecting cylinder had to be changed more frequently (10–15 minutes). Each specimen was tested for the following: (1) Acidity by titration against NaOH (N/50) to pH 7·4, using a glass electrode pH meter coupled to an automatic titrator (Radiometer). (2) Na^+ and K^+ by flame photometry (Perkin Elmer, external standards). (3) Cl^- by potentiometric titration using the automatic titrator (Lehmann, 1939; Muller, 1942). (4) Pepsin using the haemoglobin substrate method (Harrison, 1964). (5) Total osmolarity was measured in seven samples of high concentration using a freezing point osmometer. (6) In one animal the stomach was irrigated with $NaHCO_3$ by the technique of Piper *et al.* (1963) and the electrophoretic pattern of the gastric juice estimated by Piper (1966).

Samples of blood were taken from five animals and the total osmolarity, Na^+, K^+, and Cl^- concentration of the plasma were measured by the above techniques.

The figures were analysed in several ways. The interrelationships of ions, volume, pepsin for both concentration and output were determined with the assistance of the digital computer, SILLIAC. The correlation coefficients between pepsin and H^+, K^+, and Cl^- were obtained. In addition observations were made on the response to histamine, and histamine augmented with subcutaneous histamine and subcutaneous insulin.

RESULTS

The characteristics of the serum of the wombat are shown in Table 1, together with the total osmolarity of gastric juice secreted at maximal acid concentration. It can be seen that the osmolarity and concentration of ions in the serum of these animals is roughly the same as that in other animals more frequently used in gastric research. The osmolarity of human, dog, and cat plasma ranges from 300 to 330 m. osmoles/litre (Houssay, 1955; Spector, 1956).

TABLE 1

Serum osmolarity and the osmolarity of concentrated gastric juice in milli osmoles/litre, and the concentration of Na^+, K^+ and Cl^- (mEq/l.) from the serum of the wombat, ±S.D.
The figure in brackets is the number of specimens analysed

Total osmolarity serum	286·2±20·8 (5)
Ions (serum):	
Na	134·8± 3·3 (5)
K	4·4± 0·35 (5)
Cl	96·8±10·1 (5)
Gastric juice (whole stomach) ..	281·4± 33·2 (7)

The electrophoretic pattern of the gastric juice showed a main band that moved towards the anode and had the electrophoretic mobility of albumin. In addition there was a more rapidly moving anodal band (Band 6) and several bands of intermediate mobility. The latter are almost entirely mucopolysaccharides. The pattern resembles that found in human gastric juice (Piper, 1966; Piper *et al.*, 1963).

The response of the whole stomach (Group 1) and the isolated cardiogastric gland (Group 2) to histamine infusion was similar to other animals. After the start of the infusion the volume and acidity of gastric juice increased until after about one hour a peak was reached (Fig. 1). There was a tendency after the establishment of a peak for the secretion rate to diminish, while the acidity remained at a plateau. Supplementary subcutaneous injections of histamine caused a temporary increase in gastric output, but no increase in the concentration of acid. The injection of insulin was followed by a considerable increase in both the volume and the acidity of the gastric juice. The volume of gastric juice and the output of acid taken over all experiments were closely related ($r = 0{\cdot}80$).

The pepsin concentration remained at a high and fluctuating level for some hours and then declined. The correlation of pepsin on volume was poor ($r = 0{\cdot}29$), neither the injection of histamine nor of insulin affected the decline of peptic concentration. A typical result is shown in Fig. 2. The concentration of K^+ closely followed the concentration of pepsin in all the fluctuations ($r = 0{\cdot}63$).

The concentration of all the ions measured in all experiments followed the usual relationships. Na^+ concentration fell as the acidity rose, and Cl^- and K^+ followed each other closely (Table 2).

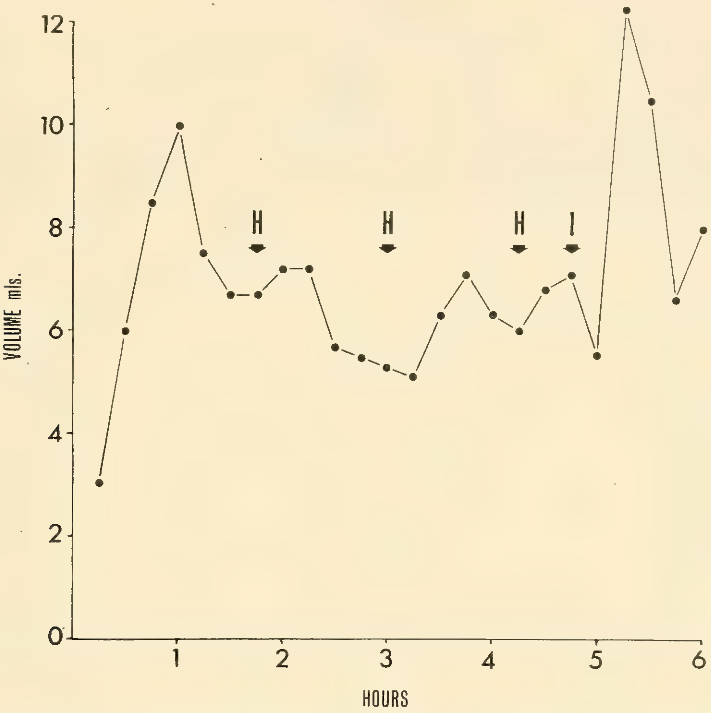

Fig. 1. Volume of gastric juice secreted from the whole stomach preparation described in the text. Histamine stimulation was commenced at 0 time. Note the rise to a peak after 1 hour and the decline despite continuing stimulation. Booster doses of histamine produced some increase in output, but a considerable increase in output followed the administration of insulin. H—histamine, I—insulin.

When comparing the maximum secretory capacity of the cardiogastric gland (Group 1) and the whole stomach including the cardiogastric gland (Group 2) it is necessary to take into account the effectiveness of the septum separating the gland from the body of the stomach. In one animal this septum was not adequate to exclude leakage from the body of the stomach into the cardiogastric gland area; the animal was excluded when the comparisons were made. Table 3 shows the maximum concentration of ions excreted by

TABLE 2

Correlation coefficients (r) for acidity (H) on Cl, Na, K and also for pepsin (P) on H, Na, Cl and K

The concentrations of all ions were in mEq/l. and pepsin in 10^3 units/l.

L.C. Ions	r	Pepsin (P)	r
H Vs Cl	0·78	P Vs H	−0·21
H Vs Na	−0·83	P Vs Cl	0·05
H Vs K	−0·27	P Vs Na	−0·05
		P Vs K	0·63

four isolated cardiogastric gland areas and the maximum concentration from the whole stomach. There was no significant difference between any of the figures obtained for H^+, Cl^-, Na^+, K^+ and pepsin (Table 3).

The Hollander (1932) two-component theory of gastric secretion is based on the assumption that gastric juice is made up of two isotonic solutions.

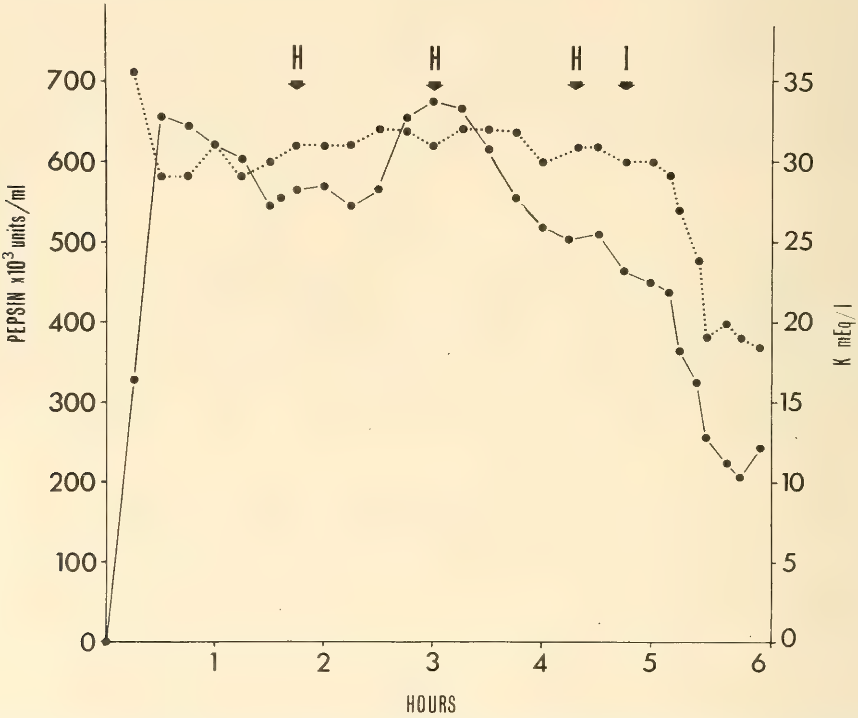

Fig. 2. Concentration of pepsin (Units 10^3/ml.) and K^+ (mEq/l.) from the gastric juice obtained from the animal shown in Fig. 1. The concentrations of pepsin and acid show similar fluctuations.

If this assumption is valid for the wombat there will be a linear relation between the concentrations x, y of different ions, taken two at a time, of the form—

$$y = a + bx \tag{1}$$

where the constant b is given by

$$b = \frac{\sqrt{xy}}{\sqrt{xx}}$$

xy being the co-variance
xx being the variance.
The constant "a" is found by taking mean values in equation (1).

$$\bar{y} = a + b\bar{x}$$

or

$$a = \bar{y} - b\bar{x} \tag{2}$$

The ionic relationships obtained in this manner are:

$$Cl^- = 0{\cdot}58H + 91{\cdot}4 \quad (r = 0{\cdot}77) \tag{3}$$

$$Na^+ = -0{\cdot}521H + 86{\cdot}9 \quad (r = -0{\cdot}83) \tag{4}$$

$$K^+ = -0{\cdot}083H + 26{\cdot}46 \quad (r = -0{\cdot}27) \tag{5}$$

The nomenclature used to express the Hollander two-component theory is shown in Table 4.

If the two compounds are isotonic

$$p + q = b + c + d \tag{6}$$

The relations between the ionic concentrations have been outlined by James (1957), and if x is the proportion of the parietal cell component in gastric juice, the relevant equations are:

$$Cl^- = bx + (c+d) \tag{7}$$

$$Na^+ = (c+b)\ (1-x) \tag{8}$$

$$K^+ = qx + d\ (1-x) \tag{9}$$

$$H^+ = (p+b)\ x - b \tag{10}$$

We require to know the concentrations of Cl^-, Na^- and K^+ in terms of H^+ as in equations (3), (4) and (5). Therefore by eliminating x from equations (7), (8), (9) and 10 we obtain:

$$Cl^- = \frac{b}{p+b} H + \frac{b^2}{p+b} + c + d \tag{11}$$

$$Na^+ = -H \frac{(c+b)}{(p+b)} + p \frac{(c+b)}{(p+b)} \tag{12}$$

$$K^+ = -H \frac{(d+q)}{(p+b)} + \frac{bq+pd}{p+b} \tag{13}$$

$$H^+ = K \frac{c+d}{d-q} - q \frac{c+d}{d-q} \tag{14}$$

The volumes of Cl^-, Na^+, K^+ and H^+ represent the total concentration of each ion in whole gastric juice. By solving the equations relevant for each ion, e.g., (11) and (3) for Cl^-, and (12) and (4) for Na^+ a series of values is obtained as in Table 5 which are in best agreement with the Hollander theory.

TABLE 3

Maximum concentration of Na, Cl, H and K at mEq/l. and of Pepsin × 10^3 units/ml. ±S.D. obtained from four isolated cardiogastric glands and four total gastric pouch experiments

	Whole Stomach (Group 1)	Cardiogastric Gland (Group 2)
H	129·0± 4·6	117·0± 20·1
Cl	170·5± 2·6	170·5± 5·0
Na	16·3± 3·8	24·7± 10·5
K	30·0± 4·8	19·9± 4·9
P	490·7±137·0	624·7±232·3

In these results the parietal and non-parietal components are not isotonic.

The ionic relations calculated from equations (11) to (14), using the values in Table 5 are:

$$Cl^- = 0{\cdot}58H + 168 \tag{15}$$

$$Na^+ = -0{\cdot}584H + 96 \tag{16}$$

$$K^+ = -0{\cdot}0835H + 14 \tag{17}$$

These relations are closest in the equations (3) to (5) in the present analysis. For comparison, we also found the best fit on the assumption that the total molarity of the non-parietal secretion was 170 mM., making it isotonic with the parietal secretion.

The best fit was found for the following values:

$$\begin{array}{lr} NaHCO_3 & b = 120\text{ mM.} \\ NaCl & c = 35 \\ KCl & d = 15 \\ \hline & 170 \end{array}$$

which give the following theoretical relations:

$$Cl^- = 0{\cdot}42H + 100 \qquad (18)$$

$$Na^+ = -0{\cdot}54H + 90 \qquad (19)$$

$$K^+ = -0{\cdot}052H + 9 \qquad (20)$$

which again agree adequately with the experimental results (compare equations 3–5 with 18–20).

TABLE 4

Parietal cell secretion (Concentration)		Non-parietal cell secretion (Concentration)	
HCl	p	$NaHCO_3$	b
KCl	q	NaCl	c
		KCl	d

The figure of 170 mM. concentration assumed for both parietal and non-parietal solutions in the last analysis is not inconsistent with the measured osmolarity of 281·4 ml./l. (Table 1), since the latter figure is weighted strongly by the fully ionised solutes by a factor of two. However, the non-parietal figures given in Table 5 are probably inconsistent with the measured osmolarity.

TABLE 5

Parietal cell secretion (Concentration mEq/l.)			Non-parietal secretion (Concentration mEq/l.)		
HCl	p	167	$NaHCO_3$	b	232
KCl	q	0	NaCl	c	0
			KCl	d	33·4
Total concentration		167			265·4

The results were analysed to determine whether it was justified to group together the results for whole stomachs and for glands. From this analysis it appears that the Cl^-/H^+ and the Na^+/H^+ relations are the same for both gland and for stomach, but that the K^+/H^+ relations are different. We find for the cardiogastric gland alone

$$K = -0{\cdot}30H + 54 \quad (r = -0{\cdot}52)$$

whereas for the whole stomach alone

$$K = -0{\cdot}14H + 37{\cdot}2 \ (r = -0{\cdot}47).$$

The separation into two sets is seen to improve the correlation. These results taken together with the relations (3) and (4) give the Hollander analysis of the secretions (Table 6), which suggests that the parietal cells of the stomach secrete a small amount of HCl (20 mM.), whereas the parietal cells of the cardiogastric gland do not.

DISCUSSION

The wombat is a member of the Phascolomydiae family of the marsupials. The primitive forms of the marsupial separated from the ancestors of the present day mammals, in the remote past, probably about 70 million years ago.

Although in the intervening periods the marsupial has undergone considerable changes, especially in the larger Australian varieties, there is still an enormous gulf between the marsupial and the placental mammal. It is therefore of some interest to compare the secretory ability of this animal with that of more usual laboratory animals and man. On the whole the function of this "antique" stomach shows a remarkable resemblance to that of man. The stomach responded to histamine stimulation with a brisk ouptput of gastric juice and the concentration was only slightly lower than the maximum concentration achieved by man, dog and cat. The relationships of the different ions to one another were similar to those of the mammals. The Hollander two component theory still broadly fits the secretory pattern of this animal. The fit between theory and the observed results was not so close as has been observed in the cat (Milton *et al.*, 1963). This may be partly explained by the fewer number of experiments and the more restricted scatter of the observed ionic concentrations. The electrophoretic pattern of the gastric juice also resembled that of man.

TABLE 6

Parietal cell secretion			Non-parietal cell secretion		
	Gland	Stomach		Gland	Stomach
HCl	167	167	$NaHCO_3$ ..	100	100
KCl	0	20	NaCl ..	35	35
			KCl	55	55

The close correlation between K^+ and pepsin, if confirmed in man, could be a useful indication of peptic concentration in human gastric function tests, as it is easier to measure K^+ concentration than pepsin.

Much has been written about the "maximal" gastric secretory capacity. These findings show that in this animal, when the stomach is secreting at close to the limit of its power as a response to histamine, then a considerable boost in secretion can be achieved by the addition of insulin to the stimulus. Stimulation with combined agents may therefore give a higher maximal level than the use of one agent alone.

The finding that the cardiogastric gland secretes juice of about the same concentration as the body of the stomach agrees with the histological findings that the cells composing the cardiogastric gland are similar to those of the corpus (Hingson and Milton, 1968). It was not feasible in these experiments to compare in detail the output of the cardiogastric gland to the rest of the stomach in terms of ml. per minute; a large number of animals would be required to do this and it would be necessary to standardise the size of the stomach and gland in each case. But in the intact animal the cardiogastric gland must secrete a large proportion of the gastric juice. The reason for the slight difference in the relationship between K^+/H^+ in the whole stomach and the gland is not clear, but it could be related to the very large number of chief cells in the gland area and their intimate relationship to the parietal cells, so that during acid secretion in the gland the cells extract some K^+ from the adjacent chief cells.

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THE MUCOSA OF THE STOMACH OF THE WOMBAT (*VOMBATUS HIRSUTUS*) WITH SPECIAL REFERENCE TO THE CARDIOGASTRIC GLAND

DICKSON J. HINGSON* and G. W. MILTON†
(*Communicated by Dr. Mervyn Griffiths*)

(Plates III–V)

[Read 27th March, 1968]

Synopsis

The specialised cardiogastric gland region of wombat stomach which is characteristic of koala and beaver stomachs as well, is located on the lesser curve near the oesophageal opening. The cardiogastric gland in the wombat is distinctive because of its complex group of mucosal sacculations which open into the stomach lumen via 25 or 30 large crater-like ostia. The mucosa of this gland contains long, straight, closely packed, unbranched gastric glands composed of the cell types found elsewhere in the stomach, with chief cells concentrated at the base of the glands. Parietal cells are present in great abundance. Typical surface and neck mucous and argyrophilic cells are also present. The bizarre cardiogastric specialisation in the wombat is thus not cytologically a separate organ from the stomach. However, it does contribute greatly to the total secretory cell mass of the stomach.

INTRODUCTION

The stomach of the wombat (*Vombatus*), koala bear (*Phascolarctos*) and beaver (*Castor*) are of unusual anatomical interest due to the presence of a convoluted mucosal specialisation, or cardiogastric gland on the lesser curve, near the oesophageal opening. The first reported observations on the stomach of a wombat were made by Everard Home (1808); since then only brief descriptions of gross anatomical features of the stomach have been published (Oppel, 1896; Mackenzie, 1918; Milton, 1962). Some histological aspects of the cardiogastric gland region were studied by Johnstone (1898), but the techniques of that day did not permit micro-photography of the cytological organisation of the mucosa. This study was undertaken in order to clarify the organisation of this unusual stomach.

MATERIAL AND METHODS

Twenty-four adult wombats of both sexes (species: *Vombatus hirsutus*) were trapped in rural areas of Victoria and New South Wales. The animals were killed and the stomach was removed within five minutes of death, distended with 10% formal saline and immersed in this fixative. One stomach was sectioned and blocks placed in osmic acid-zinc iodide fixative, to stain the postganglionic unmyelinated parasympathetic nerve fibres (Maillet, 1963). Material for light microscopy was embedded in paraffin wax and sections 7–8 microns in thickness were stained by various methods. These included haematoxylin and eosin, periodic-acid-Schiff reaction (PAS), block silver impregnation (Masson, 1928), thionin and methylene blue. An incubation time of 36 hours was found preferable for the block silver impregnation.

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* Research Student, Johns Hopkins University, Baltimore, U.S.A. Present address: Department of Anatomy, Harvard Medical School, Boston, Massachusetts, U.S.A.

† Department of Surgery, University of Sydney.

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Observations

General Features of Wombat Stomach

The wombat stomach resembles that of the human in shape, and thus the usual regional nomenclature will be used: cardia, fundus, corpus and pylorus. The cardiogastric gland is found immediately distal to the cardiac region, hence its name (suggested by Smith *et al.*, 1911) for the analogous structure of the beaver.

The stomach wall varies considerably in thickness, from 0·6 mm. in the fundic region to 2·0 mm. in the corpus and pyloric region. The cardiogastric gland is the notable exception, as the thickness of the stomach wall in this region varies from 4 to 8 mm. The empty stomach measures 30 to 35 cm. along the greatest length from fundus to pylorus. It is thrown into several longitudinal folds which appear to converge on the cardiogastric gland except at the pyloric border. These disappear when the stomach is distended.

The cardiogastric gland can be identified externally on the lesser curve by several criteria:

(1) Its bulging position just distal to the oesophageal-gastric junction.
(2) A ruddy brown colouration due to the skeletal muscle fibres which run over it from the oesophagus, parallel with the longitudinal axis of the stomach. These fibres terminate, though not abruptly, near the pyloric border of the gland.
(3) A fold of lesser omentum and large stomach vessels which are seen crossing the stomach wall, just distal to the gland. However, the gland borders are not sharply outlined on the serosal surface.

The cardiogastric gland, on the luminal side, is distinguished by 25–30 crater-like outlets into the lumen of the stomach (Pl. III, Figs 1 and 2). These outlets, as shown in Figs 1 and 2 are convoluted within; they are not simple ostia. The trapezoid shape of the gland is well defined by these outlets, although convolutions of mucosa underlie the surface epithelium for a few millimetres peripheral to the outlets. The gland has its axis on the lesser curve; it converges to its narrowest dimension at the oesophageal opening. The mean surface area of these "gland trapezoids" as measured in six wombats was 15·0 cm^2. The outlets are often missing from the axis itself with only simple ridging present instead. Occasionally an outlet can be seen somewhat peripheral to and isolated from the main mass of the gland.

Regional Organisation of mucosa

The Cardia.—Typical cardiac, or mucus-secreting glands, are present in a narrow ring-shaped area (2 mm.) surrounding the oesophageal opening. Parietal cells begin to appear in the more peripheral part of this band. Only mucous cells are present immediately adjacent to the oesophago-gastric junction. The cardiogastric gland adjoins the cardiac area.

The Fundus.—The gastric glands in the fundus are much shorter and more coiled than in other regions. The mucosal thickness here is only about one-third that of the corpus and cardiogastric gland. Surface and neck mucous, parietal, chief, and argentaffin cells are all present, but the chief cells are much more abundant, relative to parietal cell population, than in the corpus and cardiogastric gland. Chief cells almost exclusively occupy the basal half of the individual gastric glands, with only occasional parietal cells or mucous neck cells wedged in among them. The luminal half of the glands is composed of surface mucous cells.

The Corpus.—This region is composed of long, straight, simple gastric glands. They are densely packed, parallel to each other, and perpendicular to the muscularis mucosae. The glands contain all five major cell types, and

and empty into gastric "pits" or foveolae. The distribution of cells and thickness of mucosa closely approximates the situation in the cardiogastric gland, and will be described under that heading. The only difference between this region and the cardiogastric gland is that here the mucosa forms a simple lining sheet without convolutions and impocketings. The corpus mucosa blends gradually into the mucosa of other regions.

The Cardiogastric Gland.—The mucosa of the cardiogastric gland is folded upon itself in an elaborate manner, so that sac-like impocketings result. The nature of these impocketings is best understood by sections through the edge of the cardiogastric gland, where the mucosa is beginning to fold under itself (Pl. III, Fig. 3). The sacs thus formed are simple, branched, tubular, and do not anastomose. Muscularis mucosae closely invests these sacs and their branches. The ostia of the sacs are 1–5 mm. across, and represent the 15–30 crater-like openings seen macroscopically. Because of the large volume occupied by the impocketings relative to the smaller area required for their ostia, the underlying mass of sacs bulges beyond the outer rows of ostia. Thus it is that the peripheral rim of the cardiogastric gland underlies a simple epithelial sheet that does not bear openings (Pl. III, Fig. 3). As Fig. 3 also shows, the submucosa sweeps up among the sacs, bringing in its areolar tissue nerve, lymph and blood supply to the sacs, as well as some smooth muscle slips which are probably derived from the muscularis mucosae and externa. The muscularis and serosal coats simply pass underneath the whole mucosal mass, without investing individual sacs. The collection of longitudinally oriented striated muscle fibres, just deep to the serosa, is easily seen histologically (Pl. III, Fig. 4). For a more detailed description of the muscularis layers the reader is referred to Johnstone's account (1898).

A section cut transversely across the lesser curve (the axis of the gland) may show a bifid ridged median leaf of submucosa, with no underlying sacs, and correspondingly thickened submucosa and muscularis layers (Pl. III, Fig. 4).

The mucosa of the gland is similar to that of the corpus in cytological organisation. While its single-sheet thickness (0·63 mm.) is approximately that of the corpus, the mucosa is piled up so that the mean total thickness of mucosa in a given section is four to ten times that of any other stomach region.

The individual glands are simple, straight and densely packed, opening near the lumen of the stomach into foveolae (Pl. IV). These contain the five principal cell types found in other mammalian stomachs. The chief cells are concentrated in the basal fifth of the glands, with occasional parietal cells wedged among them. A few argentaffin cells are near the base of some of the glands. A large number of parietal cells are present in every gland in its middle three fifths with mucous neck cells or, occasionally, surface mucous cells interspersed. Approximately 500 cells constitute a single gland.

Connective tissue, capillaries, fibroblasts, and a few smooth muscle fibres fill in the spaces between glands. The capillary plexus is particularly rich in the muscularis mucosae and near the gastric foveolae, just beneath the surface mucous cells. Large, thin-walled vessels, packed with blood cells, are often seen between foveolae.

The Pylorus.—The mucosa of the corpus gradually loses its parietal and chief cells as the pyloric opening is approached, although argentaffin cells remain. The epithelium becomes thinner, and foveolae eventually extend halfway to the muscularis mucosae. The glands become entirely composed of mucus-secreting and argentaffin cells. There is an intermediate zone, approximately 2 cm. wide, containing both corpus glands and pyloric glands. This zone begins at the pyloric edge of the cardiogastric gland and continues around towards the greater curve. Near the pylorus the glands become widely spaced, and considerable connective tissue, fibroblasts, and smooth muscle fills the spaces between glands. The glands themselves are coiled and may show simple branching. A suggestion of villi is seen in the few millimetres immediately surrounding the pyloro-duodenal junction, with several gland foveolae opening into each villus.

Cytology of the Gastric Glands.—Except where stated otherwise, these observations apply equally to cardiogastric gland and other regions of the stomach. Five distinct mucosal cell types are evident; surface mucous, neck mucous, parietal, chief and argyrophilic cells.

Surface Mucous Cells.—Surface mucous cells line the foveolae of the gastric glands and bridge the mucosa between the foveolae. They are tall, columnar cells, with a height of 15 to 20 microns and a width of about four microns. The nucleus is spherical and basally or centrally placed. A large nucleolus may be present. These cells are easily identified in PAS sections (Pl. v, Fig. 1) by the heavily striated mucous granules in the cytoplasm. These granules are densely packed and are present in the apical half of the cell. They do not encroach on the nucleus so as to flatten it, and usually a clear zone is seen between nucleus and mucus accumulations.

Neck Mucous Cells.—Neck mucous cells are found among the parietal cells along the elongated neck of the glands. They are low columnar or cuboidal and about 5μ in diameter. The shape of these cells is variable, and the cell may have a broad base and narrow apex, or vice versa. The nucleus is basally located and flattened by an encroachment of mucous granules on its apical side. Sometimes PAS-positive material is found on the basal side of the nucleus.

Chief Cells.—Chief cells are localised in the basal regions of the gastric glands, and stain readily with basic dyes. They are cuboidal or low columnar, and measures 5–10μ in diameter. The nucleus is spherical and centrally located. Accumulations of chromophil substance are present in the basal part of the cell. This substance is distributed in parallel, concentric or radially oriented rows, which give the cytoplasm a clearly striated appearance (Pl. v, Fig. 2). "*Nebenkerns*" (concentric spirallying ergastoplasmic rings) are clearly evident in some cells. The striations often seem centered about or actually attached to the nuclear membrane. The thickness of each striation is 0·2 microns or less. Accurate measurement is not possible because of the limited resolving power of the light microscope.

The apical portion of the cell has a pale, bubbly or frothy appearance suggestive of the zymogen granules characteristic of these cells. The vacuolations are spherical and are about 1μ in diameter. The top of the cell is frequently seen bulging into the lumen of its gland tubule. This distension is evidently caused by local accumulation of the secretory product. In certain regions of the mucosa most chief cells are seen to be almost full of the zymogen granules, with the ergastoplasm confined to the extreme base of the cell. In other mucosal regions the reverse is true, with ergastoplasm occupying the entire cell.

Parietal Cell.—Parietal cells are easily distinguished by their large size (diameter 10–25μ), and acdiophilic cytoplasm. They are confined mainly to the middle three fifths of the gastric glands, but occasionally wedge among both surface mucous cells and the basally located chief cells. Parietal cells appear to have a slightly larger mean diameter in the cardiogastric gland than in other stomach regions, although this has not been statistically verified. Parietal cells are spherical or pyramidal in shape. The nucleus is large, centrally located and may contain a nucleolus. The cytoplasm has a definite granular appearance. An intracellular canaliculus is present, staining negatively in haematoxylin-eosin preparations. The canaliculus is sharply outlined occasionally in PAS-treated material, as PAS-positive substances in the canaliculus cause a definite purplish ring (Pl. v, Fig. 3). This canaliculus surrounds the nucleus in a nearly completed "horseshoe", the open ends of which join the lumen of the gastric gland. The canaliculus follows a course midway between nuclear membrane and external limiting membrane.

The Argyrophilic Cell.—Argentaffin and other argyrophilic cells are present throughout the stomach mucosa, though not in great numbers. Both are demonstrated by the Masson stain. When present, they are usually basally located in the gastric glands. Their size is difficult to measure, owing to the great variety of shapes they assume (Pl. v, Fig. 4). Some cells are spherical and are about 10μ in diameter, others are greatly elongated (up to 30μ in length), with a narrow width (5μ) corresponding to the diameter of the nucleus. The nucleus itself is spherical and may be centrally placed in some cells. Not infrequently the nucleus may be centered at one end of the cell, with most of the cytoplasm concentrated around it. In such cases a long tapering extension of cytoplasm extends in one direction away from the nucleus, thus giving the cell a flask or club-shaped appearance. This extension may narrow considerably until it resembles a thread-like neuron process, $0{\cdot}2\mu$ in diameter. The argyrophilic cell seems to adapt its flexible shape to directly conform with its neighbours, and does not necessarily abut on the lumen of the gland tubules. The cytoplasm contains hundreds of small granules which may be stained by silver impregnation methods. Many of these granules are attached to the nuclear membrane.

Nervous Tissue.—Anterior and posterior vagal trunks are present on the oesophagus in its lower portion. These send branches to the cardiogastric gland as well as to the remainder of the stomach. A definite "spray" of fibres is often seen entering the cardiogastric gland.

Ganglia and nerve fibres were poorly or incompletely demonstrated in haematoxylin-eosin and the various special stains which it was hoped would distinguish them. However, the existence of the myenteric plexus of Auerbach in the muscularis externa was clearly demonstrated, with both nerve fibres and large multipolar neurons present. The submucous plexus of Meissner was not clearly seen.

Discussion

Some earlier observers, as well as the present authors, have seen that the cardiogastric gland of the wombat is not histologically a separate organ from the stomach (Oppel, 1896; Johnstone, 1898). Its mucosa is composed of the same types of secretory cells which are found in other stomach regions and in other mammalian stomachs. The similarities of thickness and cell distribution in corpus mucosa and cardiogastric gland mucosa do not suggest a unique function attributable to the cardiogastric gland.

The parietal cells of the wombat cardiogastric gland appear larger than those elsewhere in the stomach, an observation which had been previously made in beaver stomach (Nasset, 1953). However, we cannot verify in the wombat any increased height of mucosa or density of parietal cells in the cardiogastric mucosal lining as compared to neighbouring mucosa in the stomach body; such an increase has been reported in the beaver (Nasset, 1953). No comparisons based on those parameters have been reported for the koala stomach. It must be recognised that the total amount of enzyme and acid-secreting mucosa in the gland represents a very considerable fraction of the total stomach mucosa. While the localisation of this mucosa has been carried to an extreme in the wombat, koala and beaver, regional concentrations of parietal cells have been observed in other mammals. In man, dog, cat and rat the greatest density of parietal cell population exists in the stomach body on the greater curve (Oi *et al.*, 1958). The rabbit has the greatest concentration in the fundus, while the guinea pig has its greatest parietal cell concentration in the same site on the lesser curve as does the wombat (Oi *et al.*, 1958). The guinea pig does not possess a cardiogastric gland. Of interest is the fact that in human embryos gastric pits and differentiating gastric epithelial cells are first seen along the lesser curve, particularly in the oral part (Salenius, 1962).

The subcellular features of the mucosal cells in the cardiogastric glands or in other regions of the stomach were not unusual. However, the clarity and organised patterns of the ergastoplasmic striations in the chief cells were of some interest and are believed to be a well-defined rough endoplasmic reticulum. These striations have been described in the chief cells and pancreatic acinar cells of other mammals (Hagenau, 1958; Dalton, 1951).

Johnstone (1898) and Oppel (1896) have speculated about the significance of the cardiogastric gland in mammalian evolution and the genetic differences which may underlie its development. Oppel believed that the glandular apparatus of the wombat and koala blossomed into the cardiogastric gland in order to facilitate assimilation of large amounts of food. Thus the gland is viewed as an accessory structure which in practice augments the limited circumference of the stomach and represents a beneficial evolutionary development. It is not certain, however, in what way the digestion of large amounts of food is particularly enhanced by this gland. We have obtained considerable quantitative data on the acid, enzyme, and electrolyte composition of sections from the cardiogastric gland. Further discussion of the physiologic role of this anatomical specialisation is put forward by Milton, Hingson and George (1967).

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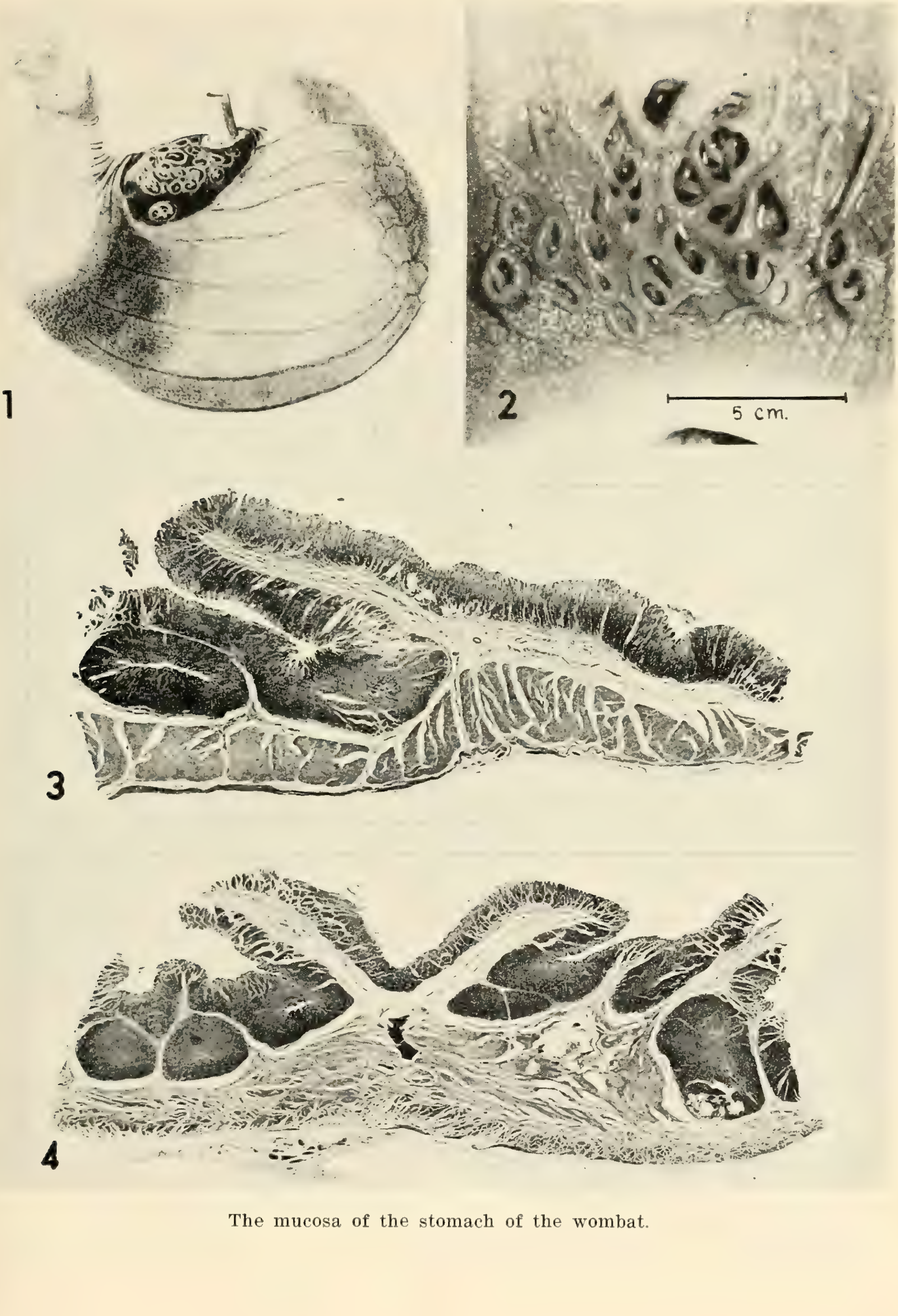
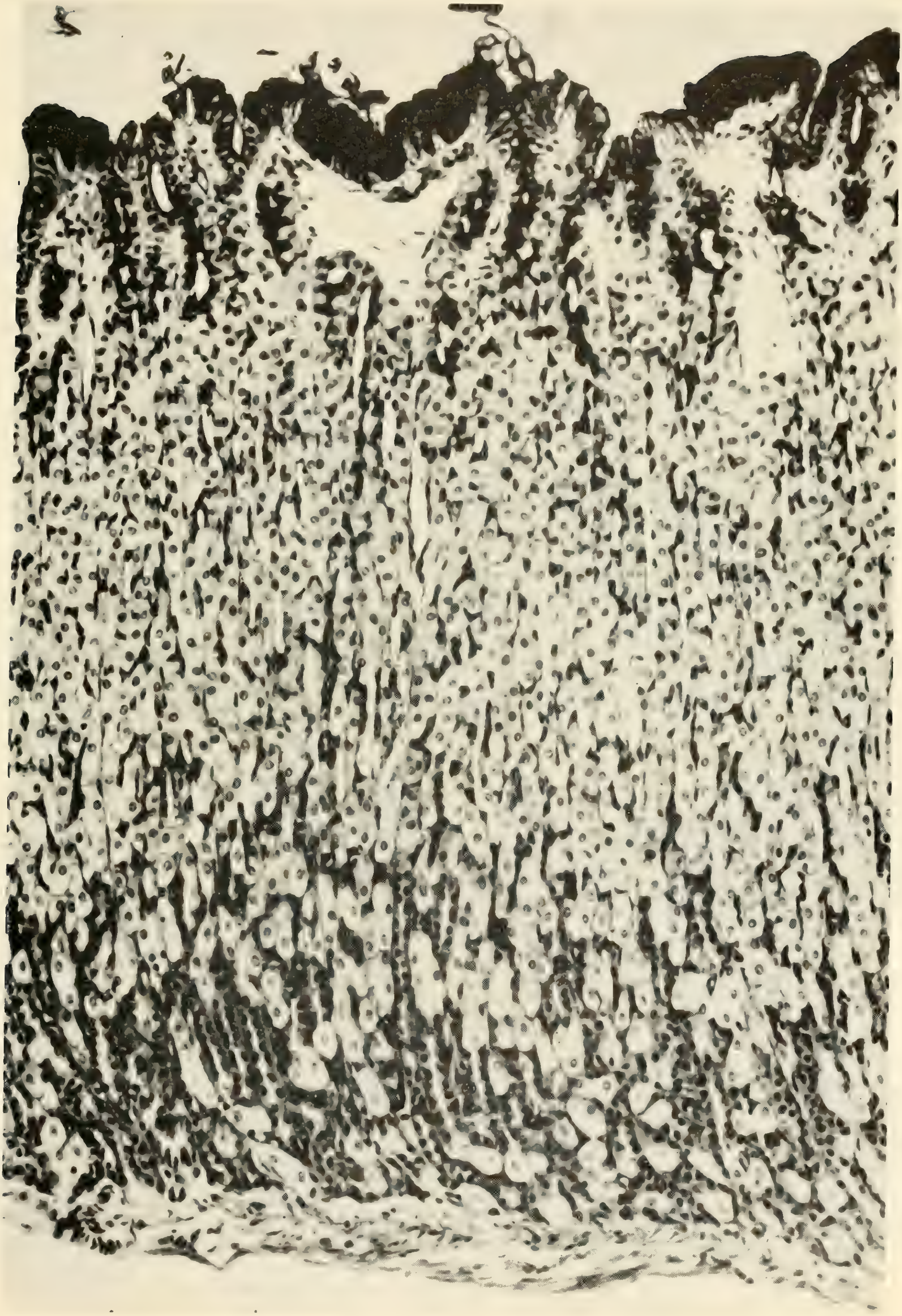
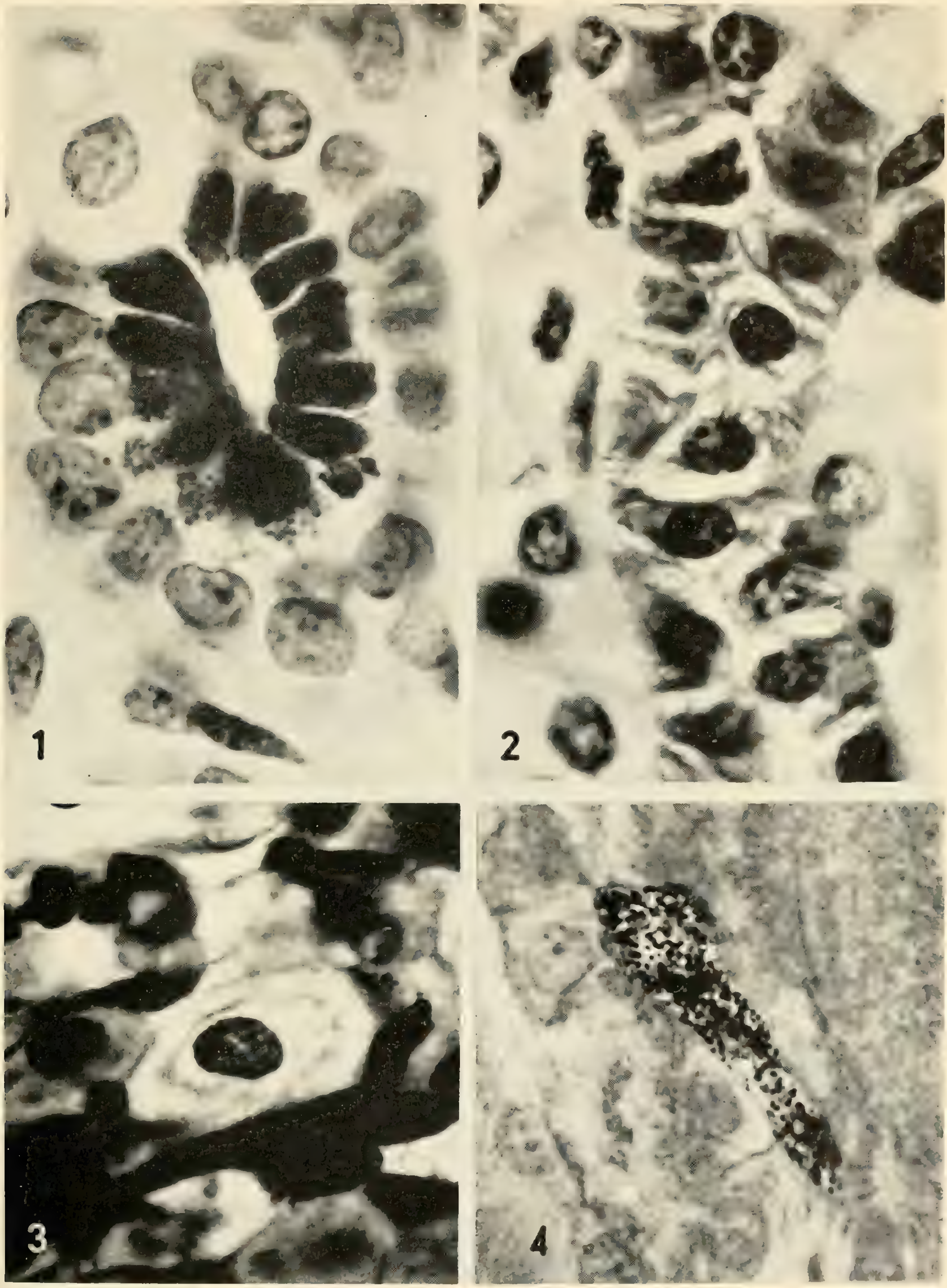


The mucosa of the stomach of the wombat.



The mucosa of the stomach of the wombat.



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EXPLANATION OF PLATES III–V

PLATE III

Fig. 1. The stomach of the wombat turned inside out and distended, from E. Home (1808). The gland area is well shown on the lesser curve close to the oesophagus.

Fig. 2. Close-up photograph of the cardiogastric gland. The oesophagus is the opening in the upper part of the picture. The edge of the antrum is at the extreme bottom. The cardiogastric gland ostia spread out close to the oesophagus on the lesser curve.

Fig. 3. Low power section, stained with haematoxylin-eosin through anterior edge of wombat cardiogastric gland. A typical sacculation with its ostium is visible, resulting from an impocketing of the stomach mucosa. Muscularis mucosae and submucosa invest the sacs, whereas muscularis externa passes deep to the whole of the gland mass. ×9.

Fig. 4. Low power section, stained with haematoxylin-eosin, of cardiogastric gland. The lesser curve has been transversely cut, and the axis of the gland lies approximately through the V-shaped median ridge in the centre of the photograph. Mucosal impocketings and sacs are on both sides of this ridge, which is characterised by a thinner mucosa than seen elsewhere in the gland. Bundles of skeletal muscle fibres, transversely cut, are just deep to the serosa. ×10.

PLATE IV

Section of cardiogastric gland mucosa, stained with PAS and counterstained with haematoxylin. Gastric glands are seen to be simple and unbranched. Chief cells are concentrated at the base of the glands and stain with haematoxylin. Parietal cells remain unstained, while neck and surface mucous granules are stained intensely with the PAS reaction. ×240.

PLATE V

Fig. 1. Transverse section through a gastric tubule from wombat cardiogastric gland. The section has been stained with PAS and counterstained with haematoxylin. Tall columnar mucous cells line the foveola, with dark-staining mucin granules evident in the apical portion of the cells. An unstained parietal cell is seen wedged among these cells at the upper left, communicating with the lumen through an intercellular cleft. ×2000.

Fig. 2. Section through the base of a gastric tubule in the cardiogastric gland, stained with haematoxylin-eosin. Prominently striated ergastoplasm is seen in all of the chief cells. The strands are oriented in a parallel, concentric, or radial pattern. The cell in the centre of the microphotograph contains haemophilic strands which are centered about or attached to the nuclear membrane. ×2000.

Fig. 3. Section through cardiogastric gland mucosa, stained with PAS and counterstained with haemotoxylin. The intracellular canaliculus of the parietal cell is prominently stained. ×2000.

Fig. 4. A photomicrograph of an argentaffin cell from the cardiogastric gland. The granules have been stained with Masson silver impregnation. Intensely silvered granules fill much of the cytoplasm of the argentaffin cells, with other gastric epithelial cell types almost entirely unstained. ×2000.

A REVIEW OF THE GENUS *HALOCYNTHIA* VERRILL, 1879

PATRICIA KOTT
Zoology Department, University of Queensland

[Read 27th March, 1968]

Synopsis

The genus *Halocynthia* Verrill is reduced by synonymy to six closely related species distinguished only by the condition of the gonads and the branchial and atrial spines. Considerable variation in external appearance is demonstrated within a single species.

Species occur in the littoral fringe of land masses and generally have a wide latitudinal range. Their distribution appears to be limited mainly by deep waters. The genus appears to be an ancient one and it may represent a relict of the Tethys Sea fauna.

INTRODUCTION

The genus *Halocynthia* Verrill, is an homogeneous one, comprising only a limited number of closely related species. These generally have a wide cosmopolitan distribution from north to south along the sub-littoral fringe of land masses in depths up to about 200 m. Geographic isolation is not always a major factor in speciation and phylogeny of the genus is discussed. An attempt is made in the present work to define the limits of intraspecific variation and to clarify the taxonomy of the genus.

Genus HALOCYNTHIA Verrill, 1879

Type Species.—Ascidia papillosa Linnaeus, 1767.

Test produced into spines. Longitudinal glandular plications and arborescent liver lobes present in the pyloric region. Gonads form, on each side of the body, a parallel series of tubular ovaries surrounded by testis lobes, each gonad terminating in a ♀ and ♂ duct directed toward the atrial opening. On the left the gonads are in the gut loop and the ducts extend across the descending limb of the intestine. A double series of languets present along the dorsal line.

Species of this genus are present in sand, gravel or on rocks but never in mud. The genus has been recorded, on several occasions, with the phanerogam, *Posidonia*, which also flourishes on a sandy substrate (*H. papillosa* in the Mediterranean and *H. hispida* in South Australia). Further, the genus is invariably taken in fairly shallow water (up to 200 m. but generally less) in sheltered waterways and estuaries where terrestrial run-off and/or melting ice might be expected to affect the salinity of the water, e.g., Upper St. Vincent's Gulf, Port Jackson, D'Entrecasteaux Channel, Akkeshi Bay, Puget Sound, Massachusetts Bay, Gulf of St. Lawrence, Iceland, Greenland, etc.

Key to the Species of Halocynthia

1 Spines around apertures with secondary spines 2
Spines around apertures without secondary spines 4
2(1) 1 or 2 gonads per side, not parallel, no spinules on shaft of spines.......... .... *H. igaguri* Tokioka
(Inland Sea, Japan)
Spinules on shaft of spines 3

3(2) More than 2 parallel gonads per side .... *H. hispida* (Herdman)
(Hokkaido, Ceylon, East Australia and South Australia)
2 parallel gonads joining ventrally to form a U .... *H. spinosa* Sluiter
(South Africa, East Africa, Red Sea)
4(1) 2 parallel gonads joining ventrally to form a U .... *H. papillosa* (Linnaeus)
(Mediterranean, Adriatic)
More than 2 parallel gonads joined ventrally 5
5(4) Surface of test raised into small spine bearing elevations (*H. aurantium* (Pallas)) 6
Surface of test not raised into small spine bearing elevations *H. roretzi* (Drasche)
(Northern Japan, Japan Sea)
6(5) North Pacific .... *H. aurantium* sub. sp. *typicum*
North Atlantic .... *H. aurantium* sub. sp. *pyriformis*

HALOCYNTHIA HISPIDA (Herdman, 1881)

(Text-fig. 1)

Cynthia hispida Herdman, 1881, p. 61; 1882, p. 146; *Cynthia crinitistellata* Herdman, 1899, p. 34; 1906, p. 313; *Halocynthia hispida*; Kott, 1952, p. 283 var. *typica*; 1952, p. 284 var. *crinitistellata*; 1954, p. 129 var. *crinitistellata*; *Cynthia hilgendorfi* Traustedt, 1885, p. 36; Oka, 1935, p. 436; *Halocynthia hilgendorfi*; Hartmeyer, 1906, p. 6; Tokioka, 1959, p. 233; f. *ritteri*, 1962, p. 18; *Halocynthia owstoni* Oka, 1906, p. 42; *Halocynthia ritteri* Oka, 1906, p. 43; *Halocynthia igaboja* Oka, 1906, p. 45; Van Name, 1945, p. 362; *Halocynthia okai* Ritter, 1907, p. 11; Ritter and Forsyth, 1917, p. 441; *Pyura okai;* Hartmeyer, 1909-11, p. 134; *Tethyum igaboja* Huntsman, 1912, pp. 114, 115, 136; Van Name, 1945, p. 362; *Cynthia pachyderma* Oka, 1926, p. 559; *Cynthia cactus* Oka, 1932, p. 131; *Halocynthia cactus;* Tokioka, 1953, p. 285; Rho, 1966, p. 213; 1966*a*, p. 366; ? *Halocynthia simaensis* Tokioka, 1949, p. 62.

Description.—The body is rounded, maximum diameter from 3 to 10 cm. Individuals are often crowded together and the body becomes misshapen. The colour is always red-orange. Posteriorly the test is produced into irregular root-like processes. The test may be fairly thick and is always tough and very leathery externally. The surface of the body is even; or produced into tubercular prominences which are evenly distributed about 5 mm. apart over the whole surface, or irregularly distributed. These tubercular prominences are especially noticeable in the siphonal region where they are best developed. Generally there seems to be a tendency to loss of the tubercular prominences on the body with an increase in size although they do persist in the siphonal region. There is also a tendency for the surface of the body to become increasingly rough and wrinkled with increasing size.

Long spines of 2 to 3 mm. or more are often present either distributed evenly over the body surface (*C. cactus* Oka, 1936); or supported by the tubercular prominences singly or in groups of 2 to 3 (*C. crinitistellata* Herdman, 1899; Kott, 1952; *C. hilgendorfi*; Oka 1935; *H. igaboja* Oka, 1906; Van Name, 1945). These long spines are absent altogether from some specimens (*C. hispida* Herdman, 1882; Kott, 1952. H. *ritteri* Oka, 1906; Tokioka, 1962). In the present collection from St. Vincent's Gulf all varieties of test spine development are present:

Carickalinga Heads, 20 to 15 ft., "in caves and on vertical rock faces":

(1) Even surface, globular body with slightly protruberant siphons. Only few inconspicuous longer spinous processes from the test. Smaller test spines covering the surface consist of 6 to 8 long radiating processes and a single terminal process. Single specimen.

(2) Thickly distributed long spinous processes over the surface, longer anteriorly, these are not always supported by tubercular prominences. Small test spines covering the surface. Single specimen.

Off Port Stanvac, on steel wreckage:

Surface uneven, rounded tubercular prominences especially anteriorly, supporting single median, or several long spines. Smaller test spines with 6 to 8 stiff radiating processes. Single specimen.

St. Vincent's Gulf, Posidonia beds:

Surface generally uneven with tubercular prominences, or irregular transverse wrinkles. Long spinous processes present all over the body or confined to the region around the siphons. Smaller test spines with 6 to 8 stiff radiating processes. Numerous specimens.

No constant condition in the distribution of the spines and tubercular prominences has been observed in the specimens from any one area which would suggest geographical subspecies: and specimens with spine arrangement intermediate between those types described above are constantly encountered. It is possible that the differences reflect to some extent environmental factors (see below). Spines sometimes increase in length anteriorly and in larger specimens become leathery. They have secondary spines terminally and in 2 to 3 concentric rings along the shaft. The secondary spines tend to lose their concentric arrangement as the spines become more leathery and their distribution consequently becomes less regular. The shafts of the spines are covered by regularly spaced minute spinules.

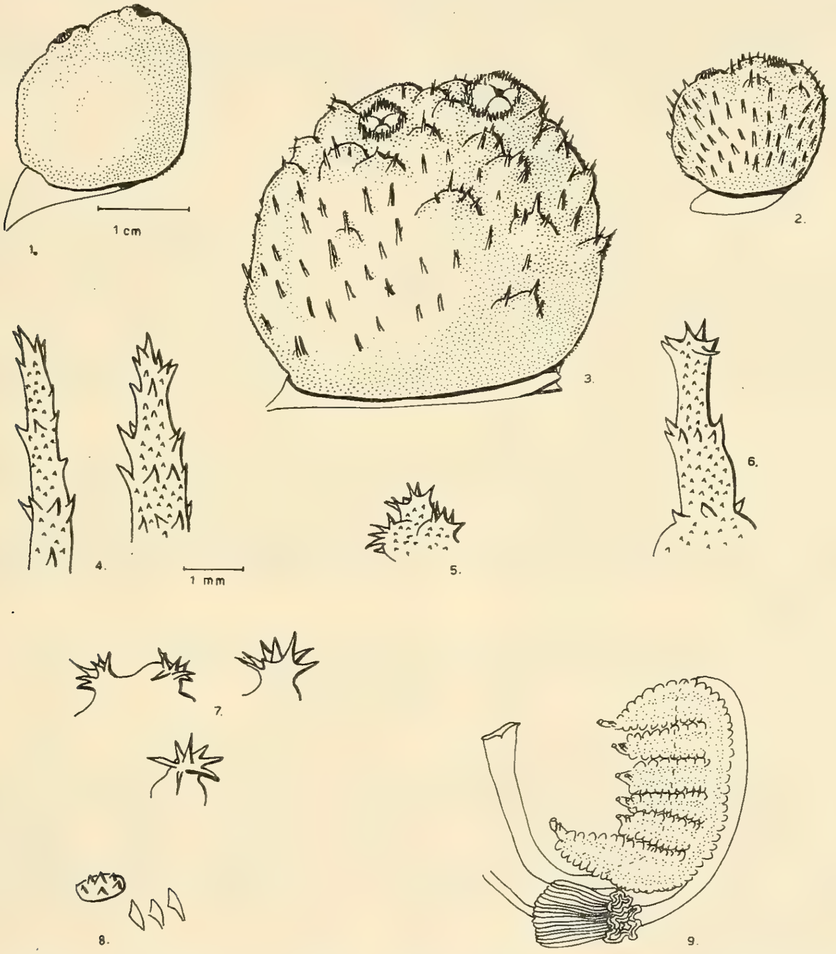
Over the whole surface of the test, between the longer spines, minute, almost confluent papillae support 6 to 8 radiating spines or processes; or they occasionally terminate in a single spine. The surface of these papillae is also covered with spinules as on the shaft of the longer spines. These papillae and the processes they support give to the surface of the test a downy appearance. Always present around the apertures is a circle or thicket of larger spines sometimes branched, and similar to those found elsewhere on the test in the majority of specimens. They have secondary spines terminally and in concentric circles along the shaft and they have spinules on the shaft.

In the siphon linings scale-like swellings continuous with the small spine bearing papillae of the test extend in a single row down the folds which correspond to the branchial and atrial lobes. These support one or more small spines and in the furrows between the folds are reduced to single conical spines or papillae.

Branchial tentacles vary from 8 to 16 with well-developed primary branches supporting a fringe of minute secondary branches. Dorsal tubercle forms a double spiral cone and rarely deviates from this condition. Dorsal lamina consists of a row of pointed languets, closely placed; and to the right of this a second row of similar languets but not so closely placed. The branchial sac has 9 to 10 folds on each side of the body. The most central fold on each side is often rudimentary. The maximum number of vessels on a single fold is from 18 in a specimen of 1·8 cm. high up to 25 to 37 in specimens greater than 5 cm. There are from 1 to 3 longitudinal vessels between the folds. Stigmata per mesh vary from 4 to 10 in individuals of 2 to 7 cm. *H. cactus*; Tokioka, 1953, 8 cm. high had 20 to 23 stigmata in the largest meshes but Oka's specimens from the same locality and otherwise identical with the former have a smaller number of stigmata in each mesh.

The gut loop is simple and closed. The ascending rectum extends anteriorly to terminate in a smooth rimmed anus. Anterior glandular plications are present in the pyloric region and distal to these a collection of arborescent liver lobules form a half ring around the gut usually on its mesial surface. However, these may be displaced anteriorly around the intestine.

Gonads vary from 2 to 10 parallel ovarian tubes on each side of the body, directed toward the atrial opening. They are joined ventrally by an antero-posteriorly oriented connective. Testes lobes are arranged along both sides of the ovaries and in mature specimens extend as a continuous mat between and on the parietal side of the ovaries. Testes ducts join on the surface of each ovarian tube and form a vas deferens to open adjacent to the oviduct. Occasionally gonads are missing or reduced on the right side of the body. On the left they are present in the gut loop.



Text-figure 1.—*Halocynthia hispida* (from St. Vincent's Gulf). 1 and 2. Specimens from Carickalinga Heads; 3. Specimen from Posidonia beds; 4. Spines from thicket around apertures; 5. Small spines on lobes of apertures; 6. Long test spine; 7. Small test spines evenly distributed over surface; 8. Spines from inner lining of apertures; 9. Diagram of gut and gonads on the left.

New Records.—From Posidonia beds, St. Vincent's Gulf, South Australia, 5 fm.; 4 mls off Pt. Stanvac, South Australia, on steel wreckage, 15 fm.

Carickalinga Heads, 15 to 20 ft. in caves and on vertical rock faces, South Australia. Coll. S. A. Shepherd.

Previous Records.—D'Entrecasteaux Channel, Tasmania, 5 fm. (Kott, 1952); off Maria Island, Tasmania, 174–155 m., 676–128 m. (Kott, 1954); Bass Strait, 38–40 fm. (Herdman, 1882); Port Jackson (Herdman, 1899; Kott, 1952); Ceylon, 6–9 fm. (Herdman, 1906); Hokkaido, Japan (Traustedt, 1885; Oka, 1906); Honshu, Kyushu, Japan (Oka, 1906, 1932, 1935; Tokioka, 1949, 1953, 1959, 1962); British Columbia to California, 10–90 fm. (Ritter, 1907; Huntsman, 1912, 1921; Van Name, 1945).

Distribution.—In 5–90 fm. in the Pacific Ocean from Hokkaido to southern Australia in the west and from British Columbia to California in the east. The species has not been recorded from New Zealand; nor from any other islands in the Pacific and its spread may be limited by deeper waters. Records are lacking from the Malayan Peninsula, Indonesia, west and north-east Australia. Further collecting may establish some continuity between the Japanese, Ceylon and Australian specimens as there is no morphologically stable characters which might suggest isolated communities in these areas. Nor is its recorded distribution continuous across the north Pacific Ocean from Hokkaido to British Columbia.

Habitat.—Van Name (1945) describes the species as present on a sandy or gravelly bottom. The present specimens are described as "thick in Posidonia beds"; "vertical rock faces". Specimens from d'Entrecasteaux Channel were from scallop beds.

Remarks.—Externally therefore specimens of this species vary in external appearance and may be characterised as belonging to the following types:

(*a*) Long spines absent from body of the individual; surface even: *Cynthia hispida*, Herdman, 1882, Bass Strait; *Halocynthia hispida* var. *typica* Kott, 1952, d'Entrecasteaux Channel; *Halocynthia ritteri* Oka, 1906; Tokioka, 1962, Japan.

(*b*) Long spines randomly distributed over the body of the individual; surface even: *Halocynthia cactus* Oka, 1932; Tokioka, 1953, Sagami Bay, Japan; *Halocynthia igaboja* Oka, 1906; Van Name, 1945, Japan and East Pacific.

(*c*) Some spines present on parts of the body (intermediate between (*a*) and (*b*)): *Cynthia hilgendorfi* Traustedt, 1885; f. *ritteri* Tokioka, 1959, Japan.

(*d*) Surface of body raised into tubercular prominences supporting longer spines: *Cynthia crinitistellata* Herdman, 1899; Herdman, 1906, Port Jackson, Ceylon; *Halocynthia hispida* var. *crinitistellata* Kott, 1952, Port Jackson; Kott, 1954, off Maria Island, Tasmania; *Halocynthia hilgendorfi*; Oka, 1935, Japan.

It has not been possible to divide specimens demonstrating these various conditions of the test into geographical sub-species. However, it is possible that the variations occur in response to some environmental factor.

The species resembles *H. spinosa* Sluiter in the form of the longer spines on the test; however, in the latter species the smaller spines which cover the test and cause its granular consistency are supported on small scale-like areas rather than papillae, similar to the condition in *H. aurantium* but distinct from the homologous structures in *H. hispida*. *Cynthia crinitistellata* Herdman, 1906 from Ceylon has papillae rather than scales supporting the test spines and despite its location geographically is undoubtedly a synonym of *H. hispida*.

H. simaensis Tokioka is listed as a doubtful synonym of this species. Although externally the specimen resembles larger specimens of the present species the glandular plications of the pyloric region are subdivided into lobes; and spines are absent from the siphonal lining. So far only a single specimen is known. Further collection may confirm these characters as indicating specific distinctions rather than individual abnormality or the effects of age. The absence of gonads on the right is not necessarily significant as the number of gonads, especially on the right, varies considerably.

Herdman (1899) considers *Cynthia dumosa* Stimpson, 1855, a very likely synonym of the present species. However, Stimpson's specimen was not the characteristic orange-red colour of *H. hispida*; and was taken from Port Jackson on a muddy substrate which is unusual for *H. hispida*.

HALOCYNTHIA AURANTIUM (Pallas, 1787)

(Text-fig. 2, (10-12))

Ascidia aurantium Pallas, 1787, p. 24. (For further synonymy see accounts of subspecies below.)

Description.—*Halocynthia aurantium* (Pallas, 1787) from the north Pacific and *H. pyriformis* (Rathke, 1806) from the north Atlantic both have papillary swellings all over the test supporting pointed spines singly or in groups. The spines, however, do not radiate as in *H. hispida* but are shorter, project forwards, and have a central spine which is longer than those which surround it. The species lacks the longer branched spines of *H. hispida* although a circle of enlarged spines is present around the apertures with minute spinules or barbs along the shaft. Other characters resemble those in *H. hispida.* The two subspecies are distinguished from one another only by the numbers of gonads on each side of the body: 3 to 7 for sub. sp. *pyriformis* and 3 to 4 for sub. sp. *aurantium.* This, as observed by Van Name (1945) and Arnbäck (1928) does not constitute a very convincing distinction and relationships are better indicated by subspecific than by specific rank.

HALOCYNTHIA AURANTIUM (Pallas, 1787)
sub. sp. *typica*

(Text-fig. 2, (11-12))

Ascidia aurantium Pallas, 1787, p. 240; *Cynthia pyriformis*; Traustedt, 1885, p. 34 (part); *Cynthia superba* Ritter, 1900, p. 590; Pratt, 1916, p. 667; *Cynthia deani* Ritter, 1900, p. 590; *Halocynthia superba*; Oka, 1906, p. 41; Hartmeyer, 1903, p. 200; *Halocynthia deani;* Hartmeyer, 1903, p. 200; *Tethyum aurantium*; Huntsman, 1912, pp. 114, 115, 136; 1912*a*, p. 173; Redikorzev, 1916, p. 169 (part); *Halocynthia aurantium*; (part) + *forma koreana* Hartmeyer, 1903, pp. 195, 200; *Halocynthia aurantium*; Ritter, 1913, p. 448; + *H. superba* Michaelsen, 1919, p. 11; Hartmeyer, 1921, pp. 30, 33; Arnbäck 1928, p. 84; Pratt, 1935, p. 748; Van Name, 1945, p. 362; Tokioka, 1951, p. 17; 1967, p. 219; Monniot, 1965, p. 115.

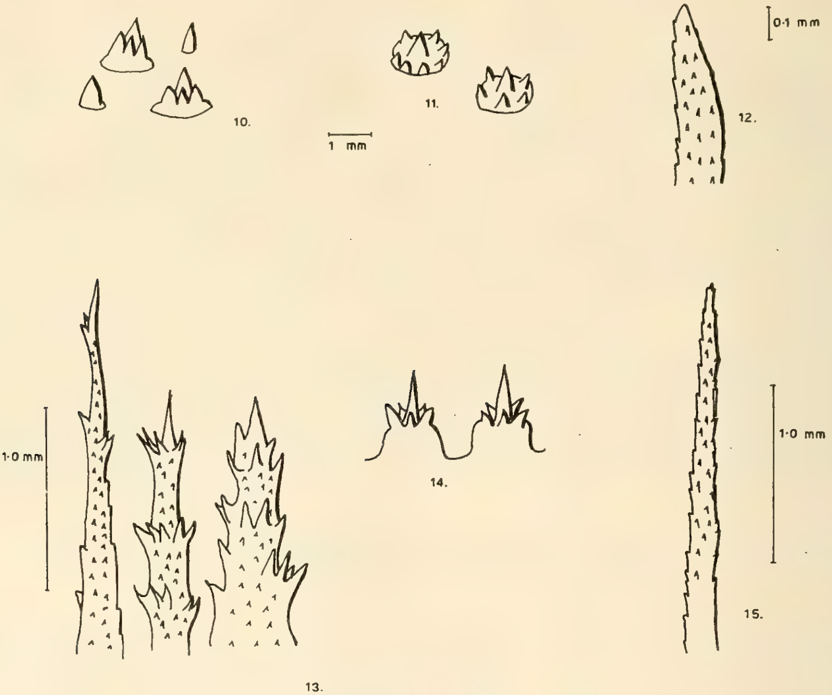
Records.— Korea (Hartmeyer, 1903); Hokkaido (Traustedt, 1885; Oka, 1906; Tokioka, 1951, 1966); Kuril Is. (Pallas, 1787); Vladivostok, Okhotsok Sea (Redikorzev, 1916); Bering Sea, Bering Straits, Puget Sound (Huntsman, 1912, 1912*a*; Ritter, 1900, 1913); Alaska, Pribilof Islands (Ritter, 1913).

Distribution.—A continuous distribution is recorded from the Bering Sea to overlap limits of *H. hispida* off Hokkaido and Korea in the north-western Pacific and off north-west America south to Puget Sound.

Habitat.—The subspecies is taken in waters from 10 to 180 m. on sand, sand with stones and shells, and sometimes on rocks (Arnbäck, 1928).

HALOCYNTHIA AURANTIUM (Pallas, 1787)
sub. sp. *pyriformis* (Rathke, 1806)
(Text-fig. 10)

Ascidia pyriformis Rathke, 1806, p. 41; Sars, 1851; *Cynthia papillosa*; (part) Traustedt, 1880, p. 407; Non Gunnerus, 1765; *Cynthia pyriformis*: Stimpson, 1854, p. 20; 1860, p. 1; Packard, 1863, p. 412; Binney, 1870, p. 17; Dall, 1870, p. 255; 1872, p. 157; Morse, 1871, p. 352; Kiaer, 1893, p. 67; 1896, p. 12; Metcalf, 1900, p. 510; Hartmeyer, 1901, p. 49; 1915, p. 313, *Rhabdocynthia pyriformis*; Verrill, 1879, p. 27; Whiteaves, 1901, p. 268; Michaelsen, 1918, p. 11; Hartmeyer, 1920, p. 127; 1921, p. 30; 1923, p. 163; Arnbäck, 1928, p. 33; Pratt, 1935, p. 748; Van Name, 1945, p. 359; Millar, 1966, p. 99; *Tethyum pyriforme*; Hartmeyer, 1914, p. 1103; Berrill, 1935, p. 257; *Tethyum pyriforme americanum* Huntsman, 1912, pp. 112, 148; Berrill, 1929, pp. 46, 48; 1935, p. 269; *Pyura pyriformis*; Procter, 1933, p. 284; *Cynthia nordenskjoldi* Wagner, 1885, p. 156; Herdman, 1891, p. 577; *Cynthia papillosa*; Jacobson, 1892, p. 156; *Halocynthia arantium*; Hartmeyer, 1903, p. 195 (part); Bjerkan, 1908 (part); Michaelsen, 1918, p. 11; Harant, 1929, p. 66; *Pyura aurantium*; Hartmeyer, 1909–11, p. 1331; Van Name, 1912, p. 532; *Tethyum aurantium*; Redikorzev, 1916, p. 169; *Pyura pectinicola* Michaelsen, 1908, p. 262; Hartmeyer, 1909–1911, p. 1341; *Tethyum microspinosum* Van Name, 1921, p. 443.



Text-figure 2.—*Halocynthia aurantium* subsp. *pyriformis* (after Millar, 1966). 10. Small test spines. *Halocynthia aurantium* subsp. *typica* (after Tokioka, 1951). 11. Small test spine; 12. Spine from thicket around apertures. *Halocynthia spinosa*. 13. Spines from around apertures (after Michaelsen, 1918); 14. Small test spines (after Millar, 1962). *Halocynthia papillosa* (after Michaelsen, 1918). 15. Spine from around apertures.

Records.—Massachusetts Bay, Gulf of St. Lawrence, Labrador (Van Name, 1912, Huntsman, 1912); Ellesmeere Land, west coast of Greenland, Iceland (Traustedt, 1880, Arnbäck, 1928); Faroe Is., Spitzbergen, Barents Sea (Redikorzev, 1916, Arnbäck, 1926); north-western Norway (Arnbäck, 1928, Millar, 1966); Bergen (Rathke, 1906, Hartmeyer, 1901, 1923) White Sea; Murman coast (Redikorzev, 1916).

Distribution.—A continuous distribution across the north Atlantic with its most southern extent at Bergen in the east and Massachusetts in the west. In the north it extends from Ellesmeere Land the west coast of Greenland, Iceland, the Faroe Is., Spitzbergen and the Barents Sea. It is therefore present much further to the north than *H. aurantium* sub. sp. *typica* of which the most northern limit is the Bering Straits. There are no records from further east than the White Sea.

Habitat.—The species is taken from rock, sand, stones and shell in waters of 0 to 114 m.

HALOCYNTHIA SPINOSA Sluiter, 1905

(Text-fig 2, (13, 14))

"An *Ascidia quadridentata* L." Forskal, 1776, p. 9; *Halocynthia spinosa* Sluiter, 1905, p. 16; Michaelsen, 1918, p. 7; *Pyura spinosa*; Hartmeyer, 1909, p. 1341; *Pyura (Halocynthia) spinosa*; Hartmeyer, 1912, p. 181; *Halocynthia spinosa* f. *defectiva* Millar, 1962, p. 201; *Halocynthia arabica* Monniot, 1965, p. 121; f. *defectiva*; Monniot, 1965, p. 121; ? *Halocynthia* sp. Harant, 1929, p. 67.

Description.—In this species the longer spines on the body and in a thicket around the apertures are similar to those of *H. hispida*, with terminal secondary spines and secondary spines more or less in concentric rings along the shaft. Spinules are also present on the shaft of these spines. However, the species is distinguished by the U-shaped gonads on each side of the body similar to the gonads of *H. papillosa*; and by the distribution and form of the small test spines, supported on scale-like thickenings of the test 0·5 mm. in diameter and consisting of a central spine 0·5 mm. long surrounded by 5 to 6 smaller spines 0·25 mm. long distributed around the border of the scale. These minute test spines are also similar to those of *H. papillosa*.

Records.—Red Sea, Gulf of Aden (Michaelsen, 1918); Somaliland (Sluiter, 1905); Cape Province, South Africa, 0—13 m. (Millar, 1962); ? West of Gibraltar, eastern Atlantic, 3745 m. (Harant, 1929).

Habitat.—The specimens from South Africa were all taken from rock. There is no information on the type of substrate from which specimens from other localities were taken.

Remarks.—Millar's f. *defectiva*, taken from three different locations between January and March, was so named due to the absence of gonads on the right side of the body. While in Michaelsen's specimens of the present species gonads were absent on the right side. This absence of gonads from one side occasionally occurs in other species of this genus but its significance is not apparent.

The small specimen taken from 3745 m. west of Gibraltar (Harant, 1929) has test spines typical of the present species, and, although the gonads are not developed, probably represents an individual of this species. There are no other records of *H. spinosa* from the Atlantic coast of Africa and this single specimen may represent a relict population in deeper water.

The derivation of *H. spinosa* from the Mediterranean species *H. papillosa* by the development of secondary spines on the longer spines of the test is suggested by their otherwise close morphological similarity. Spread of the ancestral species is unlikely through the Suez area as no continuity of the marine environment existed there previous to the opening of the Suez canal in the nineteenth century. *Halocynthia papillosa* has been known from the Mediterranean since the seventeenth century and Forskal's report of an *Ascidia quadridentata* (synonym of *H. spinosa*) is from the Red Sea in the eighteenth century. The presence of *H. spinosa* in eastern Atlantic as indicated by Harant's (1929) specimen suggests a (not necessarily contemporary) circum African distribution for the species. It is therefore most likely that the ancestral species was continuous from the western Mediterranean and around via South Africa to the Red Sea. The Straits of Gibraltar subsequently provided a sufficient barrier for the isolation of two distinct populations representing the species *H. spinosa* and *H. papillosa*.

The significance of the close morphological relationship between this species and *H. hispida* is also puzzling. In view of the wide distribution of this and other species of the genus, there is no apparent isolating barrier between *H. hispida* from Ceylon (Herdman, 1906) and the present species from the Red Sea. The relationships of these and other species of the genus are indicated in Text-fig. 3 and Table 1.

HALOCYNTHIA PAPILLOSA (Linnaeus, 1767)

(Text-fig. 2 (15))

Ascidia papillosa Linnaeus, 1767, p. 1087; *Tethyum papillosum* Gunnerus, 1765, p. 100; *Cynthia papillosa*; Savigny, 1816, p. 143; Heller, 1877, p. 249; Lacaze Duthiers and Délage, 1892, p. 126; Roule, 1885, p. 180; Herdman, 1891, p. 576; *Halocynthia papillosa*; Hartmeyer, 1904, p. 322; Michaelsen, 1918, p. 10; Harant, 1929, p. 66; Harant and Vernieres, 1933, p. 24; Pérès, 1958, p. 161; Monniot, 1965, p. 113; *Pyura papillosa*; Hartmeyer, 1909, p. 1340; 1912, p. 181; *Ascidia rustica* Risso, 1826, p. 274; non Linné, 1772.

Description.—This species closely resembles *H. aurantium* in the distribution and form of the small test spines, and in the distribution and form of the larger spines which are present around the siphons. The larger spines lack secondary spines but have spinules. However, the species are distinguished by the U-shaped gonads of *H. papillosa*.

Records.—Western Mediterranean (Pérès, 1958, Harant and Vernieres, 1933); Adriatic (Heller, 1877); Atlantic coast of France (Harant and Vernieres, 1933, Lacaze Duthier and Délage, 1892).

Habitat.—From amongst coralline algae, *Posidonia* sp., sand and shell.

Remarks.—The morphological relationships between the present species and *H. aurantium* in the north Atlantic and *H. spinosa* in the Red Sea are indicated in Table 1.

HALOCYNTHIA IGAGURI Tokioka, 1953

Halocynthia igaguri Tokioka, 1953, p. 20.

Description.—This species is distinguished from all others by the gonads which appear to be of a simple styelid type with tubular oviduct surrounded by pyriform testes lobes. The long spines on the test have secondary spines but no spinules and between these there are minute papillae evidently without terminal spines as in *H. hispida, H. aurantium* and *H. papillosa*. There are only 7 branchial folds per side and Tokioka has not described a double series of languets along the dorsal line.

Record.—Inland Sea, Japan (Tokioka, 1953).

Remarks.—The condition of the gonads, number of branchial folds and the dorsal lamina are not typical of this genus. However, there are the usual glandular plications and liver lobes in the pyloric region.

Halocynthia roretzii (Drasche, 1884)

(*Styela?*) *Cynthia roretzii* Drasche, 1884, p. 376. For further synonymy see Tokioka, 1953, p. 282.

Description.—Specimens are up to 14 cm. long. This species has circles of spines around the apertures similar to those of *H. aurantium* with spinules but no secondary spines. The surface of the test is divided into scale-like areas without spines, as in *H. aurantium.* In older specimens large mammillary or finger-like processes develop from the test sometimes bearing a terminal spine. There are very numerous branchial folds—up to 18 on each side with 60 to 70 longitudinal vessels on each fold. Gonads are numerous—7 to 11.

Younger specimens have neither mammillary nor finger-like processes and no polygonad scale-like areas; the surface has instead a number of spines with spinules similar to those present around the apertures of the adult.

Table 1

Morphological relationships between common species of the genus Halocynthia

		Gonads	
		U-shaped gonads	Many parallel gonads
Secondary spines on Test spines	Absent	*H. papillosa* Mediterranean	*H. aurantium* North Atlantic North Pacific
	Present	*H. spinosa* South Africa Red Sea	*H. hispida* North Pacific Indo-Malayan

For fuller description see Tokioka, 1953, p. 282.

Records.—"Coasts of Hokkaido, Honsyu, Sikoku and Kyusyu but not from south coast of Sikoku and Kyusyu . . . also distributed throughout the coast of Tyosen and the coast of Shantung Peninsular in North China." (Tokioka, 1953, p. 285.)

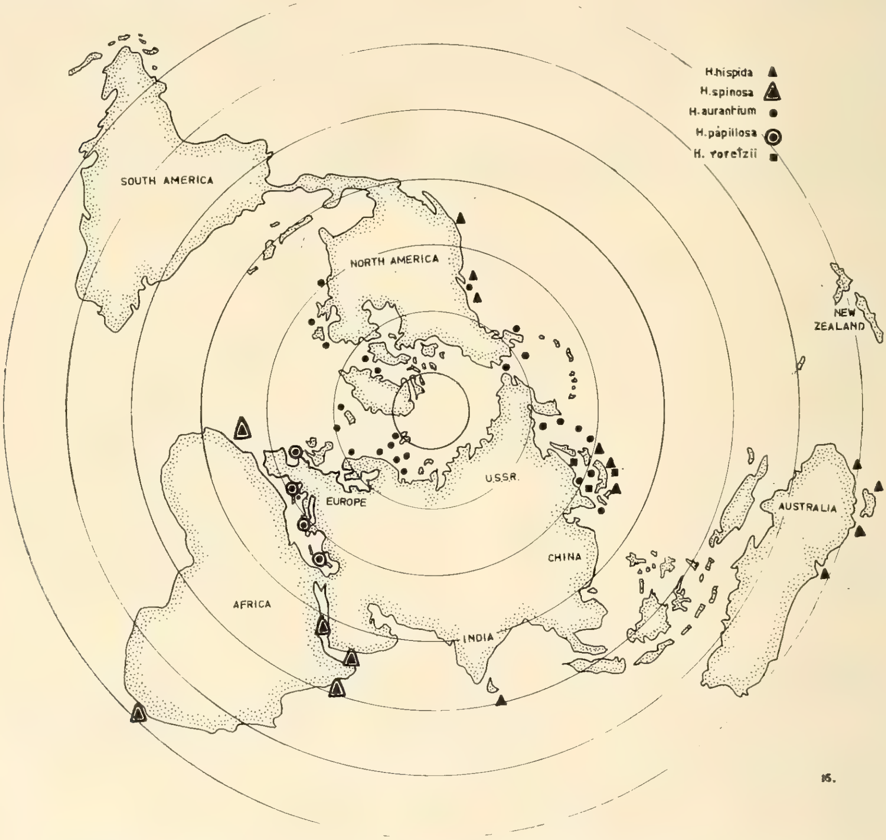
Distribution.—In fairly shallow water in a limited area around Japan and the northern part of the Japan Sea.

Remarks.—The species is probably related to *H. aurantium* and its distinguishing characters are largely a result of the greater development of those characters than occurs in *H. aurantium.*

Phylogeny

(Table 1, Text-fig. 3)

The four most widespread species of this genus present interesting morphological and geographical relations. From the condition in the Mediterranean species *H. papillosa* with U-shaped gonads, simple spines, and spine-bearing scales on the test, *H. aurantium* in the north Atlantic is differentiated by development of the gonads; and *H. spinosa* from South Africa and the Red Sea develops secondary branches on the test spines but retains the U-shaped gonads. This distribution of closely related species suggest that this genus represents a relict of Tethys Sea fauna. The extension of *H. aurantium* into the north Pacific through the Bering Straits probably occurred later. However, *H. spinosa*, radiating from west of the Mediterranean southwards around Africa and north into the Red Sea could have been a Tethys component of the tropical Atlantic-West Pacific fauna. The combination of characters found in *H. hispida* may result from *H. aurantium* by the development of secondary spines, or from *H. spinosa* by the increase in the gonads. The distribution of *H. hispida* in the north Pacific and Indo-Malayan areas, as well as its morphology, is intermediate between *H. aurantium* and *H. spinosa* and its origin is probably more recent than either of the latter species.



Text-figure 3. Map showing world distribution of species of *Halocynthia*.

Acknowledgements

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A NEW BDELLOURID-LIKE TRICLAD TURBELLARIAN ECTOCONSORTIC ON MURRAY RIVER CHELONIA

LAURENCE R. RICHARDSON*

[Read 24th April, 1968]

Synopsis

A new genus is provided for a small acephalous, sedentary turbellarian with posterior adhesive discs, a posterior male complex, and general form resembling *Bdelloura candida*, a maricolous triclad on the gills of *Limulus*. It differs significantly otherwise so that it is a novelty in the Maricola as well as the Paludicola, but is provisionally placed in the latter. "Perigrinatic" is proposed for consortism other than parasitic, symbiotic, and commensal.

This paper describes a triclad turbellarian found in the limb-pits of turtles from a lake near Griffith, N.S.W. As freshwater triclads these would be expected to be Paludicola, but they possess in addition to an anterior adhesive pad, longitudinal marginal adhesive bands and paired posterior adhesive discs. They are acephalous and the single pair of eyes is in a posterior position. These and other features are exceptional in the Paludicola, seen in some Maricola but as yet no Maricola are known from freshwater. The copulatory bursa is situated at the anterior end of the male terminal reproductive organs, dorsolateral to them not fully anterior as in Paludicola, and since the genital pore is posterior, marginal, located between the posterior adhesive discs, the "probursal" condition is possibly secondary. I place these animals provisionally and with much reservation in the Paludicola.

The relationship to the turtles does not fall into the usual consortic categories when these are used in their proper sense, and I propose that it be termed perigrinatic, in the sense of Virgil: "one travelling in a foreign land". There is nothing to indicate that this triclad may not be free-living. It is not parasitic in the sense that it draws nourishment from the host, as does the sanguivorous leech, g. *Placobdella*, which is found with it. It is not symbiotic in the correct usage of this term. There is nothing to indicate it benefits the host or benefits from it. It does not share the food of the host since it is microphagous, and so should not be termed commensal even recognising that this category has become the catch-pot for any kind of consortism which is neither parasitic or symbiotic.

Four specimens came to me from Dr. R. E. Barwick who found them and others along with many egg-capsules in the limb-pits of *Emydura macquarii* and *Chelodina longicollis* taken at Lake Wyangan, near Griffith, N.S.W. during the course of experimental fishing operations carried out by officers of the N.S.W. Inland Fisheries Research Station towards the end of May, 1967.

The stalked egg-capsules immediately recalled those of the bdellourid *Syncoelium* and of some other Planariidae. The animals were fully bdellourid like, even to the presence of two white bodies suitably placed to be the paired copulatory bursae characteristic of this family. It was not until I had studied serial sections that I could persuade myself that these animals could be Paludicola, even though this also gave evidence of characteristics more suited

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* 4 Bacon Street, Grafton, N.S.W., 2460.

to the Maricola than to the Paludicola. Should it later be found that they are maricolous, I see no genus there which will accept them (Hyman, 1951*b*; Grasse, 1961). The absence of a direct connection from the bursa to the exterior excludes them from both the Bdellouridae and the Uteroporidae. Otherwise there is the exceptional g. *Puiteca* in the Procerodidae which has anterior and posterior adhesive discs and a posterior genital pore, but this has the single pair of ovaries in the post-pharyngeal position and lacks a bursa.

If paludicolous, the internal muscle layer of the pharynx includes a circular layer uninterrupted by other muscle cells as is characteristic of the Planariidae and Kenkidae. The latter is restricted to North America and contains white, eyeless cave planarians with resemblance to the g. *Phagocata*. There are only three genera (Hyman, 1951*a*), none suitable for the present species. This presents a combination of characters which I have not found in the various genera of the Paludicola (Hyman, 1951*a*, *b*; Grasse, 1961), and certainly not in the Planariidae. Accordingly, I propose a new genus as below.

METHODS

After preliminary study of the live specimens which provided information mainly on the alimentary canal, the animals were narcotised in a drop of water on a slide inverted over a drop of chloroform in a covered petri dish. Then covered with a cover-slip, and 50% alcohol run in under the cover-slip, the rate of flow being regulated to maintain just such pressure as held the animal flat. A specimen was stained in acetic alum carmine, cleared in glycerine, subsequently sectioned at 10 mu. and stained with Delafield Haematoxylin and eosin.

BDELLASIMILIS, n. g.

Triclad bdellourid-like Turbellaria having a small anterior adhesive pad continuous with narrow longitudinal marginal adhesive bands which expand into two round ventral sucker-like posterior terminal adhesive discs; acephalous; a single pair of eyes placed about ⅓rd of the length from the anterior end; a single pair of ovaries close behind the eyes, prepharyngeal; copulatory bursa connects by a duct into the penis antrum; testes branching, tubular, preocular and also lateral to the pharyngeal region; sperm vesicles, paired, almost post-pharyngeal; sperm ducts join terminally into a common median duct which connects to the penis where the cavity is central; no bulbar cavity; genital aperture, posterior, median, marginal; no adenodactyl; no genito-intestinal connection; posterior limbs of intestine transversely connected behind peripharyngeal chamber; egg-capsules, stalked, cylindroid.

Type Species.—Bdellasimilis barwicki, n. sp. as follows:

BDELLASIMILIS BARWICKI, n. sp.

(Fig. 1, 2)

A whitish or partly grayish, self-coloured, semitransparent, bdellourid-like triclad of small size with a single pair of posteriorly placed eyes, and with obvious paired posterior sucker-like adhesive discs.

Contracted (8·0 mm.) rather bluntly rounded anteriorly, the width about 2·0 mm. at the level of the eyes which are placed about 2·5 mm. from the anterior end; maximum width of 3·0 mm. at the level of the posterior end of the pharynx about 4·0 to 5·0 mm. from the anterior end. The margins then curve obtusely so that the posterior end is obtusely rounded with the two adhesive discs partly showing behind the margin of the body and separated by a wide and shallow notch where the elongated genital aperture opens ventrally. The body is generally low convex above, flat below. When strongly contracted, the surface shows numerous short striae which are transverse. In extension it may nearly double its length, the preocular region becoming elongate, tapering acutely to the narrow tip but the width and length of the post-pharyngeal region are little changed from the contracted condition.

The anterior adhesive pad is transverse, short, only about 0·08 mm. in length and continuous with the longitudinal marginal bands which are 0·10 mm. wide and run slightly medial to the lateral edge of the body which overhangs them as though an eave. The bands expand posteriorly into the adhesive discs which are 0·3 mm. wide and slightly longer than wide, with narrow raised rims surrounding a flat central area which is richly supplied with eosinophilic gland cells as also in the marginal bands and anterior pad. The relationship of the rim to the disc is the same as the lateral edge of the body to the marginal band. When the animal is detached from the substratum and placed on its back, the rims of the discs may roll up, thicken, become continuous, presenting the appearance of a single sucker which may be the actual form of this organ: a single wide adhesive pad which appears as two discs because of the emargination of the disc when attached to the substrate.

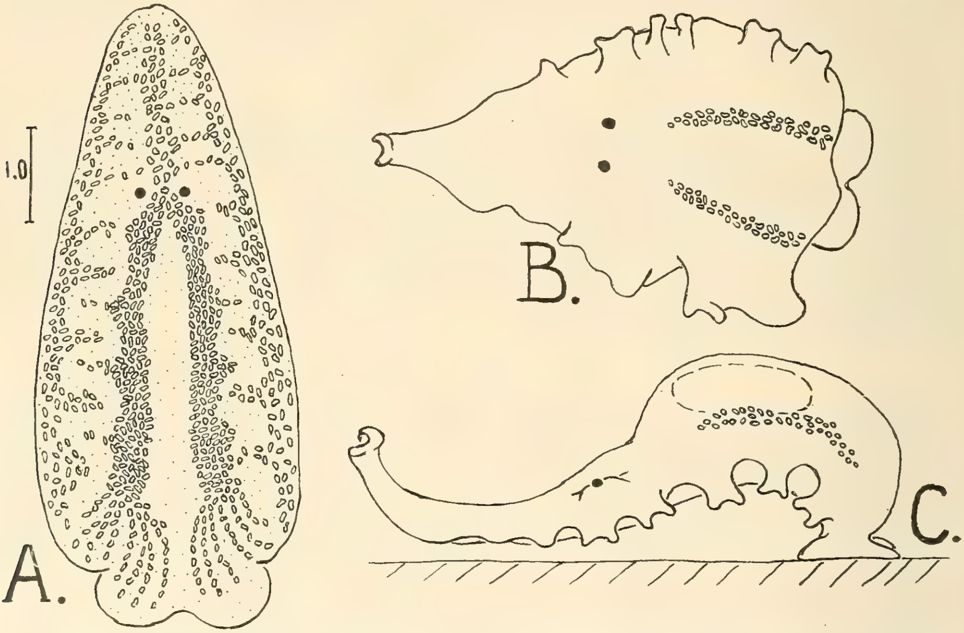

Fig. 1. *Bdellasimilis barwicki.* A. Dorsal view of preserved specimen showing distribution of chromatophores. B. Dorsal and C. lateral views showing the feeding posture. Scale in mm.

Seen with reflected light, the animal is whitish excepting for the black and obvious eyes and pale brown chromatophores which are concentrated as a longitudinal row on either side of the peripharyngeal chamber, the two rows converging shortly behind the eyes and extending anteriorly between them as a more diffuse median row nearly reaching the anterior end of the body. Marginal bands of more widely scattered chromatophores run along each side of the body. Between the paramedian row and the marginal row there are scattered chromatophores suggesting possible transverse bars and others arranged over the posterior region of the body seem to be in radiating lines. It is possible that the dorsum might be patterned when the chromatophores are extended. I have not seen this.

Alimentary System (Fig. 2D.)

The ventral opening into the peripharyngeal chamber is about $\frac{3}{5}$ths of the length of the body from the anterior end. It is transverse, narrowly elliptical to slit-like, and the chamber wider and longer than the pharynx and about $\frac{1}{5}$th of the length of the body. The floor, walls and roof of the chamber are much plicated internally and the whole chamber can be greatly enlarged in the extended animal, especially dorsally as the roof is thin. The pharynx, about $\frac{1}{8}$th of the length of the body is directed posteriorly and in life, I did not see it protruded from the chamber. The pharynx is thick-walled, the parenchyme towards the anterior end is rich in eosinophilous gland cells which are densely packed also around the origin of the limbs of the canal and along the anterior limb nearly to the level of the ovaries. There are only one or two very short small lateral diverticula on the anterior limb between the pharynx and the eyes. Anterior to the eyes there are some seven or eight briefly ramifying elongate tubular diverticula on either side of this limb, short in the sense that they reach only about half way to the margin, and they diminish in length anteriorly. This limb reaches nearly to the anterior end of the body.

The posterior limbs are nearly circular in section as they arch around the anterior end of the peripharyngeal chamber, and depressed elliptical lateral and posterior to the chamber. Lateral to the chamber, they carry a few very small medial diverticula. There is a transverse canal joining the two posterior limbs behind the chamber, followed by more numerous small medial diverticula along the last portion which terminates bluntly near the posterior margin at the level of the end of the penis. The lateral diverticula are more lobed than tubular in their subdivisions, uniform in size along the pharyngeal region and then diminish progressively in diameter and length.

Reproductive System (Fig. 2D, E). (Note: Dimensions given are taken from sections.)

Testes, sperm ducts, vitellaria, and bursa could not be seen in the live animal.

In sections, the testes and sperm ducts appear as a paired ramifying tubular system anterior to the spermiducal vesicles and commencing about 0·75 mm. from the anterior end of the body so that the system is in part preocular. The sperm ducts are somewhat coiling or tortuous, about 0·07 mm. in width in the preocular region and slightly diminished in width as they approach the spermiducal vesicles. The main ducts run just medial to the longitudinal cords of the nervous system. If a side branch from the duct is followed laterally, it closes off in simple blunt-ended tubules and there is no spermatic tissue beyond this. From this, it seems the testes are ramifying tubular lateral branches from the main duct, and openly continuous with the duct. The histology of the contents of both tubules and ducts are the same, both containing spermatocytes and spermatids. The ducts enter the obliquely aligned somewhat ovoidal spermiducal vesicles located lateral to the posterior end of the peripharyngeal chamber. These thin-walled vesicles contain only mature sperm as also the following thin-walled narrow convoluted tubular sperm ducts which are about 0·03 mm. in diameter and extend to the level of the penis bulb when each bends abruptly anteriorly to join into a thick-walled transverse tube about 0·04 mm. in diameter and with a narrow lumen. From the middle of this tube, a thick-walled median tube with a narrow lumen extends back and enters the penis. There is no bulbar cavity. The canal is central in the penis which is about 0·04 mm. in diameter and 0·12 mm. long, tapering, conical and protrudes into and almost fills the proximal portion of the genital antrum. This antrum expands into a second terminal chamber beyond the end of the penis and the slit-like genital aperture opens ventrally from this second chamber. There is an

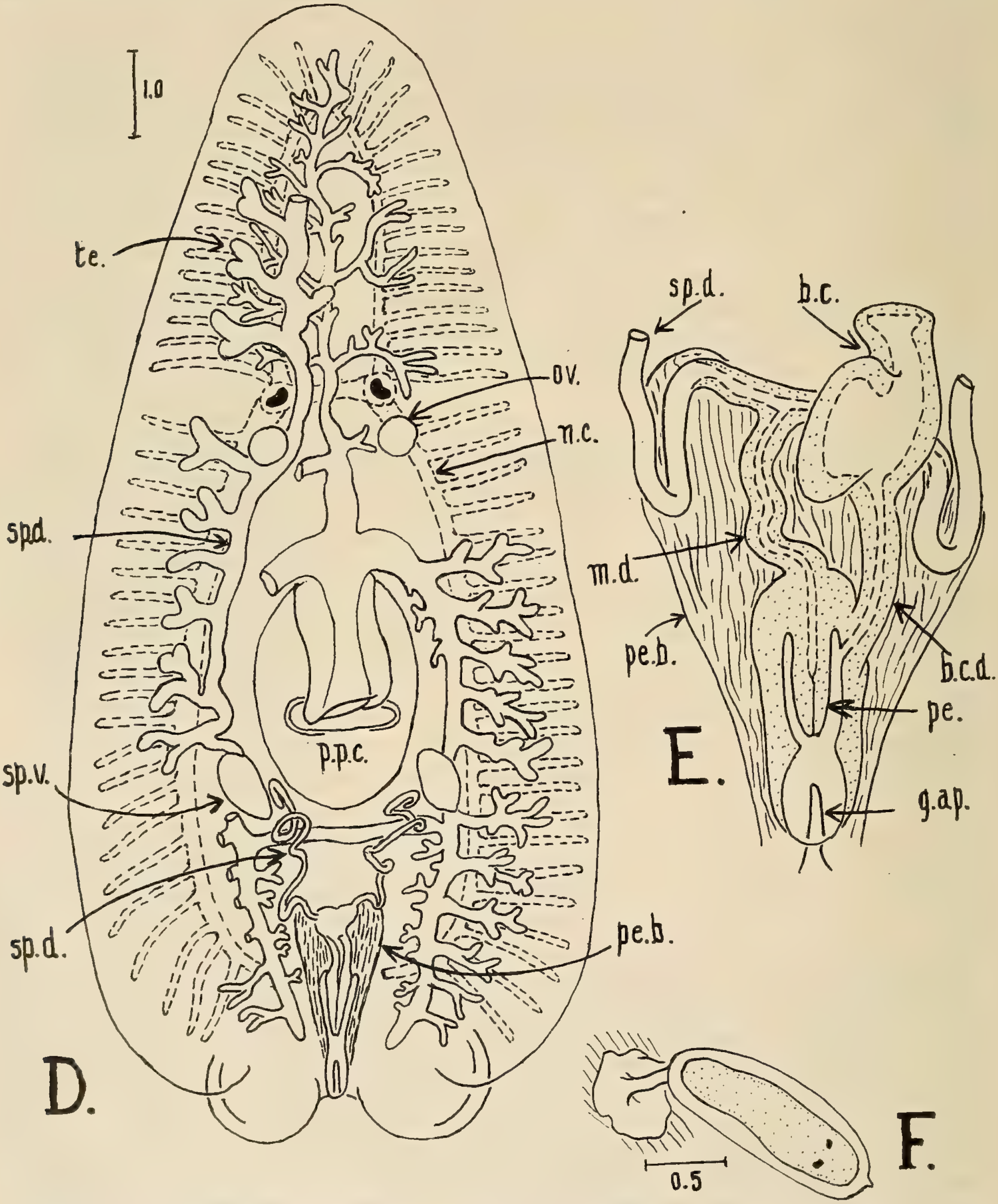

Fig. 2. *Bdellasimilis barwicki.* D. General morphology, composite based on the living specimen, a stained whole mount, and serial sections. E. Free-hand reconstruction from serial sections of terminal male organs, copulatory bursa and duct. F. Egg-capsule. b.c., copulatory bursa; b.c.d., bursal duct; g.ap., genital pore; n.c., longitudinal nerve cord; m.d., median duct; ov., ovary; pe., penis; pe.b., penis bulb; p.p.c., peripharyngeal chamber; sp.d., sperm duct; sp.v., sperm vesicles; te., testis. Scale in mm.

elevation of the dorsal and lateral walls protruding into the antrum as though dividing the proximal from the terminal chamber and leaving them in communication only ventrally; but it is very short and the sections too thick for me to determine the form of this structure.

The single pair of spherical ovaries are situated close behind the cerebral ganglia and the eyes. They are 0·08 mm. in diameter and contain oocytes. The vitellaria show in sections as irregular aggregations of cells chiefly in the region of the ovaries and behind the ovaries, the greater part dorsal above the anterior limb of the alimentary canal, and only some few cells between the diverticula. There is no obvious pattern or distribution which might indicate the path of a duct and I have been unable to detect a duct. The oviducts could not be seen with sufficient regularity to indicate a path and no terminal connections to the reproductive antrum or bursal sac or duct could be found although the wall of both the proximal and terminal portions of the antrum is thickly muscular. There are paired latero-dorsal brief grooves on the inner face of the anterior end of the terminal portion of the antrum suggestive of terminations of oviducts, but these grooves cannot be traced into the muscular wall.

The copulatory bursa was not seen in either the live animal nor in stained whole mounts. In sections it commenced as a slightly widened end to a muscular cylinder about 0·1 mm. in length with a short bulbous caecum on the dorsal aspect so that expanded it might become bilobate. It narrows rapidly to a bursal duct of about the same length. This is thick walled and with a narrow lumen. The duct extends briefly along the dorso-lateral aspect of the penis bulb, enters obliquely to terminate by opening about half way along and into the lateral aspect of the penis antrum. The thick walls of the bursa and duct show no indication of the entry of oviducts and there are no genito-intestinal connections.

The egg-capsules contain only a single embryo. There is an attachment disc of the diameter or wider than the capsule, rather irregular in outline and with some thin raised edges. The stalk is solid, short, cylindrical, its length about equal to the diameter of the capsule which is 0·5 mm. wide and about 1·3 mm. long, terminating obtusely with a minute spike. The colour is brownish; the appearance, chitinoid; the wall, single; the surface, smooth. A short cap detaches by a smooth-edged break running completely around the capsule to release the young.

Type.—Whole mount stained specimen prepared by R. E. Barwick, Coll. No. W 4174, Australian Museum, Sydney.

General Observations

Dr. Barwick noted that although he collected these turbellarians from both *Chelodina longicollis* and *Emydura macquarii*, there were few egg-capsules and these only in the limb-pits of the latter in contrast to such numbers in *C. longicollis* as to be described as dense masses in the order of up to a hundred in one limb-pit alone, and also a few on the skin of the legs elsewhere. On this evidence alone, it is clear there is a continued association between *B. barwicki* and these Chelonia, for he found only a few turbellarians which is suggestive of an extended period of capsule deposition as is known in some triclads.

Of the four live specimens I received, two stayed persistently in the water in the vial; two remained on the lower surface of the cap closing the vial. They did not change position in 24 hours and seem to be strongly sedentary in habit.

The appearance is that of a glossiphonid leech when the body is extended in contact with the surface, but it can be raised to the near vertical with the animal erect on the posterior discs and then the lateral margins are thrown into short rugae as though coarsely frilled. This attitude may be sustained for five minutes and more. There is no movement such as the respiratory movement in leeches when the body is raised clear of the surface.

When stimulated to move over a surface, the motion quite strongly suggests euglenoid creeping. The prepharyngeal region is extended, narrowed, but the pharyngeal and postpharyngeal regions are not greatly reduced in width or length. The prepharyngeal region then widens and shortens and the posterior region is drawn forward. It is not a rapid movement. I did not see it exhibit typical smooth turbellarian progression. Various attempts to persuade the animal to swim were unsuccessful. When dropped into water, it sank slowly to the bottom, rolling up and unrolling lengthwise and partly twisting the anterior portion of the body, but with no control. In this it differs from *Bdelloura candida* which is a capable swimmer (Verrill, 1892).

When detached from the surface and placed on its back, it is unable to right itself. One was held in water in a watch-glass for three hours in this position. During this time, it rolled up lengthwise repeatedly and extended in attempts to find a hold for the anterior adhesive pad, but with no success. It seemed to have no ability to twist the anterior portion of the body sufficiently to obtain a hold. The posterior end of the body has even less flexibility. The level of the water was reduced until the surface film was within the reach of the animal but it made no attempt to utilise this to re-orientate itself. In this inability to right itself, *B. barwicki* contrasts with other Paludicola and with such Maricola as I know.

It is a most difficult animal to manipulate. When detached from the surface by a needle, the body is wrapped lengthwise or crosswise on the needle adhering by the marginal bands, the anterior pad and posterior discs. It cannot be shaken from the needle or displaced by even violent agitation in water. As the animal is in fact firm bodied, it can be handled by using two needles, transferring it from one to the other until it is moved to the point of a needle, and it is unable to maintain a hold on this.

It is unusually light sensitive. An abrupt exposure to direct bright light leads to strong contraction, and a gradual relaxation when the light is turned off. When this is repeated several times, the animal acts as though conditioned and remains contracted for ten to twenty minutes with the light turned off. It does not respond to light from below even with very much higher intensities than produces contraction with direct light above. The pigmented optic cups open dorsally which apparently shields the light-sensitive retinal structures from light from below. I have not found this response in *Dugesia* or *Curtisia* spp. which I have known elsewhere.

B. barwicki has a distinct feeding posture (Fig. 1C). Attached by the posterior adhesive discs, the body is raised and held parallel to the substratum. The postocular region is convex in profile; the extended preocular region, concave above with the margins of the body rolled ventrally to form a furrow which is open at the anterior tip of the body. The lateral margins are undulate to irregularly rugose but without movement. The peripharyngeal chamber is enlarged and obvious through the thin body wall roofing over it. At intervals as frequent as ten minutes, the margins of the preocular region are folded inwards, the body raised slightly as a whole, and the preocular region curved ventrally and passed back under the ocular region and to the back of the pharyngeal region, the whole as though forming a sac beneath the peripharyngeal chamber. This attitude is held for a matter of a minute or so, and then the former stance is resumed.

During this action, the opening of the peripharyngeal chamber is large, twice and more the width of the pharynx, and the latter swings from side to side, extends and shortens, as though probing all regions in the peripharyngeal chamber. On one occasion, a considerable mass of unicellular green algae was accumulated in the enlarged peripharyngeal chamber. The margin of the enlarged opening into the chamber was thickened, as though a band holding the mass of algae within the chamber while the pharynx probed around and into it.

This manner of feeding suggested the possibility that there might be something here of the nature of a ciliated mucous filter feeding mechanism based on the mucus secreted from the anterior pad and marginal bands; but I could not detect any signs of currents of water moving toward or away from the animal such as would be expected in the presence of this type of feeding mechanism. In fact, I was not able to detect any indication of external ciliation in the live animal. The mass of uncellular algae in the peripharyngeal chamber seemed to be a loosely formed accumulation and the pharynx seemed to move freely into and through it with no indication that the algae were trapped in mucus.

Acknowledgements

The specific name is given in appreciation of the assistance given to me on this and other occasions by Dr. R. E. Barwick, Australian National University. I desire to thank also Mr. N. Call of the same institution who prepared the sections, and Dr. J. C. Yaldwyn, of the Australian Museum, who has been most helpful on many occasions. I thank the Science and Industry Endowment Fund for the loan of microscopic and other equipment.

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THE PLANTS GRAZED BY RED KANGAROOS, *MEGALEIA RUFA* (DESMAREST), IN CENTRAL AUSTRALIA

G. M. CHIPPENDALE*

Forest Research Institute, Forestry and Timber Bureau, Canberra, A.C.T.

(Plates VI–VIII)

[Read 24th April, 1968]

Synopsis

A study of the diet of red kangaroos in an area of central Australia shows that grass (75% to 99%) is the preferred fodder, with *Eragrostis setifolia* Nees being the most important single species grazed. Forbs are significantly grazed only for short periods in spring, and trees and shrubs are only grazed in small amounts with some increases in summer.

During drought grazed *Eragrostis setifolia* is higher in moisture content than ungrazed.

A pattern of grazing by kangaroos is suggested from the results obtained, but there is evidence that a larger amount of grazing takes place in gilgais than on the open plain.

INTRODUCTION

Preliminary analysis of the diet of red kangaroos, *Megaleia rufa* (Desmarest), in central Australia indicated that green herbage, and in particular the grass *Eragrostis setifolia* Nees predominated (Chippendale, 1962). As Newsome (1965*a*, *b*, *c*; 1966) has shown the supply of green herbage to be vital to the red kangaroo in central Australia, breeding, survival of young, and distribution and abundance depending on it, the plant species grazed by kangaroos in different seasons were studied in detail. The Burt Plain, an important drought refuge for kangaroos (Newsome, 1965*a*), about 32 miles north of Alice Springs, was chosen as a study area.

HABITAT

The Burt Plain lies between the Burt and Harry Creeks and is cut by the Stuart Highway (Fig. 1). To the east of the highway, the open grassland varies from *Astrebla pectinata* (Lindl.) F. Muell. ex Benth. communities which were depauperate during the investigation to small water channels and some gilgais carrying *Eragrostis setifolia* Nees and other grasses. To the west of the highway, the grassland is predominantly *Eragrostis setifolia* in and around gilgais, often mixed with *Eragrostis xerophila* Domin. The gilgais had a particular assemblage of other species, including *Swainsona campylantha* F. Muell., *Psoralea cinerea* Lindl., *Neptunia dimorphantha* Domin., *Alternanthera angustifolia* R.Br., *Abutilon malvifolium* (Benth.) J. M. Black, *Centipeda thespidioides* F. Muell., *Marsilea exarata* A.Br., and *Portulaca oleracea* L. Occasional deeper gilgais were almost completely dominated by *Marsilea exarata*. After rains, particularly in summer, annual grasses grew on the plain and in the gilgais.

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* Formerly Animal Industry Branch, Northern Territory Administration, Alice Springs, N.T.

The gilgais are marked depressions into which water runs after rain, and at times (Plate VI) 50 or more points of rain would be sufficient to fill a gilgai. The response of the vegetation to this water was spectacular (Plate VII), with far more growth in the gilgai than on the surrounding open plain.

Tripogon loliiformis (F. Muell.) C. E. Hubbard occurred on the higher parts of the plain after rain, and was most common in the heavy soil area of Cotton Bush, *Kochia aphylla* R. Br.

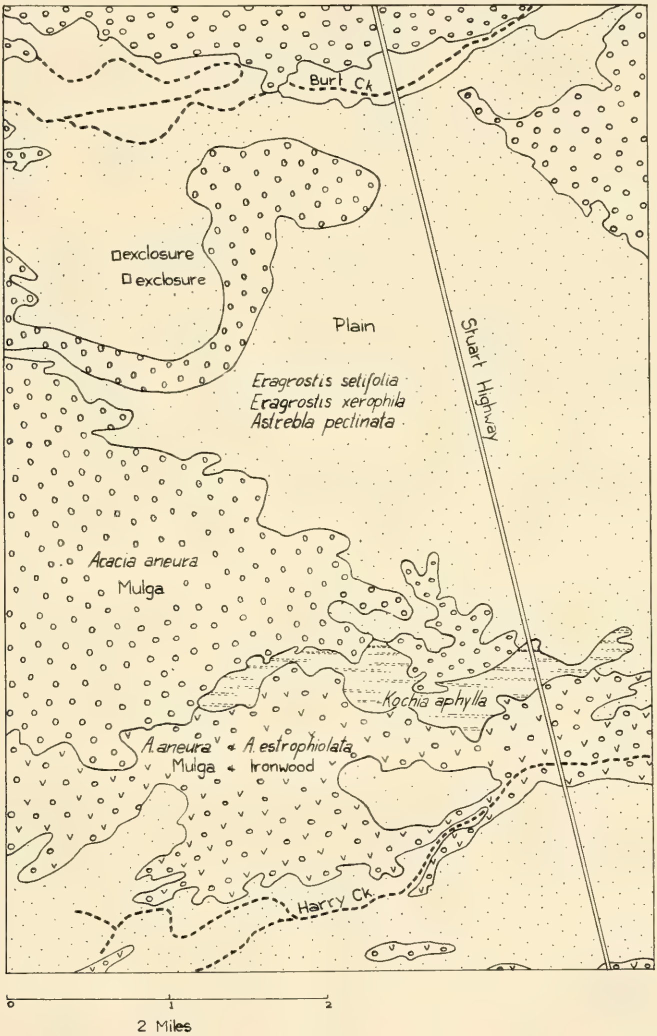

FIG 1.

The grasslands were surrounded by *Acacia aneura* F. Muell. ex Benth. woodland with sparse *Eragrostis eriopoda* Benth. present, and beyond the mulga was the creek bank association with *Eucalyptus camaldulensis* Dehnh., *Eremophila longifolia* (R.Br.) F. Muell., *Santalum lanceolatum* R.Br., *Dichanthium sericeum* (R.Br.) A. Camus, and *Chloris acicularis* Lindl.

The rainfall on the Burt Plain, including for several months prior to sampling, is shown in Table 1.

Cattle were present in small numbers for periods of several months during the investigation.

METHODS

Samples from the stomach contents of kangaroos were taken at frequent intervals from October, 1959 to October, 1961, except for five months in 1960, the kangaroos being shot after dark, usually when feeding on the plain west of the highway.

TABLE 1

Rainfall on the Burt Plain (points)

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1959	8	8	155	—	190	6	5	—	1	85	98	53
1960	385	78	—	44	58	9	12	27	61	99	58	52
1961	88	22	—	236	—	—	—	—	—	—	9	—

The samples, approximately 20% of the stomach contents, were washed in a fine sieve, dried in the sun and stored in packets until examined. They were later examined under a binocular microscope on an extension arm, using the point frame method of Chamrad and Box (1964). A frame of crossed threads sat squarely on the dried sample which was spread evenly in a 12″ × 10″ enamel dish. The microscope was used to identify the fragment at each of the 100 points where threads crossed.

Artificial samples containing known percentages by weight were made up by a Technical Assistant and examined by the author who had no knowledge of the contents. Results of the test are shown in Table 2. It can be seen that the accuracy for major constituents is better than for minor constituents, and there is the possibility of missing some minor constituents.

TABLE 2

Results of test of point frame method, using artificial samples

Species	Quantities (Percentage)							
	1st Test		2nd Test		3rd Test		4th Test	
	Actual	Point Frame	Actual	Point Frame	Actual	Point Frame	Actual	Point Frame
Eragrostis setifolia ..	95·0	95·0	50·0	52·0	80·0	82·75	97·0	99·25
Enneapogon polyphyllus	1·0	3·0	—	—	2·0	5·75	—	—
Portulaca oleracea ..	2·0	0·75	10·0	5·25	2·0	0·75	—	—
Euphorbia drummondii	0·5	0·5	—	—	2·0	2·0	—	—
Salsola kali	1·0	0·75	—	—	2·0	0·75	1·0	—
Acacia aneura ..	0·5	—	10·0	8·75	2·0	0·75	1·0	0·5
Acacia victoriae ..	—	—	10·0	12·75	2·0	1·5	—	—
Tribulus terrestris ..	—	—	10·0	11·0	2·0	0·5	—	—
Atriplex elachophylla ..	—	—	10·0	10·25	2·0	0·5	—	—
Boerhavia diffusa ..	—	—	—	—	2·0	2·75	—	—
Indigofera dominii ..	—	—	—	—	2·0	1·5	—	—

In using the point frame method, four estimates were made for each sample, two each by a Technical Assistant and the author, and the results for each sample averaged.

Fragments were identified by reference to a standard set of plant fragments collected on the Burt Plain, and by checking with authentic specimens in the Herbarium of the Northern Territory, Alice Springs. Owing to the difficulty of identification of grasses from minute fragments, mostly less than 1·0 mm. long, scores in the point frame were given as "grass" initially, so that only a total grass percentage was obtained. Subsequently, the sample was scanned under the microscope to identify the grass species present and to assess relative dominance, but percentages for individual species were not obtained. Grasses were sometimes identified by portions of spikelets or spikes in the sample, and these in turn were related to leaf or stem fragments associated in same sample. This information provided a guide for identification in those samples in which leaves only were present. When dealing with *Eragrostis* species, which were often present as leaf fragments only, a means of separating these was sought. Examination of the hairs on the inside of the convolute leaves was satisfactory; the angle and arrangement of these hairs varied slightly in *E. setifolia*, *E. xerophila* and *E. eriopoda* (Plate VIII), these being the main species available. Test determination of fragments from herbarium specimens showed about 90% positive accuracy, with the remainder being doubtful; there were no errors.

Fragments of leaves, stems, fruits and seeds in the samples aided the identification of forb and topfeed species, but when there was doubt, specimens were collected from the Burt Plain for comparison.

A number of kangaroo-proof exclosures each five metres square were erected on the Burt Plain; two of these are pertinent to this project, each being on a gilgai. Six transects across each exclosure were each continued for a further five metres outside the fence on two sides; periodic measurements were made of the basal length of any species on each transect. All measurements were reduced to percentage density cover.

After results were known, the moisture content in grazed and ungrazed *Eragrostis setifolia* was measured by weight from monthly samples.

RESULTS

The stomach contents of red kangaroos on the Burt Plain contained some green plant material at all times, though dried basal material predominated in drier periods. This accords reasonably with the results reported by Griffiths and Barker (1966) for Cunnamulla.

Table 3 shows that grass species dominated the diet, almost exclusively doing so during the hot months, representing from 75% to 99% of the plants eaten.

Of 189 samples, 154 contained *Eragrostis setifolia*, and of the remainder, 9 contained *Eragrostis xerophila* and *Tripogon loliiformis*, 9 more contained *Eragrostis xerophila*, 8 more contained *Tripogon loliiformis*, 1 contained *Astreba pectinata* and *Chloris acicularis*, 7 contained mainly an assemblage of annuals, and 1 contained unidentified grass species.

In dry times, such as from October, 1959 to January, 1960, *Eragrostis setifolia* and *Eragrostis xerophila* were grazed by most animals; other species found in the samples in this period were only as traces. With good summer rain, *Tripogon loliiformis* became dominant in the diet in February, 1960.

After little effective rain during the winter, *Eragrostis setifolia* and *Enneapogon polyphyllus* (Domin.) N. T. Burbidge were grazed by most animals during August and September, 1960, but some short ephemeral grasses also contributed to the diet. Moderate rain in September and October caused the diet in early November, 1960 to be mainly *Eragrostis setifolia*, *Eragrostis xerophila*, *Tripogon loliiformis* and *Enneapogon polyphyllus*. By late November and until March, 1961, only dry vegetation was available, and *Eragrostis setifolia* dominated the diet; *Eragrostis xerophila* was commonly grazed in February.

TABLE 3

The quantity of grass and the species contained in samples from kangaroo stomach contents

D=dominant ; C=common ; r=rare

						Perennials							Annuals						
Sample Period	Field Conditions	Number of Samples	Average Quantity (%)	Range of Quantity (%)	Relative Abundance	*Eragrostis setifolia*	*Eragrostis xerophila*	*Tripogon loliiformis*	*Chloris acicularis*	*Digitaria ammophila*	*Astrebla pectinata*	*Bothriochloa ewartiana*	*Enneapogon polyphyllus*	*Iseilema membranaceum*	*Iseilema vaginiflorum*	*Dactyloctenium radulans*	*Brachiaria gilesii*	*Tragus australianus*	Other Species
1959																			
13–19 Oct.	Dry basal grass	14	96	92–98	D	6	3	—	1	—	—	—	—	—	—	—	—	—	1
					C	1	3	2	—	—	—	—	—	—	—	—	—	—	—
					r	—	—	1	—	—	2	—	3	—	—	1	—	—	2
11–18 Dec.	Dry grass stems ; water in gilgais	10	96	90–99	D	1	3	—	—	—	—	—	—	—	—	—	—	—	—
					C	2	4	5	—	—	—	—	—	—	—	—	—	—	2
					r	—	—	—	—	—	—	—	—	2	—	—	2	—	4
1960																			
8–14 Jan.	Dry basal grass ; water in gilgais	7	95	90–97	D	4	—	—	—	—	—	—	—	—	—	—	—	—	—
					C	3	—	3	—	—	—	—	—	—	—	—	—	—	—
					r	—	1	—	—	—	1	—	—	—	—	2	—	—	1
21 Jan.	Green growth in gilgais	10	99	97–99	D	2	2	—	—	—	—	—	—	—	—	—	—	—	—
					C	2	5	5	—	—	—	—	—	—	—	—	—	—	—
					r	—	—	—	1	—	1	—	—	2	—	2	—	—	3
4–12 Feb.	Green	4	99	98–99	D	—	—	2	—	—	—	—	—	—	—	—	—	—	—
					C	2	—	2	—	—	—	—	—	—	—	—	—	—	—
					r	—	—	—	—	—	—	—	—	—	—	1	2	—	2
19 Aug.	Dry	10	75	28–99	D	3	—	—	—	—	—	—	—	—	—	—	—	—	—
					C	7	—	—	—	—	—	—	7	—	—	—	—	—	—
					r	—	—	5	—	—	—	—	—	4	—	4	—	4	—
26 Aug.	Dry	10	88	73–98	D	—	—	—	—	—	—	—	—	—	—	—	—	—	—
					C	10	—	3	1	1	—	—	7	—	—	—	—	—	—
					r	—	1	3	4	3	—	2	—	4	—	8	3	2	3

TABLE 3—*Continued*

The quantity of grass and the species contained in samples from kangaroo stomach contents—Continued

Sample Period	Field Conditions	Number of Samples	Average Quantity (%)	Range of Quantity (%)	Relative Abundance	Perennials							Annuals						
						Eragrostis setifolia	*Eragrostis xerophila*	*Tripogon loliiformis*	*Chloris acicularis*	*Digitaria ammophila*	*Astrebla pectinata*	*Bothriochloa ewartiana*	*Enneapogon polyphyllus*	*Iseilema membranaceum*	*Iseilema vaginiflorum*	*Dactyloctenium radulans*	*Brachiaria gilesii*	*Tragus australianus*	Other Species
1960																			
5 Sept.	Some green	10	85	61–97	D	1	—	—	—	—	—	—	1	—	—	—	—	—	—
					C	5	—	6	1	—	—	—	6	—	—	—	—	—	—
					r	—	—	—	4	2	—	9	—	9	—	8	3	1	1
3 Nov.	Green	10	97	95–99	D	1	—	—	—	—	—	—	—	—	—	—	—	—	—
					C	9	6	8	—	—	—	—	8	—	—	—	—	—	—
					r	—	—	—	2	1	—	3	—	5	1	2	1	—	1
16 Nov.	Drying	10	91	84–98	D	—	—	—	—	—	—	—	1	—	—	—	—	—	—
					C	8	6	5	—	—	—	—	8	—	—	—	—	—	—
					r	—	—	—	1	2	—	—	—	6	5	2	—	—	2
28 Nov.	Dry basal grass	10	92	85–97	D	2	—	—	—	—	—	—	—	—	—	—	—	—	—
					C	8	3	2	—	—	—	—	7	—	—	—	—	—	—
					r	—	—	—	1	—	1	4	—	2	7	3	1	2	2
20 Dec.	Dry	10	97	84–100	D	9	—	—	—	—	—	—	—	—	—	—	—	—	—
					C	1	1	—	—	—	—	—	—	—	—	—	—	—	—
					r	—	—	3	1	—	2	—	2	2	—	4	2	—	—
1961																			
16 Jan.	Dry	10	94	87–99	D	10	—	—	—	—	—	—	—	—	—	—	—	—	—
					C	—	—	—	—	—	—	—	—	—	—	—	—	—	—
					r	—	2	1	1	—	2	—	2	—	—	1	1	—	—
22 Feb.	Dry	10	96	91–99	D	2	—	—	—	—	—	—	—	—	—	—	—	—	—
					C	8	8	—	—	—	—	—	—	—	—	—	—	—	—
					r	—	—	3	1	1	—	—	—	—	4	1	2	—	—

TABLE 3—*Continued*

The quantity of grass and the species contained in samples from kangaroo stomach contents—Continued

Sample Period	Field Conditions	Number of Samples	Average Quantity (%)	Range of Quantity (%)	Relative Abundance	Perennials							Annuals						
						Eragrostis setifolia	*Eragrostis xerophila*	*Tripogon loliiformis*	*Chloris acicularis*	*Digitaria ammophila*	*Astrebla pectinata*	*Bothriochloa ewartiana*	*Enneapogon polyphyllus*	*Iseilema membranaceum*	*Iseilema vaginiflorum*	*Dactyloctenium radulans*	*Brachiaria gilesii*	*Tragus australianus*	Other Species
1961																			
29 Mar.	Dry basal grass	10	86	79–95	D	7	—	—	—	—	—	—	—	—	—	—	—	—	—
					C	3	—	—	—	—	—	—	—	—	—	—	—	—	—
					r	—	3	3	—	—	—	—	3	—	—	—	—	—	—
27 Apr.	Green	10	99½	99–100	D	—	—	10	—	—	—	—	—	—	—	—	—	—	—
					C	10	—	—	—	—	—	—	—	—	—	—	—	—	—
					r	—	1	—	—	—	—	—	—	—	—	—	3	1	—
25 May	Green	10	99	98–100	D	—	—	—	—	—	—	—	—	—	—	3	—	—	—
					C	5	—	5	—	—	—	—	2	—	—	7	1	1	—
					r	—	—	—	1	1	—	—	4	9	—	—	7	9	1
22 June	Dry	10	95	85–100	D	1	—	—	—	—	—	—	—	—	—	—	—	—	—
					C	8	—	8	1	1	—	—	—	—	—	—	—	—	—
					r	—	—	—	3	1	—	2	7	9	—	7	7	5	3
29 Aug.	Dry	10	84	70–98	D	2	—	—	—	—	—	—	—	—	—	—	—	—	—
					C	8	—	8	—	—	—	—	—	—	—	—	—	—	—
					r	—	—	—	3	—	—	—	4	10	—	4	4	6	—
24 Oct.	Dry	4	89	80–98	D	3	—	—	1	—	—	—	—	—	—	—	—	—	—
					C	—	—	—	—	—	—	—	—	—	—	—	—	—	—
					r	—	—	—	—	1	—	1	1	3	—	—	1	2	—
					D	54	8	12	2	—	—	—	2	—	—	3	—	—	1
					C	100	36	62	3	2	—	—	45	—	—	7	1	1	2
Totals		189	—	—	r	—	8	19	23	12	9	21	26	67	17	50	39	32	25
						154	52	93	28	14	9	21	73	67	17	60	40	33	28

Following the good rain in early April, 1961, *Tripogon loliiformis* predominated in the diet, with *Eragrostis setifolia*. In May, 1961 with no further rain, annual grass species contributed most to the diet, *Dactyloctenium radulans* (R.Br.) Beauv., *Tragus australianus* S. T. Blake and *Brachiaria gilesii* (Benth.) Chase predominating, with *Iseilema membranaceum* (Lindl.) Domin. and *Enneapogon polyphyllus*; seeding heads were common in the samples at this time and *Eragrostis setifolia* and *Tripogon loliiformis* were grazed by fewer animals. In June to August, 1961, *Tripogon loliiformis* and *Eragrostis setifolia* were grazed by almost all animals with annual species being grazed by slightly fewer animals. In October, 1961, the indication is that *Eragrostis setifolia* had again become the main grass in the diet, supported with some annual material.

Table 4 shows that forb species were mostly grazed in small percentages and that the total forbs in the diet only exceeded 10% for short periods. *Calotis hispidula* F. Muell., *Marsilea exarata* and *Portulaca oleracea* were the most consistently recorded annual forbs, and *Helipterum floribundum* DC. tended to become important during the months of August and September. Several other species increased from trace amounts to at least 1% of the diet for brief periods of from one month to several months, and these were *Helipterum charsleyae* F. Muell. (included as "other Compositae") in August, September and October, *Psoralea cinerea* in September, 1960 and March, 1961, *Alternanthera angustifolia* in January to March, 1961. A number of other forbs were consistently recorded as being grazed in trace amounts usually by less than half of the animals sampled at any period, and these were *Euphorbia drummondii* Boiss., *Neptunia dimorphantha*, *Indigofera dominii* Hj. Eichler, *Abutilon malvifolium*, and various *Bassia* species. Other forbs were grazed in trace amounts during isolated periods by few animals.

Table 5 shows that woody species rarely comprised more than 1% of the diet and then only for brief periods. *Acacia aneura* was the predominant tree or shrub species grazed, being recorded in almost all months, but only grazed by about half of the animals. When the amount of this species in the diet increased from trace amounts to 3% in January, 1960 and to 2% in March, 1961, the number of animals grazing the tree also increased, as did the number of tree species being grazed. *Acacia tetragonophylla* F. Muell. was 6% of the diet in October, 1961, after a long rainless period. *Acacia sessiliceps* F. Muell. was grazed as 1% in January, 1961 and 2% in March, 1961 (listed under other species). Other woody species were recorded as trace amounts by few animals or in isolated periods.

Table 6 gives the percentage ground cover in and around two exclosures, and it can be assumed that the cover inside would represent the available fodder on the plain with no grazing while the cover outside reflects grazing as well as an indication of actual available fodder on the plain. Table 6 considered with Tables 3–5 shows that on 16th November, 1960, there were more forbs than *Eragrostis* spp. on the Burt Plain; yet grass comprised 91% of the kangaroos' diet. The diet remained about the same on 29th November, 1960, with available forbs now less than the grass. Grazing of forbs and topfeed was increased on 29th March, 1961, when *Eragrostis setifolia* had been markedly reduced outside the exclosure. Good rains from 10th to 19th April, 1961, resulted in about equal amounts of forbs and grass being available inside, but herbage was less than half the amount of grass outside; the diet at 27th April, 1961 was 99·5% grass with *Eragrostis setifolia* and *Tripogon loliiformis* dominating. Forbs were again more plentiful than grass on 26th May, 1961, but grass was still 99% of the diet, with the annual grasses

TABLE 4

The quantities of forb species identified in samples from kangaroo stomach contents

Sample Period	Number of Samples	Quantity (%)	Average percentage/number of samples in which recorded																					
			Portulaca oleracea	*Calotis hispidula*	*Marsilea exarata*	*Helipterum floribundum*	*Neptunia dimorphantha*	*Lepidium rotundum*	*Alternanthera angustifolia*	*Abutilon malvifolium*	Other Compositae	*Bassia* spp.	*Boerhavia diffusa*	*Indigofera dominii*	*Psoralea cinerea*	*Euphorbia drummondii*	*Sida* spp.	*Tribulus* spp.	*Solanum* spp.	*Goodenia* spp.	Other Leguminosae	*Atriplex* spp.	*Kochia* spp.	Other Species
1959																								
13–19 Oct. ..	14	3	x/1	x/14	1/7	x/8	x/7	x/7	—	—	x/6	x/5	—	—	—	x/3	x/1	—	—	x/1	x/3	x/1		—
11–18 Dec. ..	10	3	x/4	2/10	x/5	—	x/2	—	x/1	—	x/3	x/3	x/4	—	—	x/3	—	x/5	—	x/1	—	—		—
1960																								
8–14 Jan.	7	1	x/1	x/4	x/3	—	x/1	—	x/2	—	—	x/1	—	—	—	—	x/1	x/1	x/2	x/1	—	—		x(1)
21 Jan. ..	10	¼	x/1	x/2	x/2	—	x/1	—	—	—	—	—	—	—	—	x/1	—	—	—	—	—	—		—
4–12 Feb. ..	4	½	x/1	x/1	—	—	x/1	—	—	—	x/1	—	—	—	—	—	—	—	—	—	—	—		—
19 Aug. ..	10	24¾	x/6	x/3	x/1	23/10	—	x/5	—	—	—	—	—	—	—	—	—	1/2	x/2	x/1	x/2	—		x(2)
26 Aug. ..	10	11½	1/7	1/10	x/6	7/10	—	x/3	x/3	x/2	x/3	x/3	x/1	—	—	x/1	x/4	2/2	—	x/1	—	x/1		—
5 Sept. ..	10	14½	1/6	1/8	x/3	4/10	x/2	x/3	x/3	x/3	3/8	x/3	—	x/4	4/3	x/2	x/1	x/1	—	—	—	x/1		x(1)
3 Nov. ..	10	2¾	2/10	x/4	x/2	x/2	x/1	x/5	—	x/2	—	—	—	x/3	—	—	—	x/1	—	x/1	—	—		—
16 Nov. ..	10	8¾	7/10	x/4	x/2	—	x/3	x/1	—	x/4	—	x/1	x/1	x/5	—	x/1	—	—	—	x/1	—	x/1		—
28 Nov. ..	10	7¾	5/10	x/3	x/3	—	x/6	x/1	x/2	x/7	—	x/1	—	x/2	—	x/1	x/1	—	x/3	x/3	x/2	—		—
20 Dec. ..	10	2¾	x/6	x/2	2/6	—	x/2	—	x/3	x/7	x/1	x/1	—	x/2	—	—	—	x/1	x/1	—	—	—		—
1961																								
16 Jan. ..	10	5	3/10	x/3	x/5	—	x/5	x/1	1/9	x/5	x/1	—	x/1	x/3	x/4	—	—	—	x/2	—	—	—		—
22 Feb. ..	10	4	x/7	x/2	1/7	—	1/4	—	1/10	x/4	—	—	x/1	x/2	x/7	—	—	—	—	x/1	—	—		—
29 Mar. ..	10	8	2/10	x/5	1/4	—	—	—	1/6	—	—	x/1	—	x/3	3/8	x/1	—	—	x/3	—	—	x/1		1(3)
27 Apr. ..	10	¼	—	—	—	—	x/1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		—
25 May ..	10	¾	x/4	—	x/1	—	x/2	x/1	x/2	—	—	—	x/2	—	—	—	—	—	—	—	—	—		—
22 June ..	10	4¾	2/9	x/4	x/4	x/2	x/1	x/5	x/5	x/7	—	—	x/1	—	—	—	x/5	—	x/1	x/1	—	—		x(2)
9 Aug. ..	10	15¾	x/1	x/4	1/5	13/9	x/1	x/1	x/2	x/1	1/4	—	x/2	—	x/3	—	—	—	x/1	—	—	—		—
24 Oct. ..	4	4	x/1	x/2	x/1	x/1	x/2	x/1	2/2	—	1/3	x/1	—	x/1	—	—	—	—	—	—	—	—		—
Total number of samples in which species occurred (of 189) ..			105	85	67	52	42	34	50	42	30	20	13	25	25	13	13	13	15	12	7	5	—	9

x = less than 1%.

now being selected by more animals. A similar situation showed on 22nd June, 1961, although the perennial grasses and some forbs were being grazed. By 24th October, 1961, after no rain for six months, negligible amounts of forbs were available on the plain and the perennial grasses were still the dominant items in the diet but forbs represented about 4% of the diet, with topfeed 7%.

Figure 2 shows the amounts of moisture in samples of grazed and ungrazed *Eragrostis setifolia* collected in and near gilgais on the Burt Plain from November, 1963 to January, 1965. Rainfall is also shown. It can be seen that during dry times the shorter grazed shoots contained more moisture than the dry ungrazed grass.

TABLE 5

The quantities of woody species identified in samples from kangaroo stomach contents

Sample Period	Number of Samples	Quantity (%)	Average percentage/number of samples in which recorded				
			Acacia aneura	*Acacia estro-phiolata*	*Acacia tetra-gonophylla*	*Acacia victoriae*	Other Species
1959							
13–19 Oct. ..	14	1	1/11	x/1	x/3	x/3	x/2
11–18 Dec. ..	10	1	x/6	x/6	—	x/1	x/2
1960							
8–14 Jan. ..	7	4	3/6	x/3	x/3	x/1	x/2
21 Jan. ..	10	¾	x/7	x/1	—	—	x/1
4–12 Feb. ..	4	½	x/4	x/1	—	—	—
19 Aug. ..	10	¼	x/3	—	x/1	—	—
26 Aug. ..	10	½	x/5	x/1	—	—	—
5 Sept. ..	10	½	x/4	—	—	—	—
3 Nov. ..	10	¼	x/4	—	—	—	—
16 Nov. ..	10	¼	x/2	x/1	—	—	—
28 Nov. ..	10	¼	x/6	—	—	—	—
20 Dec. ..	10	¼	x/2	—	—	—	—
1961							
16 Jan. ..	10	1	x/3	—	—	x/1	1/4
22 Feb. ..	10	—	—	—	—	—	—
29 Mar. ..	10	6	2/6	—	1/3	1/3	2/7
27 Apr. ..	10	¼	x/4	—	—	—	—
25 May ..	10	¼	x/3	—	—	—	—
22 June ..	10	¼	x/2	—	—	—	—
9 Aug. ..	10	¼	x/3	—	—	—	x/1
24 Oct. ..	4	7	x/3	x/1	6/3	x/2	—
Total number of samples in which species occurred (of 189)			85	15	13	11	18

x=less than 1%.

DISCUSSION AND CONCLUSIONS

Green grass is the preferred diet of the red kangaroo in central Australia.

Within a month, possibly within several weeks, of effective rain at any time, the diet is almost exclusively grass. Observations at such times have shown that *Eragrostis setifolia* and *Tripogon loliiformis* have soft green regrowth, and this regrowth predominated in the stomach contents. Effective rain in autumn caused annual grasses *Tragus australianus*, *Dactyloctenium radulans*, *Iseilema membranaceum*, *Brachiaria gilesii*, and *Enneapogon polyphyllus* to be grazed by almost all of the animals sampled. These species would probably be grazed after summer rain as they respond in summer.

It is notable that *Eragrostis eriopoda*, which is widely available to the kangaroos in areas of *Acacia aneura*, was not recorded as grazed. Similarly, *Astrebla pectinata* which is available on the open plain, was rarely grazed.

With little effective rain in winter, the forb content of the diet increased to its highest point of about 24% in August, 1960 and 16% in August, 1961. At these times, the rapidly growing ephemeral *Helipterum floribundum* was apparently selected, as high percentages were recorded. Perennial grasses would be in poor condition at this time.

Portulaca oleracea, a succulent annual herb, was particularly selected, although in comparatively small amounts, from November, 1960 to June, 1961. This species, and *Marsilea exarata*, *Neptunia dimorphantha*, *Indigofera dominii*, *Psoralea cinerea*, *Alternanthera angustifolia* and *Abutilon malvifolium* were usually grazed as an assemblage of plants, and as a group, comprised from 1% to about 9% of the diet. As these grow in the gilgais with *Eragrostis setifolia*, it indicates that most grazing takes place in finite areas, the gilgais.

TABLE 6

Percentage cover in two exclosures on the Burt Plain

Date	*Eragrostis setifolia*		Other Species, predominantly Forbs	
	Inside	Outside	Inside	Outside
16.11.1960	4·3	2·7	7·6	7·6
29.11.1960	8·6	6·4	7·8	5·0
20.12.1960	9·8	4·7	20·1	3·5
16. 1.1961	9·2	4·6	7·5	1·3
22. 2.1961	13·1	5·5	20·6	3·6
29. 3.1961	9·3	2·3	3·2	0·2
27. 4.1961	9·9	9·9	9·4	4·4
26. 5.1961	12·1	8·0	21·4	9·2
22. 6.1961	16·1	7·4	21·0	4·9
9. 8.1961	12·2	3·9	9·5	0·7
5. 9.1961	12·6	3·2	5·6	0·4
17.10.1961	11·4	3·8	3·8	0·2
27.11.1961	8·3	2·0	2·1	0·0

The extra water which runs into gilgais makes the grass more succulent, and the moisture content of short shoots of *Eragrostis setifolia* which are grazed ranges from 10% to 20% higher than that of taller ungrazed material of the same species. Although water content was studied several years after the main project, it is likely that similar conditions applied during the project period.

Browse species are unimportant in the diet, for the main woody species eaten, Mulga *Acacia aneura*, only comprised 2% to 3% of the diet during January to March when extra roughage may be sought to balance the soft grass after rain; it was grazed much less at other times. Other browse species were mainly represented as traces. These small amounts would seem consistent with small sporadic grazing in the *Acacia aneura* scrub where the animals mainly rest during the day.

It is concluded that the short green shoots of the perennial grass Neverfail, *Eragrostis setifolia*, in gilgais, was preferred by kangaroos on the Burt Plain as the bulk of fodder all through the year. *Tripogon loliiformis*, which is a perennial with a short growth period and is indicatively known as Five Minute Grass, was also favoured in periods immediately after rain, and probably as long as green leaf shoots are present. In late winter or early spring, some annual herbage was mixed with the perennial grasses, and in summer the animals select *Portulaca oleracea* with smaller quantities of other annual herbs growing in gilgais. Several annual grasses are selected during summer, and in mid-summer after rain small amounts of topfeed, notably *Acacia aneura*, were eaten. Annual grasses again contributed during autumn.

From this pattern, and from observations, the kangaroo may not seriously affect natural pastures, but certainly grazes the basal portions of perennial grasses in dry times, and in a long drought, this could be serious. Trees are rarely grazed, and no traces of bark or wood were seen in the samples. Field observations confirm that the animals eat the soft regrowth of perennial grasses in gilgais and also graze to a lesser degree other plants which may be green. Similarly, tall grasses are not grazed; it was common to see mature stands of *Eragrostis* spp. on the open plain as ungrazed, while at the same time, tracks, faecal pellets, and signs of grazing in gilgais were common. An explanation seems to be that more or less constant grazing in the gilgais kept the grasses actively growing, and it seems possible that the congregation of faecal matter at these points together with the run-on effect of rainfall may give added recovery power to the grass.

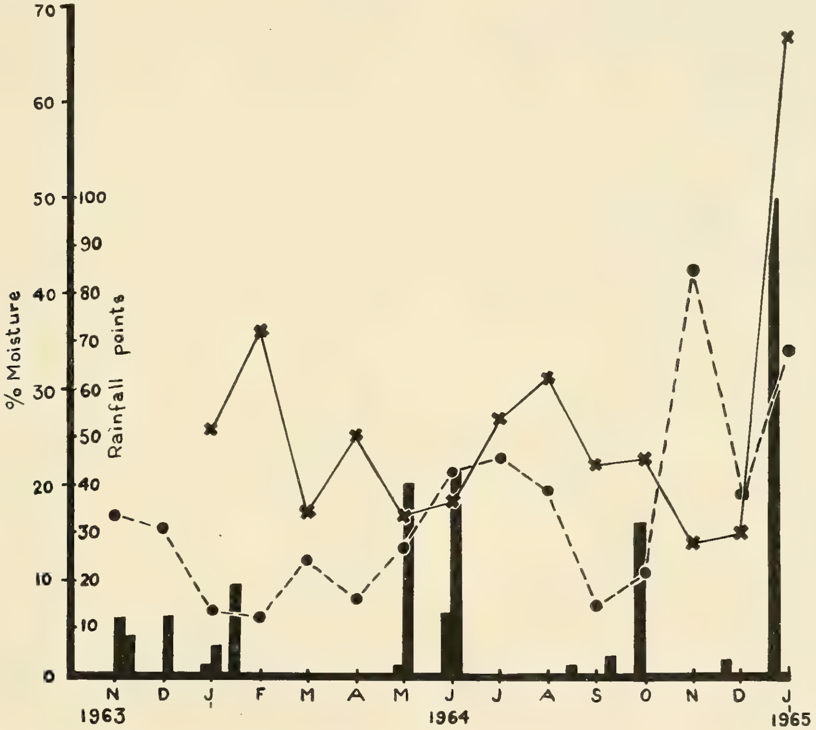

Fig. 2. Moisture contents of samples of *Eragrostis setifolia*: ——— grazed, in gilgais; - - - - - not grazed, near gilgais.

As the perennial grass *Eragrostis setifolia* is the most important single species in the diet of the kangaroo in central Australia, it is possible that this grass in gilgais, and the red kangaroo, may at times form an interdependent relationship.

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I appreciated criticism of my manuscript by Dr. A. E. Newsome, Division of Wildlife, C.S.I.R.O., Canberra, A.C.T.

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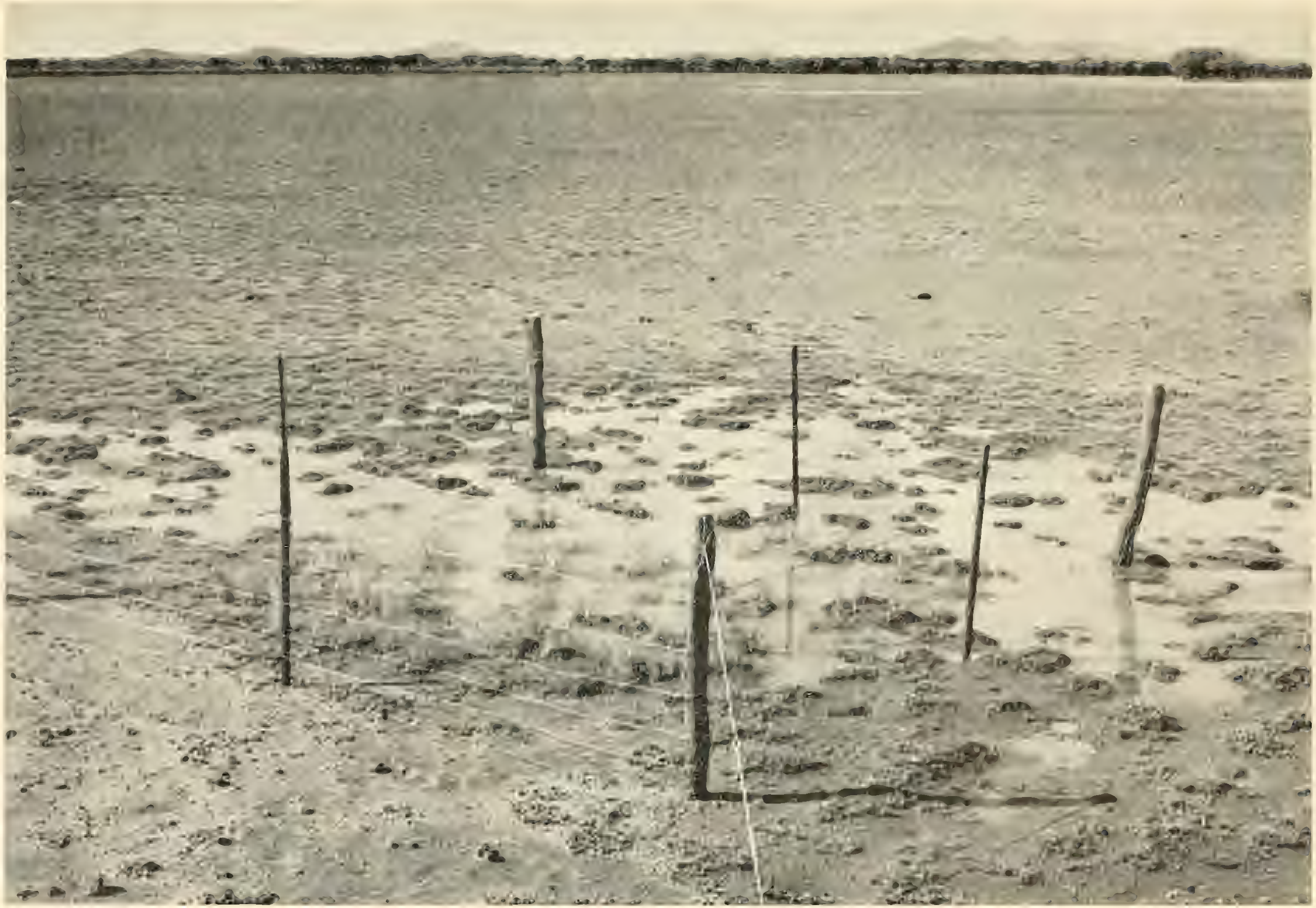
EXPLANATION OF PLATES

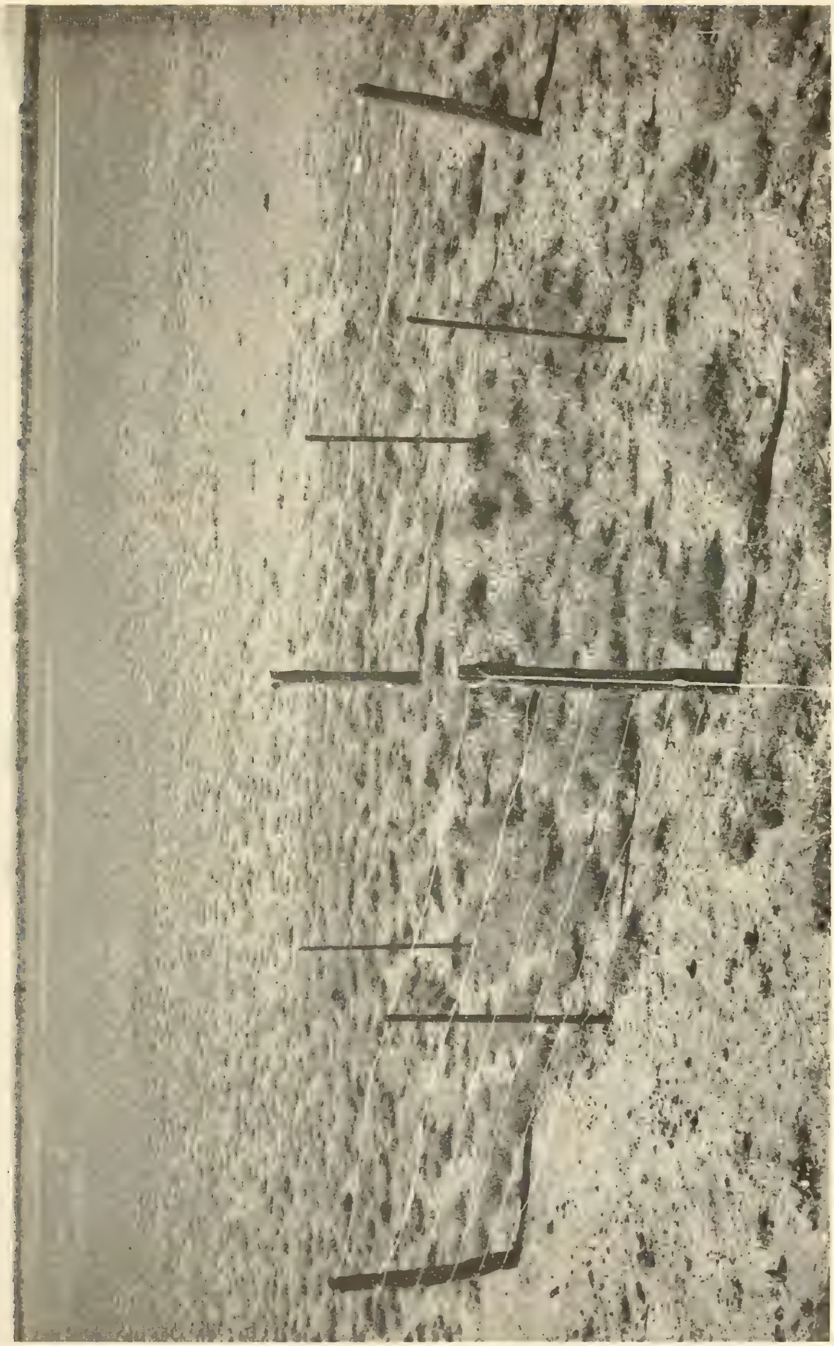
PLATE VI. An exclosure on a gilgai on the Burt Plain, central Australia, 19th April, 1961.

PLATE VII. The same exclosure and gilgai, 27th April, 1961.

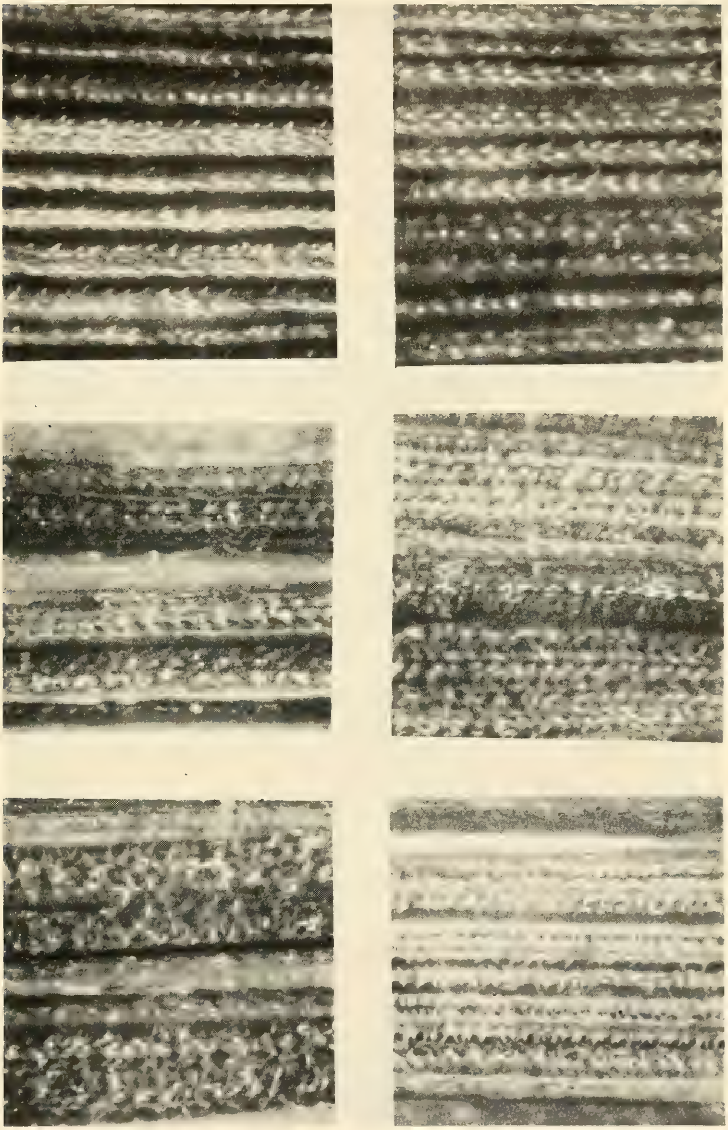
PLATE VIII. Patterns of hairs on inner surface of the convolute leaves of: Top left, *Eragrostis xerophila* from herbarium specimen R. Winkworth 617, right NT313; Centre left, *Eragrostis setifolia* from NT9011, right NT9012; Bottom left, *Eragrostis eriopoda* from M. Lazarides 5189, right N. Burbidge and M. Gray 4544.



An enclosure on a gilgai on the Burt Plain, 19th April, 1961



An enclosure on a gilgai on the Burt Plain, 27th April, 1961.



Pattern of hairs on leaves of *Eragrostis* species.

THE LOWER AND MIDDLE PALAEOZOIC STRATIGRAPHY AND SEDIMENTARY TECTONICS OF THE SOFALA–HILL END–EUCHAREENA REGION, N.S.W.

G. H. Packham

(Plates ix–xii)

[Read 24th April, 1968]

Synopsis

Ordovician andesitic volcanics are the oldest rocks in this region of about 1,000 square miles. They are overlain about Sofala in the east of the region, by Silurian limestones and shales, rhyolitic volcanics, subgreywackes, dacitic tuffs and further subgreywackes, and west near Euchareena by rhyolitic volcanics, limestone and shale. The source of the sediments lay to the west and south-west except for the highest subgreywacke unit in the Sofala sequence which was derived from the underlying formations as a result of the uplift of a structure to the east (the Capertee Geanticline). Dacitic vulcanism on this geanticline in the early Devonian provided directly or indirectly, much of the detritus comprising the greywackes and tuffs of the Crudine Group and the Merrions Tuff which were deposited in the Hill End Trough in the Sofala-Hill End area. In the Euchareena district more restricted andesitic and dacitic vulcanism occurred at this time. During the later Lower Devonian and perhaps part of the Middle Devonian, greywacke sedimentation took place in the Hill End Trough while limestones and shales were deposited in the Limekilns area. Near Euchareena limestones, shales and lithic calcarenites were being laid down. The youngest rocks deposited in the region prior to the Upper Devonian are acid tuffs overlying the limestone-shale sequence at Limekilns perhaps unconformably. The region is folded into a broad synclinorium which has a culmination in the vicinity of Hill End and is overthrust to the east near Sofala. The rocks of the central part are strongly cleaved and belong to the green schist metamorphic facies.

Introduction

The region of over a thousand square miles, described in this paper contains folded strata ranging in age from Ordovician to Devonian. Within the region there are three palaeogeographic and tectonic entities (Figure 1), which have been discussed in previous publications (Packham, 1960, 1962, 1968). They are from east to west, the Capertee Geanticline, the Hill End Trough and the Molong Geanticline. This paper presents the stratigraphic evidence on which the recognition of these features was originally based.

Within the Capertee Geanticline, which came into existence at about the end of the Silurian, the sediments are normally uncleaved and only moderately folded. Limestones occur in the Lower Devonian and indicate that shallow water environments occurred in that part of the succession at least. The geanticline has as its western boundary the Wiagdon Thrust, a structure which is now known to extend from north of Mudgee to south of Yetholme, a distance of about 100 miles.

The Hill End Trough which occupies most of the region under discussion contains greywacke-type sediments throughout the exposed Silurian and Devonian section. Folding is moderate to strong, with slaty cleavage developed everywhere in the finer sediments and in the coarser rocks in the central part of the trough. The cleavage fans on a regional scale, dipping to the west in the eastern part and east in the west. It is approximately vertical in the vicinity of Hill End. The highest grade of metamorphism reached is in the central part of the trough where biotite is developed over a width of about 10 miles across the strike. On the western side of the trough, the greywacke sequence passes into fossiliferous sediments on the eastern flank of the Molong Geanticline where limestones occur in the Ordovician, Silurian and Devonian Systems.

The region is one in which outcrop is generally good. It is essentially a plateau with an elevation of about 3,200 feet in the east and 2,500 feet in the west, strongly dissected by the Turon and Macquarie Rivers and their tributaries. Exposures along the rivers and the major tributaries are excellent.

The description of the stratigraphy is divided into three sections (a) the Sofala-Limekilns district of the eastern side of the Hill End Trough and the western edge of the Capertee Geanticline (*b*) the Hill End district, in the centre of the trough and (*c*) the Euchareena district on the western side of the trough and the eastern side of the Molong Geanticline.

Rock specimens mentioned in the text are in the rock collection of the Department of Geology and Geophysics, University of Sydney.

THE STRATIGRAPHY OF THE SOFALA–LIMEKILNS DISTRICT

In the Sofala district there is an essentially conformable sequence of strata, ranging in age from Upper Ordovician at the base to possibly Middle Devonian at the top. The highest unit in the Limekilns area, the Winburn Tuff, may be unconformable on the Limekilns Group. The successions in the Sofala-Turondale area and the Limekilns area are as follows (in descending order):

Sofala-Turondale		Limekilns	
		Winburn Tuff	2000+′
Cunningham Formation	2800′	Limekilns Group	2500′
Merrions Tuff	2000′	Merrions Tuff	1500′
Crudine Group	3700′	Crudine Group	2500′
Cookman Formation	1500′	Cookman Formation	600′
Chesleigh Formation	3500′	Chesleigh Formation	3500′
Bell's Ck. Volcanics	1500′		
Tanwarra Shale	250′	Tanwarra Shale	0–250′
Sofala Volcanics	?	Sofala Volcanics	7000+′

The Limekilns sequence is east of the Wiagdon Thrust and the Sofala sequence is west of this fault in the Hill End Trough.

SOFALA VOLCANICS

The type section of the Sofala Volcanics is exposed along the Turon River, commencing one and a half miles west of Sofala, extending ten miles to the east where the formation is thrust over Upper Devonian sandstones. No underlying formation has been recognized so that the base of the Sofala Volcanics cannot be defined. In the type section, approximately 7,000 feet of strata consisting dominantly of clastic and pyroclastic detritus with a small proportion of lavas, are exposed. Occasional horizons of chert represent concentrations of pelagic elements.

Type section. In the lower part of the section medium to fine-grained sediments are dominant, typically in beds a foot thick, displaying graded bedding, convolute bedding and slump structures. Fine-grained sediments in the section are very dark grey to black in colour and have a sub-conchoidal fracture. Three types of coarser sediments occur in the section. There are breccias containing a small amount of matrix, composed almost entirely of fragments of rocks of the same lithology as the fine-grained sediments in the section (Plate IX, fig. 1). The second type consists of an abundant fine-grained matrix including rounded cobbles and boulders of andesite and siltstone blocks up to a foot or so in diameter. The third kind, composed of angular blocks of intermediate lavas occurs sporadically in the lower part of the type section but is abundant in the upper part. About the middle of the sequence (about 2½ miles east of Sofala) there is a chert horizon several hundred feet thick which extends north and south of the Turon River for several miles.

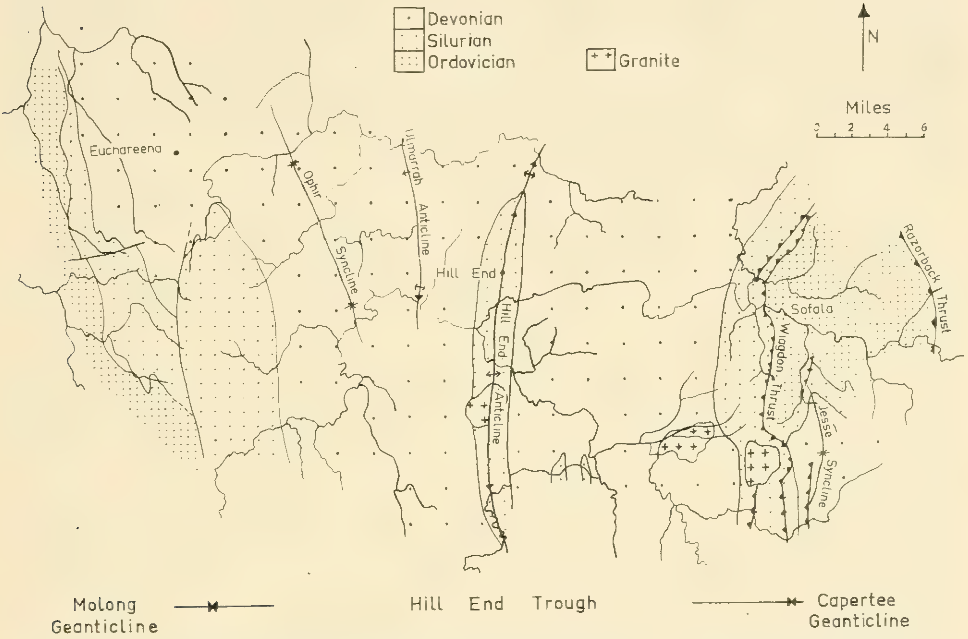


Figure 1. General regional map showing distributions of Ordovician, Silurian and Devonian Systems and major structures and tectonic units mentioned in the text.

The upper part of the formation consists almost entirely of tuffs, abundant andesite breccia and some andesites. West of Sofala these are transgressed by dykes and other minor intrusions of rocks of lamprophyre affinities, apparently basic differentiates of the andesites. The increase in the coarseness of the volcanics and the presence of the related intrusives suggest that the vent (or vents) responsible for the deposition of the upper part of the section may have been close at hand.

Regional distribution and variation. In the upper part of the sequence, limestone blocks occur in breccias in Big Oaky Creek just east of Wattle Flat, and a limestone lens occurs one and a half miles north-north-west of Wattle Flat. The limestones may have resulted from the rapid building up of volcanic debris in the upper part of the section. Apart from this, the formation maintains the general characteristics of the type section throughout its outcrop.

Except in close proximity to the Wiagdon Thrust where cleavage is developed, the rocks of the Sofala Volcanics are massive and indurated. Even the fine-grained sediments have little tendency to split along bedding planes. Small movements along joints are observable in almost every outcrop.

Petrography. Apparently most of the lavas of the Sofala Volcanics were originally andesitic. They contain phenocrysts of plagioclase, augite and/or hornblende. Occasional lavas have groundmasses containing small plagioclase laths but in most the groundmass is very fine and even grained. These latter may have been originally glassy. The plagioclase in all the thin-sections which were examined is albite. The ferromagnesian minerals are fresh in most rocks, except in the area north-west of Sofala. Two types of hornblende occur in the relatively unaltered rocks; green hornblende with a pleochroic scheme, Z = olive green, Y = yellow green, and X = pale yellow with $Z \wedge C$ about 24° and brown with $Z \wedge C$ about 18°. The green amphibole often shows signs of resorption and the brown amphibole occasionally contains inclusions of pyroxene. The pyroxenes are pale green in thin section and have a moderate 2V and an extinction of about 45°.

The lamprophyres which occur to the west of Sofala are petrographically very similar to the andesites except for the absence of felspar phenocrysts. An almost identical association has been described from the Wellington District by Basnett (1942). The Sofala lamprophyres are amphibole-rich, but at least some of this replaces pyroxenes as is evidenced by the typical pyroxene form of some of the amphibole crystals and the presence of rare irregularly shaped cores of pyroxene. The replacing mineral has a $Z \wedge C$ of 20° and X = colourless, Y and Z = pale green. This mineral also replaces darker amphibole in which X = yellow, Y = brown and Z = brownish green and $Z \wedge C$ is about 27°. The groundmasses of these rocks are highly altered, now consisting of albite, pale green amphibole and epidote with calcite abundant in some.

The volcanic breccias are composed almost entirely of fragments of various types of andesites. There is no sign of rounding even in the larger fragments. The matrix consists of small rock fragments and grains of felspar and pyroxene. Near the top of the succession where there is considerable alteration, it is not clear whether those rocks containing angular blocks up to several inches across are actually lavas including fragments of andesite similar to those described by Basnett and Colditz (1946) from rocks of comparable age at Wellington, or whether they are actually breccias. The presence of numbers of clastic fragments in some localities suggests an original sedimentary origin for the rocks. The matrix in which the fragments now occur is composed of an interlocking mass of albite, epidote and pale green amphibole. In the lower part of the sequence, relatively unrecrystallized breccias consist of fragments of lavas (generally a variety of types), pale green pyroxene a little felspar (albite) in a matrix of chlorite, calcite and epidote.

Like the breccias, the rocks of intermediate grainsize consist almost entirely of volcanic material. Except in the upper part of the formation where the bedding is obscure, the sandy sediments are greywackes. They are poorly sorted. Felspar (albite) is the dominant mineral, the grains are either idiomorphic or broken crystal fragments. Green and brown hornblende and augite are present. A little quartz occurs, this shows signs of magmatic corrosion and is hence probably volcanic in origin. Rock fragments are rare, those present are grains of the groundmass of andesite. The matrix, which usually comprises some 20 percent of the rock, is composed of chlorite, albite and a little calcite.

The finer grained rocks have a mineralogy similar to that of the arenites. The finest of these sediments are chert-like in hand specimen and are difficult to distinguish from the occasional radiolarian cherts which occur throughout the sequence. The radiolarian rocks themselves, consist of poorly preserved radiolaria, making up roughly 10 percent of the rock, in a fine-grained groundmass of material showing weak double refraction and a refractive index higher than canada balsam—presumably quartz. Large numbers of minute black granules, possibly carbonaceous, and a few percent of albite and chlorite grains of silt size are scattered through the fine groundmass of the radiolarian rocks. Several series of quartz veins must have been deposited soon after deposition of the sediment since where fragments of the radiolarian rocks are incorporated in intraformational breccias, they sometimes contain quartz veins predating their incorporation (Plate IX, fig. 1). If the fragments were derived from older formations it is most unlikely that in such a sediment all the fragments would be angular and of precisely the same lithology as the finer sediments in the Sofala Volcanics. Deformation seen in some of the early formed veins in the radiolarian rocks is probably the result of the continuation of compaction of the sediment after the formation of veins.

Depositional environment and direction of origin. The association of sedimentary structures in the lower part of the Sofala Volcanics is as follows: graded-bedding, convolute-bedding and slump structures. Cross bedding is absent. This association together with the presence of graptolites and radiolarian cherts suggests a deep water environment of deposition.

The beds of coarse sediment with rounded andesitic cobbles and boulders with a large proportion of matrix are not simple pyroclastic sediments. The rounding of the andesite cobbles indicates some transportation before final deposition. Slumping or some form of mass movement seems to be the only way to explain the association of these sediments with what are almost certainly deep water sediments. Contemporaneous movements have resulted in the breaking up of some of the fine-grained sediments of the sequence resulting in breccias composed almost entirely of fragments of those rocks.

Towards the top of the formation the appearance of limestone in blocks and lenses suggests that there was some shallowing which may be due to orogenic movement, local volcanic accumulation or filling of the entire basin.

Slump structures observed in the type section, a short distance upstream from Eaglehawk Gully indicate movement from west to east. Thus an easterly sloping sea floor can be inferred.

Age. Poorly preserved graptolites have been found about the middle of the Sofala Volcanics in Eaglehawk Gully. The graptolites appear to be *Glyptograptus teretiusculus* which is found in uppermost Darriwillian and Gisbornian strata. If this identification can be relied upon, then it is probable that much of the Ordovician is represented by the volcanics since the graptolites occur a little below the middle of the exposed section of the formation. The top of the formation pre-dates the Tanwarra Shale, the age of which, from the contained graptolites and other lines of evidence, is probably Upper Llandovery or early Wenlock. The upper possible limit of the Sofala Volcanics is within the Lower Silurian.

Tanwarra Shale

This formation rests, with a slight break, on top of the Sofala Volcanics. The junction of the two formations is obscured in many localities by overthrust faulting on the Wiagdon Thrust. The base of the Tanwarra Shale is marked by a conglomerate or sandstone resting on top of the Sofala Volcanics.

This basal member is composed almost entirely of material derived from the erosion of the andesites, together with some fossil detritus.

Type section. The type section of the formation is in Portion 516 of the Parish of Sofala, in the headwaters of Spring Creek and Bell's Creek, south of Mount Tanwarra after which the formation is named. This section is 250 feet thick. The basal conglomerate is of the order of forty feet in thickness and contains limestone pebbles with "*Halysites*" in addition to andesitic detritus. Above, is an impure limestone about twenty feet thick. This limestone consists of alternating bands of fossil material and sandy calcareous shale. The larger coral fossils are preserved in their living environment or have been transported only a short distance. The fauna is as follows: *Phaulactis shearsbyi*, *Mucophyllum liliiforme*, *Heliolites daintreei*, *Acanthohalysites* cf. *gamboolicus*, *Alveolites* sp., *Atrypa* sp., cf. *Barrandina* sp. and *Encrinurus* sp. Above this horizon there are a few feet of shales and sandy shales. The shales which make up the remainder of the formation are green, grey and black in colour, all are poorly bedded and contain occasional fossil remains, mostly poorly preserved small brachiopods. Ten feet above the limestone there are sparse graptolite remains. The forms present are: *Monograptus* cf. *paradoxus* and *M. priodon.*

The top of the formation is recognised by the appearance of bands of acid tuff marking the beginning of the Bell's Creek Volcanics.

Regional distribution and variation. North of the type section, the formation is considerably sheared. The stratigraphy of the formation in this area is not clear. It is possible that north of the Turon River some of the rocks mapped as Tanwarra Shale may actually be Chesleigh subgreywacke. The sediments are rolled out to such an extent that in many exposures bedding has been completely destroyed and replaced by a crude alternation of silty and shaly material parallel to the cleavage.

To the south of the type section there is a small outcrop of fossiliferous marl a mile to the west of the top of Wiagdon Hill which may be a southwards continuation of the formation; from this *Encrinurus* sp. was collected. At Wiagdon Hill on the Bathurst Road, the formation is represented only by a thin limestone and some shales; this is on the overthrust side of the Wiagdon Thrust. In the creeks to the south-east along the strike the formation is missing, apparently faulted out. Underlying the Bell's Creek Volcanics three miles south of Wiagdon Hill there is a sequence of shales representing a continuation of the Tanwarra Shale.

There is only one known occurrence of the Tanwarra Shale on the eastern side of the fault. This is in the head of the Spring Creek in Portion 245 of the Parish of Sofala near the western border of Portion 253, three and a quarter miles east of Wattle Flat. The succession is similar to that of the type section four and a half miles to the west, except that graptolites have not been found at this second locality. The fauna includes: cf. *Phaulactis shearsbyi*, *Mucophyllum crateroides*, *Tryplasma* sp., *Spirinella caecistriata* and *Encrinurus* sp. Fossils are considerably more abundant and better preserved than in the type section.

In the sections east of the Wiagdon Thrust where the Tanwarra Shale is absent the Sofala Volcanics are followed by a breccia composed of andesitic detritus. This is succeeded by the Chesleigh Formation without the intervention of the Bell's Creek Volcanics.

Age. The age of the formation is clearly Silurian. If the *Monograptus* cf. *paradoxus* is in fact *M. paradoxus* then the age is almost certainly Upper Llandovery; if not, then the age could be anywhere from the base of the

Upper Llandovery to half way up the Wenlock. The presence of "*Halysites*" in the shelly fauna is also in agreement with an age in the lower half of the Silurian.

BELL'S CREEK VOLCANICS

The Bell's Creek Volcanics is a succession of rhyolitic tuffs and lavas which conformably overlies the Tanwarra Shale. The formation varies considerably in thickness along the strike and is confined to the western side of the Wiagdon Thrust.

Type section. The type section, 1,500 feet thick, is exposed in the valleys of Bell's Creek and Jew's Creek, two miles south-west of Sofala. This is the maximum thickness known for the formation. The basal part consists dominantly of tuffs, succeeded by rhyolite and then by another tuffaceous unit. Overlying is the Chesleigh Formation, the lower part of which is non-volcanic. The lavas of the Bell's Creek Volcanics form a high ridge to the west of Bell's Creek while the underlying tuffs and a dolerite sill occupy the floor and the eastern side of the valley. The tuffs at the top of the formation occupy the small valley of Middle Creek to the west of the ridge of rhyolites.

Regional distribution and variation. North of the Turon River the formation is considerably diminished in width as a result of thrust faulting. It is possible that the contact between the Bell's Creek Volcanics and the Tanwarra Shale north of the Turon River might be a tectonic one.

The Bell's Creek Volcanics outcrop in the Wiagdon Hill road section as tuffs, slates and chert-like rocks. Half mile to the south-east very poorly preserved graptolites occur in a cherty shale in the formation. They are straight monograptids but no further identification is possible. Further south in the vicinity of Cheshire's Creek, lavas are once more abundant. The volcanics can be traced for eighteen miles along the strike but to the east of the Wiagdon Thrust the formation is unknown. This is unexpected in view of the considerable extension of the volcanics along the strike and it is the first indication of a significantly different stratigraphic succession on either side of the thrust.

Petrography. The rhyolites are pale green or buff coloured rocks with a subconchoidal fracture. Flow-banding is only rarely visible in hand specimen. In thin section these rocks have either a uniform groundmass or irregular flow structure. Phenocrysts, which are not abundant, are dominantly quartz and orthoclase, with minor amounts of albite (about Ab_{95}). Idiomorphic phenocrysts are rare, mostly they are corroded or fractured. Ferromagnesian minerals, present in only small quantities, are confined to the groundmass. They are either biotite, pleochroic from yellow to very dark brown, or chlorite, which is apparently the alteration product of the biotite. Epidote and clinozoisite are present in some rocks occurring as small individual crystals scattered through the rock and as aggregates up to 1 mm. across. The lavas are cut by quartz veins some of which also contain clinozoisite or epidote. The groundmass shows a good deal of textural variation even within the one section; it varies from a very fine-grained to a coarse-grained mosaic of interlocking quartz and felspar grains.

The tuffaceous lithologies in the formation range from coarse breccias to extremely fine-grained rocks with a flinty appearance. Their mineralogy is similar to that of the rhyolites with which they are associated. The medium-grained tuffs are composed of broken quartz and felspar grains, biotite and devitrified glass shards, together with a little apatite. The finer tuffs are banded with some evidence of graded-bedding on a small scale. The extremely fine-grained tuffs are generally pale green flinty rocks, without bedding in hand specimen or with broadly developed irregular banding. In thin-section these are seen to consist of an interlocking mass of quartz and felspar with some calcite, chlorite and epidote.

Chesleigh Formation

The Chesleigh Formation takes its name from the property "Chesleigh" (three miles west of Sofala) on which it outcrops as a prominent strike ridge and conformably overlies the Bell's Creek Volcanics. It is non-volcanic in the lower part of its section, thus the base can be defined as the top of the last tuff horizon.

Type section. The formation is 3,500 feet thick in this section which is that exposed along the Turon River in Portions 48, 47 and the eastern part of Portion 46 of the Parish of Waterbeach. The lowest unit, a massive subgreywacke, 2,000 feet thick, outcrops on the south bank of the Turon River and forms a large cliff in which bedding is poorly defined. Overlying this is 500 feet of interbedded slate and subgreywacke. The beds vary from a few inches to ten feet in thickness. In the top thousand feet of the formation, the amount of felspar increases, subgreywackes pass into greywackes and there are some interbedded crystal tuff horizons in which the beds are up to twenty feet thick. The uppermost beds are thinly bedded fine-grained felspathic siltstones and slates. These siltstones which are green and red are followed by the first of the quartz-rich sediments of the Cookman Formation.

Regional distribution and variation. In spite of the large size of outcrops along the Turon River, there is very little fresh rock exposed in the type section. Two miles to the north, on Two Mile Creek, the bedding characteristics of the lower massive subgreywacke can be seen. Bedding planes are spaced six to eight inches apart and each bed is to some extent graded. The clarity of this grading is obscured by the small size range—from fine sandstone to siltstone. The bedding features are further obscured as a result of tectonic movement which has taken place within the formation. This movement is particularly evident on the banks of Crudine Creek between Two Mile Creek and the Turon River, where slaty cleavage is strongly developed in interbedded slates and subgreywacke. To the south of the type section, the subgreywacke lithology is dominant and the upper tuffaceous part of the formation consists only of slates and fine tuffs with a cherty appearance.

The Chesleigh Formation occurs on the eastern side of the Wiagdon Thrust with lithology and thickness similar to those of the type section, but differing in that cherty rocks are common in the upper part of the formation. In this region, the Chesleigh Formation rests directly on the Sofala Volcanics except in the headwaters of Spring Creek where the Tanwarra Shale occurs. The contact between the Tanwarra Shale and the Chesleigh Formation in this area has not been observed.

The absence of the Bell's Creek Volcanics and the restriction of the Tanwarra Shale on the eastern side of the Wiagdon Thrust, suggests that the base of the Chesleigh Formation in that area is an erosional surface. The extension of the missing formations along the strike is such that they might be expected to continue across the strike as well. However, it has been already pointed out that the Bell's Creek Volcanics vary considerably from place to place. Similarly, since the Tanwarra Shale was, at least in part, laid down in a shallow water environment, it may perhaps have not been deposited in some localities. Breccia composed of andesitic material underlying the Chesleigh Formation east of Wattle Flat, mapped as part of the Sofala Volcanics, might be the time equivalent of the Tanwarra Shale. Even if there is no erosional break below the Chesleigh Formation, the significant feature is that the Wiagdon Thrust brings into juxtaposition two significantly different stratigraphic sequences. Differences between the sections on either side of the thrust are maintained in most of the formations overlying the Chesleigh Formation.

Petrography. In the type section the subgreywacke (Plate IX, fig. 2) which makes up the lower part of the formation contains fifty to seventy percent of quartz. Most of the grains show some sign of rounding, though this is more evident in the largest grains (0·5 mm.). The sorting is poor, all gradations exist between the largest grains and the finest material constituting the matrix. This matrix makes up twenty percent or more of the rock. Apart from quartz silt, the matrix is composed of chlorite and pale green, weakly pleochroic mica. A small proportion of rock fragments is present; these fragments are of two types. Firstly, shales consisting of a fine-grained aggregate of quartz, chlorite and sericite and in some cases a little carbonate. Secondly, there are fragments composed of interlocking quartz grains with small amounts of chlorite either included in the grains or concentrated in their margins. These latter rock fragments are probably fragments of thermally metamorphosed sediments. Felspar is absent. In the matrix there are occasional grains of muscovite. The heavy mineral assemblage is varied and includes: tourmaline (variety of shapes, sizes and colours), zircon, sphene, apatite and rutile.

In the upper part of the formation, the rocks which have been called greywackes differ from the underlying subgreywackes only in the addition of felspar and a corresponding decrease in the percentage of quartz. Orthoclase is more abundant than plagioclase (albite).

The tuffs of the Chesleigh Formation are massive with grainsizes ranging from fine sand to breccias. Their interpretation in thin-section is difficult. There is a good deal of secondary albite in the matrix and replacing orthoclase, as well as in veins. Quartz and carbonate are the abundant secondary minerals in some specimens while in others the assemblage is albite, quartz and epidote. The detrital minerals are quartz, orthoclase, plagioclase (now albite) and chlorite. In some of the coarser rocks fragments of acid porphyritic rocks occur.

The lithology of the formation on the eastern side of the Wiagdon Thrust is very similar to that of the type section. Some of the subgreywackes however, contain a small proportion of felspar (orthoclase and albite), and have a greenish colour in hand specimen instead of the normal grey colour. The variation of colour is attributable to the presence of additional chlorite.

Depositional environment and origin of the detritus. A variety of sedimentary structures indicative of a deep-water depositional environment, are present in the Chesleigh Formation. They include graded bedding, load casts (Plate IX, fig. 8), small slumps, small-scale cross-bedding, and flute-casts. The last three structures have yielded evidence indicating the direction of slope of the seafloor at the time of deposition.

Small-scale slump structures occur near the top of the Chesleigh Formation in the type section and in Dam Creek, in fine-grained siltstone beds four to eight inches thick. The direction of movement which has been determined by measuring the inclination of a number of slump fold axes in each locality, is consistently towards the east-north-east.

A similar direction of movement is indicated by flute-casts beautifully exposed on the bases of overturned beds two miles north of Cheshire's Creek and a locality on Cheshire's Creek half a mile east of the Wattle Flat–Peel road. At the first locality the direction of movement is corroborated by the dip of small-scale cross-bedding in a similar direction.

The detritus in the lower part of the formation is apparently first or second cycle detritus derived from a granitic terrain. The low proportion of felspar and the presence of sedimentary rock fragments suggest the former rather than the latter. It is known that there were folding movements in the Tasman Geosyncline (the Benambran Orogeny) roughly at the end of the Ordovician Period and continuing into the Silurian (see Packham, 1967*a*). The Ordovician sediments exposed in the southern highlands of New South Wales by these movements were slates, shales and subgreywackes which were derived from granitic rocks directly or indirectly forming an ideal source for the detritus for the Chesleigh Formation.

In the upper part of the Chesleigh Formation acid volcanic material is common but detritus of the type which makes up the lower part of the formation is still present.

Fauna. No fossils have been found in this formation.

COOKMAN FORMATION

The Cookman Formation which consists of quartz-rich greywackes, occasional grits and conglomerates interbedded with slates overlies the Chesleigh Formation. Its base is recognized by the first appearance of the characteristic light-coloured quartzite-like subgreywacke and sublabile greywacke.

Type section. The type section of the Cookman Formation, one thousand five hundred feet thick, is in the eastern half of Portion 46 of the Parish of Waterbeach on the south bank of the Turon River immediately west of the type section of the Chesleigh Formation. The formation takes its name from the Cookman Range which is the strike ridge that the formation makes to the north of the Turon River. The type section consists dominantly of slates with interbedded fine-to-medium-grained sandstones and only a few beds of coarse sandstones and conglomerates. Most of the sandy beds, several inches to a foot thick, display no obvious internal structure, but the beds of the order of three feet thick are graded-bedded. Frequently, casts of worm-tracks appear on the under surfaces of the sandy beds. At the top of the formation there is a thick slate which is overlain by the lowest coarse-grained beds of the Crudine Group.

Regional distribution and variation. The Cookman Formation maintains the features of the type section along its strike. It can also be recognized east of the Wiagdon Thrust overlying the Chesleigh Formation. In Cheshire's Creek in the southern part of Portion 119 (Parish of Wiagdon), the formation is similar in lithology to the type section but only six hundred feet thick. It can be traced north from Cheshire's Creek for some distance but is lost in the area of poor outcrops south-east of Wattle Flat.

Petrography. The typical quartz-rich medium-grained arenite (grains up to 0·6 mm.) is moderately sorted with only a small percentage of matrix (Plate IX, fig. 4). The quartz grains vary from rounded to angular. Identifiable mineral inclusions are rare, though rutile, apatite and yellow tourmaline have been observed. Flakes of muscovite up to half a millimetre long are scattered through the rock. The matrix is composed of quartz silt with white mica and some chlorite. In the heavy mineral assemblage zircon is the most abundant mineral, both idiomorphic and rounded grains of comparable size are present; the rounded ones are far more abundant. Grey-green, brown and blue tourmalines have been noted; almost all show signs of rounding. Occasional grains of rutile occur. The most significant, yet least abundant mineral present in the heavy mineral assemblage is hornblende, pleochroic from yellow-green to grass-green. The finer-grained sandstones have a smaller percentage of felspar than the medium-grained ones and the sorting is better; the number of large grains is reduced with decreasing grain-size though the percentage of matrix remains much the same. The coarser sediments are more varied in their features. Micrometric analyses of some of the rocks of the formation are given in Table 1. Felspar and rock fragments become increasingly abundant in the coarser rocks. Both orthoclase and plagioclase (albite) are present; occasionally the plagioclase crystals have rows of inclusions arranged in zones indicating that there were once composition differences within the crystals. Some orthoclase is partially replaced by albite. The rock fragments are mostly finegrained, dominantly fragments of the groundmasses of acid porphyritic rocks. Occasional large aggregates of quartz and felspar are present, possibly derived from granitic rocks. Rare detrital grains of microcline endorse this view. A little detrital carbonate is present both as crystalline rock fragments and as patches in the matrices of these coarser sediments.

TABLE 1

Micrometric analyses of Arenites from the Cookman Formation

	A	B	C	D
Quartz	81	60	49	30
Rock fragments	8	6	3	39
Muscovite	1	—	—	—
Chlorite grains	1	—	—	—
Felspar (Or and Ab)	1	8	2	5
Sericite-quartz matrix	10	26	46	18
Calcite	—	—	—	8

A. S 387. Maximum grain-size 0·6 mm. One mile south of type section.
B. TS 109. Maximum grain-size 1·5 mm. Type section.
C. TS 110. Maximum grain-size 3 mm. Type section.
D. TS 118. Maximum grain-size 5 mm. Type section.

The slates of this formation are composed of white mica, chlorite, and variable proportions of quartz silt. The abundance of mica is responsible for their pale grey colour in hand specimen.

Depositional environment and source of the sediment. East of the Wiagdon Thrust flute casts are well exposed on the bases of the overturned beds. The lobes of the flute-casts are narrower and less rounded than those in the Chesleigh Formation. Good exposures of these structures which are found on Cheshire's Creek and three miles north of it, indicate a direction of flow a little south of east. This is the opposite to that in the Chesleigh Formation. Thus, the change in direction of slope of the sea-floor implies the uplift of an area to the east. This eastern land mass incidentally, had an extremely important role in the later history of the region. The petrography of the Cookman Formation suggests that a variety of rocks were eroded off this newly exposed area, including acid volcanics (indicated by rock fragments and corroded quartzes), sediments which were quartz-rich (rounded quartzes, heavy mineral assemblage with abundant rounded zircon and less abundant rounded tourmaline), possibly granite (microcline, quartz-felspar aggregates and possibly idiomorphic zircons) and basic igneous rocks (amphibole in the heavy mineral assemblage). All of these source rocks can be accounted for in the underlying formations except for the possible granite. The material derived from the acid volcanics may have come from the erosion of the volcanics at the top of the Chesleigh Formation or the Bell's Creek Volcanics. The sediments which gave rise to the majority of the heavy mineral assemblage belonged, in all probability, to the Chesleigh Formation which would in addition, have provided the greater part of the quartz of the Cookman Formation.

The increase in the proportion of unstable rock and mineral fragments in the coarser fractions of the sediments of the Cookman Formation may be explained by considering the weathering characteristics of the suggested source rocks. The subgreywackes of the Chesleigh Formation which at this stage would be still unconsolidated, and therefore erode by disaggregation of the grains yielding small particles. The tuffs may erode by a similar process but the coarser types would give rise to the larger particles. The lavas would be eroded by the normal processes of weathering and abrasion and give rise to particles of a variety of sizes. Thus, if a sediment is composed of larger grains, then it must, of necessity, be derived from a source other than the subgreywackes of the Chesleigh Formation. The medium to fine-grained sediments of the Cookman Formation would, on the other hand, be composed dominantly of material derived from those subgreywackes. The presence of amphibole can be related to the Sofala Volcanics, mainly on the grounds that there are no other formations in the sequence known to contain amphibole. The location and age of the granite which was suggested as a possible contributor to the detritus is completely unknown.

The environment of deposition of the Cookman Formation seems to have been a deep-water one. There is some evidence of life on the sea-floor in the presence of worm tracks. The greater elongation of the flute casts in Cookman Formation suggests that the slope may have been greater in this area during the deposition of the Chesleigh Formation.

Age. No fauna has been found in this formation but fragmentary plant material was collected on the top of the high hill formed by the formation, three quarters of a mile south of the Turon River. These fragments are sometimes Y-shaped and are similar to some of the plant material found in the Silurian and Devonian in Victoria. Their age is certainly no older than early Ludlow.

CRUDINE GROUP

The Crudine Group is so called because much of the valley of Crudine Creek is cut into these sediments. There is a sharp change from the quartz-rich sediments of the Cookman Formation to the massive tuff and breccia at the base of the Crudine Group. The top of the group is the base of the very thick and massive Merrions Tuff. This is a distinctive boundary since the upper formation of the Crudine Group is one which consists of greywackes and slates and contains no tuff horizons.

The Crudine Group is several thousand feet thick and contains a variety of rock types, all typical of eugeosynclinal sedimentary associations; pyroclastics which range from coarse breccias, down to fine-grained chert-like tuffs and the normal clastic sediments which include breccias, conglomerates, sands, silts and muds all of the greywacke suite, but no chemical and organic sediments. It is difficult to distinguish between tuffaceous rocks and greywackes in some instances because the dominant source of the sediments is volcanic.

Type section. The group consists of two formations; the Turondale Formation below and the Waterbeach Formations above. The aggregate thickness of the type sections of the two formations is 3,700 feet.

a. Turondale Formation. The type section of this formation, which takes its name from the nearby village of Turondale, is on the south bank of the Turon River in Portion 46 of the Parish of Waterbeach overlying the type section of the Cookman Formation. The Turondale Formation is 2,020 feet in this section and consists of three units (Figure 2).

The lowest division of the formation, 830 feet thick, is composed almost entirely of tuffaceous material. Only 120 feet are not derived directly from volcanic sources, these are slates and fine-grained sandstones. The basal bed of the formation is a coarse conglomerate in which the matrix is at first fine-grained and makes up a large proportion of the rock but towards the top of the bed the amount of matrix decreases to about half of the rock and becomes sandy. The pebbles in the conglomerate are mainly of acid volcanic rocks with some of limestone, shale and tuff. Limestone pebbles and boulders are more abundant in the lower part of the bed. Angular shale blocks contemporaneously derived, are often very large; the largest seen had exposed dimensions of ten feet by three feet. The conglomerate passes upwards into volcanic breccia. This breccia and the succeeding tuff, which are typical of the tuffaceous sediments in the Crudine Group and the Merrions

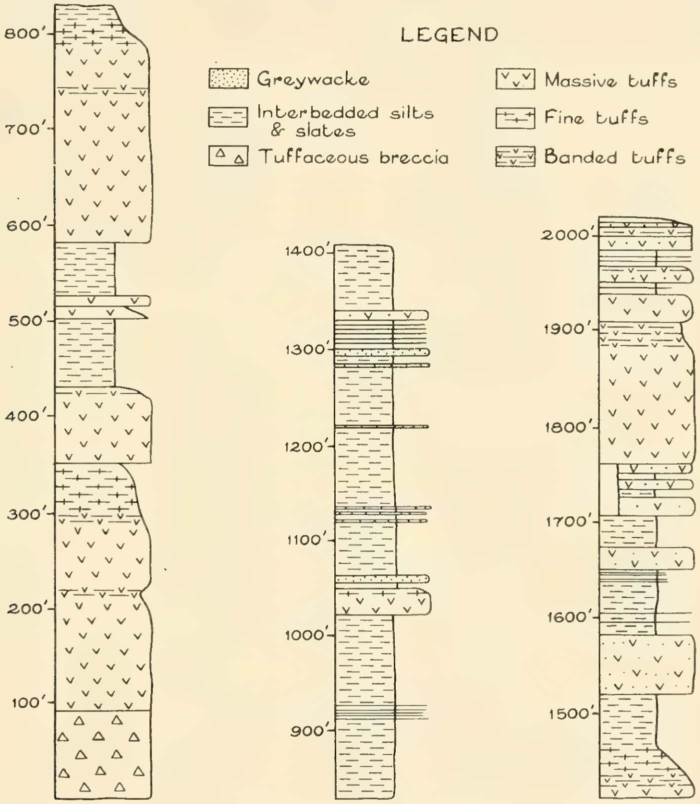


Figure 2. Type section of the Turondale Formation measured on the south bank of the Turon River in Por. 46, Parish Waterbeach. Greywacke beds less than 2 feet thick are shown as thin horizontal lines.

Tuff, consist of quartz, felspar, chlorite and epidote. They are hard and massive, pale green rocks with only poorly developed bedding planes with beds of the order of tens of feet thick (Figures 2, 6, 8). Graded bedding is commonly developed over the entire thickness of the bed. The coarser phases often contain a small percentage of shale fragments and rounded felsite pebbles but most of the fragments are irregular, flattened chloritic bodies. These latter generally have inclusions of quartz and felspar, which are often embayed. Epidote and zircon are also present (Plate IX, fig. 3). The constant appearance of these bodies in sediments rich in volcanic debris in the region suggests that they have a volcanic origin. A possible explanation is that they were originally angular glassy fragments which have been subsequently converted to chlorite, possibly having passed through an intermediate stage of palagonite. This type of phenomenon has been described by Tyrrell and Peacock (1926) and Raw (1943). Other products of this process were, in all probability, subsequently converted to epidote. The very fine-grained rocks at the top of this basal bed have ill-defined bedding and a conchoidal fracture and are often translucent on the thin edges of fresh specimens. Their colour ranges from pale green through greenish-grey to dark grey. Sometimes they have spots several millimetres in diameter scattered through them in indefinite bands; these are apparently the result of local concentrations of chlorite and epidote. Above these tuffaceous sediments there are interbedded fine-grained greywackes and slates which are followed by more massive tuffaceous rocks.

The second unit, 580 feet thick, is dominantly slate and silt with bands of greywacke and a few tuffaceous beds. The tendency of these greywacke beds to occur in groups is a striking feature which is repeated at higher levels in the Waterbeach Formation and, to a lesser extent, in the Cunningham Formation. The greywacke beds differ in appearance from the tuffaceous beds below in a number of ways. The greywackes are thinner, mostly one to three feet thick, but ranging from several inches to ten feet. Shale pebbles are the most common of the larger rock fragments. Graded bedding is common but by no means universal. When present there is a gradation from greywacke to shale, whereas the tuffs, as described above, grade into cherty rocks. The slates interbedded with the greywackes are in units several inches thick, the bedding being marked by a thin silt band which occasionally shows suggestions of small-scale cross-bedding and graded bedding.

The upper part of the Turondale Formation, 610 feet thick in the type section, contains a proportion of tuffaceous material which is reminiscent of the lower part of the Turondale Formation, but the thicknesses of the beds are closer to those of the middle unit. In hand specimen, these rocks are seen to contain few rock fragments, chloritic patches are rare and so are shale fragments. There is little indication of graded bedding, where present the gradation is into shale in some beds and cherty rocks in others. In the fine to medium sand size-range some beds have alternating pale green and dark green bands, one to three inches thick, resulting from variation of the proportion of chlorite in the rock.

b. Waterbeach Formation. This formation takes its name from the parish in which the type section is defined. This section, 1,690 feet thick, is on the south bank of the Turon River in Portions 69, 74 and 49, a little over a mile west of the type section of the Turondale Formation. In the Waterbeach Formation, shaly rocks are far more abundant than sandy ones and tuffaceous rocks are absent. The base of the formation is the top of the last tuffaceous band of the Turondale Formation. There is a marked change in the characteristics of the sedimentation at this point. The greywackes are in distinct groups at 300, 800, 1,100 and 1,300 feet above the base of the formation. With the exception of shale pebble bands which occasionally occur at the bases of the thicker greywackes, conglomeratic rocks are absent from the section. A generalized stratigraphic column is given in Figure 3.

The sandy zones may represent times of greater local tectonic activity which aided erosion and hence provided coarser detritus, or alternatively, the control could be purely climatic, since periods of greater rainfall would have the same effect. Eustatic changes provide a third possible mechanism.

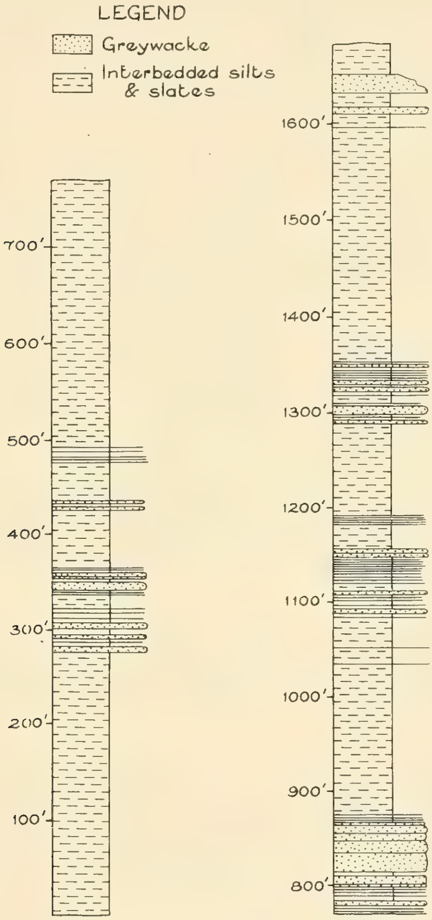


Figure 3. Type section of the Waterbeach Formation measured on the south bank of the Turon River in Portions 41, 74 and 69, Parish Waterbeach. Greywacke beds less than 2 feet thick are shown as thin horizontal lines.

It is unlikely that they represent volcanic outburts because there are no tuff horizons associated with them. Further, the petrography of the sediments indicates that material has been only partly derived from a volcanic source.

The majority of beds of greywacke and siltstones (over four inches thick) are graded-bedded. Some of the thinner silt beds are graded-bedded, passing up gradually into the overlying slate. Others form overall graded units with oscillations of grainsize within the unit. Still others have no grading, they have distinct silt bands with irregular bedding, small scale cross-bedding, or cross bedded ripple marks. In all types the silts have sharp bases frequently infilling animal trails on the top of the underlying slate unit. The silty units are generally thinner than the slate between them, the distance from the base of one silt unit to the next varying from two to six inches (Plate x, fig. 1). The thinnest beds of greywackes are the most abundant and there is a progressive decline in the frequency of occurrence of beds with increasing thickness. The thickest bed observed has a thickness of twenty-four feet. In the composite graded beds which occur occasionally, there is no parting along the junction of the coarse greywacke with the underlying fine greywacke. Occasionally, the lower unit has been dragged up into the upper unit during the deposition of the latter. Most of the graded beds maintain almost the same grain-size over the lower three quarters of their thickness then decrease gradually in grain-size in the remainder of the bed. This upper part of the bed which is normally fine greywacke or siltstone, generally has bedding planes spaced about a quarter of an inch apart. Only very infrequently is there a gradation into slate. It is possible that the beds which have no graded bedding observable in the field are beds in which the upper finer grained part of the bed has not been deposited.

The greywackes often contain angular fragments of shales which have been derived, in all probability, from contemporaneously deposited sediments by the erosive action of sediment charged turbidity currents. Normally, shale fragments included in the greywackes are four to five inches long and an inch or so thick. The largest shale fragment observed in this formation has exposed dimensions of five feet long and five inches thick. It is in a greywacke bed only three and a half feet thick. Shale fragments are the only fragments coarser than sand size found in this section of the formation.

Groove casts, flute-casts and load-casts occur on the bases of some of the greywacke beds in this formation, but their frequency is difficult to determine because the bases of the beds are infrequently exposed. Only a few slumps have been observed in this section, all of them are in the thinly bedded slate-siltstone part of the sequence. Each slump involves a foot or less of strata.

Regional variation of the Crudine Group. The Turondale Formation changes its character both across and along the strike. The most important new feature is the appearance of conglomeratic phases in the upper unit. These conglomerates are found north and south of the type section but have their greatest development three to five miles south of the Turon River where they are several hundred feet thick. In this conglomerate there is at least 60 percent of medium-grained greywacke matrix keeping the pebbles well separated (Plate x, fig. 2). The pebbles are varied in type; they include quartzite, quartz porphyry, limestone and shaly rocks. Quartzite and quartz porphyry are rounded, their size varying from less than an inch to six to eight inches along their greatest diameter. The limestone and shale fragments have been deformed along with the matrix during the folding of the succession and as a result they are flattened into lenses in the cleavage plane. By far the largest block of limestone observed measures 80 feet by 30 feet; it occurs in Portion 45 of the Parish of Waterbeach. The occurrence of this block of pure limestone containing tabulate corals, in a coarse conglomerate and its general association with graded-bedded rocks, together with the absence of any other limestone lenses and the remains of shelly fossils from the associated sediments all support the contention that it is a derived block. It is most unlikely that large pebbles and cobbles were carried by a turbidity current; it is more likely that they were carried by a mud-flow, or deposited by sliding or slumping. Further south, conglomerates are less frequent. In spite of this variation the Turondale Formation is dominated throughout by detritus of volcanic origin. The Waterbeach Formation is more constant in its characters. The only significant change in features is that to the north of the type section commencing a mile from the Turon River, a thick greywacke unit containing some conglomeratic phases is developed near the base of the formation.

The section east of the Wiagdon Thrust. The section here is thinner (2,500 feet), the tuffaceous beds are more distinct, graded-bedding does occur (Plate x, fig. 3), but is not common. The coarser beds are better sorted than in the Turon River section. Further to the east, on the eastern limb of the Jesse Syncline near the top of the group, there are fragmentary brachiopods in mudstone; this is the only locality in the Crudine Group where invertebrate fossils other than those occurring in limestone boulders have been found. One horizon of coarse conglomerate consisting of large quartz porphyry cobbles in a matrix of sand derived from similar material is exposed on Cheshire's Creek.

Direction of source of the sediments. The lithological variation described above leads one to conclude that the sediments in the eastern side of the Wiagdon Thrust are closer to their source than the rocks to the west. This view is backed up by the evidence provided by the sedimentary structures which occur in the Crudine Group. In the type section of the Waterbeach Formation between 1,100 feet and 1,350 feet above the base of the formation, there are a number of structures, flute-casts and small-scale cross-bedded current-ripples, which indicate a direction of sediment flow towards a little north of west. Three and a half miles north of the type section near the top of the Waterbeach Formation and five miles south of the type section at much the same horizon there are occurrences of small-scale cross-bedding. The former indicates a direction of flow a little south of west and the latter towards the west. Similar structures occur high in the Crudine Group east of the Wiagdon Thrust one mile west of Limekilns Public School site. At this locality, the structures indicate a slope towards the west-north-west.

Thus, at all the localities where there is any evidence of slope of the sea-floor, the general direction of slope indicated is towards the west. So the same palaeogeographic conditions must have existed during the deposition of the Crudine Group as existed at the time when the Cookman Formation was deposited.

Petrography and mode of deposition of the sediments. The sediments of the Crudine Group have few constituents. The grains of sand and silt size are: quartz, felspar, igneous rock fragments and occasional grains of calcite. These are set in a matrix of chlorite and epidote with zircon, pyrite and apatite as minor constituents. Micrometric analyses of these rocks are set out in Tables 2 and 3.

The tuffaceous rocks of the Turondale Formation differ somewhat from the greywackes of the Waterbeach Formation. The greywackes contain a larger proportion of rock fragments, a larger proportion of quartz relative to felspar and a smaller proportion of epidote in the matrix. These differences are brought out in Figure 4. Figure 5 illustrates the general resemblances between the sediments. All these arenites fall into the field of labile greywackes (Packham, 1954) and are thus distinct from the sediments of the underlying Cookman Formation which fall into the fields of subgreywackes and sublabile greywackes.

The most striking difference between the formations is in the nature of the bedding. The frequency of occurrence of greywacke beds of a given thickness in the Waterbeach Formation is roughly inversely proportional to the thickness of the bed. The tuffaceous rocks of the Turondale Formation do not show this feature at all; if anything, the thicker beds are more common than the thinner ones. This is also true of the Merrions Tuff which overlies the Waterbeach Formation. Figure 6 illustrates this difference clearly.

The problem which now arises is that of determining the mode of deposition of the tuffs. The tuffaceous rocks have normal graded-bedded sediments overlying, underlying and interbedded with them, and it is difficult to maintain that emergence has taken place so that the tuffs could be deposited in shallow water. In any case the beds lack any characters which would positively distinguish them as shallow water sediments. The Merrions Tuff extends across the strike for twenty miles and a greater distance along the strike. Such a distribution is out of keeping with the sediments being simply the result of explosive volcanic activity. It is clearly impossible for material of sand size and larger to be hurled such distances. In any case, massive beds of the thickness found could not have been deposited by such a process.

TABLE 2

Micrometric analyses of Tuffaceous Arenites from the Turondale Formation

	A	B	C	D
Quartz	20	8	12	27
Felspar	34	32	31	27
Igneous rock fragments ..	9	6	2	8
Chlorite patches	6	—	3	2
Chlorite matrix	31	54	52	36

All specimens are from the type section of the formation.

A. TS 55. 250 feet above the base of the formation.
B. TS 48. 875 feet above the base of the formation.
C. TS 45. 1,300 feet above the base of the formation.
D. TS 39. 1,470 feet above the base of the formation.

TABLE 3

Micrometric analyses of Greywackes from the Waterbeach Formation

	A	B	C	D	E	F
Quartz	15	16	28	17	13	14
Felspar	21	12	9	19	17	4
Igneous rock fragments ..	23	30	27	20	30	37
Sedimentary rock fragments	—	1	4	2	—	4
Chlorite-silt matrix ..	41	41	32	42	40	41

All specimens are from the type section of the formation.

A. TS 34. 280 feet above the base of the formation.
B. TS 38. 440 feet above the base of the formation.
C. TS 24*a*. 1,100 feet above the base of the formation.
D. TS 20. 1,350 feet above the base of the formation.
E. TS 18. 1,350 feet above the base of the formation.
F. TS 16. 1,600 feet above the base of the formation.

Textural similarity of the tuffaceous rocks and the normal greywackes (Tables 2, 3; figs 4, 5; Plate IX; figs 5, 6, 7) and the negative arguments cited in the previous paragraph lead me to the conclusion that the tuffaceous rocks were deposited by the same sort of mechanism as the greywackes, i.e., by turbidity currents or as mudflows. A terrestrial mudflow, the Osceola mudflow, described by Crandell and Waldron (1956) has a number of features resembling the tuffaceous beds of the Turondale Formation and the Merrions Tuff. The Osceola mudflow has a maximum thickness of 350 feet where it has been restricted in a narrow gorge, but the thickness decreases to less than 20 feet on the plain below. The formation is coarsely graded-bedded (the concentration of boulders being much higher at the base than the top). The proportion of clay and silt in the sample analysed by Crandell and Waldron is 39·6 percent. This accords reasonably well with the results I have obtained for the sediments of the Turondale Formation and the Merrions Tuff (Tables 2, 4) where the range is from 31 to 54 percent. Apart from the greater proportion of boulders in the Osceola mudflow, its similarity to the tuffaceous rocks of the Turondale Formation and the Merrions Tuff is a close one. The lateral change of upper part of the Turondale Formation from tuffaceous rocks to greywacke conglomerate can be explained by assuming that the mudflow involved had not moved a great distance and that the variation of composition represents the influence of varied source materials.

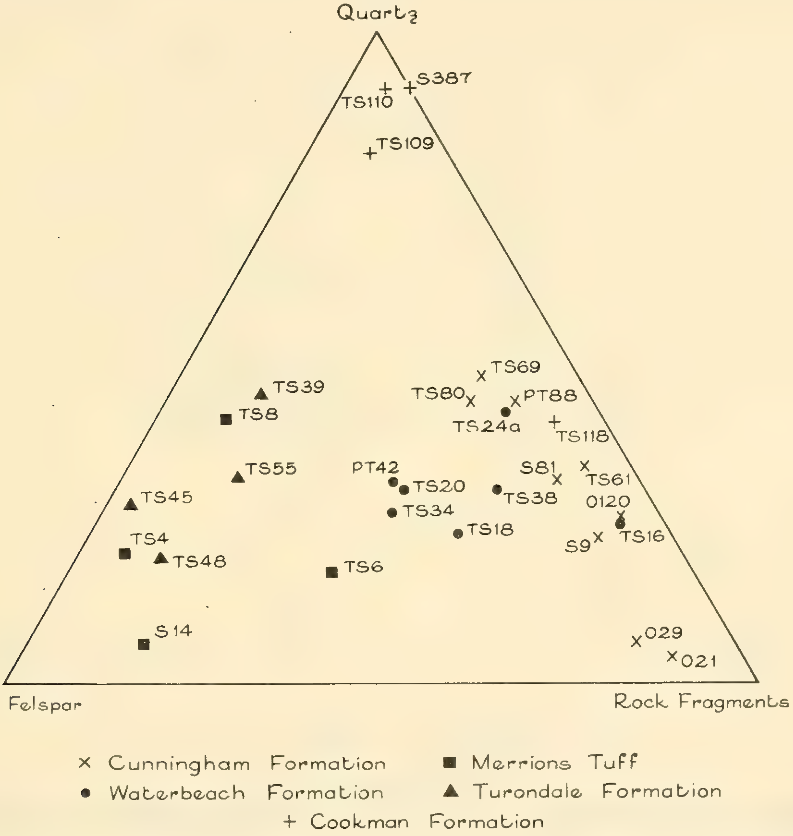


Figure 4. Plot of composition of the sand fractions of arenites listed in Tables 1–7.

If the tuffaceous sediments are, in fact, mudflows, then strictly speaking, it is not advisable to call such sediments "tuffs", because although they may have been intially deposited near a volcano, they were later transported to their present location. I have, however, retained the term "tuff" to distinguish these sediments from the greywackes which, though clearly derived from volcanic rocks for the most part, show no petrographic evidence that they were contemporaneous with the vulcanism.

If alternating intervals of vulcanism and quiescence are postulated, the differences between the two types of sediment may be explained. During the volcanic episodes, large amounts of detritus of sand grade were made available, hence there is a preponderance of sandy detritus over finer material. In the quiescent episode normal erosion of the terrain took place yielding large amounts of silt and clay. Weathering of felspar in this terrain was probably responsible for the increase of the quartz relative to felspar in the Waterbeach Formation. Erosion of lavas extruded in the vicinity of the vents could explain the larger proportion of rock fragments.

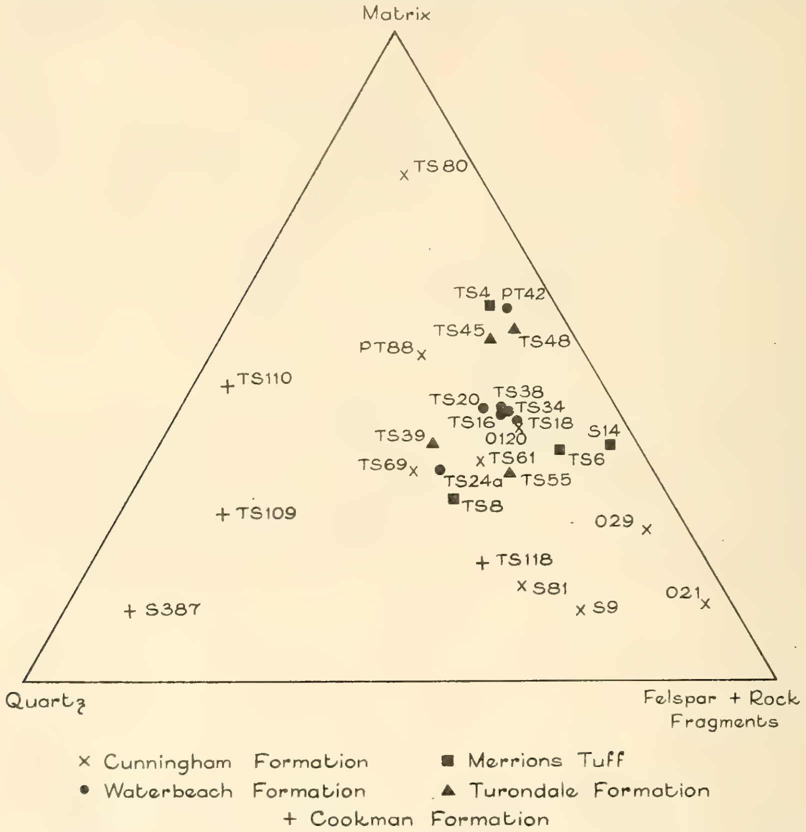


Figure 5. Plot of composition of the sand fractions of arenites listed in Tables 1–7.

Comparison of the frequency of occurrence of beds in this succession with those obtained by Potter and Siever (1955), for the Lower Pennsylvanian and Upper Chester sandstones (orthoquartzites) in Illinois (Figure 7), clearly brings out the difference between deep-water geosynclinal deposition and shallow-water deposition. In the geosynclinal environment the frequency of the beds in the one to four feet class is very high (70 percent) and drops rapidly, while in the shallow water environment the frequency of sandstones rises to a maximum of 20 percent in the four to eight feet class, and then falls slowly with increasing thickness.

The quartz grains in the tuffaceous sediments in the Turondale Formation are mostly angular but occasional grains have bipyramidal form, generally with slightly rounded angles. Corrosion embayments are common and are filled with fine grained material which constituted the groundmass of a lava or filled with chlorite. The largest quartz grains are two millimetres in diameter and it is these which are most frequently bipyramidal and embayed. Plagioclase (about Ab_{95}) is more abundant than orthoclase. The grains of albite are always cloudy occasionally with inclusion of epidote and almost always surrounded by epidote which has developed in the chlorite matrix. The albite grains have the same maximum grainsize as the quartz grains and, like them, sometimes have corrosion embayments filled with chlorite. The albite grains are more often idiomorphic than the quartz grains. The morphological characteristics of the orthoclase grains are similar to those of the albite. In a number of thin-sections from the Turondale Formation the orthoclase grains have patchy replacement by albite similar to those in the upper part of the Chesleigh Formation. Glass shards, now replaced by albite, are common in some of the tuffaceous sediments; these offer positive evidence of a volcanic origin for at least some of the detritus. Very rarely, the sediments contain grains of brown amphibole. In the darker rocks, chlorite and epidote make up the entire matrix, in the lighter ones, albite is present also. Rock fragments are not common in the tuffaceous rocks, when they are present, they are acid lavas similar in mineralogy to the tuffaceous rocks.

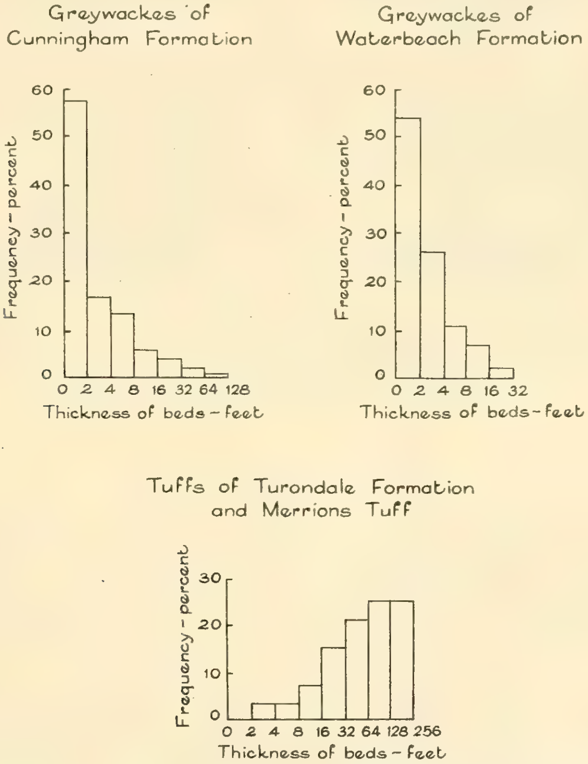


Figure 6. Frequency distribution of bed thicknesses in the type sections of the Merrions Tuff, the Cunningham and Waterbeach Formations.

The petrography of these tuffaceous rocks confirms the pyroclastic origin of the detritus in a number of ways; glass shards are present. Quartz and felspar grains show signs of corrosion (for some of the quartz grains this is certainly magmatic, in others it might have been post-depositional). Chlorite patches, probably derived from glassy rock fragments, are common. There is no evidence from the petrography of the sediments or the associated conglomeratic pebbles that the quartz and felspar grains were derived from a plutonic source. The small proportion of rock fragments in the sandy fraction precludes the possibility of the sediments being the result of the weathering and erosion of acid lavas and porphyries.

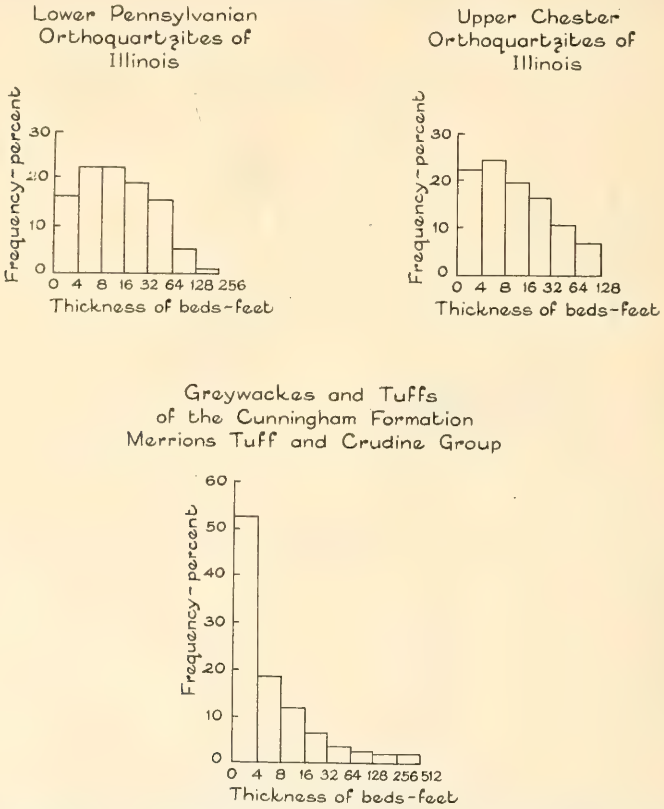


Figure 7. Frequency distribution of bed thicknesses in shallow-water sandstones in Illinois and greywackes of the Hill End Trough.

The greywackes of the Waterbeach Formation are finer-grained than the typical tuffaceous sediments of the Turondale Formation. The quartz and felspar (albite with minor orthoclase) grains are smaller and more angular in the greywackes. Igneous rock fragments are far more abundant in the greywackes than in the tuffaceous rocks. Fragments over a millimetre in diameter are normally rounded, smaller ones are angular. Shale fragments are the most abundant sedimentary rock fragments, they are frequently large and almost always angular. Limestone fragments are seen in thin-section. The matrix is of chlorite, quartz, felspar and some scattered grains of epidote. The proportion of epidote is much smaller than in the tuffaceous rocks. The proportions of the various constituents in the coarse and medium-grained greywackes do not vary greatly with grainsize in any one bed. The micrometric analyses of TS 18 and 19 (from the top and bottom respectively of a graded-bedded greywacke, Plate IX, figs 7, 6) illustrate this. The proportion of rock fragments decreases noticeably only in the finer sandstones and siltstones.

The mineralogy of the siltstones and slates throughout much of the Crudine Group is closely related to that of the coarser grained rocks associated with them. The ratio of quartz to felspar is similar and so far as can be determined in thin-section, the remainder of the rock is chlorite. The distinctive appearance of fine-grained chert-like sediments of the Turondale Formation results from their having a smaller proportion of chlorite than the slates, considerable quantities of epidote and interlocking grains.

Fauna and age. The only fossils found in the Crudine Group are ones which have been transported from their living environment. Near the top of the group approximately 5 miles north of Limekilns in Portion 107 of the Parish of Jesse a mudstone has yielded a brachiopod fauna from which Wright (1966) has identified *Dolerorthis*, sp., *Skenidioides* sp., *Isorthis* sp., *Schizophoria* sp., *Plectadonta* sp., *Notanoplia* sp., *Schelwienella* ? sp., *Eospirifer* sp., *Ivanothyris* ? sp., *Spinatrypa* sp., *Lissatrypa lenticulata* and the coral *Pleurodictyum*. In the type section of the Turondale Formation, limestone pebbles at the base of the formation contain *Tryplasma* sp., *Favosites* sp. and Pentamerid brachiopods. Near the top of the same section very poorly preserved plant remains have been found. Three miles to the south, in the upper part of the formation, limestone blocks contain *Favosites* sp. close to *F. richardsi*. The age indicated by the brachiopod fauna at the top of the group is Lower Devonian.

MERRIONS TUFF

This formation is extremely widespread and has proved of great value in elucidating the structure and succession of the region. The base of the formation is the base of the first tuff horizon after the greywacke succession of the Waterbeach Formation. Its top is the top of the highest tuff bed in the Hill End Trough succession where Merrions Tuff is overlain by the slates and greywackes of the Cunningham Formation. In the vicinity of Limekilns, the Merrions Tuff is overlain by shales of the lower part of the Limekilns Group. In all sections, the Merrions Tuff consists dominantly of medium sand-grade in massive beds of the order of tens of feet thick, these beds often show grading on a large scale, from breccias at the base to fine chert-like rocks at the top. Dacitic lava flows occur but make up only small proportion of the formation.

The large-scale graded-bedded units commence with a basal breccia which contains large chloritic bodies (Plate X, fig. 4) of the type described in the account of the Turondale Formation, sometimes angular blocks of shale and less frequently, rounded pebbles of quartz porphyries and limestone. The matrix is composed of coarse sand-grade mineral fragments (albite, orthoclase, quartz with interstitial chlorite and epidote). This is succeeded by progressively finer detritus with an alternation of light and dark bands several inches thick, the colour banding apparently resulting from variation of the chlorite content. Sometimes just below the banded rocks there is a zone which has a mottled appearance. This too, results from an uneven distribution of chlorite through the rock. The banded rocks pass upwards into finer tuffs, poorly bedded, light in colour and often with indefinite slump structures. These rocks have a chert-like appearance and are frequently spotted. They have been described in the discussion of the Turondale Formation.

Type section. The type section (Figure 8) of this formation is along the south bank of the Turon River in Portion 41 of the Parish of Waterbeach, overlying the type section of the Waterbeach Formation. The name of the formation is derived from Merrions Trig. Station south of the type section on a high ridge formed by the outcrop of the formation. The measured thickness of the type section is 2,020 feet, this order of thickness is typical of the formation. The formation can be divided into four units in this

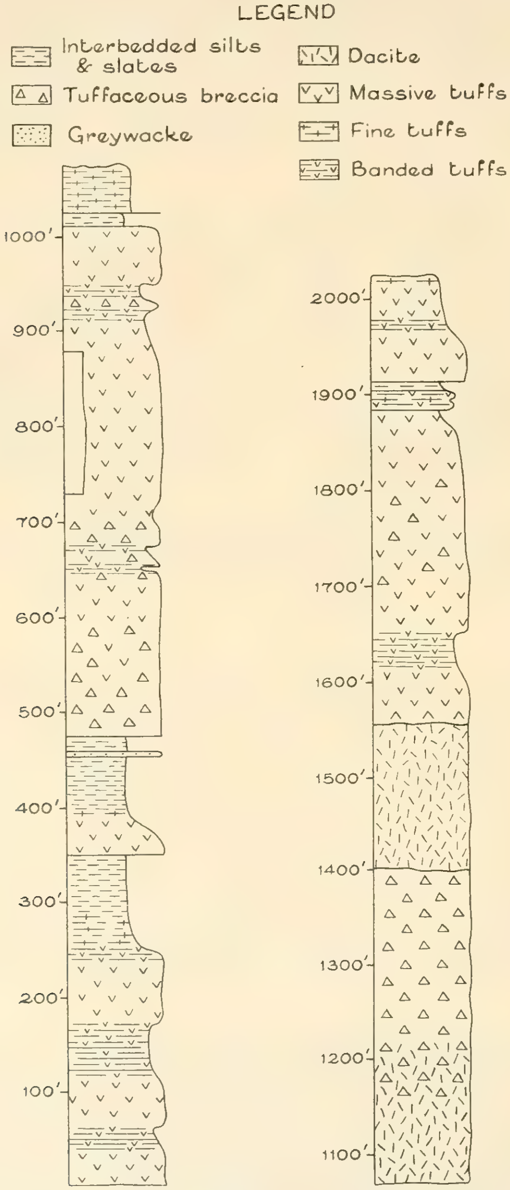


Figure 8. Type section of the Merrions Tuff measured on the south bank of the Turon River in Portion 31, Parish Waterbeach.

section. The lowest 475 feet of the formation contains four thick tuff beds. The lower two commence with coarse tuff and pass upwards into banded tuff which is followed abruptly by coarse tuff. The upper two tuffaceous beds pass into indurated shaly rocks with characters similar to those of the Waterbeach Formation. Interbedded with the fine-grained sediments at about 470 feet above the base of the formation there are two greywacke beds with all the characters of the typical greywackes of the Waterbeach Formation except that they contain a larger proportion of quartz and felspar and a correspondingly smaller proportion of rock fragments.

The next 600 feet of the formation is almost entirely coarse tuff. Two exceptionally thick beds occur. The lower one is over 150 feet thick and the upper one is over 200 feet thick. Shale blocks included in the base of the lower one are up to two feet across while the upper one has large chloritic blocks at its base.

Five hundred feet of rock containing tuff and lava flows then follow. At the base lava rests with an irregular contact against cherty rocks at the top of the underlying unit. This lava passes upwards into brecciated lava—possibly a flow breccia then into a breccia more closely resembling the coarser phases of the tuff. This is followed by another lava flow.

The remaining 460 feet of the formation commences with a very coarse breccia (Plate x, fig. 4) which grades up into finer sediments. The next bed is over two hundred feet thick, it has some fluctuations in grainsize but becomes finer in the upper part. Above is an alternation of tuff and cherty rock followed by seven feet of sediments with the bedding features of the shaly rocks of the Waterbeach Formation. The formation concludes with a hundred foot unit which grades from breccia at the base into cherty rocks at the top.

Regional distribution and variation. South of the Turon River the formation remains much the same as the type section, but to the north there is lateral change in the lowest unit of the formation, where an increase in the proportion of intercalated strata takes place and some of the tuffs pass into conglomerates with cobbles of felsitic rocks. The lavas, too, in the north differ somewhat in hand specimen from those in the type section; vesicular types are common, the cavities being filled with epidote, prehnite and calcite.

The general lithological identity and bedding characteristics of the formation are maintained in the Limekilns area on the east side of the Wiagdon Thrust where the formation is of the order of 1,500 feet thick. There is a felsitic lava flow at the base to the north-east of Limekilns. Overlying the tuff is a black shale (the Rosedale Shale) which is poorly bedded and contains no tuffaceous material. The junction with the Merrions tuff is sharp.

Petrography. Apart from minor differences, the sediments (Plate III, fig. 1) of this formation are the same as the tuffaceous rocks of the Turondale Formation. Amphibole is still rare but is more common than in the Turondale Formation. It has the following optical properties: Z = slightly greenish mid-brown; X = very light brown; $Z \wedge C$ about 17°; moderately large 2V. Orthoclase, often partly sericitized, is common only in coarser tuffaceous rocks; the mineral has more albite patches than in the type section of the Turondale Formation. Comparison of the micrometric analyses of sediments from the two formations (Tables 2, 4) and their positions on Figures 4 and 5 bring out this similarity. The mode of deposition of the tuffaceous rocks is discussed above.

The lavas associated with the Merrions Tuff are altered dacites; they are tough dark grey to greenish grey rocks. The phenocrysts are mainly of felspar (1·0 mm.), very rich in soda (about Ab_{95}) and frequently corroded. Quartz phenocrysts are not abundant but are always corroded. In one thin-section a pale green non-pleochroic pyroxene was found. Amphibole similar to that in the tuffs is occasionally present. The groundmass of the lavas is composed of plagioclase laths (0·1 mm. long), granular quartz, grains of epidote and wisps of chlorite. The degree of alteration in these rocks is considerable; in most slides chlorite and epidote pseudomorphs after amphiboles are common.

TABLE 4

Micrometric analyses of Tuffaceous Arenites from the Merrions Tuff

	A	B	C	D
Quartz	3	27	10	8
Felspar	51	35	30	31
Igneous rock fragments ..	6	—	19	3
Sedimentary rock fragments ..	—	—	5	—
Chloritic patches	4	7	—	3
Chloritic matrix	36	31	36	55

All specimens are from the type section of the formation.

A. TS 14. 50 feet above the base of the formation.
B. TS 8. 350 feet above the base of the formation.
C. TS 6. 850 feet above the base of the formation.
D. TS 4. 1,030 feet above the base of the formation.

CUNNINGHAM FORMATION

This formation is named after the parish in which the type section occurs. The formation consists of slates, siltstones, greywackes and conglomerates. Lavas and tuffs are absent. Some of the greywacke beds are thicker than those of the Waterbeach Formation but at the same time considerably thinner than typical beds of the Merrions Tuff.

Type section. This is along the banks of the Turon River in Portion 138 of the Parish of Cunningham, conformably overlying the type section of the Merrions Tuff. The stratigraphic column is given in Figure 9. The type section which is a little over 2,800 feet has been measured to the top of the highest bed exposed.

The proportion of sandy material and the grainsize of the coarser beds is greater in this section, than in the type section of the Waterbeach Formation. These two features have associated with them, an increase in thickness of the coarsest beds and a less distinct alternation of sequences of fine sediments with groups of greywacke beds than in the type sections of the Waterbeach Formation and the middle part of the Turondale Formation. In the Cunningham Formation type section, the coarser beds are more abundant between 300 and 900 feet, 1,050 and 1,150 feet, 1,250 and 1,550 feet, 1,750 and 1,850 feet, and 2,130 and 2,350 feet above the base. The coarsest greywackes in this formation are in thick beds—the thickest is 70 feet, one is 60 feet thick and there are a number over 30 feet. This contrasts with the type section of the Waterbeach Formation on which the thickest bed is 20 feet. On the basis of number per hundred feet of section, thinner greywacke beds are more abundant in the Cunningham Formation than in the Waterbeach Formation. Most beds up to four or five feet thick are graded-bedded but the thicker beds display irregular fluctuations of grainsize. The siltstones and slates are similar to those in the Waterbeach Formation.

At two places in the type section, namely 1,450 and 2,150 feet above the base, beds quite different in texture from the greywackes occur; the first is 18 feet thick and the second is 50 feet in thickness. These are massive, dark grey in colour, consisting dominantly of clay and silt size material (see Table 5, Plate xi, fig. 2) but with a small proportion of coarser material.

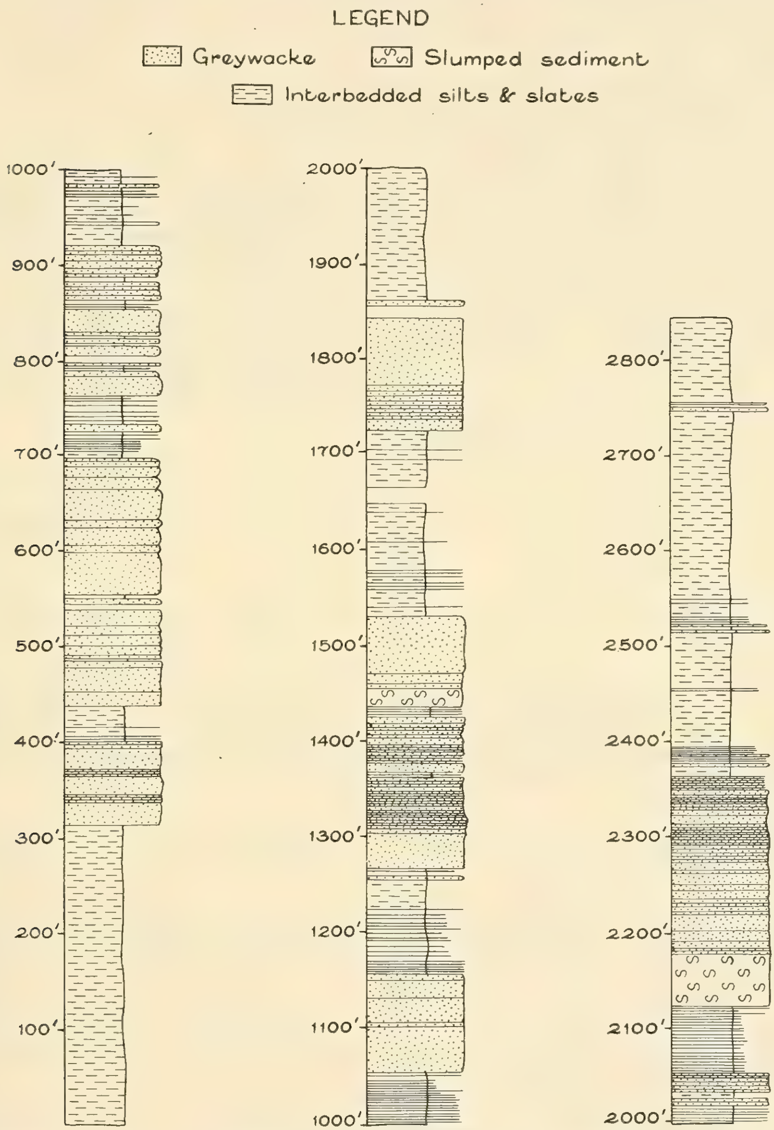


Figure 9. Type section of the Cunningham Formation measured on the south bank of the Turon River, Portions 41, 50, Parish Waterbeach. Greywacke beds less than 2 feet thick are shown as thin horizontal lines.

In the lower one the largest pebbles are 2 to 3 inches in diameter, whilst in the upper one the maximum size is 6 inches. The lower bed contains deformed blocks of shale up to two feet in diameter in a matrix which has folded banding. One brachiopod fragment was found in this bed. The upper bed is composed dominantly of a finer banded phase with about 80 percent clay and silt and a second phase which contains an appreciable proportion of sand sized grains. The boundaries between the two phases are sharp but very irregular (Plate x, fig. 6). Both are boulder bearing. The best explanation of the origin of these two beds is that they are mudflow or highly mobile slump deposits. The sporadic banding of the rock, the irregular distribution of boulders through the bed, the incomplete mixing of the fine-grained and sandy phases of the upper bed and the contortion of the banding of the lower bed are all in agreement with this conclusion. The symmetry of the contortions, incidentally, suggests that the direction of flow was from east to west. The inclusion of the brachiopod in the lower bed suggests that the flow was initiated in a fairly shallow-water environment.

The observations made regarding the origin of the alternation slate-rich and greywacke-rich zones (p. 29) apply equally to the Cunningham Formation. A volcanic origin can be definitely ruled out because there is no indication of vulcanism during the deposition of the Cunningham Formation. It is interesting to note that the upper mudflow horizon occurs at the base of a greywacke cycle which is over 200 feet thick. This commences with thickly bedded greywackes but the thickness of the beds gradually diminishes upwards. This may have been caused by an uplift in the source area or fall in sea level, erosion gradually obliterating the effects of the change and the supply of sandy debris gradually diminishing.

Regional variation. The formation is confined to the western margin of the area under discussion but some variation in the proportion of various lithologies occurs. Greywackes with an abundance of shale fragments are more common to the south and to the west there is a rapid decrease in the abundance of coarse sediment.

Source direction of the sediments. Flute-casts and small-scale cross-bedding occurring at intervals throughout the type section and the flow-deformed banding in the lower mudflow horizon all indicate a direction of sediment flow towards the west. Small-scale cross-bedding indicating a similar direction of flow occurs near the base of the formation at Gimlet Creek (four and a half miles due south of the type section) and again at several points in the section exposed by Winburndale Rivulet.

Thus the same direction of slope of the sea-floor was maintained from the time of deposition of the Cookman Formation until the deposition of the Cunningham Formation.

Petrography and sedimentation. Because of the higher proportion of shale fragments the appearance of the Cunningham Formation greywackes differs from that of the Waterbeach Formation greywackes. The coarser phases of the Cunningham greywackes may contain up to fifty percent of shale fragments. The grey colour of the Cunningham Formation greywackes contrasts with the greenish grey of those of the Crudine Group which contain a higher proportion of epidote.

Micrometric analyses of some of the sediments of the Cunningham Formation are given in Table 5 and are plotted in Figures 4, 5. The proportion of felspar is significantly lower in the Cunningham Formation than in the Waterbeach Formation. The thin-section characteristics of the various types of detrital minerals and rock fragments are identical in both formations. There are fragments of porphyritic acid igneous rocks, limestone, shale and quartzite. A single pebble of granite found in a conglomerate phase of the Cunningham Formation does not necessarily indicate any change in the source area because a few granite pebbles have been found in the Waterbeach Formation in the Hill End area. The siltstones and slates of the Cunningham

Formation are poorly sorted; they differ from those of the Waterbeach Formation only in that they contain a higher percentage of detrital quartz. The percentage of matrix in the Cunningham greywackes is more variable and often considerably lower than in the Waterbeach greywackes (Plate xi, figs 4, 5), and the beds are often considerably thicker; only two percent of the greywacke beds in the type section of the Waterbeach Formation are over 16 feet thick, while 10 percent of those of the Cunningham Formation type section exceed this value. If the initial slope from the shallow-water environment into the trough in which the Cunningham Formation was deposited, was steeper than for the Waterbeach Formation, and if, the trough had a flatter floor, then I think the differences could be explained. The steeper slope would allow flowing grain layers (Sanders, 1965) or turbidity currents with a smaller amount of fine material to flow; the sediments found in the type section of the Cunningham Formation may have been deposited at the foot of such a slope as a submarine fan. The rarity of slumps in this section offers evidence against deposition on the slope. Had the slope continued further to the west, it would be expected that the coarse sediments would be common for a considerable distance in this direction. This is not the case.

TABLE 5

Micrometric analyses of Greywackes from the Cunningham Formation in the Sofala district

	A	B	C	D	E
Quartz	31	22	10	20	27
Felspar	9	4	3	9	9
White mica	—	—	7	—	—
Igneous rock fragments . .	25	32 ⎫	3	57	48
Sedimentary rock fragments	2	8 ⎭		3	2
Matrix	33	34	77	11	14

A. TS 69. Type section, 330 feet above the base of the formation.
B. TS 61. Type section, 1,380 feet above the base of the formation.
C. TS 80. Type section, 2,150 feet above the base of the formation.
D. S 9. Sofala-Hill End road, ½ mile west of the eastern boundary of the formation.
E. S 89. Sofala-Hill End road, ¾ mile west of the eastern boundary of the formation.

Fauna. Apart from a brachiopod fragment in one of the mudflow horizons, no fossils have been found in this formation other than those occurring in limestone pebbles in the coarser sediments. Tabulate corals are the most abundant. The forms found are favositids, one is doubtfully *Emmonsia* sp., the others are *Favosites* sp. One rugose coral, possibly an Acanthophyllid has been found.

Age. The best evidence for the age of this formation comes from its correlation with the Devonian Limekilns Group (see below). The Cunningham Formation can be traced westwards to the Euchareena area where it passes laterally into shallow-water sediments containing Lower Devonian fossils.

LIMEKILNS GROUP

This group consists of three formations which overlie the Merrions Tuff in the vicinity of Limekilns, five miles south-east of Wattle Flat. These three formations were first described by Hawkins (1953). In ascending order, the formations are the Rosedale Shale, the Jesse Limestone and the Limekiln Creek Shale. There is no indication of contemporaneous vulcanism within the group though it is overlain and underlain by thick pyroclastic formations, the Winburn Tuff and the Merrions Tuff respectively.

The age of the limestone in this group has been known to be Devonian for many years but the limestone was not mapped stratigraphically until it was studied by Hawkins (1953). The Limekilns Group has an important place in the interpretation of the palaeogeography of the region since it contains neritic benthonic organisms in their living environment and is of the same age as the Cunningham Formation which is a typical geosynclinal deep-water succession. The evidence for this correlation rests on a number of different lines of approach. First, they both overlie the Merrions Tuff conformably. Then the lithologies are comparable, in that they are both non-volcanic; this is not a common feature in the succession. Again, sedimentary structures in the Cunningham Formation in the Turon River section show that the sediment has been transported from east to west, indicating the existence of an area with a shallow water environment somewhere to the east.

The thickness of the Limekilns Group in the Limekilns area is of the order of 2,500 feet. This may be an overestimate because faults are difficult to detect in the Rosedale Shale and the Limekiln Creek Shale.

a. *Rosedale Shale.* This formation which has been named after a property at Limekilns, has its type section (as designated by Hawkins, 1953) in Pender's Creek in Portions 1, 16 and 63 of the Parish of Jesse. A sharp contact with the Merrions Tuff marks the lower boundary. The shale is dark grey to black, well jointed and fisile but with macroscopic bedding planes every six to eight inches. Pyrite is common. The shale is composed of quartz and felspar silt set in a fine-grained matrix of chlorite and sericite. Chlorite is the more abundant. Fossils are rare, there are only occasional linguloid brachiopods and poorly preserved plant remains. The thickness quoted by Hawkins for this formation is 700 feet.

b. *Jesse Limestone.* This formation conformably overlies the Rosedale Shale. The outcrops to the east of Limekilns are thickly bedded limestones and breccias, while those to the west are dominantly calcarenites 50–100 feet thick, in which individual beds can be traced for distances of at least a mile. Hawkins (1953) designated the section of the clastic facies exposed in Diamond Creek as the type section. The base and top of the formation in the type section are respectively the base of the first calcarenite bed and the top of the highest one.

The limestone is highly fossiliferous, though the massive limestone is less abundantly so than the detrital facies to the west. *Syringaxon* ? sp., *Phillipsastraea currani*, *Hexagonaria tunkanlingensis*, *Disphyllum* sp., *Dendrostella* sp., *Spongophyllum* sp., *Acanthophyllum mansefieldensis*, *Grypophyllum* sp., *Lyrielasma* sp., *Tryplasma* sp., *Pseudamplexus* sp., *Plasmophyllum australe*, *Calceola* sp. and *Receptaculites australis* have been identified by Wright (1966). Brachiopods, stromatoporoids, tabulate corals, fish plates and conodonts are also known from the formation. Preliminary identifications of the conodont fauna are: *Bellodella devonica*, *B. resima*, *Hindeodella prescilla*, *Lonchidina* sp., *Neoprioniodus excavatus*, *Neoprioniodus* sp., *Ozarkodina denckmanni*, *Paltodus acostatus*, *P. unicostatus*, *P. valgus*, *Polygnathus linguiformis foveolata*, *Spathognathodus exiguus*, *Synprioniodina* sp. and *Trichonodella* sp. The assemblage is apparently a late Lower Devonian one (Emsian).

Towards the north, along the Limekilns-Wattle Flat road, the limestone thins very considerably and the formation is represented by a few impure calcareous arenites. These contain, apart from detrital carbonate, porphyritic acid igneous rock fragments as the most abundant constituent with quartz grains less abundant and felspar least abundant. This the same order of abundance as the various types of detritus in the greywackes of the Cunningham Formation.

c. *Limekiln Creek Shale.* This formation was also defined by Hawkins (1953). It has its type section in Cheshire's Creek in Portion 253 and the eastern part of Portion 127 of the Parish of Wiagdon. The thickness of the formation given by Hawkins is 1,500 feet. It overlies the Diamond Creek Limestone and underlies the Winburn Tuff. The lithology and fossil content are similar to those of the Rosedale Shale.

Winburn Tuff

The formation has its type section in Cheshire's Creek, in Portion 127 of the Parish of Wiagdon (Hawkins, 1953). The formation is named after a parish which has Cheshire's Creek as its boundary and so the south bank of the creek in the type section is actually south of Limekilns, in the Parish of Winburn. The dips of the underlying shales are frequently discordant with the boundary of the tuff which may lie unconformably on the Limekilns Group.

The formation occurs in the core of a synclinal structure truncated to the west by a thrust fault. The section is thus incomplete but over 2,000 feet of it is preserved. Lithologically, the formation is very similar to the Merrions Tuff. The beds are thick and the greatest part of the formation is composed of tuff of coarse sand size. The remainder is composed of finer tuffaceous sediments.

No indication of vulcanism has been found within the Cunningham Formation and this is taken as an indication that the Cunningham Formation pre-dates the Winburn Tuff and so may be equated with the Limekilns Group. There is no formation to the west with which the Winburn Tuff can be correlated.

There is a general textural and mineralogical resemblance between the Winburn Tuff and the Merrions Tuff. The rocks are poorly sorted and composed of white and pink felspar, quartz, epidote and chlorite; rock fragments are not abundant. Orthoclase is the dominant felspar, it is often partly replaced by albite in patches about a tenth of a millimetre long or less commonly, by narrow veins along the cleavage. The detrital plagioclase in the rock is albite. Epidote is less abundant than in the Merrions Tuff.

The Stratigraphy of the Hill End District

There have been three previous geological maps of the Hill End region, each covering an area of about 100 square miles surrounding the town. The first was by Pittman (1881); his map showed that the town, and thus the mineralized zone, lay on the crest of an anticline, but he made no attempt to subdivide the succession. The second map was produced by Harper (1918) who, because he misinterpreted some sedimentary structures in the succession, considered that an unconformity was present. The third study was by Jopling (1950) who reaffirmed the original simple concept of Pittman, but again there was no serious attempt to divide the sequence into units, since the purpose of Jopling's study was to investigate the gold mineralization. The anticline on which the town of Hill End is situated gives the most complete section in the central part of the region. The sequence of formations from the Chesleigh Formation to the Cunningham Formation, described in the Sofala district can also be recognized in the Hill End area. The geological map accompanying (Plate IV), incorporates the Hill End area.

CHESLEIGH FORMATION

The lowest part of the section consists of massive subgreywackes, with tuffs and thin beds of slates at the base. Above this, massive tuffaceous rocks appear which have sorting akin to that of greywackes; these tuffaceous rocks are reminiscent of those in the Turondale Formation of the Crudine Group, but their association with massive subgreywackes is one unknown in that formation to the east. The exposed thickness of the formation in the Hill End area is about 1,700 feet, in all probability representing the upper part of the Chesleigh Formation which, in the type area, contains volcanic material.

Unfortunately, it has not been possible to obtain any evidence of the direction of transportation of the sediments in the Chesleigh Formation outcropping in the Hill End area; the direction of source of the Chesleigh Formation in the Sofala-Wattle Flat area is from the west or a little to the south of west. The Hill End area would be expected to be a little closer to the source area; this seems to be reflected in the lithology of the sediments. The non-volcanic sediments are more felspathic; a notable addition is the presence of a small amount of microcline. There is also a suggestion of coarsening of grainsize, indicated by a greater abundance of shale blocks in the subgreywackes. Volcanic material is also more abundant here than in the type section, again suggesting a closer proximity to the source region.

The outcrop in the Hill End district, is confined to the axial region of the Hill End Anticline, and occupies a strip, less than two miles in width, commencing two miles north of the town of Hill End and extending south for 16 miles. The outcrop is cut off to the north and the south by the gentle plunge of the fold.

COOKMAN FORMATION

In the Hill end Anticline, the Chesleigh Formation is flanked by the Cookman Formation with an outcrop width of just under half a mile on both limbs. Good cliff sections exist where the Cookman Formation crosses the Turon and Macquarie Rivers. The Cookman Formation also outcrops to the east of the Hill End Anticline in the axial regions of three small anticlines along the Macquarie River upstream from its junction with the Winburndale Rivulet. Only the upper part of the formation is exposed in each case. The thickness of the Cookman Formation in the Hill End area is about 2,300 feet, *i.e.*, considerably thicker than in the type section (1,500 feet). The coarser sediments like those of the type section, are almost all quartz-rich with a few percent of argillaceous matrix; they occur in beds mostly one to two feet thick. Unlike the type section, graded-bedding is well developed although the size range is rather more restricted here. These features suggest a location for the Hill End sections of the Cookman Formation further from the source of the sediments. The indications in the Sofala area were that the sea-floor sloped to the west during deposition of the Cookman Formation in contrast with the general easterly slope at the time of deposition of the Chesleigh Formation. In the Turon River cliff section of the formation exposed on the eastern side of the Hill End Anticline slipped load-casts, small-scale cross-bedding and slumps are occasionally found and these indicate a westerly slope on the seafloor.

In hand specimen, the subgreywackes of this formation differ in appearance from those in the Sofala area. This difference results from the greater degree of metamorphism in the Hill End area. Thus, instead of the rock being moderately indurated and quartzite-like with individual grains fairly distinct, it has been converted to a very hard, brittle, somewhat translucent and hornfels-like rock in which the grains are entirely interlocking. Under the microscope it is difficult to determine the nature of the original texture.

Crudine Group

Both the Turondale and the Waterbeach Formation can be traced into this area and maintain many of the characteristics found in their type sections.

Turondale Formation

This overlies the Cookman Formation in the Hill End Anticline and outcrops over the whole length of the anticline in the area mapped. Although it does not appear in any of the anticlines to the west of the Hill End Anticline it does outcrop extensively east of it, in the anticlinal structure west of the junction of the Macquarie River and the Winburndale Rivulet. This outcrop has a width of three miles on the southern border of the map, interrupted only by three small inliers of the Cookman Formation. To the north this anticlinal structure plunges north so that the Turondale Formation disappears under higher formations.

The thickness of the formation seems to be fairly constant in the region and of the same order as the thickness measured in the Turon River section at Hill End, that is, 2,200 feet (in the type section it is 2,000 feet). The lithology likewise is similar—mainly tuffaceous rocks and greywackes. The beds are thick but for the most part the coarse rocks characteristic of the lowest part of the formation in the type section are not present. This means that the junction of the Turondale Formation with Cookman Formation is not such a distinct one as in the Sofala area but it can be recognized by an increase in the thickness of beds, the presence of some beds of coarse sand size and the presence of acid tuffs and most important, the change from dominantly quartz detritus to lithic and felspathic debris. Although there has been a reduction of the maximum grainsize of the sediments in this formation in the Hill End area, the abundance of coarse-grained sediments is far greater here than in the Waterbeach Formation. Some of the thicker beds of the Turondale Formation contain blocks of shale—one of these observed in Washing Gully of Hill End is ten feet long. Indications of slumping movements are often seen in these beds. The tuffaceous rocks range from coarse sand-size through to fine cherty types.

A porphyry, twenty to thirty chains wide in outcrop, occurs within the Turondale Formation, at the same stratigraphic level, on both sides of the Hill End Anticline. Even where its contacts are exposed there is no clear evidence that the porphyry is intrusive and, further, it has obviously been involved in the folding movements since it is strongly deformed. It may be a flow. An inclusion of granite with a rounded outline, measuring approximately two feet by one foot is exposed in the porphyry in the bed of Washing Gully a mile and a quarter west of Hill End. The inclusion shows some signs of disruption for small groups of crystals, evidently derived from the granite, are seen separated from the inclusion by a narrow vein of the porphyry. There is no indication of the development of any kind of reaction rim around the inclusion.

The evidence of the direction of slope of the sea-floor is in harmony with what has been found in the Sofala area. The general indication is that the slope was from east to west, which means that the Hill End section was further from the shore. This accords with the lithological data such as the absence of the coarsest tuffs and the increase in proportion of greywacke. The data indicating the slope are a slump structure in tuffaceous sediments on the Macquarie River three miles south-east of the junction of the Turon and Macquarie Rivers and the occurrence of cross-bedded ripple marks near the base of the formation 300 yards west of the same river junction. Small-scale cross-bedding exposed on the bank of the Macquarie River, 15 miles south of Hill End on the western limb of the Hill End Anticline, indicates an easterly downward slope of the sea-floor. Thus, the axis of the trough in which the Turondale Formation was deposited lay in the vicinity of the Hill End Anticline.

Waterbeach Formation

This formation outcrops extensively in the Hill End area. It appears on both limbs of the Hill End Anticline and, on the eastern side towards the south of the area, can be traced around several folds to the junction of Winburndale Rivulet and the Macquarie River. About 6 miles west of the Hill End Anticline the Waterbeach Formation outcrops in the axial region of the Ulmarrah Anticline (Figure 1).

The appearance of the Waterbeach Formation in most sections is closely similar to that in the type section with the notable exception of the inlier in the Ulmarrah Anticline described below. The usual features are: an absence of tuffs, a preponderance of slates over greywackes, and well developed graded-bedding, especially in the slates. This graded-bedding is better developed than in the type section. The same tendency characterizes the Cunningham Formation in this area.

In a number of places in the section of the Waterbeach Formation exposed on the western limb of the Hill End Anticline, flute casts and small-scale cross-bedding indicate a down-slope of the sea-floor from east to west. Hence, the same direction of slope persisted from Sofala at least as far west as this section.

The thickness of the Waterbeach Formation south of Hill End on the Turon River is 2,000 feet, 350 feet thicker than the type section.

In the Ulmarrah Anticline immediately underlying the Merrions Tuff there is over 900 but less than 1,500 feet of extremely deformed sediment. This material is part of a huge slump, the base of which is not exposed. The sediment in the deformed zone is coarse greywacke and slate, which have been mutually involved in the slip. The greywacke (Plate xi, fig. 7) is not a normal one; it contains a proportion of matrix much larger than is normal and the sorting is poorer (cf. Table 6). In the field it is also unusual, for included in it are blocks of a great variety of rocks, the largest and commonest being shale. Blocks 15 feet across are common. Other inclusions are not only far less frequent, but of considerably smaller size, being for the most part rounded boulders up to 2 feet in diameter. Rock types represented are: quartz-felspar porphyries, biotite-granite, limestone, dacitic tuff, quartzite and quartz. In places the boulder-bearing material and deformed slates are overlain by little-deformed graded-bedded slates but elsewhere the slate is clearly injected by irregular masses of the greywacke (Plate x, fig 7); these injection movements clearly pre-date the regional cleavage. These relationships may be the result of first, the slumping of the coarse material into a position of temporary stability, then deposition of graded-bedded shales on top followed by a later slip of both the first slump and its cover. This process may have been repeated a number of times. Some of the contact between the two phases might represent a slide-plane within the whole slump mass. As it has not been possible to recognize any systematic arrangement of folds within the slumped material, no direct evidence of the direction of source of the slump is available.

By far the best exposures of the slump mass are in the gorge of Pyramul Creek on the northern edge of the area mapped. To the south, outcrops in the axial region of the anticline are poor but the occurrence of poorly sorted greywackes and boulder beds, suggests that the slump extends for at least six miles along the axis of the anticline. Further south the Waterbeach Formation is concealed by the overlying Merrions Tuff. To the east, in the Hill End Anticline, there is no certain indication of the slump, despite good exposures. The only possible disturbed area is on the west limb of the anticline on Pyramul Creek where some of the interbedded slates and greywackes are rather more folded than usual; this folding, however, might be tectonic. Although the evidence for the direction of origin of the slump mass is negative, it suggests that the slump was derived from the west since, if it had come from the east the effect certainly would be clearly noticeable in the exposures in the Hill End Anticline. Again, if the slump had moved from the east to the west the distance of movement would have to be very considerable since boulder-bearing horizons are rare in the Waterbeach Formation within the area mapped. Since sediments in the Waterbeach Formation, on the western limb of the Hill End Anticline, indicate a westerly slope of the sea-floor, the axis of the trough in which the formation was deposited must have lain in the vicinity of the Ulmarrah Anticline or slightly to the east of it.

TABLE 6

Micrometric analysis of Greywacke Matrix of Ulmarrah Slump

	Pt
Quartz	12·2
Felspar	12·7
White mica	2·8
Rock fragments	13·8
Matrix	58·2

Locality: Axis of Ulmarrah Anticline in Pyramul Creek.

Another boulder-bearing greywacke, this time a very thin bed, by comparison with the slump described above (the thickness of sediment involved is only of the order of tens of feet), outcrops in the core of an anticline some twelve miles south-east of the Ulmarrah Slump but is east of the Hill End Anticline and so is unrelated to the large slump.

MERRIONS TUFF

In the Hill End Area, this formation maintains the character of its type area at Sofala better than the underlying units. North of the Turon River it outcrops on both the eastern and western limbs of the Hill End Anticline but to the south occurs only along the western limb. On the eastern limb the Merrions Tuff outcrops over a considerable area between the Macquarie and Turon Rivers due to the northerly plunge of several folds of moderate amplitude west of the Hill End Anticline. East of these structures the formation again strikes southwards along the western side of the synclinal structure continuing south from Sally's Flat. To the west of the Hill End Anticline the tuff outcrops on both limbs of the Ulmarrah Anticline as far south as the Macquarie River. The unit again occurs in a southerly-plunging anticline on the northern edge of the area mapped, between the Hill End Anticline and the Ulmarrah Anticline. The Merrions Tuff in the Ulmarrah Anticline is the most westerly outcrop of the formation in the region under discussion. The area east of the Hill End Anticline is structurally different from other areas in which the tuff outcrops for here it is tightly folded into sharp crests and troughs whereas elsewhere it behaves in a more competent fashion.

Lithological and bedding characteristics similar to those of the formation in the type section are maintained in the Hill End area, where the thickness is over 2,000 feet on the eastern limb of the Hill End Anticline. To the west of Hill End the formation contains less coarse material and the section is thinner (about 1,000 feet at Ulmarrah). Altered dacitic lavas are present in nearly all exposed sections and generally they occur at, or near, the base of the formation. The lavas sometimes have columnar jointing and, as a result of the regional deformation in which they have been involved, the north-south dimension of the columns is generally one and a half times the east-west dimension.

The lithological continuity of the Merrions Tuff and the decrease in thickness to the west are such that it must have been derived from the east. A shift to the west of the axis of the trough must be postulated to account for the extension of the sediment as far west as the western limb of the Ulmarrah Anticline. During the time of deposition of the underlying Waterbeach Formation the axis lay in the vicinity of the Ulmarrah Anticline.

Cunningham Formation

The type section of the Cunningham Formation which is described above is on the western side of a synclinal structure running through Sally's Flat. South of the Turon River the formation is restricted by the complex anticlinal structure occurring between the river and the Hill End Anticline but northwards the formation extends across to the anticline. West of the Hill End Anticline the Cunningham Formation outcrops over a very large area in a broad synclinal structure (the Ophir Syncline, Figure 1) roughly ten miles wide. The continuous outcrop is broken only by the lower rocks in the Ulmarrah Anticline and the small structure between it and the Hill End Anticline. The Cunningham Formation can be traced west to Euchareena; the outcrops there are discussed below.

The thickness of the Cunningham Formation in the Ophir Syncline is of the order of 12,000 feet. This is far greater than the thickness of the type section (2,800 feet). But it is not certain whether the formation has thickened to the west since there is no formation overlying the type section of the Cunningham Formation.

The lithology of the Cunningham Formation in the Hill End area differs from that of the type section principally in the proportions of the various rock types. Fine-grained sediments are far more common here and conglomeratic greywackes are very rare. To the west of Hill End greywackes are rare except near the base of the formation and there they are rich in felspar apparently derived from tuffaceous rocks. Between 5,000 and 6,000 feet above the base of the formation, a few thin graded-bedded and slumped bands of arenite and rudite composed largely of calcareous debris, outcrop on the banks of the Macquarie River between Curragurra Creek and Pyramul Creek. The detritus was apparently derived from the west where the Cunningham Formation passes into limy sediments. The formation here consists almost entirely of slate. Individual bands of silt are not common. Almost all of the silty material occurs at the base of graded slaty beds. These graded units are thicker than those described as occuring in the type section of the Waterbeach Formation. The general order of thickness of beds is six inches in the Cunningham Formation in this area.

The location of the axis of the trough in which the formation was deposited seems to have been in the vicinity of the Hill End Anticline. This is suggested by two lines of evidence. First, the shale-pebble conglomerates which are so characteristic of the formation in the eastern part of the region only extend as far west as the eastern limb of the Hill End Anticline. Secondly, there are frequent slump structures west of the Hill End Anticline; these make their appearance on the western limb of the anticline and are found commonly in most sections to the west of it. Good examples of these slump structures are exposed in Tambaroora Creek upstream from Washing Gully and at a number of places along the Macquarie River between Tambaroora Creek and Lewis Ponds Creek west of the axis of the Hill End Anticline. No direct evidence of the direction of movement of the sediment has been obtained by an examination of the structures because the amount of movement has almost completely destroyed the bedding. The deformed material, largely of clay and silt size, is often cut by veins of silty material probably deposited while water was being squeezed from the plastic mass after its final deposition. The indications of graded-bedding and other structures, which remain suggest that the initial deposition of the sediment was in deep water. The fine-grained nature of the sediments involved in these slumps and the absence of similar structures on the eastern side of the Hill End Anticline suggest an easterly slope of the sea-floor as far as the Hill End Anticline. Convolute bedding is common locally in very fine silts just west of the Ulmarrah Anticline and near the junction of Lewis Ponds Creek and the Macquarie River.

The Stratigraphy of the Euchareena District

The Devonian limestones and some of their associated sediments in the valleys of Nubrigyn and Boduldura Creeks, west of Euchareena and Stuart Town have been mapped and petrographically examined by Wolf (1965). Apart from this, there have been only two significant contributions to the geology of the area, the original mapping by Carne and Jones (1919) of the limestones studied by Wolf and the reconnaissance mapping of the western margin of the area by Joplin and others (1952).

Oakdale Formation

The oldest rocks in the Euchareena district are andesitic volcanics, representing a southern extension of the Oakdale Formation from the Mumbil District (Strusz, 1960). The Ordovician age of the volcanics has been established by the finding of graptolites at four localities. The northernmost is in Portion 10, Parish of Nubrigyn. Sherrard (1954) states that the graptolites here are: *Climacograptus bicornis*, *Climacograptus scharenbergi*, *Orthograptus* cf. *apiculatus* and *Lasiograptus* ? *harknessi*. Two miles to the south on the boundary of Portions 4 and 48 of the same parish there are fragments of *Dicellograptus* sp. Further south again on the Bell River just east of the Silurian Nandillyan Limestone (Joplin and others, 1952), I have found *Orthograptus* cf. *apiculatus* and *Glossograptus hinksii*. The fourth locality is 2¼ miles west of Mullion Creek Railway Station, by the side of the Belgravia Road. The forms identified are *Orthograptus apiculatus* and *Climacograptus* sp.

These andesitic volcanics occupy the same position in the succession as the Sofala Volcanics and are of comparable age. There is some difference in the general appearance of the rocks in the two areas. The andesitic volcanics in the western area are far less indurated than the Sofala volcanics and the interbedded fine-grained rocks are shales rather than chert.

An important section occurs on the eastern margin of this formation in the northern-western corner of the area mapped, in a gully flowing into Nubrigyn Creek through Portion 10 of the Parish of Nubrigyn. The section is as follows:

The lowest rocks exposed are andesites, overlying these is a thin limestone followed by shales with the fauna containing *Climacograptus bicornis* mentioned above; this in turn is followed by marls and a second thin limestone containing a fauna of tabulate corals overlain by a thick succession of arenites consisting of material derived from andesites and finally a Silurian limestone at the base of the Mumbil Formation, containing Pentamerids, *Tryplasma* sp., and a rugose coral close to *Phaulactis shearsbyi*. The exposed section below the Mumbil Formation is about a thousand feet thick.

The fauna of the lowest limestone in this sequence is highly significant; it includes halysitid corals, *Syringopora* sp., *Heliolites* sp., and *Multisolenia* sp. A comparable fauna has been found in the Oakdale Formation, about thirteen miles to the north (Strusz, 1960). The graptolite assemblage has been placed by Sherrard (1954) in the zone she calls the Zone of *Climacograptus peltifer* but there is no clear reason why it should be placed in that zone. The fauna is compatible with the assemblage two zones higher in what she calls the Zone of *Orthograptus calcaratus* and *Plegmatograptus nebula*. Thus the field observations indicate that the *Halysites* fauna extends down into the Upper Ordovician at least as far as the last-mentioned zone.

Mullions Range Volcanics

In the Mullions Range this formation occupies the axial region of an anticline plunging to the north. Unfortunately no older formations outcrop in the structure so that it has not been possible to determine the thickness of the formation in the Mullions Range. The formation outcrops to the west of the Mullions Range as a gradually narrowing strip, running slightly west of north. It has been traced as far north as Eadvale.

There are at least 5,000 feet of the volcanics exposed in the Mullions Range, but in the well-exposed section along Kerr's Creek, chosen as the type section, the volcanics are only 1,500 feet thick. The thickness of the formation diminishes rapidly towards the north. In the type section there is a dacite flow at the base, followed by breccias of similar composition and then another dacite flow. On top of this are more clastic sediments—tuffs and coarse sandstones. The section ends with a flow of banded rhyolite. The changes in thickness within the formation seem to be an original feature, since there is no local indication of an erosional break at the top. A volcanic centre in the vicinity of the Mullions Range, may account for the distribution of the formation. The Mullions Range Volcanics rest on the Ordovician andesitic rocks described above (Oakdale Formation).

The volcanics are almost exclusively dacites and rhyolites. The coarsest rocks are porphyry-like types; these grade in grain-size to types containing only a very small percentage of minute phenocrysts. The fine-grained types are difficult to identify positively in the field because of their similarity to the inter-bedded, indurated clastic rocks. The fine-grained lavas are pale greenish-grey when fresh and only very rarely banded, so very few dips and strikes can be obtained within the outcrop of the formation. The phenocrysts in the lavas are orthoclase, plagioclase (albite) and quartz. Felspar and quartz are roughly equal in abundance. The groundmass is composed of interlocking grains of quartz and felspar, with only minor amounts of biotite (X = pale yellow-brown and Z = very dark brown), mostly altered to chlorite. Epidote is common, occurring as grains in the groundmass.

The clastic sediments in the formation are all highly indurated. They range from fine silts to coarse sandstones and are composed of material derived from the lavas. Glass shards are common in some of the tuffs.

The age of this formation will be discussed after the description of the overlying formations.

Mumbil Formation

The Mumbil Formation originally described by Strusz (1960) in the Mumbil district, conformably overlies the Mullions Range Volcanics. It has been mapped from the northern extremity of the area, south to Kerr's Creek, around the margin of the Mullions Range in the Parish of Trudgett and then down the eastern side of the range to Frederick's Valley Creek. In the northern part of the area the formation rests directly on rocks older than the Mullions Range Volcanics.

The section in Frederick's Valley Creek is 1,200 feet thick consisting of grey and greenish-grey slate, commonly containing large pyrite cubes, and is almost devoid of bedding. The cleavage developed in the type section is not typical of the formation as a whole. To the west, the cleavage gradually diminishes in intensity, from Nubrigyn Creek to Kerr's Creek it is virtually absent. The formation is non-volcanic and composed of fine-grained sediments. The base of the formation, where it rests on the Mullions Range Volcanics is taken as the top of the last lava or tuff band of the volcanics. At the northern extremity of the area the formation rests on the Oakdale Formation. The upper boundary is the base of the first tuff band of the Bay Formation in the vicinity of the Mullions Range. In the Nubrigyn Creek area where the thickness is only about 300 feet, the base is the lowest tuff band or andesite flow of the Cuga Burga Volcanics. Just to the west of Kerr's Creek where neither the Mullions Range Volcanics nor the Cuga Burga Volcanics is present, the mapping of the Mumbil Formation is very difficult since it is overlain by the Cunningham Formation which contains few sandy bands here. The top of the Mumbil Formation has been taken in this area as the place in the sequence where the greenish colour of the claystones gives way to the grey shales and siltstone bands of the Cunningham Formation.

A number of limestone lenses have been recognized within the Mumbil Formation as shown on the map; they are probably equivalent to the Narragal Limestone (Strusz, 1960). The fauna of the northern-most one includes *Tryplasma* sp., *Phaulactis shearsbyi* and pentamerid brachiopods.

Bay Formation

The Bay Formation outcrops around the northern and eastern flanks of the Mullions Range. Outcrop commences near Kerr's Creek Railway Station passing around the northern end of the Mullions Range, along the eastern side through Bay Trigonometrical Station (after which the formation is named), and then south to Frederick's Valley Creek. The Bay Formation overlies the Mumbil Formation and underlies the Cunningham Formation but there is apparently an erosional break between the Bay Formation and the overlying Cunningham Formation. West of Kerr's Creek the Bay Formation is absent and the Cunningham Formation rests on the Mumbil Formation. The type section of the Bay Formation is exposed in Curragurra Creek at the northern extremity of the outcrop of the formation. The thickness in this section is approximately 400 feet, from here the thickness increases steadily along the eastern margin of the Mullions Range reaching about 1,500 feet at Frederick's Valley Creek. The proportions of the various lithologies making up the formation change throughout its outcrop. The type section is representative of the northern and more westerly part of the formation. It consists dominantly of tuffs of dacitic composition lithologically very similar to the variety of types found in the Merrions Tuff, ranging from coarse-grained crystal tuffs with chlorite-rich patches, to fine-grained chert-like types with a conchoidal fracture. A small proportion of siltstones and slates are present. By contrast, sections exposed to the south-east contain a higher proportion of slates and silts. In Frederick's Valley Creek, tuffs are less abundant than slates and silts and some greywackes are present. The top of the formation is taken as the top of the last tuff bed. It is overlain by greywackes, conglomerates and slates of the Cunningham Formation.

Cuga Burga Volcanics

Like the Bay Formation, the Cuga Burga Volcanics conformably overlie the Mumbil Formation. The volcanics occur only in the north-western corner of the area, extending south as far as the head of Weandre Creek. The volcanics have been traced intermittently into the Mumbil District whence they were first described (Strusz, 1960). The best exposed section in the Euchareena district is seen in the vicinity of Eadvale, in the east-west gully in Portion 58 of the Parish of Nubrigyn. The exposure there consists of about 1,000 feet of andesite flows which exhibit pillow structures in places, overlain by about 500 feet of interbedded shales and tuffaceous rocks. These latter are similar to the tuffs of the Bay Formation, containing abundant felspar, some quartz and chlorite. The beds of tuff are thin, of the order of one to three feet thick. The top of the formation is the uppermost bed of tuff.

Cunningham and "Nubrigyn" Formations

The Cunningham Formation is by far the most extensive stratigraphic unit in the Euchareena area, outcropping from Nubrigyn Creek to the Macquarie River. Limestones, impure calcarenites and conglomerates interdigitate with the western margin of the outcrop of the Cunningham Formation. The limestones were mapped by Carne and Jones (1919) who gave them the name of the Nubrigyn (limestone) belt. All the limestone lenses were collectively called the Nubrigyn Limestone by Packham (1958). Wolf (1965) modified this term by including the clastic calcareous and lithic sediments as well as the limestones in the Nubrigyn Formation. The southern and eastern limits of the formation have not been defined closely, so at present it seems best to use the term "Nubrigyn Formation" provisionally until its stratigraphic and geographic limits are established. The approximate limits of the rocks of "Nubrigyn Formation" lithology are shown on the regional geological map.

The basal beds of the Cunningham-"Nubrigyn" sequence along the western margin of the outcrop are shales which are overlain by interbedded calcareous labile sandstones, polymictic conglomerates and shales, containing limestone lenses which Wolf (1965) regards as algal bioherms. The limestone lenses occur abundantly over about six square miles mainly south of Boduldura Creek but extend south over about nine miles. Wolf (1965) divided the sequence above the basal shale into four units in the Boduldura Creek area. The lowest consists of well-bedded impure calcareous sandstones, calcarenite, shale and large algal bioherms. The second is not so well bedded, the algal bioherms are smaller and more frequent, local areas of andesite occur (? flow remnants) and there are limestone breccias developed around some of the limestone pods. The third unit contains abundant volcanic detritus and further ? flow remnants. Current bedding is common in the arenites. The highest part of the exposed section is an algal bioherm. The thickness of these strata preserved in this area is of the order of 1,700 feet.

Much of the calcareous material in the "Nubrigyn Formation" contains obscure organic structures which Wolf (1965) regards as algal. From the better preserved material Johnson (1964) has described the following algae: *Hedstroemia australe*, *Garwoodia primitiva*, *Litanaia robusta*, *L. cracens*, *Abacella deliculata*, *Lancicula wolfi*, *Uva* sp., *Litopora spatiosa*, *Girvanella* sp. aff., *Girvanella ducii*, *Rothpletzella devonicum* and *Renalcis devonicus*. Johnson also records the presence of the encrusting foram *Wetherdella*. Many other fossil groups are present, tabulate and rugose corals are common, stromatoporoids, brachiopods and conodonts have been found. The coral fauna recorded by Strusz (1968) is *Acanthophyllum* (*Neostringophyllum*) *implicatum*, *Calceola* sp., *Eridophyllum immersum*, *Hexagonaria approximans cribellum*, *Pseudochonophyllum pseudohelianthoides* and *Xystriphyllum dunstani*. *Pseudamplexus princeps*, *Tryplasma* spp. and *Receptaculites* sp. are also present. A number of conodonts have been isolated from beds in the lower part of the formation 0·6 miles north-north west of the junction of Boduldura and Nubrigyn Creeks. The forms present include *Spathognathodus linearis*, *S. inclinatus wurmi*, *S.* cf. *steinhornensis*, *Icriodus pesavus*, *Ozarkodina* sp. cf. *O. jaegeri*, *O. media*, *O. denckmanni*, *Trichonodella* sp., *Neoprioniodus* sp., *Hindeodella* sp. and *Panderodus unicostatus*. The age of the formation is Lower Devonian, its precise position is discussed later in this paper.

The other material in these sediments is igneous and metamorphic; fragments of andesites, basalts, dolerite, fine-grained acid volcanic rocks, quartzite and granite are all present. The first two were probably derived from the underlying Oakdale Formation, the Cuga Burga Volcanics or possible contemporaneous flows. The dolerite fragments are very altered and very little can be determined of their original petrography. Dolerites are known to intrude Ordovician and Silurian rocks to the south-west in the Cargo-Cudal district (Stevens, 1950), to the north in the Wellington district (Basnett and Colditz, 1946), and closer at hand to the north in the Mumbil district (Strusz, 1960); intrusions of this type are a likely source for the dolerite fragments in this formation. The acid volcanic fragments bear a strong resemblance to the rocks of the Mullions Range Volcanics, part of which could have been exposed at the time. The fragments in question bear very little resemblance to the Silurian Canowindra Porphyry (Stevens, 1950; Ryall, 1965) which outcrops to the west but could be compared with the early Devonian lavas of the same region, i.e., the Bull's Camp Volcanics (Packham and Stevens, 1955), the Duladerry Rhyolite (Stevens, 1954) and similar rocks in the Cumnock area (Joplin and others, 1952). The last mentioned is only 12 miles west of Nubrigyn Creek. The quartzite and granite pebbles are more difficult to account for, they apparently came from further afield.

The arenites and conglomerates in the vicinity of Nubrigyn Creek are well sorted (see Table 7) and occasionally cross-bedded. The arenites have a carbonate cement (Plate xi, fig. 6) or a small proportion of chlorite matrix (Plate xi, fig. 8). Individual beds are lenticular. These features, as well as their intimate association with the algal limestones, point to deposition in a shallow water environment.

To the east of the calcareous facies of the "Nubrigyn Formation" both arenites and conglomerates are rare and almost all of the succession consists of slates and silts. Patches of conglomerate have been found in three localities, viz., two and a half miles west of Euchareena, by the side of the Molong road; in the first railway cutting to the north of Euchareena Railway Station; on the road one and a half miles west of Store Creek Railway Platform. The first and second localities are important since the conglomerates contain fossils: *Acanthophyllum* sp. and *Calceola* sp. at the first, and *Acanthophyllum* sp. and *Syringopora flaccida* at the second locality. In view of the association of these conglomerates with fine-grained sediments and their occurrence in small masses it seems likely that they are slide deposits.

South of Nubrigyn Creek, sandy beds are not common in the lower part of the Cunningham Formation. In the vicinity of Kerr's Creek, the coarsest beds are laminated siltstone to very fine sandstone bands. To the east of this latter area, where the Cunningham Formation is in contact with the Bay Formation, some of the basal beds of the Cunningham Formation in the vicinity of the Mullions Range are conglomeratic, containing pebbles of acid lavas and quartzite. These conglomerates differ from those occurring to the north-west in the vicinity of the Nubrigyn Limestone in that they contain a larger proportion of matrix. The arenites and the conglomerates of the southern area are of the greywacke suite (Plate xi, fig. 5, Table 7) in contrast to those of the labile sandstone suite in the north-west.

TABLE 7

Micrometric analyses of arenites from the Cunningham Formation in the Euchareena district

	A	B	C	D
Quartz	21·2	13·8	5·0	3·6
Felspar	5·1	5·4	10·0	8·8
Igneous rock fragments ..	13·6	36·1	61·5	73·4
Sedimentary rock fragments ..	9·5	5·0	14·7	5·4
Matrix	50·6	39·7	8·1	8·8

A. PT 88. Greywacke, Curragurra Creek, 3 miles east of Euchareena.
B. O 120. Greywacke at base of Cunningham Formation, Curragurra Creek, 4 miles south-east of Euchareena.
C. O 21. Labile sandstone, from "Nubrigyn Formation", 4 miles west of Euchareena.
D. O 29. Labile sandstone, from "Nubrigyn Formation", 7½ miles north-west of Euchareena.

East of Store Creek and Euchareena, arenites are extremely rare. In the entire section exposed in Curragurra Creek there are only two or three beds of greywacke (the micrometric analysis of one of these is given in Table 7). Graded-bedding is common only east of the railway line. The silts have occasional bands of small-scale cross-bedding and convolute bedding. Unfortunately most of these structures have been observed in loose blocks on the sides of hills and it has not been possible to use them as indicators of the direction of slope of the sea-floor.

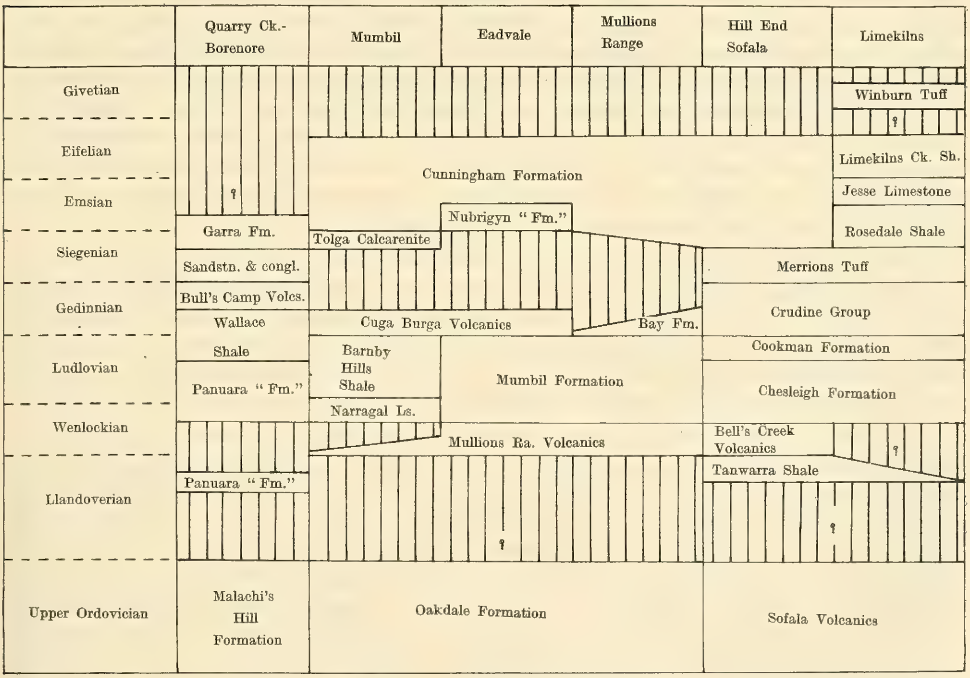
A magnificent slump structure is exposed in the narrow gorge of Curragurra Creek, four miles east of Euchareena. The structure is not so spectacular as the Ulmarrah Slump in the Hill End district because here the rock types involved are limited to interbedded silts and slates and the mass is only about 200 feet thick. The original bedding is still preserved, normally in folds with axial planes close to the regional dip. In places the sandy beds are reduced to contorted fragments in a shaly matrix; some of these fragments of beds are ten or so feet long (Plate x, fig. 8). Examination of the folds in this slump indicate that the anticlines, recognizable by the presence of graded bedding in the silts, have their crests facing east, suggesting that the slump has moved towards the east and hence the sea-floor must have sloped downwards in that direction. This accords with the facies change of the formation towards shallow-water to the west and establishes the existence of a trough (the Hill End Trough) of sedimentation to the east. The eastern margin of this trough has been shown to lie to the east of the Wiagdon Thrust where shallow water sediments are again developed in the Limekilns area.

It is not known whether this slump is a local phenomenon or whether it forms an extensive slump sheet. The suggestion was made in the description of slump structures in the Hill End area (p. 66) that they originated to the west of Hill End and moved eastwards to their present locations. They could have originated anywhere on the easterly-sloping sea-floor and thus it may not be possible to trace them back to the western limb of the Ophir Syncline. The degree to which bedding has been destroyed in the slumps just to the west of Hill End indicates that they have moved considerably further than the slump in Curragurra Creek.

AGES OF FORMATIONS IN THE EUCHAREENA DISTRICT

The Oakdale and Mumbil Formations of the Euchareena district represent the southern extension of the two oldest formations of the Mumbil district (see Table 8). Their occurrence at Mumbil and their fauna have been described by Strusz (1960, 1961). Although Upper Ordovician graptolites occur in the Oakdale Formation at Mumbil, the highest beds, which contain limestone lenses, are Upper Ordovician or Lower Silurian on the evidence of their contained coral fauna. Strusz (1960) considered the overlying Mumbil Formation to range from "the topmost Llandoverian through most or all of the Wenlockian". Beds which Strusz regarded as basal beds of the Narragal Limestone (the lower member of the Mumbil Formation) contain some distinctive forms, including: *Palaeophyllum* sp., *Multisolenia tortuosa* and *Acanthohalysites australis*. Forms occuring in the main part of the limestone include: *Phaulactis shearsbyi* and *Entelophyllum latum*. *Monograptus bohemicus* (Lower Ludlow) occurs low in the overlying Barnby Hills Shale, which is the upper member of the Mumbil Formation. Dr. Strusz

TABLE 8
Regional correlation table



	Quarry Ck.-Borenore	Mumbil	Eadvale	Mullions Range	Hill End Sofala	Limekilns
Givetian	▥	▥	▥	▥	▥	▥ Winburn Tuff ▥ ?
Eifelian	▥	Cunningham Formation	Cunningham Formation	Cunningham Formation	Cunningham Formation	Limekilns Ck. Sh.
Emsian	▥ ? Garra Fm.	Cunningham Formation	Cunningham Formation Nubrigyn "Fm."	Cunningham Formation	Cunningham Formation	Jesse Limestone Rosedale Shale
Siegenian	Garra Fm. Sandstn. & congl.	Tolga Calcarenite ▥	▥	▥	Merrions Tuff	Merrions Tuff
Gedinnian	Bull's Camp Volcs. Wallace	▥ Cuga Burga Volcanics	▥ Cuga Burga Volcanics	▥ Bay Fm.	Crudine Group	Crudine Group
Ludlovian	Shale Panuara "Fm."	Barnby Hills Shale Narragal Ls.	Mumbil Formation	Mumbil Formation	Cookman Formation Chesleigh Formation	Cookman Formation Chesleigh Formation
Wenlockian	▥	▥ Mullions Ra. Volcanics	Mullions Ra. Volcanics	Mullions Ra. Volcanics	Bell's Creek Volcanics	▥ ?
Llandoverian	Panuara "Fm." ▥	▥	▥ ?	▥	Tanwarra Shale ▥	Tanwarra Shale ▥ ?
Upper Ordovician	Malachi's Hill Formation	Oakdale Formation	Oakdale Formation	Oakdale Formation	Sofala Volcanics	Sofala Volcanics

and I recently revisited the area and found that the limestones which he regarded as basal beds of the Narragal Limestone are separated from it by a thin succession of acid to intermediate volcanics, and thus the "basal" limestones are either part of or rest directly on the Oakdale Formation. The fauna is the same as that in the Oakdale Formation, and has little in common with the Narragal Limestone. There is no clear evidence then, that the Narragal Limestone extends far below the top of the Wenlock. In the vicinity of Euchareena, the Mullions Range Volcanics occur between the Oakdale and Mumbil Formations. These volcanics can be correlated with the acid to intermediate volcanics which underlie the Mumbil Formation at Mumbil (Table 8).

Further afield at Quarry Creek, 24 miles south-south-west of Euchareena, the Silurian sequence can be dated with some accuracy by means of the contained graptolite faunas (Packham, 1968). Beds at Quarry Creek, containing *Monograptus bohemicus* and therefore equivalent to the lower part of the Barnby Hills Shale are underlain by shales containing Upper Wenlock graptolites (principally *M. testis*). These are in turn underlain by cross-bedded sandstones, derived from acid volcanics. Below these sandstones are shales and fine quartzitic sandstones containing Upper Llandovery graptolites (*M. marri* is the most common). There is therefore a break in sedimentation between the Upper Llandovery and the Upper Wenlock, the result of an uplift called the Quarry Creek Phase of the Benambran Orogeny by Packham (1967*a*). Limestone (the Quarry Creek Limestone) underlies the Upper Llandovery sandstones and shales and overlies Upper Ordovician andesitic volcanics which can be correlated with the Oakdale Formation. The clastic succession with limestone bands at the top of what has been mapped as the Oakdale Formation near Nubrigyn Creek might contain Llandovery beds and be separate from the volcanics.

In view of the break in sedimentation recognized at Quarry Creek below the late Wenlock succession it seems likely that the Mumbil Formation ranges from Upper Wenlock to Ludlow and the Mullions Range Volcanics fall within the gap in the Quarry Creek succession. The absence of the volcanics at Quarry Creek and at other localities closer to the Mullions Range implies that interruption of deposition took place after the extrusion of the volcanics.

The Cuga Burga Volcanics which overlie the Barnby Hills Shale are on present evidence equivalent to the Bay Formation and have been placed just above the Silurian-Devonian boundary by Packham (1968) since there is a considerable thickness of shale above the occurrence of *Monograptus bohemicus* in the Barnby Hills Shale. This is a little higher than Strusz (1960) placed the Cuga Burga Volcanics. The Tolga Calcarenite which overlies the Cuga Burga at Mumbil has not been recognized in the area studied, but it has been found by Wolf (1965) and Kemezys (1959) a few miles to the north. The latter has found it to be unconformable on the volcanics. The calcarenite is apparently equivalent to or older than the shale unit in the Nubrigyn Creek area overlying the volcanics and below the limestones and lithic arenites. I suggested (Packham, 1967*a*) that the Tolga Calcarenite may be equivalent to part of the Garra Formation. This latter unit described by Strusz (1965) is a succession of shales and limestones over 4,000 feet thick, forming an outcrop extending about sixty miles north-south and about five miles east-west. Outcrop commences approximately nine miles west of the base of the Nubrigyn Formation. I also suggested (Packham, 1968) that the calcareous "Nubrigyn Formation" because of its considerable content of terrigenous sands and conglomerates may be younger than the Garra Formation in which such detritus is rare.

Based on his work on the corals, Strusz (1968) has suggested an Emsian age for the Garra Formation and from the few corals known from the "Nubrigyn Formation" a correlation with the higher beds of the Garra Formation would be indicated. Although the conodont faunas of the two formations are only very sketchily known, no great disparity in age is apparent. Rare platform conodonts (possibly *Polygnathus linguiformis dehiscens*) have been recovered from the highest parts of the Garra Formation (Philip, 1967). The upper part of the "Nubrigyn Formation" has to date yielded only small faunas but no platform types have been found. The conodonts from the lower part of the "Nubrigyn Formation" resemble those recorded from the lower beds of the Garra Formation by Philip (1967) but the corals suggest the highest levels. *Polygnathus linguiformis foveolata* incidentally, occurs in the Jesse Limestone at Limekilns. It is clear that some compromise has to be reached. Accordingly, in Table 8, it is suggested (*a*) that the Tolga Calcarenite is equivalent to the base of the Garra Formation, (*b*) that the lower part of the Garra Formation may be late Siegenian and (*c*) that the upper part is Emsian and equivalent in age to the lower part at least, of the Nubrigyn Formation but older than the Jesse Limestone.

Stratigraphic Correlations Throughout the Region

Although the fossil evidence at present available does not permit precise dating of the formations, it does, combined with the lithologically established successions, enable the relative ages of the various stratigraphic units in the region to be established with some confidence.

Commencing at the base of the succession, the oldest formation on the east, the Sofala Volcanics may be correlated generally with the Oakdale Formation, the oldest formation in the west. Whilst Ordovician graptolites occur in both formations it is possible that the formations might extend into the early Silurian. In the west there is no definite evidence of Llandovery sediments but the Tanwarra Shale of the Sofala area is best assigned to the Upper Llandovery or Lower Wenlock, at the latest. The overlying formation, the Bell's Creek Volcanics may then be correlated approximately with the Mullions Range Volcanics; both are probably Middle Silurian.

The approximate correlation of the Wenlock to Ludlow Mumbil Formation with the Chesleigh Formation follows from the lithological mapping of higher formations between Mudgee and Wellington along the Cudgegong River by Dickson (1962), Shatwell (1962) and Jones (1962). This mapping has enabled the relationship of the Cuga Burga Volcanics to the Crudine Group to be established. On the western limb of a large anticlinal structure south of Wuuluman and ten miles east of Wellington, the Cuga Burga Volcanics are overlain by slates and siltstones and above them is the Merrions Tuff. In the next anticline to the east, the Cuga Burga Volcanics are not present but are replaced by tuffs and greywackes of the Turondale Formation. This relationship indicates that the Turondale Formation and the Cuga Burga Volcanics can be correlated approximately and so too can the formations underlying them, the Chesleigh and Mumbil Formations respectively.

No formations in the Euchareena district are at present correlated with the Waterbeach Formation and the Merrions Tuff. There was apparently erosion in the west at that time.

The Cunningham Formation which is represented in the central and western parts of the region, passes laterally both eastwards and westwards into calcareous sediments. The Tolga Calcarenite and at least the lower part of the "Nubrigyn Formation" are older than the Jesse Limestone judging by the conodont assemblages (see p. 52). The possibility that the Tolga Calcarenite and the "Nubrigyn Formation" are equivalent to the Waterbeach Formation and the Merrions Tuff has not been entirely ruled out. There is, however, no clear evidence of calcareous detritus being shed into the western part of the geosynclinal region even in small quantities from the west until the deposition of some 5,000 feet of the Cunningham Formation had taken place. The highest formation in the east, the Winburn Tuff has no known equivalent in the central and western parts of the region.

Intrusive Rocks

This whole region is remarkably free from intrusive bodies compared with other parts of the Lower Palaeozoic Belt of eastern Australia. Apart from minor intrusions associated with the andesitic volcanics, the intrusives fall into two types, viz. granitic masses and dolerite dykes and sills.

Three small, massive, granitic bodies outcrop in the area: the Wiagdon Granite (named after the Parish of Wiagdon), the Millah Murrah Granite (named after the Parish of Millah Murrah) and the Bruinbun Granite (named after a locality on the Macquarie River south of Hill End). In each case the contacts are sharp and cross-cutting. These granites are probably part of, or are related to, the Bathurst Granite which outcrops very extensively to the south.

The dolerites occur in two groups roughly symmetrically placed on both sides of the region. They occur towards the margins of the central strongly cleaved zone. In the east, they are most common in the upper part of the Chesleigh Formation. They have been involved in the general low grade metamorphism of the region.

Structure

Folding

Throughout the greater part of the region, the folds have steeply-dipping axial planes. In the central part of the area a strong cleavage has developed. This cleavage first appears in the slates and as the degree of deformation increases it penetrates the coarse rocks as well. Overturned beds occur in the central part of the area but their dips are steep. It is only in the vicinity of the Wiagdon Thrust to the south of Wattle Flat that overturned beds dipping at less than 45° are encountered.

There is a general concordance between the stratigraphy and the structure of the region. The central area of maximum deposition during Crudine and Cunningham "times" is the most deformed and has been thrust eastward over a more stable area. The axial planes of the folds in the western part of the region dip to the east at angles of 70 to 80 degrees. To the east dips gradually steepen until at Hill End the axial planes are approximately vertical; still further to the east they dip steeply to the west. Along the Turon River, east of Hill End and extending to the north, is a zone in which the Cunningham Formation has been almost isoclinally folded and the overturned limbs of the folds dip steeply to the west. This gives an asymmetry to the regional structure because there is no corresponding zone to the west of Hill End. The asymmetry is further emphasized by the thrust faults which occur to the east. The Hill End anticline marks a very considerable culmination in the folds of the trough, the sediments exposed along its crest being some 20,000 feet stratigraphically lower than those in the trough of the Ophir Syncline to the west and about 15,000 feet below the highest beds in the isoclinally folded zone of the Cunningham Formation rocks to the east, about Sally's Flat.

The regional cleavage mentioned above seems to be an axial plane cleavage. It first appears at about the meridian of the Orange-Wellington railway line and extends eastwards as far as the Wiagdon Thrust. Although the rocks of the eastern side of the Wiagdon Thrust, in the area north-east of Peel, are most strongly overturned, having their axial planes dipping at 20° or so, cleavage is not developed in them.

Apart from the change in dip of the axial planes of the folds there is also a swing in strike across the region. In the north the change is from N 30°W on the western side to N 20°E on the east. The fold axes are closer packed to the south and they are generally parallel, striking approximately N 20°W. The plunge is gently towards the north in most folds.

Where grain elongations have been observed and these are common in the greywackes of the Cunningham Formation, they are approximately perpendicular to the fold axes and the bedding-cleavage intersections. Pyrite "shadows" have a similar orientation.

The metamorphism which affected the region was of low grade being no higher than green-schist facies, though there is an increase in its intensity from the margins of the area where chlorite, albite and muscovite occur, towards the centre, where biotite is common. This parallels the stronger folding and the more intense development of cleavage in the central part of the region. In addition, accompanying the northerly structural plunge there is some narrowing of the width of the biotite-bearing zone northwards. Along the southern margin of the area mapped the zone has a width of about 20 miles while at the latitude of Hill End it is about 17 miles wide.

Faulting

Minor Faults

As far as can be determined at the scale of mapping, faulting is remarkably rare in this region. Three minor faults have been mapped; one is a cross fault in the west of the region near Kerr's Creek, the second is a high-angle thrust fault six miles east of Hill End. The third is, in all probability, also a high angle thrust fault cutting off the Mullions Range Volcanics along the western side of the Mullions Range. Two localities have been found where the cleavage has been disturbed by later movements. In neither case did it seem that faulting significant on the scale of mapping had taken place. One of these localities is on the Winburndale Rivulet about half a mile from the Macquarie River and the other on the Macquarie River, one and a quarter miles upstream from its junction with Lewis Ponds Creek.

The Wiagdon Thrust System

The Wiagdon Thrust fault is the most important tectonic feature of the region. At present it is known to extend from Gulgong in the north to the Bathurst Granite near Yetholme in the south, a distance of some eighty miles. The thrust dips to the west but at varying angles. North of Sofala the dip is of the order of ten degrees—in some places even less. Near Wiagdon Hill the dip is considerably steeper and is of the order of sixty degrees. The strike likewise is very variable. North of Sofala, it is parallel to the fold axes of the area (N 30°E), and after crossing the Turon River runs approximately north-south. At Wiagdon Hill, south of Wattle Flat, the fault swings suddenly towards the south-east and then returns to N 10°E and continues in that direction to Cheshire Creek. This variation in strike, which affects the folds to the west as well as the fault, appears to be a reflection of the configuration of the mass against which the sediments to the west were folded and thrust. In the discussion of the stratigraphy of the Sofala

Volcanics some evidence was presented for the existence of a local volcanic focus near Sofala in the last stages of the vulcanism.

North of Wiagdon Hill, the thrust is apparently parallel to the bedding of the over-riding sediments, with the thrust plane occurring at about the Tanwarra Shale (sometimes within it and sometimes just below it in the Sofala Volcanics).

To the south at Wiagdon Hill, the thrust occurs within the Sofala Volcanics and several hundred feet of the volcanics have been thrust over the Chesleigh Formation. Towards the southern edge of the area mapped the fault plane passes into the Chesleigh Formation as the result of the development of an overturned anticline at the base of the overthrust mass. Two minor thrusts occur on the foreland side in the south.

Instead of the Sofala Volcanics being swept clean of later formations on the foreland side by the thrust, south-east of Wiagdon Hill the entire sequence has been preserved. This is the direct result of a southerly plunge of the folds on the foreland side which may be attributed indirectly to the suggested thinning of the volcanic pile at the top of the Sofala Volcanics. Just to the east of the thrust in this southern area the greatest degree of overturning in the whole area has been observed. Overturned dips between 65° and 20° are normal. In exceptional cases the beds are horizontal (overturned) and in one local pucker a dip of 40° to the east was observed; this overturned zone is bounded by a minor thrust which dies out to the north where the main thrust swings to the west.

North of the Turon River, the thrust structures again become complex. About a mile north of the river a new dislocation becomes apparent, this time to the west of the main thrust line. It appears within the Chesleigh Formation bringing the upper part of the Chesleigh Formation against the Bell's Creek Volcanics and then, further north, the Cookman Formation against the Bell's Creek Volcanics. The main Wiagdon Thrust is again in the Tanwarra Shale or just within the Sofala Volcanics.

The Wiagdon Thrust can be observed where it crosses the Turon River and at a number of localities about five miles north of Sofala in tributaries of Cookman Creek. In these planes there is a transitional zone from sheared andesite of the Sofala Volcanics to phyllite derived from the Tanwarra Shale. The original bedding of the Tanwarra Shale is broken down but deformed traces of it remain both on the microscopic and the macroscopic scale.

Razorback Thrust

This fault was discovered by Day (1961) four miles north of the Turon River in the vicinity of the Razorback Mine from which it takes its name. This fault is on the extreme east of the area and brings the Sofala Volcanics up against westerly-dipping Upper Devonian sandstones cutting off the western limb of the synclinal structure in which the sandstones lie. There is sufficient relief in the vicinity of the Turon River to determine that the fault plane dips steeply to the west. It is the only structure in the area for which a post-Upper Devonian age can be demonstrated.

General Summary of Depositional History

Ordovician

Ordovician rocks are exposed on the eastern and western margins of the region and andesitic volcanic material dominates both areas. The few sedimentary structures observed in the lower part of the Sofala Volcanics suggest an eastward slope of the sea-floor and the deposits represent a turbidite facies.

Higher, pyroclastic debris becomes more abundant and the presence of occasional limestone lenses in the upper part of the formation implies some shallowing but this may be only of local significance. The stratigraphy of the Oakdale Formation is unknown in detail but limestone lenses occur within the higher parts of the Upper Ordovician in the formation and at lower stratigraphic levels further west (e.g., at Molong and Bowan Park). This evidence, though fragmentary is consistent with the palaeogeographic pattern which existed in the later Silurian. The sea-floor sloped generally to the east into a region of turbidite deposition (the Hill End Trough) and commencing at the western margin of the region under discussion and extending further west, was an elevated zone (the Molong Geanticline). A second trough of turbidite deposition, the Cowra Trough, was probably in existence at this time west of the geanticline (Packham, 1967).

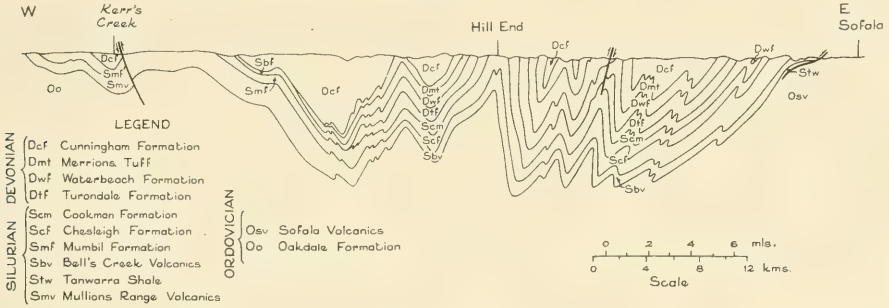


Figure 10. Cross-section from Sofala to Kerr's Creek. Section projected to depth to demonstrate stratigraphic relationship between formations in eastern and western margins of the Hill End Trough.

Silurian

It is not known whether the Sofala Volcanics and the Oakdale Formation extend into the Silurian. The possibility exists that deposition may have been interrupted by early phases of the Benambran Orogeny. The Tanwarra Shale though not definitely proven to be Lower Silurian, is probably of that age or basal Wenlock at the latest. The conglomerate at the base of the formation represents an erosional break which might be correlated with one of the two Lower Silurian orogenic phases of the Benambran Orogeny in the Orange district, the Cobbler's Creek Phase at about the base of the Llandovery or the Panuara Phase at about the middle of the Llandovery (Packham, 1968). If the correlation can be made the later one is the more likely.

The two acid volcanic formations which follow, the Mullions Range Volcanics in the west and the Bell's Creek Volcanics in the east are apparently Middle Silurian. It was suggested that the Mullions Range Volcanics lay within the gap in deposition from late Llandovery to Upper Wenlock found to occur at Quarry Creek. Mapping of the base of the volcanics has failed to reveal the presence of Llandovery beds beneath them except perhaps in the north, giving the impression that there is at least a disconformity between the Mullions Range Volcanics and the Oakdale Formation. Because of the absence of the Mullions Range Volcanics in nearby sections to the west, such as the one along the Bell River only four miles west of the 1,500 feet-thick type section of the volcanics, it is likely that the volcanics antedate the Quarry Creek Phase of the Benambran Orogeny. The regional distribution of the Bell's Creek Volcanics is also suggestive of tectonic movements post-dating them. The Chesleigh Formation which normally overlies the Bell's Creek Volcanics, overlies the Sofala Volcanics in the vicinity of Wattle

Flat, east of the Wiagdon Thrust. If these relations are the result of a local uplift, the uplift is roughly contemporaneous with the Quarry Creek Orogenic Phase.

The lower parts of the Chesleigh Formation and the Barnby Hills Shale are composed of sediments consisting of quartz, white mica and some chlorite; volcanic debris is rare. Deposits of this composition are common in Ludlow successions in the southern highlands of New South Wales, and sedimentary structures in the Chesleigh Formation in the Sofala area indicate a downward slope of the sea-floor to the east-north-east. The detritus was probably derived from Ordovician sediments (with minor contributions from granitic sources), exposed in the southern highlands of New South Wales and eastern Victoria as a result of the Benambran Orogeny. The sediments might have been transported northwards along the trend of the Benambran structures and thence into the trough. The sediments deposited on the Molong Geanticline at this stage, apart from the Narragal Limestone and its equivalents, are fine-grained (siltstones and shales) although their environment of deposition is unknown. The sediments in the Hill End Trough are coarser, consisting of interbedded slates, siltstones and fine-grained greywackes and having the typical features of a turbidite facies.

The dacitic volcanic debris in the upper part of the Chesleigh Formation, which is intermingled with detritus similar to that in the lower part, has no known equivalent in the Euchareena area. It occurs in both the Hill End and Sofala occurrences of the formation, though in the latter it is a minor constituent south of the Turon River, increasing rapidly in abundance northwards. Deposition throughout is in turbidite facies and the directional features of the sedimentary structures are consistent with those of the lower part of the formation. The volcanic centre supplying the detritus probably lay to the west or south-west of Hill End. It has not as yet been identified.

The highest formation regarded as Silurian in the Sofala area is the Cookman Formation. At its base, an important change in the pattern of sedimentation took place. Sedimentary structures indicate a reversal of the direction of source of the sediments. From this formation onwards, in the Hill End and Sofala areas, detritus came from the east. The Cookman Formation is a sequence of slates and quartz-rich greywackes. Their petrography is consistent with their having been derived from the Chesleigh Formation with minor contributions from underlying formations. The uplift of the structure to the east (the Capertee Geanticline) which considerably restricted the Hill End Trough can be regarded as part of the Bowning Orogeny and may be contemporaneous with the Yarralumla Phase (Öpik 1958). The upper part of the Barnby Hills Shale was probably deposited at the same time as the Cookman Formation.

Devonian

The new palaeogeographic pattern established with the commencement of deposition of the Cookman Formation persisted throughout the remainder of the history of the Hill End Trough. At approximately the beginning of the Devonian, vulcanism was renewed, this time on a grand scale, especially in the east. After the basal breccias of the Crudine Group, the remainder of the Turondale Formation consists of thickly bedded dacitic tuffs, greywackes composed of tuffaceous material, conglomerates and interbedded slates and siltstones. The Cuga Burga Volcanics were poured out in the northern part of the Euchareena area and northwards extending down into the Hill End Trough. Dacitic vulcanism responsible for the Bay Formation produced clastic sediments similar to those of the Turondale Formation in the southern part of the Euchareena area at about this time. The axis of the trough lay west of the Hill End Anticline as it must have done during the deposition of the Cookman Formation.

The Waterbeach Formation (the upper part of the Crudine Group) is free from evidence of contemporaneous volcanic activity. Nevertheless its greywackes are composed almost entirely of material ultimately of volcanic origin and similar to that of the Turondale Formation. Except for the sediment contained in the Ulmarrah Slump which is the most westerly occurrence of the formation, the detritus appears to have been derived from the east. The axis of the trough remained just west of the Hill End Anticline.

Wolf (1965) and Kemezys (1959) have mapped an erosional junction at the top of the Cuga Burga Volcanics and the distribution of the Cuga Burga Volcanics and the Bay Formation in the Euchareena area is compatible with such a contact. Any uplift on the western side of the trough would have probably increased the slope on the eastern side of the Molong Geanticline and initiated the Ulmarrah Slump.

The axis of the trough seems to have been at its western limit during the deposition of the Merrions Tuff, lying at least eight miles west of the Hill End Anticline and less than 16 miles east of the present outcrop of the Oakdale Formation. The thick beds of dacitic pyroclastic material of the Merrions Tuff, like those of the Turondale Formation have been interpreted as some kind of turbidite deposit. While it is possible that turbidites could have flowed up the western side of the trough to some extent, the distance was probably not significant, especially since dacite flows within the formation are found west of the Hill End Anticline. The westward shift of the axis may have been the result of infilling from the east.

Vulcanism in the trough ended with the Merrions Tuff, and with the return of normal greywacke sedimentation in the Cunningham Formation, the axis of the trough moved eastwards to about the Hill End Anticline. The sediments of the central part of the trough are fine but in the east pass into a zone in which greywackes and conglomerates are common. In some of these beds the amount of matrix is small. This distribution suggests that the slope was short and perhaps steep and that the main part of the trough was flat. The slope on the west may have been more regular since slump structures are common as far east as Hill End. The Limekilns Group which overlies the Merrions Tuff, east of the Wiagdon Thrust is correlated with the Cunningham Formation. The age of the limestone in the middle of the Group is Emsian to perhaps basal Eifelian on the basis of its conodont fauna. Judging by its fauna the Limekilns Group was deposited largely in the neritic environment. No indication of turbidite deposition has been found in it. On the west, the Cunningham Formation passes into the calcareous facies of the "Nubrigyn Formation". The transition is extremely rapid. The "Nubrigyn Formation" apparently represents a near-shore turbulent environment with algal reefs, limestone breccias, abundant coarse terrigenous material derived from a variety of sources with evidence of local vulcanism. These pass eastwards rapidly into sequences of slates and siltstones with rare greywackes, boulder horizons and calcareous turbidite beds. The basal part, if not all, of the "Nubrigyn Formation" is older than the Jesse Limestone.

Overlying the Limekilns Group in the vicinity of Limekilns and extending south for some miles is the Winburn Tuff, a formation which has lithological features very similar to those of the Merrions Tuff but is much richer in orthoclase. The field relations are strongly suggestive of a unconformity with the Limekilns Group. The Winburn Tuff is in turn overlain unconformably by quartzites and shales of the Upper Devonian Lambie Group. The latter unconformity is representative of a phase of the Tabberabberan Orogeny. The former might be regarded as related to an earlier phase of the same orogeny.

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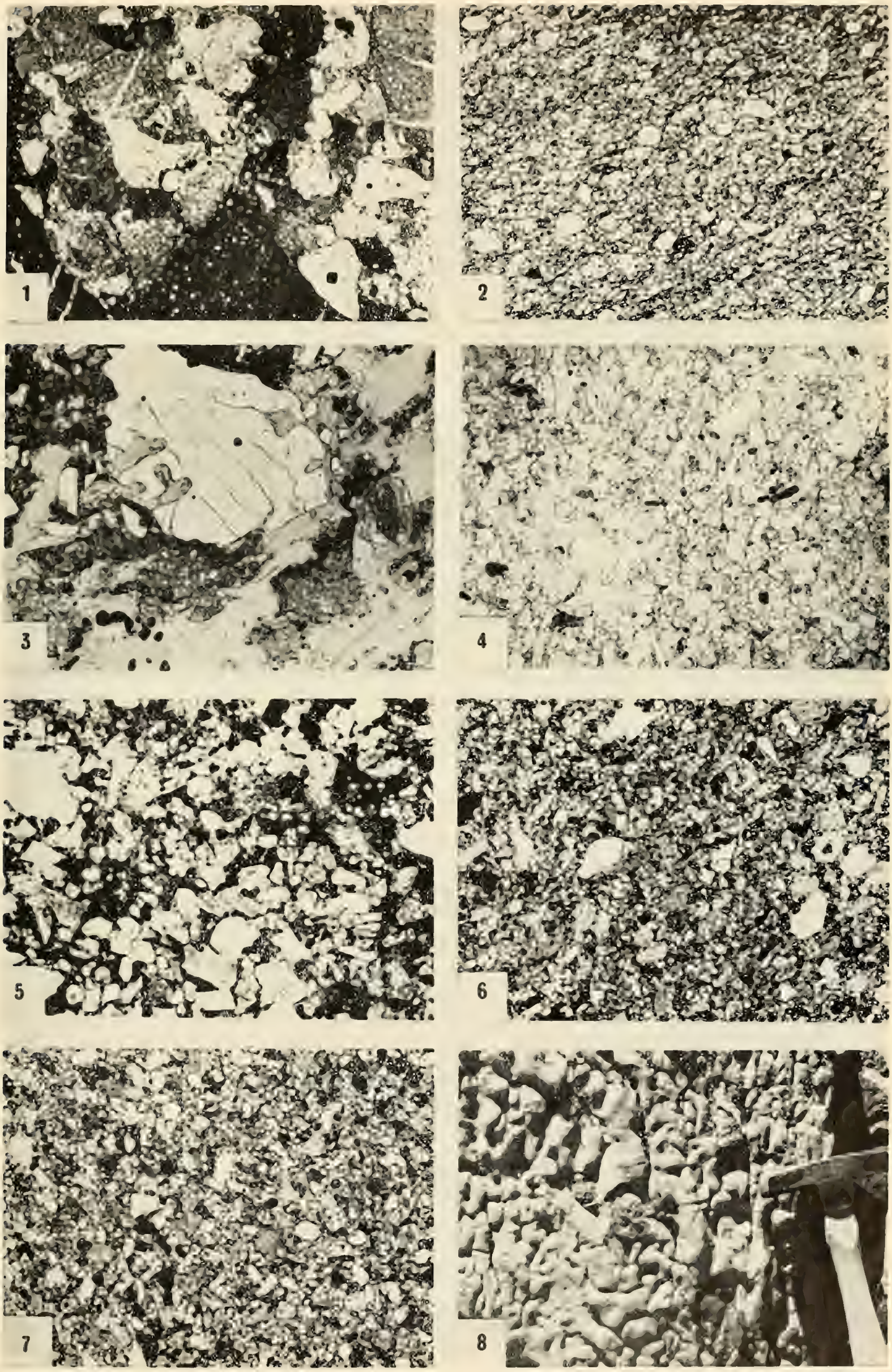
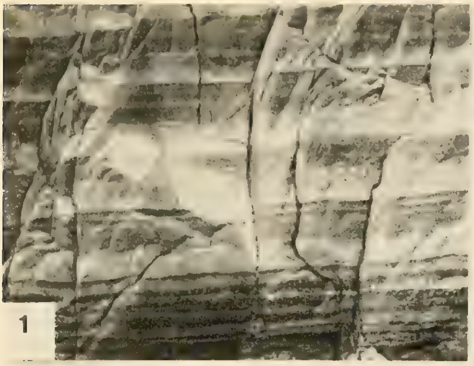


The Lower and Middle Palaeozoic stratigraphy and Sedimentary Tectonics of the Sofala-Hill End–Euchareena region, N.S.W.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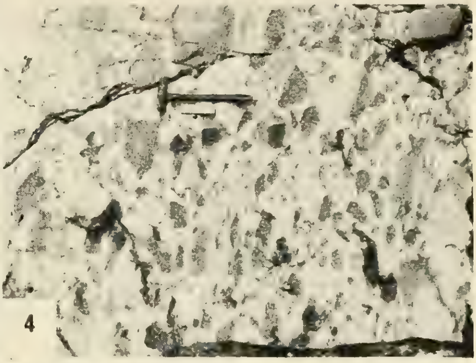
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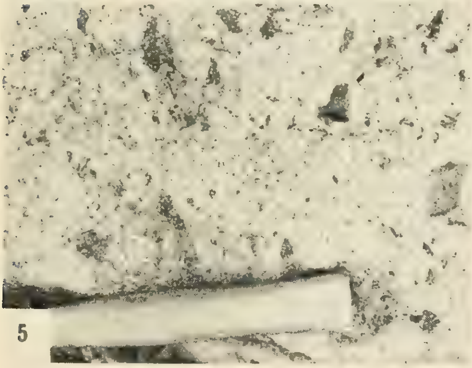
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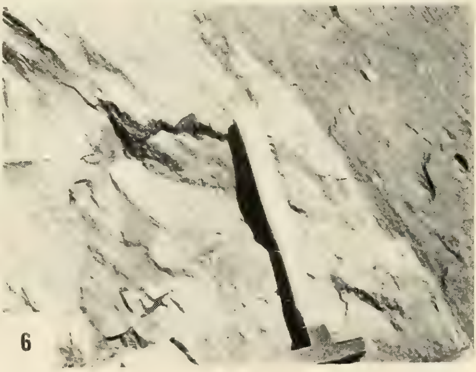
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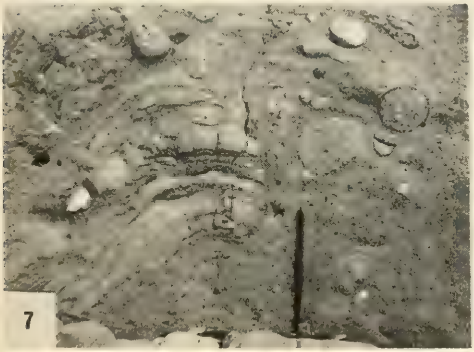
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8

The Lower and Middle Palaeozoic stratigraphy and Sedimentary Tectonics of the Sofala-Hill End–Euchareena region, N.S.W.

PLATE XII

GEOLOGICAL MAP OF THE EUCHAREENA-HILL END-SOFALA AREA

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EXPLANATION OF PLATES

PLATE IX

Fig. 1. Breccia composed of fine-grained sedimentary rocks, some containing quartz veins. ×8. Sofala Volcanics, Turon River, Portion 53 Parish of Stewart. Fig. 2. Subgreywacke. ×8. Chesleigh Formation, upper part of Wiagdon Hill, 2½ miles south of Wattle Flat. Fig. 3. Chloritic patch in tuffaceous arenite. ×8. Turondale Formation, 1½ miles south-east of Turondale. Fig. 4. Subgreywacke. ×8. Cookman Formation, Type section of formation, Turon River, 3½ miles west of Sofala. Fig. 5. Tuffaceous arenite. ×8. Turondale Formation, Type-section, Turon River, 1,300 feet above the base of the formation. Fig. 6. Greywacke from the base of bed 80″ thick. ×8. Waterbeach Formation, Type-section, Turon River, 1,350 feet above the base of the formation. Fig. 7. Greywacke from same bed as above. 70′ above the base of the bed. ×8. Fig. 8. Load casts on the base of a subgreywacke. Chesleigh Formation, 3¼ miles west-north-west of Limekilns.

PLATE X

Fig. 1. Graded-bedded silts and slates. The photograph represents three feet of section. Waterbeach Formation, junction of the Macquarie River and Winburndale Rivulet. Fig. 2. Greywacke conglomerate with a large proportion of matrix. Turondale Formation, Turon River, 2 miles north of Turondale. Fig. 3. Graded-bedding in silts and slates in overthrust beds east of the Wiagdon Thrust. Crudine Group, 3 miles north-west of Limekilns. Fig. 4. Coarse breccia containing blocks of dacite. Merrions Tuff, Type section, Turon River, 1,550 feet above the base of the formation. Fig. 5. Tuffaceous arenite with chloritic patches. Merrions Tuff, 2 miles north of Limekilns. Fig. 6. Outcrop of mudflow horizon (the hammer rests on sandy phase) showing contact between sandy and muddy phases. Cunningham Formation, Type section, Turon River, 2,150 feet above the base of the formation. Fig. 7. Boulder bearing greywacke injected into slates or siltstones in the Ulmarrah Slump. Waterbeach Formation, Ulmarrah Anticline, Pyramul Creek. Fig. 8. Contorted siltstone band in slump structures. Cunningham Formation, Curragurra Creek, 5 miles north-north-east of Euchareena.

PLATE XI

Fig. 1. Tuffaceous arenite containing abundant epidote. ×8. Merrions Tuff, Type section, Turon River, 850 feet above the base of the formation. Fig. 2. Matrix of mudflow horizon. ×8. Cunningham Formation, Type section, Turon River, 2,150 feet above the base of the formation. Fig. 3. Greywacke. ×8. Cunningham Formation, ¾ mile west of eastern boundary of the formation on the Sofala-Sally's Flat road. Fig. 4. Greywacke. ×8. Cunningham Formation, Type section, Turon River, 2,500 feet above the base of the formation. Fig. 5. Greywacke. ×8. Base of Cunningham Formation, Curragurra Creek, 4 miles south-east of Euchareena. Fig. 6. Labile sandstone with carbonate cement. ×8. "Nubrigyn Formation", 4 miles west of Euchareena. Fig. 7. Greywacke matrix of the Ulmarrah Slump. Waterbeach Formation, Ulmarrah Anticline Pyramul Creek. Fig. 8. Labile sandstone. ×8. "Nubrigyn Formation", 4 miles west of Euchareena.

PLATE XII

Geological Map of the Sofala-Hill End-Euchareena Region.

THE CONSTITUTION, DISTRIBUTION AND RELATIONSHIPS OF THE AUSTRALIAN DECAPOD CRUSTACEA

A PRELIMINARY REVIEW*

D. J. G. GRIFFIN and J. C. YALDWYN
The Australian Museum, Sydney, N.S.W.

[Read 24th April, 1968]

Synopsis

Approximately 1200 species are recorded from Australia, representing 57 of the 73 known decapod families. These are placed in 361 genera. About 54% of the species belong to the Brachyura. Xanthid and majid crabs as well as parastacid crayfish are well represented. Little is known of many natant groups. The majority of species are tropical and many are widespread northern forms; there are a smaller number of widespread southern forms. The tropical fauna shows close affinities with the faunas of other Indo-West Pacific areas.

INTRODUCTION

There are approximately 1,200 species of Crustacea Decapoda currently recognized and recorded from the Australian area representing 57 of the 73 families into which the living members of this order are at present divided. The Australian species range in size from the transparent, planktonic, sergestid shrimp *Lucifer*, a few mm. in length, through the whole range of variously-sized prawns, crayfish, hermit crabs and true crabs, up to the giant xanthid crab of the southern continental shelf, *Pseudocarcinus gigas*, reaching at least 30 lb. in weight and 13 inches across the carapace. Decapods are found on land, in freshwater, on sandy beaches, in mangrove swamps and in the sea, from the surface of the open ocean through all depths, and on all bottoms, down to the floor of the nearby hadal trenches of this area. On the continent itself, species occur from the upper slopes of the Snowy Mountains, through the streams and swamps of almost all land and vegetation types, to the intermittent waters of some parts of the inland deserts.

The present review is an attempt to systematize certain aspects of the currently available knowledge of the diversity, distribution and relationships of the Australian Decapod fauna.

The data used in this review come from a series of largely uncritical family and subfamily checklists prepared from the decapod literature index held in the Crustacea Department at the Australian Museum. This index was initiated by A. R. McCulloch early this century, but has been greatly expanded and developed by F. A. McNeill since then. McNeill in fact, since his retirement as Curator of Crustacea in 1961, has still remained largely responsible for keeping this unique and invaluable index up to date. Without its help we would have been unable to present this study in its present form. The index is basically a cross-referenced file of decapod species recorded in published literature for Australia and nearby areas. It pays special regard to synonymy, recorded localities and illustrations. It also contains numerous unpublished observations, new records, extensions to range, suspected

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* The revised text of a paper presented at the Australian/New Zealand Meeting on Decapod Crustacea, Sydney, October 24–28, 1967.

synonyms, drawings, photographs and colour sketches. Though incomplete, its imperfections are largely known, and it is being continually expanded and developed. There are at present approximately 28,000 items individually indexed and systematically arranged in this file.

The present review is restricted to Australian species and localities actually published, in press or in draft manuscript known to us in July, 1967. In a very few cases certain clear, specific omissions or new state records, known to several workers on our fauna, and not in the above categories, are included. Many new records for Australia, recorded only in the Museum literature file, or known only to workers with an Australian group under review, are not included in the present study. No attempt has been made to search the collections of the Australian Museum, or other State museums, for extensions of range or to confirm the presence or absence of species from areas considered in the tables below. Such a search was not considered necessary or practicable at this stage; in the opinion of the authors, the extra details obtained would not alter to any significant extent the overall conclusions about relationships and distribution patterns drawn here.

The classification used at the suprageneric level in this review is mainly that set out in Balss (1957), though this has been modified in some instances to suit our views. For example, Holthuis (1955) is followed for the caridean shrimps and prawns, Griffin (1966) for the majid spider crabs and Stephenson and Campbell (1960) for the portunid swimming crabs.

HISTORICAL

The only previous attempt to review the Australian decapod Crustacea was made by Haswell in 1882. His well-known "Catalogue of the Australian Stalk- and Sessile-Eyed Crustacea" was published by the Australian Museum as the first of a series of similar catalogues on various groups of the Australian fauna. Haswell's section on the Decapoda in this volume includes 381 species representing 152 genera. These genera are distributed among 37 families or family equivalents. Geographical information is very sparse and usually restricted to one or two individual localities for each species; no summary or distribution analysis is included in this work. Assuming that all the species recorded by Haswell still stand in the Australian list, the 1882 Catalogue covers only 32% of the decapods now known from this area.

Since Haswell's major work on this order, a number of family and generic reviews have appeared, covering either the whole of Australia or a restricted area. A number of important expedition reports, covering usually one major collection for a restricted area, have also been issued in this period. Only three groups of Australian decapods are considered to be adequately covered by modern systematic reviews: the penaeid prawns (Dall, 1957; Racek and Dall, 1965), the majid spider crabs (Griffin, 1966) and the portunid swimming crabs (Rees and Stephenson, 1966; Stephenson, 1961, 1962; Stephenson and Campbell, 1959, 1960; Stephenson and Hudson, 1957; Stephenson, Hudson and Campbell, 1957). Other published systematic and geographic accounts of major significance are as follows: freshwater parastacid crayfish (Clark, 1936, 1941; Riek, 1956); parastacid crayfish of Queensland, of Western Australia and of Tasmania (Riek, 1951*b*, 1967*a*, 1967*b*); porcellanid crabs of Western Australia (Haig, 1965); oxystome and gymnopleuran crabs of Western Australia (Tyndale-Biscoe and George, 1962); freshwater potamid crabs and the zoogeography of freshwater decapods in general (Bishop, 1963, 1967); *Ocypode* crabs of Western Australia (George and Knott, 1965), and an illustrated account of the decapods of South

Australia (Hale, 1927). Expedition reports of importance are as follows: Abrolhos Islands, Western Australia (Percy Sladden Trust Expedition—Montgomery, 1931); Low Isles and adjacent reefs, Queensland (Great Barrier Reef Expedition—McNeill, 1968); Port Curtis district, Queensland (Grant and McCulloch, 1906); continental shelf off Sydney, New South Wales (*Thetis* Expedition—Whitelegge, 1900); continental shelf off south-eastern and southern Australia (*Endeavour* Expedition—Rathbun, 1918, 1923; Schmitt, 1926); shelf and deep waters off Tasmania and southern Australia (B.A.N.Z.A.R. Expedition—Hale, 1941), and south-western Australia (Hamburg Museum Expedition—Balss, 1935).

Size and Constitution of the Fauna

The 1200 or so species of decapod crustaceans recorded from Australia belong to 361 genera and 57 families. The largest systematic group is the Brachyura or true crabs which includes about 54% of the total species (Table 1). The smallest group is the Macrura Reptantia (crayfish and allies) which contains almost as many species as the Anomura or hermit crabs but only half the number of genera; the Natantia (shrimps and prawns) comprise less than three times as many species as the reptant macrurans, but spread through almost four times as many genera.

Table 1

Size of the four major systematic groupings in the Australian decapod fauna

Group	——	Number of Families	Number of Genera	Number of Species	Percentage of Total Species
Natantia ..	Shrimps and prawns	16	82	299	25·1
Macrura Reptantia	Crayfish, etc.	4	21	119	10·0
Anomura ..	Hermit crabs, etc.	14	41	129	10·8
Brachyura	True crabs	23	217	643	54·1
Total		57	361	1190	100·0

The largest family is the Xanthidae with 47 genera and 166 species (Table 2). The largest genera are the xanthids *Actaea* and *Pilumnus* with 27 species each. The Parastacidae with only 11 genera contains at least 91 species; included are three particularly large genera, *Cherax*, *Euastacus* and *Engaeus*. The average number of genera per family is 6·3, the average number of species per family is 21 and the average number of species per genus is 3·3.

Considering the larger families and genera (Table 2) we find that 17 of the families (30% of the familial total) contain more than 5 genera (in all 273 genera—75% of the generic total), that 23 families (42·1% of the familial total) contain 998 species (83·9% of the specific total) and that 23 genera (6·4% of the generic total) account for 365 species (30·4% of the specific total). In these larger groups then, the average number of genera per family is 16, the average number of species per family is 45 and the average number of species per genus is 16.

Among the best represented groups of decapods in Australia are the Parastacidae (freshwater crayfish)—probably about 80% of the total world species; the Mictyridae (soldier crabs)—all three species are represented in Australia, and the anomuran family, the Lomisidae (one species), which is confined to Australia. The intertidal grapsid crabs, although one of the larger families (4% of the total marine species, Table 5), is in fact rather poorly represented in Australia—less than 25% of the total known species occur here; particularly noticeable is the paucity of varunines. The terrestrial groups—Gecarcinidae (land crabs) and Coenobitidae (robber crabs and land hermits)—are very poorly represented with only three species out of a world total of about 15. Several families of natants are poorly represented in the Australian fauna. Particularly noticeable is the paucity of pandalid and crangonid shrimps. These families are especially well represented in northern hemisphere waters. The Australian fauna includes at present only six pandalids (world total about 112) and 10 crangonids (world total about 140). A number of other natant families—stenopodids, sergestids and processids—present in Australia in small numbers, conform to a general world familial pattern of a few species, often with a limited geographical distribution, in each major area. Less than 1/5 of the known Atyidae (freshwater shrimps) and less than 1/10 of the Potamidae (freshwater crabs) occur in Australia—this contrasts with the strong representation of the other freshwater family, the parastacid crayfish.

TABLE 2

List of the large families (containing more than 10 genera) and genera (containing 10 or more species)

		Family	No. of Genera	No. of Species	Genus	No. of Species	Genus	No. of Species
20 or more genera	100 species	Xanthidae	47	166	Actaea	27	Pilumnus	27
					Carpilodes	10	Xantho	10
	50–99 species	Majidae	43	93	Hyastenus	13		
11–19 genera		Parastacidae	11	91	Cherax	24	Euastacus	19
					Engaeus	15		
					Thalamita	23	Portunus	18
		Portunidae	15	80	Charybdis	14		
		Leucosiidae	19	74	Leucosia	15	Ebalia	10
		Paguridae	15	58	Pagurus	12		
		Penaeidae	15	50	Metapenaeopsis	10		
	20–49 species	Palaemonidae	19	48	Macrobrachium	12		
		Grapsidae	17	43	Sesarma	15		
		Ocypodidae	11	41	Macrophthalmus	15	Uca	13
		Goneplacidae	14	21				
6–10 genera		Porcellanidae	8	38	Petrolisthes	10		
		Alpheidae	6	31	Alpheus	17		
		Parthenopidae	10	29	Parthenope	16		
		Dromiidae	9	24				
	10–19 species	Hippolytidae	9	19				
		Atyidae	6	19				
5 genera or less		Scyllaridae	5	15	Scyllarus	10		
		Calappidae	3	14				
		Pinnotheridae	3	12				
		Palinuridae	4	11				
		Galatheidae	3	11				
		Hymenosomidae	3	10				

MAJOR HABITAT GROUPINGS

The vast majority of the species (90%) are exclusively marine. However, all of the four major systematic groupings are represented on land or in freshwater. The list below gives the names of the families (and in some cases genera) occurring in freshwater, on land and in the various zones of the sea. Three families, including 18 genera and more than 116 species, are confined to freshwater and four other genera (of three families) also occur in freshwater. Two genera containing four species belonging to two families are found on land.

The intertidal zone is dominated by representatives of five families which do not normally occur subtidally (a total of more than 100 species). Thirteen other families are strongly represented intertidally or immediately subtidally; the most important of these are the xanthids, portunids, majids and leucosiids.

Five families contain mainly pelagic or bathypelagic oceanic species and the representatives of 20 families are characteristic of the shelf. Particularly important shelf groups are the majids, parthenopids, leucosiids, portunids and dromiids. A list of these habitat groupings is given below.

Freshwater Families and Genera

Restricted freshwater families: Atyidae, Parastacidae, Potamidae.

Freshwater genera or species: *Macrobrachium* and *Palaemonetes* (in part) (Palaemonidae); *Halicarcinus lacustris* (Hymenosomidae); *Varuna litterata* (partly) (Grapsidae).

Terrestrial Families

Restricted terrestrial families: Coenobitidae, Gecarcinidae.

Littoral (i.e., Intertidal) Families

Restricted littoral families: Thalassinidae, Lomisidae, Mictyridae, Grapsidae, Ocypodidae.

Other families with some littoral (but not exclusively littoral) representatives: Palaemonidae, Alpheidae, Gnathophyllidae, Hippolytidae, Stenopodidae, Axiidae, Callianassidae, Dromiidae, Calappidae, Leucosiidae, Majidae, Portunidae, Xanthidae.

Oceanic Families

Restricted pelagic or bathypelagic families: Penaeidae (in part only), Sergestidae, Oplophoridae, Pasiphaeidae, Grapsidae (*one* genus only—*Planes*).

Families characteristic of Shelf and Shallow Waters

Penaeidae, Ogyrididae, Stenopodidae, Palinuridae, Scyllaridae, Laomediidae, Galatheidae, Albuneidae, Dromiidae, Raninidae, Calappidae, Homolidae, Leucosiidae, Majidae, Parthenopidae, Hymenosomidae, Portunidae, Xanthidae, Goneplacidae, Cancridae.

COMMERCIAL GROUPS

The commercial species are largely macrurous—natant prawns and reptant crayfish. The major families are the Penaeidae, Palinuridae and Portunidae (part only) with 13 genera and about 50 species being fished commercially. The Scyllaridae and Parastacidae are of minor economic importance.

GEOGRAPHICAL DISTRIBUTION WITHIN AUSTRALIA

The main feature of the patterns of geographical distribution of the marine decapods in Australia is the fairly clear partitioning of the fauna into a northern (tropical) group and a southern (temperate) group, the former being very much the larger. However, there is no clear geographical dividing line between these two groups and the junction is in the form of a broad transition zone on the east and west coasts. This is well shown by plotting the distributions of a large number of tropical and temperate species on the one map (Fig. 1). In the case of the majid spider crabs (22 species occurring mainly in northern waters, 15 in temperate areas), it can be seen that this transition zone extends on the east coast from about Cape Howe in the south to Hervey Bay in the north, and on the west coast from about Cape Leeuwin in the south to about Shark Bay in the north.

About 160 species have a wide northern distribution extending from north-western Australia to Queensland and sometimes further south to New South Wales or Victoria (Tables 3 and 4, Fig. 2). Particularly notable in this regard are the relatively large number of portunids, leucosiids, parthenopids, calappids, palinurids, porcellanids and penaeids; a smaller proportion of the larger families, such as Xanthidae and Majidae, are also widespread northern forms. It should be pointed out that although the distributions of these species are considered to be continuous, a very large number (about 2/3) of these widespread northern species are not known from the Gulf of Carpentaria and the Torres Strait area.

Fig. 1. Map of Australia showing known distributions of 22 mainly northern species and 15 mainly southern species of majid crab, indicating the extent of the transition zones between the northern tropical and southern temperate faunas.

More than 40 species have widespread southern distributions extending from New South Wales or Victoria to south-western Australia. Particularly notable here are majids, grapsids and hymenosomids; the dromiids are also well represented in this southern group, although their distributions are more limited according to the information currently available. Five of these widespread southern species occur from southern Queensland to central Western Australia.

Less obvious than these northern and southern groups are ones which are either eastern or western (Fig. 7). The number of species extending along the whole eastern or western coasts are few and generally eastern species are either northern or southern. Inasmuch as some species are known only from either the east or west coasts there appear to be transition zones in the north around the Torres Strait area and in the south around eastern South Australia. The area around Spencers Gulf in South Australia contains several species which are otherwise common in tropical areas (Fig. 1).

TABLE 3

Number of species showing particular distribution—northern, eastern and southern

Family	Distributional Limits															
	Total Species	W.A.–N. Qld.	W.A.–Qld.	W.A.–N.S.W.	N. Qld.–Qld.	N. Qld.–N.S.W.	N. Qld.–Vict.	Qld.–N.S.W.	Qld.–Vict.	Qld.–S.A.	N.S.W.–S.A.	N.S.W.–W.A.	Vict.–W.A.	S.A.–W.A.	N.S.W.–Vict.	Vict.–S.A.
Xanthidae ..	58	1	15	10	18	3	—	2	—	2	3	2	1	1	—	—
Majidae	38	2	10	1	3	—	2	1	2	2	3	5	3	1	3	—
Portunidae	41	—	12	17	3	2	—	3	—	—	2	—	—	1	1	—
Leucosiidae	25	6	9	2	1	—	—	1	1	—	2	—	1	—	2	—
Paguridae	16	—	2	2	2	—	—	2	—	—	1	1	—	—	5	1
Palaemonidae ..	13	1	2	—	5	—	—	—	—	—	2	1	—	—	—	2
Grapsidae	20	—	2	2	6	—	—	3	1	1	—	1	1	—	—	3
Ocypodidae ..	22	2	6	5	3	—	—	4	1	—	—	—	—	—	—	1
Penaeidae	18	1	2	9	2	—	—	1	2	—	—	—	—	1	—	—
Porcellanidae ..	12	—	9	2	—	—	—	—	—	—	—	—	1	—	—	—
Alpheidae	8	1	1	—	—	3	—	—	—	—	1	—	—	1	—	1
Parthenopidae ..	18	2	4	1	7	—	—	3	—	—	—	—	—	1	—	—
Dromiidae	7	—	—	—	—	—	—	1	—	—	4	—	—	—	—	2
Goneplacidae ..	4	—	—	—	1	—	—	1	—	—	1	—	1	—	—	—
Hippolytidae ..	6	—	1	1	—	—	—	—	—	—	3	1	—	—	—	—
Palinuridae	8	—	5	—	—	—	—	1	—	—	—	1	—	—	1	—
Calappidae	10	—	3	5	—	—	—	1	—	—	—	—	—	1	—	—
Others	40	2	4	5	—	—	—	5	1	3	3	6	4	—	4	3
Total ..	364	18	87	62	51	8	2	29	8	8	25	18	12	7	16	13

Approximately 130 species have a widespread distribution along the east coast. The majority of these occur along the Queensland coast often to northern New South Wales but a large number occur from Queensland or New South Wales to Victoria, Tasmania or South Australia. One widespread majid, *Oncinopus aranea*, extends from northern Queensland to South Australia and eight others have only slightly more limited distributions. Particularly notable in this eastern group are the Xanthidae with a very large number of species confined to Queensland. At least 20 species of decapods appear to have a central eastern distribution extending from southern Queensland to northern Victoria.

No separate analysis of western species is given as our distributional data were summarized under State headings only and subdivision of the long Western Australian coastline has not been attempted in detail.

Summarizing the distribution patterns of species occurring outside a single State, the most common is a northern one with a smaller group of species having widespread southern distributions. These two major types are characteristic of particular taxonomic groups. Thus portunids, penaeids, parthenopids, ocypodids, porcellanids and palinurids are almost entirely restricted to northern Australia.

TABLE 4

Examples of very widely distributed species

Family	Species	Area							
		S.A.	W.A.	N. Qld.	Qld.	N.S.W.	Vict.	S.A.	W.A.
Penaeidae ..	*Penaeus latisulcatus*	×	×	×	×	×			
	Hymenopenaeus sibogae		×	×	×	×	×		
Palaemonidae ..	*Anchistus custos*	×	×	—	×				
Alpheidae ..	*Alpheus edwardsii*		×	—	×	×	—	×	
Upogebiidae ..	*Upogebia darwinii*	×	×	×					
Hippidae ..	*Hippa adactyla*	×	×	×	×	×			
Porcellanidae ..	*Polyonyx transversus*		×	—	×	×	×		
	Pisidia dispar	×	×	—	×	×			
Dromiidae ..	*Petalomera lateralis*				×	×	×	×	×
Leucosiidae ..	*Leucosia anatum*		×	×	×	×	—	×	
	Myra mammilaris	×	×	—	×				
Calappidae ..	*Calappa hepatica*	×	×	—	×	×			
	Matuta granulosa	×	×	×	×				
Parthenopidae ..	*Ceratocarcinus dilatatus*	×	×	×	×				
Majidae ..	*Huenia proteus*	×	×	—	×	×			
	Zewa varians		×	×	×	×	×		
	Hyastenus diacanthus		×	×	×	×	×		
	Achaeus brevirostris		×	×	×	×	×		
	Leptomithrax sternocostulatus ..				×	×	×	×	×
	Schizophrys aspera	×	×	×	×				
	Micippa philyra	×	×	×					
Xanthidae ..	*Cryptocoeloma haswelli*	×	×	×	×				
	Actaea calculosa	×	×	×	×	×			
	Actumnus setifer	×	×	×					
	Pilumnus fissifrons				×	×	×	×	×
	Pilumnus semilanatus	×	×	—	×				
	Ozius truncatus				×	×	—	×	×
Portunidae ..	*Thalamita sima*	×	×	×	×	×			
	Portunus pelagicus	×	×	×	×	×	×	×	×
	Macropipus corrugatus				×	×	×	×	×
	Lissocarcinus polybioides	×	×	—	×	×			
Grapsidae ..	*Leptograpsus variegatus*				×	×	×	×	×
	Cyclograpsus audouinii				×	×	×	×	×

A very large number of species in every group is not known from more than one State. In the case of nine families (Oplophoridae, Crangonidae, Callianassidae, Paguridae, Majidae, Palicidae, Xanthidae, Goneplacidae and Grapsidae) more than 2/3 of the species are recorded at present from only one State.

Different families are represented in quite different proportions in different areas as can be seen from Tables 3 to 6 and Fig. 3. Figures 4 and 5 give examples of some of the distribution patterns discussed above. The families Xanthidae, Majidae and Grapsidae possess several widespread northern as well as southern species. The Hymenosomidae is the only family with 10 species or more which is virtually restricted to southern waters (Queensland species are known, but not, as yet, adequately recorded in the literature). The different distributions are summarized in Table 3 and Fig. 2*b*.

Extra-Australian Geographical Relationships

Examination of the distribution patterns of the decapod genera represented in Australia shows that almost 50% of those found outside Australia possess species in the Indo-West Pacific area but not outside it, whilst a very slightly smaller number are distributed throughout the Indian, Pacific and Atlantic Oceans. The list below groups the families according to the relationships of the included genera.

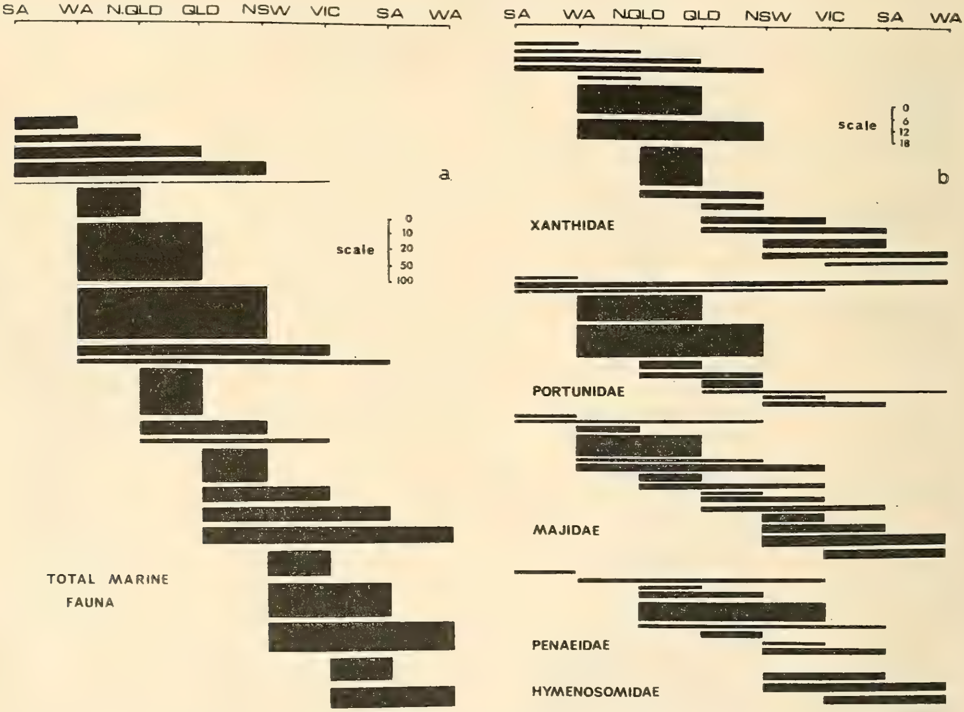

Fig. 2. Diagram showing distribution patterns of Australian marine decapod species known to occur in more than one State; width of each bar is proportional to number of species showing each particular pattern of distribution according to the scales given. a—distribution of all Australian species; b—distribution patterns of the species belonging to five selected families.

Families with more than 2/3 of their Genera World-Wide in Distribution

Large families (i.e., with 10 or more Australian species): Penaeidae, Scyllaridae, Paguridae, Porcellanidae, Galatheidae, Calappidae.

Small families (i.e., with less than 10 Australian species): Sergestidae, Pasiphaeidae, Pandalidae, Oplophoridae, Rhynchocinetidae, Processidae, Crangonidae, Stenopodidae, Nephropsidae, Axiidae, Upogebiidae, Pylochelidae, Coenobitidae, Chirostylidae, Albuneidae, Homolidae, Dorippidae, Cancridae, Gecarcinidae, Hapalocarcinidae.

Families with more than 2/3 of their Genera Indo-West Pacific in Distribution

Large families (i.e., with 10 or more Australian species): Leucosiidae, Majidae, Parthenopidae, Hymenosomidae, Ocypodidae.

Small families (i.e., with less than 10 Australian species): Ogyrididae, Thalassinidae, Laomediidae, Corystidae, Atelecyclidae, Mictyridae.

Families with between 1/3 and 2/3 of their Genera World-Wide or Indo-West Pacific in Distribution

Large families (i.e., with 10 or more Australian species): Palaemonidae, Alpheidae, Hippolytidae, Palinuridae, Dromiidae, Xanthidae, Portunidae, Goneplacidae, Grapsidae, Pinnotheridae.

Small families (i.e., with less than 10 Australian species): Gnathophyllidae, Callianassidae, Hippidae, Raninidae, Palicidae.

TABLE 5

Percentage of total marine decapod species in each state made up by each family

Family		Area—Percentage of Species					
		Qld.	N.S.W.	Vic. and Tas.	S.A.	W.A.	All States
Approx. number of species		700	300	200	200	400	1070
Xanthidae	166	16	12	8	10	18	15
Majidae	93	7	12	18	12	10	9
Portunidae	80	10	10	3	4	11	8
Leucosiidae	74	8	4	6	5	8	7
Paguridae	58	4	5	6	2	3	5
Palaemonidae	48	4	2	—	3	3	4
Grapsidae	43	5	5	6	4	2	4
Ocypodidae	41	5	3	1	0·5	4	4
Penaeidae	51	8	6	4	2	4	4
Porcellanidae	38	4	2	3	1	7	3
Alpheidae	31	3	2	4	7	1	2
Parthenopidae	29	4	1	—	1	2	2
Dromiidae	24	1	2	3	6	2	2
Goneplacidae	21	2	3	3	2	0·5	1·5
Hippolytidae	19	0·5	1	1·5	3	1·5	1·5
Scyllaridae	15	1	2	1	—	1·5	1·5
Calappidae	14	1·5	2	—	1·5	3	1·5
Pinnotheridae	12	1	0·5	1·5	1·5	1	1
Palinuridae	11	1	1·5	1	0·5	1·5	1
Galatheidae	11	1	2	2	0·5	0·5	1
Hymenosomidae	10	—	1	2·5	2·5	1	1
Others	111	13	21	24·5	34	13·5	21

Families and Genera with Asiatic Representation

The families Atyidae and Potamidae (both freshwater), and representatives of the following families: Majidae (*Leptomithrax, Sargassocarcinus*); Xanthidae (*Hypothalassia, Calvactea, Liagore*); Grapsidae (*Utica*); Palicidae (*Pleurophrycus*).

Genera with a Wide, Southern Temperate Distribution

Genera, with family name in brackets, as follows: *Nauticaris* (Hippolytidae); *Campylonotus* (Campylonotidae); *Jasus* (Palinuridae); *Notomithrax* (Majidae); *Halicarcinus* (Hymenosomidae); *Leptograpsus* and *Cyclograpsus* (in part) (Grapsidae); *Nectocarcinus* (Portunidae).

Some Genera with Other Distributions

Indopacific and South Atlantic: *Mursia* (Calappidae).

Indopacific and West African: *Epixanthus, Heteropanope, Pilumnopeus* (Xanthidae).

Indopacific and West Indies: *Chlorodiella, Carpilius, Phymodius* (Xanthidae); *Ovalipes* (Portunidae).

Indopacific and Eastern Pacific (but not Atlantic): *Pugettia* (Majidae); *Daira, Carpilodes, Trapezia* (Xanthidae).

More than two thirds of the included genera in almost one half of the families occur throughout the world, whilst 1/5 of the families are mainly Indo-West Pacific. Slightly less than one third of the families have mixed relationships. A few genera, each including only a small number of species in Australia, are distributed mainly through the southern temperate areas of the Indo-Pacific. The freshwater families, Atyidae and Potamidae, as well as a few marine genera, are largely confined to Australia and the Indo-Malayan area. Finally, a small number of genera, mainly xanthids, have unusual distributions.

TABLE 6

Number of species per state expressed as a percentage of the total number of species in each family

Family	Approx. Number of Species	Area—Percentage of Species				
		Qld.	N.S.W.	Vic. and Tas.	S.A.	W.A.
Xanthidae	166	61	20	7	10	42
Majidae	93	48	36	34	23	41
Portunidae	80	75	38	10	7	56
Leucosiidae	74	71	15	13	12	46
Paguridae	58	40	26	15	7	19
Palaemonidae	48	48	11	0	11	22
Grapsidae	43	80	38	22	20	21
Ocypodidae	41	81	25	5	2	47
Penaeidae	51	90	35	11	9	34
Porcellanidae	38	61	16	7	5	74
Alpheidae	31	60	16	20	47	20
Parthenopidae	29	80	10	0	10	29
Dromiidae	24	31	26	21	40	31
Goneplacidae	21	49	40	20	20	5
Hippolytidae	19	15	15	15	40	30
Scyllaridae	15	51	48	12	0	34
Calappidae	14	70	50	0	22	80
Pinnotheridae	12	40	9	25	25	45
Palinuridae	11	85	61	24	10	75
Galatheidae	11	85	72	48	9	18
Hymenosomidae	10	0	40	50	50	40
Others	111	90	50	70	65	60

Twenty-nine genera are not known outside Australia; many of these are monotypic. The following is a list of these restricted and often poorly known taxa.

Genera Endemic (i.e., restricted) to Australia

Freshwater genera and families: *Caridinides, Stygiocaris* (Atyidae); ten genera of Parastacidae (i.e., all except *Cherax*).

Marine genera, with family names in brackets, as follows: *Vercoia* (Crangonidae); *Lomis* (Lomisidae); *Epipedromia* (Dromiidae); *Lisso-*

Fig. 3. Histogram showing percentage of total species per family per State for each of four selected families compared with percentage State representation of total Australian marine decapod fauna.

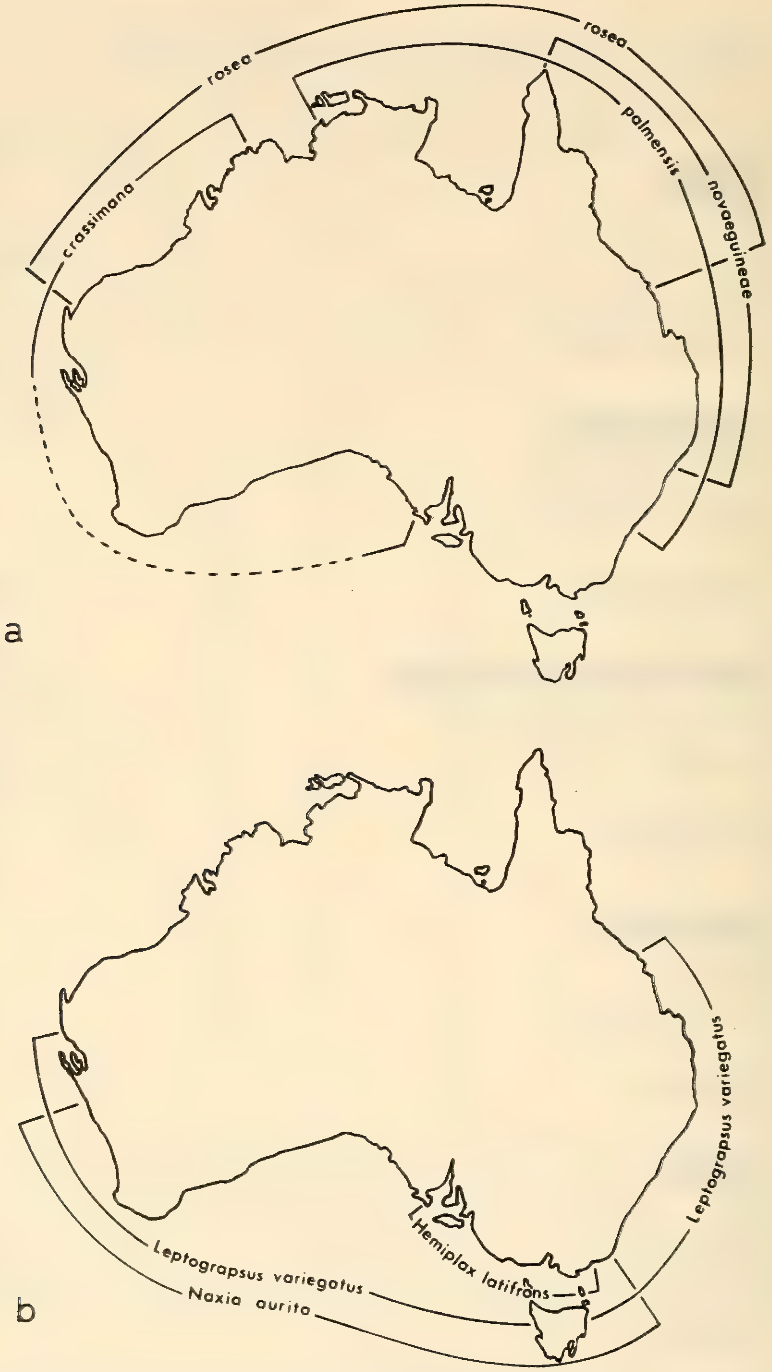

Fig. 4. a—Distribution of the stridulating group of penaeid prawns of the genus *Metapenaeopsis* showing various patterns of northern distribution. b—Distribution of of the ocypodid crab *Hemiplax latifrons*, the majid crab *Naxia aurita* and the grapsid crab *Leptograpsus variegatus* showing three patterns of southern distribution.

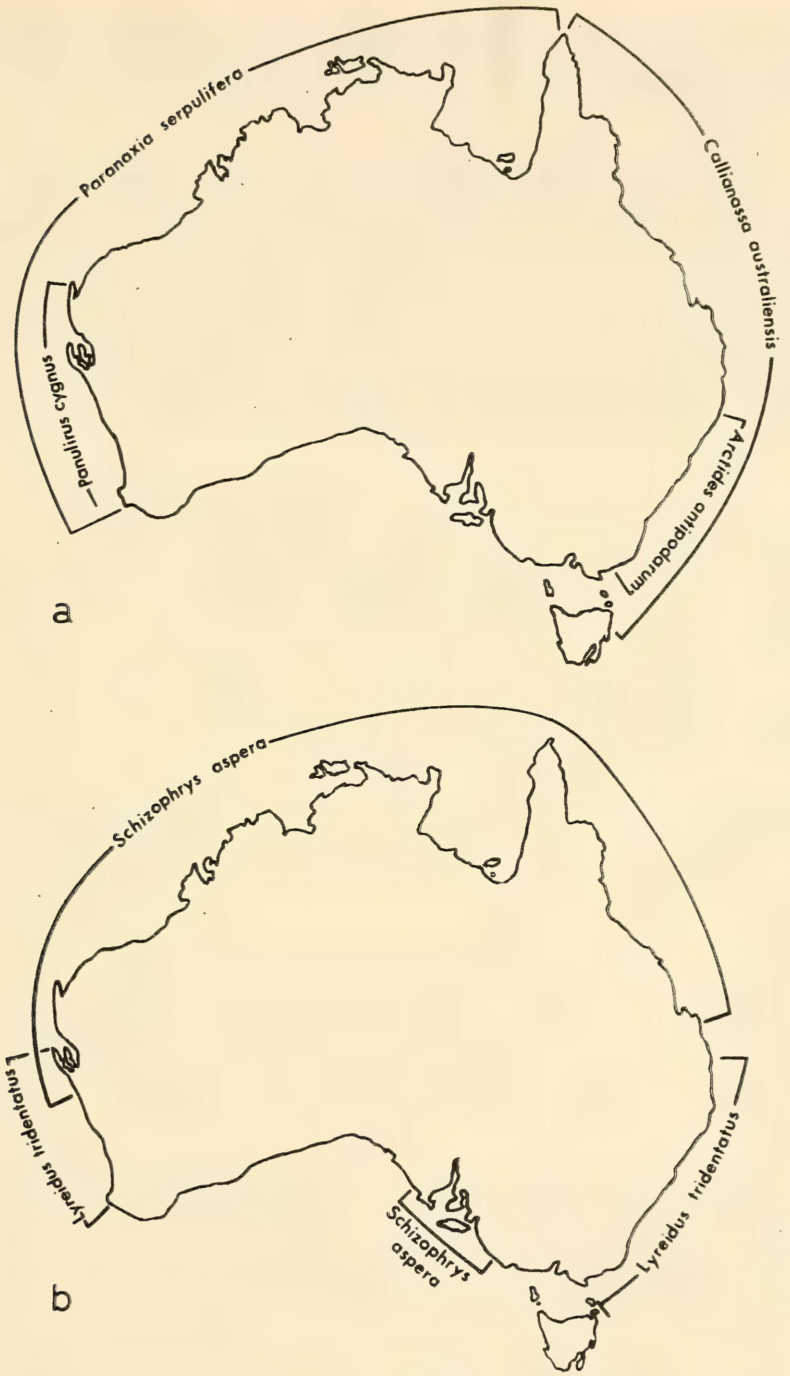

Fig. 5. a—Distribution of the palinurid crayfish *Panulirus cygnus* and the majid crab *Paranaxia serpulifera* showing two types of western distribution pattern; and of the callianassid "yabby" *Callianassa australiensis* and the scyllarid lobster *Arctides antipodarum* showing two types of eastern distribution pattern. b—Distribution of the raninid crab *Lyreidus tridentatus* and the majid crab *Schizophrys aspera* showing two types of discontinuous distribution.

morpha (Leucosiidae); *Tumulosternum, Paramithrax, Paranaxia, Ephippias* (Majidae); *Leptograpsodes, Helograpsus, Paragrapsus* (Grapsidae); *Banareiopsis, Paraetisis, Pseudocarcinus, Prolybia* (Xanthidae); *Heloecius, Australoplax* (Ocypodidae).

Tropical and Temperate Species and their Distributions

An analysis of the distributions of the species belonging to five family groups (Table 7) show that a large proportion of the tropical species are widespread throughout the Indo-West Pacific. Generally a smaller proportion is either shared with part of the Indian Ocean or the Western Pacific, though a sizeable number of Australian species are not known outside the Indo-Malayan Archipelago—in the penaeine prawns this last group is particularly large. The temperate group is characterized by a very large number of species which are restricted to Australia; among the temperate majids a small percentage is shared with southern temperate areas outside Australia.

Table 7

Distributions of species outside Australia for five family groups

Family	Total No. Species	Percentage of Total Species per Distribution Type Partitioned according to Area						Percentage of Total	
		Restricted	Indo-Malay	Indian Ocean	West Pacific	Widespread	Southern		
Portunidae ..	80	19	10	11	8	52	0	91	Tropical Australia
		66	0	0	0	34	0	9	Temperate Australia
Majidae ..	93	17	15	10	15	43	0	65	Tropical Australia
		67	0	2	11	6	14	35	Temperate Australia
Oxystomata..	45	17	4	24	9	46	0	82	Tropical Western Australia
		66	6	22	0	12	0	18	Temperate Western Australia
Porcellanidae	30	21	11	12	18	38	0	88	Tropical Western Australia
		100	0	0	0	0	0	12	Temperate Western Australia
Penaeinae ..	40	38	21	8	15	18	0	92	Tropical Australia
		100	0	0	0	0	0	8	Temperate Australia

The fauna as a whole is not as yet well enough known to allow an analysis of the representation of the main Indo-Pacific elements in the various areas of Australia. Thus in the majids, whilst at present the western Australian fauna appears to contain a larger percentage of Indian Ocean species than does the eastern Australian fauna, this may be due to the fact that the western Australian fauna is the poorer known.

Conclusions—Present and Future Work

Much of what has been outlined above would apply to most groups of Australian marine animals—tropical groups tend to be widely distributed, whereas cool temperate animals tend to have limited distributions. Zoogeographically, the Australian decapod fauna appears to have been derived almost entirely from the tropical Indo-Pacific region. There seems to be no good evidence to suggest that temperate species have reached Australia directly from temperate areas outside Australia.

The following concluding remarks attempt to summarize what is at present known about each of the main systematic groups. It should be pointed out that few parts of the Australian coastline, continental shelf and off-shore oceanic waters have been well sampled thus far, whilst the continental slope beyond 100 fms. is virtually unknown. Almost the whole of the area around north-western Australia and the Great Australian Bight is unexplored.

The penaeid prawns are continuing to be actively investigated by A. A. Racek of the University of Sydney. Almost nothing is known about the identity and distribution of the pelagic and bathypelagic shrimps (Sergestidae, Pasiphaeidae, Oplophoridae), nor about the shelf and archibenthal, possibly commercial, natants (e.g., Pandalidae and Crangonidae); only the *Challenger* Expedition (1873–76) has provided as yet any substantial information on these groups in Australian offshore waters. However, New Zealand representatives have been recently reviewed (Richardson and Yaldwyn, 1958; Yaldwyn, 1960).

Among the most complex and taxonomically difficult groups of natants are the Alpheidae (snapping shrimps—see Banner and Banner, 1966), the Australian members of which are currently being revised by A. H. and Dora M. Banner of the University of Hawaii. The other main natant group—the Palaemonidae—is perhaps reasonably well known; the pontonines (mainly tropical commensals—see Bruce, 1967) are now being studied by A. J. Bruce of the C.S.I.R.O. Division of Fisheries and Oceanography and the palaemonines have been briefly investigated by a few workers (e.g., Holthuis, 1952). Our comprehension of the freshwater species of the genus *Macrobrachium* and of the freshwater shrimps of the family Atyidae, is almost abysmal—nothing definitive is known of the individual distributions, or of the range of variation in these forms. The general zoogeography and relationships of all freshwater decapod genera has, however, been reviewed in detail by Bishop (1967).

For most of the reptant macrurans our knowledge is more advanced. The status of the palinurids is probably better known than that of any other group of decapods, and they are under continuing study by R. W. George of the Western Australian Museum and L. B. Holthuis of the Rijksmuseum, Leiden (George and Holthuis, 1965). Holthuis has also nearly completed revisionary studies on the Scyllaridae. Two major systematic revisions of the Parastacidae are being completed by E. F. Riek of the C.S.I.R.O. Division of Entomology and D. D. Francois of the N.S.W. Chief Secretary's Department Fisheries Division.

Not a great deal is known of the very large and varied group, the Anomura. Only the Porcellanidae are reasonably well known, the western species having recently been studied by Janet Haig of the Allan Hancock Foundation, Los Angeles (Haig, 1965) and she is soon to commence intensive studies on the remainder of the Australian fauna. Information about the pagurids is almost totally absent for the whole Indo-Pacific (with the exception of south-east Asia where the species have been studied by Fize and Serène, 1955); this is in contrast to the fairly well-known Atlantic fauna (see Gordan, 1956). The position of the monotypic Lomisidae has been investigated recently by Pilgrim (1965).

In the Brachyura a few groups have been studied in varied detail, but most are still poorly known. Knowledge of the leucosiids, calappids and raninids has been given a basis in the recent studies by Marina Tyndale–Biscoe and R. W. George (1962), and by W. Stephenson of the University of Queensland (pers. comm.). These oxystomes are one of the groups where further revisionary studies could be completed fairly easily in the near future.

In the case of the oxyrhynchs (Majidae, Parthenopidae and Hymenosomidae), one of us (D.J.G.G.) is continuing investigation of the majids; a fairly large number of new species remain to be added to the fauna and many species known from eastern Australia are present in western waters, but have not so far been recorded formally. Studies on the parthenopids have been initiated; the most recent relevant studies are by Flipse (1930) and Serène (1954, 1955). The Hymenosomidae exhibit their greatest diversity in Australasia (Tesch, 1918*a*), yet knowledge of them is almost entirely lacking; the work of J. S. Lucas, of the University of Western Australia (pers. comm.), on reproductive isolation and general biology, should provide a sound basis for future work on the Australian species.

The portunids continue to undergo intensive study by W. Stephenson and his co-workers at the University of Queensland; this group is one of the best known of Australian crabs. The very large and complex group, the Xanthidae, are currently being revised on a world-wide basis by Danièle Guinot of the National Museum, Paris (see Forest and Guinot, 1961); previous knowledge of Australian species comes mainly from the works of Melbourne Ward (see Whitley, 1967). The Goneplacidae appear at present to make up rather a small proportion of the brachyuran fauna but it should be pointed out that several small and taxonomically difficult subfamilies await study; many Indo-West Pacific species have been recently documented by Serène (1964).

The behaviourally and ecologically very interesting shore crabs of the families Grapsidae and Ocypodidae are perhaps reasonably well known in the Indo-Pacific (Banerjee, 1960; Crosnier, 1965) and several groups are currently under review in Australia. Local species of the first family are being studied by B. M. Campbell of the Queensland Museum (Campbell, 1967; Campbell and Griffin, 1966) who is particularly interested in the complex group belonging to the genus *Sesarma*. R. Serène of the National Museum, Singapore, is revising at the same time the Indo-Pacific species of *Sesarma*, and one of us (D.J.G.G.) is investigating the distribution of, and variation in, several widespread shore crab species (Griffin, in press). The macrophthalmine ocypodids are currently being revised by R. S. K. Barnes (1966*a*, *b*). The fiddler crabs (*Uca* species) are in an unusual position taxonomically (see Crosnier, 1965); a very sound basis for work on these species was provided by studies on American species in the 1940's by Jocelyn Crane who has more recently briefly investigated most of the Indo-Pacific species (Crane, 1957). Several workers in Australia are variously interested in this group and know something of the distribution and status of local species, based mainly on recent ecological studies by W. Macnae (1966) of Witwatersrand University, Johannesburg. However, nothing substantial is at present being done by anybody on Australian members of this genus. The western Australian ghost crabs (*Ocypode* species) have recently been studied by R. W. George and Mary Knott (1965).

Nothing is known of two interesting families of mainly commensal species; the Pinnotheridae (see Tesch, 1918*b*; Serène, 1964), which undoubtedly contain many more Australian species than are currently recognised and the Hapalocarcinidae of which almost nothing is known in Australia, although the south-east Asian fauna has recently been thoroughly documented by Fize and Serène (1957).

Undoubtedly a lot of work remains to be done. Most importantly, knowledge must be obtained of the distributions and patterns of variation within species. Work along these lines might be considered as preceding systematic rearrangements and generic revisions in those cases where identification of taxa at the generic level is not impossible. It is to be earnestly hoped that currently available knowledge concerning some groups will be fully exploited in the near future in conjunction with ecological studies. Species exist in nature, not merely in a bottle or in a person's mind, it is the systematist's job to find them.

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THE EMBRYOLOGY OF *EPALTES AUSTRALIS* LESS. (COMPOSITAE)

GWENDA L. DAVIS

Department of Botany, University of New England, Armidale, N.S.W.

[Read 24th April, 1968]

Synopsis

The capitula of *E. australis* are heterogamous and, although all the florets are tubular, those of the outermost seven or eight whorls are filiform and female. Along any radius of the capitulum, the anthers develop in acropetal succession whereas the ovules form and mature in a basipetal manner.

Microsporogenesis is regular and the pollen is three-celled when shed.

Embryo sac formation follows the Polygonum type but only two antipodal cells are formed and the micropylar cell is binucleate. No secondary multiplication of antipodals occurs and the cells persist into post-fertilization stages. Fusion of the polar nuclei occurs immediately before fertilization and after the premature degeneration of the synergids.

Endosperm formation is *ab initio* Cellular and embryogeny conforms to the Asterad type.

INTRODUCTION

Of the three species of *Epaltes* endemic to Australia, *E. australis* is the most widely distributed and, according to Black (1957), it occurs in all states except Western Australia. It has also been reported from Formosa where it was possibly introduced in Australian wheat or wool.

The plant is herbaceous with procumbent stems which may reach 30 cm. in length and the hemispherical capitula are borne on short pedicels in the axils of the obovate leaves.

No member of this genus has previously been the subject of an embryological investigation although its component species are endemic to tropical Africa, Mexico, Brazil, tropical Asia and China, as well as Australia.

MATERIALS AND METHODS

The material on which this investigation was based was collected from 40 miles east of Wanaaring, far western New South Wales, and fixed in F.A.A. by Professor N. C. W. Beadle of the University of New England.

After embedding, sections were cut at 8–10μ and stained with Delafield's haematoxylin and Johansen's safranin.

FLORAL MORPHOLOGY

The capitula are hemispherical and heterogamous and the naked receptacle is slightly concave at maturity. The florets are all tubular and do not exceed the ovate, obtuse, involucral bracts, their number varying with the size of the capitulum. According to Black (1957), about 100 female florets surround the 8–25 bisexual disc florets but, in the Wanaaring material, the ratio of female to bisexual florets was approximately 12:1 in a total of up to 400 florets per capitulum.

The filiform female florets occupy the outermost 7 or 8 whorls and, at maturity, the stylar arms protrude through the small aperture at the apex of the corolla tube (Text-fig. 1). Their outer surfaces are finely papillate and no definite stigmatic lines could be identified at their margins (Text-fig. 3).

The bisexual disc florets are shortly 4-lobed (Text-fig. 2) and the filaments of the four epipetalous stamens are inserted near the base of the corolla tube. Although the anthers are closely associated, they do not cohere into an anther tube. The stylar arms are lanceolate and taper sharply into the slender apices (Text-fig. 4). Finely papillate stigmatic lines occupy their margins and the large papillae on their outer surfaces are continuous with those on the distal end of the style proper. A ring-like nectary surrounds the base of the style and has no counterpart in the female florets.

The fruits of the bisexual florets are slightly broader than those of the females but both types are longitudinally ribbed and bear a microscopic rim which represents the pappus (Text-figs 1–2).

MICROSPORANGIUM

The anthers are tetrasporangiate with sterile apices and are proximally tailed. Within the epidermis the fully formed anther wall is made up of endothecium, middle layer and tapetum and its method of formation follows the Dicotyledonous type (Davis, 1966). The cells of the amoeboid tapetum become multinucleate during meiosis in the adjacent microspore mother cells, and this may be accompanied by nuclear fusion. When the microspore tetrads are formed, the tapetal cells are 2- or 4-nucleate and, on breakdown of the tetrads, periplasmodium formation occurs.

Microsporogenesis and male gametogenesis follow the same sequence of events as described in *Podolepis jaceoides* (Davis, 1961) and the pollen grains are 3-celled when shed after the longitudinal dehiscence of the anther.

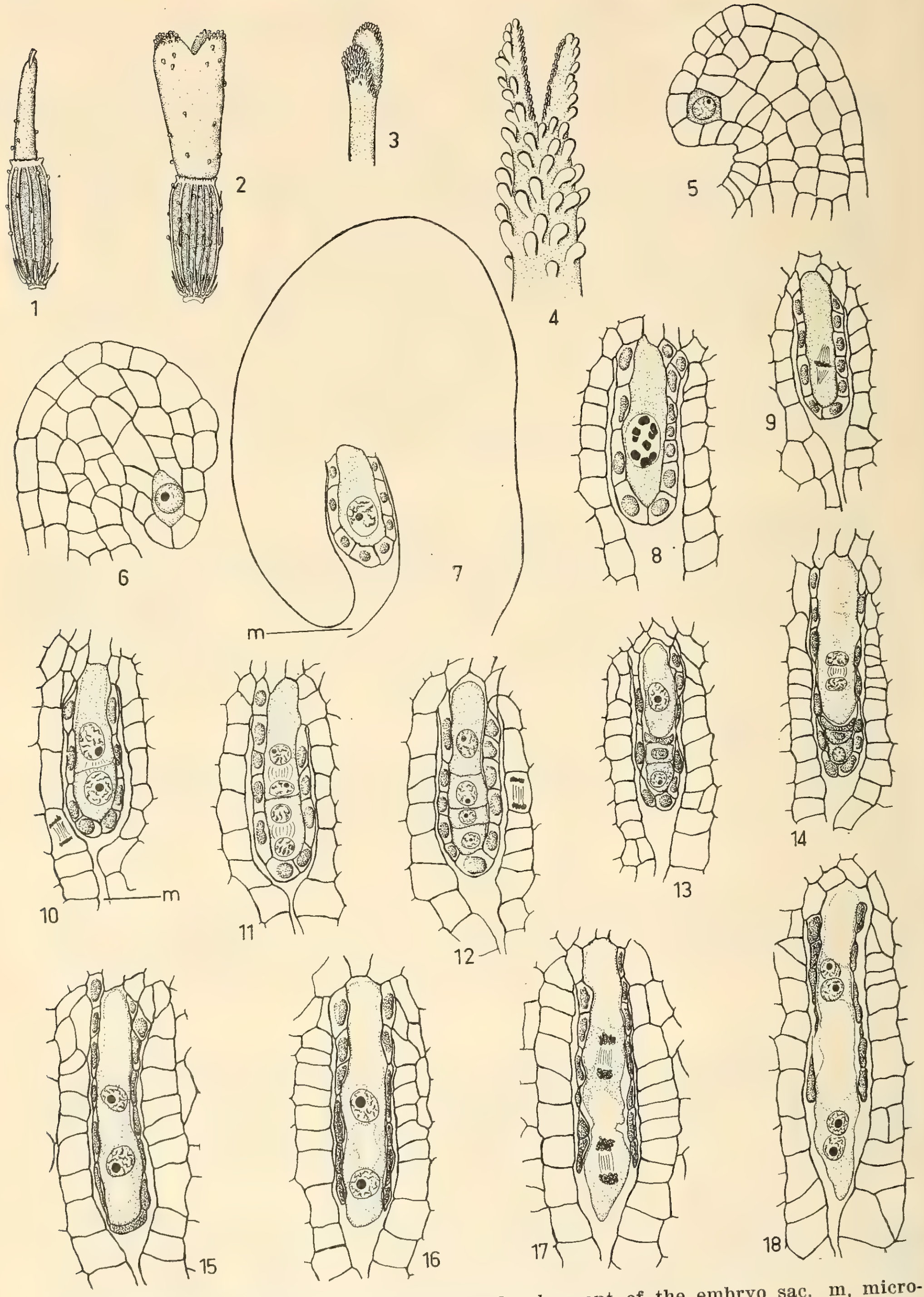
MEGASPORNAGIUM

The initially atropous ovule becomes anatropous with the development of the single massive integument which overgrows the nucellus until it meets the funicle (Text-figs 5–7). As in other Compositae, the ovule is tenuinucellar and arises from the base of the inferior ovary.

Megasporogenesis

An archesporial cell differentiates at the apex of the nucellus in a sub-epidermal position and gives rise directly to the megaspore mother cell (Text-figs 5–7). The enlargement of this cell is accompanied by active cytoplasmic synthesis and it is accommodated in the nucellar lobe by anticlinal divisions of the overlying nucellar epidermal cells.

When the growth of the integument is completed, meiosis is initiated in the megaspore mother cell whose nucleus is situated towards the micropylar pole (Text-figs 8–9). Cytokinesis after meiosis 1 is therefore unequal and the chalazal dyad cell is larger than its micropylar counterpart (Text-fig. 10). Meiosis 11 takes place simultaneously in both dyad cells (Text-fig. 11) and is followed by wall formation but, whereas the two micropylar megaspores are the same size, the chalazal dyad cell divides unequally and the chalazal megaspore of the linear tetrad is the largest (Text-fig. 12). Although all the



Text-figs 1–18.—Floral morphology and development of the embryo sac. m, micropyle. Text-figs 1, 2 × 17; 3, 4 × 100; 5, 6, 8–18 × 600; 7 × 433.

megaspores may develop vacuoles and, consequently, are said to germinate, only the chalazal megaspore increases in size and the three non-functional megaspores degenerate (Text-fig. 13).

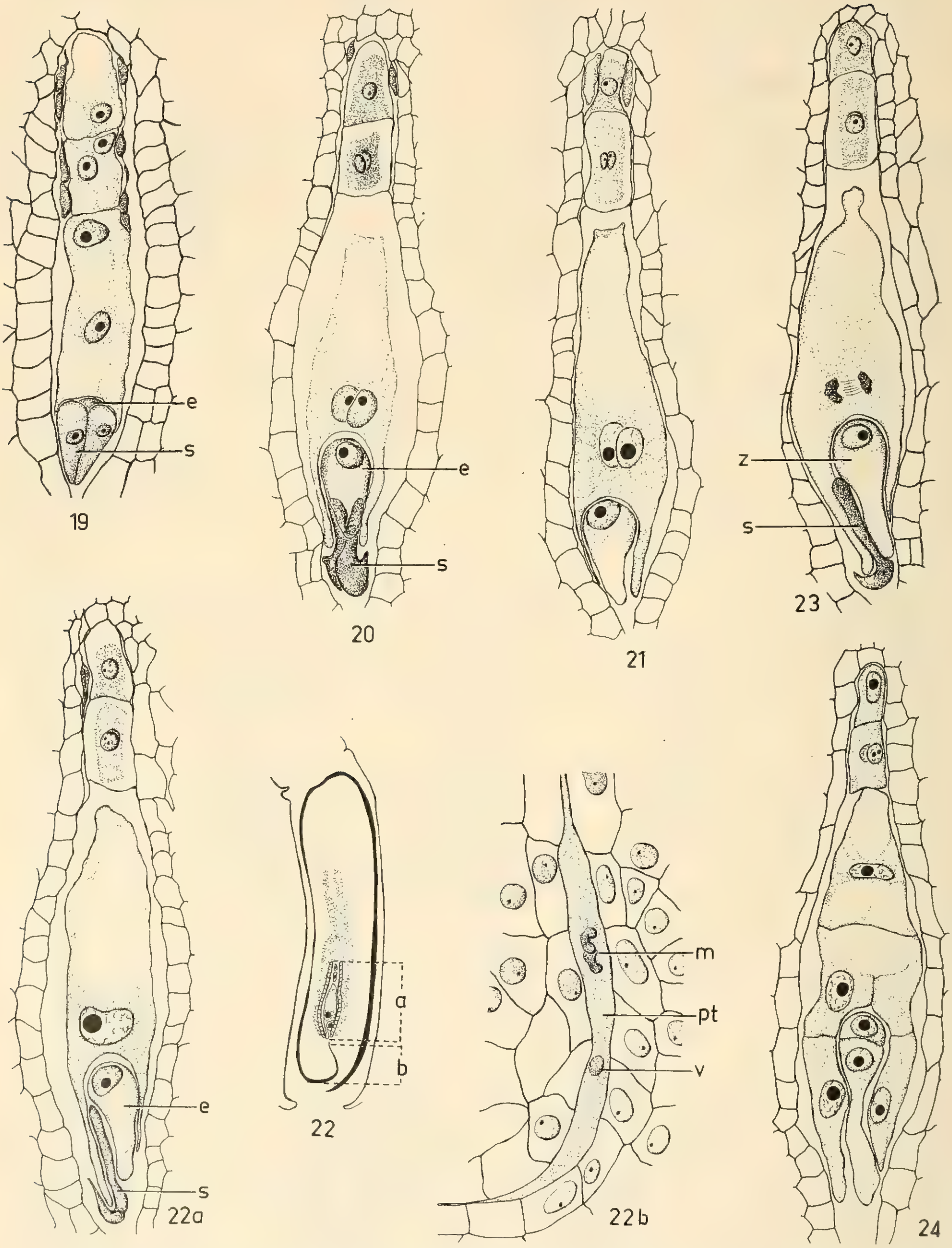
Embryo sac formation

When the functional megaspore enlarges, the nucellar epidermis becomes tangentially stretched and its cells do not divide anticlinally. The transition from the functional megaspore stage to the 1-nucleate embryo sac is purely a matter of size increase and is not associated with any anatomical characteristics. In most Compositae, the 1-nucleate embryo sac fills the nucellar lobe after the dissolution of the non-functional megaspores, but in *E. australis* the latter are still in evidence when the nucleus of the embryo sac divides (Text-fig. 14). A vacuole forms between the daughter nuclei and, following the eventual absorption of the crushed non-functional megaspores, the 2-nucleate embryo sac comes into direct contact throughout its length with the nucellar epidermis (Text-fig. 15). Further enlargement of the embryo sac results in its apex penetrating the nucellar epidermis and taking up its position at the throat of the micropyle (Text-fig. 16). Although the cell contents of the nucellar epidermis are in a degenerated condition, the layer itself persists until maturity of the embryo sac and its remains can be recognised internal to the endothelium.

The second embryo sac mitosis leads to the 4-nucleate stage in which the nuclei occupy the 2+2 configuration, the two pairs being separated by a large vacuole which was formed after the preceding nuclear division (Text-figs 17–18). The third and last embryo sac mitosis, as well as the following free 8-nucleate stage, were not observed but, after cytokinesis, differentiation occurs and the development of the embryo sac is, therefore, of the Polygonum type.

The differentiated embryo sac is 6-celled (Text-fig. 19), due to the formation of only two antipodal cells, of which the micropylar is invariably 2-nucleate. In the newly-formed embryo sac, the antipodal cells are vacuolate and their cytoplasm stains lightly but, at maturity, the vacuoles disappear and each cell becomes filled with dense cytoplasm. No nuclear divisions occur and the two cells remain in this condition until they degenerate when embryogeny is well advanced. In the endosperm mother cell, the two polar nuclei initially occupy opposite poles and are separated by the large vacuole which has persisted since the 2-nucleate stage of the embryo sac. The chalazal polar nucleus then migrates to the micropylar portion of the cell where it becomes closely associated with its micropylar counterpart. Fusion of the polar nuclei to form a secondary nucleus is delayed until just before fertilization. As in other Compositae, the three cells of the egg apparatus are partially enclosed by the hood-like micropylar portion of the endosperm mother cell. When the synergids are first formed, they are slender basally vacuolate cells which taper towards their apices at the throat of the micropyle. However, during their degeneration, each develops a lateral fold which appears hook-like in section (Text-fig. 20). In *Epaltes australis* the breakdown of the synergids is premature in that it commences before the formation of the secondary nucleus and is not associated with the entrance of the pollen tube into the embryo sac. The egg is an elongated cell which is deeply enfolded by the endosperm mother cell and its micropylar half is occupied by a large vacuole (Text-figs 20–21).

The micropylar chamber, which contains the nucellar lobe, is bounded by the innermost cell layer of both the integument and the raphe. These cells



Text-figs 19–24.—Mature embryo sac, fertilization and endosperm formation. e, egg; m, male gametes; pt, pollen tube in micropyle; s, sygergids; v, vegetative nucleus; z, zygote. Text-figs 19 × 600; 20, 21, 23, 24 × 433; 22 × 67; 22a, 22b × 1000.

divide only anticlinally (Text-figs 10, 12) and, by the time the megaspore mother cell enters meiosis, they have formed the endothelium. In cell arrangement and staining capacity, this cell layer is sharply demarcated from the remainder of the integumentary cells and it reaches its maximum development at maturity of the embryo sac. Its cells show signs of degeneration after endosperm formation has been initiated and it can be distinguished only by its position by the time the young embryo has become heart-shaped. The development of an endothelium is invariable in the Compositae and it is a character of tenuinucellar ovules in general, where the embryo sac comes into direct contact with the integument after the breakdown of the nucellus. Circumstantial evidence indicates that it may play a part in the nutrition of the embryo sac by producing enzymes which digest the contents of the integumentary cells external to it. In text-figure 22 this process of digestion is well advanced and a region of empty collapsed cells extends outwards from the endothelium, within which is the mature embryo sac.

Fertilization

Syngamy was not observed, but in one ovule (Text-fig. 22) in which a secondary nucleus was present and the synergids had degenerated (Text-fig. 22a), a pollen tube was present in the micropyle and contained two closely associated vermiform male gametes as well as the vegetative nucleus from the pollen grain (Text-fig. 22b).

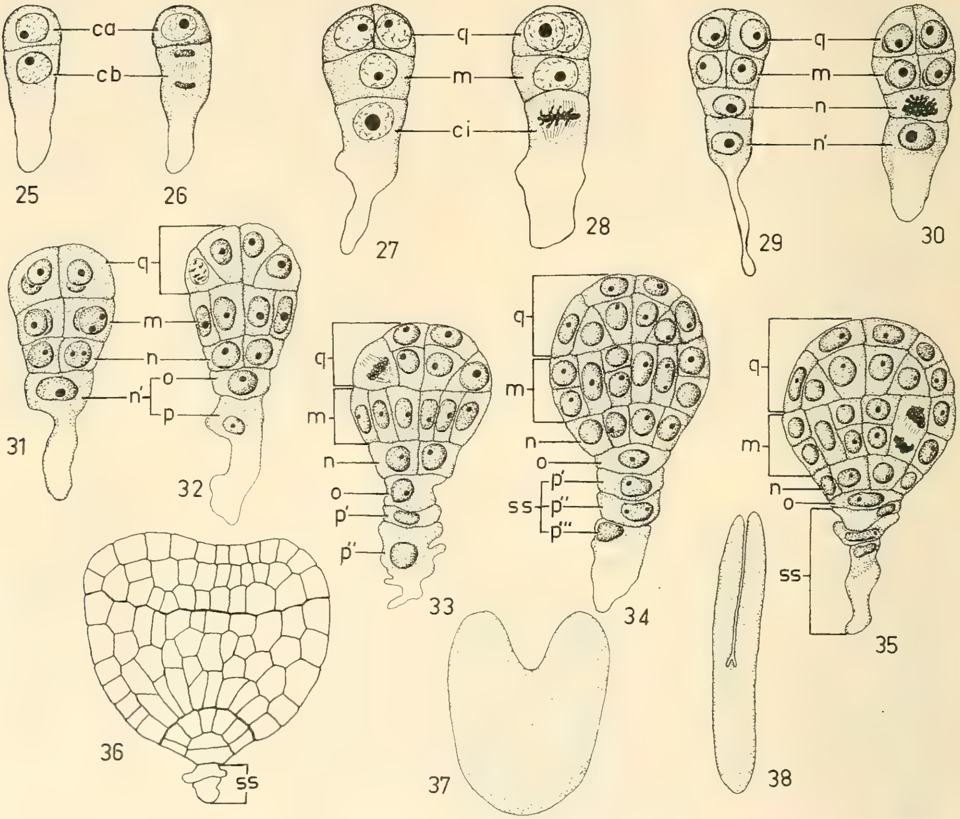
Post-fertilization Events

Endosperm formation

Division of the primary endosperm nucleus precedes that of the zygote. The mitotic spindle lies at right angles to the long axis of the embryo sac and a wall is laid down across the telophase spindle (Text-fig. 23). Endosperm formation is therefore of the *ab initio* Cellular type and subsequent divisions follow rapidly. By the time the proembryo is 2-celled, endosperm formation is well advanced (Text-fig. 24) but there is no evidence of its digestion before the embryo has reached the stage shown in text-figure 35. When the embryo is fully grown all the endosperm has been utilized with the exception of a layer of regular thick-walled cells within the remains of the integument. The seed, therefore, is not strictly exalbuminous.

Embryogeny

After formation of five or six endosperm cells, the zygote divides transversely to form the superposed cells *ca* and *cb* of the two-celled proembryo (Text-fig. 25). Vertical division of *ca* gives rise to the tier *q* and *cb* divides transversely to form the cells *m* and *ci* of the four-celled proembryo (Text-figs 26–27). A vertical division in *q* and *m* converts the first into a quadrant and the second into two juxtaposed cells, while *ci* divides transversely to form *n* and *n′* (Text-figs 28–29). The eight-celled proembryo is now made up of four tiers of cells, *q*, *m*, *n* and *n′*; further vertical divisions transform *m* into a quadrant and replace the single cell of *n* by two juxtaposed cells (Text-figs 30–31). This is the final stage of the proembryo and, after transverse division of *n′* into *o* and *p*, the four-tiered embryo proper is delimited from the suspensor which originates from *p*. Because *ca* undergoes a vertical division and cells derived from both *ca* and *cb* take part in the formation of the embryo proper, the embryogeny of *E. australis* conforms to the Asterad type. The quadrant *q* now becomes an octant and a periclinal division of each cell of *m* cuts off a central quadrant (Text-fig. 32). The cells of *q* divide periclinally, further vertical and periclinal divisions occur in *m*, *n* becomes a quadrant and *p* forms *p′* and *p″* (Text-fig. 33). Transverse divisions cause *m* to become two-tiered and the three-celled suspensor (ss) is established (Text-figs 34–35). The embryo proper has now assumed a globular form and the suspensor cells become highly vacuolate and of irregular outline. Their contents disappear and, although the suspensor can still be identified when the embryo becomes heart-shaped (Text-fig. 36), no trace of it remains after the initiation of the cotyledons (Text-figs 37–38).



Text-figs 25–38.—Embryogeny. (Lettering follows the system of Souège.) Text-figs 25–35 × 600; 36 × 433; 37 × 270; 38 × 50.

Maturation Gradients in the Capitulum

The capitulum being a racemose inflorescence, its florets mature in acropetal succession and the youngest occupy a central position. There is therefore a gradient expressed in the maturation of both anthers and ovules along any radius. In *E. australis*, however, although the stages of microsporogenesis were found to conform to this centripetal pattern, a reverse gradient was observed in the development of the ovules. In all the capitula examined the central florets contained the youngest anthers and the most mature ovules, whereas the peripheral female florets contained the youngest ovules. This phenomenon of opposite maturation gradients in the male and female reproductive structures of a capitulum has not been reported previously and, in order to investigate it more closely, the ovules of florets occupying three sites in median sections of five capitula were compared:

	Central Bisexual Floret	Innermost Female Floret	Outermost Female Floret
1.	Growth of integument almost completed	Integument development initiated	Ovule atropous
2.	Megaspore tetrad	Meiosis 11	Meiosis 1
3.	2-Nucleate embryo sac	Functional megaspore	Megaspore tetrad
4.	4-Nucleate embryo sac	First embryo sac mitosis	Functional megaspore
5.	2-Cellerd poembryo	2-Celled proembryo	Mature embryo sac

Due to their earlier maturation, the florets at the centre of the capitulum are the first to be pollinated and proembryos are found in their ovules before fertilization occurs in the peripheral florets. During embryogeny, the maturation gradient becomes less apparent and, in the infructescence, the ovaries of all florets contain a seed with a fully developed embryo.

DISCUSSION

Although embryo sac formation follows the Polygonum type, cytokinesis is such that invariably the chalazal antipodal nucleus is enclosed in one cell and the remaining two in the second. This nuclear disposition is in agreement with all other reports in the Compositae where there are only two antipodal cells and there is no record of the chalazal cell ever being the binucleate one. Variation does occur, however, in the behaviour of these cells. For example, in *Synedrella nodiflora* (Banerji and Pal, 1955) and *Tridax trilobata* (Hjelmqvist, 1951) fusion may occur between the nuclei in the micropylar cell so that both cells are then uninucleate, and in *Bidens biternata* (Deshpande, 1964*b*) and *Gerbera jamesonii* (Maheswari Devi, 1957) the nuclei divide and each cell becomes multinucleate. The commonest condition, however, is where nuclear division is accompanied by cell division. This secondary multiplication of antipodal cells has been reported by Harling (1951) in *Chrysanthemum arcticum*, *Erigeron canadensis* and *Matricaria globifera* and later (1954) in *Vittadinia triloba*. In *Epaltes australis* no embryo sac was observed with more than two antipodal cells and, although the two nuclei in the micropylar cell were closely associated, fusion did not occur. In this respect, this species is similar to *Chrysanthemum flosculum* (Harling, 1951), *Flaveria repanda* (Misra, 1957), *Matricaria chamomilla* (Harling, 1951), *Senecio glutinosus* (Afzelius, 1924), *Tridax procumbens* (Maheshwari and Roy, 1952), *Volutarella ramosa* (Deshpande, 1964a) and *Wedelia calendulacea* (Ghosh, 1962) although the occasional occurrence of three antipodal cells is reported in these examples.

The premature degeneration of the synergids is an unusual feature of the embryology of *E. australis*. This appears to be an autonymous breakdown of the cells because it occurs before the entry of the pollen tube and while the embryo sac is still immature. No comparable examples of this phenomenon have been traced in the literature.

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APHROPHYLLUM (RUGOSA) FROM LOWER CARBONIFEROUS LIMESTONES NEAR BINGARA, NEW SOUTH WALES

R. K. JULL*
University College of Townsville, Townsville, Queensland

(Communicated by Mr. R. H. Anderson)

(Plate XIII)

[Read 26th June, 1968]

Synopsis

The hystero-ontogeny of the type species of *Aphrophyllum*, *A. hallense* Smith, is described and *A. smithi*, sp. nov. is proposed. Both species are known only from Viséan (Lower Carboniferous) limestones at Halls Creek, near Bingara. Some similarities between the youthful and adult characters of *A. hallense* and those of *Thysanophyllum orientale* Nicholson and Thomson, type species of *Thysanophyllum*, and *Lonsdaleia* spp. suggest that *Aphrophyllum* may lie with the *Lonsdaleiidae*; other features, however, suggest that it lies in a separate, new family of rugose corals.

INTRODUCTION

Studies of Lower Carboniferous corals from New South Wales by Pickett (1967) and work in progress by the writer on Queensland forms have shown *Aphrophyllum* Smith to be an important and diverse genus endemic to the Viséan of eastern Australia. Its affinities are in doubt, with Smith (1920) and Jones (1933) suggesting a possible relationship with *Endophyllum* Edwards and Haime, Hill (1956) and Dobrolyubova (1962) relating it to *Palaeosmilia* Edwards and Haime, and Pickett (1967) placing the genus with the Lonsdaleiidae. With the intention of clarifying this problem, the following discussion is devoted to the details of the hystero-ontogeny of its type species *A. hallense* Smith. *Aphrophyllum smithi*, sp. nov., which is also described herein, provides some measure of the variability of the genus in the area of provenance of its type species.

Material for this study is from limestones at Halls Creek, some 17 miles south of Bingara, New South Wales (Text-fig. 1). Pickett (1967) considered these beds to be Middle Viséan in age and correlated them with the upper part of the Namoi Formation.

All fossil and locality numbers ("F" and "L" numbers) are registered in the catalogue of the Department of Geology and Mineralology, University of Queensland, Brisbane with the exception of those prefixed with "AM" which are in the Australian Museum, Sydney, and with "BM", in the British Museum (Natural History), London. The terminology applied to hystero-ontogeny is that as outlined by Jull (1965).

SYSTEMATIC DESCRIPTION

Genus APHROPHYLLUM Smith

APHROPHYLLUM HALLENSE Smith

(Pl. XIII, figs 1–3; Text-fig. 2)

Holotype: AM F17640 (not F17648 or F17684 as quoted respectively by Hill, 1934, p. 73 and Pickett, 1967, p. 29) with thin sections AM1036-38-39-40 in the Australian Museum, Sydney (listed as B8 by Smith, 1920, p. 64) and A5051 in the Sedgwick Museum, Cambridge.

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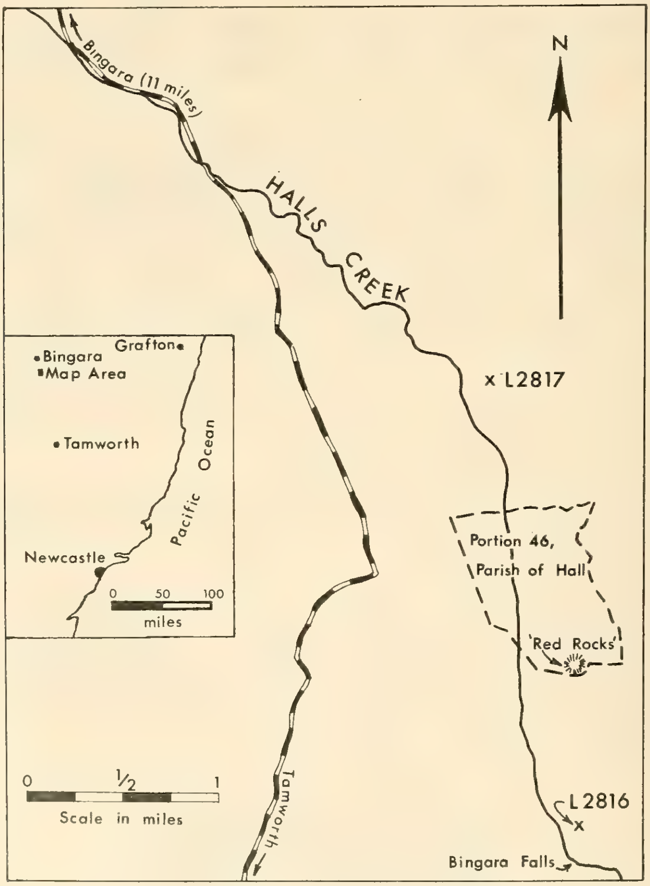
* Now at the Department of Geology, University of Windsor, Windsor, Ontario, Canada.

Locality and Age: The species is known only from a few localities at probably nearly the same stratigraphic horizon in Viséan limestones in the vicinity of Halls Creek, in Parish Hall, County Murchison, some 17 miles south of Bingara, New South Wales. Smith (1920, p. 51) in proposing the species, did not list a specific locality in these limestones for the holotoype and paratype. However, Benson who collected the material, reported (1917, p. 242) a fauna in this limestone in Portion 46, Parish Hall. As this is his only mention of a fossiliferous limestone in the area, presumably this is the type locality. I did not visit this spot during my trip to the area in 1964, but Mr. F. W. Mitchell, property owner on Halls Creek, who provided accurate information on other outcrops of the limestone, described to me the occurrence of a fairly prominent limestone outcrop immediately west of Red Rocks, a locality marked in Portion 46 of the Parish Map (see Text-fig. 1). This is possibly coincident with Professor Benson's collecting site.



Text.-fig. 1. Map of the Halls Creek area showing localities of specimens collected. Site of the type locality of *Aphrophyllum hallense* Smith is probably near "Red Rocks".

Material for this study was collected from two localities in this limestone. One (L2816) is 300 yards north along strike from Bingara Falls and about three-quarters of a mile south of the presumed type locality. The other (L2817) is on the east side of Halls Creek, 25 yards west of the serpentine and approximately one and one-half miles north of Benson's site. The limestones outcrop discontinuously in the area but the three localities are likely to prove to be nearly at the same horizon. There is no doubt that all material in question is conspecific.

Diagnosis: Cerioid, with irregularly shaped corallites averaging 18 mm. in diameter; usually 20 to 24 septa of each of two orders are present; the long often pinnately arranged major septa sometimes meet at the axis to form an irregular axial structure, and the minor septa are well developed; lonsdaleoid dissepiments occupy a variably wide zone and are naotically modified in part; tabulae are domed with flat or upturned ends; increase is lateral, rarely parricidal peripheral; trabeculae are monacanthne.

Description: A. Adult characters. Smith (1920), Hill (1934) and Pickett (1967) have all described the adult characters in adequate detail. Pickett (1967) placed in *Nothaphrophyllum gregarium* Pickett the specimen from Chatham Quarry, Taree, considered by Hill (1934) to belong to the present species.

B. Hystero-ontogeny. All known representatives of *A. hallense* are more or less crushed and this, together with the abundant stereome in the species which tends to obscure detail, and the fact that the axial septa are not obvious, makes the study of corallite development difficult. Amongst eleven coralla, only F46028 from L2816 yielded nearly complete details of hystero-ontogeny from examination of closely spaced acetate peel sections of the specimen. The following description is based principally on one corallite of this specimen, illustrated in Text-fig. 2. In general detail, this example of corallite development is typical of other youthful corallites which were observed in thin sections from other specimens including the holotype. Figure references, viz. F46028/18–23, refer to details in Text-fig. 2.

Lateral increase.

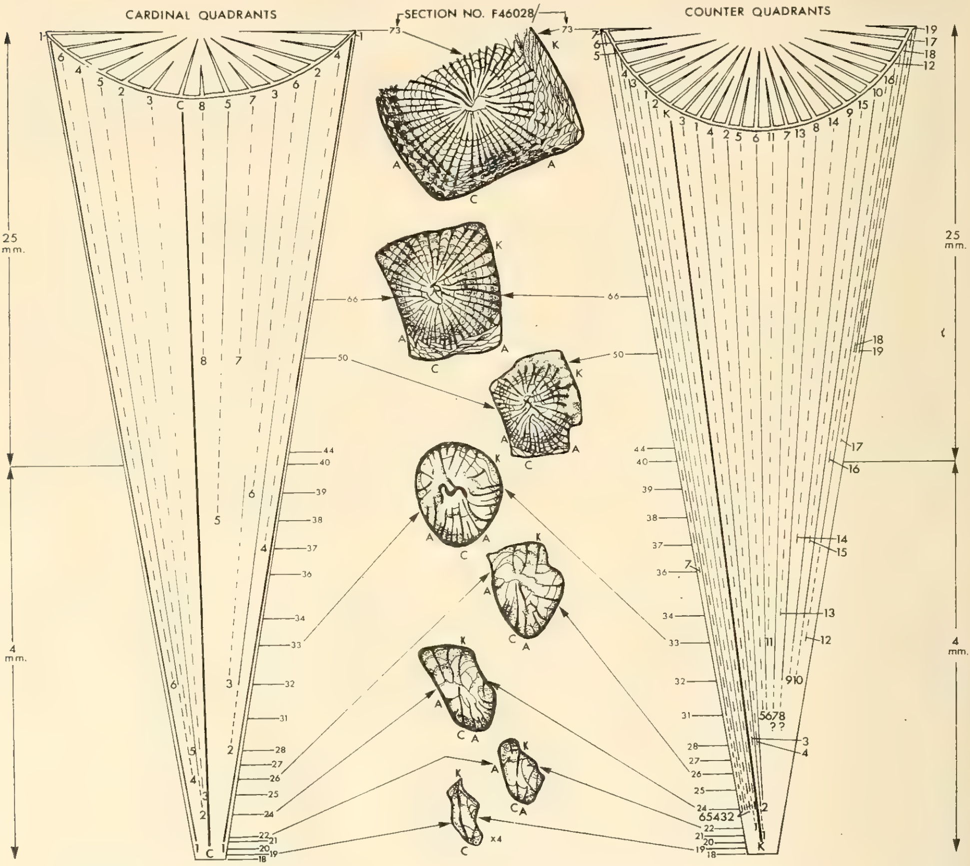
Increase is typically lateral but parricidal peripheral increase has been observed in one instance, this being described after the section on lateral increase. The laterally arising corallite developed within the lonsdaleoid dissepimentarium of the parent and all of its septa are independently inserted; they do not represent continuation of growth of parts of the septa of the parent. Stereome is abundant throughout development.

Hystero-brephic stage (F46028/18–23). The daughter corallite is first obvious as a small area within the lonsdaleoid dissepiments of the parent, and approximately 0·25 mm. distally axial septa appear. The axial plane is orientated radially to the axis of the parent with the cardinal septum on the outer side, furthest from the axis of the parent. Axial septa are initially united but almost immediately separate into counter and cardinal septa which never come into direct contact with each other again during development. Simultaneous with their separation is the appearance of alar septa, followed shortly by counter-lateral septa. After the shortening of the axial septa, none of the six septa are in contact during this stage of development which ranges over approximately 0·45 mm. of growth.

Hystero-neanic stage (F46028/24-38): This stage commences with the appearance of metasepta, and includes most of the septal insertion in the daughter corallite. Insertion is somewhat irregular, with septa arising from the wall of the corallite in fossulae which are not obvious. Newly inserted septa are not contratingent.

Most major septa are inserted before minor septa in a regular manner in the right cardinal quadrant. Insertion in the left cardinal quadrant would probably have been similar had not this side of the corallite been constricted during development with the result that major septum number 4 in this quadrant is late in appearing.

Insertion in the counter quadrants is characterized by periods of rapid insertion of major and minor septa. In general, major septa alternate with minor septa in order of appearance. A disproportionately large number of septa are inserted in the left counter quadrant (the reverse of the diagrammatic corallite in Text-fig. 2), resulting in the lateral migration of the counter septum during corallite growth so that axial septa cease to lie opposite each other. Possibly it was adjacent to the left counter quadrant that the daughter met with the least resistance to corallite expansion.



Text-fig. 2. Hystero-ontogeny in *Aphrophyllum hallense* Smith, F46028, from L2816. The diagrammatic representations of cardinal and counter quadrants illustrate the order of septal insertion; note the change in vertical scale. C= cardinal septum; K= counter septum; A= alar septum; solid lines= long major septa; short dashed lines= short major septa; long dashed lines= minor septa. Number 1 septa in the cardinal quadrants are alar septa. Numbers opposite the diagrammatic quadrants are those of pertinent acetate peel sections. Numbers 18 to 23 are through the hystero-brephic stage, 24-38 through the hystero-neanic stage, 39-72 through the late neanic stage, and 73 through the ephebic stage. Lower five corallites × 2·2, upper three corallites × 1·1.

During the early part of the hystero-neanic stage, major septa do not reach the axis, but they lengthen with further corallite development so that by the end of the hystero-neanic stage, some extend to the axis and an irregular axial structure is consistently present.

Throughout the hystero-neanic stage, the daughter corallite is subcircular in outline and lonsdaleoid dissepiments are absent, except for the occasional small one. Interseptal dissepiments are absent at first, but by the end of this stage of development, a single row is developed entirely around the corallite.

Approximately 2·75 mm. of growth occurs during the hystero-neanic stage. The end of this stage and the commencement of the late neanic stage are transitional.

Late neanic stage (F46028/39-72): The daughter corallite now acquires sharp corners and some lonsdaleoid dissepiments. A few pairs of major septa alternating with minor septa in order of appearance, are inserted at the wall in the cardinal and alar fossulae. A small axial structure of twisted lamellae is present until just before the achievement of the ephebic stage; in some corallites this axial structure persists into adulthood. Little development of the lonsdaleoid dissepimentarium occurs until the later part of this stage. At this time, a wide zone of lonsdaleoid dissepiments develops around the corallite, and many of these dissepiments become naotically modified. With this development, the corallite reaches adulthood, after 20 mm. of growth during this stage and a total of about 23 mm. of growth.

Parricidal peripheral increase.

In the observed example of parricidal peripheral increase, four corallites arose in the calice of the parent, and these soon expanded to occupy the entire area of the calice. A fifth corallite appeared somewhat later than the rest and may have arisen by lateral increase from its developing neighbour. The early stages of development of these corallites have been destroyed by crushing. In general, their hystero-ontogeny resembles that observed in the above described example of lateral increase, except that a lonsdaleoid dissepimentarium is developed earlier, but nevertheless not widened nor naotically modified until the final stage of development. Three of these corallites are illustrated in the lower-left of pl. XIII, fig. 1.

Remarks: The variable nature of the adult morphology of the species is likewise reflected in the nature of corallite development, and it is difficult to assess which features of the latter are typical of the species. Certainly the character of axial septa ceasing to oppose one another after early development in the example illustrated is one of individual variation, and so also is the exact pattern of septal insertion. However, the rather general pattern during hystero-neanic development of major septa appearing before the minor septa in the cardinal quadrants, and major and minor septa appearing alternately in the counter quadrants, is probably fairly typical of the species; it somewhat resembles insertion in laterally arising corallites of *Lithostrotion* (see Jull, 1965). Other apparently significant characters are the initially united axial septa which are radially orientated with respect to the axis of the parent during hystero-brephic development; and the late neanic appearance of an irregular axial structure and of lonsdaleoid dissepiments which are mainly formed as such and not as modifications from interseptal dissepiments.

Increase in *A. hallense* differs in a number of characters from that in the type species of *Thysanophyllum*, *T. orientale* Thomson and in *Lonsdaleia* spp. (see Jull, 1967). United axial septa during hystero-brephic development, and minor septa appearing in the counter quadrants at the start of the hystero-neanic stage are unknown in *T. orientale* and *Lonsdaleia.* They also generally lack the formation of lonsdaleoid dissepiments *per se*, these structures forming rather from interseptal dissepiments by the withdrawal of septa from the wall.

In lateral increase in *Lonsdaleia*, commonly as many as five corallites develop nearly simultaneously from the same parent and some of these corallites are orientated with their axial planes as much as 90 degrees away from the parent; neither of these characters have yet been observed in either *A. hallense* or *T. orientale.*

APHROPHYLLUM SMITHI, sp. nov.

(Pl. XIII, figs 4–5)

Holotype: F46073, from L2816, located in Viséan limestones at Halls Creek 300 yards north along strike from Bingara Falls, Portion 62, Parish Hall, County Murchison, New South Wales.

Diagnosis: Similar to *A. hallense* but with smaller corallites having fewer septa, a narrower lonsdaleoid dissepimentarium, and flatter tabulae.

Description: Based on the holotype and three topotypes, all of which have been partially crushed.

The corallum is cerioid and consists of irregularly shaped polygonal corallites which average 11 mm. and range from 7·5 to 14 mm. in diameter. Intercorallite walls are sinuous or undulating as seen in transverse section of the corallite, and are 0·4 to 0·5 mm. in width. Stereome lines the dissepiments and in some corallites, it may almost totally infill the interstices of the skeletal elements.

Septa are straight or slightly wavy and have irregular outlines. Corallites have from 18 to 22 septa of each order. Major septa generally do not reach the axis in the holotype, but in most corallites of the other specimens (pl. XIII, fig. 5) they extend close to the axis or reach it. Long septa are pinnately arranged in elongate corallites. An axial structure is absent. Minor septa are less than half as long as major septa.

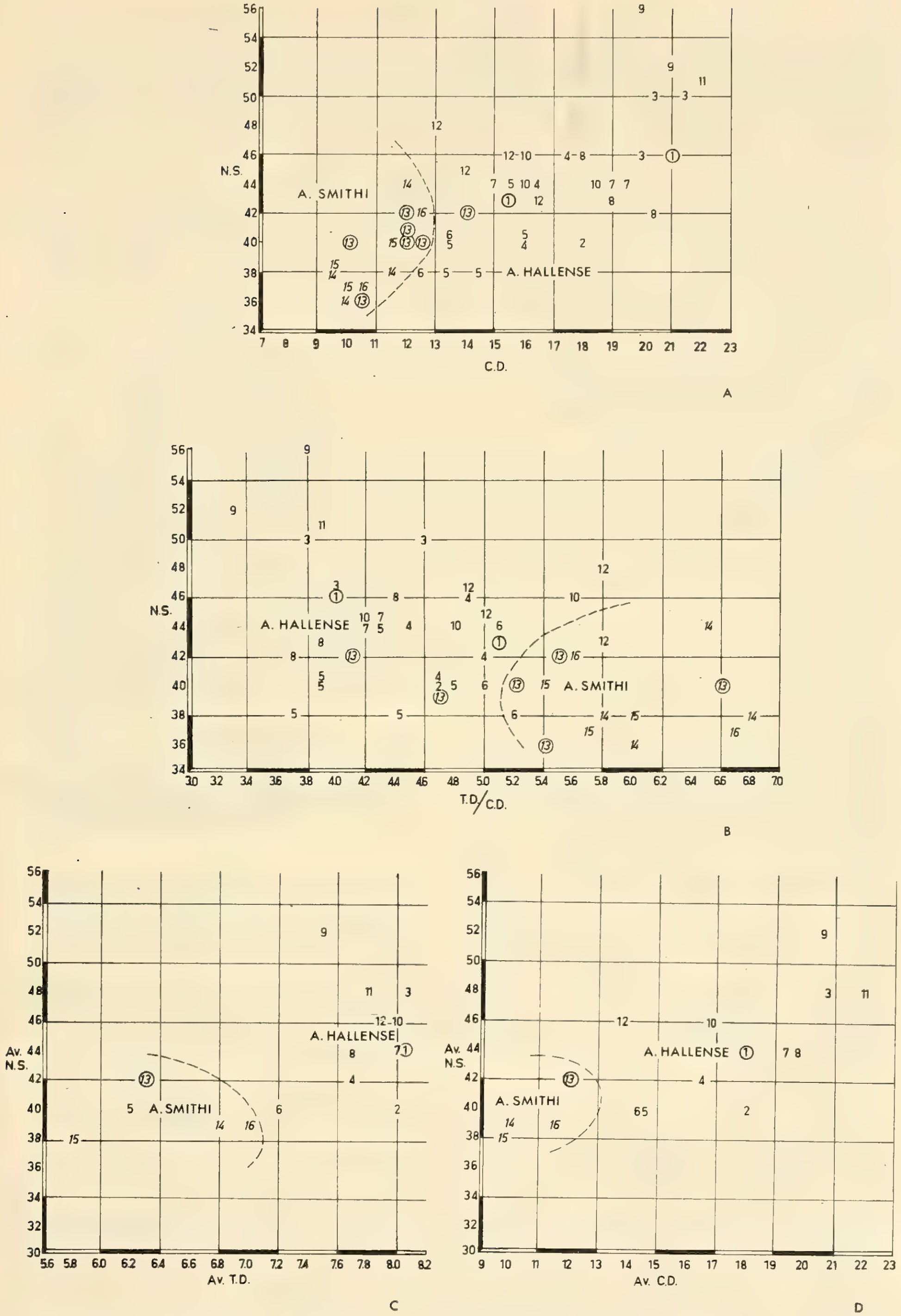
The dissepimentarium consists of one to three rows of steeply inclined interseptal dissepiments bounded by variably developed lonsdaleoid dissepiments which are usually crushed. Lonsdaleoid dissepiments are developed entirely around the corallite, or are present only in a narrow zone in the corners or ends of corallites. Naotic developments are uncommon. The tabularium ranges from 5·5 to 7 mm. in diameter. Tabulae are gently arched or domed if septa extend close to the axis, or flat or sagging if septa are short. The ends of tabulae are flat or upturned, and approximately 20 tabulae occur in a 10 mm. interval.

Hystero-ontogeny: The few youthful corallites observed appear to have arisen by lateral increase. They are similar to those in *A. hallense*, but an axial structure was not observed.

Microstructures: Septal trabeculae are monacanthine and similar to those in *A. hallense* (see Text-fig. 4) except that trabeculae are more closely spaced, being at approximately 0·075 mm. intervals, rather than 0·1 to 0·125 mm. as they are in *A. hallense.*

Distribution: The species is known only at the type locality.

Remarks: The species is named in honour of Dr. Stanley Smith who first described corals from the limestones at Halls Creek. Apart from possessing



Text-fig. 3. Graphical comparison of *Aphrophyllum smithi*, sp. nov. and *A. hallense* Smith. N.S. = number of septa of both orders; C.D. = corallite diameter (the mean of the maximum and minimum dimensions in mm.); T.D. = tabularium diameter (in mm.); Av. = average. Each corallum studied was assigned a number, and all corallites measured in a corallum are recorded on the graphs with the number of their particular corallum. Vertical numbers are of corallites in *A. hallense*, and inclined numbers are of *A. smithi*. Circled numbers are of corallites in the holotypes. Only uncrushed or slightly crushed corallites were measured.

smaller dimensions overall, *A. smithi* is similar to *A. hallense*, and larger than average corallites in this species may be mistaken for *A. hallense* although corallites of the latter usually have a wider lonsdaleoid dissepimentarium and more strongly arched tabulae. The two are graphically compared in Text-fig. 3, and some overlap in parameters is evident, especially in graph B.

AFFINITIES OF APHROPHYLLUM

Although the adult and youthful morphology of *A. hallense* is now well known, the affinities of the genus are still not readily evident. This is partly due to the paucity of information on the hystero-ontogeny of rugose corals in general so that the significance of particular characters is yet not fully appreciated.

Aphrophyllum was considered by both Hill (1956, p. F290) and Dobrolyubova (1962, p. 316) to be related to *Palaeosmilia*; Hill placed the genus in the Amygdalophyllinae.

For the following reasons, however, the affinities of the genus might appear to be with the Lonsdaleiidae, as was first suggested by Pickett (1967). The tabulae of *A. hallense* and *A. smithi* resemble those in *Thysanophyllum orientale*; this last species, the type of *Thysanophyllum*, was concluded by Jull (1967) to lie in the Lonsdaleiidae. When naotic developments are absent in *Aphrophyllum*, a common situation in this genus, the lonsdaleoid dissepimentarium is similar to that in typical lonsdaleid corals. Moreover, corallites of *Aphrophyllum* in which septa do not reach the axial region closely resemble the typical morphology of *Thysanophyllum*; this especially applies to some undescribed Queensland species, such as *Aphrophyllum* sp. illustrated by Hill and Woods (1964, pl. C2, fig. 1).

Other characters of *Aphrophyllum*, on the other hand, are unknown in typical representatives of *Lonsdaleia* and *Thysanophyllum*. These are the pinnate arrangement of septa in all known species of *Aphrophyllum*, some details of the hystero-ontogeny of *A. hallense*, as discussed above, and the nature of the axial structure.

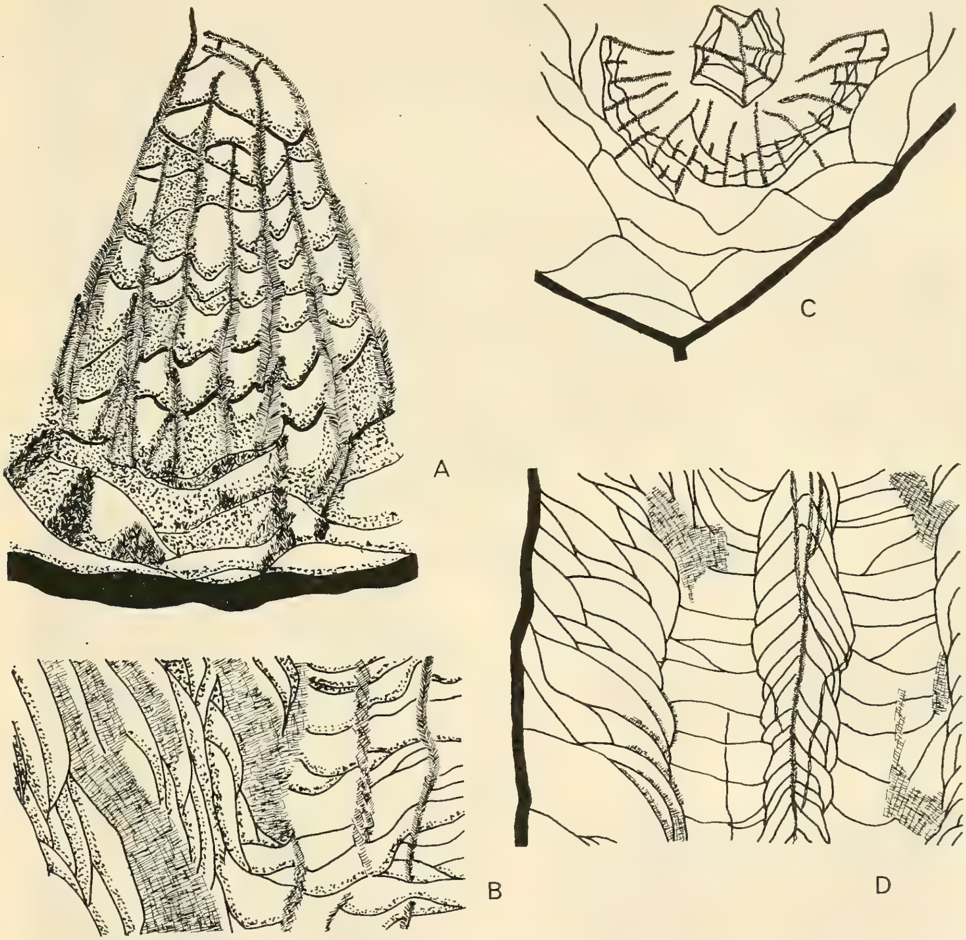
Septa in *Aphrophyllum*, *Lonsdaleia* and *Thysanophyllum* are composed of monacanthine trabeculae (Text-fig. 4). In *A. hallense*, trabeculae are larger than is normal in these other genera, and the peripheral ends of septa in some corallites are composed of two or more rows of trabeculae and may be split or cavernous. Multiple rows of trabeculae are a common situation in some corals showing naotic developments, but are unknown in *Lonsdaleia* and *Thysanophyllum*. Wang (1950) has earlier remarked on septal structure in these genera.

There is thus a strong suggestion that *Aphrophyllum* lies in a separate, new family of rugose corals. Further work on other species of *Aphrophyllum* is currently in progress by the writer and may assist in elucidating the taxonomic position of this genus.

Finally, Smith (1920, p. 55) and Jones (1933, p. 60) have both remarked on the similarity of *Aphrophyllum hallense* to *Endophyllum*; superficially at least, the former differs significantly only by having naotically modified dissepiments. *Endophyllum* is widely distributed in Middle to Upper Devonian beds and three cerioid species described by Gorsky (1935) from the Tournaisian of Novaya Zemlya appear to belong to the genus (see Soshkina and Dobrolyubova, 1962). Possibly hystero-ontogenetic studies of *Endophyllum* may show that *Aphrophyllum* is descended from this line.

Acknowledgements

I am very grateful to Professor D. Hill, F.R.S., both for her criticism of the manuscript of this paper and her advice during my studies at the University of Queensland, of which this paper is part of the outcome. Mr. O. H. Fletcher, formerly of the Australian Museum, Sydney, helpfully provided photographs and information on the type material of *A. hallense*, and I gladly acknowledge the assistance of Dr. B. Runnegar, of the University of New England, during our visit to the Halls Creek area in 1964 to collect the present material.



Text-fig. 4. Monacanthine septal trabeculae in A, B, *Aphrophyllum hallense* Smith, F46043 from L2816, and in C, D, *Lonsdaleia floriformis floriformis* (Martin), B.M. R17160, from Viséan D_2 zone beds at Coalbrookdale, Shropshire, England. All figs approx. ×7.

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EXPLANATION OF PLATE XIII

All figures × 2.

Figs 1–3. *Aphrophyllum hallense* Smith. 1, transverse section of F46028 from L2816; 2, transverse section of topotype, AM 1037; 3a–b, transverse and longitudinal sections of F46071 from L2817.

Figs 4–5. *Aphrophyllum smithi*, sp. nov. 4a–b, transverse and longitudinal sections of holotype, F46073 from L2816; 5, transverse section of topotype F46074 from L2816.


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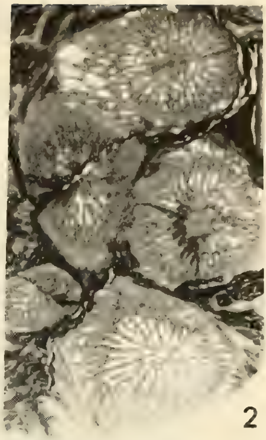
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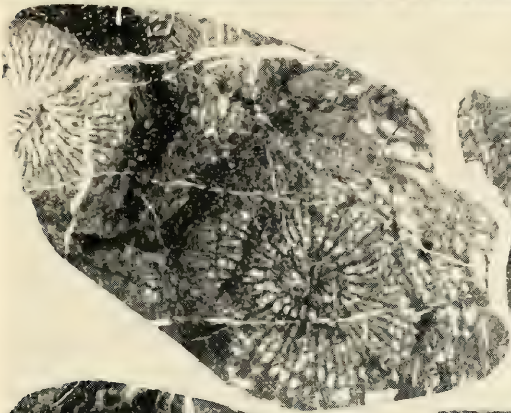
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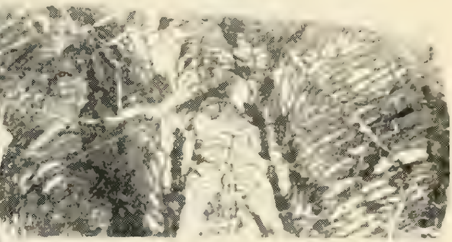
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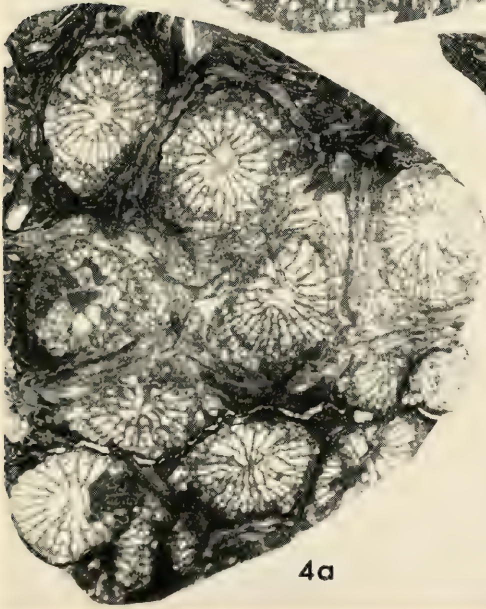
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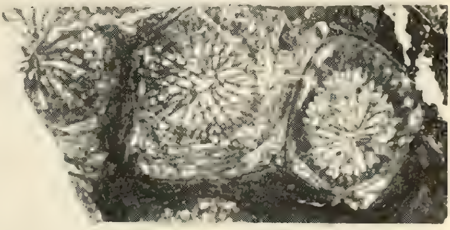
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Aphrophyllum hallense Smith and *A. smithi*, sp. nov.

TYPE SPECIMENS IN THE MACLEAY MUSEUM, UNIVERSITY OF SYDNEY

I. Fishes

P. J. Stanbury

The Macleay Museum, School of Biological Sciences, University of Sydney

(Communicated by Dr. D. T. Anderson)

[Read 26th June, 1968]

Introduction

The Macleay collection was started around 1790 by Alexander Macleay (1767-1848). He collected insects. He caught specimens himself and acquired others by exchange among his friends; but probably the major part of his collection resulted from purchases at auctions of historic collections. In this way Macleay obtained specimens originally collected by Captain Cook's naturalists, Surgeon General White, Charles Sturt and Sir Stamford Raffles as well as many other less well known figures (Fletcher, 1920).

Alexander Macleay brought his collection to Australia in 1825-26 when he was appointed the first Colonial Secretary. His son, William Sharp Macleay (1792-1865), helped his father collect and after William Sharp inherited it, he enlarged it considerably. When he died the collection passed to his cousin, Sir William Macleay (1820-1891), the first President of the Linnean Society of New South Wales.

Sir William Macleay decided to expand the collection to include all branches of the Animal Kingdom as well as anthropological and geological specimens. He employed collectors all over the world and amassed a huge collection that overflowed from his large house at Elizabeth Bay, Sydney, into a museum-building 115 × 36 feet in the garden. When this became full, and having no heir, he decided to offer the entire collection to the University of Sydney. The Senate accepted Sir William's gift in 1888 and the Government contributed £16,000 to erect a Museum building in the University grounds. The collection was moved in 1889, and the building was opened to the public in 1890.

Sir William Macleay died in 1891. The curator he had appointed, George Masters, died in 1912. In 1917, the University started to use part of the building for other purposes. The collection became neglected and its space was severely curtailed as described by my predecessor (Anderson, 1965). In the last few years, however, some attention has been given to the Museum and the following table gives an idea of what remains.

An account of the history of the Macleays was given by J. J. Fletcher in his Presidential Address to the Linnean Society of New South Wales, 14th June, 1920. This account was completed after Fletcher's death from his notes by A. B. Walkom (Fletcher, 1929). The story of Sir William Macleay's collecting trips has been told by D. N. S. MacMillan in his book "A Squatter Went to Sea" (1957).

So far as I can discover, the only lists of type specimens in the collection that have been published are:

(i) Copland, S. J., 1945, 1946.—Catalogue of Reptiles in the Macleay Museum, Parts 1 and 2. Proc. Linn. Soc. N.S.W., 70: 291-311; 71: 136-144. These papers dealt in detail with three species of lizards.

(ii) Hahn, D. E.—A list of the designated type specimens in the Macleay Museum: Insecta. Duplicated at the University of Sydney, 1962. This listed about 2,000 type specimens.

Table 1

An estimate of the number of specimens in the Macleay Museum, University of Sydney, in January, 1968

Specimen	Total	Approximate Number of Types
Coelenterates	300	—
Sponges	200	3
Corals	250	—
Annelids	100	—
Insects	1,000,000	2,000+
Shells	50,000	150
Other molluscs	300	—
Echinoderms	500	—
Fishes	9,000	75
Amphibians	1,000	7
Reptiles	2,000	60
Birds	9,000	12+
Mammals	1,500	8
Anthropological	2,000	Many
Fossils	200	Some

I propose to publish lists of the other type specimens in the Macleay Museum. This will be done in the following order: Fishes; Amphibians Reptiles; Birds; Mammals; and Shells.

This paper contains a list of the fishes of the Macleay Museum from which new species were described.

The Fish Types

Nearly all the fish types in the Museum were described by Sir William Macleay. The original descriptions were published in the Proceedings of the Linnean Society of New South Wales. Most of them were reprinted at Sydney in 1881 by F. W. White, in the "Descriptive Catalogue of Australian Fishes" (Vols. I and II).

The bulk of Sir William Macleay's type specimens are in the Macleay Museum, although about 40 are in the Australian Museum, Sydney (Whitley, 1957).

Macleay collected fishes from specially chartered vessels such as the "Galatea" and the "Peahen" which dredged up and down the coast of New South Wales (Fletcher, 1929), and the "Chevert" which sailed into New Guinea waters (MacMillan, 1957). Macleay also acquired unusual fish from the Sydney Fish Market and from friends.

The following list includes all the fishes that I can find in the Museum that Macleay described as new species. Most of his names have since been superseded, some many times. Further types may lie unrecognised in the Macleay Museum. The fish are stored in bottles in 70% alcohol.

The classification in the list is based on that given by D. S. Jordan, "The Genera of Fishes and a Classification of Fishes" (1963) and the family numbers are Jordan's. The F numbers are the Macleay Museum Register numbers.

The data for each type in the list that follows is arranged in the following order: Family name/Family number/Scientific name under which described/Kind of type/Number of specimens/Locality/Reference in *Proc. Linn. Soc.*, N.S.W./Macleay Museum register number.

Hemiscyllidae 51 *Chiloscyllium furvum* Macleay H 1 Port Jackson VI. 364, No 1094, 1881 F7

Squalidae 67 *Acanthias megalops* Macleay H 1 Port Jackson VI 367, No 1101, 1881 F24

Myliobatidae 84 *Myliobatus australis* Macleay H 1 Port Jackson VI. 380, No 1124, 1881 F41(a)

Dussumieriidae 148 *Etrumeus jacksoniensis* Macleay C 2 Port Jackson III. 36, 1878 F66

Galaxiidae 173 *Galaxias bongbong* Macleay C 10 Moss Vale VI. 233, No 849, 1881 F82

Galaxiidae 173 *Galaxias nebulosa* Macleay C 2 Long Bay nr. Sydney VI. 234, No 850, 1881 F83

Galaxiidae 173 *Galaxias planiceps* Macleay C 9 Rankin's Lagoon; Bathurst VI. 233, No 848, 1881 F85

Galaxiidae 173 *Galaxias coxii* Macleay C Approx. 14 Mount Wilson VI. 232, No 847, 1881 + V p. 46, 1880 F87

Sternoptychidae 185 *Sternoptychides amabilis* Ogilby C Damaged H 1 + bits Lord Howe Island III. pt. 3, p. 1313, 1888 F93

Alabidae 197 *Chilobranchus rufus* Macleay C Approx. 15 Port Jackson VI. 266, No 909, 1881 F96

Alabidae 197 *Chilobranchus rufus* Macleay C Approx. 15 Tasmania VI. 266, No 909, 1881 F96(a)

Echelidae 216 *Muraenichthys australis* Macleay C 2 Lane Cove VI. 272, No 921, 1881 F114

Echelidae 216 *Myrophis chrysogaster* Macleay H 1 Port Darwin VI. 271, No 918, 1881 F115

Echelidae 216 *Myropterura laticaudata* Ogilby C 2 Fiji XXII. 247, 1879 F116

Plotosidae 245 *Copidoglanis longifilis* Macleay C 2 Long Is. Torrest Straits. "Chevert" Exp. 1875 VI. 207, No 809, 1881 F158

Synodontidae 271 *Saurida truculenta* Macleay H 1 Port Jackson VI. 219, No 830, 1881 F174

Synodontidae 271 *Saurida argentea* Macleay C 2 Endeavour River VI. 220, No 830, 1881 F175

Belonidae 302 *Belone gracilis* Macleay C 4 Port Jackson VI. 243, No 865, 1881 F190

Gadidae 310 *Lotella marginata* Macleay C 2 Port Jackson VI. 114, No 767, 1881 F209

Bothidae 326 *Rhomboidichthyls spiniceps* Macleay H 1 Port Jackson VI. 127, No 783, 1881 F211

Bothidae 326 *Arnoglossus bleekeri* Macleay H 1 Endeavour River VII. 124, No 779, 1881 F217

Bothidae 326 *Lophorhombus cristatus* Macleay H 1 Port Jackson VII. 14, 1882 F1160

Paralichthyidae 327 *Teratorhombus excisiceps* Macleay H 1 Port Jackson VI. 126, No 782, 1881 F218

Soleidae 333 *Solea macleayana* Ramsay C(?) 1 Port Jackson V. 462, 1880 F1167

Synapturidae 334 *Synaptura sclerolepis* Macleay H 1 Port Darwin II. p. 363, pl. 10, fig. 4, 1877 F225

Synapturidae 334 *Synaptura nigra* Macleay C 3 Port Jackson V. 1881 48-9 F225(a)

Synapturidae 334 *Synaptura fasciata* Macleay H 1 Port Jackson VII. 1882 14 F1168

Cynoglossidae 335 *Plagusia guttata* Macleay H 1 Endeavour River II. 362, pl. 10, fig 3, 1877 F226

Cynoglossidae 335 *Plagusia guttata* Macleay C 6 Port Darwin II. 362, pl. 10, fig 3. 1877 F226(a)

Cynoglossidae 335 *Plagusia unicolor* Macleay C 2 Port Jackson VI. 138, No 801, 1881 F1162

Holocentridae 348 *Holocentrum goldiei* Macleay C 3 Port Moresby VII. p. 352, No 127, 1882 F241

Syngnathidae 356 *Leptoichthys cristatus* Macleay H 1 Western Australia VI. 296, No. 964, 1881 F256(a)

Syngnathidae 356 *Ichthyocampus maculatus* Alleyne and Macleay H 1 Darnley Is. "Chevert" Exp. 1875 I. 353 pl. 17, fig 2, 1875 F261

Syngnathidae 356 *Ichthyocampus annulatus* Macleay C 2 Port Darwin II. 364, pl. 10, fig 6, 1875 F262

Syngnathidae 356 *Stigmatophora depressiuscula* Macleay H 1 King George's Sound VI. 299, No 969, 1881 F280

Centriscidae 362 *Amphisile komis* Macleay H 1 Yap Is. III. 1876 p. 165 F290

Melanotaeniidae 372 *Aristeus rufescens* Macleay C 2 Rivers of Northern Queensland V. 625, No 538 1880 F294(a)

Melanotaeniidae 372 *Aristeus lineatus* Macleay H 1 Richmond River V. 626, No 539, 1880 F294(b)

Melanotaeniidae 372 *Atherinosoma jamesonii* Macleay C 6 Bremer R. Qld. IX. 171, 1884 F295

Mugilidae 374 *Mugil delicatus* All and Macleay C 4 Cape York "Chevert" Exp. 1875 I. 341, pl. 15, fig. 1, 1875 F306

Polynemidae 376 *Polynemus caecus* Macleay H 1 Port Darwin II. 354, pl. 9, fig. 1, 1877 F325

Thunnidae 378 *Pelamys australis* Macleay H 1 Port Jackson V. 557, No 397, 1880 F333

Carangidae 401 *Caranx edentulus* All and Macleay C 4 Percy Is. I. 327, pl. 11, fig. 2 1875 F349

Carangidae 401 *Caranx bucculentus* All and Macleay C. 2 Cape York I. 326, pl. 11, fig. 1, 1875 F350

Carangidae 401 *Caranx radiatus* Macleay H(?) 1 Rockingham Bay V. 537, No. 362, 1880 F351

Carangidae 401 *Caranx cheverti* All and Macleay H 1 Katow; New Guinea, 1875 I. 324, pl. 10, fig. 1, 1875 F357

Carangidae 401 *Caranx obtusiceps* Macleay C 9 Port Moresby VII. 357, No 151, 1882 F360

Carangidae 401 *Caranx mandibularis* Macleay C 2 Port Moresby VII. 356, No 150, 1882 F363

Carangidae 401 *Caranx laticaudis* All and Macleay H 1 Hall Sound, New Guinea 1875 I. 325, pl. 10, fig. 2, 1875 F365

Carangidae 401 *Caranx papuensis* All and Macleay H 2 Hall Sound, New Guinea I. 325, pl. 10, fig. 3, 1875 F366

Carangidae 401 *Caranx moresbiensis* Macleay H 1 Port Moresby VII. 358, No 152, 1882 F369

Apogonidae 414 *Apogon guttulatus* All and Macleay C Approx 20 Darnley Island. "Chevert" Exp. 1875 I. 267, pl. 5, fig. 1, 1875 F402

Apogonidae 414 *Apogon cookii* Macleay C 10 Endeavour River V. 344, No 88, 1880 F403

Apogonidae 414 *Apogon cookii* Macleay C(?) 7 Port Moresby V. 344, No 88, 1880 F409

Apogonidae 414 *Apogon opercularis* Macleay C 12 Port Darwin II. 347, pl. 7, fig. 1, 1877 F406

Apogonidae 414 *Apogonichthys darnleyensis* All and Macleay H 1 Darnley Is. "Chevert" Exp. 1875 I. 268, pl. 5, fig. 3, 1875 F418

Apogonidae 414 *Apogonichthys marmoratus* All and Macleay C. 2. Cape Grenville I. 368, pl. 5, fig. 2, 1875 F421

Apogonidae 414 *Apogonichthys roseobrunneus* Macleay H 1 Northern Rivers Qld. V. 348, No 105, 1880 F424

Ambassidae 417 *Pseudoambassis castelnaui* Macleay C 4 Murrumbidgee V. 339, No 79, 1880 F427

Ambassidae 417 *Ambassis elevatus* Macleay C 6 Endeavour River V. 338, No 75, 1880 F432

Ambassidae 417 *Ambassis jacksoniensis* Macleay C. Approx. 20 Port Jackson V. 340, No 81, 1880 F434

Ambassidae 417 *Pseudoambassis ramsayi* Macleay H 1 Port Jackson V. 340, No. 80, 1880 F436

Ambassidae 417 *Ambassis papuensis* All and Macleay C 2 Hall Sound, New Guinea 1875 I. 266, pl. 5, fig. 4, 1875 F438

Latidae 422 *Pseudolates cavifrons* All and Macleay C 3 Port Darwin I. 262, pl. 3, 1875 F442(a)

Latidae 422 *Lates darwiniensis* Macleay H 1 Port Darwin II. 345, No 2, 1877 F442(b)

Oligoridae 424 *Oligorus gibbiceps* Macleay H 1 Murrumbidgee (Yass) X. 267, 1885 F443

Epinephelidae 426 *Murrayia jenkinsi* Macleay H 1 Murrumbidgee (nr. Yass) X. 268, 1885 F448(a)

Serrenidae 427 *Serranus goldiei* Macleay H 1 Port Moresby VII. 226, No 9, 1882 F477

Serranidae 427 *Serranus alatus* All and Macleay H 1 Hall Sound, New Guinea "Chevert" Exp. 1875 I. 264, pl. 4, fig. 2, 1875 F482

Serranidae 427 *Serranus guttulatus* Macleay H 1 Port Jackson III. 33, 1878 F1166

Serranidae 427 *Dules haswellii* Macleay C 3 Rockingham Bay V. 359, No 126, 1880 F908

Pseudochromidae 431 *Cichlops filamentosus* Macleay C Approx. 10 Port Darwin V. 570, No 423, 1880 F497

Pempheridae 434 *Pempheris macrolepis* Macleay C. 2 King George's Sound V. 516, No 323, 1880 F503

Lutjanidae 441 *Genyoroge bidens* Macleay C 2 Port Moresby III. 230, 1882 F524

Lutjanidae 441 *Mesoprion obscurus* Macleay H 1 Endeavour River V. 331, No 64, 1880 F527

Lutjanidae 441 *Genyoroge unicolor* All and Macleay C 2 Percy Is. "Chevert" Exp. 1875 I. 266, pl. 4, fig. 1, 1875 F528

Lutjanidae 441 *Mesoprion roseigaster* Macleay H 1 Rockingham Bay V. 331, No 65, 1880 F530

Pomadasidae 444 *Diagramma papuense* Macleay C 4 Port Moresby VII. 237, No 49, 1882 F535

Pomadasidae 444 *Diagramma multivittatum* Macleay C 2 Port Darwin II. 349, pl. 7, fig. 2, 1877 F545

Pomadasidae 444 *Diagramma crassilabre* All and Macleay H 1 Hall Sound New Guinea 1875 I. 271, pl. 5, fig. 5, 1875 F546

Theraponidae 445 *Therapon truttaceus* Macleay H 1 Endeavour River V. 366, No 141, 1880 F573

Theraponidae 445 *Therapon truttaceus* Macleay (?) 1 Endeavour River V. 366, No 141, 1880 F573(a)

Lethrinidae 447 *Lethrinus punctulatus* Macleay C 6 Port Darwin II. 351, pl. 8, fig. 2, 1877 F584

Lethrinidae 447 *Lethrinus laticaudis* All and Macleay H 1 Percy Is. "Chevert" Exp. 1875 I. 276, pl. 8, fig. 2, 1875 F589

Lethrinidae 447 *Lethrinus papuensis* All and Macleay H 1 Hall Sound, New Guinea "Chevert" Exp. 1875 I. 276, pl. 8, fig. 1, 1875 F590

Lethrinidae 447 *Lethrinus fusciceps* Macleay H 1 Port Darwin II. 350, pl. 8, fig. 1, 1877 F596

Lethrinidae 447 *Lethrinus aurolineatus* Macleay C 2 Port Moresby VII. 247, No 108, 1882 F1159

Girellidae 451 *Pachymetopon squamosum* All and Macleay H 1 Hall Sound, New Guinea "Chevert" Exp. 1875 I. 275, pl. 9, fig. 1, 1875 F609

Girellidae 451 *Girella elevata* Macleay H 1 Port Jackson V. 408, No 235 1880 F1155

Gerridae 458 *Gerres longicaudus* All and Macleay C 4 Cape Grenville "Chevert" Exp. 1875 I. 272, pl. 7, fig. 2, 1875 F615

Gerridae 458 *Gerres cheverti* All and Macleay C 2 Cape Grenville "Chevert" Exp. 1875 I. 722, pl. 7, fig. 1, 1875 F617

Gerridae 458 *Gerres profundus* Macleay C 2 Port Darwin II. 350, pl. 7, fig. 3, 1877 F618

Gerridae 458 *Gerres carinatus* All and Macleay C 2 Darnley Island "Chevert" Exp. 1875 I. 273, pl. 7, fig. 4, 1875 F620

Gerridae 458 *Gerres bispinosus* All and Macleay C 2 Hall Sound, New Guinea "Chevert" Exp. 1875 I. 273, pl. 7, fig. 3, 1875 F621

Scorpidae 481 *Scorpis vinosa* All and Macleay H 1 Cape York I. 277, pl. 9, fig. 2, 1875 F674

Chaetodontidae 488 *Chaetodon aureofasciatus* Macleay C 6 Port Darwin II. 351, pl. 8, fig. 3, 1877 F686

Chaetodontidae 488 *Chaetodon ocellipinnis* Macleay H 1 King George's Sound III. 33, pl. 3, fig. 1, 1878 F692

Scorpaenidae 493 *Tetraroge darnleyensis* All and Macleay H 1 Darnley Island I. 278, pl. 6, fig. 1, 1875 F761

Scorpaenidae 493 Centropogon echinatus Macleay H 1 Endeavour River V. 436, No 296, 1880 F764

Platycephalidae 506 *Platycephalus castelnaui* Macleay H 1 King George's Sound V. 587, No 456, 1880 F786

Platycephalidae 506 *Platycephalus longispinis* Macleay H 1 Trawled outside Sydney Heads IX. 170, 1884 F1163

Pomacentridae 532 *Heptadecanthus longicaudis* All and Macleay C 3 Cape Grenville "Chevert" Exp. 1875 I. 343, pl. 15, fig. 3, 1875 F820

Pomacentridae 532 *Dascyllus fasciatus* Macleay H 1 Port Darwin II. 361, pl. 10, fig. 2, 1878 F825

Pomacentridae 532 *Pomacentrus obscurus* All and Macleay C 4 Torres Straits I. 343, pl. 15, fig. 2, 1875 F826

Pomacentridae 532 *Pomacentrus dolii* Macleay C 2 Port Jackson VI. 65, No 672, 1881 F1164

Labridae 536 *Chaerops notatus* All and Macleay H 1 Cape Grenville 1875 I. 344, pl. 16, fig. 1, 1875 F862(a)

Labridae 536 *Trochocopus rufus* Macleay C 2 King George's Sound III. 35, pl. 5, fig. 3, 1878 F1169

Coridae 537 *Coris pallida* Macleay H 1 Endeavour River VI. 100, No 739, 1881 F893

Coridae 537 *Coris papuensis* Macleay H 1 Port Moresby VIII. 275, No 378, 1883 F898

Coridae 537 *Coris cyanea* Macleay C 2 Port Moresby VII. 588, No 216, 1882 F899

Coridae 537 *Labrichthys melanura* Macleay C 3 Port Jackson VI. 89, No 719, 1881 F920

Coridae 537 *Labrichthys dorsalis* Macleay H 1 Port Jackson VI. 87, No 716, 1881 F920(a)

Coridae 537 *Labrichthys maculata* Macleay H 1 King George's Sound VI. 89, No 718, 1881 F920(b)

Coridae 537 *Labrichthys nigromarginata* Macleay H 1 Port Jackson III. 35, pl. 3, fig. 3, 1878 F922

Coridae 537 *Platyglossus immaculatus* Macleay H 1 Port Darwin II. 362, pl. 10, fig. 1, 1877 F935

Coridae 537 *Cheilolabrus magnilabrus* All and Macleay Cotypes of genus and species 4 Darnley Island "Chevert" Exp. 1875 I. 345, pl. 16, fig. 2, 1875 F1154

Coridae 537 *Labrichthys labiosa* Macleay H 1 Port Jackson VII. 88, No 717, pl. 1, fig. 2, 1881 F1158

Sparisomidae 539 *Heteroscarus castelnaui* Macleay C 2 Port Jackson III. 36, pl. 5, fig. 2, 1878 F952

Scaridae 540 *Pseudoscarus flavolineatus* All and Macleay C 3 Cape Grenville I. 346, pl. 16, fig. 3, 1875 F881

Scaridae 540 *Pseudoscarus frontalis* Macleay H 1 Port Moresby VII. 590, No 228, 1882 F901

Scaridae 540 *Pseudoscarus goldiei* Macleay C 2 Port Moresby VII. 590, No. 227, 1882 F1165

Scaridae 540 *Pseudoscarus labiosus* Macleay H 1 Port Moresby VII. 591, No 231, 1883 F938

Scaridae 540 *Pseudoscarus moresbyensis* Macleay C 2 Port Moresby VII. 591, No 232, 1882 F883

Scaridae 540 *Pseudoscarus nudirostris* All and Macleay H 1 Cape Grenville I. 346, pl. 17, fig. 1, 1875 F880

Scaridae 540 *Pseudoscarus zonatus* Macleay H 1 Port Moresby VII. 591, No 230, 1882 F890

Odacidae 541 *Olistherops brunneus* Macleay C 2 Port Jackson III. 36, pl. 5, fig. 1, 1878 F957

Odacidae 541 *Odax brunneus* Macleay H 1 Port Jackson VI. 109, No 759, 1881 F957(a)

Eleotridae 544 *Eleotris compressus* Macleay H 1 Port Jackson II. 358, pl. 9, fig. 7, 1877 F998

Eleotridae 544 *Eleotris elongata* Alleyne and Macleay H 1 Darnley Island I. 334, pl. 13, fig. 1, 1875 F962

Eleotridae 544 *Eleotris taeniura* Macleay H 1 Low. Is. Torres Straits V. 624, No 534, 1880 F963

Eleotridae 544 *Agonostoma darwiniensis* Macleay C Approx 10 Port Darwin II. 360, pl. 9, fig. 8, 1877 F970

Gobiidae 545 *Eleotris compressus* Macleay H1 Port Jackson II. 358 pl. 9, fig. 7 1877 F998

Gobiidae 545 *Gobius lateralis* Macleay C 3 King George's Sound V. 602, No. 485, 1880 F983

Gobiidae 545 *Gobius semifrenatus* Macleay C 5 Port Jackson V. 598, No 478, 1880 F984

Gobiidae 545 *Gobius scabriceps* Macleay C 2 Endeavour River Qld. V. 603, No 487, 1880 F990(a)

Gobiidae 545 *Gobius nigripinnis* All and Macleay C 6 Palm Is. Torres Straits I. 332, pl. 12, fig. 2, 1875 F992

Gobiidae 545 *Gobius darnleyensis* All and Macleay C 3 Darnley Island I. 331, pl. 12, fig. 1, 1875 F992(a)

Gobiidae 545 *Gobius cristatus* Macleay C Approx. 10 Port Jackson V. 610, No 500, 1880 F993

Gobiidae 545 *Gobiodon verticalis* All and Macleay C 8 Endeavour River, Darnley Island (in coral) I. 333, pl. 12, fig. 4, 1875 F987(b)

Gobiidae 545 *Apocryptes lineatus* All and Macleay C 8 Gape Grenville I. 332, pl. 12, fig. 3, 1875 F994

Gobiidae 545 *Apocryptes bivittatus* Macleay C 4 Port Darwin II. 357, pl. 9, fig. 5, 1877 F994(c)

Gobiidae 545 *Gobius maxillaris* Macleay H 1 Port Darwin II. 357, pl. 9, fig. 2, 1877 F999

Gobiidae 545 *Gobiosoma guttulatum* Macleay C Approx 8 Port Darwin II. 357, pl. 9, fig. 6, 1877 F1001

Gobiidae 545 *Gobius flavidus* Macleay C Original label only: No specimen Port Jackson V. 602, No 486, 1880 F1156

Gobiidae 545 *Gobius gibbosus* C 5 Endeavour River V. 601, No 485, 1880 F1157

Callionymidae 561-2 *Callionymus lateralis* Macleay H 1 Port Jackson V. 628, No 543, 1880 F1015

Callionymidae 561-2 *Callionymus calcaratus* Macleay C 6 Port Jackson V. 628, No 542, 1880 F1016

Opistognathidae 579 *Opistognathus jacksoniensis* Macleay C 3 Port Jackson V. 570, No 422, 1880 F1019

Opistognathidae 579 *Opistognathus darwiniensis* Macleay C 3 Port Darwin II. 355, pl. 9, fig. 3, 1877 F1020

Opistognathidae 579 *Opistognathus maculatus* All and Macleay H(?) 1 Torres Straits "Chevert" Exp. 1875 I. 280, pl. 9, fig. 3, 1875 F1021

Clinidae 585 *Lepidoblennius marmoratus* Macleay C 3 King George's Sound III. 34, pl. 3, fig. 2, 1878 F1025

Clinidae 585 *Lepidoblennius geminatus* Macleay H 1 Port Jackson VI. 13, No 571, 1881 F1026

Clinidae 585 *Cristiceps pictus* Macleay H 1 Port Jackson VII. 25, No 589, 1881 F1029

Clinidae 585 *Cristiceps fasciatus* Macleay H 1 Port Jackson VI. 19, No. 579 1881 F1030

Blenniidae 589 *Blennius castaneus* Macleay H? 1 Port Stephens (should be Port Jackson) VI. 5, No 550, 1881 F1034

Blenniidae 589 *Salarias filamentosus* All and Macleay H 1 Cape York I. 337, pl. 14, fig. 1, 1875 F1035

Blenniidae 589 *Petroscirtes guttatus* Macleay C 2 Port Jackson VI. 9, No 557, 1881 F1037

Blenniidae 589 *Petroscirtes wilsoni* Macleay H 1 Port Jackson IX. 170, pl. 1, 1884 F1037(a)

Blenniidae 589 *Petroscirtes cristiceps* Macleay C 4 Port Jackson VI. 9, No 559, 1881 F1037(b)

Blenniidae 589 *Petroscirtes fasciolatus* Macleay C Approx. 10 Port Jackson VI. 8, No 556, 1881 F1038

Blenniidae 589 *Petroscirtes rotundiceps* Macleay C 2 Port Jackson VI. 9, No 558, 1881 F1041

Blenniidae 589 *Salarias irroratus* All and Macleay H 1 Low Is. Torres Straits I. 337, pl. 13, fig. 4, 1875 F1042

Blenniidae 589 *Salarias spaldingi* Macleay C Approx. 10 Port Darwin II. 358, pl. 9, fig. 4, 1877 F1045

Blenniidae 589 *Salarias atratus* Macleay C 2 Port Moresby VII. 361, No 170, 1882 F1047

Blenniidae 589 *Salarias geminatus* All and Macleay C 2 Torres Straits I. 336, pl. 13, fig. 3, 1875 F1050

Blenniidae 589 *Salaris cristiceps* All and Macleay H 1 Darnley Island 1875 I. 338, pl. 14, fig. 3, 1875 F1050(b)

Blenniidae 589 *Salarias auridens* All and Macleay H 1 Darnely Island, Torres Straits I. 338, pl. 14, fig. 2, 1875 F1051

Blenniidae 589 *Salarias cheverti* Macleay C Approx. 10 Darnley Island VI. 12, No 570, 1881 F1051(a)

Blenniidae 589 *Salarias lineolatus* All and Macleay H(?) 1 Port Darwin I. 336, pl. 13, fig. 2, 1875 F1052(a)

Monacanthidae 620* *Monacanthus fuliginosus* Macleay C 2 Port Moresby VII. 596, No 261, 1882 F1084

Monacanthidae 620* *Monacanthus nigricans* Macleay H 1 Port Moresby VII. 596, No 260, 1882 F1087

Monacanthidae 620* *Monacanthus guttulatus* Macleay H 1 King George's Sound III. 37, pl. 4, fig. 2, 1878 F1092

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* Now called Aleuteridae.

Monacanthidae 620* *Monacanthus macrurus* Macleay H 1 Port Jackson VI. 330, No 1029, 1881 F1098

Monacanthidae 620* *Monacanthus guntheri* Macleay C 2 Port Jackson VI. 314, No. 998, 1881 F1161

Tetraodontidae 624 *Tetraodon fasciatus* Macleay C Approx. 8 Port Darwin II. 365, pl. 10, fig. 5, 1877 F1138

Antennariidae 629 *Antennarius asper* Macleay H 1 Darnley Island V; 580, No 442, 1880 F1146

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REPLACEMENT NAME FOR THE PREOCCUPIED GENUS NAME *ODINIA* PERRIER, 1885 (ECHINODERMATA: ASTEROIDEA)

Alan J. Dartnall,* David L. Pawson,† Elizabeth C. Pope,‡ and Brian J. Smith§

[Read 26th June, 1968]

It was recently brought to the attention of one of us (E.C.P.) that the generic name *Odinia* Perrier, 1885 (Echinodermata: Asteroidea) is a junior homonym of *Odinia* Robineau-Desvoidy, 1830 (Insecta: Diptera).

We propose here a new name for the asteroid:

Subclass Asteroidea de Blainville, 1830
Order Forcipulatida Perrier, 1884
Family Brisingidae Sars, 1876
Novodinia nom nov. pro *Odinia* (preoccupied)

Type-species: *Odinia semicoronata* Perrier, 1885, by subsequent designation of Fisher, 1917.

Etymology: *Novodinia* is of feminine gender, derived from the original name.

Remarks: *Novodinia* is a widely distributed genus, being represented in deep water in the Atlantic, Pacific and Indian oceans. In the Southern Hemisphere two species are known, *N. australis* (H. L. Clark) from off Victoria, Australia, and *N. novazealandiae* (H. E. S. Clark) from off the Chatham Islands, New Zealand.

Acknowledgement

The authors' thanks are due to Mr. David McAlpine of The Australian Museum who drew attention to the existence of the genus *Odinia* in the Diptera.

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* A. J. Dartnall, Department of Invertebrates, Tasmanian Museum, Hobart, Tasmania.

† D. Pawson, Division of Echinoderms, U.S. National Museum, Smithsonian Institution, Washington, D.C., U.S.A.

‡ Elizabeth C. Pope, Department of Echinoderms, The Australian Museum, Sydney, New South Wales.

§ B. J. Smith, Invertebrate Department, The National Museum of Victoria, Melbourne, Victoria.

PERMIAN FAUNAS AND SEDIMENTS FROM THE SOUTH MARULAN DISTRICT, NEW SOUTH WALES

R. E. Wass and I. G. Gould
Department of Geology and Geophysics, University of Sydney

(Plates xiv–xv)

[Read 26th June, 1968]

Synopsis

A richly fossiliferous Permian outlier is described from the South Marulan District. Fauna and flora consist of 41 species of which one, *Elimata prima* is new. Correlation of these sediments with beds situated about the Wandrawandian Siltstone-Nowra Sandstone boundary in the South Coast Permian sequence is suggested.

The spatial arrangement of pelitic sediments containing leaves, and sandstones containing a marine fauna enables interpretation of the beds as lagoonal and littoral shoreline deposits which are associated with a Permian transgression. Alternatively, they may represent a simple stratigraphic sequence.

Introduction

The earliest workers in the Marulan-South Marulan district, approximately 120 miles south-west of Sydney, were Woolnough (1909) and Craft (1931). Studies made by Osborne (1931, 1949) and Osborne and Lovering (1952) considered petrological aspects of the batholithic and related rocks. Additional unpublished results are included in theses by Hind (1950), Lovering (1950) and Svenson (1950). Woolnough (1909, p. 786) and Craft (1931, Text-fig. 2) record the small areas of Permian sediments overlying older rocks. The most recent geological map of the area, the Wollongong 1:250,000 Geological Series Sheet SI 56–9 (2nd edn) has been compiled by the Geological Survey of New South Wales. This shows the south-westerly extent of Permian strata referred to the Megalong Conglomerate and undifferentiated Berry Formation to be approximately 4 miles north-east of Permian sediments described herein. One or two isolated outcrops also occur on the Ordovician-Devonian contact approximately 1½ miles north-east of South Marulan.

Pertinent differences can be observed between this map and the geology represented on Text-fig. 1, the latter resulting from a study by Gould (1966). The Silurian acid volcanics and interbedded sediments are separated from Devonian batholithic rocks. On the Wollongong 1:250,000 geological map the distribution of these units suggests that they are not completely separated. Another major difference is that the fault separating Ordovician and Silurian strata near South Marulan is interpreted here as an unconformity.

General Palaeozoic Sratigraphy

The lowest stratigraphic unit is the Tallong beds. They are composed of an undifferentiated sequence of isoclinally folded slates, quartzites and phyllites considered by Sherrard (1949) to be late Upper Ordovician in age.

Unconformably overlying the Tallong beds is the Bungonia limestone. The basal portion is massive limestone but this becomes increasingly arenaceous towards the top. Because of the associated fauna, *Favosites* *gothlandicus* and *F. allani*, *Heliolites*, *Tryplasma*, stromatoporoids and pentamerid brachiopod casts (Svenson, 1950; Flinter, 1950; Gould, 1966) the unit is regarded as Middle-Upper Silurian in age. Toscanites, tuffs and tuffaceous labile and sublabile sandstones with minor pelites previously included in the batholithic rocks are named the Tangerang volcanics. On field evidence they are considered to overlie conformably the Bungonia limestone and to be Upper Silurian in age, probably extending into the Lower Devonian.

The Glenrock granodiorite, a term used by Woolnough (1909) for a major component of the Marulan Batholith, intrudes the three units already discussed. Naylor (1939) and Browne (1950) assign to the granodiorite a probable late Middle Devonian and a Tabberabberan age respectively.

Permian sediments are composed of leaf-rich pelites and fine to medium grained labile and sublabile calcareous sandstones which contain a rich marine fauna and plant detritus. Their position on the Bungonia limestone-Tangerang volcanics contact coincides with a major physiographic break which extends in a southerly direction towards the Shoalhaven River gorge. They outcrop approximately one mile south-west of South Marulan at Grid Ref. 70493024 Wollongong 1:250,000 geological map. Outcrop, which is mainly rubble, covers a kidney-shaped area of approximately 40,000 square yards.

The pelites in the southern portion of the outcrop are composed of 95% clay size particles and brown organic matter, probably leaves. There are small amounts of quartz, zircon and mica.

The major portion of the body consists of detritus comprising quartz (45%), feldspar (25%), rock fragments (25%) with accessory muscovite, biotite and heavy minerals, including hornblende, tourmaline and opaques. Matrix constitutes up to 5% of the rock. Sorting is fair with grains ranging in size from 0·05 mm. to 2·5 mm. in mean diameter. Mineral grains are angular to subangular while most lithic fragments are subrounded to rounded.

Quartz grains cover the entire grain size range and are dominantly of two types. Some grains show undulose extinction, mosaic domains and often with included zircon needles, minute dusty inclusions and rare feldspar laths. The second type commonly exhibits clear extinction and trails of small inclusions. Fragment shapes often suggest hexagonal peripheries while pseudo-inclusions and resorbed rims are apparent.

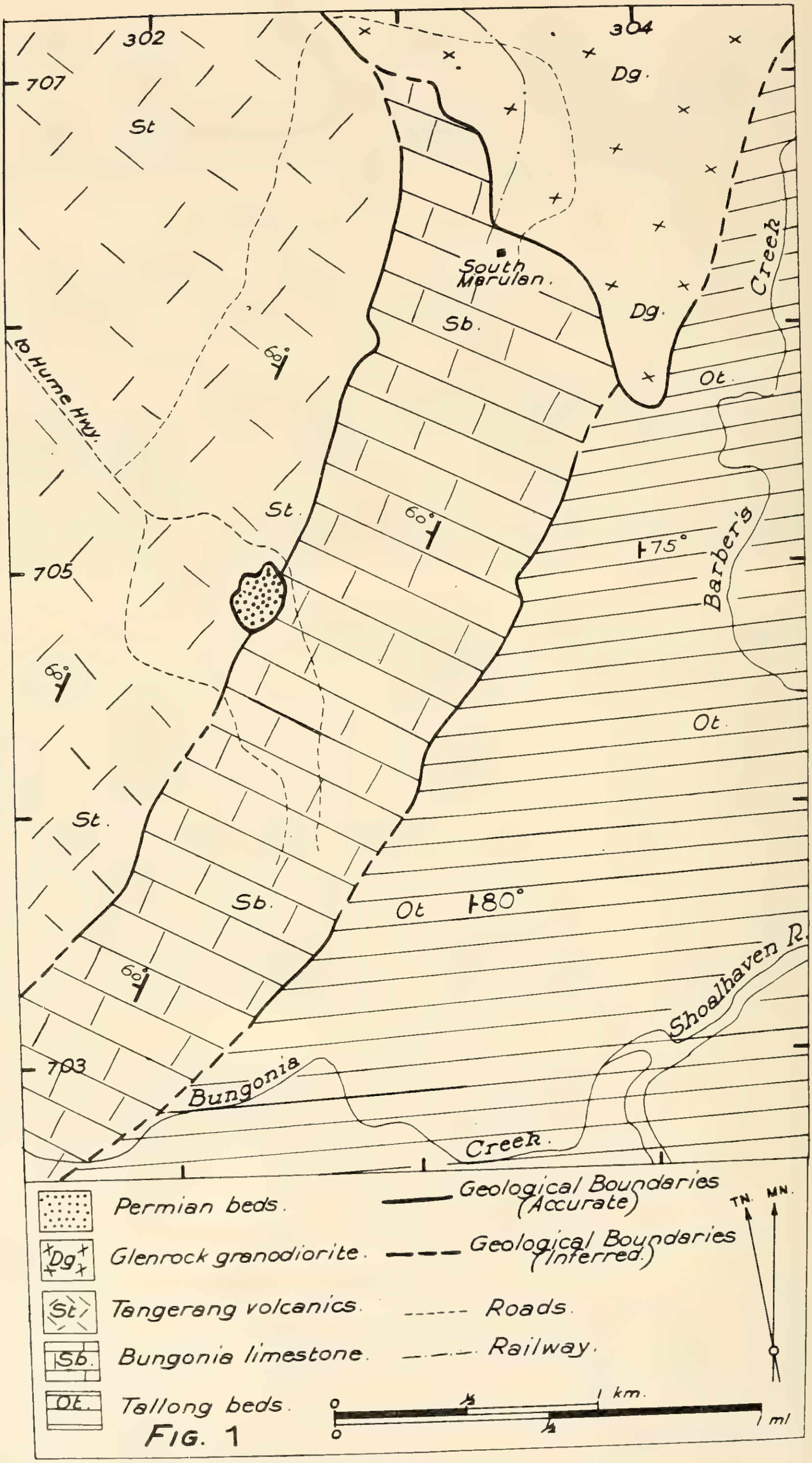
Feldspar grains generally range in mean diameter from 0·4 mm. to 1·0 mm. although rare grains are only 0·05 mm. across. Potassic feldspar and plagioclase occur in approximately equal proportions. K-feldspar is often perthitic and may show sericitisation. Rare myrmekitic growths rim some grains. Some show crosshatched twinning and may be identified positively as microcline. Plagioclase is more commonly altered to chloritic products.

Colourless muscovite and altered biotite flakes are scattered throughout. Heavy minerals are accessory and consist of (i) opaques, (ii) amphibole lath fragments up to 0·5 mm. long, mostly chloritised and (iii) rare tourmaline, pleochroic from blue-green to yellow-green.

Lithic fragments generally show extensive alteration and may be separated into four groups:

(i) acid volcanics showing embayed quartz, feldspar and biotite in a once glassy mesostasis,

(ii) granitic fragments composed of a mosaic of quartz grains and perthitic feldspar,



Text-fig. 1. General Geological Map of the South Marulan area (after Gould, 1966).

(iii) trachytic (?) fragments with abundant feldspar laths defining a flow foliation in a once glassy ? groundmass, and

(iv) rare and extremely fine grained fragments of slates.

Matrix consists of very fine detrital grains with abundant clay minerals. Patchy iron staining is prevalent. Post depositional mineralogical change is evident where areas of complete chloritisation occur. The chlorite forms intergrowths of radiating spherules. These are colourless to pale yellow and generally show grey interference colours but are rarely isotropic.

Consideration of detritus present indicates three major sources.

1. The Tangerang volcanics as evidenced by the second type of quartz discussed and also by recognisable acid volcanic fragments,

2. the batholithic rocks themselves due to the first type of quartz and granitic fragments, and

3. the regionally metamorphosed Tallong beds as evidenced by slate fragments and the pleochroic tourmaline, characteristic of these strata.

Fauna and Flora

Fauna and flora identified are listed below. The fauna occurs in the sandstone. Leaf detritus is found dominantly in the pelites but some is enclosed in the sandstone. In the list, an asterisk (*) indicates the species is discussed later and a stroke (/) indicates the species is figured.

Cladochonus sp.
Conularia inornata Dana
Conularia cf. _tuberculata_ Fletcher
Fenestella canthariformis (Crockford)
Fenestella dispersa (Crockford)
Fenestella granulifera (Crockford)
Polypora woodsi (Etheridge, Jr)
Protoretepora ampla (Lonsdale)
*/_Stenopora gracilis_ (Dana)
Ambikella cf. _ingelarensis_ (Campbell)
/_Ambikella_ cf. _isbelli_ (Campbell)
Ambikella cf. _mantuanensis_ (Campbell)
/_Ambikella_ cf. _undulosa_ (Campbell)
*/_Fletcherithyris_ cf. _amygdala_ (Dana)
/_Fletcherithyris parkesi_ Campbell
/_Gilledia ulladullensis_ Campbell
*/_Notospirifer_ cf. _minutus_ Campbell
/_Strophalosia clarkei_ Etheridge Sr
Strophalosia clarkei var. _minima_ Maxwell
Terrakea solida (Etheridge and Dun)
*/_Terrakea_ sp.
Trigonotreta stokesi Koenig
/_Pleurikodonta_ cf. _elegans_ Runnegar
Atomodesma (_Aphanaia_) sp.
*/_Conocardium_ sp.
Aviculopecten subquinquelineatus McCoy
*/_Elimata prima_ sp. nov.
*/_Stutchburia costata_ (Morris)
Schizodus sp.
Vacunella cf. _curvata_ (Morris)
Merismopteria sp.
Myonia corrugata? Fletcher
Keeneia minor (Fletcher)
Keeneia ocula (Sowerby)
Peruvispira cf. _elegans_ (Fletcher)
Peruvispira trifilata (Dana)
Strotostoma inflata Fletcher
Tribrachiocrinus sp.
Phialocrinus cf. _konincki_ (Clarke)
Glossopteris ampla Dana
Glossopteris sp.

The occurrence of these sediments on the edge of the Sydney Basin together with the spatial arrangement of leaf-rich pelites and sandstones containing a marine fauna indicated that a shoreline may have extended over the area. Because of this the surrounding area was surveyed accurately to obtain the outcrop pattern and to plot the boundary between the pelites and sandstones. Using a scale of 1 inch equals 60 feet, a theodolite stadia traverse established control with sufficient accuracy for a 2 feet contour interval. This has been increased on the final plan to avoid congestion. Detail and geological boundaries were obtained using a telescopic alidade and plane table. The accuracy of the Permian-Silurian boundary to the east may be doubted due to the movement of Permian talus downslope and the superficial similarity of the Permian sandstone and Bungonia limestone lithologies. The heavily wooded nature of the terrain also hindered surveying.

The map resulting from the survey appears as Text-fig. 2.

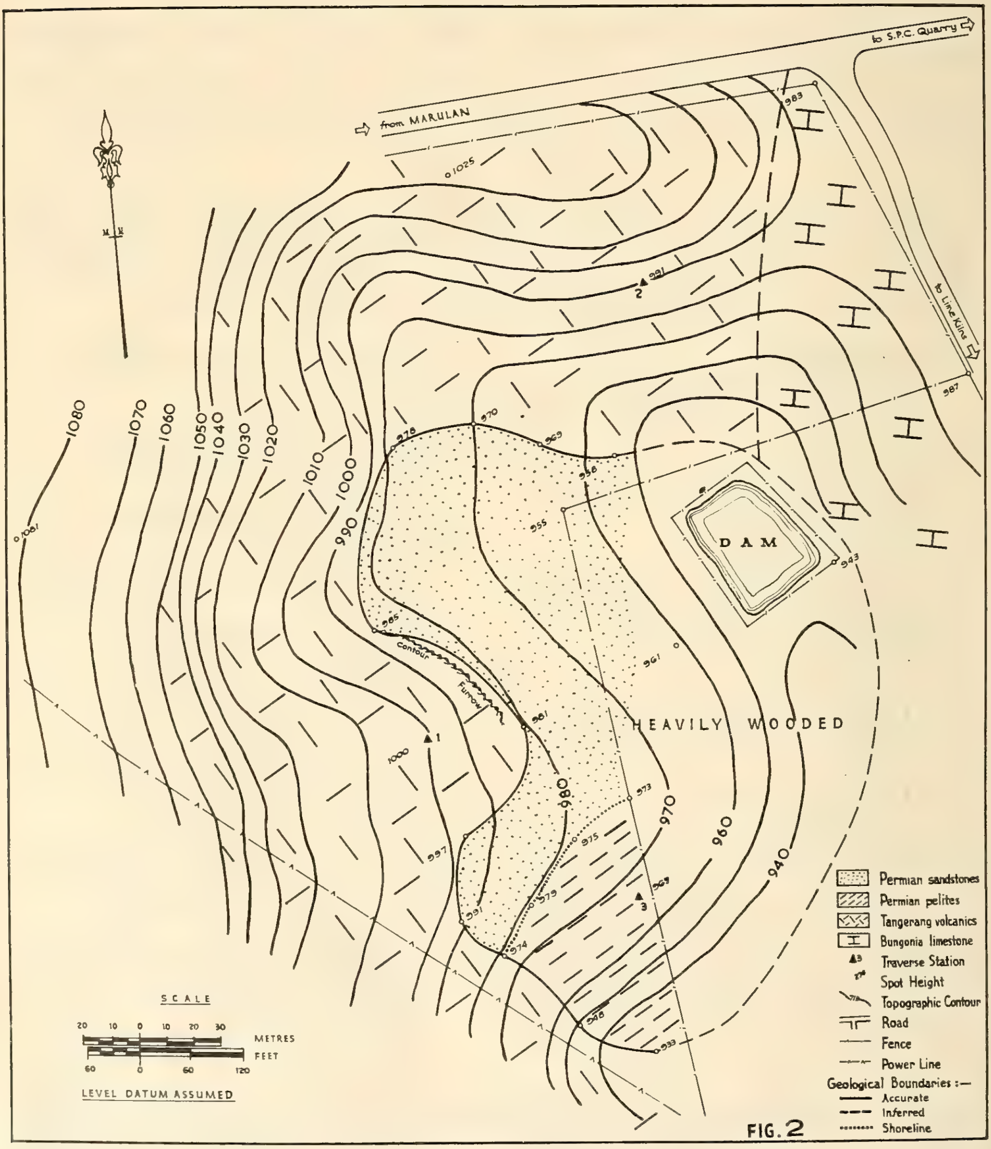


FIG. 2

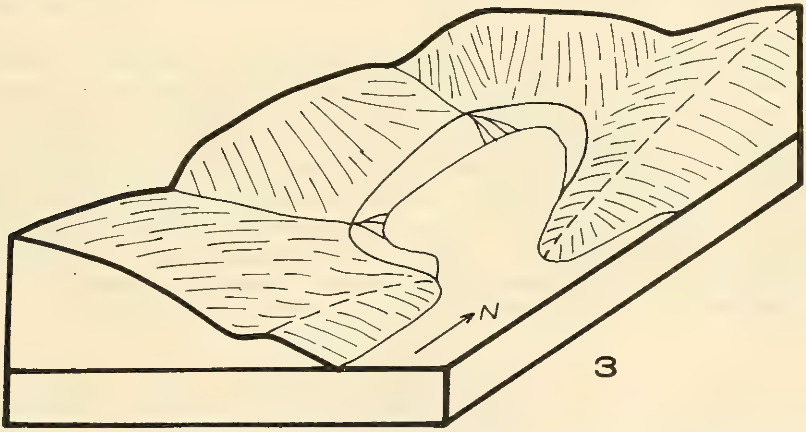
Text-fig. 2. Geological and Survey map of the Permian outlier and surrounding area.

DEPOSITIONAL INTERPRETATION

A division between pelites and sandstones is developed in the southern part of the Permian outcrop along an assumed topographic level of 973 feet to 979 feet. This is approximately 110 feet below the ridge top of Tangerang volcanics to the west. The lowest occurrence of Permian sediment is some 130 feet below this ridge. The ridge of Tangerang volcanics to the north and the eastern ridge formed by the Bungonia limestone are not as high topographically but enclose the Permian sediments on three sides with a topographical opening to the south.

In other areas on the edge of the Sydney Basin, the Permian is thin and in places is abnormal in character. The base of the Permian traces an irregular junction with older rocks so sediments such as these could have been deposited on a surface of some relief. It is possible that this area, affected by a period of Permian transgression contained many inlets and bays which received sediment transported from an eroding high composed of older rocks to the west. The South Marulan area may be interpreted as an inlet with the sandstones being in a littoral environment and the pelitic sediments representing a lagoonal or deltaic environment on the edge. The division between pelites and sandstones could be interpreted then as a shoreline. Subsequent erosion related to a period of regression in the Permian and post-Permian erosion would remove some of the sediments giving rise to the disposition of beds as in Text-fig. 2.

A possible reconstruction of the area in Permian time appears as Text-fig. 3.



Text-fig. 3. Block diagram showing possible topographic elements during deposition of South Marulan strata during Permian time.

We do not feel that the deposits can be representative of both transgression and regression. The marine sediments can be referred to a transgression but it is unlikely that the pelites are part of a regressive phase as one would expect sediments associated with such a regression to become coarser. A regression followed by a transgression is out of the question as the latter must be invoked to allow marine environment to cover the area.

The possibility that the sandstones may overlie pelites must be recognized. To the north and east, shorelines are formed and coarse sediments are overlain by finer sediments with a northerly or north-easterly dip (Craft, 1931). With such a situation here, the dip would be south-easterly but this would depend to some extent on associated Permian topography. Unfortunately no dips can be recorded from the South Marulan sediments.

If the marine deposits are littoral in origin, one would expect to find some evidence of turbulence near the junction with the pelitic sediments and evidence of quieter conditions some distance from this region. The fauna close to the supposed shoreline consists entirely of broken polyzoan detritus, ramose colonies of stenoporids and fenestellids with a large proportion of leaves. This supports a littoral origin. With increasing distance from the pelitic sediments, brachiopod and mollusc individuals increase in number with their valves united. Polyzoan colonies become more complete. Only near the edge of the littoral deposits is there evidence supporting turbulence. Elsewhere the fauna seems to have lived in relatively quiet conditions in shallow water. This would be in keeping with the possible physiographic position and the palaeogeography.

In considering the palaeogeography of the south-western portion of the Sydney Basin, one must take into account the study made by Gostin (1968). His thesis has shown that along the far south-western margin of the Basin in Permian time, sediments unconformably overlying pre-Permian basement become younger in a general north-westerly direction. This is based on faunal and field evidence. In the far south of the Basin, the lowest unit of the Conjola Formation unconformably overlies basement whereas to the west of Ulladulla, the topmost unit of the Conjola Formation, and further to the north-west, the Wandrawandian Siltstone and Nowra Sandstone overlie basement. In other words, there is a progressive transgressive phase in a north-westerly direction along the south and south-western margins of the Basin. The precise direction of the transgression cannot be determined at this stage due to the lack of satisfactory control points in the Nowra-Berry district.

Faunal evidence to support this transgression is adequate. Faunas in the lowest unit of the Conjola Formation are considered by Runnegar (in press) to be Dalwood equivalent, possibly correlative with the Allandale Formation. Further to the north-west, younger faunas in the topmost unit of the Conjola Formation and the Ulladulla Mudstone reveal similarities to faunas in the lower part of the Branxton Formation in the Hunter Valley. Therefore, it is not surprising that an analysis of the South Marulan fauna reveals that it is equivalent to fauna in high Wandrawandian Siltstone-low Nowra Sandstone. It is probably correlative with high Branxton or low Muree Formation. This is discussed in more detail subsequently.

Systematic Descriptions

Phylum Mollusca

Class Pelecypoda

Superfamily ?

Family Conocardiidae Neumayr

Genus *Conocardium* Bronn, 1835

Type Species: (by monotypy) *Cardium* (*Conocardium*) *elongatum* Sowerby, 1812, p. 188, pl. 82, fig. 3.

Diagnosis: See La Rocque, 1950, p. 317.

Conocardium sp.

(Pl. xiv, Figs 10–14)

In the description the shell is oriented in the sense of Branson (1942) and La Rocque (1950) and is the opposite of Fletcher (1943).

Description: Shells are equivalve and small. Anteriorly they are alate with a flattened area near the hinge line. A characteristic key-hole shaped ventral gape is developed along more than half the anterior ventral margin which is slightly curved. The region adjacent to the gape on an internal mould is crenulate with more than 13 crenulations present. They decrease in size and are more closely spaced posteriorly, and can be traced from the margin to the umbonal region. Concentric ornament is not developed as strongly. Carinae are not well developed. The semi-crecentic posterior area is ornamented with 15 or more radial, and concentric plicae, producing small inflections on the slightly curved margin. The posterior tube is produced closer to the umbones than to the posterior extremity. Umbones are small and centrally situated. The hinge line is straight and long. The anterior ligament area is long and narrow and the posterior area is large and wide.

On an external mould, 24 primary radial ribs can be traced from the umbonal region to the anterior ventral margin. This number increases near the margin as secondary ribs arise between the primaries.

Discussion: This species has morphological resemblances to *Conocardium robustum* Fletcher, 1943, because of its strongly inflated carinal area, the shape of the anterior gape and the oblique nature of the carina. It is much smaller than this species but this may be due to immaturity. The species has a more oblique carina than *Conocardium australe* (McCoy).

Specimens catalogued from South Marulan are S.U.P. (Sydney University Palaeontological Collection) 12622 A, B, C.

Dimensions: These are related to the long, straight anterior region.

12622 (right valve)	Length......27 mm.
	Height......20
	Thickness...10

Superfamily Carditacea ?
Family Myochonchidae Newell
Genus *Stutchburia* Etheridge, Jr, 1900

Type Species: (by original designation) *Orthonota* ? *costata* Morris, 1845, p. 273, pl. 11, fig. 1, from the Permian of the Illawarra region, New South Wales.

Diagnosis: See Dickins, 1963, p. 95.

Stutchburia costata (Morris), 1845
(Pl. xiv, Figs 1–5)

Diagnosis: Shell slightly expanded towards rear; radial plications confined to posterior portion of the shell.

Description: Shells become slightly higher and elongate posteriorly; umbones are not prominent; a long deep ligament groove is placed posterior to the umbones. There is a great variation in size. Morphology developed is constant except for the muscle scars. On all specimens the anterior adductor scar has a prominent posterior buttress. This is higher dorsally and wider anteriorly. However, on small specimens the anterior region of this scar overhangs the margin. This is not so with larger specimens in which the anterior adductor scar is divided into a dorsal one-third and a ventral two-thirds by a low ridge which is higher dorsally. Posterior scars are nearly semi-circular with the diameter paralleling the hingeline but they are slightly asymmetrical towards the anterior. Anterior scars are oval. Elongate, narrow pedal scars are evident in front of the umbo on all specimens. The pallial line is entire meeting the anterior scar at its postero-lateral margin and the posterior scar in its ventral region. The hinge is edentulous with a slight twist to the right in front of the umbones. Ornamentation consists of concentric growth lines and upwards of 5 strong radial plicae in the posterior region.

Discussion: The occurrence of a form possessing coarse costae with a subdivision of the anterior adductor scar by a ridge is interesting as Etheridge (1900) stated that the coarse costae were characteristic of *S. costata* whereas the latter feature was characteristic of *S. compressa.* Further studies may show the two species to be identical.

Specimens catalogued are S.U.P. 12610–12614, 12615, A, B, C, 23573 A, B, C.

Dimensions: (right valve)

	Length	Height	Thickness
23573A	63·0	25.0	9·5 mm.
12610	9·6	6·0	2·5 mm.
12611	5·1	2·9	1·0 mm.

Superfamily PECTINACEA
Family LIMIDAE d'Orbigny
Genus *Elimata* Dickins, 1963

Type Species: (by original designation) *Elimata guppyi* Dickins, 1963, p. 93, pl. 15, figs 6–13, from the base of the Permian, Poole Sandstone, Western Australia.

Diagnosis: See Dickins, 1963, p. 93.

ELIMATA PRIMA, sp. nov.
(Pl. XIV, Figs 6–9)

Holotype: 12607 S.U.P. from the northern section of Permian sediments at 70493024 Wollongong 1:250,000 Geological Series Sheet SI 56–9, approximately one mile south-west of South Marulan, New South Wales.

Diagnosis: Robust, convex, markedly opisthocline shells with a short, straight hinge line.

Description: Shells are opisthocline with a short, straight hinge line. Weakly developed umbonal ridges separate small flattened areas from the rest of the shell. The posterior ridge is sharper and more distinct than the rounded anterior ridge which produces a steep slope on the dorsal antero-lateral region of the shell. Concentric growth lines are present and sometimes fine radiating plicae can be observed near the ventral margin.

Discussion: This species is larger, more opisthocline and possesses a shorter hinge line than the type species. This is the first published record of the genus from the Eastern Australian Permian strata. Dickins (1964) referred to *Elimata* sp. nov. from the Ingelara Formation in the south-western portion of the Bowen Basin, Queensland.

Specimens catalogued from South Marulan are S.U.P. 12606–12609.

Dimensions: (right valve)

	Length	Height	Thickness
12607	13	12	2·0 mm.
12609	13+	15	2·5 mm.

Phylum BRACHIOPODA
Class ARTICULATA
Order TEREBRATULIDA
Family DIELASMATIDAE Schuchert
Genus *Fletcherithyris* Campbell, 1965

FLETCHERITHYRIS cf. AMYGDALA (Dana), 1847
(Pl. xv, Figs 7, 11)

Remarks: Specimens assigned to this species show some variation from those described by Campbell. One has a characteristic V-shaped septalium with growth lines normal or directed slightly posteriorly to its length. This is different from *F. amygdala* (Dana) where they are directed mainly anteriorly (Campbell, 1965, pl. 6, figs 24, 32) and *F. farleyensis* Campbell in which they are directed posteriorly (Campbell, 1965, pl. 6, fig. 4). The septalium developed is of similar length to *amygdala* and similar to *farleyensis* in height. The lateral commissure is intermediate between these two species (Campbell, 1965, pl. 6, figs 7, 29).

A specimen smaller than the normal *farleyensis* may be *F. farleyensis faba* Campbell but the characteristics anterior flattening of the pedicle valve in the latter species is not conspicuous. Growth lines on the septalium are normal to its length.

Specimens catalogued are S.U.P. 25557–25558.

Dimensions:

	Length	Width	Height
25557	31	22	13·5 mm.
25558	21	14	8·0 mm.

Order SPIRIFERIDA
Family MARTINIIDAE Waagen
Genus *Notospirifer* Harrington, 1955

Type Species: (by original designation) *Spirifer darwini* Morris, 1845, p. 279 from the Permian, ? Muree Formation at Glendon, Hunter Valley, New South Wales.

Diagnosis: See Campbell, 1959, p. 342; Waterhouse and Vella, 1965, p. 70.

NOTOSPIRIFER cf. MINUTUS Campbell, 1960
(Pl. xv, Figs 1–5)

Remarks: Specimens from South Marulan show much variation in external morphology. In none could the fold in the brachial valve be described as being flat on top. There is a gradation from folds with a shallow sinus to folds with a strong sinus developed. Specimens with the latter feature are considered to be gerontic, this being based also on the nature of the plications. The sulcus of the pedicle valve can have a small fold developed along its midline. In mature specimens, the number of plications is the same in *N. minutus* but they are more strongly developed. In younger specimens the greatest width is more posterior than in older specimens.

Internally the ventral adminicula are similar to those figured by Campbell (1960, pl. 140, fig. 7) and only in small specimens do they tend to become subparallel posteriorly. Dorsal adminicula are shorter than the ventral and widely divergent. They are noticeably longer on specimens with five well developed plicae.

Specimens catalogued from South Marulan are S.U.P. 25544, 25549–52, 25555, 25560, 25561, 25565, 25572, 25573, 25576.

Dimensions: (brachial valve)

	Length	Width	Height
25551	15	28	6·8 mm.
25552	13	23	9·0 mm.
25572	20	36	8·0 mm.
25573	20	39	10·0 mm.

Order STROPHOMENIDA
Family LINOPRODUCTIDAE Stehli
Genus *Terrakea* Booker, 1930

Type Species: *Productus brachythaerus* Morris, 1845, from the Permian of New South Wales. (See Maxwell, 1956, Heming, 1957.)

Diagnosis: See Moore, 1965, p. H503.

TERRAKEA sp.
(Pl. XIV, Fig. 19)

Remarks: Fragmentary remains from South Marulan reveal a wide, straight hinge line. Umbonal shoulders are not steep and the umbo which is blunt and not strongly thickened only slightly overhangs the hinge line. Diductors are longitudinally striated; adductors are finely dendritic.

Features of the umbonal region indicate that this species is remarkably similar to *Terrakea* sp. from the Ingelara Formation and Catherine Sandstone of the Springsure 1:250,000 Sheet area of Queensland. The blunt nature of the umbo with an absence of strong thickening enables a separation from *Terrakea solida* which is found generally at a higher stratigraphic horizon.

Specimens catalogued from South Marulan are S.U.P. 25540, 25545.

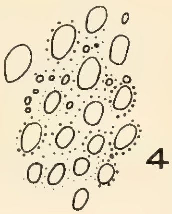
Phylum POLYZOA
Class GYMNOLAEMATA
Order TREPOSTOMATA
Family STENOPORIDAE Waagen and Wentzel
Genus *Stenopora* Lonsdale, 1844

Type Species: (by subsequent designation of Ulrich, 1890, p. 375) *Stenopora tasmaniensis* Lonsdale, 1844, p. 178 from the Permian of Southern Tasmania.

Diagnosis: Zoarium massive, ramose, encrusting, bilaminar; zooecial tubes thin walled in axial region and exhibiting a definite annulated habit in the peripheral region; diaphragms absent; apertures oval or rounded, mesopores and acanthopores present; maculae and monticules may be developed.

STENOPORA GRACILIS (Dana), 1849
(Text-fig. 4)

Diagnosis: Ramose zoarium with a narrow peripheral region and two or three rows of annulations; mesopores not well developed, acanthopores numerous; maculae irregular.



Text-fig. 4. Oblique tangential section through *Stenopora gracilis*, 16431, × 10.

Remarks: Specimens from South Marulan possess ramose zoaria with a diameter of 1·0–5·0 mm. The peripheral region is 1·2 mm. wide in a zoarium of diameter 5·0 mm. Zooecial tubes leave the axis at an angle of 35°–40° and in the peripheral region they are normal to the periphery.

The small, ramose zoaria and the nature of the peripheral region are considered adequate to include these specimens in *Stenopora gracilis*. The species, *S. nigris* Crockford is similar to *S. gracilis*. According to Crockford (1943) both are charaterised by a narrow, peripheral region with two rows of annulations, numerous acanthopores and few mesopores. *S. gracilis* is the finer species but an examination of S.U.P. material reveals that measurements are more similar to *S. nigris* than those stated by Crockford.

Specimens catalogued are S.U.P. 16431–16438.

AGE AND CORRELATION

Recent work by Campbell (1965), Dickins, Gostin and Runnegar (in press), Gostin (1968) and Runnegar (in press) together with studies made during this decade in the Permian of Queensland, particularly by Dickins (in press) enable a reasonable correlation and stratigraphic analysis of the South Marulan fauna to be made with similar faunas on the South Coast and Hunter Valley in New South Wales and with the Bowen Basin in Queensland. Many species are long ranging and of little value. A conspicuous feature of the fauna is the absence of genera such as *Taeniothaerus*, *Grantonia*, *Deltopecten* and *Eurydesma* and particular species of the genera *Notospirifer*, *Cancrinella*, *Terrakea and Ambikella*. This immediately indicates that the fauna is younger than Fauna II in the Bowen Basin and similar faunas elsewhere. However, species such as *Keeneia ocula*, *Gilledia* cf. *ulladullensis*, *Fletcherithyris parkesi*, *Ambikella* cf. *isbelli* and *A.* cf. *undulosa* are recorded from the Conjola Formation, partly equivalent to Fauna II (Dickins *et al.*, in press).

The use of species of *Ambikella* for correlative purposes in the South Coast and Hunter Valley Permian sequences has limited value as most species were originally described from Queensland and those in the Sydney Basin are in urgent need of critical examination. Therefore, all species of *Ambikella* from South Marulan are prefixed by cf. It is worthy of note that the species possess a shallow sulcus and the adminicula are elongated in the brachial valve. These are considered to be features of *Ambikella* spp. in Fauna III of the Bowen Basin.

Species from South Marulan regarded as significant and of use in correlation are *Fletcherithyris* cf. *amygdala*, *Notospirifer* cf. *minutus*, *Terrakea* sp., *T. solida*, *Pleurikodonta* cf. *elegans* and *Vacunella* cf. *curvata*. The occurrence of *Elimata prima*, sp. nov. may be of some value as is the absence of the terebratuloid *Marinurnula*. In the southern region of the Sydney Basin the absence of this genus is of stratigraphic significance as it indicates that the fauna is not younger than the Nowra Sandstone (Campbell, 1965).

Of the South Marulan species, Dickins *et al.* (in press) record *Strophalosia* cf. *clarkei*, *Terrakea* sp. and *Fletcherithyris amygdala* from the Wandrawandian Siltstone and *Vacunella* cf. *curvata*, *Notospirifer* cf. *minutus*, *Strophalosia* cf. *clarkei* and *Ambikella* cf. *isbelli* from Nowra Sandstone. Of the other species considered significant, *Pleurikodonta elegans* has been recorded by Runnegar (1965) from Fauna IV and possibly high Fauna III in the Bowen Basin. This is the first record of the genus outside this area. *Atomodesma* (*Aphanaia*) sp. has been identified from the Oxtrack Formation (low Fauna IV) and in the Springsure area, *Elimata* occurs first in the Ingelara Formation (middle Fauna III) and in strata containing a high Fauna III there is an incoming of *Terrakea* sp. and *Notospirifer* cf. *minutus*. The boundary between the Nowra Sandstone and the Wandrawandian Siltstone may be equivalent to the upper part of the Gebbie Subgroup (high Fauna III) in the Bowen Basin. It seems therefore, that the South Marulan strata may be best correlated with the strata about the Wandrawandian Silstone-Nowra Sandstone boundary. Considering the Hunter Valley sequence in terms of the South Marulan fauna, correlation with the upper part of the Branxton Formation or low Muree Formation is suggested.

Terrakea solida occurs only in Fauna IV. *Aviculopecten subquinquelineatus, Keeneia minor, Stutchburia costata, Gilledia ulladullensis, Fletcherithyris parkesi* and *Fenestella canthariformis* together with species of *Ambikella* appear high or low in the sequence and it seems that correlatives of Fauna III in the southern Sydney Basin contain species found in Faunas II and IV as well as Fauna III of the Bowen Basin. Dickins *et al.* (in press) have already recognised this feature and consider that it may be due to either an hiatus during Fauna III time in the South Coast sequence or to the faunas appearing at slightly different times due to geographical and environmental factors.

A complete faunal study of the South Coast Permian sequence, especially the productids, spiriferids and pelecypods would be beneficial and as a result, correlation of the South Marulan strata with the South Coast sequence may need revision.

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EXPLANATION OF PLATES

Plate XIV

Stutchburia costata

Fig. 1. 23573A, internal mould of a right valve, ×1. Fig. 2. 23573C, external cast of ornament, ×1. Fig. 3. 23573A, internal mould showing hinge line, ×1. Fig. 4. 12611, internal mould of right valve showing overhang of anterior adductor scar, × 8. Fig. 5. 23573A, internal mould of left valve showing ridge in anterior adductor scar, pedal retractor and pallial line, ×3.

Elimata prima, sp. nov.

Fig. 6. 12607, internal mould of left valve, × 2. Fig. 7. 12606, internal mould of right valve, × 2. Fig. 8. 12609, internal mould of right valve, × 2. Fig. 9. 12607, side view of internal mould of left valve, × 2.

Conocardium sp.

Fig. 10. 12622C, external cast of ornament on right valve showing secondary ribs developing between primaries, × 2. Fig. 11. 12622A, internal mould of right valve, × 1·5. Fig. 12. 12622A, internal mould showing keyhole shaped ventral gape, × 1·5. Fig. 13. 12622A, umbonal view of internal mould showing straight hinge line and posterior tube, × 1·5. Fig. 14. 12622A, posterior view of internal mould showing position of posterior tube and inflections on margin produced by plicae, × 1·5.

Pleurikodonta cf. *elegans*

Fig. 15. 12624A, anterior view of internal mould, × 2. Fig. 16, 12624B, external mould showing crenulate commissure, × 3. Fig. 17. 12616, internal mould showing megadesmatid tooth fold, ×4.

Strophalosia cf. *clarkei*

Fig. 18. 25539, internal mould of pedicle valve, × 1·5.

Terrakea sp.

Fig. 19. 25540, oblique view of umbonal region on internal mould of pedicle valve, × 1.

Plate XV

Notospirifer cf. *minutus*

Fig. 1. 25572, internal mould of brachial valve, × 2. Fig. 2. 25551, posterior view of internal mould, × 2. Fig. 3. 25572, posterior view of internal mould showing sinus in fold of brachial valve, × 2. Fig. 4. 25552, internal mould of pedicle valve, × 2. Fig. 5. 25551, internal mould of anterior commissure, × 2.

Fletcherithyris parkesi

Fig. 6. 23452, internal mould of brachial valve, × 1·5. Fig. 12. 23452, internal mould of anterior commissure, × 1·5.

Fletcherithyris cf. *amygdala*

Fig. 7. 25557, lateral commissure on internal mould, × 1·5. Fig. 11. 25557, internal mould of brachial valve, × 1·5.

Gilledia ulladullensis

Fig. 8. 25559, internal mould of brachial valve, × 1·5. Fig. 9. 25559, internal mould of pedicle valve, × 1·5. Fig. 10. 25559, anterior commissure on internal mould, × 1·5. Fig. 13. 25559, lateral commissure on internal mould, × 1·5.

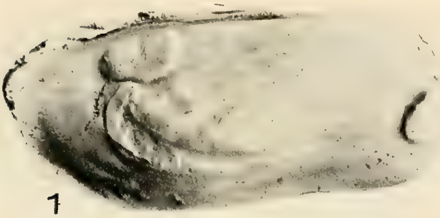
Ambikella cf. *isbelli*

Fig. 14. 23451, anterior commissure on internal mould, × 1. Fig. 15. 23451, internal mould of pedicle valve, × 1·5. Fig. 16. 23451, posterior view of internal mould, × 1·5.

Ambikella cf. *undulosa*

Fig. 17. 25579, internal mould of pedicle valve, × 1.

PLATE XIV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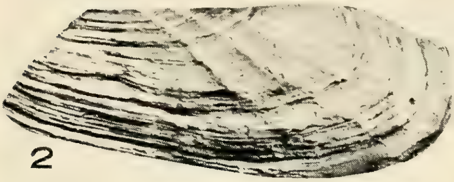
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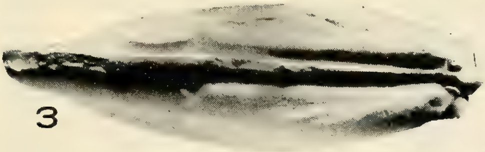
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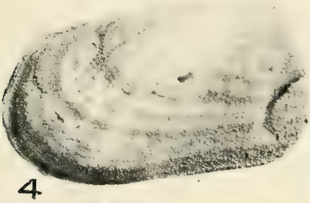
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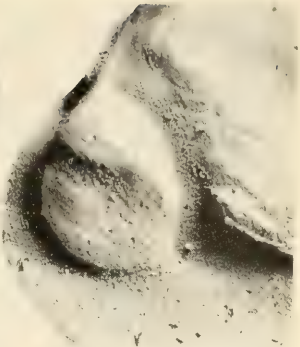
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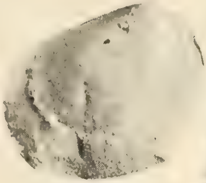
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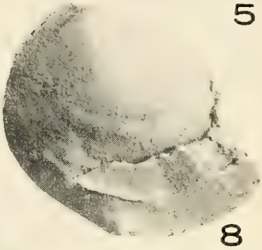
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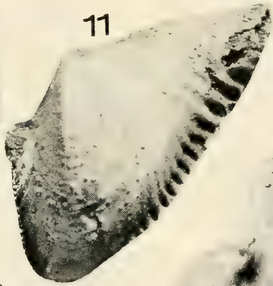
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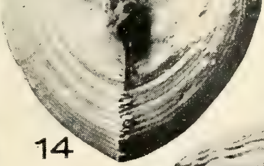
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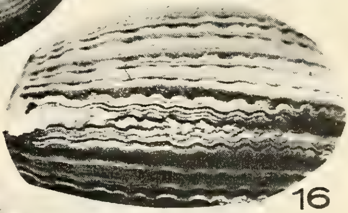
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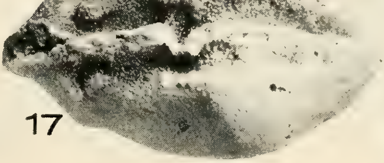
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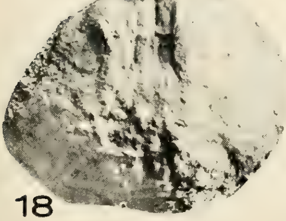
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ON THE FIRST OCCURRENCE OF A *CLIMACOGRAPTUS BICORNIS* WITH A MODIFIED BASAL ASSEMBLAGE, IN AUSTRALIA

HENRY MOORS
University of Melbourne

[Read 31st July, 1968]

Synopsis

This paper describes the first *Climacograptus bicornis* with basal spines modified by the presence of accessory spines, found in Australia, at Tallong, N.S.W. It is compared with a more complicated species *Cl. venustus* found in China and its position with respect to the evolution of *Cl. venustus* from *Cl. bicornis* discussed. The structure of the basal assemblage is described more fully than, and compared with, the Chinese species and its possible function discussed.

INTRODUCTION

In 1959, S. C. Hsu (Hsu, 1959) described a new species of *Climacograptus* with a peculiar basal modification from northwestern Hupeh, China, naming it *Cl. venustus* and showed a possible line of evolution of the species from and through other recognized species. Hsu states (*op. cit.*, p. 351) "It appears hardly possible that the complicate appendage consisting of the powerful principal spines with fully developed accessory ones could have developed directly from the simplest form with only two thin lateral spines. There must be some forms intermediate between them, which have not yet been discovered at present." He then showed how *Cl. venustus* could have been developed from *Cl. bicornis* and backed this line of descent by an analogy with the line of descent of *Cl. peltifer* from *Cl. bicornis*. However, Hsu had only two specimens, both of the same degree of development, and so could only make a guess at the evolution of his species. The finding of this specimen at Tallong, N.S.W., may help to clarify the evolutionary trend as it appears to be of intermediate development between *Cl. venustus* and *Cl. bicornis*.

SYSTEMATICS

Family DIPLOGRAPTIDAE Lapworth

Genus *Climacograptus* Hall

Climacograptus bicornis Hall subspecies.

DESCRIPTION

The polypary has a minimum length of 20·7 mm., excluding spines, but would have reached a greater length as the specimen studied was incomplete. The width at the sicula is only 0·8 mm. and the rhabdosome expands constantly to a maximum of 1·8 mm. at about 1 cm., after which it decreases gradually to 1·6 mm. distally. A virgula, or median septum, can be seen to run through the middle of the rhabdosome after the fourth thecal pair.

The thecae are typically climacograptid and appear to be slightly introtorted causing the aperture to be introverted into an apparently very shallow, small excavation, about 1/6th the width of the rhabdosome. Proximally the thecae number about 13 in 10 mm. with a length of about 0·7 mm., a width of 0·3 mm. and overlap each other by about 1/3 of their lengths, while distally they number just under 10 in 10 mm. and are 1·7 mm. in length.

No sicula could be seen, but the proximal end is typified by two large horizontal spines with a single accessory spine on each. The principal spines (in the terminology of Hsu, 1959) are both crescentric and together form a parabolic curve. One is over 4½ mm. in length while the other, being incomplete, measures only 3¼ mm., and both have maximum widths of approximately 0·3 mm. About one quarter of the way from the sicula each spine carries an accessory which is parallel to the rhabdosome, and measures approximately 1 mm. in length (1·1 mm. and 0·8 mm.); it is of constantly tapering shape and maximum width of 0·2 mm. The principal spines are made up of two portions (Fig. 1, a), the main portion being a solid (?) rod extending for the whole length of the spine and supporting underneath it a thin tube for about two thirds of its length. The solid rod does not appear to be affected by the accessory spines.

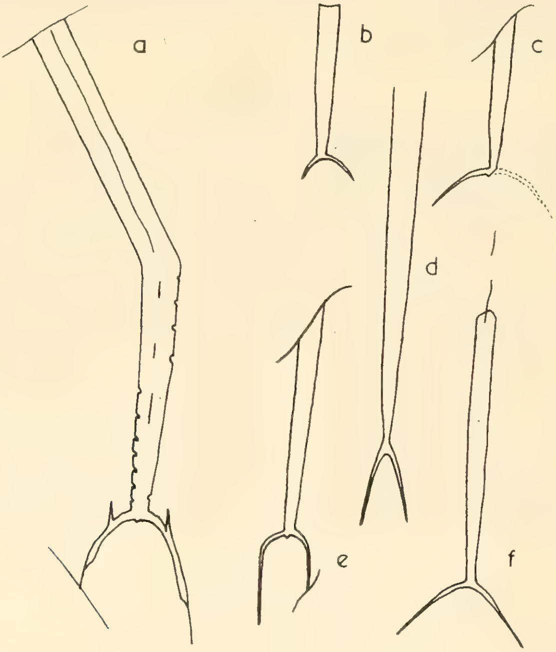

Fig. 1. Camera lucida drawings of actual specimens from locality 9, Tallong. (a) The *Climacograptus* described in this paper, × 5. (b) to (f) *Cl. bicornis* from the same locality as (a) showing the large range of size of rhabdosome and modifications of basal spines; all × 2½.

This assemblage is markedly asymmetrical, the spines are of different lengths (one is incomplete but by comparison with the other can be estimated to be shorter); in this obverse aspect the right hand spine is larger than the left and also carries an accessory spine larger than that carried by the other.

Discussion

The specimen here described varies little from both *Cl. bicornis* and *Cl. venustus* appearing to be a natural link between the two.

The nature of the principal spines is apparently clearer here than in Hsu's two specimens, and the relationship of the various components better shown. The spines can be seen to consist of a tube of almost constant diameter supported by a thin rod which continues past its end (see Fig. 1, a) rather than Hsu's constantly tapering tube with central rod. Also there does not appear to be any constriction of the tube in the vicinity of the auxilliary spines as described by Hsu (an examination of his figures does show some irregularities in width but not as rhythmic as suggested by his description, but they could have been badly drawn).

The accessory spines appear to differ in some respects from those of Hsu. Firstly those of *Cl. venustus* are almost radially disposed on the principal spines (though less so away from the rhadbosome), Hsu comparing it to a high toothed cog, while in this specimen the accessory spines lie parallel to the rhabdosome. Although they are somewhat shorter than in Hsu's specimens, this can be explained by their more tangential position on the principal spines compared to the more radially situated spines of *Cl. venustus*, as explained above.

The function of the accessory spines must remain theoretical (see Hsu, *op. cit.*, p. 351, for some ideas and references) but the suggestion that they could be modified apertures to allow egress of internal tissue does not seem valid as the accessory spines end in a very fine point, limiting any aperture that could be there to very small dimensions, and the principal spines appear to have apertures of their own, where the supporting rod emerges from its tube. For the development of the spines of *Cl. bicornis* see Bulman, 1947, pp. 59-62.

Climacograptus bicornis is a very widespread species, specimens having been found from probably all the graptolite bearing strata of appropriate age. It is very diagnostic in appearance and is easily identified *sensu lato*. However, it is exceedingly variable in size, and shape of the basal assemblage, and already has been subdivided into a number of species and subspecies on the basis of these. The validity of many of these differentiates must be questionable as there is often a complete gradation from one to the next or to *Cl. bicornis sensu lato*.

Ruedemann (1908, pp. 80–85, 1947, pl. 72, fig. 52) and many others have shown the variability of the basal assemblage and size of the rhabdosome, and Fig 1, b–f shows the great variation found at just one locality. This makes one wonder at the value of separating the species into a number of subspecies as there must be only arbitrary divisions between them and they are apparently of little stratigraphic use (many different forms found together). So far apparently only three specimens (two of *Cl. venustus* and this one) have been found indicating that this stage of development of *Cl. bicornis* would be of academic rather than practical interest. The specimen here described is therefore not separated from, but merely indicated to be, a subspecies of *Cl. bicornis*.

EVOLUTION

Hsu envisaged a line of descent (see Fig. 2, a–d) from *Cl. bicornis* with straight extended spines, step (i), through one with drooping spines (ii), then drooping spines with short projections (iii) to *Cl. venustus* with large projections, step (iv). The finding of this specimen would rather indicate that step (iii) should be a species with drooping spines and only one fully grown projection, and an extra step with two fully grown extensions added before the final stage *Cl. venustus* (h–a). Hsu's concept of small size and excess spinosity pointing to the probability of it being a relic form seems to be backed up stratigraphically here.

Material

Only one specimen was found, preserved as a flattened metallic film in fine black slate. The specimen was incomplete, both the distal and part of the proximal end lying off the slab (see Fig 1, a). The graptolite had undergone deformation before fossilisation being bent about 1 cm. from the sicula and the distal portion undergoing some torsion as well. The specimen was given to the National Museum of Victoria where it holds the number P26392.

Horizon and Locality

The specimen came from the Shoalhaven River Gorge near Tallong, N.S.W., and from Sherrard's locality 9 in that area (Sherrard, 1949, p. 77).

From this locality Sherrard has identified *Dicellograptus angulatus*, *D. caduceus*, *Climacograptus bicornis*, *Cl. tridentatus*, *Cl. minimus*, *Orthograptus truncatus pauperatus*, *O. calcaratus basilicus*, *Cryptigraptus tricornis* and *Retiolites* (*Plegmatograptus*) nebula, from which she had deduced an age of Elles and Wood's "Zone 12" or the *Dicranograptus clingani* zone (*op. cit.*, pp. 64, 80, Elles and Wood, 1912). She also further subdivides the zone, stating that locality 9 represents a higher part of it. This is lower than Hsu's Wufengian or Ashgillian (zone of *Dicellograptus complanatus*) and would support the supposition that this is a link between *Cl. bicornis* and *Cl. venustus*.

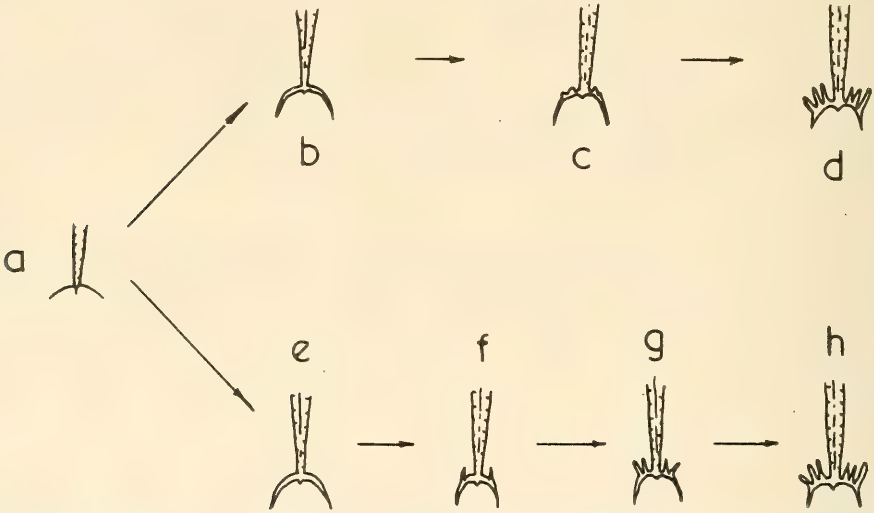

Fig. 2. Postulated evolutionary sequence of forms developing from *Cl. bicornis*, all approximately ×2. (a) to (d) as proposed by Hsu (1959, pl. 1, figs 7, 11, 12, 13), (a), (e) to (h) as proposed in this paper.

Appendix

This area (Tallong) is distinctive in that all the species related to *Cl. bicornis* have their basal appendages enlarged to greater than normal size. Sherrard says (*op. cit.*, p. 69) "The development of the appendages in the former varieties which Ruedemann has studied and figured (1908, p. 80, Plate A) can be paralleled and surpassed at this place, where the length of the virgella in *Cl. tridentatus* and the size of the wings on the shield in *Cl. peltifer* greatly exceeds anything shown in Ruedemann's plate." Apparently, conditions which suited the function of an elaborate basal appendage must have prevailed in the environment where these forms lived during this period. (See Hsu *op. cit.*, p. 351 for suggestions and references.)

Acknowledgements

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CHROMOSOME LOCATION AND LINKAGE STUDIES INVOLVING THE *Pm3* LOCUS FOR POWDERY MILDEW RESISTANCE IN WHEAT

R. A. McIntosh and E. P. Baker
Department of Agricultural Botany, University of Sydney

(Plates XVI–XVII)

[Read 31st July, 1968]

Synopsis

The chromosome location of the incompletely dominant gene conditioning resistance to powdery mildew in Asosan wheat was confirmed as 1A by nullisomic F_2 analysis. This gene, formerly designated Ml_a, is now known to be an allele at the *Pm3* locus and is redesignated *Pm3a* following the recommendations for gene nomenclature in wheat. Repulsion phase linkage studies, using F_2 genotypic classification verified from progeny tests, indicated a crossover value of 4·81 ± 0·52 per cent between *Pm3a* and the gene *Hg* conditioning pubescent glumes.

INTRODUCTION

The loci for certain of the genes conferring resistance to powdery mildew, *Erysiphe graminis* DC. f. sp. *tritici* Em. Marchal, in common or bread wheat, *Triticum aestivum* L. ssp. *vulgare* (Vill.) have been located on specific chromosomes by aneuploid analyses (Sears and Rodenhiser, in Sears (1954); Nyquist, 1957; Briggle and Sears, 1966; Law and Wolfe, 1966; McIntosh, Luig and Baker, 1967). In other instances linkage values have been determined between genes for mildew resistance and previously localised factors which condition other characters (*e.g.*, Briggle and Sears, 1966). Such studies on gene location and linkage intensity have contributed to the rapid expansion of the wheat genetic map in recent years. The studies to be reported are concerned with the chromosome location of a gene conferring mildew resistance in the variety Asosan and with the determination of the linkage value between this gene and that conditioning pubescent glumes.

LITERATURE REVIEW

Pugsley (1961) identified a dominant gene Ml_a for seedling resistance to powdery mildew in the wheat variety Asosan. Briggle (1966) assigned permanent numerals to three loci conditioning mildew resistance, giving the symbol *Pm3* to the locus at which Ml_a is located. Briggle and Sears (1966) reported the presence of a multiple allelic series at this locus in various wheat varieties. Alternatively they proposed that close linkage could be implicated. On the basis of allelism they suggested that as many as five alleles were involved. One group of varieties included Asosan, in which the gene for resistance was effective from the first-leaf stage to maturity. A second group included the variety Indian 1A, in which resistance was not expressed until the three to four-leaf stage. In the studies by Briggle and Sears tests for mildew reactions on the progenies of disomic F_2 plants from crosses between the Chinese Spring monosomic series and Indian identified no chromosome unequivocally as the carrier of *Pm3*. However, tests of Indian substitution line 1A, in which chromosomes 1A of Indian were substituted for their homologues in Chinese Spring by means of a series of six backcrosses to Chinese Spring monosomic 1A, showed clearly that this chromosome carried *Pm3*.

A single gene difference between pubescent and glabrous glumes has been indicated in most instances (see Ausemus *et al.* (1946)). Sears (1953) by nullisomic analysis placed the single dominant gene for pubescent glume *Hg* (Tsunewaki, 1966) in the variety Indian on chromosome 1A.

From backcross data Briggle and Sears (1966) found strong linkage in coupling between *Hg* and *Pm3*, the crossover value being 0·82 map units.

MATERIALS AND METHODS

A backcross mildew-resistant derivative Asosan × Federation^3 W2583* was used in the investigations. It carries the mildew-resistance gene Ml_a from Asosan, possesses glabrous glumes and is distinguished morphologically from Federation in having grains with red pericarp.

The chromosome location of Ml_a was determined by crossing Asosan × Federation^3 as the pollen parent with the series of twenty-one Chinese Spring monosomics, which are mildew susceptible. Monosomic F_1 plants were distinguished from disomic sibs by meiotic examinations of pollen mother cells, stained with acetocarmine, from anthers in spikes fixed in Farmer's fixative. The segregation ratios for reaction types on the primary seedling leaves were studied in the progenies of monosomic F_1 plants in each cross.

The mildew susceptible variety Yalta W1373, with pubescent glumes due to the gene *Hg*, was crossed with Asosan × Federation^3 in order to estimate the recombination value between Ml_a and *Hg*. The progenies of five F_1 plants were studied, about half the spikes on each plant being bagged to prevent possible outcrossing. Since on previous evidence recombination between the genes under study was rare, outcrossing could affect estimates of the recombination value. Seed on bagged spikes of each hybrid plant was threshed and bulked, but kept separated from seed produced by open pollination. Each plant progeny was analysed separately. F_2 seedlings were classified for mildew reaction type on the primary leaf, sprayed with an appropriate fungicide to control further mildew development, transplanted to the field and grown to maturity. The phenotypic classification for glume pubescence was made macroscopically. In doubtful cases a binocular microscope was used for final classification. Segregates with pubescent glumes were classified into two classes, one fully pubescent and the other intermediate in degree of development and in length of the trichomes on the glumes.

The mildew reactions of progenies from F_2 plants classified for mildew reaction type and degree of glume pubescence were determined. On the basis of these tests residue seed from apparent F_2 recombinants between Ml_a and *Hg* was space-planted in the field and F_3 lines classified for pubescent versus glabrous glumes at maturity.

A strain of wheat powdery mildew designated S.U.1 (McIntosh and Baker, 1966) was used in the investigations. Mildew reaction types were scored according to the scheme described by Newton and Cherewick (1947).

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* Refers to Sydney University Wheat Accession Register.

Experimental Results

Chromosome location of Pm3 *locus*

Asosan × Federation^3 was virtually immune to mildew, exhibiting "0;" reaction types on the primary seedling leaf, in contrast to the susceptible "3+" reaction type pustules shown by the Chinese Spring monosomics. Asosan × Federation^3 showed some mildew on the coleoptile, but this was ignored in the investigations. Hybrid plants exhibited slightly higher ("1") reaction types, indicating incomplete dominance of the resistant reaction type. Segregation ratios for mildew reaction type in populations from monosomic F_1 plants from crosses involving various Chinese Spring monosomics are presented in Table 1. Some resistant seedlings showed reaction types similar to Asosan × Federation^3, but the majority, presumably heterozygous in genotype, exhibited "1" types similar to the F_1 plants. Populations from 20 of the 21 monosomics gave segregation ratios conforming with expectation for a single incompletely dominant factor pair in Asosan. For the cross involving monosome 1A (XIV) a highly significant deviation ($P < 0{\cdot}001$) was shown on this hypothesis. The deficiency in the number of susceptible segregates in the cross involving only 1A implies that the gene conditioning mildew resistance in Asosan is located on this chromosome.

Table 1

Segregation for seedling mildew reaction type in progenies of monosomic F_1 plants from crosses between the various Chinese Spring monosomic lines and Asosan × Federation^3

Chromosome involved	Reaction types "0;, 11+" (resistant)	 "3+" (susceptible)	Total	$\chi^2_{(3:1)}$	P value
1A	224	15	239	44·69	0·001
1B	119	40	159	0·002	0·99–0·95
1D	51	15	66	0·18	0·95–0·50
2A (II)	43	15	78	0·02	0·95–0·50
2B (XIII)	60	16	76	0·63	0·50–0·20
2D	62	18	80	0·27	0·95–0·50
3A	52	19	71	0·12	0·95–0·50
3B	48	16	64	0·00	1·00
3D	44	19	63	0·89	0·50–0·20
4A	78	27	105	0·03	0·95–0·50
4B	43	20	63	1·53	0·50–0·20
4D	54	20	74	0·16	0·95–0·50
5A	51	21	72	0·67	0·50–0·20
5B	56	16	72	0·30	0·95–0·50
5D	17	8	25	0·65	0·50–0·20
6A	69	16	85	1·73	0·20–0·10
6B	33	7	40	1·20	0·50–0·20
6D	65	14	79	2·23	0·20–0·10
7A	49	12	61	0·01	0·95–0·50
7B	38	18	56	1·52	0·50–0·20
7D	44	18	62	0·54	0·50–0·20
Total (excluding 1A)	1,076	355	1,431	0·03	0·95–0·50

Three seedlings chimaeric for reaction types ("1–" and "3+") closely approaching the parental types were observed among the progeny of the monosomic 1A F_1 plant (Pl. xvi). In all cases the longitudinal division line between the resistant and susceptible sectors was at, or very close to, the leaf midrib. Presumably chimaerism resulted from loss in an early embryonic division of the Asosan 1A chromosome in a seedling monosomic or monotelosomic for this chromosome. Chimaeric seedlings were grouped with the resistant class on the basis of this assumed origin.

Linkage intensity between Pm3 *and* Hg

The genotypes of Asosan × Federation[3] and Yalta can be designated *Pm3Pm3 hghg* and *pm3pm3 HgHg* respectively and linkage was studied therefore in the repulsion phase. In mildew resistant F_2 segregates two distinct groups of seedlings were observed. One group exhibited "0;" reaction types similar to the resistant parent and the other "11+" reaction types. Tests in F_3 confirmed the latter class as the heterozygous genotype. Glume pubescence was also incompletely dominant. The intermediate phenotype in the F_2 group is shown in Plate XVII together with the fully pubescent and glabrous glumed phenotypes. Behaviour of F_3 again confirmed that the intermediate class was heterozygous. Behaviour of F_3 lines for mildew reaction verified generally the accuracy of F_2 genotypic classification for mildew reaction type and indicated few misclassification errors.

An inspection of F_2 data, in which the genotypic classification for mildew reaction type was verified or corrected from progeny tests, indicated certain recombinant classes resulting from crossing over between *Pm3* and *Hg* in repulsion in F_1 gametogenesis. Individuals in such classes were checked by F_3 tests for the correctness or otherwise of F_2 genotypic classification at the *Hg* locus. Progeny tests for this purpose were of homozygous resistant plants which were pubescent in F_2, of plants heterozygous for mildew reaction type classified as homozygous dominant or homozygous recessive at the *Hg* locus, and of homozygous susceptible plants classified as heterozygous at the *Hg* locus. Lines in which plants were scored for pubescent versus glabrous glumes at maturity confirmed genetic recombination and revealed accurate classification of *Hghg* and *hghg* F_2 genotypes. In 3 cases out of 36, plants classified as homozygous pubescent in F_2 were found to be heterozygous on the basis of F_3 tests. No significant differences in segregation were found in the populations derived from bagged versus open-pollinated F_1 spikes and the data were pooled for analysis. The F_2 genotypic totals for mildew reaction type, confirmed or amended in a few instances on the basis of progeny tests, were 216 homozygous resistant, 432 heterozygous and 194 homozygous susceptible. However, 44 seedlings classified for reaction type to mildew failed to survive transplantation and produced neither adult plants for pubescent glume classification nor seed for progeny testing. These were not distributed at random in the three mildew reaction categories, 9 being from the homozygous resistant, 14 from the heterozygous and 21 from the homozygous susceptible classes. Despite spraying for mildew control, survival was strongly biassed against susceptible seedlings. The final figures were adjusted therefore in each mildew reaction genotype. F_2 plants which died were included to remove the possible effect of differential survival on linkage estimation. The distribution within glume pubescence genotypes of the plants which failed to survive was based on that shown for surviving plants in each category. The adjusted numbers in the different genotypes for mildew reaction and pubescence genotypes are shown in Table 2.

From maximum likelihood equations, recombination between *Pm3* and *Hg* was calculated to be 4·81 ± 0·52 per cent.

DISCUSSION AND CONCLUSIONS

The current investigations using nullisomic analysis demonstrated that chromosome 1A carried the gene Ml_a for mildew resistance in Asosan. This confirmed the findings of Briggle and Sears (1966) who used the chromosome substitution technique to place an allele in Indian on this chromosome. Briggle (1966) designated the locus at which Ml_a is situated as *Pm3* and proposed that alleles at a locus be indicated by lower case letters. On the basis of this recommendation we propose that the gene in Asosan previously referred to by Pugsley (1961) as Ml_a be designated *Pm3a*. This symbolism seems logical and orderly, especially as this gene exhibits the lowest reaction type on the primary seedling leaf of alleles at this locus.

The postulated origin of chimaeras for mildew reaction in three F_2 seedlings in the progeny of a monosomic 1A F_1 plant provided additional evidence that chromosome 1A carried the *Pm3* locus. In disomic heterozygotes it would be necessary to invoke an unusually high rate of mitotic instability to explain their occurrence. It is highly probable that such seedlings were initially monosomic for chromosome 1A carrying the *Pm3a* allele and hence hemizygous for this gene. A high rate of mitotic instability is more characteristic of monotelocentric than normal chromosomes in *Agropyron* addition lines to wheat (Baker, unpublished); Steinitz-Sears (1966) reported also that telocentrics for the short arm of monosome 3B in wheat were unstable somatically. This suggests that the chimaeric seedlings may have been produced, in fact, from individuals monotelocentric for the arm of 1A carrying the *Pm3a* gene. Assuming the constitution of the chimaeric sectors is as postulated, a comparison of the reaction types in the resistant sector with those exhibited by Asosan × Federation³ (Pl. XVI) indicates that *Pm3a* is slightly less effective in the hemizygous than the homozygous state. However, the reaction types appeared lower than in the heterozygous state in identical backgrounds under the same environmental conditions.

TABLE 2

Numbers of plants in various F_2 genotypes from five hybrids between Asosan×Federation³ (Pm3aPm3a hghg) *and Yalta* (pm3apm3a HgHg)*

Genotype	Number of plants
Pm3aPm3a HgHg	1·04
Pm3aPm3a Hghg	18·75
Pm3aPm3a hghg	205·21
Pm3apm3a HgHg	14·45
Pm3apm3a Hghg	403·67
Pm3apm3a hghg	27·88
pm3apm3a HgHg	195·05
pm3apm3a Hghg	19·95
pm3apm3a hghg	0·00
Total	886·00

* Adjusted to include 9 mildew-resistant (*Pm3aPm3a*) plants, 14 plants heterozygous for mildew reaction type (*Pm3apm3a*) and 21 mildew-susceptible (*pm3apm3a*) plants which failed to survive after transplantation.

χ^2_2 (1 *Pm3aPm3a* : 2 *Pm3apm3a* : 1 *pm3apm3a*) = 0·26 ; P = 0·95–0·50.

χ^2_2 (1 *HgHg* : 2 *Hghg* : 1 *hghg*) = 1·15 ; P = 0·95–0·50.

In crosses both with Chinese Spring monosomics and Yalta, *Pm3a* was incompletely dominant. The heterozygous genotypes in crosses with Yalta showed somewhat higher ("11+") reaction types than with Chinese Spring ("1"). This may have been due to the higher temperatures prevailing when the Yalta crosses were tested.

The estimate of linkage intensity between *Pm3* and *Hg* in coupling by Briggle and Sears (1966) from testcross data, using the variety Chancellor with the double recessive genotype as the male parent, indicated close linkage with a crossover value of 0·82 per cent. The value of 4·81 ± 0·52 per cent in the current investigations from F_2 studies with linkage in repulsion is significantly higher. In maize there is evidence that crossing over for many of the chromosomes is considerably higher in male than female gametogenesis (Rhoades, 1941; Burnham, 1949). Briggle and Sears estimate restricted crossing over to female gametogenesis whereas in the current studies crossing over occurred in both sexes. It is not known how widespread the phenomenon of higher crossing over in the pollen is in higher plants. Ramage (1960), in fact, found crossing over higher in the female in barley. In any case estimates of linkage frequently vary in different investigations. In barley, for example, Woodward (1957) and Wells (1958) obtained recombination percentages of 26·5 and 18·0 respectively between the loci for rough versus smooth awn (*Rr*) and long versus short-haired rachilla (*Ss*).

It is of interest that Briggle (1966) described a group of five mildew resistant varieties, all with pubescent glumes, in which resistance was not expressed until the three to five-leaf stage and in which three different alleles appeared to be involved at the *Pm3* locus. Selections have been made in appropriate F_3 lines in the current investigations to isolate *Pm3aPm3a HgHg* genotypes. These together with the progeny of the single *Pm3aPm3a HgHg* recombinant F_2 individual classified in the studies will furnish a useful genetic stock carrying two dominant closely linked markers which are readily classifiable genotypically and in which the mildew reaction classification can be made at the primary leaf stage.

Briggle and Sears (1966) from the phenotype of a plant monotelosomic for the long arm of an Indian chromosome 1A in a Chinese Spring background and an analysis of its progeny concluded that the *Pm3* and *Hg* loci were both on the short arm of this chromosome. The distances of each gene from the centromere can be determined by using a telocentric for the short arm of 1A in mapping but as yet this aneuploid stock is not available. In view of the close proximity of the two loci it will be of interest to determine if the technique is sufficiently precise to place their order with respect to the centromere should the genes be situated at some distance from it. Should the loci be close to the centromere the difference between the recombination value obtained in the current investigations and that published by Briggle and Sears (1966) may be due, in part at least, to differences in frequencies of crossing over in male and female gametogenesis since Rhoades (1941) found differences more accentuated in regions near the centromeres in maize.

Acknowledgements

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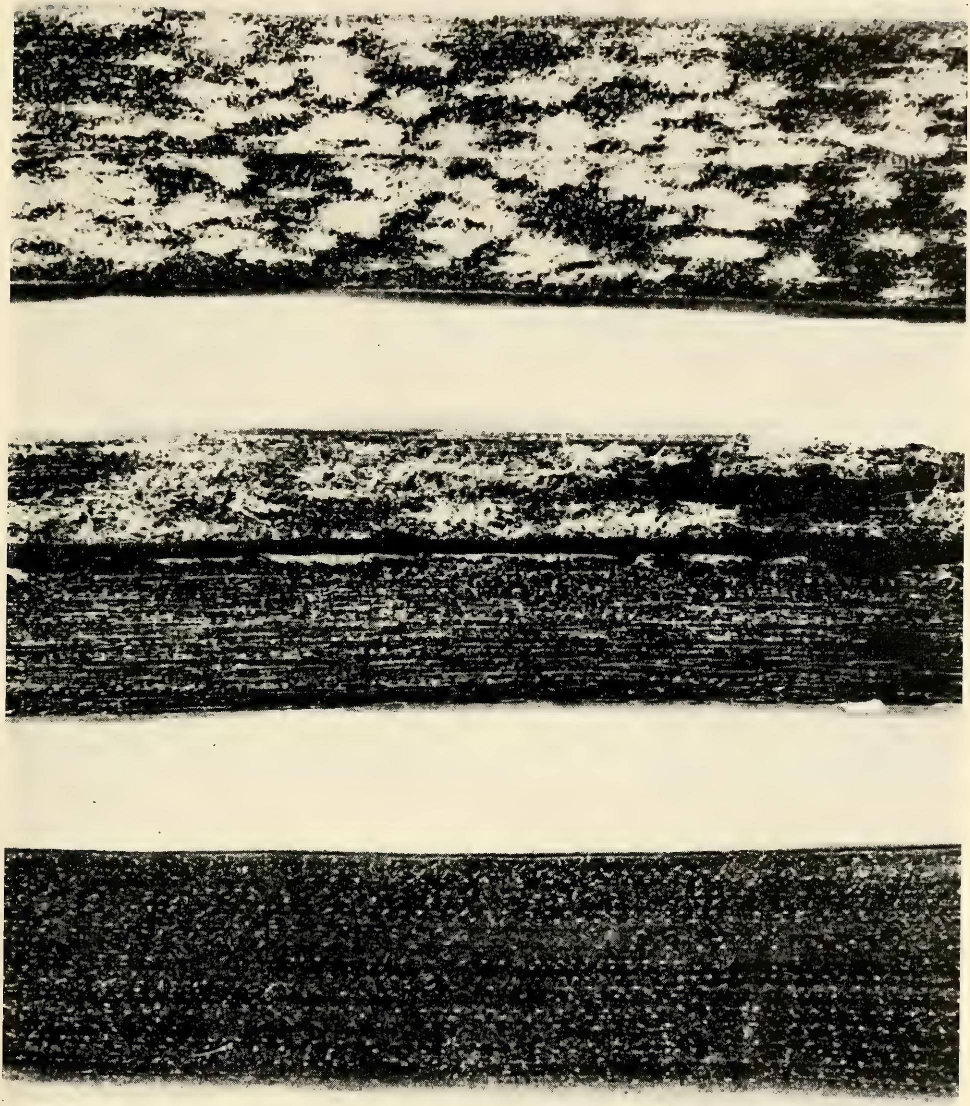
EXPLANATION OF PLATE XVI

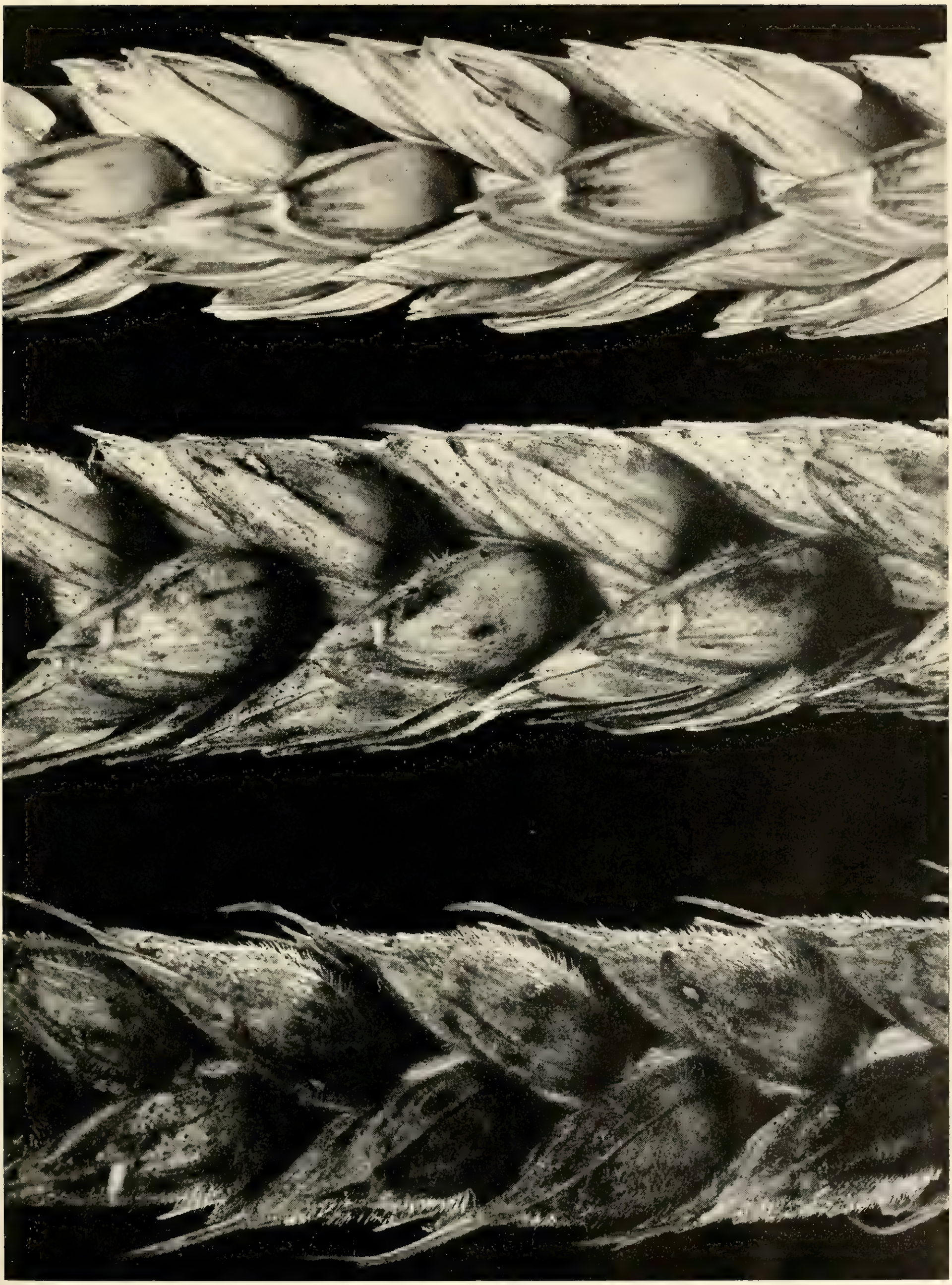
Portions of leaves of F_2 segregates from monosomic F_1 plants in cross Chinese Spring monosomic 1A × (Asosan × Federation^3) showing reaction types to powdery mildew. Left—resistant segregate. Middle—chimaeric segregate. Resistant (left) and susceptible (right) sectors. Right—susceptible segregate. (× 8.)

EXPLANATION OF PLATE XVII

F_2 segregation for glume pubescence in cross (Asosan × Federation^3) × Yalta. Left—homozygous pubescent segregate. Middle—heterozygous pubescent segregate. Right—glabrous segregate. (× 3·75.)



Chimaerism for mildew reaction type in wheat.



Phenotypic expression of pubescent glumes in wheat.

THE VEGETATION OF THE BOORABBIN AND LAKE JOHNSTON AREAS, WESTERN AUSTRALIA

J. S. Beard
King's Park and Botanic Garden, Perth
(Communicated by Mr. R. H. Anderson)

(Plates XVIII–XXII)

[Read 31st July, 1968]

Synopsis

The purpose of this paper is to present two vegetation maps from Western Australia on the scale of 1 : 250,000. The two are contiguous and conform to the standard series of topographic maps on this scale. The locality is east of the Western Australian wheatbelt in undeveloped country between Southern Cross and Coolgardie, Lake King and Norseman. Mapping was done from aerial photography. Methods of the survey and the classification and terminology adopted are outlined. A mapping notation developed for the purpose is presented for the first time. Factors of the environment are described and the mapped communities dealt with in detail as to physiognomy and composition. Three shrubland and five woodland types are recognized which combine variously into five vegetation systems, in which the plant communities and their related soils occur in catenary sequences.

GENERAL DESCRIPTION

This paper relates to the two contiguous map sheets of the 1 : 250,000 Series, Boorabbin and Lake Johnston which cover country between 31° and 33° S. latitude, 120° and 121·30° E. longitude. The area concerned lies in general terms to the south-west of Coolgardie, which is only ten miles off the Boorabbin sheet at its north-west corner. The area then extends 90 miles westwards from Coolgardie towards Southern Cross, and 140 miles southwards towards Esperance and the coast, excluding Norseman which, like Coolgardie, lies just off the margin of the area. Road, rail, water and telegraph communications between the west coast and the eastern goldfields traverse the north of the Boorabbin sheet. Similar lines of communication from Coolgardie to Esperance cross the north-east corner of the Boorabbin sheet and continue southwards just east of both map margins for their entire length. A main road crosses the southern part of the Lake Johnston sheet from Daniel to Lake King, a road which is readily traversable and in good condition. A rather less frequented graded track crosses the northern part of the same sheet from Norseman to Hyden. Otherwise, as the country is uninhabited, there are virtually no roads and only a few bush tracks.

The first exploration of this area took place from the south under J. S. Roe in 1849, when Peak Charles was named after the Governor, Charles Fitzgerald. In 1863 H. M. Lefroy traversed the northern portion. The Johnston Lakes were named by a prospector, Frank Hann, in 1901 after the Surveyor-General, H. F. Johnston. Following the discovery of gold at Coolgardie in 1892 communications with the coast along the present line of the railway and water pipeline were established, and in 1893 Holland pioneered a route from Broome Hill near Katanning to Coolgardie. This route, "Holland's Track", crossed the Boorabbin sheet diagonally from S.W. to N.E. The northern part of it from Pigeon Holes to Coolgardie has become a graded road, but the southern portion has been lost.

We have little precise record of any botanical collecting in the area. Diels and Pritzel travelled through by train in 1901 and recorded some observations. In recent years collecting has been done by such botanists as C. A. Gardner and R. D. Royce and the plant cover is reasonably well known in a general way. The area was included in the Coolgardie District of the Eremaean Botanical Province by Diels (1906), which was maintained by Gardner and Bennetts (1956). Burbidge (1960), however, has placed the Coolgardie District in an interzone lying between the Eremaean and Southwestern Provinces. Gardner's (1942) map of the vegetation of Western Australia shows the whole area as Sclerophyllous Woodland but this clearly is intended as a broad generalization, having regard to the scale of the map (about 1:8,000,000). Other vegetation maps which include Western Australia such as in Williams (1955) are equally generalized, due to their scale and the absence of detailed field work.

The Boorabbin area was geologically mapped by J. Sofoulis and W. Bock in 1960, and a geological map at 1:250,000 with explanatory memoir published in 1963. The Lake Johnston area has not been geologically examined in detail, nor mapped. In May 1964 the writer travelled through the Boorabbin area with J. Sofoulis, who explained the correlations between vegetation and underlying soil and geology which had been observed in the course of geological mapping. Botanical specimens were collected and numerous important plants, especially the trees, identified. In October 1964 the writer, assisted by F. Lullfitz, traversed the Lake Johnston area from Lake King to Norseman with diversions to Hatter's Hill, Lake Hope and Peak Charles, and returned from Norseman on the Hyden Road as far as Forrestania with a diversion to the Bremer Range, then going north to Southern Cross and east along the main road to do spring collecting in the Boorabbin scrub heath. Four hundred botanical specimens were collected and subsequently identified, partly by Mr. C. A. Gardner and partly by the Curator and staff at the Western Australian Herbarium, whose assistance is gratefully acknowledged. The object of the field work, however, was not to obtain comprehensive collections to establish the total floristic composition of each plant community, desirable though that would be. This would have required very much more time in the field, and in any case there would have been no facilities for identifying a much greater number of specimens. The objective has been ecological, to determine the plant communities occurring in the area, to map them, and to furnish the essential details of their composition and physiognomy.

Following the field reconnaissance, the mapping was done from controlled 1-mile to 1-inch aerial photo-mosaics furnished by the Department of Lands and Surveys. Much time was saved by the kindly loan by the Geological Survey of the original photographs used by the geological field party in 1960 for the Boorabbin area, since after consultation with the party leader, Mr. J. Sofoulis, his interpretations could be readily adapted for vegetation mapping. In this part of the country rock exposures are few and the underlying strata are buried beneath a thick overburden. The geological map is thus to a large extent essentially a soil map and was prepared by interpreting vegetation patterns on the aerial photographs as soil. In the Boorabbin sheet there will be found to be a general similarity between the boundaries shown on the vegetation and geological maps. The main differences consist in the subdivision for vegetation purposes of the "Residual Sandplain" areas into scrub heath and broombrush thicket, and the inclusion of all the areas of basic rocks and included granites in the northeastern sector within a single association of sclerophyll woodlands.

The Lake Johnston sheet was mapped purely from original photo-interpretation by the writer on the scale 1 : 62,500. The outlines were reduced photographically by the Department of Lands and Surveys and prepared for publication at King's Park.

Factors of the Environment

Physiography

The country included in these map sheets is a part of the interior plateau of Western Australia and lies between 700 and 1500 feet above sea level. With the exception of the group of the abrupt Fitzgerald Peaks in the south-east, of which the largest, Peak Charles, reaches a height of 2160 feet, relief is subdued. Ridges are broad and flat and alternate gently with valleys which are also broad and flat, the difference in level from ridge to flat being rarely more than 300 feet with slopes falling about 25 feet per mile.

The area is divided into five Vegetation Systems (see page 259), distinguished as the Boorabbin, Coolgardie, Cave Hill, Bremer Range and Lake Hope Systems (Fig. 1). Each of these has a characteristic physiography, geological structure and soil association as well as its characteristic vegetation pattern. In the Boorabbin System the country consists mainly of a dissected upland developed on granite with widely spreading sandy plateau surfaces up to 1500 feet in altitude and valleys down to 1200 feet, draining mainly to the north. In midslope there may at times be a small lateritic scarp or "breakaway" and also bare outcrops of granite which are moderately common. They have a low outline and rarely project much above the surrounding country. The valleys are relatively narrow and contain chains of small salt lakes. The Cave Hill System is also a granite upland, but much more strongly dissected, so that little of the old sandy plateau remains; it is hilly on a smaller scale and granite outcrops are very abundant, Except for the Fitzgerald Peaks, however, they rarely form prominent features. Valleys are broader and there are some larger salt lakes. The Lake Hope System is again a granitic upland, but developed under a higher

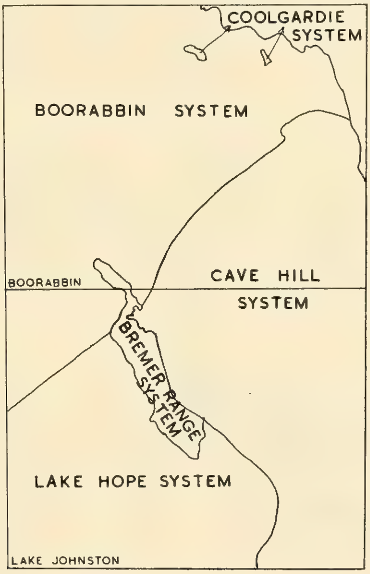


Fig. 1 VEGETATION SYSTEMS

rainfall to a still more advanced stage of dissection. Traces of the sands and lateritic gravels of the "old plateau" surface on high ground are rare and granite outcrops quite rare. Solonetzic soils carrying mallee vegetation have developed over the rising ground, valleys are very broad and flat and contain large salt lakes. Relief is from 800 to 1100 feet above sea level.

The Coolgardie and Bremer Range Systems are developed upon greenstones, mainly basic rocks such as ancient basaltic lavas and metasediments, with included granites. These outcrops tend to occur in belts trending N.N.W.–S.S.E. and form small hilly ranges with rounded rocky hills and broad alluvial areas at their foot. Relative elevation in the Bremer Range is only 300 feet.

The physiography of the whole area of these two maps is dominated by a main watershed (see Fig. 2) running more or less diagonally across the Boorabbin sheet from S.W. to N.E. and at a general height of 1300–1500 feet. A second parallel ridge 1000 to 1200 feet high occurs 40–50 miles to the S.E., and it is between these two ridges that the extensive and complicated system of the Johnston Lakes has developed. In the whole region there are no permanent streams, and indeed there are hardly any well-defined channels for flood run-off. None the less the country shows a definite pattern of ridge and valley which must have been excavated by

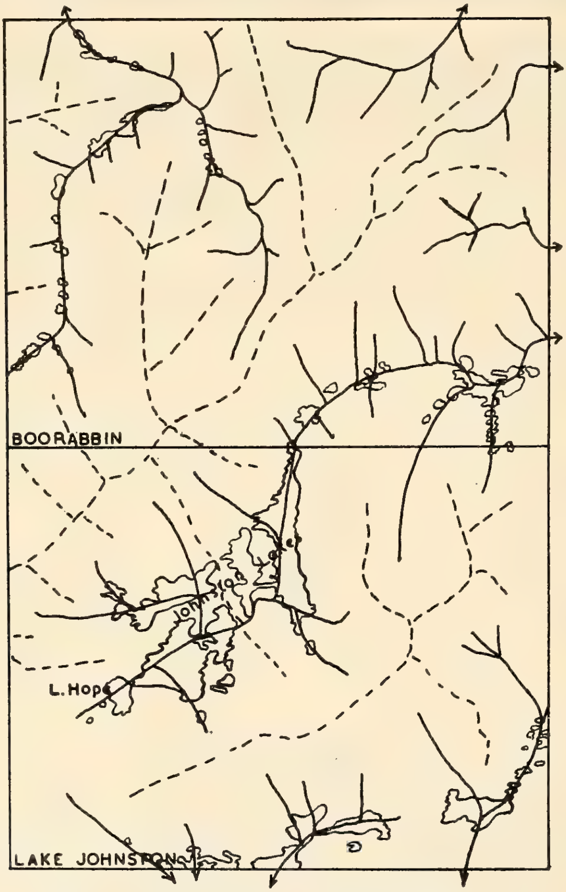


Fig. 2 DRAINAGE PATTERNS

a coherent river system, presumably in earlier times under a higher rainfall régime. Figure 2 is an attempt to sketch the ancient drainage system by inserting hypothetical streams in the valley bottoms where today there are only chains of salt lakes with little or no actual flow from one to the other. Crests of the interfluves are shown dotted. North of the main ridge the valleys trend northwards and it is thought that this drainage originally passed westward to the Swan River. On the east side of the Boorabbin sheet drainage is eastwards towards Lake Lefroy. Elsewhere, south of the main ridge, the country slopes generally towards the sea, and it is reasonable to suppose an original connection with those river channels which still actually exist on the south coast such as the Oldfield and Lort Rivers.

The Bremer Range forms a ridge following the line of strike of the basic rocks, which is thus at right angles to the main direction of the ridge and valley system developed upon the granite. However, the ridge is a low one and appears to have been breached by the ancient river system.

In the present epoch the process must be one of filling up the ancient valleys by silt and evaporites derived from nearby hills. Some parts of the valleys would tend to receive more deposit than others, raising the level relatively more and leading to ponding elsewhere. Evaporation then leads to accumulations of salts, vegetation is killed at a certain critical level and playa lakes come into being. These may be extended later by wind action and by further salt accumulation.

If it is postulated that in the past a period of higher rainfall is necessary to account for the development of the present topography, or more than one such period, then one or more periods of greater aridity are equally reasonable and indeed are evidenced elsewhere on the continent. During an arid phase aggradation of valleys might well occur more rapidly than at present, and have initiated the formation of the salt lakes. It might be possible by careful study to discover the effects of such climatic fluctuations upon landform.

*Climate**

As most of this country is unsettled, rainfall records are available only for a few places near the northern boundary. Maps based on these records and others reasonably close to the area show that the 11 inch isohyet runs roughly northwest–southeast through the northern part of Lake Johnston, dividing the area approximately into halves. The lowest rainfall is just below 10 inches in the far northeast, and the highest is 13 inches, on the eastern part of the southern border. In about 90% of the area annual rainfall is between 10 and 12 inches, there being only a comparatively small area near the southern border with 12 to 13 inches, and a still smaller area in the north with less than 10 inches.

In the southern part the wettest six monthly period is the same as in most of the agricultural area, i.e. May to October. However, further north, and in about four-fifths of the area, the wettest period is March–August. Almost throughout the area, the average rainfall is higher in March than in April, and in the north, where the late autumn and winter rains are comparatively light, this results in the March–August period being wetter than May–October.

In the far south, monthly averages give the impression of almost uniform rainfall, as at Salmon Gums, for instance, they exceed one inch in the period March to October inclusive, and are between three-quarters of an inch

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* The data which follow were contributed by the Commonwealth Bureau of Meteorology by courtesy of the Regional Director, Perth.

and one inch in each of the remaining four months. However, the comparatively high averages of these four months are due not to consistent totals of about three-quarters of an inch to one inch, but to many dry months, a smaller number of moderately wet months and a few very wet ones.

Table 1 shows rainfall data for Coolgardie, Widgiemooltha and Salmon Gums.

TABLE 1

Rainfall data

(Points)

	No. of Years	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Coolgardie														
Average ..	63	65	98	96	89	109	112	93	98	54	68	60	65	1,007
Median ..	72	26	60	52	52	94	105	87	65	44	36	31	41	
Highest month	72	643	933	527	415	454	469	297	356	364	309	306	350	
Lowest month	72	0	0	0	0	1	7	0	3	0	0	0	0	
Highest day ..	72	462	533	230	203	167	193	112	186	92	259	154	190	
Widgiemooltha														
Average ..	65	74	98	110	104	116	116	93	98	67	78	73	66	1,093
Median ..	65	38	40	50	60	90	105	74	77	50	53	54	30	
Highest month	65	543	1,054	592	569	591	463	326	330	384	393	342	407	
Lowest month	65	0	0	0	0	0	0	3	0	0	0	0	0	
Highest day ..	65	345	1,050	220	273	172	220	150	122	147	198	203	208	
Salmon Gums														
Average ..	43	83	95	110	104	131	155	146	131	125	108	77	76	1,341
Median ..	43	42	41	58	87	117	138	140	124	100	80	60	49	
Highest month	43	553	410	694	416	435	410	333	381	374	326	280	288	
Lowest month	43	0	0	0	0	4	45	25	21	12	0	0	3	
Highest day ..	40	355	323	415	178	170	132	95	153	268	120	138	131	

Evaporation

Evaporation ranges from 55 inches per year at the southwestern corner to 92 inches in the far northeast. The rate of evaporation is highest in January, when totals for the month at these places are 10 inches and 15 inches respectively. They are lowest in July, when the range is from 1·7 to 2·5 inches.

Growing Season

The length of the growing season may be estimated from curves of "effective" rainfall (based on evaporation) and average rainfall. These values are applicable to introduced species drawing their moisture supply from a comparatively shallow depth, and are not necessarily applicable to native vegetation. However, they enable growing conditions in this area to be compared with those in the agricultural area and are included for that reason.

The growing season is longest on the southern border of the region, where it reaches four months, and is about the same length as in much of the wheat belt along a line from Kellerberrin to Northampton. In about one-third of the area the length of the season is between four and three months, this being equivalent to the season in the marginal wheat belt country. In a little more than one-third of the area the length is between three and two months, while in the northeastern quadrant it is less than two months.

Although the length of the season in the southern part of this area is about the same as in much of the wheat belt, there is a smaller surplus of rainfall here during the growing season. On the other hand, a small surplus of rainfall above the average for the months preceding or following the normal growing season, would cause a greater increase in the length of the season in this region than in the main wheat belt.

Temperature

In summer, temperature increases northward, the range in February, the hottest month, being from a mean maximum of 85° in the southeastern corner to 94° in the northwest corner. In winter, mean minimum temperature is lowest in the southern half of the area, but increases towards the southern border, and also over the northern half of the area. The range of mean minimum is from a little below 39° in the coldest part to a little over 41° in the far northeast.

It has been found that light frosts occur with screen temperatures of 36°. In an area with a mean minimum of 39° it is obvious that frosts will occur frequently, and some will be severe. Table 2 shows temperature data for Southern Cross, Coolgardie and Salmon Gums, the climatological stations closest to the area. The frequency of temperatures below 36° has been included in this table as an indication of frost frequency.

Wind

One station in this area (Boorabbin), recorded wind for 2½ years, and the 9 a.m. records for this centre show that from November to April winds are mainly easterlies, E./S.E. being a little more frequent than E./N.E. in January and February, and the reverse in the other four months. There are very few winds with a westerly component during the December–March period, but they become more frequent in April, and from May to August westerlies predominate, though not to the same extent that the easterlies did earlier in the year. Winds in excess of 30 knots were recorded only three times, from directions of W.S.W., W. and W.N.W. Most of the winds in excess of 20 knots were from the northwest quadrant.

At Norseman, winds from the northeast quadrant predominate from January to May, with W./N.W. winds becoming more frequent in May, and predominating from June to September. In October winds become more variable and although there are still a fair number from W./W.N.W. there are more from S./S.S.E. and from N.E./N.N.E. In the November and December southerlies prevail, but are not much more frequent than northeasterlies.

At Coolgardie the prevailing direction at 9 a.m. is N.E./N. from October to April, and S.W./W. from May to September. At 3 p.m. N.E./N. winds prevail from November to March, N./N.W. in April, and S.W./W. from May to October.

Table 3 shows the diurnal variation of prevailing wind at Southern Cross. In this table winds from the direction preceding the stroke are more frequent than from the direction following it.

Human Influences

Owing to the low rainfall of the Boorabbin and Lake Johnston areas there has been virtually no agricultural settlement, the only developed section being confined to approximately 900 acres in the extreme south-east centred upon Kumarl, which lies a few miles east of the sheet boundary. There are no pastoral leases at the present time, though two areas of 56,400 and

TABLE 2

Temperature Data

	Number of Years	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Southern Cross														
Mean maximum ..	43	94·3	93·0	87·0	78·9	69·5	63·0	61·7	64·7	72·0	77·7	86·5	92·3	78·4
Mean minimum ..	43	62·2	62·2	58·4	51·7	45·1	41·5	39·1	40·3	43·1	47·9	55·0	59·9	50·5
Highest	64	115·0	117·0	112·0	103·2	92·2	81·5	80·0	85·9	94·6	102·8	110·2	114·6	117·0
Lowest	64	42·0	42·0	38·2	30·0	26·0	24·3	23·0	25·0	26·0	30·6	35·6	40·8	23·0
Average number ≥ 100°	24	12	7	3	0	0	0	0	0	0	0	2	5	27
,, ,, ≥ 90°	24	24	18	13	3	0	0	0	0	0	3	10	19	88
,, ,, ≤ 36°	10	0	0	0	0·4	3·0	7·9	10·8	8·6	4·4	1·0	0	0	36·1
Coolgardie														
Mean maximum ..	30	91·9	91·4	84·9	76·9	68·9	62·5	61·2	64·6	72·1	77·4	84·9	89·9	77·2
Mean minimum ..	30	62·6	62·6	59·6	53·2	47·4	43·4	41·4	42·4	46·3	50·5	56·3	60·4	52·2
Highest	65	115·0	114·3	110·0	103·0	91·8	79·3	81·0	85·5	94·0	103·0	109·0	111·0	115·0
Lowest	65	46·0	46·6	41·0	36·0	33·2	30·2	29·0	30·8	31·0	34·0	37·4	43·0	29·0
Average number ≥ 100°	44	7	5	2	0	0	0	0	0	0	0	2	4	20
,, ,, ≥ 90°	44	18	15	10	3	0	0	0	0	0	3	9	16	74
,, ,, ≤ 36°	10	0	0	0	0	0·7	2·3	3·6	3·2	0·9	0	0	0	10·7
Salmon Gums														
Mean maximum ..	14	85·4	84·5	81·4	73·9	66·9	62·2	60·6	63·3	69·0	73·7	79·8	83·5	73·7
Mean minimum ..	14	56·0	55·7	54·8	49·0	43·8	41·4	39·1	40·2	41·8	44·9	49·5	53·4	47·5
Highest	24	114·0	110·0	108·5	102·0	90·0	89·9	90·6	81·9	96·0	101·7	105·3	109·2	114·0
Lowest	24	38·6	37·6	34·0	29·2	27·5	22·5	24·3	23·6	24·0	27·0	30·0	34·7	22·5
Average number ≥ 100°	12	3	2	1	0	0	0	0	0	0	1	1	2	10
,, ,, ≥ 90°	12	10	7	6	1	0	0	0	0	0	2	5	8	39
,, ,, ≤ 36°	—	0	0	0·2	0·8	2·9	6·2	9·9	7·3	5·9	4·4	0·5	0	38·1

52,149 acres at the Johnston Lakes were taken up from 1955–1957 with the intention of utilizing country where the woodland has a saltbush understory. The leases were abandoned due to lack of water supplies. There are settlements along the goldfields lines of communication across the north and east of the Boorabbin sheet, but these are not agricultural and have effected virtually no clearance of the plant cover. There has been mining development in the Coolgardie system, but this likewise has effected virtually no clearance of the natural vegetation. All mines are closed down at the time of writing. There is no longer any Aboriginal population in the area.

On the other hand, woodcutting has been in progress steadily for many years to provide mining timber and firewood for the goldfields and water pumping stations. More or less all the woodland in the eastern half of the Boorabbin sheet was cut over at one time, working from tram lines which no longer exist, but are shown on the geological map. Most of the woodland on the remainder of the Boorabbin sheet is now being tapped by motor truck working from roads running south from the Great Eastern Highway. The Lake Johnston sheet on the other hand is much more remote and untouched, and timber getting is confined to a belt about 10 miles wide along the southern half of the eastern margin of the sheet. Fellings which are very selective have had the effect of making the woodland more open. Regeneration seems generally to be satisfactory from seed except in *Eucalyptus salmonophloia* stands where it may be very slow to appear.

TABLE 3

Diurnal Variation of Prevailing Wind

Southern Cross

Hour	Number of Years	Direction											
		Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
0600	5	SE/S	SE/S	SE/S	SE/S	N/NE	N/NW	NW/W	NW/W	W/NW	SE/S	SE/S	SE/S
0900	5	NE/N	NE/N	NE/N	NE/N	NE/N	N/NE	N/NE	W/NW	NE/N	NE/N	NE/E	NE/E
1200	5	N/NE	N/NE	NE/N	N/NE	NE/N	N/NE	NW/W	W/NW	W/SW	W/SW	W/SW	N/NE
1500	5	SW/W	SE/S	NE/N	NE/N	W/SW	N/NE	W/SW	W/NW	W/NW	W/SW	W/SW	S/SW

The wind data are of interest in view of the attention drawn by Sofoulis (1963) in the geological memoir to the elongation of the playa lakes in a NNW–SSE direction with an apparent migration of the lakes to the NNW and piling up of sand on the SSE side. During winter, the rainy season when the lakes may contain water, westerlies predominate and nearly all the strong winds (>20 knots) are from the north-west quadrant. This would account for the transport of sand to the south-east, and it must be assumed that the wave motions set up tend to form sandy beaches on the SE and to undercut the banks in the NW, even though at first sight the opposite would seem likely to be the case.

While human land utilization pressure in this area is minimal, it is quite another matter with that other anthropogenic factor, the bush fire. All large contiguous areas of scrub, thicket and mallee show burn patterns in air photographs, so much so that interpretation is often difficult. The taller sclerophyll woodlands burn only rarely and with difficulty if at all, owing to the sparseness of the ground layer and openness of the tree canopy, but the much denser shrublands burn all too easily. In the south, where woodland is shorter and denser and merges into mallee, it, too, will burn readily and there may be difficulty in distinguishing on photographs between mallee and burnt woodland. We can be certain that fire has occurred since time immemorial in this vegetation, at least as far back as the earliest human occupation, but the probability seems to be that it has become more frequent since the arrival of Europeans. Burn patterns show recent fires to have started on roads and tracks, or to have spread from settled country in the direction of Southern Cross. Sofoulis (1963) has drawn attention to features detectable in burn patterns in aerial photographs which he describes as "sandplain lineaments", and attributes to lines of taller vegetation representing some source of underground water supply such as faults and joints in the underlying rock. It is difficult to subscribe to this view since the patterns radiate fanwise from the source of origin of a fire and extend along the direction in which the fire has moved most rapidly. Further, in the sandplain country the underlying rock is deeply buried and unlikely to affect surface vegetation. However, this is something that requires further investigation.

Description of the Vegetation

Plant Formations

The Plant Formations occurring in this area are only six in number. Describing them in the simplest terms only, they are as follows:

1. *Scrub Heath*: Popularly "sand heath" or "sand plain", a mixed, stratified, partly open shrub assemblage with Proteaceae and Myrtaceae prominent, found on leached sands.

2. *Broombush Thicket*: Popularly "tamma scrub", a less diverse single-layered very dense shrub assemblage consisting mainly of *Casuarina, Acacia* and *Melaleuca* species, found on shallow sandy soil underlain by laterite ironstone and gravel, or by unweathered granite.

3. *Rock Pavement Vegetation* consisting of lichen and moss on soil-less outcrops of granite, with aquatic plants in pools and shrubs in crevices or occasional soil patches.

4. *Mallee*: Open to closed eucalypt shrub assemblage with variable low shrub ground layer, found on leached granite soils in the south of the area.

5. *Sclerophyll Woodland*:
    - (*a*) Mixed sclerophyll woodland, a medium-tall (40–50′) open eucalypt woodland occupying eluvial soils in the north of the area.
    - (*b*) Salmon Gum woodland, tall ($> 60'$) open eucalypt woodland occupying alkaline alluvial soils throughout the area.

6. *Halophytes*: Communities of succulent or more or less succulent subshrubs occupying highly saline depressions.

All of these formations are well developed upon the acid rocks which underlie the greater part of the area. Where there are outcrops of basic rocks, formations of 5(*b*) and 6 continue to occur as before on alluvial soils, 1, 3 and 4 are absent, while 2 and 5(*a*) occur with a distinctly different floristic composition.

It will be observed that two different terms, "scrub" and "thicket" have been used for shrubland formations, and this demands a word of explanation. Just as it is useful to distinguish between closed and open tree-dominated formations as "forest" and "woodland" respectively, so it seems necessary to distinguish in the same way between closed and open shrublands as "thicket" and "scrub". "Mallee", the eucalypt shrubland which has physiognomic properties of its own, should strictly be referred to as "mallee scrub".

Physiognomy

1. *Scrub Heath*

It is difficult to describe a characteristic structure for this formation, since the vegetation is burnt so frequently that a mature structure has little chance to develop. On regeneration after fire by coppice and seedling growth, a layer of low shrubs appears, at first open and then more or less closed. With further growth the naturally taller species begin to outstrip the smaller, and stratification begins to develop into a lower layer of small ericoid shrubs with emergent taller species with larger leaves. In time the upper layer, while remaining irregular due to the varying mature sizes of its components, may tend to close up and partially suppress the lower layer. The latter grows from 1–2½ ft in height, its components typically belonging to the Myrtaceae, with leaves leptophyll in Raunkiaer size. Some of these have a corymbose habit of growth, others are erect, thin and straggly. The components of the upper layer may reach 15 ft in height, belong typically to the Proteaceae and have very deeply divided, harsh, prickly leaves which are difficult to assess for leaf area but would be mainly microphyll in Raunkiaer size. There is some admixture of *Casuarina* from the adjacent thicket formation and low mallees tend to occur where there is some clay in the subsoil. All components are evergreen, with simple (though in many cases deeply divided) leaves. There is scope for considerable further investigation into the life form of scrub heath plants, their regeneration after fire and other aspects.

The structure is illustrated in the diagrams of Fig. 3, which are drawn from actual measured strips 50 ft long, 10 ft wide and represent what appear to be early and later stages of development. In the "early" stage

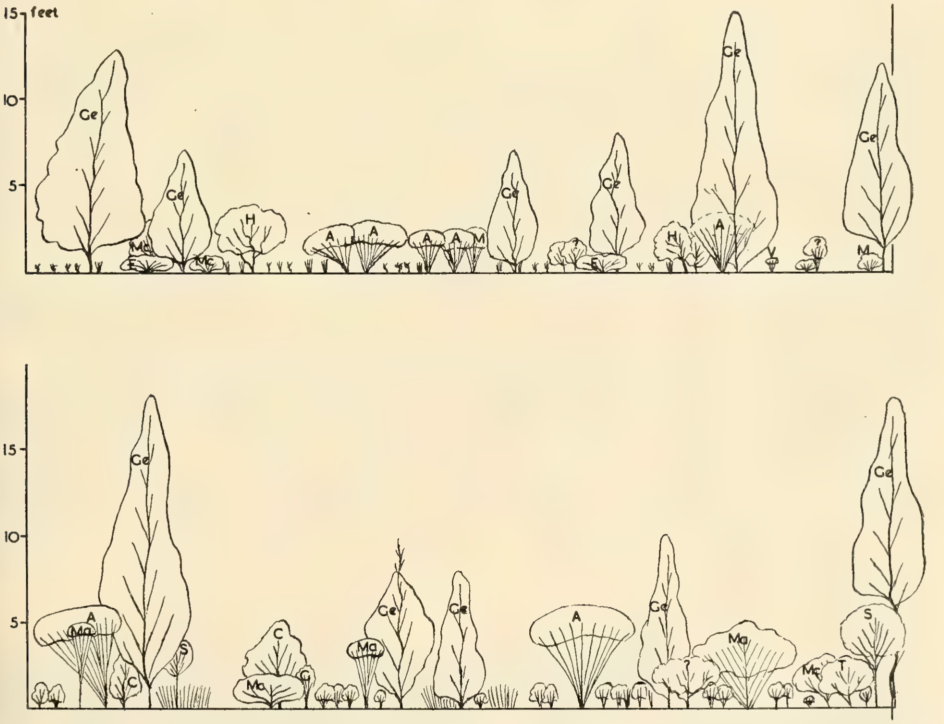

Fig. 3. Profile diagrams of Scrub Heath. Top—early stage. Bottom—late stage. Both near 255 mile peg, Hyden – Norseman Road. For key to species see p. 257.

the tall, pyramidal *Grevillea excelsior* shrubs have reached 10 ft–15 ft in height and a lower layer of 2–3 ft high shrubs has become established, interspersed with small clumps of sedge, small caespitose aphyllous plants and prostrate woody plants such as *Balaustion pulcherrimum* and *Borya nitida*. In the "later" stage many of the Grevillea are much taller, and all of them are beginning to show signs of senility. One in the left centre of the profile is recorded as stagheaded. Broombrush Acacias and Melaleucas have grown up to 6 ft in height, and there appears to be invasion in progress by *Callitris preissii, Santalum acuminatum* and a *Hakea* sp. In the vicinity of this profile but not recorded in it, other such invaders were observed to include *Hakea multilineata, Calothamnus quadrifudus* and *Casuarina corniculata*. The supposed invaders are all relatively young plants of species which are known to become much larger. It seems probable that *Grevillea excelsior* is a pioneer species in scrub heath following fire and that a succession can be recognized. The ground layer of the "later" stage differs in that there are large and well established sedge clumps, with numerous small ericoid shrubs of 1–1½ ft.

2. *Broombush Thicket*

In its purest form the thicket is a dense, closed, single-layered community of relatively simple floristic composition. It grades, however, very gradually into scrub heath where the two adjoin, so that there are intermediate structures such as the addition of a ground layer of small ericoid shrubs. Like the scrub heath the thicket is subject to frequent fires by which it is destroyed, regenerating from seed. Height of the vegetation therefore depends largely on the time that has elapsed since the last fire, up to 12 or 15 ft being possible. Where undershrubs occur they naturally will flourish mainly in the early stages, becoming suppressed later. The dominant components of the thicket are virtually confined to different species of *Casuarina, Acacia* and *Melaleuca,* all of which have the same habit of growth: the stem divides repeatedly into a large number of thin, largely erect branchlets terminating at the same height and giving a dense, gently domed crown to the bush. This may be referred to as the "Broom-bush" habit. It is perhaps analogous to the mallee habit of eucalypts. In *Casuarina* leaves are reduced to scales and their function taken over by the thin, terete, green twigs. The fruits are held on the bush until it dies or is killed by fire, when seed is liberated. The *Acacia* species have phyllodes, narrow, linear and about 2 in. long. The seed is shed but is protected by a hard seed coat: germination takes place copiously after burning. Melaleucas have small ericoid leaves and their fruits behave like those of *Casuarina*.

Two profiles have been measured to illustrate the structure of this formation and appear in Fig. 4, being an "early" and "late" stage as in the case of the heath scrub. There is no essential difference except that the virtually closed canopy formed already at about 4 ft in the "early" stage has advanced to 8 ft in the "late" stage. Heath components such as *Banksia, Hakea* and *Isopogon* have grown rather less in height and are becoming suppressed by the broom-bushes.

3. *Rock Pavement Vegetation*

The numerous bare outcrops of granite rock, devoid of soil, throughout this area, are for the most part unable to support any plant cover except aquatics in rock pools and some thin crust of lichen. Accumulations of peaty matter may occur in hollows, which support low woody plants and shrubs.

4. Mallee

Mallee is a shrub-eucalypt formation. Each plant has an underground rootstock about one cubic foot in size from which arise numerous slender stems giving a bushy crown similar to the "broom-bush habit". Mallee is subject to frequent fires which destroy the top growth, regeneration taking place from coppice. It is not clear to what extent the mallee habit is genetically controlled or due to fire. Certainly any small eucalyptus tree of a species having the power to coppice would automatically assume a mallee habit if frequently burnt, and very many mallee species can also be found in tree form, either moderately sized or in the small but single-stemmed tree form known as "marlock" in Western Australia. The structure of mallee is extremely variable, its height varying with age from the last fire, and its density and associates varying also. The most typical form of mallee is a closed community of mallee habit rising from 10–15 ft in height with an understory of small ericoid shrubs of the genus *Melaleuca*. The understory may elsewhere consist of mixed shrubs belonging to the heath scrub where there is a transition to the latter formation, of salt-bush under alkaline soil conditions or of hummock-grass on red sand. In this area the last two types occupy only small patches which are not mappable. The same species of mallee eucalypts may occur over different understories and vice-versa, and the stature of the eucalypts may vary without change of species from true mallee to marlocks and small trees. Profile diagrams measured in mallee are presented in Figs 5 and 6, the former a low form

Fig. 4. Profile diagrams of Broombush Thicket. Top—early stage. Bottom—later stage. Top—285 mile peg, Hyden – Norseman Road. Bottom—233 mile peg. For key to species see p. 257.

Fig. 5. Profile diagram of low Mallee, 254 mile peg, Hyden – Norseman Road. For key to species see p. 257.

and the latter a tall. It is believed that these represent early and late growth stages. In both cases the mallee forms an almost closed canopy layer, at 7 ft and 20 ft respectively, with a discontinuous lower layer of Melaleuca broom-bushes. Occasional small clumps of grass were the only ground vegetation in both cases.

5. *Sclerophyll Woodland*

Like the mallee, the sclerophyll woodland is eucalypt-dominated, there are several different floristic associations and structural types. In general, growth consists of a tall but open stand of trees with extremely sparse undergrowth with the result that the woodland is subject to burning to only a minor extent. Where fire passes, the trees are killed and do not coppice but regenerate from seed, an even-aged stand resulting. Study is required of the extent to which existing stands are even-aged, and of the regeneration of the various species. If it should prove that fire, even at very long intervals, is the agent responsible for regeneration of these woodlands, then as with the other formations height and density are a function of age and structure is not altogether meaningful. There is in general a correlation between height and density in that the lowest woodlands tend to be the densest, and the tallest the most open. There is every gradation from the low dense mallee to the very tall stands of over 80 ft in height where the trees are extremely scattered. However, one may distinguish two broad classes, the mixed woodlands of 40–60 ft in height on residual soils, and the Salmon Gum (*Eucalyptus salmonophloia*) woodlands of alluvial flats, which exceed 60 ft. In the former type trees are irregularly scattered so that in part their crowns touch and in part there are large open spaces. Diameters of the dominants are 9–12 in. The trunk forks into a number of ascending branches at about a third of tree height and the rather flat crown is thin and casts little shade as the leaves hang downwards. Except at times in gaps the only tree layer is that of the dominants forming the canopy, but there are two highly sparse layers of shrubs, the one 6–12 ft high and mainly of "broom-bush" habit, the other of low shrubs under 2 ft. Locally the latter may be saltbush. On soil derived from granite the trees in this formation are smooth-barked, but on basic rocks the majority of the species have persistent rough bark on the lower trunk or on the trunk and lower limbs. The significance of this is not understood. Fig. 7 illustrates a measured profile in an example of this mixed woodland in which *Eucalyptus*

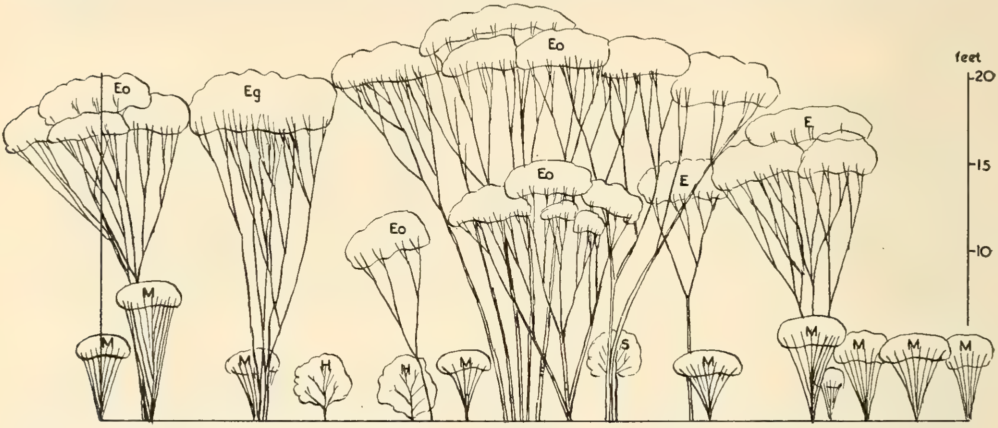

Fig. 6. Profile diagram of tall Mallee near 260 mile peg, Hyden – Norseman Road. For key to species see p. 257.

transcontinentalis is dominant. One outstanding tree reaches 75 ft in height, but most of the dominants attain between 40 and 60 ft. There is an understory of eucalypts in mallee form. Low shrub and herb layers are virtually absent. The profile demonstrates the irregularity of the woodland and the openness of the canopy. There are wide gaps between groups of dominants which tend to occur in clusters, the result no doubt of group regeneration. Much more work could usefully be done on the structure and stability of these woodlands.

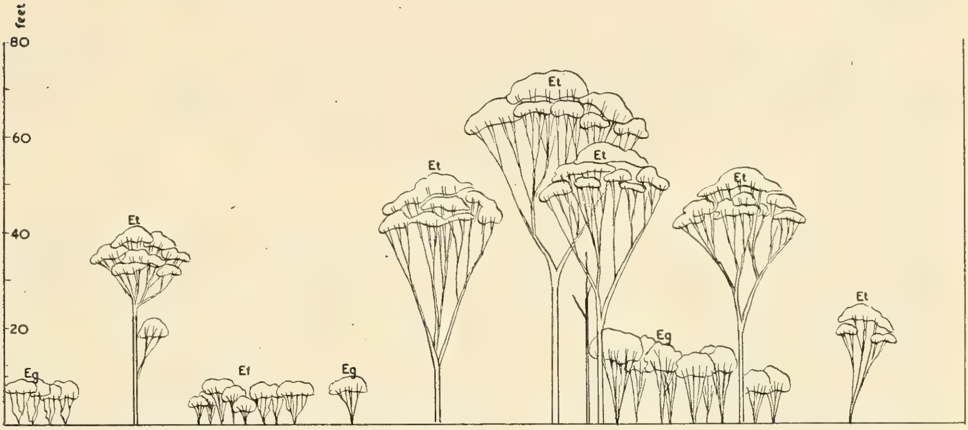

Fig. 7. Profile diagram of sclerophyll woodland – *Eucalyptus transcontinentalis*. For key to species see p. 257.

The taller woodland of *Eucalyptus salmonophloia* and its associates is generally over 60 ft tall, with a maximum of about 90 ft, very open with the trees as much as 200 ft apart. There is a very strong trunk, in most cases up to 3 ft in diameter and extending to half the height of the tree. The shrub layers are as in the mixed woodland, a saltbush understory being common in the vicinity of salt lakes and on alluvia derived from basic rocks. Both smooth and rough-barked trees are present but, as before, the rough bark appears to indicate a higher base status in the soil.

Fig. 8 shows a profile measured in pure salmon gum woodland, an example which is probably of a denser stand than normal (compare

Fig. 8. Profile diagram of sclerophyll woodland – *Eucalyptus salmonophloia* association measured 26 miles south of Hyden on Hyden—Newdegate Road. For key to species see p. 257.

photograph). Density is frequently irregular and clustered as with the *Eucalyptus transcontinentalis* woodland, and a typical group occurs in the centre of the measured profile. Height of the dominants is generally greater than that of *Eucalyptus transcontinentalis* and its associates. Seedlings, saplings and young pole-sized *Eucalyptus salmonophloia* are a rarity, but there is very frequently a tall shrub layer of the *Melaleuca* species known as "Boree".

In all the eucalypt types including mallee, the adult leaves are evergreen, simple, mesophyll in Raunkiaer size, falcate and pendant, hanging vertically. There is a complete absence of lianes and epiphytes, and of any such special plant forms as palms, cycads and bamboos, even grass trees.

6. *Halophytes*

The most extreme communities of halophytes are the small ($<$ 12 in.) succulent chenopodiaceous shrubs which occupy raised beds on the floors of the larger salt lakes. Rather rarely here, one may find a *Frankenia* zone of small ericoid shrubs round the lake margin. Alluvial flats bordering lakes tend to have a saltbush understory in woodland and in some places on the north-east side of a lake the tree cover may be very sparse or virtually absent, leaving a pure saltbush community. Sandhills to the south-east of lakes tend to carry a woodland of special floristic composition which is described in the appropriate place, but has not been mapped. Halophyte communities have otherwise been mapped where they occur.

Classification, Terminology and Notation

The broad principles of classification adopted are those stated by the author in previous work (Beard, 1944, 1955). To recapitulate briefly, the basic unit is the plant association which is a floristic grouping, being the largest possible group with consistent dominants, either of the same or closely allied species. Associations may be divided into minor floristic groups, to which it was proposed to apply the Clementsian terminology. Also they may be termed consociations if they are single-dominant communities. The associations may be grouped together according to their physiognomy (structure and life-form) into formations. The formation is thus a physiognomic group and can be treated without reference to floristics. A higher grouping of formations into formation-series was proposed by Beard for tropical America (*ibid.*) and the applicability of this concept to Australia is discussed below.

Coming down from principles to practical considerations, there is a need for some consistent and logical system of classification, some consistent terminology and a mapping notation, for use in the description of vegetation and in the cartography. On the other hand it is not possible to predict accurately in advance of a survey what vegetation units are going to be found in Western Australia, and how they need to be treated. In a general way, of course, the vegetation types of the State are known, but it would be unwise to adopt a rigid classification and terminology in advance. It would be better to consider this towards the end of a general survey and to adopt in the meantime a flexible system. It is therefore proposed to distinguish plant formations by local names, e.g., jarrah forest, mallee, mulga and pindan, and to relate these in each paper as they occur to recognized classification systems.

At the highest level of classification we have the system put forward by Küchler (1949) and elaborated by Dansereau (1951) which was designed to be of universal application on a world scale and to facilitate valid comparisons between vegetation units in different parts of the world. A recent paper (G. Ross Cochrane, 1963) has applied a slightly modified Küchler system to the description of Australian vegetation types on a continental scale. There have been other cases in different countries where the Küchler system has also been applied and it seems desirable that we should also participate. For the benefit of those interested in comparative vegetation on a world scale it is proposed to give both Küchler and Dansereau notations, and Dansereau diagrams, for our vegetation types in descriptive memoirs, though in point of fact the value of this where Australian vegetation is concerned may be questioned. Comparisons are valueless if not valid, and it may be objected that Australian vegetation has so many unique features unrepresented elsewhere that comparisons between it and other world vegetation may not be valid at all. The fundamental idea behind methods of description and classification designed to be of universal application is that vegetation is the expression of environment and that if we can equate vegetation units in different areas we can be assured that they express (within narrow limits) the same environment. This, however, may very well be a false assumption when totally different floras are involved in the comparison and it is strongly suspected that this point will be proven when more exact physiognomic comparisons between Australian and other vegetation become possible. At least by stating our vegetation types in Küchler and Dansereau terms we are making a contribution to such study, and it can be done without proclaiming any faith in the outcome of it.

Both Küchler and Dansereau, followed by Ross Cochrane, have spoken of their systems as "classifications", but they are in effect descriptive notations. A classification would appear rather to be an ordered system of arrangement of vegetation types linked to a terminology, both of which serve to emphasize and clarify the relationships and differences between these types. In this sense, a genuine classification of Australian vegetation types is of the kind published by Williams (1955), with its physiognomic key and its terminology based on kinds of forest, woodland, savannah and so on. There appears to be no generally accepted and satisfactory system of classification for Australian vegetation, but Williams seems to have been the closest to approach the goal. His treatment contains some inconsistent features and may not in the long run be workable without modification, but it may be accepted provisionally and any difficulties can be discussed as they arise.

In addition to these arrangements for classification and terminology, we require for use on maps a notation system similar to that employed by geologists, e.g., Ts, tertiary sandstone; Ag, Archaean granite. In our case the notation should be of reasonable brevity and should if possible convey the diagnostic features of the vegetation which are:

1. Nature and size of the dominant stratum and of other strata if of diagnostic importance.
2. Dominant or diagnostic plant species.
3. Density of the strata referred to in 1.

It should be possible to arrive at a 3-letter notation to embrace the above. A mapping notation must above all be brief and long alphabetical formulae which are involved in Küchler's system, and even more so in Dansereau's, are too cumbersome. The only Australian community cited by Dansereau (1951), that of *Ceratopetalum australiense,* has the formula Tteazc.Ltehzb.Etegxi.Ftevzc.Hmevzb. and even Küchler's much simpler system still produces Tropical Rain Forest = Btml.ejuy.Hlmp. These could never appear on any map and it is unlikely that it was ever intended that they should, the purpose being symbolic description of vegetation, rather than mapping. However, it is possible to borrow from Küchler and Dansereau in the construction of a simpler system as follows:

1. Physiognomy of Dominant Stratum

T	Tall trees > 25m. tall
M	Medium trees 10–25m. tall
L	Low trees < 10m. tall
S	Shrubs > 1m. tall
Z	Dwarf shrubs < 1m. tall
G	Graminoids other than spinifex
H	Hummock grass (spinifex)
F	Forbs
X	Lichens and mosses (Hepatics)
C	Succulents (Chemopods)
T_d	Tall deciduous trees
M_d	Medium deciduous trees
L_d	Low deciduous trees

2. Floristic

e	Eucalypt
a	Acacia
t	Triodia
x	Heterogeneous (mixed or other)

(To be differentiated as e_1; e_2 for individual species. Other species may be added as required, e.g., m = Melaleuca.)

3. Density

c	Closed or continuous
i	Open, not touching; incomplete cover
p	Scattered groups
r	Rare but conspicuous
b	Barren — vegetation largely absent

The actual formulae are to be written with the floristic category first, e.g., eMc; aLi meaning respectively a eucalypt-dominated closed medium tree community (a eucalypt forest in fact) and an acacia-dominated woodland (mulga). The formulae are designed in this "triangular" form in order to be more readily comprehended at a glance. The central capital letter conveys the most important feature, physiognomy; the left hand one floristics and the right hand one density. This may be found aesthetically more pleasing, and more efficient, than the usual formula beginning with a capital and tailing off into a string of small letters whose order and position may often be confusing.

The principal, capital-lettered category, is based upon Küchler's group 1: Height, and is intended to accord mention primarily to the dominant stratum, e.g., eMc. If two or more strata are considered co-dominant, their symbols may be written together, e.g., xSZi. Any diagnostically important strata may be included in this manner—eLr.aSr.pHi—which is the formula for sandhill desert, i.e., an open Hummock-grassland of Plectrachne with scattered acacia shrubs and low eucalypt trees. It is not intended, however, to deal exhaustively with all synusiae in the manner of Dansereau. This is a mapping notation which sets out to describe salient features only.

The floristic category serves to name the species or genera which are dominant or diagnostic, but as most West Australian communities are of simple composition or even single-dominant associations, this category will also to a large extent convey — from the known morphology of the species — a life-form characteristic of the community. In Australia a relatively few genera dominate and provide a characteristic form for whole communities in this way — *Eucalyptus, Acacia* and *Triodia* (or *Plectrachne*), rather more rarely *Melaleuca, Casuarina,* etc. A category "heterogeneous" is provided for mixed communities in which no definite dominance asserts itself. The actual species concerned may be nominated if desirable by subscript numbers. This category is basically the same in conception as Küchler's initial one, which he writes in capitals, using the classes evergreen broadleaf, deciduous broadleaf, evergreen needleleaf, etc. These were obviously designed for a North American environment and represent basic life-forms to a large extent characteristic of taxonomic groups, e.g., conifers and angiosperms. In Australia life-form is even more closely related to taxonomic groups and at a lower level. If a community is said to be eucalyptoid, acacioid or triodioid a characteristic life-form is at once conveyed to the reader.

The third category "Density" is the same as Küchler's Group II. Küchler's Group III is not directly included: the characters which it deals with will have been already incorporated in our series if important, i.e., if they are "salient features", otherwise they are disregarded. Dansereau has set up three other categories in his system, Function, Leaf Shape and Size, Leaf Texture. All of these will be found to be conveyed by our first cataegory Floristic and are therefore not separately required. There are presented here first a number of actual profiles of vegetation (Figures 3–8), secondly "Dansereau diagrams" (Figures 9–13) in which these diagrams are converted into pictograms according to the method of Dansereau (1951) and thirdly a series of comparative formulae according to the system of notation proposed above and those of Dansereau (1951) and Küchler (1949) in Table 4.

TABLE 4

Plant formations of the Boorabbin-Lake Johnston area	Beard formula	Küchler formula	Dansereau formula
Scrub heath	xSZc	Bszc	Fteaxi.Fmeaxc
Broombush thicket	cSc	Bsc	Fmejaxc
Rock pavement vegetation ..	xXi	Li	Mljgki
Mallee	eSZc	Bszc	Fleaxc.Fmeaxc
Sclerophyll woodland	eMi	Bmli.szr	Tmeaxi.Fmleaxb
Halophytes	xCi	Oik	Fljgki

KEY TO SPECIES APPEARING ON DIAGRAMS

A *Acacia;* B *Banksia elderana;* C *Callitris preissii;* Ca *Casuarina acutivalvis;* Cs *Casuarina campestris;* Cc *Casuarina corniculata;* Er *Eremaea pauciflora;* Ef *Eucalyptus flocktoniae;* Eg *Eucalyptus gracilis;* Eo *Eucalyptus oleosa* var.; Es *Eucalyptus salmonophloia;* Et *Eucalyptus transcontinentalis;* E *Eucalyptus* species unidentified; G *Goodenia* sp.; Ge *Grevillea excelsior;* H *Hakea;* I *Isopogon scabriusculus;* Ma *Melaleuca acuminata;* Mc *Melaleuca cordata;* Mp *Melaleuca pauperiflora;* M *Melaleuca* sp. unidentified; S *Santalum acuminatum;* T *Thrytomene;* V *Verticordia.*

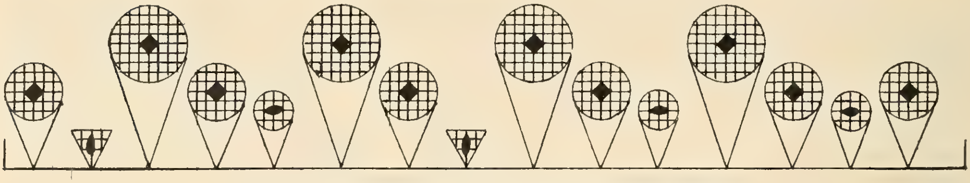

Fig. 9. Dansereau diagram for Scrub Heath.

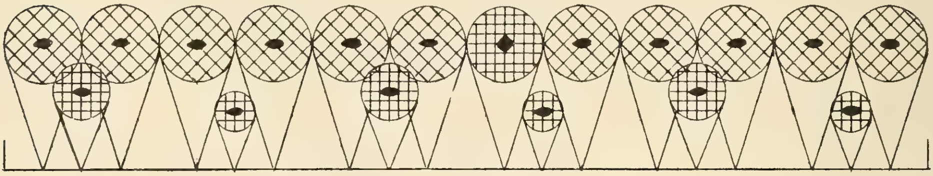

Fig. 10. Dansereau diagram for Thicket.

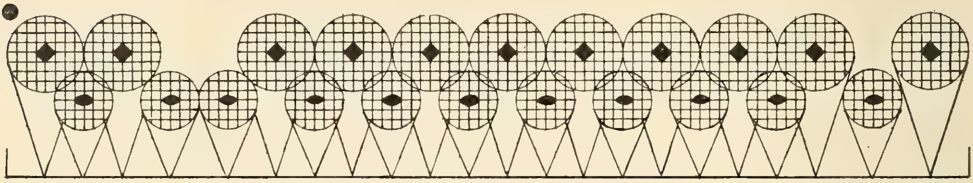

Fig. 11. Dansereau diagram for Mallee.

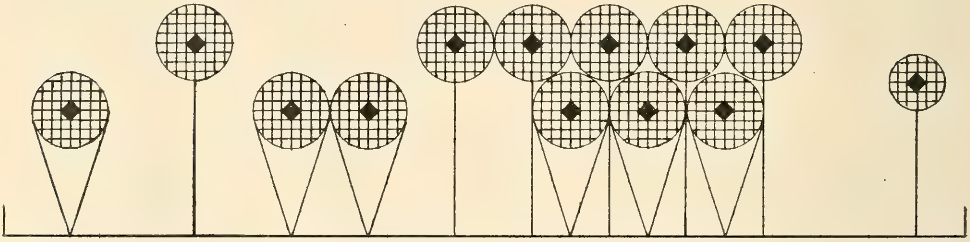

Fig. 12. Dansereau diagram for sclerophyll woodland *Eucalyptus transcontinentalis – E. flocktoniae* association.

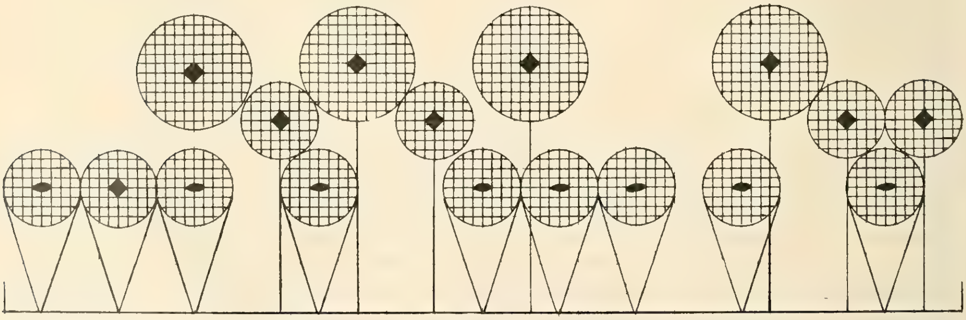

Fig. 13. Dansereau diagram for sclerophyll woodland – *Eucalyptus salmonophloia* Association.

VEGETATION SYSTEMS

Beard's work in Tropical America (1944, 1955) based primary classification upon floristics (the plant association), secondary classification upon structure and life-form (the plant formation) and a tertiary classification upon habitat (formation-series). At the tertiary level, five series of related formations could be built up with descending structure radiating from an optimum, each series within the same general kind of environment or "essential habitat", their descent reflecting decreasing availability of moisture or other comparable factors. Under Australian conditions, while this approach may still be fruitful for certain purposes and in a fuller state of our knowledge, it would appear at present that for vegetation survey a regional approach analogous to the Land System classification used by the C.S.I.R.O. (e.g., Speck 1960; Mabbutt 1963) would be more immediately valuable.

A Land System is defined (*loc. cit.*) as an "area or group of areas throughout which there is a recurring pattern of topography, soils and vegetation", and all three aspects of the landscape, together with geology and climate, are studied and interwoven into Land Research work. A vegetation survey, like a topographic, soil and geological survey, studies one aspect in particular with reference to the others, but the same recurring patterns will be observed and can be used to characterize unit areas. A vegetation survey will be expected to discover such patterns which will be dependent upon topographic and/or soil features, in the same way that it is already accepted practice for a soil survey to recognize recurrent patterns of soil types dependent upon topographic and/or geological features and characterized by distinctive vegetation. Working in East Africa, Milne (1935) discovered that soil types recurred in a definite position according to slope and originated the concept of the soil catena. Since that time the catena with modifications has come into general acceptance in British soil survey work. The Soil Survey of Scotland uses the Soil Association, a term originated by J. H. Ellis in Canada in 1932, which is a drainage catena. The term Soil Catena is used in the Soil Survey of England and Wales for a "sequence of repetitive soil series which recurs in a manner dependent upon topographic features" (Clarke, 1937), but it is the practice to speak of Soil Mosaics where the patterns are not topographically controlled. In the light of existing C.S.I.R.O. Land Research work in Western Australia, it can be confidently expected that as the Vegetation Survey proceeds patterns of vegetation will emerge closely corresponding to soil catenas and mosaics which will be termed catenary sequences of vegetation and vegetation mosaics. It may be expected that catenary sequences will predominate on the interior plateau and mosaics, possibly, on the coastal plains.

It will be desirable to recognize unit areas within which the same patterns recur, and to find a term for these. Although these are geographical areas, in a vegetation survey they rank as vegetation units. They are not, therefore, land systems, though it may logically be expected that if complete land research comes to be done the vegetation of the area will be found to be the vegetation of a co-extensive land system. We have in this case had to search for a term for our own use. The term Soil Association suggests Plant Association as an equivalent, but this is pre-empted for plant communities at a lower level of classification corresponding to Soil Type. "Vegetation System" seems to be the best choice of term. Since we have already from Diels, Gardner and Bennetts a division of Western Australia into Botanical Districts and Provinces, it will probably be the most convenient to regard Vegetation Systems as subdivisions of districts. As the Survey builds up, the boundaries of the Districts and Provinces, which are at present highly generalized, will become more exactly defined, and this itself is a desirable objective.

The relation between the classification adopted in the Vegetation Survey of Western Australia for vegetation units and major world systems of soil classification would then become as follows:

TABLE 5

	Unit 1	Unit 2	Unit 3	Unit 4	Unit 5	Unit 6
Vegetation classification	Faciation, society, etc.	Plant association (floristic)	Plant formation (physiognomic)	Vegetation system	Botanical district	Botanical province
U.S. Soil Survey classification	Soil phase or variant	Soil types	Soil series and soil complex	—	—	—
British Soil Survey	Subtype	Soil type	Soil series and soil complex	Soil Association (Scotland) Catenas and mosaics (England)	Major region	—
Russian Soil Survey	Soil individual	Soil variety	Soil Complex	Elementary Landscape	Soil Region	Soil Province

As indicated in the section on Physiography, it is possible to recognize five vegetation systems in the area studied.

1. *The Boorabbin System*

At the highest points and in the centre of the widest interfluves, broad plateaux of deep yellow sand carry a pure scrub heath association. For several months in the spring this type is filled with brilliantly flowering plants of all colours. Down slope it merges very gradually, so that sharp boundaries can never be drawn, into the broom-bush thicket. There is at first a general mixture then heath plants are relegated to an understory and finally disappear. Within these two zones outcrops of granite occur, with their rock pavement vegetation. Down slope under the broom-bush scrub the yellow sand becomes shallower and is bottomed by a lateritic hardpan which eventually comes to the surface often with a small scarp or "breakaway". Below this there is an abrupt change to sclerophyll woodland, at first the mixed association of *Eucalyptus transcontinentalis* and *Eucalyptus flocktoniae* on a relatively shallow red loam soil overlying granite. Further down in the valley bottom on deep alluvium there is a gradual change to the taller *Eucalyptus salmonophloia* association. The latter species is general throughout on light loam. *Eucalyptus longicornis* comes in on heavier soil, *Eucalyptus salubris* on stiff clay and *Eucalyptus melanoxylon* where kunkar is abundant.

2. *The Cave Hill System*

In the Cave Hill System there is very little scrub heath due to dissection of the sandy plateau surfaces. The interfluves are mainly characterized by granite outcrops surrounded by thicket growing on shallow decomposing rock or residual ironstone. On the lower ground the same woodland types are found as in the Boorabbin system.

3. *The Lake Hope System*

Here there is a relative scarcity of both scrub heath and thicket with their associated plateau soils. Instead the uplands are covered with the mallee formation with its typical sand over clay profile. On lower ground this merges patchily into very variable mixed woodland, variable both in structure and composition between the extremes of mallee and typical woodland. There is much less of the *Eucalyptus salmonophloia* type in this system and it tends to become restricted to "reefs" or narrow belts mainly in valley bottoms, but also at times on higher ground.

4. *The Coolgardie System*

This system is mainly developed in the Eastern Goldfields area to the north-east, and a relatively small portion of it only is included in the north-east corner of the Boorabbin sheet. The component communities are mainly sclerophyll woodland with some mallee and broombush thicket. The basic rocks or greenstones tend to form small, hilly ranges, in which the highest and stoniest hills are covered with broom-bush scrub mainly of Acacia, and the less rocky ridges with sclerophyll woodland of the *Eucalyptus torquata-Eucalyptus le soeufii* association. It is possible that the *Acacia* scrub maybe associated with rock of a particular lithological type. Woodland on the lower, less hilly and rocky ground corresponds in structure to the mixed *Eucalyptus transcontinentalis* woodland of the three vegetation systems on acid rocks described above, but is of quite different composition, characteristic species being *Eucalyptus le soeufii, Eucalyptus clelandii, Eucalyptus campaspe.*

The commonest of these are "blackbutts", that is, there is a persistent scaly bark on at least the lower part of the trunk, whereas on the acid rocks components tend to be smooth-barked. On low-lying alluvia the *Eucalyptus salmonophloia* association is found, with a preponderance of salt-bush in the understory. Occasionally on the higher ground there may be sandy plateaux, mainly on included granites, the sand being red in colour. On deep sand, in small patches, one finds mallee with spinifex, a mallee form of *Eucalyptus oleosa* with an understory of *Triodia scariosa.* Otherwise the plant cover of these plateaux is broom-bush thicket similar to that on acid rocks.

5. *The Bremer Range System*

While the Bremer Range is similar in geology and topography to the Coolgardie area its plant communities are entirely different. On the rocky knolls one finds a broom-bush thicket of *Casuarina* and a complete absence of *Eucalyptus torquata* and *Eucalyptus le soeufii.* In local patches the thicket breaks away to a grassland with shrubs. Footslope areas carry a fine sclerophyll woodland of *Eucalyptus dundasii* and *Eucalyptus longicornis* (both blackbutts), with no other associated trees except that where the woodland has been destroyed by fire the regeneration in addition to the above two species contains much *Eucalyptus corrugata.* The latter species appears to be relatively shortlived in competition with the others and under undisturbed conditions appears to be confined to a narrow belt between the woodland and the thicket. On low alluvial country there is the usual *Eucalyptus salmonophloia* association.

Botanical Provinces and Districts

From external evidence it would appear that the Lake Hope System, in which mallee is the dominant member of the catena, forms part of the Eyre District of the Southwestern Province, whereas the others belong to the Coolgardie District of the Southwestern Interzone.

Floristic Composition

The purpose of this section is primarily to distinguish floristically the various plant communities recognized. To do this the names of dominant, diagnostic and common or conspicuous species have to be listed, but there is no necessity to aim at a complete list of components. This would only be the objective if a complete botanical survey were being undertaken. As it is, the plant lists are being made as complete as possible within the scope of our knowledge, but it should be understood that they are only collectors' lists and of necessity incomplete.

1. Scrub Heath

This formation is by far the richest floristically of any of those in the locality and is also without any definite and consistent dominants so that it is not at present possible to characterize associations within it. There is scope for interesting and useful ecological research in studying the composition of this formation in detail. All that can be said as regards dominance is that *Grevillea excelsior* and in the northern part *Grevillea pterosperma* may assume physical dominance by growing to a much greater height than other components and may at times be quite abundant. They are very conspicuous and thus tend to appear typical species although their occurrence is very irregular. On the other hand it is suspected that *Grevillea excelsior* is actually a pioneer species and is relatively short-lived, dying out a certain number of years after the fire which regenerated it and giving way to slower-growing, slower-regenerating shrubs. There is an indication of this in the profile diagrams, as discussed earlier.

Further, *Grevillea excelsior* is essentially typical of deep yellow sand and occurs sparingly if at all wherever ironstone gravel predominates. Here *Dryandra* or *Casuarina* replace it. There is no distinct boundary between the scrub heath on its yellow sand and the broom-bush scrub on its ironstone gravel, the two soils and the two vegetations merging into one another. The ecotone is characterized by a broom-bush upper layer with *Casuarina*, *Acacia* and *Melaleuca*, and a heath lower layer of small, ericoid, mainly Myrtaceous, shrubs. At an early stage after fire the latter is re-established and appears to be a similar early stage of pure scrub heath. Later, however, the broom-bushes grow up and suppress it and give the opposite impression. The character of the vegetation in the ecotone thus varies according to time elapsed since the last fire.

This process has been described also for the pure heath scrub when dealing with physiognomy. In the plant lists which follow, an attempt has been made to define those species which in matured scrub would form part of the upper layer, as distinct from those which remain part of the lower layer.

Mallees are found sporadically in the scrub heath and may often, as in the case of *Eucalyptus burracoppinensis* and *Eucalyptus leptopoda*, be typical of it and not found to occur in any actual mallee formation.

Composition of the Scrub Heath in the Boorabbin System

Tall emergent shrubs: *Grevillea excelsior, G. pterosperma.*

Upper layer: *Acacia beauverdiana, A. fragilis, A. hynesiana, A. resinomarginea, A. rossei, A. sterophylla, A.* spp. J.S.B.3353–4, *Banksia audax, B. elderana, B.* sp. inedit. J.S.B.3879, *Callitris preissii* subsp. *verrucosa, Casuarina acutivalvis, C. campestris, C. corniculata, C. dielsiana, C. helmsii, Dryandra* sp. J.S.B.3871, *Eucalyptus burracoppinensis, E. foecunda, E.*

incrassata, E. leptopoda, E. platycorys, Grevillea apiciloba, G. biformis, G. ceratocarpa, G. didymobotrya, G. hookeriana, G. rufa, Hakea falcata, H. platysperma, H. roei, Isopogon scabriusculus, Persoonia saundersiana, Petrophile conifera, P. ericifolia, P. semifurcata.

Lower layer: *Adenanthos flavidiflora, Baeckea leptospermoides, Balaustion pulcherrimum, Boronia ternata, Brachysema chambersii, Burtonia hendersonii, Calytrix breviseta, Chamelaucium pauciflorum, Conospermum brownii, C. stoechadis, C. teretifolia, Cyanostegia microphylla, Dampiera lavandulacea, D. luteiflora, D. stenostachya, Daviesia croniniana, Eremaea pauciflora, Erichsenia uncinata, Eriostemon brucei, E. coccineus, Goodenia pinifolia, Grevillea haplantha, Halgania tomentosa, Hemigenia dielsii, Hibbertia stricta, H. uncinata, Jacksonia hakeoides, Lachnostachys bracteosa, Leptospermum roei, Leucopogon* sp. J.S.B.3339, *Melaleuca cordata, M. holosericea, M. subtrigona, Microcorys ericifolia, Micromyrtus racemosa, Phebalium drummondii, Persoonia coriacea, Petrophile circinata, Pityrodia caerulea, P. lepidota, P. uncinata, Plectrachne rigidissima, Pultenaea georgei, Stylidium limbatum, Tetratheca efoliata, Thryptomene kochii, Verticordia chrysantha, V. insignis, V. pennigera, V. picta, V. pritzelli, V. roei, Waitzia acuminata, Wehlia thryptomenoides.*

Composition of the Scrub Heath in the Cave Hill and Lake Hope Systems:

Tall emergent shrubs: *Grevillea excelsior.*

Upper layer: *Banksia elderiana, B. laevigata, B. media, Callitris preissii* subsp. *verrucosa, Calothamnus quadrifidus, Casuarina acutivalvis, C.* sp. *C. microstachya, Dryandra erythrocephala, D.* sp. J.S.B.3681, *Dodonaea stenozyga, Eucalyptus eremophila, E. flocktoniae, Grevillea* sp. aff. *asparagoides, G. concinna, G. didymobotrya, G. hookerana, G. incrassata, G. integrifolia, G. rufa, G. teretifolia, Hakea falcata, H. multilineata, H. roei, H. subsulcata, Isopogon axillaris, I. scabriusculus, I.* sp. inedit. aff. *teretifolius, Petrophile semifurcata, P. seminuda.*

Lower layer (shrubs, subshrubs and herbs): *Adenanthos flavidiflora, Astroloma serratifolium, Baeckea crispiflora, Calythrix* aff. *decandra, C. breviseta, Casuarina humilis, Chamelaucium megalopetalum, C. pauciflorum, C. virgatum, Comesperma drummondii, Cyanostegia angustifolia, Dampiera juncea, D. lavandulacea, D. wellsiana, Eremaea pauciflora, Grevillea eryngioides, G. prostrata, Halgania integerrima, Hemigenia eutaxioides, Isopogon villosus, Leptospermum roei, Leschenaultia expansa, L.* sp. inedit., J.S.B.3785, *Logania tortuosa, L.* sp. inedit., J.S.B.3737, *Lysinema ciliatum, Melaleuca cordata, M. subtrigona, Microcorys exserta, Mirbelia spinosa, Persoonia teretifolia, P. tortifolia, Phebalium* sp., *Pimelea sulphurea, Pityrodia axillaris, Olearia ciliata, Oxylobium ciliatum, Stylidium bulbiferum, S. zeicolor, Verticordia chrysantha, V. insignis, V. mitchelliana, V. picta, V. roei, Xanthorrhoea nana.*

As the plant lists are not complete, much of the difference between the northern and southern areas may be more apparent than real, and represent the vagaries of collecting. However, there are certainly some real differences, which in the present state of our knowledge appear to be the following:

Absence in the south of *Grevillea pterosperma, Acacia hynesiana, Acacia rossei, Banksia audax, Casuarina corniculata, Eucalyptus burracoppinensis, Eucalyptus leptopoda, Balaustion pulcherrimum, Verticordia pritzelii.*

Absence in the north of *Banksia laevigata, Banksia media, Isopogon* sp. inedit. aff. *teretifolius, Adenanthos flavida, Casuarina humilis, Chamelaucium megalopetalum, Leschenaultia* spp., *Xanthorrhoea nana.*

2. *Broom-bush Thicket*

When of mature structure this formation is a closed community, and the characteristic species are those of its canopy layer. Under certain conditions an understory of scrub heath species may be present as previously described, and these need not be further listed. The broom-bush scrub is developed on two different substrata, ironstone gravels capping granitic uplands, and rocky knolls occurring in outcrops of basic rocks. The composition is slightly different in these two cases.

On granite the principal components are: *Acacia fragilis, A. resinomarginea, A. stereophylla, A.* sp. J.S.B.3400, A. sp. J.S.B.3415, *A.* sp. J.S.B.3774, *A.* sp. J.S.B.3775, *Casuarina acutivalvis, C. campestris, C. corniculata, C. dielsiana* or var., *C. helmsii, Eucalyptus foecunda, E. leptopoda, E. oleosa, Melaleuca acuminata, Tryptomene appressa, T. kochii.*

Not all of these species may be present at any one time, in fact it appears that three species of *Casuarina* and two of *Acacia* would be a normal association, but such local variations have not yet been studied.

Where this community presents a sharp boundary, as it sometimes does to granite outcrops or to sclerophyll woodland, one may find along the margin the small mallee *Eucalyptus grossa.*

On Mount Day in the Bremer Range, which is an outcrop of fine-grained basaltic rock forming a low dome of altitude approximately 1500 ft, the top and slopes (except partially in the steepest parts) are clothed with a broom-bush scrub. This was 4 ft tall in October, 1964, but dead, fire-killed relics of 8 ft were present. Composition was observed to be: *Casuarina campestris,* v.a.; *Calothamnus asper,* a.; *Eremophila* sp. 3841, o.; *Dodonaea ptarmacifolia,* o.; *Acacia* sp. 3843, o.; *Melaleuca uncinata,* o.; *Cassia eremophila,* o.; *Scaevola oxyclona,* o.; *Eucalyptus oleosa, forma,* o. (mallee, up to 10 ft); *Triodia scariosa, r.*

On the steepest part of the east slope the scrub breaks into grass with scattered shrubs, the grasses including *Stipa juncifolia* and *Aristida arenaria* with herbs *Brunonia australis* and *Waitzia acuminata* and the subshrub *Ptilotus obovatus.* The major shrubs are the above *Dodonaea, Calothamnus, Acacia, Melaleuca* and *Cassia* with *Pittosporum phillyraeoides.* At the foot of the steep slope the dense scrub is reformed, consisting almost entirely of *Casuarina, C. campestris, C. helmsii* and *C.* sp. inedit. J.S.B.3838.

Such scrub knolls with grassy openings are frequent in the Bremer Range, but composition was not examined elsewhere.

Scrub on basaltic hilltops in the Coolgardie system is rather taller and consists mainly of *Acacia* sp. 3377.

3. *Rock Pavement Vegetation*

The numerous granite outcrops throughout this region consist typically of low domes of almost bare rock exfoliating in thin sheets. The rock is not quite bare, but clad sparsely with lichens, while here and there are depressions and holes filled with water after rain which have a certain growth of algae and mosses, and patches of soil, perched upon the rock. The vegetation of these patches varies according to their size and depth. Where they are thin and small, the typical plant is *Borya nitida* growing in herbaceous tussocks. With more soil, certain shrubs characteristic of this habitat appear, notably *Kunzea sericea,* less typically *Calothamnus quadrifidus, Thryptomene australis, Melaleuca leiocarpa* and *Dodonaea attenuata,* with sedges, Restionaceae and herbs such as *Isotoma petraea.* Large patches of deep soil and boulders will tend to develop shrubs and small trees of *Casuarina huegeliana* and *Acacia* spp. Around the outer edge of the outcrop the soil is at first shallow, though supplied with additional moisture by run-on. Shallow patches tend to resemble those on the rock itself, but the shrub *Melaleuca elliptica* is especially typical of this situation. Deep soil adjoining rocks carries dense groves of *Casuarina huegeliana* to 20 ft in height, or of an *Acacia* (unidentified Ac. 3352?). These usually merge into adjoining sclerophyll woodland with a belt containing *Eucalyptus loxophleba.*

Peak Charles differs rather markedly from other granite outcrops in size, height, steepness and other respects, and its vegetation has correspondingly unique features. The rock rises to 2160 feet above sea level, which implies about 1500 ft above the surrounding country, and consists of a pink granite. In many places the slopes are precipitous and bare of vegetation except lichens, but elsewhere patches of soil cling to the rock and scrub has developed. The summit is largely bare, with a few old, gnarled bushes of *Leptospermum* sp. inedit. (J.S.B.3821), 2 ft tall, growing in crevices. The middle slopes bear shrub thickets 4 to 6 ft tall, containing *Leptospermum* 3821, *Calothamnus quadrifidus* and *Calothamnus gilesii, Melaleuca fulgens, Callitris preissii,* subsp. *verrucosa, Baeckea behrii, Darwinia* sp., *Hibbertia mucronata, Labichea lanceolata, Anthocercis genistoides, Philotheca ericoides, Oxylobium parviflorum.*

On the lower slopes these also very largely occur with the addition of other species such as *Grevillea teretifolia, Santalum acuminatum* and *Santalum spicatum, Acacia* spp., *Casuarina humilis.* Besides this scrub, however, there are groves of *Casuarina huegeliana,* a tree up to 20 ft, or of mallee with *Eucalyptus loxophleba* and *Eucalyptus eremophila.* At the foot of the rock the tall scrub is joined by *Acacia acuminata* and *Pittosporum phillyraeoides.*

Kunzea sericea was not observed on Peak Charles, its niche being occupied by *Melaleuca fulgens,* which is characteristic of granite outcrops in the Esperance area to the south-east. The range of *Kunzea sericea* is to the north-west as far as the Darling Range.

4. Mallee

The most consistent and abundant species in the mallee formation of this area is *Eucalyptus eremophila,* a variable species which occurs in a number of different forms and varieties. Associates are *Eucalyptus oleosa* vars., *Eucalyptus redunca, Eucalyptus incrassata, Eucalyptus pileata, Eucalyptus leptophylla, Eucalyptus flocktoniae, Eucalyptus loxophleba.* Up to four species, of which *Eucalyptus eremophila* is normally one, tend to occur together in any one locality. Mallee which has resulted from burnt woodland may contain or consist of *Eucalyptus salubris* and *Eucalyptus gracilis.*

There are many variations in the ground layer beneath the mallee, from virtual absence to dense and continuous cover of low shrubs 2 to 4 ft tall. In the latter case *Melaleuca pungens* is the usual component. On sandy soil heath shrubs may be abundant, notably *Banksia media, Hakea laurina, Callitris preissii* subsp. *verrucosa, Melaleuca cordata, Leptospermum roei, Calytrix* aff. *decandra, Leschenaultia* sp. inedit., *Verticordia mitchelliana.* On heavy soil undergrowth is relatively sparse, but includes a number of typical shrub species, such as *Grevillea huegelii, Grevillea oncogyne, Eremophila calorhabdos, Eremophila dichroantha, Eremophila ?decipiens, Olearia adenolasia, Prostanthera arenicola,* and *Rulingia craurophylla.*

Mallee communities noted on the traverses were as follows:

Lake King-Norseman Road, at S.W. corner of Lake Johnston sheet—*Eucalyptus eremophila, Eucalyptus flocktoniae, Eucalyptus foecunda, Eucalyptus oleosa* var., *Eucalyptus* sp. unidentified (J.S.B.3740).

Ditto, vicinity of the 100-Mile Tank—*Eucalyptus eremophila, Eucalyptus flocktoniae, Eucalyptus pileata, Eucalyptus* sp. unidentified, with white fruits.

100-Mile Tank to Lake Hope—*Eucalyptus eremophila, Eucalyptus foecunda.* Young thickets of *Eucalyptus salubris* and *Eucalyptus gracilis* representing sclerophyll woodland in process of regeneration.

Norseman-Hyden Road, 315–300 Mile Peg—*Eucalyptus eremophila, Eucalyptus gracilis, Eucalyptus foecunda, Eucalyptus redunca.*

South of Woolgangie—*Eucalyptus eremophila, Eucalyptus loxophleba, Eucalyptus oleosa* var.

Woolgangie to Bullabulling—*Eucalyptus eremophila, Eucalyptus foecunda, Eucalyptus incrassata.*

No mallee has been observed in this area on greenstone.

5. *Sclerophyll Woodland*

In this formation there are a number of different association which may be readily recognized.

(*a*) *Eucalyptus transcontinentalis*-Eucalyptus flocktoniae* association on the "granite eluvium" of the geological survey, i.e. red loam developed *in situ* on granite. Associated trees are *Eucalyptus gracilis* (o), *Eucalyptus corrugata* (f), *Eucalyptus salubris* (l.a.), *Eucalyptus melanoxylon* (l.f.). Undergrowth may be almost entirely lacking, but the few scattered shrubs seen include: *Alyxia buxifolia, Comesperma spinosum, Daviesia anthoclona, Dodonaea stenozyga, Eremophila dempsteri, Eremophila saligna, Eremophila* sp. inedit. J.S.B.3825, *Grevillea huegelii, Grevillea oncogyne, Melaleuca pauperiflora, Melaleuca pubescens, Melaleuca sheathiana, Santalum acuminatum, Scaevola spinescens, Westringia rigida.*

In places, mainly south of the Johnston Lakes, a low woodland may be encountered intermediate in structure between mallee and sclerophyll woodland proper, and composed of *Eucalyptus flocktoniae* and *Eucalyptus eremophila,* mostly with a dense understory of *Melaleuca pungens.*

(*b*) *Eucalyptus* aff. *striaticalyx-Eucalyptus leptophylla* association on sand ridges. These tend to occur to the south-east of salt lakes, in curved lines, conforming to the present lake margin. The ridges are low, well vegetated, and too limited in extent to be mapped. There are good examples between the 380 and 370 mile pegs on the Norseman–Hyden Road. The dominant species is a tree suggesting *Eucalyptus striaticalyx,* up to 40 ft tall, with persistent stringy bark on the lower trunk, together with a few salmon gum, *Eucalyptus salmonophloia,* and the sand salmon gum *Eucalyptus leptophylla.* The latter is only a small tree, but may form pure stands locally. Undergrowth consists of a fairly dense ground layer (2 ft) of spinifex *Triodia scariosa,* and the cyperaceous reed *Lepidosperma viscidum.*

(*c*) *Eucalyptus torquata-Eucalyptus le soeufii* association on rocky greenstone ridges. This association occurs only in the Coolgardie system and is of limited extent in this area. *Eucalyptus torquata* and *Eucalyptus*

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* For convenience, since these are important ecotypes readily recognizable in the field, it is preferred to use the forms *Eucalyptus transcontinentalis* Maiden and *Eucalyptus longicornis* F. Muell. rather than *Eucalyptus oleosa* F. Muell. var. *glauca* Maiden and var. *longicornis.* F. Muell.

le soeufii are co-dominant, abundant and characteristic. Associated trees are *Eucalyptus corrugata, Eucalyptus clelandii, Eucalyptus campaspe* and *Casuarina cristata.* There is an open shrub understory, largely of *Eremophila* spp. up to 6 ft tall and of "broom-bush" habit, notably *Eremophila scoparia, Eremophila glabra, Eremophila oldfieldii,* also *Dodonaea, Cassia* and *Acacia* species, interspersed with glaucous 4 ft shrubs of the "Old Man Saltbush", *Atriplex nummularia.* Forbs include *Ptilotus exaltatus.*

(*d*) *Eucalyptus le soeufii-Eucalyptus oleosa* association on deep soils developed on the greenstones and included granites. This also is confined to the Coolgardie system and is of limited extent within the Boorabbin map sheet. Composition is related both to that of the *Eucalyptus transcontinentalis-Eucalyptus flocktoniae* and *Eucalyptus torquata-Eucalyptus le soeufii* associations, all eucalypt components of both being present except for *Eucalyptus torquata* which is entirely absent, being confined to rocky ridges. A newcomer is *Eucalyptus oleosa* var. *obtusa.* Thus we have: *Eucalyptus le soeufii,* v.a.; *Eucalyptus oleosa* var. *obtusa,* l.a.; *Eucalyptus transcontinentalis* (*Eucalyptus oleosa* var. *glauca*), a.; *Eucalyptus clelandii,* f.; *Eucalyptus corrugata,* f.; *Eucalyptus campaspe,* l.f.; *Eucalyptus flocktoniae,* f.; *Eucalyptus gracilis,* o.

The understory does not differ significantly from that in the *Eucalyptus transcontinentalis-Eucalyptus flocktoniae* association.

(*e*) *Eucalyptus dundasii-Eucalyptus longicornis* association on deep soil over greenstone in the Bremer Range. The woodland shows a co-dominance of *Eucalyptus dundasii* and *Eucalyptus longicornis* (*Eucalyptus oleosa* var. *longicornis*), sometimes in mixture, sometimes in pure patches. The former of these is characteristic of greenstone soils further east, around and to the south of Norseman, and the latter of greenstone soils further west around Forrestania and in other localities. This woodland appears to be rather readily destroyed or damaged by fire and in many places there are young saplings and pole-sized stands consisting largely of *Eucalyptus corrugata* in addition to the above two species. Since *Eucalyptus corrugata* was nowhere observed in mature stands it may be that it is a relatively short-lived pioneer species: this merits further investigation. In the transition to *Casuarina* scrub on Mt Day there is a narrow band of *Eucalyptus celastroides* and *Eucalyptus* sp. (unidentified). Undershrubs are extremely sparse, but the following were noted: *Eremophila* sp. inedit., J.S.B.3825; *Eremophila densifolia; Dodonaea stenozyga; Acacia* spp. On the low ground a saltbush *Cratystylis conocephala* is common.

(*f*) *Eucalyptus salmonophloia* consociation on alluvial soils, derived from both granite and greenstone. The composition of this association is very simple. Very commonly and most typically the tree layer consists of nothing but *Eucalyptus salmonophloia* and this seems to be associated with a light loam soil. Changes in soil tend to bring in some admixture, *Eucalyptus longicornis* on clay-loam, *Eucalyptus salubris* on stiff clay. *Eucalyptus melanoxylon* appears to indicate high base status, usually the presence of Kunkar. Under ecotonal conditions appropriate mixtures can be seen, e.g., with *Eucalyptus transcontinentalis, Eucalyptus flocktoniae* and their associates or with *Eucalyptus flocktoniae* and *Eucalyptus eremophila* (in marlock form) where the boundary is with mallee. In these cases, *Eucalyptus salmonophloia* being of superior stature, a layered woodland is formed. There is commonly a tall shrub layer of *Melaleuca* spp., e.g., *Melaleuca pauperiflora, Melaleuca pubescens,* and/or *Melaleuca sheathiana.* Shrubs are extremely sparse, but include many species of *Eremophila* and *Acacia, Daviesia* *nematophylla* and *Daviesia anthoclona.* Where the soil is somewhat saline, there is a ground layer solely of saltbush, 18 inches high.

6. *Halophytes.* The vegetation of saline areas may be divided into two types, saltbush and samphire. The former may be found on alluvial soils in the vicinity of salt lakes, while the latter occurs in the lakes themselves, usually on raised beds forming a marked pattern in the lake. Not all lakes have these beds. The saltbush type begins as a ground layer under *Eucalyptus salmonophloia, Eucalyptus melanoxylon* or *Eucalyptus flocktoniae,* which become more and more scattered as salinity increases. On the east side of some lakes the trees may thin out completely to leave pure saltbush and grass as at Lake Hope, where the saltbushes *Atriplex paludosa* and *Frankenia interioris* and grasses *Danthonia setacea, Stipa elegantissima* were recorded. Occasionally at lake margins trees of *Eucalyptus kondininensis* are found, but this tree does not seem to be common in the area.

Samphires have not been studied and are assumed to be *Arthrocnemum* spp.

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EXPLANATION OF PLATES

PLATE XVIII

Top left. Sandheath east of Hyden, October, 1964. Stage of regeneration with abundant *Grevillea excelsior,* lower story of ericoid shrubs, *Verticordia roei* flowering.

Top right. Sandheath east of Lake King near the rabbit-proof fence, October, 1964. Intermediate stage, well-developed Proteaceous shrubs (*Banksia elderana, Isopogon*) and *Casuarina* with low ericoid ground layer.

Bottom left. Broombush thicket of *Casuarina* spp. Near Koorarawalyee, October, 1964.

Bottom right. Grassy opening in thicket, Mount Day in the Bremer Range, October, 1964. Foreground: *Ptilotus obovatus* with *Stipa* and *Aristida,* behind shrubs of *Dodonaea, Calothamnus,* etc., and *Eucalyptus oleosa.*

Scrub heath east of Hyden.

Scrub heath east of Lake King.

Broombush thicket of *Casuarina* spp.

Grassy opening in thicket.

The vegetation of the Boorabbin and Lake Johnston areas.

Mallee.

Mixed sclerophyll woodland.

Eucalyptus flocktoniae and saltbush

Salmon Gum (Eucalyptus salmonophloia).

The vegetation of the Boorabbin and Lake Johnston areas.

Sclerophyll woodland of alluvial soils.

Sclerophyll woodland on sand ridges.

Vegetation on granite outcrop.

Vegetation on Peak Charles.

The vegetation of the Boorabbin and Lake Johnston areas.

AUSTRALIA 1 : 250,000

BOORABBIN

VEGETATION SURVEY OF WESTERN AUSTRALIA

SHEET SH 51-13

Mapped by J. S. Beard 1964-65

BOORABBIN

SHEET SH 51-13 1968

AUSTRALIA 1 : 250,000

LAKE JOHNSTON

VEGETATION SURVEY OF WESTERN AUSTRALIA

SHEET SI 51-1

Mapped by J. S. Beard 1964-65

LAKE JOHNSTON

SHEET SI 51-1 1968

PLATE XIX

Top left. Mallee between 100-mile tank and Lake Hope, October, 1964. *Eucalyptus eremophila, E. gracilis. Melaleuca* understory.

Top right. Mixed sclerophyll woodland, between 100-mile tank and Lake Hope, October, 1964. Fairly young stand. *Eucalyptus transcontinentalis, E. salubris, E. melanoxylon, E. gracilis.* "Boree" *Melaleuca* at right.

Bottom left. *Eucalyptus flocktoniae* and saltbush, open woodland in salt country on the east side of Lake Hope.

Bottom right. Unlogged stand of salmon gum (*Eucalyptus salmonophloia*) 6 m. south of Queen Victoria Rock.

PLATE XX

Top left. Sclerophyll woodland of alluvial soils. Stand of Gimlet (*Eucalyptus salubris*) with understory of "boree" *Melaleuca* and *Atriplex.* Norseman – Hyden Road.

Top right. Sclerophyll woodland on sand ridges. *Eucalyptus* sp. aff. *striaticalyx, Triodia scariosa.*

Bottom left. Vegetation of a typical granite outcrop. Queen Victoria Rock, May, 1964. *Kunzea sericea* in crevices.

Bottom right. Vegetation on middle slopes of Peak Charles. October, 1964. *Calothamnus, Callitris, Leptospermum, Melaleuca fulgens, Restionaceae.*

PLATE XXI

Vegetation map of Boorabbin.

PLATE XXII

Vegetation map of Lake Johnston.

Species designated in mapping: E.8, *Eucalyptus salmonophloia*; E.9, *E. longicornis*; E.10, *E. transcontinentalis;* E.11, *E. flocktoniae;* E.12, *torquata;* E.13, *le soeufi;* E.14, *dundasii;* E.15, *eremophila.*

SIR WILLIAM MACLEAY MEMORIAL LECTURE, 1968

WILDLIFE CONSERVATION

H. J. Frith
Division of Wildlife Research, CSIRO, Canberra, A.C.T.

[Delivered 31st July, 1968]

I. Introduction

The distinguished career of Sir William Macleay in Australia, from 1839 to 1891, covered the period when the inland was being occupied by settlers and domestic stock. He was in the forefront of this occupation when, soon after his arrival, he took up country on the Murrumbidgee River west of the present town of Darlington Point.

This country is now in the heart of the Riverina, the district that became the cradle of the wool industry, the location of many of the famous studs, the birth-place of many of the bush ballads and the folk-lore of shearers and jumbuks, shanties and riverboats. Yet, when William Macleay went there, only eleven years after Sturt had probed his way down the river, this was all in the future. We are told that as late as 1842 "very little was known of the country situated on the western side of the main road passing from New South Wales to Victoria on the lower Murray, Edward, Billabong, Murrumbidgee, Lachlan and Darling Rivers. The general impression was that all this lower country to the westward was too dry, too flat and too arid for any purpose, and the few who travelled over it described it as a miserable, wretched, useless country" (Fletcher, 1893).

The actual site of William Macleay's squatterage is not certain. There were many runs on the Murrumbidgee and the Macleays held several and, no doubt, some were registered in the names of financial backers rather than the man actually on the spot. However, by the end of the nineteeth century between Hay and Darlington Point the various squatterages, runs and blocks had consolidated into four stations, "Eli Elwah", "Burrabogie", "Toganmain" and "Kerarbury". The Macleays had had interests in all except the first, and Sir William had held "Kerarbury", part of which had formerly been known as "Uratta", since the fifties. "Kerarbury" has since been subdivided and, although a Kerarbury Station still exists, the block where the original homestead is thought to have been is immediately to the west and is known as "The Homestead".

To a naturalist, however, of greater concern is not that the old homestead has disappeared and its location is not certain, but that most of the wildlife of the region has also disappeared and its original composition even is not certain.

II. Small Mammals

In many years' research on the Murrumbidgee plains, apart from rabbits, domestic stock and feral foxes and cats, the only mammals seen have been red and grey kangaroos, *Megaleia rufa* and *Macropus giganteus*, an occasional marsupial mouse, *Sminthopsis crassicaudata*, and a few brush-tailed possums, *Trichosurus vulpecula*, wherever there is some timber. There are probably also a few water rats, *Hydromis chrysogaster*, somewhere on the river, but I have not seen them.

In 1958 Marlow published maps of marsupial distribution based on his own observations and on museum records. The startling fact of these maps is that apart from the red kangaroo, grey kangaroo, brush-tailed possum and fat-tailed marsupial mouse, all of which are common today, there are virtually no historical records of marsupials in western New South Wales. The records of native rodents are likewise poor. Either inland New South Wales was without small mammals at the beginning of settlement, or there has been a disastrous decline in most species. The latter is, of course, probably the case.

It is one of the tragedies of the early settlement of this country that the mammal fauna of the inland was allowed to perish without even having been described. There seems to have been no organized collecting or recording done in the Riverina, and many animals that could have been common have disappeared from the State and in some cases from the whole continent.

We will never know with certainty the original composition of the fauna of the inland plains, and can only try to build up a picture from the few records from the surrounding areas and from what little we know of the biology of some of the animals that have survived elsewhere in the continent.

Most of the information on inland marsupials comes from the results of an expedition led by William Blandowski in 1856–1857 and from the work of John Gould in 1839–1840. The former expedition was financed by the Victorian Government and led by William Blandowski, but Gerard Krefft was the report writer and published papers on the expedition. Wakefield (1966) has examined the literary accounts and the surviving records. The expedition was in the field for a year, and, having reached the Murray River near Echuca, followed it to about the present site of Mildura, where they camped for several months. Excursions were made in several directions, including one of about 300 miles to the north-east. They found a very rich fauna and collected several hundred mammals representing over 30 species. Judging from the numbers collected of some species, they must have been very common. John Gould collected on the Upper Hunter River and on the Liverpool Plains to the west of the Divide and north-westward from there.

Although both these areas are some distance from the Murrumbidgee, it is a fair assumption that species collected both at Liverpool Plains and the junction of the Murray and Darling Rivers would probably also have occurred along the Murrumbidgee. Among these are the barred bandicoot, *Perameles fasciata*, that has not been recorded in New South Wales since Krefft's 1857 expedition and is not known to occur anywhere today, and *Bettongia penicillata*, that has not been recorded in New South Wales for 50 years and is now only known with certainty in south-western Australia; the bettong was also recorded near Gundagai in 1832. The rufous rat-kangaroo, *Aepyprymnus rufescens*, was common on the Murray, but is now found nowhere inland; the brown hare wallaby, *Lagorchestes leporides*, was also recorded near Booligal in 1890, but this was the last record for New South Wales, and it is not known to occur anywhere today; the bridled nail-tail wallaby, *Onychogalea frenata*, has not been seen anywhere for 30 years; the mouse, *Thetomys gouldii*, also seems to have gone as there has been no information for a long time.

Some species recorded by Krefft, but not by Gould, probably did not reach as far east as "Kerarbury", but some certainly did. The rabbit-eared bandicoot, *Macrotis lagotis*, had a wide distribution in New South Wales, but the last record was near Wagga in 1912. The pig-footed bandicoot, *Chaeropus ecaudatus*, was known in south-western New South Wales until 1880, but is now probably extinct. Lesueur's rat-kangaroo, *Bettongia lesueuri*, was abundant in much of inland New South Wales, but is now known for certain only on islands off the coast of south-west Australia.

Kershaw (1909) recorded the hairy-nosed wombat between Deniliquin and Billabong Creek, not far south of "Kerarbury", in 1884, and these were apparently the only examples ever collected in New South Wales. It was long believed that they were the same as the South Australian species *Lasiorhinus latifrons*, but Crowcroft (1967) has shown them to be of the southern Queensland species *L. gillespiei* which is also extinct. It may have also occurred on the Murrumbidgee.

The native rodent, *Leporillus apicalis*, which is now probably extinct, probably extended to the Murrumbidgee, and perhaps also *Notomys mitchelli*. There may have been other native rodents in the area, particularly in the *Pseudomys* group of genera, as Krefft recorded several at the Murray – Darling junction and Gould and others collected some of these and other species on the Liverpool Plains.

Marlow points out that of the 52 species of marsupials that have been recorded in New South Wales, 42% are presumed extinct or rare. Calaby (1963) considers that of the 119 marsupials in Australia, five are extinct and 34 are endangered. The position with the native rodents is similar but less well documented, largely because of taxonomic difficulties. Needless to say, virtually nothing is known of the biology of any of these animals, and surviving collections in museums are hopelessly inadequate.

One of the significant things about this disaster is that most of the animals that have disappeared or are endangered have never been persecuted, or very little. Their disappearance, often unnoticed, is an incidental and insidious byproduct of alteration of the habitat by stock.

III. Kangaroos

While the small marsupials of the inland declined before settlement, the red kangaroo, *Megaleia rufa*, for a time prospered. Krefft recorded in 1857: "The Red Kangaroo (*Osphranter rufa*) is to all appearance very scare as not a single specimen was brought in during our stay at Gunbower by the natives." Many of the explorers' journals in New South Wales and elsewhere in the inland also give the impression that red kangaroos were not numerous, yet towards the end of the 19th century organized drives in the Riverina and elsewhere were accounting for many thousands in quite small areas. By 1957 it was widely held that they were in "plague proportions" in the inland, in places outnumbered the sheep, and were a major pest. There was accordingly a great deal of research on this and other kangaroos, and it has been possible to judge these claims and to learn a lot about the biology of the animals. Should a determined effort be made to conserve them, the essential biological data on which to base these efforts are now available.

Much of the Murrumbidgee flood plain is now grassland, with scattered clumps of boree, pine and black box. The most extensive grasslands are of *Danthonia* and *Stipa/Danthonia*. There is general agreement among plant ecologists (Beadle, 1948; Moore, 1953*a*, *b*; Williams, 1955) that these are disclimax communities produced by grazing. Originally the area was mainly a low shrub woodland of boree and other small trees.

Aerial counts of the density of kangaroo populations between Hay and Darlington Point have shown that in the period 1960–1963 the wallaby grass plains supported on the average 4·1 kangaroos to the square mile, but of the woodlands pine-belah supported only 0·1 and the belah-rosewood 1·5 kangaroos to the square mile. Of the total animals counted, 79% were on the wallaby grass plains (Frith, 1964; Frith and Calaby, 1969). These results, combined with the common observation that red kangaroos are usually most numerous on short green grass and least numerous on long dry herbage, leave little doubt that the abundance of kangaroos in the area is related to grazing on the virgin habitats.

Newsome (1965) has reported similar results from central Australia with land grazed by cattle, and there is further evidence from the north-west corner of New South Wales that the abundance of red kangaroos can be attributed to sheep grazing also (Bailey, 1967). Ealey (1968) in north-west Australia has concluded that the abundance of euros, *Macropus robustus*, also is a direct result of the impact of sheep on a delicately balanced natural vegetation; the sheep overgrazed it to the point of their own destruction, but created ideal euro habitat.

This kind of situation, of course, means that kangaroos pose quite different conservation problems than do many animals. They are abundant in a particular stage of botanical succession and, if the composition of the pasture changes due to increases or decreases in the stocking rate with domestic stock, the size of the kangaroo populations will fluctuate also. In the meantime, because of their abundance, they are held to be serious competitors with stock by many, and several States have allowed uncontrolled slaughter both by pastoralists and by those who shoot the animals for their meat and hides. The main features of the biology of the red kangaroo are now known, and it is possible to be rather more definite about the factors that control kangaroo populations than it was a few years ago when the controversy about kangaroos in inland New South Wales was at its height.

They are not nearly so wide-ranging as has been thought. In mild weather no marked animal has been found more than 30 miles from the place of marking, although in drought some have moved up to 130 miles. The amount of food eaten is not several times that of a sheep as has been often claimed; in bulk it is similar. It is not possible, however, to equate sheep with kangaroos as forage removers unless their food preferences are the same. A current study shows that, although there is a broad similarity in the plants eaten, there are significant differences. Many plants, relished by sheep, are avoided by kangaroos and vice versa. The two animals have specific food preferences and so are not in complete competition. There are similar results from central Australia with red kangaroos and cattle (Newsome, 1967).

Mortality in the pouch varies with the climatic conditions. In a favourable environment loss of pouch young is about 15%, but in mild drought the number failing to leave the pouch increases (Frith and Sharman, 1964). A further adaptation to drought is that many females fail to have a post-partum oestrus and cease breeding until rain falls.

In the recent drought breeding of red kangaroos ceased, most of the pouch young and young at foot perished, and the adults dispersed, fell in condition and many perished. Yet all the time uncontrolled shooting continued. It is no wonder the populations declined and kangaroos became uncommon over very large areas. On the Murrumbidgee between 1960 and 1963 the average density fell from 8·6 to the square mile to 2·7, and on the Darling River it fell from 6·3 to 2·2 and in both places there were later obvious declines that were not measured (Frith, 1964). In the north-west corner of the State the density fell from 6·3 to the square mile to 1·2 between 1964 and 1966, and in central Australia between 1959 and 1966 it fell from about 10·0 to 1·9 animals to the square mile (Newsome, 1966).

Faced with this dramatic decline, New South Wales and Northern Territory strengthened their administrative machinery to control it, but neither New South Wales nor any other State at present has the manpower to institute and conduct an effective management programme. Until this is done kangaroo conservation must remain a matter of chance.

There is no doubt that red kangaroos can be preserved, as a species, in reserves. However, the animal is a valuable resource and it seems appropriate that they should also be conserved on land devoted to pastoral industries. Since the original settlement the stock numbers in inland New South Wales have followed the common pattern for arid areas. The numbers of sheep initially are high, but very quickly decline. In the Western Division, for example, at the end of last century, there were thirteen million sheep, but due to degradation of the rangeland the area now can only carry seven million. However, the biomass of animals is probably still much the same, the missing six million sheep being in the form of kangaroos which are in themselves a valuable resource. Kangaroo management depends on the Australian community and Governments realising that domestic stock are not the only means of utilizing much of the arid zone. A long-term husbandry based on both stock and kangaroos will probably be less productive than one based on stock alone, but certainly more permanent.

IV. Waterfowl

The Murrumbidgee plains have been an appropriate place to study another complex problem of wildlife conservation, that of several species of waterfowl. Although the problems of kangaroo conservation are difficult, they are not insoluble. The position of waterfowl, however, is more complicated as they demand the management of water conservation schemes with the needs of waterfowl in mind just as much as other products of more economic value.

Australian waterfowl were apparently never very numerous, and in the erratic, semi-arid environment one might assume that the populations would be quite delicately balanced and not need a great deal of interference with their habitat to upset them. This interference has been applied at several critical points in the life history of many species and they now are declining rapidly. The reasons are quite well known, but those responsible for wildlife conservation have been able to do little to halt the decline.

The inland waterfowl need a breeding place, a nearby refuge for dry weather and a permanent refuge for extended dry periods and droughts. These can be separated by great distances, but, unless they are available at the appropriate time, the populations cannot survive. At present, all these types of habitat are vulnerable to settlement and are being steadily destroyed.

The inland rivers wind across their flood plains and local rainfall has little effect on their level; the level is controlled by rain or melting snow on the highlands, hundreds of miles to the east. In years of adequate rain the rivers rise, often in spring, but at whatever season the rain falls the billabongs, lagoons and effluent streams fill. In times of heavy rain there are great floods that cover thousands of square miles with water a few inches deep. In extreme years the waters of the Murrumbidgee and the Murray, over one hundred miles to the south, join across the plains. In dry years the billabongs do not fill or rise in level only slightly. In very dry years the rivers cease to flow or become dry and so do the billabongs.

In the northern hemisphere, where much of the pioneer work on the factors controlling the breeding seasons of birds was done, birds tend to have fairly regular breeding seasons and nest at a fixed time each year. It has been concluded that, in general, the sexual cycle is controlled by the increase in day length that occurs at a fixed time each spring and that the actual breeding season is timed, within these quite narrow limits, by more immediate environmental factors such as the availability of nest sites, etc. (Lack, 1954; Rowan, 1926). Such a mechanism in semi-arid Australia would, more often than not, result in the ducklings being hatched at a time when the rivers were low and the billabongs dry with a resultant disaster to the young of that year.

It has now been shown that Australian waterfowl can breed at any time of the year that suitable conditions exist for the survival of the young. In unfavourable years they do not breed at all. The breeding season is directly geared to changes in waterlevel in the billabongs. Even though the plains may be gripped by drought, should rain on the catchments cause a local increase of a suitable speed and extent in the waterlevel of the billabong, the birds breed (Frith, 1959*c*). In this way it is ensured that the waterfowl do not breed when the habitat is unfavourable and also that favourable circumstances are not missed, no matter at what time of the year they occur.

All the common waterfowl of the billabongs receive a sexual stimulus from the rising waterlevel, but the speed of the reaction varies from species to species. The grey teal, *Anas gibberifrons*, is the most rapid, and ovulation can follow within a few days of the first sign of the rising water. The pink-eared duck, *Malacorhynchus membranaceus*, also receives an immediate stimulus, but the eggs are not laid until it is certain that the rise in waterlevel is going to be maintained and actual flooding of the plains will follow. This difference is related to the food requirements of the two birds; the grey teal can use a very wide variety of food from many sources and this is made available by the rising water. The most important insects also have breeding seasons geared to the rising waterlevel and the shallows become dense with their young by the time the ducklings hatch. The pink-eared duck is a food specialist and lives on microscopic plants and animals that are only abundant in shallow drying floodwater. Other ducks have different speeds of response; the black duck, *A. superciliosa*, breeds as the waterlevel approaches its maximum, the hardhead, *Aythya australis*, breeds immediately after the maximum level, and the freckled duck, *Stictonetta naevosa*, a little after that (Frith, 1959*c*, 1965). There are two species, the blue-billed duck, *Oxyura australis*, and the musk duck, *Biziura lobata*, that are restricted to the few deep semi-permanent cumbungi swamps in the region and, being in a "safe" habitat, have no need for an erratic breeding season. They breed at a regular time each year and there is reason to believe that these have retained a photoperiodic effect in the timing of their breeding seasons (Braithwaite and Frith, 1969).

How the rising waterlevel stimulates the sexual cycle of species with erratic breeding seasons has been the cause of some speculation — did the waterlevel act as a visual stimulus or did it operate through some other intermediate factor. Recent work with nine species, ranging from those with the most regular breeding seasons to those with the most erratic, has suggested that in some species the waterlevel change affects the abundance of food which in turn affects the nutrition of the birds and this permits breeding. In those species having erratic breeding seasons the normal germinal cell division for spermatogenesis and the necrosis of these cells are not separated; they occur concurrently, so that at any time the testis is primed, as it were, for an immediate response to suitable nutrition of the bird. Both processes are reversible, so that, should a bird receive a stimulus that is not maintained, it can rapidly reverse the spermatogenic cycle. Some species can continue sperm production throughout the year, even during moult (Braithwaite, 1969; Braithwaite and Frith, 1969).

Floods and even full billabongs are not permanent features of the inland plains, and as the water areas decrease the birds must disperse. It has been shown that these movements are multidirectional (Frith, 1959*d*). The movement is an explosive random dispersal with birds moving in all directions. The degree of mobility varies from species to species and the distance travelled depends on the abundance of habitat. The birds apparently fly in straight lines until a suitable swamp is found and there they remain until it in turn becomes unsuitable. There is then another random dispersal. A bird having left the Murrumbidgee only returns by chance. Those that do not find a suitable swamp on the outward movement carry on, and many presumably fly out to sea and perish (Frith, 1962, 1963).

Very few of the drought refuges are in the inland as little permanent water exists there. The few cumbungi swamps that do exist are crowded each summer with great numbers of many species of waterfowl. It has been possible to show that, although as many as nine species can crowd together on the one swamp for long periods, they are effectively isolated ecologically by having different bill structures, enabling different feeding methods, different feeding places; e.g., some dive to the bottom of deep water and others feed only on the surface and have different abilities to use different food items (Frith, Braithwaite, and McKean 1969). They seldom compete for food. The cumbungi swamps are capable of supporting the birds for long periods, but eventually they must move again to the ultimate drought refuges, the coastal lagoons of the eastern, south-eastern and northern coasts, where they remain until the inland rivers flood once more.

The causes of the decline in waterfowl populations are now apparent. The needs of water conservation and hydro-electric power have led to continuing efforts to control the flow of the inland rivers and to prevent their flooding. Each water conservation structure built in the highlands and each weir built on the plains to divert water for irrigation decrease the frequency with which the water level in the billabongs increases in level and thus decrease the frequency of breeding of the waterfowl. Even those birds that do breed are finding it increasingly difficult to find a suitable drought refuge. The trend of agriculture on the coast is to drain every swamp and pool whether this will produce productive land or not. Perhaps the productivity of many farms would be increased more by pasture improvement on existing pastures than by draining a few acres to produce another boggy tussocky pasture.

If waterfowl are to survive in south-eastern Australia, it must be recognized that they need living space, and very positive efforts need to be made to ensure their conservation.

V. Wildlife Conservation

Australia's record towards its wildlife has been generally poor. Those animals that do not provide products whose value can be measured in money, or that are not useful as game, have been ignored so that their survival in the face of increasing pastoral and agricultural use of the land has been purely a matter of chance. Those that were hardy enough or adaptable enough to withstand the changes to the environment have survived; those that were not have declined seriously or have disappeared. Most of those that do provide economic products have been exploited to the point where they are incapable of providing anything.

I can find no example of successful management of an animal that has been used to provide economic products. In each case the treatment has followed the same pattern. The exploitation of the animal is uncontrolled until the populations have been reduced to a low level. Attempts to control the industry are then applied, but are often based on legislation rather than on biology or are not effectively policed or both. The animals continue to decline in numbers to the point where the industry is no longer profitable, having destroyed its own resources. By this time public opinion is so outraged that the animal is afforded complete and virtually unalterable protection.

Apart from the few mammals and birds that have been the subject of special studies, conservation is hindered because the wildlife generally is not well known, so that it is difficult to set targets, and little is known of the biology of even common species so that reserves can be sensibly managed.

The need for active management of the wildlife in reserves is shown by many examples in other countries, but in Australia little has been documented. There are many cases of reserves failing to serve their main purpose in the long term because of inadequate knowledge of the animals and lack of management. I have already mentioned how red kangaroos depend on short green pastures that is not a permanent feature of the ungrazed inland plains. It might be inferred that large populations of the animals can only be retained in reserves if the ground cover is kept in a suitable state by grazing some domestic stock. On the other hand, the mallee fowl was long thought to be endangered by the depredations of foxes, but a study of the bird showed that this was not so; the real reason for the decline was competition with the birds for food by stock and rabbits; mallee fowl cannot be conserved unless grazing stock are excluded and rabbits eradicated from the reserve. The re-discovered Leadbeater's possum needs an early stage of the regeneration of *Eucalyptus regnans* with trees 25 to 30 years old so that a dense tangle of *Acacia* grows below (Warneke, pers. comm.). Its retention in numbers would depend on rotational clearing of parts of the reserve.

Colonies of koalas appear on the closely settled coast and often are too closely protected from interference by the local communities. The problem with many of these is that they are in small isolated areas of habitat where regeneration of the trees is prevented by dairy cows and, due to the very close protection, the koalas increase in numbers to the point where they overgraze and destroy the mature trees with disaster to the whole colony.

The recently re-discovered New Holland mouse, *Pseudomys novaehollandiae,* promises to show the full cycle of man's unconscious management of an area. Only one had been seen in 130 years when it was found to be abundant near Port Stephens, N.S.W. The reason for its abundance is considered to be a disclimax community of *Acacia* and bracken caused by frequent accidental burning of the forest, but the next phase of the development is to destroy the area during mining for rutile and other minerals. But for the chance encounter by an experienced observer the animal might have disappeared unnoticed for another 130 years (Keith and Calaby, 1968).

Even if the naturalists of the early days had recognized the extreme vulnerability of the small ground-living mammals, it is difficult to imagine how they might have prevented the decline then when we still fail today. Even had reserves been created on the plains and fenced against stock in an age when it was not normal to fence even pastoral holdings, this could hardly have been done before the rabbit invasion which would have destroyed the habitat anyway. In that age, before it was realized that a knowledge of an animal's ecology is essential for its conservation and the management of reserves, before it was even realized that the science of ecology existed, the management of any reserves secured on the plains would have been a very chancy affair. Perhaps the best contribution the early naturalists could have made would have been to ensure that there was documentation of the animals' distribution, adequate collections in the museums, and the establishment of captive colonies against the day when the Governments would be able to secure and staff adequate reserves.

Today there is improved legislation and a wider interest in conservation. There are many reserves of varying value and, although few have been chosen for their wildlife values, this is being rectified in places. Nevertheless, there are very few reserves where the wildlife is adequately studied and properly managed so that it will remain abundant. There is no educational establishment that provides training in the techniques of wildlife management.

VI. Conclusion

In this talk I have tried to show that wildlife conservation is a complex process. A great deal of the wildlife has disappeared and many species are still declining, even though the essential facts to halt their decline are now known.

The mammal fauna of inland New South Wales disappeared very early in the history of settlement due to changes in the environment induced by settlement. It is important to realize that these and similar changes are still going on, not only in the closely settled areas but the remote ones and in the reserves, and that, unless care is taken, other wildlife species will fail.

If wildlife conservation in Australia is to be a fact and not merely a pious hope, a greatly increased effort in research and management is needed.

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A STUDY OF SOME SMUTS OF *ECHINOCHLOA* SPP.

R. A. Fullerton and R. F. N. Langdon
Department of Botany, University of Queensland

(Plates xxiii–xxviii)

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Synopsis

The structure and development of sori of *Ustilago tricophora* on *Echinochloa* spp. have been described. There is no essential difference between the sori formed in floral parts and those occurring in vegetative parts of the host. Sporogenous hyphae growing from the region of the columella form spores progressively, the first formed spores being those just beneath the soral covering. The latter is composed of a fungal sheath overlain by a hispid covering of host origin. A study of the development of the smut in both inoculated plants and naturally infected plants and a scrutiny of herbarium specimens of smut of *Echinochloa* from many parts of the world have shown that the smut which occurs in floral organs or in vegetative parts and which is ornamented by spines is *Ustilago tricophora* (Link) Kunze. The names *Ustilago sphaerogena*, *U. crus-galli*, *U. globigena* and *U. panici-frumentacei* have been applied to smuts which have now been shown to be indistinguishable from *U. tricophora*.

Introduction

Smut fungi are known as parasites of species of *Echinochloa* (Gramineae) in many parts of the world. Seven species of *Ustilago* have been described from these grasses, the earliest being an ovary smut, *Ustilago tricophora* (Link) Kunze on *Echinochloa colonum* from Egypt. Apart from its formal description by Kunze (1830) almost nothing has been written about that smut. Another ovary smut, *Ustilago sphaerogena* Burrill, described in 1888, has been studied briefly by Fischer (1953) and is recorded from New South Wales (Anon., 1958). *Ustilago crus-galli* Tracy & Earle was described in 1895 as affecting both the inflorescence and the vegetative parts, and McAlpine (1910) has recorded the occurrence of this smut in Australia. *Ustilago panici-frumentacei* Bref., *U. globigena* Speg., *U. paradoxa* Syd. & Butl. and *U. holubii* Syd. which were described in 1895, 1898, 1911 and 1935 respectively have a number of points in common with the smuts described in earlier years, though the last mentioned entirely destroys the panicle while the others form sori in only some of the spikelets in an inflorescence. Fullerton (1966) in a short report of his studies of soral development of a smut in parts of the inflorescence of *Echinochloa colonum* referred that smut to *Ustilago sphaerogena* Burrill, using the work of Fischer (1953) as a guide to its identity. Fullerton found that galls similar to those in the floral parts were sometimes developed on the vegetative parts of plants that had been inoculated with the ovary smut known to him as *U. sphaerogena*. He also pointed out that the differences between *U. sphaerogena* and *U. crus-galli* were differences of degree rather than of kind and foreshadowed a taxonomic investigation of smuts of *Echinochloa*.

Species of *Ustilago* on *Echinochloa* have been studied and the results are reported in this paper. An account is given of the development and structure of sori and of sporogenesis in both reproductive and vegetative parts of the host. Using these and other data, a taxonomic revision of certain smuts has been made.

It will be convenient in the following discussions of the smuts of *Echinochloa* to refer to some of the specimens in terms related to the type of sorus, i.e., the symptoms, induced in the host and to the form of the spines developed on the spore wall. Sori developed separately from various organs of the floret are referred to as the *U. sphaerogena* form and sori on vegetative parts or developed in the inflorescence as galls not specific to particular organs are termed the *U. crus-galli* form. Spines on the spores are referred to as being of the *U. sphaerogena* form or the *U. crus-galli* form when they resemble the spines occurring on the spores in the type material of these species.

MATERIALS AND METHODS

Specimens of *Echinochloa colonum* infected by a smut of the *Ustilago sphaerogena* form were collected in the Rosewood district of south-eastern Queensland during the late summer and autumn months (Feb.–May) of 1964 and 1965. In May, 1966, specimens were collected from the Meandarra and Goondiwindi districts of Queensland. Some of the material from these collections was dried, the remainder being preserved in Formalin Acetic Alcohol (FAA).

In October, 1964 and September, 1965, seeds of *Echinochloa colonum* were dusted with spores of the *U. sphaerogena* form of smut and planted in a garden plot at St. Lucia. A number of these plants developed sori. A detailed study was made of the morphological and anatomical features of the various soral types represented. Sori in different stages of development were fixed in FAA. Material to be sectioned was dehydrated in a tertiary butyl alcohol series and embedded in paraffin wax of MP 54–56° C. Blocks were serially sectioned at 10μ, sori being cut both longitudinally and transversely. Two methods of staining were used, Safranin-Fast Green (Johansen, 1940) and Periodic acid-Schiff's Reagent (Conn, 1960) with a Fast Green counterstain. Both methods were satisfactory for differentiating mycelium and host tissues.

Details of spore formation were elucidated by examining the appropriate parts of the serial sections by phase contrast microscopy. Some useful supplementary information was obtained by hand teasing young sori, treating the sporogenous hyphae with concentrated potassium hydroxide to remove gelatinous material, mounting in clear lactophenol and examining by phase contrast microscopy.

For the taxonomic work on the smuts of *Echinochloa* spp. specimens from a number of herbaria were obtained. These were supplemented by material collected from plants in the field and smut-inoculated plants grown in garden plots in the grounds of the University of Queensland at St. Lucia, Brisbane. Spores for microscopic examination were mounted in Shear's mounting fluid (Graham, 1959). Herbaria from which specimens have been made available are as follows: United States National Fungus Collection, U.S.D.A., Beltsville (BPI); National Herbarium, Department of Agricultural Technical Services, Republic of South Africa (PRE), New South Wales Department of Agriculture, Rydalmere (DAR); Instituto de Botanica C. Spegazzini, La Plata, Argentina (LPS), Commonwealth Mycological Institute (IMI); Department of Botany, University of Queensland (BRIU).

MORPHOLOGY OF SORI

The sori on *Echinochloa* spp. are readily detected because parts of the plants where the fungus sporulates increase in size and bear numerous hairs on the surface. The hirsute nature of the soral covering was noted by Kunze (1830) when he described *Ustilago tricophora,* and similar observations have been made Burrill (1888), Tracy and Earle (1895) and

Mundkur (1943) in their descriptions of various species of *Ustilago* which occur on *Echinochloa* spp. Magnus (1896) in describing the smut galls on *E. crus-galli* referred to the presence of a sheath of fungal hyphae underlying the host tissue that covered the swollen areas. McAlpine (1910) also has commented briefly on the structure of the galls studied by Magnus but added no new information of any significance. The development of sori in vestigial ovaries in staminate spikelets of *Buchloe dactyloides* infected by *Tilletia buchloeana* was recorded by Norton (1896). Hansing and Lefebvre (1941) described sori of *Sphacelotheca sorghi* and *S. cruenta* where stamens as well as the ovaries had been transformed by the smut and they referred also to sori developing in the rudimentary ovaries of staminate spikelets of *Andropogon furcatus* infected by *Sorosporium everhartii*. Fullerton (1966) has shown that smuts of *Echinochloa* spp. which could be referred to *Ustilago sphaerogena* were not confined to the ovary but spored in various organs of the floret and in stems and leaves.

STRUCTURE OF SORI IN INFLORESCENCES

Since the form of the sori is influenced by the structure of the organs or parts in which sporulation occurs, the morphology of floral parts of *Echinochloa colonum* is described briefly here. Spikelets consist of two florets, the lower floret being sterile and the upper one fertile. The sterile floret has a lemma and a membranous palea only. The fertile floret has a lemma which is hard and shiny with inrolled margins. With a thin palea it encloses the floral organs. Small unicellular hairs occur on the outer surfaces of the glumes, the sterile lemma and the pedicel of the spikelet below the glumes. On the axes of the panicles are long, pointed, unicellular hairs which arise in the epidermis.

The ovary is smooth, sub-globose and glistening white, about 0·5 mm. long, with two styles and feathery stigmas. The ovary wall surrounding the ovule is two cells thick. The ovule is anatropous with two integuments surrounding the nucellus. There are three stamens and two lodicules. The latter are flattened and fan-shaped, up to 0·5 mm. long, expanding at the time of anthesis to 1·5 mm. diameter and becoming cup-shaped.

Macroscopic features of sori

Sori in inflorescences may be restricted to the floral parts of a minority of spikelets, a condition which can be termed the *Ustilago sphaerogena* form of smut expression (Plate XXIII).

Where sori replace organs of the floret, a spikelet bears a number of globose, green, hispid sori up to 3 mm. diameter. In any infected spiklet there are up to six sori of varying dimensions. When the maximum number of sori is developed one sorus occupies the position of the ovary, three are present in positions where stamens usually are placed, and a further two occur lower down on the axis in the position normally occupied by lodicules (Plate XXIII). There is, however, great variation in this pattern. Not uncommonly fusion of smutted floral organs leads to the formation of a large and somewhat irregular sorus on the apical part of which may be seen remnants of tissue recognizable as styles or stigmas, stamens or lodicules. Sometimes parts of the lemma and palea are incorporated in such a sorus. The sterile floret sometimes is changed, the palea being abnormally hairy at the base. A small hispid structure, the origin of which could not be determined, sometimes develops between the lemma and palea. All sori retain their green colour until maturity, when the soral covering splits irregularly to disclose a dark spore mass in which one or more columellae become visible as the spores are dispersed.

A second sort of smut expression in inflorescences is that which might be termed the *Ustilago crus-galli* form since sori occur in stems and leaves and extend to inflorescences in some plants only. In the latter case almost every spikelet in the inflorescence may be smutted and those not affected are usually infertile. Various components of the spikelets may be affected individually or in combinations to form a large number of irregularly shaped sori. Sporulation in the sterile florets is common, lemmas and paleas being sites for the formation of sori. Phyllody is a characteristic feature. This is partly due to the extension of the distal ends of many sori into flattened green leaf-like structures, but short vegetative shoots also grow from the axis of the inflorescence. Unlike the sori of the *U. sphaerogena* form, these sori do not maintain a regular shape for any one organ of origin and there is considerable disparity between sori. Because of phyllody and the range of plant structures involved it is difficult to identify with certainty the origin of many of the individual sori (Plate XXIV).

Microscopic appearance of sori

The soral covering with layers of host and of fungal origin is a feature common to all sori. The structure of the sori and of the collumellae contained therein varies according to the part of the plant in which sporulation has occurred.

The columella

The term columella is used in reference to the region where the fungus and host tissues are in close contact. The columella in sori developed from organs of the floret is a columnar structure extending upwards from the base of the sorus and ending bluntly in the soral cavity. In sori in vegetative tissues and sometimes in sori in inflorescences (the *U. crus-galli* form) the columella is a pad of tissue with an undulating surface with which hyphae are in close contact. In each case the columella is composed of cells of the host (parenchyma and tracheal elements) and abundant intercellular and intracellular hyphae.

The soral covering

The soral covering consists of two distinct layers, the outer one being tissue of the host plant and the inner layer a fungal sheath (Plate XXIV). The fungal sheath lining the soral cavity is a dense mass of interwoven hyphae which can be separated from the host tissue by gentle manipulation with needles. This sheath is present at an early stage of sporulation and remains virtually unchanged in thickness as the sorus expands and matures. The thickness of the host layers and the fungal layers in soral coverings varies, as shown in Table 1. The host tissue has three to five layers of cells which vary in size, ranging in diameter from 10 to 30μ. In some places large epidermal cells are grouped together to form cushions. It is from cells

TABLE 1
Thickness of layers in the soral covering

Type of sorus	Thickness of host tissue layer	Thickness of fungal layer
	(All figures in microns)	
Fully developed ovary sorus ..	30–50	30–50
Dehiscing sorus in ovary	10–20	30–40
In stamen	50 (100 at cushions)	10–20
Fused ovary and stamen	10–40	10–20
In lodicule	30–80	10–30

of these cushions that most of the hairs of the soral covering arise, although soral hairs occasionally develop from smaller epidermal cells. The hairs are unicellular, elongate, tapering and sharply pointed structures. They vary in length and usually reach 1 to 2 mm. with a basal diameter of 16 to 20μ. These hairs resemble those found on axes of the inflorescence and are much larger than the hairs found on parts of normal spikelets. While spore formation progresses the soral coverings increase to accommodate the expanding spore mass. As the sorus approaches maturity, cells of the host tissue distort and flatten as they dry and in some areas they may peel off, exposing the fungal sheath which then is the only covering over the spores.

Sori in ovaries

Sori developed from the ovary alone have in most cases a distinct papilla situated on the distal end of the sorus and bearing two styles and stigmas. A light coloured strip extending from this papilla down the anterior side of the sorus can be seen in practically all sori of this type. In this region there are two walls enclosing a flattened, elongate cavity. The outer wall enclosing this cavity consists of three to four layers of parenchymatous cells bounded inside and out by a distinct epidermis. There is profuse hair development on both sides of the outer wall and also on the epidermis of the inner wall.

Dissection showed that remnants of an ovule were often present in this cavity which therefore has been interpreted as being the distorted locule of the ovary. The form and the position of the ovule varied. In some sori it was located in the papillate distal part of a sorus, somewhat removed from the region of sporulation. Its structure then was approximately that of the ovule in a non-infected ovary except that the integuments were densely clothed on both sides with short, hyaline, unicellular hairs. In other sori the ovule appeared to be placed directly on the wall of the sorus and the normal morphological characters of the ovule were no longer evident (Plate xxv, *a, b*).

In the early stages of development of sori in ovaries, mycelium sometimes proliferates in the region of ovule attachment. In other cases the mycelium grows into the funicle and may reach the base of the nucellus. The consequent amount and type of distortion appear to be related to the position in the ovary at which massing of mycelium occurs.

Sori in stamens

These sori were up to 2 mm. diameter, globose to flask-shaped, often surmounted by a filament up to 0·5 mm. long and bearing an anther. Such anthers did contain pollen, although it was not determined whether this pollen was fertile.

The first evidence of infection in filaments was a slight swelling and marked hairiness close to the base of the filament. At a later stage a mass of mycelium was found to be present inside the swollen portion. Further growth resulted in the formation of a globose sorus with a typical cylindrical columella inside (Plate xxvi).

Alteration of the staminal filament may extent for some distance above the sorus proper, the remaining length of filament often being distinctly swollen, tapering from sorus to anther and exhibiting marked hairiness.

Sori in lodicules

Sori in lodicules are up to 2 mm. diameter, but even in a single floret there may be one much bigger than the other. The fungal sheath and its overlying hispid covering are similar to those of sori in other organs. The columella is broadly triangular in section and flattened in the plane of the broad axis of the normal lodicule.

Other sori in inflorescences

The irregular sori of the *Ustilago sphaerogena* form originate in the floral axis, and the regions of sporulation may include basal parts of floral organs, lemmas and paleas. The soral cavity is continuous although invaginations of the soral wall indicate where various host parts have grown together. The columella of these compound sori is broad at the base and divided apically, the points corresponding to the several components of the sorus.

Some sori in inflorescences are not confined to the spikelets and resemble the sori in vegetative parts of the plant. These sori of the *Ustilago crus-galli* form, whether in inflorescences or in vegetative parts, have the soral covering and the columella of the form already described. Other matters of structure are discussed in a later section.

STRUCTURE OF SORI IN VEGETATIVE PARTS

Sori form as irregular blister-like swellings on various vegetative parts of the plant (Plate VII *a, b*). They are usually largest and most numerous, often coalescing, in the nodal regions but occur commonly on the leaf bases, leaf blades and internodes of the stem. The sori, which have green, hispid coverings, vary from smoothly rounded to cerebriform. At nodes and on leaf bases sori may reach a size of 1·0–2·0 cm. diameter. On leaf blades and in internodal regions sori are usually much smaller, 1–several mm. diameter, occurring as isolated blisters or by coalescence forming sori which lie along the leaf or stem. Normal inflorescences are commonly produced by the infected culms. The presence of smut in nodal regions of these culms may stimulate development of axillary buds leading to a rosette of short, leafy axillary shoots emanating from a complex mass of sori. Inflorescences are seldom produced from such shoots. The microscopic structure of the sori is the same as that of galls in inflorescences except for certain details of the form of the columella. The points of difference are mentioned below.

SPORE FORMATION

Kukkonen and Vaissalo (1964) have reviewed the rather limited information that there is on spore formation in smut fungi. Their own electron microscope studies of sporogenesis in *Anthracoidea aspera* confirm earlier work on species of *Ustilago* by De Bary (1887), Lutman (1910) and Hutchins and Lutman (1938) who found that spore initials were embedded in an almost homogeneous gelatinous mass produced by swelling of the sporogenous hyphae. Magnus (1896) and McAlpine (1910) have recorded some details of development of *Ustilago crus-galli.* In that smut gelatinization of hyphae was observed, and weight was given to the supposed basipetal formation of spores in the sporogenous hyphae. The latter observation was the reason for these authors' inclusion of the species in the genus *Cintractia.* De Bary (1887) defined the genus *Sphacelotheca,* emphasising the columella and the fungal sheath surrounding the spore mass as characters by which it was distinguished from *Ustilago.* He said that the development and mature structure of the spore mass of *Sphacelotheca* were the same as those of *Ustilago.* For the latter he described the gelatinization of hyphae synchronously with or even before the basipetal development of the spores.

During the present investigation the modes of spore formation of sori of the *Ustilago sphaerogena* and *U. crus-galli* forms respectively were found to be essentially the same. Sori of the former tend to be symmetrical about the columella while the latter usually have the columella oriented so that the sporulation is above it and not around it. There is a continual production of hyphae at the columella. The walls of these hyphae become gelatinized and hyphal characters disappear. Spore initials then appear in the gelatinous matrix a short distance from the columella, and when first visible are opaque bodies about 3μ in diameter, almost indistinguishable from the rest of the matrix. The spore initials then rapidly expand to a size approaching that of mature spores. Concurrent with the development and expansion of spore initials is the formation of dense echinulations which outline the spores, no spore walls being visible at this stage. Soon after the appearance of echinulations the spore walls become well defined. At first hyaline, they soon become pigmented. As the initials are expanding and maturing, the gelatinous matrix gradually disappears until the spores are connected by thin strands of gelatinous material. In young sori spore masses are agglutinated and possibly the cementing material may be remnants of this matrix. In older sori spores become powdery.

The production of sporogenous mycelium in young sori proceeds at a greater rate than its gelatinization. Thus the columella becomes surrounded by mycelium which is hyaline, thick walled, septate, much branched and 1·0–3·0μ in diameter. It closely resembles the mycelium of the sheath that surrounds the spores.

The gelatinization of sporogenous mycelium that grows around or above the columella tends to be concentrated in a number of discrete regions. The continued growth of mycelium between the regions of rapid gelatinization produces hyphal columns which extend into the developing sorus, the columns being more numerous in the sori in vegetative parts than in floral sori. These columns in which the hyphae lie parallel to one another are associated with crests on the undulating surface of the columella (Plate XXVII). Gelatinization of hyphae of the columns later reduces considerably the extent to which the columns penetrate out into the mature spore mass.

During development of the sorus, spores in all stages of formation can be found. When production of sporogenous mycelium ceases, spore formation continues and mature spores are finally developed very close to the columella.

TAXONOMY

Ustilago tricophora (Link) Kunze. Flora, 13, 369. 1830. *Caeoma tricophorum* Link in Willdenow, Sp. Pl., 6 (2), 3. 1825. *Ustilago sphaerogena* Burrill in Saccardo, Sylloge Fung., 7, 468. 1888. *Ustilago crus-galli* Tracy & Earle, Bull. Torrey bot. Club, 22, 175. 1895. *Ustilago panici-frumentacei* Brefeld, Unters. Gersammt. Mykol., 12, 103. 1895. *Cintractia seymouriana* Magnus, Ber. dt. bot. Ges., 14, 217. 1896. *Cintractia crus-galli* (Tracy & Earle) Magnus, Ber. dt. bot. Ges., 14, 392. 1896. *Ustilago globigena* Speg., Anal. Mus. nac., 6, 208. 1898. *Cintractia sphaerogena* (Burrill) Hume, Proc. Iowa Acad. Sci., 9, 233, 1902. *Ustilago tricophora* (Link) Kunze var. *pacifica* Lavroff, Trudy biol. nauchno-issled. Inst. tomsk. gos. Univ., 2, 9. 1936. *Ustilago tricophora* (Link) Kunze var. *crus-galli* (Tracy & Earle) Lavroff, Trudy biol. nauchno-issled. Inst. tomsk. gos. Univ., 2, 9. 1936.

Sori in organs of the floret, in parts of the inflorescence or in vegetative parts, variable in size and form, with a hispid covering of host tissue. Spore mass agglutinated at first, later pulverulent, surrounded by a fungal sheath up to 50μ thick. Spores globose, subglobose or ellipsoid, dark, 6–14μ at greatest diameter, ornamented with spines varying in density of distribution, length and shape.

Specimens examined: On *Echinochloa colonum* (L.) Link, Egypt, Ehrenberg, no date (IMI); Sudan, S. A. J. Tarr, 12. x. 1954 (IMI 59760); Louisiana, U.S.A., Atkinson & Forbes, 28. viii. 1936 (BPI); Louisiana, U.S.A., C. R. Ball, 16. viii. 1898 (BPI); Louisiana, U.S.A., I. L. Forbes, 13. ix. 1940 (BPI); Cuba, F. S. Earle, 9. x. 1924 (BPI); Amberley, Qld., R. F. N. Langdon, 29. iii. 1947 (BRIU 415); Lawes, Qld., W. J. Bissett, 28. ii. 1941 (BRIU 501); Nambour, Qld., J. C. Johnson, 26. iii. 1951 (BRIU 270); Cleveland, Qld., O. R. Byrne, 1951 (BRIU 1209); St. Lucia, Qld., R. A. Fullerton, iii. 1966 (BRIU 2283), iii. 1966 (BRIU 2284), iii-iv. 1966 (BRIU 2286), 3. iv. 1966 (BRIU 2287); Meandarra, Qld., R. A. Fullerton, 1. v. 1966 (BRIU 2288); Goondiwindi, Qld., R. A. Fullerton, 2. v. 1966 (BRIU 2289, 2290); Pilliga, N.S.W., J. A. O'Reilly, vi. 1958 (DAR 4863). On *Echinochloa turneriana* Domin., Windorah, Qld., P. J. Skerman, 26. vii. 1946 (BRIU 399), 24. vi. 1949 (BRIU 529). On *Echinochloa holubii* (Stapf) Stapf, Transvaal, Sth. Africa, I. B. Davy, 15. iii. 1912 (PRE 2247, BPI) (TYPE, *Ustilago crus-galli* Tracy & Earle var. *minor* Zundel). On *Echinochloa walteri* (Purch) Heller, Connecticut, U.S.A., G. M. Reid, 14. ix. 1919 (BPI). On *Echinochloa crus-galli* (L.) Beauv., Utah, U.S.A., Tracy & Evans, no. 651, 8. x. 1887 (BPI) (TYPE, *Ustilago crus-galli* Tracy & Earle); Illinois, U.S.A., A. B. Seymour, no. 1892, ix. 1884 (BPI) (TYPE, *Ustilago sphaerogena* Burrill); Argentina, C. Spegazzini, no. 3025, 13. v. 1917 (LPS) (*Ustilago globigena* Speg., det. C. Spegazzini); Nanking, China, F. L. Tai, 3. x. 1929 (BPI); Japan, quarantine interception at Seattle, U.S.A., iii. 1941 (BPI); Mandalay, Burma, A. McKerrel, 17. viii. 1922 (BPI); Arizona, U.S.A., D. F. Cook, 22. ix. 1923 (BPI); California, U.S.A., W. W. Mackie, xii. 1928 (BPI); Colorado, U.S.A., A. S. Hitchcock, 28. viii. 1906 (BPI); Colorado, U.S.A., E. Bartholomew, 4. ix. 1914 (BPI); Connecticut, U.S.A., G. P. Clinton, 22. ix. 1906 (BPI); Connecticut, U.S.A., G. L. Zundel, 30. ix. 1926 (BPI); Florida, U.S.A., H. W. Wedgeworth, 3. vii. 1940 (BPI); Illinois, U.S.A., M. B. Waite, 2. x. 1888 (BPI); Indiana, U.S.A., F. D. Fromme, 1. x. 1913 (BPI); Iowa, U.S.A., L. H. Pammel, 20. ix. 1909 (BPI); Maryland, U.S.A., H. H. McKinney, 25. x. 1944 (BPI); Massachusetts, U.S.A., A. B. Seymour, 10. ix. 1910 (BPI); Minnesota, U.S.A., D. Griffiths, viii. 1896 (BPI); Missouri, U.S.A., J. B. Norton, ix. 1896 (BPI); Nebraska, U.S.A., T. A. Williams, 11. ix. 1890 (BPI); Nevada, U.S.A., O. F. Smith, viii. 1940 (BPI); New Jersey, U.S.A., F. L. Scribner, 24. ix. 1880 (BPI); New Mexico, U.S.A., E. W. D. Holway, 13. ix. 1896 (BPI); New York, U.S.A., R. Latham, 1. x. 1916 (BPI); Oklahoma, U.S.A., W. H. Long, 28. xii. 1909 (BPI); Oregon, U.S.A., J. R. Kienholz, 15. ix. 1937 (BPI); Pennsylvania, U.S.A., G. L. Zundel, 22. ix. 1938 (BPI); Utah, U.S.A., A. D. Garrett, 16. x. 1904 (BPI); Virginia, U.S.A., P. Klaphaak, 12. x. 1922 (BPI); Washington, U.S.A., W. N. Suksdorf, 3. x. 1894 (BPI); Washington, D.C., U.S.A., M. B. Waite, 30. x. 1888 (BPI); Wyoming, U.S.A., A. Nelson, 27. viii. 1904 (BPI); Spain, collector not stated, viii. 1946 (BPI); Morocco, G. Malencon, 9. xi. 1932 (BPI); Nigeria, A. Thompson, 2. iv. 1920 (BPI); Cape Province, South Africa, A. O. D. Mogg, 7. iii. 1934 (PRE 27384; and BPI, as *Ustilago crus-galli* var. *minor* Zundel, det. Zundel); Argentine, T. Rojas, v. 1906 (BPI); New York, U.S.A., R. Latham, x. 1922, and D. Reddick, 25. x. 1941 (BPI, as *Ustilago crus-galli* var. *minor* Zundel, det. Zundel); Transvaal, South Africa, A. O. D. Mogg, 3. vii. 1934 (BPI, as *Ustilago crus-galli* var. *minor* Zundel, det. Zundel); Richmond, N.S.W., W. M. Carne, iii. 1911 (DAR 721), A. Murphy, v. 1961 (DAR 6152); Yenda, N.S.W., collector not stated, iv. 1934

(DAR 1002); Yanco, N.S..W., P. Kable, iii. 1962 (DAR 6981); Baulkham Hills, N.S.W., collector not stated, 1956 (DAR 4862). On *Echinochloa crus-galli* (L.) Beauv. var. *frumentaceae* W. F. Wight, Aspley, Qld., J. G. Morris, iv. 1952 (BRIU 583).

In addition to the specimens already listed, 32 other specimens on *Echinochloa crus-galli* from localities in 14 States of the United States of America were examined. These fungi did not differ significantly from the collections on that grass from the U.S.A. which have been formally listed above.

Notes on specimens examined

(*a*) *Type specimens*

Ustilago sphaerogena Burrill. The specimen consists of two smutted spikelets. Floral parts are affected individually. In one spikelet there is a large sorus in the position of the ovary, bearing remnants of the styles on its papillate apex. Three smaller sori surround the large central sorus, occupying the positions of the stamens. Each of these three sori bears an anther on a thin projection from the apex. Two small sori occupy the positions of the lodicules. All sori are covered by hairy tissue of the host. The other spikelet bears several sori occupying the positions of the floral parts. The spores are globose to subglobose, 6–12μ diameter, densely and sharply echinulate (Plate XXVIII).

Ustilago crus-galli Tracy & Earle. The specimen is a small length of stem with a single node and part of a leaf. An axillary shoot is developed from the node. Sori are developed in two hairy leaf galls each about 2·0 mm. diameter. The spores are globose to subglobose, 9·0–13·5μ diameter, echinulate. The spines are broader at the base (i.e. blunter) and less densely crowded than in *U. sphaerogena* (Plate XXVIII).

Ustilago crus-galli Tracy & Earle var. *minor* Zundel. The spores of this specimen are not distinguishable from those of type material of *U. crus-galli.*

(*b*) *Authentic specimens*

Ustilago globigena Speg. The specimen is part of an inflorescence with a few smutted spikelets. The sori are developed in floral parts and resemble closely the sori found in the type specimen of *U. sphaerogena.* The spores are not smooth, as stated by Spegazzini (1899), but are echinulate and as suggested by Hirschhorn (1939) are very similar to those of *U. sphaerogena.*

(*c*) *Other specimens*

Ustilago tricophora (Link) Kunze. Type material could not be located. By courtesy of the Director of the Commonwealth Mycological Institute we have been able to view a slide made by one of his staff from a smutted specimen of *Echinochloa colonum* which is now in a phanerogamic herbarium (not specified). The specimen had been collected in Egypt by Ehrenberg, who was also the collector of the material from Egypt on which *Ustilago tricophora* is based. There is a strong possibility that Ehrenberg's collection from Egypt went partly to Link and partly to a phanerogamic herbarium, especially as the inflorescence smut of *Echinochloa* affects only a small proportion of the spikelets. The spores of this specimen are globose to subglobose, 9–11μ diameter and densely echinulate. The spines are slightly coarser and not quite as long as the spines of *Ustilago sphaerogena.* A specimen of smut on *Echinochloa colonum* from the Sudan is very similar to type material of *Ustilago sphaerogena,* as also is smut on *Echinochloa crus-galli* from Cape Province, Union of South Africa. It is believed that these specimens from Africa, including one in the type host from the type locality of *Ustilago tricophora,* can be accepted as reliable evidence as to the characteristics of *Ustilago tricophora.*

Ustilago sphaerogena Burrill and *U. crus-galli* Tracy & Earle. A majority of the specimens received under the name *Ustilago sphaerogena* bore sori in the floral parts which were the same as those seen in the type specimen of this fungus. The spores also were characteristic of that species. Similarly, most of the specimens which were labelled *Ustilago crus-galli* had the soral and spore characters of the type material of that species. The dimensions of the spores in some specimens varied a little from those of the type specimens of these two species. Specimens of the *U. sphaerogena* form in all except three cases had spores which were within the limits of size of spores of the type specimen, and these exceptions exceeded the upper limit by only one micron. With *U. crus-galli* material the type specimen had spores ranging from 9 to 13·5μ diameter but in a majority of specimens spores with lower limits down to 6μ were found. A few specimens included spores which had their longest dimensions one or two microns greater than what were observed in the type specimen. Spores which exhibited these deviations from the limits of size of the type specimen were nearly all markedly subglobose or tending to ellipsoid. For both species the variations in dimensions are not regarded as being of any significance. All specimens include spores with dimensions within the range exhibited by the type specimens.

The type specimen of *Ustilago sphaerogena* exemplifies a form of *Echinochloa* smut where sori are developed in the floral parts alone. The ornamentation of the spores of certain specimens with these symptoms was not typical of *Ustilago sphaerogena.* In some the spines were less densely spaced and the form of the spines tended towards that found in spores of *U. crus-galli,* i.e., somewhat shorter and more broadly based than in *U. sphaerogena.* Three specimens from Louisiana, U.S.A. (collected by Ball in 1898, Atkinson and Forbes in 1936 and Forbes in 1940 respectively) exhibited this intermediate condition of the spines. In specimens from Cuba (coll. Earle, 1924), China (coll. Tai, 1929) and Spain (collector not stated, 1946), the ornamentation of the spores was typical of that found in spores of type material of *U. crus-galli.* A specimen from Nigeria (coll. Thompson, 1920) had spores with the *U. crus-galli* form of spines but with the spines more sparsely placed than in *U. crus-galli.* A few spores of this specimen were smooth. A collection from Oregon, U.S.A., by Kienholz in 1937 which had the *U. sphaerogena* form of sorus had very short, broadly based and sparsely placed spines which could be considered to be within the range of variation of *U. crus-galli,* and indeed this specimen, identified by R. Sprague, came to us under the name *U. crus-galli.*

Two specimens with stem sori typical of *Ustilago crus-galli* (Burma, coll. McKerrel, 1922, and Connecticut, U.S.A., coll. Clinton, 1906) had spores with ornamentation tending towards the form typical of *U. sphaerogena.* The former was labelled *U. sphaerogena,* the latter *U. crus-galli.* Both are intermediate in form between the "typical" conditions of those species.

Specimens of smut on *Echinochloa colonum* from Queensland included some specimens collected in the countryside and others from plants grown in plots at St. Lucia. Most plants from the field bore sori of the *Ustilago sphaerogena* form only and had spores which conformed to those described for *U. sphaerogena.* Exceptions to this were BRIU 2288 which had sori on vegetative parts only, BRIU 2289 which had sori in both vegetative parts and inflorescences, the sori in the latter being of two kinds, the *U. crus-galli* form and the *U. sphaerogena* form, and BRIU 2290 with sori of the *U.*

crus-galli form in both vegetative parts and inflorescences. Plants grown from smut-inoculated seed also included some which bore sori of both the *U. crus-galli* and the *U. sphaerogena* forms (BRIU 2283, 2284, 2286) and one with the *U. crus-galli* form of sorus in vegetative tissues only (BRIU 2287). The ornamentation of the spores in these specimens was variable. In some sori forms of spine were found which were intermediate between the *U. sphaerogena* and *U. crus-galli* forms in width and in distribution on the spore surface. In others, spores of the typical *U. crus-galli* form were found. In essence, the spores and the sori on plants inoculated with spores from the *U. sphaerogena* form of sorus showed variability covering the range of characters which earlier workers had used to delimit two species, namely *U. sphaerogena* and *U. crus-galli.*

Notes on synonymy

Three names have been listed as synonyms of *Ustilago tricophora,* namely *U. panici-frumentacei, U. tricophora* var. *pacifica* and *U. tricophora* var. *crus-galli,* although type or authentic specimens have not been seen. Mundkur (1943) has studied *U. panici-frumentacei* and considered its relationship to *U. tricophora.* A small difference in spore size was the only character by which Mundkur could differentiate these two species. Our present studies do not support a concept of species differentiation by size differences of about one micron. Lavroff (1936) included *U. panici-frumentacei* with *U. tricophora,* giving it varietal status in the latter species. He also reduced *U. crus-galli* to the status of a variety of *U. tricophora* (Petrak, 1950).

Mundkur (1943) after examining type material of *U. paradoxa* reported that its spores were entirely smooth. He noted that its mode of germination differs from that of *U. crus-galli* and *U. panici-frumentacei.* In our studies only two specimens, one from Nigeria (BPI) and the other from Queensland (BRIU 2284), have exhibited spores lacking spines. In these fungi the smooth spores were exceptional, the great majority being echinulate. *U. paradoxa* is accepted as being distinct from *U. tricophora* although its habit of attacking only some spikelets in an inflorescence and its hispid soral covering indicate its possible relationship to *U. tricophora.*

Discussion

Several species of *Ustilago* have been described from *Echinochloa* from various parts of the world. One of them, *U. holubii,* destroys the inflorescence and the sorus may extend into the stem below. This characteristic and the smooth to minutely verruculose spores distinguish it from other smuts of these grasses. Common to the rest of the species of *Ustilago* described from *Echinochloa* is a hispid membrane, developed from tissues of the host, covering the fungal structures in the region of sporulation. In a taxonomic study of smuts of this kind we have retained *Ustilago paradoxa,* which has smooth spores, and have grouped the other smuts to make a single species, *Ustilago tricophora.* The description of the latter species has been amended in this paper and it now includes all those smuts of *Echinochloa* which form sori with coverings formed conjointly of fungal tissue and hispid tissue of host origin and which have spores ornamented by spines.

Certain smuts of *Echinochloa* may evoke similar host reactions which are reflected by the uniformity of the host tissues that cover sori and by resemblances between sori on various parts of the plant. Apparent differences in soral structure, e.g. in shape and size, are related to the organ or part of the plant in which sporulation has occurred. Similarities in soral characters are not in themselves indicative of a taxonomic relationship between smuts. Evidence for such a relationship for the smuts now referred to *Ustilago tricophora* is to be found in the experimental work on inoculation of plants with smut, in patterns of sporogenesis in the different forms of sori, and in comparisons of spore characters of a large number of herbarium specimens.

It has been shown that when *Echinochloa colonum* was inoculated with spores from the *Ustilago sphaerogena* form of sorus individual plants bearing sori of both the *U. sphaerogena* and the *U. crus-galli* forms could be found. In these sori supposedly typical of two different species of smut, there were marked similarities in the development of fungal structures, e.g., columella and fungal sheath, and in sporogenesis. In the inoculated plants as well as in the herbarium specimens, spores representing the intergrades between the *U. sphaerogena* form and the *U. crus-galli* form were found. The extreme cases were the occurrence of the *U. crus-galli* form of spores in sori in the *U. sphaerogena* form of sorus, and vice versa.

Fullerton (1966), who reported on the structure of the sori of the *Ustilago sphaerogena* form of smut of *Echinochloa colonum* suggested that *Sphacelotheca* might be a genus more appropriate than *Ustilago* for the species of smut he studied. The basis for that suggestion was that the smut of *Echinochloa* appeared to have the characteristics of spores enclosed by a fungal sheath and basipetal formation of spores around a columella which in recent years have been accepted as characteristic of the genus *Sphacelotheca* (Fischer, 1953; Fischer and Holton, 1957). Hirschhorn (1939) and McAlpine (1910) have doubted the validity of *Sphacelotheca* as a genus distinct from *Ustilago.* McAlpine noted that a columella occurs in other smuts such as species of *Cintractia* and *Sorosporium,* and that there are ". . . various gradations in the formation of a fungus membrane enclosing the spores . . .". He indicated that there were difficulties in deciding whether a sheath should be regarded as evanescent or persistent. Concerning the other characters for distinguishing *Sphacelotheca* from *Ustilago,* namely the basipetal formation of spores in the former which is lacking in the latter, there seems to be no grounds for accepting such a distinction. De Bary (1887) declared that in the smut on which *Sphacelotheca* was based, namely *Ustilago hydropiperis,* ". . . the development and mature structure of the spore-mass are the same as those of *Ustilago* . . .". In the sections cut from *Ustilago tricophora* in various stages of development we have noted that for some time there is production of sporogenous hyphae around the columella. Spores develop from the first-formed hyphae and are pushed outwards as more sporogenous hyphae grow. Spore formation is a continuous process that occurs progressively while sporogenous hyphae are forming rather than being the basipetal formation of spores from a mass of pre-formed hyphae, progressing from the region of the fungal sheath towards the columella. The basipetal formation of spores often quoted as a characteristic of the genus *Sphacelotheca* may be more apparent than real. Further studies of sporogenesis in smut fungi which at present are included in *Sphacelotheca* are in progress. For the present no change in the generic position of the species *tricophora* will be made.

Acknowledgements

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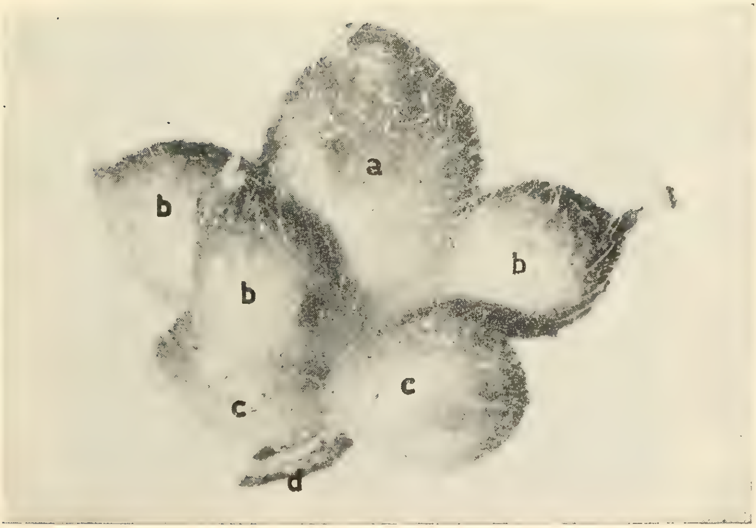
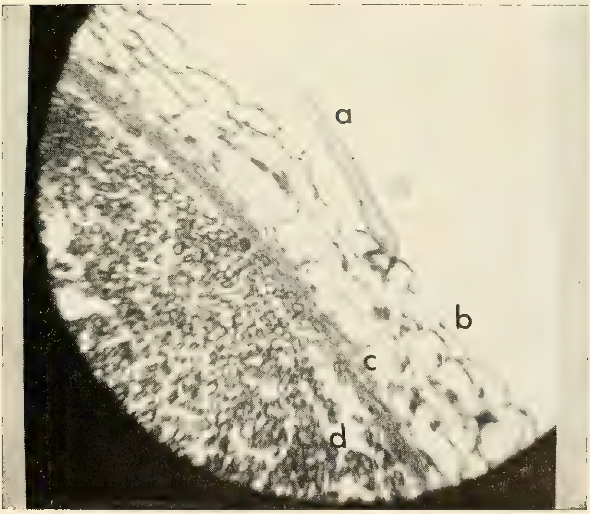
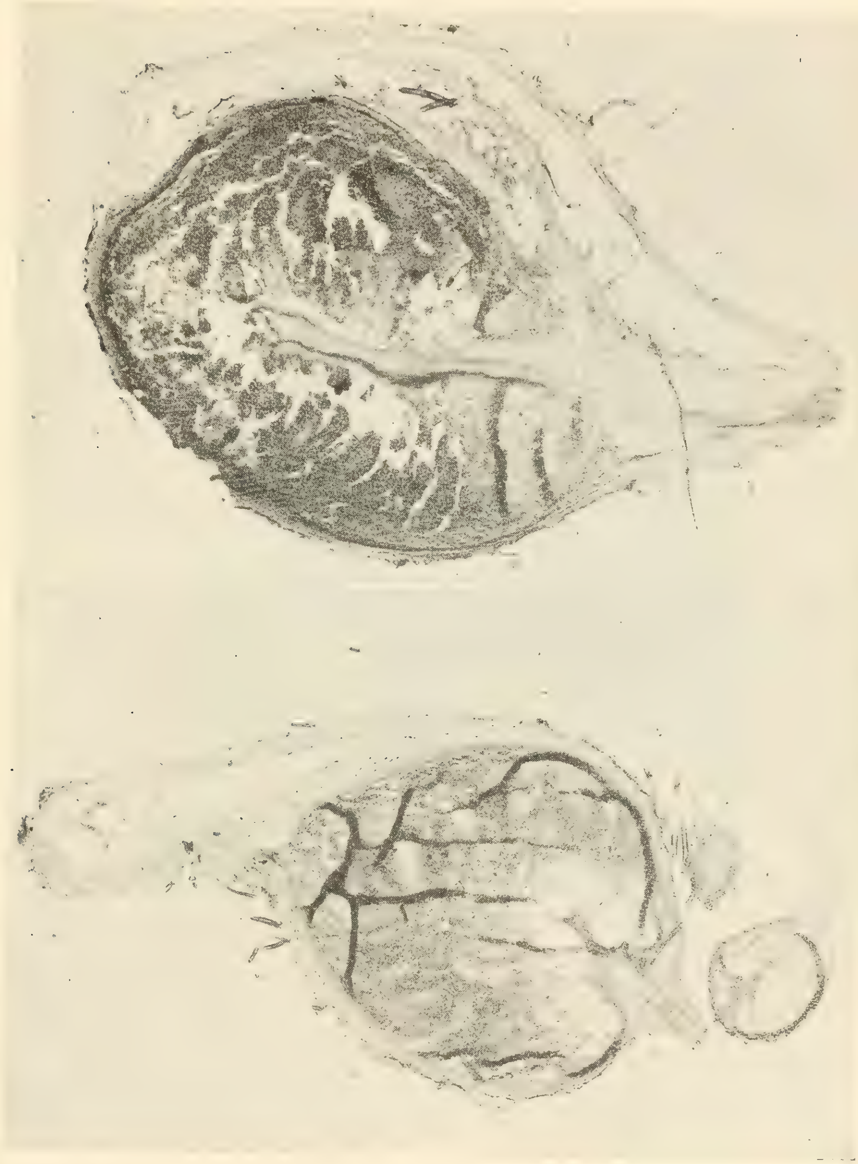


Top.—Echinochola colonum with *Ustilago sphaerogena* form of smut.
Bottom.—Sori developed in floral parts of *Echinochloa colonum.*

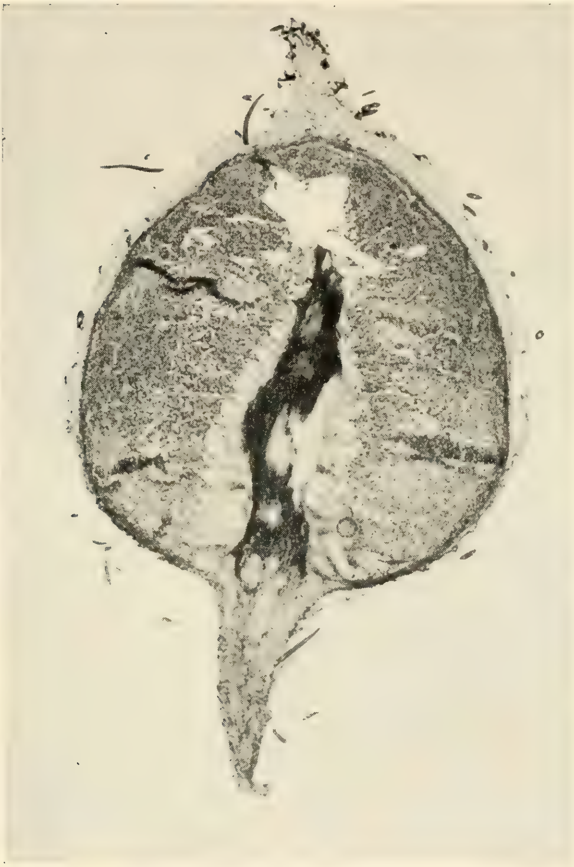


Top.—*Echinochloa colonum* with *Ustilago crus-galli* form of smut.

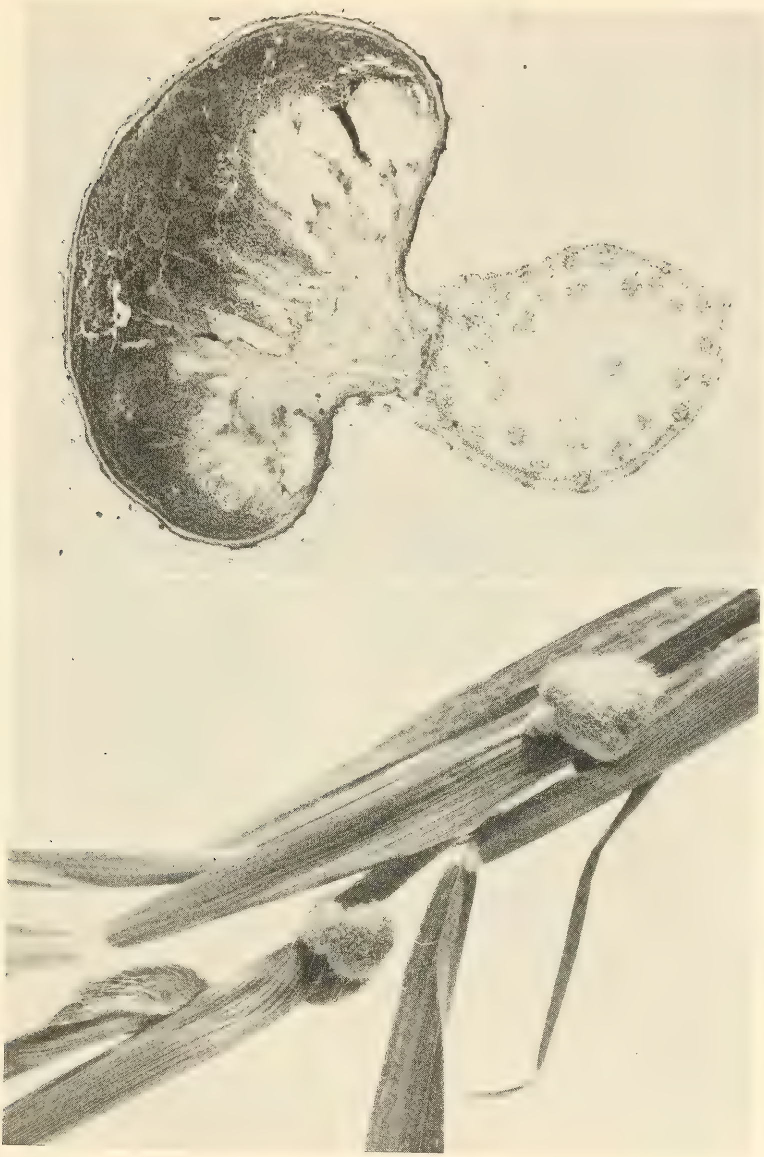
Bottom.—Section showing features of soral covering of sori on *Echinochloa colonum.*



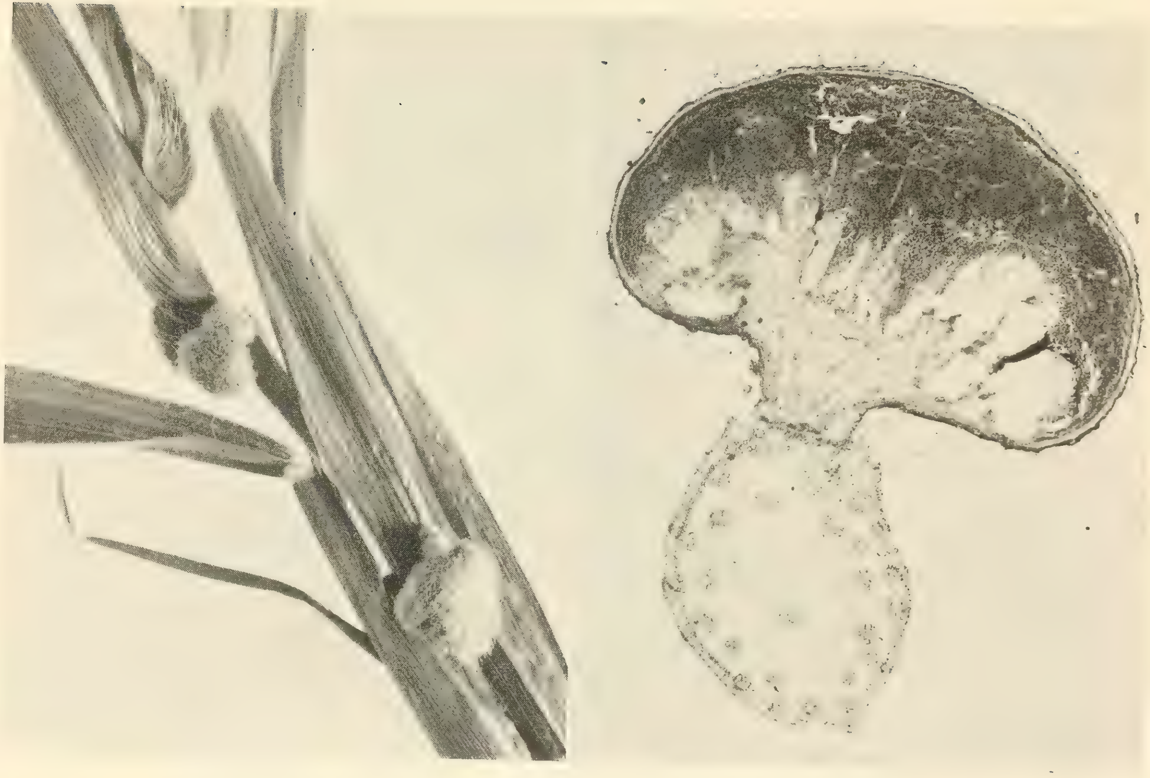
Longitudinal sections of sorus in ovary of *Echinochloa colonum.*



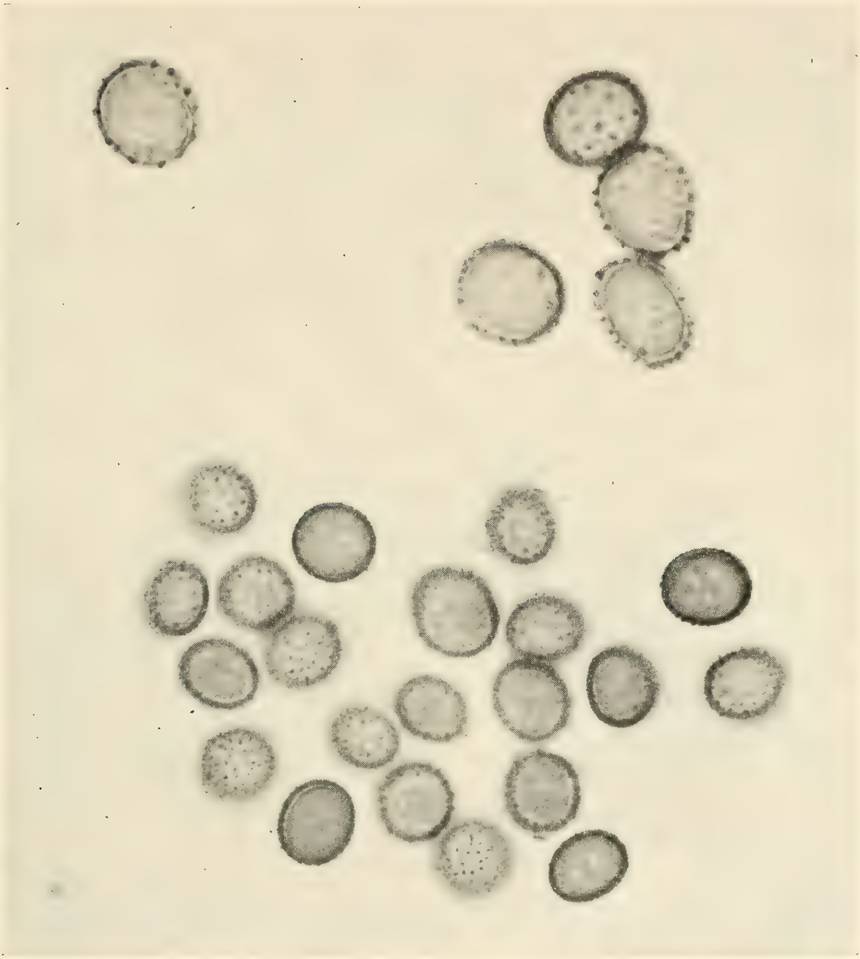
Longitudinal section of sorus in staminal filament of *Echinochloa colonum*.



Left side.—Sori on nodes and leaf sheaths of *Echinochloa colonum*.
Right side.—Section through sorus on stem of *Echinochloa colonum*.



Left side.—Sori on nodes and leaf sheaths of *Echinochloa colonum*.
Right side.- Section through sorus on stem of *Echinochloa colonum*.



Left side.—Spores of the *Ustilago sphaerogena* form

Right side.—Spores of the *Ustilago crus-galli* form.

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EXPLANATION OF PLATES

Plate XXIII

Top. *Echinochloa colonum* with *Ustilago sphaerogena* form of smut expression in floral parts (× 3).

Bottom. Sori developed in floral parts of *Echinochloa colonum* (× 14) (*a*) in ovary; (*b*) in staminal filaments, with anthers still attached; (*c*) in lodicules; (*d*) upper glume and fertile lemma.

Plate XXIV

Top. *Echinochloa colonum* with *Ustilago crus-galli* form of smut expression in inflorescence (× 3).

Bottom. Section showing features of soral covering of sori on *Echinochloa colonum* (× 160). (*a*) epidermal hairs; (*b*) host tissue; (*c*) fungal sheath; (*d*) spore mass.

Plate XXV

Left side. Longitudinal section of sorus in ovary of *Echinochloa colonum* with ovule in papilla above sorus (× 35).

Right side. Longitudinal section of sorus in ovary of *Echinochloa colonum* with ovule on wall of sorus (× 30).

Plate XXVI

Longitudinal section of sorus in staminal filament of *Echinochloa colonum* (× 40).

Plate XXVII

Left side. Sori on nodes and leaf sheaths of *Echinochloa colonum* (× 3).

Right side. Section through sorus on stem of *Echinochloa colonum* (× 30).

Plate XXVIII

Left side. Spores of the *Ustilago sphaerogena* form (× 1000).

Right side. Spores of the *Ustilago crus-galli* form (× 1200).

A VIVIPAROUS SPECIES OF *PATIRIELLA* (ASTEROIDEA, ASTERINIDAE) FROM TASMANIA

A. J. Dartnall

The Tasmanian Museum, Hobart, Tasmania

(Plate xxix)

[Read 25th September, 1968]

Synopsis

A viviparous species of asterinid sea star of the genus *Patiriella* is described. Attention is drawn to its restricted distribution in the littoral of S.E. Tasmania and the significance of its mode of development is noted. Some comparisons are drawn with other Australian species of *Patiriella*.

Introduction

The new species of *Patiriella* discussed in this paper was known formerly from specimens held by the Tasmanian Museum and the Zoology Department of the University of Tasmania. The specimens had been attributed to *Patiriella exigua* (Lamarck), 1816 and *Asterina scobinata* Livingstone, 1933.

Class Stelleroida

Subclass Asteroidea

Family Asterinidae Gray, 1840

Genus *Patiriella* Verrill, 1913

Patiriella vivipara, sp. nov.

(Plate xxix)

Description of holotype.—A small asterinid sea star with five arms. The interradial edge is hardly concave; the entire animal having the appearance of a slightly rounded pentagon.

The abactinal, radial area is covered with imbricate, crescentic plates. A papular pore is enclosed by the concavity of each crescentic plate. The papulae are arranged in five (5) rows on each side of the abactinal axis of the arms. Papulae are absent from most of the interradial area of the abactinal surface and the plates of this area are without a papular notch. The abactinal plates carry 4 to 13 cylindrical, slightly capitate, granular spinelets. The number of spinelets on each abactinal plate increases towards the centre of the disc.

The madreporite is sub-triangular, channelled and perforate.

The anus is protected by six (6) spinelets inclined obliquely over the aperture.

The inferomarginal plates are distinct, each carrying four (4) spinelets on the outer margin, and form a conspicuous edge to the actinal surface.

The actinal plates are imbricate and arranged in chevrons in the interradial area. Each plate is granular and carries one (1) bluntly pointed spine. Towards the disc margin two (2) spines are present on some plates.

The adambulacral plates bear two (2) furrow spines and one (1) subambulacral spine. The adambulacral plate proximal to the oral plate carries three (3) furrow spines. The furrow spines are basally webbed, broad and bluntly pointed. Each oral plate carries six (6) oral spines (the largest being the innermost) and one (1) suboral spine.

Colour in life.—Life colour is a constant orange-yellow, slightly lighter on the actinal surface.

Type material.—*Holotype.* R = 8·5 mm., r = 6·8 mm., Midway Point, Pittwater, Tasmania (42°49′ S., 147°31′ E.). Littoral rock shelf. 23. iv. 1967. Collected, A. J. Dartnall, Tasmanian Museum Reg. No., H371.

Paratype series.—Thirty-three (33) specimens ranging in size from R = 1·0 mm. to R = 10·5 mm. Two individuals fixed with emerging young. (All are spirit specimens.) Locality details as for holotype. Tasmanian Museum Reg. No. H372.

Distribution and Habitat.—Patiriella vivipara is known from four localities extant — all in south-eastern Tasmania — and is probably extinct in a fifth locality due to recent modification of the foreshore (see Fig. 1).

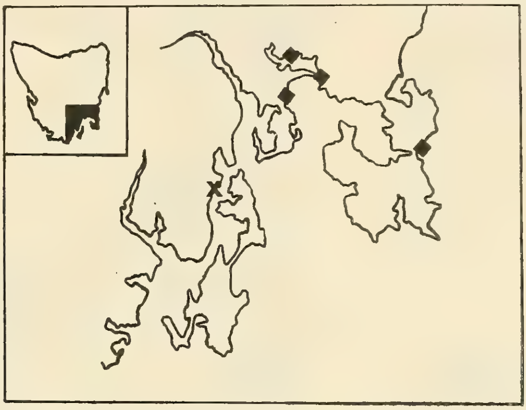

Figure 1. Distribution of *P. vivipara*, sp. nov., in S.E. Tasmania. Solid blocks show sites where the species is known to be extant; the cross the station where it occurred recently, but from where it is absent now.

The species is found on gently sloping, sheltered shores, characterized by rocks, often no more than a foot high, littered on a rock platform which gives way to sand in the lower littoral. It is found under rocks in the *Galeolaria* zone of the shore and it can be demonstrated to be more negatively phototatic than both *Patiriella exigua* and *Patiriella regularis* (Verrill), 1867.

Remarks.—Interest in this species stems from its viviparous habit. The young develop in sacs derived from the gonads and when a size of 1–2 mm. R is attained they rupture the incubatory sac, enter the coelom and emerge between the abactinal plates of the adult. *P. vivipara* breeds throughout the year.

Retention of young during embryonic development in specially adapted structures within or upon the body of the parent is common amongst echinoderms. Boolootian (1966) lists thirty-three species of Asteroidea which exhibit brooding habits, coelomic and ovarian incubation is known among the Holothuroidea and bursal incubation in the Ophiuroidea.

P. vivipara is the only asteroid known to exhibit embryonic development in a sac derived from the gonad and adds another reproductive variant to the family Asterinidae.

Affinities.—Patiriella vivipara is very similar to *P. exigua.* Both species possess six oral spines (sometimes 5 or 7) at a size of 10–11 mm. R and differences of ambulacral, actinal and abactinal spinulation and plate arrangement, if any, are not distinct. Juvenile examples of *P. regularis,* which may be confused with both *P. vivipara* and *P. exigua* in Tasmanian waters, can be separated by the smaller number of oral spines (5 at 10–11 mm. R). (See Table 1.)

P. vivipara attains maximum size at 14 mm. R, this being exceeded by all the Australian species of *Patiriella.*

Reproductive characteristics may be used to separate the species and *P. vivipara* is distinguished from other members of the genus, particularly *P. exigua,* primarily on this basis. Amongst the species available for study in Tasmania *P. regularis, P. gunnii* (Gray), 1840 and *P. calcar* (Lamarck), 1816 possess gonopores opening abactinally and free swimming larvae; in *P. exigua* the gonopore opens actinally and the larvae undergo a shortened development and in *P. vivipara* development is internal, there is no gonoduct and the young emerge in the shear-plane of the interradial arc (see Nichols, 1962).

TABLE 1

Some characteristics of species of Patiriella *in Australia*

Species	Number of rays	Number of Oral spines	Number of Spines per actinal plate	Origin of data
P. vivipara	5	6*	1	Tasmanian Museum collections
P. exigua	5	6*	1	,, ,, ,,
P. regularis	5	5*	1	,, ,, ,,
P. nigra	5	†	1–2	H. L. Clark, 1938
P. inornata	5	4	1	A. A. Livingstone, 1933
P. mimica	5	5	1	,, ,, ,,
P. calcar	8	3–4	1	Tasmanian Museum collections
P. gunnii	6	5–6	2	,, ,, ,,‡
P. brevispina	6	4–5	2	H. L. Clark, 1938‡

* At a size of 10–11 mm. R.

† H. L. Clark's description mentions the close resemblance of *P. regularis* to *P. nigra* but gives little quantitative data about the latter species.

‡ See A. M. Clark, 1966, for comments on the specific characters of *P. gunnii* and *P. brevispina*.

Colour in life may be used to separate the species in the field. *P. vivipara* is constantly orange/yellow; in *P. exigua* the actinal surface is blue-green and that of *P. regularis* off-white. *P. calcar* is noted for its wide range of colour and pattern and reddish-purple, six armed forms are attributed to *P. gunnii* (A. M. Clark 1966).

Acknowledgements

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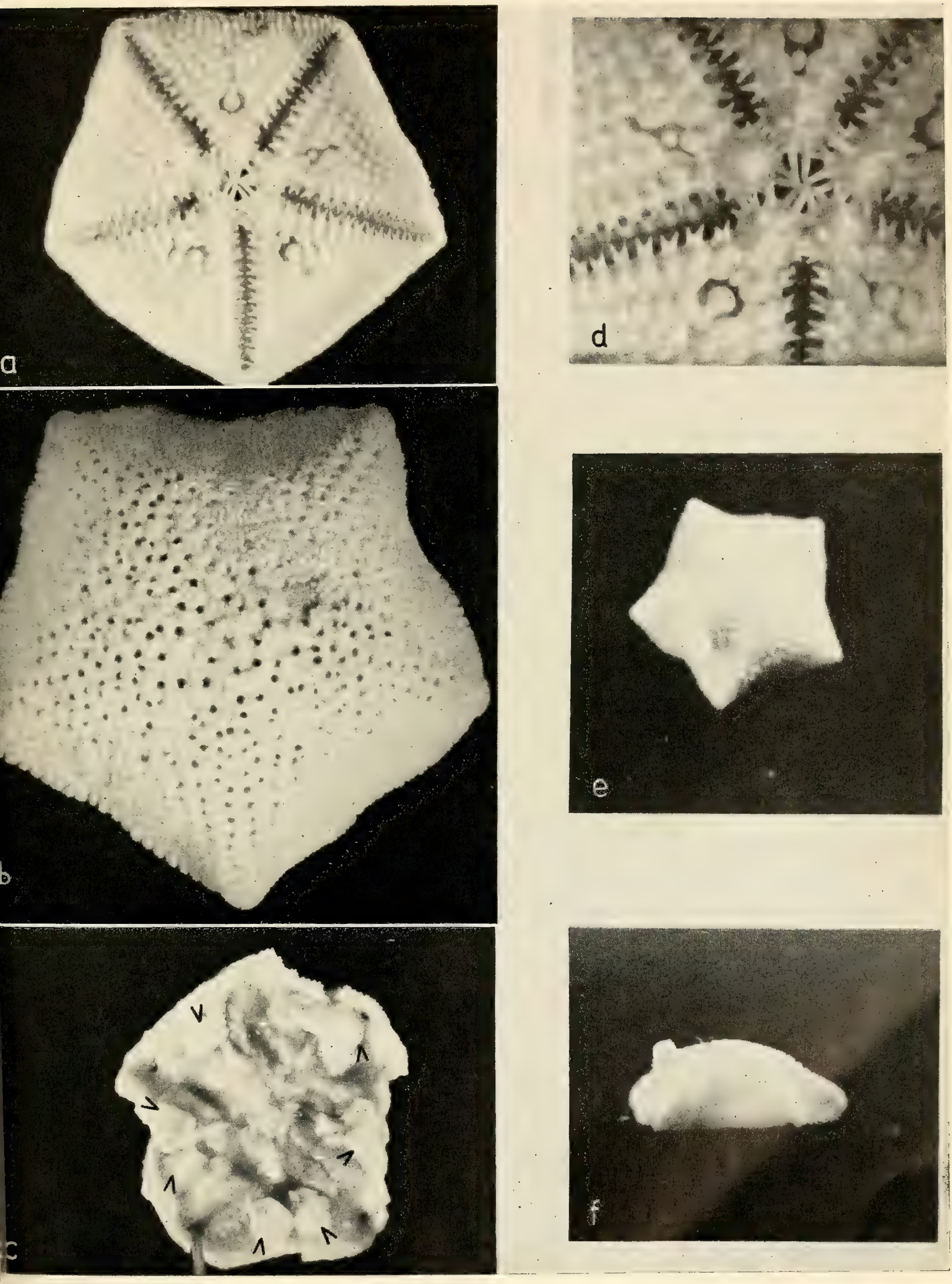
EXPLANATION OF PLATE XXIX

P. vivipara, sp. nov. a. Actinal surface (H372). b. Abactinal surface (H372). (Photo. C. G. Harrison.) c. A specimen with the actinal surface removed. The sacs containing the young and developing embryos are indicated. d. Detail of oral and adambulacral spinulation (H372). e and f. Young emerging through the abactinal surface of adult (H404).



Patiriella vivipara, sp. nov.

THE NASAL MITES OF QUEENSLAND BIRDS (ACARI: DERMANYSSIDAE, EREYNETIDAE, AND EPIDERMOPTIDAE)

ROBERT DOMROW
Queensland Institute of Medical Research, Brisbane

(Plates xxx-xxxi)

[Read September 25, 1968]

Synopsis

Native and introduced birds of 211 genera and 330 species have been examined for nasal mites in Queensland. At a generic level, this represents 64% of the Australian, and 75% of the Queensland fauna. At a specific level, the corresponding figures are 45% and 58%. Of the Queensland fauna, 53% of the genera and 36% of the species were found to be infested. Three families of mites were discovered in this microhabitat: Dermanyssidae (eight genera, 99 species), Ereynetidae (four genera, 19 species), and Epidermoptidae (six genera, six species). Keys are provided to all genera and species known to occur in Australian birds.

The following 12 dermanyssid species have been described as new: *Tinaminyssus megaloprepiae* from *Megaloprepia magnifica* (Columbidae), *T. myristicivorae* and *T. welchi* from *Myristicivora spilorrhoa* (Columbidae), *Ruandanyssus artami* from *Artamus cinereus* and *A. minor* (Artamidae), *Ptilonyssus neochmiae* from *Neochmia phaeton* (Ploceidae), *P. struthideae* from *Struthidea cinerea* (Corvidae), *P. corcoracis* from *Corcorax melanorhamphus* (Corvidae), *P. orthonychus* from *Orthonyx temminckii* (Timaliidae), *P. monarchae* from *Monarcha trivirgata* (Muscicapidae), *P. setosae* from *Rhipidura setosa* and *R. rufifrons* (Muscicapidae), *P. gerygonae* from *Gerygone palpebrosa* (Sylviidae), and *Sternostoma neosittae* from *Neositta striata* (Sittidae).

The following three ereynetid species have been described as new: *Boydaia myzomelae* from *Myzomela sanguinolenta* (Meliphagidae), *B. maluri* from *Malurus amabilis* and *M. melanocephalus* (Sylviidae), and *Ophthalmognathus accipitris* from *Accipiter fasciatus* (Accipitridae).

Fourteen dermanyssid, eight ereynetid, and one epidermoptid species have been recorded from Australia for the first time, as have the genera *Rhinoecius* (Dermanyssidae), *Ophthalmognathus* (Ereynetidae), and *Mycteroptes* (Epidermoptidae).

Forty-nine new host-records have been detailed for 24 dermanyssid species, and one each for one ereynetid and one epidermoptid species.

Forty generic and 56 specific names (of which 25 and 36, respectively, are new synonyms) have been discarded as being based on too typological an approach to taxonomy, without due regard to intraspecific variation and zoogeography.

Five habitats have been sampled more or less intensively, *viz.* rain-forest, tropical woodland, tropical tussock grassland, semi-arid savannah, and coastland.

Host-specificity is well marked, each genus or species of mite being restricted to a particular family, genus, or species of bird. This is true both of cosmopolitan and Old World groups of birds that occur in Australia (even if represented by only one species), and of birds such as the honeyeaters (Meliphagidae) that have radiated in, and are restricted to the Australian zoogeographical region.

The rhinonyssine genera (Dermanyssidae) are considered monophyletic and separable only on ecological grounds from the ectoparasitic macronyssine species found on both birds and mammals. In both subfamilies, the protonymph has well developed chelicerae like those of the adult female, while the deutonymph, with poorly developed chelicerae like those of the larva, is a non-feeding stage. The genera have developed along three lines. *Tinaminyssus*, a simple genus retaining extensive dorsal shields and a tritosternum in species parasitizing ground-birds, leads, by reductions of the dorsal armature and the respiratory apparatus, to three genera restricted to birds of the shore and open water (*Larinyssus*, *Rallinyssus*, and *Rhinonyssus*). All four possess normal chelicerae with two unreduced digits. In *Ruandanyssus* and *Rhinoecius*, the fixed digit is absent, leaving a falcate movable digit of normal proportions. In *Ptilonyssus* and *Sternostoma*, both digits are considerably reduced, with a concomitant tapering of the distal half of the cheliceral shaft.

CONTENTS

I. INTRODUCTION

The first nasal mites of birds were described, sporadically, by European workers (Giebel, 1871; Berlese and Trouessart, 1889; Trägårdh, 1904; Hirst, 1921*a, b,* 1923), and this work was reveiwed and extended by Vitzthum (1935). More recently, considerable work in Brazil by de Castro (1948), Pereira and de Castro (1949), and do Amaral (1962 *et seq.*) has been supplemented by studies in the U.S.A. by Furman (1957), Strandtmann (1951 *et seq.*), Hyland (1961), and Clark (1958 *et seq.*). Fain's reviews of the Rhinonyssinae (1957*e*), Speleognathinae (1963*c*), and Turbinoptinae (1960*c*) are based on his numerous papers, particularly on the African and European fauna, but augmented by material from birds of all kinds dying at the Antwerp Zoo. Zumpt and Till (1955) have also studied the African fauna, Bregetova (1964 *et seq.*) has initiated useful studies in the U.S.S.R., and Wilson (1964 *et seq.*) is working up extensive collections from S.E. Asia and New Guinea. Lesser papers by several other workers are mentioned whenever necessary in the text below, and reveiws have been published by Hyland (1963) and Fain (1965*a*). Ticks and chiggers (Acari: Argasidae and Trombiculidae) have each been once recorded from similar microhabitats in birds (Amerson, 1966; Brennan, 1965), but are not considered below. Another oddity is the single specimen of *Halarachne miroungae* Ferris, specific for seals (Pinnipedia : Phocidae), found in the larynx of a gentoo penguin, *Pygoscelis papua* Forster, kept in the same enclosure (Fain and Mortelmans, 1959; Domrow, 1962).

Ptilonyssus trouessarti Hirst (1921*b*) was the only species known from Australia when the present study was commenced five years ago. At first, I published small instalments as material came to hand (Domrow, 1964*a et seq.*), but have, for the past three years, determined to assemble material until the law of diminishing returns had run its course. This last instalment therefore comprises the briefest possible summary of previous records, as well as details of all new material collected. Its text was closed on June 30, 1968. An attempt has also been made to list all mite species, which, while not yet collected, can be expected to occur, together with their hosts, in Australia. A complete host-parasite list is also given, together with an indication of the groups of birds that have not yet been examined (Tables 2 and 3), that future collecting, both in Queensland and elsewhere in Australia, may be directed towards the birds (and habitats) most likely to prove rewarding. Thus, although no swifts (Apodiformes : Apodidae) have been examined, this group is known to harbour three rhinonyssines overseas (Fain, 1957*e*; Sakakibara, 1967).

All holotypes have been deposited in the Australian National Insect Collection, C.S.I.R.O. (Canberra), and paratypes, when available, have been lodged in this Institute, the Prince Leopold Institute of Tropical Medicine (Antwerp : Dr. A. Fain), and the Bernice P. Bishop Museum (Honolulu : Dr. R. W. Strandtmann).

The initials of the collectors, apart from my own, are those of G. J. Barrow, H. Battam, E. H. Derrick, I. D. Fanning, M. L. Friel (*née* Emanuel), B. H. Kay, H. J. Lavery, H. I. McDonald, D. J. Moss, J. Nielsen, H. A. Standfast, J. S. Welch, and R. H. Whitehead.

II. LOCALITIES AND HABITATS

The localities in Queensland mentioned in Section IV below are indicated in Fig. 1a, and have been divided into five major categories, with vegetational notes after the "Atlas of Australian Resources" (Department of National Development : Canberra, 1955). Of the New South Wales localities, the Tweed River flows through an area of subtropical rain-forest, while Urbenville is in sclerophyll, and Mt. Keira (near Wollongong) in wet sclerophyll forest.

(*a*) *Rain-forest.*—Of the northern localities, the tropical rain-forest studied at Maalan and Jordan Ck. (both on the escarpment of the Atherton Tableland near Millaa Millaa) have been discussed more fully by Domrow (1967*b*). The rain-forest at Ella Bay reaches right to the beach, and is relatively undisturbed, but that around Innisfail has been largely destroyed as a result of extensive sugar-cane farming. The Mt. Jukes locality has also been detailed by Domrow (1967*b*).

Webb (1959) has pointed out a difference in the rain-forest environment to the south of Sarina, and the three submontane areas studied in S. E. Queensland are therefore better classified as subtropical rain-forest. These are Mt. Glorious, Upper Brookfield, and Wilson's Peak (Plate xxx, Fig. 1).

(*b*) *Tropical woodland.*—Apart from Chillagoe and Charters Towers, in relatively drier areas of north Queensland, the remaining localities in this category are in the far south-east of the state (Esk, Cobble Ck., Mt. Nebo, Samford, Brisbane, Mt. Cotton, Logan Village, Tamborine Village, Oxenford, and Palen Ck.). These are all in open eucalypt forest, but, in certain valleys with higher precipitation and denser vegetation, birds typical of rain-forest, *e.g. Macropygia phasianella* (Temminck) and *Chibia bracteata* (Gould), are commonly seen. The Esk area (Plate xxx, Fig. 2) will be treated in more detail elsewhere (Domrow, 1969).

(*c*) *Tropical tussock grassland.*—This category, mixed with tropical woodland, is typified by Kowanyama (fomerly the Mitchell River Mission), and has been treated in detail by Doherty *et al.* (1963), Standfast (1965), and Domrow (1967). Viruses isolated from wild birds at this locality have been detailed by Whitehead *et al.* (1968). Longreach Lagoon lies between Gamboola and Highbury cattle stations.

(*d*) *Semi-arid savannah.*—Condamine is in an area of tropical woodland mixed with layered scrub, while Mitchell, Charleville, and Augathella are in an extensive area of tropical woodland mixed with arid scrub. To the south, Cunnamulla is surrounded by semi-arid, low-tree savannah, and, further inland, Winbin Ck. lies in mixed semi-arid shrub savannah and arid scrub. Finally, Windorah, in semi-arid tussock grassland, sees the beginning of the red dunes of the inland desert (Plate xxxi, Fig. 1).

(*e*) *Coastland.*—The estuary of Topsy Ck. and Half Tide are open ocean beaches with large areas of sand. Tin Can Bay is a sheltered, very shallow inlet with a narrow sandy beach above extensive mudflats, the latter being exposed only at low tide (Plate xxxi, Fig. 2). Cowley Beach and Chelona are examples of mixed coastal woodland, characterized by low forest on impoverished soil, with extensive areas of mangroves along the water margins.

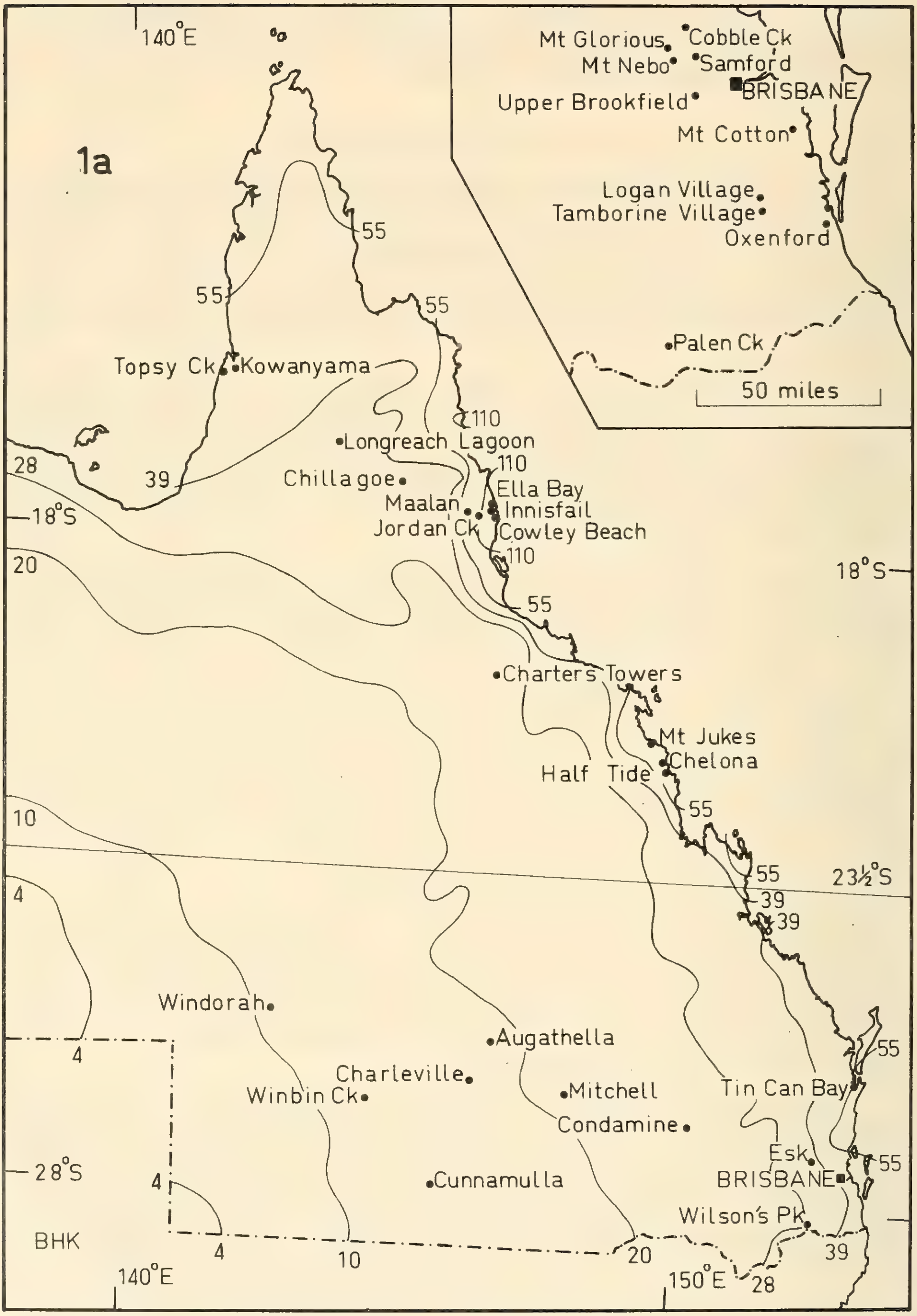


Fig. 1a. Map of Queensland showing localities mentioned in text (isohyets in inches/year).

III. METHODS AND MATERIALS

The classical method of collection of intranasal mites is that of Fain (1957*e*), and I can do no better than repeat his essentials: *"La récolte des Acariens a été pratiquée généralement peu de temps après la mort de l'Oiseau . . . le bec est largement ouvert. Au moyen d'une paire de ciseaux à mors fins on découpe le palais, le plus près possible du bec et sur une grande longueur de façon à bien exposer la région qui correspond aux narines. Les tissus excisés sont . . . examinés ultérieurement . . . Pour examiner les narines par l'intérieur il est souvent nécessaire de disséquer les cornets situés profondément ou les lamelles cornées qui cachent plus ou moins leur orifice interne.*

"Les Epidermoptidés sont généralement cantonnés à l'intérieur même des narines et ce n'est qu'en cas de forte infestation qu'on peut les voir envahir la profondeur des fosses nasales. A cause de leur petite taille ils sont souvent difficiles à découvrir et il est nécessaire d'utiliser un grossissement déjà assez puissant . . . Les Rhinonyssidés vivent également dans les narines, on peut cependant les rencontrer aussi dans le mucus qui recouvre les cornets, mais ils ne s'aventurent jamais très loin à l'intérieur des fosses nasales. Les Epidermoptidés comme les Rhinonyssidés sont animés de mouvements lents et ne se déplacent probablement que très peu. Il n'en est pas de même des Speleognathes qui sont très rapides et circulent dans toute l'étendue des fosses nasales, envahissant même les cellules osseuses".

I would only add that I have supplemented this palatal approach with a dissection inwards and backwards from the nostrils sufficiently deep to expose the air-sacs of the skull, thus facilitating the collection of speleognathines. Even this, if neatly performed, does not preclude the preparation of the skins for museum purposes, and, in any case, the viscera of many of the specimens were taken for virological and parasitological studies. Both Fain (1965*a*) and I (1967*a*) have commented on the fact that nasal mites are not found, except for *Sternostoma tracheacolum* Lawrence and occasional stragglers, in the internal respiratory tract. The work of Maa and Kuo (1965) would confirm this.

The above method allows the collection of virtually every mite present in the nasal passages of each bird, and therefore provides a basis for quantitative population studies. One such study (Domrow, 1967*a*) showed no significant difference in rhinonyssine populations during the wet (March-April) and dry (October-November) seasons at Kowanyama. However, in the present study, only one other locality (Esk) was visited regularly, and work here was directed rather towards a thorough sampling of the bird fauna. Consequently, once a species was found and confirmed to harbour nasal mites, it was not collected intensively or ignored at later visits. Further quantitative data on populations have been supplied by ter Bush (1963) and Amerson (1967).

The material was fixed in cold 70% ethyl alcohol containing 5% glycerine, and cleared within a month in warm lactic acid, the latter procedure causing the legs to extend conveniently (excessive heating causes cuticular exfoliation, but this is often of little consequence as the setal bases stand firm). The specimens were then mounted singly (or in pairs if belonging to a common species) in Hoyer's formula for gum-chloral medium (distilled water 50 cc., gum arabic 30 g., chloral hydrate 200 g., glycerine 20 cc., mixed in that sequence at room temperature), and the slides dried in an oven at 37°C. Hoyer's, a water-soluble medium, has many advantages over polyvinyl alcohol, which becomes virtually insoluble and contracts to an extreme degree with age. I have used Hoyer's routinely since 1959, and in the warm-temperate climate of Brisbane, even with its rather humid summers, no crystallization or blackening has taken place, and ringing the coverslip with varnish is not necessary. I fancy the presence of a little lactic acid renders the preparation less prone to dry out at the edge (see also Womersley, 1943).

IV. Systematics

In this section, the material collected will be dealt with in systematic sequence, as detailed in Table 1. The following three sections will deal with host-specificity and zoogeography, the phylogeny of the rhinonyssine genera, and host-parasite relationships.

I have accepted Evans and Till's terminology (1965) for the dorsal shields of the idiosoma, except that I have preferred "mesonotal shieldlets" to "mesonotal scutellae" (these authors themselves use the term "shield" for the larger sclerotizations). Also, in the case of the peritrematalia (a term dating at least from Vitzthum, 1935), I have called the accompanying sclerotization, which invariably lies behind the stigma (and peritreme, which is reduced if present at all), the poststigmatic, and not the peritrematal shield.

Table 1

Systematic synopsis of the mites collected

Family	Genera Represented	No. of Species	Family	Genera Represented	No. of Species
Dermanyssidae	*Tinaminyssus*	18	Ereynetidae	*Boydaia*	8
(Rhinonyssinae)	*Larinyssus*	2	(Speleognathinae)	*Neoboydaia*	5
	Rallinyssus	4		*Ophthalmognathus*	3
	Rhinonyssus	6		*Speleognathopsis*	3
	Ruandanyssus	2	Epidermoptidae	*Turbinoptes*	1
	Rhinoecius	2	(Turbinoptinae)	*Passerrhinoptes*	1
	Ptilonyssus	53		*Oxleya*	1
	Sternostoma	12		*Schoutedenocoptes*	1
				Rhinoptes	1
				Mycteroptes	1

No rigid nomenclature has been adopted for the dorsal setation, as the frequent reduction renders it difficult always to identify the setae according to Lindquist and Evans' system (1965). Nevertheless, it is recognized that many of the setae present in the Rhinonyssinae have their counterparts in this system. Thus, on the podonotal shield, my verticals are surely their j_1, and my anterolaterals the intermediate members of their j and z series, while the commonly seen posterodiscal arch of four setae would be their pairs j_5 and z_5. The midposterior pair, which, in *Ptilonyssus* Berlese and Trouessart, may or may not be left free in the cuticle depending on the degree of truncation of the shield, is j_6. The five pairs of setae between the posterolateral angles of the shield and the stigmata are r_3, r_{5-6}, and s_{5-6} (s_5 being on or off the shield depending on the degree of its reduction, and absent in some species of *Sternostoma* Berlese and Trouessart). The central eight members of the transverse band of ten setae immediately behind the mesonotal shieldlets in *Ptilonyssus* are the pairs J_{1-2} and Z_{1-2}. Finally, the pygidial setae would be J_5 or Z_5. That these setae of the adult are most easily recognized from Evans and Till's figure (1965) of the dorsum of the protonymph of *Macronyssus flavus* (Kolenati), a macronyssine ectoparasite of bats, is an indication of the reduction common in this endoparasitic group.

The terminology used for the structures on the venter is also that of Evans and Till (1965), except that I have preferred the widely used (and purely Latin) term "adanal" to the hybrid "paranal" for the two setae flanking the anus. The term "cribrum" for the patch of aciculations behind the postanal seta also dates at least from Vitzthum (1935). I have not definitely assigned the setae on the ventral cuticle, but, again, the common occurrence of two setae immediately behind the genital shield, followed by a transverse row of about six, mirrors more closely the nymphal than the adult macronyssine pattern.

The legs have been described according to Evans (1963*a*), in which the tarsal setae designated ad_1 and pd_1, reduced and often difficult to see in the rhinonyssines, are equivalent to the two setae noted, but not included in the tarsal formulae by Domrow (1966*b*).

Finally, Evans (1963*b*) and Evans and Till (1965) have been followed for the terminology of the capitulum, a term they discard in favour of "gnathosoma", although, for its basal portion, they use "basis capituli". I have also preferred to consider the appendage of the palpal tarsus a claw rather than an apotele (Camin *et al.*, 1958), and have followed Sellnick (1965, 1967) in preferring "epistome" to "tectum". The palpal setal formulae commence with the trochanteral setae, and continue, if possible, to the tibiae; they include the two dorsodistal sensory rods on the tibiae.

Additional morphological studies have been made on the chelicerae, the genital aperture, the spermatheca and its ducts, and the coxal and femoral glands (Fain, 1960*e*, 1963*b*, *f*, 1966*a*).

The foregoing paragraphs refer essentially to the Rhinonyssinae, but Fain (1962*b*, 1963*g*, *h*) has also discussed sexual dimorphism, the invaginated sensory organ of tibia I, and the solenidia of the Speleognathinae.

Family DERMANYSSIDAE

Subfamily RHINONYSSINAE

This is the classification of Evans and Till (1966), the first serious attempt in two decades to elucidate the suprageneric taxa of the "dermanyssoid" and "laelapoid" complexes.

The initial dichotomies of the following key (those based on the nature of the chelicerae of the adult female, and leading to couplets 3, 6, and 7) follow the first of Fain's classifications (1957*a*), in which the Rhinonyssidae, treated as a full family, were divided into three subfamilies : Rhinonyssinae Trouessart, Rhinoeciinae Fain, and Ptilonyssinae de Castro. The subfamily Agapornyssinae Gretillat *et al.* (1959), based on a synonym of *Sternostoma* (*v. infra*), is a synonym of the Ptilonyssinae. Fain was later (1960*d*) to erect a fifth subfamily, Larinyssinae, monotypic for *Larinyssus* Strandtmann, which, however, I prefer to leave among his rhinonyssine genera.

Further, in more recent work, at least ten new genus-group taxa have been raised (Brooks and Strandtmann, 1960; Fain, 1964*d*; Fain and Aitken, 1967; Bregetova, 1965*a*, *b*, 1967). Some of these, with composite generic names, cut across Fain's lines of division. For example, *Rhinosterna* Fain and *Sternoecius* Fain and Aitken each show characters of *Sternostoma* (Ptilonyssinae), and of *Rhinonyssus* Trouessart (Rhinonyssinae) on the one hand and of *Rhinoecius* Cooreman (Rhinoeciinae) on the other. Both are placed as synonyms of *Sternostoma* below.

Also, it is clear that other of these taxa are synonyms, even though certain faunas, *e.g.* the neotropical and oriental, require further study. For example, *Trochilonyssus* Fain and Aitken shows the process on coxae II and the elongate sternal and genital shields characteristic of many species of *Ptilonyssus*, and, apart from the chelicerae and the armature of the stigmata, keys directly to that genus in Fain's system of 1960*d*. *P. maluri* Domrow also shows abnormally long cheliceral digits, and the lack of peritremes is a criterion, which, in the case of *Ptilonyssus* and *Passeronyssus* Fain, is shown below no longer to hold.

Bregetova (1964) favours a diphyletic system, recognizing an older group (Rhinonyssidae) and a younger, for which she proposes the new family Neonyssidae.* In one case, the chelicerae of both nymphal stages are said to be similar to those of the adult. In the other, there is alleged a "marked difference between the chelicerae of the feeding protonymph and the non-feeding deutonymph, the chelicerae of the latter reverting to the form in the non-feeding larva". (I use Evans and Till's words of 1965, but should note they were phrased for a different context.)

However, this system also cuts across Fain's, placing *Rhinoecius* and *Sternostoma* among the rhinonyssids, and *Ruandanyssus* Fain among the neonyssids, and I believe it to be based on incorrect observation. I have examined both protonymphs and deutonymphs of *Tinaminyssus* Strandtmann and Wharton (many species from pigeons, parrots, kingfishers, and herons), *Larinyssus*, *Rhinonyssus*, *Ruandanyssus*, and *Ptilonyssus*, one protonymph of *Rhinoecius*, and two deutonymphs of *Sternostoma* (I have no immature specimens of *Rallinyssus* Strandtmann), and, in all cases, they confirm Evans and Till's findings, even in such genera as *Rhinoecius* and *Ruandanyssus*, in which the chelicerae lack the fixed digit. Mitchell (1963) has also shown the phenomenon of alternate feeding stages in his detailed morphological study of *Rhinonyssus rhinolethrum* Trouessart, while the pioneer work on this point was that of Strandtmann (1961).

I therefore consider the Rhinonyssinae a monophyletic group of macronyssine origin (see Section VI below), and recognize no intermediate grade between subfamily and genus.

Key to Australian genera of RHINONYSSINAE *(females)**

* This and the following keys are all based on Australian material only.

1. Cheliceral shafts of uniform diameter, the digits occupying more than one-eighth of the total length 2
Chelicerae attenuate in distal half, the digits normally occupying less than one sixteenth of the total length (but one-eighth in *Ptilonyssus maluri* Domrow) 7
2 (1). Both cheliceral digits present 3
Fixed cheliceral digit absent 6
3 (2). Stigmata with peritremes 4
Stigmata without peritremes .... *Rhinonyssus* Trouessart
4 (3). Peritrematalia in normal position above coxae III-IV. Anus normal 5
Peritrematalia situated near caudal extremity of idiosoma. Some species with delicate circumanal frill .... *Rallinyssus* Strandtmann
5 (4). Podonotal shield always entire. Opisthonotal shield entire, fragmentary, or absent .... *Tinaminyssus* Strandtmann and Wharton
All dorsal shields fragmentary .... *Larinyssus* Strandtmann
6 (2). Opisthonotal shield and tritosternum present .... *Ruandanyssus* Fain
Opisthonotal shield and tritosternum absent .... *Rhinoecius* Cooreman

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* Unfortunately, this author, apparently from a lack of literature, uses some genera in an outmoded sense. In particular, *Neonyssus* Hirst has been shown by Fain and Hyland (1962*b*) to be a synonym of *Ptilonyssus*, and her Neonyssidae therefore falls to de Castro's Ptilonyssinae (1948).

7 (1). Stigmata normally with peritremes, but, if not, gnathosoma terminal (except in *P. neochmiae*, n. sp.) and anal shield ventral, normally formed, and bearing postanal seta .... *Ptilonyssus* Berlese and Trouessart

Stigmata without peritremes. Gnathosoma withdrawn ventrally between coxae I at least to level of trochantero-femoral articulation of palpi. Anal shield terminal, usually regressed, and always lacking postanal seta ....*Sternostoma* Berlese and Trouessart

Genus TINAMINYSSUS Strandtmann and Wharton

Tinaminyssus Strandtmann and Wharton, 1958, *Contr. Inst. Acar. Univ. Md*, 4: 161. Type-species *Neonyssus* (*Ptilonyssoides*) *trappi* Pereira and de Castro, 1949, *Archos Inst. biol., S Paulo*, 19: 229; do Amaral, 1967, *Ibid.*, 34: 137. *Mesonyssus* Fain, 1960, *Revue Zool. Bot. afr.*, 61: 313, 62: 102. Type-species *Neonyssus treronis* Fain, 1956, *Ibid.*, 53: 394. New synonymy. *Mesonyssoides* Fain and Nadchatram, 1962, *Bull. Annls Soc. r. ent. Belg.*, 98: 271. Type-species *Mesonyssoides malayi* Fain and Nadchatram, 1962, *Loc. cit.*, 272. New synonymy. *Mesonyssoides* Strandtmann and Clifford, 1962, *J. Parasit.*, 48: 723. Type-species *Mesonyssoides ixoreus* Strandtmann and Clifford, 1962, *Loc. cit.*, 723. New synonymy. *Psittanyssus* Fain, 1963, *Revue Zool. Bot. afr.*, 68: 69. Type-species *Psittanyssus baforti* Fain, 1963, *Loc. cit.*, 70. New synonymy. *Falconyssus* Fain, 1966, *Revue Zool. Bot. afr.*, 74: 85. Type-species *Falconyssus elani* Fain, 1966, *Loc. cit.*, 86. New synonymy.

Both Fain (1963*e*) and do Amaral (1967) consider the two species originally placed in *Tinaminyssus* belong to *Mesonyssus*, thereby contravening Art. 23, since the former has priority.

I do not believe the mere absence of the opisthonotal shield in *Falconyssus* justifies its separation from a genus in which this character is notoriously variable (see couplets 2 and 3 in the following key, which include the three species known from Australian psittacids). In any case, this shield is present in *T. milvi* (Fain, 1962*c*), n. comb., and *T. epileus* (Wilson, 1964), n. comb., both of which also have falconiform hosts, and Fain himself has commented (1963*e*) : *"à notre avis le nombre des écussons dorsaux ne devrait pas être utilisé commé caractère générique dans la famille Rhinonyssidae".*

Key to females of Australian species of TINAMINYSSUS

1\. Tritosternum present 2

Tritosternum absent 4

2 (1). Opisthonotal shield entire .... *kakatuae* (Domrow), n. comb.

Opisthonotal shield not entire 3

3 (2). Anterior fragment of opisthonotal shield entire, bearing several long, sinuous setae Postanal seta absent .... *aprosmicti* (Domrow), n. comb.

Anterior fragment of opisthonotal shield divided, bearing several short, stiff setae. Postanal seta present .... *trichoglossi* (Domrow), n. comb.

4 (1) Opisthonotal shield present 5

Opisthonotal shield absent 17

5 (4). Adanal setae behind anus 6

Adanal setae in front of anus or at least level with its centre 7

6 (5). Opisthonotal shield subrectangular, with margins distinct. Femur I (1-4/2-1), II (1–4/1–1), III (1–3/1–1), IV (1–3/1–0). Genua I–III (1–4/2–1), IV (1–4/1–0). Capitular setae absent ...... *belopolskii* (Bregetova), n. comb.

Opisthonotal shield subpentagonal, with eroded margins. Femora 8.7.4.4. Genua 8.6.6.4. Capitular setae present ....*epileus* (Wilson), n. comb.

7 (5). No setae inflated basally 8

Some setae, particularly on coxae, strongly inflated basally 15

8 (7). Postanal seta present 9

Postanal seta normaly absent, but minute in specimens of *T. geopeliae* (Fain) from *Geopelia cuneata* (Latham) 11

9 (8). Postanal seta at least as long as adanals .... *melloi* (de Castro), n. comb.
Postanal seta less than half as long as adanals 10
10 (9). Adanal setae at least as long as anus. Venter of opisthosoma with about 10 pairs of rather short setae. Basitarsi II–IV 3.3.3 .... *ocyphabus* (Domrow), n. comb.
Adanal setae barely half as long as anus. Venter of opisthosoma with about 20 pairs of quite long setae. Basitarsi II-IV 4.4.4 *hirtus* (Wilson), n. comb.
11 (8). Adanal setae at least as long as anus 12
Adanal setae considerably shorter than anus ....*columbae* (Crossley), n. comb.
12 (11). Cribrum absent. Basitarsi II-IV at least 4.4.3. Capitular setae absent 13
Cribrum present. Basitarsi II-IV 3.3.3. Capitular setae present 14
13 (12). First pair of setae between genital and anal shields minute. All coxae unarmed. Basitarsi II-IV 4.4.4. All claws subequal ...... *ptilinopi* (Wilson), n. comb.
All setae between genital and anal shields subequal. Coxae II-III armed with crescentic bosses. Basitarsi II-IV 4.4.3. Claws I considerably stronger than II–IV..*myristicivorae*, n. sp.
14 (12). All setae between genital and anal shields subequal. Coxae without rounded bosses .... *megaloprepiae*, n. sp.
First pair of setae between genital and anal shields considerably weaker than remainder. Coxae II-IV with distinct, rounded bosses ....*geopeliae* (Fain), n. comb.
15 (7). Adanal setae shorter than anus. Only one seta on coxa I inflated basally. Basitarsi II-IV 4.4.4 .... *phabus* (Domrow), n. comb.
Adanal setae at least as long as anus. Both setae on coxa I inflated basally. Basitarsi II-IV 4.4.3 16
16 (15). Opisthonotal shield rectangular, confined entirely to dorsum. Setae on ventral surface of opisthosoma simple, including first minute pair. Coxae each with crescentic boss. All claws subequal. Capitular setae present ....*macropygiae* (Wilson), n. com.b
Opisthonotal shield subcircular, encroaching onto venter. Most setae between genital and anal shields inflated basally. Coxae II-IV each with stout spur. Claws I stronger than II-IV. Capitular setae absent *welchi*, n. sp.
17 (4). Four setae in centre of dorsal surface of opisthosoma much larger than remainder. SI-II set on sternal shield. Postanal seta present..*halcyonus* (Domrow), n. comb.
All setae on dorsal surface of opisthosoma subequal. Only SI set on sternal shield. Postanal seta absent .... *daceloae* (Domrow), n. comb.

TINAMINYSSUS KAKATUAE (Domrow), n. comb.

Mesonyssoides kakatuae Domrow, 1964, *J. ent. Soc. Qd,* 3: 35. *Mesonyssus kakatuae,* Domrow, 1966. PROC. LINN. SOC. N.S.W., 90: 191; Wilson, 1966, *Pacif. Insects,* 8: 759.

Previous records (both Psittacidae, Psittaciformes).—Red-tailed black cockatoo, *Calyptorhynchus banksii* (Latham), Kowanyama. Rose-breasted cockatoo, *Kakatoe roseicapilla* (Vieillot), Condamine.

New host record.—Cockatiel, *Leptolophus hollandicus* (Kerr) (Psittacidae), Condamine, 12.i.1966, R. D., D. J. M., and J. S. W. (6 ♀♀, 2 ♂♂).

TINAMINYSSUS APROSMICTI (Domrow), n. comb.

(Figs 1-6, 8-15)

Mesonyssoides aprosmicti Domrow, 1964, *J. ent. Soc. Qd,* 3: 26. *Mesonyssus aprosmicti,* Wilson, 1968, *J. Parasit.,* 54: 395. *Mesonyssoides platycerci* Domrow, 1964, *J. ent. Soc. Qd,* 3: 27. New synonymy.

Previous records (both Psittacidae, Psittaciformes).—Red-winged parrot, *Aprosmictus erythropterus* (Gmelin), Condamine. Also Kowanyama. Pale-headed rosella, *Platycercus adscitus* (Latham), Condamine. Also Esk, Charleville, and Longreach Lagoon.

New host records (all Psittacidae).—King-parrot, *A. scapularis* (Lichtenstein), Oxenford, 1.vii.1967, B. H. K. (9 ♀♀, 3 ♂♂, 1 deutonymph). Ring-neck parrot, *Barnardius barnardi* (Vigors and Horsfield), Charleville, 19.i and 1.ii.1967, R. D. and J. S. W. (14 ♀♀, 2 ♂♂); Winbin Creek, 20.i.1966, R. D., D. J. M., and J. S. W. (1 ♀). Mulga parrot, *Psephotus varius* Clark, Charleville, 23.i.1967, R. D. and J.S.W. (3 ♀♀, 2 ♂♂, 1 protonymph). Red-backed parrot, *P. haematonotus* (Gould), Orchard Hills, N.S.W., 22.xii. 1968, D. Himsley (1 ♀). (This specimen was obtained while I was reading proof, and is taken into account only here and in Table 4. It is typical of *T. platycerci* as originally described.)

The original material of the two taxa here combined was separable according to the following couplet:

1. Anterior fragment of posterior dorsal shield with cluster of 10 enormous setae. Sternal plate poorly defined. Metasternal setae present. From an Australian parrot (*Aprosmictus* Gould) .... *aprosmicti* Domrow
Anterior fragment of posterior dorsal shield with cluster of 12 enormous setae. Sternal plate well defined. Metasternal setae absent. From an Australian parrot (*Platycercus* Vigors) .... *platycerci* Domrow

The central cluster of enlarged mesonotal setae in 17 female paratypes from *A. erythropterus* numbers 9 twice, 10 twelve times, and 11 three times, while 19 additional females from this host at Kowanyama show 8 once, 9 nine times, and 10 nine times. The cluster is not flanked laterally by an additional pair of strong setae as described for *T. platycerci.*

The central cluster is larger in 9 females from *A. scapularis* (Fig. 1), comprising 12 setae three times, 13 twice, 14 twice, and 15 twice (2 of the cluster of 14 in one specimen are not enlarged). Further, these specimens do show this central cluster flanked exteriorly by a further pair of enlarged setae, arranged 1.0 once, 1.1 four times, 1.2 three times, and 0.2 once.

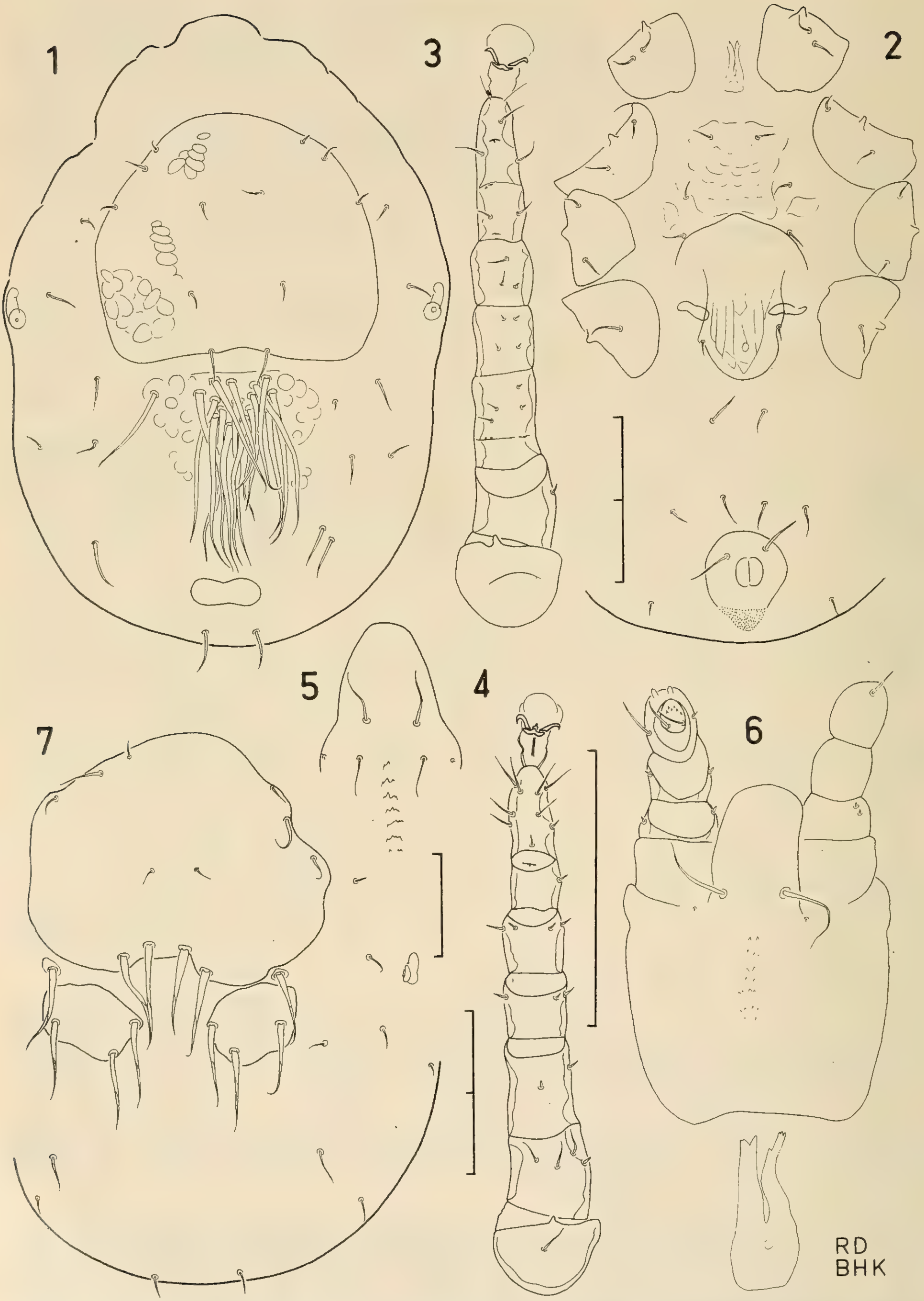
In 43 ♀♀ and 6 ♂♂ from *P. adscitus,* the entire complex of enlarged mesonotal setae numbers 12 in 37 ♀♀ and 2 ♂♂. Five ♀♀ and 3 ♂♂ show 11 setae, lacking one of the exteriormost pair or one of the central cluster. One ♂ and 1 ♀ show 10 setae, the male lacking two setae from the central cluster, and the female one of the exteriormost pair and one from the central cluster. In one female, two setae of the central cluster are completely fused basally, and set in a single correspondingly larger alveolus.

All specimens from *B. barnardi* lack the outermost pair of the complex, the number of setae in the central cluster being 10 five times, 9 ten times (including both males), and 8 once.

The sternal shield is weakly sclerotized and ill-defined in specimens from both species of *Aprosmictus,* but dense and sharply delineated in material from *Platycercus* and *Barnardius* Bonaparte. Metasternal setae are present in all the specimens from *A. erythropterus,* although one paratype and four of the later specimens show a metasternal seta on one side only. The specimens from *A. scapularis* (Fig. 2) are uniformly 3.3 (except 3.2 once), as are those from *Platycercus* and *Barnardius* (in both of which latter, SI is borne on the sternal shield).

The two other species of *Tinaminyssus* recorded from Australian psittacids by Domrow (1964*a*) are *T. trichoglossi* from various lorikeets, and *T. kakatuae* from crested psittacids (cockatoos and the cockatiel). Considerable clinal variation is allowed below in the former species, and the material now discussed from members of a third psittacid group, the parrots, is similarly considered conspecific.

The material from the mulga parrot (*Psephotus* Gould) typically shows only eight enlarged dorsal setae in the mesonotal cluster, and has a sternal shield intermediate between those of *T. aprosmicti* and *T. platycerci* as

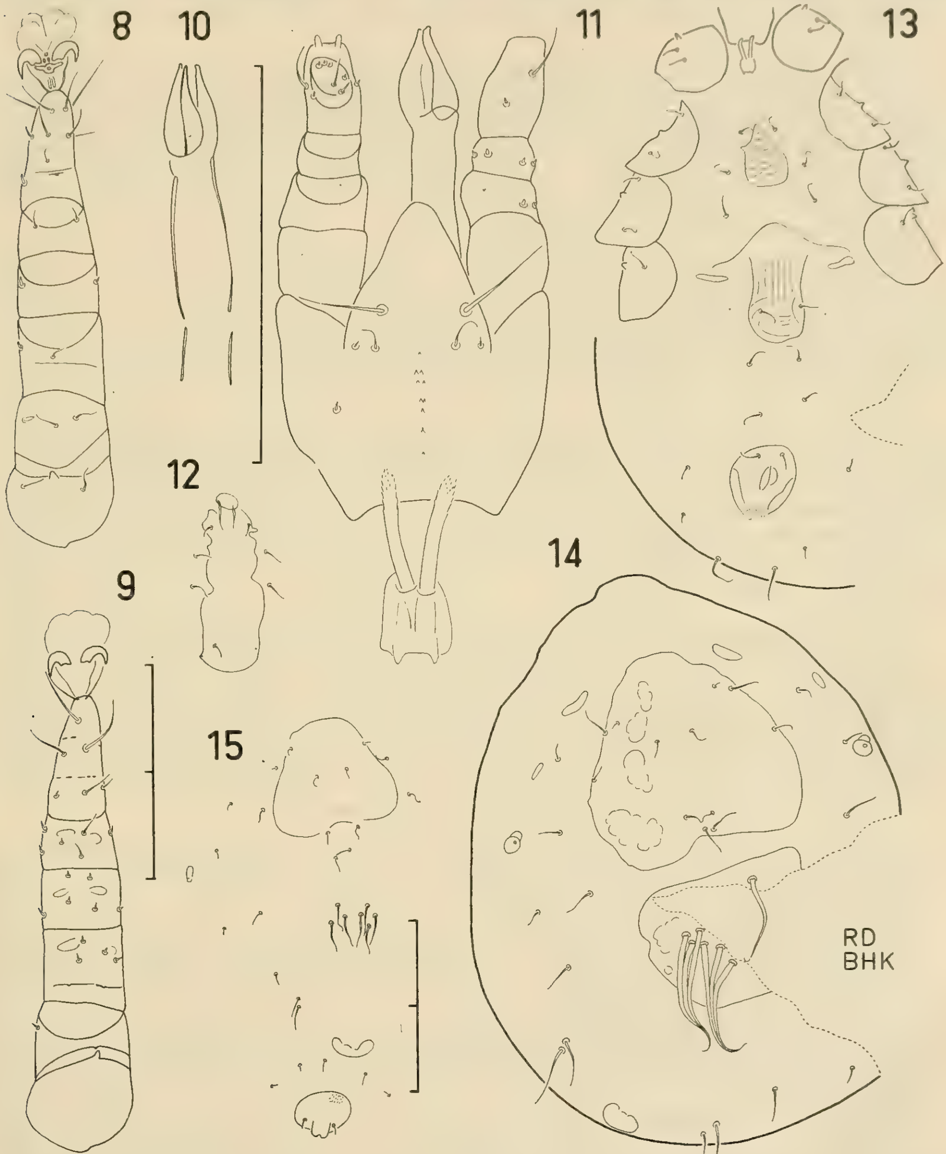


Figs 1–6. *Tinaminyssus aprosmicti* (Domrow) (♀ from *Aprosmictus scapularis*).–1–2, Dorsal and ventral views of idiosoma. 3–4, Dorsal and ventral views of leg IV. 5, Deutosternum and hypostome, with typical setation. 6, Ventral view of capitulum, with atypical hypostomal setation, *i.e.* with HI absent (left palp in dorsal view). (Each division on the scales equals 100μ.)

Fig. 7. *Tinaminyssus trichoglossi* (Domrow) (♀ from *Glossopsitta pusilla*).–Dorsal view of idiosoma.

originally described, being tapered anteriorly, leaving S1 free in the adjacent cuticle. Further, there is a concentration of the four midposterior setae on the podonotal shield not shown in the other material, so best the material be described, but within my broadened concept of *T. aprosmicti*.

Female.—A rounded species when engorged, idiosoma 625μ long (calculated from ruptured specimen illustrated). Podonotal shield (Fig. 14) as long as wide, 231-264μ long, 235-259μ wide, well defined, subtriangular, but with rounded corners and irregular posterior margin; surface closely



Figs 8–15. *Tinaminyssus aprosmicti* (Domrow) (from *Psephotus varius*).– 8–9, Ventral and dorsal views of leg III of ♀. 10, Chelicera of ♂. 11, Ventral view of capitulum of ♀ (left palp in dorsal view). 12, Sternogenital shield of ♂. 13–14, Ventral and dorsal views of idiosoma of ♀. 15, Dorsal view of idiosoma of protonymph.

punctate and marked by muscle insertions. Shield with three setae on each anterolateral margin; also three pairs of setae in mid-longitudinal line, of which the central pair is set decidedly further back than in remaining material. Anterior (mesonotal) fragment of opisthonotal shield not as strongly delimited, almost semicircular behind rectilinear anterior margin; with eight (rarely seven) enlarged setae. Posterior (pygidial) fragment of opisthonotal shield transversely oval; asetose. Stigmata with much abbreviated peritremes. Dorsal body cuticle with four shieldlets anterolaterally, and seven pairs of setae (sixth and seventh pairs enlarged and approximated as in original illustration of *T. platycerci*).

Sternal shield (Fig. 13) well defined, reticulate, and with some punctae; tapered distinctly between SI and extending back just behind SII. SI-III free in cuticle. Metasternal setae absent. Genital shield ligulate, irregularly marked, and bearing two setae; associated pores free in cuticle. Anal shield rounded anteriorly, more heavily sclerotized laterally; cribrum present. Anus centrally placed, preceded by adanal setae; postanal seta absent. Ventral cuticle with ten setae arranged 2.4.4.

Legs with setae short and spinose on anterodorsal aspect, but long and tapering ventrodistally (Figs 8-9). Coxae 2.2.2.1. Trochanter I (0-1/2-0), II (2-0/2-0), III-IV (1-0/3-0). Femur I (2-4/2-2), II (2-4/1-1), III (1-4/1-0), IV (1-3/0-0). Genu I (2-4/2-2), II-III (2-4/0-2), IV (2-4/1-1). Tibiae (2-3/2-1). Tarsi—.18.18.18 (*mv* present). Ambulacrum I weaker than II-IV.

Basis capituli (Fig. 11) normally with two capitular setae, but one often absent. Several fine deutosternal denticles present. Hypostome with three pairs of setae, HI strongest, HIII weakest. Palpal tarsus obscured dorsally by tibia; setal formula 0.2.4.7(6), mostly minute, but one or two on tibia long and slender. Chelicerae 80-85μ long, chelate portion occupying one-quarter of total length. Tritosternum with hyaline edges on base, and two distally spiculate laciniae.

Male.—Idiosoma 460μ long in relatively unengorged specimen. Dorsum as in female, but shields slightly smaller; podonotal shield 223×223μ.

Sternogenital shield (Fig. 12) irregular in outline, bearing SI, but SII-III free in cuticle; genital setae on shield (one missing on one side of one specimen), with accompanying pores on shield in one specimen, off in other. Genital aperture in front of SI. Texture of sternal and genital areas as in female. Remainder of venter as in female.

Legs as in female, but one seta may be lacking on genua-tibiae III-IV; one specimen also shows femur IV 4.5.

Capitulum as in female, except for spermatodactyl on chelicera (Fig. 10).

Protonymph.—Dorsum (Fig. 15) as in adult, but shields and mesonotal setae not so strongly developed.

Sternal area with six setae. Ventral cuticle immediately behind coxae IV probably with six setae arranged 2.?4. Anal shield flanked posteriorly by about five setae.

Chaetotaxy of coxae and trochanters as in adult, but trochanter IV not very clear. Femur I as in adult, II probably (1-4/1-1), III (1-3/1-0), IV as in adult on one side, (1-3/1-0) on other. Genu I (1-4/2-1), II-IV (1-4/0-1). Tibiae (1-3/2-1). Tarsi—.17.17.17 (*mv* absent). Tarsus I essentially as in adult.

Capitulum essentially as in female.

Tinaminyssus trichoglossi (Domrow), n. comb.

(Fig. 7)

Mesonyssoides trichoglossi Domrow, 1964, *J. ent. Soc. Qd*, 3: 29. *Mesonyssus trichoglossi,* Wilson, 1964, *Pacif. Insects*, 6: 378; 1966, *Ibid.*, 8: 766; 1968, *J. Parasit.*, 54: 400. Domrow, 1966, Proc. Linn. Soc. N.S.W., 90: 191. *Mesonyssus neopsittaci* Wilson, 1964, *Pacif. Insects*, 6:372; 1966, *Ibid.*, 8: 759; 1968, *J. Parasit.*, 54: 397. New synonymy. *Mesonyssus domicellae* Wilson, 1964, *Pacif. Insects,* 6:375; 1968, *J. Parasit.*, 54:397. New synonymy. *Mesonyssus chalcopsittae* Wilson, 1968, *J. Parasit.*, 54: 395. New synonymy.

Previous records (all Psittacidae, Psittaciformes).—Rainbow-lorikeet, *Trichoglossus moluccanus* (Gmelin), Tamborine and Logan Villages. Also Esk and Kowanyama. Scaly-breasted lorikeet, *T. chlorolepidotus* (Kühl), Tamborine and Logan Villages. Also Esk. Little lorikeet, *Glossopsitta pusilla* (Shaw), Esk.

The above four nominal taxa were based on variation in number and strength of setae, beginning on the dorsal shields and free segments of the legs, and extending finally onto the coxae and venter. Moreover, host-specificity is not absolute (Wilson, 1966*b*), and I now consider this variation clinal, in the direction: *T. neopsittaci*—unnamed form from *Glossopsitta* (Fig. 7)—typical form of *T. trichoglossi*—unnamed form from *Trichoglossus* recognized by Domrow (1964*a*) and figured by Wilson (1964)—*T. domicellae*—*T. chalcopsittae*.

The following specimens housed in the Australian Museum, Sydney, and examined through the courtesy of Mr. C. N. Smithers, are listed for historical reasons, being among the first nasal mites of birds ever collected. Prior to 1892, all known species were European, one having been described by Giebel (1871) and three by Berlese and Trouessart (1889). The first Australian rhinonyssine was described by Hirst (1921*b*), and work in this region was resumed by Domrow (1964*a et seq.*).

The series comprises 3♀♀ (in fair condition) from *T. moluccanus* (listed on the label under its synonym *T. multicolor* (Gmelin)), Tweed River, N.S.W., ii.1892, T. Steel (Carter, 1926, Proc. Linn. Soc. N.S.W., 51: vii, gives a brief biography). All the specimens agree with the variety noted in the original description.

Tinaminyssus belopolskii (Bregetova), n. comb.

Neonyssus belopolskii Bregetova, 1950, *Dokl. Akad. Nauk SSSR,* 71: 1005; Strandtmann, 1956, *J. Kans. ent. Soc.,* 29: 137; Mitchell, 1961, *SWest. Nat.,* 6: 105. *Mesonyssus belopolskii,* Domrow, 1965, *Acarologia,* 7: 433: 1966, Proc. Linn. Soc. N.S.W., 90: 191; Wilson, 1968, *J. med. Ent.,* 5: 213. *Neonyssus ardeae* Zumpt and Till, 1955, *J. ent. Soc. sth. Afr.,* 18: 63; Fain, 1957, *Annls Mus. r. Congo belge Sér. 8vo,* 60:53, 137. *Neonyssus bubulci* Zumpt and Till, 1955, *J. ent. Soc. sth. Afr.,* 18: 66; Fain, 1957, *Annls Mus. r. Congo belge Sér. 8vo,* 60: 54. New synonymy. *Neonyssus ixobrychi* Fain, 1956, *Revue Zool. Bot. afr.,* 53:134; 1957, *Annls Mus. r. Congo belge Sér. 8vo,* 60: 54. New synonymy. *Neonyssus marcandrei* Gretillat, Capron, and Brygoo, 1959, *Acarologia,* 1: 379. *Mesonyssus belopolskii nycticoracis* Fain, 1961, *Acarologia,* 3: 516.

Previous records (all Ardeidae, Ciconiiformes).—Plumed egret, *Egretta intermedia* (Wagler). Little egret, *E. garzetta* (Linnaeus). Cattle egret (introduced), *Bubulcus ibis* (Linneaus). White-faced heron, *Notophoyx novaehollandiae* (Latham), Esk. Also Charleville, Tin Can Bay, Mt. Jukes, and Kowanyama. Pied heron, *Notophoyx picata* (Gould), Kowanyama. Little bittern, *Ixobrychus minutus* (Linnaeus).

I have been able to examine the following material of *N. bubulci* from the type-host, *B. ibis*: 1 ♀ and 1 ♂ paratype (Transvaal), 1 ♀ and 1 ♂ (Bechuanaland), and 2 ♀♀ (Rwanda), the last four specimens bearing Fain's identifications. As described, this taxon shows the opisthonotal shield broader than is usual in the other five taxa listed above, but one of the two specimens from Rwanda is intermediate in this respect, and I therefore accept the synonymy. The synonymy of *N. ixobrychi,* reasonably clear from the published data, is confirmed by a study of the holotype ♀ from Rwanda. All six taxa are restricted to ardeid hosts.

TINAMINYSSUS EPILEUS (Wilson), n. comb.

Mesonyssus epileus Wilson, 1964, *Pacif. Insects,* 6: 358; 1965, *Ibid.,* 7: 638.

Previous record.—Crested hawk, *Aviceda subcristata* (Gould) (Accipitridae, Falconiformes).

Three paratype ♀♀ from the above (type) host all show trochanter II 5, rather than 4.

TINAMINYSSUS MELLOI (de Castro), n. comb.

Neonyssus (Neonyssus) melloi de Castro, 1948, *Archos Inst. biol., S Paulo,* 18: 270. *Mesonyssus melloi,* Domrow, 1965, *Acarologia,* 7: 434; 1966, PROC. LINN. SOC. N.S.W., 90: 192; Wilson, 1966, *J. Parasit.,* 52: 1211. *Mesonyssus melloi streptopeliae* Fain, 1962, *Revue Zool. Bot. afr.,* 65: 310. *Mesonyssus streptopeliae,* Fain, 1965, *Revue Zool. Bot. afr.,* 72: 159. *Neonyssus hirsutus* Feider, 1962, *Studii Cerc. stiint. Iăsi,* 13: 58. New synonymy.

Previous records (all introduced Columbidae, Columbiformes).—Domestic pigeon, *Columba livia* Gmelin, Brisbane. Indian turtle-dove, *Streptopelia chinensis* (Scopoli), Brisbane. Senegal dove, *S. senegalensis* (Linnaeus).

New host records.—White-headed pigeon, *C. norfolciensis* Latham, Wilson's Peak, 15.v.1967, R. D. and B. H. K. (16 ♀♀, 11 ♂♂). Wonga pigeon, *Leucosarcia melanoleuca* (Latham) (Columbidae), Mt. Keira, 19.xi. 1967, H. B. (1 ♀).

This latter host was banded by Mr. H. Battam, Cronulla, who noted several of these mites in and around the right nostril. When they were disturbed, two or three crawled into the open beak, others withdrew into the nostril, and only one was captured.

TINAMINYSSUS OCYPHABUS (Domrow), n. comb.

Mesonyssus ocyphabus Domrow, 1965, *Acarologia,* 7: 437.

Previous record.—Crested pigeon, *Ocyphaps lophotes* (Temminck) (Columbidae, Columbiformes), Samford and Condamine. Also Esk, Charleville, Augathella, Longreach Lagoon, and Kowanyama.

New host record.—Squatter-pigeon, *Geophaps scripta* (Temminck) (Columbidae), Kowanyama, 1.iv.1965, R. D. (2 ♀♀).

My original comparison (1965*c*) of the legs of this species with those of *T. geopeliae* Fain (1964*c*) would imply that ambulacrum I is modified. In fact, it does not differ appreciably from II-IV.

Both specimens from *Geophaps* Gray are typical of the original description, except that the posterior seta on coxae I–III is relatively weaker, only 6–7 pairs of setae are present on the ventral body cuticle, and the central two pairs of setae on the opisthonotal shield are obsolescent or absent. Leg chaetotaxy as in specimens from the type host, *O. lophotes*. Coxae 2.2.2.1. Trochanters I–III (1–0/2–1), IV (1–0/3–1). Femora I–II (1–4/3–1), III–IV (1–3/1–0). Genu I (1–4/2–1), II–III (1–4/0–1), IV (1–3/0–0). Tibiae (1–3/2–1). Tarsi—.17.17.17 (*mv* present; basitarsi trisetose).

TINAMINYSSUS HIRTUS (Wilson), n. comb.

Mesonyssus hirtus Wilson, 1966, *J. Parasit.*, 52: 1210; 1968, *J. med. Ent.*, 5: 215.

This species, originally described from a member of the genus *Chalcophaps* Gould in the Philippines and New Guinea, may now be recorded from Australia: 4 ♀♀ from a green-winged pigeon, *C. chrysochlora* (Wagler) (Columbidae, Columbiformes), Wilson's Peak, 15.v.1967, R. D. and B. H. K.

TINAMINYSSUS COLUMBAE (Crossley), n. comb.

Neonyssus (*Neonyssus*) *columbae* Crossley, 1950, *Proc. ent. Soc. Wash.*, 52: 309. *Mesonyssus columbae*, Domrow, 1965, *Acarologia*, 7: 440; Wilson, 1966, *J. Parasit.*, 52: 1211.

Previous records (both Columbidae, Columbiformes).—Domestic pigeon (introduced), *Columba livia* Gmelin. Crested pigeon, *Ocyphaps lophotes* (Temminck), Esk.

TINAMINYSSUS MEGALOPREPIAE, n. sp.

(Figs 16–24)

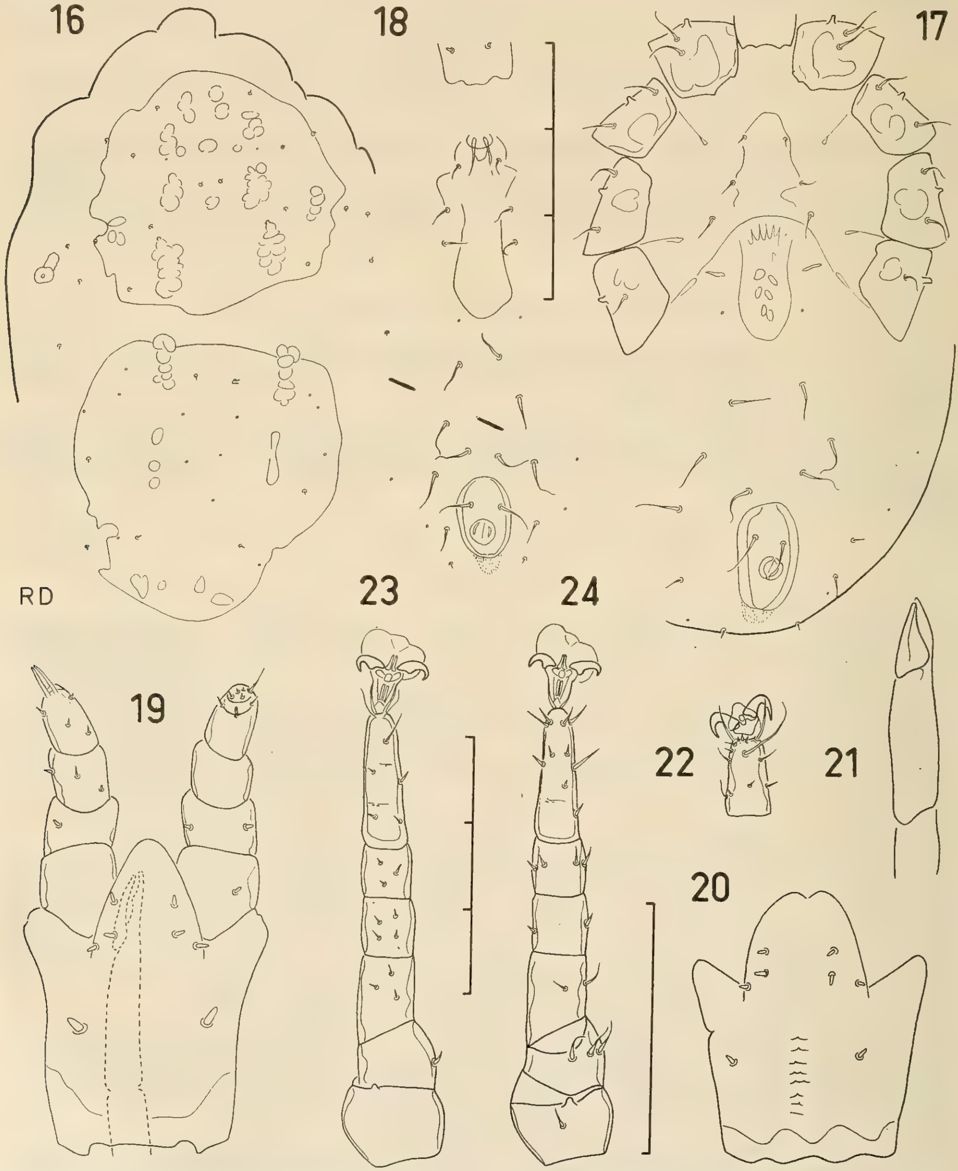
Diagnosis.—In Wilson's key (1964) to the species of *Tinaminyssus* from columbiforms, *T. megaloprepiae* comes nearest to *T. ptilinopi* (Wilson). However, the new species differs in showing (*i*) the opisthosomal setae few and uniform ventrally, *i.e.* midanterior pair not obsolescent; (*ii*) a cribrum; and (*iii*) distinct capitular setae and deutosternal denticles. The setal formulae for the legs given below also differ from those provided by Wilson, although I should note that, in a paratype from *Ptilinopus perlatus zonurus* Salvadori, trochanter I is (1–0/2–1) and the tibiae (1–3/2–1).

Specimens of *T. phassae* (Wilson, 1966*a*), n. comb., lacking the postanal seta would also key to this couplet, but *T. megaloprepiae* is distinct in the same three items cited above. There are also differences in the setal formulae of the leg segments, although I should note that a paratype of *T. phassae* shows trochanter I (1–0/2–0), genu I (1–4/2–1), and tarsi—.18.18.17 (*mv* present, basitarsi II–III with four, but IV with three setae).

Types.—Holotype female, allotype male, two paratype males, and one protonymph from a wompoo pigeon, *Megaloprepia magnifica* (Temminck) (Columbidae, Columbiformes), Maalan, 17.viii.1965, R. D. and J. S. W. Holotype and allotype N. I. C.; paratypes R. D.

Female.—Idiosoma 737μ long in slightly distorted specimen figured. Podonotal shield (Fig. 16) 281×304μ, well defined, but with irregular margins; surface reticulate, closely punctate, and marked by muscle insertions; with 13 setae and two pores. Opisthonotal shield 322×317μ, of similar texture, narrowed posteriorly, and not encroaching onto venter; with six setae (one of which is double) and 13 pores arranged as figured. Marginal cuticle with about four pairs of setae. All dorsal setae minute, slightly tapered rods. Peritremes as long as diameter of stigmata; poststigmatic shields absent.

Sternal shield irregular (Fig. 17), delimited only by cessation of cuticular striae, textures except for few punctae, without pores. SI–III increasing in length in that order, slightly inflated basally; SI-II submarginal, III free in cuticle. Metasternal setae absent. Genital shield drop-



Figs 16–24. *Tinaminyssus megaloprepiae*, n. sp. (from *Megaloprepia magnifica*).– 16–17, Dorsal and ventral views of idiosoma of ♀. 18, Ventral shields of ♂. 19, Ventral view of capitulum of ♀, with deutosternum omitted (right palp in dorsal view). 20, Ventral view of basis capituli of ♂. 21, Chelicera of ♂. 22, Dorsal view of tarsus I of ♀. 23–24, Dorsal and ventral views of leg IV of ♀.

shaped, shagreened, with muscle insertions and rayed operculum. Genital setae absent, but attendant pores present in adjacent cuticle. Anal shield almost twice as long as wide (134×76μ), rounded anteriorly, and with subparallel, sclerotized lateral margins. Definite cribrum present. Anus centrally placed, preceded by elongate adanal setae; postanal seta absent. Ventral cuticle with several pores and 12 basally expanded setae, of which mid-anterior two are not at all reduced, although posterior five are.

Legs with setae on coxae and trochanters similar to those on venter, but remainder generally much shorter and more spinose, particularly on dorsal aspect (Figs 23–24). Coxae without ventral excrescences. Coxae 2.2.2.1. Trochanter I (1–0/2–1), II (2–0/2–1), III–IV (2–0/2–0). Femur I (1–4/2–1), II (1–4/1–1) on one side and (1–4/2–1) on other, III (1–4/1–0), IV (1–3/1–0). Genu I (1–4/2–1), II–IV (1–4/0–1). Tibiae (1–3/2–1). Tarsi –. 17.17.17 (*mv* present, but basitarsi trisetose). Ambulacrum I with pretarsus much shorter, claws slightly stronger (and with correspondingly larger articulatory sclerites), and pulvillus less extensive than II-IV (Fig. 22).

Basis capituli with two capitular setae (Fig. 19); deutosternal denticles as in male (Fig. 20). Hypostome with three pairs of setae. Palpal tarsus not completely obscured dorsally by tibia; setal formula 1.3.3/2.8 (vague, apparently internal structure figured between two ventrodistal setae of tibia may be remnant of claw). All setae on capitulum in form of stout rods, except those on more distal segments of palpi (especially one on tarsus). Chelicerae not in full lateral view, but 116μ long, with chelate portion occupying one-quarter of total length. Tritosternum absent.

Male.—Idiosoma 550–605μ long in slightly distorted specimens. Dorsum as in female, but with some tendency for opisthonotal shield to encroach onto sides of body. Podonotal shield 250–264μ long, 273–286μ wide.

Venter as in female, except for genital aperture in front of SI (Fig. 18).

Legs as in female, but femur I (1–4/1–1) once, II (1–4/2–1) twice, III (1–4/0–0) twice and (1–3/0–0) twice; genu IV (1–3/0–1) once. One specimen is teratological, showing femur-tibia I (1–0/2–1) because all 4.4.3 setae on dorsal aspect are lacking.

Capitulum as in female, with distinct deutosternal denticles (Fig. 20). Chelicerae with spermatodactyl (Fig. 21).

TINAMINYSSUS GEOPELIAE (Fain), n. comb.

Mesonyssus geopeliae Fain, 1964, *Revue Zool. Bot. afr.*, 70: 33; Domrow, 1965, *Acarologia,* 7: 440; 1966, PROC. LINN. SOC. N.S.W., 90: 192; Wilson, 1966, *J. Parasit.,* 52: 1211.

Previous records (both Columbidae, Columbiformes).—Peaceful dove, *Geopelia placida* Gould, Kowanyama. Also Charleville. Bar-shouldered dove, *G. humeralis* (Temminck), Samford. Also Esk and Kowanyama.

New host record.—Diamond-dove, *G. cuneata* (Latham), Charleville, 1.ii. 1967, R. D. and J. S. W. (6 ♀♀, 4 ♂♂).

The specimens from *G. cuneata* closely resemble the original descriptions, except that a minute postanal seta is present, and the seta in the posterior angles of coxae I–III, and the bosses on coxae II–IV are weaker.

TINAMINYSSUS PTILINOPI (Wilson), n. comb.

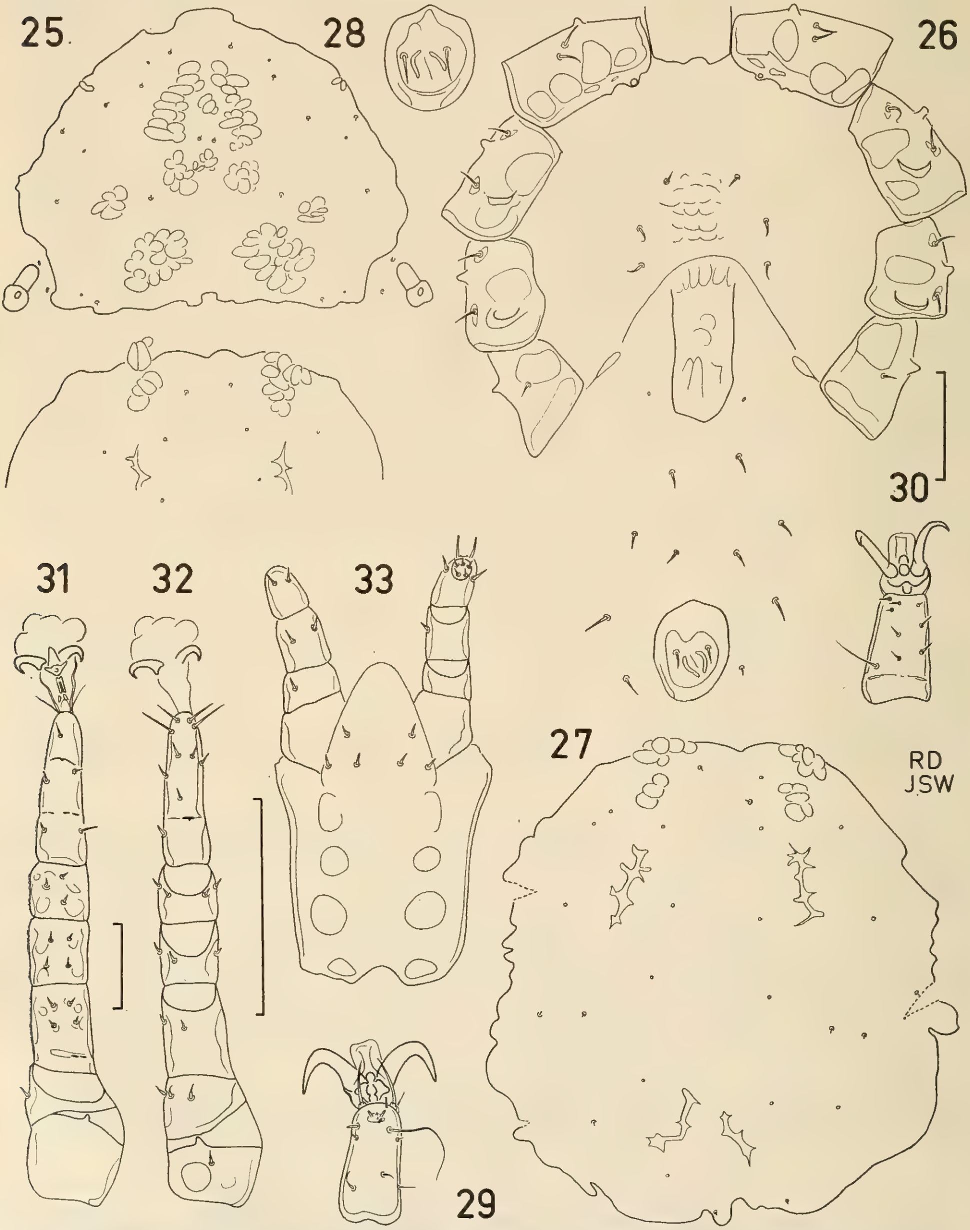
Mesonyssus ptilinopi Wilson, 1964, *Pacif. Insects,* 6: 366; 1965, *Ibid.,* 7: 638; 1966, *J. Parasit.,* 52: 1212; 1968, *J. med. Ent.,* 5: 221.

Previous record.—Purple-crowned pigeon, *Ptilinopus superbus* (Temminck) (Columbidae, Columbiformes).

TINAMINYSSUS MYRISTICIVORAE, n. sp.
(Figs 25–33)

Mesonyssus sp. *"A"* Domrow, 1967, PROC. LINN. SOC. N.S.W., 91: 215.

Diagnosis.—In Wilson's key (1964) to the species of *Tinaminyssus* from columbiform birds, *T. myristicivorae* comes nearest *T. treronis* (Fain), n. comb. However, the new species differs in showing (*i*) considerably shorter setae ventrally on the legs and opisthosoma, on which latter the midanterior



Figs 25–33. *Tinaminyssus myristicivorae*, n. sp. (♀ from *Myristicivora spilorrhoa*).–25–26, Dorsal and ventral views of idiosoma (opisthonotal shield incomplete). 27, Opisthonotal shield (much flattened). 28, Anal shield. 29–30, Dorsal and ventral views of tarsus I. 31–32, Dorsal and ventral views of leg IV. 33, Ventral view of capitulum (right palp in dorsal view).

pair is not obsolescent; (*ii*) claw I considerably stronger than II–IV; and (*iii*) no elongate seta on the palpal tibiotarsus.

There are also differences in leg chaetotaxy, that of the holotype of *T. treronis* being coxae 2.2.2.1; trochanter I (0–1/2–1), II (0–0/3–1), III (1–0/3–0), IV (1–0/4–0); femur I (0–4/3–1), II (0–4/2–1), III (0–4/2–0), IV (0–3/2–0); genu I (1–4/2–1), II–III (0–4/2–1), IV (0–4/2–0); tibiae (1–3/2–1); tarsi—.17.17.17 (*mv* present, but basitarsi trisetose).

T. myristicivorae is separable from the more recently described *T. phassae* (Wilson, 1966*a*) in showing considerably enlarged claws on tarsi I and uniform ventral opisthosomal setae. See also above diagnosis of *T. megaloprepiae*, n. sp., for comments on the leg setation of *T. phassae*, which also differs in detail from that of *T. myristicivorae*.

Types.—Holotype female and two paratype females from a Torres Strait pigeon, *Myristicivora spilorrhoa* (Gray) (Columbidae, Columbiformes), Kowanyama, 22.x.1966, R. D. Holotype N. I. C.; paratypes R. D.

Female.—Idiosoma 605–638μ long in ruptured specimens. Podonotal shield (Fig. 25) 273–276μ long and 366–370μ wide; well defined anteriorly and posteriorly, but with eroded margins and posterolateral excavations at level of peritremes. Surface reticulate, closely punctate, and marked by muscle insertions; with eight pairs of minute setae and three pairs of pores. Opisthonotal shield (Fig. 27) of similar texture, expanded posterolaterally to encroach onto venter; with four or five pairs of minute setae and about eight pairs of pores arranged as figured. Marginal cuticle with few pores near peritremes. Poststigmatic shields absent.

Sternal shield (Fig. 26) indicated only by cessation of cuticular striae; without pores, but with few scale-like markings. SI submarginal, but II–III free in adjacent cuticle. Metasternal setae absent. Genital complex as in *T. megaloprepiae*, n. sp. Anal shield (Fig. 28) slightly longer than wide, 102×94μ, more heavily sclerotized marginally; without cribrum. Anus centrally placed, with adanal setae near its anterior margin; postanal seta absent. Ventral cuticle with about five pairs of short setae, which are only slightly expanded basally, and of which midanterior pair is not obsolescent.

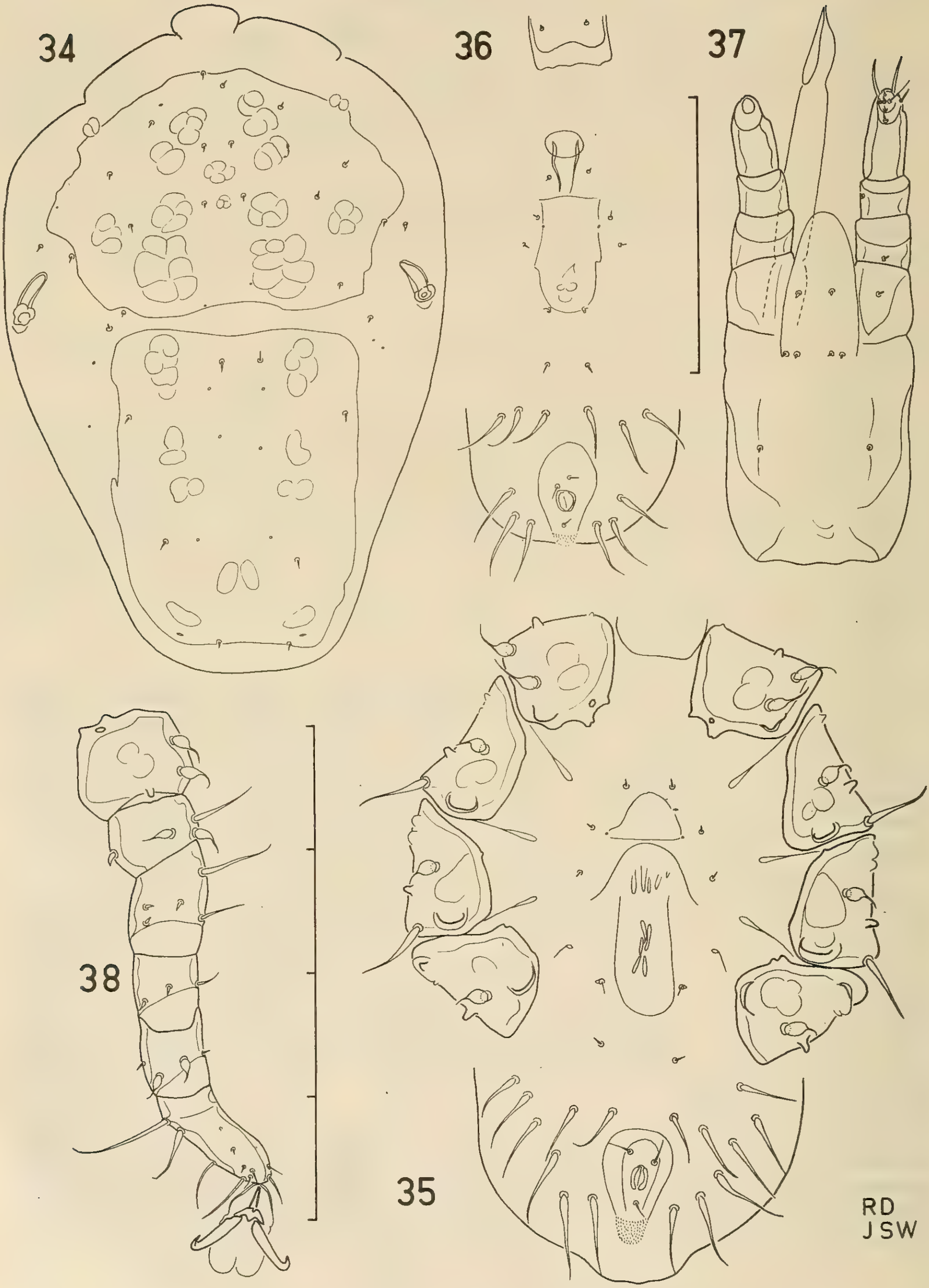
Leg setae also short, particularly on dorsal surface (Figs 31–32). Coxae II–III with sclerotized crescent posteroventrally. Coxae 2.2.2.1. Trochanter I (1–0/2–1), II (2–0/2–1), III–IV (2–0/2–0). Femur I (1–4/3–1) but (1–4/2–1) twice, II (1–4/2–1), III (1–4/1–1) but (1–4/2–1) once, IV (1–4/1–0). Genu I (1–4/2–1), II–III (1–4/0–1), IV (1–4/1–1). Tibiae (1–3/2–1). Tarsi—.18.18.17 (*mv* present; basitarsi II–III with four, but IV with three setae). Ambulacrum I (Figs 29–30) with very short pretarsus and internally sclerotized, truncate pulvillus. Claw I very considerably stronger than II–IV.

Basis capituli (Fig. 33) without capitular setae and deutosternal denticles. Hypostome with three pairs of subequal, spinose setae. Palpal tarsus completely obscured dorsally by tibia; setal formula 0.1.3.6. Chelicerae 116μ long, with chelate portion occupying one-quarter of total length. Tritosternum absent.

TINAMINYSSUS PHABUS (Domrow), n. comb.

Mesonyssus phabus Domrow, 1965, *Acarologia*, 7: 435.

Previous record.—Common bronzewing, *Phaps chalcoptera* (Latham) (Columbidae, Columbiformes), Esk. Also Charleville.



Figs 34–38. *Tinaminyssus macropygiae* (Wilson) (from *Macropygia phasianella*).–34–35, Dorsal and ventral views of idiosoma of ♀. 36, Ventral shields of ♂. 37, Ventral view of capitulum of ♀, with dorsal setation of right palp not shown. 38, Ventral view of leg I of ♀.

TINAMINYSSUS MACROPYGIAE (Wilson), n. comb.

(Figs 34–38)

Mesonyssus macropygiae Wilson, 1966, *Pacif. Insects*, 8: 607; 1968, *J. med. Ent.*, 5: 215.

This species may now be recorded from Australia, the original series being from New Guinea and the Philippines: 19 ♀♀ and 4 ♂♂ from brown pigeons, *Macropygia phasianella* (Temminck) (Columbidae, Columbiformes), Ella Bay and Jordan Creek, 4 and 18.viii.1965, respectively, R. D. and J. S. W.; also 10 ♀♀ and 2 ♂♂, Wilson's Peak, 15.v.1967, R. D. and B. H. K.

Dr. Wilson has kindly confirmed the identity of my material.

TINAMINYSSUS WELCHI, n. sp.

(Figs 39–47)

Mesonyssus sp. *"B"* Domrow, 1967, PROC. LINN. SOC. N.S.W., 91: 215.

Diagnosis.—In Wilson's key (1964), *T. welchi* falls near *T. gourae* (Wilson), n. comb. The two species also show ambulacrum I modified and (as far as can be judged from Wilson's heavily stippled figure) podonotal and opisthonotal shields similar in both their shape and their setation. However, the basally expanded setae on all coxae and the venter of *T. welchi* immediately separate the two species, and further minor differences are to be seen in the armature of coxa IV and the width of the genital shield.

Of the more recently described species from the Australian region, *T. phabus* (Domrow, 1965*c*) and *T. macropygiae* (Wilson, 1966*a*) also show coxal processes and basally expanded setae on the legs, but differ from *T. welchi* in the details of this armature as well as in the shape and setation of the opisthonotal shield and the setation of the venter.

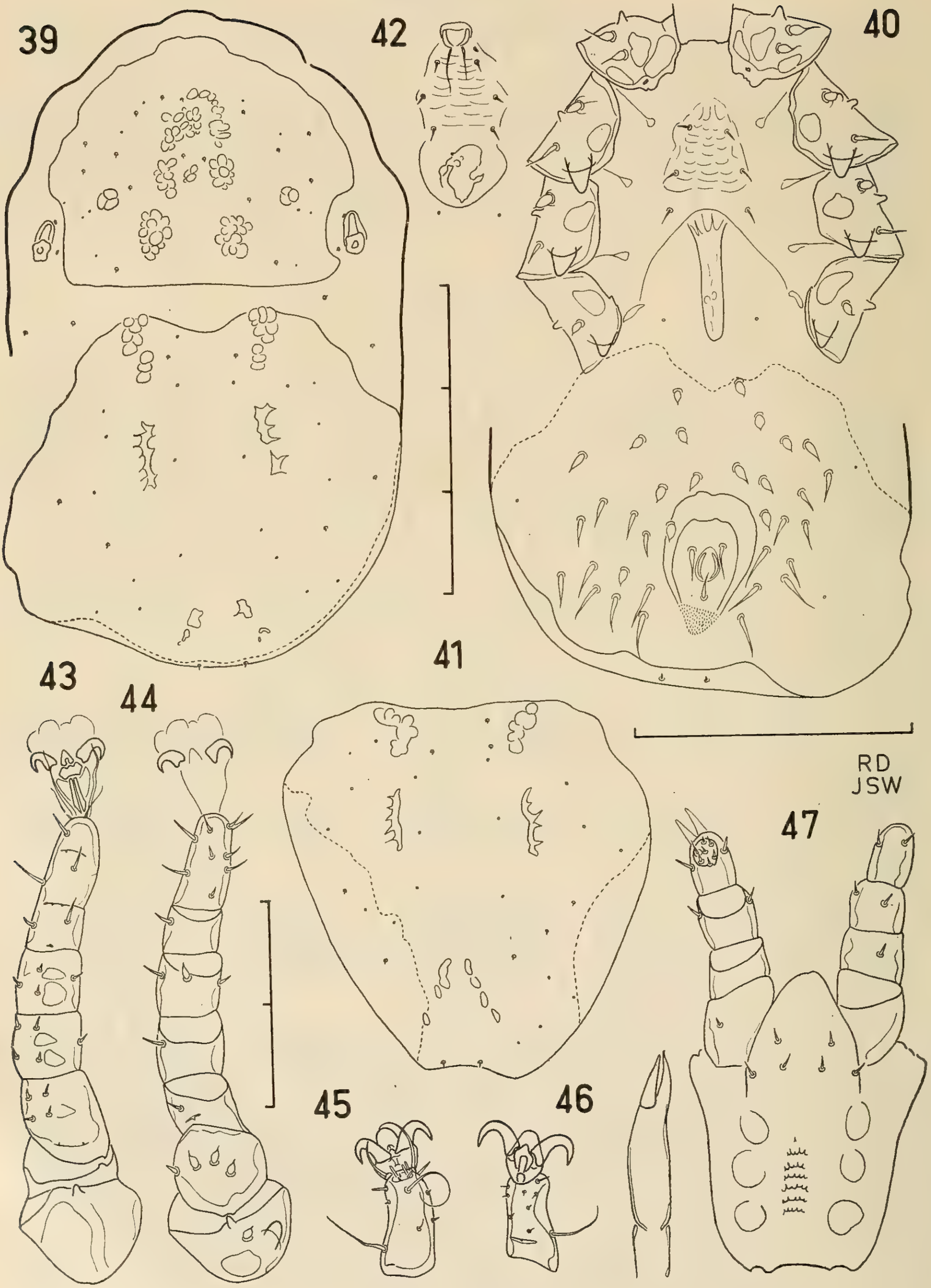
Of the remaining two parasites of columbids briefly diagnosed by Wilson (1966*a*, 1968*b*), *T. angustus* (Wilson), n. comb., is said to have a rectangular opisthonotal shield, and *T. peleiae* (Wilson), n. comb., distinct poststigmatic shields.

Finally, *T. welchi* recalls the neotropical *T. castroae* (do Amaral, 1963*a*), n. comb., which is, however, unique in showing basally expanded genital and sternal setae as well.

Types.—Holotype female, allotype male, five paratype females, and one deutonymph from a Torres Strait pigeon, *Myristicivora spilorrhoa* (Gray) (Columbidae, Columbiformes), Kowanyama, 22.x.1966, R. D. Holotype and allotype N. I. C.; paratypes R. D. and A. F.

Female.—Idiosoma (moderately engorged) 627–660μ long and 385–396μ wide in four somewhat compressed specimens; 627 x 374μ in one unflattened specimen. Podonotal shield (Fig. 39) irregularly arched anteriorly, excavated posterolaterally around stigmata, and rectilinear posteriorly; with eight pairs of minute setae in addition to paired pores and muscle insertions. Opisthonotal shield concave anteriorly and expanded posterolaterally to encroach broadly (Fig. 41) onto venter in unfed, and slightly so in fed specimens; with four pairs of setae (including pygidial pair) in addition to paired pores and muscle insertions. Both shields distinctly reticulate and heavily stippled in entirety. Stigmata with short peritremes; poststigmatic shields absent; adjacent cuticle with four pairs of minute setae.

Sternal shield (Fig. 40) subpentagonal, delineated only by cessation of cuticular striae, very weakly sclerotized, and textureless except for weak scalation; SI and II on shield, III free in cuticle (only one SI in one specimen). Metasternal setae absent. Genital shield narrow, shagreened, and with



Figs 39–47. *Tinaminyssus welchi*, n. sp. (from *Myristicivora spilorrhoa*).–39–40, Dorsal and ventral views of idiosoma of ♀. 41, Opisthonotal shield of unengorged ♀. 42, Sternogenital shield of ♂. 43–44, Dorsal and ventral views of leg IV of ♀. 45–46, Dorsal and ventral views of tarsus I of ♀. 47, Ventral view of capitulum of ♀, with inset of chelicera (left palp in dorsal view).

weak muscle insertions; operculum rayed; genital setae as in *T. megaloprepiae*, n. sp. Anal shield well sclerotized marginally, but transparent centrally; adanal setae level with front of anus, subequal to postanal seta; cribrum present. Ventral cuticle with two to four pores and 34–42 setae, of which 14–16 are basally expanded, with short terminal filament, while remainder are normal, *i. e.* elongate.

Coxae II–IV armed posteriorly—this armature is not simply the crescentic thickening found in *T. ocyphabus* (Domrow, 1965*c*), or the rosette of *T. geopeliae* (Fain, 1964*c*), but a strong, distinctly protruding spur analogous to those present in many species of *Echinonyssus* Hirst and *Trichosurolaelaps* Womersley (see Domrow, 1966*a*). Coxae 2.2.2.1. Trochanter I (1–0/2–1), II (1–0/3–1) but (1–0/3–0) once, III–IV (1–0/3–0). Femur I (1–4/3–1), II (1–4/2–1) but (1–4/3–1) twice and (1–4/2–0) once, III (1–5/1–0) but (0–5/1–0) once, IV (1–4/0–0) but (0–4/0–0) once. Genu I (1–4/2–1), II–IV (1–4/0–1). Tibiae (1–3/2–1). Tarsi—.18.18.17 (*mv* present; basitarsi II–III with four, but IV with three setae). Only the above six variations were noted in the 270 segments checked. Both setae on coxa I, anterior seta on coxae II and III, and seta on coxa IV modified; posterior seta on coxa II and III normal. Modified setae present on venter of remaining segments as follows: one to three on disc of trochanters, and one (often weak) on femur-tibia I and femora and tibiae II–IV. Some tarsal setae slightly expanded basally. Tarsus I incrassate (Figs 45–46), strongly sclerotized, and with dorsodistal sensory islet; pretarsus shorter, claws stronger, and pulvillus smaller (yet less diaphanous) than II–IV.

Basis capituli (Fig. 47) well sclerotized; with about six rows of deutosternal denticles, but without capitular setae. Hypostome with three pairs of subequal setae. Palpi with five free segments, but tarsus obscured dorsally by tibia; setal formula 1.1.4.6. Tarsus with about seven minute setae. All setae on capitulum spine-like. Chelicerae with digits occupying one-quarter of total length (Fig. 47). Tritosternum absent.

Male.—Similar to female, but smaller, idiosoma 495μ long.

Genital area of sternogenital shield hyaline marginally, with very irregular, but strongly sclerotized patch discally (Fig. 42). Venter of opisthosoma with four expanded setae on one side and seven on other; eleven normal setae on each side.

Leg chaetotaxy as in female, except coxa II lacking *pv*, femur III (0–5/1–0), and IV (1–4/1–0) (all on one side only).

Spermatodactyl as long as cheliceral digits.

TINAMINYSSUS HALCYONUS (Domrow), n. comb.

Mesonyssus halcyonus Domrow, 1965, *Acarologia*, 7: 443; Wilson, 1966, *Pacif. Insects*, 8: 609; 1968, *J. med. Ent.*, 5: 213. *Falconyssus halcyonus*, Fain, 1966, *Revue Zool. Bot. afr.*, 74: 86.

Previous records (both Alcedinidae, Coraciiformes).— Sacred kingfisher, *Halcyon sanctus* Vigors and Horsfield, Logan Village and Brisbane. Also Esk, Charleville, Winbin Ck., Half Tide, Innisfail, and Kowanyama. Mangrove-kingfisher, *H. chloris* (Boddaert).

New host records.—Red-backed kingfisher, *H. pyrrhopygius* Gould, Kowanyama, 27 and 30.iii, and 17.iv.1965, R. D. and J. S. W. (11♀♀, 2♂♂, 4 nymphs). Forest kingfisher, *H. macleayii* Jardine and Selby, Innisfail, 3.viii.1965, R. D. and J. S. W. (22♀♀, 6♂♂, 3 nymphs); Kowanyama, 29.iii, 7 and 14.iv.1965, and 12.iii.1967, R. D., B. H. K., H. A. S., and J. S. W. (8♀♀, 1♂).

All specimens are similar dorsally. However, those from *H. pyrrhopygius* and *H. macleayii* show pointed, not spatulate tarsal claws, while the setae on the ventral cuticle are only slightly inflated basally in the former series, and barely at all in the latter.

TINAMINYSSUS DACELOAE (Domrow), n. comb.

Mesonyssus daceloae Domrow, 1965, Acarologia, 7: 445. *Falconyssus daceloae,* Fain, 1966, *Revue Zool. Bot. afr.,* 74: 87.

Previous records (both Alcedinidae, Coraciiformes).—Laughing kookaburra, *Dacelo gigas* (Boddaert), Samford and Esk. Also Condamine and Mt. Jukes. Blue-winged kookaburra, *D. leachii* Vigors and Horsfield, Chelona. Also Kowanyama.

I regret having formed this specific name in the first, rather than the third declension—*Dacelo* Leach is an anagram of *Alcedo* Linnaeus, and is the basis of the subfamily Daceloninae (see Thomson, 1964). Art. 32, however, forbids any change (Stoll *et al.,* 1964).

Genus LARINYSSUS Strandtmann

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

Key to females of Australian species of LARINYSSUS

1. Ventral surface of opisthosoma with about ten pairs of setae. Capitular setae present. Two pairs of hypostomal setae present ....*benoiti* Fain
Ventral surface of opisthosoma with about three pairs of setae. Capitular setae absent. Three pairs of hypostomal setae present ....*orbicularis* Strandtmann

LARINYSSUS BENOITI Fain

Larinyssus benoiti Fain, 1961, *Revue Zool. Bot. afr.,* 63: 128; 1964, *Annls Mus. r. Afr. cent. Sér. 8vo,* 132: 134; Domrow, 1966, PROC. LINN. SOC. N.S.W., 90: 196.

Previous records (both Glareolidae, Charadriiformes).— Australian pratincole, *Stiltia isabella* (Vieillot), Kowanyama. Oriental pratincole, *Glareola pratincola* (Linnaeus).

Fain's single female (1960*b*) was originally misidentified as the following species (personal communication).

LARINYSSUS ORBICULARIS Strandtmann

Larinyssus orbicularis Strandtmann, 1948, *J. Parasit.,* 34: 507; Zumpt and Patterson, 1951, *J. ent. Soc. sth. Afr.,* 14: 78; Bregetova, 1951, *Parazit. Sb.,* 13: 117; Fain, 1956, *Revue Zool. Bot. afr.,* 53: 157. *Larinyssus petiti* Gretillat, 1961, *Vie Milieu,* 12: 155. New synonymy.

Previous records (all Laridae, Charadriiformes).—White-winged black tern, *Chlidonias leucoptera* (Temminck). Gull-billed tern, *Gelochelidon nilotica* (Gmelin). Common tern, *Sterna hirundo* Linnaeus. Sooty tern, *Sterna fuscata* Linneaus. This record is based on host-relationship (Amerson, 1967), and I have been unable to obtain specimens to confirm it. Southern black-backed gull (vagrant), *Larus dominicanus* Lichtenstein.

This widespread parasite of gulls and terns may now be recorded from Australia: 16 ♀♀, 2 ♂♂, and 1 protonymph from a crested tern, *Sterna bergii* Lichtenstein (Laridae), estuary of Topsy Creek, 29.x.1966, R. D. and H. A. S.

Repeated attempts to borrow material of Gretillat's species have been in vain, but the host data and some of the original figures make me certain the synonymy is correct. The alleged single dorsal shield, bearing the stigmata and peritremes, is clear evidence that Gretillat has misinterpreted the dorsal surface of this cosmopolitan parasite of larids.

Genus Rallinyssus Strandtmann

Rallinyssus Strandtmann, 1948, *J. Parasit.*, 34: 512; Wilson, 1965, *Pacif. Insects*, 7: 623. Type-species *Rallinyssus caudistigmus* Strandtmann, 1948, *Loc. cit.*, 512. *Rallinyssoides* Fain, 1960, *Bull. Annls Soc. r. ent. Belg.*, 96: 295. Type-species *Rallinyssus congolensis* Fain, 1956, *Revue Zool. Bot. afr.*, 53: 396; 1957, *Annls Mus. r. Congo belge Sér. 8vo*, 60: 58.

Key to females of Australian species of Rallinyssus

1. Circumanal frill absent 2
Circumanal frill present 3
2 (1). Opisthonotal shield present .... *amaurornis* Wilson
Opisthonotal shield absent .... *congolensis* Fain
3 (1). Podonotal shield about as long as wide, with margin extended laterally beyond sublateral row of muscle insertions. First pair of setae behind podonotal shield closely set, not separated by midposterior convexity of shield .... *gallinulae* Fain
Podonotal shield decidedly longer than wide, with margin not extended laterally beyond sublateral row of muscle insertions. First pair of setae behind podonotal shield widely set, separated by midposterior convexity of shield .... *caudistigmus* Strandtmann

Rallinyssus amaurornis Wilson

Rallinyssus amaurornis Wilson, 1965, *Pacif. Insects*, 7: 624; 1967, *Philipp. J. Sci.*, 95: 215; 1968, *J. med. Ent.*, 5: 221.

Previous record.—White-browed crake, *Poliolimnas cinereus* (Vieillot) (Rallidae, Gruiformes).

Rallinyssus congolensis Fain

Rallinyssus congolensis Fain, 1956, *Revue Zool. Bot. afr.*, 53: 396; 1957, *Annls Mus. r. Congo belge Sér. 8vo*, 60: 58. *Rallinyssus porzanae* Wilson, 1967, *Philipp. J. Sci.*, 95: 215. New synonymy.

Previous record.—Spotless crake, *Porzana tabuensis* (Gmelin) (Rallidae, Gruiformes).

In view of the variation of the podonotal shield discussed under the following species, the two taxa documented above are also synonymized.

Rallinyssus gallinulae Fain

Rallinyssus gallinulae Fain, 1960, *Bull. Annls Soc. r. ent. Belg.*, 96: 295; Domrow, 1965, *Acarologia*, 7: 450; Wilson, 1965, *Pacif. Insects*, 7: 634; 1968, *J. med. Ent.*, 5: 221. *Rallinyssus rallus* Wilson, 1965, *Pacif. Insects*, 7: 631. New synonymy.

Previous records (all Rallidae, Gruiformes).—Lewin water-rail, *Rallus pectoralis* Temminck. Banded landrail, *Hypotaenidia philippensis* (Linnaeus), Innisfail. Eastern swamphen, *Porphyrio melanotus* Temminck.

Australian specimens show the podonotal shield, and its accompanying four shieldlets and sixteen setae, arranged as in Wilson's Fig. 4B. However, the shield, while longer than wide, is rounded laterally, and therefore intermediate between Wilson's eroded, and Fain's subcircular form (Fain's Fig. 1, where, incidentally, there is also a trace of the second pair of accessory shieldlets on the right hand side).

Having established this synonymy, it should be pointed out that, by accepting even further reduction of the podonotal shield as still falling within the range of intraspecific variation, the question is raised of the synonymy of the following species (which has priority), and even of *R. verheyeni* Fain (1963*d*), described from *Rallus* Linnaeus. There is nothing in the way of host-specificity to argue against such a step (see Section V below), and the concept of a single, cosmopolitan species with a circumanal frill, from a wide range of rallids, is not unattractive.

In view of the peculiarly displaced stigmata in this genus, one might postulate that the mites assume some definite spatial orientation in the nasal passages of their hosts.

Rallinyssus caudistigmus Strandtmann

Rallinyssus caudistigmus Strandtmann, 1948, *J. Parasit.*, 34: 512; Bregetova, 1951, *Parazit. Sb.*, 13: 118; Domrow, 1966, Proc. Linn. Soc. N.S.W., 90: 196; Wilson, 1968, *J. med. Ent.*, 5: 221.

Previous records (both Rallidae, Gruiformes).—Dusky moorhen, *Gallinula tenebrosa* Gould, Esk. Coot, *Fulica atra* Linnaeus.

Genus Rhinonyssus Trouessart

Rhinonyssus Trouessart, 1894, *C. r. Séanc. Soc. Biol.*, (10) 1: 723. Type-species *Rhinonyssus coniventris* Trouessart, 1894, *Loc. cit.*, 724. See also note below on *Sternostomum* Trouessart, 1895.

Sommatericola Trägårdh, 1904, "Monographie der arktischen Acariden" (Inaugural Dissertation: Uppsala), p. 28. Type-species *Sommatericola levinseni* Trägårdh, 1904, *Loc. cit.*, 29. This genus is based on *Somateria* Leach, and Neave (1940) also lists the later spelling *Sommateria* Kaup. However, as both these spellings antedate Trägårdh's paper, and it is unlikely he made a change from *Somateria* on his own accord, no change in his spelling seems necessary.

Key to females of Australian species of Rhinonyssus

1. Anal shield present. Distal segments of palpi forming a compact cone barely larger than trochanter 2
Anal shield obsolescent. Distal segments of palpi cylindrical, noticeably longer than trochanter 3
2 (1). Podonotal shield entire. Setae on venter of opisthosoma normal .... *rhinolethrum* (Trouessart)
Podonotal shield fragmented. Setae on venter of opisthosoma in form of stout spines .... *poliocephali* Fain
3 (1). Sternal shield absent. Genital shield elongate .... *coniventris* Trouessart
Sternal shield present. Genital shield as long as broad 4
4 (3). Podonotal shield with posterior margin subrectilinear. Ventral surface of opisthosoma with 10-12 pairs of setae .... *himantopus* Strandtmann
Podonotal shield with distinct posteromedian extension. Ventral surface of opisthosoma with considerably more, or considerably fewer setae 5
5 (4). Ventral surface of opisthosoma with 20-30 pairs of setae .... *sphenisci* Fain and Mortelmans
Ventral surface of opisthosoma with one pair of setae .... *minutus* (Bregetova)

Rhinonyssus rhinolethrum (Trouessart)

Sternostomum rhinolethrum Trouessart, 1895, *Revue Sci. nat. appl.*, 42: 393. This is the spelling given in the title and in the formal listing of the new name. The usage *"rinolethrum"* a few lines later is an example of multiple original spelling and should be corrected under Art. 32. van Eyndhoven (1964) says the labels bear a third spelling. Also Bregetova, 1951, *Parazit. Sb.*, 13: 114.

Rhinonyssus rhinolethrum, Strandtmann, 1951, *J. Parasit.*, 37: 132; 1956, *Proc. ent. Soc. Wash.*, 58: 137; Fain, 1956, *Revue Zool. Bot. afr.*, 53: 149; 1958, *Bull. Soc. r. Zool. Anvers*, 9: 9; 1960, *Revue Zool. Bot. afr.*, 61: 108, 62: 91; Mitchell, 1960, *SWest. Nat.*, 5: 107; 1963, *J. Parasit.*, 49: 506; van Eyndhoven, 1964, *Zoöl. Meded., Leiden*, 39: 303; Wilson, 1964, *Pacif. Insects*, 6: 383; 1968, *J. med. Ent.*, 5: 222.

Rhinonyssus rhinolethrus Domrow, 1966, PROC. LINN. SOC. N.S.W., 90: 196. Trouessart was at pains to indicate that he considered the correct original spelling *Sternostoma* neuter (Arts 30 and 32,), even to the extent of publishing (1895) the unjustified emendation *Sternostomum* (Art. 33) (*v. infra*). I had therefore considered *rhinolethrum* adjectival and amended its termination under Art. 30. However, I now find *rhinolethrum* is formed neither exactly from the adjective ὀλέθριος (*olethrius*) nor the substantive ὄλεθρος (*olethrus*), and, in the absence of a clear statement by Trouessart that his specific name be treated adjectivally rather than substantivally, revert to the original (indeclinable) spelling *rhinolethrum*.

Rallinyssus rhinolethrum Fain, 1962, *Bull. Annls Soc. r. ent. Belg.*, 98: 265. As this entry is immediately preceded by the heading "Genre *Rhinonyssus* . . .", the slip of the pen is obvious, and should therefore be corrected under Art. 32. It should not, presumably, be treated as a new combination.

Sommatericola levinseni Trägårdh, 1904, "Monographie der arktischen Acariden" (Inaugural Dissertation: Uppsala), p. 29. *Sternostomum levinseni*, Bregetova, 1951, *Parazit. Sb.*, 13: 114. *Sternostomum levinsi* (*sic*) Vitzthum, 1935, *J. Orn., Lpz.*, 83: 569. *Rhinonyssus levinseni*, van Eyndhoven, 1964, *Zoöl. Meded., Leiden*, 39: 300. *Rhinonyssus Dartevellei* Fain and Vercammen-Grandjean, 1953, *Revue Zool. Bot. afr.*, 48: 35. The original spelling contravenes Art. 28 and should be corrected to *dartevellei* under Art. 32.

Previous records (all Anatidae, Anseriformes).—Domestic goose, *Anser anser* (Linnaeus). Whistling tree-duck, *Dendrocygna arcuata* (Horsfield) Kowanyama. Black duck, *Anas superciliosa* Gmelin. Garganey teal, *Anas querquedula* Linnaeus. Mallard (introduced), *Anas platyrhynchos* Linnaeus.

New host records.—Maned goose, *Chenonetta jubata* (Latham) (Anatidae), Charleville, 25.i.1967, R. D. and J. S. W. (1 ♀). Grey teal, *Anas gibberifrons* (Müller), Charters Towers, 10.iii.1966, H. J. L. (1♂). Greenshank, *Tringa nebularia* (Gunnerus) (Scolopacidae, Charadriiformes), Kowanyama, 11.xii.1967, R. D. and H. A. S. (1 deutonymph).

Like the single specimen recorded by Strandtmann (1956) from a coot (*Fulica* Linnaeus, Rallidae, Gruiformes) in Thailand, the new specimen from *Tringa* Linnaeus is also best regarded as a straggler — its host was taken at a small swamp where ducks abound. Strandtmann's paper (1958) on the correlation between gregariousness and host-specificity in the Rhinonyssinae should also be consulted. Hirst (1921*a*) compares this species with *R. scoticus,* but the latter is a *nomen nudum,* possibly a discarded manuscript name for one of the other species of *Rhinonyssus* described in the same paper.

RHINONYSSUS POLIOCEPHALI Fain

Rhinonyssus poliocephali Fain, 1956, *Revue Zool. Bot. afr.*, 53: 149; 1957, *Annls Mus. r. Congo belge Sér. 8vo*, 60: 45; Domrow, 1965, *Acarologia*, 7: 450.

Previous record.—Little grebe, *Podiceps ruficollis* (Vroeg) (Podicipidae, Podicipiformes), Esk. Also Kowanyama.

RHINONYSSUS HIMANTOPUS Strandtmann

Rhinonyssus himantopus Strandtmann, 1951, *J. Parasit.*, 37: 136; 1956, *Proc. ent. Soc. Wash.*, 58: 132; 1959, *J. Kans. ent. Soc.*, 32: 134; Fain, 1956, *Revue Zool. Bot. afr.*, 53: 149; 1957, *Annls Mus. r. Congo belge Sér. 8vo*, 60: 44; 1958, *Bull. Soc. r. Zool. Anvers*, 9: 10; *Explor. Parc natn. Albert deux. Sér.*, 6: 9; 1960, *Revue Zool. Bot. afr.*, 62: 92; 1964, *Annls Mus. r. Afr. cent. Sér. 8vo*, 132: 137; Gretillat, 1961, *Vie Milieu*, 12: 155; Domrow, 1966, PROC. LINN. SOC. N.S.W., 90: 195. *Rhinonyssus strandtmanni* Fain and Johnston, 1966, *Bull Soc. r. Zool. Anvers*, 38: 25. New synonymy.

Previous records (all Charadriidae, Charadriiformes).—Red-kneed dotterel, *Erythrogonys cinctus* Gould, Kowanyama. Spur-winged plover, *Lobibyx novaehollandiae* (Stephens), Esk. Masked plover, *L. miles* (Boddaert), Kowanyama. Black-fronted dotterel, *Charadrius melanops* Vieillot, Kowanyama.

New host record.—White-headed stilt, *Himantopus leucocephalus* Gould (Recurvirostridae, Charadriiformes), Kowanyama, 27.x.1966, R. D. and R. H. W. (2 ♀ ♀).

Strandtmann (1951, 1959) has figured two forms of this species. The original series from *H. mexicanus* (Müller) shows the margin of the podonotal shield behind the level of the stigmata almost *rounded*, but with indications of three shallowly convex lobes. The second form, from *Charadrius vociferus* Linnaeus, shows the same bell-shaped shield, but with the posterolateral corners *angulate* and the medial curve less pronounced.

Fain and Johnston (1966) also figured a specimen from *C. vociferus*, but show the posterolateral margin somewhat *eroded*.

The present series from *H. leucocephalus* shows the rounded, and the specimens recorded by Domrow (1966*b*) from *Lobibyx miles* and *L. novaehollandiae* the angulate form. However, I can now refer the specimens from *Erythrogonys cinctus* and *C. melanops* to the eroded, and not to the original rounded form merely because they were non-angulate (Domrow, 1966*b*). I therefore accept all these specimens as falling within the range of individual variation of a single species.

RHINONYSSUS SPHENISCI Fain and Mortelmans

Rhinonyssus sphenisci Fain and Mortelmans, 1959, *Bull. Soc. r. Zool. Anvers*, 12: 13. *Rhinonyssus sphenisci schelli* Fain and Hyland, 1963, *Bull. Soc. r. Zool. Anvers*, 32: 4. New synonymy. *Rhinonyssus schelli*, Wilson, 1967, *Antarctic Res. Ser.*, 10: 41.

Previous record.—Adélie penguin (vagrant), *Pygoscelis adeliae* (Hombron and Jacquinot) (Spheniscidae, Sphenisciformes).

The synonymy is obvious from the descriptions, and both records are

RHINONYSSUS MINUTUS (Bregetova)

Sternostomum minutus Bregetova, 1950, *Dokl. Akad Nauk SSSR*, 71: 1007. *Sternostoma minutus*, Furman, 1957, *Hilgardia*, 26: 483. *Rhinonyssus minutus*, Fain, 1961, *Acarologia*, 3: 514; Domrow, 1965, *Acarologia*, 7: 450. *Rhinonyssus pluvialis* Fain and Johnston, 1966, *Bull. Soc. r. Zool. Anvers*, 38: 27. New synonymy.

Previous records (all Charadriidae, Charadriiformes).—Eastern golden plover, *Pluvialis dominicus* (Müller). Red-capped dotterel, *Charadrius alexandrinus* Linnaeus, Half Tide. Also Tin Can Bay and estuary of Topsy Ck. Ringed plover (vagrant), *C. hiaticula* Linnaeus.

The synonymy is obvious from the descriptions, and all hosts are charadriiforms.

RHINONYSSUS CONIVENTRIS Trouessart

(Figs 48–57)

Rhinonyssus coniventris Trouessart, 1894, *C. r. Séanc. Soc. Biol.*, (10) 1: 724; Hirst, 1921, *Proc. zool. Soc. Lond.*, 1921: 361; Strandtmann, 1951, *J. Parasit.*, 37: 130; 1956, *Proc. ent. Soc. Wash.*, 58: 130; Mitchell, 1961, *SWest. Nat.*, 6: 103; Fain, 1963, *Bull. Annls Soc. r. ent. Belg.*, 99: 88; Domrow, 1965, *Acarologia*, 7: 450. *Rhinonyssus echinipes* Hirst, 1921, *Proc. zool. Soc. Lond.*, 1921: 359. *Rhinonyssus neglectus* Hirst, 1921, *Proc. zool. Soc. Lond.*, 1921: 359; Bregetova, 1951, *Parazit. Sb.*, 13: 117. *Rhinonyssus tringae* Fain, 1963, *Bull. Annls Soc. r. ent. Belg.*, 99: 96. *Rhinonyssus* sp. Domrow, 1967, PROC. LINN. SOC. N.S.W., 91: 216.

Previous records (all Charadriiformes).—Turnstone, *Arenaria interpres* (Linnaeus) (Charadriidae). Grey plover, *Squatarola squatarola* (Linnaeus) (Charadriidae). Eastern golden plover, *Pluvialis dominicus* (Müller) (Charadriidae). Red-capped dotterel, *Charadrius alexandrinus* Linnaeus, Half Tide. Also Tin Can Bay. Ringed plover (vagrant), *Charadrius hiaticula* Linnaeus. Wood-sandpiper, *Tringa glareola* Linnaeus (Scolopacidae). Sanderling, *Crocethia alba* (Vroeg) Scolopacidae). Dunlin (vagrant), *Erolia alpina* (Linnaeus) (Scolopacidae). Knot, *Calidris canutus* (Linnaeus) (Scolopacidae).

New host record.—Red-necked stint, *Erolia ruficollis* (Pallas) (Scolopacidae), estuary of Topsy Ck., 29.x.1966, R. D. (1 ♀).

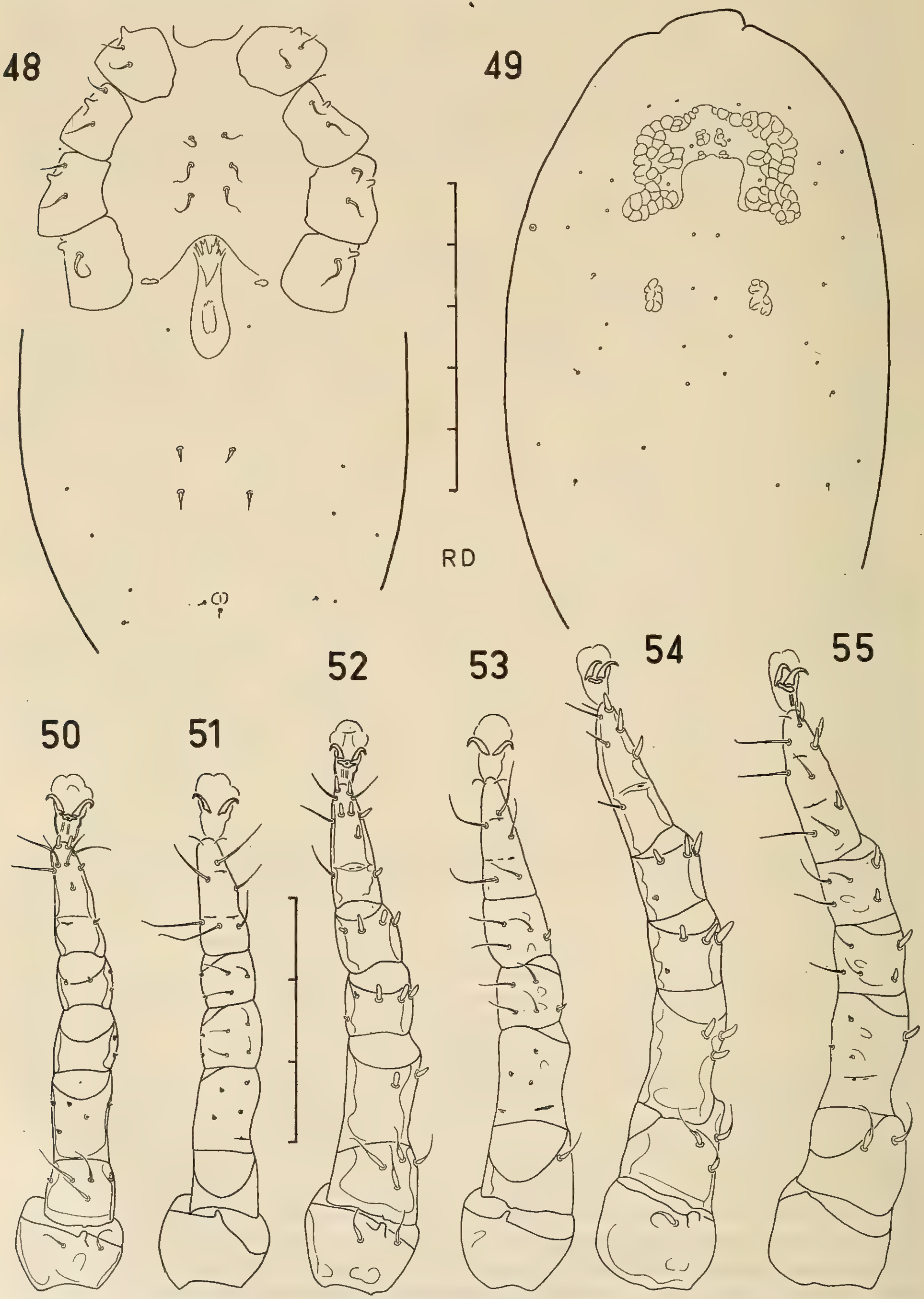
Two considerations underline the artificiality of distinguishing, even as subspecies, the three nominal taxa of Trouessart and Hirst, whose hosts include a range of charadriiform birds. On a morphological level, Strandtmann (1951), studying material from Trouessart's type-host, *A. interpres,* figured a female with a *coniventris*-like, and a male with a *neglectus*-like podonotal shield. Indeed, the degree of erosion of the podonotal shield shows clinal variation in the direction *R. echinipes*—*R. coniventris*—*R. neglectus*, but a convincingly identical pattern of muscle insertions is retained in all three. Further, Fain (1963*a*), in an *addendum,* records specimens from the same host, which bridge another morphological gap (setation of femur IV) in the first couplet of his key attempting to separate the three forms.

On an ecological level, Fain (1963*a*) lists *R. c. echinipes* from *Charadrius alexandrinus* in Europe, and suggests this form is host-specific for *Charadrius* Linnaeus. However, in Queensland, two further series (3 ♀ ♀ and 1 ♂, Tin Can Bay, 29.vi and 17.viii.1966, R. D. and J. S. W.) confirm my earlier record (1965*c*) of a *neglectus*-like form from *C. alexandrinus*.

The female from *E. ruficollis* recalls *R. tringae* in the shape of its podonotal shield, but perhaps even here the same pattern of muscle insertions noted above can be made out (Fig. 56), and I therefore maintain the synonymy. (A paratype of *R. tringae* agrees well with Fain's illustration, but shows a distinct setal remnant towards the rear of each arm of the podonotal shield.)

The new Queensland specimen is illustrated in detail (Figs 48–57) because its setation (*e.g.* on the sternal shield and tarsus IV) differs somewhat from that of Fain's material. Apart from tarsus I, which is identical ventrally with Fain's Fig. 10, leg I is similar to leg II, except that (*i*) only two filamentous setae are present on the trochanter; (*ii*) seven minute setae are present ventrally on the femur; and (*iii*) two additional minute setae are present on the ventrodistal margin of the genu. The setal formulae, therefore, are: coxae 2.2.2.1; trochanters 4.5.5.5; femora 11.10/9.5.7; genua 10.8.10.9; tibiae 9.9.8.9; tarsi–.18.18.18 (*mv* present).

A species such as *R. coniventris,* morphologically much reduced and with a world-wide distribution throughout a group of birds as extensive as the Charadrii, may be expected to show a wider range of individual variation than a more zoogeographically restricted species.



Figs 48–55. *Rhinonyssus coniventris* Trouessart (♀ from *Erolia ruficollis*).–48–49, Ventral and dorsal views of idiosoma. 50–55, Ventral and dorsal views of legs II–IV.

Genus Ruandanyssus Fain

Ruandanyssus Fain, 1957, *Annls Parasit. hum. comp.*, 32: 148. Type-species *Ruandanyssus terpsiphonei* Fain, 1957, *Loc. cit.*, 148.

Key to females of Australian species of RUANDANYSSUS

1. Opisthonotal shield considerably narrower than podonotal shield, and tapering posteriorly. Most idiosomal setae reaching at least half way to the base of the next nearest seta. Tritosternum with fully formed laciniae........ ....*terpsiphonei* Fain

Opisthonotal shield almost as wide as podonotal shield, and somewhat truncate posteriorly. Most idiosomal setae falling far short of the base of the next nearest seta. Tritosternal laciniae obsolescent .... *artami*, n. sp

Ruandanyssus terpsiphonei Fain

(Figs 58–68)

Ruandanyssus terpsiphonei Fain, 1957, *Annls Parasit. hum. comp.*, 32: 148; 1960, *Revue Zool. Bot. afr.*, 62: 98; Domrow, 1965, *Acarologia*, 7: 432. *Ruandanyssus terpsiphonei terpsiphonei*, Sakakibara, 1968, *J. med. Ent.*, 5: 17. *Ruandanyssus terpsiphonei echongi* Sakakibara, 1968, *J. med. Ent.*, 5: 15. New synonymy.

Previous records (all Passeriformes).—Spectacled flycatcher, *Monarcha trivirgata* (Temminck) (Muscicapidae), Mt. Jukes. Also Innisfail. Black-faced cuckoo-shrike, *Coracina novaehollandiae* (Gmelin) (Campophagidae), Esk. Little cuckoo-shrike, *C. robusta* (Latham), Esk. Rufous whistler, *Pachycephala rufiventris* (Latham) (Pachycephalidae), Esk and Mt. Jukes. Apostle-bird, *Struthidea cinerea* Gould (Corvidae), Condamine.

New host records (all Passeriformes).—Leaden flycatcher, *Myiagra rubecula* (Latham) (Muscicapidae), Brisbane, 15.ix.1965, Esk, 13.ii.1968, and Innisfail, 3.viii.1965, R. D., B. H. K., and J. S. W. (16 ♀ ♀, 4 ♂ ♂, and 1 protonymph). White-winged triller, *Lalage tricolor* (Swainson) (Campophagidae), Kowanyama, 25.x.1966, R. D. (2 ♀ ♀, 1 ♂). White-browed scrub-wren, *Sericornis frontalis* (Vigors and Horsfield) (Sylviidae), Esk, 6.x.1966, R. D. and J. S. W. (13 ♀ ♀, 1 ♂). Masked wood-swallow, *Artamus personatus* (Gould) (Artamidae), Charleville, 24.i.1967, R. D. and J. S. W. (1 ♀). Golden whistler, *Pachycephala pectoralis* (Latham) (Pachycephalidae), Esk, 14.vii.1965, R. D. and J. S. W. (15 ♀ ♀, 4 ♂ ♂, 1 protonymph). Grey whistler, *P. griseiceps* Gray, Innisfail, 8.vii, and 1 and 10.ix.1965, G. J. B. and H. I. McD. (36 ♀ ♀, 5 ♂ ♂, 1 proto-, and 1 deutonymph).

As presaged by the absence of one genital seta, the female I illustrated (1965*c*) is confirmed as an extreme individual variant lacking both metasternal setae. On checking a long series of both sexes, both metasternals were invariably found present (as originally figured for the male), except in one specimen, where one is lacking (Figs 67–68).

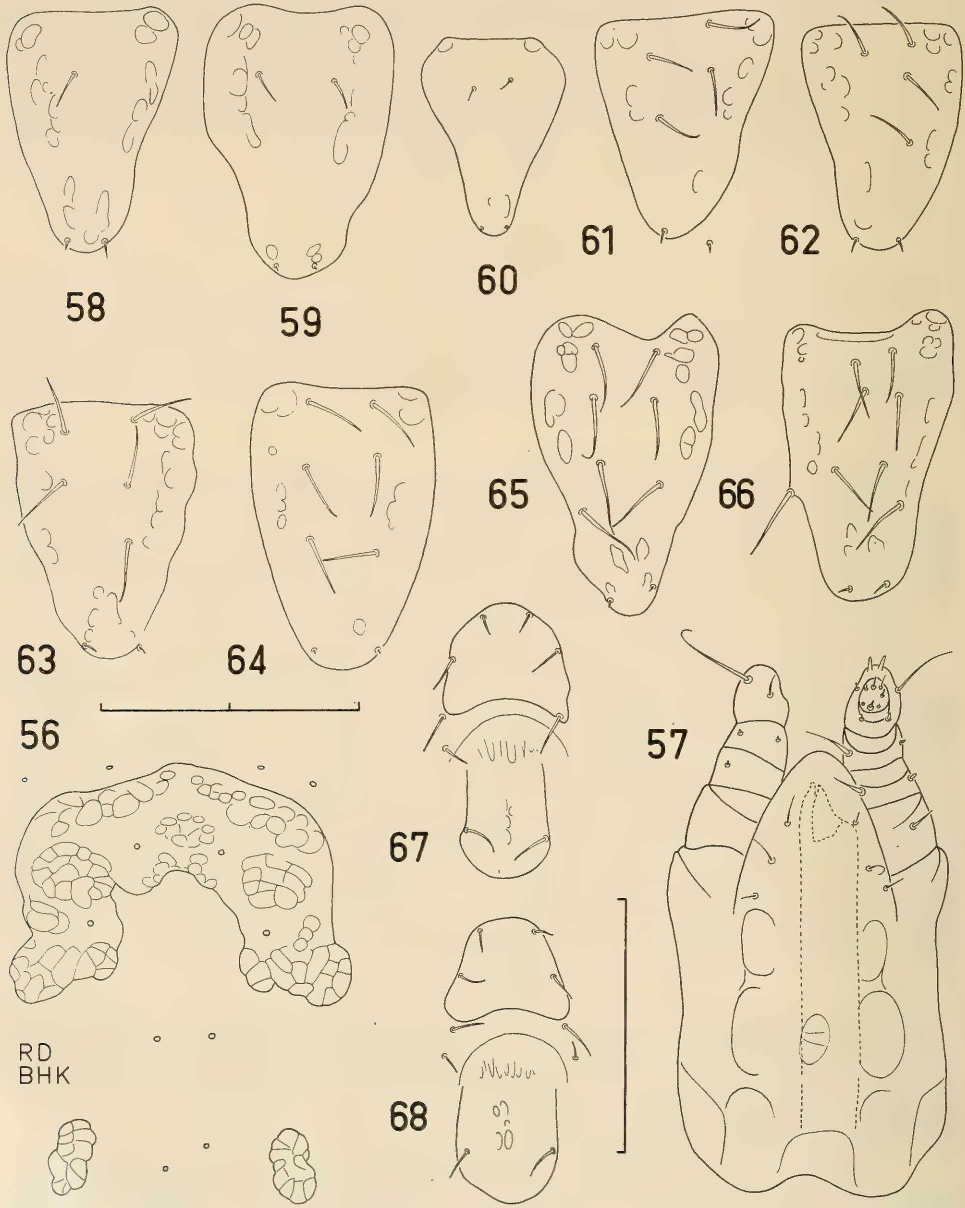
Further, an examination of 75 specimens yielded no aberrancies from the 1.1 discal setae figured by Fain and myself on the opisthonotal shield except 1.0 three times (Figs 58–60). However, the material from *Myiagra rubecula* differs in showing additional longitudinally arranged pairs of discal setae on the opisthonotal shield. The following formulae were noted: 1.3 once, 2.2 once, 2.3 four times, 3.3 nine times, 3.4 three times, and 4.4 once (Figs 61–66). I do not feel these minor varieties merit a name.

RUANDANYSSUS ARTAMI, n. sp.

(Figs 69–74, 161–164)

Ruandanyssus sp. Domrow, 1967, Proc. Linn. Soc. N.S.W., 91: 217.

Diagnosis.—*R. artami* is readily separable from the preceding, and only other known species, *R. terpsiphonei* Fain (1957*a*), by using the key above.



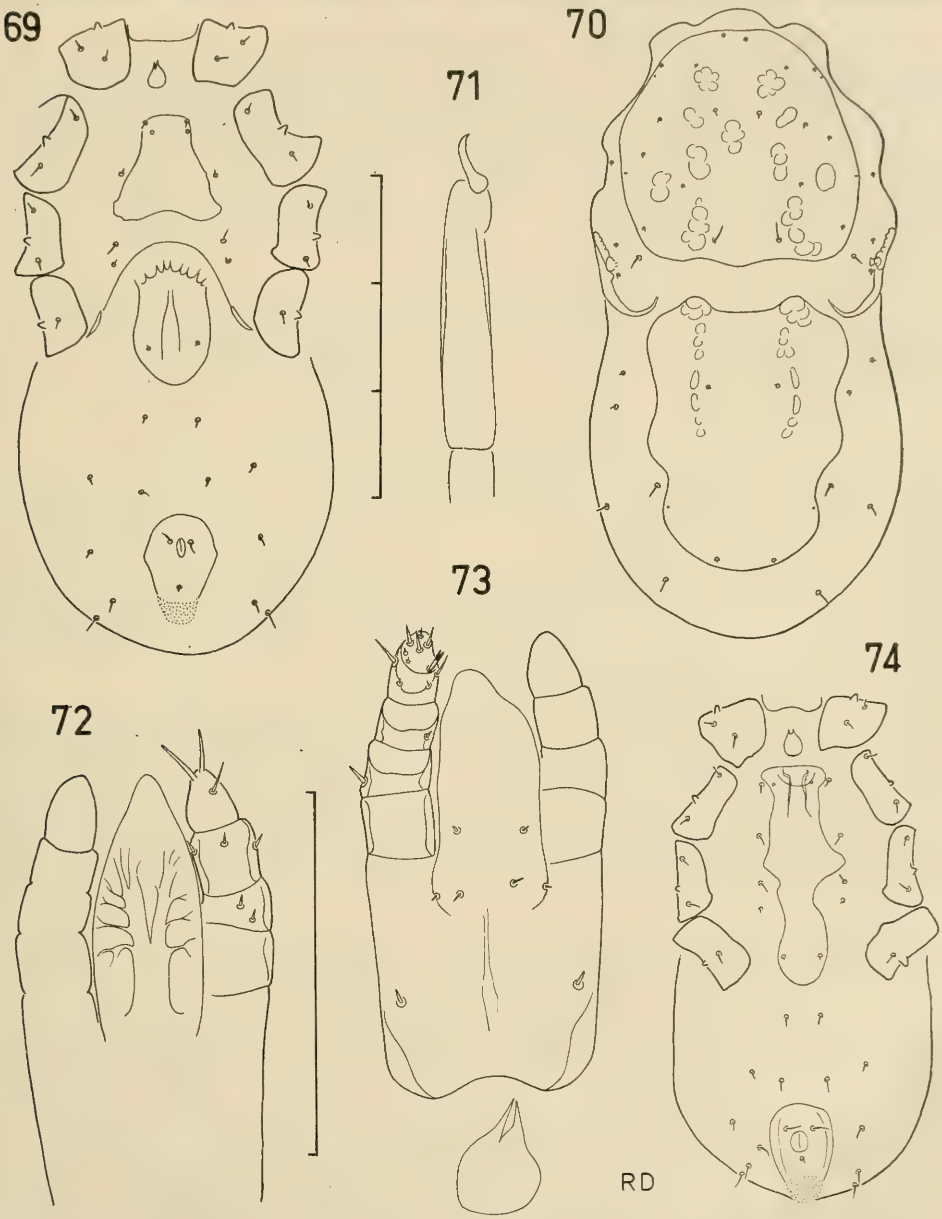
Figs 56–57. *Rhinonyssus coniventris* Trouessart (♀ from *Erolia ruficollis*).–56, Podonotal shield and mesonotal shieldlets. 57, Ventral view of capitulum (right palp in dorsal view).

Figs 58–68. *Ruandanyssus terpsiphonei* Fain.–58, Opisthonotal shield of ♂ from *Monarcha trivirgata*. 59–60, Opisthonotal shield of ♀♀ from *Pachycephala rufiventris* and *Sericornis frontalis*. 61–62, Opisthonotal shield of ♂♂ from *Myiagra rubecula*. 63–66, Opisthonotal shield of ♀♀ from *M. rubecula*. 67–68, Sternal and genital shields of ♀♀ from *P. griseiceps*.

Types.—Holotype female, allotype male, and two paratype females from black-faced wood-swallows, *Artamus cinereus* Gould (Artamidae, Passeriformes), Kowanyama, 27.iii and 1.iv.1965, R. D. and J. S. W. Holotype and allotype N. I. C.; paratypes R. D and A. F.

Also 3 ♀ ♀, 1 ♂, and 2 protonymphs from a little wood-swallow, *A. minor* Vieillot, Charleville, 23.i.1967, R. D. and J. S. W.

Female.—Idiosoma 585–595μ long in little compressed specimens (one containing embryonic larva, another with undeveloped ovum extruded),



Figs 69–74. *Ruandanyssus artami*, n. sp. (from *Artamus cinereus*).–69–70, Ventral and dorsal views of idiosoma of ♀. 71, Chelicera of ♀. 72–73, Dorsal and ventral views of capitulum of ♀. 74, Ventral view of idiosoma of ♂.

slightly constricted behind stigmata. Podonotal shield (Fig. 70) as long as wide, rather evenly rounded anteriorly and laterally, but with posterior margin weakly trilobate; with nine pairs of setae (only midposterior pair prominent), and two pairs of submarginal pores. Opisthonotal shield concave anteriorly, roundly convex posteriorly, and trilobate laterally; with one pair of small setae discally in addition to terminal pygidial pair. Both shields closely granulate (except for narrow marginal strip), and further marked by paired muscle insertions. Dorsal cuticle with nine pairs of setae of varying size. Stigmata provided with short peritremes and followed by lateroventrally-directed poststigmatic shields.

Sternal shield (Fig. 69) subtriangular, well sclerotized, granulate, but with indefinite margins; bearing SI (with attendant pores) and flanked by SII–III; metasternal setae present, but small. Genital shield drop-shaped, weakly granulate, with some longitudinal strengthening discally, and rounded, rayed operculum; genital setae small. Anal shield longer than wide, well rounded at front, and denser at sides; cribrum present. Anus set well forward, with adanal setae near its anterior edge; postanal seta smaller, set well back from anus. Ventral cuticle with twelve setae arranged 2.4.6. All body setae simple, with rather blunt tips.

Leg setae similar (Figs 163–164). Coxae 2.2.2.1. Trochanter I (1–0/2–1), II (1–1/2–1), III–IV (1–0/2–1). Femur I (2–3/1–2), II (1–4/2–1), III (1–4/1–0), IV (1–4/0–0). Genu I (1–4/1–1), II–III (1–4/0–1), IV (1–3/0–0). Tibia I (1–4/2–1), II–IV (1–3/2–1). Tarsi – .17.17.16 (*mv* lacking on II–IV; ad_2 also lacking on IV). Minor variants common on femora (I with 1 *pl*, II with 1 *v* or 0 *pl*, III with 0 *v*, IV with 3 *d*), and tarsi (III lacking al_2 or av_2, IV lacking al_2 or al_3). Tarsus I with 21 setae in addition to dorsodistal sensory islet of five rods (Figs 161–162). Two lyriform fissures present, one dorsally and one posterolaterally (I) or anterolaterally (II–IV), between basi- and telofemora. Tarsi II–IV with four lyriform fissures, one dorsobasally on basitarsus, one middorsally on telotarsus, and one dorsally (divided) and one ventrally between basi- and telotarsus. Tarsus I with two fissures only (first and last of above four). Ambulacrum I similar to II–IV, but pretarsus slightly stouter.

Basis capituli (Figs 72–73) with indication of deutosternum, but without denticles; with two capitular setae. All six hypostomal setae present, but small. Epistome hyaline marginally, with denser dendritic area discally. Palpi with usual five free segments; setal formula 0.3.4.7. Genu with dorsobasal lyriform fissure. Tarsus obscured dorsally by tibia; with about six small setae. Claw bifid. Cheliceral shaft of uniform diameter; single (movable) digit falcate, occupying one-sixth of total length (Fig. 71). Tritosternum hyaline, with base well developed, but laciniae obsolescent.

Male.—Idiosoma 485μ long in slightly compressed specimen. Essentially as in female except for fusion of sternal, metasternal, and genital complexes (Fig. 74), and presence of spermatodactyl on chelicerae.

Protonymph.—Podonotal shield as in female, but with only eight pairs of setae (verticals lacking). Pygidial shield indistinct, but with two barbulate setae twice as strong as strongest of simple dorsal setae. Setal arrangement on dorsal cuticle as in female, but including pair of setae taken in discally by expansion of pygidial shield into opisthonotal shield. Stigmata with peritremes, but unarmed.

Sternal shield with two pores near SI; SI–III submarginal. Anal shield as in female. Ventral cuticle with eight setae arranged 2.4.2.

Chaetotaxy of coxae, genua, tibiae, and tarsi as in adult (minute ventrodistal setae on plantar surface of tarsus I difficult to see even at ×500), with following individual variation: coxa III lacking *pv* once, and genu IV (1–2/0–0) twice. Trochanters as in adult, except IV (1–0/2–0), with following individual variations: II (1–0/2–1) once, and III (1–0/2–0) once. Femur I as in adult, II (1–4/1–0), III (1–3/1–0), IV (1–3/0–0), with following individual variation: II (1–4/1–1) once. Lyriform fissures arranged as in adult, but dorsobasal fissure on basitarsus I absent, and dorsal fissure between basi- and telotarsi II–IV undivided.

Capitulum as in female, but with five deutosternal denticles in single file.

Genus RHINOECIUS Cooreman

Rhinoecius Cooreman, 1946, *Bull. Mus. r. Hist. nat. Belg.*, 22: 1. Type-species *Rhinoecius oti* Cooreman, 1946, *Loc. cit.*, 1. *Zumptnyssus* Fain, 1959, *Bull. Annls Soc. r. ent. Belg.*, 95: 112. Type-species *Ruandanyssus buboensis* Fain, 1958, *Revue Zool. Bot. afr.*, 58: 292. New synonymy.

The presence or absence of a tritosternum, as indicated under *Tinaminyssus* above, and *Ptilonyssus* below, has no meaning at a generic level. Further, both genera are restricted to owls.

Key to females of Australian species of RHINOECIUS

1. Podonotal shield entire .... *cooremani* Strandtmann
Podonotal shield fragmentary, with one larger anterior, and four smaller posterior fragments .... *tytonis* Fain

RHINOECIUS COOREMANI Strandtmann

(Figs 75–77)

Rhinoecius cooremani Strandtmann, 1952, *Proc. ent. Soc. Wash.*, 54: 208.

This genus, previously recorded only from strigid owls in Europe, Africa, and the U.S.A., may now be added to the Australian fauna: 9 ♀ ♀ and 1 protonymph from a boobook owl, *Ninox novaeseelandiae* (Gmelin) (Strigidae, Strigiformes), Esk, 5.i.1966, R. D. and J.S.W.

I have examined paratypes of Strandtmann's three species (two of which have been further illustrated by do Amaral, 1962), and my specimens differ from his *R. cooremani* only in showing (*i*) the anteriormost pair of dorsal cuticular setae apparently set on the margin of the podonotal shield (Fig. 77) (I say "apparently" because the cuticle on the specimens available is somewhat exfoliated, and could have come, together with its setae, to lie over the edge of the shield); and (*ii*) the postanal seta present, but rather weaker than the adanals (Figs 76–77). The capitulum is depicted in Fig. 75.

RHINOECIUS TYTONIS Fain

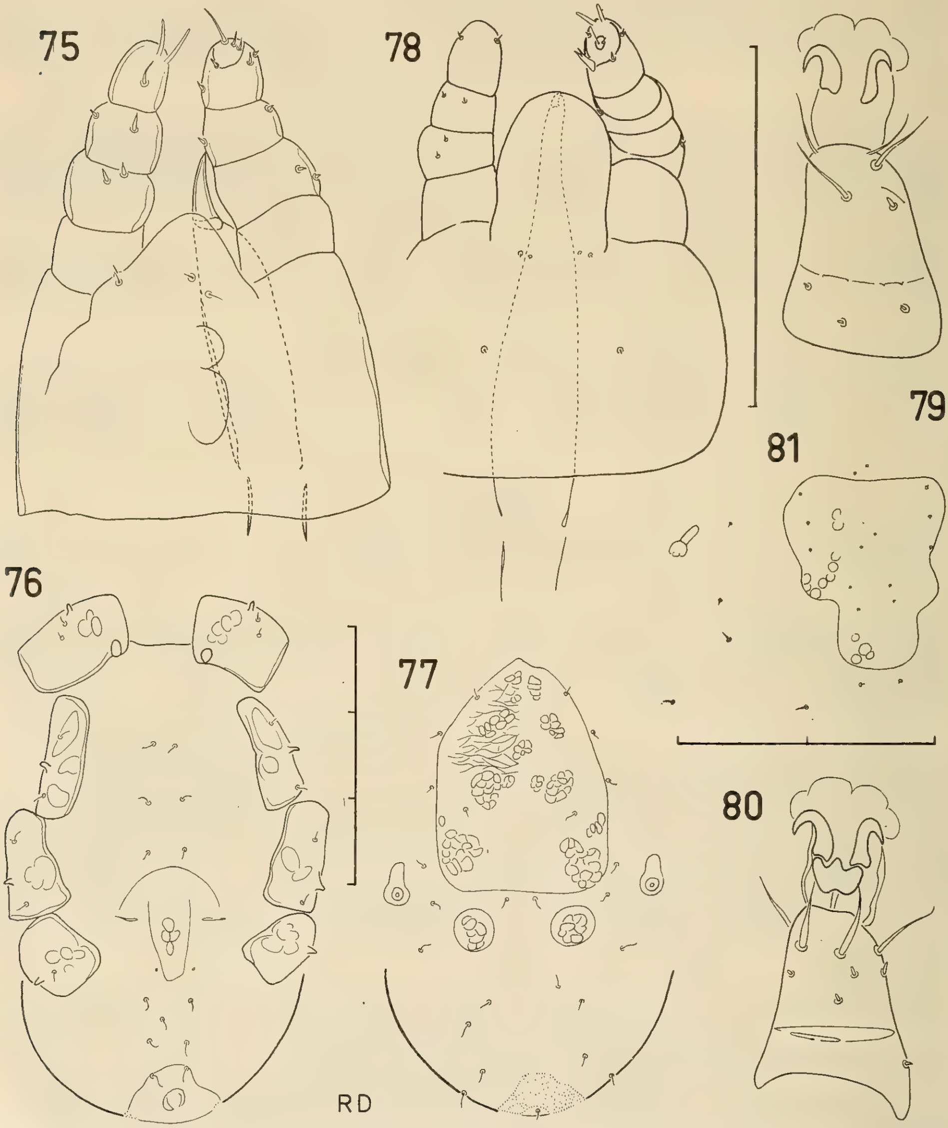
Rhinoecius tytonis Fain, 1956, *Revue Zool. Bot. afr.*, 53: 394; 1957, *Annls Mus. r. Congo belge Sér. 8vo*, 60: 131, 138.

Previous record.—Barn-owl, *Tyto alba* (Scopoli) (Tytonidae, Strigiformes).

Genus PTILONYSSUS Berlese and Trouessart

Ptilonyssus Berlese and Trouessart, 1889, *Bull. Biblioth. scient. Ouest*, 2: 128. Type-species *Ptilonyssus echinatus* Berlese and Trouessart, 1889, *Loc. cit.*, 129. *Rhinonyssoides* Hirst, 1921, *Proc. zool. Soc. Lond.*, 1921: 770. Type-species *Rhinonyssoides trouessarti* Hirst, 1921, *Loc. cit.*, 770. *Neonyssus* Hirst, 1921, *Proc. Zool. Soc. Lond.*, 1921: 771. Type-species *Neonyssus intermedius* Hirst, 1921, *Loc. cit.*, 771. *Neonyssoides* Hirst, 1923, *Proc. zool.*

Soc. Lond., 1923: 975. Type-species *Rhinonyssus* (*Neonyssoides*) *nucifragae* Hirst, 1923, *Loc. cit.*, 975. Hirst's three type-species have since been described and illustrated by Fain (1960*a*), Fain and Hyland (1962*b*), and Bregetova (1967). *Ptilonyssoides* Vitzthum, 1935, *J. Orn., Lpz.*, 83: 581. Type-species *Ptilonyssoides triscutatus* Vitzthum, 1935, *Loc. cit.*, 581. *Rhinacarus* de Castro, 1948, *Archos Inst. biol., S Paulo*, 18: 257, *nec* Nehring, 1884, *Sber. Ges.*



Figs 75–77. *Rhinoecius cooremani* Strandtmann (♀ from *Ninox novaeseelandiae*).–75, Ventral view of capitulum (right palp in dorsal view). 76–77, Ventral and dorsal views of idiosoma.

Figs 78–80. *Ptilonyssus neochmiae*, n. sp. (♀ from *Neochmia phaeton*).–78, Ventral view of capitulum (right palp in dorsal view). 79–80, Dorsal and ventral views of tarsus III.

Fig. 81. *Ptilonyssus cinnyris* Zumpt and Till (♀ from *Cyrtostomus frenatus*).–Opisthonotal shield.

naturf. Freunde Berl., 1884: 64. Type-species *Rhinonyssus* (*Rhinacarus*) *angrensis* de Castro, 1948, *Loc. cit.*, 257. New synonymy. The relevant paragraph of Nehring runs: "*Der Name* Halarachne *erscheint mir nicht sehr glücklich gewählt, da diese Milbe nach den bisherigen Beobachtungen keineswegs frei im Meerwasser lebt, sondern ihre Existenz an die Nasenhöhle der Kegelrobben (vielleicht auch anderer Pinnipedier) bindet und sich vermuthlich nur von Thier zu Thier überträgt. Ich würde sie* Rhinixodes *oder* Rhinacarus *nennen, wenn sie neu zu benennen wäre.*" Nehring's use of the subjunctive indicates that he did not mean to erect these names for possible use in the future, but that he was only indicating what names he himself might have used had he been naming the taxon. Indeed, he did not even show a preference for either name, and it could be argued that the names were not proposed for taxonomic use (Art. 1). On the other hand, assuming these names were proposed for taxonomic use, they can only be considered as synonyms of *Halarachne* Allman, as did Nehring himself, since he continued to use *Halarachne*. Thus, as names first published as synonyms, they are unavailable under Art. 11.

Flavionyssus de Castro, 1948, *Archos Inst. biol., S Paulo*, 18: 266. Type-species *Ptilonyssus* (*Flavionyssus*) *rabelloi* de Castro, 1948, *Loc. cit.*, 266. *Rochanyssus* de Castro, 1948, *Archos Inst. biol., S Paulo*, 18: 272. Type-species *Neonyssus* (*Rochanyssus*) *werneri* de Castro, 1948, *Loc. cit.*, 272. *Paraneonyssus* de Castro, 1948, *Archos Inst. biol., S Paulo*, 18: 274. Type-species *Neonyssus* (*Paraneonyssus*) *enriettii* de Castro, 1948, *Loc. cit.*, 274. *Travanyssus* de Castro, 1948, *Archos Inst. biol., S Paulo*, 18: 276. Type-species *Neonyssus* (*Travanyssus*) *paranensis* de Castro, 1948, *Loc. cit.*, 276. *Vitznyssus* de Castro, 1948, *Archos Inst. biol., S Paulo*, 18: 277. Type-species *Dermanyssus nitzschi* Giebel, 1871, *Z. ges. Naturw.*, 38: 31. New synonymy. *Cas* Baker and Wharton, 1952, "An introduction to acarology" (Macmillan: New York), p. 81 (unnecessary *nomen novum* for *Rhinacarus* de Castro). Type-species as for *Rhinacarus* de Castro, *v. supra*. New synonymy. *Astridiella* Fain, 1957, *Riv. Parassit.*, 18: 94. Type-species *Ptilonyssus scotornis* Fain, 1956, *Revue Zool. Bot. afr.*, 53: 148. New synonymy. *Hapalognatha* Butenko, 1959, *Nauch. Dokl. vysh. Shk.*, 2: 17; 1960, *Zool. Zh.*, 39: 1490. Type-species *Hapalognatha prima* Butenko, 1959, *Loc. cit.*, 17 (*nomen nudum* under Art. 13); 1960, *Loc. cit.*, 1490. *Passeronyssus* Fain, 1960, *Revue Zool. Bot. afr.*, 61: 110; 1962, *Ibid.*, 66: 139; Fain and Nadchatram, 1962, *Bull. Annls Soc. r. ent. Belge.*, 98: 275. Type-species *Ptilonyssus viduae* Fain, 1956, *Revue Zool. Bot. afr.*, 53: 147; 1957, *Annls Mus. r. Congo belge Sér. 8vo*, 60: 120. New synonymy. *Tyranninyssus* Brooks and Strandtmann, 1960, *J. Parasit.*, 46: 418. Type-species *Tyranninyssus tyrannus* Brooks and Strandtmann, 1960, *Loc. cit.*, 419. New synonymy. *Locustellonyssus* Bregetova, 1964, "Some problems of evolution of the rhinonyssid mites" (Nauka: Leningrad). *Locustellonyssus* is not mentioned in the text of this article, but occurs in an accompanying photograph of a table on host-specificity. This does not constitute publication under Art. 8; and, in any case, as no type-species is given, *Locustellonyssus* is unavailable here under Art. 13. Also 1965, *Zool. Zh.*, 44: 1093. Type-species *Locustellonyssus amurensis* Bregetova, 1965, *Loc. cit.*, 1093. New synonymy. *Periglischrodes* Baker and Delfinado, 1964, *Pacif. Insects*, 6: 589. Type-species *Periglischrodes gressitti* Baker and Delfinado, 1964, *Loc. cit.*, 589. *Otocorinyssus* Bregetova, 1967, *Parazit. Sb.*, 23: 127. Type-species *Neonyssus* (*Otocorinyssus*) *melanocoryphae* Bregetova, 1967, *Loc. cit.*, 127. New synonymy. *Frigilonyssus* Bregetova, 1967, *Parazit. Sb.*, 23: 130. Type-species *Ptilonyssus coccothraustis* Fain and Bafort, 1963, *Bull. Annls Soc. r. ent. Belg.*, 99: 447. New synonymy. *Spizonyssus* Bregetova, 1967, *Parazit. Sb.*, 23: 131. Type-species *Ptilonyssus serini* Fain, 1956, *Revue Zool. Bot. afr.*, 53: 139; 1957, *Annls Mus. r. Congo* *belge Sér. 8vo,* 60: 90. New synonymy. *Neotyranninyssus* Fain and Aitken, 1967, *Bull. Inst. r. Sci. nat. Belg.,* 43: 27. Type-species *Neotyranninyssus fluvicolae* Fain and Aitken, 1967, *Loc. cit.,* 29. New synonymy. *Trochilonyssus* Fain and Aitken, 1967, *Bull. Inst. r. Sci. nat. Belg.,* 43: 29. Type-species *Trochilonyssus trinitatis* Fain and Aitken, 1967, *Loc. cit.,* 32. New synonymy. *Pipronyssus* Fain and Aitken, 1967, *Bull. Inst. r. Sci. nat. Belg.,* 43: 36. Type-species *Pipronyssus manaci* Fain and Aitken, *Loc. cit.,* 36. New synonymy.

The number of synonyms for *Ptilonyssus s. l.* is already large, but I make no apology for increasing it further. The reason that the boundaries between these taxa have been drawn, and redrawn, is the simple one that they correspond to nothing at all, their only purpose having been to divide, in the light of arbitrary and trivial morphological characters, a group of which all other considerations emphasize the fundamental unity. The smaller the taxon, the greater should be the morphological and ecological gap between it and its nearest relatives.

It has proved difficult to arrange this large series in a completely orderly system, and I have therefore compromised between the order of the key and the order of the hosts. This point is discussed further in Section V below on host-specificity.

Key to females of Australian species of PTILONYSSUS

1. Stigmata provided with peritremes 2

Stigmata not provided with peritremes 49

2 (1). Dorsal armature (excluding mesonotal shieldlets) comprising three units: podonotal, opisthonotal, and pygidial, of which the latter two may, or may not be fused 3

Dorsal armature (excluding mesonotal shieldlets) comprising two units: podonotal and pygidial, of which the latter may be obsolescent or absent 14

3 (2). Mesonotal sclerotization with two pairs of strong, peg-like setae in tandem. Postanal seta absent .... *ailuroedi* Domrow

Mesonotal complex otherwise. Postanal seta normally present, but absent in *P. pygmaeus* (Bregetova) 4

4 (3). Cribrum present 5

Cribrum absent 13

5 (4). Pygidial shield fused with opisthonotal shield 6

Pygidial shield free 12

6 (5). Metasternal setae normally present, but absent in specimens of *P. carduelis* Fain from *Chloris chloris* (Linnaeus) 7

Metasternal setae absent 11

7 (6). Podonotal shield with four setae considerably stronger than remainder on dorsum .... *carduelis* Fain

All setae on dorsum uniform in size 8

8 (7). Podonotal shield strongly convex laterally 9

Podonotal shield parallel-sided .... *maluri* Domrow

9 (8). Opisthonotal shield widest anteriorly. Adanal setae near front of anus. Coxal setae uniform in length 10

Opisthonotal shield widest at its middle. Adanal setae near back of anus. Seta on coxa IV elongate .... *hirsti* (de Castro and Pereira)

10 (9). Postanal seta present .... *emberizae* Fain

Postanal setae absent .... *pygmaeus* (Bregetova), n. comb.

11 (6). Opisthonotal shield subtriangular, with four pairs of setae in addition to pygidials. Tarsi II-IV with al_1, av_1, pv_1, al_2, av_2, and pv_2 in form of strong, slightly curved spurs, which, at their apex, curve distinctly while tapering rapidly .... *colluricinclae* Domrow

Opisthonotal shield subrectangular, with one pair of setae in addition to pygidials. Tarsi II-IV with al_1, av_1, pv_1, and pl_1 irregularly inflated.... .... *capitatus* (Strandtmann)

12 (5). Opisthonotal shield fully as wide as podontal, and considerably larger than pygidial shield. Anus occupying entire anterior angle of elongate anal shield, preceding all three anal setae .... *triscutatus* (Vitzthum)

Opisthonotal shield much narrower than podonotal, and subequal to pygidial shield. Anus centrally placed on anal shield, flanked laterally by adanal setae .... *sittae* Fain

13 (4). Opisthonotal shield entire, with pygidial complex obliterated .... *struthideae*, n. sp.
Opisthonotal shield fragmented, with pygidial remnants possibly present .... *corcoracis*, n. sp.

14 (2). Distinct tritosternum with well developed laciniae present .. *nitzschi* (Giebel)
Tritosternum rarely present, and then represented only by merest remnant, without laciniae 15

15 (14). Postanal seta normally present, but absent in specimens of *P. terpsiphonei* Fain from *Carterornis* Mathews and *Monarcha melanopsis* (Vieillot) .. 16
Postanal seta absent 41

16 (15). Podonotal shield not flanked on each side by small accessory shield 17
Podonotal shield flanked on each side by small accessory shield 38

17 (16). Podonotal shield at least as wide as long, with lateral margins concave in their posterior half, and therefore divergent behind the peritrematalia. Posterolateral angles of shield full and rounded, resulting in a wide, shallowly 3-lobed posterior margin 18
Podonotal shield normally clearly longer than wide, but if not, not formed as above 20

18 (17). Podonotal shield not sufficiently reduced posteriorly to leave midposterior pair of setae free in cuticle immediately in front of mesonotal shieldlets .... *cractici* Domrow
Podonotal shield with posterior margin sufficiently eroded medially to leave midposterior pair of setae free in cuticle 19

19 (18). Pygidial shield present, either entire or divided .... *motacillae* Fain
Pygidial shield absent .... *langei* (Butenko), n. comb.

20 (17). Podonotal shield not sufficiently reduced posteriorly to leave midposterior pair of setae free in cuticle immediately in front of mesonotal shieldlets 21
Podonotal shield truncate posteriorly, leaving midposterior pair of setae free in cuticle immediately in front of mesonotal shieldlets 31

21 (20). Two setae on posterior margin of podonotal shield subequal to remainder on shield 22
Two setae on posterior margin of podonotal shield considerably stronger than remainder on shield 30

22 (21). Pygidial shield normally entire, but divided in specimens of *P. philemoni* from *Meliphaga notata* (Gould) and *M. gracilis* (Gould) 23
Pygidial shield divided or absent 29

23 (22). Palpal setae not as long as their corresponding segment. Ventral surface of opisthosoma with 6-14 pairs of setae 24
Four setae on ventrolateral aspect of each palp considerably longer than their corresponding segments. Ventral surface of opisthosoma with about 28 pairs of setae .... *balimoensis* Sakakibara

24 (23). All coxal setae normally sharply tipped, but blunt and peg-like on coxa I of *P. terpsiphonei* Fain 25
All coxal setae inflated, subglobular .... *trouessarti* (Hirst)

25 (24). Genital setae on genital shield 26
Genital setae in cuticle adjacent to genital shield .... *philemoni* Domrow

26 (25). All leg setae sharply pointed. Seta *mv* absent on tarsi II-IV 27
Legs with a *mélange* of pointed and blunt, peg-like setae. Seta *mv* present on tarsi II-IV .... *terpsiphonei* Fain

27 (26). Adanal setae in front of anus .... *microecae* Domrow
Adanal setae behind anus 28

28 (27). Podonotal shield larger in posterior half, with posterior margin subrectilinear and bearing four setae. Metasternal setae present. Ventral surface of opisthosoma with about six pairs of setae .. *nudus* Berlese and Trouessart
Podonotal shield larger in anterior half, with posterior margin fully curved and bearing two setae. Metasternal setae absent. Ventral surface of opisthosoma with 8-10 pairs of setae .... *orthonychus*, n. sp.

29 (22). Podonotal shield with seven pairs of setae, of which only four are submarginal. Pygidial shields distinct. Adanal setae in front of anus .... *myzanthae* Domrow
Podonotal shield with six pairs of setae, all submarginal. Pygidial shield obsolescent. Adanal setae behind anus .... *myzomelae* Domrow

30 (21). Adanal setae in front of anus. Pygidial shield entire .... *acrocephali* Fain
Adanal setae behind anus. Pygidial shield divided .... *pittae* Domrow

31 (20). Pygidial shield entire 32
Pygidial shield divided or absent 36

32 (31). Podonotal shield at least as long as wide 33
Podonotal shield noticeably wider than long 35

33 (32). Podonotal shield convex laterally, with at least six pairs of setae (including vertical pair). Adanal setae in front of anus 34
Podonotal shield concave laterally, with only three pairs of setae (including vertical pair). Adanal setae behind anus .... *stomioperae* Domrow

34 (33). Podonotal shield with two pairs of setae posteriorly .... *setosae*, **n. sp.**
Podonotal shield with one pair of setae posteriorly .... *gerygonae*, **n. sp.**

35 (32). Setae between podonotal shield and peritrematalia undistinguished. Coxa II without anterodorsal process .... *dicaei* Domrow
Two setae between podonotal shield and peritrematalia on each side considerably stronger than remainder. Coxa II with anterodorsal process .... *ruandae* Fain

36 (31). Podonotal shield widest near its middle. Pygidial shields present, even if small 37
Podonotal shield clearly widest anteriorly. Pygidial shields completely absent .... *cinnyris* Zumpt and Till

37 (36). Podonotal shield with three pairs of setae in midline (including verticals). Pygidial shields subcircular, well formed .... *rhipidurae* Domrow
Podonotal shield with four pairs of setae in midline. Pygidial shields evanescent .... *lymozemae* Domrow

38 (16). Coxal setae inflated, subspherical .... *echinatus* Berlese and Trouessart
Coxal setae elongate, slenderly tapering 39

39 (38). Adanal setae behind anus 40
Adanal setae in front of anus .... *thymanzae* Domrow

40 (39). Podonotal shield distinctly broader in anterior half, with six pairs of setae .... *gliciphilae* Domrow
Podonotal shield narrowly subrectangular, with four pairs of setae (including vertical pair) .... *meliphagae* Domrow

41 (15). Pygidial shield entire 42
Pygidial shield absent .... *cerchneis* Fain

42 (41). Podonotal shield* not sufficiently reduced posteriorly to leave midposterior pair of setae free in cuticle immediately in front of mesonotal shieldlets 43
Podonotal shield truncate posteriorly, leaving midposterior pair of setae free in cuticle immediately in front of mesonotal shieldlets 47

43 (42). Setae on coxae and venter of opisthosoma slenderly tapering 44
Setae on coxae and venter of opisthosoma truncate, rod-like 46

44 (43). Coxa II without anterodorsal process 45
Coxa II with anterodorsal process .... *monarchae*, **n. sp.**

45 (44). A stout species when engorged. Podonotal shield strongly cordate, with regular margins .... *sphecotheris* Domrow
An elongate species when engorged. Podonotal shield with lateral margins very irregular, and noticeably narrower in posterior third .... *sturnopastoris* Fain

46 (43). Chelicerae attenuate only at extreme tip .... *novaeguineae* (Hirst)
Chelicerae attenuate in distal half .... *grallinae* Domrow

47 (42). Chelicerae attenuate only at extreme tip .... *novaeguineae* (Hirst)
Chelicerae attenuate in distal half 48

48 (47). Podonotal shield with six pairs of setae. Setae on dorsum of opisthosoma in form of heavy spines .... *psophodae* Domrow
Podonotal shield with five pairs of setae. Setae on dorsum of opisthosoma in form of minute rods .... *macclurei* Fain

49 (1). Extensive opisthonotal or mesonotal shield present, irrespective of pygidial complex 50
Only pygidial shield present on opisthonotum .... *bradypteri* (Fain), **n. comb.**

50 (49). Pygidial complex, if present, fused to opisthonotal shield 51
Pygidial shield discrete 53

51 (50). Opisthonotal shield extended back to include pygidial complex. Sternal shield wider than long .... *neochmiae*, **n. sp.**
Mesonotal shield not extending back to pygidium; pygidial shield absent. Sternal shield longer than wide 52

52 (51). Genital setae off shield. Sternal, genital, and ventral setae in form of weak rods .... *elbeli* (Strandtmann), **n. comb.**
Genital setae on shield. Sternal, genital, and ventral setae in form of heavy pegs .... *angrensis* (de Castro), **n. comb.**

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* The nature of the podonotal shield is unknown in *P. novaeguineae* (Hirst) (see Fain and Hyland, 1962*b*), and it is therefore keyed out through both halves of this couplet.

53 (50). Opisthonotal shield elongate, bearing three pairs of setae. SI on shield. Anal shield evenly sclerotized. Leg setae in form of small spines .... *dioptrornis* Fain

Opisthonotal shield quadrate, bearing two pairs of setae. SI off shield. Anal shield with heavily sclerotized band between anus and cribrum. Many leg setae large and inflated .... *dicruri* Fain

Ptilonyssus maluri Domrow

Ptilonyssus maluri Domrow, 1965, *Acarologia*, 7: 451. *Neonyssus maluri*, Bregetova, 1967, *Parazit. Sb.*, 23: 133.

Previous record.—Red-backed wren, *Malurus melanocephalus* (Latham) (Sylviidae, Passeriformes), Esk.

Ptilonyssus colluricinclae Domrow

Ptilonyssus colluricinclae Domrow, 1964, *Acarologia*, 6: 596. *Neonyssus colluricinclae*, Bregetova, 1967, *Parazit. Sb.*, 23: 133.

Previous record.—Grey shrike-thrush, *Colluricincla harmonica* (Latham) (Pachycephalidae, Passeriformes), Brisbane. Also Wilson's Peak and Esk.

New host records.—Rufous shrike-thrush, *C. megarhyncha* (Quoy and Gaimard), Innisfail, vi–ix. 1965, G. J. B., R. D., H. I. McD., and J. S. W. (52♀♀, 10 protonymphs); Esk, 14.vii.1965, R. D. and J. S. W. (47♀♀, 5 nymphs). Golden whistler, *Pachycephala pectoralis* (Latham), Innisfail, 1.ix.1965, H. I. McD. (11♀♀). Grey whistler, *P. griseiceps* Gray, Innisfail, 9.vii.1965, G. J. B. and H. I. McD. (1♀).

Ptilonyssus capitatus (Strandtmann)

(Figs 82–89)

Paraneonyssus capitatus Strandtmann, 1956, *J. Kans. ent. Soc.*, 29: 133. *Astridiella capitatus*, Fain, 1959, *J. ent. Soc. sth. Afr.*, 22: 21. *Neonyssus* (*Otocorinyssus*) *capitatus*, Bregetova, 1967, *Parazit. Sb.*, 23: 127.

This species may now be recorded from Australia: 2♀♀ from a Horsfield bushlark, *Mirafra javanica* Horsfield (Alaudidae, Passeriformes), Kowanyama, 3.iv.1965, R. D. The only previous record is from an American lark (*Otocoris* Bonaparte).

Ptilonyssus carduelis Fain

Ptilonyssus carduelis carduelis Fain, 1962, *Bull. Annls Soc. r. ent. Belg.*, 98: 253. *Neonyssus* (*Frigilonyssus*) *carduelis carduelis*, Bregetova, 1967, *Parazit. Sb.*, 23: 130. *Ptilonyssus carduelis chloris* Fain, 1962, *Bull. Annls. Soc. r. ent. Belg.*, 98: 257. New synonymy. *Neonyssus* (*Frigilonyssus*) *carduelis chloris*, Bregetova, 1967, *Parazit. Sb.*, 23: 130.

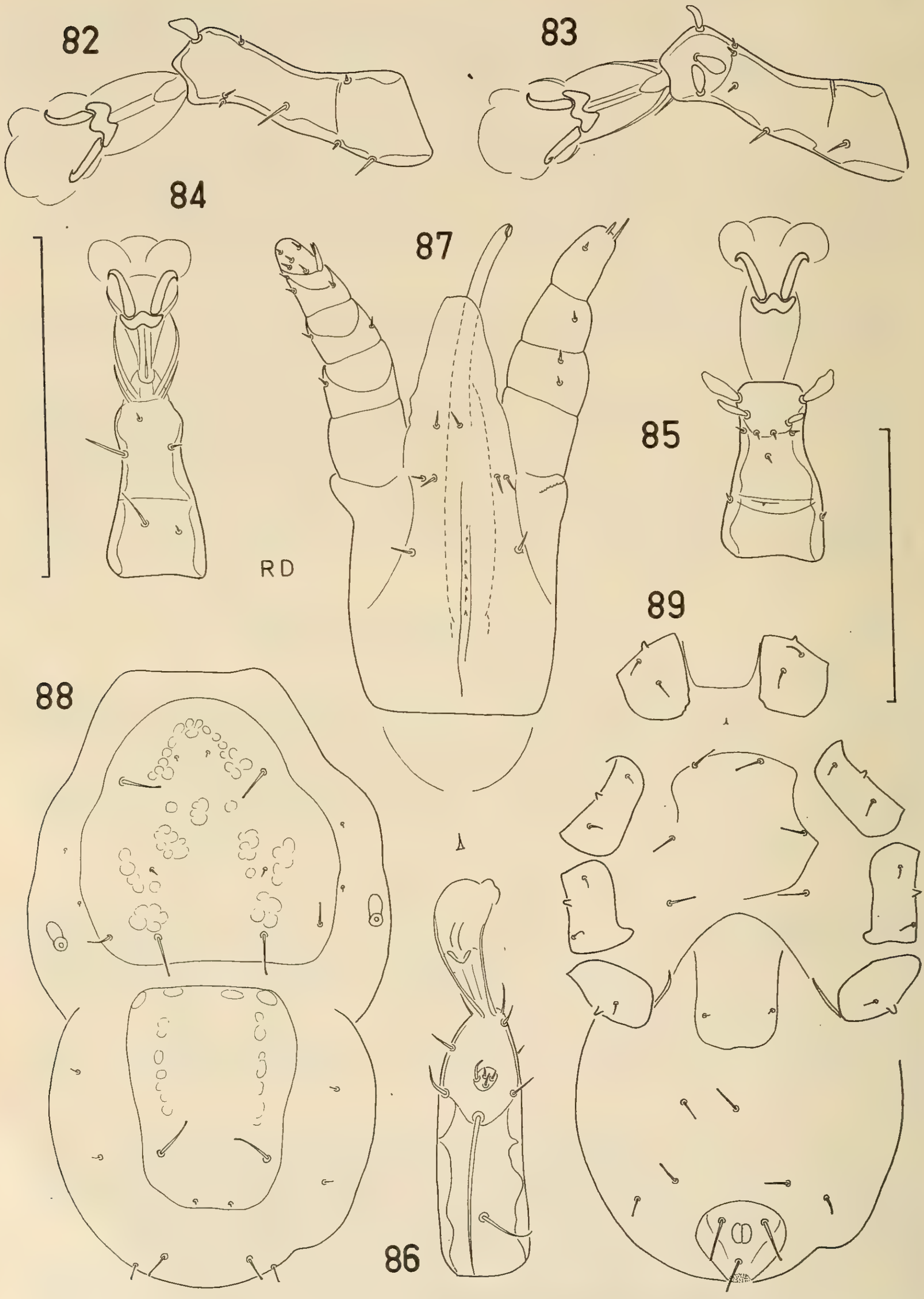
Previous record.—Greenfinch (introduced), *Chloris chloris* (Linnaeus) (Fringillidae, Passeriformes).

Ptilonyssus emberizae Fain

Ptilonyssus emberizae Fain, 1956, *Revue Zool. Bot. afr.*, 53: 140; 1957, *Annls Mus. r. Congo belge Sér. 8vo*, 60: 95; 1958, *Bull. Soc. r. Zool. Anvers*, 9: 7; 1963, *Bull. Annls Soc. r. ent. Belg.*, 99: 168. *Neonyssus* (*Paraneonyssus*) *emberizae*, Bregetova, 1967, *Parazit. Sb.*, 23: 133.

Previous records (both Passeriformes).—Common swallow (vagrant), *Hirundo rustica* Linnaeus (Hirundinidae). Gouldian finch, *Poephila gouldiae* (Gould) (Ploceidae).

Fain (1963*d*) comments on the close relationship between this species and *P. icteridius* (Strandtmann and Furman, 1956). Should they prove synonymous, the former has priority by six months.



Figs 82–89. *Ptilonyssus capitatus* (Strandtmann) (♀ from *Mirafra javanica*).–82–83, Lateral views of tarsus IV. 84–85, Dorsal and ventral views of tarsus II. 86, Dorsal view of tarsus I. 87, Ventral view of capitulum (left palp in dorsal view). 88–89, Dorsal and ventral views of idiosoma, with anal shield foreshortened.

PTILONYSSUS PYGMAEUS (Bregetova), n. comb.

Neonyssus (*Spizonyssus*) *pygmaeus* Bregetova, 1967, *Parazit. Sb.*, 23: 131.

Previous record.—Goldfinch (introduced), *Carduelis carduelis* (Linnaeus) (Fringillidae, Passeriformes).

PTILYONYSSUS HIRSTI (de Castro and Pereira)

Neonyssus hirsti de Castro and Pereira, 1947, *Archos Inst. biol., S Paulo*, 18: 129; Porter and Strandtmann, 1952, *Tex. J. Sci.*, 4: 394. *Paraneonyssus hirsti*, Feider, 1962, *Studii Cerc. stiint. Iăsi*, 13: 48. *Ptilonyssus hirsti*, Fain, 1963, *Bull. Annls Soc. r. ent. Belg.*, 99: 170; Domrow, 1964, *Acarologia*, 6: 608. *Ptilonyssus nudus* Berlese, 1892, "Acari, myriapoda, et scorpiones hucusque in Italia reperta, ordo Mesostigmata" (Patavii), fasc. 54, No. 1 (♂), *nec* Berlese and Trouessart, 1889, *Bull. Biblioth. scient. Ouest*, 2: 130. *Ptilonyssus nudus* Hirst, 1916, *J. zool. Res.*, 1: 73 (♀), *nec* Berlese and Trouessart, *Loc. cit.*

Previous record.—House-sparrow (introduced), *Passer domesticus* (Linnaeus) (Fringillidae, Passeriformes), Brisbane.

This material compares well with specimens from the United States.

PTILONYSSUS NEOCHMIAE, n. sp.
(Figs 78–80, 90–91)

Diagnosis.—According to Thomson (1964), *Vidua* Cuvier, *Hypochera* Bonaparte, and *Steganura* Reichenbach are a group of three very similar genus-group taxa of ploceid affinities, from which nasal mites of the genus *Ptilonyssus* have been described as follows: *P. viduae* Fain (1956, 1957*e*), *P. hypocherae* (Fain, 1963*e*), n. comb., and *P. steganurae* Fain (1967*b*).

P. viduae is the type-species of *Passeronyssus* Fain (1960*f*, 1962*c*), the genus in which *P. hypocherae* was originally placed, and neither species shows the stigmata extended anteriorly into peritremes. However, in *P. steganurae*, and in the species with which Fain originally thought to associate it, *P. intermedius* (Hirst, 1921*b*) (see also Fain, 1960*a*; Fain and Hyland, 1962*b*), peritremes are present.* Fain also compares *P. steganurae* with *P. ploceanus* Fain (1956), a species he treats more fully in 1957*e*, together with several other related species, all possessing peritremes, from other ploceid and fringillid genera. It is clear, therefore, that we are in the presence of congeners, and the essential criterion of difference listed by Fain between *Ptilonyssus* and *Passeronyssus* (peritremes present or absent) no longer holds good.

The new ploceid parasite, *P. neochmiae*, lacking peritremes, but possessing an extensive opisthonotal shield, is therefore best compared, not with *P. viduae*, but with *P. hypocherae*. It is readily separable, however, by the absence of anterolateral extensions to the podonotal shield, the relatively broader dimensions of the opisthonotal shield, and the length and position of the anal setae.

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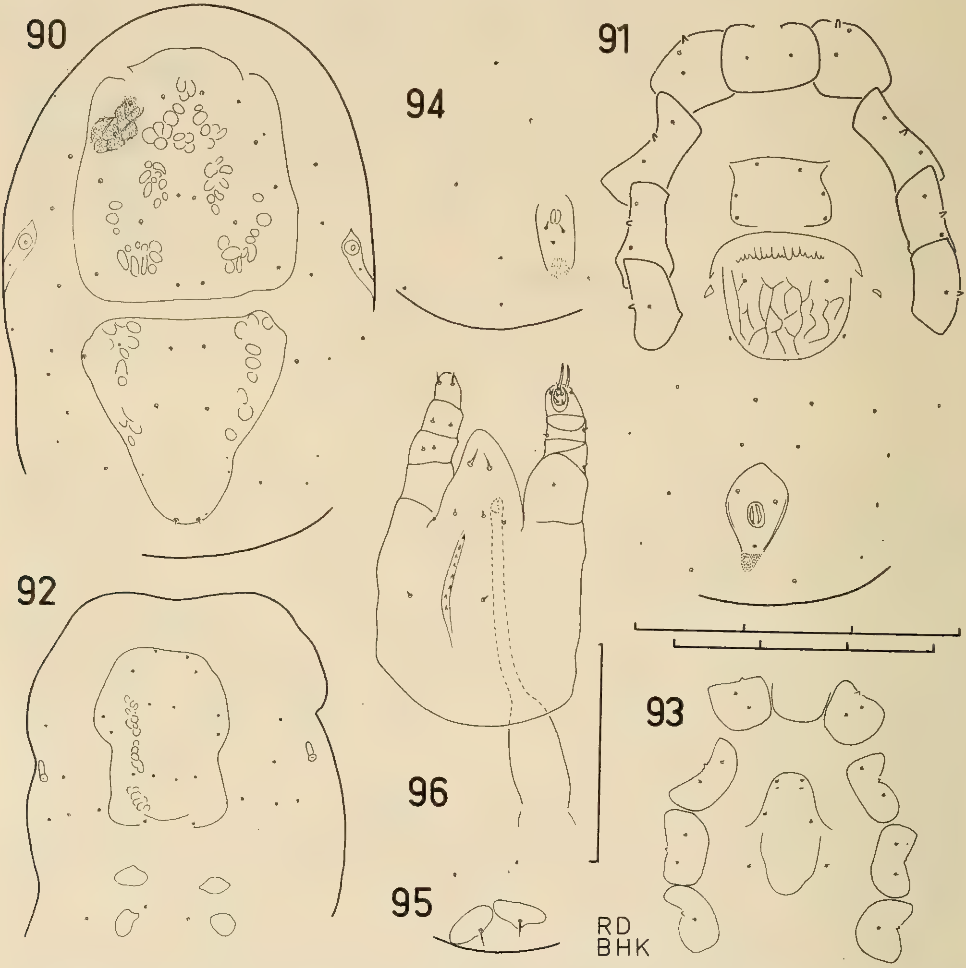
*The unique specimen of *P. intermedius* is alleged on Trouessart's label to have come from a Malagasy bird, but it should always be kept in mind that, as this worker collected much of his material from dried museum skins, his data should always be verified by fresh material. For example, listrophorid mites said by Trouessart to have come from an African rodent, and described by Lawrence (1956) as *Cricetomysia andrei*, proved to be *Campylochirus chelopus* Trouessart (1893), a parasite of a peculiarly Tasmanian marsupial (Domrow, 1958). Also, Trouessart himself (1896) expressed the probability that *Chirodiscus amplexans* Trouessart and Neumann (1890), described from the feathers of an Australian bird, will also prove to belong to the Listrophoridae, a family modified towards a lifelong attachment to single mammalian hairs.

Types.—Holotype female and four paratype females from a crimson finch, *Neochmia phaeton* (Hombron and Jacquinot) (Ploceidae, Passeriformes), Innisfail, 3.viii.1966, M. L. F. Holotype N. I. C.; paratypes R. D. and A. F.

Female.—Idiosoma 510μ long in slightly distorted specimen figured. Podonotal shield (Fig. 90) slightly longer than wide, 230–240μ long, 210–220μ wide; anterior margin irregularly convex, sides subparallel, and posterior margin straight. Setae in eight pairs; surface reticulate, strongly punctate, and marked by muscle insertions. Opisthonotal shield sub-triangular, with rounded corners, length 192–196μ, width 187–192μ. Six setae normally present anteriorly, in hexagonal arrangement; pygidial setae present. Dorsal cuticle with three pairs of setae flanking podonotal, and several setae and pores flanking opisthonotal shield. Stigmata without peritremes, borne on weakly sclerotized, posteriorly extended stigmatic shields.



Figs 90–91. *Ptilonyssus neochmiae*, n. sp. (♀ from *Neochmia phaeton*).–Dorsal and ventral views of idiosoma.

Figs 92–96. *Ptilonyssus sittae* Fain (protonymph from *Climacteris picumnus*).–92–93, Dorsal and ventral views of podosoma. 94, Anal shield. 95, Pygidium. 96, Ventral view of capitulum (right palp in dorsal view).

Sternal shield (Fig. 91) very weakly sclerotized, with SI–III, but no pores, on shield proper. Metasternal setae absent. Genital shield short and broad, reticulate and shagreened, and with narrow, rayed operculum. Genital setae set well forward on shield, with associated pores set free in cuticle near posterior margin of shield. Anal shield angularly convex anteriorly, and with cribrum posteriorly. Anus centrally placed, preceded by adanal, and followed by postanal seta. Ventral cuticle with several pairs of setae and pores. All body setae minute.

All leg setae minute, except for those at apex of tarsi II–IV (Figs 79–80). Coxae 2.2.2.1. Trochanter I (1-0/2–1), II (1–0/3–1), III–IV (1–0/3–0). Femora I–II (1–4/1–1), III (1–3/1–0), IV (1–2/1–0); genua I–III (1–4/2–1), IV (1–4(3)/1–0). Tibiae (1–3/2–1). Tarsi –.17.17.17 (*mv* absent). Setae al_1, av_1, pv_1, and pl_1 on tarsi II–IV, particularly ventral pair, considerably stronger than remainder of setae on ventral aspect. Claws I weak, but not clearly visible; ambulacrum I also weaker and more slender than II–IV.

Basis capituli (Fig. 78) with pair of weak capitular setae, but deutosternum absent. HI absent, II–III present, but very weak. Palpal setae weak, apart from two dorsodistal tibial rods. Tarsus obsolescent, with two slender setae. Strong claw present. Chelicerae attenuate in distal half, with chelate portion occupying one-thirteenth of total length. Tritosternum absent.

PTILONYSSUS STRUTHIDEAE, n. sp.

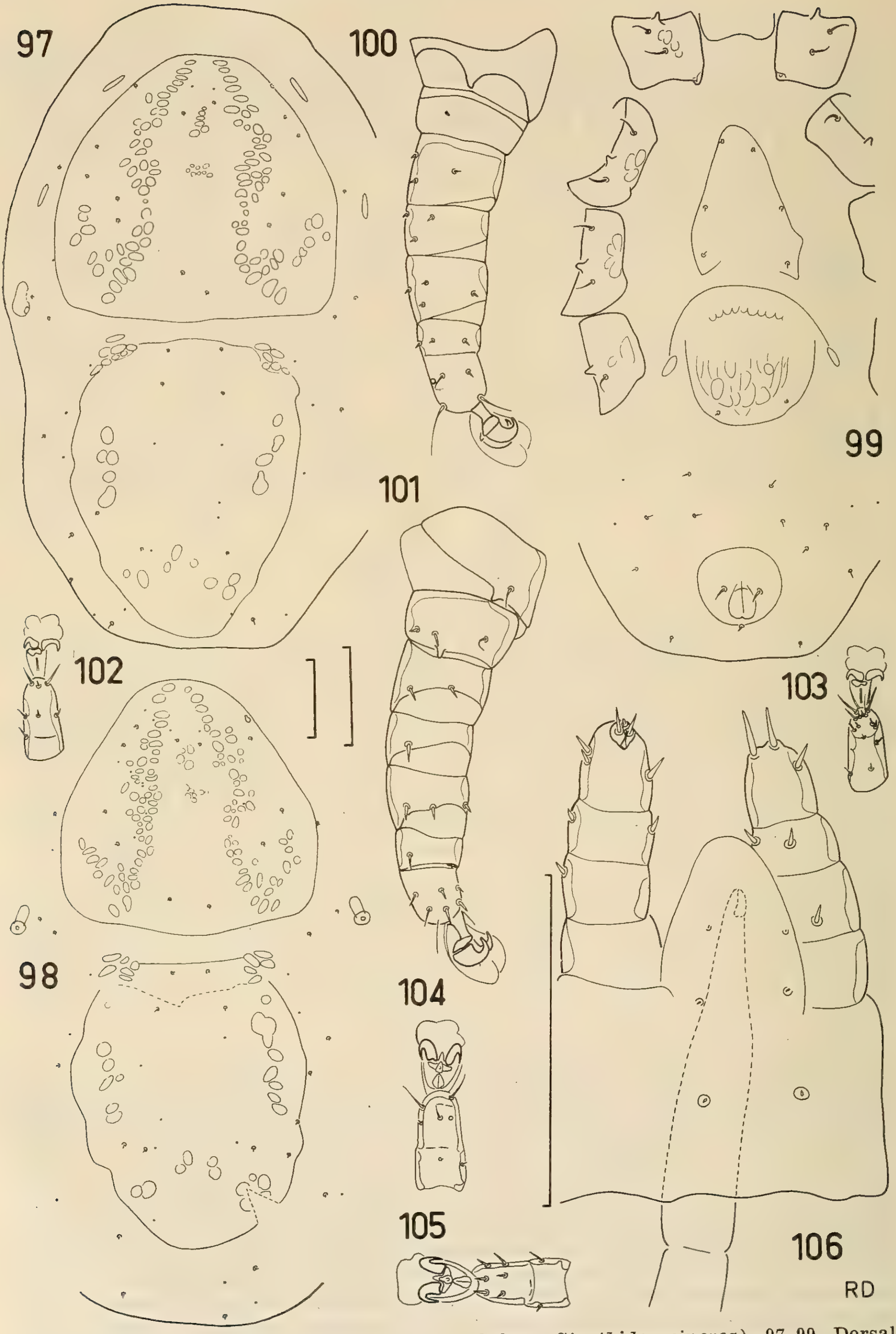
(Figs 97–106)

Diagnosis.—Leach (1958), whose classification of Australian birds I am presently using, places *Struthidea* Gould and *Corcorax* Lesson among the Corvidae and *Grallina* Vieillot as the sole member of the Grallinidae. However, Mayr and Amadon (1951) have grouped these three genera — mainly on a characteristic habit, all build a bowl-shaped mud nest — into the Grallinidae, recognizing two subfamilies, Grallinae (*sic*) for the peculiar *Grallina* and Corcoracinae for the more closely related *Struthidea* and *Corcorax*.

This subfamilial classification parallels that of their respective nasal mites — the slender-bodied *Ptilonyssus grallinae* Domrow (1964*c*) is quite distinct from the thick-set *P. struthideae*, n. sp., and *P. corcoracis*, n. sp., in showing the following characters: podonotal shield strongly excavated posterolaterally, thereby flanking peritrematalia; pygidial shield distinct; anal shield elongate, with distinct cribrum, but without postanal seta; body setae strong and peg-like; coxa II with anterodorsal process; leg chaetotaxy: coxae 2.2.2.1; trochanters I–II (0–0/3–1), III (2–0/2–0), IV (1–0/5–0); femur I (2–4/0–2), II (1–4/1–1), III (1–3/1–0), IV (1–3/2–0); genua I–III (1–4/0–1), IV (1–3/0–0); tibiae (1–3/2–1); tarsi –.17.17.17 (*mv* lacking); palpal chaetotaxy 1.2.4.6.

However, both in general (*facies*) and in particular (chaetotaxy of legs and palpi), the two new species are very similar indeed and are separable, as noted above, only on the degree of sclerotization of the dorsal shields and the setation of tarsus IV.

In view of the uncertain relationships of their two host genera, it is difficult to point to any species of *Ptilonyssus* as a possible relative, even confining one's attention to the species with extensive opisthonotal shields. Of the Australian species in this category — omitting *P. hirsti* (de Castro and Pereira, 1947) from the introduced *Passer domesticus*, a fringillid — *P. ailuroedi* Domrow (1964*b*), from ptilonorhynchids, is readily separable by its four immense mesonotal setae; *P. colluricinclae* Domrow (1964*c*), from pachycephalids, by the shape and setation of the dorsal shields and the armature of tarsi II–IV; and *P. maluri* Domrow (1965*c*), from a sylviid, by the presence of metasternal setae and a distinct deutosternum.



Figs 97–106. *Ptilonyssus struthideae*, n. sp. (♀ from *Struthidea cinerea*).–97–99, Dorsal and ventral views of idiosoma. 100–101, Dorsal and ventral views of leg IV. 102–103, Ventral and dorsal views of tarsus I. 104–105, Dorsal and ventral views of tarsus IV. 106, Ventral view of capitulum (left palp in dorsal view).

It has since come to my notice that *P. struthideae* is much more closely related to *P. nucifragae* (Hirst, 1923) (see also Fain, 1960*a*; Bregetova, 1967), whose host, *Nucifraga caryocatactes* (Linnaeus) is likewise a corvid (Thomson, 1964), a relationship which would urge caution in accepting Mayr and Amadon's findings (1951). I have seen two pairs of Hirst's species, but the new species is readily distinguished by the different shapes of both its dorsal shields, the posterior reduction of its anal shield, and the uniformity in length of its coxal setae.

Types.—Holotype female and two paratype females from apostle-birds, *Struthidea cinerea* Gould (Corvidae, Passeriformes), Condamine, 29.v.1965, H. A. S.; Condamine, 6.vii.1963, I. D. F.; and Charleville, 1.ii.1967, R. D. and J. S. W. Holotype N. I. C.; paratypes R. D.

Female.—Idiosoma relatively stout, 660μ long in somewhat flattened specimen. Podonotal shield (Figs 97–98) very slightly wider than long, strongly arched anterolaterally, and virtually straight posteriorly; bearing six or seven pairs of minute setae. Opisthonotal shield one-third again as long as wide, tapering irregularly to convex posterior margin; bearing two pairs of setae anteriorly, and three to five irregularly arranged setae posteriorly, none of which appear to be pygidials. Both shields closely punctate except for very narrow marginal strip, marked by distinct muscle insertions, and showing few weak pores. Body cuticle with four shieldlets and six setae flanking podonotal, and about eight setae and pores flanking opisthonotal shield. Stigmata provided with short peritremes.

Sternal shield (Fig. 99) narrower anteriorly, virtually textureless, and outlined only by cessation of cuticular striae; bearing SI–III, but without pores. Metasternal setae absent. Genital shield short and broad, showing few muscle insertions and reticulate pattern more densely sclerotized than remainder of shield; with rayed operculum anteriorly and two minute setae posteriorly. Anal shield weakly sclerotized, with anus almost at posterior margin; adanal setae near anterior of anus, postanal submarginal; cribrum quite absent. Cuticle with about six pairs of setae and few pores.

Legs stout, with truncate tarsi bearing ambulacra ventrodistally (Figs 100–101). Setae generally short and spinose. Coxae 2.2.2.1. Trochanter I (1–0/2–1), II (0–0/3–1), III (1–0/3–0), IV (1–0/2–0). Femur I (1–4/2–1), II (1–4/1–1), III–IV (1–3/1–0). Genu I (1–4/2–1), II–III (1–4/0–1), IV (1–3/0–0). Tibiae (1–3/2–1). Tarsi –.17.17.16 (II–IV lacking *mv*; IV also lacking ad_2, its relative position in II and III being indicated in Figs 100 and 104 by a small circle; av_1 and pv_1 slightly stronger). Ambulacra II–IV (Figs 104–105) with strong articulatory sclerites supporting heavy claws. Ambulacrum I similar (Figs 102–103), but much smaller.

Tritosternum and deutosternum absent (Fig. 106). Capitular and hypostomal setae III minute; remaining two pairs of hypostomals obsolescent or absent. Palpi with usual five segments, but tarsus much reduced and completely obscured dorsally by tibia. Setal formula 0.2.4.6. Tarsus with one smaller and two larger setae; claw present, with indication of bifid tip under oil immersion. Cheliceral shaft of uniform diameter basally, but tapering in distal third; chelatae portion occupying one-fifteenth of total length.

PTILONYSSUS CORCORACIS, n. sp.

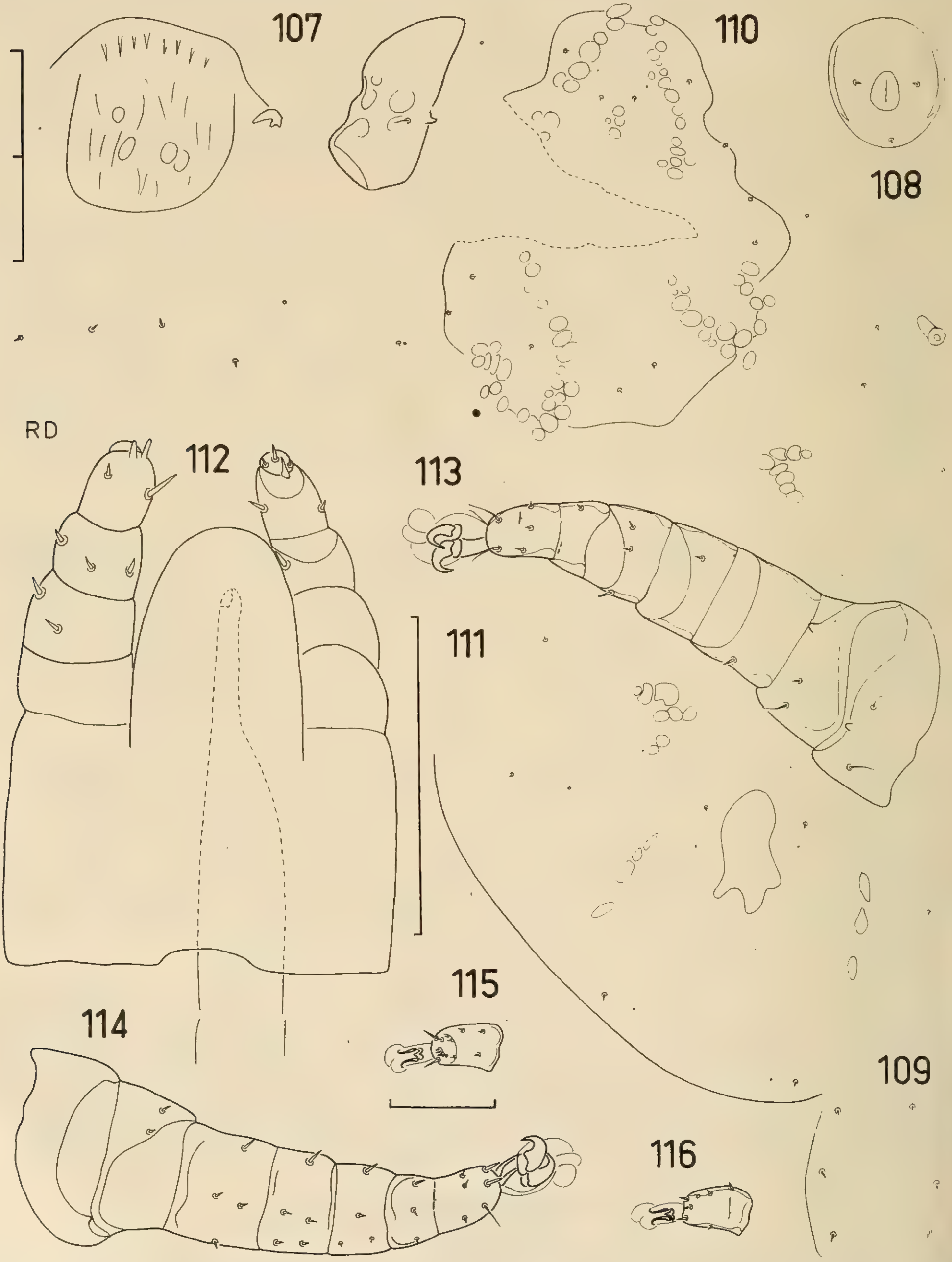
(Figs 107–116)

Diagnosis.—See that for *P. struthideae,* n. sp., above.

Types.—Holotype female from a white-winged chough, *Corcorax melanorhamphus* (Vieillot) (Corvidae, Passeriformes), Condamine, 6.vii.1963, I. D. F. Holotype N. I. C.

Also 6♀♀ and 2♂♂ from *C. melanorhamphus*, Charleville, 28.i.1967, R. D. and J. S. W.

Female.—Idiosoma about 880μ long in mounted, somewhat compressed material. Podonotal shield (Fig. 110) approximately as wide as long, but



Figs 107–116. *Ptilonyssus corcoracis*, n. sp. (♀ from *Corcorax melanorhamphus*).–107, Sternal shield and coxa IV. 108, Anal shield. 109, Sternal setae. 110, Podonotum, with one mesonotal shieldlet. 111, Opisthonotum, with other mesonotal shieldlet. 112, Ventral view of capitulum, with basis not clear (right palp in dorsal view). 113–114. Ventral and dorsal views of leg III. 115–116, Dorsal and ventral views or tarsus I.

narrower anteriorly and slightly convex midposteriorly; outline generally indistinct and eroded, particularly around anterior and posterolateral muscle insertions; bearing six pairs of minute setae and two pores; surface granulate, marked by regular pattern of muscle insertions. Mesonotum with two shieldlets. Posteromedially an irregular, asetose shield (Fig. 111) flanked on each side by seta and pore: this possibly represents the pygidial complex, although further to each side—and, I fancy, behind—there are additional shieldlets. Body cuticle with occasional setae and pores whose pattern is indiscernable. Stigmata provided with short peritremes.

Sternal plate (Fig. 109) obsolescent, flanked by short, spinose SI–III. Metasternal setae absent. Genital shield (Fig. 107) as in *P. struthideae*, n. sp. Anal shield (Fig 108) subcircular, very weakly sclerotized, without cribrum; anus centrally placed, flanked by three weak anal setae.

Leg chaetotaxy (Figs 113–114) as in *P. struthideae*, but genu IV (1–4/0–0) on one side of holotype, and tarsi –.17.17.17 (*mv* absent; ad_2 present on IV). Tarsus I is depicted in Figs 115–116.

Basis capituli and hypostome obscured in holotype, but other specimens show deutosternum absent, weak capitular setae present, and hypostomal setae (particularly I) obsolescent or absent (Fig. 112). Dorsodistal rods on palpal tibia weaker than in *P. struthideae*. Chelate portion occupying one-twentieth of total length. Tritosternum absent.

PTILONYSSUS TRISCUTATUS (Vitzthum)

Ptilonyssoides triscutatus Vitzthum, 1935, *J. Orn., Lpz.*, 83: 581. *Ptilonyssus triscutatus*, Fain, 1957, *Annls Mus. r. Congo belge Sér. 8vo*, 60: 121; Domrow, 1966, PROC. LINN. SOC. N.S.W., 90: 196.

Previous record.—Rainbow-bird, *Merops ornatus* Latham (Meropidae, Coraciiformes), Esk. Also Kowanyama.

PTILONYSSUS DIOPTRORNIS Fain

Ptilonyssus dioptrornis Fain, 1956, *Revue Zool. Bot. afr.*, 53: 137; 1957, *Annls Mus. r. Congo belge Sér. 8vo*, 60: 124; 1959, *J. ent. Soc. sth. Afr.*, 22: 26. *Passeronyssus dioptrornis*, Fain, 1960, *Revue Zool. Bot. afr.*, 61: 110; 1962, *Ibid.*, 66: 139; Nadchatram, McClure, and Lim, 1964, *J. fed. Malay St. Mus.*, 9: 105. *Ptilonyssoides dioptrornis*, Strandtmann, 1960, *J. Kans. ent. Soc.*, 33: 142. *Passeronyssus enicuri* Fain and Nadchatram, 1962, *Bull. Annls Soc. r. ent. Belg.*, 98: 276. New synonymy. *Passeronyssus lusciniae* Fain, 1962, *Revue Zool. Bot. afr.*, 66: 140. New synonymy.

This species may now be recorded from Australia: 11 ♀ ♀, 1 ♂, 2 deutonymphs (one enclosing well developed ♀), and 4 protonymphs from pale-yellow robins, *Eopsaltria capito* Gould (Muscicapidae, Passeriformes), Innisfail, 6.vii and 11.viii.1965, G. J. B. and H. I. McD., and Wilson's Peak, 15.v.1967, R. D. and B. H. K.*

The three nominal species comprising this parasite of Turdidae and Muscicapidae (two groups often considered merely as muscicapid subfamilies) do not differ in any way that I would consider beyond the range of individual variation. I have noted above on several occasions that many recent taxa, both at species- and genus-group levels, have been erected with only minor *differences* in mind. It is convenient here to note that it is perhaps even more important to keep *similarities* in mind.

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* The type-host of *P. lusciniae*, the nightingale, *Luscinia megarhynchos* Brehm (Turdidae), was once introduced into Australia, but failed to become established (Cayley, 1963).

PTILONYSSUS DICRURI Fain

Ptilonyssus dicruri Fain, 1956, *Revue Zool. Bot. afr.*, 53: 137; 1957, *Annls Mus. r. Congo belge Sér. 8vo,* 60: 122. *Ptilonyssoides dicruri,* Strandtmann, 1960, *J. Kans. ent. Soc.*, 33: 140. *Passeronyssus dicruri,* Domrow, 1965, *Acarologia,* 7: 451. *Ptilonyssoides faini* Strandtmann, 1960, *J. Kans. ent. Soc.,* 33: 142.

Previous record.—Spangled drongo, *Chibia bracteata* (Gould) (Dicruridae, Passeriformes), Samford and Esk. Also Kowanyama.

I have examined one Thai specimen identified as *P. dicruri* by Strandtmann.

PTILONYSSUS SITTAE Fain
(Figs 92–96, 219–222)

Ptilonyssus sittae Fain, 1965, *Revue Zool. Bot. afr.,* 72: 158; 1966, *Bull. Annls Soc. r. ent. Belg.,* 102: 117.

This species, originally described from a European species of *Sitta* Linnaeus (Sittidae), may now be recorded from Australia: 1 protonymph from a brown tree-creeper, *Climacteris picumnus* Temminck (Certhiidae, Passeriformes), Winbin Creek, 20.i.1966, R. D., D. J. M., and J. S. W.

Keast (1957) placed *Climacteris* Temminck in the family Sittidae, and the matter is further discussed by Thomson (1964).

PTILONYSSUS AILUROEDI Domrow

Ptilonyssus ailuroedi Domrow, 1964, *Acarologia,* 6: 31, 619; Wilson, 1964, *Pacif. Insects,* 6: 381.

Previous record.—Green catbird, *Ailuroedus crassirostris* (Paykull) (Ptilonorhynchidae, Passeriformes), Mt. Glorious. Also Wilson's Peak.

Also 1 ♀ and 1 ? (in poor condition) from *A. crassirostris* (listed on the label under its synonym *A. smithi* (Vigors and Horsfield)), Tweed River, N.S.W., ii.1892, T. S. (see comments above on *Tinaminyssus trichoglossi*).

PTILONYSSUS ELBELI (Strandtmann), n. comb.

Cas elbeli Strandtmann, 1960, *J. Kans. ent. Soc.,* 33: 137. *Sternostoma bruxellarum* Fain, 1961, *Bull. Annls Soc. r. ent. Belg.,* 97: 53. New synonymy.

Previous records (both Sturnidae, Passeriformes).—European starling (introduced), *Sturnus vulgaris* Linnaeus. Common myna (introduced), *Acridotheres tristis* (Linnaeus).

I have examined one of Strandtmann's paratypes.

PTILONYSSUS ANGRENSIS (de Castro), n. comb.

Rhinonyssus (*Rhinacarus*) *angrensis* de Castro, 1948, *Archos Inst. biol., S Paulo,* 18: 257. *Cas angrensis,* Baker and Wharton, 1952, "An introduction to acarology" (Macmillan: New York), p. 81; Strandtmann and Wharton, 1958, *Contr. Inst. Acar. Univ. Md,* 4: 169.

This is the first record of this parasite of swallows outside the Americas: 7 ♀♀ from the welcome swallow, *Hirundo neoxena* Gould (Hirundinidae, Passeriformes), Kowanyama, 21.x.1966, R. D. and H. A. S. They compare well with 1 ♀ from the United States.

PTILONYSSUS NITZSCHI (Giebel)

Dermanyssus Nitzschi Giebel, 1871, *Z. ges. Naturw.,* 38: 32. The original capitalized spelling should be corrected under Art. 32. *Rhinonyssus nitzschi,* Vitzthum, 1935, *J. Orn., Lpz.,* 83: 572 (*pro parte*). *Neonyssus* (*Vitznyssus*) *nitzchi* (*sic*) de Castro, 1948, *Archos Inst. biol., S Paulo*, 18: 277. *Ptilonyssus* (*Rhinonyssoides*) *nitschi* (*sic*) Pereira and de Castro, 1949, *Archos Inst. biol., S Paulo*, 19: 222. *Vitznyssus nitzschi*, Strandtmann and Wharton, 1958, *Contr. Inst. Acar. Univ. Md*, 4: 175; Strandtmann, 1960, *J. Kans. ent. Soc.*, 33: 131. *Astridiella caprimulgi* Fain, 1957, *Riv. Parassit.*, 18: 96.

Previous record.—Large-tailed nightjar, *Caprimulgus macrurus* Horsfield (Caprimulgidae, Caprimulgiformes).

I agree with Strandtmann and Wharton (1958) that (*i*) it is unnecessary to delete *D. nitzschi*, the first nasal mite described from birds, from the nomenclature; and (*ii*) it would be legitimate to consider the holotype of *A. caprimulgi* as the neotype of *D. nitzschi*. See discussion on *Boydaia crassipes* (Berlese and Trouessart) below.

It is noteworthy that two of the hosts of *P. nitzschi* listed by Fain (1957*e*) also harbour *P. scotornis* Fain (1956, 1957*b*). However, the proportions of the anal shield and the chelicerae appear to distinguish the two taxa. It was, however, illegal of Fain to discard his original holotype of *P. scotornis* for a better specimen from a different host.

Ptilonyssus echinatus Berlese and Trouessart

Ptilonyssus echinatus Berlese and Trouessart, 1889, *Bull. Biblioth. scient. Ouest*, 2: 129; Strandtmann, 1960, *J. Kans. ent. Soc.*, 33: 146; George, 1961, *J. Kans. ent. Soc.*, 34: 114; Domrow, 1964, *Acarologia*, 6: 607. *Hapalognatha platytricha* Butenko, 1959, *Nauch. Dokl. vȳssh. Shk.*, 2: 17 (*nomen nudum*); 1960, *Zool. Zh.*, 39: 1494. *Ptilonyssus chalybeaedomesticae* do Amaral, 1967, *Archos Inst. biol., S Paulo*, 34: 169. New synonymy. *Ptilonyssus echinatus taperaefuscae* do Amaral, 1967, *Archos Inst. biol., S Paulo*, 34: 199. New synonymy.

Previous records (both Hirundinidae, Passeriformes).—Welcome swallow, *Hirundo neoxena* Gould, Brisbane. Also Kowanyama. Common swallow (vagrant), *H. rustica* Linnaeus.

New host record.—Tree-martin, *Hylochelidon nigricans* (Vieillot) (Hirundinidae), Charleville, 31.i.1967, R. D. and J. S. W. (1♀).

All Australian specimens show the pygidial shield divided, as does 1♀ from *H. rustica* from the United States.

The above taxa would seem to provide another example of clinal variation. All are parasites of swallows.

Ptilonyssus pittae Domrow

Ptilonyssus pittae Domrow, 1964, *Acarologia*, 6: 26, 618.

Previous record.—Noisy pitta, *Pitta versicolor* Swainson (Pittidae, Passeriformes), Upper Brookfield. Also Innisfail.

Ptilonyssus cractici Domrow

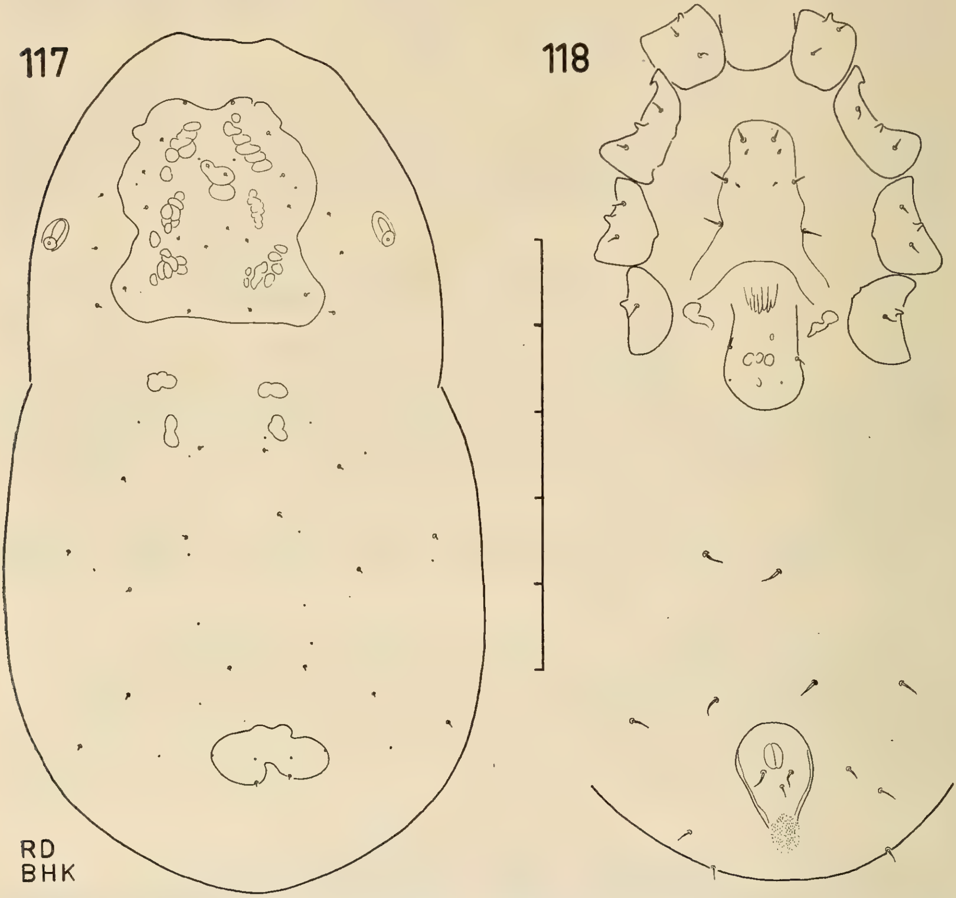
(Figs 117–126)

Ptilonyssus cractici Domrow, 1964, *Acarologia*, 6: 598, 616; 1966, Proc. Linn. Soc. N.S.W., 90: 196.

Previous records.—Laughing kookaburra, *Dacelo gigas* (Boddaert) (Alcedinidae, Coraciiformes), Esk. White-winged triller, *Lalage tricolor* (Swainson) (Campophagidae, Passeriformes), Kowanyama. Also Charleville. Black-backed magpie, *Gymnorhina tibicen* (Latham) (Cracticidae, Passeriformes), Brisbane and Condamine. Also Esk. Pied butcher-bird, *Cracticus* *nigrogularis* (Gould), Logan Village. Grey butcher-bird, *C. torquatus* (Latham), Esk. Black-backed butcher-bird, *C. mentalis* Salvadori and d'Albertis, Chillagoe.

New host record.—Pied currawong, *Streptera graculina* (Shaw) (Cracticidae), Esk, 10.vii.1967, R. D. and B. H. K. (7 ♀♀).

The leg chaetotaxy of specimens from cracticids is as follows. Coxae 2.2.2.1. Trochanters 4.5.4.4. Femur I (2–4/1–2), II (1–4/1–1), III–IV (1–3/0–0). Genua I–III (1–4/0–1), IV (1–2/0–0). Tibiae I–II (1–3/2–1), III–IV (1–3/2–0). Tarsi –.17.17.17. The two posterodorsal setae on genu III are set in relatively larger alveoli. Specimens from *Lalage* Robineau–Desvoidy differ only in showing trochanter II 4. The specimen from *Dacelo* shows a different chaetotaxy on two segments, *viz.* femur IV (1–3/1–0) and tibia IV (1–3/2–1). See also note below on *P. sphecotheris* Domrow.



Figs 117–118. *Ptilonyssus cractici* Domrow. (♀ from *Lalage tricolor*).—Dorsal and ventral views of idiosoma.

One magpie in subadult plumage (Esk, 13.ii.1968, R. D. and B. H. K.) yielded 105 ♀♀, 9 ♂♂, 7 deuto-, and 22 protonymphs. This extremely heavy infestation was confined to the nasal passages, the mites in the drier anterior portions near the nostrils being partially encased in dried nasal secretions. No mites were found in the trachea or lungs.

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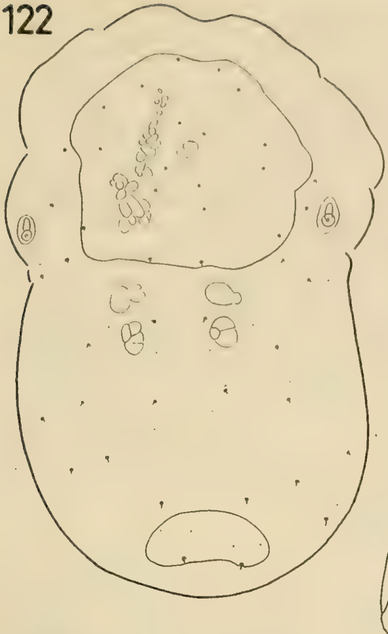

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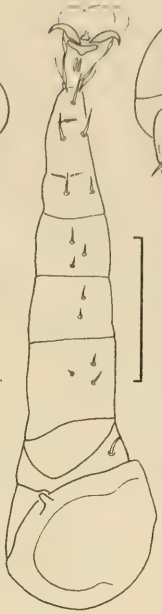

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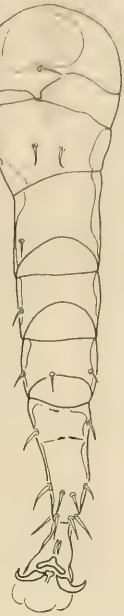

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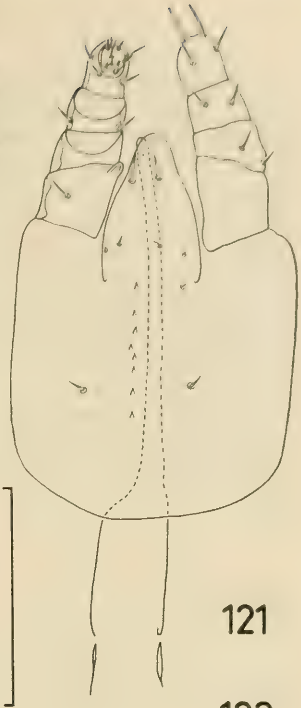

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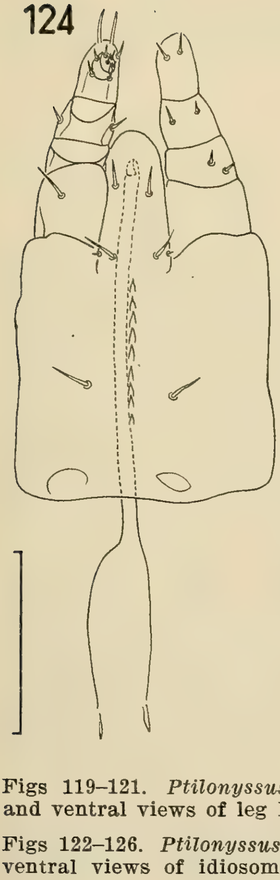

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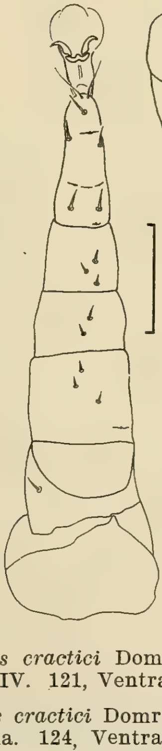

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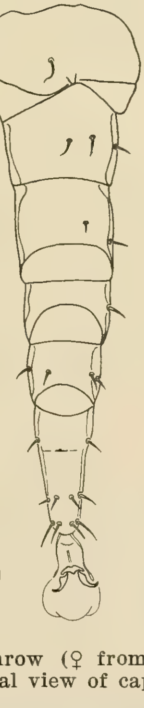

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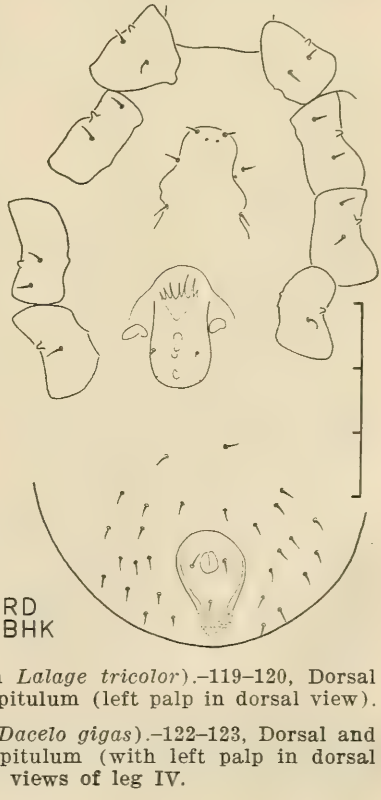


Figs 119–121. *Ptilonyssus cractici* Domrow (♀ from *Lalage tricolor*).–119–120, Dorsal and ventral views of leg IV. 121, Ventral view of capitulum (left palp in dorsal view).

Figs 122–126. *Ptilonyssus cractici* Domrow (♀ from *Dacelo gigas*).–122–123, Dorsal and ventral views of idiosoma. 124, Ventral view of capitulum (with left palp in dorsal view). 125–126, Dorsal and ventral views of leg IV.

PTILONYSSUS MOTACILLAE Fain

(Figs 127–132)

Ptilonyssus motacillae Fain, 1956, *Revue Zool. Bot. afr.*, 53: 143; 1957, *Annls Mus r. Congo belge Sér. 8vo,* 60: 104, 137; 1959, *J. ent. Soc. sth. Afr.*, 22: 24; 1960, *Revue Zool. Bot. afr.*, 61: 109; 1962, *Ibid.*, 66: 128; Domrow, 1964, *Acarologia,* 6: 600; 1965, *Ibid.*, 7: 460. *Ptilonyssus motacilla* (*sic*) Gretillat, 1961, *Vie Milieu,* 12: 155. *Ptilonyssus estrildicola* Fain, 1959, *J. ent. Soc. sth. Afr.*, 22: 22. New synonymy. *Ptilonyssus fringillicola* Fain, 1959, *J. ent. Soc. sth. Afr.*, 22: 28; 1962, *Bull. Annls Soc. r. ent. Belg.*, 98: 262. New synonymy. *Hapalognatha prima* Butenko, 1959, *Nauch. Dokl. vȳssh. Shk.*, 2: 17 (*nomen nudum*); 1960, *Zool. Zh.*, 39: 1490. The two species headings on this latter page are transposed. *Ptilonyssus lobatus* Strandtmann, 1960, *J. Kans. ent. Soc.*, 33: 147. New synonymy. *Ptilonyssus cinnyricincli* Fain, 1962, *Revue Zool. Bot. afr.*, 66: 132. New synonymy. *Ptilonyssus estrildicola taeniopygiae* Fain, 1963, *Revue Zool. Bot. afr.*, 68: 74; Nadchatram, McClure, and Lim, 1964, *J. fed. Malay St. Mus.*, 9: 105. New synonymy. *Ptilonyssus motacillae phoenicuri* Fain, 1966, *Revue Zool. Bot. afr.*, 74: 90. New synonymy. *Ptilonyssus* sp. Fain and Nadchatram, 1962, *Bull. Annls Soc. r. ent. Belg.*, 98: 280. See also Domrow (1966*b*).

Previous records (all Passeriformes).—Rufous whistler, *Pachycephala rufiventris* (Latham) (Pachycephalidae), Mt. Cotton and Samford. Also Esk and Kowanyama. Australian pipit, *Anthus australis* Vieillot (Motacillidae), Esk. Yellow wagtail (vagrant), *Motacilla flava* Linnaeus. Goldfinch (introduced), *Carduelis carduelis* (Linnaeus) (Fringillidae). Zebra finch, *Taeniopygia castanotis* (Gould) (Ploceidae). Common myna (introduced), *Acridotheres tristis* (Linnaeus) (Sturnidae).

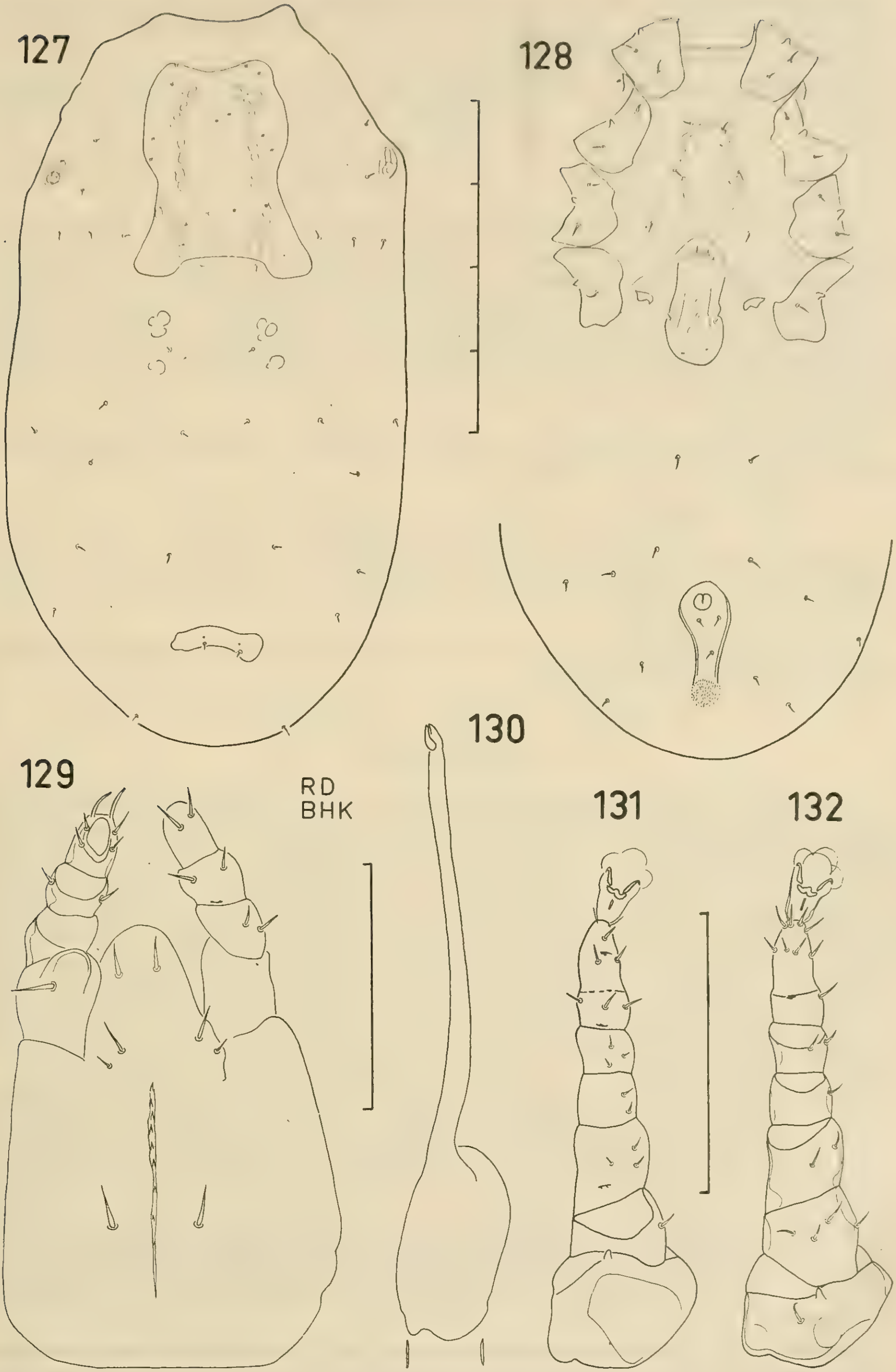
New host records (both Passeriformes).—Rose-robin, *Petroica rosea* Gould (Muscicapidae, Passeriformes), Esk, 17.iv.1967, R. D. and B. H. K. (4 ♀♀, 1 deutonymph). Spice finch (introduced), *Lonchura punctulata* (Linnaeus) (Ploceidae), Innisfail, 3.viii.1965, R. D. and J. S. W. (1♀).

Fain (1962*c*) stated that "P. motacillae *présente des légères variations en rapport avec la nature de l'hôte parasité. Ces variations portent sur la forme et les dimensions des écussons et des poils dorsaux, les dimensions du corps et des différents organes, la structure de l'écusson pygidial (simple ou double). Comme il existe tous les intermédiaires entre les formes extrêmes il ne semble pas indiqué de donner à ces variations un rang spécifique ni même subspécifique*". Later (1966*b*), however, he was to describe *P. m. phoenicuri.* A further Australian variant from *Petroica* Swainson is figured on page 353.

In the former paper, Fain also described *P. cinnyricincli* as intermediate between *P. motacillae* and *P. lobatus* in showing incipient mesonotal lobes. Weaker lobes are also present in *P. m. phoenicuri* and in Australian specimens from *Pachycephala* Vigors.

Fain (1959, 1962*a*) noted variation in the pygidial shield of specimens of *P. fringillicola* from *Emberiza* in Africa and *Carduelis* Brisson in Europe, and one of the latter specimens is very similar to *P. motacillae.* In particular, it shows a process anterodorsally on coxa II as well as ventrointernally on the palpal trochanter. The African *P. estrildicola* and its Australian subspecies, *P. e. taeniopygiae,* would also be synonymous by the present criteria. The two-toned illustrations of *P. tillae* Fain (1959), from an African starling, are too dense to allow of a decision on its status.

There has also been described (de Castro, 1948; George, 1961; Fain, 1964*b*) a group of closely related taxa from neotropical and nearctic passerines, but I have no experience of them. Their *chefs de file* are *P. sairae* de Castro and *P. japuibensis* de Castro.



Figs 127–132. *Ptilonyssus motacillae* Fain (♀ from *Petroica rosea*).– 127–128, Dorsal and ventral views of idiosoma. 129, Ventral view of capitulum, with palpal tarsus not clear (left palp in dorsal view). 130, Ventrolateral view of chelicera. 131–132, Dorsal and ventral views of leg IV.

The only tangible way in which the specimens from *Petroica* Swainson differ from the earlier Australian material is that the pygidial shield is entire rather than divided (Fig. 127).

Specimens from all three Australian hosts have the following leg chaetotaxy. Coxae 2.2.2.1. Trochanters 4.4.4.5. Femur I (2–4/1–2), II (1–4/1–1), III (1–3/0–0), IV (1–3/1–0). Genua I–III (1–4/0–1), IV (1–2/0–0). Tibiae I–II (1–3/2–1), III–IV (1–3/2–0) but often (1–3/1–0). Tarsi –.17.17.17 (*mv* absent).

Fain's *P. e. estrildicola* came from various African ploceids, and his later *P. e. taeniopygiae* from *T. castanotis* which died in Antwerp shortly after their importation from Australia. In view of the large number of species of various families of mites parasitizing the nasal passages of birds now known to occur in related African, S.E. Asian, and Australian hosts, I would accept this record as a natural infestation. The specimen from *L. punctulata* shows the three anal setae in almost the same transverse line, *cf. P. e. taeniopygiae.*

I have been able to examine 1 ♀ from *Carduelis* (labelled *P. fringillicola*) and 6 ♀ ♀ paratypes of *P. lobatus.*

PTILONYSSUS LANGEI (Butenko), n. comb.

Hapalognatha langei Butenko, 1959, *Nauch. Dokl. vȳssh. Shk.,* 2: 17 (*nomen nudum*); 1960, *Zool. Zh.,* 39: 1490. The two species headings on this latter page are transposed.

Previous record.—Common swallow (vagrant), *Hirundo rustica* Linnaeus (Hirundinidae, Passeriformes).

PTILONYSSUS ORTHONYCHUS, n. sp.

(Figs 133–137)

Diagnosis.—This morphologically nondescript species seems best compared with *P. malaysiae* Fain (1964*a*), originally described from the fairy bluebird, *Irena puella* (Latham). *Irena* Horsfield, incidentally, is placed at the end of the family Aegithinidae by McClure (1963), leading immediately into the Timaliidae, to which *Orthonyx* Temminck, the host of the new species, belongs. However, in all the following characters, *P. malaysiae* is at variance with *P. orthonychus*: podonotal shield associated with seven pairs of setae (excluding five pairs set between the shield and the peritrematalia — these are commonly present throughout the species of *Ptilonyssus*); genital setae not set on shield; adanal setae set in front of anus; coxa II with anterodorsal process; tarsi II–IV with av_1 and pv_1 spur-like; capitular setae absent.

If the Timaliidae are considered merely a subfamily of the Muscicapidae (Keast, 1961; Thomson, 1964), the only Australian species recalling *P. orthonychus* is *P. microecae* Domrow (1966*b*). The two may, however, be separated by setational details of the podonotal and anal shields, legs, and capitulum.

Types.—Holotype female and eight paratype females from southern chowchillas, *Orthonyx temminckii* Ranzani (Timaliidae, Passeriformes), Wilson's Peak, 15.v.1967, R. D. and B. H. K. Holotype N. I. C.; paratypes R. D. and A. F.

Female.—A lightly sclerotized species with particularly weak setation (Fig. 133); idiosoma 825μ long in engorged, somewhat flattened specimen figured. Podonotal shield suboval, but slightly broader and weakly concave anteriorly, length 245–286μ, breadth 183–250μ; associated setae in nine pairs, of which verticals and one or two anterolateral pairs are normally free in adjacent cuticle. Cuticle between shield and peritremes with additional five pairs of setae arranged 1.1.3. Mesonotum with usual four shieldlets and transverse band of ten setae. Pygidial shield entire, transverse, with two setae and accompanying pores, and surrounded by about five pairs of setae slightly stronger than remainder of dorsal series.

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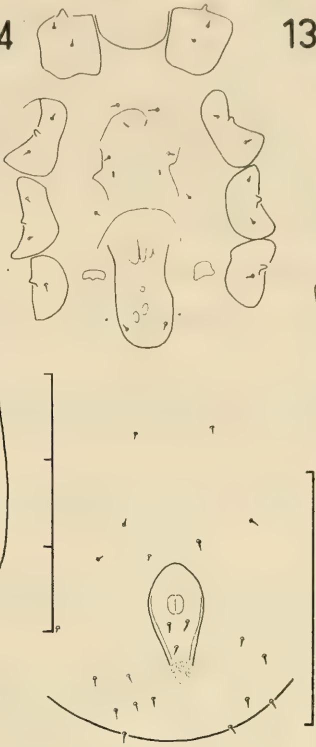

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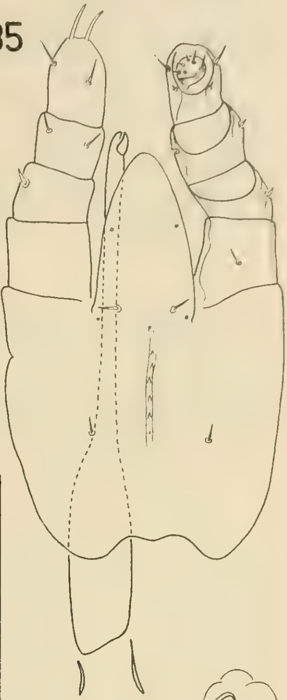

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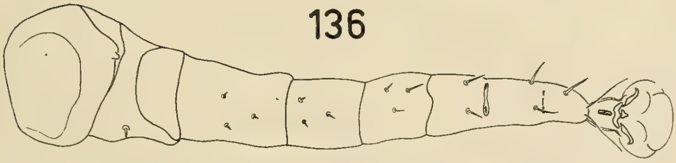

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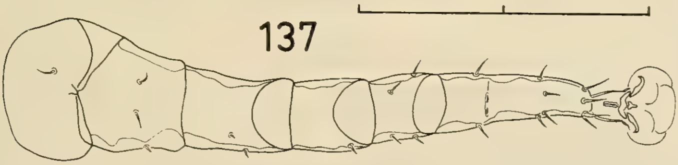

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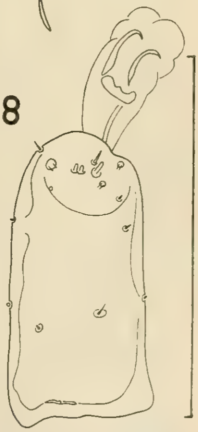


Figs 133–137. *Ptilonyssus orthonychus*, n. sp. (♀ from *Orthonyx temminckii*).–133–134, Dorsal and ventral views of idiosoma. 135, Ventral view of capitulum (right palp in dorsal view). 136–137, Dorsal and ventral views of leg IV.

Fig. 138. *Sternostoma neosittae*, n. sp. (♀ from *Neositta striata*).–Dorsal view of tarsus I.

Sternal shield (Fig. 134) evanescent, marked only by cessation of cuticular striae, bearing four pores and SII, leaving SI and III free in cuticle. Metasternal setae absent. Genital shield ligulate, with few indications of muscle insertions and rayed operculum; genital setae set on shield, but attendant pores free in cuticle. Anal shield elongate, strongly arched anteriorly; anus in front of all three anal setae; cribrum present. Ventral cuticle with about ten pairs of slightly stronger setae.

Coxa II without anterodorsal process and leg setation undistinguished (Figs 136 and 137). Coxae 2.2.2.1. Trochanters I–II (1–0/2–1), III–IV (1–0/3–0). Femur I (2–4/1–2), II (1–4/1–1), III (1–3/0–0), IV (1–3/1–0). Genua I–III (1–4/0–1), IV (1–3/0–0). Tibiae (1–3/2–1). Tarsi –.17.17.17 (*mv* absent; II–IV with av_1 and pv_1 only very slightly enlarged).

Basis capituli (Fig. 135) with two capitular setae and about seven small denticles in single file in deutosternal groove. Hypostome with HIII subequal to capitular setae, but HI and II obsolescent. Palpal setal formula 1.2.4.8. Tarsus with several weak setae and remnant of claw. Chelicerae attenuate in distal three-fifths, chelate portion occupying one-twentieth of total length. Tritosternum absent.

Ptilonyssus microecae Domrow

Ptilonyssus microecae Domrow, 1966, Proc. Linn. Soc. N.S.W., 90: 196; 1967, *Ibid.*, 91: 219.

Previous records. — Jacky winter, *Microeca fascinans* (Latham) (Muscicapidae, Passeriformes), Esk. Also Charleville and Kowanyama. Lemon-breasted flycatcher, *M. flavigaster* Gould, Kowanyama.

Ptilonyssus terpsiphonei Fain

(Figs 139–152)

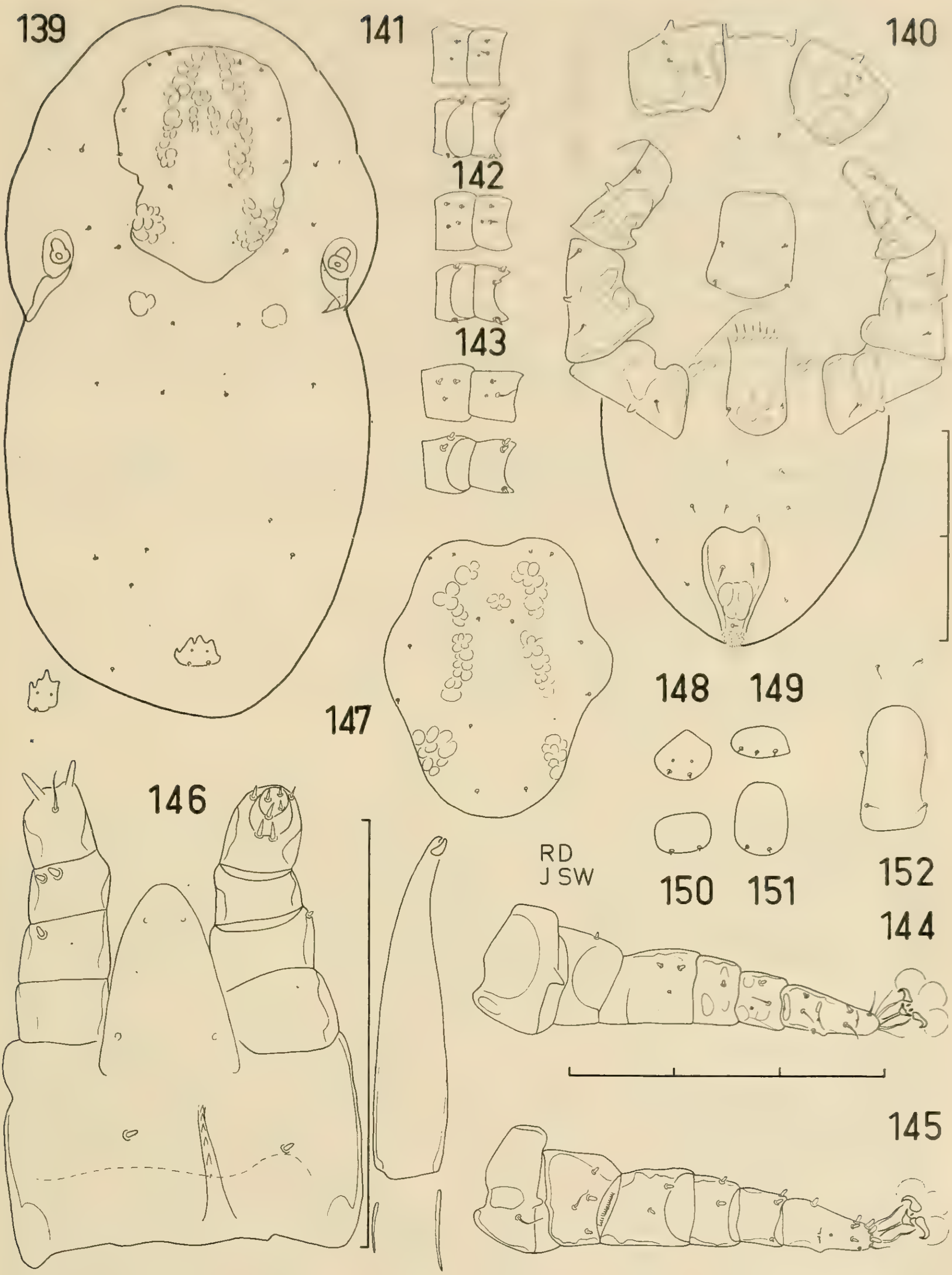
Ptilonyssus terpsiphonei Fain, 1956, *Revue Zool. Bot. afr.*, 53: 145; 1957, *Annls Mus. r. Congo belge Sér. 8vo*, 60: 104, 137; 1959, *J. ent. Soc. sth Afr.*, 22: 22; Domrow, 1965, *Acarologia*, 7: 453.

Previous records (all Muscicapidae, Passeriformes).—Black-faced flycatcher, *Monarcha melanopsis* (Vieillot), Esk. Spectacled flycatcher, *M. trivirgata* (Temminck), Mt. Jukes. Also Innisfail. White-eared flycatcher, *Carterornis leucotis* (Gould), Chelona. Also Innisfail.

New host records (all Muscicapidae).—Leaden flycatcher, *Myiagra rubecula* (Latham), Esk, 6.x.1966, R. D. and J. S. W. (6 ♀♀). Restless flycatcher, *Seisura inquieta* (Latham), Esk, 5.i.1966 and 17.iv.1967, R. D., B. H. K., and J. S. W. (4 ♀♀, 3 ♂♂, 1 protonymph). Australian pied flycatcher, *Arses kaupi* Gould, Innisfail, 5.viii.1965, R. D. and J. S. W. (1 ♀). Shining flycatcher, *Piezorhynchus alecto* (Temminck), Innisfail, 3 and 6.viii.1965, R. D. and J. S. W. (8 ♀♀, 4 ♂♂).

Individual variation in this material is considerable, but does not dispel the conviction that only one species is involved. Fain (1957*e*) illustrated three pairs of setae along the midposterior line of the podonotal shield in his African material, and this is also the case in specimens from *M. trivirgata* (Fig. 147). However, in all other Australian material, the anteriormost pair is absent (except in one specimen from *Seisura*, where one seta of the pair is present). Moreover, in specimens from *Myiagra* Vigors and Horsfield, any one or two of the remaining four setae may be rudimentary or absent (Fig. 139). Variation in the pygidial shield is indicated in Figs. 148–151. Distinct poststigmatic shields are always present.

The sternal setae are normally filiform (Fig. 152), but SI are rod-like in material from *Seisura*, and all are so modified in that from *Myiagra* (Fig. 140). The postanal seta is absent in specimens from *M. melanopsis* and *Carterornis* Mathews, minute in those from *Arses* Lesson and *Piezorhynchus* Gould, and otherwise normal.



Figs 139–152. *Ptilonyssus terpsiphonei* Fain.–139–140, Dorsal and ventral views of idiosoma of ♀ from *Myiagra rubecula*, with inset of pygidial shield from another specimen from same host. 141, Dorsal and ventral views of genu-tibia III of ♀ from *M. rubecula*. 142–143, Dorsal and ventral views of genua-tibiae III–IV of ♀ from *Monarcha trivirgata*. 144–145, Dorsal and ventral views of leg IV of ♀ from *M. rubecula*. 146, Ventral view of capitulum (right palp in dorsal view), with inset of chelicera, both from ♀ from *M. rubecula*. 147, Podonotal shield of ♀ from *M. trivirgata*. 148–151, Pygidial shield of ♀♀ from *Seisura inquieta*, *Arses kaupi*, *Piezorhynchus alecto*, and *M. trivirgata*. 152, Sternal shield of ♀ from *Carterornis leucotis*.

The legs present a *mélange* of rod-like and filiform setae (Figs 144–145). Both setae on coxa I are always rod-like, and so is usually the anterior seta on coxa II in material from *Myiagra, Seisura, Piezorhynchus,* and *M. trivirgata* (Fig. 140). Otherwise, the coxal setae are filiform. The major variant in the leg setation occurs on the genua of specimens from both species of *Monarcha* Vigors and Horsfield: I (1–4/2–1), II–III (1–4/0–1), IV (1–3/1–0), compared with I (1–2/2–1), II–III (1–2/0–1), IV (1–1/1–0) in other specimens (Figs 141–143). I include the one specimen from *Arses* in the latter category, although it shows I (1–3/2–1), II (1–2/0–1), III (1–2/1 *av*–1) and (1–2/1 *pv*–1), IV (1–1/1–0) and (1–1/2–0) — indeed, the setation in this specimen varies on the four segments trochanter–tibia. The femoral formulae vary slightly, but this is to be expected on the most setose of the segments. An all-encompassing formula would be 10/9.8/7.5/6.5/6. The remaining segments are constant: coxae 2.2.2.1; trochanters 4.4.4.5; tibiae I–II (1–3/2–1), III–IV (1–3/2–0); tarsi –.18.18.18 (*mv* present, see Fig. 145).

The capitular setae are normally present (Fig. 146), but appear to be absent in material from *M. melanopsis.* The palpal formula (trochanter-genu) is generally 0.2.2 (Fig. 146), but increases to 0.2/3.4 in specimens from *Monarcha* and *Carterornis.*

PTILONYSSUS BRADYPTERI (Fain), n. comb.

Passeronyssus bradypteri Fain, 1962, *Revue Zool. Bot. afr.,* 66: 143; Domrow, 1966, PROC. LINN. SOC. N.S.W., 90: 196.

Previous record.—Rufous songlark, *Cinclorhamphus mathewsi* Iredale (Sylviidae, Passeriformes), Esk.

PTILONYSSUS ACROCEPHALI Fain

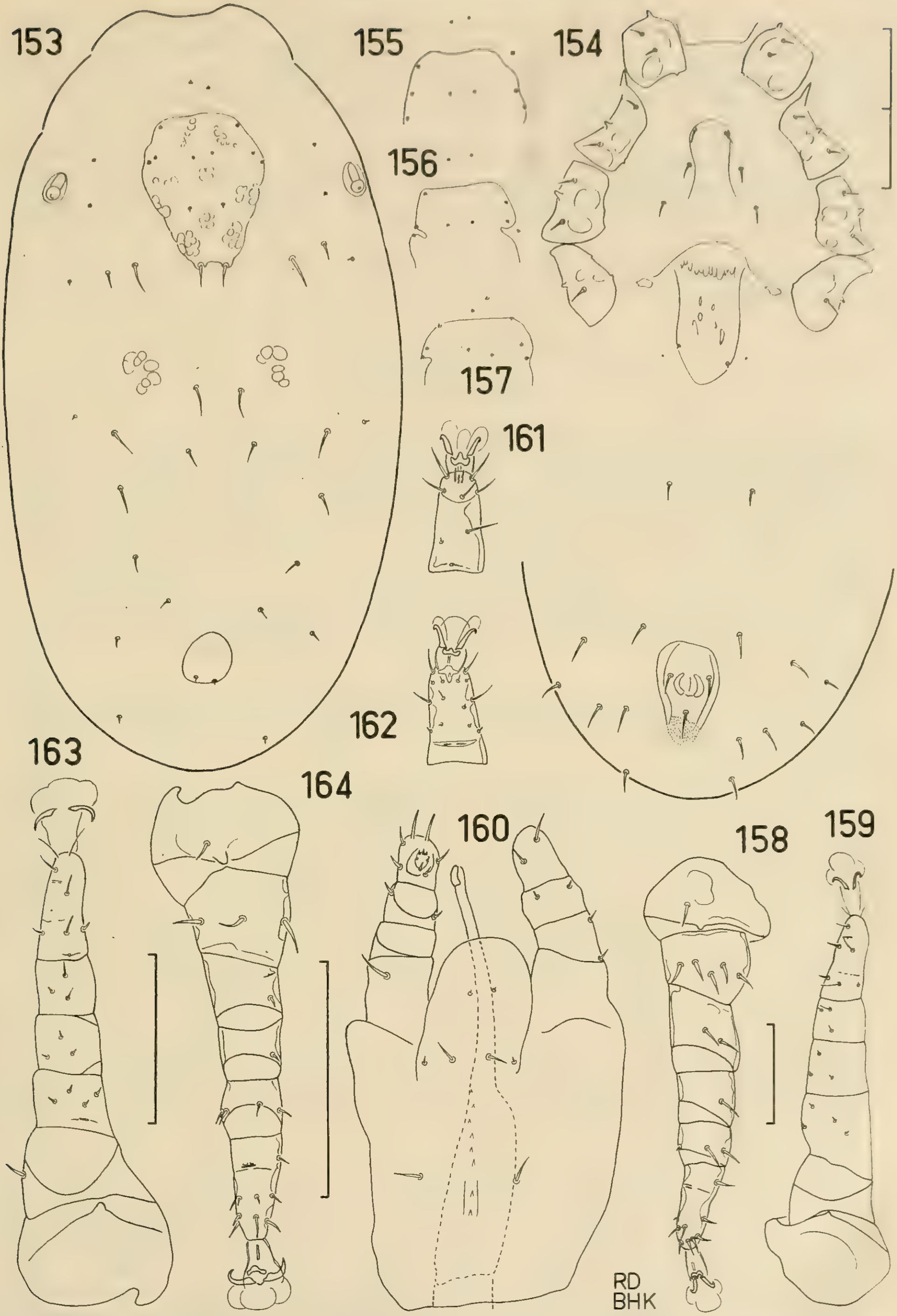
(Figs 153–160)

Ptilonyssus acrocephali Fain, 1964, *Bull. Annls Soc. r. ent. Belg.,* 100: 55.

This species, originally described from a European species of *Acrocephalus* Neumann, may now be recorded from Australia: 5 ♀♀ and 1 protonymph from Australian reed-warblers, *A. australis* (Gould) (Sylviidae, Passeriformes), Esk, 6.x.1966, and Kowanyama, 12.iii.1967, R. D., B. H. K., H. A. S., and J. S. W. The leg chaetotaxy (Figs 158–159) of these specimens is as follows. Coxae 2.2.2.1. Trochanters 4.4.4.5. Femur I (2–4/1–2), II (1–4/1–1), III–IV (1–4/1–0). Genua I–III (1–4/0–1), IV (1–3/0–0). Tibiae I–II (1–3/2–1), III–IV (1–3/2–0). Tarsi –.17.17.17 (*mv* absent). One more, or one less seta was occasionally noted on trochanter IV, femora I–III, and tibia III. The arrangement of setae on the capitulum is shown in Fig. 160.

The genital shield of Australian specimens (Fig. 154) takes in the genital setae as in *P. calamocichlae* Fain (1956, 1957*e*), while these setae are shown as free in Fain's figure of *P. acrocephali.* Moreover, the degree of posterolateral erosion of the podonotal shield (Fig. 153) is such that the subposterior pair of setae is discal, again as in *P. calamocichlae,* rather than marginal as in *P. acrocephali.* The anterolateral margins of the shield are irregular in Australian material (Figs 155–157). Actually, these two taxa are otherwise very similar, and it may be that they are conspecific. At the moment, however, the situation is clouded by several additional taxa recently described from sylviids.

P. calamocichlae Fain (1956, 1957*e*) was originally described from five African genera of Sylviidae: *Calamocichla* Sharpe, *Hippolais* Balderstein, *Cisticola* Kaup, *Prinia* Horsfield, and *Apalis* Swainson. The material from *Hippolais* has since been given subspecific status as *P. c. hippolaisi* by Fain



Figs 153–160. *Ptilonyssus acrocephali* Fain (♀ from *Acrocephalus australis*).–153–154, Dorsal and ventral views of idiosoma. 155-157, Variations in setation of anterior half of podonotal shield. 158–159, Ventral and dorsal views of leg IV. 160, Ventral view of capitulum (left palp in dorsal view).

Figs 161–164. *Ruandanyssus artami*, n. sp (♀ from *Artamus cinereus*).–161–162, Dorsal and ventral views of tarsus I. 163–164, Dorsal and ventral views of leg IV.

(1963*e*), while the material from the remaining three genera had earlier been given specific rank as *P. cisticolarum* by Fain (1959). Finally, the material from *Prinia* and *Apalis,* showing the pygidial shield divided rather than entire as in the three preceding taxa, was given specific rank as *P. elongatus* by Fain (1964*d*).

In the meantime, two further taxa with even more strongly divided pygidial shields were described from Belgian sylviids by Fain (1962*a*, 1963*d*): *P. phylloscopi* from *Phylloscopus* Boie and *P. ruandae sylviae* from *Sylvia* Scopoli.

Material from another Australian sylviid genus (*Gerygone* Gould) is considered below.

PTILONYSSUS MONARCHAE, n. sp.

(Figs 165–170)

Diagnosis.—Of the described species of *Ptilonyssus* from Australian flycatchers, only two species, *P. terpsiphonei* Fain (1956, 1957*e*) and *P. microecae* Domrow (1966*b*), show the podonotal shield complete enough posteriorly to take in the median pair of setae set immediataely in front of the mesonotal shieldlets. This is also true of *P. monarchae,* which may best be compared with *P. microecae.* However, while the anterior process on coxa II is absent, and the postanal seta present in the former, the opposite obtains in the latter. There are also minor differences in the setation of the podonotal shield and the position of the adanal setae relative to the anus.

Types.—Holotype female from a spectacled flycatcher, *Monarcha trivirgata* (Temminck) (Muscicapidae, Passeriformes), Innisfail, 31.viii.1965, H. I. McD. Holotype N. I. C.

Female.—Idiosoma 670μ long in unengorged condition, broader in anterior half. Podonotal shield (Fig. 165) half again as long as wide, 256 × 178μ, narrower in posterior third; anterior margin subrectilinear, posterior margin convex; with muscle insertions and seven pairs of setae as indicated. Peritremes short, borne on oval shieldlets with poststigmatic portions more heavily sclerotized. Body cuticle between and around podonotal shield and peritremes with 13 setae. Mesonotum with two shieldlets and transverse band of ten setae. Pygidium with entire shield and eight pairs of setae.

Sternal shield (Fig. 166) evanescent, with six setae, but apparently without pores. Metasternal setae absent. Genital shield drop-shaped, with rayed operculum and two genital setae, the latter accompanied by pores in adjacent cuticle. Anal shield elongate, with anus in front of adanal setae; postanal seta absent, but cribrum present. Body cuticle with fifteen setae arranged 2.5.8.

Coxa II with slender process on anterodorsal margin. Coxae 2.2.2.1. Trochanters I–II (1–0/2–1), III (2–0/2–0), IV (1–1/3–0). Femur I (2–4/1–2), II (1–4/1–1), III (1–3/1–0), IV (1–3/2–0). Genua I–III (1–4/0–1), IV (1–2/0–0). Tibiae (1–3/2–1). Tarsi –.17.17.17 (*mv* absent; I with one ventrodistal seta stronger, II–IV with av_1 and pv_1 stronger, see Figs 167–168).

Basis capituli with two, and hypostome with six setae; HII smaller, remainder subequal (Fig. 170). Deutosternum with single file of ten denticles. Palpal setal formula 1.3.4.8. Tarsus with about seven minute setae and bifid claw. Chelicerae (Fig. 169) attenuate for slightly more than half their length; digits occupying one-fifteenth of total length. Minute tritosternal remnant present.

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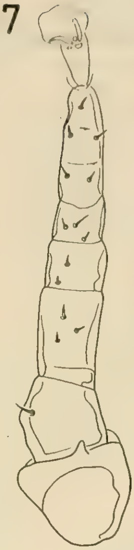

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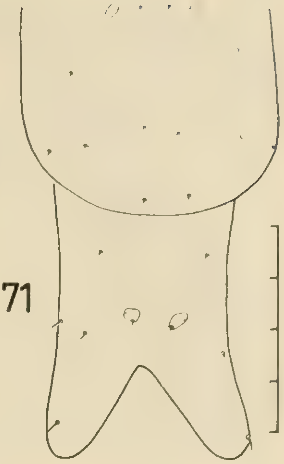

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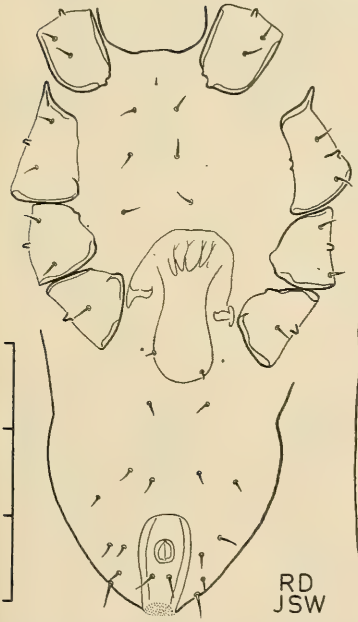

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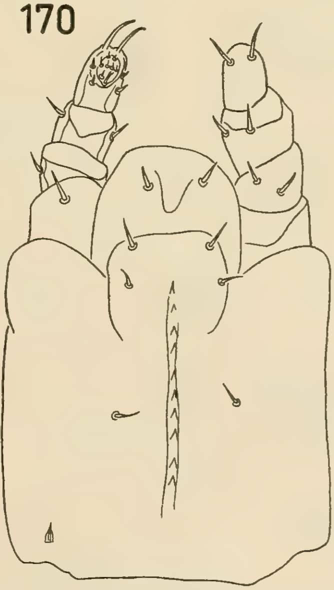

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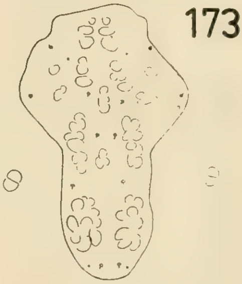

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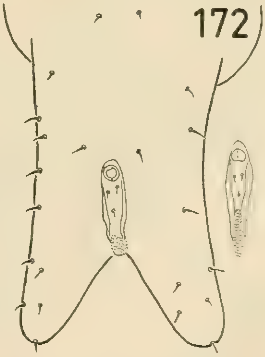


Figs 165–170. *Ptilonyssus gliciphilae* Domrow (♀ from *Myzomela pectoralis*).–165–166, Dorsal and ventral views of idiosoma. 167–168, Dorsal and ventral views of leg IV. 169, Chelicera. 170, Ventral view of capitulum with inset showing tritosternum (left palp in dorsal view).

Figs 171–173. *Ptilonyssus gliciphilae* Domrow (♀ from *Myzomela pectoralis*).–171–172, Dorsal and ventral views of opisthosoma. 173, Podonotal shield.

PTILONYSSUS SETOSAE, n. sp.

(Figs 174–186)

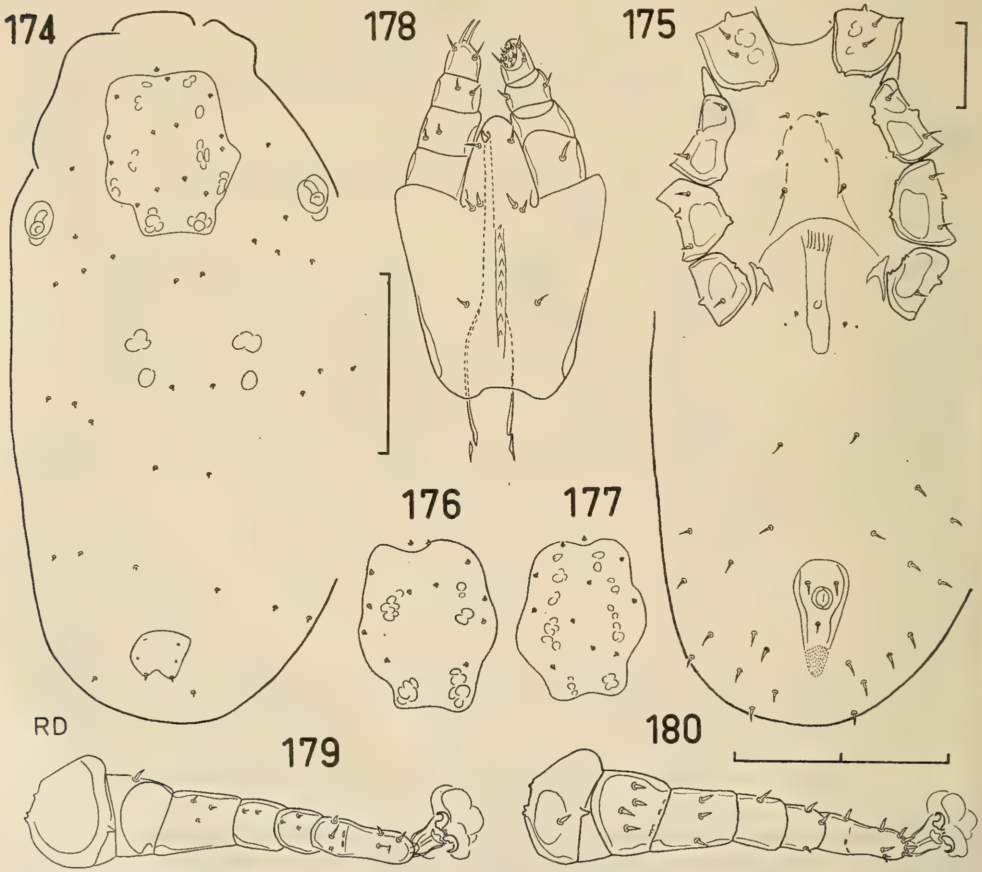
Diagnosis.—The species of *Ptilonyssus* known from *Rhipidura* Vigors and Horsfield (see Fain, 1963*e*, and Domrow, 1966*b*) may be separated by the following couplets:

1. Vertical setae present, *i.e.* podonotal shield with seven pairs of setae. Postanal seta present 2
Vertical setae absent, *i.e.* podonotal shield with six pairs of setae (including submarginal anterolateral pair). Postanal seta absent .... *macclurei* Fain
2 (1). Pygidial shield entire. Adanal setae in front of anus .... *setosae*, n. sp.
Pygidial shield divided. Adanal setae behind anus .... *rhipidurae* Domrow

Types.—Holotype female and seven paratype females from a northern fantail, *Rhipidura setosa* (Quoy and Gaimard) (Muscicapidae, Passeriformes), Ella Bay, 4.viii.1965, R. D. and J. S. W. Holotype N. I. C.; paratypes R. D.

The following specimens are assigned to the new species, but do not form part of the type series: 6 ♀♀ and 1 protonymph from rufous fantails, *R. rufifrons* (Latham), Innisfail, 24 and 29.vi.1965, G. J. B. and H. I. McD.

Female.—Idiosoma 594–616μ long, 322μ wide in unfed specimens, and up to 814–880μ long, 385–418μ wide in engorged material (all mounted).



Figs 174–180. *Ptilonyssus setosae*, n. sp. (♀ from *Rhipidura setosa*).–174–175, Dorsal and ventral views of idiosoma. 176–177, Variations in setation of podonotal shield. 178, Ventral view of capitulum (right palp in dorsal view). 179–180, Dorsal and ventral views of leg IV.

Podonotal shield rather variable in shape, but generally slightly concave anteriorly and posteriorly, with midlateral convexity; usually in range 178–201μ long, 156–171μ wide, but one specimen smaller, 169×147μ. Five specimens show six pairs of setae on shield (Fig. 176), but I believe normal complement to be seven pairs, attained only when midposterior arch of four is full (Fig. 174). One specimen (Fig. 177) is grossly abnormal, both lacking one anterolateral on each side and one median, as well as having midposterior four irregularly arranged. Surface of shield weakly granulate and marked by muscle insertions. Cuticle surrounding shield with six pairs of setae. Peritremes present, with weak poststigmatic shields. Mesonotum with four shieldlets and ten setae. Pygidial shield entire, subquadrate, with two setae and some pores; surrounded by about eight setae. Dorsal setae in form of stout spines.

Sternal shield delineated only by cessation of cuticular striae, without evident texture (Fig. 175), bearing six setae and four pores submarginally. Metasternal setae absent. Genital shield elongate, with longitudinal granulations and weakly marked muscle insertions; operculum rayed. Genital setae and accompanying pores free in cuticle. Anal shield broadest towards front, with adanal setae in front of anus; postanal seta and cribrum present. Ventral cuticle with about 10–12 pairs of spinose setae.

Legs provided with stout, spine-like setae ventrally, and much weaker setae dorsally (Figs 179–180). Coxae 2.2.2.1 (on one side of one specimen the seta on coxa IV is bifid). Trochanters 4.4(5).4.5. Femur I (2–4/1–2), II (1–4/1–1), III (1–3/1–0), IV (1–3/2–0). Genua I–III (1–4/0–1) but I often (1–3/0–1), IV (1–2/0–0). Tibiae I–II (1–3/2–1), III–IV (1–3/2–0). Tarsi –.17.17.17 (*mv* lacking). Ambulacrum I more elongate, and with weaker, straighter claws than II–IV.

Basis capituli and hypostome with four pairs of subequal, spinose setae (Fig. 178). Deutosternum with about nine denticles in single file. Palpal setal formula 1.2.4.7. Chelicerae suddenly attenuate in distal half, with digits occupying one-twentieth of total length. Tritosternum absent.

Remarks.—The above description is based on specimens from *R. setosa.* Those from *R. rufifrons* differ in the following respects. Idiosoma 737×330μ in moderately fed, 814–847μ long and 352–363μ wide in engorged, and 880×374μ in gravid specimens. Podonotal shield as long as wide, length 167–178μ, breadth 174–180μ; broadly arched anterolaterally and slightly concave posteriorly. All dorsal setae in form of blunt rods (Fig. 181).

Venter with sternal and opisthosomal setae stouter (Fig. 182).

Setae on ventral aspect of legs in form of blunt rods (Figs 185–186). Genua I and II often (1–3/0–1). Femur IV (1–3/1–0). In fact, all three species included in the above key show the same gross setal formulae as given by Domrow (1966*b*) for *P. rhipidurae*, except that specimens of *P. setosae* from *R. setosa* show an additional ventral seta on femur IV.

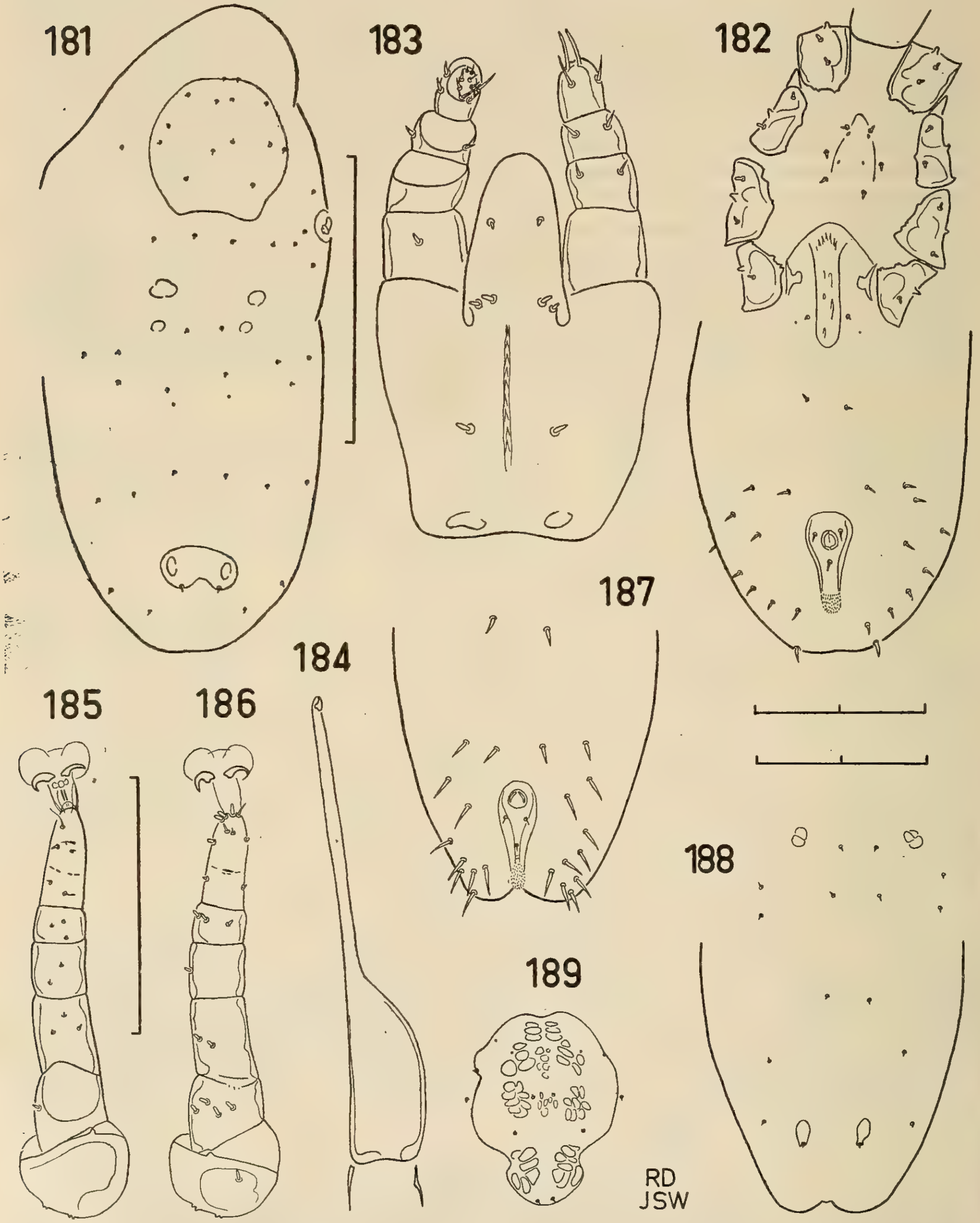
Capitulum also with rod-like setae on basis and hypostome (Fig. 183). Chelicerae as in Fig. 184.

PTILONYSSUS GERYGONAE, n. sp.

(Figs 190–194)

Ptilonyssus sp. Domrow, 1967, PROC. LINN. SOC. N.S.W., 91: 217.

Diagnosis.—Of the taxa from sylviid genera discussed above under *P. acrocephali* Fain, *P. gerygonae* is most closely related to *P. calamocichlae hippolaisi* Fain (1963*e*). However, the setae on the ventral surface of the opisthosoma and in the transverse row of six immediataely behind the podonotal shield are undistinguished in the new species, while they are considerably enlarged in *P. c. hippolaisi.* Also, on the posterior tarsi, the setae on the leading edge are retrorse, and av_1 and pv_1 divergent in *P. c. hippolaisi,* but normally curved and with opposed tips, respectively, in the new species. Finally, the bulbous basal portion of the chelicerae is relatively longer in *P. c. hippolaisi* with respect to the attenuate distal portion.

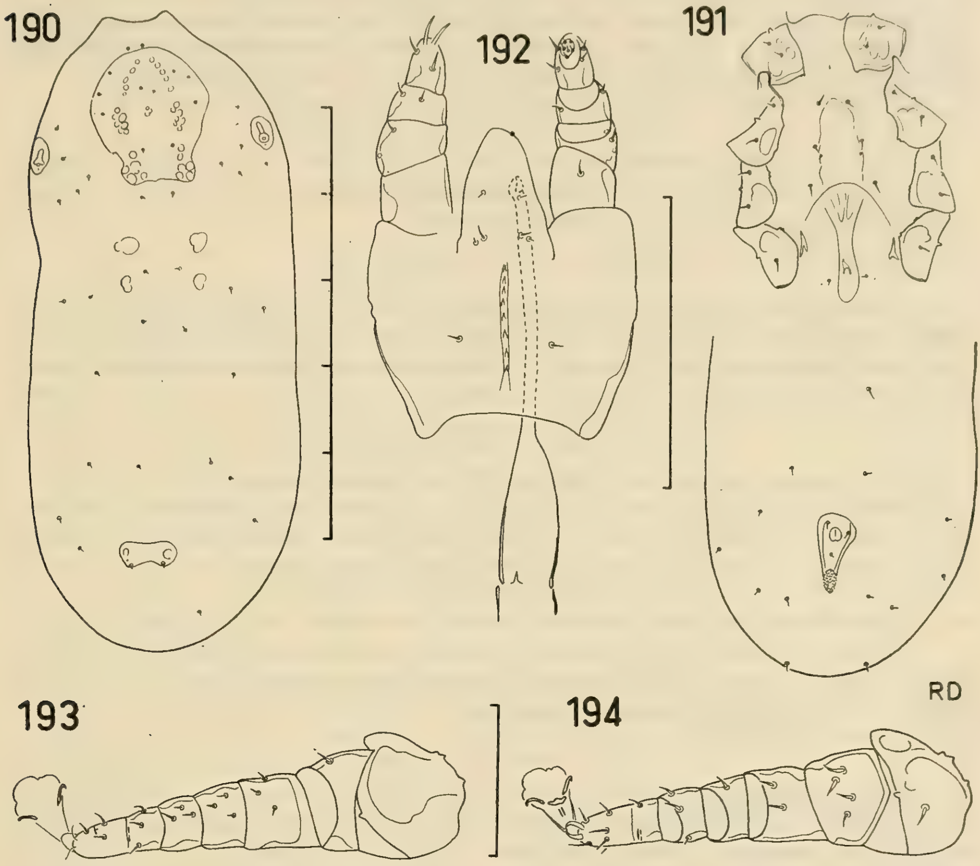


Figs 181–186. *Ptilonyssus setosae,* n. sp. (♀ from *Rhipidura rufifrons*).–181–182, Dorsal and ventral views of idiosoma. 183, Ventral view of capitulum (left palp in dorsal view). 184, Chelicera. 185–186, Dorsal and ventral views of leg IV.

Figs 187–189. *Ptilonyssus philemoni* Domrow (♀ from *Meliphaga notata*).–187–188, Ventral and dorsal views of opisthosoma. 189, Podonotal shield.

Types.—Holotype female, six paratype females, and one protonymph from black-throated warblers, *Gerygone palpebrosa* Wallace (Sylviidae, Passeriformes), Innisfail, 1.vii. and 16.viii.1965, G. J. B., R. D., H. I. McD., and J. S. W. Holotype N. I. C.; paratypes R. D.

Female.—Idiosoma 704–836μ long, 253–319μ wide depending on degree of engorgement. Podonotal shield (Fig. 190) 150–161μ long, 138–147μ wide; broadly arched anterolaterally, irregularly bilobed posteriorly; bearing six pairs of setae (including vertical pair); surface weakly granulate and marked by muscle insertions. One pair of setae immediately behind shield, and five pairs arranged 1.1.3 between shield and peritrematalia. Mesonotum with usual four shieldlets and transverse band of ten setae. Pygidial shield entire, transverse, with two setae and pores; surrounded by about eight setae. All dorsal setae in form of slender spines.



Figs 190–194. *Ptilonyssus gerygonae*, n. sp. (♀ from *Gerygone palpebrosa*).–190–191, Dorsal and ventral views of idiosoma. 192, Ventral view of capitulum (right palp in dorsal view) (note tritosternum). 193–194, Dorsal and ventral views of leg IV.

Sternal shield weakly outlined and textureless, with two pores; SI–III in adjacent cuticle (Fig. 191). Metasternal setae absent. Genital shield narrowly drop-shaped, leaving genital setae and attendant pores free in cuticle. Anal shield small, elongate, with adanal setae in front of, and postanal seta behind anus; cribrum present. Ventral cuticle with about six pairs of setae.

Legs with slender, spine-like setae ventrally (Figs 193–194). Coxae 2.2.2.1. Trochanters 4.4.4.5. Femur I (2–4/1–2), II (1–4/1–1), III (1–3/0–0), IV (1–3/1–0). Genua I–III (1–4/0–1), IV (1–3/0–0). Tibiae I–II (1–3/2–1), III–IV (1–3/2–0). Tarsi –.17.17.17 (*mv* absent; av_1 and pv_1 stronger, with opposed points).

Capitular setae and all hypostomal setae present (Fig. 192). Deutosternum with about eight denticles in single file. Palpal setal formula 1.2(3).4.8. Chelicerae bulbous in basal two-fifths, with chelate portion occupying one-twentieth of total length. Minute tritosternal remnant present.

PTILONYSSUS RHIPIDURAE Domrow

Ptilonyssus rhipidurae Domrow, 1966, PROC. LINN. SOC. N.S.W., 90: 199.

Previous record.—Grey fantail, *Rhipidura fuliginosa* (Sparrman) (Muscicapidae, Passeriformes), Esk. Also Innisfail.

PTILONYSSUS MACCLUREI Fain

Ptilonyssus macclurei Fain, 1963, *Revue Zool. Bot. afr.,* 68: 72; Domrow, 1964, *Acarologia,* 6: 609, 617; 1966, PROC. LINN. SOC. N.S.W., 90: 201.

Previous record.—Willie wagtail, *Rhipidura leucophrys* (Latham) (Muscicapidae, Passeriformes), Palen Ck., Brisbane, and Esk. Also Kowanyama.

PTILONYSSUS PSOPHODAE Domrow

Ptilonyssus psophodae Domrow, 1964, *Acarologia,* 6: 29, 618.

Previous record.—Eastern whipbird, *Psophodes olivaceus* (Latham) (Falcunculidae, Passeriformes), Upper Brookfield. Also Esk and Innisfail.

PTILONYSSUS GRALLINAE Domrow

Ptilonyssus grallinae Domrow, 1964, *Acarologia,* 6: 611, 618.

Previous record.—Magpie-lark, *Grallina cyanoleuca* (Latham) (Grallinidae, Passeriformes), Brisbane and Condamine. Also Urbenville (N.S.W.), Esk, Charleville, Chelona and Kowanyama.

PTILONYSSUS RUANDAE Fain

Ptilonyssus ruandae Fain, 1956, *Revue Zool. Bot. afr.,* 53: 395; 1957, *Annls Mus. r. Congo belge Sér. 8vo,* 60: 109; Domrow, 1964, *Acarologia,* 6: 608. *Ptilonyssus ruandae alcippei* Fain and Nadchatram, 1962, *Bull. Annls Soc. r. ent. Belg.,* 98: 279.

Previous record.—Grey-backed silvereye, *Zosterops lateralis* (Latham) (Zosteropidae, Passeriformes), Brisbane. Also Wilson's Peak, Mt Jukes, and Innisfail.

PTILONYSSUS DICAEI Domrow

Ptilonyssus dicaei Domrow, 1966, PROC. LINN. SOC. N.S.W., 90: 201.

Previous record.—Mistletoe-bird, *Dicaeum hirundinaceum* (Shaw) (Dicaeidae, Passeriformes), Mt Jukes.

PTILONYSSUS CINNYRIS Zumpt and Till

(Fig. 81)

Ptilonyssus cinnyris Zumpt and Till, 1955, *J. ent. Soc. sth. Afr.,* 18: 78; Fain, 1957, *Annls Mus. r. Congo belge Sér. 8vo,* 60: 86; 1958, *Bull. Soc. r. Zool. Anvers* 9: 7; Nadchatram, McClure, and Lim, 1964, *J. fed. Malay St. Mus.,* 9: 104.

This parasite of African and Malayan sunbirds may now be recorded from the only Australian member of the family: 3 ♀♀ and 1 protonymph from yellow-breasted sunbirds, *Cyrtostomus frenatus* (Müller) (Nectariniidae, Passeriformes), Innisfail, 2.viii and 17.ix.1965, R. D., H. I. McD., and J. S. W. The podonotum is shown in Fig. 81.

PTILONYSSUS MYZANTHAE Domrow

Ptilonyssus myzanthae Domrow, 1964, *Acarologia,* 6: 603, 617.

Previous records (both Meliphagidae, Passeriformes).—Noisy miner, *Myzantha melanocephala* (Latham), Condamine. Also Esk. Little wattle-bird, *Anthochaera chrysoptera* (Latham), Palen Ck.

New host record.—Yellow-throated miner, *M. flavigula* Gould, Charleville, 19.i.1967, J. N. and J. S. W. (5 ♀♀, 1 protonymph); Winbin Ck., 20.i.1966, R. D., D. J. M., and J. S. W. (2♀♀).

PTILONYSSUS PHILEMONI Domrow
(Figs 187–189)

Ptilonyssus philemoni Domrow, 1964, *Acarologia,* 6: 600, 617; 1965, *Ibid.,* 7: 460.

Previous records (all Meliphagidae, Passeriformes).—Blue-faced honeyeater, *Entomyzon cyanotis* (Latham), Logan Village and Condamine. Also Esk and Kowanyama. Noisy friar-bird, *Philemon corniculatus* (Latham), Logan Village. Also Palen Ck., Esk, Charleville, and Mt Jukes. Little friar-bird, *P. citreogularis* (Gould), Brisbane, Samford, and Esk. Also Charleville, Chelona, Longreach Lagoon, and Kowanyama.

New host records (all Meliphagidae).—Striped honeyeater, *Plectorhyncha lanceolata* Gould, Esk, 10.vii.1967, R. D. and B. H. K. (11 ♀♀, 4 nymphs); Charleville-Cunnamulla road, 19.v.1965, H. A. S., D. J. M., and B. H. K. (3♀♀). Lesser Lewin honeyeater, *Meliphaga notata* (Gould), Innisfail, 3 and 22.vi, and 15.ix.1965 (17 ♀♀, 1♂). Graceful honeyeater, *M. gracilis* (Gould), Innisfail, 30.vi, 5–21.viii, and 14.ix.1965, G. J. B., R. D., H. I. McD., and J. S. W. (27 ♀♀).

The new specimens from *Plectorhyncha* Gould are quite typical of the original description, although in one specimen the pygidial shield shows far to one side a very narrow longitudinal fissure with striate cuticle, and may fairly be said to be divided.

However, the specimens from *Meliphaga* Lewin, although they show the same evenly tapering chelicerae and cordate podonotal shield with 5–6 characteristically arranged pairs of setae figured for *P. philemoni* Domrow (1964*c*), may be separated by the following features: (*i*) the adanal setae are set well behind the anus; and (*ii*) the pygidial shield is divided, the two longitudinal fragments being widely separated. Other minor differences are detailed in the description below.

Female.—Idiosoma 583–660μ long when unengorged, but up to 825–990μ when fully fed and mounted; weakly cleft posteriorly. Podonotal shield (Fig. 189) usually 220–231μ long, 170–176μ wide, but occasionally smaller (209–214μ long, 165–168μ wide); cordate, but margins somewhat eroded, leaving one or two of three anterolateral pairs of setae free in cuticle; two discal pairs set in stronger arch than in original series; posterior pair submarginal. Surface irregularly granulate, with very distinct muscle insertions. Cuticle between narrowed posterior third of shield and peritremes with three pairs of setae. Two mesonotal shieldlets accompanied by eight setae arranged 4.4. Halves of pygidial shield (Fig. 188) elongate, widely separated, each with terminal seta; preceded by arch of six setae.

Sternal shield somewhat stronger than in original series, with some granulation, usually bearing SI and II submarginally, and with two pores between SII; SI not as strong as pygidial setae, SII larger, and SIII approaching anteroventral opisthosomal setae in size. Metasternal setae absent. Genital shield typical. Anal shield (Fig. 187) elongate, 140–162μ long, 40–46μ wide; anus well forward, and well in front of three subequal and weak anal setae. Ventral body cuticle with nine to 14 (usually 10–12) pairs of stout setae.

Setae on coxae and trochanters slightly more expanded than in original series; those on ventral surface of other segments (including av_1 and pv_1 on tarsi II–IV) somewhat weaker, but still with delicate tips. Setae on dorsum of legs weaker, evenly tapering. Coxae 2.2.2.1. Trochanters I–II (1–0/2–1), III (2–0/2–0), IV (2–0/4–0). Femur I (2–4/1–2), II (1–4/2–1), III–IV (1–3/1–0). Genua I–II (1–4/0–1), III (1–4/0–2), IV (1–3/1–0). Tibiae (1–3/2–1). Tarsi –.17.17.17 (*mv* absent). The formulae of the original series differ in the following respects: trochanter IV with five setae; basifemur I often with tenth seta ventrally; femur III with four to six setae; genua III–IV usually (1–4/0–1) (1–3/0–0), but (1–4/0–2) (1–3/1–0) in large specimens from *P. corniculatus*.

Capitulum as in original series except as follows: basis without spinulae at ventroexternal angles; hypostomal setae very weak, anteriormost pair absent. Palpal setal formula 1.2.4.8 in both series.

Male.—Idiosoma 473μ long. Dorsum as in female.

Venter essentially as in female, except for genital aperture in front of SI (area between coxae IV not clear). Anal shield 135 × 40μ, flanked by five stout setae on one side and six on other.

Legs and capitulum undistinguished.

PTILONYSSUS BALIMOENSIS Sakakibara

(Figs 195–203)

Ptilonyssus balimoensis Sakakibara, 1968, *J. med. Ent.*, **5**: 17.

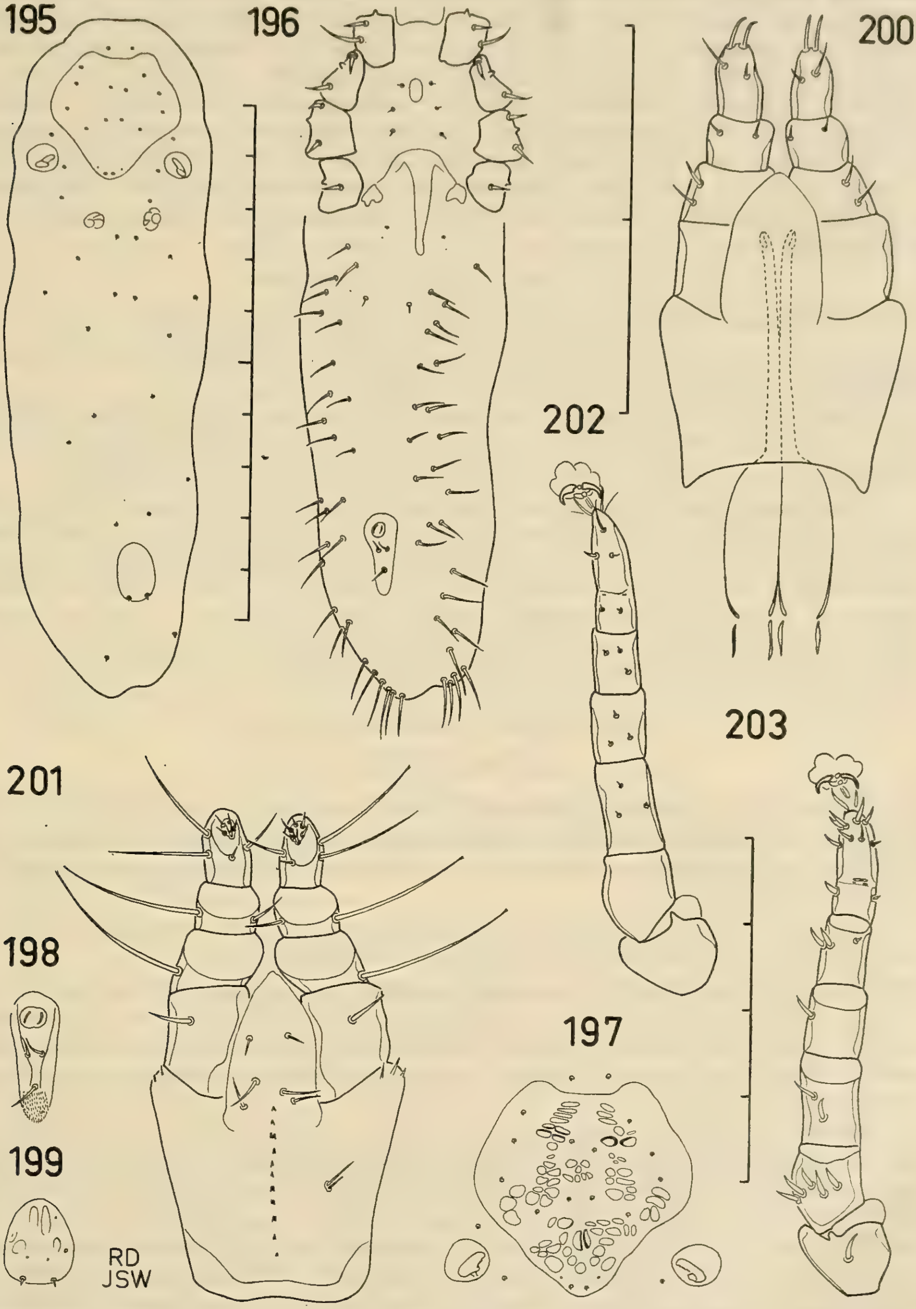
I had already figured and described this striking new species before seeing the above reference, and therefore restrict the present text to additional descriptive notes and figures. The podonotal shield immediately recalls that of *P. philemoni* Domrow (1964*c*), but the two species may easily be separated by the shape of the cheliceral shafts, and the setation of the ventral face of both opisthosoma and palpi.

The new material comprises 2 ♀♀ from a Macleay honeyeater, *Meliphaga macleayana* (Ramsay) (Meliphagidae, Passeriformes), Ella Bay, Innisfail, 12.viii.1965, R. D. and J. S. W.

Female.— Idiosoma (Figs 195–196) 1300μ long in slightly compressed material. Podonotal shield (Fig. 197) broadly cordate, as long as wide; shagreened over entire surface (except for narrow marginal strip), showing quite strongly marked muscle insertions, and bearing two subposterior pores and seven pairs of setae. Pygidial shield (Fig. 199) longitudinally shagreened (particularly in mid-line), bearing four or five pores and two spinose pygidial setae. All dorsal setae minute, particularly on podosoma.

Sternal shield without pores. Genital shield longitudinally shagreened, with indications of muscle insertions. Anal shield (Fig. 198) shagreened laterally. Ventral cuticle with 26–31 setae on either side, all of which are very strong except one midanterior pair.

Coxa II without anterodorsal process, but anterior seta borne on tubercle. Setae on ventral aspect of legs considerably longer and stronger than those on dorsal, occasionally bifid at extreme tip (Figs 202–203). Coxae 2.2.2.1. Trochanters I-II (1–0/2–1), III (2–0/2–0), IV (2–0/3–0). Femur I (2–4/3–2) (including one seta present ventrally on basifemur), II (1–4/2–1), III (1–4/1–0), IV (1–3/1–0). Genua I–III (1–4/0–1) (but II with only 3 *d* once), IV (1–3/0–0). Tibiae I–II (1–3/2–1), III (1–3/2–0) in one specimen



Figs 195–203. *Ptilonyssus balimoensis* Sakakibara (♀ from *Meliphaga macleayana*).– 195–196, Dorsal and ventral views of idiosoma. 197, Podonotal shield. 198, Anal shield. 199, Pygidial shield. 200–201, Dorsal and ventral views of capitulum. 202–203, Dorsal and ventral views of leg IV.

(1–3/1 *av*–0) in other, IV (1–3/2–0) (but with only 1 *v*, and that *av*, once). Tarsi–.17.17.17 (*mv* absent; av_1 and pv_1 stronger on tarsi II–IV). Ambulacrum I little different from II–IV, all with two subequal claws and diaphanous pulvillus.

Basis capituli (Figs 200–201) slightly teratological in both specimens, showing two setae set in contiguous or single alveolus on left side only, rather than typical 1.1; spinulose externally near trochanteral articulation. Tritosternum absent, but deutosternal groove present, showing about eleven uni- or bidentate denticles. Palpi five-segmented, with setal formula 1.3.4(5).8(7); four external setae on femur-tibia preternaturally long for genus, sometimes bifid at extreme tip. Tarsus weak, completely obscured dorsally by tibia; with about five weak setae and small bifid claw. Chelicerae suddenly attenuate in distal half; chelate portion occupying one-twentyfifth of total length.

Ptilonyssus myzomelae Domrow

Ptilonyssus myzomelae Domrow, 1965, *Acarologia*, 7: 455.

Previous record.—Scarlet honeyeater, *Myzomela sanguinolenta* (Latham) (Meliphagidae, Passeriformes), Samford. Also Esk.

New host record.—Dusky honeyeater, *M. obscura* Gould, Innisfail, 30.vi, 6.viii, and 30.ix.1965, G. J. B., R. D., H. I. McD., and J. S. W. (3 ♀ ♀, 1 deutonymph); Jordan Ck., 18.viii.1965, R. D. (2 ♀ ♀, 1 protonymph).

Specimens from the type host, *M. sanguinolenta,* show the pygidial shield completely lacking, although the short, stumpy pygidial setae (and their accompanying pores) are easily made out among the elongate, tapering opisthosomal series. Specimens from *M. obscura,* however, show widely separated, small, rounded pygidial shields, each bearing a seta and pore, although on one side of one specimen the pygidial seta is separated from its shield and pore by five complete cuticular annulations.

Ptilonyssus gliciphilae Domrow

(Figs 171–173)

Ptilonyssus gliciphilae Domrow, 1966, Proc. Linn. Soc. N.S.W., 90: 204.

Previous record.—Brown honeyeater, *Gliciphila indistincta* (Vigors and Horsfield) (Meliphagidae, Passeriformes), Esk and Chelona. Also Charleville and Kowanyama.

New host record.—Banded honeyeater, *Myzomela pectoralis* Gould (Meliphagidae), Kowanyama, 16, 18, and 23.x.1965, R. D. (11 ♀ ♀, 1 ♂).

The podonotal shield of the new material is very similar to that of the original. However, apart from host-specificity, the new form is readily separable by showing the pygidial shield distinctly divided, and two setae ventrally on basifemur I. Further minor differences are noted in the description below.

Female.—Idiosoma 780μ long in one unengorged specimen, but elongate and reaching 1320–1430μ in fully fed, mounted material; terminal bifurcation quite evident in life, even to naked eye. Podonotal shield (Fig. 173) usually 290–308μ long and 187–192μ wide, but extreme range 286–319μ long and 176–205μ wide; more parallel-sided in posterior half, and with anteriormost pair of median setae set further back than in original series; surface strongly granulate, with well-defined muscle insertions. Arrangement of adjacent setae and shieldlets around podonotal shield and on mesonotum as in original series. Halves of pygidial shield (Fig. 171) small, well separated, each with seta and pore; flanked by three or four pairs of stronger setae.

Venter as in original series, but anal shield (Fig. 172) narrower (220–253μ long, 52–55μ wide) and less well-defined anteriorly. Genital shield on raised lobe between coxae IV in engorged specimens.

Coxae 2.2.2.1. Trochanters I–II (1–0/2–1), III (2–0/2–0), IV (2–1/2–0). Femur I (2–4/3–2) (including two setae ventrally on basifemur), II (1–4/2–1), III (1–3/2–0), IV (1–3/1–0). Genu I (1–4/0–1), II (1–4/1–1), III (1–4/1–2), IV (1–3/1–0). Tibiae (1–3/2–1). Tarsi –.17.17.17 (*mv* absent; av_1 and pv_1 as in original series). The original series shows a similar chaetotaxy, except femur I (1–4/1–2) (*i.e.* no setae ventrally on basifemur), III (1–3/1–0); genu III (1–4/1–1). Setae on ventral face of legs similar to those on coxae, but those on dorsum rather weaker. Ambulacrum I only very slightly weaker than II–IV. Coxa II with strong anterodorsal process.

Capitulum as in original series, but setal formula of palpi 1.3(2).4.9 due to presence of additional seta dorsally on femur and tibia. Tritosternum absent.

Male.—Idiosoma 596μ long, evenly rounded posteriorly. Dorsum entirely as in female, but podonotal shield smaller, 219 × 120μ.

Sternal shield as in female, but extended into diffuse genital area between coxae IV; genital setae free in cuticle. Sexual aperture in front of SI. Anal shield as in female, but only 120μ long; surrounded by five pairs of setae rather than 10–12 pairs in female.

Leg setation as in female, but with five setae on one trochanter II; av_1 and pv_1 on tarsi II–IV sharply pointed, though still upturned at tip.

Capitulum as in female. Chelicerae not attenuate, spermatodactyl occupying two-fifths of total length of 120μ.

PTILONYSSUS LYMOZEMAE Domrow

Ptilonyssus lymozemae Domrow, 1965, *Acarologia*, 7: 453.

Previous record.—Scarlet honeyeater, *Myzomela sanguinolenta* (Latham) (Meliphagidae, Passeriformes), Logan Village and Samford. Also Esk.

PTILONYSSUS STOMIOPERAE Domrow

Ptilonyssus stomioperae Domrow, 1966, PROC. LINN. SOC. N.S.W., 90: 206.

Previous records (both Meliphagidae, Passeriformes).—Yellow honeyeater, *Meliphaga flava* (Gould), Kowanyama. White-gaped honeyeater, *Stomiopera unicolor* (Gould) Kowanyama.

PTILONYSSUS THYMANZAE Domrow

Ptilonyssus thymanzae Domrow, 1964, *Acarologia*, 6: 604, 617; 1966, PROC. LINN. SOC. N.S.W., 90: 204.

Previous records (all Meliphagidae, Passeriformes).—Lewin honeyeater, *Meliphaga lewinii* Swainson, Esk. Also Wilson's Peak and Innisfail. Lesser Lewin honeyeater, *M. notata* (Gould), Innisfail. Yellow-faced honeyeater, *M. chrysops* (Latham), Samford. Noisy miner, *Myzantha melanocephala* (Latham), Logan Village and Condamine. Also Brisbane and Esk. Little wattle-bird, *Anthochaera chrysoptera* (Latham), Palen Creek.

New host records (all Meliphagidae).—White-plumed honeyeater, *Meliphaga penicillata* Gould, Charleville, 10 and 24.i.1967, R. D., J. N., and J. S. W. (4 ♀ ♀); Winbin Ck., 21.i.1966, R. D., D. J. M., and J. S. W. (2 ♀ ♀). Yellow-throated miner, *Myzantha flavigula* Gould, Winbin Ck., 20.i.1966, R. D., D. J. M., and J. S. W. (2 ♀ ♀). Spiny-cheeked honeyeater, *Acanthagenys rufogularis* Gould, Charleville, 14.i.1966 and 1.ii.1967, R. D., D. J. M., and J. S. W. (2 ♀ ♀).

PTILONYSSUS MELIPHAGAE Domrow

Ptilonyssus meliphagae Domrow, 1964, *Acarologia,* 6: 606.

Previous record.—Yellow-faced honeyeater, *Meliphaga chrysops* (Latham) (Meliphagidae, Passeriformes), Mt Cotton. Also Esk.

New host record.—White-throated honeyeater, *Melithreptus albogularis* Gould (Meliphagidae), Esk, 6.x.1966 and 17.iv.1967, R. D., B. H. K., and J. S. W. (4 ♀♀); Kowanyama, 15.iii.1966, R. D. (1 ♀).

The pygidial complex of the original specimen from *Meliphaga* was not detected, but I have since seen two more females from this host. These show the pygidial shield widely divided into two elongate fragments little wider than the alveoli of the pygidial setae. A pore accompanies each seta.

The specimens from *Melithreptus* Vieillot all show an entire, transverse pygidial shield, although in two specimens it is narrowly and asymmetrically divided as in the specimen of *P. philemoni* discussed above. Indeed, in one specimen, the teratology affects the entire distal portion of the opisthosoma, as ventrally the anal shield is also atypical, lacking the postanal seta.

PTILONYSSUS NUDUS Berlese and Trouessart

Ptilonyssus nudus Berlese and Trouessart, 1889, *Bull. Biblioth. scient. Ouest,* 2: 130; Berlese, 1892, "Acari, myriapoda, et scorpiones hucusque in Italia reperta, ordo Mesostigmata" (Patavii), fasc. 53, No. 10 (♀); de Castro and Pereira, 1947, *Archos Inst. biol., S Paulo,* 18: 127; Bregetova, 1951, *Parazit. Sb.,* 13: 118; Porter and Strandtmann, 1952, *Tex. J. Sci.,* 4: 394; George, 1961, *J. Kans. ent. Soc.,* 34: 116; Fain, 1963, *Bull. Annls Soc. r. ent. Belg.,* 99: 171; *nec* Hirst, 1916, *J. zool. Res.,* 1: 73. *Ptilonyssus* (*Ptilonyssus*) *nudus,* de Castro, 1948, *Archos Inst. biol., S Paulo,* 18: 260.

Previous records (both Fringillidae, Passeriformes).—Tree-sparrow (introduced), *Passer montanus* (Linnaeus). House-sparrow (introduced), *P. domesticus* (Linnaeus).

I have been able to examine specimens of this species from Europe and the United States.

PTILONYSSUS STURNOPASTORIS Fain
(Figs 204–213)

Ptilonyssus sturnopastoris Fain, 1963, *Acarologia,* 5: 1.

This species, originally described from an Indian starling (*Sturnopastor* Blyth), may now be recorded as follows: 2 ♀♀ and 2 protonymphs from Australian shining starlings, *Aplonis metallica* (Temminck) (Sturnidae, Passeriformes), Ella Bay, 4.viii.1965, R. D. and J. S. W.

PTILONYSSUS SPHECOTHERIS Domrow

Ptilonyssus sphecotheris Domrow, 1964, *Acarologia,* 6: 613.

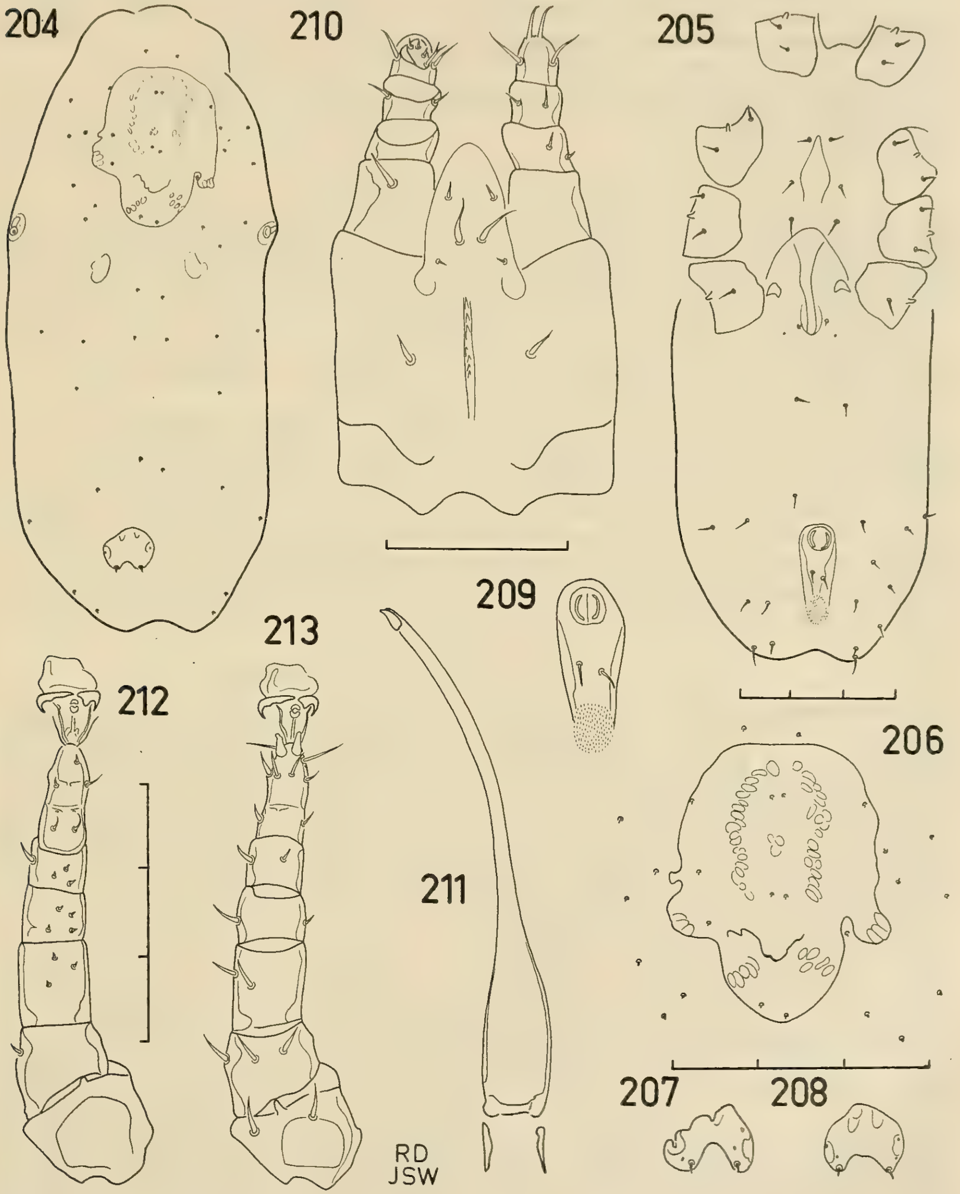
Previous record.—Southern figbird, *Sphecotheres vieillotii* Vigors and Horsfield (Oriolidae, Passeriformes), Brisbane. Also Samford.

New host records.—Yellow figbird, *S. flaviventris* Gould, Ella Bay, 4.viii.1965, R. D. and J. S. W. (41 ♀♀, 6 ♂♂, 1 deuto-, and 1 protonymph). Great bower-bird, *Chlamydera nuchalis* (Jardine and Selby) (Ptilonorhynchidae, Passeriformes), Kowanyama 18.iii.1966, R. D. (1 ♀).

I have not been able to distinguish the lattermost specimen from paratypes of this species. Its presence in a ptilonorhynchid rather than the usual oriolid is not due to any error of labelling, either in the field or the laboratory. As with the single specimens above of *P. cractici* from *Dacelo* and *R. rhinolethrum* from *Tringa,* I was quite aware at the time of collection that a novelty had been obtained.

Ptilonyssus trouessarti (Hirst)

Rhinonyssoides trouessarti Hirst, 1921, *Proc. zool. Soc. Lond.*, 1921: 770. *Ptilonyssus trouessarti,* Fain and Hyland, 1962, *Ann. Mag. nat. Hist.*, (13) 5: 346; Domrow, 1964, *Acarologia*, 6: 608. *Ptilonyssus orioli* Fain, 1956, *Revue Zool. Bot. afr.*, 53: 144; 1957, *Annls Mus. r. Congo belge Sér. 8vo*, 60: 114; 1962, *Bull. Annls Soc. r. ent. Belg.*, 98: 264; Strandtmann, 1960, *J. Kans. ent. Soc.*, 33: 150.



Figs 204–213. *Ptilonyssus sturnopastoris* Fain (♀ from *Aplonis metallica*).–204–205, Dorsal and ventral views of idiosoma. 206, Podonotal shield. 207–208, Variations in pygidial shield. 209, Anal shield. 210, Ventral view of capitulum (left palp in dorsal view). 211, Chelicera. 212–213, Dorsal and ventral views of leg III.

Previous records (both Oriolidae, Passeriformes).—Olive-backed oriole, *Oriolus sagittatus* (Latham), Logan Village. Also Esk and Innisfail. Yellow oriole, *O. flavocinctus* (King), Kowanyama.

Domrow (1946*c*) has discussed the misidentification of the original host of this species.

PTILONYSSUS NOVAEGUINEAE (Hirst)

Rhinonyssus novae-guineae Hirst, 1921, *Proc. zool. Soc. Lond.*, 1921: 769. The original spelling (with hyphen) is corrected above under Art. 32. *Passeronyssus novae-guineae*, Fain, 1960, *Revue Zool. Bot. afr.*, 61: 313. *Ptilonyssus novae-guineae*, Fain and Hyland, 1962, *Ann. Mag. nat. Hist.*, (13) 5: 346.

Previous record.—Magnificent rifle-bird, *Ptiloris magnificus* (Vieillot) (Paradiseidae, Passeriformes).

PTILONYSSUS CERCHNEIS Fain

Ptilonyssus cerchneis Fain, 1957, *Annls Mus. r. Congo belge Sér. 8vo,* 60: 133; Strandtmann, 1962, *Proc. ent. Soc. Wash.*, 64: 100; Bregetova, 1964, "Some problems of evolution of the rhinonyssid mites" (Nauka: Leningrad), p. 5; Domrow, 1965, *Acarologia,* 7: 457.

Previous records.—Brown hawk, *Falco berigora* Vigors and Horsfield (Falconidae, Falconiformes), Esk. Also Kowanyama. Nankeen kestrel, *F. cenchroides* Vigors and Horsfield, Mt Jukes. Also Esk.

Most of my specimens were heavily engorged when collected, and the opisthosomal cuticle has accordingly ruptured and crumpled during mounting procedures. One unfed specimen, however, does show the two areas of non-striate cuticle on the opisthonotum described by Strandtmann (1962), as well as a second, smaller pair slightly behind, and outside the first pair. Neither pair bears a seta and associated pore, and it would therefore seem that Strandtmann is correct in questioning whether these structures belong to the pygidial complex. I have examined 2 ♀ ♀ from the United States.

Genus STERNOSTOMA Berlese and Trouessart

Sternostoma Berlese and Trouessart, 1889, *Bull. Biblioth. scient. Ouest,* 2: 126; Furman, 1957, *Hilgardia,* 26: 474. Type-species *Sternostoma cryptorhynchum* Berlese and Trouessart, 1889, *Loc. cit.*, 127. *Sternostomum* Trouessart, 1895, *Rev. Sci. nat. appl.*, 42: 392. Unjustified emendation under Art. 33. Furman (1957) has pointed out the error of Vitzthum (1935) and his school in considering *Sternostoma* and *Sternostomum* distinct genera, even though Trouessart had explicitly stated that the type-species of the former was also that of his unjustified emendation. Nor is either name to be confused with *Rhinonyssus* Trouessart, 1894, *v. supra,* type-species *Rhinonyssus coniventris* Trouessart, 1894. *Agapornyssus* Gretillat, Capron, and Brygoo, 1959, *Acarologia,* 1: 376. Type-species *Agapornyssus faini* Gretillat *et al.,* 1959, *Loc. cit.*, 376. *Sternostomoides* Bregetova, 1964, "Some problems of evolution of the rhinonyssid mites" (Nauka: Leningrad). *Sternostomoides* is not mentioned in the text of this article, but occurs in an accompanying photograph of a table on host-specificity. This does not constitute publication under Art. 8; and, in any case, as no type-species is given, *Sternostomoides* is unavailable here under Art. 13. Also 1965, *Ent. Obozr.*, 44: 709. Type-species *Sternostomum technaui* Vitzthum, 1935, *J. Orn., Lpz.*, 83: 569. New synonymy. *Rhinosterna* Fain, 1964, *Revue Zool. Bot. afr.*, 70: 125. Type-species *Rhinosterna aymarae* Fain, 1964, *Loc. cit.*, 126. New synonymy. *Sternoecius* Fain and Aitken, 1967, *Bull. Inst. r. Sci. nat. Belg.*, 43: 24. Type-species *Sternoecius piprae* Fain and Aitken, 1967, *Loc. cit.*, 24. New synonymy.

Sternostomoides was erected for a group of three parasites of turdids (all considered conspecific below), which lack the opisthonotal shield. However, the existence of *S. inflatum* Fain (1963*c*) and *S. dureni* Fain (1956, 1957*c*), also from turdids, in which the opisthonotal shield is eroded and complete, respectively, makes the synonymy clear.

The cheliceral modifications in the last two taxa should be considered only of specific value, since the two species involved are otherwise typical of *Sternostoma.*

Key to females of Australian species of STERNOSTOMA

1. Podonotal shield evenly rounded anteriorly. Opisthonotal shield at most accompanied by small mesonotal shieldlets, or absent 2

Podonotal shield deeply excavated anteriorly. Opisthonotal shield accompanied by two extensive lateral shields .... *fulicae* Fain and Bafort

2 (1). Opisthonotal shield present 3

Opisthonotal shield absent .... *technaui* (Vitzthum)

3 (2). Posterolateral margin of podonotal shield with four setae (two medial and one in each corner) 4

Posterolateral margin of podonotal shield with two setae (medial) 9

4 (3). Two mesonotal shieldlets present. Palpal tibiotarsus twice as long as wide .... *thienponti* Fain

Mesonotal shieldlets absent. Palpal tibiotarsus at most only slightly longer than wide 5

5 (4). Setae al_{1-2}, av_{1-2}, pv_{1-2}, and pl_{1-2} on tarsi II-IV variously formed, but not as follows 6

Setae al_{1-2}, av_{1-2}, pv_{1-2}, and pl_{1-2} on tarsi II-IV slender, with expanded tips .... *cooremani* Fain

6 (5). Opisthonotal shield subquadrate. Setae al_{1-2}, av_{1-2}, pv_{1-2}, and pl_{1-2} on tarsi II-IV digitate ....*cuculorum* Fain

Opisthonotal shield at least one and a half times as long as wide Setae al_{1-2}, av_{1-2}, pv_{1-2}, and pl_{1-2} on tarsi II-IV variously formed, but not as above 7

7 (6). Dorsal shield heavily and evenly punctate. Palpal tibial sensory rods minute 8

Dorsal shield with strong subhexagonal reticulation giving the effect of honeycomb. Palpal tibial sensory rods more than half as long as tibiotarsus ....*gliciphilae* Domrow

8 (7). Sternal shield weakly and evenly granulate. Some of setae al_{1-2}, av_{1-2}, pv_{1-2}, and pl_{1-2} on tarsi II-IV peculiarly crimped .... *dureni* Fain

Sternal shield with distinct transverse reticulation. Setae al_{1-2}, av_{1-2}, pv_{1-2}, and pl_{1-2} on tarsi II-IV minute, unmodified .... *tracheacolum* Lawrence

9 (3). Lateral margins of podonotal shield evenly convex 10

Lateral margins of podontal shield triconcave .... *paddae* Fain

10 (9). Podonotal shield with five pairs of setae. Mesonotal shields absent 11

Podonotal shield with four pairs of setae. Mesonotal shields present........ .... *boydi* Strandtmann

11 (10). With one pair of setae between genital and anal shields. Setae al_{1-2}, av_{1-2}, pv_{1-2}, and pl_{1-2} on tarsi II-IV unmodified .... *neosittae*, n. sp.

With two pairs of setae between genital and anal shields. Setae al_{1-2}, av_{1-2}, pv_{1-2}, and pl_{1-2} on tarsi II-IV expanded ....*cryptorhynchum* Berlese and Trouessart

STERNOSTOMA THIENPONTI Fain

Sternostoma thienponti Fain, 1956, *Revue Zool. Bot. afr.*, 53: 152; 1957, *Annls Mus. r. Congo belge Sér. 8vo*, 60: 68; Domrow, 1965, *Acarologia*, 7: 449; 1966, PROC. LINN. SOC. N.S.W., 90: 194. *Sternostoma thieponti* (*sic*) Strandtmann, 1960, *J. Kans. ent. Soc.*, 33: 135.

Previous records (all Passeriformes).—Black-backed magpie, *Gymnorhina tibicen* (Latham) (Cracticidae), Condamine. Black butcher-bird (black and red phases), *Cracticus quoyi* (Lesson and Garnot), Innisfail. Spangled drongo, *Chibia bracteata* (Gould) (Dicruridae).

New host record.—Pied butcher-bird, *Cracticus nigrogularis* (Gould), Kowanyama, 8.iv.1965, R. D. and J. S. W. (7 ♀♀).

STERNOSTOMA COOREMANI Fain

Sternostoma cooremani Fain, 1956, *Revue Zool. Bot. afr.,* 53: 154; 1957, *Annls Mus. r. Congo belge Sér. 8vo,* 60: 72; Domrow, 1965, *Acarologia,* 7: 448; 1966, PROC. LINN. SOC. N.S.W., 90: 192. *Sternostoma cooremani halcyoni* Fain and Nadchatram, 1962, *Bull. Annls Soc. r. ent. Belg.,* 98: 280.

Previous records (all Coraciiformes).—Laughing kookaburra, *Dacelo gigas* (Boddaert) (Alcedinidae), Condamine. Also Esk. Mangrove-kingfisher, *Halcyon chloris* (Boddaert) (Alcedinidae). Rainbow-bird, *Merops ornatus* Latham (Meropidae), Esk. Also Windorah.

STERNOSTOMA CUCULORUM Fain

Sternostoma cuculorum Fain, 1956, *Revue Zool. Bot. afr.,* 53: 155; 1957, *Annls Mus. r. Congo belge Sér. 8vo,* 60: 74; Nadchatram, McClure, and Lim, 1964, *J. fed. Malay St. Mus.,* 9: 106; Domrow, 1965, *Acarologia,* 7: 449. *Sternostoma cuculorum* var. *urolestis* Fain, 1959, *J. ent. Soc. sth. Afr.,* 22: 32. See Art. 45. New synonymy. *Sternostoma laniorum* Fain, 1956, *Revue Zool. Bot. afr.,* 53: 156; 1957, *Annls Mus. r. Congo belge Sér. 8vo,* 60: 76; Domrow, 1965, *Acarologia,* 7: 449; 1966, PROC. LINN. SOC. N.S.W., 90: 193. New synonymy. *Sternostoma laniorum* var. *batis* Fain, 1957, *Annls Mus. r. Congo belge Sér. 8vo,* 60: 77; Fain and Nadchatram, 1962, *Bull. Annls Soc. r. ent. Belg.,* 98: 281; Strandtmann, 1960, *J. Kans. ent. Soc.,* 33: 135. See Art. 45. New synonymy. *Sternostoma batis,* Fain, 1962, *Revue Zool. Bot. afr.,* 66: 146; Nadchatram, McClure, and Lim, 1964, *J. fed. Malay St. Mus.,* 9: 106. *Sternostoma zosteropus* Domrow, 1966, PROC. LINN. SOC. N.S.W., 90: 194. New synonymy.

Until more tangible characters can be found to divide the above taxa, I would prefer to consider them conspecific. The character of the claws originally noted for *S. zosteropus* does not, in fact, hold good. It may be that in this (and in one other case, *viz. Ptilonyssus motacillae, v. supra*); I have been too radical in my synonymy, but it is virtually impossible to key their component taxa as presently described.

Previous records.—Fan-tailed cuckoo, *Cacomantis pyrrhophanus* (Vieillot) (Cuculidae, Cuculiformes), Esk. Also Innisfail and Kowanyama. Willie wagtail, *Rhipidura leucophrys* (Latham) (Muscicapidae, Passeriformes), Esk. Also Kowanyama. Leaden flycatcher, *Myiagra rubecula* (Latham) Muscicapidae), Innisfail. Pale-yellow robin, *Eopsaltria capito* Gould (Muscicapidae), Innisfail. Rufous strike-thrush, *Colluricincla megarhyncha* (Quoy and Gaimard) (Pachycephalidae, Passeriformes), Innisfail. Crested bellbird, *Oreoica gutturalis* (Vigors and Horsfield) (Falcunculidae, Passeriformes), Mitchell. Grey-backed silvereye, *Zosterops lateralis* (Latham) (Zosteropidae, Passeriformes), Mt. Jukes.

New host records.—Brush cuckoo, *C. variolosus* (Vigors and Horsfield), Kowanyama, 14.iv.1965, R. D. (22 ♀♀). Koel, *Eudynamys orientalis* (Linnaeus) (Cuculidae), Esk, 6.x.1966, R. D. and J. S. W. (14 ♀♀). Australian pied flycatcher, *Arses kaupi* Gould (Muscicapidae), Innisfail, 5.viii.1965, R. D. and J. S. W. (19 ♀♀). Spectacled flycatcher, *Monarcha trivirgata* (Temminck) (Muscicapidae), Innisfail, 31.viii.1965, H. I. McD. (10 ♀♀).

STERNOSTOMA DURENI Fain

Sternostoma dureni Fain, 1956, *Rev. Zool. Bot. afr.,* 53: 153; 1957, *Annls Mus. r. Congo belge Sér. 8vo,* 60: 68.

This species, whose type-host is an African thrush, may now be recorded from Australia: 4 ♀♀ from an Australian ground-thrush, *Oreocincla lunulata* (Latham) (Turdidae, Passeriformes), Wilson's Peak, 15.v.1967, R. D. and B. H. K.

STERNOSTOMA TRACHEACOLUM Lawrence

Sternostoma tracheacolum Lawrence, 1948, *J. Parasit.*, 34: 366; Bregetova, 1951, *Parazit. Sb.*, 13: 116; Furman, 1957, *Hilgardia*, 26: 478; Fain, 1957, *Annls Mus. r. Congo belge Sér. 8vo*, 60: 65; Fain and Hyland, 1962, *Parasitology*, 52: 404; Strandtmann, 1960, *J. Kans. ent. Soc.*, 33: 137; Domrow, 1965, *Acarologia*, 7: 449; 1966, PROC. LINN. SOC. N.S.W., 90: 194; Murray, 1966, *Aust. vet. J.*, 42: 262. *Sternostoma meddai* Lombardini, 1953, *Redia*, 38: 187. *Sternostoma castroae* Fain, 1956, *Revue Zool. Bot. afr.*, 53: 393. *Agapornyssus faini* Gretillat, Capron, and Brygoo, 1959, *Acarologia*, 1: 376.

Previous records (all Passeriformes except the first).—Budgerygah (aviary-bred), *Melopsittacus undulatus* (Shaw) (Psittacidae, Psittaciformes). Common swallow, *Hirundo rustica* Linnaeus (Hirundinidae). Australian reed-warbler, *Acrocephalus australis* (Gould) (Sylviidae). Yellow-breasted sunbird, *Cyrtostomus frenatus* (Müller) (Nectariniidae). Goldfinch (introduced), *Carduelis carduelis* (Linnaeus) (Fringillidae). House-sparrow (introduced), *Passer domesticus* (Linneaus) (Fringillidae). Canary (introduced cage-bird), *Serinus canaria* (Linneaus) (Fringillidae). Gouldian finch (aviary-bred), *Poephila gouldiae* (Gould) (Ploceidae), Sydney.

This mite is the cause of severe respiratory complications in cage-birds (Fain and Carpentier, 1958; Fain and Hyland, 1962*a*; Murray, 1966; Mathey, 1967).

STERNOSTOMA GLICIPHILAE Domrow

Sternostoma gliciphilae Domrow, 1966, PROC. LINN. SOC. N.S.W., 90: 192.

Previous record.—Brown honeyeater, *Gliciphila indistincta* (Vigors and Horsfield) (Meliphagidae, Passeriformes), Esk.

STERNOSTOMA NEOSITTAE, n. sp.

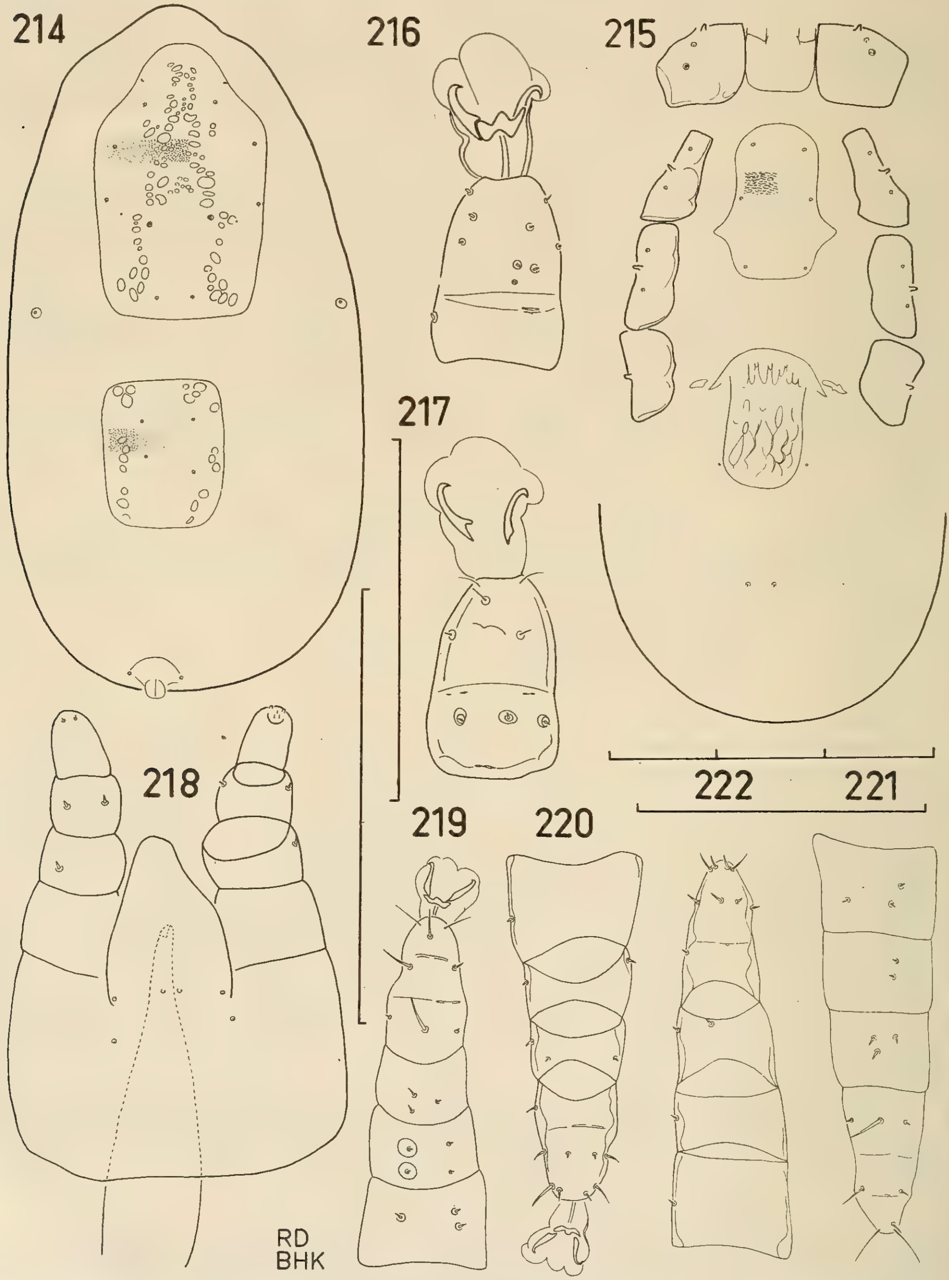
(Figs. 138, 214–218)

Sternostoma sp. Domrow, 1967, PROC. LINN. SOC. N.S.W., 91: 217.

Diagnosis.—The new species, which lacks setae in the posterolateral angles of the podonotal shield, and does not show the digitate, or even apically expanded setae al_{1-2}, av_{1-2}, pv_{1-2}, and pl_{1-2} on tarsi II–IV characteristic of such species as the type, *S. cryptorhynchum* (well figured from the original material by Furman, 1957, and Fain, 1957*e*), may best be compared with *S. boydi* Strandtmann (1951) and *S. inflatum* Fain (1963*e*). The former (originally described from the sanderling, Scolopacidae, Charadriiformes) is separable by the presence of only four pairs of setae on the podonotal shield (*v. infra*), the presence of two pairs of setae, not one, behind the genital shield, and its relatively unmodified anal shield. The latter (from a thrush, Turdidae, Passeriformes) is separable by the eroded margins of its opisthonotal shield, and the presence, again, of two pairs of setae behind the genital shield.

Types.—Holotype female, sixteen paratype females, and two deutonymphs enclosing developing males from a striated sittella, *Neositta striata* (Gould) (Sittidae, Passeriformes), Kowanyama, 7.iv.1965, R. D. and J. S. W. Holotype N. I. C.; paratypes R. D., A. F., and R. W. S.

Female.—Idiosoma 495μ long in unengorged specimen, and from 640–690μ in engorged mounted specimens like that illustrated. Podonotal shield (Fig. 214) 260–270μ long, 160–165μ wide; anterior quarter narrower and strongly convex, sides subparallel, and posterior margin rectilinear. Surface with punctae heavier towards midline, particularly where two rows of muscle insertions converge. Setae in three anterolateral, and two posteromedian pairs; two pairs of pores present. Opisthonotal shield rectangular, 140–150μ long, 110–115μ wide, bearing four setae, and again showing punctae heaviest near muscle insertions. Stigmata without peritremes, unarmed. Dorsal cuticle without additional setae.



Figs 214–218. *Sternostoma neosittae*, n. sp. (♀ from *Neositta striata*).–214–215, Dorsal and ventral views of idiosoma. 216–217, Ventral and dorsal views of tarsus III. 218, Ventral view of capitulum (right palp in dorsal view).

Figs 219–222. *Ptilonyssus sittae* Fain (protonymph from *Climacteris picumnus*).–Dorsal and ventral views of femora-tarsi III–IV.

Sternal shield (Fig. 215) longer than wide, somewhat expanded between coxae II and III; surface lightly shagreened; SI–III present in longitudinal rows, but metasternal setae absent. Genital shield drop-shaped, with distinct recticulation and punctation; rayed operculum present; genital seta-pore complex reduced to remnant just off shield. Anal shield terminal, very weakly sclerotized, and without cribrum. Adanal setae present, but postanal absent. Ventral cuticle with one pair of setae behind genital shield. All body setae minute.

Leg setae again minute, barely longer than diameter of their alveoli. Coxal formula 2.2.2.0. Tarsus I with dorsodistal sensory islet as in Fig. 138. Tarsal formula—.18.18.18 (*mv* present). Tarsi and ambulacra II–IV stouter than I (Figs 216–217).

Capitulum undistinguished (Fig. 218). Capitular setae well forward, with one, or even both of pair frequently absent. HI not detected, II–III very weak. Dorsodistal rods on tibia very short. Tarsus obsolescent, with no trace of claw. Tritosternum absent.

STERNOSTOMA CRYPTORHYNCHUM Berlese and Trouessart

Sternostoma cryptorhynchum Berlese and Trouessart, 1889, *Bull. Biblioth. scient. Ouest,* 2:127; Furman, 1957, *Hilgardia,* 26:475; Fain, 1957, *Annls Mus. r. Congo belge Sér 8vo,* 60: 70.

Previous record.—House-sparrow (introduced), *Passer domesticus* (Linnaeus) (Fringillidae, Passeriformes).

STERNOSTOMA PADDAE Fain

Sternostoma paddae Fain, 1958, *Bull. Soc. r. Zool. Anvers,* 9: 8.

Previous record.—Java sparrow (introduced cage-bird), *Padda oryzivora* (Linnaeus) (Ploceidae, Passeriformes).

Fain and Bafort (1963) report this mite associated with severe conjunctivitis in this host.

STERNOSTOMA BOYDI Strandtmann

Sternostoma boydi (*sic*) Strandtmann, 1951, *J. Parasit.,* 37: 138 (a solecism now allowable under Rec. 31—the species was named for Dr. Elizabeth M. Boyd); Furman, 1957, *Hilgardia,* 26: 480; Fain, 1956, *Revue Zool. Bot. afr.,* 53: 151; 1960, *Ibid.,* 62: 95; Mitchell, 1961, *SWest Nat.,* 6: 103.

Previous records (all Charadriiformes).—White-winged black tern, *Chlidonias leucoptera* (Temminck) (Laridae). Sooty tern, *Sterna fuscata* Linnaeus (Laridae). This record is based on host-relationship (Amerson, 1967), and I have been unable to obtain specimens to confirm it. Turnstone, *Arenaria interpres* (Linnaeus) (Charadriidae). Common sandpiper, *Tringa hypoleuca* Linnaeus (Scolopacidae). Wood-sandpiper, *T. glareola* Linnaeus. Greenshank, *T. nebularia* (Gunnerus). Sanderling, *Crocethia alba* (Vroeg) (Scolopacidae). Knot, *Calidris canutus* (Linnaeus) (Scolopacidae).

I have examined eight ♀♀ of this species from Rwanda and the United States, all with the podonotal shield showing three pairs of anterolateral setae in addition to the single posteromedian pair originally figured.

STERNOSTOMA TECHNAUI (Vitzthum)

Sternostomum technaui Vitzthum, 1935, *J. Orn., Lpz.,* 83: 569. *Sternostoma technaui,* Furman, 1957, *Hilgardia,* 26: 482; Fain, 1963, *Bull. Annls Soc. r. ent. Belg.,* 99:174. *Sternostomoides technaui,* Bregetova, 1965, *Ent. Obozr.,* 44: 709. *Sternostoma turdi* Zumpt and Till, 1955, *J. ent. Soc. sth.*

Afr., 18: 85; Furman, 1957, *Hilgardia*, 26: 481; Fain, 1962, *Bull. Annls Soc. r. ent. Belg.*, 98: 264; 1963, *Ibid.*, 99: 176. New synonymy. *Sternostomoides turdi*, Bregetova, 1965, *Ent. Obozr.*, 44: 712. *Sternostoma spatulatum* Furman, 1957, *Hilgardia*, 26: 480. New synonymy.

Previous records (all Turdidae, Passeriformes).—Blackbird (introduced), *Turdus merula* Linnaeus. Song-thrush (introduced), *T. philomelos* Brehm. Australian ground-thrush, *Oreocincla lunulata* (Latham).

New Australian record.—*O. lunulata*, Wilson's Peak, 15.v.1967, R. D. and B. H. K. (1 ♀).

I do not believe the three nominal species above reflect more than the intraspecific variation to be expected in any cosmopolitan parasite. All are parasites of turdids.

STERNOSTOMA FULICAE Fain and Bafort

Sternostoma fulicae Fain and Bafort, 1963, *Bull. Annls. Soc. r. ent. Belg.*, 99: 474.

Previous record.—Coot, *Fulica atra* Linnaeus (Rallidae, Gruiformes).

Family EREYNETIDAE

Subfamily SPELEOGNATHINAE

As the type-genus, *Speleognathus* Womersley (1936), was consistently so spelled by the original author, his rendering of the family-group name as "Spelaeognathidae" contravenes Art. 29. An obvious *lapsus calami*, it should be corrected under Art. 32.

Comments on the labile nature of most, if not all characters used in the three most recent classifications of the Speleognathinae (Fain, 1958*b*, 1962*d*, 1963*c*) continue to appear (Clark, 1964, 1967; Domrow, 1961, 1965*a*), and I therefore accept only the genera of the third of Fain's systems.

Key to adults of Australian genera of SPELEOGNATHINAE

1\. All body and leg setae barbulate. Dorsal shield absent. Eyes normally absent, but present in *B. myzomelae*, n. sp. Sensillae weakly clavate. Palpi with three segments .... *Boydaia* Womersley
Body and leg setation with an admixture of filamentous setae. Dorsal shield and eyes absent, weak, or substantial. Sensillae normally filamentous, but globose in *Neoboydaia merops* (Fain). Palpi with one, two, or three segments 2

2 (1). Dorsal shield absent or minute. Palpi with one, two, or three segments 3
Dorsal shield substantial. Palpi with three segments .... *Speleognathopsis* Cooreman

3 (2). Eyes absent. Palpi with one or two segments .... *Neoboydaia* Fain
Eyes present. Palpi with two or three segments .. *Ophthalmognathus* Dubinin

Genus BOYDAIA Womersley

Boydaia Womersley, 1953, *Trans. R. Soc. S. Aust.*, 76: 82. Type-species *Speleognathus sturni* Boyd, 1948, *Proc. ent. Soc. Wash.*, 50: 9, *nec Boydaia angelae* Womersley (1953) as stated by Ford (1959) and Brooks and Strandtmann (1960). The latter is a species of *Lawrencarus* Fain (1957*c*) (Ereynetidae, Lawrencarinae), a genus inhabiting the nasal passages of frogs and toads.

Key to adults of Australian species of BOYDAIA

1\. Coxal setae not 1.1.1.1. Hypostomal setae 2.2 2
Coxal setae 1.1.1.1. Hypostomal setae 1.1 .... *falconis* Fain

2 (1). External seta on coxa I normal 3
External seta on coxa I minute .... *hirundoae* Fain

3 (2). Trochanteral setae 1.1.0.0. Femoral setae 6.4.3.2 or more. Tibial setae 5.3.3.3 4
Trochanteral setae 1/0.0.0.0. Femoral setae 6.4.3.1. Tibial setae less than 5.3.3.3 7
4 (3). Femoral setae 6.4.3.2 5
Femoral setae 7.4.3.3 6
5 (4). Coxal setae slender, parallel-sided, about twice as long as diameter of their alveoli. Solenidion on tarsus II set in depression, but free. Posteroventral margin of basis capituli uniformly sclerotized .... *zosteropis* Fain
Coxal setae short, clavate, barely as long as diameter of their alveoli. Solenidion on tarsus II concealed in narrow invagination. Sclerotization of posteroventral margin of basis capituli interrupted medially .... *sturni* (Boyd)
6 (4). Eyes absent. Coxal setae 2.1.1.0 .... *spatulata* Fain
Eyes present. Coxal setae 2.1.2.0 .... *myzomelae*, n. sp.
7 (3). Tibial setae 5.3.2.3........ *crassipes* (Berlese and Trouessart), n. comb.
Tibial setae 4.2.2.2 .... *maluri*, n. sp.

BOYDAIA STURNI (Boyd)

Speleognathus sturni Boyd, 1948, *Proc. ent. Soc. Wash.*, 50: 9; 1951, *J. Parasit.*, 37: 79 (where the author lists the locality of some Indian specimens in the form of a binomen allegedly identifying one of the mynas); *nec* Porter and Strandtmann, 1952, *Tex. J. Sci.*, 4: 394. *Boydaia sturni*, Fain, 1961, *Bull. Annls Soc. r. ent. Belg.*, 97: 57; 1963, *Bull. Inst. r. Sci. nat. Belg.*, 39: 56; *Z. ParasitKde*, 22: 371.

Previous records (both introduced Sturnidae, Passeriformes).—Starling, *Sturnus vulgaris* Linnaeus. Common myna, *Acridotheres tristis* (Linnaeus).

New Australian record.—*S. vulgaris*, Esk, 6.x.1966, R. D. and J. S. W. (13 adults, 4 larvae).

BOYDAIA ZOSTEROPIS Fain

Boydaia zosteropis Fain, 1963, *Bull. Inst. r. Sci. nat. Belg.*, 39: 43.

This species, previously known only from an African silvereye, may now be recorded from Australia: 2 adults and 2 larvae from a grey-backed silvereye, *Zosterops lateralis* (Latham) (Zosteropidae, Passeriformes), Mt. Nebo, 17.xi.1965, E. H. D.

BOYDAIA HIRUNDOAE Fain

Boydaia hirundoae Fain, 1956, *Annls Parasit. hum. comp.*, 31: 661; 1958, *Revue Zool. Bot. afr.*, 58: 180; 1963, *Bull. Annls Soc. r. ent. Belg.*, 99: 179; Domrow, 1965, *Acarologia*, 7: 43.

Previous records (both Hirundinidae, Passeriformes).—Welcome swallow, *Hirundo neoxena* Gould, Brisbane. Common swallow (vagrant), *H. rustica* Linnaeus.

New host record.—Fairy martin, *Hylochelidon ariel* (Gould) (Hirundinidae), Windorah, 20.i.1966, R. D., D. J. M., and J. S. W. (1 larva).

BOYDAIA FALCONIS Fain

Boydaia falconis Fain, 1956, *Annls Parasit. hum. comp.*, 31: 657.

This African species is now known also to occur in Australia: 35 adults and 1 larva from brown hawks, *Falco berigora* Vigors and Horsfield (Falconidae, Falconiformes), Kowanyama, 27.x and 9.xi.1965, R. D.

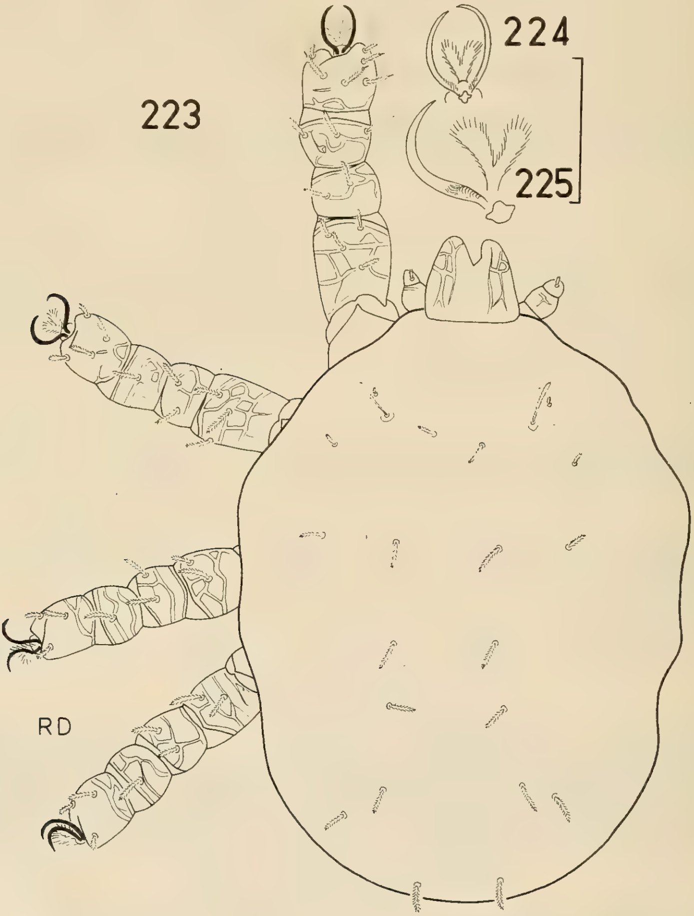
BOYDAIA SPATULATA Fain

(Figs. 223–226)

Boydaia sturni var. *spatulata* Fain, 1955, *Annls Soc. belge Méd. trop.*, 35: 695. See Art. 45. *Boydaia spatulata*, Fain, 1956, *Riv. Parassit.*, 17: 33; 1956, *Revue Zool. Bot. afr.*, 53: 43; 1956, *Annls Parasit. hum. comp.*, 31: 651.

Fain (1963*c*) has detailed a group of five African and European species centred around *B. spatulata,* which, while distinguishable as larvae, are scarcely separable as adults. In the absence of immatures, I now record Fain's species from three new Australian hosts (Meliphagidae, Passeriformes): 1 ♀ from a banded honeyeater, *Myzomela pectoralis* Gould, Kowanyama, 23.x.1965; 1 ♀ from a noisy friar-bird, *Philemon corniculatus* (Latham), Esk, 5.x.1965; and 1 ♀ from a little friar-bird, *P. citreogularis* (Gould), Charleville, 14.i.1966, R. D., D. J. M., and J. S. W.

The specimen illustrated is from *Myzomela* Vigors and Horsfield, and has the following measurements: idiosoma 410μ long, 314μ wide; capitulum 93μ long, 82μ wide; palpi 35μ long; leg I 315, II 266, III 249, IV 270μ long. Setal formulae for legs: coxae 2.1.1.0; trochanters 1.1.0.0; femora 7.4.3.3; genua 4.4.3.3; tibiae 5.3.3.3; tarsi 12.8.7.7. The specimens from *Philemon* Vieillot are considerably larger, but show identical chaetotaxy, although, in fact, the following minor variants occur: genital setae 5.4 (*Myzomela*); hypostomal setae 2.1 (*P. corniculatus*); femora I–II 7.4/6.3, genu II 4.3, and tibia IV 3.4 (*P. citerogularis*—some broken cuticle from the body is



Figs 223–225. *Boydaia spatulata* Fain.–223, Dorsal view of adult from *Myzomela pectoralis*. 224–225, claws and pulvilli of adults from *M. pectoralis* and *Philemon citreogularis* (at twice indicated scale).

folded over one leg IV, but the four setae in question appear to lie beneath it, and, therefore, to belong to the tibial, and not to the idiosomal series. Some measurements are: capitulum 116μ long, 103μ wide; palpi 54μ long; leg II 350–365, III 320–340, IV 345–375μ long (excluding ambulacra, but including coxae).

The sensillae in the series from *Myzomela* are 32μ long and about one-tenth as broad; in specimens from *Philemon*, they are 43–45μ long and noticeably more slender (one-fifteenth as broad as long).

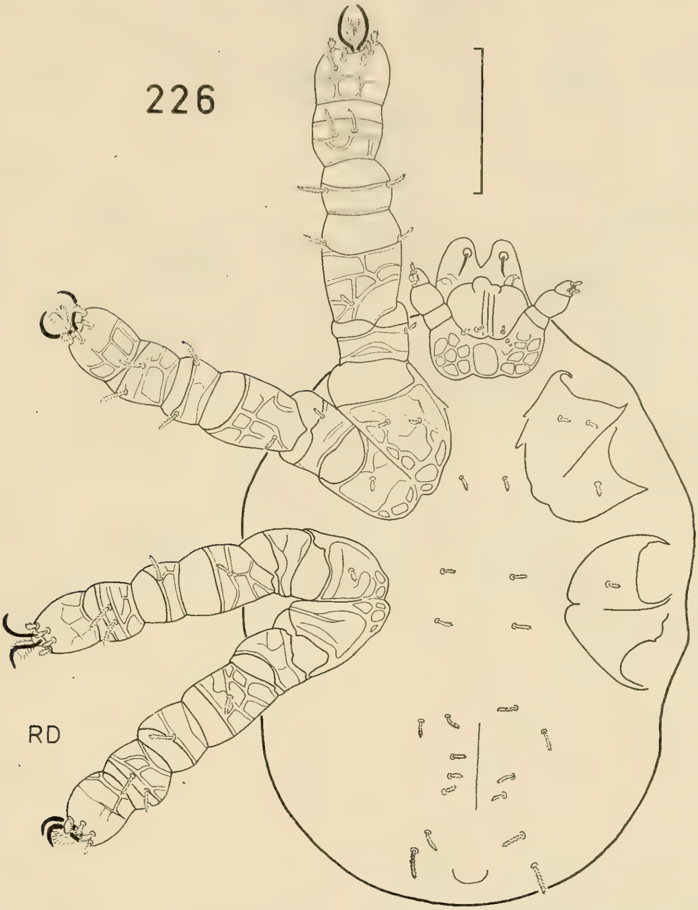


Fig. 226. *Boydaia spatulata* Fain.–Ventral view of adult from *Myzomela pectoralis*.

BOYDAIA MYZOMELAE, n. sp.

(Figs. 227–229)

Diagnosis.—*B. myzomelae* is related, on chaetotaxy, to the five species centred around *B. spatulata* (see Fain, 1963*c*, and discussion on that species above), but may easily be separated from them by the coxal formula (2.1.2.0, not 2.1.1.0) and the presence of distinct eyes.

Two other species of *Boydaia*, *B. hirundoae* and *B. psalidoprocnei* Fain, show a coxal formula 2.1.2.0, but are distinct from *B. myzomelae* both morphologically (external seta on coxa I minute) and ecologically (hosts swallows, Hirundinidae, Passeriformes) (see Fain, 1963*c*).

Types.—Holotype female from a scarlet honeyeater, *Myzomela sanguinolenta* (Latham) (Meliphagidae, Passeriformes), Esk, 6.x.1966, R. D. and J. S. W. Holotype N. I. C.

Female.—Idiosoma engorged, ruptured during mounting procedure, 465μ long, 315μ wide across humeral prominences. Cuticle finely striate-punctate.

Figs 227–228. *Boydaia myzomelae*, n. sp. (adult from *Myzomela sanguinolenta*).–227, Dorsal view. 228, Pulvillus (at twice indicated scale).

Eyes sharply outlined, with corneae (Fig. 227). Sensillae 32μ long, very slightly clavate. Presensillary setae small, 2 in number. Postsensillary setae 3.4.2.2.4.2.

Sternal setae 2+2.2. Genital setae 2.3/3.2 Anal setae 2.2 (Fig. 229).

Legs with reticulate subcuticular markings, I 302, II 275, III 250μ long (IV lacking except for coxae and one trochanter). Setal formulae: coxae 2.1.2.0; trochanters 1.1.0.0; femora 7.4.3.–; genua 4.4.3.–; tibiae 5.3.3.–; tarsi

12.8.7.–. Tarsi I and II with solenidion; tibia I with invaginated sensory organ.* Claws equal, of uniform diameter except at tip, roughened internally near basal angulation; retractable into dorsodistal pits in tarsi. Pulvilli directed upwardly between claws, bifid, with each arm expanded distally and flared externally; with many filaments on plantar surface (Fig. 228).

229

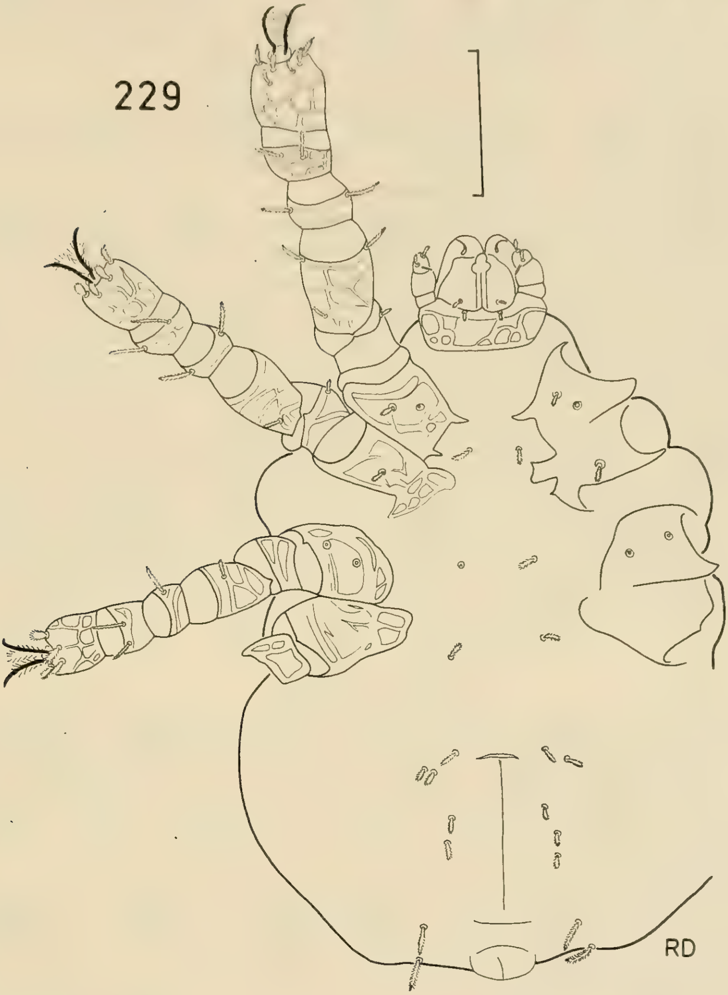


Fig. 229. *Boydaia myzomelae*, n, sp.–Ventral view of adult from *Myzomela sanguinolenta*.

Capitulum 80μ long, 90μ wide, reticulate; hypostomal setae 2.2. Palpi 3-segmented, 40μ long; setal formula 0.0.3; solenidion present on tarsus.

All setae barbulate (many on dorsum of idiosoma and legs appear, at lower magnification, to terminate in hyaline expansion, which, however, under oil-immersion, is seen to comprise merely shorter terminal setules); six setae on tarsus I and one on tarsus II with rod-like, hyaline extension apically.

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* These organs are treated more fully by Fain (1962*b*). They are reminiscent of the chemoreceptors of insects classified as *sensilla coeloconica* by Imms (1957).

BOYDAIA CRASSIPES (Berlese and Trouessart), n. comb.

Ereynetes crassipes Berlese and Trouessart, 1889, *Bull. Biblioth. scient. Ouest,* 2: 141. *Speleognathus sturni* Porter and Strandtmann, 1952, *Tex. J. Sci.,* 4: 394, *nec* Boyd, 1948, *Proc. ent. Soc. Wash.,* 50: 9. See Fain (1958*b*). *Boydaia nigra* Fain, 1955, *Annls Soc. belge Méd. trop.,* 35: 695; 1956, *Riv. Parassit.,* 17: 32; *Revue Zool. Bot. afr.,* 53: 44; *Annls Parasit. hum. comp.,* 31: 658; 1957, *Revue Zool. Bot. afr.,* 55: 254; 1958, *Ibid.,* 58: 179; 1962, *Bull. Annls Soc. r. ent. Belg.,* 98: 266; 1963, *Z. ParasitKde,* 22: 371; *Bull. Annls Soc. r. ent. Belg.,* 99: 179. New synonymy.

Previous records (all Passeriformes).—Yellow wagtail (vagrant), *Motacilla flava* Linnaeus (Motacillidae). Goldfinch (introduced), *Carduelis carduelis* (Linnaeus) (Fringillidae). House-sparrow (introduced), *Passer domesticus* (Linnaeus) (Fringillidae).

New host record.—White-winged triller, *Lalage tricolor* (Swainson) (Campophagidae, Passeriformes), Charleville, 14.i.1966, R. D., D. J. M., and J. S. W.; Kowanyama, iv.1965, R. D. (33 adults, 9 larvae).

I accept the synonymy suggested by Fain (1957*c*). As in the case of *Ptilonyssus nitzschi* above, I believe this procedure preferable to accepting both a *nomen dubium* and a later taxon which is almost certainly its junior synonym. It should be confirmed by the formal designation of a neotype when the group is next revised (Art. 75). Neither Lombardini (1936) nor Fain (1964*e*), in their listings of the ereynetids in the Berlese collection in Florence, mention this species, and Dr. M. H. Naudo tells me there is none in the Trouessart collection in Paris. As with all these mites, the true locality is the nasal passage of their specific host wherever it may exist, rather than any fixed geographical area, so I see no objection to choosing one of Porter and Strandtmann's specimens, providing they are in good condition.

BOYDAIA MALURI, n. sp.

(Figs 230–235)

Diagnosis.—*B maluri* falls among those small species of *Boydaia* with a considerably reduced leg setation (Fain, 1963*c*), and may best be compared with *B. trochila* Fain (1958*a*). However, the two species may be separated by the setation (3, not 2 or 1) of genu IV, and the presence or absence of a solenidion on the palpal tarsus. Lesser differences appear to lie in the claws and pulvilli.

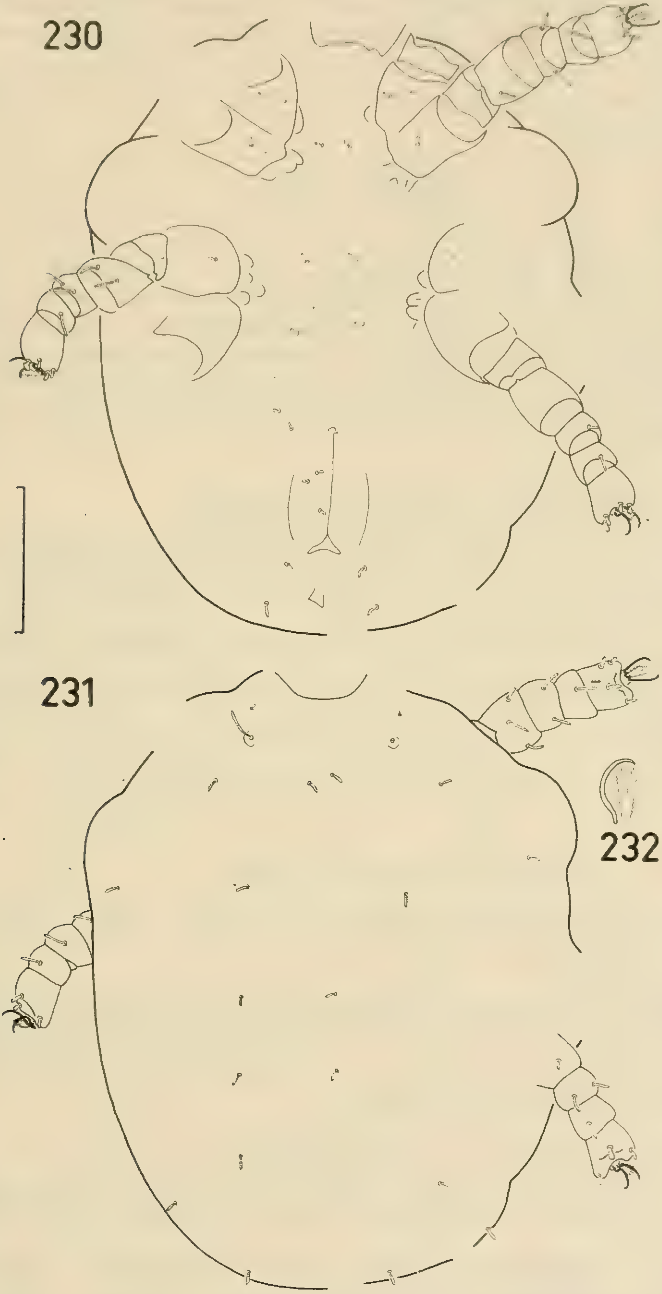
The host relationships should also be noted. *B. maluri* is from peculiarly Australian "wrens" (Sylviidae, Passeriformes), while *B. trochila* was described from hummingbirds, which belong to the neotropical family Trochilidae (Apodiformes).

Types.—Holotype female from a lovely wren, *Malurus amabilis* Gould (Sylviidae, Passeriformes), Cowley Beach, 9.viii.1965, R. D. and J. S. W. Three females one of which is designated paratype) from a red-backed wren, *M. melanocephalus* (Latham), Kowanyama, 22.xi.1965, R. D. Holotype N. I. C.; paratype R. D.

Female.—Idiosoma (Fig. 231) engorged and pigmented in all specimens, with humeral prominences; from 374x308, through 432x345 (figured), to 528x385μ depending on degree of compression during mounting procedure. Cuticle minutely striate-punctate. Eyes absent. Sensillae 24–27μ long, very slightly clavate. Presensillary setae minute, 2 in number. Postsensillary setae 4.4.2.2.4.2.

Sternal setae 2+2.2. Genital setae 2.3/3.2 Anal setae 2.2 (Fig. 230).

Legs (Figs. 234–235) with reticulate subcuticlar markings, 213, 193, 186, and 205μ long in two specimens figured. Setal formulae: coxae 2.1.1.0; trochanters 1.0.–.– (*M. amabilis*), 0.0.0.0 (*M. melanocephalus*); femora 6.4.3.1; genua 4.4.3.3; tibiae 4.2.2.2; tarsi 12.8.7.7. Tarsi I and II with solenidion;



Figs 230–232. *Boydaia maluri*, n. sp. (adult from *Malurus melanocephalus*).–230–231, Ventral and dorsal views. 232, Pulvillus (at twice indicated scale).

Figs 233–235. *Boydaia maluri*, n. sp. (adult from *Malurus amabilis*).–233, Ventral view of capitulum. 234–235, Ventral and dorsal views of leg I.

tibia I with invaginated sensory organ. Claws equal, simple, of uniform diameter except at tip; retractable into dorsodistal excavations in tarsi. Pulvilli (Fig. 232) directed upwardly between claws, apparently entire except for weak distal cleft; with numerous filaments on plantar surface.

Capitulum (Fig. 233) 80μ long, 85μ wide, reticulate; hypostomal setae 2.2. Palpi 3-segmented, 36μ long; setal formula 0.0.3; solenidion present on tarsus.

All setae barbulate; six on tarsus I and one on tarsus II with expanded, hyaline extension distally.

Genus NEOBOYDAIA Fain

Neoboydaia Fain, 1958, *Revue Zool. Bot. afr.*, 58: 177. Type-species *Boydaia philomachi* Fain, 1956, *Riv. Parassit.*, 17: 27. *Ralliboydaia* Fain, 1962, *Revue Zool. Bot. afr.*, 66: 365. Type-species *Neoboydaia* (*Ralliboydaia*) *latiralli* Fain, 1962, *Loc. cit.*, 365. The original spelling is a *lapsus calami* based on the host-genus *Laterallus* Bonaparte, and was subsequently corrected to *lateralli* under Art. 32 by Fain (1964*b*). *Aureliania* Fain, 1958, *Revue Zool. Bot. afr.*, 58: 177. Type-species *Boydaia aureliani* Fain, 1955, *Annls Soc. belge Méd. trop.*, 35: 694.

Key to adults of Australian species of NEOBOYDAIA

1. Presensillary setae minute. Palpi with two segments 2
Presensillary setae normal. Palpi with one segment 3
2 (1). Genital setae 6.6. Anal setae 1.1. Coxal setae 2.1.1.0. Femoral setae 5.4.3.2. Palpal setae 0.3 .... *philomachi* Fain
Genital setae 4.4. Anal setae 2.2. Coxal setae 2.1.1.1. Femoral setae 4.3.2.2. Palpal setae 1.2 .... *psittaculae* Fain
3 (1). First pair of postsensillary setae present. Sensillae filamentous. Hypostomal setae 2.2 4
First pair of postsensillary setae absent. Sensillae globose. Hypostomal setae 0.0 .... *merops* (Fain)
4 (3). Sternal setae 2.2.0. Coxal setae 1.1.1.1. Trochanteral setae 0.0.0.0. .... *aureliani* (Fain)
Sternal setae 2.2.2. Coxal setae 2.1.1.1. Trochanteral setae 1.1.0.0.................................... *colymbiformi* Clark

NEOBOYDAIA PHILOMACHI (Fain)

Boydaia philomachi Fain, 1958, *Riv. Parassit.*, 17: 27; 1964, *Annls Mus. r. Afr. cent. Sér. 8vo*, 132: 141; Clark, 1964, *J. Parasit.*, 50: 160; Domrow, 1965, *Acarologia*, 7: 43.

Previous records (all Scolopacidae, Charadriiformes).—Bar-tailed godwit, *Limosa lapponica* (Linnaeus), Half Tide. Wood-sandpiper, *Tringa glareola* Linnaeus. American pectoral sandpiper, *Erolia melanotos* (Vieillot). Ruff (vagrant), *Philomachus pugnax* (Linnaeus).

NEOBOYDAIA PSITTACULAE Fain

Neoboydaia psittaculae Fain, 1962, *Bull. Annls Soc. r. ent. Belg.*, 98: 318.

Previous record.—Peach-faced lovebird (introduced cage-bird), *Agapornis roseicollis* (Vieillot) (Psittacidae, Psittaciformes).

New host records (both Psittacidae).—Rainbow-lorikeet, *Trichoglossus moluccanus* (Gmelin), Kowanyama, 1.xi.1965, R. D. (1 adult). Varied lorikeet, *Psitteuteles versicolor* (Lear), Kowanyama, 3.xi.1965, R. D. (1 adult).

NEOBOYDAIA AURELIANI (Fain)

Boydaia aureliani Fain, 1955, *Annls Soc. belge Méd. trop.*, 35: 694; 1956, *Revue Zool. Bot. afr.*, 53: 36. *Boydaia* (*Aurelinia*) *aureliani*, Fain, 1958, *Revue Zool. Bot. afr.*, 58: 177. *Neoboydaia* (*Aureliania*) *aureliani*, Fain, 1963, *Bull. Annls Soc. r. ent. Belg.*, 99: 181; *Bull. Inst. r. Sci. nat. Belg.*, 39: 52.

Previous record.—Barn-owl, *Tyto alba* (Scopoli) (Tytonidae, Strigiformes).

NEOBOYDAIA MEROPS (Fain)

Boydaia merops Fain, 1955, *Annls Soc. belge Méd. trop.*, 35: 694; 1956, *Riv. Parassit.*, 17: 30; Domrow, 1966, PROC. LINN. SOC. N.S.W., 90: 210.

Previous record.—Rainbow-bird, *Merops ornatus* Latham (Meropidae, Coraciiformes), Esk and Innisfail. Also Kowanyama.

NEOBOYDAIA COLYMBIFORMI Clark

Neoboydaia colymbiformi Clark, 1964, *J. Parasit.*, 50: 158.

This species may now be recorded from Australia: 1 adult from a little grebe, *Podiceps ruficollis* (Vroeg) (Podicipidae, Podicipiformes), Esk, 15.v. 1965, I. D. F. and J. S. W. The only previous record is from an American grebe (*Colymbus* Linneaus, a name proscribed in favour of *Podiceps* Latham, see Thomson, 1964).

Genus OPHTHALMOGNATHUS Dubinin

Ophthalmognathus Dubinin, 1957, *Trudy leningr. Obshch. Estest.*, 73: 66. Type-species *Ophthalmognathus dogieli* Dubinin, 1957, *Loc. cit.*, 68. (=*Speleognathus schoutedeni* Fain, *v. infra*). *Neospeleognathus* Fain, 1958, *Revue Zool. Bot. afr.*, 58: 178. Type-species *Speleognathus schoutedeni* Fain, 1955, *Annls Soc. belge Méd. trop.*, 35: 695. New synonymy. *Trispeleognathus* Fain, 1958, *Revue Zool. Bot. afr.*, 58: 178. Type-species *Speleognathus striatus* Crossley, 1952, *J. Parasit.*, 38: 385. New synonymy. *Metaboydaia* Fain, 1962, *Bull. Inst. r. Sci. nat. Belg.*, 38: 7. Type-species *Speleognathus poffei* Fain, 1955, *Annls Soc. belge Méd. trop.*, 35: 695; 1956, *Revue Zool. Bot. afr.*, 53: 23. New synonymy.

The decision to accept *Ophthalmognathus* (see Fain, 1958*b*) leaves one only to note that, in the question of considering *Neospeleognathus* and *Trispeleognathus* (both originally raised as subgenera of *Speleognathus* by Fain, 1958*b*) as subgenera of a genus in its own right, Fain (1963*c*), as first reviser, was free under Rec. 24 to choose the latter for the generic name, although the former has precedence of position. Presumably, he was influenced by his intermediate classification (1962*d*), in which *Trispeleognathus* was given full generic rank, while *Neospeleognathus* was considered a subgenus of *Neoboydaia* Fain.

Key to adults of Australian species of OPHTHALMOGNATHUS

1\. Coxal setae 2.1.1.1. Femoral setae more than 5.4.3.2. Hypostomal setae 1.1. Palpi with three segments, setation 0.1.3 2

Coxal setae 2.1.1.0. Femoral setae 5.4.3.2. Hypostomal setae 2.2. Palpi with two segments, setation 0.0.2. .... *schoutedeni* Fain, n. comb.

2 (1). Genital setae 5.5. Femoral setae 5.4.3.3. .... *striatus* (Crossley), n. comb.

Genital setae 4.4 Femoral setae 6.4.3.4 .... *accipitris*, n. sp.

OPHTHALMOGNATHUS STRIATUS (Crossley), n. comb.

Speleognathus striatus Crossley, 1952, *J. Parasit.*, 38: 385; Fain, 1956, *Revue Zool. Bot. afr.*, 53: 18. *Speleognathus* (*Trispeleognathus*) *striatus*, Fain, 1958, *Revue Zool. Bot. afr.*, 58: 178. *Trispeleognathus* (*Trispeleognathus*) *striatus*, Fain, 1963, *Bull. Inst. r. Sci. nat. Belg.*, 39: 53. *Trispeleognatus striatus* (*sic*) do Amaral, 1963, *Archos Inst. biol., S Paulo,* 30: 91.

Previous record.—Domestic pigeon (introduced), *Columba livia* Gmelin (Columbidae, Columbiformes).

OPHTHALMOGNATHUS ACCIPITRIS, n. sp.
(Figs 236–237)

Diagnosis.—Three species of *Ophthalmognathus s. s.** (*i.e.* with 3-segmented palpi) are known. *O. striatus* and *O. womersleyi* (Fain), n. comb., are both listed from Africa and the Americas, from various pigeons (Columbi-

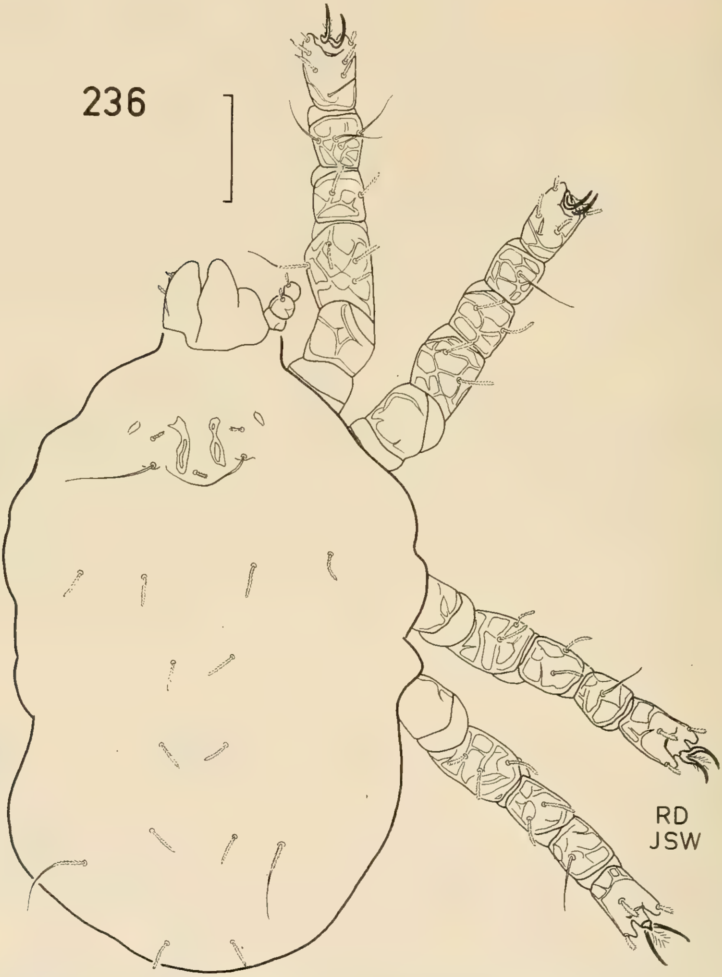


Fig. 236. *Ophthalmognathus accipitris*, n. sp.–Dorsal view of adult from *Accipiter fasciatus.*

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*It is a pity to have to note that acarological literature is becoming increasingly crowded with misspellings of numerous terms in common taxonomic use. This one and its partner are especially prone to suffer (*sensu stricta, sensu latu, sensu latus*), but other examples are common, *e.g. genus incertus, nomine nuda, species novum, sp. novo,* and *status novum.* There are also lapses in taxonomic names (*dividus, femuralis, flumenicola, inexspectatus,* and *omniphagous*); in morphological terms (endapodal, metatarsii, scutae, tarsae, and ventrum); and in general (a *corrigenda*, atennuated, detritis, hiati, and *in statuo quo*). This unconcern for a language which is both exact and the backbone of scientific terminology is inexcusable, and, regrettably, even the *Code* (Stoll *et al.*, 1964), in reducing Art. 31 to a mere Recommendation, has taken a step towards the stand that "scientific names . . . are meaningless since Latin is no longer an effective scientific language".

formes) and ducks (Anseriformes), respectively (Clark, 1958; Fain, 1963*c*; do Amaral, 1963*b*). Full morphological details are given by Fain (1963*c*), and *O. accipitris,* from an Australian goshawk (Falconiformes), may be separated from both by the setal formulae of the genitalia (4.4, not 5.5) and femora (6.4.3.4, not 5.4.3.3). *O. accipitris* further differs from *O. womersleyi* in showing two pairs (not one) of anal setae, and lacking the single seta on the palpal tibia.

The third known species, from a Brazilian pigeon, is *O. curicoi* (do Amaral, 1965), n. comb. It is not as well characterized, but differs from all three species discussed above in showing a coxal formula 2.0.1.0 rather than 2.1.1.1, and two pairs of gnathosomal setae rather than one.

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Fig. 237. *Ophthalmognathus accipitris,* n. sp.–Ventral view of adult from *Accipiter fasciatus.*

Types.—Holotype female and one paratype female from an Australian goshawk, *Accipiter fasciatus* (Vigors and Horsfield) (Accipitridae, Falconiformes), Kowanyama, 25.x.1966, R. D. Holotype N. I. C.; paratype R. D.

Female.—Idiosoma 594 and 616μ long in somewhat compressed condition. Cuticle finely striate on body, minutely, but densely aciculate on appendages.

Eyes present, but small, evident more by cessation of cuticular striae than by any definite corneae. Scutum divided into two longitudinal fragments (Fig. 236). Sensillae filamentous, simple. Dorsal setal formula (including presensillary pair) 2.2(1).4.2.2.4.2, all barbulate (except exterior pair of subposterior row, which are drawn out distally into filaments).

Sternal setae 2.2.1 in both specimens, but presumably 2.2.2 normally. Genital setae 1.3/3.1; anal setae 2.2(1). All barbulate (Fig. 237).

Setal formulae for legs as follows: coxae 2.1.1.1; trochanters 1.1.0.0; femora 6.4.3.4; genua 4.4.3.3; tibiae 5.3.3.3; tarsi 12.8.7.7. All barbulate except as follows: one seta on anterior margin of femur I distinctly, and occasional seta on some genua and tibiae slightly filamentous distally; tibiae with 3.1.1.1 dorsal setae entirely filamentous; some rounded, barbulate setae at tips of tarsi I–II with short, hyaline, apically expanded extensions. Tarsi I–II each with dorsal solenidion. Tibia I with invaginated sensory organ. Claws paired, subequal, retractable into dorso-distal excavations in tarsi. Pulvilli entire, bearing filaments.

Capitulum and legs with distinct reticulate pattern beneath cuticle. Palpi 3-segmented. Tibia with one seta dorsally; tarsus with one seta dorsally, and two setae and solenidion ventrally. Only two fully formed hypostomal setae present. All capitular setae barbulate, omitting vestiges of second hypostomal pair present between normal pair. Chelicerae drawn out distally into ventrally-directed stylets.

OPHTHALMOGNATHUS SCHOUTEDENI (Fain), n. comb.

Speleognathus schoutedeni Fain, 1955, *Annls Soc. belge Méd. trop.*, 35: 695; 1956, *Revue Zool. Bot. afr.*, 53 : 18. *Ophthalmognathus dogieli* Dubinin, 1957, *Trudy leningr. Obshch. Estest.*, 73: 68. New synonymy.

A third species of this genus may also be recorded from Australia: 6 adults from nankeen night herons, *Nycticorax caledonicus* (Gmelin) (Ardeidae, Ciconiiformes), Esk and Kowanyama, 5.i.1966 and 6.iv.1965, R. D. and J. S. W. The only previous records are African, *N. nycticorax* (Linnaeus) and *Ardeola idae* (Hartlaub).

I accept the synonymy suggested by Fain (1958*b*). Both taxa were described from herons.

Genus SPELEOGNATHOPSIS Cooreman

Speleognathopsis Cooreman, 1954, *Annls Parasit. hum. comp.*, 29: 428. Type-species *Speleognathopsis galli* Cooreman, 1954, *Loc. cit.*, 429.

Key to adults of Australian species of SPELEOGNATHOPSIS

1. Presensillary setae present. Four or more setae in first postsensillary row. Anal setae 3.3. Coxal setal formula commencing 2.1.1 (seta on coxa II of *S. benoiti* Fain minute). Femoral setae more than 5.4.3.2 2
Presensillary setae absent. Two setae in first postsensillary row. Anal setae 1.1 Coxal setae 1.0.1.0 Femoral setae 5.4.3.2 ...... *galli* Cooreman
2. (1). Scutum transverse. Seta on coxa II of normal size. Pulvilli simple. Palpal setae 0.3 .... *porphyrionis* Domrow
Scutum elongate. Seta on coxa II minute. Pulvilli bifid. Palpal setae 1.3 .... *benoiti* Fain

SPELEOGNATHOPSIS GALLI Cooreman

Speleognathopsis galli Cooreman, 1954, *Annls Parasit. hum. comp.*, 29: 429; Fain, 1963, *Bull. Inst. r. Sci. nat. Belg.*, 39: 53.

Previous records (both Galliformes).—Domestic fowl (introduced), *Gallus gallus* (Linnaeus) (Phasianidae). Guinea fowl (introduced), *Numida meleagris* (Linnaeus) (Numididae).

Since writing this, I have seen 7 adults of this species, previously known only from Rwanda, from the nasal sinuses and nares of domestic fowls in villages in the Western Sepik District (near Irian Barat border), v.1966, N. Talbot.

SPELEOGNATHOPSIS PORPHYRIONIS Domrow

Speleognathopsis porphyrionis Domrow, 1965, *Acarologia,* 7: 44.

Previous record.—Eastern swamphen, *Porphyrio melanotus* Temminck (Rallidae, Gruiformes), Samford.

SPELEOGNATHOPSIS BENOITI Fain

Speleognathopsis benoiti Fain, 1955, *Annls Soc. belge Méd. trop.,* 35: 696; 1956, *Revue Zool. Bot. afr.,* 53: 29; Domrow, 1965, *Acarologia,* 7: 44; 1966, PROC. LINN. SOC. N.S.W., 90: 210; McDaniel, 1967, *Tex. J. Sci.,* 19: 94. *Speleognathopsis charadricola* Fain, 1964, *Revue Zool. Bot. afr.,* 70: 35. *Speleognathopsis wai* Fain, Vercammen-Grandjean, and Wagner, 1966, *Acta zool. path. antverp.,* 41: 115. New synonymy.

I have already noted (1966*b*) considerable intraspecific variation in this parasite of charadriiforms, and commend to the reader Marshall's statement on taxonomy (in Parker and Haswell, 1962).

Previous records (all Charadriidae, Charadriiformes).— Red-kneed dotterel, *Erythrogonys cinctus* Gould, Kowanyama. Masked plover, *Lobibyx miles* (Boddaert), Kowanyama. Grey plover, *Squatarola squatarola* (Linnaeus). Black-fronted dotterel, *Charadrius melanops* Vieillot, Esk. Also Kowanyama.

Family EPIDERMOPTIDAE

Subfamily TURBINOPTINAE

This latter group has usually been accorded full familial status in recent years, but this period has also seen the erection of annectant taxa such as the Heterocoptidae (Fain, 1967*a*). I therefore return the group to its original family, the Epidermoptidae, noting that, while the epidermoptines are skin-parasites of birds, the turbinoptines inhabit the outermost parts of the nasal cavity. Such a treatment is parallel to that accorded the other two groups of nasal parasites of birds discussed above.

Even though I have used the characters of the female genitalia and the male clasping apparatus in the primary dichotomies in the following key to genera, it should be noted that the groups so obtained are not correlated. For example, while females of *Rhinoptes* de Castro and Pereira and *Schoutedenocoptes* Fain both key out through the second half of couplet 2, males of the former diverge from those of the latter at couplet 7. Nor do the two genera show similar tarsal modifications, yet both parasitize phasianoids (Galliformes).

Key to Australian genera of TURBINOPTINAE

1.	Females	2
	Males	7
2 (1).	Endogynium absent. Vulva transverse	3
	Endogynium present. Vulva in form of inverted Y	4
3 (2).	All tarsi with two claws	*Turbinoptes* Boyd
	All tarsi with one claw	*Passerrhinoptes* Fain
4 (2).	All tarsi with two claws	*Oxleya* Domrow
	All tarsi not with two claws	5
5 (4).	All tarsi very short and heavily sclerotized, with at least one claw	6
	Only tarsi I-II very short and heavily sclerotized. Tarsi I-II with one claw. Tarsi III-IV without claws	*Schoutedenocoptes* Fain

6 (5). Tarsi I-II with two claws. Tarsi III-IV with one claw ....
.... *Rhinoptes* de Castro and Pereira
All tarsi with one claw .... *Mycteroptes* Fain
7 (1). Body rounded posteriorly. Anal suckers minute 8
Body bilobed posteriorly. Anal suckers distinct 10
8 (7). Tarsi I-II with two claws. Tarsi III-IV with one claw ....
....*Rhinoptes* de Castro and Pereira
All tarsi with one claw 9
9 (8). Epimera I free .... *Mycteroptes* Fain
Epimera I fused .... *Passerrhinoptes* Fain
10 (7). All tarsi with two claws. Legs III-IV subequal 11
Tarsi I-II with one claw. Tarsi III-IV without claws. Leg IV considerably smaller than III ....*Schoutedenocoptes* Fain
11 (10). Dorsum unarmed except for minute propodosomal shield .... *Oxleya* Domrow
Dorsum with extensive hysterosomal shield in addition to propodosomal shield .... *Turbinoptes* Boyd

Genus Turbinoptes Boyd

Turbinoptes Boyd, 1949, *J. Parasit.,* 35: 295. Type-species *Turbinoptes strandtmanni Boyd,* 1949, *Loc. cit.,* 295.

Turbinoptes strandtmanni Boyd

Turbinoptes strandtmanni Boyd, 1949, *J. Parasit.,* 35: 295; Fain, 1956, *Revue Zool. Bot. afr.,* 54: 222; 1960, *Ibid.,* 62: 101; 1962, *Bull. Annls Soc. r. ent. Belg.,* 98: 266; 1963, *Ibid.,* 99: 179; Dubinin and Snegireva, 1957, *Zool. Zh.,* 36: 204; Domrow, 1965, *Acarologia,* 7: 90.

Previous records (all Charadriiformes).—Silver gull, *Larus novaehollandiae* Stephens (Laridae), Half Tide. Whimbrel, *Numenius phaeopus* (Linnaeus), Scolopacidae. Common sandpiper, *Tringa hypoleuca* Linnaeus (Scolopacidae).

New host record.—Eastern curlew, *Numenius madagascarensis* (Linnaeus), Tin Can Bay, 22.viii.1966, R. D. and J. S. W. (32♀♀, 17♂♂, 6 nymphs).

New Australian record.—*N. phaeopus,* Tin Can Bay, 26.x.1966, R. D. and J. S. W. (7♀♀, 5♂♂).

Genus Passerrhinoptes Fain

Passerrhinoptes Fain, 1956, *Revue Zool. Bot. afr.,* 54: 216. Type-species *Passerrhinoptes andropadi* Fain, 1956, *Loc. cit.,* 217; 1957, *Annls Mus. r. Congo belge Sér. 8vo,* 60: 30.

Passerrhinoptes pomatostomi Domrow

Passerrhinoptes pomatostomi Domrow, 1966, Proc. Linn. Soc. N.S.W., 90: 213.

Previous record.—Grey-crowned babbler, *Pomatostomus temporalis* (Vigors and Horsfield) (Timaliidae, Passeriformes), Esk. Also Condamine.

Genus Oxleya Domrow

Oxleya Domrow, 1965, *Acarologia,* 7:85. Type-species *Oxleya podargi* Domrow, 1965, *Loc. cit.,* 85.

Oxleya podargi Domrow

Oxleya podargi Domrow, 1965, *Acarologia,* 7: 85.

Previous record.—Tawny frogmouth, *Podargus strigoides* (Latham) (Podargidae, Caprimulgiformes), Samford and Cobble Ck. Also Esk.

Genus SCHOUTEDENOCOPTES Fain

Schoutedenocoptes Fain, 1956, *Revue Zool. Bot. afr.*, 54: 210. Type-species *Schoutedenocoptes numidae* Fain, 1956, *Loc. cit.*, 211.

SCHOUTEDENOCOPTES NUMIDAE Fain

Schoutedenocoptes numidae Fain, 1956, *Revue Zool. Bot. afr.*, 54: 211: 1957, *Annls Mus. r. Congo belge Sér. 8vo,* 60: 17.

Previous record.—Guinea fowl (introduced), *Numida meleagris* (Linnaeus) (Numididae, Galliformes).

Genus RHINOPTES de Castro and Pereira

Rhinoptes de Castro and Pereira, 1951, *Archos Inst. biol., S Paulo,* 20: 67. Type-species *Rhinoptes gallinae* de Castro and Pereira, 1951, *Loc. cit.*, 67.

RHINOPTES GALLINAE de Castro and Pereira

Rhinoptes gallinae de Castro and Pereira, 1951, *Archos Inst. biol., S Paulo,* 20: 67; Domrow, 1965, *Acarologia,* 7: 90. *Rhinoptes pternistis* Fain, 1956, *Revue Zool. Bot. afr.*, 54: 221; 1957, *Annls Mus. r. Congo belge Sér. 8vo,* 60: 37. New synonymy.

Previous records (both Phasianidae, Galliformes).— Domestic fowl (introduced), *Gallus gallus* (Linnaeus). Brown quail, *Synoicus australis* (Latham), Dayboro and Chelona.

I would confirm here the synonymy implicit in an earlier note (Domrow, 1965*b*).

Genus MYCTEROPTES Fain

Mycteroptes Fain, 1956, *Revue Zool. Bot. afr.*, 54: 219. Type-species *Mycteroptes basilewskyi* Fain, 1956, *Loc. cit.*, 220.

MYCTEROPTES BASILEWSKYI Fain

Mycteroptes basilewskyi Fain, 1956, *Revue Zool. Bot. afr.*, 54: 220; 1957, *Annls Mus. r. Congo belge Sér. 8vo,* 60: 33.

This genus and species, previously known only from an African roller of the genus *Coracias* Linnaeus may now be recorded from Australia: 17 ♀♀, 1 ♂, and 6 nymphs from an eastern broad-billed roller, *Eurystomus orientalis* (Linnaeus) (Coraciidae, Coraciiformes), Esk, 5.x.1965, R. D. and J. S. W.

V. HOST-SPECIFICITY AND ZOOGEOGRAPHY

At the beginning of this study, I was surprised to find so many species, originally described from overseas birds, also present in Australia, but it soon became clear that this was due simply to the fact that these mites had never been searched for in Australia. Thus only 39 (39%) of the 99 rhinonyssines, four (21%) of the 19 speleognathines, and two (33%) of the six turbinoptines now known (or expected to occur) in Australia have proved to be new species. This represents an overall figure of 36% (45 out of 124 species). In the following discussion on the host-specificity and zoogeography of the Australian fauna, the species are discussed, as far as possible, in systematic order. Those I have described as new since the beginning of this study are indicated by an asterisk, as it is interesting to consider to what extent the hosts of these species are restricted to the Australian zoogeographical region.

(*a*) *Tinaminyssus*

The three species from psittacids are the only Australian members of this genus to retain the tritosternum. This structure is, however, in the process of regression, and is absent in other species from extra-Australian psittacids, *e.g. T. baforti* (Fain), n. comb., and *T. phalliger* (Fain), n. comb. (see Fain, 1963*e*, 1965*b;* Domrow, 1964*a; Wilson,* 1964, 1966*b*). The opisthonotal shield is also regressing in this group. The host-specificity of these three species is discussed in detail above in Section IV under *T. aprosmicti.* In essence, each has several hosts within well defined psittacid groups: *T. kakatuae** parasitizes crested species (cockatoos and the cockatiel), *T. aprosmicti** various parrots, and *T. trichoglossi** various lorikeets. However, although the Psittacidae (as well as the Columbidae and Alcedinidae, *v. infra*) have undergone considerable radiation in the Australian region, all three families are virtually cosmopolitan, and some of their newly described parasites have already been recorded in New Guinea, Indonesia, and the Philippines (Wilson, 1964, 1966*a, b,* 1968*a, b*). There is no reason therefore, not to expect them even further afield.

T. belopolskii has been recorded from all the continents except South America, and is restricted to the Ardeidae.

T. epileus is, as yet, known only from New Guinea, but it parasitizes a falconid which extends well into Australia.

The largest series (11 species) of Australian species of *Tinaminyssus* is that restricted to columbids. The simpler species, *i.e.* those lacking basally inflated setae on the legs and venter, may be divided into two groups depending on the postanal seta, yielding the sequences—(*i*) postanal seta present: *T. melloi, T. ocyphabus** and *T. hirtus;* and (*ii*) postanal seta absent: *T. columbae, T. megaloprepiae,* T. geopeliae, T. ptilinopi,* and *T. myristicivorae.** The widespread *T. melloi* occurs in all three introduced ground-pigeons (Columbinae), which are primarily seed-eaters. Its remaining two hosts (*Columba norfolciensis* and *Leucosarcia melanoleuca*) are jungle-dwelling, seed- and fruit-eating members of the same subfamily. *T. ocyphabus* is known only from the peculiarly Australian *Ocyphaps* Gray, while *T. hirtus* is known from *Chalcophaps* Gould in the Philippines, New Guinea, and Australia. These are again columbines, the former typical of open forest, the latter of rain-forest. *T. columbae* is also widespread in the domestic pigeon, and has been once recorded from *Ocyphaps,* while *T. geopeliae* is restricted to *Geopelia* Swainson in Malaysia, the Philippines, New Guinea, Australia, and Hawaii (introduced). The remaining three species of the sequence are parasites of jungle-dwelling fruit-pigeons (Treroninae). *T. ptilinopi* has been recorded from *Sphenurus* Swainson in Taiwan, and is widespread from S. E. Asia to New Guinea in *Ptilinopus* Swainson, one of the known hosts extending well into Australia. *T. megaloprepiae* and *T. myristicivorae* are known only from their original Australian hosts.

The second group comprises *T. phabus,** recorded only from *Phaps* Selby, an Australian columbine of the open forest, *T. macropygiae,* restricted to a jungle-dwelling columbine (*Macropygia* Swainson) in the Philippines, New Guinea, and Australia, and *T. welchi,** a parasite of a treronine. Clearly, there is a tendency for the more advanced species of this genus to be found parasitizing the jungle-dwelling treronines rather than the more typical columbines.

There remain two species from alcedinids: *T. halcyonus** is common in *Halcyon* Swainson in the Philippines, New Guinea, and Australia, while *T. daceloae** has only been recorded from *Dacelo,* an Australian genus.

(b) *Larinyssus*

Of the two known species, *L. orbicularis* is cosmopolitan in the Laridae, and *L. benoiti* has been recorded from African and Australian glareolids.

(c) *Rallinyssus*

This compact genus is cosmopolitan and restricted to rallids. Of the two species without circumanal frills, *R. amaurornis* is known from two hosts in Taiwan and the Philippines, and *R. congolensis* from a further two in Rwanda and the Philippines. The range of one host of each species extends into Australia. Of the two species with circumanal frills, *R. gallinulae* has been recorded from Belgium, New Guinea, and Australia, and *R. caudistigmus* from the U.S.A., South Africa, New Guinea, and Australia. Host-specificity is again low, the former species having been recorded from five genera, and the latter from three of the same five (Wilson, 1965, 1967).

(d) *Rhinonyssus*

This genus is confined to water birds of several types, and the primary dichotomy in the key in Section IV above is based on the work of Strandtmann (1959). Of the species with a definite anal shield and compacted palpi, *R. rhinolethrum* is cosmopolitan in a very wide range of anseriform genera, while *R. poliocephali* is known from a single species of *Podiceps* Latham in both Africa and Australia. Of the species with the anal shield obsolescent and normal palpi, both *R. coniventris* and *R. minutus* are cosmopolitan parasites of a wide range of charadriiforms, while *R. sphenisci* has only been recorded from Sphenisciformes.

(e) *Ruandanyssus*

Of the two known species, *R. terpsiphonei* has a wide range of African and Australian passeriform hosts, while *R. artami** is as yet known only from Australian artamids. However, the latter may be expected to coexist with its host-family, which extends to S. E. Asia.

(f) *Rhinoecius*

This genus comprises several species, all restricted to the Strigiformes. Of the Australian species, *R. cooremani,* originally recorded from *Strix* Linnaeus in the U.S.A., here parasitizes *Ninox* Hodgson (also a strigid), while *R. tytonis* probably coexists with the widespread barn-owl, *Tyto alba* (Tytonidae).

(g) *Ptilonyssus*

Apart from three species noted below (*P. triscutatus, P. nitzschi,* and *P. cerchneis*), the 53 Australian members of this genus are restricted to the Passeriformes, and may conveniently be split into two major divisions depending on whether or not the opisthonotal shield is reduced merely to a pygidial complex. (The presence of metasternal setae is often, but not always correlated with this division.) The first division may again be once divided. Firstly, a group may be commenced with *P. maluri** and *P. colluricinclae** (parasites of peculiarly Australian sylviids and pachycephalids, two taxa often considered only as muscicapid subfamilies, see Thomson, 1964), which lead by way of *P. capitatus* (a widespread parasite of alaudids) to *P. carduelis, P. emberizae, P. pygmaeus, P. hirsti,* and *P. neochmiae** (all parasites of fringillids and ploceids, two widespread families of small granivores). (*P. neochmiae* lacks peritremes, but this minor morphological point should not be allowed to override an otherwise convincing unity.) The group closes with *P. struthideae** and *P. corcoracis,** two species lacking a cribrum and parasitizing two monotypic, and peculiarly Australian corvid genera. They appear closely related to *P. nucifragae,* a parasite of *Nucifraga* Brisson, a palaearctic member of the same family.

The second group, involving increasing fragmentation and reduction of the opisthonotal shield, includes seven species. In *P. triscutatus, P. dioptrornis, P. dicruri,* and *P. sittae,* the pygidial shield is discrete. The first is a parasite of meropids (Coraciiformes), while the other three parasitize muscicapids (including turdids), dicrurids, and sittids (including certhiids), respectively. All are widespread in Africa, Eurasia, and Australia. *P. ailuroedi,** an aberrant species with considerable mesonotal modifications, probably also belongs here. Its hosts belong to the Ptilonorhynchidae, a peculiarly Australian family near the end of the passerine series. On the other hand, *P. elbeli* and *P. angrensis* both lack a pygidial shield, the former being a parasite of Eurasian sturnids, while the latter parasitizes the cosmopolitan family Hirundinidae.

The second major division is best commenced with *P. nitzschi,* from a widespread caprimulgid (Caprimulgiformes). It is the only species to retain a fully developed tritosternum. However, from this point onward, it becomes increasingly difficult to correlate morphology and host-specificity. Thus the three major dichotomies used in the key in Section IV above (those depending on the degree of posterior truncation of the podonotal shield, the presence or absence of the postanal seta, and the condition of the pygidial shield) all lead to incongruities with the system based on host order that will now largely be followed.

Both *P. echinatus,* an isolated and widespread species from hirundinids, and some species from meliphagids (*v. infra*) show accessory podonotal shields, but the two groups do not seem otherwise related. Likewise, *P. pittae** (from an Australian pittid) is not necessarily close to the widespread sylviid parasite *P. acrocephali* (*v. infra*) merely because both have a pair of enlarged setae set close together on the posterior margin of the podonotal shield. It is possibly closer to *P. cractici,** *P. motacillae,* and *P. langei,* a trio comprising members of the so-called *sairae* species-group of Fain (1959, 1962*c*). Of these, the first is a parasite of three genera of Cracticidae (a peculiarly Australian family), the second is widespread and recorded from a variety of hosts, while the third is known only from the original record from a hirundinid in the U.S.S.R.

There now follows a group of eleven species from the Muscicapidae (or families sometimes included therein, see Keast, 1961). As mentioned above, it is difficult to arrange them naturally, but the degree of truncation of the podonotal shield has been given precedence over the absence of the postanal seta, and the division of the pygidial shield has been considered least likely to indicate true relationships. These criteria yield the sequences (only non-muscicapine hosts are indicated)—(*i*) species with podonotal shield not truncate, pygidial shield entire, and postanal seta present: *P. orthonychus** (from a timaliid), *P. microecae,** *P. terpsiphonei, P. bradypteri* (from a sylviid), and *P. acrocephali* (again from a sylviid) (*P. bradypteri* is the only species of the entire sequence to lack peritremes, but this alone does not, I believe, necessarily make it more closely related to any of the species listed above which also lack this character, *i.e.* the other species formerly included in *Passeronyssus* and *Cas,* see synonymy of *Ptilonyssus* in Section IV above. Clearly, many characters are polyphyletic in this weakly sclerotized group of endoparasites. *P. bradypteri* is therefore placed before *P. acrocephali*, the first species of the sequence to show an anterodorsal process on coxa II. This latter character then persists throughout the sequence, except for the last species, *P. psophodae*); (*ii*) similar to (*i*), but postanal seta absent: *P. monarchae*;* (*iii*) similar to (*i*), but podonotal shield truncate: *P. setosae** and *P. gerygonae** (from a sylviid); (*iv*) similar to (*iii*), but pygidial shield divided: *P. rhipidurae*;* and (*v*) similar to (*iii*), but postanal seta absent: *P. macclurei* and *P. psophodae** (from a falcunculid).

Of these eleven species, four have been recorded outside Australia. *P. terpsiphonei* has a very wide host range in Africa and S. E. Asia. *P. bradypteri* and *P. acrocephali* were originally recorded from Africa and Europe, respectively (the Australian host of the latter is also a species of *Acrocephalus* Naumann). *P. macclurei* was described from a Malayan species of *Rhipidura* Vigors and Horsfield, and is restricted, in Australia, to *R. leucophrys*. Of the other three Australian species of *Rhipidura*, *R. fuliginosa* carries only *P. rhipidurae*, while the two rain-forest species, *R. setosa* and *R. rufifrons*, each bear a variant of a third species, *P. setosae*. *P. monarchae* is known only from the original record, but *P. microecae* is known from two species of *Microeca* Gould, and *P. orthonychus* and *P. gerygonae* have both been taken a second time in their original host species. *P. psophodae* is certainly restricted to *Psophodes olivaceus*.

The family Muscicapidae is cosmopolitan, and, although it has radiated considerably in Australia, the parasites of muscicapines, at least, may be expected outside Australia, just as the widespread *P. terpsiphonei* is established in a wide range of Australian genera. The parasites of such peculiarly Australian branches of this radiation as the pachycephalines and malurines, however, may be restricted to this region. Finally, this group of eleven species from muscicapids provides the best Australian example of host-specificity at three levels: its members may be restricted to a single host family, genus, or species.

*P. grallinae** is an isolated species restricted to *Grallina cyanoleuca*, the sole Australian member of the small and aberrant Australopapuan family Grallinidae (see also diagnosis for *P. struthideae* in Section IV above).

There are four families of Old World and Australian nectar-feeders, the Zosteropidae (silvereyes), the Dicaeidae (flower peckers), the Nectariniidae (sunbirds), and the Meliphagidae (honeyeaters). *P. ruandae* and *P. dicaei*,* two species with short, characteristically broad podonotal shields, are restricted to the first two, and *P. cinnyris* to the third of these families. *P. dicaei* is still only known from the original record from *Dicaeum* Cuvier in Australia, but the other two species are common in other members of their respective families both in S. E. Asia and Africa.

Some evidence is given above for a burst of speciation within *Ptilonyssus* in peculiarly Australian flycatchers. A similar burst is perhaps still in progress among the parasites of honeyeaters (which, unlike the cosmopolitan flycatchers, are virtually restricted to Australia), and variants of both *P. philemoni* and *P. gliciphilae* have been described in Section IV above. Such morphological gaps, correlated with host-specificity, are suggestive of isolation at a subspecific level, but it is difficult to confirm sexual isolation in a group with such specialized habits. In any case, mere experimental confirmation of sexual isolation is of doubtful value, and since it is as much an error to describe a true species as a subspecies as the reverse, the use of trinomina for these variants has been foregone (Mayr *et al.*, 1953).

Only one of the three major dichotomies discussed above under the species from flycatchers is available to divide the species from honeyeaters, *viz.*

the degree of truncation of the podonotal shield (the pygidial shield is variable in many species, and the postanal seta is always present). The application of this criterion yields the following two sequences—(*i*) podonotal shield not truncate: *P. myzanthae,* P. philemoni,* P. balimoensis, P. myzomelae,** and *P. gliciphilae;** and (*ii*) podonotal shield truncate: *P. lymozemae,* P. stomioperae,* P. thymanzae,** and *P. meliphagae.** In addition to this posterior truncation, there is also a lateral reduction of the podonotal shield in some species, leaving free accessory shieldlets. This occurs in both sequences, the species concerned being *P. gliciphilae, P. thymanzae,* and *P. meliphagae* (see note on *P. echinatus* above). As the honeyeaters are often gregarious, and several species may be seen feeding in the same flowering tree, strict host-specificity is not to be expected. Indeed, double infestations are not uncommon, see Section VII below. Thus *P. thymanzae* is known from eight species belonging to four genera, and *P. philemoni* from six species of four genera, though it should be noted that these genera are all toward the end of the sequence given by Leach (1958). Most of the remaining species are known from two, or occasionally three host-genera, but there is evidence that both *P. myzomelae* and *P. lymozemae* and restricted to *Myzomela* Vigors and Horsfield. The striking *P. balimoensis,* originally described from an unidentified meliphagid in New Guinea, occurs in *Meliphaga macleayana* in Australia.

The isolated *P. nudus* keys out near the parasites of muscicapids, but is restricted to the introduced domestic sparrow (Fringillidae), and, like many of the species with a complete opisthonotal shield parasitic in other fringillids and ploceids, retains the metasternal setae.

P. sturnopastoris is a parasite of S. E. Asian and Australian sturnids.

*P. sphecotheris** and *P. trouessarti* are restricted to Australian oriolids, the former to the two species of *Sphecotheres* Vieillot and the latter to the two species of *Oriolus* Linnaeus. They have characteristically cordate podonotal shields, but key out separately because the postanal seta is absent in the former and present in the latter.

The imperfectly known *P. novaeguineae* was described from a paradiseid species which penetrates into Australia.

This leaves *P. cerchneis,* a characteristic and widespread species restricted to the genus *Falco* Linnaeus (Falconiformes). It is perhaps related to the group of species from neotropical falconiforms detailed by Pereira and de Castro (1949) and Fain and Johnston (1966).

(*h*) *Sternostoma*

The members of this nondescript and difficult genus, unlike the preceding one (*Ptilonyssus*), show no predilection for passeriform hosts, and host-specificity is normally above the familial level. *S. thienponti* is common in Australian cracticids, although the only previous records are from African and Asian dicrurids. This finding is of interest, as Thomson (1964) notes that the relationships of the dicrurids are a "matter of speculation". The following four species are virtually cosmopolitan, or at least widespread in the Old World: *S. cooremani* in two coraciiform families, *S. boydi* in various charadriiforms, and *S. dureni* and *S. technaui* in turdids.

S. cuculorum has numerous hosts, among which cuculids and muscicapids figure prominently. Of the three recorded cuculid hosts, *Cacomantis variolosus* usually chooses birds that build open, cup-shaped nests in small trees *etc.,* particularly muscicapids, as foster-parents, and Cayley (1963) notes that the remaining three Australian hosts also build cup-shaped nests.

C. pyrrhophanus, on the other hand, prefers hosts which build a domed nest near the ground, while the larger *Eudynamys orientalis* prefers the nests of orioles and large meliphagids. If I have not over-simplified my concept of *S. cuculorum,* these findings differ from those of Strandtmann and Furman (1956) and Clark (1963), who found that, in the parasitic American cowbirds (Icteridae, Passeriformes), "host specificity of nasal mites is operative even in the face of ample opportunities for cross transmission of parasites".

S. tracheacolum, a pest in aviaries, particularly of fringillids and ploceids, tends to spread to unusual hosts in these circumstances. It has also been recorded from a wide range of small passeriforms in the wild (Fain and Hyland, 1962*a*). *S. paddae,* known only from the original record, is associated with conjunctivitis in an Oriental ploceid, and *S. cryptorhynchum* is widespread in the house-sparrow.

The remaining three species (*S. gliciphilae,* S. neosittae,** and *S. fulicae*) have not been collected since the original series. The first is the only species of the genus recorded from a peculiarly Australian host family (Meliphagidae), but the second may be expected to occur in other sittids overseas. The third is a parasite of the coot (Rallidae).

(*i*) *Boydaia*

This large genus, unlike the remaining three speleognathine genera discussed below, is essentially restricted to passeriform hosts, although, of the Australian species, *B. falconis* is widespread in the genus *Falco. B. spatulata* and *B. crassipes* are both widespread parasites of a variety of hosts, but *B. sturni, B. zosteropis,* and *B. hirundoae,* though widespread, are restricted to sturnids, zosteropids, and hirundinids, respectively. *B. myzomelae** and *B. maluri** are newly described from two peculiarly Australian groups, the Meliphagidae and Malurinae (Sylviidae).

(*j*) *Neoboydaia*

The five Australian members of this genus (*N. philomachi, N. psittaculae, N. aureliani, N. merops,* and *N. colymbiformi*) are all widespread, showing a low level of host-specificity for five different non-passeriform orders (Charadrii–, Psittaci–, Strigi–, Coracii–, and Podicipiformes, respectively).

(*k*) *Ophthalmognathus*

O. schoutedeni is widespread in ardeids, and *O. striatus* in columbids. *O. accipitris,** newly described from an Australian accipitrid, may also have a wider range.

(*l*) *Speleognathopsis*

S. benoiti is a widespread parasite of various charadriiforms, while *S. galli* and *S. porphyrionis** are known, as yet, only from galliforms in Africa and a gruiform in Australia, respectively.

(*m*) *Turbinoptes*

T. strandtmanni is a widespread parasite of various charadriiforms.

(*n*) *Passerrhinoptes*

*P. pomatostomi** is known only from an Australian timaliid, but may extend, with this family, as far as Africa.

(*o*) *Oxleya**

*O. podargi** was described from an Australian caprimulgiform, which, however, extends into the Orient.

(*p*) *Schoutedenocoptes*

S. numidae is known only from a domesticated numidid.

(*q*) *Rhinoptes*

R. gallinae was also described frôm a domesticated phasianid, but also occurs wild in an Australian member of the same host-family.

(*r*) *Mycteroptes*

M. basilewskyi is widespread in coraciids.

In conclusion, the anatomy of all birds is very similar, and their relatively recent emergence, their low rate of extinction, and their poor fossil record have further contributed to the difficulty in providing a classification and a detailed history of the phylogeny of the various bird orders.

The birds began to diverge from reptilian stock in the late Jurassic (150 million years ago), shortly after the emergence of the first mammals, but the earliest line (the Archaeornithes, which included only *Archaeopteryx* Meyer) is long extinct.

The Neornithes, which include the remaining fossil groups as well as all living birds, arose in the Cretaceous (120 m. years ago), and even by this time some birds had evolved which can be referred to orders still extant. During the Tertiary, the birds (and the mammals) gained ascendancy over the reptiles, and most of the orders, both of land-and water-birds, evolved (Eocene, 50 m. years ago), modern genera began to appear (Oligocene-Miocene, 35–25 m. years ago), and many modern species were already present (Pliocene, 10 m. years ago).

Both groups of modern birds are cosmopolitan. The palaeognaths (or flightless ratites) include only the ostrich of Africa and (formerly) S. W. Asia, the emu and cassowaries of Australia and New Guinea, the kiwis and recently extinct moas of New Zealand, the rheas of South America, *etc.* To the best of my knowledge, the only ratites examined for nasal mites are three emus (*Dromaius* Vieillot) (*v. infra*) and two cassowaries (*Casuarius* Brisson) (Wilson, personal communication). All were uninfested. The neognaths therefore include all the known hosts of nasal mites. They comprise all the remaining orders, but, as noted above, it is difficult to classify a group so diverse as to include the tinamous, penguins, grebes, petrels, ducks, hawks, pigeons, parrots, owls, swifts, *etc.* on the one hand, not to mention the equally large series of passeriform families on the other (Young, 1950; Thomson, 1964).

It seems clear, therefore, that mites of three suborders entered the nasal cavities of birds at an early period, and spread with their hosts, so that such widely differing groups of birds as grebes, herons, swallows, larks, *etc.* now bear their own distinctive mites throughout their cosmopolitan ranges. The same is true of groups confined to the Old World, even in the case of families possessing numerous species in Africa and Asia that are represented in Australia only by one. The Coraciidae, Meropidae, Nectariniidae, Sturnidae, and Dicruridae come immediately to mind, and all have carried their specific parasite(s) into Australia. A similar situation occurs even with such introduced species as the starling and house-sparrow, and this conservatism is opposed only by the parasites of groups of birds, like the meliphagids, that have been free to radiate in isolation at the end of this chain in Australia.

VI. PHYLOGENY OF THE RHINONYSSINE GENERA

Although no firm relationship with other arachnids can be established from the meagre fossil record, mites have been reported from the Devonian and Carboniferous, while, by the Tertiary, all the principal families are represented, particularly in amber (Woolley, 1961). Vitzthum's concept (1935, 1942) of the Dermanyssidae (then included in the Laelapidae) as primitively humus-dwelling predators, various lines of which became paraphages of insects, nidophiles, ectoparasites, and finally endoparasites of a wide range of vertebrate hosts, was maintained by Zumpt and Patterson (1951), and Evans and Till (1966) have recently retreated the matter in detail.*

It therefore seems reasonable to look for the primitive hosts of the Rhinonyssinae among the land-birds. The simplest species of *Tinaminyssus* (those retaining two well developed dorsal shields) are, indeed, those from pigeons, hawks, and parrots, the one exception, *T. belopolskii,* being a parasite of herons. The tritosternum, another structure quickly lost in an endoparasitic group, is also retained in some species from parrots. Some fragmentation, or occasionally the disappearance of the opisthonotal shield takes place in other species from hawks and parrots, and the species from tinamous (neotropical ground-birds) also show a divided opisthonotal shield. The species of *Tinaminyssus* from kingfishers generally lack the opisthonotal shield, as do those of the related genera *Larinyssus* and *Rallinyssus, T. tanysipterae* (Wilson, 1966*a*), n. comb., and *R. amaurornis* Wilson (1965) being exceptions. *Larinyssus* is restricted to various waders and *Rallinyssus* to rails. The latter, because of its peculiarly displaced stigmata and anal *accoutrements*, is presumably the more evolved. The fragmentation of the dorsal shield in these two genera extends to the podonotal shield, and this is to be correlated with the decreasing danger of desiccation and anoxia in the nasal passages of fresh-water and marine birds. The genus *Rhinonyssus,* in which the peritremes (porous anterior extensions of the respiratory stigmata) are lost, closes this line of evolution. The simpler species of this genus are parasites of penguins and a wide variety of waders, but one compact species-group with peculiarly modified palpi is found both in ducks and grebes (Strandtmann, 1959). It should be noted, however, that penguins are much closer to the Procellariiformes (petrels, albatrosses, *etc.*) than to the waders, and that the grebes are not ducklings, as I have heard bushmen heatedly affirm. In this case, the gregarious habits of the hosts in salt– and fresh-water are more important in determining host-specificity than true phylogenetic relationships (Strandtmann, 1958). To recapitulate, in this series of four small genera, all with unmodified chelicerae, the movement has been towards, and not away from water-birds.

A second line of development is to be seen in the two small genera *Ruandanyssus* and *Rhinoecius,* in which the fixed cheliceral digit has been lost, leaving a falcate movable digit of moderate length. The former parasitizes a range of passeriform birds, while the latter is restricted to owls.

A third line is characterized by a considerable reduction in size of the cheliceral digits, with a concomitant attenuation of the distal half of the cheliceral shafts (the seemingly bulbous, but normally developed basal portion is drawn out ventrally to form this slender portion). The species of *Ptilonyssus* which have retained two large dorsal shields and (often)

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*The classification of the two other groups of nasal mites of birds is still fluid. The Ereynetidae are divided by Fain (1962*d*) into the Ereynetinae (essentially free-living predators, but including one ectoparasite of pulmonate gastropods and one intranasal parasite of a Malaysian bird, see Fain, 1964*e*, and Fain and Nadchatram, 1962), the Lawrencarinae (intranasal parasites of frogs), and the Speleognathinae (intranasal parasites of warm-blooded vertebrates). The turbinoptines are close relatives of epidermoptine genera which scavenge on the skin *débris* of birds.

metasternal setae are principally parasites of small granivores, while the remainder have radiated, and are still radiating among a wide range of passeriforms. An occassional species of this very large genus has been recorded from non-passeriforms (hawks, swifts, nightjars, and bee-eaters), but none is known from water-birds. The species of *Sternostoma,* found as a rule deeper in the nasal tract, have lost their peritremes, and one, with a reduced opisthonotal shield, is found in waders. The remainder are parasites particularly of passeriforms, but, rather more frequently than is the case with *Ptilonyssus,* also of non-passeriform groups.

These three lines are the subfamilies Rhinonyssinae, Rhinoeciinae, and Ptilonyssinae discussed, and abandoned in Section IV above, together with Bregetova's theory (1964) of a diphyletic origin of the rhinonyssines. Indeed, the rhinonyssines with a well developed tritosternum are so little differentiated from some of the ectoparasites of mammals and birds, *e.g. Ornithonyssus* Sambon and *Pellonyssus* Clark and Yunker, that Zumpt and Till (1961) placed *Ruandanyssus* and *Astridiella* (here considered a synonym of *Ptilonyssus*) among the macronyssine rather than the rhinonyssine genera. If a distinction must be maintained between the Macronyssinae and the Rhinonyssinae, it can be made only on ecological grounds, because the presence or absence of the tritosternum is useless as a taxonomic character, as discussed above in the synonymies of *Tinaminyssus, Rhinoecius,* and *Ptilonyssus.* Indeed, even this ecological separation is weakened by the habits of some related species. The tropical fowl-mite, *Ornithonyssus bursa* (Berlese) (Macronyssinae), unlike the northern fowl-mite, *O. sylviarum* (Canestrini and Fanzago), does not spend its whole time on its host (Furman, 1963), and the chicken-mite, *Dermanyssus gallinae* (Degeer) (Dermanyssinae) feeds only for one or two hours at night, spending the rest of the day in crevices in fowlhouses (Kirkwood, 1963). Such behaviour undoubtedly led to the entry of "protorhinonyssines" into the intricate, warm, and moist nasal passages of birds. I therefore believe the Rhinonyssinae to be a monophyletic unit clearly derived, and separable only with difficulty from the Macronyssinae, the former name having priority.

VII. Host-parasite List

As the revision of the official checklist of Australian birds (Leach *et al.,* 1926) has not yet been completed, I have used the classification of Leach (1958)* in the present study. This authority lists 735 species, 330 genera, 82 families, and 20 orders (including 11 genera and 17 species of introduced and vagrant birds), while an unpublished checklist of Queensland birds on a similar basis (Lavery, personal communication) lists 570 species and 280 genera. It is therefore clear that, since Queensland, of all the states, has by far the largest proportion of the birds on the Commonwealth list (78% of the species, and 85% of the genera), an intensive study of the fauna of that state will have relevance beyond its borders. Leach's system is summarized in Tables 2 and 3, with an indication of the fauna still to be examined. However, as with many of Australia's rarer marsupials, it is unlikely that some groups, *e.g.* night parrots (*Geopsittacus* Gould) and scrub-birds (*Atrichornis* Stejneger), will ever be thoroughly examined for parasites.

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*As I am not a bird taxonomist, I have accepted uncritically the Latin names of this authority, although several are obviously in error. Thus, while the use of adjectival specific names with masculine terminations (*pyrrhopygius, sanctus*) in the feminine genus *Halcyon* contravenes Art. 30, the original spelling of the specific name *tenuirostris,* not being adjectival, stands under Art. 32, and cannot be forced into a neuter form on its transferal to *Edoliisoma* Pucheran. I have, however, dispensed with the hyphen in specific names such as *novaehollandiae* (Art. 32).

I have examined just over half (287 species) of the Queensland total, while another 43 widespread species known to be infested overseas have not yet been so found in Australia (some of this latter group occur in Queensland; others do not). Of those I have examined, 158 species (55%) were infested (of which eight are likely to yield still further mite species), while a further 51 species can be expected to yield nasal mites. In total, 330 species are known to have been examined, of which nasal mites have been recorded from 209 (63%).

TABLE 2

Analysis of Australian and Queensland genera and species of birds examined and found infested with nasal mites

Order	Number of Genera				Number of Species			
	Australia	Queensland*	Examined	Infested	Australia	Queensland*	Examined	Infested
Casuariiformes ..	2	2	1	0	2	2	1	0
Galliformes ..	8	6	5	3	9	7	5	3
Turniciformes ..	2	2	1	0	8	7	1	0
Columbiformes ..	17	14	12	12	27	22	17	16
Gruiformes	12	10	9	7	16	15	9	7
Podicipiformes ..	1	1	1	1	3	3	1	1
Sphenisciformes ..	3	1	1	1	5	1	1	1
Procellariiformes ..	16	12	0	0	37	26	0	0
Charadriiformes ..	38	32	28	20	76	75	44	31
Ciconiiformes ..	14	12	11	5	20	21	17	7
Anseriformes ..	15	12	8	4	22	18	11	7
Pelecaniformes ..	6	6	4	0	15	14	6	0
Falconiformes ..	14	14	8	3	26	24	12	4
Strigiformes ..	2	2	2	2	9	8	4	2
Psittaciformes ..	23	19	13	12	58	36	20	14
Caprimulgiformes ..	4	4	3	2	8	7	3	2
Coraciiformes ..	7	7	5	4	12	12	10	8
Apodiformes ..	3	3	0	0	3	5	0	0
Cuculiformes ..	7	7	6	2	14	12	8	3
Passeriformes ..	136	114	93	72	365	255	160	103
Total..	330	280	211	150	735	570	330	209
Percentage :								
Australia ..	100	85	64	45	100	78	45	28
Queensland ..	—	100	75	53	—	100	58	36
Examined ..	—	—	100	71	—	—	100	62

* Lavery's figures (personal communication) for the Galliformes, Turniciformes, Gruiformes, and Charadriiformes have been adjusted to conform to Leach's order (1958) to facilitate comparison of the two sets of figures.

The number of individual host-parasite records, however, is somewhat larger. My own collections have yielded 205 such records (Rhinonyssinae from 175, Speleognathinae from 23, and Turbinoptinae from 7 hosts), and, taking into account birds on the Australian list that are known to be infested overseas, this number may be increased to 295 (Rhinonyssinae from 248, Speleognathinae from 37, and Turbinoptinae from 10 hosts). These figures are neither maximal nor minimal, since some birds examined in small numbers only will probably prove later to be infested, while others, of which only a single specimen has been examined, have proved infested (with, in at least one case, *Oreocincla lunulata,* two species of mites).

The reason for this difference is that one host-species may harbour two or more species of mites, and, in fact, 30 hosts are known, in Australia, to harbour two, seven three, and one four parasites. However, no multiple infestations were noted in the present study, but the following 22 cases of natural double infestations occurred, 14 involving two rhinonyssine species,

TABLE 3

Synopsis of genera and species of Australian birds examined and found infested with nasal mites

Order	Family	Number of Genera			Number of Species		
		Total	Examined	Infested	Total	Examined	Infested
Casuariiformes	Dromaiidae	1	1	0	1	1	0
	Casuariidae	1	0	0	1	0	0
Galliformes	Megapodiidae	3	2	0	3	2	0
	Phasianidae	4	2	2	5	2	2
	Numididae	1	1	1	1	1	1
Turniciformes	Turnicidae	1	1	0	7	1	0
	Pedionomidae	1	0	0	1	0	0
Columbiformes	Columbidae	17	12	12	27	17	16
Gruiformes	Rallidae	11	8	7	15	8	7
	Megalornithidae	1	1	0	1	1	0
Podicipiformes	Podicipidae	1	1	1	3	1	1
Sphenisciformes	Spheniscidae	3	1	1	5	1	1
Procellariiformes	Hydrobatidae	5	0	0	5	0	0
	Procellariidae	8	0	0	24	0	0
	Pelecanoididae	1	0	0	1	0	0
	Diomedeidae	2	0	0	7	0	0
Charadriiformes	Laridae	6	4	4	21	8	7
	Stercorariidae	2	0	0	3	0	0
	Haematopodidae	1	1	0	2	1	0
	Charadriidae	8	7	6	16	10	9
	Recurvirostridae	3	2	1	3	2	1
	Scolopacidae	11	9	7	24	18	12
	Rostratulidae	1	0	0	1	0	0
	Jacanidae	1	1	0	1	1	0
	Glareolidae	2	2	2	2	2	2
	Burhinidae	2	1	0	2	1	0
	Otitidae	1	1	0	1	1	0
Ciconiiformes	Threskiornithidae	3	3	0	5	5	0
	Ciconiidae	1	1	0	1	1	0
	Ardeidae	10	7	5	14	11	7
Anseriformes	Anatidae	15	8	4	22	11	7
Pelecaniformes	Phalacrocoracidae	1	1	0	5	3	0
	Anhingidae	1	1	0	1	1	0
	Sulidae	1	1	0	4	1	0
	Fregatidae	1	0	0	2	0	0
	Phaethontidae	1	0	0	2	0	0
	Pelecanidae	1	1	0	1	1	0
Falconiformes	Accipitridae	12	7	2	18	9	2
	Falconidae	1	1	1	7	3	2
	Pandionidae	1	0	0	1	0	0
Strigiformes	Strigidae	1	1	1	4	2	1
	Tytonidae	1	1	1	5	2	1
Psittaciformes	Psittacidae	23	13	12	58	20	14
Caprimulgiformes	Podargidae	1	1	1	4	1	1
	Aegothelidae	1	1	0	1	1	0
	Caprimulgidae	2	1	1	3	1	1
Coraciiformes	Coraciidae	1	1	1	1	1	1
	Alcedinidae	5	3	2	10	8	6
	Meropidae	1	1	1	1	1	1
Apodiformes	Apodidae	3	0	0	3	0	0
Cuculiformes	Cuculidae	7	6	2	14	8	3
Passeriformes	Menuridae	1	0	0	2	0	0
	Pittidae	1	1	1	3	1	1
	Atrichornithidae	1	0	0	2	0	0
	Hirundinidae	3	3	2	5	5	4
	Muscicapidae	16	11	10	37	18	15
	Campophagidae	4	4	2	9	9	3
	Timaliidae	5	2	2	14	2	2
	Sylviidae	21	9	5	78	22	6

TABLE 3—*Continued*

Synopsis of genera and species of Australian birds examined and found infested with nasal mites—Continued

Order	Family	Number of Genera			Number of Species		
		Total	Examined	Infested	Total	Examined	Infested
Passeriformes	Artamidae	1	1	1	6	5	3
	Grallinidae	1	1	1	1	1	1
	Pachycephalidae	2	2	2	17	5	5
	Falcunculidae	3	3	2	6	3	2
	Turdidae	4	3	2	8	4	3
	Pycnonotidae	1	0	0	1	0	0
	Cracticidae	3	3	3	14	6	6
	Paridae	2	0	0	5	0	0
	Sittidae	1	1	1	6	3	1
	Certhiidae	1	1	1	9	3	1
	Zosteropidae	1	1	1	4	1	1
	Dicaeidae	2	2	1	9	5	1
	Nectariniidae	1	1	1	1	1	1
	Meliphagidae	23	13	11	69	25	21
	Motacillidae	2	2	2	2	2	2
	Alaudidae	2	1	1	2	1	1
	Fringillidae	4	4	4	5	5	5
	Ploceidae	13	10	5	23	12	5
	Sturnidae	3	3	3	3	3	3
	Oriolidae	2	2	2	4	4	4
	Dicruridae	1	1	1	1	1	1
	Paradiseidae	2	1	1	4	3	1
	Ptilonorhynchidae	6	4	2	10	6	2
	Corvidae	3	3	2	5	4	2

and eight one rhinonyssine and one speleognathine species (turbinoptines were never involved): *Tinaminyssus myristicivorae* and *T. welchi* from *Myristicivora spilorrhoa; Rhinonyssus minutus* and *Speleognathopsis benoiti* from *Charadrius melanops* (twice); *Ruandanyssus terpsiphonei* and *Ptilonyssus struthideae* from *Struthidea cinerea; Ruandanyssus terpsiphonei* and *Sternostoma cuculorum* from *Myiagra rubecula; Ptilonyssus triscutatus* and *Neoboydaia merops* from *Merops ornatus; Ptilonyssus dioptrornis* and *Sternostoma cuculorum* from *Eopsaltria capito; Ptilonyssus cractici* and *Sternostoma thienponti* from *Gymnorhina tibicen; Ptilonyssus terpsiphonei* and *Sternostoma cuculorum* from *Arses kaupi; Ptilonyssus monarchae* and *Sternostoma cuculorum* from *Monarcha trivirgata; Ptilonyssus ruandae* and *Sternostoma zosteropis* from *Zosterops lateralis; Ptilonyssus myzanthae* and *P. thymanzae* from *Myzantha melanocephala* (four times); *Ptilonyssus myzanthae* and *P. thymanzae* from *Myzantha flavigula; Ptilonyssus philemoni* and *Boydaia spatulata* from *Philemon corniculatus; Ptilonyssus gliciphilae* and *Boydaia spatulata* from *Myzomela pectoralis; Ptilonyssus lymozemae* and *Boydaia myzomelae* from *Myzomela sanguinolenta; Ptilonyssus cerchneis* and *Boydaia falconis* from *Falco berigora* (twice); and *Sternostoma dureni* and *S. technaui* from *Oreocincla lunulata.*

The complete host-parasite list occupies Table 4 below, in which the following typographical conventions have been used: (*i*) asterisks indicate birds known to occur in Australia as introductions or vagrants, but not listed in Leach (1958); (*ii*) scientific names of birds printed in roman rather than in italics indicate species not examined in the present survey; and (*iii*) scientific names of mites similarly printed indicate host-parasite relationships established overseas, but not yet noted in Australia.

TABLE 4

List of Australian birds examined and their recorded nasal mite parasites

	Casuariiformes	
	Dromaiidae	
Dromaius novaehollandiae (Latham)	Emu	
	Galliformes	
	Megapodiidae	
Megapodius freycinet Gaimard	Scrub-fowl	
Alectura lathami Gray	Brush-turkey	
	Phasianidae	
Gallus gallus (Linnaeus)*	Domestic fowl	Speleognathopsis galli Rhinoptes gallinae
Synoicus australis (Latham)	Brown quail	*Rhinoptes gallinae*
	Numididae	
Numida meleagris (Linnaeus)*	Guinea-fowl	Speleognathopsis galli Schoutedenocoptes numidae
	Turniciformes	
	Turnicidae	
Turnix varia (Latham)	Painted quail	
	Columbiformes	
	Columbidae	
Ptilinopus regina Swainson	Red-crowned pigeon	
Ptilinopus superbus (Temminck)	Purple-crowned pigeon	Tinaminyssus ptilinopi
Megaloprepia magnifica (Temminck)	Wompoo pigeon	*Tinaminyssus megaloprepiae*
Myristicivora spilorrhoa (Gray)	Torres Strait pigeon	*Tinaminyssus myristicivorae* *Tinaminyssus welchi*
Columba livia Gmelin*	Domestic pigeon	*Tinaminyssus melloi* Tinaminyssus columbae Ophthalmognathus striatus
Columba norfolciensis Latham	White-headed pigeon	*Tinaminyssus melloi*
Macropygia phasianella (Temminck)	Brown pigeon	*Tinaminyssus macropygiae*
Streptopelia chinensis (Scopoli)	Indian turtle-dove	*Tinaminyssus melloi*
Streptopelia senegalensis (Linnaeus)	Senegal dove	Tinaminyssus melloi
Geopelia placida Gould	Peaceful dove	*Tinaminyssus geopeliae*
Geopelia cuneata (Latham)	Diamond-dove	*Tinaminyssus geopeliae*
Geopelia humeralis (Temminck)	Bar-shouldered dove	*Tinaminyssus geopeliae*
Chalcophaps chrysochlora (Wagler)	Green-winged pigeon	*Tinaminyssus hirtus*
Phaps chalcoptera (Latham)	Common bronzewing	*Tinaminyssus phabus*
Geophaps scripta (Temminck)	Squatter-pigeon	*Tinaminyssus ocyphabus*
Ocyphaps lophotes (Temminck)	Crested pigeon	*Tinaminyssus ocyphabus* *Tinaminyssus columbae*
Leucosarcia melanoleuca (Latham)	Wonga pigeon	*Tinaminyssus melloi*
	Gruiformes	
	Rallidae	
Rallus pectoralis Temminck	Lewin water-rail	Rallinyssus gallinulae
Hypotaenidia philippensis (Linnaeus)	Banded landrail	*Rallinyssus gallinulae*
Porzana tabuensis (Gmelin)	Spotless crake	Rallinyssus congolensis
Poliolimnas cinereus (Vieillot)	White-browed crake	Rallinyssus amaurornis
Amaurornis ruficrissus (Gould)	Bushhen	
Gallinula tenebrosa Gould	Dusky moorhen	*Rallinyssus caudistigmus*
Porphyrio melanotus Temminck	Eastern swamphen	Rallinyssus gallinulae *Speleognathopsis porphyrionis*
Fulica atra Linnaeus	Coot	Rallinyssus caudistigmus Sternostoma fulicae
	Megalornithidae	
Grus rubicundus (Perry)	Brolga	

TABLE 4—*Continued*

List of Australian birds examined and their recorded nasal mite parasites—Continued

	Podicipiformes Podicipidae	
Podiceps ruficollis (Vroeg)	Little grebe	*Rhinonyssus poliocephali* *Neoboydaia colymbiformi*
	Sphenisciformes Spheniscidae	
Pygoscelis adeliae (Hombron and Jacquinot)*	Adélie penguin	Rhinonyssus sphenisci
	Charadriiformes Laridae	
Chlidonias hybrida (Pallas)	Whiskered tern	
Chlidonias leucoptera (Temminck)	White-winged black tern	Larinyssus orbicularis Sternostoma boydi
Gelochelidon nilotica (Gmelin)	Gull-billed tern	Larinyssus orbicularis
Sterna hirundo Linnaeus	Common tern	Larinyssus orbicularis
Sterna bergii Lichtenstein	Crested tern	*Larinyssus orbicularis*
Sterna fuscata Linnaeus	Sooty tern	Larinyssus orbicularis Sternostoma boydi
Larus novaehollandiae Stephens	Silver gull	*Turbinoptes strandtmanni*
Larus dominicanus Lichtenstein*	Southern black-backed gull	Larinyssus orbicularis
	Haematopodidae	
Haematopus ostralegus Linnaeus	Pied oystercatcher	
	Charadriidae	
Arenaria interpres (Linnaeus)	Turnstone	Rhinonyssus coniventris Sternostoma boydi
Erythrogonys cinctus Gould	Red-kneed dotterel	*Rhinonyssus himantopus* *Speleognathopsis benoiti*
Lobibyx novaehollandiae (Stephens)	Spur-winged plover	*Rhinonyssus himantopus*
Lobibyx miles (Boddaert)	Masked plover	*Rhinonyssus himantopus* *Speleognathopsis benoiti*
Zonifer tricolor (Vieillot)	Banded plover	
Squatarola squatarola (Linnaeus)	Grey plover	Rhinonyssus coniventris Speleognathopsis benoiti
Pluvialis dominicus (Müller)	Eastern golden plover	Rhinonyssus minutus Rhinonyssus coniventris
Charadrius alexandrinus Linnaeus	Red-capped dotterel	*Rhinonyssus minutus* *Rhinonyssus coniventris*
Charadrius melanops Vieillot	Black-fronted dotterel	*Rhinonyssus himantopus* *Speleognathopsis benoiti*
Charadrius hiaticula Linnaeus*	Ringed plover	Rhinonyssus minutus Rhinonyssus coniventris
	Recurvirostridae	
Himantopus leucocephalus Gould	White-headed stilt	*Rhinonyssus himantopus*
Recurvirostra novaehollandiae Vieillot	Red-necked avocet	
	Scolopacidae	
Numenius madagascarensis (Linnaeus)	Eastern curlew	*Turbinoptes strandtmanni*
Numenius phaeopus (Linnaeus)	Whimbrel	*Turbinoptes strandtmanni*
Mesoscolopax minutus (Gould)	Little whimbrel	
Limosa lapponica (Linnaeus)	Bar-tailed godwit	*Neoboydaia philomachi*
Limosa limosa (Linnaeus)	Black-tailed godwit	
Tringa hypoleuca Linnaeus	Common sandpiper	Sternostoma boydi Turbinoptes strandtmanni
Tringa brevipes (Vieillot)	Grey-tailed tattler	
Tringa glareola Linnaeus	Wood-sandpiper	Rhinonyssus coniventris Sternostoma boydi Neoboydaia philomachi
Tringa nebularia (Gunnerus)	Greenshank	*Rhinonyssus rhinolethrum* Sternostoma boydi

TABLE 4—*Continued*

List of Australian birds examined and their recorded nasal mite parasites—Continued

Crocethia alba (Vroeg)	Sanderling	Rhinonyssus coniventris Sternostoma boydi
Erolia ruficollis (Pallas)	Red-necked stint	*Rhinonyssus coniventris*
Erolia acuminata (Horsfield)	Sharp-tailed sandpiper	
Erolia melanotos (Vieillot)	American pectoral sandpiper	Neoboydaia philomachi
Erolia ferruginea (Brunnich)	Curlew-sandpiper	
Erolia alpina (Linnaeus)*	Dunlin	Rhinonyssus coniventris
Calidris canutus (Linnaeus)	Knot	Rhinonyssus coniventris Sternostoma boydi
Gallinago hardwickii (Gray)	Australian snipe	
Philomachus pugnax (Linnaeus)*	Ruff	Neoboydaia philomachi
	Jacanidae	
Irediparra gallinacea (Temminck)	Lotus-bird	
	Glareolidae	
Stiltia isabella (Vieillot)	Australian pratincole	*Larinyssus benoiti*
Glareola pratincola (Linnaeus)	Oriental pratincole	Larinyssus benoiti
	Burhinidae	
Burhinus magnirostris (Latham)	Southern stone-curlew	
	Otitidae	
Eupodotis australis (Gray)	Australian bustard	
	Ciconiiformes Threskiornithidae	
Threskiornis molucca (Cuvier)	Australian white ibis	
Threskiornis spinicollis (Jameson)	Straw-necked ibis	
Plegadis falcinellus (Linnaeus)	Glossy ibis	
Platalea regia Gould	Royal spoonbill	
Platalea flavipes Gould	Yellow-billed spoonbill	
	Ciconiidae	
Xenorhynchus asiaticus (Latham)	Jabiru	
	Ardeidae	
Egretta intermedia (Wagler)	Plumed egret	Tinaminyssus belopolskii
Egretta alba (Linnaeus)	White egret	
Egretta garzetta (Linnaeus)	Little egret	Tinaminyssus belopolskii
Bubulcus ibis (Linnaeus)*	Cattle egret	Tinaminyssus belopolskii
Notophoyx novaehollandiae (Latham)	White-faced heron	*Tinaminyssus belopolskii*
Notophoyx pacifica (Latham)	White-necked heron	
Notophoyx picata (Gould)	Pied heron	*Tinaminyssus belopolskii*
Demigretta sacra (Gmelin)	Reef-heron	
Nycticorax caledonicus (Gmelin)	Nankeen night heron	*Ophthalmognathus schoutedeni*
Butorides striata (Linnaeus)	Mangrove-heron	
Ixobrychus minutus (Linnaeus)	Little bittern	Tinaminyssus belopolskii
	Anseriformes Anatidae	
Anser anser (Linnaeus)*	Domestic goose	Rhinonyssus rhinolethrum
Anseranas semipalmata (Latham)	Pied goose	
Nettapus pulchellus Gould	Green pigmy goose	
Chenonetta jubata (Latham)	Maned goose	*Rhinonyssus rhinolethrum*
Dendrocygna arcuata (Horsfield)	Whistling tree-duck	*Rhinonyssus rhinolethrum*
Tadorna radjah (Garnot)	White-headed shelduck	
Anas superciliosa Gmelin	Black duck	Rhinonyssus rhinolethrum
Anas querquedula Linnaeus	Garganey teal	Rhinonyssus rhinolethrum
Anas gibberifrons (Müller)	Grey teal	*Rhinonyssus rhinolethrum*
Anas platyrhynchos Linnaeus*	Mallard	Rhinonyssus rhinolethrum
Aythya australis (Eyton)	Hardhead	

TABLE 4—*Continued*

List of Australian birds examined and their recorded nasal mite parasites—Continued

	Pelecaniformes Phalacrocoracidae	
Phalacrocorax sulcirostris (Brandt)	Little black cormorant	
Phalacrocorax varius (Gmelin)	Pied cormorant	
Phalacrocorax melanoleucus (Vieillot)	Little pied cormorant	
	Anhingidae	
Anhinga novaehollandiae (Gould)	Australian darter	
	Sulidae	
Sula dactylatra Lesson	Masked gannet	
	Pelecanidae	
Pelecanus conspicillatus Temminck	Australian pelican	
	Falconiformes Accipitridae	
Accipiter novaehollandiae (Gmelin)	Grey goshawk	
Accipiter fasciatus (Vigors and Horsfield)	Australian goshawk	*Ophthalmognathus accipitris*
Accipiter cirrocephalus (Vieillot)	Collared sparrow hawk	
Aquila audax (Latham)	Wedge-tailed eagle	
Haliaeetus leucogaster (Gmelin)	White-breasted sea-eagle	
Haliastur sphenurus (Vieillot)	Whistling eagle	
Milvus migrans (Boddaert)	Black kite	
Elanus notatus Gould	Australian black-shouldered kite	
Aviceda subcristata (Gould)	Crested hawk	Tinaminyssus epileus
	Falconidae	
Falco longipennis Swainson	Little falcon	
Falco berigora Vigors and Horsfield	Brown hawk	*Ptilonyssus cerchneis* *Boydaia falconis*
Falco cenchroides Vigors and Horsfield	Nankeen kestrel	*Ptilonyssus cerchneis*
	Strigiformes Strigidae	
Ninox novaeseelandiae (Gmelin)	Boobook owl	*Rhinoecius cooremani*
Ninox connivens (Latham)	Winking owl	
	Tytonidae	
Tyto alba (Scopoli)	Barn-owl	Rhinoecius tytonis Neoboydaia aureliani
Tyto novaehollandiae (Stephens)	Masked owl	
	Psittaciformes Psittacidae	
Agapornis roseicollis (Vieillot)*	Peach-faced lovebird	Neoboydaia psittaculae
Trichoglossus moluccanus (Gmelin)	Rainbow-lorikeet	*Tinaminyssus trichoglossi* *Neoboydaia psittaculae*
Trichoglossus chlorolepidotus (Kühl)	Scaly-breasted lorikeet	*Tinaminyssus trichoglossi*
Psitteuteles versicolor (Lear)	Varied lorikeet	*Neoboydaia psittaculae*
Glossopsitta pusilla (Shaw)	Little lorikeet	*Tinaminyssus trichoglossi*
Calyptorhynchus banksii (Latham)	Red-tailed black cockatoo	*Tinaminyssus kakatuae*
Kakatoe galerita (Latham)	White cockatoo	
Kakatoe roseicapilla (Vieillot)	Galah	*Tinaminyssus kakatuae*
Kakatoe sanguinea (Gould)	Little corella	
Leptolophus hollandicus (Kerr)	Cockatiel	*Tinaminyssus kakatuae*
Aprosmictus scapularis (Lichtenstein)	King-parrot	*Tinaminyssus aprosmicti*
Aprosmictus erythropterus (Gmelin)	Red-winged parrot	*Tinaminyssus aprosmicti*
Platycercus elegans (Gmelin)	Crimson rosella	
Platycercus adscitus (Latham)	Pale-headed rosella	*Tinaminyssus aprosmicti*
Platycercus eximius (Shaw)	Eastern rosella	

TABLE 4—*Continued*

List of Australian birds examined and their recorded nasal mite parasites—Continued

Barnardius barnardi (Vigors and Horsfield)	Ring-neck parrot	*Tinaminyssus aprosmicti*
Psephotus varius Clark	Mulga parrot	*Tinaminyssus aprosmicti*
Psephotus haematonotus (Gould)	Red-backed parrot	*Tinaminyssus aprosmicti*
Neophema pulchella (Shaw)	Turquoise parrot	
Melopsittacus undulatus (Shaw)	Budgerygah	Sternostoma tracheacolum
	Caprimulgiformes Podargidae	
Podargus strigoides (Latham)	Tawny frogmouth	*Oxleya podargi*
	Aegothelidae	
Aegotheles cristata (Shaw)	Owlet-nightjar	
	Caprimulgidae	
Caprimulgus macrurus Horsfield	Large-tailed nightjar	Ptilonyssus nitzschi
	Coraciiformes Coraciidae	
Eurystomus orientalis (Linnaeus)	Eastern broad-billed roller	*Mycteroptes basilewskyi*
	Alcedinidae	
Alcyone azurea (Latham)	Azure kingfisher	
Alcyone pusilla (Temminck)	Little kingfisher	
Dacelo gigas (Boddaert)	Laughing kookaburra	*Tinaminyssus daceloae* *Ptilonyssus cractici* *Sternostoma cooremani*
Dacelo leachii Vigors and Horsfield	Blue-winged kookaburra	*Tinaminyssus daceloae*
Halcyon pyrrhopygius Gould	Red-backed kingfisher	*Tinaminyssus halcyonus*
Halcyon sanctus Vigors and Horsfield	Sacred kingfisher	*Tinaminyssus halcyonus*
Halcyon macleayii Jardine and Selby	Forest kingfisher	*Tinaminyssus halcyonus*
Halcyon chloris (Boddaert)	Mangrove-kingfisher	Tinaminyssus halcyonus Sternostoma cooremani
	Meropidae	
Merops ornatus Latham	Rainbow-bird	*Ptilonyssus triscutatus* *Sternostoma cooremani* *Neoboydaia merops*
	Cuculiformes Cuculidae	
Cuculus saturatus Blyth	Oriental cuckoo	
Cacomantis pyrrhophanus (Vieillot)	Fan-tailed cuckoo	*Sternostoma cuculorum*
Cacomantis variolosus (Vigors and Horsfield)	Brush cuckoo	*Sternostoma cuculorum*
Chalcites basalis (Horsfield)	Horsfield bronze-cuckoo	
Chalcites plagosus (Latham)	Golden bronze-cuckoo	
Scythrops novaehollandiae Latham	Channel-billed cuckoo	
Eudynamys orientalis (Linnaeus)	Koel	*Sternostoma cuculorum*
Centropus phasianinus (Latham)	Pheasant-coucal	
	Passeriformes Pittidae	
Pitta versicolor Swainson	Noisy pitta	*Ptilonyssus pittae*
	Hirundinidae	
Hirundo neoxena Gould	Welcome swallow	*Ptilonyssus angrensis* *Ptilonyssus echinatus* *Boydaia hirundoae*
Hirundo rustica Linnaeus*	Common swallow	Ptilonyssus emberizae Ptilonyssus echinatus Ptilonyssus langei Sternostoma tracheacolum Boydaia hirundoae

TABLE 4—*Continued*

List of Australian birds examined and their recorded nasal mite parasites—Continued

Cheramoeca leucosterna (Gould)	White-backed swallow	
Hylochelidon nigricans (Vieillot)	Tree-martin	*Ptilonyssus echinatus*
Hylochelidon ariel (Gould)	Fairy martin	*Boydaia hirundoae*
	Muscicapidae	
Microeca fascinans (Latham)	Jacky winter	*Ptilonyssus microecae*
Microeca flavigaster Gould	Lemon-breasted flycatcher	*Ptilonyssus microecae*
Petroica rosea Gould	Rose-robin	*Ptilonyssus motacillae*
Petroica goodenovii (Vigors and Horsfield)	Red-capped robin	
Melanodryas cucullata (Latham)	Hooded robin	
Rhipidura fuliginosa (Sparrman)	Grey fantail	*Ptilonyssus rhipidurae*
Rhipidura setosa (Quoy and Gaimard)	Northern fantail	*Ptilonyssus setosae*
Rhipidura rufifrons (Latham)	Rufous fantail	*Ptilonyssus setosae*
Rhipidura leucophrys (Latham)	Willie wagtail	*Ptilonyssus macclurei* *Sternostoma cuculorum*
Myiagra rubecula (Latham)	Leaden flycatcher	*Ruandanyssus terpsiphonei* *Ptilonyssus terpsiphonei* *Sternostoma cuculorum*
Seisura inquieta (Latham)	Restless flycatcher	*Ptilonyssus terpsiphonei*
Arses kaupi Gould	Australian pied flycatcher	*Ptilonyssus terpsiphonei* *Sternostoma cuculorum*
Piezorhynchus alecto (Temminck)	Shining flycatcher	*Ptilonyssus terpsiphonei*
Monarcha melanopsis (Vieillot)	Black-faced flycatcher	*Ptilonyssus terpsiphonei*
Monarcha trivirgata (Temminck)	Spectacled flycatcher	*Ruandanyssus terpsiphonei* *Ptilonyssus terpsiphonei* *Ptilonyssus monarchae* *Sternostoma cuculorum*
Carterornis leucotis (Gould)	White-eared flycatcher	*Ptilonyssus terpsiphonei*
Eopsaltria capito Gould	Pale-yellow robin	*Ptilonyssus dioptrornis* *Sternostoma cuculorum*
Eopsaltria chrysorrhoa Gould	Northern yellow robin	
	Campophagidae	
Pteropodocys maxima (Rüppell)	Ground cuckoo-shrike	
Coracina novaehollandiae (Gmelin)	Black-faced cuckoo-shrike	*Ruandanyssus terpsiphonei*
Coracina hypoleuca (Gould)	White - breasted cuckoo - shrike	
Coracina papuensis (Gmelin)	Papuan cuckoo-shrike	
Coracina lineata (Swainson)	Barred cuckoo-shrike	
Coracina robusta (Latham)	Little cuckoo-shrike	*Ruandanyssus terpsiphonei*
Edoliisoma tenuirostre (Jardine)	Jardine caterpillar-eater	
Lalage tricolor (Swainson)	White-winged triller	*Ruandanyssus terpsiphonei* *Ptilonyssus cractici* *Boydaia crassipes*
Lalage leucomela (Vigors and Horsfield)	Varied triller	
	Timaliidae	
Orthonyx temminckii Ranzani	Southern chowchilla	*Ptilonyssus orthonychus*
Pomatostomus temporalis (Vigors and Horsfield)	Grey-crowned babbler	*Passerrhinoptes pomatostomi*
	Sylviidae	
Smicrornis brevirostris (Gould)	Brown weebill	
Smicrornis flavescens Gould	Yellow weebill	
Gerygone olivacea (Gould)	White-throated warbler	
Gerygone fusca (Gould)	Western warbler	
Gerygone richmondii (Mathews)	Brown warbler	
Gerygone mouki Mathews	Northern warbler	
Gerygone palpebrosa Wallace	Black-throated warbler	*Ptilonyssus gerygonae*
Cinclorhamphus mathewsi Iredale	Rufous songlark	*Ptilonyssus bradypteri*
Acrocephalus australis (Gould)	Australian reed-warbler	*Ptilonyssus acrocephali* Sternostoma tracheacolum
Cisticola exilis (Vigors and Horsfield)	Fantail-warbler	
Chthonicola sagittata (Latham)	Speckled warbler	

TABLE 4—*Continued*

List of Australian birds examined and their recorded nasal mite parasites—Continued

Acanthiza pusilla (Shaw)	Brown thornbill	
Acanthiza uropygialis Gould	Chestnut-tailed thornbill	
Acanthiza chrysorrhoa (Quoy and Gaimard)	Yellow-tailed thornbill	
Acanthiza reguloides Vigors and Horsfield	Buff-tailed thornbill	
Sericornis lathami (Stephens)	Yellow-throated scrub-wren	
Sericornis frontalis (Vigors and Horsfield)	White-browed scrub-wren	*Ruandanyssus terpsiphonei*
Sericornis magnirostris (Gould)	Large-billed scrub-wren	
Malurus melanotus Gould	Black-backed blue wren	
Malurus lamberti Vigors and Horsfield	Variegated wren	
Malurus amabilis Gould	Lovely wren	*Boydaia maluri*
Malurus melanocephalus (Latham)	Red-backed wren	*Ptilonyssus maluri* *Boydaia maluri*
	Artamidae	
Artamus superciliosus (Gould)	White-browed wood-swallow	
Artamus personatus (Gould)	Masked wood-swallow	*Ruandanyssus terpsiphonei*
Artamus cyanopterus (Latham)	Dusky wood-swallow	
Artamus cinereus Gould	Black-faced wood-swallow	*Ruandanyssus artami*
Artamus minor Vieillot	Little wood-swallow	*Ruandanyssus artami*
	Grallinidae	
Grallina cyanoleuca (Latham)	Magpie-lark	*Ptilonyssus grallinae*
	Pachycephalidae	
Colluricincla harmonica (Latham)	Grey shrike-thrush	*Ptilonyssus colluricinclae*
Colluricincla megarhyncha (Quoy and Gaimard)	Rufous shrike-thrush	*Ptilonyssus colluricinclae* *Sternostoma cuculorum*
Pachycephala pectoralis (Latham)	Golden whistler	*Ruandanyssus terpsiphonei* *Ptilonyssus colluricinclae*
Pachycephala rufiventris (Latham)	Rufous whistler	*Ruandanyssus terpsiphonei* *Ptilonyssus motacillae*
Pachycephala griseiceps Gray	Grey whistler	*Ruandanyssus terpsiphonei* *Ptilonyssus colluricinclae*
	Falcunculidae	
Psophodes olivaceus (Latham)	Eastern whipbird	*Ptilonyssus psophodae*
Falcunculus frontatus (Latham)	Eastern shrike-tit	
Oreoica gutturalis (Vigors and Horsfield)	Crested bellbird	*Sternostoma cuculorum*
	Turdidae	
Turdus merula Linnaeus	Blackbird	Sternostoma technaui
Turdus philomelos Brehm	Song-thrush	Sternostoma technaui
Oreocincla lunulata (Latham)	Australian ground-thrush	*Sternostoma dureni* *Sternostoma technaui*
Epthianura tricolor Gould	Crimson chat	
	Cracticidae	
Gymnorhina tibicen (Latham)	Black-backed magpie	*Ptilonyssus cractici* *Sternostoma thienponti*
Cracticus nigrogularis (Gould)	Pied butcher-bird	*Ptilonyssus cractici* *Sternostoma thienponti*
Cracticus torquatus (Latham)	Grey butcher-bird	*Ptilonyssus cractici*
Cracticus quoyi (Lesson and Garnot)	Black butcher-bird	*Sternostoma thienponti*
Cracticus mentalis Salvadori and d'Albertis	Black-backed butcher-bird	*Ptilonyssus cractici*
Strepera graculina (Shaw)	Pied currawong	*Ptilonyssus cractici*
	Sittidae	
Neositta chrysoptera (Latham)	Orange-winged sittella	
Neositta leucocephala (Gould)	White-headed sittella	
Neositta striata (Gould)	Striated sittella	*Sternostoma neosittae*

TABLE 4—*Continued*

List of Australian birds examined and their recorded nasal mite parasites—Continued

	Certhiidae	
Climacteris picumnus Temminck	Brown tree-creeper	*Ptilonyssus sittae*
Climacteris melanota Gould	Black tree-creeper	
Climacteris leucophaea (Latham)	White-throated tree-creeper	
	Zosteropidae	
Zosterops lateralis (Latham)	Grey-backed silvereye	*Ptilonyssus ruandae* *Sternostoma cuculorum* *Boydaia zosteropis*
	Dicaeidae	
Dicaeum hirundinaceum (Shaw)	Mistletoe-bird	*Ptilonyssus dicaei*
Pardalotus ornatus (Gmelin)	Red-tipped pardalote	
Pardalotus punctatus (Shaw)	Spotted pardalote	
Pardalotus rubricatus Gould	Red-browed pardalote	
Pardalotus melanocephalus Gould	Black-headed pardalote	
	Nectariniidae	
Cyrtostomus frenatus (Müller)	Yellow-breasted sunbird	*Ptilonyssus cinnyris* Sternostoma tracheacolum
	Meliphagidae	
Melithreptus albogularis Gould	White-throated honeyeater	*Ptilonyssus meliphagae*
Plectorhyncha lanceolata Gould	Striped honeyeater	*Ptilonyssus philemoni*
Myzomela sanguinolenta (Latham)	Scarlet honeyeater	*Ptilonyssus myzomelae* *Ptilonyssus lymozemae* *Boydaia myzomelae*
Myzomela pectoralis Gould	Banded honeyeater	*Ptilonyssus gliciphilae* *Boydaia spatulata*
Myzomela obscura Gould	Dusky honeyeater	*Ptilonyssus myzomelae*
Acanthorhynchus tenuirostris (Latham)	Eastern spinebill	
Gliciphila fasciata Gould	White-breasted honeyeater	
Gliciphila indistincta (Vigors and Horsfield)	Brown honeyeater	*Ptilonyssus gliciphilae* *Sternostoma gliciphilae*
Conopophila albogularis (Gould)	Rufous-banded honeyeater	
Meliphaga fusca Gould	Fuscous honeyeater	
Meliphaga lewinii Swainson	Lewin honeyeater	*Ptilonyssus thymanzae*
Meliphaga notata (Gould)	Lesser Lewin honeyeater	*Ptilonyssus philemoni* *Ptilonyssus thymanzae*
Meliphaga gracilis (Gould)	Graceful honeyeater	*Ptilonyssus philemoni*
Meliphaga chrysops (Latham)	Yellow-faced honeyeater	*Ptilonyssus thymanzae* *Ptilonyssus meliphagae*
Meliphaga macleayana (Ramsay)	Macleay honeyeater	*Ptilonyssus balimoensis*
Meliphaga penicillata Gould	White-plumed honeyeater	*Ptilonyssus thymanzae*
Meliphaga flava (Gould)	Yellow honeyeater	*Ptilonyssus stomioperae*
Stomiopera unicolor (Gould)	White-gaped honeyeater	*Ptilonyssus stomioperae*
Myzantha melanocephala (Latham)	Noisy miner	*Ptilonyssus myzanthae* *Ptilonyssus thymanzae*
Myzantha flavigula (Gould)	Yellow-throated miner	*Ptilonyssus myzanthae* *Ptilonyssus thymanzae*
Anthochaera chrysoptera (Latham)	Little wattle-bird	*Ptilonyssus myzanthae* *Ptilonyssus thymanzae*
Acanthagenys rufogularis Gould	Spiny-cheeked honeyeater	*Ptilonyssus thymanzae*
Entomyzon cyanotis (Latham)	Blue-faced honeyeater	*Ptilonyssus philemoni*
Philemon corniculatus (Latham)	Noisy friar-bird	*Ptilonyssus philemoni* *Boydaia spatulata*
Philemon citreogularis (Gould)	Little friar-bird	*Ptilonyssus philemoni* *Boydaia spatulata*
	Motacillidae	
Anthus australis Vieillot	Australian pipit	*Ptilonyssus motacillae*
Motacilla flava Linnaeus*	Yellow wagtail	Ptilonyssus motacillae Boydaia crassipes
	Alaudidae	
Mirafra javanica Horsfield	Horsfield bushlark	*Ptilonyssus capitatus*

TABLE 4—*Continued*

List of Australian birds examined and their recorded nasal mite parasites—Continued

	Fringillidae	
Chloris chloris (Linnaeus)	Greenfinch	Ptilonyssus carduelis
Carduelis carduelis (Linnaeus)	Goldfinch	Ptilonyssus pygmaeus Ptilonyssus motacillae Sternostoma tracheacolum Boydaia crassipes
Passer montanus (Linnaeus)	Tree-sparrow	Ptilonyssus nudus
Passer domesticus (Linnaeus)	House-sparrow	*Ptilonyssus hirsti* Ptilonyssus nudus Sternostoma tracheacolum Sternostoma cryptorhynchum Boydaia crassipes
Serinus canaria (Linnaeus)*	Canary	Sternostoma tracheacolum
	Ploceidae	
Taeniopygia castanotis (Gould)	Zebra finch	*Ptilonyssus motacillae*
Steganopleura bichenovii (Vigors and Horsfield)	Banded finch	
Donacola castaneothorax (Gould)	Chestnut-breasted finch	
Aidemosyne modesta (Gould)	Plum-headed finch	
Aegintha temporalis (Latham)	Red-browed firetail	
Bathilda ruficauda (Gould)	Star finch	
Neochmia phaeton (Hombron and Jacquinot)	Crimson finch	*Ptilonyssus neochmiae*
Poephila atropygialis Diggles	Black-tailed finch	
Poephila personata Gould	Masked finch	
Poephila gouldiae (Gould)	Gouldian finch	Ptilonyssus emberizae *Sternostoma tracheacolum*
Lonchura punctulata (Linnaeus)*	Spice finch	*Ptilonyssus motacillae*
Padda oryzivora (Linnaeus)*	Java sparrow	Sternostoma paddae
	Sturnidae	
Sturnus vulgaris Linnaeus	Starling	Ptilonyssus elbeli *Boydaia sturni*
Acridotheres tristis (Linnaeus)	Common myna	Ptilonyssus elbeli Ptilonyssus motacillae Boydaia sturni
Aplonis metallica (Temminck)	Australian shining starling	*Ptilonyssus sturnopastoris*
	Oriolidae	
Oriolus sagittatus (Latham)	Olive-backed oriole	*Ptilonyssus trouessarti*
Oriolus flavocinctus (King)	Yellow oriole	*Ptilonyssus trouessarti*
Sphecotheres vieillotii Vigors and Horsfield	Southern figbird	*Ptilonyssus sphecotheris*
Sphecotheres flaviventris Gould	Yellow figbird	*Ptilonyssus sphecotheris*
	Dicruridae	
Chibia bracteata (Gould)	Spangled drongo	*Ptilonyssus dicruri* Sternostoma thienponti
	Paradiseidae	
Ptiloris paradiseus Swainson	Paradise rifle-bird	
Ptiloris victoriae Gould	Victoria rifle-bird	
Ptiloris magnificus (Vieillot)	Magnificent rifle-bird	Ptilonyssus novaeguineae
	Ptilonorhynchidae	
Ptilonorhynchus violaceus (Vieillot)	Satin bower-bird	
Ailuroedus crassirostris (Paykull)	Green catbird	*Ptilonyssus ailuroedi*
Ailuroedus melanotus (Gray)	Spotted catbird	
Chlamydera maculata (Gould)	Spotted bower-bird	
Chlamydera nuchalis (Jardine and Selby)	Great bower-bird	*Ptilonyssus sphecotheris*
Sericulus chrysocephalus (Lewin)	Regent bower-bird	
	Corvidae	
Corvus coronoides Vigors and Horsfield	Australian raven	
Corvus cecilae Mathews	Australian crow	
Struthidea cinerea Gould	Apostle-bird	*Ruandanyssus terpsiphonei* *Ptilonyssus struthideae*
Corcorax melanorhamphus (Vieillot)	White-winged chough	*Ptilonyssus corcoracis*

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ADDENDA

Recent visits to Kowanyama have necessitated the following changes to the list of birds recorded there by Standfast (1965) and Domrow (1967*a*). Delete *Dupetor flavicollis* and *Ptilonorhynchus violaceus* as misidentifications of *Nycticorax caledonicus* (juvenile) and *Eudynamys orientalis*, respectively. Add *Tringa nebularia* (D), *Gallinago hardwickii* (W), *Hamirostra melanosterna* (D), *Acrocephalus australis* (W), and *Anthus australis* (D). *Alectura lathami* and *Porphyrio melanotus* are confirmed as occurring in the area, where 139 species of birds are now known.

Two recent papers by Sakakibara should be noted (1968, *J. med. Ent.*, 5: 298–309; 1968, *Acarologia*, 10: 426–431). His description of the exact nature of the dorsal shields of *Ptilonyssus novaeguineae* (Hirst), which is keyed out above on the assumption that it possesses only the podonotal and pygidial shields typical of the vast majority of species, allows its more exact placement in couplet 12, which includes *P. triscutatus* (Vitzthum) and *P. sittae* Fain. It is immediately separable by the shape and proportions of its three dorsal shields and the nature of the leg setation.

I would place *P. paradisaeus* Sakakibara as a synonym of *P. novaeguineae*—the minor setational differences alleged are essentially in characters prone to considerable variation in this group, and both are from paradiseids (Sakakibara lists grackles, Icteridae, among the hosts, but this neotropical family does not occur in New Guinea—this recalls Womersley and Audy's caution (1957, *Stud. Inst. med. Res. F.M.S.*, 28: 231–296) on the tendency for the laconic "rat" and "mouse" on field labels later to be interpreted as "*Rattus*" and "*Mus*".

Likewise, I would place *P. trouessarti pseudotrouessarti* Sakakibara as a synonym of *P. trouessarti* (Hirst). Sakakibara also recognizes *P. orioli* Fain, but his illustration of a paratype is at variance with Fain's, and until the holotypes are compared, I maintain *P. orioli* under the synonymy of *P. trouessarti*. Oriolids figure largely among the hosts of these taxa.

Two other species discussed above (*P. terpsiphonei* Fain and *P. estrildicola* Fain) are also recorded from New Guinea.

P. missimensis Sakakibara is the form of *P. philemoni* Domrow described and figured above from *Meliphaga* spp., and is accordingly synonymized under that species.—March 5, 1969.

Messrs. E. T. Bulfin, A. L. Dyce, H. A. S., and R. D. collected these novelties (not entered in Tables) at Kowanyama in April 1969:

Rhinonyssus coniventris, 4 ♀ ♀, 1 ♂, *Erolia ruficollis* (the variety described with ♂ differing from ♀ only in primary sexual characters).

Rhinoecius cooremani, 3 ♀ ♀, *Ninox connivens* (deep in nares).*

Ptilonyssus neochmiae, 1 ♀, *Neochmia albiventer* Mathews.*†‡

Ptilonyssus echinatus, 1 ♀, *Hylochelidon ariel* (pygidial shields small, well separated).*‡

Neoboydaia psittaculae, 1 ♀, *Aprosmictus erythropterus* (differs from Fain's chaetotaxy in showing femora 4.3.2.3; specimen from *Trichoglossus* shows femora 4/3.2.2.2 and tibiae 5.3.2.3; specimen from *Psitteuteles* shows tibiae 4.2.2.2).*

G. et sp. indet. (Speleognathinae), 1 ♀, *Turnix velox* (Gould).*†‡

Mycteroptes basilewskyi, 4 ♀ ♀, *Eurystomus orientalis* (* represents new host record, † bird new to Table 4, and ‡ bird new to Kowanyama).

Additional species clearly sighted by R. D. at Kowanyama are *Numenius phaeopus, Erolia ferruginea, Ardea sumatrana* Raffles, *Dupetor flavicollis* (Latham), *Tyto alba,* and *Artamus minor,* making a total of 148.

Finally, *Sternostoma tracheacolum* caused respiratory symptoms in aviary-bred *Serinus canaria,* Burnie, Tas., iv. 1969, R. W. Mason and A. Little.

Sternostoma borceanum Feider and Mironescu, 1968, *Anal. stiint. Univ. Al. I. Cuza,* 14: 105, from various European turdids, is an obvious synonym of *S. technaui.*—May 27, 1969.

Index of Families, Genera, and Species of Mites Discussed

(Accepted names in italics; synonyms in roman, with original termination)

Plate xxx

Fig. 1. Rain-forest (3,000 ft.) with Wilson's Peak in background.
Fig. 2. Tropical woodland along Cressbrook Ck., near Esk.

Plate XXXI

Fig. 1. Semi-arid vegetation and sand dune near Windorah.

Fig. 2. Protected beach flats at low tide, Tin Can Bay.

TYPE SPECIMENS IN THE MACLEAY MUSEUM, UNIVERSITY OF SYDNEY

II. AMPHIBIANS AND REPTILES

JUDY GOLDMAN, L. HILL and P. J. STANBURY
School of Biological Sciences, University of Sydney

[Read 30th October, 1968]

Synopsis

The existing amphibian and reptilian type specimens in the Macleay Museum are listed by families in current phylogenetic order.

INTRODUCTION

The Macleay Museum at the University of Sydney contains a comprehensive zoological collection including a number of Australian type specimens. Lists of insect types (Hahn, 1962) and fish types (Stanbury, 1968) have been published. Further lists are being compiled. This paper lists the existing amphibian and reptilian type specimens in the Macleay Museum and their current taxonomic status. In all 7 amphibian and 58 reptilian types are catalogued.

The majority of the amphibian and reptilian types were collected on the "Chevert" expedition led by William Macleay to coastal north Queensland, Torres Straits and the southern coast of New Guinea in 1875 (Macmillan, 1957). All these were named and described by Macleay (1877*a*, *b*, *c*, *d*). Other type material was collected for Macleay by collectors in Australia, but since his death few types have been lodged in the Museum.

Several Macleay types appear to have been lost. The Museum has had a varied history (Anderson, 1965) with changes in location during which some specimens were presumably misplaced. In addition there have been periods without adequate curatorship when some types, particularly the geckos, dried out. As a result, some of the species described by Macleay have had to be ignored in subsequent taxonomic studies, particularly as his original descriptions now seem inadequate to define the species.

The types are stored in glass jars in 70% alcohol. The Macleay Museum Register numbers (R numbers) were entered in 1965 by the previous curator, Mrs. J. Anderson. These numbers were combined with the numbers given to some, but not all, specimens by S. J. Copland in 1945. Copland numbers have been given the prefix MR and where applicable they appear after the present R numbers in the list of type specimens.

AMPHIBIAN TYPES

From the collection of the "Chevert" expedition, Macleay (1877*d*) described five new species of frogs, of which two are lodged in the Macleay Museum, two in the Queensland Museum, and one, *Litoria dorsalis*, appears to have been lost. Neither Boulenger (1882) nor Fry (1913) were able to classify this species on the basis of Macleay's description. Apart from Macleay's specimens, five other amphibian types are lodged in the Museum.

REPTILIAN TYPES

ORDER SQUAMATA

Fam. *Scincidae.* Of the 19 scincid type specimens in the Museum, the majority were collected on the "Chevert" expedition (Macleay 1877*b*), and many still stand as holotypes. However, some of the material could not be identified further than genus and status of such specimens is doubtful. Three species described by Macleay could not be located in the collection. The missing types are *Heteropus bicarinatus* (1877*b*), *Tetradactylus guttulatus* (1885) and *Hinulia picta* (1885). Of these, the first is of the most importance, as it stands as the holotype of *Leiolopisma bicarinata* (Macleay) (see Loveridge, 1934). *Tetradactylus guttulatus* was ascribed to the genus *Lygosoma* by Boulenger (1887), and *Hinulia picta* was synonymized with *Tiliqua gerrardii* (Gray) by Mitchell (1950).

Fam. *Gekkonidae.* The gekkonid series in the Museum includes 10 types described by Macleay (1877*c*), only one of which, *Peripia dubia,* is missing. These types were examined in detail by Kluge (1963), who clarified their systematic status as follows:

Diplodactylus annulatus = ? *Phyllodactylus annulatus* (Macleay) R487–488
Peripia papuensis = *Hemidactylus frenatus* Dumeril and Bibron R480–481
Peripia ornata = *Lepidodactylus lugubris* (Dumeril and Bibron) R484–485
Peripia longicaudis = *Gehyra variegata* (Dumeril and Bibron) R482
Peripia dubia *Gehyra variegata* (Dumeril and Bibron) Not present
Peripia marmorata = *Gehyra baliola* (Dumeril) R477
Peripia brevicaudis = *Gehyra baliola* (Dumeril) R475
Heteronota fasciata = *Cyrtodactylus pelagicus* (Girard) R176
Heteronota marmorata = *Cyrtodactylus pelagicus* (Girard) R178, 181–183
Heteronota eboracensis = *Cyrtodactylus pelagicus* (Girard) R207.

Fam. *Agamidae.* Five new agamid species were described by Macleay (1877*c,* 1883), but only three types are still present in the Museum. Of the two missing, one, *Grammatophora jugularis* (1877*c*), cannot be placed further than the genus *Amphibolurus* (Boulenger 1885), and the other, *Tiaris longii* (1877*c*), has been placed in synonomy with *Gonyocephalus godeffroyi* (Boulenger 1885).

ORDER SERPENTES

Fam. *Colubridae.* Nine new colubrid snakes were collected on the "Chevert" expedition (Macleay 1877*a*) and are all present in the Museum today. Six additional species described by Macleay (1875, 1877*e*, 1883, 1884, 1888) are also listed. However, three of Macleay's types are missing; viz. *Tropidonotus ater* (1885), *Fordonia variabilis* (1877*e*) and *Dendrophis olivacea* (1877*e*).

Fam. *Elapidae.* Two new species of elapids were collected on the "Chevert" expedition (Macleay 1877*a*). An additional eight type species (Macleay 1878, 1884, 1885, 1887, 1888) are present in the Museum.

LIST OF TYPES

The types are listed by families in current phylogenetic order.

An asterisk in the locality column indicates that the specimen(s) was collected on the "Chevert" expedition.

References are given for the scientific name under which a type was originally described and for the present name.

AMPHIBIA Family	Name under which Described and Reference Proc. Linn. Soc. N.S.W.	Present Names and Reference	Type of Type, No. and Condition	Locality	M.M. Reg. No.
Leptodactylidae	*Philocryphus flavoguttatus* Fletcher, 1894. 8 : 233	*Heleiporus australiacus* (Shaw) Moore, 1961. Bull. Am. Mus. Nat. Hist., 121 : 179	Lectotype, 1 male, fair condition	Mt. Victoria, Blue Mountains. New South Wales	R49
			Allotype, 1 female, fair condition	Thornleigh, Sydney, New South Wales	R50
	Notes : Moore (p. 183) : " I have never found a reference to the existence of the type *Rana australiaca* ", and it is therefore suggested that Fletcher's specimens stand as lectotype (R49) and allotype (R50)				
	Phanerotis fletcheri Boulenger, 1890. 5 : 593	*Lechroidus fletcheri* (Boulenger) Loveridge, 1935. Bull. Mus. Comp. Zool., 78 : 22	Cotype 1, good condition	Dunoon, Richmond River, New South Wales	R57
	Notes : Collected Fletcher				
	Ranaster convexiusculus Macleay, 1877. 2 : 136	*Limnodynastes convexiusculus* (Macleay) Moore, 1961. Bull. Am. Mus. Nat. Hist., 121 : 354	Not present 1968	Katow (Binaturi River), New Guinea *	
	Notes : Moore (p. 354) : Holotype in Queensland Museum				
Hylidae	*Litoria guttata* Macleay, 1877. 2 : 137	*Hyla infrafrenata infrafrenata* Gunther Loveridge, 1948. Bull. Mus. Comp. Zool., 101 : 402	Type 1, poor condition	Katow (Binaturi River), New Guinea *	R145
Microhylidae	*Hylophorbus rufescens* Macleay, 1877. 2 : 136	*Asterophrys rufescens* (Macleay) Loveridge. 1948. Bull. Mus. Comp. Zool. 101 : 416	Type 1, poor condition	Katow (Binaturi River), New Guinea *	R144
	Austrochaperina robusta Fry, 1912. Rec. Aust. Mus. p : 93	*Sphenophryne robusta* (Fry) Moore, 1961. Bull. Am. Mus. Nat. Hist., 121 : 333	Cotypes 6, good condition	Russell River, N. Queensland	R53
	Notes : Holotype in Australian Museum				
	Austrochaperina ornata Fry, 1912. Rec. Aust. Mus., 9 : 91	*Cophixalus ornatus* (Fry) Loveridge, 1935. Bull. Mus. Comp. Zool., 78 : 55	Cotype 1, fair condition	Russell River, N. Queensland	R54
	Notes : Holotype in Australian Museum				

Family	Name under which Described and Reference Proc. Linn. Soc. N.S.W.	Present Names and Reference	Type of Type, No. and Condition	Locality	M.M. Reg. No.
Microhylidae	*Chaperina punctata* van Kampen, 1913. Nova Guinea. 9 : 643	*Sphenophryne macrorhyncha* (van Kampen) Loveridge, 1948. Bull. Mus. Comp. Zool., 101 : 421	Cotype 1, fair condition	Went Range, Dutch New Guinea 1050 m.	R56
	Notes : Collected on Dutch New Guinea expedition, October, 1909. This specimen was forwarded from the curators of the Amsterdam Museum in 1914				
Ranidae	*Hylarana nebulosa* Macleay, 1877. 2 : 137	*Rana daemeli* (Steindachner) Loveridge, 1948. Bull. Mus. Comp. Zool., 101 : 410	Not present, 1968	Cape York, N. Queensland	
	Notes : Moore (1961, p. 345) : Holotype in the Queensland Museum				
REPTILIA Scincidae	*Hinulia pardalis* Macleay, 1877. 2 : 63	*Sphenomorphus pardalis pardalis* (Macleay) Copland, 1945. Proc. Linn. Soc. N.S.W., 70 : 292	Type 1, fair condition	Barrow Island, N.E. Australia *	R93, MR21
	Notes : Copland gives a detailed redescription of this type, and discusses the distribution of the species and its taxonomic relationships				
	Mocoa nigricaudis Macleay, 1877. 2 : 63	*Sphenomorphus nigricaudis nigricaudis* (Macleay) Copland, 1945. Proc. Linn. Soc. N.S.W., 70 : 299	Type series 5, fair to good condition	Darnley Island, Torres Straits *	R74, MR376–380
	Notes : Copland (1945) has redescribed Macleay material, and selected MR378 as the lectotype and MR376, 377, 379 and 380 as paratypes				
	Hinulia spaldingi Macleay, 1877. 2 : 63	*Sphenomorphus spaldingi* (Macleay) Loveridge, 1934. Bull. Mus. Comp. Zool., 77 : 346	Type series 4, good condition	Endeavour River, N. Queensland *	R82, MR418–421
	Notes : Boulenger (1887, p. 225) synonymized this species with *Lygosoma* (*Hinulia*) *lesuerii* Gray, although it obviously fits his description of the closely related species *Lygosoma* (*Hinulia*) *dorsale* Boulenger (p. 226). Loveridge (1934) placed Macleay's *Hinulia spaldingi* and *Lygosoma dorsale* Boulenger in synonymy as *Sphenomorphus spaldingi* (Macleay). Copland (1946) in his description of the Macleay specimens, selected MR419 as a lectotype and 418, 420, 421 as paratypes				
	Hinulia papuensis Macleay, 1877. 2 : 62	*Sphenomorphus megaspila papuensis* (Macleay) Loveridge, 1948. Bull. Mus. Comp. Zool., 101 : 346	Type 1, good condition	Katow (Binaturi River), New Guinea *	R66, MR383
	Notes : Boulenger (1887, p. 247) places this species as a ? synonym of *Lygosoma* (*Hinulia*) *jobiensis* Meyer. It fits Boulenger's description closely with the exception of the presence of 6 supraoculars against 5 in *L. jobiensis*. Boulenger also synonymizes *Hinulia megaspila* Gunther into *L. jobiensis* but Loveridge removes the former to the genus *Lygosoma* (*Sphenomorphus*) *megaspila megaspila* (Gunther) and places Macleay's *H. papuensis* as a second subspecies. Advancing the subgenus *Sphenomorphus* to generic level, the species now stands as *Sphenomorphus megaspilus papuensis* (Macleay)				

Family	Name under which Described and Reference Proc. Linn. Soc. N.S.W.	Present Names and Reference	Type of Type, No. and Condition	Locality	M.M. Reg. No.
Scincidae	*Lygosoma ornatum* Macleay, 1877. 2 : 64	? *Sphenomorphus crassicaudus* (A. Dumeril) Boulenger, 1887. Cat. Liz. Brit. Mus., 3 : 325	Type 1, good condition	Endeavour River, N. Queensland *	R1012, MR367
	Notes :	This species agreed with Boulenger's description of *Lygosoma* (*Homolepida*) *crassicauda* A. Dumeril. Loveridge (1934, p. 307) discusses *Omolepida crassicaudum* (A. Dumeril) (with no mention of Macleay's *Lygosoma ornatum*), then in 1948 (p. 318) he lists it as *Lygosoma* (*Lygosoma*) *crassicauda* A. Dumeril. Mittleman (1952) lists the species as *Sphenomorphus crassicaudus* (A. Dumeril) but since both the last two papers do no more than list this species, it can only be suggested that *Lygosoma ornatum* Macleay stands as *Sphenomorphus crassicaudus* (A. Dumeril)			
	Lygosoma fragile Macleay, 1877. 2 : 64	*Sphenomorphus ? sp.*	Type 1, fair condition	Hall Sound, New Guinea *	R51, MR392
	Notes :	Boulenger (1887, p. 209) ascribes this species only to the genus *Lygosoma* Gray. An attempt to identify this specimen from Boulenger's key only resulted in its classification to the subgenus *Hinulia* (Gray), i.e. genus *Sphenomorphus* Fitzinger (Mittleman, 1952)			
	Hinulia atrocostata Macleay, 1877. 2 : 62	*Sphenomorphus ? sp.*	Type 1, good condition	Katow (Binaturi River), New Guinea *	R91, MR381
	Notes :	Boulenger (1887, p. 209) ascribes this species only to the genus *Lygosoma* Gray. As with *Lygosoma fragile* this species could not be identified further than the subgenus *Hinulia* by Boulenger's key, i.e. genus *Sphenomorphus* Fitzinger (Mittleman, 1952)			
	Mabouia irrorata Macleay. 1877. 2 : 66	*Emoia atrocostata irrorata* (Macleay) Loveridge, 1948. Bull. Mus. Comp. Zool., 101 : 372	Type 1, good condition	Hall Sound, New Guinea *	R106, MR188
	Mabouia marmorata Macleay, 1877. 2 : 65	*Emoia atrocostatum* (Lesson) Boulenger, 1887. Cat. Liz. Brit. Mus., 3 : 295	Type 1, good condition	Long Island, Torres Straits *	R59, MR465
	Notes :	Boulenger listed this species as a ? synonym of *Lygosoma* (*Emoa*) *atrocostatum* (Lesson) which was verified by examination of the Macleay specimen			
	Euprepis simillimus Macleay, 1877. 2 : 69	*Emoia cyanogaster* (Lesson) Boulenger, 1887. Cat. Liz. Brit. Mus., 3 : 292	Type series 3, good condition	Katow (Binaturi River), New Guinea *	R67–69, MR438–440
	Notes :	Boulenger (1887, p. 292) lists this species as a synonym of *Lygosoma* (*Emoa*) *cyanogaster* (Lesson) and this was verified by comparison of Macleay's specimen with Boulenger's description. The specmens are smaller than Macleay's *Euprepis longicaudis*, which also key to *L. cyanogaster* and are possibly juveniles			

Family	Name under which Described and Reference Proc. Linn. Soc. N.S.W.	Present Names and Reference	Type of Type, No. and Condition	Locality	M.M. Reg. No.
Scincidae	*Euprepis longicaudis* Macleay, 1877. 2 : 68	*Emoia cyanogaster* (Lesson)	Type series 5 fair condition	Darnley Island, Torres Straits *	R97, MR537–541
	Notes : Boulenger (1887, p. 297) lists this species as a synonym of *Lygosoma* (*Emoa*) *nigrum* (Hombron and Jacquinot). However, from Boulenger's key and descriptions, *Euprepis longicaudis* agrees with *L.* (*Emoa*) *cyanogaster* (Lesson) (Boulenger, 1887, p. 292)				
	Euprepis submetallicus Macleay, 1877. 2 : 69	*Emoia baudinii pallidiceps* Vis.	Type series 3, fair condition	Hall Sound, New Guinea *	R75–77, MR518–520
	Notes : Boulenger (1887, p. 209) refers this species (as *Euprepis metallicus*) to the genus *Lygosoma* only. From Boulenger's key and descriptions, it is identified as *Lygosoma* (*Emoa*) *baudinii* (Dumeril and Bibron) (p. 296). Loveridge (1948, p. 370) gives a key to the subspecies of *Emoia baudinii* from which Macleay's specimen is classified as *Emoia baudinii pallidiceps* Vis.				
	Eumences brunneus Macleay, 1877. 2 : 66	*Riopa rufescens* (Shaw) Boulenger, 1887. Cat. Liz. Brit. Mus., 3 : 303	Type series 3, 2 in good condition, 1 in fair condition	Darnley Island, Torres Straits *	R94–96, MR242–244
	Mabouia uniformis Macleay, 1877. 2 : 65	*Riopa rufescens* (Shaw) Boulenger, 1887. Cat. Liz. Brit. Mus., 3 : 303	Type 1, good condition subadult	Cocoanut Island, Torres Straits *	R100, MR513
	Heteropus variegatus Macleay, 1877. 2 : 66	*Leiolopisma fuscum variegatum* (Macleay) Mitchell, 1953. Rec. S.A. Mus., 11 : 78	Cotypes 3, fair condition	Darnley Island, Torres Straits *	R103–105, MR389–391
	Notes : Boulenger (1887, p. 382) synonymized five of Macleay's species, viz. *Heteropus longipes*, *H. sexdentatus*, *H. variegatus*, *H. cheverti* and *H. quinquecarinatum*, into *Lygosoma* (*Leiolopisma*) *fuscum* (Dumeril and Bibron). Loveridge (1948, pp. 361–365) divides this species into several subspecies without reference to Macleay's specimens, but from his key the first two species of Macleay fit into *Lygosoma* (*Leiolopisma*) *fuscum fuscum* (Dumeril and Bibron), and the last three into *Lygosoma* (*Leiolopisma*) *fuscum luctuosum* (Peters and Doria). The group was revised by Mitchell (1953) and his examination of Macleay's material verified these two subspecies, but since Macleay's material has priority over that of Peters and Doria, the second subspecies was changed to *Leiolopisma fuscum variegatum* (Macleay), and MR390 was selected as the lectotype.				
	Heteropus quinquecarinatus Macleay, 1877. 2 : 67	*Leiolopisma fuscum variegatum* (Macleay) Mitchell, 1953. Rec. S.A. Mus., 11 : 78	Type series 5, good condition	Darnley Island, Torres Straits *	R98, MR422–426
	Heteropus cheverti Macleay, 1877. 2 : 67	*Leiolopisma fuscum variegatum* (Macleay) Mitchell, 1953. Rec. S.A. Mus., 11 : 78	Type series 2, good condition	Barrow Island, N.E. Australia *	R112–113, MR384–385

Family	Name under which Described and Reference Proc. Linn. Soc. N.S.W.	Present Names and Reference	Type of Type, No. and Condition	Locality	M.M. Reg. No.
Scincidae	*Heteropus longipes* Macleay, 1877. 2 : 66	*Leiolopisma fuscum fuscum* (Dumeril and Bibron) Mitchell, 1953. Rec. S.A. Mus., 11 : 77	Type 1, good condition	Endeavour River, N. Queensland *	R101, MR427
	Heteropus sexdentatus Macleay, 1877. 2 : 67	*Leiolopisma fuscum fuscum* (Dumeril and Bibron) Mitchell, 1953. Rec. S.A. Mus., 11 : 77	Type series 3, good condition	Cape Grenville, N. Queensland *	R78–80, MR462–464
Agamidae	*Lophognathus lateralis* Macleay, 1877. 2 : 103	*Physignathus temporalis* (Gunther)	Type 1, good condition	Katow (Binaturi River), New Guinea *	R362, MR723
	Notes : Boulenger (1885, p. 395) ascribes this species only to the genus *Physignathus*. On examination, the specimens agreed with Boulenger's key and description of *Physignathus temporalis*, with the exception of Macleay's specimen having only one femoral and one preanal pore on each side, whereas *P. temporalis* is described with two of each per side				
	Tiaris papuensis Macleay, 1877. 2 : 101	*Gonyocephalus papuensis* (Macleay) Boulenger, 1885. Cat. Liz. Brit. Mus., 1 : 297	Type 1, good condition	Hall Sound, New Guinea *	R335, MR833
	Tiaris boydii Macleay, 1883. 8 : 432	*Gonyocephalus boydii* (Macleay) Boulenger, 1885. Cat. Liz. Brit. Mus., 1 : 297	Type series 2, good condition	Herbert River, N. Queensland	R366–367, MR1003–1004
	Notes : Collected J. A. Boyd				
Typhlopidae	*Typhlops batillus* Waite, 1884. 9 : 9	*Typhlops batillus* Waite	Type 1, good condition	Wagga Wagga, New South Wales	R669
Boidae	*Nardoa crassa* Macleay, 1885. 10 : 66	*Liasis fuscus* Peters Boulenger, 1893. Cat. Snakes Brit. Mus., 1 : 78	Type 1, good condition	Herbert River, N. Queensland	R877
	Notes : Collected J. A. Boyd, 1885				
Colubridae	*Pappophis flavigastra* Macleay 1877 2 : 39	*Boiga irregularis irregularis* (Merrem) Loveridge, 1938. Bull. Mus. Comp. Zool., 101 : 387	Type 1, fair condition	Katow (Binaturi River), New Guinea *	R982

Family	Name under which Described and Reference Proc. Linn. Soc. N.S.W.	Present Names and Reference	Type of Type, No. and Condition	Locality	M.M. Reg. No.
Colubridae	*Pappophis laticeps* Macleay, 1877. 2 : 39	*Boiga irregularis irregularis* (Merrem) Loveridge, 1948. Bull. Mus. Comp. Zool., 101 : 387	Type series 4, fair condition	Hall Sound, New Guinea *	R936–39
	Dipsas boydii Macleay, 1884. 9 : 548	*Boiga fusca* (Gray) Loveridge, 1934. Bull. Mus. Comp. Zool., 77 : 274	Type 1, good condition	Herbert River, N. Queensland	R927
	Dipsas ornata Macleay, 1888. 3 : 416	*Boiga fusca* (Gray) Kinghorn, 1929. Rec. Aust. Mus., 17 : 84	Type 1, fair condition	King Sound, N.W. Australia	R926
	Notes : Kinghorn synonymized *D. ornata* with *B. fusca* and states that the type has 19 midbody scale rows, not 15 as described in the original note by Macleay				
	Lycodon darnleyensis Macleay, 1877. 2 : 38	*Stegonotus cucullatus* (Dumeril and Bibron) Boulenger, 1893. Cat. Snakes Brit. Mus., 1 : 365	Type 1, good condition	Darnley Island, Torres Strait *	R586
	Notes : Boulenger lists this species as a ? synonym of *Stegonotus cucullatus*. On examination, the type specimen fits the description of this species				
	Herbertophis plumbeus Macleay, 1883. 8 : 434	*Stegonotus plumbeus* (Macleay) Boulenger, 1893. Cat. Snakes Brit. Mus., 1 : 368	Type 1, good condition	Herbert River, N. Queensland	R981, MR1245
	Notes : Collected J. A. Boyd. On the basis of this specimen, Macleay erected a new genus, but use of the key in Boulenger confirms the decision to synonymize it with *Stegonotus*. Although the specimen is superficially similar to *S. modestus*, it appears to warrant separate species identification				
	Mainophis robusta Macleay, 1877. 2 : 36	*Brachyorrhus albus* (Linné) Boulenger, 1893. Cat. Snakes Brit. Mus., 1 : 305	Type series 2, good condition	Katow (Binaturi River), New Guinea *	R615–16
	Katophis plumbea Macleay, 1877. 2 : 36	*Tropidonotus picturatus* Schlegel Boulenger, 1893. Cat. Snakes Brit. Mus., 1 : 215	Type series 4, good condition	Katow (Binaturi River), New Guinea *	R618–21
	Tropidonotus angusticeps Macleay, 1883. 8 : 433	*Tropdionotus picturatus* Schlegel Boulenger, 1893. Cat. Snakes Brit. Mus., 1 : 215	Type 1, fair condition	Herbert River, N. Queensland	R591
	Notes : Boulenger lists this as a possible synonym. Use of his key confirms this				

Family	Name under which Described and Reference Proc. Linn. Soc. N.S.W.	Present Names and Reference	Type of Type, No. and Condition	Locality	M.M. Reg. No.
Colubridae	*Fordonia papuensis* Macleay, 1877. 2 : 35	*Fordonia leucobalia* (Schlegel) Boulenger, 1896. Cat. Snakes Brit. Mus., 3 : 21	Type series 3, good condition	Katow (Binaturi River). New Guinea *	R912–14
	Notes : Boulenger (1896, p. 23) suggests that *F. papuensis*, with 22 midbody scale rows, may be based on an aberrant specimen, and he thus synonymizes this species with *Fordonia leucobalia*. Re-examination of all the specimens in the type series shows that they have 25–33 midbody scale rows and not 22 as stated in Macleay's description. Thus the synonymy with *F. leucobalia*, as suggested by Boulenger, is verified				
	Dendrophis bilorealis Macleay, 1883. 8 : 435	*Dendrophis punctulatus* (Gray) Boulenger 1896. Cat. Snakes Brit. Mus., 3 : 629	Type series	Herbert River	R561–2
			Topotype series 5, good condition	Herbert River, N. Queensland	R557–9
	Notes : Boulenger synonymizes this species with *Dendrophis punctulatus* and lists this species as a colour variant along with *D. gracilis*				
	Dendrophis gracilis, Macleay, 1875. 1 : 15	*Dendrophis punctulatus* (Gray) Boulenger, 1894. Cat. Snakes Brit. Mus., 2 : 82	Type series 3, excellent condition	Townsville, N. Queensland	R569-71
	Notes : Collected by Mr. Spalding				
	Dendrophis breviceps Macleay, 1877. 2 : 37	*Dendrophis lineolatus* Hombron and Jacquinot Boulenger, Cat. Snakes Brit. Mus., 2 : 85	Type series 3, good condition	Katow (Binaturi River), New Guinea *	R581–3
	Notes : Boulenger lists this species as a ? synonym of *Dendrophis lineolatus*. Examination of the specimen confirms this				
	Dendrophis darnleyensis Macleay, 1877. 2 : 37	*Dendrophis calligaster* Gunther Boulenger, 1894. Cat. Snakes Brit. Mus., 2 : 80	Type 2 series, excellent condition	Darnley Island, Torres Straits *	R565–6
	Dendrophis katowensis Macleay, 1877. 2 : 37	*Dendrophis calligaster* Gunther Boulenger, 1894. Cat. Snakes Brit. Mus., 2 : 80	Type series	Katow (Binaturi River), New Guinea *	R563–4, MR563-4

Family	Name under which Described and Reference Proc. Linn. Soc. N.S.W.	Present Names and Reference	Type of Type, No. and Condition	Locality	M.M. Reg. No.
Elapidae	*Elapocephalus ornaticeps* Macleay, 1877. 2 : 221	*Demansia psammophis* (Schlegel) Kinghorn, 1941	Type 1, good condition Juvenile	Port Darwin, Northern Territory	R705 MR1305
	Diemenia papuensis Macleay, 1877. 2 : 40	*Demansia psammophis papuensis* (Macleay) Loveridge, 1934. Bull. Mus. Comp. Zool., 77 : 277	Type 1, good condition	Hall Sound, New Guinea *	R713
	Notes : Boulenger (1896, p. 322) synonymized this species with *Demansia psammophis*, whilst Loveridge suggested that *Demansia spammophis papuensis* is a geographical race				
	Diemenia atra Macleay, 1884. 9 : 549	*Demansia psammophis olivacea* (Gray) Loveridge, 1934. Bull. Mus. Comp. Zool., 77 - 277	Type 1, good condition	Herbert River, N. Queensland	R708
	Notes : Boulenger (1896, p. 323) notes that *D. atra* is probably a melanotic specimen of *D. olivacea*. Loveridge recognizes this synonymy and reduces *olivacea* to subspecific rank, as *D. psammophis olivacea*				
	Diemenia angusticeps Macleay, 1888. 3 : 417	*Demansia psammophis olivacea* (Gray) Loveridge, 1934. Bull. Mus. Comp. Zool., 77 : 277	Type 1, fair condition	King's Sound, N.W. Australia	R712
	Notes : Boulenger (1896, p. 323) synonymized *D. angusticeps* with *D. olivacea*, which was reduced to subspecific rank in *D. psammophis* by Loveridge				
	Hoplocephalus brankysi Macleay, 1878. 3 : 52	*Australeps superba* (Gunther) Worrell, 1963. Aust. Rep. Park Rec., 1	Type	Moss Vale, New South Wales	R541, MR1362
	Notes : Collected C. S. Bransky. Boulenger (1896, p. 343) synonymized this species with *Denisonia superba* but Worrell erected a new genus *Austrelaps* and discussed reasons for removing it from *Demansia*				
	Hoplocephalus assimilis Macleay, 1885. 10 : 68	*Crytophis nigrescens* (Gunther) Worrell, 1961. W. Aust. Nat., 8 : 26	Type 3, good condition	Herbert River, N. Queensland	R507–9
	Notes : Collected J. A. Boyd. Boulenger (1896, p. 343) synonymized this species with *Denisonia nigrescens* but Worrell erected a new genus and discussed its relationship to *Demansia*				

Family	Name under which Described and Reference Proc. Linn. Soc. N.S.W.	Present Names and Reference	Type of Type, No. and Condition	Locality	M.M. Reg. No.
Elapidae	*Hoplocephalus carpentariae* Macleay, 1877. 2 : 403	*Unechis carpentariae* (Macleay) Worrell, 1961. W. Aust. Nat., 8 : 25	Type 1, fair condition	Normanton, Gulf of Carpentaria	R505, MR1317
	Notes : Collected Dr. Cox, 1887. Boulenger (1896, p. 344) lists this species as *Denisonia carpentariae*, which stood until 1961, when Worrell erected a new genus *Unechis* to accommodate it, and discussed his reasons for removing it from *Denisonia*. It should be noted that the type specimen differs from Macleay's description in having 19 scale rows and not 15 as is usually stated (e g. Loveridge, 1934, p. 289)				
	Pseudechis darwinensis Macleay, 1877. 2 : 220	*Pseudechis australis* (Gray) Thomson, 1930. Aust. J. Exp. Biol. & Med. Sci., 7 : 125	Type 1, good condition	Port Darwin, Northern Australia	R649
	Notes : Collected Mr. Spalding				
	Brachysoma simile Macleay, 1877. 2 : 221	*Pseudelaps diadema* (Schlegel) Boulenger, 1896. Cat. Snakes Brit. Mus., 3 : 319	Type series 4, fair condition	Port Darwin, Northern Australia	R664–7, MR1421–4
	Notes : Collected Mr. Spalding				
	Acanthophis laevis Macleay, 1877. 2 : 40	*Acanthophis antarcticus antarcticus* (Shaw) Boulenger, 1896. Cat. Snakes Brit. Mus., 3 : 355	Type 1, good condition	Katow (Binaturi River), New Guinea *	R693

Acknowledgement

The skeleton of this list was compiled by the previous curator of the Macleay Museum, Mrs. J. M. E. Anderson, to whom we are indebted.

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NOTES ON VITTADINIA TRILOBA sens. lat. (COMPOSITAE)

NANCY T. BURBIDGE
Division of Plant Industry, C.S.I.R.O., Canberra, Australia

(Communicated by Dr. Joyce W. Vickery)
[Read 30th October, 1968]

Synopsis

Five taxa which have been included in *Vittadinia triloba* by some authors are discussed. A new name is supplied, *V. muelleri* N. T. Burbidge, for a species believed to represent part of Sonder's *Eurybiopsis hookeri* var. *angustifolia* and also a new name, *V. blackii* N. T. Burbidge is supplied for South Australian material formerly regarded as *V. tenuissima* (Benth.) J. M. Black.

The genus *Vittadinia* A. Rich., Ess. Fl. Nouv.Zel. 250 (1832), is distributed in Australia, New Guinea, New Caledonia and New Zealand, the main group of species being in the continental area. In the "Flora Australiensis" Bentham took a broad view of species limits and it has long been evident that a critical revision is required. In particular, the name *V. australis* A. Rich. was applied to a range of material showing considerable diversity and wide distribution in southern and eastern Australia. In more recent Australian botanical literature this name has been replaced with *V. triloba* Gaud. Preliminary study has indicated that some clarification of this assemblage is possible and, pending a more intensive treatment, five component taxa are considered below.

It has been found that achene characters are of diagnostic significance. The outline is usually spathulate to oblanceolate or cuneate and there is some asymmetry which varies with position in the head, but the prominence of the ribs on the flattened sides, as well as the nature and arrangement of the hairs, varies from species to species.

V. TRILOBA (Gaud). DC., Prodr. 5: 281 (1836); *Brachycome triloba* Gaud., Bot., Freyc. Voy. 467 (1830); *V. australis* A. Rich. sensu Bentham, Fl. Austral. 3: 490 (1866); *Eurybiopsis scabrida* J. D. Hook., Lond. J. Bot. 6: 110 (1847); *E. hookeri* F. Muell. ex Sond. var. *scabra* Sond., Linnaea 25: 454 (1853); *V. scabra* DC. sensu J. D. Hook., Fl. Tasm. 1: 181 (1856) non DC. (1836).

The name *V. australis* A. Rich., to which Bentham referred the Australian material, was based on a New Zealand plant in which the ligulate florets are white, the inner involucral bracts about 5 mm. long and the trilobed leaves are glandular-pubescent with ciliate margins. Since the Australian plants have violet-coloured ligules, the inner involucral bracts are at least 6 mm. long and the vestiture of the leaves is different, separation seems justified. The type of Gaudichaud's species was collected in the Port Jackson area.

The plants are scabrid with spreading multicellular hairs on stems and leaves and also up the mid-line of the acuminate scales of the involucres: the hairy achenes are narrowly turbinate-spathulate, ribbed and slightly flattened. The distribution appears to be mainly in New South Wales, Victoria and Tasmania. See Fig. 1 A (achene).

V. CUNEATA DC., Prodr. 5: 281 (1836); J. D. Hook., Fl. Tasm. 1: 182 (1856); *Eurybiopsis gracilis* J. D. Hook., Lond. J. Bot. 6: 110 (1847); *E.*

hookeri F. Muell. ex Sond. var. *incana* Sond., Linnaea 25: 454 (1853); *V. triloba* var. *lanuginosa* J. M. Black, Trans. & Proc. Roy. Soc. S. Aust. 52: 229 (1928).

This species is distinguished by the woolly vestiture, especially on the stems, the achenes are more flattened and more hairy than in *V. triloba* and their narrow bases are clothed with appressed hairs. It is found in eastern New South Wales, Victoria, south eastern parts of South Australia and in Tasmania. See Fig. 1 B (achene) B_1 (bifid hairs).

V. MUELLERI, nom. nov.

Eurybiopsis hookeri F. Muell. et Sond. var. *angustifolia* Sond., Linnaea 25: 454 (153) quoad "Van Diemensland (Stuart)".

Holotype.—"Rockbank" adjoining Black Mountain Station, Wulgulmerang, N. E. Gippsland, alt. 2800 feet approx., J. H. Willis, 27.xi.1962 (MEL 30013).

Plantae ascendentes, minute glanduloso-pubescentes. Folia angusta, conduplicata, 1–4 cm. longa, integer vel lobis lateralibus, lobi angusti, divaricati, marginibus sparse ciliatis. Bracteae involucrales minute glanduloso-pubescentes vel minute tuberculatae, marginibus membranaceis, apicibus obtusis, ciliolatis. Achaenia striata, dimidio inferiore villis appressis, dimidio superiore pubescentia praeter marginibus, villis clavatis.

The plants are tufted, the minutely glandular-pubescent stems ascendent with the narrow, more or less conduplicate leaves entire or with narrow spreading lobes slightly above the middle, but leaves almost lacking from the peduncles. Inner bracts of the involucres obtuse, without long hairs though minutely glandular-pubescent or the surface appearing minutely tuberculate, the margins ciliolate towards the apices. Achenes flattened, cuneate-spathulate, the thickened margins glabrous, the lower portion with appressed hairs grading into slender clavate (sometimes minutely bifid) hairs spreading from between the ribs of the upper part, the ribs often inconspicuous on immature fruits. Distribution widespread in eastern New South Wales, Victoria and Tasmania. See Fig. 1 D (achene) D_1 (hairs).

New South Wales: 10 miles W. of Yarrowyck, New England, R. W. Jessup & M. Gray 1794, 17.x.1952 (CANB); 2 miles N. of Dumaresq, R. W. Jessup & M. Gray 1794, 17.x.1952 (CANB); Chiswick, 10 miles S. of Armidale, R. W. Jessup & M. Gray 1750, 23.x.1952 (CANB); Cherry Hill, Armidale district, R. Roe R548, 16.ii.1945 (CANB); Kentucky, R. Roe R569, 21.ii.1945 (CANB); 8 miles S. of Cessnock, R. Story 6708, 2.x.1959 (CANB); Fairfield, O. D. Evans, 3.xii.1929 (CANB); Concord, O. D. Evans, 4.ii.1927 (CANB); Mt. Jerrabomberra, S. of Queanbeyan, N. T. Burbidge 6696, 6.xi.1960 (CANB); *Australian Capital Territory*: near Burbong Village, Molonglo River, P. J. Darbyshire 541, 21.xii.1961 (CANB, N.S.W.); Turner, Canberra, R. Pullen, 1267, 21.ii.1959 (CANB); Black Mountain, C. W. E. Moore, 5.x.1945; also W. Hartley, 12.iv.1944 and R. Pullen 2061, 23.ii.1960 (all CANB); Kambah-Tharwa road, 3 miles past Kambah turn-off, M. Gray 3582, 18.xii.1958 (CANB); Michelago, New South Wales, H. S. McKee 7487, 23.x.1960 (CANB); *Victoria*: Heathcote, J. H. Willis, 7.xi.1961 (MEL 30018); *Tasmania*: Mt. Nelson, C. E. Lord, January 1930 (CANB); Tasmania, Stuart (MEL 30015).

Sonder listed two specimens under the variety *angustifolia,* one from Van Diemensland and the other from Holdfast Bay (South Australia) collected by Mueller in May. At Melbourne there is a Mueller specimen of 1851 from the Sonder Herbarium which is believed to represent the second.

No Stuart material that might be definitely associated as having been examined by Sonder has been located. There is however a specimen on which the label reads: "Eurybiopsis hookeri ferd Mll. var. laciniata, Tasmaniae Stuart" in Mueller's handwriting. Until proved otherwise this may be part of the specimen seen by Sonder since it does, in fact, agree more closely with his description than does the plant from Holdfast Bay. Sonder's text reads: "foliis . . . glabris vel subtus setulosis marginibus ciliolatis, inferiore plerumque incisodentatis . . . achaenia puberulis."

In the opinion of the writer the two specimens represent distinct species, one described here and the other agreeing with material wrongly referred to *V. tenuissima* (Benth.) J. M. Black and discussed below.

V. TENUISSIMA (Benth.) J. M. Black, Trans. & Proc. Roy. Soc. S. Aust. 52: 229 (1928) quoad comb., descr. excl.; *V. australis* A. Rich. var. *tenuissima* Benth., Fl. Austral. 3: 491 (1866).

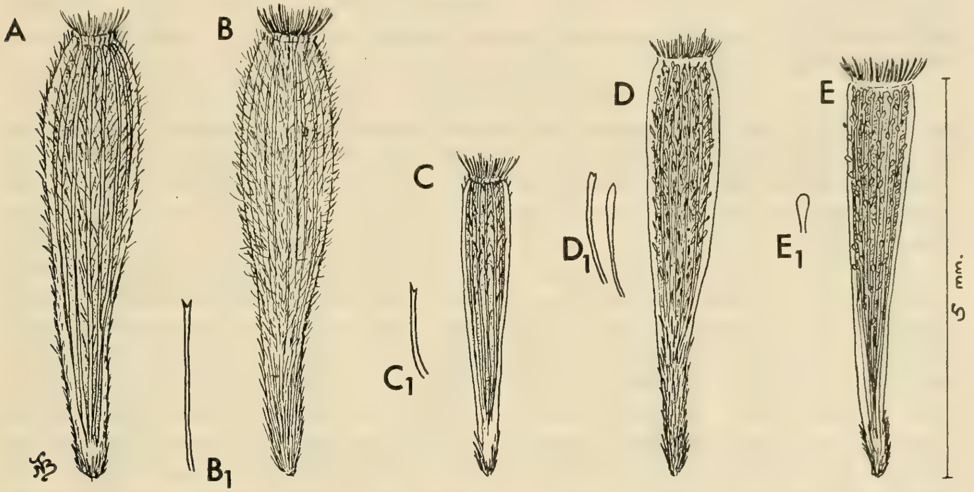


Fig. 1. A. *Vittadinia triloba*: achene. (from "Glenfield, O. D. Evans, 27.vii.1928."). B. *V. cuneata*: achene; B_1 hair. (from "Jerilderie, N.S.W., E. D'Arnay 388"). C. *V. tenuissima*: achene; C_1 hair. (from "Grose Vale, Carne, N.S.W. 101651."). D. *V.* mueller: achene; D_1 hairs from upper part of achene. (from "Tharwa road Kambah, A.C.T., Gray 3582.") E. *V. blackii* achene; E_1 hair. (from holotype.)

Bentham quoted Port Jackson specimens collected by Robert Brown and by Woolls and a Mueller specimen from Burnett River (Queensland). Judging by photographs of the first and third of these and by specimens in the New South Wales Herbarium, the leaves are extremely slender and almost or quite glabrous though the stems, which have a pronounced tendency to branch corymbosely in the upper half above a simple base, are minutely hairy. As noted by Bentham, the heads are small, the involucres being only 4–5 mm. long and the achenes 3·5–4·5 mm. long. This species is apparently distributed from south east Queensland through the Northern Tablelands of New South Wales and south through coastal districts to near the Victorian border. Fig. 1 C (achene) C_1 (hair).

Though Black based his combination on Bentham's varietal name his description does not fit the type material. He states "involucrum 7–8 mm. longum . . . achaenia 4–5 mm. longa puberula utrinque circiter 6–costata . . ."

He also mentions the ligules as numbering 15–20 which is higher than in the eastern Australian specimens examined. It is thus evident that though his combination is the correct name for the species typified as Bentham's var. *tenuissima,* his description covers a different species. This latter is discussed below.

V. BLACKII, nom. nov.

V. tenuissima (Benth.) J. M. Black quoad descr., basion. excl.; *Eurybiopsis hookeri* F. Muell. et Sond. var. *angustifolia* Sond., Linnaea 25: 454 (1853) quoad "Holdfast Bay, Mai".

Holotype.—Old Stockade Hill, Northfield, ca. 10 km. N.N.E. of Adelaide, South Australia, D. N. Kraehenbuehl 153, 5.iii.1960 (AD 96422044).

Plantae minute glanduloso-pubescentes, villis septatis sparsim ornatae. Folia lineari-teretia vel lineari-conduplicata, 1–1·5 (–3) cm. longa. Bracteae involucrales minute glanduloso-pubescentes, marginibus membranaceis, apicibus ciliatis. Achenia striata, dimidio inferiori glabra villis appressis infra exceptis, dimidio superiori minute pubescentia, villis brevibus crassis clavatis etiam ornata.

Plants subshrubby, 10–30 cm. high, older stems more or less decumbent and woody, stems much branched, bearing septate hairs mixed with minute glandular pubescence. Leaves linear, conduplicate but usually so narrow as to appear terete and channelled above; mostly 1–1·5 cm. long but occasionally longer with sparse scattered hairs and few minute glandular ones, the surface more or less glistening. All stems terminating in solitary heads, involucres 7–9 mm. long, bracts with green centres bordered with minute glandular hairs, a few longer hairs sometimes present, margins membranous and ciliolate towards the acuminate apex. Achenes shorter than innermost bracts, flattened, narrow cuneate, deeply ribbed, with scanty appressed hairs at base but otherwise glabrous in lower half, the upper half with projecting short clavate hairs, margins glabrous, pappus bristles very numerous, smooth towards base but barbellate above. Fig. 1 E (achene) E_1 (hair). Distribution mainly restricted to South Australia but also recorded from western New South Wales and north eastern Victoria with one record from Western Australia.

This species can be separated from *V. muelleri* by the septate hairs on the stems, the scattered hairs of the leaves and by the deeply ribbed achenes with fewer and short clavate hairs attached to the ribs rather than between them.

Western Australia: Halfway between Mt. Ragged and Victoria Spring, Miss S. Brooks, 1886 (MEL 30012); *South Australia*: Birksgate, M. Koch, Sept. 1902 (NSW 101654); Lake Eyre Basin, Schomburgk (AD 96826384); Hambidge Flora and Fauna Reserve (ca. 140 km. N. of Port Lincoln) Eyre Peninsula, C. R. A. Alcock 1103, 10.x.1966 (AD 96711206); Thrington on Thrington-Moonta road, Upper Yorke Peninsula, B. Copley 163, 27.iii.1966 (AD 96622021); Maitland, Yorke Peninsula, J. M. Black, April 1917 (AD 96826385); ca. 2½ km. S. of Hamilton on road to Kapunda, Mt. Lofty Range, Hj. Eichler 12074, 7.xii.1955 (AD 95902036); Freeling Cemetery, ca. 55 km. N.N.E. of Adelaide, D. N. Kraehenbuehl 1505, 18.ix.1965 (AD 96724004); Adelaide Plains near Adelaide, J. M. Black, April 1917 (AD 9682385); North bank of Dry Creek, east of Yatala Prison Farm, Adelaide Plains, D. N. Kraenhenbuehl 465, 13.ix.1961 (AD 96426228); Brighton, J. M. Black, 18.ix.1904 (AD 96826386); Echunga district, R. F. Parsons 212, 27.x.1961 (AD 96348243); Murray Bridge, J. H. Maiden, January 1907

(NSW 101655); Sandergrove, O. E. Menzel, Oct. 1896 (AD 96826380); Port Elliot, Fleurieu Peninsula, J. B. Cleland, 25.i.1925 (AD 9682383); sine loc., Behr, 10.ii.1845 (MEL 30009) (type of *Aster behrii?*) *New South Wales*: Interior, Behr (MEL 30016); *Victoria*: Murray Desert, Behr (MEL 30011); Pine Plains, Wimmera, Behr 215 (MEL 30017).

Key to species discussed

1. Leaves spathulate, oblanceolate or cuneate, entire or 3–lobed at the apex. Achenes 5–6 mm. long, narrowly oblanceolate, vestiture on both sides and margins consisting of slender hairs with bifid apices above underlying glandular pubescence.

2. Plants clothed with soft woolly hairs; basal part of achene with dense appressed hairs, the hairs of the upper part spreading and obscuring the ribs:
cuneata

2a. Plants scabrid with spreading septate hairs; lower part of achene almost glabrous except for short appressed hairs at base, upper part prominently ribbed, slightly flattened but turgid, hairs spreading:
triloba

1a. Leaves filiform, linear or narrowly elliptical-oblanceolate, entire or sometimes with a pair of spreading narrow lobes near or above the middle; achenes narrowly cuneate or spathulate-cuneate, margins glabrous or almost so.

3. Leaves filiform, almost or quite glabrous; involucres 4–5 mm. long, achenes 3·5–4 mm. long; lower half glabrous apart from short appressed hairs at base, upper half with sparse slender spreading hairs with bifid apices; glandular pubescence lacking:
tenuissima

3a. Leaves sparsely hairy, hairs septate; involucres 6–9 mm. long; achenes 4·5–5 mm. long, minute glandular pubescence present below hairs.

4. Leaves with scanty hairs on margins and on midrib of lower surface; lower part of achene clothed with slender appressed bifid-tipped hairs which grade into slender obtuse or bifid-tipped clavate hairs growing between the ribs which are often inconspicuous before maturity:
muelleri

4a. Leaves with scattered hairs; achenes with appressed slender hairs at base of glabrous lower half, deeply striate above with 6–7 prominent ribs on each side even when young, the ribs bearing short clavate hairs:
blackii

A REVIEW OF THE FAMILY AGNESIIDAE HUNTSMAN 1912; WITH PARTICULAR REFERENCE TO *AGNESIA GLACIATA* MICHAELSEN, 1898

PATRICIA KOTT

Zoology Department, University of Queensland

[Read 27th November, 1968]

Synopsis

Known species of the family Agnesiidae are reviewed and their relationships are clarified. Particular attention has been given to the genus *Agnesia* and the synonymy and distribution of *Agnesia glaciata*. New occurrences are recorded for *Agnesia glaciata* and *Adagnesia opaca*.

Similar modifications of body musculature to operate specialized closing mechanisms are demonstrated in each genus of the family. The development of this protective closing mechanism is associated with the extent to which the test is made brittle and rigid with encrusting sand thus preventing the general contraction of the body as a defence mechanism. The three known genera are closely related and distinguished by branchial sac modifications from *Caenagnesia* through *Adagnesia* to *Agnesia*. *Adagnesia opaca* and *Agnesia glaciata* are the most specialized species. The family appears to be an ancient one and records indicate relict populations of all species.

INTRODUCTION

The family Agnesiidae of the Suborder Phlebobranchia contains a limited number of closely related and highly specialized genera. Records of the family are not common, although often large numbers of individuals are taken together.

The following genera are known:

(1) *Caenagnesia* Ärnbäck, 1938, is known only from Antarctica and is represented by two species.

(2) *Agnesia* Huntsman, 1912, is represented by one species from the north Pacific; a second species extends from California to Tierra del Fuego and the Antarctic Peninsula, North Island, New Zealand, South Africa, Moreton Bay, Queensland, and Japan; a third species is known from abyssal depths of the north Atlantic.

(3) *Adagnesia* Kott, 1963, of which 2 species are known, one from a single specimen off Macquarie Island, and one from a limited area of the Australian coast.

In the present work the inter-relationships of species of this family are discussed, especially in regard to the increasing specialization of body musculature.

Family AGNESIIDAE Huntsman, 1912

Gut on the left side of the branchial sac; internal longitudinal vessels reduced to papillae on the transverse vessels; stigmata spiral; branchial tentacles arranged in 4 concentric circles; the border of the branchial and atrial apertures produced into 6 and 7 pronounced lobes respectively: muscle bands reduced in length, often considerably.

Throughout the family Agnesiidae there is an increasing reduction in the numbers of papillae on the transverse vessels; reduction in numbers of infundibula; and a reduction in the number of transverse vessels present. The musculature becomes highly specialized and there is a progressive reduction in numbers and length of muscle bands throughout the family.

Despite the specialized nature of body musculature in the Agnesiidae, the homologues of the cionid musculature can be traced. In *Ciona intestinalis,* the most primitive species known, the external layer of musculature is represented by longitudinal bands and the internal layer consists of circular fibres. Only on the siphons, anterior to the tentacular band, does the circular muscle layer become superficial to the longitudinal bands. The internal transverse musculature, present more posteriorly in Agnesiidae, represents the inner layer of circular fibres in *Ciona.* While the anterior and superficial transverse bands represent the continuation of the circular bands which in *Ciona* are confined to the siphons. The inner circular bands associated with the tentacular ring in Agnesiidae are also a vestige of the inner circular layer of *Ciona.* The most significant departure from the cionid condition observed in the musculature of Agnesiidae is the reduction in length and number of longitudinal muscle bands; and the interruption of circular bands to form shorter transverse bands confined to the dorsal and ventral borders of the body. True circular bands are, in Agnesiidae, confined to the siphons. On the rest of the body the circular musculature is interrupted first laterally (*Caenagnesia* spp.) and then also in the median dorsal and ventral lines (*Agnesia* spp. and *Adagnesia* spp.).

The shortened muscle bands of Agnesiidae are associated with increasing rigidity of the test due to encrustation with sand. The body is consequently less contractile and the functions of the muscles become more specialized. In *Caenagnesia bocki, Agnesia glaciata* and *Adagnesia opaca* the shortened muscle bands pull lips or folds of test, which is generally rigid with sand, across the apertures to form a closing mechanism. This undoubtedly serves as a protective device for these non-contractile species existing in a vulnerable sublittoral locality.

The subfamily Rhodosomatinae of the family Corellidae, also of the suborder Phlebobranchia, contains monotypic *Rhodosoma turcicum* (Savigny), the only species outside the present family which exhibits a similar closing mechanism protecting the apertures. In *Rhodosoma* this is less symmetrical but more conspicuous than in the Agnesiidae and a fold involving the body wall and test is developed only on the right side of the apertures to form a lid. This is operated by the transverse muscle bands at the base of the siphons, particularly those across the mid line between the apertures, which extend out into the fold (Kott 1952). The mechanism is similar in Agnesiidae where the circular muscles surrounding the base of the siphons are interrupted laterally and operate across the dorsal midline from the base of the test fold on either side of the apertures. The mechanism appears to develop independently in each genus of the family. Closing lips are formed in *Caenagnesia bocki* and are present but not so well developed in *Adagnesia antarctica* which appears to have been derived from *Caenagnesia.* In *Adagnesia opaca* the closing mechanism achieves its greatest development and in *Agnesia,* a genus which probably evolved from a primitive *Adagnesia* sp. a gradual specialization of musculature to operate closing lips is observed within a single species, *Agnesia glaciata,* where, in its most specialized form, it closely resembles the mechanism found in *Adagnesia opaca.*

Genus CAENAGNESIA Ärnbäck, 1938

Traces of longitudinal vessels remain as bifid papillae on the transverse vessels of the branchial sac. Dorsal lamina retains the primitive condition of a plain edged membrane. Primary transverse vessels bearing papillae are present between each row of infundibula. Branchial papillae are more numerous than the number of infundibula in each row and more than a single papilla corresponds to each infundibulum. There are at least 12 primary transverse vessels present.

CAENAGNESIA SCHMITTI Kott

(Text Fig. 1)

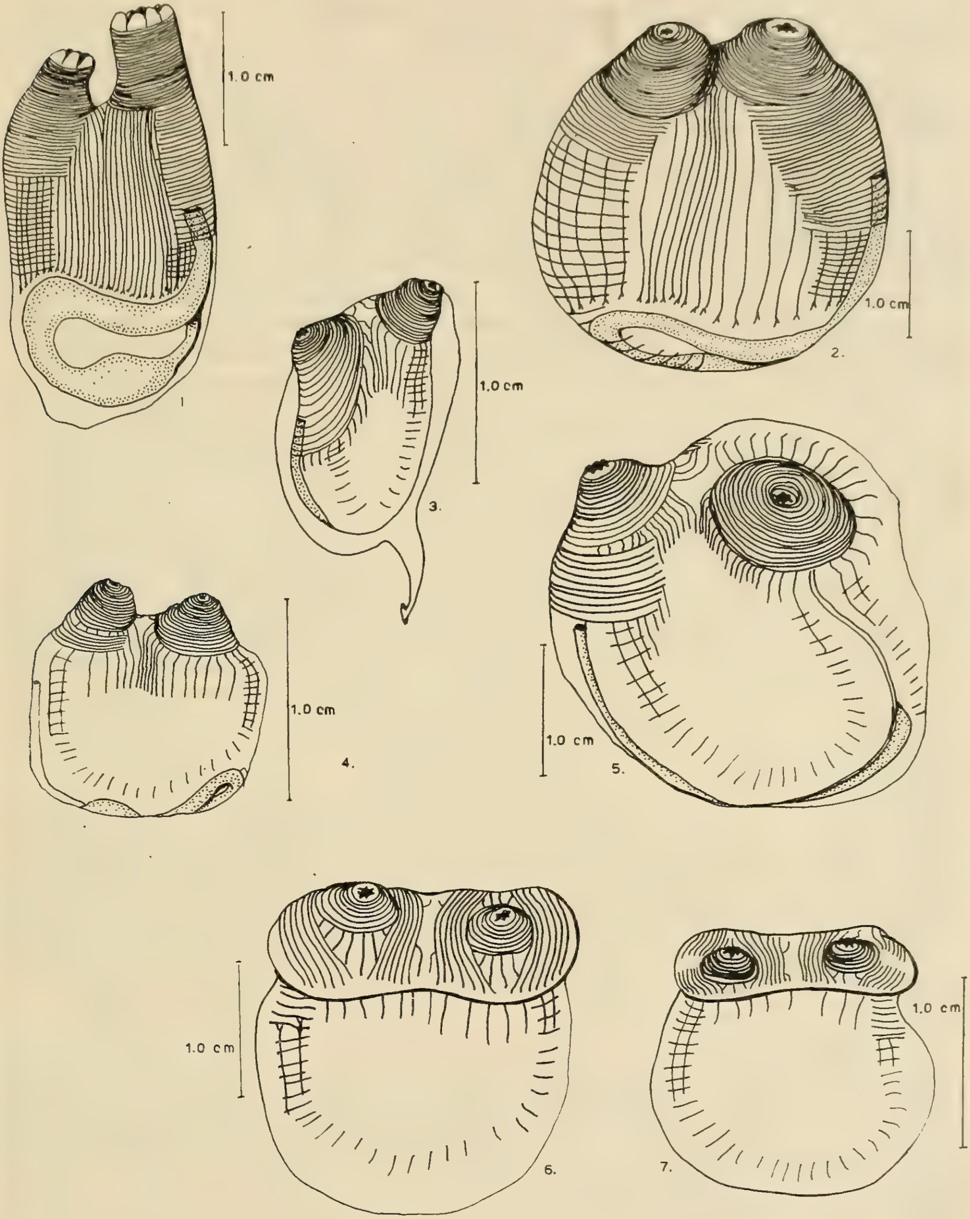
Caenagnesia schmitti Kott, 1969, p. 94.

Specimens examined.—U.S. National Museum: South Shetlands, "Eltanin", St. 428, 662–1120 m; coll. W. Schmitt, St. 66/63, 62 m. Victoria Land, S. W. Robertson Bay, 400 m (Holotype USNM 11968). (Single specimens from each station.)

Remarks.—The body is cylindrical, the test is thin and the body wall highly contractile. The apertures are on short cylindrical siphons which are furrowed along their length. The longitudinal muscle bands are especially numerous (about 50 on each side) and extend the whole length of the body on the right and as far as the gut loop on the left. Contraction of these muscles tends to draw the gut loop up along the branchial sac; however, in relaxed specimens the gut loop appears to lie behind the branchial sac reminiscent of the situation in *Ciona intestinalis.* Circular muscles are present around the siphons, external to the longitudinal muscles and numerous fine circular bands are present internally, associated with the 4 circles of branchial tentacles. Ventrally a superficial layer of transverse muscles is present anteriorly and is continuous across the endostyle. About 5 of the most posterior bands of this series overlap, in the middle of the body, with an inner transverse series present posteriorly on either side of the endostyle but not continuous across it. Dorsally a similar series of superficial transverse muscles is continuous across the dorsal line in the anterior two thirds of the body. These overlap with approximately the 5 most anterior bands of an inner transverse series which are interrupted across the dorsal line. The anterior superficial transverse bands, continuous across the dorsal surface, extend across the distal part of the rectum; while the inner and more posterior bands, interrupted across the dorsal surface, allow for some expansion of the stomach and proximal part of the rectum. Ventral transverse muscles are longer than the dorsal bands and neither extend across the sides of the body. In the branchial sac the number of rows of infundibula (60) and the number of infundibula in each row (25) are especially numerous for species of this family. The number of papillae on the transverse vessels are also numerous, with especially long biramous arms. There is a simple dorsal lamina as in *Ciona intestinalis* and other families of Phlebobranchia.

Occurrence.—Antarctica, probably circum-antarctic continent 74 m to 1000 m (Kott 1969).

Discussion.—The shape of the body, the furrowed external siphons, the thin test and the large numbers and length of the longitudinal muscles are unspecialized and reminiscent of *Ciona intestinalis.* The branchial sac also shows primitive affinities, as the number of rows of stigmata and the number



Text-figure 1–7 (Semi-diagrammatic showing body musculature) 1. *Caenagnesia schmitti* (Relay Bay, Antarctica). 2. *Caenagnesia bocki* (South Shetlands, Antarctica). 3. *Agnesia septentrionalis* (St. Georges Sound, Probilof Is.). 4. *Agnesia glaciata* (Corona del Mar, California). 5. *Agnesia glaciata* (South Shetlands, Antarctica). 6. *Agnesia glaciata* (Antarctic Peninsular, Antarctica). 7. *Agnesia glaciata* (Moreton Bay, Queensland).

of papillae per row is reduced in more specialized forms; and the retention of long biramous arms on the papillae suggests that the reduction of the longitudinal vessels has not proceeded as far as in other species with smaller papillae.

Caenagnesia bocki Ärnbäck

(Text Fig. 2)

Caenagnesia bocki Ärnbäck, 1938, p. 41. Van Name 1945, p. 202. Millar 1960, p. 94. Kott 1969, p. 96. *Agnesia complicata* Kott 1954, p. 151.

Specimens examined.—U.S. National Museum: Weddell Sea, "West Wind", St. 4, 796 m; "Edisto", St. TR6, 394 m; South Shetlands, coll. W. Schmitt, St. 9/63, 57 m; "Eltanin", St. 437, 267–311 m. Australian Museum: BANZARE Collection: Enderby Land, 220 m. (Single specimens.)

Remarks.—The species is dorso-ventrally flattened and the almost sessile apertures are fairly close together on the upper surface. Folds of test are formed along each side of the apertures into which the body wall projects. These folds may meet along the median line, thus covering and protecting the apertures. The test is firm and transparent and is sometimes brittle with sand. Due to the dorso-ventral flattening of the body the gut appears to lie across the posterior surface only slightly to the left. The longitudinal muscles are numerous (about 20) on each side. They extend the whole length of the body on the right but only to the gut loop on the left. There are circular muscles on the siphons external to the longitudinal muscle. Internally there are about 11 circular muscles associated with the 4 circles of tentacles. In a continuous series with the external circular siphonal muscle bands there are transverse bands across the dorsal border of the body in the anterior two thirds. Similar transverse muscles are present in the anterior one third of the body ventrally. The most anterior of these transverse muscle bands are inserted into the body wall at the base of the protective folds of test. Overlapping with the external transverse muscles there is a layer of internal transverse musculature across the dorsal border on the inner surface of the proximal part of the gut loop; and across the endostyle ventrally. More diffuse musculature across the posterior end of the body is gathered into bands which are inserted into the area enclosed by the pole of the gut loop where they are obscured by gonad lobes. All transverse muscles are interrupted across the sides of the body. The protective closing mechanism operates by the contraction of the external transverse muscle bands anteriorly which pull the lips together; meanwhile the siphonal musculature closes the apertures.

The branchial sac in this species is reduced from the condition found in *C. schmitti.* There are primarily 12 rows of 13 to 14 spiral infundibula. With growth the number of rows multiplies and a specimen of 30 mm (Kott 1954) has 24 rows of about 17 spirals. Biramous papillae with long arms are present on the transverse vessels between each row of infundibula. There are about 3 corresponding to each spiral.

Occurrence.—South Shetlands, Antarctic Peninsula (Ärnbäck 1938, Millar 1960, Kott 1969); South Georgia (Millar 1960); Weddell Sea (Kott 1969); Enderby Land (Kott 1954); at 57–800 m.

Discussion.—This species is distinguished from *C. schmitti* especially by the reduced numbers of branchial papillae, transverse vessels and infundibula.

and by the protective lips which cover the apertures. The reduced number and length of longitudinal muscle bands and the reduction in number of internal circular muscles associated with the tentacular sphincter is probably related to the development of a closing mechanism associated with the loss of a flexible body. The internal muscle bands are continuous posteriorly and dorsally across the mesial surface of the gut loop beneath the retropharyngeal groove that extends from the oesophageal opening at the base of the dorsal lamina to the posterior end of the endostyle. In Aplousobranchia the musculature of the body wall extends outside the gut loop, generally to the posterior end of the body. It has been suggested (see Kott 1969, p. 190) that the position of the gut loop on the side of the branchial sac could have resulted from a backwards extension of the branchial sac to the right or left of the gut loop. The muscle bands would, in this case remain outside the gut loop. The presence of the internal transverse muscle bands on the mesial surface of the gut loop in the present species suggests that, at least in this family, the gut has been drawn up on the left side of the branchial sac by relative shortening of the longitudinal muscle bands, leaving the inner transverse muscles across the posterior end of the body.

Genus Agnesia Michaelsen, 1898

Simple undivided flat triangular papillae present on transverse vessels. Dorsal lamina absent. Area of flat unperforated membrane crossed by primary transverse vessels present along mid dorsal line of branchial sac. Enlarged triangular papillae on the primary transverse vessels to the left of the dorsal line may correspond to dorsal languets. The number of infundibula present in each row always exceeds the number of papillae present on the transverse vessels. Four primary transverse vessels present (crossing the mid dorsal line).

Agnesia septentrionalis Huntsman

(Text Fig. 3)

Agnesia septentrionalis Huntsman, 1912, p. 118; 1912*a*, p. 106. Van Name, 1945, p. 200. *Agnesia beringia* Ritter, 1913, p. 493.

Specimens examined.—U.S. National Museum (Cat. No. 10633): coll. G. W. Hanna, St. George Island, Alaska (5 specimens). American Museum of Natural History (Cat. No. 1896): coll. G. Hanna, St. Georges Sound, Pribilof Islands, 74 m (3 specimens).

Remarks.—Rounded oval body from 0·5 to 1·5 cm long, usually supported by a delicate short stalk from the posterior end of the body. The stalk may be 1 cm long on a specimen of 0·8 cm but is generally much shorter than this. The test is thin and glassy, with few hairs and adherent sand grains. The apertures protrude on short rounded siphons, the branchial aperture anterior, and the atrial aperture antero-dorsal. There are 4 rows of equally long and closely placed branchial tentacles and posterior to these, at the base of the siphon, a ring of about 6 circular muscles which may coalesce into a single wide band in the rim of the tentacular velum. About 30 longitudinal muscle bands radiate from each siphon for only a very short distance. Externally each siphon has about 22 circular muscle bands. On the atrial siphon these extend well down the dorsal surface to cross the rectum. Short transverse muscle bands are arranged in single series on either side of the dorsal and ventral median lines, beneath the longitudinal muscles, and, especially on the dorsal surface, these extend anteriorly beneath the circular siphonal musculature. In this species the branchial sac is well developed. There are 4 primary transverse vessels, bearing large flattened tongue-like papillae. Between successive primary transverse vessels 4 rows of 22 infundibula develop from double rows of 11 primary spirals. Secondary transverse vessels develop about 7 papillae corresponding to those on the primary vessels. Intermediate transverse vessels of a third order separating the double rows of infundibula between the primary and secondary vessels also develop papillae but these are generally incomplete. Each infundibulum develops a maximum of 4 to 5 coils.

Occurrence.—Bering Sea (Ritter 1913); British Columbia (Huntsman 1912, 1912*a*); Alaska, Pribilof Islands (Ritter 1913); at 27 to 78 m.

Discussion.—Differences between this species and *A. glaciata* involve the development of the body musculature which is less complex in the present species and the siphonal muscles in particular are not modified to operate a special closing mechanism. Apertures close by simple sphincter muscles around the siphons and these circular muscles are never interrupted. Similarly the branchial tentacles are more conspicuous in the present species and the inner circular muscles at the base of the branchial siphon associated with a velum are better developed. Development of the branchial sac depends, in the present species, on a proliferation of primary infundibula. In *A. glaciata* growth is accompanied by increase in the number of coils of each infundibulum.

AGNESIA GLACIATA Michaelsen

(Text Figs 4–7)

Agnesia glaciata Michaelsen, 1898, p. 370; Van Name, 1945, p. 200; 1900, p. 76; 1907, p. 75; Millar, 1960, p. 92; Kott 1969, p. 97. *Agnesia krausei* Michaelsen 1912, p. 181. *Agnesia capensis* Millar 1955, p. 191. *Agnesia himeboja* Oka 1915, p. 1. *Agnesia sabulosa* Oka 1929, p. 152. *Agnesia septentrionalis;* Van Name, 1945, p. 201, Part (specimens from Newport Harbour, Southern California).

Specimens examined.—U.S. National Museum: Antarctic Peninsula, coll. W. Schmitt, St. 27/63, 75 m; 66/63, 74–92 m (single specimens); South Shetlands, coll. W. Schmitt, St. 64/63, 86 m (2 specimens). American Museum of Natural History (catalogue Nos. 1570, 1571, 1572, identified as *A. septentrionalis* by Van Name 1945): coll. MacGinitie; Corona del Mar California. Queensland Museum (Registration No. G5214): coll. W. Stephenson, Moreton Bay, Queensland 27°14′50″S, 153°18′00″E, 23 m; 27°16′20″S 153°20′50″E, 24 m (numerous specimens on muddy sand).

Remarks.—Mature specimens vary in size from less than 1·0 cm in diameter to 4 cm long. They are generally more or less rectangular and contracted specimens may be dorso-ventrally or laterally flattened. Both siphons are sessile and are present on the anterior surface. Variations in morphological characters occur in association with increasing size or increasing rigidity of test due to sand encrustation. Without sand the test is thin and semitransparent and may have fine hairs especially from the posterior end.

In large specimens from the South Shetlands (coll. W. Schmitt, 3 to 4 cm long) the test is free of sand and is very delicate posteriorly while the anterior half of the body is thickened, except for an area immediately surrounding the siphons. On contraction, the anterior thickened portion of the test forms a protective dome over the dorso-ventrally contracted body and the siphons are drawn down into, and are protected by, the surrounding thicker test. Smaller specimens from California (Newport Harbour coll. MacGinitie, 1·0 cm) and from Patagonia (*A. krausei* Michaelsen 1898, 0·9 cm) have the test thickened in a similar way although there is some sand adhering. Contraction causes a withdrawal of the apertures which are protected by the sandy ridge of thickened test surrounding them. Specimens from Moreton Bay (1·5 cm), from Tierra del Fuego (Michaelsen 1898, 1·8 cm) and the specimen from the Antarctic Peninsula (Kott 1969, 2 cm) are heavily encrusted with sand causing the test to be rigid. Here the area of test surrounding the apertures is extended into a fold involving the body wall. On contraction the body is laterally flattened and the fold, especially from the right side, closes over the apertures.

The body musculature basically consists of about 20 superficial circular muscles around the branchial siphon and usually more associated with the atrial siphon. The basal muscles on the atrial siphon are not continuous around the anterior side of the siphon. These are referred to as posterior atrial muscles and they extend well down the dorsal surface. There is only a single circular band associated with the tentacular velum. From each side of the siphons longitudinal bands radiate not more than half-way down the body. There are more longitudinal bands from the branchial than from the atrial siphons. The proximal 8 to 10 circular bands around each aperture have fibres joining the longitudinal bands; and the posterior atrial muscles also have some fibres joining the distal extent of the longitudinal muscles.

In specimens from California there are about 20 circular bands around the branchial siphon; about 15 circular bands around the atrial siphon; and 6 posterior atrial bands. There are 14 longitudinal bands from each side of the branchial siphon and 8 from each side of the atrial siphon. In the specimens from the South Shetlands there are 18 longitudinal bands from either side of the branchial aperture; 15 from either side of the atrial aperture and 6 to 15 posterior atrial bands. The circular bands vary from 20 to 50 on both siphons. Where a protective fold of test is developed (specimens from Moreton Bay) the anterior 8 circular muscles of the branchial and atrial siphons remain unmodified and remain associated with the proximal extent of the longitudinal bands. However the next 4 to 7 circular bands break up into fibres dorsally, ventrally and on both sides of each siphon in the fold of the body wall associated with the test fold. These bands are not associated with the longitudinal bands. Posteriorly to these, a further 10 muscle bands on either side of the dorsal line are homologous with the posterior atrial bands in other specimens and some fibres branch into the longitudinal bands; 5 similar bands on either side of the ventral line represent modified circular bands from the base of the branchial siphon and are also associated with the longitudinal bands. In these specimens there are 11 longitudinal bands on either side of the branchial siphon and 6 longitudinal bands on either side of the atrial siphon. In the larger specimen from the Antarctic Peninsula 12 circular bands remain uninterrupted around the apertures and the next 7 circular muscles are associated with the protective folds and break into fibres on each side of the apertures. In this specimen these muscles are continuous across the dorsal and ventral surfaces. This is a more posterior group of muscles than those associated with the fold in the Moreton Bay specimens and only 5 short bands remain posterior to the folds, on either side of the dorsal line and associated with the longitudinal bands. In this specimen there are 25 longitudinal bands per side.

The data given above indicate that, with an increase in size of the body, there is an increase in the number of longitudinal muscle bands and the numbers of bands associated with the siphons. There is also considerable variation in the relative numbers of bands utilized for different functions. The longitudinal muscles are never involved with the fold or ridge surrounding the apertures and their function appears to be to draw the apertures down into the body and to dorso-ventrally flatten the body. They are consequently longer when the test is less rigid. The uninterrupted circular bands act as siphonal sphincters. However, when the protective fold is developed, it is the circular bands from the middle of the siphons which, together with a varying number of posterior atrial muscles, break into fibres and operate the protective folds of test. The number of circular bands which remain entire in the anterior extent of the siphon affects the number of posterior atrial muscles which become involved with the closing mechanism and seems to depend on the extent to which the siphons are developed. Consequently, in the large specimen from the Antarctic Peninsula where 12 muscle bands operate as a sphincter, the posterior atrial bands contribute to the operation of the closing mechanism leaving only a few of these below the folds. In the Moreton Bay specimens 8 muscle bands operate as a sphincter, the remainder of the circular siphonal muscles are modified to operate the closing mechanism, and the posterior atrial muscles, interrupted across the dorsal line, all remain behind the protective fold and probably contribute to the lateral flattening of the body. Unmodified posterior atrial bands, inserted into the body wall where it is associated with the thicker test around the siphons, probably draw the atrial siphon towards the branchial siphon and draw the test in more closely around both siphons.

In addition to the muscle bands described above short muscle bands deep to the longitudinal bands are continuous around the dorsal and ventral borders of both sides of the body. These muscles tend to flatten the body.

The dorsal tubercle is a simple slit and there is a tongue-like evagination of the body wall projecting from the region of the dorsal gland. The branchial sac has 6 double rows of 11 infundibula. Transverse vessels between each double row bear triangular papillae which are enlarged to the left of dorsal line. These transverse vessels are continuous over the dorsal membrane. A dorsal lamina is not formed. Only in the specimen from the Antarctic Peninsula are papillae developed also on the intermediate transverse vessels. The latter do not cross the dorsal line. Stigmata form 8 to 10 spirals. These are often interrupted in the vertical or horizontal axis and are crossed by radial vessels.

Occurrence.—Antarctic Peninsula, South Shetlands (Kott 1969); Tierra del Fuego (Michaelsen 1898); Patagonian Shelf (Michaelsen 1912, Millar 1960); California (Van Name 1945); New Zealand (Millar 1960); South Africa (Millar 1955, 1960); Moreton Bay, Queensland (New records); Japan (Oka 1915, 1929); at 23 and 115 m.

Discussion.—The tremendous variation in the disposition of the body wall musculature together with the widely dispersed records suggests that more than a single species is involved here. It is apparent however that the muscles are disposed merely in response to the degree of rigidity of the test. Where a heavy sand incrustation prohibits contraction of the anterior test around the withdrawn siphons the test instead folds over the siphons and the muscle bands break up into fibres in the folds. The numbers of muscle bands which are modified to effect the various contractions required of the body wall are immensely varied and the most posterior circular bands may either be involved in the protective fold or may remain superficial to the longitudinal bands posterior to the fold. This may depend to some extent on the size of the fold; or on the relative size of the body; or the development of the siphons.

In younger specimens (*A. capensis* Millar, *A. himeboja* Oka, *A. sabulosa* Oka, *A. krausei* Michaelsen), the apertures remain in the primitive position, the branchial aperture anteriorly and the atrial aperture antero-dorsally and the ridge of test protecting them has not developed. The interrupted muscles bands behind the atrial siphon, the number of coils in each fundibulum, the number of infundibula and transverse vessels and the single muscle band in the tentacular velum all indicate that these specimens do fall within the range of variation of the species.

The species is distinguished from *Agnesia septentrionalis* by the larger number of spirals in each infundibulum; by the fact that at least some circular muscles are not completely continuous around the siphons; and by single muscle band associated with the tentacular velum.

AGNESIA DEPRESSA Millar

Agnesia depressa Millar, 1955*a*, p. 1.

Remarks.—Millar's specimens (4) ranged from 0·8 to 1·1 cm in greatest diameter and this species resembles other *Agnesia* spp. in the presence of hair like processes from the test and in the numbers and arrangement of transverse vessels and infundibula. The species is distinguished only by the reduction of the branchial papillae and is apparently closely related to *Agnesia glaciata.*

Occurrence.—Swedish Deep-sea Expedition Sta. 371; N 24°12′, W 63°23′ to N 24°28′, W 63°18′; 5850 to 5860 m (Millar 1955*a*).

Discussion.—It is remarkable that a species from this depth shows so little deviation from other species. Apart from the longer test hairs it demonstrates none of the usual modifications, especially of the branchial sac, which are usually associated with abyssal species.

Genus ADAGNESIA Kott, 1963

Bifid papillae on the transverse vessels. Dorsal lamina absent. Area of flat unperforated membrane crossed by primary transverse vessels present along mid-dorsal line of branchial sac. Enlarged triangular papillae on the primary transverse vessels to the left of the dorsal line may correspond to dorsal languets. The number of infundibula always exceeds the numbers of branchial papillae in each row. Always more than 4 primary transverse vessels present.

ADAGNESIA ANTARCTICA Kott

Adagnesia antarctica Kott, 1969, p. 99.

Specimen examined.—U.S. National Museum: West of Macquarie Island, "Eltanin", St. 1418, 86–101 m. (Holtype U.S.N.M. 11966.)

Remarks.—The single available specimen is rounded and 1·5 cm in diameter. The test is thin but brittle and encrusted with sand. The apertures are surrounded by a rim of thickened test around the upper surface. There are about 20 circular muscles around each siphon and 35 longitudinal muscles on each side of the body extending only a short distance from the base of the siphons. Short transverse muscle bands are present in rows around the dorsal and ventral borders on either side of the body. In the branchial sac there are 7 double rows of spiral infundibula separated by 6 primary transverse vessels. Biramous papillae with long arms are present on the primary transverse vessels but there is never more than one of these papillae corresponding to each spiral and often there are fewer. Along the dorsal line a large single languet develops from each primary transverse vessel, as in *Agnesia.*

Occurrence.—Only the holotype from west of Macquarie Island is known.

Discussion.—The species is distinguished from *Caenagnesia* spp. by reduction in the numbers and length of longitudinal muscle bands, a reduction in the length of transverse bands and their interruption over the mid line, and a reduction in the numbers of circular siphonal muscle bands; a reduction in the numbers of primary transverse vessels, infundibula and branchial papillae; the loss of the dorsal lamina and the presence of enlarged dorsal languets on the primary transverse vessels on the dorsal line. In the condition of the dorsal lamina and numbers of infundibula in each row, the species resembles *Agnesia* spp. However, other reductions in the branchial sac and body musculature in the latter genus are greater than in *Adagnesia antarctica* which retains the biramous branchial papillae of *Caenagnesia* and may be considered phylogenetically intermediate between *Caenagnesia* and *Agnesia.*

ADAGNESIA OPACA Kott

Adagnesia opaca Kott, 1963, p. 76.

Specimens examined.—Queensland Museum (Reg. No. G4907): coll. W. Stephenson *et al.*, Moreton Bay, Queensland (numerous specimens). Australian Museum: coll. J. MacIntyre, 16.6.65, 140 m, off Cronulla, N.S.W. (fragments only).

Remarks.—This is a particularly large species (3 to 4 cm diameter) and represents the most highly specialized genus of the family in regard to its closing mechanism. The test is thin and completely rigid and brittle with sand. On both sides of the apertures folds of test form lips so shaped that the excurrent aperture is directed upwards and the incurrent aperture is directed downwards toward the substrate on which the animal lies. The body musculature is correspondingly specialized and bears a relationship to that of *Agnesia glaciata.* Only a limited number of circular muscle bands are present around the siphons, superficial to short radiating longitudinal bands which extend no further than the base of the siphons. Both anterior and posterior to the circular muscles of both siphons, there are very strong transverse bands extending across the dorsal line from the base of the protective folds of test. Their contraction draws these folds together. The general body musculature is reduced to very short muscle bands around the anterior, dorsal, posterior and ventral borders of both sides of the body. These short bands along the dorso-lateral border are arranged in parallel to the long axis of the body and may represent the remnants of the distal portions of longitudinal bands which radiate from the siphons. The remaining short muscle bands which appear to be deeper in the body wall than those along the dorsal border, are probably homologues of similar muscles in *Agnesia glaciata* and represent the remnants of the inner circular body musculature. About 30 transverse vessels, each supporting about 32 bifid papillae, alternate with single rows of about 60 infundibula. However, although there are triangular languets on each transverse vessel to the left of the dorsal line large languets alternate with small languets suggesting that those transverse vessels bearing the latter have developed later as a result of proliferation of the branchial sac. In the posterior part of the branchial sac this proliferation can be observed occurring and single infundibula tend to subdivide into two to increase the number of spirals in each row and then further subdivision occurs to increase the number of rows of infundibula so that 4 spirals, arranged in a square, result from the subdivision of a single spiral infundibulum. In association with the highly developed closing mechanism the gonoducts are directed anteriorly and the species is probably viviparous.

Occurrence.—Moreton Bay, Queensland (Kott 1963); off Cronulla, N.S.W., 140 m (New Record).

Discussion.—The reduction of body musculature has proceeded beyond the condition found in *Adagnesia antarctica* and indeed, beyond the degree of reduction and specialization of this musculature known in *Agnesia* spp. However the condition of the dorsal lamina and branchial papillae, and the numbers of branchial papillae in relation to the numbers of infundibula in each row establish its relationship to *Adagnesia antarctica* from which it has diverged by modifications of the musculature to operate a highly specialized closing mechanism, by the secondary development of numerous transverse vessels in the branchial sac and proliferation of the numbers of infundibula in each row and by a corresponding increase in the numbers of branchial papillae on the transverse vessels. The similarity of the branchial sac of this species to that of *Caenagnesia* spp. is due to this proliferation of infundibula and transverse vessels together with the retention of biramous branchial papillae. However the reduced number of branchial papillae associated with each infundibulum in the present species together with the condition of the dorsal lamina clearly distinguish the species from *Caenagnesia*. The large numbers of infundibula in the branchial sac is a secondary development perhaps related to the large size characteristic of individuals of this species.

ZOOGEOGRAPHY

The widely dispersed records of *Agnesia glaciata* suggest that this represents an ancient species with a well established cosmopolitan distribution, and that today records of this species from the Pacific, Antarctic and Indian Oceans may represent relict populations now isolated. The occurrence of 2 species of the family exclusively in the Antarctic also probably represent relict populations now isolated by the submergence of land or submarine bridges. Despite the fact that it is the phylogenetically primitive genus *Caenagnesia* which is today endemic in the Antarctic it is not thought possible for the family to have developed there and to have then radiated northwards as far as northern boreal waters. If this had occurred one would not expect, in isolated areas, so very few species. It is the wide distribution and morphological homogeneity of *Agnesia glaciata* which suggests that the species (and the family) was well established a long time ago and persists today as a highly successful relict form.

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TYPE SPECIMENS IN THE MACLEAY MUSEUM UNIVERSITY OF SYDNEY

III. BIRDS

P. J. STANBURY
School of Biological Sciences, University of Sydney

[Read 27th November, 1968]

INTRODUCTION

There are about 9000 bird skins in the Macleay Museum at the University of Sydney. At least 57 of these are types or belong to a type series. This paper lists them together with associated pertinent information. As noted in the other papers in this series (Stanbury 1968, Goldman, Hill and Stanbury 1969) further types may lie unrecognized in the Museum.

THE BIRD TYPES

Some of the bird types were collected on the "Chevert" expedition to north Queensland and New Guinea waters in 1875 (see Macmillan 1957). Others were obtained from collectors in the northern parts of Australia. The new species were described by G. Masters (the first curator of the Macleay Museum[1]) and by E. P. Ramsay.

A few of the type specimens are mounted but most are stuffed skins. All are kept in the dark in air-tight drawers.

In the table that follows the BT numbers refer to the numbers of the compartments in which the specimens are stored. At present there is no complete register of birds; a register has been started but it is unlikely to be completed before the end of 1969. When the register is complete each type specimen will be numbered with the prefix B. (The BT number will appear in brackets on the same label.)

The classification in the table is that devised by A. Wetmore of the Smithsonian Institute, Washington, in 1960.

The reference to the original description of each type specimen is given. In addition the revised name used by G. M. Mathews (in the two parts of Systema Avium Australasianarum, published in 1927 and 1930 by the British Ornitholigists Union) is given. Reference to the page quoted will usually provide a list of earlier synonymous names.

The Australian Museum holds some types of which the Macleay Museum also holds individuals of the same species collected from the same locality in about the same year.

In view of the relations of Sir William Macleay with the Australian Museum and with the University of Sydney it is possible that some of such specimens in the Macleay Museum are part of a type series. I have therefore labelled these "type series?". In these instances the reference number of the Australian Museum type specimen also is given in the table.

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[1] The curators of the Macleay Museum were G. Masters 1888–1912; J. Shewan 1913–1933; K. E. W. Salter 1934–1944; J. R. Henry 1945–1958; Elizabeth Hahn 1958–1962; and Jennifer M. E. Anderson 1963–1966; all of whom have contributed either directly or indirectly to this list. I am especially grateful to my immediate predecessor, Mrs. J. Anderson, for her work in this regard.

List of Specimens

Family	Scientific name under which originally described	Reference PROC. LINN. SOC., N.S.W.	Name in Mathews : *Systema Avium Australasianarum* and page reference	No. of specimens and sex where known	Type or type series	Locality and date collected where known	Macleay Museum Reg. No.	Type specimen number in Australian Museum
Megapodiidae	*Megapodius assimilis* Masters, 1875	1 : 59	*Megapodius reinwardt* Dumont, p. 13	3 1 ? 2 female	Type series	Dungeness Island, Bet Island, Torres Straits	BT20	None
Laridae	*Sterna nigrifrons* Masters, 1875	1 : 62	*Sterna dougallii* Montagu, p. 138	1 1 male	Type	Warrior Reef, Torres Straits 17.7.1875	BT15	None
Laridae	*Larus longirostris* Masters, 1877	2 : 113	*Bruchigavia novaehollandiae* (Stephens), p. 147	6	Type series	King George's Sound	BT16	None
Columbidae ?	*Macropygia rufo-castanea* Ramsay, 1879	4 : 314	*Macropygia rufa* Rams., p. 61	1	Type series ?	Solomon Islands	BT25	0.18711 male
Podargidae	*Podargus gouldi* Masters, 1875	1 : 45	*Podargus strigoides* (Latham), p. 355	1 1 male	Type	Gulf of Carpentaria, June, 1875	BT19	None
Muscicapidae	*Gerygone simplex* Masters, 1875	1 : 52	*Ethelornis mastersi* (Sharpe), p. 464	2 1 male 1 female	Type series	Gulf of Carpentaria	BT1	None
Muscicapidae	*Pachycephala robusta* Masters, 1875	1 : 49	*Pachycephala robusta* Masters, p. 668	1 1 female	Type	Cape York	BT2	None
Muscicapidae	*Pachycephala kandavensis* Ramsay, 1875	1 : 66	*Pachycephala pectoralis* (Lath.), p. 667	4 2 male 2 female	Type series	Kandavu, Fiji	BT3	None
Muscicapidae	*Pachycephala occidentalis* Ramsay, 1877	2 : 212	*Pachycephala pectoralis* (Lath.), p. 664	5 4 male 1 female	Type series ?	Western Australia and King George's Sound	BT4	0.18570
Muscicapidae	*Pachycephala dubia* Ramsay, 1879	4 : 99	*Muscitrea griseiceps* (Gray), p. 680	2	Type series ?	Astrolabe Bay, New Guinea	BT5	0.18575

List of Specimens—Continued

Family	Scientific name under which originally described	Reference Proc. Linn. Soc., N.S.W.	Name in Mathews : *Systema Avium Australasianarum* and page reference	No. of specimens and sex where known	Type or type series	Locality and date collected where known	Macleay Museum Reg. No.	Type specimen number in Australian Museum
Muscicapidae	*Sericornis brunneopygius* Masters, 1875	1 : 53	*Sericornis minimus* Gould, p. 615	6 3 male 3 female (7 originally collected)	Type series	Cape York	BT6	None
Muscicapidae	*Sauloprocta cockerelli* Ramsay, 1879	4 : 81	*Leucocirca cockerelli* (Ramsay), p. 498	2	Type series ?	Solomon Islands	BT7	0.18716 male 3849 male ? 3848 female
Muscicapidae	*Monarcha brodiei* Ramsay, 1879	4 : 80	*Piezormona barbata* (Ramsay), p. 516	1	Type series ?	Solomon Islands	BT8	0.18724 male
Muscicapidae	*Myiagra pallida* Ramsay, 1879	4 : 79	*Submyiagra ferrocyanea* (Ramsay), p. 501	2	Type series ?	Solomon Islands	BT9	3839 male 3838 male ? 3840 female
Muscicapidae	*Myiagra ferrocyanea* Ramsay, 1879	4 : 78	*Submyiagra ferrocyanea* (Ramsay), p. 501	4	Type series ?	Solomon Islands	BT10	3833 male 3837 male 0.18720 male ? 3835 female
Muscicapidae	*Eopsaltria inornata* Ramsay, 1874	*Proc. Zool. Soc. Lond.*, 1874, p. 604	*Muscitrea griseiceps* (Gray), p. 679	1	Type series ?	Endeavour River	BT11	0.32614
Sternidae	*Sternula inconspicua* Masters, 1875	1 : 63	*Sternula albifrons* (Vroeg), p. 140	4 1 male 3 female (5 specimens originally collected)	Type series	Cape York, 19.6.1875, and 22.9.1875	BT14	None

List of Specimens—Continued

Family	Scientific name under which originally described	Reference Proc. Linn. Soc., N.S.W.	Name in Mathews: *Systema Avium Australasianarum* and page reference	No. of specimens and sex where known	Type or type series	Locality and date collected where known	Macleay Museum Reg. No.	Type specimen number in Australian Museum
Meliphagidae	*Ptilotis frenata* Ramsay, 1874	*Proc. Zool. Soc. Lond.*, 1874, p. 603	*Meliphaga frenata* (Ramsay), p. 775	1	Type series ?	Rockingham Bay	BT23	0.18560 male 0.18561 female 0.18562 female
Dicaeidae	*Pardalotus assimilis* Ramsay, 1877	2 : 180	*Pardalotus striatus* (Gm.), p. 723	3	Type series ?	New South Wales	BT24	0.18593
Zosteropidae	*Zosterops flavogularis* Masters, 1876	1 : 56	*Zosterops albiventris* Reichenb., p. 699	7 4 male 3 female	Type series	Cape Grenville	BT12	None
Zosteropidae	*Zosterops ramsayi* Masters, 1875	1 : 56	*Zosterops lateralis* (Lath.), p. 709	2 2 male	Type series	Palm Island, N.E. Australia	BT13	None

Acknowledgements

I wish to express my thanks to the Curator of Birds at the Australian Museum Mr. H. J. de S. Disney, and especially to Mr. K. A. Hindwood, Honorary Associate of the same Museum, who very kindly sorted through a selection of suspected type specimens.

I am also grateful to Mrs. Karen Paynter and to Miss Kerry Smith for their proficient technical assistance in the compiling of the several drafts of this list.

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TYPE SPECIMENS IN THE MACLEAY MUSEUM UNIVERSITY OF SYDNEY

IV. MAMMALS

P. J. STANBURY
School of Biological Sciences, University of Sydney

[Read 27th November, 1968]

INTRODUCTION

The Macleay Museum has nearly 1,200 mammalian specimens. At least 8 of these are types. As noted in the earlier papers in this series (Stanbury 1968, Goldman, Hill and Stanbury 1969, Stanbury 1969) further types may lie unrecognized in the Museum.

THE MAMMALIAN TYPES

Six of the mammalian types were collected on the "Chevert" expedition to New Guinea in 1875 (see Macmillan 1957). The other two, from North Western Australia, were collected by W. W. Froggatt, one of Sir William Macleay's collectors.

All but one of the specimens are mounted or stuffed skins. *Sminthopsis froggatti* is stored in spirit. All the specimens are stored in the dark. Some fading is apparent on most of the specimens. One, *Dorcopsis beccarii* has lost about 40% of its fur.

RARE MARSUPIALS

The Macleay Museum also possesses a number of rare marsupial specimens which are not types but which now are extinct or virtually so: for example *Onychogalea fraenata* (Lower Murrumbidgee, N.S.W.), *Myrmecobius rufus* (S. Australia), *Antechinus apicalis* (King Georges Sound, W. A.) and *Thylacinus cynocephalus* (Tasmania).

Acknowledgements

I am indebted to the previous curators of the Museum, and especially to Mrs. J. Anderson (1963–1966). I wish also to thank Drs. W. D. L. Ride and J. L. Bannister of the Western Australian Museum who checked the first draft of this list and made many helpful suggestions.

References

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

MACMILLAN, D. N. S., 1957.—"A Squatter went to Sea." Currawong Publishing Company, Sydney.

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STANBURY, P. J., 1969.—Type specimens in the Macleay Museum, University of Sydney III. Birds. PROC. LINN. SOC. N.S.W., 93 : 457-461.

List of Specimens

Family	Scientific name under which originally described	No. of specimens, sex and kind of type	Locality	Reference (Proc. Linn. Soc., N.S.W.)	Macleay Museum Reg. No.	Notes
Macropodidae	*Macropus gracilis* Miklouho-Maclay	1 male, Holotype	Port Moresby, New Guinea	9 (1884) : 894 Plate 39, figs 7 and 8	M382	
Macropodidae	*Macropus jukesii* Miklouho-Maclay	1 female, Holotype	Port Moresby, New Guinea	9 (1884) : 891 Plate 39, figs 1–6	M380	Skull removed (slightly affected by magnesium chloride as noted by de Miklouho-Maclay)
Macropodidae	*Dorcopsis beccarii* Miklouho-Maclay	1 female, Holotype	Port Moresby, New Guinea	10 (1885) : 146 Plate 20, figs 1–4	M383	Poor condition. Much fur and one foot missing
Macropodidae	*Dorcopsis macleayi* Miklouho-Maclay	1 male, Holotype	Port Moresby, New Guinea	10 (1885) : 149 Plate 20, figs 5–9	M381	
Macropodidae	*Petrogale assimilis* Ramsay	1 female, Holotype	Palm Island	1 (1876) : 360	M422	A male M423 exists, collected from the same locality and possibly at the same time (contradicting Ramsay's remark (p. 361))
Dasyuridae	*Antechinus* (*Podabrus*) *froggatti* Ramsay	1 female, Holotype	Derby, W. Australia	2 (Series 2) : 552	M1177	On loan to the Australian Museum since 1959 and now catalogued there M8019. The skin is in spirit, the skull separate
Peramelidae	*Perameles auratus* Ramsay	1 male, Holotype	Derby, W. Australia	2 (Series 2, 1887) : 551	M468	The type specimen is a male with a malformed tail. A female collected from the same locality has an apparently normal tail. Both specimens have had their skulls removed and these are stored separately
Pteropidae	*Pteropus* (*Epomops* ?) *epularis* Ramsay	1 male, Paratype ?	Katow, New Guinea	2 (1877) : 8	M235	

HATCHING AND LARVAL DEVELOPMENT OF *HAPLOSTOMELLA AUSTRALIENSIS* GOTTO (COPEPODA, FAM. ASCIDICOLIDAE), A PARASITE OF THE ASCIDIAN *STYELA ETHERIDGII* HERDMAN

D. T. Anderson and G. T. Rossiter

School of Biological Sciences, University of Sydney

[Read 27th November, 1968]

Synopsis

H. australiensis produces paired cylindrical ovisacs each containing 70–100 eggs. Hatching occurs as a lecithotrophic, positively phototropic nauplius which swims briefly then moults to a demersal first copepodite. This stage exhibits sexual dimorphism and is probably the infective stage of the life cycle. Hatching is osmotic in the usual copepod manner and is stimulated by light and mechanical agitation. The obligatory light stimulus ensures that hatching occurs after the ovisac is discharged from the host. The response to mechanical agitation ensures a synchronous hatching which ruptures the tough wall of the ovisac. The hatching mechanism is specialized and the larval development is abbreviated compared with those of other ascidicolous copepods.

INTRODUCTION

During the course of a general survey of copepods of the Sydney area, in search of species suitable for embryological study, the authors collected specimens of a large worm-like parasitic copepod inhabiting the oesophagus and stomach of the simple ascidian *Styela etheridgii* Herdman. The parasite was identified by Dr. R. V. Gotto of Queen's University, Belfast, as a new species of the genus *Haplostomella* Chatton and Harant 1924, family Ascidicolidae. The four previously described species of *Haplostomella* have all been collected from northern hemisphere localities, where they occur in compound ascidians. The new species, named *H. australiensis* Gotto, has been described by Gotto (1968). In the present paper, we present observations on the general breeding activity, hatching and larval development of this animal.

MATERIALS AND METHODS

Adult females of *H. australiensis* were collected at intervals during June, July and August, 1967. The animals were taken from specimens of *Styela etheridgii* living at low tide level on Bottle and Glass Rocks on the south shore of Sydney Harbour. Records were kept of the frequency of occurrence of egg masses attached to the animals, and the later embryonic development, hatching and first two larval stages were studied using egg masses cultured in the laboratory.

The egg masses were cultured in glass tubes, the lower ends of which were closed with fine nylon gauze and immersed in well-aerated, filtered sea water. The water was changed regularly and tubes cleaned of algal film every 2 days. The cultures were maintained at 20°C. The water temperature in the natural habitat of the copepods at the time of collection ranged from 13 to 18°C.

The aquarium containing the culture tubes was at no time subjected to direct sunlight, but the laboratory was illuminated through windows on its northerly aspect during the day. Fluorescent lighting supplemented natural illumination during working hours. At all times, the culture tubes were shaded from light from above by a sheet of white paper placed over their upper ends. Mention is made of these facts because it was subsequently determined that the embryos are sensitive to bright light stimulation as a causative factor in hatching.

The sequence of events in hatching was observed for individual embryos and for whole egg masses. The finer details of hatching of individual embryos, including the rupture of egg membranes and accurate measurements of changes in volume, were recorded by mounting eggs in sea water on a cavity slide sealed with a cover slip and observing hatching by phase contrast microscopy.

The sensitivity of the embryos to bright light stimulation was studied using a sharply focussed microscope lamp to deliver either flashes or longer periods of bright light stimulation. By this technique, the days on which embryos could be induced to hatch by stimulation with bright light were determined, relative to the day of hatching of unstimulated embryos of the same age. This difference is referred to in the following account as days before "normal" hatching.

The hatching response of embryos in solutions of different osmotic strengths was also studied, in accordance with the view expressed by Marshall and Orr (1954) and Davis (1959) that a common osmotic mechanism underlies hatching in copepods. Embryos were immersed in hypotonic or hypertonic sea water in Petri dishes brightly illuminated under a binocular microscope. Newly emerged nauplii, or the embryos if hatching failed to occur within a fixed period, were then transferred back to normal sea water. Controls remained in normal sea water throughout. Hypotonic sea water, osmotically equivalent to a 2·4% salt solution, was prepared by diluting sea water (3·5% salt solution) to 70% with distilled water. Hypertonic sea water (7·5% salt solution) was prepared by adding 4 gm. sodium chloride per 100 ml. to normal sea water.

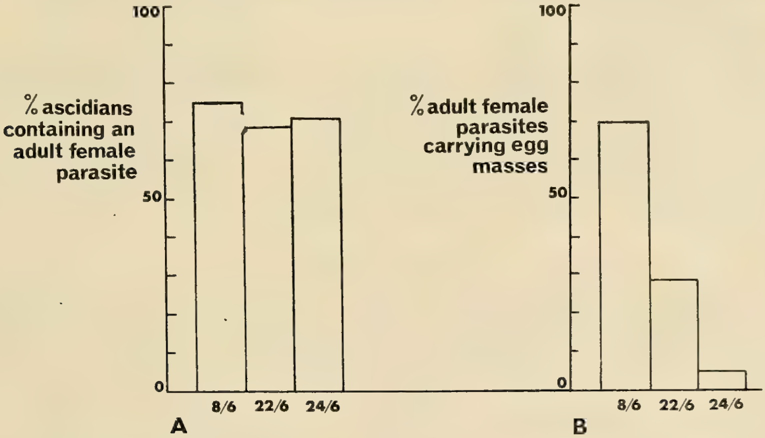

Fig. 1 A, % occurrence of adult female *Haplostomella* in three samples of *Styela* from a single population; B, % of parasites in each sample bearing egg masses.

RESULTS

Occurrence and breeding of adult females

The percentage occurrence of *H. australiensis* females in the ascidian *Styela etheridgii* in three separate samples collected at Bottle and Glass

Rocks is shown in Fig. 1A. The percentage, in each sample, of females which carried egg masses is shown in Fig. 1B. The decline in the percentage of ovigerous females in the second and third samples suggests a trend towards termination of a breeding cycle. The number of ascidians examined in the samples were 16, 75 and 88 respectively.

In none of the ascidians examined was there more than one adult female *Haplostomella*. The minimum length of the specimens was 4 mm., while the average length was 5 mm.

Culturing of egg masses and larvae

Most of the difficulties previously associated with the laboratory culture of egg masses from parasitic copepods (Wilson 1905, 1907*a*, 1907*b*, 1911*a*, 1911*b*) were experienced again in the present work. From the culture of 32 egg masses, only 6 pairs of masses already containing embryos at an advanced stage of development when collected remained viable until hatching. From 3 of these masses, embryos which had received no form of artificial stimulation hatched after 9, 13 and 17 days of culture respectively. Egg masses with embryos at very early stages of development, for example, cleavage or gastrulation, remained viable in culture for about 15 days. Maintenance of the hatched larval stages in the laboratory also proved difficult. About 95% of the nauplii hatched from egg masses in the laboratory failed to survive the first moult into a first copepodite stage. Because of the low survival rate, the few first copepodites which did emerge were fixed while intact, and development was not followed beyond this stage.

The egg masses

H. australiensis, like many copepods, lays its eggs into paired cylindrical ovisacs attached to the genital apertures of the female. The eggs when laid are spherical and 180μ in diameter. Seventy to 100 eggs are closely packed within each ovisac, which measures about 3 mm. × 0·8 mm. The eggs tend to be flattened slightly in the early stages of development, due to their close packing. They then gradually assume a regular ellipsoidal shape, 200μ long and 160μ in diameter.

The ovisacs function as brood chambers and remain attached to the female at least until the embryos reach a late stage of development. The period of development is estimated to be 6–8 weeks, taking into account the observation of 2 weeks of early development and 2½ weeks of later development of embryos in culture. No ovisacs with embryos at an intermediate stage of development were collected.

The newly hatched larva

The newly hatched nauplius of *H. australiensis,* 200μ in length, is illustrated in Fig. 2G. The nauplius is free-swimming and lecithotrophic. The antennules, antennae and mandibles all bear swimming setae, but feeding spines are absent. The labrum is also poorly defined. The post-naupliar region is large and swollen, but shows no external signs of segmentation or limb rudiments. The nauplius is markedly phototropic and is a very rapid swimmer.

The sequence of events in hatching

Towards the end of embryonic development, for almost a week before hatching, the embryo shows peristaltic movements of the gut and irregular, rather infrequent twitching of the body. Just before hatching is initiated, there is a marked increase in activity. For a period of one or two minutes, the embryo exhibits vigorous movements of the whole body and especially of the three pairs of limbs.

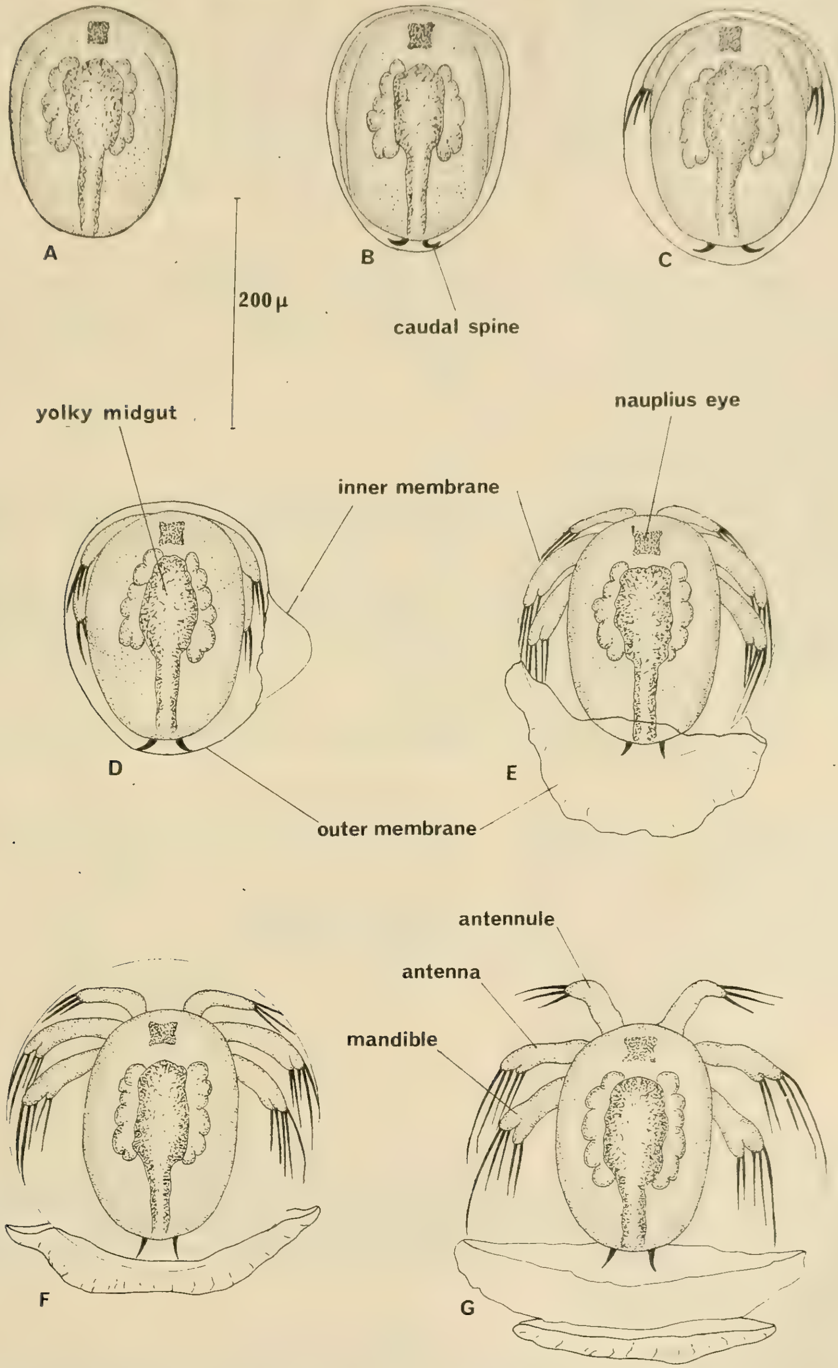

Fig. 2. The hatching sequence of *H. australiensis* (for description, see text).

After this phase of vigorous movement, the nauplius becomes quiescent and a thin film of fluid appears between the nauplius and the egg membranes (Figs 2A, 2B). The increasing volume of the fluid causes the membranes to swell, usually in the equitorial plane. The outer egg membrane ruptures, revealing the transparent inner membrane (Figs 2C, 2D). During this phase of swelling, the naupliar limbs move passively with the expanding inner membrane until they are in the extended swimming position (Fig. 2E). The volume of fluid within the inner membrane continues to increase until the membrane forms a sphere 270μ in diameter (Fig. 2F). The average time for expansion is 1–2 minutes; and the volume increases by a factor of 4·3=1. The nauplius, which fills the egg membranes before swelling begins, shows no increase in volume during the hatching process.

The nauplius remains quiescent within the inner membrane for a further period of 1–2 minutes after the inner membrane has ceased to expand. The inner membrane is then ruptured as the nauplius swims rapidly forwards (Fig. 2G). The nauplius, freed from its egg membranes, swims immediately to the surface and towards the light.

Physical factors influencing hatching

(i) Exposure to bright light:

The marked phototropism of the newly hatched nauplius is preceded by sensitivity to bright light for a number of days before hatching. During those days, muscular twitching of the embryo can be evoked on exposure to flashes of bright light, and the embryo can be stimulated to hatch prematurely by continuous exposure to bright light. The sensitivity to light of embryos from a single egg sac, measured for five days preceding normal hatching, is summarized in Table I.

TABLE I

Sensitivity to light of embryos from a single ovisac of Haplostomella australiensis

Days before normal hatching	Number of embryos tested	Period of exposure to bright light required to initiate hatching (minutes)	Average exposure period (minutes)
5	3	One hatched after 180 minutes. Two failed to hatch in this time	>180
4	3	120–180	150
3	10	30–90	80
2	15	4–20	15
1	25	1–7	3

As can be seen, the exposure time required to induce hatching falls rapidly as the day of normal hatching approaches. The sensitivity of the twitch response to a flash of bright light also increases during the final days of embryonic development.

(ii) Mechanical agitation:

Mechanical agitation also hastens the onset of hatching. In one embryo two days before normal hatching, mechanical agitation with needles under bright light caused hatching to commence after 3 minutes. The average time of exposure to bright light required to initiate hatching in embryos of this age is 15 minutes, and the minimum time is 4 minutes (Table I). A second embryo, one day before normal hatching, began to hatch while being removed from the ovisac with needles, even before being exposed to bright light.

For 5 embryos spread out in a Petri dish and exposed to bright light, 15 minutes elapsed between the first sign of hatching in the first embryo to hatch and in the last to hatch. For 20 embryos from the same ovisac, kept in contact inside part of the ovisac, the interval was only 6 minutes. In this case, the vigorous prehatching movements of the first embryo to hatch caused mechanical agitation of adjacent embryos and a rapid spread of the hatching response ensued.

The synchronization of hatching

Hatching under bright light stimulation was induced and observed for three intact ovisacs. In each case, the sequence of hatching and its timing for individual embryos within the ovisac was found to be the same as that previously described for individual embryos removed from their ovisacs and studied in isolation. Moreover, the functional significance of the sensitivity of the hatching response to mechanical agitation was revealed by these observations. The vigorous prehatching movements induced by the bright light stimulus began at first in only a few scattered embryos, but spread quickly through adjacent embryos until the whole ovisac vibrated. This mass activity persisted for about 3 minutes, and then almost all of the embryos simultaneously became quiescent as the 1–2 minute phase of expansion of the egg membranes began. The simultaneous increase in volume of the inner membranes, in addition to rupturing the outer membranes, generated a collective pressure sufficient to rupture the ovisac longitudinally. Most of the embryos, still quiescent within their expanding inner membranes, spilled out through the rupture and completed their hatching outside the ovisac. Those remaining within the ovisac hatched and escaped through the longitudinal slit.

The importance of synchronous hatching in promoting escape from the ovisac was confirmed by another experimental observation. Five embryos, one day before normal hatching, were loosely packed and sealed off in part of an ovisac. Simultaneous hatching was then induced by exposure to bright light, but the expansion of the egg membranes was able to be accommodated without rupture of the surrounding ovisac wall. The nauplii thus escaped within the closed ovisac. Although they made vigorous swimming movements, the nauplii were unable to rupture the tough ovisac wall and escape into the surrounding water.

Natural hatching

The hatching of embryos in the laboratory without bright light stimulation was not observed directly, but several batches of nauplii hatched in culture from ovisacs which had been observed to be intact on the previous day. Such hatching was noticed at about 9 a.m., by which time most of the nauplii had entered the quiescent period preceding the moult to a first copepodite (see below). This quiescence follows a 2–3 hour period of activity, indicating that the nauplii had hatched synchronously at about dawn. The associated ruptured ovisacs gave further indication that natural hatching proceeds in the same synchronous manner as experimentally induced hatching.

Hatching in hypotonic and hypertonic sea water

(i) Hypotonic sea water:

The hatching sequence was not altered by immersion of eggs in hypotonic sea water, but the rate of hatching was accelerated (Fig. 3). The duration of both the phase of prehatching activity and the phase of expansion of the inner membrane were shortened. When returned to normal sea water after hatching, the nauplii which had been hatched in hypotonic sea water did not differ in behaviour or further development from those hatched in normal sea water.

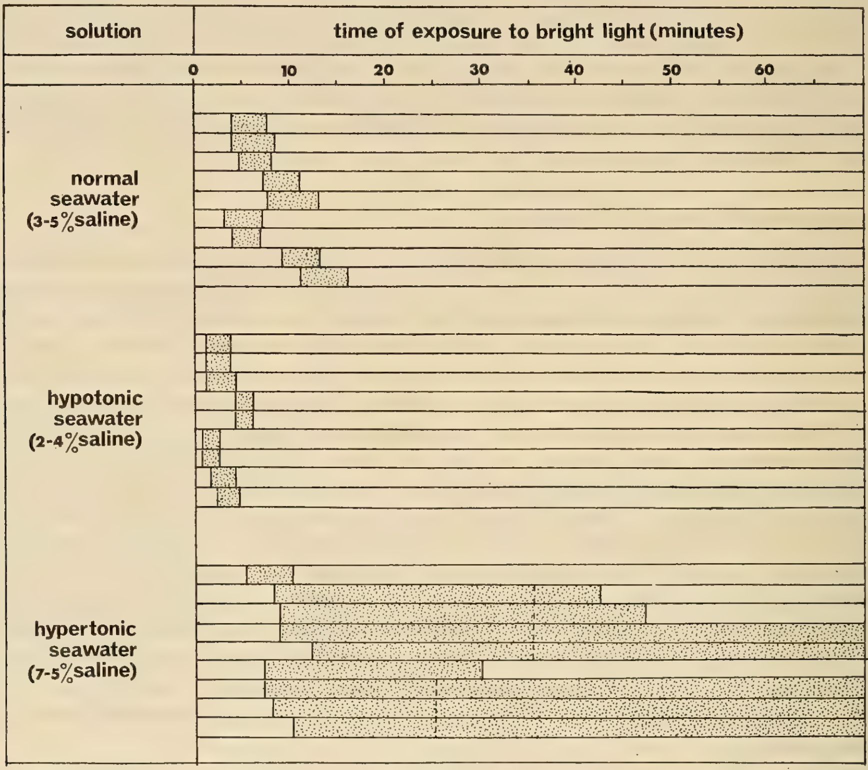

Fig. 3. The timing of light-stimulated hatching of *H. australiensis* in hypotonic and hypertonic sea water, for embryos 2 days before normal hatching. Each shaded block represents the time for one embryo to complete the hatching sequence.

(ii) Hypertonic sea water:

Following immersion in hypertonic sea water, both the hatching sequence and the rate of hatching were altered. In response to the stimulus of bright light, the embryos began their prehatching movements in the usual way, but the swelling of the egg membranes was completely inhibited. Only one embryo out of nine attained hatching in the hypertonic solution, in approximately normal time (Fig. 3). Of the remaining 8, three underwent delayed hatching after return to normal sea water, while the remainder failed to hatch. Although prehatching activity was prolonged, no swelling of the egg membranes ensued even after return to normal sea water.

Larval development

(i) The nauplius:

The nauplius, described and illustrated above, remains active at the surface of the water for 2–3 hours after hatching. It then sinks and becomes quiescent, entering the moult to the first copepodite stage.

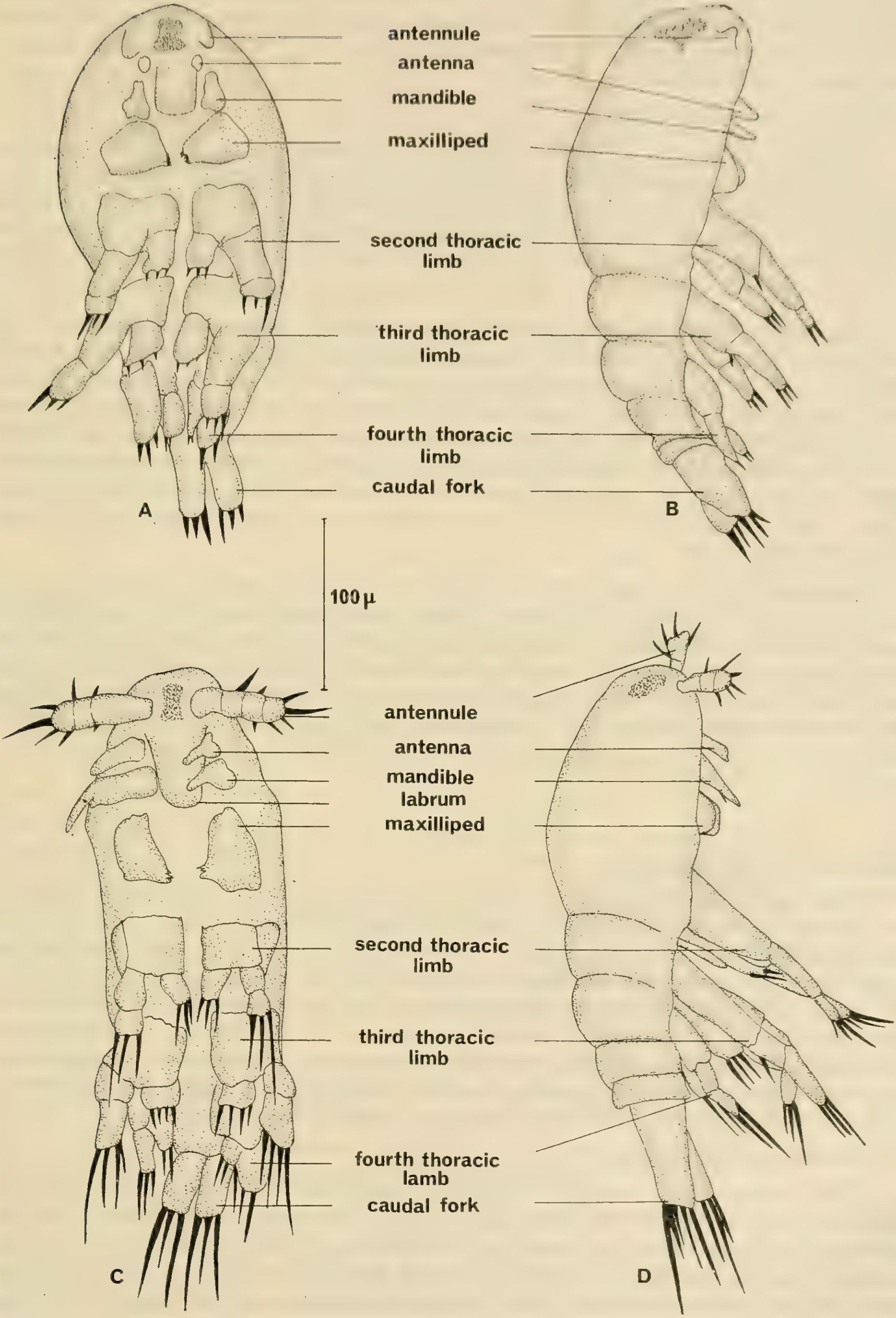

Fig. 4. The first copepodite of *H. australiensis.* A, female, ventral view; B, female, lateral view; C, male, ventral view; D, male, lateral view.

The nauplius swims in the manner typical of newly hatched copepod nauplii (Gauld, 1959), by rapid, synchronous beating of the three pairs of naupliar limbs. Swimming follows a spiral course. At no time does the nauplius display the slower, rhythmic movements typical of the later naupliar stages of planktonic copepods. The main propulsion comes from the action of the long, setose antennae and mandibles, with a lesser contribution from the shorter antennules.

(ii) The first copepodite:

Three to four hours after the onset of quiescence, the nauplius moults, yielding a first copepodite stage (Fig. 4). This larva is 280–300μ long. The naupliar appendages are greatly reduced, while the first three pairs of biramous trunk limbs are exposed as functional swimming limbs. The copepodite is not phototropic, and swims at or near the bottom of its container. Probably this stage or the next is the stage which enters the ascidian host.

The first copepodite of *H. australiensis* already shows sexual dimorphism. The male (Figs 4C, 4D) can be diagnostically distinguished from the female (Figs 4A, 4B) by the antennules, which are distinct and segmented in the male, small and inconspicuous in the female, a difference reflecting the specialized later function of the antennules as claspers in male ascidicolid copepods (Lang, 1948). In addition, the remaining naupliar limbs and trunk limbs of the male are generally larger and more setose than those of the female, and a greater space is observed between the maxillipeds and first pair of swimming limbs.

Neither the copepodite stage nor the adult female show traces of maxillules or maxillae. In view of the vermiform character and reduced limbs of the adult female, it is clear that further female larval stages would show the acquisition of two more pairs of trunk limbs, followed by reduction and simplification of the five pairs. The adult male of *H. australiensis* has not been identified, but probably resembles the *Cyclops*-like male of *Ascidicola* (Gotto, 1957) and has a more typical later larval development.

Discussion

Duration of development

The apparent duration of embryonic development in *H. australiensis,* 6–8 weeks, is comparable with those reported by Wilson (1905, 1907*a*, 1907*b*, 1911*a*, 1911*b*) for a great number of parasitic copepods. Such periods are long compared with the few days of embryonic development in *Cyclops* and the even shorter 1–2 days in *Calanus* (Marshall and Orr, 1954). The extended embryonic development of parasitic copepods is a reflection of a combination of larger eggs and prolonged direct development to a late larval stage before hatching. *Ascidicola rosea,* with a smaller egg, takes 18 days (Gotto, 1957), and *Gonophysema* 19–20 days (Bresciani and Lützen, 1961).

The hatching mechanism

The sequence of events in hatching, and the operation of the osmotic hatching mechanism in *H. australiensis* are comparable with those described for marine planktonic copepods by Marshall and Orr (1954) and for fresh water copepods by Davis (1959). Each of these shows the phase of vigorous activity just before hatching, the osmotic expansion of the inner membrane and rupture of the outer membrane, and the quiescence of the embryo during expansion of the membranes.

The observation for *H. australiensis* that immersion in hypotonic sea water affects the rate of hatching but not the time of onset of hatching, suggests that the hatching mechanism can be resolved into two components. The first is a light-sensitive component which, when activated, sets in motion the second, an osmotic component. It can be inferred that osmotic stress is set up between the contents of the space between the embryo and its membranes on the one hand, and the surrounding water on the other, as a result of the prehatching activity of the embryo. This activity could result either in secretion of an osmotically active substance or in a change in the structure and permeability of the inner membrane, or both. All that is obvious at the present time is that the activity has a light-sensitive trigger and that the osmotic stress resulting from the activity leads to membrane swelling and escape of the nauplius.

Hatching in natural conditions

Gotto (1957) observed through the transparent wall of *Corella parallelogramma* (Müller) that *Ascidicola rosea,* which normally inhabits the oesophagus of the host, migrates to the stomach of the host before releasing its ripe egg masses. Here the inner membranes of the eggs swell and burst forth from the clustered outer membranes, but remain intact around the nauplii during passage through the intestine and rectum. Escape of the nauplii from the swollen inner membranes occurs in the exhalent water current of the host.

Styela etheridgii has an opaque test, and events intervening between release of the egg sacs by *Haplostomella australiensis* and ensuing natural hatching of the nauplii can only be inferred. In almost 200 ascidian hosts examined, however, no trace was found of detached ovisacs or hatched nauplii of the parasite. This suggests that the ovisacs released by the parasite are carried quickly through the gut and out of the exhalent siphon of the host before hatching takes place. Furthermore, no ovisacs were obtained that hatched normally in less than 9 days. Presumably, ovisacs closer to hatching than 9 days have already been released. The light-sensitivity of hatching is probably significant in preventing hatching before the ovisac has escaped the host since, in contrast to *A. rosea,* the nauplii hatch from their inner membranes as soon as these have swollen and would be exposed to digestive enzymes within the host. Similar light sensitivity in hatching is common among endoparasitic trematodes and cestodes (Smyth, 1961).

Sensitivity to mechanical stimulation probably plays a different role. When the ovisac is released from the female, it is closed off as a tough-walled bag. Experimentation shows that rupture of this bag, essential for the escape of the nauplii, depends on synchronous swelling of the contained egg membranes. The prehatching activity which leads to swelling, although dependent on light stimulation, is accelerated in its onset by mechanical stimulation. Synchrony of the hatching process is assured by this response, since mechanical stimulation spreads rapidly in an ovisac as soon as one embryo makes the prehatching response to light.

During a period of 5 days at 20°C., the embryos become more and more sensitive to both light and mechanical stimulation, until a slight stimulus of either kind will set off synchronous hatching. Presumably this extended gradient of increasing sensitivity permits some margin of delay in escape from the host, while at the same time ensuring eventual hatching even in conditions of relatively low illumination which might be encountered.

Synchronous hatching in parasitic copepods with sac-like ovisacs may be a common phenomenon. Wilson (1911*a*, 1911*b*) noted split, empty ovisacs of lernaeopodid and ergasilid copepods after overnight mass hatchings, and also observed that the ovisac ruptured in *Ergasilus* as the egg membranes swelled.

Larval stages

It is well known that the notodelphyiniform copepods inhabiting ascidians hatch as a phototropic, free-swimming nauplius with reduced limbs and an enlarged, ovoid, yolk-filled body (Canu, 1892; Gray, 1933*b*; Gurney, 1933; Lang, 1948; Gotto, 1957; Gage, 1966). The Enterocolidae also have a nauplius of this type, although lacking the positive phototropy displayed in the notodelphyiniform species (Canu, 1892; Gray, 1933*a*; Lang, 1948). The further development of the nauplius has been studied in only a few species (*Ascidicola, Notodelphys, Enterocola;* Gotto, 1957; Gage, 1966; Canu, 1892) but has been consistently found to pass through four free-swimming naupliar stages and two copepodite stages, of which the second gradually adopts a demersal habit and is probably the infective stage. The free-swimming period of these species is several days.

Haplostomella australiensis has a much more abbreviated larval development. The nauplius conforms to the usual type, being similar to that of *Ascidicola rosea*, but is free-swimming for only a few hours before moulting to the demersal first copepodite stage. Furthermore, this stage already manifests sexual dimorphism, which probably indicates that it is the infective stage, as in lernaeopodids (Wilson, 1911*a*). The only comparable brevity known at the present time for the free-swimming stages of a copepod parasitizing ascidians is that of *Gonophysema gullmarensis*. This aberrant species also has a single, brief naupliar stage and a single copepodite stage infective to new hosts (Bresciani and Lützen, 1961).

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HATCHING AND LARVAL DEVELOPMENT OF *DISSONUS NUDIVENTRIS* KABATA (COPEPODA, FAM. DISSONIDAE), A GILL PARASITE OF THE PORT JACKSON SHARK

D. T. Anderson and G. T. Rossiter

School of Biological Sciences, University of Sydney

[Read 27th November, 1968]

Synopsis

D. nudiventris lays typical, uniseriate, caligid egg strings, but hatches as a nauplius which remains attached to the egg-string by paired caudal threads and has reduced naupliar limbs. The nauplius moults, yielding a free-swimming, demersal copepodite which is probably the infective stage of the life cycle. The peculiarities of hatching and development in *D. nudiventris* support the removal of the genus from the Caligidae to the monogeneric family Dissonidae, proposed on morphological grounds by Yamaguti.

Introduction

While the number of specific descriptions of copepods parasitizing fishes in Australian waters is gradually increasing (Heegaard, 1962; Kabata, 1965, 1966), nothing has been recorded of their larval stages. The genus *Dissonus,* comprising a small number of caligoid species associated with elasmobranch fishes, is a particularly interesting one. Created by Wilson (1906), this genus remained within the Caligidae until 1963, when it was removed by Yamaguti (1963) to a separate family Dissonidae on the basis of a number of small but significant morphological differences. *Dissonus nudiventris* was first collected by the British, Australian and New Zealand Antarctic Expedition of 1929–1931, from *Heterodontus phillipi* Blainville at Hobart, Tasmania, but the material was described and named as a new species only by Kabata (1965). Although Kabata followed Yamaguti in assigning the species to the family Dissonidae, the first words of his specific description read "A typical caligid copepod————", emphasizing the fact that the adults of *D. nudiventris* are similar in general form to the well known caligids.

Wilson (1905, 1907*a*, 1907*b*), Gurney (1934) and Heegaard (1947) have stressed the uniformity in structure and habits of caligid larvae. The following description of the hatching and early larval development of *D. nudiventris* shows that in Yamaguti's newly proposed family, larval development differs markedly in the early stages from that of the Caligidae.

Materials and Methods

Male and female adults of *Dissonus nudiventris* were collected from the gill filaments of the Port Jackson shark, *Heterodontus portjacksoni* (Meyer). The fishes came from the marine aquarium at Manly, N.S.W. Of four individuals examined, one yielded 23 females and 6 male parasites, a second 65 females only and a third 1 female only, while the fourth was uninfested.

In all, fourteen egg strings of *D. nudiventris* containing advanced embryos were cultured. The egg strings were found to be highly susceptible to bacterial and protozoan attack in the conditions of the culture. Using movements of the gut in the embryos as a convenient index of viability. it was found that the embryos remained alive for no more than five days. Hatching was observed only if it took place during this period. Numerous nauplii were hatched, but very few survived the first moult to the first copepodite stage, and no larvae were carried beyond this stage.

In spite of these difficulties, which are well known for parasitic copepods (Wilson, 1905, 1907*a*, 1907*b*; Heegaard, 1947), the results obtained revealed a unique pattern of hatching and larval development in *Dissonus nudiventris*, quite unlike that of any caligid.

RESULTS

The egg string

D. nudiventris produces paired egg strings of typical caligid form. Each egg string is cylindrical, 4–6 mm. long, 0·35 mm. in diameter, and contains a single row of flattened, disc-shaped eggs, closely packed together with their flattened surfaces almost touching. Each egg lies in a separate cell of the egg string, with diameters of 350 × 320μ and a thickness of 70μ. The wall of the cell is relatively rigid and tough. As the embryos develop, it can be seen that the flattening of the egg is a dorso-ventral one. The dorsal surface of each embryo faces the ventral surface of the next embryo of the string. Furthermore, the anterior ends of the embryos, marked in later stages by the nauplius eyes, are also aligned. The embryos all face in one direction along the length of the string.

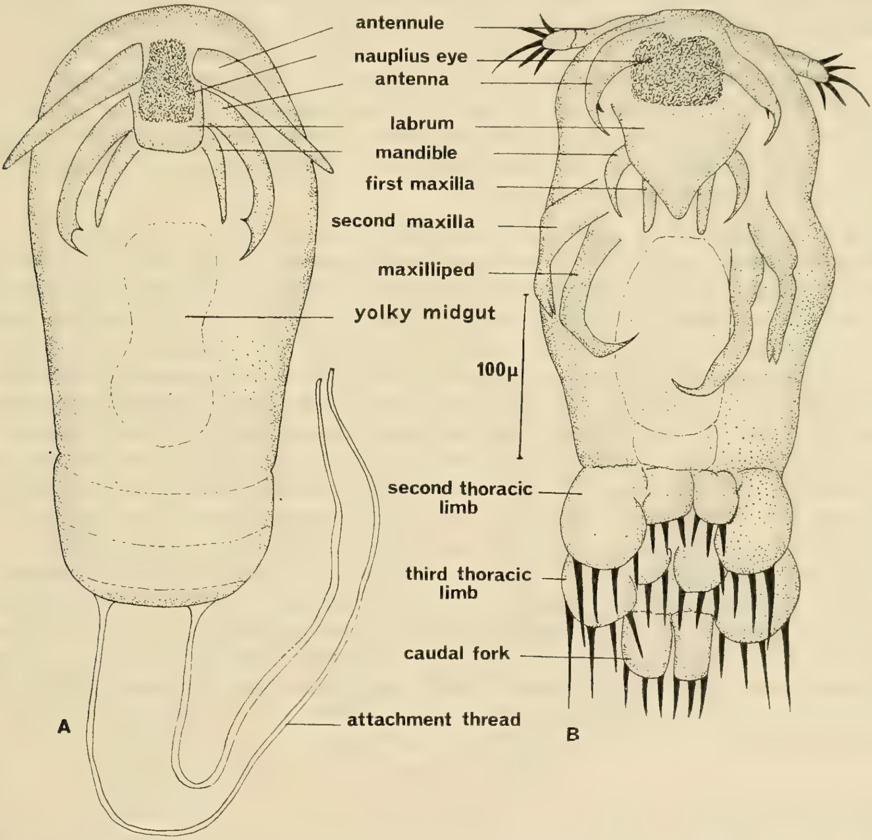

Fig. 1. *Dissonus nudiventris*. A. The newly hatched nauplius, ventral view. B. The first copepodite, ventral view.

The newly hatched larva

The newly hatched nauplius which emerges from a cell of the egg string in *D. nudiventris* is unique among Crustacea. Although diagnostically a nauplius, with 3 pairs of naupliar limbs and an externally unsegmented post-naupliar region (Fig. 1A), it is non-feeding and non-swimming. The nauplius remains permanently attached to the wall of the egg string by a pair of fine, fibrous threads arising from the posterior end of the larva. The post-naupliar region is elongated, and the naupliar limbs are short, devoid of swimming setae or feeding spines, ventrally disposed and generally similar to the form they take in the next larval stage.

Hatching

Hatching of each individual nauplius from its cell in the egg string is a relatively prolonged process. A variable period of activity, which may continue sporadically for many minutes, precedes hatching. The first sign of hatching is a slight swelling of the membrane around the embryo, accompanied by formation of a film of fluid between the embryo and the membrane (Figs 2A, 2B). The embryo rounds up slightly from its previous flattened form. Further swelling of the membrane, resisted by the tough wall of the cell, gradually carries the nauplius out through an aperture formed in the wall of the cell, immediately in front of the nauplius eye (Fig. 2C). The formation of this aperture is imperceptible. Vigorous movements of the embryo occur during this phase of hatching. The increase in volume of the membrane is approximately fourfold.

As the nauplius is gradually extruded from its cell, the caudal threads become apparent (Fig. 2C) and gradually extend (Fig. 2D). When the swollen membrane breaks and the nauplius finally emerges, the threads continue to restrain it. At this stage, they measure about twice the length of the nauplius, which itself is about 370μ long. The nauplius continues to twitch its limbs and body after hatching, but makes no swimming movements and shows no photosensitivity. The duration of hatching of individual nauplii emerging from three different egg strings ranged from a few minutes to three hours. Hatching within any one egg string was asynchronous and was not promoted by exposure to light. It was, however, sensitive to the osmotic concentration of the surrounding medium. Immersion of part of an egg string, from which some nauplii had already hatched, in hypotonic sea water (2·4% saline), caused 10 more nauplii to hatch within 5 minutes, a degree of synchrony never observed in normal hatching. Conversely, immersion of another part of the same egg string in hypertonic sea water (7·5% saline) inhibited all further hatching. It can be inferred that, as in other copepods (Marshall and Orr, 1954; Davis, 1959; Anderson and Rossiter, 1968), the swelling of the egg membrane during hatching in *D. nudiventris* has an osmotic basis.

Larval development

(i) The nauplius:

The nauplius (Fig. 1A) remains unchanged in external appearance until it moults, after 2–5 hours, into a first copepodite. The nauplius remains attached to the egg string by the caudal threads, and shows only sporadic twitching. The large, curved, spatulate caudal spines of the typical caligid free-swimming nauplius, referred to by Wilson (1905) as balancing organs, are conspicuously absent.

(ii) The first copepodite:

The first copepodite (Fig. 2B) emerges through a longitudinal split in the anterior dorsal midline of the naupliar cuticle, leaving the exuvia intact and still attached to the egg string by the paired caudal threads. The first copepodite retains the same size and general shape as the nauplius, but shows three new features:

(*a*) further modification of the naupliar limbs. The antennules become segmented and setose. The antennae become more hook-like, approximating to their adult form. The stylet-like mandibles come into closer association with the labrum, which itself becomes larger and pointed;

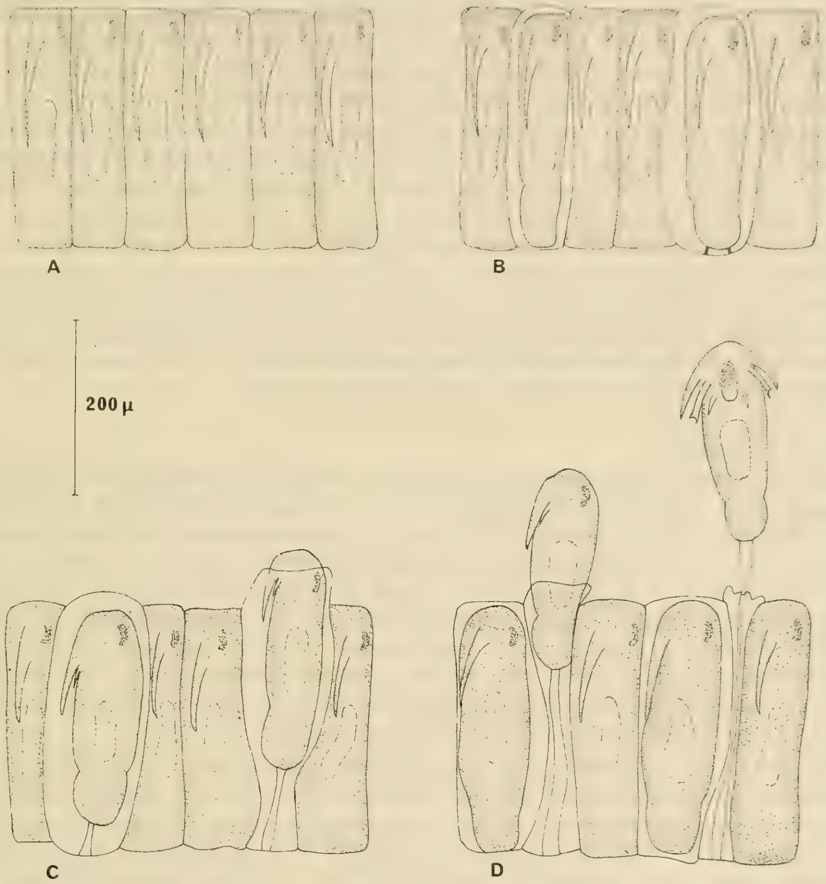

Fig. 2. The hatching sequence of *Dissonus nudiventris* (for description, see text).

(*b*) emergence of the maxillules, as stylets associated with the labrum and of elongated maxillae with chelate tips;

(*c*) emergence of three trunk segments, with a pair of long clawed maxillipeds anteriorly on the first and two pairs of functional, biramous swimming limbs posteriorly on the second and third segments.

The first copepodite is lecithotrophic, free-swimming and demersal, swimming about near the bottom of the container. There is no sign of a frontal filament, the thread by which typical caligid copepods (the chalimus stage) attach themselves to their hosts before completion of the larval stages (Wilson, 1907; Gurney, 1934; Heegaard, 1947; Baer, 1952).

No sexual dimorphism is observed in the first copepodite of *D. nudiventris* but, as noted by Kabata (1965), sexual dimorphism is not marked in the adults of this species. Apart from differences in proportion in the genital segments, the adult female differs from the male only in the absence of the vestiges of a sixth pair of thoracic limbs.

DISCUSSION

The egg strings and hatching

The egg strings of *D. nudiventris* are similar to those of the many caligid species described by Wilson (1905) and others. The sensitivity of the embryos and larvae in conditions of artificial culture also reiterates the findings of Wilson and of Heegaard (1947) for the eggs of many copepods parasitizing fish. Generally, these parasites experience very efficient ventilation, the absence of which may be a critical factor in culture.

Associated with this difficulty, the long duration of hatching from the egg string in *D. nudiventris* may not be a true indication of hatching in natural conditions. Wilson (1905, 1907) observed that hatching from a typical caligid egg string takes place more or less simultaneously, and in view of the synchrony of development of the eggs in the egg string of *D. nudiventris,* synchronous hatching is to be expected. Since each embryo emerges independently from its own cell in the egg string, however, the role of synchronous hatching in rupturing the ovisac in the ascidicolid copepod *Haplostomella australiensis* and other species with sac-like ovisacs (Anderson and Rossiter, 1968) is irrelevant in *D. nudiventris.*

Larval development

While passage through most or all of naupliar development within the egg membranes is a feature of lernaeid and lernaeopodid copepods parasitizing fishes (Wilson, 1911*a*; Baer, 1952) and of *Gonophysema gullmarensis* and *Haplostomella australiensis* parasitizing ascidians (Bresciani and Lützen, 1961; Anderson and Rossiter, 1968) there has been no previous record of a non-swimming nauplius which hatches and yet remains attached by paired threads to the egg string, as in *D. nudiventris.* This nauplius is a remarkable exception to the rule noted by C. B. Wilson (1911*a*) that "all copepod nauplii, as well those of parasitic forms as those of free swimmers, seek the surface of the water and there swim about freely".

The brief attached naupliar stage of *D. nudiventris* can be interpreted as an exotic means of shortening the duration of free larval stages, alternative to the prolonged direct development within the egg seen in lernaeopodids and many other Crustacea. It contrasts strongly with the typical succession of two phototropic, free-swimming naupliar stages and two demersal copepodite stages seen in caligid development (Heegaard, 1947). The caligid larvae provide a prolonged dispersal and host-seeking phase in the life cycle. The elimination of the free-swimming naupliar stages in *D. nudiventris,* with retention of the demersal first copepodite, greatly restricts dispersal, apparently in favour of protected, more direct development. This loss may not be important, however, since both male and female adults of *D. nudiventris* can leave the host and swim freely, at least for short periods.

Associated with the loss of naupliar swimming, the naupliar limbs develop directly towards their later adult form, and the first copepodite already has mouthparts approximating in structure to those of the adult. Since the larva is also lecithotrophic, slow-swimming and demersal, it seems likely to be the immediate host-seeking and attachment stage. It follows that the peculiar attached nauplius is in all probability an adaptation to completion of the life cycle of *D. nudiventris* on a single host shark, with the emergent first copepodite stage attaching directly to the gills on to which it emerges. This might well be advantageous in view of the solitary habits and scattered distribution of the Port Jackson shark, leaving host transfer to the adult during moments of host contact, e.g. in mating. Infestation by one ovigerous female would then be sufficient to ensure rapid parasitization of a previously unparasitized host. It is notable that of the sharks examined, one was totally uninfested.

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ABSTRACT OF PROCEEDINGS

ORDINARY GENERAL MEETING

27th March, 1968

Professor T. G. Vallance, President, in the chair.

The minutes of the last Ordinary General Meeting (29th November, 1967) and of the Special General Meeting (29th November, 1967) were taken as read and signed.

The Chairman announced that the Council had elected the following Ordinary Members of the Society: Messrs. D. F. Blaxell, D.D.A., B.Sc., University of New South Wales, Kensington; and J. R. J. French, B.Sc.(For.), A.I.W.Sc., Cremorne, N.S.W.

The Chairman announced that library accessions amounting to 53 volumes, 290 parts or numbers, 9 bulletins, 4 reports and 3 pamphlets, total 359, had been received since the last meeting.

The Chairman drew the attention of members to the Australasian Native Orchid Society, its objects and its publication "Orchadian"; also to the Australian Research Grants Committee, Department of Education and Science, Canberra, and its research projects.

PAPERS READ

(By title only, an opportunity for discussion to be given at the April Ordinary General Meeting)

1. The Rhaphidophoridae (Orthoptera) of Australia. Part 7. A new genus from the Nullarbor Plain, South-western Australia. By Aola M. Richards.

A new genus is erected, and the new species is described from limestone caves on the Nullarbor Plain in south-western Australia.

2. A review of the genus *Halocynthia* Verrill 1879. By Patricia Kott.

The genus *Halocynthia* Verrill is reduced by synonymy to six closely related species distinguished only by the condition of the gonads and the branchial and atrial spines. Considerable variation in external appearance is demonstrated within a single species. Species occur in the sublittoral fringe of land masses and generally have a wide latitudinal range. Their distribution appears to be limited mainly by deep waters. The genus appears to be an ancient one and it may represent a relict of the Tethys Sea fauna.

3. The mucosa of the stomach of the wombat (*Vombatus hirsutus*) with special reference to the cardiogastric gland. By D. J. Hingson and G. W. Milton. (*Communicated by Dr. Mervyn Griffiths.*)

The specialized cardiogastric gland region of wombat stomach which is characteristic of koala and beaver stomachs as well, is located on the lesser curve near the oesophageal opening. The cardiogastric gland in the wombat is distinctive because of its complex group of mucosal sacculations which open into the stomach lumen via 25 or 30 large crater-like ostia. The mucosa of this gland contains long, straight, closely packed, unbranched gastric glands composed of the cell types found elsewhere in the stomach, with chief cells concentrated at the base of the glands. Parietal cells are present in great abundance. Typical surface and neck mucous and argyrophilic cells are also present. The bizarre cardiogastric specialization in the wombat is thus not cytologically a separate organ from the stomach. However, it does contribute greatly to the total secretory cell mass of the stomach.

4. The secretory capacity of the stomach of the wombat (*Vombatus hirsutus*) and the cardiogastric gland. By G. W. Milton, D. J. Hingson and E. P. George. (*Communicated by Dr. Mervyn Griffiths.*)

The secretory capacity of the stomach of the wombat (*Vombatus hirsutus*), and of the cardiogastric gland of this animal has been studied. It was found that the secretory power of this stomach resembles that of man and animals commonly used in gastric research. The concentrations of ions in gastric juice generally fitted the Hollander two-component theory of gastric secretion. A close correlation between the concentration of pepsin and of K^+ was demonstrated. The electrophoretic pattern of the gastric juice of the wombat resembled that obtained from the gastric juice of man. The maximum secretory capacity of the stomach of this animal was lower than that of man. It was found that a considerable increase in the gastric output could be obtained by augmenting the effects of histamine stimulation by injections of insulin.

5. A taxonomic review of the genus *Mixophyes* (Anura, Leptodactylidae). By I. R. Straughan.

Two new species of *Mixophyes* Gunther are described and the two subspecies already defined are elevated to species.

OTHER BUSINESS

Dr. I. V. Newman drew attention to signs he had observed of preparations to lay a sewer line on the surface beside the bed of the Lane Cove River near its headwaters between Wahroonga and Normanhurst. The steepness of the valley sides in the uppermost reaches mean great scarring and destruction. In certain parts of this region is some of the best forest in the Sydney region. He pointed out that the price of Conservation is Eternal Vigilance.

ORDINARY GENERAL MEETING

24th April, 1968

Professor T. G. Vallance, President, occupied the chair.

The minutes of the last Ordinary General Meeting (27th March, 1968) were read and confirmed.

The Chairman announced that the Council had elected the following office-bearers for the 1968–69 session: *Vice-Presidents*: Mr. L. A. S. Johnson, Professor R. C. Carolin, Dr. D. T. Anderson and Miss Elizabeth C. Pope; *Honorary Treasurer*: Dr. A. B. Walkom; *Honorary Secretary*: Mr. R. H. Anderson.

The Chairman announced that the Council had elected Mrs. Elizabeth J. Hayden, B.Sc. (Melb.)., Burwood, N.S.W., and Dr. A. E. Wood, B.Sc.Agr., Ph.D., Bexley, N.S.W., Ordinary Members of the Society.

The Chairman announced that library accessions amounting to 15 volumes, 181 parts or numbers, 7 bulletins, 7 reports and 4 pamphlets, total 214, had been received since the last meeting.

The Chairman drew the attention of members to the notice notifying that the Australian Research Grants Committee is at present calling applications for support for research projects in 1969.

The Chairman also announced that no Ordinary General Meeting will be held in May.

PAPERS READ

1. A new bdellourid-like triclad turbellarian ectoconsortic on Murray River *Chelonia*. By L. R. Richardson.

2. The stratigraphy of the Sofala–Hill End–Euchareena region. By G. H. Packham.

3. The constitution, distribution and relationships of the Australian Decapod Crustacea. By D. J. G. Griffin and J. C. Yaldwyn.

4. The embryology of *Epaltes australis* Less. (*Compositae*). By Gwenda L. Davis.

5. Plants grazed by Red Kangaroos, *Megaleia rufa* (Desmarest), in central Australia. By G. Chippendale.

LECTURETTE

Dr. F. H. Talbot, Director of the Australian Museum, Sydney, delivered a very interesting lecturette, illustrated with colour transparencies, entitled "Fishes and Corals—ecological results of a study on One Tree Island Reef, Great Barrier Reef".

ORDINARY GENERAL MEETING

26th June, 1968

Professor T. G. Vallance, President, occupied the chair.

The minutes of the last Ordinary General Meeting (24th April, 1968) were read and confirmed.

The Chairman announced that library accessions amounting to 28 volumes, 453 parts or numbers, 3 bulletins, 11 reports and 47 pamphlets, total 542, had been received since the last meeting.

The Chairman announced that "Australian Natural History", Vol. 14, No. 8 (December, 1963) is missing from the Society's set and is now out of print. He suggested that some member with a copy might be willing to make it available to complete the set.

PAPERS READ

1. *Aphrophyllum* (Rugosa) from Lower Carboniferous limestones near Bingara, New South Wales. By R. K. Jull. (*Communicated by Mr. R. H. Anderson.*)

2. Type specimens in the Macleay Museum, University of Sydney. I. Fishes. By P. J. Stanbury. (*Communicated by Dr. D. T. Anderson.*)

3. Replacement name for the preoccupied genus name *Odinia* Perrier 1885 (Echinodermata : Asteroidea). By A. J. Dartnall, D. L. Pawson, Elizabeth C. Pope and B. J. Smith.

4. Permian faunas and sediments from the South Marulan district, New South Wales. By R. E. Wass and I. G. Gould.

EXHIBIT

Mr. G. P. Whitley exhibited two unpublished photographic portraits, from the Australian Museum's archives, of naturalists active in Australia over a century ago. One was of George French Angas (1822–1886) who had been Secretary of the Australian Museum and is famous for his artistic illustrations; the other of Gerard Krefft (1830–1881), a former Curator and the zoologist who first described the Queensland lungfish.

LECTURETTE

Miss Elizabeth C. Pope, Australian Museum, Sydney, gave a lecturette on the "Star fishes of the Fiji reefs", illustrated by colour transparencies.

ORDINARY GENERAL MEETING

31st July, 1968

Professor T. G. Vallance, President, occupied the chair.

The minutes of the last Ordinary General Meeting (26th June, 1968) were taken as read and confirmed.

The Chairman announced that Dr. F. H. Talbot, Director of the Australian Museum, had been elected a member of Council in place of Professor J. M. Vincent.

The Chairman announced that library accessions amounting to 11 volumes, 138 parts or numbers, 8 bulletins, 5 reports and 3 pamphlets, total 165, had been received since the last meeting.

PAPERS TAKEN AS READ

(By title only, an opportunity for discussion to be given at the September Ordinary General Meeting):

1. On the first occurrence of a *Climacograptus bicornis* with a modified basal assemblage in Australia. By H. Moors.
2. Chromosome location and linkage studies involving the Pm3 locus for powdery mildew resistance in wheat. By R. A. McIntosh and E. P. Baker.
3. The vegetation of the Boorabbin and Lake Johnston areas, Western Australia. By J. S. Beard. (*Communicated by Mr. R. H. Anderson.*)

ORDINARY GENERAL MEETING

25th September, 1968

Professor T. G. Vallance, President, occupied the chair.

The minutes of the last Ordinary General Meeting (31st July, 1968) were read and confirmed.

The Chairman announced that the Council had elected the following Ordinary Members of the Society: Mr. James Burns, Avalon Beach, 2107; Miss Estelle M. Canning, Canberra, 2600; Miss Margaret L. Debenham, Strathfield, 2135; Dr. R. N. Richards, Armidale, 2350; and Dr. Peter Stanbury, Macleay Museum, University of Sydney, 2006.

The Chairman extended, on behalf of members, congratulations to Mr. Abdul Khan on his appointment to a lectureship at the new University at Lahore, Pakistan.

The Chairman announced that library accessions amounting to 19 volumes, 148 parts or numbers, 6 bulletins, 4 reports and 2 pamphlets, total 179, had been received since the last meeting.

The Chairman also announced that the Council is prepared to receive applications for Linnean Macleay Fellowships tenable for one year from 1st January, 1969, from qualified candidates. Each applicant must be a member of this Society and be a graduate in Science or Agricultural Science of the University of Sydney. The range of actual (tax-free) salary is, according to qualifications, up to a maximum of A$3,200 per annum. Applications should be lodged with the Honorary Secretary, who will give further details and information, not later than Wednesday, 6th November, 1968.

The Chairman drew the attention of members to a "Symposium on Arid Lands" sponsored by the Australian Academy of Science, Canberra, on 19–21 May, 1969.

The Chairman drew the attention of members to an invitation by the Wildlife Preservation Society of Australia to attend a function on 6th November in honour of Mr. Allen Strom.

PAPERS READ

1. A study of some smuts of *Echinochloa* spp. By R. A. Fullarton and R. F. N. Langdon.
2. A viviparous species of *Patiriella* (Asteroidea, Asterinidae) from Tasmania. By A. J. Dartnall.
3. The nasal mites of Queensland birds (Acari : Dermanyssidae, Ereynetidae and Epidermoptidae). By R. Domrow.

LECTURETTE

An illustrated lecturette entitled "Some new aspects of Crustacean development" was delivered by Dr. D. T. Anderson, Department of Zoology, University of Sydney.

ORDINARY GENERAL MEETING

30th October, 1968

Professor T. G. Vallance, President, in the chair.

The minutes of the last Ordinary General Meeting (25th September, 1968) were read and confirmed.

The Chairman, on behalf of members, extended congratulations to Dr. Beryl Nashar on her appointment as Dean of the Faculty of Science, Newcastle University.

The Chairman announced that Miss Christine D. Clarke, Milson's Point, and Mr. L. A. Nielsen, Jandowae, Queensland, had been elected by the Council to membership of the Society.

The Chairman announced that library accessions amounting to 13 volumes, 162 parts or numbers, 8 bulletins, 8 reports and 3 pamphlets, total 194, had been received since the last meeting.

The Chairman announced that the Council is prepared to receive applications for Linnean Macleay Fellowships tenable for one year from 1st January, 1969, from qualified candidates.

PAPERS READ

1. Type specimens in the Macleay Museum, University of Sydney. II. Amphibians and reptiles. By Judy Goldman, L. Hill and P. J. Stanbury.

2. Notes on *Vittadinia triloba* sens. lat. (Compositae). By Nancy T. Burbidge. (*Communicated by Dr. Joyce W. Vickery.*)

LECTURETTE

An illustrated lecturette entitled "Some local Charophytes" was delivered by Dr. A. T. Hotchkiss, Department of Botany, University of Sydney.

ORDINARY GENERAL MEETING

27th November, 1968

Professor T. G. Vallance, President, in the chair.

The minutes of the last Ordinary General Meeting (30th October, 1968) were read and confirmed.

The Chairman announced that the following had been elected by the Council to membership of the Society: Mr. D. R. Goodfellow, Carlingford, N.S.W.; Mr. J. H. Phippard, B.Pharm., University of Queensland, Brisbane, Queensland; Dr. C. J. Quinn, B.Sc.(Hons.), Ph.D., University of New South Wales, Kensington, N.S.W., and Mr. B. V. Timms, B.Sc.(Hons.), Avondale College, Cooranbong, N.S.W.

The Chairman announced that the Council had re-appointed Miss Alison K. Dandie, B.Sc.(Hons.), to a Linnean Macleay Fellowship in Botany for one year from 1st January, 1969.

The Chairman referred to the death on 2nd November, 1968, of Sir Harold Raggatt, a distinguished geologist, who had been a member of the Society since 1929.

The Chairman also announced that library accessions amounting to 36 volumes, 253 parts or numbers, 10 bulletins, 5 reports and 2 pamphlets, total 306, had been received since the last meeting.

PAPERS READ

1. A revision of the family Agnesiidae Huntsman 1912, with particular reference to *Agnesia glaciata* Michaelsen 1898. By Patricia Kott.

2. Type specimens in the Macleay Museum, University of Sydney. III. Birds. By P. J. Stanbury.

3. Type specimens in the Macleay Museum, University of Sydney. IV. Mammals. By P. J. Stanbury.

4. Hatching and larval development of a species belonging to the Copepod family, Ascidicolidae, a parasite of the ascidian, *Styela etheridgii* Herman. By D. T. Anderson and G. T. Rossiter.

5. Hatching and larval development of *Dissonus nudiventris* Kabata (Copepoda, Fam. Dissonidae), a gill parasite of the Port Jackson shark. By D. T. Anderson and G. T. Rossiter.

NOTES AND EXHIBITS

Mr. G. P. Whitley exhibited, and commented upon, some Japanese papers on poisonous crabs, a topic which had been discussed at last August's seminar on ichthyosanotoxism arranged by the South Pacific Commission at Tahiti.

Dr. A. Hotchkiss discussed the ripening and after-ripening in fruits of *Ruppia spiralis* Dumort. The fruits of *Ruppia spiralis* were shown in photographs illustrating several stages in ripening. At the stage of maturity on the plant the fruits are covered with smooth, green, soft outer tissues. The fruits are immediately deciduous and undergo a period of after-ripening for about two weeks during which the inner pericarp hardens and darkens, the outer tissues die, decay and eventually are sloughed off both the fruit and the stipe. The fruit at this stage is terminated by a slender beak, and its surface is covered with stout spines composed of thick-walled, irregularly branched sclereids projecting from the outer surface of the pericarp wall. At germination, a calyptra bends back from the convex side, pushed outward by the emerging radical.

The President, Professor T. G. Vallance, referred to the centenary (1967) of the Rev. W. B. Clarke's work *"Remarks on the Sedimentary Formations of New South Wales"*. From a summary statement some 15 pages in length the work grew in the space of eleven years (and four editions) to become a book of 165 pages, completed only a fortnight before Clarke's death in June, 1878. Clarke has been called the "Father of Australian Geology", and this series of editions provides a means of examining the development of his ideas and attitudes on Australian stratigraphy. Close, comparative study of these documents would amply repay the attention of some historian of geology.

Some examples of Clarke's developing stratigraphical synthesis, such as his increasing confidence in the existence of Devonian strata and doubts as to the ages of the upper part of the coal sequence and the strata above it in the Sydney basin, were briefly discussed.

Copies of the four editions were exhibited. Brief details of these were listed because the first three issues, at least, are not readily traceable.

Ist edition—pp. 65–80 in *Catalogue of the Natural and Industrial Products of New South Wales forwarded to the Paris Universal Exhibition of 1867, by the New South Wales Exhibition Commissioners.* Government Printer, Sydney, 1867.

2nd edition—pp. 505–531 in *Industrial Progress of New South Wales: being a report of the Intercolonial Exhibition of 1870, at Sydney; together with a variety of papers illustrative of the industrial resources of the colony.* Government Printer, Sydney, 1871.

3rd edition — pp. 149–206 in *New South Wales Intercolonial and Philadelphia International Exhibition. Mines and Mineral Statistics of New South Wales, and notes on the geological collection of the Department of Mines,* .... Government Printer, Sydney, 1875.

4th edition—*Remarks on the Sedimentary Formations of New South Wales.* .... Government Printer, Sydney, 1878.

LIST OF MEMBERS

(15th December, 1968)

ORDINARY MEMBERS

(An asterisk (*) denotes Life Member)

1940 Abbie, Professor Andrew Arthur, M.D., B.S., B.Sc., Ph.D., c/- University of Adelaide, Adelaide, South Australia, 5000.
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 Biological Sciences, Botany Building, Sydney University, 2006.
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., 51 Ocean Street, Woollahra, N.S.W., 2025.
1922 Anderson, Robert Henry, B.Sc.Agr., 19 Kareela Road, Chatswood, N.S.W., 2067.
1965 Andrew, Mrs. Phillipa Audrey, M.Sc. (*née* Croucher), 10 Black Street, Watsonia, Victoria, 3087.
1963 Ardley, John Henry, B.Sc. (N.Z.), Messrs. William Cooper and Nephews (Australia) Pty. Ltd., P.O. Box 12, Concord, N.S.W., 2137.
1927 *Armstrong, Jack Walter Trench, " Cullingera ", Nyngan, N.S.W., 2825.
1952 Ashton, David Hungerford, B.Sc., Ph.D., 92 Warrigal Road, Surrey Hills, Victoria, 3127.
1912 Aurousseau, Marcel, B.Sc., 229 Woodland Street, Balgowlah, N.S.W., 2093.

1961 Bain, Miss Joan Maud, M.Sc., Ph.D., 18 Onyx Road, Artarmon, N.S.W., 2064.
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., 113 Lucinda Avenue South, Wahroonga, N.S.W., 2076.
1950 *Barber, Professor Horace Newton, M.S., Ph.D., F.A.A., School of Biological Sciences, Department of Botany, University of N.S.W., P.O. Box 1, Kensington, N.S.W., 2033.
1955 Barlow, Bryan Alwyn, B.Sc., Ph.D., School of Biological Sciences, The Flinders University of South Australia, 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.
1960 Batley, Alan Francis, A.C.A., 123 Burns Road, Wahroonga, N.S.W., 2076.
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.
1946 Bearup, Arthur Joseph, B.Sc., 66 Pacific Avenue, Penshurst, N.S.W., 2222.
1940 Beattie, Joan Marion, D.Sc. (*née* Crockford), 2 Grace Avenue, Beecroft, N.S.W., 2119.
1964 Bedford, Geoffrey Owen, B.Sc., 87 Jacob Street, Bankstown, N.S.W., 2200.
1952 Bennett, Miss Isobel Ida, Hon.M.Sc., School of Biological Sciences, Department of Zoology, Sydney University, 2006.
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.
1958 Blake, Clifford Douglas, B.Sc.Agr., Ph.D., Faculty of Agriculture, Sydney University, 2006.
1941 Blake, Stanley Thatcher, D.Sc. (Q'ld.), 1110 Waterworks Road, The Gap, Queensland, 4061.
1968 Blaxell, Donald Frederick, D.D.A., B.Sc., School of Biological Sciences, University of New South Wales, P.O. Box 1, Kensington, N.S.W., 2033.
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.
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., 2927.
1949 Burden, John Henry, 1 Havilah Street, Chatswood, N.S.W., 2067.

1931 *Burges, Professor Norman Alan, M.Sc., Ph.D., Professor of Botany, University of Liverpool, Liverpool, England.
1959 Burgess, The Rev. Colin E. B. H., Parks and Gardens Section, Department of the Interior, Canberra, A.C.T., 2600.
1962 Burgess, Ian Peter, B.Sc.For., Dip.For., The Forestry Office, Coff's Harbour, N.S.W., 2450.
1968 Burns, James, A.A.S.A., 127 Plateau Road, Avalon Beach, N.S.W., 2107.

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, Division of Entomology, C.S.I.R.O., P.O. Box 109, City, Canberra, A.C.T., 2601.
1968 Canning, Miss Estelle Margaret, B.Sc. (Melb.), c/- Canberra Botanic Gardens, Parks and Gardens Branch, Department of Interior, Canberra, A.C.T., 2600.
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., C.S.I.R.O., Division of Entomology, P.O. Box 109, City, Canberra, 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., Entomological Branch, N.S.W. Department of Agriculture, Private Mail Bag, No. 10, Rydalmere, N.S.W., 2116.
1936 *Chadwick, Clarence Earl, B.Sc., Entomological Branch, N.S.W. Department of Agriculture, Private Mail Bag No. 10, Rydalmere, N.S.W., 2116.
1956 Chambers, Thomas Carrick, M.Sc. (N.Z.), Ph.D., Botany School, University of Melbourne, Parkville, Victoria, 3052.
1966 Child, John, M.A., B.Comm. (N.Z.), D.Phil. (Oxon.), Department of Economics, Otago University, Box 56, Dunedin, New Zealand.
1959 Chippendale, George McCartney, B.Sc., 4 Raoul Place, Lyons, A.C.T., 2606.
1947 Christian, Stanley Hinton, Malaria Research Unit and School, Kundiawa, Eastern Highlands, Territory of Papua and New Guinea.
1932 *Churchward, John Gordon, B.Sc.Agr., Ph.D., " 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 109, City, Canberra, A.C.T., 2601.
1968 Clarke, Miss Christine Dorothea, B.Sc.(Hons.), 26A Alfred Street, Milson's Point, N.S.W., 2061.
1961 Clarke, Miss Lesley Dorothy, Ph.D., 4 Gordon Crescent, Eastwood, N.S.W., 2122.
1947 Clarke, Mrs. Muriel Catherine, M.Sc. (*née* Morris), 122 Swan Street, Morpeth, N.S.W. 2321.
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., School of Biological Sciences, Department of Botany, Sydney University, 2006.
1966 Clyne, Mrs. Densey, 7 Catalpa Crescent, Turramurra, N.S.W., 2074.
1956 Cogger, Harold George, M.Sc., Department of Zoology, Macquarie University, North Ryde, N.S.W., 2113.
1946 Colless, Donald Henry, Ph.D. (Univ. of Malaya), c/- Division of Entomology, C.S.I.R.O., P.O. Box 109, City, Canberra, 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 109, City, Canberra, A.C.T., 2601.
1966 Conroy, Brian Alfred, International House, Sydney University, 2006.
1942 Copland, Stephen John, M.Sc., 15 Chilton Parade, Warrawee, N.S.W., 2074.
1947 Costin, Alex Baillie, B.Sc.Agr., C.S.I.R.O., Division of Plant Industry, P.O. Box 109, City, Canberra, A.C.T., 2601.
1964 Craddock, Miss Elysse Margaret, 36 Lyons Road, Drummoyne, N.S.W., 2047.
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.

1965 Dandie, Miss Alison Kay, B.Sc.(Hons.), Dip.Ed., 69 Waitara Parade, Hurstville, N.S.W., N.S.W., 2220.
1960 Dart, Peter John, B.Sc.Agr., Ph.D., Soil Microbiology Department, Rothamsted Experimental Station, Harpenden, Herts., England.
1968 Dartnall, Alan John, B.Sc., 7 Forbes Avenue, West Hobart, Tasmania, 7000.
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.
1968 Debenham, Miss Margaret Lee, B.Sc., 42 Hunter Street, Strathfield, N.S.W., 2135.

1967 De Nardi, Mrs. Jan Christina, B.Sc. (Q'ld.) (*née* Morrow), 6/81 New South Head Road, Vaucluse, N.S.W., 2030.
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.
1960 Dorman, Herbert Clifford, J.P., A.S.T.C. (Dip.Chem.), Dip.Soc.Stud. (Sydney), Rodgers Street, Teralba, N.S.W., 2284.
1954 Douglas, Geoffrey William, B.Agr.Sc., Deputy Chairman, Vermin and Noxious Weeds Destruction Board, Department of Crown Lands and Survey, Treasury Place, Melbourne, Victoria, 3002.
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.
1964 Florence, Ross Garth, M.Sc.For., Ph.D., The Australian National University, Department of Forestry, P.O. Box 4, Canberra, A.C.T., 2600.
1966 Ford, Miss Judith Helen, 18 Central Avenue, Mosman, N.S.W., 2088.
1930 Fraser, Miss Lilian Ross, D.Sc., 1 Laurence Street, Pennant Hills, N.S.W., 2120.
1968 French, John Richard Joseph, B.Sc.(For.), A.I.W.Sc., 5 Brierley Street, Cremorne, N.S.W., 2090.

1935 *Garretty, Michael Duhan, D.Sc., Box 763, Melbourne, Victoria, 3001.
1944 Greenwood, William Frederick Neville, 11 Wentworth Avenue, Waitara, N.S.W., 2077.
1965 Griffin, David Michael, M.A., Ph.D. (Cantab.), School of Agriculture, Sydney University, 2006.
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 109, City, Canberra, A.C.T., 2601.
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.
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., 183 Richmond Road, Kingswood, N.S.W., 2750.
1960 Hartigan, Desmond John, B.Sc.Agr., 75 Northwood Road, Northwood, N.S.W., 2066.
1968 Hayden, Mrs. Elizabeth Jean, B.Sc. (Melb.), Botany Department, Australian National University, P.O. Box 4, Canberra, A.C.T., 2600.
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., Senior Lecturer in Chemistry, University of Malawi, Limbe, Malawi, Africa.
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, Miss Dorothy, M.Sc., Ph.D., Department of Geology, University of Queensland, Brisbane, Queensland, 4067.
1943 *Hindmarsh, Miss Mary Maclean, B.Sc., Ph.D., 4 Recreation Avenue, Roseville, N.S.W., 2069.
1956 *Holder, Miss Lynette Anne, B.Sc., 48 Rutledge Street, Eastwood, N.S.W., 2122.
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 Botany, University of New England, Armidale, N.S.W., 2350.
1942 Humphrey, George Frederick, M.Sc., Ph.D., C.S.I.R.O. Marine Biological Laboratory, Box 21, Cronulla, N.S.W., 2230.

1960 Ingram, Cyril Keith, B.A., B.Ec., Office of Inspector of Schools, 2/306 Malton Road, Epping North, N.S.W., 2121.

1957 Jackes, Mrs. Betsy Rivers, B.Sc., Ph.D. (Univ. Chicago) (*née* Paterson), 21 Nebo Road, Mackay, Queensland, 4740.
1963 Jacobs, Miss Janice Lorraine, B.Sc., School of Biological Sciences, Department of Botany, Sydney University, 2006.
1938 Jacobs, Maxwell Ralph, D.Ing., M.Sc., Dip.For., 32 Arthur Circle, Forrest, A.C.T., 2603.
1966 Jacobs, Surrey Wilfred Laurence, 7 Yarrara Road, Pymble, N.S.W., 2073.
1961 Jacobson, Miss Constance Mary, M.Sc., Ph.D., School of Biological Sciences, Department of Zoology, Sydney University, 2006.
1960 James, Sidney Herbert, M.Sc., 54 Holmfirth Street, Mt. Lawley, Western Australia, 6050.
1964 Jancey, Robert Christopher, M.Sc., Ph.D., c/- Department of Botany, University of Western Ontario, London, Ontario, Canada.
1963 Jefferies, Mrs. Lesly Joan, 14 Denman Street, Hurstville, N.S.W., 2220.
1960 Jenkins, Thomas Benjamin Huw, Ph.D., Department of Geology and Geophysics, Sydney University, 2006.
1952 Jessup, Rupert William, M.Sc., 6 Penno Parade North, Belair, South Australia 5052.
1947 Johnson Lawrence Alexander Sidney, B.Sc., c/- National Herbarium, Royal Botanic Gardens, Sydney, 2000.
1945 Johnston, Arthur Nelson, B.Sc.Agr., 22A Greville Street, Chatswood, N.S.W., 2067.
1960 Jolly, Violet Hilary, M.Sc., Ph.D., Metropolitan Water, Sewerage and Drainage Board, P.O. Box 2, Guildford, N.S.W., 2161.
1958 Jones, Edwin Llewelyn, B.A., P.O. Box 196, Leeton, N.S.W., 2705.
1963 Jones, Leslie Patrick, Department of Animal Husbandry, Sydney University, 2000.
1930 Joplin, Miss Germaine Anne, B.A., Ph.D., D.Sc., Department of Geophysics, Australian National University, Canberra, A.C.T., 2600.
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 Vertebrate Zoology, Queen's University, Kingston, Ontario, Canada.
1951 Kerr, Harland Benson, B.Sc.Agr., Ph.D., Summer Institute of Linguistics, P.O. Ukarumpa, E.H.D., Territory of New Guinea.
1937 Kesteven, Geoffrey Leighton, D.Sc., c/- Division of Fisheries and Oceanography C.S.I.R.O., P.O. Box 21, Cronulla, N.S.W., 2230.
1966 Khan, Abdul Ghaffar, M.Sc., Botany Department, Panjab University, New-Campus, Lahore, West-Pakistan.
1957 Kindred, Miss Berenice May, B.Sc., Fachbereich Biologie, Universitat Konstanz, 775 Konstanz, Postfach 733, Germany.

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., 35 Gordon 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.
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.
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., C.S.I.R.O., Ian Clunies Ross Animal Research Laboratory, P.O. Box 144, Parramatta, N.S.W., 2150.

1951 Macdonald, Colin Lewis, 7 Watford Close, North Epping, N.S.W., 2121.
1948 Macintosh, Professor Neil William George, M.B., B.S., Department of Anatomy, Sydney University, 2006.
1961 Mackay, Miss Margaret Muriel, B.Sc.(Hons.), M.Sc., M.I.Biol., J.P., 6 Woodford Street, Longueville, N.S.W., 2066.
1922 Mackerras, Ian Murray, M.B., Ch.M., B.Sc., C.S.I.R.O., Division of Entomology, P.O. Box 109, City, Canberra, A.C.T., 2601.
1931 *Mair, Herbert Knowles Charles, B.Sc., Royal Botanic Gardens, Sydney, 2000.
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.
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, 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., 12 St. Thomas Street, Bronte, N.S.W., 2024.
1932 McCulloch, Robert Nicholson, M.B.E., D.Sc.Agr., B.Sc., Cattle Tick Research Station, Wollongbar, N.S.W., 2480.
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.), c/- Royal Botanic Gardens, Kew, Richmond, Surrey, England.
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, 64 Treatts Road, Lindfield, N.S.W., 2070.
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., 89 Kentucky Street, Armidale, N.S.W., 2350.
1948 Millerd, Miss Alison Adèle, Ph.D., C.S.I.R.O., Division of Plant Industry, P.O. Box 109, City, Canberra, 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., Department of Zoology, University College of Townsville, Pimlico, Townsville, Queensland, 4810.
1963 Moore, Barry Philip, B.Sc., Ph.D., D.Phil., C.S.I.R.O., Division of Entomology, P.O. Box 109, City, Canberra, A.C.T., 2601.
1958 Moore, Kenneth Milton, Cutrock Road, Lisarow, N.S.W., 2251.
1960 Moore, Raymond Milton, D.Sc.Agr., 94 Arthur Circle, Forrest, A.C.T., 2603.
1964 Moors, Henry Theodore, B.Sc., Department of Geology and Mineralogy, University of Melbourne, Parkville, Victoria, 3052.
1955 Morgan, Mrs. Eva, M.Sc., 5317 Borland Road, Los Angeles, California, 90032, U.S.A.
1961 Morrison, Gordon Cyril, 34 Leuna Avenue, Wahroonga, N.S.W., 2076.
1958 Moss, Francis John, 37 Avenue Road, Mosman, N.S.W., 2088.
1955 Muirhead, Warren Alexander, B.Sc.Agr., C.S.I.R.O., Irrigation Research Station, Private Mail Bag, Griffith, N.S.W., 2680.
1926 Mungomery, Reginald William, c/- Bureau of Sugar Experiment Stations, 99 Gregory Terrace, Brisbane, Queensland, 4000.
1965 Murray, David Ronald, B.Sc., 14 Consul Road, Brookvale, N.S.W., 2100.

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., School of Biological Sciences, Macquarie University, North Ryde, N.S.W., 2113.
1967 Nicholls, Anthony Oldham, B.Sc., School of Botany, University of Melbourne, Parkville, Victoria, 3052.
1922 Nicholson, Alexander John, C.B.E., D.Sc., F.R.E.S., C.S.I.R.O., Box 109, City, Canberra, A.C.T., 2601.
1968 Nielsen, Lloyd Alwyn, P.O. Box 12, Jandowae, Queensland, 4410.
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.

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., 34 Invergowrie Avenue, Highgate, South Australia, 5063.
1950 Oxenford, Reginald Augustus, B.Sc., 107 Alice Street, Grafton, N.S.W., 2460.

1952 Packham, Gordon Howard, B.Sc., Ph.D., Department of Geology, Sydney University, 2006.
1940 *Pasfield, Gordon, B.Sc.Agr., 20 Cooper Street, Strathfield, N.S.W., 2135.
1966 Patrick, John William, B.Sc.Ag.(Hons.), School of Biological Sciences, Macquarie University, North Ryde, N.S.W., 2113.
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 109, Canberra City, A.C.T., 2601.
1964 Pedder, Alan Edwin Hardy, M.A. (Cantab.), 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, University of New England, Armidale, N.S.W., 2350.
1947 Phillips, Miss Marie Elizabeth, M.Sc., Ph.D., Parks and Gardens Section, Department of the Interior, Canberra, A.C.T., 2600.
1935 Pope, Miss Elizabeth Carington, M.Sc., C.M.Z.S., Australian Museum, P.O. Box A285, Sydney South, N.S.W., 2000.
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., 2600.

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 109, City, Canberra, A.C.T., 2601.
1958 Rigby, John Francis, B.Sc., 152 Holland Road, Blackburn South, Victoria, 3130.
1932 *Robertson, Sir Rutherford Ness, C.M.G., F.R.S., B.Sc., Ph.D., F.A.A., Professor of Botany, University of Adelaide, Adelaide, South Australia, 5000.
1967 Rodd, Anthony Norman, Royal Botanic Gardens, Sydney, 2000.
1964 Rothwell, Albert, D.P.A., 11 Bonnie View Street, Cronulla, N.S.W., 2230.

1960 Salkilld, Barry William, Dip.Soc.Stud. (Univ. Syd.), 71 Beresford Road, Thornleigh, N.S.W., 2120.
1932 *Salter, Keith Eric Wellesley, B.Sc., School of Biological Sciences, Department of Zoology, Sydney University, 2006.
1962 Sands, Miss Valerie Elizabeth, M.Sc., Flat 3, 2 William Street, Dunedin, New Zealand.
1919 *Scammell, George Vance, B.Sc., 7 David Street, Clifton Gardens, N.S.W., 2088.
1965 Selkirk, David Robert, School of Biological Sciences, Botany Building, Sydney University, 2006.
1961 Selwood, Mrs. Lynne, B.Sc., Ph.D., (*née* Bedford), School of Anatomy, University of New South Wales, P.O. Box 1, Kensington, N.S.W., 2033.
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., 23 Princes Street, Turramurra, N.S.W., 2074.
1959 Simons, John Ronald, M.Sc., Ph.D., 242 Kissing Point Road, Turramurra, N.S.W., 2074.
1955 Slack-Smith, Richard J., 7 Kingston Street, Shenton Park, Western Australia, 6008.
1953 Smith, Eugene Thomas, 22 Talmage Street, Sunshine, Victoria, 3020.
1943 Smith-White, Spencer, D.Sc.Agr., F.A.A., 51 Abingdon Road, Roseville, N.S.W., 2069.
1967 South, Stanley A., B.Sc., 47 Miowera Road, Turramurra, N.S.W., 2074.
1945 Southcott, Ronald Vernon, M.B., B.S., 13 Jasper Street, Hyde Park, South Australia, 5061.

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., 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, Neville George, M.Sc. (N.Z.), Ph.D. (Lond.), School of Biological Sciences, Department of Zoology, Sydney University, 2006.
1965 Stephenson, Professor William, B.Sc. (Hons.), Ph.D. (Durham, Eng.), Diploma of Education, member Aust. Coll. Educ., Fellow Zoological Society, Department of Zoology, University of Queensland, St. Lucia, Queensland, 4067.
1962 Strahan, Ronald, M.Sc., Director, Taronga Zoo, P.O. Box 20, Mosman, N.S.W., 2088.
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 Sweeney, Anthony William, Malaria Institute, Public Health Department, Rabaul, Territory of Papua and New Guinea.
1962 *Swinbourne, Robert Frederick George, 4 Leeds Avenue, Northfield, South Australia, 5085.

1965 Talbot, Frank Hamilton, M.Sc., Ph.D., 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 Gardiner, B.Sc.Agr. (*née* Garden), 21 Middle Head Road, 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 Anatomy, Sydney University, 2006.
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.
1946 Tipper, John Duncan, A.M.I.E.Aust., 26 Kuring-gai Avenue, Turramurra, N.S.W., 2074.
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, 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.
1934 *Voisey, Professor Alan Heywood, D.Sc., School of Earth Sciences, Macquarie University, North Ryde, N.S.W., 2113.

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 Branch, N.S.W. Department of Agriculture, Private Mail Bag No. 10, Rydalmere, N.S.W., 2116.
1909 Walkom, Arthur Bache, D.Sc., 5/521 Pacific Highway, Killara, N.S.W., 2071.
1967 Wallace, Michael Joseph, B.Sc., 66 Parry Avenue, Beverly Hills, N.S.W., 2209.
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.
1911 Wardlaw, Henry Sloane Halcro, D.Sc., F.R.A.C.I., 71 McIntosh Street, Gordon, N.S.W., 2072.
1966 Wass, Robin Edgar, B.Sc. (Hons., Q'ld.), Ph.D., Department of Geology and Geophysics, Sydney University, 2006.
1936 Waterhouse, Douglas Frew, D.Sc., F.R.S., C.S.I.R.O., P.O. Box 109, City, Canberra, 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.
1927 Waterhouse, Professor Walter Lawry, C.M.G., D.Sc.Agr., M.C., D.I.C., F.L.S., F.A.A., 30 Chelmsford Avenue, Lindfield, N.S.W., 2070.
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.
1963 Webster, Miss Elsie May, 20 Tiley Street, Cammeray, N.S.W., 2062.
1946 Wharton, Ronald Harry, M.Sc., Ph.D., C.S.I.R.O., 677 Fairfield Road, Yeerongpilly, Queensland, 4105.
1963 White, Mrs. Mary Elizabeth, M.Sc., 7 Ferry Street, Hunter's Hill, N.S.W., 2110.
1926 *Whitley, Gilbert Percy, F.R.Z.S., Australian Museum, P.O. Box A285, Sydney South, N.S.W., 2000.
1962 Whitten, Maxwell John, Ph.D., C.S.I.R.O., Division of Entomology, P.O. Box 109, City, Canberra, A.C.T., 2601.
1960 Wildon, David Conrad, B.Sc.Agr., Box 108, Rozelle, N.S.W., 2039.
1954 Williams John Beaumont, B.Sc., University of New England, Armidale, N.S.W., 2350.
1954 Williams, Mrs. Mary Beth, B.Sc. (*née* Macdonald), 902D Rockvale Road, Armidale, N.S.W., 2350.
1960 Williams, Neville John, B.Sc., Zoologisch Laboratorium der Rijksuniversiteit te Groningen, Rijksstraatweg 78, Haren (Gr.), Nederland.
1952 Williams, Owen Benson, M.Agr.Sc. (Melbourne), c/- C.S.I.R.O., The Ian Clunies Ross Animal Research Laboratory, P.O. Box 144, Parramatta, N.S.W., 2150.
1950 Willis, Jack Lehane, M.Sc., A.A.C.I., 26 Inverallan Avenue, Pymble, N.S.W., 2073.
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., Geology Department, Victoria University of Wellington, P.O. Box 196, Wellington, C.1., New Zealand.

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 MEMBER

1949 Jensen, Hans Laurits, D.Sc.Agr. (Copenhagen), State Laboratory of Plant Culture, Department of Bacteriology, Lyngby, Denmark.

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