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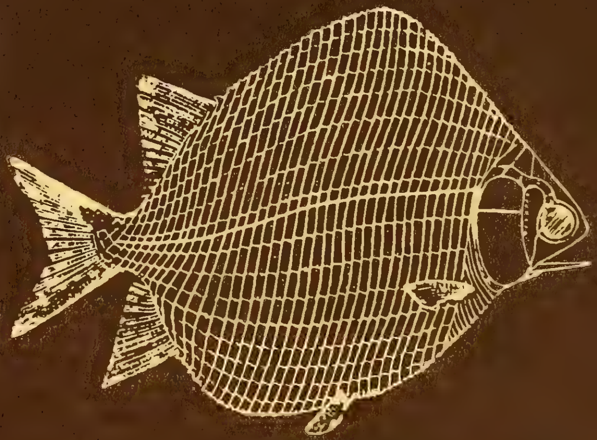
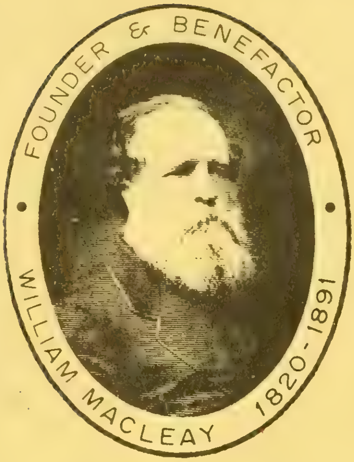


NATURAL HISTORY IN ALL ITS BRANCHES

THE LINNEAN SOCIETY OF NEW SOUTH WALES



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The Society exists to promote 'the Cultivation and Study of the Science of Natural History in all its Branches'. It holds meetings and field excursions, offers annually a Linnean Macleay Fellowship for research, contributes to the stipend of the Linnean Macleay Lecturer in Microbiology at the University of Sydney, and publishes the *Proceedings*. Meetings include that for the Sir William Macleay Memorial Lecture, delivered biennially by a person eminent in some branch of Natural Science. The Society's extensive library is housed at the Science Centre in Sydney.

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PROCEEDINGS
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VOLUME 103
PART 1

THE SIR WILLIAM MACLEAY MEMORIAL LECTURE 1978

Natural History Today

D. T. ANDERSON, F.R.S.

School of Biological Sciences, University of Sydney

[Delivered 16 March 1978]

The Sir William Macleay Memorial Lecture is an occasion on which to honour the memory and legacy of one of the most important pioneers of scientific endeavour in the State of New South Wales and in Australia generally. Prime architect and benefactor of the Linnean Society of New South Wales, Sir William Macleay was foremost a naturalist, at a time when that term was a respectable admission both for a gentleman and for a man of science.

Arriving in New South Wales from England in 1839 at the age of 19, he had already spent some time as a medical student, but opportunities and family associations were to divert him wholly from this course (Walkom, 1942). He became quickly involved in the management of property on the Murrumbidgee near Wagga, where he lived almost permanently for 15 years. It was from this formative period of direct and intimate contact with the flora and fauna of the Australian bush, that William Macleay developed a devotion and a commitment to the study of nature that was to dominate the rest of his life. He returned to residence in Sydney in 1857, and to comfortable circumstances which allowed him in 1862, at the age of 42, to make the decision to give his whole attention to Natural History. Out of this decision arose many investigations, expeditions and benefactions in the study of the biological sciences generally in Australia, all of which retain their importance even after the passage of nearly 120 years. Among them was the formation of the Linnean Society of New South Wales, in 1874. In initiating this move, in association with a number of other zoologists, botanists and geologists of the day, Macleay called for the formation of "A Society of Natural History". Ten years later, in a Presidential Address to the then well established Society (Fletcher, 1893), he included the following comment: "Our rules state that the Society is for the promotion of the study of Natural History in all its branches". In the course of time the objectives of the Society were redefined as the promotion of the study of Natural Science, but the practice of the Society has been to retain the spirit of Sir William's major intention, in fostering the development of research and scholarship in Zoology, Botany and Geology. During the twentieth century, with the increasing penetration of science into more and more esoteric concepts and technologies, these disciplines have broadened and become cross-linked, and the Society has now come to embrace the Biological Sciences and Earth Sciences as its domain — a move which Sir William would have thoroughly approved.

I feel, however, that because Sir William came to be a scientist and a promoter of scientific endeavour through his observation and appreciation of nature, and not through any formal early training, he might also have been concerned to see that the focal point of his view of Natural History, namely the continued comprehension of the faunal, floral and geological diversity of the earth, was not lost to sight in the search for ever more powerful theoretical abstractions.

For example, with his interest in bacteriology (commemorated, for instance, in the

Linnean Macleay Lectureship in Microbiology at the University of Sydney), Sir William would no doubt have been delighted with the discoveries of modern microbial genetics; but would also have seen, I think, that these do not assist our ability to conceptualize the diversity and biology of, say, the marsupials. To do this properly one needs, among other things, a vast array of comparative descriptive and experimental data — on the animals themselves, their habits, their reproduction, their interactions with other animals and with many species of plants, their distribution, their fossil history, and the relationship of this history with the geological history of the earth in the Mesozoic and Tertiary. The same argument applies to any other group of animals or to any group of plants, with varying degrees of difficulty depending on the group. This kind of science, which focuses on the systematization of diversity, was what people meant in the nineteenth century when they talked about Natural History. Its importance was obvious at that time, because of the need to try to systematize and manage the flood of information on diversity being gathered from all parts of the world. Gradually everything fell into place with the acceptance of the idea of Evolution, which provided a means of dealing with diversity in a unified way. But from this in turn has stemmed in the present century an array of astonishing achievements in experimental biology, which has brought us to the brink of control over the fundamental processes of life, and to the powerful theoretical constructs of molecular biology and population biology.

What possible significance, then, can Natural History continue to have today? Can it continue to contribute significantly to understanding, or is it a Dodo, a relic from the past that has now been knocked on the head and made extinct as a profitable, professional scientific discipline.

Modern dictionary definitions of Natural History are not encouraging. Natural History, says the Shorter Oxford Dictionary (1959 edition), is the systematic study of all natural objects, animal, vegetable and mineral — so far, so good — but, *now* restricted to the study of animal life, usually in a popular manner. Example, another incident in natural history is, "Toads eat larks".

Websters Dictionary (1926 edition) is even more interestingly denigrating. Natural History, it says, was formerly the study, description and classification of animals, plants, minerals and other natural objects, thus including the sciences of zoology, botany, mineralogy, etc. in so far as they existed at that time (the time is not specified, but the implication is that of Aristotle and Pliny), but *now* commonly restricted to a study of these subjects in a more or less superficial way, at least without making use of modern anatomical and analytical methods.

A DODO INDEED!

In fact, a more constructive definition of scientific Natural History can be developed by contemplating the thoughts and work of some of its founders as contributing scientists. I present two examples, both Englishmen, Gilbert White in the eighteenth century and Charles Darwin in the nineteenth century.

Gilbert White, although he wrote only one book in his entire life (White, 1788), is one of the most interesting characters in the history of Zoology. He was born in 1720. His father was a barrister and his mother was the daughter of the then vicar of Selborne, a small village in rural Hampshire in southern England. Gilbert himself, after pursuing a liberal education and taking an M.A. at Oxford in 1746 at the age of 26, entered the church. For some 15 years he moved among different parishes in England, to become eventually in 1761, at the age of 40, a curate in the village of his birth, Selborne. Here he remained until his death at 72. The Selborne Parish Register records that the Reverend Mr White officiated on June 10th, 1793, at the burial of one of his parishioners, a 16-year-old girl. During this sad duty, White caught a cold, to which he succumbed before the end of the month.

In the 32 years of his settled curacy at Selborne, Gilbert White became, like many educated men of his time, an ardent naturalist. His uniqueness in this pursuit lies in the manner of his investigations and in the book that he wrote on his observations, "The Natural History of Selborne". White spent more time on Natural History than he did on the business of his parish. He identified and described many species hitherto unrecognized, thus contributing directly to the major academic activity of the zoology of the day, dominated by none other than Linnaeus himself. But he also, and this is the crucial point, observed, recorded and interpreted the daily lives and activities of these species. White's are among the first accurate and constructive observations on such matters as — the species specificity of bird songs and their use in distinguishing closely related species; the functional significance of animal colouration; the phenomenon of territoriality in birds; the phenomenon of bird migrations; the occurrence of pseudo-copulation of frogs; and the nocturnal activities of bats, large and small. Never formally trained in zoology, he set in motion an emphasis on field studies and the observation of living animals, of which James Fisher, in his introduction to the 1947 edition of *The Natural History of Selborne* (Fisher, 1947), had this to say: "The theory of organic evolution could never have been propounded, as it was, in the middle of the nineteenth century, without two centuries or more of serious classification, and fifty years or more of serious field observation. It was useless to know how animals were built without knowing the quality of their lives". Gilbert White investigated the quality of their lives. He wrote, for example, of the night-jar *Caprimulgus* feeding on chafers at an oak tree, that "I saw it distinctly, more than once, put out its short leg while on the wing, and, by a bend of the head, deliver somewhat into its mouth. If it takes any part of its prey with its foot, as I have now the greatest reason to suppose it does these chafers, I no longer wonder at the use of its middle toe, which is curiously furnished with a serrated claw". The approach is modern — field observation, cautious interpretation, emphasis on living function. In fact, the claw now appears to be more important in preening — but at least White based his remarks on an observation of nature and not on an imaginative interpretation of dead specimens. Not that he was loath to investigate a dead specimen in connection with his studies if necessary. Take, for example, these comments on a species of large bat. "This summer through I have seen but two of that large species —— ; I procured one of them and found it to be a male; and made no doubt, as they accompanied together, that the other was a female; but happening in an evening or two to procure the other likewise, I was somewhat disappointed when it appeared to be of the same sex — amply furnished with the parts of generation, much resembling those of a boar." Here is evidence of detailed anatomical as well as field observation.

White was, in fact, the epitome of the well rounded, eighteenth century clerical gentleman. He even adhered to the tradition of the day by writing poetry, though alas without the perceptiveness and discrimination that he applied to his observations of Nature:

> "Is this the scene that late with rapture rang,
> Where Delphy danced, and gentle Anna sang;
> With fairy step, where Harriet tripped so late,
> And on her stump reclined the musing Kitty sate?"

The curate's calling is more evident here, in a portion of an ode on a visit by three eligible sisters to his bachelor field haunts. It is perhaps no wonder that Gilbert remained a bachelor. Nevertheless, he understood the meaning and purpose of Natural History in a remarkable way.

The inspiration engendered by the observational techniques of the Reverend Gilbert White soon encouraged a deeper investigation of animals in the field rather than in museums. From about 1820, one begins to see a vast increase in interest in Natural History as recorded from field observations, in a period that was to last through much of the century and was to see the birth of the Theory of Evolution as a consequence. There is no doubt that the unparalleled contributions to Biology made by Charles Darwin had their origin, among other things, in the experiences he gained during his participation in the five years voyage of the Beagle. In the preface to his remarkable account of these experiences, the "Voyage of the Beagle", Darwin (1845) directs attention to the following matters:

1. That the volume contains a history of the voyage and a sketch of those observations in Natural History and Geology which possess some interest to the general reader.
2. That in a larger publication, the Zoology of the Voyage, he had appended to the description of each species (described systematically by various specialists of the day) an account of its habits and range.

It was this awareness of habits and range, that is, of observations on the lives of species in their natural habitat, and the relating of these observations to structure and adaptation, which gave all of Darwin's work its modern feel and which led him with great insight to the possibility of a system of generalization through which all such phenomena might be comprehended. He was supremely aware of the diversity, functional interrelatedness and temporal instability of living phenomena, and of the relationships between those endless minutiae of detail concerning animals and plants that can be expressed verbally and graphically, but cannot be reduced to mathematical or chemical formulations. And he could express this awareness with the most penetrating simplicity: "The slimy, disgusting Holothuriae, which the Chinese gourmands are so fond of, also feed largely on corals; and the bony apparatus within their bodies seems well adapted to this end. These Holothuriae, the fish, the numerous burrowing shells, and nereidous worms, which perforate every block of dead coral, must be very efficient agents in producing the fine white mud which lies at the bottom and on the shores of the lagoon" (*Voyage of the Beagle,* p. 463, Keeling Island). And again: "It was most striking to be surrounded by new birds, new reptiles, new shells, new insects, new plants, and yet by innumerable trifling details of structure, and even by the tones of voice and plumage of the birds, to have the temperate plains of Patagonia, or the hot dry deserts of Northern Chile, vividly brought before my eyes. Why, on these small points of land, which within a late geological period must be covered by the ocean, which are formed of basaltic lava, and therefore different in geological character from the American continent, and which are placed under a peculiar climate — why were their aboriginal inhabitants, associated, I may add, in different proportions in both kind and number from those on the continent, and therefore acting on each other in a different manner — why were they created on American types of organization?" (*Voyage of the Beagle*, p. 393, Galapagos Archipelago).

One can perhaps sum up and define Natural History as Darwin understood it in the following way. It is the investigation of:

the diversity of animal and plant life,
the relation of structure to habit and environment,
the perpetuation of diversity through reproduction
and the evolution of diversity through time *and* the distillation from these observations of generalizations which summate this diversity.

Using this definition, we can now address the question, whether Natural History has a role today. In my opinion it has, and for the following reasons:

Our knowledge of diversity has increased enormously in the twentieth century. Vast numbers of new species have been identified and named. The amount of information on the distribution, structure, functional organization, activities, reproduction and life cycles of known species has increased to a torrent. A similar plethora of information has been gathered on fossil species, especially of invertebrates, and new techniques have permitted fossil material to be interpreted in much more detail with respect to modes of life, interrelationships and temporal distribution and spatial distribution. All of this information needs to be incorporated into new generalizations which convey our present level of understanding, and not simply tacked on to generalizations which were propounded in the nineteenth century. Let me trace through an example with which I am familiar, progress in the understandings of barnacles. Darwin's two classic monographs (1851, 1854), systematized all there was to know about barnacles at that time and provided a comprehensive statement about the phylogeny, evolution and biology of this group. Subsequent studies have modified this statement in various directions, concerned with feeding, reproduction, embryonic development, larval development, population biology and fossil history. With the exception of the latter, however, these studies have been conducted in relation to various kinds of experimental conceptualizations in physiology, ecology and developmental biology. Only the palaeontologists have kept in mind that questions about barnacles can be most usefully framed in the context of a comprehensive overview of the group, and have tried to improve on Darwin's overview in the light of new information. This endeavour has now culminated in an extensive revision by Newman and Ross (1976) of the phylogeny and classification of the balanomorph barnacles, based on recent and fossil skeletal structure; but much of the other information gathered on structure, function and reproduction in barnacles during the last 120 years still lies outside this framework. It is easy to see what happens as a result. The natural history of barnacles continues to be expressed in outmoded terms, and erroneous conceptions of our basic knowledge of these animals continue to be incorporated into otherwise sophisticated physiological, developmental and ecological investigations.

Suppose, for example, that one wishes to investigate an ecological problem involving knowledge of the pattern and composition of food intake by a particular species of barnacle. Is the information available? Probably not. In order to obtain it, what does one have to use? The techniques of natural history. In order to apply these successfully, what does one have to know? How to describe and interpret one's observations in the general context of information about feeding mechanisms and their evolution in the Cirripedia. Where can this information be found? In Darwin (1854) ; and then in a random scatter of observations that have never been correlated one with another or used to modify, as they must, Darwin's initial interpretation.

We could do better. As was so eloquently argued by J. W. Evans (1965), we should do better. We should encourage the improvement of comparative, whole-organism descriptive and experimental biology (Natural History) all the time, by professional biologists for professional biologists, so that we can continue to come to terms with diversity as well as with causality. Both are aspects of the same truth.

In fact, I would be prepared to go one step further and plead the cause of professional scientific Natural History in its contribution to the larger human endeavour. The conflict between exploitation and conservation must be resolved if we are not all to sink into the mire of a murdered world. We, as biologists, have a prime responsibility in promoting the conservation of nature. Part of this responsibility can be met by professional scientific work leading to suitable management techniques — but this work is often highly mathematical and always too high powered for the average person to grasp. Yet the community at large has to be persuaded, because it eventually has to foot the bill in limiting exploitation and accepting that conservation has advantages. Education in Natural History, which builds on a natural link between man and nature, which presents the familiar, shows it to be complex and worthy of respect, and puts this complexity in visual, verbal, graspable terms, can provide one of the few means of communication that can prevent the community from becoming disenchanted with science.

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Review of the Australian Dipteridaceae

RAFAEL HERBST
(Communicated by J. F. RIGBY)

HERBST, R. Review of the Australian Dipteridaceae. *Proc. Linn. Soc. N.S.W. 103* (1), *(1978) 1979*: 7-21.

A critical examination is made of the available fossil fern specimens included in the family Dipteridaceae from Australian collections. All valid fossil species from Australia are reviewed, but extant species are not considered.

Poorly-described species are redescribed, and illustrated, with lectotypes selected where necessary. *Thaumatopteris shirleyi* sp. nov. is erected, being the first record of the genus from Australia; doubtfully, *Clathropteris* is cited for the first time.

The species *Dictyophyllum rugosum, D. obtusilobum?* and *Hausmannia buchii* are shown to be absent from Australia.

Rafael Herbst, Faculty of Sciences, 9 de Julio 1449, Corrientes, Argentina;
manuscript received 11 October 1977.

INTRODUCTION

Other than in South America, the Gondwana record of fossil members of the fern family Dipteridaceae seems to be a meagre one. Very little is known of the family from South Africa and India, and only a few ill-defined species had been described many years ago from Australasia. Considering the relative wealth of species and specimens from South America this always seemed rather strange to me. Thus, while studying Triassic plants, and having found some good specimens of these ferns, I decided to review the whole group from Australia and New Zealand without restricting it to Triassic representatives.

This contribution is to clarify some names, to revalidate and redescribe some poorly known but sound species and to describe the recently found *Thaumatopteris shirleyi* sp. nov. A list of all references to fossil Dipteridaceae was compiled, and after critical examination of the specimens themselves, many were excluded and some others were re-identified. The resulting list of taxa, here considered valid, comprises seven species included in three genera, and the doubtful presence of a fourth genus. Fortunately most of the original specimens could be located in museum collections, mainly in Queensland, therefore lectotypes and paratypes could be selected and designated. I did not see New Zealand material.

Repositories of specimens are abbreviated as follows:

GSQ = Geological Survey of Queensland, Brisbane
MUDG = Department of Geology and Palaeontology, University of Melbourne, Melbourne
QM = Queensland Museum, Brisbane
SUP = Department of Geology and Geophysics, University of Sydney, Sydney
UQ = Department of Geology and Mineralogy, University of Queensland, Brisbane

SYSTEMATIC REVIEW

Previous Records of Australasian Fossil Dipteridaceae

The following list is compiled from all literature available to me in which identification of actual specimens is made:

Original citation	*Source*	*Present status*
1. *Dictyophyllum bremerense*	Shirley, 1898	*D. bremerense*
2. *Dictyophyllum rugosum*	Walkom, 1917	*D. bremerense*
3. *Dictyophyllum davidi*	Walkom, 1917	*D. davidii*
4. *Dictyophyllum acutilobum*	Arber, 1917	*D. acutilobum*
5. *Dictyophyllum obtusilobum?*	Arber, 1917	*D.* sp. cf. *D. acutilobum*
6. *Hausmannia buchii*	Walkom, 1917	not Dipteridaceae
7. *?Dictyophyllum* sp.	Walkom, 1919	not Dipteridaceae
8. *Dictyophyllum rugosum*	Walkom, 1924	*D. davidii*
9. *Hausmannia wilkinsi*	Walkom, 1928	*H. wilkinsii*
10. *Dictyophyllum bremerense*	Jones and de Jersey, 1947	*D. bremerense*
11. *Dictyophyllum* sp. 1	Jones and de Jersey, 1947	not Dipteridaceae
12. *Dictyophyllum* ? sp. 2	Jones and de Jersey, 1947	not Dipteridaceae
13. *Dictyophyllum ? davidi*	Jones, 1948	not Dipteridaceae
14. *Dictyophyllum ? rugosum*	Hill, 1951	*D. davidii*
15. *Dictyophyllum bremerense*	Derrington, 1954	*D. davidii*
16. *Hausmannia* ? sp.	White, 1961	*H. (P.)* sp. cf. *H. (P.) deferrariisii*
17. *Hausmannia (Protorhipis)* sp.	Hill et al.	*H. (P.)* sp. cf. *H. (P.) deferrariisii*
18. *Hausmannia* sp.	White, 1966	*H. (P.)* sp. cf. *H. (P.) deferrariisii*
19. *Hausmannia wilkinsi*	White, 1967	*H.* sp. cf. *H. wilkinsii*
20. *Hausmannia* sp.	Douglas, 1969	*H. bulbaformis*
21. *Dictyophyllum* sp. cf. *D. ellenbergi*	White, 1969	*D. bremerense*
22. *Hausmannia wilkinsi*	White, 1972	*H.* sp. cf. *H. wilkinsii*
23. *Hausmannia* sp. cf. *H. deferrariisii*	Gould, 1974	*H. (P.)* sp. cf. *H. (P.) deferrariisii*
24. *Hausmannia* sp.	Gould, 1975	*H. (P.) sp. cf. H. (P.) deferrariisii*
25. *Hausmannia bulbaformis*	Douglas, 1973	*H. bulbaformis*

From the foregoing list, apart from the misidentified species which have been placed in synonymy, the following names are rejected or excluded from the Australasian Dipteridaceae:

5. *D. obtusilobum*? (Arber, 1917) : this doubtful fragment most probably is a small bit of *D. acutilobum* as Arber himself expressed originally.

6. *H. buchii* (Walkom, 1917) : this is a fragment of a fossil leaf with no visible margin at all. The veins dichotomize, but do not show traces of the anastomosing network of the Dipteridaceae. It is excluded from the record.

7. ? *Dictyophyllum* sp. (Walkom, 1919) : this is a fragmentary specimen which does not show any veins or other detail except its outline. It is improbable that it belongs to the Dipteridaceae.

11. and 12. *Dictyophyllum* sp. *1* and *Dictyophyllum?* sp. *2* (Jones and de Jersey, 1947) : two small fragments which do not show any trace of venation and are incomplete; they are excluded from the record.

13. *Dictyophyllum? davidi* (Jones, 1948) : another fragmentary specimen which only very vaguely reminds one of *Dictyophyllum*; a mid-vein and some lateral veins can be distinguished, but the fragment more probably is a portion of *Dicroidium* sp.

Specimens attributed to other species are quoted either in the synonymy or in the respective discussion below, according to the degree of confidence with which they are regarded as belonging to a particular species.

The following taxa stand as valid:

Dictyophyllum bremerense Shirley
Dictyophyllum davidii Walkom

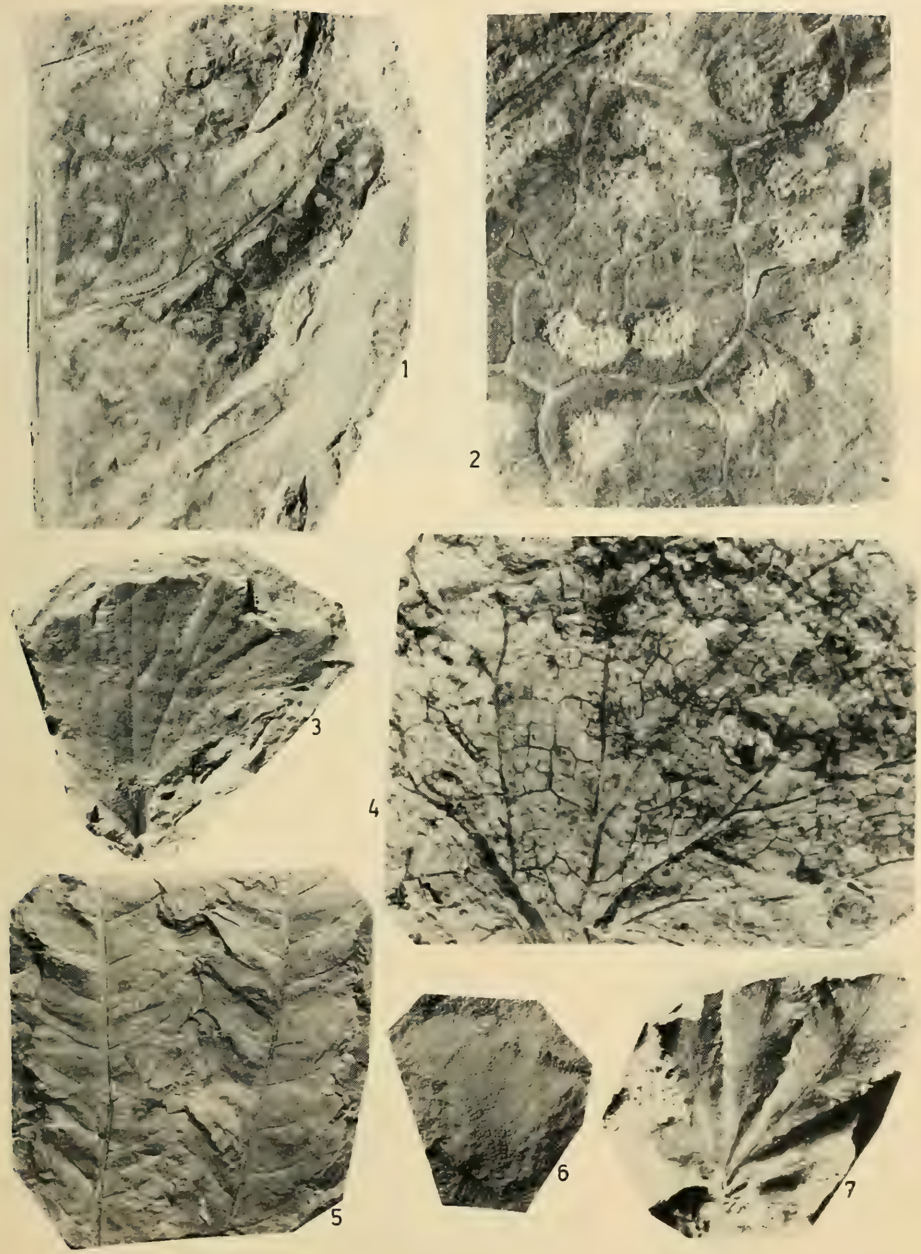

Fig. 1. 1, 2 – *Dictyophyllum bremerense* Shirley, 1898 (1) UQ F64068 ×2⅓; (2) UQ F64068 ×8. 3 – *Hausmannia wilkinsii* Walkom, 1928 GSQ F1943b ×1⅔. 4 – *Clathropteris* sp. UQ F23071 ×1⅓. 5 – *Dictyophyllum bremerense* Shirley, 1898 SUP 20007b ×1. 6 – *Hausmannia (Protorhipis)* sp. cf. *H. (P.) deferrariisii* Feruglio, 1937 Bureau of Mineral Resources, Canberra, specimen F22699, from Helen Springs, Northern Territory (photo kindly supplied by Mrs M. E. White) ×⅔. 7 – *Dictophyllum davidii* Walkom, 1917 GSQ F165 Holotype ×⅔.

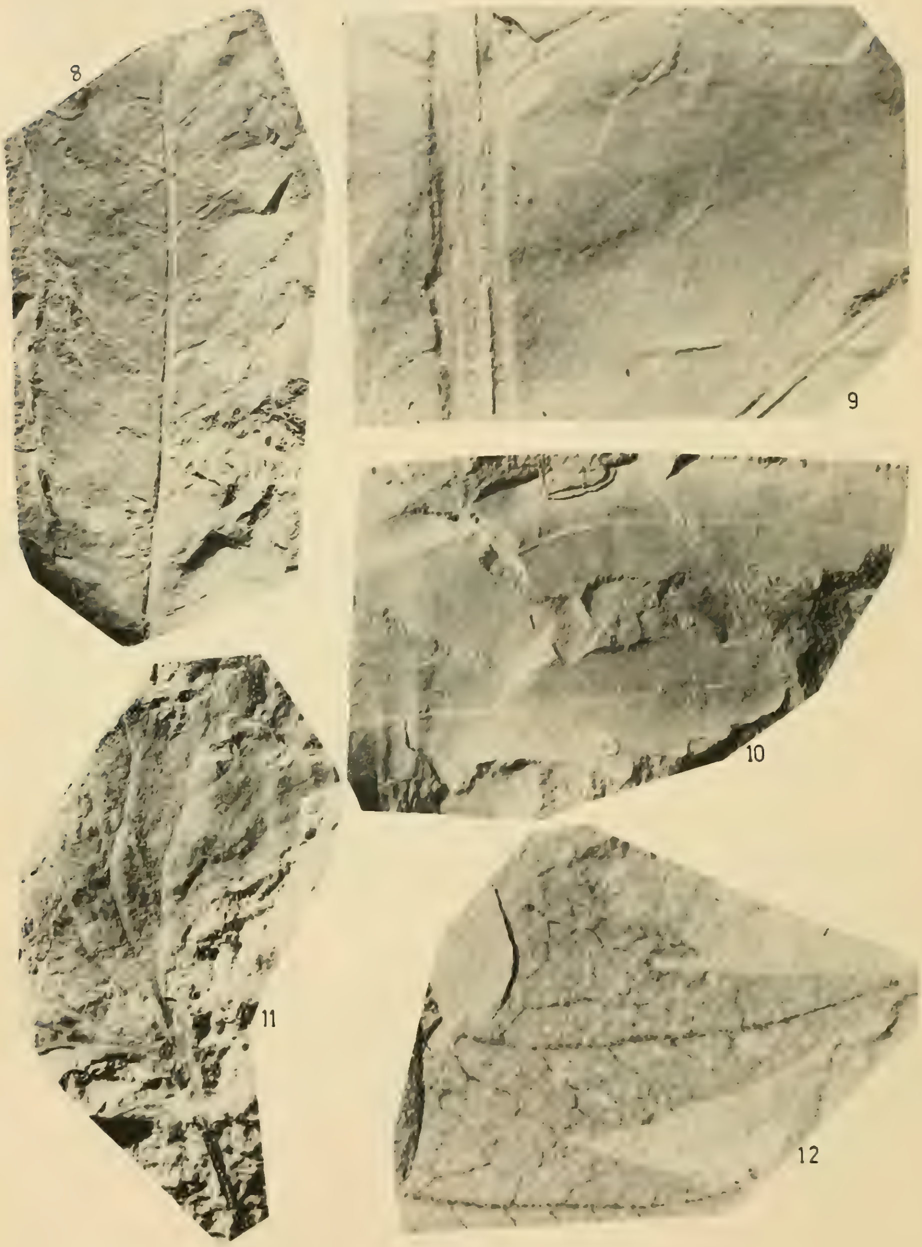

Fig. 2. **8** — *Dictyophyllum bremerense* Shirley, 1898 GSQ F12041 ×1⅓. **9, 10** — *Thaumatopteris shirleyi* n. sp. **(9)** UQ F64280 ×3⅓; **(10)** No. 2995 (CTES-PB, Argentina) ×2. **11** — *Hausmannia wilkinsii* Walkom, 1928 GSQ F8857 ×2⅔. **12** — *Dictyophyllum davidii* Walkom UQ F48643 ×2.

Dictyophyllum acutilobum (Braun) Schenk
Thaumatopteris shirleyi n. sp.
Hausmannia (Hausmannia ?) wilkinsii Walkom
Hausmannia (Protorhipis) sp. cf. *H. (P.) deferrariisii* Feruglio
Hausmannia (Hausmannia) bulbaformis Douglas
cf. *Clathropteris* sp.

SYSTEMATIC PALAEOBOTANY

Dictyophyllum bremerense Shirley, 1898

Fig. 1. 1 ,2, 5 ; Fig. 2. 8 ; Fig. 3. 1-8.

1898, *Dictyophyllum bremerense* Shirley, *Geol. Surv. Queensl., Publ.* 128: 25, pl. 13, figs 2a/b.

1917, *Dictyophyllum rugosum* Walkom, *Geol. Surv. Queensl., Publ.* 257: 9 pl. 4, fig. 3; pl. 6, fig. 4B; pl. 9, fig. 3.

1947, *Dictyophyllum bremerense* Shirley, *in* Jones & de Jersey, *Univ. Queensland., Pap. Dept. Geol.* 3(3) : 13; pl. 1, fig. 6; pl. 4, fig. 1b.

Description: Frond palmate (?) with at least seven large pinnae united at the base, and free apically. Free parts of pinnae up to 100 mm long, probably longer, 50 mm wide, rather pinnatifid.

Midrib of pinnae strong and straight; second order lateral veins (the midvein of each "pinnule") arising at 60°, slightly falcate (or apically, concavely arched), reaching the apex of each "pinnule".

"Pinnules" generally falcate, their free portions up to 20 mm long, by 8-9 mm wide basally; apex is generally acute, both margins strongly curved. Distance along midrib between where lateral, second order veins arise is variable, from 6-7 mm to 15-17 mm.

Third order veins (second order lateral veins) arise at 60°-70°, then by successive dichotomous divisions form a network of somewhat elongated, rectangular to polygonal meshes. The highest order meshes are 4-5 mm diameter, and, when elongated, their longest axis lies parallel to the second order veins. From the second order veins, smaller ones of successively higher orders are given off, which themselves form smaller meshes of successively higher orders. The meshes are polygonal, 4-7 sided, with the smallest, highest order, measuring about 0.5 mm diameter. Most higher order meshes are elongated, and tend to be arranged with their longest axis parallel to the second order veins. Venation is similar throughout the lamina.

Fertile specimens are rare, but some show sporangia arranged in "sori" (?) either along lateral veins of second order as elongated bodies 7-8 mm long and 1 mm wide (Fig. 3. 4) or/and distributed randomly on the lamina as oval or rounded bodies 2-3 mm diameter (Fig 3. 4, 7). The shape of these "sori" (Fig. 3. 5) is not clear as all available impressions are from the upper surface, and it is possible that the sporangia are distributed evenly or in irregular patches over the whole lamina.

Individual sporangia are indistinct, they are about 0.05 mm in diameter. An annulus is faintly visible in some.

Discussion: When Shirley erected this species, there were few others to compare it with. Subsequent authors, other than Jones & de Jersey (1947), have ignored it. No more recently erected species are synonymous with it although it is quite similar to *D. tenuifolium* Stipanicic & Menendez, and *D. ellenbergi* Fabre & Greber, and less similar to *D. davidii* Walkom and *D. acutilobum* (Braun) Schenk. All but the last are Gondwanan species, and it is felt that they form a natural, closely related group.

Material Studied: Lectotype: GSQ F 166a (here designated), figured by Shirley

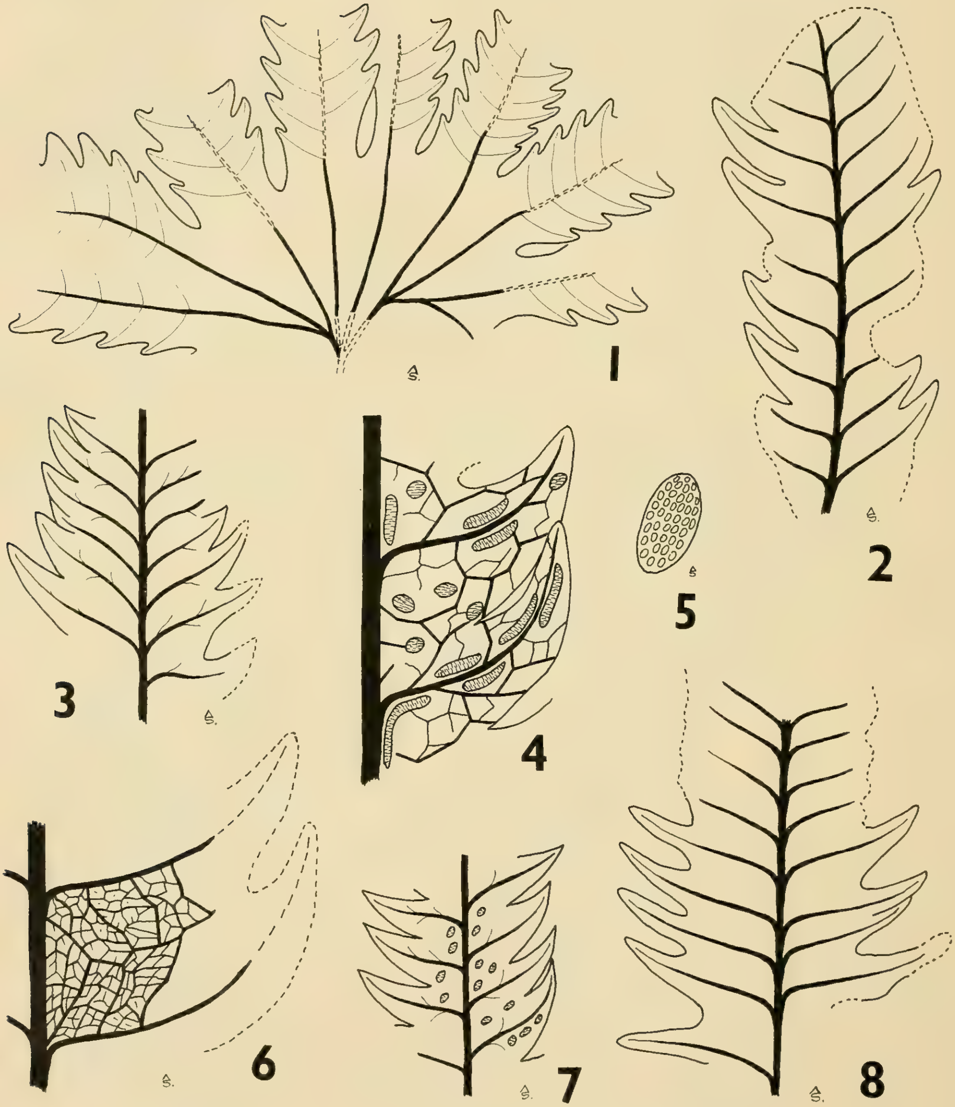

Fig. 3. **1-8** – *Dictyophyllum bremerense* Shirley, 1898 **(1)** GSQ F549, partly reconstructed × ⅔; **(2)** GSQ F12041 × ⅔; **(3)** UQ F2685 × ⅔; **(4)** UQ F64068 × 1⅓; **(5)** UQ F64068, sorus showing probable arrangement of sporangia × 6⅔; **(6)** UQ F43868 × 2; **(7)** UQ F64068 × ⅔; **(8)** UQ F2668 × ⅔.

(1898), pl. XIII, fig. 2; Denmark Hill, Ipswich, Qld; Late Triassic age. *Paratype* GSQ F 166, figured by Shirley (1898), pl. XIII, fig. 3; and counterpart UQ F 5981; from the same locality.

Other Specimens: Denmark Hill, Blackstone Formation (upper part of the Ipswich Coal Measures) of Karnian age (de Jersey, 1972): GSQ F 549, 12033-12044; UQ F 2342, 2668, 2685, 5983, 5984, 44313; 5981 (counterpart of GSQ F 166) and 8199 both figured by Jones & de Jersey (1947; pl. 1 fig. 6; pl. iv, fig. 1b respectively).

Dinmore Quarry, Qld, Blackstone Formation: Mr N. Petty's collection nos. 259, 264 a/b, 539, 607.

Ipswich (details unknown), Qld. SUP 20007 a,b.

Dictyophyllum davidii Walkom, 1917

Fig. 1. 7; Fig. 2. 12; Fig. 5. 15-17

1917, *Dictyophyllum davidi* Walkom. *Geol. Surv. Queensl., Publ.* 257: 10, pl. 3, fig. 2.
1924, *Dictyophyllum rugosum* Walkom. *Mem. Queensl. Mus.,* 8:2, pl. 21, fig. 1.
1954, *Dictyophyllum bremerense,* Shirley, in Derrington — unpublished thesis, University of Queensland: 45.
1975, *Dictyophyllum davidii* Walkom, *in* Flint & Gould, *J. Proc. R. Soc. N.S.W.* 108: 71, pl. 1, fig. 3.

Description: Frond palmate, with at least eight pinnae. The leaf is definitely petiolate, the petiole divides once into two main veins, which in turn divide over short intervals giving off four veins each to form the pinnae.

The type-specimen has incomplete pinnae up to 50 mm long by 20 mm wide; in another big specimen they reach 100 mm long by 30 mm wide.

Pinnae are only slightly pinnatifid, with small free "pinnules" only 4-5 mm long; it seems better to describe the pinnae as strongly dentate rather than pinnatifid, First order lateral veins arise at 70-75°, one for each "pinnule" or "tooth", reaching their apex, slightly falcate. Veins of successive order cannot be clearly differentiated; they form a network of polygonal (4-7 sided) meshes. The meshes are somewhat elongated with their main axis parallel to the pinna rachis, but become more isodiametric towards the margins and pinnae apices. The former are around 1.5 mm by 1 mm and the latter about 1 mm diameter.

Only one fertile specimen is available; it shows elongated sori, 1.2-2 mm long by 0.8-1.2 mm wide, arranged mainly along the pinna rachis and first order lateral veins; very occasionally they seem to be on other parts of the lamina. Each sorus contains 25-30 sporangia but no details of these can be made out.

Discussion: This species was believed to be closely related to the well known *Dictyophyllum rugosum* (L. & H.) and was sometimes mistaken with it. But the redescription given by Harris (1961) for this species shows very clearly that *D. davidii* is a different species, with a general morphological similarity. Additionally the soral characters herein described for *D. davidii* very strongly support this difference.

As already stated it is felt that *D. davidii* belongs to a natural "group" of species together with *D. bremerense, D. tenuifolium, D. ellenbergi* and *D. acutilobum.*

Material Studied: Holotype (here designated): GSQ F 165, from "Challivet", portion 28, parish Biarra, near Esk, Qld; Esk Formation of Middle Triassic age, largely Anisian (de Jersey, 1972).

Other Specimens: Esk Formation of Middle Triassic age. "Challivet", portion 28, parish Biarra, near Esk, Qld: GSQ F 168, 933, 12043; Various sites at or around

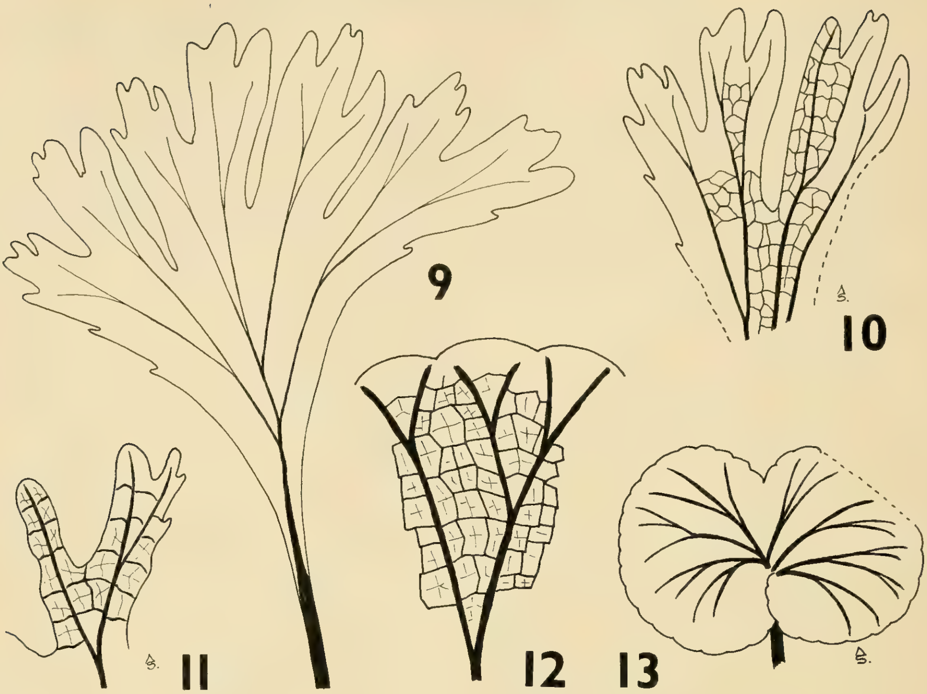

Fig. 4. **9-11** *Hausmannia wilkinsii* Walkom, 1928 **(9)** GSQ F1943a, combined with GSQ 8857 to give the reconstruction of a leaf ×2⅔; **(10)** GSQ F1943a, detail of venation ×2⅔; **(11)** GSQ F8843, detail of venation ×1⅔. **12, 13** – *Hausmannia (Protorhipis)* sp. cf. *H. (P.) deferrariisii* Feruglio, 1937 **(12)** UQ F50306, detail of venation ×3⅓; **(13)** UQ F50306, reconstruction of a leaf ×1⅓.

Wivenhoe Hill, parish Wivenhoe, Qld; UQ F 2010, 2046, 2051, 2359, 5812, 12853, 17068, 17069, 26754, 64177. Mandura 1:63 360 map sheet at grid reference 936629 (quoted from Derrington, 1954), Qld: UQ F 17394 a/b. Caboolture 1:63 360 map sheet at grid reference 645257, Qld: UQ F 17079 a/b. Portion 42, parish Wivenhoe, Qld: QM F 1468 (Walkom, 1924, pl. 21, fig. 1).

Bundamba Group of latest Triassic to Middle Jurassic age (Cranfield & Schwarzbock, 1972), horizon within the Bundamba Group unknown. Precipice Creek (tributary of the Dawson River), 4 km SW of Rose's Shack, Qld (Hill, in Shell Report, 1951): UQ F 48643, 48654.

Dictyophyllum acutilobum (Braun) Schenk

1917, *D. acutilobum* (Braun) Schenk, in Arber, E.A.N., *Paleont. Bull. N.Z. Geol. Surv.* 6:34, pl. XII, figs 2-4.

Discussion: I have not seen the original specimens described by Arber, but there is little doubt that they can confidently be regarded as belonging to the species.

D. acutilobum has a rather wide distribution (Sweden, Germany, Persia and New Zealand) and was also quoted, without illustrations, by Zeiller (1875) from the "Rhaetic" of Chile; later Solms-Laubach, while describing plants from the same locality, quoted a different species of Dipteridaceae, but did not illustrate his species.

The fragment found at Purga, Qld, described below is very similar to illustrations

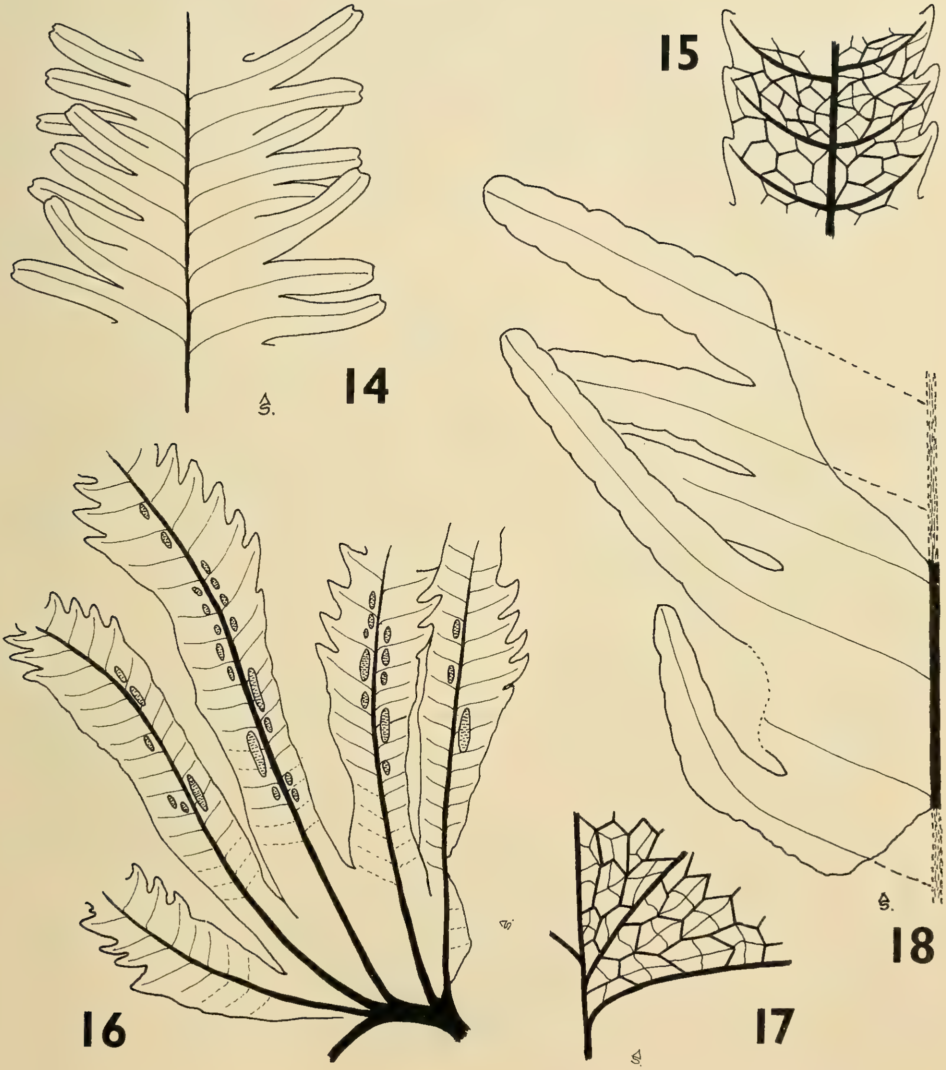

Fig. 5. **14, 18** – *Thaumatopteris shirleyi* n. sp. (14) UQ F64280, reconstruction of part of the leaf based on the holotype × ⅓; (18) UQ F64280, holotype × 1. **15-17** – *Dictyophyllum davidii* Walkom, 1917 (15) GSQ F165, holotype × 2⅔; (16) UQ F64177 × ⅔; (17) GSQ F165, detail of venation of the holotype × 4.

of this species figured by other authors, and therefore I consider that it most probably belongs here, but because of its fragmentary nature must be regarded as a comparison.

Dictyophyllum sp. cf. *D. acutilobum* (Braun) Schenk

Fig. 6. **16**

Description: This pinna fragment is 28 mm long by 20 mm wide with two "pinnules" on each side. These are sub-triangular with a slightly curved midvein arising at about 45° from the rachis, and continuing to the apex of the "pinnules". The free part of each "pinnule" is one third of the total width.

From each midvein, secondary veins arise which, by successive divisions form a network of polygonal meshes. Those of the first order are about 4-5 mm diameter, and are filled with higher order meshes, the smallest one (highest order) are about 0.9-1 mm diameter.

Material Studied: Purga, Qld; Walloon Coal Measures, mainly Middle Jurassic: UQ F 5856.

Thaumatopteris shirleyi n. sp.

Fig. 2. **9, 10**; Fig. 5. **14, 18**

Diagnosis: The biggest fragment represents a portion of pinna with a strong rachis 2 mm wide. First order lateral veins arise at 30° to enter the pinnules and reach their apex. The lamina forms a continuous wing along the rachis up to 22 mm wide, thereafter the pinnules are free. They are up to 72 mm long by 11 mm wide at the base, diminishing very slowly to 5 mm wide at the rounded apex. A small pinnule measures only 23 mm long by 5 mm at the base. Margins of the pinnules are crenated, each crena slightly asymmetrical, and about 3.5 mm long.

Second order lateral veins (laterals of pinnules) emerge at 40-45°, and are spaced 4-6 mm apart. Those on the winged lamina are immediately dichotomized forming a net of polygonal first order meshes of 7 by 5 mm diameter, with their longest axis along the main rachis. Inside these, successively smaller meshes are formed, the smallest about 0.5 to 1 mm diameter; in many cases a free terminal veinlet in these ultimate meshes can be seen. In the pinnules only the small last order meshes stand out clearly.

All specimens are sterile, but one of them shows some bulgings of the lamina which could correspond to underlying bodies (sporangia?). These bulgings coincide with the interior of the ultimate meshes.

Discussion: I could not find a species among the Dipteridaceae which can be closely compared with *T. shirleyi.* There are several forms with long "pinnules" but the lamina adjoining the rachis, the size and venation characters differ quite a bit.

Although not known from complete leaves, *T. shirleyi* seems to be one of those cases where it is difficult to decide between *Thaumatopteris* or *Dictyophyllum* as the best to house the species; the former name is preferred on account of the above-mentioned long "pinnules".

Material Studied: Holotype: UQ F 64280, *Paratypes:* UQ F 64204 a/b from Dinmore Quarry, Ipswich, Qld in the Blackstone Formation (upper part of Ipswich Coal Measures) of mainly Karnian age (de Jersey, 1972).

Other specimens: CTES-PB no. 2995, University of the Northeast, Corrientes, Argentina.

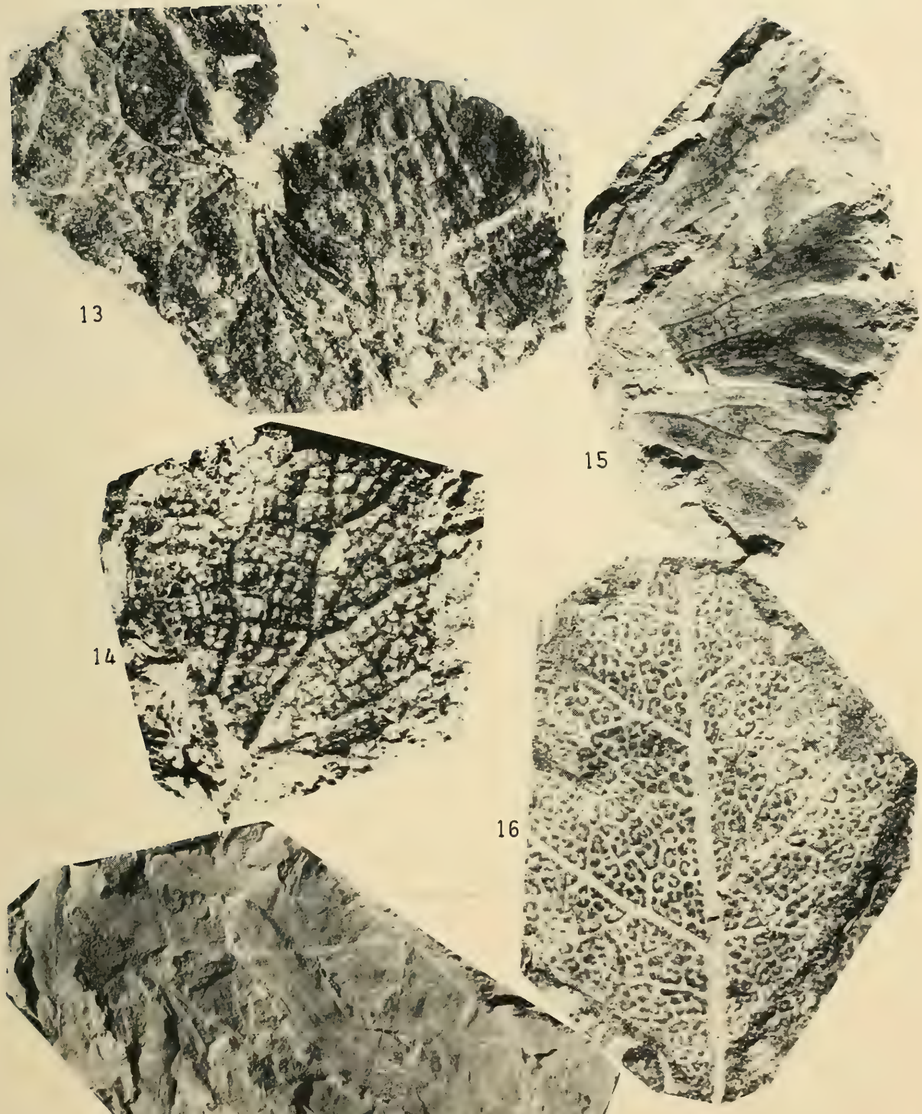

Fig. 6. **13, 14** – *Hausmannia (Protorhipis)* sp. cf. *H. (P.) deferrariisii* Feruglio, 1937 (13) UQ F50305 ×2⅔; (14) UQ F64201 ×4⅔. **15** – *Hausmannia wilkinsii* Walkom, 1928 GSQ F1943a ×2. **16** – *Dictyophyllum* sp. cf. *D. acutilobum* (Braun) Schenk, 1874 UQ F5868 ×2⅔. 17 – *Thaumatopteris shirleyi* n. sp. UQ F64280, holotype ×⅔.

Hausmannia (Hausmannia ?) wilkinsii Walkom, 1928
Fig. 1. **1**; Fig. 2. **11**; Fig. 6. **15**; Fig. 4. **9, 10, 11**

1928, *Hausmannia wilkinsi* Walkom. *Proc. Linn. Soc. N.S.W.*, 53 (2): 148, pl. xiii, figs 3, 4.
1967, *Hausmannia wilkinsi* Walkom, *in* White. *Rep. Bur. Miner. Resour. Aust.*, 1967/78: fig. 3.
1972, *Hausmannia wilkinsi* Walkom, *in* White, *Rep. Bur. Miner. Resour. Aust.*, 1972/1: figs 6, 7.

Description: Complete(?) or half leaf(?) flabelliform, petiolate; the lamina is dissected into four main segments which in turn are again dissected but not so deeply. The four main segments correspond with each of the main veins into which the petiole splits; they dichotomize several times, each final vein reaching the apex of the ultimate portion of the dissected lamina. Veins of higher order arise at right angles and form a network of more or less quadrangular to 5-sided meshes of about 4-5 mm diameter. These are filled with successively smaller meshes, the smallest being about 1-1.5 mm diameter.

Discussion: The few more or less fragmentary specimens of *H. wilkinsii* seem to show that it could be an intermediate form between the classical forms included in the subgenera *Protorhipis* and *Hausmannia* (s.s.) more probably inclined towards the latter.

For its size and venation it was correctly placed in a separate species from those known to Walkom in 1928 and this difference still stands.

Since erected by Walkom (1928), *Hausmannia wilkinsii* has only been used by White (see synonymy) for some fragmentary specimens, which appear to be correctly identified. These specimens came from the Nullawurt Sandstone Member of the Bungil Formation of Early Cretaceous age, and the Gilbert River Formation of Jurassic-Early Cretaceous age, in Queensland.

Material Studied: Lectotype (here designated) GSQ F 1943, from Lower Camp, Plutoville, Cape York Peninsula, Qld, of Early Cretaceous age. Figured by Walkom (1928) pl. xiii, fig. 4. *Paratype* GSQ F 1944, figured by Walkom (1928) pl. xiii, fig. 3.

Other specimens: GSQ F 8843, 8844, 8851, 8857, 8858. All specimens come from the type locality.

Hausmannia (Protorhipis) sp. cf. *H. (P.) deferrariisii.* Feruglio, 1937
Fig. 1. **6**; Fig. 6. **13, 14**; Fig. 4. **12, 13**

1961, *Hausmannia* sp., in White, *Rep. Bur. Miner. Resour. Aust.*, 1961/146 fig. 15.
1966, *Hausmannia (Protorhipis)* sp., in Hill, Playford & Woods, *Jurassic Fossils of Queensland* (Queensl. Palaeontographical Soc.), pl. J1, fig. 9.
1966, *Hausmannia* sp., in White, *Rep. Bur. Miner. Resour. Aust.*, 1966/111, fig. 1.
1974, *Hausmannia* sp. cf *H. (Protorhipis) deferrariisii* Feruglio, *in* Gould, *Proc. R. Soc. Queensl.*, 85 (3): 35.

Description: Leaf entire, composed of two half laminae separated by a deep lower and a short upper sinus. Each half lamina is more or less oval, 20-23 mm long by 15-20 mm wide, margins markedly crenate. The strong petiole, which probably was originally at right angles to the lamina, gives off four primary veins into each half lamina. Each vein divides dichotomously several times to form a network of more or less quadrangular to hexagonal meshes of successively higher orders, the smallest measure about 0.4-0.5 mm diameter.

The first dichotomy of the primary veins occurs halfway to the margin, and successive dichotomies along the primary veins branch at about 45°. Higher order veins and veinlets branch almost at right angles.

All specimens are sterile.

Discussion: Several good specimens of this species are in the University of Queensland collection, but even so it is difficult to establish definitely their complete identity with *H. (P.) deferrariisii* Feruglio, which was originally described from the Middle to Upper Jurassic of Patagonia. There seem to be slight differences in size and venation characters, as well as considerable geographical separation between localities. As the Australian specimens are not completely identical with the Argentinian ones, the best procedure is to designate a comparison. Gould (1974) adopted a similar procedure.

Some specimens quoted by White (1961, 1966) are too fragmentary to allow a definite determination, however they are most probably Early Cretaceous in age. The specimen originally figured by White (1966, fig. 1; reproduced here as Fig. 1. **6**; the photograph was kindly supplied by Mrs White) seems to be fertile. It very strongly resembles *H. (P.) papilio* (Feruglio) Herbst, a closely allied species.

Material Studied: Walloon Coal Measures, mainly Middle Jurassic; Tannymorel Colliery, Tannymoreal, Qld. UQ F 50305, 50306, 64192, 64193, 64194 a/b, 64195-64197, 64198 a/b, 64199, 64200. Mt Elliott Mine, Rosewood, Qld. UQ F 64201, 64202.

Other Specimens: Walloon Coal Measures, mainly Middle Jurassic. Kleinton Clay Pit (via Toowoomba), Qld. QM F 2901. Near Kalbar, parish of Fassifern, Qld. QM F 2905.

Hausmannia (Hausmannia) bulbaformis Douglas, 1973

1954, ?Angiosperm, in Medwell, *Proc. R. Soc. Vict.*, 65: 21.
1969, *Hausmannia* sp. indet., in Douglas, *Mem. geol. Surv. Vict.*, 28: 224; fig. 4, 2.
1969, *Hausmannia* sp., in Douglas, *Mem. geol. Surv. Vict.*, 28: 232; pl. 42, fig. 4.
1973, *Hausmannia bulbaformis* Douglas, *Mem. geol. Surv. Vict.*, 29: 96-97; pl. 33, fig. 3; fig. 7, 44.

Discussion: Only two specimens are available and both are rather fragmentary. Specimen MUGD 3533A, the holotype, from the Koonwarra fish-beds shows some details of venation, thus it can be ascertained that the leaf belongs to the Dipteridaceae, and most probably to *Hausmannia*. It is a petiolate incomplete leaf, with several main veins dividing in a fan-like way which by successive divisions form a network of polygonal, slightly elongated, meshes about 1 mm in diameter. The lamina seems to have been quite thin and filmy.

I think it is rather risky to erect a new species on such fragmentary material, but on the other hand it can be stated that the specimen does not resemble any of the known Australasian species of *Hausmannia*. Therefore I shall provisionally accept Douglas' classification hoping that in the future more findings and better preserved material will justify the erection of this species.

Material Studied: Koonwarra Fish Beds, near Leongatha, Vic.; Wonthaggi 1:63 360 map sheet grid reference 3966, 2457. Early Cretaceous: MUDG 3533 A, B. Killara Bluff, allotment 4, section A, Parish of Killara, Vic. Early Cretaceous: MUDG 2014.

cf. *Clathropteris* sp.

Fig. 1. 4

Description: Fragments of lamina with typical "clathropteroid" quadrangular network of meshes. None of the available specimens shows any part of the original margin, but the biggest one shows what appears to be the main rachis from which at least six first order (?) veins depart in a more or less palmate arrangement. They dichotomize at angles of 45°, and from their branches the veins of successive orders start at right angles to form the abovementioned quadrangular network with meshes about 3-3.5 mm diameter.

Further away from the base, these meshes become more polygonal (5-6 sided), but remain about the same size. The ultimate meshes are about 1-1.5 mm each side, and again quadrangular at the base, and slightly more polygonal away from it.

Material Studied: Cooroy 1:63 360 map sheet at grid reference 098146, Qld; Walloon Coal Measures, mainly Middle Jurassic: UQ F 23068-23072, UQ F 23074-23076.

Discussion: All known fragments are too small and fragmentary to allow a definite classification, but from the few diagnostic characters it can be concluded that the pieces most probably belong to *Clathropteris.*

The venation is different from all other known species hitherto described for Australasia.

ACKNOWLEDGEMENT

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A new species of the *Litoria peronii* Complex (Anura: Hylidae) from Eastern Australia

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and the late J. J. LOFTUS-HILLS

MARTIN, A. A., WATSON, G. F., GARTSIDE, D. F., LITTLEJOHN, M. J., & LOFTUS-HILLS, J. J. A new species of the *Litoria peronii* complex (Anura: Hylidae) from eastern Australia. *Proc. Linn. Soc. N.S.W. 103* (1), *(1978) 1979*: 23-35.

A new species of hylid frog, *Litoria tyleri*, is described from coastal eastern Australia. *L. tyleri* is a member of the *L. peronii* complex; it differs from the other Australian members of the complex (*L. peronii* and *L. rothi*) in adult morphology and mating-call structure. *L. tyleri* is sympatric with *L. peronii* and *in vitro* hybridization tests show the two species to be reciprocally genetically incompatible; they also differ biochemically.

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INTRODUCTION

The *Litoria peronii* group of species includes *L. peronii* in Australia, *L. amboinensis, L. darlingtoni* and *L. everetti* in New Guinea and associated islands, and *L. rothi* in both Australia and New Guinea (Tyler, 1968; Menzies, 1976). In addition, Straughan (1966) and Tyler (1968) noted that an undescribed member of this complex occurs near Brisbane, Queensland. We have collected this undescribed species along eastern coastal Australia from south-eastern Queensland to Jervis Bay, New South Wales. The purpose of the present paper is to describe the new taxon and compare it with *L. peronii* and *L. rothi.*

Because we have encountered *L. rothi* only infrequently in the field, comparative data for this species include only morphology of preserved adults and larvae, and mating-call structure. For the new species and *L. peronii*, however, we have considerable field and experimental data, encompassing adult morphology, mating-call structure, life history, larval morphology, reciprocal artificial hybridization tests, and electrophoresis of haemoglobins and plasma proteins.

METHODS

Adult Morphology

Comparative morphological study was restricted to sexually mature males, and measurements were taken (to 0.1 mm) with vernier calipers or with a stereoscopic microscope and eyepiece micrometer. We have followed the methods and terminology of Tyler (1968), except that head length was measured to the mid-point of the tympanum. Abbreviations used in the text are: E-N/IN = eye to naris distance/internarial span; HL/HW = head length/head width; TL/S-V = tibia length/snout to vent length.

Mating-Call Structure

Mating calls were recorded in the field using a variety of tape recorders and microphones (e.g. EMI L2B, Nagra IIIBH, Tandberg 11-2 tape recorders; Beyer M-69, Beyer M-88, Grampian DP-1 microphones). Where possible, the recorded specimens were collected and lodged in the Department of Zoology, University of Melbourne research collection. Wet-bulb air temperatures (which approximate those of small frogs calling from elevated positions) were taken at or near the calling sites.

Recordings were analysed on an audiospectrograph (Kay 6061-B Sona-Graph) with playback on a Tandberg 11-2 tape recorder. One call of each individual was analysed, generally the last clear call in the recording sequence. Note and spectral characteristics were obtained from a note at or near the middle of each call. Characteristics of the calls were measured on the audiospectrograms using calibrated scales.

Artificial Hybridization Tests and Life History

Artificial hybridization tests were carried out in the field using the technique of Rugh (1962). *In vitro* crosses were made between individuals of the new taxon and *L. peronii,* all collected from a sympatric breeding assemblage at Ryan's Swamp, Caves Beach Reserve, A.C.T. For each interspecific cross a simultaneous intraspecific (control) cross was made. Progeny of control crosses provided material for life history descriptions; and for *L. peronii* additional larval material from Sarsfield, Victoria, derived from an *in vivo* fertilization on 3rd December, 1965, was examined. Embryos and larvae were reared initially in the field under fluctuating temperature conditions and, on return to the laboratory, in Holtfreter's Solution at 20 ± 0.5°C. Larvae were fed on boiled lettuce. Larvae of *L. rothi* were collected at Kununurra, W.A. on 24th February, 1977. Methods of fixation, measurement and illustration of embryonic and larval material follow those of Martin and Littlejohn (1966).

Blood Proteins

Plasma proteins and haemoglobins from 12 individuals of *L. peronii* (6 from Caves Beach Reserve; 6 from Ourimbah, N.S.W.) and 9 of the new taxon (7 from Caves Beach Reserve; 2 from Ourimbah) were analysed. Animals were etherized and ventrally dissected to expose the cardiac cavity. A *truncus arteriosus* was cut, and blood collected in heparinized microhaematocrit tubes. The tubes were flame-sealed, centrifuged at low speed (approximately 25 g) for 10 minutes, then broken at the interface between plasma and cells.

Electrophoresis was carried out on horizontal 5% acrylamide gel slabs using the method described by Gartside (1972). All separations were performed at room temperature using a continuous tris (tris-hydroxymethyl aminomethane) borate buffer (0.3 M tris; pH 8.7) and 250 volts constant voltage, provided by a Vokam stabilized power supply. Five μl of plasma were analysed from each individual. Electrophoresis of plasma was continued until bromphenol blue dye, added to human plasma controls on each gel, had migrated 7 cm from the origin: this took about two hours.

Plasma proteins were stained in 1% amidoschwartz 10B (Chroma Gesellschaft) in 7% acetic acid. Haemoglobins, prepared by washing cells twice in 0.9% sodium chloride and haemolysing them in a mixture of equal parts of toluene and distilled water, were stained in o-dianisidine using the technique of Owen and Smith (1961). All blood samples were fresh when analysed.

DESCRIPTION

Litoria tyleri n. sp.

Types

Holotype, mature male No. R64754, Australian Museum, Sydney; male paratypes: Nos R64755-R64764; female paratypes: Nos R64765, R64766. Type locality: Ryan's Swamp, Caves Beach Reserve, A.C.T., 14 km S of Huskisson, Shire of Shoalhaven, N.S.W. (35° 09′ 45″ S, 150° 40′ 00″ E). Collected by D. F. Gartside, M. J. Littlejohn, J. J. Loftus-Hills, A. A. Martin, I. F. Spellerberg and G. F. Watson, 21st October, 1969. South Australian Museum Nos R12248, R12251, R12254, R13267A, R13267B, R13267C, R13338A, R13338B, R13338C, all mature males from the Ourimbah area, N.S.W., are also nominated as paratypes.

Diagnosis

The *Litoria peronii* group is distinguished from all other frogs in Australia by the combination of the following characteristics:

(i) well-developed webbing and discs on both fingers and toes;
(ii) second finger longer than first;
(iii) dorsum light grey to brown with minute green flecks in life; and
(iv) posterior surfaces of thighs patterned with yellow and black.

L. tyleri can be distinguished from *L. peronii* and *L. rothi* by means of the following characters. In both *L. peronii* and *L. rothi* there is a dark edging on the supratympanic ridge; this dark line is absent in *L. tyleri*. In *L. rothi* the axilla is black, and the posterior surface of the thigh is black with a few yellow spots. In *L. peronii* the axilla is yellow with large black spots, and the thigh is yellow with coarse

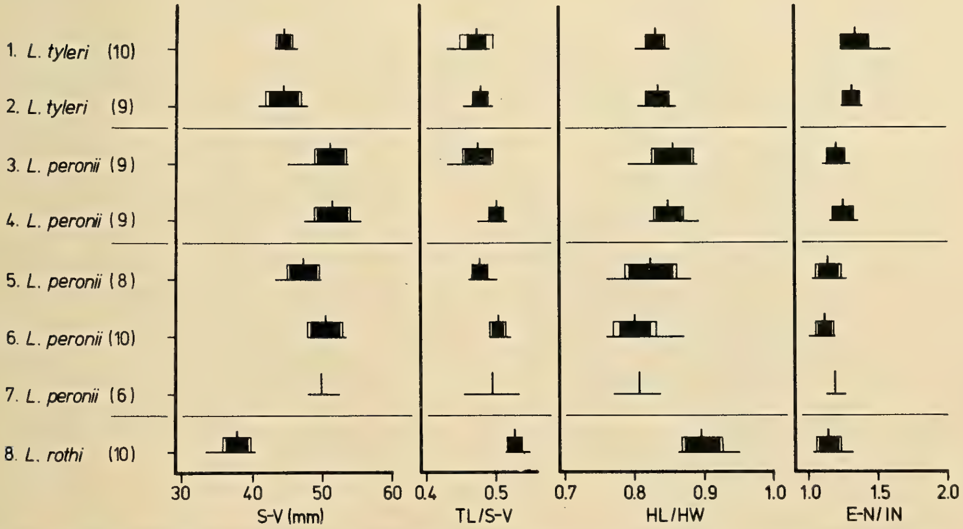

Fig. 1. Body dimensions and ratios of samples of *Litoria tyleri, L. peronii* and *L. rothi.* The number in parentheses after the species name is the sample size. The short vertical line is the sample mean and the horizontal line is the observed range of variation. The black bar represents the 95% confidence limits on either side of the mean and the open bar plus one-half of the black bar indicates one standard deviation of the mean. Sample localities are: 1 and 3, Caves Beach Reserve, A.C.T.; 2, Palm Grove, Ourimbah, N.S.W.; 4, Mallacoota, Vic.; 5, 5-19 km W of Coonabarabran, N.S.W.; 6, Narrandera, N.S.W.; 7, Yarrawonga area, Vic.; 8, Laura, Qld.

black variegation. In *L. tyleri* the axilla is yellow with few or no black spots, and the thigh is yellow with fine black variegation. The texture of the back is rough and warty in *L. peronii,* much less warty in *L. tyleri,* and virtually smooth in *L. rothi.* The mating calls of the three species are distinctive. *L. tyleri* has a greater S-V length than *L. rothi* (Fig. 1). Crosses between individuals of *L. tyleri* and *L. peronii* show the species to be reciprocally genetically incompatible (Table 1).

TABLE 1

Results of *in vitro* crosses between *Litoria tyleri* and *L. peronii* from Ryan's Swamp, Caves Beach Reserve, A.C.T.

Cross	No. of Eggs	No. Fertilized	% Hatched*
		L. tyleri ♀ × *L. peronii* ♂	
Control	110	96	100
Experimental	67	67	0
Control	100	100	80
Experimental	61	61	0
		L. peronii ♀ × *L. tyleri* ♂	
Control	40	40	70
Experimental	77	77	0
Control	65	65	60
Experimental	74	74	0

*Failure to hatch was associated with developmental breakdown, particularly abnormal neurulation.

The three species may readily be identified by the use of the following key:

1. A black line bordering the supratympanic ridge; axilla black, or yellow with heavy black spots; posterior surface of thigh heavily marked with black 2

   Supratympanic ridge without a black line; axilla yellow, sometimes with 1-2 small black spots; posterior surface of thigh yellow with fine black variegation . . . . *L. tyleri*

2. Body length of mature males more than 42 mm; head length 76-88% of head width; back warty; posterior surface of thigh yellow with heavy black variegation. . . . . *L. peronii*

   Body length of mature males less than 42 mm; head length 86-95% of head width; back smooth; posterior surface of thigh black with a few yellow spots . . . . *L. rothi*

Description

A medium-sized species of moderately slender habitus (Fig. 2). Vomerine teeth between the internal nares; tongue broad and with a posterior nick. Head broader than long (HL/HW = 0.80-0.85); snout rounded. External nares much closer to tip of snout than to eye; internarial span less than distance between eye and naris (E-N/IN = 1.23 −1.59). Canthus rostralis slightly concave but not sharply defined; loreal region sloping. Eye diameter slightly greater than distance from eye to naris,

Fig. 2. Male paratype of *Litoria tyleri,* snout-vent length 44.0 mm.

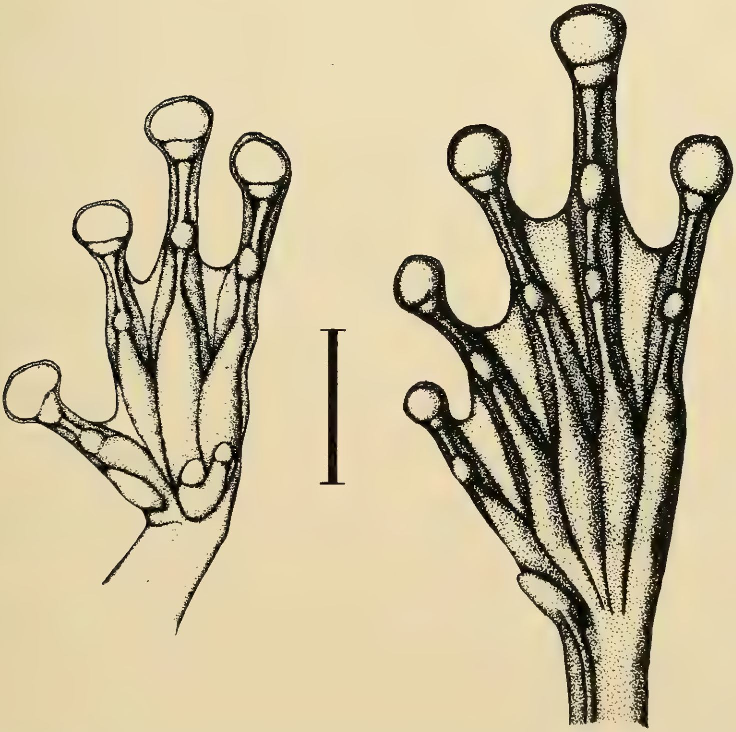

Fig. 3. Palmar view of left hand and plantar view of left foot of holotype of *Litoria tyleri.* The bar represents 5 mm.

and considerably greater than tympanum diameter. Tympanum prominent, bordered dorsally by a ridge running from behind the eye to the axilla.

Webbing on fingers well-developed (Fig. 3); discs prominent, disc diameter being about 1.5-2 times phalanx width. Sequence of lengths 3 > 4 > 2 > 1.

Hind limbs moderately short; TL/S-V = 0.43-0.49. Webbing extends to penultimate phalanx of fourth toe and almost to discs of other toes (Fig. 3). Sequence of lengths 4 > 5 = 3 > 2 > 1. Inner metatarsal tubercle small, oval; no outer metatarsal tubercle.

Dorsal skin mottled, light grey to medium brown, with minute emerald spots; texture finely warty. Ventral skin distinctly granular, off-white to yellowish. Gular region dusky brown in breeding males; no nuptial pads. Axilla with a yellow pterygial membrane, sometimes with 1-2 small black spots. Groin yellow with black mottling; posterior surface of thigh with finely divided yellow and black markings.

Dimensions of holotype are: snout-vent length, 43.4 mm; tibia length, 20.3 mm; head length, 12.8 mm; head width, 15.2 mm; eye to naris distance, 4.3 mm; internarial span, 3.1 mm; eye diameter, 4.7 mm; tympanum diameter, 3.3 mm.Dimensions and ratios of males in the type series are shown in Fig. 1. Dimensions of the two female paratypes are: snout-vent length, 47.6 and 45.6 mm; tibia length, 22.8 and 21.7 mm; head length, 14.3 and 14.1 mm; head width, 15.4 and 15.3 mm; eye to naris distance, 4.2 and 4.5 mm; internarial span, 3.7 and 3.7 mm; eye diameter, 4.9 and 4.4 mm; tympanum diameter, 3.8 and 3.5 mm.

Variation and Comparison with Other Species

The type series of *L. tyleri* shows little morphological variation, and a sample of males from Ourimbah, N.S.W., conforms with the type series (Fig. 1). Also shown in Fig. 1 are selected dimensions and ratios of two samples of *L. peronii* from coastal N.S.W. and Victoria, three samples of *L. peronii* from inland N.S.W. and Victoria, and a sample of *L. rothi* from Laura, Queensland.

L. rothi is the most distinctive member of the complex, having the smallest body size, longest legs and narrowest head. It also has the least warty dorsal skin and the greatest amount of black pigmentation in the axilla, groin and thighs.

Males of *L. tyleri* are intermediate between those of *L. rothi* and *L. peronii* in body size and degree of wartiness of the dorsal skin. On the other hand, *L. tyleri* has the shortest legs and the least amount of black colouration in the axilla, groin and thigh region.

Some differentiation between coastal and inland populations of *L. peronii* is evident, with the coastal samples tending to have a greater body size, narrower head and higher E-N/IN ratio.

Mating-Call Structure

The mating calls of the three species are of similar basic structure and consist of trains of regularly-repeated notes (Fig. 4), each of which is pulse modulated (Table 2).

Although there are insufficient data to assess the effects of temperature on call structure in the *L. peronii* group, general trends are evident for vocalizations in other species of anurans (Littlejohn, 1978). There is an inverse relationship with temperature for durations of calls and notes, and a direct relationship for repetition rates of calls, notes and pulses. The numbers of notes per call and pulses per note, and dominant frequency, usually are not markedly affected by temperature. Hence, allowance must be made for temperature variation when comparing calls.

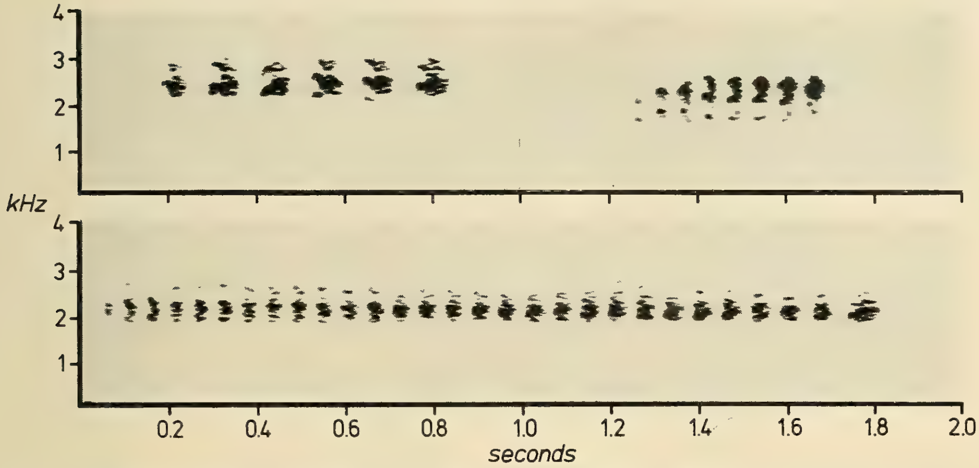

Fig. 4. Audiospectrograms of mating calls of: upper left, *Litoria tyleri,* Palm Grove, Ourimbah, N.S.W.; upper right, *L. rothi,* Kununurra, W.A.; lower, *L. peronii,* Palm Grove, Ourimbah, N.S.W. The trace for *L. peronii* is the latter half of a call.

Even so, it is clear that the calls of *L. peronii* are much longer than those of the other two species, and that the dominant frequencies are slightly higher and note repetition rates slightly lower in calls of *L. tyleri* (Table 2). There are more notes in the call of *L. peronii,* and more pulses in the notes of *L. tyleri* (Table 2). These latter meristic characters should be only minimally associated with temperature, and thus could be most useful in diagnosis.

Life History and Larval Morphology

The following descriptions are based on embryos and larvae reared from eggs of *L.. tyleri* and *L. peronii* fertilized *in vitro* at Caves Beach Reserve on 22nd October, 1969. The dimensions of seven newly-fertilized *L. tyleri* eggs (mean and range) are: embryo diameter, 1.32 mm (1.28-1.36); capsule diameter, 3.49 mm (3.20-3.60). The comparable figures for *L. peronii* are 1.52 mm (1.48-1.56) and 3.00 mm (2.80-3.12). Thus *L. tyleri* eggs are smaller, but with slightly larger capsules. In both species the animal pole is dark brown, the vegetal pole creamy-white, and the jelly capsule three-layered.

When 44 hours old, embryos of both species were at stage 18 of Gosner (1960). Those of *L. tyleri* are slender, medium brown in colour, and approximately 3 mm in total length. The *L. peronii* embryos are plumper, lighter in colour and shorter (length about 2.4 mm).

The embryos of *L. tyleri* hatched after 57 hours, at stage 20, when their total length was about 4.8 mm. Three pairs of external gills are present. Newly-hatched embryos of *L. peronii* are very similar but slightly lighter in colour; they hatched at an age of 70 hours.

All larvae were preserved at the age of 49 days, when they had reached stages 25-26. The dimensions (mean and range) of four *L. tyleri* larvae are: total length, 13.96 mm (12.80-14.72); tail length, 9.36 mm (8.80-9.76). Those of five *L. peronii* larvae are: total length, 19.50 mm (17.00-21.90); tail length, 12.20 mm (10.90-13.90). Apart from the difference in size, the larvae are generally similar, with those of *L. tyleri* having slightly heavier pigmentation and narrower tail fins. The mouth discs are not fully developed, but in the larvae of *L. tyleri* heavier pigmentation

TABLE 2

Physical characteristics of mating calls of *Litoria tyleri, L. peronii* and *L. rothi*
Means and ranges are given

Species and Locality	Wet Bulb Air Temp. °C	Sample Size	Duration (msec)	Notes/Call	Note Repetition Rate (notes/sec)	Note Near Middle			
						Duration (msec)	Pulses/Note	Pulse Rep. Rate (pulses/sec)	Dominant Frequency (Hz)
Litoria tyleri									
Caves Beach Reserve, A.C.T.	12.0-13.0	4	1570 1270-2135	7.8 6-10	4.7 4.4-5.4	122 114-128	23.0 17-30	186 127-258	* 2250-2750
Palm Grove, Ourimbah, N.S.W.	20.8	4	614 455-830	6.0 5-8	9.3 8.6-10.3	64 60-68	23.8 23-25	374 347-392	2475 2350-2550
12.8 km NW of Coffs Harbour, N.S.W.	21.5	3	595 510-645	5.7 5-6	9.0 8.9-9.2	68 61-75	22.7 22-24	333 295-357	* 2150-2650
Litoria peronii									
Gipsy Point, Vic.	14.25-14.5	3	2647 2310-3270	34.7 29-44	12.9 12,4-13.3	43 38-51	10.7 9-12	239 220-276	* 1700-2000
Palm Grove, Ourimbah, N.S.W.	16.9-17.5	3	2425 2120-2800	42.0 36-50	17.3 16.9-17.9	30 25-33	9.3 9-10	308 267-356	* 1900-2100
Litoria rothi									
Kununurra, W.A.	25.6	3	443 370-490	8.3 7-9	17.8 17.4-18.2	25 25-26	10.0 9-11	378 356-400	1933 1850-2000

*Two equal peaks present in some calls.

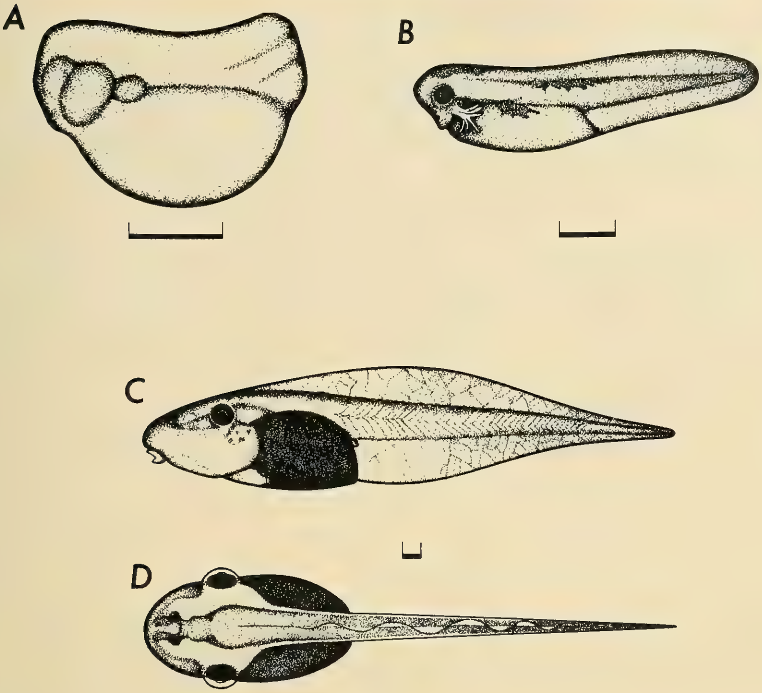

Fig. 5. Stages in development of *Litoria peronii*, Sarsfield, Vic. A, stage 17; B, stage 20 (newly-hatched); C and D, stage 29. The bar in each case represents 1 mm.

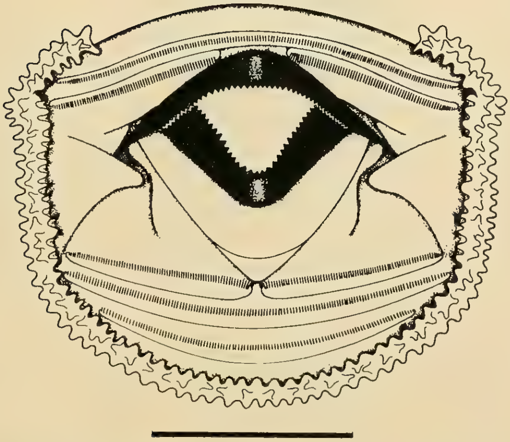

Fig. 6. Mouth disc of larva at stage 29 of *Litoria peronii,* Sarsfield, Vic. The bar represents 1 mm.

of the labial papillae is evident. In both species the spiracle is sinistral and the anus dextral.

Because a complete developmental series of *L. tyleri* from eggs to advanced larvae was not obtained, a series of *L. peronii* stages from Sarsfield, Vic., has been used for illustration (Fig. 5). Available material of *L. tyleri* indicates that the embryonic and larval stages of the two species are similar, and Fig. 5 shows the general characteristics of both species.

Live *L. peronii* larvae are pale golden-yellow, with a dark lateral stripe extending from the snout through the eye and along the dorsal edge of the body and tail musculature. The intestinal peritoneum is dark dorsally but silvery-white ventrally, and the oral and branchial areas are almost transparent but for scattered golden chromatophores. The most advanced larva in the series (stage 41) has a total length of 44.2 mm and tail length of 26.8 mm.

The mouth disc (Fig. 6) is typical of most Australian hylid larvae (Martin and Watson, 1971). There are two rows of teeth in the upper labium and three in the lower; 2-3 rows of papillae extend around the sides and back of the mouth disc. The mouth formula is

$$\frac{1 \quad 1 \quad 1}{1 \quad 2 \quad 1}$$

The Sarsfield larvae took about 190 days to develop from fertilization to metamorphosis, but the larval life-span of *L. tyleri* is unknown.

Fig. 7. Two-banded haemoglobin phenotypes of A, *Litoria peronii* and B, *L. tyleri,* both from Palm Grove, Ourimbah, N.S.W.

Fourteen *L. rothi* larvae from Kununurra, W.A., range in total length from 26.5 mm (stage 25) to 67.7 mm (stage 41). In general morphology they closely resemble the larvae of *L. peronii* and *L. tyleri*; however, their oral structure is distinctive. The lower jaw is much more robust than in the other species, and the third lower row of labial teeth is absent, or reduced to a small median structure bearing less than ten teeth.

Artificial Hybridization

Two *in vitro* crosses were made in both reciprocal combinations between *L. tyleri* and *L. peronii* (Table 1). While the control crosses displayed some degree of abnormality, the experimental crosses in both combinations were characterized by

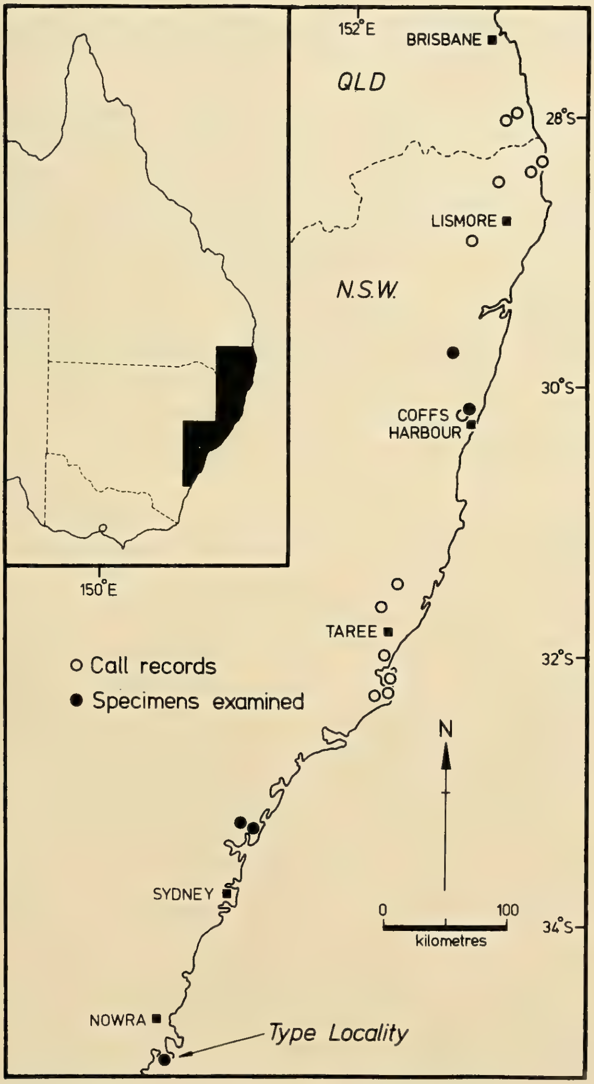

Fig. 8. The geographic distribution of *Litoria tyleri.* The inset shows the area of eastern Australia covered by the main map.

total developmental breakdown. No hybrid embryo successfully completed neurulation. This high degree of incompatibility is suggestive of crosses between diploids and tetraploids (as in the American *Hyla versicolor* and *H. chrysoscelis*; Wasserman, 1970), and a study of karyotypes would be of interest.

Blood Proteins

Fig. 7 shows the typical electrophoretic pattern for haemoglobins, each species having two anodally-migrating bands. The mobility of the leading band is similar in both taxa, while the mobility of the second band is consistently different. Migration of the second band is much faster in *L. tyleri* than in *L. peronii.* For plasma proteins, one set of bands appeared to be species-specific, although other bands in the complex plasma pattern differed in mobility or staining intensity between individuals. Despite this individual variability, bands which are presumed to be transferrins (based on experience with other hylids) are of similar mobility in every individual of both taxa.

Breeding Biology

Males of *L. tyleri* have been heard calling in October, November and January. Males called from the banks of permanent ponds and swamps, or from elevated positions (0.5-1.0 m above the water) in emergent or marginal vegetation. Wet bulb air temperatures at calling sites ranged from 11.0-21.5°C.

Reproductively active females have been collected in October.

Distribution

L. tyleri is distributed along the east coast of Australia from southern Queensland to the Jervis Bay area, N.S.W. (Fig. 8). The geographic range of *L. tyleri* is entirely included within that of *L. peronii* (see Moore, 1961, Fig. 50). Neither species is known to be sympatric with *L. rothi,* which is distributed along the northern and north-eastern coasts (Cogger, 1975).

Etymology

The species is named for Michael J. Tyler of the University of Adelaide, in recognition of his contributions to our knowledge of Australo-Papuan hylid frogs.

CONCLUSIONS

The three species of the *Litoria peronii* complex in Australia are readily distinguishable. The sympatric forms, *L. tyleri* and *L. peronii*, are highly distinctive in most aspects studied, including mating-call structure, blood-protein characteristics, and genetic incompatibility. The apparently absolute level of post-mating isolation between them renders the occurrence of hybridization extremely improbable. In any case, hybrids should be recognizable on grounds of adult morphology (e.g. Martin, 1972), mating-call structure (e.g. Zweifel, 1968) or blood-protein patterns (e.g. Brown and Guttman, 1970). None of our data for these characteristics is suggestive of the occurrence of hybridization.

ACKNOWLEDGEMENTS

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A New Species of *Microscolex (Diplotrema)* (Annelida: Oligochaeta) from New South Wales

G. R. DYNE

(Communicated by B. G. M. JAMIESON)

DYNE, G. R. A new species of *Microscolex (Diplotrema)* (Annelida: Oligtochaeta) from New South Wales. *Proc. Linn. Soc. N.S.W. 103* (1), (*1978*) *1979:* 37-41.

A new species of *Microscolex (Diplotrema),* the first record of the subgenus from New South Wales, is described and figured. This species, defining the known southerly limit of *Diplotrema* in Australia, is shown to have close affinities with the subgeneric type, *D. fragilis.* These species, together with an undescribed form from Ban Ban Springs, Queensland, appear to form a discrete species-group quite distinct from more northerly representatives of the subgenus.

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INTRODUCTION

The endemic Australian acanthodriline earthworm subgenus *Microscolex (Diplotrema)* contains sixteen described species, with a distribution extending from Gayndah (S.E. Queensland) to North-Western Australia, including a large nucleus of species in the Northern Territory. Spencer (1900) erected the genus *Diplotrema* (type, *D. fragilis*) on the basis of the arrangement of the male terminalia, the openings of the vasa deferentia and prostatic ducts supposedly separate, but both on segment XVIII. Stephenson (1930) in devising an elaborate phylogenetic scheme, incorporated *Diplotrema* as a necessary intermediate between the primitive acanthodrilin condition (male pores on XVIII, two pairs of prostatic pores on XVII and XIX), and the more advanced megascolecin condition, with combined male and prostatic pores.

However, re-examination of Spencer's material (Jamieson, 1971) showed the original description to be grossly erroneous, *D. fragilis* in fact having the acanthodrilin arrangement of male terminalia. The redefined *Diplotrema* could not then maintain separate status from the type of *Eodrilus, E. cornigravei* Michaelsen, 1907, and consequently the large number of species formerly assigned to this genus were regrouped (Jamieson, 1971). Those forming an homogeneous assemblage with *D. fragilis* with respect to Australian endemicity and the possession of modified genital setae remained in *Diplotrema,* whilst the majority of species were placed in *Notiodrilus* Michaelsen, 1950. Subsequent analysis (Jamieson, 1974) resulted in the relocation of the entire complex (as subgenera *Notiodrilus* and *Diplotrema*) in *Microscolex* Rosa, 1887, largely because the microscolecin arrangement of combined male and prostatic pores on XVII, characteristic of *Microscolex,* had been shown in some instances to vary to the acanthodrilin condition intraspecifically (Pickford, 1932). A re-examination of the type-species of *Notiodrilus, N. georgianus* Michaelsen 1888, demonstrated sufficient differences from the type of *Microscolex, M. phosphoreus* (Dugès 1837) to warrant subgeneric rank for *Notiodrilus.* This subgenus, within *Microscolex,* embraced a small number of species with vesiculate nephridia and a distinctive setal arrangement; *Diplotrema* was incorporated as a third subgenus within *Microscolex,* differing from *Notiodrilus* primarily in the universal occurrence of genital setae within the species of *Diplotrema* recognized at that time (Jamieson, 1974).

Finally, a study of a number of new *Diplotrema* species from the Northern Territory, Australia, which exhibited marked variation in the arrangement of genital setae, and which included species lacking such setae, led to a further redefinition of the subgenus (Jamieson and Dyne, 1976). *Diplotrema* nevertheless retains a pronounced morphological and endemic identity.

SYSTEMATIC DESCRIPTION

Genus MICROSCOLEX Rosa, 1887

Subgenus DIPLOTREMA Spencer 1900 Emend.

Diplotrema tyagarah sp. nov.

Fig. 1 A-D, table 1

Material Examined: 149° 49′ E, 30° 07′ S, 26 km north of Narrabri on Newell Highway, in black moist clayey soil under dry grass, W. Nash and R. Raven, 19 July 1975 — Holotype (H) (AM W 6622), paratype, P1 (AM W 6623); 149° 37′ E, 29° 49′ S, 42 km south of Moree on Newell Hwy, in black clayey soil, just below surface in flat grassy country, W. Nash and R. Raven, 19 July 1975 — Paratype, P 2 (AM W 6624). l = 51, 49.5 + mm (posterior amputee); w (midclitellar) = 2.2, 2.1 mm; s = 142, 76 +; (H, Pl). Form uniformly circular in cross-section; pigmentless buff in alcohol. Prostomium epilobous ⅓, peristomium somewhat furrowed. First dorsal pore 7/8. Setae 8 per segment, in regular longitudinal rows throughout, setae *a* and *b* of XVII and XIX modified as penial setae; setae *a* and *b* modified as spermathecal genital setae in VII but absent from XVIII.

Nephropores inconspicuous on the clitellum (in *cd*?). Clitellum annular, strongly developed, XIII-XVII (extending dorsally into ½ XII) setae visible on the clitellum, intersegmental furrows faint, dorsal pores obscured. Male pores minute orifices in broad seminal grooves, in mid-XVIII, slightly later of *b*-lines; prostatic porophores 2 pairs, in XVII and XIX, on slight protruberances forming the four corners of a roughly square male field, delimited laterally by a pair of broad seminal grooves joining the prostatic porophores; within the male field a diamond arrangement of small elliptical markings, each a slightly glandular area with pore-like centre, in 17/18 and 18/19; a large transversely elliptical tumescence with raised rim and median ridge, with slightly sunken centre in XVI, pressing anteriorly to meet the indented posterior edge of the clitellum; a diffusely glandular area immediately posterior to the male field, extending to 20/21, and within it, a faintly visible marking, similar to those within the male field, median, in XIX, close to 19/20.

Female pores conspicuous openings presetally in *ab* (closer to *a*) near intersegment 13/14, in XIV, surrounded by an elliptical, paler region on the clitellum. Spermathecal pores 2 pairs, closely paired in *a*-lines in 7/8 and 8/9, on protruberant lips. A large pair of glandular swellings in VII associated with the genital seta follicles, extending laterally to *c*, and filling the segment.

Septa 6/9-10/11, slightly thickened, 6/7-8/9 moderately strongly thickened, 5/6 moderately thickened. Dorsal blood vessel single, continuous onto pharynx. Last hearts in XIII, supraoesophageal vessel IX-XIII, adherent to roof of oesophagus; commissurals in X-XIII larger than the remainder, and sending a narrow connective

TABLE 1

Intersetal Distances in Segment XII of *M. (Diplotrema) tyagarah*

% of circumference

	aa	ab	bc	cd	dd	dc	cb	ba	u (in mm.)
HOLOTYPE	9.3	2.1	14.5	2.1	51.8	1.9	16.0	2.3	5.25
PARATYPE 1	11.8	2.2	14.3	1.6	51.2	1.8	15.0	2.0	5.51
PARATYPE 2	10.3	2.5	15.3	2.0	51.3	2.0	14.0	2.5	4.37
mean	10.5	2.3	14.7	1.9	51.4	1.9	15.0	2.3	5.04

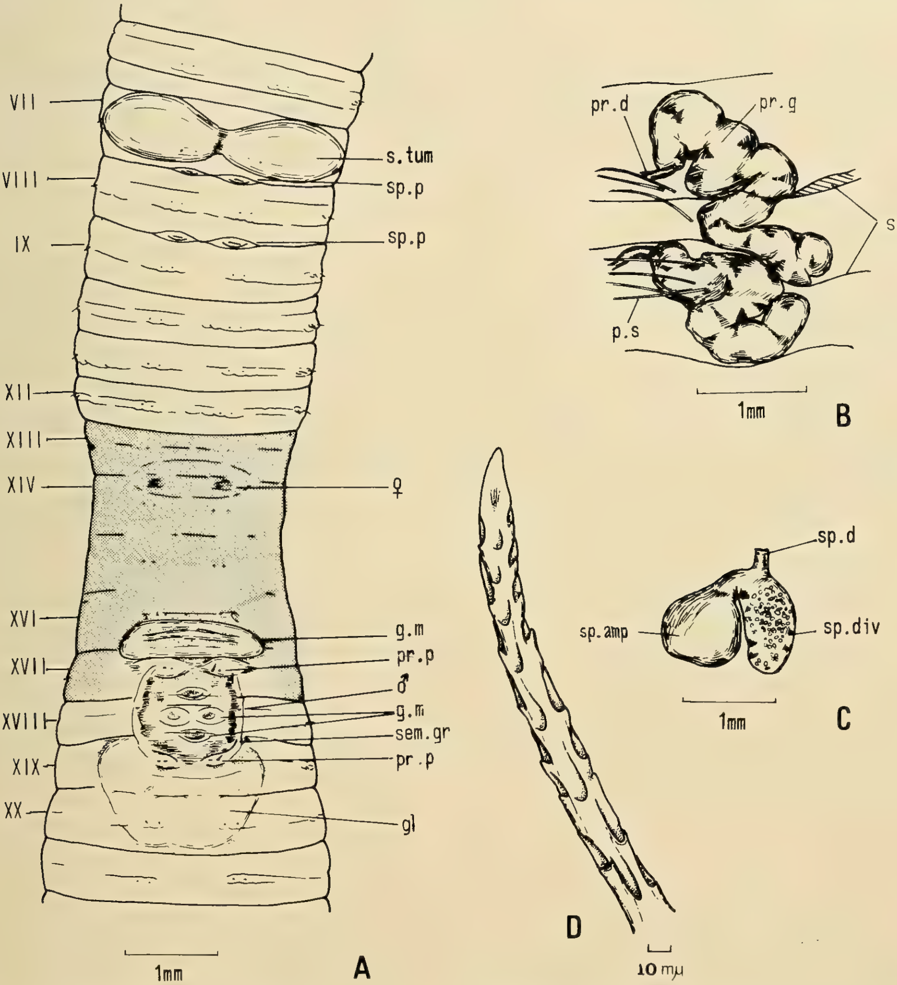

Fig. 1. M. (Diplotrema) tyagarah sp. nov. A.— Genital field of Holotype. B.— Right prostates of Holotype *in situ*. C.— Right spermatheca (IX) of Holotype. D.— Mature genital seta from Holotype.

Abbreviations used in illustrations and text: gl — glandular area; g.m — accessory genital marking; pr.p — prostatic pore; pr.d — prostatic duct; pr.g — prostate gland; p.s — penial seta; s — septum; s.tum — tumescence associated with genital setae; sem.gr — seminal groove; sp.amp — spermathecal ampulla; sp.d — spermathecal duct; sp.div — spermathecal diverticulum; sp.p — spermathecal pore; ♂ — male pore; ♀ — female pore; H — holotype; P — paratype; l — length; w — width; s — number of segments; u — total circumference.

to both the dorsal and supraoesophageal vessels, remaining commissurals very small and dorso-ventral only. Gizzard small-medium, soft and compressible, in V; oesophagus VI-XIV, rather narrow, not well vascularized, with conspicuous rugae on its inner walls; intestinal origin in XV, with abrupt expansion, a definite typhlosole absent. Nephridia stomate holonephridia throughout, the medium sized nephrostomes preseptal and usually in *ab*; the wide, thin-walled ducts entering the parietes slightly pre-setally in *cd*; the nephridial body invested in a high peritoneum appearing as a discrete sheaf of tissue in each segment; no tufting demonstrable in the pharyngeal region. Holandric; large flocculent sperm masses and very large, brightly iridescent sperm funnels in X and XI; seminal vesicles ill-defined, 2 pairs, one very small pair in IX, and a more prominent mass in XII, with apparent stalk-like connection to the funnels of the preceding segment. Coiled, tubular prostate glands 2 pairs, in XVII and XIX, somewhat flattened, and with stout muscular ducts; the anterior pair conspicuously the larger encroaching into XVIII. Penial seta follicles thin and transparent, with little copulatory musculature; *a* and *b* follicles conjoined; the setae moderately long, ectally tapering shafts with some irregular blunt toothing on the distal eighth. Length of mature seta = 1.54 mm; midshaft diameter = 19.2 μm (mean of 3).

Ovaries in XIII, comprising small sheafs of oocytes and large pleated funnels. Spermathecae 2 pairs, subequal, in VIII and IX, each comprising a bulbous, ovoid ampulla joined by a short stalk to a clavate diverticulum, the walls of which are packed with innumerable iridescent spheroidal sperm chambers; whereas the ectal duct and diverticulum appear continuous, the stalked ampulla appears to be an appendage. Length of right spermatheca of IX (from apex of ampulla to pore) = 1.5 mm; total length = 5.6 × length of duct and 1.4 × length of diverticulum. Genital seta follicles conspicuous in VII, *a* and *b* follicles inseparable; the setae stout shafts conspicuously ornamented with deep longitudinal notching which becomes more elongate entally; length of mature seta = 0.65 mm, midshaft diameter = 22.2 μm (mean of 2).

Remarks:

Diplotrema tyagarah is readily distinguishable from the remainder of the subgenus by the unique configuration of genital markings associated with the male field. The closest affinities of the species lie with the subgeneric type, *D. fragilis,* with which it shares such characters as similar general appearance of the genital field and clitellum, identical position of the first dorsal pore, lobular peritoneum-invested nephridial bodies, intestinal origin in XV, and a striking similarity in the form of the spermathecae. *D. tyagarah* is nevertheless separable on the basis of genital field details and setal ratio data.

DISCUSSION

Diplotrema tyagarah constitutes the first record of *Diplotrema* from New South Wales, extending the distributional range of the subgenus southwards by some 480 kilometres. The species thus forms the southernmost limit of a staggered chain of *Diplotrema* species extending from the Northern Territory, across to Cape York, and down the eastern coast of Queensland.

Despite remoteness from northern relatives, *D. tyagarah* has maintained most of the characteristics which contribute to the homogeneity of the subgenus as a whole, including holandry, possession of peculiarly modified setae in the vicinity of the spermathecae, retention of penial setae, and consistency in the number of spermathecae and their diverticula.

Together with an undescribed species from Ban-Ban Springs (S.E. Qld), *D. tyagarah* and the subgeneric type, *D. fragilis* form a morphologically compact aggregate rather distinct from the more northerly representatives of the subgenus (*vide* Jamieson and Dyne, 1976 for descriptions and key). Radiation from a common ancestry is likely to have taken place within the last 10-50 thousand years, when increasing post-Pleistocene aridity was effectively isolating numerous earthworm populations. The members of species-groups have presumably resisted such isolating factors for a longer period, and remain closely related at the present time. More intensive collecting in and near the regions separating *D. tyagarah* from its close allies may reveal further isolates of similar affinities.

ACKNOWLEDGEMENTS

The author is indebted to Dr B. G. M. Jamieson, Department of Zoology, University of Queensland, for helpful advice and criticism during the course of this study.

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The family Hypoderidae (Acari) in Australia

ALEX FAIN and ROBERT DOMROW

FAIN, A., & DOMROW, R. The family Hypoderidae (Acari) in Australia. *Proc. Linn. Soc. N.S.W. 103* (1), (*1978*) 1979: 43-46.

Mites of the family Hypoderidae are recorded from Australia for the first time: *Neottialges (Pelecanectes) evansi* Fain from *Phalacrocorax carbo* (Linnaeus) (Phalacrocoracidae) (Tasmania), *N. (P.) tasmaniensis*, n. sp., from *P. fuscescens* (Vieillot) and *P. sulcirostris* (Brandt) (Tasmania and New South Wales, respectively), and *N.* (*P.*) *plegadicola* Fain from *Threskiornis spinicollis* (Jameson) (Threskiornithidae) (Victoria).

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manuscript received 26 July 1977, in revised form 25 January 1978.

Hypoderid mites are in general free-living, but the hypopial stage invades the subcutaneous tissues of birds and mammals (Fain and Laurence, 1974). A few species were listed from birds either of widespread distribution or introduced into Australia (Fain, 1967), but no specifically Australian material was previously known. We now record three species (of which one is new) taken from birds in south-eastern Australia.

Genus NEOTTIALGES Fain

Neottialges Fain, 1966: 325. Type-species *N. (N.) geopeliae* Fain.

Subgenus PELECANECTES Fain

Pelecanectes Fain, 1966: 326. Type-species *N. (P.) evansi* Fain.

Key to Australian species of *Neottialges*

1. Genital sclerite either complete or represented only by anterior half. Setae d_4 very long 2
   Genital sclerite interrupted at mid-length. Setae d_4 short . . . . *tasmaniensis*, n. sp.
2. Genital sclerite complete . . . . *evansi* Fain
   Genital sclerite represented only by anterior half . . . . . *plegadicola* Fain

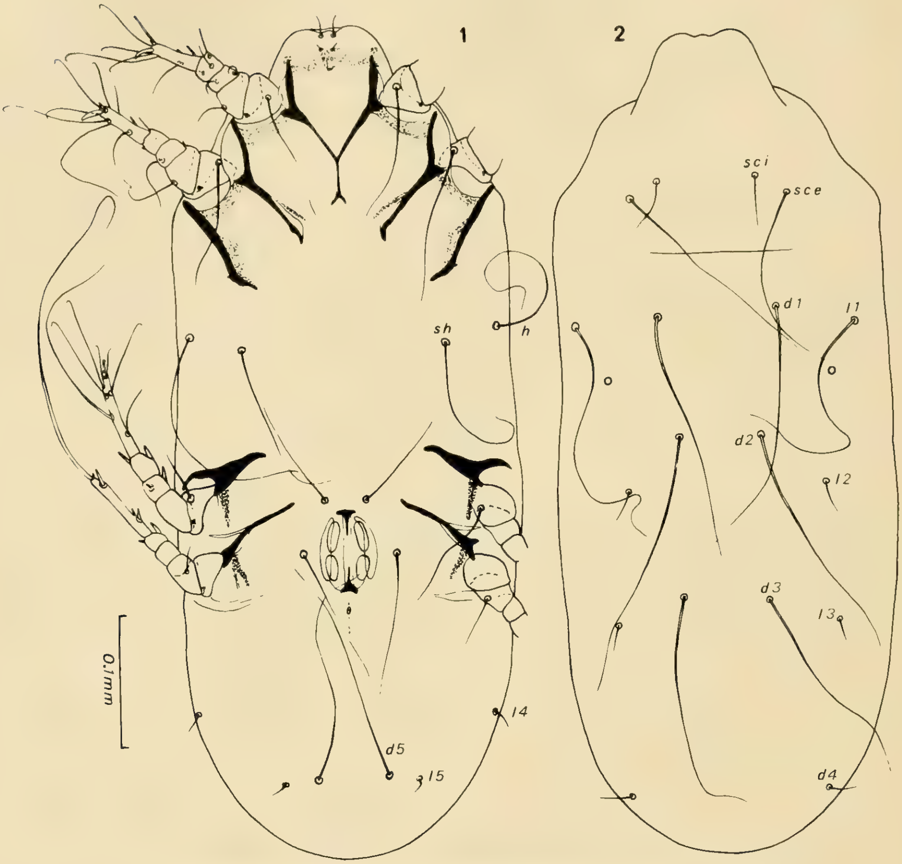
Neottialges (Pelecanectes) evansi Fain

N. (P.) evansi Fain, 1966: 327; 1967: 88; Černý, 1969: 272; Pence, 1972: 435; Schwan and Sileo, 1978: 522.

P. evansi (Fain) : Fain and Beaucournu, 1972: 374.

Material. Many hypopial specimens from "subcutaneous nodule", black cormorant, *Phalacrocorax carbo* (Linnaeus) (Pelecaniformes: Phalacrocoracidae), near Scottsdale, Tasmania iii. 1977, R. W. Mason. In authors' institutes.

Notes. The only previous records were from various cormorants, *Phalacrocorax* spp., in England, France, Kenya, Cuba and the U.S.A.



Figs 1-2. Neottialges (Pelecanectes) tasmaniensis holotype hypopus. 1. Venter. 2. Dorsum.

Neottialges (Pelecanectes) tasmaniensis, n. sp.
(Figs 1-5)

Material. Holotype and 20 paratype hypopial specimens from "subcutaneous fascia infiltrated by mites", white-breasted cormorant, *P. fuscescens* (Vieillot), Beechford, Tasmania, 10.vi.1973, B. L. Munday. Holotype and one paratype (on same slide, holotype *à g.,* i.e. to left, nearer red label) in Australian National Insect Collection, CSIRO, Canberra; remaining paratypes in authors' institutes. Many specimens (not types), same data, in spirit.

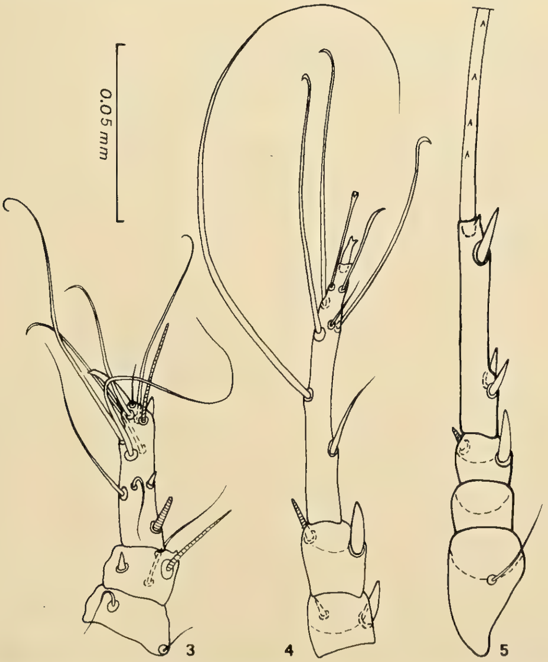
Also many hypopial specimens (not types) found "subcutaneously on legs, neck and in particularly large concentration on the breast", little black cormorant, *P. sulcirostris* (Brandt), Lake Cowal, New South Wales, 18.v.1977, W. J. M. Vestjens. In ANIC and authors' institutes.

Hypopus. Idiosoma not constricted at mid-length, 630 × 270 μm (holotype), 640 × 265 μm (paratype). Cuticle poorly sclerotized; dorsum and coxae without punctate shields. Palposomal sclerite wider (33 μm) than long (15 μm) (Fig. 1). Epimera I fused; sternum proper forked posteriorly, 36 μm long. Genital suckers longer than wide, not divergent posteriorly. Genital sclerite represented by anterior T-shaped and posterior inverted T-shaped parts. Dorsal setae d_{1-3}, $_{5}$ and l_1 very long (175-225 μm); l_{2-5} and d_4 short (not above 25 μm) (Fig. 2). Legs not unduly shortened. Tarsi I-IV 39, 42, 72 and 60 μm long, respectively. Tarsus I with eight piliform setae, three spines and two solenidia (terminal spine on tarsi I-II shorter than corresponding segment) (Fig. 3); tarsus III with eight piliform setae and one terminal spine (Fig. 4); tarsus IV shorter than tarsus III, with three spines (two basals at same level) and one elongate, barbulate terminal seta (Fig. 5).

Notes. The new species is known only in the hypopial stage. It belongs to a small group characterized by the centrally interrupted genital sclerite and the short to very short setae l_{2-5} and (usually) d_4. The group previously contained three species: *N. (P.) bassani* (Montagu) from a sulid (Europe and southern Atlantic), and *N. (P.) ajajae* Fain and *N. (P.) montagui* Fain, both from a threskiornithid (transported from North America to the Antwerp Zoo). The new species differs from *N. (P.) bassani* in having seta d_4 set more laterally, tarsi III-IV of unequal lengths and no spine on tarsus III at midlength. It differs from *N. (P.) ajajae* in having seta d_4 much shorter, tarsi III-IV of more unequal lengths and a different disposition of spines on tarsus IV. Nearest to *N. (P.) montagui,* to which it runs in Fain's key (1967), it differs therefrom in having the body smaller, the palposomal sclerite much wider than long, the sternum longer, tarsi I-II much shorter (39 and 42 μm *vs* 48 and 51 μm, respectively), a different disposition of basal spines on tarsus IV (at same *vs* different levels) and the trochanteral setae much longer.

Neottialges (Pelecanectes) plegadicola Fain

N. (N.) plegadicola Fain, 1966: 326.
N. (N., sic — recte P.) plegadicola Fain: Fain, 1967: 94.



Figs 3-5. Neottialges (Pelecanectes) tasmaniensis hypopus. 3. Leg I. 4. Leg III. 5. Leg IV.

Material. Hypopial specimens from "subcutaneous tissue around the cloaca . . . in clumps and in fairly large numbers", straw-necked ibis (adult), *Threskiornis spinicollis* (Jameson) (Ciconiiformes: Threskiornithidae), rookery on Lake Corangamite, Victoria, ix.1973, J. H. Arundel and K. Harrigan. In authors' institutes.

Notes. The only previous record was from the glossy ibis, *Plegadis falcinellus* (Linnaeus) (Threskiornithidae), in Belgium. This bird species also occurs in Australia.

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Corrigendum:
These *Proceedings*, vol. 101, page 200, line 38 — delete "(?)"

An Early Triassic Megafossil Flora from the Lorne Basin, New South Wales

W. B. K. HOLMES and S. R. ASH

HOLMES, W. B. K., & ASH, S. R. An Early Triassic megafossil flora from the Lorne Basin, New South Wales. *Proc. Linn. Soc. N.S.W. 103* (1), (*1978*) *1979*: 47-70.

A small late Early Triassic flora is described in this paper from the lower part of the Camden Haven Group in the Lorne Basin of eastern New South Wales. It includes 17 identifiable species and several unidentified forms. New taxa in the flora are *Coniopteris? ramosa* sp. nov., *Cladophlebis carnei* sp. nov., *Dicroidium voiseyi* sp. nov., the supposed micro- and megasporophylls of *Dicroidium zuberi* (Szajnocha) Archangelsky var. *feistmantelii* (Johnston) Retallack, *Karibacarpon feistmantelii* sp. nov., and *Pteruchus barrealensis* (Frenguelli) var. *feistmantelii* comb. et var. nov., and the coniferous cone *Voltziopsis townrovii* sp. nov. The flora is similar and probably contemporaneous with that from the upper part of the Narrabeen Group of the Sydney Basin of New South Wales.

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INTRODUCTION

Plant fossils of Early Triassic age occur at several localities in the Lorne Basin of northeastern New South Wales (Fig. 1). A few authors (Carne 1897, 1898; Voisey 1939; Pratt 1970) noted these occurrences, some listed the fossils they found but none of the fossils has been described. In this report we describe the recognizable plant megafossils that occur in the Lorne Basin at five localities near Laurieton (Fig. 1) and correlate the flora with the better known Triassic floras of the adjacent Sydney and Clarence-Moreton Basins of New South Wales. The fossils described are in the collections of the Geology Department, University of New England, Armidale (UNEF), The Mining and Geological Museum, Sydney (MMF), Australian Museum, Sydney (AMF), and the Geology and Geophysics Department of Sydney University (SUGD).

PREVIOUS INVESTIGATIONS

The geology of what is now known as the Lorne Basin was first studied in 1896 by J. E. Carne, a Geological Surveyor with the Geological Survey of New South Wales. During the course of his investigation Carne discovered plant megafossils in a bed of grey shale at the base of the coastal headland called Camden Head (Fig. 1) in rocks now believed to be of late Early Triassic age and referred to the Camden Head Claystone (Fig. 2). Carne collected a few fossils and these were examined by W. S. Dun, Assistant Palaeontologist and Librarian of the N.S.W. Geological Survey, who reported (in Carne 1897, 1898) that the collection contained: *Thinnfeldia odontopteroides* (Morris) Feistmantel 1878, *Alethopteris lindleyana* Royle 1833, *Equisetum,* cycad frond — probably *Ptilophyllum, Gleichenites?, Cardiocarpum* Brongniart 1828, and *Phyllotheca* sp. He also reported that the collection contained a poorly preserved fern which was somewhat similar to *Didymosorus (Gleichenites)*

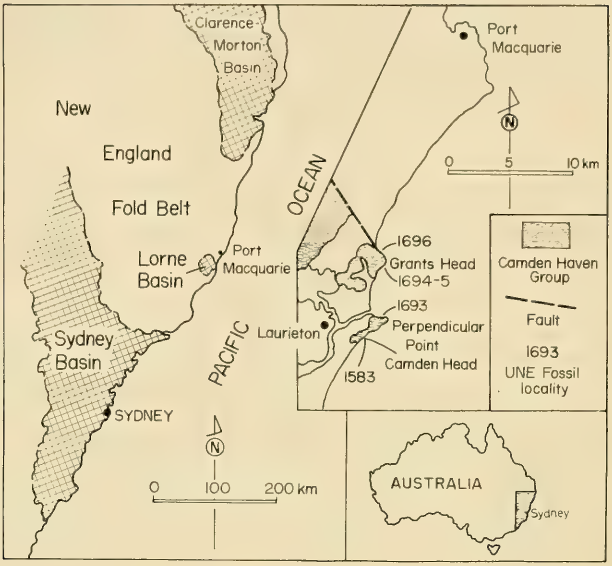


Fig. 1. Map showing the location of the Lorne Basin and major tectonic features in southeastern Australia and a more detailed locality map. The tectonic map is adapted from the Tectonic Map of Australia (Geol. Soc. Australia, 1971) and the locality map is adapted from the Hastings 1:250 000 geological sheet (1966).

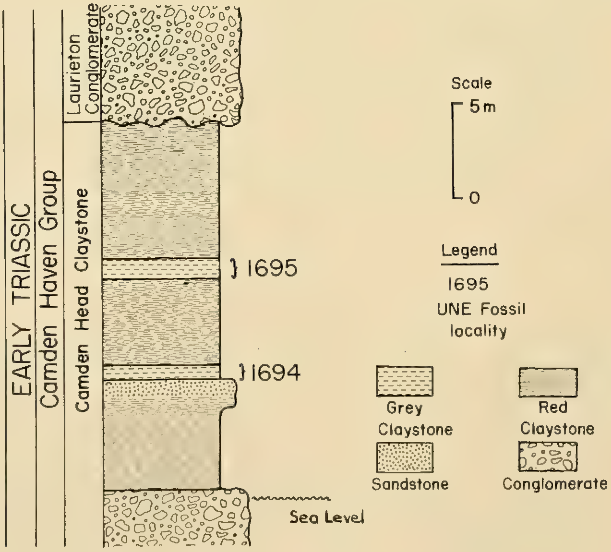


Fig. 2. Stratigraphic section of the lower part of the Camden Haven Group exposed near the base of Grants Head, N.S.W. showing the positions of localities 1694 and 1695.

gleichenoides Oldham and Morris 1862. Carne concluded that the fossils showed that the strata could be correlated with the Clarence Coal Measures of Triassic age.

During the 1930s A. H. Voisey studied the geology of the Lorne Basin and proposed (1939) that name for the area. Voisey (1939) also proposed the name Camden Haven Series for the Triassic rocks in the basin and collected plant fossils from what was apparently Carne's locality at the base of Camden Head. Some of them were exhibited at the Ordinary Monthly Meeting of the Linnean Society of New South Wales on 29th September 1937, according to the Proceedings of the Society for that year (p. xlii). Voisey's collection was studied by A. B. Walkom who reported (in Voisey 1939) that it contained *Thinnfeldia feistmantelii* Johnston 1895, *Cladophlebis* sp. and a seed. Walkom also suggested that the fossil determined to be *Thinnfeldia odontopteroides* by Dun (in Carne 1897, 1898) was probably the same as the fossil he called *T. feistmantelii.* In the same report Voisey mentioned the occurrence of Triassic plant fossils at several additional localities in the Lorne Basin but he did not identify any of them. We have been unable to locate the collections of Carne and Voisey.

Goodwin (1962) studied the geology of part of the Lorne Basin and reported the occurrence of plants at several localities including one on the north side of Perpendicular Point (probably near locality 1693 of this paper). She, however, did not describe or illustrate any of the fossils.

Packham (1969) summarized the geology of the Lorne Basin and named the Triassic strata there the Camden Haven Group.

G. W. Pratt, who has studied the geology of the Lorne Basin for many years collected a few plants from Carne's locality at the base of Camden Head. They were identified by Dr John Pickett (in Pratt 1970) as *Cladophlebis australis* (Morris) Seward 1904, *Dicroidium feistmantelii* (Johnston) Gothan 1912, *?Williamsonia* sp., and *?Neocalamites*. Pratt and Herbert (1973) discussed the geology of the Lorne Basin in some detail and subdivided the Camden Haven Group into three formations: Camden Head Claystone (at the base), Laurieton Conglomerate, and Grants Head Formation (at the top). They suggested that the sequence was of Early Triassic age and correlated it with the upper part of the Narrabeen Group in the Sydney Basin.

Helby (1972) has studied the pollen and spore content of sediments from two localities in the Lorne Basin. A sample from UNE locality 1583 yielded only three forms, none of which was of significance for dating purposes and a sample from the Grants Head locality 1695 yielded 10 species of palynomorphs. Helby (1973) stated that the association resembled the *Aratrisporites tenuispinosus* Playford 1965 assemblage of late Early Triassic age in the Sydney Basin.

G. J. Retallack has collected from the Camden Head Claystone at the base of Camden Head and has examined several collections of plant megafossils made by others from this locality. He lists (Retallack 1977) the following species: *Cladophlebis* sp., *Dicroidium lancifolium* var. *lineatum* (Tenison-Woods) Retallack 1977, *D. zuberi* (Szajnocha) Archangelsky 1968, *"Pterorrachis" barrealensis* Frenguelli 1942, *Umkomasia* sp., *Lepidopteris madagascariensis* Carpentier 1935, and *Voltziopsis wolganensis* Townrow 1967. In the same report Retallack places this flora in the Dicroidetum zuberi Association.

Bocking (1977) collected specimens from the Grants Head localities. He identified several species of *Dicroidium* from fragmentary remains. The best preserved specimen is included below as *D. dubium* var. *australe* (Jacob & Jacob) Retallack.

STRATIGRAPHY OF THE CAMDEN HAVEN GROUP

The lowest member of the Camden Haven Group, the Camden Head Claystone, consists principally of red-brown claystone and siltstone and small amounts of grey fossiliferous claystone, sandstone and conglomerate. It is thick bedded and ranges from 0 to at least 75 m in thickness (Pratt and Herbert 1973, p. 108). The Camden Head Claystone which is thickest along the coastline thins westward and is absent in the western part of the Lorne Basin. The Camden Head Claystone unconformably overlies Palaeozoic rocks and is overlain by and intertongues with the Laurieton Conglomerate. Bocking (1977) regards the Camden Head Claystone as being wholly contained within the Laurieton Conglomerate. The Laurieton Conglomerate is massive bedded and yellow to brown in colour. It is composed of rounded to subangular pebbles and cobbles in a sandy to clayey matrix and ranges from 45 m to 210 m in thickness. The unit is thinnest along the coast and thickens to the west where it overlaps the underlying Camden Head Claystone and rests unconformably on Palaeozoic rocks in the western parts of the Lorne Basin. The Grants Head Formation, the uppermost member of the Camden Haven Group, consists of greyish sandsone, conglomerate and fossiliferous siltstone. It is thin to medium bedded and may be in excess of 150 metres thick.

LOCALITIES

The fossils described here were collected from five localities in the Camden Haven Group near Laurieton on the north coast of New South Wales, as shown on Fig. 1. Each locality is described below together with the assigned University of New England locality number. The grid reference numbers are taken from the Camden Haven 1: 100 000 sheet.

1583 Camden Head Claystone. In a lens of hard grey siltsone at the base of Camden Head. This is the locality from which Carne (1897, 1898), Voisey (1939), Pratt (1970) and Retallack (1977) have collected. It is commonly called the Perpendicular Point locality but the original locality descriptions given by these authors indicate that their collections actually came from the base of Camden Head not Perpendicular Point. G. R. 846984.
1693 Camden Head Claystone. In thin bedded grey siltstone exposed at the base of the sea cliffs on the north side of Perpendicular Point. G. R. 850990.
1694 Camden Head Claystone. In a bed of nodular grey siltstone near the base of the sea cliffs at Grants Head. About 19 m below the Laurieton Conglomerate of the Camden Haven Group (Fig. 2). G.R. 854034.
1695 Camden Head Claystone. In a lens of nodular grey siltstone in the sea cliffs at Grants Head. About 10 m below the Laurieton Conglomerate of the Camden Haven Group (Fig. 2). G.R. 854034.
1696 Grants Head Formation. In thin-bedded siltstone in the sea cliffs at the northern end of Bartletts Beach. G.R. 850045.

SYSTEMATIC PALAEOBOTANY

Division Tracheophyta
Class Lycopsida
Order Lepidodendrales
Genus *Skilliostrobus* Ash 1979
Skilliostrobus australis Ash 1979
Fig. 3, 1 and 11

Description. This recently described cone is represented in the flora by isolated examples of its distinctive sporophylls. The proximal portions of the sporophyll are wedge shaped and have a maximum width of 12 mm and a length of about 1 cm. The limbs have a width of about 3 mm and a length of about 4.5 mm but the apices of the limbs are missing. Megaspores characteristic of *S. australis* were extracted from one of the megasporophylls (Fig. 3, **11**).

Discussion. *S. australis* occurs in the lower part of the Gosford Formation of Early Triassic age near Terrigal, New South Wales and in the Parmenteer Supergroup near Hobart, Tasmania (Ash 1979).

Material. AMF 59457 from locality 1695 and specimen UNEF 15510 from locality 1583.

Lycopod Stems of Uncertain Position

?Lycopod stem a

Fig. 3, 2

Description. A stem 12 cm in length and 1.5 cm in width shows a surface covered with oval scars approximately 2.5 mm × 1 mm.

The preservation of this fossil makes it difficult to identify. It does superficially resemble the stem of *Pleuromeia longicaulis* (Burges) Retallack (1975, fig. 5A) so we presume that it is a lycopod stem. The scars, however, are somewhat similar to those that occur in *Psaronius* and it is possible that the fossil is a fern stem.

Material. Specimens AMF 59416 and UNEF 15509 from locality 1583.

Lycopod stem b

Fig. 3, 3

Description. A fragment of a lepidendroid stem which has three vertical rows of slightly concave rhomboidal leaf cushions in a steep spiral arrangement. The cushions are attenuated vertically, the height being about 16 mm and the width 8 mm. The top of each cushion is level with the midpoint of the horizontally adjacent cushions. Structureless carbonaceous material crusts the surface of each cushion and no leaf scars or pits are preserved.

Discussion. The orientation of the specimen in life is unknown and the description given above applies to the specimen as aligned in the illustration. Lepidodendroid stems with similar but smaller rhombic leaf cushions also occur in the Newport Formation at UNEL 1436 specimen UNEF 13829, and in the Basin Creek Formation at UNE locality 1489 (WBKH collection).

Material. AMF 59418 from locality 1583.

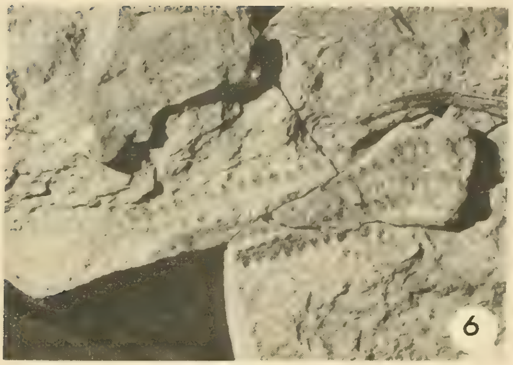
Division Sphenopsida

Equisetaceous stems

Fig. 3, 4

Description. Fragments of longitudinally ribbed equisetaceous stems have been collected from all recorded localities. At locality 1693 these fragments constitute the bulk of recognizable remains. Carne (1897) recorded *Equisetum* and *Phyllotheca* sp. and Pratt and Herbert (1970) listed *?Neocalamites* from locality 1583. None of the specimens examined by us have any diagnostic characters preserved that would allow a specific determination. Stems vary in width from about 2.5 mm to 30 mm and the number of ribs varies from 8 to 12 per cm. On most stems the internodes are apparently very long as few nodes are present. On stems with nodes the longitudinal ribs continue without interruption through the node. Rounded scars on these nodes may be branch or leaf bases. These stems could be referred to *Paracalamites* Zalessky 1927.

Discussion. Similar stems have been recorded as *Phyllotheca australis* Brongniart,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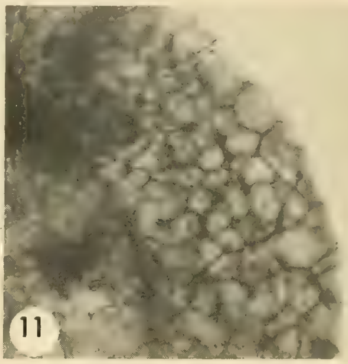
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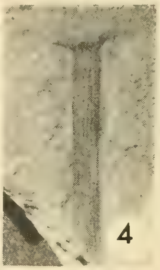
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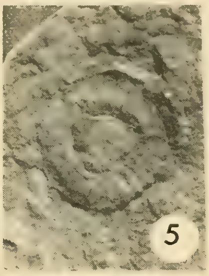
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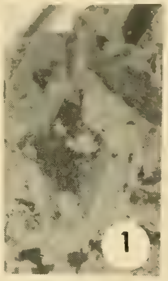
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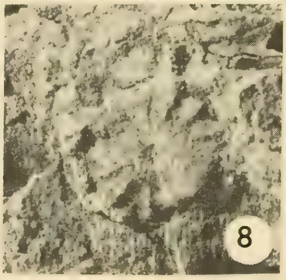
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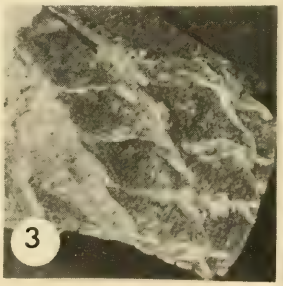
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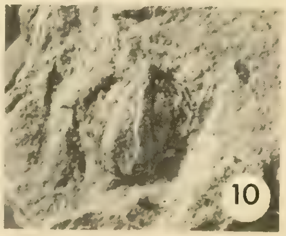
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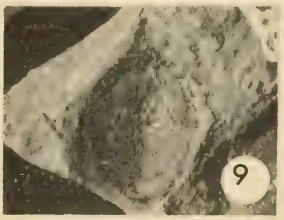
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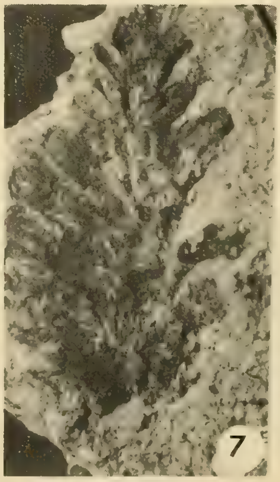
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Schizoneura sp. or *Neocalamites* sp. from the Esk Beds (Hill *et al.* 1965. pl. T1, fig. 5; Walkom 1924, pl. 16, fig. 1), the Narrabeen Group (Walkom 1925, pl. 24, fig. 1) and Leigh Creek (Chapman and Cookson 1926, pl. 19, figs 2-6 and pl. 20, fig. 1).
Material. MMF 16038, AMF 59424 and UNEF 15511, UNEF 15513, UNEF 15515 from locality 1583.

Nodal Diaphragms

Fig. 3, 5

Two specimens are in the present collection. One is damaged and has some vascular bundles 1 mm apart still attached. The external diameter is approximately 18 mm. The other specimen consists of a circular sediment-filled cavity 10 mm in diameter surrounded by a 6 mm wide ring of about 28 segments.

The specimen illustrated here in Fig. 3 compares rather closely with the nodal diaphragm from the Late Triassic of Greenland which Harris (1931, pl. 3, fig. 13) has called *Equisetites doratodon,* and those illustrated as *Neocalamites* cf. *carreri* from the Middle Triassic Blackstone Formation of Queensland in Hill *et al.* (1965, pl. T1, fig. 3).
Material. AMF 59423 and UNEF 15512 from locality 1583.

Class Filicopsida
Order Filicales
Family Dicksoniaceae
Genus *Coniopteris* Brongniart 1849
Coniopteris ?ramosa sp. nov.

Fig. 4, 1 and 2

Diagnosis. Bi-(?tri-) pinnate leaf; penultimate segments pinnate-pinnatifid. Pinnae opposite, acutely triangular. Pinnules sub-opposite, oval, entire; imbricate near rachis but coalescing distally; a single vein entering each pinnule and forking several times.
Description. Portion of a bi-(?tri-) pinnate leaf 30 mm in length with base and apex missing. Six pairs of opposite, acutely-triangular pinnae about 12 mm in length are attached almost at right angles to this length of rachis which is 1 mm in width. The pinnules near the main rachis are oval and contracted basally; 1.3 mm wide and 1.7 mm long; inserted at an angle of approximately 60°; margins entire and overlapping. The pinnae taper evenly throughout their length so that each succeeding pair of sub-opposite pinnules is slightly smaller and in the distal half become coalescent. A single vein enters the pinnule and branches up to seven times, radiating throughout the lamina. The specific epithet *ramosa* alludes to this character.
Holotype. AMF 59428 and its counterpart AMF 59429.
Locality. 1695 in grey siltstone lens in sea cliffs at Grants Head, N.S.W.
Horizon. Camden Head Claystone, Camden Haven Group, Late Early Triassic.
Discussion. This fragment of a sterile fern leaf resembles in outline, sterile leaves of some other Triassic *Coniopteris* species, e.g. *C. walkomi* Frenguelli (1950, fig. 4) from Argentina and *C. lobata* (Oldham) Walkom (1925, pl. 29, figs. 4-6) from the

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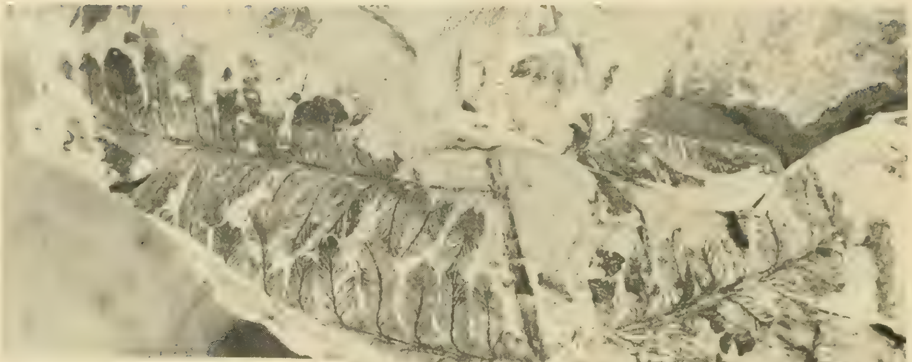
Fig. 3. Note: Specimens natural size unless stated otherwise. Those photographed under kerosene are marked with an asterisk (*).
1 *Skilliostrobus australis* Ash, *, Detached megasporophyll, AMF59457. 2 ?Lycopod stem a, *, AMF 59416. 3 Lycopod stem b, AMF 59418. 4 Equisetaceous stem, AMF 59424. 5 Nodal diaphragm, AMF 59423. 6 *Microphyllopteris* sp., AMF 59417. 7 Cone?, AMF 59420. 8 Circular ribbed object, AMF 59419, × 2. 9 Dispersed seed c, AMF 59421, × 2. 10 Dispersed seed b, *, AMF 59422, × 2. 11 Side of a megaspore extracted from the detached megasporophyll attributed to *Skilliostrobus australis* Ash in 1 AMF 59457, × 100.



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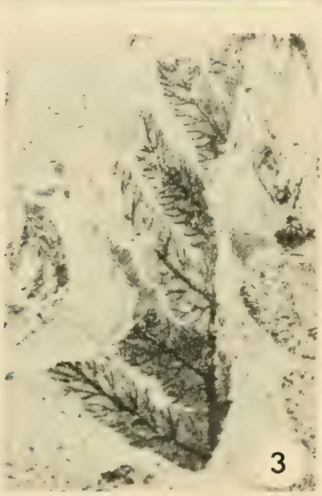

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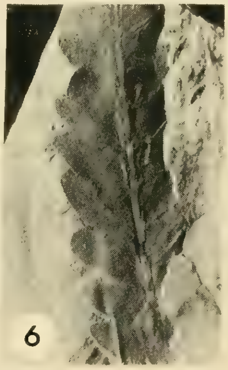

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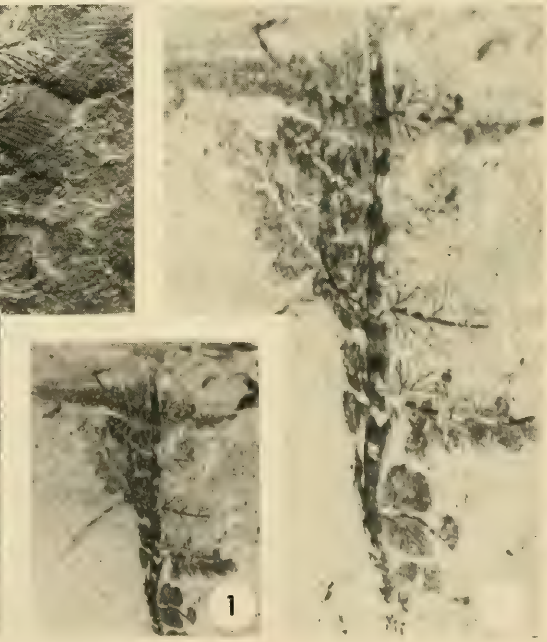

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Sydney Basin, but these species differ by having pinnular venation which branches once only. Sterile leaves of the Jurassic *C. hymenophylloides* (Brongn.) Seward have pinnules with veins that branch several times but the pinnules are lobed or finely divided (Harris 1961, fig. 53). Fertile specimens of *C. ? ramosa* are required to establish the correct generic assignment of this leaf.

?Coniopteris burejensis (Zalessky) Seward 1912

Fig. 5, 1 and 2

Description. A sterile fern pinna, 28 mm in length and tapering only slightly. Pinnules alternate, rhomboidal with acute apices 2 mm wide and 3 mm long; inserted on rachis at an angle of about 45°; acroscopic lobe larger than the basiscopic lobe. Pinnule midrib giving off a pair of opposite or three or more alternate lateral veins which sometimes branch again before reaching the margin.

Discussion. This specimen agrees in shape and venation with sterile fragments of *C. burejensis* from Yorkshire illustrated by Harris (1961, figs. 51 F-H) and is doubtfully assigned to that species. *C. burejensis* is widespread in the Jurassic of Eastern Asia, Siberia and Europe.

Material. AMF 59435 from locality 1583.

Fern Form Genera of Uncertain Position

Genus *Cladophlebis* Brongn. emend. Frenguelli 1947

Cladophlebis cf. *mendozaensis* (Geinitz) Frenguelli 1947

Fig. 4, 3

Description. A poorly preserved fragment of one side of a fern pinna 20 mm in length with parts of five oblong-lanceolate pinnules attached by the whole of their bases to the rachis, has venation in the pinnules somewhat characteristic of this species from the Late Triassic of Argentina (Frenguelli 1947, pl. 11, fig. 3). The majority of secondary veins visible on this specimen leave the pinnule midrib at an angle of approximately 45° and divide into two branches; the upper branch then divides again.

Material. AMF 59426 from locality 1583.

Cladophlebis carnei sp. nov.

Fig. 4, 4 and 5

Diagnosis. Bipinnate leaf; pinnae opposite, linear. Pinnules catadromic; the first pinnule attached in the angle between the main rachis and the pinna rachis; the rest of the pinnules opposite or sub-opposite. Pinnules of irregular length, oblong or slightly tapering, obtuse; entire; inserted on pinna rachis at 75°-90°; midrib decurrent, persisting to or almost to the apex. Lateral veins catadromic, alternate to sub-opposite, mostly once divided. The basal lateral veins on either side of the midrib differ in shape from the other lateral veins. The first basiscopic vein is inserted at right angles to the base of the decurrent midvein or directly to the pinna rachis; dividing once and passing straight or slightly recurved to the margin. The first acroscopic lateral vein is attached close and parallel to the pinna rachis, then decurving to follow parallel around the acroscopic basal lobe of the pinnule. This vein is simple, or if

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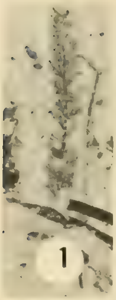
Fig. 4. Note: Specimens natural size unless stated otherwise. Those photographed under kerosene are marked with an asterisk (*).

1-2 *Coniopteris ? ramosa* sp. nov., *, AMF 59428, holotype, **1**, ×1.2, ×3. **3** *Cladophlebis* cf. *mendozeansis* (Geintz) Frenguelli, *, AMF 59426, ×3. **4-5** *Cladophlebis carnei* sp. nov., *, AMF 59425, holotype, **4**, ×1.5, ×2. **6** *Cladophlebis* sp. indet., *, UNEF 15501. **7** *Cladophlebis* sp. indet., *, counterpart of specimen in **6**, AMF 59427, ×2.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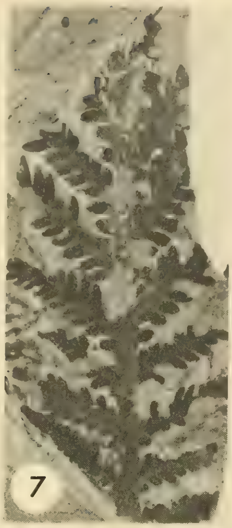
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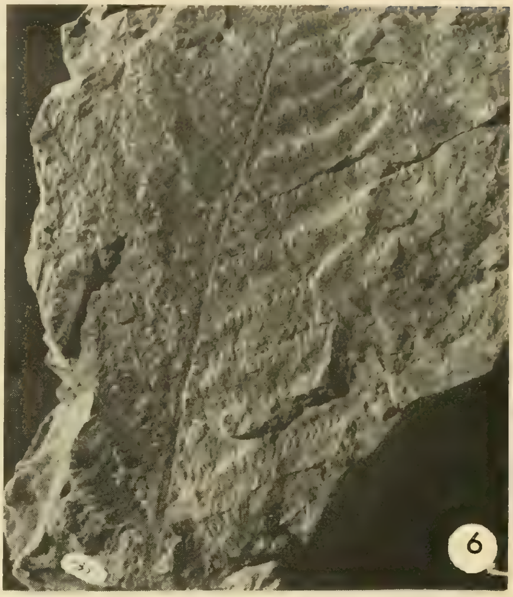
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forked, the two branches run close and parallel. The following lateral veins leave the midrib at 20°-30°, dividing once near the midrib into two branches which diverge only slightly and curve to the margin at 45°-60°. The last two pairs of apical lateral veins are usually undivided.

Description. Bipinnate leaf with portions of four opposite pinnae preserved. The pairs of pinnae are inserted at 75° and spaced about 23 mm apart on the main rachis which is 2.5 mm in width. The maximum preserved length of a pinna with a distal portion missing is 6 cm. Pinnules catadromic; first pinnule attached in the angle between the main and pinna rachis; following pinnules opposite, becoming subopposite to alternate distally. Pinnules slightly variable in length and width, 10 mm-13 mm × 3.5 mm-5 mm; oblong or slightly tapering; obtuse, entire; attached to the pinna rachis at 75°-90°. Pinnules decurrent, acroscopically contracted; the decurrent base of the next pinnule almost, or slightly, coalescing with the previous pinnule. Pinnule midrib decurrent and persistent almost to the apex. Lateral veins catadromic, alternate to sub-opposite; the first basiscopic and first acroscopic lateral veins differ in their course from the following veins. The first basiscopic lateral vein is inserted at right angles to the base of the decurrent midrib or directly to the pinna rachis; dividing once and passing straight or slightly recurved to the margin. The first acroscopic lateral vein is attached close and parallel to the pinna rachis; and then decurving to follow parallel around the acroscopic basal lobe of the pinnule; simple, or if forked, the two branches run close and parallel. The following lateral veins are inserted at 20°-30°; dividing once near the midrib; the branches diverging only slightly and curving to meet the margin at 45°-60°. The last one or two apical pairs of veins are usually undivided. 18-21 lateral veins leave the midrib, with 34-40 reaching the margin.

This species is named in honour of J. E. Carne [1855-1922] who made the first recorded collection of fossil plants from the Lorne Basin.

Holotype. AMF 59425.

Locality. 1583 in grey siltstone lens at base of sea cliffs on southern side of Camden Head.

Horizon. Camden Head Claystone, Camden Head Group. Late Early Triassic.

Discussion. C. carnei bears a superficial resemblance to *Merianopteris major* Feist. 1881, and to *Cladophlebis roylei* (=*Alethopteris lindleyana* Royle) (Arber 1905, figs 34 and 32 respectively) and may be the fern leaf collected by Carne and identified by Dun as the latter species (Carne 1897). Our species differs from both the above species by having twice as many lateral veins which divide only once — commonly twice in *C. roylei*. In *Merianopteris major* the pinnules are coalescent, with the lower lateral veins anastomosing between pinnules. The *C. roylei* of Jack and Etheridge (1892, pl. 17, figs 3 and 4) and *Merianopteris major* of Tenison-Woods (1883, pl. 8, figs 2 and 3) both differ from the types of these species and also from *Cladophlebis carnei*. The fragment referred to *C.* sp. cf. *oblonga* Halle, 1913a in Bourke *et al.* (1977, fig. 3.2) is *C. carnei. C. oblonga* differs in having undifferentiated lateral veins at the base of the pinnules.

Cladophlebis sp. indet.

Fig. 4, 6 and 7

Fig. 5. Note: Specimens natural size unless stated otherwise. Those photographed under kerosene are marked with an asterisk (*).
1-2 *Coniopteris burejensis* (Zalessky) Seward ?, *, AMF 59435, 1, ×1. 2, ×2.5. 3-4 *Dicroidium zuberi* (Szajnocha) Archangelsky var. *feistmantelii* (Johnston) Retallack. 3, AMF 59430, *, ×0.5. 4, AMF 59431. 5 *D. dubium* var. *australe* (Jacob & Jacob) Retallack. Apical portion of leaf, *, AMF 59432. 6-7 *Lepidopteris madagascariensis* Carpentier. 6, AMF 59433, ×0.5. 7, *, AMF 59434.

Description. Some fragments of linear fern pinnae have very closely spaced, ovate to slightly falcate alternate pinnules with entire margins and rounded apex. The pinnules are closely spaced but not conjoined and are attached by the whole of the base and are slightly decurrent on the pinna rachis; 10-14 mm long and 4-6 mm wide; inserted at an angle of 50°-60°. Midrib slightly decurrent then curving outwards and continuing straight to within 1 mm of the pinnule apex where it divides into 2 or 3 secondary veins. The lateral veins are arranged alternately; the first basiscopic vein emerging at right angles from the decurrent base of the midrib or even lower from the rachis itself; dividing once and decurving through 70°-90° to the pinnule margin. The rest of the lateral veins, on both sides of the midrib, depart from it at an angle of about 30° and curve outwards to meet the margin at angles of 50°-75°. In the proximal two-thirds of the pinnule the lateral veins dichotomize twice in the first half of their length, but approaching the apex there is only one dichotomy or even undivided veins. About 20 lateral veins leave the midrib, dividing into 50 or more around the margin.

Material. AMF 59427 and UNEF 15501 from locality 1583.

Discussion. This pinna fragment is similar in dimensions to *C. carnei* sp. nov. but differs in having falcate pinnules; more divisions in the lateral veins and in the first acroscopic lateral vein being similar to the other lateral veins. The pinnules are shorter and broader and more closely spaced than those of *C. australis* (Morris) Halle 1913b, *C. oblonga* Halle has similarly shaped and spaced pinnules but differs in the lateral venation. In *C. oblonga* the lateral veins normally fork once only about midway from the midrib to the margin.

Genus *Microphyllopteris* Arber 1917

Microphyllopteris sp.

Fig. 3, 6

Description. A fragment of a bipinnate leaf with portions of four parallel and closely spaced linear pinnae is placed in this form genus which was created by Arber for leaves formerly placed in the *Gleichenites* genus but without evidence of fructifications to support their affinities with the present genus *Gleichenia.* The longest pinna fragment is 5.5 cm in length and decreases in width from 6 mm to 4 mm. The pinna rachis tapers gradually from 1 mm in width. The closely spaced opposite pinnules are 2 mm wide and 2.5 mm long and are attached by the whole of their base; slightly falcate to triangular with an acute apex near the primary rachis but decreasing gradually in size and becoming more rounded distally. No venation is preserved.

Discussion. This leaf may be the same species as Carne's specimens which were identified by Dun (Carne 1897, 1898) as *Gleichenites* or *Didymosorus (Gleichenites) gleichenoides* Oldham and Morris 1862. The apices of the pinnules on our specimen are not rounded as in specimens of *Gleichenites gleichenoides* from the Rajmahal Series of India (Oldham and Morris 1862, pl. 25 and pl. 26, figs 1 and 3), or as narrow and acute as *Microphyllopteris acuta* Walkom 1919, from the Burrum Series of Queensland; Herbst (1974, p. 80) suggests that *M. acuta* may be a conifer. Our fossil compares closely with *Todites narrabeenensis* Burges (1935) from the Narrabeen Group of New South Wales and also in outline with the fertile fern *Gleichenites wivenhoensis* Herbst 1974 from the Esk Formation of Queensland.

Material. AMF 59417 from locality 1583.

Class Cycadopsida

Order Pteridospermales

Family Corystospermaceae

Genus *Dicroidium* Gothan, emend. Townrow 1957

Dicroidium voiseyi sp. nov.

Fig. 7, 1 and 2

Diagnosis. Pinnate frond with linear pinnules confluent on rachis. Lateral veins in pinnae well spaced, leaving midrib at acute angle and dichotomizing once, rarely twice.

Description. Small pinnate forked(?) frond. Portion preserved (base and apex missing) 70 mm long and 40 mm wide. Main rachis 1.5 mm wide and gradually tapering upwards. Pinnae alternate, leaving rachis at angle of 40°-50°, bases confluent giving rachis a winged appearance; linear, with straight or slightly undulate margins, parallel for three-quarters of length then slowly tapering to a bluntly acute apex. Pinnae in mid-portion of frond 2.5-4 mm in width and 30-40 mm in length. A straight midrib runs the whole length of each pinna, the first lateral vein attached directly to the main rachis, the rest of the lateral veins leaving the midrib at an angle of 30°-45° and soon dichotomizing once with a very acute angle and continuing straight to the margin; occasionally a vein branches a second time; about 6 pairs of veins leave the midrib in 10 mm. This species is named in honour of Professor A. H. Voisey who pioneered the geology of the Lorne Basin.

Holotype. AMF 59447 and counterpart AMF 56478.

Paratype. AMF 59448.

Locality. 1583 in grey siltstone lens at base of cliffs on southern side of Camden Head, N.S.W.

Horizon. Camden Head Claystone, Camden Haven Group. Late Early Triassic.

Discussion. Retallack (1977, microfiche Frame G7) identified specimen AMF 56478, the counterpart of the holotype of *D. voiseyi* as *D. lancifolium* var. *lineatum* (Tenison-Woods) Retallack. However, the lectotype of *D. lancifolium* var. *lineatum,* SUGD SUM 34 which was illustrated by Tenison-Woods (1883, Pl. 3, fig. 6) is a poorly preserved lower portion of a forked leaf which differs from *D. voiseyi* in having apparently grouped and numerous veins in acutely-triangular pinnules with contracted bases. *D. pinnis-distantibus* (Kurtz) Frenguelli 1943 appears to be coriaceous in contrast to the thin textured pinnae of *D. voiseyi.* The former species also has more distantly spaced and more tapering pinnae with a different venation. The sparse venation of *D. voiseyi* resembles that of *Alethopteris medlicottiana* Oldham (in Feistmantel 1876), from the Jabalpur Group of the Upper Gondwanas of India (Feistmantel 1886, pl. 1, figs 12-14). In outline *D. voiseyi* resembles *Supaia linaerifolia* White 1929, fig. 1, from the Permian Hermit Shale of Arizona.

Thinnfeldia indica var. *aquilina* and *T. indica* var. *falcata* of Shirley (1898, pl. 6, fig. 2 and pl. 7, fig. 2) are close to *Dicroidium voiseyi* but differ in the size and shape of the pinnae and in the venation. Walkom (1917a, p. 24) took Shirley's illustrated specimen of *Thinnfeldia indica* var. *falcata* as the type for *T. acuta* — later *Dicroidium acutum* (Walkom) Frenguelli 1943. Retallack (1977, p. 271) synonymized *D. acutum* under *D. lancifolium* var. *lineatum* (Tenison-Woods) Retallack. We consider *D. acutum* to be significantly different and should retain its specific status.

Dicroidium zuberi (Szajnocha) Archangelsky, var. *feistmantelii* (Johnston) Retallack 1977

Fig. 5, 3 and 4

Description. Bipinnate leaves with forked rachis. Although none of the specimens is complete the fragments suggest that the larger leaves were at least as wide as 20 cm and 35 cm or more in length. The primary rachis of the leaf is 4-12 mm in width and has a punctate or papillate surface. The pinnae range from 2 cm to 10 cm in length and from 8 mm to 20 mm in width; attached to the primary rachis at an angle of 45°-80°. The pinnae are divided to the pinna rachis into somewhat elongated subtriangular or rhombic pinnules 3 mm to 6 mm wide and 4 mm to 12 mm long, except towards their distal ends and near the leaf apex where they are coalescent and resemble similar portions of leaves of *D. dubium* and *D. lancifolium*. The pinnules are inserted at an angle of about 45° and have subacute to rounded or somewhat flattened apices. Several veins enter each pinnule from the pinna rachis and follow a curving path to the pinnule margins. Each vein typically forks twice before reaching the margin.

Discussion. This species is a common element in the flora and is marked by a great variation in the size of the leaves. These fossils compare more closely with the variety *D. zuberi* var. *feistmantelii* (Johnston) Retallack 1977, but in some specimens the pinnules are more rhombic than rounded and come close to *D. zuberi* var. *zuberi* (Szajnocha) Archangelsky 1968. However, both the supposed male and female reproductive organs of the var. *feistmantelii* differ significantly from the South American fructifications attributed to the var. *zuberi*, which suggests that all our leaves should be placed in the var. *feistmantelii*.

D. zuberi var. *feistmantelii* also occurs in the Narrabeen Group in the Sydney Basin (Walkom 1925, 1932), the Basin Creek Formation (Retallack *et al.* 1977) and the Esk Beds of Queensland (Walkom 1924).

Material. AMF 59430, AMF 59431, and UNEF 15514 from locality 1583.

Dicroidium dubium var. *australe* (Jacob & Jacob) Retallack 1977

Fig. 5, 5

Description. A medium sized bipinnatifid leaf. Pinna bases decurrent, pinna lobes rounded, venation indistinct.

Discussion. Fragments of bipinnatifid pinnae are common at locality 1695 and probably belong to this species. The apical pinnae of the bipinnate *D. zuberi* group of leaves become bipinnatifid and may be confused with the above species.

Material. AMF 59432 from locality 1583 and SUGD 81.8 from locality 1695.

Genus *Karibacarpon* Lacey 1976

Type species: *Karibacarpon problematicum* Lacey 1976

Emended Diagnosis. Megasporophyll composed of a stout rachis and several oppositely arranged lateral and a pair of terminal seed-bearing branches. Seeds contained in stalked, dorsiventrally flattened, fan-shaped, ribbed cupules. Seeds oval, large, ridged, with acute bifid micropyle. Empty cupules opening to form large star-shaped structures composed of 5 to 9 lobes.

Karibacarpon feistmantelii sp. nov.

Fig. 6, 1-8

Diagnosis. Small *Karibacarpon* fructification on a bipinnate megasporophyll. Closed cupules with inconspicuous ribs, 5-9 in number, usually 6. Mature cupules with lobed or petaloid margins, each enclosing one ovate platyspermic ovule. Empty cupules opening to form star-shaped "flowers".

Description. The megasporophyll consists of a stout primary rachis with opposite lateral branches bearing two or more pairs of opposite pedicellate cupules and a terminal pair of single cupules. Secondary rachis 3 mm or more in width and up to 5 cm in length. Pedicels of varying length and 3 mm to 4 mm in width at point of attachment to side of cupule which is of a very thick woody (?) texture. Closed cupules circular, oval or reniform, with 5 to 9, usually 6 inconspicuous ribs radiating from the pedicel across the upper surface. The dorsal surface averages 18 mm × 14 mm and the sides are 2 mm deep (as compressed). Maturing cupules develop lobed margins with the ribs as suture lines between the lobes. The lobes become increasingly separated and form elongate acute "bracts" clasping the ovule. The lobes of empty cupules are expanded and when compressed form star-like "flowers", 2 cm to 4 cm in diameter. The 5 to 9, usually 6 petal-like lobes are more or less acutely pointed and range from 6 mm to 16 mm in length, with a maximum width of 3.5 mm at the base. Most expanded cupules have been converted to a thick mass of structureless granular coal, suggesting that the organ was highly lignified. Occasionally the surface of the coal has a peculiar puckered appearance with irregular rounded ridges and furrows crossing the lobes at right angles. Walkom's specimen (1925, p. 29, fig. 9) and Fig. 6, **6** of this paper illustrate examples of this type of preservation.

The mature ovules are ovate and vary only slightly from the average size of 12 mm × 8 mm. A low medial ridge or fold extends the length of most ovules. The linear curved micropyle 1 mm in length is rarely preserved.

Syntypes. AMF 59436 portion of megasporophyll (counterpart UNEF 15521)
AMF 59439 closed cupule
AMF 59437 lobed cupules with seeds (counterpart AMF 59438)
AMF 59440 expanded cupule
AMF 59445 dispersed seed

Type locality. 1583 in a grey siltstone lens at the base of sea cliffs on southern side of Camden Head, N.S.W.

Horizon. Camden Head Claystone, Camden Haven Group. Late Early Triassic.

Discussion. The genus *Karibacarpon* was proposed by Lacey (1974) and erected (Lacey 1976) for a large cupulate fructification found in association with dispersed seeds and a large leafed *Dicroidium, D. narrabeenense* var. *bursellii* (Lacey) Retallack 1977. Lacey (1976, p. 10) believed they were all derived from the one plant. Fertile organs of a similar nature have also been recorded by Lacey (1976, p. 11) in association with *D. lancifolium.* Both forms, which occur in the Molteno Succession in Rhodesia, are larger than *Karibacarpon feistmantelii* sp. nov., have more ribs and are relatively much deeper, although the latter feature may be a result of preservation due to different types of enclosing sediments (Walton 1936).

Thomas (1933) described three genera of female cupulate fructifications; *Umkomasia, Pilophorosperma* and *Spermatocodon,* from the Molteno Beds of Natal. On the evidence of similar cuticles and on the fact of association, he included these reproductive organs and the leaves of *Dicroidium* Gothan, *Xylopteris* Frenguelli, *Pachypteris* in part, and *Johnstonia* Walkom, in the family Corystospermaceae. In *Umkomasia* and *Pilophorosperma* the arrangement of the fertile branches is similar to *K. feistmantelii* sp. nov., but in those two genera the cupules are much smaller and divide into only two lobes by clefts in the plane of branching. The margins of older cupules of *Spermatocodon* have 3-4 small lobes but the infloresence is spirally branching. The largest cupule of *S. sewardi* Thomas (1933, fig. 31b) is less than one-quarter the average size of the cupules of *K. feistmantelii.*

Frenguelli (1944) attributed cupulate ovuliferous fructifications to *Dicroidium zuberi* (=*Zuberia zuberi*) and compared them with *Lagenostoma.* These cupules were borne on slender branches and opened into three lobes, (see Frenguelli 1944, figs. 10, 11) giving them an appearance quite different from *Karibacarpon feistmantelii* sp. nov.

Examples of expanded cupules have been long known in the Early Triassic floras of the Sydney Basin. From the Newport Formation, Walkom (1925, Pl. 29, figs 7-9) illustrated specimens which he referred to *?Williamsonia* sp. (flowers). Fig. 6 on pl. 31

in the same paper shows a lateral branch of a *Karibacarpon* megasporophyll and fig. 9 shows a closed cupule. Figs 3-5 are probably dispersed seeds of *K. feistmantelii* sp. nov. Walkom (1932, p. 15, figs 4 and 5) again referred typical expanded cupules to *?Williamsonia* sp. flowers. A 10 lobed organ showing parallel veins from the Ipswich Series (Walkom 1917b, p. 14, pl. 4, fig. 5) may be a *Karibacarpon*. Jones and de Jersey (1947, p. 35, fig. 23) illustrate a possible *Karibacarpon* cupule that has been compressed sideways. Specimens of expanded cupules from other areas include SUGD 13006 and SUGD 14004 from Brookvale; MMF 3107 and AMF 52170 from Clarence Siding, AMF 58795 and AMF 58797 from Mt Piddington and UNEF 13923-5 from the Newport Formation. The latter specimens were collected by G. J. Retallack who, in a comprehensive thesis on the Newport Formation (Retallack 1973) was the first to suggest that they were corystospermous and referred them to *Umkomasia* sp. In a recent paper Retallack (1976, fig. 7) shows a reconstruction of *Dicroidium zuberi* var. *feistmantelii* with its reproductive organs which agrees well with the Lorne Basin material. Other specimens from the Lorne Basin include AMF 59463, AMF 59462, AMF 59464, AMF 59461, UNEF 15516-15520 from locality 1583 and UNEF 15523 from locality 1695.

Genus *Pteruchus* Thomas 1933 emend. Townrow 1961

Pteruchus barrealensis (Frenguelli) var. *feistmantelii* comb. et var. nov.

Fig. 6, 9-11

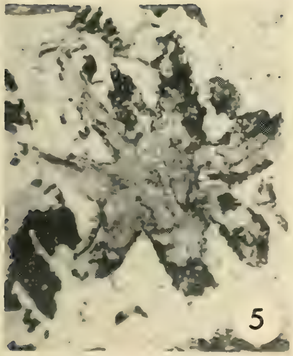
Description. A long microsporophyll consisting of a strap-shaped lamina bearing pendant, cigar-shaped pollen sacs. The laminae range from 5-18 mm in width and 30-80 mm in length and sometimes show undulate margins. A short stalk about 1.5 mm in width and up to 2.5 cm long is sometimes present. The pollen sacs are 4-5 mm long and 0.5 mm wide, some with rounded ends and others, possibly dehisced, with ragged ends; very numerous. Specimens AMF 59442, AMF 59443, AMF 59444, AMF 59455 and UNEF 15525-6 from locality 1583 and UNEF 15522 from locality 1695.

Discussion. These microsporangiate organs are similar to but even longer than *Pterorrachis barrealensis* Frenguelli (1942) from the Late Triassic of Argentina. That species was synonymized with *Pteruchus dubius* by Townrow (1961) although the Argentinian fossil is much longer than the type of *Pteruchus dubius* from South Africa (Thomas 1933). We support the contention of Retallack (1977) that it should be reassigned to *Pteruchus* but not to the species *dubius*. The difference in length between our species and the Argentinian *Pterorrachis barrealensis* is obvious when comparing the reconstruction of this organ by Frenguelli (1944, fig. 12) with that of Retallack (1976, fig. 7) and suggests a geographical variation corresponding to the variation in leaf forms.

On the basis of association and cuticular similarities, Thomas (1933), Frenguelli (1944), Townrow (1961), Archangelsky (1968) and Retallack (1973, 1976) have suggested that *Pteruchus* (including *Pterorrachis*) is part of the same plant which bore the leaf *Dicroidium*. *Pterorrachis barrealensis* was correlated with *Dicroidium zuberi* (Frenguelli 1944) and it is also likely that our *Pteruchus barrealensis* var.

Fig. 6. Note: Specimens natural size unless stated otherwise. Those photographed under kerosene are marked with an asterisk (*).

1-8 *Karibacarpon feistmantelii* sp. nov. 1, Portion of megasporophyll, *, syntype, AMF 59436. 2, Dorsal surface of closed cupule, syntype, AMF 59439, ×2. 3, Portion of megasporophyll with cupules containing ovules, syntype, AMF 59437. 4, Counterpart of specimen in 3, AMF 59438. 5, Expanded cupule, syntype, AMF 59440. 6, Fragment of expanded cupule, AMF 59441, ×2. 7, Dispersed seed showing micropyle, syntype, AMF 59445, ×2. 8, Dispersed seed, AMF 59446, ×2. 9-11 *Pteruchus barrealensis* (Frenguelli) var. *feistmantelii* comb. et var. nov. 9, AMF 59442. 10, AMF 59443. 11, AMF 59444.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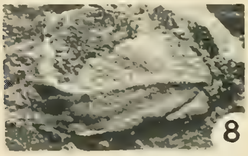
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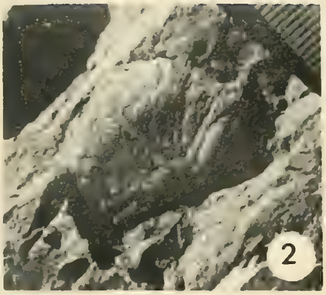
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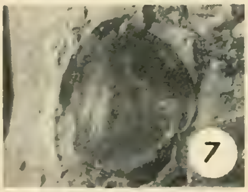
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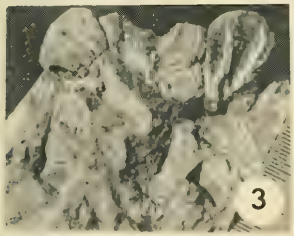
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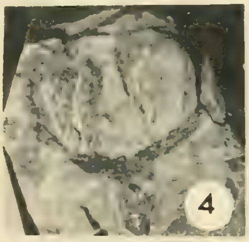
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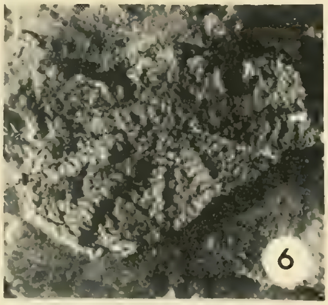
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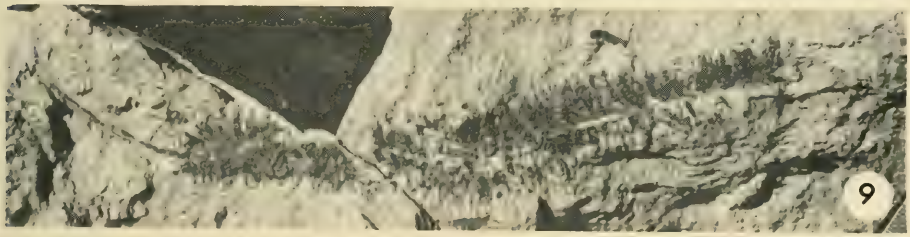
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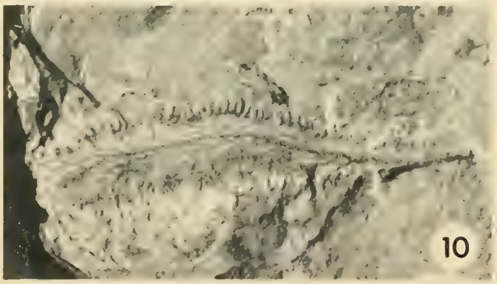
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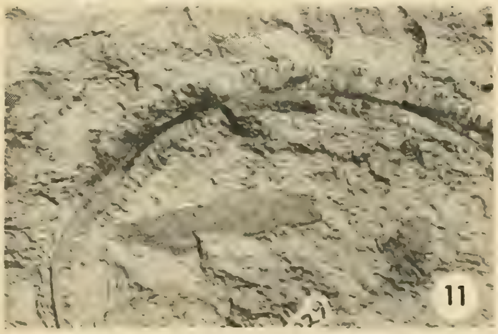
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feistmantelii sp. nov. is the microsporangiate organ of *Dicroidium zuberi* var. *feistmantelii*.

This fructification also occurs in the Newport and Garie Formations of the Sydney Basin (Retallack 1973) and possibly in the Nymboida Coal Measures of the Clarence-Moreton Basin (Retallack *et al.* 1977).

Family Peltaspermaceae
Genus *Lepidopteris* Schimper emend. Townrow 1956
Lepidopteris madagascariensis Carpentier 1935
Fig. 5, **6** and **7**

Description. This species is represented by an almost complete frond 17 cm long and 11 cm wide, and numerous smaller fragments. The pinnae are as long as 6 cm, having elongated pinnules 1-1.5 mm wide and 2-5 mm long with entire or crenate margins, attached at 75°-90°. The pinnule bases are decurrent and the apices are rounded. The venation is extremely indistinct. Rounded pinnules are attached to the main rachis between the pinnae, and the rachis is covered with small lumps as is characteristic of this species (Townrow 1966).

Discussion. These leaves are very similar to those occurring in the upper part of the Newport Formation of the Sydney Basin but are not as robust as those from the Clarence-Moreton Basin.

Material. AMF 59433, AMF 59434, AMF 56476 and AMF 59465 from locality 1583.

Dispersed Seeds, Probably Pteridospermous
Seed a
Fig. 7, **9**

Spherical mould of seed 4 mm in diameter. Surrounding flattened border is cordate — with flattened base and obtuse apex. At sides, the border is 0.5 mm wide and at apex projects 2 mm above the presumed nucellus.

Material. AMF 59454 from locality 1583.

Seed b
Fig. 3, **10**

Ovate seed 7 mm × 4 mm with crescent-shaped lateral wings 2 mm at widest point. An acutely triangular ridge traverses the seed from base to apex.

Material. AMF 59422 from locality 1583.

Seed c
Fig. 3, **9**

Oval seed 6 mm × 8 mm with encircling wing 1 mm wide. An acute ?micropyle 2 mm in length projects vertically. May be compared with *Cordaicarpus ovatus* Lele (1961) and "Seed-like body" Type I of Banerji *et al.* (1976, pl. 3, fig. 42).

Material. AMF 59421 from locality 1583.

Order Cycadales
Cycadaceous leaves of uncertain position
Genus *Taeniopteris* Brongniart 1832
Taeniopteris lentriculiforme (Etheridge) Walkom 1917a
Fig. 7, **7**

Description. Elliptic leaves; petiolate, simple, entire, obtuse. Midrib distinct, tapering to apex. Lateral veins leaving midrib at 70° and passing straight to the margin. Some veins near the base are divided once but most are undivided. The most complete leaf is 4 cm wide at midpoint of lamina and estimated to have been at least 8 cm long. The density of the veins is about 12 in 10 mm.

Discussion. These leaf fragments agree well with the original material described from the uppermost Newport Formation at Gosford and Freshwater (Etheridge 1894, pl. 8, figs 1-3). Specimens attributed to this species from Ipswich, Qld (Shirley 1898, pl. 7, fig. 3 and Walkom 1917a, fig. 11) and from the Basin Creek Formation (Flint and Gould 1975, pl. 3, figs 8 and 9) have a greater number of dichotomous veins.
Material. AMF 59453 and UNEF 15526 from locality 1696.

Class Coniferopsida
Order Coniferales
Family Voltziaceae
Genus *Voltziopsis* Potonie 1899
Voltziopsis townrovii sp. nov.

Fig. 7, 3-5

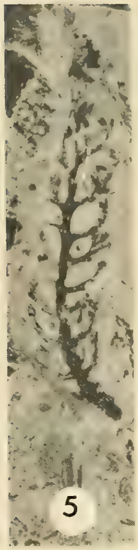
Diagnosis. Seed cone elongate, 3.5 to more than 7 cm long, 1.5 cm wide at maximum, bearing numerous spirally attached cone units composed of a conjoined bract and cone scale. Cone scales 7 mm long, divided into five lobes at midpoint, each lobe bearing a single flattened ovate seed. Bracts tapering and forked, up to 14 mm long.
Description. Terminal female cones from 3.5 cm to over 7 cm long and 1.5 cm wide, the axis tapering distally from a width of 3.5 mm at the lowermost cone unit. One cone is attached to a leafless stem 5 cm in length. The cone units, consisting of conjoined bract and cone scale, are arranged spirally; attached to the axis at about 45° and later expanding to 75°; numerous (as many as 70 estimated to be on the largest specimens). The acutely tapering and (?) forked bracts are up to 14 mm in length. The scales are about 7 mm in length; divided at their midpoint into five obtuse lobes. A single flattened ovate seed may be attached to the surface of each lobe. The basal and apical cone units are not well developed.
Holotype. AMF 59449.
Locality. 1583 in grey siltstone lens at base of seacliffs on southern side of Camden Head, N.S.W.
Horizon. Camden Head Claystone, Camden Haven Group. Late Early Triassic.
Discussion. These cones are similar to *V. wolganensis* Townrow 1967 except for being up to almost three times the length of Townrow's specimen. They appear to expand and shed the bracts on maturity. Preservation of the specimens is three dimensional and the matrix can be excavated to reveal the branched and forked nature of the bracts and scales. There is a similarity in form between these cones and the "hermaphroditic flower" *Irania hermaphroditica* Schweitzer (1977, pl. 3, figs 1-5 and pl. 5, fig. 4) from the Rhaetic of Iran.
Material. AMF 59450, AMF 59451, UNEF 13993 and UNEF 15527 from locality 1583 and UNEF 15528-9 from locality 1695.

Voltziopsis sp. foliage shoot

Fig. 7, 6

A single example of a foliage shoot 24 mm long, with close spaced, linear, acute, spirally attached leaves, 3 mm to 7 mm long and 1 mm or less wide, has the general appearance of *V. angusta* (Walkom) Townrow (1967, fig. 1b), but our leaves are twice the size of that species.
Material. AMF 59452 from locality 1695.

Order Ginkgoales
Form Genus *Rhipidopsis* Schmalhausen 1879
Rhipidopsis ?narrabeenensis Walkom 1925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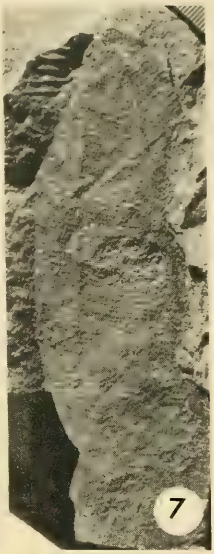
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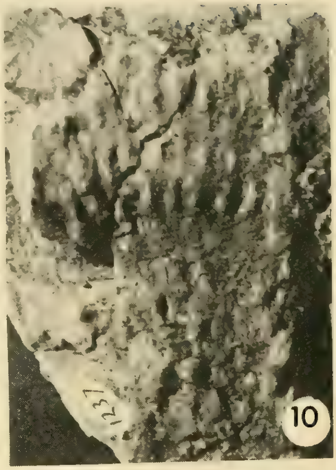
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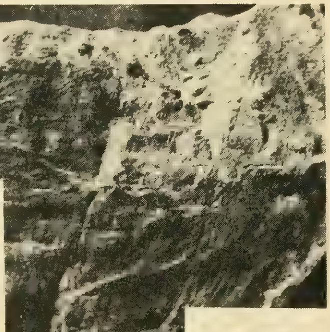
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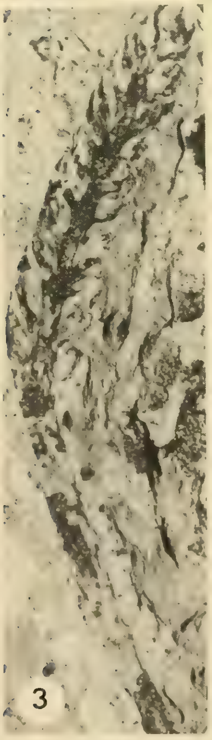
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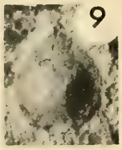
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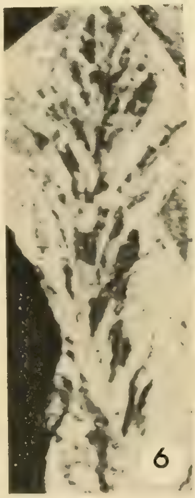
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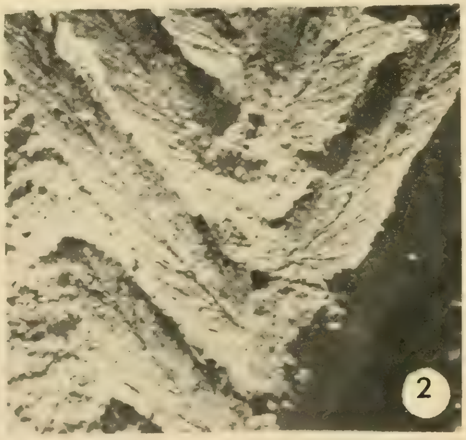
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Fig. 7, 8

Description. An apical portion of a wedge-shaped leaf, divided vertically into two segments, resembles an illustrated specimen from the Newport Formation of the Sydney Basin (Walkom 1925, pl. 30, fig. 4). The segments are 43 mm and 30 mm in width across the truncate apex; the length is estimated to have been from 8 to 10 cm. Straight veins about 1 mm apart radiate to the apex. There is no evidence of anastomosing to suggest that these leaves may be *Chiropteris* Kurr, but they may be better placed in *Ginkgophytopsis* Boureau. Burges (1935, p. 262, fig. 9) illustrated more complete specimens, probably from the same locality as Walkom's. Other similar leaves are *Rhipidopsis densinervis* Feist. from Argentina (Kurtz 1921, Pl. 6, figs 51 and 53) and possibly *R. ginkgoides* Schmalhausen (?) var. *sussmilchi* Dun (1910, Pl. 51) from the roof shales of the Bulli Coal Seam under Sydney.

Material. AMF 59455 from locality 1583.

Plantae Sedis Incertae

Stem?

Fig. 7, 10

A poorly preserved example of a ? stem with scars possibly representing leaf bases resembles a specimen from the Narrabeen Group figured by Walkom (1925, Pl. 30, fig. 2) as *? Williamsonia* sp.

Material. AMF 59456 from UNEL 1583.

Cone?

Fig. 3, 7

An ovate, woody organ 52 mm × 38 mm suggests a coniferous female cone similar to *Pinus* or *Sequoia*. Oblong — spathulate bracts or scales 10 mm × 5 mm are attached at an angle of 60° to a central axis.

Material. AMF 59420 from UNEL 1583.

Circular Ribbed Object

Fig. 3, 8

A round object 8.5 mm in diameter with a depressed centre and about 10 raised spoke-like ridges radiating to the circumference. This fossil may represent an equisetaceous nodal diaphragm.

This fossil compares with the fossils from the Rhaeto-Liassic of Greenland which Harris (1931, p. 11-12) called "star-caps". Similar fossils have been reported from the Late Triassic — Early Jurassic of Queensland by Jones (1948, pl. 1, fig. 1) who called them "star-caps". Such fossils also have been observed in the Middle Triassic Basin Creek flora at Nymboida by WBKH.

Harris (1931) found that "star-caps" were borne terminally on equisetaceous axes and he suggested that they are formed from a modified leaf-sheath in which the teeth have been bent over the stem apex and have adhered together.

Material. AMF 59419 from locality 1583 and UNEF 15530 from locality 1695.

Fig. 7. Note: Specimens natural size unless stated otherwise. Those photographed under kerosene are marked with an asterisk (*).

1-2 *Dicroidium voiseyi* sp. nov., *, holotype, AMF 59447. **2**, Specimen showing lateral venation. Paratype. AMF 59448, ×4. **3-5** *Voltziopsis townrovii* sp. nov., *, Female cone. **3**, AMF 59449, holotype. **4**, AMF 59450. **5**, AMF 59451. **6** *Voltziopsis* sp., *, Foliage shoot, AMF 59452, ×3. **7** *Taeniopteris lentriculiforme* (Etheridge) Walkom, AMF 59453. **8** *Rhipidopsis ? narrabeenensis* Walkom, AMF 59455. **9** Dispersed seed a, AMF 59454, ×2. **10** Stem ?, AMF 59456.

CONCLUSION

On the basis of common forms, the Lorne Basin flora probably correlates best with that occurring in the Early Triassic Upper Newport Formation of the Sydney Basin. There are few forms which occur also in the Anisian-Ladinian floras described by Retallack (in Retallack, Gould, and Runnegar 1977) from the Clarence-Moreton Basin. On palynological evidence Helby (1973, p. 146) suggests that the Camden Haven Group is probably late Early Triassic in age, a determination which we believe is supported by the macroflora described in this paper.

Pratt and Herbert (1973) reconstructed the Lorne Basin palaeoenvironment as being an area of alluvial fans debouching from the south-west, west and north-west onto a widespread plain crossed by meandering streams. An arid climate was suggested. The localities from which the bulk of our flora was collected all represent a single environment, that of back-swamps bordering streams and filled by overbank flooding.

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We thank Dr R. E. Gould, Dr B. C. McKelvey and Dr G. J. Retallack for much helpful discussion. We very much appreciate Dr Retallack allowing us unrestricted access to his unpublished thesis on the palaeobotany of the Newport Formation. The curators at the Australian Museum, The Mining and Geological Museum, Sydney and the Universities of Sydney and New England kindly allowed access to their fossil collections. Mrs Felicity Holmes greatly assisted with the collecting, photographing and typing. Dr Gould photographed some of the specimens and Mrs Rhonda Vivian did the final typing of the manuscript. S.A. received assistance from the United States-Australia Cooperative Science Program and was provided with research facilities in the Department of Geology of the University of New England.

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A natural habitat of the insect Pathogenic Fungus *Culicinomyces* in the Sydney area

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RUSSELL, R. C., DEBENHAM, M. L., & LEE, D. J. A natural habitat of the insect pathogenic fungus *Culicinomyces* in the Sydney area. *Proc. Linn. Soc. N.S.W. 103* (1), *(1978) 1979*: 71-73.

One possible source of a mosquito pathogenic fungus, *Culicinomyces* sp., which appeared in a Sydney laboratory colony in 1972, was considered to be McCarr's Creek near Sydney. After several seasons' search, larvae of the mosquito *Aedes rupestris* Dobrotworsky, collected from rock pools in the creek in late 1976 and early 1977, were found to be infected with *Culicinomyces*. The fungus was cultured *in vitro* and tested for pathogenicity.

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INTRODUCTION

A sudden increase in larval mortality occurring in February, 1972, in a colony of *Anopheles amictus hilli* Woodhill & Lee maintained at the School of Public Health and Tropical Medicine, University of Sydney, was traced to an infection with a pathogenic fungus, but attempts to identify the fungus were unsuccessful (Sweeney *et al.,* 1973). In September, 1972, a similar phenomenon was observed by Prof. J. N. Couch and associates in colonies of *Anopheles quadrimaculatus* Say maintained at the University of North Carolina, Chapel Hill, N.C. In 1974 Couch, Romney & Rao described the Chapel Hill fungus as a new species, *clavosporus,* of a new genus *Culicinomyces,* stating that the fungus had been introduced to the mosquito colonies in water from University Lake, Chapel Hill, and adding that it also occurred "in mosquitoes in water from a lake near Sydney, Australia (Dr Lee and associates)". Apart from the implication that the two fungi are conspecific — and they have as yet only been determined to be congeneric (Sweeney, 1975a) — this statement is misleading, as at that time the source of introduction of the fungus to the S.P.H. & T.M. colony was unknown, although Professor Couch had been informed that one of the suspect sources was McCarr's Creek near Sydney.

SOURCE OF THE FUNGUS

A review of the situation in the mosquito colony at the time of introduction of the fungus revealed three possible sources:

(i) it had persisted undetected at a low level since the colony's development from larvae originating in Gove, N.T., twelve months previously, but had reached epizootic level following a change in pupal separation procedures;

(ii) it was introduced with *Aedes australis* (Erichson) which had recently been colonized in the laboratory from specimens collected in brackish rock pools at Tamarama, Sydney.

(iii) it was introduced with water brought from McCarr's Creek, French's Forest, Sydney, which was used for culture of the *An. amictus hilli* larvae.

When temperature and salinity tolerances of the fungus were considered (Sweeney, pers. comm.), (iii) was accepted as the most likely source, and investigations of this area were begun in an attempt to find the natural habitat of the fungus. *Culicinomyces* is pathogenic to several species in a number of different families of Dipterous insects in their aquatic larval stage (Sweeney, 1975b); it has also been found in adult mosquitoes from an infected laboratory colony, but only rarely (Debenham & Russell, 1977). Thus, over several seasons, collections were made of aquatic Dipterous larvae, and samples were taken of water, vegetation, substrate and organic debris for laboratory examination, but until recently no evidence of the presence of *Culicinomyces* was detected in any of these collections.

Then, on 5th January, 1977, several dead *Aedes rupestris* Dobrotworsky larvae, part of a collection of aquatic Dipterous larvae made at McCarr's Creek on 23rd December, 1976, were found to be showing extensive growth of a fungus identifiable as a species of *Culicinomyces*. These larvae all came from a single small, shallow rock pool, with bottom organic debris over gravel, in the partially dry creek bed. This pool was only a few metres above the site from which the water for the colony is collected. The larvae had been maintained since their collection in the water in which they were collected, and kept in a laboratory separated from that in which *Culicinomyces* cultures were stored. Care had been taken to eliminate any chance of contamination from these cultures.

The infected larvae were washed in 50 ml of distilled water, then plated onto nutrient agar containing 0.1% streptomycin and 0.02% neomycin. The washings were retained. Growth of *Culicinomyces* and other fungi occurred on these plates, and the *Culicinomyces* was selectively removed and replated. Subsequent examination showed a pure culture of *Culicinomyces* had been obtained, and this was transferred to nutrient agar slopes on which it is currently being maintained.

On 6th January, 1977, further collections of Dipterous larvae were made from rock pools in the creek bed. Prior to this collection some rain had fallen and water had flowed over these pools, but they did not appear to have been completely flushed out. On 10th January a number of *Aedes rupestris* larvae from this collection, taken from the same pool as the larvae found infected on the previous occasion, and maintained in the same way, were also found to be infected with *Culicinomyces*. These larvae were washed and plated, and the fungus established on nutrient agar as before.

Following heavy rains the McCarr's Creek area was re-investigated on 25th January, 1977, but the rock pools had been completely flushed through, and very few Dipterous larvae could be collected. Examination of these, and of larvae collected here and from similar creeks in the vicinity on other occasions, has so far not produced any further evidence of *Culicinomyces* in this area.

PATHOGENICITY OF THE FIELD ISOLATIONS

Spores washed or cut from nutrient agar cultures of the field-isolated fungus were added to test trays of *An. amictus hilli* larvae, and the development of these compared with larvae in trays to which no spores had been added. In all cases most of the larvae in the inoculated trays were dead within seven days, and growth of *Culicinomyces* was observed in many of the dead larvae. Larvae in control trays developed and emerged normally. Qualitatively, the pathogenicity of the field-isolated fungus appeared comparable to that of the laboratory-derived culture.

Following a suggestion by Mr M. O'Keeffe, S. P. H. & T. M., the field-isolated fungus was also established on a *Nocardia* medium (Tsukamura, 1969 — 10 g glucose, 4 g sodium glutamate, 0.5 g KH_2PO_4, 0.5 g $MgSO_4.7H_2O$, 20 g agar, 1 l distilled water, with pH adjusted to 7.0 by the addition of 10% w/v KOH). After establishment, fungus grown on this medium was tested for pathogenicity to mosquito larvae in the manner described above, with similar results.

For additional confirmation of pathogenicity a small number of *An. amictus hilli* larvae were added to the 50 ml of distilled water which had been used to wash the infected larvae from McCarr's Creek prior to plating them. After four days all larvae were dead, and one showed good growth of *Culicinomyces*, but the remaining larvae were too heavily contaminated with Protozoa for the cause of death to be determined.

CONCLUSION

It has been found that the insect pathogenic fungus *Culicinomyces* exists naturally in McCarr's Creek, French's Forest, Sydney, and that it infects larvae of the mosquito *Aedes rupestris* in this area. It is not yet known whether mosqito larvae are the natural hosts of the fungus in this habitat or whether such infections are incidental to the natural cycle of the fungus.

ACKNOWLEDGEMENTS

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THE LINNEAN SOCIETY OF NEW SOUTH WALES

Record of the Annual General Meeting, 1978

The one hundred and third Annual General Meeting of the Society was held in the Science Centre, 35 Clarence Street, Sydney, on Wednesday 29 March 1978 at 7.30 pm.

The President, Professor B. D. Webby, occupied the Chair. The minutes of the one hundred and second Annual General Meeting, held 28 March 1977, were read and confirmed.

Report on the Affairs of the Society for the Year 1977–8

Publications

The Society's *Proceedings* were issued on the following dates:

Vol. 101, Part 3	6 April 1977
Vol. 101, Part 4	28 July 1977
Vol. 102, Part 1	28 September 1977
Vol. 102, Part 2	26 October 1977

During the year a Committee of Council reviewed suggestions regarding style and format for future issues of the *Proceedings*. A number of recommended changes have been approved by Council. These include a new cover design, changes to the layout of abstracts and headings of papers, use of a better quality paper which will allow half tones to be placed at appropriate places in the text (and not, as hitherto, printed as plates separate from the text) and publication of the *Proceedings* in two double issues per volume in the hope of attracting the Book Bounty which could lead to a saving of up to 25% on printing costs. It is planned to incorporate these changes into Volume 103, the first double issue of which should appear late in 1978 or early in 1979.

The LINN SOC NEWS continued to be produced quarterly to keep members informed of Society activities, forthcoming events and other items of interest.

Membership

During the year 5 new members were elected, 12 resigned and one died. At 1 March 1978 the society consisted of 255 Ordinary Members, 26 Life Members and 5 Corresponding Members, making a total membership of 286.

Miss Kathleen English, who died in August 1977, had been a member since 1930. She was an authority on Tabanid flies and published the results of her research into their life histories and taxonomy in our *Proceedings*.

We have recently learned of the death of Dr Hans Laurits Jensen, Macleay Bacteriologist from 1929 to 1947 and Corresponding Member of the Society since 1949. The work that he did as Macleay Bacteriologist is held in world-wide esteem. Dr Jensen contributed more than 30 papers to the *Proceedings*.

Meetings

The eleventh Sir William Macleay Memorial Lecture was delivered by Professor D. T. Anderson of the University of Sydney. The lecture entitled *Natural History Today* was given at the Science Centre on 16 March 1978 and was followed by a dinner. Professor Anderson's text appears elsewhere in this issue of the *Proceedings*.

At general meetings during the year members heard talks by distinguished speakers on a wide range of topics. On 27 April 1977, Mr David Colby of the Australian Atomic Energy Commission spoke about 'The Uranium Debate'. 'Discovering the Australian Desert Culture' was the subject chosen by Professor R. A. Gould, Department of Anthropology, University of Hawaii, for his talk on 27 July. Finally, on 14 December, Dr J. A. Dulhunty of the Department of Geology & Geophysics, University of Sydney, presented 'The Lake Eyre Story'.

Two Field Days were held, the first being to examine aboriginal rock carvings at West Head under the guidance of Ku-ring-gai Chase National Park Rangers in June 1977, the second (in August) was led by Dr D. Adamson and directed to the problems of invasion of exotic plants in several natural bushland sites around Sydney.

To complete the record, note is made of the very successful full-day symposium on 'The Natural History of the Myall Lakes Sand Masses'. This meeting, organized by Dr P. Myerscough, was held on 12 November 1977.

Library

Since the appointment in July of our new Librarian, Mrs Johanne Buttigieg, the backlog of work has been brought up to date and the library is now functioning normally.

Linnean Macleay Fellowship

Mrs Jennifer Anderson has completed her second year as Linnean Macleay Fellow at the University of New South Wales. Her tenure has been extended for a third year. She is studying seasonal cycles of development in some Australian ladybirds (Coleoptera: Coccinellidae).

Her particular interest is reproductive diapause. Factors that induce, maintain and terminate diapause are being investigated in the laboratory, in conjunction with a seasonal field study. Species being studied include the aphidophagous *Scymnodes lividigaster* (Mulsant) and the mycophagous *Leptothea galbula* (Mulsant).

Linnean Macleay Lectureship in Microbiology

Dr K. Y. Cho reports that his research work in the past year has been aimed at characterizing the membrane of *Azotobacter vinelandii.* The membrane lipids have been analysed and the antegenecity of the membrane studied by cross immunoelectrophoresis. In June 1977 Dr Cho participated in a UNESCO training course held in Hong Kong on the cultivation of edible fungi.

Staff Appointments

Following the resignation of Mr A. M. Ginges from the post of Secretary to the Society in June 1977, Council appointed Mrs Barbara Stoddard to the position as from 4 July.

On 25 July, 1977, Mrs Johanne Buttigieg was appointed Librarian.

Office

The Society now has an office near the Library on the 6th floor of the Science Centre. The Librarian is in attendance on Mondays and Wednesdays from 9 am until 1 pm and the Secretary all day on Tuesdays. The office is closed on Thursdays and Fridays.

The Society's telephone number is 290 1612.

Science Centre

During the year the Science Centre has become recognized as a source of services to the scientific and professional community and has attracted interest as a model for others. The Earl of Shannon, chairman of the proposed Science Centre in London, inspected the building during his recent visit to Sydney and had discussions on problems related to instituting such a project.

In spite of unfavourable economic conditions, the Science Centre has progressed to the stage where all the office space has been let except for a portion of the 5th floor, all shops and car-parking spaces are taken and the Secretarial Services division has doubled in size. The use of meeting rooms and facilities has increased to the point at which there are meetings held in the building on most week-nights. The restaurant on the ground floor which closed in December 1977 is expected to reopen under new management in April 1978.

The income of the Science Centre now exceeds operating expenses but is not yet sufficient to meet more than a part of the interest owing on the bank loan.

A notable item of decor on the exterior wall of the Auditorium on the 1st floor is a mural of appropriate design in copper created by Mr Auriel Ragus and donated by Mr E. J. Selby, a member of the Linnean Society of New South Wales who serves as one of its directors on the board of Science House Pty Ltd.

REPORT OF THE HONORARY TREASURER FOR THE YEAR 1977

The Balance Sheet and the Income & Expenditure accounts of the Society's General Account give cause for considerable concern. Again, we have suffered a deficiency, this year of $3516. Our Accumulated Funds, at over half a million dollars, might suggest that we are a wealthy Society but four-fifths of this amount is invested in the Science Centre building which has not yet reached the stage of providing any income to the Society and is unlikely to do so for some time. Our invested funds amount only to rather less than $93,000, from which we received interest of $8903.

Under Expenditure, a new item Fellowship Grant appears. Council decided that the amount which it is legally entitled to pay its Fellow from the Fellowships Account had to be supplemented in this way to bring the emolument nearer the value of scholarships awarded by other organizations. The cost of printing the *Proceedings* is much higher this year, partly because of further increases in the printer's charges and partly because two parts of the *Proceedings* for 1976 were not paid for until 1977. The new item Room Hire represents the cost of hiring meeting rooms for the Society's functions in the Science Centre. The item Rent is for the small office on the 6th floor of Science Centre which we occupied for part of 1977 and is much less than the rent for 1976 when, for most of the year, we had rooms in Science House. Secretarial Services includes a fee of $4000 for editing and processing the *Proceedings,* which underlines the fact that the cost of publishing a journal is much more than the actual printing costs.

The main sources of income in the General Account are the Membership Subscriptions and

Subscriptions to the *Proceedings*, Interest on investments, the surplus income from the Fellowships Account and, in 1977, Sales chiefly of back numbers of the journal. This last fortunately was higher than usual this year but cannot be depended upon for consistent results in the future.

In the Fellowships Account investments yielded more Interest in 1977 than previously because of turnover of lower interest-yielding stocks to an investment earning higher interest. As we employed a Fellow for the whole twelve months no transfer was made to the Fellowships Capital Account. After paying the salary of the Linnean Macleay Fellow the surplus of $7250 was transferred to the General Account.

In the Bacteriology Account the Interest received increased slightly this year. The sum of $2500 was donated to the University of Sydney towards the salary of the Linnean Macleay Lecturer in Microbiology. The deficiency of $102 simply means we donated slightly more than we received as interest during 1977 but the reserve balance is still quite adequate.

The Scientific Research Fund has been augmented by Interest of $1659 and Donations of $2000; the balance now stands at $17,773.

Following presentation of the Honorary Treasurer's Report and discussion, a motion that the Audited Balance Sheets for 1977 be adopted was passed unanimously by the members present.

The President, Professor B. D. Webby, then delivered his Presidential Address entitled *The Ordovician Stromatoporoids.* [The text of Professor Webby's address appears in Vol. 103, part 2 of the *Proceedings.*]

No other nominations having been received, the Chairman declared the following duly elected for the ensuing year:

President: Mr J. T. Waterhouse.
Members of Council: Dr D. A. Adamson, Dr A. E. Greer, Dr L. A. S. Johnson, Mr A. N. Rodd, Dr C. N. Smithers, Professor N. G. Stephenson.
Auditors: W. Sinclair & Co.

Professor Webby then invited Mr Waterhouse to take the Chair. Before closing the meeting Mr Waterhouse called on Dr A. Ritchie to propose a vote of thanks to the Retiring President. Dr Ritchie made special reference to Professor Webby's efforts while President to update the format of the *Proceedings*: his vote of thanks was carried by acclamation.

LINNEAN SOCIETY OF NEW SOUTH WALES

GENERAL ACCOUNT

Balance Sheet as at 31st December, 1977

1976 $		$
	Accumulated Funds—	
	Balance, 1st January, 1977	503,918.96
	Less deficiency for the year	3,516.11
503,919	Balance, 31st December, 1977	500,402.85
	Reserves—	
1,143	Bookbinding	1,142.66
	Science House Pty Limited—	
	Donations held	236.00
$505,062		$501,781.51

1976 $		$	$
	Fixed Assets—		
	Furniture, Fixtures & Fittings — At Cost	1,670.91	
1,538	*Less* Depreciation written off	247.91	
			1,423.00
	Office Machines — At Cost	984.00	
583	*Less* Depreciation written off	489.00	
			495.00
	Investment — At Cost—		
1	Share — Science House Pty Limited		1.00
2,122	Total Fixed Assets		1,919.00
	Investments—		
	Deposits—		
8,310	N.S.W. Permanent Building Society	410.22	
36,700.00	Australian Resources Development Corp.	36,700.00	
1,000	Commonwealth Loans — At Cost	1,000.00	
	Debentures — At Cost		
	C.B.F.C. Limited	20,000.00	
5,000	Colonial Sugar Refining Co. Limited	—	
	Metropolitan Water, Sewerage & Drainage		
32,100	Board	22,100.00	
12,750	Mutual Acceptance Limited	12,750.00	
95,860	Total Investments		92,960.22
	Current Assets—		
	Loans — Science House Pty Limited—		
400,000	Science Centre Account	400,000.00	
3005	Management Account	3004.60	
304	Sundry Debtors	311.00	
	Linnean Macleay Fellowships Account	39.87	
101	Cash on Hand	35.21	
3,670	Cash at Bank	3,511.61	
407,080	Total Current Assets		406,902.29
$505,062			$501,781.51

LINNEAN SOCIETY OF NEW SOUTH WALES

Income and Expenditure Account for the Twelve Months Ended 31st December, 1977

1976 $	EXPENDITURE	$	1976 $	INCOME	$	$
450	Audit Fees	450.00		Subscriptions —		
1,037	Cleaning	66.00	988	Members	927.50	
122	Depreciation	202.54	3,251	Proceedings	5,047.26	
864	General Expenses	410.23				
—	Fellowship Grant	600.00	4,239			5,974.76
1,041	Illustrations	1,416.95		Proceedings — Printing Costs —		
34	Insurance	33.34	1,351	Donations received		25.50
—	Legal Expenses	250.00	—	Insurance Refund		33.76
216	Library	139.83	9,349	Interest Received		8,903.11
50	Life Assurance Premium	—				
193	Light and Power	266.21		Fellowships Account —		
100	Linnean Macleay Lecturer's Fee	—	6,115	Surplus Income for the year ended		
1,022	Postages	1,200.42		31st December, 1977		7,413.26
4,929	Proceedings — Printing Costs	9,157.22				
449	Printing and Stationery	316.51	—	Donations Received		6.00
93	Referees Fees	70.00	766	Reprint Sales		789.20
116	Repairs and Maintenance	1117.00	1,159	Sales		5,249.11
1,160	Reprints	1,273.25				
—	Room Hire	216.00	22,979	Total Income		28,394.70
3,986	Salaries	4,132.68				
3,334	Science House Rent	314.08	3,272	Deficiency for Year Transferred to		
6,492	Secretarial Services	11,090.23		Accumulated Funds		3,516.11
563	Telephone	188.32				
$26,251	Total Expenditure	$31,910.81	$26,251			$31,910.81

AUDITORS' REPORT

We have audited the books and records of the Linnean Society of New South Wales for the twelve months ended 31st December, 1977 and are of the opinion that the above Balance Sheet and accompanying Income and Expenditure Account correctly sets forth the position of the financial affairs as at 31st December, 1977, according to the explanations given to us as disclosed by the books of the Society.

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

DATED at Sydney this seventh day of March, 1978.

JOYCE W. VICKERY,
Hon. Treasurer.
7th March, 1978.

LINNEAN SOCIETY OF NEW SOUTH WALES

LINNEAN MACLEAY FELLOWSHIPS ACCOUNT

Balance Sheet as at 31st December, 1977

1976 $		$	$
	Accumulated Funds —		
	Balance, 1st January, 1977 —		
	Amount Bequeathed by Sir William Macleay	70,000.00	
	Transfers from Income Account	59,873.10	
	Increase in Value of Assets	272.02	130,145.12
	Less adjustment of transfers to general account in respect of interest received		318.69
130,145	Balance, 31st December, 1977		129,826.43
4,587	Bank Overdraft		
	General Account —		
	Interest not transferred		39.87
$134,732			$129,866.30

1976 $		$
	Fixed Assets —	
46,200	Commonwealth Loans — At Cost	46,200.00
13,500	Australian Savings Bond — At Cost	13,500.00
	Debentures — At Cost —	
200	British Petroleum Company of Australia Ltd	200.00
1,000	Electricity Commission of New South Wales	1,000.00
1,263	F.N.C.B. — Waltons Corporation Limited	1,262.90
18,500	Metropolitan Water, Sewerage & Drainage Board	13,000.00
13,250	Mutual Acceptance Limited	13,250.00
6,000	Telecom Australia	6,000
	Deposits —	
29,700	Australian Resources Development Bank	35,400.00
4,800	N.S.W. Permanent Building Society	—
319	Permanent of Australia Building Society Ltd	39.87
134,732	Total Investments	129,852.77
	Current Assets —	
	Cash at Bank	13.53
$134,732		$129,866.30

Income and Expenditure Account for the Twelve Months Ended 31st December, 1977

1976 $		$
2,800	Salary of Linnean Macleay Fellow	3,199.92
400	Transfer to Capital Account	— —
6,115	Surplus for the year transferred to General Account	7,250.41
$9,315		$10,450.33

1976 $		$
9,315	Interest Received	10,450.33
$9,315		$10,450.33

AUDITORS' REPORT

We have audited the books and records of the Linnean Society of New South Wales for the twelve months ended 31st December 1977 and are of the opinion that the above Balance Sheet and accompanying Income and Expenditure Account correctly sets forth the position of the financial affairs of the Linnean Macleay Fellowships Account as at 31st December, 1977, according to the explanations given to us and as disclosed by the books of the Society.

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

DATED at Sydney this Seventh day of March, 1978.

JOYCE W. VICKERY,
Hon. Treasurer.
7th March, 1978.

LINNEAN SOCIETY OF NEW SOUTH WALES

BACTERIOLOGY ACCOUNT

Balance Sheet as at 31st December, 1977

1976 $	Accumulated Funds—	$	$	1976 $	Investments—	$
	Balance, 31st December, 1977—			26,900	Commonwealth Loans – At Cost	26,900.00
	Amount bequeathed by Sir William Macleay	24,000.00		1,600	Australian Savings Bonds — At Cost	1,600.00
36,900	Transfers from Income Account etc.	12,90.00			Australian Resources Development Bank	
			36,900.00	8,000	Transferrable Deposits — At Cost	8,000.00
	Macleay Lecturer in Microbiology					
	Reserve—				Debentures—	
	Balance, 1st January, 1977	2,666.70		200	British Petroleum Company of Australia Ltd	200.00
2,667	*Less* Deficiency for Year	102.00			Metropolitan Water, Sewerage & Drainage	
				200	Board — At Cost	200.00
	Balance, 31st December, 1977		2,564.70	36,900		36,900.00
					Current Assets—	
				2,667	Cash at Bank	2,564.70
$39,567			$39,464.70	$39,567		$39,464.70

Income and Expenditure Account for the Twelve Months Ended 31st December, 1977

1976 $			1976 $		$
2,300	University of Sydney — Salary of Lecturer	2,500.00	2,186	Interest Received	2,398.00
			114	Deficiency for Year	102.00
$2,300		$2,500.00	$2,300		$2,500.00

AUDITORS' REPORT

We have audited the books and records of the Linnean Society of New South Wales for the twelve months ended 31st December 1977 and are of the opinion that the above Balance Sheet and accompanying Income and Expenditure Account correctly sets forth the position of the financial affairs of the Bacteriology Account as at 31st December, 1977, according to the explanations given to us and as disclosed by the Books of the Society.

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

DATED at Sydney this Seventh day of March, 1978.

JOYCE W. VICKERY,
Hon. Treasurer.
7th March, 1978.

LINNEAN SOCIETY OF NEW SOUTH WALES

Scientific Research Fund Account

Balance Sheet as at 31st December, 1977

1976 $		$	$
	Accumulated Funds—		
	Balance, 1st January, 1977	14,114.44	
	Interest Received	1,659.18	
	Donations Received	2,000.00	
14,114	Balance, 31st December, 1977		17,773.62
$14,114			$17,773.62

1976 $		$
	Investments—	
	Debentures — At Cost—	
—	Australian Guarantee Corporation Ltd	1,800.00
3,600	Beneficial Finance Corporation Ltd.	3,600.00
1,200	British Petroleum Company of Australia Ltd	1,200.00
2,700	Commercial & General Acceptance Limited	2,700.00
3,100	Finance Corporation of Australia Ltd	3,100.00
1,021	F.N.C.B. — Waltons Corporation Limited	1,021.00
—	General Credits Ltd.	1,900.00
1,200	Industrial Acceptance Corporation Ltd	1,200.00
1,200	Mutual Acceptance Limited	1,200.00
14,021		17,721.00
	Current Assets—	
93	Cash at Bank	52.62
$14,114		$17,773.62

AUDITORS' REPORT

We have audited the books and records of the Linnean Society of New South Wales for the twelve months ended 31st December 1977 and are of the opinion that the above Balance Sheet correctly sets forth the position of the financial affairs of the Scientific Research Fund Account as at 31st December, 1977 according to the explanations given to us and as disclosed by the Books of the Society.

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

DATED at Sydney this Seventh day of March, 1978.

JOYCE W. VICKERY,
Hon. Treasurer.
7th March, 1978.

PROCEEDINGS
of the
LINNEAN SOCIETY
of
NEW SOUTH WALES

VOLUME 103
PART 2

PRESIDENTIAL ADDRESS

The Ordovician Stromatoporoids

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Department of Geology & Geophysics, University of Sydney

(Delivered 29 March 1978)

Synopsis

Stromatoporoids are sessile, dominantly Early-Middle Palaeozoic, frame-building, calcareous fossils, probably nearest to present-day sclerosponges or hydrozoans. The Ordovician representatives, which formed important constituents of the earliest coral-stromatoporoid-algal patch reef and carbonate bank communities, include members of three markedly different families — the Labechiidae, the Clathrodictyidae and the Cliefdenellidae. The labechiids are the most diverse and abundant Ordovician group with some nineteen genera, and a maximum development in the Middle-Late Ordovician. The clathrodictyids are a predominantly Silurian family, but three genera had already appeared in the preceding Ordovician. The cliefdenellids are restricted to one, exclusively Ordovician, genus. A systematic review of all the constituent Ordovician genera is presented.

The distribution of the genera is depicted in terms of the known Ordovician stratigraphical ranges and geographical spread. The labechiids exhibit a strikingly rapid period of diversification in the Middle Ordovician (in North American stratigraphical terminology, between Chazy and 'Blackriver' times). Most genera appear to have dispersed fairly rapidly along the band-like Ordovician 'equatorial' belt, but a few like *Pachystylostroma* and *Aulacera* seem to have migrated much more slowly, having taken until late in the Ordovician to achieve a circum-equatorial distribution. The clathrodictyids and cliefdenellids made their first appearances in the Australian region in the late Middle Ordovician (North American 'Trenton'). *Clathrodictyon* and *Ecclimadictyon* also migrated very slowly, taking until the end of the Ordovician to attain a circum-equatorial dispersal. While the clathrodictyids may have evolved from a simple 'vesicular' Middle Ordovician labechiid, it is more difficult to derive the complex morphology of *Cliefdenella* from such an ancestor. *Cliefdenella* is only recorded from Australia and Siberia.

The supposed Cambrian 'stromatoporoids' cannot be positively confirmed as the ancestral stocks to later stromatoporoids. They have a temporally and geographically restricted occurrence in the Early Cambrian of the Altai Sayan mountain region of Siberia, have archaeocyathan associations and morphological resemblances to some members of the class Irregulares, and they are separated by a period of 110 million years from indubitable Middle Ordovician and later stromatoporoids. An earlier ancestry would help to explain the sharp morphological differences between individual families and to resolve the problem of the derivation of *Cliefdenella,* but the origins may have been in non-skeletonized stocks rather than in the supposed Cambrian 'stromatoporoids'. The first Ordovician appearance of each family seems more likely to reflect the beginnings of skeletonization in the particular group rather than to depict the initial radiation of a new lineage. The review concludes with an account of the adaptive radiation of skeletonized Middle-Late Ordovician labechiid genera, and an outline of the alternatives for deriving the clathrodictyids and the cliefdenellids.

INTRODUCTION

The year 1978 marked the centenary of the introduction by Nicholson & Murie of the term Stromatoporoidea. Members of this problematical group of fossil organisms have calcareous skeletons of hemispherical, laminar, encrusting, cylindrical and ramose growth form, and are composed internally of a meshwork of plate-like elements (cysts or laminae) and intersecting, vertical, rod-like pillars, or less commonly, an amalgamate network. Nicholson & Murie (1878) reviewed the structure and affinities of stromatoporoids — published incidentally in the journal of our kindred society, the Linnean Society of London — arguing against their affinity with marine plants ('Nullipores'), Foraminifera, hexactinellid sponges, Bryozoa and corals. They noted the close resemblances to hydrozoans and to calcareous sponges, favouring a grouping with the sponges. Later, Nicholson (1886a) revised this view in favour of interpreting stromatoporoids as hydrozoans rather than sponges, having become convinced of the existence in various typical stromatoporoids of 'tubes' or 'cells' which may have served to house living zooids as in a coelenterate colony.

Both Nicholson & Murie's earlier interpretation and Nicholson's later grouping have their modern adherents. Stearn (1975) has summarized the divergence of opinion as between 'those who maintain that they are hydrozoans whose closest living relative is *Hydractinia* and those who believe that their closest living relatives lie in the Phylum Porifera. In favouring the assignment of them to a separate subphylum of the Porifera (the Stromatoporata), Stearn (1972; 1975) noted the morphological similarities, especially the presence of astrorhizae (possibly representing the excurrent canal system as in a sponge), and the principal difference in lacking siliceous spicules. He interpreted the stromatoporoids like modern sclerosponges as secreting a skeleton of fibrous aragonite and living as individual (non-colonial) filter feeders.

On the other hand, Birkhead (1967), Flügel & Flügel-Kahler (1968), Sleumer (1969), Mori (1969; 1970), Bogoyavlenskaya (1969), Kaźmierczak (1971) and Bolshakova (1973), among modern specialists of the group, prefer to view them as having an affinity with hydrozoans. Kaźmierczak (1976), though, in the latest expression of his views, radically departs from his earlier interpretation, and now proposes that stromatoporoids be removed fron the animal kingdom, and included with stromatolites in the Cyanophyta (blue-green algae). Thus the precise affinities and systematic relationships of stromatoporoids are now little closer to being settled than they were in Nicholson's day, despite the enormous increase in knowledge of the group, including the especially important contributions on microstructure (Stearn 1966; St. Jean 1967) and soft tissue reconstructions based on analogies with living sclerosponges (Stearn 1975).

The majority of past and present-day specialists have viewed the Stromatoporoidea as being a reasonably homogeneous group. However, a small band of European workers, notably Heinrich (1914), Tripp (1929), Kühn (1927; 1939) and Alloiteau (1952), have considered them to be heterogeneous, with representatives of the family Labechiidae taken to be a separate subdivision not allied to stromatoporoids proper. These workers maintained that the coenosteum (or skeleton) of members of the order Stromatoporoidea in exhibiting a meshwork of open, gallery-like passages and a ramifying, tube-like astrorhizal system, differed fundamentally from labechiids which typically have a closed vesicular form and lack astrorhizae. The labechiids were therefore assigned to a separate order. The majority of present-day specialists of the group (Yavorsky 1962; Nestor 1964; 1966a; 1966b; Stearn 1966; Flügel & Flügel-Kahler 1968; Webby 1969; Bogoyavlenskaya 1969; Mori 1969; 1970; Bolshakova 1973; Khalfina & Yavorsky 1973; Khromych 1974a; and Kapp & Stearn 1975), however, include the labechiids in the Stromatoporoidea. As Nestor (1966a) has said, 'the differences between the vesicular and other stromatoporoids are by no means so sharp and fundamental as to justify assigning them to different orders'.

Many previous workers have alluded to the difficulties of interpreting — more specifically identifying — stromatoporoids because of their susceptibility to alteration both by the processes of diagenesis and recrystallization. Stearn's (1972; 1975) explanation that stromatoporoids initially secreted a more unstable aragonite skeleton recalls Nicholson's (1886a, p. 35) original statement. He wrote: 'There is, in fact, considerable reason for concluding that the skeleton was originally composed of arragonite, and that in almost all, or perhaps all, specimens which have not been silicified, the arragonite has become more or less extensively replaced by calcite'. Other calcareous fossil groups such as brachiopods, bryozoans and some corals (notably heliolitids) usually exhibit better preservation than the associated stromatoporoids (Kapp & Stearn 1975).

Not only are there problems of interpreting the effects of secondary alteration of the original structure, but there are difficulties in recognizing the limits of the original variability within many fossil species. For instance, within a single coenosteum exhibiting alternate banding of two distinctive morphologies, one may be inferred to be more completely calcified than the other (see further discussion p. 87, and Yavorsky, 1961, pl. 19, figs 1-6; pl. 20, figs 1-2). The coenosteum may have been better calcified at certain periods of growth than at others (Kapp & Stearn 1975).

The first, indubitable representatives of the Stromatoporoidea appeared in the Middle Ordovician (Chazy) of eastern North America (Galloway 1957; Kapp & Stearn 1975), and the group rapidly attained a wide distribution through Europe, Asia, North America and Australia. The position of the problematical, Early Cambrian stromatoporoids from the Altai Sayan fold belt of south west Siberia (Khalfina & Yavorsky 1967) remains in doubt (see later discussion p. 112). The Middle-Late Ordovician stromatoporoids accumulated in carbonates mainly in isolated occurrences, small clusters or bank-type deposits (biostromes). In a few places they are also reported as constituting a conspicuous component of patch reefs (bioherms), for instance, in the early Middle Ordovician Chazy Group of Vermont (Kapp 1975), in the late Middle Ordovician Mjøsa Limestone of Norway (Skjeseth 1963), and in the Late Ordovician (Richmond) of Anticosti Island (Bolton 1972; Copper, 1974). The Ordovician stromatoporoids merit close attention for a fuller understanding of the structure and development of the early members of the group.

In an attempt to maintain uniformity of usage throughout this review, I have followed North American practice of regarding the Whiterock, Chazy, 'Blackriver' and 'Trenton' as Middle Ordovician, and the Eden, Maysville and Richmond as Late Ordovician (see Fig. 8). Specimens illustrated in Figs 1-7 are from the following repositories: palaeontology collection of Sydney University (SUP), geology collection of the University of Tasmania (UTGD), Paleontologisk Museum, Oslo (PMO), and the Sedgwick Museum, Cambridge (SM).

SYSTEMATIC REVIEW

In general Ordovician stromatoporoid faunas tend to be less well preserved, and less diverse and abundant than their Middle Palaeozoic counterparts. Representatives of only three families have been confirmed as occurring in Ordovician strata (Webby 1969; Webby & Morris 1976) — the Labechiidae Nicholson 1879 being the largest and most varied family with its maximum development in the Middle-Late Ordovician, the Clathrodictyidae Kühn 1939, a relatively inconspicuous component of the Middle-Late Ordovician fauna, and the Cliefdenellidae Webby 1969, limited to a single, exclusively Ordovician genus.

(a) Family Labechiidae

The conception of the family adopted herein is similar to that given by Galloway (1957), Yavorsky (1962) and Stearn (1966) — it appears to be a natural grouping, and is not easily amenable to subdivision. The group could be enlarged to superfamily rank but is still not easily subdivisible. It constitutes the elements of 'Gruppe 1' of Flügel & Flügel-Kahler (1968). The family includes a wide range of forms characterized by imperforate, compact tissue, cyst-like to laminar plates, sometimes exhibiting denticles, sometimes pillars (occasionally both), and with very rare obscure occurrences of astrorhizae (Yabe & Sugiyama 1930; Nestor 1966b; 1976; Mori 1970).

Some workers (Kühn 1927; 1939; Lecompte 1956) have separated the cylindrical to branching forms from the rest of the group, placing them in the family Aulaceridae Kühn 1927. However others, such as Bogoyavlenskaya (1969; 1971) and Khalfina & Yavorsky (1973), regard the shape of the coenosteum as a feature of generic not family rank.

Bogoyavlenskaya (1969; 1974) has raised labechiids to the level of an order, and Khalfina & Yavorsky (1973) and Nestor (1974; 1976) to that of a superfamily. New family subdivisions have been added — Stromatoceriidae Bogoyavlenskaya 1969, Plumataliniidae Bogoyavlenskaya 1969, Rosenellidae Yavorsky *in* Khalfina & Yavorsky 1973, and Platiferostromatidae Khalfina & Yavorsky 1973 — but all seem to be unnatural divisions and should be rejected. Also, Khalfina & Yavorsky assign without comment the family Stromatoceriidae (genus *Stromatocerium* Hall) to stromatoporaceans rather than labechiaceans.

The erection of the family Lophiostromatidae Nestor 1966 (superfamily Lophiostromatacea Nestor 1974) seems to be another unnecessary subdivision of the labechiid group, introduced in order to accommodate those elements with more massive tissue (the genera *Lophiostroma* Nicholson 1891 and *Dermatostroma* Parks 1910).

Nestor (1974) proposed a four-fold subdivision of the superfamily Labechiacea — families Labechiidae, Stromatoceriidae, Aulaceridae and Plumataliniidae. In a subsequent paper, Nestor (1976) offered a different four-fold subdivision adding the Rosenellidae and subtracting the Stromatoceriidae. He radically changed the generic composition of the various families from his earlier subdivision. For example, the Aulaceridae which formerly included only the cylindrical forms (such as *Aulacera, Sinodictyon* and *Cryptophragmus*) was modified to include *Cystistroma* Etheridge and *Stromatocerium* Hall, and to exclude *Cryptophragmus* and *Sinodictyon* — to group together the cystose forms with 'hollow' pillars irrespective of their growth form. The 'hollow' pillars of *Stromatocerium,* as Kapp & Stearn (1975) have remarked, may form by diagenetic processes from solid ones, and therefore may have little or no taxonomic significance.

Khromych (1974a; 1974b) has given as the basis for subdividing the labechiids, the presence or absence of continuous pillars with an inverted cone-like structure, but has actually provided a most arbitrary and artificial subdivision of the group. Clathrodictyids are associated with forms like *Stromatocerium* (Stromatoceriidae) and *Cystostroma* (Cystostromatidae Khromych 1974a) in the same superfamily (Cystostromacea), and representatives of the family Labechiidae (restricted) are placed with members of the family Actinostromatidae in the superfamily Labechiacea. *Stromatocerium* which has close ties to *Labechia* and *Labechiella* (differing chiefly in having angular to blade-like instead of round pillars) is thus grouped in a separate superfamily from *Labechia* and *Labechiella* — placed in the superfamily Cystostromacea (and associated with *Clathrodictyon*). This is as extreme and as unacceptable as Khalfina & Yavorsky's (1973) grouping of *Stromatocerium* in the superfamily Stromatoporacea.

Kaźmierczak (1971) has employed a two-fold morphological grouping with subdivisions (lineages) based on inferred evolutionary trends. Morphological group

A, lineages I-IV, contain many common labechiid genera, but the individual lineage subdivisions fall well short of acceptable natural groupings. The worst example is the association of the morphologically distinctive, non-labechiid *Cliefdenella* Webby with the labechiid *Forolinia* Nestor in lineage IV.

The Ordovician representatives of the family Labechiidae exhibit a wide variety of growth form. As Parks (1910) noted, they range from 'delicate incrustations of *Dermatostroma papillatum*' to giant cylindrical columns of *Aulacera* like those found on Anticosti Island up to 5 metres long and 350 mm in diameter (Galloway & St. Jean 1961, p. 26). They occur, however, more commonly in hemispherical to sheet-like masses — for example, the hemispherical masses of *Cystistroma donnellii* Etheridge from the Cliefden Caves Limestone of New South Wales attain dimensions of 280 mm across and 200 mm in height (Webby 1969), and *Labechia huronensis* (Billings) from the Late Ordovician of Ontario, Indiana and Ohio has a size of up to 270 mm across and 120 mm in height (Galloway & St. Jean 1961). Some masses of *Cystostroma* such as *C. fritzae* Galloway & St. Jean from the Late Ordovician of Ontario attain larger dimensions — 600 mm across and 250 mm in height. Kapp (1974; 1975) reported the occurrence of a still larger conical to columnar coenosteum of *Pseudostylodictyon lamottense* (Seely), more than 1 metre in width and height from the Chazy Group of eastern North America.

(i) *Cystostroma* Galloway & St. Jean *in* Galloway 1957 — Kapp & Stearn (1975) questioned the validity of the genus *Cystostroma* based on the type species *C. vermontense* Galloway & St. Jean from the Crown Point Formation (Chazyan) on Isle La Motte. In a survey of some 400 specimens from the type area, the morphology of *C. vermontense* was only found at the bases of coenostea of *Labechia prima* Kapp & Stearn and some other species. However in the type material re-examined by Kapp & Stearn only the vesicular *Cystostroma* cyst-type structure is preserved.

The problem of intergrowths of two distinct morphologies in one coenosteum is highlighted by another example from the Late Ordovician of the Kolyma Basin, north-eastern U.S.S.R. Identified by Yavorsky (1961) as an intergrowth of *Labechia mirabilis* Yavorsky and *Cystostroma rarum* Yavorsky this labechiid exhibits alternating phases of growth with cysts only, giving a *Cystostroma* morphology, and with both cysts and pillars producing a *Labechia*-type structure. In another example of an undescribed species from the lower part of the Gordon Limestone Subgroup near Mole Creek, Tasmania, the bands of cysts alternate with sediment layers (less commonly diagenetic silt). Some individual coenostea (Fig. 2E-F) show little trace of pillars, while others exhibit, in varying stages of preservation, solid pillars or 'walless rods' (Kapp & Stearn 1975). It is therefore assigned to *Labechia*.

Many of the designated species of *Cystostroma* exhibit denticles, and some even show impersistent pillars, of the type formed by superposition of denticles through more than one cyst. The problem is where to draw the line between forms with denticles only and forms with impersistent pillars. The type species *C. vermontense* (based on the type material) and *C. cliefdenense* Webby seem to lack all traces of pillars, whereas Nestor's (1964) *C. estoniense* is recorded as having rare, short, 'hollow' pillars, and *C. concinnum* Ivanov *in* Ivanov & Myagkova from the Late Ordovician of the Urals (Bogoyavlenskaya 1973) also has occasional slender, tubule-like pillars. Nestor (1976), who includes forms with impersistent pillars in his conception of the genus, has listed some thirteen species from the Middle-Late Ordovician.

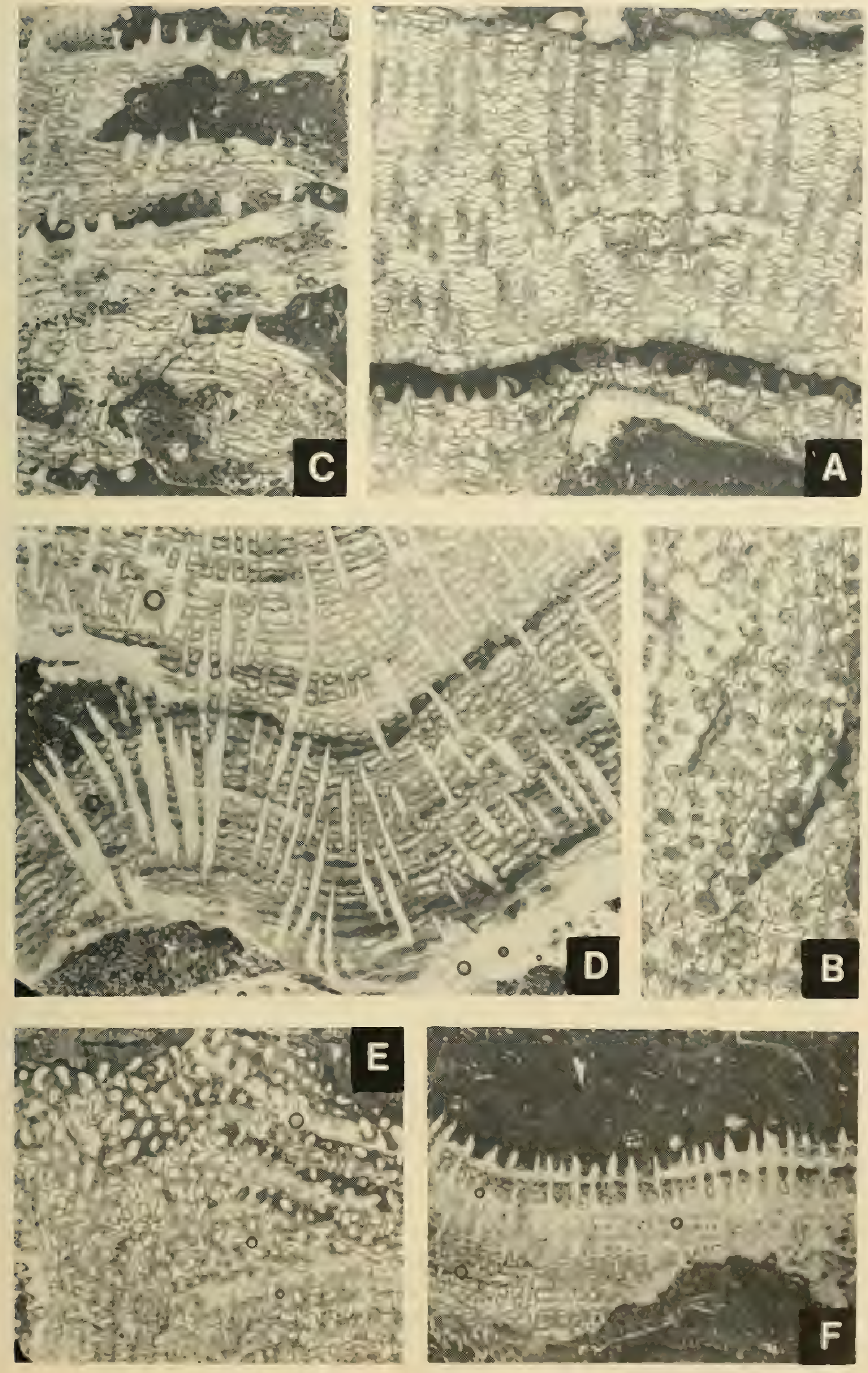
Little has been written on the ontogeny of species as a basis for determining stromatoporoid ancestry and phylogeny (see Galloway 1957). The basal row of cysts or laminae of the coenosteum (and the basal rows of successive latilaminae) may provide some clues to the early developmental stages of a particular line. In this context, Kapp & Stearn's (1975) observation that the structure of *C. vermontense* is only preserved in the bases of coenostea of *Labechia prima* and other species may be significant in supporting arguments that *Cystostroma* is the 'ancestral' stock. The base of the coenosteum of *Labechia* cf. *L. pustulosa* (Safford) — see Kapp & Stearn (1975, pl. 4, fig. 3) — and the base of a latilamina of *L. aldonesis* Webby (1977, pl. 1d) similarly exhibit a *Cystostroma*-type structure.

(ii) *Pseudostylodictyon* Ozaki 1938 — The type species, *P. poshanense* Ozaki 1938, following the definitions of cysts and laminae given by Kapp & Stearn (1975,p. 167), exhibits both cysts and laminae, but in some parts of the coenosteum it is difficult to distinguish between them. The laminae seemingly form parallel to the growth surface of the coenosteum, and represent successive depositional floors. The cysts, both large and small, fill interspaces between successive depositional floors in two main areas, on the slopes of the mamelons and in the troughs between the mamelons. Denticles may be present or absent. The problem of whether the laminae are original, laterally continuous, plate-like structures, or formed secondarily by the destruction of inclined-vertical side walls of long-low cysts in certain rows during diagenesis or recrystallization, is unresolved. At least in *P. inequale* Webby (1969, pl. 119, figs 1-3) its laterally continuous concentric plates appear to represent original primary laminae (Fig. 3F).

Kapp & Stearn (1975) have expressed inconsistent statements bearing on the early stages of stromatoporoid evolution. On the one hand (p. 169) they claim that *Labechia eatoni* (Seely) with its rows of similar-sized long-low cysts arose from *Pseudostylodictyon lamottense* (Seely) with its pattern of predominant laminae, and on the other (p. 167), they maintain that 'primitive' species have large, strongly convex cysts of variable size and shape, while more advanced forms have smaller, more uniform long-low cysts, implying a more probable derivation of the Chazy *Labechia* from a vesicular *Cystostroma*-like ancestor. If *Pseudostylodictyon* is indeed ancestral to *Labechia,* why do not the bases of coenostea of *Labechia* exhibit a 'laminar' *Pseudostylodictyon* structure?

Plumatalinia Nestor 1960 has been distinguished from *Pseudostylodictyon* by having a fine subreticulate tissue in the mamelon columns (Nestor 1964). However, it remains uncertain as to whether this tissue is of primary or secondary origin. If the latter, then the original vesicular plates of the mamelon columns have broken down into a secondary subreticulate tissue; and hence the genus should be regarded as a synonym of *Pseudostylodictyon.* In an opposed view, Bogoyavlenskaya (1969) has argued that *Plumatalinia,* because of its morphology of vesicular plates resembling laminae, and reticulate column network, could well be the ancestor of 'laminar' stromatoporoids, for instance the clathrodictyids. She introduced the family Plumataliniidae to accommodate this genus.

Fig. 1. A-B, *Labechia conferta* (Lonsdale 1839), × 5, SUP 285 from the Silurian of Dudley, England. A, vertical section showing solid pillars protruding upward into the sediment. B, tangential section. C-F, *Stromatocerium* sp. nov., × 5; from the lower part of the Gordon Limestone Subgroup (Middle Ordovician) of Tasmania. C, vertical section of UTGD 94642 from the Cashions Creek Limestone of the Florentine Valley showing peripheral part of latilaminate coenosteum. D, vertical section of UTGD 94639 exhibiting diagenetically altered, sparry calcite-filled pillars. E, tangential section of UTGD 94640. F, vertical section of UTGD 94641 showing sparry calcite-filled (replaced) pillars protruding into the overlying sediment. D-F, from the lower part of section on the south-west side of Sassafras Creek in the Mole Creek area.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(iii) *Labechia* Milne-Edwards & Haime 1851 — The internal structure of *Labechia* based on the type species *L. conferta* (Lonsdale) from the Middle Silurian of England has been fully investigated by Nicholson & Murie (1878) and Nicholson (1879), and shown to be composed of a large number of stout, vertically aligned pillars with a series of lenticular, upwardly convex vesicles filling the interspaces (Fig. 1A-B). The pillars, Nicholson (1879; 1886a) noted, protrude onto the upper surface of the coenosteum as solid tubercles (papillae), but may show axial canals elsewhere. Because of the irregular arrangement of the vesicles (Nicholson 1886a), the coenosteum exhibits little tendency to split concentrically as in typical stromatoporoids with 'concentric laminae'. Lecompte (1956), Galloway (1957), Galloway & St. Jean (1961), Yavorsky (1962), Nestor (1966b) and Mori (1970) offered a similar generic conception to that given by Nicholson, emphasizing the long, stout, round pillars, vesicular cyst plates and compact microstructure. The pillars may have an upwardly-directed cone-in-cone appearance, zigzag-shaped outer edges and axial canals as seen in vertical section, and concentric banding with lighter, apparently hollow centres (intersected axial canals) as seen in tangential section (Stearn 1966; Nestor 1966b). In fact the axial canals are not strictly hollow but have an infilling of sparry calcite.

Only a few Ordovician species, like *Labechia huronensis* from the Late Ordovician of Canada (Galloway & St. Jean 1961), bear close morphological similarity to the type species, *L. conferta*. Other forms, with only a patchy development of pillars, and with more consistency in the regularity of horizontal cyst rows than in the continuity of vertical pillars, have been included in the genus; see, for example, *Labechia eatoni* (Seely 1904), *L. prima*, Kapp & Stearn 1975 and *L. aldonensis* Webby 1977. In the group including these species (*L. prima* group), the coenosteum has an overall appearance of more conspicuous horizontal elements than vertical (Figs 2D; 3C-D), in contrast to those closely allied to the type species (*L. conferta* group) with the continuity of strong, vertical pillars as the dominating feature of their coenostea (Fig. 1A-B). The *L. prima* group is well developed in the Middle-Late Ordovician, from the middle Chazyan onwards, and probably represents an early stage in the evolutionary development of *Labechia*.

Stearn (1966) noted that the cysts of virtually all labechiids appear to be without pores except in the genus *Forolinia* Nestor 1964. He suggested that if the supposed foramina in the cysts of this genus are leached or recrystallized pillars then the genus would be difficult to distinguish from *Labechia*. Kapp & Stearn (1974) have added that if the 'canals' of Nestor (1964) are interpreted as altered pillars, then *Forolinia* should be regarded as a synonym of *Labechia*.

(iv) *Labechiella* Yabe & Sugiyama 1930, *Labechiellata* Sugiyama 1940 and *Tuvaechia* Bogoyavlenskaya 1971 — Yabe & Sugiyama (1930) introduced *Labechiella* as a subgenus of *Labechia* but misinterpreted the flattened cyst plates

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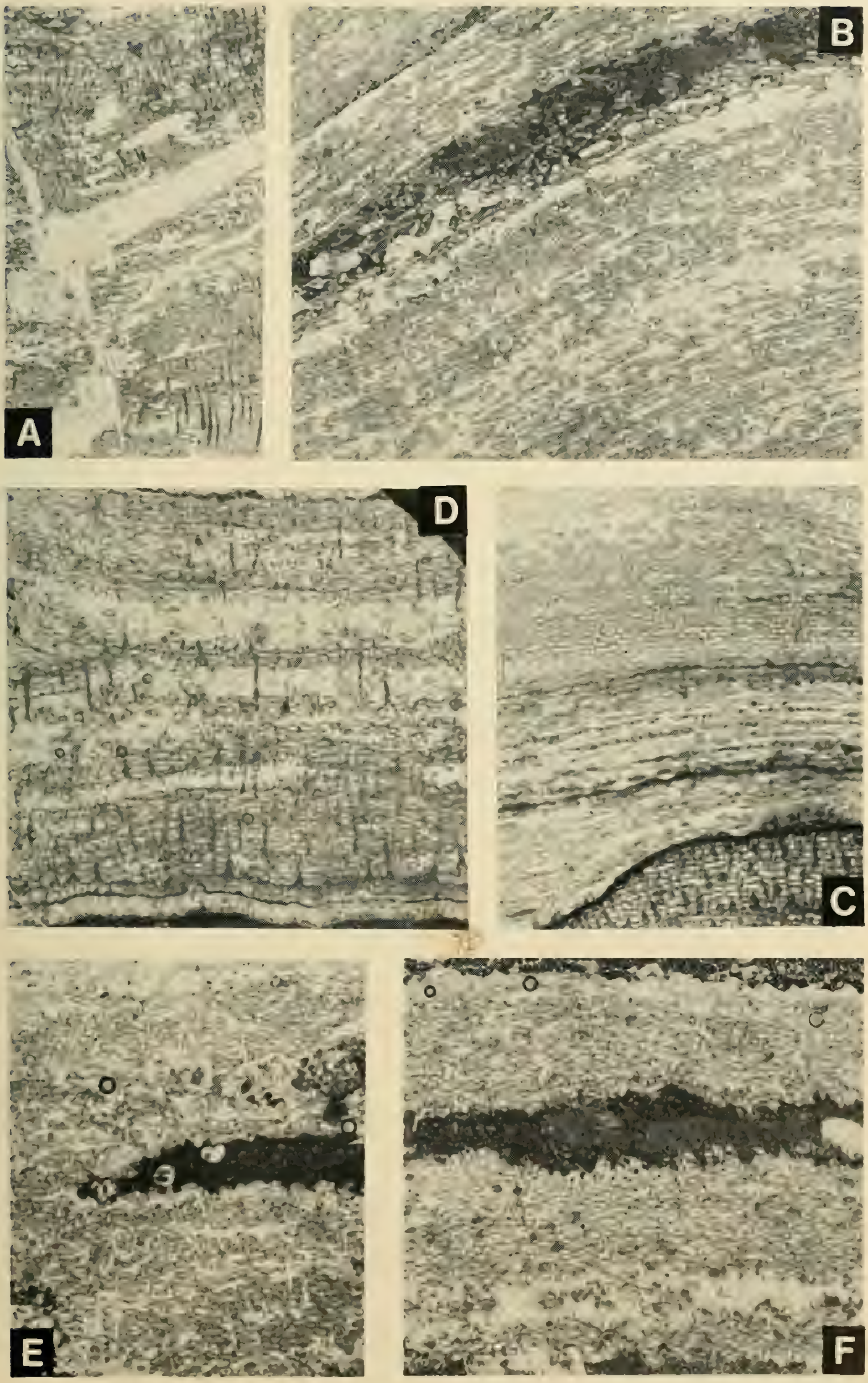
Fig. 2. A-B, *Stratodictyon* sp. nov., from the lower part of the Gordon Limestone Subgroup on south-west side of Sassafras Creek, Mole Creek area, Tasmania. A, vertical section of UTGD 94643 showing pillars. Note coenosteum is cut by large calcite vein. B, vertical section of UTGD 94644 with banding seemingly partially due to replacement of rows of long-low cysts. Sparry calcite fills the diagenetically altered areas — the scattered former pillars (now 'walless rods') and the rows of cysts (in part resembling laminae). C, association of holotype of *Stratodictyon ozakii* Webby 1969 on *Labechiella regularis* (Yabe & Sugiyama 1930); SUP 26252, × 5, from lower part of Cliefden Caves Limestone at Licking Hole Creek, central western New South Wales. D, vertical section of *Labechia* of the *L. prima* type from the lower part of the Gordon Limestone Subgroup, south-west side of Sassafras Creek, Mole Creek area, Tasmania; UTGD 94645, × 5. E-F, *Labechia* sp. A, × 5, latilaminate coenostea from lower part of the Gordon Limestone Subgroup in cliff section on north side of Sassafras Creek, Mole Creek area. E, vertical section of UTGD 94646 showing a few traces of former pillars — now 'walless rods'. F, vertical section of UTGD 94647, which in contrast lacks all traces of pillars.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(laminae) of the type species *Labechia serotina* Nicholson from the Middle Devonian of England as rod-like horizontal elements. The rounded pillars of *L. serotina,* as seen in tangential section, characteristically unite into chain-like groups (Galloway, 1957).

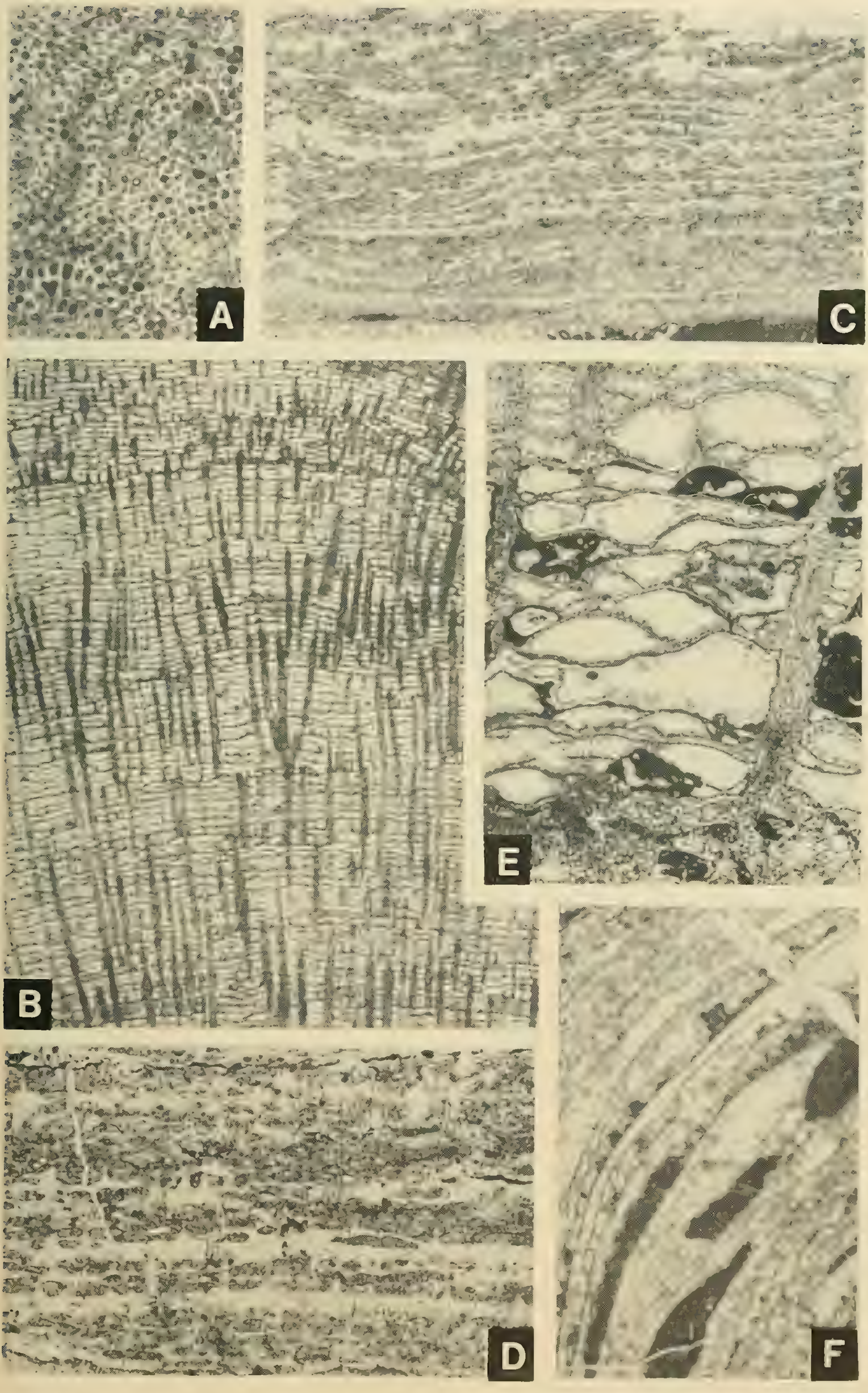
Following the introduction of *Labechiella* Sugiyama (type species *Labechiella regularis* Sugiyama 1939 from the Silurian of Japan) in 1939, Sugiyama appears to have realized his error of using a preoccupied name, for in the errata column of his 1940 paper he substituted the new name *Labechiellata* Sugiyama 1940. In his next paper Sugiyama (1941) again referred to *Labechiellata.* The type species of *Labechiella* Yabe & Sugiyama 1930 and the type species of *Labechiellata* Sugiyama 1940 are closely similar except for the spacing of pillars; in *Labechiella serotina* they are close spaced and tend to form chain-like links as seen in tangential section, while in *Labechiellata regularis,* the vertical rod-like pillars are widely spaced. Galloway (1957) has argued that Sugiyama (1939; 1940) incorrectly claimed credit for erecting the genus *Labechiella* based on *L. regularis* Sugiyama, and that the introduction of the name *Labechiellata* Sugiyama 1941 (*sic*) could only be explained by a memory lapse on Sugiyama's part. However, as outlined above, Sugiyama's actions seem to be more readily explained in terms of his recognition of the error and substitution of the new name *Labechiellata.*

Bogoyavlenskaya (1971) has added the new genus *Tuvaechia* (type species *Labechia regularis* Yabe & Sugiyama 1930, *non Labechiella regularis* Sugiyama 1939). Nestor (1976) in discussing the relationships between *Tuvaechia* and *Labechia* pointed out the lack of clear-cut distinctions between the shape of the vesicles, the spacing of the pillars and the stratigraphical distribution of the two forms. The differentiation between *Tuvaechia* and *Labechiella* is even more difficult. *Tuvaechia,* like *Labechiellata* is distinguished from *Labechiella* only by the wider spacing of the pillars. Like *Labechiellata* it should be regarded as a junior synonym of *Labechiella. Labechiella regularis* Sugiyama 1939 thus becomes a subjective junior synonym of *Labechiella regularis* (Yabe & Sugiyama 1930) and must be renamed; I propose *Labechiella sugiyamai* sp. nov.

Whether *Labechiella* (Fig. 3A-B) was derived from a *Labechia* by flattening of cyst plates to form laminae or from a *Pseudostylodictyon* by superposition of the denticles to form strong continuous pillars remains in doubt. Galloway (1957, p. 393) claimed a derivation of *Labechiella* from *Labechia.* The developmental trend proposed by Bogoyavlenskaya (1971) involving evolution first of *Labechia* from *Tuvaechia* (= *Labechiella*), and second of *Labechiella* from a *Labechia,* does not seem to accord with present known facts about morphological relationships and stratigraphic distribution (see Nestor 1976, p. 37).

(v) *Stratodictyon* Webby 1969 — The conception of *Stratodictyon* is here

Fig. 3. A-B, *Labechiella regularis* (Yabe & Sugiyama 1930) from the lower part of the Cliefden Caves Limestone, central western New South Wales; × 5. A, tangential section of SUP 26240 from west of Boonderoo shearing shed. B, vertical section of SUP 26236 from Licking Hole Creek. Note well developed primary laminae. C, *Labechia* sp. B; vertical section of PMO 97117 from Mjøsa Limestone south of Bergvika, Norway, showing diagenetically produced, 'secondary' laminae; × 5. D, *Labechia aldonensis* Webby 1977; vertical section of paratype SM.A97446 from Stinchar Limestone near Girvan, Scotland, exhibiting incipient, diagenetically formed, secondary laminae; × 5. E, *Cystistroma donnellii* Etheridge 1895; vertical section of assumed topotype SUP 28246 from lower part of Cliefden Caves Limestone at Fossil Hill, central western New South Wales, × 4. Note small denticles on upper surfaces of cysts. F, *Pseudostylodictyon inequale* Webby 1969; vertical section of paratype SUP 29134 from Clearview Limestone Member of Ballingoole Limestone (Bowan Park Group), Malachi's Hill, central western New South Wales; × 10. Note the presence of both cysts and primary laminae.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restricted to include only those fine textured, latilaminate forms with horizontal elements composed of regular, close-spaced rows of long-low cysts resembling incipient laminae, vertical elements consisting of denticles and small, discontinuous pillars occupying some areas of the coenosteum but not others, and seemingly lacking astrorhizae (cf. Webby 1969). The notion of Galloway (1957, p. 364) and Kapp & Stearn (1975, p. 167) that 'primitive species have cysts which are large, strongly convex, and variable in shape and size' and that more advanced forms have smaller cysts with a higher length/height ratio and more uniform character may be used to imply that *Stratodictyon* — the type species *S. ozakii* Webby (Fig. 2C), and *S. columnare* Webby, from the Cliefden Caves Limestone of New South Wales, an undescribed species from the Gordon Subgroup of Tasmania (Fig. 2A-B), and *S. valcourensis* (Kapp & Stearn) from the late Chazyan of eastern North America — is a more advanced form than the representatives of the *Labechia prima* group. In *L. prima* Kapp & Stearn, *L. eatoni* (Seely) and *L. aldonensis* Webby, the cysts are less regular in size and shape, and they are less conspicuously aligned in regular rows appearing as incipient laminae.

(vi) *Rosenella* Nicholson 1886a — This morphologically simple genus is typified by its exhibiting variably sized, usually large, cysts, with or without denticles (Nicholson 1886a; 1886b; Galloway 1957; Galloway & St. Jean 1961). *Rosenella* (Fig. 5D) may be distinguished from *Cystostroma* by having relatively much larger and more variably sized cysts, and from *Pseudostylodictyon* by lacking clearly defined laminae.

(vii) *Pachystylostroma* Nestor 1964 — As pointed out elsewhere (Webby 1979), the selection of the type species of *Pachystylostroma, P. ungerni* (Rosen) from the early Silurian of Estonia, seems to have been an unfortunate choice, for it lacks indubitable pillars (see Nestor 1962; 1964). Indeed, at the generic level, it is indistinguishable from a *Pseudostylodictyon,* and even bears a resemblance to the type species of that genus, *Pseudostylodictyon poshanense* Ozaki 1938. *Pachystylostroma fragosum* Nestor is the only Estonian Late Ordovician form referrred to the genus (Nestor 1964); and it also lacks pillars and would seem more correctly allied to *Pseudostylodictyon* or perhaps to *Rosenella.* It is to be hoped that pillars will eventually be found in *Pachystylostroma ungerni* to validate this now well-accepted genus, characterized by the presence of both cysts and laminae, as well as pillars and denticles (Nestor, 1964; Mori 1969; Kapp & Stearn 1975). Nestor's (1976) reference to the division of thick cyst walls into a 'basic plate' and a 'covering plate' as a diagnostic feature of *Pachystylostroma* seems totally unacceptable. The genus (Fig. 4B-F) differs from *Pseudostylodictyon* in having pillars, from *Labechia* in having laminae, from *Labechiella* in exhibiting both denticles and cysts, and from *Rosenella* in showing both pillars and laminae.

Nestor's (1976) tentative assignment of *Rosenella woyuensis* Ozaki 1938 to *Pachystylostroma* seems unjustified on the grounds that Ozaki's (1938) type specimens from China, and the New South Wales material of *R. woyuensis* (see Webby, 1969),

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Fig. 4. Pseudostylodictyon aff. *poshanense* Ozaki 1938; vertical section of SUP 26235 from the lower part of the Cliefden Caves Limestone west of Boonderoo shearing shed, central western New South Wales; × 5. B-C, *Pachystylostroma* sp. A from the Mjφsa Limestone north of Bergvika, Norway; PMO 97112; × 5. B transverse section. C, vertical section. D-F, *Pachystylostroma* sp. B, × 5. D, vertical section of UTGD 94649 from the middle part of the Gordon Limestone Subgroup just below the *Pliomerina* siltstones, Mole Creek, Tasmania. E, vertical-oblique section of UTGD 25374 from Gordon Limestone Subgroup at Gunns Plains. F, transverse section of UTGD 94648 from same horizon and locality as Fig. 4. D. G-H, new genus allied to *Stromatocerium* from Mjφsa Limestone south of Bergvika, Norway; PMO 97113, × 5. G, vertical section. H, tangential section.

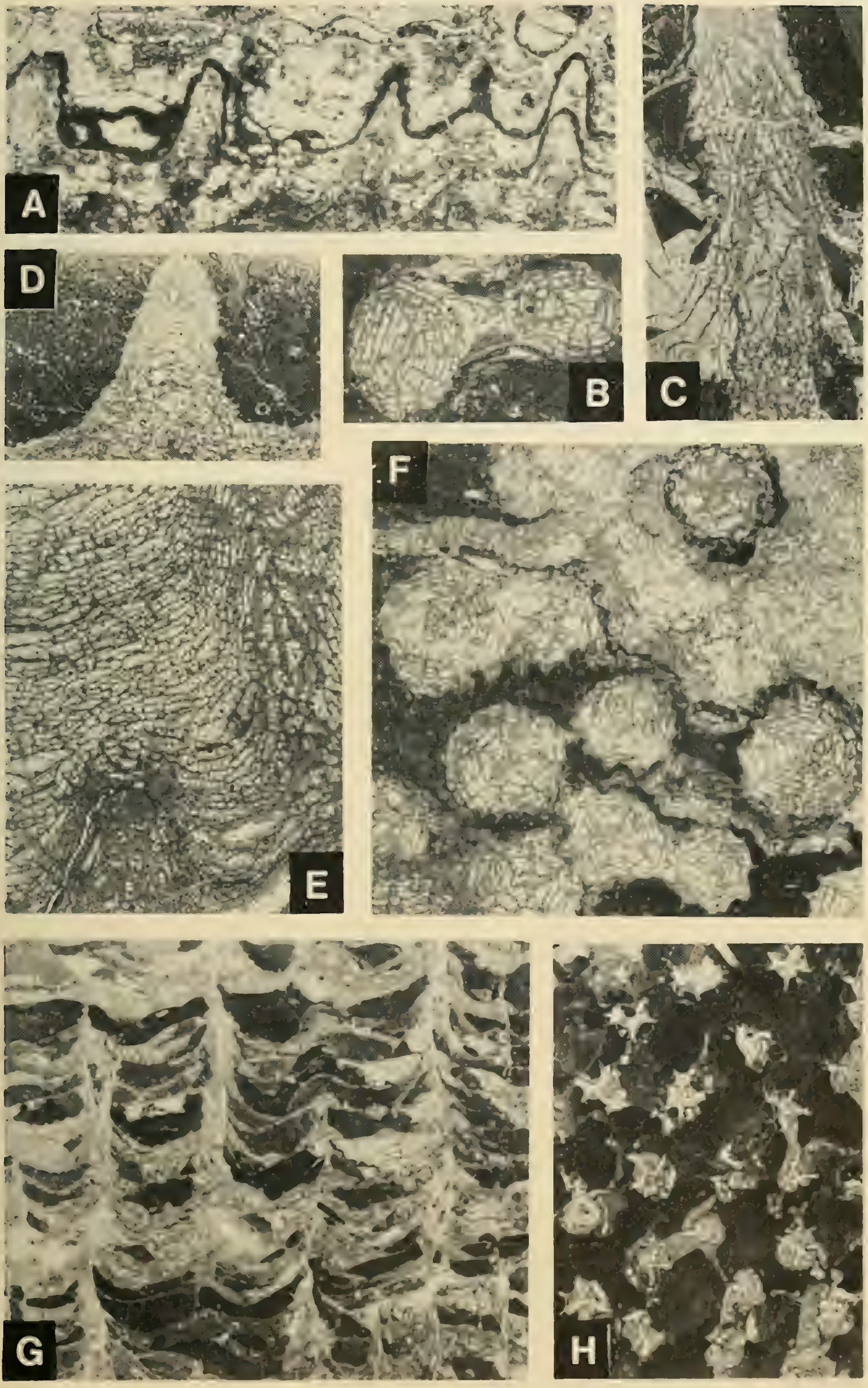
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exhibit large and small cysts (but no laminae) and denticles (but no true pillars). Occasional pillars are exhibited by *Rosenella amzassensis* Khalfina 1960a from the late Ordovician of Gornaya Shoriya and in material from the Moiero River of northern Siberia, both included by Nestor (1976) in his conception of *woyuensis*. It would seem preferable to group the Gornaya Shoriya and Moiero material in *amzassensis* and, despite the lack of well defined laminae, tentatively assign it to the genus *Pachystylostroma*. This species is not synonymous with *Rosenella woyuensis*.

(viii) *Stromatocerium* Hall 1847 — The genus resembles *Labechiella* but the pillars have angular, meandriform, stellate or flanged outlines, as seen in tangential section. The cyst plates are frequently but not always flattened into long-low cysts or laminae. Denticles are not present. Pillars of virtually all described species of *Stromatocerium* appear to be secondarily altered, possibly mainly by diagenetic leaching of the interiors of the pillars, and subsequent infilling by sparry calcite. Even the upwardly protruding tips of the pillars on the upper surfaces of the coenostea are replaced and filled with sparry calcite (Fig. 1C-F). Had the pillars been originally hollow as suggested by Nestor (1964; 1976) and Kaźmierczak (1971), they would not have been preserved as upwardly protruding tubercles in the sediment. To explain the formation of sparry calcite filled 'hollow pillars' or 'walless rods' requires a process of diagenetic alteration (Kapp & Stearn, 1975) probably involving selective subaerial leaching of solid pillars and subsequent infill with sparry calcite. It follows that the irregular to angular pillars of many forms may have been derived by secondary processes from large, solid, possibly originally rounded vertical elements of *Labechia* or *Labechiella* type, suggesting that *Stromatocerium* at best should be viewed as a form genus.

Nestor (1976) has recently recommended that the conception of the genus be restricted to representatives of the *S. rugosum* group, and that members of the *S. michiganense* group should be included in a separate genus. Pillars of the first type are 'hollow', wall-like, of variable cross-sectional shape, usually radiating from centres which may include associated mamelons (group A of Fig. 10). Pillars of the second type are thin, complexly bent and intermeshed vertical plates, not radiating outward from centres (group C of Fig. 10). A third group, the *S. canadense* group, were assigned by Nestor (1976) to the genus *Cystistroma* Etheridge 1895. Nestor's *S. canadense* group has at least one form exhibiting denticles and therefore strictly equatable with *Cystistroma* but there are others with 'hollow', rounded to angular pillars and no denticles which should be included in a separate group (group B of Fig. 10). A good example is the new species (Fig. 1C-F) presently under description from the lower part of the Gordon Subgroup in Tasmania (Webby, in press b).

In their classification of stromatoporoids, Khalfina & Yavorsky (1973) introduced the genus *Platiferostroma* to accommodate forms with *Stromatocerium*-like pillars and upwardly convex cysts (like the type species of *Labechia*). They assigned *Stromatocerium huronense* Billings, described by Parks (1910) from the Late Ordovician of North America, to the new genus. However, this species was subsequently revised by Galloway & St. Jean (1961) and assigned in part to *Labechia huronensis* (Billings) and in part to *Stromatocerium granulosum* (James). The former has round pillars and the latter does not have conspicuously arched cyst plates. The former should be retained in *Labechia* and the latter in *Stromatocerium*. The genus *Platiferostroma* (with its type species *Stromatocerium hydridium* Dong 1964) is thus best regarded as restricted to the lowest levels (Etreoungtian) of the Carboniferous.

(ix) *Cystistroma* Etheridge 1895 — Like *Stromatocerium* it typically exhibits a coarse-textured structure of large pillars and cysts, but the pillars have a rounded to irregular or serrated outline in tangential section, and tiny denticles occur on upper surfaces of cyst plates and in places on outer surfaces of the large pillars (Fig. 3E). It is likely that the large pillars of *Cystistroma* were derived from mamelon columns of a form like *Pseudostylodictyon poshanense* Ozaki (Fig. 4A), as outlined previously (Webby, 1969). There is little likelihood, owing to the markedly different order of magnitude of size difference between the pillars and denticles, of the pillars being derived by superposition of the denticles as in other labechiids such as *Labechia* and *Pachystylostroma* (Kapp & Stearn, 1975). *Stromatocerium canadense* Nicholson & Murie 1878 from the Middle Ordovician of eastern North America (and perhaps the Estonian counterparts including *S. sakuense* Nestor 1964) should be assigned to *Cystistroma*. North American specimens have denticles on the upper surface of cyst plates and 'short, spine-like flanges' on the pillars (Parkes, 1910; Galloway & St. Jean, 1961, p. 60).

(x) New genus allied to *Stromatocerium* — The distinctive *Stromatocerium*-like morphology with long, slender, 'composite' vane-like pillars and denticles (Fig. 4G-H) is currently being described as a new genus based on material from the Middle Ordovician Mjøsa limestone of Norway (Webby, in press, a). *Pachystylostroma* and the related *Stylostroma* Gorsky 1938 (also including forms previously assigned to *Pseudolabechia* Yabe & Sugiyama 1930 but now excluded because *Pseudolabechia* proved to be an actinostromatid not a labechiid — see Mori, 1969; 1970) both exhibit well developed, upwardly and outwardly radiating pillars within the mamelon columns (*Pachystylostroma* also has them in other parts of the coenosteum). In longitudinal section the pillars may be fused to form a vertically continuous, vane-like structure — see, for example, *Stylostroma gracile* (Yavorsky, 1957, pl. 19, figs 1-3) — while in tangential section they exhibit a stellate pattern of outwardly radiating pillars centred on the axis of the mamelon. The 'composite' vane-like pillars of the new genus appears to have been derived from former mamelon columns. To what extent these structures are primary, and to what extent they are modified by secondary diagenetic alteration processes is uncertain.

(xi) *Lophiostroma* Nicholson 1891 — Nicholson (1891), Kühn (1927; 1939), Lecompte (1956) and Yavorsky (1962) all assigned *Lophiostroma* to labechiids, but Galloway (1957) preferred a grouping with the actinostromatids on the basis of the thickened skeletal tissue and laminae inflected into columns and, more recently, Khalfina & Yavorsky (1973) classified *Lophiostroma* with the clathrodictyids. Nestor (1966b) and Mori (1970), excluded the genus from the labechiids, assigning it instead to the family Lophiostromatidae Nestor 1966b — more recently (Nestor 1974; 1976) to the superfamily Lophiostromatacea — on the grounds of it having undifferentiated skeletal tissue completely filling the interior of the coenosteum. The series of sharply undulating 'laminae' (possibly representing pauses of growth rather than true laminae) defines the positions of the conical pillar-like structures, seen as papillae on the upper surface of the coenosteum. The papillae in the type species of *Lophiostroma, L. schmidti* (Nicholson) from the Silurian of Gotland (Mori, 1970, pls 19-20), are remarkably similar in size and appearance to those of the type species of *Labechia, L. conferta* (Lonsdale) from the Silurian of England and Gotland. The only named Ordovician species closely resembling the type species is *Lophiostroma shantungensis* Yabe & Sugiyama 1930 from the Middle Ordovician of China. Its coenosteum is almost completely filled with poorly differentiated skeletal tissue, but there are traces of pillars with upwardly-directed cone-in-cone structure, and a few large, calcite-filled cysts. This species appears to be unquestionably a labechiid, possibly derived by massive thickening of its skeletal tissue from a *Labechiella*, or a

Labechia. Lophiostroma elandiense Khalfina 1960a from the Late Ordovician of the Altai region seems to represent a rather poorly preserved *Labechiella.*

(xii) *Dermatostroma* Parks 1910 — This problematical, thin, encrusting labechiid typically exhibits a papillose upper surface appearance like a *Labechia* or *Lophiostroma* (see illustration of *D. scabrum* in Galloway & St. Jean 1961, pl. 13, fig. 1), but has a less well defined internal structure. The genus seems to be restricted to the Middle-Late Ordovician horizons of North America (Parks 1910; Galloway & St. Jean 1961). The first group has a few laminae and pillars, the second, radially crystalline prisms (possibly representing much thickened pillars) and the third exhibits a structureless mass of calcite crystals. The first group may be allied to *Labechiella,* the second to *Lophiostroma* and the third is of uncertain affinities (but has a constant encrusting association on species of *Aulacera*). Nestor (1974; 1976) has included *Dermatostroma* in the family Lophiostromatidae (and superfamily Lophiostromatacea) thus separating it from other labechiids like *Labechiella.* In spite of its need for revision, this genus should continue to be associated with the labechiids.

(xiii) *Sinodictyon* Yabe & Sugiyama 1930 and *Ludictyon* Ozaki 1938 — Both forms come from the Middle Ordovician of China. *Sinodictyon* is a fasciculate to cylindrical form with large, denticled cysts axially, and rows of smaller, long-low cysts with denticles and pillars laterally. The morphology of the axial zone resembles *Rosenella,* and the lateral zone, a *Labechia* of the *L. prima-L. eatoni* type. Galloway (1957) included the genus *Ludictyon* Ozaki in synonymy with *Sinodictyon,* but *Ludictyon* has a more-or-less broadly cylindrical coenosteum with less well defined axial and lateral zones, a pattern of alternating large and small cysts in the axial zone, rows of smaller cysts laterally, and denticles in both axial and lateral zones (Ozaki 1938). It does not seem to be a convincing junior synonym of *Sinodictyon.* Apart from its broad columnar form, *Ludictyon* exhibits close morphological similarities with laminar-hemispherical *Rosenella,* and appears to represent an earlier stage in evolutionary development from a *Rosenella*-type ancestor than does *Sinodictyon.*

(xiv) *Cryptophragmus* Raymond 1914, *Thamnobeatricea* Raymond 1931 and *Cladophragmus* Raymond 1931 — These slender North American Middle Ordovician forms have been grouped together as representatives of a single genus, *Cryptophragmus* by Galloway (1957) and Galloway & St. Jean (1961), even though there are distinctive differences between them. As Raymond (1931) noted, *Cryptophragmus* is unbranched, *Thamnobeatricea* has lateral branching and *Cladophragmus* exhibits bifurcating branches. *Cryptophragmus* has an axial column with a narrow lateral zone, and an outer sheath with the structure of *Labechia* which is rarely seen in continuity with the axial column. It needs to be resolved whether *Cryptophragmus* represents the growth of one or more than one organism. *Cladophragmus,* on the other hand, has no lateral zone or sheath.

The relationships of these slender cylindrical genera (Fig. 5C) to laminar-

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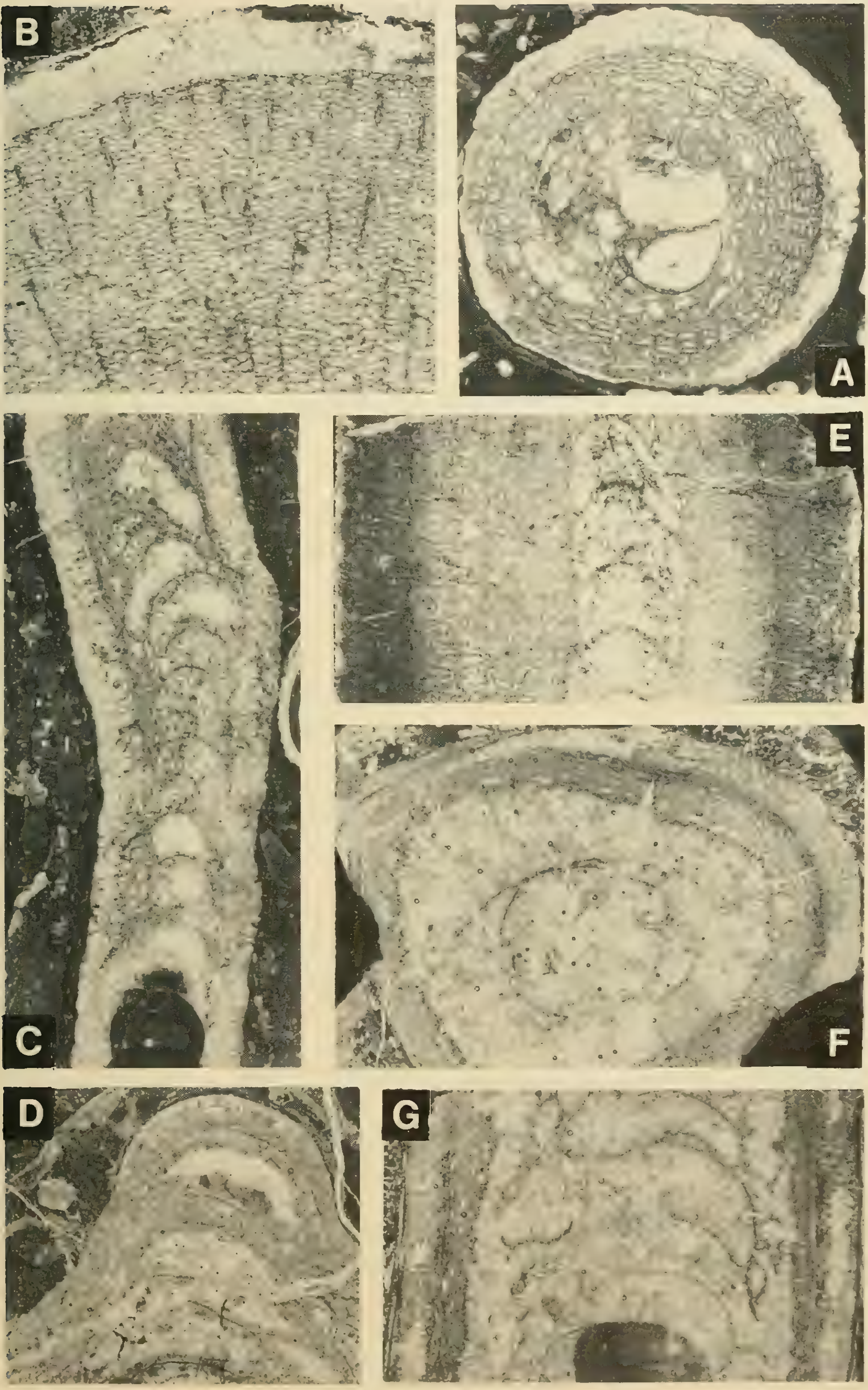
Fig. 5. A, *Alleynodictyon nicholsoni* Webby 1971 from the Gerybong Limestone Member, Daylesford Limestone (Bowan Park Group) at The Ranch, Bowan Park area, central western New South Wales; transverse section of holotype SUP 34170, × 4. B, *Aulacera* sp. A from the uppermost part of the Gordon Limestone Subgroup at The Den, Mole Creek area, Tasmania; transverse section of outer zone of large specimen, UTGD 94651, × 4. C, *Cryptophragmus*? sp. from the Lower Limestone Member of the Benjamin Limestone (Gordon Limestone Subgroup) in the Florentine Valley; vertical section of UTGD 94654, × 4. D, *Rosenella* sp. from the Gordon Limestone Subgroup at Ida Bay; vertical section of UTGD 94650, × 4, showing prominent mamelon-like upgrowth. E, *Aulacera* sp. B from the uppermost part of the Gordon Limestone Subgroup at The Den, Mole Creek area; vertical section of UTGD 94652, × 2. F-G, *Aulacera* sp. C from the upper part of the Gordon Limestone Subgroup at Gunns Plains; × 2. F, transverse section. G, vertical section.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hemispherical labechiids are not clearly established. They may have evolved from mamelon-like columns extending upwards off a laminar-hemispherical base, but such bases have not yet been found. They may have been derived from a strongly mammillated representative of *Cystostroma, Pseudostylodictyon* or *Rosenella* with its mamelons exhibiting large 'axial' cysts.

(xv) *Alleynodictyon* Webby 1971 — The genus (Fig. 5A) appears to be more closely related to *Cryptophragmus* and its allies than to *Sinodictyon* and *Ludictyon*. It differs from all other cylindrical labechiids by exhibiting blade-like pillars. Representatives of *Stromatocerium* and the *Stromatocerium*-like new genus with blade-like pillars provide a clue to the possible mode of derivation of the pillars of *Alleynodictyon*. In the new genus, the outwardly radiating, 'composite' vane-like pillar structure (Fig. 4 G-H) seems to have formed from the many upwardly and outwardly inclined, small pillars fusing in continuous vertical rows and linking axially. Each such 'composite' pillar seems to have been derived at the axis of a former, *Pachystylostroma*-like mamelon column by apparent coalescence of numerous small pillars (Fig. 4 B-F). *Alleynodictyon* (if the cylindrical branches are viewed as modified mamelon columns) have a differentiated coenosteum with a lateral zone and an axial column. The small pillars which are similarly formed by fusion into vertical rows are however confined to the lateral zone. They resemble septa in rugose corals.

(xvi) *Aulacera* Plummer 1843 (= *Beatricea* Billings 1857) — The coenosteum of *Aulacera* is unbranched, and it has a relatively wider lateral zone than in other cylindrical labechiids. The axial column is usually sharply differentiated from the lateral zone, and exhibits a series of large, superposed cysts; the lateral zone shows rows of imbricated, smaller cysts with pillars distributed, usually sporadically, in the outer part (Fig. 5B, E-G). Specimens of large dimensions have been recorded from the Late Ordovician of Anticosti Island (Twenhofel 1928). In places along the coast of Anticosti, they occur so thickly 'as to resemble piles of petrified logs'. They protrude like hollowed trunks 'suggesting small cannon projecting from a wall' (Twenhofel, 1927, p. 105) in a cliff face on Anticosti, appropriately named Battery Point. Mostly they lie in the plane of bedding, but occasionally a specimen is seen to be orientated in a vertical or upright (?growth) position. Attachment bases have not been positively confirmed.

Most workers (Schuchert 1919; Twenhofel 1927; Yavorsky 1955; 1957; Galloway & St. Jean 1961) have interpreted *Aulacera* as having had an erect life orientation, growing up vertically off an attachment base. However, Copper (1974, p. 379) has argued that *Aulacera* may have rolled around on the sea floor instead of growing vertically ! In preferring a vertical mode of growth, it should be emphasized that only a relatively small part of the total preserved length of the coenosteum (observed to a maximum of 5 m) — the apical growing area of Webby (1971) — may have projected above the sea floor at any one time, and upward growth may have kept pace with the adjoining sediment accumulation. However, a period of intense erosion and bodily transport of these giant columnar 'structures' would have been required to reorientate them into their final resting place, in the plane of bedding.

Aulacera, though apparently confined to the Richmond (Late Ordovician) of North America first appears in stratigraphically lower levels in Tasmania (possibly equatable with the Eden or Maysville), and possibly from still lower horizons in China — *Aulacera peichuangensis* Ozaki 1938 being recorded from the Middle Ordovician ('Blackriver' or 'Trenton') of China.

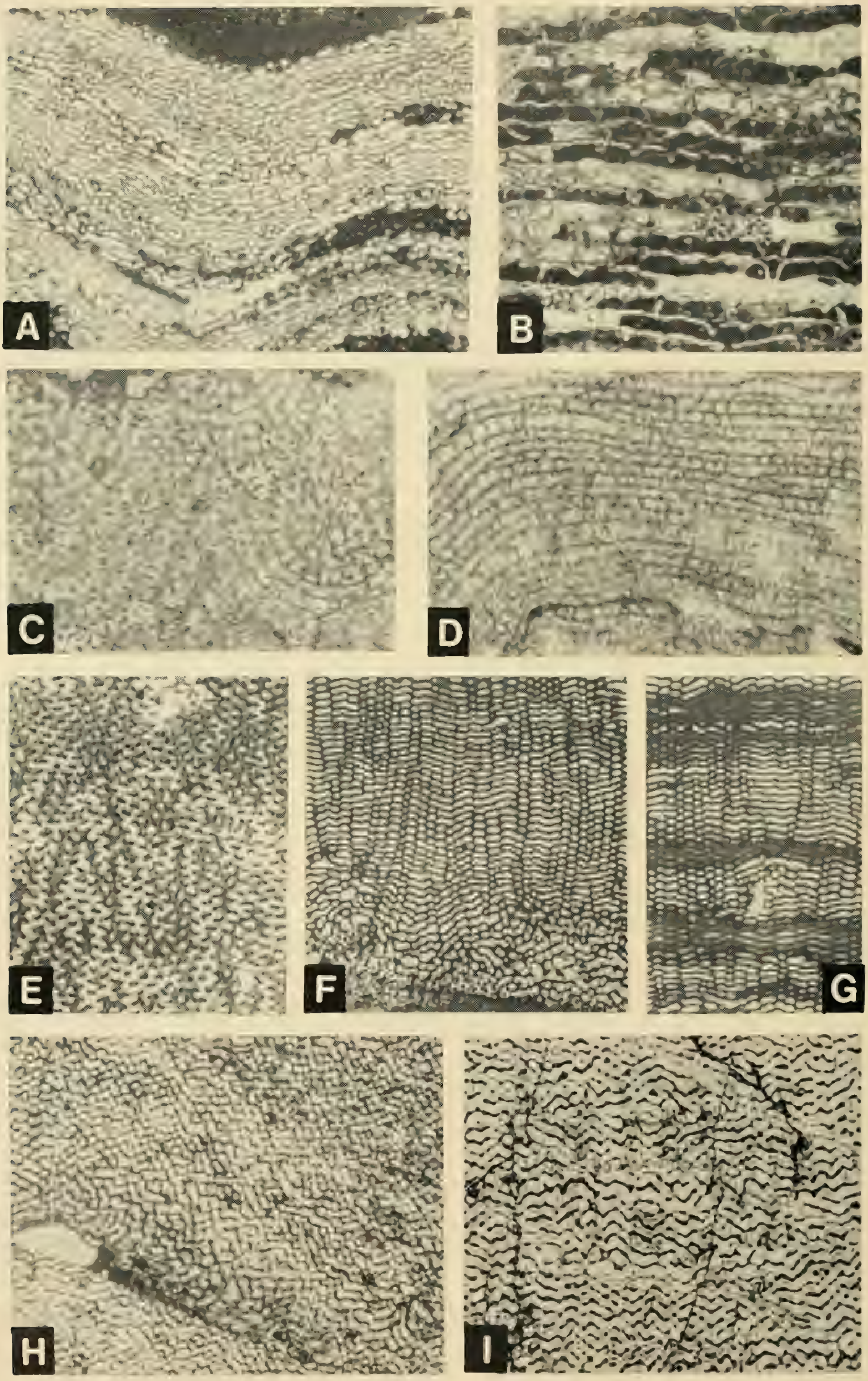
(b) *Family Clathrodictyidae*

Galloway (1957) in an outline of the phylogeny of Stromatoporoidea regarded the Labechiidae with their simple morphology and earliest appearance as ancestral directly or indirectly to all other stromatoporoid families. Galloway viewed the Clathrodictyidae as having evolved from a member of the labechiids in the Late Ordovician, the overlapping or imbricated cysts of labechiids being replaced by 'the side-by-side placing of the cysts' of clathrodictyids. A similar derivation of clathrodictyids ('laminar' stromatoporoids) from labechiids ('vesicular' stromatoporoids) through a succession of developmental stages from Late Ordovician to Early Silurian time is inferred by Nestor (1966a). He depicted a trend from a *Cystostroma*-like ancestor composed of imbricate, upbranched cyst plates, but not arranged in orderly rows, to *Clathrodictyon vormsiense* Riabinin from the Late Ordovician (Vormsi horizon) of Estonia with regular rows of long-low cyst plates, to more typical representatives of the genus, in the very topmost beds of the Ordovician (Porkuni horizon of Estonia) — forms such as *Clathrodictyon gregale* Nestor and *C. zonatum* Nestor with irregular laminae. Bogoyavlenskaya (1969) and Kaźmierczak (1971) have made similar suggestions regarding the derivation of 'laminar' stromatoporoids from *Cystostroma*. It is perhaps significant that both labechiids and clathrodictyids typically exhibit a microstructure of non-porous, speckled, compact tissue (Stearn 1966).

Neither Galloway, Nestor, Bogoyavlenskaya nor Kaźmierczak explained precisely how the pillars of *Clathrodictyon* were formed. Typically confined to a single interlaminar space (Stearn, 1966), the pillars are not as Galloway (1957) contended, strictly the downward continuations of the edges of the cysts, otherwise the intersected cyst walls would appear as circles or polygonal outlines in tangential sections (Khalfina & Yavorsky 1967). The funnel-like (or inverted cone-shaped) pillars of some species of *Clathrodictyon* (Stearn, 1966; Stearn & Hubert 1966) may reflect an origin of the pillars from intersections of downwardly-inflexed cyst plates. However, usually the pillars show little or no trace of associated downwardly-inflexed cyst tissue. If *Clathrodictyon* evolved from the labechiids then the 'labechiid-type' cyst walls must have broken down or failed to calcify. The regularity in the spacing of pillars may be explained by the pillars having been derived at points of intersection of former downwardly-inflexed cysts.

(i) *Clathrodictyon* Nicholson & Murie 1878 — Characteristically *Clathrodictyon* is a Silurian genus with a widespread and abundant distribution (Nestor 1964; 1966b; 1976; Birkhead 1967; Mori 1969; 1970; Bolshakova 1973). Its Late Ordovician record is more restricted but not confined to Estonia and Anticosti Island as previously indicated by Galloway (1957). Nestor (1964) described some five species from Estonia, and proposed two of them as name-bearers from his Late Ordovician stromatoporoid zones. Webby & Banks (1976) have recorded an additional four species from the Late Ordovician (probably about Late Caradoc in age) of Tasmania (Fig. 6 C-D). One Tasmanian species *C. idense* is notable among Ordovician forms for exhibiting dissepiments which link the pillars and subdivide the galleries. Species allied to the Estonian forms have also been reported by Webby (1969) from the Late Ordovician of New South Wales (Fig. 6A-B), and by Bogoyavlenskaya (1973) from the western Urals.

(ii) *Ecclimadictyon* Nestor 1964 — The genus has a similar distribution and stratigraphic range to that of *Clathrodictyon*. It is related to *Clathrodictyon* but differs in exhibiting zigzag-shaped laminae, and relatively less conspicuous pillars. Although not clearly developed in all species, the pillars are confined to interlaminar spaces and tend to be alternating, not superposed; they formed from downwardly inflected laminae seemingly also at intersections of 'cyst plates'. A distinctive orderly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meshwork is represented in tangential section by the pattern of distribution of the pillars and intersecting downwardly inflected chevron-shaped laminae.

Nestor (1974) has inferred a derivation of *Ecclimadictyon* either from *Clathrodictyon* or, less certainly, directly from *Cystostroma*. In the Estonian successions, the first clathrodictyids to make their appearance are *Clathrodictyon vormsiense* and *C. microundulatum* whereas in New South Wales *Ecclimadictyon nestori* (Fig. 6H) first appears stratigraphically well below the first representative of *Clathrodictyon* (see Webby & Morris 1976, fig. 1). It comes in, indeed it defines, the base of Fauna 2, at a stratigraphical level which is no later than Early Eastonian (= middle Caradoc, or late Middle Ordovician in terms of North American or Baltic successions).

Late Ordovician species of *Ecclimadictyon* include *E. porkuni* (Riabinin) and *E. koigiense* Nestor from Estonia (Nestor 1964), *E. geniculatum* Bogoyavlenskaya 1973 from the Urals, *E. amzassensis* (Khalfina) from south-west Siberia and New South Wales (Khalfina 1960a; Webby 1969), *E. nestori* Webby 1969, *E. cribratum* Webby & Morris 1976 from New South Wales, and *E. undatum* from Tasmania (Webby & Banks 1976). Both the Estonian species are from the uppermost (Porkuni horizon) part of the Ordovician, and differ from the others in exhibiting dissepiments. Two other species are especially distinctive — *E. amzassensis* exhibits overall vertical continuity in alignment of zigzag-shaped rows of pillars (Fig. 6E-G), and *E. cribratum* has patches of horizontal tissue with 'hexactinellid' rod-like radial processes (Fig. 6I).

(iii) *Plexodictyon* Nestor 1966b — Nestor (1966b), Stearn (1969) and Bogoyavlenskaya (1973) have regarded the genus *Plexodictyon* as restricted to Late Silurian strata. However, *P. ?cascum* Webby & Morris 1976 from the Late Ordovician of New South Wales (Fig. 7D), is a species with close morphological similarities to the late Silurian representatives of the genus, and suggests a much earlier derivation of *Plexodictyon* from *Ecclimadictyon* than previously thought. It may be significant that a *Plexodictyon*-like structure develops in mamelon-like upgrowths of the coenostea of some of the earliest known species of *Ecclimadictyon* and *Clathrodictyon* (see Webby & Banks, 1976, p. 131, pl. 2, fig. 5 and Webby & Morris 1976 p. 132, Fig. 5D).

(c) *Family Cliefdenellidae*

Webby (1969) and Webby & Morris (1976) have discussed relationships between Cliefdenellidae and other stromatoporoid groups. The family contains only the one genus, *Cliefdenella* Webby 1969. No other Ordovician stromatoporoid exhibits such a complex association of primary laminae with denticles on upper surfaces, dissepiments and a ramifying meshwork of horizontal astrorhizal canals filling interlaminar spaces,

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Fig. 6. Clathrodictyon cf. *microundulatum* Nestor 1964 from the Clearview Limestone Member of the Ballingoole Limestone (Bowan Park Group), near Malachi's Hill, central western New South Wales; vertical section of SUP 29133, × 5. B, *Clathrodictyon* aff. *mammillatum* (Schmidt 1858) from the Davy's Plains Limestone Member of the Daylesford Limestone (Bowan Park Group) at Quondong, central western New South Wales; vertical section of SUP 43173, × 10. C-D, *Clathrodictyon plicatum* Webby & Banks 1976 from the uppermost part of the Gordon Limestone Subgroup in Tasmania, × 10. C, tangential section of holotype UTGD 94626 from roadside locality leading to main quarry west of The Den, Mole Creek. D, vertical section of paratype UTGD 94629 from The Den. E-G, *Ecclimadictyon amzassensis* (Khalfina 1960a) from the upper part of the Cliefden Caves Limestone at The Island, Cliefden Caves, central western New South Wales, × 5. E-F, tangential and vertical sections of SUP 26206. G, vertical section of SUP 26207. H, *Ecclimadictyon nestori* Webby 1969 from the upper part of the Cliefden Caves Limestone at The Island; vertical section of paratype SUP 26200, × 10. I, *Ecclimadictyon cribratum* Webby & Morris 1976 from limestone breccia at the top of the Malongulli Formation, near Malongulli Trig., central New South Wales; vertical section of holotype SUP 78266, × 10.

and vertical astrorhizal columns with associated updomed laminae, astrorhizal canals and vertical spine-like elements (Fig. 7A-C). It resembles a *Plexodictyon*-type structure (Webby & Morris 1976) with the addition of the complex astrorhizal system and 'tube-like' pillars. The vertical elements of the coenosteum — the 'tube-like' pillars and the astrorhizal columns — seem to retain their independence as discrete units and never appear to exhibit interconnection one with the other. Origins of this group are obscure. *Cliefdenella* makes its first appearance in beds of Fauna 2 (about middle Eastonian or, in North America terms, 'Trenton') of the N.S.W. succession, only about 100 m stratigraphically above the first incoming of clathrodictyids (Webby & Morris, 1976). The genus is known through a stratigraphical range in N.S.W. from the middle Eastonian to early Bolindian (Faunas 2-3 of Webby 1969), and from the Late Ordovician of Salair in south-west Siberia (Khalfina & Yavorsky 1974).

STRATIGRAPHIC DISTRIBUTION

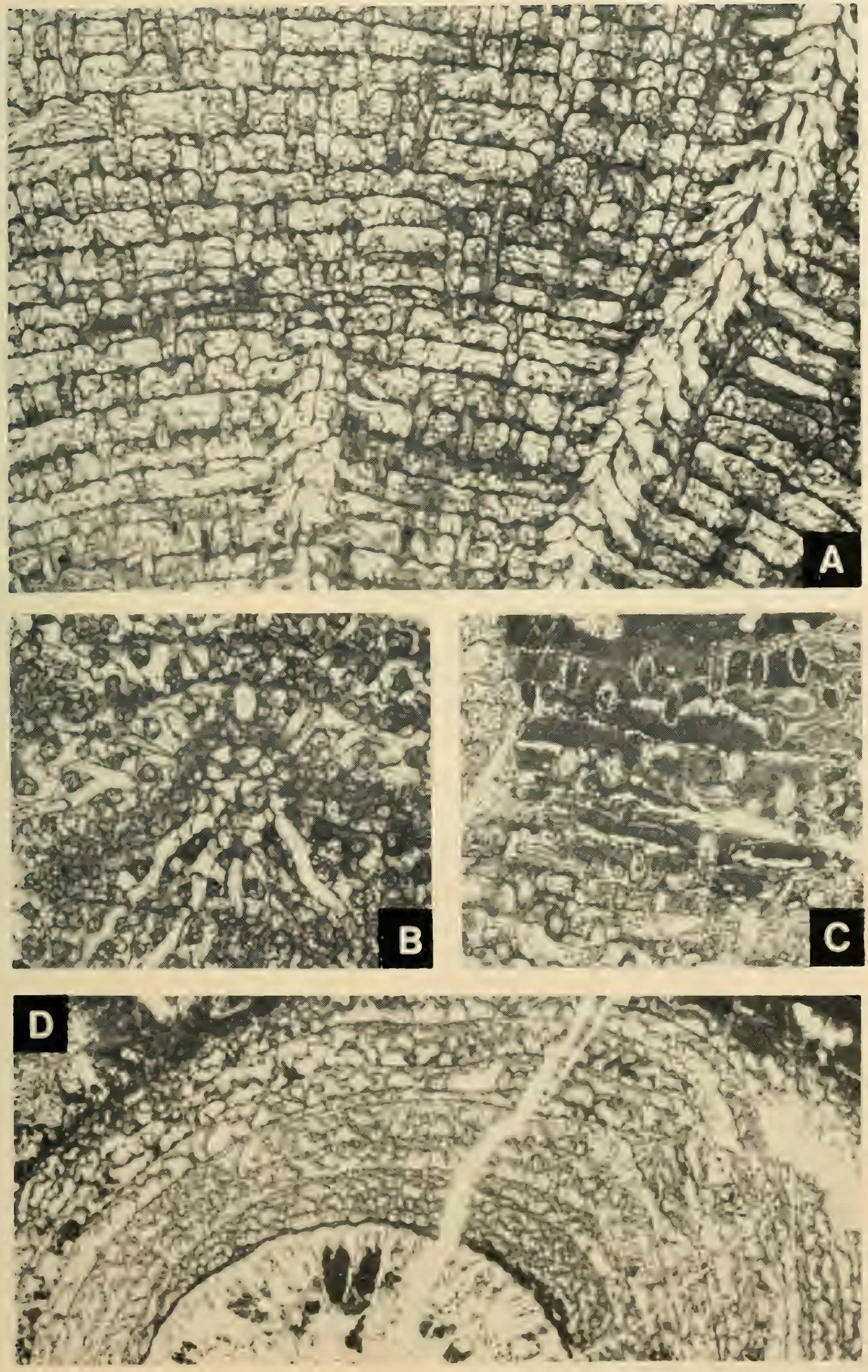
(a) *Australia*

(i) *New South Wales.*— Three biostratigraphically distinct coral and stromatoporoid faunas (Faunas 1, 2 and 3) have been recognized from the Late Ordovician (Gisbornian-Bolindian) limestone successions of central western New South Wales (Webby 1969; 1971; 1975). The labechiids, *Pseudostylodictyon* aff. *poshanense* Ozaki, *Stratodictyon ozakii* Webby, *S. columnare* Webby, *Rosenella woyuensis* Ozaki, *Labechiella regularis* (Yabe & Sugiyama), *Cystistroma donnellii* Etheridge and *Alleynodictyon nicholsoni* Webby appear in Fauna 1 (Fig. 8), of probable late Gisbornian age. In terms of the North American sequence, this level would be roughly equivalent to a late Porterfield? or early Wilderness age (i.e., in the older nomenclature, a 'Blackriver' age). This is the oldest stromatoporoid fauna known from New South Wales; and it already exhibits considerable diversity from the basic labechiid stock.

The first appearance of clathrodictyids defines the base of Fauna 2, in sequence some 94 m above the top of the lower, thinly bedded member of the Cliefden Caves Limestone (Webby & Morris, 1976). On the basis of present correlations, these clathrodictyids (*Ecclimadictyon nestori* Webby and *Plexodictyon* ? sp.) probably first appeared about the beginning of the Eastonian and the first cliefdenellids in the middle Eastonian. The stratigraphic distribution of the Ordovician clathrodictyid and cliefdenellid stromatoporoids was shown in fig. 1 of Webby & Morris (1976). The labechiid component of Fauna 2 includes *Cystostroma cliefdenense* Webby, *Pseudostylodictyon inequale* Webby and *Labechiella variabilis* (Yabe & Sugiyama). *Cystostroma cliefdenense* seems to be in no way closely linked or related to the first clathrodictyids. Indeed the clathrodictyids actually appear stratigraphically below the first occurrences of *C. cliefdenense*. In terms of North American successions, Fauna 2 would equate with the 'Trenton' (Fig. 8), or in the revised terminology of Sweet & Bergström (1976), the Rocklandian-Shermanian.

Fauna 3 spans an interval from the late Eastonian to the early Bolindian, broadly equivalent to the Eden-Maysville interval of North America (Fig. 8). The

Fig. 7. A-C, *Cliefdenella etheridgei* Webby 1969 from the upper part of the Cliefden Caves Limestone, The Island, Cliefden Caves area, central western New South Wales; × 5. A, vertical section of holotype SUP 24157. B, tangential section of paratype SUP 24154. C, oblique-vertical section of paratype SUP 24156. D, *Plexodictyon? cascum* Webby & Morris 1976 from the Clearview Limestone Member of the Ballingoole Limestone (Bowan Park Group) of central western New South Wales; vertical section of paratype SUP 77277, × 7.7. Note the association with the rugosan *Palaeophyllum patulum* McLean & Webby 1976.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stromatoporoids occur mainly in the upper part of the respective limestone successions at Bowan Park and elsewhere, and may represent a mainly 'early Bolindian' fauna. They include cliefdenellids, clathrodictyids (including *Plexodictyon? cascum*) and the labechiid, *Pseudostylodictyon inequale*. No stromatoporoids have been found in higher Ordovician horizons of New South Wales.

(ii) *Tasmania.* — Carbonates of the Gordon Subgroup accumulated through much of Ordovician time on the Tasmanian Shelf (Banks, 1962; Webby 1976; 1978). Only the clathrodictyid stromatoporoids from the upper part and labechiids from the lowest part of the sequence have so far been studied in detail (Webby & Banks, 1976; Webby, in press b). The bulk of the fauna consists of labechiids (no cliefdenellids are known), and comprises a very diverse and abundant component of the total biota. Corbett & Banks (1973) have outlined the general faunal and floral succession in the Gordon Subgroup of the Florentine Valley area as consisting of some eight stratigraphically distinct 'faunas', probably ranging from about Castlemainian (late Arenig) to early Bolindian. The first three 'faunas' lack stromatoporoids but the fourth contains *Stromatocerium* in an assemblage with *Maclurites* and *Girvanella*. It occurs in the Cashions Creek Limestone of probable Darriwilian age — approximately equivalent to middle-late Chazy of North America. The stromatoporoid faunas from this horizon to the top of the subgroup (from the fourth to eighth 'faunas' inclusive) are more complete and better preserved in the Mole Creek section than in the Florentine Valley.

The first stromatoporoids to appear in the basal part of the Gordon Subgroup of the Mole Creek area are *Stromatocerium, Stratodictyon* and *Labechia* (Figs 1D-F; 2A-B, D). Stratigraphically higher, in the *'Lichenaria'* beds, exposed in the cliffs above Sassafras Creek, *Labechia* (Fig. 2E-F) is exposed in latilaminate, dome to sheet-like 'colonies' up to 550 mm across and 220 mm in height. *Rosenella* and a branching cylindrical form, possibly *Cryptophragmus,* make their appearance towards the top of the cliffs. Still higher the first *Pachystylostroma* comes in. These occurrences together with the first appearances of *Tetradium* and *Eofletcheria* suggest a correlation with the earliest N.S.W. coral/stromatoporoid fauna (Fauna 1).

Stratigraphically much higher, immediately beneath the *Pliomerina* siltstones, the stromatoporoids include abundant *Pachystylostroma* (Fig. 4D, F) and less common *Labechia, Labechiella* and *Rosenella*. *Palaeophyllum* and heliolitids have been observed from this part of the sequence indicating a correlation with N.S.W. Fauna 2. Above the *Pliomerina* siltstones, the faunas are rather sparse and the record of stromatoporoids incomplete. However, towards the top of the sequence of the Gordon Subgroup, at The Den and in the vicinity of the large working quarry farther west, there is a rich stromatoporoid fauna comprising *Labechia, Labechiella, Rosenella, Aulacera* (Fig. 5B, E) and the clathrodictyids *Ecclimadictyon undatum* Webby & Banks, *Clathrodictyon plicatum* Webby & Banks, *C. molense* Webby & Banks and *C.* sp. The fauna is associated with abundant corals including favositids, halysitids, *Favistina* and other characteristic elements of Fauna 3. It is very tentatively correlated with the Eden-Maysville of North America (Fig. 8), despite the occurrence of *Aulacera,* which tends to be restricted to the Richmond of North America (Galloway & St. Jean 1961).

Appearances of Ordovician stromatoporoid genera in Australian successions are depicted in Fig. 8. The maximum period of diversification of stocks seems to have occurred in the Gisbornian, with the appearance of Fauna 1. The species of *Stromatocerium, Stratodictyon* and *Labechia* in the lowest part of the limestone at Mole Creek are distinctly different forms (Figs 1D-F; 2A-B, D) and cannot easily be linked through intermediate forms back to a common ancestor. The species of

Stratodictyon and *Labechia* may have evolved from an early Chazy representative of *Pseudostylodictyon,* like *P. lamottense,* thought by Kapp & Stearn (1975) to be the oldest North American stromatoporoid, but *Pseudostylodictyon* has not been found in the lowest stromatoporoid-bearing beds of the Gordon Subgroup of Tasmania. The species of *Stromatocerium,* has no known progenitor unless it is interpreted as having descended from Khalfina & Yavorsky's (1974) supposed Early Cambrian *Stromatocerium* of the Kuznetsky Alatau region, Siberia (see later discussion, p. 113). From the initial *Stromatocerium, Labechia* and *Stratodictyon* stocks in these lowest horizons of the Gordon Subgroup, it would not have been difficult to derive the more diverse Fauna 1 assemblage.

(b) *North America*

Kapp & Stearn (1975) have traced the evolutionary history of the oldest stromatoporoids in North America. They have interpreted *Pseudostylodictyon lamottense* which first appears in the Day Point Formation (zone 1) of the Chazy Group, and has 'denticled laminae and large irregular cysts', as representing the earliest stage of stromatoporoid evolution. Diversification from this ancestral stock took place along two main paths, typified by the genera *Labechia* and *Pachystylostroma.* Both genera make their appearance in the Crown Point Formation (zone 2) of the Chazy Group — *Labechia eatoni, L. prima* and *Pachystylostroma goodsellense,* the first to exhibit vertical pillars supposedly secreted to strengthen the coenosteum. In the next stage of evolutionary development through the middle-late Crown Point and Valcour Formations (mid-late Chazy) a further two species of *Labechia* and three species of *Pachystylostroma* appeared, presumably derived from the main stock of *L. eatoni* and *P. goodsellense.*

The genus *Cystostroma* which is formed solely of cysts without laminae or pillars has as its type species *C. vermontense* originally described from the Crown Point Formation, and considered by many workers, most notably by Galloway (1957) and Nestor (1964; 1966a), as the most primitive stromatoporoid. Unfortunately, Kapp & Stearn (1975) were unable to confirm the presence of this species and have suggested it to be a very rare species or 'an abnormal representative of *Labechia prima*'.

A stratigraphic break in the record of deposits and hence a gap in the course of evolutionary development occurs between the top of the Chazy Group and the base of the overlying Black River Group. According to Kapp & Stearn (1975) the basal formation of the Black River Group is the Pamelia Formation and it contains the problematical cylindrical stromatoporoid *Cryptophragmus.* The succeeding Lowville and Leray Formations have a new stromatoporoid fauna apparently dominated by *Stromatocerium rugosum.* In addition to *Cryptophragmus* and *Stromatocerium,* Galloway & St. Jean (1961) have noted the first appearance of *Rosenella* and the enigmatic encrusting stromatoporoid *Dermatostroma* Parks 1910 in horizons of 'Blackriver' age. With the exception of *Cryptophragmus* most of the labechiid genera seem to range at least to the top of the Ordovician. *Cryptophragmus* however is confined to the North American late Middle Ordovician (i.e., 'Blackriver' and possibly 'Trenton').

The large, unbranched, cylindrical stromatoporoid *Aulacera* Plummer is characteristic of Richmond (Late Ordovician) horizons of North America (Galloway & St. Jean 1961). Also *Clathrodictyon* has been reported by Twenhofel (1927, p. 107) from a similar level in the succession of Anticosti Island. The species recently figured by Copper (1974, p. 378) from a bioherm of the Ellis Bay Formation (late Richmond) on Anticosti seems to be the same species of *Clathrodictyon* as Dr T. E.

Bolton of the Canadian Geological Survey (pers. comm.) has shown me from Member 6 of this formation. It is a representative of the *Clathrodictyon boreale* group of Nestor (1964). Workum, Bolton & Barnes (1976) have also recorded *Labechia, Cystostroma*? and *Aulacera* from the Ordovician succession of Akpatok Island, north-east Canada.

(c) *Europe*

The oldest stromatoporoid in European successions appears to be *Labechia aldonensis* Webby 1977 from the Stinchar Limestone of the Girvan district of Scotland. It occurs in an horizon of approximately middle-late Llandeilo age (Williams, 1962; Williams *et al.*, 1972).

On the island of Helgϕya in the Nes-Hamar district of Norway, Stϕrmer (1953) recorded the presence of a spectacular 'stromatoporoid reef' some 9-10 m thick in the Mjϕsa Limestone. The Mjϕsa Limestone is correlated with the Upper Chasmops Limestone (stage 4bδ) of Oslo, or in terms of Estonian subdivisions, equivalent to the Oandu (D_{III}) or Rakvere (E) stages (middle-late Caradoc). As noted by Skjeseth (1963) the core of the reef near the shore of Lake Mjϕsa consists of a massive framework of stromatoporoids. Sampling of the Mjøsa Limestone in the vicinity of Bergvika on the island of Helgϕya has produced a varied stromatoporoid fauna with a few individual coenostea attaining dimensions of up to 1.3 m across and 0.4 m in height. The fauna includes representatives of *Labechia, Pachystylostroma* and a new genus allied to *Stromatocerium* (Webby, in press a). To the south the Encrinite Limestone of similar age to the Mjϕsa Limestone also contains stromatoporoids.

Kaljo, Klaamann & Nestor (1963) have recorded two stromatoporoids from the Ashgill of Norway — *Clathrodictyon microundulatum* Nestor from stage 5a, and *Pachystylostroma* sp. nov. ex gr. *fragosa* Nestor from stage 5b. These elements correspond quite closely to faunas of the Pirgu (F_{Ic}) and Porkuni (F_{II}) stages of Estonia.

The Estonian Ordovician stromatoporoid succession has been fully described and analysed by Nestor (1964; 1966b). As outlined by him (1966b) the vesicular labechiids (*Stromatocerium, Cystostroma* and *Plumatalinia*) are typical of the period, but begin to be replaced by 'vesicular-laminar' clathrodictyids (*Clathrodictyon* and *Ecclimadictyon*) by Ashgill times. Two species of *Stromatocerium* are the first to appear in the Oandu (D_{III}) stage of middle-late Caradoc age. No stromatoporoids have been recorded from the succeeding Rakvere (E) and Nabala (F_{Ia}) stages, but the first clathrodictyids, *C. microundulatum* and *C. vormsiense* appear in the next stage, the Vormsi (F_{Ib}), about early-middle Ashgill time. The succeeding Pirgu (F_{Ic}) stage contains *Stromatocerium, Cystostroma* and *Plumatalinia* in addition to *C. microundulatun.* The topmost stage of the Ordovician in Estonia, the Porkuni (F_{II}), is characterized by new species of *Clathrodictyon, C. gregale, C. mammillatum* and *C. zonatum,* by the first *Ecclimadictyon* (*E. koigiense* and *E. porkuni*) and by *Pachystylostroma fragosum.*

On the western slope of the Urals, Bogoyavlenskaya (1973) has described an Ordovician stromatoporoid fauna comprising *Cystostroma concinnum* (Ivanov), *Stromatocerium definitum* (Ivanov), *Clathrodictyon microundulatum* Nestor and *Ecclimadictyon geniculatum* Bogoyavlenskaya. The species come from two horizons — the Typyl (topmost Middle Ordovician) and Rassokha (Late Ordovician, about the level of the zone of *Pleurogr. linearis*). The species of *Ecclimadictyon* is unusual in occurring in the older Middle Ordovician (Typyl) horizon (approximately equivalent to the level of *Dicranogr. clingani,* or to the Oandu stage, D_{III}, of Estonia; Whittington & Williams, 1964).

(d) *Asia*

In the Moiero River section in the northern part of the Siberian Platform, Nestor (1976) has recorded a succession of Middle-Late Ordovician stromatoporoid faunas. All are labechiids, and the oldest is *Cystostroma insuetum* Nestor from the Krivoluk stage of possible 'Blackriver' (Nestor 1976, p. 9) or ?Chazy (Sokolov *et al.,* 1960 p. 49) age. *Stromatocerium* cf. *sakuense* Nestor 1964 occurs in an higher, Middle Ordovician (?'Trenton') horizon, and a much larger fauna appears in the Late Ordovician Dolbor stage. This latter fauna comprises *Cystostroma evenkiense* Nestor 1976, *Stromatocerium australe* Parks 1910, *S. pergratum* Nestor 1976, *Lophiostroma* sp. and *Pachystylostroma? amzassensis* (Khalfina 1960) — see earlier discussion p. 96. *Aulacera tenuipunctata* (Yavorsky 1955) occurs in still higher beds near the top of the Ordovician. Another form, reported by Yavorsky (1955) from the Late Ordovician of the Siberian Platform (Stony Tunguska and Moiero Rivers), is *Labechiella regularis* (Yabe & Sugiyama).

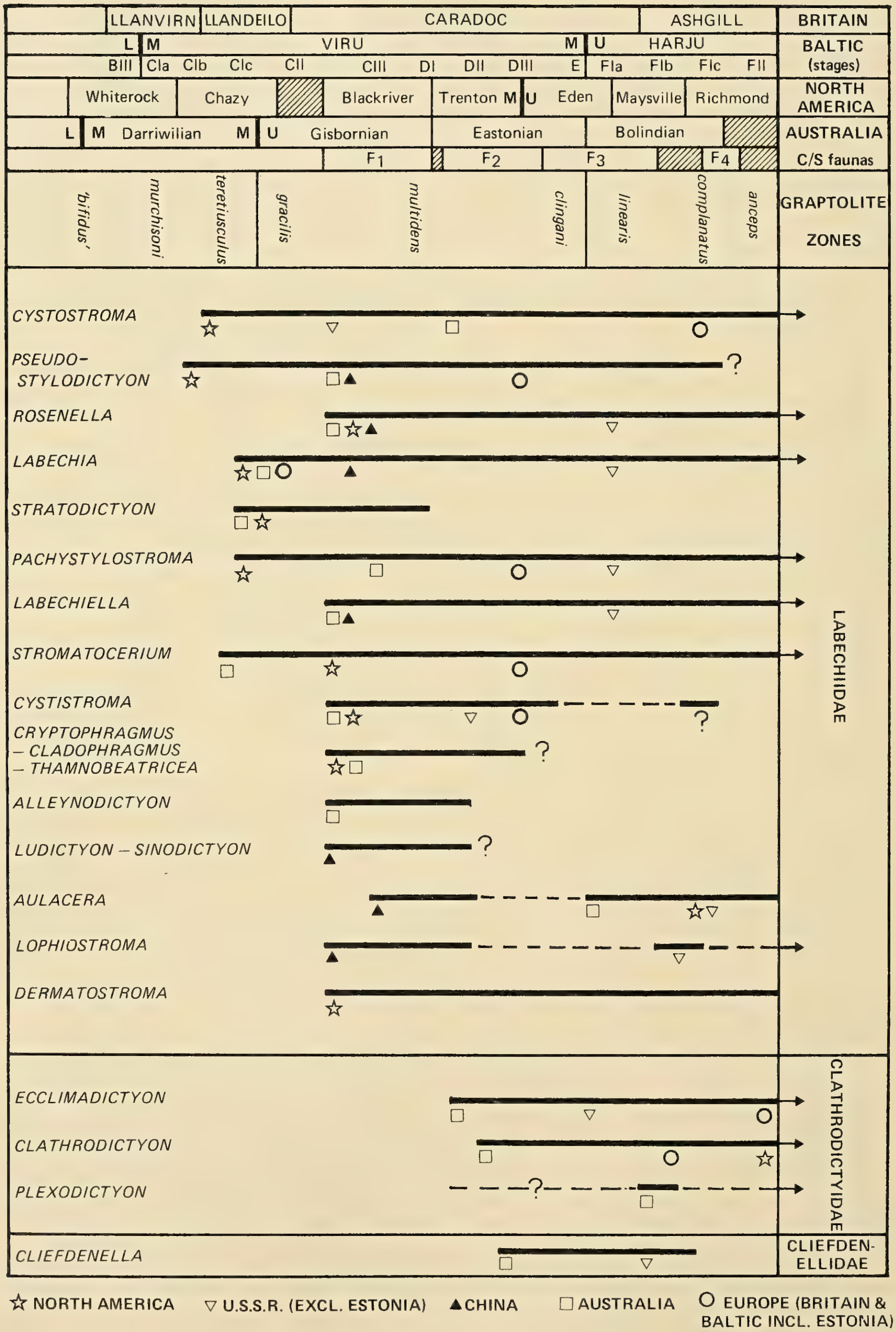
In the folded zone of the Altai Sayan mountain region of south-west Siberia there are many isolated records of Ordovician stromatoporoids. Khalfina (1960a) has described *Labechiella lophiostromoides* (Khalfina), *L. elandiense* (Khalfina), *Pachystylostroma? amzassensis* (Khalfina) and *Ecclimadictyon amzassensis* (Khalfina) from the upper part of the Amzass Formation (Late Ordovician) of Gornaya Shoriya and from similar levels in Gorny Altai. In approximate terms, the upper part of the Amzass Formation correlates with the zone of *Pleurogr. linearis* (Sokolov *et al.,* 1960). Khalfina & Yavorsky (1974) recorded *Cliefdenella permirum* from the Late Ordovician of Salair, and Bogoyavlenskaya (1971) referred to the presence of *Cystostroma* in the Middle and Late Ordovician of Tuva, and *Labechiella regularis* (Yabe & Sugiyama) and *Labechia huronensis* (Billings) from Late Ordovician horizons.

From the Late Ordovician Dulankara horizon in Kazakhstan, Khalfina (1958) has described (without illustration) *Labechiella kasachstanica,* and from the Late Ordovician of the Chatkal Range of Kirgizia, Middle Asia, Yavorsky (1961) has recorded *Cystostroma sarytschelekense.*

Another species of *Cystostroma, C. rarum* Yavorsky, of uncertain validity because of its intergrowth with *Labechia mirabilis* Yavorsky, is described by Yavorsky (1961) from the Late Ordovician of the Kolyma Basin of the north-eastern U.S.S.R.

In addition, many species of *Aulacera* have been described from Late Ordovician horizons from various parts of the Soviet Union by Yavorsky (1955; 1957; 1963), in particular from the Urals, from Novaya Zemlya, from the Vilyuy and Stony Tunguska Rivers of the Siberian Platform, and from eastern Siberia. A species of *Cryptophragmus, C. gracilis* is also recorded from the Ordovician of eastern Siberia by Yavorsky (1955).

Ordovician stromatoporoids have been reported from a number of regions of Eastern Asia — Shantung, Shansi and Liaotung (Southern Manchuria) provinces of North China, and North Korea (Yabe & Sugiyama 1930; Endo 1932; Ozaki 1938; Sugiyama 1941; Yang & Dong 1962). These occurrences all fall within the geographical limits of the major Hwangho Basin, and come from horizons of the Toufangian Series (and equivalents) of 'Middle' Ordovician (post Llandeilo and pre-Ashgill) age. Kobayashi (1969) has noted that stromatoporoids are the third largest fossil group in the Toufangian fauna of the Hwangho Basin, more specifically they occur mostly in horizons of the Toufangkou Limestone and the Ssuyen Formation (i.e., in the middle or upper parts of the Toufangian Series). There is no evidence of a faunal succession — merely an abundance of elements through a relatively restricted stratigraphical range, probably equivalent to the 'Blackriver', and possibly the


LLANVIRN
LLANDEILO
CARADOC
ASHGILL
BRITAIN
L M VIRU M U HARJU
BALTIC (stages)
BIII Cla Clb Clc CII CIII DI DII DIII E Fla Flb Flc FII
Whiterock
Chazy
Blackriver
Trenton M U Eden
Maysville
Richmond
NORTH AMERICA
L M Darriwilian M U Gisbornian
Eastonian
Bolindian
AUSTRALIA
F1 F2 F3 F4
C/S faunas
'bifidus'
murchisoni
teretiusculus
gracilis
multidens
clingani
linearis
complanatus
anceps
GRAPTOLITE ZONES
CYSTOSTROMA
PSEUDO-STYLODICTYON
ROSENELLA
LABECHIA
STRATODICTYON
PACHYSTYLOSTROMA
LABECHIELLA
STROMATOCERIUM
CYSTISTROMA
CRYPTOPHRAGMUS – CLADOPHRAGMUS – THAMNOBEATRICEA
ALLEYNODICTYON
LUDICTYON – SINODICTYON
AULACERA
LOPHIOSTROMA
DERMATOSTROMA
LABECHIIDAE
ECCLIMADICTYON
CLATHRODICTYON
PLEXODICTYON
CLATHRODICTYIDAE
CLIEFDENELLA
CLIEFDEN-ELLIDAE
?
☆ NORTH AMERICA
▽ U.S.S.R. (EXCL. ESTONIA)
▲CHINA
☐ AUSTRALIA
○ EUROPE (BRITAIN & BALTIC INCL. ESTONIA)

'Trenton' as well. The varied fauna includes records of some thirteen species from Shantung, nine from Liaotung, two from Shansi and two from North Korea. The genera include *Pseudostylodictyon, Labechia, Labechiella, Lophiostroma, Rosenella, Sinodictyon, Ludictyon* and *Aulacera*. The species of *Aulacera, A. peichuangensis* Ozaki, possibly represents the earliest record of the genus, earlier than the 'Eden-Maysville' appearances of the genus in Tasmania (Fig. 8). The association of *Aulacera* with other cylindrical forms (*Sinodictyon* and *Ludictyon*) may imply an evolutionary connection, with the Chinese fasciculate, branching 'Middle' Ordovician forms ancestral to the unbranched *Aulacera* (Fig. 10).

(e) *General significance*

The Ordovician labechiids exhibit a strikingly rapid period of diversification through the interval from the Llandeilo to the early Caradoc (from Chazy to 'Blackriver' using North American terminology, see Fig. 8). The earliest (Chazy) stocks, judging from Australian and North American first appearances, include *Pseudostylodictyon* (N. Amer.), *Cystostroma* (N. Amer. & ?Aust.), *Labechia* (N. Amer. & Aust.), *Stromatocerium* (Aust.), *Stratodictyon* (Aust.) and *Pachystylostroma* (N. Amer.). They are followed by appearance of *Rosenella* (Aust.), *Labechiella* (Aust.), *Cystistroma* (Aust.), *Dermatostroma* (N. Amer.) and the first cylindrical forms — *Cryptophragmus* (N. Amer.) and *Alleynodictyon* (Aust.) — in the early Caradoc ('Blackriver') and correlatives (see Fig. 8).

With the records of *Lophiostroma, Sinodictyon, Ludictyon* and *Aulacera* in the 'Middle Ordovician' of China — possibly from equivalent 'Blackriver' (or ? 'Trenton') levels — it seems that the maximum period of generic diversification of labechiids from basic Chazy stocks occurred early in the history of the group. They maintained their presence as the major stromatoporoid group through the Middle and Late Ordovician (from 'Blackriver' to Richmond times) but declined in importance from the Silurian onwards. Less than half the Ordovician genera of labechiids (and none of the cylindrical forms) survived beyond the end of the Ordovician (Fig. 8). *Aulacera* whose cylindrical columns attained very large dimensions (5 m in height?) in beds of the latest Ordovician was perhaps the most spectacular form to become extinct.

From the apparent band-like spread of occurrences (Fig. 9), it appears that the Ordovician labechiids had approximately an equatorial distribution, perhaps limited to within 20° either side of the palaeoequator. The Middle Ordovician stocks seem to have a more restricted geographical spread — confined to eastern North America, Scotland, China and S.E. Australia — than the Late Ordovician forms (Fig. 9).

Despite the inadequacies of the preserved fossil record and the unevenness in the reliability of available data, it may be suggested that some of the labechiid elements like *Labechia* and *Cystostroma* seem to have achieved an 'equatorial' distribution during the Chazy, while others — *Pseudostylodictyon, Pachystylostroma, Stromatocerium* and *Aulacera* — seem to have migrated very slowly to adjoining regions (Fig. 9). Others again appear to represent endemic elements, for instance, the

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Fig. 8. Chart showing the known stratigraphic ranges of Ordovician stromatoporoid genera. The first appearance of each genus is shown by symbols for each major region. Those genera known to survive beyond the end of the Ordovician are depicted with arrows at the top of their Ordovician ranges. Correlations between the respective British, Baltic, North American and Australian stratigraphic subdivisions are only tentative. However, it should be noted that the boundaries between the Lower and Middle Ordovician, and between the Middle and Upper Ordovician, as shown in the columns by symbols L, M and U, occur at different levels in the respective Baltic, North American and Australian successions. C/S faunas — coral/stromatoporoids faunas of Webby (1969) and Webby & Morris (1976).

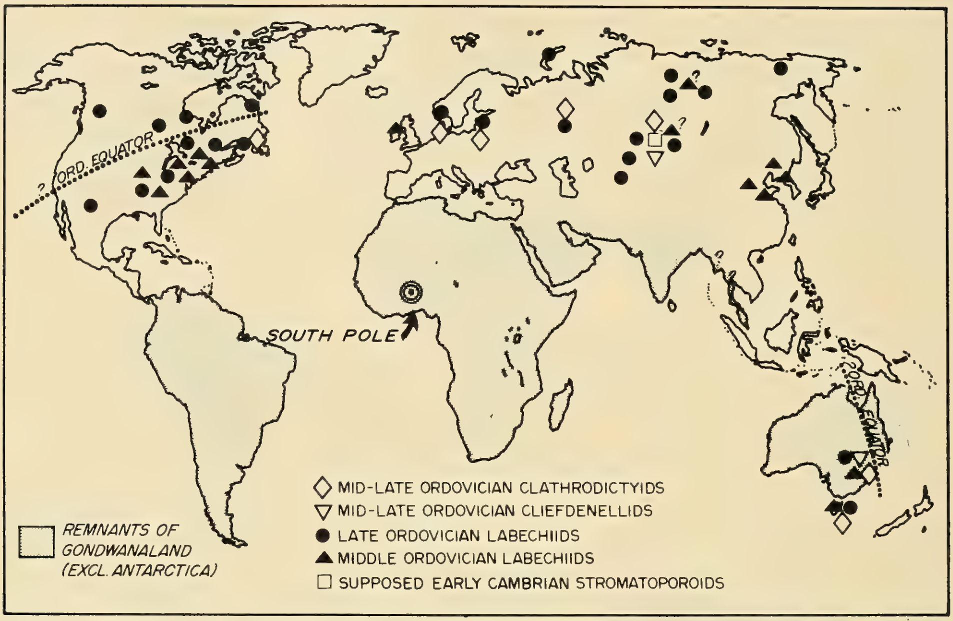

Fig. 9. Map illustrating the world-wide spread of Ordovician stromatoporoid faunas. Note also the single occurrence of the supposed Cambrian 'stromatoporoids' from the Altai Sayan mountain region of Siberia. Ordovician equatorial positions based on suggestions by Webby (1978) for Australia and Ross (1976) for North America.

problematical, encrusting *Dermatostroma* of North America, cylindrical *Sinodictyon* and *Ludictyon* of China, and cylindrical *Alleynodictyon* of Australia.

The clathrodictyid genera *Clathrodictyon* and *Ecclimadictyon* also exhibit patterns of slow global migration like a number of the labechiid genera. The genus *Clathrodictyon* which first appears in 'Trenton' correlatives in New South Wales, Australia, took until the Maysville (early Ashgill) to reach Estonia, and until the late Richmond to make its first appearance in North America, on Anticosti Island.

ORIGINS AND INTERRELATIONSHIPS

(a) *Supposed Cambrian 'Stromatoporoids'*

Although most workers have claimed the Middle Ordovician 'vesicular' labechiids to be the earliest representatives of the Stromatoporoidea with *Cystostroma* (Galloway, 1957; Galloway & St. Jean, 1961; Nestor, 1964; 1966a; Bogoyavlenskaya, 1969) or *Pseudostylodictyon* (Kapp & Stearn, 1975) seen to be ancestral to all later forms, a small group of Soviet specialists, notably Yavorsky (1932; 1940; 1947), Khalfina (1960a; 1960b; 1971), Vlasov (1961) and Khalfina & Yavorsky (1967; 1974), have maintained that the Ordovician stromatoporoids were derived from earlier, Cambrian stocks. The supposed stromatoporoid fauna occurs exclusively in the Early Cambrian of the Altai Sayan mountain region of south-west Siberia (Fig. 9). The fauna includes representatives of exclusively Cambrian genera (*Altaicyathus* Vologdin 1932; *Korovinella* Khalfina 1960b; *Praeactinostroma* Khalfina 1960b; *Cambrostroma* Vlasov, 1961), and others which may be linked with established post-

Cambrian forms — the genera *Clathrodictyon* Nicholson & Murie 1878, *Rosenellina* Radugin 1936 and *Stromatocerium* Hall 1847.

Korovinella (type species *Clathrodictyon sajanicum* Yavorsky) is the best known genus, typically exhibiting porous laminae, short, rod-like pillars, and vertical canals, the latter possibly analogous to the astrorhizal columns of stromatoporoids (Khalfina 1960a; 1960b). The porous nature of the laminae, on the other hand, is noted by Nestor (1966a) to ally the genus to archaeocyathans. *Praeactinostroma* (type species *Actinostroma vologdini* Yavorsky) has both discontinuous rod-like horizontal elements and pillars forming an incomplete, reticulate network also intersected by vertical canals. It appears to have closer affinities to stromatoporoids by resembling the Silurian genus *Plectostroma* Nestor 1964 and Mesozoic genus *Actinostromaria* Chalmas *in* Dehorne 1920 (see Nestor 1966a). Of the other forms, Nestor (1966a) has viewed *Cambrostroma* as a junior synonym of *Korovinella,* he has noted that Radugin's Cambrian species of *Rosenellina* has never been described and cannot be discussed further, and he has observed that Vlasov's species of *Clathrodictyon* (*C. formozovae*) is based on such small fragments that they cannot be satisfactorily revised.

Altaicyathus (type species *A. notabilis*) was originally described as an archaeocyathan by Vologdin (1932), but it was later included by Yavorsky (1940), Zhuravleva (1955; 1960), Khalfina (1960b) and Vologdin (1966) in stromatoporoids. *Korovinella* Khalfina 1960b has been regarded by Vlasov (1967) as a junior synonymn of *Altaicyathus* Vologdin 1932 (see also Hill, 1972, p. E142, and Flügel & Flügel-Kahler, 1968, p. 525), so perhaps both *Korovinella* and *Cambrostroma* should be included in *Altaicyathus.* However at least one species of *Korovinella, K. edelsteini* (Yavorsky), has recently been equated with the archaeocyathan *Abakanicyathus karokolensis* Konjuschkov — see Zhuravleva & Miagkova (1974, pl. 2, fig. 2).

Two species of *Stromatocerium, S. pospelovi* Khalfina *in* Khalfina & Yavorsky 1974 and *S. cambricum* Khalfina *in* Khalfina & Yavorsky 1974 are recorded as coming from the Cambrian of the Kuznetsky Alatau, south-west Siberia. With their meandriform pillar structures, the species seem to have more in common with forms from the Early Carboniferous of China — like *Stromatocerium kwangsiense* Dong 1964 — than with typical Ordovician species of the genus (Parks, 1910; Galloway & St. Jean, 1961).

Galloway (1957) noted that the supposed Cambrian stromatoporoids of Yavorsky (1932) were not composed of simple cysts as would be expected if they were ancestral to *Cystostroma* and *Pseudostylodictyon* but included more complex structures with laminae, pillars and astrorhizae. He implied (see also Galloway & St. Jean, 1961, p. 7) that the forms were collected from younger horizons than the Cambrian. Galloway also thought that the stromatoporoids as a group may have evolved from the archaeocyathans, from a form like *Exocyathus* Bedford & Bedford, but did not, in view of his doubts about the stratigraphic position of Yavorsky's finds, explore the possibility of the supposed Cambrian forms being transitional between archaeocyathans and stromatoporoids. The more recent work of Yavorsky, Khalfina and Vlasov has proved beyond doubt that the bulk of the forms come from the Early Cambrian of the Altai-Sayan mountain region; typically they have an association with archaeocyathans, even within the one specimen.

Nestor (1966a) interpreted the supposed Cambrian stromatoporoids (excluding the recently reported species of *Stromatocerium*) as archaeocyathans being only convergently similar to stromatoporoids. According to him, the forms disappeared from the stratigraphic record towards the end of the Early Cambrian and had no successors in the Middle-Late Cambrian or the Early Ordovician. He argued against them being the ancestors of the Middle Ordovician stromatoporoids, the earliest being the 'vesicular' labechiids. On the other hand, archaeocyathan specialists such as Vologdin (1966) and Hill (1972) have excluded the supposed Cambrian 'stromatoporoids' from a grouping with archaeocyathans.

Khalfina & Yavorsky (1967) in reply to Nestor reiterated that the Cambrian forms were the oldest stromatoporoids, and that they were morphologically distinct from archaeocyathans. They noted that vertical canals were shown to be arranged like the astrorhizal canals of stromatoporoids, and the external and internal walls of typical archaeocyathans were lacking. The coniform-cylindrical 'coenostea' of forms like *Korovinella* and *Praeactinostroma* were seen to bear similarities to cylindrical coenostea of some later Palaeozoic (post Ordovician) stromatoporoids, for example, in exhibiting similar patterns of laminae arranged transversely to the axial canal (*Paramphipora*), lateral processes (*Idiostroma, Stachyodes*) and a single axial canal (*Amphipora, Idiostroma*). The genus *Clathrodictyon* was seen by Khalfina & Yavorsky to be unrelated to 'vesicular' stromatoporoids, and possibly to have been derived from Cambrian 'stromatoporoids' with perforate laminae. The porous nature of the laminae in *Korovinella* was regarded as being different from the arrangement of pores in tabulae of irregular archaeocyathans (Suborder Archaeosyconina), and the mode of lamina formation in *Korovinella* similar to that of stromatoporoids like *Actinostroma* (another post Ordovician form). I question these latter assertions. First, the perforate laminae of *Korovinella* closely resemble the porous tabulae of irregular archaeocyathans like *Hupecyathus* Debrenne 1964. Secondly, the perforate laminae of *Korovinella* differ markedly from the laminae of *Actinostroma* (composed of an hexactinellid network of radial processes — see Stearn, 1966, p. 86).

Zhuravleva (1970) has noted that the skeletal structures of archaeocyathans of the class Irregulares with 'colonial' form may be practically indistinguishable from stromatoporoids like *Clathrodictyon* (Zhuravleva & Miagkova, 1974). The tabulae, vertical rods and central cavities of irregular archaeocyathans are recognized as having equivalents in the laminae, pillars and astrorhizae of stromatoporoids. Zhuravleva & Miagkova (1974) have emphasized the morphological similarities between stromatoporoid *Amphipora* and irregular archaeocyathan *Protopharetra,* and between *Korovinella* and *Archaeosycon.* They have additionally shown the supposed Cambrian 'stromatoporoids' *Korovinella edelsteini* and *Praeactinostroma* to be indistinguishable from irregular archaeocyathans *Abakanicyathus karakolensis* Konjuschkov and *Claruscyathus cumfundus* (Vologdin), respectively (Zhuravleva & Miagkova, 1974, pl. 2).

In terms of presently accepted views of morphology and classification of stromatoporoids the Cambrian 'stromatoporoid' genera of Yavorsky, Khalfina and Vlasov include three (possibly four) stocks, each of which may be grouped in a different family. *Altaicyathus* (= *Korovinella*) belongs to the exclusively Cambrian family Korovinellidae Khalfina 1960b, *Praeactinostroma* should probably be included in the family Actinostromatidae Nicholson 1886 (a group which has no confirmed Ordovician record) and *Clathrodictyon* is a member of the Clathrodictyidae. A possible fourth is the presumed *Stromatocerium* (family Labechiidae). The korovinellids are the best known group but have the least close resemblances to Middle Ordovician or later stromatoporoids. *Praeactinostroma* bears no close relationships to Middle-Late Ordovician stromatoporoids. *Clathrodictyon* and *Stromatocerium* remain too inadequately documented. *Clathrodictyon* is based on totally insufficient material and *Stromatocerium* has yet to be confirmed as coming from undoubted Cambrian horizons. Their essentially localized occurrence with archaeocyathans in the

Altai Sayan mountain region of Siberia and morphological resemblances with members of the class Irregulares, and their physical separation by such an enormous break in continuity of record of some 110 m.y. from Middle Ordovician stromatoporoids, make it impossible to establish them as the earliest, indubitable stromatoporoids. The occurrences of *Clathrodictyon* and *Stromatocerium* may represent the earliest records of clathrodictyids and labechiids, respectively, but they may equally well be viewed as homeomorphs of later stromatoporoids (either offshoots of irregular archaeocyathans, or members of an independent group). There is no record of such structures after the extinction of the reef-forming archaeocyathans at the end of the Early Cambrian, until the Middle Ordovician when skeletal reef habitats reappeared.

(b) *Outline of Evolutionary Development of Ordovician Stromatoporoids*

The Middle Ordovician stromatoporoids formed an important 'skeletonized' constituent of the earliest 'coral-stromatoporoid-algal' reef communities (Pitcher, 1971; Heckel, 1974; Copper, 1974; Kapp, 1975). Their skeletal remains were among the more prominent components of Middle-Late Ordovician patch reef and carbonate bank deposits. The advent of skeletonization may have represented an adaptive breakthrough allowing for a dramatic increase in size (some Chazy stromatoporoids are up to 1 m in width and height), providing the necessary support for the mantling soft tissues, and elevating the individuals above the substrate to facilitate their filter feeding (Stearn, 1972), epifaunal mode of life. The sessile stromatoporoid animal evidently lived in a moderately competitive, near-equatorial, shallow-water patch reef or carbonate bank-type environment.

The main burst of adaptive radiation of the labechiids occurred in the Middle Ordovician, seemingly with the genera derived from a *Cystostroma* or *Pseudostylodictyon*-like ancestor, as shown in Fig. 10. From the nature of the radiation of skeletonized genera (Figs. 8, 10), it appears that we are viewing a genuine invasion of patch reef and bank habitats previously relatively free from competitors. The early appearance of *Stromatocerium* from the Tasmanian 'Middle Ordovician' (Fig. 8), an 'advanced' form in terms of its occurrence at the end of an evolutionary pathway (see *Stromatocerium* group B in Fig. 10) may merely serve to indicate how rapidly the adaptive radiation took place in the Chazy, rather than to suggest links with a supposed Early Cambrian *Stromatocerium* archetype (Khalfina & Yavorsky, 1974).

Recognition in some labechiids of immature and mature (or alternating) growth stages — the basal layers of coenostea (and the bases of latilaminae) exhibiting immature stages of growth — may be significant in clarifying phylogenetic relationships within the group (Galloway, 1957). For example, Galloway (1957, p. 394) noted in one specimen of *Cystistroma canadensis* the presence of a *Rosenella*-type 'immature' stage, and Kapp & Stearn (1975) have observed *Cystostroma* as the 'immature' stage of *Labechia prima*.

Morphologically the most simple, calcified laminar hemispherical forms are *Cystostroma, Pseudostylodictyon* and *Rosenella* (Fig. 10). They typically exhibit rows of simple cysts (or laminae in *Pseudostylodictyon*) arranged in an imbricated manner, denticles on their upper surfaces and mamelons but no pillars. By simple superposition of denticles to form rounded pillars, the genera *Labechia* (*L. prima* group), *Stratodictyon* and *Pachystylostroma* may be derived. In view of the growth stages exhibited by *Labechia* (Yavorsky, 1961; Kapp & Stearn, 1975) *Cystostroma,* rather than *Pseudostylodictyon,* should be regarded as its ancestor. *Stratodictyon* appears to have been derived from a member of the *L. prima* group, or less likely, directly from

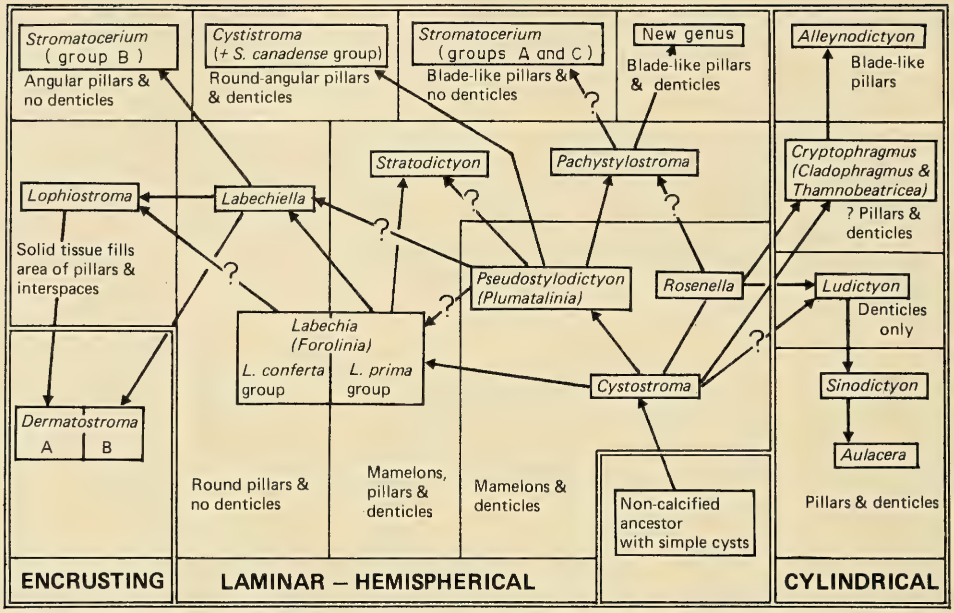

Fig. 10. Diagram showing possible evolutionary pathways for the Ordovician genera of labechiid stromatoporoids.

Pseudostylodictyon (Webby, 1969, p. 653), while *Pachystylostroma* appears to have evolved, as Kapp & Stearn (1975) have outlined, from *Pseudostylodictyon*. The culmination of the trend towards long and continuous pillars derived from superposed denticles leads to representatives of *Labechia* (*L. conferta* group) with cysts and *Labechiella* with laminae. *Stromatocerium* (*S. rugosum* group) is derived from *Labechiella* and has irregular (secondarily altered) pillars. None of these latter forms exhibits denticles.

Derivation of *Lophiostroma* and *Dermatostroma* is more problematical. The clue to the derivation of *Lophiostroma* with its poorly differentiated internal structures owing to a completely solid infill of tissue is seen in the Middle Ordovician species *L. shantungensis* which shows traces of original pillars and a few large unfilled cysts in the interspaces, as in a *Labechiella* or *Labechia*. Furthermore the upper surface of the coenosteum of the respective type species of *Lophiostroma* and *Labechia* have an identical papillose appearance. The encrusting genus *Dermatostroma* includes forms with solidly fused vertically aligned prisms which may be allied to *Lophiostroma* (*Dermatostroma* A in Fig. 10), and forms with a few laminae and pillars which may be related to *Labechiella* (*Dermatostroma* B in Fig. 10).

Cystistroma, as previously suggested by Webby (1969, p. 653), may have been derived from *Pseudostylodictyon* with the large, rounded-angular pillars evolving from mamelons, not from denticles. The new *Stromatocerium*-like genus (Webby, in press a) bears similarities to *Cystistroma* in exhibiting denticles on upper surfaces of cysts in the interspaces between the large pillars but differs in having 'composite' vane-like pillars, each apparently developed at the site of a former mamelon. It seems to have a different derivation from *Cystistroma,* probably from a *Pachystylostroma.* Other forms with large 'hollow' wall-like radiating pillars of *S. rugosum* type (group A of Fig. 10) and slender, intermeshed, 'composite' blade-like pillars, referred to the

Stromatocerium michiganense group (group C of Fig. 10) may have a similar origin, but they lack denticles.

The cylindrical labechiids appear to have evolved from the laminar-hemispherical forms by the development of extended mamelon-like upgrowths perhaps from a *Cystostroma*-like base (Galloway & St. Jean, 1961). The relationships have not been clearly established but there would appear to be two main trends (Fig. 10) — one through the Chinese fasciculate-cylindrical genera *Ludictyon* and *Sinodictyon* to the large unbranched *Aulacera,* and the other through the slender North American forms of *Cryptophragmus, Cladophragmus* and *Thamnobeatricea* to *Alleynodictyon,* a genus with blade-like pillars (Webby, 1971). Both lines would appear to commence with a simple *Rosenella* or *Cystostroma*-like ancestor.

Clathrodictyids may have been derived from a simple labechiid ancestor, but evolved pillars from downward inflections of laminae rather than by superposition of denticles as in labechiids, and developed walled astrorhizae. Adequate time seems to have been available for these morphological changes to have taken place, given a line of descent from a Chazy, *Cystostroma*-like ancestor to the first appearance of clathrodictyids in the 'Trenton' (Fig. 8). The alternative is a much earlier, independent ancestry for the group, possibly from the Early Cambrian *Clathrodictyon* of Vlasov (1961) and Khalfina & Yavorsky (1967). To be directly ancestral to Middle Ordovician and later representatives of the genus would imply that the supposed Early Cambrian *Clathrodictyon* lost its ability to preserve a mineralized skeleton for a period of 110 m.y. to the Middle Ordovician.

It is more difficult to derive the complex morphology of the cliefdenellids from a labechiid. The group may have evolved from a clathrodictyid like *Plexodictyon* but there would seem to be too limited a period of time within the 'Trenton' (Fig. 8) to make all the necessary morphological changes, viz., addition of denticles to the upper surface of its primary laminae, large tube-like pillars and complex astrorhizae. A more realistic view allowing for the development of the complex morphological features is to suggest that cliefdenellids arose as an independent Ordovician group from an earlier, possibly Cambrian soft-bodied ancestor.

The marked morphological differences between the three separate families of Ordovician stromatoporoids favour a much earlier origin possibly from a common (? soft-bodied) ancestor in the Cambrian (very doubtfully from within the irregular archaeocyathans, suborder Archaeosyconina), with independent lines of descent through the Ordovician. The initial Middle Ordovician record of each family is based on the appearance of its first skeletonized remains, and does not necessarily coincide with the origins of the individual group.

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Freshwater Sponges from the Northern Territory (Porifera: Spongillidae)

J. STANISIC

STANISIC, J., Freshwater sponges from the Northern Territory (Porifera: Spongillidae). *Proc. Linn. Soc. N.S.W. 103* (2), (*1978*) *1979*: 123-130.

Three spongillids are recorded from a freshwater billabong in Arnhem Land, Northern Territory, Australia.

Metania ovogemmata sp. nov. and *Radiospongilla streptasteriformis* sp. nov. are figured and described. *M. ovogemmata* represents the first record of the genus *Metania* Gray in Australia and its discovery establishes a connection between the Australian and South American spongillid faunas. *R. streptasteriformis* extends the range of the genus *Radiospongilla* Penney and Racek in Australia and a study of its relationship to other members of the genus indicates that there has been a radiation of radiospongillids in Australia. *Eunapius sinensis* (Annandale), previously recorded from the eastern states of Australia, is recorded for the first time from the Northern Territory.

This new information forms the basis for further speculation on the origins and relationships of Australian spongillids.

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INTRODUCTION

Following the comprehensive revision of a worldwide collection of freshwater sponges by Penney and Racek (1968), Racek (1969) completely revised the freshwater sponges of Australia and produced keys to all the described species. However, Racek's conclusions regarding the origin, dispersal and distribution of the Australian spongillid fauna were based on only limited material from the remote areas of central and northern Australia. Apart from the single record of *Radiospongilla hispidula* Racek from Darwin and two specimens of *Radiospongilla philippinensis* (Annandale) from Derby (W.A.), the material treated by Racek (1969) came from localities in the eastern states.

The paucity of material from these remote areas is largely due to their inaccessibility to previous collectors. However, with the establishment of the Crocodile Research Facility at Maningrida in Arnhem Land (N.T.), the author was able to obtain a collection of spongillids from Australia's far north. Detailed taxonomic studies of this collection revealed the presence of two new species of spongillids and the first record of the genus *Metania* Gray from Australia.

The sponges described in this paper provide new information on the distribution of the Australian spongillid fauna. More importantly however, this new information enables a reassessment of the possible origin of some of Australia's freshwater sponges to be made.

The taxonomic and morphological terminology used here follows Penney and Racek (1968). Preparation of the material followed the outlines presented by Gee (1931).

TAXONOMY

Genus *Metania* Gray

Metania Gray, 1867, p. 551
Metania Penney and Racek, 1968, p. 147 (and synonymy)
Type species: Spongilla reticulata Bowerbank (1863)

This genus, as redefined by Penney and Racek (1968), includes those species which possess a single layer of radially arranged tubelliform gemmoscleres and free microscleres. The genus is restricted to tropical areas of Asia, Africa and South America. The new species, which is described below is the first representative recorded from Australia.

Metania ovogemmata sp. nov.

Material: Freshwater billabong ('Benamanarka Gunora') near Maningrida, Arnhem Land, Northern Territory, 12°00'S, 134°20'E, coll. G. Wells, 6. x. 76, holotype (Australian Museum Z3693).

Description: Sponge forming encrustations of variable thickness (1-3 mm) on logs in shallow water; surface reticulate and markedly hispid with spicules projecting through the dermal membrane. Skeleton consisting of tracts of spicules which form vague triangular meshes. Oscula conspicuous. Consistency of dry sponge firm.

Megascleres of two distinct size classes. The larger series forms the primary skeleton of the sponge, while the smaller series is mainly restricted to the vicinity of the gemmules, forming a spicular envelope around each gemmule. The larger series (Fig. 1 a-c) consists of stout fusiform amphioxea; slightly curved, ranging from smooth to incipiently spined except on the distal portions of the sclere. Length range 220-290 μm, width range 10-20 μm. Those in the smaller series (Fig. 1d,e) are short, stout, hastate amphioxea; curved and covered with numerous conical spines which tend to form whorl-like aggregations at the scleral apices. Length range 195-230 μm, width range 12-20 μm.

Microscleres (Fig. 1f,g) slender, fusiform amphioxea; straight to slightly curved and covered with numerous spines. In the central portion of the sclere these spines become longer and complex. Length range 60-90 μm width range 2-4 μm.

Gemmoscleres (Fig. 1h-1) tubelliform with an almost circular rotule at one end and terminating in a smooth knob at the other. The face of the rotule is clear of any striations while the margins are strongly recurved. The shaft of the sclere possesses a number of large conical spines. Length range 25-35 μm, width of shaft 2-4 μm, diameter of rotule 16-21 μm, width of terminal knob 3-7 μm.

Gemmules (Fig. 1m,n) large and oviform; abundant and scattered throughout the skeletal meshwork. The pneumatic layer of the gemmule is thin with the gemmoscleres embedded radially so that the terminal knob is to the outside. The knob does not project beyond the outer gemmular membrane. Surface of the gemmule is granular. The foramen of the gemmule is tubular and the porus tube projects a short distance beyond the outer gemmular membrane. The gemmules are surrounded by an envelope of spiny megascleres. Dimensions of gemmules 420-520 μm (long axis) by 260-370 μm (short axis).

Type: Holotype with slides and vial of gemmules in the Australian Museum.

Distribution: Hitherto known only from the type locality in Arnhem Land, Northern Territory.

Colour: Spirit specimen black.

Discussion: The discovery of this new species in tropical northern Australia fills an important gap in the distribution of the genus *Metania*. Although known to occur in tropical areas, the absence of material from Australia puzzled Penney and Racek (1968), who concluded that the genus had a discontinuous distribution. It now appears that *Metania,* like other groups of spongillids, has a continuous southern distribution.

The presence of two classes of megascleres and the peculiar arrangement of the smaller series around the gemmule, suggest that this species is most closely related to *Metania reticulata* (Bowerbank) which occurs in the Amazon River of South

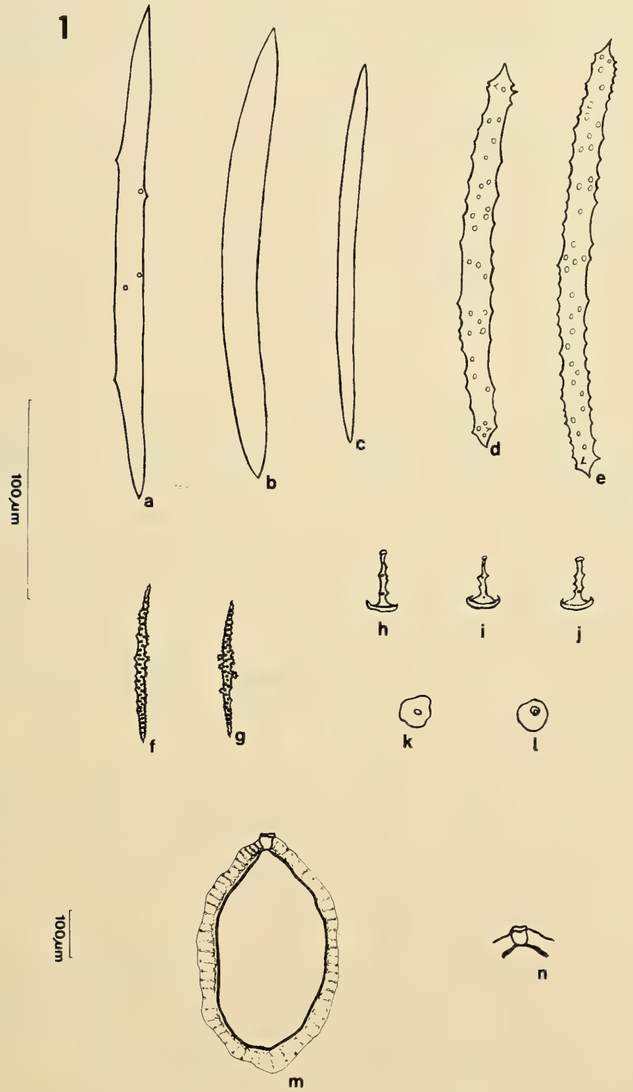

Fig. 1. *Metania ovogemmata* sp. nov.

a-c. larger series of megascleres
d-e. smaller series of megascleres
f-g. microscleres
h-j. gemmoscleres

k-l. rotules of gemmoscleres
m. gemmule
n. micropyle apparatus

America. However, the difference in the size of the megascleres of the two species and the fact that these are amphioxea in *M. ovogemmata* as opposed to amphistrongyla in *M. reticulata,* indicate that *M. ovogemmata* deserves separate specific status.

The striking arrangement of the hastate amphioxea in *M. ovogemmata* around the gemmule, appears to be an adaptation indicative of species which have small gemmoscleres and an associated small pneumatic layer in the gemmule. Similar capsules are found in *Trochospongilla* Vejdovsky, *Uruguaya* Carter and *Drulia* Gray, all of which have small radially arranged gemmoscleres and small pneumatic layers.

Considering the presence of the two congeners, *Metania vesparia* (von Martens) and *Metania vesparioides* (Annandale) in the Asian region, the relationship of *M. ovogemmata* to a South American species has important implications regarding the possible origin of this genus. These implications will be discussed later.

Genus Radiospongilla Penney and Racek

Radiospongilla Penney and Racek, 1968, p. 61 (and synonymy).
Radiospongilla Racek, 1969, p. 279.
Type species: Spongilla sceptroides Haswell (1882).

Penney and Racek (1968) introduced this genus as a link between those spongillids with acerate gemmoscleres and those with birotulate gemmoscleres, showing that the previous grouping of the spongillids into the two sub-families Spongillinae and Meyeninae was unwarranted. Hitherto six species are known from Australia.

Radiospongilla streptasteriformis sp. nov.

Material: Freshwater billabong ('Benamanarka Gunora') near Maningrida, Arnhem Land, Northern Territory, 12°00'S, 134°20'E, coll. G. Wells, 6. x. 76, holotype (Australian Museum Z3695).

Description: Sponge forming very thin encrustations in the corrugations of bark from logs in shallow water. Surface of the sponge is an irregular network of spicules with some of these projecting through a poorly developed dermal membrane giving the sponge a slightly hispid appearance.

Megascleres (Fig. 2a,b) slender to stout, curved fusiform amphioxea; strongly spined over the entire length with no distinct aggregation of the spines. Length range 160–200 μm, width range 4–10 μm.

2

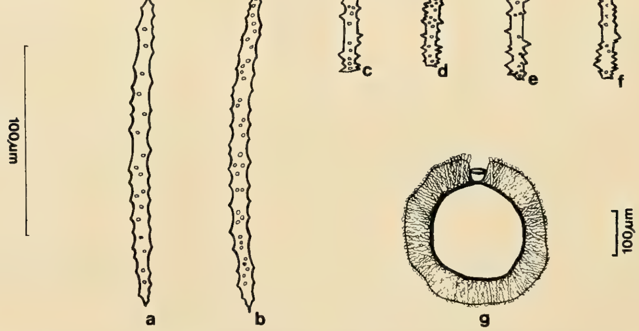

Fig. 2. *Radiospongilla streptasteriformis* sp. nov.

a-b. megascleres
c-f. gemmoscleres
g. gemmule

Microscleres absent.

Gemmoscleres (Fig. 2c-f) short, stout abrupt amphistrongyla covered with numerous long straight spines. Occasionally the central portion of the sclere is less spined than the distal portions. Straight to slightly curved. Length range 40-65 μm, width range 4-6 μm.

Gemmules (Fig. 2g) abundant and scattered throughout the symplasm of the sponge. These are large and spherical with a well developed pneumatic layer.

The gemmoscleres are embedded radially in the pneumatic layer and project beyond the outer gemmular membrane, making the surface of the gemmule distinctly hispid. The porus tube does not project beyond the outer gemmular membrane and is surrounded by a conical depression. Diameter of gemmule 340-440 μm.

Type: Holotype with slides and vial of gemmules in the Australian Museum.

Distribution: Hitherto known only from the type locality in Arnhem Land, Northern Territory.

Colour: Not reliably recorded.

Discussion: The discovery of *Radiospongilla streptasteriformis* in the alkaline waters of Australia's north, suggests that the genus *Radiospongilla* Penney and Racek may not be as restricted in distribution as Racek (1969) indicated. Based largely on collections from the eastern seaboard, Racek suggested that most species of this genus preferred acidic waters.

The gemmoscleres of *R. streptasteriformis* which are small and evenly spined abrupt amphistrongyla, readily separate this species from its congeners. However, the dimensions of the megascleres and gemmoscleres indicate that this species is closely related to *Radiospongilla synoica* Racek and *Radiospongilla cantonensis* (Gee). These three spongillids are characterized within the radiospongillids by their small megascleres and small gemmoscleres. They show a range of gemmosclere structure from amphioxea (*R. synoica*) through abrupt amphistrongyla (*R. streptasteriformis*) to the formation of almost perfect pseudorotules (*R. cantonensis*).

As *R. synoica* is endemic to eastern Australia and *R. cantonensis* is also present in eastern Australia (unpublished data), the distribution of these three species indicates a localized radiation from the central stem of radiospongillids as represented by the extant species *Radiospongilla cerebellata* (Bowerbank) and *Radiospongilla philippinensis* (Annandale). The evolutionary importance of the genus *Radiospongilla* (Penney and Racek, 1968; Racek, 1969; Racek and Harrison, 1975), makes the occurrence of such a radiation in the Australian region assume particular relevance in discussions concerning the origins of spongillids. The significance of this point will be discussed later.

Genus *Eunapius* Gray

Eunapius Gray, 1867, p. 552

Eunapius Penney and Racek, 1968, p. 21 (and synonymy).

Eunapius Racek, 1969, p. 271

Type species: Spongilla carteri Bowerbank (1863)

This genus is characterized by species which have a tangential arrangement of gemmoscleres around the gemmule and which lack free microscleres. Members of the genus are widely distributed and four species are recorded from Australia. *Eunapius sinensis* (Annandale) is known from the eastern and western river systems in New South Wales and Queensland. It is here recorded for the first time from the Northern Territory.

Eunapius sinensis (Annandale)

Spongilla (Stratospongilla) sinensis Annandale, 1910, p. 183.
Eunapius sinensis Penney and Racek, 1968, p. 35 (and synonymy).
Eunapius sinensis Racek, 1969, p. 273.

Material: Freshwater billabong ('Benamanarka Gunora') near Maningrida, Arnhem Land, Northern Territory, 12°00'S, 134°20'E, coll. G. Wells, 6. x. 76 (AM Z3695).

Type: Of *S. sinensis* in the collection of the United States National Museum.

Distribution: According to Penney and Racek (1968), ranging from USSR through Manchuria and mainland China to Australia. Not known from SE Asia.

Discussion: The characteristics of this specimen in both its mode of growth and spicular components make it fully comparable with the previously recorded Australian specimens. Racek (1969) considered that the thick pneumatic coat of the gemmule, which is reinforced by tangential layers of robust gemmoscleres, makes this species particularly suited to harsh environments.

The specimen was found growing in very close association with *M. ovogemmata.* However, the pavement layers of gemmules of *E. sinensis* were readily discernible from the more loosely scattered gemmules of *M. ovogemmata.*

GENERAL DISCUSSION

Origins and Relationships of the Australian Spongillids

Racek (1969) believed that most of the Australian spongillids were a southern extension or represented mere races of the Asian fauna. He based this assessment on the distribution of the extant spongillids in these two areas. More recently however, Racek and Harrison (1975) have reconsidered this theory.

Racek and Harrison examined the phylogenetic position of the fossil spongillid *Palaeospongilla chubutensis* Ott and Volkheimer which was discovered in the lacustrine sediments of the Cretaceous of Argentina. Consideration was given to the southern distribution of a number of the extant spongillids which showed close affinity with the fossil. In particular, Racek and Harrison referred to the presence in Australia of members of the genus *Radiospongilla* Penney and Racek, which could be related to the Cretaceous fossil, and the distribution of *Spongilla alba* Carter in both Australia and South America. These workers considered the pattern of continental drift in an attempt to reconstruct dispersal routes leading from the Cretaceous fossil to the present day distribution of spongillid fauna.

Racek and Harrison concluded that it was more reasonable to consider that Asia and Australia had independent faunal gains along dispersal routes which existed prior to the dismemberment of the great southern continent Gondwanaland. Two dispersal routes leading west-east were suggested. One route was along the connected South American, Antarctic and Australian plates, while the other was through Africa and Indo-Pakistan. Subsequently there may have been interchange between the Asian and Australian faunas. However, the evidence for these conclusions was based almost solely on the assumption that the extant fauna was directly related to the Cretaceous fossil.

With the discovery of *Metania ovogemmata* sp. nov. in Australia, a reassessment of spongillid dispersal routes is possible. It has already been demonstrated that *M. ovogemmata* is more closely related to *Metania reticulata* (Bowerbank) of South America than to its Asian congeners. The affinity between these extant spongillids can only be reasonably explained by divergence from a common stock. In order to account for the present distribution of these two species, subsequent dispersal would have required connected land masses which were present during the Mesozoic when Australia and South America were part of Gondwanaland (Smith, 1971).

Although Racek and Harrison (1975) came to similar conclusions regarding the importance of Gondwanaland in spongillid dispersal they considered only dispersal routes which were west-east along the Mesozoic continuity. A study of the distribution of the genus *Metania* Gray reveals the possibility of dispersal in an east-west direction. *Metania vesparia* (von Martens) and *Metania vesparioides* (Annandale) which occur through Africa, Burma, Borneo and Indonesia indicate dispersal and speciation from South America to Africa and Indo-Pakistan. As *M. ovogemmata* possesses a number of ancestral traits, e.g. two classes of amphioxeous megascleres, it is possible to demonstrate an evolutionary series from *M. ovogemmata* through *M. reticulata* to the Asian congeners. Therefore, in this case dispersal and speciation has most probably occurred in an east-west direction with the genus *Metania* having its origins in the Australian region.

Although little is known of the origin of the spongillids with birotulate gemmoscleres (e.g. *Metania*), they are considered to have arisen from an hypothetical stock from which the extant genus *Radiospongilla* Penney and Racek has also been derived (Penney and Racek, 1968). The gemmoscleres of *Radiospongilla cantonensis* (Gee) and *Radiospongilla crateriformis* (Potts) possess almost perfect rotules, suggesting that these two species share a common ancestry with the birotulate genera. In order to demonstrate more conclusively the emergence of birotulate genera in Australia, it is necessary to consider the distribution of radiospongillids which are considered to be phylogenetically related to these genera. However, this requires a reassessment of the suggested relationships within the genus *Radiospongilla*.

Penney and Racek (1968) considered that *R. cantonensis* and *R. crateriformis* form part of an evolutionary line within the radiospongillids. Their conclusions were based on the fact that the gemmoscleres of both these species possessed pseudorotules. This view implies that the birotulate genera have had a monophyletic origin. Such a view, however, does not explain the marked morphological diversity of the birotulate genera. Moreover, this view leads to difficulties in explaining relationships between the distribution of these radiospongillids and the distribution of the birotulate genera.

Recent developments based on the work of Poirrier (1974, 1976) and Stanisic (1977) enable an alternative view to be put forward. These workers have shown that using gemmoscleral form as a first principle for establishing relationships within genera, is not entirely valid. Such features are subject to ecomorphic variation which can mask true relationships. If, on the other hand one considers the length of the megasclere as a basis for assessing relationships, a new and more reasonable argument presents itself.

The difference in the lengths of the megascleres of *R. cantonensis* and *R. crateriformis* indicates that these two species have diverged from the central line of the radiospongillids at different times. The central line is represented by the *Radiospongilla cerebellata* (Bowerbank) group. Hence it is possible that the birotulate genera have arisen from more than one ancestor and that their origins are polyphyletic. Using megasclere length as a criterion, it is now also reasonable to suggest that *R. cantonensis* is more closely related to *Radiospongilla synoica* Racek and *Radiospongilla streptasteriformis* sp. nov. as all three spongillids have small megascleres. In view of the fact that these three spongillids occur almost solely in the Australian region, it is probable that they represent a radiation from a common ancestor in this region. Therefore, if *R. cantonensis* shares a common ancestry with some of the birotulate genera in Australia it is possible to document the emergence of birotulate genera in Australia. This not only supports the views of the present study regarding the origins of the genus *Metania* but also the view of Racek (1969), who considered that *Heterorotula* Penney and Racek evolved in Australia.

Inter-generic relationships within the family Spongillidae still need to be reliably established. The broad hypothesis regarding the relationship of the genus *Radiospongilla* to the birotulate genera which was put forward by Penney and Racek (1968), while providing some insight, is too vague to provide the explanatory and predictive powers which would make such a hypothesis useful in determining relationships. On the other hand, the specific arguments which have been presented above, can be used to demonstrate the emergence of birotulate genera in Australia. It is now also possible to predict a relationship between the radiospongillids mentioned above and these birotulate genera. Although highly speculative, such a hypothesis is favoured by the fact that its restrictive nature makes it open to testing by future research and discoveries.

As mentioned at the beginning of the discussion, the origins and affinities of the Australian freshwater sponges have been discussed by Racek (1969) and Racek and Harrison (1975). The new material documented in the present study, has enabled a further assessment to be made of the considerations initiated by these workers and it is now possible to show a definite connection with the unique South American spongillid fauna. Reconsideration of inter-generic relationships and distribution patterns indicate the possibility of an Australian origin for some of the birotulate genera, in particular *Metania*. The information provided by this new material however, emphasizes the need for further collecting within the Australian region.

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Hans Laurits Jensen, 1898-1977

MACLEAY BACTERIOLOGIST, 1929-1947

(*Memorial Series No. 26*)

Hans Laurits Jensen was born 27 June 1898 at Frederiksund, Denmark, and died in Copenhagen on 5 October 1977. He came to Australia in 1929 to take up the position of Macleay Bacteriologist of the Society, a post which he occupied for the next eighteen years until his return to the State Plant Laboratory at Lyngby in Denmark. Before coming here he trained in agronomy at his home university (the Royal Danish Veterinary and Agricultural High School), after which he had been appointed Bacteriologist in the State Plant Laboratory. A Rockefeller Grant then enabled him to work for two years with H. G. Thornton at the Rothamsted Experimental Station before his Linnean Society post in which he was to make such a notable contribution. Work on free-living nitrogen fixation which largely occupied the middle part of his Australian period earned Jensen the doctorate of his university. From 1943 to 1947 he combined his continuing research programme with lecturing in Bacteriology to science students at the University of Sydney. Returning to Denmark in 1947, he was in charge of bacteriology in the State Plant Laboratory, completing his service with seven years as Director until his retirement in 1968.

During his career Dr Jensen published more than 170 articles, of which 35 were very substantial contributions to the *Proceedings* of this Society. He became recognized as an outstanding agricultural microbiologist, particularly in connection with organic matter decomposition, nitrogen fixation and soil fertility; he was the recipient of many awards, both in his native Denmark and on the world scene. Hans Jensen played a significant editorial role in several internationally recognized journals and was commonly consulted as examiner and research adviser. It was a measure of the man's influence, and of the high regard in which he was held, that colleagues and friends commemorated his seventieth birthday with a volume of scientific articles by thirteen contributors from eight countries representative of north-south and east-west hemispheres.*

Dr Jensen's research interests were wide indeed, ranging from several major contributions to the activity, nature and systematics of soil bacteria (notably actinomycetes and corynebacteria) to more immediately practical matters concerned with the decomposition of soil organic matter, the degrading of diverse herbicides and other potent organic molecules which under present day farming practice find their way into the soil. At no stage did Jensen restrict himself to a narrow field although, of course, the emphasis was adjusted from time to time. For example his interest in biological nitrogen fixation was maintained over some thirty years and included many investigations with both free-living and symbiotic forms. Particularly it was Jensen's critical quantitative studies of the significance and requirements of non-symbiotic nitrogen fixation which brought about a more realistic re-assessment of its limited contribution to maintaining soil nitrogen under conditions of agricultural practice in Australian wheat production. At the same time Jensen contributed most significantly to a better knowledge of the taxonomy of the free-living aerobic nitrogen-fixing bacteria as well as the pasture legume: *Rhizobium* association. Study of the latter was initiated during the last part of his period as Macleay Bacteriologist, at a time when

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*Festskrift til Hans Laurits Jensen — Gadgaard Nielsens Bogtrykkeri, Lemvig, 1968.

there had been very little sound work along these lines accomplished on the Australian scene, but when this country's work on symbiotic nitrogen fixation was about to take off at a greatly accelerated pace. Jensen's work in Australia and, less intensively, after his return to Denmark, remains a valuable part of our body of knowledge of this vastly important symbiosis.

Besides these major continuing interests Jensen was responsible for comprehensive articles in the wider field of soil microbiology and methodology. According to the needs of the occasion (including the war years) he was also prepared to give his time ungrudgingly to the investigation of practical aspects of microbiology which took in such diverse topics as the suitability of substitute agars, dew-retting of flax, ensilage, antifungal preservatives and the safe storage of blood.

For most of his stay in Australia Jensen was of necessity a lone worker, obliged to make the best he could of a quasi-official arrangement between the Society and the University of Sydney. A shrinking effective budget as post-war inflation leapt ahead at the same time as the income from the Macleay bequest remained static, or declined, was a constant restraint. The late Professor Hugh Ward helped by extending the hospitality of the Bacteriology Department to provide accommodation and some basic facilities; considerable support was provided by several Banks, particularly in providing a greenhouse and permitting the employment of a graduate research assistant. Despite these limitations Jensen was able by temperament and ability to use his time in Australia as probably the most productive period of his career. He did this with a series of deceptively simple but beautifully designed and executed experiments that gave clear answers to well directed questions. At times indeed so economical of time and effort was his experimentation, so free his work area of clutter, it seemed that papers could be written directly from the laboratory bench. Hans Jensen truly belonged to the classic tradition of Winogradsky and Beijerinck; his work was a conjunction of impeccable technique and ability to think a problem through to a logical and practical significant conclusion — qualities sometimes missing from contemporary "black-box, publish-or-perish" exponents of the art.

We count ourselves privileged to have enjoyed his professional co-operation and personal friendship both in Australia and when we visited him, his wife Helene and his family in Denmark. Agricultural microbiology is in so many ways the better for Hans Jensen's long and distinguished contributions.

Y. T. TCHAN J. M. VINCENT

A KEY TO THE MEMORIAL SERIES OF THE LINNEAN SOCIETY OF NEW SOUTH WALES (1928-1978)

In October 1978, the Council of the Society resolved to commission an essay on the late Dr Hans Laurits Jensen, Macleay Bacteriologist from 1929 to 1947, for the Memorial Series. The essay, twenty-sixth in the series, is printed in this issue (pp. 131-132). It is the latest in a line now spanning more than fifty years of publication. Council believes members will be interested in the record of that half-century and, accordingly, has ordered the issue of a key to the series.

A footnote to the first article, dated 1928, explained the original intention: 'The Memorial Series will comprise memorials prepared, from time to time, under the direction of Council, of distinguished Members of the Society who have died'. That has remained a guide to successive Councils. As a result the Society possesses a valuable biographical record, a record believed to be unique among the scientific societies of this country until the Australian Academy of Science began to publish memorials of its deceased Fellows about twenty years ago.

Each memorial article was published in the Society's *Proceedings* and in limited numbers of separate offprints for private distribution. Until at least the early 1960s separate issues generally appeared with distinctive olive-green or grey printed covers. More recently they have come in humbler style.

Of the entries in the following list, only that for J. J. Fletcher calls for particular comment. It alone was not printed as such in the *Proceedings*. In fact, only the separate issue indicates its place in the series. This unusual situation arose because the appreciation by Baldwin Spencer had already appeared in the journal before Council decided to establish the Memorial Series. The Haswell memorial set a pattern and so when Council resolved to commemorate Fletcher in the same style a list of his publications was needed to supplement Spencer's article. That list, compiled by the then Secretary (A. B. Walkom) was printed in the *Proceedings* for 1929. The separate issue of the Fletcher memorial (1929) consists of the list of papers appended to reprints of the text and portrait first published two years earlier. Like its immediate neighbours in the series, the Fletcher separate has pagination different from that of copy in the *Proceedings*. The practice of re-numbering pages for offprints was abandoned after issue of No. 3.

THE MEMORIAL SERIES Nos. 1-25 (1928-1978)

1 William Aitcheson Haswell, 1854-1925 (By H. J. C[arter])
Proceedings 53, 1928: 485-498. Plate.

2 Joseph James Fletcher, 1850-1926 (By W. B[aldwin] S[pencer] (and) [A. B. Walkom])
Proceedings 52, 1927: xxxiii-xliii. Plate.
Proceedings 54, 1929: 686-687.

3 Joseph Henry Maiden, 1859-1925 (By A. H. S. L[ucas])
Proceedings 55, 1930: 355-370. Plate.

4 Richard Hind Cambage, 1859-1928 (By E. C. A[ndrews])
Proceedings 59, 1934: 435-447. Plate XIX.

5 Charles Hedley, 1862-1926 (By C. A[nderson])
Proceedings 61, 1936: 209-220. Plate X.

6 Tannatt William Edgeworth David, 1858-1934 (By H. J. C[arter] and W. R. B[rowne])
Proceedings 61, 1936: 341-357. Plate XVII.

7 Arthur Henry Shakespeare Lucas, 1853-1936 (By H. J. C[arter])
Proceedings 62, 1937: 243-252. Plate XII.

8 Walter Wilson Froggatt, 1858-1937 (By A. B. W[alkom])
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9 Herbert James Carter, 1858-1940 (By A. B. W[alkom])
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10 Alexander Greenlaw Hamilton, 1852-1941 (By E. C. A[ndrews])
Proceedings 69, 1944: 176-184. Plate III.

11 Robin John Tillyard, 1881-1937 (By J. W. E[vans])
Proceedings 71, 1946 (1947): 252-256. Plate XVII.

12 Carl Adolph Sussmilch, 1875-1946 (By E. C. Andrews)
Proceedings 73, 1948: 242-248. Plate XIV.

13 ERNEST CLAYTON ANDREWS, 1870-1948 (By W. R. B[rowne] and A. B. W[alkom])
Proceedings 77, 1952: 98-103. Plate II.
14 GUSTAVUS ATHOL WATERHOUSE, 1877-1950 (By A. B. W[alkom] and A. J. N[icholson])
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15 GEORGE DAVENPORT OSBORNE, 1899-1955 (By W. R. B[rowne])
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16 WILLIAM NOEL BENSON, 1885-1957 (By W. R. B[rowne])
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17 SIR DOUGLAS MAWSON, 1882-1958 (By J. B. C[leland])
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18 ANTHONY MUSGRAVE, 1895-1959 (By G. P. W[hitley])
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21 ANTHONY REEVE WOODHILL, 1900-1965 (By D. J. Lee and D. F. Waterhouse)
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22 WALTER LAWRY WATERHOUSE, 1887-1969 (By I. A. Watson)
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23 GILBERT PERCY WHITLEY, 1903-1975 (By T. G. Vallance)
Proceedings 101, 1976 (1977) : 256-260.
24 WILLIAM ROWAN BROWNE, 1884-1975 (By T. G. Vallance)
Proceedings 102, 1977: 76-84.
25 ARTHUR BACHE WALKOM, 1889-1976 (By T. G. Vallance)
Proceedings 102, 1977 (1978) : 148-155.

T. G. VALLANCE

Corrigendum

In the W. R. Browne memorial (*Proceedings,* 102, 1977) on page 80, lines 28-29, the words '. . . had graduated from the university.' should have been printed '. . . left the university.', as in the original typescript.

ADVICE TO AUTHORS

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> BULLOUGH, W. S., 1939. — A study of the reproductive cycle of the minnow in relation to the environment. *Proc. zool. Soc. Lond.*, Ser. A, 109: 79-108.

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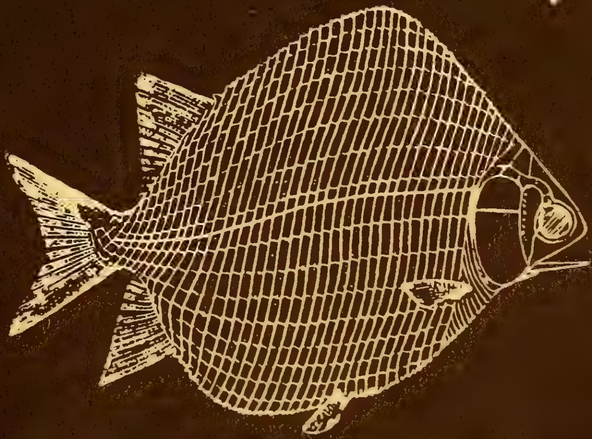

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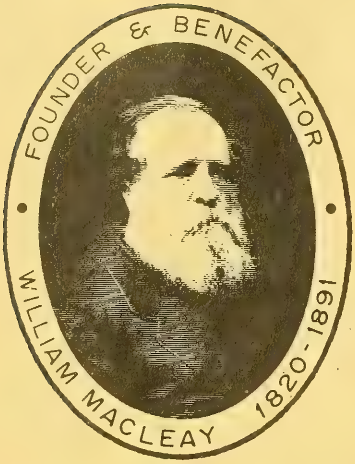

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Cover motif: *Cleithrolepis granulata* Egerton
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PROCEEDINGS
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VOLUME 103
PART 3

Fenestrate Bryozoans with Large Apertural Form in the Carboniferous of Eastern Australia

BRIAN A. ENGEL

ENGEL, B.A. Fenestrate bryozoans with large apertural form in the Carboniferous of eastern Australia. *Proc. Linn. Soc. N.S.W.* 103 (3), (1978) 1979: 135-170.

Study of Australian Carboniferous cryptostome fenestrate bryozoans has revealed that the number of rows of zooecial apertures per branch is transitional between species of *Fenestella* Lonsdale and *Polypora* M'Coy and is thus not necessarily the best basis for generic distinction. Apertural studies have demonstrated that simple fenestrate apertures fall into two size distributions with the larger diameter forms bearing a wide, low, peristomal collar in association with an operculum-like covering which bears a central boss-like projection. Species belonging to this group include most Australian Carboniferous forms previously referred to *Polypora* together with several two-rowed species which, otherwise, would normally be assigned to *Fenestella*. To separate these large apertural forms, two very closely related genera have been erected, *Australopolypora* gen. nov. and *Australofenestella* gen. nov., the former containing the multi-rowed species and the latter the two-rowed species.

Six species have been assigned to *Australopolypora* of which two are new: *Australopolypora rawdonensis* and *Australopolypora keppelensis parvula*. Seven species have been referred to *Australofenestella*, four of which are new: *Australofenestella brookeri, Australofenestella trevallynensis, Australofenestella* (?) *keepitensis,* and *Australofenestella stroudensis minuta*.

Brian A. Engel, Department of Geology, University of Newcastle, Newcastle, Australia 2308; manuscript received 10 January 1978, accepted in revised form 26 June 1978.

INTRODUCTION

Previously described species of fenestrate bryozoans with three or more rows of apertures per branch, from the Carboniferous strata of eastern Australia, have all been placed in *Polypora* M'Coy (1844) without generic comment, obviously because this broadly defined genus was the only available taxon suitable for their reception. In total, eight such species have been described, five by Crockford (1947, 1949) and three by Campbell (1961).

The original diagnosis of *Polypora* (M'Coy 1844) required these fenestrate forms to have "three to five rows of apertures per branch, apertural peristomes which were never raised and non-poriferous dissepiments". These broad generic limitations were not strictly observed even by M'Coy who in the same paper described *Polypora verrucosa* M'Coy, in which the peristomal collars were strongly elevated (*vide* Miller 1963). It is thus not surprising that several of the above Australian species, which also exhibit strong peristomal exsertion, were placed by their authors in *Polypora*.

Over the long interval since M'Coy's diagnosis of *Polypora* was first published, it has been common practice to place regular fenestrate species, with non-poriferous dissepiments, into either *Fenestella* or *Polypora,* depending for the primary generic assignment almost entirely upon the number of rows of zooecial apertures per branch. Effectively, this aspect has assumed a weighting in taxonomy considered to be out of proportion to its importance for reasons given below. The relatively few species which have escaped this rigid dichotomy have depended upon the presence of some exotic structural aspect, as can be found in various contemporary genera such as *Archimedes* Owen 1838, *Hemitrypa* Phillips 1841 and *Semicoscinium* Prout 1859.

Because of the virtually uncontrolled addition of many hundreds of species to *Fenestella* and *Polypora,* both broadly-defined genera have become totally unwieldy, impractical units for which only tentative efforts have been made in more recent times to devise some scheme of subdivision. With respect to the genus *Polypora,* the only major attempt at a key classification has been made by Russian palaeontologists who, as a result of their experience over some forty years, have based their grouping of species largely upon the number of rows of zooecia per branch, thus extending the style of demarcation between *Fenestella* and *Polypora* to the various species of *Polypora* with higher numbers of zooecial rows. Australian experience with a limited Carboniferous-Permian sample would suggest that this method can have direct stratigraphic relevance but at the same time it obscures some of the more basic morphological and genetic relationships which may lead to a more satisfactory subdivision.

Revised diagnosis of POLYPORA *M'Coy.* Appreciating the problems accompanying the unrestricted growth of *Polypora,* Miller (1963) re-described M'Coy's type material with the object of establishing a suitable standard for subsequent investigations. This emended generic diagnosis appears to have been written largely with the morphology of the type species in mind. In this respect it is rather restrictive in some morphological aspects, variations of which may be considered legitimately to fall within the limits of the genus. In particular, apart from the regular multi-rowed fenestrate features, *Polypora* is additionally re-defined as having (a) non-carinate branches; (b) regularly spaced, elevated nodes situated on the centreline of the branch; (c) hexagonal-polygonal zooecial bases arranged side by side on a flat basal plate; (d) a microstructure of tubules in the branch wall surrounding apertural margins and forming cores of nodes.

Australian Carboniferous species do not readily conform with some of these requirements for the following reasons.

Nodes, if developed at all, are scattered in a relatively haphazard fashion over the branch surface being placed adjacent to the proximo-central rim of an aperture in any row. There is a tendency to approach a vaguely central arrangement in a number of the species but none of them has "regularly spaced, elevated nodes situated on the centreline of the branch", the lack of which, given the current assessment of nodal function, is not considered to be sufficient reason for their exclusion from the genus.

In addition, the Australian material is preserved only as external and internal moulds with an absence of primary skeletal remains and hence the inclusion of tubular microstructure as an essential aspect becomes an impractical requirement. It is perhaps relevant to comment that an apparent lack of data on both nodes and microstructure in *Polypora marginata* M'Coy did not deter Miller (1963) from regarding it as a legitimate member of the revised genus.

As a possible alternative to the key classification of the Russian school, Miller suggested that further subdivision of *Polypora* could ultimately be based upon the following features: (a) presence or absence of nodes on the obverse of the branches; (b) arrangement of these nodes with respect to a central carina; (c) organization and location of the zooecial chambers in relationship to the 'basal plate'.

Apparently this suggested scheme was intended to result in new genera/subgenera, for the absence of nodes and the presence of a median carina would appear to be incompatible with his emended diagnosis of *Polypora.*

Over the decade since these suggestions were put forward, ideas on the importance of nodes have changed, a situation foreshadowed by Miller (1963, p.168).

Personal experience with Australian fenestrates appears to downgrade nodal distribution to the species or even varietal level, and it is difficult to justify any greater importance in taxonomy. Tavener-Smith (1973) has also questioned the validity of Miller's revised diagnosis regarding nodal occurrence and has rejected the requirements as unwarranted and over-restrictive.

Morphological Considerations

Having questioned the conventional relationship between *Fenestella* and *Polypora* and finding little else in the definition of either genus that is convincingly diagnostic, a further search was made for other features which could be of some value. An intensive morphological and statistical treatment was made of approximately 300 specimens including all type specimens of Australian Carboniferous species previously referred to either *Fenestella* or *Polypora*. This study has demonstrated predictably that much more attention should be given to individual zooecial characteristics. Whilst inter- and intra-zooecial variation is obviously basic in all descriptions, zoarial details have tended to dominate taxonomic studies at the generic/specific level almost to the exclusion of individual zooecial details. Historically, it has been easier, largely because of indifferent preservation, to record such items as zooecial spacing rather than to delineate the characteristics of individual chambers. In more recent years, most authors have realized the need to include zooecial characteristics and such items as the basal outline of zooecial chambers now form a common component of most new descriptions.

The following observations on morphological details have arisen from the present study:

Number of zooecial rows per branch. The conventional method of subdivision of species between *Fenestella* and *Polypora* on the basis of either two or three (and more) zooecial rows per branch was found to be increasingly impractical for Australian Carboniferous fenestrates. There exists a trend for two-rowed species, commonly assigned to *Fenestella,* to develop a third row of apertures prior to each branch bifurcation throughout the Carboniferous interval. Low zonal species have no pre-bifurcation apertures, mid-zonal species normally have one or two additional pre-bifurcation apertures and by the late Carboniferous there are commonly at least five or six and often more apertures arranged in a very distinct third row which extends for a considerable distance back towards the previous branch division. Since dominantly three-rowed species, normally placed in *Polypora,* commonly have a reduction to two rows of apertures for some distance immediately post-bifurcation, it is readily apparent that these tendencies lead to species which are obviously neither two- nor three-rowed in character (Fig. 3, 9). This problem of generic separation has already been cited by Campbell (1961) in the case of *Fenestella*? *altinodosa* Campbell where after doubtfully assigning the species to *Fenestella,* this author concluded that "perhaps it would be equally well placed in *Polypora*" (Campbell, 1961, p.459), a change which has now been proposed herein for other morphological reasons.

Many previous authors have noted the undoubtedly polyphyletic nature of both *Fenestella* and *Polypora* but none appears to have questioned the validity of using the number of apertural rows as a primary generic indicator. Based upon the present study of Australian species, it is suggested that at least some of the present taxonomic difficulties stem from this assumption. The change from two to three rows of apertures would appear to be a transitional one which does not seem to have been discussed previously with sufficient clarity. Excellent support for this transitional change comes from the genus *Septatopora* (Engel, 1975), where other highly diagnostic morphological features result in this one genus containing a group of species which progressively change from two to four or five zooecial rows per branch over the duration of the Carboniferous Period.

Zooecial apertures. The most significant information to emerge from the present investigation was that zooecial apertures could be assigned to three compact varieties as outlined below:

1. Fenestellid type — a simple, circular aperture with a narrow peristomal rim, the degree of exsertion of which was from weak to moderate depending upon the obverse branch profile. Mean apertural diameter was in the range of 0.08-0.14mm. The group contained no apparent internal apertural structures and included most but not all Carboniferous species previously referred to *Fenestella* by Australian authors. Further subdivision of this group seems quite possible when coupled with additional morphological features.
2. Polyporid type — a large, simple, circular or oval aperture with a very broad peristomal collar which may be either entire (Fig. 2, 5) or open proximally in a horseshoe shape (Fig. 1, 4). Both conditions can be observed in the one specimen. External moulds of all members of the group reveal the presence of an operculum-like lid over the aperture. This cover bears either an elevated perforation or a spine-like projection, the exact nature of which is not evident in this form of preservation (Fig. 1, 7). The structure is usually placed in the centre of the lid but can be eccentric in some cases (Fig. 3, 8). Rare specimens have been observed to bear minute septa-like projections around the margin of the aperture as recorded in the type species *Polypora dendroides* M'Coy by Miller (1963). Mean apertural diameter is between 0.14-0.23mm. Species belonging to this group include most of the Australian Carboniferous forms previously referred to *Polypora* together with a small group of uncommon species which in all other aspects would have been reasonably placed in *Fenestella*.
3. Septatoporid type — a circular, strongly exserted to stalked aperture with a thin, high, calice-like peristome. Within the aperture there are eight vestibular septa radiating from a small central orifice. Mean apertural diameter is between 0.07-0.13mm. Species of this group were previously placed in either *Fenestella* or *Polypora* depending upon the number of rows of zooecial apertures per branch. Apart from the apertures, other morphological aspects of this group leave little doubt of its separate status which has been elaborated elsewhere (Engel, 1975).

With reference only to the fenestellid and polyporid types, it is significant that there is a separation of apertures into two size ranges with the larger forms bearing a low, wide, peristomal collar coupled with an operculum-like covering over the orifice. It is also important that this separation does not conform with the conventional generic demarcation, based upon the number of rows of zooecial apertures per branch.

The fact that some apertures bear traces of up to sixteen, weak, septal projections would support the contention (Engel, 1975) that there is an undoubtedly close relationship between the polyporids and the new genus *Septatopora* Engel.

Zooecial chamber outline. The use of this feature as a diagnostic aspect for fenestrate genera is not without considerable risk of error. Wass (1968) has demonstrated that chamber outline is very sensitive to the exact level at which it has been recorded relative to the 'basal plate' of the specimen. Therefore, the use of random tangential thin sections for the identification of shape must remain a hazardous process, unless all shape changes have been recorded by serial sectioning.

Morozova (1974) has expressed great confidence in the diagnostic value of chamber shape by using it with several other mesh characteristics to fragment the genus *Fenestella* (s.l.) into fourteen new genera. The present study does not entirely support the method adopted because of the difficulty in quantifying the actual shapes observed. When a chamber is studied as a three-dimensional internal mould, the distinction between triangular, trapezoidal and pentagonal shapes becomes a function of the branch width and the extent to which the chamber has been exposed down the sides of the branch. It is possible to recognize all three shapes on different branches within the one colony, given variable branch widths and different amounts of stripping of the outer calcareous layers. Thin sections cut at varying levels may record all of the above shapes, terminating with a bean-shaped outline when the section is deep enough to intersect the distal extension of the vestibule which leads to the obverse external aperture.

Experience with Australian material would suggest that much more intensive serial sectioning of fenestrate species is necessary before zooecial chamber shape can be applied as a reliable diagnostic feature. There is no doubt, however, that the feature has a role to play in future classifications of fenestrate species.

Nodes. In the species with three or more rows of apertures, described in this paper, nodes are frequently lacking. In the few cases where they are present, they occur randomly in any row being situated adjacent to the proximo-central rim of a particular aperture (Fig. 1, 8 & 9). This forms an interesting contrast to the contemporary *Septatopora* genus where the nodes are located on the distal rim of the apertures. Due to the width of the peristomal collar in the polyporids, it is not uncommon to see the node fused into the margin of the collar (Fig. 1, 8). The point to be noted is that there is a very close relationship of each node with a particular aperture and that there is not the development of a regular central row of nodes as recorded in the type species. Nodes in the dominantly two-rowed species described in this paper follow a regular, linear, nodal pattern when developed.

Modes of preservation. One of the central difficulties experienced in working with fenestrate species concerns variation in the modes of preservation of specimens.

Eastern Australian Carboniferous material is almost entirely preserved as external and internal moulds, with a consequent lack of primary skeletal material. Whilst this effectively prevents the preparation of thin sections, it undoubtedly provides excellent preservation of all external characteristics coupled with useful internal reconstructions of the original zooecial chambers.

The few silicified specimens extracted from local limestones have a worn, open skeletal appearance which compares very badly with the surface details available from moulds. This is possibly due to incomplete replacement or post-depositional abrasion, for the criticism is not true of this style of preservation in other regions.

A major problem arises in comparative studies because of different modes of preservation. Many Russian species are illustrated only with figures of thin sections which have been made at unspecified levels within the zoarium. It is impossible to compare these with the fine surface sculpture available from moulds. Comparative work is therefore reduced to the level of mesh comparisons which are, in themselves, insufficient for positive diagnosis in many cases. Undoubtedly these constraints of preservation have led to much duplication in the published literature.

TAXONOMY

Biologically, it would seem that the morphological details and dimensions of individual zooecia may have more relevance than the number of them that can be packed into an ever expanding branch width. This opinion needs substantiation from other workers since many older publications are deficient in this type of data, making literature comparisons very inconclusive.

Pending wider consideration of the classification value of individual zooecial details as proposed in this paper, a relatively conservative taxonomic approach has been adopted. Instead of grouping all the species within one genus, two new genera are proposed namely *Australopolypora* gen.nov. and *Australofenestella* gen.nov. In the former, all multi-rowed, non-carinate species are grouped together into an evolving stream which permits reasonable comparison with the many existing species of *Polypora* M'Coy. Similarly, the dominantly two-rowed, carinate species are placed together in the second genus facilitating a ready comparison with species of *Fenestella* Lonsdale. Thus instead of being incompatible with the classical dichotomy based on rows of apertures, the new genera build on that basis and extend the definitions to include the apertural characteristics.

This compromise reduced the strength of the argument that like apertures should be grouped together but it is the only realistic course to adopt in the confused field of fenestrate bryozoan taxonomy. It must be stressed however that the new genera exhibit a much closer relationship than the nomenclature would suggest.

Reluctance to make major changes in the present generic status flows from the fact that the eastern Australian Carboniferous occurrence of fenestrate species is very restricted and is not necessarily representative of world-wide distribution. The present review of this fauna has revealed, after contractions by synonymy, a current total of fifteen species of *Fenestella,* seven species of *Australofenestella,* six species of *Australopolypora* and nine species of the new genus *Septatopora* (Engel, 1975) together with less common examples of *Archimedes, Hemitrypa* and *Semicoscinium.* On the basis of such a small sample it is unwise to propose major taxonomic shifts. However, the morphological trends evident in this pilot study of a relatively uncomplicated fauna could possibly have wider implications for the considerably larger and more diverse faunas in other parts of the world.

Abbreviations. All abbreviations used in the statistical treatment of fenestrate mesh are of standard form as cited in Engel (1975, p.577).

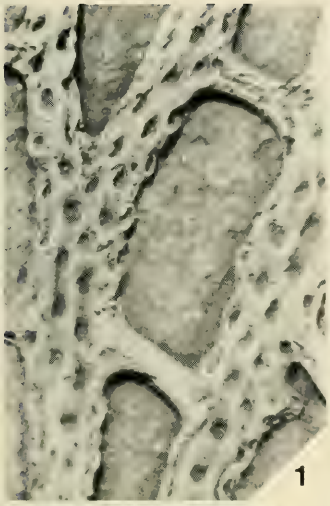
Repositories. Catalogued specimens have their number prefixed by the letter 'F', preceded by the following Museum coding:
QU = Queensland University; QGS = Queensland Geological Survey; NEU = University of New England; NU = University of Newcastle; SU = University of Sydney.

Fig. 1. (All except 6 prepared from latex casts.)

1-3. *Australopolypora palenensis* (Crockford). **1, 2,** obverse surface showing wide, distally-inclined apertures with distinct, low, peristomal collars of similar orientation, QUF62187, locality Mt. Barney, x20, x30 respectively. **3,** obverse surface showing similarly arranged apertures and peristomes, QUF32248, locality Ridgelands (188848), x20.

4-5. *Australopolypora rawdonensis* sp.nov. **4,5,** obverse view of paratype showing horseshoe-shaped peristomes arranged in a fan-like form across the branch, NUF2345, locality NUL258, x15, x10 respectively.

6-9. *Australopolypora altinodosa* (Campbell). **6,** reverse view showing shape and arrangement of internal moulds of three rows of zooecial cells, NEUF4708A, locality NUL9, x20. **7-9,** obverse views of holotype illustrating: two-three zooecial row development; large open apertures with a boss-like projection on operculum; pseudo-carinal ornament in two-rowed branches; and large, broken, ribbed, surface spines, NEUF4708A, locality NUL9, x20, x20, x10 respectively.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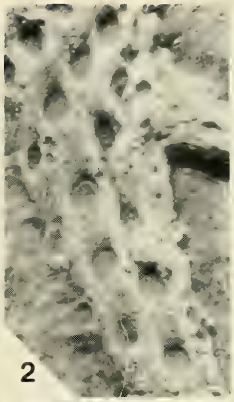
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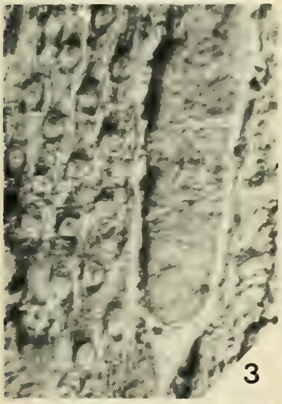
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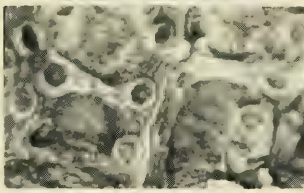
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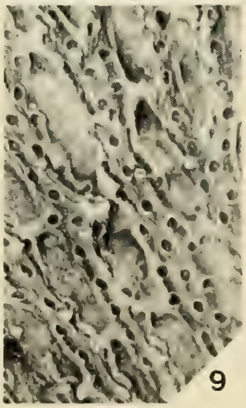
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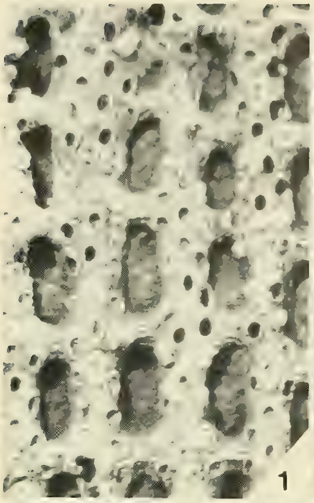
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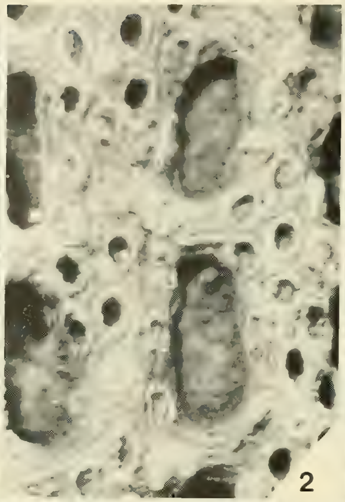
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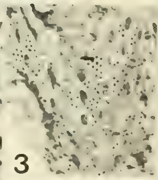
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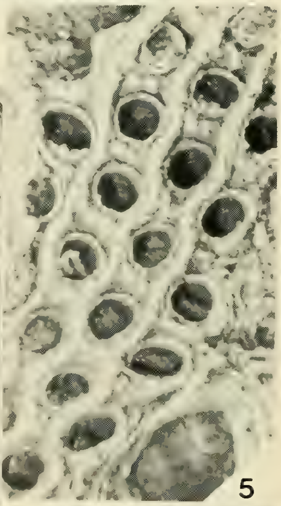
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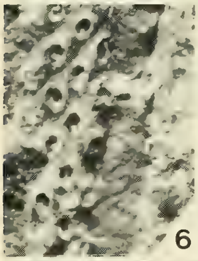
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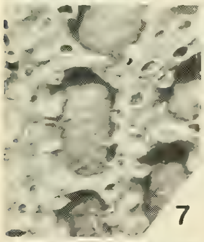
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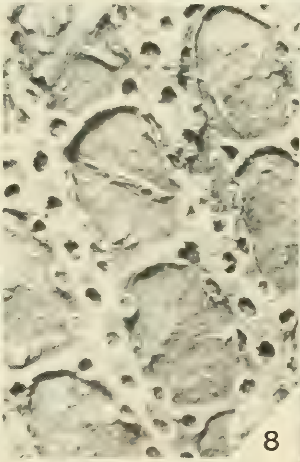
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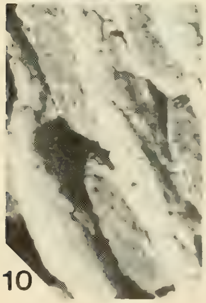
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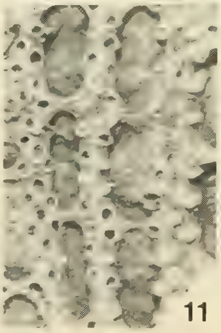
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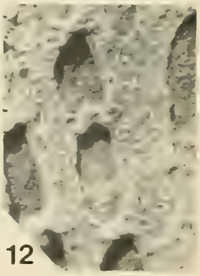
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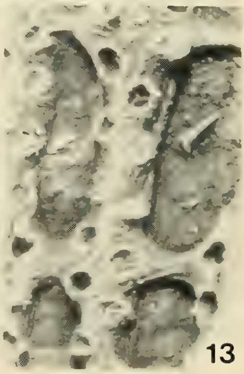
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Fossil localities. Where appropriate, localities are given by their number from the University of Newcastle Locality Index (NUL). Localities not in that index are given in full detail in the text. NUL9 — 3km east of Booral, N.S.W. (Campbell, 1961); NUL39 — Cameron's Bridge, Rouchel Brook, N.S.W. (Crockford, 1947); NUL258 — Barrington, N.S.W. (Cvancara, 1958); NUL454 — Isaacs Formation, Booral, N.S.W. (Campbell, 1961); NUL472 — Ridgelands 1 mile Military Map (Grid Reference 194827), Queensland (Fleming, 1969); NUL514 — Rawdon Vale, N.S.W. (Cobark 1:31680 Grid Reference 739454); NUL529 — Bonnington Formation, Trevallyn, N.S.W. (Roberts, 1965).

Photographic methods. Most specimens are preserved as internal or external moulds from which blackened latex casts were prepared for photographic purposes. These casts were then whitened with a layer of ammonium chloride before being photographed with a camera attached to a stereobinocular microscope.

SYSTEMATIC DESCRIPTIONS

Order CRYPTOSTOMATA Shrubsole & Vine 1882

Family FENESTELLIDAE King 1850

Genus *AUSTRALOPOLYPORA* gen.nov.

Type species. A. palenensis (Crockford) (= *Polypora palenensis* Crockford, 1949).
Diagnosis. Unifoliate or funnel-shaped fenestrate expansions comprising a uniform mesh of radiating, straight or gently sinuous, usually non-carinate branches joined by regular, non-poriferous, transverse dissepiments; zooecial apertures in three or more rows on obverse branch surface with increase and reduction in number of rows at branch bifurcations; apertures with low, broad, entire or horseshoe-shaped peristome, scarcely raised above the branch surface; apertures with an operculum which bears a raised boss; nodes, if developed, situated on the proximo-central rim of an aperture; reverse surface may bear spiny projections; both obverse and reverse branches may be smooth, granular or longitudinally striate.
Geological range. Late Visean — Permian.
Remarks. The distinctive apertural form and nodal development of this genus set it apart from the polyphyletic genus *Polypora* M'Coy.

Fig. 2. (All except **9** & **10** prepared from latex casts.)
1-2. *Australopolypora keppelensis parvula* subsp.nov. **1, 2,** obverse surface of holotype showing large, circular apertures with strong peristomal collars. Note nodal development and regular mesh, QUF32296, locality Ridgelands (194827), x20, x40 respectively.
3-5. *Australopolypora scalpta* (Campbell). **3-5,** obverse surface of holotype showing close packing of the large, circular apertures. Peristomal collars are depressed below branch level, NEUF4720B, locality NUL9, x3, x10, x30 respectively.
6-13. *Australopolypora neerkolensis* (Crockford). **6,** obverse surface of holotype, QUF25005, locality Mt. Barney, x10. **7, 11, 13** obverse surface illustrating low, peristomal collars surrounding wide apertures and sinuate longitudinal branch ornament. Note extended development of two zooecial rows after branch bifurcation, QUF10893, locality Ridgelands (265791), x10, x10, x20 respectively. **8,** obverse surface of specimen QUF10892, x10, locality Ridgelands (265791). **9, 10,** obverse view of eroded specimen showing erect vestibules leading up to the external apertures; and reverse view of zooecial cells showing irregularly pentagonal to elongate rhomboidal form, QUF43162, locality Yarrol (QUL2654), x10, x15 respectively. **12,** obverse view of specimen which has been flattened during preservation, NEUF5667, locality NUL390, x10.

Australopolypora rawdonensis sp.nov.

Fig. 1, 4-5

Diagnosis. Coarse form with wide branches and narrow dissepiments forming a rectangular mesh; zooecia in three or four rows per branch with five to nine apertures per fenestrule; apertures oval, with horseshoe-shaped peristomes arranged in a fan-shaped arrangement across each branch.

Description. Zoarium: Fan-shaped, being composed of radiating branches of unknown orientation; maximum radius 35mm. *Obverse surface:* (a) *Branches.* Very wide (m.BW 0.56mm), straight or broadly curved; branch cross section circular to slightly oval, commonly deflated; ornament of longitudinal, sinuous, pustulose ridges which meander around and between zooecial apertures. (b) *Dissepiments.* Narrow to medium width (m.DW 0.16mm) with only slight expansion at branch junctions; level with or below branches; ornament or ridges continuous on to branches. (c) *Fenestrules.* Sub-rectangular to rectangular; coarse, irregular, fan-shaped mesh; fenestrule openings equal to or greater than branch width resulting in an open meshed appearance; long, wide fenestrules (m.FL 2.71mm; m.FW 1.24mm). (d) *Carina.* Absent. (e) *Nodes.* Absent; a few specimens have rare, large, distant, irregularly spaced spines of presumed attachment significance. (f) *Zooecial apertures.* Medium size, oval (m.max.ZD 0.17mm); surrounded by a strongly pustulose, moderately elevated, horseshoe-shaped peristome, open on the proximal margin; aperture closed by a poorly-preserved, centrally-perforated plate. Oval-shaped apertures in central rows with long axis parallel to branch length; marginal rows with long axis at 45° to branch length, with peristome gap facing centre of branch, or drawn out into a proximally-directed club-shape. Apertures alternate in adjoining rows with strong marginal indentation of fenestrules but without dissepimental stabilization; zooecia in three or four rows per branch with increase to five pre-bifurcation and decrease to three post-bifurcation; apertures moderately spaced (m.Z-Z 0.37mm) with from 5 to 9 zooecia per fenestrule (m.Z/F 7.3).

Reverse surface. (a) *Form.* Round branches joined by level or depressed, narrower dissepiments; reverse normally deflated; ornament of fine, longitudinal ridges comparable with those of the obverse surface; several strong spines developed at base of zoarium. (b) *Zooecial bases.* Oval bases arranged in non-overlapping rows.

Material. Holotype NUF2343a/b (NUL258); Paratypes NUF2344, 2345, 2347, 2349a/b (NUL258); NUF2353 (NUL514); Others NUF2346, 2348 (NUL258); NUF2350, 2351, 2352, 2354, 2355 (NUL514).

Remarks. No other Carboniferous species of *Australopolypora* has been found with a comparable apertural arrangement. Pustulose, horseshoe-shaped peristomes of similar form can be found at a lower stratigraphic level in such species as *Fenestella allynensis* Roberts (1965). The specific name is derived from the locality of Rawdon Vale, N.S.W.

Stratigraphy. Of major significance is the fact that *A. rawdonensis* is the first development of a three-four rowed species in the Australian Carboniferous sequence. It is found to be of common occurrence in the *Rhipidomella fortimuscula* zone at various localities in the Stroud-Gloucester Syncline, N.S.W. This stratigraphic distribution would indicate that *Australopolypora* first appeared in the Australian record in the mid-late Visean in marked contrast to the much earlier Northern Hemisphere distribution of *Polypora* M'Coy.

Australopolypora palenensis (Crockford, 1949)

Fig. 1, 1-3

1949 *Polypora palenensis* Crockford, pp.427-8, text fig. 12.

1972 *"Polypora" palenensis* Crockford; Fleming, pp.7-8, pl.3, figs. 1-3.

Revised diagnosis. Coarse form with very wide branches and large sub-oval to rectangular fenestrule openings; zooecia in three to four rows per branch, five to nine apertures per fenestrule; apertures circular, distant, inclined distally with proximal rim level with branch and distal rim depressed below branch level.

Revised description. Zoarium: Fan-shaped, composed of radiating branches of unknown orientation; maximum radius 40mm. *Obverse surface:* (a) *Branches.* Very wide (m.BW 0.60mm) straight or broadly curved in an irregular pattern due to frequent bifurcation; cross-section circular to oval, but commonly deflated into a broad strap-like form; zooecial rows separated by faint longitudinal meandering ridges; interapertural spaces and sides of branch with similar sculpture. (b) *Dissepiments.* Slender to wide (m.DW 0.23mm); narrow forms have only slight expansion at branch junction; wide forms expand continuously from centre to branch junction resulting in variably-shaped fenestrules. (c) *Fenestrules.* Sub-oval to rectangular; coarse, irregular, fan-shaped mesh; fenestrule openings large, resulting in an open meshed appearance; long to very long, wide fenestrules (m.FL 3.1mm; m.FW 1.37mm). (d) *Carina.* Absent. (e) *Nodes.* Absent. (f) *Zooecial apertures.* Medium size, circular (m. ZD 0.14mm), but frequently deformed during preservation; peristome entire, uniform, low, but well developed, and inclined distally; apertures closed by a poorly-preserved, perforated plate. Zooecial chambers elongated proximally, with a distally-directed vestibule meeting the branch at a low angle, resulting in the apertural face also being distally inclined to the branch surface; this is achieved by having the proximal rim level with, or above the branch surface and the distal rim depressed into the branch in a suitable cavity; resultant longitudinal obverse branch profile is a sawtooth pattern along each row of apertures. Fenestrule indentation slight or lacking; apertures not stabilized with respect to dissepiments; zooecia in three to four rows per branch with increase to five or six pre-bifurcation, and decrease to two or three post-bifurcation; apertures distantly spaced (m.Z-Z 0.48mm) with from five to nine zooecia per fenestrule (m.Z/F 6.4).

Reverse surface: (a) *Form.* Rounded branches joined by narrower dissepiments generally situated below branch level; reverse commonly deflated; ornament of fine longitudinal striations normally obscured by a thin smooth overgrowth. (b) *Zooecial bases.* Oval with little or no overlap between rows.

Material. Holotype QUF25008, Neerkol Series, Por. 127V/202, Par. Palen, Mt. Barney, Queensland; Paratype QUF25009 (type area); Others QUF62187, QGSF10931a/b (type area); QGSF10909 (Neerkol Fm., Malchi Creek, Ridgelands 1 mile map ref. 265791); QUF32248 (Neerkol Fm., Ridgelands 1 mile map ref. 188848).

Remarks. Fleming (1972) amplified the brief description of Crockford (1949), and gave the first photographic illustration of the species. However, he omitted to emphasize the apertural inclination and its resultant obverse branch profile which, apart from the very coarse mesh, is the most diagnostic feature of the species. The low angle of intersection of the straight vestibule and branch surface has resulted in a distinctive form which has not been observed in any of the other described species of *Australopolypora.*

Small apertural septa noted by Fleming (1972) have not been observed in the material available to the writer. Some external moulds display a ring of very strong pustules around the peristome which are possibly equivalent to the tubules surrounding the apertures of *P. dendroides* M'Coy.

Stratigraphy. The majority of specimens of *A. palenensis* (Crockford) come from the Mt. Barney region or from Malchi Creek, near Rockhampton, Queensland. Lack of recognition of the species in other areas is probably a product of the brief description and inadequate type material upon which the species was based.

Though not common in New South Wales, it has been found in the present study at a number of localities where it was not listed by previous authors. In all cases it occurs with a *Levipustula levis* fauna, but because of an inability to establish the time equivalence of many of the occurrences of this fauna, it is not possible to assign *A. palenensis* a restricted range as Fleming (1972) has done for its occurrence in Queensland.

Australopolypora altinodosa (Campbell, 1961)

Fig. 1, **6-9**

1961 *Fenestella* (?) *altinodosa* Campbell, pp.458-9, p1.57, figs. 2a,b.

Revised diagnosis. Medium to coarse fenestrate with wide branches arranged in a sub-rectangular mesh; zooecia in two to three rows per branch, with three to four apertures per fenestrule; apertures large, distant with strong circular peristome; nodes very large and distantly spaced; branch ornament of strong ribbing.

Revised description. Zoarium: Small, fan-shaped fragment of unknown orientation; maximum radius 20mm. *Obverse surface:* (a) *Branches.* Straight, wide (m.BW 0.46mm), commonly deflated; obverse branch profile centrally elevated but without median carina; ornament of strong, longitudinal ribbing, about six in number with central rib becoming carina-like on two-rowed branches; some ribs continuous and sinuate, others only developed interaperturally; ribs on lateral slope of branch bear fine pustules; rib number rises to twelve pre-bifurcation. (b) *Dissepiments.* Medium width (m.DW 0.17mm); centrally straight with moderate expansion at branch junction; situated level with branches; ornament of strong ribs continuous on to branches. (c) *Fenestrules.* Elongate sub-rectangular to sub-oval; medium length and width (m.FL 1.75mm, m.FW 0.93mm). (d) *Carina.* Absent; role assumed by central prominent, sinuate, surface rib; early development of three rows of zooecia results in two such ribs over considerable distances. (e) *Nodes.* Very large, circular, oval-based with a diameter of 0.16-0.24mm; nodes very tall (⩾0.4mm), generally sloping distally with neither obvious termination nor superstructure evident; ornament of longitudinal ribbing; distantly spaced (m.N-N 0.90mm), irregularly placed along a central row; nodes on three-rowed branches are situated between the apertures of the central row but seldom on the centre line of the branch. (f) *Zooecial apertures.* Circular to slightly oval, large (m.ZD 0.20mm), surrounded by a prominent, moderately-exserted peristome; each aperture closed by an axially-perforated, domed, diaphragm-like plate; apertures alternate in lateral and median rows and are not stabilized with respect to the dissepiments; marginal rows with little or no fenestrule indentation; zooecia in two rows per branch with three rows developing up to 5mm prior to bifurcation; apertures distantly spaced in each row (m.Z-Z 0.49mm) with from three to four zooecia per fenestrule (m.Z/F 3.6).

Reverse surface: (a) *Form.* Branches with broadly semi-circular profile tapering slightly from obverse; dissepiments level with or slightly below branches; ornament of fine, straight, longitudinal ribbing. (b) *Zooecial bases:* Elongate, irregularly pentagonal in marginal rows with the central row being rhomboidal in shape.

Material. Holotype NEUF4708A, Booral, N.S.W. (NUL9).

Remarks. Campbell (1961) noted several unusual features about this species which caused him to have doubts about its correct generic category. His final choice of doubtfully grouping it with *Fenestella* Lonsdale is at variance with other morphological aspects, here considered to place it more appropriately with *Australopolypora*.

Unusual features noted by Campbell (1961) include: very high nodes placed randomly on any part of the obverse branch surface, an absence of any clearly defined median carina, and the very early development of a third row of apertures up to 5 mm prior to each branch bifurcation.

In addition to these aspects, the apertural form of the species is considered to align it closely with other Australian Carboniferous species of *Australopolypora.* It shares with them a very large circular aperture which is surrounded by a broad peristomal collar of distinctive appearance. It also exhibits the flat, centrally perforated plate which is presumed to have closed the aperture.

As discussed earlier, these apertural features are considered to be of greater diagnostic value than the number of rows of apertures which does not clearly group the species with either of the available generic categories. No comparable species has been described in available literature.

Stratigraphy. The single known specimen was described by Campbell (1961) from just below the main *Levipustula* bed at Booral, N.S.W., a locality considered to be of early Westphalian age. No other comparable material has been recovered from the type locality or elsewhere.

Australopolypora neerkolensis (Crockford, 1949)

Fig. 2, **6-13**

1949 *P.neerkolensis* Crockford, pp.426-7, text-fig. 10.
1962 *P.neerkolensis* Crockford, Campbell, pp.46-7, pl.13, figs. 1a-d.
1964 *P.neerkolensis* Crockford, Maxwell, p.58, [non pl. 13, figs. 8-9].
1964 *P. neerkolensis* Crockford, Hill & Woods, p.c.8, pl.C4, figs. 3-4.
1972 *P.neerkolensis* Crockford, Fleming, pp.5-6, pl.3, figs. 4-7.

Revised diagnosis. Medium-sized form with very wide branches and wide dissepiments set in a variable mesh of oval to sub-rectangular fenestrules; zooecia in three rows per branch, with three to five apertures per fenestrule; apertures large, circular, with centrally-perforated domed plate; carina lacking; nodes irregularly developed.

Revised description. Zoarium: Sub-parallel branches set in a narrowly-radiating fan-shaped zoarium of unknown orientation; maximum radius 50mm. *Obverse surface:* (a) *Branches.* Very wide (mBW 0.64mm); branch cross-section oval but commonly flattened by deflation, ornament of fine pustules with variable development of longitudinal ridges between apertures; ornament strong on branch sides; two-rowed branches can have a raised central rib of carina-like form. (b) *Dissepiments.* Medium to broad (m DW 0.27mm); outline highly variable with some expanding continuously from their centre to the branch junction, whilst others are narrow and straight without expansion; most dissepiments are inclined rather than vertical in position; situated level with or just below branches; ornament of strong ribbing continuous on to the branch surface. (c) *Fenestrules.* Oval to sub-rectangular; medium-sized mesh of variable appearance; some specimens have fenestrule openings equal to or narrower than branches resulting in a closed mesh appearance whilst others have thin extended dissepiments which produce an open-meshed form; medium length, medium to wide fenestrules (m FL 1.74mm; m FW 1.10mm). (d) *Carina.* Absent in all but short post-bifurcation segments where a central prominent rib can develop a carina-like appearance between the two rows of apertures which are present in that region. (e) *Nodes.* Irregularly developed nodes occur on some specimens, being placed adjacent to, or forming part of, the apertural peristome on its proximal side in any apertural row. (f) *Zooecial apertures.* Large (m ZD 0.20mm), circular to oval, being surrounded by a prominent, entire peristome; apertures crossed by an arched, centrally perforated plate which in external moulds bears a raised central boss which can rise above the level of the peristome; usually three rows per branch with increase to four or five pre-bifurcation and decrease to two or three rows post-bifurcation; apertures distantly spaced in each row (m Z-Z 0.44mm) with from three to five apertures per fenestrule (m Z/F 4.3); apertures in adjoining rows very closely packed with less than a zooecial diameter separating them diagonally; apertures may indent fenestrule margin according to the degree of branch deflation, and are not stabilized with respect to dissepiments.

Reverse surface: (a) *Form.* Narrowly-rounded branches joined by level or slightly depressed dissepiments; thin outer surface smooth beneath which are developed numerous fine, longitudinal striations. (b) *Zooecial bases.* Elongate oval to elongate rhomboidal; irregularly pentagonal in two-rowed segments.

Material. Holotype QUF25005, Por.127V/202 Par. Palen, Mt. Barney; (Paratype — Specimen QUF24999 listed by Crockford (1949) as a paratype is actually a specimen of *Septatopora pustulosa*). Other specimens mentioned by Crockford are missing; Others QGSF10929-10930, 10934 (Type locality); QGSF10892-10894, Malchi Creek, Stanwell; QUF32189 Neerkol Creek, Stanwell; QUF32290, NUF2367-2368 (NUL472); QUF43162, 43199 Yarrol (Maxwell, 1964); NEUF5656-5670 Oaky Creek (Campbell, 1962).

Remarks. Crockford (1949) based this species on a poorly-preserved holotype which has resulted in considerable confusion with later determinations. Better-preserved material described by Campbell (1962) and Fleming (1972) has resulted in a clearer understanding of the species.

In the present study, considerable doubts have been entertained with respect to the conspecific nature of all the material placed by Fleming (1972) in this species. Features which exhibit most variation include: (a) *Mesh form.* Most specimens have broad, curved dissepiments associated with a closed-mesh appearance. A few specimens (QGSF10892-4) have thin, extended dissepiments with a resultant open mesh. This variation could be due to meshwork changes within a complete zoarium, but larger specimens from other regions do not support such a proposal. (b) *Zooecial apertures.* Well preserved branches have a round profile with moderately-exserted apertures which indent the fenestrule margin, thus having a somewhat similar appearance to that of *Septatopora pustulosa* (Crockford) with which it was confused by both Crockford (1949) and Maxwell (1964). Many other specimens have strongly-deflated, strap-like branches in which the apertures are also flattened. The difference in appearance between these two states of preservation requires a very detailed inspection for transitional stages between the two extremes. (c) *Apertural diameter.* Open-meshed specimens (QGSF10892-4) have a consistently larger zooecial diameter than that of most other specimens. The combination of this feature plus the mesh form may be significant, but, as it is possible to observe transitional stages, some uncertainty persists as to the correct specific designation. The holotype is most certainly too badly preserved to enable a positive diagnosis of the morphological limits of the species.

Stratigraphy. A. neerkolensis occurs in the *Levipustula levis* zone at various localities in New South Wales and Queensland.

Queensland specimens have been recovered from various levels in the Neerkol Formation (Stanwell), from the Poperima Formation (Yarrol), and from the type locality at Mt. Barney. New South Wales specimens have been recorded from the Kullatine 'Series' at Oaky Creek (Campbell, 1962) and from several localities of the *Levipustula levis* assemblage in the Gloucester-Bulahdelah region.

Fleming (1972) suggests that *A. neerkolensis* is restricted to the early portion of the *Levipustula levis* zone in the Neerkol Formation and its equivalents. Re-examination of specimens placed by Fleming (1960, 1969) in *Polypora* cf.*woodsi* from the *Auriculispina levis* zone, together with extra material collected from that zone (QUF32290, NUF2367, NUF2368) leave little doubt that they belong to *A. neerkolensis*. In these circumstances it would appear that this species is a long ranging one extending through the whole of the Neerkol Formation (2100m).

Australopolypora scalpta (Campbell, 1961)

Fig. 2, 3-5

1961 *P. scalpta* Campbell, pp.461-2, pl.60, fig.11.

Revised diagnosis. Medium-sized form of closely-meshed appearance; composed of very wide branches and very small, oval fenestrules; carina and nodes absent; apertures large, oval, medium-spaced being located in branch depressions from which a thin, entire peristome rises almost to branch level; apertures usually in four rows per branch.

Revised description. Zoarium: Gently-radiating branches of unknown orientation; maximum radius 12mm. *Obverse surface:* (a) *Branches.* Very wide (m.BW 0.86mm), generally flattened in cross-section; ornament of sinuous, longitudinal ridges between apertural rows; surface pustulose. (b) *Dissepiments.* Very wide (m.DW 0.74mm); strongly expanded at branch junction; level with branches; ornament of some surface ribbing, more evident on sides of both branches and dissepiments. (c) *Fenestrules.* Oval; very closely-meshed form dominated by wide branches and small fenestrules, resulting in a very closed mesh appearance; medium length, medium to wide fenestrules (m.FL 1.56mm; m.FW 1.14mm); actual fenestrule opening is approximately 0.8mm long by 0.3mm wide. (d) *Carina.* Absent; three to five linear rows of apertures are separated by prominent, sinuous ridges. (e) *Nodes.* Absent. (f) *Zooecial apertures.* Large, slightly oval (long diameter m.ZD 0.23mm); surrounded by a narrow, raised, entire peristome which does not quite rise to the level of the longitudinal, interzooecial, sinuous ridges, due to the moderate depression of the apertures below branch level; apertures in four rows per branch with increase to five pre-bifurcation and decrease to three post-bifurcation; apertures moderately to distantly spaced (m.Z-Z 0.41mm) with from three to four zooecia per fenestrule (m.Z/F 3.8); apertures in adjoining rows closely crowded, being separated diagonally by a distance of about half the zooecial diameter; fenestrules not indented by apertures which are also not stabilized with respect to the dissepiments.

Reverse surface: (a) *Form.* Flattened to weakly-rounded branches joined by broad, level dissepiments; branches bear weak, finely pustulose striations usually obscured by secondary thickening. (b) *Zooecial bases.* Broadly flattened, elongate-hexagonal or oval in outline.

Material. Holotype NEUF4720A/B, Booral, N.S.W. (NUL9).

Remarks. This highly distinctive species is readily recognizable by its depressed apertures and peristomes which are situated below the prominent, longitudinal, sinuous ridges separating the zooecial rows. No other comparable form has been observed in the literature.

The holotype remains the only known specimen despite intensive collecting at the type locality.

Stratigraphy. The type locality was recorded by Campbell (1961) as being above the main *Levipustula levis* bed at Booral, New South Wales (NUL9).

Australopolypora keppelensis (Crockford, 1946)

1946 *P. minuta* Crockford, p.133, text fig. 9.

[non] 1932 *P. minuta* Deiss, p.28. [*vide* Crockford, 1962].

1962 *P. keppelensis* Crockford, p.840.
1968 *P. keppelensis* Crockford, Wass, p.47, pl.12, fig.2.

Diagnosis. Medium to fine form; zooecia in three rows with three zooecia opposite each fenestrule; surface ornamented by discontinuous ridges and grooves between the apertures, and by a few small nodes.

Holotype. QUF7974a, Lakes Creek Beds (*Trachypora* horizon behind quarry), Rockhampton, Queensland. (Artinskian).

Geological age. Late Carboniferous — late Permian.

Australopolypora keppelensis parvula subsp.nov.
Fig. 2, 1-2

Diagnosis. Medium to fine species; regular mesh with wide branches and dissepiments forming uniform oval fenestrules; carina absent; nodes irregularly disposed adjacent to some apertures; apertures large, closely spaced in three rows per branch; peristome wide being either entire or proximally open; apertures closed by a flat, centrally perforated plate.

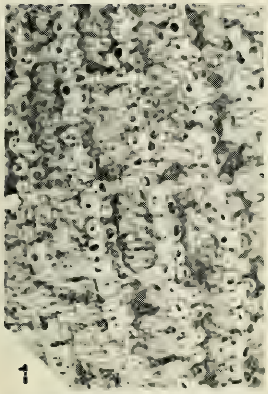
Description. Zoarium: Moderately-radiating, sub-parallel branches in flat expansion of unknown orientation; maximum radius 22mm. *Obverse surface:* (a) *Branches.* Medium to wide (m.BW 0.41mm) with circular cross-section becoming oval at bifurcation; ornament of sinuous ribbing between and around the apertures. (b) *Dissepiments.* Wide (m.BW 0.23mm), expanded from centre in a semicircular curve to the branch junction; level with branches; ornament of strong ribbing continuous on to branches. (c) *Fenestrules.* Oval to sub-oval; mesh fine to medium-sized and very regular; fenestrule openings and branch width of similar dimensions producing a very uniform mesh appearance; fenestrules short and of medium width (m.FL 0.84mm; m.FW 0.64mm). (d) *Carina.* Absent. (e) *Nodes.* Numerous, round (diam.ca. 0.1mm), bluntly-pointed, irregularly-developed nodes associated with apertures in all zooecial rows, but tending towards a near central arrangement; absent over large areas, but when present usually placed adjacent to the proximal rim of an aperture. (f) *Zooecial apertures.* Medium to large (m.ZD 0.15mm), circular to oval in outline; peristome prominent, slightly raised and faintly pustulose; peristome can be entire, but more frequently has a horseshoe-shaped appearance, with the proximal margin being smoothed over in a lip-like form; each aperture covered by a centrally-perforated plate; apertures in three rows per branch with increase to four pre-bifurcation, and decrease to two post-bifurcation; fenestrule indentation slight, and apertures not stabilized with respect to the dissepiments; apertures directed perpendicular to the curvature of the branch with some marginal elevation of the peristomes in the lateral rows; branch surface depressed between apertures which are closely spaced (m.Z-Z 0.26mm) with from two to four zooecia per fenestrule (m.Z/F 3.2); apertures in adjoining rows very close being diagonally separated by about half a zooecial diameter.

Fig. 3. (All except **6** prepared from latex casts.)

1-2. *Australofenestella brookeri* sp.nov. **1**, **2**, obverse surface of holotype showing large apertural form in a two-rowed species. Some apertures exhibit a central axial boss, NUF2541, x15, x30 respectively.

3. *Australofenestella stroudensis minuta* subsp.nov. **3**, obverse surface of holotype showing large apertural form and a low, central, nodose carina, NUF2396, locality NUL258, x20.

4-9. *Australofenestella stroudensis stroudensis* (Campbell). **4**, obverse surface of specimen previously referred to *Fenestella anodosa* Campbell, NEUF4701, locality NUL9, x20. **5**, obverse surface of holotype of *F. anodosa,* NEUF4700C, locality NUL9, x20. **6**, reverse surface of holotype of *A. s. stroudensis* showing arrangement of zooecial cells, NEUF4704B, x15, locality NUL9. **7-9**, obverse surface of holotype of *A. s. stroudensis* illustrating the large apertural form and distinct development of a strong boss or spine on the operculum covering the apertures, NEUF4704B, x20, x30, x10 respectively.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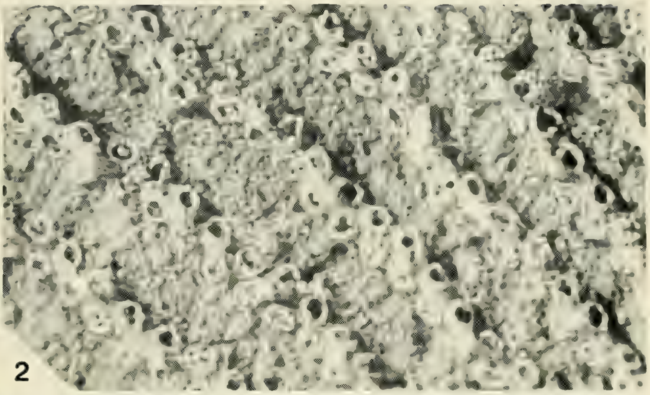
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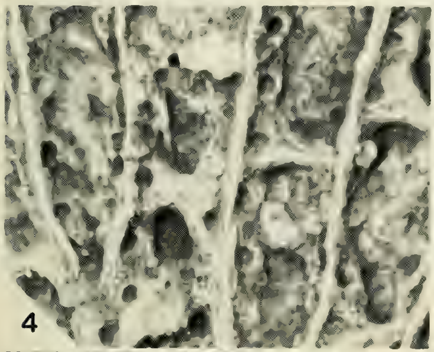
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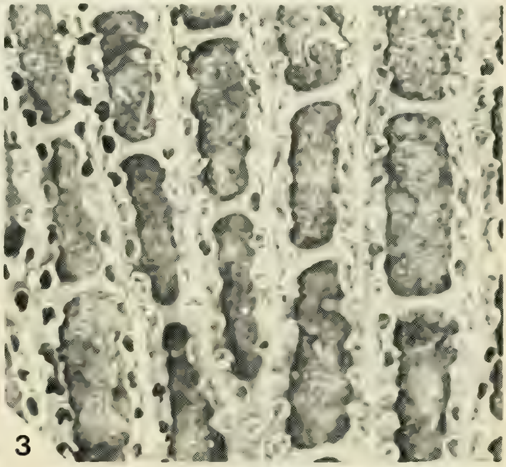
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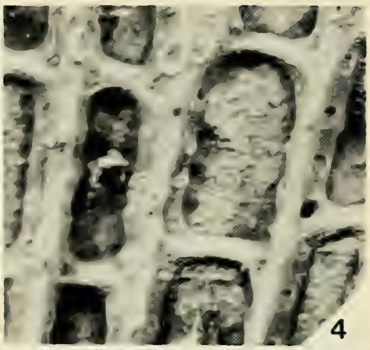
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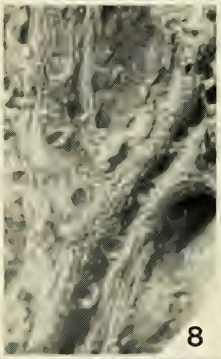
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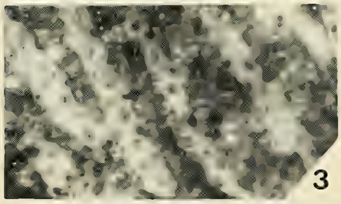
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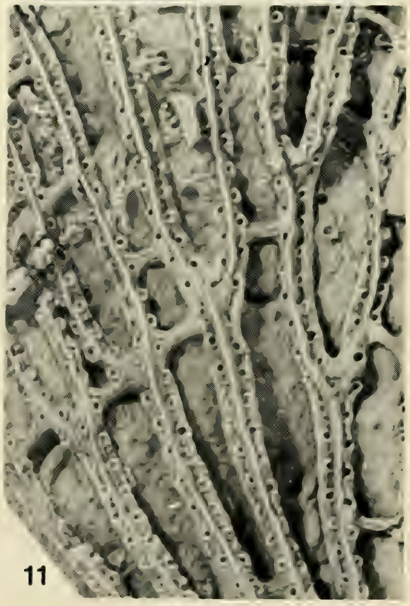
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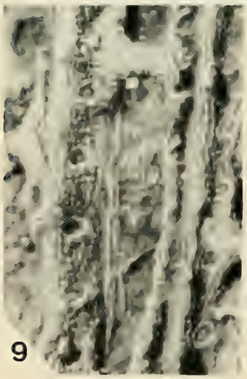
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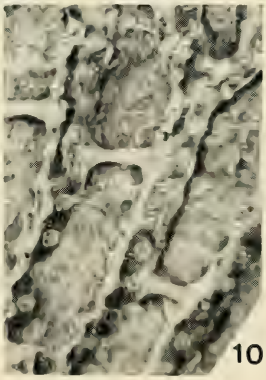
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Reverse surface: (a) *Form.* Rounded branches joined by medium-width dissepiments slightly below branch level; ornament of a smooth, thin, outer layer covering longitudinal striations. (b) *Zooecial bases.* Irregularly pentagonal in lateral rows with a rhomboidal form in the central rows.

Material. Holotype QUF32296 (NUL472); Paratypes QUF32297, QUF32295 (NUL472).

Remarks. The specimens which form the basis of this new subspecies were collected by Fleming (1960) who gave an unpublished description of them under the open nomenclature of *Polypora* cf. *keppelensis* Crockford. The same material was listed again in this form in Fleming (1969). Fleming considered his material to be identical with *A. keppelensis* except for their consistently shorter fenestrule length.

An examination of measurements made upon the type specimens of *A. k. keppelensis* and the specimens of *A. k. parvula,* given in Table 1, reveals that there are significant differences in fenestrule length and width, dissepiment width and zooecial spacing with consequent discrepancies in the associated space counts. Apart from these mesh differences, both groups display considerable similarity in apertural form and arrangement with some apertures of both having a proximal break in the peristome with an associated lip-like structure.

Based upon the present material from the late Carboniferous Neerkol Formation as well as that from the Artinskian Lakes Creek Beds (Crockford, 1946) and from younger Permian beds in the Bowen Basin (Wass, 1968), the following stratigraphic changes support the erection of the new subspecies: (a) there is a noticeable change in mesh dimensions from *A. k. parvula* in the Neerkol Formation to *A. k. keppelensis* from the Lakes Creek Beds with only slight further change in the later Permian specimens. (b) With the mesh change, the fenestrule form also changes from the regular oval shape in *A. k. parvula* to sub-oval to sub-rectangular in *A. k. keppelensis* from the Lakes Creek Beds to a normally sub-rectangular form in the younger *A. k. keppelensis* from the Bowen Basin. (c) Nodes of irregular distribution are very common in *A. k. parvula,* becoming rarer and finally absent in the Permian representatives.

Stratigraphy. All specimens of *A. k. parvula* were collected by Fleming (1960) from the locality NUL472 (QGSL1000) as geologically described by Fleming (1969). This location, east of the Ridgelands-Stanwell Road, occurs in the top 300m of the Neerkol Formation and has been assigned a late Carboniferous age.

A. k. keppelensis Crockford (1946) was originally described from the Lakes Creek Beds, east of Rockhampton. Because of breaks in the sequence, the section

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Fig. 4. (All except 3 & 6 prepared from latex casts.)

1-3. *Australofenestella (?) keepitensis* sp.nov. **1, 2,** obverse surface of holotype illustrating the close, irregular nodal distribution and the occasional development of a third central row of apertures. Note nodal variation (whiter marks) in **2** with both linear and zig-zag form. **3,** obverse fragment of holotype showing three-rowed zooecial arrangement, NEUF7466A, locality NEUL318, x6, x30, x10 respectively.

4-9. *Australofenestella malchi* (Crockford). **4, 5,** obverse surface of holotype showing large apertures, peristomal collars and large surface hemispherical depressions, QUF24952, locality Malchi Creek, x20, x20 respectively. **6,** reverse view of zooecial chambers, QUF10903, locality Malchi Creek, x20. **7,** obverse surface of specimen previously referred to *Fenestella cerva* Campbell. Note carinal development at branch bifurcations, NEUF4705H, locality NUL454, x20. **8, 9,** obverse views of holotype of *F. cerva* illustrating profile change as a result of deformation. Note boss-like projections within the apertures on **9,** NEUF4709A, locality NUL454, x20, x20 respectively.

10, 11. *Australofenestella cincta* (Crockford). **10,** obverse surface of deformed specimen showing strong boss-like structures within the peristome, NEUF4715E, locality NUL9, x10. **11,** obverse surface of well preserved specimen, QGSF10897, showing strong nodeless carina separating two rows of large apertures, locality Ridgelands (265791), x10.

connecting these two faunas is not known. On other faunal evidence, the Lakes Creek Beds were assigned an Artinskian age by Crockford, a determination supported by Kirkegaard, Shaw & Murray (1970).

Genus *AUSTRALOFENESTELLA* gen.nov.

Type species. Australofenestella malchi (Crockford) (=*Fenestrellina malchi* Crockford, 1949, pp.422-423, fig. 4)

Diagnosis. Unifoliate or funnel-shaped fenestrate expansions comprising a uniform mesh of radiating, straight or gently sinuous, weakly to strongly carinate branches joined by regular, non-poriferous dissepiments; large size zooecial apertures in two rows with variable increase in rows prior to bifurcation; apertures with low, broad, entire or horseshoe-shaped peristome raised only on branches with acutely triangular cross-section; apertures with an operculum which bears a raised boss; nodes vary from obsolete to blunt, widely-spaced cones arranged in a central row on the carina; obverse and reverse branch surfaces may be smooth, granular or striate.

Geological range. Carboniferous-Permian.

Remarks. The distinctive apertural form in this genus readily separates it from *Fenestella* Lonsdale. Features which separate it from *Australopolypora* include the number of apertural rows, the median carina and the different arrangement of the nodes.

Australofenestella brookeri sp.nov.

Fig. 3, 1-2

Diagnosis. Medium-sized form with medium-width branches forming a sub-oval to sub-rectangular, regular mesh; branches bear no distinct central carina but a central row of large, broadly cone-shaped, distantly-spaced, nodes; apertures occur in two rows with a third row appearing only in the fork at bifurcation; apertures large, close to medium-spaced with a low, wide, entire peristome; zooecial bases elongate triangular to irregularly pentagonal.

Description. Zoarium. Gently expanding fragments of unknown orientation; maximum radius 30mm. *Obverse surface:* (a) *Branches.* Medium width (m.BW 0.33mm) near straight; branch cross-section broadly rounded without carina; no ornament observed. (b) *Dissepiments.* Medium width (m.DW 0.17mm); dissepiments expand in a broad curve from their centre to the branch junction where they join just below branch level; ornament of moderate ribbing which continues on to branch sides. (c) *Fenestrules.* Sub-oval to sub-rectangular; medium-sized, moderately regular mesh (m.FL 1.49mm; m.FW 0.72mm). (d) *Carina.* Absent; some indistinct low ridging occurs between nodes. (e) *Nodes.* Wide-based, cone-shaped nodes which narrow rapidly to a fine point; distantly spaced (m.N-N 0.71mm) in a central row. (f) *Zooecial apertures.* Medium to large, circular (m.ZD 0.15mm); surrounded by a low, entire, broad, moderately raised peristome; apertures arranged in two rows with a third appearing only in the fork at each bifurcation; apertures alternate in adjoining rows and are situated on the broad obverse slope of the branch where they are directed with slight lateral inclination towards the fenestrule; they are not stabilized with respect to the dissepiments and have moderate fenestrular indentation; apertures close to medium-spaced (m.Z-Z 0.29mm) with from 4 to 6 zooecia per fenestrule (m.Z/F 5.1).

Reverse surface. (a) *Form.* Unknown. (b) *Zooecial bases.* Elongate triangular to irregularly pentagonal.

Material. Holotype NUF2541 (NUL39).

Remarks. Diagnostic aspects of this species include its apertural form and position, branch form and nodes.

The need to document these distinctive, rare elements of the Australian Carboniferous fenestrate fauna justifies the generally undesirable practice of erecting a new species based upon a single specimen.

The specific name honours a resident of the Rouchel Brook district, Mr B. Brooker.

A. brookeri shares with *A. stroudensis minuta* and *A. stroudensis stroudensis* the development of large cone-shaped nodes, wide, circular apertures, no carina, and a similar broad branch profile. Further, in order of stratigraphic appearance, *A. brookeri* has one aperture in the fork at branch bifurcation, *A. s. minuta* has two apertures and *A. s. stroudensis* can have between five and ten extra apertures in a third row prior to a branch division. This morphology would suggest that these three taxa form a lineage throughout the Carboniferous sequence.

Stratigraphy. The only known material has been discovered in the Waverley Formation at Cameron's Bridge, Rouchel Brook, where it is associated with a fauna of the *Pustula gracilis* subzone of the *Schellwienella* cf. *burlingtonensis* zone.

Australofenestella stroudensis (Campbell, 1961)

1961 *F. stroudensis* Campbell, p.458, pl.56, figs. 1a-c.
1961 *F. anodosa* Campbell, p.457, pl.57, figs. 3a-c.

Revised diagnosis. Fenestrate species with medium to coarse, regular mesh; carina low, poorly defined with moderate to distantly spaced nodes of variable form; two rows of apertures increase to three some distance before branch bifurcation; apertures large, with entire peristome; branch ornament of longitudinal ribbing; zooecial bases irregularly pentagonal.

Geological range. Late Visean-Westphalian.

Australofenestella stroudensis stroudensis (Campbell, 1961)

Fig. 3, 4-9

Synonymy. As above.

Revised diagnosis. Medium to coarse species with wide branches arranged in a regular mesh; carina low, ill-defined, with distant, poorly developed obsolete nodes; apertures in two rows per branch with the appearance of a third row, containing up to ten apertures, before bifurcation; apertures large, distant, with entire circular peristome; branch ornament of sinuous, pustulose ribbing; zooecial bases irregularly pentagonal.

Description. *Zoarium:* Expanding zoarial fragments of unknown orientation; maximum radius 60mm. *Obverse surface:* (a) *Branches*. Straight, wide (m.BW 0.45mm), commonly deflated; obverse branch profile centrally elevated with a low, ill-defined carina; ornament of sinuous, longitudinal, pustulose ribbing between and surrounding apertures. (b) *Dissepiments*. Medium width (m.DW 0.17mm); centrally straight with moderate expansion at branch junction; situated level with branches; ornament of coarse to fine ribbing which expands laterally on to branch sides. (c) *Fenestrules*. Sub-rectangular, medium to coarse, moderately regular mesh; fenestrules medium to long and wide (m.FL 1.91mm; m.FW 0.97mm). (d) *Carina*. Low, rounded to blunt keel of variable preservation due to frequency of branch deflation; it may appear as a high, bladed structure if branches are depressed on either side of this central plate or alternatively, if the whole branch is flattened, it may be barely apparent on the obverse surface; two carinae develop with the very early appearance of a third row of zooecia before bifurcation; because of the very large apertures, the carina tends to be sinuate or resorbed by the apertures. (e) *Nodes.* Some regions on the type material display low, indistinct, rounded elevations which may be taken to represent an obsolete row of nodes. (N-N. ca. 0.60mm). (f) *Zooecial apertures.* Large, circular, prominent (m.ZD 0.19mm); slightly raised apertures surrounded by an entire peristome which may rise on to or replace the low carina; apertures arranged in two rows with a third row, containing from two up to ten apertures (max. length 5mm), appearing prior to each branch bifurcation; apertures alternate in adjoining rows and are partially stabilized with respect to the dissepiments; apertures placed on obverse branch surface, being either erect or gently inclined towards the fenestrule, unless distorted by preservation; fenestrular margin very slightly indented, if at all; apertures medium to widely spaced (m.Z-Z 0.43mm) with from 4 to 5 zooecia per fenestrule (m.Z/F 4.5). (g) *Additional features.* Zooecial diameter at the peristome is maintained vertically for the length of the vestibule, giving the appearance of a very wide, open aperture; at the base of this deep, erect vestibule the chamber turns in a sharp right-angle bend in the proximal direction, where it expands into an elongate zooecial chamber. A few branches display spherical depressions on the branch surface between apertures which may possibly represent the site of ovicellular development.

Reverse surface: (a) *Form.* Rounded branches joined by narrow, level dissepiments; bifurcations preceded by a very gradual spread in branch width associated with the obverse development of a third row of apertures; many branches exhibit deflation effects on the reverse; ornament of longitudinal striations on branches and dissepiments, partly obscured by overgrowth in proximal parts of the zoarium; some large anchoring spines occur near the base of a few zoaria. (b) *Zooecial bases.* Irregularly pentagonal.

Material. Holotype NEUF4704A/B (NUL9); Paratype NEUF4703 (NUL9); Others NEUF4700B/C, 4701 (NUL9).

Remarks. Detailed comparison of *A. stroudensis* (Campbell) and *A. anodosa* (Campbell) has revealed that most apparent differences are the result of the highly distorted state in which the type materials have been preserved.

Type specimens of *A. stroudensis* have been subjected to vertical compression which has produced a general flattening of the obverse surface. Specimens of *A. anodosa* have been deformed by lateral compression in addition to the vertical loading. Whilst general deflation of the branch has taken place, the carinal plate has not been crumpled so that it now appears as a high, usually inclined, bladed carina. On either side of this carina, the weaker apertural surface has collapsed into a channel located between the carina and the doubled-over side walls of the branch, which now appear as two lateral carinae. Dissepiments are generally undeformed, but are snapped off at the branch junction, and pushed up over the apertural surface or into the side of the branch. Restoration of the profile would result in a form indistinguishable from that of *A. stroudensis.*

Both species were originally described as being nodeless. However, intensive study has revealed traces of very poorly preserved, low nodes on a few branches, a conclusion already noted by Wass (1968, p. 83). In both cases it is apparent that the nodes were very close to obsolescence. The existence of stronger, but similar nodes upon the stratigraphically older *A. stroudensis minuta* would support this conclusion.

The only mesh variation between *A. anodosa* and *A. stroudensis* occurs in the zooecial spacing which is slightly greater in *A. anodosa.* This difference is not considered to be significant.

In strict order of appearance in the one paper, *A. anodosa* is the senior specific name, but because it is considered inappropriate to apply this name to a species which does in fact bear nodes, *A. stroudensis* has been selected as the more suitable, available taxon.

Stratigraphy. All known specimens have been found associated with the *Levipustula levis* zone at Booral, N.S.W. (Campbell, 1961).

Australofenestella stroudensis minuta subsp.nov.

Fig. 3, 3

Diagnosis. Medium-sized fenestrate, with narrow branches arranged in a regular, open, sub-rectangular mesh; branches bear a low, ill-defined carina with small, moderately spaced nodes; apertures in two rows, with a third row appearing one or two apertures before bifurcation; apertures large, closely spaced with thin, entire peristomes; branch ornament of moderately developed longitudinal ribbing; zooecial bases irregularly pentagonal.

Description. Zoarium: Moderately expanding, laminar, zoarial fragment of unknown orientation; maximum radius 30mm. *Obverse surface:* (a) *Branches.* Straight, narrow (m.BW 0.29mm); branch cross-section rounded with a gentle slope on either side of an ill-defined carina; ornament of moderately developed ribbing or otherwise smooth. (b) *Dissepiments.* Narrow (m.DW 0.08mm); centrally straight with greatest expansion at branch junction; situated level with branches and ornamented with coarse ribbing which expands laterally on to branch sides. (c) *Fenestrules.* Sub-rectangular; regular, open mesh with fenestrules of medium length and width (m.FL 1.37mm; m.FW 0.72mm). (d) *Carina.* Low, rounded, ill-defined central carina, partly resorbed by apertural peristomes. (e) *Nodes.* Central row of small, circular or oval-based nodes with moderate spacing (m.N-N 0.44mm). (f) *Zooecial apertures.* Large, circular, prominent (m.ZD 0.17mm) slightly raised apertures surrounded by a thin, entire peristome which can replace portion of the carina; wide vestibular diameter is maintained until further expansion occurs into the zooecial chamber; apertures arranged in two rows per branch, with a third row appearing up to two apertures prior to branch bifurcation; apertures alternate in adjoining rows and are situated on the broad obverse slope of the branch, being directed upwards or with slight lateral inclination; apertures partly stabilized with respect to dissepiments and only with slight marginal indentation of the fenestrules; apertures closely spaced (m.Z-Z 0.30mm) with from 4 to 6 zooecia per fenestrule (m.Z/F 4.6).

Reverse surface. (a) *Form.* Broadly rounded branches joined by narrow, near level dissepiments; ornament of fine, longitudinal ribbing. (b) *Zooecial bases.* Irregularly pentagonal.

Material. Holotype NUF2396 (NUL258).

Remarks. The sub-specific name alludes to the diminutive size of this specimen as compared with that of *A. s. stroudensis.*

Principal differences at the subspecific level include: (a) *A. s. minuta* has an overall smaller mesh, with significant differences in most dimensions. Whilst size alone is not of major importance, the lack of intermediate material makes it unwise to group these specimens into a single taxon; (b) *A. s. minuta* has a regular, central row of small nodes not developed on *A. s. stroudensis,* where the nodes are either poorly preserved or vestigial in form; (c) *A. s. minuta* has fewer pre-bifurcation apertures than *A. s. stroudensis.*

Generally *A. s. minuta* is closely related to *A. s. stroudensis* but displays sufficient transitional differences between *A. brookeri* and *A. s. stroudensis* to justify its treatment as a separate subspecies. Differences between *A. s. minuta* and *A. brookeri* are noted in the description of the latter species.

Stratigraphy. This specimen has been collected from the Barrington area (NUL258) where it is associated with a *Rhipidomella fortimuscula* fauna (Cvancara, 1958).

Australofenestella trevallynensis sp.nov.

Fig. 5, 4-8

Diagnosis. Medium-sized, irregular, crenulated fenestrate with narrow to medium width, straight or broadly curved, weakly carinate branches forming a rectangular to sub-rectangular mesh; nodes medium size, moderately to distantly spaced; apertures medium to large size, not stabilized, directed obversely or slightly sideways; zooecia in two rows with a third row appearing up to two apertures before bifurcation; zooecial bases elongate triangular/trapezoidal trending to irregularly pentagonal on wide branches.

Description. Zoarium: Expanding, crenulated fragments of unknown orientation; maximum radius 60mm. *Obverse surface:* (a) *Branches.* Narrow to medium width (m.BW 0.30mm), straight or slightly irregular; radiating proximally, sub-parallel distally; cross-section broadly tapered to rounded but frequently deformed; ornament of strong, pustulose, longitudinal ribbing often obliterated by smooth overgrowth. (b) *Dissepiments.* Narrow to medium width (m.DW 0.15mm); centrally straight with moderate expansion at branch junction; some junctions inflated to house an enlarged zooecium; ornament of strong ribbing with central rib having a carinate form. (c) *Fenestrules.* Rectangular to sub-rectangular; irregular mesh with fenestrules of medium length and width (m.FL 1.57mm; m.FW 0.73mm). (d) *Carina.* Moderately to weakly developed, low carina connecting elongated nodal bases; generally about one third of branch width. (e) *Nodes.* Medium-sized, pointed, circular nodes with elongated bases; medium to distantly spaced (m. N-N 0.59mm) in a central row. (f) *Zooecial apertures.* Medium to large (m. ZD 0.14mm); circular to slightly oval-shaped; one specimen has a few enlarged zooecia (ca. 0.2mm) located at branch-dissepiment junctions; peristome circular, slightly raised on fenestrular margin and covered with an operculum-like plate which bears a central boss; apertures in two unstabilized rows with a third row of one or two apertures prior to bifurcation; apertures closely spaced (m. Z-Z 0.31mm) with from four to six apertures per fenestrule (m. Z/F 5.1).

Reverse surface: (a) *Form.* Evenly rounded or slightly tapered branches joined by medium-width dissepiments; ornament of fine striations with weak pustules usually rendered smooth by overgrowth. (b) *Zooecial bases.* Elongate triangular/trapezoidal trending to irregularly pentagonal on wider branches.

Fig. 5. (All except 8 prepared from latex casts.)

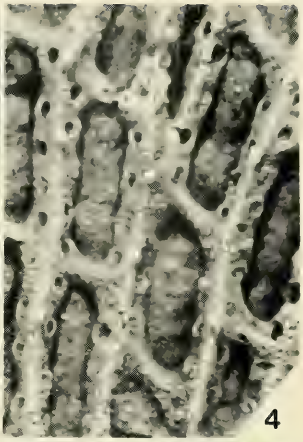
1-3. *Australofenestella cincta* (Crockford). **1, 2,** obverse surface of neotype showing large mesh form and very high, nodeless carina; **2** illustrates the development of large hemispherical pits superimposed on some apertures, within which it is still possible to observe the boss-like projection, QGSF10898, locality Ridgelands (265791), x10, x25 respectively. **3,** obverse view of one branch showing the strong boss-like projections in each aperture, NEUF4715E, locality NUL9, x20.

4-8. *Australofenestella trevallynensis* sp.nov. **4-7,** obverse surface of holotype showing large apertural form, peristomal collars and an ill-defined carina with evenly spaced, distant nodes, NEUF6918, locality NUL529, all figs. x20. **8,** reverse of zooecial cells showing triangular-trapezoidal form, NEUF6908, locality NUL529, x20.

9-11. *Australofenestella macleayensis* (Campbell). **9,11,** obverse surface of holotype showing large apertures separated by a strong carina upon which the nodes are very difficult to observe, NEUF5738, locality NUL390, x10, x5 respectively. **10,** obverse surface of holotype of *A. crockfordae* (Campbell) showing the typical crushed appearance of the material placed in that species, NEUF4699A, locality NUL9, x10.


1


2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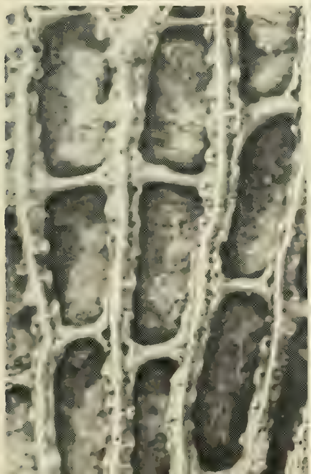
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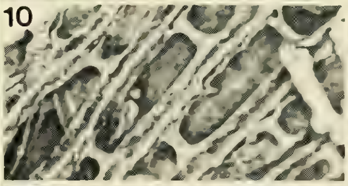
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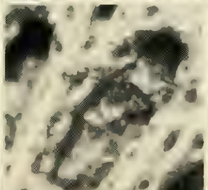
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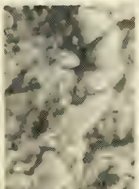
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Material. Holotype NEUF6918a/b (NUL529); Paratype NEUF6908/6909 (NUL529); Others NUF2429a/b, 2433 (NUL258); NEUF6918, (?)6919 (NUL529).

Remarks. Features including carinal form, branch profile and apertural form display considerable variation in this species, largely as a result of structural deformation during preservation. Specimens from NUL258 (Barrington) tend to have little carinae, more exserted apertures and occasional enlarged zooecia whereas those from the type locality are more carinate and less exserted.

The specimens from NUL529 (Trevallyn) were formerly grouped by Roberts (1965) in *F. allynensis* Roberts. They can be readily separated from the latter species which has large, ear-like apertural hoods, rounded carinae, much closer nodes and irregularly pentagonal zooecial bases.

A. trevallynensis is quite similar to *F. gresfordensis* Roberts (1963) which is distinguished by its possession of much closer nodes; distinct, high-bladed carinae; weakly-hooded, proximally inclined apertures; and very distinctive, flanged, zooecial bases.

Stratigraphy. This species has been identified from the Trevallyn locality of Roberts (1965) in a formation containing an *Orthotetes australis* fauna. It has also been found in the *Rhipidomella fortimuscula* zone at Barrington (Cvancara, 1958), but not as yet in the intervening *Delepinea aspinosa* zone.

Australofenestella malchi (Crockford, 1949)

Fig. 4, 4-9

1949 *Fenestrellina malchi* Crockford, pp.422-423, fig. 4.
1961 *Fenestella malchi* (Crockford) Campbell, p.460.
1961 *F. cerva* Campbell, pp.455-456, pl.59, figs. 1a-c.
1964 *F. malchi* (Crockford) Maxwell, p.38, pl.12, fig. 13.
1972 *F. malchi* (Crockford) Fleming, p.4, pl.2, figs. 1-3.

Revised diagnosis. Regular fenestrate with medium-width, straight branches forming a uniform sub-rectangular mesh; branches broadly rounded with distinct carina which bears large, circular, widely spaced nodes; apertures in two rows with a third appearing before bifurcation; apertures medium-sized, circular, not stabilized, with operculum-like plate bearing a central boss; ornament of pustulose striations; zooecial bases elongate, irregularly pentagonal.

Description. Zoarium: Gently to rapidly expanding fan-shaped fragments of unknown orientation; maximum radius 60mm. *Obverse Surface:* (a) *Branches.* Medium to wide (m.BW 0.40mm), frequently collapsed and distorted during preservation; branches sub-parallel to radiating in arrangement; branch cross-section rounded to triangular on either side of a sharply defined, broad carina; ornament of fine, wavy, pustulose striations. (b) *Dissepiments.* Medium width (m.DW 0.16mm), centrally straight, expanding only at branch junctions; ornament as on branches. (c) *Fenestrules.* Rectangular to sub-rectangular; regular mesh of medium length, medium width fenestrules (m.FL 1.63mm; m.FW 0.91mm). (d) *Carina.* Strong, massive, high carina varying from broad to sharp profile within one zoarium, the variation being a product of distortion during preservation; at bifurcation, carina swings on to one branch with a second, new carina commencing near a small node in the fork, or forming outside the third row of zooecia sometimes developed just before bifurcation. (e) *Nodes.* Large, circular nodes with elongate oval bases; distantly spaced (m. N-N 0.81 mm) in a single central row. (f) *Zooecial apertures.* Medium size, circular (m.ZD 0.14mm); surrounded by a low, circular peristome, best developed on the fenestrular rim; each bears an operculum-like plate with a central boss; apertures distantly spaced (m. Z-Z 0.42mm) with from three to five zooecia per fenestrule (m. Z/F 4.0); apertures in two unstabilized rows per branch with a third row up to 1mm before branch bifurcation. (g) *Additional features.* Hemispherical depressions (0.8-0.9mm diam.) occur on obverse surface near base of zoarium.

Reverse surface. (a) *Form.* Rounded branches joined by medium-width dissepiments; branch width increases very close to bifurcation producing a distinctive tuning-fork shape; ornament of pustulose striations together with distally-directed irregular spines on a few branches. (b) *Zooecial bases.* Elongate, irregularly pentagonal.

Material. Holotype QUF24952 (Malchi Creek); Paratypes QUF24953 (Malchi Creek), QUF25006 (Por. 201-2, Parish Palen, Mt. Barney), SUF7432 (NUL9); Others QGSF10903, 10904 (Malchi Creek), NEUF4705H, 4709A, 4718, 4739 (NUL454).

Remarks. Deflation during preservation has caused much confusion with this species. The styles of deformation present are discussed with *A. s. stroudensis* (Campbell).

Campbell (1961) described two species *A. malchi* (Crockford) and *A. cerva* (Campbell) from Booral, N.S.W. and it is suggested in this paper that most of the differences between these two are a direct result of preservation. Distinguishing features listed by Campbell for *A. cerva* include large fenestrules, more zooecia per fenestrule, a more defined carina and peristomes (not recorded for *A. malchi*). The first two differences have been bridged in the present study by intermediate forms and the latter two are preservational aspects, rather than specific differences. Tall nodes recorded on *A. cerva* by Campbell have also been found in specimens of *A. malchi.* For these reasons, the two taxa have been contracted into *A. malchi* in the present description.

A. malchi is also similar to *A. macleayensis* (Campbell, 1961), the major differences being largely that of size of fenestrules, branches and nodal spacing. Since the present study has failed to produce transitional material, these two taxa have been retained in their present form.

Stratigraphy. A. malchi occurs in the *Levipustula levis* zone at Malchi Creek and Mt. Barney in Queensland and at several localities in the Stroud-Gloucester and Myall Synclines (including Booral) in New South Wales. Present information suggests that the species ranges throughout most of the brachiopod assemblage zone.

Australofenestella macleayensis (Campbell, 1961)

Fig. 5, **9-11**

1961 *F. crockfordae* Campbell, pp.457-458, pl.59, figs. 2a-b.
[non] 1960 *F. (Minilya) crockfordae* Burckle, p.1088.
1962 *F. macleayensis* Campbell, p.48, pl.11, figs. 11a-c.

Revised diagnosis. Fenestrate with coarse, regular, sub-rectangular mesh; straight, wide, broadly rounded branches with a high, rounded, well-defined carina which bears distant nodes; two rows of unstabilized apertures per branch with increase to three rows prior to bifurcation; apertures medium-sized, erect with entire peristome within which there is an operculum-like plate with a central boss; branch ornament of fine pustulose striations; zooecial bases elongate, irregularly pentagonal.

Description. Zoarium: Flat, slightly expanding fragment of unknown orientation; maximum radius 50mm. *Obverse surface:* (a) *Branches.* Straight, wide (m. BW 0.47mm), commonly deflated; profile broadly rounded with a sharply-defined central carina; ornament of fine pustulose striations. (b) *Dissepiments.* Medium to wide (m. DW 0.18mm); centrally straight with gradual expansion to branch junction; ornament as for branches. (c) *Fenestrules.* Sub-rectangular, coarse, regular mesh; fenestrules long and wide (m. FL 2.62mm; m. FW 1.04mm). (d) *Carina.* High, prominent, well-rounded, medium to broad, being less than one third of the width of the branches; with deflation, carinae become much broader in profile; two carinae develop with the early appearance of a third row of zooecia before bifurcation. (e) *Nodes.* High, bladed nodes situated on the central carina; spacing very distant and irregular (m. N-N 1.10mm); nodes poorly preserved on holotype. (f) *Zooecial apertures.* Medium-sized, circular (m. ZD 0.15mm), with slightly raised peristome producing erect, cup-shaped apertures; apertures display an operculum-like plate with a central boss; apertures not stabilized; widely spaced (m. Z-Z 0.43mm) with from three to six and one half zooecia per fenestrule (m. Z/F 6.1) being arranged in two rows with a third row appearing up to 1.6mm pre-bifurcation.

Reverse surface. (a) *Form.* Rounded branches joined by rounded dissepiments less than half branch width; ornament of fine, close striae generally obscured by overgrowth. (b) *Zooecial bases.* Elongate, irregularly pentagonal.

Material. Holotype NEUF5738 (NUL390 — Oaky Creek, Kempsey); Others NEUF4698, 4699 (NUL9 — Booral).

Remarks. Campbell (1961) erected a new species *A. crockfordae* (Campbell) which is pre-occupied by *F. (Minilya) crockfordae* Burckle (1960) and therefore must be replaced. Campbell (1962) described a further new species *A. macleayensis* which in the opinion of Wass (1968, pp. 83, 85) and the present writer is specifically identical with *A. crockfordae* (Campbell). The former name has therefore been selected for this taxon.

Reasons for the contraction are based upon the following: Campbell (1962) noted that the two species were comparable, but decided that *A. crockfordae* (Campbell) was distinctive because of its large nodes and very wide carina. As *A. macleayensis* was described as being nodeless, this represented a significant difference. However, careful re-examination of the latter holotype reveals that it does have nodes which are difficult to observe because of their very poor preservation. When measured they have identical spacing with those of *A. crockfordae* (Campbell). Carinal differences between *A. crockfordae* (Campbell) and *A. macleayensis* are due to different modes of deformation during preservation as discussed in the remarks with *A. stroudensis* (Campbell). As a result, it becomes apparent that only one species is now required.

Stratigraphy. This species is known only from the *Levipustula levis* zone in New South Wales.

Australofenestella cincta (Crockford, 1949)

Fig. 4, **10-11**; Fig. 5, **1-3**

1949 *Fenestrellina cincta* Crockford, p.425, text-fig. 8.
1961 *Fenestella* cf. *cincta* (Crockford), Campbell, p.460.
1964 *F. cincta* (Crockford), Maxwell, p.38, pl.13, fig. 1.
1972 *F. (Bajoola) cincta* (Crockford), Fleming. p.4, pl.2, figs. 4-6.

Revised diagnosis. Coarse fenestrate with very wide, rapidly-bifurcating branches forming a coarse, irregularly rectangular mesh; branches with triangular profile, bearing a strong, very high, nodeless carina; apertures in two rows with no pre-bifurcation increase; apertures large, circular, erect, and of cup-like form with the peristome being raised on the fenestrular margin; branch ornament of distinctive, pustulose, longitudinal striations; zooecial bases very elongate, irregularly pentagonal.

Description. Zoarium: Narrowly radiating to sub-parallel, mature fragments of unknown orientation; maximum radius 40mm; branch bifurcation frequent. *Obverse surface:* (a) *Branches.* Straight to slightly wavy, sub-parallel; very wide (m. BW 0.55mm); rapid spread of branches after bifurcation followed by sub-parallel development has produced a distinctive 'tuning-fork' arrangement; cross-section triangular to sub-rounded, tapering steeply upwards to a very prominent central carina; ornament of fine to coarse, longitudinal, pustulose, sinuous ribbing. (b) *Dissepiments.* Medium to wide (m. DW 0.19mm); centrally straight with minor expansion at branch junction; situated at or just below branch level; ornament of prominent ribbing which is continuous on to branch sides. (c) *Fenestrules.* Very coarse, irregular mesh; high frequency of bifurcation, and the growth of dissepiments not always perpendicular to branches, disrupts an otherwise rectangular outline; fenestrules of variable dimensions; usually very long and wide with some fenestrules being very short (m. FL 3.39mm, O.R. 1.59-6.9mm; m. FW 1.23mm, O.R. 0.7-2.0mm). (d) *Carina.* Acutely triangular, very high, slightly sinuous median carina; considerably steeper than branch profile from which it is separated by a marked change of slope; carina continuous on one branch at bifurcation, showing a temporary loss of profile adjacent to the zooecial aperture in the fork, new carina on the other branch forms up from one of a group of prominent surface ribs located on the side of the branch, there being no obvious connection back to the primary carina. (e) *Nodes.* Absent. (f) *Zooecial apertures.* Large, circular (m. ZD 0.19mm) surrounded by an entire, strongly developed, exserted peristome; apertural profile low, adjacent to carina, but with maximum elevation on the fenestrular margin giving the aperture a cup-like form on the obverse slope of the branch; zooecia arranged in two rows with no pre-bifurcation increase except for one aperture being located on the fork at each branch division; apertures alternate in position in adjoining rows being not stabilized with respect to the dissepiments and displaying very slight fenestrular indentation; apertures closed by operculum-like plates, each of which bears a variably-placed, spine-like projection; apertures very widely spaced (m. Z-Z 0.49mm) with from 3 to 12 zooecia per fenestrule (m. Z/F 7.0). (g) *Additional features.* Occasional resorbed apertures are surrounded by a semi-circular pit located on the branch between the carina and a narrow semi-circular ridge which extends beyond the edge of the branch (0.36-0.42mm long by 0.24-3mm wide). The aperture in the base of the pit has a very reduced peristome but still has the opercular plate present. One aperture was observed to have a small spherical sac obscuring it. An ovicellular function has been postulated.

Reverse surface: (a) *Form.* Rounded branches joined by small, medium-width level dissepiments; branch surface longitudinally ornamented with fine, pustulose ribbing; similar, but coarser, ribbing occurs on the dissepiments. (b) *Zooecial bases.* Very elongate, irregularly pentagonal.

Material. Holotype lost; Neotype (Fleming, 1972) QGSF10898 (Neerkol Fm., Ridgelands 1 mile map ref. 265791); Others QGSF10891, 10897 (topotypes); NEUF4715E, 4719, 4700A (NUL9); NUF2377 (NUL472); numerous additional localities in the Stroud-Gloucester-Bulahdelah region, N.S.W.

Remarks. This most distinctive, very large species exhibits strong development of the operculum-like plate, with its variably placed boss-like projection, which closes the external aperture. The function of the projection on the plate cannot be determined from the external moulds available. It is considered to represent either a spine on the surface or a tube-like extension through the plate.

A. cincta differs from all other species described in this paper in possessing a very high, bladed, nodeless carina which separates the two rows of apertures on each branch. In this respect, the inclusion of *A. cincta* in this paper is somewhat anomalous except for the apertural development which is considered to be its most significant feature.

Fleming (1966) placed *A. cincta* in his subgenus *Fenestella (Bajoola)*, which was defined to include species of *Fenestella* with strong nodeless carinae. Detailed comparison of the type species *F. (Bajoola) capellae* Fleming with the present species reveals a number of dissimilarities which would suggest that the grouping is possibly inappropriate. Significant differences in the structure of the carina and of the zooecial apertures and chambers, form the basis upon which the grouping has not been perpetuated. Other Early Carboniferous species (*F. roucheli* Crockford, *F. propinqua* de Koninck and *F. brownei* Roberts) have much more in common with the type species and may possibly be grouped with it at some future date.

A. cincta remains a solitary form without obvious affinity to any other species known to the writer. No useful comparisons can be offered from the literature at this stage.

Stratigraphy. A. cincta is widely found associated with the *Levipustula levis* zone. Its occurrence has been reported in Queensland from the Stanwell district (Crockford, 1949; Fleming, 1972) and the Yarrol district (Maxwell, 1964) in beds equated to various levels in the Neerkol Formation. New South Wales material has been described from Booral (Campbell, 1961) and has been found in the present study in a number of other localities in the Stroud-Gloucester-Bulahdelah region.

Australofenestella (?) keepitensis sp.nov.

Fig. 4, 1-3

1963 *Fenestella* sp.1. Campbell & Engel, pp.67-68, pl.1, figs. 4-5.

Diagnosis. Coarse, irregular fenestrate with wide, straight to slightly wavy, non-carinate branches forming a sub-oval to sub-rectangular mesh; nodes very large, widely spaced, irregularly distributed; apertures moderately large, not stabilized, situated low on branch sides; zooecia in two rows with a third, intermittently developed, central row of apertural-sized pits which are developed unrelated to branch bifurcations; zooecial bases large irregularly pentagonal in lateral rows and rhomboidal in the central row when developed.

Description. Zoarium: Expanding fragment of unknown orientation; maximum radius 65mm. *Obverse surface:* (a) *Branches.* Wide (m. BW 0.46mm), straight to slightly wavy with gently radiating arrangement; branch cross section rounded; ornament of fine pustulose striations obscured by secondary overgrowth. (b) *Dissepiments.* Wide (m. DW 0.42mm); branch junctions rounded to sub-rounded; situated below branch level; no ornament observed. (c) *Fenestrules.* Sub-rectangular to sub-oval; irregular mesh of long, wide fenestrules (m. FL 2.61mm; m. FW 1.10mm). (d) *Carina.* Absent; some low ridging occurs between nodes. (e) *Nodes.* Very large, prominent oval-based, round nodes (basal diameter 0.25-0.4mm); medium to distant spacing (m. N-N 0.49mm); node arrangement extremely irregular, varying from a central row, to a zigzag pattern, to a few cases of two nodes being placed alongside each other; nodal variation is irregular without relationship to branch bifurcations. (f) *Zooecial apertures.* Medium to large, circular (m. ZD 0.16mm); surrounded by low peristome, best developed on the fenestrular rim; apertures in two unstabilized rows situated low on branch sides where the apertures face into the fenestrule; apertures distantly spaced (m. Z-Z 0.47mm) with from five to six zooecia per fenestrule (m. Z/F 5.6); irregularly developed short rows of aperture-like pits occur along the centre line of some branches. Development is unrelated to branch bifurcations but the branches show some thickening in the region of these extra rows. The pits are located between nodes and represent the brief, intermittent development of a third row of apertures.

Reverse surface: (a) *Form.* Irregular branches, varying from straight to zigzag in an anastomosing format; dissepiments equal in dimension to, and level with, branches; surface smooth. (b) *Zooecial bases.* Large, irregular, pentagonal in lateral rows and rhomboidal where a third row is developed.

Material. Holotype NEUF7466A/B (NEUL318 — Swaines Gully, Werrie Syncline).

Remarks. Evidence that the irregular central occurrence of small pits represents additional apertural development comes from the observation of three rows of zooecial chambers in some parts of the zoarium. Peristomal development is very weak on these central apertures.

The distribution of nodes and the erratic development of a third central row of apertures together with the absence of a central carina make it very unlikely that this species belongs to *Fenestella* Lonsdale. Although zigzag nodes are a feature of the subgenus *F. (Minilya)* Crockford, the nature of their development in the present species prevents any viable comparison being made.

No other species in the literature at present available can be usefully compared with *A.* (?) *keepitensis* which can only be dubiously assigned to this genus.

Stratigraphy. The species is known only from the Tulcumba Sandstone where it is associated with a *Spirifer sol* assemblage of early Tournaisian age.

COMPARATIVE GROUPING OF SPECIES

Tables 1 and 2 detail the descriptive and statistical aspects of all the species/subspecies described in this paper.

Multi-rowed species. Stable, unifying features which justify the grouping of the multi-rowed species adopted in this paper include: (a) Apertures of large size, and medium to distant spacing, all of which bear a wide, low, peristomal collar which may be entire, or horseshoe-shaped with a proximal opening. All apertures bear a transverse plate or operculum and this plate carries a raised spine or boss-like projection, the position of which is usually central, but can be eccentrically placed; (b) Straight, wide to very wide branches of oval to flattened cross-section. Most species bear moderate to very strong development of distinctive, pustulose ribbing. All species lack a central carina having at most a low, internodal rise of very poor development; (c) Nodes are generally absent from the group but where developed are located on the proximo-central rim of an aperture in any zooecial row. In two species (*Australopolypora rawdonensis* and *Australopolypora altinodosa*), the obverse surface bears large, widely-spaced spines of presumed attachment significance because of their robust construction and lack of outward termination.

Some species exhibit a greater degree of similarity than others and the following discussion relates to these forms:

(1) *Australopolypora rawdonensis* and *Australopolypora palenensis.* These two species have the coarsest mesh of the multi-rowed species with a fenestrule length close to 3mm and a width of about 1.3mm. From the reverse, the form, ornament and zooecial bases are very similar. The major distinction lies in the position, form, and spacing of the zooecial apertures.

Australopolypora rawdonensis has horseshoe-shaped peristomes surrounding oval apertures which are placed in a fan-like arrangement. Central apertures have their long axis parallel to the branch length whereas the side apertures are inclined at 45 degrees to the length. By contrast, *Australopolypora palenensis* has apertures which are distally inclined to the branch surface, having the proximal

TABLE 1

A descriptive comparison of the important morphological features of the fenestrate mesh of all species of *Australopolypora* gen.nov. and *Australofenestella* gen.nov. described in this paper.

Genus	Species		FL mm	FW mm	BW mm	DW mm	ZD mm	Z-Z mm	N-N mm	Nº	F/10	B/10	Z/5	Z/F
AUSTRALOPOLYPORA	*rawdonensis*	x̄	2·71	1·24	0·56	0·16	0·17	0·37	0·87	140	3·7	8·2	13·5	7·3
		s	*0·558*	*0·212*	*0·092*	*0·043*	*0·015*	*0·034*	-					
		O.R.	1·20-4·40	0·88-1·92	0·34-0·80	0·10-0·32	0·12-0·20	0·32-0·49	0·62-1·14					
	palenensis	x̄	3·11	1·37	0·60	0·23	0·14	0·48	—	100	3·2	7·3	10·4	6·4
		s	*0·473*	*0·215*	*0·121*	*0·065*	*0·013*	*0·056*						
		O.R	2·08-4·40	1·00-2·12	0·44-1·00	0·14-0·40	0·12-0·18	0·38-0·62						
	altinodosa	x̄	1·75	0·93	0·46	0·17	0·20	0·49	0·90	20	5·7	10·7	10·2	3·6
		O.R.	1·40-2·10	0·66-1·10	0·40-0·54	0·14-0·24	0·18-0·22	0·40-0·60	0·42-1·26					
	neerkolensis	x̄	1·74	1·10	0·64	0·27	0·20	0·44	1·00	260	6·2	10·1	12·4	4·3
		s	*0·205*	*0·205*	*0·130*	*0·091*	*0·025*	*0·060*	-					
		O.R.	1·14-2·30	0·64-1·80	0·36-1·16	0·12-0·52	0·16-0·28	0·30-0·62	0·72-1·20					
	scalpta	x̄	1·56	1·14	0·86	0·74	0·23	0·41	–	20	6·4	8·7	12·2	3·8
		O R	1·20-1·84	0·88-1·60	0·60-1·16	0·52-1·12	0·20-0·24	0·34-0·56						
	keppelensis keppelensis	x̄	1·01	0·92	0·50	0·14	0·16	0·33	rare	40	9·9	10·9	15·1	3·1
		s	*0·064*	*0·141*	*0·057*	*0·012*	*0·014*	*0·039*						
		O.R.	0·90-1·14	0·70-1·20	0·40-0·60	0·12-0·16	0·12-0·18	0·28-0·40						
	keppelensis parvula	x̄	0·83	0·64	0·41	0·23	0·15	0·26	present	40	12·0	15·6	19·3	3·2
		s	*0·062*	*0·072*	*0·058*	*0·030*	*0·013*	*0·030*						
		O.R.	0·68-0·95	0·50-0·84	0·32-0·60	0·20-0·30	0·12-0·18	0·22-0·32						
AUSTRALOFENESTELLA	*brookeri*	x̄	1·49	0·72	0·33	0·17	0·15	0·29	0·71	20	6·7	13·9	17·2	5·1
		O R.	1·10-1·72	0·60-0·90	0·28-0·38	0·12-0·20	0·14-0·18	0·26-0·32	0·54-0·90					
	stroudensis minuta	x̄	1·37	0·72	0·29	0·08	0·17	0·30	0·44	20	7·3	13·9	16·8	4·6
		O R.	0·56-1·94	0·50-0·92	0·26-0·34	0·04-0·12	0·14-0·18	0·26-0·34	0·28-0·60					
	stroudensis stroudensis	x̄	1·91	0·97	0·45	0·17	0·20	0·43	0·60	80	5·2	10·3	11·8	4·5
		s	*0·152*	*0·123*	*0·048*	*0·026*	*0·020*	*0·063*	*0·086*					
		O R	1·64-2·40	0·70-1·30	0·34-0·56	0·12-0·22	0·16-0·24	0·32-0·54	0·42-0·72					
	trevallynensis	x̄	1·57	0·73	0·30	0·15	0·14	0·31	0·66	100	6·4	13·8	16·2	5·1
		s	*0·218*	*0·127*	*0·035*	*0·029*	*0·017*	*0·025*	*0·081*					
		O R	0·76-2·30	0·46-1·00	0·22-0·38	0·08-0·22	0·10-0·20	0·26-0·38	0·46-0·84					
	malchi	x̄	1·63	0·91	0·40	0·16	0·14	0·42	0·81	160	6·2	11·1	12·2	4·0
		s	*0·252*	*0·189*	*0·073*	*0·045*	*0·015*	*0·056*	*0·120*					
		O R	1·12-2·26	0·38-1·40	0·24-0·64	0·08-0·28	0·10-0·16	0·32-0·56	0·44-1·12					
	macleayensis	x̄	2·62	1·04	0·47	0·18	0·15	0·43	1·10	60	3·8	9·8	11·6	6·1
		s	*0·339*	*0·223*	*0·066*	*0·041*	*0·017*	*0·047*	*0·193*					
		O R	2·08-3·92	0·56-1·66	0·32-0·60	0·12-0·30	0·12-0·18	0·34-0·54	0·56-1·80					
	cincta	x̄	3·39	1·23	0·55	0·19	0·19	0·49	—	120	3·1	8·2	10·5	7·0
		s	*1·136*	*0·267*	*0·082*	*0·037*	*0·019*	*0·075*						
		O R	1·60-6·90	0·70-2·04	0·40-0·78	0·12-0·30	0·16-0·24	0·30-0·66						
	(?) keepitensis	x̄	2·61	1·10	0·46	0·42	0·16	0·47	0·49	20	3·8	9·1	10·8	5·6
		O R	2·16-3·28	0·76-1·48	0·36-0·56	0·28-0·52	0·14-0·18	0·38-0·56	0·36-0·80					

rim of the peristome level with the surface and the distal rim depressed below branch level.

(2) *Australopolypora altinodosa* and *Australopolypora neerkolensis*. These two species have very close mesh dimensions. *A. altinodosa* has slightly narrower branches in keeping with its more extensive development of two rows of zooecia.

bear large attachment spines as noted above. In most respects, these species strong affinity with the number of zooecial rows being the principal distinc- Since *A. neerkolensis* has not been found at the one locality where *A.* *dosa* occurs, it is possible that the latter is just a local variant of *A.* *olensis* at Booral, N.S.W. Lack of further material precludes a definite ion.

remaining taxa *Australopolypora scalpta* and *Australopolypora keppelensis* *la* are distinctive in their own right and exhibit no obvious grouping res.

TABLE 2

l summary of the mesh dimensions of all species of *Australopolypora — Australofenestella* n this paper. Species known only by a single specimen have only their means and observed ranges or explanations of abbreviations see Engel (1975, p.577).

ies	Mesh	Branch Width Form Profile	Fenestrules	Nodal Spacing & Size	Apertural Size & Spacing	Zooecial Rows			Zooecia per Fenestrule	Zooecial Bases	Special Features
						post bif.	norm -al	pre bif			
ensis	coarse; open, irregular	very wide, straight; round-oval	sub-rectangular to rectangular; long; wide	distant spines	large; oval; medium	3 / 3-4 / 4-5			5 to 9	oval, no overlap	horseshoe peristomes
nsis	coarse; open, irregular	very wide; straight, round-oval	sub-oval to rectangular, long; wide	–	medium; round, distant	2-3/3-4/4-5			5 to 9	oval, no overlap	distally inclined peristomes
dosa	medium; open, irregular	wide, straight, oval	sub-oval to rectangular, med. length/width	distant spines	large, round, distant	2 / 2-3 / 3			3 to 4	irregularly pentagonal rhomboidal	strong central ribbing
lensis	medium; open, regular	very wide, straight; oval	oval to sub rectangular; med. length/width	frequent; irregular	large, round, distant	2-3/ 3 /4-5			3 to 5	elongate oval - rhomboidal	variable mesh
ta	medium, closed, regular	very wide, straight; oval	oval medium length, medium width	—	large, oval, medium	3 / 4 / 5			3 to 4	elongate hexagonal	depressed peristomes
lensis *parvula*	medium, even, regular	wide, straight, round-oval	oval to sub-oval; short length, medium width	frequent; irregular	large, round, close	2 / 3 / 4			2 to 3·5	irregularly pentagonal rhomboidal	horseshoe & complete peristomes
keri	medium, even; regular	narrow, straight, round	sub-oval to sub-rectangular; med. length/width	distant, blunt, cones	large, round, close	2 / 2 / 3			4 to 6	triangular-irregularly pentagonal	blunt nodes peristomes
densis *minuta*	medium; open, regular	narrow, straight, round	sub-rectangular; medium length, medium width	medium regular small	large, round, close	2 / 2 / 3			4 to 6	irregularly pentagonal	conical nodes
densis *udensis*	coarse, open; regular	wide, straight, round	sub-rectangular; long, wide	vestigial	large; round, distant	2 / 2-3 / 3			4 to 5	irregularly pentagonal	weak nodes, no carina
lynensis	medium, open, irregular	medium, straight, triangular	sub-rectangular to rectangular, med. length/width	distant, regular; medium	medium, round, close	2 / 2 . 2-3			4 to 6	triang-trap-irregularly pentagonal	variable mesh
hi	medium; even, regular	medium, straight, triangular	rectangular to sub-rectangular; med. length/width	distant, regular; large	medium, round, distant	2 / 2 /2-3			3 to 5	elongate irregularly pentagonal	preservation distortion
eayensis	coarse, open, regular	wide, straight, triangular	sub-rectangular; long, wide	distant, irregular; bladed	medium, round; distant	2 / 2 /2-3			3 to 6·5	elongate irregularly pentagonal	preservation distortion
ta	coarse, open, irregular	very wide, straight, triangular	rectangular, very short to very long, wide	—	large, round, distant	2 / 2 / 2			3 to 12	very elongate irregularly pentagonal	very high nodeless carina
epitensis	coarse, open, irregular	wide, straight, round	sub-rectangular to sub-oval, long, wide	medium irregular large	large, round, distant	2 / 2-3 / 2			5 to 5	irregularly pentagonal -rhomboidal	erratic nodes & zooecia

CORRECTIONS:

Proc. Linn. Soc. N.S.W., 103 (3), pp. 166–167.

The tabulated matter of Table 1 has been printed under the heading for Table 2, and vice versa. The editor apologizes for failing to correct these printer's errors.

TABLE 1

A descriptive comparison of the important morphological features of the fenestrate mesh of all *Australopolypora* gen.nov. and *Australofenestella* gen.nov. described in this paper.

Genus	Species		FL mm	FW mm	BW mm	DW mm	ZD mm	Z-Z mm	N-N mm	Nº	F/10	B/1
AUSTRALOPOLYPORA	*rawdonensis*	x̄	2·71	1·24	0·56	0·16	0·17	0·37	0·87	140	3·7	8·2
		s	*0·558*	*0·212*	*0·092*	*0·043*	*0·015*	*0·034*	-			
		O.R.	1·20-4·40	0·88-1·92	0·34-0·80	0·10-0·32	0·12-0·20	0·32-0·49	0·62-1·14			
	palenensis	x̄	3·11	1·37	0·60	0·23	0·14	0·48	—	100	3·2	7·3
		s	*0·473*	*0·215*	*0·121*	*0·065*	*0·013*	*0·056*				
		O.R.	2·08-4·40	1·00-2·12	0·44-1·00	0·14-0·40	0·12-0·18	0·38-0·62				
	altinodosa	x̄	1·75	0·93	0·46	0·17	0·20	0·49	0·90	20	5·7	10·7
		O.R.	1·40-2·10	0·66-1·10	0·40-0·54	0·14-0·24	0·18-0·22	0·40-0·60	0·42-1·26			
	neerkolensis	x̄	1·74	1·10	0·64	0·27	0·20	0·44	1·00	260	6·2	10·1
		s	*0·205*	*0·205*	*0·130*	*0·091*	*0·025*	*0·060*	–			
		O.R.	1·14-2·30	0·64-1·80	0·36-1·16	0·12-0·52	0·16-0·28	0·30-0·62	0·72-1·20			
	scalpta	x̄	1·56	1·14	0·86	0·74	0·23	0·41	–	20	6·4	8·7
		O R	1·20-1·84	0·88-1·60	0·60-1·16	0·52-1·12	0·20-0·24	0·34-0·56				
	keppelensis keppelensis	x̄	1·01	0·92	0·50	0·14	0·16	0·33	rare	40	9·9	10·9
		s	*0·064*	*0·141*	*0·057*	*0·012*	*0·014*	*0·039*				
		O R	0·90-1·14	0·70-1·20	0·40-0·60	0·12-0·16	0·12-0·18	0·28-0·40				
	keppelensis parvula	x̄	0·83	0·64	0·41	0·23	0·15	0·26	present	40	12·0	15·6
		s	*0·062*	*0·072*	*0·058*	*0·030*	*0·013*	*0·030*				
		O R.	0·68-0·95	0·50-0·84	0·32-0·60	0·20-0·30	0·12-0·18	0·22-0·32				
AUSTRALOFENESTELLA	*brookeri*	x̄	1·49	0·72	0·33	0·17	0·15	0·29	0·71	20	6·7	13·9
		O R	1·10-1·72	0·60-0·90	0·28-0·38	0·12-0·20	0·14-0·18	0·26-0·32	0·54-0·90			
	stroudensis minuta	x̄	1·37	0·72	0·29	0·08	0·17	0·30	0·44	20	7·3	13·9
		O R	0·56-1·94	0·50-0·92	0·26-0·34	0·04-0·12	0·14-0·18	0·26-0·34	0·28-0·60			
	stroudensis stroudensis	x̄	1·91	0·97	0·45	0·17	0·20	0·43	0·60	80	5·2	10·3
		s	*0·152*	*0·123*	*0·048*	*0·026*	*0·020*	*0·063*	*0·086*			
		O R	1·64-2·40	0·70-1·30	0·34-0·56	0·12-0·22	0·16-0·24	0·32-0·54	0·42-0·72			
	trevallynensis	x̄	1·57	0·73	0·30	0·15	0·14	0·31	0·66	100	6·4	13·8
		s	*0·218*	*0·127*	*0·035*	*0·029*	*0·017*	*0·025*	*0·081*			
		O R	0·76-2·30	0·46-1·00	0·22-0·38	0·08-0·22	0·10-0·20	0·26-0·38	0·46-0·84			
	malchi	x̄	1·63	0·91	0·40	0·16	0·14	0·42	0·81	160	6·2	11·1
		s	*0·252*	*0·189*	*0·073*	*0·045*	*0·015*	*0·056*	*0·120*			
		O R	1·12-2·26	0·38-1·40	0·24-0·64	0·08-0·28	0·10-0·16	0·32-0·56	0·44-1·12			
	macleayensis	x̄	2·62	1·04	0·47	0·18	0·15	0·43	1·10	60	3·8	9·8
		s	*0·339*	*0·223*	*0·066*	*0·041*	*0·017*	*0·047*	*0·193*			
		O R	2·08-3·92	0·56-1·66	0·32-0·60	0·12-0·30	0·12-0·18	0·34-0·54	0·56-1·80			
	cincta	x̄	3·39	1·23	0·55	0·19	0·19	0·49	—	120	3·1	8·2
		s	*1·136*	*0·267*	*0·082*	*0·037*	*0·019*	*0·075*				
		O.R	1·60-6·90	0·70-2·04	0·40-0·78	0·12-0·30	0·16-0·24	0·30-0·66				
	(?) keepitensis	x̄	2·61	1·10	0·46	0·42	0·16	0·47	0·49	20	3·8	9·1
		O R	2·16-3·28	0·76-1·48	0·36-0·56	0·28-0·52	0·14-0·18	0·38-0·56	0·36-0·80			

rim of the peristome level with the surface and the distal rim depresse branch level.

(2) *Australopolypora altinodosa* and *Australopolypora neerkolensis*. The species have very close mesh dimensions. *A. altinodosa* has slightly n branches in keeping with its more extensive development of two rows of z

Both bear large attachment spines as noted above. In most respects, these species show strong affinity with the number of zooecial rows being the principal distinction. Since *A. neerkolensis* has not been found at the one locality where *A. altinodosa* occurs, it is possible that the latter is just a local variant of *A. neerkolensis* at Booral, N.S.W. Lack of further material precludes a definite decision.

(3) The remaining taxa *Australopolypora scalpta* and *Australopolypora keppelensis parvula* are distinctive in their own right and exhibit no obvious grouping features.

TABLE 2

A statistical summary of the mesh dimensions of all species of *Australopolypora* — *Australofenestella* described in this paper. Species known only by a single specimen have only their means and observed ranges recorded. For explanations of abbreviations see Engel (1975, p.577).

	Species	Mesh	Branch Width Form Profile	Fenestrules	Nodal Spacing & Size	Apertural Size & Spacing	Zooecial Rows			Zooecia per Fenestrule	Zooecial Bases	Special Features
							post bif.	norm -al	pre bif			
AUSTRALOPOLYPORA	*rawdonensis*	coarse; open, irregular	very wide; straight; round-oval	sub-rectangular to rectangular; long; wide	distant spines	large; oval; medium	3	3-4	4-5	5 to 9	oval, no overlap	horseshoe peristomes
	palenensis	coarse; open; irregular	very wide, straight, round-oval	sub-oval to rectangular; long; wide	–	medium; round, distant	2-3	3-4	4-5	5 to 9	oval, no overlap	distally inclined peristomes
	altinodosa	medium; open; irregular	wide; straight; oval	sub-oval to rectangular, med. length/width	distant spines	large, round, distant	2	2-3	3	3 to 4	irregularly pentagonal rhomboidal	strong central ribbing
	neerkolensis	medium; open, regular	very wide, straight; oval	oval to sub rectangular; med. length/width	frequent; irregular	large, round, distant	2-3	3	4-5	3 to 5	elongate oval - rhomboidal	variable mesh
	scalpta	medium, closed; regular	very wide, straight; oval	oval medium length, medium width	–	large, oval, medium	3	4	5	3 to 4	elongate hexagonal	depressed peristomes
	keppelensis parvula	medium, even, regular	wide, straight, round-oval	oval to sub-oval; short length, medium width	frequent; irregular	large, round, close	2	3	4	2 to 3·5	irregularly pentagonal rhomboidal	horseshoe & complete peristomes
AUSTRALOFENESTELLA	*brookeri*	medium, even, regular	narrow, straight, round	sub-oval to sub-rectangular; med length/width	distant, blunt, cones	large, round, close	2	2	3	4 to 6	triangular-irregularly pentagonal	blunt nodes peristomes
	stroudensis minuta	medium; open, regular	narrow, straight, round	sub-rectangular; medium length; medium width	medium regular small	large, round; close	2	2	3	4 to 6	irregularly pentagonal	conical nodes
	stroudensis stroudensis	coarse, open, regular	wide, straight, round	sub-rectangular; long, wide	vestigial	large; round, distant	2	2-3	3	4 to 5	irregularly pentagonal	weak nodes, no carina
	trevallynensis	medium, open, irregular	medium, straight, triangular	sub-rectangular to rectangular, med length/width	distant, regular; medium	medium, round, close	2	2	2-3	4 to 6	triang.-trap.-irregularly pentagonal	variable mesh
	malchi	medium, even, regular	medium, straight, triangular	rectangular to sub-rectangular; med length/width	distant, regular; large	medium, round, distant	2	2	2-3	3 to 5	elongate irregularly pentagonal	preservation distortion
	macleayensis	coarse, open, regular	wide, straight, triangular	sub-rectangular; long, wide	distant, irregular; bladed	medium, round; distant	2	2	2-3	3 to 6·5	elongate irregularly pentagonal	preservation distortion
	cincta	coarse, open, irregular	very wide, straight, triangular	rectangular, very short to very long, wide	—	large, round, distant	2	2	2	3 to 12	very elongate irregularly pentagonal	very high nodeless carina
	(?)keepitensis	coarse, open, irregular	wide, straight, round	sub-rectangular to sub-oval, long, wide	medium irregular large	large, round, distant	2	2-3	2	5 to 6	irregularly pentagonal -rhomboidal	erratic nodes & zooecia

Two-rowed species. The inclusion of eight two-rowed species in this paper is based substantially upon their common development of large-sized apertures which are very similar to those of the multi-rowed species. In all cases, these apertures are closed by an operculum-like lid which bears an axial boss or elevated perforation.

In contrast to the multi-rowed, most of the two-rowed species have a regular central row of nodes, the exceptions to this being *Australofenestella cincta* which is nodeless and *Australofenestella (?) keepitensis* which displays very irregular nodal development. In addition, most species exhibit some carinal development although this aspect is highly variable within the group from almost no development to the very attenuated form of *A. cincta*.

Grouping of the two-rowed species is as follows:

(1) *Australofenestella brookeri, Australofenestella stroudensis minuta* and *Australofenestella s. stroudensis.* These three taxa form a developmental series throughout the duration of the Carboniferous interval. Principal variations include: (a) Nodes in *A. brookeri* are large, bluntly cone-shaped features arranged along a vague central ridge. In *A. s. minuta* the nodes are much smaller and in *A. s. stroudensis* they are very vague, blunt prominences of vestigial form. In all cases the carinal development is weak; (b) As noted above, the number of pre-bifurcation apertures in the third, central row increases in the younger species such that the generic assignment based upon the number of apertural rows becomes increasingly contentious; (c) Mesh variations, depicted in Tables 1 and 2, illustrate a continuing enlargement of the zoaria through geological time.

(2) *Australofenestella trevallynensis, Australofenestella malchi* and *Australofenestella macleayensis. A. trevallynensis* and *A. malchi* are two stratigraphically separated species which have a great deal in common. Mesh differences are small but consistently larger in the younger species *A. malchi.* In addition, *A. trevallynensis* has an irregular, crenulated mesh with weak carinal development, small nodes and closer apertures whereas in *A. malchi,* the mesh is regular and branches have well defined broad carinae which bear stronger nodes. Differences also exist in the position of onset of the third row of zooecia before bifurcation, in the reverse branching pattern and in the outline of the zooecial bases which are transitional in form between the two species.

A. macleayensis is a considerably larger species which continues the trends evident in *A. malchi.* The former species exhibits much greater fenestrule length, branch width, and nodal spacing. However since there is no material which presently bridges the dimension gap between these two species, both taxa have been retained.

In summary, all three species share a similar morphology which is emphasized by the common presence of the strong apertures with a distinctive covering.

STRATIGRAPHIC SUMMARY

Detailed stratigraphic distribution of each species is included with the respective descriptions. They are also illustrated in Fig. 6. From these data, some further conclusions are of significance.

The first record of the multi-rowed species of *Australopolypora* in eastern Australian strata appears to be that of *Australopolypora rawdonensis* from the late Visean *Rhipidomella fortimuscula* assemblage zone. Phillips Ross (1961) makes no mention of multi-rowed species in her summary of the Ordovician-Silurian-Devonian Bryozoa of Australia, and the present study has failed to reveal any older Carboniferous forms. The first multi-rowed fenestrate to appear in the record belongs to *Septatopora* which therefore just slightly predates the first australopolyporid. Together, they constitute

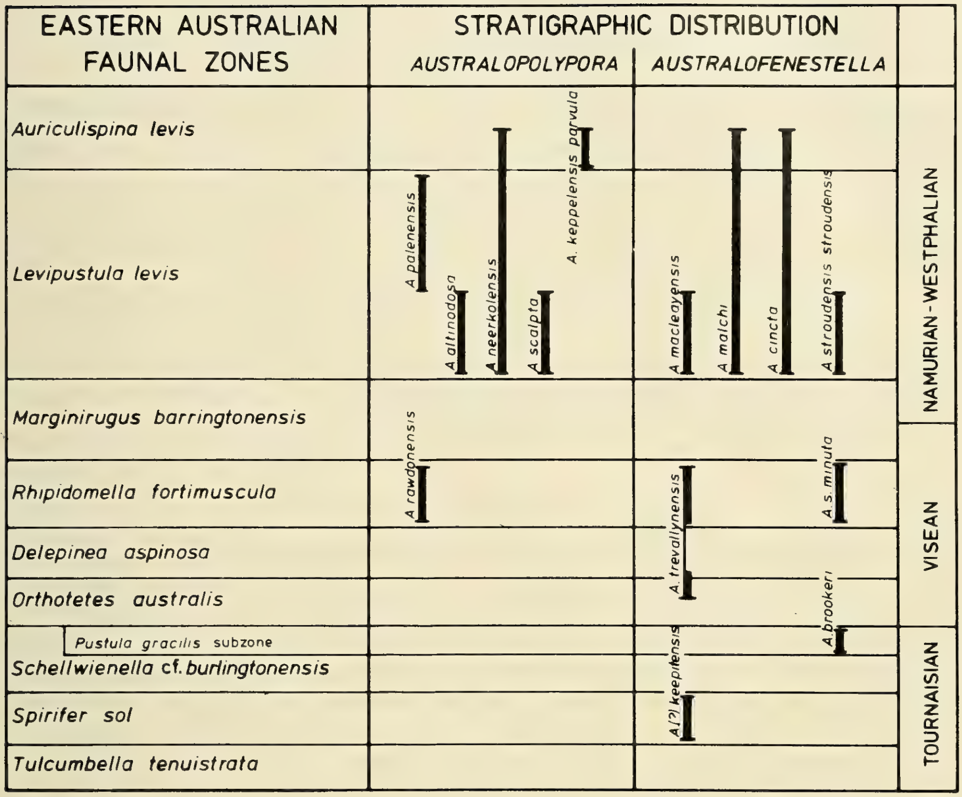

Fig. 6. Stratigraphic distribution of the various species of *Australopolypora* gen.nov. and *Australofenestella* gen.nov. in terms of eastern Australian Carboniferous brachiopod assemblage zones. Tentative correlation with European zonation is also included.

an excellent marker horizon in the Australian sequence. *Australopolypora* becomes a more abundant fossil in late Carboniferous and Permian strata but at no stage is there a large number of available taxa. This record is in marked contrast to the more extensive Northern Hemisphere distribution. Of the six multi-rowed species recorded in this paper, only *A. rawdonensis* and *A. keppelensis parvula* appear to mark distinctive stratigraphic levels.

No great stratigraphic importance can be assigned to the *Australofenestella brookeri — Australofenestella stroudensis* lineage due to the comparative rarity of the constituent members. Their real significance lies in their apertural conformity with the multi-rowed species, despite the fact that they commonly bear only two rows of zooecial apertures.

ACKNOWLEDGEMENTS

Thanks are due to Mr P. J. G. Fleming, Geological Survey of Queensland, for helpful assistance and the provision of facilities to study the type material in his custody; to Emeritus Professor D. Hill, C.B.E., F.R.S., of the University of Queensland and Professor B. Runnegar and Mr G. Brown of the University of New England for their generous provision of access to, or loan of, type materials housed in their respective collections.

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The Final Larval Instar of *Phaenocarpa (Asobara) persimilis* Papp (Hymenoptera, Braconidae, Alysiinae) from Australia

J. R. T. SHORT

SHORT, J. R. T. The final larval instar of *Phaenocarpa (Asobara) persimilis* Papp (Hymenoptera, Braconidae, Alysiinae) from Australia. *Proc. Linn. Soc. N.S.W.* 103 (3), (1978) 1979: 171-173.

The characters of the final larval instar of *Phaenocarpa persimilis* Papp are described and figured. The systematic position of *Phaenocarpa* within the Alysiinae is discussed in relation to recent classification schemes for Braconidae.

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INTRODUCTION

Papp (1977) has described the adult of *Phaenocarpa (Asobara) persimilis* from Australia. Like other members of the Alysiinae, it is an endoparasite of Diptera, emerging from the host puparium. Prince (1976) has studied the behaviour and physiology of this braconid and sent me a parasitized culture of *Drosophila melanogaster* Meigen. Present knowledge on the distribution of this parasite and its drosophilid field hosts is outlined by Prince. The characters of the final larval instar have not been described for any species of *Phaenocarpa*.

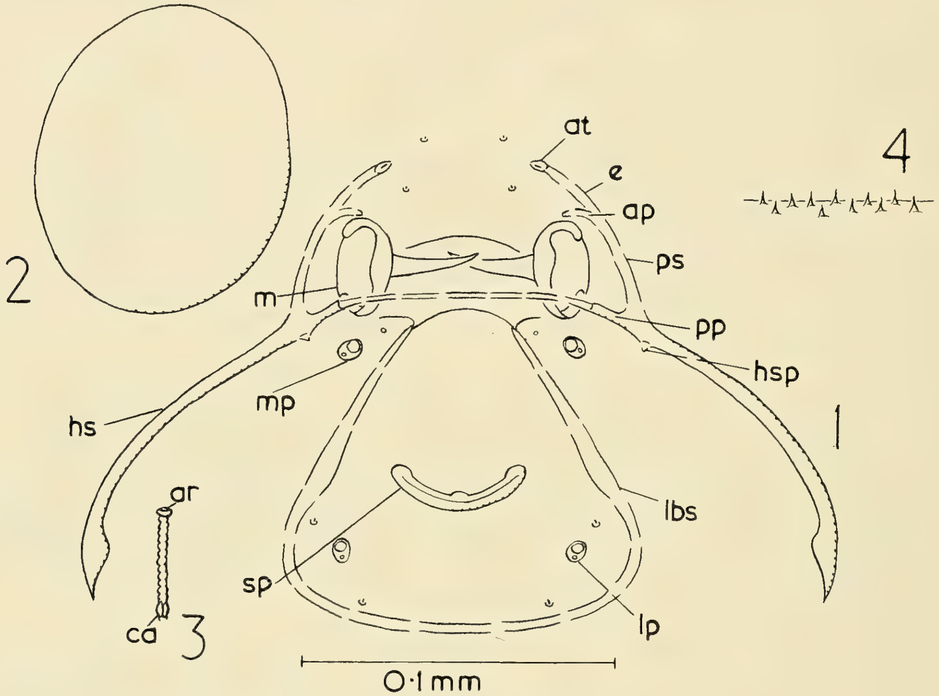
METHODS

Because of the small size of this braconid I could not follow standard methods (Short, 1978) of preparing and mounting ichneumonoid larvae. The final larval instars were dissected out of *Drosophila* puparia and a slit made in the larval body behind the head. The larvae were then washed in distilled water to clear away as much as possible of the body contents without distorting the delicate head. They were then mounted in Faure's fluid in cavity slides with the anterior surface of the head displayed. Enough of the body contents had been removed for the larvae to clear rapidly in this fluid and allow the examination of head parts and sense organs. The terminology of the head parts, together with its basis in comparative morphology, is given in Short (1952). Six larvae were studied. The slide preparations will be deposited in the Australian National Insect Collection.

LARVAL CHARACTERS

Of the head sclerites (Fig. 1), epistoma (e) unsclerotized above anterior tentorial pits (at); pleurostomae (ps) very lightly sclerotized; posterior pleurostomal processes (pp) and hypostomae (hs) sclerotized; hypostomal spur (hsp) represented by very small and lightly sclerotized projection from hypostoma; stipital sclerite absent; labial sclerite (lbs) very lightly sclerotized; maxillary (mp) and labial palps (lp) disc-like and with two sensilla, one large and one very small; silk press (sp) sclerotized; prelabial sclerite absent; labral sclerite absent; setae and sensilla of head very small; mandible (m) with lightly sclerotized base and relatively long, curved, slender, sclerotized blade; very lightly sclerotized bar present connecting posterior pleurostomal processes across dorsal surface of food meatus anterior to mandibles;

antennae (Fig. 2) disc-shaped and showing no sensilla on membrane; spiracle (Fig. 3) with small, shallow atrium (ar) and closing apparatus (ca) separated from atrium by length of trachea approximately equal in length to blade of mandible; skin (Fig. 4) with numerous spines, but no visible setae.



Figs. 1-4. Final larval instar of *Phaenocarpa (Asobara) persimilis* Papp.
1 Anterior view of head.
Abbreviations: ap anterior pleurostomal process, at anterior tentorial pit, hs hypostoma, hsp hypostomal spur, lbs labial sclerite, lp labial palp, m mandible, mp maxillary palp, pp posterior pleurostomal process, ps pleurostoma, sp silk press.
2 Antenna.
3 Spiracle.
Abbreviations: ar atrium, ca closing apparatus.
4 Cuticle.

DISCUSSION

In this account Capek (1970, 1973) and van Achterberg (1976) are followed in considering the Alysiinae to consist of the tribes Alysiini and Dacnusini.

The Alysiinae is a definite group on adult characters (van Achterberg, 1976) but the final larval instar characters differ from the almost complete set of head sclerites in *Alysia* (Short, 1952, fig. 33A) to the condition in *Aspilota* (Short, 1952, fig. 33B) where the only sclerotized structures are the epistoma and mandibles. *Dapsilarthra* may be a heterogeneous group. De la Baume Pluvinel (1915) figures an almost complete set of head sclerites in *D. gahani* de la Baume Pluvinel. Čapek (1970) figures *D. apii* Curtis with only the mandibles and pleurostomae sclerotized.

In the key to the genera of final larval instar braconids given by Čapek (1973), *Phaenocarpa* keys out in the second couplet with *Alysia* since the labial sclerite is present, although very lightly sclerotized. *Alysia* differs from *Phaenocarpa* in having the lateral parts of the labial sclerite well sclerotized. The form of the silk press, spiracles, antenna and cuticle are generally similar in these genera.

The larva of *Phaenocarpa* shows two very unusual features which have not been described in any other braconid. The mandibles, with their lightly-sclerotized oval-shaped bases and slender, curved sclerotized blades are similar to, but not identical with, the mandibles of the larvae of the more specialized genera of the ichneumonid subfamily Mesochorinae (Short, 1976). The very lightly sclerotized bar which extends between the posterior pleurostomal processes across the anterior surface of the food meatus is an unusual structure. It is difficult to suggest a function for it. A similar structure is present in some ichneumonids of the subfamilies Banchinae (Lissonotinae) and Metopiinae (Short, 1978). In *Phaenocarpa* the bar is clearly anterior to the mandibles; it does not form a ventral edge to the labrum.

Since *Alysia* and *Phaenocarpa* stand apart from other Alysiinae in showing a labial sclerite, it can be argued that *Phaenocarpa* represents one line of specialization from *Alysia*. *Phaenocarpa* spins only a very slight cocoon within the host puparium and reduction of the cocoon-spinning apparatus is seen in the very lightly sclerotized labial sclerite, the much-reduced hypostomal spur and the absence of the stipital sclerite. The general structure of the silk press, spiracle, antenna and cuticle of *Alysia* has been retained. The mandibles and bar between the posterior pleurostomal processes of *Phaenocarpa* are specialized structures.

ACKNOWLEDGEMENTS

I wish to thank the Australian Research Grants Committee for financial support and Dr G. J. Prince for sending a parasitized culture of *Drosophila*.

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Late Ordovician Articulate Brachiopods from Gunningbland, Central Western New South Wales

IAN G. PERCIVAL

PERCIVAL, I. G. Late Ordovician articulate brachiopods from Gunningbland, central western New South Wales. *Proc. Linn. Soc. N.S.W.* 103 (3), (1978) 1979: 175-187.

Brachiopods described and illustrated from the lower (Caradoc age-equivalent) part of the Goonumbla Volcanics at Gunningbland, central western New South Wales, include the new genus *Infurca* (Strophomenidae, Furcitellinae) with type species *I. tessellata* sp. nov., and the new species *Sowerbyella anticipata* and *Scaphorthis? aulacis.* Other forms recorded include *Doleroides* sp., *Oepikina?* sp., and aff. *Leptellina* sp. The occurrence in the Gunningbland fauna of several brachiopod genera formerly known only from contemporaneous strata in Kazakhstan confirms strong zoogeographic relationships between central western New South Wales and Kazakhstan during the middle to late Ordovician.

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INTRODUCTION

Within the lower part of the late Eastonian — early Bolindian (late Caradoc equivalent) Goonumbla Volcanics at Gunningbland, 32 km west of Parkes, a unit of massive tuffaceous sandstone occurs which yields an abundant well-preserved fauna dominated by brachiopods and trilobites. This sandstone unit immediately overlies limestone containing corals and stromatoporoids indicative of a Fauna III age in the local biostratigraphic scheme established by Webby (1969). Further stratigraphic and locality data are given in Percival (1978).

Inarticulate brachiopods, and the most abundant plectambonitacean strophomenoid brachiopods from this locality have previously been described (Percival, 1978, 1979). Presented below are descriptions of other important elements of the brachiopod fauna.

SIGNIFICANCE OF THE FAUNA

Late Ordovician brachiopod faunas of central western New South Wales are characterized by a high degree of endemism especially at specific (and to a lesser extent, generic) level, as evidenced by the large proportion of new taxa described herein and previously (Percival, 1978, 1979). The biogeographically-significant non-endemic elements of these faunas, in particular those from the Gunningbland area, are divisible into two groups: one including cosmopolitan genera such as *Sowerbyella* and *Paterula,* and the other comprising forms showing pronounced affinities with genera previously recorded only from Kazakhstan. This latter assemblage includes *Kassinella, Dulankarella?* (Percival, 1979), and aff. *Leptellina* herein. Species of these genera closely comparable with those occurring at Gunningbland are recorded in Kazakhstan from the late Caradoc Anderken and Dulankara horizons, correlated with the Zones of *Dicranograptus clingani* and *Pleurograptus linearis* (Nikitin, 1972), and thus broadly contemporaneous with the stratigraphic position of the Gunningbland fauna. In addition, an undescribed species referred to '*Chonetoidea simorini* M. Borisyak in coll.' by Sokolskaya (1960, pl.27, figs. 24-25) is possibly congeneric with

Durranella Percival, 1979, described from Gunningbland and elsewhere in central western N.S.W.; the age of '*C. simorini*' is, however, not given more precisely than mid-Ordovician. The restricted occurrence of the cited brachiopod genera in Kazakhstan and New South Wales confirms the strong zoogeographic relationship between these areas in the middle and late Ordovician, recognized by Webby (1974) from studies of the trilobite distribution.

Systematic Descriptions

Morphological terminology used herein follows that of the *Treatise on Invertebrate Paleontology, Part H, Brachiopoda* (Williams and Rowell, 1965), with modifications employed by Percival (1979). Classification follows Pope (1976) for the superfamily Strophomenacea and Havliček (1977) for Orthida. Specimens prefixed SUP are catalogued in the Palaeontological Collections of the Department of Geology and Geophysics, University of Sydney.

Abbreviations appearing in tables of measurements are as follows:

L, W, length, width of valve;

T, thickness of single valve;

Lmf, Wmf, maximum dimensions of muscle field from beak and midline respectively;

similarly for platform (Lpl, Wpl), socket ridges (Lsr, Wsr), brachiophore bases (Lbb, Wbb) and dental plates (Ldp, Wdp). Lengths and widths for last two parameters measured on internal moulds.

Ls, maximum extension of median ridge or septum from beak in designated valve;

N, OR, $\bar{x}$, s, number of specimens, observed range, mean, standard deviation from mean.

Order	ORTHIDA	Schuchert and Cooper, 1932
Suborder	ORTHIDINA	Schuchert and Cooper, 1932
Superfamily	PLECTORTHACEA	Schuchert, 1929
Family	PLECTORTHIDAE	Schuchert, 1929
Subfamily	PLECTORTHINAE	Schuchert, 1929
Genus	*DOLEROIDES*	Cooper, 1930

Type species: Orthis gibbosa Billings, 1857; original designation of Cooper, 1930, p. 375.

Doleroides sp.

Fig. 1, **13-16**

Material: Five specimens (SUP 62555 a/b, 62556 - 62559) from tuffaceous sandstone unit in lower part of Goonumbla Volcanics, near 'Currajong Park' homestead, just north of Gunningbland (locality L51 of Percival, 1978).

Description: Exterior of valves. Subequally biconvex, brachial valve slightly deeper; broad dorsal fold and corresponding ventral sulcus developing anteriorly, anterior commissure noticeably uniplicate. Evenly broadly convex in posterior transverse profile; maximum height of pedicle valve about one-fifth valve length; brachial valve between one-fifth and three-eighths as high as long. Outline transversely subquadrate; length averaging three-quarters valve width; maximum width at or slightly posterior to midlength. Beaks slightly projecting; hingelines of both valves five-eighths to two-thirds as wide as maximum width; cardinal extremities obtusely rounded, lateral and anterolateral margins broadly convex, anterior margin tending to be truncated. Ornament costellate with rounded ribs increasing by bifurcation (rarely by intercalation); 8 to 10 ribs in 5 mm at anterior valve margin. Concentric ornament either absent, or inconspicuous, comprising widely-spaced growth lines.

Ventral interarea high, curved; strongly apsacline to catacline; with wide, open delthyrium. Dorsal interarea lower, orthocline; notothyrium without covering plates.

Pedicle valve interior. Teeth large and stout, with deep oblique fossettes, supported from dorsal margin of hingeline by secondary callus replacing discrete dental plates. Muscle field elongately subcordate, extending to approximately one-third length, and one-quarter width, of valve, and enclosed laterally by low slightly convergent ridges; small linear adductor scars bisected by faint median ridge and contained anteriorly by low swelling at front of muscle field; diductors do not enclose adductors. Mantle canal impressions not observed, save for long divergent *vascula media.*

Brachial valve interior. Cardinal process linear, differentiated into thick smooth shaft and narrower short crenulated myophore, flanked by deep notothyrial cavities (Fig. 1, 14). Brachiophores long, rod-like, moderately divergent, supported for about half their length by bases converging anterior to shaft of cardinal process; prominent fulcral plates (Fig. 1, 14) bound large deep sockets anterolaterally. Median septum variable in development but generally indistinct beyond midlength of valve. Impressions of muscle scars and mantle canals obscure.

Measurements		L	W	L/W	T	Lmf	Wmf	Lsr	Wsr
SUP 62555 a/b	(Pedicle valve)	15.9	22.0	0.72	3.1	5.4	5.2	—	—
SUP 62556	(Brachial valve)	11.5	15.5	0.74	2.3	—	—	—	—
SUP 62557	(Brachial valve)	10.0	15.0	0.67	—	—	—	1.1	3.7
SUP 62558	(Brachial valve)	13.8	16.0	0.86	3.9	—	—	—	—
SUP 62559	(Brachial valve)	12.1	15.4	0.79	2.7	—	—	2.4	4.4

Remarks: Although insufficient material is available to warrant the establishment of a new species, or for adequate comparison with previously-described species, this form differs from most *Doleroides* in having longer, less widely-flaring brachiophores.

Subfamily ORTHOSTROPHIINAE Schuchert and Cooper, 1931

Genus *SCAPHORTHIS Cooper, 1956*

Type species: Scaphorthis virginiensis Cooper, 1956, p.502 (original designation).

Scaphorthis? aulacis sp. nov.

Fig. 1, **1-11**; Table 1

Etymology: aulacis (Latin) = furrow, in reference to the prominent dorsal sulcus.

Diagnosis: Subquadrate *Scaphorthis?* with high ventral fold and well-defined dorsal sulcus; convergent plates supporting brachiophores rudimentary to absent; median dorsal ridge lacking.

Material: Holotype (SUP 62549) and eleven paratypes (SUP 62543 - 62548, 62550 - 62554 a/b) from tuffaceous sandstone unit in lower part of Goonumbla Volcanics, near "Currajong Park" homestead, just north of Gunningbland; one paratype (SUP 62574) from underlying siltstone (locality L49 of Percival, 1978) also near "Currajong Park" homestead.

Description: Exterior of valves. Small ventribiconvex shells with deep dorsal median sulcus extending from posterior to anterior margins. Brachial valve gently convex laterally; pedicle valve with subangular median fold highest at about one-third valve length from posterior margin, becoming subdued anteriorly; height of pedicle valve equal to between one-quarter and one-fifth valve length, and about three-times height of corresponding brachial valve. Outline subquadrate to transversely subquadrate; lengths of sample populations of pedicle and brachial valves average seven-eighths and


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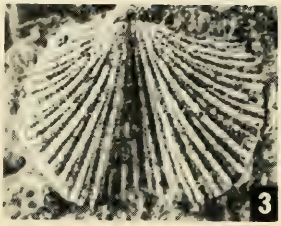
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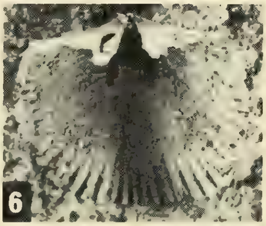
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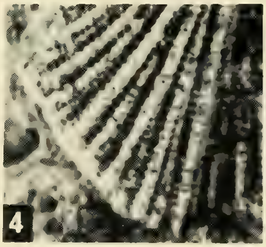
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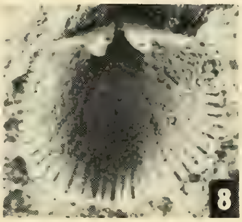
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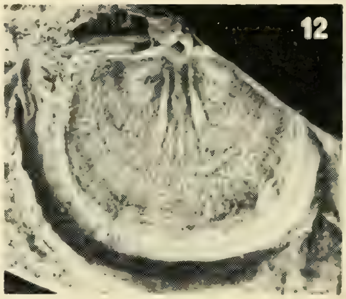
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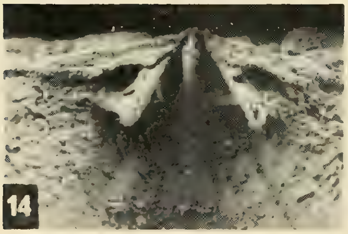
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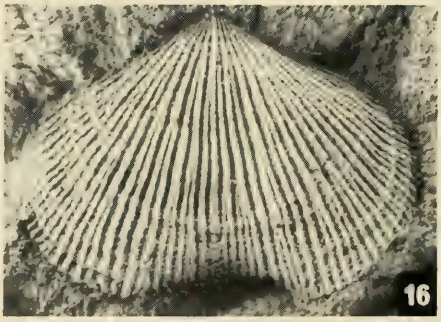
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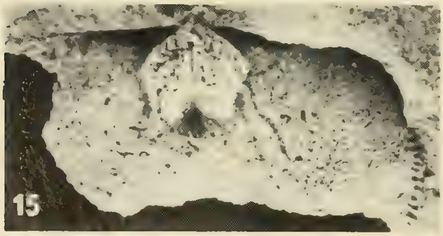
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four-fifths of respective valve widths; hingeline slightly less than maximum width which occurs at approximately midlength. Beaks weakly projecting; cardinal extremities obtusely rounded, lateral and anterior margins broadly convex. Anterior commissure weakly sulcate. Ornamentation costellate, costellae curved away from median line, increasing by bifurcation with 4 to 5 ribs per 1 mm at anterolateral margins of specimens 5 mm in length; ventral median rib may be slightly accentuated. Ribs cancellated by very fine closely spaced concentric filae (Fig. 1, 3, 4), approximately 9 to 11 per 1 mm of radius of valve, imparting reticulate appearance to shell surface. Shell substance fibrous.

Ventral interarea moderately high, planar, apsacline; delthyrium narrowly triangular, open, but with very short transversely striated pedicle collar apically (Fig. 1, **7, 8**). Dorsal interarea low, anacline, approximately same width as that of pedicle valve; notothyrium open.

Pedicle valve interior. Teeth small, simple, with oblique fossettes; supported by divergent receding dental plates extending to about one-sixth valve length; umbonal chambers small but deep. Muscle field short, subcordate, restricted to vicinity of delthyrial cavity, and occupying one-third valve width; adductor and diductor impressions not distinct. Mantle canal impressions obscure except for long *vascula media* divergent from anterior extremity of muscle field. Periphery of valve bears plicate impressions of external ribbing.

Brachial valve interior. Cardinal process a thin simple ridge not extending anteriorly beyond notothyrial chamber; notothyrial platform not thickened; median septum not developed. Brachiophores are moderately long stout blades (Fig. 1, **10, 11**) supported by divergent bases on valve floor for most or all of their length; brachiophore bases extend to approximately one-fifth valve length and are about one-quarter valve width apart at their distal extremities. Minute anterior extensions of bases in holotype (Fig. 1, **10,11**) faintly convergent (observed in this specimen only). Small deeply conical sockets excavated between brachiophores and hingeline; fulcral plates rudimentary or absent. Muscle scars and mantle canal impressions not observed. Measurements are given in Table 1.

Remarks: In external and internal morphology the new species described above closely resembles some of the early dalmanellidines. Such similarity is apparently superficial, as a fragment of shell adherent to a ventral internal mould (SUP 62574) attributed to this species proved to be impunctate when sectioned. Comparable examples of homeomorphy are known from other orthidine groups. Havlíček (1977) noted two families of orthaceans (Ranorthidae; Nanorthidae) of early Ordovician age which also are of dalmanellid appearance, yet are impunctate. Several plectorthacean genera (family Plectorthidae) are also superficially similar in

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Fig. 1. Specimens from tuffaceous sandstone unit in lower part of Goonumbla Volcanics, Gunningbland, New South Wales.

1-11. *Scaphorthis? aulacis* sp. nov. All x5 except **4, 11** both x10. **1.** Latex impression from pedicle valve external mould, paratype SUP 62547. **2.** Latex impression from brachial valve external mould, paratype SUP 62545/b. Interarea of attached pedicle valve visible. **3-4.** Latex impression from brachial valve external mould, paratype SUP 62550, showing ornament in detail. **5-6.** Pedicle valve internal mould, and latex impression from same, paratype SUP 62548. Interarea above tooth on left side of **6** damaged by air bubble in latex. **7-8.** Pedicle valve internal mould, and latex impression from same, paratype SUP 62546. **9-11.** Brachial valve internal mould, latex impression from same, and enlargement of cardinalia, holotype SUP 62549. Note attitude of brachiophores and their supporting bases.

12. *Oepikina?* sp. x1.3. Latex impression from brachial valve internal mould, SUP 62568.

13-16. *Doleroides* sp., **13, 15-16** x2.5; **14** x5. **13-14.** Latex impression from brachial valve internal mould, and enlargement of cardinalia of same (slightly tilted), SUP 62559. **15-16.** Pedicle valve internal mould, and latex impression from pedicle valve external mould, SUP 62555 a/b.

TABLE 1

Measurements of *Scaphorthis? aulacis* sp. nov.

		L	W	L/W	Ldp	Wdp	$\frac{\text{Ldp}}{\text{L}}$	$\frac{\text{Wdp}}{\text{W}}$	Lbb	Wbb	$\frac{\text{Lbb}}{\text{L}}$	$\frac{\text{Wbb}}{\text{W}}$
Holotype SUP 62549 (Brachial valve)		3.5	4.6	0.76	—	—	—	—	0.8	1.0	0.23	0.22
Paratype SUP 62548 (Pedicle valve)		5.5	6.2	0.89	0.8	2.0	0.15	0.32	—	—	—	—
Pedicle valves	N	9	9	9	4	4	4	4				
	OR	3.4–6.8	4.0–7.8	0.75–0.96	0.5–0.9	1.5–2.0	0.15–0.18	0.25–0.38	—	—	—	—
	$\bar{x}$	5.2	6.0	0.88	0.8	1.8	0.16	0.32				
	s	1.0	1.1	0.06	0.2	0.2	0.01	0.05				
Brachial valves	N	11	11	11					5	5	5	5
	OR	3.5–5.8	4.3–7.0	0.71–0.94	—	—	—	—	0.7–1.0	1.0–1.4	0.15–0.26	0.21–0.30
	$\bar{x}$	4.3	5.3	0.81					0.8	1.2	0.20	0.25
	s	0.8	0.9	0.07					0.1	0.2	0.04	0.04

appearance to dalmanellidines. Of these, *Scaphorthis* Cooper (in particular *S. sulcata* Wright) is most like the form described above. Wright (1964, p.202) in establishing *S. sulcata* commented on the "dalmanelloid appearance of the shell and the style of cardinalia" of this species, and of *Corineorthis* Stubblefield, *Giraldiella* Bancroft, and *Scaphorthis* in general.

The new species does not conveniently fit into either the Orthacea or Plectorthacea. In the holotype (the best-preserved brachial valve) rudimentary concave plates converge beneath the anterior ends of the brachiophores (Fig. 1, **10, 11**). This feature suggests affinities with the Plectorthacea, especially in view of other similarities (discussed below) with *Scaphorthis sulcata.* However, in most other examples of the new species, the anteriorly-divergent brachiophores are attached to the valve floor throughout the majority of their length. Thus the Gunningbland species could equally well be assigned to the Orthacea (Ranorthidae), and compared with *Eodalmanella* Havlíček (presently known only from one species of Llanvirn age from Czechoslovakia). Overall it would seem best tentatively to refer the new species to *Scaphorthis,* a more widespread genus of middle and late Ordovician age.

Like the Portrane Limestone species *S. sulcata* Wright, of Ashgill age, *S.? sulcata* displays a reticulate external appearance imparted by closely-set growth lines intersecting the fascicostellate radial ornament. As noted by Wright (1964, p.203) this feature distinguishes *S. sulcata* from American species of *Scaphorthis.* In addition (and again serving to differentiate them from the American species), both *S. sulcata* and *S.? aulacis* are characterized by the presence of a well-defined dorsal sulcus and the absence of a thickened internal median ridge in the brachial valve. A pedicle callist is present in both species. However, *S.? aulacis* is much less transverse in outline than *S. sulcata,* and more importantly lacks the distinct convergent plates supporting the brachiophores as developed in the latter. Differences are also noted in relative dimensions of cardinalia and ventral muscle fields of the two species. The ranorthid *Eodalmanella* Havlíček differs from *S.? aulacis* in lacking a pedicle callist and in displaying well-defined muscle scars and vascular impressions in the brachial valve. Another distinguishing feature is valve outline, *Eodalmanella* being widest at the hingeline whereas the maximum width of *S.? aulacis* coincides more or less with midlength.

Order STROPHOMENIDA Öpik, 1934
Suborder STROPHOMENIDINA Öpik, 1934
Superfamily PLECTAMBONITACEA Jones, 1928
Family LEPTELLINIDAE Ulrich and Cooper, 1936
Subfamily LEPTELLININAE Ulrich and Cooper, 1936

aff. *Leptellina* sp.
Fig. 2, **6-9**

Material: Five specimens (SUP 61461, 62539-62542) from tuffaceous sandstone unit in lower part of Goonumbla Volcanics, near "Currajong Park" homestead, just north of Gunningbland.

Description: Valves plano- to concavo-convex; subquadrate to subrectangular; length five-eighths to seven-tenths valve width; maximum width at about midlength; cardinal extremities acutely angular, lateral margins sigmoidal, anterior margin broadly convex. Details of ornament unknown. Dorsal interarea anacline; orientation of ventral interarea unknown, pseudodeltidium small.

Pedicle valve interior. Teeth stout, pointed, with narrow oblique fossettes, supported by thickened wall of delthyrial cavity. Muscle field cordate, extending to almost midlength and occupying one-third valve width; bisected by thin median ridge; adductor scars not distinguished from diductors. Low arcuate bars of shell material anterolateral to muscle scars bear shallow impressions of mantle canals.

Brachial valve interior. Cardinal process trilobed, low and broad; socket ridges short, straight and widely divergent, with thickened distal extremities recurved posteriorly. Prominent elongately conical median septum rises abruptly at about one-third valve length from callus anterior to low notothyrial platform; sharply ventrally-peaked anterior end of septum at approximately seven-tenths valve length bears shallow tubular posteriorly-directed excavation; septum does not extend to platform rim. Platform wide and long, occupying eight to nine-tenths valve length and width, with high flared and slightly undercut rim in adults; rim barely indicated in juveniles. Elongate adductor scars deeply excavated on either side of septum in central portion of platform (Fig. 2, **6**). Pair of *vascula media* canals lies along sides of median septum, extending beyond its termination through anteromedian gap in platform rim; two pairs of long straight canal impressions *(vascula myaria)* diverge anterolaterally, *vascula genitalia* indistinct.

Measurements		L	W	L/W	Lmf	Wmf	Lsr	Wsr	Ls	Lpl	Wpl
SUP 61461	(Pedicle valve)	4.4	7.0	0.63	1.9	2.4	—	—	—	—	—
SUP 62539	(Brachial valve)	4.1	5.8	0.71	1.1	1.7	0.7	2.3	2.9	3.2	4.9
SUP 62540	(Brachial valve)	4.0	6.1	0.66	1.1	2.3	0.9	2.6	2.7	3.4	5.1
SUP 62541	(Brachial valve)	3.8	5.8	0.66	—	—	0.7	2.3	2.7	3.2	4.5
SUP 62542	(Brachial valve)	4.2	6.2	0.68	—	—	0.9	2.7	3.0	3.8	5.1

Remarks: This distinctive form, characterized by a large ventral muscle field bisected by a thin median ridge, and thick dorsal median septum not extending to platform rim, is best left in open nomenclature until further material displaying the ornament is available. Close comparison is possible with only one other described species — *Leptelloidea multicostata* Rukavishnikova (1956, p.132) from the Anderken and Otarsk horizons (mid-late Caradoc) of Kazakhstan. This species was referred to variously by Nikitin (1972) as *Leptelloidea? multicostata, Leptellina multicostata,* and *Leptellina? multicostata,* in addition to the original designation of Rukavishnikova (1956). It belongs, however, to neither *Leptelloidea* nor *Leptellina,* differing from both in appearance of the dorsal median septum, especially termination of the latter posterior to the platform rim. The cardinalia of the Kazakh and Gunningbland species are *Leptellina*-like, but their ventral muscle fields are quite distinctly different in size, shape and arrangement from those of species of *Leptellina*. The ventral muscle field of *Leptelloidea* is also unlike those of the Kazakh and Gunningbland forms, although arcuate ridges in the pedicle valve of aff. *Leptellina* sp. suggest similarity with some species of *Leptelloidea* possessing a low concentric submarginal ventral rim. It is apparent that the Kazakh and Gunningbland species are representatives of a new genus related to both *Leptellina* and *Leptelloidea*.

Family SOWERBYELLIDAE Öpik, 1930
Subfamily SOWERBYELLINAE Öpik, 1930
Genus *SOWERBYELLA* Jones, 1928

Type species: *Leptaena sericea* Sowerby, 1839; original designation of Jones, 1928, p.384.
Diagnosis: See Williams, 1965, pp. H378-9.

Sowerbyella anticipata sp. nov.
Fig. 2, 1-5

Etymology: In reference to advanced features of this species, foreshadowing later denticulate sowerbyellids (Latin *anticipatus:* foretell).
Diagnosis: Large *Sowerbyella* with deeply inset ventral adductors; dorsal muscle field and septa not thickened; rudimentary accessory pair of ventral denticles and dorsal sockets present on hingeline.
Material: Holotype (SUP 62570) and three paratypes (SUP 62571-62573) from tuffaceous sandstone unit in lower part of Goonumbla Volcanics, near "Currajong Park" homestead, just north of Gunningbland.
Description: Exterior of valves. Moderately concavo-convex shell, depth approximately one-fifth valve length; outline transverse, maximum width at hingeline; valve length between half and three-fifths width. Cardinal extremities subrectangular to acute, lateral and anterior margins broadly rounded. Brachial valve with broad shallow sulcus rapidly widening anteriorly; ornament unequally parvicostellate (available exterior inadequately preserved for measurements of rib distribution); indistinct short oblique rugae present adjacent to posterolateral hingeline. Pedicle valve ornament not seen; interarea apsacline; delthyrium wide, pseudodeltidium small, apical. Dorsal interarea anacline to catacline; notothyrium covered by small chilidial plates. Shell substance pseudopunctate.
Pedicle valve interior. Oblique ridge-like teeth project laterally from wall of delthyrial cavity. Additional low tubercle present on hingeline on each side of beak about one-third distance toward cardinal extremities (Fig. 2, 5) presumably also assisted in articulation, being accommodated in shallow linear socket (buttressed anteriorly by short ridge) on brachial valve hingeline (Fig. 2, 1). Muscle field bilobed; adductor scars small, elliptical, with posterior ends deeply inserted beneath small pedicle callist in delthyrial cavity. Adductors separated by short median septum which forks at 70°-80°, between one-fifth and one-quarter valve length from beak, into low ridges outlining rectangular diductor scars; latter extend to between half and five-eighths valve length, and occupy one-third to two-fifths valve width. Mantle canal pattern lemniscate.
Brachial valve interior. Ridge-like cardinal process laterally fused to chilidial plates, forming arcuate shelf over deeply excavated alveolus; socket ridges very short, straight, widely divergent. Median septum weak, commencing at three-tenths valve length and extending to seven-tenths length, flanked by stronger moderately divergent submedian septa commencing beneath cardinalia; submedian septa not thickened anteriorly. Muscle field indistinct, lacking thickened floor and lateral bounding

ridges, crossed by divergent weakly-developed transmuscle septa. Mantle canal pattern not preserved.

Measurements		L	W	L/W	T	Lmf	Wmf	Ls	Lsr	Wsr
SUP 62570	(Pedicle valve)	12.9	21.9	0.59	2.4	6.4	7.8	3.0	–	–
SUP 62571	(Pedicle valve)	13.0	22.0	0.59	2.5	5.6	8.7	2.8	–	–
SUP 62572	(Brachial valve)	12.3	22.8	0.54	–	–	–	–	–	–
SUP 62573	(Brachial valve)	8.7+	15.3	–	–	–	–	–	1.6	3.9

Remarks. The large size and deeply inserted ventral adductor muscles imply that this is an advanced species of *Sowerbyella;* broadly similar North American forms are of Trenton and Eden age (Howe, 1972). Of considerable significance is the rudimentary accessory hingeline denticulation which, according to Howe (1972, p.443), is a feature of *Eoplectodonta* or *Thaerodonta* rather than *Sowerbyella.* The species described here, which in all other details conforms to *Sowerbyella,* possibly represents a transitional form approaching *Eoplectodonta.*

Sowerbyella anticipata is distinguished from all known *Sowerbyella* sensu stricto by absence of thickening of the dorsal muscle field and septa, and development of rudimentary accessory denticulation. There is little similarity between this species and *S. lepta* occurring in slightly older strata at "New Durran" south-east of Gunningbland (Percival, 1979). The two differ most noticeably in size, profile, dimensions and appearance of muscle fields in both valves, and in details of cardinalia.

Superfamily STROPHOMENACEA King, 1846
Family OEPIKINIDAE Sokolskaya, 1960

Oepikina? sp.
Fig. 1, 12

Material: One brachial valve internal mould, SUP 62568, from tuffaceous sandstone unit in lower part of Goonumbla Volcanics, near "Currajong Park" homestead, just north of Gunningbland.

Description: Brachial valve subquadrate, widest at hingeline; length three-quarters width; planar to weakly convex with narrow dorsally-geniculate anterolateral and anterior margins. Interarea anacline. Cardinal process bilobed above alveolus excavated posteriorly in low notothyrial platform; socket ridges short, straight, very widely divergent, sharply recurved toward hingeline distally. Short median septum extends anteriorly from notothyrial platform, dividing at one-quarter valve length into three indistinct subparallel septa terminating at about midlength, and flanked by stronger bladelike pair of subparallel submedian septa. Muscle scars suboval, extending to three-eighths valve length and width; transmuscle septa lacking. Mantle canals indistinct but pattern apparently saccate. Conspicuous subperipheral rim present. *Pedicle valve* unknown.

Measurements: Length 25.3 mm, width 33.5 mm.

Remarks: The specimen differs from other species of *Oepikina* in form and arrangement of its septa, development of a circular alveolus (rather than a longitudinal groove) beneath the cardinal process lobes, and in the extended recurved distal portions of the socket ridges. Although it exhibits the characteristic subperipheral rim of *Oepikina,* generic determination remains uncertain until the pedicle valve is known.

A single brachial valve external mould (SUP 62569) of weakly concave profile and subquadrate outline possibly belongs to the same species as that described above. Although this specimen, measuring 13.5 mm in length and 17.5 mm width, is only about half the size of SUP 62568, the two have almost identical length: width ratios. The external mould indicates that the ornament comprised fine multicostellae crossed


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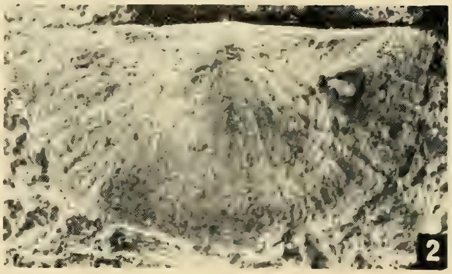
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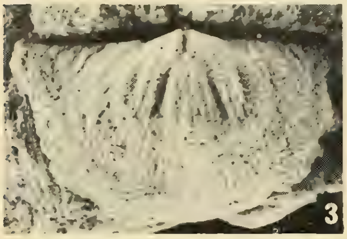
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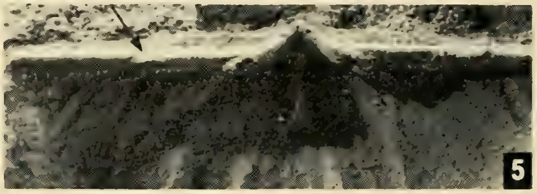
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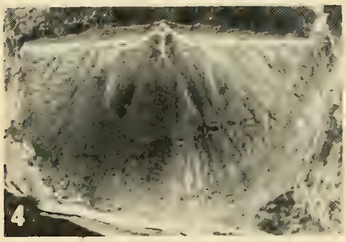
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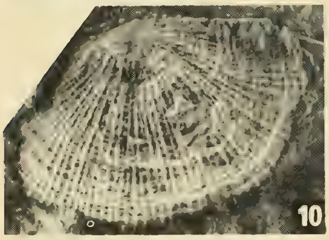
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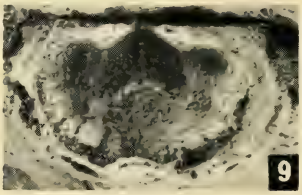
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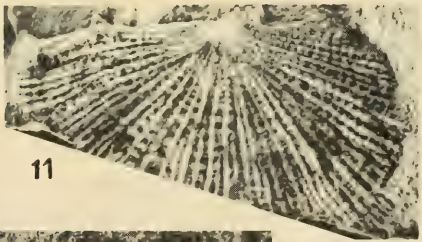
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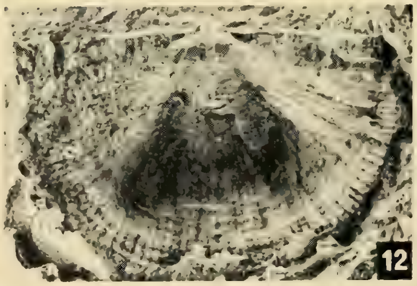
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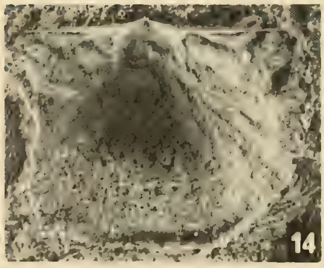
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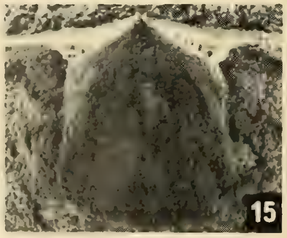
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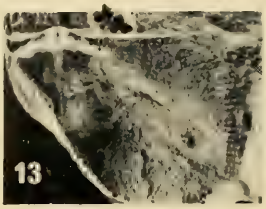
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by delicate crowded concentric filae, with three to four costellae per mm at the anterior margin; this ornament resembles that of the type species of *Oepikina, O. septata* Salmon (Cooper, 1956, pl. 239B, fig. 21).

Family STROPHOMENIDAE King, 1846
Subfamily FURCITELLINAE Williams, 1965
Genus *INFURCA* gen. nov.

Type species :*Infurca tessellata* gen. et sp. nov.
Etymology: Alluding to undivided dorsal median septum, *in-* without, *furca* fork (Latin).
Diagnosis: Convexo-planar to dorsibiconvex furcitellin with conspicuous concentric lamellae intersecting multicostellate ornament; pseudodeltidium small, foramen apparently absent; teeth denticulate, supported by weakly divergent plates laterally bounding pentagonal muscle field; dorsal median septum undivided, other dorsal septa inconspicuous or lacking.
Discussion: Multicostellate ornament, valve profile, and form of ventral muscle field are consistent with the assignment of the new genus to the Furcitellinae, although it differs from other genera of that subfamily in having only a small pseudodeltidium, and in apparently lacking a pedicle foramen. However, available external moulds were not entirely suitable for preservation of the internal infilling of such a structure if it existed, and subsequent material may reveal the presence of a small apical foramen. Reduction in number and degree of development of dorsal septa is also a distinguishing feature of *Infurca,* recalling the early furcitellin *Trotlandella* Neuman, 1974, from Llanvirn age strata near Trondheim, Norway. Other features common to *Infurca* and *Trotlandella* include small ventral muscle field restricted to delthyrial cavity, and multicostellate ornament intersected by conspicuous concentric rugae-like growth lamellae. *Infurca* is readily distinguished from *Trotlandella* in lacking the large pseudodeltidium of the latter, and in having divergent dental plates (rather than anteriorly convergent as in *Trotlandella*). Perhaps the most fundamental distinction between these genera concerns relative development of cardinalia; the cardinal process lobes of *Infurca* are considerably more prominent than those of *Trotlandella* which also is characterized by elevated sockets — a feature not present in *Infurca.* Other Ordovician furcitellins, such as *Furcitella* Cooper and *Holtedahlina* Foerste, differ from *Infurca* in having more robust cardinalia and strongly developed dorsal ridges with an anteriorly bifurcating median septum. Early Silurian species of *Katastrophomena* Cocks exhibit weak development of dorsal septa comparable to *Infurca* and display a similar ornament (termed *scoticoid* by Pope, 1976), but differ from the new genus in their resupinate profile.

Fig. 2. Specimens from tuffaceous sandstone unit in lower part of Goonumbla Volcanics, Gunningbland, New South Wales.

1-5. *Sowerbyella anticipata* sp. nov. **1.** Latex impression from brachial valve internal mould, paratype SUP 62573, x3. **2.** Latex impression from brachial valve external mould, paratype SUP 62572, x2.5. **3-5.** Pedicle valve internal mould, latex impression from same, and enlargement of hingeline (slightly tilted), holotype SUP 62570. Arrow on 5 indicates position of accessory hingeline denticulation. **3, 4** x2; **5** x4.

6-9 aff. *Leptellina* sp., all x5. **6, 7.** Latex impressions from brachial valve internal moulds, SUP 62540 and SUP 62542 respectively. **8.** Latex impression from juvenile brachial valve internal mould, SUP 62541. **9.** Latex impression from pedicle valve internal mould SUP 61461.

10-15. *Infurca tessellata* gen. et sp. nov. **10.** Latex impression from brachial valve external mould, paratype SUP 62563, x2. **11.** Latex impression from pedicle valve external mould, paratype SUP 62566, showing ornament, x3. **12.** Latex impression from brachial valve internal mould, holotype SUP 62560, x2.5. **13.** Latex impression from brachial valve internal mould, paratype SUP 62562, x2. **14-15.** Latex impression from pedicle valve internal mould, and enlargement showing denticles on dental plates, and muscle field, SUP 62564, x2 and x5 respectively.

Infurca tessellata gen. et sp. nov.

Fig. 2, 10-15

Etymology: Referring to chequered appearance of ornament; Latin *tessellatus* chequered.

Diagnosis: Characters of genus.

Material: Holotype (SUP 62560) and seven paratypes (SUP 62561 – 62567) from tuffaceous sandstone unit in lower part of Goonumbla Volcanics, near "Currajong Park" homestead, just north of Gunningbland.

Description: Exterior of valves. Convexo-planar to dorsibiconvex transversely subquadrate shells with obtusely-rounded cardinal extremities and broadly-rounded lateral and anterior margins; maximum width at about one-third valve length from beak, valve length three-fifths to seven-tenths width. Pedicle valve approximately one-tenth as deep as long, with subdued median fold of variable width, flanked laterally by triangular depressed areas; posterolateral corners of valve flattened or slightly oblique to plane of commissure, anterior and anterolateral margins frequently narrowly geniculate. Brachial valve has indistinct median sulcus in posterior half of valve; prominently convex medially; between one-sixth and one-quarter as deep as long, and (estimated) about twice depth of corresponding pedicle valve; posterolateral corners flattened. Both valves ornamented with coarse concentric rugae-like growth lamellae, imparting chequered appearance to exterior. Costellae and growth lamellae equally prominent or, more commonly, costellae slightly stronger in development bearing small nodes at junction with concentric lamellae. Superimposed on chequered ornament are more-widely-spaced step-like growth hiatuses. Ten to twelve costellae occupy 5 mm along front margin of valves. Pedicle valve interarea apsacline; delthyrium wide, pseudodeltidium small, apical, highly convex; foramen not apparent. Brachial valve interarea lower, anacline to catacline; notothyrium covered by low convex chilidium with shallow median sinus.

Pedicle valve interior. Teeth denticulate (Fig. 2, 15), with denticles extending posteriorly along walls of delthyrial cavity; teeth supported by thin weakly divergent dental plates extending anteriorly to about three-eighths valve length, and laterally bounding pentagonal muscle field. Latter is shallowly impressed, lacks containing ridges anteriorly, and extends to two-fifths valve length and one-fifth valve width; adductor and diductor scars not distinguished. Mantle canals indistinct. Valve periphery flattened laterally, narrowing anterolaterally and inflected towards brachial valve anteriorly.

Brachial valve interior. Twin erect lobes of cardinal process separated by minute ridge within narrow cleft, and supported on anchor-shaped notothyrial platform. Socket ridges short, widely divergent, recurved distally parallel to hingeline. Narrow weakly-developed median septum extends anteriorly from notothyrial platform, through indistinct muscle field, to between one-third and half valve length; other septa inconspicuous to absent. Mantle canals obscure. Periphery of valve thickened slightly, incised by closely-spaced grooves.

Measurements		L	W	L/W	T	Lmf	Wmf	Lsr	Wsr
Holotype SUP 62560	(Brachial valve)	13.3	20.0	0.67	2.1	—	—	1.2	3.9
Paratype SUP 62561	(Pedicle valve)	17.7	26.8	0.66	—	—	—	—	—
Paratype SUP 62562	(Brachial valve)	15.4+	27.0	—	—	—	—	2.3	7.8
Paratype SUP 62563	(Brachial valve)	13.2	22.0	0.60	3.0	—	—	—	—
Paratype SUP 62564	(Pedicle valve)	14.5	21.6	0.67	1.4	5.7	4.4	—	—
Paratype SUP 62565	(Brachial valve)	17.9	26.1	0.69	3.0	—	—	—	—
Paratype SUP 62566	(Pedicle valve)	10.6+	17.5+	—	—	—	—	—	—
Paratype SUP 62567	(Pedicle valve)	10.0+	21.2+	—	—	—	—	—	—

Remarks: The genus *Infurca* is at present represented only by its species *I. tessellata*.

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I am grateful to Associate Professor B. D. Webby for helpful criticism of the manuscript, and to Dr G. A. Cooper and an anonymous referee for comments on taxonomic problems. For their hospitality during fieldwork I thank the Buchan and Trotman families of Gunningbland. Mrs D. Garbler and Miss C. A. Johnson kindly typed the manuscript. This research was conducted during tenure of a Commonwealth Postgraduate Award at the Department of Geology and Geophysics, University of Sydney.

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PROCEEDINGS
of the
LINNEAN SOCIETY
of
NEW SOUTH WALES

VOLUME 103
PART 4

Some Dermanyssid Mites (Acari), mostly from Australasian Rodents

ROBERT DOMROW

DOMROW, R. Some dermanyssid mites (Acari), mostly from Australasian rodents. *Proc. Linn. Soc. N.S.W.*, 103 (4), (1978), 1979: 189-208.

Results are presented from three sponsored expeditions to collect parasitic mites from mammals, mostly rodents, in remote parts of Australasia. Three new species of *Laelaps* are described from native-mice (*Pseudomys* spp.) in Western Australia: *L. janalis* from *P. occidentalis, L. bycalia* from *P. albocinereus,* and *L. lybacia* from *P. praeconis.* Additional data, including new hosts and localities, and previously unknown males and immature stages, are given for a further 22 species in nine genera: *Mesolaelaps* (3), *Haemolaelaps* (2), *Peramelaelaps* (1), *Laelaps* (9), *Eulaelaps* (1), *Echinonyssus* (1), *Trichosurolaelaps* (2), *Ornithonyssus* (2) and *Halarachne* (1). A small group of intractable specimens of *Laelaps* with both setae on coxa I simple is still under study.

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This paper assembles results from three Australian Biological Resources Study grants, gratefully acknowledged — one to Dr C. H. S. Watts, Institute for Medical and Veterinary Research, Adelaide, for a circum-Australian sampling of rats (Robinson *et al.,* 1978) and two to me to collect ectoparasites in remote areas of Queensland. For brevity, collectors are omitted from Dr Watts' offering (with map coordinates), but I hasten to add that they were A. C. & J. F. Robinson. Their material will be deposited in the Australian National Insect Collection, CSIRO, Canberra. The data for my contributions are: Bamaga, near Cape York, iii.1975, R. Domrow and J. S. Welch; and Kowanyama (formerly Mitchell River Mission), east coast of Gulf of Carpentaria, vi.1976, R. Domrow. These two collections will be divided between the Queensland Museum, Brisbane, and my institute (QIMR). Lastly, a few recent accessions in QIMR are added, with data in full. I thank all concerned.

Terminology is largely after Evans and Till (1965), with tarsi II-IV after Evans (1969). Hosts are after Ride (1970), with subspecies for rats supplied after Taylor and Horner (1973).

Mesolaelaps australiensis (Hirst)

Laelaps (Mesolaelaps) australiensis Hirst, 1926, *Proc. zool. Soc. Lond.,* 1926: 840.

Material. Three ♀♀, *Rattus fuscipes fuscipes* (Waterhouse) (three rats), 22 km NE Jurien (30°8′, 115°8′), W.A., 12-13.iv.1975; 10 ♀♀, *R. f. coracius* Thomas (three rats), 41 km SE Cairns (17°15′, 145°56′), Qd, 16.xi.1974; seven ♀♀, *R. leucopus leucopus* (Gray), Bamaga; one ♀, *R. lutreolus lutreolus* (Gray), 20 km SW Port Macquarie (31°37′, 152°50′), N.S.W., 2.ii.1975; 14 ♀♀, *R. sordidus sordidus* (Gould) (three rats), Iron Range, 23 km S Portland Roads (12°47′, 143°18′), Qd, 2-3.xi.1974; two ♀♀, *R. s. sordidus* (two rats), 37 km S Cooktown (15°48′, 145°14′), Qd, 9.xi.1974; 10 ♀♀, *R. s. sordidus* (four rats), 16 km S Cairns (17°4′, 145°47′), Qd, 14.xi.1974; eleven ♀♀, one deutonymph (hereafter abbreviated as dn), *R. s. sordidus* (four rats), 11 km NE Atherton (17°12′, 145°33′), Qd, 22.xi.1974; one ♀, *R. s. villosissimus* (Waite), 2 km NE Mount Isa (20°38′, 139°30′), Qd, 19.x.1974; one ♀, *R. s. villosissimus,* 32 km W Windorah (25°20′, 142°18′), Qd, 15.x.1974; one ♀, *R. tunneyi tunneyi* (Thomas), 14 km S Nourlangie Camp (12°54′, 132°39′), N.T., 18.vi.1975; one ♀, *R. t. culmorum* (Thomas and Dollman), 58 km N Maryborough (25°6′, 152°33′), Qd, 14.i.1975; one ♀, *Hydromys chrysogaster* Geoffroy, Maslin Creek, Atherton (17°15′, 145°29′), Qd, 24.xi.1974; one ♀, *Melomys littoralis* (Lönnberg), 11 km NE Atherton (17°12′, 145°33′), Qd, 22.xi.1974; one ♀, *M. littoralis,* 9 km SE Dunwich, Stradbroke Island (27°32′, 153°30′), Qd, 19.i.1975.

Deutonymph. Capitulum 355 μm long, as in *M. antipodianus* (Hirst) (see Domrow, 1977), but setae c and h_3 well exceeding sides of basis. Epistome an equilateral triangle, free sides ever so slightly convex, with weak denticulations and broad, but fine, submarginal dendritic pattern. Chelicerae stronger, 248 μm long, with digits more elongate, occupying one-quarter of total length.*

Idiosoma 780 μm long, 530 μm wide (somewhat engorged). Dorsal shield 715x335 μm, holotrichous, differing from that of *M. antipodianus* only in that setae are slightly more elongate. Most of Z and S setae broken, but Z_3 certainly elongate. Setae on cuticle longer and more widely spaced than in *M. antipodianus* (as is case in adults of two species).

Venter as in *M. antipodianus,* but genital portion of sternogenital shield tapering very sharply behind metasternal setae, parallel-sided, only half as wide as space between genital setae; setae on cuticle again longer and more widely spaced. Postanal seta broken off, but its insertion well exceeded by adanals. At least one small metapodal shield on each side.

Legs holotrichous except for one additional v seta on tibia I (2-6/4-2) as in *M. antipodianus* (♀ also showing this additional seta). Longest seta on dorsum of tarsus IV 140 μm.

Notes. M. australiensis is widespread in Australia, showing a low level of host-specificity (Domrow, 1961, 1962a, 1967). At a subspecific level, *R. f. fuscipes, R. l. leucopus, R. s. villosissimus, R. t. tunneyi* and *R. t. culmorum* are new host-records, *R. t. tunneyi* extending the range of this mite into the Northern Territory. Extra-Australian records (New Guinea, New Zealand and Kermadec Islands) were summarized by Tenorio and Radovsky (1974).

Mesolaelaps bandicoota (Womersley)

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

Material. Two ♀♀, *Rattus fuscipes assimilis* (Gould), Mount Stanley, 38 km E Kingaroy (26°30′, 152°13′), Qd, 16.i.1975; four ♀♀, *R. f. assimilis* (two rats), 56 km SE Canberra (35°41′, 149°32′), N.S.W., 14.ii.1975; one ♀, *R. f. assimilis,* 20 km NE Mallacoota (37°27′, 149°57′), N.S.W., 17.ii.1975; two ♀♀, *R. lutreolus lutreolus,* 6 km SW Bemm River (37°47′, 148°54′), Vic., 21.ii.1975.

Notes. This material confirms earlier records (Domrow, 1963, 1973). All specimens show the anterior seta on coxae II-III normal (unexpanded) and the dorsal shield holotrichous, except one female from near Canberra with three setae at J_4 (Domrow, 1977).

Mesolaelaps anomalus (Hirst)

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

Material. Two ♀♀, *Isoodon macrourus* (Gould), Bamaga.

Notes. This material confirms previous records (Domrow, 1962a, 1967).

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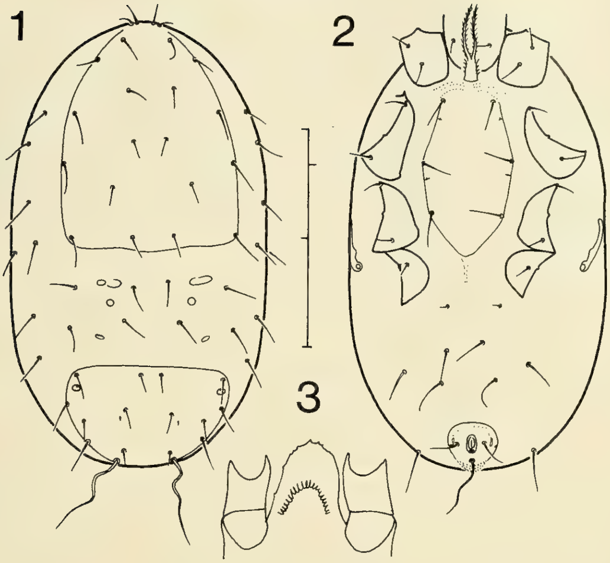
*Proportions, rather than absolute measurements, seem important with single deutonymphal specimens, since prefemales differ from premales only in their larger size.



Figs 1-3. Haemolaelaps domrowi. 1-2. Idiosoma in dorsal and ventral views, pn. 3. Epistome, ♀. Note: the subdivisions on scales with Figs 1-23 represent 100 μm.

Haemolaelaps domrowi Womersley

(Figs 1-3)

Haemolaelaps domrowi Womersley, 1958, *Proc. Linn. Soc. N.S.W.,* 82: 301.

Material. Six ♀♀, one ♂, two protonymphs (hereafter abbreviated pn), *Isoodon macrourus,* Bamaga.

Female. Epistome slightly shorter and more rounded than in *H. flagellatus* Womersley (see Domrow, 1977), with fewer, slightly stronger denticles and submarginal dendritic pattern as in *H. calypso* Domrow, 1966.

Protonymph. Basis capituli slightly longer than wide, with setae c slightly more than half as long as interspace, exceeding sides of basis; deutosternum with at least five rows of denticles, mostly double. Hypostome with setae $h_3>h_1>h_2$; h_1 almost one and a half times as long as interspace; h_3 slightly more than one and a half times as long as interspace, slightly exceeding sides of basis. Labial cornicles pale, but with opposed tips. Epistome anticipating that of ♀. Palpal setation (trochanter-tibia) holotrichous, i.e. 1.4.5.12 (including two dorsodistal rods); seta al_1 on genu spatulate; tarsus with one of three v elongate; claw bifid. Chelicerae as in ♀, i.e. fixed digit straight, weak, edentate, with elongate pilus dentilis (small dorsal seta present, but pores not detected); movable digit stronger, with two small teeth near incurved tip.

Idiosoma 410-455 μm long, 260-300 μm wide. Surface of dorsal shields marked by paired muscle insertions and reticulate. Podonotal shield with three extremely shallow lobes posteriorly; podonotum holotrichous, with 16 pairs of setae (eleven on shield, five on cuticle). Pygidial shield semicircular, with pair of very distinct pores in anterolateral angles in front of setae S_4. Opisthonotum holotrichous, with 14 pairs of setae (eight on shield, six on cuticle). All setae subequal except for slightly smaller j_2 and J_5, and much longer Z_5 (lattermost sinuous, but this may be artifact of mounting).

Tritosternal base with a few distinct barbs laterally as in adult; laciniae ciliated. Sternal shield elongate, with some sign of reticulation; anterior margin weak, preceded by narrow zone of striae; lateral margins straight between insertions of setae; posterior margin triangular, with indication of short backward extension; with usual three pairs of setae and two pairs of pores. Genital complex represented only by pair of small setae. Anal shield appearing slightly foreshortened posteriorly, with postanal seta twice as long as adanals. Ventral cuticle with three pairs of setae in front of, and one pair flanking, anal shield. Peritremes short, not reaching forward beyond articulations on coxae III; peritrematal shields, if present, completely lateral and out of sight.

Legs largely folded under, but setation seen to be holotrichous. No *d* seta on femora-genua I-II unduly lengthened.

Notes. Immatures of this species were previously undescribed. The material confirms earlier records (Domrow, 1962a, 1967).

Haemolaelaps penelope Domrow

Haemolaelaps penelope Domrow, 1964, *Proc. Linn. Soc. N.S.W.,* 89: 156.

Material. One ♀, *Trichosurus caninus* (Ogilby), Clouds Creek, N.S.W., ix.1977, J. H. Arundel.

Notes. The only previous record of this species was from S.E. Queensland.

Peramelaelaps bandicoota Womersley

(Figs 4-7)

Peramelaelaps bandicoota Womersley, 1956, *Linn. Soc. J., Zool.,* 42: 574.

Material. Eleven ♀♀, five ♂♂, two dn, one pn, *Isoodon macrourus,* Bamaga.

Female. Basis capituli longer than wide, with setae *c* of moderate length, about two-fifths as long as interspace, just reaching sides of basis; deutosternum with six rows of one to three denticles. Hypostome with setae $h_3>h_1>h_2$; h_1 slightly longer than interspace; h_3 one and a quarter times longer than interspace, well exceeding sides of basis. Labial cornicles pale, but with opposed tips. Labrum slowly tapering, pointed, spiculate. Epistome soft and diaphanous, with smooth margin and submarginal trace of dendritic pattern reaching to midlength, about twice as long as basal width and roundly pointed, reaching just beyond distal margins of palpal femora. Palpal setation (trochanter-tibia) holotrichous, i.e. 2.5.6.14 (including two dorsodistal rods); seta al_1 on genu spatulate; tarsus with one of three *v* elongate; claw bifid. Chelicerae with fixed digit pale, straight, edentate (dorsal seta and pores not detected); movable digit well sclerotized, with two teeth more distinct than originally figured.

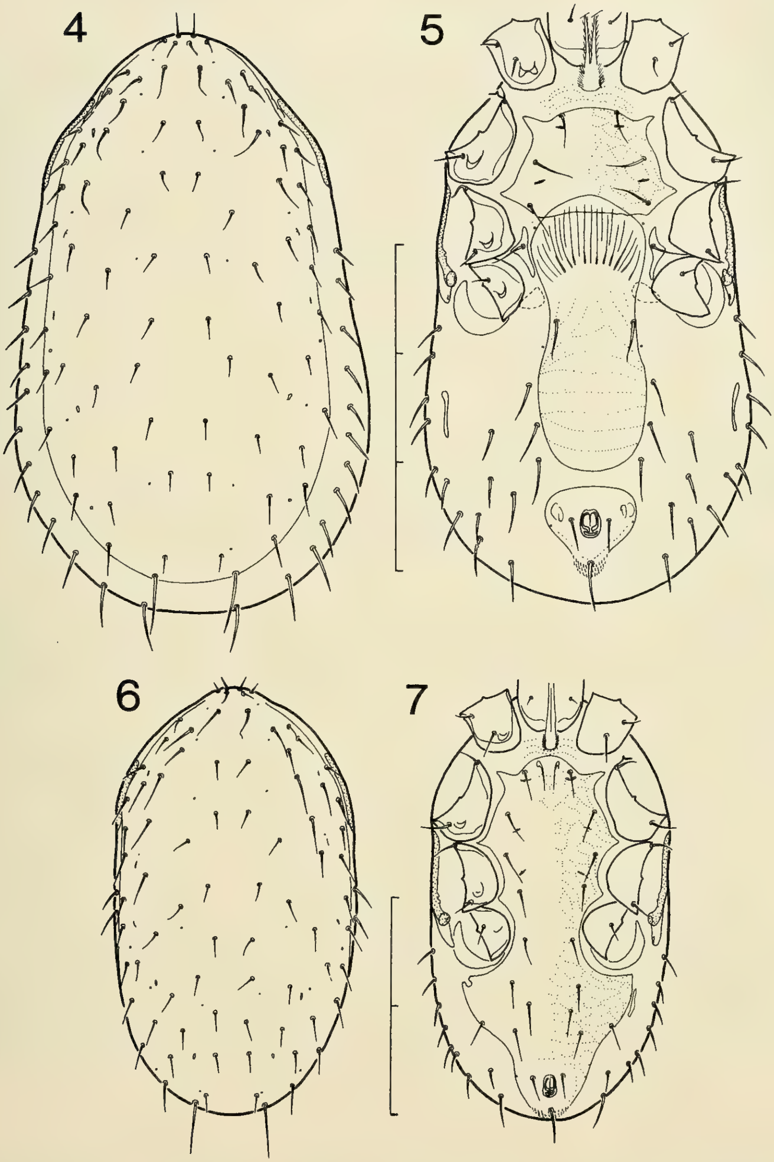
Dorsal shield with surface weakly marked by paired muscle insertions, not reticulate except for vertical, humeral and lateral band that narrows and disappears posteriorly; pores probably more numerous than figured; setation holotrichous (22 pairs of podonotal setae, 17 pairs of opisthonotals — S_2 lacking on one side of specimen figured).

Tritosternal base with fine, soft fringe laterally, *cf. H. domrowi* above.

Leg setation holotrichous. No *d* seta on femora-genua I-II unduly lengthened.

Male. Capitulum as in ♀ except for shorter setae h_3 (about half as long as interspace, falling short of sides of basis) and spermatodactyl. Latter with spermatophore-carrier stout, abruptly and shortly bent apically around tip of somewhat reduced movable digit.

Idiosoma 380-395 μm long, 210-240 μm wide. Dorsum as in ♀, but almost completely covered by dorsal shield and with only about two pairs of setae on cuticle.



Figs 4-7. Peramelaelaps bandicoota. 4-5. Idiosoma in dorsal and ventral views, ♀. 6-7. Idiosoma in dorsal and ventral views, ♂.

Sternal portion of holoventral shield as in ♀, but more arched anteriorly to accept genital aperture; ventral portion expanded and normally sharply angulate behind coxae IV, with four (at times five) pairs of usurped ventral setae. Ventral cuticle with about eight pairs of setae of increasing length posteriorly. Metapodal shields at times insensibly fused into holoventral shield. Peritremes a little shorter than in ♀.

Legs as in ♀, but spurs on coxae simpler and some ventral setae on II strengthened: *av* on femur, *av* and *pv* on genu (to some extent) and tibia, av_{2-3} and pv_2 on tarsus.

Deutonymph. Capitulum not clear in either specimen, but essentially predicting that of ♀.

Idiosoma 475 μm long, 265 μm wide (enclosing developing ♀); 405 μm long, 235 μm wide (enclosing developing ♂). Dorsal shield with lateral incisions narrow, reaching slightly past midpoint between setae J_1 and Z_1; setation of prefemale obscured by that of developing adult, but shield of premale torn free of developing adult and clearly holotrichous (22 pairs of podonotal setae, 17 pairs of opisthonotals).

Sternogenital shield with four pairs of setae and three pairs of pores; ligulate posteriorly, leaving genital setae and pores free in cuticle. Remainder of venter not clear due to doubling, but peritremes elongate.

Leg setation not clear due to doubling, but probably holotrichous. Spurs on coxae simple.

Protonymph. Capitulum predicting that of ♀; palpal setation not clear because of doubling, but probably holotrichous.

Idiosoma 385 μm long, 210 μm wide (enclosing developing deutonymph). Podonotal shield lightly trilobed posteriorly, median lobe strongest. Pygidial shield almost straight anteriorly, but with slight median prominence; with pair of very distinct pores in front of setae S_4 as in *H. domrowi* above. Setation not clear because of doubling, but probably holotrichous.

Sternal shield with three pairs of setae and two pairs of pores, but outline not clear. Genital complex represented at least by a pair of small setae. Ventral cuticle with three pairs of setae in front of, and one pair flanking, anal shield. Peritremes abbreviated.

Leg setation not clear because of doubling, but probably holotrichous.

Notes. The above description of the female of this species is only so full as to complete Womersley's text; the male and immatures were previously undescribed. These specimens confirm earlier records (Domrow, 1962a, 1967).

Laelaps southcotti Domrow

Laelaps southcotti Domrow, 1958, *Proc. Linn. Soc. N.S.W.,* 82: 364.

Material. Six ♀♀, two pn, *Uromys caudimaculatus* (Krefft) (two rats), Iron Range, 19 km SW Portland Roads (12°43′, 143°17′), Qd, 2.xi.1974; four ♀♀, *U. caudimaculatus* (two rats), 40 km SE Cairns (17°15′, 145°56′), Qd, 15-16.xi.1974; three pn, *U. caudimaculatus,* 19 km SE Atherton (17°25′, 145°31′), Qd, 25.xi.1974.

Notes. This material confirms the original record.

Laelaps sp.

Material. Many specimens, *Rattus leucopus leucopus,* Bamaga; ten ♀♀, four dn, three pn, *R. l. leucopus* (three rats), Iron Range, 19 km SW Portland Roads (12°43′, 143°17′), Qd, 3.xi.1974; one ♀, one dn, *R. l. leucopus* (two rats), Iron Range, 20 km SW Portland Roads (12°44′, 143°16′), Qd, 31.x.1974; one dn, one pn, *R. l. leucopus,* Iron Range, 27 km S Portland Roads (12°49′, 143°18′), Qd, 2.xi.1974; three ♀♀, one ♂, three dn, *R. sordidus sordidus* (two rats), Iron Range, 23 km S Portland Roads (12°47′, 143°18′), Qd, 2.xi.1974; two ♀♀, *R. tunneyi culmorum,* 58 km N Rockhampton (22°52′, 150°41′), Qd, 5.i.1975.

Notes. These difficult specimens, with both setae on coxa I simple, will be treated later.

Laelaps nuttalli Hirst

Laelaps nuttalli Hirst, 1915, *Bull. entomol. Res.*, 6: 183.

Material. Two ♀♀, *Rattus rattus* (Linnaeus), Mamara, Guadalcanal, Solomon Islands, 12.xi.1975, J. A. R. Miles; one ♀, *R. rattus,* Mendana, Ndende, Santa Cruz Group, Solomon Islands, 31.x.1975, J.A.R.M.; two ♀♀, one dn, *R. rattus,* 11 km NE Atherton (17°12′, 145°33′), Qd, 22.xi.1974; one ♂, *R. exulans* (Peale), Honiara, Guadalcanal, 28.x.1975, J.A.R.M.; three ♀♀, *R. exulans,* Pamua, Makira (= San Cristobal), Solomon Islands, 8.xi.1975, J.A.R.M.; four ♀♀, one ♂, *R. exulans,* Kira Kira West, Makira, 9.xi.1975, J.A.R.M.; one ♀, *R. exulans,* Mendana, 31.x.1975, J.A.R.M.; one ♀, *R. exulans,* Graciosa Bay, Ndende, 1.xi.1975, J.A.R.M.; nine ♀♀, two ♂♂, *R. exulans,* Onetar, Gaua, Banks Islands, New Hebrides, 23.x.1975, J.A.R.M.; five ♀♀, *R. lutreolus lutreolus* (two rats), 20 km SW Port Macquarie (31°37′, 152°50′), N.S.W., 1.ii.1975; one ♀, *R. sordidus sordidus,* Kowanyama; six ♀♀, *R. s. sordidus* (three rats), Iron Range, 23 km S Portland Roads (12°47′, 143°18′), Qd, 2.xi.1974; three ♀♀, two ♂♂, four dn, one pn, *R. s. sordidus* (three rats), 16 km S Cairns (17°4′, 145°47′), Qd, 14.xi.1974; three ♀♀, one ♂, one dn, *R. s. sordidus* (three rats), 11 km NE Atherton (17°12′, 145°33′), Qd, 22.xi.1974; three ♀♀, *R. s. villosissimus,* 56 km SE Boulia (15°22′, 140°), Qd, 18.x.1974; five ♀♀, one ♂, *R. s. villosissimus,* 77 km SE Boulia (15°35′, 140°8′), Qd, 17.x.1974; two ♀♀, one ♂, *R. s. villosissimus,* 2 km NE Mount Isa (20°38′, 139°30′), Qd, 19.x.1974; eight ♀♀, six ♂♂, seven dn, one pn, *R. s. villosissimus* (two rats), 33 km SE Richmond (20°49′, 143°28′), Qd, 20.x.1974; 12 ♀♀, one ♂, four dn, one pn, *R. s. villosissimus* (three rats), 32 km W Windorah (25°20′, 142°18′), Qd, 15.x.1974; 21 ♀♀, one dn, *R. s. colletti* (Thomas) (eight rats), South Alligator River, 175 km E Darwin (12°42′, 132°32′), N.T., 7-8.vi.1975; six ♀♀, two dn, one pn, *R. s. colletti* (four rats), Leanyer Swamp, 15 km E Darwin (12°23′, 130°56′), N.T., 11.vi.1975; two ♀♀, one ♂, one dn, *R. tunneyi tunneyi* (two rats), 7 km SE Nourlangie Camp (12°49′, 132°42′), N.T., 13.vi.1975; one ♀, *Pseudomys gracilicaudatus* (Gould), 98 km NW Bundaberg (24°31′, 151°28′), Qd, 10.i.1975; four ♀♀, one ♂, *Melomys cervinipes* (Gould) (two rats), 32 km S Cooktown (15°45′, 145°18′), Qd, 7.xi.1974; one ♀, *M. cervinipes,* 40 km SE Cairns (17°15′, 145°56′), Qd, 15.xi.1974; one ♀, *M. littoralis,* 22 km S Cooktown (15°39′, 145°13′), Qd, 7.xi.1974; one ♀, *M. littoralis,* Leanyer Swamp, 15 km NE Darwin (12°22′, 130°56′), N.T., 11.vi.1975.

Notes. All previous Australian records of this cosmopolitan parasite of small rodents were from Queensland (e.g. Domrow, 1958, 1962a). Its range is now extended to the Northern Territory and New South Wales. At a subspecific level, *R. l. lutreolus, R. s. colletti* and *R. t. tunneyi* are new host-records. Two recent references of a wider (Pacific) interest are Mitchell (1964) and Marshall (1976).

Laelaps assimilis Womersley

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

Material. One ♂, *Rattus rattus,* 50 km NE Newcastle (32°39′, 152°9′), N.S.W., 4.ii.1975; five ♀♀, two ♂♂, *R. fuscipes assimilis* (three rats), Mount Stanley, 38 km E Kingaroy (26°30′, 152°13′), Qd, 16.i.1975; three ♀♀, two ♂♂, one dn, three pn, one larva (hereafter abbreviated l), *R. f. assimilis* (three rats), 20 km NE Mallacoota (37°27′, 149°57′), N.S.W., 16-17.ii.1975; two ♀♀, *R. f. assimilis,* 5 km SW Bemm River (37°47′, 148°55′), Vic., 19.ii.1975.

Notes. This material confirms the original record. The specimen from *R. rattus* is a straggler.

Laelaps wasselli Domrow

Laelaps wasselli Domrow, 1958, *Proc. Linn. Soc. N.S.W.,* 82: 363.

Material. Three ♀♀, *Hydromys chrysogaster,* Kowanyama; three ♀♀, *H. chrysogaster,* Iron Range, 26 km SW Portland Roads (12°49′, 143°18′), Qd, 1.xi.1974; one pn, *H. chrysogaster,* 29 km SE Innisfail (17°46′, 146°7′), Qd, 4.xii.1974.

Notes. This material confirms the original record.

Laelaps echidninus Berlese

Laelaps (Iphis) echidninus Berlese, 1887, *Acari, Myriapoda et Scorpiones hucusque in Italia reperta.* Patavii. Fasc. 39, No. 1.

Material. Eight ♀♀, *Rattus exulans,* Mendana, Ndende, Santa Cruz Group, Solomon Islands, 31.x.1975, J.A.R.M.; one ♀, *R. exulans,* Loh, Torres Islands, New Hebrides, 16.x.1975, J.A.R.M.; five ♀♀, one ♂, *R. fuscipes assimilis* (two rats), 56 km SE Canberra (35°41′, 149°32′), N.S.W., 14.ii.1975; three ♀♀, *R. f. assimilis,* Wragge Creek, Kosciusko National Park (36°23′, 148°28′), N.S.W., 11.ii.1975; two ♀♀, one dn, *R. f. assimilis* (three rats), 20 km NE Mallacoota (37°27′, 149°57′), N.S.W., 17.ii.1975; one ♀, *R. f. assimilis,* 6 km SW Bemm River (37°47′, 148°54′), Vic., 20.ii.1975; many specimens, *R. leucopus leucopus,* Bamaga; 29 ♀♀, *R. l. leucopus* (three rats), Iron Range, 19 km SW Portland Roads (12°43′, 143°17′), Qd, 1-3.xi.1974; two ♀♀, *R. l. leucopus,* Iron Range, 26 km SW Portland Roads (12°44′, 143°14′), Qd, 31.x.1974; one pn, *R. l. leucopus,* Iron Range, 20 km SW Portland Roads (12°44′, 143°16′), Qd, 31.x.1974; nine ♀♀, *R. l. leucopus,* Iron Range, 24 km S Portland Roads (12°47′, 145°18′), Qd, 31.x.1974; one ♀, *R. l. leucopus,* Iron Range, 27 km S Portland Roads (12°49′, 143°18′), Qd, 2.xi.1974; 21♀♀, *R. l. cooktownensis* Tate (five rats), 32 km S Cooktown (15°45′, 145°18′), Qd, 7-9.xi.1974; many ♀♀, *R. l. cooktownensis,* Mossman, Qd, vi.1970 and v.1971, R. Domrow and R. W. Campbell.

Notes. At a subspecific level, *R. l. leucopus* and *R. l. cooktownensis* are new host-records. Campbell *et al.* (1977) isolated a new paramyxovirus from *R. f. assimilis* and *R. l. cooktownensis,* and from mites of this species found on the latter host.

Laelaps aella Domrow

Laelaps aella Domrow, 1973, *Proc. Linn. Soc. N.S.W.,* 98: 65.

Material. Three ♀♀, *Pseudomys gracilicaudatus,* 98 km NW Bundaberg (24°31′, 151°28′), Qd, 10.i.1975; five ♀♀, *P. nanus* (Gould), 7 km SE Nourlangie Camp (12°49′, 132°42′), N.T., 13.vi.1975; one ♀, *P. nanus,* 14 km S Nourlangie Camp (12°54′, 132°38′), N.T., 18.vi.1975; nine ♀♀, *P. nanus,* 346 km S Darwin (15°36′, 131°7′), N.T., 1.vi.1975; one ♀, *P. nanus,* 18 km NE Kimberley Research Station (15°33′, 128°6′), W.A., 28.v.1975; one ♀, *P. nanus,* 246 km E Derby (17°7′, 125°43′), W.A., 21.v.1975; four ♀♀, *P. nanus* (two rats), 165 km E Derby (17°6′, 125°10′), W.A., 15.v.1975.

Notes. The only previous record of this species was from the Northern Territory. The considerable extension of range both eastward and westward now noted takes in all but the western extreme (New Norcia, W.A.) of the combined ranges of the two known hosts, if indeed they are specifically distinct (Ride, 1970). Their mites are indistinguishable.

Laelaps rothschildi Hirst

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

Material. Seven ♀♀, *Melomys cervinipes* (four rats), 32 km S Cooktown (15°45′, 145°18′), Qd, 7-9.xi.1974; 18 ♀♀, *M. cervinipes* (four rats), 40-41 km SE Cairns

(17°15′, 145°56′), Qd, 15-16.xi.1974; four ♀♀, *M. cervinipes,* 19 km SE Atherton (17°25′, 145°31′), Qd, 25.xi.1974; one ♀, *M. cervinipes,* 61 km N Rockhampton (22°51′, 150°40′), Qd, 5.i.1975; two ♀♀, *M. cervinipes,* 98 km NW Bundaberg (24°32′, 151°28′), Qd, 12.i.1975; 21 ♀♀, *M. littoralis* (six rats), Iron Range, 21-26 km S Portland Roads (12°44-48′, 143°16-18′), Qd, 1-3.xi.1974; nine ♀♀, *M. littoralis* (four rats), Mount Simon, 22 km S Cooktown (15°39′, 145°13′), Qd, 8.xi.1974; three ♀♀, *M. littoralis* (two rats), 37 km S Cooktown (15°48′, 145°15′), Qd, 7.xi.1974; two ♀♀, *M. littoralis,* 25 km N Atherton (17°3′, 145°26′), Qd, 21.xi.1974; one ♀, one pn, *M. littoralis,* 11 km NE Atherton (17°12′, 145°33′), Qd, 22.xi.1974; 12 ♀♀, *M. littoralis* (five rats), 17 km S Cairns (17°5′, 145°47′), Qd, 14.xi.1974; one ♀, *M. littoralis,* 29 km SE Innisfail (17°46′, 146°7′), Qd, 3.xii.1974; three ♀♀, *M. littoralis* (two rats), 58 km N Rockhampton (22°52′, 150°41′), Qd, 5.i.1975; three ♀♀, *M. littoralis,* 58 km N Maryborough (25°6′, 152°32′), Qd, 14.i.1975; 13 ♀♀, one dn, one pn, *M. littoralis* (three rats), 9 km SE Dunwich, Stradbroke Island (27°32′, 153°30′), Qd, 19-20.i.1975; three ♀♀, *M. littoralis,* Leanyer Swamp, 15 km NE Darwin (12°22′, 130°56′), N.T., 11.vi.1975; two ♀♀, *Melomys* sp., Kowanyama; six ♀♀, *Melomys* sp., 62 km NW Coen (13°27′, 142°57′), Qd, 29.x.1974.

Notes. This species is common on *Melomys* in New Guinea and coastal N.E. Australia (Domrow, 1973), but was not previously recorded from the Northern Territory.

Laelaps pammorphus Domrow

Laelaps pammorphus Domrow, 1973, *Proc. Linn. Soc. N.S.W.,* 98: 69.

Material. Seventeen ♀♀, two ♂♂, *Zyzomys argurus* (Thomas) (six rats), Mount Simon, 22 km S Cooktown (15°39′, 145°13′), Qd, 7-9.xi.1974; eight ♀♀, two ♂♂, *Z. argurus* (five rats), Torola Pool, Fortescue River (21°18′, 116°11′), W.A., 8.v.1975; 29 ♀♀, three ♂♂, *Z. argurus* (11 rats), 165 km E Derby (17°6-7′, 125°10′), W.A., 15-17.v.1975; six ♀♀, *Z. woodwardi* (Thomas) (three rats), Canon Hill, 225 km E Darwin (12°23′, 132°56′), N.T., 21.vi.1975.

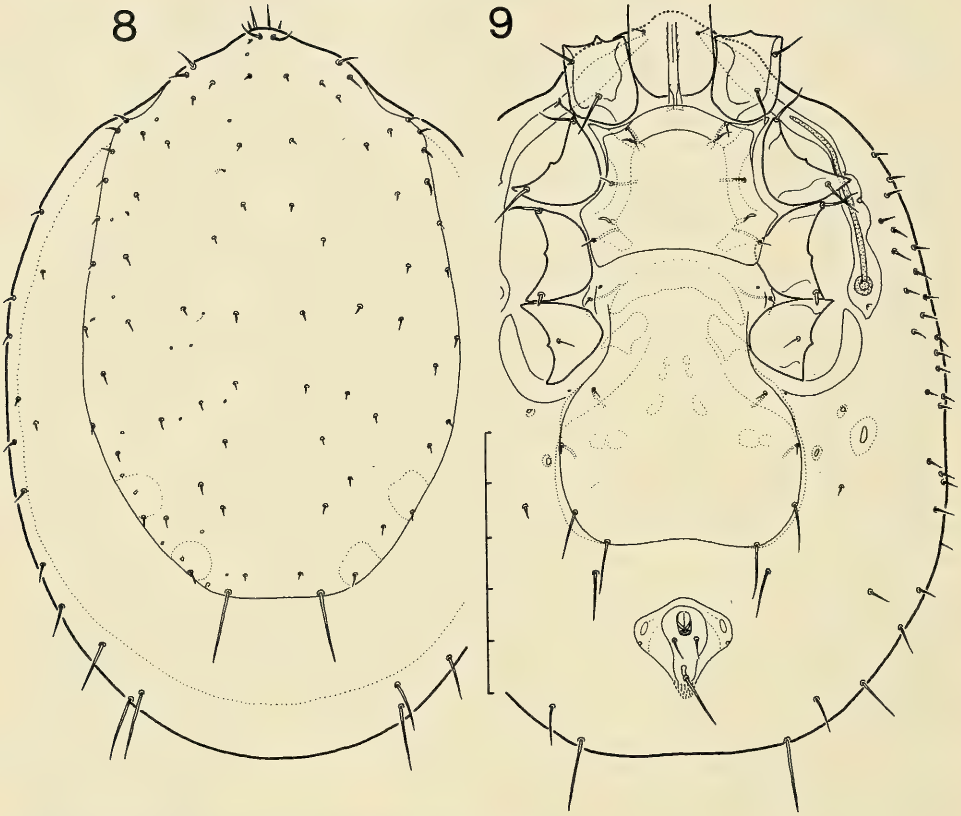
Notes. The only previous records of this species were from the Northern Territory. The considerable extension of range both eastward and westward now noted takes in all but the westernmost portion (the Pilbara, W.A.) of the combined ranges of the two known hosts (Ride, 1970). The strengthened setae J_1 and Z_1 originally noted on the dorsal shield of specimens from *Z. woodwardi* are visible at x30 in spirit when suitably lit.

Laelaps janalis, n. sp.

(Figs 8-9)

Types. Holotype ♀ and four paratype ♀♀, *Pseudomys occidentalis* Tate (two rats), 17 km NE Bendering (32°21-22′, 118°28′), W.A., 1.iv. 1975; one paratype ♀, same data as holotype, but 30.iii.1975.

Female. Basis capituli longer than wide, with setae *c* short, about one-quarter as long as interspace, falling short of sides of basis; deutosternum with six denticles mostly in single file, but first and last denticle at times multiple. Hypostome with setae $h_3 > h_1 > h_2$; h_1 about one-fifth longer than interspace; h_2 short, $= c$; h_3 almost twice as long as interspace, well exceeding sides of basis. Labial cornicles well formed. Labrum spiculate, hastate. Epistome soft and diaphanous, apparently with two small lobes in median indentation. Palpal setation (trochanter-tibia) holotrichous, i.e. 2.5.6.14 (including two dorsodistal tibial rods); seta v_2 on trochanter elongate, slightly flared; seta al_1 on genu slightly spatulate; tarsus with one of three *v* elongate; claw bifid, tines with extended, hyaline, minutely barbed edges. Chelicerae with basal segment subequal in diameter to, but only half as long as, shaft of distal segment; digits occupying one-fifth of total length. Fixed digit with incurved tip and one distal tooth,



Figs 8-9. Laelaps janalis. Idiosoma in dorsal and ventral views, ♀.

between which is set short, stiff pilus dentilis about as long as diameter of digit at that level; with subbasal seta dorsally, but associated pores not detected. Movable digit with incurved tip and two external teeth, between which is accepted armature of fixed digit. Corona comprised of about ten subequal ciliations.

Idiosoma 1,230-1,375 μm long, 900-1,045 μm wide (not gravid); 1,440 μm long, 1,080 μm wide (carrying fully developed larva). Dorsal shield well sclerotized, surface marked by paired muscle insertions and with obvious reticulation; with usual sinuous vertical and humeral margins, with sides then very slightly diverging to two-thirds length, and finally converging rather more sharply to truncate posterior margin; podonotum with normal 22 pairs of setae, mostly short (j_{1-6}, z_{1-6}, s_{1-6}, r_{2-5}); opisthonotum with normal 17 pairs of setae, all short except Z_5 (J_{1-5}, Z_{1-5}, S_{1-5}, px_{2-3}); pores in 22 pairs, those in front of S_{4-5} overlain by extensive patch of transparent cuticle. Dorsal cuticle sclerotized except for narrow marginal strip, with about 12 pairs of setae of increasing length posteriorly.

Tritosternal base unarmed; laciniae lightly ciliated, reaching forward to insertions of labial cornicles. Sternal shield strongly sclerotized, especially a broad band on anterior and lateral margins, and with heavy cornua between coxae I-II; surface without any obvious reticulation except laterally; anterior margin roundly convex; posterior margin shallowly concave, without any median extension; shield with three pairs of short, slender setae and two pairs of pores (each provided with canaliculus). Metasternal shields small, each bearing small seta (provided with canaliculus), but pore free in adjacent cuticle. Genitoventral shield strongly sclerotized, with cuticle encroaching on lateral margins; surface marked by paired muscle insertions, but without obvious reticulation; shield expanded behind coxae IV, with sides subparallel and posterior margin shallowly concave; with pair of short genital setae and three pairs of usurped ventral setae (first pair short, other two pairs long), but pores free in adjacent cuticle; operculum broadly arched, sclerotized internally and supported by strong genital apodemes. Anal shield well sclerotized except for elongate clear central patch bearing anus and setae; lateral angles each with muscle insertion and marginal pore; shield slightly longer than wide, with both antero- and posterolateral margins slightly concave; adanal setae set just behind anus, falling well short of long postanal seta, and latter far exceeding cribrum. Metapodal shields and two pairs of shieldlets between them and genitoventral shield all largely encroached on by cuticle. Peritremes of medium length, extending forward only to level of anterior margins of coxae II, borne on peritrematal shields that run forward to fuse with dorsal shield vertically but are free of broadly crescentic exopodal shields IV behind. Ventral cuticle with about 30 pairs of setae of increasing length posteriorly, including one long pair immediately behind genitoventral shield.

Legs with setation called for by Evans and Till (1965) for dermanyssids in general, and for *L. echidninus* in particular (i.e. holotrichous except for one additional *pl* seta on genu IV, 2-5/1-2). Coxa III with *pv* a heavy spine. Trochanters I-II with *al*, and III-IV with *al* and *d* strengthened, but still sharply pointed. Femora I-II with pd_1 lengthened, reaching distal margin of tibia in former, but barely as long as basal diameter of segment in latter; II with *av* slightly, and III with *v* heavily, spinose. Genu I with pd_3 lengthened, a little longer than ad_1 on femur I. Tarsi II-IV with ad_1 and pd_1 minute and other setae, especially ventrodistally, strengthened (in particular, al_1, av_1 and pl_1 on II and al_{1-2} on III); II without ad_3 unduly lengthened as in *L. albycia* Domrow, 1965.

Larva. Details not clear within ♀, but podonotum holotrichous, with 10 pairs of setae ranging from 90 (j_1) to 290 μm (j_6) in length; opisthosoma also with several pairs of elongate setae.

Notes. This fine new species will not go beyond the first couplet in Domrow's (1965, 1973) keys and diagnoses. In showing a relatively full complement of setae on the dorsal shield and peritremes of at least medium length, it fits with the *nuttalli, spatanges* and *hapaloti* groups; but the minute genital and first pair of usurped ventral setae on the genitoventral shield indicate the *finlaysoni* group.

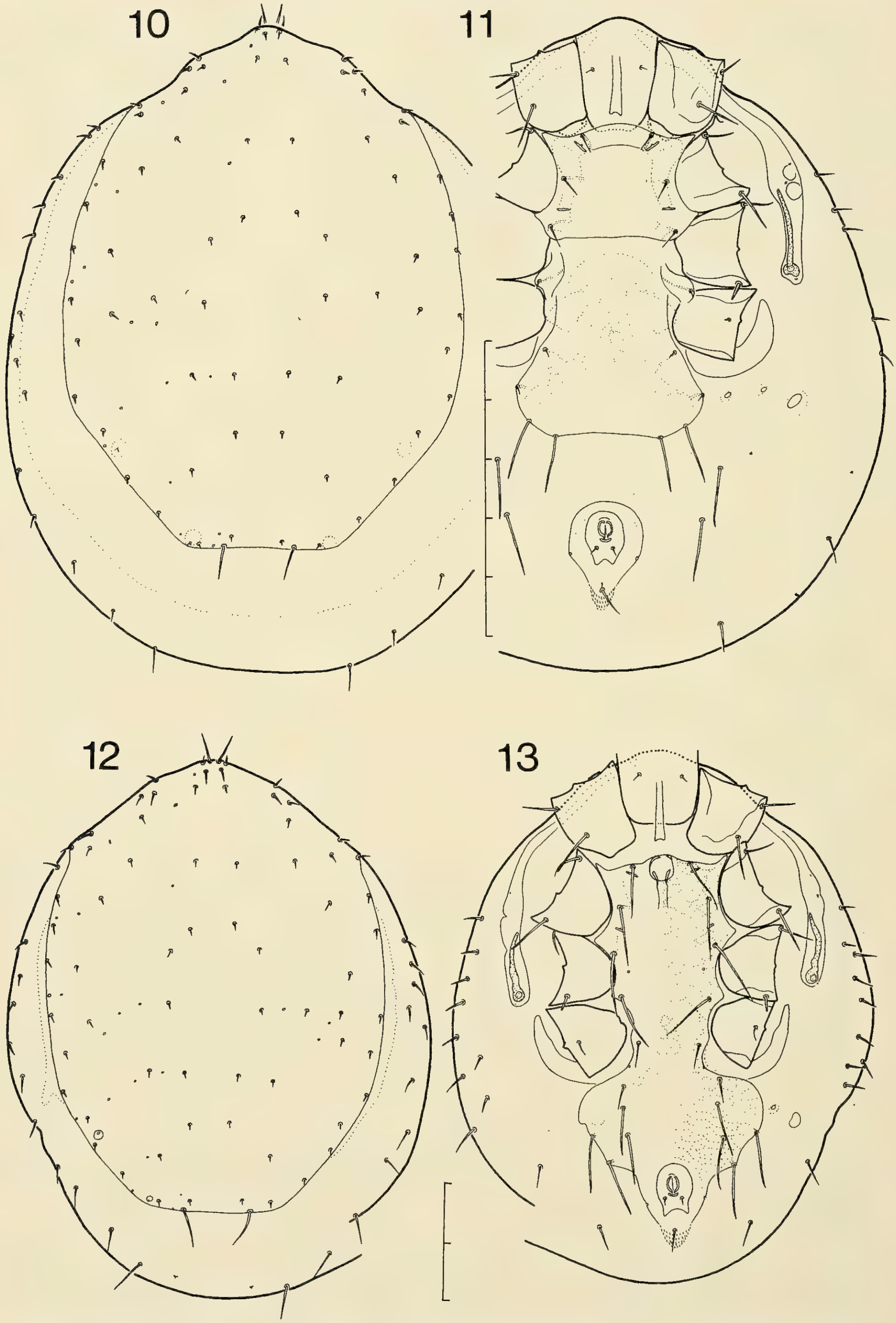
A review of the Australian *Laelaps* spp. awaits study of a collection from the Kimberley region of Western Australia (this includes further new species, but cannot be treated here by reason of the conditions of loan).

The specific name is a Latin adjective, *janal-is, -e,* of Janus, the Roman god of the year, who looked both to the front and back.

Laelaps bycalia, n. sp.
(Figs 10-17)

Types. Holotype ♀, allotype ♂, two paratype ♀♀, one morphotype dn and one morphotype pn, *Pseudomys albocinereus* (Gould) (two rats), 22 km NE Jurien (30°8′, 115°9′), W.A., 13.iv.1975.

Female. Capitulum as in *L.albycia* except as follows. Setae *c* shorter, about one-quarter as long as interspace, falling short of sides of basis. Setae h_2 slightly longer; h_3 longer, about three-quarters as long as interspace. Epistome with four small, weak median lobes. Basal segment of chelicerae one-tenth shorter than shaft of distal segment.



Figs 10-13. Laelaps bycalia. 10-11. Idiosoma in dorsal and ventral views, ♀. 12-13. Idiosoma in dorsal and ventral views, ♂.

Idiosoma 1,100 μm long, 905 μm wide (older specimen bearing larva); 990 μm long, 825 μm wide (recently moulted, non-gravid specimen). Dorsal shield moderately well sclerotized, surface marked by paired muscle insertions but without reticulation; outline essentially as in *L. janalis,* but tapering more sharply in posterior third, more sharply truncate posteriorly and of rather broader proportions; podonotum with 20 pairs of setae, mostly short (first two, somewhat isolated pairs on dorsal cuticle could well be r_{3-4}, thereby making up normal 22 pairs); opisthonotum with 15 pairs of setae, all short except Z_5 (px_{2-3} lacking); pores as in *L. janalis,* but patches of transparent cuticle in front of S_{4-5} smaller. Dorsal cuticle sclerotized except for marginal strip (evident in recently moulted specimen only as slight granulation of cuticle), with about 12 pairs of setae of slightly increasing length posteriorly (excluding two isolated anterior pairs noted above).

Venter as in *L. janalis* except as follows. Sternal shield with posterior margin almost straight and all setae rather longer, st_3 well exceeding posterolateral angles. Genitoventral shield with outline almost straight between genital setae and first pair of usurped ventral setae, then rounding sharply to ever so slightly concave posterior margin; difference between two types of setae on shield more marked. Anal shield with clear central patch not extending to cribrum; anterior margin strongly arched; anal setae smaller, especially adanals. Peritremes abbreviated, situated entirely above coxae III. Ventral cuticle marginally with about seven pairs of setae of increasing length posteriorly and two marked pairs immediately behind genitoventral shield.

Legs with setation called for by Evans and Till (1965) for dermanyssids in general, and for *L. echidninus* in particular (i.e. holotrichous except for one additional *pl* seta on genu IV, 2-5/1-2). Details as in *L. janalis* except on tarsi: II-III (but not IV) with setae, especially ventrodistally, strengthened; II as in *L. albycia,* i.e. al_1 and pl_1 strengthened (but still pointed), ad_3 and (to lesser extent) av_3 lengthened, and one seta on basitarsus (ad_4) strengthened; III with al_{1-2}, av_3 and (on basitarsus) al_4 strengthened.

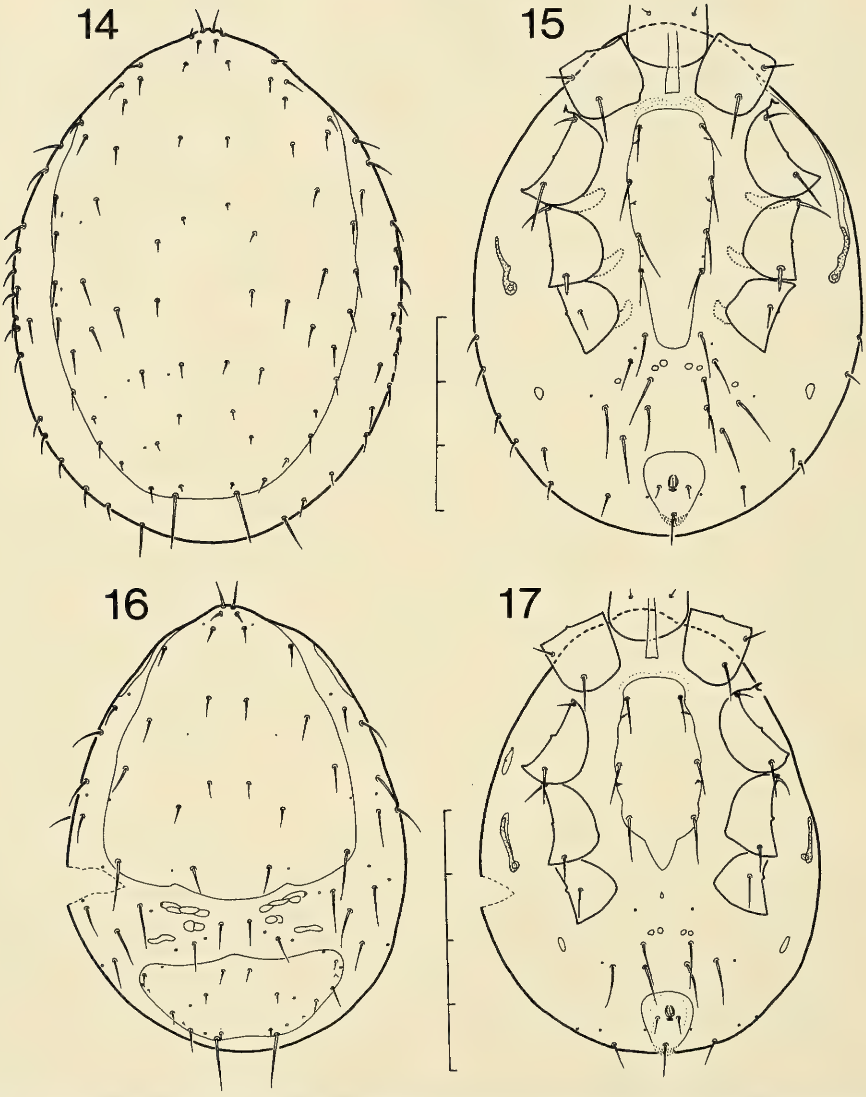
Male. Capitulum as in ♀ except as follows. Some deutosternal denticles multiple. Hypostomatal setae subequal, h_1 about two-thirds as long as interspace. Labial cornicles softer, flared at tips. Chelicerae with fixed digit soft, gently tapering and edentate, 55 μm long, 8 μm wide basally. Spermatodactyl 110 μm long, occupying five-sixteenths of total cheliceral length; lightly upcurved, with edentate, but firmly pointed, remnant of movable digit just beyond half length. Neither chelicera protruded far and corona not detected.

Idiosoma 890 μm long, 705 μm wide (slightly ruptured). Dorsum as in ♀ except as follows. Dorsal shield less angulate in posterior third; podonotum with 21 pairs of setae, i.e. taking in r_3, but presumptive r_4 (lacking on one side) still free in cuticle; also irregular in lacking one z_6 and one S_1, and in doubling of one Z_1. Strip of sclerotized cuticle narrow, irregular and largely incomplete posteriorly.

Venter as in ♀ except as follows. Holoventral shield reticulate except for elongate patch extending from level of metasternal setae to disc of genitoventral portion; setae st_{1-3} and metasternal setae far longer; genitoventral portion with genital setae and five pairs of usurped ventral setae, difference between two types of setae less marked. Metapodal shields simpler.

Leg setation as in ♀ except as follows. Coxa IV with *v* much longer. Some other setae stronger, resembling *pv* on coxa III: femora I four *v,* II pv_1, IV *v*; genua I, III *pv,* II *av* and *pv,* IV pl_1; tibiae I, III-IV *pv,* II *av* and *pv.*

Deutonymph (enclosing ♂). Capitulum as in ♂ except that chelicerae resemble those of ♀.



Figs 14-17. Laelaps bycalia. 14-15. Idiosoma in dorsal and ventral views, dn. 16-17. Idiosoma in dorsal and ventral views, pn.

Idiosoma 790 μm long, 620 μm wide. Dorsum as in ♀, but shield less angulate in posterior third, with longer setae (r_5 free in cuticle on one side), showing only traces of lateral incisions between podonotal and opisthonotal halves, and not invested by strip of sclerotized cuticle.

Venter with same setation as ♂, but sternogenital shield discrete and peritrematal shields less developed.

Leg setation anticipating that of ♂, including genu IV.

Protonymph. Capitulum holotrichous, anticipating that of ♀.

Idiosoma 670 μm long, calculated to be 550 μm wide. Podonotal shield with three shallow lobes posteriorly; podonotum holotrichous, with 16 pairs of setae (eleven on shield, five on cuticle). Pygidial shield transverse, slightly concave anteriorly but with slight median convexity; opisthonotum normally holotrichous, with 14 pairs of setae (eight on shield, six on cuticle — superficial count would give thirteen pairs, but closer examination reveals S_4 lacking on one side of shield and S_5 on other).

Sternal shield elongate, with posterior margin distinctly triangulate; with usual three pairs of setae and two pairs of pores. Genital complex represented only by pair of distinct pores. Ventral cuticle with four pairs of setae. Peritrematal shields in three fragments.

Leg setation holotrichous except for one additional *pl* seta on genu IV (1-4/0-1), predicting that of ♀ except for coxae: III with *pv* hardly strengthened, IV with *v* elongate.

Larva. Details not clear within ♀, but podonotum holotrichous, with 10 pairs of setae ranging from 18 (s_6) and 25 (j_1) to 135 μm (j_6) in length. Opisthosoma with a few pairs of setae resembling s_6.

Notes. This new species keys out near *L. finlaysoni* Womersley, 1937, see Domrow (1963, 1965), but the outlines of both the dorsal and genitoventral shields in the female show clear differences. Further, although both species show 35 pairs of setae on the dorsal shield, there also appear to be fundamental differences in the *J* and *px* series on the opisthonotal portion; these await further study, see notes on *L. janalis* above.

The specific name of this, and the other new species below, are both anagrams of *calabyi,* and are to be treated as nouns (nominative singular) in apposition to *Laelaps*.

Laelaps cybiala Domrow

Laelaps cybiala Domrow, 1963, *Proc. Linn. Soc. N.S.W.,* 88: 206.

Material. Two ♀♀, *Mastacomys fuscus* Thomas, Wragge Creek, Kosciusko National Park (36°23′, 148°28′), N.S.W., 10.ii.1975.

Notes. This material confirms the original record.

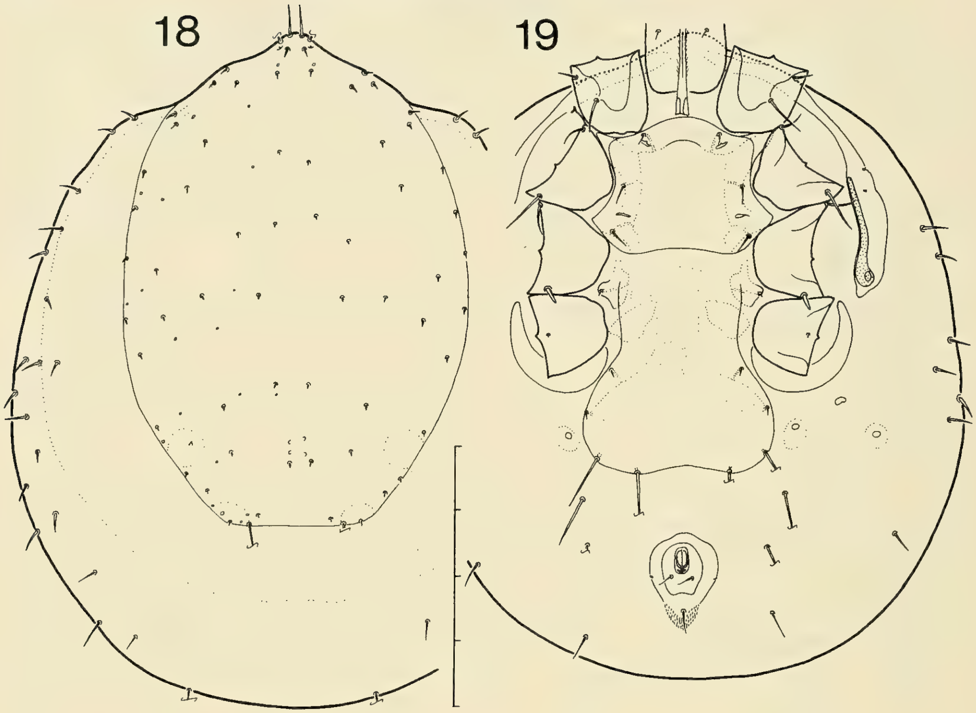
Laelaps lybacia, n. sp.

(Figs 18-19)

Types. Holotype ♀, *Pseudomys praeconis* Thomas, Bernier Island (24°55′, 113°8′), W.A., 22.iv.1975.

Female. Capitulum as in *L. albycia* except as follows. Setae *c* much shorter, about one-eighth as long as interspace, falling well short of sides of basis. Setae h_1 not fully clear, but shorter than interspace; h_3 longer, about three-fifths as long as interspace. Epistome not clear. Basal segment of chelicerae one-fifth shorter than shaft of distal segment.

Idiosoma 1,035 μm long, 845 μm wide. Dorsal shield moderately well sclerotized, surface marked by paired muscle insertions but without reticulation except for two or three weak humeral lines; outline intermediate between those of *L. janalis* and *L. bycalia;* podonotum with 19 pairs of setae, mostly short (z_3 lacking, first of two, somewhat isolated pairs on dorsal cuticle could well be r_{3-4}); opisthonotum with 14 pairs of setae, all short except Z_5 (S_3 lacking, *J* and *px* series requiring further study); pores as in *L. janalis,* but patches of transparent cuticle in front of S_{4-5} slightly smaller. Dorsal cuticle sclerotized except for broad marginal strip, with about 17 pairs of setae of slightly increasing length posteriorly (excluding two isolated anterior pairs noted above).



Figs 18-19. Laelaps lybacia. Idiosoma in dorsal and ventral views, ♀.

Venter as in *L. bycalia* except as follows. Sternal shield with posterior margin slightly concave and setae st_1 short compared to st_{2-3}. Genitoventral shield rounded laterally and more concave posteriorly. Adanal setae stronger, postanal weaker.

Legs with setation called for by Evans and Till (1965) for dermanyssids in general, and for *L. echidninus* in particular (i.e. holotrichous except for one additional *pl* seta on genu IV, 2-5/1-2). Details as in *L. bycalia.*

Notes. This new species keys out near *L. finlaysoni,* see Domrow (1963, 1965), but differs therefrom in lacking setae z_3 and S_3 on the dorsal shield, and in its broader genitoventral shield. The *J* and *px* series on the dorsal shield show certain fundamental similarities, but await further study, see notes on *L. janalis* and *L. bycalia* above.

Eulaelaps stabularis (Koch)

Gamasus stabularis Koch, 1839, *Deutschlands Crustaceen, Myriapoden und Arachniden.* Regensburg: Herrich-Schäffer. Heft 27: No. 1.

Material. Two ♀♀, *Felis catus* Linnaeus, Hamilton, Vic., xi.1975, A.M. Freemantle.

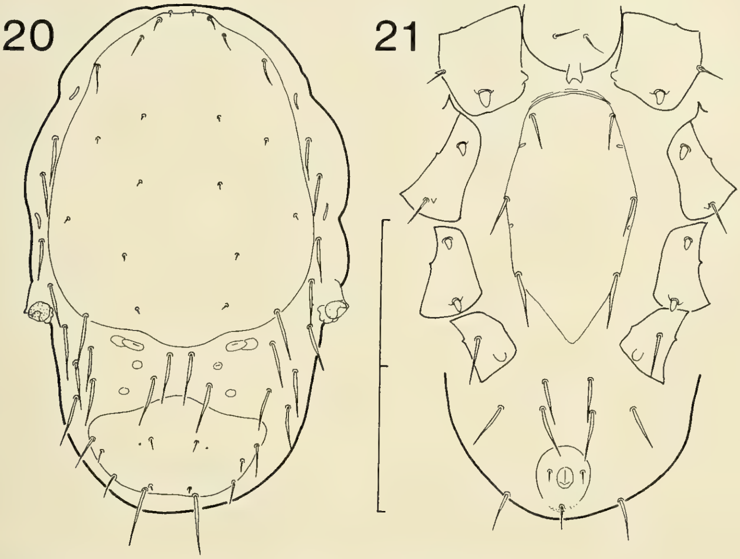
Notes. The only other record of this apparently recently introduced Holarctic and Oriental species in Australia is from *Mus musculus* Linnaeus in Tasmania (Domrow, 1973).

Echinonyssus butantanensis (da Fonseca)

Ichoronyssus butantanensis da Fonseca, 1932, *Mem. Inst. Butantan,* 7: 135.

Material. One ♀, *Rattus rattus,* 26 km NE Perth (31°13′, 116°9′), W.A., 4.iv.1975.

Notes. Previous Australian records of this introduced species were all from the east: Womersley (1956, as *Hirstionyssus arcuatus* (Koch); Glenfield is near Sydney, N.S.W., not in Qd) and Domrow (1961, 1963, as *H. musculi* (Johnston)). The specific name now used is after Evans and Till (1966) and Herrin (1974).



Figs 20-21. Trichosurolaelaps crassipes. Idiosoma in dorsal and ventral views, pn.

Trichosurolaelaps crassipes Womersley
(Figs 20-21)

Trichosurolaelaps crassipes Womersley, 1956, *Linn. Soc. J., Zool.,* 42: 564.

Material. Six ♀♀, *Trichosurus vulpecula* (Kerr), Belbora, Kowanyama, iv.1969, R. Domrow and E. T. Bulfin; three ♀♀, two ♂♂, *T. vulpecula,* Kowanyama; three ♀, *T. vulpecula,* D'Aguilar, Qd, 1.iv.1957, R. Domrow; one ♂, *T. vulpecula,* Grovely, Qd, 24.ii.1965, E. H. Derrick; eight ♀♀, one ♂, *T. vulpecula,* Brookfield, Qd, 30.iii.1973, G. Wolf; six ♀♀, *T. vulpecula,* Woodridge, Qd, 29.x.1963, R. Domrow and I. D. Fanning; three ♀♀, *T. vulpecula,* Bonalbo, N.S.W., 2.vi.1961, K. Keith and D. L. McIntosh; two ♂♂, one dn, one pn, *T. vulpecula,* Taronga Park Zoo, Sydney, N.S.W., 18.viii.1967, M. D. Murray; five ♀♀, five ♂♂, four dn, four pn (sample only), *T. vulpecula,* Sunbury, Vic., v.1977, J. H. Arundel; one ♀, three ♂♂, *T. vulpecula,* North Midlands, Tas., 2.vii.1962, R. H. Green; one ♀, one ♂, *T. vulpecula,* Kelso, Tas., 16.ii.1961, B. C. Mollison; eight ♀♀, two ♂♂, *T. vulpecula,* Maydena, Tas., 10.v.1961, B. C. Mollison.

Deutonymph. Details of capitulum and legs as in adult, but armature of legs weaker, betraying its setal origin (e.g. in prefemale, more than in premale, seta av_2 on genu-tibia I is spinose basally, but then strongly notched and setiform distally).

Idiosoma 450-460 μm long, 285-290 μm wide (prefemale); 445-470 μm long, 295-310 μm wide (premale). Dorsal shield not incised laterally between podonotal and opisthonotal portions; setation as in ♂, but setae on margin of shield (behind level of coxae II) and those on cuticle distinctly bladed.

Sternogenital shield with four pairs of setae and three pairs of pores, gently tapering behind setae st_2 to terminate roundly between genital setae (genital pores not detected). Anal shield as in ♀. Setae of ventral cuticle bladed, in eight to ten pairs. Peritremes much abbreviated both in prefemale and in premale, barely as long as diameter of stigmata (characteristic adult form clear in one enclosed ♀).

Protonymph. Palpal trochanter-genu holotrichous.

Idiosoma 310-340 μm long, 190-220 μm wide (in front of peritremes). Podonotal shield trilobed posteriorly, median lobe the strongest; podonotum holotrichous, with 16 pairs of setae (11 on shield, five on cuticle — j_{1-3} and z_2 of differing lengths; j_{4-6}, z_{4-5} and s_4 minute; s_5 and five pairs on cuticle long and bladed). Pygidial shield semicircular, but with median convexity on anterior margin; opisthonotum bideficient, with 12 pairs of setae (six on shield, six on cuticle — J_{4-5} minute, as is submarginal Z_4 between marginal S_{4-5} of medium length; Z_5 long but simple; six pairs on cuticle long and bladed).*

Sternal shield with usual three pairs of setae (of increasing length posteriorly; st_2 slightly, and st_3 clearly, bladed) and two pairs of pores. Metasternal and genital complexes not detected. Anal shield predicting that of ♀. Ventral cuticle with three pairs of bladed setae in front of, and one pair of stout setae flanking, anal shield. Stigmata strong, protuberant, without peritremes.

Leg setation holotrichous except that tibia IV is unideficient posterolaterally (1-3/2-0). Armature already predicting that of adult.

Notes. These records document Domrow's (1972) bald statement that this species is common on this host in eastern Australia. Kowanyama is the northernmost record.

Troughton (1965: 105) noted that small [unidentified] mites caused annoyance and irritation in *Schoinobates volans* (Kerr), especially when sickly. Species of *Trichosurolaelaps* may now be linked with tissue damage in their hosts, at least in zoo conditions. The series of *T. crassipes* from Taronga Park Zoo stemmed from areas of alopecia and keratinization around the head, elbows, hocks and perineum, with evidence of intense itching; that from Sunbury from the back of a mature female possum that, having been held captive for six months, had been biting at the area for two to three weeks, the mites apparently being quite irritating. The series of *T. striatus* below from Dandenong was from a skin scraping; that from Werribee from a heavily infested possum with a large area of hair loss consistent with trauma induced by irritation.

Trichosurolaelaps striatus Domrow

Trichosurolaelaps striatus Domrow, 1958, *Proc. Linn. Soc. N.S.W.,* 82: 356.

Material. Many specimens, *Pseudocheirus peregrinus* (Boddaert), Mosman, N.S.W., 26.v.1966, A. L. Dyce; two ♀♀, *P. peregrinus,* Dartmouth, Vic., 22.xi.1973, I. Beveridge; three ♀♀, one ♂, *P. peregrinus,* Dandenong, near Melbourne, Vic., vii.1977, N. J. Barton; many specimens, *P. peregrinus,* Werribee, Vic., ix.1977, J. H. Arundel.

Notes. Domrow (1961) extended the range of this species from S.E. Queensland to Tasmania, but without intermediate records. See also notes on preceding species.

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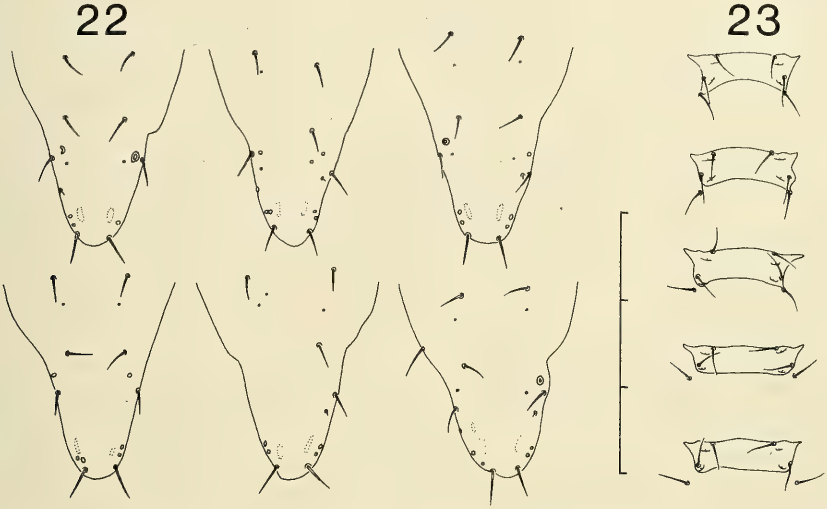
*Setae J_4 and Z_4 are assigned these signatures because the former is set just inside a wideset pair of pores (*cf.* holotrichous condition in Figs 1 and 16), and the latter because its position allows only this interpretation. Domrow (1972), writing before immatures were known in this genus, but knowing that J_{3-4} and Z_{3-4} all occur in the holotrichous condition, arbitrarily considered the posteriormost seta possible to be the absent one in the case of deficiencies in the adults. When further immatures are known, the situation can again be analysed.

Ornithonyssus bacoti (Hirst)

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

Material. Two pn, *Rattus rattus*, 26 km NE Perth (31°13′, 116°9′), W.A., 4.iv.1975.

Notes. This species, the tropical rat mite and a minor pest of man, is widespread in Australia (Hirst, 1914; Domrow, 1963, 1973). Closer examination quickly showed that these two nymphs did not belong with the female of *E. butantanensis* above that was collected on the same rat.



Figs 22-23. Ornithonyssus sylviarum. 22. Six variants of tapered posterior portion of dorsal shield, ♀ (four pairs of longer, and one pair of shorter, setae are normal complement; 12 pairs more anteriorly). 23. Five variants of sternal shield, ♀ (second from bottom most typical).

Ornithonyssus sylviarum (Canestrini and Fanzago)

(Figs 22-23)

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

Material. Seven ♀♀, one pn, nestling *Hirundo neoxena* Gould, Campania, Tas., 9.i.1974, P. Park.

Notes. These specimens, from a new host, underline the widespread occurrence of this pest of poultry on native birds in temperate southern Australia (Domrow, 1973). A customary key character for this species is the disassociation of setae st_3 from the sternal shield, but the condition varies considerably from specimen to specimen (as does the setation of the posterior portion of the dorsal shield); see also Allred (1970).

Halarachne miroungae Ferris

Halarachne miroungae Ferris, 1925, *Parasitology,* 17: 166.

Material. Two l, *Mirounga leonina* (Linnaeus), Macquarie Island, Southern Ocean, summer of 1976, I. Morgan.

Notes. The previous nearest record of this species to Australia probably originated from Kerguelen, some 5,000 miles to the west (Domrow, 1962b, 1974).

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Feeding Habits and Structure of the Gut of the Australian Freshwater Prawn *Paratya australiensis* Kemp (Crustacea, Caridea, Atyidae)

PREM GEMMELL

GEMMELL, P. Feeding habits and structure of the gut of the Australian freshwater prawn *Paratya australiensis* Kemp (Crustacea, Caridea, Atyidae). *Proc. Linn. Soc. N.S.W.* 103 (4), (1978) 1979: 209-216.

A study of the feeding habits and histological details of the alimentary canal of *Paratya australiensis* is presented. Functional morphology and histology of the various regions of the gut are described and discussed in relation to food and feeding habits.

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INTRODUCTION

Alimentary adaptations in decapod crustaceans have attracted the attention of workers since the beginning of the century. Parker (1876), Calman (1909), Yonge (1924), and Patwardhan (1934, 1935) were pioneers in the field. Recently George *et al.* (1955), Fryer (1960), Schaefer (1970) and Powell (1974) have contributed considerably to the study of decapod alimentary organization.

Paratya australiensis (Kemp) is a common freshwater small prawn that favours vegetated areas. It occurs in a wide variety of permanent inland waters (coastal streams, rivers, lakes, farm dams and ponds). Williams (1977) described its occurrence in south-eastern South Australia, south-western New South Wales extending northwards into Queensland. The present investigation is the first study of the alimentary adaptations of this species in relation to its feeding habits.

MATERIALS AND METHODS

Specimens of *Paratya australiensis* were collected monthly from Manly Dam, N.S.W., during the period October 1972 to February 1973. The specimens were brought to the laboratory alive and were kept at a constant temperature of 18°C for further observations. For histological studies specimens were fixed in alcoholic Bouin's fluid for 24 hours. The antennules, antenna, thoracic and abdominal appendages were cut right to the base and the carapace was completely removed to allow easy penetration of the fixative. The fixed material was subsequently washed, dehydrated, embedded in paraffin (M.P. 56°C) and sectioned at 6 μm. The sections were stained in Delafield haematoxylin and eosin and mounted in D.P.X. mounting medium.

OBERVATIONS

FEEDING HABITS

Paratya australiensis is a browser and filter feeder. During browsing the food is collected by chelipeds. The food which consists of fine particles and insects is scraped off the substratum by the strong toothed spines. As the fingers of the chela approach the substratum, they open widely; on contact with the substratum the terminal spines and setae become splayed out. As the chela closes and begins to be withdrawn its setae come together; their elasticity ensures that the extremities are held closely to the substratum and a considerable area is scraped. The scraped material is held by the opposed sets of setae. The serrated edges of the toothed spines of chela are responsible for scraping the substratum and loosening the detritus. Larger particles are picked up by the combed, and the finer ones by the brush setae. The loaded spines then pass into the mouth parts where the grid setae of the first maxilliped strip off the food. The chelipeds are also used for breaking down the larger particles of food.

During filter feeding, *Paratya* holds itself in a slanting position near the surface of the tank. Strong water currents are produced by the metachronal beatings of the endites of the first maxilla and scaphognathite of the second maxilla, these appendages are fringed with long dorsally directed setae which pass the food in the midventral line towards the mouth. The direction of food currents during this action is firstly towards the animal from the sides and secondly, from behind forwards along the mid-ventral line. Small particles of food suspended in water are taken up by the toothed and plumose setae on the inner side of the endites of the first and second maxillipeds. The stout spinous setae of the first maxilla help in scraping off the food from the setae of the more posterior appendages. The food is passed into the buccal cavity via the mandibles.

Fig. 1. T.S. through the oesophagus of *Paratya australiensis* showing the disposition of the oesophageal folds. C = chitin, C.M.F. = circular muscle fibres, D.F. = dorsal fold, EP. = epithelium, L.M.F. = long muscle fibres, M = mouth, MAN. = mandible, OES. = oesophagus, SM. = submucosa. Magnification: approx. x90.

Fig. 2. T.S. through mouth, oesophagus and the cardiac proventriculus showing the cardio-oesophageal junction. C = chitin, C.OES.O = cardio-oesophageal orifice, C.PROV. = cardiac proventriculus, D.F. = dorsal fold, L.F. = lateral fold, P.PROV. = pyloric proventriculus, S = seta. Magnification: approx. x90.

STRUCTURE OF THE GUT

The alimentary canal of *Paratya australiensis* consists of a foregut, midgut and hindgut.

FOREGUT

The foregut includes the mouth, oesophagus and the tventriculus. The mouth (M′) is ventral between the two mandibles. In front the labrum overlaps the mouth and the incisor processes of the mandibles.

The oesophagus (Fig. 1) is a narrow tube ascending from the mouth and opening into the cardiac proventriculus. The cardiac end of the oesophagus is dilated and thrown into three folds — one dorsal and two lateral (D.F. and L.F.). The wall of the oesophagus is lined internally by chitin, columnar epithelium, thick submucosa of loose connective tissue, circular and longitudinal muscle layers and an external layer of connective tissue.

The proventriculus (Fig. 2) is divided into an anterior large cardiac proventriculus (C.PROV.) and a posterior small pyloric proventriculus (P.PROV.). The two are separated by a prominent depression.

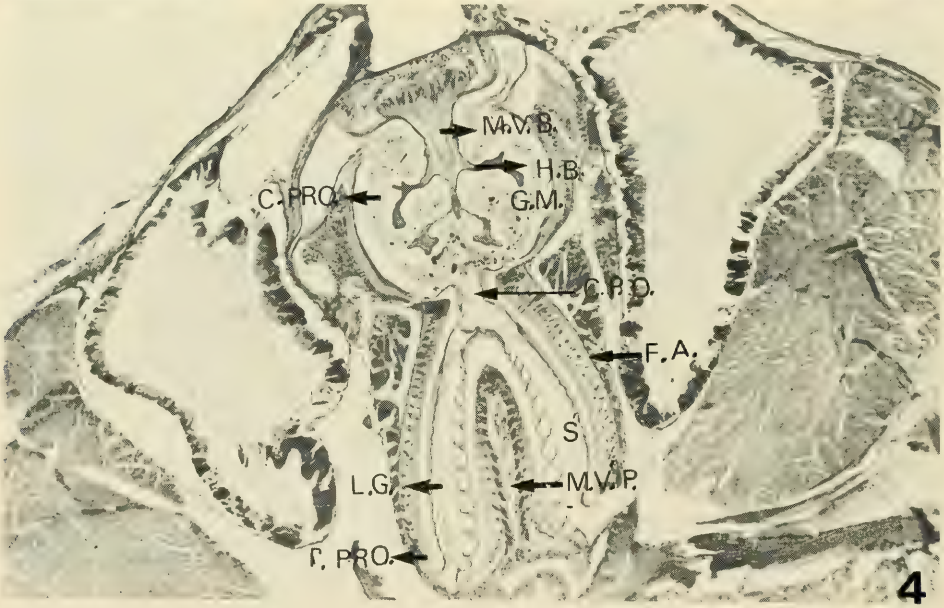
The cardiac proventriculus is a dilated pouch in which food can be accumulated. Regurgitation of food from the cardiac chamber into the oesophagus is prevented by the oesophageal folds (D.F. and L.F.) at the termination of the oesophagus. The cuticular lining (C.) of the cardiac proventriculus constitutes a setose gastric mill (G.M.)

The cardiac proventriculus in *Paratya* shows a median vertical bar (M.V.B.) extending from the anterior to nearly the posterior end of the chamber. Two pairs of short horizontal bars (H.B.) attached to its sides are covered with chitin (C.). The lateral bars show serrated edges on both sides; probably to increase the triturating surface. The chitinous lining (C.) of the cardiac proventriculus is produced into long fine setae (S.) which are inwardly and downwardly directed (Fig. 2).

The chitinous lining of the pyloric proventriculus is produced into a number of setae (S.) forming the filter apparatus (Figs 3 and 4). From the base of the pyloric proventriculus arises a median ventral piece (M.V.P.) that extends up to the anterior end dividing the pyloric proventriculus into two narrow lateral grooves (L.G.); one on either side of the median piece. The chitinous lining of the pyloric proventriculus is produced into a number of spines (S.) all along its lateral edges. The spines are inwardly and upwardly directed, becoming progressively smaller from the base to the apex. The lateral edges of the median ventral piece (M.V.P.) are similarly produced into small groups of spines at regular intervals. The spines are large at the base, becoming smaller towards the apex. The larger spines overlap the smaller ones in front of them producing a many-pocketed sieve-like structure. Between the two sets of spines, that is the ones along the lateral lining of the pyloric chamber and those on the median ventral piece is a narrow space — the lateral groove (L.G.) which ultimately releases fine food particles into the midgut (M.G.) (Fig. 5). The coarse particles are retained for further action. This observation is supported by the presence of large food particles in the cardiac and fine in the pyloric proventriculus.

The pyloric filter apparatus of *Paratya* is continued into the midgut in the form of chitinous pyloric sheath (P.S.). The sheath collects coarser food particles from the filter apparatus and prevents it from mixing with fine food particles. The pyloric sheath (P.S.) in *Paratya* consists of only two semicircular chitinous folds lying opposite each other lateromedially and slightly overlapping at the sides.

The epithelium lining the proventriculus is tall columnar, supported by a thin basement membrane (B.M.); a submucosa of loose connective tissue, circular muscle fibres and a peripheral layer of loose connective tissue.



Figs 3 & 4. T.S. through the proventriculus showing details of the gastric mill, filter apparatus and the disposition of the digestive glands. B.M. = basement membrane, C. = chitin, C.M.F. = circular muscle fibres, C. PROV. = cardiac proventriculus, C.P.O. = cardiopyloric orifice, EP. = epithelium, F.A. = filter apparatus, G.M. = gastric mill, H.B. = horizontal bar, INT. C. = intestinal caeca, L.G. = lateral groove, M.V.B. = median vertical bar, M.V.P. = median ventral piece, S = spine, SM. = submucosa. Magnification: approx. x110.

MIDGUT

The midgut (Figs 5 and 6) is a short tube. Two long diverticulae — the intestinal caecae (INT.C.) arise from its anterior end and extend on either side of the proventriculus. The midgut is lined by columnar epithelium supported by a thin layer of loose connective tissue, an inner layer of circular muscle fibres and an outer layer of longitudinal muscle fibres followed by a thin investing sheath.

HINDGUT

The hindgut is short and narrow. The inner surface is thrown into a number of broad folds (Fig. 7). The wall consists of the following layers — an inner layer of columnar epithelium covered by chitin, submucosa of loose connective tissue, inner layer of circular (C.M.F.), outer layer of longitudinal muscle fibres (L.M.F.) and a thin limiting membrane.

DIGESTIVE GLANDS

The digestive glands are complex greenish-yellow tubular structures occupying most of the cephalothorax. The lobules of the glands are arranged around a lobular duct. These ducts join together to form the main duct that opens into the midgut. The lumen is lined by tall columnar secretory cells that are highly vacuolated, the resting cells showing a number of granules in the cytoplasm. The epithelium is supported by connective tissue and smooth muscles which encourage the discharge from the secretory units.

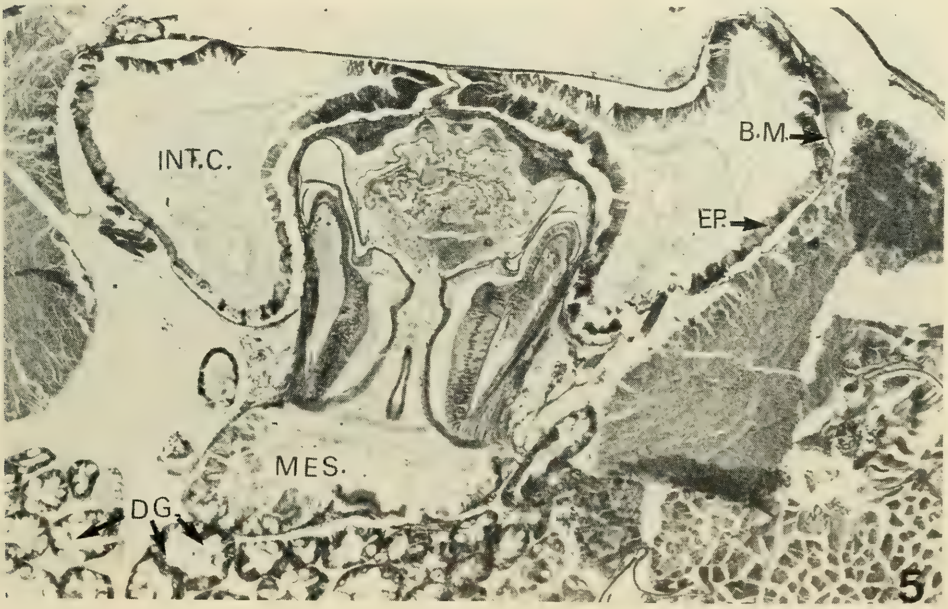


Fig. 5. T.S. through the proventriculus and the mesenteron showing the opening of the filter apparatus into the mesenteron. B.M. = basement membrane, DG. = digestive glands, EP. = epithelium, INT. C. = intestinal caeca, MES. = mesenteron. Magnification: approx. x110.

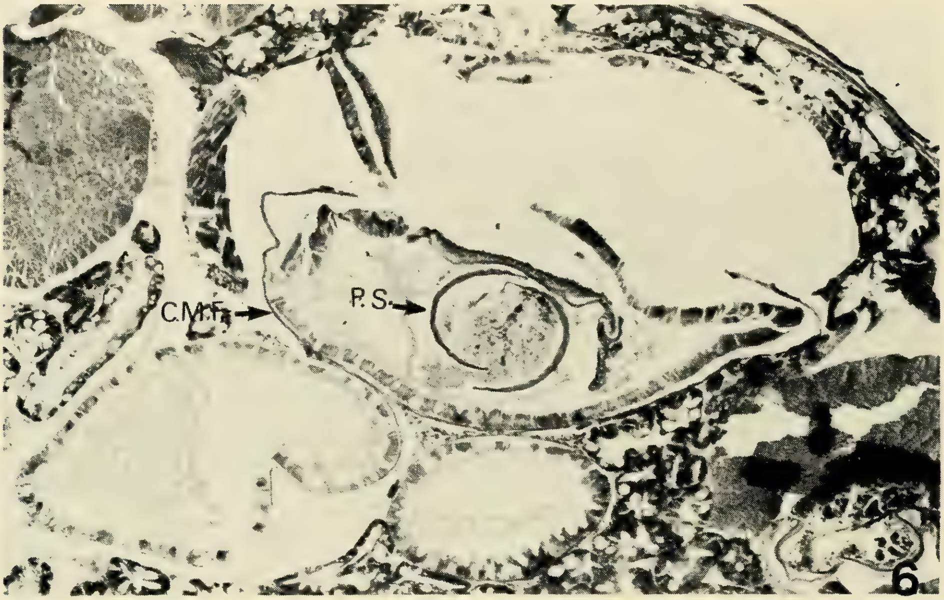


Fig. 6. T.S. through the mesenteron showing the position of the pyloric sheath. C.M.F. = circular muscle fibres, P.S. = pyloric sheath. Magnification: approx. x110.

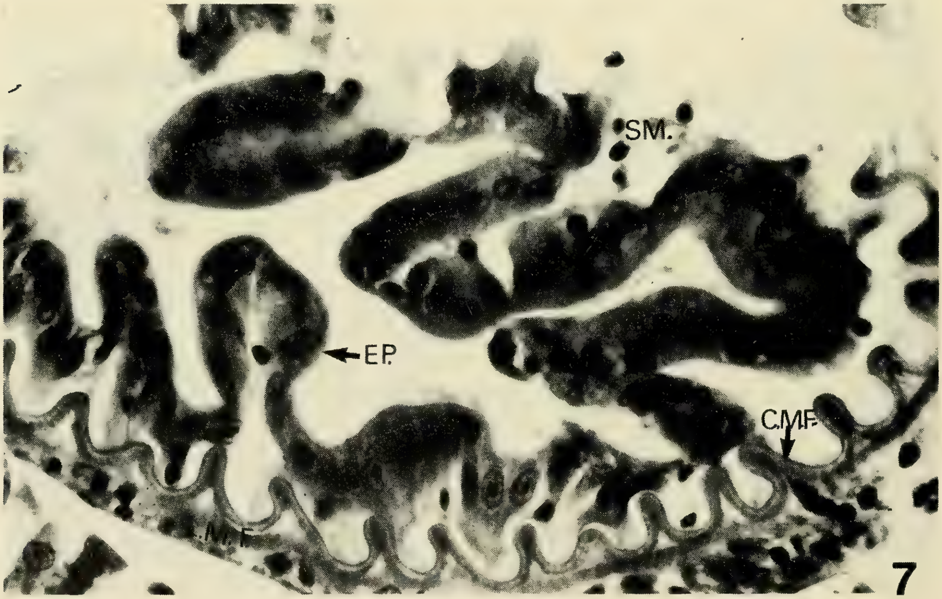


Fig. 7. T.S. through the proctodaeum. C.M.F. = circular muscle fibres, EP. = epithelium, L.M.F. = longitudinal muscle fibres, SM. = submucosa. Magnification: approx. x250.

DISCUSSION

The maxillae in *Paratya australiensis* are adapted for producing water currents. The endites of the first maxilla and the scaphognathite of the second maxilla along with the maxillipeds produce strong water currents. Smaller particles of food are picked up by the thickly arranged setae on these appendages and passed to the mouth. The chelipeds are used for picking up larger particles of food, breaking it into bits and their final transference to the mouth. The chelipeds are also responsible for scraping, collecting the detritus and its transfer to the mouth. The present investigations are in accord witth the finds of Fryer (1960) on *Caridina africana* and *C. nilotica* and Kotpal (1971) on *Penaeus lamarrei*.

The morphology and histology of the gut give ample evidence of the structural modifications of the gut to suit its food and mode of feeding. *Paratya* is seen to feed continuously for long intervals. The presence of a distensible oesophagus permits these quantities of food to be swallowed at a time. The oesophageal folds prevent regurgitation of food. Similar observations have been recorded in *Panulirus* (George *et al.,* 1955), *Metapenaeus bennettae* (Dall, 1967) and *Callianassa* (Powell, 1974).

The stomach of crustaceans has been described as the gastric mill by various authors, for instance Parker (1876), Huxley (1880), Patwardhan (1935), Reddy (1935), George *et al.* (1955) and Schaefer (1970).

Review of the literature reveals in every case the stomach is differentiated into two regions, the anterior masticatory portion — the gastric mill — and a posterior pyloric portion — the filter apparatus. The size, shape and the structure of the gastric mill is variable in different groups. A strong gastric armature as identified by the presence of large calcified ossicles is mainly dependent on the size of the animal and the hard nature of the diet of shelled molluscs and arthropods. Though the word gastric mill is used by all the workers for its masticatory function the details given are highly variable.

Paratya australiensis is a small freshwater prawn feeding primarily on aquatic plants, algae, diatoms and insects. In association with the soft nature of the diet, and well-developed mandibles, the gastric mill in *Paratya* does not show any calcified ossicles as described by Huxley (1880), Patwardhan (1935) and Reddy (1935). The filter apparatus in the pyloric proventriculus is mainly used for sieving finer particles of food before they enter the midgut for digestion. The details of the filter apparatus show a strong resemblance to those observed in *Caridina laevis* (Pillai, 1960), *Corophium volutator* and *Caprella linearis* (Aggarwal, 1963, 1964), *Metapenaeus bennettae* (Dall, 1967) and *Callianassa* (Powell, 1974). The pyloric brushes described by Powell were, however, absent in *Paratya*.

The pyloric sheath in the mesenteron is a simple structure in *Paratya* and is functionally comparable to the terminal lappets of *Penaeus setiferous* (Young, 1959) and pyloric fingers of *Callianassa* (Powell, 1974).

Microscopic studies of the gut wall of *Paratya* show an inner layer of circular muscle fibres and an outer layer of longitudinal muscle fibres which are contrary to the observations of George *et al.* (1955) in *Panulirus,* and Vonk (1960) in *Astacus*. Pillai (1960) and Dall (1969), however, observed the arrangement of muscle fibres in the gut wall of *Caridina laevis* and *Metapenaeus bennettae* to be similar to that of *Paratya*.

The digestive glands open into the mesenteron, which is the site for digestion and absorption of food. Intestinal caeca showing identical histological details to that of mesenteron can be inferred to perform similar functions. The present investigations are in agreement with the findings of George *et al.* (1955), Aggarwal (1963, 1964) Dall (1967) and Powell (1974).

ACKNOWLEDGEMENTS

I thank Professor D. T. Anderson, School of Biological Sciences, University of Sydney, Sydney, for his help in the preparation of this manuscript. My sincere thanks are due to Dr G. C. B. Poore, Senior Research Officer, Marine Studies Group, Victoria, for his helpful criticism of the manuscript.

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Three New Species of *Amblyseius* Berlese (Acarina: Phytoseiidae) from Australia

E. SCHICHA

SCHICHA, E., Three new species of *Amblyseius* Berlese (Acarina: Phytoseiidae) from Australia. *Proc. Linn. Soc. N.S.W.* 103 (4), (1978) 1979: 217-226.

Adults and immature stages of *Amblyseius lailae* n. sp. from papaw, adults of *Amblyseius neolentiginosus* n. sp. from *Pinus radiata*, and adults of *Amblyseius neovictoriensis* n. sp. from Indian coral tree (*Erythrina* sp.), all from coastal New South Wales, are described and illustrated.

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INTRODUCTION

The three new species described here were collected in late summer 1978 during collecting trips along the coast of N.S.W. They are suspected of being predators of phytophagous mites.

If not indicated otherwise, three specimens were measured of each of the developmental stages described, values being the range in micrometres (μm). BCRI is the abbreviation for Biological and Chemical Research Institute, Rydalmere.

Genus AMBLYSEIUS Berlese

Amblyseius Berlese, 1914: 143. Type-species by original designation: *Zercon obtusus* Koch, 1839.

Amblyseius lailae, n.sp.

(Figs 1-22)

Diagnosis. — In the adult stage, *A. lailae* is similar to *A. pafuriensis* van der Merwe (1968). However, in females of *lailae* setae D4, M2, L3, L8 and L9 are slightly longer and setae D1 and L4 are considerably longer than those in *pafuriensis*. In *lailae* the macrosetae on genu III and tibia III are slightly shorter and on genu I, II and IV, tibia IV and basitarsus IV they are considerably shorter. The movable digit of the chelicerae in *lailae* has three teeth, while that in *pafuriensis* has only one. In *lailae* the peritremes reach to the bases of D1 whereas in *pafuriensis* they only reach to the bases of L1.

Types. — NEW SOUTH WALES: on leaves of papaw, Alstonville, 18.iv.1978, M. Elshafie. *Holotype* ♀ (*A.lai.*1) in BCRI; 4 ♀♀ (*A.lai.*2-5) and six ♂♂ (*A.lai.*6-7) *paratypes*; all in BCRI.

Female (Figs 1-7)

Dorsum. — Dorsal shield 343-372 long, 179-199 wide at L4, smooth, with 17 pairs of setae, six dorsal, two median, four prolateral, five postlateral: D1 30-32 long, D2 and D3 6-8, D4 8-9, D5 9-10, D6 7-8, M1 6-8, M2 9, L1 45-48, L2 8-10, L3 8-9, L4 63-71, L5 8-10, L6 11-12, L7 10-14, L8 7-10, L9 57-59. L9 slightly serrated, all other setae smooth. All setae shorter than distances between their bases and bases of setae following next in series, except for L1 which is longer than interspace L1/L2. Five pairs of large pores and two pairs of small pores as figured. S1 16-17 and S2 9-11 long.

Figs 1-9. Amblyseius lailae, n.sp., female: 1, dorsum. 2, sternal shield. 3, ventrianal shield. 4, chelicera. 5, spermatheca. 6, leg III. 7, leg IV; male: 8, ventrianal shield. 9, spermatodactyl. The dimensions of these and other characters illustrated in Figs 1-38 are given in the text.

Peritremes extending forward to bases of D1 (Fig. 1).

Venter. — Sternal shield 68-73 long, 84 wide, with three pairs of setae, two pairs of pores and lobate posteriorly. Fourth pair of setae on metasternal shields (Fig. 2). Vase-shaped ventrianal shield 116-121 long, 73-79 wide, with three pairs of preanal setae of equal length and one pair of preanal pores 34-37 apart (Fig. 3).

Chelicera. — Fixed digit 33-37 long, with nine teeth plus pilus dentilis. Movable digit 37-39 long, with three backward pointing teeth (Fig. 4).

Spermatheca. — Tube-like cervix 33-38 long, atrium occupying whole width where cervix fuses with macroduct, the latter very short (Fig. 5).

Legs. — Seven macrosetae: spiniform on genu I 36 long, genu II 36-40, genu III 43-44, tibia III 36-37 (Fig. 6); tapering apically and ending with a little knob on genu IV 73-77, tibia IV 61-62, basitarsus IV 106-111 (Fig. 7).

Male (Figs 8-9) (two specimens measured)

Dorsum. — Dorsal shield 280-290 long, 128-145 wide at L4, smooth, with chaetotaxy resembling that of female: D1 22-25 long, D2 to D4 4-5, D5 6-7, D6 5-6, M1 6, M2 8, L1 35-36, L2 6, L3 8-9, L4 45-49, L5 to L7 8-10, L8 6-7, L9 43-46. S1 16 and S2 7, on interscutal membrane.

Venter. — Imbricated ventrianal shield 114-117 long, 156-158 wide, with three pairs of preanal setae of equal length, the posterior two pairs on a transverse line, and a pair of pores 22-25 apart (Fig. 8).

Spermatodactyl. — Shaft narrow; small foot broad with blunt toe and protruding heel (Fig. 9).

Legs. — Seven macrosetae similar to those of female: on genu I 28, genu II 27, genu III 31, tibia III 27, genu IV 52-53, tibia IV 41-43, basitarsus IV 71-85.

Deutonymph (Figs 10-13)

Female (two specimens measured)

Dorsum. — Smooth dorsal shield 296-319 long, 142-145 wide at L4, with 17 pairs of setae, six dorsal, two median, four prolateral, five postlateral: D1 28-30 long, D2 to D6 5-8, M1 6-7, M2 9, L1 43-44, L2 8, L3 8-10, L4 55-58, L5 11-12, L6 12-13, L7 12-14, L8 6-10, L9 46-48. L9 slightly serrated, all other setae smooth. L1 as long as interspace L1/L2; all other setae shorter than distances between their bases and bases of setae following next in series. Five pairs of large pores and three pairs of small pores as figured. S1 14-16 and S2 25 on interscutal membrane. Peritremes extending to L2 (Fig. 10).

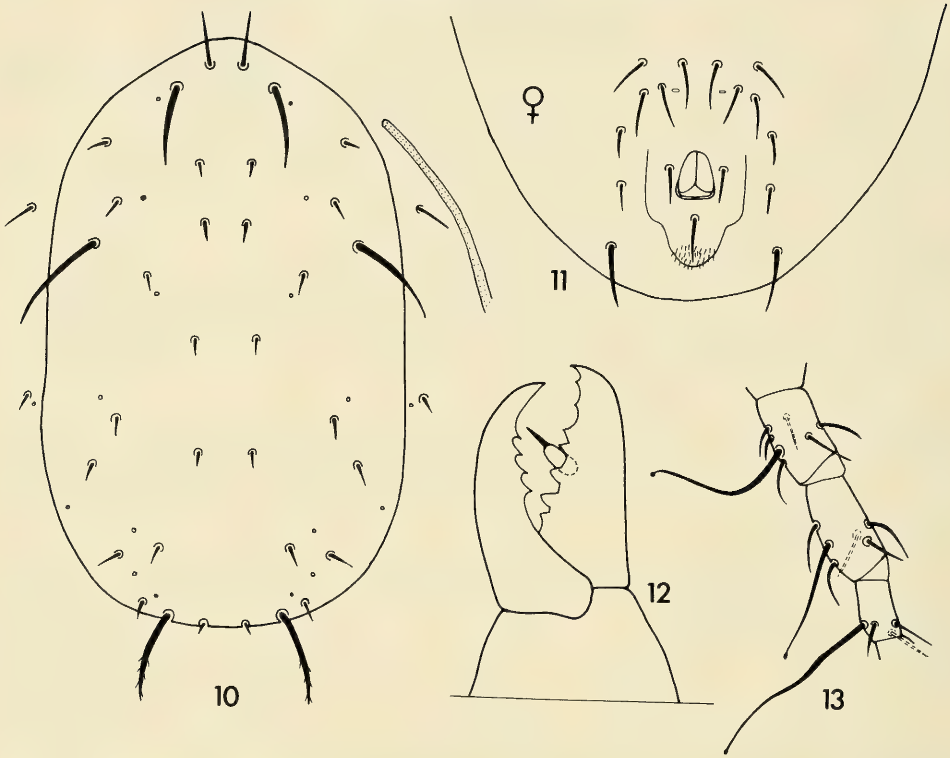
Venter. — Two pairs of preanal setae, two pairs of lateroventral setae, two pairs of posteroventral setae and one pair of caudal setae 32-33 long. Preanal pores 26-30 apart (Fig. 11).

Chelicera. — Fixed digit 25-29 long, with 7-8 teeth and pilus dentilis. Movable digit 28-29 long with three backward pointing teeth (Fig.12).

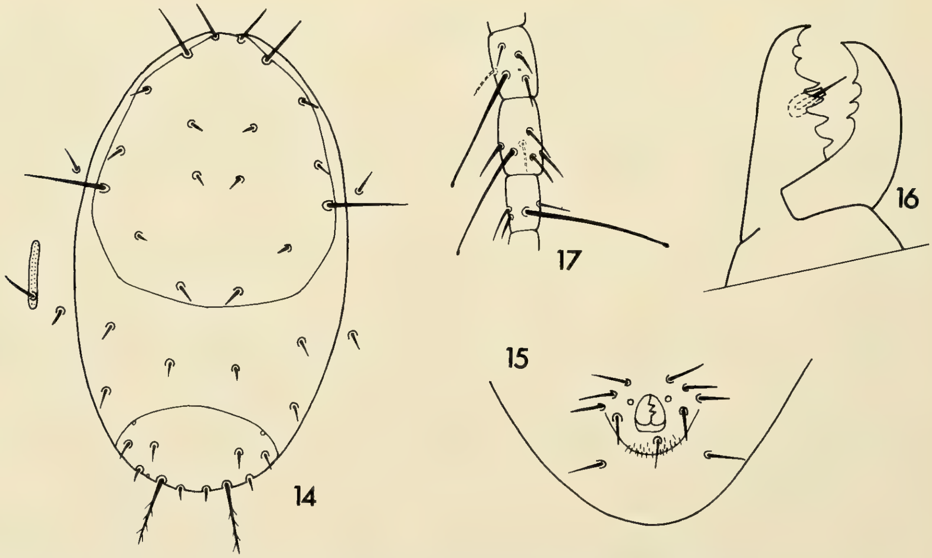
Legs. — Seven macrosetae similar to those of female (holotype): on genu I 35-36, genu II 36-37, genu III 48-49, tibia III 39-40, genu IV 67-71, tibia IV 51-61, basitarsus IV 94-95 (Fig.13).

Protonymph (Figs 14-17) (one specimen measured)

Dorsum. — Smooth dorsal surface 232 long, 122 wide at L4, bearing two shields. Anterior shield with nine pairs of setae, four dorsal, one median, four lateral; posterior shield with five pairs of setae, one dorsal, one median, three lateral; between



Figs 10-13. Amblyseius lailae, n.sp., deutonymph female: 10, dorsum. 11, venter. 12, chelicera. 13, leg IV.



Figs 14-17. Amblyseius lailae, n.sp., protonymph: 14, dorsum. 15, venter. 16, chelicera. 17, leg IV.

the two shields three pairs of setae, one dorsal, two lateral: D1 20 long, D2-D6 3-7, M1 4, M2 9, L1 28, L2 and L3 7, L4 43, L5 to L8 5-9, L9 36. L9 slightly serrated, all other setae smooth. L1 as long as interspace L1/L2; all other setae shorter than distances between their bases and bases of setae following next in series. Peritremes 34 long (Fig. 14).

Venter. — Two pairs of preanal setae, one pair of lateroventral setae, one pair of caudal setae, all of near equal length (Fig. 15).

Chelicera. — Both digits 38 long. Fixed digit with six teeth and pilus dentilis; movable digit with three backward pointing teeth (Fig. 16).

Legs. — Seven macrosetae similar to those of female (holotype): on genu I 28, genu II 30, genu III 36, genu IV 65, tibia IV 62, basitarsus IV 78 (Fig. 17).

Larva (Figs 18-22) (one specimen measured)

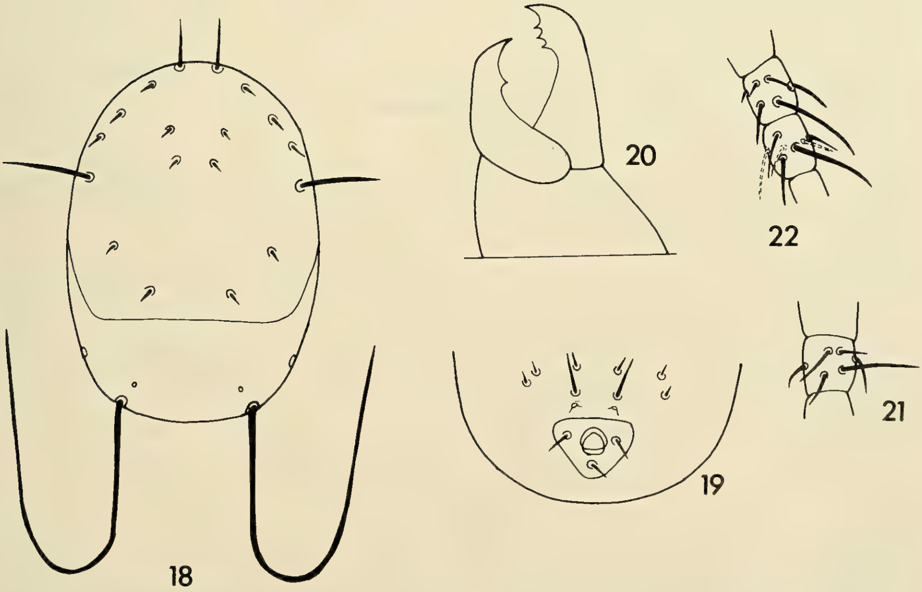
Dorsum. — Smooth dorsal shield 218 long, 116 wide at L4. Ten pairs of smooth setae, four dorsal, one median, four prolateral, one caudolateral: D1 24 long, D2 and D3 3, D4 7, M1 5, L1 and L2 7, L3 8, L4 47, L9 171.

All setae shorter than distances between their bases and bases of setae following next in series. One pair of large pores between L4 and L9 and one pair of small pores near L9 (Fig. 18).

Venter. — Two pairs of preanal setae, posterior pair three times longer than anterior. Two pairs of lateroventral setae short. Preanal pores 19 apart (Fig. 19).

Chelicera. — Both digits 21 long. Fixed digit with three teeth; movable digit with one tooth (Fig. 20).

Legs. — Four macrosetae: on genu I 26, genu II 38, genu and tibia III 50 (Figs 21-22).



Figs 18-22. Amblyseius lailae, n.sp., larva: 18, dorsum. 19, venter. 20, chelicera. 21, leg II. 22, leg III.

Amblyseius neolentiginosus, n.sp.
(Figs 23-30)

Diagnosis. — In the adult stage, *A. neolentiginosus* is similar to *A. lentiginosus* Denmark and Schicha (1975). However, in *neolentiginosus* setae D1 are shorter and setae M2, L1, L4, S1, S2 and all three macrosetae on leg IV are considerably shorter than those in *lentiginosus.* In addition, in *neolentiginosus* setae L4 are only approx. half as long as those in *lentiginosus.* In *neolentiginosus* the fixed digit of the chelicerae has 10 teeth whereas that in *lentiginosus* has only seven teeth. *Neolentiginosus* has a well developed atrium between cervix and macroduct of the spermatheca, while *lentiginosus* has no distinct atrium.

Types. — NEW SOUTH WALES: on *Pinus radiata* tips of branches, Narara, 2.ii.1978, E. Schicha. *Holotype* ♀ (*A.neol.* 1); two ♀♀ (*A.neol.* 2-3), one ♂ (*A.neol.* 4) *paratypes;* all in BCRI.

Female (Figs 23-28)

Dorsum. — Smooth dorsal shield 360-365 long, 177-183 wide at L4, with 17 pairs of setae, six dorsal, two median, four prolateral, five postlateral: D1 22-24 long, D2 to D6 4-8, M1 4-5, M2 77-78, L1 35-36, L2 and L3 7-10, L4 44-50, L5 to L8 4-7, L9 113-115. M2 and L9 slightly serrated, all other setae smooth. L1 as long as interspace L1/L2, all other setae shorter than distances between their bases and bases of setae following next in series. Five pairs of large pores as figured. S1 and S2 4 long, on interscutal membrane. Peritremes extending forward beyond bases of D1 (Fig. 23).

Venter. — Sternal shield 60-62 long, 75-80 wide, with three pairs of setae and two pairs of pores as figured. Fourth pair of setae on metasternal shields (Fig. 24). Smooth pentagonal ventrianal shield 114-120 long, 94-100 wide, with three pairs of short preanal setae and a pair of preanal pores 17-19 apart (Fig. 25).

Chelicera. — Both digits 33 long. Fixed digit with ten teeth plus pilus dentilis, movable digit with three teeth (Fig. 26).

Spermatheca. — Tube-like cervix 16-18 long, atrium occupying whole width where cervix fuses with macroduct (Fig. 27).

Legs. — Six macrosetae: on genu I 22-24, genu II 28-31, genu III 36-39, genu IV 53-71, tibia IV 43-48, basitarsus IV 57-62 (Fig. 28).

Male (Figs 29-30) (one specimen measured)

Dorsum. — Dorsal shield 272 long, 156 wide at L4, with chaetotaxy resembling that of female, but all setae relatively shorter: D1 20 long, D2 to D6 4-5, L1 31, L2 and L3 6, L4 37, L5 to L8 4-5, L9 90. S1 and S2 4 on interscutal membrane.

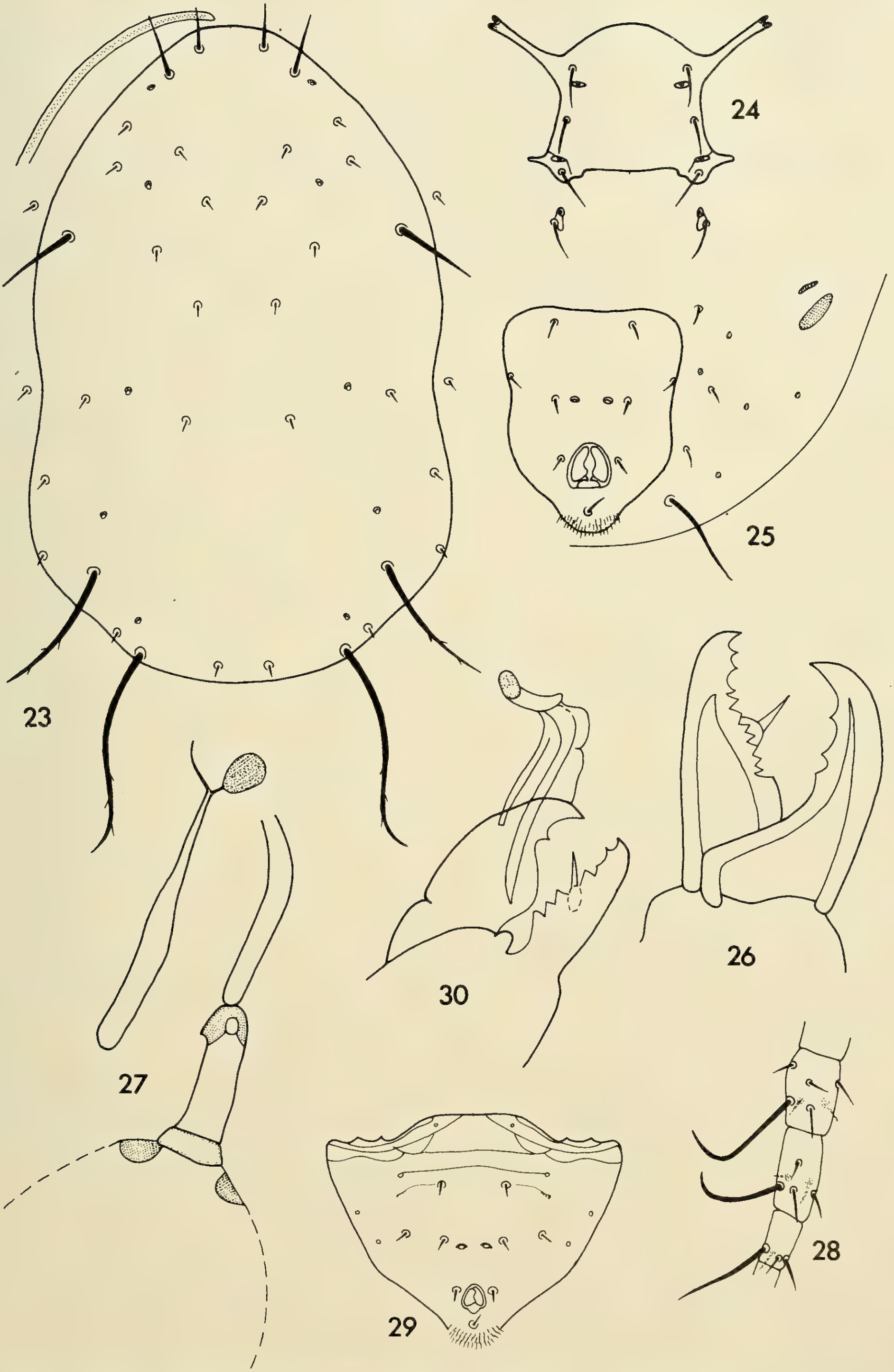
Venter. Slightly creased ventrianal shield 114 long, 156 wide, with three short preanal setae, four pairs of small pores and a pair of large preanal pores 17-19 apart (Fig. 29).

Spermatodactyl. — Shaft 17 long, foot ending with a knob (Fig. 30).

Legs. — Six macrosetae similar to those of female: on genu I 19 long, genu II 21, genu III 23, genu IV 50, tibia IV 32, basitarsus IV 48.

Amblyseius neovictoriensis, n.sp.
(Figs 31-38)

Diagnosis. — In the adult stage, *A. neovictoriensis* is similar to *A. victoriensis* (Womersley) (Womersley, 1954; see also Schicha, 1977). However, in *neovictoriensis* the dorsal shield is narrower and shorter, setae D1 are shorter, and setae L2 and L3 are approx. half as long as those in *victoriensis.* In *neovictoriensis* setae L4 are longer



Figs 23-30. Amblyseius neolentiginosus, n.sp., female: 23, dorsum. 24, sternal shield. 25, ventrianal shield. 26, chelicera. 27, spermatheca. 28, leg IV; male: 29, ventrianal shield. 30, spermatodactyl.

Figs 31-38. Amblyseius neovictoriensis, n.sp., female: 31, dorsum. 32, sternal shield. 33, ventrianal shield. 34, chelicera. 35, spermatheca. 36, leg IV; male: 37, ventrianal shield. 38, spermatodactyl.

and setae, L6, L7 and L8 are approx. twice as long as those in *victoriensis*. The fixed digit of the chelicerae in *neovictoriensis* has 4 teeth, while that of *victoriensis* has 7 teeth. The two species differ in addition in the shape of their macrosetae of legs III and IV, their spermathecae and their spermatodactyli.

Types. — NEW SOUTH WALES: on Indian coral tree (*Erythrina* sp.), Coffs Harbour, 15.ii.1978, E. Schicha. *Holotype* ♀ (*A.neo*.1) in BCRI; two ♀♀ (*A.neo*.2-3) and one ♂ (*A.neo*.4) *paratypes* all in BCRI.

Female (Figs 31-36)

Dorsum. — Dorsal shield 285-319 long, 182-186 wide at L4, reticulated anterolaterally, with 17 pairs of setae, six dorsal, two median, four prolateral, five postlateral: D1 28-31 long, D2 to D6 6-8, M1 6-7, M2 9-11, L1 35-39, L2 33-34, L3 36-41, L4 43-46, L5 9-12, L6 17-21, L7 23-28, L8 23-31, L9 59-60. L9 slightly serrated, all other setae smooth. L1 longer than interspace L1/L2; L3 as long as interspace L3/L4. All other setae shorter than distances between their bases and bases of setae following next in series. Five pairs of pores as figured. S1 and S2 9-14, on interscutal membrane. Peritremes extending forward to base of L2 (Fig. 31).

Venter. — Sternal shield 58-62 long, 71-76 wide, with three pairs of setae and two pairs of pores as figured. Fourth pair of setae on metasternal shields (Fig. 32). Vase-shaped ventrianal shield 89-94 long, 75-78 wide, with three pairs of long preanal setae and one pair of preanal pores 27-30 apart. Membrane surrounding ventrianal shield with three pairs of setae and four pairs of small shields. Caudolateral setae 32-37 long. Primary metapodal shield 11-14 long; secondary metapodal shield missing (Fig. 33).

Chelicera. — Both digits 24-26 long. Fixed digit with four teeth plus pilus dentilis. Movable digit with one backward pointing tooth (Fig. 34).

Spermatheca. — Sack-like cervix 11-13 long, atrium occupying whole width where cervix fuses with macroduct (Fig. 35).

Legs. — Six macrosetae: spiniform on genu II 26-28 long, genu III 31-34, tibia III 28-30, genu IV 46-51, tibia IV 36-43, basitarsus IV 63-71 (Fig. 36).

Male (Figs 37-38) (one specimen measured)

Dorsum. — Dorsal shield 236 long, 148 wide at L4, with chaetotaxy resembling that of female: D1 26 long, D2 to D6 4-8, M1 6, M2 10, L1 32, L2 30, L3 31, L4 40, L5 8, L6 17, L7 19, L8 26, L9 46. S1 and S2 14, on interscutal membrane.

Venter. — Imbricated ventrianal shield 94 long, 156 wide, with three pairs of preanal setae, arranged in an almost straight line, and a pair of preanal pores 22 apart (Fig. 37).

Spermatodactyl. — Shaft including foot 25 long; shaft narrow, pronounced heel rounded, toe ending with a suctorial disc (Fig. 38).

Legs. — Six macrosetae similar to those of female: on genu II 19 long, genu III 26, tibia III 25, genu IV 37, tibia IV 33, basitarsus IV 48.

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Biota of a Temperate Shallow Water Reef

JEANETTE E. WATSON

WATSON, J. E. Biota of a temperate shallow water reef. *Proc. Linn. Soc. N.S.W.* 103 (4), (1978) 1979: 227-235.

This study describes the total flora and fauna of a small (1 m²) but representative area of temperate water reef 23 m deep near Sydney, New South Wales. Excluding Foraminifera, the biota totalled 150 species comprising 29 algal, 120 invertebrate and 1 fish species. Hydroids are dominant in terms of species (13%) and sessile invertebrates comprise 51% of community biomass and 61% of species. Algae comprise 19% of species and 36% of community biomass. Populations of numerable animals are dominated by polychaetes (18%) and amphipods (17%). The sample yielded 8 new species, one new genus, extended the Australian provincial distribution of 17 species and provided 4 new records for Australia.

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INTRODUCTION

In recent years there have been a number of studies on the species composition, distribution and ecology of the soft bottom littoral and sublittoral estuarine communities of the south-eastern Australian coastline (King *et al.,* 1971; Stephenson *et al.,* 1974; Poore & Rainer, 1974; Hutchings & Recher, 1974). There are however, few published reports upon the epibiota of sublittoral reefs. These include several detailed studies of the ecology of benthic Algae in South Australian waters by Shepherd and Womersley (1970, 1971, 1976), and generalized accounts of the benthic ecology of Gulf St. Vincent and Investigator Strait in South Australia (Shepherd & Sprigg, 1976; Richardson & Watson, 1975a, 1975b), of Westernport Bay in Victoria (Smith *et al.,* 1975), and of the central New South Wales coast near Sydney (Laxton, 1976, 1977; Jones, 1977. None of these studies has, however, been directed towards a complete analysis of the epibiota at any one sampling site.

As part of a wider survey involving pollution studies at other localities on the central New South Wales coastline, the biota of a flat-topped sandstone reef in an unpolluted environment at 23 m depth was sampled at a site 500 m east of Jibbon Bombora in the ocean off Port Hacking (34° 01′ 20″ S., 151° 14′ 20″ E.) in September 1976.

SAMPLING METHODS

Following preliminary inspection, a site representative of the biota of the reef top was selected for sampling. A hoop of 0.33 m² was then thrown randomly on the site and the enclosed biota completely scraped into a fine mesh bag. This was repeated to give a total sampling area of 1 m².

The samples were later sorted under the microscope to species level and individual organisms counted. Colonial organisms were drained, blotted, and estimated as damp weight. This method of estimation of biomass was adopted since damp weighing does not destroy specimens which may later require detailed taxonomic examination.

Only Foraminifera were not examined in detail.

RESULTS

The list of species, together with numbers of individuals animals and the biomass of larger colonial organisms is given in the Appendix. Smaller colonial organisms are assigned a rank order of abundance from 1 (rare); 2 (common), to 3 (abundant).

The biota of the total sampling area of 1 m^2 comprises 150 species, of which 29 (19%) are Algae belonging to 29 genera. One hundred and twenty species are invertebrates, referable to at least 100 genera (not including sponges), and there is 1 species of fish. In terms of numbers of species, hydroids are the most abundant invertebrate group with 19 species (13% of total invertebrate species present), followed by Bryozoa (15 species, 10%), polychaetes (15 species, 10%), amphipods (12 species, 8%), sponges (11 species, 7%), bivalves (10 species, 7%), and gastropods (8 species 5%). The collection contains 155 invididual non-colonial animals with the polychaetes contributing the greatest number (28 invididuals, 18%), followed by amphipods (27 individuals, 17%), gastropods (26 individuals, 17%), bivalves (25 individuals, 16%), and ophiuroids (17 individuals, 11%).

The colonial polychaetes *Phyllochaetopterus socialis, Serpula vermicularis* and *Filograna implexa,* with relative abundances of (3), (2) and (1) respectively, would, if counted as individuals, considerably augment the polychaete population.

Total biomass of Algae and animals amounts to some 700 g damp weight. In terms of biomass, the sponges, with 283 g (40% of biomass) are the most abundant group, followed by Algae with 255 g (36% of biomass), and the single alcyonarian colony, *Capnella gaboensis,* with 36 g (5% of biomass). The remaining biomass is made up of gastropods (3%), one species of ascidian, *Polycarpa pedata* (3%), bivalves and Bryozoa (each 2%), and hydroids (1%).

The more important groups of the biota are discussed below:

Algae

Of the 29 algal species recorded, 26 are red Algae and the remainder brown. All are small, low growing, turf-like species. Three are new records for New South Wales and include *Antithamnion pinnafolium* Wollaston, previously unknown outside South Australia, *Anotrichum crinitum* (Kuetzing) Baldock, which has a recorded distribution of southern Australia and New Zealand, and *Schottera nicaeense* (Duby) Guiry and Hollenberg, a Mediterranean species. Two as yet undescribed species, *Propagula* sp., and *Mediothamnion* sp., only recently discovered in Port Phillip Bay, Victoria, were also present in the sample. Several other species may also represent new taxa, but the material is insufficient for determination.

Sponges

This group comprises 11 species in 4 families. Only one, *Callyspongia* sp., a small grey dish-shaped sponge, could be identified to genus. The next most abundant sponge is an erect orange-coloured species belonging to the Raspailiidae. All are common sponges along this part of the New South Wales coastline.

Hydroids

The shallow water hydroid fauna of the New South Wales coast is known only from records of Bale (1884, 1888) and from the reports of the "Thetis" Expedition (Ritchie, 1911) and occasional incidental references in the literature. The 19 species of hydroids in the collection include 2 undescribed species, one belonging to the genus *Hebella,* and the other to *Antennella.* There are also 6 new records for the central east coast of Australia. Several of the newly recorded species are abundant in the sample and include the large plumose hydroid, *Plumularia asymmetrica* Bale, formerly recorded from the Great Australian Bight (Bale, 1915; Watson, 1973); *Scoresbia daidala* Watson, a small, obligatory epiphyte on the brown alga *Zonaria crenata* J.

Agardh, recorded once previously from the type locality in Gulf St. Vincent, South Australia, *Monostaechus quadridens* McCrady, formerly recorded from Queensland (Pennycuik, 1959), and *Sertularia olseni* Watson, a hydroid associated with sponges, recorded once, from the type locality in the Great Australian Bight (Watson, 1973).

Only 2 of the hydroids, *Tubularia australis* Stechow, and *Eudendrium* sp., are athecate species. Of the 17 thecate species, 13 are small epiphytes growing among the algal turf, and the remainder, with the exception of the epilithic *Plumularia asymmetrica,* are epizooites, growing upon tubiculous polychaetes or 'on other hydroids.

Alcyonaria

This group is represented by 3 species, including one large colony of *Capnella gaboensis* Verseveldt. Although only recently described (Verseveldt, 1977), this is a common shallow water alcyonarian of New South Wales coastal reefs.

Bryozoa

The bryozoan fauna of the New South Wales coastline is not well known, and of the 12 species represented in the sample, 5 are new records for this part of the Australian coastline. There are 7 species of crustose (membraniporiform) Bryozoa, 4 erect jointed (cellariiform) species and 1 erect (vinculariiform) species. The cellariiform species, *Crisia acropora* Busk and *Emma triangula* Hastings, are among the new locality records and are also the most abundant species in the sample. *C. acropora* is known from Bass Strait (Busk, 1875) and *E. triangula* is known from this locality as well as from New Zealand (Hastings, 1939).

Polychaetes

Of the 15 species of polychaetes present, tubiculous forms are the dominant group in terms of numbers and include 5 species of serpulids. *Phyllochaetopterus socialis* Claparède is the most abundant polychaete in the sample (abundance (3)), the clustered tubes providing substrate for a number of small sessile species, including hydroids and Bryozoa. The cosmopolitan *Nematonereis unicornis* Grube is recorded for the first time in Australian waters. The nearest locality record for this species is the Indo-west Pacific.

Approximately half of the polychaete species and the major part of the polychaete population are filter feeders, including all of the tubiculous species. The remainder may be either omnivores or predators but there is little information on their feeding habits.

Mollusca

The shelled molluscs are all small reef dwelling species well known from the literature. The sample comprises 26 gastropods belonging to 8 species and 25 individuals of 10 bivalve species.

The predatory boring gastropod, *Torvamurex denudatus* (Perry) is the most abundant mollusc with 11 individuals in the sample. Since few bored bivalve shells were found, it seems likely that this species may be an unspecific predator or scavenger.

The algal browsing seahare, *Aplysia sydneyensis* Sowerby, is represented by one specimen. The type locality of this circumglobal species is Port Jackson. The remaining 2 species of opisthobranchs are undescribed species of the genera *Philine* and *Trapania,* the latter being a first record of this cosmopolitan genus for Australia.

Amphipoda

There are 2 undoubted, and possibly 5 additional undescribed species, reflecting the poor state of knowledge of the taxonomy of the group. *Mallacoota subcarinata*

(Haswell), commonly occurring throughout south-eastern Australia, is the only species whose distribution is known. Half of the 11 amphipod species and the tanaid *Paratanais* cf. *ignotis* (Chilton) are tubiculous forms which are usually responsible for stabilization of substrate, accumulating silt and detritus in and around their tubes.

Isopoda

Of the 3 species of isopods recorded, only one, *Cymodoce aspersa* (Haswell), whose type locality is Port Jackson, has been fully described. A single juvenile female is probably *Cilicaeopsis granulata* (Whitelegge). Jibbon Head, adjacent to the sampling site, is one of the localities where this species was collected by Whitelegge (1902). The third species, represented in the sample by 2 adult males is an undescribed species which may also be worthy of separate generic status (W. Seed, pers. comm.). A similar, unnamed specimen was recorded from Masthead Island on the Great Barrier Reef by Baker (1926).

Ophiuroidea

The 4 species of ophiuroids include one new genus and one new record for the Australian east coast. The undescribed genus is an amphiurid related to the cosmopolitan shallow water species *Amphipholis squamata* (Delle Chiaje) (A. Baker, pers. comm.), and the new record is *Ophiacantha alternata* A. M. Clark, a small sublittoral form previously known from Port Phillip Bay, Victoria. The 2 other species, *Ophioactis resiliens* Lyman and *Ophiothrix caespitosa* Lyman are common components of the immediate sublittoral algal-sponge-bryozoan fauna of temperate Australia.

Holothuroidea

Of the 3 species identified, *Pentacta australis* Ludwig is a common form widely distributed along the Australian coastline. The other two species comprise *Neocucumis ? watasei* (Oshima), known only from Japan, and an undescribed species of *Thyone*.

Other Species

The brachiopod *Magellania flavescens* (Lamarck) represented by one small specimen, is a widely, but sparsely distributed species in shallow ocean waters of temperate Australia. *Balanus trigonus* (Darwin) is one of the commonest barnacles of the sublittoral of the New South Wales coastline, where it has been dredged from depths of up to 108 m (Pope, 1945). The ascidian *Polycarpa pedata* Herdman, is a very common solitary ascidian of the sublittoral of the south-eastern coast. It frequently grows in association with the stalked ascidian, *Pyura spinifera* (Quoy & Gaimard) (J. E. W. unpub.).

DISCUSSION

The 150 species belonging to 104 genera include a new genus of ophiuroid and a probable new genus of isopod. Eight are probable new species (2 hydroids, 2 opisthobranchs, 2 amphipods, 1 isopod and 1 holothurian). The ranges of 4 algal species, 6 hydroids, 5 bryozoans and 1 ophiuroid are extended to the temperate east coast from the cool temperate southern region and the range of one isopod species is extended southwards from the Great Barrier Reef. There are 4 new records for Australia with the discovery of the cosmopolitan polychaete *Nematonereis unicornis,* the holothurian *Neocucumis ?watasei,* previously recorded from Japan, the opisthobranch, *Trapania* sp., and the Mediterranean red alga, *Schottera nicaeense.* This number of new species and new records is all the more remarkable when the small size of the sampling area, and its situation in a region considered to be relatively well known scientifically, is taken into account.

With the exception of *Callyspongia,* the larger of which was 10 cm in diameter, and the ascidian *Polycarpa pedata,* the biota comprised small to very small organisms, most of which are dependent upon the algal turf for substrate, food and shelter. The algal community is dominated by small filamentous rhodophytic species; there are only 3 small species of brown Algae, and green Algae are absent.

Sessile invertebrates comprise 51% of the biomass of the community and 61% of the species present. Algae account for 36% of the biomass and 19% of the species; algal cover was subjectively estimated at 50% of the sampling area.

Analysis of community trophic structure shows that the greatest contribution to the animal community biomass (48%) is by the suspension feeding component, dominated by sponges. In terms of species, however, carnivores, mainly microcarnivores, comprise the largest single feeding class with 42% of the total species present. Using photographic techniques in benthic studies off the New South Wales coastline, Laxton (1976, 1977) and Jones (1977), found that microcarnivores contributed the greatest percentage cover on most rocky substrates in areas where water turbidity is high. Pequengnat (1964), using species and population counts, found that suspension feeders were the most abundant components of a Californian reef-top habitat. Analysis of the present very limited sample supports Laxton's findings; it is quite likely however, that habitat or geographical differences as well as sampling methods may lead to widely varying results.

The new locality records from this sample provide further information upon the biogeographic affinities of south-eastern Australia with the Indo-Pacific and Japan. The sample also provides additional evidence for the close relationship of the Australian Peronian with the southern Flindersian Province west of Bass Strait.

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APPENDIX

LIST OF SPECIES

Numbers after the species name represent individual organisms.

Numbers in parentheses are an estimation of rank order of abundance of colonial organisms and algae, (1) = rare, (2) = common, (3) = abundant.

New records are marked *.

Probable new genera or new species are marked$^+$.

ALGAE	
Phaeophyta:	
Halopteris platycena Sauvageau	(2)
Dictyota alternifida J. Agardh	(2)
Zonaria sinclairii Hooker & Harvey	(3)
Rhodophyta:	
Delisea fimbriata (Lamouroux) Mont.	(1)
Cheilosporum sagittatum (Lamouroux) Aresch.	(1)
Jania sp.	(1)
Thamnoclonium sp.	(1)
Callophyllis sp.	(1)
**Schottera nicaeense* (Duby) Guiry & Hollenberg	(1)
Glioderma sp.	(1)
Aglaothamnion sp.	(1)
**Anotrichium crinitum* (Keutzing) Baldock	(1)
**Antithamnion pinnafolium* Wollaston	(1)
Balliella sp.	(1)
Callithamnion sp.	(1)
Ceramium sp.	(3)
**Mediothamnion* sp.	(3)
Platythamnion sp.	(3)
**Propagula* sp.	(1)
Pleonosporium sp.	(1)
Spongoclonium sp.	(1)
Acrosorium decumbens (J. Ag.) Kylin	(1)
Phycodris sp.	(2)
Dasya wilsonis J. Agardh	(1)
Heterosiphonia australis (J. Ag.) De Toni	(1)
Aphanacladia sp.	(1)
Amplisiphonia sp.	(1)
Dasyclonium incisum (J. Ag.) Kylin	(1)
Polysiphonia sp.	(1)
INVERTEBRATA	
Porifera:	
Callyspongiidae	
Callyspongia sp.	(2)
Raspailiidae	(3)
Suberitidae	(3)
Spongiidae	(2)
Hydroida:	
Athecata:	
Tubularia australis Stechow	(1)
Eudendrium sp.	(1)
Thecata:	
**Clytia* sp.	(1)
Obelia sp.	(3)
Hebella scandens (Bale)	(1)
$^+$*Hebella* sp.	(1)
Hincksella cylindrica (Bale)	(1)
Halecium sessile Norman	(1)
**Halecium ?fragile* Hodgson	(1)
Halecium delicatulum Coughtrey	(1)
**Scoresbia daidala* Watson	(2)

Sertularella simplex Coughtrey	(2)
**Amphisbetia olseni* Watson	(1)
Antennella secundaria Gmelin	(3)
+*Antennella* sp. 2	(2)
**Monostaechus quadridens* McGrady	(3)
Plumularia spinulosa Bale	(2)
Plumularia obliqua Saunders	(3)
**Plumularia asymmetrica* Bale	(3)
Actinaria:	
Anemone sp.	1
Alcyonaria:	
Capnella gaboensis Verseveldt	(3)
Alcyonaria sp. 2	(1)
Alcyonaria sp. 3	(1)
Bryozoa:	
**Aetea anguina* (Linnaeus)	(3)
Chaperia cervicornis (Busk)	(1)
Caberea helicina Hastings	(1)
**Emma triangula* (Hastings)	(3)
**Celleporaria intermedia* (MacGillivray)	(1)
Celleporaria (Sinuporaria ?) hastigera	(1)
Discopora vultur (Hincks)	(1)
Smittoidea acaroensis (Busk)	(1)
Celleporina sp.	(3)
**Crisia acropora* Busk	(3)
Bicrisia edwardsiana (d'Orbigny)	(1)
**Pustulopora ? intricaria* (Busk)	(2)
"Retepora" sp.	(2)
Scuticella ventricosa (Busk)	(2)
Amathia biseriata Krauss	(1)
Polychaeta:	
Ophiodromus sp.	1
Haplosyllis spongicola Grube	2
Pionosyllis sp.	1
Typosyllis sp.	8
Exogone sp.	1
Platynereis australis (Schmarda)	1
**Nematonereis unicornis* (Grube)	4
Phyllochaetopterus socialis Claparède	(3)
Idanthyrsus pennatus (Peters)	1
Branchiomma nigromaculata (Baird)	2
Hydroides ? brachycantha Rioja	1
Pomatostegus polytrema (Philippi)	1
Filograna implexa Berkley	(1)
Serpula vermicularis Linnaeus	(2)
Spirobranchus giganteus (Pallas)	5
Sipunculida:	
Sipunculid sp.	1
Nemertina:	
Nemertine sp.	2
Brachiopoda:	
Magellania flavescens (Lamarck)	1
Gastropoda:	
Torvamurex denudatus (Perry)	11
Dentimitrella lincolnensis (Reeve)	1
Cypraea sp.	1
Notosinister maculosa (Hedley)	4
Mitra carbonaria Swainson	2
Austrosassia parkinsoniana (Perry)	3
Vermicularia sp.	2
Murexsul brazieri (Angas)	2

Ophisthobranchia:	
Aplysia sydneyensis Sowerby	1
+*Philine* sp.	1
+*Trapania* sp.	1
Bivalvia:	
Dosinia sp.	1
Venerupis exotica Lamarck	1
Hiatella australis (Lamarck)	3
Diplodonta globulosa A. Adams	1
Marikelllia solida (Angas)	1
Cardita calyculata (Linnaeus)	4
Atrina tasmanica (Tenison Woods)	2
Lanistina impacta (Hermann)	1
Lima nimbifer Iredale	4
Trichomya hirsuta (Lamarck)	7
Crustacea:	
Amphipoda:	
Photis sp.	3
Aora sp.	2
Gammaropsis sp.	1
Amphithoid sp. 1	1
Amphithoid sp. 2	1
Cerapus sp.	4
+Phlianthid sp.	1
+*Liljeborgia* sp.	2
Mallacoota subcarinata (Haswell)	6
Tethygeneia cf. *elanora* Barnard	1
? Corophiid sp.	4
Amaryllis macrophthalmus (Haswell)	1
Tanaidacea:	
Paratanais cf. *ignotus* (Chilton)	1
Isopoda:	
Cymodoce aspersa (Haswell)	2
+cf. *Cymodoce* sp.	1
Cilicaeopsis granulata (Whitelegge)	1
Brachyura:	
Plagusia chabrus (Linnaeus)	1
Halicarcinus ovatus Stimpson	2
Micippa tuberculosa (H. Milne Edwards)	1
Leptomithrax sternocostulatus (H. Milne Edwards)	3
Anomura:	
Paguristes sulcatus Baker	1
Cirripedia:	
Balanus trigonus Darwin	4
Pycnogonida:	
Achelia sp.	2
Nymphon molleria	1
Echinodermata:	
Ophiuroidea:	
Ophiothrix caespitosa Lyman	13
+*Pholiostigma watsonae* (Baker m.s.)	2
**Ophiacantha alternata* A. M. Clark	1
Ophiactis resiliens Lyman	1
Holothuroidea:	
Pentacta doliolum (Pallas)	1
**Neocucumis ?watasei* (Ohshima)	1
+*Thyone* sp.	1
Ascidiacea:	
Polycarpa pedata Herdman	1
PISCES	
Gobiosocidae	1

A New Species of *Limnadia* (Crustacea: Conchostraca) from the Granite Belt in Southern Queensland and Northern New South Wales

J. A. WEBB and G. D. BELL
Communicated by A. RITCHIE

WEBB, J. A., & BELL, G. D. A new species of *Limnadia* (Crustacea: Conchostraca) from the Granite Belt in southern Queensland and northern New South Wales. *Proc. Linn. Soc. N.S.W.* 103 (4), (1978) 1979: 237-245.

Eulimnadia is synonymized with *Limnadia,* as the character separating the two, the presence or absence of a spine on the lower distal angle of the telson, is gradational and therefore unsatisfactory. *Limnadia urukhai* sp. nov. is distinguished from other species of the genus by the evenly curved dorsal margin and moderate size of its carapace (up to 6.7 mm by 4.3 mm), its few growth lines (maximum 10), small number of pairs of legs (15-16), two almost equal segments of the sixth endite in the first pair of claspers, and lack of a spine on the lower distal angle of the telson. On the basis of the variability noted in some morphological characters both by previous workers and in the present study, the Australian species *Limnadia cygnorum* and *L. rivolensis* may be synonymous.

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INTRODUCTION

The Queensland conchostracan fauna has been little studied; of the 23 previously known Australian species, only 3 have been recorded from Queensland. These are *Limnadia rivolensis* (Brady 1886) and *Caenestheria berneyi* (Gurney 1927) from the Longreach district (Gurney, 1927), and *Cyclestheria hislopi* (Baird 1859) from Rockhampton (Sars, 1887). In addition, in the Queensland Museum there are specimens from Stradbroke Island provisionally identified as *Lynceus* cf. *tatei* (Brady 1886), and from Cunnamulla labelled *Cyzicus* cf. *dictyon* (Spencer and Hall 1896).

Thus it is of considerable interest that several populations of conchostracans collected from small rainwater pools in the Granite Belt of southern Queensland and northern New South Wales proved on close examination to be a new species of *Limnadia*.

Genus *Limnadia* Brongniart

Limnadia Brongniart 1820, p.84; Daday 1925, p.147; Ueno 1927, p.281; Brehm 1933, p.31; Straskraba 1965a, p.263.

Eulimnadia Packard 1874, p.55; Sars 1895, p.14; Daday 1926, p.1; Barnard 1929, p.251; Mattox 1954, p.6.

Paralimnadia Sars 1896, p.15; Daday 1925, p.146.

Type Species. Limnadia lenticularis (Linnaeus 1761).

Diagnosis. Umbo lacking, lines of growth restricted to marginal portion of shell (i.e. large larval valve), dorsal margin smooth; frontal organ on top of pyriform appendage; first antennae long, unsegmented (after Straskraba, 1965a).

Discussion. The differences between *Limnadia* and *Eulimnadia* have been treated differently by different authors. Packard (1874) erected *Eulimnadia* for species that were distinguished from those in *Limnadia* by having a narrower shell with a straighter dorsal margin, fewer lines of growth, larger gills, shorter flabellae, and fewer pairs of legs. But, as Sars (1895) and Straskraba (1965a) pointed out, the size and shape of the shell and the number of growth lines can be very unreliable characters; they are closely related to environmental conditions and the age of the individual (Massal, 1954), and often cannot be used to differentiate between species. The validity of using the size of the gills has been questioned by Brehm (1933) and Daday (1925), who felt that this feature also could be strongly altered by external conditions. The flabellum length varies considerably between species, from shorter than to nearly twice as long as the leg to which it is attached. The number of pairs of legs shows a similar variability from 16 to 26.

For these reasons Sars (1895) questioned the validity of *Eulimnadia,* although he considered that one feature could definitely be used to separate the 2 genera: no males were known for any species of *Limnadia.* Daday (1925) and Barnard (1929) thought this an insufficient criterion, as although only females have been recorded for several limnadiid species, in most cases this is probably due to the small number of specimens collected (*L. lenticularis* is an exception). Daday instead proposed a single morphological distinction: the presence (*Eulimnadia*) or absence (*Limnadia*) of a spine on the lower distal angle of the telson. Since there is a complete gradation between these two extremes (Fig. 1), this character is somewhat unsatisfactory, as Barnard (1929), Straskraba (1965a) and even Daday (1925) have noted. Daday (1925) felt that *Eulimnadia* and *Limnadia* should be subgenera but retained them as genera for "historical and practical reasons".

Ueno (1927) adopted the position that species with numerous growth lines and 12-13 segments in the flagellae of the second antennae should be *Limnadia,* whereas those with 4-6 growth lines and 9-10 antennae segments would be referred to *Eulimnadia.* However, Brehm (1933) found that the subdivisions in the second antennae were indistinct, difficult to count, and could vary from 8 to 12 in one individual.

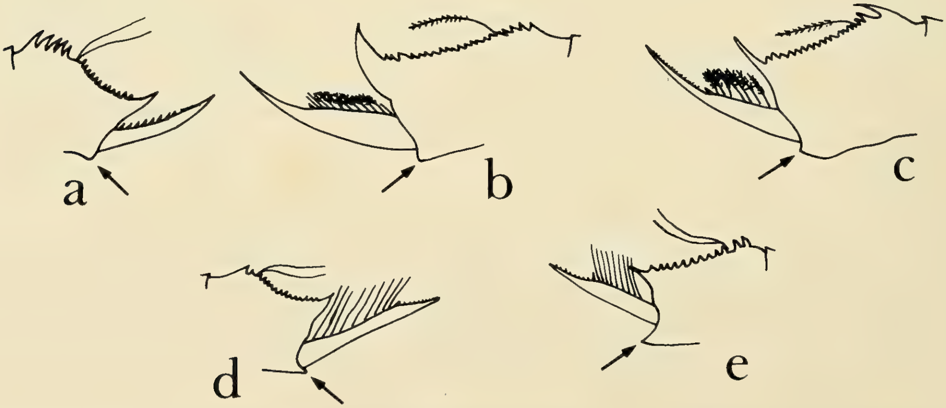


Fig. 1. Telsons of (a) *Limnadia lenticularis* (Linnaeus 1761), (b) *L. rivolensis* (Brady 1886), (c) *L. victoriensis* (Sayce 1903), (d) *L. texana* (Packard 1874), and (e) *L. similis* (Sars 1900), showing variation in shape of lower distal angle (indicated by arrows). From Daday (1925), Straskraba (1965a), Sayce (1903), and Daday (1926).

Mattox (1954) reaffirmed that the number of pairs of legs, the shape of the lower distal angle of the telson, and the number of segments in the second antennae could be used to separate *Eulimnadia* from *Limnadia*.

Some species can be assigned to either genus, depending which of the above criteria are used. *L. urukhai* sp. nov. would be referred to *Limnadia* on the basis of its telson shape, but the presence of males, and the small number of pairs of legs (15-16) and antennae segments (8-10) would place it in *Eulimnadia*. Most authors have relied entirely on the outline of the lower distal angle of the telson. Although this appears to show little variability within species, the gradation illustrated by Fig. 1 indicates that it is not a satisfactory character for distinguishing genera. Therefore *Eulimnadia* should be synonymized with *Limnadia*.

Sars (1896) differentiated *Paralimnadia* from *Limnadia* on the almost straight dorsal margin in the male carapace of the former, its large number of growth lines (up to 30), and relatively small larval valve (as little as 25% of overall valve length). However, the dorsal margin and larval valve of the female shell are only slightly different from those of many other limnadiid species, some of which have more growth lines. Daday (1925) synonymized the 2 genera and this is followed here.

Distribution. World-wide.

Limnadia urukhai, sp. nov.

(Figs 2-25)

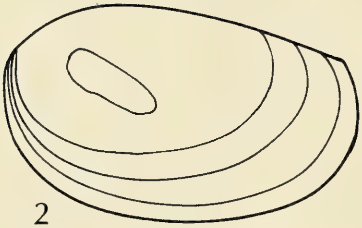
Types. Queensland: Sow and Pigs, near Stanthorpe, 26.iii. 1978, G. Bell, 1 ♂ (holotype, W7499), 5 ♂, 9♀ (W7500); Mt. Norman, near Stanthorpe, 9.iv. 1978, J. Surridge, 10 ♂, 19 ♀, 4 juveniles (W7502); Stanthorpe, Nov. 1929, H. Jarvis, 4 ♂, 2♀ (W268). New South Wales: Bald Rock, near Tenterfield, 26.iii. 1978, A. Ewart, 7 ♂, 1♀ (carapaces only) (W7501). All specimens housed in the Queensland Museum.

Diagnosis. Bisexual; male and female carapaces similar, with evenly curved dorsal margins, large larval valves, and up to 10 growth lines, maximum size 6.7 mm by 4.3 mm; 15-16 pairs of legs; 2 segments in sixth endite on first pair of claspers almost equal in length; no spine on lower distal angle of telson.

Male. Dorsal margin of carapace always smoothly curved (Figs 2-5); antero-dorsal and postero-dorsal corners usually obtuse and angular (Fig. 3), but occasionally rounded (Figs 2, 4); rarely slight concavity ventral to postero-dorsal angle (Fig. 5). Maximum carapace measurements 6.7 mm by 4.3 mm, with 10 growth lines present. Larval valve constitutes as little as 55% of overall carapace length. Elliptical shell gland (or muscle scar) always contained entirely within larval valve, and greatest dimension 20-35% of overall carapace length.

Colour of carapace varies during ontogeny: juveniles with no growth lines transparent; adults dark brown on larval valve with yellowish growth segments, and clear spot close to ventral margin of larval valve (Fig. 4, dotted circle), forming "window" through which claspers often visible. With increase in number of growth segments, clear spot increases in size and shifts ventrally (Fig. 5). Micro-ornament of shell very subdued punctate, although ridges between punctae sometimes reticulate, rarely showing indistinct radiating pattern.

Basal stalk of pyriform appendage undifferentiated in immature individuals (Fig. 6); normally very short in adults (Figs 8, 9), occasionally long (Fig. 7). Eye lobe (prominence carrying paired eyes) close or immediately adjacent to frontal organ; angular projection on anterior side usually noticeable (Figs 6-8), occasionally very small and indistinct (Fig. 9b). Occipital notch commonly right-angled although obtuse in immature specimens (Fig. 6). Ocellus elongate triangular to tear-drop in shape, rarely sub-elliptical. Rostrum extends beyond ocellus for approximately length



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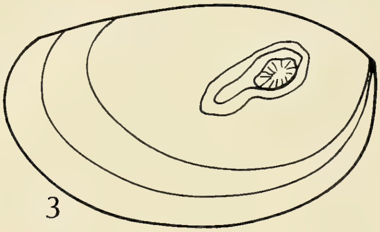

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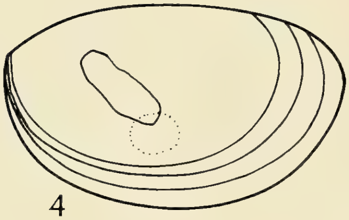

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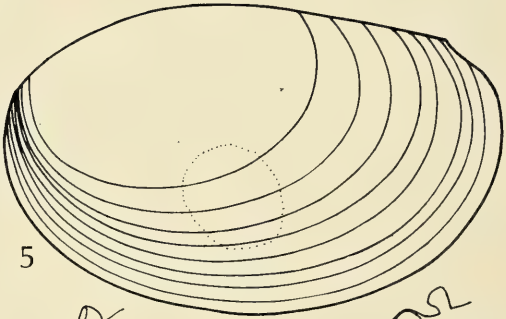

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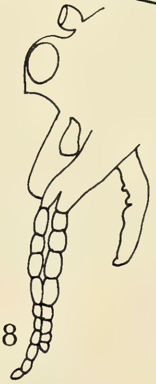

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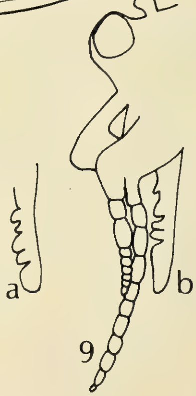

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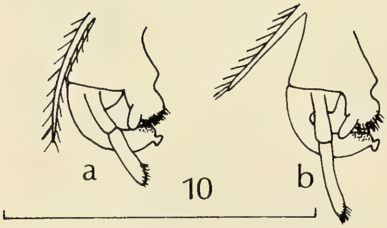

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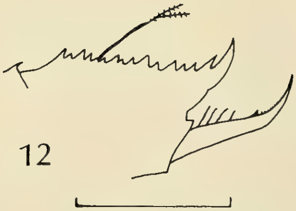

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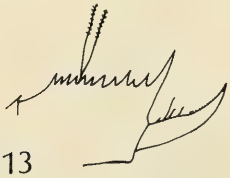

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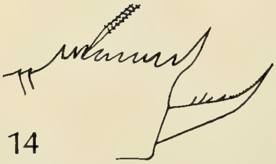

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of ocellus, with well-rounded termination, rarely pointed in immature individuals (Fig. 6).

First antennae long, reaching second, third or fourth segment of second antennae, with 3 to 6 non-setose papillae on anterior side, Size and distinctness of papillae vary considerably, even within one individual (Figs 9a, b).

Scape of second antenna extends slightly beyond rostrum; each flagella has 7 to 10 segments, often poorly differentiated towards tip and difficult to count. Flagellae normally almost equal in length, rarely one only half as long as the other (Fig. 9b).

Fifteen to 16 pairs of legs, first 2 modified as claspers. Third endite of claspers varies in length, and projection below fourth endite (thumb) often indistinct (Fig. 10a). Sixth endite (subapical appendage) in first pair of claspers bipartite, apical segment slightly longer than basal (Figs 10a, 11). Tip carries short setae, but none at joint between segments. Apical segment of sixth endite in second pair of claspers much longer than basal (Fig. 10b), otherwise the two pairs of claspers similar.

Posterior 8 to 12 abdominal segments typically with 1 to 2 dorsal spines, but occasionally middle 5-8 segments each have up to 8 dorsal setae.

Dorsal margin of telson armed with 10 to 15 spines; posterior spine longest and straight, curved, or protruding beyond posterior margin of telson (Figs 12-14). Other dorsal spines vary irregularly in size, even between two halves of telson of one individual. Forked filament between third and fifth spines from anterior end. Caudal claws as long as or slightly shorter than dorsal margin of telson, with few small setae and usually one small spine on dorsal surface. Lower distal angle of telson right-angled or slightly obtuse, and corner angular or slightly rounded.

Female. Female carapace occasionally with more arched dorsal margin (Fig. 16) and smaller dimensions (maximum 6.2 mm by 4.1 mm) than male; otherwise very similar (Fig. 15), except lacks clear spot mentioned previously.

Female head (Figs 17, 18) resembles that of male except occipital notch obtuse and rounded, becoming less obtuse in older specimens. Rostrum extends short distance past ocellus, termination rounded and right-angled.

First antennae extend only to first or second segments of second antennae, and have 2 to 3 poorly differentiated papillae (Fig. 18), or occasionally up to 5 well-marked papillae (Fig. 17).

Second antennae, number of pairs of legs and dorsal modifications of abdominal segments same as for male.

Ninth and tenth legs each possess long narrow flabellum (Fig. 19), up to 1.5 times as long as leg.

Posterior spine on dorsal margin of telson generally protrudes beyond and inclined to posterior margin (Figs 20, 21); this is less common in males.

Eggs 0.14 to 0.20 mm in diameter, covered with irregular or semi-regular pattern of ridges (Figs 25 a-c). Largest clutch carried by any female about 80.

Juvenile. Shell of smallest individual collected transparent with no growth lines, measuring 2.3 mm by 1.3 mm; dorsal margin only slightly curved (Fig. 22). At least 12 pairs of legs differentiated (posterior legs difficult to count), 6 to 7 segments in flagella of second antennae, and 9 spines on dorsal margin of telson (Fig. 24). No

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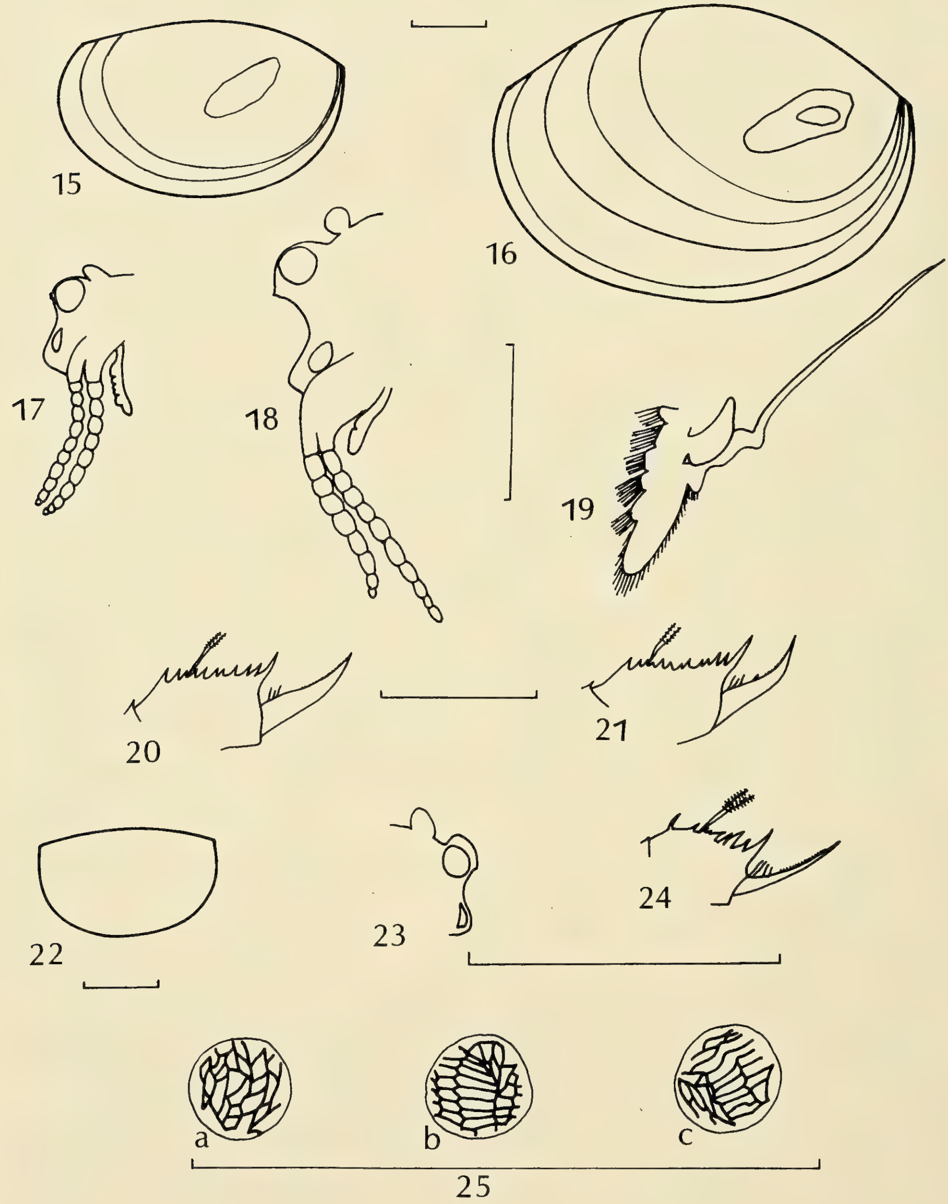
Figs 2-14. 2. Carapace (♂), W7502. 3. Carapace (♂), W7499 (holotype). 4. Carapace (♂), W7502, showing clear spot (dotted circle). 5. Carapace (♂), W7501, showing clear spot. 6. Head (♂), W7502. 7. Head (♂), W7500. 8. Head (♂), W7499 (holotype). 9a, b. Head (♂) W7500, showing both first antennae. 10a, b. First and second claspers, respectively, W7502. 11. First clasper, W7499 (holotype). 12. Telson (♂), W268. 13. Telson (♂), W7500. 14. Telson (♂), W7499 (holotype).

All scale lines represent 1 mm. For the sake of clarity, setae at joints between segments of second antennae have been omitted.



Figs 15-25. 15. Carapace (♀), W7502. 16. Carapace (♀), W7500. 17. Head (♀), W7502. 18. Head (♀), W7500. 19. Flabellum, W7502. 20. Telson (♀), W7500. 21. Telson (♀), W268. 22. Carapace (juvenile), W7502. 23. Head (juvenile), W7502. 24. Telson (juvenile), W7502. 25a-c. Eggs, showing pattern of surface ridges.
All scale lines represent 1 mm. For the sake of clarity, setae at joints between segments of second antennae have been omitted.

flabellae, claspers, or eggs developed. Frontal organ well differentiated, although pyriform appendage lacks basal stalk (Fig. 23).

On slightly larger specimen, still with no growth lines, 15 pairs of legs visible while other features the same. With one growth line, number of segments in second antennae 7 to 10. In specimens with 2 growth segments dorsal margin more curved, 12 dorsal spines on telson, pyriform appendage has basal stalk, and flabellae present in females. These specimens have adult complement of legs, second antennae segments, and telson spines. Individuals with 3 growth lines show claspers or eggs, indicating full sexual maturity. The previous descriptions of males and females were based on such specimens.

Ontogenetic variation in some characters can still occur after the onset of sexual maturity, as indicated already for the occipital notch in both sexes and the rostrum in males.

Discussion. Limnadia urukhai differs from species previously assigned to *Eulimnadia* in its lack of a spine on the lower distal angle of the telson. With regard to the other species of *Limnadia,* it is readily differentiated from *L. stanleyana* King 1855, since in the latter the male carapace has an almost straight dorsal margin, whereas that of the female is strongly curved; furthermore the larval valve of *L. stanleyana* constitutes as little as 20% of the overall shell length. *L. grobbeni* Daday 1925 and *L. woltereckí* Brehm 1933 are both very large, reaching 19 by 13 mm and 22.3 by 16.6 mm respectively, with up to 45 growth lines. The dorsal margin in both species displays a slight concavity absent in *L. urukhai.*

L. urukhai can be distinguished from the three Australian species *L. cygnorum* (Dakin 1914), *L. rivolensis,* and *L. badia* (Wolf 1911) by its smaller number of legs (15-16 as against 18-20), and by the two almost equal segments of the sixth endite of its first clasper, where the other species have the apical segment twice as long as the basal or have 3 segments. *L. lenticularis* differs in that no males of this species have ever been described (despite extensive collections), the female rostrum is very acute, and there are 22-24 abdominal segments.

The work of several previous authors, notably Straskraba (1965a), demonstrated that intraspecific variation in some characters is considerable, and the present study has enlarged on this. Putting this information together reveals that the following characters are not taxonomically useful for limnadiids: presence of angular projection on eye lobe, ocellus shape, number and distinctness of papillae on first antennae (particularly in females), relative lengths of flagella of second antennae, dorsal modifications of abdominal segments, presence of small spine halfway along caudal claw, and inclination of posterior spine on dorsal margin of telson to that margin. In addition, Brehm (1933) found that the number of segments in the flagella of the second antennae can range from 8 to 12 in one individual, and illustrations in Daday (1926) and Barnard (1929) show that setae at the joints of the sixth endite of the claspers may be absent or present. Figures in Sars (1895) reveal that in *L. stanleyana* the surface of eggs varies from ridged to subdued spinose, and Dakin (1914) found that the shell gland may or may not be confined to the larval valve.

The following characters, although they show considerable variation, are thought to be useful if treated cautiously: prominence of projection below thumb of clasper, shape of rostrum and occipital notch, length of first antennae, number and relative lengths of joints of sixth endite of first clasper, number of pairs of legs, number of dorsal spines on telson, number of setae on caudal claw, shape of lower distal angle of telson, shape of dorsal margin and maximum dimensions and number of growth lines of carapace, and relative sizes of larval valve and shell gland. Ontogenetic variation in any of these must be taken into account.

TABLE 1

Differences between *Limnadia cygnorum* and *L. rivolensis*

	L. cygnorum	*L. rivolensis*
frontal organ	slightly elongated	normal
number of pairs of legs	18	20
spine halfway along caudal claw	absent	present
projection below thumb of clasper	prominent	moderately well-marked
number and relative lengths of segments in sixth endite of first clasper	2, apical one twice as long as basal	3, subequal
surface of eggs	subdued spinose	spinose

Of the other characters, the following may be important but too little is known of their variability: size and shape of frontal organ, length of flabellae, presence of setae on first antennae, and colour and micro-ornament of shell.

Among the 24 Australian conchostracan species there are probably several synonymies, as suggested by Williams (1968) ; detailed studies of European and North American faunas have considerably reduced the number of species there (Straskraba, 1965 a, b, 1966; Sissom, 1968; Wiltshire, 1974). Applying the above knowledge of character variability to the Australian limnadiids reveals that *L. cygnorum* and *L. rivolensis* may be synonymous, as intimated by Glauert (1924). Table 1 lists the differences between them; the only significant one refers to the sixth endite of the first clasper. If the apical segment in *L. cygnorum* is in fact divided in half, a possibility admitted by Dakin (1914) in his original description, then the differences separating the species are within the limits of intraspecific variation and they are synonymous. A final decision must await re-examination of the original specimens, as the published descriptions omit certain features.

Distribution. Probably throughout the Granite Belt of southern Qld., extending into at least the northern portion of the New England Tableland in N.S.W.

Ecological notes. The specimens of *L. urukhai* collected occurred in small (1 to 2m^2 area) shallow (4 to 5 cm deep) rainwater pools on bare granite outcrops. However, only the larger of these pools were occupied by conchostracans, in association with slugs and chironomiid insect larvae. The insect larvae appear to eat the soft parts of dead conchostracans, such that dead individuals left overnight had only their shells remaining in the morning. One population of *L. urukhai* on Mt. Norman was bright green due to a heavy infestation of algae, particularly on the legs. This was identified as *Characium* spp. by Dr A. B. Cribb, Dept. Botany, University of Qld. In some pools there were large numbers of individuals, many vigorously copulating. *L. urukhai* is an active species; it generally swims with the long dimension of the shell at about 45° to the horizontal and its head upwards, but can adopt any other position. At the surface it turns upside down and moves along venter upwards. When frightened or resting it buries itself sideways or venter upwards in the bottom sediment. Many specimens were observed feeding in the algae on the pool bottoms.

Specimens at the Sow and Pigs were believed to be about 9 days old when collected, since the only rain for several months had fallen 10 days previously. They survived for 3 days after collection, when they had a maximum of 4 growth segments.

Relative proportions of males and females varied considerably in different collections, females making up 30% to 85% of the specimens.

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Records of Little-Known Sharks from Australian Waters

A. J. BASS

Communicated by J. R. PAXTON

BASS, A. J. Records of little-known sharks from Australian waters. *Proc. Linn. Soc. N.S.W.* 103 (4), (1978) 1979: 247-254.

Chlamydoselachus anguineus, Hemipristis elongatus, Cirrhigaleus barbifer, Centroscymnus crepidater and *Centroscymnus owstoni* are recorded from Australia for the first time, illustrated and briefly described. A further record of *Hexanchus griseus* is noted.

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INTRODUCTION

The shark fauna of Australia is not well known and many species often go unrecognized due to a lack of readily available descriptions. This paper attempts a partial remedy by recording and describing several obscure but possibly quite abundant species. Terminology and methods are as described in Bass *et al.* (1976). All study material is in the collections of the Australian Museum, Sydney (AMS) and the Western Australian Museum, Perth (WAM).

Family CHLAMYDOSELACHIDAE

Chlamydoselachus anguineus Garman 1884

Chlamydoselachus anguineus Garman 1884: 47, figs (type locality: Japanese seas).

Study material: 1315 mm mature male (AMS I.19157-001) trawled from 512-585 m of water off Brush Island, New South Wales (35°35-29'S, 150°44-47'E), F.R.V. "Kapala", 9 June 1976.

This specimen is illustrated (Fig. 1) and its proportional dimensions summarized (Table 1). A vertebral count was not attempted as the lack of calcification in *Chlamydoselachus* renders most of the centra invisible in radiographs. The teeth number 13-13/12-1-12. Distinguishing features include the blunt snout, elongate body, single dorsal fin, anal fin, distinctive tricuspid teeth which are similar in the upper and lower jaws, and six gill-slits of which the first pair are joined across the throat.

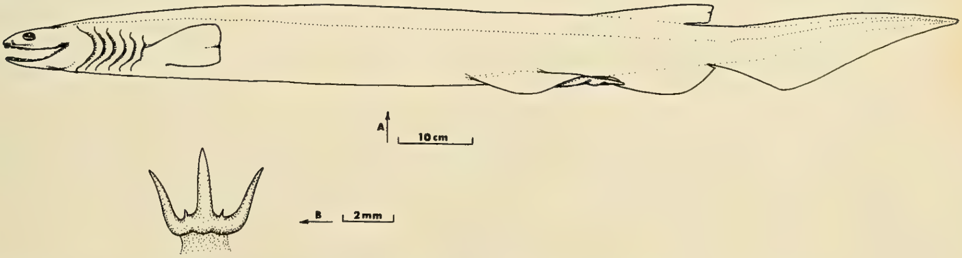

Fig. 1. 1315 mm mature male *Chlamydoselachus anguineus* (AMS I.19158-001). A — lateral view, B — tooth from near centre of lower jaws.

Stead (1907) recorded *Chlamydoselachus* from New South Wales on the basis of a skull with part of a vertebral column measuring over three metres in length. I agree with Whitley (1940) that this identification is highly doubtful. First described from Japanese seas where it is relatively common, *C. anguineus* has also been caught in the north-eastern Atlantic on several occasions and twice off California (Roedel and Ripley, 1950). The only definite records from the southern hemisphere are of two sharks trawled at different times off South West Africa (Smith, 1967; Bass *et al.*, 1975b). To these may now be added the record from New South Wales.

Family HEXANCHIDAE

Hexanchus griseus (Bonnaterre 1788)

Squalus griseus Bonnaterre 1788: 663 (type locality: Mediterranean).

Study material: Jaws of a 4250 mm, 348 kg female (AMS I.19110-001) caught on a bottom long-line in 420 m of water off Norah Head, New South Wales (33°15′S, 152°15′E), J. Dulhunty, 6 June 1976.

No detailed measurements of this shark are available as only the jaws were preserved. The tooth count is 18-19/9-VI-1-VI-8, the Roman numerals referring to the large multicuspid teeth found in the lower jaws of all hexanchid sharks. This group is distinguished by the presence of six or seven gill-slits (all widely separated across the throat), an anal fin, a single dorsal fin, and markedly different teeth in the upper and lower jaws. Of the four currently accepted species, *Notorynchus cepedianus* (Peron 1807) and *Heptranchias perlo* (Bonnaterre 1788) are relatively common and well known in Australian waters. *Heptranchias dakini* Whitley 1931 is a synonym of *H. perlo* (see Garrick and Paul, 1971a). The third species, *Hexanchus griseus* (Bonnaterre 1788), was first noted in Australian waters by Stead (1963) and then described and figured by Lynch (1964) on the basis of a 219 cm male caught in Victoria. The present study material constitutes the second definite record of *H. griseus* from Australia, for some of Stead's specimens may have belonged to the fourth species, *Hexanchus vitulus* Springer and Waller 1969. A demersal shark of warm waters, *H. vitulus* has been recorded in the western Atlantic — Gulf of Mexico region, the south-western Indian Ocean and the Philippines (see Bass *et al.*, 1975b). In case of doubt the following key should serve to identify all four hexanchid species.

Key to species of the family HEXANCHIDAE

1	Six gill-slits	2
—	Seven gill-slits	3
2	Lower jaws with five rows of large teeth on each side; dorsal fin height about twice anal height; mouth width about 1½ × mouth length	*Hexanchus vitulus*
—	Lower jaws with six rows of large teeth on each side; dorsal fin height about 1½ × anal height; mouth width more than twice mouth length	*Hexanchus griseus*
3	Snout sharp, its length more than 1½ × distance between nostrils; body plain, without any small dark or white spots	*Heptranchias perlo*
—	Snout blunt, its length much less than 1½ × distance between nostrils; upper surface of body with numerous small dark or white spots	*Notorynchus cepedianus*

Family CARCHARHINIDAE

Hemipristis elongatus (Klunzinger 1871)

Dirrhizodon elongatus Klunzinger 1871: 665 (type locality: Red Sea).

Study material: 656 mm immature male (WAM P.24547) from Exmouth Gulf, Western Australia (22°10′S, 114°20′E), D. Heald, 6 July 1973; head and one pelvic fin of 1250 mm mature male (AMS I.19438-005) taken in a gill-net in 1-6 m of water off Lizard Island, Queensland (14°40′S, 145°27′E), Australian Museum party, 1-12 November 1975.

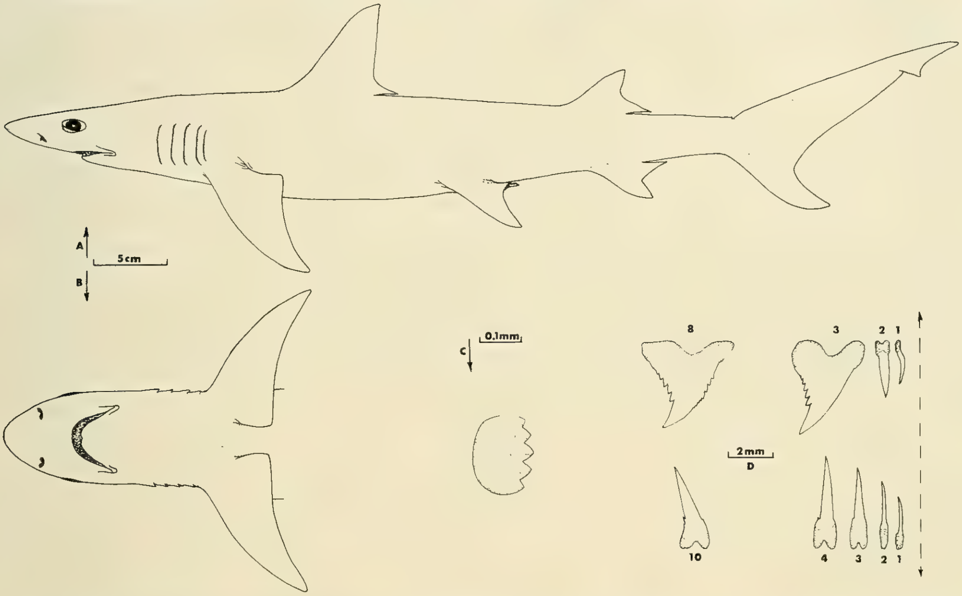

Fig. 2. 656 mm immature male *Hemipristis elongatus* (WAM P.24547). A — lateral view, B —ventral view, C — denticle from side below first dorsal fin, D — teeth from right side of upper jaws. Dashed line indicates position of symphyses; numbers indicate position of tooth rows counting from centre of jaws.

The smaller of these two specimens is illustrated (Fig. 2) and its proportional dimensions summarized (Table 1). Vertebrae number 51 monospondylous in 101 precaudal and a total of 187. The teeth number 14-14/17-17 (13-13/16-16 in the larger shark). Colour (in alcohol) is a pale greyish brown, lighter ventrally, with no conspicuous markings on the fins. The head of the mature male (also in alcohol) is dark grey dorsally, pale cream below. *H. elongatus* is usually described as having spiracles which is not the case with the present study specimens. An interdorsal ridge is variously described as present or not (see Bass *et al.,* 1975a). A definite ridge is present on the anterior half of the interdorsal space of the smaller of the two Australian sharks. Identification is based on the following suite of characters: distinctive teeth (Fig. 2D); definite upper and lower lip grooves; internal nictitating lower eyelids; first dorsal origin approximately over inner pectoral corner; second dorsal fin about half as high as first dorsal, its origin anterior to the anal fin origin; anal fin slightly shorter than second dorsal fin; caudal peduncle without lateral ridges; precaudal pits present (the lower pit may be faint); caudal fin with a distinct lower lobe and subterminal notch; and falcate pectoral and pelvic fins, especially the latter which have acutely pointed tips to the lateral lobes.

The Australian fauna includes a number of carcharhinid sharks, many of them poorly known and usually not identified correctly. The specimens described above constitute the first record of *Hemipristis elongatus* from Australia. Previous records range from southern Africa and Madagascar north to the Red Sea and east to Vietnam.

TABLE 1
Summary of proportional dimensions, shown as percentages of total length

	C.anguineus 1315mm male	*H.elongatus* 656mm male	*C.barbifer* 704mm female	*C.crepidater* 338mm male	*C.owstoni* 975mm female
Snout to outer end nostrils	0.8	3.8	2.7	3.6	1.5
inner end nostrils	0.9	4.0	3.7	5.0	3.1
mouth	0.2	7.2	7.8	14.5	7.7
eye	2.1	6.3	5.0	10.7	5.2
spiracle	—	—	10.1	18.3	11.8
1st gill-slit	8.0	16.3	16.3	24.3	17.2
pectoral origin	14.7	21.5	18.3	27.8	20.9
1st dorsal origin	61.3	29.0	30.1	34.6	29.7
pelvic origin	48.5	49.5	51.7	58.3	61.5
upper caudal origin	76.4	76.5	79.5	77.5	81.0
Horizontal eye diameter	1.4	2.4	4.0	5.9	2.6
Spiracle length	—	—	1.7	2.1	1.1
Upper ends 1st to last gill-slits	6.7	5.5	3.0	3.8	3.5
1st to 2nd dorsal origins	—	30.5	30.8	28.4	34.3
Pectoral to pelvic origins	33.7	25.9	33.2	33.1	41.5
Pelvic to anal origins	12.2	17.1	—	—	—
Pelvic to lower caudal origins	—	—	26.6	14.8	17.4
Anal to lower caudal origins	13.2	14.2	—	—	—
Last dorsal to upper caudal origins	15.1	17.1	17.8	16.6	17.0
Nostril length	0.7	1.5	2.4	2.7	1.6
Distance between inner ends nostrils	3.3	4.0	3.7	4.1	3.6
Mouth width	7.6	5.6	7.8	6.2	6.7
Mouth length	6.4	4.1	—	—	—
Upper lip groove	—	1.4	1.1	5.6	2.2
Lower lip groove	—	0.9	2.1	1.8	3.1
1st gill-slit	6.3	4.1	2.6	1.2	2.3
3rd gill-slit	5.4	4.0	2.7	1.5	2.1
Last gill-slit	4.3	2.9	2.3	1.2	1.7
1st dorsal height	2.6	9.3	8.8	3.8	2.7
base	10.0	10.4	8.9	8.9	12.8
posterior lobe	2.6	2.6	5.0	6.2	5.6
2nd dorsal height	—	4.4	8.0	4.4	4.4
base	—	7.2	9.5	8.9	10.2
posterior lobe	—	2.3	4.5	7.4	5.8
Anal height	4.2	3.5	—	—	—
base	12.6	6.4	—	—	—
posterior lobe	1.4	2.4	—	—	—
Pectoral base	3.5	4.7	4.8	4.7	5.1
inner edge	5.2	4.6	7.2	6.5	5.6
length	8.2	15.9	13.9	11.5	12.7
Pelvic anterior edge	6.8	9.5	8.1	7.4	9.8
origin to tip	12.8	8.2	11.6	10.1	15.4
Caudal upper lobe	23.8	29.4	21.2	23.4	19.6
lower lobe	8.3	11.6	11.5	12.4	12.8
Subterminal notch to caudal tip	4.4	7.0	—	4.1	5.9

Family SQUALIDAE

Cirrhigaleus barbifer Tanaka 1912

Cirrhigaleus barbifer Tanaka 1912: 151, pl. 141, figs 156-162 (type locality: Tokyo market, Japan).

Study material: 704 mm female (AMS I.19154-001) trawled from 494 m of water off Brush Island, New South Wales (35°34′S, 150°45-46′E), F.R.V. "Kapala", 6 July 1976.

This shark is illustrated (Fig. 3) with the proportional dimensions summarized (Table 1). Definite keels are present on the caudal peduncle while the caudal fin lacks any trace of a subterminal notch. No marked precaudal pits are present but a faint shallow notch at the upper caudal origin could be construed as an incipient (or vestigial) precaudal pit. Vertebrae number 50 monospondylous in 85 precaudal and a total of 114. The teeth number 13-14/12-12. Colour (when freshly dead) dark grey above, white below, the fins with white trailing edges accentuated by somewhat darker colouring adjacent to the white edges.

C. barbifer, distinguished by extremely long nasal barbels and by a lack of precaudal pits, was known only from two Japanese specimens until Garrick and Paul (1971b) recorded three from New Zealand and noted the existence of at least four others from Japan. The example from off Brush Island represents the first record from Australia.

Garrick and Paul (1971b) commented on the close similarities between *Squalus* and *Cirrhigaleus* but regarded the latter as valid. Bass *et al.* (1976) pointed out that the recently described *Squalus asper* Merrett 1973 bridges the gap between the two genera and concluded that they should probably be merged. For the present, however, I retain the genus *Cirrhigaleus* while emphasizing its close relationship with *Squalus asper*.

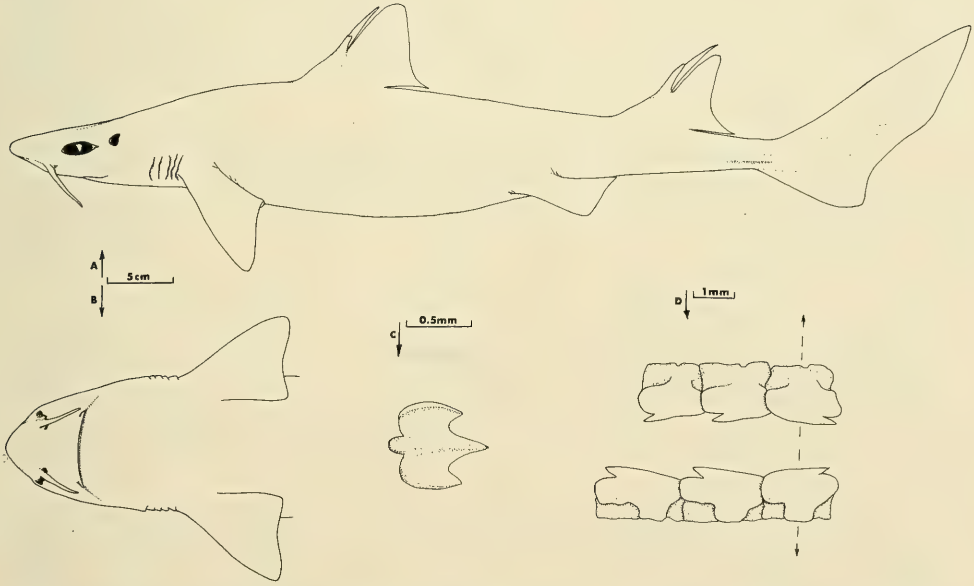

Fig. 3. 704 mm female *Cirrhigaleus barbifer* (AMS I.19154-001). A — lateral view, B — ventral view, C — denticle from side below first dorsal fin, D — teeth from right side of upper jaws. Dashed line indicates position of symphyses.

Genus *Centroscymnus* Bocage and Capello 1864

Four genera of Squalinae have laterally grooved fin spines and unicuspid teeth that are dissimilar in the upper and lower jaws. They are best distinguished by the characters used in the following key (after Bass *et al.,* 1976).

Key to some genera of the subfamily SQUALINAE

1 Distance from snout to mouth longer than that from mouth to pectoral origin .... *Deania* Jordan & Snyder 1902
— Distance from snout to mouth equal to or less than that from mouth to pectoral origin 2
2 Upper teeth set close together, at least some of the bases overlapping to form an interlocking band .... *Centrophorus* Muller & Henle 1837
— Upper teeth set apart, the bases not overlapping to form an interlocking band 3
3 Upper teeth midway along either side of upper jaws distinctly longer than those towards centre; denticles of adults with a long median ridge, without a conspicuous median cavity .... *Scymnodon* Bocage & Capello 1864
— Upper teeth midway along either side of upper jaws not distinctly longer than those towards centre; denticles with median ridge absent or restricted to posterior part, with a conspicuous median concavity .... *Centroscymnus* Bocage & Capello 1864

Genus *Centroscymnus* Bocage and Capello 1864

Centroscymnus, as defined above, was not known from the southern hemisphere until Garrick (1959a) recorded two species in New Zealand. *Centroscymnus crepidater* (Bocage and Capello 1864) has since been taken off Namibia (Pinchuk and Permitin, 1970) while *C. owstoni* Garman 1906 has been caught in the south-western Indian Ocean (Forster *et al.,* 1970). The occurrence of these two sharks in Australian waters is therefore not unexpected. The species are distinguished according to the following key.

Key to Australian species of the genus *Centroscymnus*

1 Preoral clefts almost meeting in the midline of the upper jaws ... *C. crepidater*
— Preoral clefts short, the distance between their inner ends at least as great as the distance between the inner ends of the nostrils .... *C. owstoni*

Centroscymnus crepidater (Bocage and Capello 1864)

Centrophorus crepidater Bocage and Capello 1864: 260 (type locality: Portugal).

Study material: 305 mm immature male (AMS I.15987-013) trawled from 549 m of water 48 km north-east of Jervis Bay, New South Wales (34°40′-35°01′S, 151°10-07′E), F.R.V. "Kapala", 7 July 1971; 338 mm immature male (AMS I.17868-003) trawled from 777 m off Sydney, New South Wales (33°40-43′S, 151°56-59′E), F.R.V. "Kapala", 6 December 1972.

The larger of these two specimens is illustrated here (Fig. 4) with the proportional dimensions summarized (Table 1). The colour (in alcohol) is a uniform dark brown. The denticles are typical of young *Centroscymnus;* larger sharks have denticles similar to those illustrated for *C. owstoni* (Fig. 5C, see also Garrick, 1959a, fig. 4). Both specimens had 75 precaudal vertebrae with 54 (338 mm male) and 55 (305 mm male) monospondylous vertebrae. The caudal vertebrae were insufficiently calcified to make clear images on radiographs. Tooth numbers were 36/16-1-16 (338 mm male) and 37/16-1-16 (305 mm male).

Centroscymnus owstoni Garman 1906

Centroscymnus owstoni Garman 1906: 207 (type locality: Japan).

Study material: 440 mm female (AMS IB.5327) trawled from 823 m of water east of Eden, New South Wales (37°04′S, 149°55′E), J. Henry, 29 August 1961 (in poor

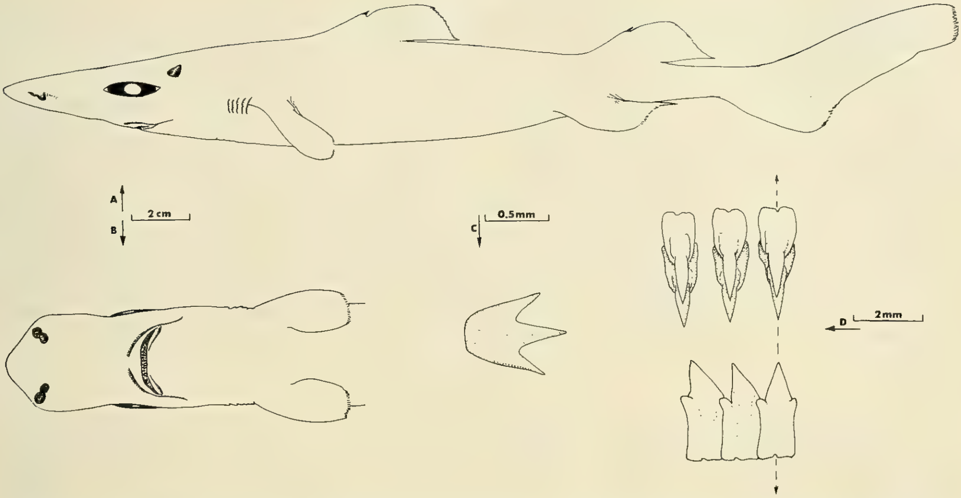

Fig. 4. 338 mm immature male *Centroscymnus crepidater* (AMS I.17868-003). A — lateral view, B — ventral view, C — denticle from side below first dorsal fin, D — teeth from right side of upper jaws. Dashed line indicates position of symphyses.

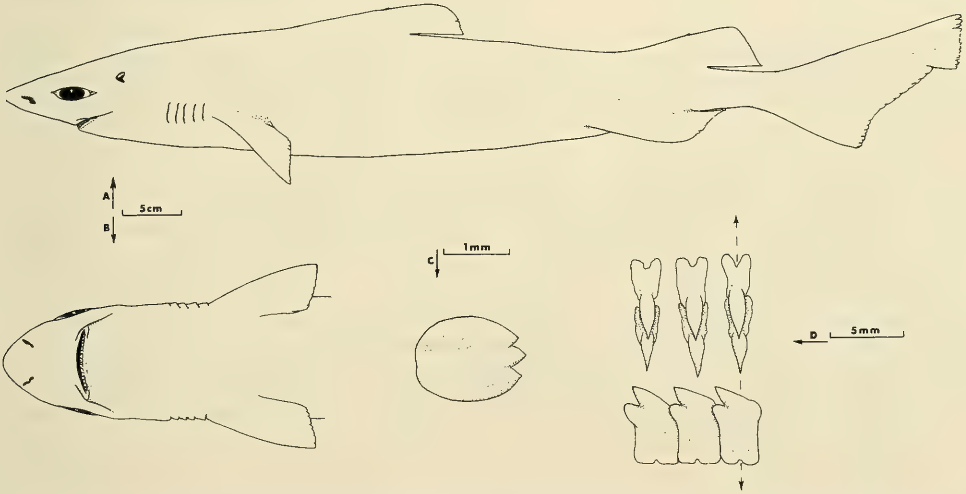

Fig. 5. 975 mm mature female *Centroscymnus owstoni* (AMS I.16147-001). A — lateral view, B — ventral view, C — denticle from side below first dorsal fin, D — teeth from right side of upper jaws. Dashed line indicates position of symphyses.

condition); 975 mm mature female (AMS I.16147-001) trawled off Sydney, New South Wales (151°E, 33°S), F.R.V. "Kapala", August 1971.

The 975 mm female is illustrated (Fig. 5) with the proportional dimensions summarized (Table 1). Many of the differences in proportions between this mature shark and the immature *C. crepidater* illustrated in Fig. 4 are due to growth changes rather than specific differences. Trends in the changes of proportional dimensions with growth in squaloid sharks are summarized by Garrick (1960). The colour (in alcohol) is a uniform dark brown. Vertebrae numbered 57 monospondylous in a precaudal total of 75 (caudal vertebrae not counted). The teeth numbered 37/17-1-17.

The smaller of these two specimens of *C. owstoni* was identified as *Scymnodon plunketi* Waite 1910 by Whitley (as noted in the Australian Museum fish register). *S. plunketi* had previously been recorded from south-eastern Australia by Cowper and Downie (1957) together with *Centroscymnus waitei* (Thompson 1930). Garrick (1959b) has since shown that *C. waitei* is the juvenile of *S. plunketi*. The specimens noted by Cowper and Downie included *Centrophorus squamosus* (Bonnaterre 1788), *Centroscymnus owstoni* and one shark which probably was *S. plunketi* (pers. comm., J. A. F. Garrick). *S. plunketi* could well appear in catches of deepwater sharks from Australian seas. Apart from the tooth and denticle characters noted in the generic key above, it is readily distinguished from *C. crepidater* and *C. owstoni* by a shorter snout tip (distance between inner ends nostrils about 1½ × that from tip of snout to inner ends nostrils in *S. plunketi*, about equal in *C. crepidater* and *C. owstoni*).

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A Key to the Australian Genera of the Agaricales

A. E. WOOD

WOOD, A. E. A key to the Australian genera of the Agaricales. *Proc. Linn. Soc. N.S.W.* 103 (4), (1978) 1979: 255-273.

A key is provided to the genera of Agaricales found in Australia. The limits of the genera are those outlined by Singer, and most of the diagnostic characters have been incorporated in the key.

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INTRODUCTION

In recent years there have been great developments in the concepts of genera in the Agaricales. However, there has been little work carried out to apply these new concepts to the local agaric flora. This paper is an attempt to do this. The generic concepts used have been those of Singer (1975). In a few cases the generic limits are wider than those accepted by Singer. In almost all of these cases, the wider sense follows the use of British Check List (Dennis, Orton and Hora, 1960). The genera which have been included in other genera are as follows:

Anellaria is included in *Panaeolus*
Armillariella is included in *Armillaria*
Copelandia is included in *Panaeolus*
Galerella is included in *Conocybe*
Gerronema is included in *Mycena* and *Omphalina*
Tectella is included in *Panellus*.

Lentinellus and *Schizophyllum* are still included, despite their exclusion from the order by Singer. This conclusion is not universally accepted and for convenience they are still included in the key.

In recent years I have collected and studied the local species and compared them with the genera accepted by Singer. In no case so far has it been necessary to propose a new genus. The genera included in the key are those that have been found in Australia together with those genera that may possibly occur here but have not so far been recorded. In this latter category are included large cosmopolitan genera and other genera where the distribution almost certainly includes Australia. Most of the collecting has been carried out in New South Wales, but there is reason to believe that the key will prove satisfactory for most of Australia.

The key is based on the concepts outlined in Singer (1975) and Dennis, Orton and Hora (1960) and is dichotomous, with several genera being keyed out several times. Spore colours unless otherwise stated, refer to the colour of a spore print. Where possible, macroscopic features have been used, to allow the key to be used in the field.

KEY

1a.	Fruit body lamellate	2
1b.	Fruit body soft, poroid (tough to woody species, see Polyporaceae)	147
2a.	(1) Lamellae narrow, fragile or flexible, crowded (space between lamellae < four times thickness of lamella) ; spore colour variable	9

2b.	Lamellae very thick, waxy, distant (space between lamellae > four times thickness of lamella); spore colour mostly white	3
3a.	(2) Spores brown, smooth, elongate; cystidia present, usually large and encrusted; basidia not very elongate ($\ell/d<6$)	*Gomphidius*
3b.	Spores white, smooth or rough, non-amyloid; basidia elongate or not	4
4a.	(3) Basidia not very elongate ($\ell/d<6$); spores smooth or rough	5
4b.	Basidia elongate ($\ell/d>6$); spores smooth	6
5a.	(4) Spores elongate, smooth; cap margin grooved; pigment present that turns green in alkali	*Anthracophyllum*
5b.	Spores globose, spiny; cap margin smooth; no unusual pigment present	*Laccaria*
6a.	(4) Lamellae shallow, decurrent, anastomosing or reduced	*Cantharellus** (Cantharellaceae)
6b.	Lamellae well developed, decurrent or not, not anastomosing	7
7a.	(6,42) Lamellar trama distinctly bilateral; cap viscid; lamellae usually decurrent; stipe apex usually rough with dots; veil often present	*Hygrophorus*
7b.	Lamellar trama not bilateral	8
8a.	(7) Lamellar trama strongly interwoven; lamellae often decurrent; fruit body not bright red or bright yellow; cap never viscid; stipe smooth	*Camarophyllus*
8b.	Lamellar trama regular, mostly of wide hyphae; lamellae decurrent or not; colour of fruit body usually bright red or bright yellow; cap often viscid; stipe smooth	*Hygrocybe*
9a.	(2) Flesh soft, fibrous; spores of various colours, amyloid, dextrinoid or non-amyloid	11
9b.	Flesh granular (containing sphaerocysts); spores white to pale buff, amyloid, ornamented	10
10a.	(9) Cap with latex when broken; intermediate lamellae always present	*Lactarius*
10b.	Latex absent; intermediate lamellae mostly absent	*Russula*
11a.	(9) Stipe central	28
11b.	Stipe eccentric, lateral or absent	12

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* This is not a true agaric, but it is included because of superficial similarity which might cause it to be confused with this group.

12a.	(11) Spores mainly white or pale brown; almost always on wood	14
12b.	Spores pink or purple;	13
13a.	(12) Spores purple; cuticle filamentous, gelatinized; on wood	*Melanotus*
13b.	Spores pink and *either* polygonal *or* with ridges	90
14a.	(12) Fruit body soft and fleshy	15
14b.	Fruit body tough and leathery	23
15a.	(14) Spores pinkish-brown to ochre-brown	16
15b.	Spores white, non-amyloid	17
16a.	(15) Spores pinkish-brown to clay-brown; lamellae not anastomosing; trama ><* regular	*Crepidotus*
16b.	Spores cigar-brown to ochre-brown; lamellae decurrent >< anastomosing, readily separated from cap flesh; trama bilateral; sometimes on the ground	*Paxillus*
17a.	(15) Gelatinized layer in flesh; encrusted, thick-walled marginal cystidia present	*Hohenbuehelia*
17b.	No gelatinized layer in flesh; ± cystidia of various types	18
18a.	(17) Cap surface with stiff dextrinoid hairs; thin or thick-walled cystidia present; fruit body sessile, with constricted base	*Chaetocalathus*
18b.	Cap surface of unspecialized hyphae	19
19a.	(18) Fruit body resupinate; thick-walled cystidia absent	*Resupinatus*
19b.	Fruit body sessile or stipe eccentric	20
20a.	(19) Lamellae distant (space between lamellae > four times thickness of lamella); cap margin grooved; spores cylindric; cystidia absent; pigment present that turns green in alkali	*Anthracophyllum*
20b.	Lamellae crowded (space between lamellae < four times thickness of lamella); cap smooth	21
21a.	(20) Spores ellipsoid to cylindric; stipe eccentric, rarely absent; >< thick-walled cystidia present	*Pleurotus*
21b.	Spores sub-globose	22
22a.	(21) Fruit body sessile; thin-walled cystidia present or absent; cap thin	*Nothopanus*
22b.	Stipe eccentric; cystidia absent; cap fleshy, luminescent	*Omphalotus*

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* >< = more or less.

23a.	(14) Lamellae splitting longitudinally	*Schizophyllum*
23b.	Lamellae not splitting	24
24a.	(23) Margin of lamellae entire	25
24b.	Margin of lamellae serrate	27
25a.	(24) Spores amyloid; cystidia absent	*Panellus*
25b.	Spores non-amyloid	26
26a.	(25) Cystidia present; lamellae crowded	*Panus*
26b.	Cystidia absent; lamellae distant; cap margin grooved	*Anthracophyllum*
27a.	(24) Spores non-amyloid, cystidia absent	*Lentinus*
27b.	Spores amyloid, cystidia present	*Lentinellus*
28a.	(11) Spores white or pale green or pale pink	29
28b.	Spores deep pink	90
28c.	Spores rust, clay or cigar brown (not chocolate)	98
28d.	Spores chocolate, cocoa brown, purple or black	138
29a.	(28) Stipe with *either* volva, volval remains *or* bulbous base *and/or* a distinct annulus (at least in young specimens)	30
29b.	Stipe with *neither* volva *nor* annulus	41
30a.	(29) Stipe with *either* volva, volval remains *or* bulbous base; annulus mostly present; spores amyloid or not, never dextrinoid	*Amanita*
30b.	Stipe with no volval remains, but with a distinct annulus	31
31a.	(30) Lamellae adnate to decurrent	32
31b.	Lamellae free; fruit body normally on the ground	35
32a.	(31) Cap cuticle filamentous; fruit body normally on wood	33
32b.	Cap cuticle cellular or with a covering of cellular granules; fruit body mostly on the ground	34
33a.	(32) Cap smooth or with small scales	*Armillaria*
33b.	Cap with prominent, large, erect, conical warts	*Cyptotrama*
34a.	(32) Cap mostly viscid; cap cuticle cellular; large cystidia present	*Oudemansiella*
34b.	Cap not viscid; cap and stipe with a covering of spherical cells in granules; cystidia not prominent	*Cystoderma*
35a.	(31) Cap viscid; lamellar trama bilateral; spores small, sub-globose, non-amyloid	*Limacella*
35b.	Cap dry; lamellar trama never bilateral; spores dextrinoid	36
36a.	(35) Lamellae and spores >< green	*Chlorophyllum*
36b.	Spores white	37

37a.	(36,53) Spores metachromatic in cresyl blue, with prominent germ pore; cap fleshy or membranous	38
37b.	Spores not metachromatic in cresyl blue, without prominent germ pore; cap fleshy	40
38a.	(37) Disc of cap with palisade structure; clamp connections present; cap large, fleshy; spores without metachromatic plug	*Macrolepiota*
38b.	Disc of cap without palisade structure; clamp connections absent	39
39a.	(38) Cap large, fleshy; spores without metachromatic plug	*Leucoagaricus*
39b.	Cap membranous; spores with metachromatic plug	*Leucocoprinus*
40a.	(37) Cuticle cellular but not a palisade; spores with thin walls; clamp connections present or absent; cystidia usually present	*Lepiota*
40b.	Cuticle flat filamentous; spore walls somewhat thickened; clamp connections absent; cystidia absent	*Pseudobaeospora*
41a.	(29) Lamellae >< strongly decurrent	42
41b.	Lamellae not strongly decurrent	53
42a.	(41) Lamellae thick; basidia very long (ℓ/d>6)	7
42b.	Lamellae thin; basidia not unusually long	43
43a.	(42) Spores non-amyloid or dextrinoid	44
43b.	Spores amyloid	50
44a	(43) Spores smooth	45
44b.	Spore wall rough, uneven or heterogeneous	48
45a.	(44) Small species (cap diameter usually < 2 cm); stipe often tough to cartilaginous; lamellar trama irregular; clamp connections present or absent	*Omphalina*
45b.	Large species (cap diameter usually > 2 cm) stipe typically fleshy; lamellar trama regular or irregular; clamp connections present	46
46a.	(45) Lamellae repeatedly forked	*Hygrophoropsis*
46b.	Lamellae not forked	47
47a.	(46) Fruit body bright yellow to orange, luminescent; lamellar trama irregular to >< regular; on wood	*Omphalotus*
47b.	Fruit body not bright coloured, not luminescent; lamellar trama >< regular; mostly on the ground	*Clitocybe*
48a.	(44) Spores with heterogeneous or uneven walls; cystidia present; fruit body drab coloured	*Fayodia*

48b.	Spores distinctly spiny; cystidia absent		49
49a.	(48) Spores white to cream	*Clitocybe*	
49b.	Spores pink	*Lepista*	
50a.	(43) Stipe tough, with yellow to rust basal mycelium; fruit body somewhat reviving; spores smooth, thin-walled; cystidia present; on wood or humus	*Xeromphalina*	
50b.	Stipe more fleshy; basal mycelium not coloured; fruit body not reviving; cystidia present or absent		51
51a.	(50) Cystidia absent; spores short-ellipsoid to sub-globose, smooth, thin-walled; on wood	*Clitocybula*	
51b.	Cystidia present; on wood or on the ground		52
52a.	(51) Spores with smooth, simple wall, ellipsoid to short-cylindric; on wood	*Clitocybula*	
52b.	Spores with thick, more or less uneven, wall, >< subglobose; on wood or on the ground; cuticular hyphae sometimes gelatinized	*Fayodia*	
53a.	(41) Lamellae free; spores dextrinoid		37
53b.	Lamellae free, adnate or sinuate; spores not dextrinoid (rarely dextrinoid and then lamellae not free)		54
54a.	(53) Cap and stipe with a covering of granules consisting of spherical cells; spores amyloid, non-amyloid or dextrinoid	*Cystoderma*	
54b.	Cap and stipe without a cellular covering		55
55a.	(54) Lamellae adnate; spores thick walled, dextrinoid, without germ pore; stipe fleshy, without annulus; cap fleshy, smooth, viscid; cuticle filamentous	*Hebelomina*	
55b.	Spores not dextrinoid; lamellae free, adnate or sinuate		56
56a.	(55) Spores rough (or at least heterogeneous)		57
56b.	Spores smooth		64
57a.	(56) Spores amyloid		58
57b.	Spores non-amyloid		59
58a.	(57) Hyphae without clamp connections; large pointed marginal cystidia, with crystal coated apex present (may be rare); cuticle filamentous; spores with plage; fruit body usually fleshy with sinuate lamellae	*Melanoleuca*	
58b.	Hyphae with clamp connections; prominent cystidia absent; cuticle filamentous; spores without plage; fruit body usually fleshy with sinuate lamellae	*Leucopaxillus*	

59a.	(57) Lamellae thick, distant, (space between lamellae > four times thickness of lamella), broadly adnate; cuticle filamentous; spores without plage; basidia without carminophile granules	*Laccaria*
59b.	Lamellae thin, crowded (space between lamellae < four times thickness of lamella), often sinuate; spores without plage	60
60a.	(59) Cuticle cellular, usually above a gelatinous layer; large prominent cystidia present; lamellae attached; clamp connections mostly present	*Oudemansiella*
60b.	Cuticle filamentous; cystidia absent or present (and then not very large); clamp connections present	61
61a.	(60) Basidia without carminophile granules	62
61b.	Basidia with carminophile granules; spores white	63
62a.	(61) Spores pale pink; spore wall thin, coarsely to finely roughened	*Lepista*
62b.	Spore print white; spore wall thick, heterogeneous or uneven	*Fayodia*
63a.	(61) Fruit body grey	*Lyophyllum*
63b.	Fruit body bright coloured (rarely white)	*Calocybe*
64a.	(56) Spores amyloid	65
64b.	Spores non-amyloid	71
65a.	(64) Cystidia rare or absent	66
65b.	Cystidia present, conspicuous	69
66a.	(65) Fruit body large (cap diameter usually > 2 cm), fleshy, on the ground; lamellae often sinuate	67
66b.	Fruit body small (cap diameter usually < 2 cm), on wood	68
67a.	(66) Hyphae with clamp connections	*Leucopaxillus*
67b.	Hyphae without clamp connections	*Melanoleuca*
68a.	(66) Lamellae well developed	*Clitocybula*
68b.	Lamellae mostly reduced to veins; fruit body white, fragile	*Delicatula*
69a.	(65) Fruit body with large pointed marginal cystidia with crystal coated apex (may be rare); hyphae without clamp connections; fruit body mostly large, fleshy; lamellae usually sinuate	*Melanoleuca*
69b.	Fruit body with conspicuous or inconspicuous cystidia, but these never crystal coated; hyphae with clamp connections	70
70a.	(69) Cystidia not conspicuous; fruit body mostly large (cap diameter usually > 2 cm), fleshy; lamellae often sinuate	*Leucopaxillus*

70b.	Conspicuous cystidia present; fruit body mainly small (cap diameter usually < 2 cm), cap conical; lamellae ascending, >< free	*Mycena*
71a.	(64) Cap cuticle normal filamentous, without hairs or cystidia	72
71b.	Cap cuticle diverticulate to cellular, or filamentous with hairs or cystidia	80
72a.	(71) Stipe fleshy; fruit body mostly large (cap diameter usually > 2 cm); lamellae typically sinuate	73
72b.	Stipe tough; fruit body seldom large; lamellae typically adnate	76
73a.	(72) Cystidia present, marginal, >< globose; on wood	*Tricholomopsis*
73b.	Cystidia inconspicuous or absent; usually on the ground	74
74a.	(73) Baidia without carminophile granules; cystidia absent	*Tricholoma*
74b.	Basidia with carminophile granules	75
75a.	(74, 77) Fruit body grey (rarely white, and then basidia long)	*Lyophyllum*
75b.	Fruit body bright coloured (when white, basidia not long)	*Calocybe*
76a.	(72) Gloeocystidia present	*Lactocollybia*
76b.	Gloeocystidia absent	77
77a.	(76) Basidia without carminophile granules	78
77b.	Basidia with carminophile granules	75
78a.	(77) Stipe not insititious; cuticle not gelatinized; fruit body not reviving	*Collybia*
78b.	Stipe insititious; cuticle gelatinized or not; fruit body reviving	79
79a.	(78) Cuticle gelatinized *or* stipe with black rhizomorphs; odour usually unpleasant	*Micromphale*
79b.	Cuticle usually not gelatinized; rhizomorphs absent; odour not unpleasant	*Marasmiellus*
80a.	(71) Cap cuticle filamentous	81
80b.	Cap cuticle diverticulate to cellular	83
81a.	(80) Cap with long stiff hairs; fruit body fragile, mostly white; cap dry	*Crinipellis*
81b.	Cap with cystidia	82
82a.	(81) Cap with large cystidia (length up to 60 μm); fruit body large (cap diameter usually > 2 cm), coloured; on wood; cap viscid	*Flammulina*
82b.	Cap with small cystidia (length up to 30 μm); fruit body small (cap diameter usually < 2 cm) delicate, white; cap >< hygrophanous	*Hemimycena*

83a.	(80) Fruit body small (cap diameter usually < 2 cm), white, non-reviving; lamellae with no marginal cystidia; cap cuticle diverticulate	*Hemimycena*
83b.	Fruit body not combining these characters	84
84a.	(83) Cap cuticle cellular to sub-cellular	85
84b.	Cap cuticle nodulose to diverticulate	88
85a.	(84) Cystidia inconspicuous or absent; basidia with carminophile granules; fruit body not reviving	*Calocybe*
85b.	Conspicuous cystidia present; basidia without carminophile granules	86
86a.	(85) Fruit body not reviving; stipe fleshy; sub-cuticular layer of cap usually gelatinous	*Oudemansiella*
86b.	Fruit body reviving or not; stipe tough to cartilaginous; sub-cuticular layer of cap not gelatinous	87
87a.	(86) Fruit body reviving; cap cuticle without cystidia; cells of cuticle smooth or rough to irregular; clamp-connections mostly present	*Marasmius*
87b.	Fruit body not reviving; cap cuticle with cystidia; cells of cuticle regular, smooth; clamp-connections absent	*Pseudohiatula*
88a.	(84) Stipe not insititious; fruit body not reviving; marginal cystidia present or absent, not conspicuous	*Collybia*
88b.	Stipe insititious; fruit body usually reviving; marginal cystidia mostly present	89
89a.	(88) Stipe tough but not cartilaginous; cap cuticle diverticulate but not rough	*Marasmiellus*
89b.	Stipe thin, cartilaginous; cap cuticle diverticulate and roughened	*Marasmius*
90a.	(13, 28) Stipe eccentric, lateral or absent *and* spores ribbed	*Clitopilus*
90b.	Stipe usually central	91
91a.	(90) Spores polygonal, smooth; lamellae not free; cap and stipe not separable; mostly on soil	*Rhodophyllus*
91b.	Spores smooth or rough, not polygonal (if somewhat angular then also rough)	92
92a.	(91) Spores rough; lamellae not free; cap and stipe not separable	93
92b.	Spores smooth	94
93a.	(92) Clamp connections absent; cystidia present or absent; cuticle >< parallel filamentous; spores ovoid to somewhat angular	*Rhodocybe*
93b.	Clamp connections present; cystidia absent; cuticle interwoven filamentous; spores ovoid	*Lepista*

94a.	(92) Large, elongate, thin-walled, hyaline cystidia on lamellae and cap surface (length up to 60 μm); lamellae sub-free; cap and stipe not easily separable	*Macrocystidia*
94b.	Large cystidia absent; lamellae free; cap and stipe easily separable	95
95a.	(94) Well developed cup shaped volva present; on the ground or wood	96
95b.	Volva absent; lamellar trama inverse; spores non-amyloid	97
96a.	(95) Lamellar trama inverse; spores non-amyloid; on the ground or wood	*Volvariella*
96b.	Lamellar trama bilateral; spores amyloid; on the ground	*Amanita*
97a.	(95) Annulus present	*Chamaeota*
97b.	Annulus absent	*Pluteus*
98a.	(28, 114) Fruit body fragile, soon decaying; cap viscid, striate or pleated; cuticle cellular; cystidia not abruptly capitate; lamellar trama regular; stipe with no brown pigment towards base; spores rust-brown, occasionally dull-brown	*Bolbitius*
98b.	Fruit body not delicate, fragile	99
99a.	(98) Stipe with membranous ring at maturity	100
99b.	Stipe with cobweb partial veil or veil absent (cobweb partial veil, when present, mostly only visible in young stages, adult specimens may show fine fibrillar remains on stipe)	108
100a.	(99) Cuticle filamentous	101
100b.	Cuticle cellular	106
101a.	(100) Spores smooth	102
101b.	Spores rough	105
102a.	(101) Lamellae thick, distant (space between lamellae > four times thickness of lamella), decurrent, often waxy; spores elongate, without germ pore; cystidia present, usually large and encrusted (length up to 60 μm); cap mostly viscid	*Gomphidius*
102b.	Lamellae thin, crowded (space between lamellae < four times thickness of lamella), not waxy, rarely decurrent	103
103a.	(102) Spores truncate, with prominent germ pore; chrysocystidia absent; cap hygrophanous, not scaly; mainly on wood	*Kuehneromyces*
103b.	Spores without prominent germ pore; chrysocystidia present or absent	104

104a.	(103) Mainly on wood; stipe mostly >< scaly; lamellae not decurrent; spores ovoid or non-ovoid; chrysocystidia often present; cap not hygrophanous; fruit body usually large, fleshy (cap diameter usually > 3 cm.)	*Pholiota*
104b.	Mainly on the ground; cap or stipe not scaly; chrysocystidia absent; spores ovoid; fruit body mostly small (cap diameter usually < 3 cm)	*Galerina*
105a.	(101) Fruit body large (cap diameter usually > 3 cm), fleshy; spores without plage; veil *either* double, forming annulus on upper part of stipe and annulus or belts on lower part of stipe *or* single	*Rozites*
105b.	Fruit body mostly small (cap diameter usually < 3 cm), fragile, striate; spores with plage; veil single	*Galerina*
106a.	(100) Spores rust-brown, smooth, with germ pore; cystidia not abruptly capitate	*Pholiotina*
106b.	Spores buff-brown; cystidia not abruptly capitate	107
107a.	(106) Spores smooth, with germ pore	*Agrocybe*
107b.	Spores rough, without germ pore, without plage	*Descolea*
108a.	(99) Cuticle cellular or sub-cellular or with abundant cystidia; mostly small species (cap diameter usually < 3 cm); spores smooth or rough	109
108b.	Cuticle filamentous, without cystidia; small or large species; spores smooth or rough	117
109a.	(108) Spores rust-brown to cigar-brown	110
109b.	Spores chocolate-brown	141
110a.	(109) Cuticle strictly cellular, with or without cystidia; spores smooth, with prominent germ pore; cystidia >< abruptly capitate	111
110b.	Cuticle sub-cellular, with or without cystidia; spores smooth or rough, without prominent germ pore; cystidia not abruptly capitate	115
111a.	(110) Spores cigar-brown; cystidia not abruptly capitate; cap without cystidia, convex to flattened	*Agrocybe*
111b.	Spores rust-brown	112
112a.	(111) Cystidia abruptly capitate; stipe brown towards the base; cap without cystidia	*Conocybe*
112b.	Cystidia not abruptly capitate	113

113a.	(112) Stipe brown towards the base; cystidia often present on cap	*Pholiotina*
113b.	*Either* stipe white to the base *or* cuticle not strictly cellular	114
114a.	(113) Stipe white to the base; spores with germ pore	98
114b.	Stipe coloured; germ pore inconspicuous or absent; cystidia often present on cap	115
115a.	(110, 114) Spores rough, cigar-brown; cap cuticle >< a layer of cystidia or >< cellular	*Alnicola*
115b.	Spores smooth, cigar-brown or rust-brown	116
116a.	(115, 124) Fruit body hygrophanous; spores cigar-brown; cap cuticle a layer of cystidia	*Simocybe*
116b.	Fruit body non-hygrophanous; spores rust-brown; cap cuticle of broad elongate cells, heavily encrusted, often in chains	*Phaeomarasmius*
117a.	(108) Spores smooth	118
117b.	Spores rough or nodulose (this may need to be determined under oil immersion)	132
118a.	(117) Spores clay-brown or cigar-brown or grey-brown	119
118b.	Spores rust-brown	120
119a.	(118) Spores clay-brown or cigar-brown; chrysocystidia seldom present	124
119b.	Spores some shade of grey-brown; chrysocystidia often present	141
120a.	(118, 131) Spores truncate, with prominent germ pore; chrysocystidia absent; fruit body hygrophanous; lamellae not free	*Kuehneromyces*
120b.	Spores not truncate, without prominent germ pore (narrow indistinct pore may be present in some cases)	121
121a.	(120) Spores thin-walled, often collapsing in water, >< hyaline *sub. micr.*	122
121b.	Spores usually not collapsing in water, coloured *sub. micr.*	123
122a.	(121) Clamp connections present; lamellae broadly adnate to sub-decurrent; marginal cystidia narrow; facial cystidia absent	*Tubaria*
122b.	Clamp connections absent; lamellae ascending, >< free; cap conic to hemispherical, normally striate; marginal cystidia narrow; facial cystidia present	*Galerina*
123a.	(121) Fruit body mostly medium to large (cap diameter usually > 3 cm); cap ><	

convex; lamellae usually attached; *either* cap scaly *and/or* chrysocystidia present *and/or* spores non-ovoid *Pholiota*

123b. Fruit body mostly small (cap diameter usually < 3 cm); cap >< conical; lamellae ascending, >< free; cap not scaly; chrysocystidia absent *Galerina*

124a. (119) Cap cuticle filamentous, of the normal type 125

124b. Cap cuticle of >< barrel-shaped cells or chains of broad elongate cells 116

125a. (124) Lamellae decurrent; lamellar trama bilateral 126

125b. Lamellae rarely decurrent; lamellar trama regular 128

126a. (125) Lamellae thick, distant (space between lamellae > four times thickness of lamella), often waxy; spores elongate without germ pore; cystidia present, usually large and encrusted; cap mostly viscid *Gomphidius*

126b. Lamellae thin, crowded (space between lamellae < four times thickness of lamella), not waxy, >< anastomosing; cap rarely viscid 127

127a. (126) Lamellae readily separating from flesh; cystidia often present, not encrusted; spores not elongate *Paxillus*

127b. Lamellae not readily separating from flesh; cystidia present, often encrusted; spores elongate; cap cuticle turns blue with ammonia *Phylloporus*

128a. (125) Cap mostly conical, generally radially fibrillose or splitting; cystidia striking, *either* thick-walled and with crystal coated apex *or* thin-walled, naked, cylindric; spores ovoid, without germ pore *Inocybe*

128b. Cap mostly convex, not radially fibrillose; cystidia not striking 129

129a. (128, 141) Spores not truncate and without prominent germ pore 130

129b. Spores truncate or with red line at junction of wall layers when mounted in KOH 131

130a. (129) Spores thin-walled, often collapsing in water, >< hyaline *sub. micr.* *Tubaria*

130b. Spores firm-walled, not collapsing, coloured *sub. micr.*, without reddish line at junction of wall layers when mounted

	in KOH; *either* cap scaly *and/or* chrysocystidia present *and/or* spores non-ovoid	*Pholiota*
131a.	(129) Chrysocystidia absent; spores truncate, with prominent germ pore	120
131b.	Chrysocystidia present; spore print some shade of grey-brown; spores mounted in KOH show reddish line at junction of wall layers	141
132a.	(117) Spores angular, nodulose, clay-brown or cigar-brown	*Inocybe*
132b.	Spores spiny or warted, but not nodulose	133
133a.	(132) Spore wall punctate due to embedded spines	*Tubaria*
133b.	Spore wall with true spines or warts	134
134a.	(133) Spores rust-brown	135
134b.	Spores clay-brown or cigar-brown	137
135a.	(134) Cystidia typically absent (when present, >< globose, thin-walled); veil cobweblike; spores rough-warted	*Cortinarius*
135b.	Cystidia typically present, not globose	136
136a.	(135) Fruit body bright coloured, often on wood; cap >< convex; veil present or absent (always on wood when present); clamp connections present; spores without plage	*Gymnopilus*
136b.	Fruit body mostly not bright coloured; cap conic to hemispherical, normally striate; lamellae ascending; mostly on the ground; clamp connections present; spores with plage (rarely without plage, but then clamp connections absent)	*Galerina*
137a.	(134) Cap often large (diameter usually > 3 cm), viscid; spores without germ pore; cystidia present; cap cuticle normal filamentous, without cystidia	*Hebeloma*
137b.	Cap usually small, (diameter usually < 3 cm) dry; spores without germ pore; cystidia present; cap cuticle >< a layer of cystidia or >< cellular	*Alnicola*
138a.	(28) Cap and stipe readily separable; lamellae free; spores cocoa-brown to purple-brown; annulus present	*Agaricus*
138b.	Fruit body otherwise	139
139a.	(138) Fruit body normally autodigesting; lamellae parallel-sided; spores black or rarely chocolate	*Coprinus*
139b.	Fruit body not autodigesting	140
140a.	(139) Cuticle filamentous; spores deep brown to violet; fruit body not very fragile	141

140b.	Cuticle cellular; spores black or deep brown; fruit body fragile	144
141a.	(140, 109, 119, 131) Spores drab-brown to blackish-violet, often non-ovoid; spores *sub. micr.* in KOH greyish or with a reddish line at the junction of the wall layers	142
141b.	Spores yellow-brown to deep rust-brown or grey rust-brown, rarely non-ovoid; spores *sub. micr.* in KOH yellow-brown, without a reddish line at the junction of the wall layers	129
142a.	(141) Sub-cuticular layer of cap sub-cellular; cap typically dry, with no separable pellicle; chrysocystidia always present; often tufted and on wood; veil cobweb-like, rarely annulate; lamellar trama regular, of narrow hyphae (rarely also with a central strand of swolllen cells)	*Naematoloma*
142b.	Sub-cuticular layer of cap not sub-cellular; cuticle typically a separable pellicle; chrysocystidia present or absent	143
143a.	(142) Chrysocystidia normally present (where absent, stipe with glutinous covering); annulus present (may be fugacious); lamellar trama of interwoven hyphae of unequal diameter	*Stropharia*
143b.	Chrysocystidia absent; veil mostly sparse or absent; lamellar trama sub-regular	*Psilocybe*
144a.	(140) Spores discolouring to a grey colour (*sub. micr.*) in conc. H_2SO_4; lamellae not mottled; spores smooth (rarely rough)	145
144b.	Spores not discolouring in conc. H_2SO_4 (*sub. micr.*); lamellae mottled; spores smooth or rough	146
145a.	(144) Cap smooth; hymenium without pseudoparaphyses; stem white	*Psathyrella*
145b.	Cap pleated, grooved; hymenium with pseudoparaphyses	*Coprinus*
146a.	(144) Spores smooth	*Panaeolus*
146b.	Spores rough	*Panaeolina*
147a.	(1) Spores smooth, white or coloured	148
147b.	Spores rough, black, or nearly so	159
148a.	(147) Spores white	149
148b.	Spores yellow, pink, fawn, brown, olivaceous or black	150
149a.	(148) Fruit body fragile, white; spores ellipsoid to sub-globose, amyloid	*Filoboletus*

149b.	Fruit body fleshy to somewhat tough; surface of cap buff to brown; spores cylindric, non-amyloid	*Polyporus arcularius** (Polyporaceae)
150a.	(148) Spores not black	151
150b.	Spores black and *either* very large *or* with a very thick wall	159
151a.	(150) Clamp connections present and easily found; spores short	152
151b.	Clamp connections absent, sparse or present (when present, spores elongate and tubes arranged radially)	153
152a.	(151) Tubes >< free around the apex of the stipe; spores yellow	*Gyroporus*
152b.	Tubes >< decurrent; spores brown to olive-brown	*Gyrodon*
153a.	(151) *Either* pores arranged radially *or* fruit body entirely red to pink	*Suillus*
153b.	Fruit body with none of the above characters	154
154a.	(153) Spores ferruginous-brown, fawn or pink; flesh never blueing	*Tylopilus*
154b.	Spores olivaceous-brown	155
155a.	(154) Stipe scabrous from squamules which are white at first, but soon discolour black or brown; stipe rarely cylindric or ventricose; pores never red	*Leccinum*
155b.	Stipe not scabrous	156
156a.	(155) Veil pulverulent to arachnoid, sulphur yellow	*Pulveroboletus*
156b.	Veil otherwise	157
157a.	(156) Cap viscid; cuticle not cellular	*Pulveroboletus*
157b.	Cap viscid or dry, when viscid, cuticle >< cellular	158
158a.	(157) Stipe reticulate *and/or* tubes red at first; tube trama with strongly divergent hyphae which are much paler than the central tissue	*Boletus*
158b.	Stipe not as above; tube trama with slightly divergent hyphae which are only a little paler than the central tissue	*Xerocomus*
159a.	(147, 150) Spores globose to subglobose; cap woolly or warted; spores almost black	*Strobilomyces*
159b.	Spores elongate	160
160a.	(159) Spores with embedded spines or pegs (occasionally smooth); young tubes white to pale grey; spores red-brown to dark-brown	*Porphyrellus*

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* This is not a true agaric, but it is included because of superficial similarity which might cause it to be confused with this group.

160b.	Spores with longitudinal ridges (occasionally with embedded spines or smooth); young tubes yellow; spores almost black	*Boletellus*

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A New Species of *Dakinomyia* from Queensland (Diptera: Asilidae)

G. DANIELS

DANIELS, G. A new species of *Dakinomyia* from Queensland, (Diptera: Asilidae). *Proc. Linn. Soc. N.S.W.* 103 (4), (1978) 1979: 275-281.

Dakinomyia secuta sp. nov. is described from central Queensland, the genus previously having been recorded only from Western Australia. Prey is recorded for the new species and additional distribution records of *D. froggattii* (Dakin and Fordham) are noted.

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INTRODUCTION

Hull (1962) records three Australian asilid genera, *Opseostlengis* White, *Questopogon* Dakin and Fordham and *Dakinomyia* Hardy, as being confined to the higher rainfall area of south-west Western Australia, each genus being considered as monotypic.

Daniels (1976) recorded four species of *Questopogon* from all states except Tasmania and the Northern Territory. The known distribution of *Dakinomyia* is extended to Queensland where it is represented by *D. secuta.* Presumably collecting in inland Queensland, South Australia and Northern Territory will confirm the presence of the genus in intermediate localities.

Material was examined and is housed in the following collections, abbreviated as:

AM	Australian Museum, Sydney
ANIC	Australian National Insect Collection, Canberra
BM	British Museum (Natural History), London
GD	Author's collection, Sydney
MM	Macleay Museum, Sydney
WAD	Western Australian Department of Agriculture, Perth.

DAKINOMYIA Hardy

Dakinomyia Hardy, 1934: 25. Type-species by original designation:
Neosaropogon froggattii Dakin and Fordham, 1922.

Flies of this genus are readily distinguished from all other Australian asilids by the distinct wing venation, the long, distal extension of the second, third and fourth posterior cells being very characteristic. They are large flies of bare aspect with a long subcylindrical and tapered abdomen. The male terminalia are rotated 90°. The facial bristles are restricted to the dorsal epistomal margin.

Hardy (1934: 25) recorded *Dakinomyia secuta* sp. n. from Eidsvold, Queensland under the incorrect name *Neosaropogon claripennis* Ricardo. An examination by Mr R. Leeke of the 'type' of *N. claripennis* at the British Museum shows that *N. claripennis* is not congeneric. At present *N. claripennis* is retained in *Neosaropogon.*

Dakinomyia secuta sp. n.

Figs 1-7

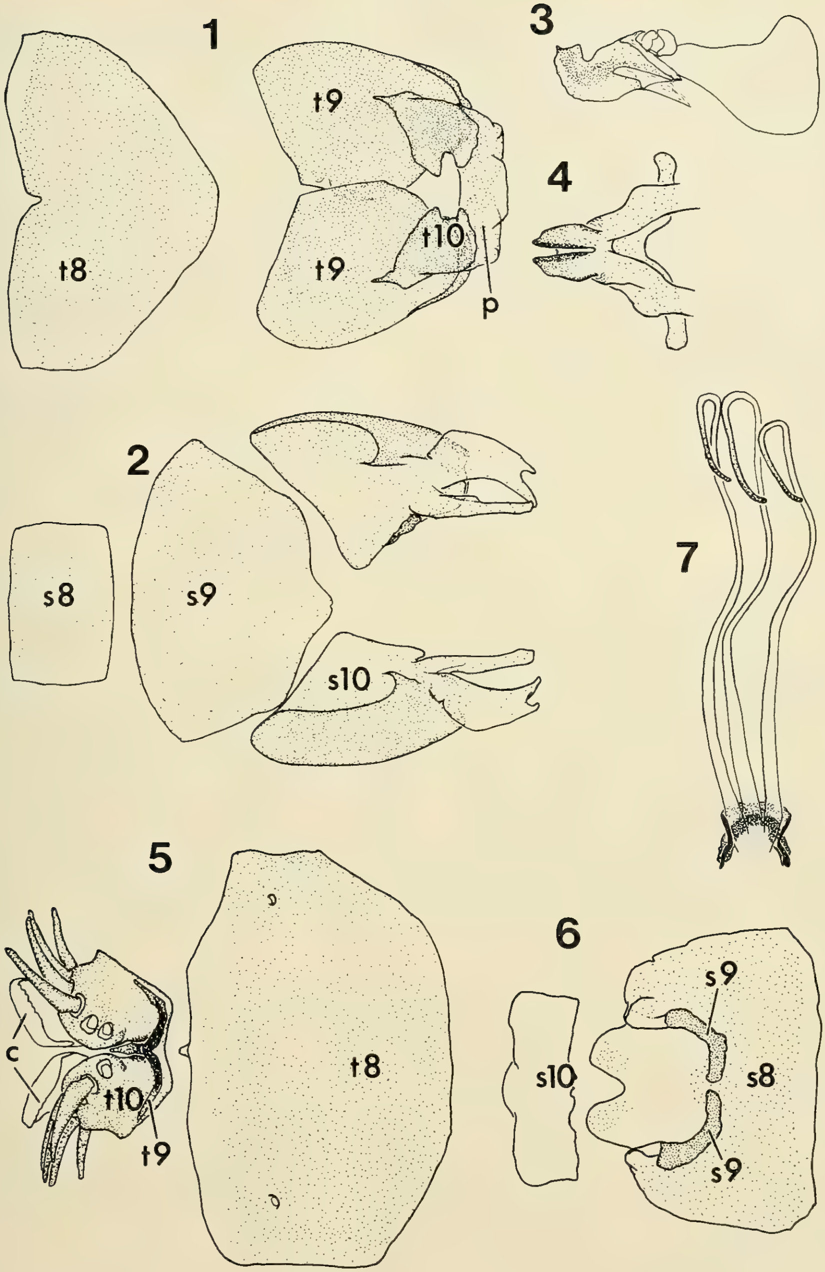
Dakinomyia claripennis (Ricardo); Hardy (1934: 25), misidentification.

Holotype. ♂, QUEENSLAND: Blackdown Tableland, Expedition Range, 6.i.1976, G. Daniels, (AM). *Paratypes.* QUEENSLAND: 14 ♂, 10 ♀, same data as holotype except 6-9.i.1976 (1 ♂, 1♀, BM; G.D); 1 ♀, same data as holotype except 23.xii.1972, M. S. Moulds, (G.D.); Eidsvold, 11.iv.1924, x.1929-iv.1930, ii-vi.1923 (4 ♂, 2 ♀, AM, 2 ♂, 2 ♀, ANIC), C. Gibbons, T. L. Bancroft (1 ♀ from Eidsvold identified as *Neosaropon claripennis* in G. H. Hardy's handwriting).

Other Material Examined (Non-Type): Eidsvold, no data, (1 ♂, 1♀ AM, 1 ♂, 1 ♀ ANIC); 1 ♂, Eidsvold, ii-vi.1923, Mackerras (MM).

MALE. *Head.* Frons, face, occiput and vertex pale yellow pollinose. Mystax comprised of 2 or 3 rows of erect, stout, pale yellow bristles confined to dorsal margin of epistoma. Fronto-orbital bristles absent but a group of 4-8 stout, admixed black and yellow bristles present on lower anterior corner of ocellar tubercle. Ocellar bristles confined to apex of occellarium, comprised of 3 or 4 pair of long stout black bristles with several weaker scattered elements. Palpi brownish, white haired; second distal segment with laterally offset apical pore. Proboscis black, with a laterally compressed dorsal ridge. Occipital bristles pale yellow, more or less confined to a single row with some weaker elements along each side. Antennae orange; first and second segments dusted yellow, setae black; third segment with an apical pit at an oblique angle on inner margin, the pit bearing a short blunt concealed spine. Relative lengths of antennal segments 1:1.05-1.15:3.14-3.86.

Thorax. Mesoscutum brownish with broad blackish medial line and pre- and postsutural dorsocentral areas, the latter sometimes narrowly joined dorsally. Scutellum brownish. Pleura grey dusted. Pronotum with a row of moderately stout yellowish bristles with a posterior and anterior row of weak erect bristles. Posterior pronotum laterally with 2-7 strong erect long black bristles surrounded by weaker white elements. Mesoscutum with abundant short appressed black setae. The medial setae are in a double row and have a bare submedial line either side. Dorsocentral areas bare except for a few anterior setae on dark presutural mark. Dorsocentral bristles not extending anteriorly to suture, posterior elements incurved. Humeral callus with 5 or 6 bristles anteriorly, mixed black and yellowish; posterior surface setate. 5-7 strong black presutural, 3 supra alar and 2 or 3 postalar bristles. Scutellar disc bare; margin with a pair of long, black convergent bristles. Metanotum strongly bulbous; micropubescent only. Mesopleuron, pteropleuron and anepisternite micropubescent. Pleurotergite with a double row of fine bristles, dorsally being finer and denser, sometimes forming a 'tuft'. Metapleuron with some weak bristles posteriorly. *Legs.* Orange-brown. Fore and mid femora with dense appressed black setae and only a single short subapical bristle posteriorly on fore femur and 1 or 2 similar bristles on mid femur. Fore tibia with a row of 2-4 antero- and 5 or 6 posterodorsal short bristles; a row of 6 posteroventral bristles, short except for a single long stout bristle at apical third, usually being the fifth bristle in the row; apically with a fan of 6 or 7 bristles of varying lengths. Tibia dark brown on apical fourth. First 3 tarsal segments yellow, with dense appressed setae; third segment occasionally deep brown on apical third; segments 4 and 5 deep brown; basitarsus twice as long as succeeding segment. Mid tibiae with dense short appressed setae; dark brown on apical fourth; a row of 4 to 6 short dorsal bristles; 3 evenly spaced, long, anterodorsal bristles; a row of 3-5 short anteroventral bristles; 2 long ventral bristles arising from mid point and apical fourth of tibia; a row of 4 or 5 anteroventral bristles. Mid tarsus similar to fore tarsus. Hind femur with dense appressed setae, deep brown on apical sixth; a weak bristle present anteriorly on mid point of femur. Hind tibia yellow, deep brown on apical third; with dense short appressed black setae. A row of 4 long dorsal bristles, 3 long anterodorsals, 2 being before basal half and one on apical third; a row



Figs 1-7. Dakinomyia secuta sp.n., terminalia: (1) tergites of male, ventral view; (2) sternites of male, dorsal view; (3) aedeagus, lateral view; (4) aedeagus, ventral view; (5) tergites of female, dorsal view; (6) sternites of female, dorsal view; (7) spermathecae and furca, dorsal view. Setae are omitted from Figs 1, 2, 5 and 6. c = cerci, p = proctiger, s = sternite, t = tergite.

of 4 or 5 anteroventrally. Hind tarsus deep brown; first and second segments yellow on basal sixth and half respectively. Basitarsus about 2.5 times as long as succeeding segment. *Wings*. Venation and shape similar to *D. froggattii* as illustrated in Hull, 1962 fig. 510.

Abdomen. Strongly tapered; orange-brown. First tergite mostly black, narrowly orange-brown along posterior margin. Second tergite blackish brown on basal fourth, this same area being white pruinescent. White pruinescent stripe on lateral margin of tergites 1-7. Fine short appressed setae present on tergites. Lateral margin of tergites 1-4 with fine pile, relatively long and dense on first tergite and becoming shorter and less dense on each succeeding tergite. Sternites white pruinescent with fine white erect setae. Segment 8 orange, recessed into preceeding segment. *Terminalia* (Figs 1-4) black, rotated 90°.

FEMALE. Similar to male except as follows:

Abdomen. Tergites 5-8 shining, with sparse, erect white setae. Tergites 7 and 8 black. Tergites 1-5 with lateral white pruinescent line. *Terminalia* (Figs 5 and 6) black. Acanthophorites with 6 or 7 pairs of long, stout, blunt spines.

DIMENSIONS: length of body, ♂ 26.0 - 30.1 mm, ♀ 26.5 - 32.5 mm; length of thorax, ♂ 6.5 - 7.4 mm; ♀ 6.8 - 7.7 mm; length of wing, ♂ 17.5 - 19.2 mm; ♀ 17.5 - 19.7 mm.

MORPHOLOGY OF THE FEMALE TERMINALIA

The female terminalia, as herein discussed, comprise the genital and postgenital segments (abdominal segments 8-11).

SEGMENT EIGHT

Tergite 8 (Fig. 5). On the expanded female abdomen, tergite 8 (t8) is a medium sized, easily observable sclerite and is relatively unmodified. The anterior margin is convex, a similar condition existing on the posterior margin, although less strongly so. The posterior margin is somewhat membranous centrally. The ratio of medial length to maximum width is 3.7 to 6.8.

Sternite 8 (Fig. 6). Like t8, sternite 8 (s8) is a relatively large and conspicuous sclerite although it is a more complex structure than t8 and has undergone diverse modifications. A medial recess is present and the submedial area is extended posteriorly. The posterior margin has a submedial lobe extending along the inner surface of s8.

SEGMENT NINE

Tergite nine (and tergite ten) (Fig. 5). Tergite 9 (t9) and tergite 10 (t10) cannot be entirely separated as they appear to be fused. t9 would appear to be reduced to a small narrow, double crescent shaped sclerite at the anterior margin of the deeply, medially divided t10, with a narrow pointed medial extension posteriorly.

Sternite nine (Fig. 6). Sternite 9 (s9) appears as a small sclerite, apparently fused to each of the lateral, anteriorly directed, posterior margins and extends anteriorly and medially to a point slightly posterior to the posterior margin of the furca. Each sclerite is concave posteriorly and more or less sharply angulate anteriorly.

SEGMENT TEN

Tergite ten (Fig. 5). t10 is a rounded sclerite medially divided posteriorly, the division extending towards the anterior margin but not reaching it. Each acanthophorite, as this divided tergite is generally referred to, possesses strongly modified setae, usually six in number but occasionally seven.

Sternite ten (? plus *eleven*) (Fig. 6). Sternite 10 (? plus 11) (s10) is a broad and narrow membranous sclerite that partially overlaps the medial extension of s8. Each anterior lateral corner overlies part of s9. The medial lateral margin appears to be joined with the ventral margin of s10.

CERCI (Fig. 5).

The cerci are attached to the posterior margin of t10 and bear a row of blunt spine-like bristles along the extreme posterior margin. The remaining ventral surface is densely covered with short, fine, hair-like bristles.

FEMALE REPRODUCTIVE SYSTEM

The female reproductive system comprises a pair of tubular accessory glands on long slightly narrower ducts (Fig. 7), 3 elongate spermathecae with brownish vesicles, the spermathecal ducts being approximately twice the diameter of the spermathecae and have a short common duct before entering the median oviduct. Viewed dorsally the furca is semicircular with a vertical rib on the dorsal surface. This rib is concave laterally and is flared anteriorly. The ovaries (omitted from Fig. 7) are long and narrow, extending from the posterior margin of segment 1 to the anterior margin of segment 8 and have a short oviduct.

MORPHOLOGY OF THE MALE TERMINALIA

The male terminalia comprise the eighth to eleventh abdominal segments.

SEGMENT EIGHT

Tergite eight (Fig. 1). t8 is a medium sized, easily observable sclerite and has undergone some modification. The anterior margin is concave whilst the posterior margin is convex and tends to form a lobe medially. The ratio of medial length to maximum width is 4.8 to 9.3

Sternite eight (Fig. 2). s8 is a small relatively inconspicuous sclerite, and is rectangular in shape with the posterior margin slightly convex.

SEGMENT NINE

Tergite nine (epandrium) (Fig. 1). t9 is slightly longer than t8 and fully cleft medially, the two halves rounded, obtuse and converging posteriorly. The dorsal margin of each half is rounded, forming a small lobe. The anterior margin is straight but angled to the medial axis.

Sternite nine (hypandrium) (Fig. 2). s9 is a well-developed sclerite with a distinctly convex anterior margin. The lateral margins are narrowed posteriorly and the posterior margin has a distinct medial projection.

SEGMENT TEN

Tergite ten (Fig. 1). t10 is reduced to a pair of sclerites lying below the posterior margin of t9. The anterior margin is at approximately 45° to the medial line and slightly concave. The anterolateral margin is extended into a narrow lobe. The lateral margins are almost straight with a convex lateral projection towards anterior margin. Medially, each sclerite has a distinct recess just behind the convex posterior margin.

Sternite ten (coxite) (Fig. 2). s10 appears as a pair of short curved processes ('styles') which arise subapically from the inner surface. The ventral style has parallel sides for most of its length, being bluntly rounded apically and slightly enlarged basally. The dorsal style is much stouter than the ventral style, generally about 3 times as wide. At about one fourth of the length of this process a small dorsal spur is present.

PROCTIGER

The *proctiger* (Fig. 1) is a rectangular membranous sclerite with the anterior margin slightly wider than the posterior margin, extending slightly beyond s10 and has an indistinct medial crease. The posterior margin is almost straight with a small setose lobe on each lateral corner and a broad indistinct convex lobe medially.

AEDEAGUS

The *aedeagus* (Figs 3 and 4) is short, widened anteriorly and sulcate posteroventrally. The anterior dorsal margin and a lateral ventral groove are membranous.

D. secuta differs from *D. froggattii* in the following characters:

D. froggattii has 3rd antennal segment brownish; thorax with dorsum uniformly brown-black; 1st abdominal tergite black dorsally on basal third and on lateral margin sublaterally tergites 2-5 with a black line, extreme margin orange-brown, with a yellow pruinescent line, tergites 6-8 black orange-brown lateral margin; sternites deep black-brown; femora red-brown, dorsally black, and apically widened tibia with, at most, basal third yellow; coxae orange-brown to deep brown; first tergite with black microtrichiae dorsally, white haired laterally, and with 4-5 black stout bristles laterally; tergites two to five with extremely fine, stout orange microtrichiae.

FORAGING AND PREDATION

Observations at Expedition Range, Queensland

While awaiting prey, the asilids rest on rocks, soil and sticks close to the ground, though the greatest preference is for large, bare rocks. The flies land on sunny areas and if even partly covered by shadow will usually move immediately. Upon alighting, these flies take up a characteristic position with their bodies turned perpendicularly to the sun. The bodies were normally held high off the substrate with the tip of the abdomen held slightly above the substrate. Predation was observed mostly in the morning from about 7.00 am to 10.30 am.

When prey is sighted, the predator's whole body turns to face it. Forage flights were usually short, ranging from about 30 cm to a metre. Prey was taken only in the air and was usually impaled upon being captured. After capturing prey, the asilid would fly up to 3 m to find a suitable perch to manipulate prey, either a grass stem or twig about 30-45 cm above the ground. Upon alighting one of the fore legs was used as an anchor whilst the other fore leg and the middle legs manipulated the prey. However if a fly was disturbed whilst feeding it would seek a large bare area of rock or soil and continue feeding.

Prey selection is presented only to generic level as specific identifications are not available.

It is noteworthy that the prey of all female asilids captured were Hymenoptera and three of the Hymenoptera were males.

Prey taken:
1 ♀ with *Ropalidea* sp. (Hymenoptera: Vespidae)
1 ♂ with *Rhytidoponera* sp. (Hymenoptera: Formicidae)
1 ♂ with nr *Dasypogon* sp. (Diptera: Asilidae)
1 ♀ with *Apis mellifera* (L.) (Hymenoptera: Apoidea)
1 ♀ with *Tachytes* sp. (Hymenoptera: Sphecidae)
1 ♀ with *Campsomeris* sp. (Hymenoptera: Scoliidae)
1 ♂ with Hemiptera: Cicadidae
1 ♂ with Diptera: Asilidae (undetermined genus)

Dakinomyia froggattii (Dakin and Fordham)

Neosaropogon froggattii Dakin and Fordham, 1922: 523.
Dakinomyia froggattii (Dakin and Fordham) — Hardy 1934: 25.

The only recorded locality for this species is the type locality, Bremer Bay, Western Australia. The following specimens extend the distribution approximately

430 km to the north east:

1 ♀ Lake Cronin, W.A. 16.iii.1970 K. T. Richards (WAD)
1 ♀ Bakers Hill W.A. 24.ii.1969 T. Burbidge (WAD)

ACKNOWLEDGEMENTS

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