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NATURAL HISTORY IN ALL ITS BRANCHES

THE LINNEAN SOCIETY OF NEW SOUTH WALES

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Cover motif: Transverse section (×2.4) of the Devonian coral described by A. J. T. Wright as *Melrosia rosae* gen. et sp. nov. From the Mount Frome Limestone, Mudgee district, N.S.W.
Adapted by Len Hay from *Proc. Linn. Soc. N.S.W.* 90, 1966, p. 266 (fig. 3).

PROCEEDINGS
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VOLUME 109
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THE SIR WILLIAM MACLEAY MEMORIAL LECTURE 1984

New Light on the Extinction of the Australian Megafauna

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[Delivered 18 July 1984]

Coming as I do from the University of Sydney I frequently encounter the name of Sir William Macleay. The energies of the staff of the Macleay Museum ensure that his name is kept in front of us.

The subject of Oceanic prehistoric archaeology has an important place within the Macleay Museum. Thus my sort of archaeology is, within the University of Sydney, associated with the name of Macleay. By contrast archaeology has not been so associated, at least in this century, with your Society. I have looked at the contents of your *Proceedings* and suspect that mine may be the first contribution in prehistoric archaeology for some eighty years. I therefore feel that it is a double honour for me to be giving the Sir William Macleay Memorial Lecture to your Society. The honour is both a personal one, and one for the discipline of prehistoric archaeology within Australia.

Of course, much of Australian archaeology is not relevant to the aims of your Society. I would not expect you, for instance, to find a place for research into the manufacturing sequence of stone tools, or a study of their functions. However the study of megafaunal extinctions, incorporating as it does such studies as zoology and botany, is clearly relevant to your Society.

Extinctions is so manifestly a topic of what used to be called natural history that some of you may be wondering why I should be claiming it as also a topic for study by archaeologists. Let me give you two reasons why it should be. The first reason is chronological, and the second methodological. The chronological evidence that megafauna and prehistoric humans overlap is increasing. The period of overlap was evidently some tens of millennia. The methodical reason, related to the chronological one, is that archaeologists, in their approach to studying past events in the field, are accustomed to paying minute attention to stratigraphic detail. Of course such attention is not restricted to prehistorians: indeed we have recently seen some palaeontologists, examining the extinction of dinosaurs at the end of the Cretaceous, reducing their research objective to the study of the chemical properties of a band of dust 10mm thick. Nevertheless, though they do not possess a technique peculiar to themselves, archaeologists have a strong tradition of relishing the fine detail of the context in which their specimens are found, as much as they relish the specimens. We do not dig for specimens as we might dig for potatoes.

Field work designed to establish the relationship between humans and megafauna will always require fine attention to contextual detail. From this point of view it is fortunate that the question of Pleistocene extinctions, in both the Americas and Australia, is being answered by the use of archaeological methods.

It has not always been thought that the question of Pleistocene extinctions in Australia was one for archaeologists. Until a decade ago in Australia one could respectably argue, though with some opposition, that megafaunal extinctions pre-dated the first settlement of this continent by the ancestors of the Australian Aborigines. Where were the archaeological sites, with unambiguous stratigraphy and radiocarbon dates, at which the sceptical excavator could repeatedly find artifacts and megafauna in association? After decades of armchair speculation and (I would say) desultory field work there were none. Indeed it was questionable whether there was any overlap in time. For example a Holocene date for a tooth of *Diprotodon* from Orroroo, in South Australia, was about 7,000 years old: less frequently reported, by the supporters of recent megafaunal extinctions, was a date of greater than 40,000 years for the contents of the stomach of the same beast (Jones, 1968). Another critical site, for the adherents of early extinctions, was Lake Mungo. Archaeologists, studying in detail Lake Mungo's artifacts and food remains at stratified locales older than 20,000 years, were absolutely unable to find any extinct species (Bowler *et al.*, 1970).

Yet in spite of its attractiveness an extinction that pre-dated human arrival was not a view that was strongly argued, largely because it left unanswered the question of what else might have caused the extinctions. So a different explanation came into favour. Rhys Jones (influenced by Paul Martin, that doyen of the American debate about extinctions) provided us with a respectable hypothesis of human causation. The argument that gained strength in the 1960s was an extinction caused by the initial human settlement of Australia towards the end of the Pleistocene (Jones, 1968). It was thought to be sudden and ecologically catastrophic.

There were several observations that made plausible the hypothesis of extinctions soon after first human settlement:

1. Species stable since the Tertiary (notably *Diprotodon*, short-faced macropods such as *Procoptodon* and *Sthenurus*, and the carnivorous phalanger *Thylacoleo*) suddenly became extinct at the end of the Pleistocene. There might be room for argument about how synchronous the extinction of the various species was, but by the vast scale of Cainozoic chronostratigraphy there could be no doubt that the extinctions were sudden.
2. The species that became suddenly extinct had survived numerous climatic oscillations, of precipitation and temperature, that had earlier taken place in the 2-3 million years of the Pleistocene. They not only survived these oscillations but, by their fossil distribution across latitudes and coastal-inland gradients, showed themselves not to be sensitively adapted to specialized environmental conditions. They were, in other words, species tolerant of diverse environmental conditions, in the same way that the grey kangaroo is tolerant. The largest species (those allied to the genera of *Diprotodon* and *Zygomaturus*) have been collected as fossils from Papua-New Guinea to Tasmania, and out west to the lakes of the Lake Eyre basin. Even allowing for diachronic variations in palaeoclimates it would be hard to argue that *Diprotodon* was anything but a very tolerant animal.
3. While not precisely knowing the habits of the extinct megafauna it is possible, from a study of the functional anatomy of the teeth, to identify the majority as browsers. Of especial interest was *Diprotodon*, evidently a riverine browser. *Thylacoleo* was plausibly interpreted in a quite different way, namely as a leopard-sized carnivore. In these two cases (and in others) species became extinct in niches that were then left unfilled. The principle of competitive exclusion could not be invoked as a cause of extinction.
4. It was argued that climate could also not be invoked. Palaeoclimatologists the world over had not detected, towards the end of the Pleistocene, a climatic event that was novel. True, we saw the severely cold and dry pleniglacial event,

centred on 18,000 years ago, with particular clarity, but we saw it in that way because it was so recent and had left so complete a record of its effects. However even a cursory study of older landforms indicated that events just as severe had been recurring events in the Australian Pleistocene.

5. There was only one discernibly novel event at the end of the Pleistocene in Australia, namely the arrival of human beings. The question was whether we were to see them as ecologically neutral or as analogous to a new disease.

All the considerations outlined above applied to the Americas as well, where ground sloth and mastodon became extinct at the end of the Pleistocene. Again we know that it was at that time that humans arrived.

Thus developed the idea of the extinction of a naive fauna faced by a novel predator in the form of humans. The fauna was thought to be naive in the sense manifested by animals that live today in areas not previously occupied by humans, such as certain ocean islands, areas of the Arctic and all of the Antarctic. The absence of humans in those places has meant that the animals evolved no behaviour specific to humans as predators.

In 1973 Martin, writing about the Americas, sharpened up the general theory of human predation to a specific one. He argued that newly-arrived humans, and their descendants, formed an advancing predatory front. This front had become adapted to the naive resource of megafauna. Martin argued that the first Americans swept the Western Hemisphere and killed off the megafauna (the largest species being the most economical part, for such a human adaptation, of the total mammalian biomass) within 1,000 years (Martin, 1973). This new and extreme theory for the precise mechanism of extinction fitted with the fact the radiocarbon dates in Tierra del Fuego were as early as dates from the north of North America, namely around 11,000 years old.

Though not explicitly extended to Australia, this blitzkrieg model attracted Australian archaeologists. Here too dates in the south were as early as dates in the north, and no sites associating artifacts and megafauna, in reliable and repeatedly observable stratigraphic association, had been found.

It is perhaps not immediately obvious to you why the absence of blitzkrieg sites was expected by the proponents of this model for megafaunal extinctions. The answer is (and it is a reasonable one, even though it might be thought to retain overtones of special pleading) that in terms of the probability of discovery we cannot expect to find the short-lived blitzkrieg event materialized in the archaeological record. After all, and on a vastly broader timescale, millions of individual *Diprotodon* must have lived in New South Wales alone, yet the specimen from Tambar Springs is the only individual for which we have more than half the bones in the skeleton. Indeed we can note in passing that when the blitzkrieg argument was being put together we did not have even the Tambar Springs specimen. This marvellously unique skeleton, that is now on display in the Australian Museum, was found only in 1979. The argument in brief is that since we have so few fossils, compared with the individuals that lived, why should we expect to be fortunate enough to find those dating from the short-lived blitzkrieg. The implications of the blitzkrieg model for field research are depressing.

My field research into the question of megafaunal extinctions did not start until 1974, well after the opposing armies of climatic and humanly-induced extinctions had taken to the field. Had I earlier joined the theoretical fray I have no doubt that I would have favoured the arguments for humanly-induced extinction. I was certainly attracted by the bold explanatory power of the blitzkrieg model.

I now have to stress that, regardless of its theoretical appeal, the blitzkrieg model for Pleistocene extinctions is seriously threatened by the stratigraphic evidence emerging from the archaeological sites that I am going to make the subject of the rest of this lecture.

In order to set this current field work in context I shall briefly describe some earlier excavations carried out, by myself and several colleagues, near Melbourne in the 1970s (Gillespie *et al.*, 1978). At the site of Lancefield we were able to date the megafauna to 26,000 years ago. This is a date not for extinction itself, but rather for a still-extant megafauna. Extinction in Victoria took place at some still unknown date after the deposits at Lancefield were laid down.

Now a date of 26,000 years ago is a suspiciously late date if the blitzkrieg model is to hold. We knew before we dated Lancefield that human occupation at Lake Mungo was at least 34,000 years old. Furthermore after we published Lancefield we were to learn that there is, for the Western Australian site of Upper Swan, reliable evidence for humans at, or earlier than, 40,000 years ago (Pearce and Barbetti, 1981). By 'reliable' I mean stones that are irrefutably artifacts, *in situ*, and with repeated radiocarbon dates.

In brief, then, a period of several thousand years of overlap between humans and megafauna was fatal for the blitzkrieg model. Yet the implications of Lancefield went further than the mere overlap of radiocarbon dates with archaeological sites elsewhere. We found at Lancefield two stone artifacts that could be stratigraphically related to the bone bed — one, under conditions of impeccable control, was found in a little channel under the bone bed and was therefore earlier than an occurrence of megafauna on grounds of relative dating alone.

Though it was (and still is) a site that seriously challenges the blitzkrieg model, Lancefield had a severe deficiency. It had no extended stratified sequence in which artifacts and megafauna could be found in association in successive layers. The deposits at Lancefield happened during a short period around 26,000 years ago when the spring-fed swampy depression was filled with shallow water. The depression filled up and, as the pollen record shows, no more free water was available. There was therefore no attraction for animals, or rather there were no depositional processes that preserved their visitations. So the archaeologist at Lancefield excavates down through two metres of recent deposits of sandy clay, across an unconformity and into the bone bed. Importantly the charcoal used for dating was recovered from just under the undisturbed bone bed, with (as I have already mentioned) an artifact. So in spite of the absence of a continuous association I found the stratification beyond reproach as regards the late date for megafauna. Furthermore the two dates of 26,000 years were obtained from separate parts of the site. Nevertheless we did depend entirely on the reliability of the two radiocarbon dates for the recent age of the megafauna, and we had no continuous sequence, associating humans and megafauna, that could be dated from top to bottom and provide some chronological history of the association.

One might have supposed that a site with better stratigraphic properties than Lancefield would have been easy to find. Yet it has been the case that since we published our findings the discovery of a stratified sequence on the mainland of Australia has proved elusive, but, if the dates from Lancefield are correct, the discovery of such a stratified sequence is to be expected.

As an improvement on our work at Lancefield our recent work on the Liverpool Plains of New South Wales looks encouraging. It is to this work that I shall now turn. The Tambar Springs Project, as it is informally called, has for the first time provided direct stratigraphic evidence for a prolonged and continuous overlap of humans and megafauna at a single site. Thereby the evidence from Lancefield has been markedly improved upon.

In providing you with an account of the Tambar Springs Project I stress that there are many loose ends to the work so far done. This lecture is therefore a report on work in progress. It is also a report on work done in collaboration with others, currently David Horton (of the Australian Institute of Aboriginal Studies) and Judith Fethney of the University of Sydney. Students of the University of Sydney have provided the labour that these labour-intensive sites require. The work has been supported in part by the Australian Research Grants Scheme.

We have been excavating at two sites on the Liverpool Plains, called Lime Springs and Trinkey. Both sites are spring-fed swamps, unimpressive depressions in the landscape. Each is less than 100m in diameter. Neither is identifiable as a site on aerial photographs, yet their unimpressive appearance belies their scientific importance. We discovered both sites by ground survey, and into the banks of the swampy depressions we dug blind, since no archaeological evidence outcrops on the surface.

The sites are 3km apart. Both have essentially the same stratigraphy. The prehistoric stratigraphic units, from the top down, are: —

1. The Grey Silt, an aeolian dust dating to 6,000 years old: up to 0.8m thick.
2. The Black Swamp, an organic-rich black sandy clay dating from 6,000-c. 20,000 years old: up to 1.3m thick.
3. The Buff Silt, an aeolian dust c. 26,000 years old: up to 0.5m thick.

In substantiating a recent date of megafaunal extinctions it is the Black Swamp that holds the clues. Wherever we have dug, and at both sites, the Black Swamp contains stone artifacts and megafauna. All the mammalian remains (both extinct and extant species) have been identified from fragments of the enamel of their teeth. Bits of bone are fragmented, and nearly one third are burned, suggesting that they are the remains of human activity around the spring-fed swamps.

At Lime Springs (by far the richer of the two sites) extinct species present include *Diprotodon*, *Macropus titan*, *Protemnodon*, *Procoptodon* and *Sthenurus* (Gorecki *et al.*, 1984:118). In the same levels we found thousands of artifacts, including 1988 that were greater than 10mm in minimum dimension. From the point of view of the age of extinctions it is critical to note that the upper levels of the Black Swamp at Lime Springs (dated by analogy with Trinkey to 6,000 years old) have as much extinct fauna as the lower levels.

When we published the site of Lime Springs we had only one date, and that was for the base of the Black Swamp unit. Now we have several dates and they are all consistent.

We have the remarkable evidence of the megafauna living through to the Holocene. As my late mentor Louis Leakey used to say, the textbooks will have to be rewritten. Indeed a Holocene megafauna is not the only remarkable attribute of the Black Swamp unit at both sites, since we also find high groundwater discharge from the springs through the pleniglacial period centred on 18,000 years ago and which, to the south and west of the Liverpool Plains, has been shown to be exceptionally arid. Another unexpected discovery is cultural: at the top of the Black Swamp (and therefore dating to about 6,000 years ago) we find the first occurrence at our sites of the horsehoof cores of the Kartan industry. This industry (previously undated with any precision) is found in arid areas to the west; the Liverpool Plains represent the most easterly occurrence of this fascinating prehistoric industry (Lampert, 1983). I will comment again on the significance of the Kartan industry when I describe the uppermost unit called the Grey Silt.

The sandy clays of the Black Swamp unit, though below the water-table, retain well-differentiated cultural stratigraphy. We were able to use correspondence factor analysis of the excavated units, taking as data the counts of the rock types used to make artifacts, to demonstrate that the site was not disturbed (Gorecki *et al.*, 1981:119). Since, in addition, we cannot differentiate the state of preservation of extant and extinct species we have very strong *prima facie* evidence for a Holocene megafauna on the Liverpool Plains.

These two sites are better than Lancefield for the simple reason that each has a sequence, covering some 14,000 years, during which artifacts and megafauna are associated. For the first time claims for coexistence do not depend on casual and unrepeatable observation. It is possible to invite a sceptic to excavate a square metre and guarantee that the association will reveal itself again. Repeatability is one of the essentials of good science.

It is important to note that our findings, surprising though they are, do not fly in the face of findings from other archaeological sites on the central and western slopes. There are no other sites yet excavated. True, extinctions in the fragile ecosystems of the lakes in western New South Wales were complete by 27,000 years ago (Hope *et al.*, 1983). Yet we must remember that our area is (today at any rate) so well-watered as not to be so easily disturbed by climate or humans. Let us consider an environmental parallel. Giraffes and rhinoceroses went extinct in the Sahara following minor climatic changes, but flourish to this day in the well-watered Serengeti. We do not think of African environments in a monistic way, yet we tend to fall victim to the cliche of Australia being the driest continent. The driest continent it may well be, but this statement of average overlooks the hundreds of thousands of fertile square kilometres in the well-watered east. My point is that the fragile ecosystems to the west give us no reason to predict synchronicity of extinctions in the different ecosystems of the east. The only theory that requires synchronicity is blitzkrieg: Lancefield, Lime Springs and Trinkey indicate that continent-wide extinctions are not attributable to initial human impact.

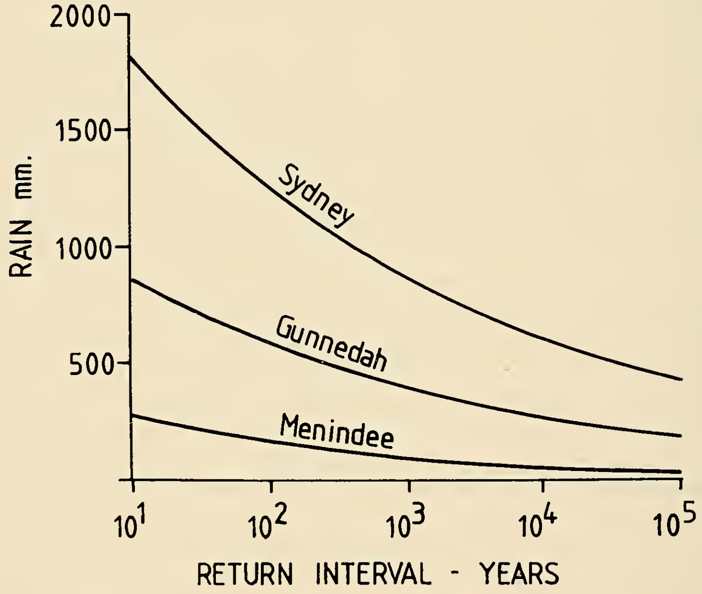

Fig. 1. Return intervals of droughts, computed from the rain falling in Year *J* + Year *J*-1. Gunnedah, on the Liverpool Plains is proofed against drought in a way that Menindee, representing the western lakes of New South Wales, is not.

We published (Gorecki *et al.*, 1984:117) a graph showing the theoretical importance, when studying extinctions, of summer rainfall on the Liverpool Plains. Fig. 1 extends this line of thinking into the statistics of the return intervals of droughts. The graph is calculated from the rainfall statistics of the last hundred years (in lieu of statistics from the Pleistocene!). The algorithms for computing return intervals are taken from

Gumbel (1958). To make the statistics more ecologically meaningful I have computed the return intervals not for annual rainfall but for the rainfall of Year *J* + Year *J*-1. Thus we are looking at the return intervals of droughts calculated from the sum of two year's rainfall.

How can we make use of Fig. 1 to illustrate the stability of the Liverpool Plains? Let us suppose that we assume a total of only 200mm of rainfall, spread over two years, as locally catastrophic to large mammals and hunter-gatherer humans in any environment. Fig. 1 indicates that the average return interval of such an amount at Menindee is in the order of once every one hundred years. At Gunnedah the return interval exceeds one hundred thousand years. Thus we can see that the Liverpool Plains not only have better absolute rainfall than the western lakes (including a critical peak of summer rainfall) but they are far better proofed against crippling droughts.

The enduring stability of the Black Swamp unit was destroyed 6,000 years ago when the Grey Silt was blown in. This remarkable unit is best represented at Trinkey, where nearly a metre of calcareous aeolian dust sits conformably on the Black Swamp unit. At Lime Springs, where the silt lies below the water-table, it has evidently been decalcified so that only the siliceous component remains. The deposition of Grey Silt represents a rude interruption to the swampy ecosystem since no more swamp deposits formed until post-European times, when the clearing of the land caused a rise in the water-table.

This calcareous dust is foreign to the area. Certainly it is not a source-bordering dune, since weathering products of the Pilliga Sandstone surround the two swamps. Moreover the Grey Silt is found at its deepest within the Trinkey depression and to the west, not as a dune on the eastern margin.

The theory that I am working on is that the Grey Silt was blown off fluviatile sediments along the Darling River and was trapped by the dense vegetation (such as the reed *Phragmites*) growing in the swamps.

Having been so trapped the calcareous material in the dust was in part eluviated down the profile of the Grey Silt. At its base, and in the top of the underlying unit of Black Swamp, calcareous nodules have formed — chemically aiding the preservation of bones and teeth in what would otherwise have been an acid black sandy clay.

Whatever the final explanation for this extraordinary dust may be, it is clearly a rare event. The underlying deposits of the Black Swamp show no sign of dust. In scale it is an event not to be compared with the trivial dust storms of today. The absence of soils developed within it suggests that it was a single event. If it was blown from the Darling River it perhaps represents either the onset of an arid period, with destabilization of alluvial materials previously stabilized by wet-loving vegetation, or it represents the occurrence of a flood of rare magnitude followed by a rare hot northwesterly wind.

That there occur floods with a magnitude vastly exceeding anything we have seen in historic times is implicit in Fig. 2. Again I have used Gumbel statistics, this time to estimate the return intervals for floods, of specified discharges, on the Darling at Bourke. The mind boggles at the implications, for deposits of alluvium on the flood plain of the Darling, of the flood with a return interval of 1,000 years.

Detailed sedimentological work must now be done on the Grey Silt and an attempt made to estimate its source and climatological significance. In many ways I would like to be able to interpret it as an arid event, because we could then link the aridity with the arrival of the Kartan industry — aridity pushing to the east people whose industrial traditions had, for some thousands of years, been stably settled well to the west.

Some answers to the environmental implications of the Grey Silt may come from a study of pollen spectra immediately before, during and after its deposition. Alas, no swamp deposits formed after its deposition at Lime Springs and Trinkey. Moreover

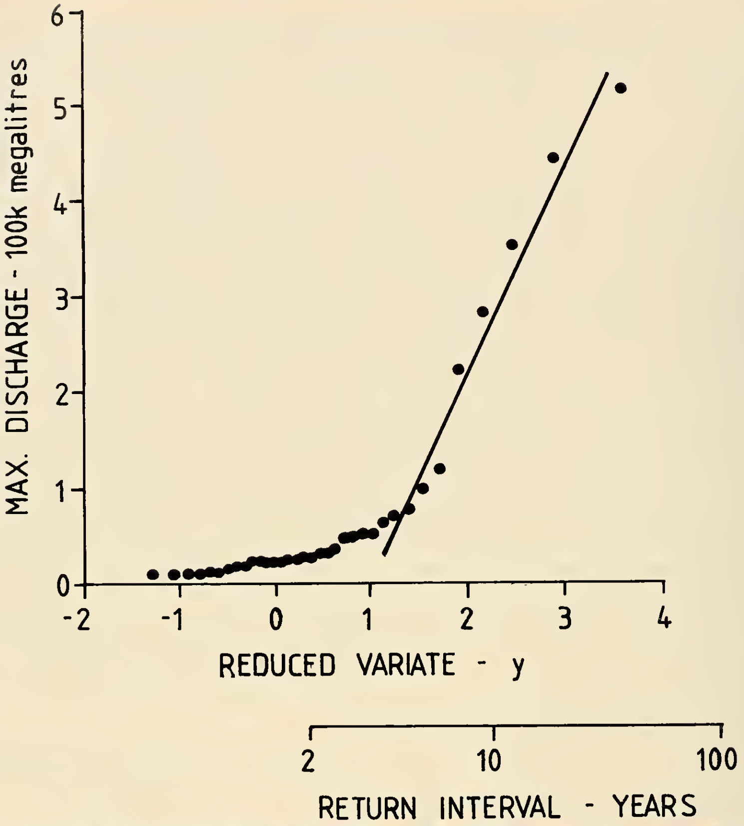

Fig. 2. Return intervals of floods on the Darling at Bourke. Note the implications, in the steepness of the line, for the magnitude of the thousand year flood. See text for relevance of flooding to origins of the aeolian Grey Silt unit at the site of Trinkey.

there is no pollen in the underlying Black Swamp unit. Pollen is to be expected in such organic-rich deposits, so evidently it was destroyed when the swamps dried 6,000 years ago, a process of destruction that would have been abetted by the calcareous contribution from the Grey Silt. I regard it as a primary objective of our field work to find a swamp that has remained damp and thereby preserved pollen from these critical prehistoric periods.

Meanwhile it is indeed tempting to rush in and explain the extinction of megafauna, on the Liverpool Plains, as 'caused' by the Grey Silt. However at Trinkey, underlying the Black Swamp, we have another dust, called the Buff Silt and tentatively dated to 26,000 years. The megafauna clearly survived this event — not only its environmental effects (whatever they may have been) but also the co-occurrence of humans at that time. For we have undoubted artifacts in the Buff Silt at Trinkey.

We can now seen an unexpected twist emerging from these two sites. Not only have we threatened the blitzkrieg hypothesis, but also the climatic explanation for extinction. For how can one appeal to an arid event at 6,000 years ago when an earlier event has survived unscathed? Moreover we have also threatened any hybrid model, which seeks to explain extinctions as a bit of climate with a bit of human interference, for humans were also on the spot when the dust blew 26,000 years ago.

Does all the work we have done leave us with no explanation for extinctions? Yes, for the Liverpool Plains. Certainly a crude explanation (in terms of climate, humans or both combined) will not work. I will therefore leave you with some speculation. Let us remember the important theoretical point, put forward by the proponents of humanly-induced extinction, whereby they ask what was new at the end of the Pleistocene. For the Liverpool Plains we must ask what was new after 6,000 years.

Two answers emerge. The first is the small-tool tradition, reasonably interpreted as an improved hunting technology. The other is the appearance of the dingo. Both events are thought to have happened around 5,000 years ago. It may well be hard to bring these events into archaeological focus and to relate them, in a mechanistic sense, to the process of megafaunal extinctions. Yet, over the next decade we shall seek to do just this in our field work.

As an audience you represent various disciplines in the natural sciences. I invite you to visit the critical sections we are establishing at our archaeological sites and to cast a constructive, if sceptical eye, over the diverse sorts of evidence we are uncovering. The question to which we are seeking answers is not scientifically trivial and certainly needs the attention of diverse experts. The cause of megafaunal extinctions is one of the most challenging ecological questions facing science in Australia.

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Aquatic Angiosperms in Coastal Saline Lagoons of New South Wales.

I. The Vegetation of Lake Macquarie

R. J. KING

KING, R. J. Aquatic angiosperms in coastal saline lagoons of New South Wales. I. The vegetation of Lake Macquarie. *Proc. Linn. Soc. N.S.W.* 109 (1), 1986: 11-23.

The distribution and relative abundance of the four aquatic angiosperms in Lake Macquarie have been mapped. The seagrasses occupied an estimated 14.17km^2 or 12.3% of the lake surface area with *Zostera capricorni* (11.57km^2) and *Halophila ovalis* (5.59km^2) most widespread. There were some 2.01km^2 of *Posidonia australis* in the central lake region nearest the ocean entrance. The halotolerant *Ruppia megacarpa* was found in small amounts, and only in Chain Valley Bay.

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INTRODUCTION

Barrier estuaries or estuarine lagoons are characteristic of much of the south-east Australian coast (Barnes, 1980). These barrier estuaries range in size from large estuaries such as Wallis Lake and Lake Macquarie, which are over 100km^2, to small estuaries on the south coast e.g. Wallaga, Merimbula and Pambula Lakes. All are characterized by narrow, elongated entrance channels with broad tidal and backbarrier sand flats (Roy, 1984). Away from these active channels the lakes are shallow, low-energy environments with the margins often densely covered by seagrasses.

Three of these barrier estuary systems (Lake Illawarra just south of Wollongong and Lake Macquarie and Tuggerah Lakes on the N.S.W. Central Coast) are of special interest. These lakes all support some commercial fishing and prawning, but are in areas of rapid urbanization with increasing recreational use. Proximity to major population centres and coal deposits has made these lakes suitable sites for steam-generating power stations (Fig. 1). All of these power stations use steam-driven generating units and lake water is continuously drawn from an inlet channel to cool the condensers.

This paper is part of a series reporting the results of a long-term study on the aquatic vegetation in the Central Coast lagoons. An introductory paper on *Zostera capricorni* in Illawarra Lake has already been published (Harris *et al.*, 1980). The broad aim of these studies is to provide detailed qualitative and quantitative data on the aquatic vegetation in these lakes, to monitor long term changes, and to assess the effects of cooling water discharges from the power stations.

LAKE MACQUARIE

Lake Macquarie (Fig. 1) is a large barrier estuary some 90km north of Sydney, and just south of the industrial city of Newcastle. The lake has a surface area of 110km^2 and an irregular foreshore of some 166km. It extends 22km in a north south direction and the maximum width is 9km. The easterly projection of Wangi-Wangi Point, and the western sandy shallows from Swansea divide the lake into two natural parts. The lake was formed by the inundation of coalescing river valleys, but the ocean entrance which was initially much wider is now narrow and shallow due to sand deposition (Baas Becking *et al.*, 1959). Roy (1984) considers that the lake represents a youthful stage of a barrier estuary with characteristic rocky and highly irregular shoreline. The average depth of

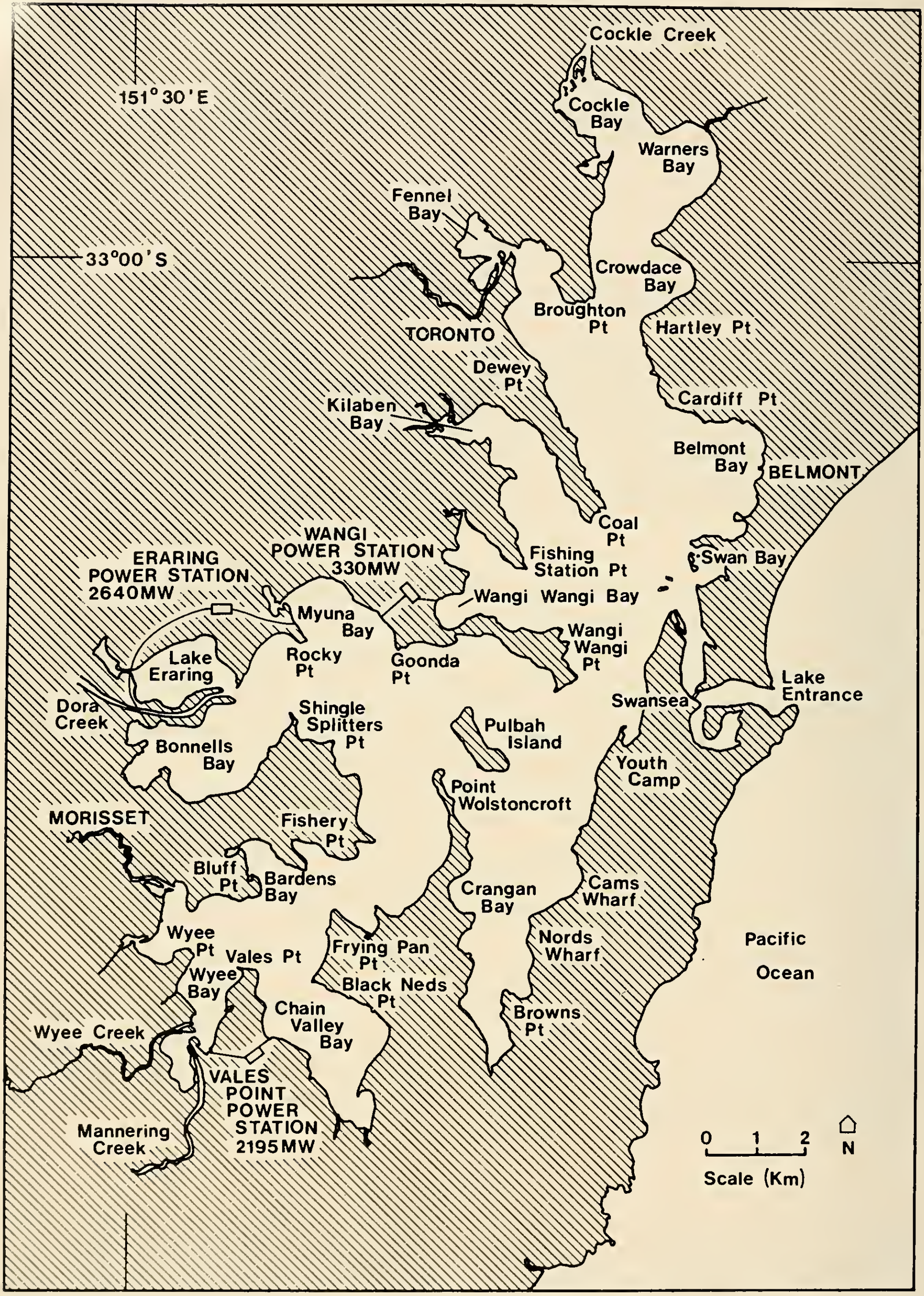

Fig. 1. Lake Macquarie, showing localities mentioned in the text and position of power stations.

the lake is 6.7m with a maximum depth of 11m east of Pulbah Island. At the entrance the spring tidal range is 1.25m but at the western end of the entrance channel it is only 0.15m. Average tidal range in the lake is only 6mm (State Pollution Control

Commission, N.S.W., 1983) and wind-induced currents are more important in producing water level changes (Roy and Peat, 1975). It is estimated that only one per cent of the lake volume is exchanged on each tidal cycle (State Pollution Control Commission, N.S.W., 1983) and salinity levels are thus highly dependent on catchment run-off and the flushing action of storm flows. Salinity is usually in the range 25-33.

PREVIOUS STUDIES

The seagrass communities of Lake Macquarie were first discussed in relation to an alleged depletion of fish (Wood, 1959a; MacIntyre, 1959). The former dealt with the seagrasses in only two pages and included a single map (scale approx. 1:180,000) showing the distribution of seagrasses within the entire lake. The latter made some cursory comments on seagrasses in relation to the benthic macrofauna. Since that time there have been a number of unpublished reports dealing with the seagrass distribution in various parts of Lake Macquarie, and often with specific reference to faunal community structure (State Pollution Control Commission, N.S.W., 1983). The only publications since Wood (1959a) surveying the total lake are those of Evans and Gibbs (1981) and West *et al.* (1985). Both surveys were based on aerial photographs.

The aim of the present study is to provide a detailed set of maps showing the present (1985) distribution and composition of the seagrass beds within Lake Macquarie with an indication of the relative contribution of the various species.

METHODS

The lake was surveyed during late February/early March (1985). Observations on the extent, pattern of cover and species composition of seagrasses were made by use of transects run perpendicular to the shoreline at intervals of 50-200 metres, depending on the uniformity of the vegetation. The transects were extended until the deepest limit of the vegetation was reached, or in some cases were continued to the opposite shoreline. The methods of observation included direct viewing from a boat, raking with a long-handled rake, snorkelling, and wading in very shallow areas. The methods used at any site depended on turbidity and depth. The distance from the shore was measured using a rangefinder [Rangematic MK5: Ranging Inc. for distances over 50m (accuracy 99% at 100m, 95% at 500m, 90% at 1000m) and a Ranging Optimeter 620 for shorter distances].

The distribution of seagrasses was plotted on maps at an initial scale of 1:25,000. Two subjective scales were used: a scale of abundance and a measure of growth or sociability. Each scale has three categories:

Abundance 1. Sparse growth (< 15% cover); 2. Moderate growth (15-50%); 3. Abundant growth (> 50%).

Sociability: a. individual strands or clumps; b. patches of growth up to 10m; c. beds of relatively even distribution.

Thus the designation of a weed bed as Z1aH2c indicates a mixed bed of *Zostera* (sparse in individual strands or clumps) and *Halophila* (moderate growth and relatively evenly distributed). The area covered by weed beds was measured from enlarged copies of the maps using an *Apple 2E* microcomputer coupled to a graphics tablet.

RESULTS AND DISCUSSION

This paper provides the basic distribution of seagrasses in Lake Macquarie in Summer 1985.

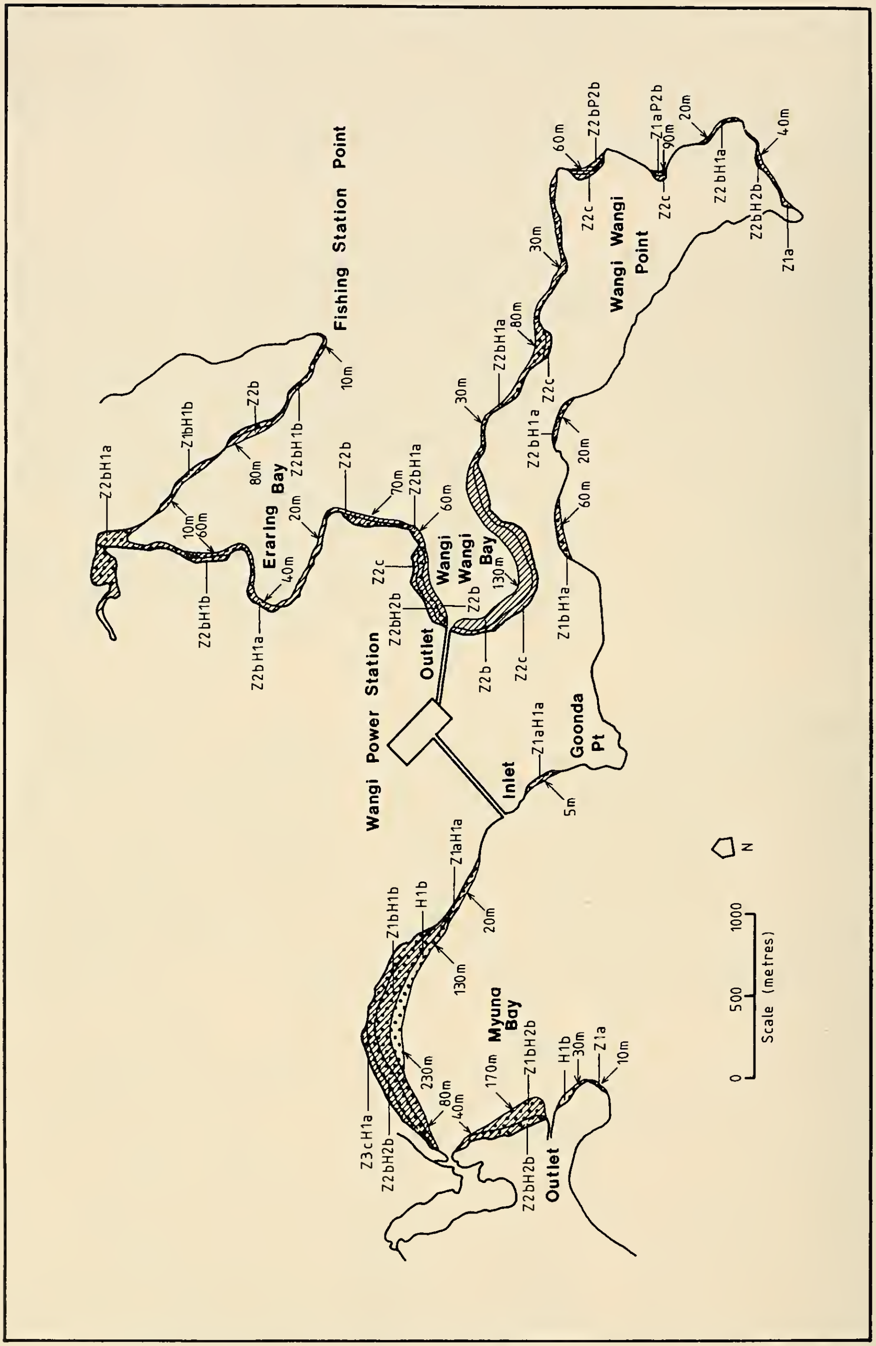

Fig. 2. Distribution of seagrasses in Lake Macquarie: Fishing Station Point to Rocky Point, western margin of lake.

Key to Figs 2-8:

Zostera ▧	*Halophila* ⁙	*Ruppia* ▨	*Posidonia* ▥

For key to abundance and sociability see text.

The results of the main survey are given in Figs 2-8. A full account of the survey is available in King (1986). The total area occupied by seagrass was 14.7km^2. The area occupied by each species, is presented in Table 1 along with information for the major regions and bays in the lake.

The magnitude and predictability of seasonal change and differences from year to year are discussed in King and Hodgson (1986). The data give some indication of the relative abundance of each species. For *Zostera capricorni* this information can be converted to estimates of total and above ground biomass (King and Barclay, 1986).

TABLE 1

Areas (km^2) of seagrasses in Lake Macquarie, survey of January-February 1985

	Reference figure	*Zostera*	*Halophila*	*Posidonia*	*Ruppia*	Total
Lake Macquarie (all areas)[1]		11.57	5.59	2.01	0.15	14.17
Myuna Bay (Eraring Outlet — Goonda Point)	2	0.25	0.29	—	—	0.29
Goonda — Fishing Station Point	2	0.47	0.26	0.01	—	0.48
Northern Lake (Fishing Station Point — Cardiff Point)	3 & 4	1.30	0.46	—	—	1.58
Central eastern (Cardiff Point — 'Youth Camp')	3	3.69	0.52	1.67	—	5.10
Crangan Bay ('Youth Camp' — Pt Wolstoncroft	5	1.05	0.31	0.02	—	1.07
Chain Valley Bay (Frying Pan Point — Vales Pt)	7	1.21	1.22	—	0.15	1.25
Wyee Bay inc. Mannering Bay	7	0.16	0.83	—	—	0.83
Wyee Point — Bluff Pt	7	0.62	0.60	—	—	0.74
Bonnells Bay (Shingle Splitters Point — Rocky Point)	8	2.00	1.08	—	—	2.00

[1] total includes several small areas not listed separately

There are three major species of seagrass in Lake Macquarie:

Zostera capricorni Ascherson is the only species of *Zostera* present. References by Wood (1959a) to *Z. muelleri* in Lake Macquarie are incorrect and result from the fact that Wood (1959b) did not appreciate the wide phenotypic variation which occurs in *Z. capricorni* (see Robertson, 1984).

Halophila ovalis (R. Brown) Hooker f.

Posidonia australis Hooker f.

In addition, the salt-tolerant genus *Ruppia* has been recorded. Following Jacobs and Brock (1982) this material is referred to *R. megacarpa* Mason.

Zostera capricorni was the most widely distributed and abundant of the seagrasses in Lake Macquarie. It covered 11.57km^2 or 10 per cent of the lake area either in monospecific stands, or mixed with other seagrasses. *Halophila ovalis* occurred in 25% of the area of *Zostera*. The largest *Zostera* beds are in Belmont Bay and the areas just south of the entrance. Only 12 per cent of *Zostera* occurs in the northern half of the lake. The values

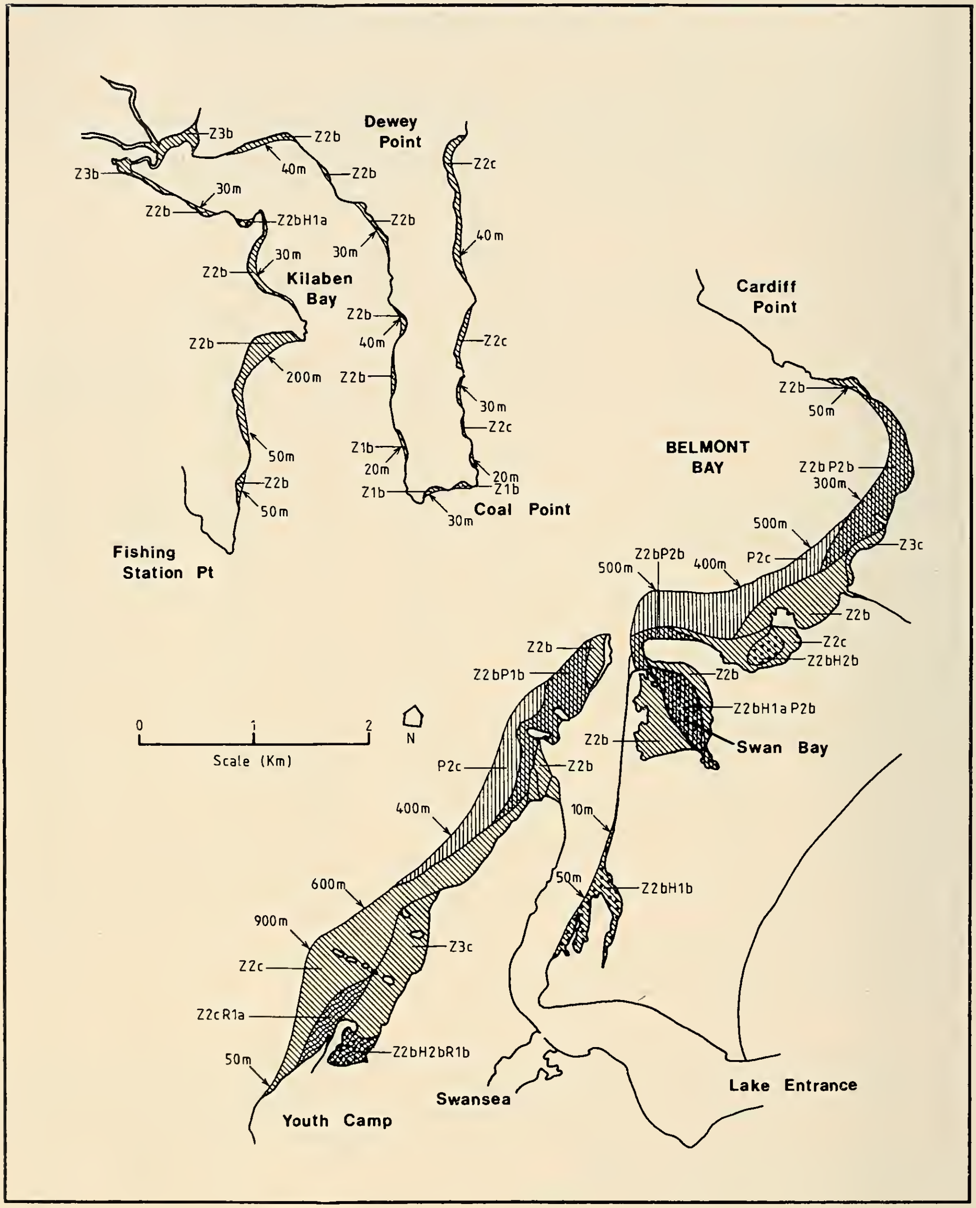

Fig. 3. Distribution of seagrasses in Lake Macquarie: central region of the lake: western margin (Dewey Point to Fishing Station Point); eastern margin (Cardiff Point to 'Youth Camp'). For key see legend to Fig. 2.

obtained in this study are comparable with data from West *et al.* (1985) and Evans and Gibbs (1981) (Table 2). In the latter study the total for all seagrasses was greater than in the present study but the area occupied by *Zostera* was estimated to be 12.24km^2, cf. 11.57km^2 here.

TABLE 2

Comparison of the areas of seagrasses in Lake Macquarie with values recorded in published surveys

Reference	Time of survey	Area of seagrass (ha)	Percentage of lake area[1]
Wood (1959a)	August 1953	2331	20
MacIntyre (1959)	August 1953	2548	22
Evans and Gibbs (1981)[2]	Aerial photographs: Nov., 1971; May, 1975 Field surveys: May, 1978	1788	15.5
West *et al.* (1985)	Aerial photographs: June, 1981 and March, 1982 (West, pers. comm)	1339	11.6
Present study[3]	Feb.-March (1985)	1417	12.3

Notes

1 Various estimates of lake area are available. Values calculated here are based on a mapped water area of 11511ha (West *et al.*, 1985).

2 Areas quoted for Lake Macquarie in Evans and Gibbs need to be increased by a factor of four (P. Gibbs; pers. comm). This correction has been applied to figures in the table above.

3 Lake Eraring was not included in this study but is included in all the other studies.

Halophila ovalis occurred over an area of 5.59km^2 often intermixed with *Zostera*. It was most common in shallow bays and especially in Mannering Bay and the southern end of Wyee Bay where it formed substantial monospecific beds. Evans and Gibbs (1981) reported only 0.55km^2 of *Halophila* in the lake but given the nature of their survey using aerial photographs it is likely that mixed beds were recorded as *Zostera* only, since the *Zostera* dictates the overall appearance of the beds. Wood (1959a) considered that *Halophila* was never in sufficient quantity to make it an important member of the seagrass community, a conclusion which is contradicted by the results obtained here.

Posidonia australis has a limited distribution and covered an area of only 2.01km^2, some 1.67km^2 on the eastern shore near the lake entrance. This compares with a total area of 0.53km^2 recorded by Evans and Gibbs (1981). It occurred alone in patches or beds of relatively even distribution offshore from *Zostera* and mixed *Zostera/Halophila* beds, with which it was sometimes interspersed (Fig. 3). There were small isolated patches of *Posidonia* in Crangan Bay just south of Cams Wharf; on the east side of Pulbah Island; and on the western lake shore of Wangi-Wangi Point.

Ruppia megacarpa was recorded in only 0.1km^2 in Chain Valley Bay, though Wood (1959a) showed *Ruppia* to be the dominant seagrass in backwaters (Mannering Bay and the southern portion of Chain Valley Bay) as well as the flats to the west of Swansea. The abundance of *Ruppia* shows great fluctuations in other coastal saline lagoons such as Smiths Lake and Tuggerah Lakes and this aspect is discussed in detail in King and Hodgson (1986).

In addition to aquatic angiosperms, benthic algae, especially *Gracilaria verrucosa* (Hudson) Papenfuss, *Microdictyon umbilicatum* (Velley) Zanardini and *Cystophyllum onustum* (Mertens) J. Agardh, may be locally abundant.

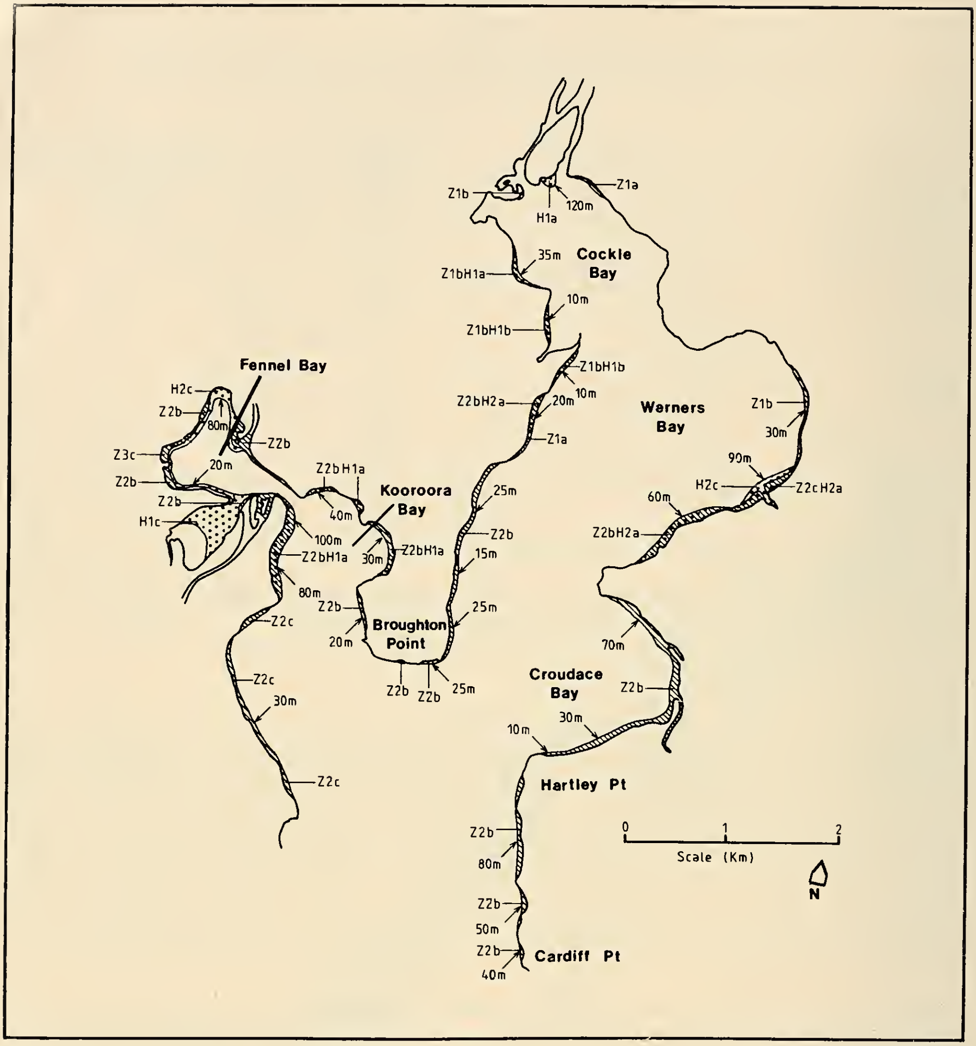

Fig. 4. Distribution of seagrasses in Lake Macquarie: northern portion of the lake (Dewey Point to Cardiff Point). For key see legend to Fig. 2.

The method of survey adopted in this study has proved to be very satisfactory for broad scale vegetation mapping and estimations of abundance. It has several advantages over mapping from aerial photographs:

- the surveys can be undertaken at an appropriate time, e.g. at the time of maximum biomass rather than based on photographs generally taken for some other purpose;
- species and mixed-species populations can be recognized at the time of survey, and hence changes within small areas will be recorded;
- measures can be made of species abundance as well as distribution. The scheme of recognizing three levels of abundance and three levels of sociability is far simpler than, for instance, a direct Braun-Blanquet type scale of 0-9 of the type used by Kirkman (1978). This is especially so where comparable results are required from different field workers.

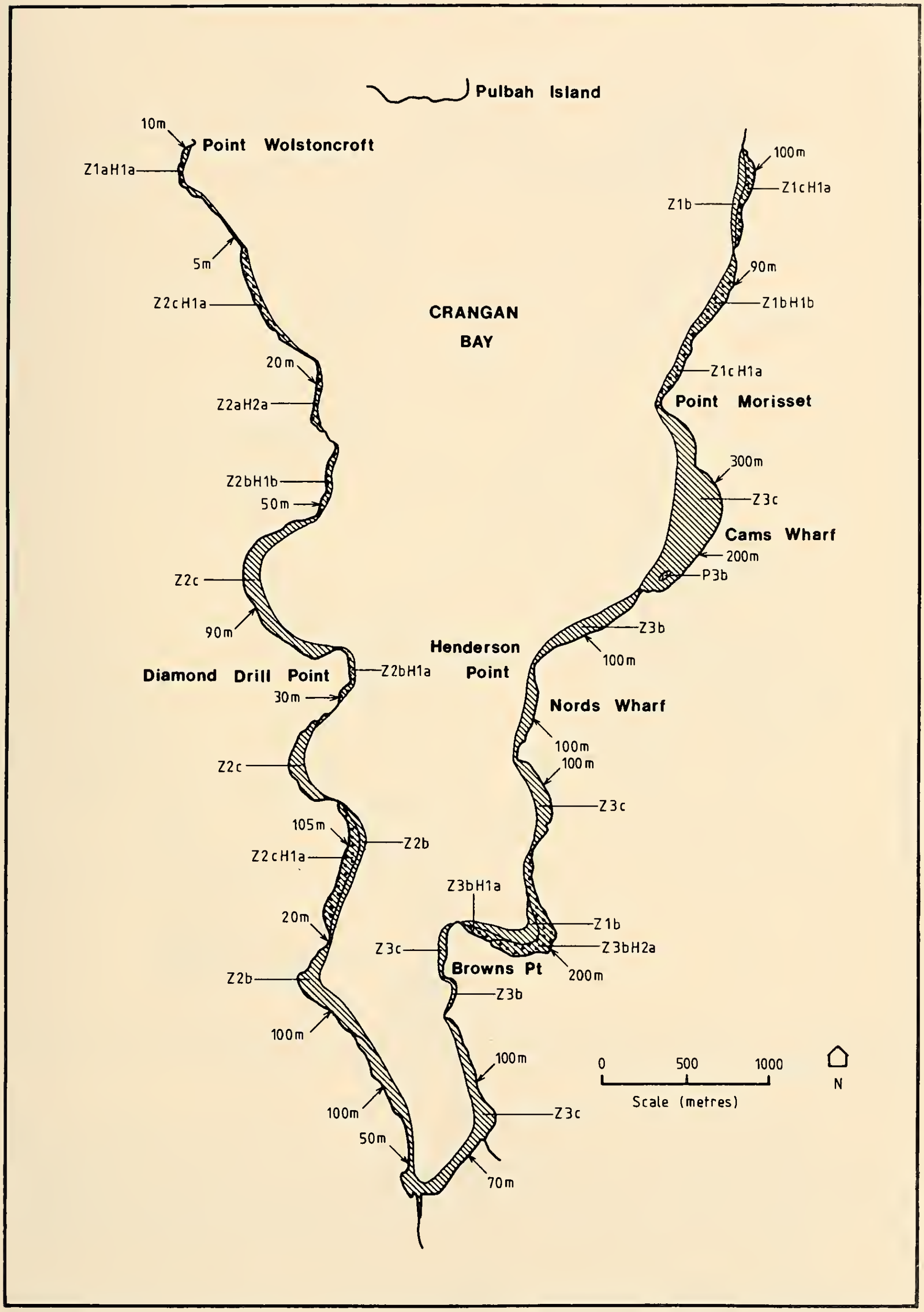

Fig. 5. Distribution of seagrasses in Lake Macquarie: southeastern section (Crangan Bay). For key see legend to Fig. 2.

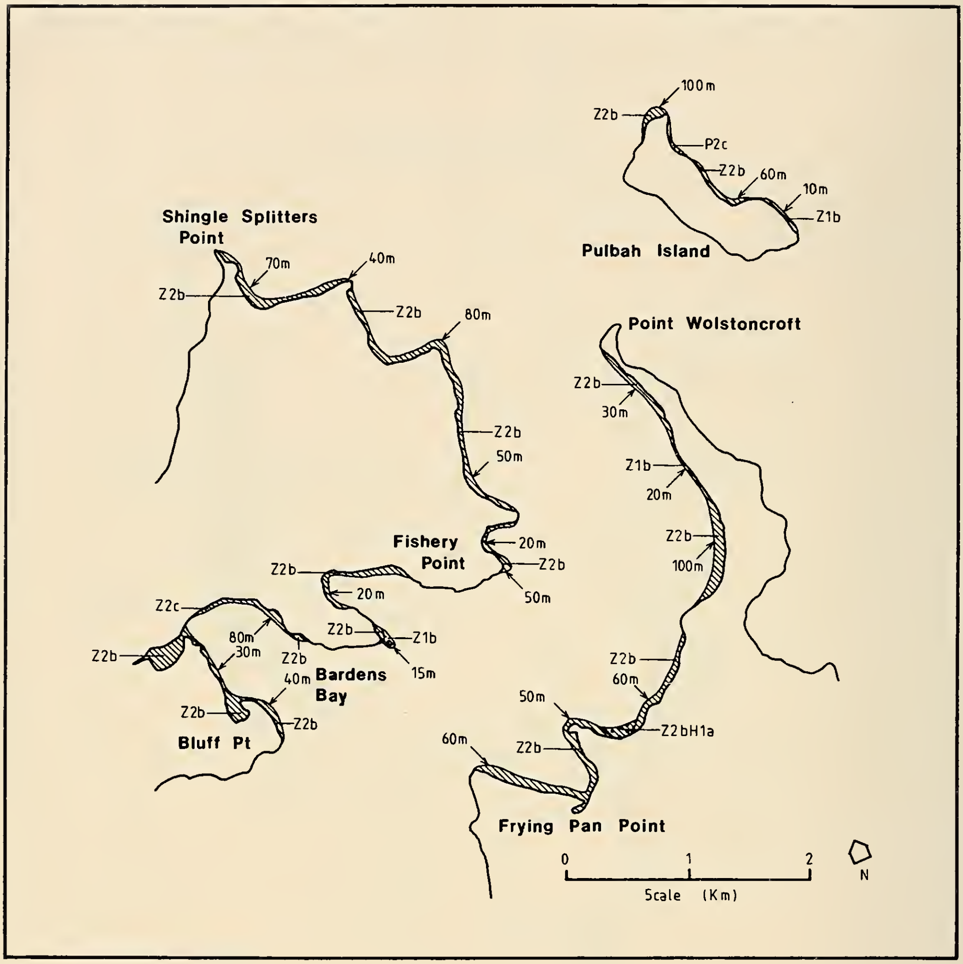

Fig. 6. Distribution of seagrasses in Lake Macquarie: southern region of the Lake (Point Wolstoncroft to Frying Pan Point and Bluff Point to Shingle Splitters Point). For key see legend to Fig. 2.

- since the accuracy of the final estimates of area occupied by seagrass is ultimately dependent on the scale of the original maps, this type of survey can be much more accurate. For example reading areas from maps of the scale of that in Wood (1959a) is impossible, even assuming that the map itself is reasonably accurate. The problem is compounded by the difficulty of measuring in areas where the seagrasses occur as narrow fringing beds. The provision of the absolute values for the width of the beds as in the present survey can be useful for later detailed comparisons in specific areas.
- the scale or intensity of the survey can be readily adapted to suit specific requirements of the user.

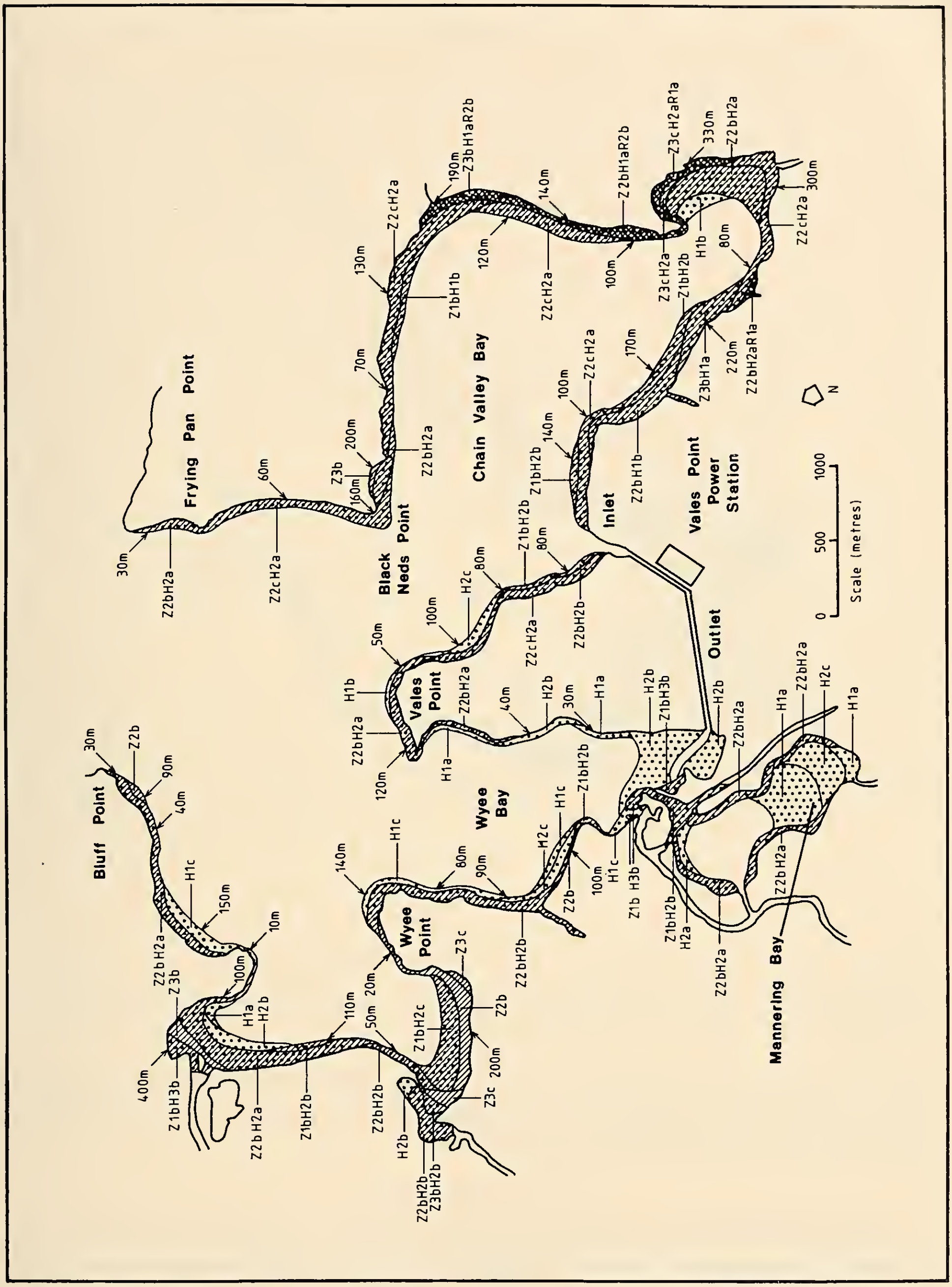

Fig. 7. Distribution of seagrasses in Lake Macquarie: southwestern portion of the lake (Wyee Bay and Chain Valley Bay). For key see legend to Fig. 2.

The methods adopted for surveys of seagrass beds will depend on the use to which the data will be put. Data to provide a base-line against which future change might be measured should be at least as detailed as this method allows. However there are still considerable problems with interpretation of changes over time (King and Hodgson,

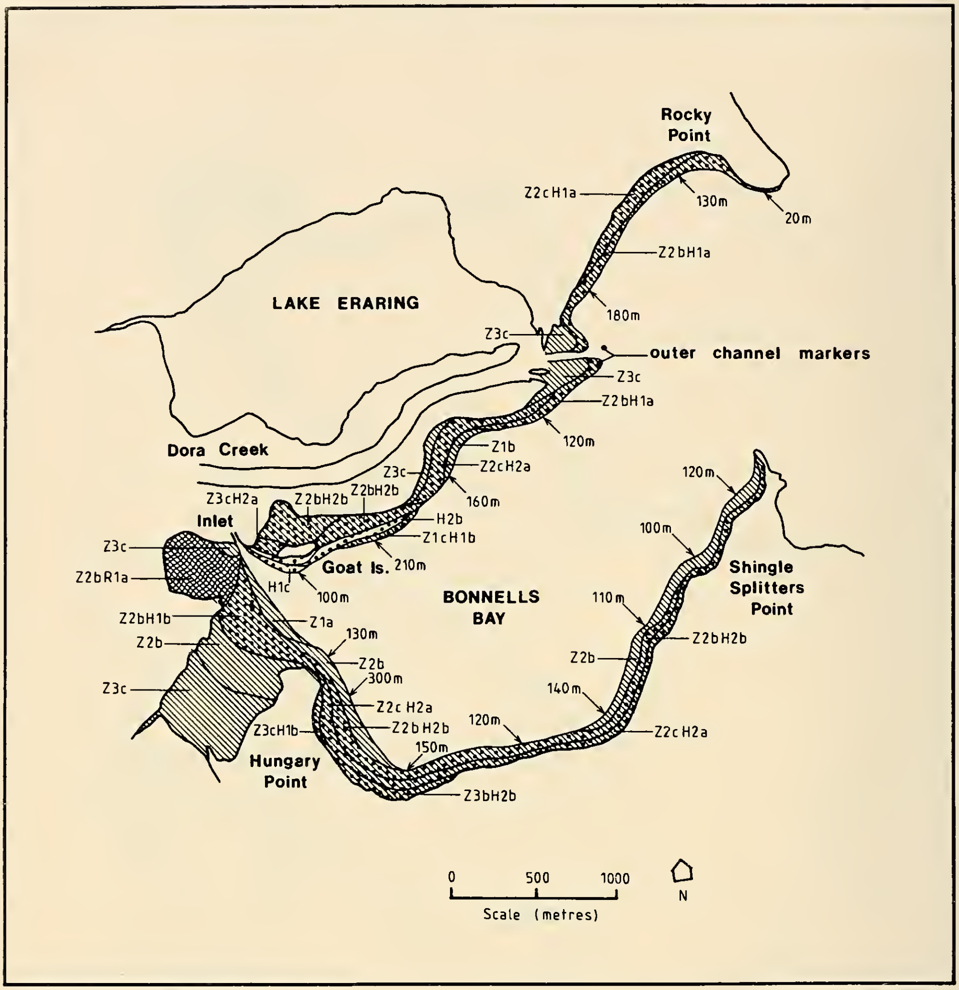

Fig. 8. Distribution of seagrasses in Lake Macquarie: western portion of the lake, Bonnells Bay (Shingle Splitters Point to Rocky Point). For key see legend to Fig. 2.

1986). The major disadvantage of the method used here is that it is time consuming. Hence it would be inappropriate to the provision of a broad scale inventory of seagrass resources of the type provided by West *et al.* (1985).

ACKNOWLEDGEMENTS

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I am pleased to acknowledge technical staff involved with this survey, N. Jacobs, S. McOrrie and L. G. Watson.

During the course of this project I have discussed many of the ideas with colleagues. I thank them all, particularly Dr P. Farrant, Dr P. Adam, and Dr B. Hodgson.

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Aquatic Angiosperms in Coastal Saline Lagoons of New South Wales.
II. The Vegetation of Tuggerah Lakes, with Specific Comments on the Growth of *Zostera capricorni* Ascherson

R. J. KING and V. M. HOLLAND

KING, R. J., & HOLLAND, V. M. Aquatic angiosperms in coastal saline lagoons of New South Wales. II. The vegetation of Tuggerah Lakes, with specific comments on the growth of *Zostera capricorni* Ascherson. *Proc. Linn. Soc. N.S.W.* 109(1), 1986: 25-39.

The distribution and relative abundance of the three aquatic angiosperms in the Tuggerah Lakes system have been mapped. The seagrasses occupy an estimated 19.11km^2 or 25% of the area of the lakes. *Halophila ovalis* occurs over an area of 10.40km^2 and *Ruppia megacarpa* over 8.24km^2. The growth rate of *Zostera capricorni* was measured in the field using a hole-punching technique. Growth rates measured over a year ranged from 0.8mg.shoot^{-1}.day^{-1} in winter to a summer maximum of 2.6mg.shoot^{-1}.day^{-1}. There were marked seasonal changes in the storage and use of starch in the rhizomes, from a maximum at the end of summer (226mg.g^{-1}dwt of rhizome) to a minimum value of 20mg.g^{-1} at the end of winter.

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INTRODUCTION

The aquatic vegetation of Tuggerah Lakes was surveyed by Higginson (1965) and some ecological effects of pollution documented (Higginson, 1971). Since that time there have been a number of detailed surveys of the aquatic vegetation of the lakes but these have not been published in full or in generally available literature. A single value for the area of seagrass beds is given by West *et al.* (1985).

This paper provides a full survey of the distribution of seagrasses in Tuggerah Lakes in summer 1985. In addition data are provided on the seasonal aspects of growth of *Zostera capricorni* Ascherson which is the most abundant marine angiosperm in the lakes. Basic data are provided on seasonal variation in shoot length, shoot weight, reproductive status and rhizome starch reserves. Seasonal change in the rate of growth of the vegetative shoot was estimated by the rate of production of new leaf tissue.

TUGGERAH LAKES

Tuggerah Lakes, approximately 100km north of Sydney on the east Australian coast (Fig. 1) are a series of three interconnected coastal lagoons: Lake Munmorah, 7.8km^2; Lake Budgewoi, 11.2km^2; Tuggerah Lake, 58km^2 (total area 77km^2) (Interdept. Comm., 1979). West *et al.* (1985) measured the water surface area at only 70.29km^2 and this reflects the shallow topography: a small fall in the lake level exposes much of the lake bottom especially on the Budgewoi Flats on the eastern margin of Lake Budgewoi. The lakes extend 16km in a north—south direction and 5km east—west with a perimeter of approximately 110km. The lakes are a barrier estuarine system at a relatively youthful stage (Roy, 1984) and are thought to have been formed by long shore currents building a series of sand bars across an indentation in the coastline. The eastern foreshores are thus of a sand-dune nature (Bird, 1984). The lakes are shallow, the average depth being

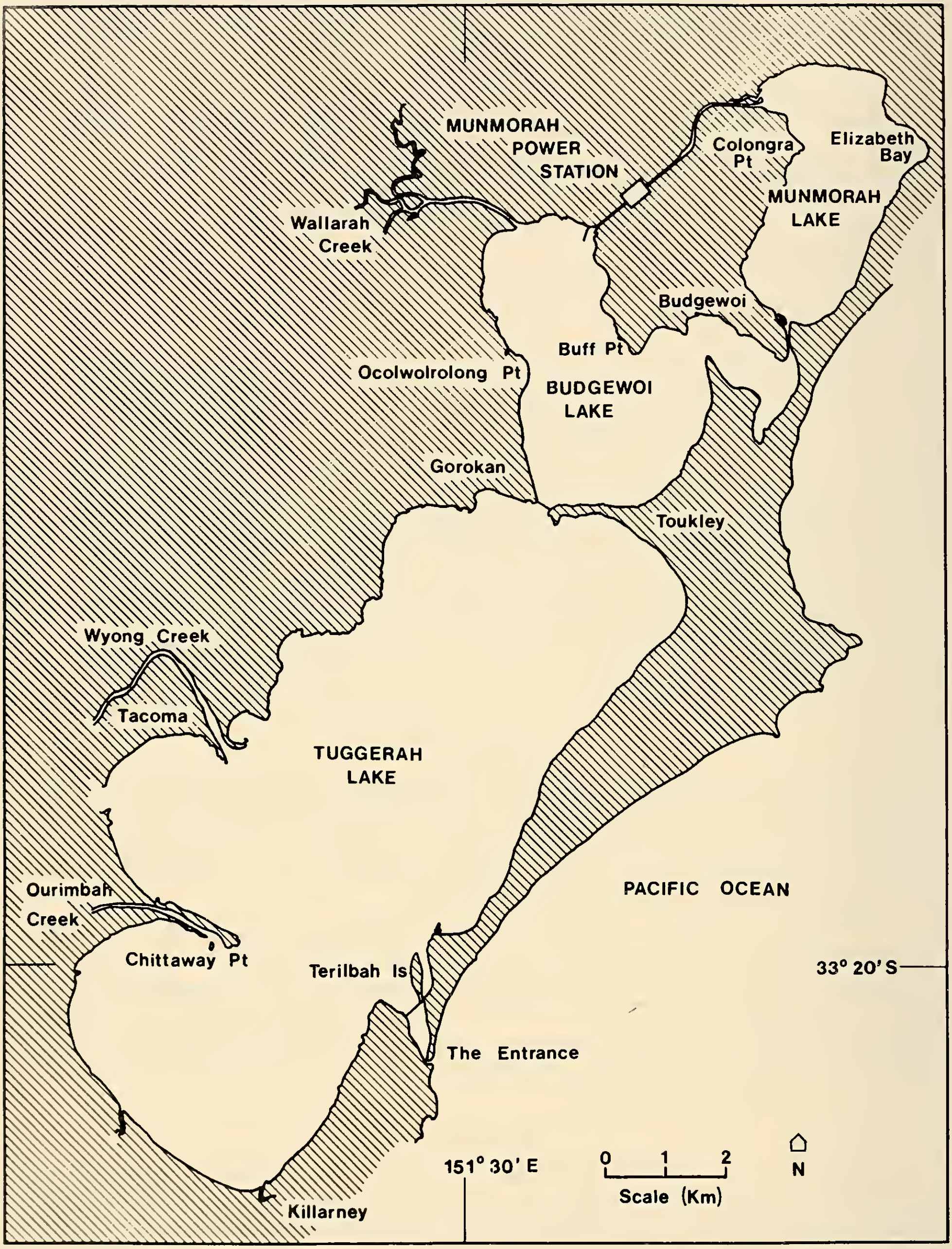

Fig. 1. Tuggerah Lakes showing localities mentioned in the text, and the principal study site for growth studies.

1.9m, and the greatest depth 4.9m under the Toukley bridge between Budgewoi and Tuggerah Lake. The lake system is connected to the sea by a narrow channel at 'The Entrance' and this connection is only rarely completely closed. Tidal flushing is low, with an exchange of only about one per cent of lake volume; tidal action within the lakes is negligible. Salinity is thus dependent on rainfall in the catchment of 670km^2

(Interdept. Comm., 1979). Salinity is generally in the range 17-28 though salinities as low as 5 after heavy rainfall, and 49 after drought, have been recorded (Higginson, 1971).

METHODS

A. *Seagrass distribution survey*

The seagrass distribution was surveyed and mapped using the method outlined in King (1986b), then plotted using the same scale: abundance [1= sparse growth, (<15% cover); 2= moderate growth (15-50%); and 3= abundant growth (>50%)] and sociability [a= individual strands or clumps; b= patches to 10 m; and c= beds of relatively even distribution].

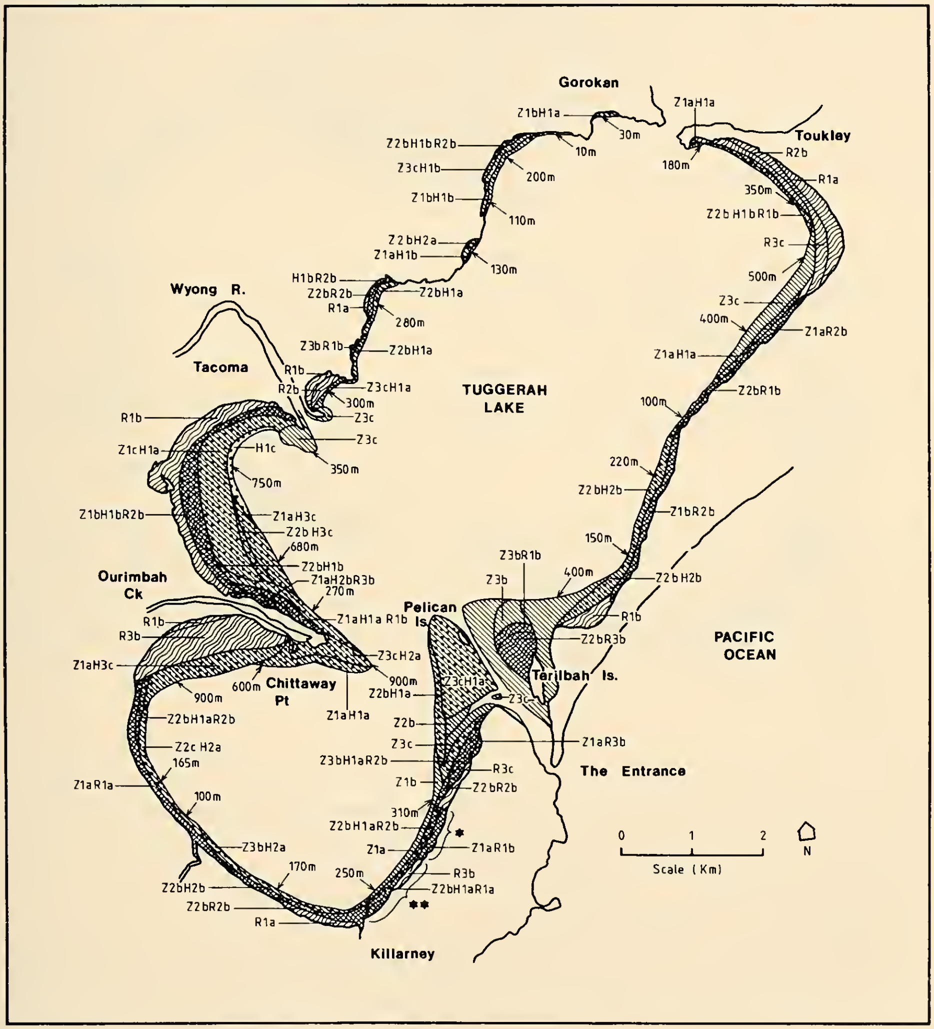

Fig. 2. Distribution of seagrasses in Lake Tuggerah.

▧ *Zostera* ▒ *Halophila* ▨ *Ruppia*

For key to abundance and sociability see text.

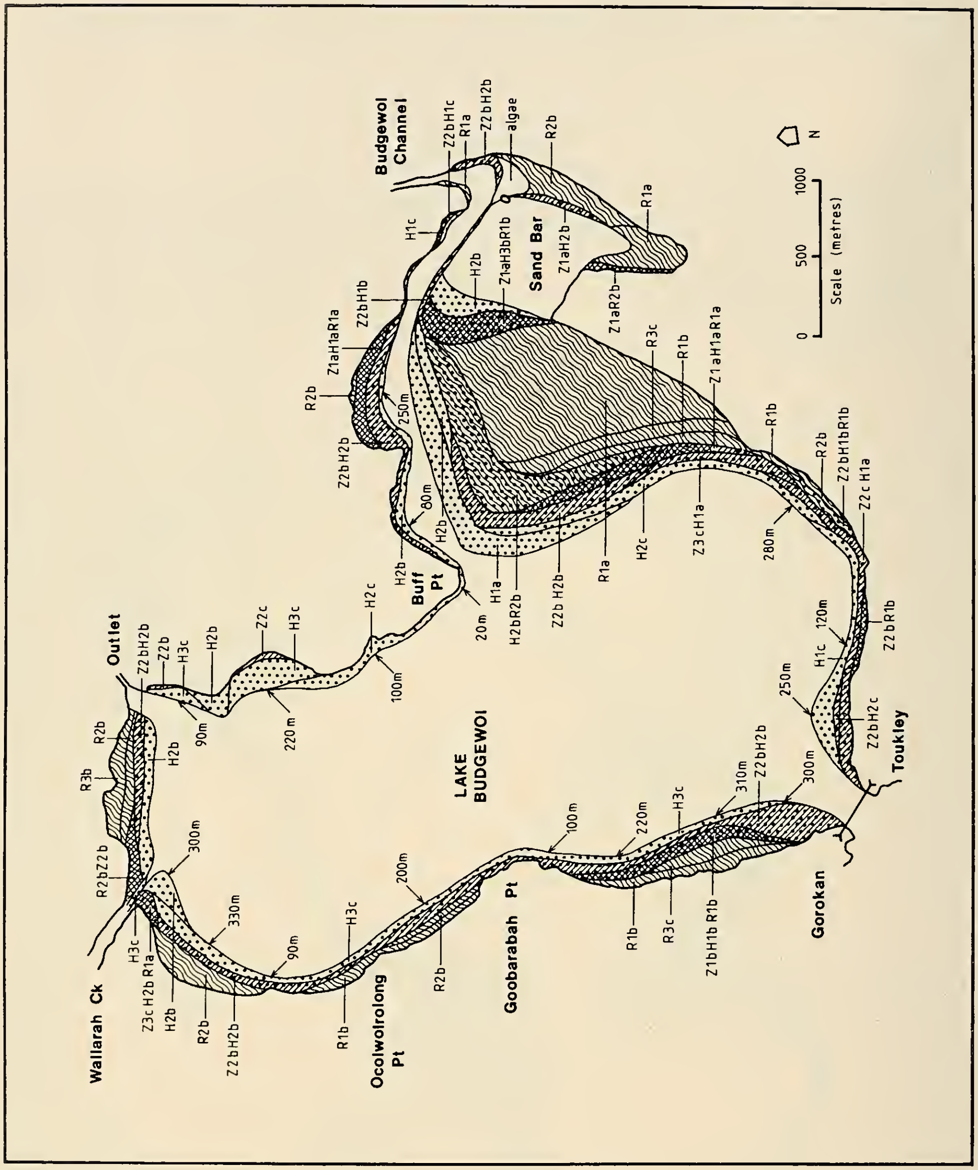

Fig. 3. Distribution of seagrasses in Lake Budgewoi (see legend for Fig. 2).

B. *Seasonal studies on* Zostera capricorni

Study site:

The principal study site for seasonal growth studies was located in a depth of 0.5m in the northwestern end of Lake Munmorah. This site was selected as representative of relatively undisturbed *Zostera* beds. It was well beyond the thermal influence of the Munmorah power station and urban pressure in terms of housing construction, and hence increase in siltation and nutrients, is low. There is little recreational use of these shallow flats. Extensive beds of *Zostera capricorni* up to 500m wide, in some places mixed with *Halophila ovalis*, occurred in this area of the lake (Fig. 4).

1. Leaf growth

Leaf-blade growth rates were estimated using a modification of the leaf-marking technique of Zieman (1974). In these experiments the datum mark in a shoot was a small hole punched through the group of leaves using a pair of 'tongue forceps', the prong of which had been ground to a sharp point. The scissor-like instrument minimizes damage to the leaf blade, which is not crushed. In a preliminary experiment to test the use of this method, holes were punched along the *Zostera* leaves at 2cm intervals, the first hole being about 2mm from the shoot — rhizome junction. The plants were then grown in perspex tanks in a growth cabinet at 25°C for 7 days. Individual leaves on each shoot were then examined to determine possible effects of the marking method, elongation between successive holes, and the relationship between leaf age and elongation rate.

Growth experiments were carried out at 2-month intervals (Oct. 1978 — Feb. 1979) and then at monthly intervals from March 1979 to February 1980. Samples of the *Zostera* were collected from the study site using a 20cm corer, 'planted' in plastic containers, marked and returned to the field. Plants were then harvested after an interval of 12 days and the dry weight (constant weight at 105°C) obtained for new tissue and leaf material above the datum mark. All epiphytes were removed. Growth rates were calculated as increase in biomass per shoot, per day. Each growth experiment was replicated four times.

2. Population data

The following data were obtained in conjunction with the growth experiments:

Shoot length — the length of the longest leaf on each of 50 randomly-selected intact shoots was measured.

Shoot weight — data on shoot weight were obtained directly from the leaf growth study.

Reproductive shoots — only vegetative shoots were used in the calculation of growth rates. The frequency of reproductive shoots was estimated for all core samples.

3. Rhizome starch reserves

Living rhizome segments were collected from September 1978 to February 1980. Each sample consisted of segments from 10-15 plants. The rhizome segments were washed free of sediment, the roots and shoots were removed, and the samples were then frozen and stored at -15°C until extraction. The quantity of starch in the rhizomes was determined using the extraction and assay procedure of Hassid and Neufeld (1964).

RESULTS

A. *Seagrass distribution*

Three aquatic angiosperms occurred in the Tuggerah Lakes in sufficient amounts and widely distributed enough to be mapped at the scale used. These were *Zostera capricorni* Ascherson; *Halophila ovalis* (R. Brown) Hooker f.; and *Ruppia megacarpa* Mason. The maps constructed from the vegetation survey are presented as Figs 2-4. A full copy of the survey is available in King (1986a). The total area occupied by seagrass was 19.11km^2 and the area occupied by each species is presented in Table 1. Data are given separately for each lake in the Tuggerah Lakes system, as well as for the Budgewoi Flats region.

B. *Seasonal studies*

Preliminary growth studies

In the preliminary experiments on material grown in the growth cabinet all leaf elongation occurred within 4cm of the shoot base. Over 90% of growth occurred in the

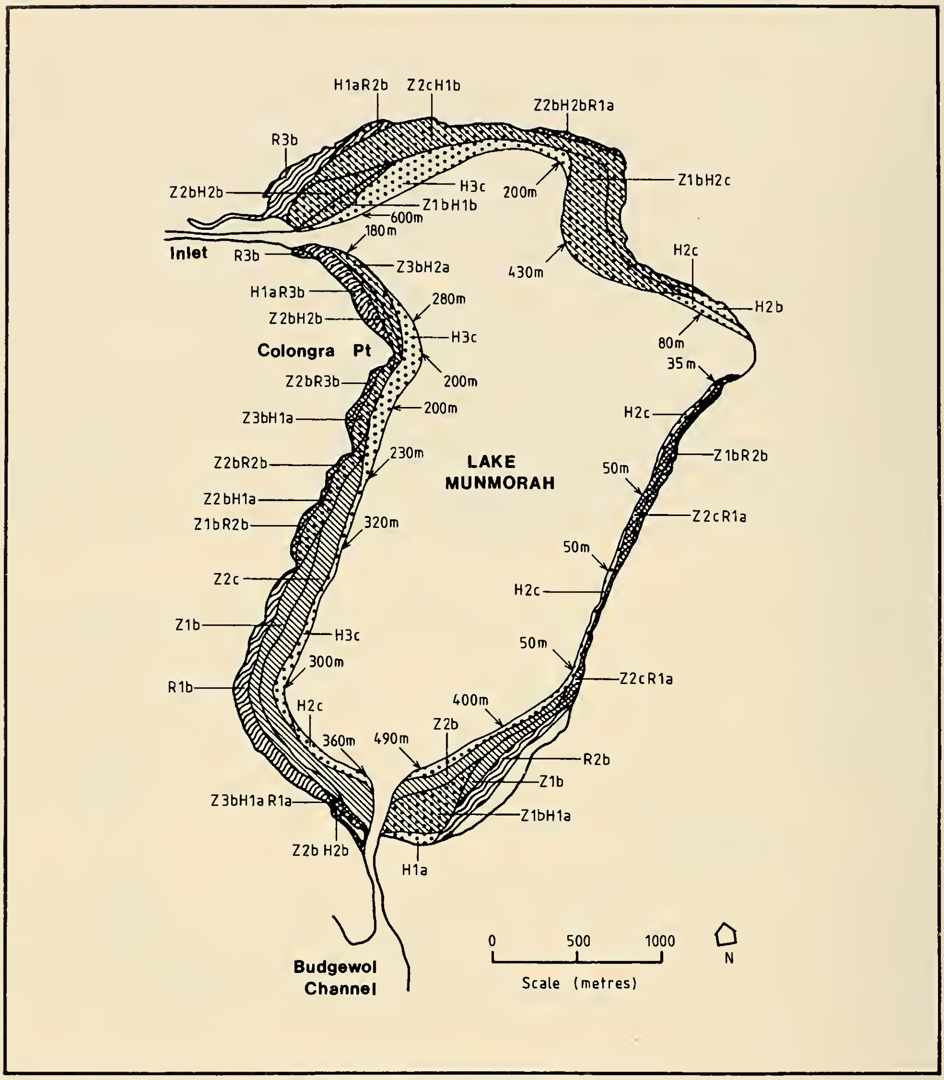

Fig. 4. Distribution of seagrasses in Lake Munmorah (see legend for Fig. 2).

TABLE 1

Areas (km^2) of seagrasses in Tuggerah Lakes, survey of January-February 1985

	Zostera	*Halophila*	*Ruppia*	Total area of seagrass
Tuggerah Lakes (all areas)	12.26	10.40	8.24	19.11
Tuggerah Lake	9.58	6.43	5.48	12.69
Budgewoi Lake	1.19	2.49	2.22	4.03
Budgewoi Flats (within L. Budgewoi)	0.59	1.34	1.71	2.63
Lake Munmorah	1.49	1.48	0.54	2.39

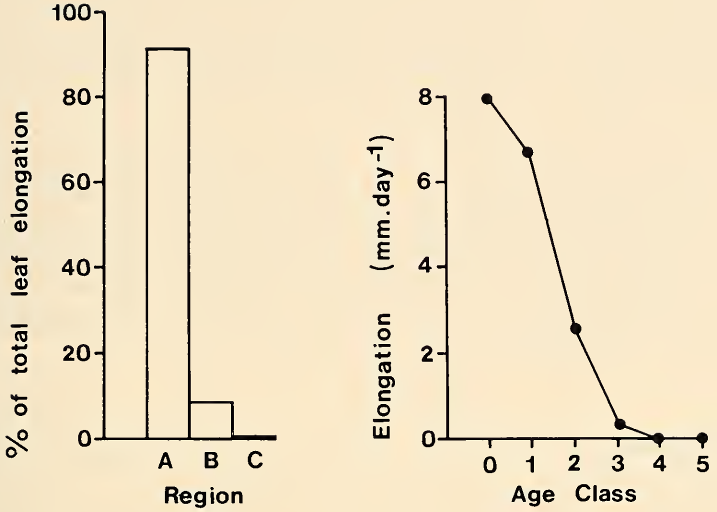

Fig. 5. a (left), Elongation between successive holes in *Zostera capricorni.* A represents the growth below the datum (0 cm), B (0-2 cm), C (2-4 cm) and D (above 4 cm). **b** (right), Elongation rates of leaves of different age classes. The youngest marked leaf is referred to age class 1; leaves arising during the course of the experiment as age class '0'.

region below the first hole (at 2mm) and 99.5% below the 2cm datum mark (Fig. 5a). A datum mark 2cm from the base was selected therefore for use in all further experiments. The number of leaves per shoot varied from 3 to 6, and the rate of growth was directly related to leaf age (Fig. 5**b**). Leaves which arose during the harvest interval are indicated as age class '0', and the elongation rate was estimated on the assumption that these new leaves were present on average for half the experimental growth period (Sand-Jensen, 1975).

Leaf growth

The growth rate of new leaf tissue ranged from 2.6 ± 0.5mg. shoot^{-1}.day^{-1} in summer to 0.8mg. shoot^{-1}. day^{-1} in late autumn (Fig. 6). Leaf tissue production was closely related to the weight of the shoot. Shoot viability, (i.e. the percentage of shoots alive at the end of the harvest interval) was generally high (90-100%) except in November and December 1979 when it was 72 and 57% respectively.

Population data

Shoot length

Mean shoot length was at its lowest in late summer, and it ranged from 22.7 ± 0.8 cm in March to a winter maximum of 53.9 ± 1.8cm in July (Fig. 7). Analysis of variance showed that monthly differences were significant ($P < 0.005$) and application of Tukey's test (Zar, 1974) showed that a difference in shoot length of 7.3cm was statistically significant.

Shoot weight

Mean weight of shoots was highest in January 1980 (251 ±12mg. shoot^{-1} and lowest in May 1979 (89 ± 8mg. shoot^{-1}). The data are plotted in Fig. 8.

Reproductive shoots

Flowering commenced in October 1978, and in 1979 in early August. Seed set occurred soon after flowering and in both years reproductive shoots persisted in the population until December. The density of flowering shoots (shoots.m^{-2}) differed markedly in the two years: in 1978 densities of 188 (Oct) and 113 (Dec) were recorded and for the months Aug-Dec 1979 densities were 24, 63, 90, 35, and 31 respectively.

Rhizome starch reserves

Starch made up to 22.6% of the dry weight of the rhizome of *Zostera capricorni*, and there was a marked seasonal change in the quantity stored (Fig. 9). There was a rapid build up in summer with a maximum value of 226mg.g dwt^{-1} in February 1979 and a decline in autumn to a minimum of 20mg.g dwt^{-1}. The method of starch extraction was accurate but time consuming and therefore replicate samples were analysed in only four months. The variability between replicates in these samples was low (coefficients of variation between 7.1 and 18.2%).

DISCUSSION

A. *Seagrass distribution*

In this survey seagrasses were recorded as covering 19.11km^2 or 25% of the area of Tuggerah Lakes. *Zostera capricorni* was the most widely distributed seagrass occurring over 12.26km^2 or approximately 16% of the lake area. *Halophila ovalis* occurred over 10.40km^2 (14%) and *Ruppia megacarpa* over 8.24km^2 (11%). The only other recent figure is that of West *et al.* (1985) who estimated from aerial photographs that seagrass covered 11.62km^2 of the whole lake system. This considerably lower area may result from the fact that *Halophila* beds were not detected from aerial photographs whereas *Zostera* which forms conspicuous beds was. Also West *et al.* (1985) measured a surface area for the lakes 6.7km^2 less than that in the Interdept. Comm. (1979). If this represents a real difference due to the lowering of the water level in the lakes this reduction would be in the marginal area normally occupied by seagrasses, and particularly the Budgewoi Flats would have been not included.

The areas of seagrass recorded in this survey are considerably lower than those found by Higginson (1965; 1968). The areas of seagrass which he recorded in 1963, 1965 and 1966 were 42%, 31% and 28% of the lake area respectively. Not only has the area occupied by seagrass decreased but also the relative importance of the different species. Higginson's maps, based on a survey in May 1963 (Higginson, 1965), showed Lake Budgewoi almost filled with seagrass (76.2% of lake covered cf. 36% in the present study). The whole central region was occupied by *Ruppia* (42% of the lake area). *Ruppia* was also dominant in deeper water in the southern part of Lake Tuggerah so that approximately one-third of the beds were *Ruppia*-dominated communities. By 1966 there was no *Ruppia* in the lake system (Higginson, 1968). The results presented here show that *Ruppia* had again become established in Tuggerah Lake but it was not found in deeper water; rather in shallow areas inshore of the *Zostera* beds. The places where *Ruppia* was dominant were west of Chittaway Point and just south of Toukley in Tuggerah Lake, and on the Budgewoi Flats. The central portion of each of the three lakes was devoid of seagrasses. Details of long period changes in the vegetation are discussed in King and Hodgson (1986).

B. *Seasonal Studies*

The modification of Zieman's (1974) method of measuring seagrass leaf growth was shown to be an appropriate method.

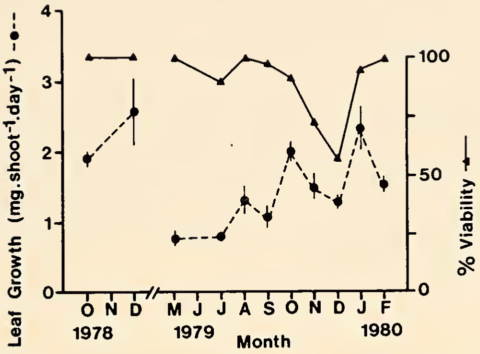

Fig. 6. Seasonal changes in leaf growth recorded on *Zostera capricorni* in the field. Data for early 1979 lost due to vandalism.

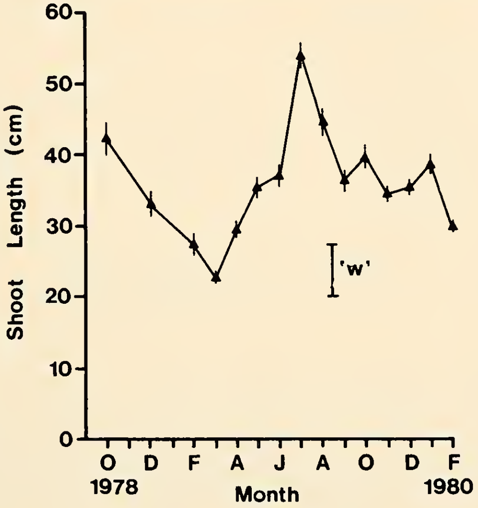

Fig. 7. Seasonal variation in mean shoot length of *Zostera capricorni.* The standard error is shown; the vertical bar (Tukey's 'W') represents a significant difference in shoot length of 7.3 cm.

In the seagrass genera *Thalassia, Posidonia* and *Zostera* the leaf-initiating meristem is at the base of the shoot, just above the rhizome. The meristem is enclosed and protected by the older leaves and leaves are produced distichously from the leaf primordium (den Hartog, 1970). Measurement of leaf growth by marking leaves (Zieman, 1974) assumes that vegetative growth occurs only at the base of the shoot, below a fixed point — the datum mark. Growth involves both the production of new cells and their subsequent expansion, and these two processes are spatially separated. Growth measured as increase in size or weight is mainly due to the process of cell expansion, which occurs in an area adjacent to the meristem (Preston, 1974). In *Zostera* this zone occurs immediately above the meristem and results principally in elongation, since leaf width changes very little during growth (Mukai *et al.*, 1977). This means that leaf growth can be estimated by measuring the single parameter of leaf length, but it is imperative that holes are punched above the zone of cell expansion.

Preliminary experiments indicated that a point 2cm above the shoot—rhizome junction was appropriate as a datum as 99.5% of leaf growth elongation occurred below this point. No deleterious effects due to the hole-punching technique were observed, and all shoots remained healthy over the seven day harvest interval. The holes, though small, were easily located in all leaves. There are advantages in using a punched hole rather than other datum marks such as staples. All leaves can be marked simultaneously, increasing both accuracy and speed. Also the datum mark can be placed below the ligule, through the sheath. In *Zostera* the younger leaves are successively enclosed by the leaf sheaths of older leaves and this restricts alternative types of datum marks to areas above the sheath (Sand-Jensen, 1975). This creates difficulties because of the need to estimate the growth of new unmarked leaves.

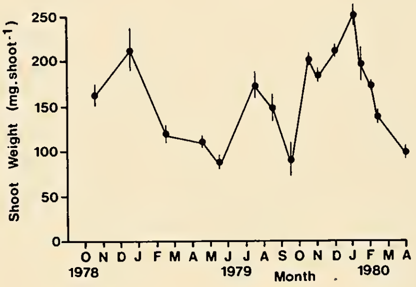

Fig. 8. Seasonal variation in the mean shoot weight of *Zostera capricorni* (± standard error).

In studies of the leaf growth of *Posidonia australis* in altered salinity, Tyerman *et al.* (1984) showed that damage to the leaf sheath killed or inhibited leaf growth. In the present experiments the hole made by the tongue forceps is small and the sheath may reseal. Certainly, there was no visible damage, but it is possible that all new leaf growth was inhibited.

The comparison of growth rates of *Zostera* measured here with those measured in other studies on seagrasses is hampered by the lack of uniformity in the units in which growth rates are expressed, coupled with the fact that the magnitude of the differences is a function of the unit in which growth is measured. In Table 2 data from Botany Bay and Port Hacking are summarized. In so far as generalizations may be drawn from such data one can conclude that the relative differences in growth rates between summer and winter are similar at all these study sites and that even though the measures of relative growth rate are calculated on different bases they are comparable.

The viability of shoots was low during November and December (Fig. 6) and this is reflected in a reduced growth rate during the period.

The range of shoot lengths (22.7cm, late summer—53.9cm in winter) is comparable to that reported by Larkum *et al.* (1984) for *Zostera capricorni* in Botany Bay except that there the pattern is virtually the reverse with a maximum of 45cm in late summer and a minimum of 17.2cm in winter. A similar pattern to that found by Larkum *et al.* (1984) in Botany Bay was reported by Harris *et al.* (1980) for Lake Illawarra, and by Higginson (1968) for Lake Budgewoi. The length of the longest leaves has been used to indicate the seasonal growth cycle (Harris *et al.*, 1980) and the marked seasonal die back which is reported to occur in winter (Wood, 1959b; Larkum *et al.*, 1984). Comparison of the data on maximum shoot length with the leaf growth rates presented above makes it clear that in this case there is no relationship between the two. If *Zostera capricorni* were always to show the marked seasonal fluctuations reported by Wood (1959b) the relationship might be expected but rapid changes in seagrass beds may be caused by factors other than normal seasonal ones, e.g. heavy rainfall (Harris *et al.*, 1980), depredation by swans (Wood, 1959a,b), and wave damage (Kirkman *et al.*, 1982). These factors may be more important in shallow protected lakes such as Lake Munmorah than in open bays, such as Botany Bay. In Lake Illawarra full leaf development has been maintained in some years into early spring, by which time new leaf growth had commenced. Given this it would be better to use the leaf length frequency rather than longest leaf length to establish comparative growth rates (see for example Kirkman *et al.*, 1982).

TABLE 2

Comparative Data for Zostera capricorni *on the New South Wales Coast*

	Summer	Winter
Tuggerah Lakes (present study)		
Measured shoot growth mg. shoot^{-1}.day^{-1}	2.6	0.8
Calculated growth rate* g. g^{-1}.day^{-1}	0.0104	0.0089
Botany Bay (Larkum *et al.*, 1984)		
Leaf growth cm. day^{-1}	1.62	0.38
'Proportional growth rate' g. g^{-1}.day^{-1}	0.0308	0.0213
Production rate g. m^{-1}.day^{-1}	8.92	1.37
Calculated shoot growth** mg. shoot^{-1}.day^{-1}	4.1	0.8
Port Hacking (Kirkman *et al.*, 1982)		
Production rates g. m^{-1}.day^{-1}	2.5	0.3
'Relative growth rate' g. g^{-1}.day^{-1}	0.028	0.014

* rate calculated using mean shoot biomass data for Munmorah Lake.
** rate calculated on the basis of mean shoot density.

The data on vegetative shoot weights are not directly comparable with other published data where biomass is generally expressed on the basis of area. Conversion of the data in Larkum *et al.* (1984) gives values ranging from 36mg. shoot^{-1} in winter to 133mg. shoot^{-1} in summer (cf. 89 and 251 in this study). On the basis of average shoot weights the growth rates in the present studies can be expressed in g.g.$^{-1}$.day^{-1} and thus be compared with the proportional growth rate of Larkum *et al.* (1984). The values obtained are 0.0089 in winter (comparable values for Botany Bay and Port Hacking 0.0213 and 0.008 respectively) and 0.0104 in summer (0.0308 and 0.035). The relative similarity between the rates for summer and winter obtained in this study reflects the less marked seasonal change in above ground biomass compared to that in the other two studies.

Zostera capricorni commences flowering in spring or early summer. Various times for flowering appear in the literature (November — Wood, 1959b; September — Harris *et al.*, 1980; Larkum *et al.*, 1984). In 1978 flowering commenced in October but in 1979 it commenced in early August. The factors initiating flowering have not been investigated but they are possibly related to temperature. In 1979 winter temperatures were relatively mild with the lowest temperature being 13.8°C in July, whereas Electricity Commission data show a minimum generally in the range 11-12°C. Studies on the northern hemisphere *Zostera marina* have implicated temperature in anthesis and seed production (Setchell, 1929; McRoy, 1970; Churchill and Riner, 1978) though Jacobs (1979) suggested that light intensity may be the controlling factor.

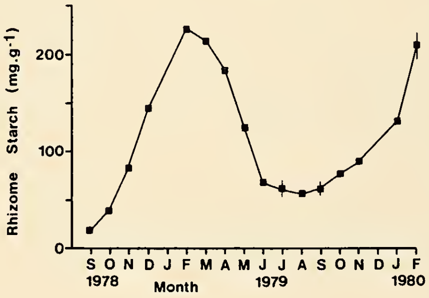

Fig. 9. Seasonal variation in the quantity of starch in the rhizomes of *Zostera capricorni*.

The data on the prevalence of flowering are of the same order as those of Larkum *et al.* (1984) who recorded up to 312 flowers.m^{-2}. The presence of reproductive shoots is apparently not related to the 'success' of *Zostera capricorni* in the Tuggerah Lakes, since establishment from seedlings has not been observed.

The principal storage product in seagrasses is starch, and starch grains are prominent in the cortical cells of rhizomes of *Zostera capricorni* (Fig. 10). Soluble carbohydrates, principally sucrose, are also found in quantity in both the rhizomes and leaves of seagrasses. Drew (1980) reported that *Zostera capricorni* leaves contained 4.7% sucrose, 1.6% myo-inositol and 0.4% fructose while the rhizomes contained 17.1% sucrose.

The extraction method used here (Hassid and Neufeld, 1964) produces a pure starch fraction. This represents stored reserves which need to be enzymatically mobilized before they are available to the plant. Rapid incorporation of starch occurred in summer (approx. 1.5-2.0mg.g^{-1}.day^{-1}) leading to a maximum in early autumn after which the shoot weight began to decline. During autumn and winter the starch level fell rapidly, presumably due to mobilization and use of the reserves by the plant. This fall in the quantity of starch occurred at the same time as the seasonal drop in light intensity and temperature.

Marked seasonal changes in the quantity of both soluble and insoluble carbohydrates are known especially in alpine plants where high levels are essential to initiate rapid growth in the spring growing season (Mooney and Billings, 1960; Bannister and Ward, 1981). The seasonal pattern in aquatic plants differs with low levels of carbohydrates in the rhizomes during winter/spring with rapid incorporation during summer (Haag and Gorham, 1977; Dawes and Lawrence, 1980; Livingston and Patriquin, 1981). The reserves accumulated in summer allow the species to survive low winter light intensities (Dawes and Lawrence, 1980). A comparable situation has been demonstrated in Arctic kelps (Chapman and Lindley, 1980). Defoliation studies with the tropical seagrass *Thalassia testudinum* suggested that rhizome reserves also support leaf-blade regeneration (Dawes and Lawrence, 1979) and Drew (1980) has shown the utilization of endogenous soluble carbohydrates, especially sucrose, by *Zostera angustifolia* leaves starved in the dark.

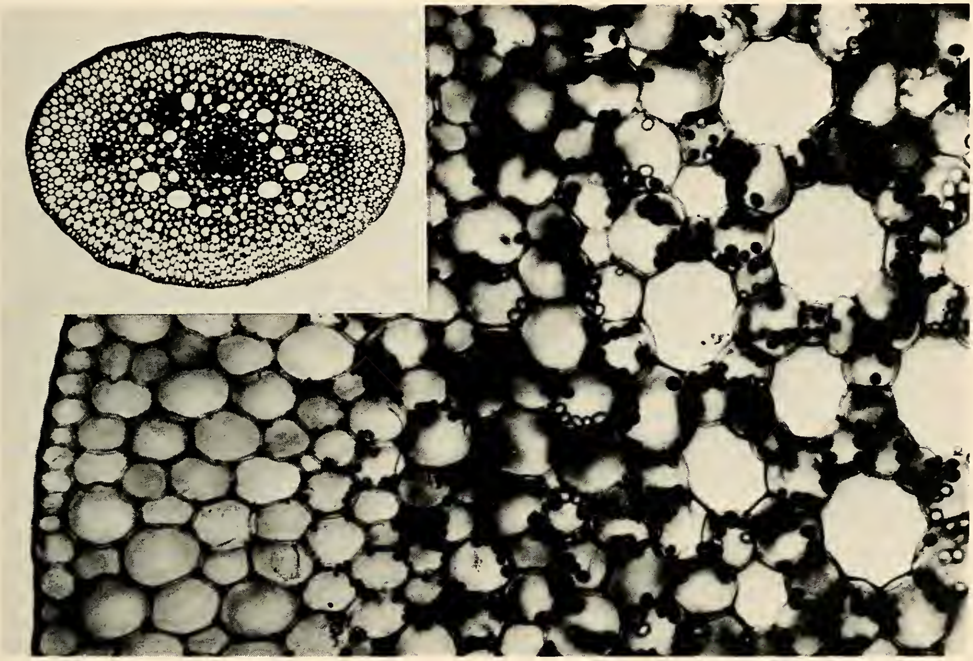

Fig. 10. Transverse section of the rhizome of *Zostera capricorni* showing starch grains in the cortical cells. Material collected late summer, 1985.

ACKNOWLEDGEMENTS

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Aquatic Angiosperms in Coastal Saline Lagoons of New South Wales. III. Quantitative Assessment of *Zostera capricorni*

R. J. KING and J. B. BARCLAY

KING, R. J., & BARCLAY, J. B. Aquatic angiosperms in coastal saline lagoons of New South Wales. III. Quantitative assessment of *Zostera capricorni.*, *Proc. Linn. Soc. N.S.W.* 109 (1), 1986: 41-50.

Data on *Zostera capricorni* (total biomass, below-ground, detrital leaf, flowering stems and living shoot) and shoot measurements (percentage cover, density, leaflength and width) and biomass of *Halophila ovalis* and *Ruppia megacarpa* for summer and winter 1978-79 are presented for 7 sites in Lake Macquarie and 5 sites in Tuggerah Lakes. Regression equations are established relating *Zostera capricorni* total biomass and living shoot biomass to percentage cover for these sites in winter and summer and these equations applied to field survey data. The total biomass of *Zostera* in Lake Macquarie in summer 1985 was estimated as 1454 tonnes over an area of 11.57km^2; living shoot biomass was 330 tonnes. Comparable figures for Tuggerah Lakes are 1255 tonnes total biomass and 453 tonnes living leaf biomass over an area of 12.26km^2.

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INTRODUCTION

The distribution of aquatic angiosperms in the estuaries and coastal lagoons on the central and southern coast of New South Wales has been the subject of a number of papers but these have been quantitative only in the sense that the broad areas occupied by seagrasses have been mapped and in some cases surface area covered has been estimated (Wood, 1959, for Lake Macquarie; Higginson, 1965, for Tuggerah Lakes; Harris *et al.*, 1980, for Lake Illawarra; Evans and Gibbs, 1980, for 5 lagoons including Lake Macquarie and Lake Illawarra). West *et al.* (1985) provided an estuarine inventory for New South Wales but in this the only information on seagrasses was a value for the total area of seagrass and a list of those seagrasses occurring in each estuarine system. Detailed information on the distribution, relative abundance and the area occupied by seagrasses is available for Lake Macquarie (King, 1986b) and Tuggerah Lakes (King and Holland, 1986).

Despite the information in these publications and in the plethora of unpublished reports by State Government authorities until now there have been no biomass data available for these estuarine ecosystems except for two isolated values for the maximum total biomass of all species in Tuggerah Lakes in 1964 and 1967 (Higginson, 1971). Indeed it is only in the last few years that any data have been published for Botany Bay (Larkum *et al.*, 1984).

In both Lake Macquarie and Tuggerah Lakes the most abundant and widespread macrophyte is the seagrass *Zostera capricorni* Ascherson. It covers 11.57km^2 of Lake Macquarie (total seagrass area 14.17km^2) (King, 1986b), and 11.66km^2 (total seagrass area 20.44km^2) of the Tuggerah Lakes (King and Holland, 1986). *Zostera* commonly occurs with *Halophila ovalis* (R. Brown) Hooker f. but while *Halophila* is widespread (5.59km^2 and 9.82km^2 of Lake Macquarie and Tuggerah Lakes respectively) it is not such a significant contributor to biomass. The fibre-weed *Posidonia australis* Hooker f. does not occur in Tuggerah Lakes and is of restricted distribution in Lake Macquarie. *Ruppia megacarpa* R. Mason occurs in both systems but at the commencement of this study was relatively unimportant. Changes in the vegetation of Tuggerah Lakes since that time indicate that more attention should be paid to this species.

In this report we present basic data on biomass of *Zostera capricorni* of selected sites in both Lake Macquarie and the Tuggerah Lakes system. This information is then used to establish the relationship between various biomass attributes (total biomass, root, living leaf, detrital leaf and flowering stem) and shoot measures (percentage cover, shoot density, leaf height and leaf width). Relationships between percentage cover, and both total biomass and biomass of standing leaf stock are applied to data collected in the general surveys (King, 1986a,b; King and Holland, 1986).

TABLE 1

Scale used to rate seagrass distribution, with estimations of percentage leaf cover

	Sociability		
Abundance	a Individual strands or clumps	b Patches up to 10 m diameter	c Beds of relatively even distribution
1 Sparse growth (<15%)	5%	10%	15%
2 Moderate growth (15-50%)	15%	25%	35%
3 Abundant growth (>50%)	inappropriate measure	60%	65%

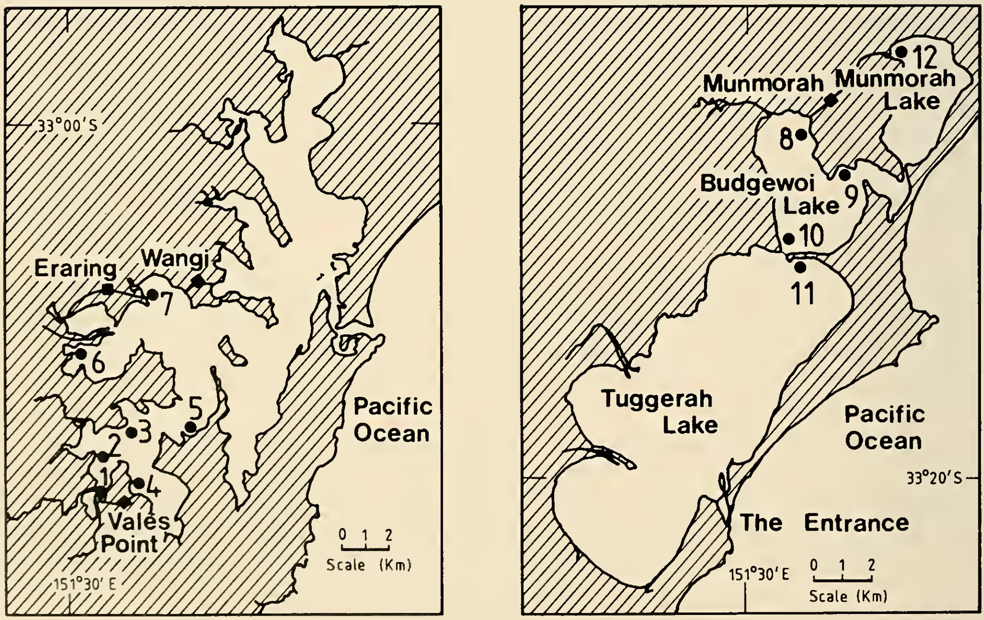

Fig. 1. a (left), sampling sites in Lake Macquarie: b (right), sampling sites in Tuggerah Lakes. See also Tables 2 and 3.

METHODS

Sampling for the quantitative analysis

Twelve sampling locations were selected to cover a range of seagrass density: sites 1-7 in Lake Macquarie and sites 8-12 in Tuggerah Lakes (Fig. **1a**,**b**). These included sites in power station cooling water discharge plumes and sites near the edge of the plumes. Sites 1 to 5 are in the Vales Point power station cooling water plume, and sites 8 to 10 are in the Munmorah power station plume. Seagrasses at each locality were sampled in winter of 1978 and summer 1978/79 except for site 6 (Lake Macquarie) and sites 10 and 11 (Tuggerah Lakes) which were sampled in winter only.

In winter at least 10 quadrats were sampled at each site. These were located randomly within a grid 20m × 5m parallel to the shore, and at approximately 1m depth. In shallower water in these lakes seagrasses are sometimes physically damaged due to wave action created by both wind and motor boat activity, and this may upset any general relationships involving the leaf component. Samples were collected complete with sediment using a diver-held corer with an internal diameter of 15cm.

Percentage cover of *Zostera capricorni* was visually estimated in quadrats 25cm × 25cm using a scheme similar to that of Kirkman (1978) but with 7 cover grades:

Grade	% Cover Range	Midpoint	Description
6	>80	90	occupying almost the entire quadrat
5	61-80	70	approx. three quarters quadrat
4	41-60	50	approx. half quadrat
3	25-40	33	approx. third quadrat
2	12-24	18	approx. fifth quadrat
1	2-11	7	1/10-1/20 quadrat
+	<2	1	very sparse, occasional leaves

The random location of quadrats in winter proved somewhat unsatisfactory since in areas of mosaic weed growth some quadrats contained no seagrass at all (see sample numbers in Tables 2 and 3 which summarize the data for all quadrats containing seagrasses). In summer the samples were taken in areas subjectively assessed (Kirkman, 1978) as having intermediate weed cover for that particular locality: the size of the core samples was increased to 18.5cm diameter, and the number of samples was standardized at 5 at each locality. Localities 10 and 11 in Tuggerah Lakes were sampled in winter only.

At the field site all plant material was washed free of sediment in a 1.5mm mesh sieve, bagged and then either preserved in formalin or frozen. In the laboratory the samples were treated following the recommendations of Wetzel (1965) and Vollenweider (1974). The macrophytes were separated into the different species, washed to remove salt and physically cleaned of macrophytes. The *Zostera* was sorted into four components: root and rhizome, detrital leaf, living leaf, and flowering stems. Fresh weights were obtained after a standard spinning of each component in a simple kitchen 'salad dryer'. Dry weights were obtained by drying to constant weight at 105°C. Percentage ash-free weights of subsamples were obtained after oxidation to constant weight in a muffle furnace at 550°C.

The following measurements were made for each core sample: number of upright living shoots per unit area ('density'); average length of the two longest living leaves per shoot ('leaf height'); average width of leaves, 10cm from the base of 10 mature living leaves ('leaf width'). A high level of correlation was found between biomass levels and leaf

TABLE 2

Seagrass biomass (g. dry wt. m^{-2}), and Zostera *shoot measurements, as mean ± standard error from sites in Lake Macquarie, 1978-1979*

					Zostera biomass					*Zostera* shoot measurements			
SITE (Fig. 1a)		TIME	NO. SAMPLES	*Halophila* BIOMASS	TOTAL INC. DETRITUS	BELOW GROUND	DETRITAL LEAF	FLOWERING STEM	LIVING LEAF	% COVER	DENSITY (shoots.m^{-2})	LENGTH (cm)	WIDTH (mm)
Vales Point Power Station outlet	1	Winter	7	142 ± 19	0	0	0	0	0	0	0	0	0
		Summer	5	179 ± 8	0	0	0	0	0	0	0	0	0
Wyee Bay (north west)	2	Winter	9	10 ± 5	127 ± 40	77 ± 16	31 ± 9	0	19 ± 4	20 ± 5	1032	10 ± 2	3.0 ± 0.2
		Summer	5	12 ± 3	163 ± 47	81 ± 22	24 ± 7	0	59 ± 19	50 ± 12	1888 ± 288	11 ± 2	3.0 ± 0.1
Bluff Point	3	Winter	10	5 ± 1	258 ± 19	209 ± 17	23 ± 2	0	25 ± 2	–	–	–	–
		Summer	5	4 ± 1	372 ± 31	221 ± 11	37 ± 5	14 ± 4	100 ± 13.	71 ± 2	1280 ± 128	26 ± 2	3.5 ± 0.1
Chain Valley Bay Station inlet	4	Winter	10	1 ± 1	245 ± 19	164 ± 14	69 ± 6	0	[13 ± 4][1]	[13 ± 3	1184 ± 160	9 ± 2	2.3 ± 0.1][1]
		Summer	5	17 ± 4	182 ± 48	115 ± 30	27 ± 6	1 ± 1	39 ± 11	30 ± 6	544 ± 112	20 ± 3	3.1 ± 0.7
Summerland Point	5	Winter	8	0	320 ± 20	197 ± 12	109 ± 12	0	14 ± 2	22 ± 2	336 ± 64	16 ± 2	2.7 ± 0.1
		Summer	5	0	639 ± 36	332 ± 17	120 ± 8	15 ± 11	172 ± 14	83 ± 4	1360 ± 192	43 ± 3	3.3 ± 0.1
Bonnells Bay	6	Winter	10	24 ± 8	186 ± 56	(135 ± 23	74 ± 33)[2]	0	19 ± 4	–	1520 ± 352	–	–
Myuna Bay Eraring Station outlet	7	Winter	11	0	379 ± 18	(217 ± 17	120 ± 12)[3]	0	28 ± 4	30 ± 3	1120 ± 224	19 ± 2	2.8 ± 0.1
		Summer	5	0	303 ± 29	169 ± 14	52 ± 6	13 ± 5	68 ± 10	60 ± 4	832 ± 64	27 ± 2	3.2 ± 0.1

Where full data sets are not available these are indicated: [1]data for 6 quadrats only
[2]data for 4 quadrats only
[3]data for 8 quadrats only

TABLE 3

Seagrass biomass (g. dry wt. m^{-2}), and Zostera *shoot measurements, as mean ± standard error from sites in Tuggerah Lakes, 1978-1979*

SITE (Fig. **1b**)		TIME	NO. SAMPLES	*Ruppia* BIOMASS	*Halophila* BIOMASS	*Zostera* biomass					*Zostera* shoot measurements			
						TOTAL INC. DETRITUS	BELOW GROUND	DETRITAL LEAF	FLOWERING STEM	LIVING LEAF	% COVER	DENSITY (shoots.m^{-2})	LENGTH (cm)	WIDTH (mm)
Munmorah Power Station outlet	8	Winter Summer	10 5	No Seagrasses 0	92 ± 2	0	0	0	0	0	0	0	0	0
Buff Point Budgewoi Lake	9	Winter Summer	4 5	0 0	6 ± 3 16 ± 5	37 ± 8 114 ± 29	23 ± 8 57 ± 11	4 ± 2 23 ± 11	0 0	10 ± 1 34 ± 8	10 ± 3 30 ± 6	688 ± 304 688 ± 144	8 ± 2 18 ± 3	2.4 ± 0.5 2.4 ± 0.1
Southern Budgewoi Lake	10	Winter	8	0.8 ± 0.8	0	64 ± 9	(58 ± 11	11 ± 4)[1]	0	11 ± 3	12 ± 2	848 ± 192	5 ± 1	1.8 ± 0.6
Northern Tuggerah Lake	11	Winter	10	11 ± 8	4 ± 1	161 ± 52	(133 ± 52	27 ± 14)[2]	0	39 ± 19	28 ± 9	976 ± 144	12 ± 3	2.2 ± 0.2
Munmorah Lake near station inlet	12	Winter Summer	9 5	0 0	2 ± 1 2 ± 1	81 ± 10 201 ± 58	(47 ± 9 79 ± 26	6 ± 3)[3] 51 ± 19	0 0	24 ± 6 68 ± 16	18 ± 3 53 ± 10	800 ± 160 880 ± 144	11 ± 1 23 ± 3	2.7 ± 0.1 3.2 ± 0.2

Where full data sets are not available these are indicated: [1] data for 6 quadrats only
[5] data for 5 quadrats only
[6] data for 6 quadrats only

measurements (Barclay, 1983). This suggests the potential of using regression analysis to estimate biomass with non-destructive sampling. The most relevant to broad scale surveys are those relating biomass to estimates of percentage cover.

Data for total biomass of *Zostera* (excluding detrital material) and biomass of standing leaf stock were related to percentage cover through regression analysis. Using the data on area and abundance of *Zostera* (King, 1986a,b; King and Holland, 1986) these data have been used to give biomass figures for the entire lake systems. The categories of sociability and abundance used in the field surveys have been combined in a two-way table. For each category the cover was visually estimated, as above, and the percentage cover (to the nearest 5%) assigned to each (Table 1). The category 3a is unused since *Zostera* communities in which plants grow as individual strands or clumps cannot exhibit abundant growth.

RESULTS

The full data set on seagrass biomass and *Zostera* shoot measurements for Lake Macquarie and Tuggerah Lakes are given in Tables 2 and 3 respectively. The biomass figures are expressed in terms of per metre square but since the data refer only to quadrats in which plant material occurred they cannot be used in any comparative sense or to indicate biomass typical of an area. All data are expressed in terms of dry weight. The ratios of dry weight to fresh weight, and the organic contents as a percentage of dry weight for *Halophila* and *Zostera* are given in Table 4.

TABLE 4

Dry weight as a percentage of fresh weight of Zostera *and* Halophila *for sites in Lake Macquarie. Mean ± s.e; n = 82*
Organic weight as percentage of total dry weight of Zostera *and* Halophila *in both Lake Macquarie and Tuggerah Lakes. Mean ± s.e.; n = 110*

		Zostera below ground	 detrital leaf	 live leaf	*Halophila*
Dry weight as percentage fresh weight	Lake Macquarie	9.6 ± 0.3	8.2 ± 0.5	10.5 ± 0.7	8.8 ± 0.5
Organic contents as percentage dry weight	Lake Macquarie	76.5 ± 1.5	78.5 ± 1.7	85.9 ± 1.0	69.7 ± 1.0
	Tuggerah Lakes	65.4 ± 2.0	67.3 ± 2.6	81.5 ± 2.7	

The relationship between percentage cover with both total biomass and leaf standing stock is described by the series of equations given in Table 5. Separate equations are provided for each season and for both Lake Macquarie and Tuggerah Lakes. Site 2 (Wyee Bay in Lake Macquarie) differs from other sites in a number of ways (Barclay, 1983) and is treated separately. In these equations biomass is expressed as a logarithmic scale since there appeared to be a logarithmic relationship between percentage cover and biomass (cf. Larkum *et al.*, 1984).

DISCUSSION

There are relatively few studies which deal with the estimation of seagrass standing stock or biomass in broad surveys, yet such data are important for management purposes and especially so if vegetation change is to be monitored. In regions where there is

TABLE 5

Linear regression equations relating $\log_{10}$ (total biomass) and $\log_{10}$ (living leaf biomass) to percentage cover for sites in southern Lake Macquarie and Tuggerah Lakes.
X_1 = percentage cover

SOUTHERN LAKE MACQUARIE				
All sites except those in Wyee Bay				
Summer				
$\log_{10}$ (total biomass)	=	$0.012X_1 + 0.525$	r = 0.933 (n = 20)	$p<0.001$
$\log_{10}$ (living leaf biomass)	=	$0.014X_1 - 0.200$	r = 0.941 (n = 20)	$p<0.001$
Winter				
$\log_{10}$ (total biomass)	=	$0.016X_1 + 0.697$	r = 0.686 (n = 26)	$p<0.001$
$\log_{10}$ (living leaf biomass)	=	$0.026X_1 - 0.586$	r = 0.833 (n = 25)	$p<0.001$
Wyee Bay (Site 2)				
Summer				
$\log_{10}$ (total biomass)	=	$0.010X_1 - 0.223$	r = 0.806 (n = 5)	$0.02<p<0.5$
$\log_{10}$ (living leaf biomass)	=	$0.017X_1 - 0.434$	r = 0.986 (n = 5)	$p<0.001$
Winter				
$\log_{10}$ (total biomass)	=	$0.035X_1 - 0.063$	r = 0.894 (n = 9)	$p<0.001$
$\log_{10}$ (living leaf biomass)	=	$0.030X_1 - 0.638$	r = 0.917 (n = 9)	$p<0.001$
TUGGERAH LAKES				
Summer				
$\log_{10}$ (total biomass)	=	$0.010X_1 + 0.417$	r = 0.910 (n = 10)	$p<0.001$
$\log_{10}$ (living leaf biomass)	=	$0.011X_1 - 0.037$	r = 0.959 (n = 10)	$p<0.001$
Winter				
$\log_{10}$ (total biomass)	=	$0.016X_1 + 0.240$	r = .836 (n = 18)	$p<0.001$
$\log_{10}$ (living leaf biomass)	=	$0.023X_1 - 0.501$	r = .826 (n = 31)	$p<0.001$

a marked seasonal growth pattern peak biomass may also be used as an indicator of productivity (Nienhuis and de Bree, 1977). In broad-scale survey work normal destructive methods of vegetative sampling are rarely appropriate, not only because they are time-consuming, but also, because the removal of vegetation may itself affect the result, particularly if the survey area is ecologically sensitive or has only a sparse vegetation cover.

Percentage cover has been used successfully to estimate 'above-ground' biomass of aquatic angiosperms by a number of workers: Rorslett *et al.* (1978) in studies of freshwater macrophytes; Kirkman (1978) in monitoring the decline of *Zostera capricorni* in Moreton Bay, Queensland; and locally by Larkum *et al.* (1984) in assessing total above ground stock of *Zostera capricorni* in Botany Bay. A more sophisticated population density index was used by Sheldon and Boylen (1978) to estimate cover and subsequently biomass in a large freshwater lake in N.Y. State. In a broad-scale survey Mukai *et al.* (1980) used a similar approach to that here to estimate the biomass of *Zostera marina* in Odawa Bay, central Japan. They used somewhat fewer data, 9 samples only in an area of 68 hectares.

In the study of Larkum *et al.* (1984) percentage cover was related logarithmically to both underground biomass and shoot biomass. A similar association was found in this project in Lake Macquarie and Tuggerah Lakes. In other studies, (Nienhuis and de Bree, 1977), in the Netherlands; McRoy, 1970, in Alaska) linear relationships were established between the standing stock of *Z. marina* and percentage cover. Larkum *et al.* (1984) suggested that the logarithmic relationship may indicate a 'synergistic effect of the presence of one plant on the growth of another', but whether this is caused by a more favourable redox potential and/or enhanced nutrient availability in dense stands (Orth, 1977) was not determined.

Non-destructive methods of estimating abundance were generally restricted to above-ground material and in seagrass studies root biomass has often been ignored; as indeed it is in most ecosystem studies (Caldwell, 1979). If the root to shoot ratio is any indication of the energy investment in root systems then it is clear that the importance of the root component has been underestimated. There are, however, several reports on below-ground productivity in seagrasses which indicate that it is much less than would be predicted by this ratio (see West and Larkum, 1983). The root/living shoot ratio of *Z. capricorni* was in the range of 1.16-2.94 in summer (data from Tables 2 and 3). Such ratios are compatible with observations made on a wide variety of communities where below-ground productivity has been shown to account for 50-80% of total net production (Caldwell, 1979). In winter when the living shoots die back the ratio of root/shoot is much greater and more variable, but the picture is complicated by the impossibility of distinguishing between living and non-living components and the root biomass.

The regressions established in this survey indicate that total biomass and standing stock of living leaves can be estimated from percentage cover. Separate regressions are required for the seasons (winter and summer). In this study separate regressions were required for data from site 2 (Wyee Bay, 1.5km from the Vales Point power station outlet). These regressions differed significantly from those at all other sites in Lake Macquarie.

When considering the calculated biomass data the following qualifications should be borne in mind:

(i) it is assumed that the relationship between biomass measures and percentage cover at various sites and in various seasons has remained constant during the period of the surveys,

(ii) there is a compromise between breadth and intensity of survey such that only 8 categories of percentage cover of *Zostera* are mapped. Hence there is a built-in error in the estimation of biomass for any category of abundance/sociability even assuming a particular area is accurately identified. This error could be especially critical when small areas of the lake are considered separately,

(iii) the equations do not take into account any possible variation in the relationship between percentage cover and biomass with depth (cf. Larkum *et al.*, 1984).

There are few relevant data with which to compare the biomass figures calculated using these relationships (Table 6). Larkum *et al.* (1984) recorded a total above-ground biomass of 81 ±4.2 tonnes for the 309ha of *Zostera capricorni* beds in Botany Bay. They pointed out that this figure was considerably less (by a factor of 6-10) than would have been estimated by taking the product of the area of the beds and biomass from a typically healthy bed. Their estimate took into account the patchy distribution of the beds. The average biomass figure in tonnes per square kilometre of 26 for Botany Bay is comparable to the average values of 28 tonnes.km^{-2} for Lake Macquarie and 37 tonnes.km^{2} in Tuggerah.

The only published estimates of the dry weight standing biomass for either Lake Macquarie or Tuggerah Lakes are those of Higginson (1971) for Tuggerah Lakes. A single maximum value for 1964 and a single minimum value (1967) were given: 21000 tons (21333 tonnes) and 2300 tons (2337 tonnes) respectively. These figures include all species and related to the much larger area of the lake which was then colonized by plants. The figures were said to represent the equivalent of 2.5 tons.acre^{-1} (627 tonnes.km^{-2}) and 0.4 tons acre^{-1} (100 tonnes.km^{-2}). These values seem inordinately high

TABLE 6

Total biomass (tonnes) and shoot biomass of Zostera capricorni *in summer 1985 calculated using the linear regressions in Table 5 in conjunction with the area and relative abundance of* Zostera *shown on maps for Lake Macquarie (King, 1986b) and Tuggerah Lakes (King and Holland, 1986). Note that the total of Lake Macquarie includes seagrass from several small areas not listed separately*

	Total biomass (T)	*Zostera capricorni* Shoot biomass (T)	Area (km^2)
LAKE MACQUARIE			
Myuna Bay	26	6	0.29
Goonda — Fishing Station Pt	52	11	0.26
Northern Lake (Fishing Station Pt — Cardiff Pt)	161	35	1.30
Central eastern Lake	364	78	3.69
Crangan Bay	227	55	1.05
Chain Valley Bay	171	39	1.21
Wyee Bay inc. Mannering Bay	4	4	0.16
Wyee Pt — Bluff Pt	72	16	0.62
Bonnells Bay	289	67	2.00
Total — Lake Macquarie	1454	330	11.57
TUGGERAH LAKES			
Tuggerah Lake	1052	376	9.58
Budgewoi Lake	89	34	1.19
Munmorah Lake	114	43	0.59
Total — Tuggerah Lakes	1255	453	12.26

when compared with the range (10-55g.m^{-2} or 10-55 tonnes.km^{-2}) for *Zostera* species in Australia (see review of McComb *et al.*, 1981) and values in the range 70-156g.m^{-2} for mature stands of *Zostera capricorni* in summer in Botany Bay (Larkum *et al.*, 1984). The highest values for any site in this survey were 172 ± 14g.m^{-2} (n = 5) for site 5 (Summerland Point) in summer. Higginson (1971) included all plants in his biomass but again published data for 'apparently healthy growing stands of plants' are 49.9g.m^{-2} for *Halophila* (see McComb *et al.*, 1981) and 403g.m^{-2} for *Ruppia*; considerably less than the values anticipated throughout the lakes. Unfortunately Higginson (1971) did not indicate the way in which he derived his values. The method of estimating biomass described here is appropriate to broad-scale surveys but it could be readily adapted to more detailed surveys. It is especially useful when there is a need to embrace wide variability in both time and space but resources are limited. Although correlations are high the field data are still prone to subjective assessment of the percentage cover. A multiple regression based on several measured leaf characters (Barclay, 1983) is potentially more accurate but the general applicability of such equations would need to be investigated.

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Aquatic Angiosperms in Coastal Saline Lagoons of New South Wales. IV. Long-term Changes

R. J. KING and B. R. HODGSON

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The area occupied by aquatic angiosperms and the biomass of *Zostera capricorni* have been documented for southern Lake Macquarie and the Tuggerah Lakes from 1980 to 1985. The area of seagrasses in Lake Macquarie ranged from 4.81 to 6.75km^2, and the total biomass of *Zostera* from 543 to 1099 tonnes. Winter biomass was significantly greater than summer biomass. In the Tuggerah Lakes the area was 13.13-19.11km^2 and total biomass of *Zostera* 840-1888 tonnes. Differences between years were not significant because of the wide variation shown in both parameters. The data show no time-related trends or predictable changes. When vegetation survey is to function as baseline data this inherent variability in seagrass populations must be recognized.

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INTRODUCTION

The disturbance of seagrass beds by natural and artificial causes and the recognition of the potential of such disturbances on commercial and recreational fishing have led to the recent increased interest in the biology of these plants (McRoy and Helfferich, 1977; Phillips and McRoy, 1980; McComb *et al.*, 1981). In Australia where some 11.4% of the coastline consists of coastal lagoons (Cromwell, 1971, in Barnes, 1980), and with the increasing residential and industrial development in proximity to the coastal water ways, such studies have especial relevance. In investigations of seagrass communities on the New South Wales coast there are few detailed early studies. Hence baseline studies, in which data are collected and analysed in order to specify the present state of the community, are a prime requirement. Generally such studies anticipate some environmental changes. The so-called 'baseline data' are essential to monitoring since change can only be detected in relation to the unimpacted state. When the impact has to be inferred from temporal change alone the sampling and statistical analysis is suboptimal in that a control area defined *a priori* is lacking (Green, 1979). In cases where any future impact is potentially able to affect a wide area, or act over a long time, the sampling of baseline data is critical. The problem is always to obtain sufficient quantitative information that takes into account natural fluctuations so that later comparisons can be meaningful.

In the long term studies in the coastal saline lagoons of the New South Wales coast there have been detailed studies relating seagrass growth to specific environmental factors (e.g. Harris *et al.*, 1980; Higginson, 1965) and very broad distribution studies in which the results are essentially qualitative (e.g. Wood, 1959a; Evans and Gibbs, 1981; West *et al.*, 1985). Studies of the former type at least allow some predictions to be made on the basis of environmental tolerances: from studies in the latter category change can usually only be confirmed when the seagrass is no longer present.

This paper provides data on areas of seagrass coverage and biomass of *Zostera capricorni* in two seagrass-dominated coastal lagoons on the central coast of New South

Wales (Lake Macquarie and Tuggerah Lakes). Long-term vegetation changes are discussed.

STUDY AREA

The two study sites, Lake Macquarie and the Tuggerah Lakes, are on the central New South Wales coast and their aquatic vegetation is described in King (1986a,b) and King and Holland (1986). Both lake systems support commercial fishing and prawning, but are in areas with rapid urbanization and increasing recreational use. Proximity to major population centres and to coal deposits have made the lakes suitable sites for steam-generating power stations: Wangi (330MW), Vales Point (2195MW), and Eraring (2640MW) power stations on Lake Macquarie, and Munmorah power station (1400MW) on the Tuggerah Lakes. These power stations use steam-driven generating units, and the lake water is continuously drawn from an inlet channel to cool the condensors. The Electricity Commission of New South Wales commenced funding of long-term seagrass surveys in the early 1960s in the Tuggerah Lakes and in the early 1970s in Lake Macquarie. These early surveys evolved to the present quantitative surveys. The cooling-water discharges result in the production of artificial warm water effluents (5-9°C above ambient) in localized areas of the lakes. Given the potential impact of these cooling-water discharges as well as changes such as the increasing turbidity and levels of phosphorus in Lake Macquarie (State Pollution Control Commission, 1983), and comparable environmental changes in the Tuggerah Lakes, there was a perceived need for quantitative data on the seagrass communities.

METHODS

Since winter 1980 the aquatic vegetation in the southern half of Lake Macquarie and in the Tuggerah Lakes has been mapped quantitatively on a regular basis. All areas were mapped in winter 1980 and 1981 and all areas have been mapped every summer since. In addition areas in Lake Macquarie, Myuna Bay and Wyee Bay, have been mapped every winter.

The vegetation was mapped and the areas of seagrass calculated using the techniques outlined in King (1986b) but in surveys prior to 1984 the distance from the shoreline to the seagrass boundary was measured using a marked tape rather than optical range-finders. The formulae relating percentage cover and biomass measures established in King and Barclay (1986) were used to convert the data from the maps into estimates of total biomass and living shoot biomass.

RESULTS AND DISCUSSION

The results are given in a series of tables:

Table 1	Area occupied by seagrasses in southern Lake Macquarie (1980-1985).
Table 2	Biomass, total and living leaf, for seagrasses in southern Lake Macquarie (1980-1985).
Table 3	Area occupied by seagrasses in Tuggerah Lakes (1980-1985).
Table 4	Biomass, total and living leaf, for seagrasses in the Tuggerah Lakes (1980-1985).

A complete copy of the vegetation surveys (1980-1986) is available (King, 1986a).

LAKE MACQUARIE

The range of estimates for total area of seagrass in southern Lake Macquarie for winter 1980 – summer 1985 was 4.81km^2-6.75km^2 (Table 1) and differences between

TABLE 1

Areas (km^2) of seagrass in southern Lake Macquarie in the years 1980-1985

Season & Year	W80	S81	W81	S82	W82	S83	W83	S84	W84	S85
LAKE MACQUARIE (Southern Lake) — areas listed separately below										
Zostera	5.28	5.15	6.66	3.85		4.02		4.65		5.81
Halophila	1.16	3.58	3.29	2.68		2.24		3.85		4.59
Ruppia	—	—	—	0.07		—		0.19		0.15
Posidonia	0.03	0.05	0.02	0.01		0.07		0.02		0.01
Total	5.49	5.99	6.75	4.92		4.81		5.00		6.65
MYUNA BAY (Eraring Power Stn outlet to Goonda Pt excluding Whiteheads Lagoon)										
Zostera	0.38	0.42	0.71	0.40	0.19	0.25	0.44	0.32	0.32	0.25
Halophila	0.16	0.37	0.35	0.24	0.08	0.27	0.37	0.27	0.30	0.29
Total	0.38	0.42	0.71	0.41	0.20	0.27	0.46	0.32	0.33	0.29
GOONDA POINT – FISHING STATION POINT										
Zostera	0.52	0.54	0.85	0.51		0.38		0.53		0.47
Halophila	0.02	0.09	—	—		0.19		0.32		0.26
Posidonia	0.01	0.02	0.01	0.01		0.01		0.02		0.01
Total	0.53	0.62	0.86	0.51		0.39		0.53		0.48
CRANGAN BAY ('Youth Camp' — Pt Wolstoncroft)										
Zostera	0.79	1.21	1.08	0.34		0.87		0.72		1.05
Halophila	—	0.31	0.33	—		0.09		0.19		0.31
Posidonia	0.02	0.03	0.01	+		0.06		+		+
Total	0.81	1.37	1.09	0.35		0.92		0.72		1.07
CHAIN VALLEY BAY (Vales Pt — Frying Pan Point)										
Zostera	1.30	1.12	1.53	1.05		0.87		1.02		1.16
Halophila	0.31	1.01	1.14	0.93		0.58		0.74		1.22
Ruppia	—	—	—	0.07		—		0.19		0.15
Total	1.43	1.33	1.58	1.33		1.04		1.05		1.25
WYEE BAY including MANNERING BAY (Vales Pt — Wyee Pt)										
Zostera	0.05	0.05	0.07	0.05	0.01[1]	0.09	0.16	0.21	0.20	0.27
Halophila	0.09	0.38	0.09	0.45	0.25[1]	0.43	0.82	0.53	0.83	0.83
Total	0.10	0.40	0.09	0.60	0.25[1]	0.48	0.84	0.53	0.86	0.83
WYEE POINT – BLUFF POINT										
Zostera	0.38	0.38	0.36	0.23		0.27		0.42		0.61
Halophila	0.23	0.40	0.35	0.36		0.17		0.32		0.60
Total	0.38	0.40	0.36	0.36		0.41		0.47		0.74
BONNELLS BAY (Shingle Splitters Pt — Rocky Pt)										
Zostera	1.86	1.43	2.06	1.27		1.29		1.43		2.00
Halophila	0.35	1.02	1.03	0.70		1.09		1.43		1.08
Total	1.86	1.45	2.06	1.36		1.30		1.43		2.00

1 Data for Mannering Bay only

values for different years and different seasons were not significant. Even within specific areas of the lake differences in the area occupied by seagrass were not significant. In Table 5 the data for seagrass areas are summarized along with comparative figures for 1953. The values for 1953 were measured by planimetry using an original map from the CSIRO 1953 survey. The error in measuring such small areas is great (approx. 10%) but based on the values presented there appears to have been an overall reduction in seagrass beds of about one third. This reduction is apparent in all areas of the lake. Part of this loss may be attributable to sedimentation though the estimate for loss of lake area due to this is only one to two hectares per year (SPCC, 1983). Secchi disc data indicate that lake turbidity has increased, and since the lower limit of seagrasses is thought to be limited by light this would also reduce the area of seagrass.

TABLE 2

Biomass (tonnes) of Zostera capricorni *in southern Lake Macquarie, Winter 1980 — Summer 1985. Winter surveys from 1982 onwards have included only Myuna and Wyee Bays. Maps of individual areas are given in King (1986)*

LAKE MACQUARIE	W80	S81	W81	S82	W82	S83	W83	S84	W84	S85
Total biomass										
Myuna Bay	87	34	231	47	55	43	115	72	69	26
Goonda-Fishing Stn Pt	117	51	264	75	—	65	—	64	—	52
Crangan Bay	188	115	296	52	—	176	—	132	—	227
Chain Valley Bay	340	166	299	153	—	142	—	229	—	171
Wyee Bay	13	1	2	1	<1	1	14	3	18	4
Wyee Pt-Bluff Pt	62	40	115	29	—	74	—	112	—	72
Bonnells Bay	292	136	548	174	—	201	—	427	—	289
TOTAL	1099	543	1755	531		702		1039		841
Above-ground biomass										
Myuna Bay	9	8	39	10	9	10	17	18	7	6
Goonda-Fishing Stn Pt	13	11	41	17	—	15	—	14	—	11
Crangan Bay	25	24	40	12	—	42	—	31	—	55
Chain Valley Bay	38	38	29	35	—	34	—	56	—	39
Wyee Bay	2	1	1	<1	<1	1	3	2	3	4
Wyee Pt-Bluff Pt	5	9	17	6	—	19	—	28	—	16
Bonnells Bay	24	29	74	39	—	46	—	107	—	67
TOTAL	116	120	241	120		167		256		198

There are no data with which to compare the values for areas occupied by individual seagrass species (Table 2) nor the values for *Zostera capricorni* biomass.

While the area occupied by seagrasses remained relatively constant the biomass changed considerably. Part of this is probably due to the marked seasonal change in the biomass of *Zostera*. In winter the ratio of above-ground biomass to total biomass was about 1:8 and in summer it was about 1:4. If the number of living leaves on the plants varies and is influenced by non-seasonal factors such as King and Holland (1986) suggested then the biomass estimates will be affected accordingly. Another factor influencing the changes between years is the relative contribution of other seagrass species to the area occupied.

TUGGERAH LAKES

In Tuggerah Lakes the range of values for the area occupied by seagrasses is 13.13km^2 to 19.11km^2 and again there are no trends in the data (Table 3). A comparison of the percentage of the total area of the lakes occupied by each of the three seagrass species over the period 1980-1985 and 1963-1966 (Higginson, 1968) is given in Table 6. This indicates a marked reduction in the area occupied by *Zostera capricorni*.

The area occupied by *Halophila ovalis* appears to have increased dramatically but in Higginson's surveys *Halophila* would have been recorded only when it grew in single species stands. When *Halophila* occurs in mixed communities it is almost always the other species which give the beds their overall physiognomy. In the period 1980-1985 *Ruppia megacarpa* had more than trebled in the area occupied, from 2.52km^2 to 8.24km^2. In the period during which Higginson observed the distribution of weeds in the

TABLE 3

Areas (km^2) of seagrass in Tuggerah Lakes in the years 1980-1985

Season & Year	W80	S81	W81	S82	S83	S84	S85
TUGGERAH LAKES — (Total)							
Zostera	10.92	8.66	15.96	12.85	16.69	14.61	12.26
Halophila	4.10	9.14	10.98	9.71	13.36	7.51	10.40
Ruppia	2.52	1.76	3.13	2.20	2.73	5.01	8.24
Total	14.34	13.13	17.60	14.19	18.64	16.28	19.11
TUGGERAH LAKE							
Zostera	7.31	5.60	11.05	8.93	13.12	10.27	9.58
Halophila	0.67	6.05	7.16	4.53	8.15	3.77	6.43
Ruppia	2.50	1.76	3.12	1.71	2.73	3.75	5.48
Total	9.93	9.76	12.06	9.04	13.12	11.43	12.69
BUDGEWOI LAKE							
Zostera	2.86	2.17	3.61	2.12	2.75	3.21	1.19
	(1.91)*	(1.24)	(2.01)	(1.06)	(0.98)	(2.12)	(0.58)
Halophila	2.55	2.19	2.20	2.94	3.96	2.62	2.49
	(1.83)	(1.27)	(1.89)	(1.76)	(2.19)	(1.93)	(1.34)
Ruppia	0.02	–	0.01	0.33	–	0.98	2.22
	(–)	(–)	(–)	(0.06)	(–)	(0.44)	(1.71)
Total	3.05	2.28	3.82	3.00	4.19	3.43	4.03
MUNMORAH LAKE							
Zostera	0.75	0.89	1.30	1.80	0.82	1.13	1.49
Halophila	0.88	0.90	1.61	2.24	1.25	1.12	1.48
Ruppia	–	–	–	0.16	–	0.28	0.54
Total	1.36	1.09	1.72	2.25	1.33	1.42	2.39

*Data in brackets are for the Budgewoi Flats.

Tuggerah Lakes (1963-1966) the percentage of the area which was occupied by *Ruppia* fell from 13.3% to zero. Such wild fluctuations in the populations of *Ruppia* have also been observed in Smiths Lake (Myall Lakes system) but the factors involved have not yet been recognized. From the data available on the total area occupied by seagrass it does not appear that the increase in the area occupied by *Ruppia* is completely at the expense of *Zostera* and *Halophila* (Fig. 2).

The only biomass figures available for Tuggerah Lakes are not directly comparable with the data in Table 4 since they are for all seagrasses. The values were a maximum, in 1964, of 21,000 tons, and a minimum, in 1967, of 2,300 tons. These values seem to have been arrived at by multiplying the dry weight values obtained for quadrat samples by the area of the lake occupied by *Zostera* and the upper limit is considerably more than could be anticipated (see King and Holland, 1986). The range is far wider than that recorded here, 840-1888 tonnes (Table 4). In Tuggerah Lakes the ratio of above-ground biomass to total biomass was about 3 at all seasons.

The justification for many environmental surveys in the marine and coastal zones is that they are base-line studies against which man-induced change can be measured. Gray (1976) has noted that many such surveys are inadequate to the task of monitoring subtle, naturally-occurring changes and that they generally neglect the majority of the living constituents in the ecosystem.

Examination of the published data on the seagrasses of the Central Coast lakes reveals three problems:

TABLE 4

Biomass (tonnes) of Zostera capricorni *in Tuggerah Lakes, Winter 1980-Summer 1985*

TUGGERAH LAKES	W80	S81	W81	S82	S83	S84	S85
Total biomass							
Tuggerah Lake	627	747	1514	945	1159	1258	1052
Budgewoi Lake	169	127	236	219	242	456	89
Munmorah Lake	44	45	138	157	67	88	114
TOTAL	840	919	1888	1321	1468	1802	1255
Above-ground biomass (living leaf)							
Tuggerah Lake	213	291	642	369	443	499	376
Budgewoi Lake	50	47	78	86	92	183	34
Munmorah Lake	12	16	53	60	25	33	43
TOTAL	275	354	773	515	560	715	453

TABLE 5

Areas of seagrass in Lake Macquarie (km^2) 1980-1985, compared with values measured from CSIRO maps, 1953 (R. J. MacIntyre, pers. comm.)

	Year of Survey	
	1980-85	1953
Lake Macquarie (all areas)	14.17*	21.34
Myuna Bay (Eraring Power Stn outlet to Goonda Pt excluding Whiteheads Lagoon)	0.20-0.71	0.78
Goonda Pt to Fishing Station Point	0.39-0.86	1.22
Northern lake (Fishing Station Point to Cardiff Point)	1.58*	3.22
Central eastern part of lake (Cardiff Point — 'Youth Camp')	5.10*	7.28
Crangan Bay ('Youth Camp' — Pt Wolstoncroft)	0.35-1.37	0.65
Chain Valley Bay (Frying Pan Point to Vales Point) .	1.04-1.58	2.05
Wyee Bay including Mannering Bay (Vales Point to Wyee Point)	0.09-0.86	1.56
Wyee Point to Bluff Point	0.36-0.74	1.53
Bonnells Bay (Shingle Splitters Point to Rocky Point)	1.30-2.06	2.49

* value for 1985 summer only.

1. All surveys are a compromise between the area covered and the detail of information collected. Earlier surveys of both Lake Macquarie and Tuggerah Lakes showed presence and absence of the seagrass species and these were presented as maps for each of the lake systems, but at very small scale [(1:*c*.180,000 for Lake Macquarie (Wood, 1959a) and 1:*c*.190,000 for Tuggerah Lakes (Higginson, 1965)]. These surveys also included global figures for the area covered by seagrass, and Higginson (1971) presented biomass figures for all aquatic angiosperms in the entire Tuggerah Lakes system.

   From these sorts of data absolute conclusions can only be drawn when seagrass has entirely disappeared from an area which it formerly colonized. The scale of the published maps makes it impossible to draw conclusions about specific areas of the lakes which may have been 'impacted'.
2. The seagrass beds in the Central Coast lakes occur in an area undergoing rapid urbanization. As well as thermal effects associated with power stations there are environmental changes due to other factors, especially increasing sedimentation, toxic metal pollution, and increased nutrient levels from fertilizers and sewage (Higginson, 1971; Interdept. Comm., 1979). In the absence of information on species inter-

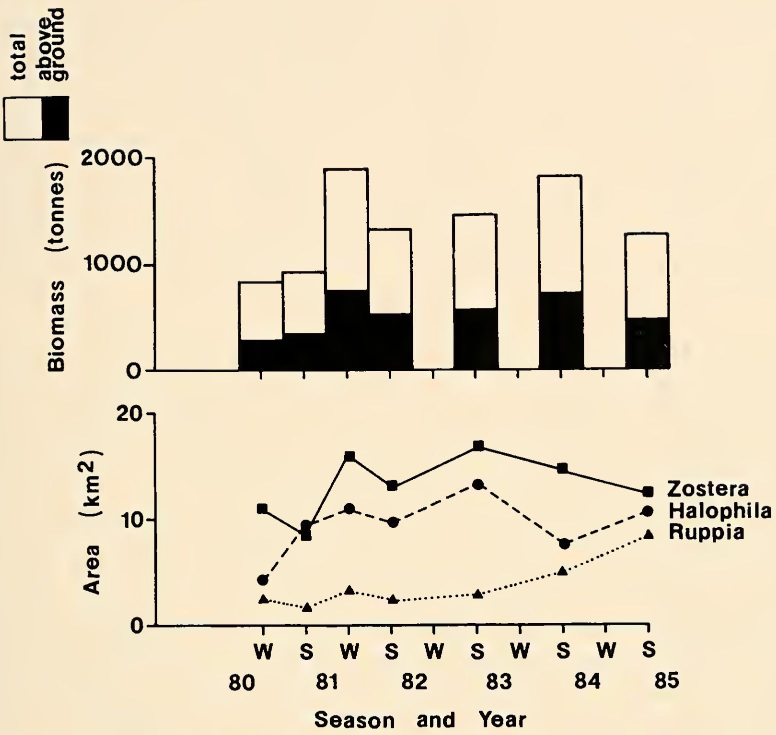

Fig. 1. Areas (km^2) occupied by the three aquatic angiosperms: *Zostera capricorni*; *Halophila ovalis*; and *Ruppia megacarpa* in Tuggerah Lakes, and biomass for *Zostera*.

actions, between even the common species and the environment, it is not possible to attribute community change to any one of the concomitant environmental perturbations.

Optimal impact study design requires the selection of a control area, or spatial control (Green, 1979). Whether such a control area, which is uninfluenced by the 'impact' under study but in other ways is similar to the area under investigation, can be designated *a priori* is a matter which can be generally argued (Gray, 1976). On the basis of the data available for the present study it seems unlikely.

3. In the absence of an adequate control area impact must be inferred from temporal change alone. In order to interpret such changes long-term systematic sampling and recording is necessary, and it must be assumed that observed changes would not have occurred if the area had not been environmentally altered.

With vegetation which changes as rapidly, as unpredictably and by such a magnitude as the present data indicate such an assumption may be unwarranted. Changes would need to be extensive and long lasting before firm conclusions could be drawn.

Wood (1959b) was able to state — 'the taxonomy of the Australian sea-grasses has been dealt with by several workers, but no ecological studies have been made'. In the same year he published his preliminary study on the plant communities of Lake

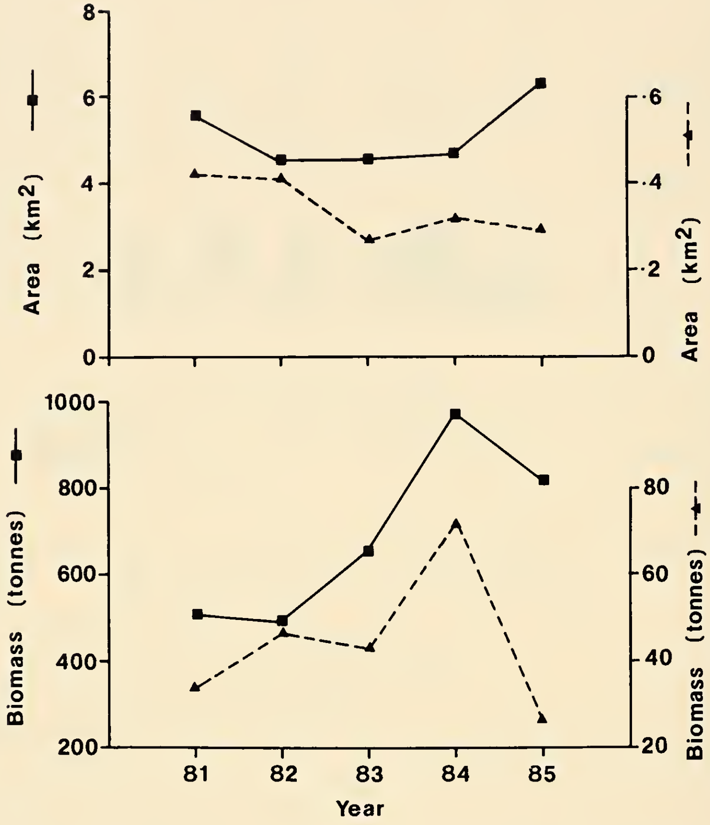

Fig. 2. Area (km^2) and total biomass occupied by aquatic angiosperms in Myuna Bay compared wtih value for the total area of southern Lake Macquarie.

Macquarie (Wood, 1959a) and their significance, *and* in an enviable display of honesty stated — 'only generalities are possible regarding the requirements of the sea-grasses'. Since that time seagrass ecology has received a great deal of attention but the unexplained variability in species composition, distribution, and biomass of seagrass beds in the Central Coast lakes still leaves us in a position where we could state very little without qualification. There is certainly some evidence from Australian studies and elsewhere that seagrass beds undergo drastic changes even under natural (non-impacted) conditions (Larkum and West, 1983). One specific area which remains unstudied is the means by which populations cope with environmental change. What is the importance of acclimatization in environmental response, and/or ecotypic variation?

In North America Phillips (*in* Phillips and McRoy, 1980: 29-40) has reported the use of leaf width to indicate environmental stress: narrow leaves indicate stress, broader leaves more optimum conditions. There have been no such morphometric studies in eastern Australia, though Larkum *et al.* (1984) recorded leaf widths at various sites for *Zostera capricorni* in Botany Bay.

TABLE 6

Area of seagrass in Tuggerah Lakes expressed as a percentage of the total lake area, compared with values given by Higginson (1968). Note that the values given in Higginson are for the community dominants only whereas data in the present study record all species in mixed beds

	Higginson (1968)			Present study
	May '63	Aug '65	Aug '66	Period: Winter '80/Summer '85
Zostera capricorni	27.8	27.5	27.7	11.2-21.7
Halophila ovalis	0.8	0.5	0.6	5.3-17.4
Ruppia megacarpa	13.3	3.3	0.0	2.3-10.7
Total seagrass	41.9	31.2	28.2	17.1-25.0

CONCLUSIONS

Long-term studies in southern Lake Macquarie and the Tuggerah Lakes, of both the area covered by seagrasses and the biomass of the major species, *Zostera capricorni*, showed that marked fluctuations are inherent in the nature of the communities. Over the period 1980-1985 these fluctuations did not appear to follow any regular or even predictable pattern. Data such as those presented by Higginson (1965, 1968), King (1986b) and King and Holland (1986) cannot be directly used as baseline data since they present the results of only single surveys and therefore fail to take into account this variation in time. Long-term changes can be recognized by comparing earlier data with those here but most earlier information is less detailed. Relative changes in abundance and distribution of seagrass can be detected by following long-term change, in which case the extent of change must be greater than the magnitude of the changes due to inherent variability, or by comparison against a control area. The selection of a control area is difficult since apart from the habitat both the species and their distribution must be similar. It is doubtful whether such control areas exist let alone can be recognized. In the case of a specific impact such as the discharge of cooling water effluent into Myuna Bay since early 1982 it may be valid to use the combined data for all other sites in southern Lake Macquarie as a control. When this was done there were no significant differences between Myuna Bay and the 'control' area for either area of seagrass or biomass of *Zostera capricorni* (Fig. 2) but such areas require monitoring to see if the trends which are apparent from the graph are continued.

Even large changes in seagrass distribution must be interpreted with caution. The disappearance of *Ruppia megacarpa* from large areas of the Tuggerah Lakes in 1965 could have been interpreted as resulting from drought conditions which existed at that time and its reappearance in quantity since 1984 may be due to subsequent environmental change. Such marked fluctuations are not a peculiarity of this lake system. Personal observations in Smiths Lake (Myall Lake system) show that *Ruppia* populations there exhibit changes of a similar magnitude.

On the basis of what few data are available from earlier studies it is apparent that the area of seagrass recorded in earlier studies of both Lake Macquarie and Tuggerah Lakes has decreased. In both cases this may be attributed to increasing turbidity, but this has not been demonstrated.

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Non-contemporaneity in the Marulan Batholith

PAUL F. CARR and BRIAN G. JONES

CARR, P. F., & JONES, B. G. Non-contemporaneity in the Marulan Batholith. *Proc. Linn. Soc. N.S.W.* 109 (2), 1986: 63-67.

The Lockyersleigh Adamellite and Chapmans Creek Granodiorite crop out near Brayton New South Wales and form part of the composite Marulan Batholith. A Rb-Sr whole-rock isochron for these two plutons indicates an emplacement age of 326 ± 6Ma with an initial $^{87}Sr/^{86}Sr$ ratio of 0.7049. These isotopic data are very similar to published data for the Carboniferous Bathurst Batholith (mean age of 310Ma) but differ significantly from published data which indicate a Devonian age (approximately 400Ma) for other plutons in the Marulan Batholith. The low initial $^{87}Sr/^{86}Sr$ ratio implies that the two plutons at Brayton were derived from an isotopically relatively unevolved I-type source.

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INTRODUCTION

The Marulan Batholith and comagmatic igneous rocks of the Bindook Volcanic Complex crop out in the eastern part of the Lachlan Fold Belt of New South Wales (Fig. 1) and comprise a series of plutonic rocks and associated lavas and pyroclastics which have an outcrop area of approximately 1350km^2. Naylor (1939) considered that the batholith was intruded during Devonian time and isotopic dating by Carr *et al.* (1980) and Flood *et al.* (1982) has confirmed this age of emplacement. Two plutons of the batholith which occur near Brayton (Fig. 1) were assigned a Devonian age by Naylor (1939) whereas Brunker and Offenberg (1968) regarded these intrusions as Carboniferous. Isotopic data for the Brayton plutons have not been published previously and the present investigation, which is part of a larger project on the Marulan Batholith and Bindook Volcanic Complex, was undertaken to resolve the age of these intrusions by using Rb-Sr isotopic techniques.

MARULAN BATHOLITH

Plutons of the composite Marulan Batholith form approximately 36% of the outcrop area of the southern half of the Bindook Volcanic Complex and show a compositional range from tonalite and granodiorite through adamellite to granite and alkali feldspar granite. Most plutons are relatively small and are elongate meridionally.

AGE CONSTRAINTS

The youngest stratified units with age-diagnostic fossil assemblages which are intruded by plutons of the Marulan Batholith are the Bungonia Limestone and the overlying Tangerang Formation. The Bungonia Limestone contains Ludlovian (Late Silurian) fossils in the lower part and a Lochkovian (earliest Devonian) fauna near the top of the formation (Jones *et al.*, 1981), and Lochkovian faunas have been recorded from the basal part of the Tangerang Formation (Jones *et al.*, 1984; Jones *et al.*, 1986; Mawson, 1975). The oldest rocks which unconformably overlie plutons of the batholith are Late Devonian marine and terrestrial strata which crop out to the west of Bungonia (Naylor, 1939). These stratigraphic data indicate that the batholith in general is younger than earliest Devonian but older than Late Devonian.

Fig. 1. Simplified geological map showing location of the Bathurst Batholith and the Marulan Batholith together with the comagmatic Bindook Volcanic Complex. Sample locations and detailed geology of the Brayton district are shown in the inset.

Evernden and Richards (1962) obtained a Carboniferous age (313Ma; as recalculated using the constants of Steiger and Jager, 1977) for a biotite separate from a pluton of the batholith and commented on the discordance between the stratigraphic age and the isotopic data. Vallance (*in* Packham, 1969: 198) and O'Reilly (1972) were also aware of the anomaly.

K-Ar dates on biotite separates from three different plutons of the southern part of the batholith indicate a mean age of emplacement of 398Ma (Carr *et al.*, 1980). The average Rb-Sr biotite age for the Marulan Batholith is 400Ma (Flood *et al.*, 1982) and both the K-Ar and Rb-Sr biotite data are consistent with a 12-point whole-rock Rb-Sr isochron age of 419 ± 33 (Flood *et al.*, 1982).

BRAYTON PLUTONS

The oldest rocks in the Brayton district (Fig. 1) are a Late Ordovician sequence of isoclinally folded slate, quartzite and phyllite which is unconformably overlain by sedimentary strata and basic volcanic rocks of Silurian age (MacRae, 1978). These basic volcanic rocks are overlain by, or faulted against, dacite and tuff of the Bindook Volcanic Complex which Carr *et al.* (1980) and Jones *et al.* (1984) have equated with the Early Devonian Tangerang Formation of the Bungonia region.

The Ordovician to Early Devonian sequence at Brayton was intruded by two plutons of the Marulan Batholith, the Lockyersleigh Adamellite and Chapmans Creek Granodiorite. O'Reilly (1972) referred to the latter intrusion as the Towrang granodiorite but as the name Towrang Beds has priority (Brunker and Offenberg, 1968) the intrusion is named herein as the Chapmans Creek Granodiorite. Tertiary basalts, dolerites and sedimentary strata post-date the adamellite and granodiorite (O'Reilly, 1972).

Stratigraphic criteria impose only broad limits on the age of the Lockyersleigh Adamellite and Chapmans Creek Granodiorite. The intrusive relationship with the rocks of the Bindook Volcanic Complex indicates a post-Early Devonian emplacement whereas the non-metamorphosed Tertiary rocks indicate intrusion prior to the Tertiary. The petrography of the various rocks and the contact metamorphic effects associated with the intrusion of the adamellite and granodiorite have been described in detail by O'Reilly (1972). Both plutons are composed of holocrystalline, granular rocks containing perthitic alkali feldspar, plagioclase, quartz, biotite and accessory sphene, iron-titanium oxides, zircon and apatite. Hornblende occurs in the adamellite but is absent from the granodiorite. Aplite veins composed of alkali feldspar and quartz occur in both plutons.

TABLE 1

Rb-Sr data for Lockyersleigh Adamellite (LA) and Chapmans Creek Granodiorite (CCG)

SAMPLE	PLUTON	Rb (ppm)	Sr (ppm)	$^{87}Rb/^{86}Sr$	$^{87}Sr/^{86}Sr$ ($\pm 2\sigma$)
1120	LA	167	534	0.905	.70899 ± 19
1121	LA	50	1029	0.141	.70553 ± 11
1122	CCG	140	671	0.606	.70802 ± 05
1170	CCG	140	164	2.471	.71638 ± 05
1188	LA	152	615	0.715	.70827 ± 05

Rb-Sr data have been determined for five whole-rock samples from the two plutons at Brayton and the results are presented in Table 1 and Fig. 2. Regression of the data for all five samples yields an age of 328 ± 6Ma (Table 2) but the high value for the mean square of the weighted deviates (MSWD = 15.00) indicates that the scatter is in excess of that attributable to analytical uncertainty alone. Exclusion of sample 1122 from the regression reduces the MSWD to an acceptably low value of 2.48 (Table 2) but does not make a significant difference to the date (326±6Ma). The resultant initial $^{87}Sr/^{86}Sr$ ratio is 0.7049.

TABLE 2

Regression analyses for Lockyersleigh Adamellite and Chapmans Creek Granodiorite

SAMPLES FOR MODEL 1 ISOCHRON	INITIAL $^{87}Sr/^{86}Sr$ (± 2σ)	AGE (Ma) (± 2σ)	MSWD
1120, 1121, 1122, 1170, 1188	.7049±1	328±6	15.00
1120, 1121, 1170, 1188	.7049±1	326±6	2.48

Age calculated using $\lambda = 1.42 \times 10^{-11}$ yr^{-1}

DISCUSSION

The Rb-Sr isochron for the four samples indicates that the two plutons at Brayton were emplaced during the Carboniferous and are not contemporaneous with other plutons from the Marulan Batholith which have been dated by Carr *et al.* (1980) and Flood *et al.* (1982). The age of the Lockyersleigh Adamellite and Chapmans Creek Granodiorite does imply a temporal correlation with the Bathurst Batholith which crops out over an area of at least 1600km^2 in the Bathurst region of New South Wales (Fig. 1) and has a mean age of emplacement of 310Ma (Facer, 1979). In addition, the initial

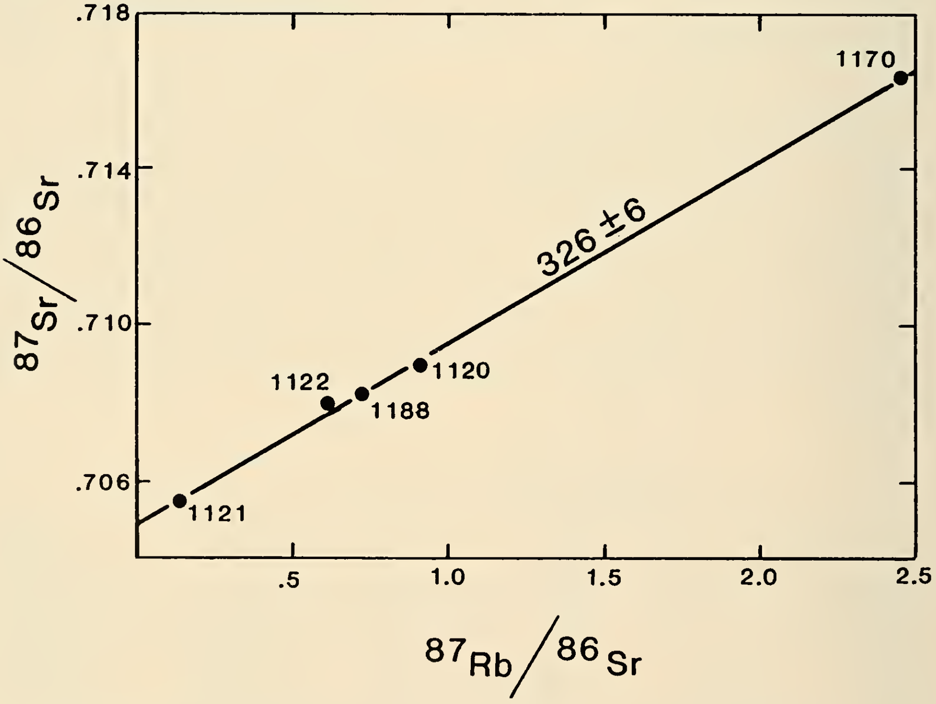

Fig. 2. Isochron diagram for the Lockyersleigh Adamellite and Chapmans Creek Granodiorite.

$^{87}Sr/^{86}Sr$ ratio of 0.7049 for the Brayton plutons is indistinguishable from the initial ratio of 0.7047 for the Bathurst Batholith (Flood *et al.*, 1982) but is significantly different from the initial ratio of 0.7061 for the Marulan Batholith and the Bindook Volcanic Complex (Flood *et al.*, 1982).

The K-Ar biotite age of 313Ma (recalculated) obtained by Evernden and Richards (1962) for a pluton of the Marulan Batholith is similar to the mean age of the Bathurst Batholith (310Ma) and the plutons at Brayton (326Ma). This similarity in age may be fortuitous due to the loss of radiogenic argon or it may indicate the presence of another Carboniferous pluton in the Marulan Batholith.

Mineralogical, chemical and isotopic properties of the granitic rocks of the Lachlan Fold Belt generally permit subdivision into one of two groups (White and Chappell, 1983) which reflect derivation by partial melting of igneous rocks ('I-type granitoids') or sedimentary rocks ('S-type granitoids'). The low initial $^{87}Sr/^{86}Sr$ ratio (0.7049) obtained in the present study indicates that the plutons at Brayton were generated from an isotopically relatively unevolved source and the ratio is consistent with the I-type mineralogical and chemical characteristics which White and Chappell (1983) have documented for the Marulan and Bathurst Batholiths.

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An Atlas of Seeds and Fruits from Macquarie Island

DANA M. BERGSTROM

BERGSTROM, D. M. An atlas of seeds and fruits from Macquarie Island. *Proc. Linn. Soc. N.S.W.* 109 (2), 1986: 69-90.

Seeds and fruits of 30 members of the vascular flora from subantarctic Macquarie Island are described and illustrated. The atlas was constructed to aid in identification of fossils found in peat deposits on the island.

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INTRODUCTION

Macquarie Island, (158°57′E, 54°30′S) in the Southern Ocean, is one of a number of small isolated islands in the subantarctic zone. Like other subantarctic islands it has a small vascular flora (Greene and Walton, 1975). The island's flora consists of about 45 vascular plant species and 110 bryophyte species. Table 1 lists vascular species and includes all recent taxonomic revisions.

Climate during the Holocene has enabled extensive peat formations to develop on the island. Fossil evidence of past vegetation, in the form of pollen grains, spores, seeds, leaf and stem fragments, is preserved in these peat deposits. This atlas was constructed to aid in the identification of seeds and fruits found in peat samples. Analysis of the fossil record from peat deposits is providing valuable insight into vegetation dynamics and tectonic processes on the island (Selkirk *et al.*, 1983; Selkirk *et al.*, 1984; Bergstrom, 1985). The usefulness of macrofossil analysis, in association with microfossil analysis, in the reconstruction of past vegetation is becoming increasingly apparent (GreatRex, 1983; Griffin, 1977; Bergstrom, 1985; Huckerby and Oldfield, 1976; Campbell *et al.*, 1973). GreatRex (1983) reported that most seeds and fruit found in surface samples of mires in Britain came from within 1m of the sampling point. Seeds coming from greater distances were adapted for dispersal by wind or water. He suggested that reconstruction of past communities from assemblages in a single sample would apply only to the immediate vicinity of the sampling point.

There have been numerous comments in the literature on the stability of the morphology of seeds (Montgomery, 1977; Corner, 1976; Berggren, 1969), with the last two authors suggesting the value of the use of seed morphology as a tool in systematics.

METHODS

Collections

Seeds and fruits were collected from plants on Macquarie Island during the summers of 1979-80, 1983-84. The dry seeds and fruits are part of the Herbarium, School of Biological Sciences, Macquarie University, but will be lodged with the National Herbarium of New South Wales, Royal Botanic Gardens, Sydney, as voucher specimens. Of the 40 angiosperm species known from the island, 10 have not been collected with either seeds or fruits, or with mature seeds or fruit.

Form of Descriptions

All descriptions are for identification of seeds and fruits under a dissecting microscope. They are for the smallest dispersal unit, be it a seed or indehiscent fruit such as an achene. On occasions when it was hard to determine whether seeds or fruit were dispersed, descriptions for both seed and fruit are given.

The descriptions are divided into a number of sections.

a) **Dimensions**

The position of the hilum or basal scar is taken as the base of the seed or fruit. The

TABLE 1

Extant Vascular Flora of Macquarie Island

Nomenclature after Copson (1984) and Seppelt *et al.* (1984) except where indicated

Lycopodiaceae —	*Lycopodium* sp.
Blechnaceae —	*Blechnum penna-marina*
Grammitidaceae —	*Grammitis poeppigeana*
Hymenophyllaceae —	*Hymenophyllum peltatum*
Aspidiaceae —	*Polystichum vestitum*
Apiaceae —	*Azorella selago*
	Hydrocotyle sp.
Araliaceae —	*Stilbocarpa polaris*
Asteraceae —	*Cotula plumosa*
	Pleurophyllum hookeri
Brassicaceae —	*Cardamine corymbosa*
Callitrichaceae —	*Callitriche antarctica*
Caryophyllaceae —	*Cerastium fontanum*
	Colobanthus muscoides
	C. quitensis
	Stellaria decipiens
	S. media
Crassulaceae —	*Crassula moschata*
Cyperaceae —	*Carex trifida*
	Isolepis aucklandicus(1)
	* *Uncinia divaricata*
	* *U. hookeri*
Haloragaceae —	*Myriophyllum triphyllum*
Juncaceae —	*Juncus scheuchzerioides*
	Luzula crinita var. *crinita*(2)
Onagraceae —	*Epilobium brunnescens* var. *brunnescens*(3)
	E. pedunculare(4)
Orchidaceae —	*Corybas macranthus*
Poaceae —	*Agrostis magellanica*
	Anthoxanthum odoratum
	Deschampsia chapmanii
	D. penicillata
	Festuca contracta
	Poa annua
	P. foliosa
	P. hamiltonii
	P. litorosa
	Puccinellia macquariensis
Polygonaceae —	*Rumex crispus*
Portulacaceae —	*Montia fontana*
Ranunculaceae —	*Ranunculus biternatus*
Rosaceae —	*Acaena magellanica*
	A. minor
Rubiaceae —	*Coprosma pumila*
	Galium antarcticum

(1) = *Scirpus aucklandicus* (Wilson, 1981); (2) = *Luzula campestris* (Edgar, 1975); (3) = *Epilobium nerteroides* (Raven and Raven, 1976); (4) = *Epilobium linnaeoides* (Raven and Raven, 1976).

* = specimens identified Karen Wilson (pers. comm., 1985).

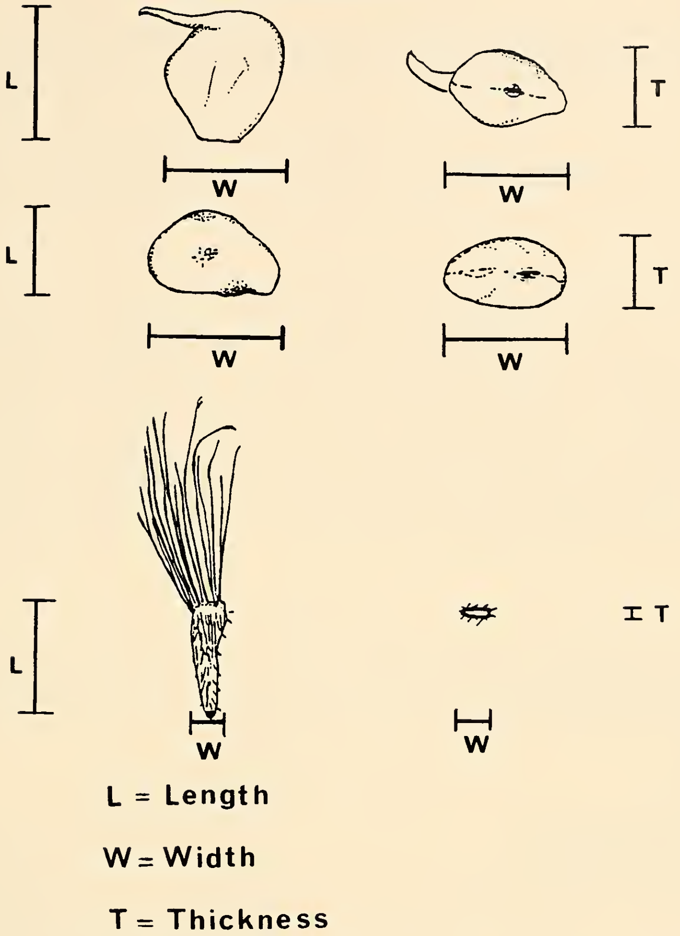


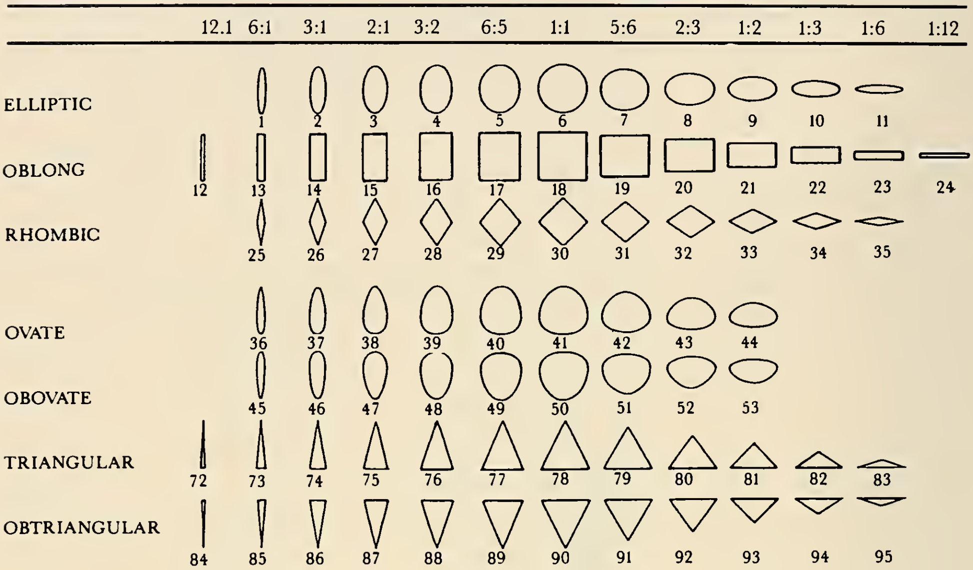
Fig. 1. Diagram illustrating how dimensions were determined. Three different seed/fruit types are shown.

length is measured from the base to the apex or, where a style is present, to the base of the style. The width is perpendicular to this and the thickness, perpendicular to the 2 axes. All measurements are taken at the widest point of the seeds or fruits. Fig. 1 shows how length, width and thickness measurements on three types of seeds and fruits were determined. The measurements given are the means of measurements on 10 seeds + standard error. The standard error by no means gives the range within the species, but Montgomery (1977) suggests that although seeds may vary in size, depending on growth conditions, the ratio of the measurements is usually constant. When 10 seeds were not available the number of seeds measured is given in the form of n = x, where x is the number measured.

b) Shape

The shape has been given in terms of longitudinal section (l.s.) and cross section (c.s.). These sections have been considered as simple symmetrical plane shapes. The shapes are delimited mathematically as ratios:

- in the case of l.s., length : width
- in the case of c.s., thickness : width.



Language equivalents:

ELLIPTIC
1-2 narrowly elliptic
3-4 elliptic
5 broadly elliptic
6 circular
7 transversely broadly elliptic
8-9 transversely elliptic
10-11 transversely narrowly elliptic

OBLONG
12 linear
13-14 narrowly oblong
15-16 oblong
17 broadly oblong
18 square
19 transversely broadly oblong
20-21 transversely oblong
22-23 transversely narrowly oblong
24 transversely linear

RHOMBIC
25-26 narrowly rhombic
27-28 rhombic
29 broadly rhombic
30 quadrate rhombic
31 transversely broadly rhombic
32-33 transversely rhombic
34-35 transversely narrowly rhombic

OVATE
36-37 narrowly ovate
38-39 ovate
40-41 broadly ovate
41-42 very broadly ovate
43-44 depressed ovate

OBOVATE
45-46 narrowly obovate
47-48 obovate
49-50 broadly obovate
50-51 very broadly obovate
52-53 depressed obovate

TRIANGULAR
72 linear triangular
73-74 narrowly triangular
75-76 triangular
77-78 broadly triangular
78-79 very broadly triangular
80-81 shallowly triangular
82-83 very shallowly triangular

OBTRIANGULAR
84 linear-obtriangular
85-86 narrowly obtriangular
87-88 obtriangular
89-90 broadly obtriangular
90-91 very broadly obtriangular
92-93 shallowly obtriangular
94-95 very shallowly obtriangular

Fig. 2. Chart of plane shapes and descriptive terminology (after Montgomery, 1977, after Systematics Association, 1962).

The numbers following the shape descriptions are serial numbers given by the Systematics Association Committee for Descriptive Biological Terminology (1962) to plane shapes, shown in Fig. 2.

c) **Comments**

Comments are self-explanatory. A glossary is provided at the end of the descriptions.

d) **Colour**

Colours of dry seeds and fruits were ascertained by use of the 'Revised Standard Soil Color Chart' by Oyana and Takehara (1967). This standard was chosen as it is widely available. The description method is based on a system in which colour can be measured by three attributes: **Hue** which represents the dominant spectral colour such as red or blue; **Value** — which represents the relative lightness of colour; **Chroma** — the relative purity of spectral colour. A serial number is given. Thus, Hue 7.5YR 6/8 consists first of the hue number (Hue 7.5YR), then the value number (6), followed by the chroma number (8). A description of the colour is also given (e.g. orange) based on terminology used by Oyana and Takehara (1967). All colours were assessed under the same natural light conditions.

PHOTOGRAPHS

The photographs (Figs 3-10) show seeds and fruits against a background of grey plasticine. The length-wise orientation of the figures has the hilum or fruit scar pointing towards the caption. Where possible seeds and fruits were positioned so that both the l.s. and c.s. could be viewed. The scale on each photograph indicates 1mm.

DESCRIPTIONS OF SEEDS AND FRUITS

APIACEAE

Azorella selago (Fig. 3**A**)
Length: 1.61 ±0.04mm
Width: 0.91 ±0.05mm
Thickness: 0.68 ± 0.06mm
Shape: —
Longitudinal section: elliptic (3-4) or irregular.
Cross section: varied, due to distortion from other mericarps at the commissure.
Comments: Mericarps. Surface rough with 5 distinct irregular longitudinal ridges. Persistent style 1.48 ± 0.5mm long. Floral remnant may be present.
Colour: Hue 10YR 7/6 bright yellow brown.

ARALIACEAE

Stilbocarpa polaris (Fig. 3**B**,**D**)
Length: 2.24 ± 0.03mm
Width: 0.92 ± 0.05mm
Thickness: 1.14 ± 0.05mm
Shape: —
Longitudinal section: broadly ovate (41-42).
Cross section: transversely elliptic (8-9) or irregular.
Comments: Seeds borne in black, shiny, spherical fruit, centre of which is hollow. Seed surface coarse, often with fleshy endocarp still attached. No hilum. Cream, persistent Y-shaped vascular trace on one surface. In arms of 'Y' there is a hole.
Colour: Hue 7.5YR 4/6 brown.

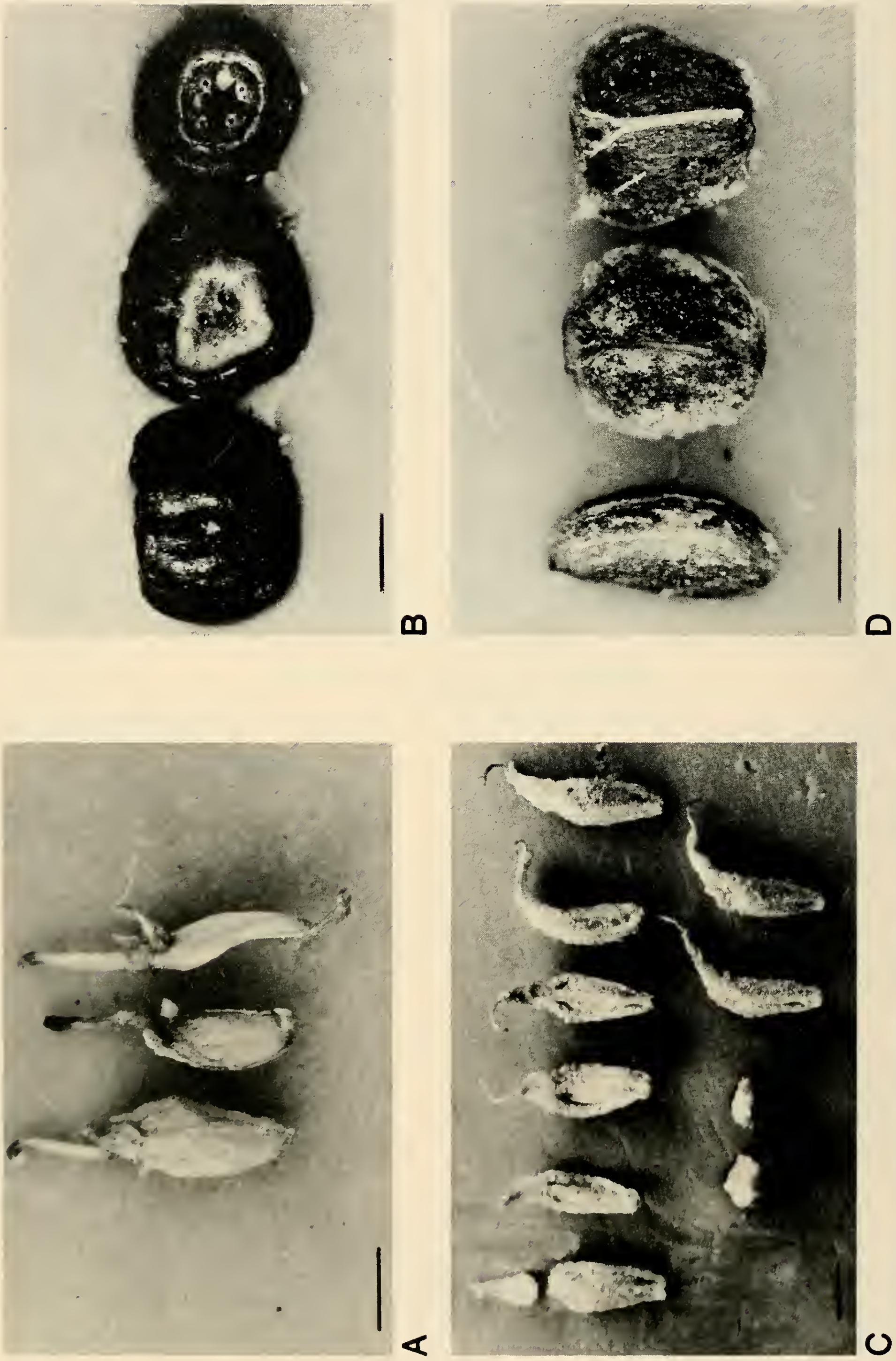


Fig. 3. **A** = *Azorella selago* mericarps. **B & D** = *Stilbocarpa polaris*, **B** = fruits, **D** = seeds. **C** = *Cotula plumosa* achenes. 1mm scales.

Fig. 4. **A** = *Pleurophyllum hookeri*, achenes. **B** = *Cardamine corymbosa*, seeds. **C** = *Cerastium fontanum* seeds. **D** = *Colobanthus muscoides* seeds. 1mm scales.

ASTERACEAE

Cotula plumosa (Fig. 3**C**)
Length: 2.04 ± 0.04mm
Width: 1.18 ± 0.03mm
Thickness: 0.94 ± 0.03mm
Shape: —
Longitudinal section: obovate (47).
Cross section: transversely elliptic (8).
Comments: Achene. Longitudinal axis curved. Surface of achene reticulate and coarsely punctate. Persistent style and tubular corolla.
Colour: Hue 10YR 7/4 dull yellow orange.

Pleurophyllum hookeri (Fig. 4**A**)
Length: 3.0 ± 0.14mm
Width: 0.88 ± 0.05mm
Thickness: 0.54 ± 0.02mm
Shape: —
Longitudinal section: narrowly obovate (45-46) to triangular (85-86).
Cross section: transversely oblong (21).
Comments: Achene with plumose pappus. Surface of achene velutinous, hairs white. Stylar and perianth remnants often present. Pappus hairs approximately 6mm long, unequal in length and bristly.
Colour: Hue 2.5YR dull reddish brown.

BRASSICACEAE

Cardamine corymbosa (Fig. 4**B**)
Length: 1.3 ± 0.02mm
Width: 1.0 ± 0.02mm
Thickness: 0.4 ± 0.02mm
Shape: —
Longitudinal section: elliptical to broadly elliptic (4-5).
Cross section: depressed ovate (44) or irregular.
Comments: Cotyledons accumbent with cotyledons and radicle indicated by a sulcus. Surface undulating, puncticulate and shiny. In c.s. the seeds compressed at margins. Funicular remnant light yellow orange (Hue 10Y).
Colour: Hue 10R 5/8 red, margins and hilum darker.

CARYOPHYLLACEAE

Cerastium fontanum (Fig. 4**C**)
Length: 0.7 ± 0.15mm
Width: 0.68 ± 0.01mm
Thickness: 0.54 ± 0.01mm
Shape: —
Longitudinal section: broadly obovate (49-50) or irregular.
Cross section: transversely oblong (19-20).
Comments: Hilum within deep notch. Surface coarsely papillate. Papillae low and rounded with ovoid stellate bases. Arrangement of papillae may be concentric, particularly along margins. Small, hyaline, protoxylem remnant attached to hilum.
Colour: Hue 5YR 5/8 bright reddish brown.

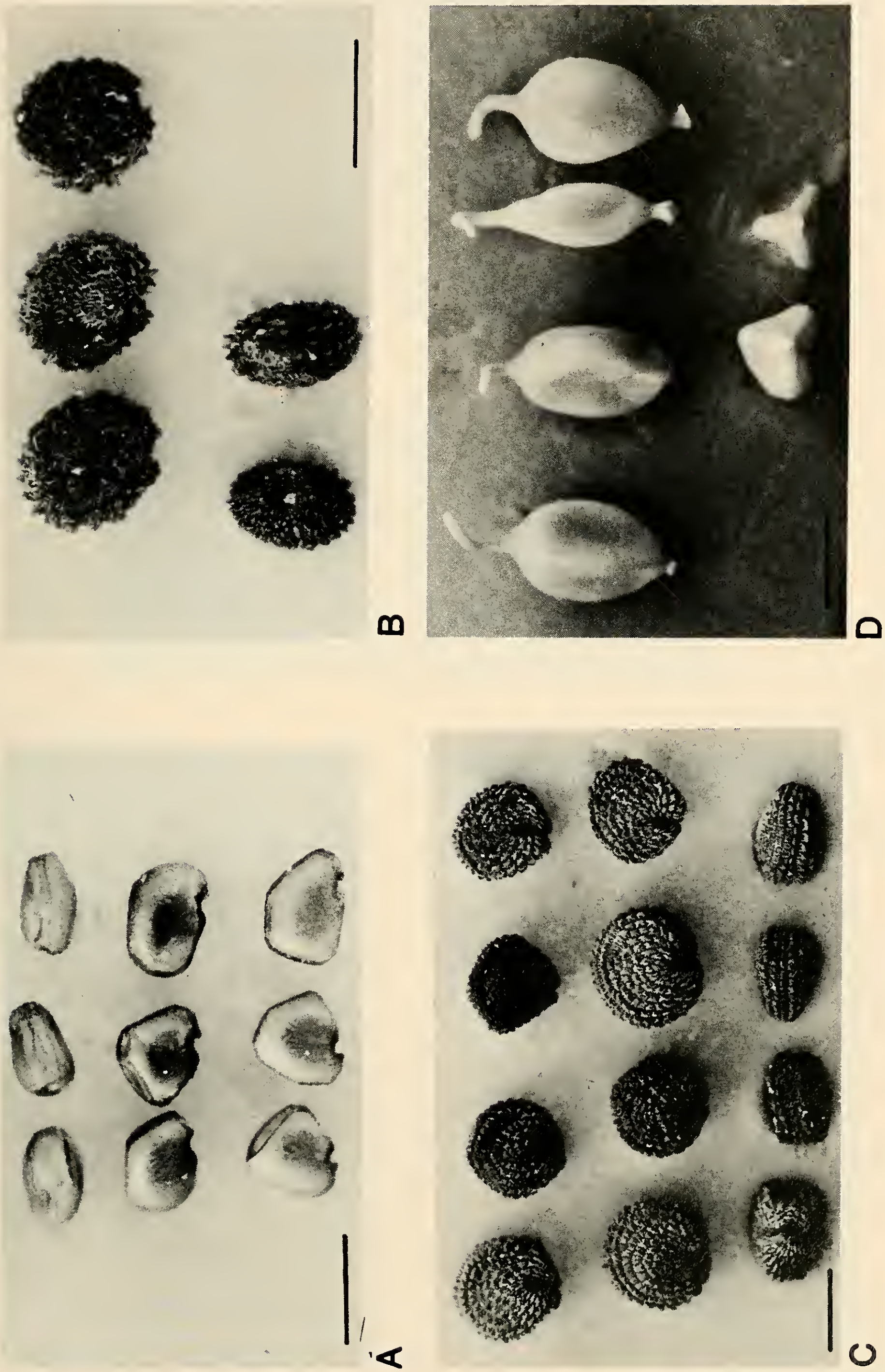


Fig. 5. **A** = *Colobanthus quitensis* seeds. **B** = *Stellaria decipiens* seeds. **C** = *Stellaria media* seeds. **D** = *Carex trifida* achenes. 1mm scales.

Colobanthus muscoides (Fig. 4**D**)
Length: 0.38 ± 0.002mm
Width: 0.65 ± 0.002mm
Thickness: 0.34 ± 0.002mm
Shape: —
Longitudinal section: depressed ovate (43-44) or irregular.
Cross section: transversely elliptic (8-9) or irregular.
Comments: Seeds slightly reniform. Margins often depressed forming sulcus (hence irregular in l.s.). Surface faintly colliculate and translucent. Minute white caruncle.
Colour: Hue 7.5YR 5/8 bright brown.

Colobanthus quitensis (Fig. 5**A**)
Length: 0.55 ± 0.02mm
Width: 0.62 ± 0.02mm
Thickness: 0.38 ± 0.01mm
Shape: —
Longitudinal section: depressed obovate (52-53), or irregular.
Cross section: transversely elliptic (8-9).
Comments: Margins often depressed forming sulcus (hence irregular in l.s.). Surface translucent and very faintly colliculate. Minute white caruncle.
Colour: Hue 5YR 5/8 bright reddish brown.

Stellaria decipiens (Fig. 5**B**)

Length: 0.98 ± 0.05mm	n = 7
Width: 0.97 ± 0.05mm	n = 7
Thickness: 0.64 ± 0.05mm	n = 7

Shape: —
Longitudinal section: circular (6) to irregular.
Cross section: transversely elliptic (8-9).
Comments: Hilum in deep notch. Concentric to irregular papillose surface. Papillae irregular and elongate, especially along margin and towards the hilum/base.
Colour: Hue 7.5R 4/8, 3/4, 3/6 red to dark red.

Stellaria media (Fig. 5**C**)
Length: 1.25 ± 0.04mm
Width: 1.26 ± 0.04mm
Thickness: 0.8 ± 0.01mm
Shape: —
Longitudinal section: broadly elliptic (5-7) or broadly obovate (48-51) or irregular.
Cross section: transversely elliptic (8-9), or oblong (20-21) or irregular.
Comments: Hilum in deep notch. Concentric rings of low rounded papillae on surface. Papillae arise from raised irregular or star-shaped bases.
Colour: Hue 7.5R 4/8 red.

CYPERACEAE

Carex trifida (Fig. 5**D**)

Length: 1.79 ± 0.02mm	n = 6
Width: 1.05 ± 0.06mm	n = 6
Thickness: 0.85 ± 0.06mm	n = 6

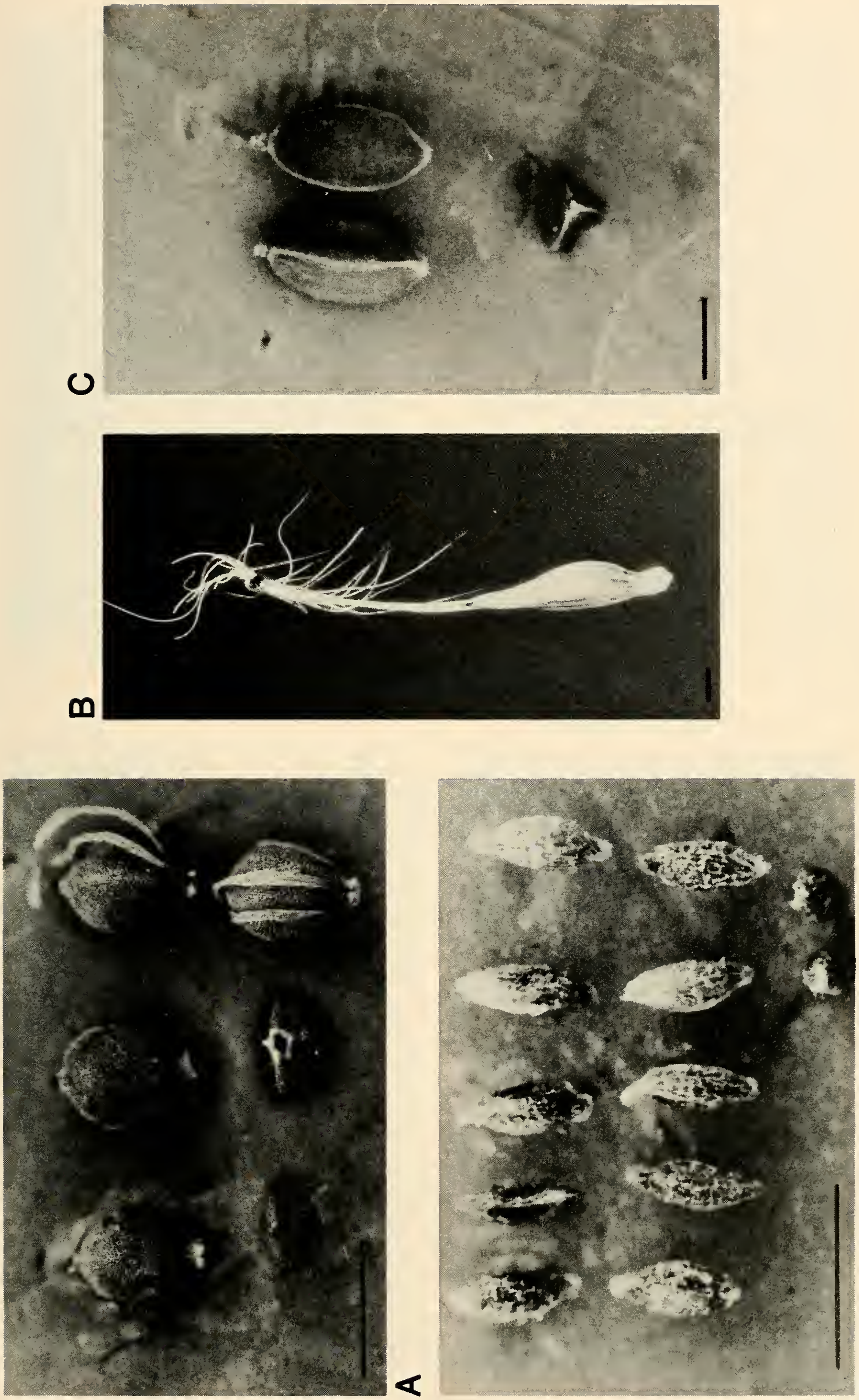


Fig. 6. **A** = *Isolepis aucklandicus* seeds. **B & C** = *Uncinia divaricata*, **B** = perigynium, **C** = achenes. **D** = *Juncus scheuchzerioides* seeds. 1mm scales.

Shape: —

Longitudinal section: elliptic (3-4).

Cross section: triangular to shallowly triangular (80-82).

Comments: Achene. Longitudinal axis concave-convex. Surface puncticulate and lustrous. Persistent, slender and contorted stylar remnant or just stylar base present. Fruit borne in papery perigynium which is ovate in l.s., transversely elliptic in c.s. (approximately 0.5mm long), somewhat fusiform with stipitate base.

Colour: Hue 10YR 8/6-8/8 yellow-orange.

Isolepsis aucklandicus (Fig. 6**A**)
Length: 1.01 ±0.01mm
Width: 0.73 ±0.01mm
Thickness: 0.45 ±0.01mm
Shape: —

Longitudinal section: broadly obovate (49-50).

Cross section: shallowly triangular (81-82), tending to planoconvex.

Comments: Margins slightly ridged, base stipitate. Surface areolate. Stylar base obtuse. Three loose, ligulate bristles from base, approximately 2× longer than achene.

Colour: Hue 7.5YR 4/6 brown.

Uncinia divaricata (Fig. 6**B**,**C**)
Length: 2.43 ±0.02mm
Width: 1.21 ±0.04mm
Thickness: 0.79 ±0.04mm
Shape: —

Longitudinal section: elliptic (3).

Cross section: shallowly triangular (80).

Comments: Achene. Sides slightly convex, edges rounded. Surface with profuse, low, rounded papillae. Achene borne in perigynium. Stylar remnant that, if intact, protrudes from perigynium and terminates in a hook. Surface of perigynium striated.

Colour: Hue 5YR 6/6-6/8 orange.

JUNCACEAE

Juncus scheuchzerioides (Fig. 6**D**)
Length: 0.7 ±0.01mm
Width: 0.25 ±0.01mm
Thickness: 0.25 ±0.01mm
Shape: —

Longitudinal section: elliptic (3).

Cross section: circular (6) or irregular.

Comments: Seed fusiform. Coarsely striate, whitish membranous coating on surface. There is often a prominent longitudinal ridge of tissue. Base is usually nodulous or sometimes minutely pointed.

Colour: Hue 5YR 5/8-6/8 bright reddish-brown to orange.

Luzula crinita var. *crinita* (Fig. 7**A**)
Length: 1.03 ± 0.01mm
Width: 0.53 ± 0.01mm
Thickness: 0.43 ± 0.01mm

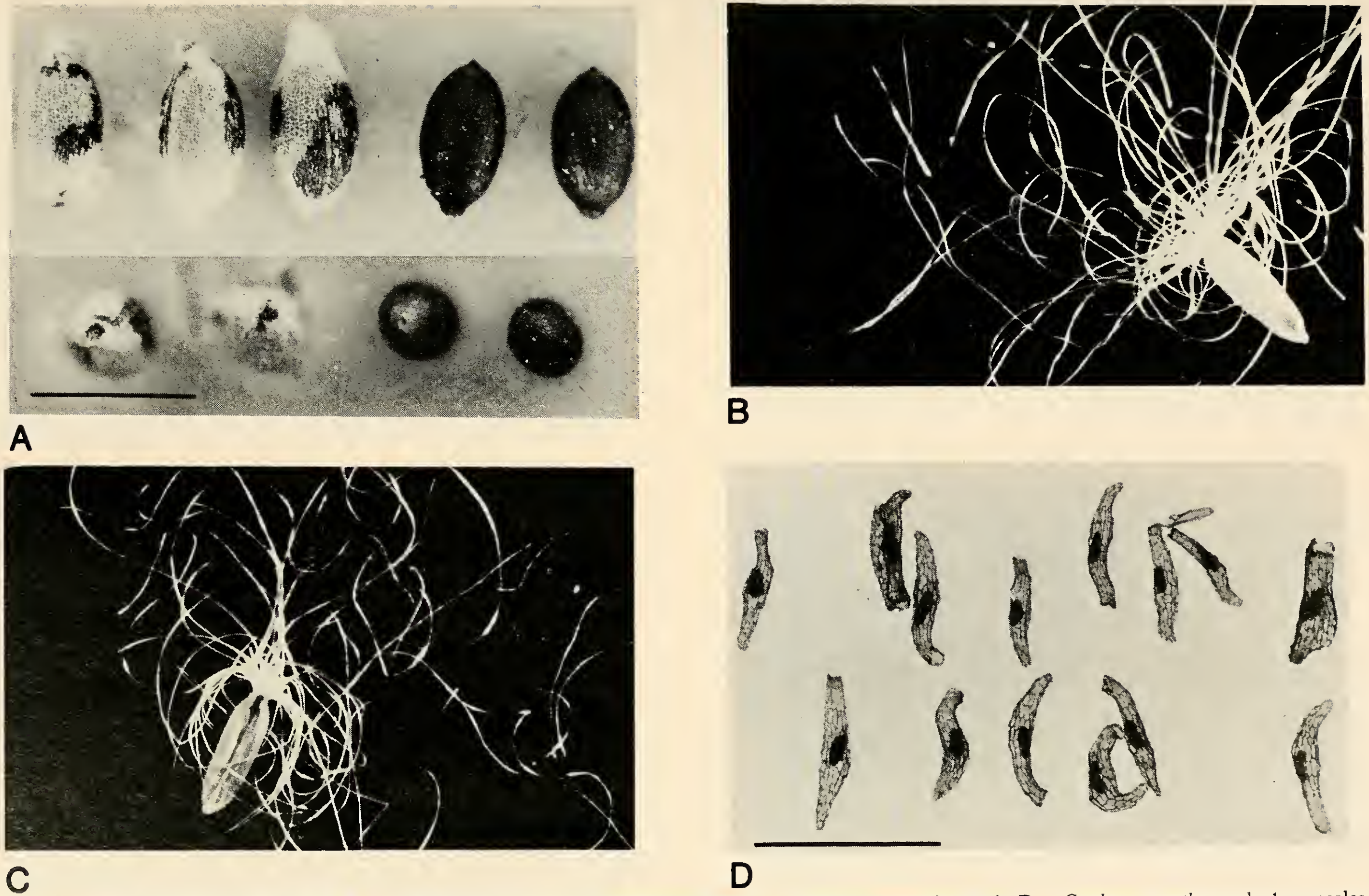


Fig. 7. **A** = *Luzula crinita* var *crinita* seeds. **B** = *Epilobium brunnescens* var. *brunnescens* seeds. **C** = *Epilobium pedunculare* seeds. **D** = *Corybas macranthus* seeds. 1mm scales.

Shape: —

Longitudinal section: elliptic (3).

Cross section: very broadly ovate (41-42).

Comments: Seed fusiform with minutely pointed apex and obtuse nodulous base, hilum inconspicuous. A large (1.26 ± 0.01mm, n = 10) whitish aril completely envelops the seed. Surface of seed reticulate and glistening. Surface of caruncle faintly striated and areolate.

Colour: Hue 7.5R 3/4-3/6 dark red, base darker.

ONAGRACEAE

Epilobium brunnescens var. *brunnescens* (Fig. 7**B**)

Length: 0.81 ±0.01mm

Width: 0.62 ± 0.01mm

Thickness: 0.2 ± 0.01mm

Shape: —

Longitudinal section: narrowly obovate to obovate (46-47).

Cross section: transversely oblong (20-21).

Comments: Sides often depressed. Longitudinal sulcus, deepening towards apex, terminating with cream coma. Surface longitudinally papillose.

Colour: Hue 5YR 6/8 orange.

Epilobium pedunculare (Fig. 7**C**)

Length: 0.70 ± 0.01mm

Width: 0.29 ± 0.01mm

Thickness: 0.21 ±0.04mm

Shape: —

Longitudinal section: narrowly obovate (46-47).

Cross section: transversely oblong (20-21).

Comments: Sides often depressed. Surface longitudinally papillose. Longitudinal sulcus, deepening towards apex, and terminating with cream coma. Base minutely pointed.

Colour: Hue 5YR 6/8 orange.

ORCHIDACEAE

Corybas macranthus (Fig. 7**D**)

Length: 0.67 ± 0.03mm

Width: 0.12 ± 0.01mm

Thickness: approx. 0.1mm

Shape: —

Longitudinal section: elliptic (1) or irregular (e.g. twisted).

Cross section: circular (6) or irregular.

Comments: Small spherical embryo in transparent membranous reticulate seed coat. Base tapering or blunt.

Colour: Hue 10YR 8/3 light yellow-orange.

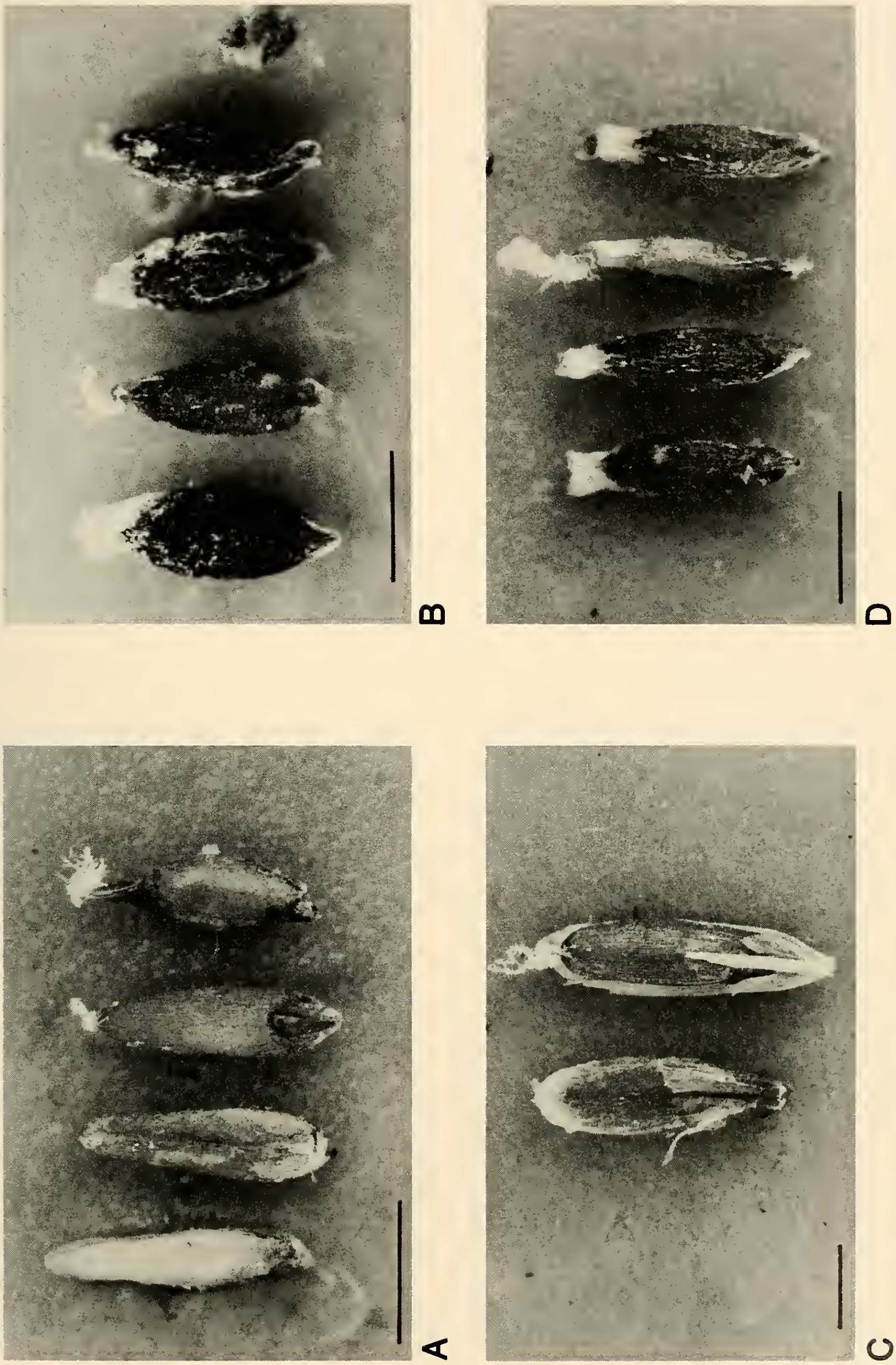


Fig. 8. **A** = *Agrostis magellanica* caryopsis. **B** = *Deschampsia chapmanii* caryopsis. **C** = *Festuca contracta* caryopsis. **D** = *Poa annua* caryopsis. 1mm scales.

POACEAE

Agrostis magellanica (Fig. 8**A**)
Length: 1.5 ± 0.01mm n = 7
Width: 0.52 ± 0.03mm n = 7
Thickness: 0.42 ± 0.02mm n = 7
Shape: —
Longitudinal section: narrowly elliptic (2-3).
Cross section: broadly elliptic (5).
Comments: Caryopsis. Apex minutely pointed. Small coma present. V-shaped groove near fruit scar. Surface sometimes concave.
Colour: Hue 7.5YR 7/8 yellow-orange.

Deschampsia chapmanii (Fig. 8**B**)
Length: 1.02 ± 0.03mm
Width: 0.47 ± 0.02mm
Thickness: 0.45 ± 0.01mm
Shape: —
Longitudinal section: obovate (47).
Cross section: circular (6).
Comments: Caryopsis fusiform. Nodulous apex terminating in small coma. Apiculate base with lacerate fruit scar. Surface rugose.
Colour: Hue 7.5YR 5/8.

Festuca contracta (Fig. 8**C**)
Length: 3.19 ± 0.01mm n = 2
Width: 1.16 ± 0 n = 2
Thickness: 0.58 ± 0.04mm n = 2
Shape: —
Longitudinal section: narrowly obovate (46).
Cross section: depressed obovate (43).
Comments: Caryopsis. Base minutely pointed, oblique fruit scar. Apex obtuse with exocarp extending into wing. Dark stripe on concave surface. Surface rugulose.
Colour: Hue 7.5YR 5/8 bright brown.

Poa annua (Fig. 8**D**)
Length: 1.48 ± 0.06mm n = 5
Width: 0.57 ± 0.02mm n = 5
Thickness: 0.38 ± 0.02mm n = 5
Shape: —
Longitudinal section: narrowly elliptic (2-3).
Cross section: irregular.
Comments: Caryopsis. Base blunt, apex terminating in a short white coma. Surface rugose.
Colour: Hue 10YR 6/8.

Poa foliosa (Fig. 9**A**)
Length: 1.9 ± 0.02mm
Width: 0.44 ± 0.01mm
Thickness: 0.43 ± 0.01mm

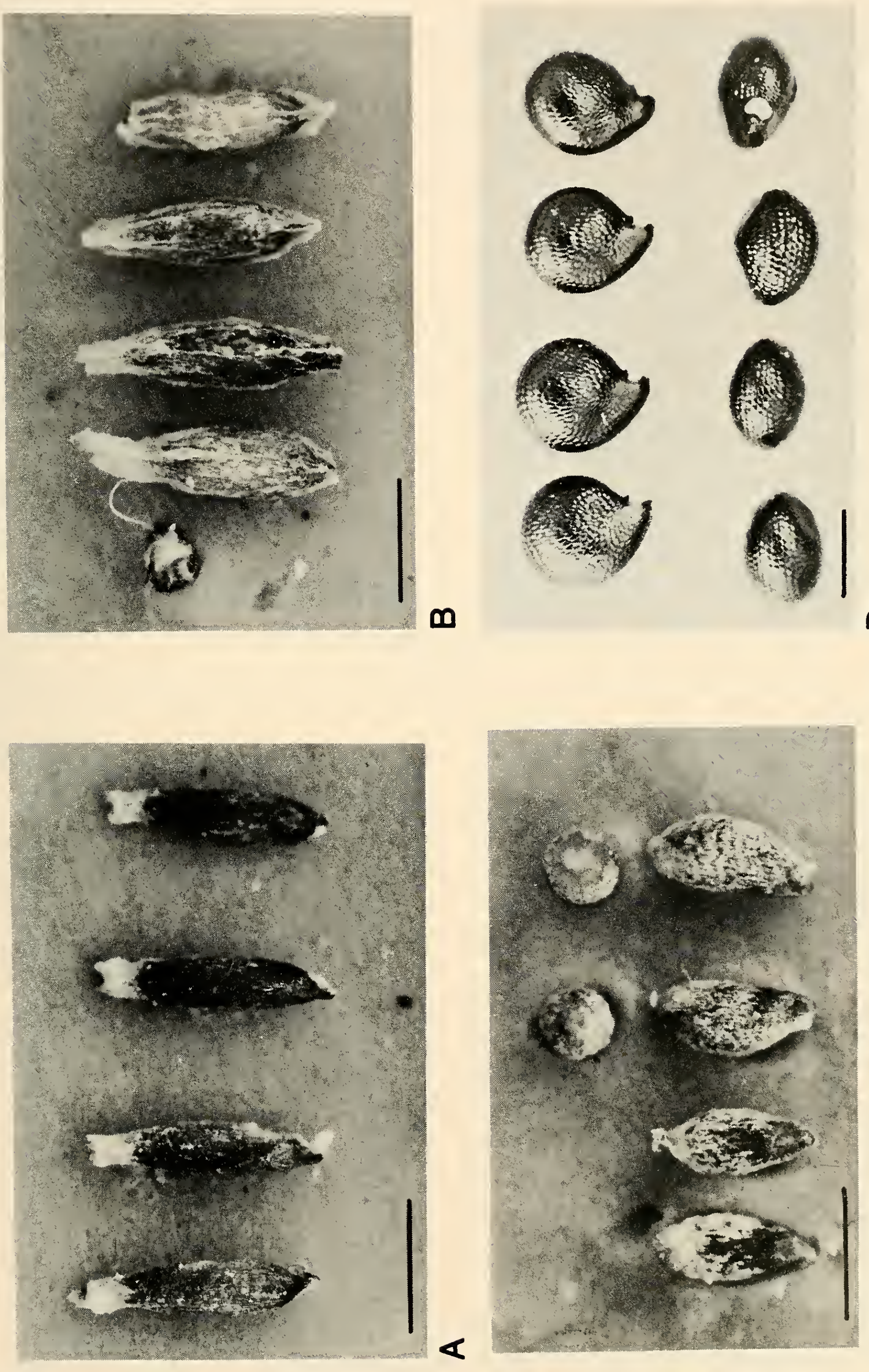


Fig. 9. **A** = *Poa foliosa* caryopsis. **B** = *Poa hamiltonii* caryopsis. **C** = *Puccinellia macquariensis* caryopsis. **D** = *Montia fontana* seeds. 1mm scales.

Shape: —
Longitudinal section: narrowly elliptic (1-2).
Cross section: broadly triangular (78).
Comments: Caryopsis. Sides often concave. Apex minutely pointed. Fruit-scar white, rough surfaced and blunt. Surface translucent and rugulose.
Colour: Hue 7.5YR 5/8 bright brown.

Poa hamiltonii (Fig. 9**B**)
Length: 1.94 ± 0.06mm
Width: 0.56 ± 0.01mm
Thickness: 0.53 ± 0.02mm
Shape: —
Longitudinal section: narrowly elliptic (1-2).
Cross section: circular (6) or irregular.
Comments: Caryopsis. Exocarp extending beyond rest of fruit by approximately 0.5mm and terminating in small white coma at apex.
Colour: Hue 7.5YR 5/8 bright brown.

Puccinellia macquariensis (Fig. 9**C**)
Length: 1.67 ± 0.04mm
Width: 0.56 ± 0.02mm
Thickness: 0.47 ± 0.02mm
Shape: —
Longitudinal section: narrowly elliptic to elliptic (2-3).
Cross section: broadly elliptic to circular (4-6).
Comments: Caryopsis fusiform, apex minutely pointed. Seed coat forming cream fruit-scar at base. Surface rugose.
Colour: Hue 2.5YR 4/8 reddish brown.

PORTULACACEAE

Montia fontana (Fig. 9**D**)
Length: 1.5 ± 0.22mm
Width: 1.2 ± 0.01mm
Thickness: 0.9 ± 0.01mm
Shape: —
Longitudinal section: obovate to broadly obovate (48-49).
Cross section: transversely elliptic (8).
Comments: Embryo coiled. Compressed, keeled edge ascending from hilum. Surface colliculose with regular, tending to concentric pattern. Very shiny (lustrous). Obvious pale yellow caruncle (Hue 2.5Y 8/4) with areolate surface.
Colour: Hue 5RP 1.7/1 purplish black.

RANUNCULACEAE

Ranunculus biternatus (Fig. 10**A**)
Length: 1.9 ± 0.03mm
Width: 1.8 ± 0.04mm
Thickness: 1.3 ± 0.02mm
Shape: —
Longitudinal section: very broadly ovate (41-42).
Cross section: broadly ovate (40-41).

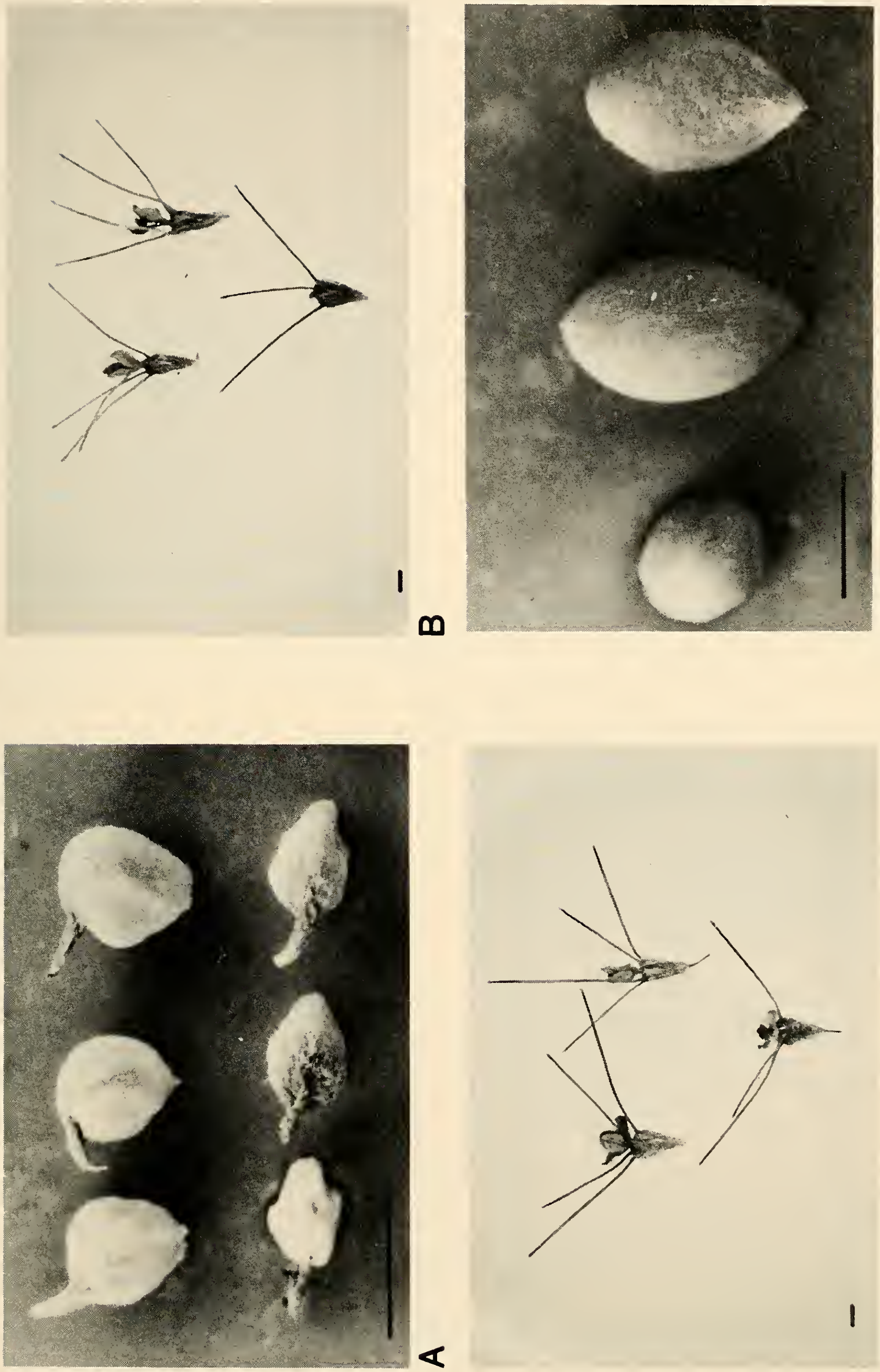


Fig. 10. **A** = *Ranunculus biternatus* achene. **B** = *Acaena magellanica* achenes. **C** = *Acaena minor* achenes. **D** = *Coprosma pumila* seeds. 1mm scales.

Comments: Achene. Deep sulcus ascending from hilum and fruit scar to base of lateral persistent style. Style often recurved with terminal hook. Surface irregular and rugose.
Colour: Hue 10YR 8/1.2-8/4 light grey to light yellow-orange. Apex and style darker.

ROSACEAE

Acaena magellanica (Fig. 10**B**)
Length: 3.1 ±0.06mm
Width: 1.11 ±0.03mm
Thickness: 1.11 ±0.03mm
Shape: —
    Longitudinal section: obtriangular (87).
    Cross section: broadly oblong to square (17-18).
Comments: Achene enclosed in hardened villous calyx (hairs white) which is endowed with 4 subulate spines approximately 8mm long. Spines barbed at tip. Corolla and stylar remnant, or at least persistent stylar base, present.
Colour: 2.5Y 7/6 bright yellowish brown.

Acaena minor (Fig. 10**C**)
Length: 3.16 ± 0.1mm
Width: 1.1 ±0.03mm
Thickness: 1.0 ± 0.03mm
Shape: —
    Longitudinal section: obtriangular (87).
    Cross section: broadly oblong to square (17-18).
Comments: Achene enclosed in hardened villous calyx (hairs white) which is endowed with 4 subulate spines approximately 6mm long. Spines barbed at tip. Corolla and stylar remnant, or at least persistent stylar base, present.
Colour: Hue 7.5YR 6/8 orange.

RUBIACEAE

Coprosma pumila (Fig. 10**D**)
Length: 2.5 ± 0.1mm
Width: 1.58 ± 0.03mm
Thickness: 1.3 ± 0.01mm
Shape: —
    Longitudinal section: obovate (48).
    Cross section: broadly elliptic (5).
Comments: Seed fusiform. Longitudinal axis curved. The base is minutely pointed with hilum inconspicuous. Surface rugulose.
Colour: Hue 10YR 7/6 bright yellow brown.

GLOSSARY

Accumbent Lying face to face
Achene A dry, indehiscent, one-seeded fruit
Areolate Having a distinct but fine network of spaces
Aril An appendage or outer covering of a seed, growing from hilum or funiculus
Bristle A stiff hair
Caruncle An aril at or about the hilum or funiculus
Colliculate Covered with small, rounded elevations, or hillocks
Coma A tuft of hairs covering apex

Commissure A junction or seam
Fruit Scar Scar on fruit indicating point of attachment to parent plant
Fusiform Swollen in the middle and tapering towards the ends
Funiculus Stalk by which a seed is attached to ovary wall or placenta
Hilum Scar on a seed indicating point of attachment to funiculus
Indehiscent Not opening
Ligulate Strap-shaped
Mericarp 1-seeded portion of fruit which may/may not split at maturity
Nodulous With small knobs
Papillate Small, nipple-shaped projections
Perigynium Sheath which envelops achenes belonging to the Cyperaceae
Punctate Marked with dots or depressions
Puncticulate Finely punctate
Reticulate Netted, more distinct than areolate
Rugose Coarsely wrinkled
Rugulose With very fine wrinkles
Stellate Star-like
Stipitate With a short stalk
Sulcus A groove or furrow
Velutinous Having fine straight hairs
Villous Having long silky hairs

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Notes on the Biology of Adult and Immature Amycterinae (Coleoptera, Curculionidae)

ANNE T. HOWDEN
(Communicated by C. N. SMITHERS)

HOWDEN, A. T. Notes on the biology of adult and immature Amycterinae (Coleoptera, Curculionidae). *Proc. Linn. Soc. N.S.W.* 109 (2), 1986: 91-105.

Adults of the endemic Australian weevil subfamily Amycterinae feed primarily on monocotyledons but a few eat dicotyledons. The varied morphology of the adult mouthparts is shown to correspond to the texture of the food plant. Species which feed on wiry stems have stout, blunt mandibles and a pronounced 'gular roll'; at the opposite extreme, species which feed on the most tender lily leaves have thin-edged slicing mandibles and no gular roll, leaving the maxillae and prementum completely exposed.

Notes on the biology of the immature stages of ten genera of amycterines are reported. Oviposition is apparently in the soil. Larvae of one species feed on the tender new growth of *Xanthorrhoea* crowns; other species observed feed on underground stems, tubers and rhizomes, and possibly roots. Pupation takes place in the soil.

The function of the modified 8th sternite (the 'forceps') of male *Phalidura* is discussed.

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INTRODUCTION

The endemic Australian weevil subfamily Amycterinae includes an estimated 500 species. The weevils are favourites of collectors because of their unusual and often spectacular structural modifications, but their biology was almost unknown as recently as 1970 (Britton, 1970: 619). The few published references to biology concern mainly the weevils' hiding places and supposed food sources. Many of the food records, such as *Eucalyptus* bark (Ferguson, 1921: 29, 30) and dry, dead wood (Macleay, 1865: 201) are spurious. So little is known concerning the biologies of the species that even precise localities and dates of collection are worthwhile contributions.

Information is recorded herein concerning immature stages of ten genera of Amycterinae and the adult food of another five genera. In addition, the morphology of the adult mouthparts of amycterines is discussed as it relates to the texture of their food plants, and the morphology of the ovipositor is discussed as it relates to method of oviposition.

METHODS

E. C. Zimmerman, Curator of Weevils Emeritus, Commonwealth Scientific and Industrial Research Organization, Canberra, assisted with the identifications of the adults, and I have personally examined many of the types of Blackburn, Ferguson, Lea, Macleay, Pascoe, Sloane, and Waterhouse. No nomenclatural changes are made in this paper, because a comprehensive work including the Amycterinae is in preparation by E. C. Zimmerman. At his suggestion, all references to higher classification are omitted here because of his anticipated changes to the system. Genera are discussed using the nomenclature and taxonomic sequence found in the *Coleopterorum Catalogus* (Schenkling and Marshall, 1931).

Immature stages are being described in a separate publication by Brenda May, Department of Scientific and Industrial Research, Auckland, New Zealand.

Voucher specimens of adult and immature stages will be deposited in the Australian National Insect Collection, Canberra, and, where sufficient material exists, in the New Zealand Arthropod Collection, Auckland, and the Howden collection.

Biological observations were made over a period of nine years during four trips to Australia, totalling 16 months of field time. These trips were: (1) December 1974 to June 1975, in eastern Australia between Atherton, Queensland, and Canberra, Australian Capital Territory; July 1975, in southwestern Western Australia. (2) July and August 1978, Sydney, New South Wales; Canberra, Australian Capital Territory; across the Nullarbor Plain; and the Western Australian districts of South West, Murchison, Gascoyne, and Pilbara north to Point Samson. (3) August to November 1981, Sydney, New South Wales; Western Australian districts of South West and Murchison; Yorke Peninsula, South Australia. (4) July and August 1983, Sydney, New South Wales; Western Australian districts of South West and Murchison; Australian Capital Territory and New South Wales between Canberra and northwestern New South Wales and adjacent territory.

THE FOOD AND MOUTHPARTS OF ADULT AMYCTERINAE

Adults feed on a variety of plants, mostly monocotyledons, but also on some dicotyledons, namely legumes and myrtaceous plants. According to the growth form of these plants, amycterines feed at ground level (on *Arthropodium*, *Bulbine*, etc) to over a metre above ground (on *Acacia*, *Bossiaea*). Table 1 summarizes the observed and suspected food plants of adults and larvae. Note that the classification of these plant taxa apparently does not closely follow the classification of the weevils at the generic level. There is, however, a correlation between the **texture** of the plants and the weevil genera. If the plant taxa were rearranged according to the relative tenderness of the tissues consumed by the weevils and then compared to the type of mouthparts of the weevil, the correlation would be striking.

TABLE 1

Plant-Amycterinae Associations

Plant species	Location	Amycterine species and stage	adult	egg	larva	pupa
POACEAE						
Astrebla pectinata	Tibooburra, E to 85km W, NSW	*Cubicorrhynchus taurus*	X			
Cenchrus ciliaris	3km NW Pt Augusta, SA	*Cubicorrhynchus* sp.	X			
Enneapogon nigricans	Pt Augusta and 3km NW, SA	*Cubicorrhynchus* sp.	X		X[a]	
Eragrostis eriopoda	100km SE Tibooburra, NSW	*Cubicorrhynchus* sp.			X[a]	
	70-100km NW Tibooburra, NSW	*Cubicorrhynchus taurus*	X			
Eragrostis eriopoda?	Waka Hsd (90km W Tibooburra), NSW	*Cubicorrhynchus taurus*	X		X[a]	
	Warri Warri Gate and N, Qld	*Cubicorrhynchus taurus*	X		X[a]	
Nassella trichotoma	nr Yass, NSW	*Phalidura assimilis*	X		X	X
		Phalidura elongata	X			X
		Cubicorrhynchus sp.	X		X[a]	X
Stipa sp.	56km E Kimba, SA	*Cubicorrhynchus calcaratus*	X		X[a]	
	Damboring (N Ballidu), WA	*Cubicorrhynchus* sp.			X[a]	
Stipa nitida	91km NW Bourke, NSW	*Cubicorrhynchus* sp. nr *taurus*	X			X
	87km E Wilcannia, NSW	*Cubicorrhynchus* sp. nr *taurus*	X		X[a]	
	125km E Wilcannia, NSW	*Cubicorrhynchus* sp. nr *taurus?*	X		X[a]	
Triodia basedowii	1km S tip North West Cape, WA	*Notonophes auriger*	X		X[a]	
Unidentified grasses	nr Yass, NSW	*Acantholophus spinifer*	X			

TABLE 1 (concluded)

Plant species	Location	Amycterine species and stage	adult	egg	larva	pupa
POACEAE						
Unidentified grasses	Oodlawirra, SA	*Cubicorrhynchus* sp.	X		X[a]	
		Acantholophus planicollis	X		X[a]	
	Mt Horner, WA	*Cubicorrhynchus crenicollis*	X		X	X
	Onslow, WA	*Chriotyphus tibialis*	X		X[a]	
		Notonophes sp.	X			
	36km W Yalgoo, WA	Gen. indet.			X	
	Yellowdine, WA	*Acantholophus maximus*			X[a]	
	50km NW Yuna, WA	*Acantholophus maximus*	X			
CYPERACEAE						
Lepidosperma sp. nr *gracile*	55km S Marvel Loch, WA	*Talaurinus* sp.	X			
		Acantholophus transitus	X			
Lepidosperma sp. nr *viscidum*	80km S Marvel Loch, WA	*Acantholophus transitus*	X			
ECDEIOCOLEACEAE						
Ecdeiocolea monostachya	52km E Kalbarri, 42km NW Yuna, 65km S Wurarga, WA	*Acantholophus maximus*	X		X[a]	
RESTIONACEAE						
Lepidobolus preissianus	90 Mile Tank, WA	*Macramycterus draco*	X			
LILIACEAE						
Gen. indet.	Thomas River, WA	*Talaurinus echinops*	X			
Arthropodium capillipes	28km W Yalgoo, WA	*Dialeptopus echinatus*	X	X	X	
		Polycreta metrica	X			
	56km S Mullewa, WA	*Ennothus fallax*	X		X	
Bulbine alata	Tibooburra, Menindee, Bourke, Wilcannia, NSW	*Bubaris pubescens*	X		X	X
Dianella revoluta	Lake Bryde, Mt Madden, WA	*Mythites* sp. indet.	X		X	
	52km E Kalbarri, 20km N Northampton, 18km S Wurarga, WA	*Mythites basalis* var. *nodosus*	X		X	X
Stypandra imbricata	Mt Madden, WA	*Cucullothorax horridus*	X			
AMARYLLIDACEAE						
Doryanthes excelsa	Engadine, NSW	*Acantholophus marshami*	X			
XANTHORRHOEACEAE						
Lomandra sp.	Congo, NSW	*Talaurinus simillimus*	X		X	X
Lomandra longifolia	Clyde Mt, NSW	*Mythites granulatus*	X			
		Talaurinus rugifer	X			
	Atherton, Qld	*Talaurinus subvittatus*	X			
Xanthorrhoea spp.	Engadine, NSW	*Acantholophus marshami*	X		X[a]	
	Glenbrook, NSW	*Acantholophus marshami*			X[a]	
FABACEAE						
Acacia sp.	55km E Mullewa, WA	*Dialeptopus echinatus*	X			
	28km W Yalgoo, WA	*Dialeptopus echinatus*	X			
Bossiaea linophylla	30km W Pemberton, WA	*Acantholophus* sp. A nr *aureolus*	X			
Daviesia teretifolia	Cape Le Grand, WA	*Hyborrhinus prodigus*	X			
		Acantholophus sp. B nr *aureolus*	X			
Jacksonia foliosa	18km S Wurarga, WA	*Sclerorinus* sp.	X			
Jacksonia foliosa?	Hopetoun, WA	*Acantholophus* sp. B nr *aureolus*	X			
MYRTACEAE						
Melaleuca sp.	90 Mile Tank, WA	*Acantholophus* sp.	X			
Leptospermum sp.	Northcliffe, WA	Gen. indet.	X			

[a] Identification of larva questionable.

The mouthparts of adult amycterines exhibit a relatively wide range of form for one subfamily. The base of the oral cavity and the mandibles especially show modifications at the generic level. At one extreme, the mandibles of *Polycreta metrica* Pascoe (Figs 5, 6) have a thin, blade-like cutting edge, and the ventral surface of the rostrum is not modified at the base of the oral cavity. The leaves of *Arthropodium capillipes* on which *P. metrica* feeds are as tender as young onion leaves. At the other extreme, the mandibles of *Macramycterus draco* Macleay (Fig. 3) are massive and blunt-edged. The base of the oral cavity is grossly developed into a thick lip or 'gular roll' (Dohrn, 1872: 144) which extends forward 1mm or more to conceal the prementum. The leafless stems of *Lepidobolus preissianus*, on which this *Macramycterus* feeds, are extremely tough and wiry. However, the stout mandibles of *M. draco* do not prevent it from also feeding on tender plants such as ryegrass. The neat little slices of the unknown plant in Fig. 2 were regurgitated by the *M. draco* in Fig. 1.

It seems likely that the heavily reinforced base of the oral cavity provides structural strength for the operation of the mandibles. The thickest lip is associated with the toughest food plants; moderate modification consists of a moderate lip with a sinuous edge and is associated with leathery food plants; and so forth, until the extreme condition in which there is no apparent modification of the base of the oral cavity associated with the softest plants. Additional discussions of mouthparts in relation to texture of plants are found under particular species, especially *Talaurinus*, *Acantholophus* sp. nr. *hypoleucus* (Boheman), and *Mythites*.

Table 1 shows also that all the dicot records refer to adults only. It is possible that adults have a wider range of food plants and that immature stages are associated only with monocots. For example, *Dialeptopus echinatus* Lea in captivity fed and bred on the lily *Arthropodium capillipes* but was observed in the field on *Acacia* and other plants.

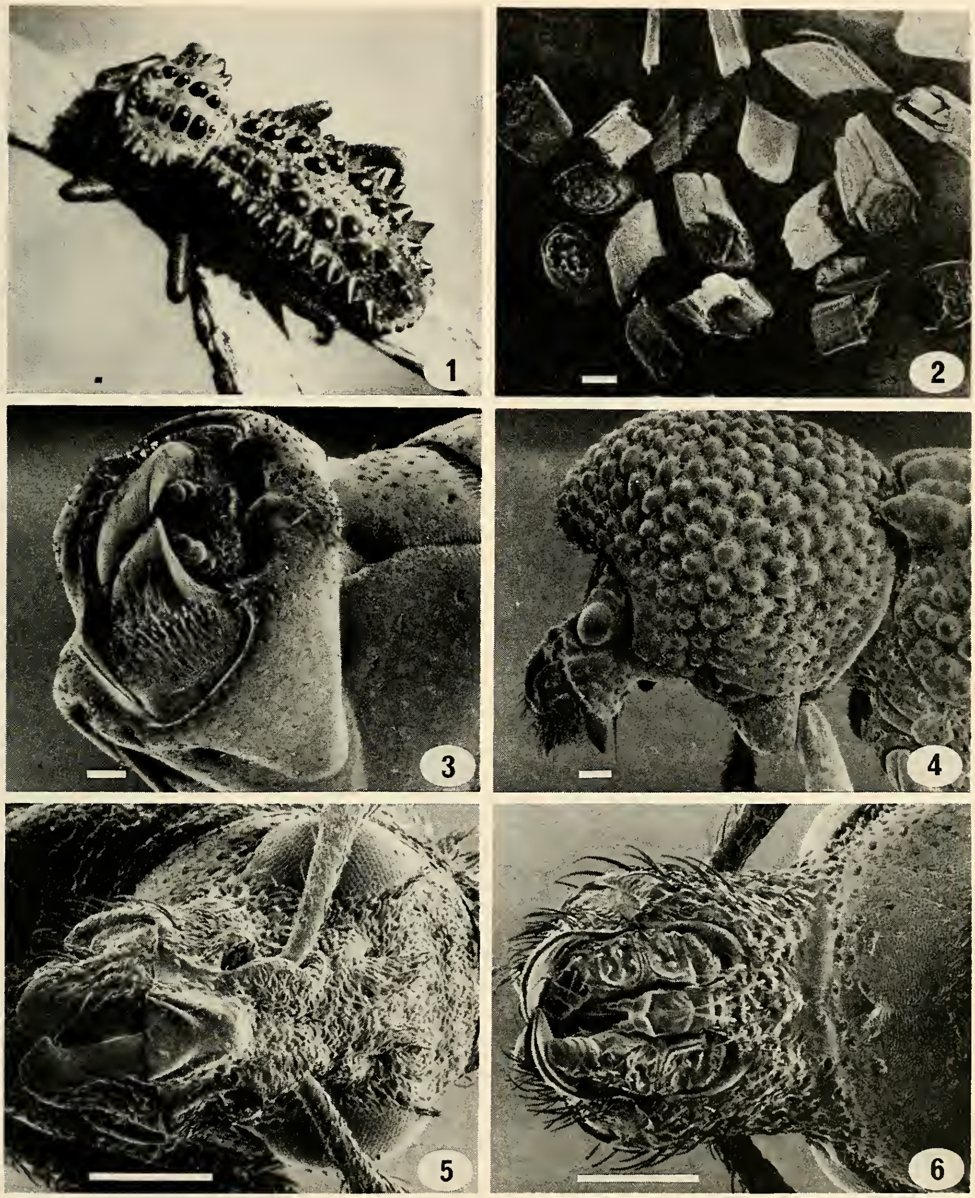
GENERAL OBSERVATIONS ON THE LIFE HISTORY OF AMYCTERINAE

Oviposition and morphology of the ovipositor

Oviposition apparently takes place in the soil, as the following evidence indicates. Numerous attempts to rear confined adults of many species resulted in eggs and a larva of *Dialeptopus echinatus*. The large, creamy yellow eggs were dropped on the surface of the soil, and after two weeks of extreme conditions, the eggs were dead. However, one egg had apparently been placed in the soil, and a larva was found in the container a month after the adults were confined. This suggests that dropping the eggs on the surface was a response to stress or infertile eggs and that placing the egg in the soil was the norm.

Newly eclosed larvae of *Bubaris pubescens* and *Mythites* spp. begin feeding on the exterior surface of the underground stem of their food plant and not from a position already within the stem which would be the case if the egg had been inserted into the plant tissue.

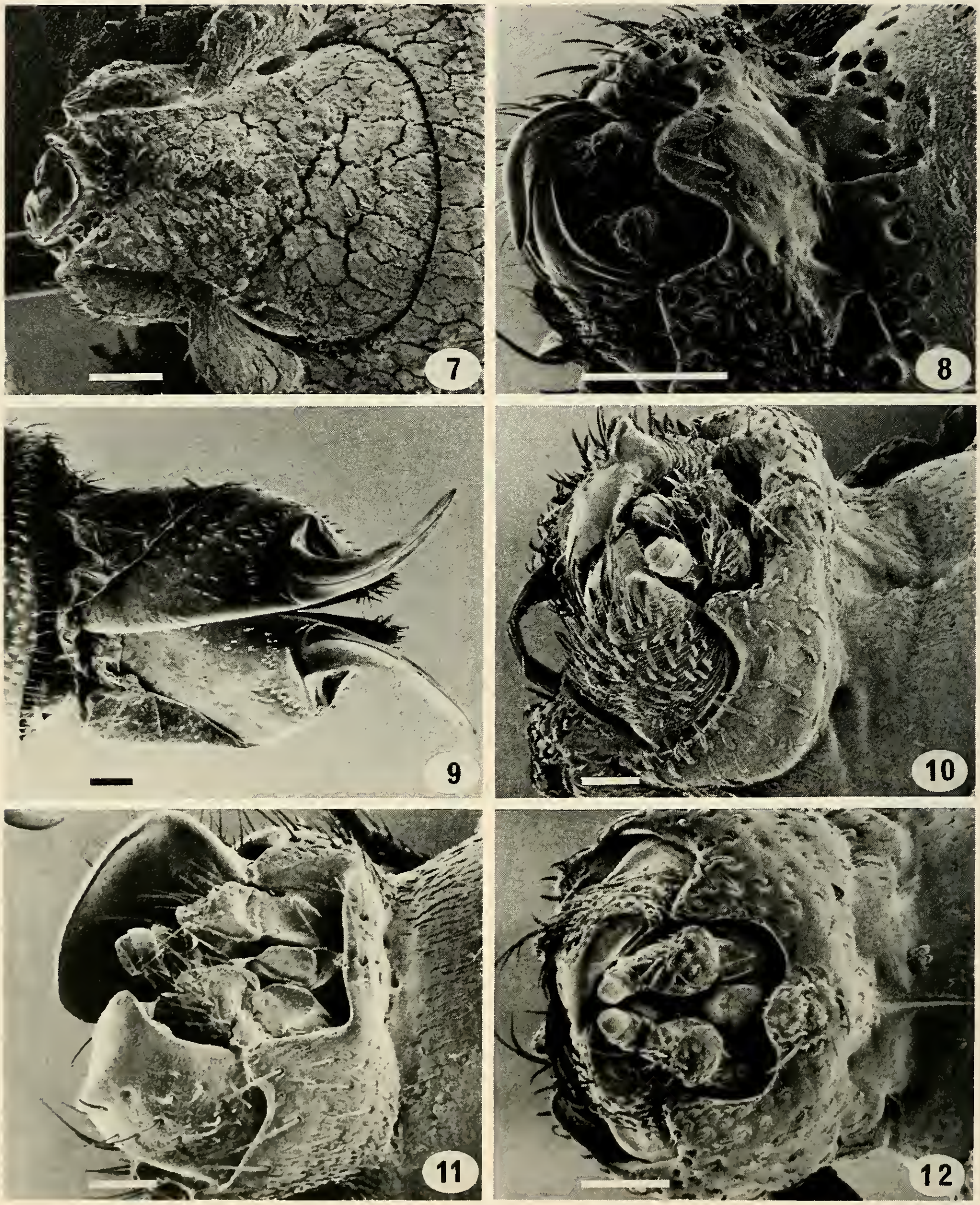
The morphology of the ovipositor also seems to be consistent with oviposition in the soil. In amycterines the stylus, near the apex of the coxite dorsally, has evolved into a free, heavily sclerotized, outwardly-directed blade (Fig. 9). In most species the blade is crescent-shaped, with or without a tooth on its dorsal edge, and ranges in shape from a paddle to a simple scoop (*Mythites*). This same type of free sclerite is found in the South African subfamily Hipporhininae and in at least some Tanyrhynchinae, but oviposition has not been observed in these groups either. An analagous, but not homologous, ovipositor is found in some North American Leptopiinae which are known to oviposit in the soil.



Figs 1-6. Figs 1-3. *Macramycterus draco* Macleay, male: 1) sunning on twig, 2) slices of plant regurgitated by specimen in Fig. 1, 3) oblique ventral view of mouthparts. Fig. 4 *Cucullothorax horridus* Ferguson, female, profile of head and prothorax. Figs 5,6. *Polycreta metrica* Pascoe, male, mouthparts: 5) anterior view; 6) ventral view. Scale line = 0.5mm.

Larval stage

With one exception (*Acantholophus marshami* (Kirby)?), all larvae found to date feed underground. Species associated with grasses (e.g., *Phalidura*, *Cubicorrhynchus*, etc.) feed on the subterranean crowns and there is no direct evidence of their feeding on roots.



Figs 7-12. Figs 7, 8. *Bubaris pubescens* Lea: 7) dorsal view head and rostrum of female with typical dirt encrustation, 8) oblique ventral view mouthparts of reared male. Fig. 9. *Macramycterus* sp., apex of female genitalia, dorsal view. Fig. 10. *Talaurinus subvittatus* Ferguson, male oblique ventral view of mouthparts. Fig. 11. *Acantholophus* sp. nr. *hypoleucus* (Boh.), female, oblique ventral view of mouthparts. Fig. 12. *Mythites basalis* var. *nodosus* Ferguson, female, ventral view of mouthparts. Scale line = 0.5mm.

Species that feed on Liliales feed on the subterranean stems and tubers or rhizomes, and again there is no direct evidence of their feeding on roots.

Pupal stage

Larvae pupate where they have fed or only a few centimetres away (*Cubicorrhynchus crenicollis* Waterhouse, *Bubaris pubescens* Lea), or they may travel some distance to pupate. On two occasions, *Acantholophus* sp. pupae were dug from the centre of a sand track a metre or more away from any vegetation. The presence of the pupae was indicated by a slight disturbance on the surface of the soil directly over the vertical cell.

BIOLOGICAL OBSERVATIONS BY SPECIES

Phalidura spp.

Male *Phalidura* are characterized by a pair of grotesque 'forceps' protruding from the abdomen. These 'forceps' of the vernacular are the highly modified male 8th sternite which is divided into a pair of massive, free, elongate sclerites up to half the length of the weevil, and which together strongly resemble a pair of forceps. The function of the forceps, '. . . so far as one can reasonably infer, is to grip the female right round the hinder end of her body . . .' (Gahan, 1918: cxxi). However, in repeated observations, copulating pairs of *P. elongata* Macleay and *P. grandis* Ferguson never used the forceps in this manner, and furthermore, it seems physically impossible. The apices of the forceps can only be moved apart by approximately 2mm; the minimum width of *Phalidura* females is much greater. The sides of the 7th sternite confine the forceps at the base and prevent greater lateral movement. The forceps extend into the abdomen by several millimetres and are prevented from being pulled out any farther by a connecting vertical internal disc which is approximately 3.5mm in diameter.

The copulatory posture observed in *P. elongata* and *P. grandis* is as follows. The abdomen of the male is extended to the maximum amount so that the massive, heavily sclerotized penultimate tergite is directed ventrally and slightly anteriorly; the last tergite is completely horizontal and anteriorly directed; the forceps are parallel to each other and likewise extend the maximum distance, their apices almost reaching the female's metasternum and presumably pressing upwards. This pressure may be the only function of the forceps. The forceps also bear species-specific arrangements of setae which suggests a recognition function (*see* Baker and Thompson, 1978).

Phalidura assimilis Ferguson and *P. elongata* Macleay

These species were reported by Barry Moore (1978: 138; and *in litt.*) breeding and feeding on *Nassella trichotoma* near Yass, New South Wales. The larva of *P. assimilis* is illustrated in Moore (1980: 13).

Phalidura grandis Ferguson

A short series was taken in Tibooburra, New South Wales, in August feeding in a small yard planted in Kikuyu and other grasses.

Talaurinus spp.

Two species of *Talaurinus* (*rugifer* and *subvittatus*) were observed feeding on *Lomandra longifolia*, and a third species of *Talaurinus* (*simillimus*) is associated with a *Lomandra* sp. The leaves of *L. longifolia* are very tough and the mouthparts of both species observed feeding on them are heavily reinforced with a conspicuous gular roll (Fig. 10). The other food plants listed below for *Talaurinus* spp. are likewise tough to very tough and the mouthparts of the weevils are similar to those in Fig. 10.

Talaurinus echinops (Pascoe)

One specimen was taken at Thomas River, Western Australia, in October in debris of a *Patersonia*-like plant.

Talaurinus molossus Pascoe (*Sclerorinus* in Schenkling and Marshall, 1931)

A series was taken at Newdegate, Western Australia, in July walking on bare ground at midday.

Talaurinus rugifer (Boisduval)

One male was observed at Clyde Mountain, New South Wales, in April feeding on a leaf of *Lomandra longifolia*.

Talaurinus simillimus (Macleay)

One adult, eight larvae, and one pupa were collected by Murray S. Upton at Congo, New South Wales, in March with *Lomandra* (B. May, *in litt.*).

Talaurinus subvittatus Ferguson

A short series was observed at Atherton, Queensland, in February feeding on *Lomandra longifolia*.

Talaurinus sp.

One male from Marvel Loch, Western Australia, in September was associated with *Lepidosperma*.

Molochtus gagates Pascoe

A series was taken 23km west of Yalgoo, Western Australia, in July under mulga logs and under bark of mulga logs on the ground.

Chriotyphus tibialis Ferguson

A series was taken at Onslow, Western Australia, in July in grass clumps growing in sand near the beach. One amycterine larva (genus?) was in the same grass.

Chriotyphus sp.

A series was taken at Coral Bay, Western Australia, August, in grass clumps growing in sand near the beach.

Sclerorinus spp.

A series was taken 18km south of Wurarga, Western Australia, in August at night after 2200 hours in matted stems of *Jacksonia foliosa* about 5-10cm above ground level.

Sclerorinus spp. were common on the Nullarbor Plain between Caiguna and Madura, Western Australia, in August under glasswort.

Macramycterus spp.

Macramycterus species appear to be strictly diurnal in their activities, including copulating (July and September) and sunning on a perch 45cm above ground (Fig. 1).

Macramycterus draco Macleay

A short series at 90 Mile Tank, Western Australia, in September displayed a typical feeding behaviour consisting of walking up to a stem of *Lepidobolus preissianus*, chewing off the stem near the ground and eating the stem. In captivity a weevil facing down on a stem of *L. preissianus* was observed to cut the stem off beneath itself (about 5cm above the ground), to cling to the cut portion as it fell to the ground, and to continue feeding on the freshly cut end, consuming about 2.5cm in 5 minutes. Mouthparts of *Macramycterus* are discussed elsewhere in this paper (see p. 94).

Acantholophus spp.

The large genus *Acantholophus* is highly varied in its biology. There are many more nocturnal than diurnal observations. Perambulating larvae of *Acantholophus* are described below.

Acantholophus sp. A near *aureolus* (Boheman)

A large series was observed 30km west of Pemberton , Western Australia, between 1930 and 2200 hours in a light rain, feeding on *Bossiaea linophylla* and two other species of shrubs at 0.5 to 1.2mm above ground.

Acantholophus sp. B near *aureolus* (Boheman)

A series was taken at Cape Le Grand, Western Australia, in October on cool overcast days under very dense *Daviesia teretifolia*, well-camouflaged on the ground in the sparse debris of grey, dead leaves of the same size and colour as the weevils. All specimens regurgitated green matter, presumably *Daviesia* foliage.

One adult at Esperance, Western Australia, in October was walking at night, in a temperature near freezing, in the vicinity of *Daviesia*.

Two specimens were found at Hopetoun, Western Australia, in August on the ground under *Jacksonia* sp.

Acantholophus sp. nr *hypoleucus* (Boheman)

A short series at Arrowsmith River, Western Australia, July, was taken under dead grass trees; the mouthparts (Fig. 11) indicate food of moderate texture.

Acantholophus marshami (Kirby)

Described by Froggatt (1896: 77) as '. . . the common Amycterid about the neighbourhood of Sydney. Most of the members of this large genus live upon the grass, but this one climbs up the leaves of the grass-tree, and clinging round them gnaws pieces out.'

A colony of amycterines at Engadine (40km south of Sydney), New South Wales, has been monitored for several years by the G. A. Holloway family and is apparently this species. The Holloways report (*in litt.*) larvae present from early May to mid November. One male *A. marshami* (det. A. Howden) was taken 9 May on the crown of a *Xanthorrhoea* containing amycterine larvae (det. B. May). The larvae are always in the crown, a metre or more above ground, in head-up position in a column of chewed matter, and feed on the innermost tender white leaves. Some larvae were of buff colour instead of white on 1 November; several weeks later all larvae were absent from *Xanthorrhoea*. Observations are continuing.

The Holloways also report amycterine larvae from other species of grass trees and from Glenbrook in the Blue Mountains.

Although the ectophytic behaviour of these larvae appears to be anomalous among amycterines, it is possibly only an extension of feeding in ground-level crowns of plants.

Three males of *A. marshami* were taken at Engadine (same site as above) in August under leaf scales of a standing dead flower stalk of the Gymea lily, *Doryanthes excelsa*.

Acantholophus maximus (Macleay)

Single adults and series were taken at four sites between 52km east of Kalbarri and 65km south of Wurarga, Western Australia, in August in clumps of *Ecdeiocolea monostachya*. A single amycterine larva was excavated at two of the sites, each larva 7.5cm below the surface of the ground in the crown of a plant.

Acantholophus planicollis Waterhouse

One adult was taken at Oodlawirra, South Australia, in August; nearby grass yielded six amycterine larvae of unknown genus.

Acantholophus spinifer Macleay

Adults and larvae, according to Moore (1978: 138), are associated with grass near Yass, New South Wales.

Acantholophus transitus Macleay

A short series was taken 55-80km south of Marvel Loch, Western Australia, in clumps of *Lepidosperma* spp. near *gracile* and near *viscidum*; adults were also taken in the vicinity of Lake King and Newdegate in July.

Cubicorrhynchus spp.

All *Cubicorrhynchus* species collected to date have been associated with either native or introduced species of Poaceae except for occasional instances in which the weevils appeared to be hiding only. *Cubicorrhynchus* larvae taken from the crowns of grass plants often regurgitated green material, indicating they had fed on underground stems and not the roots. Adults are primarily nocturnal.

Cubicorrhynchus calcaratus Macleay

Adult fragments and a larva were taken 56km east of Kimba, South Australia, in August in a clump of *Stipa* sp.

Cubicorrhynchus crenicollis Waterhouse

A colony near Mt Horner, Western Australia, was located in an unidentified species of native grass growing in an isolated strip of relatively undisturbed coastal heath. On 14 July larvae and fragments of adults were excavated from clumps of the grass. On 9 September, seven larvae and 17 pupae (some with larval exuviae still attached) were excavated. Pupae were 10-50mm deep in the soil in cylindrical excavations approximately 7mm in diameter, at the outer edge of the root mass of the clump.

Three adults were reared from pupae collected 9 September, ecdysis occurring in 5, 34, and 52 days. The first two adults emerged from pupae which had remained on the surface of the soil in the rearing tin. The third pupa was located in a cell in the bottom of the rearing tin and was still white 11 days before its ecdysis was artificially accelerated by increasing the moisture and temperature in the tin. Thus it appears that the duration of the pupal period varies greatly, and pupae deeper in the soil might be expected to have a longer pupation because warm temperatures and superficial rains would not reach them.

The inferred life cycle is thus: larva — July to September, pupa — August to November, adult emergence — September to November and later.

Cubicorrhynchus taurus Blackburn and related species

Several species may be included in this unit of specimens distinguished by having the fore coxae contiguous and the hind tibia of the male nodose and produced into a conspicuous lobe on the inner edge medially. The range is throughout the northwest corner of New South Wales and adjacent Queensland and South Australia, specifically, Tibooburra, southeast to Wilcannia, southwest to Menindee, through Broken Hill and northwest to Frome Downs. Specimens west of the Flinders Ranges are a different species (*Cubicorrhynchus* sp. from Port Augusta). Eighteen adults from a granite outcropping at Tibooburra were smaller and less developed in secondary sexual characters than specimens from the clay or sandy areas and may be a different species.

Adults and a few larvae collected July through August were associated with a variety of grasses especially *Astrebla pectinata* (Mitchell grass) and *Eragrostis eriopoda* (woollybutt). Dissected females contained no eggs but an abundance of fat. A sample of both sexes from various localities contained green plant matter in the digestive tract although the grasses were only beginning to show green after recent rains.

Caged specimens fed on grass by climbing up the blade and while still facing up, ate the blade from the tip down, backing down as necessary. One female observed cut the top 2cm from a blade of grass and carried it back and forth, pausing to feed on it. Many pieces of cut grass accumulated on the soil of the cage. This weevil cut the grass blade not with a single cut, but with an up and down rasping motion not observed in other amycterines. The mandibles and reinforced base of the oral cavity of this species indicate the ability to cut very tough material.

Cubicorrhynchus sp. near *taurus* Blackburn

This species resembles *C. taurus*, but males lack the conspicuous lobe on the hind tibia; the range is central New South Wales from 87km east of Wilcannia to 68km west of Cobar and north to 91km northwest of Bourke. At the latter locality one pupa was found 8cm deep in the ground under *Stipa nitida*. Larvae (presumably of this species) were found at several sites in the crowns and root masses of *Stipa nitida*. Abundant *Eragrostis* in the area yielded no amycterine adults or immatures.

Cubicorrhynchus sp. from Port Augusta

This species is related to *C. taurus* by the contiguous fore coxae, but the hind tibia of the male is straight for the proximal two-thirds, then strongly curved forward, its inner edge bearing a conspicuous tooth or prong at the distal fifth. The species was taken in South Australia from Port Augusta southwest to 9km west of Iron Knob, and north of Port Augusta to Quorn on the west side of the Flinders Ranges. Adults were taken in late July and late August in clumps of *Cenchrus ciliaris*, *Enneapogon nigricans*, and *Stipa nodosa*; larvae were taken in late July in *Enneapogon nigricans* and *Stipa nodosa*.

Notonophes auriger Ferguson

Adults were taken at Onslow, Western Australia, in July in debris washed around the base of grass; adult carcasses were found at the North West Cape in late July near a larva 3-5cm deep in soil under a tussock of *Triodia basedowii* (spinifex).

Notonophes gascoynensis Baker (1972: 123)

Adults at Carnarvon, Western Australia, in August were sheltering under *Salicornia australis* (samphire); the weevils are similar in colour and form to the debris under the plants.

Hyborrhinus Marshall (1946: 94) (= *Hyborrhynchus* Macleay in Shenkling and Marshall, 1931)

Hyborrhinus prodigus (Macleay) was taken at Cape Le Grand, Western Australia, in October, in debris under *Daviesia teretifolia*.

Mythites spp.

Two Western Australian species of *Mythites* (*basalis* var. *nodosus* Ferguson and sp. indet.) are associated only with *Dianella revoluta*, spreading flax-lily. The plant is discussed here because of its importance to *Mythites* and other amycterines. Old leaves of the plant remain stiff and upright, and old clumps of *Dianella* can be a metre or more wide, retaining thick layers of their own litter or windswept debris of *Eucalyptus* leaves, etc. Occasionally adults of other amycterines are found in the shelter of *Dianella revoluta* clumps, e.g., *Acantholophus* sp., *Acantholophus maximus*, *Acherres mamillatus* Pascoe, *Cubicorrhynchus bohemani* (Boheman), *Dialeptopus echinatus*, *Macramycterus* sp., and *Notonophes cichlodes* (Pascoe). However, all larvae excavated from *D. revoluta* are *Mythites* (B. May, *in litt.*).

Mythites adults usually feed by cutting out portions of the leaf margin, but caged beetles cut off the flower stalk of one *D. revoluta* at 9cm above ground. Mouthparts of *M. basalis* var. *nodosus* (Fig. 12) indicate a food plant of moderate texture.

Mythites basalis var. *nodosus* Ferguson

This species was observed and collected in a semicircle around Geraldton from north of Northampton to the Kalbarri turnoff, east to Wurarga, southeast to 55km east of Mullewa, south of Mullewa and west to Arrowsmith. Larvae were found 12 July to 10 September, pupae 7 September, adults 7 August through September. In the earliest observation, newly eclosed larvae 5-8cm below ground level had eaten into the underground *Dianella* stem from without; in addition, one large larva was found in a rhizome. In an August examination of a heavily infested *Dianella* clump, the rhizomes were found to be extensively excavated by larvae. Two pupae were found 2.5cm deep in the soil of a *D. revoluta* clump, one in a vertical cylindrical hole.

Mythites sp. indet.

Adults and larvae were taken at Lake Grace, Lake Bryde, and Mt Madden in southwestern Western Australia, on four occasions between 22 September and 13 October in clumps of *Dianella revoluta*. Some larvae were just below the surface of the soil above the roots and rhizomes. Other larvae had burrowed into the rhizomes and were feeding in cavities they had excavated from the exterior. Adults were found in all clumps of *Dianella* containing larvae.

Mythites granulatus Lea

One female at Clyde Mountain, New South Wales, on the morning of 8 April was observed feeding on *Lomandra longifolia*.

Bubaris pubescens Lea

Adults and immature stages were found in August in the large area of red sand plains of northwestern New South Wales ranging from Menindee north to Tibooburra and the Queensland border, southeast of Tibooburra towards Wanaaring, from Wilcannia to 87km east of Wilcannia and north to 35km north of Bourke.

Adults and larvae feed on the leek lily, *Bulbine alata*, a small lily with an onion-like cluster of tender leaves and a short flower stalk. The roots do not bear tubers, nor is there a swollen base or bulb.

The following synopsis is based on hundreds of observations at the many localities listed above. Newly eclosed larvae eat directly into the base of the underground portion of the stem, immediately above the roots, usually 4-25mm below the surface of the soil. Older larvae feed externally on the underground stem while encased in a hollowed concretion of sand grains which adheres to the stem. When injured, the lily stem bleeds a slightly viscous sap and this seems to cause or contribute to the accretion of the sand. Usually there is only one larva per plant; infestation by two or three larvae per plant is uncommon and when it occurs involves only small larvae. By the time larvae leave a plant, the plant is usually in seed and (1) showing no obvious above-ground evidence of distress (infrequently), or, (2) at least the outer leaves are dead and pinkish in colour (commonly), or, (3) the plant is completely dead (infrequently). Older larvae may travel underground to feed or to pupate; large larvae are sometimes seen feeding on very small, previously untouched lilies. Pupae and prepupae are found in an earthen cell as far as 2.5cm from the host plant, but are usually directly beneath the plant and 0.6-15.0cm below the surface of the soil. Pupal cells are approximately 15-20mm long and 5-6mm wide. No freshly emerged adults were found, but a pupa collected 24 August was reared to adult in 21 days.

Since *Bulbine alata* responds very quickly to rain, local showers can have a strong influence on the availability of food for larvae. By waiting under bushes where the *Bulbine* seedlings will first appear, adults can oviposit as soon as suitable lilies are available. As with other species living in arid and semi-arid country with irregular rains, the life cycle of *Bubaris pubescens* is probably influenced more by precipitation than by the calendar.

The naturalized onion weed, *Asphodelus fistulosus*, is similar in plant form to *Bulbine alata*, and the two species may grow intermingled in one area. At Menindee, a large number of both plants in equal numbers was examined; only the *Bulbine* was infested with amycterine larvae. However, a large *Bubaris* larva confined for five days with only an *Asphodelus* plant for food ate a typical spherical hole 3mm in diameter in the base of the underground stem.

Adults of *B. pubescens* have a dense coat of short, wiry, curled 'setae' distributed everywhere except around the apex of the rostrum and ventral surface of the head (Figs 7, 8). These setae may produce a gummy exudate. The prothorax has closely spaced cylindrical tubercles 0.3-0.5mm high, and the elytra have similar but fewer tubercles. The result of this ornamentation is that the weevil becomes encrusted with particles of soil firmly wedged and glued in place (Fig. 7). This crust is very good camouflage.

Dialeptopus spp.

Dialeptopus have long, slender legs and many of the Western Australian species can be seen running quickly and conspicuously over the ground in the daylight hours of the winter months.

Dialeptopus echinatus Lea

Adults are common east and southeast of Geraldton, Western Australia, in the winter months. Copulating pairs were taken on *Acacia* at several localities and on a 'sedge.' Caged beetles fed only on *Arthropodium capillipes* when given a sample of vegetation from the Yalgoo area which included *Dianella revoluta* and *Acacia. Arthropodium capillipes* is a delicate lily with fleshy leaves and a tall flower spike appearing in the early spring. The roots are fibrous and many terminate in small tubers. Leaves were eaten by the weevils from the margin towards the centre of the leaf. One pair of weevils caged for a month produced seven eggs, one of which eclosed, and the larva during that month excavated almost one-quarter of a tuber on the end of a root.

Dialeptopus plantaris Pascoe

Two very active specimens were taken 82km north of Carnarvon, Western Australia, in July on spinifex.

Cucullothorax horridus Ferguson

One female (Fig. 4) was taken at Mt Madden, Western Australia, in July on *Stypandra imbricata*; additional specimens were taken at 90 Mile Tank (September) and carcasses of specimens at Marvel Loch.

Sosytelus lobatus Pascoe

One specimen was taken near Sydney, New South Wales, in August walking during the day.

Ennothus fallax Pascoe — *Polycreta metrica* Pascoe complex

These two monotypic Western Australian taxa are probably congeneric, *Ennothus* being the senior name. Specimens from 56km southwest of Mullewa and from Tunney are referable to *Ennothus fallax*. Specimens from 28-29km west of Yalgoo and 55km south of Marvel Loch are referable to *Polycreta metrica*. This distribution suggests the range of *Polycreta metrica* is in an area of lower rainfall, i.e., outside the wheat belt and with less than 25cm of rain annually, where *Ennothus fallax* occurs in slightly higher rainfall areas.

These small, active amycterines, 5.0-8.6mm, are reminiscent of *Dialeptopus* with their long legs and distinctly spider-like appearance.

All specimens were associated exclusively with *Arthropodium capillipes*. Usually the weevils were concealed deep in the rosette of leaves at the base of the plant or under debris very close to a lily. Weevils were observed feeding on leaves of the lily, once during the day (*P. metrica*) and once at night (*E. fallax*). In captivity the weevils ate only *Arthropodium capillipes*. Mouthparts of *P. metrica* are shown in Figs 5 and 6.

At the Mullewa site in July, three larvae were found 8-10cm deep in the soil around an *Arthropodium* plant on which an *E. fallax* had been feeding. All tubers from the excavated plant were collected and examined under a microscope. One shell of a tuber contained parts of an adult male *E. fallax*; other empty tubers contained pieces of head capsules and an almost complete larval exuvia.

No immature stages were found in September, but adults were much more numerous then.

CONCLUSIONS

Biological observations have helped to interpret some of the structural modifications of adult amycterines. The varied morphology of the mouthparts relates to the texture of the food plant. The unusual stylus of the ovipositor probably relates to oviposition in the soil.

In addition, two findings indicate that amycterines are a relatively old group, namely, placing the eggs in the soil (which is plesiomorphous in Curculionidae) and larvae feeding on monocots (monocots being an older group of angiosperms than dicots).

The inferred life cycle of the species observed south of the Tropic of Capricorn is as follows. Eggs are laid in the soil in the winter. Larvae of the majority of species feed on underground stems (*Bubaris*, *Mythites*), on the crown of grasses (*Cubicorrhynchus*), on tubers (*Dialeptopus*, *Ennothus*), and on rhizomes (*Mythites*); larvae of one species feed on aerial crowns of grass trees (*Acantholophus*?). Larval development is completed in the winter or early spring. Pupation occurs in the soil and the duration of the pupal stage in arid and semi-arid areas may be influenced more by moisture and temperature than by the calendar.

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Scanning electron micrographs were taken by Lewis Ling, Biology Department, Carleton University, Ottawa, Canada.

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The Circumtropical Barnacle *Tetraclitella divisa* (Nilsson-Cantell) (Balanomorpha, Tetraclitidae): Cirral Activity and Larval Development

D. T. ANDERSON

ANDERSON, D. T. The circumtropical barnacle *Tetraclitella divisa* (Nilsson-Cantell) (Balanomorpha, Tetraclitidae): cirral activity and larval development. *Proc. Linn. Soc. N.S.W.* 109 (2), 1986: 107-116.

T. divisa is reported for the first time from Australia (Magnetic Island, north Queensland). The functional morphology and cirral activity of the species resemble those of *Tetraclitella purpurascens*, with emphasis on prolonged cirral extension in response to moderate water flow. Larvae brooded to the cyprid stage pass through 4 naupliar stages in the mantle cavity, showing vestigial limb setation and enlarged caudal papilla development. The cyprid undergoes further differentiation before release. The paradox of circumtropical insular distribution in spite of abbreviated free larval life (as a cyprid only) is discussed.

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INTRODUCTION

Tetraclitella divisa is a small tetraclitelline found under and between rocks in low intertidal habitats on tropical shores. The species, first described by Nilsson-Cantell (1921) from material collected in Sumatra and the Java Sea, was notable as the first balanomorph known to brood its embryos to the cyprid stage in the mantle cavity. Nilsson-Cantell gave a brief description of a brooded metanauplius and a description and figure of the cyprid.

Since its original discovery, *T. divisa* has been found in the Hawaiian Islands (Pilsbry, 1928; Edmondson, 1933; Ross, 1961), Formosa (Hiro, 1939), Kyusyu and Ryukyu Islands (Utinomi, 1949), South China Sea (Zevina and Tarasov, 1963), tropical west Africa (Bassindale, 1961; Stubbings, 1967), Dominica (Ross, 1968), India (Ross, 1971), Aldabra and Fiji (Foster, 1974). It thus has a circumtropical insular and occasional mainland distribution. Dense populations may occur, as in Fiji (Foster, 1974), where the species may cover up to 100% of available surfaces. B. A. Foster (pers. comm.) has also found *T. divisa* at Norfolk Island. The present paper reports the first discovery of *T. divisa* from Australia. Brooding to the cyprid stage in the mantle cavity was confirmed by Hiro (1939) and Ross (1961, 1968). Among other balanomorphs, this phenomenon has been described only in *Solidobalanus masignotus* (Henry and McLaughlin, 1967; Newman and Ross, 1971), and in a small tesseroporan from Hawaii (Newman and Ross, 1977) and various other Pacific islands (B. A. Foster, W. A. Newman, pers. comm.).

Some aspects of the anatomy of *T. divisa* were described by previous authors. The external appearance, wall plates and opercular plates were variously presented and figured by Nilsson-Cantell (1921), Hiro (1939), Ross (1961, 1968), Zevina and Tarasov (1963), Stubbings (1967) and Foster (1974). The individual mouthparts, though not the oral cone, were described by the same authors with the exception of Ross (1961) and were well figured by Stubbings (1967). Brief descriptions of the cirri, including podomere counts, were given by Nilsson-Cantell (1921), Hiro (1939), Zevina and Tarasov (1963) Stubbings (1967) and Ross (1968). The functional morphology and cirral activities of the species have not been investigated. Descriptions of development are also very brief, being confined to the two stages given by Nilsson-Cantell (1921). In the present work, the opportunity is taken to describe the anatomy of the animal in more detail, to report on its cirral activities and to examine the sequence of development based on a full series of stages.

MATERIALS AND METHODS

Specimens were obtained from the undersurface of a coral boulder from the low intertidal of Picnic Bay, Magnetic Island, north Queensland in August 1982. The boulder was collected by Dr John Collins of the James Cook University of North Queensland, who presented the animals to me as a frequently occurring but unidentified species from that habitat.

Observations were made on the living animals, including an investigation of cirral responses to water currents generated across the aperture by means of a Pasteur pipette. The specimens were then fixed in 0.5% formalin-seawater (V/V). Anatomical investigations were carried out by dissection following the methods of Anderson (1981). Developmental stages found in the mantle cavities of 25 specimens were removed and transferred through alcohol to methyl benzoate, benzene and finally liquid paraffin. These specimens were studied microscopically as wet whole mounts in liquid paraffin.

RESULTS

The Anatomy of *T. divisa*

Wall and Operculum. Previous workers have described the wall plates and operculum of *T. divisa* in some detail. A resumé of these descriptions is given here, and illustrated from the Queensland material, as a preliminary to a more detailed consideration of structure and function.

The animal is of low conical shape in external view (Fig. **1A**), with a basal diameter of 6-11mm. The basal margin of the wall is rounded in outline. There is a small, diamond-shaped to hexagonal orifice with a length about one quarter of the basal diameter. The four wall plates are distinct, with broad radii on the compound rostrum and laterals. The radii have horizontal summits and exhibit dark striations indicative of internal tubes. The external surface is covered by a pale brown chitinous cuticle marked by close set, imbricating growth lines fringed with fine chitinous hairs. Each plate may be strengthened by three or more ribs that protrude little or not at all beyond the margin. The parietes are penetrated by 2-6 rows of longitudinal tubes, quadrangular to hexagonal in cross section, filled with greyish mantle tissue. The basis is membranous, sometimes calcareous around the periphery only, or calcareous throughout. The internal space enclosed by the wall is small and subcylindrical. The ratio of external to internal basal diameter is approximately 2.3:1.

The yellowish operculum, set superficially within a shallow sheath, is of typical tetraclitelline form. In the closed position, the scuta occupy most of the orifice (Fig. **1A**). Each scutum is long rostrocarinally and short apicobasally (Fig. **1B**). The external surface has a broad median depression. The internal surface (Fig. **1B**) shows poor definition of the adductor muscle scar and adductor ridge, and there are no crests for the insertion of the rostral and lateral scutal depressor muscles. The articular ridge and furrow, however, remain broad and prominent. The tergum, as in other tetraclitellines, is short and wide (Fig. **1B**), with a broad, shallow tergal spur clearly separated from the basiscutal angle and 4-8 crests for attachment of the tergal depressor muscles.

Little raising and rostral rotation of the opercular valves is involved in the opening of the aperture. The main movement is a lateral upswing of the valves on the hinge formed by the opercular membrane.

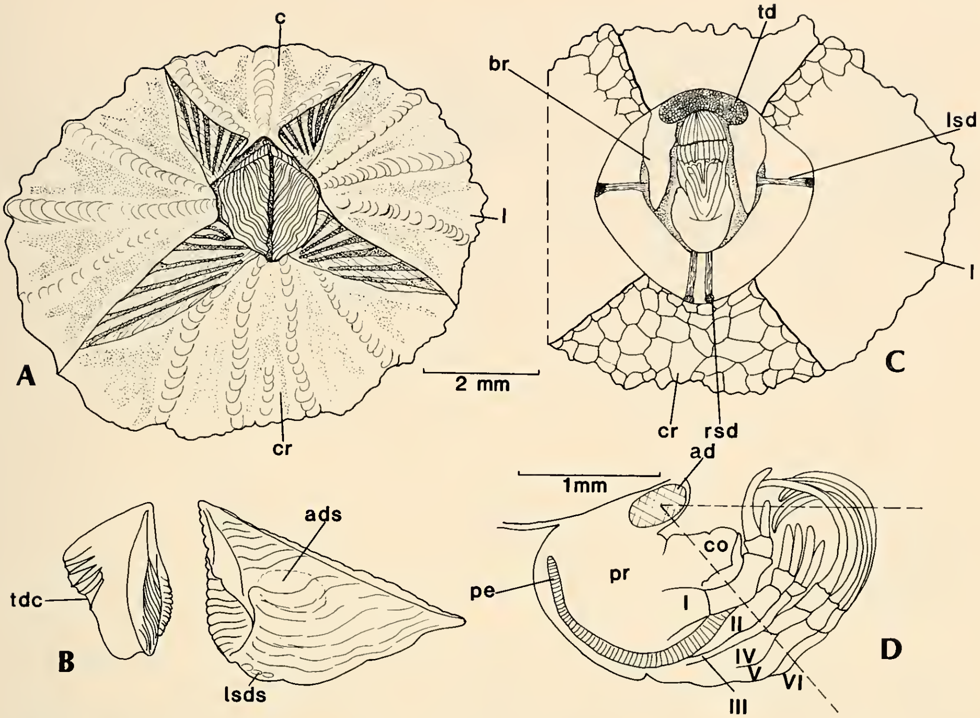

Fig. 1. T. divisa. **A.** — External apical view. **B.** — Right scutum and tergum, anterior view. **C.** — Basal view. **D.** — Body and limbs, right lateral view. *ad*, adductor scutorum; *ads*, adductor scutorum scar; *br*, branchia; *c*, carina; *co*, oral cone; *cr*, compound rostrum; *l*, lateral; *lsd*, lateral scutal depressor muscle; *lsds*, lateral scutal depressor scar; *pe*, penis; *pr*, prosoma; *rsd*, rostral scutal depressor muscle; *td*, tergal depressor muscle; *tds*, tergal depressor muscle crests; I-VI, cirri I-VI.

Body, Mantle Cavity and Depressor Muscles. Commensurate with the low profile of the wall and the small interior space, the body of *T. divisa* shows the typical long, low configuration of a tetraclitelline (Fig. 1**D**) and is small relative to the size of the animal as a whole (Fig. 1**C**). The prosoma protrudes well forward of the level of the adductor scutorum, to occupy the rostral part of the mantle cavity. A pair of long, pointed branchiae lies lateral to the body and limbs. The paired tergal depressor muscles are large and fill the carinal end of the mantle cavity. The lateral and rostral scutal depressor muscles are thin.

Cirri. The cirri are not well described in previous accounts, but conform to the general tetraclitelline pattern. The maxillipeds (cirri I-III) have short rami, while those of the captorial cirri (IV-VI) are of moderate length.

Cirrus I (Fig. 2**A**) has a long, curved protopod and an exopod of 8-10 podomeres, recurved carinally. The exopod carries apically directed, serrulate setae on the median face and tip. The shorter endopod of 4-6 podomeres also has serrulate setae, but these are directed posteriorly. Four long, serrulate setae project postero-apically from the basis.

Cirrus II (Fig. 2**B**) has a long protopod but short rami, the exopod having 6-8 and the endopod 5-7 podomeres. The serrulate setae of the protopod and both rami are directed anteriorly, except for a sparse, postero-apically directed fringe along the posterior margin of each ramus. The apical podomere of each ramus also carries several forwardly

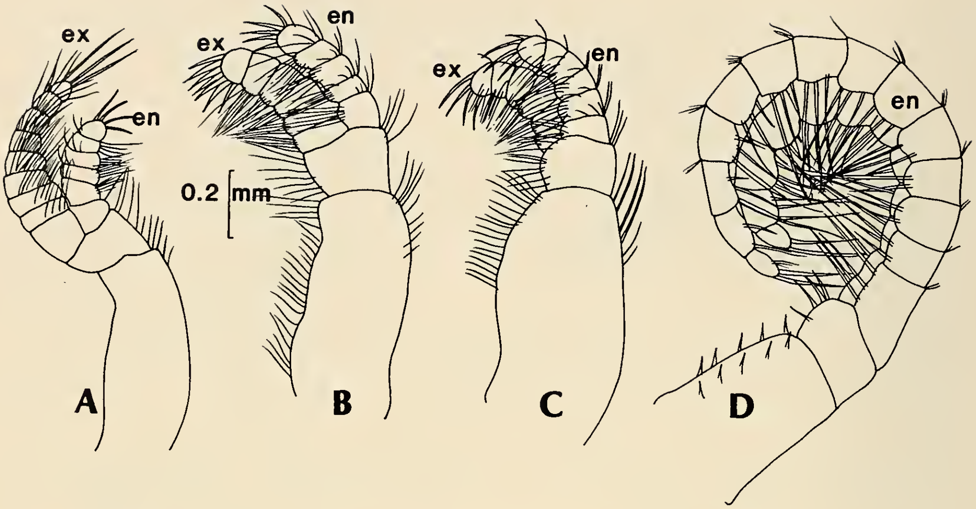

Fig. 2. T. divisa. **A-E.** — Left cirri in median view. **A.** — Cirrus I. **B.** — Cirrus II. **C.** — Cirrus III. **D.** — Cirrus V. *en*, endopod; *ex*, exopod.

curved, serrate setae with a double row of heavy setules along the concave margin. A few pappose setae project from the postero-apical corner of the coxa and basis.

Cirrus III (Fig. 2**C**) is slightly shorter than cirrus II, with a broad protopod as well as short rami. The exopod and endopod have 6-7 and 5-7 podomeres respectively. Setation is similar to that of cirrus II, except for an additional intermixture of serrate setae among the anteriorly pointing, serrulate setae of the endopod.

Cirri IV-VI (Fig. 2**D**) are typical captorial cirri. Representative podomere numbers are 13/11, 15/13 and 15/14 for the exopod and endopod. The podomeres carry 2 long pairs and 1 short pair of serrulate setae anterolaterally. The protopod carries sparse anterior spines.

Mouthparts. The general configuration of the oral cone has not been described for *T. divisa.* The individual mouthparts have been well described and figured by previous workers (e.g. Hiro, 1939; Stubbings, 1967).

The oral cone (Figs 3**A**, 3**B**) is low and wide and the labrum is only weakly bullate. In posterior view, the large, obliquely inclined mandibular palps obscure the labrum. Curved setae on each palp fringe the entrance to the preoral cavity. The short maxillae are set well on to the dorsal surface of the oral cone and point more posteriorly than ventrally.

The labrum (Fig. 3**C**) has a shallow median indentation on the posterior margin, with 3-4 low protuberances and a fringe of short hairs on either side. The long mandibular palps have serrulate setae apically and a fringe of jointed setae along the median edge. The mandible (Fig. 3**D**) is quadridentoid, with a prominent incisor tooth and subsidiary cusps on the 2nd-4th teeth. The molar process carries a group of 4 sharp spines of variable length. The maxillule (Fig. 3**E**) has two large and two small spines above a small notch. 6-8 spines occupy the cutting edge below the notch, and a group of smaller spines occupies the median angle. The maxilla (Fig. 3**F**) is typical, with an apical lobe carrying serrulate setae and a proximoventral lobe with jointed setae.

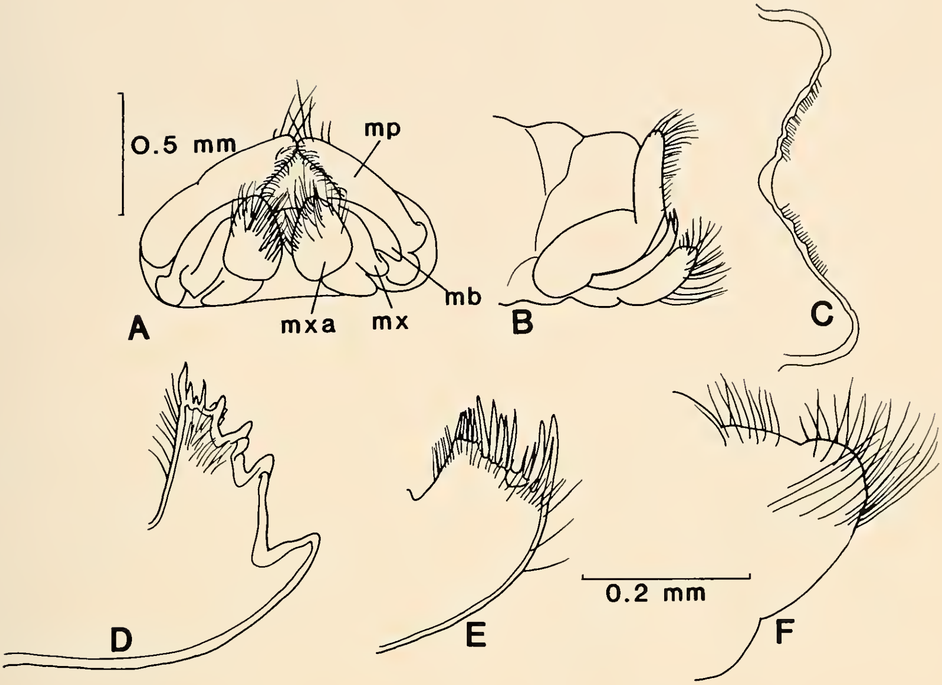

Fig. 3. T. divisa. **A** and **B.** — Posterior and right lateral views of oral cone. **C.** — Labrum, ventral view. **D.** — Right mandible, lateral view. **E.** — Right maxillule, lateral view. **F.** — Left maxilla, median view. *mb*, mandible; *mp*, mandibular palp; *mx*, maxillule; *mxa*, maxilla.

Cirral activity in *T. divisa*

Prior to cirral activity, the small opercular valves swing open at a low angle, with very little uplift. In still water, the opercular valves are held open and pumping beat commences. The curled long cirri emerge slightly above the carinal end of the aperture on each beat. The exopods of the first cirri also emerge, apposed and upright, in front of the long cirri. The pumping beat becomes more active in response to mechanical vibration induced by light tapping on the rock surface adjacent to the animal.

The application of a gentle water current across the orifice immediately evokes prolonged cirral extension. The cirral fan is held upright as long as the water current flows. Rotation of the extended fan up to 70-80° in either direction occurs in response to water currents impinging on the animal either laterally or carinally. Responses to stronger currents were not investigated.

Larval development in *T. divisa*

As mentioned above, only Nilsson-Cantell (1921) described any of the developmental stages of the larvae brooded in the mantle cavity of *T. divisa.* He distinguished a metanauplius stage, 0.84mm long, with a rounded body and well developed thoracic limb rudiments. The larva retains the three pairs of naupliar limbs, but with reduced setation. The second stage described by Nilsson-Cantell was the cyprid, 0.62mm long, with a typical bivalve carapace, eyes and antennules, but with a prominent thoraco-abdominal process.

The present material has yielded a longer sequence of stages which reveal the major progression of development. The embryos, deposited in the mantle cavity as paired adherent masses, are not embedded in typical gelatinous lamellae. Early embryos are brownish, yolk-filled and ovoid, with diameters of 450 × 350μm. Within the egg membrane, embryonic development proceeds with little increase in volume, yielding naupliar limb rudiments and a small caudal papilla (Fig. 4**A**). These rudiments become more conspicuous, and a median eyespot develops anteriorly. The embryo then hatches from the egg membrane, freeing the naupliar limbs, and changes slightly in shape (diameters 450 × 330μm). The body of the hatched, embryonized nauplius remains yolk-filled (Fig. 4**B**). The naupliar limbs are simple, with short, vestigial setae at the tip of each limb. The antennae are slightly longer than the antennules and mandibles.

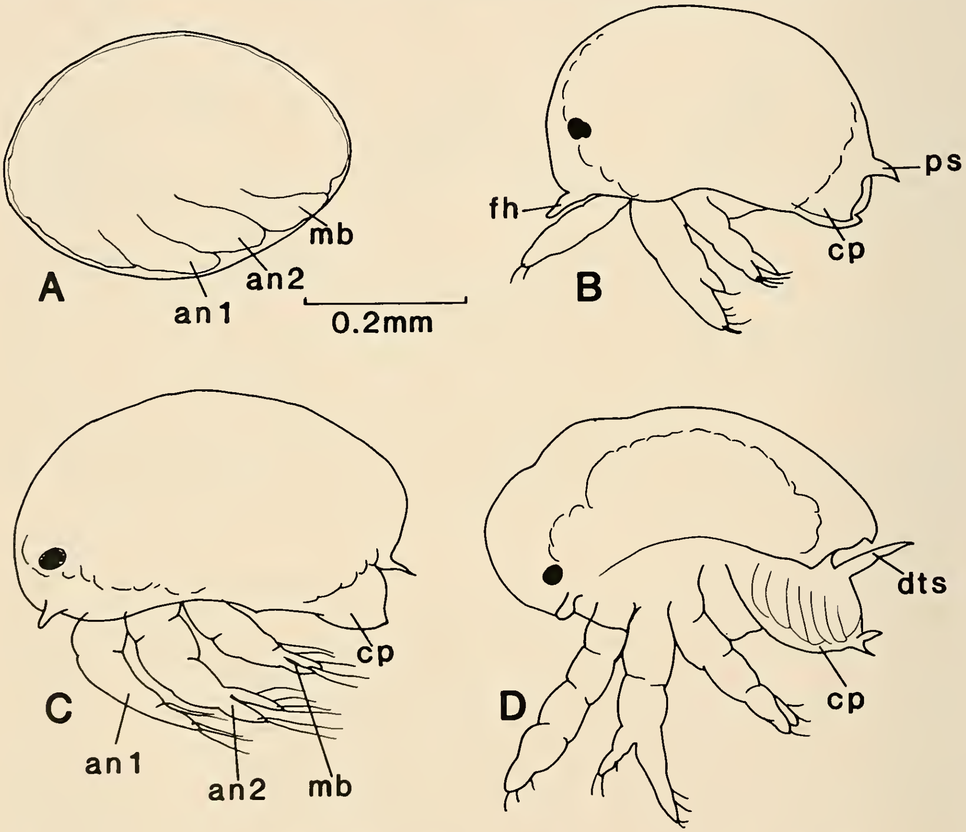

Fig. 4. T. divisa. **A-D.** Developmental stages from the mantle cavity. **A.** — Embryo before hatching. **B.** — Stage I nauplius; **C.** — Stage II nauplius. **D.** — Stage III nauplius. *an1*, antennule; *an2*, antenna; *cp*, caudal papilla; *dts*, dorsal thoracic spine; *fh*, frontolateral horn; *mb*, mandible; *ps*, posterior shield spine.

The first stage nauplius increases in volume and undergoes a moult to a second stage (Fig. 4**C**) in which the caudal papilla becomes more prominent. The antennae and mandibles develop more clearly bifid tips. At the second moult, the third stage nauplius (Fig. 4**D**) shows considerable enlargement of the caudal papilla and a dorsal thoracic spine, reduction of the posterior shield spine and some reduction in the volume of yolk within the body. The lateral margins of the dorsal shield are now sharply delineated and the setation of the limbs is reduced. During this stage, the caudal papilla begins to show signs of segmentation. Another moult then follows, yielding a fourth stage nauplius (Fig. 5**A**), the last before the cyprid. The caudal papilla is further enlarged, while the naupliar limbs show a reduction in the number of vestigial setae. Paired compound eyes develop anteriorly and paired, setose thoracic limbs are conspicuous in the caudal papilla. The outline of the body changes towards that of a more typical, late stage tetraclitid nauplius, with a broad straight front. Internally, the outlines of internal organs become defined, although much yolk remains.

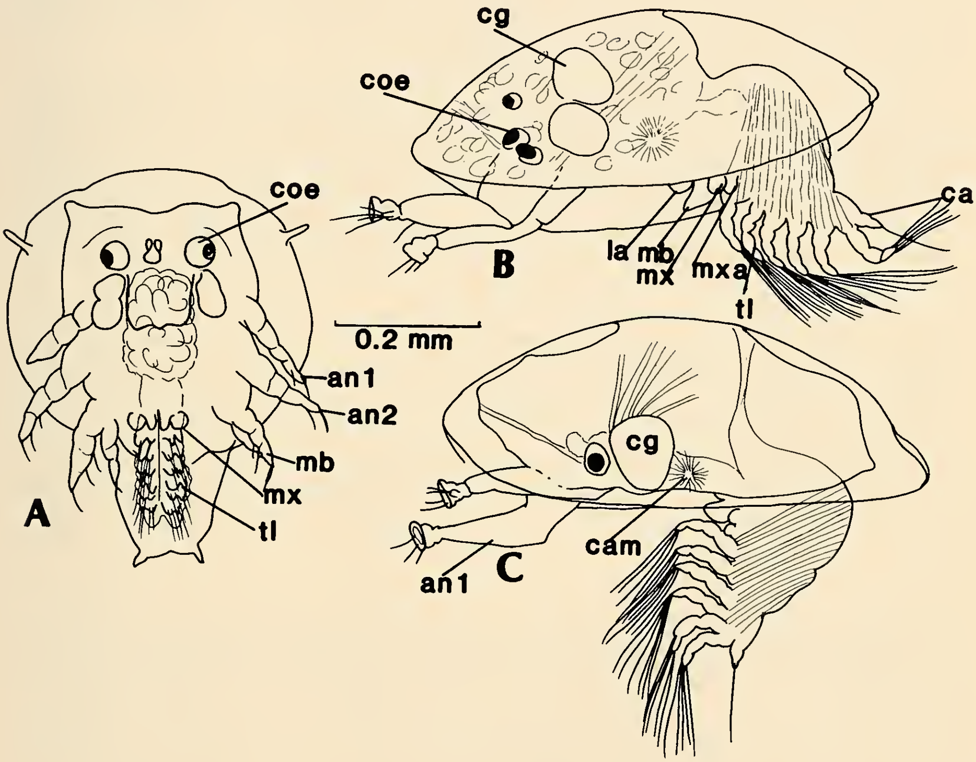

Fig. 5. T. divisa. **A-C.** — Later developmental stages from the mantle cavity. **A.** — Stage IV nauplius; **B.** — Early cyprid. **C.** — Late cyprid. *an1*, antennule; *an2*, antenna; *ca*, caudal appendage; *cam*, cyprid adductor muscle; *cg*, cement gland; *coe*, compound eye; *la*, labrum; *mb*, mandible; *mx*, maxillule; *mxa*, maxilla; *tl*, thoracic limbs.

The young cyprid, apart from the continuing yolk content, is of the usual cyprid structure (Fig. 5**B**). As the cyprid continues its development and the yolk is used up, (Fig. 5**C**), the 6 pairs of setose thoracic limbs and their musculature become fully differentiated and the compound eyes and cement glands become more conspicuous, but there is still little sign of development of the gut. The 3 pairs of mouthpart rudiments are obvious but not functionally differentiated. Cyprids must escape the mantle cavity at this stage, but it seems likely that free-swimming life is brief. Little reserve material remains within the larva, and feeding is not possible.

DISCUSSION

Functional Morphology. Anderson and Anderson (1985), studying *Tetraclitella purpurascens*, drew attention to the many generalized balanomorph features retained in the Tetraclitellinae, some of which had already been recognized by Ross (1969). They include a low conical profile maintained by diametric growth: associated broad radii; weak articulation of the wall plates; a flattish operculum with large tergal depressor muscles, small scutal depressor muscles and no scutal depressor muscle scars; a small mantle cavity with little free space for respiratory flow; an elongate prosoma and thorax with limbs in serial array; short maxillipeds, but a high, narrow oral cone. Anderson and Anderson also showed that the diametric growth of the tetraclitelline wall is based on a unique specialization, open-sided tubiferous parietes capable of circumferential growth. This feature was figured by Hiro (1939) but its significance in promoting rapid diametric growth has only recently been appreciated.

The same pattern of morphological organization, except for a lower profile to the oral cone, is displayed by *Tetraclitella divisa*, at a much smaller maximum size than *T. purpurascens*. Concomitantly, the two species share a common mode of opercular and cirral activity. Anderson and Buckle (1983) observed that *T. purpurascens* performs respiratory pumping beat in still and slowly flowing water, and responds to moderate external water flow by prolonged cirral extension. Anderson and Anderson (1985) found that the opercular movements associated with these cirral activities in *T. purpurascens* are simple, involving a hinge-like opening and closing action on a thick opercular membrane, with only moderate uplift. *T. divisa* exhibits similar opercular movements, performs respiratory pumping beat in still water and enters into prolonged cirral extension in response to slow to moderate external water flow. Both species also have a limited rotational capacity of the extended cirral fan, to not more than 90° in either direction.

Thus in spite of obvious differences in size and distribution, *T. divisa* and *T. purpurascens* epitomize a functional organization that is probably characteristic of all tetraclitelline species, combining a generalized balanomorph pattern of respiration and feeding with a hypobiontic habit and a capacity for rapid diametric growth. Further studies on other species of *Tetraclitella* from this point of view would be of particular interest.

Larval Development. In the light of the morphological conservatism of the tetraclitellines, the unusual modifications of larval development in *T. divisa* are particularly striking. Embryonic and larval development described in some other species of the genus follow the characteristic balanomorph mode, with eggs of moderate size (approx. 200μm) hatching as typical stage I nauplii and passing through the usual sequence of six planktotrophic naupliar stages followed by a cyprid stage (Anderson, 1969; Karande, 1974, 1982; Barker, 1976; Egan and Anderson, in preparation). *T. divisa* has a secondarily enlarged, yolky egg (450×350μm), hatches as a lecithotrophic stage I nauplius with vestigial setation, remains within the mantle cavity throughout its lecithotrophic development to the cyprid stage and is free-swimming only as a cyprid. During this brooded development, the number of moults is reduced, yielding only four naupliar stages before the cyprid. The naupliar limb setation remains vestigial in all naupliar stages, and the main emphasis is on development of a large caudal papilla. Some yolk still remains when the moult to the cyprid takes place, and the cyprid undergoes considerable further differentiation at the expense of this yolk, including functional elaboration of the antennules, the thoracic limbs and their musculature, and the cement glands, before reaching the stage of release. Development of the cyprid organization is thus a more direct and gradual process in *T. divisa* than in typical planktotrophic balanomorph larvae. Convergently similar modifications towards direct development through a reduced number of lecithotrophic naupliar stages, followed by release from the mantle cavity at the cyprid stage, have been noted in the lepadomorph *Ibla idiotica* (Batham, 1945) and in most Acrothoracica (Turquier, 1972, 1985). The developmental sequences in the two other balanomorphs known to release their larvae at the cyprid stage have not yet been described.

Distribution. As pointed out by Newman and Ross (1977), the distribution of *T. divisa* presents a paradox. The species is circumtropical and mainly insular, occurring as a series of widely separated, geographically isolated, intertidal populations. At the same time its planktonic larval phase is very abbreviated. The present work indicates that the cyprid retains no yolk reserves when released, and is like other cyprids in being unable to feed. Settlement in the vicinity of the adult population is thus favoured, resulting in the known build-up of dense local populations; but dispersal as planktonic larvae over long distances is not possible. The circumtropical insular distribution therefore suggests oceanic transport on floating objects, for which some evidence was provided by Newman and Ross (1977). On arrival at a suitable location, the mode of cyprid release would facilitate rapid colonization, in a manner analogous to that of many ascidians with brood retention and abbreviated larval life. The selective forces that led a few, scattered balanomorph species into this mode, however, with its increased egg size and consequent modifications towards direct development, remain a mystery.

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Metagenesis as a Possible Key to Animal Form

JEAN J. CARTER

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The origin of metazoan form is attributed to the evolutionary modification of a metagenic life cycle, a model for which is proposed, based on two alternating diploid entities, here termed *troph* and *gōne*. These are expressed in the Hydrozoa and Scyphozoa in their most readily identifiable form as independent polyps and medusae. Budding of the *troph* and the strobilation of the *gōne* are seen as characteristic expressions of asexual reproduction, by which means each entity replicates its own generation. The formation of the *gōne* by the *troph*, however, involves a change in the nature of the unit and additional trophs can only be formed by way of a zygote. The integration of the two entities (i.e. *troph* and *gōne* or *troph* and *gōne* plus strobilus) is considered as the underlying cause of the development of the triploblastic and coelomate condition and the role of the 1D cell is interpreted as the '*gōne* primordium'. This integration is termed *syngenean*.

Recognition of the *troph*- and *gōne*-derived elements in segmented protostomes identifies the adult mandibular segment as the first primary *gōne* (G1). The effects on cephalization of reduction of the *troph*, of its invasion by *gōne* tissue and of use of the *troph* or *gōne* mouth by the adult, are considered.

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INTRODUCTION

Metagenesis is the term for a life cycle in which an asexually reproducing (budding) generation, arising from a zygote, alternates with a sexually reproducing generation (Haeckel, 1866). In the animal kingdom, metagenesis is a phenomenon that occurs so sporadically and in so small a number of seemingly unrelated groups of lower metazoans, that little phylogenetic significance has been attached to it beyond its relevance to the phylogeny of the cnidarians. Early writers on the subject (Steenstrup, 1845; Allman, 1864; Haeckel, 1866) recognized that, in its basic form, metagenesis consisted of an alternation of a 'vegetative', 'nurse' or 'feeding' generation and a 'fruiting' or gamete-producing generation. Later, others (Strasburger, 1894; Bower, 1908) characterized the alternating generations in plants in terms of chromosome numbers and identified the initiation of the gametophyte generation with the occurrence of meiosis and, although its value as the basis for a generalization was challenged from time to time (Svedelius, 1927), its precision and convenience have led to its wide acceptance as a working hypothesis (cf. Weier *et al.*, 1974).

The discovery of apogamy in pteridophytes, although confusing the issue (Lang, 1898; Farmer and Digby, 1907), has since been attributed to certain irregular mitotic figures (Steil, 1939) and accommodated as a secondary phenomenon. Although the generations are sometimes viewed as subdivisions of a single cycle (Darlington, 1978), there can be no doubt that a vegetative (or asexually reproducing) phase is followed by a sexual phase in the life cycles of all plants.

Zoologists, confronted by alternating asexual and sexual stages in the lower invertebrates, in which the haploid cells are restricted to the gonads and gametes (Campbell, 1974), were unable to establish an equivalence between the life cycles of the lower plants and animals. Many workers, following Brooks (1886), have favoured the view that metagenesis in cnidarians is a secondary condition and discussion has centred on whether the ancestral form was polypoid or medusoid, sessile or free (Thiel, 1966; Campbell, 1974; see also Boudreaux, 1979: 17, 18).

The interpretation of animal form presented in this paper depends largely on recognition of the universality of potential polypoid and medusoid phases, or their equivalents, in that order, in the life cycles of all metazoans and it attempts to follow their separate evolutionary progress in representative types within the Metameria. It could be argued that there is room for a new approach since no comprehensive theory of the relationships between the invertebrate phyla has emerged from two recent symposia of the Systematics Association (House, 1979; Conway Morris, 1985).

In hydrozoans, the polyps, gonostyles and medusae which succeed each other as distinct morphological entities, retain continuity of the body layers as the polypoid generation buds to form the medusoid generation. Though some doubt still exists about the metagenic status of the (young) scyphopolyp and (older) scyphistoma, consensus of opinion favours a polypoid interpretation (Campbell, 1974; Thiel, 1966; Chapman, 1966). The direct transformation of the strobilating scyphistoma into ephyrae (e.g. in *Aurelia*) and the development of gonads in the lucernarian scyphopolyp (Hornell, 1893; Hyman, 1940: 509), however, demonstrate that ultimately a specific region must become medusoid in nature. In the normal process of ephyra production, the apical disc or, on occasion, the first three discs, either degenerates or resumes a polypoid existence (Thiel, 1966: 16-20). The pedal disc can also be regarded as part of the polypoid tissue, since it reverts to a typical polyp after the liberation of the last ephyra and a scyphistoma has been figured with a well-developed ring of polyp-like tentacles at the base of a stack of developing ephyrae (Agassiz, 1860). As in hydrozoans, the scyphozoan medusa is formed from a population of cells by transformation of part of the body wall. Campbell (1974) has pointed out that because of this and because of the diploid nature of the medusa as a whole, some workers feel that the polyp should be considered as a larval phase. This continuity of body layers from one 'generation' to the next would be comparable with the condition in pteridophytes if the 'gametophyte generation' had been defined to include the diploid tissue of the sporangia as well as the haploid prothallus formed from spore germination. In higher plants, the equivalent of the *gōne* generation in animals would then be found in the stamens and carpels, rather than in the haploid tissue alone. In other words, the haploid phase would represent only part of the 'gametophyte generation'. The implication of this alternative interpretation is that, whereas in the plant kingdom the sporophyte or asexual generation forms the conspicuous vegetative unit, in animals it is the sexual generation that has become dominant in body form (see below) and the analogy of the asexual polypoid phase should be sought in the premetamorphic 'primary marine larvae' (Jägersten, 1972) or their embryonalized equivalents.

The precocious formation of the sexual entity and the concurrent embryonic development of both phases of the life cycle offer a simple explanation for both the transformation of the vegetative polyp into part of an integrated and usually motile organism and for the increasing complexity of some tissues and organ systems. It would appear that, as in the higher plants, the identity of the two units in animals may have become progressively obscured during evolution as their tissues became more intimately associated. The relative dominance of the polypoid versus medusoid elements has subsequently contributed a fundamental though simple source of variation at the higher taxonomic levels.

THE SYNGENEAN MODEL

To challenge this concept, a new approach to morphology is proposed. In the present discussion, the anatomy of selected types is related to a series of models for which the following terminology is introduced (see Fig. 1). The term *troph* refers to the

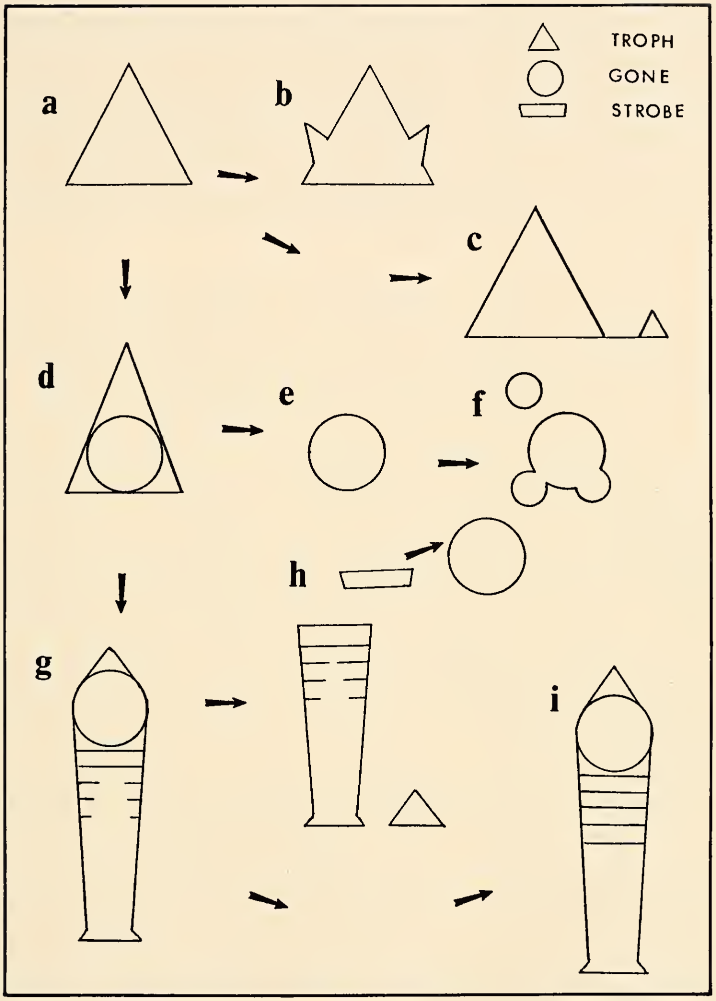

Fig. 1. Diagrammatic representation of methods of asexual reproduction. **a.** *Troph.* **b.** Asexual reproduction of *troph* by budding. **c.** Asexual reproduction of *troph* by alternative budding method. **d.** Metagenic formation of *gōne* by *troph.* **e.** *Gōne* independent of *troph.* **f.** Asexual production of *gōnes* by budding. **g.** Asexual production of *gōnes* (strobes) by strobilation. **h.** Liberation and maturation of strobes and re-settling of apical *troph.* **i.** Strobilated syngenean individual.

asexually reproducing, polypoid form or phase of the life cycle or to a primary larva of the trochophore (or related marine group) or to its embryonalized equivalent. The term *gōne* is used for an individual of the gamete-forming, medusoid generation, or for an equivalent entity in the sexual generation of the life cycle. The term *syngenean* refers to single organisms formed by the integration of the *troph* entity with one or more *gōne* entities and the term *strobilus* is used here for a segmented series and the term *strobe* refers to a single unit in the series of *gōne* entities that may or may not have secondarily lost its primary reproductive function and may or may not have become tagmatized.

Hyman's (1951) rejection of the scyphistoma as a candidate for the ancestry of the Metameria was based partly on the difficulty of homologizing the head and anal 'segments' with the other body segments and partly on the assumption that 'a free-swimming animal reproducing in this manner would lose its head at each fission' (Hyman, 1951: 30). Clark's account of the corm theory (Clark, 1964: 22), like Hyman's, does not recognize a metagenic difference between the oral and pedal discs and the intervening ephyrae. Neither does it distinguish conceptually between the strobilus of a scyphistoma, the stolons of syllids, the chains of 'budding' turbellarians and the serial proglottids of cestodes. The metagenic status of each of these structures needs to be better understood because they can only be homologous if each represents the same unit or block of units.

THE COELOM AND PRIMARY GERM LAYERS

Before attempting to establish the equivalence or otherwise of these units or blocks of units, the nature of the coelom and germ layers and the position of the mouth relative to the blastopore are reconsidered. The presence of a coelom is a definitive adult characteristic of all taxa with a primary marine larva (i.e. trochophore, nauplius, actinotrocha, cyphonautes, tornaria and auricularia). By contrast, the acoelomate condition is so characteristic of the carnivorous, coprophagous or parasitic platyhelminths and nemathelminths that one must ask whether this is, in fact, the primitive condition or whether it was initially related in some way to a more advanced or symbiotic way of life.

There has been considerable interest in the method of formation of the coelom (as a schizocoel or an enterocoel) and its evolutionary origin (as a gonocoel, nephrocoel or enterocoel) (Clark, 1964). Discussion of these aspects, however, has failed to emphasize that, despite the mechanics and phylogeny of its origin, its ultimate relationship to the primary organ systems is remarkably constant. As with the formation of medusae in cnidarians, the manner of their origin may vary (contrast *Obelia* and *Aurelia*), but the results are clearly comparable.

By temporarily lessening the emphasis on the mechanism of formation in favour of its ultimate expression, we could hypothesize a situation in which a *troph* and a *gōne*, each with its own ectoderm, endoderm and mesenchyme, are integrated in such a way that the corresponding ectodermal and endodermal layers of each become confluent or intermingled. In this condition, the mesenchyme of *troph* and *gōne* would be equivalent, despite possible differences in their origin and the primary cavity within the *gōne* would be equivalent to that of the *troph* and therefore to its blastocoel. Whereas the haemocoel is recognized to be a persistent blastocoel (i.e. *troph* cavity), the coelom has not previously been considered as its counterpart in the *gōne* generation. If the *troph* and *gōne* are separate entities or the *troph* has been reduced, a cavity in the *gōne* mesenchyme will not be recognized as a coelom and an acoelomate condition will result.

Although the relationship of the three primary layers of the *troph* to their counterparts in the *gōne* unit will be influenced by the relative degree of development of each and by their physical disposition, it is to be expected that some association or co-ordination will occur between functionally equivalent units of the two generations. It will be evident that although this interpretation accepts the existence of three primary germ layers, ectoderm, endoderm and mesenchyme (including mesoderm), it modifies the concept of each by recognizing their possible dual origin. This may help explain the invasion of the annelid prostomium and its appendages by the trunk mesoderm (cf. Åkesson, 1968: 215) and the histolysis and cell migration that characterizes the pre-oral tissues of arthropods during metamorphosis (Anderson, 1966, 1973; Green, 1971; Manton, 1928), as well as the dual embryological origin and physiological control of some organ systems. Willmer's (1970) concept of the two cell-types (epithelium and mesohyl), instead of the traditional three, is equally applicable to the syngenean interpretation and reflects the

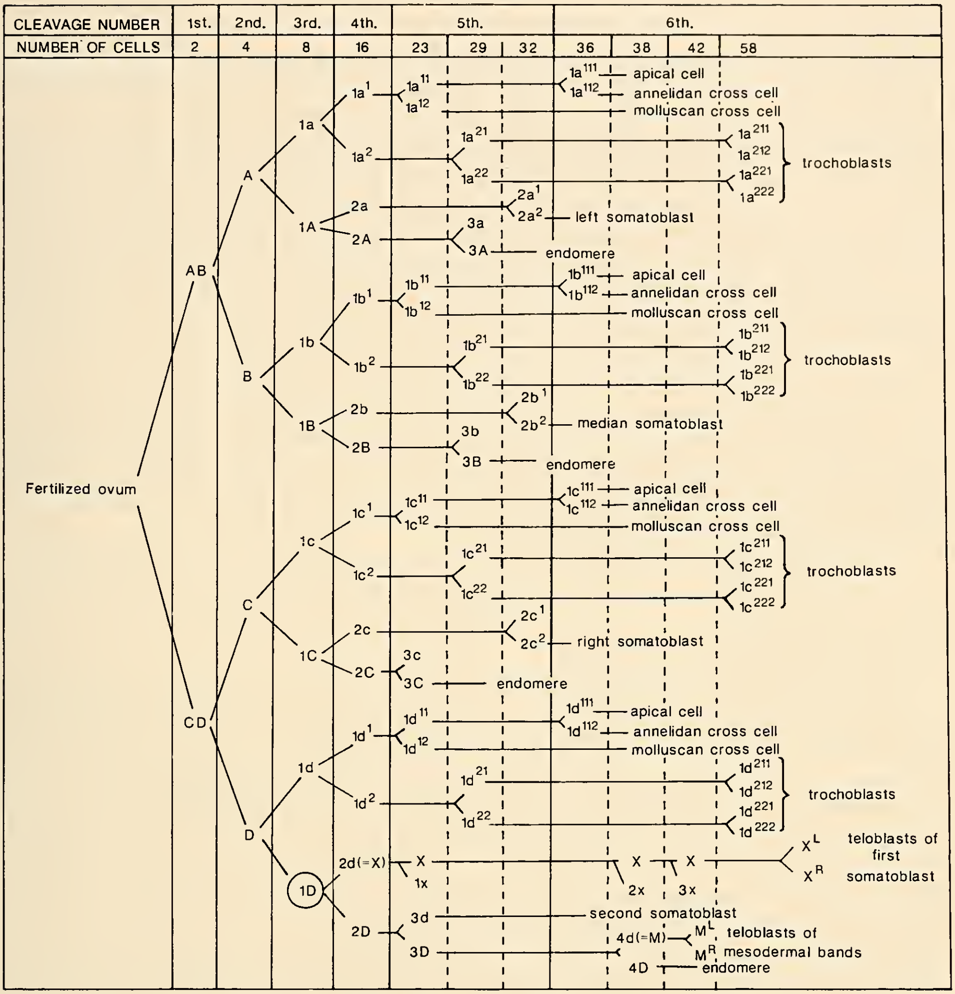

Fig. 2. Cell lineage of *Nereis* (Polychaeta) (after Okada, 1968). Note the idiosynchronous division of the 1D cell, postulated here as the *gōne* primordium.

dissatisfaction with the conventional interpretation of the germ layers (Oppenheimer, 1940).

Detailed studies of embryonic cell lineages in the protostomatous phyla (Wilson, 1892; Cather, 1971; Clement, 1971; Åkesson, 1962; Kumé and Dan, 1968), which characteristically exhibit spiral cleavage, have shown that while the behaviour and fate of the A, B, C and 1d cells are comparable, that of the 1D lineage is unique (Fig. 2). Not only is the timing of its divisions unrelated to the synchrony of the other cells, but its derivatives contribute to the final structure in a unique manner. The attention that has been directed to 4d (or M), as the 'mother cell' of the mesoderm and the sex cells, has obscured the range and sum of the other 1D derivatives. In *Nereis*, 2d (=X) is the teloblast of the ectoderm of the first trunk segment and also forms the proctodaeum; 3d contributes to the posterior wall of the stomodaeum; 4d gives rise to some of the mesodermal elements of the mid-gut as well as to the mesoblast (M) with its coelom, and the 4D contributes endoderm to and behind the posterior pharyngeal region tissues. These 1D derivatives collectively fulfil the requirements of the first medusa-equivalent (or the primary *gōne*) and succeeding units of the strobilus.

Comparison of the cell lineages of the polychaete *Nereis*, the cirripede *Mitella* and the phyllopod *Polyphemus* reveals a general similarity. From these examples, the difference between the annelid and crustacean lineages appears to be that the D lineage achieves a 'potentially self-sufficient' identity, comprising ectoderm, endoderm, mesoderm and germ cells after the third cleavage in *Nereis* (i.e. the 1D cell) (Okada, 1968) and after the second, the D^{II} (i.e. the D cell) (Shiino, 1968), in the crustaceans *Polyphemus* and *Mitella*. However, the origin of the endoblast and primordial germ cell of *Polyphemus* is comparable with *Nereis* rather than with *Mitella* (see Fig. 2), suggesting that variation in the details of cell lineage within a phylum (in this case Arthropoda) may be as great as that between related phyla.

Prior to metamorphosis, the nereid trochophore (with the exception of the 1D derivatives) can be compared with a *troph* or a coelenterate polyp which has transformed its mesogloea into mesenchyme. After metamorphosis, the original *troph* tissue is separated by the vigorous growth of the 1D derivatives, so that the pre-oral region and pygidium assume a relationship to the entire organism comparable with that of the oral and pedal regions of a scyphistoma.

Let us, therefore, consider the consequences of the proposition that the triploblastic, coelomate condition owes its origin to the development of the *gōne* (identifiable in *Nereis* as the 1D lineage, see Fig. 2) in intimate association with the *troph*, formed from the derivatives of cells A, B, C and 1d.

If each *gōne* has the metagenic status, function and anatomical potential of a medusa and the strobilus is essentially a stack of such medusae, each strobe will retain a potential self-sufficiency until this is irreversibly changed by evolution resulting in a division of labour between strobes. With progressive differentiation of a strobilus, it is to be expected that the leading units will have developed the *gōne*-orientated sensing and feeding systems to a greater degree than those following. By recognizing the first post-metamorphic (i.e. the most anterior trunk or jaw-bearing) segment in *Nereis* as G1 (see Table 1), the dual origin of the adult mouth and pharynx becomes clear. The cephalization of G2 and G3 in arthropods makes the evolution of more specialized mouth parts possible. The doubt that surrounds the homology of the peristomium in polychaetes (Schroeder and Hermans, 1975) is largely due to conflicting definitions. These doubts can be resolved, in part, by recognizing the errant polychaetes to be annelids with a well-developed and persistent *troph* and the sedentarians to be forms in which the *troph* is reduced. The role of the peristomium as the sensory and oral region of G1 (cf. the manubrium of the first medusa) is supported by the definition of Schroeder and Hermans (1975) and by embryological evidence. The peristomial appendages, together with the sub-oesophageal ganglion and invasive mesohyl which supplements the pre-metamorphic and pre-oral structures, can be regarded as elements of the first or primary *gōne*. The reciprocal growth of axons to and from the supra- and sub-oesophageal ganglia also support the concept of this *gōne* actively establishing operational partnership with the *troph* (cf. Henry, 1947).

Once the positional and functional relationships between *troph* and *gōne* are recognized, it becomes possible to interpret the proto- and deuterostomatous conditions, irrespective of assumed phylogenetic relationships. This will be deferred, however, until certain aspects of segmentation, stolonization and tagmatization have been considered.

SEGMENTATION, TAGMATIZATION AND STOLONIZATION

The segmentation of annelids and arthropods is almost ubiquitous and widely regarded to be a primitive feature of both groups. Its partial obliteration in some arthropods may occur during maturation, as in the parasitic crustaceans, or during the embryonic stages, as in the acarine and araneid arachnids. In all these cases, the lack of segmentation is clearly secondary. Tagmatization usually accompanies and possibly precedes a loss of segmentation. It is characteristic of a specific functional specialization such as feeding, locomotion or reproduction, the obliteration of segmentation being commonly associated with the reproductive region of the body.

There is much variation and some uncertainty about the precise origin of the germ cells in the various arthropod taxa. They have been found in representative polychaetes, crustaceans and insects in all segments of the strobilus, including the mandibular (G1), but not in the pre-oral or caudal 'segments' (Green, 1971; Anderson, 1973; Snodgrass, 1935; Bitsch, 1973). Because these exceptions coincide with the postulated *troph* tissues, it is concluded that the *gōne* or the strobilus itself is the potentially fertile unit and that evolution has favoured the migration of the germ cells to restricted regions or metameres, usually those posterior to the stomach and digestive glands. Variability in the position of the genital ducts in the lower crustaceans and, therefore, in the extent of the fertile (cephalo-) thorax, contrasts sharply with the rigid patterns that characterize the malacostracans, insects, myriapods and chelicerates. In the oligochaetes, the sterile region posterior to the fertile tagma is usually reduced or secondarily modified.

TABLE 1

Segmental equivalence of the anterior appendages of the Metameria based on the syngenean interpretation of animal form

SYNGENEAN UNIT	ANNELIDA	ARTHROPODA		
	POLYCHAETA	CRUSTACEA	INSECTA	ARACHNIDA
T 1	PROSTOMIAL TENTACLES AND PALPS	ANTENNULES	——	——
T 2		ANTENNAE	ANTENNAE	——
T 3		LARVAL MANDIBLES	INTERCALARY SEGMENT	——
G 1	PERISTOMIAL TENTACLES AND PHARYNGEAL JAWS	ADULT MANDIBLES	ADULT MANDIBLES	CHELICERAE
G 2	APPENDAGES OF TRUNK SEGMENTS 2nd.	FIRST MAXILLA	FIRST MAXILLA	PEDIPALPS
G 3	3rd.	SECOND MAXILLA	SECOND MAXILLA	PROSOMAL (WALKING) LEGS 1st.
G 4	4th.	WALKING LEGS (OR MAXILLIPEDS) 1st.	THORACIC LEGS 1st.	2nd.
G 5	5th.	2nd.	2nd.	3rd.
G 6	6th.	3rd.	3rd.	4th.
G 7	etc.	etc.		

T: *troph*; G: *gōne*

By identifying, as the essential feature of the onset of metamorphosis in crustaceans, the simultaneous histolysis of the pre-oral musculature of the nauplius, its replacement by invasive somitic mesoderm and the development of the *adult* elements of the mandibular segment, the nauplius can serve as a point of reference for the morphogenesis of the adult jaw-bearing segment of both annelids and the egg-nauplius. The entity G1 (or the 'primary *gōne*') and the subsequent strobes (G2, G3 etc.) can then be identified and their tagmatization compared without the necessity for establishing homology of the pre-oral tagmata. The advantages of this are evident in interpreting the homologies of tagmata in arachnids and onychophorans where pre-oral (or *troph*-equivalent) structures appear to be reduced.

By adopting the nauplius in preference to the trochophore as a 'standard' or reference for the fully-developed 'primary larva' of the protostomatous phyla, the three paired appendages (antennules, antennae and *larval* mandibles), together with the proto-, deuto- and trito-cerebra, the larval eyes and the larval alimentary system (stomodaeum, larval stomach and digestive glands and the anterolateral region of the adult pharynx), can be identified as parts of the mature *troph*. In Crustacea, the replacement of larval by adult appendage musculature, like the development of pharyngeal jaws in the first trunk segment of polychaetes, is due to the activity of cells derived from the mesodermal teloblasts and ultimately to the 1D lineage (cf. Manton, 1928; Green, 1971; Anderson, 1973).

The pharyngeal region of annelids and the (adult) mandibular segment of crustaceans appear to be structures of dual origin, derived in part from the *troph* and in part from the *gōne*, the development of each component varying with the taxon, but those of the *gōne* invariably developing after those of the *troph*.

In insects, the intercalary segment, now widely accepted as being innervated by the tritocerebrum (Bitsch, 1973; Rempel, 1975) would, by the same reasoning, be part of the *troph* and the equivalent of the larval mandibular region of a nauplius. In the holometabolous insects, it seems to be the sudden burst of growth of *gōne* tissue, initially and precociously formed during the early embryonic period, but latent during the secondary larval ('caterpillar') stage, which causes metamorphosis by completing the differentiation of each strobe and by modifying and replacing some of the *troph*'s characteristic structures — e.g. the larval eye spots and simple pre-oral appendages. In the mosquito, for example, the larval feeding brushes are replaced at metamorphosis by the highly specialized structures that form the feeding mandibles. In orthopterans, cells derived from a mesodermal somite migrate into the rudimentary antennae and proliferate to form the segmented adult antennae (Wheeler, 1893: 111). Although the 1D cell is not identifiable as such in insects, the somitic mesoderm clearly belongs to the strobilus. As such, it can be interpreted as another instance of the integration of equivalent tissues of the two generations to form a single functional structure. Although the spiral cleavage and, therefore, the possibility of recognizing the 1D lineage is replaced by superficial cleavage in the peracaridean crustaceans and the insects, there seems to be no reason to doubt the homology of the mandibular and strobilar regions of either group with their counterparts in the lower crustaceans if the adult mandibular segment is G1 in all cases. Here again, we see that although the details of differentiation may differ, the results are closely comparable because no one doubts the homology of isopod structures with their counterparts in other crustaceans.

Table 1 shows the strobilar patterns of certain metameric invertebrates, using the post-metamorphic mandibular segment as the critical means of identifying G1. This homology has not previously been justified because of the difference in form between the pre-oral appendages of the major groups. Once the pre-metamorphic appendages are recognized as the homologues of the peri-oral tentacles of a *troph*, their initial radial symmetry can be seen as secondarily modified to a paired bilateral arrangement. This change in symmetry is best understood in relation to the establishment of the antero-posterior axis of the typical syngenean metazoan, the establishment of a composite mouth and increased 'streamlining' of the head.

A reduction of the *troph* appears to have occurred within most of the major phyla during their early evolution and has possibly been a significant factor affecting variation at class level and above. The scyphozoan coelenterates, the tubicolous polychaetes, oligochaetes and hirudinean annelids as well as the chelicerate arthropods exemplify the dominance of the *gōne* within the larger taxa. In segmented forms, this results in greater prominence of the derivatives of the first strobe in the pre-oral tissues and of the first two or three strobes in the composition of the mouth and gnathocephalon.

The development of multi-segmental blocks, or epitokal 'stolons' in some annelids, particularly syllids, though regarded by some earlier writers as a kind of alternation of generations (cf. Potts, 1911), is now more widely interpreted as a form of regeneration. Okada (1934) and Berrill (1952) have described the development of a new prostomium as part of the stolon head and the regeneration of a typical head when the anterior segments are amputated. At first sight, this suggests the replacement of *troph* tissue by *gōne* tissue. However, the formation of the new head blastema is closely linked with the arrival of multipotent neoblasts, formed as 'syncitial nests of small mesenchyme cells' (Berrill, 1952: 414), lying in the angles of the septum and nerve cord. If the neoblasts arise directly from the larval mesenchyme or if ectoderm derived from A, B, C or 1d lineages (e.g. $2a^2$, $2b^2$, $2c^2$ — the right, median and left somatoblasts respectively: cf. Fig. 2) contributes to the new head, there is no departure from the principle of head formation from *troph*-derived tissue. The development of epitokal heads in certain polychaetes may, therefore, be a consequence of the distribution of *troph* tissue in the adult worm.

Experimental studies (Wada, 1968; Clement, 1962) have shown that embryos of protostome larvae cannot undergo metamorphosis without the D cell. However, the D cell alone, although capable of producing a 'normal' post-trochal region, dies before it can reach the stage of metamorphosis, suggesting that a normally-functioning *troph* is necessary for the development of the *gōne*.

PROTOSTOMATOUS AND DEUTEROSTOMATOUS TAXA

Grobben (1908) and some later authors (e.g. Beklemishev, 1969) have used the method of mouth formation, *inter alia*, to distinguish what they believe to be two major, fundamentally divergent stocks of metazoans: the Deuterostomia and the Protostomia. Neither group, however, has been universally accepted. For example, the validity of the deuterostomes has been under challenge in recent years (Brien, 1974; Løvtrup, 1975) and some undoubted protostomes (e.g. onychophorans; Manton, 1949) have been shown to possess a mouth that arises *de novo* and not from the blastopore or its point of closure. There seems little doubt, however, that the annelid-arthropod-mollusc-turbellarian group does possess features that indicate a true relationship between them.

The syngenean interpretation offers a solution to the dilemma about homology in regarding the mouth of the polyp in the cnidarians to be the equivalent of the mouth of the *troph* in protostomatous metazoans. The Protostomia are then seen to be a group of phyla in which the *troph* mouth remains as part of the functional adult mouth, however formed. Any exceptions to this among protostomes can be accommodated as specializations comparable with the degree of variation in cnidarian gastrulation (i.e. by epiboly, ingression or delamination). The deuterostomes, collectively identified more by the absence of protostome features, lack the homogeneity of the protostomes and appear in most, if not all, cases to be taxa in which the distinctive features of the *troph* are reduced and the oral aperture of the *gōne* becomes the functional mouth.

In these deuterostomes, where the adult mouth arises independently of the blastopore, the way in which the mouth originates lends itself to the interpretation that it is derived from the *gōne* while the blastopore is largely confined to the pygidial area. In such cases, the *troph* is still able to contribute to the sensory and neural structures of the head or lophophore. The extent to which it does so is an expression of the relative contributions of *troph* and *gōne* to the adult body form and appears to provide a simple explanation for some of the differences that exist between the 'lophophorate deuterostomes' and the 'true deuterostomes'. Close relationship between these groups would not have to be assumed in order to explain their embryological similarities.

CONCLUSIONS AND SUMMARY

If the Metazoa evolved from the Protista (Sleigh, 1979: 50-52), there is reason to argue that because metagenesis is so widespread in the Protista and Cnidaria, it could well be a fundamental characteristic of the Metazoa. In an *a priori* interpretation of metagenesis in the metazoans, the more primitive form is the free *troph* (larva) while the embryonalized equivalent (e.g. the egg-nauplius; Shiino, 1968) is its phylogenetic successor. The general trend appears to have been towards direct development, the precocious formation of the *gōne* (sexual generation) and the syngenean state. A hypogenic interpretation of the life cycle, on the other hand, offers no basis for seeking an evolutionary progression from alternating generations towards the development of primary larvae and thence to progressive embryonalization and permits the marine primary larvae to be considered as a series of individual late adaptations.

When the metagenic model is applied to the higher invertebrates, the existence and metamorphosis of the marine primary larvae become explicable without need to identify the direct or hypothetical ancestors. The introduction of the concept of *troph* and *gōne*, as models for the polyp and medusa equivalents respectively, also allows the two forms to be considered as homologues each capable of their own maturity, modifications and evolution. It also suggests that through integration they could form a syngenean animal, the morphology of which would vary depending on the relative contributions made by the *troph* and *gōne* components. The degree of development and persistence of each entity controls such features as the degree of cephalization, the presence or absence of a coelom, segmentation and tagmatization, as well as the type of mouth development. By this *a priori* approach and the avoidance of traditional assumptions, an alternative interpretation of animal form can now be offered.

The recognition of metagenesis and the almost simultaneous and integrated development of the two generations can explain the trend toward embryonalization of the larval form as an evolutionary advance. By recognizing the contribution which the *troph* and *gōne* entities each make to the functional morphology of the adult, it is possible to trace an increasing specialization of the *troph*'s sensory role in the developing brain and its decreasing role in food uptake and locomotion. Against this background, other functional systems can be isolated in similar fashion by embryological criteria and the direction of any progressive morphological series can be determined independently of existing theories about phylogeny.

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NOTE ADDED IN PROOF

'Tagmatization' is used here to describe the progressive differentiation of a block of strobes into a tagma. It is distinct from tagmosis, in which the *troph* may be incorporated with *gōne* units, as in cephalization.

'Embryonalization' is defined as the gradual suppression of the free-living primary marine larvae (the *troph* generation) and the modification or loss of their morphological identity due to the precocious development of the *gōne* before hatching. This requires recognition of a distinction between larval (*troph*) ectoderm, endoderm and mesenchyme and the *gōne*-derived ectoderm, endoderm and mesoderm. Its range is exemplified in crustaceans where hatching may occur at any stage from a nauplius to a miniature adult. The word is identified with the syngenean interpretation of animal form and is suggested as the 'unknown force' or 'adult pressure' which lies behind adultation and acceleration as discussed by Jägersten (1972: 6, 218).

THE LINNEAN SOCIETY OF NEW SOUTH WALES

RECORD OF THE ANNUAL GENERAL MEETING, 1985

The one hundred and tenth Annual General Meeting was held in the Maiden Theatre of the National Herbarium, Royal Botanic Gardens, Sydney, on Wednesday, 27th March 1985, at 7.30 p.m.

The President, Mr G. R. Phipps, occupied the Chair. The minutes of the one hundred and ninth Annual General Meeting were adopted by the members present.

REPORT ON THE AFFAIRS OF THE SOCIETY FOR THE YEAR 1984-85

Publications

The Society's *Proceedings* were published as follows:—

Volume 107 (1982), Nos. 3 & 4	December, 1984.

This larger-than-usual issue contained papers presented to an international symposium on the Evolution and Biogeography of Early Vertebrates held in Sydney and Canberra, February 1983.

In addition, the Society also published in December 1984 a special volume containing 36 papers presented to the First International Polychaete Conference.

Dr P. A. Hutchings edited the Polychaete volume; Prof. T. G. Vallance continued to edit the *Proceedings*. The honorary service of these two members is gratefully acknowledged.

Newsletter

The Linnean Society News, edited by Dr Helene Martin up to and including No. 33 (July 1984), and thereafter by Mr G. R. Phipps, has been issued quarterly and distributed to members. It continues to spread details of our programme, reports of Council resolutions, titles and authors of papers accepted for publication in the *Proceedings*, news of grants from Joyce W. Vickery Scientific Research Fund and other items believed to be of interest to members. Dr Martin and Mr Phipps are thanked for the time and effort they have devoted to the News.

Membership

During the year, 8 full members were elected. Two members transferred to associate membership, one to senior membership and three members resigned. At 26th March 1985, the roll stood at 280 full members, 21 associate members and one senior member.

Dr Peter Stanbury of the Macleay Museum, University of Sydney, was congratulated by the Society on his being awarded the Medal of the Order of Australia.

Meetings

On Sunday, 3rd June, members and friends met at Connell's Hill to walk through the intertidal wetlands of southern Botany Bay and to examine the characteristic communities there under the guidance of Drs P. Adam and R. J. King and Prof. A. W. D. Larkum.

On Wednesday, 20th June, at the Australian Museum, Mr Alan Andrews of the Metropolitan Water, Sewerage, and Drainage Board gave an illustrated talk on Mount Kosciusko and the nineteenth-century scientists and others who explored and studied the area.

The Macleay Memorial Lecture for 1984 was heard on the 18th July. The lecturer, Prof. R. V. S. Wright, of the Department of Anthropology, University of Sydney, entitled his address: 'New Light on the Extinctions of the Australian Megafauna'. We await submission of the text for publication in the *Proceedings*.

An excursion led by Dr L. A. S. Johnson, Director of the Royal Botanic Gardens, Sydney, to the gardens' annexe at Mount Tomah was held on 23rd September.

On Wednesday, 24th October, at the Australian Museum, Dr Marilyn Fox (Royal Botanic Gardens) gave an illustrated talk on the year-to-year variations in the vegetation of western New South Wales.

The Society joined the Institute of Biology in Australia on 21st November for a combined visit to the Division of Entomology Research Station at Warrawee. The meeting included four short talks by members of the station staff on the general theme of biological control of pest arthropods.

Our first meeting in 1985 was as a co-sponsor, with the Institute of Biology in Australia, the Royal Zoological Society of New South Wales and the Australian Museum Society, of a symposium entitled: 'In Defence of Science: A Response to Creationism'. Speakers at the symposium, held on Saturday, 9th March, at the N.S.W. Conservatorium of Music, were Mr Ron Strahan (National Photo Index of Australian Wildlife), Prof. Ron Brown (Monash University), Dr Alex Ritchie (Australian Museum), Prof. Mike Archer (University of New South Wales), and Dr David Briscoe (Macquarie University).

The Joyce W. Vickery Scientific Research Fund

Grants totalling $2,413 were awarded during the year to assist seven research projects. Details were announced in Linnean Society News nos. 34 and 35.

Linnean Macleay Fellowship

The appointment of Mr R. W. Johnstone as Linnean Macleay Fellow was noted in the last annual report. Mr Johnstone has now supplied the following account of his investigation of 'Detrital Fluxes of Carbon and Nitrogen in Coral Reef Sediments: One Tree Island Lagoon'.

'As the title suggests, this project examines the flow of nitrogen and carbon through sediments in a coral reef lagoon on One Tree Island, southern Barrier Reef, Queensland.'

'Work in 1984 centred primarily on the collection of data relating to the seasonal variations in sediment carbon and nitrogen levels, with emphasis on the different nitrogen species. The data collected show a marked difference in the levels of sediment ammonia between the very fine and coarse sediments and a significantly higher level of ammonia in sediments during the summer months.'

'In conjunction with this work, time was spent developing a polarographic oxygen sensor for measuring oxygen micro-gradients within sediment types. The results from this show interstitial oxygen levels to be negligible below 2cm in all sediment types. Such a result was not found using coarser techniques but does comply with the discovery of high H_2S levels within the sediment.'

'The later part of 1984 was also spent carrying out nitrogen enrichment experiments in the field. As may have been expected, all sediment types showed varying levels of nitrogen uptake outside that due to diffusion. This aspect of my work represents the main area of interest for 1985 and several different methods will be developed to monitor the fate and uptake kinetics of nitrogen supplied to the different sediment types.'

At the Council meeting held on 24th October, it was resolved that Mr Johnstone's Linnean Macleay Fellowship be renewed for 1985.

Office

The Society's office at 6/24 Cliff Street, Milsons Point, is open from 9.30 a.m. to 5 p.m. every Tuesday. The telephone number is (02) 929 0253.

Linnean Macleay Lectureship in Microbiology

Dr Kai Yip Cho, of the Department of Microbiology, University of Sydney, reports progress in the following terms.

'The work this year is concerned with the introduction of a wide variety of edible mushrooms to Australian growers. The use of liquid spawn to replace conventional grain spawn is extensively studied.'

Dr Cho adds that he has received a research grant of $55,000 from the N.S.W. government, through the Advanced Technology Development Assistance Fund. He hopes that his project will 'boost production, diversification and profitability for mushroom growers in New South Wales within the next few years'.

The Society congratulates Dr Cho on his success and notes, with pleasure, how far his efforts go to confirm the vision of Sir William Macleay.

PRESIDENTIAL ADDRESS

Mr G. R. Phipps delivered his Presidential Address on the ornithology of the *Chevert* expedition to New Guinea, sponsored and led by Sir William Macleay in 1875. Illustrating his address with specimens from the Macleay Museum, Mr Phipps discussed his own recent systematic studies and related them to the history of the expedition and its bird collection. It is hoped to publish the address in the *Proceedings* in due course.

DECLARATION OF ELECTIONS

As the number of nominations did not exceed the number of vacancies, no voting was necessary. The following members were therefore declared elected to the Council for the year 1985-86:

President — Dr P. M. Martin
Members of Council — Prof. M. Archer
Mr L. W. C. Filewood
Dr P. M. Martin
Dr I. G. Percival
Auditor — W. Sinclair & Co.

Mr G. R. Phipps then introduced Dr P. M. Martin as the President for 1985-86 and invited him to take the Chair. The meeting closed with a vote of thanks to the retiring President.

LINNEAN SOCIETY OF NEW SOUTH WALES

GENERAL ACCOUNT

Balance Sheet as at 31st December, 1984

1983 $			$
	Accumulated Funds—		
	Balance 1st January, 1984		547,496.33
	Add Surplus for the year		12,212.26
			559,708.59
	Less Science House Pty Limited		
	Provision for Doubtful Debt	396,959.57	
	Investment — One Share	1.00	396,960.57
547,496	Balance 31st December, 1984		162,748.02
	Reserve—		
1,143	Bookbinding		1,142.66
	Science House Pty Limited—		
30	Donations held		—
$548,669			$163,890.68

1983 $		$	$
	Fixed Assets—		
	Furniture, Fixtures & Fittings — At Cost	1,670.91	
891	*Less* Depreciation written off	846.37	824.54
	Office Machines — At Cost	2,048.88	
649	*Less* Depreciation written off	1,496.88	552.00
	Investment — At Cost		
1	Share — Science House Pty Limited		—
1,541	Total Fixed Assets		1,376.54
	Investments—		
	Deposits—		
19	N.S.W. Permanent Building Society	20.30	
48,800	Australian Resources Development Ltd	48,800.00	
1,000	Commonwealth Loans — At Cost	—	
20,526	Australian Savings Bonds — At Cost	20,526.00	
	N.S.W. Premier State Bonds — At Cost	3,000.00	
	Debentures — At Cost		
2,400	Esanda Limited	16,100.00	
5,000	Metropolitan Water Sewerage and Drainage Board	5,000.00	
12,750	Mutual Acceptance Limited	—	
90,495	Total Investments		93,446.30
	Current Assets —		
	Loans — Science House Pty Limited (in liqn)		
416,990	Science Centre Account	20,000.00	
3,005	Management Account	—	
1,444	Sundry Debtors	3,117.99	
1,141	Linnean Macleay Fellowships Account	1,720.83	
33,903	Cash at Bank	44,079.02	
150	Deposit	150.00	
456,633	Total Current Assets		69,067.84
$548,669			$163,890.68

LINNEAN SOCIETY OF NEW SOUTH WALES

Income & Expenditure Account for the Twelve Months ended 31st December, 1984

1983 $	EXPENDITURE	$
750	Audit Fees	800.00
49	Bank Charges	101.10
110	Cleaning	—
187	Depreciation	163.85
503	Donations	—
1,082	General Expenses	754.14
151	Insurance	205.81
—	Lecturers' Fees	100.00
40	Library	458.15
439	Light and Power	184.28
—	Macleay Dinner & Lecture	142.48
1,609	Postages	1,571.74
6,394	Proceedings — Printing Costs	6,706.46
288	Printing and Stationery	758.48
2,664	Rent	4,419.96
381	Photocopying Expenses	652.39
4,428	Salaries	5,342.64
5,619	Secretarial Services	2,467.50
287	Telephone	271.25
24,981	Total Expenditure	25,100.23
13,611	Surplus for Year Transferred to Accumulated Funds	12,212.26
$38,592		$37,312.49

1983 $	INCOME	$	$
	Subscriptions —		
1,491	Members	1,348.30	
7,405	Proceedings	9,092.95	
8,896			10,441.25
12,795	Interest Received		12,888.84
	Photocopying Receipts		38.00
—	Macleay Dinner & Lecture		162.00
250	Sundry Income		527.00
265	Linnean Society Dinner		—
	Fellowships Account —		
13,336	Surplus Income for the year ended 31st December, 1984		9,805.82
260	Donations Received		—
	Reprints Sales		
2,790	General	662.60	
—	Polychaete Vol.	2,772.28	3,434.88
—	Sales		14.70
38,592	Total Income		37,312.49
$38,592			$37,312.49

AUDITORS' REPORT

We have audited the books and records of the Linnean Society of New South Wales for the twelve months ended 31st December, 1984 and are of the opinion that the accompanying Balance Sheet and Income and Expenditure Account subject to the Liquidators determination of the amount payable in respect of the loan due from Science House Pty Ltd (In Liqn) correctly sets forth the position of the financial affairs as at 31st December, 1984 according to the explanations given to us and as disclosed by the Books of the Society.

W. SINCLAIR & CO.
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DATED at Sydney this First Day of March, 1985.

A. RITCHIE
Hon. Treasurer.
March, 1985.

LINNEAN SOCIETY OF NEW SOUTH WALES

LINNEAN MACLEAY FELLOWSHIPS ACCOUNT

Balance Sheet as at 31st December, 1984

1983 $			$	1983 $			$
	Accumulated Funds —				Fixed Assets —		
	Balance 1st January, 1984			4,400	Commonwealth Loans — At Cost		—
	Amount bequeathed by Sir William Macleay	70,000.00		18,631	Australian Savings Bonds — At Cost		5,131.50
	Transfers from Income Account	59,873.10		—	N.S.W. Premier State Bonds — At Cost		55,300.00
	Increase in Value of Assets	384.32	130,257.42		Debentures — At Cost		
	Less Adjustment of Transfers to General			200	British Petroleum Company of Australia Ltd.		200.00
	Account in respect of Interest Received		318.69	13,600	Esanda Limited		22,800.00
129,826	Balance 31st December, 1984		129,938.73	1,263	Barclays Credit Corporation Ltd		375.20
	General Account —			2,000	Metropolitan Water Sewerage & Drainage Board		—
1,141	Interest not Transferred		1,720.83	12,450	Mutual Acceptance Limited		—
				6,000	Telecom Australia		6,000.00
					Deposits—		
				37,900	Australian Resources Development Bank		37.900.00
				2,147	St George Building Society Ltd		2,312.13
				32,330	N.S.W. Permanent Building Society Ltd		544.53
				130,921	Total Investments		130,563.36
					Current Assets		
				13	Cash at Bank	1063.53	
				33	Sundry Debtors	32.67	
				46	Total Current Assets		1096.20
$130,967			$131,659.56	$130,967			$131,659.56

Income and Expenditure Account for the Twelve Months ended 31st December, 1984

1983 $		$	1983 $		$
5	Bank Charges	1.12	13,341	Interest Received	13,006.97
—	Salaries	3,200.03			
13,336	Surplus for the Year transferred to General Account	9,805.82			
$13,341		$13,006.97	$13,341		$13,006.97

AUDITORS' REPORT

We have audited the books and records of the Linnean Society of New South Wales for the twelve months ended 31st December, 1984 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, 1984 according to the explanations given to us and as disclosed by the Books of the Society.

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DATED at Sydney this First Day of March, 1985

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Hon. Treasurer.
March, 1984.

LINNEAN SOCIETY OF NEW SOUTH WALES

BACTERIOLOGY ACCOUNT

Balance Sheet as at 31st December, 1984

1983 $		$	$
	Accumulated Funds—		
	Balance 31st December, 1984 —		
	Amount Bequeathed by Sir William Macleay	24,000.00	
36,900	Transfers from Income Account etc.	12,900.00	36,900.00
	Macleay Lecturer in Microbiology Reserve—		
	Balance 1st January, 1984	4,253.10	
	Add Surplus for Year	3,122.56	
4,253	Balance 31st December, 1984		7,375.66
$41,153			$44,275.66

1983 $			$
	Investments—		
1,600	Commonwealth Loans — At Cost		–
1,600	Australian Savings Bonds — At Cost		–
–	N.S.W. Premier State Bonds — At Cost		26,900.00
	Australian Resources Development Bank		
8,000	Transferable Deposits — At Cost		8,000.00
	Debentures—		
200	British Petroleum Company of Australia Ltd.		200.00
24,000	Esanda Limited		1,600.00
	Deposits —		
1,658	N.S.W. Permanent Building Society		395.89
37,058			37,095.89
	Current Assets		
4,050	Cash at Bank	7,135.03	
45	Sundry Debtors	44.74	
4,095	Total Current Assets		7,179.77
$41,153			$44,275.66

Income & Expenditure Account for the Twelve Months ended 31st December, 1984

1983		
5,000	University of Sydney — Salary of Lecturer	–
6	Bank Charges	0.24
	Surplus for Year	3,122.56
$5,006		$3,122.80

1983		
4,004	Interest Received	3,122.80
1,002	Deficiency for Year	–
$5,006		$3,122.80

AUDITORS' REPORT

We have audited the books and records of the Linnean Society of New South Wales for the twelve months ended 31st December, 1984 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, 1984 according to the explanations given to us and as disclosed by the Books of the Society.

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DATED at Sydney this First Day of March, 1985

A. RITCHIE.
Hon. Treasurer.
1st March, 1985.

LINNEAN SOCIETY OF NEW SOUTH WALES

JOYCE W. VICKERY SCIENTIFIC RESEARCH FUND ACCOUNT

Balance Sheet as at 31st December, 1984

1983 $		$	$	1983 $		$
	Accumulated Funds—				Investments—	
	Balance 1st January, 1984	68,286.11		5,132	Australian Savings Bonds — At Cost	.5,131.50
	Surplus on Redemption of Debentures	16.70		–	N.S.W. Premier State Bonds — At Cost	20,000.00
	Interest Received	8,683.89			Debentures — At Cost	
				2,500	Australian Guarantee Corporation Ltd	–
		76,986.70		1,200	British Petroleum Company of Australia Ltd	1,200.00
	Less Research Fund Grant	2,343.00		2,249	Barclays Credit Corporation Limited	366.20
68,286	Balance 31st December, 1984		74,643.70	22,000	Citicorp Aust. Ltd.	11,000.00
	Current Liabilities—			18,000	Custom Credit Corporation Limited	18,000.00
132	Sundry Creditors		131.50	1,200	Mutual Acceptance Limited	–
				–	Esanda Ltd	13,000.00
					Deposits—	
				124	St George Building Society	133.59
				52,405		68,831.29
					Current Assets—	
				16,013	Cash at Bank	5,943.91
$68,418			$74,775.20	$68,418		$74,775.20

AUDITORS' REPORT

We have audited the books of the Linnean Society of New South Wales for the twelve months ended 31st December, 1984 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, 1984 according to the explanations given to us and as disclosed by the Books of the Society.

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DATED at Sydney this First Day of March, 1985

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1st March, 1985.

ADVICE TO AUTHORS

The Linnean Society of New South Wales publishes in its *Proceedings* original papers and review articles dealing with biological and earth science. Papers of general significance are preferred but the *Proceedings* also provides a medium for the dissemination of useful works of more limited scope. Any work considered for publication in the *Proceedings* is subject to careful scrutiny by one or more external referees.

Manuscripts will be received for assessment from non-members as well as members of the Society though non-members must communicate their works through a member. Subject to acceptance, a member's paper may be given priority in publication over that of a non-member.

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PREPARATION OF MANUSCRIPTS

Copy must be typewritten, double-spaced throughout, on one side only of good quality A4 (210 × 297 mm) paper. Margins not less than 25 mm wide all round are required. All pages should be numbered serially and securely fastened together. The desired positions for all figures and tables should be indicated in the left-hand margin of the text. For taxonomic papers the Botanical or Zoological Codes of Nomenclature, as appropriate, must be followed. Generic and specific names should be clearly marked by underlining.

Papers should be written in clear, concise English. The *Style Manual for Authors and Printers of Australian Government Publications* (Second Edition, 1972) is a useful guide. Spelling should conform to that preferred by the *Oxford English Dictionary*.

The general design of a paper should follow the scheme:

(1) Title and author's name — all in capitals.
(2) A concise Abstract, complete in not more than 200 words, indicating the scope of the paper. Authors should adopt the lay-out used in this issue of the *Proceedings*, including details of postal address but leaving spaces for editorial insertions.
(3) Main text. Footnotes should be avoided. The text may be divided into sections introduced by short headings set out as in this issue.
(4) Acknowledgements, if any.
(5) References. These should be cited in the text by author's name and date, e.g., Bullough (1939) or (Bullough, 1939) according to the context and listed alphabetically by authors under *References* thus:

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

Titles of periodicals should be abbreviated as in the *World List of Scientific Periodicals*. If more than one work by the same author published in the same year is cited, use a, b, etc., after the year in both text and list of references. Titles of books should be quoted in full together with the place of publication, the name of the publisher and the edition if other than the first.

Illustrations: Authors should note that illustrative matter (both photographs for half-tone reproduction and line drawings) is now printed in the text, not as separate plates. All illustrations must therefore be marked as figures. A number of small photographs may be arranged to form one figure. The individual parts of such a composite illustration should be clearly marked (preferably by capital letters) and identified in the caption. All captions must be typed on a separate sheet or sheets.

The maximum printed dimensions for figures will normally be 125 × 200 mm; larger formats will be considered only in exceptional circumstances. Figures must therefore be designed to yield clear images within the limits of a single page. Close attention should be paid to the matter of scale on figures. Where possible add a linear scale (with the dimension clearly marked) to the figure rather than trust that a statement of scale in the caption will be correct after the plate-maker and printer have finished their jobs.

All line drawings should be in India ink on a suitable surface, such as Bristol board, tracing linen or plastic film. In general, however, the platemaker prefers to work from good quality, glossy photographs rather than originals of various sizes. Authors are urged to supply such photographic reproductions which, if made to a scale appropriate to the size of a printed page, will show whether ornament and lettering can be read in the final print. All photographs, whether for half-tone or line illustrations, should be high-contrast, glossy prints. Each illustration should be identified (author's name, Fig. no. and orientation) in pencil on the back.

Tables should be submitted in a clear format on separate sheets. Like illustrations, they should be designed to fit a single page of the journal.

PROCEEDINGS of LINNEAN SOCIETY OF NEW SOUTH WALES

VOLUME 109

Issued 20th March 1987

NOTE: Publication of this issue, intended for December 1986, has been delayed by a serious fire at the printery that month. Editor and printer regret the inconvenience to authors and readers.

CONTENTS:

NUMBER 1

NUMBER 2

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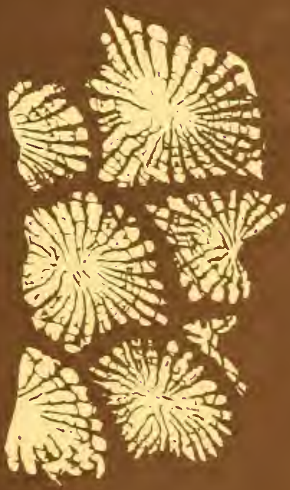
PROCEEDINGS
of the
LINNEAN SOCIETY
of
NEW SOUTH WALES

VOLUME 109
NUMBER 3
NUMBER 4



NATURAL HISTORY IN ALL ITS BRANCHES

THE LINNEAN SOCIETY OF NEW SOUTH WALES

Founded 1874. Incorporated 1884.

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.

Membership enquiries should be addressed in the first instance to the Secretary. Candidates for election to the Society must be recommended by two members. The present annual subscription is $35.00.

The current rate of subscription to the *Proceedings* for non-members is set at $50.00 per volume.

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Cover motif: Transverse section (×2.4) of the Devonian coral described by A. J. T. Wright as *Melrosia rosae* gen. et sp. nov. From the Mount Frome Limestone, Mudgee district, N.S.W. Adapted by Len Hay from *Proc. Linn. Soc. N.S.W.* 90, 1966, p. 266 (fig. 3).

PROCEEDINGS
of the
LINNEAN SOCIETY
of
NEW SOUTH WALES

VOLUME 109
NUMBER 3

PRESIDENTIAL ADDRESS

The Phylogenetic Significance of *Dracaena*-type Growth

JOHN T. WATERHOUSE F.L.S.

(Delivered 28 March 1979)

Edited from the author's notes by C. J. Quinn*

The lilies, as we know from an old comment, are arrayed in more glory than ever was Solomon. In spite of their glory which, to a modern taxonomist is but a manifestation of character-states, the lilies seem to be awaiting someone with the wisdom of Solomon to find themselves classified. Of course I use the name 'lily' rather extravagantly; in a strict recourse to nomenclature the family taxon, Liliaceae, must accept the genus *Lilium*. But the problems seem to be: what other genera might be placed with *Lilium* in the family of lilies, and which other families have, say, an ordinal relationship with the lilies?

In this comment to-night I am not going to delay with the history of the convolutions in the classification of these Monocotyledons, but the historical candidates for the Liliaceae have flowers that may be derived from a trimerous 5-whorled condition $P_{3+3}\ A_{3+3}\ G_{(3)}$. The ovary may be superior or inferior, and a whorl of stamens is sometimes missing.

Amongst the various taxonomic treatments of these candidates for the Liliaceae we can for the moment note that:

Brongniart (1813) and Lindley (1846)	disposed them in several families, including Liliaceae and Amaryllidaceae;
Engler (1897)	grouped them in a few big families;
Hutchinson (1934)	allocated them to many families in several orders (Liliales, Agavales, Amaryllidales and Haemodorales pp.);
Cronquist (1968)	has more recently become confused and has gone back to some larger-than-Engler families in a single order, Liliales;
Huber (1969) and Dahlgren and Clifford (1982)	who are enjoying some present day popularity, have lots of small families arranged in several orders (e.g., Liliales, Asparagales, Amaryllidales and Haemodorales pp.).

The differences in the above systems are not the simple matter of tribes being elevated to families and families becoming orders, for an inspection shows the content and alliances keep altering. Hence we are faced with a real systematic problem, which indicates that we have been doing something wrong — wrong in the sense that wide

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* Copy received 22 April 1987. We thank Dr Quinn for realizing the late John Waterhouse's presidential address. Dr Quinn has also prepared the Memorial to our distinguished former president that is printed in this issue (pp. 139-142).

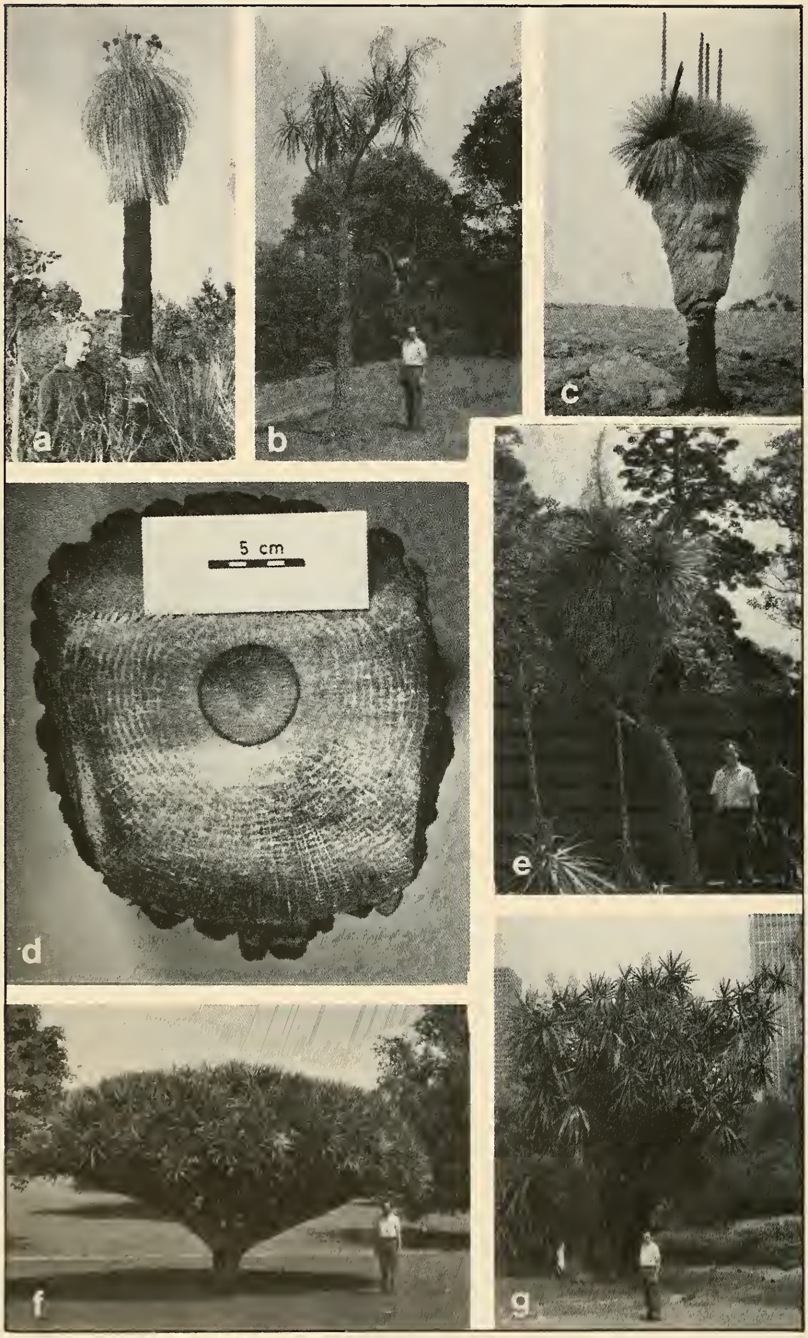


Fig. 1. Examples of pachycaulous monocotyledons.
a. *Kingia australis* with post-anthetic inflorescences: Albany, Western Australia. **b.** *Beaucania* sp. **c.** *Xanthorrhoea reflexa*; box at base of trunk is 15cm high; Beverley Western Australia. **d.** Transverse section of 1.9m high *Xanthorrhoea arborea* trunk at ground level. The primary tissues, including the basal woody cone, occupy the central region to a diameter of 8.5cm; the remainder of the trunk is secondary, arising from a perimeristem that is under the dark outer layer of leaf bases and bark (see Fig. 2a). Calga, NSW. **e.** *Yucca elephantipes*. **f.** *Dracaena draco*. **g.** *Nolina* sp. **b** and **e-g**, Royal Botanic Gardens, Sydney.

acceptance or approval is not being given to any one system. What is it we are doing wrong?

Now, one of the features of natural classification is that if we use the character-states of A, B and C to set up family number 1, we see no necessity to use another set of character-states of A, B and C to set up family number 2. It is, however, a fact of taxonomic history that character-states of the flower have, by and large, been used very successfully in setting up families and supra-specific taxa in the dicotyledons. Of course we have seen plenty of tidying up with input from more recently available data sources such as histology, karyology, biochemistry, palynology. But the tidying up was often already seen to be required. There are indeed also many monocotyledonous taxa of wide and long-time acceptance that can be well circumscribed on floral character-states.

It seems, therefore, that, following the comparative success of floral characters in the classification of most dicotyledons and many monocotyledons, we have expected the same approach to be successful over-all. This expectation, I believe, should be abandoned with reference to the Lilies and their relatives. I have come to this opinion as a result of some studies contemplating the Australian family Xanthorrhoeaceae, which consists of genera that have all been considered at some time or another candidates for the Liliaceae. The Xanthorrhoeaceae (in its present content) was set up by Hutchinson (1934), whose system for the 'lilies' in particular presented some novelty, in that attention was paid to non-floral characters — habit and leaves — as well as to floral characters, in setting up the numerous families and orders.

Hutchinson's Xanthorrhoeaceae contained genera with species of gross habit — small trees or 'shrubs' (as far as these terms can be applied to monocots; Fig. 1**a**, **c**). It included, *inter alia*, the three genera, *Xanthorrhoea* (ca 15 spp.), *Kingia* (1 sp.) and *Dasypogon* (2 spp.), and he put this family in the order Agavales along with his family Agavaceae, which again contained species of gross habit (Fig. 1**b**, **e**-**g**) belonging to such genera as *Dracaena*, *Cordyline*, *Doryanthes*, *Yucca*, *Phormium* and *Nolina*. In both families, therefore, there are species which can be described as arborescent or at least frutescent — in general, pachycaulous; so in this complex — Hutchinson's Agavales — we are dealing with big perennial robust monocotyledons with a habit that probably impressed a botanist of the northern hemisphere where monocotyledons are spring-flowering shoots produced annually from bulbs, corms and rhizomes.

In the development of a natural classification it has forever been unwise to fasten on to one character-state for setting up a taxon. Moreover, such a character-state distributed in representatives of that taxon must be seen as an homologous expression of a character. Thus, is it reasonable to postulate that *pachycauly* in Hutchinson's Xanthorrhoeaceae and Agavaceae is the result of homologous developmental processes in all the genera/species referred here?

Some years ago I started to investigate this point. It was relatively simple to show that the pachycaulous habit in members of the Xanthorrhoeaceae is the expression of two fundamentally different processes. In the course of the studies it also became obvious that Hutchinson's character of 'dry perianth' as typical of the family is also questionable; this uncertainty ultimately led to an investigation of the floral anatomy of some of the members of the family. The precise results of these investigations are to be published in full later. For the present, and to be succinct, Hutchinson's family Xanthorrhoeaceae is monstrously unnatural. However, as a result of these studies I consider there are two histological aspects in the 'lilies' (? and indeed in other monocots) that are of systematic importance:

i) features associated with the development of pachycauly; and
ii) features of the ovary wall — especially the septa.

In searching through the literature I note that there is nothing particularly novel about the features I am going to describe; it is simply that their systematic importance has not been highlighted. Moreover, the details are fairly well recorded, so I can only conclude that as systematists we are ignoring a whole pool of histological data already scored by various workers.

Regarding pachycauly, the kind of development I wish to consider tonight is that kind found in species of *Dracaena*. I am going to imply that other kinds of pachycauly in monocotyledons are very different (e.g., that in *Kingia*; Fig. 1**a**), though I am not going to describe them to you (see Staff and Waterhouse 1981). As you can see from the illustrations (Fig. 1**b**-**g**), many of the species that have the Dracaenoid kind of pachycauly are quite arborescent.

The basic histological processes producing this type of pachycauly have been known for a long time (since 1840-1870), but they really are not given much attention in accounts of general plant histology, and, if mentioned at all, the histological picture is usually described only in the transverse aspect of the stem, whereas it is in the longitudinal aspect that some of the most interesting and fundamental features of the process are to be seen.

In the transverse aspect of the primary stem (Fig. 2**d**) I want you to note:

a) the scattered vascular bundles, a typical monocotyledonous character; all tissues are of course primary;

b) that the vascular bundles are cribricentric, or nearly so, a feature found in, but not widespread in, monocotyledons;

c) that the tracheary elements are tracheids and the metaxylem ones have oblique narrow-aperture pits, features found in, but again not widespread in monocotyledons (these features are of course only ascertainable in macerated tissue);

d) the peripheral cylinder of meristematic cells, which is probably more than one cell thick.

The transverse aspect of a stem with secondary thickening is shown in Figs 1**d** and 2**a**. The points to note are:

a) the perimeristem cuts off radial rows of parenchyma cells to the inside and a few to the outside; these are appropriately termed secondary tissue;

b) proceeding centrally from the perimeristem —

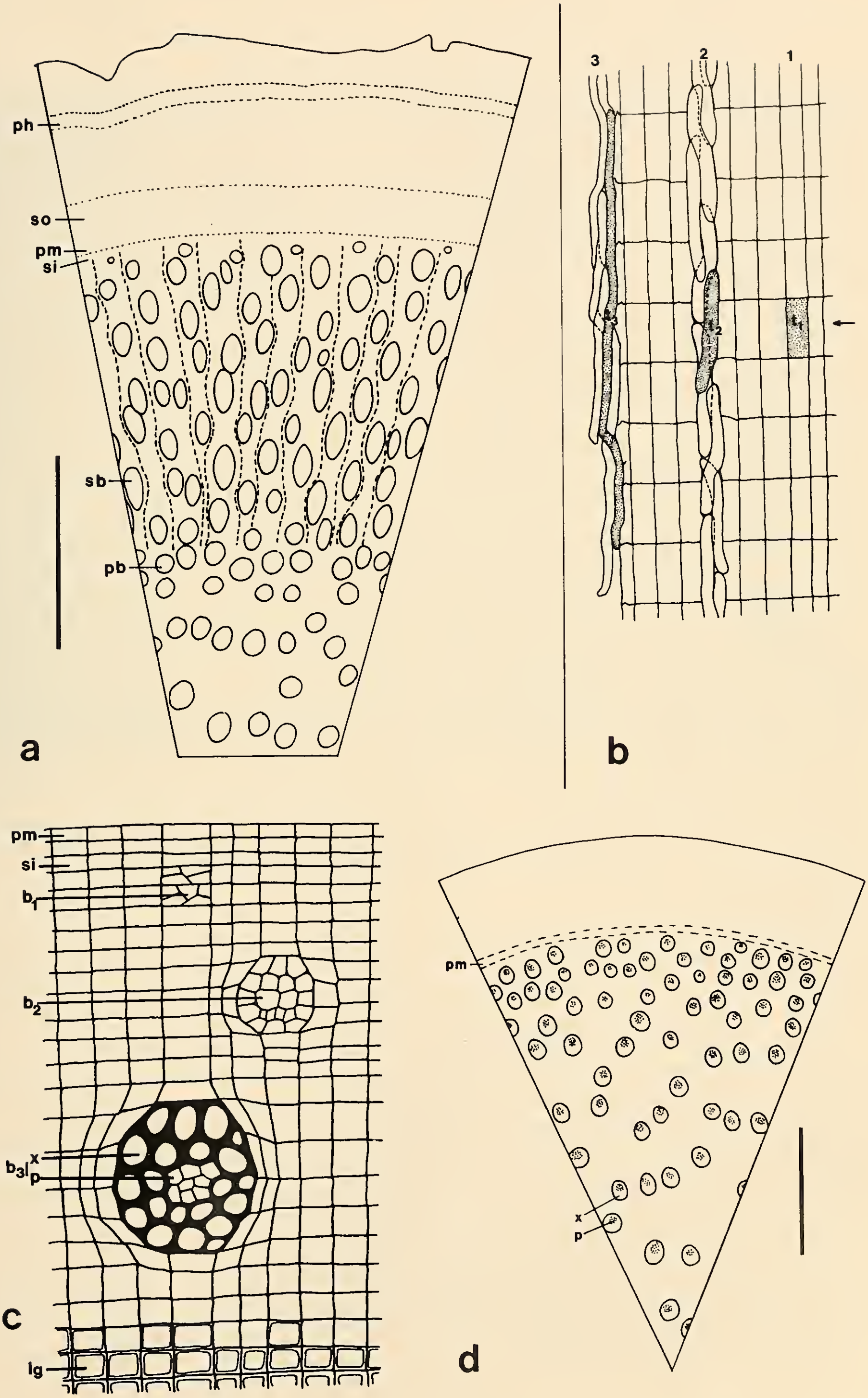
Fig. 2. Diagrams of secondary thickening in *Cordyline stricta*. *lg*, mature lignified ground tissue; *p*, phloem; *pb*, primary vascular bundle at outer limit of primary stele; *ph*, phellogen established under the leaf bases; *pm*, perimeristem; *sb*, secondary vascular bundle; *si*, secondary derivatives of the perimeristem formed on its inner face; *so*, secondary derivatives of the perimeristem formed on its outer face; *x*, xylem.

a. TS sector of outer part of mature stem showing secondary tissues. The radiating broken lines indicate the radial rows of secondary lignified ground tissue laid down by the perimeristen. Scale = 1mm.

b. Schematic representation of the longitudinal aspect of intrusive growth during the differentiation of secondary vascular bundles. Positions 1, 2 and 3 indicate successive stages in the differentiation of a vertical file of perimeristem derivatives into secondary vascular elements. The arrow indicates a horizontal row derived from a particular perimeristem initial, and members of this row in each bundle are labelled t_1, t_2 and t_3, and are stippled. At formation (position 1), only one cell of the vertical file is present in the indicated horizontal row (arrow). At position 2, file members have extended to twice their initial length, and intruded halfway into the rows immediately above and below their original position; there are thus two cells at any level in the indicated horizontal row. At position 3, each member of the file now extends through 7 vertical rows, and seven cells will be found in the indicated horizontal row; only three members of vertical file 3 are shown in the diagram for reasons of simplicity.

c. Schematic representation of the transverse aspect of differentiation of secondary vascular bundles. b_1, b_2 and b_3 indicate three successive stages in the process.

d. TS sector of young stem with perimeristem just differentiated outside the primary vascular bundles. Scale = 1mm.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d

  - i) there is an apparent cutting-up of (i.e., lots of cells divisions in) scattered single derivatives of the perimeristem;
  - ii) these strands of cells differentiate into cribricentric (or nearly so) vascular bundles similar in appearance to the primary bundles;
- c) again, the tracheary elements are tracheids of the type described above;
- d) the secondary bundle is formed within one (? always) radial row of secondary tissue;
- e) the secondary parenchyma between the mature secondary bundles becomes lignified, an aspect of the process that will not be discussed further here.

In the longitudinal aspect (RLS) of the secondary tissue it is apparent that there is a great difference between the length of the perimeristem initial and the length of the tracheid that developed from it — indeed from macerated tissue the tracheid is about 20 times the length of the perimeristem initial. Now it can only have attained this length by intrusive growth. Let us look at the process more schematically. In the diagram (Fig. 2**b**), all the members of the vertical file *1* are destined to become vascular elements; they may be considered protracheary elements. Imagine that we take up a position of inspection at the horizon marked by the arrow. At position 1 in this horizon there is one derivative in the vertical file (t_1). In position 2 each protracheary element of the file has started to elongate apically and basally, and consequently has started to intrude between the cells above and below itself (see cell t_2). The result is that at the given horizon there are now two cells where only one existed before. In position 3 (cell t_3) each protracheary element has elongated to 7 times its original length. Thus at the given horizon our original element (stippled) is now accompanied laterally by six other elements of the same vertical file, three having intruded from above, and three from below; there would be seven elements, therefore, in a transverse section of the file where there was formerly only one. This is *intrusive growth*; what looked like cell-division in the transverse aspect (Fig. 2**c**) is not. It is this elongation of the tracheids that is responsible for the lateral expansion of the secondary vascular bundle as it matures (cf. b_1, b_2 and b_3 in Fig. 2**c**). In macerated secondary tissue (Fig. 3) the tracheids can be seen to be quite twisty and to have battered looking tips as a result of having had to force their way between adjoining elements. Note also that the pitting on these elements is very similar to that on the primary tracheids, being rather like the pitting one usually finds on fibres. The block-shaped lignified parenchyma that occupy the regions between the bundles are also visible in some macerates.

A comparison of macerates from a range of genera possessing this *Dracaena*-type growth is shown in Fig. 3. These are chosen to indicate how similar the elements are, yet they constitute 2-3 different families (depending on author) disposed in 2 different orders.

The seven genera or groups of genera having *Dracaena*-type growth that are recognized in Table 1 have sub-sets of characters that distinguish each from the other. The Aristeae are probably the most out on a limb and are usually referred to the family Iridaceae, which of all the groups we might be considering here has been the most taxonomically stable. But as well as the *Dracaena*-type growth there are other shared character-states that indicate affinity. And this form of growth of stems represents a set of characters that is unlikely to have evolved more than once, and I suggest that it indicates a common origin of those taxa that have it.

Let us look at the world distribution of the generic groups as set out in Table 1. These distributions are compatible with a single origin when the continental masses were together. That is, they appear to be an ancient group that has become differentiated after continental separation.

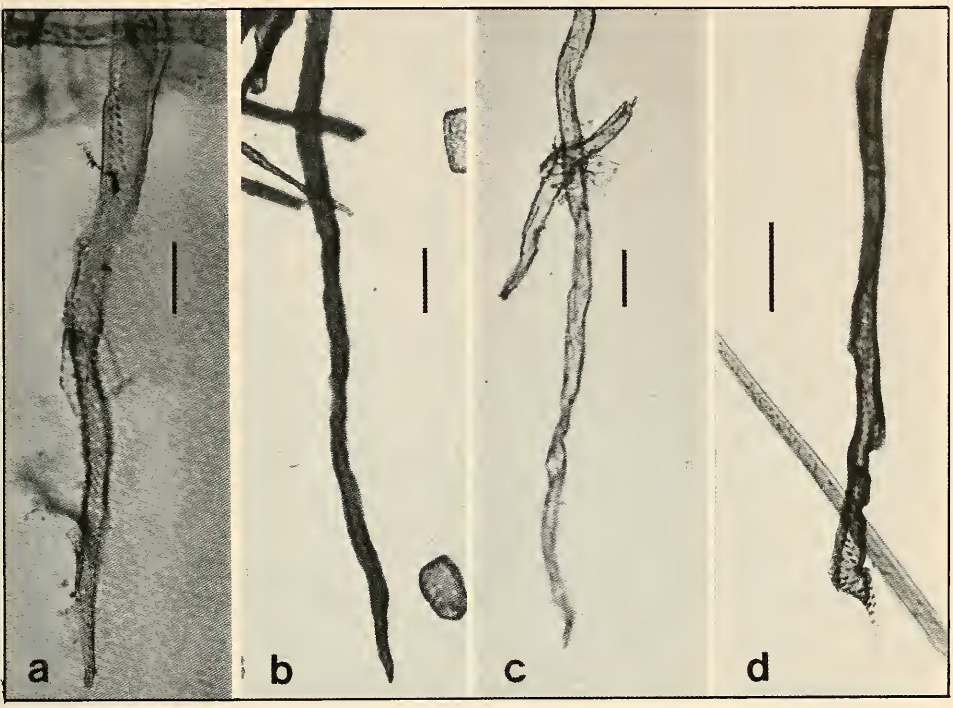

Fig. 3. Xylem tracheids from macerated secondary stem of Dracaenoid plants, showing battered looking tips resulting from intrusive growth. Scale = 100μm.
a. *Cordyline stricta.* **b.** *Aloe* sp. **c.** *Yucca* sp. **d.** *Xanthorrhoea australis.*

TABLE 1

Distribution of the taxonomic groups recognizable in the genera displaying dracaenoid thickening

GENERIC GROUP	DISTRIBUTION
Agave and *Yucca*	Central America
Nolina	North America
Xanthorrhoea	Australia
Aloe	South Africa
Lomandra	Australia, New Zealand, Hawaii
Cordyline and *Dracaena*	Australia, New Zealand, widespread in the tropics
Aristeae (Iridaceae)	South Africa, Australia

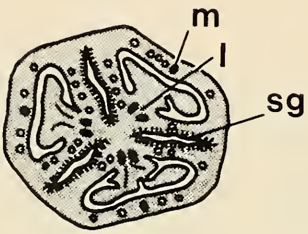

Fig. 4. Median transverse section of ovary of *Xanthorrhoea resinosa* at anthesis. The dorsal or median (*m*) and the ventral or marginal (*l*) vascular traces of each carpel are indicated in black; other vascular bundles (laterals of the dorsal trace) are in outline (see Fig. 5). *sg*, septal gland. Scale = 1mm.

As a group where do they fit is into the lilies *sensu latissimo.* This is where I believe an aspect of floral histology is important. Let us look at some features of the ovary wall. Fig. 4 shows a transverse section of the ovary of *Xanthorrhoea resinosa* in which glands can be seen clearly in each septum of the ovary. A generalized diagram is shown in Fig. 6. The gland is a pouch opening at the top of the ovary and which may extend right to the base of the ovary and even interconnect below the locules. Note also the three-armed stylar canal leading from the stigma to the locules. Similar septal glands occur in the inferior ovary of *Agave* and the superior ovaries of *Aloe* and *Yucca.*

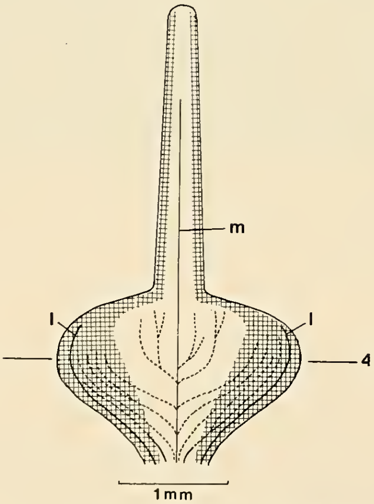

Fig. 5. Diagrammatic reconstruction of a carpel of *Xanthorrhoea resinosa* opened out flat and viewed from the adaxial side. The shaded region indicates the septal portion of the carpel. Note the highly vascularized condition with numerous laterals arising from the dorsal trace (*m*). *l*, ventral or marginal traces. *4* indicates the level of the section illustrated in Fig. 4.

Septal glands appear to occur throughout such groups as Amaryllidaceae (of either Engler or Hutchinson) and Iridaceae, although in some species they appear to have been secondarily lost, and are characteristic of Zingiberaceae, Musaceae, Cannaceae and the syncarpous Palmae. Within the lily family or families their distribution is 'taxonomically sporadic' in current systems. Certainly, Huber (1969) has considered them, but seems to be hesitant/capricious in his taxonomic use of them. Many of these same families are also characterized by a highly vascularized carpel in which the ovary wall is traversed by laterals arising from the dorsal vascular bundle (i.e., from the mid-vein of the ancestral fertile leaf; Figs 4 and 5). Both septal glands and the highly vascularized carpel are fairly complex characters that indicate a common origin of the plants that bear them.

Well, all the *Dracaena*-type genera have septal glands — this probably is also an ancient character typical of some of the so-called lilialian alliances. It is apparently common in Asphodeloid genera but not in Melanthoid genera. I have no great idea on how systematically significant the presence or absence of septal glands is, but it might be worth considering whether it has any bearing on the evolutionary hypothesis that the monocotyledon flower is a synanthium in origin rather than a strobilus; under this hypothesis each carpel plus 2 stamens is a floral unit subtended by bracts (= perianth).

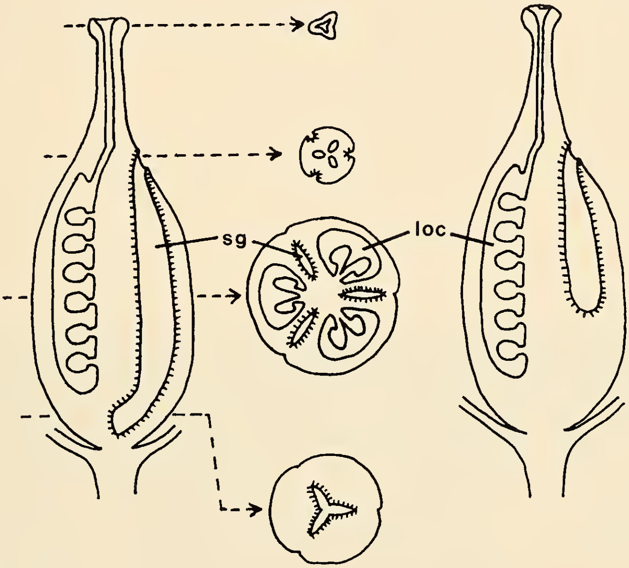

Fig. 6. Generalized diagram of syncarpous gynoecia of Dracaenoid monocotyledons showing the septal glands (*sg*) between the locules (*loc*) in both longitudinal and transverse aspects.

There is, then, a large group of ancient plants which have *Dracaena*-type growth and septal glands. How do they relate to other lilialian monocotyledons? The following points are of relevance:

1. within the group there are already small species with a vestigial amount of secondary growth
2. outside the group there are small species with vestigial amounts of secondary growth, e.g., *Chlorophytum*
3. all such species have cribricentric bundles, or collateral bundles with U-shaped xylem consisting of *Dracaena*-like tracheids, whether primary or secondary
4. there are other species with amphivasal bundles, or nearly so, with xylem consisting of tracheids that more or less resemble *Dracaena*-type primary tracheids, but which show no sign of a vestigial perimeristem. All these small species might have septal glands.

In conclusion, there appears to be a series leading to the small perennials with annual re-growth more typical of the temperate regions and much more common in the general botanical literature. But when I speak of an evolutionary series from arborescent *Dracaena*-type plants to some of the smaller species I don't mean to imply that all the smaller species have come this way. I simply believe that the *Dracaena*-type habit is ancient and the septal gland is probably also old in some of the Lilialian lines. The implication is that other Lilialian genera that do not have these histological characters are not so closely related. The *Dracaena*-type plants are not the ancestors of the lilies *sensu latissimo.* I regret we haven't found a Solomon with his wisdom yet. The problem of elucidating the relationships within this group still remains. If we are to solve it over and above determining the presence or absence of dracaenoid growth, we must:

1. describe properly the tracheary elements. There is pronounced variation from fern-like tracheids in *Dracaena* to those shown in Fig. 3, but a recent publication has them all scored simply as non-vessel elements. The distribution of the various kinds of elements is still a puzzle in the monocotyledons
2. look critically at the bundle types in the stems. Cheadle and Uhl (1948) have too many types, and we must be careful to distinguish between stems, rhizomes and leafy inflorescence axes when making comparisons
3. look for septal glands and multi-veined carpels. Huber (1969) has acknowledged these, but doesn't use data on tracheary elements.

One of the problems that must be overcome is that we must stop thinking of our taxonomy from the top of our hierarchies downwards, and start building up groups from the bottom with what we have at hand. The number of genera involved is so large that no one person can adequately survey them all. If I am going to start on the Sydney scene — with what I have at hand — my groups are going to be incomplete, lack overall world perspective and as a consequence cause, horror of horrors, later nomenclatural and circumscriptive chaos. But start we must, if our treatment of the lilies is to be improved. The remedy, I suggest, is to divorce one's groups from the code and launch them simply so that others can add to or modify them before formalizing them under the code, a procedure that has been adopted quite successfully by Pryor and Johnson (see Pryor and Johnson, 1971) in grappling with the sub-generic taxa in the genus *Eucalyptus.*

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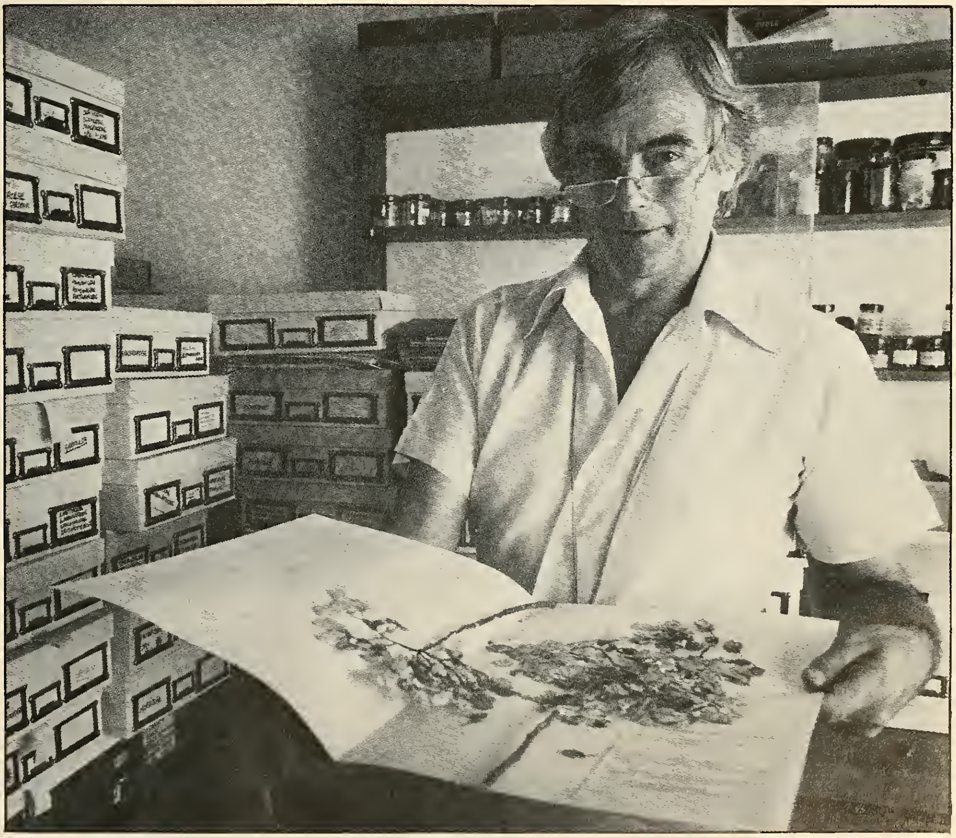
John Teast Waterhouse *1924-1983*

(Memorial Series No. 27)

Members were greatly saddened by the sudden death of Mr John T. Waterhouse at his home in Gordon, Sydney, on the night of April 1, 1983, aged 58 years.

Born on December 2nd, 1924, he received his secondary education at Tamworth Boys High School and then attended the University of Sydney, where he obtained a Bachelor of Science with First Class Honours in Botany in April, 1947. During his honours year, which was supervised by the late Dr J. McLuckie, he carried out 'A physiological investigation of the fungus, *Penicillium expansum* Link.' During the next three years he held positions as demonstrator and teaching fellow in Botany at Sydney University. In 1948 Dr A. J. Eames spent a period of leave in Sydney, and he was instrumental in directing John towards his life-long interest in arborescent monocotyledons. In 1950, however, John left the university for life on a property which he always referred to as 'The Blue Duck', a corruption of its aboriginal name, because of the problems he faced with wild ducks following introduction of irrigation for the production of lucerne. It was partly because of these problems that he returned to the University of Sydney in 1953 as a temporary lecturer in Botany, but at the end of 1954 he again opted for life on the land, this time on a grazing property, 'Burragillo', in the Collarenebri area. Throughout his time on the land he maintained and developed his



knowledge of the native flora, and started compiling a checklist for the area. It is hoped to publish this in the near future. In 1957 John was seriously injured in a fall from a horse while yarding stock, and this resulted in some lengthy periods in hospital over subsequent years. He left the rural life he loved at the start of 1962 and joined the staff of the Department of Botany at the University of New South Wales, as a Senior Tutor, just before the department moved to the Kensington Campus. Shortly after joining the department he was appointed a lecturer. He resumed his studies on Australian Grass Trees, and in 1967 presented a thesis entitled, 'Some aspects of the status of the family Xanthorrhoeaceae', for which he was awarded a Master of Science by the University of New South Wales.

In 1971-72 he spent his first study leave with Professor V. H. Heywood in the Department of Botany, University of Reading, during which he carried out a study on the tribe Anthemideae (Asteraceae), and obtained a Master of Science in Pure and Applied Taxonomy.

John joined the Linnean Society of New South Wales in 1947. He was elected to the Council of the Society in August, 1975, and remained an active and valued member until his death. He was President in 1978-1979, at a time of considerable controversy over the accumulating debt on Science House, and chaired several torrid meetings with great skill. He also devoted a great deal of time to researching the complexities of the issues, and went out of his way to inform members. He continued to make a large contribution to the solution of problems faced by the Society in his term as Vice President, 1979-1982.

In his years at the University of New South Wales John had a great impact on the teaching of botany, and was particularly active in promoting field work. He was responsible for raising taxonomy in the undergraduate syllabus above the level of plant identification, developing at first a part unit and later a full unit in the third year on the principles and methods of taxonomy. He also made a large contribution to teaching at first and second year levels. He organized the day excursion to Kurnell for First Year Biology students until the pressure of numbers made the logistics of the occasion intolerable: the last excursion involved 13 double-decker buses loaded to the gunwales. He was a mainstay of the annual second-year field camp which was held at Mount Boss State Forest from 1966 until that too outgrew the facilities. He also conducted a third year field camp in the same area for his taxonomy students for many years. John's field camps were always a happy combination of efficiently organized work by day and relaxed socialization around the fire at night, always with a few interesting specimens in his hand, and books and a plant press at his elbow. He felt that field work should be enjoyable. The combination of his quiet, easy manner and critical mind sharpened the wits of a large number of students, and stimulated many to take a deeper interest in botany. John also considered that preparation of food should receive proper attention; his third year camps were an object lesson on just what gourmet delights could be produced over an open fire, and word soon spread through the student grape vine.

Two of his research projects had their origins in student exercises on these field camps. The study of the growth of the Bangalow Palm (*Archontophoenix cunninghamiana*) was initiated on the 1967 second year camp, while his work, in collaboration with Dr M. M. Hindmarsh, on a field key to the rainforest species south of the Macleay River grew out of their key to the species of the Wilson River Primitive Area, which was tested and upgraded with the assistance of successive groups of second year students. The final key, which is based on personal examination of fresh specimens of all species, and uses characters of petiole anatomy and exudate, as well as the more usual range of vegetative characters, is now being completed by Dr Hindmarsh. It should prove a valuable aid to identification in these complex communities.

Another of his research interests centred on the Myrtaceae. Apart from his work with Dr P. G. Wilson on *Tristania* and its allies, he also studied *Eucalyptus* and the *Syzygium-Acmena* complex, and drew attention to the distinctiveness of *Syzygium floribundum*. Only the week before he died he saw '*Waterhousea*', the name for the segregate genus Hyland (1984) erected to hold this and two Queensland species, in print in the new Royal Botanic Gardens' pamphlet entitled 'A Rainforest Walk'. It is typical of him that he should protest with a grin that the name had not then been published.

During his field work, John assembled a large body of data on the eucalypts, particularly relating to venation patterns, oil gland size and distribution, and bud and capsule morphology. Although this is preserved on cards, it seems unlikely that it will ever be put to use in the construction of a key as he had envisaged.

In 1980, he embarked upon an intensive floristic survey of the Magela Creek Catchment, Northern Territory, in relation to the projected establishment of the Jabiluka uranium mine by Pancontinental Mining Ltd. He studied the area throughout the full monsoonal cycle, amassing a large collection and a wide range of field observations. Although he had produced a draft species list (Puttock and Waterhouse, 1981), and had completed studies of *Limnophila* (Wannan and Waterhouse, 1985) and *Blepharocarya* (Wannan *et al.*, 1985; 1987), much working up of this collection remained to be done, and he was looking forward to an early retirement which would allow him to devote more time to it. It is a source of great satisfaction to his colleagues that, through the good offices of the Office of the Supervising Scientist for the Alligator Rivers Region, money has now been made available so that more can be realized from this important collection of the northern Australian flora.

John considered it his duty to profess botany in the broadest sense; he was always very willing to spend time assisting those who called on his expertise, whether they were students, colleagues or members of the public who so often were directed to his door. He also devoted a great deal of effort over the years to expanding the collection held by the herbarium at the University of New South Wales, which now comprises some 45,000 specimens, and improving the level of its curation. In 1980 he registered the herbarium with the acronym UNSW, and soon afterwards obtained a special development grant from the university to enlarge the accommodation both for the collection and for associated staff and students. This reconstruction was in hand at the time of his death, and it is a suitable acknowledgement of his contribution to the teaching of taxonomy that the enlarged facility was named 'The John T. Waterhouse Herbarium' at the official opening ceremony in June 1983.

In 1973 John was elected a Fellow of the Linnean Society, London, and also became a member of the British Systematics Association. He was a foundation member of both the Australian Systematic Botany Society and a member of the founding committee of the Friends of the Royal Botanic Gardens, Sydney. John T. Waterhouse will be remembered particularly by generations of students from both the University of Sydney and the University of New South Wales as a stimulating teacher of botany, and by the botanical community as a valued colleague with a splendid sense of humour. He will also be remembered for his contributions to monocotyledonous anatomy, the taxonomy of the Myrtaceae and his work on the key to rainforest species of New South Wales. Not only the Society but the Australian botanical community at large is much the poorer for his passing.

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C. J. Quinn

Complementary feeding Habits of Golden Perch *Macquaria ambigua* (Richardson) (Percichthyidae) and Silver Perch *Bidyanus bidyanus* (Mitchell) (Teraponidae) in farm Dams

C. C. Barlow, R. McLoughlin and K. Bock

(Communicated by J. R. Merrick)

Barlow, C. G., McLoughlin, R., & Bock, K. Complementary feeding habits of golden perch *Macquaria ambigua* (Richardson) (Percichthyidae) and silver perch *Bidyanus bidyanus* (Mitchell) (Teraponidae) in farm dams. *Proc. Linn. Soc. N.S.W.* 109(3), (1986) 1987: 143-152.

A comparison was made of the diets and morphology of the alimentary tracts of golden perch *Macquaria ambigua* and silver perch *Bidyanus bidyanus*. Each species was grown in monoculture in farm dams and their diets compared with the available food sources using the prey-selection index C. The two species were then cultured together and the dietary overlap measured using Schoener's index. Golden perch proved to be a macrophagic carnivore, eating insects and crustaceans, whereas silver perch was an omnivore, feeding predominantly on zooplankton. The alimentary tract of golden perch is typical of a carnivore, whereas that of silver perch is adapted to an omnivorous diet, with a filtering mechanism on the gill rakers for capturing zooplankton. On the basis of their dietary habits, these two species are ideally suited for polyculture.

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INTRODUCTION

Large numbers of golden perch (*Macquaria ambigua* (Richardson 1845): Percichthyidae) and silver perch (*Bidyanus bidyanus* (Mitchell 1838): Teraponidae) are stocked annually in farm dams throughout eastern Australia, to provide fish for recreational angling and domestic consumption (Rowland *et al.*, 1983; Rowland, in press a,b). Management for fish production is minimal, since the primary purpose of the dams is for watering domestic stock. Consequently, fish stocking rates are usually low, in the region of 150-350 fish/ha, and the carrying capacity of the dams is only 200-500kg/ha (Barlow, in press). One method of increasing the production of fish in these dams is to stock two or more species with complementary feeding habits, that is, polyculture.

Little is known about the diets of golden perch and silver perch, although limited observations indicate that golden perch is a carnivore, feeding mainly on crustaceans, insect larvae and molluscs, and that silver perch is an omnivore, consuming small aquatic insects, molluscs, earthworms and plant material (Merrick and Schmida, 1984).

The aim of this study was to investigate the feeding habits of golden perch and silver perch reared in farm dams and thus ascertain if these fishes are suitable for polyculture. This was done by determining the preferred foods of the two species when grown separately, and then comparing their diets when grown together. The morphology of their alimentary tracts was also examined.

MATERIALS AND METHODS

The fish used in the trials were artificially bred and reared at the Inland Fisheries Research Station, Narrandera. Those used in the monoculture trial were one year old, whereas those used in the polyculture trial were three years old. The fish were stocked in earthern dams situated in flat or gently undulating pastoral country. The dams were about 0.06ha and 2-3m deep. The dam stocked with golden perch in the monoculture trial had a dense growth of red milfoil, *Myriophyllum verrucosum*, extending 2-3m from the shore and occupying the entire perimeter of the dam. The other dams did not contain macrophytes. The food available to the fish consisted of the organisms produced naturally in the dams.

MONOCULTURE TRIAL

Twenty-eight golden perch were placed in one dam and 25 silver perch in another in January 1980, and harvested with a seine net three weeks later. The fish were transported live to the laboratory in plastic bags containing water and an oxygen atmosphere. The total length and weight of each fish were recorded and the alimentary tract, from the oesophagus to the anus, removed and measured. Examination of the transporting medium showed that no regurgitation or defaecation occurred between the time of capture and dissection.

Macroinvertebrates in the guts were identified and counted. In addition, the percentage of zooplankton in the stomach contents of each silver perch was estimated volumetrically.

The available food sources, or potential prey species, were sampled with a 500μm dredge net. Samples collected with the dredge net provide an accurate estimate of the relative abundance of epibenthic animals in farm dams (Barlow *et al.*, 1982). To sample the dam containing milfoil the net was modified by removing the kick chain and attaching a rake to direct weed under the net (Topp, 1967). Ten samples were collected from each dam six days before the fish were sampled. The macroinvertebrates in all samples were later identified and counted. Three plankton samples were collected from the dam containing silver perch using an 100μm plankton net towed horizontally for 15m just below the surface.

The diet of the fish was compared with the available foods using the prey-selection index, C, which is statistically testable for any degree of selection at any sample size (Pearre, 1982). C is zero valued for no selection and has the limits -1 for complete selection and -1 for complete avoidance. Statistical tests were conducted using χ^2 tests (method 3 of Pearre (1982)).

POLYCULTURE TRIAL

The dam was stocked with 14 golden perch and 28 silver perch in November 1981 and harvested in April 1982. The fish were transported to the laboratory and dissected as described above. The diets were analysed by determining the percentage volume occupied by each food item in each stomach, as recommended by Wallace (1981).

In addition to determining the degree of interspecific overlap, the degrees of intraspecific overlap were also calculated to ascertain how well the diets of each species were characterized (Wallace and Ramsey, 1983). Specimens of each species were randomly divided into two sets and the dietary overlap calculated. This procedure was repeated 25 times for each species, and the means and standard deviations computed.

The degree of dietary overlap was determined using Schoener's index

$$\alpha = 1 - 0.5\left(\sum_{i=1}^{n} |p_{xi} - p_{yi}|\right)$$

where p_{xi} is the proportion of food item i in the diet of group x, p_{yi} the proportion of food item i in the diet of group y and n the number of food categories. Computed values range from 0 for no overlap to 1 for complete overlap. Although there is no statistical method for judging the reliability of overlap (Wallace and Ramsey, 1983), it is generally considered to be biologically significant when the value exceeds 0.60 (Zaret and Rand, 1971).

ALIMENTARY TRACT MORPHOLOGY

Analyses were conducted on all one year old fish from the monoculture experiment and a further 15 two year old golden perch and 20 two year old silver perch. All measurements were taken to the nearest millimetre on fresh specimens. Total length was measured, the digestive tract was then dissected out, laid on a dry enamel dish, and the lengths of the stomach and intestine-rectum measured immediately. The relationships between the gut length (oesophagus to anus) and total length were determined, and the ratios of intestine-rectum length : stomach length were calculated. The dentition and gill rakers were examined and illustrated.

RESULTS

MONOCULTURE TRIAL

The food organisms sampled from each dam, the dietary analysis and C values for golden perch and silver perch are given in Tables 1 and 2 respectively. The values of C indicate selection or avoidance of a food type, but the reality of selection or avoidance is shown only by the level of significance of C. Identification of the macroinvertebrates was usually possible to the species level, with the exception of the Notonectidae which could not be identified beyond family, and larval insects which usually could not be identified below order. The greater diversity of insects in the dam containing golden perch was probably due to the presence of macrophytes.

Golden perch consumed a wide range of macroinvertebrates. Corixid nymphs, which comprised about 50% by volume of the diet, were the major food. The most preferred, or actively selected, organisms were notonectids and the corixid *Agraptocorixa eurynome*. Three other comparatively abundant corixids were avoided, even though one, *Agraptocorixa parabiopunctata*, was similar in size to *A. eurynome* (approximate total length of adults 7mm and 9mm respectively). No zooplankton was found in the stomachs of golden perch.

The stomach contents of silver perch comprised 80% zooplankton, with the remainder being macroinvertebrates, allochthonous plant material and gravel. The stomach contents of 16 fish consisted entirely of zooplankton. There was comparatively little zooplankton in the intestines compared with the stomachs, but this is to be expected because of the rapid digestion of zooplankton. The percentage composition of zooplankton consumed by silver perch differed markedly from that collected from the dam, as shown below:

	Cladocera	Copepods	Ostracods
Consumed by silver perch	78%	22%	trace
Collected from dam	26%	74%	–

However, it is not known if these samples, collected from just below the surface of the dam, accurately represented the relative abundance of the zooplankton groups.

TABLE 1

Total number of each food type sampled from the dam (Na) and found in the diet (Nd) of golden perch (T.L. 224 ± 35mm, Wt. 188 ± 100g) reared in a monoculture trial; the prey selection index C and the level of significance for C.
N.S. not significant, ** P < 0.01, *** P < 0.001

FOOD TYPE	Na	Nd	C	Significance of C
Notonectidae	57	129	0.234	***
Corixidae				
Sigara spp.	640	24	-0.056	***
Agraptocorixa eurynome	321	345	0.317	***
Agraptocorixa parabiopunctata	157	0	-0.039	***
Micronecta annae group	3983	3	-0.246	***
Nymphs	4099	712	0.101	***
Dytiscidae				
Sternopriscus multimaculatus	543	1	-0.075	***
Megaporus howitti	41	49	0.120	***
Antiporus gilberti	42	1	-0.014	N.S.
Necterosoma wallastoni	9	0	-0.005	N.S.
Hydrophilidae				
Spercheus sp.	3	0	-0.003	N.S.
Laccobius sp.	0	1	0.011	N.S.
Unidentified sp.	0	1	0.011	N.S.
Hydracarina	274	1	-0.051	***
Hydraenidae	0	1	0.011	N.S.
Atyidae				
Paratya australiensis	3	0	-0.003	N.S.
Atheriniformes				
Gambusia affinis	2	0	-0.006	N.S.
Mollusca				
Physa sp.	12	0	-0.007	N.S.
Larval insects				
Trichoptera	35	22	0.059	***
Odonata	2	3	0.026	**
Coleoptera a	8	0	-0.004	N.S.
Coleoptera, Hydrophilidae	12	4	0.013	N.S.
Diptera, Culicidae	35	2	-0.007	N.S.
Diptera, Chironomidae	6	0	-0.002	N.S.
Ephemoptera a	18	0	-0.010	N.S.
Ephemoptera b	62	0	-0.023	**
Ephemoptera, Baetidae	205	5	-0.036	***
Lepidoptera, Pyralidae	3	1	0.001	N.S.
Plecoptera	94	57	-0.010	N.S.
TOTAL NUMBER	10666	1312		

Silver perch selectively fed on notonectids, but avoided both crayfish, *Cherax destructor* and mosquitofish, *Gambusia affinis*. Of the macroinvertebrates eaten by silver perch, 45 were found in the intestines and 15 in the stomachs. The large proportion of macroinvertebrates in the intestine possibly indicates a diel feeding pattern or perhaps different rates of passage through the stomach and intestine.

POLYCULTURE TRIAL

The intraspecific dietary overlap value for golden perch was 0.80 ± 0.06 and for

TABLE 2

Total number of each food type sampled from the dam (Na) and found in the diet (Nd) of silver perch (T.L. 205 ± 23mm, Wt. 111 ± 36g) reared in a monoculture trial; the prey-selection index C and the level of significance for C.
N.S. not significant, * $P < 0.1$, ** $P < 0.01$, *** $P < 0.001$

FOOD TYPE	Na	Nd	C	Significance of C
Notonectidae	29	41	0.305	***
Corixidae				
Sigara sp.	0	4	0.156	*
Nymphs	0	4	0.156	*
Dytiscidae				
Antiporus gilberti	3	2	-0.027	N.S.
Larval insect	1	4	0.106	N.S.
Parastacidae				
Cherax destructor	11	0	-0.230	**
Atheriniformes				
Gambusia affinis	34	4	-0.391	***
TOTAL NUMBER	78	59		

silver perch 0.84 ± 0.04. These values indicate that the diet of each species was well characterized, even though there were comparatively few fish in the samples. Thus, it is valid to use the present data to compare the diets of these species.

The interspecific dietary overlap value was 0.23, indicating that the diets of the two species were significantly different. The major items consumed by golden perch were trichoptera larvae (63%) and crayfish (14%). In contrast, the major foods of silver perch were chironomid larvae (34%), cladocera (14%) and ostracods (10%), while trichoptera larvae formed only 7% of the diet and crayfish were absent from the silver perch stomach contents (Fig. 1).

ALIMENTARY TRACT MORPHOLOGY

The shape of the mouth and dentition of the two species are illustrated in Fig. 2. Golden perch has a large mouth, and possesses teeth on the upper and lower jaws, vomer, palatines and roof and floor of the pharynx. The teeth are numerous, tiny and stout. All teeth are set in bony plates. In contrast, silver perch has a comparatively small mouth, and possesses teeth on the upper and lower jaws and the roof and floor of the pharynx. The villiform teeth are conical and pointed, and generally aligned to point posteriorally. An exception to this is the outer band of larger teeth on the premaxillary, which point ventro-anteriorally and in some instances protrude slightly beyond the lips. The premaxillary and mandibular teeth are set in bony plates while the upper and lower pharyngeal teeth are embedded in fleshy pads.

In both species, gill rakers form an anterior and posterior series on all four gill arches. The anterior rakers on the first arch are elongated, whereas the posterior series on the first arch and all rakers on the other arches are shorter (Fig. 3). The gill rakers of golden perch are short and firm and covered with tiny tubercules which provide a rough surface. The gill rakers of silver perch are finer and adorned with rows of villiform teeth on both margins of the flat edge of the rakers facing the pharyngeal cavity (Fig. 3). The arrangement of the rakers is such that those on adjacent arches are interposed when the arches are brought together.

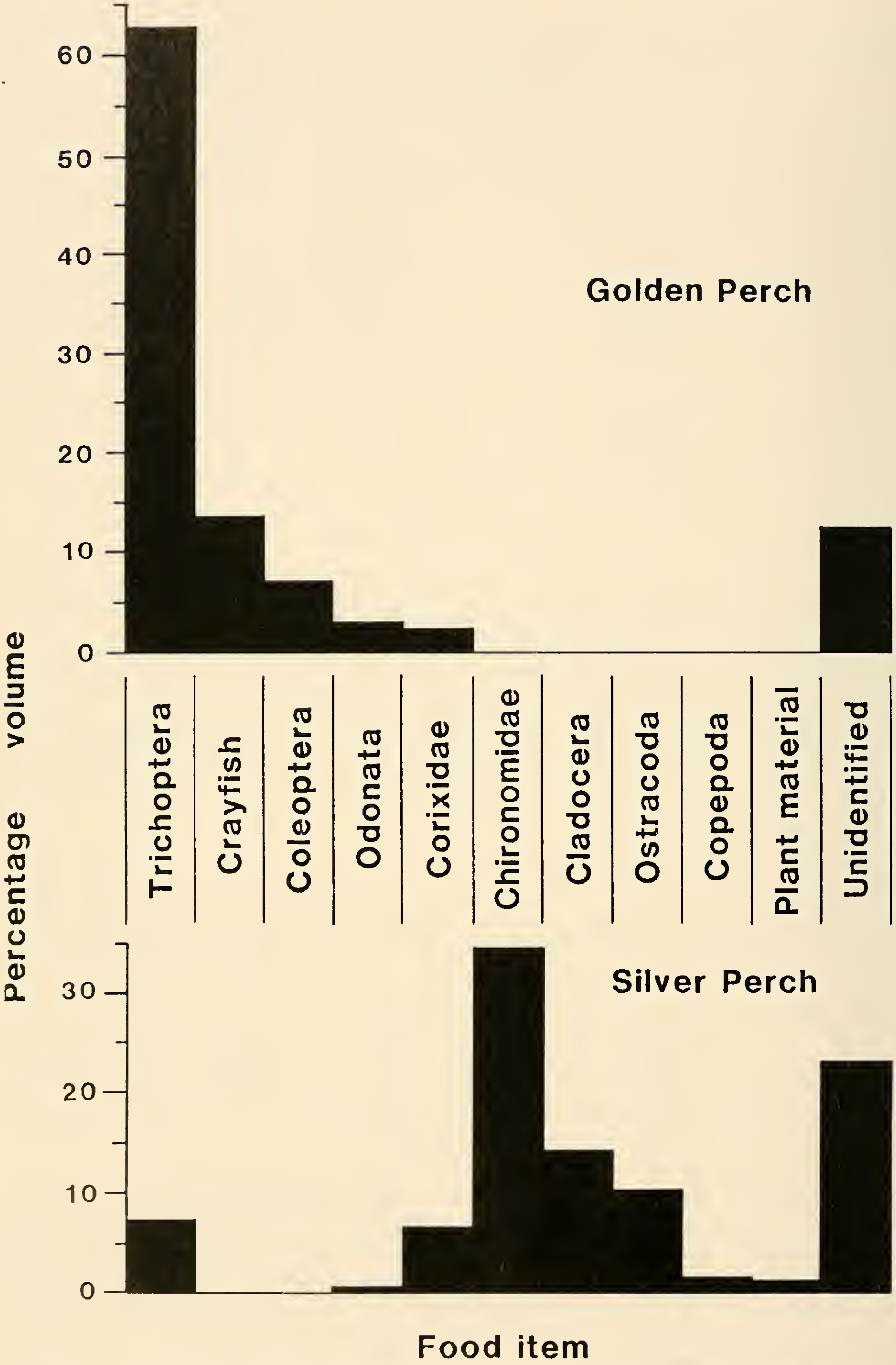

Fig. 1. Diets (average of the percentage volume of individual fish) of golden perch (T.L. 286 ± 20mm, Wt 289 ± 65g) and silver perch (T.L. 315 ± 12mm, Wt 429 ± 60g) reared in a polyculture trial.

The relationships between gut length and total length were linear for both species (Fig. 4), and were described by the following equations:

Golden perch, total length range 155-292mm,

$$GL = 0.498TL - 29.5 \quad (r=0.84,\ n=43,\ p<0.001)$$

Silver perch, total length range 175-328mm,

$$GL = 1.26TL - 106 \quad (r=0.93,\ n=45,\ p<0.001)$$

where GL = gut length and TL = total length.

The ratio of intestine-rectum length : stomach length for golden perch was 2.34 ± 0.34, and for silver perch it was 6.75 ± 1.31. That is, the alimentary tract of silver perch was longer than that of golden perch; this difference was due to the relatively longer intestine-rectum of the silver perch, rather than a difference in the size of the stomachs of the two species.

DISCUSSION

The advantage of employing a statistically measurable prey-selection index for comparing diets and potential prey species was evident in the monoculture trial. By

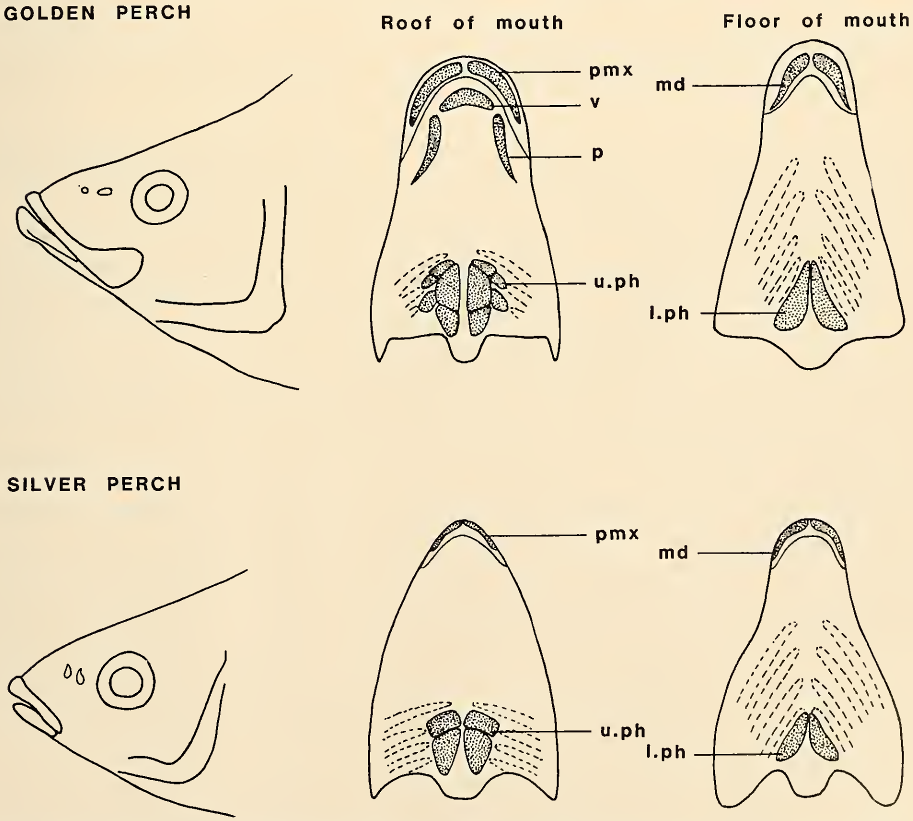

Fig. 2. Shape of the mouth and arrangement of teeth in golden perch and silver perch. (md = mandibular, pmx = premaxillary, v = vomerine, p = palatine, l.ph = lower pharyngeal, u.ph = upper pharyngeal).

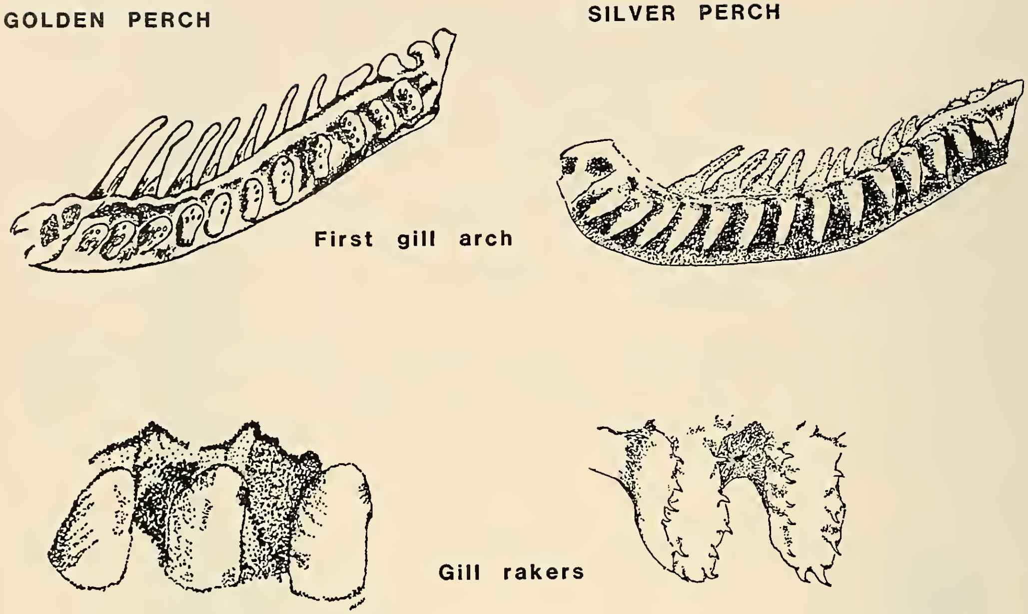

Fig. 3. The lower limb of the first gill arch of golden perch and silver perch, and magnified gill rakers showing the typical shape of the posterior rakers on the first gill arch and the anterior and posterior rakers on the second, third and fourth arches.

using C it was possible to determine which prey species were being significantly selected or avoided by the fish. Furthermore, realistic values of C could be computed even when a particular food type was absent in either the diet or the environment.

Preference ratings, however, apply only at the time of sampling; the most preferred species tend to be depleted first and the remaining species affected more or less severely according to their preference ranking and the intensity and duration of cropping (Petrides, 1975). One possible example of depletion of preferred species is the notonectids, which were actively selected by both golden perch and silver perch in the monoculture trial. However, notonectids were absent from the diets of both species in the polyculture trial, and thus presumably absent from the dam, even though notonectids are the numerically dominant insect group in farm dams in the study area (Barlow and Bock, 1981).

In the monoculture trial, golden perch fed on a wide variety of insects and the silver perch fed predominantly on zooplankton. Strict comparison of the diets was not possible because of the different available food sources. However, these apparent dietary differences were real, as indicated in the polyculture trial, in which golden perch fed mainly on trichoptera larvae and crayfish, whereas silver perch ate zooplankton and chironomid larvae. The diet of golden perch in this study agrees with published information, but the diet of silver perch indicates greater consumption of zooplankton than previous observations on the stomach contents of wild fish had indicated (Merrick and Schmida, 1984).

The morphology of the alimentary tracts also suggests that the diets of the two species are different. The large mouth of golden perch is obviously adapted for taking large prey. The numerous, tiny teeth set in bony plates, together with the stout, hard gill rakers, would aid crushing of the prey. The short intestine is also typical of a carnivore

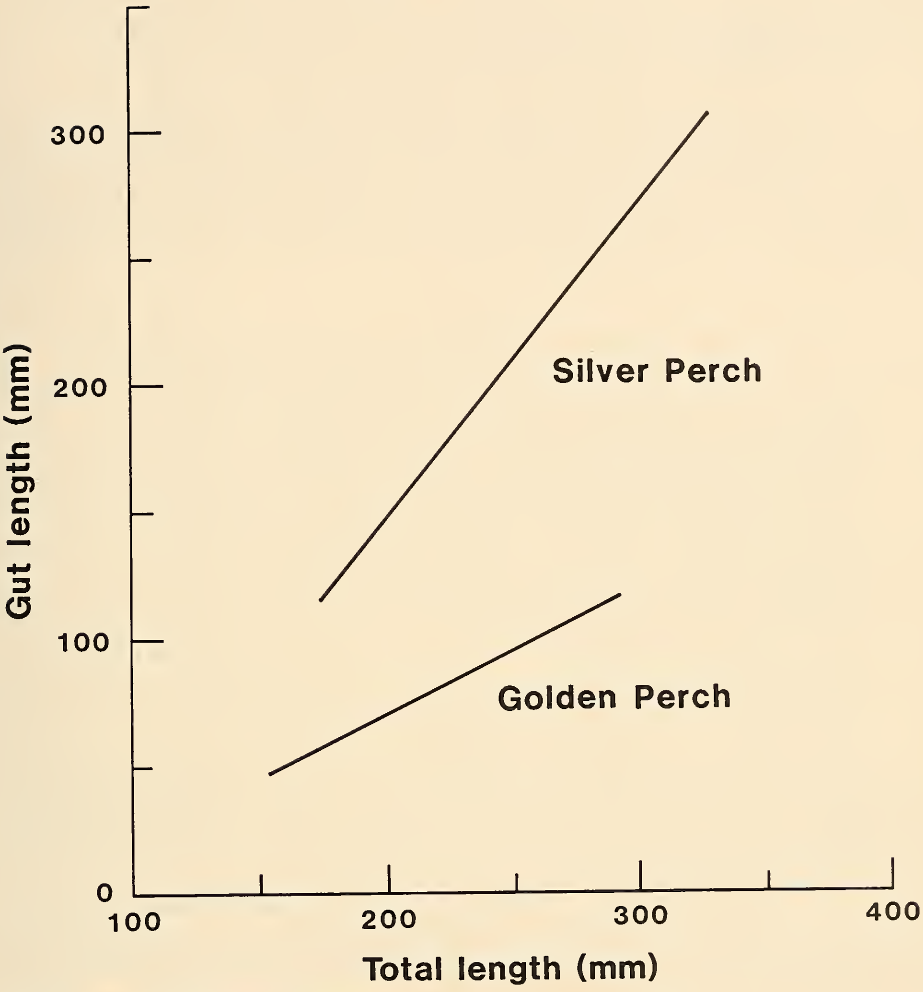

Fig. 4. Regression of gut length on total length for golden perch and silver perch.

(Das and Moitra, 1956). In contrast, silver perch has a small, terminal mouth with premaxillary teeth which are apparently capable of rasping aufwuchs from solid substrates. Aufwuchs was not present in any of the dams in this study, but periphyton has often been observed in the gut contents of silver perch from other waters (Barlow, unpublished data). Of particular interest are the villiform teeth on the gill rakers of the silver perch. These teeth form a very effective sieving device when the gill arches are brought together. Presumably, this is the mechanism silver perch uses to capture zooplankton. The comparatively long intestine of silver perch is also indicative of an omnivorous diet (Das and Moitra, 1956).

In conclusion, golden perch can be classified as a macrophagic carnivore eating insects and crustaceans, whereas silver perch is an omnivore eating mainly zooplankton, insects and aufwuchs if available. Such dietary differences indicate that these species are well-suited for rearing together in polyculture, at least in unmanaged farm dams. Although both species have many of the biological attributes necessary for successful aquaculture (Barlow, in press), research on production levels attainable in intensively managed ponds is necessary before any determination can be made regarding the economic feasibility of farming these fishes.

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Distribution and Taxonomy of the Long-eared Bats, *Nyctophilus gouldi* Tomes, 1858 and *Nyctophilus bifax* Thomas, 1915 (Chiroptera: Vespertilionidae) in eastern Australia

H. E. PARNABY

PARNABY, H. E. Distribution and taxonomy of the long-eared bats, *Nyctophilus gouldi* Tomes, 1858 and *Nyctophilus bifax* Thomas, 1915 (Chiroptera: Vespertilionidae) in eastern Australia. *Proc. Linn. Soc. N.S.W.* 109(3), (1986) 1987: 153-174.

Although recently synonymized with *N. gouldi*, *N. bifax* is shown to be a distinct species separable on a number of external, cranial and bacula features. Cranial and external characters examined show that both species are similar in size, but can be readily identified in the field on the basis of fur colour, relative ear size, and details of the snout. Striking differences exist in external phallic morphology between each species.

Additional data on the distribution of *N. bifax* and *N. gouldi* have resulted from recent field work and a re-evaluation of material in Australian collections. The distribution of both species is summarized. The known distribution of *N. gouldi* is extended north by about 1100km to Atherton, north Queensland. *N. bifax* is recorded from a number of new localities south to Iluka, New South Wales, representing a southern range extension of some 750km. These species are therefore sympatric over 1600km in eastern Australia.

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INTRODUCTION

Six species of the australo-papuan bat genus *Nyctophilus* are generally recognized from Australia (Hall, 1984): *N. geoffroyi*, *N. timoriensis*, *N. gouldi*, *N. bifax*, *N. arnhemensis*, and *N. walkeri*. This paper considers the distribution and status of eastern Australian populations of *N. gouldi* and *N. bifax*, and is part of a continuing taxonomic study of *Nyctophilus*.

Historically, the taxonomic status of *N. gouldi* has been subject to controversy. Tomes (1858) described *N. gouldi* from specimens from Moreton Bay, Queensland, and Bathurst, New South Wales. Iredale and Troughton (1934) considered *N. gouldi* to be a southeastern Australian subspecies of the widespread *N. timoriensis*. Tate (1952) regarded *N. gouldi* to be a distinct species. However, until recently the arrangement of Iredale and Troughton (1934) has been followed by most authors. There is now general agreement that *N. gouldi* and *N. timoriensis* are distinct species (Hall and Richards, 1979; Allison, 1982; Koopman, 1984) and are known to be sympatric at several localities in eastern Australia (Parnaby, unpublished). Richards (1983) summarized the known range of *N. gouldi* as southwestern Western Australia, Tasmania, Victoria, eastern New South Wales and southeastern Queensland as far north as Bundaberg.

Thomas (1915) described *N. bifax* based on material from the Torres Strait islands and north Queensland. As of 1983, *N. bifax* was recorded from northern Western Australia, the Northern Territory and across to northeastern Queensland as far south as Sarina (Allison, 1983). Within this range, two subspecies are commonly recognized: *N. bifax bifax* from Queensland, and *N. b. daedalus* from the Northern Territory and Western Australia.

Koopman (1984) believed that the criteria proposed by Thomas for the separation of *N. bifax* from *N. gouldi* were not of sufficient magnitude to warrant species status and, in view of the wide separation of their then known distribution, he tentatively placed *N. bifax* as a subspecies of *N. gouldi*. Based on the distribution data of Hall and Richards (1979), Koopman (1984) believed that the distribution of *N. bifax* and *N. gouldi* were separated by approximately 1000km in eastern Australia.

Koopman (1984), uncertain about the status of *daedalus*, placed it with *N. gouldi*, thereby tentatively proposing a single species with three allopatric subspecies: *N. gouldi gouldi* from southern Australia (but not Tasmania), *N. gouldi bifax* from north Queensland and *N. gouldi daedalus* from northern Western Australia and the Northern Territory.

Churchill *et al.* (1984) record a considerable southern extension of the known range of *N. bifax*, to the Pilbara region of Western Australia, and to Rockhampton in Queensland, thus closing the gap in the known range of this species and that of *N. gouldi* to approximately 1000km in Western Australia, and some 300km in Queensland.

Field work conducted by the author and others over the last five years, combined with a reexamination of existing Australian research collections, has resulted in further insight into the taxonomic status and distribution of these taxa. Morphologically, *N. gouldi* and *N. bifax* have been found to be readily distinguishable, both in the field and by examination of preserved material. This has facilitated the recognition of many new locality records including major range extensions of both species. Significantly, electrophoretic analysis of tissue samples collected from areas of sympatry in eastern Australia has provided unequivocal evidence of the distinct separation of *N. bifax* and *N. gouldi* (M. Adams and P. Baverstock, *pers. comm.*).

In this paper, the distribution of each species is summarized and new distribution records are presented which indicate large scale sympatry between *N. bifax* and *N. gouldi*. The major external, cranial and bacula features useful for distinguishing each species from throughout their range in eastern Australia are discussed.

Abbreviations used for research collections from which material has been examined are: Australian Museum, Sydney (AM); Australian National Wildlife Collection (CSIRO), Canberra (CM); Museum of Victoria, Melbourne (MV); South Australian Museum, Adelaide (SAM); Queensland Museum, Brisbane (QM) and Western Australian Museum, Perth (WAM).

DISTRIBUTION

N. gouldi

As noted above, this species is recorded from southwestern Western Australia, Victoria through eastern New South Wales, to southeast Queensland (Richards, 1983). Richards also records this species from Tasmania but the specimens on which this is based belong with the large Tasmanian form of *N. geoffroyi* (see Discussion).

Previously, the most northern record of this species in eastern Australia was from near Gin Gin, Queensland (Thomas, 1915). Examination of museum material, and recent field collecting, have resulted in a substantial expansion of the known range to Atherton, 1100km north from Gin Gin.

The known distributional limits of *N. gouldi* in eastern Australia are shown in Fig. 1a and localities are listed in Appendix 1. The species is usually considered to be an inhabitant of mesic eucalypt forests of the Great Dividing Range. Hall and Richards (1979) record the species from inland southern Queensland. Additional records presented here from inland Queensland and New South Wales and field work in New South Wales indicates that *N. gouldi* is widespread and probably more common throughout lower rainfall regions than was previously realized. Thus this species appears to

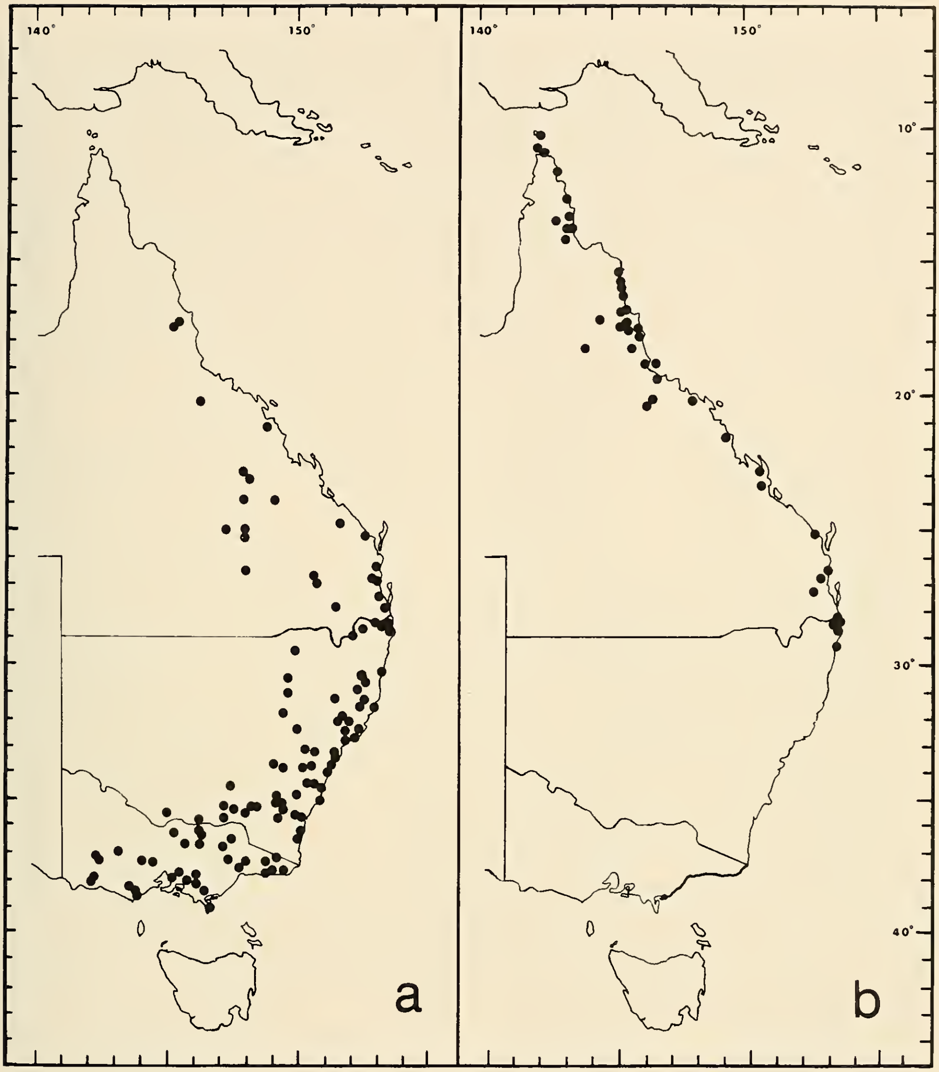

Fig. 1. Distribution of **a**, *N. gouldi* and **b**, *N. bifax* in eastern Australia.

occur in a range of habitats, including semi-arid woodland (such as in the Charters Towers region), brigalow country and sclerophyll forest.

N. bifax

The original description of *N. bifax* by Thomas (1915) was based on material from localities ranging from Torres Strait islands, south to Herberton and west to Cloncurry, northwestern Queensland. In eastern Australia, there are few published records of *N. bifax* south of Townsville; Allison (1983) depicts this species as extending south to about Sarina and Churchill *et al.* (1984) record *N. bifax* at Byfield, near Rockhampton. Examination of museum material, some of which had previously been misidentified, has resulted in a number of additional locality records in near coastal areas extending south from Townsville to southern Queensland.

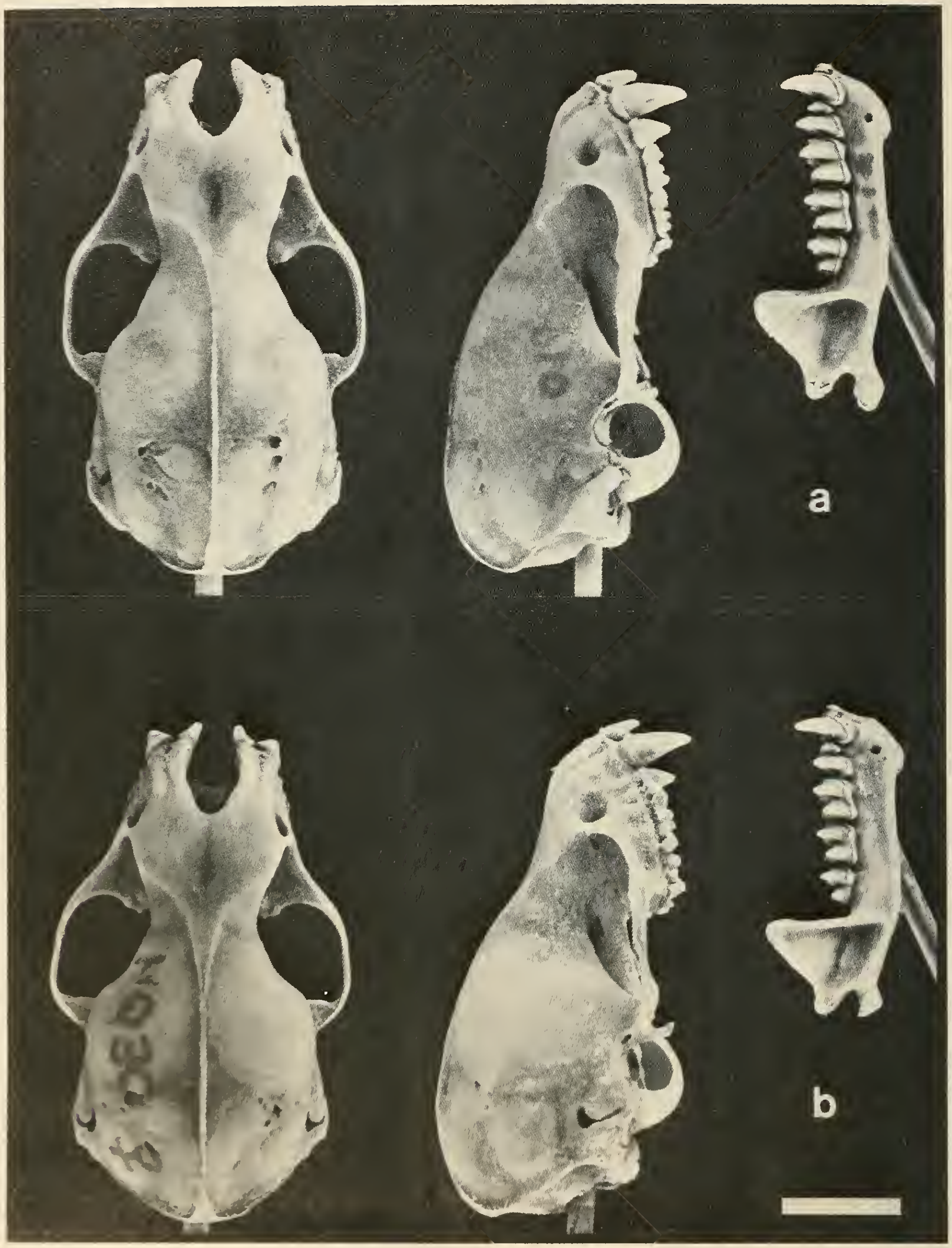

Fig. 2. Dorsal and lateral views of the skull and lateral view of the dentary of **a**, *N. gouldi* from Brisbane (QM JM5366, female); **b**, *N. bifax* from Atherton, Qld (AM M16181, female). Bar represents 4mm.

During field work in north coastal New South Wales, *N. bifax* was one of the most frequently trapped species of insectivorous bat. It was captured at low elevations at a number of localities as far south as Iluka (Parnaby, 1986), which is currently the most southern record for the species.

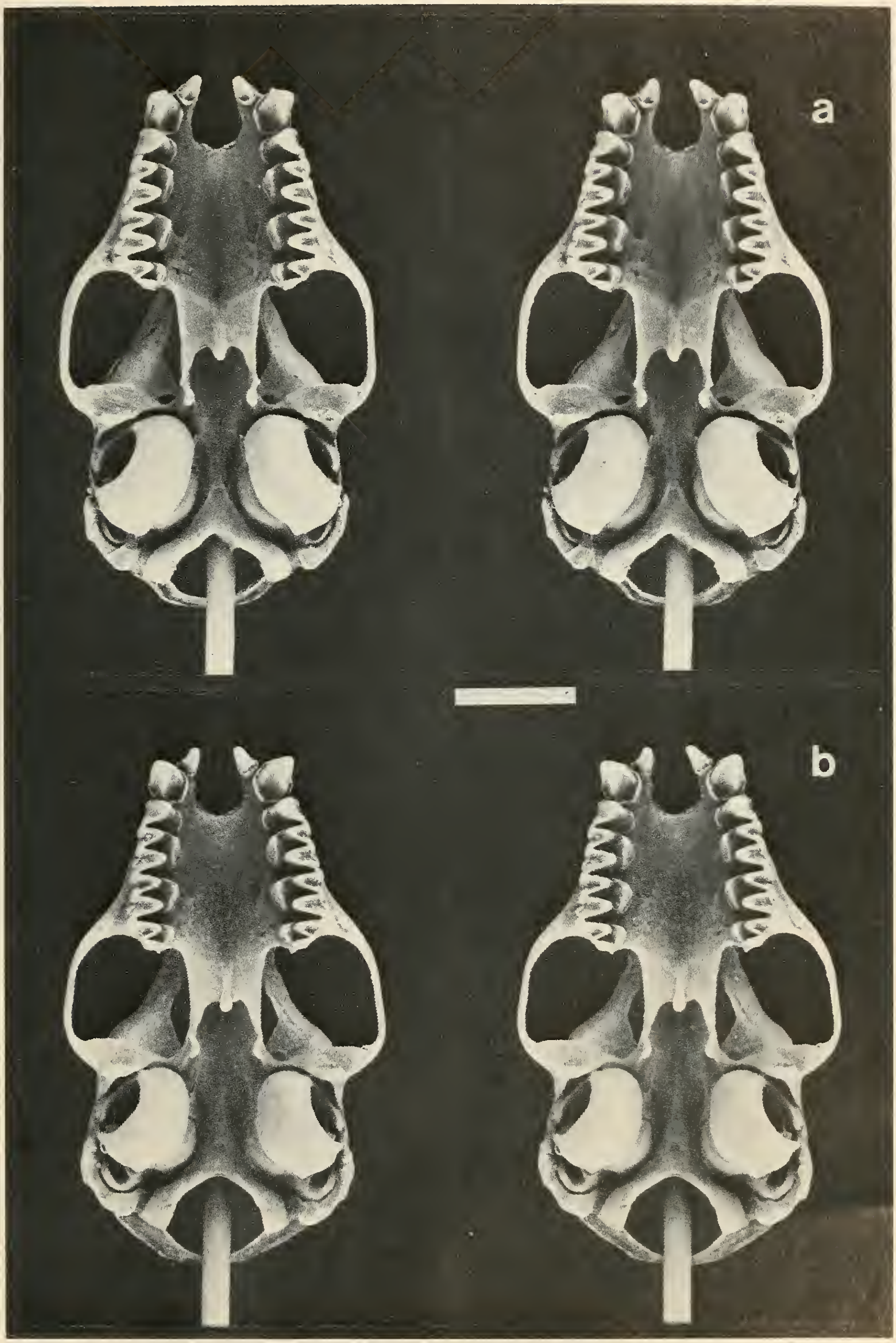

Fig. 3. Stereopairs of ventral view of **a**, *N. gouldi* from Brisbane (QM JM5366 female); **b**, *N. bifax* from Atherton (AM M16181, female). Bar represents 4mm.

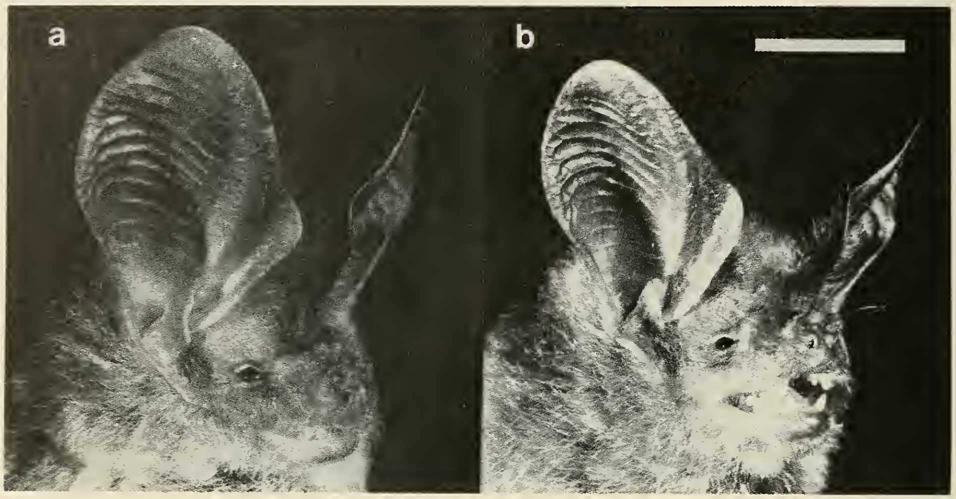

Fig. 4. Photographs illustrating differences in relative ear size between males of **a**, *N. gouldi* from Broken Head, N.S.W. (AM M13389) and **b**, *N. bifax* from Brunswick Heads, N.S.W. (AM M13388). Bar represents 1cm.

The updated distribution of *N. bifax* in eastern Australia is shown in Fig. 1**b**, and localities are listed in Appendix 1. With the exception of a specimen from the Cloncurry area (20° 42′S, 140° 30′E) reported by Thomas (1915) and one from the Einasleigh River (18° 11′S, 144° 00′E, AM M13356), most records are close to the coast. Allison (1983) notes the occurrence of this species in a variety of habitats ranging from rain forest to dry sclerophyll woodlands.

MORPHOLOGICAL DIFFERENCES

Substantial between-locality variation exists within each species throughout eastern Australia, particularly so in *N. gouldi* (see 'Metric variation' below). Despite this, diagnostic external and cranial criteria discussed in the following sections appear to hold, irrespective of locality.

Skull morphology

Compared with *N. bifax* the skull of *N. gouldi* is relatively narrow for its length, and is more slightly built (Fig. 2). In *N. gouldi* the bullae are relatively much larger, and consequently appear to be closer together medially (Fig. 3). The hamular processes of the pterygoids are slightly more ossified in *N. gouldi*. The paroccipital processes are slightiy more pronounced in *N. bifax* and are more clearly distinct from the occipital condyles.

The upper canines are laterally splayed in *N. bifax* yet in *N. gouldi* they are usually in line with the upper tooth row, however, occasional specimens of *N. gouldi* with splayed canines have been observed.

Like the skull, the dentary of *N. gouldi* is more delicately built and is shallower. The upward inflection of the postero-ventral border of the ramus is more marked in *N. bifax* and the angular process is generally shorter than that of *N. gouldi* (Fig. 2).

External Morphology

The most obvious external differences between these two species are in the relative size of the ears and general fur colour. Relative to body size, the ears are very large in *N. gouldi* (Fig. 4), while in *N. bifax* they are distinctly shorter.

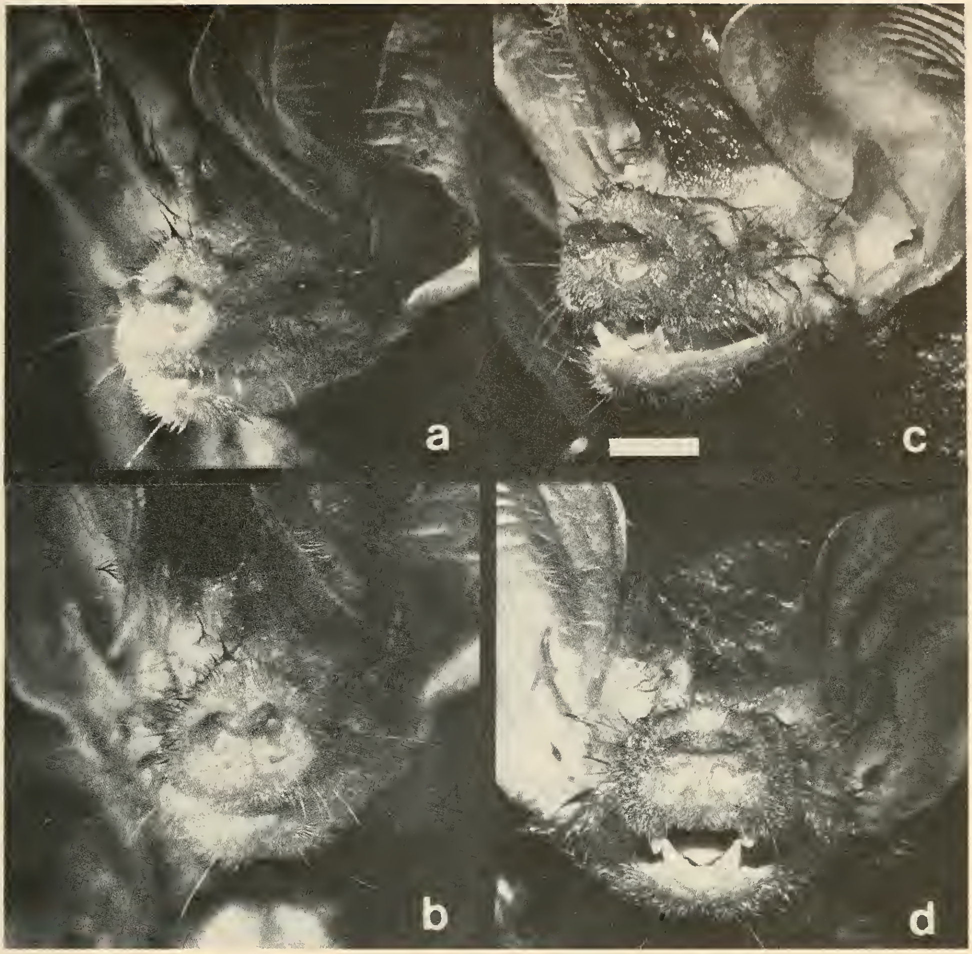

Fig. 5. Frontal and frontolateral views of the snout of **a**, and **b**, *N. gouldi* from Border Ranges, N.S.W. (AM M13412, male); **c**, and **d**, *N. bifax* from Brunswick Heads (AM M13388,male), showing differences in the post-nasal prominence. Bar represents 4mm.

From field observations, the dorsal pelage of *N. gouldi* is predominantly a slate grey or grey-brown with ash-grey ventral fur often mottled with very light buff. In *N. bifax*, the dorsum is light brown or tannish, with a lighter tannish undersurface.

There is a consistent difference in the shape of the post-nasal bump, as originally noted by Thomas (1915). Relative to the noseleaf, this structure is more developed in *N. gouldi* than *N. bifax* (Fig. 5) and in *N. gouldi* has a faint vertical groove which is weaker or absent in *N. bifax*. The specimens illustrated in Fig. 5 differ in the shape of the dorsal margin of the noseleaf; there is a median concavity in *N. gouldi* while the margin of *N. bifax* is evenly convex. However this difference is not diagnostic as the shape of the noseleaf is variable in both species.

Camera lucida drawings of a representative glans penis of an adult of each species are shown in Fig. 6. Each species differs in a number of obvious features. The lateral surfaces in *N. gouldi* are constricted in the mid-line, dividing the penis into a distinct

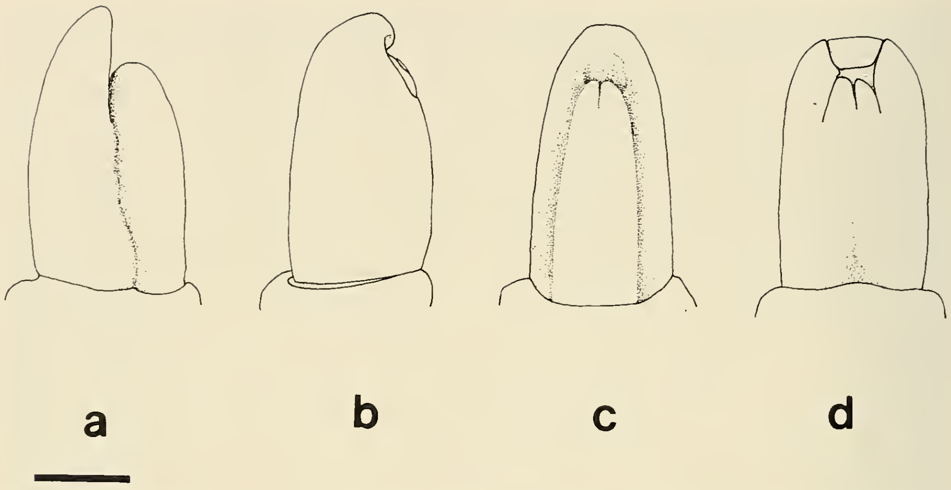

Fig. 6. Camera lucida drawings of the glans penis with prepuce removed. Lateral view of **a**, *N. gouldi* from Border Range, NSW (AM M13412), **b**, *N. bifax* from Brunswick Heads, NSW (AM M13388). Ventral view of **c**, *N. gouldi* and **d**, *N. bifax*. Bar represents 1.0mm.

dorsal and ventral element. The dorsal element forms a very distinct distal 'beak'. In marked contrast, the penis of *N. bifax* is approximately cylindrical, and the head of the penis is more truncated. Consequently, each species has a very characteristic profile which is clearly visible to the unaided eye.

Bacular morphology

As noted by Thomas (1915) *N. bifax* differs from *N. gouldi* in bacular morphology: in *N. gouldi* the baculum comes to a simple point distally whereas in *N. bifax* the tip is bifurcated by a crescentic notch.

Using X-ray photography, I have examined bacula from 17 specimens of *N. bifax* from localities scattered throughout the complete eastern Australian range of this species, from Iluka north to Lockerbie Scrub. The bifid condition is present in every specimen. Likewise, the sharp distal point is present in all 25 examples of *N. gouldi* examined from widespread locations throughout Victoria, New South Wales and Queensland. Thus, the condition of the distal tip of the baculum appears to be monomorphic in each species.

Metric Variation

A univariate and multivariate analysis of metric variation using analysis of variance, principal components analysis and canonical variates analysis of these and other species of *Nyctophilus* is in progress, and preliminary findings are outlined here.

Ten external dimensions were taken from 130 spirit-preserved specimens of *N. gouldi* from central and northern New South Wales and Queensland, and 118 spirit specimens of *N. bifax bifax* from throughout Queensland and northern New South Wales (listed in Appendix 1). Twelve cranial measurements were made on 69 skulls of *N. gouldi* and 52 of *N. bifax bifax*, all from throughout New South Wales and Queensland.

Sexual size dimorphism was found in the majority of dimensions in both species, with females on average larger than males. Consequently, sexes were treated separately in all analyses.

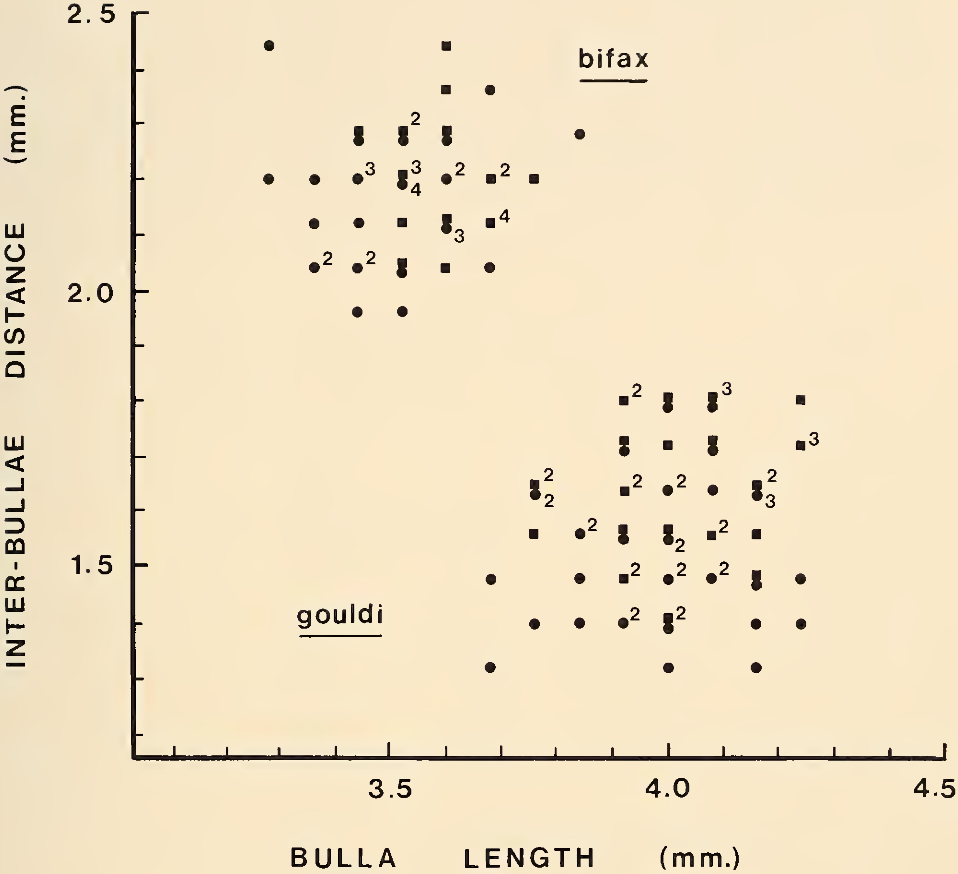

Fig. 7. Plot of interbullae distance (mm) against bulla length (mm) for 65 *N. gouldi* and 50 *N. bifax* from central and northern NSW and Qld. Both dimensions were measured in ocular units with a dissecting microscope, and the axes converted to mm. Circles represent males, squares females. Numerals indicate overlapping points.

When specimens from all localities are pooled, mensural ranges overlap between each species for all external and all but one of the 12 cranial and dental dimensions. Measurements with overlapping ranges are: ear length, measured from the notch; length of first digit; forearm length; third digit: length of metacarpal I, length of metacarpal II, length of metacarpal III; fifth digit: length of metacarpal I, II, and III; length of hind-leg; condylobasal length; greatest length of skull; length of upper tooth row (C^1-M^3); zygomatic breadth; interorbital constriction; outer breadth of upper third molars; height of braincase; skull breadth at mastoids; interbullae distance; bulla length, and basicranial length (measured from the anterior margin of foramen magnum to the anterior border of the posterior palatal emargination).

Interbullae distance is the only measurement in which the range for each species do not overlap: the range for *N. gouldi* being 2.0-2.5mm (n=65) and *N. bifax* 1.3-1.8mm (n = 50). A plot of this dimension against bulla length for all localities combined (Fig. 7) results in a clear separation of *N. bifax* and *N. gouldi*.

In both species substantial size differences were found between localities. Although analysis of these data is preliminary, observed variation seems to correspond with local climatic conditions. This is evident in a plot of forearm length against longitude for samples of *N. gouldi* from diverse sites throughout New South Wales and Queensland (Fig. 8), where increasing longitude approximates decreasing aridity. For example, mean forearm length of a sample of female *N. gouldi* from a dry inland site (Pilliga Scrub, NSW) is 38.7mm compared with 45.8mm for females from a higher rainfall site in the Great Dividing Range at a comparable latitude (Doyles River State Forest).

The between-locality size variation evident in both species might be expected to obscure differences present within a given locality. In an attempt to reduce these locality

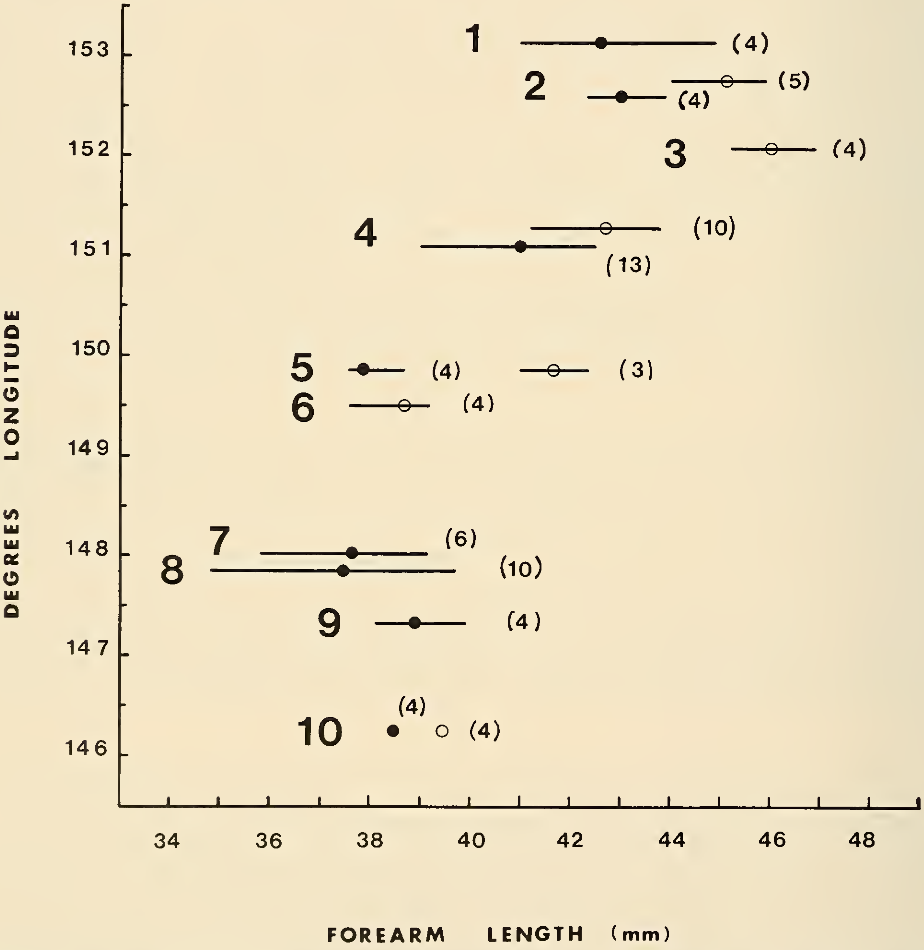

Fig. 8. Forearm length (mm) of *N. gouldi* versus longitude for samples from throughout NSW and Qld showing a trend of increase in size with longitude. Circles represent female sample means, dots male samples. Lines indicate sample range, sample size in brackets. Localities are, **1.** Tweed Rge, northern NSW; **2.** Gloucester Tops, central NSW; **3.** Doyles River State Forest, central NSW; **4.** Olney State Forest, central NSW; **5.** Cassilis region, central NSW; **6.** Pilliga State Forest, northern NSW; **7.** Tambo region, south-central Qld; **8.** Capella, central Qld; **9.** Henty region, southern NSW; **10.** Mt Leysham, north Qld. (from Churchill *et al.*, 1984).

effects, measurements of specimens from a restricted geographic region were compared. The only area of sympatry for which specimens are available in any numbers is northeastern New South Wales and far southeast Queensland. Twenty-six specimens of *N. gouldi* and 23 of *N. bifax* were examined from localities ranging from the Conondale Ranges, south to Iluka in New South Wales and inland to Tooloom. Only three of these specimens are from north of Brisbane.

Measurements of spirit specimens from within this region were pooled by sex for each species. Summary statistics for external dimensions of each species are given in Table 1, and dimensions of 19 skulls of *N. gouldi* and 11 of *N. bifax* from the same region are given in Table 2.

TABLE 1

Summary statistics for external dimensions (mm) of spirit specimens of N. bifax *and* N. gouldi *from northern N.S.W. and southeastern Qld*

Sample sizes for all dimensions are: *N. bifax* (9 males, 14 females), *N. gouldi* (10 males, 8 females)

		MEAN	S.E.	S.D.	RANGE	CV
EAR LENGTH	MALES					
	bifax	24.78	.43	1.29	21.9–26.7	5.20
	gouldi	28.33	.44	1.40	25.8–30.0	5.78
	FEMALES					
	bifax	25.16	.24	.90	23.5–26.3	3.58
	gouldi	28.55	.29	.81	27.5–30.1	2.83
FOREARM	MALES					
	bifax	41.46	.34	.10	39.3–42.5	2.42
	gouldi	42.24	.43	1.35	39.5–44.9	3.62
	FEMALES					
	bifax	42.98	.23	.87	41.0–44.4	2.06
	gouldi	43.16	.52	1.46	41.2–45.2	3.38
DIGIT I	MALES					
	bifax	6.79	.089	.27	6.3–7.1	4.12
	gouldi	6.50	.11	.35	6.1–7.1	7.67
	FEMALES					
	bifax	6.94	.064	.24	6.6–7.3	3.46
	gouldi	6.87	.52	.42	6.0–7.3	6.11
DIGIT 3, METACARPAL I	MALES					
	bifax	38.99	.32	.95	37.5–40.5	2.44
	gouldi	39.92	.60	1.89	35.8–42.7	4.73
	FEMALES					
	bifax	39.74	.22	.84	37.7–41.0	2.11
	gouldi	40.66	.46	1.31	39.2–42.5	3.22
DIGIT 3, METACARPAL II	MALES					
	bifax	15.61	.15	.46	14.9–16.3	2.95
	gouldi	15.61	.19	.59	14.7–16.3	3.78
	FEMALES					
	bifax	15.93	.14	.51	15.1–16.9	3.20
	gouldi	16.30	.30	.84	15.2–18.0	5.15
DIGIT 3, METACARPAL III	MALES					
	bifax	14.61	.11	.33	14.0–15.1	2.26
	gouldi	14.09	.22	.70	12.5–15.0	4.97
	FEMALES					
	bifax	14.66	.12	.43	13.8–15.2	2.93
	gouldi	14.14	.34	.96	12.9–15.8	6.79

TABLE 1 (continued)

		MEAN	S.E.	S.D.	RANGE	CV
DIGIT 5, METACARPAL I	MALES					
	bifax	38.91	.32	.95	37.4–40.7	2.44
	gouldi	39.74	.46	1.45	37.2–42.6	3.65
	FEMALES					
	bifax	40.01	.21	.80	38.8–41.4	2.00
	gouldi	40.52	.52	1.46	38.9–42.8	3.60
DIGIT 5, METACARPAL II	MALES					
	bifax	10.58	.12	.37	10.0–11.2	3.50
	gouldi	10.91	.17	.54	10.2–12.2	4.95
	FEMALES					
	bifax	10.84	.072	.27	10.4–11.4	2.49
	gouldi	11.43	.22	.62	10.6–12.2	5.42
DIGIT 5, METACARPAL III	MALES					
	bifax	10.71	.20	.61	9.4–11.5	5.69
	gouldi	10.00	.27	.78	9.0–12.0	7.80
	FEMALES					
	bifax	10.51	.19	.71	8.4–11.4	6.75
	gouldi	10.01	.27	.78	8.9–10.9	7.79
HINDLEG LENGTH	MALES					
	bifax	21.67	.16	.48	21.0–22.3	2.21
	gouldi	20.78	.27	.82	19.7–22.1	3.95
	FEMALES					
	bifax	21.90	.11	.42	21.2–22.7	1.92
	gouldi	21.20	.34	.95	19.8–22.6	4.48

TABLE 2

Summary statistics for skull and dental dimensions of N. bifax *and* N. gouldi *from northern N.S.W. and far southeastern Qld*

All dimensions are in mm. Note that interbullae distance, bulla length and basicranial length were measured in occular units (1 unit = 0.082mm), and converted to mm

		N	MEAN	S.E.	S.D.	RANGE	CV
CONDYLOBASAL LENGTH	MALES						
	bifax	5	15.30	.13	.29	14.9–15.6	1.89
	gouldi	11	16.36	.11	.37	15.9–17.0	2.26
	FEMALES						
	bifax	6	15.68	.098	.24	15.4–16.0	1.53
	gouldi	8	16.46	.11	.32	16.1–17.0	1.94
GREATEST LENGTH	MALES						
	bifax	5	16.64	.14	.32	16.2–17.0	1.92
	gouldi	11	17.30	.13	.42	17.3–18.2	2.43
	FEMALES						
	bifax	6	16.93	.080	.20	16.6–17.1	1.18
	gouldi	8	17.91	.11	.32	17.5–18.4	1.79
CM^{1-3} LENGTH	MALES						
	bifax	5	6.22	.037	.084	6.1–6.3	1.35
	gouldi	11	6.57	.060	.20	6.3–7.0	3.04
	FEMALES						
	bifax	6	6.32	.054	.13	6.1–6.5	2.06
	gouldi	8	6.53	.041	.12	6.4–6.7	1.84

Table 2 (continued)

		N	MEAN	S.E.	S.D.	RANGE	CV
C^1-C^1 BREADTH	MALES						
	bifax	5	4.70	.032	.071	4.6–4.8	1.51
	gouldi	11	4.82	.055	.18	4.5–5.1	3.73
	FEMALES						
	bifax	6	4.93	.033	.082	4.8–5.0	1.66
	gouldi	8	4.86	.046	.13	4.6–5.0	2.67
ZYGOMATIC BREADTH	MALES						
	bifax	5	10.54	.11	.24	10.2–10.8	2.28
	gouldi	11	10.46	.10	.33	10.0–11.1	3.15
	FEMALES						
	bifax	6	10.73	.056	.14	10.5–10.9	1.30
	gouldi	8	10.60	.10	.28	10.1–10.9	2.46
INTERORBITAL CONSTRICTION	MALES						
	bifax	5	3.52	.037	.084	3.4–3.6	2.39
	gouldi	11	3.74	.028	.093	3.6–3.9	2.48
	FEMALES						
	bifax	6	3.52	.054	.13	3.3–3.7	3.69
	gouldi	8	3.75	.050	.14	3.6–4.0	3.73
BREADTH M^{3-3}	MALES						
	bifax	5	6.78	.058	.13	6.7–7.0	1.92
	gouldi	11	6.94	.049	.16	6.7–7.3	2.30
	FEMALES						
	bifax	6	7.07	.061	.15	6.8–7.2	2.12
	gouldi	8	6.91	.055	.15	6.7–7.0	2.17
BRAINCASE HEIGHT	MALES						
	bifax	5	6.36	.081	.18	6.1–6.6	2.83
	gouldi	10	6.34	.074	.24	6.0–7.0	3.78
	FEMALES						
	bifax	6	6.42	.040	.098	6.3–6.5	1.52
	gouldi	7	6.30	.058	.15	6.1–6.5	2.38
MASTOID BREADTH	MALES						
	bifax	5	8.80	.11	.25	8.4–9.0	2.84
	gouldi	11	9.23	.060	.20	9.0–9.6	2.17
	FEMALES						
	bifax	6	9.07	.080	.20	8.9–9.4	2.20
	gouldi	8	9.16	.082	.23	8.9–9.5	2.51
INTERBULLAR DISTANCE	MALES						
	bifax	5	2.13	.045	.10	2.0–2.3	4.69
	gouldi	10	1.61	.044	.14	1.4–1.8	8.69
	FEMALES						
	bifax	6	2.23	.026	.065	2.1–2.3	2.91
	gouldi	7	1.66	.057	.15	1.4–1.8	9.03
BULLAR LENGTH	MALES						
	bifax	5	3.59	.041	.092	3.4–3.7	2.56
	gouldi	10	4.06	.038	.12	3.8–4.3	2.95
	FEMALES						
	bifax	6	3.59	.039	.095	3.5–3.8	2.65
	gouldi	7	4.08	.053	.14	3.9–4.3	3.43
BASICRANIAL LENGTH	MALES						
	bifax	5	5.54	.067	.15	5.4–5.7	2.70
	gouldi	10	6.11	.060	.19	5.8–6.6	3.11
	FEMALES						
	bifax	6	5.76	.057	.14	5.7–6.0	2.43
	gouldi	7	6.00	.072	.19	5.7–6.3	3.17

The ranges of ear length for females of each species do not overlap; this separation is shown in Fig. 9. For the remaining nine external measurements however, there is extensive overlap between each sex of each species. For all external dimensions except ear length, the two species have similar mean values for equivalent sex. As there is nearly complete overlap in the ranges of forearm length between both species, a bivariate plot of ear length against forearm length (frequently used in bat systematics) is not useful for separating males of these species (Fig. 9).

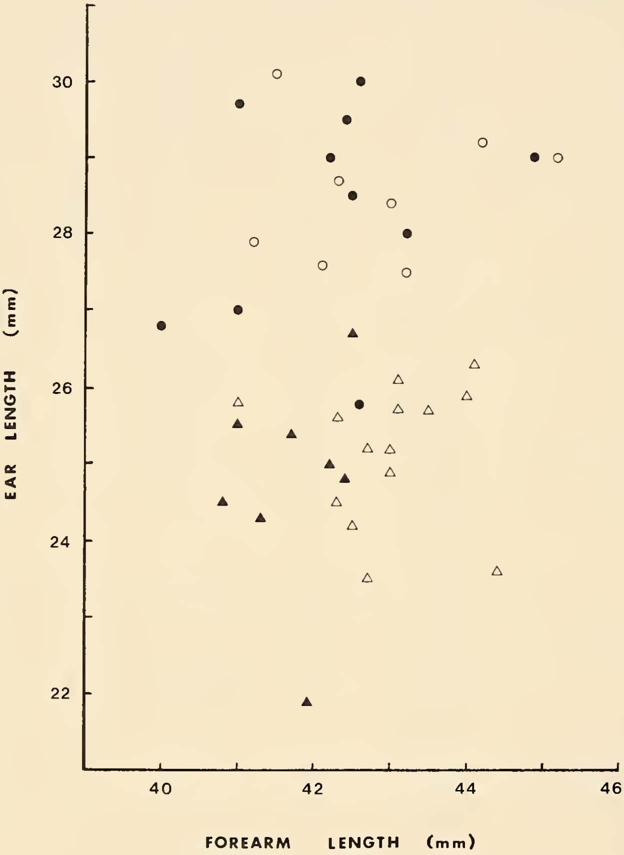

Fig. 9. Plot of ear length (mm) against forearm length (mm) for *N. gouldi* (circles) and *N. bifax* (triangles) from northern NSW and far southeastern Qld. Closed symbols represent males, open symbols females.

Skull dimensions overlap or abut in all but four characters: condylobasal length, greatest length of skull, interbullae distance and bulla length (Table 2). Clear separation of the two species results on a plot of zygomatic breadth against greatest length of skull (Fig. 10). Thus in terms of absolute size specimens of *N. gouldi* from northern New South Wales have longer skulls with bigger bullae. It remains to be seen whether these differences are maintained in larger samples.

Specimens of *N. gouldi* from this restricted region are more variable than *N. bifax* for the majority of external and cranial dimensions. This is reflected in sample coefficients of variation (see Tables 1 and 2), and is evident in a bivariate plot of zygomatic breadth against greatest length of skull (Fig. 10). This does not appear to be a site effect as individuals from the same site have measurements at either end of the scatter for these characters. The significance of this, as well as the greater variation in the majority of other dimensions of *N. gouldi* is not evident at present. Until such variation is more clearly understood, it seems prudent not to test each species for statistically significant differences between character means.

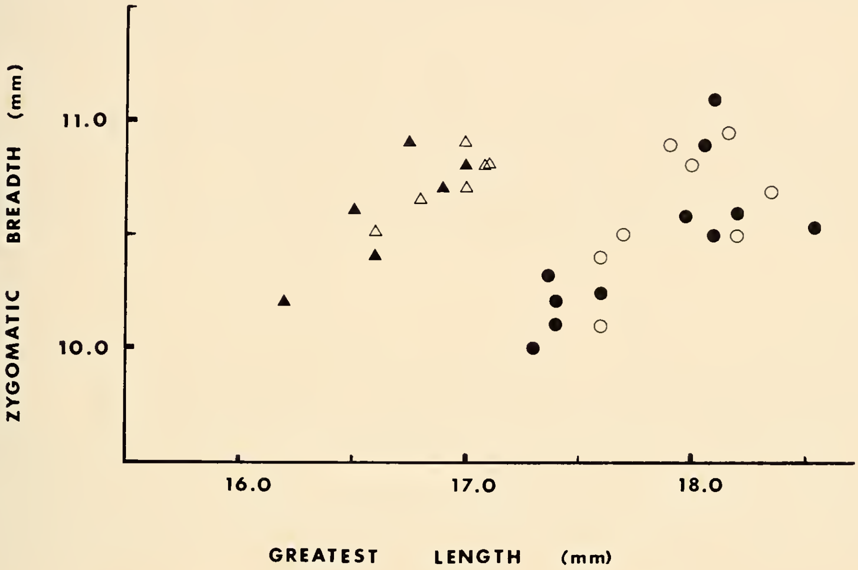

Fig. 10. Plot of zygomatic breadth (mm) against greatest length of skull (mm) for 19 *N. gouldi* (circles) and 12 *N. bifax* (triangles) from northern NSW and southeastern Qld. Males represented by closed symbols, females by open symbols.

DISCUSSION

There is little doubt that in eastern Australia, *N. gouldi* and *N. bifax* are distinct taxa. In the original description of *N. bifax*, Thomas distinguished it from *N. gouldi* by its relatively shorter ears, smaller bullae, more reduced post-nasal bump, and by the distally bifurcate baculum (compared to the simple point of *N. gouldi*). This study supports the validity of all of these criteria.

Based on specimens pooled from different localities, ranges for each species overlap for the majority of external and skull dimensions. Pooling localities, however, could obscure size differences that might exist between species at a single locality. Specimens pooled from a restricted geographic area (northern New South Wales and southeastern Queensland) were collected from a particularly diverse range of environments, but either sex of the two species could be separated using some dimensions. Adequate samples of both species from a single locality are obviously required to analyse this situation further but are not currently available.

Skulls of either sex of both species are separable on the basis of interbullae distance irrespective of locality, this character being a reflection of bullae size, a further distinguishing feature. This is significant given the extent of within-species variation and that when specimens are pooled from all localities ranges of all other dimensions examined overlap between species. This apparently reflects differences in the auditory capabilities of each species though audition in either species is little known.

As well as being broadly sympatric over a large part of their respective range, *N. bifax* and *N. gouldi* have been captured together at the same site in a number of areas. Both species were trapped at the same site in the same evening at a number of localities in northern New South Wales (Parnaby, 1986). *N. bifax* was captured frequently at near coastal localities up to 300m in elevation. By contrast, *N. gouldi* was captured in much lower numbers but at sites ranging from near sea level (such as at Broken Head Nature Reserve) to 1120m at Bar Mountain in the Tweed Range. Churchill (*pers. comm.*) captured both species at the same site in the same evening at Mt Leysham near Charters Towers, north Queensland.

I know of only three specimens of *N. gouldi* from the Atherton region, which at present represent the most northern record for this species. Cairn and Grant collected two females (AM M7024-25) from the Herberton area in 1889 while the third specimen (QM JM5381, also female) was captured in a harp trap set near a stream in dry sclerophyll forest at Atherton. Richards (1984) did not detect this species during an extensive bat survey of north Queensland rainforests, which included the Atherton region, while he found *N. bifax* to be abundant. A variety of techniques were used but he relied principally on identification of free flying bats by electronic monitoring of echolocation calls. Although more effort was concentrated on rainforest, sclerophyll forest and woodland were also sampled (Richards, *pers. comm.*). Thus *N. gouldi* appears to be uncommon in the Atherton region where it is possibly restricted to schlerophyll forest.

Electrophoretic evidence based on samples of each species taken in sympatry at several localities in northern New South Wales indicates clearly that they are good biological species. In addition, electrophoretic profiles between each species are such that hybrids between them would be readily detected (M. Adams and P. Baverstock, *pers. comm.*). However, only a small number of individuals of each species have been examined electrophoretically from areas of known sympatry.

The affinities of a number of populations variously referred to *N. gouldi*, *N. bifax* and *N. timoriensis* require clarification. Churchill *et al.* (1984) describe specimens of a *Nyctophilus* occurring sympatrically with *N. geoffroyi* and *N. bifax* from Mt Leysham, south of Charters Towers and while noting the similarity with *N. gouldi*, they were unable to allocate these animals to any known form of *Nyctophilus*.

I have examined these specimens (Queensland Museum numbers JM5248 and JM5358, not JM4361 and JM4362 as stated by Churchill *et al.* (1984), which are comparable with material from other areas of central Queensland. In view of the considerable size variation amongst *N. gouldi* from different localities, which appears to reflect local environmental conditions, there seems to be no reason for distinguishing these animals from *N. gouldi*.

A further question concerns the nature of the relationship between *N. bifax bifax* and *N. bifax daedalus*, and their distribution in north Queensland. These taxa are morphologically distinct and both could occur in the Gulf region of northwest Queensland, although sympatry has not been demonstrated. Churchill *et al.* (1984) record *N. bifax* from the Lawn Hill area. Although they did not distinguish *N. bifax bifax* from *N. bifax daedalus*, a specimen from Lawn Hill lodged by them in the Queensland Museum (JM5246) is clearly referable to *N. b. daedalus*. Of the material I have examined, the most western record of *N. bifax bifax* in Queensland is a specimen (AM M13356) from Einasleigh River (18° 11′S, 144° 00′E), west of Mt. Surprise.

McKenzie *et al.* (1977) identified a specimen of *N. bifax* from the Drysdale River National Park, northern Western Australia. They assigned this specimen (WAM M14097) to *N. b. bifax* rather than *N. b. daedalus*, on the basis of its bifurcate baculum. I have examined this specimen and believe that it is distinct from *N. b. bifax*; in bacula and dental features it is closest to *N. b. daedalus*. Thus with the possible exception of a specimen in the British Museum from Cloncurry (Thomas, 1915) which I have not examined, I am not aware of any definite record of *N. b. bifax* west of that collected from the Einasleigh River.

The status of *N. bifax daedalus* remains confused. The arrangement of Johnson (1964) is usually followed. He regarded it as the western race of *N. bifax* though its affinities have also been placed with *N. gouldi* by Troughton (1941) (as *N. timoriensis gouldi*) and Koopman (1984). Although the affinities of *daedalus* remain unclear, it does not appear to belong with *N. bifax*.

Large *Nyctophilus* from Tasmania have variously been referred to both *N. gouldi* and *N. timoriensis*. Hall and Richards (1979) record *N. gouldi* from Tasmania for the first time. The basis of this record (Richards, *pers. comm.*) is a specimen from Flinders Island, registered in the Queen Victoria Museum (reg. number 1978.1.351). In skull and baculum shape, it resembles a large version of mainland *N. geoffroyi*, and is unlike Victorian *N. gouldi*. Thus, I am not aware of any valid record in the literature of *N. gouldi* from Tasmania; the relationships of Tasmanian *Nyctophilus* require clarification.

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APPENDIX 1

SPECIMENS EXAMINED

All the following specimens have been examined by the author. A subset of these has been measured and details are available from the author.

Nyctophilus gouldi

Queensland. Atherton, 17° 16′S, 145° 29′E: 1f (JM5381); Herberton, *ca* 17° 23′S, *ca* 145° 23′E: 2f (AM M7024-25); Mt Leysham, 20° 15′S, 146° 15′E: 2m,1f (QM JM5248, JM5358, AM M12967); Finch Hatton, 21° 09′S, 148° 38′E: 1f (QM JM1113); Capella, 23° 05′S, 148° 01′E: 2m (AM M6312-13); Retro Downs Stn, Capella, 22° 52′S, 147° 54′E: 8m,1f (QM JM6184-85, JM6218-21, JM6301-03); Craigmore, 23° 55′S, 147° 53′E: 1f (QM JM2946); Blackdown Tableland, Mimosa Ck, 23° 47′S, 149° 05′E: 1f (QM JM5359); Pluto Timber Reserve, via Tambo, *ca* 25° 00′S, *ca* 147° 05′E: 1(unsexed) (CM15593); Mt Pluto, 3km E, 25° 00′S, 147° 05′E: 1m (CM4393); Mt Moffatt, 225km N of Mitchell, 25° 01′S, 147° 57′E, 1m (QM J20378); Mitchell, 26° 29′S, 147° 58′E: 1m (CM2334); Babbiloora Stn, 25° 12′S, 147° 57′E: 4m (JM5360-5363); Moolangool Stn, via Gin Gin, *ca* 24° 45′S, *ca* 151° 32′E: 2f (AM M5972, M6096(imm.)); Hervey Bay, *ca* 25° 06′S, *ca* 152° 49′E: 2f (QM JM2577, JM2596); Chinchilla, *ca* 26° 44′S, *ca* 150° 36′E: 1m,1f (AM M7634, QM J1763); Chinchilla, 32km SW, *ca* 26° 55′S, *ca* 150° 25′E: 1m (QM JM506); Conondale Rge, *ca* 26° 39′S, *ca* 152° 38′E: 1f (AM JM5364); Pomona, 26° 22′S, 152° 52′E: 1m (QM JM991); Millmerran, 27° 53′S, 151° 16′E: 1m,1f (AM M3911-12); Caloundra, 26° 48′S, 153° 08′E: 1f (QM J1762); Moggil Forest, 2f (QM JM5365-5366); Wallangara, 28° 55′S, 151° 56′E: 1m (AM M11841); Levers Plateau, NW edge, 28° 19′S, 152° 51′E: 1m,1f (AM M13411-12); North Tamborine, 27° 56′S, 153° 11′E: 1m (QM J7095); Brisbane, 27° 28′S, 153° 01′E: 1m (QM J10872).

New South Wales. Tweed River, Tyalgum 28° 22′S, 153° 12′E, 1f (AM M5450); Tweed Range, Paddys Mountain Tk, 28° 25′S, 153° 07′E: 2m (AM M13171, M13392); Tweed Range, Bar Mountain picnic area, 28° 27′S, 153° 19′E: 1m (AM M13403); Tweed Range, Airdrop Rd, 28° 24′S, 153° 03′E: 2m (AM M13393, M13406); McPherson Rge, Palm Gully area, 28° 22′S, 152° 55′E: 1m,1f (AM M13178, M13181); Tooloom, 28° 37′S, 152° 25′E: 1m,1f (CM573-574); Big Scrub Flora Reserve, 28° 38′S, 153° 20′E: 1m (AM M13243); Terania Ck, Nightcap National Park, 28° 34′S, 153° 17′E: 1f (AM M13235); Whiam Whiam State Forest, 28° 35′S, 153° 22′E: 1m,2f (AM M16029-16030, M14184); Broken Head Nature Reserve, 28° 33′S, 153° 37′E: 1m,1f (AM M13380, M13389); Woolgoolga Nature Reserve, 30° 07′S, 153° 09′E: 1m,2f (AM M13227-28, M13231); Dorrigo National Park, 30° 22′S, 152° 48′E: 2m (AM M13197-98); New England National Park, 30° 30′S, *ca* 152° 27′E: 2m,2f (AM M13200, M13202, M13208, M13213); Moree, 29° 28′S, 149° 51′E: 1f (AM M5956); Pilliga Scrub, *ca* 31° 00′S, *ca* 149° 30′E: 1m,1f (AM M5968, M8471); Pilliga Scrub, 30° 32′S, 149° 32′E: 3f (AM M16023-16025); Spear Ck, 7km E of Apsley Rv., 30° 55′S, 152° 05′E: 1f (AM M14189); Mt Boss State Forest, 31° 11′S, 152° 27′E: 4m,2f (AM M14108-M14113); Mooraduck Ck, Werrikimbie National Park, 31° 09′S, 152° 13′E: 1m (AM M12548); Doyles River State Forest, 31° 27′S, 152° 10′E: 1m,4f (AM M14114-M14118); Sea Acres Nature Reserve, Port Macquarie, 31° 28′S, 152° 56′E: 1f (AM M13434); Gloucester Tops, 3.8km WNW, 32° 02′S, 151° 34′E: 1m,3f (AM M13425-26, M13429, M13432); Upper Allyn via Eccleston, 32° 10′S, 151° 29′E: 1m (AM M9394); Canningalla Stn, 7 ml NW of Dungog, 32° 24′S, 151° 45′E: lf (AM M10002); Weabonga, 31° 13′S, 151° 19′E: lf (AM M7631); Wheogo Stn, 20km N of Dunedoo, *ca* 31° 50′S, *ca* 149° 24′E: lm,lf (AM M4284-4285); Turee, 31° 56′S, 149° 48′E: lm (AM M3746); Munghorn Gap, NE of Mudgee, 32° 25′S, 149° 50′E: 2m,2f (AM M14104-M14107); Bulahdelah, 8km SE, 32° 25′S, 152° 12′E: lm (AM M10312); Olney State Forest, 33° 06′S, 151° 18′E: 16m,10f (AM M15980-15989, M16007-16022); Anna Bay, S of Port Stephens, 32° 46′S, 152° 04′E: 2f (AM M4273, M4321); Wyong Ck, 33° 10′S, 151° 19′E: lf (CM1575); Ourimbah, 33° 22′S, 151° 22′E: lm (AM M4224); Gosford, 33° 26′S, 151° 20′E: 4f (AM M4433-4436); Ash Island, Hunter River, 32° 51′S, 151° 43′E: lm (AM M2566); Dangar Island, 33° 32′S, 151° 14′E: lm (AM M9265); Sydney area: Botany, lm (AM M2564); Carlingford, lm (AM M7618); Eastwood, lf (AM M8014); North Wahroonga, 33° 42′S, 151° 07′E: lm (AM M9191); Gymea Bay, lm (AM M7482). Hazelbrook, 33° 44′S, 150° 27′E: lm,2f (AM M3041, M3545, M3739); Lawson, 33° 43′S, 150° 26′E: lf (AM M1437); Abercrombie, Arch Cave, 33° 55′S, 149° 22′E: lf (CM2323); Jenolan Caves, 33° 49′S, 150° 02′E: lf (AM M1702); 3km S of Coco Ck Cave, Capertree Valley, *ca* 33° 08′S, 150° 10′E: lm (AM M9846); Junction of Capertree Rv. — Wolgan Rv., 33° 12′S, 150° 28′E: lm,lf (AM M11481-11482); Cob area, Culoul Rge, *ca* 33° 13′S, *ca* 150° 36′E: lm (AM M11632); Grassy Hill Tk., W of Putty Rd., *ca* 33° 22′S, *ca* 150°41′E: lm (AM M11090); Millamalong, nr. Mandurama, 33°15′S, *ca* 150° 40′E: lf (AM M3414); Pheasants Nest nr. Picton, 34° 15′S, 150° 40′E: lm (AM M11557); Campbelltown, 9km S, 34° 08′S, 150° 47′E: lm (AM M14088); Berrima, 34° 29′S, 150° 20′E: lm (AM M3436); Robertson, 34° 35′S, 150° 35′E: lf (AM M6272); Carrington Falls, 34° 38′S, 150° 41′E: lf (CM4588); Mt Keira, 34° 24′S, 150° 51′E: 2m (AM M9140, CM4587); Keiraville, 34° 25′S, 150° 50′E: lm (CM4589); Bungonia Caves, 34° 52′S, 149° 57′E: lf (AM M7638); Narooma, 36° 13′S, 150° 09′E: lf (CM1745); Jervis Bay Nature Reserve, 35° 09′S, 150° 43′E: lm,2f (AM M13438-13440); Sussex Inlet, 35° 12′S, 150° 33′E: lm (AM M14188); Araluen, 35° 39′S, 149° 49′E: lf (CM612); Mogo, 35° 47′S, 150° 09′E; lm (CM1895); 1.4km E of Wollybut Tk.. Mumbulla State Forest, 36° 33′S, 149° 52′E: lm (AM M12752); Argalong, 35° 18′S, 148° 24′E: lm (AM M4534); Tumut State Forest, 35° 22′S, 148° 12′E: lm (AM M11300); Yarrangobilly Caves, 35° 39′S, 148° 28′E: lm (CM6295); Murrumbateman, 34° 58′S, 149° 02′E: lf (CM4705); Sutton, 35° 10′S, 149° 15′E: lm (CM1457); Mt Tindery, 35° 42′S, 149° 16′E: l (CM2062); Temora, 9km W, 34° 35′S, 147° 25′E: lf (AM M11716); Temora, 15km SW, 34° 31′S, 147° 22′E: lm,lf (AM M13576-77); The Rock Nature Reserve, 35° 16′S, 147° 04′E: lm (AM M11522); Wagga Wagga, Livingstone State Forest, 35° 25′S, 147° 25′E: 2m,2f (AM M11217, M11521, M11655, M11717); Gerogery, 35° 50′S, 147° 00′E: lm (CM4029); Wahgunya State Forest, 35° 51′S, 145° 59′E: lm (AM M11494); Deniliquin, 35° 32′S, 144° 57′E: lm (MV C5159).

Australian Capital Territory. Captains Flat, 35° 35′S, 149° 27′E: lm (CM4747); Bushrangers Ck, Brindabella Rge, lm (CM4361); Canberra, 13km N, 35° 17′S, 149° 13′E: 2m (CM2382, CM2387); Lake Burley Griffith, 35° 17′S, 149° 13′E: lm,2f (CM2345, CM2386, CM2434); Black Mountain, 35° 16′S, 149° 06′E: lm (CM2077); Yarralumla, lm (CM591).

Victoria. Junction Little Bog Ck-NSW border, 37° 19′S, 149° 05′E: lm (MV C26595); Boundary Road, Wingham River, 37° 42′S, 149° 28′E: lf (C24907); Mitta Mitta, 36° 32′S, 147° 22′E: lm (CM4359); Mt Buffalo National Park, 36° 45′S, 145° 48′E; lm,3f (MV C26957-26960); Myrtleford, 24km S, 36° 45′S, 146° 44′E: lf (MV C11467); Bogong 36° 48′S, 147° 13′E: lm,lf (MV C11565-11566); Dargo, 30km NNW, 37° 11′S, 147° 12′E: 2m,1f (MV C26961-26963); Nathalia, Goulburn River, 36° 10′S, 145° 06′E: 1m (MV C25643); Mt Warby, 1.6km NNW, 36° 20′S, 146° 12′E: 2m (MV C25671-25672); Balook, 38° 26′S, 146° 34′E: 1f (MV C26952); Mt Killawarra, 36° 09′S, 146° 14′E: 1m (MV C25657); Edi, 4km WNW, 36° 38′S, 146° 24′E: 1m,3f (MV C25186-25187, C25194); Mt Macedon township, 37° 25′S, 144° 34′E: 1m (MV C7452); Daylesford area, 37° 21′S, 144° 09′E: 4f (MV C16020-16021, C16152, C26951); Maroondah Reservoir, 37° 38′S, 145° 35′E: 2m (MV C26968); Croydon, 37° 48′S, 145° 17′E: 1m,1f (MV C5419, C25476); Jindivick, 3km NNW, 38° 00′S, 145° 52′E: (MV C24907); Refuge Cove, Wilsons Promontory, 39° 03′S, 146° 28′E: 1m (MV C17129); Mt Erica, 7.1km SSW, 37° 53′S, 146° 21′E: 8m,1f (MV C25350, C25355, C25360, C25366-25367, C25372, C25374, C25386); Mt Baw Baw, 5.8km SSW, 37° 50′S, 146° 17′E: 1f (MV C25336); Willow Grove 38° 05′S, 146° 11′E: 1m (MV C25324); Nowa Nowa area, 37° 16′S, 147° 58′E: 1m,2f (MV C26093-26094, C26096); Bruthen, 8km NW, 37° 39′S, 147° 46′E: 1m,1f (MV C26965-26966); Lockup Ck, Waratah Spur Tk. 37° 24′S, 149° 06′E: 1f (MV C25905); Yalmany Rd, Roger Rv., 37° 18′S, 148° 35′E: 5m,1f (MV C25934-25939); Cooagalah block, 37° 24′S, 149° 21′E: 2m,2f (MV C25969-25972); Mt Noorinbee, 6km NNW, 37° 27′S, 149° 05′E: 1f (MV C26964); Cann River, 37° 34′S, 149° 10′E: 1m (MV C22278); Bemm River, 37° 45′S, 148° 58′E: 1m (MV C11434); Mt Ellery, 1.7km W, 37° 24′S, 148° 47′E: 1m,1f (MV C26409-26410); Teddington Reservoir, 1.5km S, 36° 52′S, 143° 16′E: 5m,6f (AM M16750, MV C26968-26978); Zumstein, 37° 05′S, 142° 22′E: 1m (MV C26967); Mt Rosea, Grampians State Forest, 37° 12′S, 142° 30′E: 1f (MV C25691); Mt Eccles National Park, 38° 05′S, 142° 00′E: 1m (MV C2605); Napier Forest, 37° 54′S, 142° 04′E: 1m (MV C23676); Otway Ranges, 38° 41′S, 143° 36′E: 3m,1f (MV C26953-26956); Grey River Scenic Reserve, nr. Kennett River, 38° 40′S, 143° 51′E: 1f (MV C25343); Irrewillipe, 38° 25′S, 143° 25′E: 1m (MV C17906).

Nyctophilus bifax

Queensland. Moa Island, 10° 11′S, 142° 16′E: 1f (MV C8800); Prince of Wales Is., *ca* 10° 41′S, *ca* 142° 09′E: 2m,1f (CM11632-34); Lockerbie Scrub, 10° 48′S, 142° 27′E: 4m,2f (CM11626-31); Carnegie Rge, Cape York, 10° 46′S, 142° 31′E: 1f (QM JM5367); Captain Billy Ck. 11° 37′, 142° 50′E: 2m,3f (QM JM5368-5372); Iron Range, 12° 43′S, 143° 19′E: 2m,1f (QM JM5373-5375); Iron Range, 12° 45′S, 143° 12′E: 4m,2f (AM M16188-16193); Archer River, 13° 27′S, 142° 57′E: 1m (QM JM5376); Archer River, 5km S, 13° 29′S, 142° 58′E: 2m,2f (AM M12958-12959, M16032-16033); Peach Ck, McIlwraith Rge, 13° 40′S, 143° 07′E: 2m,1f (QM JM5377-5379); Buthen Buthen, Cape York, 13° 21′S, 143° 28′E: 1m,2f (QM JM2429-30, JM2475); Rocky River, *ca* 13° 48′S, *ca* 143° 27′E: 1m (CM4486); Station Ck, 16km S of Coen, 14° 03′S, 143° 16′E: 2f (AM M13352, M13369); Cooktown, Jones Lagoon, 15° 26′S, 145° 10′E: 1m,1f (AM M12956-12957); Cooktown, Walker Bay, 15° 31′S, 145° 17′E: 1f (AM M12955); Bloomfield, 15° 56′S, 145° 21′E: 1m (AM M11278 imm.) Cape Tribulation, 16° 10′S, 145° 25′E: 5m,2f (AM M13344-50); Kewarra Beach, 18km N of Cairns, 16° 37′S, 145° 41′E: 1m (AM M17301); Clump Point, Tully, 17° 52′S, 146° 07′E: 1f (AM M8386); Kuranda, 16° 49′S, 145° 38′E: 2m (CM15043, QM J4409); Atherton, 17° 16′, 145° 29′E: 6m,2f (QM JM5380, JM5382, AM M13602-13605, M13611-13612); Severin Creek State Forest, Atherton Tableland, 17° 11′S, 145° 40′E: 3m,4f (AM M16183, M16185-16187, QM JM5401-5403); Wongabel State Forest, Atherton Tableland, 17° 19′S, 145° 29′E: 1m,3f (AM M16181-16182, M16184, QM JM5404); Herberton district, *ca* 17° 23′S, *ca* 145° 23′E: 1m,2f (AM M557-58, M560); Chillagoe, 17° 09′S, 144° 31′E: 1m (CM5891); Einasleigh River, Kennedy Highway, 18° 11′S, 144° 00′E: 1m (AM

M13356); Ravenshoe, *ca* 17° 36′S, *ca* 145° 29′E: lm (AM M8011); Innisfail, 17° 32′S, 146° 01′E: lm,lf (CM4834, AM M8005); Cardwell, Kirrama State Forest, *ca* 18° 10′S, *ca* 145° 40′E: lf (QM JM5383); Mt Spec, 64km N of Townsville, 18° 56′S, 146° 11′E: lf (CM4835); Palm Is., 18° 40′S, 146° 33′E: lf (QM J5274); Fanning River Stn, 19° 16′S, 146° 49′E: lm (QM JM5262); Charters Towers, 18km E, 20° 06′S, 146° 26′E: 2m (AM M13353-54); Charters Towers, Mt Leysham, 20° 15′S, 146° 15′E: lm (QM JM5384); Eungella, 21° 08′S, 148° 29′E: lm (AM M11175); East Funnell Ck, nr. Sarina, *ca* 21° 33′S, *ca* 149° 09′E: 2f (AM M7038-39); Minga Mountain, Byfield, 22° 52′S, 150° 32′E: lm (QM JM5385); Rockhampton, 23° 22′S, 150° 32′E: (QM JM5386); Hervey Bay, *ca* 25° 06′S, *ca* 152° 49′E: 2f (QM JM2571, JM2574); Noosa Heads, 26° 23′S, 153° 07′E: l(?sex) (MV M15368); Conondale Rge, *ca* 26° 39′S, *ca* 152° 38′E: lm (QM JM5387); Mt Nebo, 27° 24′S, 152° 47′E: lm (QM JM5388).

New South Wales. Reserve Ck, Murwillumbah, *ca* 29° 39′S, *ca* 150° 43′E: lm (CM4743); Billinudgel Swamp, 28° 29′S, 153° 32′E: lm,3f (AM M14090-14093); Brunswick Heads Nature Reserve, 28° 33′S, 153° 33′E: lm (AM M13388); Broken Head Nature Reserve, 28° 33′S, 153° 37′E: 5m,2f (AM M13378, M13381-83, M13385-87); Broken Head area, 28° 44′S, 153° 36′E: lf (AM M15330); Whiam Whiam State Forest, 28° 35′S, 153° 22′E: lf (AM M16031); Nightcap National Park, Terania Ck, 28° 34′S, 153° 17′E: lf (AM M13234); Big Scrub Flora Reserve, 28° 38′S, 153° 20′E: 2m,2f (AM M13240, M13247-M13249); Iluka Nature Reserve, 29° 24′S, 153° 22′E: 2m,lf (AM M13191-M13192, M13232).

Late Pleistocene Dinoflagellate Cysts from Bulahdelah, northern New South Wales

ANDREW MCMINN

(Communicated by H. MARTIN)

MCMINN, A. Late Pleistocene dinoflagellate cysts from Bulahdelah, northern New South Wales. *Proc. Linn. Soc. N.S.W.* (109(3), (1986) 1987: 175-181.

A Late Pleistocene dinoflagellate microflora has been recovered from the water bore WRC 39275 near Bulahdelah, N.S.W. Species present include *Protoperidinium* (*Protoperidinium* sect. *Quinquecuspis*) *leonis* (Pavillard), *Tuberculodinium vancampoae* (Rossignol), *Polysphaeridium zoharyi* (Rossignol), *Spiniferites mirabilis* (Rossignol), *Spiniferites ramosus* (Ehrenberg) and *Spiniferites* sp. cf. *ramuliferus* (Deflandre). This assemblage suggests a warm, nearshore, marine depositional environment.

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INTRODUCTION

A Late Pleistocene sequence was intersected in the water bore WRC 39275, which is located approximately 10km southeast of Bulahdelah, N.S.W. (Fig. 1). This sequence consists of 42m of interbedded gravels, sands and clays which can be divided into three depositional units (Fig. 2). Below 18.8m the sequence consists of fluvial lithic sands, clays and gravels, between 18.8m and 11.5m it consists of estuarine/shallow marine clay culminating in fine- to medium-grained quartz sand, and above 11.5m it is composed solely of fine- to medium-grained quartz sand of the Pleistocene Inner Barrier system (Pickett, 1983; Drury, 1982). By an analogy with nearby deposits of known age Pickett (1983) assumed the sequence to be associated with the Last Interglacial and therefore to be approximately 120,000 years old.

Four samples were investigated: from 9-11m, 14.2-18.8m, 28.0-38.8m and 40.5-40.8m. The lower three samples yielded microfloras but only one, from 14.2-18.8m, yielded a dinoflagellate cyst assemblage. This latter interval also contained foraminiferal and molluscan assemblages (Pickett, 1983). The spore-pollen component of the palynomorph assemblages is dominated by *Casuarina* (11.0-25.4%), Myrtaceae (37.5-43.0%) and *Cyathea* (10.0-29.0%); dinoflagellates comprise less than 0.5% of the uppermost assemblage and were not recovered from the underlying samples.

The samples were prepared according to standard palynological procedures, although they were not oxidized as even mild oxidation has been observed to destroy some cyst types (Dale, 1976). Palynological preparations are located in the palynological collection of the Geological Survey of N.S.W.

DINOFLAGELLATES

Fossil dinoflagellate cysts have been used extensively both to determine the age and to provide information on the depositional environments of Mesozoic and Tertiary marine sequences. Until relatively recently, however, the study of Quaternary dinoflagellate cysts has been neglected and even now is virtually restricted to the northern hemisphere. Pleistocene dinoflagellate cyst assemblages have previously been described from Great Britain (Harland and Downie, 1969; Harland, 1977; Wall and Dale, 1968; West, 1961), the North Atlantic Ocean (Harland, 1979; 1984a; 1984b), the Caribbean

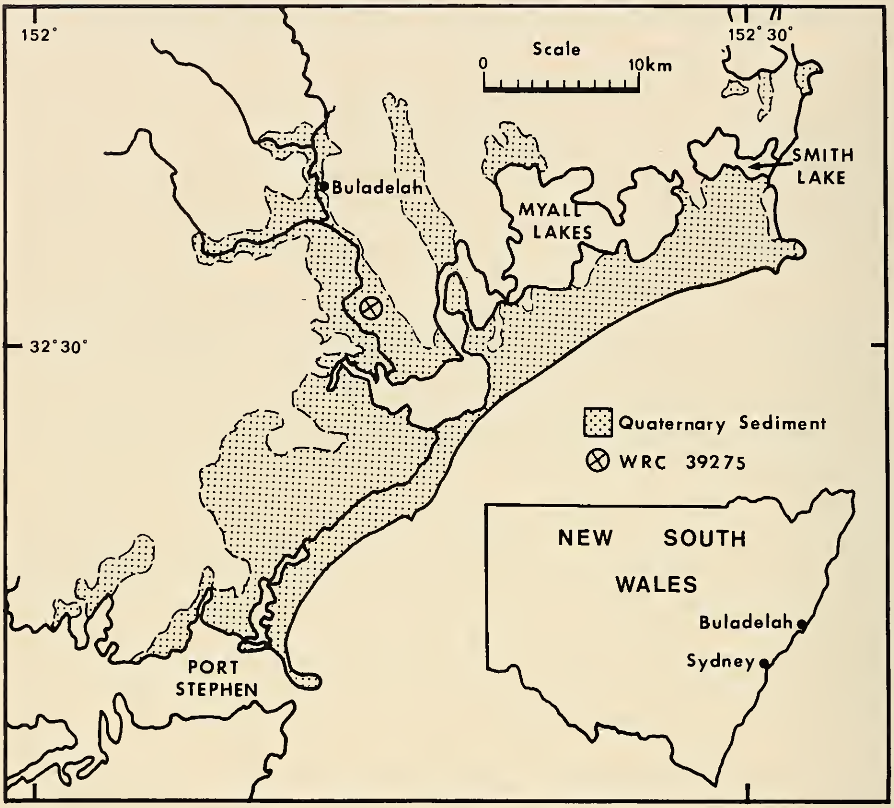

Fig. 1. Location of the bore WRC 39275 (Map reference: Newcastle 1:250 000 sheet, G.R. 5279 9865).

Sea (Wall, 1967), the North Sea (Harland *et al.*, 1978), the Black Sea (Wall *et al.*, 1973; Wall and Dale, 1973; 1974), Japan (Matsouka, 1976a; 1976b), Matsouka and Nishida, 1973), New Zealand (Wilson, 1973) and from Israel (Rossignol, 1962; 1964). There is no published account of Australian Pleistocene marine dinoflagellate cysts.

Six species, however, were recorded from Bulahdelah; these are:

Protoperidinium (*Protoperidinium* sect. *Quinquecuspis*) *leonis* (Pavillard) Balech 1974; Figs 3A-F.
Tuberculodinium vancampoae (Rossignol) Wall 1967; Figs 3**J**-**K**,**M**-**N**.
Spiniferites mirabilis (Rossignol) Sarjeant 1970; not illustrated.
Spiniferites ramosus (Ehrenberg) Mantell 1854; Figs 3**H**,**I**,**L**.
Spiniferites sp. cf. *ramuliferus* (Deflandre) Reid 1974; not illustrated.
Polysphaeridium zoharyi (Rossignol) Bujak *et al.* 1980; Fig. 3**G**.

The relative abundance of each species in the dinoflagellate assemblage is shown in Fig. 2. Absolute dinoflagellate abundance is low, being less than two cysts per gram of sediment. This compares with abundances of up to 14,000 cysts per gram in Pleistocene assemblages from Great Britain (Harland and Downie, 1969). The total number of dinoflagellate cysts observed was 54.

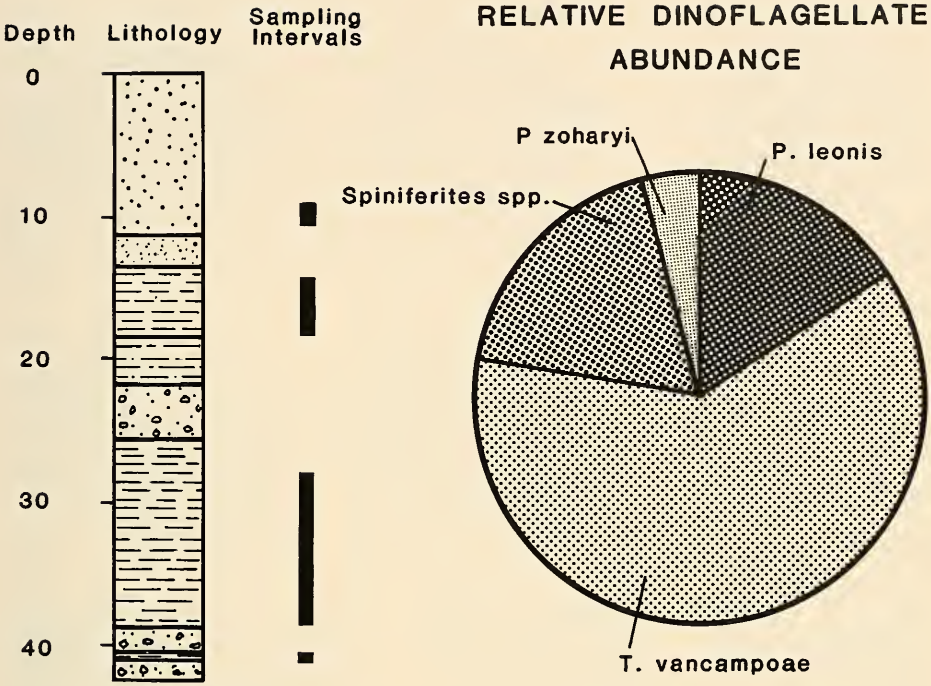

Fig. 2. Stratigraphic column, sample positions and dinoflagellate cyst abundance in the bore WRC 39275.

RECENT DISTRIBUTION OF RECORDED DINOFLAGELLATE CYSTS

Cysts of *Protoperidinium* (*Protoperidinium* sect. *Quinquecuspis*) *leonis* have been recorded from coastal areas around Great Britain, from the Caribbean and from off the coast of West Africa (Harland, 1983), and from Japan (Matsouka, 1976a). Harland (1983) suggested that this species has a tropical to temperate distribution in inner and outer neritic environments. The thecate form of this species has been recorded extensively around Australia (Wood, 1954).

Cysts of *Tuberculodinium vancampoae* have been recorded from the southern coast of eastern U.S.A., Bermuda, Bahamas, Puerto Rico, Peru and the Mediterranean Sea (Wall *et al.*, 1977), from the Persian Gulf and Red Sea (Bradford, 1973; 1975; Wall and Warren, 1969), Israel and the eastern Mediterranean Sea (Rossignol, 1962; 1964), Japan (Matsouka, 1976b; 1981; Harada and Matsouka, 1974; Shimakura *et al.*, 1971). Wall *et al.* (1977) noted that the maximum concentration of this species was in estuarine environments. Harland (1983) also observed that *T. vancampoae* was more common in tropical to subtropical areas. The highest latitude at which this cyst has been recorded is approximately 40 degrees north, in Japan. In the Australasian region the thecate form of this species (*Pyrophacus vancampoae* (Rossignol), Wall and Dale, 1971) is common in the Coral Sea and other northern seas but also extends south along the N.S.W. coastline at least as far as Sydney Harbour (new data) and Port Hacking (C. Hallegraeff, C.S.I.R.O. Marine Laboratory *pers. comm.*).

Polysphaeridium zoharyi has been recorded from Bermuda, Puerto Rico, southern coast of eastern U.S.A. and the Mediterranean Sea (Wall *et al.*, 1977), Israel and the eastern Mediterranean Sea (Rossignol, 1964; Rossignol and Pastouret, 1971), Persian Gulf and Red Sea (Bradford, 1973; 1975; Wall and Warren, 1969), the Black Sea (Roman, 1969) and Japan (Harada and Matsouka, 1974). Harland (1983) suggested that most of the reported northern European occurrences are probably misidentifications and that *Polysphaeridium zoharyi* is apparently restricted to tropical and subtropical areas. It is also apparently more abundant in estuarine and nearshore environments. In the Australasian region the thecate form of this species (*Pyrodinium bahamense* Plate 1906) has not been recorded south of New Guinea (C. Hallegraeff *pers. comm.*).

Cysts of *Spiniferites mirabilis*, *Spiniferites ramosus* and *Spiniferites* sp. cf. *ramuliferus* each have a cosmopolitan distribution. The thecate form of *Spiniferites mirabilis* and *Spiniferites ramosus* (i.e. *Gonyaulax spinifera* (Claparede and Lachmann), Diesling, 1866; Wall and Dale, 1970) is also widely distributed in the Australian region (Wood, 1954); the thecate form of *Spiniferites* sp. cf. *ramuliferus* is not known.

Discussion

The composition of the Bulahdelah assemblage bears little resemblance to any previously described assemblage. Wall *et al.* (1977) described 168 dinoflagellate cyst assemblages from a wide variety of modern marine and estuarine environments but they recorded a maximum abundance of *Tuberculodinium vancampoae*, the dominant species at Bulahdelah (66% of the assemblage), of only 11%. The unusual composition of the Bulahdelah assemblage, therefore, creates difficulties in postulating possible depositional environments. The geographically closest described Pleistocene assemblages are from the middle Pleistocene Te Piki bed, New Zealand (Wilson, 1973). These assemblages are all dominated by *Bitectatodinium tepikiense* Wilson 1973, a species usually associated with temperate and cold temperate environments and not recorded from Bulahdelah. The abundance of this species in modern environments (maximum 11% (Wall *et al.*, 1977)) does not approach that reported in the Pleistocene of New Zealand (43% to 100%). At this stage no explanation can be given for the dominance of these two species which are usually only minor elements of an assemblage.

The absence of detailed Recent cyst distribution data for the Australian region prevents a comparison of the Pleistocene Bulahdelah assemblage with modern cyst assemblages from known depositional and climatic environments; interpretations based on cyst assemblages from the northern hemisphere will of necessity rely on extrapolations. However, when those data are combined with data on the present distribution of thecate dinoflagellates in the Australasian region (Wood, 1954) it can be inferred that the Bulahdelah assemblage was deposited in a subtropical estuarine/shallow marine environment. This conclusion is consistent with results determined from foraminiferal and molluscan faunas (Pickett, 1983).

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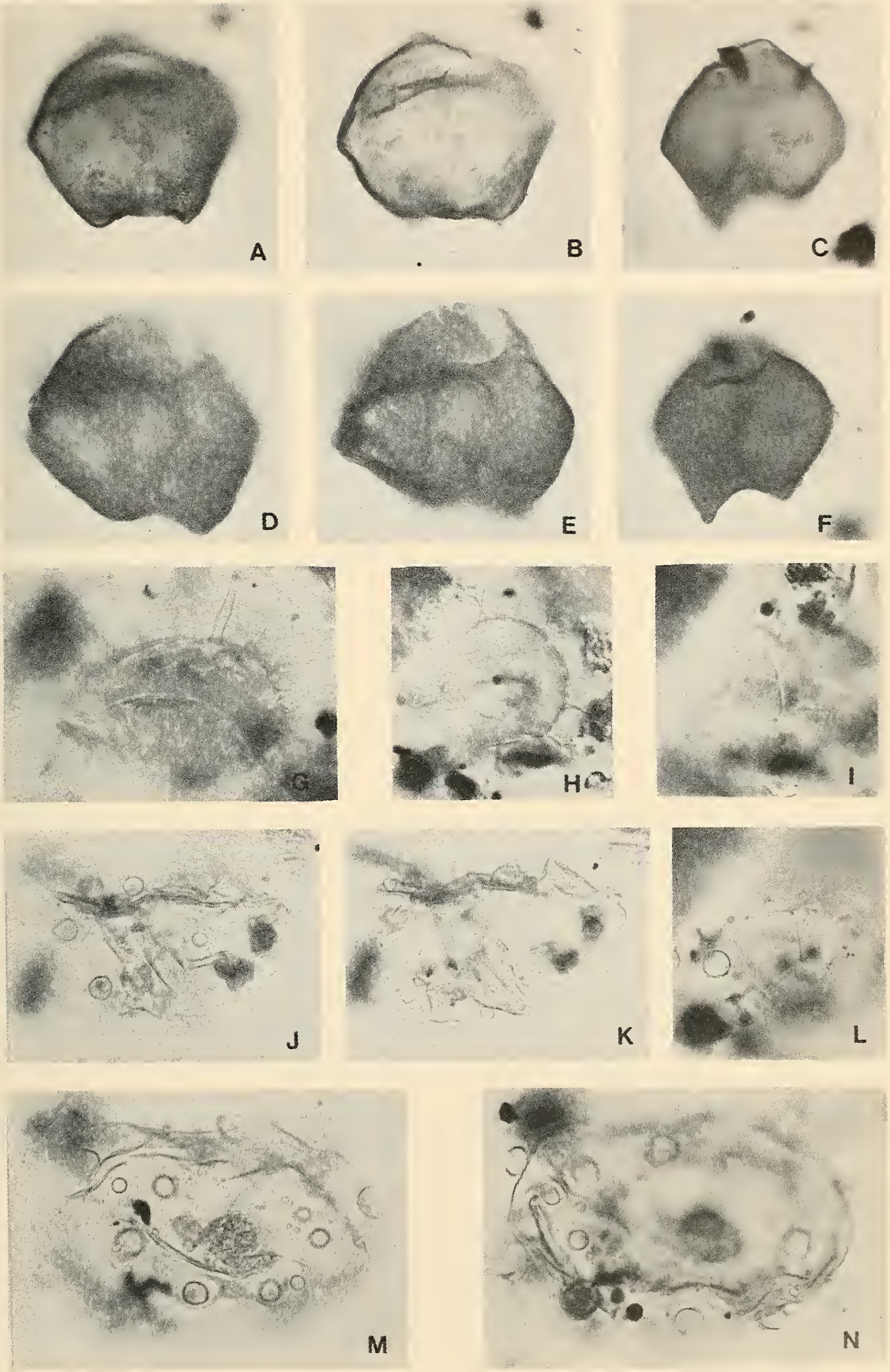
Fig. 3. **A,B** *Protoperidinium* (*Protoperidinium* sect. *Quinquecuspis*) *leonis* MMMC 01771; **C,F** *Protoperidinium* (*Protoperidinium* sect. *Quinquecuspis*) *leonis* MMMC 01772; **D,E** *Protoperidinium* (*Protoperidinium* sect. *Quinquecuspis*) *leonis* MMMC 01773; **G** *Polysphaeridium zoharyi* MMMC 01774; **H,I,L** *Spiniferites ramosus* MMMC 01775; **J,K** *Tuberculodinium vancampoae* MMMC 01776; **M,N** *Tuberculodinium vancampoae* MMMC 01777.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The echinoderm Genus *Henricia* Gray, 1840 (Asteroidea: Echinasteridae) in southern and southeastern Australian Waters, with the Description of a new Species

FRANCIS W. E. ROWE and E. LYNNE ALBERTSON

ROWE, F. W. E., & ALBERTSON, E. L. The echinoderm genus *Henricia* Gray, 1840 (Asteroidea : Echinasteridae) in southern and southeastern Australian waters, with the description of a new species. *Proc. Linn. Soc. N.S.W.* 109(3), (1986) 1987: 183-194.

Three species of *Henricia* can be identified in southern and southeastern Australian waters. These are: *H. compacta* (Sladen). *H. obesa* (Sladen), of which *hyadesi* (Perrier) is a junior synonym, and a new species, *H. kapalae*, from New South Wales. These species are herein reviewed and described.

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INTRODUCTION

Some 12 specimens of *Henricia*, collected during the 'Endeavour' Expeditions (1909-1914) from between Gabo Island, Victoria and westward to the Great Australian Bight, have been identified by H. L. Clark (1916) and echinoderm taxonomists in the Australian Museum (unpublished) as *H. hyadesi* (Perrier). Clark (1916) commented on the '. . . considerable diversity in proportions and in the spinulation . . .' of the material before him. He concluded that he was unable to recognize more than a single species, *H. hyadesi*, previously recorded from South American waters. He noted the relatively deep water from which material he had examined had been collected (91-365m) and suggested the South American and Australian *Henricia* might be distinct. Although Clark reported 11 specimens from the 'Endeavour' collections, only six of the 12 remaining in the Australian Museum collections can be confirmed, by the senior author, as having been identified by Clark. The remaining six specimens have been identified by other echinoderm taxonomists working in the Museum, who compared them with those seen by Clark.

Fisher (1940), following the examination of three of H. L. Clark's (1916) specimens, declared that the specimen from south of Gabo Island, and similarly one from east of Maria Island (Tasmania), appeared to represent *H. sufflata* (Sladen), a species described from Kermadec Islands (north of New Zealand). The third specimen, from the Great Australian Bight, appeared identifiable within a group of species including *H. compacta* (Sladen), this species having been described from New Zealand waters. Fisher did not consider any of these three specimens to be Perrier's *H. hyadesi*, a species he believed to be conspecific with *H. obesa* (Sladen).

In 1946, H. L. Clark recorded Fisher's re-identification of the three 'Endeavour' specimens. However, on re-examining those specimens, and comparing them with other material held in the Museum of Comparative Zoology at Harvard, notably two specimens of *hyadesi* from off Patagonia and a cotype of *H. compacta* var. *aucklandiae* Mortensen (1925) from New Zealand waters, Clark was unable to reach a conclusion about the 'Endeavour' specimens. He determined the best course was to leave the 'Endeavour' material identified as *hyadesi*, with the provisional note that the Great Australian Bight material probably

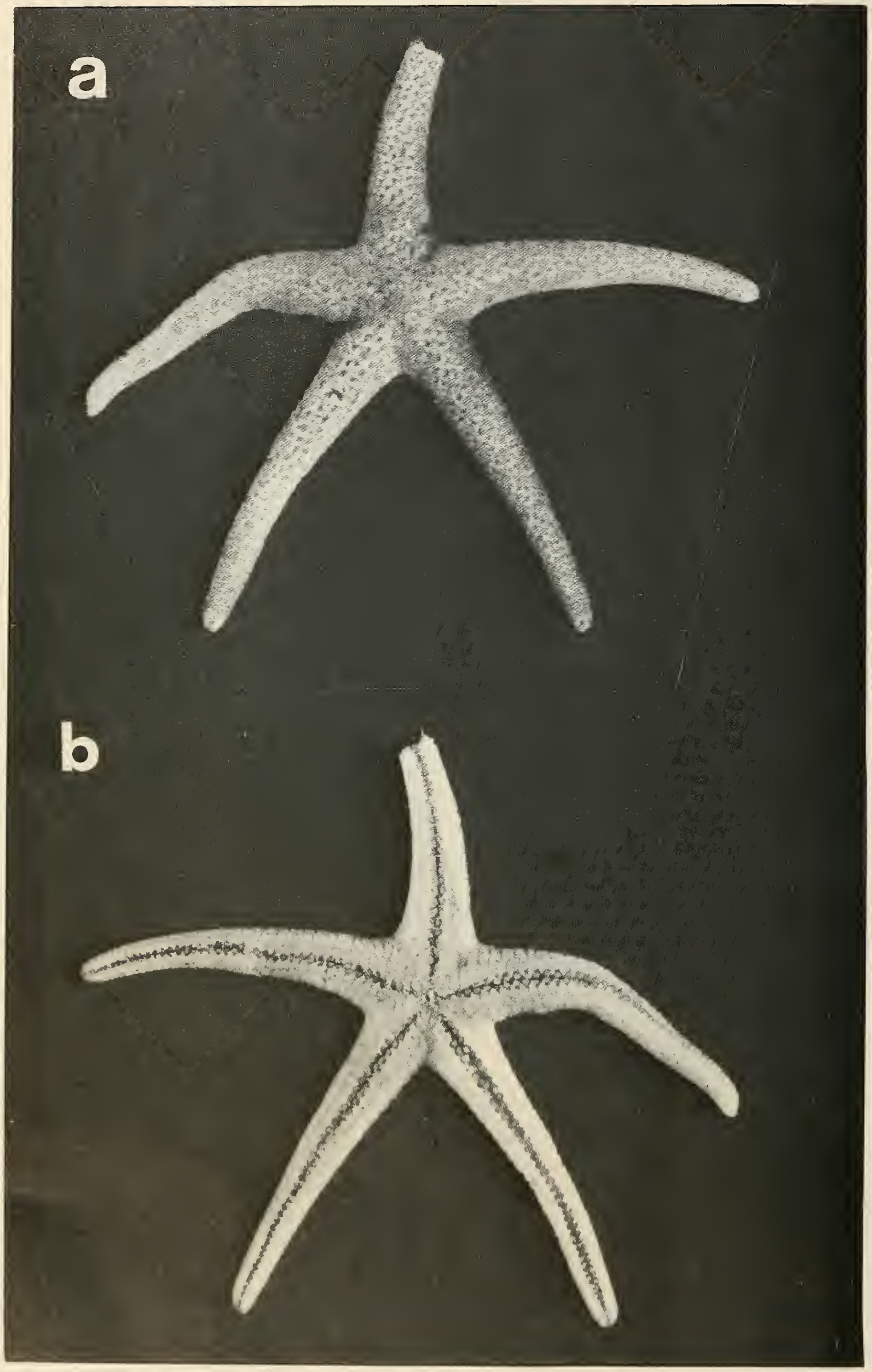

Fig. 1. Henricia compacta (holotype, BM(NH) 1890.5.7.830). a. abactinal view; **b**. actinal view. (R = 15.5mm).

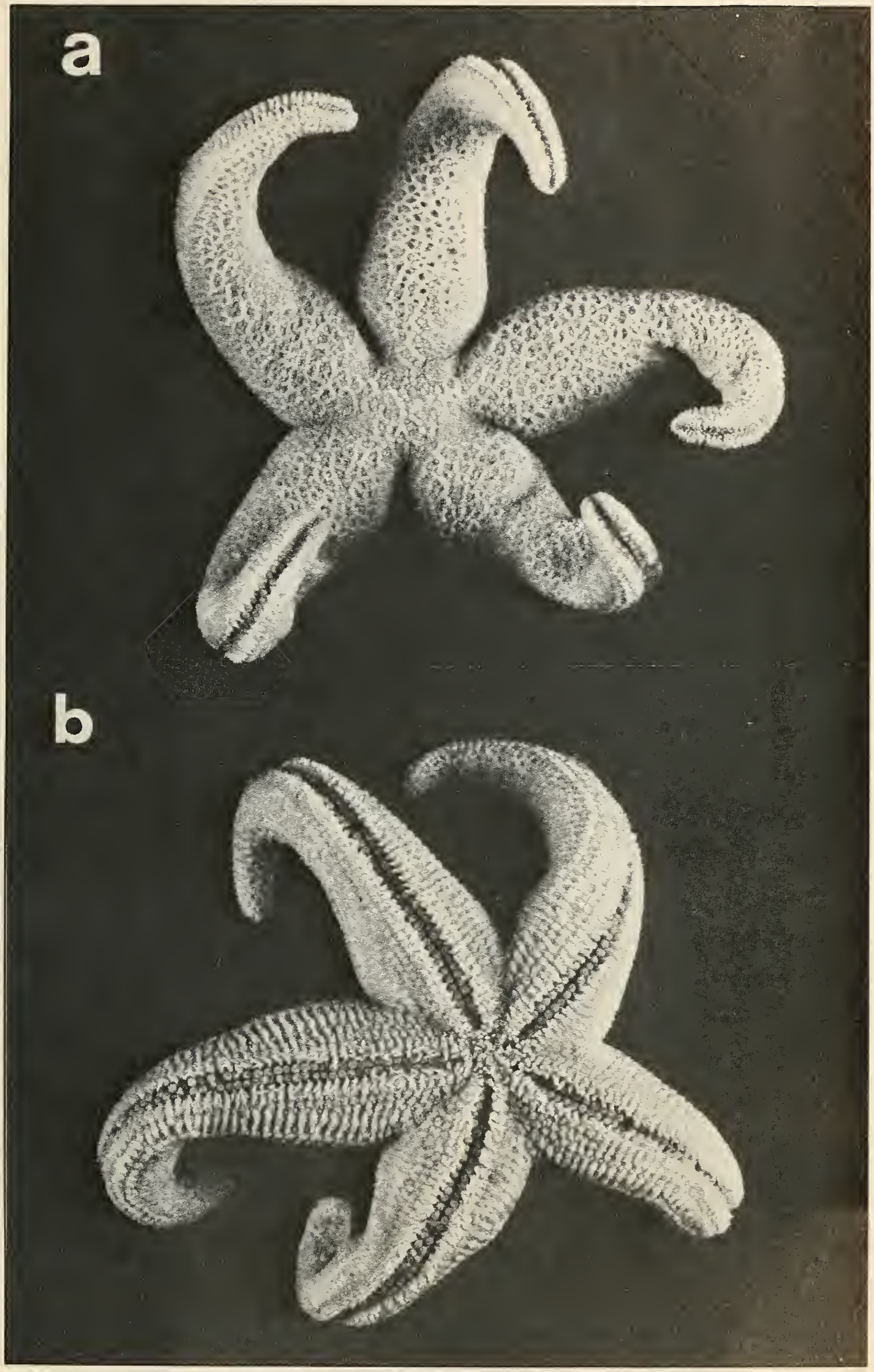

Fig. 2. Henricia obesa (holotype, BM(NH) 1890.5.7.831). **a**. abactinal view; **b**. actinal view (R = 71mm).

represented a different species from that further east in Bass Strait and off eastern Tasmania.

Fisher (1911, 1940) and Hayashi (1940) both expressed the great variability of species within the genus *Henricia*, and the extreme difficulty in satisfactorily classifying them.

According to A. M. Clark (1962), Fisher (1940) had done much to clarify the interrelationships of species within the genus *Henricia* when he grouped the Southern Ocean species into three superspecies. She (1962) noted Fisher's (1940) re-identification of three of H. L. Clark's (1916) Australian specimens of *Henricia* and accepted Fisher's (1940) synonymy of *hyadesi* (Perrier) with *obesa* (Sladen). A. M. Clark (1962) did not examine material from the Australian coast but suggested *obesa* '. . . probably occurs off the south coast of Australia'. She also provided additional information about the holotype of *H. sufflata* (Sladen).

Hayashi (1973) commenting again on the difficulty of classifying the species of *Henricia* observed that the reproductive strategy of direct development might lead to limited distribution and that '. . . this local isolation might have exerted the important influence on the differentiation of species'.

During the last decade some 250 specimens of *Henricia* have been collected from southeastern Australian waters (coast of New South Wales and eastern Victoria) during cruises of the N.S.W. State Fisheries Research Vessel 'Kapala'. These specimens have been deposited with the Australian Museum (AM) collections. This material has been examined as part of a Marine Sciences and Technologies Grants Scheme (MST) supported study of the echinoderm fauna of NSW. The material has been compared with the remaining 'Endeavour' specimens of *Henricia* held in the Australian Museum, 8 specimens from southern Australian (Victorian) waters held in the Museum of Victoria (MV), together with the holotype specimens of *H. compacta*, *H. sufflata* and *H. obesa* which are housed in the British Museum (Natural History) (BM(NH), London. Comparisons have also been made with available material of New Zealand and South American species.

As a result of this study we conclude that both *H. compacta* and *H. obesa* occur in southeastern and southern Australian waters. Additionally a new species is recognized from New South Wales. Two 'Endeavour' specimens, which were identified as *hyadesi* by H. L. Clark (1916), 16 specimens collected more recently from New South Wales waters during 'Kapala' cruises and 7 from Victorian waters have features we recognize as warranting the establishment of a new echinasterid genus. This material together with a specimen from Japan, one from Washington State (west coast of North America), (United States National Museum, Washington, D.C., U.S.A.), and two from South African waters (BM(NH)), will be dealt with by us elsewhere.

Systematic Account

Family Echinasteridae

Genus *Henricia* Gray, 1840

Henricia compacta (Sladen)

Fig. 1a-b

Cribrella compacta Sladen, 1889: 543, p. XCVI, figs 1-2, pl. XCVIII, figs 3-4.
Henricia compacta, Mortensen, 1925: 307; Fisher, 1940: 163, 164, 166; H. E. S. Clark, 1970: 4.
Henricia hyadesi, H. L. Clark, 1916: 60(part), 1946: 148(part). [Non *H. hyadesi* (Perrier) = *H. obesa* (Sladen) according to Fisher, 1940: 164].

Diagnosis: R up to 85mm, r up to 14mm, R/r = 4.4.-7.5; arms slender, tapering to a fairly acute tip; abactinal skeleton compact, plates crescentic; papular areas small, rarely contain-

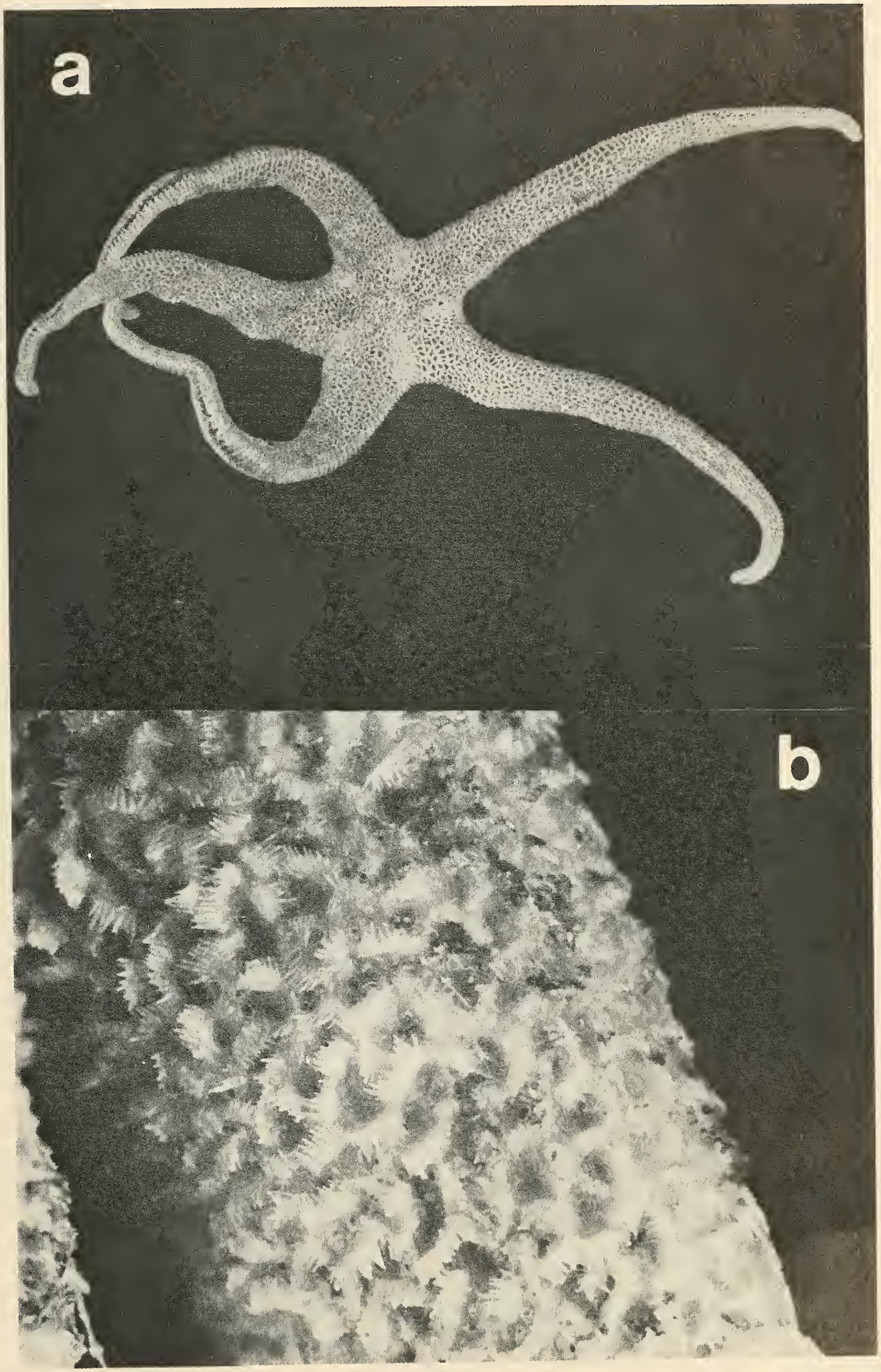

Fig. 3. Henricia kapalae sp. nov. (holotype; AM J19707). **a**. abactinal view (R = 56mm); **b**. spines on abactinal surface of ray.

ing 1-2 small accessory plates, papulae 1-3 per area; abactinal spinelets stout (up to 0.2mm long, 0.05mm wide), tapering only near the tip, terminating in a few points, up to 45 spinelets in triple, crowded rows across the plates; marginal plates not prominent unless cleaned of spines, plates quadrilobed of similar size; intermarginal plates few, extending to 3rd marginal plate in holotype (R=15.5mm) or 15th marginal plate in largest specimen (R=85mm); single row of actinal plates, extending almost to arm tip, plates squarish, with up to 35 spinelets; adambulacral plates slightly wider than long, rectangular; 2-3 furrow spines on vertical face of adambulacral plates, 2-3 prominent subambulacral spines on adradial edge of plate, behind which are 2-3 slightly smaller spines, the remainder of the plate bears up to 30-35 spinelets similar to those on the adjacent actinal plates; papulae occur between the marginal, intermarginal and inferomarginal and actinal plates along the arms.

Material examined: Holotype, BM(NH) 1890.5.7.830, 38°50′S, 169°20′E, off W coast of North Island of New Zealand, 503m; 2 specimens, AM J3075, E3773(1), Great Australian Bight, 146-274m; 1 specimen, E4716, S of Gabo Island, Victoria, 366m; 2 specimens, J19700, 58km off Mount Cann, Victoria, 205m; 2 specimens, J12886, 33°18.8′S, 127°19.3′E to 33°20.8′S, 127°29.7′E, off Terrigal, N.S.W., 300-310m; 1 specimen, J18629, 32°58.8′S, 152°41.6′E, off Newcastle, N.S.W., 1150-951m; 1 specimen, J12875, NE of Wollongong, N.S.W. 457m; 1 specimen J12863, 33°38′S, 151°57′E to 33°34′S, 152°01′E, E of Broken Bay, N.S.W., 786-805m; 1 specimen, J12860, 34°18′S, 151°26′E to 34°24′S, 151°23′E, E of Bulli (Wollongong), N.S.W. 457-476m; 2 specimens, J19701, 34°53′S, 151°08′E to 35°00′S, 151°06′E, off Lake Wollumboola, N.S.W., 412m; 1 specimen, J19699, 38°10′S, 149°52′E to 38°14′S, 149°43′E, SE of Point Hicks, Victoria, 457m; 6 specimens, J12859, 33°25′S, 152°E ′to 33°30′S, 152°07′E, off Broken Bay, N.S.W., 640m; 1 specimen, J12879, 34°18′S, 152°26′E to 34°24′S, 151°21′E, NE of Wollongong, N.S.W., 457-485m; 1 specimen, J19702, 34°28′S, 151°19′E to 34°34′S, 151°17′E, E of Port Kembla, N.S.W., 503m; 4 specimens, J12861, 34°39′S, 151°15′E to 34°32′S, 151°19′E, E of Kiama, N.S.W., 412m; 1 specimen, J12694, 33°40′S, 151°53′E to 33°46′S, 151°49′E, off Broken Bay, N.S.W., 384m; 4 specimens, J12882, 34°24′S, 151°25′E to 34°23′S, 151°25′E, SE of Sydney, N.S.W., 731-768m; 28 specimens, J13203, 33°35′S, 152°01′E to 33°32′S, 152°03′E, E of Broken Bay, N.S.W., 823m; 2 specimens J12869, 35°32′S, 150°46′E to 35°36′S, 150°43′E, E of Brush Island, N.S.W., 494m; 2 specimens, J12867, 37°48′S, 150°13′E to 33°37′S, 150°16′E, SE of Gabo Island, Victoria, 494m; 1 specimen, J19698, 38°06′S, 149°58′E to 38°00′S, 150°02′E, SE of Point Hicks, Victoria, 329m; 1 specimen, J17268, E of Nambucca Heads, N.S.W., 274m; 1 specimen, J12870, 35°32′S, 150°46′E to 35°35′S, 150°45′E, E of Brush Island, N.S.W., 503m; 5 specimens, J12881, 33°43′S, 151°46′E to 33°41′S, 151°43′E, E of Broken Bay, N.S.W., 170m; 1 specimen, J13207, 37°39′S, 159°19′E to 37°42′S, 150°18′E, SE of Gabo Island, Victoria, 731m; 19 specimens, J13193, 33°34′S, 152°02′E to 33°31′S, 152°04′E, E of Broken Bay, N.S.W., 914m; 15 specimens, J13192, 33°35′S, 152°00′E to 33°33′S, 152°02′E, off Broken Bay, N.S.W., 823m; 8 specimens, J13201(1), J17262(1), J13256(6), 34°22′S, 151°23′E to 34°19′S, 151°25′E, E of Wollongong, N.S.W., 823m; 1 specimen, J12880, 29°45′S, 153°45′E to 29°42′S, 153°46′E, off Sandon Bluffs, N.S.W., 503m; 1 specimen (eight arms), J19703, 35°02′S, 151°06′E to 34°58′S, 151°08′E, off Shoalhaven Bight, N.S.W., 439-420m; 36 specimens, J13332, 33°36′S, 152°06′E to 33°34′S, 152°08′E, E of Broken Bay, N.S.W., 914m; 3 specimens, 33°32′S, 152°06′E to 33°34′S, 152°05′E, off Broken Bay, N.S.W., 823m; 9 specimens, J13277(7), J17263(2), 33°39′S, 152°06′E to 33°37′S, 152°07′E, off Long Reef (Collaroy), N.S.W., 1006m; 6 specimens, J17265(2), J17267(4), 33°38′S, 152°02′E to 33°36′S, 152°04′E, off Long Reef (Collaroy), N.S.W., 960-988m; 1 specimen, J18618, 35°30′S, 150°52′E to 35°28′S, 150°53′E, off Brush Island, N.S.W., 933-988m.

Distribution: Southern Australia (Great Australian Bight) and Tasman Sea, from

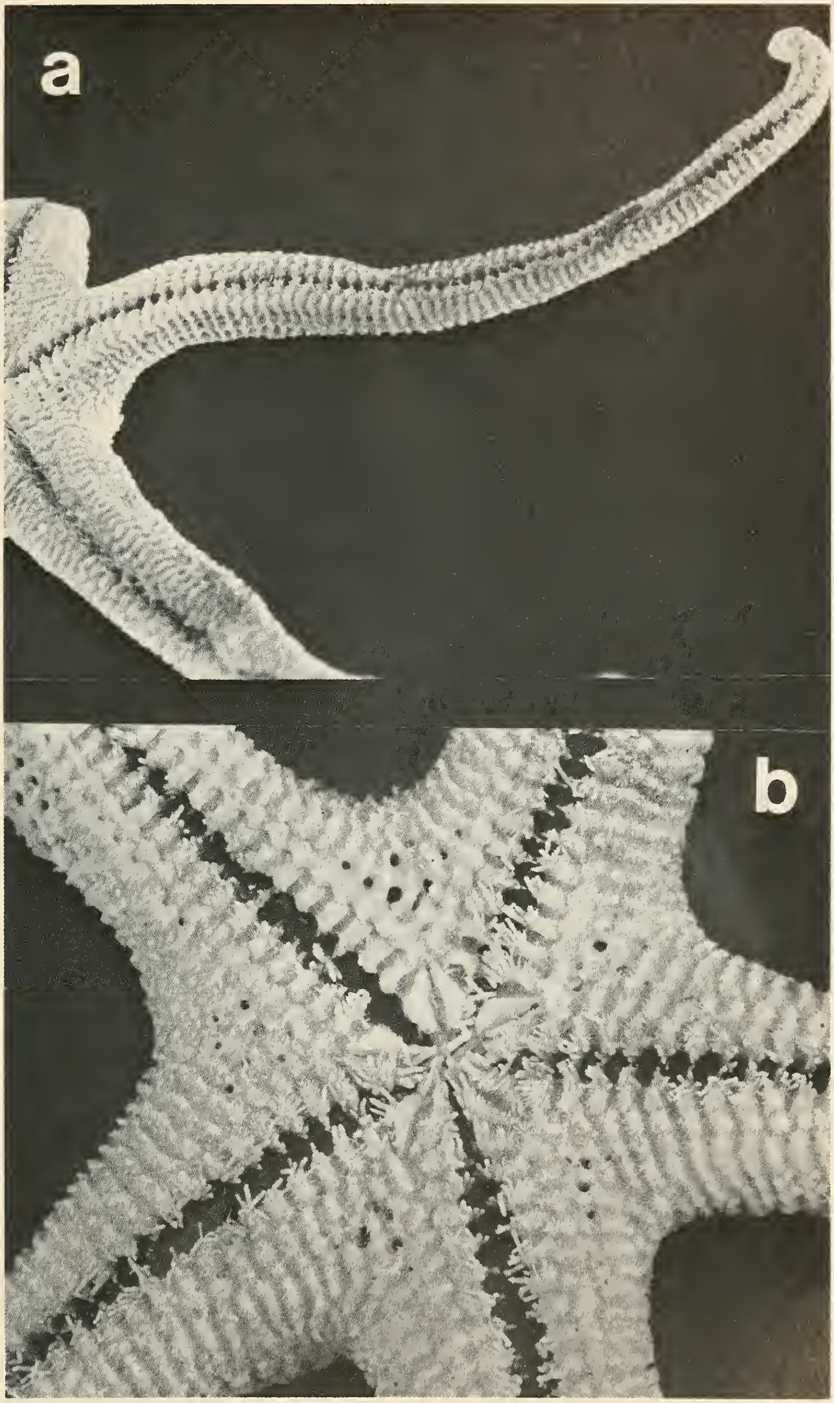

Fig. 4. Henricia kapalae sp. nov. (holotype; AM J19707). a. actinal surface and marginal plates; b. actinal surface with oral plate spine detail.

southeastern Australia (Sandon Bluffs, N.S.W. — Point Hicks, Victoria) to the west coast of New Zealand, in depths ranging from 146-1150m.

Remarks: *H. compacta* (Sladen) is based on a juvenile specimen (R=15.5mm) which Sladen considered 'sufficiently well marked to justify its being regarded as a distinct species'. He enumerated its delicate form, large plates with compact groups of numerous spinelets, small papulae areas, distinct marginals and armature of adambulacral plates as characteristic of the species. Examination of some 170 specimens in the present collection ranging from R=20-85mm has shown that the arms tend to become relatively more elongate with growth (i.e. the disc does not increase in width beyond R=c.30-40mm), that the marginal plates become less prominent beyond R=40mm and there are two (often three in larger specimens) furrow spines on the vertical face of the adambulacral plates, even in the small holotype. The relationships of this species have been discussed by Fisher (1940).

Henricia obesa (Sladen)

Fig. 2**a-b**

Cribrella obesa Sladen 1889: 544, pl. XCVI, figs 3-4, pl. XCVIII, figs 5-6.
Cribrella hyadesi Perrier, 1891: 100, pl. IX, fig. 1, pl. X, fig. 2.
Henricia hyadesi, H. L. Clark, 1916: 60(part); 1946: 148(part).
Henricia obesa, Fisher, 1940: 164; A. M. Clark, 1962: 48, figs 5n, 6a-c.

Diagnosis: R up to 100mm, r up to 14mm, R/r=4.0-5.6, rarely to 7.1; arms slightly inflated proximally, slender distally, tapering to a narrow, rounded tip; abactinal skeleton reticulate, open meshwork, 1-2 small accessory plates sometimes present in papular areas, 1-6 papulae per area; abactinal spinelets stout (0.3-0.4mm long, 0.1-0.15mm wide), rounded to slightly bulbous at the tip, terminating in many points, up to about 20 spinelets per plate, in single or double rows; marginal plates prominent in the holotype, less so in any other material without clearing of spinelets; 16-18 inferomarginal plates per 20 adambulacrals, marginal plates quadrilobed, superomarginals slightly smaller than inferomarginals; intermarginal plates, 1-3 rows proximally, reducing to one row, extending to 1/2-2/3R; two rows of actinal plates, second row extending only to 1/4R, actinal plates with up to 10 spinelets; adambulacral plates with two furrow spinelets on vertical surface; usually a single, prominent subambulacral spine on the adradial edge of the plate, behind which are 6-8 spines which decrease in size across the plate, these are arranged either 2 or 3 in single series, the remaining 4-6 spines in pairs, or all are more or less in pairs behind the innermost spine; papulae occur between the intermarginal plates and are larger and prominent between the actinal plates along the arms.

Material examined: Holotype, BM(NH)1890.5.7.831, 51°40′S, 57°50′W, Port William, Falkland Islands, 22m; 1 specimen, MV75-9, 38°44′S, 141°33′E, 30km S of Cape Nelson, Victoria, 155.4m; 2 specimens, AM E5933, 58km S of Mt. Cann, Victoria, 205m; 1 specimen, E4712, S of Gabo Island, Victoria, 365m; 1 specimen, E5031, off Babel Island, Bass Strait, 73-110m; 1 specimen, J5855, Bass Strait, trawled; 2 specimens, J8791, off Newcastle, N.S.W. trawled; 1 specimen, J19697, off Eden, N.S.W., trawled; 3 specimens, J18628, E of Gabo Island, Victoria, 402-439m; 1 specimen, J12878, 34°09′S, 151°16′E to 34°03′S, 151°21′E, E of Cronulla, N.S.W., 126-132m; 1 specimen, J13287, 34°37′S, 151°16′E to 34°44′S, 151°12′E, E of Kiama, N.S.W., 457m; 1 specimen, J12689, 34°49′S, 151°10′E to 34°56′S, 151°09′E, E of Shoalhaven Bight, 457-475m; 12 specimens, J12691, 34°53′S, 151°08′E to 35°00′S, 151°06′E, E of Shoalhaven Bight, N.S.W., 402-439m; 3 specimens, J12858, 35°38′S, 150°40′E to 35°32′S, 150°45′E, E of Brush Island, N.S.W., 393-439m; 9 specimens, J12864(6), J12876(1), J12692(2), 37°45′S, 150°12′E to 37°38′S, 150°16′E, SE of Gabo Island, 402-439m; 1 specimen, J12693, 38°10′S, 149°52′E to 38°14′S, 149°43′E, E of Cape Everard, Victoria; 1 specimen, J12690, 34°28′S, 151°19′E to

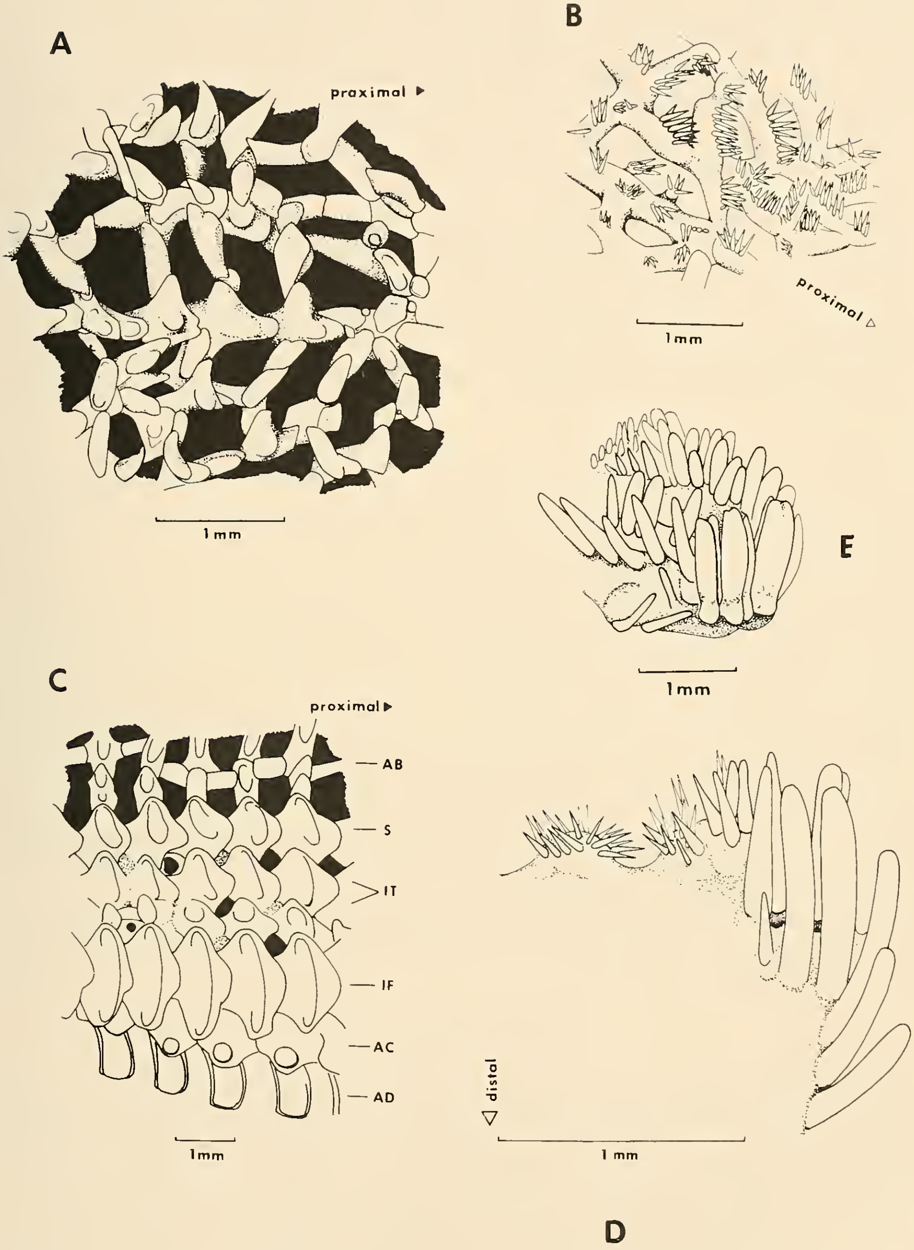

Fig. 5. Henricia kapalae sp. nov. (holotype; AM J19707). **A**. denuded abactinal plates of ray (proximal); **B**. abactinal ray spines (proximal); **C**. denuded marginal plates, from 13th to 17th inferomarginal plates. AB = abactinal plates, S = superomarginal plates, IT = intermarginal plates, IF = inferomarginal plates, AC = actinal plates, AD = adambulacral plates; **D**. adambulacral and actinal plates and spines; **E**. oral plate pair with spines.

34°34′S, 151°17′E, E of Port Kembla, N.S.W., 402m; 2 specimens, J12877, 35°29′S, 150°47′E to 35°25′S, 150°50′E, SE of Ulladulla, N.S.W., 439m; 3 specimens, J19696, 34°39′S, 151°15′E to 34°32′S, 151°19′E, E of Kiama, 412m; 4 specimens, J12872, 38°00′S, 150°02′E to 38°06′S, 149°58′E, SE of Point Hicks, Victoria, 330m; 1 specimen, J10875, 35°32′S, 150°46′E to 35°35′S, 150°44′E, E of Brush Island, N.S.W., 384m; 1 specimen, J12873, 35°36′S, 150°44′E to 35°31′S, 150°47′E, E of Bird Island, N.S.W., 604m; 3 specimens, J13195, 35°32′S, 150°46′E to 35°34′S, 150°45′E, E of Brush Island, N.S.W., 384m; 3 specimens, J12865, 35°01′S, 151°06′E to 34°58′S, 151°07′E, E of Brush Island, N.S.W., 420m; 1 specimen, J19695, 33°40′S, 151°53′E to 33°46′S, 151°49′E, off Broken Bay, N.S.W., 384m; 2 specimens, J12862, 35°32′S, 150°45′E to 35°46′S, 150°35′E, E of Brush Island, N.S.W., 219-274m; 1 specimen, J13289, 35°00′S, 151°07′E to 34°59′S, 151°08′E, off Beecroft Peninsula, N.S.W., 420m; 7 specimens; J13288, 35°02′S, 151°06′E to 34°51′S, 151°08′E, off Shoalhaven Bight, N.S.W. 365m; 3 specimens, J12857, 35°33′S, 150°45′E to 35°38′S, 150°41′E, 402m.

Distribution: Widespread in the Southern Ocean, including Tristan da Cunha (Atlantic), southern and southeastern Australia (off Newcastle, N.S.W., to Bass Strait and westward to Cape Nelson, Victoria) and Macquarie Island (south of New Zealand) in depths ranging from 22-604m.

Remarks: Comparison of the present material with the holotype of *H. obesa* leaves little doubt that it is representative of that species. Structural variation appears to be relatively slight, involving less pronounced marginal plates, the occurrence of subambulacral spines in single to double rows across the adambulacral plates, and similarly, spinelets forming single to double rows across the abactinal plates.

A. M. Clark noted (1962) that *obesa* differed from *sufflata* in its more robust abactinal skeleton, the arrangement and higher number of abactinal spinelets and in the larger size of the marginal plates relative to the adambulacral plates. Our examination of the holotype of *H. sufflata* has confirmed these differences. However, the extent of the intermarginal plates in *obesa* is greater than Clark (1962) suggests, extending in our material to at least 1/2R if not to 2/3R. We do not consider this to be of significance in determining the identity of our material. In coming to this conclusion, we therefore disagree with Fisher's (1940) identification of some of H. L. Clark's (1916) specimens as *sufflata*. In fact, H. L. Clark (1916, 1946) was substantially correct in his identification of the 'Endeavour' *Henricia* material as *H. hyadesi*, since that species is considered a junior synonym of *H. obesa* (Sladen) by Fisher (1940) and A. M. Clark (1962).

The identification of *obesa* in southern and southeastern Australian waters is now confirmed. The relationships of this species are fully discussed by A. M. Clark (1962).

Henricia kapalae sp. nov.

Figs 3a-b, 4a-b, 5A-E

Diagnosis: R=26-97mm, r=4.2-17.5mm, R/r=4.8-7.2mm, arms slender, with acute tip; skeletal reticulum relatively compact, abactinal skeletal plates with single (rarely irregularly double), webbed row of slender spinelets; marginal plates more or less distinct, inferomarginal plates twice as wide as superomarginal plates; intermarginal plates extend to 1/4R; 2 actinal rows of plates, the innermost extending to 1/4R; 2-3 spines in vertical series in furrow; 1-4 papulae per area, actinally papulae restricted to disc.

Material examined: Holotype, AM J19707, 33°39′S, 152°06′E to 33°37′S, 152°07′E, off Broken Bay, N.S.W., 990m; 16 paratypes, J19704(3), 33°35′S, 152°01′E to 33°32′S, 152°03′E, off Broken Bay, N.S.W., 450m; J19711(3), 33°30′S, 152°07′E, off Broken Bay, N.S.W., 905m; J19710(1), 33°35′S, 152°03′E, off Broken Bay, N.S.W., 823m; J19708(3), 33°39′S, 152°06′E, to 33°37′S, 152°07′E, off Broken Bay, N.S.W., 990m; J19705(1), 33°36′S, 152°06′E, off Broken Bay, N.S.W., 914m; J19709(1), 33°43′S, 151°46′E to 33°41′S, 151°43′E, off Broken Bay, N.S.W., 170m; J13323(1), 34°54′S, 151°12′E to 34°57′S, 151°11′E, off Shoalhaven, N.S.W., 540m; J18617(1), 35°29′S, 150°52′E to 35°26′S, 150°55′E, off Brush Island N.S.W., 1006m; J19679(1), 35°30′S, 150°54′E to 35°27′S, 150°55′E, off Brush Island, N.S.W., 979-1070m; J19706(1), 35°38′S, 150°40′E to 35°32′S, 150°45′E, off Brush Island, N.S.W., 393-439m.

Distribution: Between Broken Bay and Brush Island, N.S.W., in depths ranging between 170-1070m.

Etymology: Named for FRV 'Kapala' N.S.W. State Fisheries Research Vessel from which all specimens were collected.

Description: Rays 5 slender, tapering to a narrow tip, R=26-97mm, r=4.2-17.5mm, R/r=4.8-7.2, Br=4.2-17.5 (Holotype, R=56mm, r=8mm, R/r=7.0mm, Br=9mm). The disc is relatively small. The madreporite which bears small spinelets, occurs interradially, about 2/3r from the centre of the disc. Abactinal plates are irregularly bar-like to crescentic in shape, forming an irregular, relatively compact recticulum. The medial region of the plates is raised into a low ridge, which bears a single, webbed row, occasionally an irregular double row, of delicate, finely tapered spinelets. The spinelets measure up to 0.5mm in length.

There are 1-4 papulae per area abactinally. The papulae extend to the actinal surface, where they occur one per area, restricted to the disc.

Marginal plates distinct due to their regular shape and alignment. The superomarginals are much smaller and less prominent than the inferomarginals. The superomarginals are quadrilobed, about as long as wide, with a slightly oblique, actinal/abactinal directed ridge bearing spinelets. The inferomarginal plates are also quadrilobed, about twice as wide as long, and therefore twice as wide as the superomarginals. The inferomarginal plates each bear a slightly oblique ridge bearing spinelets up to 0.70mm long. The spines are usually in a single more or less uniform row but on some specimens, including the holotype, the spines occur in an irregular double row. Intermarginal plates, similar to the superomarginal plates, occur in 2-3 rows, the longest series extending to only about 1/4R. There are 25 inferomarginal plates per 20 adambulacral plates. Actinal plates occur in two rows, the first row extends only to about 1/4R, the second comprising 2-3 plates in the actinal angle. The plates are centrally ridged, and bear a group of spines, the central ones of which are the largest.

The adambulacral plates bear 2(3) stout, cylindrical spines in vertical series in the furrow. There is a single prominent, cylindrical spine on the adradial edge of the plate behind which occurs two similar spines. Behind this group of spines is a further group of three slightly shorter spines followed by up to 20 smaller, slender spines which are similar to those on the actinal and abactinal plates.

The oral plates bear the usual complement of spines.

Remarks: *H. kapalae* is immediately distinguished from *H. compacta* on skeletal morphology and spine armament, even though they show a similar shape of tapering arms. The stouter arms, shape of spinelets, fewer inferomarginal plates to adambulacral plates, less prominent marginal plates and extent of actinal papulae all serve to easily distinguish *H. obesa* from *H. kapalae*.

H. kapalae clearly falls into Hayashi's (1940) B-group of species from Japanese waters. It differs from each of those species, *H. pacifica* Hayashi, *H. aspera* Fisher, *H. ohshimai* Hayashi, *H. ohshimai acutispina* Hayashi and *H. pachyderma* in: having regularly 2 spines in vertical series in the furrow; the form of the marginal plates and spines; and spine arrangement. The very delicate, open skeletal reticulum and spine form and arrangement of *H. mutans* Koehler, from the Andaman Islands, and *H. arcystata* Fisher, from Philippine seas, excludes the identification of the N.S.W. material with either of those species.

ACKNOWLEDGEMENTS

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A new Species in the echinasterid Genus *Echinaster* Müller and Troschel, 1840 (Echinodermata: Asteroidea) from southeastern Australia and Norfolk Island

FRANCIS W. E. ROWE and E. LYNNE ALBERTSON

ROWE, F. W. E., & ALBERTSON, E. L. A new species in the echinasterid genus *Echinaster* Müller and Troschel, 1840 (Echinodermata: Asteroidea) from southeastern Australia and Norfolk Island. *Proc. Linn. Soc. N.S.W.* 109(3), (1986) 1987: 195-202.

A new species of *Echinaster*, *E. colemani*, is described from the southeastern coast of Australia between Moreton Bay, Queensland and Ulladulla, N.S.W. possibly as far south as Bass Strait, and from Norfolk Island. The relationships of *E. colemani* with the southern Australian endemic species *E. arcystatus* H. L. Clark and *E. glomeratus* H. L. Clark are discussed. The new species most likely evolved from *E. arcystatus* as a result of isolation on the east coast due to the emergence of Bass Strait during glacial periods. The most recent emergence of Bass Strait occurred 18-20,000 years ago. Distribution of *E. colemani* to Norfolk Island can only be explained by trans-Tasman larval transportation.

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INTRODUCTION

During an investigation of the echinoderm fauna of New South Wales, Lord Howe Island and Norfolk Island, a number of *Echinaster* specimens in the Australian Museum (AM) collections were examined. These specimens were without species epithet, or provisionally identified as either *E. glomeratus* H. L. Clark or *E. arcystatus* H. L. Clark. More specimens of *Echinaster* have been collected from New South Wales waters as a result of this project, which has been substantially funded by the Marine Sciences and Technologies Grant Scheme (MST). In addition, specimens from Tasman locations collected by the New Zealand Oceanographic Institution (NZOI) were examined by the senior author whilst visiting the National Museum of New Zealand, Wellington. Reappraisal of these specimens showed the occurrence of a new *Echinaster* species on the southeastern coast of Australia and at Norfolk Island. This is the first report of *Echinaster* from Norfolk Island. Table 1 lists all known species of Echinaster occurring in Australian waters with their distributions. A key is also provided for the species.

SYSTEMATIC ACCOUNT

Family Echinasteridae

Genus ***Echinaster*** Müller & Troschel, 1840

Key to Australian species of *Echinaster*

1. Abactinal spinelets large, conspicuous, up to 4-5mm long, well spaced, single, on the primary plates only, arms cylindrical.
E. callosus

1′. Abactinal spinelets smaller, <2mm long, numerous, single or in groups on primary plates, sometimes spinelets occur also on secondary abactinal plates, arms cylindrical or widened at base.
2.

2. Abactinal spinelets single, on primary plates, skeletal reticulum with relatively small papular areas, arms cylindrical or widened at the base. 3.

2′. Abactinal spinelets in small (2-4) to large (5-60) groups on primary plates, sometimes spinelets occur on secondary plates, relatively large papular areas, arms cylindrical. 6.

3. Arms cylindrical, disc small. 4.

3′. Arms widened at base, disc relatively large. *E. stereosomus*

4. 5-7 arms, autotomus, usually more than one madreporite, subambulacral spines well developed. *E. luzonicus*

4′. 5 arms, not autotomus, single madreporite, subambulacral spines not well developed. 5.

5. Abactinal and actinal spinelets include stout, chisel-shaped or club-shaped forms. *E. superbus*

5′. Abactinal and actinal spinelets uniform in size and shape, bluntly rounded at tips or truncate, some may be pitted at tip. *E. varicolor*

6. Abactinal spinelets in large discrete groups on primary plates (5-60). Papulae extend to inferomarginal line. *E. glomeratus*

6′. Abactinal spinelets in small groups on primary plates (2-4). also singly on secondary plates, papulae restricted to abactinal surface above the superomarginal line. 7.

7. Papulae 11-40 (up to about 60) per area, papular areas up to about 15.00mm diameter. *E. arcystatus*

7′. Papulae 6-8 (up to about 14) per area, papular areas up to about 6.5mm diameter. *E. colemani*

Echinaster colemani n.sp.

Figs 1**a**-**b**, 2

Diagnosis: A species of *Echinaster* with a well developed reticular abactinal skeleton; spinelets occur in groups of 2-4 on primary plates at reticular junctions and singly on secondary plates between junctions; papular areas of skeletal reticulum up to 6.5mm diameter, containing 3-14, usually 6-8 papulae; papulae occur abactinally as far as the superomarginal line.

Material examined: Holotype, AM J13076, R/r=110mm/13mm, Bate Bay, off Cronulla, N.S.W., 24.4m, rocky bottom; (14 paratypes), 1 paratype, J10862, R/r=40/8, off Moreton Bay, Qld, 76.8m; 1 paratype, J15258, R/r=85/13.5, Julian Rocks, Byron Bay, N.S.W., 24.4m; 1 paratype, J15259, R/r=43/8.4, South Solitary Islands, off Coffs Harbour, N.S.W., 27.4mm; 2 paratypes, J16541, R/r=71/10, J16534, R/r=100/13, Broughton Island, near Port Stephens, N.S.W., 18m, reef; 1 paratype, J13000, R/r=65/10.5, Broughton Island, near Port Stephens, N.S.W., 25m, on rocks; 1 paratype, J13077, R/r=92/15, off Boat Harbour, north of Cronulla, N.S.W., 39.7m; 1 paratype, J13084, R/r=75.5/13, off Cronulla, N.S.W., 30.5m; 1 paratype, J10835, R/r=80/13, Jibbon Point, Bundeena, N.S.W., 25m, sand and rubble; 1 paratype, J590, R/r=106/14.5, Newcastle Bight, N.S.W.; 1 paratype, J9182, R/r=56/12.5, Bass Point, N.S.W., 17m, bottom cover of sponge and coral; 2 paratypes J14137,

TABLE 1

Species of the genus Echinaster *occurring in Australian waters*
(H. L. Clark, 1946; L. M. Marsh, 1976; Rowe (unpublished))

Species/Author	Distribution
E. arcystatus H. L. Clark	Shark Bay, W.A. south to Waterloo Bay, Wilsons Promontory, Vict. (Endemic).
**E. callosus* von Marenzeller	Lizard Island, Qld. (Indo-west Pacific; Clark and Rowe, 1971).
E. glomeratus H. L. Clark	Abrolhos Islands, W.A., Dongarra, W.A., south to Kangaroo Island, S.A. (Endemic).
E. luzonicus (Gray)	Exmouth Gulf, W.A. north and east along the coast to Double Island Point, Qld, south to Solitary Islands, N.S.W.; offshore reefs, Rowley Shoals and Ashmore, W.A. along the Great Barrier Reef from Murray Islands south to Bunker Group, Qld. (East Indian region to islands of the south-west Pacific; Clark and Rowe, 1971).
E. stereosomus Fisher (syn. *E. acanthodes* H. L. Clark; Jangoux, 1978)	Murchison, W.A. north and east to Fraser Island, Qld, south to Brunswick Heads, N.S.W. (Philippines south to Australia; Jangoux, 1978).
E. superbus H. L. Clark	Broome south west to Dampier Archipelago (N.W. Cape). W.A. (Endemic).
E. varicolor H. L. Clark	Broome south to Esperance, W.A. (Endemic).
E. colemani n.sp.	Moreton Bay, Qld, south to Ulladulla, N.S.W., possibly to Bass Strait; Norfolk Island.

* New record based on 2 specimens held in the Australian Museum collections (AM J9674; 13096).

R/r = 137.5/18.5, 115/16.2, Ulladulla, N.S.W., 24.4m, rocky bottom; 1 paratype, ? Bass Strait, trawled (? 91-110m); 1 specimen NZOI, R/r = 137/18.5, Norfolk Island, 5-15m.

Distribution: Moreton Bay, Qld, south to Ulladulla, N.S.W., (? Bass Strait), Norfolk Island (N.E. Tasman Sea), in depths ranging from 17-40m (? possibly to 91-110m).

Description: R = 40-137mm, r = 8-18.5mm, R/r = 4.48-8.4 (av. 6.4). Arms 5, rounded in cross-section, tapering evenly to a blunt tip, though slightly constricted at the base (Figs **1a-b**). The body is covered by a thick skin. The disc is relatively small with the madreporite, which bears small spinelets, close to the interradial angle. The abactinal skeleton forms an open reticulum, the papular areas of which are more or less pentagonal and range from 3-6.5mm diameter in the specimens examined (Fig. 2). The papular areas contain 3-14 papulae, but more often 6-8 papulae. The papulae extend to the superomarginal line. Below the superomarginals groups of papula-like patches of skin occur, but these do not extend to the coelom due to a dense, fibrous tissue occluding the spaces between the plates. The primary abactinal plates at each of the 5 junctions of the pentagonal papular areas, bear groups of 2-4 small, bluntly pointed spinelets. One to four spinelets occur singly, spaced, on secondary plates delimiting the circumference of the papular areas.

Superomarginal plates are irregularly quadrilobed and bear 2-3 spinelets (1 distally on the arms). Inferomarginal plates are similarly quadrilobed, but larger than the superomarginals. They similarly bear 2-3 spinelets (1 distally). An irregular series of intermarginal plates extends to 1/5-1/4R. A number of these plates each bear a single spinelet.

Adambulacral plates are rectangular, broader than long. They bear a single, small furrow spine on the vertical surface. Across the actinal surface of the plate are 3, sometimes only 2, prominent subambulacral spines. The innermost and outermost are usually stout and cylindrical, but the middle spine may be flattened chisel-shaped towards the tip, or widened and scoop-shaped at the tip, the flattening or scooping being parallel to the furrow.

A row of actinal plates extends for about 1/5-1/4R, each plate bearing a single spinelet.

Oral plates bear 1 or 2 small furrow spinelets (where 2 are present they stand adjacent

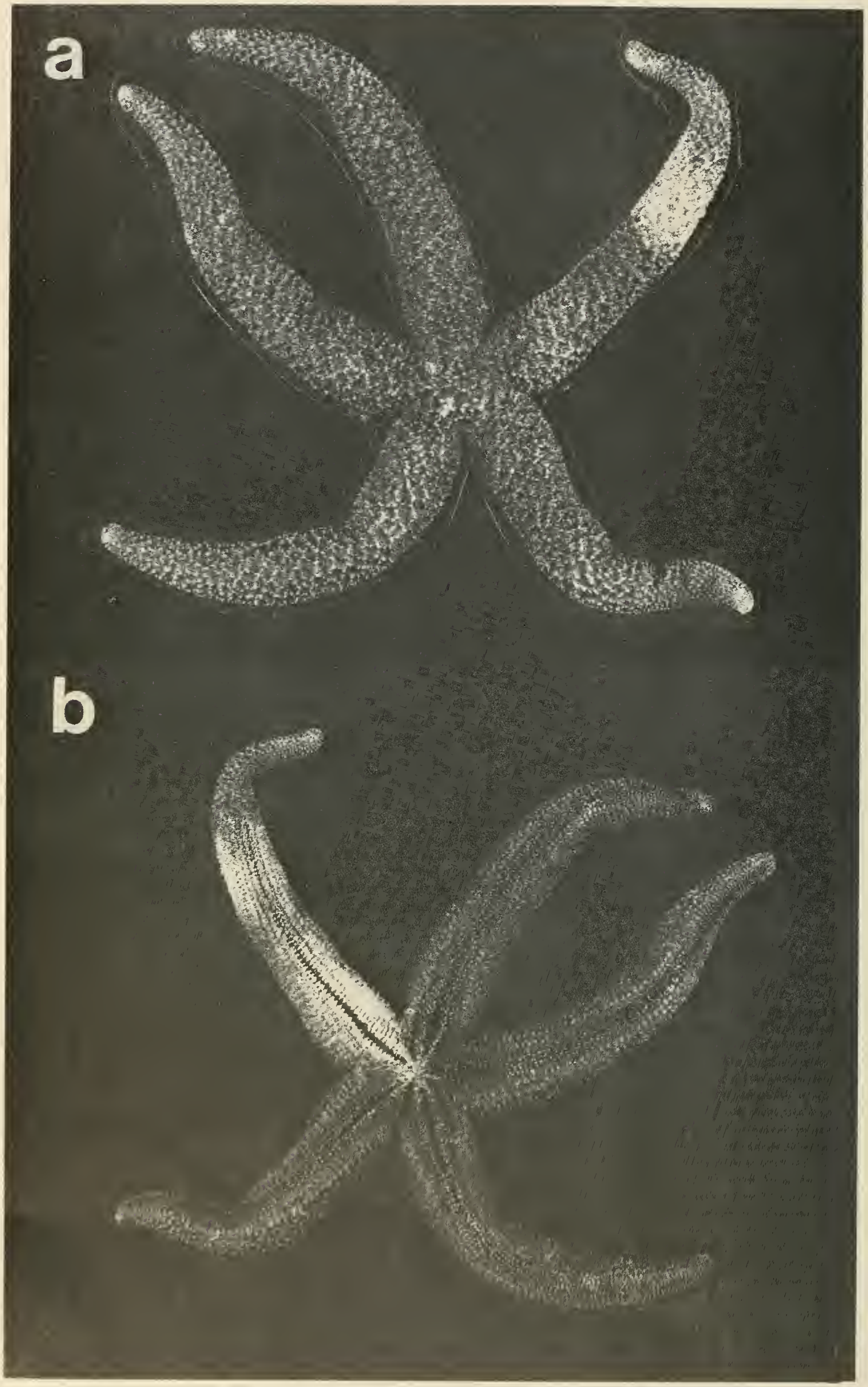

Fig. 1. Echinaster colemani sp. nov. (holotype; AM J13076). **a**. abactinal surface; **b**. actinal surface (R = 110mm).

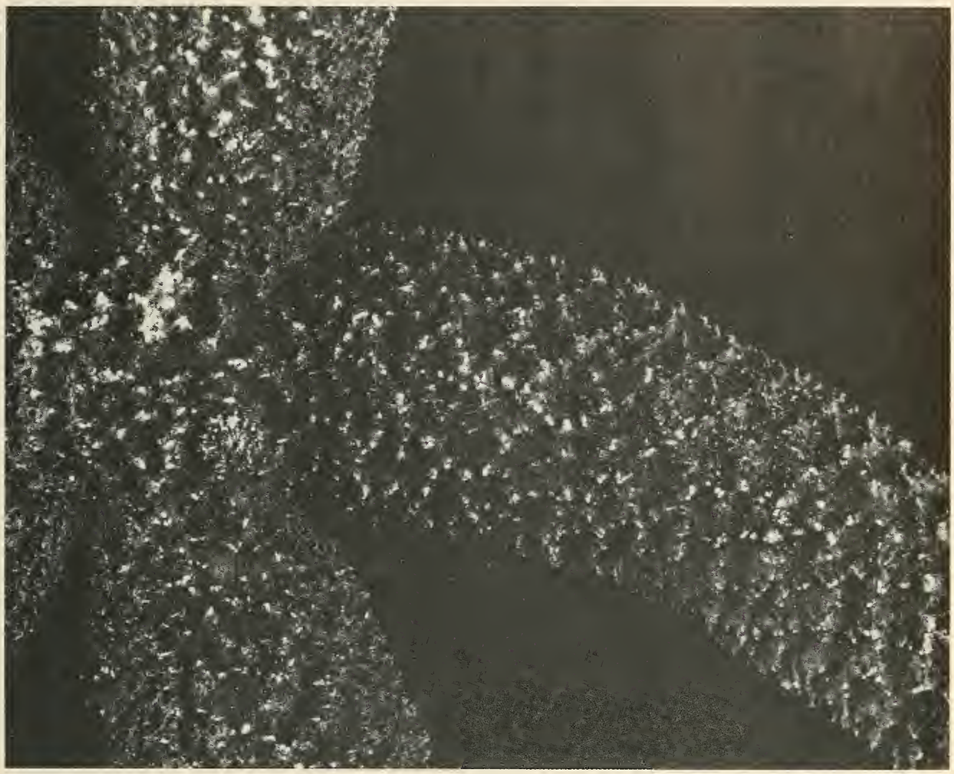

Fig. 2. Echinaster colemani sp. nov. (holotype) abactinal surface showing fine reticulation and papulae.

to one another) and 4-6 subambulacral spines. The subambulcral spines form a single or irregularly double series behind the first spine at the apex of each oral plate.

Colour: In life this species is velvet brown with purple papulae (Coleman, *pers. comm.*).

Etymology: Named for Mr Neville Coleman, who has contributed many specimens to the Australian Museum collections, including specimens of this species.

Remarks: *E. colemani* is most closely related to *E. arcystatus* H. L. Clark, 1914, (Fig. 3**a**, **b**) and *E. glomeratus* H. L. Clark, 1916, (Fig. 4). These latter species are endemic to Australia and occur sympatrically along most of the west and south coasts. All three species bear clusters of spinelets on primary abactinal skeletal plates at the reticular junctions between the papular areas. However, *E. glomeratus* is immediately distinguished from *E. colemani* and *E. arcystatus* by: its stouter abactinal skeletal spinelets, which are restricted to discrete groups of 10-20 or more (up to 60) on the primary plates (Fig. 4); the extension of papulae to the inferomarginal line; and the arrangement of its subambulacral spines. *E. colemani* and *E. arcystatus* share the restriction of papulae to the abactinal surface above the superomarginal line of plates, the occlusion of spaces between the plates below the superomarginal line, the distribution of abactinal spinelets and arrangement of subambulacral spines. *E. colemani* (Figs 1**a**-**b**, 2) differs from *E. arcystatus* (Figs 3**a**-**b**) principally in the consistently smaller size of the abactinal papular areas (up to about 6.5mm, *colemani*, up to about 15mm, *arcystatus*) and fewer papulae per area (up to 14, usually 6-8, *colemani*; up to 60, usually 11-40, *arcystatus*). The largest specimen of *colemani* known measures R=137mm; *arcystatus*

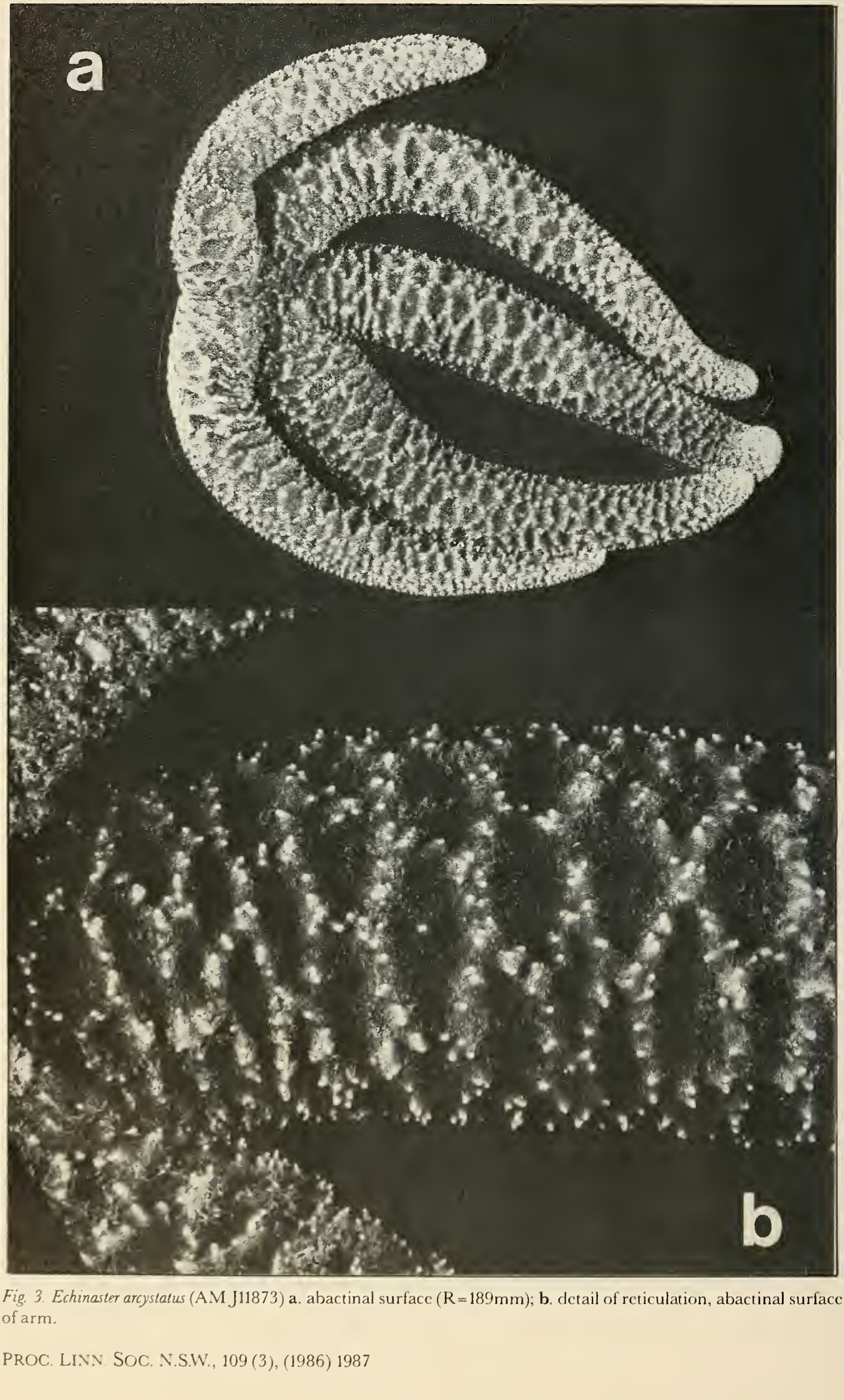

Fig. 3. Echinaster arcystatus (AM J11873) **a**. abactinal surface (R=189mm); **b**. detail of reticulation, abactinal surface of arm.

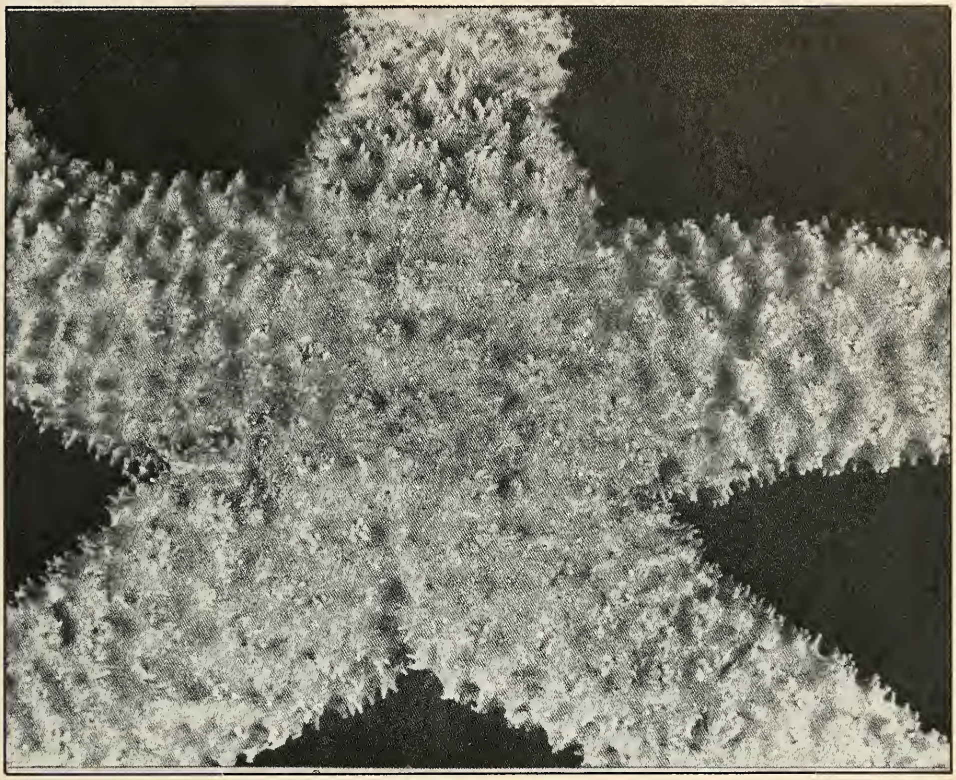

Fig. 4. Echinaster glomeratus (holotype; AM J1624) abactinal surface (R=135mm).

R=186mm. The velvet brown colour of *colemani* contrasts with the yellow/pink background colour and bright purple papulae of *arcystatus* (Coleman, *pers. comm.*).

It seems likely that *E. colemani* has evolved from *E. arcystatus*, or their common precursor, through isolation in the Tasman region, possibly as recently as 18-20,000 years ago when Bass Strait was last emergent during a glacial period. *E. arcystatus* is known to occur as far east along the south coast as Wilsons Promontory, Victoria (AM J11873).

The distribution of *E. colemani* south of Ulladulla on the New South Wales coast, however, requires confirmation. We believe there is an element of doubt regarding the Bass Strait locality attributed to the specimen (AM J8652) we identify as *E. colemani* reputedly collected during the Endeavour (1909-1914) Expedition. Since the specimen was not seen or reported by H. L. Clark (1916), it is possible that the label attached to the specimen may have been associated with it by error.

The occurrence of *E. colemani* at Norfolk Island is interesting. The reproductive strategy of *colemani* has not been determined, although its occurrence at Norfolk Island suggests a strategy involving a planktotrophic larval stage. This would facilitate dispersal across the Tasman from the coast of New South Wales in the known west to east current tracts (Rowe, 1985). The apparent absence of this shallow-water species from Lord Howe Island or other locations on the Lord Howe Ridge is perplexing. Considering the few specimens found so far, absence from such intermediate locations may be due to lack of collecting, rather than to any other agency.

In a preliminary analysis of the distributions of some 440 species which we identify as occurring on the coast of New South Wales, no fewer than 54 species (12.3%) occur either at Norfolk Island and/or Kermadec Islands and New Zealand, but not on the Lord Howe Ridge. Of these only 8 occur in shallow water (<30m), 13 occur across the continental shelf (31-200m) and the remaining 33 occur on the slope and deeper (201+m). Shallow-water species which share with *E. colemani* a distribution along the New South Wales coast and at Norfolk Island are the southern Australian asteroid species *Austrofromia polypora* and crinoid species *Antedon incommoda*. The echinoid species *Phyllacanthus parvispinus* is distributed along the New South Wales coast and occurs at the Kermadec Islands, whilst the southern Australian asteroid species *Allostichaster polyplax*, the ophiuroid species *Ophiopeza cylindrica* and holothurian species *Chiridota gigas* are known also from the coast of New South Wales and in New Zealand waters.

In discussing the distributions of species of *Asterodiscides*, Rowe (1985) suggested that populations of the southern and southeast Australian species *A. truncatus* (Coleman), which also occurs only at the Kermadec Islands and New Zealand region, might be self-sustaining and relatively phenotypically stable in their northeastern Tasman locations. He considered it is difficult to determine whether larval input was maintaining gene flow across the Tasman, despite the occurrence of appropriate current tracts. Only further sampling along the Lord Howe Ridge and in deeper waters of the Tasman Sea, together with detailed studies of reproductive strategies of these echinoderms, will help to elucidate these apparently disjunct distributions.

ACKNOWLEDGEMENTS

Mr Neville Coleman is acknowledged for his contribution of specimens to the echinoderm collections and for bringing the species, described herein, to the attention of the senior author. The senior author also wishes to thank Vicki Harriott, Lyle Vail and Anne Hoggett for their collecting effort and earlier association with his project; Dr W. del Main (New Zealand Oceanographic Institute) for the opportunity to examine the NZOI collections and Dr A. N. Baker (National Museum of New Zealand) for providing facilities and discussions on the echinoderm collections in the NMNZ. Mr W. Zeidler, South Australian Museum, is thanked for the loan of specimens of *Echinaster arcystatus*. Finally, Marine Sciences and Technologies Grants Scheme is acknowledged by the senior author for its generous support of this project (MST: 84/2092).

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Two new Species of *Delma* (Lacertilia: Pygopodidae) from northeastern Queensland and a Note on the Status of the Genus *Aclys*

GLENN M. SHEA
(Communicated by H. G. COGGER)

SHEA, G. M. Two new species of *Delma* (Lacertilia: Pygopodidae) from northeastern Queensland and a note on the status of the genus *Aclys*. *Proc. Linn. Soc. N.S.W.* 109(3), (1986) 1987:203-212.

Delma mitella sp. nov. and *Delma labialis* sp. nov. are described from two specimens each from northeastern Queensland. The new species are diagnosed on the basis of size, coloration and rostral scale shape. Records of *D. inornata* from northeastern Queensland are rejected. *Aclys* is diagnosed by two derived character states and, in the absence of a diagnosis for *Delma* that adequately demonstrates monophyly, retained as a genus distinct from *Delma*. A key to the *Delma* of Queensland and updated distribution maps are provided.

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Since the publication of Kluge's (1974) monograph of the Pygopodidae, only three new pygopodids have been described: *Pletholax gracilis edelensis* Storr, 1978, *Aprasia haroldi* Storr, 1978 and *Aprasia rostrata fusca* Storr, 1979[1]. This would suggest that knowledge of the alpha taxonomy of the family is nearly complete. The discovery of two spectacular new species of *Delma* with restricted known ranges in northeastern Queensland, described below, indicates that this is not the case.

I have followed the definitions of Kluge (1974) for measurements and body scalation, with the addition of head length, from tip of snout to rostral margin of ear, and hindlimb length, from junction of limb flap with body to distal tip of flap. The head length measurement of Kluge (1974) is here given as mouth length. The descriptions give measurement, in millimetres, followed in parentheses by the value of each measurement as a percentage of snout-vent length in the case of head length, hindlimb length and tail length, or as a percentage of head length, in the case of cephalic measurements. Measurements are linear, to the nearest 0.5mm for non-cephalic characters and to the nearest 0.05mm for cephalic characters.

Although the head shield characters defined and employed by Kluge (1974) are 'homologous quantitative characters' in terms of the reference points, they are not independent, with changes in one scale frequently affecting several characters, and do not fully describe the variation in individual scale morphology occurring between species. The stability of many head shields in *Delma* species allows the more conventional nomenclature used here. Rostral, rostral supranasal, caudal supranasal, postnasal, prefrontal, frontal, supraocular, parietal, occipital and upper temporal scales are labelled in Fig. 1. Supralabial, infralabial, nuchal and gular scale definitions follow Kluge (1974). Loreals are those scales bordering the dorsal margin of the supralabials, from the caudal margin of the postnasal up to and including the first scale contacting the enlarged subocular supralabial. Supraciliaries are those scales bordering the lateral margin of the supraoculars, from the scale contacting prefrontal to that contacting parietal. Preoculars are those small scales

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[1] Of the three species named by Wells and Wellington (1985), *'Delma wollemi'* and *'Pygopus territorianus'* are *nomina nuda* while *'Pygopus klugei'* is of uncertain status. *'P. klugei'* was differentiated from *P. nigriceps schraderi* on the basis of distinctly keeled body scales and a habitat restriction to black soil plains (*vs* smooth scales and red sand plains), and was described from a single specimen. However, Kluge (1974) included numerous specimens from black soil plains in his redescription of *P. n. schraderi*, only one of which had keeled scales.

between loreals, prefrontal, supraciliaries and the bony margin of the orbit, while suboculars are those scales bordering the dorsal margin of the subocular supralabial, but not contacting the preceding or succeeding supralabials.

Head shields are numbered rostrad to caudad, while longitudinal scale rows on body and tail are numbered from the dorsal midline.

Delma mitella sp. nov.

Figs 1,2

Holotype: Queensland Museum J32597, Herberton area, Qld. R. Russel.
Paratype: Australian Museum R65264, Koombooloomba rd, near Ravenshoe, Qld. T. Bentz, 19.xi.1967.

DIAGNOSIS: *D. mitella* differs from all other *Delma* species in its greater size (to 154mm SVL *vs* to 133mm, with only *D. fraseri*, *D. grayii*, *D. inornata* and *D. plebeia* attaining more than 115mm), almost straight or concave suture between rostral and rostral supranasals (*vs* obtusely gabled apex of rostral partly projecting between rostral supranasals) and presence of a dark line along fifth scale row from caudal body to tail, sharply demarcating dark dorsal and lateral surfaces from light ventral surface.

DESCRIPTION OF HOLOTYPE: Rostral barely projecting between rostral supranasals; rostral supranasal in broad contact with first supralabial; caudal supranasals present, in point contact with nostril; postnasal single; loreals five, subequal; preoculars nine (left) or ten (right); suboculars three, third elongate; supraciliaries five, caudalmost large and in line with preceeding series; supraoculars two, first longer; supralabials six, fourth below centre of eye, caudalmost low and elongate; infralabials seven, first pair narrowly separated on ventral midline, second pair widely separated; occipital present; upper temporals two; nuchal scales 13; gular scales 14.

Midbody scales 16; ventral scales 74; ventral body scales transversely enlarged; preanal scales three; hindlimb scales five.

Snout-vent length 150.5; head length 14.75 (9.8); mouth length 12.30 (83.4); snout length 6.35 (43.1); eye width 1.90 (12.9); postorbital length 3.85 (26.1); head width 8.60 (58.3); head depth 6.80 (46.1); rostral depth 1.35 (9.2); rostral width 2.95 (20.0); dorsal rostral length 0.90 (6.1); ventral rostral length 1.80 (12.2); hindlimb length 4.5 (3.0).

COLORATION (IN PRESERVATIVE): Dorsally and laterally mid-brown. Head slightly darker, with four narrow pale bands, irregular edged with black: first across head from third supralabial and rostral margin of orbit; second across head from fifth supralabial (where most prominent) and caudal margin of orbit; third from cranioventral margin of ear, along cranial margin of ear and across nape; fourth (very weakly defined) across nape a little way caudal to ear. Head markings do not extend ventral to supralabials.

Ventrally yellow-blue to light green, more yellow on throat, more blue ventrolaterally and on tail. A narrow dark blue-grey stripe sharply differentiating lateral from ventral surfaces, composed of small flecks on body, coalescing to a distinct stripe on fifth scale row of caudal half of body and tail.

VARIATION IN PARATYPE: Loreals four; preoculars seven; an additional subocular caudal to elongate third on right side; upper temporals fused into single scale on right side; first infralabials in contact; second infralabials moderately separated; nuchal scales 12; gular scales 15.

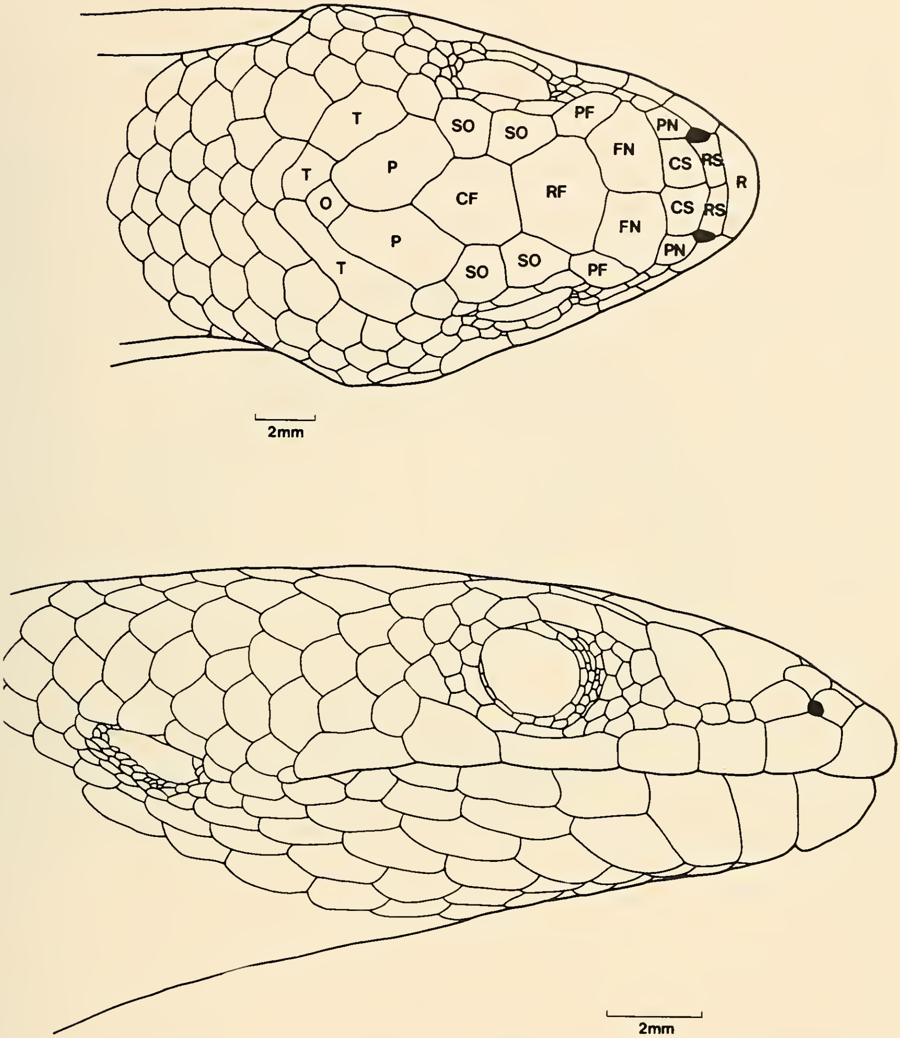

Fig. 1. Head shields of *Delma mitella*. Paratype (above) in dorsal view, holotype (below) in lateral view; CF = caudal frontal, CS = caudal supranasals, FN = frontonasals, O = occipital, P = parietals, PF = prefrontals, PN = postnasals, R = rostral, RF = rostral frontal, RS = rostral supranasals, SO = supraoculars, T = upper temporals.

Ventral scales 70; hindlimb scales four (left) or three (right); pair of ventral scales preceding preanals fused into a single v-shaped scale.

Snout-vent length 154; head length 15.50 (10.1); mouth length 13.90 (89.7); snout length 6.40 (41.3); eye width 2.10 (13.5); postorbital length 4.45 (28.7); head width 11.30 (72.9); rostral depth 1.45 (9.4); rostral width 3.50 (22.6); dorsal rostral length 0.85 (5.5); ventral rostral length 1.70 (11.0); hindlimb length 8.0 (5.2).

Coloration as for holotype, but fourth light head band almost absent.

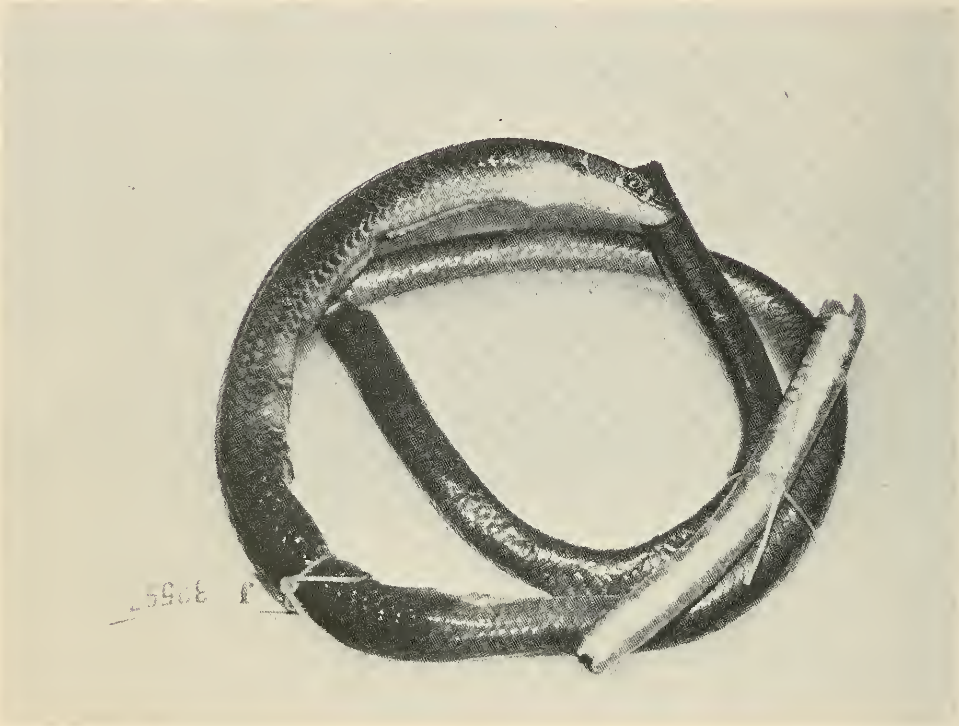

Fig. 2. Holotype of *Delma mitella.*

COLORATION (IN LIFE): A colour photograph of *D. mitella* appears on a Queensland National Parks and Wildlife Service poster, 'Reptiles of Queensland'. The specimen illustrated has body red-brown dorsally and laterally, the lateral margins of the scales slightly paler, producing an indistinct series of stripes similar to those reported for *D. inornata* (Thompson, 1980). Head dorsum mid-brown, slightly darker than body, with four narrow, irregularly black edged cream bands. Venter yellow on body and throat, but cream ventrolaterally on lips and neck, becoming blue-white ventrolaterally on body.

Iris black.

COMPARISON WITH OTHER SPECIES: *D. mitella* is a member of a group of *Delma* species possessing two pairs of supranasal scales, first supralabial distinct from rostral supranasal, fourth supralabial below centre of eye, a mode of 16 midbody scales, enlarged ventral body scales and three preanal scales. Other members of this group are *D. borea*, *D. fraseri*, *D. grayii*, *D. inornata* and *D. nasuta*.

In addition to the characters given in the diagnosis, *D. mitella* may be differentiated from *D. borea* by having 4-5 loreals (*vs* usually three), from *D. grayii* and *D. inornata* by the caudal supranasal contacting or narrowly separated from nostril (*vs* broadly separated), from the nearest populations of *D. nasuta* by its much blunter snout and lack of dark spots dorsally and ventrally on the body and from *D. fraseri* by lacking dark markings on the throat.

HABITS AND HABITATS: The paratype was found dead on road at 1905hrs.

ETYMOLOGY: The specific epithet is from the Latin *mitella*, a bandage on the head, sometimes worn to counteract the effect of wine, in allusion to the characteristic head markings of this species.

Delma labialis sp. nov.

Figs 3,4,5

Holotype: QM J45563, Paluma turnoff on Bruce Hwy, north of Townsville, Qld, in 18°59′S 146°18′E. G. V. Czechura, S. K. Wilson, 13.iv.1985.
Paratype: QM J30265, Magnetic Island, Qld. T. Low, viii.1976.

DIAGNOSIS: *D. labialis* differs from all other *Delma* species in having a lip and lateral neck pattern of alternating mid-brown and cream bars, and a dark brown stripe on the third scale row on caudal body and tail, separating dorsal from lateral surface.

DESCRIPTION OF HOLOTYPE: Rostral with obtuse apex, distinctly penetrating between rostral supranasals; rostral supranasal in moderate contact with first supralabial; caudal supranasals present, in broad contact with nostril; postnasal single; loreals four, subequal; preoculars eight (left) or ten (right); suboculars six (left) or four (right), subequal; supraciliaries five, caudalmost only slightly larger and lying medially to others; supraoculars two, first longer, second (right) divided into lateral and medial scale; supralabials six, fourth below centre of eye, caudalmost subequal to penultimate; infralabials six, first pair in broad contact on ventral midline, second pair moderately separated; occipital present; upper temporals two; nuchal scales 16; gular scales 18.

Midbody scales 16; ventral scales 72; ventral body scales transversely enlarged; preanal scales three; hindlimb scales three.

Snout-vent length 103.5; tail length 408.0 (394); head length 12.10 (11.7); mouth length 9.35 (77.3); snout length 4.95 (40.9); eye width 1.70 (14.0); postorbital length 2.05 (16.9); head width 6.65 (55.0); head depth 5.60 (46.3); rostral depth 1.20 (9.9); rostral width 2.35 (19.4); dorsal rostral length 0.70 (5.8); ventral rostral length 1.25 (10.3); hindlimb length 4.5 (4.3).

COLORATION (IN PRESERVATIVE): Dorsally and laterally mid-brown. Head slightly more yellow-brown. A series of alternating cream and mid-brown bars on lips and laterally on neck from caudal margin of orbit to cranial third of body. A narrow dark grey stripe along centre of third scale row from caudal third of body to proximal half of tail.

Ventrally immaculate cream.

VARIATION IN PARATYPE: The paratype is very desiccated and the scalation difficult to determine in places, but definitely differs from the holotype in having five infralabials on the right side (six on left); 18 midbody scales and 71 ventral scales.

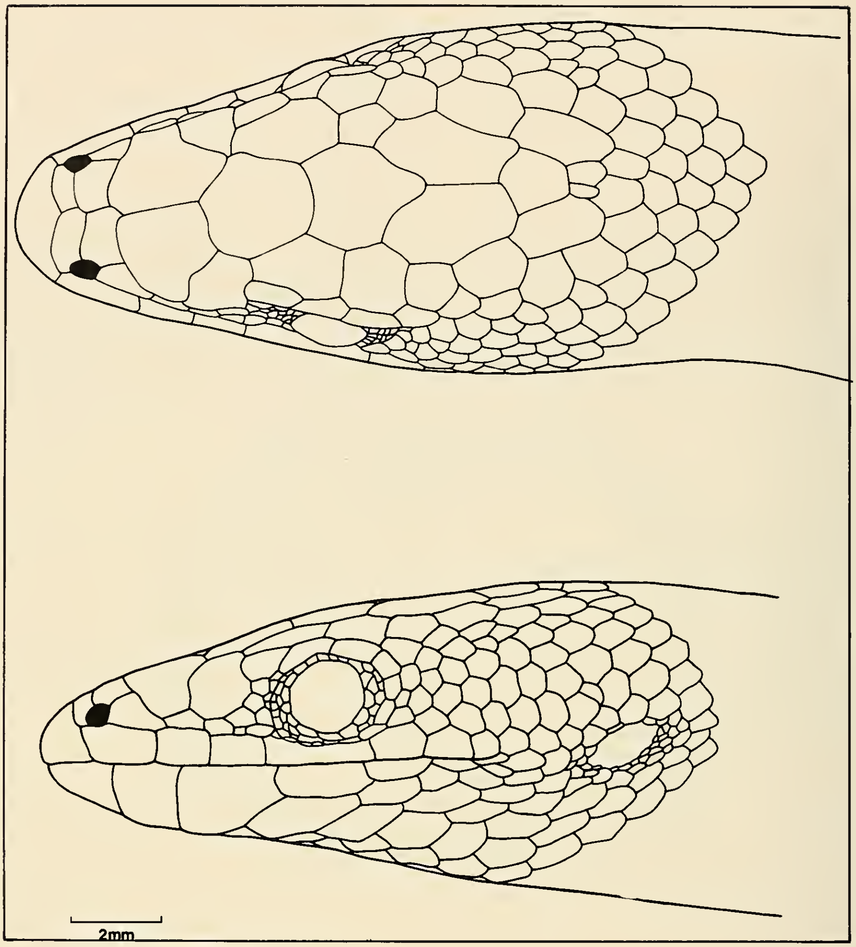

Fig. 3. Head shields of holotype of *Delma labialis*.

Snout-vent length 115.0; tail length 446.0 (388); head length 12.50 (10.9); mouth length 10.70 (85.6); snout length 4.90 (39.2); eye width 1.85 (14.8); postorbital length 2.95 (23.6); head width 6.80 (54.4); head depth 5.40 (43.2); rostral depth 1.40 (11.2); rostral width 2.55 (20.4); dorsal rostral length 1.15 (9.2); ventral rostral length 1.15 (9.2); hindlimb length 3.5 (3.0).

Coloration as for holotype.

COLORATION (IN LIFE): Kodachrome transparencies of three individuals taken by S. K. Wilson, A. Dudley and G. Husband permit the following notes on coloration in life.

Adult body dorsum red-brown becoming grey-brown on tail and cranial third of body. Slightly paler lateral margins to body scales, producing faint indications of stripes of dorsal ground. Head dorsum yellow-brown. Lip markings yellow-brown and cream. Iris black.

Juvenile body dorsum grey-brown, becoming yellow-brown on head and tail. Lip markings yellow-brown and pale yellow. Iris black.

COMPARISON WITH OTHER SPECIES: *D. labialis* is a member of the same group of *Delma* species as *D. mitella*, and may be differentiated from other members of this group by its

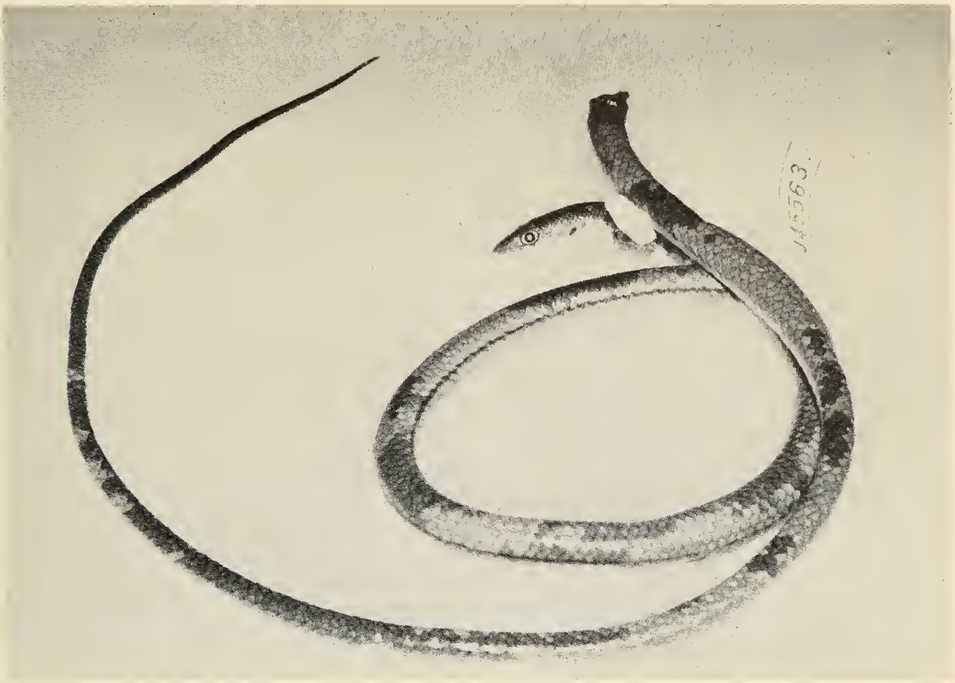

Fig. 4. Holotype of *Delma labialis*.

Fig. 5. Details of head of holotype of *Delma labialis* in life. (Photo: S. Wilson).

dorsolateral tail stripe and the nature of the head markings. It may be further differentiated from *D. borea* by its more numerous loreals (four *vs* usually three) and infralabials (5-6 *vs* 4-6, x = 4.5), from *D. grayii* and *D. inornata* by the broad contact of caudal supranasal with nostril (*vs* broadly separated), from the nearest populations of *D. nasuta* by lacking dark spots dorsally and ventrally on the body and from *D. fraseri* by lacking dark markings on throat.

HABITS AND HABITAT: The holotype was taken in low open forest with a grassy understorey, while the paratype was taken under corrugated iron near a beach. Low (1978) records this species, as *Delma inornata*(?), from 'under sheets of iron in low open forest on sand adjacent to beaches; one seen active at midday on dry, very open, rocky hill'. A. Dudley and G. Husband (*pers. comm.*) observed two specimens on Magnetic Island in February, 1985: an adult active during day in wet sclerophyll forest on the road to Nellie Beach, and a juvenile in litter in open woodland on the road to Horseshoe Bay.

ETYMOLOGY: The specific epithet is from the Latin *labium*, a lip, in allusion to the distinctive labial and lateral neck pattern of this species.

SYMPATRIC SPECIES: The only *Delma* species with a distribution overlapping those of *D. mitella* and *D. labialis* is *D. tincta* (Fig. 6; Shea, 1987), which is readily differentiated from both species by its smaller size and very different scalation. Kluge (1974) records collecting a live *D. inornata* 'a few miles south of Townsville', but does not list this specimen in his specimens examined lists or on the distribution map, nor does he question three specimens (British Museum (Natural History) 98.10.19.4-8, D. le Souef; examined) from Cooktown. These localities are respectively 620km and 1050km north of the nearest *D. inornata* locality (Marmor, Qld), itself 430km north of the main body of the species' range, which reaches Oakey, Qld (Shea, 1987), while more recent collections from both localities have not included this species. The Townsville and Cooktown records must be assumed to be in error.

THE STATUS OF *ACLYS*: Kluge (1976) reduced the monotypic *Aclys* to a subgenus of *Delma*, largely to resolve the discrepancy between relationships as suggested by external morphology (Kluge, 1974) and osteology (Kluge, 1976). This arrangement has received little acceptance. *Aclys* has been retained as a genus by Storr *et al.* (1983), Storr and Harold (1980a,b), Cogger (1983) and Cogger *et al.* (1983) without comment.

Examination of the data matrix provided by Kluge (1976) suggests that the discrepancy between data sets is partly a result of a lack of definition for *Delma* that adequately demonstrates monophyly. Of the nine skeletal characters keyed as derived for both *Aclys* and *Delma*, one, the presence of two cloacal bones per side, is shared only with *Ophidiocephalus*, while the other eight (characters 11, 19, 20, 49, 59, 65, 67 and 71 of Kluge, 1976) are all shared with two or more genera each. In contrast, only three of the thirteen phenetic external diagnostic characters (Kluge, 1974) are shared by *Aclys* and *Delma*: large external auditory meatus (primitive, and therefore unsuitable for inferring relationships), smooth scales (shared with most other pygopodid genera) and preanal pores absent (shared with *Aprasia*, *Ophidiocephalus* and *Pletholax*). *Aclys* has two uniquely derived external character states among the Pygopodidae: upper temporal scales greatly enlarged, forming a second pair of 'parietals' and rostral separating rostral supranasals on dorsal midline. There is little evidence for a sister group relationship between *Aclys* and *Delma*, and pending a more adequate diagnosis for *Delma*, the two genera are here considered distinct.

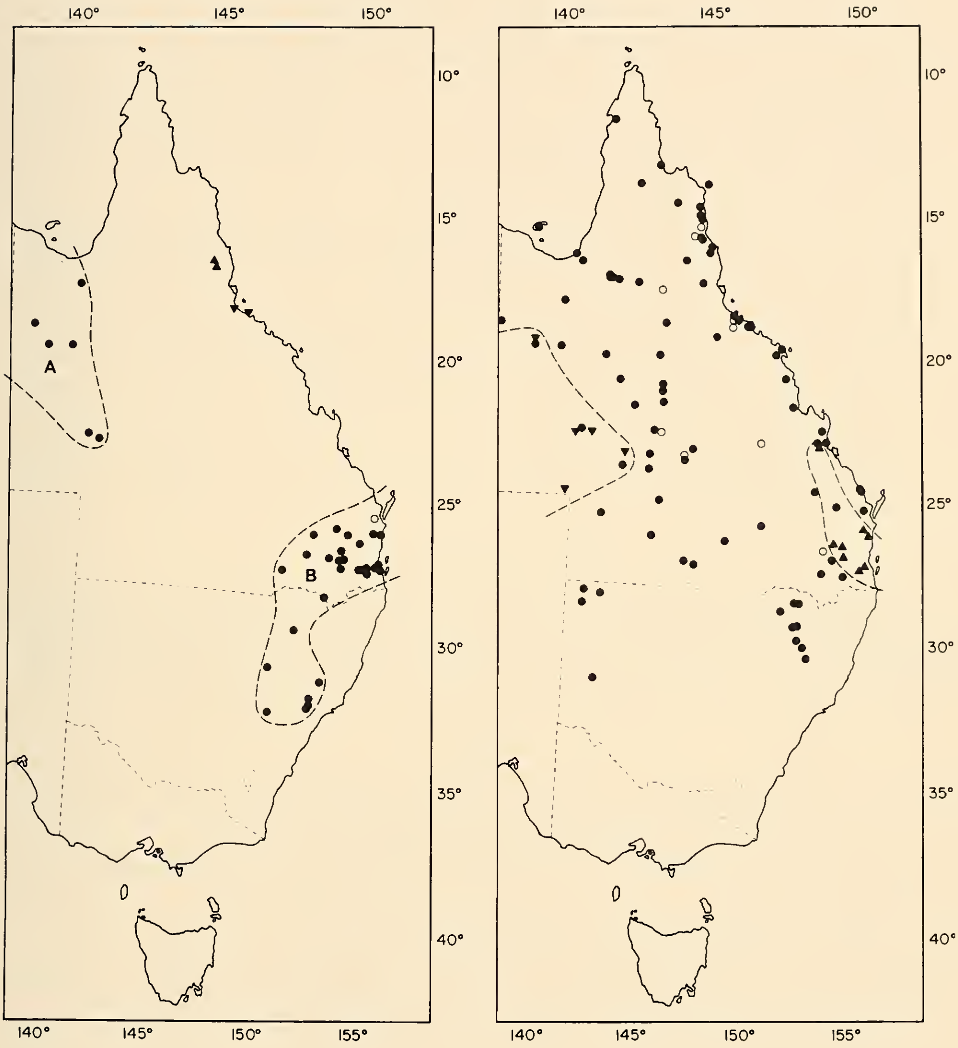

Fig. 6. Distribution of *Delma* species in eastern Australia. Left: *Delma borea* (A), *D. plebeia* (B), *D. mitella* (▲), *D. labialis* (▼). Right: *D. tincta* (●), *D. torquata* (▲), *D. nasuta* (northern form) (▼). Based on specimens examined in the Australian Museum and Queensland Museum collections. Open symbols are literature records from Kluge (1974).

KEY TO THE GENUS *DELMA* IN QUEENSLAND

1. Preanal scales two 2
   Preanal scales three 3
2. Head grey, throat white, dark collar variably present on nape, lips barred, venter cream . . . . *D. plebeia*
   Head and throat black with narrow cream or white bands, venter dark grey . . . . *D. torquata*

3. Single pair of supranasals, third supralabial below eye, midbody scales usually 14 . . . . *D. tincta*
Two pairs of supranasals, fourth supralabial below eye, midbody scales usually 16-18 4
4. Caudal supranasal broadly separated from nostril; head pattern absent; south-east Queensland . . . . *D. inornata*
Caudal supranasal narrowly separated from nostril or in contact; head pattern present or absent; north and west Queensland 5
5. Narrow dark longitudinal stripe on tail base 6
No narrow dark longitudinal stripe on tail base 7
6. Dark longitudinal tail stripe ventrolateral, sharply differentiating light ventral surface from dark lateral surface; head with faint narrow cream bands dorsally; rostral barely projecting between rostral supranasals . . . . *D. mitella*
Dark longitudinal tail stripe dorsolateral, not differentiating colour of dorsal and lateral surfaces; head without cream bands dorsally, but lips with cream bars; rostral distinctly penetrates between rostal supranasals . . . . *D. labialis*
7. Head usually with dark transverse bands; venter unmarked; usually three loreals; SVL up to 90mm . . . . *D. borea*
Head without dark transverse bands; venter usually with darker markings; 4-5 loreals; SVL up to 105mm . . . . *D. nasuta*

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Cainozoic History of the Vegetation and Climate of the Lachlan River Region, New South Wales

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(Delivered 31 March, 1982)*

SYNOPSIS

The history of the vegetation based on palynology of the late Eocene to early Pleistocene sediments is presented here for the Lachlan River region. Grey carbonaceous clays of the alluvium in the valley and in the Hillston region of the eastern edge of the Murray Basin, are the most fruitful for palynology. Pollen has not been preserved upstream of Cowra but silicified wood is found in association with basalts. Early Miocene lava flows dammed the river and the lake which was formed drowned the local vegetation (Bishop 1985a).

The palynological record and interpretations of the vegetation is one of periods of relative stability with small changes and a series of considerable, step-like change. The climate of the time is deduced from the parameters controlling generally similar modern vegetation. The main features are as follows:

1. From late Eocene to late Oligocene — early Miocene, *Nothofagus* is the most abundant pollen group and most of it is the *brassii* type. The vegetation was rainforest with reasonable diversity. The climate was very humid with a precipitation of about or above 1800mm. (The levels of precipitation given here are very general with no great accuracy: the trend is more important.)
2. In the late Oligocene — early Miocene, the *Nothofagus* content declines, particularly the *brassii* type. The vegetation was still rainforest. There was a decrease in precipitation, probably to about 1500mm.
3. In the early — mid Miocene, the Myrtaceae group was relatively more abundant. The assemblages are diverse, however, and contain many low frequency pollen types, which collectively may have accounted for a major portion of the vegetation, which was rainforest.
4. The mid Miocene was a time of considerable change. The *brassii* type of *Nothofagus* disappeared and pollen preservation ceases in the Hillston region.
5. In the ?mid — late Miocene, Myrtaceae were dominant but rainforest taxa were still present. The charcoal record, which had been low in the older, rainforest assemblages, increased considerably, suggesting that the myrtaceous vegetation was mainly wet sclerophyll. The precipitation decreased to about 1000-1500mm, with a definite dry season. Burning had become a part of the environment.
6. In the early Pliocene, *Nothofagus*, the *menziesii* and *fusca* pollen types only, reappeared in the Lachlan Valley and gymnosperms were more abundant. Rainforest had returned, the precipitation increased to more than 1500mm and burning was infrequent.
7. In the mid — late Pliocene, Myrtaceae returned to dominance, precipitation decreased to the former levels of about 1000-1500mm and burning became more frequent.
8. In the late Pliocene — Pleistocene, the rainforest element disappeared and the precipitation decreased to about 500-800mm.
9. The forest cover dwindled and in the Pleistocene Gramineae and Compositae were abundant; indicative of woodland and grassland/herbfields.

These major changes in vegetation and the inferred climatic changes may be related to changes in sea level and coincide with the major developments of circum-Antarctic oceanic circulation and ice cap formation on Antarctica.

INTRODUCTION

The Lachlan River has its headwaters in the gently undulating, swampy Breadalbane Plains at the continental drainage divide of the Central Tablelands. It flows through a

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broad upland valley around Gunning and Dalton. Downstream, the terrain increases in ruggedness and, at Narrawa, the river flows through a steep-sided granite gorge. Alluvial flats of significance commence about 13km upstream of Cowra. Valley width increases with distance downstream and the alluvial flats become extensive. After the river passes through the gap between the Jemalong and Corridgery Ranges it enters extensive plains. About the junction with Willandra Billabong, it flows onto the Western Plains, the surface of the Murray Basin, and eventually joins the Murrumbidgee River (see Fig. 1). For a delightful pictorial account of the Lachlan River and the lifestyles of the people living in the region, see Cowan and Beard (1982).

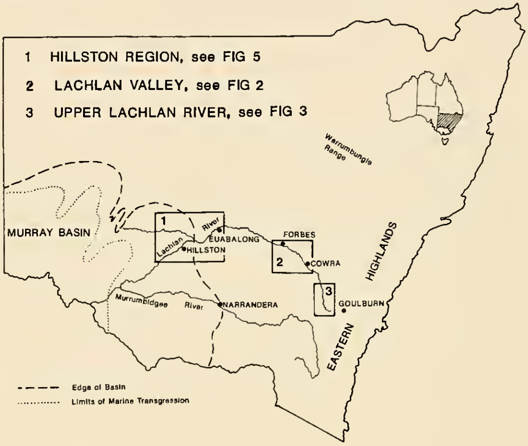


Fig. 1. Locality map. See enlargements for further detail.

In 1957, the Department of Water Resources (formerly the Water Resources Commission of New South Wales, and in 1957, the Water Conservation and Irrigation Commission) began a programme of the investigation into the ground water resources of alluvium of the Lachlan River valley, between Cowra and Forbes. Prior to this date, most bores and wells were sunk for stock water and domestic purposes and did not exceed 30m in depth. There were only a few low-yielding irrigation bores. Test drilling in the valley soon revealed good quality water at greater depths with much higher yields, suitable for irrigation and town water supplies (Williamson, 1986). At the time of writing, there are 174 high-yield bores between Cowra and Jemalong Weir, and of these 166 are used for irrigation and 8 for town water supplies. Investigation has continued downstream of Jemalong Weir and beyond Hillston.

This study of the history of the Lachlan River is based mainly on palynology, geomorphology, and geology. Water Resources has provided samples from its bores for palynology and considerable background information as well. A study of the basalts in headwaters of the Lachlan River (Bishop, 1985a) provides a history of the upper reaches of the river, beyond the extent of the alluvial flats. In all, three areas have been studied in detail and these are shown on Fig. 1.

GEOLOGY AND GEOMORPHOLOGY

The Hillston Region

The Tertiary sediments are some 100m to 170m thick near the edge of the Murray Basin. Thickness increases downstream, i.e. with distance from the edge of the basin to a maximum of about 270m in bore 36342 which is situated over the Ivanhoe Trough. When compared with the Murrumbidgee area to the south, the basement of most of the Lachlan region is shallower and the sedimentary sequence not as thick (Martin, 1984c).

The stratigraphic units used in the non-marine section of the Murray Basin have been adopted from those used in the Victorian part of the basin, with slight modification (Woolley and Williams, 1978; Woolley, 1978). Those relevant to the Lachlan area have been reviewed in Martin, (1984b; 1986a) and are briefly presented below.

The basal Warina Sand of mid — late Eocene age consists of coarse-grained quartz sands and minor dark grey clay lenses and carbonaceous clays. It is only found in the deeper parts of the basin.

The overlying Olney Formation is dominated by grey carbonacous clays and extensive sands. Elsewhere in the basin, thick lignite layers are a feature of the Olney Formation but they are not extensive in the Lachlan area. The basal part is late Eocene and extends into the Miocene.

The Calivil Sand, overlying the Olney Formation, consists of coarse sands and fine gravels with minor bands of carbonacous clay. It is thought to be late Miocene in age. The uppermost Shepparton Formation consists of polymict sands and variegated clays with yellow and brown colours dominant.

Most of the samples used for palynology come from the Olney Formation. The uppermost 60m to 80m do not yield pollen. Upstream from Euabalong to Jemalong Gap, there are few bores. Knowledge of the age of the sediments is reliant on palynology which is presented later.

Lachlan River Valley

Near Cowra, the alluvium is 3-5km wide and erosion terraces are a prominent feature. They become less pronounced further downstream and are not mappable beyond the junction of Mandagery Creek. Drilling has revealed that the alluvium reaches a maximum depth of 61m, some 6km downstream of Cowra. However, 3km upstream of Cowra, the alluvium is only 17m deep. Back Creek, which joins the Lachlan River some 12km downstream of Cowra, has alluvium extending some 48km upstream. The alluvium increases in depth with distance downstream and the maximum depth in Section 7, south of Forbes, is 133m. (See Fig. 2 for localities).

Drilling of the valley downstream of Cowra has revealed a buried 'valley-in-valley' structure. Remnants of an old valley floor are shown as a shelf which maintains a depth of 27-30m below the present drainage level, and it is present in both Back Creek and the Lachlan River valleys. However, the depth of the valley carved into the floor of the old valley, increases markedly with distance downstream (Williamson, 1964). The valley-in-valley structure is thought by Williamson (1986) to be the result of successive tectonic movements, but this is discussed further, below.

Tectonic movements near Cowra have caused a marked change in the upstream section of the Lachlan River but they have not affected Back Creek. Evidence from seismic refraction and bore data indicate that the margin of the area affected is 3km downstream of Cowra with a north-south trend. This margin is thought to be the western edge of the uplifted Eastern Highlands (Williamson, 1986). The valley-in-valley structure is shown with the palynology in Fig. 16B.

The alluvium of the Lachlan Valley consists of two quite distinct formations, the basal Lachlan Formation and overlying Cowra Formation. The characteristics of these formations have been described by Williamson (1986) and are summarized here.

The Lachlan Formation consists of a series of interbedded and interlensed sediments ranging from gravels to clays. The sands and gravels consist almost entirely of quartz of different kinds and sometimes pebbles of chert. The most significant feature of the sands

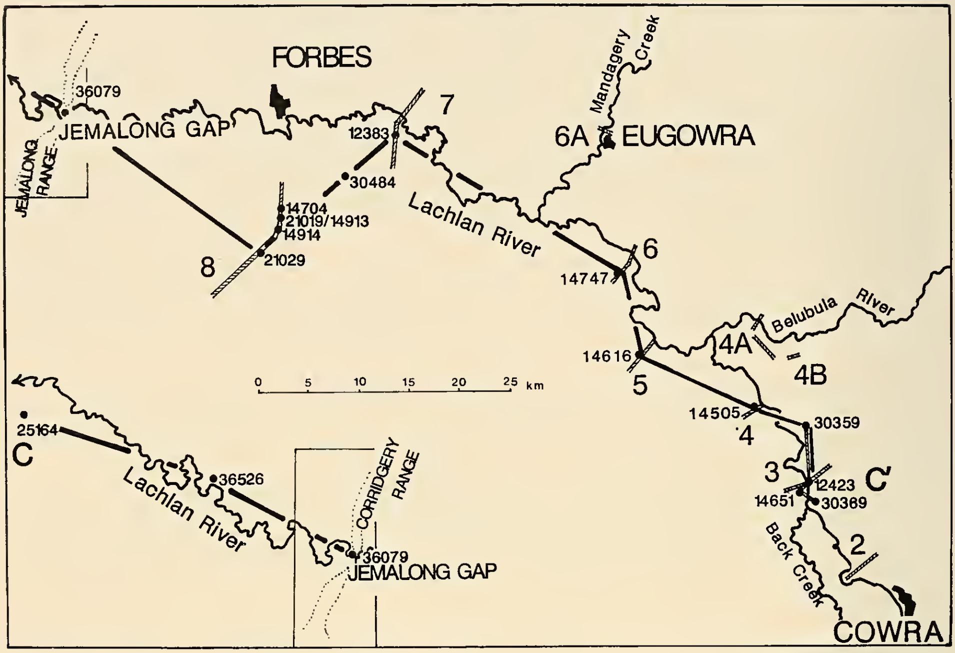


Fig. 2. Lachlan River valley locality map.

and gravels is that they do not contain the resistant rock types found in the catchment today. The fact that the sands and gravels of the Lachlan Formation consist of almost entirely quartz is important for ground water. Quartz is stable and water will become less mineralized in its passage through aquifers of the Lachlan Formation than through those of the Cowra Formation (Williamson, 1964).

The clays of the Lachlan Formation may be divided into variegated clays and carbonaceous clays. The former are usually thinly bedded and streaky. The most common colours are pale brown, yellow, grey and off-white but pink and even red are also fairly common. The carbonaceous clays are the best material for palynology. They are grey to black in colour and occur in lenses irregularly distributed through the Lachlan Formation. These lenses are usually limited in extent and often less than 1m thick though sometimes they may be correlated at the same horizon between two or three bores. These lenses may be 6m in thickness, and range up to 12m.

Wood is occasionally encountered in the sands and gravels. *Podocarpus* sp. has been identified, but most samples are too carbonized for identification (Williamson, 1986).

The Cowra Formation disconformably overlies the Lachlan Formation. The strata range from gravels to clays, all of which are predominantly brown, sometimes pale brown, red-brown, or yellow brown and rarely grey. The sands and gravels contain representatives of the various resistant rock types present in the catchment area today. In this respect, they differ significantly from the Lachlan Formation. The associated silts and clays in the Cowra Formation are predominantly brown and occasionally pale grey in thin layers. There may be greyish mottling near the surface, probably due to leaching. Carbonaceous clays are extremely rare.

Wood was encountered only once in the Cowra Formation in gravels in Bore 12437, Section 4, at a depth of 26m. It has been identified as probably *Eucalyptus resinifera* (R. K.

Bamber, *pers. comm.*), but was beyond the range of carbon dating i.e. older than 34,000 years (Williamson, 1986).

There is another formation, the Glen Logan Gravels, consisting of medium to coarse quartz gravel, usually in a red-brown silty matrix. They occur in elevated positions and often form hill cappings and are worked for road materials. It is thought that they are remnants of a formerly more extensive formation which is stratigraphically below the Lachlan Formation. Williamson (1986) postulates that the Glen Logan Gravels were probably the major source of the quartz gravels in the Lachlan Formation, but this is discussed further, below.

The test drilling in the valley has revealed facets of river history. See Fig. 2 for localities. Back Creek now joins the Lachlan River 8km downstream of Section 2 but its former junction was at Section 2. At Section 4, the ancient course of the Lachlan River went through the southern part of Section 4A instead of its present course, some 6km to the south. About Section 7, the ancient river turned south-west and passed under Section 8, some 15km south of its present course near Forbes. The ancient river passed through the gap between the Jemalong and Corridgery Ranges, as does the present river, for this is the only feasible gap (Williamson, 1986).

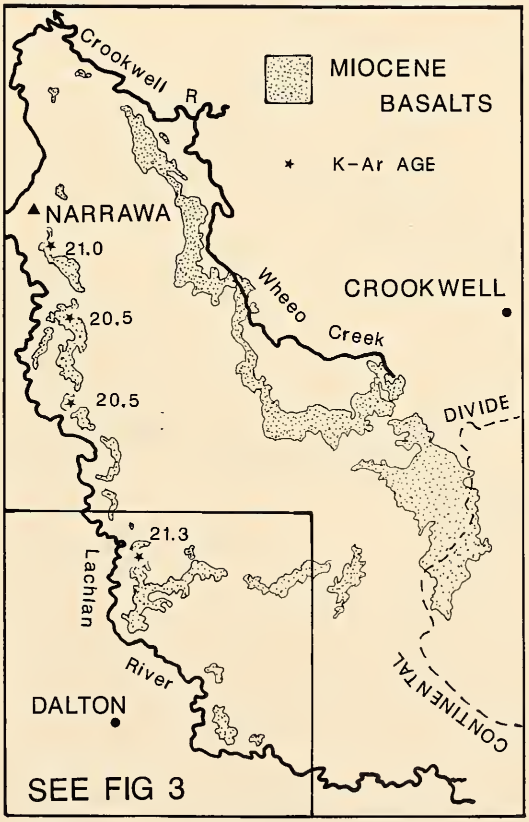


Fig. 3. The Miocene basalts of the Upper Lachlan. Modified from Bishop (1985a).

The upper Lachlan River

Near the headwaters of the Lachlan River, early Miocene channels have been preserved by long narrow tongues of basalt which were extruded into valleys and some tributaries (see Fig. 3). These basalt remnants occur as hilltop residuals as a result of relief inversion by erosion of the surrounding rock. These remnants have flat tops and are of a fairly uniform elevation, as would be expected from lava flows which did not completely fill the valleys (Bishop, Young and McDougall, 1985). The basalt remnants show that the ancient river ran parallel to the present course of the Lachlan and on the eastern side of Narrawa Mountain (Bishop, 1985a; 1987).

The lava flowed westwards down a tributary into the main river, damming the channel. It then flowed northwards for some 15km down the temporary dry river bed. A large lake, thought to be about 16,500 km^2 in area was formed (Fig. 4), presumably drowning the vegetation. Continuing lava flows engulfed the trees and preserved the wood. At least one tree stump has been preserved, apparently *in situ* and fragments of silicified wood are common in the area today (Bishop, 1985a). The stump has been identified as Myrtaceae, with affinities to *Eucalyptus* B. *Acacia* and *Nothofagus* have been identified amongst other wood fragments (Bishop and Bamber, 1985).

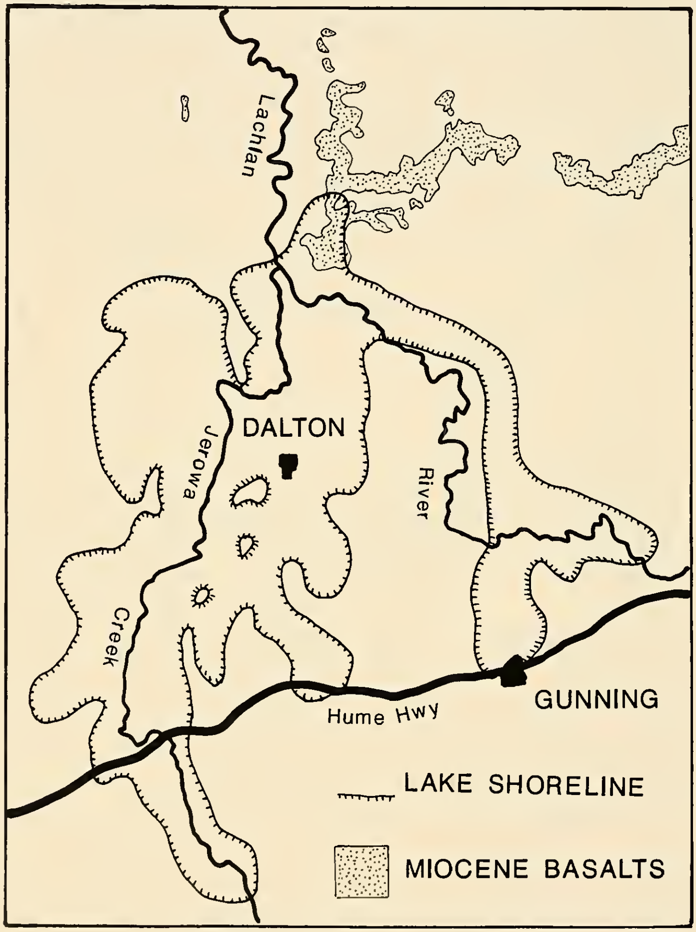


Fig. 4. Probable extent of the Miocene lake formed after the ancient Lachlan River had been damned by lava flows. Modified from Bishop (1985a).

It is not clear how long the lake persisted or what were the events associated with breaching the lava dam. It is thought that the present course of the Lachlan, in the gorge west of Narrawa Mountain, may be attributed to the catastrophic events associated with breaching the dam and draining the lake (Bishop, 1985a).

Pollen has not been preserved in the sediments of these upper reaches of the Lachlan River (Bishop, 1985a).

PALYNOLOGY

Late Eocene to mid Miocene palynofloras

The palynological zones described for the Gippsland Basin (Stover and Partridge, 1973, 1982; Partridge, 1976) are the most appropriate for this study. The zones are identified by the presence of diagnostic species in the assemblages and have been dated from independent evidence of the foraminifera found in the sequence. Extrapolation of the zones in the Gippsland Basin to the Murray Basin required some minor modifications, particularly for subdivision of thick sections of the Oligocene — early Miocene *P. tuberculatus* Zone. These modifications utilize the variation in abundance of selected species and the method is presented in Martin (1984a). Fig.5 presents the palynological zones applicable here.

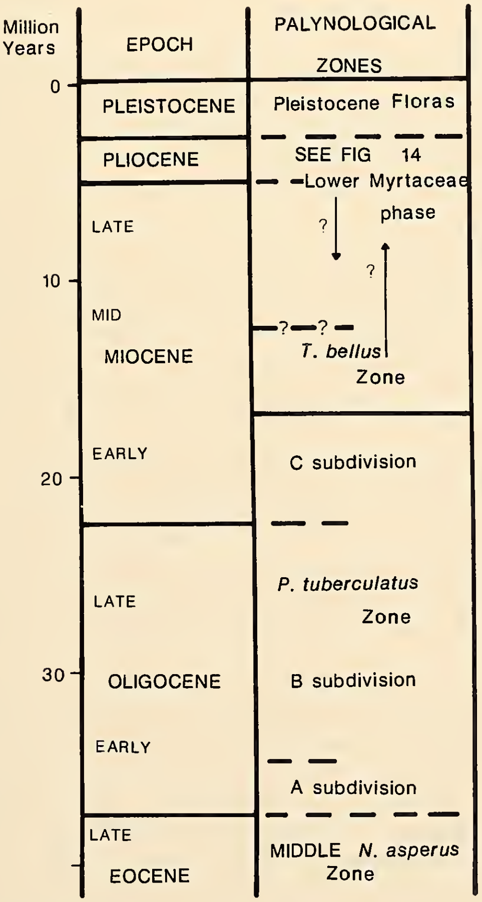


Fig. 5. Palynological zones applicable to the Hillston region. From Stover and Partridge (1973, 1982); Partridge (1976), with the modifications of Martin (1984a).

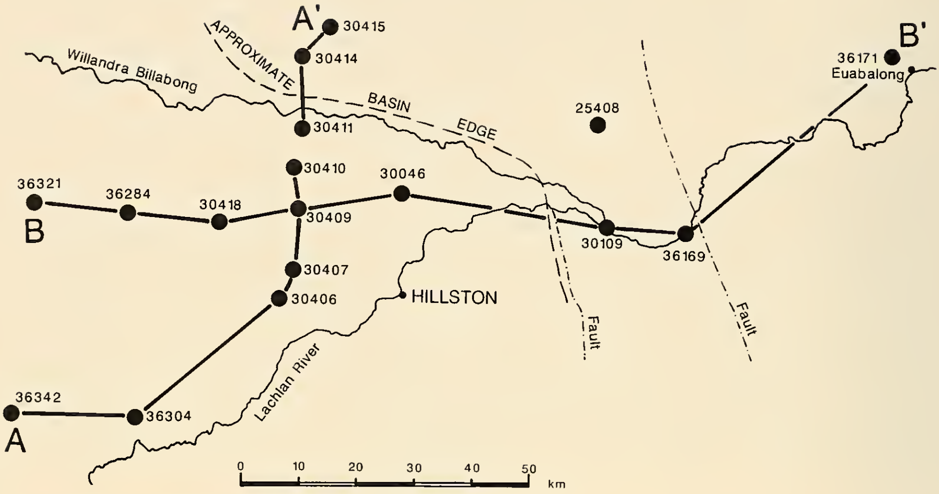


Fig. 6. Hillston region showing location of bores and sections.

Two sections in the Hillston region (see Figs 6-8) show the distribution of the palynological zones. The oldest zone present is the late Eocene Middle *N. asperus* Zone and it is restricted to the Murray Basin. Pollen preservation ceases in the early Miocene and the upper or C subdivision of the *P. tuberculatus* Zone is the youngest in the Murray Basin. Upstream of the Lachlan River, beyond the eastern edge of the basin, the younger mid Miocene *T. bellus* Zone and Pliocene sequence may be present (see Fig. 8).

Fig. 9 presents the counts of the pollen groups in Bore 36342, Tom's Lake, the deepest of this study. For a definition of the groups, see Appendix 1. There is relatively little change between the pollen groups of the Middle *N. asperus* Zone and the A and B subdivisions of the *P. tuberculatus* Zone The C subdivision shows a considerable decrease in *Nothofagus*, particularly the *brassii* type, and a slight increase in Myrtaceae. (The importance of this change is discussed further below.) Besides these abundant pollen groups, there are a number of low percentage angiosperms listed in Appendix 2. There are others which have not been named and for which botanical affinities are unknown, particularly tricolpate and tricolporate pollen types. On the whole, these assemblages are diverse.

The subdivision of the *P. tuberculatus* Zone into three parts (see Fig. 9) is only possible in the deep bores of the Lachlan region. Elsewhere, the A and B subdivisions cannot be identified. The C subdivision, however, is present over the whole area, as shown in Figs 7 and 8 (see also Martin, 1984c). In this respect, the Lachlan area of the Murray Basin differs from the Murrumbidgee area where the three subdivisions are recognized over the whole area (Martin, 1984b).

The Middle *N. asperus* Zone is distinctive with a variety of proteaceous type pollen. There may be up to nine species of *Proteacidites* which may account for 10% of the total pollen count although 5% is more common. A number of these species, mainly the larger pollen types, do not extend into the younger zone above. The diversity and abundance of the proteaceous type pollen decreases in the subsequent, younger assemblages. As well as *Proteacidites* spp. there are a number of distinctive angiosperm pollen types which are not found in younger zones (see Appendix 2).

Nothofagus is the most abundant group in the *P. tuberculatus* Zone. The *brassii* type usually accounts for most of this group but some assemblages have a high proportion of *N. flemingii* of the *fusca* pollen type (see Fig. 9). High *N. flemingii* assemblages may be found

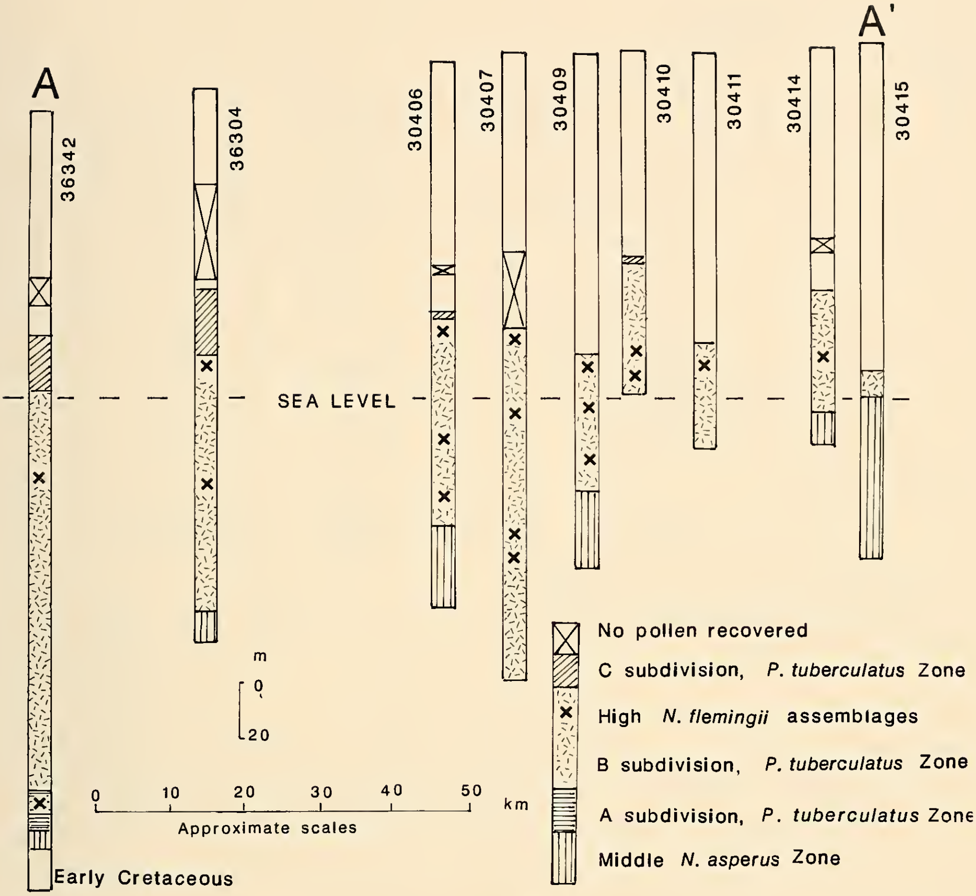


Fig. 7. The palynological zones in Section A-A^1 of the Hillston region.

anywhere in the *P. tuberculatus* Zone of the Lachlan area (see Fig. 7) of the Murray Basin, unlike the Murrumbidgee area to the south where such assemblages are restricted to two, well-defined layers (Martin, 1984b; 1986a; 1986b).

In the C subdivision of the *P. tuberculatus* Zone, the *Nothofagus* content declines, especially the *brassii* type. This decline is moderate in the Lachlan region, as shown in Fig. 9, but in the western part of the basin, the decline is much greater (Truswell *et al.*, 1985). The Myrtaceae group increases slightly here (Fig. 9), but it becomes the major pollen group with the decline in abundance of *Nothofagus* (Martin, 1986a; 1986b). As well, there is an increase in diversity and abundance of the tricolpate — tricolporate pollen types in this subdivision. The proteaceous pollen content may increase somewhat, but the pollen types are relatively small, more like *Helicia — Orites*, hence distinct from the late Eocene proteaceous content.

There are only a few of the *T. bellus* Zone assemblages and they are found upstream from the edge of the Murray Basin. The identification of this zone relies on several diagnostic species, but quantitatively, the assemblages are little different from those of the upper part of the *P. tuberculatus* Zone. Figs 10 and 11 present the counts of some *T. bellus* Zone assemblages and Appendix 2 shows the low percentage angiosperms. The seemingly poor

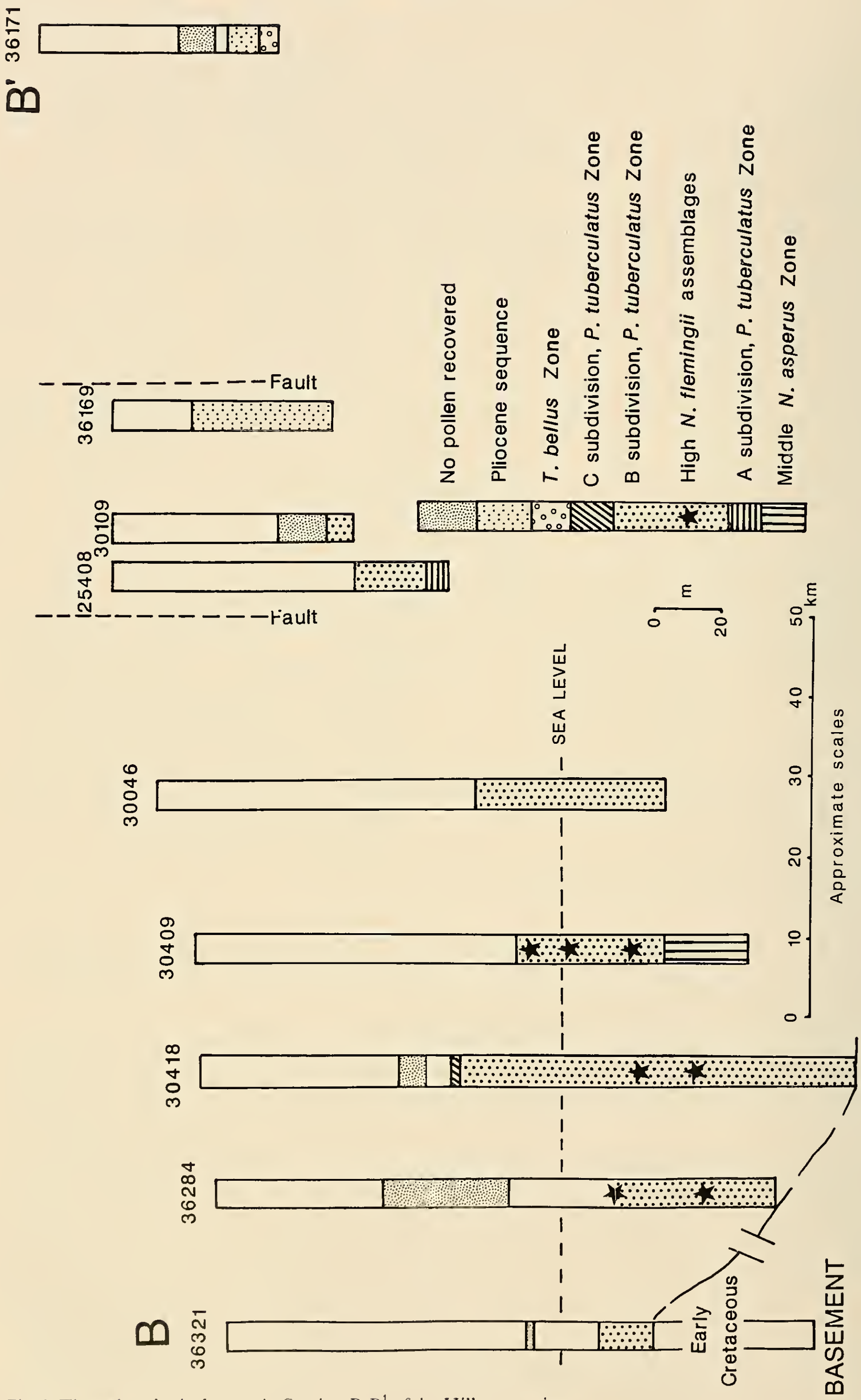


Fig. 8. The palynological zones in Section B-B^1 of the Hillston region.

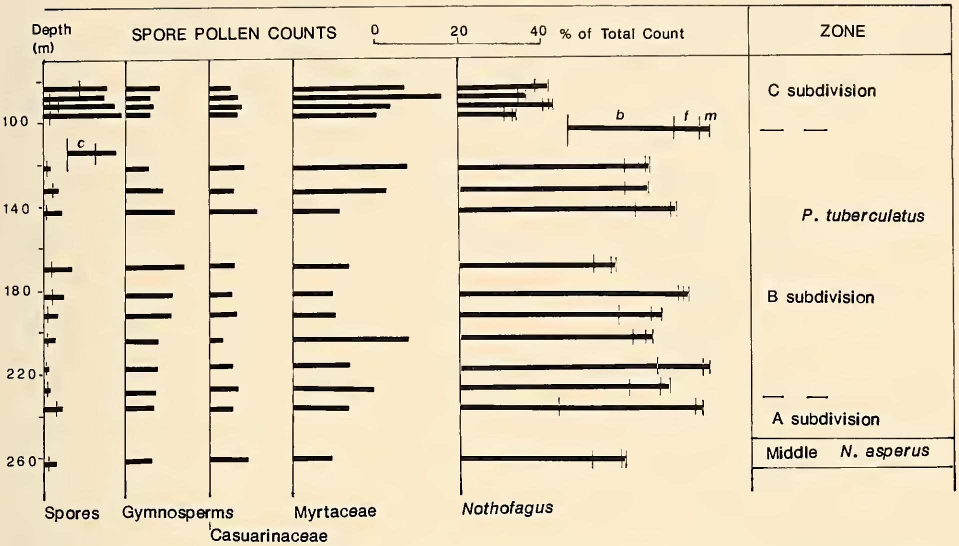


Fig. 9. The abundant pollen groups (see Appendix 1) for bore 36342 of the Hillston region. C. *Cyathea*, the left hand portion of the spore count. b, *brassii* type, f, *fusca* type and m, *menziesii* type from left to right, respectively. Those counts of *Nothofagus* showing only two divisions are the *brassii* and *fusca* types only. Low percentage taxa are not included (see Appendix 2).

representation of pollen types in Appendix 2, in comparison with the older zones is a result of many fewer of *T. bellus* zone assemblages which are, however, just as diverse as the upper part of the *P. tuberculatus* Zone. Unnamed and unknown tricolpate — tricolporate pollen types are a feature here.

The Relationship of the *T. bellus* Zone to the 'Pliocene' Sequence

The *T. bellus* Zone and a good Pliocene sequence are found in a bore at Jemalong Gap (Fig. 10). Both also occur in a bore at Euabalong (Fig. 11) but the Pliocene sequence there is not as extensive as that at Jemalong Gap. Prior to this study, only one other bore, at Narrandera (Martin, 1984b), had been found to contain both, hence a detailed comparison is warranted.

At Jemalong Gap, the *T. bellus* Zone contains two diagnostic species *Triporopollenites bellus* and *Symplocoipollenites austellus* (Stover and Partridge, 1973). The *T. bellus* Zone at Euabalong has only the latter. *S. austellus* occurs in the Myrtaceae phase immediately above the *T. bellus* Zone in both bores (and elsewhere, as discussed further below). The assignment of these assemblages to the Myrtaceae phase is based on an increase in Myrtaceae and minimal *Nothofagus*, especially the *brassii* group. The small amount of this pollen type in the basal two assemblages of the lower Myrtaceae phase at Jemalong Gap, 2% or less (see Fig. 10), could easily result from reworking of older assemblages.

Stephanocolpites oblatus, commonly present in the Pliocene sequence, is found in the *T. bellus* Zone of both bores. It is found occasionally in older zones as well (see Appendix 2). A number of distinctive early Tertiary angiosperms which range into the *T. bellus* Zone, e.g. *Malvacipollis subtilis*, *Triporopollenites endobalteus* and *Polyorificites oblatus*, as well as the nominate species of the zone, *T. bellus*, are usually lacking from the Myrtaceae phase (see Appendices 2 and 3) but, given the variability of the latter (discussed further below), this may not be entirely reliable. Thus the main feature used to differentiate the Myrtaceae

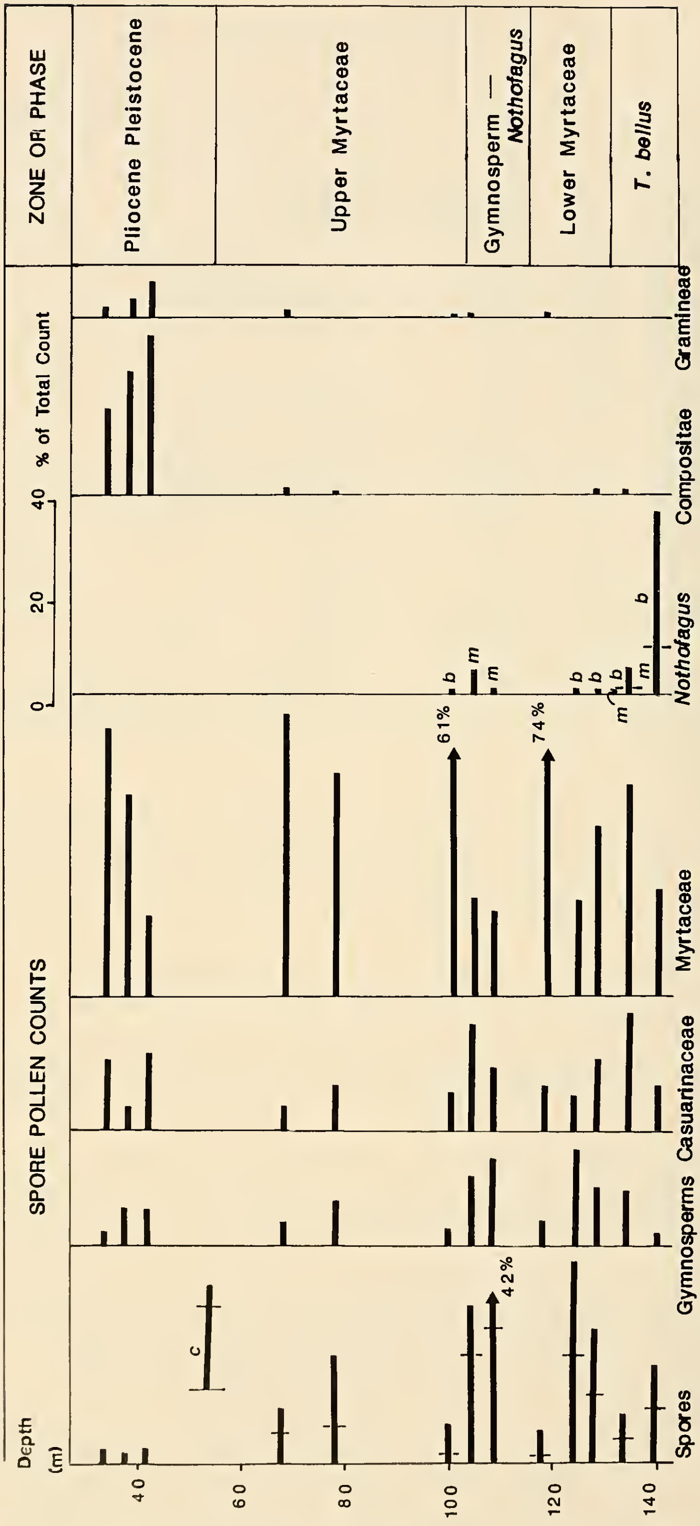


Fig. 10. The abundant pollen groups (see Appendix 1) at Jemalong Gap, bore 36079. C, *Cyathea*. b, *brassii* type. m, *menziesii* type. Low percentage taxa are not included (see Appendices 2 and 3).

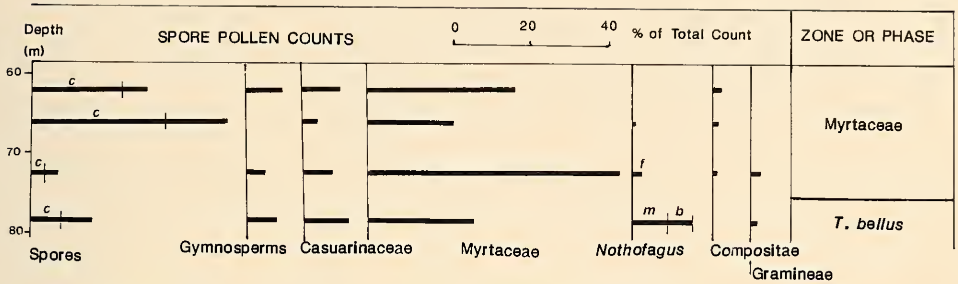


Fig. 11. The abundant pollen groups (see Appendix 1) at Euabalong, bore 36171. C, *Cyathea*. b, *brassii* type. f, *fusca* type. m, *menziesii* type. Low percentage taxa are not included (see Appendices 1 and 2).

phase from the *T. bellus* Zone is the low proportion of *brassii* type *Nothofagus*.

The upper part of the *P. tuberculatus* Zone may have a high content of Myrtaceae (discussed previously). However, near the eastern edge of the Murray Basin, it also has appreciably more than a few percent of the *brassii* type of *Nothofagus* as well as more of the typical early Tertiary angiosperms, hence is unlikely to be confused with the Myrtaceae phase. Near the western edge of the basin, the upper part of the *P. tuberculatus* Zone has more Myrtaceae and very little of the *brassii* type (Truswell *et al.*, 1985; Martin, 1986a) but a Pliocene sequence has not been identified here.

The 'Pliocene' Palynofloras

The Pliocene sequence is described in Martin (1973b) and has been divided into informal 'phases'. This description was based almost entirely on one bore, 14747 of Section 6, in which the average of all the assemblages for the phase was presented. With subsequent work, a total of some forty bores have been examined from the Lachlan River valley, hence the Pliocene sequence is re-described here with an assessment of the variability. Bore 14747, which shows the best sequence in the Lachlan River valley, is presented here again (Fig. 12) to show the variability found in the phases. This present report does not contradict or make substantial alterations to the original descriptions.

Myrtaceae phase

Myrtaceae is the abundant pollen group and usually constitutes 30-40% of the total pollen count, but some assemblages may have as much as 70%. Spore content is moderate, usually 30% or less. The content of gymnosperm pollen is moderate to low, less than 20% and *Podocarpus* is usually the most common in this group. *Nothofagus* is sometimes present but only in small amounts, 5% or less. Compositae and Gramineae are usually present in low quantities, 5% or less. Cyperaceae and Restionaceae are occasionally present, also in low quantities of 5% or less.

Some taxa are only recorded in low percentages that show little variation. These taxa usually present include *Haloragis* and Proteaceae (excluding Banksieae) whereas *Tasmannia* and *Micrantheum* are sometimes present. Infrequent occurrences include Anthocerotae, *Acacia*, *Dodonaea*, Banksieae Epacridaceae (tetrad pollen type), *Symplocos*, *Quintinia* and *Myriophyllum* whereas *Monotoca*, *Coelebogyne*, Gyrostemonaceae, *Sparganium*, *Macaranga-Mallotus* and and Goodeniaceae are rare. Unidentifiable tricolpate/tricolporate angiosperm grains usually account for 10% or less of the total pollen count.

The original description of the Myrtaceae phase included *Casuarina*, i.e. the Myrtaceae — *Casuarina* phase. High percentages of Casuarinaceae are somewhat erratic and are discussed further, below.

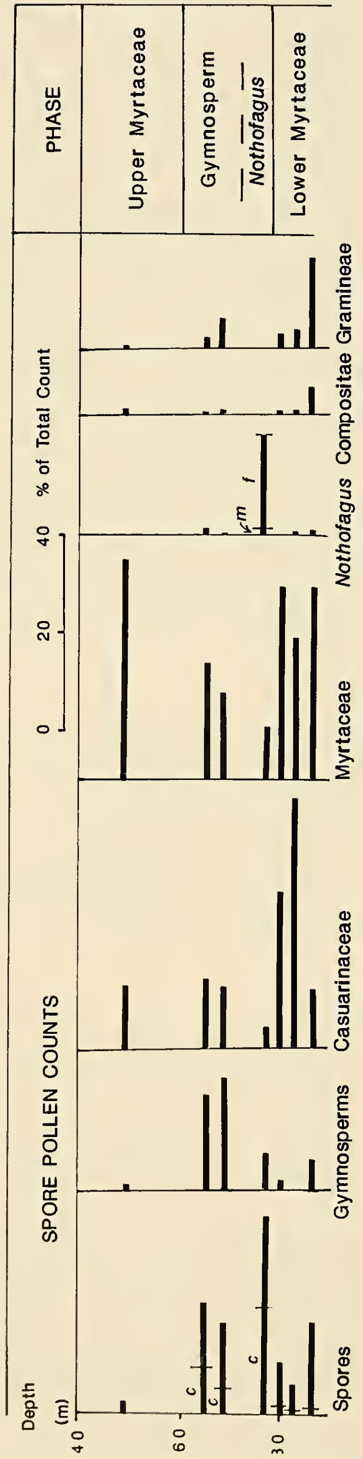


Fig. 12. The abundant pollen groups (see Appendix 1) of bore 14747, Section 6, Lachlan River valley. C, *Cyathea*. f, *fusca* type. m, *menziesii* type. Low percentage taxa are not included (see Appendix 3).

Nothofagus phase

Nothofagus is relatively abundant, over 10% with the highest value of 29%. The *fusca* pollen type, *Nothofagus brachyspinulosa*, is the most common with smaller amounts of the *menziesii* type, *Nothofagus aspera*. The *brassii* pollen type which was abundant in the early and mid Tertiary is present as very minor quantities (1-5%), and in this respect the *Nothofagus* content of these Pliocene assemblages is quite distinct from that of the older, *Nothofagus*-dominated assemblages.

Spore content is moderate (20-30%) with a slightly greater diversity than that of the Myrtaceae phase. The gymnosperm content is usually less than 20% and the composition of the group is much the same as that for the gymnosperm phase (discussed below). However, the single occurrence of *Lagerostrobus franklinii* in the Pliocene is found in the *Nothofagus* phase. The Myrtaceae content is relatively low, less than 20%. The low percentage taxa register in much the same way as that described above for the Myrtaceae phase.

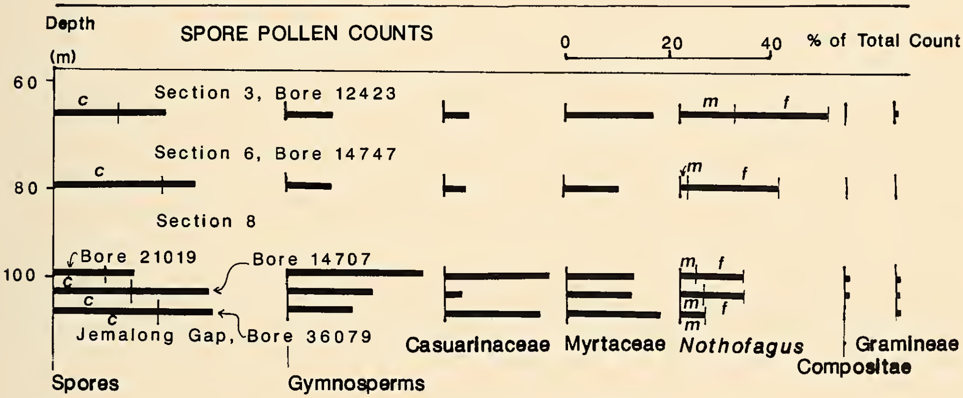


Fig. 13. The *Nothofagus* phase in the Lachlan River valley, bores arranged sequentially downstream. Jemalong Gap does not meet the definition of the *Nothofagus* phase but it is in the stratigraphic position of this phase and included for comparison. C. *Cyathea*. m, *menziesii* type. f, *fusca* type. Low percentage taxa are not included (see Appendix 3).

Fig. 13 shows the pollen spectra of the *Nothofagus* phase, sequentially downstream. The percentage of *Nothofagus* decreases with distance, downstream. Jemalong Gap, with 4.5% does not meet the definition of the *Nothofagus* phase, but there is a peak and it occurs at the expected stratigraphic level of the *Nothofagus* phase (discussed further below). This low percentage could well result from long distance transport, which, however, would coincide with the *Nothofagus* phase further upstream. Jemalong Gap is included in Fig. 13 for comparison.

The Gymnosperm phase

Gymnosperm pollen exceeds 20% of the total count. *Podocarpus* is usually the most abundant of the group, but other taxa may be more abundant, e.g. Cupressaceae, *Dacrycarpus* or *Phyllocladus*. *Dacrydium* and Araucariaceae are usually present but the latter does not exceed 6%. *Microcachrys* is occasionally present in very low frequencies.

Spores, Myrtaceae and Casuarinaceae are all moderate and values rarely exceed 20%. Occurrence of the low percentage taxa are much the same as that for the Myrtaceae phase.

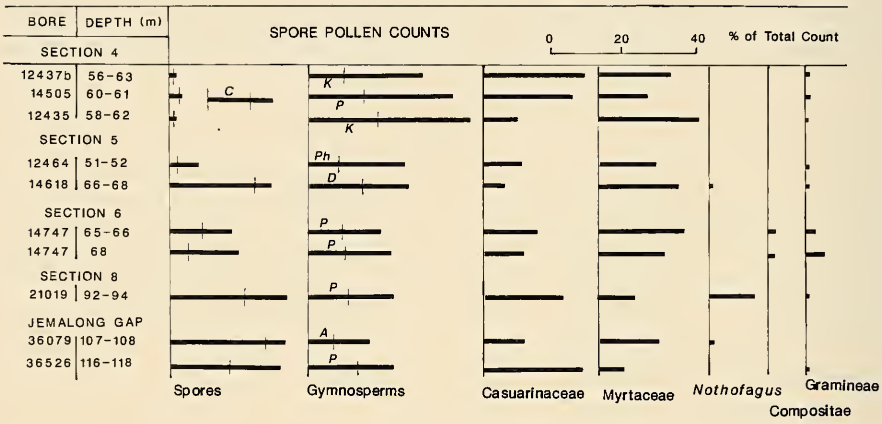


Fig. 14. The gymnosperm phase in the Lachlan River valley, bores arranged sequentially downstream. C, *Cyathea*. The most abundant gymnosperm of the group is shown thus: K, Cupressaceae, P, *Podocarpus*. Ph, *Phyllocladus*. D, *Dacrycarpus*. A, Araucariaceae. Low percentage taxa are not included (see Appendix 3).

Fig. 14 shows the pollen spectra of the Gymnosperm phase, arranged sequentially downstream. The best development is upstream at Section 4, but the decline downstream is not as marked as that for the *Nothofagus* phase. One *Nothofagus*-phase assemblage at Section B also meets the definition of the gymnosperm phase. At Jemalong Gap, the highest percentage of gymnosperms is slightly less than that in the definition, but this assemblage also contains the highest *Nothofagus* value of the Pliocene sequence in this bore , thus these two high values occur in the expected stratigraphic position (discussed further below). The Jemalong Gap high gymnosperm assemblage is included in Fig. 14 for comparison.

High Casuarinaceae Content

A more specific identification of Casuarinaceae pollen is difficult for there is continuous variation through *Gymnostoma* and *Casuarina* (Kershaw, 1970a). Some assemblages have a high content of Casuarinaceae, 50% or more of the total pollen count. These assemblages are otherwise typically those of the Myrtaceae phase. The distribution of the high percentages of Casuarinaceae do not show any clear patterns (discussed further below), hence this feature is not included in the definition of the phases.

High spore content

Some assemblages have an exceptionally high spore content (50-70%). *Cyathea* is usually the most abundant taxon throughout the Pliocene and it may be exceptionally high in these assemblages. There is usually a greater diversity of spores and most of them are ferns. Because of the high spore content, the percentages of other groups are depressed and these assemblages may not fit into any of the phases described above. Some of them, however, have an appreciable Myrtaceae content and could be included in the Myrtaceae phase.

Stratigraphic Relationships of the 'Pliocene' Sequence

As originally described (Martin, 1973b), the lower Myrtaceae phase is the oldest of the sequence and forms a relatively thin part of the sequence over the valley basement. This is overlain by the *Nothofagus* and then the gymnosperm phases, both relatively thin. Above these, the upper Myrtaceae phase forms the uppermost part of the Pliocene sequence. Thus the *Nothofagus* and gymnosperm phases divide the Myrtaceae phase into a lower and upper component, with no means of distinguishing the two from the composition of the assemblages (see Appendix 3). The upper Myrtaceae phase accounts for the largest part of the section and is usually one half to one third of the total Pliocene sequence. Fig. 15 presents the relationship of the phases.

The distribution of the Pliocene phases in the sections across the valley is shown in Fig. 16 and Fig. 17 shows C-C^1 section along the length of the valley (see Fig. 2 for localities.). It can be seen that the whole sequence increases in depth with distance downstream.

The *Nothofagus* phase has been considered as a marker horizon within the Pliocene. The evidence from the Lachlan River valley to support this hypothesis is rather sparse as only five *Nothofagus* phase assemblages have been recovered. There is no evidence to the contrary, either. In a broad sense, the *Nothofagus* phase is still considered a satisfactory marker horizon and the palaeoecological reasons for this are discussed later. However, if levels between bores are extrapolated, then a high degree of precision should not be expected for these are largely fluviatile sediments and cut and fill associated with the changes in the river system may produce a complex stratigraphy. This is probably the reason for the *Nothofagus* phase in Bore 14745 being some 12m below that in Bore 14747, which is only 0.7km distant. See section 6 in Fig. 16E.

The gymnosperm phase occurs above the *Nothofagus* phase in only one bore. All of the other gymnosperm phase assemblages occur in bores which do not have the *Nothofagus* phase or else coincide with the latter. In the upstream part of the valley, both the *Nothofagus* and gymnosperm phases occur close to the floor of the valley (see sections 3 and 4 in Fig. 16). Thus there is doubt whether the gymnosperm phase always occurs stratigraphically above the *Nothofagus* phase. Given the distribution of the two phases, an equally valid hypothesis would be a contemporary mosaic of the two kinds of vegetation (discussed further under palaeovegetation). Thus it may be more prudent to consider the *Nothofagus* and gymnosperm phases as contemporaneous events.

Stratigraphically, the high spore assemblages occur roughly about the same levels or below those of the *Nothofagus* and gymnosperm phases (see Fig. 18). Curiously, most of the high Casuarinaceae assemblages are found about these levels also (discussed under palaeovegetation).

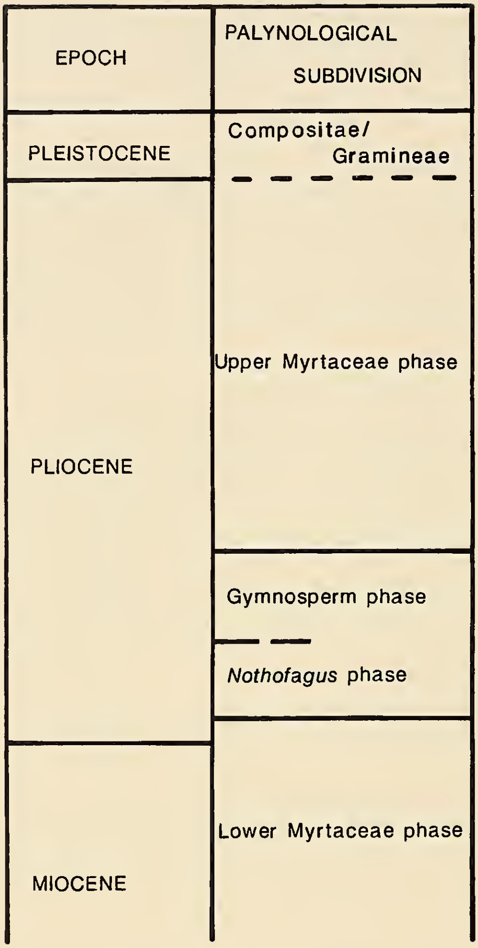


Fig. 15. The relationship of the phases in the ?mid Miocene-Pliocene sequence.

Towards the top of the upper Myrtaceae phase, diversity is reduced and the content of Compositae and Gramineae increases. It may be difficult to distinguish the uppermost Pliocene from Pleistocene assemblages (discussed further below).

Dating the 'Pliocene' Sequence

The lower Myrtaceae phase overlies the *T. bellus* Zone, as discussed previously, but dating the boundary is problematical.

In Section 6A near Eugowra on Mandagery Creek, basalt has been intersected in the bores. There is 9.4m of alluvium below the basalt (Williamson, 1986) but pollen was not recovered from these sediments. The texture, mineralogical and chemical composition of the basalt in the bores is sufficiently similar to the basalt outcrop at Toogong, some 21km upstream, to allow a common source of both the basalts (Williamson, 1986). The Toogong basalt has been dated at 12.2 million years (Wellman and McDougall, 1974).

The assemblages above the basalt contain 4-6% of *Nothofagus*, insufficient to qualify for the *Nothofagus* phase. One assemblage fits the Myrtaceae phase and the other has a high spore content. There is a good representation of rainforest taxa which is usually a feature of the older parts of the Pliocene sequence. However, the location of these bores, in the narrow, steep-sided valley of Mandagery Creek would favour rainforest taxa (discussed further below), hence its position in the sequence is uncertain. Hence the basalt date indicates that some of the Myrtaceae phase is younger than 12.2 million years.

Basalts dated at 17 million to 14 million years (Wellman and McDougall, 1974) overlie lake sediments at Chalk Mountain in the Warrumbungle Range. Two pollen assemblages from these sediments have been described (Holmes *et al.*, 1983). Both are generally similar to the oldest of the Myrtaceae phase encountered in the Lachlan River System. One assemblage has 0.5% of the *brassii* type of *Nothofagus* and there is a variety of rainforest angiosperms. However, gymnosperms are unusually abundant for the oldest part of the Myrtaceae phase. It is thought that a montane lake habitat may not be strictly comparable with the alluvial flats of a broad river valley and this may account for the difference. However, given that there is some uncertainty about the boundary between the *T. bellus* Zone and the Myrtaceae phase, an alternative interpretation is that these Chalk Mountain assemblages are youngest *T. bellus* Zone. If this alternative interpretation is accepted, then they are rather different from the *T. bellus* Zone assemblages of the Lachlan River System. Thus evidence from the Chalk Mountain assemblages suggests that the base of the lower Myrtaceae phase, i.e. the 'Pliocene' sequence, may be as old as 17 million to 14 million years, or middle Miocene.

There is no evidence to date the *Nothofagus*/gymnosperm phase. However, inference from interpretations of the palaeovegetation and changing sea levels (both topics discussed further below) suggest that it coincided with the early Pliocene highstand sea level.

'Pleistocene' Palynofloras

Only a few Pleistocene assemblages have been recovered from the Lachlan River system. They are presented here (see Fig. 18) for comparison with the Pliocene sequence.

Myrtaceae is still relatively common with some high values, about 40%. Other assemblages may have fairly low values, less than 20%. Casuarinaceae is usually quite low, less than 5% although there are a few assemblages with moderately high values of about 30%.

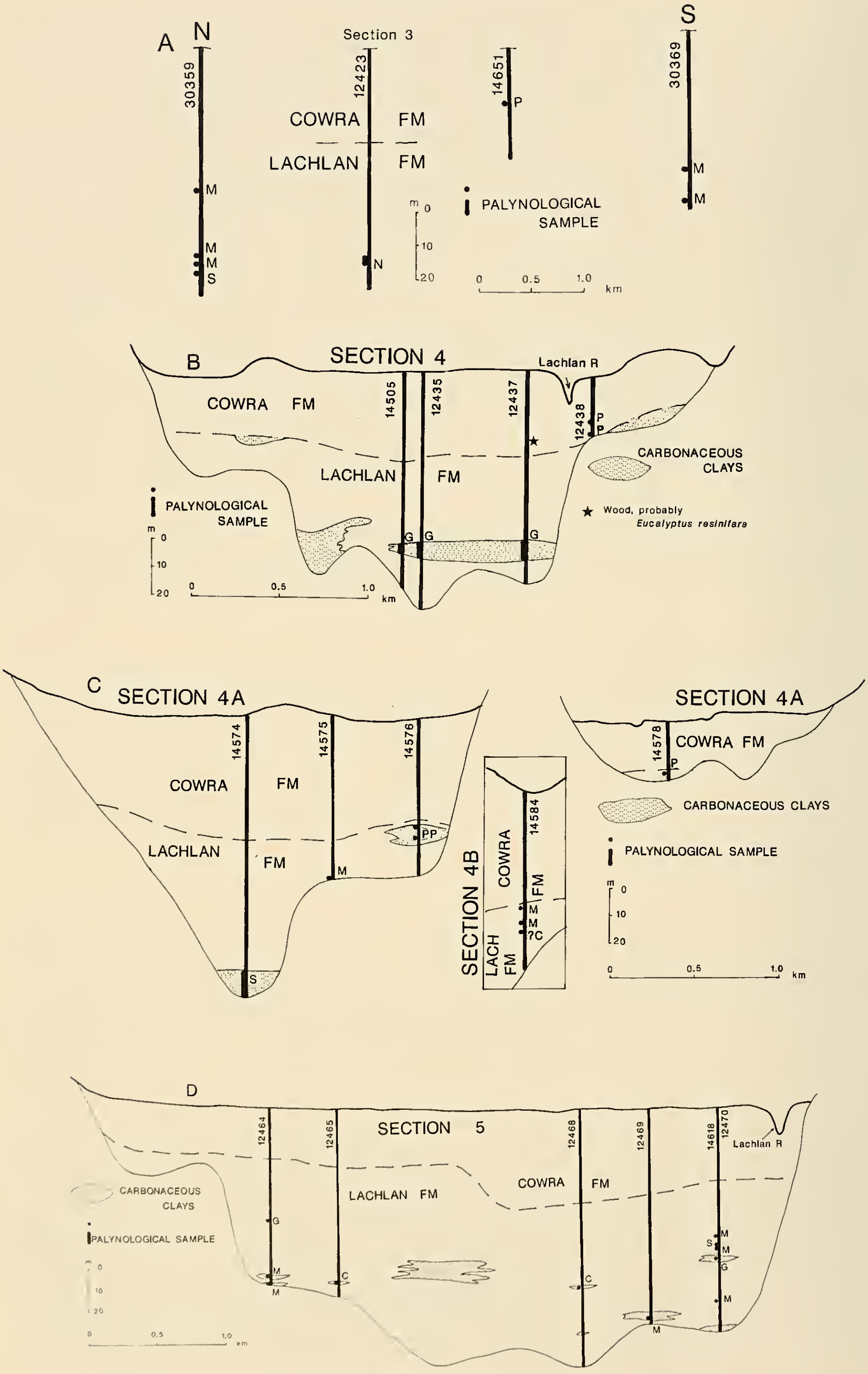
Spore content is low, usually less than 8% and of restricted diversity. Anthocerotae is usually present and the most abundant spore. *Cyathea* is absent from all except one of the assemblages and other ferns are minimal.

Gymnosperm content is low, usually less than 5%. Cupressaceae, Araucariaceae and *Podocarpus* are the only taxa found here.

Compositae is always present, usually with more than 20%. There are some very high values, the highest being 64%. Two pollen forms are almost entirely restricted to the Pleistocene, Cichorieae and *Tubulifloridites pleistocenicus*. Gramineae is usually present in values greater than 10%, sometimes up to 30%. Chenopod/amaranth is also usually present but in low quantities, less than 7%. *Polyporina granulata* is restricted to the Pleistocene. Cyperaceae and *Haloragis* are usually present whereas Restionaceae and *Sparganium* are rare.

The shrubby element, viz. *Acacia*, Banksiae, other Proteaceae, Epacridaceae, *Monotoca* and *Micrantheum* are occasionally present. Unidentifiable tricolpate/tricolporates values are usually very low. The rainforest element is absent or rare. The high pollen producers, viz. *Cyathea*, *Nothofagus* and most gymnosperms are absent or present in such low percentages that they may represent long distance transport or reworking. Other rainforest taxa such as Cupaneae, *Tasmannia*, *Quintinia* and *Symplocos* are entirely absent.

The deepest of these assemblages are intermediate between those of the Pliocene and the Pleistocene. They have a good representation of Myrtaceae and Casuarinaceae, virtually no rainforest element and relatively low Compositae.


A
N
S
Section 3
30359
12423
14651
30369
COWRA FM
LACHLAN FM
M
M
M
S
N
P
M
M
m 0
10
20
PALYNOLOGICAL SAMPLE
0 0.5 1.0 km
B
SECTION 4
Lachlan R
COWRA FM
14505
12435
12437
12438
P
P
LACHLAN FM
CARBONACEOUS CLAYS
PALYNOLOGICAL SAMPLE
Wood, probably *Eucalyptus resinifera*
G
G
G
m 0
10
20
0 0.5 1.0 km
C
SECTION 4A
14574
14575
14576
COWRA FM
LACHLAN FM
PP
M
S
SECTION 4B
14584
COWRA FM
LACH FM
M
M
?C
SECTION 4A
14578
COWRA FM
P
CARBONACEOUS CLAYS
PALYNOLOGICAL SAMPLE
m 0
10
20
0 0.5 1.0 km
D
SECTION 5
12464
12465
12468
12469
14618
12470
Lachlan R
LACHLAN FM
COWRA FM
CARBONACEOUS CLAYS
PALYNOLOGICAL SAMPLE
G
M
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C
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M
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m 0
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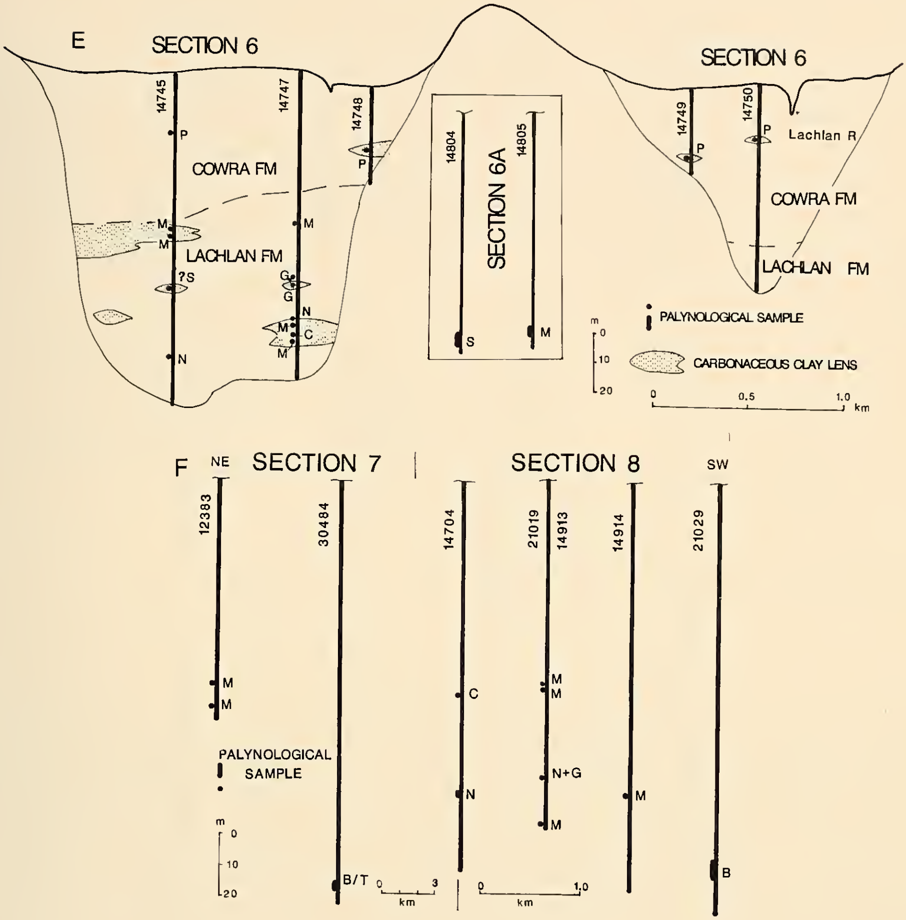

Fig. 16. The distribution of the palynological phases in sections across the valley. For location of the sections, see Fig. 2. Cross sections of valley, the distribution of carbonaceous clays and the boundary between the Lachlan and Cowra Formations from maps supplied by the Department of Water Resources. Only those bores yielding pollen are included. Legend: P — Pleistocene; PP — Pliocene-Pleistocene transition; M — Myrtaceae phase; G — Gymnosperm phase; N — *Nothofagus* phase; S — High spore assemblage; C — High Casuarinaceae assemblage; B — *T. bellus* Zone; T — *P. tuberculatus* Zone.

In summary, the most conspicuous difference of the 'Pleistocene' assemblages when compared with those of the mid Miocene-Pliocene is the virtual absence of the rainforest element, the high Compositae content, moderate Gramineae content and lower diversity. The changeover to 'Pleistocene' assemblages is recognized in other river valleys and may be used for stratigraphy (Martin, 1979, 1980, 1981) but there is no direct evidence available for dating. Wood has been retrieved once from the Cowra Formation, but it is beyond the range of radio-carbon dating, i.e. older than 35,000 to 40,000 years (Williamson, 1986).

PALAEOVEGETATION

Interpretations of the Tertiary palaeovegetation from pollen assemblages rely on general principles rather than on direct comparison with some analogous, living vegeta-

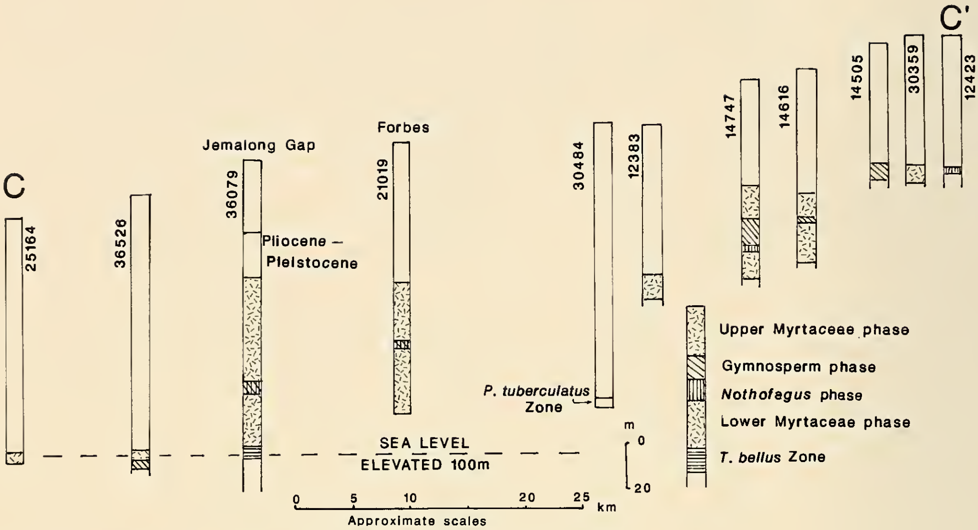

Fig. 17. Section C-C^1 running lengthwise of the Lachlan River valley.

tion. A good fit with some extant vegetation does not exist. For example, the three pollen types of *Nothofagus* are found together in the early—mid Tertiary assemblages but the living plants do not grow together anywhere in the world today. The *brassii* type only is found in New Guinea, New Caledonia and the New Hebrides, whereas the other two types may grow alone or together in southeastern Australia, Tasmania, New Zealand and South America. As a second example, *Dacrydium* and *Dacrycarpus* are found in New Guinea, New Caledonia and New Zealand today. In the early—mid Tertiary, the pollen is found with *Lagerostoma franklinii* which is restricted to Tasmania. Other examples could be given, but if a general, rather than a specific approach is adopted, floristically, comparable vegetation is found on the Australian mainland, Tasmania, New Zealand, New Caledonia and New Guinea.

Experiments with surface samples, in which the pollen assemblage on the ground is compared with the composition of the vegetation, show that changes in abundance of pollen may be interpreted as changes in abundance of the parent plant in the vegetation. For high pollen producing plants, deposition of pollen decreases exponentially from the source (Birks and Birks, 1980). An empirical value may be determined, values above which indicate local abundance of the parent plant (e.g. MacPhail, 1979). Low values may be interpreted as pollen transported in from a distance or a low occurrence of the parent plant in the vegetation. Little may be deduced about the abundance or rarity in the vegetation of low (percentage) pollen producers.

Assemblages which consist largely of tree pollen may be interpreted as closed forest (= rainforest). With a closed canopy, insufficient light reaches the ground to support a good cover of low growing, ground covering, herbaceous plants. With a good representation of the low growing plants, *viz.* Gramineae, Restionaceae, Cyperaceae and Compositae, the forest cover would have been more open. If values for these latter taxa are high, they may indicate woodland, savannah, grasslands or herbfields.

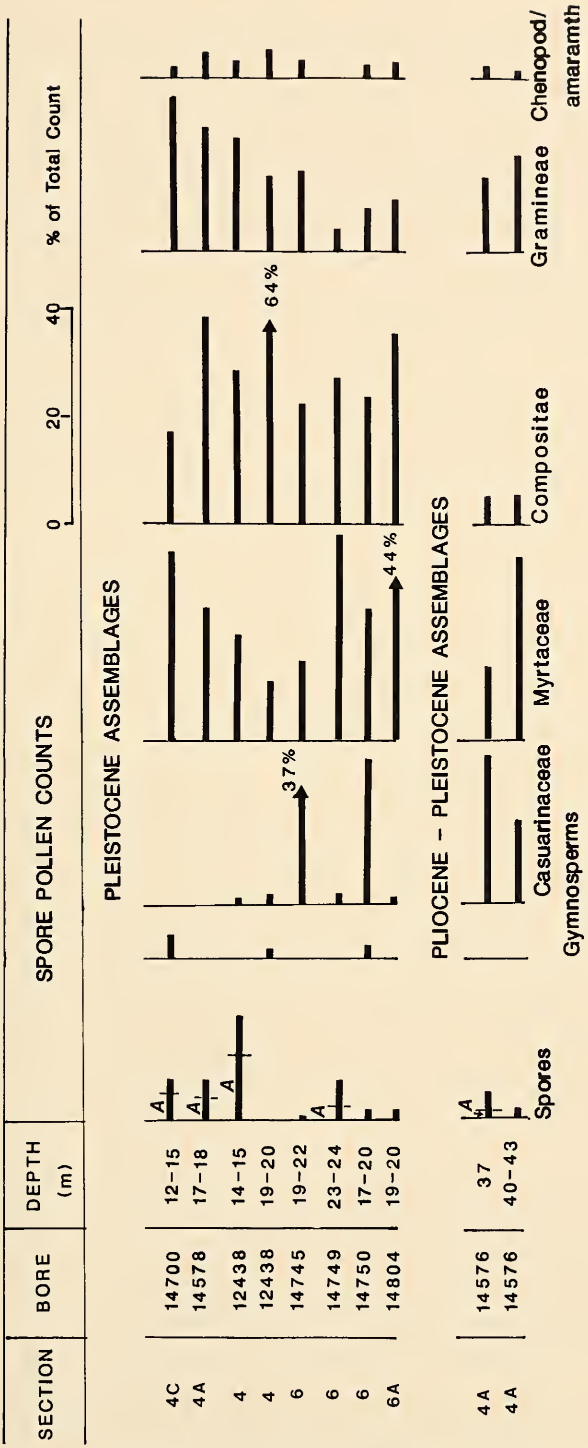

Fig. 18. Pleistocene and Pliocene — Pleistocene transitional assemblages. A, Anthocerotae.

Late Eocene to mid Miocene palaeovegetation

The vegetation throughout the whole of this period of the Tertiary must have been closed forest, judging by the extremely low content of the light-demanding, low-growing plants (see Fig. 9 and the *T. bellus* Zone in Figs 10 and 11). The *brassii* type of *Nothofagus* was prominent from the late Eocene until the late Oligocene — early Miocene when it declined and Myrtaceae became the more abundant group. This changeover in the most abundant pollen group is thought to indicate a climatic change (discussed further below).

In the Murray Basin, *N. flemingii* was more abundant in some levels of the sequence, e.g. the 230m to 240m level in bore 36342 (Fig. 9). This greater abundance may be found anywhere in the Oligocene *P. tuberculatus* Zone, A and B subdivisions, as shown in Figs 7 and 8. It is thought that *N. flemingii* required a well-drained habitat (Martin, 1984a; 1986a; 1986b) and the Lachlan region of the basin, with its slightly shallower and rather irregular basement (see Fig. 7) provided more of this habitat than the Murrumbidgee area (Martin, 1984b). Thus there was a forest mosaic, with *N. flemingii* common on well-drained sites and the *brassii* type of *Nothofagus* prominent elsewhere. This mosaic would change with time, according to changes in the course of the rivers and sedimentation. Deposition of sands with the resulting good drainage would favour *N. flemingii*.

The Myrtaceae which became prominent in the late Oligocene-early Miocene, is a heterogeneous group. The 'eucalypt type', *Myrtaceidites eucalyptoides*, which conforms with the *Angophora* — bloodwood eucalypt morphology is present but not common. Recent work shows that some species of eucalypts have pollen which is much smaller and generally unlike that of the *Angophora* — bloodwood eucalypt type (Chalson and Martin, manuscript submitted). Most of the myrtaceous pollen is generally similar to that of *Acmena*, *Baeckea*, *Backhousia*, *Syzygium*, *Tristania* and probably others as well (Martin, 1978). *Decaspermum*, *Austromyrtus* and *Rhodamnia* may be present during this time also (Truswell *et al.*, 1985). Whatever the affinities of this pollen, the very low content of ground covering plants indicates that the myrtaceous-dominated vegetation was closed forest.

The proteaceous component of the vegetation in the late Eocene may have been substantial. A number of these proteaceous types (*Proteacidites* spp.) became extinct about the end of the Eocene and during the Oligocene, but other types, e.g. *Helicia* — *Orites* are found throughout the whole period (see Appendix 2). Proteaceae pollen is under-represented in surface pollen spectra. In *Eucalyptus* forest with s sclerophyll shrub layer in which species of Proteaceae may constitute the major part, the pollen registers in low percentages only (Martin, 1978). Tree species of Proteaceae may be widespread in northeastern Queensland rainforests but their pollen is found only in low percentages in surface samples and Quaternary deposits (Kershaw, 1970b). It is thought that the ancient proteaceous types may have been higher pollen producers with more efficient pollen dispersal (Martin, 1978). A change in the pollination mechanism of the family Proteaceae is proposed by A. R. H. Martin (1981).

Diversity increases in the early Miocene C subdivision of the *P. tuberculatus* Zone, particularly amongst the tricolpate-tricolporate group. Quantitatively these account for an increase of only a few percent, from 7-9% in the Oligocene to 14-18% in the latter. Given that the parent plants would have been low pollen producers, they could have been quite significant in the vegetation. The proteaceous group, low pollen producers also, increase somewhat in the early Miocene as well (discussed previously). Collectively, these low pollen producers may have formed a substantial portion of the vegetation.

As discussed previously, early Miocene silicified woods in the upper Lachlan have been identified as Myrtaceae with affinities to *Eucalyptus* B, *Acacia* and *Nothofagus* (Bishop and Bamber, 1985). This wood assemblage cannot be placed in any palynological zone, but it further illustrates the mixed nature of the vegetation.

The mid Miocene *T. bellus* Zone vegetation would have been generally similar to that of the C subdivision, with a slight change in species composition.

?Mid Miocene-Pliocene palaeovegetation

The botanical affinities of the Myrtaceae pollen group of the Pliocene sequence is not necessarily the same as that of the group in the late Oligocene-early Miocene. Both the *Angophora* — bloodwood eucalypt type and the small-grained eucalypt type (discussed previously) are present. Other types similar to *Austromyrtus*, *Baeckea*, *Backhousia*, *Rhodamnia*, *Syzygium*, *Tristania* (Martin, 1973a) and possibly others as well are present. Whatever the identity of the Myrtaceae pollen, its association with some rainforest element (see Appendix 3) and low Gramineae/Compositae counts (see Figs 10, 11, 12) indicate a good forest cover.

The Myrtaceae phase may have been closed forest (Martin, 1978) and this interpretation would accommodate the rainforest element present in the Myrtaceae phase. However, tall open forest (= wet sclerophyll), in which species of eucalypts are dominant and some rainforest taxa are present as small trees (Ashton, 1981) is an alternative interpretation. The rainforest element present in wet sclerophyll includes myrtaceous taxa. Moreover, tree ferns are a conspicuous feature of the east coast wet sclerophyll (Ashton, 1981) and these assemblages have a considerable *Cyathea* spore content. The nature of the myrtaceous forests is considered further in the discussion.

The gymnosperm and *Nothofagus* phases would have been closed forests. It is likely that they had a patchy distribution, occupying the well-watered sites in the valley. Myrtaceous forests were present also, although probably relegated mainly to drier sites, the slopes and ridges. *Nothofagus* was more extensive upstream near Cowra, with a noticeable decline downstream, with very little at Jemalong Gap (see Fig. 13). This distribution suggests that *Nothofagus* migrated downstream from the highlands where it was probably considerably more abundant during the late Miocene. Gymnosperms were most abundant upstream also, but they were relatively common downstream as well, to beyond Jemalong Gap (see Fig. 17). *Podocarpus* was the most common gymnosperm but Cupressaceae, *Phyllocladus* and *Dacrycarpus* were sometimes abundant (see Fig. 14). Today, *Callitris* of the Cupressaceae is well known in the inland, semi-arid regions and may grow as forests in the Lachlan Valley, but there is one rainforest margin species, *Callitris macleayana* (Boland *et al.*, 1984). There are other possibilities within the family Cupressaceae. Whatever the identification of the fossil Cupressaceae pollen, its association with other rainforest taxa and a carbonaceous clay lens (indicative of a swampy environment) suggests that it was a rainforest taxon also.

Other rainforest angiosperms (see Appendix 3) were usually present. The pollen registers in low percentages, but the parent plants may have been relatively common. They may have occupied favourable habitats such as stream sides and sheltered gullies, or may have been present in the understorey layers of wet sclerophyll.

As discussed previously, a more specific identification of Casuarinaceae pollen is difficult. *Gymnostoma* may be found in rainforests. *Casuarina* is not a normal constituent of rainforest but it may be found in open forest bordering rainforest. Species of *Casuarina* may be found in most kinds of vegetation, from coastal open forests to arid shrublands. However, the high Pliocene Casuarinaceae assemblages occur stratigraphically close to the *Nothofagus* and gymnosperm phases, hence they may represent rainforest taxa or taxa which border rainforest. Riparian species may have been involved. The group may have consisted of different taxa at different times.

A shrub or small tree element may be present also (see Appendix 3). Most of the taxa in this element are represented by only a few percent and little may be deduced about their abundance. In a study of surface samples, Ladd (1979) did not recover *Acacia* pollen, yet

Acacia was co-dominant in the vegetation beneath which the samples were taken. Thus taxa in this element may have been common in the vegetation.

Fern spores are subject to water transport (Ladd, 1978; Birks and Birks, 1980). Consequently, the high spore assemblages may have been produced by runoff from a nearby gully containing abundant ferns. Such gullies would be particularly favourable for *Cyathea*.

Towards the top of the upper Myrtaceae phase, Compositae and Gramineae increase and the gymnosperms and other rainforest taxa decrease. These assemblages are thought to be transitional between the Pliocene and Pleistocene. The closed forest canopy was decreasing and open forest, woodland and grasslands were expanding.

In summary, the ?mid Miocene — Pliocene sequence is a record of gradual decline of the rainforest element. It was moderately common in the oldest part of the sequence. The vegetation was probably a mosaic of rainforest in the most favourable habitats, wet sclerophyll (further evidence for wet sclerophyll is presented in the section on fire history) covering considerable areas and with dry sclerophyll in the driest habitat. For a period, probably in the early Pliocene, rainforest expanded and would have occupied substantial areas of the valley during the *Nothofagus* and gymnosperm phases. Subsequently in the upper Myrtaceae phase, the rainforest element declined and eventually disappeared from the Lachlan Valley and its tributaries.

Pleistocene palaeovegetation

The abundance of Compositae and Gramineae (see Fig. 18) indicates open vegetation, probably woodland and grasslands/herbfields. Most of the trees would have been myrtaceous or casuarinaceous. The Casuarinaceae group, which is sometimes abundant, probably consisted of different species to those in the group during the late Miocene — Pliocene. Gymnosperms were rare and rainforest angiosperms (see Appendix 3) had disappeared from the valley and its tributaries.

The spore content is low and Anthocerotae are the most common of the group. Anthocerotae are commonly found along stream banks in open vegetation.

The Pleistocene sequence is very disjointed and nothing may be deduced about the vegetation of glacial and interglacial times. The stratigraphic position of the assemblages in the Cowra Formation (see Fig. 16) suggests most of them may be contemporaneous. It is thought these assemblages are older Pleistocene in age. It may be argued that the interglacials were more humid, being times of high sea level, and swamps necessary for preservation of pollen would be more likely at these times, hence all of the pollen assemblages presented here probably represent interglacial period(s). However, there is no direct evidence to support this argument. These Pleistocene assemblages are presented here for comparison with those of the Pliocene and to illustrate the considerable difference between the two.

Wood has been encountered in bore 12437, Section 4 at a depth of 26m (see Fig 16). It has been identified as probably *Eucalyptus resinifera* by H. K. Bamber, Forestry Commission (Williamson, 1986). *E. resinifera* is found in dry sclerophyll and wet sclerophyll (Boland *et al.*, 1984). Unfortunately, pollen was not recovered from this level in bore 12437. The identification of *E. resinifera* suggests that some relatively denser forest vegetation may have been present in the Pleistocene, probably confined to the more favourable habitats.

FIRE HISTORY

Black carbonized particles are readily recognized in palynological preparations. Such particles are usually regarded as charcoal fragments and variations in abundance of the particles are used to reconstruct Quaternary fire history (e.g. Singh *et al.*, 1981). Carbonized particles, or fusinites of the coal petrologist, may result from charring, oxidation, mouldering or fungal attack before deposition, or on the peat surface. Carbonization may also result from coalification after deposition (Teichmuller, 1982). Thus care must be exercised in the interpretation of carbonized particles, particularly for the Tertiary and older geological periods.

Fire is not essential for carbonization of plant material. It is thought that dehydration and oxidation on the swamp surface may produce fusinite. Fungal attack may cause effects similar to carbonization. For example, dry rot alters the unused part of the wood into carbon-rich, humic substances. Other fungi and other plants may produce dark material, which looks similar to carbonization. These and other factors are reviewed by Teichmuller (1982). By and large, these processes which produce carbonization without burning are not well understood, but there seems little doubt that a portion of this material may be attributed to burning (Kemp, 1981).

The re-working of carbonized particles in older sediments, particularly if they contain coal seams, may cause serious error in the deduction of a fire history. However, re-working may be detected by older palynomorphs included in a younger assemblage. A very small amount of early Tertiary re-working has been detected in the late Miocene — Pliocene sequence of the Lachlan River Valley, but no Cretaceous or older palynomorphs have been found. In particular, there is no evidence at all of re-worked Permian coals, the most likely cause of serious error. There may be a very small amount of Early Cretaceous re-working in the base of the Eocene — Oligocene sequence of the Murray Basin.

When fire is the cause of carbonization, a high degree of charring may result in very brittle fusinite which readily disintegrates into fine fragments. Less strongly charred wood may preserve the cellular structure, although probably with distortions (Teichmuller, 1982). Much of the fuel in forests is bulky and rarely, if ever, burns completely (Luke and McArthur, 1978). Fires may sweep over herbaceous swamps, burning the plant cover to water level. Fusinites of such peats shatter easily and are deposited as fine splinters. The surface of a peat swamp may occasionally dry out and ground burning may occur with the formation of a great deal of ash. This ash, however, is easily blown away or dissolved in swamp waters which are rich in carbon dioxide. Some charcoal remains on the ground, but the fine fragments are readily blown away and deposited elsewhere (Teichmuller, 1982). These are a few of the possible effects in the deposition of carbonized particles that may result from fires.

Clark (1984) reviews the effects of different pollen preparation procedures on carbonized particles and the problems of identification. The most important for this study, which presents counts of carbonized particles, is that larger particles may be broken into small pieces. Burning destroys the stratification of the cell wall (middle lamella, primary wall and secondary wall) and this feature may be used to identify charcoal from dark-coloured, unburned plant tissue (Cope and Chaloner, 1980). However, different chemical treatments may destroy stratification or produce a similar effect in cell walls which have had stratification destroyed (D. R. Selkirk, *pers. comm.*). In this study, carbonized particles were counted in preparations made for palynomorphs where treatment included a moderate oxidation process. Identification of particles was made with reference to burnt plant material which was then treated by the same chemical procedure as that used on the sediments. Particles within the size range of pollen were counted. Estimations of the area of carbonized particles (Clark, 1982) which allow for the different sizes of the particles were not possible as the preparations were made long before the decision to count carbonized particles and the methods used are unsuitable for area estimations. Counts are presented as the ratio of carbonized particles to total pollen count, in Fig. 19.

The interpretation of the abundance of carbonized particles is problematical (see review by Clark, 1983), even with the assumption that most of the particles result from burning. Charcoal particles may be transported by air currents, particularly at the time of fire, or washed from bare ground after fires. Larger particles may be broken into smaller fragments before deposition. A greater abundance of charcoal does not necessarily mean more fires, it may result from bigger fires. More charcoal probably indicates that more fuel was burnt, but even this interpretation assumes that the fuel was charred to the same degree.

The prerequisites for wild fires are

1. a fuel supply;
2. the fuel must dry out sufficiently so that it can burn; and
3. a source of ignition.

Lightning would have been the main agent (Kemp, 1981), and probably the sole source of ignition for the Tertiary and the portion of the Pleistocene under consideration here, which predates the arrival of man.

The palaeovegetation was almost entirely forests, with woodlands and grasslands becoming prominent only in the Pleistocene. Fuel is not limiting in forests (Luke, 1961). Closed forests rarely burn, except in drought periods when they are subjected to exceptional drying (Webb, 1970; Luke and McArthur, 1978). However, the pollen record is biased towards those plants growing close to the site of deposition. It may be that closed forest grew around the site of deposition and was rarely burnt, whereas a drier, more open kind of vegetation on the slopes and ridges was burnt more frequently, the charcoal being transported eventually to the site of deposition.

The interpretation adopted in this study is that an increase in carbonized particles, most of which are probably charcoal, indicates a greater frequency and/or intensity of dry periods which would allow burning, given adequate fuel. The major control of wild fires is thought to be climatic (discussed further below). Charcoal from fires anywhere in the catchment would eventually become incorporated in sediments at the site of deposition.

Counts of carbonized particles are presented in Fig. 19. In the late Eocene — early Miocene of Bore 38342 (Fig. 19A), the ratios of carbonized particles are low but increase somewhat towards the top of the sequence. In this sequence, there is a variety of dark-coloured bodies, some of which may result from the coalification process, but only particles similar to the reference burnt plant material and to the carbonized particles seen in the late Miocene — Pliocene sequence were counted.

The abundance of carbonized particles in the mid Miocene *T. bellus* Zone at Euabalong and Jemalong Gap is comparable to the early Miocene in the top of Bore 36342. In the Myrtaceae phase of the late Miocene — Pliocene sequence, the abundance is much higher. The ?*Nothofagus*-gymnosperm phase of Jemalong Gap has lower ratios of carbonized particles which are comparable with those of the *T. bellus* Zone. In Bore 14747, the *Nothofagus* phase has low ratios and the ratios of the gymnosperm phase are intermediate between the *Nothofagus* and Myrtaceae phases.

In summary, burning levels were extremely low in the late Eocene and most of the Oligocene. In the late Oligocene to mid Miocene, burning increased somewhat but it was still relatively low. Burning increased considerably in the lower Myrtaceae phase (which may be as old as mid Miocene). Burning decreased in the *Nothofagus* and gymnosperm phases (probably early Pliocene) to levels similar to those of the Oligocene — mid Miocene and increased in the upper Myrtaceae phase to the highest levels of the sequence.

THE EFFECTS OF CHANGING SEA LEVEL

Changes in sea level have an important influence on sedimentation and the environment, especially close to the shoreline. At times of high sea level, drainage is sluggish and the low-lying areas in the landscape are swampy. Sediments accumulate at these times. Evaporation is higher from the shallow seas over the continental shelves and flooded low-

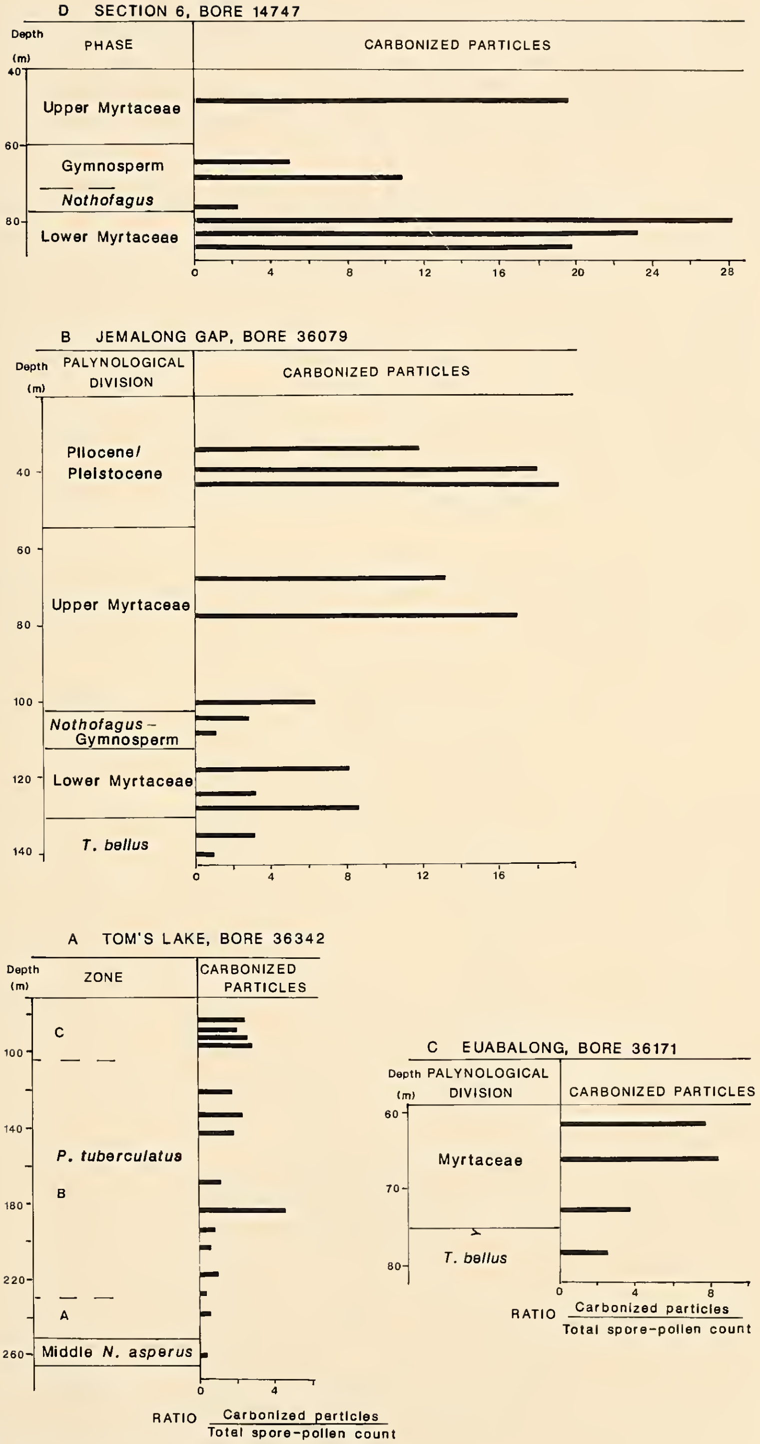

Fig. 19. Carbonized particle counts.

lying areas. As a consequence, precipitation is greater and through this effect, changing sea levels may have considerable influence a long way from the shoreline. At times of low sea level, with the shoreline close to the edge of the continental shelf, drainage is more efficient and there may be erosion and/or lack of sedimentation. Evaporation from the colder, deeper seas at the edge of the continental shelf is less, consequently precipitation is lower. At these times, the climate is more continental.

Fig. 20 presents the late Eocene to Oligocene changes in sea level, based on the sedimentary cycles recognized on the southern margin of Australia (from Loutit and Kennett, 1981). This curve is the most appropriate, for although the changes in sea level may be correlated on a worldwide basis, local tectonics may modify their expression. Sedimentary cycles have not been reported for the late Pliocene to Pleistocene on the southern margin of Australia so the global changes in sea level (from Vail *et al.*, 1977) are presented for this time range. The changes became more frequent in response to glacial-interglacial oscillations of the last 2-3 million years.

In Bore 30407 of section A-A^1 (see Fig. 7), the younger *P. tuberculatus* Zone extends almost 60m below the boundary of the older Middle *N. asperus* Zone. This depth of 60m is considerable and more than would be expected with a simple change of the river course. It is thought to illustrate downcutting at a time of low sea level and subsequent fill with younger sediments.

In the eastern edge of the Murray Basin, the Oligocene low sea level (Fig. 20) is expected to be a time of erosion. However, the effect of this low sea level is not detectable in the non-marine sediments (R. M. Williams, *pers. comm.*). It is thought that with the almost

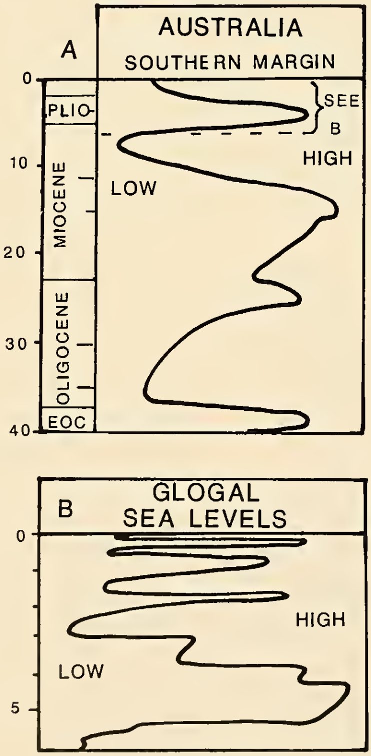

Fig. 20. Changes in sea level. The southern margin of the Australian continent from Loutit and Kennett (1981) and global sea levels from Vail *et al.* (1977).

flat terrain and a rainfall sufficiently high to maintain the forest cover, erosion would be minimal (Bishop, 1985b; Martin, 1986a; 1986b). The late Miocene low sea level, however, is evident in the sediments (R. M. Williams, *pers. comm.*). At this time, the climate was becoming drier and the cover of vegetation would be more difficult to maintain, thus allowing erosion (Martin, 1986a; 1986b). The relative scarcity of the mid Miocene *T. bellus* Zone which was deposited at a time of high sea level, may be attributed to subsequent erosion during the late Miocene low sea level.

The lower Myrtaceae phase is not as thick as would be expected if, as discussed previously, it begins in the mid Miocene. It is thought that the late Miocene low sea level, accompanied by a somewhat drier climate (discussed further below) resulted in erosion or lack of deposition and this may account for the relatively thin sections of lower Myrtaceae phase seen in Figs 10, 16 and 17. Other factors may be involved as well. Tectonics may have had some influence in the Lachlan River Valley where lower Myrtaceae phase forms a relatively thin section over the basement. As discussed previously, there is also uncertainty about the age of the transition of the *T. bellus* Zone and lower Myrtaceae phase (see Fig. 5).

The early Pliocene high sea level is expected to be a time of higher precipitation which, it is thought, allowed the *Nothofagus* and gymnosperm phases in the Lachlan River Valley. With the subsequent fall in sea level in late Pliocene, the Myrtaceae phase is evident once more.

The relatively rapid rise and fall of sea level in the Pleistocene cannot be detected in the palynological record which, as discussed previously, is extremely fragmentary. Moreover, the sea was denied access to the Murray Basin by the closure of the entrance, probably in the late Pliocene (Brown *et al.*, 1968; Abele *et al.*, 1976). As a consequence, the drainage route to the sea became much longer and this would have made a difference to the erosion/sedimentation associated with low/high sea levels (respectively).

PALAEOCLIMATE

The palaeoclimate may be deduced from the climatic requirements of comparable, present-day vegetation, but this can only be attempted at a very general level. Interpretations of the palaeovegetation are very general and as discussed previously, a good fit with some extant vegetation does not exist. However, some general climatic parameters may be deduced from the extant vegetation and applied to the palaeovegetation to illustrate climatic trends.

Brassii species of *Nothofagus* may be dominant in the mid montane zone of the New Guinea Highlands (Johns, 1982). *Nothofagus* is generally associated with high precipitation of 1500-1800mm and considerable cloudiness which reduces light intensity and maintains high humidities. It is generally absent from areas which suffer a regular and sustained water deficit (Ash, 1982). In New South Wales, one species of the *menziesii* type, *Nothofagus moorei* is present in the Eastern Highlands and may be dominant where precipitation exceeds 1800mm. It is usually restricted to sites that are commonly fog bound (Baur, 1957). Boland *et al.* (1984) give the annual rainfall of *N. mvorei*, not necessarily dominant in the vegetation, as 1500mm, with the driest months receiving 60mm, augmented by mountain mists. In general, *Nothofagus* requires a high precipitation and maintenance of relatively high humidities throughout the year.

As discussed previously, the myrtaceous vegetation may have been closed forest. In New South Wales, Myrtaceae are common in rainforests which require a precipitation of 1500mm for widespread development (Baur, 1957). Alternatively, the myrtaceous vegetation may have been wet sclerophyll (or mosaic of rainforest and wet sclerophyll) and the fire history favours this interpretation. Wet sclerophyll may be found over large tracts receiving between 1000mm and 1500mm (Ashton, 1981). Thus the Myrtaceae phase probably indicates a precipitation of somewhat less than 1500mm, probably between 1000mm and 1500mm.

The disappearance of the rainforest element from the landscape is another important parameter. The lower precipitation levels of the major eucalypt species of the drier end of the range of wet sclerophyll (in Ashton, 1981) is about 500-700mm (precipitation requirements from Boland *et al.*, 1984). The limit of subcoastal rainforest pockets across northern and northeastern Australia falls between the 600mm and 800mm isohyet (Webb and Tracey, 1981). Whichever interpretation of the Myrtaceae phase is favoured, it makes little difference to the climatic parameter at the drier end of the range.

Using these parameters and the trends shown by the carbonized particles, changes in climate may be reconstructed. It should be emphasised that there is no great precision in this reconstruction: the parameters are used more to illustrate a climatic trend.

In the Hillston region, the precipitation of the late Eocene and Oligocene was high, probably above 1800mm. High humidities were maintained throughout the year and the vegetation rarely dried out sufficient to allow burning. Fires would have been very limited in extent. There may have been a gradual, slight decrease in precipitation during the upper part of the Oligocene. In the late Oligocene — early Miocene, precipitation was probably less than 1800mm but above 1500mm. There was no definite seasonal dry period and fires were only slightly more frequent than in the preceding period. This level was maintained into the mid Miocene *T. bellus* Zone.

In the Hillston region, pollen preservation ceased in the early Miocene. Pollen preservation requires permanently wet sites which remain wet long enough for burial to a depth below the influence of the fluctuating water table. The disappearance of permanently wet sites from the landscape would have been the result, in part, of climatic change over the region as well as of a decrease of water transported into the region by the river (discussed further below). Subsequently, the sites of pollen preservation were located upstream from the edge of the Murray Basin, particularly around Jemalong Gap and in the Lachlan River Valley to Cowra.

In the ?mid Miocene, i.e. the start of the lower Myrtaceae phase, there was a further drop in precipitation probably to somewhat below 1500mm, but not less than 1000mm. A well-defined seasonal dry period became established at this time, and burning became a regular event in the landscape. The drier slopes and ridges were probably most subject to burning.

In the early Pliocene, the time of the *Nothofagus* and gymnosperm phases, precipitation increased, probably to more than 1500mm but not more than 1800mm. The level of burning decreased. In the mid — late Pliocene, the precipitation decreased once again to about or below 1500mm and the level of burning increased as well. Precipitation continued to decrease so that at the end of the Pliocene, it was probably about 500mm-800mm.

Wood recovered from the base of the Pleistocene Cowra Formation, identified as probably *Eucalyptus resinifera*, indicates a precipitation of at least 800mm, the lower limit for this species. This evidence does not contradict the above deductions, which are at best very general, and given the lack of any evidence to date the 'Pliocene — Pleistocene' boundary.

The changes in precipitation are shown diagrammatically together with the major palynological events in Fig. 21.

Today, the mean annual precipitation for Hillston is about 140mm, Forbes 200m to 210mm and Cowra, 240mm to 250mm, respectively.

The climatic parameters discussed above have been deduced from plant growth and in this context, 'precipitation' is more precisely 'effective moisture'. Effective moisture includes both rainfall and water transported by the river systems (Martin, 1986b) and the latter was probably important in the maintenance of the permanently wet sites required for pollen preservation. The climatic change described above could not occur over the Lachlan

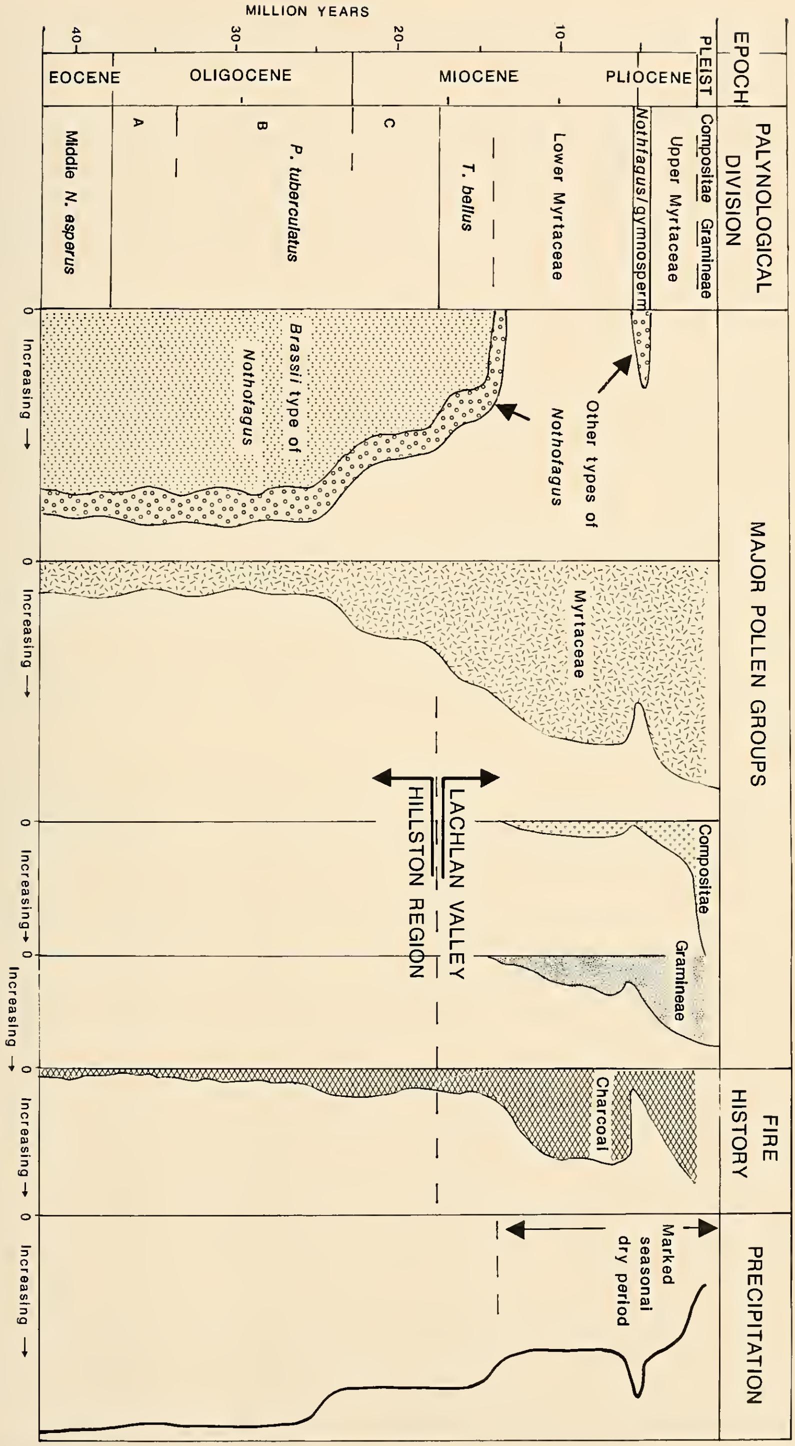

Fig. 21. Summary of major palynological events and the inferred changes in precipitation (Not to scale.)

Valley in isolation from the surrounding areas. Parallel changes would have occurred in the Eastern Highlands over the headwaters of the river and these would have been very important for the volume of water transported by the river.

Effective moisture also includes the influence of temperature through its effect on evaporation. Temperature is also very important for plant growth but it is not considered here because effective moisture is thought to be the major control. Oligocene — early Miocene temperatures were probably somewhat higher than those of today. Surface sea temperatures during the mid Miocene were about 5°C higher than those of today (Savin *et al.*, 1975; Shackleton and Kennett, 1975), hence land temperatures were probably somewhat higher also (Martin, 1986b).

Discussion

The nature of the late Miocene — Pliocene myrtaceous forests with its component of rainforest taxa has long been problematical. It was thought that they were closed forests, perhaps akin to the 'heath forests' of Borneo (Martin, 1982). This interpretation was based on an inadequate appreciation of the diversity of pollen types within the genus *Eucalyptus*. With a greater eucalypt content, an alternative interpretation of wet sclerophyll forest is possible. The record of carbonized particles is extremely important in this context. Rainforest rarely burns (Webb, 1970; Luke and McArthur, 1978) whereas 'there can be little doubt that fire is an integral part of the environment' of wet sclerophyll forests (Ashton, 1981). The great increase in carbonized particles in both the lower and upper Myrtaceae phases supports the interpretation of wet sclerophyll forest. As discussed previously, the late Miocene — Pliocene palaeovegetation was probably a mosaic of rainforest, wet sclerophyll and dry sclerophyll, each type of vegetation occupying the appropriate habitat in the landscape.

A more precise identification of myrtaceous pollen is possible. The grain may be scored for a number of characters and a combination of several character states may be distinctive. It is found that the character states of the fine detail are the most promising for this purpose (Chalson and Martin, manuscript submitted). Taxonomically closely related species may not be separable (Martin and Gadek, manuscript submitted), but pollen of the family should be divisible into a large number of groups. A more precise identification of the pollen awaits the compilation of a reference set scored for the distinctive character states. For the late Miocene — Pliocene assemblages, this set should include all species common in eastern Australian rainforests, wet sclerophyll and dry sclerophyll — a formidable task. For older assemblages, the reference set should include species in New Guinea, New Caledonia and New Zealand.

Late Oligocene — early Miocene assemblages from the western Murray Basin have a considerable myrtaceous content (Truswell *et al.*, 1985) but it should not be assumed this content is the same as that of the late Miocene-Pliocene assemblages in the Lachlan valley. A study of the carbonized particles may shed some light on this problem, but more precise identification of the myrtaceous pollen is required for the western Murray Basin also.

The major changes of palaeoclimate, as inferred from the vegetation, are thought to be linked with the development of circum-Antarctic oceanic circulation and the extent of glaciation on Antarctica (Martin, 1986b). Antarctica has had, and still has, a profound influence on world climate (Flohn, 1978), particularly on Australia because of its close proximity. About late Oligocene, circum-Antarctic circulation was established (Kennett, 1977; 1978). This factor probably reduced the efficiency of the heat transfer from the equator to the pole, thus increasing the temperature gradient between these regions. The extent of ice cover on Antarctica is uncertain but all the evidence indicates high latitude cooling and a northwards shift of westerly winds which would have influenced much of southern

Australia (Kemp, 1978; Flohn, 1978). It is thought that these events initiated the decrease in precipitation which resulted in the decline of the *brassii* type of *Nothofagus* (Martin, 1986b).

The early Miocene was a time of increasing temperatures (Savin *et al.*, 1975; Shackleton and Kennett, 1975). At the beginning of the mid Miocene, a major global climatic threshold was reached with the development of the East Antarctic ice cap (Kennett, 1977; 1978). The cause of this event remains unknown, but Kennett (1978) notes that this development occurred at a time of warmer temperatures which would have increased precipitation over Antarctica. (The mid Miocene was a time of high sea level, as discussed previously.) By the late middle Miocene, temperatures began to fall again. In the late Miocene, the ice cap retreated somewhat. It is difficult to match up the complex, poorly-dated events in the Lachlan River region with the complex developments in Antarctica. However, the mid Miocene was a time of profound change in both, and in this respect, they are in agreement. The late Miocene was a time of major cooling (Savin *et al.*, 1975; Shackleton and Kennett, 1975). Cooler oceanic temperatures result in lowered precipitation and this is in accord with the lower Myrtaceae phase of this time and the inference of reduced precipitation.

The charcoal record suggests that a well marked dry season, which allowed fires to become an integral part of the environment, dates from the ?mid — late Miocene.

A major extension of the Antarctic ice cap occurred in the late Miocene — early Pliocene (Kennett, 1977), a time of somewhat higher temperatures (Savin *et al.*, 1975) and high sea levels. This is thought to coincide with the *Nothofagus*/gymnosperm phases. Cooling continued from the mid Pliocene (Kennett, 1977; Savin *et al.*, 1975) which would have resulted in lower precipitation and the return of the Myrtaceae phase. A further global climatic threshold was passed in the late Pliocene when the glacial/interglacial oscillations commenced (Kennett, 1977). It is thought that this event coincided with the elimination of the rainforest taxa from the Lachlan River valley.

Climatic changes such as these could not .have occurred over the Lachlan valley in isolation from the surrounding areas which must have experienced similar or parallel changes. There is evidence of a climatic gradient across the Murray Basin, parallel to that of today, during the late Oligocene — mid Miocene (Martin, 1986b).

Decreasing precipitation over the Eastern Highlands would have had extremely important consequences on the activity of the rivers. The mid Miocene decrease in precipitation would have reduced the volume of water carried by the river such that it was unable to maintain the permanently wet sites in the Hillston region, but it was sufficient to maintain some permanently wet sites upstream in the Lachlan valley.

Weathering subsequent to deposition may destroy pollen and this may alternatively account for lack of pollen preservation. However, it is unlikely to be the sole cause. In the Hillston region, pollen preservation ceases in the early Miocene and the upper 80-100m of sediment are barren. In the Cowra district, however, grey carbonaceous clays containing Pleistocene assemblages may be found at depths of less than 20m. Thus the observed pattern of the cessation of pollen preservations being younger, further upstream best fits an hypothesis of a climatic gradient and a progressively diminishing volume of water carried by the river.

Changing sea levels and climate have probably played a part in shaping the Lachlan valley itself. As discussed previously, the late Miocene low sea level was a time of erosion and this would have removed most of the older sediments in the valley. Early and mid Miocene sediments are only found south of the present river near Forbes (see Figs 2 and 16F). The river once turned southwest about Section 7 and passed under Section 8, some 15km southwest of Forbes (discussed previously). When base levels were lowered and downcutting commenced, it is likely that the river adopted its present, shorter course to Jemalong Gap, thus bypassing the older sediments to the south.

The late Miocene was also a time of reduced precipitation hence the river carried a reduced volume of water which would have cut a narrower valley within the existing wide valley to produce the observed valley-in-valley structure. Williamson (1964; 1986) argues that the valley-in-valley structure was produced as a result of uplift of the highlands but Bishop *et al.* (1985) note that there does not seem any need to invoke dynamic (active) tectonism to account for the geomorphology of the Lachlan Valley. However, isostatic rebound (i.e. passive tectonism) probably occurred in response to erosional unloading (Bishop, 1985b). Moreover, signs of minor isostatic uplift may be expected mostly at the edges of the highlands (Bishop, 1987). Earthquakes in the region today show that adjustment to stresses in the earth's crust is still in progress (Denham *et al.*, 1985). Thus passive tectonism, combined with a reduced precipitation probably produced the valley-in-valley structure.

Climate has probably had an influence on the nature of the sediments themselves. With a high precipitation, various rock types would be decomposed leaving only the most resistant quartz and chert, as seen in the Lachlan Formation. The Cowra Formation, which contains an assortment of the rock types found in the catchment area, was deposited under much lower precipitation: insufficient for their decomposition. As discussed previously, Williamson (1986) postulates a formerly widespread quartz gravel formation as the source of the quartz in the Lachlan Formation. No doubt, older sediments have been reworked and they were probably mainly quartz. An hypothesis about the source of the quartz sands and gravels in the Lachlan Formation would have to be suitable for a very wide application, for all the Pliocene and older sediments of the river valleys of the western slopes of New South Wales have similar quartz gravels and sands. Experience with sediments of Cretaceous to early Oligocene age in the Gippsland, Bass and Otway Basins (Martin, unpubl.) has revealed similar quartz sands and the almost complete absence of other resistant rock types. Precipitation was also higher throughout this time span. Thus it is thought that climate has been the major factor in the production of these quartz rich sediments.

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APPENDIX 1
THE POLLEN GROUPS

SPORE/POLLEN GROUP	FOSSIL NAME	PLANT TAXA
Anthocerotae	*Cingulatisporites bifurcatus* 1	Similar to Anthocerotae
Fern spores	Numerous	Numerous pteridophyte taxa
Cyathea	*Cyathea paleospora* 1	*Cyathea* spp
Gymnosperms	*Araucariacites australis* 1	Araucariaceae, mainly *Araucaria* but *Agathis* could be included
	Cupressaceae	Cupressaceae
	Dacrycarpites australiensis 2	*Dacrycarpus*
	Dacrydium florinii 1	*Dacrydium* spp
	Microcachryidites antarcticus 1	*Microcachrys*
	Phyllocladidites mawsonii 3	*Lagerostoma* (= *Dacrydium*) *franklinii*
	P. palaeogenicus 4	*Phyllocladus* spp
	Podocarpidites ellipticus 1	*Podocarpus*
Myrtaceae	*Myrtaceidites* spp	All taxa in the family Myrtaceae
Nothofagus	*Nothofagidites, brassii* group e.g. *N. emarcidus* 3 *N. vansteenisii* 3 *N. falcatus* 3	Species of *Nothofagus* growing in New Guinea, New Caledonia and New Hebrides
	Nothofagidites, fusca group *N. brachyspinulosus* 3 *N. flemingii* 3	*Nothofagus gunnii* and all New Zealand species except *N. menziesii*. Some South American species also
	Nothofagidites, menziesii group *N. asperus* 3	*Nothofagus moorei, N. cunninghamii, N. menziesii* and some South American species
Casuarinaceae	*Haloragacidites harrisii* 3 *Casuarinidites cainozoicus* 1	All species of the family. *Gymnostoma* cannot be separated from *Casuarina* on pollen morphology (see Kershaw 1970a).
Compositae	*Tubulifloridites* spp 1	All species in the family Compositae, excluding Cichorieae
Gramineae	*Graminidites media* 1	All species in the family Gramineae

THE POLLEN GROUPS (Cont'd.)

SPORE/POLLEN GROUP	FOSSIL NAME	PLANT TAXA
Cichorieae	*Fenestrites* sp. 5	Cichorieae of the family Compositae
Chenopod/amaranth	*Chenopodipollis chenopodeaceoides* 5	Family Chenopodiaceae and some taxa of the Amaranthaceae
Proteaceous type	*Proteacidites* spp (sens. lat.)	Mainly related to Proteaceae (excluding Banksieae and *Beauprea*)

References:
1. Martin 1973a
2. Cookson & Pike 1953
3. Stover & Partridge 1973
4. Cookson & Pike 1954a
5. Truswell *et al.* 1985.

APPENDIX 2

LOW PERCENTAGE ANGIOSPERMS IN THE EARLY– MID TERTIARY

These distributions apply specifically to the Lachlan River region and are not necessarily the complete range of the species

		OCCURRENCE			
		Middle *N. asperus* Zone	*P. tuberculatus* Zone Subdivisions		*T. bellus* Zone
PLANT TAXON	FOSSIL NAME		A + B	C	
Acacia	*Polyadopollenites myriosporites* 1			+	+
Anacolosa	*Anacolosidites* ssp 1	+			
Austrobuxus (Longetia)-Dissiliaria	*Malvacipollis* 1,5	+			
	Polyorificites oblatus 2,5 = *Heliciporites astrus* 1	+	+	+	+
Banksieae	*Banksieaeidites elongatus* 1	+	+	+	+
Beauprea	*Beaupreaidites* spp 1	+	+		
Compositae	*Tubulifloridites* sp 1			+	+
Cunoniaceae	Cunoniaceae (tricolporate) 3	+	+	+	
Cunoniaceae — Eucryphiaceae	*Geissois* — *Eucryphia* comp 3	+	+	+	
Cupanieae	*Cupanieidites* spp 1	+	+	+	+
Cyperaceae	Cyperaceae 2, *Cyperaceaepollis* spp 4	+	+	+	+
Dodonaea triquetra	*Nuxopollenites* sp 4			+	
Dodonaea spp	*Dodonaea sphaerica* 2		+		
Elaeocarpus	*Elaeocarpus* comp 3	+	+		
Epacridaceae	*Ericipites* spp 1	+	+	+	
cf Goodeniaceae	—				+
Gramineae	*Graminidites media* 2	+	+	+	+
cf *Grevillea*	—			+	
Haloragis	*Haloragacidites haloragoides* 2				+
Helicia — *Orites*	*Proteacidites ivanhoensis* 2	+	+	+	+
Ilex	*Ilexpollenites* sp 1	+	+		

Low Percentage Angiosperms in the early–mid Tertiary (Cont'd.)

		OCCURRENCE			
		Middle	*P. tuberculatus* Zone Subdivisions		
PLANT TAXON	FOSSIL NAME	*N. asperus* Zone	A + B	C	*T. bellus* Zone
cf Liliaceae	*Liliacidites* spp		+	+	
Loranthaceae	Loranthaceae 3	+	+		
Macaranga — Mallotus	*Tricolporopollenites endobalteus* 5	+	+	+	
Malvaceae	—		+		
Pelargonium	*Tricolporopollenites pelargonioides* 6		+		
Polygalaceae	*Polycolpites esobalteus* 1	+	+		
Proteaceae	*Proteacidites* spp	+	+	+	+
—	*Proteacidites rectomarginis* 1	+	+		
Quintinia	*Quintinia psilatispora* 2	+	+	+	+
'Randia' chartacea	*Triporopollenites bellus* 1				+
Restionaceae, *Hypolaena* type	*Milfordia hypolaenioides* 2	+	+	+	+
Restionaceae, *Restio* type	*Milfordia homeopunctata* 1	+	+		
Santalaceae	*Santalumidites cainozoicus* 1	+			
Sapotaceae	*Sapotaceoidaepollenites rotundus* 1	+	+		+
Sparganiaceae	*Sparganiaceaepollenites* spp 2	+	+	+	+
—	*Stephanocolpites oblatus* 2		+	+	+
Symplocos	*Symplocoipollenites austellus* 1				+
Tasmannia	*Drimys tetradites* 2				+

References:
1. Stover & Patridge 1973
2. Martin 1973a
3. Luly *et al.* 1980
4. Truswell *et al.* 1985
5. Martin 1974
6. Martin 1973b

APPENDIX 3

LOW PERCENTAGE ANGIOSPERMS IN THE UPPER TERTIARY AND PLEISTOCENE OF THE LACHLAN VALLEY

(+) Present
(S) Shrub or small tree
(++) Common, present in most samples
(H) Herbaceous or ground cover
(T) Trace or rare
(R) Rainforest

PLANT TAXON	FOSSIL NAME	ELEMENT	Lower Myrtaceae Phase	*Nothofagus*/ Gymnosperm Phases	Upper Myrtaceae Phase	Pleistocene
Acacia	*Polyadopollenites myriosporites* 1	S	+	+	+	+
Banksieae	*Banksieaeidites elongatus* 1	S	+	+		
Chenopodiaceae/Amaranthaceae	*Chenopodipollis chenopodiaceoides* 4	H	+	+		
Cichorieae (of Compositae)	*Fenestrites* sp	H				+
Coelybogyne	*Psilatricolporites operculatus* 5	R	T			
Compositae	*Tubulifloridites* spp 2	H	+	+	+	++
Compositae	*Tubulifloridites pleistocenicus 2*	H				++
Cupanieae	*Cupanieidites* spp 1, 6	R		+		
Cyperaceae	*Cyperaceaepollis* spp 4	H	+	+	+	+
Dodonaea	*Dodonaea sphaerica* 2	S	+	+	+	+
Elaeocarpus	*Elaeocarpus comp* 3	R		T		
Epacridaceae	*Ericipites* sp 1	S	+	+	+	+
cf Goodeniaceae	—	S	+	T		
cf *Grevillea*	—	S		+		T
Gyrostemonaceae	—		T			
cf *Hakea*	—	S	+	+		
Haloragis	*Haloragacidites haloragoides* 1	H	++	++	++	++
Helicia-Orites	*Proteacidites ivanhoensis* 2	R	+	+	+	
Ilex	*Ilexpollenites* sp 1	R	T			
cf *Isopogon*	—	S	T	T		
cf Liliaceae	*Liliacidites* sp	H	+	T		T

APPENDIX 3 (Cont'd.)

PLANT TAXON	FOSSIL NAME	ELEMENT	Lower Myrtaceae Phase	*Nothofagus*/ Gymnosperm Phases	Upper Myrtaceae Phase	Pleistocene
Loranthaceae	Loranthaceae 3					+
Macaranga — *Mallotus*	*Triporopollenites endobalteus* 5	R	+			
Micrantheum	*Micrantheum spinyspora* 2	S	+		+	+
Monotoca	—	S	T	T	T	T
Myriophyllum	*Haloragacidites myriophylloides* 6	H	+	+	T	T
Onagraceae	Onagraceae 2	H				T
—	*Parsonsidites* 7		+			
—	*Polyporina granulata* 2					+
Proteaceae	*Proteacidites* spp	S	+ +	+ +	+	T
Quintinia	*Quintinia psilatispora* 2	R	+	+	+	
Restionaceae, *Hypolaena* type	*Milfordia hypolaenioides* 2	H	+	+	+ +	T
—	*Rhoipites alveolatus* 8 (= *Tricolporopollenites transversalis* 2)		+	+	+	+
cf. *Santalum*	—			T		
Sparganiaceae	*Sparganiaceaepollenites* sp 2	H	T		+	T
—	*Stephanocolpites oblatus* 2		+ +	+ +	+	T
cf. *Symphyonema*	*Proteacidites symphyonemoides* 2	S	+		T	
Symplocos	*Symplocoipollenites austellus* 1	R			+	
Tasmannia	*Drimys tetradites* 2	R	+	+	+ +	

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Post-Fire Demography in the Resprouting Shrub *Angophora hispida* (Sm.) Blaxell: Flowering, Seed Production, Dispersal, Seedling Establishment and Survival

TONY D. AULD

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After fire, the resprouting shrub *Angophora hispida* (Sm.) Blaxell rapidly forms an extensive canopy from epicormic and lignotuberous shoots, culminating in most plants in extensive flowering and fruiting. Flowering was virtually absent in populations which had not been recently burnt. There are virtually no predispersal seed predators in mature fruits.

Seed dispersal was minimal and confined to the immediate vicinity of the parent plant. In this study, released seeds were all viable and germinated following the first heavy rains. Seedling mortality was highest in the establishment phase (i.e., before the first leaves were produced) and declined markedly afterwards, remaining at a much lower rate for the following eight years. Seedling growth and lignotuber development were slow and after eight years the young plants may not be fire resistant. The importance of the length of inter-fire period for the survival of populations of this species is discussed.

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KEY WORDS: Demography, *Angophora hispida*, fire, resprouter.

INTRODUCTION

Two modes of post-fire regeneration have been documented. These are regeneration solely from seed following the death of all adult plants during a fire (obligate seeders), and regeneration from protected vegetative buds on surviving plants (resprouters) (see Gill, 1981). Whilst several workers have categorized plants according to their mode of recovery after fire (Purdie and Slayter, 1976; Purdie, 1977; Benson, 1985), information relating to the long-term survival and reproduction of species is sparse.

Keeley and Zedler (1978) developed a model to explain the evolutionary development of these two major modes of post-fire recovery in relation to fire frequency, in fire-prone Californian vegetation. Based on the demography of several representative species, they predicted that high fire frequencies favoured the evolution of resprouters over that of obligate seeders. One aspect of the life cycle which they did not consider was the importance of the primary juvenile period in resprouters. Bradstock (1985), who worked on two resprouting and two obligate seeding species, predicted that repeated fires of short frequencies may eliminate both resprouters and seeders. In resprouters, this was because of the slow growth rate in plants originating from seed (juveniles), and their delay in gaining fire resistance. Hence, frequent fire may prevent recruitment of plants. Abbott (1985) found a similar result for the resprouting *Banksia grandis*. Auld (1987) has shown that short fire frequencies (with <10 year intervals) are likely to reduce the abundance of the obligate seeder *Acacia suaveolens* by a decline in the buried seed bank. Consequently, any model trying to predict long-term changes in plant populations in relation to the fire regime should consider vegetative survival, growth, sexual reproduction, establishment and the subsequent length of the primary juvenile period, as well as the longevity of adult plants.

Angophora hispida is a common understorey shrub found in heaths and woodlands on Hawkesbury Sandstone around Sydney (Leach, 1986). It grows to 2-3m in height and 3-4m in width and flowers from November to January (Price, 1963). Plants are usually able to survive fire (Beadle, 1940), and regeneration occurs by a combination of lignotuberous and epicormic shoots from protected bud strands, as is typical of many species in the closely related *Eucalyptus* (McArthur, 1968).

Several components of the life cycle of the resprouter *Angophora hispida* (Sm.) Blaxell were examined using demographic methods in an effort to link post-fire regeneration to survival and reproduction. These components included seed production, dispersal, seedling recruitment and seedling survival. Predictions were made of the long-term behaviour of *A. hispida* populations under different fire regimes.

METHODS

Study sites were chosen in Ku-ring-gai Chase National Park and Manly Dam Reserve, some 10-30km north of Sydney. Annual precipitation for the region is around 1300mm with the wettest period being, on average, from January to June. The average maximum temperatures are 27°C in summer and 17°C in winter, whilst the average minimum temperatures are 17°C and 4°C, respectively.

Eleven study sites were chosen, each with a different time since fire. A range of times from one to 13 years was available, with replication for 1, 6 and 13 years. The sites are briefly described in Table 1. The soils at each site are derived from Hawkesbury Sandstone. Rainfall levels are roughly uniform across all sites throughout the study period. Rainfall data during this study were taken from the station at Manly Dam, approximately 1km from Site 1. Plant names follow Beadle *et al.* (1982).

TABLE 1

Location of study sites with time since burnt and characteristic vegetation. Vegetation type after Specht (1970)

Site	Years since fire	Vegetation and notes
1	1	Open heath with occasional emergent *Eucalyptus gummifera* and *E. haemastoma*. Understorey dominated by *A. hispida, Banksia ericifolia* and *Casuarina distyla*.
2	1 or >10	Vegetation as for site 1. This site was divided into two neighbouring populations of *A. hispida*. In both populations the fire which had burnt the site had stopped in the middle of the population, once through natural causes and once because of a small fire trail. This left one half of each population burnt and one half unburnt for at least 10 years.
3	3	Low woodland of *Angophora costata, E. gummifera, B. serrata* and *Xylomelum pyriforme*. Low (1-2m) shrub understorey of *A. hispida, Eriostemon australasius* and *Dillwynia floribunda*.
4	4	Open scrub of *A. hispida* and *B. oblongifolia*.
5	5	Open heath with occasional emergent *E. haemastoma*. Heath dominated by *A. hispida* and *B. oblongifolia*.
6	6	Open heath with *A. hispida* and *B. oblongifolia*.
7	6	Open heath with *A. hispida, B. marginata* and *Petrophile pulchella*.
8	7	Closed scrub of *A. hispida, Leptospermum attenuatum* and *P. pulchella*. Occasional emergent *E. haemastoma*.
9	10	Low woodland of *E. gummifera* and *E. haemastoma*. Understorey dominated by *A. hispida* and *D. retorta*.
10	13	Closed scrub with *A. hispida* and *P. pulchella*.
11	13	Closed scrub with *A. hispida* and *L. attenuatum*.

Fruit production

At each site, 20 individuals were randomly selected using a transect/baseline method. From randomly selected points along a baseline placed adjacent to the population to be sampled, 1m-wide transects were run into the population. A 1m interval was randomly chosen along these transects and any individuals touching the transect in this interval were sampled. The number of ripe fruits on each individual at the time of fruit maturation (February 1978) was counted. Where no fruiting individuals were encountered, the population was searched for any flowering and fruiting plants. Where possible, a sample of ripe fruits was harvested.

A further 10 individuals were similarly chosen and the number of living leaves on each counted, as an indicator of growth since the last fire, at sites 1,3,4,5,6,8,9 and 10.

For each fruiting individual that was sampled three size components were measured:

i) plant height (m);
ii) girth of the main stem (cm) at 15cm above ground; and
iii) total girth of all aerial stems (cm) at 15cm above ground.

Diameter at breast height (DBH) is not a useful measure in *A. hispida* because of the species shrubby, frequently multistemmed habit. Two girth measurements were included because of the heterogeneous nature of regeneration after fire, i.e. epicormic and/or lignotuberous regeneration. The data were analysed using a multiple regression.

An additional 21 individuals were randomly selected at Site 1 and fruit production on both types of regrowth i.e. epicormic and lignotuberous shoots recorded. This gave a better estimate of the variation in fruit production and allowed a comparison of fruiting success in relation to type of regrowth.

Predispersal seed predation

The components of each fruit harvested at Site 1 were examined to estimate the proportion of seeds that were intact, eaten by a seed predator, or undeveloped.

Seed dispersal

Initial seed fall on the soil surface was mapped along four, 50cm-wide, transects radiating from the centre of a cluster of *A. hispida* individuals.

Potential secondary dispersal by ants was examined:

i) Using 20 permanent quadrats (50 × 50cm) at Site 1 with 10 seeds of *A. hispida* and 10 seeds each of *Acacia linifolia* and *Acacia suaveolens*, both known myrmecochores (Berg, 1975; Auld, 1986). Movement of seeds by ants was observed intensively for five days. This trial was set up during seed fall for the acacias (December) and not when abundant *A. hispida* seeds were on the ground.

ii) During seed fall of *A. hispida* at Site 1 (March 1978), a permanent 1m^2 quadrat was set up near eight individuals. Thirty *A. hispida* seeds, each marked with a small white paint dot for ease of recovery, were placed in each quadrat. The fate of these seeds was followed for a month.

Seed dormancy and viability

Samples of 32 seeds from the seed lot collected from ripe fruits at Site 1 were tested for dormancy and viability monthly for six months. Seed collected from the soil surface some two weeks after seed release was also tested. Seeds were placed in petri dishes on Whatman's Seed Test Thick filter paper with distilled water. These were placed on a laboratory bench at room temperature. Germination was determined by the emergence of a radicle.

Seven replicates of 50 seeds in small hessian bags were randomly buried at a depth of between 0-5cm in Site 1. Mesh sides on the bags allowed the penetration of water, soil air and small soil animals, whilst preventing the movement of the large *A. hispida* seeds. One bag was to be recovered each month for seven months, with the component seeds being extracted and examined for dormancy, viability and signs of predation.

Seedling survivorship

The transect/baseline sampling method was used to locate 10 permanent quadrats at Site 1. Within these, the locations of 143 germinating seeds were mapped. The fate of these seeds was followed at weekly intervals for six months and then sporadically for a further seven years. Where possible, causes of mortality were identified.

At Site 1, 30 eight-year-old plants were unearthed in August 1986 and the depth of burial and size of the developing lignotuber were measured with a vernier caliper. The volume of the lignotuber was estimated by assuming it was an ellipsoid. The height and the number of live aerial stems and leaves of these plants was also measured.

Results

Fruit production

Flowering and fruit set were confined to those plants which had been burnt in the past 12 months i.e. plants at Sites 1 and 2. This was most evident at Site 2, where only half the plants had been burnt. Here burnt plants regrew extensive canopies and some flowered, whilst unburnt plants remained largely inactive and failed to produce any flowers or fruits. Whilst all burnt plants showed vigorous regrowth (Table 2) not all flowered (75% of plants at site 1 and 65% of burnt plants at site 2). No extensive, regrowth was evident at those sites not recently burnt (Table 2).

TABLE 2

Mean number of living leaves per individual

Site	Time since last fire (years)	mean number of leaves per plant (± S.E.)
1	1	2452.8 (373.1)
3	3	399.5 (107.8)
4	4	284.5 (49.5)
5	5	465.1 (173.1)
6	6	219.7 (101.1)
8	7	68.1 (22.3)
9	10	49.1 (24.2)
10	13	104.6 (27.0)

The immediate post-fire growth and reproduction were evident at other sites as indicated by either the presence of fruits from previous seasons (Sites 3 and 4), or typical inflorescence structures, i.e. terminal cymes (Sites 5-11), from past flowering.

At Site 1, significantly more fruits were produced on epicormic shoots than on lignotuberous shoots (1 — Factor Analysis of Variance (ANOVA), $P < 0.005$). This, in part, reflects the greater abundance of epicormic shoots produced after the fire. However, even where individuals produced both epicormic and lignotuberous shoots, more fruits were found on the epicormic shoots (paired t-test $0.01 > P > 0.001$). Where the main stem had a sufficient bark thickness to survive the fire and produce epicormic shoots, successful fruit production was virtually assured (94% of such plants set fruit). However, where the main stem was killed and regrowth was entirely lignotuberous, the chance of an individual successfully fruiting was greatly reduced (35%), and was confined to those plants which produced a new shoot of at least 50cm in height. Most of these plants had small fruit-crops (<100 fruits), and only one plant had a large fruit-crop which was totally lignotuberous in origin (871 fruits).

The number of fruits produced varied greatly between individuals. At Site 1, around half the fruiting plants sampled produced less than 100 fruits (Fig. 1), though some plants produced up to 1500 fruits. This variation could be partially explained by size of individuals. The linear regression of the number of fruits per fruiting plant on girth of the main stem (Fig. 2) was significant ($P < 0.001$) and accounted for some 44% of the variation in fruit-crop size. Adding the height and total girth components did not significantly improve the regression. This is expected, as all three variables were significantly correlated. A large amount of the variation in fruit production remained unexplained.

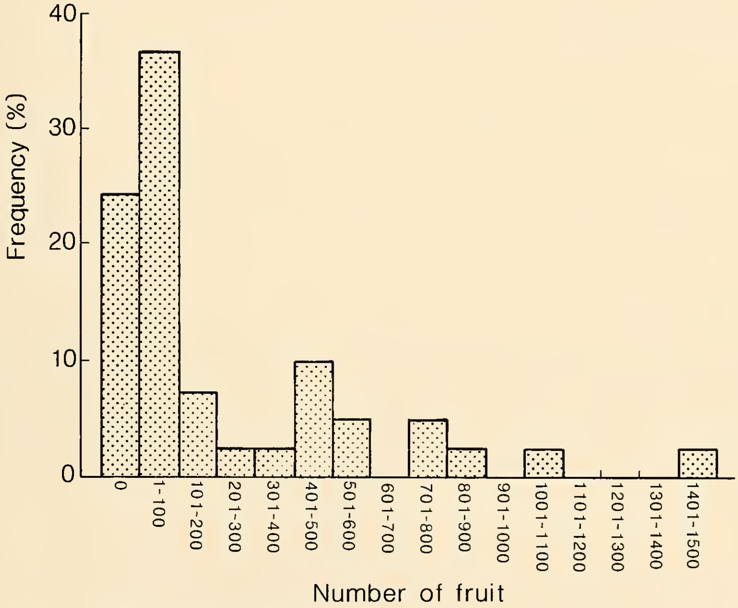


Fig. 1. Number of *A. hispida* fruits produced after fire at Site 1.

Predispersal seed predation

At Site 1, some 463 ripe fruits were harvested, with a maximum of 10 fruits being taken from any one plant. The majority of locules in a fruit contain an intact seed (Table 3). Seed predation in fruits was negligible (0.4% seeds lost), with occasional unidentified hymenopteran wasps reared from seeds.

TABLE 3

Extent of predispersal seed predation in A. hispida

	mean (± S.E.)	% of available locules
locules/fruit	2.996 (0.013)	100
intact seeds/fruit	2.361 (0.039)	78.8
seeds/fruit lost to predators	0.011 (0.005)	0.4

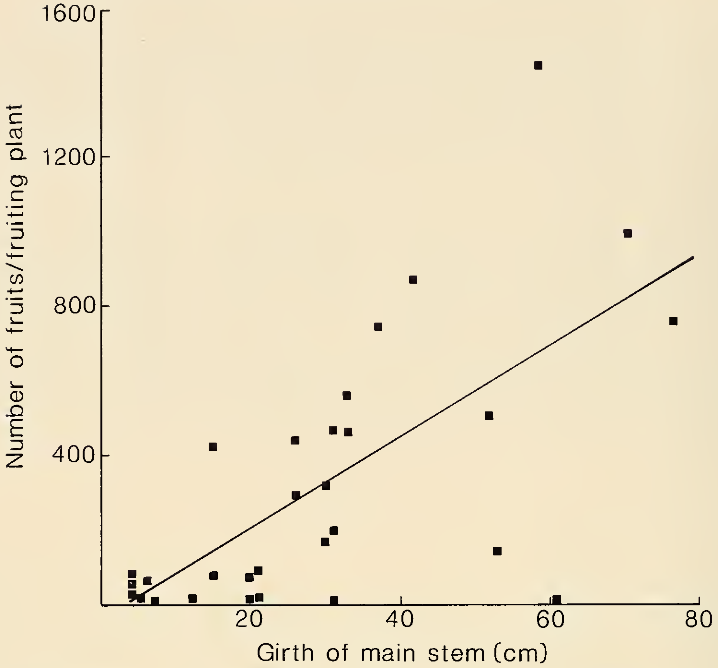


Fig. 2. Relationship between fruit production and girth of main stem for *A. hispida* at Site 1. y = -43.9 + 12.1x.

Seed dispersal

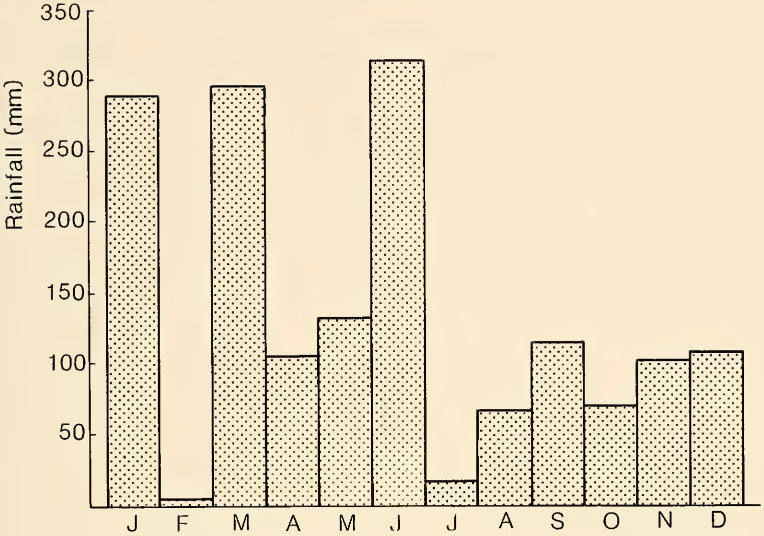
Initial seed dispersal was restricted to less than 5m around the parent plant (Fig. 3), with most seeds falling below the parent's canopy. Seed movement by ants was minimal (Table 4), indicating that *A. hispida* is not myrmecochorous. Where some ant dispersal of seeds occurred, it was only over a small distance (<50cm) and seeds may have been moved because of their close proximity to the two known *Acacia* myrmecochores.

TABLE 4

Evidence for seed movement by ants

Test species	% seeds remaining after 5 days (± S.E.)
Angophora hispida	79 (5.6)
Acacia linifolia	6 (4.7)
Acacia suaveolens	9 (5.5)

For the marked seeds, some *in situ* seed predation by an unknown seed predator occurred (20% ±7%), along with seed germination (18% ±6%) following heavy falls of rain in March 1978 (300mm). A large component of the seeds could not be traced (62% ±9%). These seeds were either: i) buried by moving sand, ii) washed away from the sampling area during heavy thunderstorms during the sampling period or iii) removed by seed predators or over small distances by ants. In all cases, the seeds would have germinated and established following sufficient rainfall in March 1978 (see below), unless they were destroyed by predators or buried too deeply for successful establishment. Seed movement during storms was small (<2m) as this was impeded by vegetation and litter.



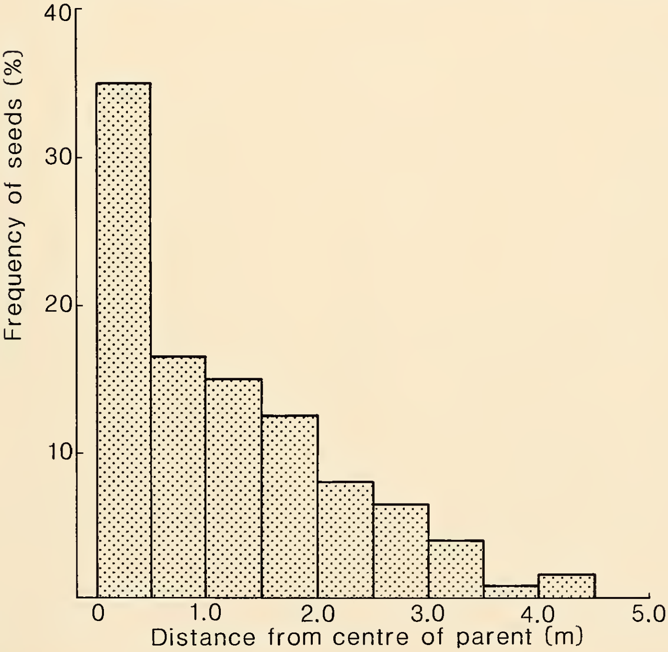


Fig. 3. Initial seed dispersal around *A. hispida* parents.

Seed dormancy and viability

All seeds showed 100% viability for up to six months after collection. There was no indication of any dormancy mechanism.

Seeds buried in hessian bags germinated within the first month of burial presumably following good rainfall in March (300mm). The remaining seed bags were retrieved two months after burial and all seeds had germinated.

TABLE 5

Size of eight year old plants, n = 30

Dimension	$\bar{x}$	s.e.	range
number of live aerial stems	1.8	0.3	1-8
number of live leaves[a]	8.1	0.9	2-27
plant height (mm)	140.2	8.0	40.5-220.2
depth to top of lignotuber (mm)	2.7	2.1	-25-29
lignotuber length (long axis) (mm)	20.3	1.6	5.9-36.1
lignotuber width (widest point) (mm)	16.4	1.0	6.3-26.7
lignotuber width (orthog.) (mm)	13.8	1.0	4.7-24.7
lignotuber volume (mm^3)	4736	780	213-16297

[a] None of the leaves sampled was of adult leaf size.

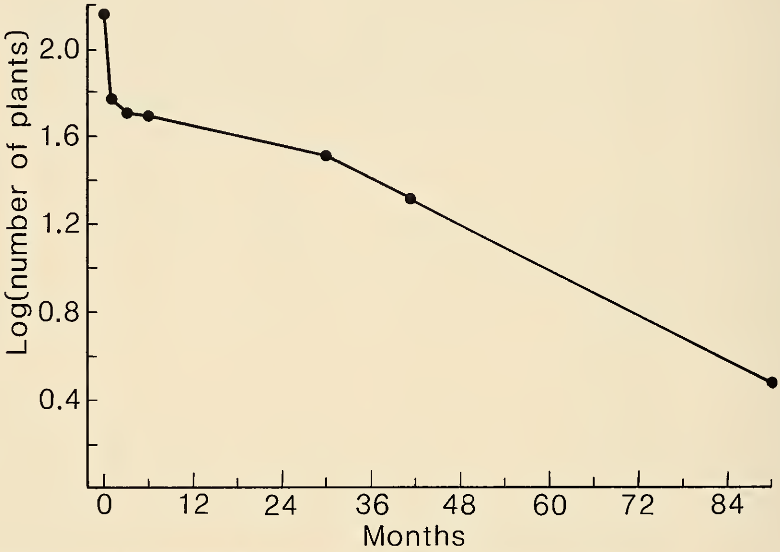


Fig. 4. The survival of *A. hispida* seedlings from germination to 8 years of age at Site 1.

Seedling survivorship

In the field, germination was confined to a 3-week period. Mortality was highest in the first few weeks after germination when the radicle was emerging and penetrating the soil surface and the cotyledons were unfolded. Once the first leaves were produced survival increased and remained relatively higher for the remainder of the study. The survival of seedlings from germination until eight years of age is shown in Fig. 4. During the first six months of seedling growth some 60% of deaths were due to desiccation; 16% to seedling predators; 5% to burial by moving sand; and 19% to unknown agents. The 8-year-old plants were small with small lignotubers close to the soil surface (Table 5).

DISCUSSION

A. hispida is a typical resprouter (Gill, 1981) with regrowth after fire from a combination of epicormic and lignotuberous shoots. It is among the fastest resprouting species in those communities in which it occurs, and where the main stem is not killed an extensive new canopy is formed some 6-8 months after fire. These mature plants have a very short secondary juvenile period and are potentially able to flower in the first flowering season (Nov-Feb) following a summer fire. Plants burnt in autumn to spring will probably not flower until the second summer as regrowth will still be incomplete in the first summer. Other resprouting species showing this same pulse of flowering in the immediate post-fire period include; geophytic orchids, lilies and herbs in South Africa (Levyns, 1966; Martin, 1966), coastal sage shrubs in California (Keeley and Keeley, 1984), *Xanthorrhoea* spp. and *Kingia* spp. in Australia (Gill and Ingwersen, 1976; Baird, 1977; Lamont and Downes, 1979). The change from a suppressed shrubby individual in long unburnt communities, to vigorous regrowth after fire, as shown by *A. hispida*, has not been recorded before in a resprouting species in Australia. The berries *Vaccinium* spp. show a similar response in the U.S.A. (Gill and Groves, 1981). Some non-sprouting plants (obligate seeders) can also grow rapidly and flower extensively in the first 18 months after fire, e.g. *Acacia suaveolens* (Auld, 1987).

In *A. hispida*, fruit production was clearly enhanced on plants resprouting via epicormic shoots. After the 1977 fire at Site 1, some 65% of plants which resprouted by lignotuberous growth only, failed to flower and may be juveniles. Most of these individuals were small. For these plants to reach maturity a sufficiently long inter-fire period is needed to allow development of a stem large enough to survive fire. However, it is important to note that one plant was able to produce a large seed-crop from a 1.5m aerial stem produced solely from the lignotuber. This is in contrast to *Banksia serrata* (Bradstock, 1985) where a minimum of 6-10 years is required for a resprouting juvenile plant to develop a stem of sufficient size to be fire resistant. Only plants of this size were capable of flowering and even then the subsequent secondary juvenile period was around two years. In *B. serrata*, repeated fires at less than 10 year intervals may produce, in a proportion of the population, continually suppressed plants which never flower. In *A. hispida*, the proportion of plants flowering will be higher.

Jacobs (1951) and Majer (1980) suggest that insect abundance is reduced at least in the short term after a fire. Although there are no studies on how fire affects the populations of predispersal seed predators, heavy flowering and fruiting after a fire may lead to reduced levels of seed predation through satiation of available seed predators e.g. *Acacia suaveolens* (Auld and Myerscough, 1986). A species which only flowers after a fire is likely to be both spatially and temporally irregular because of the irregular nature of fires. This is comparable with mast seeding species (Janzen, 1976; 1978). In contrast, other resprouting species after a post-fire secondary juvenile period, either maintain their reproductive output throughout their life span (e.g. *Banksia serrata*, Bradstock, 1985; *Arctostaphylos glandulosa*, Keeley and Keeley, 1977; and *Protea nitida*, Kruger, 1983) or show a peak after fire with a decline after approximately 2 years (*Xanthorrhoea* spp., Gill and Ingwersen, 1976; *Telopea speciosissima* and *Lambertia formosa*, Pyke, 1983) or around 10 years (*Isopogon anemonifolius*, Bradstock, 1985; and *Protea cynaroides* and *P. speciosa*, Kruger, 1983).

Dispersal of *A. hispida* seeds is minimal and seeds will remain in the boundaries of the existing population, except perhaps near its edges. Like the closely related *A. bakeri* (Auld, 1986), ant dispersal of seeds was not extensive. As well as the possibility of decreased seed predation (Majer, 1982) and increased nutrient levels (Siddiqi *et al.*, 1976) the immediate post-fire environment has ample light for developing seedlings. For *A. hispida*, with no seed dormancy, successful establishment and growth is largely dependent upon lack of discovery by post-dispersal seed predators and the amount of available moisture. Specht (1981), Bradstock and Myerscough (1981) and Bradstock (1985) have shown that the seedling establishment of several proteaceous shrubs was directly dependent upon soil moisture immediately following a fire. With high moisture availability, establishment should be high, although unless moisture levels are maintained subsequent mortality will be high. As seed of *A. hispida* maintains its viability for up to six months it is likely that sufficient rainfall will occur for germination. During drought periods, post-dispersal seed predation may severely reduce the available seed.

For recruitment in *A. hispida* to be effective, the inter-fire period must be sufficient to allow seedlings to reach a stage where they are fire tolerant. This will vary depending on the intensity of the fire and the depth of burial of the lignotuber. After 8 years, seedlings (or juveniles) were still distinct in size from all individuals which survived the 1977 fire at Site 1. Whilst the development of the lignotuber had commenced, its size was small and may not ensure survival in the next fire. Abbott (1985) found that 3½-year-old plants of the resprouter *Banksia grandis* were small in height (11cm), whilst the length of the long axis of the lignotuber of these plants was also small (1.04cm). He predicted that it takes 35 years for this species to reach maturity from seed, although no estimate was made of how large the lignotuber must be to survive fires of differing intensities. To ensure the continued survival of populations of *A. hispida* via seedling recruitment, a fire-free period of greater than eight, and possibly many more, years may be required if the small juveniles described here are not fire resistant. Clearly, for the long-term management of populations of *A. hispida*, an investigation of the minimum fire-free period that is required under varying fire intensities is required. Kruger (1983) has suggested that in fynbos the primary juvenile period is usually less than eight years, whilst for chaparral it is 8-10 years. Data from Abbott (1985), Bradstock (1985) and this study indicate that in fire-prone Australian plant communities the primary juvenile period may be much longer for resprouting species. This emphasises the importance of considering the minimum length of the fire-free interval required to maintain populations of resprouting species through seedling recruitment. Whilst many resprouters are vegetatively vigorous and floriforous after fire, this cannot be directly interpreted to mean that resprouters are capable of maintaining population levels under short fire frequencies. The length of time required for seedlings to become fire tolerant dictates the minimum fire interval, irrespective of any post-fire flushes in vegetative growth or flowering.

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A Review of the Biology of *Acacia suaveolens* (Smith) Willd. (Mimosaceae)

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(Communicated by P. J. MYERSCOUGH)

MORRISON, D. A. A review of the biology of *Acacia suaveolens* (Smith) Willd. (Mimosaceae). *Proc. Linn. Soc. N.S.W.* 109(4), (1986) 1987: 271-292.

Published and original data on a number of aspects of the biology of *Acacia suaveolens* are presented, including: taxonomy, geographical distribution, climatic, topographic, and altitudinal limitations, substratum, communities, gregariousness; response to biotic factors; performance in various habitats, effect of frost, drought, and waterlogging, morphology, chromosomes, physiology, biochemistry, perennation and reproduction, phenology, flowering and pollination, seed production and dispersal, viability of seeds and germination, seedling morphology, mycorrhiza, animal feeders and parasites, plant diseases and parasites, and history and conservation status.

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INTRODUCTION

In 1941 the British Ecological Society began publishing a series of papers on the 'Biological Flora of the British Isles' (Anon., 1941), a series that is still being actively published. This series was intended to be an introductory reference source of published and unpublished data on various aspects of the biology of the plant species occurring in Great Britain.

No similar series has been undertaken for Australian plants, partly, at least, because very few data exist for most of the species. However, extensive data do exist for a number of the more common species, particularly of the genera *Eucalyptus* and *Acacia.* This paper is an attempt to summarize the published data on one particular species, *Acacia suaveolens* (Smith) Willd., that is common in south-eastern Australia and for which considerable data do exist. The data are arranged in the format used by the British Ecological Society in publishing their Biological Flora, and I have attempted to collate whatever data exist concerning *A. suaveolens* for each of the aspects covered in that series (see Anon., 1941), and to contribute original data for aspects for which published data are not available. The references cited are mainly a subset of the bibliography of 186 sources of data on *A. suaveolens* listed in Morrison (1986).

DESCRIPTION AND TAXONOMY

Acacia suaveolens (Smith) Willd., *Sp. Pl.* 4:1050 (1806)
[*Mimosa suaveolens* Smith, *Trans. Linn. Soc. Lond.* 1:253 (1791) non Salisb. (1796); *Mimosa obliqua* Lam., *J. Hist. Nat. Paris* 1:89 (1792) non H. H. Wendl. (1798); *Mimosa ambigua* Salisb., *Prodr. Stirp.* 325 (1796); *Mimosa angustifolia* Jacq., *Pl. Hort. Schoenbr.* 3:74 (1798); *Acacia angustifolia* (Jacq.) H. H. Wendl., *Comm. Acac.* 34 (1820); *Acacia suaveolens* var. *platycarpa* DC, *Prodr.* 2:453 (1825); *Phyllodoce suaveolens* (Smith) Link, *Handbuch* 2:133 (1831); *Phyllodoce angustifolia* (Jacq.) Link, *Handbuch* 2:133 (1831); *Hecatandra suaveolens* (Smith) Raf., *Sylva Tellur.* 120 (1838)]

Subgenus *Phyllodineae* (DC) Ser.; Section *Phyllodineae* DC; Subsection *Racemosae* (Benth.) Maiden

Usually erect, slender, glabrous, little-branched, open shrub to 2(-3)m high; bark smooth, (bluish-)green. *Branchlets* terete below but acutely triquetrous above due to decurrencies, sometimes almost flattened, glabrous, brownish-green or sometimes glaucous, new growth often pinkish. *Phyllodes* alternate, erect, glaucous, coriaceous, glabrous, flat, straight or rarely slightly falcate, narrow-oblong to linear-lanceolate, acute or obtuse, acuminate or mucronate, narrowed towards the base, (5-)7-12(-20)cm long, (2-)3-7(-10)mm wide, (9-)13-27(-35) times as long as broad, one-nerved more or less central, margins thickened, yellowish-brown; pulvinus 1-2mm long; small, flat, elongated, non-porate gland (1-)2-3 (-4)mm from base of phyllode, sometimes another gland at tip. *Inflorescence* of globular heads 5-8mm in diameter, each of (3-)4-7(-12) flowers, in glabrous, axillary, often crowded, (5-)6-8(-12)-branched racemes; rhachis 1-2(-3)cm long, slender; peduncles 2-5mm long, slender; flower heads andromonoecious, usually twice as many male as hermaphrodite flowers; before development, racemes enclosed by imbricate, scarious, fimbriate, ovate, obtuse, pale yellow-brown, pink-tipped bracts to 2.5mm long, crowded at base of axis, with larger ones subtending individual peduncles, all deciduous before anthesis. *Flowers* actinomorphic, (4-)5(-6)-merous, creamy to pale lemon-yellow, protogynous, sweetly-scented. *Sepals* free, thin, linear-spathulate, acuminate, glabrous with a few hairs at the tip, 1.2-1.3mm long. *Petals* thin, free, ovate-oblong, glabrous, 1.7-3mm long, 0.7-1mm wide, less than twice as long as the calyx. *Stamens* (35-)40-55(-80), 3-5mm long; anthers small, almost round, bilobed with 4 loculi per lobe. *Ovary* unilocular, central, superior, yellow-brown, oblong, laterally compressed, acuminate, glabrous, with (4-)5-7(-8) anatropous basally-attached ovules. *Style* yellow-brown, filiform, bent, up to twice as long as the stamens; stigma simple, terminal, acute. *Pollen* grains yellow, non-reticulate, 4-porate, pores placed towards the angles of the grains, 4-furrowed; grains aggregated into polyads of 16, long equatorial diameter of the polyad 52-64μm, 1 polyad per locule. *Legume* stalked, glaucous, purplish-red at fertilization, turning bluish-green, often reddish-brown over the seeds, brown when open at maturity, glabrous, coriaceous, pruinose, (elliptic-)oblong, obtuse, apiculate, laterally compressed but slightly raised over the seeds, 2-4(-5)cm long, (10-)12-20mm wide, twice as long as wide, margins thickened. *Seeds* smooth, shiny, dark brown to brownish-black (rarely maroon), transverse, (elliptic-)oblong, 5-8mm long, 2.5-4.5mm wide, 2-3 times as long as wide; areole closed, 3-4.5mm long, 0.6 times the length of the seeds; funicle 1.5-2mm long, filiform till nearly mature then thickened into a slightly oblique, fleshy, 1-3(-4)-folded aril covering the hilar end, same colour as the seeds; no albumen present.

Variable in erectness, height, phyllode axillary angle, phyllode shape and size, and number of flowers per inflorescence, but most of this has no apparent genetic basis. In the Myall Lakes area, populations of plants with very narrow phyllodes (< 2mm wide; Armitage, 1977) are common in the sclerophyllous forest community on the Holocene sand, and this may have a strong genetic component. In the Grampians, populations with phyllodes held conspicuously close to the stem and a small rootstock can be found in the deeper sands on the west-facing slopes. Along the New South Wales coast north of Sydney, plants with a prostrate, spreading habit and much broader phyllodes are often found on thin soils on exposed headlands. Elliot and Jones (1982) also report that a form with a cream band on each side of the phyllode midvein and flowers with a deeper yellow is often cultivated, but that it 'must be propagated from cuttings to retain the variegation'.

GEOGRAPHICAL DISTRIBUTION

A. suaveolens is endemic to the southeastern coast of the Australian mainland, around the coast of Tasmania, and on the larger off-shore islands (Fig. 1). It is generally restricted to the coast, although it does occur inland, notably in the Sydney Basin, in the Grampians, and at the South Australia-Victoria border.

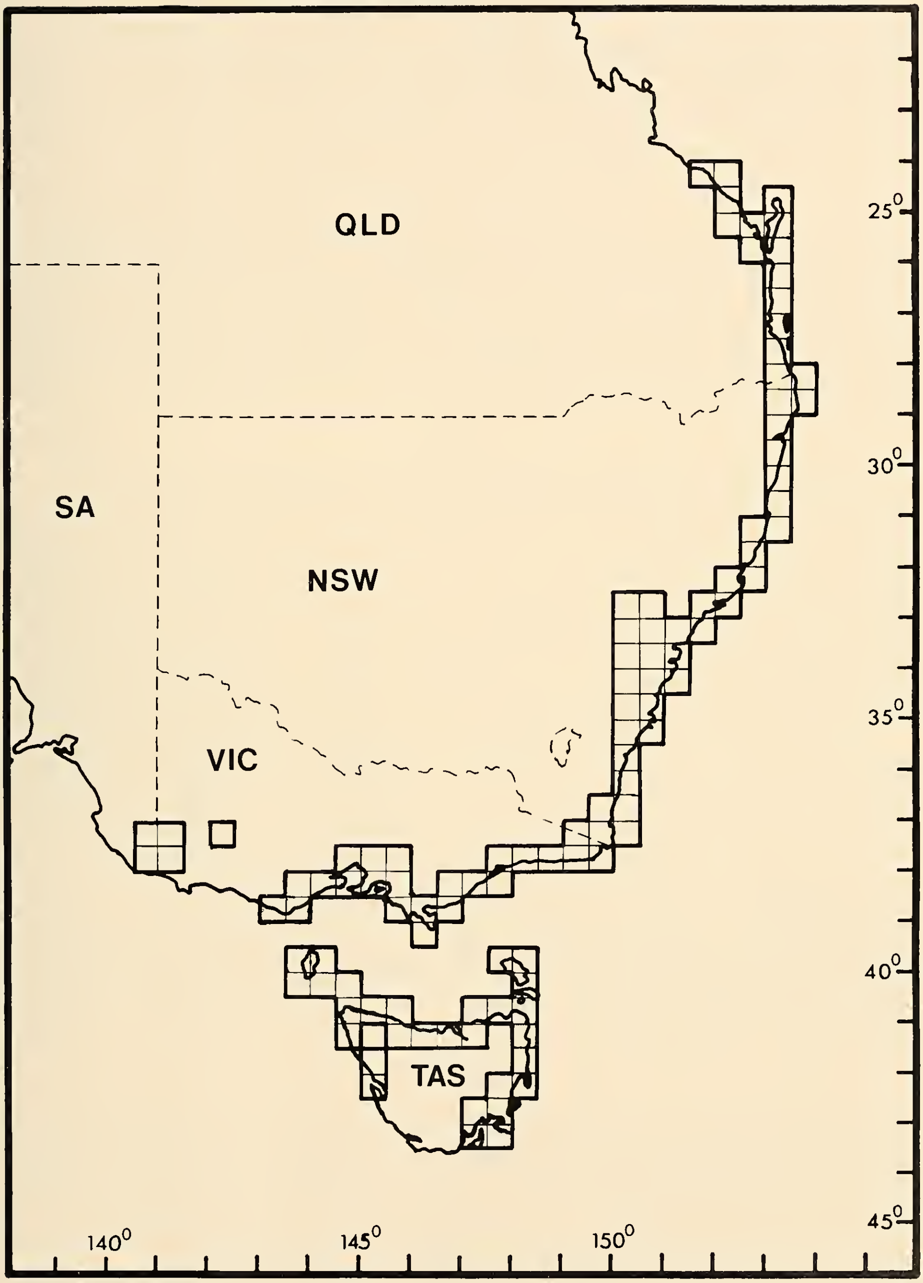

Fig. 1. Known distribution of *Acacia suaveolens*. Each outline represents at least one record on the national 0.5° × 0.5° grid. Data from dried specimens held at AD, BRI, CANB, CBG, HO, MEL, NSW, PERTH, and SYD (codes after Holmgren *et al.*, 1981).

In the literature, populations have also been recorded on the Victorian coast east of the South Australian border (Churchill and de Corona, 1972; Costermans, 1981), east of the Grampians (Churchill and de Corona, 1972; Beauglehole, 1980b; Maslin and Pedley, 1982), in the Albury district (Jacobs and Pickard, 1981; Maslin and Pedley, 1982), and in the northern tablelands of New South Wales (Simmons, 1981; Maslin and Pedley, 1982), but these records have not been confirmed and are not supported by herbarium voucher specimens (Beauglehole, 1980a; Morrison *et al.*, 1983).

CLIMATIC, TOPOGRAPICAL AND ALTITUDINAL LIMITATIONS

As a result of its large latitudinal (24°26′S to 43°15′S) and altitudinal (0-950m) range, *A. suaveolens* experiences a wide range of climatic extremes (Table 1), and does not appear to show any particular climatic preferences. It also does not exhibit any climatically-determined slope preferences. Burrough *et al.* (1977) have found plants growing at both extremes of a strong gradient of sites varying from a strongly positive to a balanced precipitation/evaporation budget over a short distance on the New South Wales central coast.

TABLE 1

Long-term temperature and precipitation extremes within the geographical distribution of Acacia suaveolens
Data from Australian Bureau of Meteorology (1975a-e) for a total of 163 meteorological stations

Climatic parameter		Value	Meteorological station
Mean annual maximum temp.: —	max.	28.5°C	Tabbimoble S.F., N.S.W.
	min.	13.4°C	Tasman Is. Lighthouse, Tas.
Highest mean monthly maximum temp.: —	max.	31.6°C	Tabbimoble S.F., N.S.W.
	min.	10.2°C	Tasman Is. Lighthouse, Tas.
Mean annual minimum temp.: —	max.	17.3°C	Tabbimoble S.F., N.S.W.
	min.	5.5°C	Geeveston (Forestry), Tas.
Lowest mean monthly minimum temp.: —	max.	22.8°C	Tabbimoble S.F., N.S.W.
	min.	0.0°C	Geeveston (Forestry), Tas.
Mean annual rainfall: —	max.	1814 mm	Alstonville Res. Stn., N.S.W.
	min.	538 mm	Geelong (S.E.C.), Vic.
Mean annual no. raindays: —	max.	235	Strahan (Vivian St), Tas.
	min.	57	Waterloo, Qld.

Populations are most commonly found within a few kilometres of the coast, and below an altitude of 300m. The only places where this species is recorded above 500m (to 600m in the McPherson Range, to 950m in the Blue Mountains, to 650m in the Budawang Range) are where the upland sandstone soils of the Great Dividing Range are contiguous with the sandy coastal plain.

SUBSTRATUM

On the mainland, *A. suaveolens* is most commonly found on the coastal Quaternary sands. The northern boundary of the distributional range is near the northern boundary of the lime-free sandy and sandy-loam soils that form the dominant soil type along the eastern Australian coast. However, coastal populations are occasionally reported from the perimeter of clay soils over sandstone (e.g. Webb, 1981); and on Wilsons Promontory the species is also found as a rare occurrence on the perimeter of sandy soils over Devonian granite (Gillham, 1960; Ashton and Webb, 1977).

Inland along the eastern coast, the species occurs on sandy soils over Jurassic sandstone in the McPherson Range, over Triassic sandstone in the Sydney Basin, over Devonian sandstone in the Budawang Range, and over Ordovician sandstone near Orbost. It is not found on the inland sandstone areas which are isolated from the coastal sandy soils.

It has also been recorded from acid Tertiary rhyolite on the Lamington Plateau (McDonald and Elsol, 1984) and on Mt Coolum (Sharpe and Batianoff, 1985).

Between Lorne and Warrnambool, populations are found on inland sandy soils over Tertiary sandstone, rather than on the uplifted Cretaceous shale of the Otway Range adjacent to the coast. The species does not occur on the coastal soils derived from the Tertiary limestone and Quaternary volcanics west of Warrnambool; and the isolated populations in the Grampians occur on Quaternary sand and on sandy soils over Devonian sandstone. Near the Victoria-South Australia border, populations are found on the inland siliceous Quaternary sands and sandy soils over Tertiary sandstone, but do not occur on the calcareous Quaternary sands nearer to the coastline.

In Tasmania, this species is common on sandy soils over the many sandstones (e.g. Silurian, Permian, Triassic, Tertiary) which form most of the northern and eastern coastline, but it only occurs sporadically on the Tertiary and Middle Proterozoic sandstones along the northwestern coastline. On the Tasman Peninsula, it is also found on thin sandy soils over Jurassic dolerite (Kirkpatrick, 1977b). In the Furneaux Group, plants occur on sandy soils over both Silurian sandstone and Devonian granite, as well as on granitic colluvium (Kirkpatrick, 1977b); and on King Island, plants are found on Middle Proterozoic sandstone soils.

A. suaveolens has been recorded from the following soil groups: — lithosols (Ashton and Webb, 1977), siliceous sands (Parsons, 1966; Firth, 1969; Durrington, 1977; Kirkpatrick, 1977a, 1977b; Benson and Fallding, 1981; Forbes *et al.*, 1982; Opie *et al.*, 1984), earthy sand (Buchanan and Humphreys, 1980), yellow earths (Benson and Fallding, 1981), humus podzols (Myerscough and Carolin, 1986), and peaty podzols (Parsons, 1966). However, it is most commonly found on siliceous sand podzols, of various colours and stages of differentiation: e.g. poorly-developed (Kirkpatrick, 1973; Myerscough and Carolin, 1986), moderately-developed (Clark, 1975; Thatcher and Westman, 1975), well-developed (Groves and Specht, 1965; Kirkpatrick, 1975; Ingwersen, 1976; Ashton and Webb, 1977; Burrough *et al.*, 1977; Clifford and Specht, 1979; Buchanan and Humphreys, 1980).

These soils may be very shallow (e.g. Cambage, 1923; Petrie, 1925; Hannon and Evans, 1963; Kirkpatrick, 1977b; Auld and Myerscough, 1986) but are usually quite deep (e.g. Groves and Specht, 1965; Ingwersen, 1976; Durrington, 1977; Kirkpatrick, 1977b; Clifford and Specht, 1979; Opie *et al.*, 1984; Myerscough and Carolin, 1986). The soils are predominantly freely-draining, but are occasionally seasonally waterlogged or permanently moist (see below). The surface pH has been recorded from 4.3-6.9 (Davis, 1941a; 1941b; Gillham, 1960; Parsons, 1966; Siddiqi *et al.*, 1972; Burrough *et al.*, 1977; Kirkpatrick, 1977b; Buchanan and Humphreys, 1980). The soils are extremely infertile, being relatively more fertile in the wetter habitats. The surface loss-on-ignition varies from 0.9-30.0% (Pidgeon, 1938; Davis, 1941a; 1941b; Ingwersen, 1976; Burrough *et al.*, 1977; Myerscough and Carolin, 1986); and total nitrogen ranges from 0.02-0.18% (Hannon, 1956; Siddiqi *et al.*, 1972; 1976; Myerscough and Carolin, 1986). Total phosphorus varies from 0.001-0.01% (Beadle, 1962; Parsons, 1966; Myerscough and Carolin, 1986), with 'available' water-soluble phosphorus ranging from 0.0002-0.0013% (Siddiqi *et al.*, 1972; 1976; Ingwersen, 1976). The exchangeable calcium is reported to be in the range 0.52-4.0 meq.%, the exchangeable potassium from 0.06-0.95 meq.%, the exchangeable magnesium from 0.2-1.77 meq.%, and the exchangeable sodium from 0.05-0.95 meq.% (Siddiqi *et al.*, 1972; 1976; Ingwersen, 1976; Burrough *et al.*, 1977; Myerscough and Carolin, 1986).

A. suaveolens grows well in the laboratory in a range of soil types with higher fertility levels than those on which it is normally found in the wild (Beadle, 1962); and the absence of plants from higher fertility soils has been ascribed to an inability to compete with faster-growing species under these conditions (Beadle, 1962).

COMMUNITIES

A. suaveolens can be regarded as a short-lived pioneer species (Clemens and Franklin, 1980), and it often occurs in early successional communities (but not in the early exposed stages) (Pidgeon, 1938; 1940) or in early phases of regeneration cycles. As a result, the presence of the species in a community is very dependent on the past history of disturbance, especially in relation to fire. The species has been recorded from a wide variety of communities, including forests, woodlands, shrublands, heaths, and sedgelands (Table 2).

TABLE 2

Plant communities in which Acacia suaveolens *has been recorded*

Alliance*	Suballiance*	Structural form +	Area	Reference†
Eucalyptus pilularis	a) *Eucalyptus pilularis*	woodland	Bulli, N.S.W.	(9)
	b) *Eucalyptus pilularis-Eucalyptus intermedia-Eucalyptus siderophylla*	open-forest	Nth Stradbroke Is., Qld.	(31)
		open-forest	Moreton Is., Qld.	(10)
	c) *Eucalyptus pilularis-Angophora costata*	open-forest	Myall Lakes, N.S.W.	(2), (21)
		open-forest	Sydney, N.S.W.	(15)
Eucalyptus botryoides		low open-forest	Sydney, N.S.W.	(5), (15)
		woodland	Sydney, N.S.W.	(26)
		low woodland	Sydney, N.S.W.	(4)
Eucalyptus gummifera-Eucalyptus racemosa-Eucalyptus sieberi	a) *Eucalyptus gummifera-Eucalyptus racemosa-Angophora costata*	open-forest	Sydney, N.S.W.	(23)
		low open-forest	Sydney, N.S.W.	(5), (23)
		low open-forest	Barren Grounds, N.S.W.	(6)
		woodland	Sydney, N.S.W.	(2), (5), (15) (23), (26)
		woodland	Barren Grounds, N.S.W.	(6)
		woodland	Jervis Bay, N.S.W.	(17)
	b) *Eucalyptus sieberi-Eucalyptus piperita-Eucalyptus racemosa*	open-forest	Sydney, N.S.W.	(3), (15)
		open-forest	Fitzroy Falls, N.S.W.	(6)
		low open-forest	Bulli, N.S.W.	(8)
		low open-forest	Macquarie Pass, N.S.W.	(11)
	c) *Eucalyptus eximia-Eucalyptus punctata*	woodland	Sydney, N.S.W.	(3)
		woodland	Bulli, N.S.W.	(9)
Eucalyptus globoidea		open-forest	East Gippsland, Vic.	(13)
		woodland	East Gippsland, Vic.	(13)
Eucalyptus baxteri		open-forest	South Australia	(29)
		low open-forest	South Australia	(32)
		woodland	Wilsons Promontory, Vic.	(1)
		low woodland	Wilsons Promontory, Vic.	(24)
Eucalyptus amygdalina		open-forest	Schouten Is., Tas.	(16)
		woodland	Tasman Peninsula, Tas.	(18)
Banksia aemula		low open-forest	Nth Stradbroke Is., Qld.	(31)
		woodland	Sydney, N.S.W.	(26)
		open-woodland	Nth Stradbroke Is., Qld.	(30)
		tall shrubland	Moreton Is., Qld.	(10)
		tall open-shrubland	Nth Stradbroke Is., Qld.	(7)
		tall open-shrubland	Moreton Is., Qld.	(10)
		closed-heath	Moreton Is., Qld.	(10)
		closed-heath	Myall Lakes, N.S.W.	(21)
		closed-heath	Sydney, N.S.W.	(27), (28)
Banksia ericifolia		open-scrub	Sydney, N.S.W.	(5)
		closed-heath	Sydney, N.S.W.	(28)
		open-heath	Macquarie Pass, N.S.W.	(11)
Banksia oblongifolia		closed-heath	Sydney, N.S.W.	(23)
		open-heath	Myall Lakes, N.S.W.	(21)
		open-heath	Sydney, N.S.W.	(27)
Banksia robur		sedgeland	Sydney, N.S.W.	(5), (15)
Banksia marginata		closed-heath	Wilsons Promontory, Vic.	(14)
		closed-heath	Rocky Cape, Tas.	(12)
		closed-heath	Ocean Beach, Tas.	(19)
		open-heath	Schouten Is., Tas.	(16)
Leptospermum myrsinoides		closed-heath	Wilsons Promontory, Vic.	(1)

TABLE 2 (Cont'd.)

Alliance*	Suballiance*	Structural form +	Area	Reference†
Leptospermum scoparium		low open-shrubland	Western Port, Vic.	(22)
		closed-heath	Flinders Is., Tas.	(20)
Casuarina littoralis-Banksia oblongifolia		closed-heath	Northern coastal N.S.W.	(2)
Casuarina distyla		closed-heath	Sydney, N.S.W.	(2)
		closed-heath	Mt. Wilson, N.S.W.	(25)
		closed-heath	Bowen Is., N.S.W.	(17)
		open-heath	Sydney, N.S.W.	(23)
Melaleuca squarrosa		open-scrub	Wilsons Promontory, Vic.	(24)
		open-heath	Wilsons Promontory, Vic.	(24)

* after Beadle (1981)

\+ after Specht (1970)

† Sources of data: — (1) Ashton and Webb (1977); (2) Beadle (1981); (3) Benson (1981a); (4) Benson (1981b); (5) Benson and Fallding (1981); (6) Burrough *et al.* (1977); (7) Clifford and Specht (1979); (8) Davis (1941a); (9) Davis (1941b); (10) Durrington (1977); (11) Fallding and Benson (1985); (12) Firth (1969); (13) Forbes *et al.* (1982); (14) Gillham (1960); (15) Hannon (1956); (16) Harris and Kirkpatrick (1982); (17) Ingwersen (1976); (18) Kirkpatrick (1973); (19) Kirkpatrick (1977a); (20) Kirkpatrick (1977b); (21) Myerscough and Carolin (1986); (22) Opie *et al.* (1984); (23) Outhred *et al.* (1985); (24) Parsons (1966); (25) Petrie (1925); (26) Pidgeon (1940); (27) Siddiqi *et al.* (1972); (28) Siddiqi *et al.* (1976); (29) Specht (1972); (30) Specht *et al.* (1977); (31) Thatcher and Westman (1975); (32) Whibley (1980)

The forest communities are usually found only on deep coastal sand masses, and have an open, heathy understorey. The woodlands also have a heath rather than a scrub understorey, and usually occur on the shallower soils. The heath communities vary from open to closed, and include both dry and wet heaths. Plants also occur occasionally in ground-water heaths, and sporadically around the edges of swamps in the northern areas (e.g. White, 1945; Hannon, 1956). The species is not found in closed coastal communities such as the exposed *Leptospermum laevigatum* and *Acacia sophorae* closed-scrubs which front many of the beaches, occurring instead in the more open woodlands or heaths slightly further inland (e.g. Giliham, 1960). Plants do, however, occasionally occur in exposed headland heaths on thin sandy soils over sandstone along the New South Wales coast (Beadle, 1981) and over dolerite on the Tasman Peninsula (Kirkpatrick, 1977b), and also on leached sands in exposed situations within the salt spray zone along the northern and eastern coasts of Tasmania (Kirkpatrick, 1977b). The species also does not appear in the coastal closed-grasslands, but plants are occasionally found in understoreys with clumped grasses.

The community dominants vary with the geographical area (Table 2) and substratum. In Queensland and northern New South Wales on low fertility soils, *A. suaveolens* is found in *Eucalyptus intermedia* open-forests, and also in the *Banksia aemula* low open-forests and tall open-shrublands on the deep sand coastal islands. On more fertile soils, but not usually in valleys, it occurs in *Eucalyptus pilularis* open-forests.

On the New South Wales central coast, it is found in *Eucalyptus botryoides* low open-forests or woodlands in the higher fertility areas on the hind-dunes, and in *E. pilularis* open-forests and low open-forests on the deep coastal sand masses and higher-fertility inland soils. More commonly, it occurs on less fertile soils in low open-forests or woodlands dominated by *Eucalyptus gummifera* (in wetter areas), *Eucalyptus sieberi* (further south), *Eucalyptus racemosa* (at higher altitudes), *Eucalyptus piperita* (in more fertile spots), and *Angophora costata* (ubiquitous). It is also common in *B. aemula* low open-forests, heaths, and shrublands on sand throughout the New South Wales coast. It is also common on sand and sandstone in dry heaths of *Banksia ericifolia* and *Casuarina distyla*, and with *Casuarina littoralis* on exposed sandy headlands. In wetter heaths, it occurs with *Banksia oblongifolia*, and occasionally with *Banksia robur*.

In Victoria, the open-forests and woodlands are dominated in the east by *Eucalyptus globoidea* (on more fertile soils) and *E. sieberi* (on less fertile soils), and in the west (and also in South Australia) by *Eucalyptus baxteri* (on the less fertile soils) and *Eucalyptus obliqua* (on the more fertile soils). In eastern Victoria, the species also occurs in *Leptospermum myrsinoides* heaths, and, in wetter more saline areas, in heaths and thickets dominated by *Melaleuca squarrosa.* On soils derived from granite, plants are occasionally found around the edges of *Banksia marginata* heaths.

In Tasmania, the species is very common in *B. marginata* heaths, especially on sand. It is also found in woodlands and open-forests of *Eucalyptus amygdalina*, often with *Eucalyptus viminalis* and *Eucalyptus tenuiramis* in more fertile areas. On the west coast, it is also a rare occurrence in open-scrub formations of *Eucalyptus nitida* and *Eucalyptus ovata* in low-fertility sand deposits, often in isolated patches among low heaths on exposed headlands.

Within the communities, *A. suaveolens* may be associated with a wide range of species. For example, in eucalypt forests along the southern coast of New South Wales and east coast of Victoria its occurrence has been found to correlate positively with 27 angiosperm species, notably *Eucalyptus gummifera*, *Leptospermum attenuatum*, *Caustis flexuosa*, and *Ricinocarpos pinifolius* (Table 3).

TABLE 3

Percentage frequency of occurrence with (+) and without (−) Acacia suaveolens *of some angiosperm plants associated with* A. suaveolens *at three sites covering two eucalypt alliances in which* A. suaveolens *is commonly found*
Data from Miller (1972), Ingwersen (1976), and Forbes et al. *(1982) respectively*

	E. gummifera — *E. racemosa* — *E. sieberi* Alliance								*E. globoidea* Alliance			
	Royal National Park				Jervis Bay Territory				East Gippsland			
Species	(+)	(−)	χ^2	+	(+)	(-)	χ^2		(+)	(-)	χ^2	
[No. quadrats]	[9]	[80]			[23]	[52]			[34]	[71]		
Acacia oxycedrus	—	—		‡	—	—			29	7	9.40	**
Actinotus minor	0	1			35	12	5.67	*	—	—		
Banksia ericifolia	22	10			39	15	5.13	*	—	—		
Banksia serrata	56	84			65	42	4.96	*	79	69		
Bossiaea ensata	—	—			48	12	11.98	***	—	—		
Cassytha glabella	33	16			26	21			74	49	5.51	*
Caustis flexuosa	78	31	7.61	**	35	13	4.53	*	24	28		
Correa reflexa	—	—			26	8			65	38	6.57	*
Dampiera stricta	—	—			61	8	24.72	***	88	83		
Darwinia taxifolia	—	—			30	10	5.06	*	—	—		
Empodisma minus	—	—			—	—			29	8	7.82	**
Epacris microphylla	22	1			39	6	13.21	***	—	—		
Eucalyptus gummifera	78	34	5.90	*	74	38	8.02	**	21	14		
Eucalyptus racemosa	—	—			43	21	4.16	*	—	—		
Gompholobium huegelii	—	—			—	—			32	10	8.19	**
Hardenbergia violacea	44	13	6.23	*	17	25			—	—		
Hibbertia fasciculata	—	—			—	—			29	8	7.82	**
Hypolaena fastigata	—	—			4	6			32	3	18.49	***
Isopogon anemonifolius	11	10			35	8	8.71	**	—	—		
Leptospermum attenuatum	67	25	6.79	**	52	10	16.48	***	47	23	6.53	*
Leucopogon collinus	—	—			—	—			62	18	19.83	***
Lycopodium fastigatum	—	—			30	12	3.97	*	—	—		
Monotoca scoparia	—	—			13	6			53	21	10.80	**
Persoonia celeyi	—	—			43	8	13.45	***	—	—		
Platysace linearifolia	89	68			39	10	9.15	**	—	—		
Ricinocarpos pinifolius	22	40			35	12	5.67	*	59	24	12.26	***
Themeda australis	—	—			13	44			26	11	3.92	*

\+ Values indicate statistical association between the species and *A. suaveolens* at that site. Lack of any details indicates that the association was NS at $P<0.05$, or that it was not tested because one of the four values in the 2×2 contingency table was <1 or more than one was <5. * $0.01<P<0.05$, ** $0.001<P<0.01$, *** $P<0.001$.

‡ Missing data indicate that the species was not recorded at that site.

GREGARIOUSNESS

Population size and density vary markedly with the past history of disturbance by fire. Monospecific stands of up to 250 plants/m^2 have been recorded in mature recently-burnt populations, although population density is usually in the range 0.8-6 plants/m^2 (Auld, 1984). In older less-disturbed habitats, plants are usually widespread but not abundant. As the plants are relatively short-lived and do not normally regenerate without fire (Auld and Myerscough, 1986; Auld, 1987), density decreases with age of the population.

RESPONSE TO BIOTIC FACTORS

Plants without rootstocks are destroyed by even the mildest fires. However, these fires render the seed coat permeable to water, and the seeds in the soil then imbibe and germinate if suitable rains fall (Bradstock, 1981; Auld, 1986c). Thus, if plants are old enough to have produced seed, the species will readily regenerate strongly immediately following a fire (e.g. Specht, 1975; Siddiqi *et al.*, 1976; Harrold, 1979); and *A. suaveolens* is often the major understorey species (commonly with *Pteridium esculentum* and *Imperata cylindrica*) in communities which have been frequently burnt.

This species does not respond well to disturbances other than fire. It does not regenerate following disturbance by sand mining without being treated with fertilizer (Clark, 1975; Thatcher and Westman, 1975), but it does compete well with exotic grass cover after this disturbance (Thatcher and Westman, 1975). Gillham (1960) has noted that this species is characteristic of the unaffected areas of sea-bird rookeries but does not occur in areas which have been dug or trampled by the birds. Similarly, Yates (1976) found that it does not regenerate well in easements under electrical transmission lines, attributing this to continued disturbance from maintenance, a higher water table, and the use of herbicides.

PERFORMANCE IN VARIOUS HABITATS

The size which plants attain varies greatly between habitats, as does the size at which they begin to flower and the number of inflorescences and fruits produced per year. Death rates vary between sites, apparently depending on the rate at which the soil dries out during summer (Auld, 1987), being greater in thin sandy soils compared with deep sands. Auld (1984) has also reported between-site variability in seed weight and seed viability.

Seed production is reduced through predation by the weevil *Melanterius corosus*, and the extent of this predation varies markedly between sites. Auld (1983) and Auld and Myerscough (1986) found losses to vary from 10-61%, with a mean of 47%, at six sites during several fruiting seasons. Populations which suffer from this weevil predation have only been found north of Jervis Bay in New South Wales; and the predation is usually more prevalent in larger populations, with scattered populations of only a few individuals commonly being free from predation.

Leaf area does not vary (range 8.0-8.3 cm^2) when grown in the laboratory in a range of soil types (Beadle, 1962), but total dry weight of the plants (as well as root nodulation) is reduced when plants are grown in swamp soils as opposed to the lower-nutrient eucalypt forest soils (Hannon, 1956).

In cultivation, plants will grow in light from filtered sun to full sun, but not in semi shade or full shade (Elliot and Jones, 1982). Response to salt winds and exposure to full salt spray is reported to be variable (Allen and Allen, 1981; Elliot and Jones, 1982), and plants vary in habitat from sheltered leeward dune slopes to fully exposed headlands.

EFFECT OF FROST, DROUGHT, AND WATERLOGGING

The altitudinal and large latitudinal range of *A. suaveolens* suggests that this species can tolerate considerable exposure to frost, and Simmons (1966) lists 18-month-old plants as surviving temperatures as low as -7°C in late June in Tasmania without frost damage.

A. suaveolens is particularly common in dry soils, which indicates that this species also has considerable tolerance to drought. However, plants show a much higher death rate during summer than at other times of the year, and Auld (1987) ascribes this to the considerably lower moisture levels of the soil during extended periods of high temperature and low rainfall.

Populations usually occur on freely-draining soils, but can be found on seasonally-waterlogged sites (e.g. Parsons, 1966; Siddiqi *et al.*, 1972; Myerscough and Carolin, 1986) and occasionally in permanently moist areas (e.g. Parsons, 1966; Siddiqi *et al.*, 1976; Benson and Fallding, 1981). However, plants were not recorded as regenerating after fire in ground-water heaths (Siddiqi *et al.*, 1976); and plants have not been recorded from sites where a standing water table reaches the shoot system.

MORPHOLOGY

The flowers are borne in axillary racemes of heads, these racemes being produced only by buds in the axils of phyllodes on those vegetative shoots that were produced during the previous December to January. Shoots produced in previous years do not usually flower. The axillary primordia may or may not expand and differentiate into floral buds. These floral buds expand lengthwise, the bracts fall off, and the flowers open. These flowers are andromonoecious, with about 13-50% of the flowers being bisexual (Morrison, 1986).

As each individual flower forms, it follows a spiral developmental sequence from the outside to the inside, described in detail by Newman (1936). Each flower is protogynous, the style first being exserted well beyond the petals, which still enclose the contorted undehisced anthers. The style is folded in bud, and pushes its way out between the overlapping petals before the bud opens, straightening progressively as the flower begins to open. The cup-shaped stigma is of the wet non-papillate type, and is sited terminally on the long narrow style. Several days after the exsertion of the style, the stamen filaments unfold and lengthen; although the style still projects well beyond them. The anthers then dehisce. Each flower head in a raceme flowers synchronously, so that each head is also protogynous. However, the racemes open subacropetally and subsynchronously, while the racemes usually open basipetally along the vegetative shoot. Therefore, each raceme and each shoot usually contains flowers at all stages of anthesis at some time.

When the ovary has been fertilized it changes colour from dull brown to reddish-maroon. The unfertilized flowers drop off early, leaving the small fruits on the bare stalks. The fruits then expand very slowly in both length and breadth for 5-8 weeks, after which they rapidly expand in length only for a further 3-5 weeks, before breadth again begins to increase. The fruits reach their final size rapidly after this, and they begin to thicken the fruit walls. The fruits then dry out and open along the ventral and then the dorsal sutures, releasing the seeds. The fruits open about 15-22 weeks after they are formed, with seed release being fairly synchronous in any one population.

The buds that form the next season's vegetative shoots are in the same axils of the phyllodes as the floral buds, and adjacent to them. Thus, the new shoots of one season are the sites of both the ensuing flowering and fruiting and also of the following season's shoot production. If no new vegetative shoots survive on a particular branch of a plant in a particular season, then that branch dies back to a branch that is supporting a surviving shoot. If no new shoots survive on a plant, then that plant dies back to the main stem, where it may or may not produce new shoots from buds that are several years old. Such plants do not usually flower again, and they die the following summer. Therefore, the successful production of new vegetative shoots is the key to the long-term survival of a plant.

If the growing points of the plants are destroyed in any way, reversion foliage consisting of pinnate or bipinnate leaves may appear on the proximal parts of branches or along the stem (Cambage, 1915; 1917; Fletcher, 1920). Similar foliage may be produced at the base of the stem if the upper shoots die back during summer, although this usually consists of small phyllodes with a number of leaflets at the tips. Plants with reversion foliage rarely produce floral buds, and they usually die within the next 3-12 months.

The leaflet buds are often found along the margins of the phyllodes as well as at the tip, resulting in the appearance at different places along the phyllode margins of pairs of reduced pinnae, pairs of leaflets, and single leaflets (Fletcher, 1920).

The phyllodes are xeromorphic microphyllous leaves. The epidermis is narrow, with a thick cuticle (Lemesle, 1965). Most of the mesophyll is composed of chlorenchymatous palisade cells, but it passes gradually into a smaller central zone of spongy cells less rich in chloroplasts (Lsmesle, 1965; Boughton, 1986). The primary and secondary veins are covered by a crescent of sclereid fibres, often with tracheids, and the surrounding tissue sometimes has calcium oxalate inclusions (Lemesle, 1965). The stomata are mesogenous, paracytic and bicytic (Grosso, 1987), fairly large ($25.0 \pm 2.5\mu m$ long; Connor and Doley, 1981), and occur on both surfaces of the phyllodes at a density of $249 \pm 21mm^{-2}$ (Connor and Doley, 1981).

The woody stems have a perennial vascular cambium, which produces very little secondary phloem. The secondary xylem consists of diffuse porous vessels with paratracheal axial parenchyma. There is no ray parenchyma, and no heartwood is formed. Periderm is present only on older stems very close to the base of the stem.

The contribution to the community biomass (i.e. wood component) in any one area is usually very small (e.g. $< 0.05\%$, Clark, 1975; 0.06-0.09%, Thatcher and Westman, 1975; 0.1%, Specht, 1979), and the percentage cover (i.e. leaf component) is also low (e.g. 0.02- 0.32%, Russell and Parsons, 1978; $> 0.17\%$, Posamentier *et al.*, 1981; 0.7-1.4%, Weste, 1981; 0.2-0.8%, Fox and Fox, 1986). The percentage cover does not apparently show any particular pattern of change with population age (Russell and Parsons, 1978).

CHROMOSOMES

$2n = 26$ in material from New South Wales (Hamant *et al.*, 1975).

PHYSIOLOGICAL DATA

Specht and Groves (1966) and Groves and Keriatis (1976) have investigated the phosphorus relations of *A. suaveolens* in water and sand cultures respectively. The plants showed little growth below 0.1ppm P, but there was a significant increase in dry weight accumulation between 0.1 and 1.0ppm P. No further dry weight increase occurred at 5.0-10.0ppm P, and all plants died at 50ppm P and above. At the higher P levels, root weight showed a greater decrease than did shoot dry weight; and the plants showed toxicity symptoms above P levels of about 4% of the shoot dry weight, with irregular necrotic areas appearing on the phyllodes before they began to die from the tips down. At levels of 50ppm P or more, the cotyledons senesced and the juvenile bipinnate leaves became red-purple, with the pinnae and petioles dying before the formation of phyllodes. At low P levels, $< 30\%$ of the dead leaves were shed and 85-90% of the P was translocated from the dead to the living tissues. The plants did not show any deficiency symptoms at low P levels. The P content of the phyllodes tended to increase with increased P levels in the substrate, and the maximum P uptake from the substrate was 57% (in water culture).

The nitrogen relations of *A. suaveolens* in sand culture have been investigated by Groves and Keriatis (1976). The plants showed no response to changing N levels from 0-250ppm without the addition of P. The most favourable combination for growth was low P concentration and high N concentration (see also Hannon, 1956). At low N levels the plants showed deficiency symptoms, with a reddening of the leaflet tips; and the N content of the phyllodes did not vary with the N concentration in the substrate. The root/shoot ratio was highest at intermediate N concentrations with no added P.

Beadle (1962) grew *A. suaveolens* plants in a range of soils in a glasshouse, and found that plants grew larger (ranging from 12 to 170cm tall after 5 months) and produced more leaves on soils with higher nutrient levels (ranging from 23 to 230ppm P). Leaf area did not differ between these treatments. Plants grown on full nutrient solution in the laboratory absorb P far in excess of field requirements (Beadle, 1968); and plants given insoluble phosphate in the form of ground fossil laterite concretions could not absorb this 'unavailable' P (Beadle, 1968).

Clark (1975) and Thatcher and Westman (1975) have shown that the addition of fertilizer to *A. suaveolens* seedlings following sand mining increases their contribution to the community biomass in the following 2-3 years (i.e. bigger plants are produced), but that by the fourth year the species has returned to its pre-mining level. Specht (1975) and Specht *et al.* (1977) have concluded that an increase in the nutrient level in the soil increases the growth rate and speeds-up the life cycle of these plants, resulting in their earlier death; and Specht *et al.* (1977) recorded the disappearance of an unusually high number of *A. suaveolens* plants during the 8 years of their fertilized treatment.

The seeds contain about 0.2% total P, 4.0% total N, 1.0% K, 1.3% Ca, and 0.4% Mg (Beadle, 1968; Groves and Keriatis, 1976; P.J. Myerscough pers. comm.). Phyllodes from field plants contain 0.01-0.05% P (Beadle, 1968; Lambert and Turner, 1987) and 1.8-2.1% N (Hannon, 1956), both increasing with increased nutrient status of the soil, and 0.01% Al, 0.40% Ca, 0.32% Mg, 0.86% K and 1.92% Cl (Lambert and Turner, 1987).

Biochemical Data

Seneviratne and Fowden (1968) and Evans *et al.* (1977) have found the following free amino acids in the seeds: S-carboxyethylcysteine (the predominant amino acid), S-carboxyethylcysteine sulphoxide, S-carboxyisopropylcysteine, β-acetyl-α,β-diaminopropionic acid, α-amino-β-ureido-propionic acid, pipecolic acid, 4-hydroxy-pipecolic acid, 5-hydroxypipecolic acid, djenkolic acid, djenkolic acid sulphoxide, γ-glutamyl-djenkolic acid. Conn *et al.* (1985) did not find any cyanogenic glucosides in either fresh leaves or herbarium material.

Perennation and Reproduction

A. suaveolens is normally a nanophanerophyte, or occasionally a microphanerophyte. Plants without rootstocks have a half-life of 3.7 years (Auld, 1987), with most populations lasting a maximum of 15-25 years (cf. Siddiqi *et al.*, 1976; Specht *et al.*, 1977; Russell and Parsons, 1978; Clemens and Franklin, 1980; Bradstock, 1981; Auld, 1987). The lifespan of the form with rootstocks is unknown. The annual death rate is about 22% up to 8 years of age, and about 12% after this (Auld, 1987).

Vegetative growth continues throughout the life of the plant, with 1-6 shoots being produced each year (Morrison, 1986). Shoot production is low for old plants, and very variable for younger plants (Morrison, 1986), with the younger plants producing much longer shoots (Morrison, 1986).

Reproduction is entirely by seed, although this species can be cultivated from cuttings (Elliot and Jones, 1982). Seedlings are rarely found in the field unless recently stimulated to germinate by a fire (Auld, 1987), with fire-free periods of 10-30 years being the most appropriate for the long-term maintenance of viable populations of this species (Auld, 1987).

Phenology

Flowering is strictly seasonal, with floral buds usually initiated in autumn, but with a distinct geographical sequence from north to south (Table 4). Flowers are most profuse in mid winter, with the fruits ripening and releasing the seeds from late spring to early summer (Table 4).

TABLE 4

Times at which flowers and mature fruits of Acacia suaveolens *have been recorded*
Data from 216 dried specimens at CBG, MEL, NSW, PERTH, *and* SYD *which had sufficiently detailed data on collection-locality and date, plus Rodway (1903), Ewart (1930), Groves and Specht (1965), Court (1972), Beadle (1976), Armitage (1977), Rogers (1978), Clifford and Specht (1979), Pedley (1979), Whibley (1980), and Beadle* et al. *(1982)*

Area	Flowers	Mature fruits
Queensland	early March — mid August	early June — end October
N.S.W. north coast*	mid March — end August	early June — end October
N.S.W. central coast and tablelands	mid March — early September	early June — end November
N.S.W. south coast+	early April — end October	end June — early December
Victoria	end April — end October	early July — mid January
South Australia	end May — end September	early September — mid January
Tasmania	mid May — mid September	early September — end January

* north of Newcastle; + south of Nowra

Flowering time is very population-specific in any one area (Morrison, 1986), but there is considerable variation from year to year, with low rainfall at the beginning of the season delaying the onset of flowering (Morrison, 1986). However, Blakely (1941) suggests that early onset of flowering is also related to low rainfall. Individual plants flower for about 4-7 weeks, but this duration decreases with plant age (Morrison, 1986). Any individual floral bud on a plant flowers for about 3-5 weeks (Morrison, 1986), with most buds opening fairly synchronously.

Fruiting phenology closely follows the flowering phenology (Morrison, 1986), except that fruits ripen and release their seeds over the same 2-3 week period each year, irrespective of when flowering was initiated (Morrison, 1986). Consequently, only early-opening flowers ever ripen fruits, as ripe fruits are usually 15-20 weeks old when they release their seeds (Morrison, 1986).

Vegetative buds are usually initiated immediately after the seeds are released. Vegetative growth continues for 8-10 weeks, when the floral buds are initiated on the new shoots.

Very small numbers of seeds germinate without stimulation from fire, and these may be found at any time of the year (Auld, 1987). Only 14 seedlings emerged at seven sites over three years, and only one of those survived longer than six months (Auld, 1984).

FLOWERING AND POLLINATION

Plants can flower within 1.5 years if germination occurs in summer, but not until the second year if germination occurs in later seasons (cf. Clemens and Franklin, 1980; Benson, 1985); however, individual plants may take up to 4-5 years to flower (Auld, 1984; Benson, 1985). 80- 93% of the plants in a population flower each year, and this is consistent from year to year for the life of the population (Morrison, 1986).

Flower production varies greatly from year to year, but there is a close inverse relationship with plant age, the first 1-4 years being the most prolific (Morrison, 1986). This pattern seems to be related to a reduced number of floral buds being produced per vegetative shoot as the plants age (Morrison, 1986), while the large inter-year variation in flower production is related to inter-year variation in the number of vegetative shoots produced (Morrison, 1986). Some plants also appear consistently to produce more flowers each year than do others (Morrison, 1986).

Superimposed on the age pattern is a relationship with rainfall, increased rainfall early in the flowering season being correlated with increased flower production (Morrison, 1986). However, floral buds produced in the middle of the season produce more flowers and ovaries than do floral buds produced early or late in the season (Morrison, 1986), and the ovaries contain more ovules.

Ovule number per ovary is not very variable, being reported as 5-6 (Newman, 1936), 5-7 (Kenrick and Knox, 1982; Knox and Kenrick, 1983), and 6-9 (Morrison, 1986). Anther number per flower is also not very variable, at 60-80 (Newman, 1936), and 44-52 (Morrison,1986). Pollen fertility is fairly high, at 85-95%, but this decreases with plant age (Morrison, 1986).

About 15-31% of the ovaries produced per plant are fertilized, with about 1-12% aborting, and 2-48% being eaten by insects (Morrison, 1986). Of the ovules produced per plant, about 3% are aborted, 12% are eaten, 1% are not fertilized in ovaries that are fertilized, 23% are fertilized, and 61% are dropped from the plant (Morrison, 1986).

Pollination of flowers is very consistent in this species at about 15-31% (Morrison, 1986), and so fruit production closely follows the pattern of flowering discussed above (Morrison, 1986). However, pollination rate is markedly decreased in floral buds opening late in the flowering season (Morrison, 1986).

The pollinators are apparently a range of non-specific insects (Morrison, 1986), including beetles (Coleoptera: Chrysomelidae, Cerambycidae, Apionidae), bees (Hymenoptera: Apidae, Halictidae), flies (Diptera: Syrphidae), ants (Hymenoptera: Formicidae), and hemipterans. However, the introduced honey bee, *Apis mellifera* (Hymenoptera: Apidae), seems to be the most effective pollinator in some areas (Morrison, 1986). Pollen is the only reward, as no nectar is secreted by the phyllode gland (Hardy, 1912; Boughton, 1981; but see also Carne, 1913b). Wind pollination is unlikely, as the 16-grain pollen polyad (see Cookson, 1954; Guinet, 1969; Kenrick and Knox, 1982; Knox and Kenrick, 1983) is not easily windborne.

SEED PRODUCTION AND DISPERSAL

Of the fruits formed on a plant, about 38-85% abort during the first 5-10 weeks after they are formed, 5-25% abort later on, 2-41% are eaten by insects, and 1-13% mature and release seeds (Morrison, 1986). The abortion of the young fruits apparently allows the plants to regulate tbe number of seeds released per plant quite closely (Morrison, 1986). About 48% of the plants in a population mature fruits in any one year (Auld and Myerscough, 1986), and there is considerable inter-year variability in the number of fruits per plant (Auld and Myerscough, 1986; Morrison, 1986). The number of fruits matured per plant follows the same inverse relationship with plant age as does flower production (Auld and Myerscough, 1986; Morrison, 1986), and there is the same increased production with increased rainfall (Auld and Myerscough, 1986).

Of the seeds formed per plant, about 60% abort while small, 12% abort later, 16% are eaten by insects while small, 7% are eaten by insects later, 3% are consumed by weevil larvae (Coleoptera: Curculionidae), and 2% are matured and released (Morrison, 1986).

The dispersal unit is the seed with its aril. Average seed weights (with aril included) per population of 23-41mg have been reported from a wide geographical range (Specht and Groves, 1966; Beadle, 1968; Groves and Keriatis, 1976; Drake, 1981; Westoby *et al.*, 1982; Auld, 1983; Morrison, 1986), and average weights from 27-41mg have been reported from populations within a few kilometres of each other (Auld, 1983; Morrison, 1986).

The seeds are released passively from the fruits. Auld (1986b) reports that the average distance of fallen seed from the parent plant is 45cm, with 90% of the seed within 1m of the parent. This distance is partly dependent on the height of the parent plant (Auld, 1986b).

Ants have been observed to move seeds to their nests in the Sydney region (Rice and Westoby, 1981; Auld, 1986b), on North Stradbroke Island (Drake, 1981), and on Wilsons Promontory (Andersen and Ashton, 1985). Drake (1981) found seeds to be removed at the rate of 10 seeds in 55 min, with *Rhytidoponera metallica* removing 9 seeds and *Aphaenogaster longiceps* removing the other. Auld (1986b) reports two unidentified species of *Pheidole* and one of *Iridomyrmex* to move seeds, although only *Pheidole* sp.A actually took them into their nests. *Pheidole* sp.A moved seeds an average of about 220cm, while the other two species only moved them about 10-15cm (Auld, 1986b). Removal rates vary from 93-100% (Drake, 1981; Auld, 1986b; Andersen and Ashton, 1985), although Auld (1986b) reported that only 38% of the seed removed by *Pheidole* sp.A was incorporated into the nests, and none of the seed removed by the other two species were. Seeds are found in the top 5cm of the soil outside ant nests, but in the top 2-15cm inside the nests (Auld, 1986b). About 65% of the seeds end up in sites that are unsuitable for germination (Auld, 1987).

All ant species drag the seeds by the tip of the aril. The elaiosome is the folded aril, which in *A. suaveolens* is unusual in being dark brown instead of the more usual whitish colour of other acacias (Vassal, 1971; 1972; Drake, 1981). This elaiosome comprises about 5% of the weight of the dispersal unit (Westoby *et al.*, 1982; Auld, 1984).

The released seeds are incorporated into the soil seed bank, at a density of 6-23 seeds/m^2 outside ant nests (Auld, 1986b). The annual decay rate of seeds in the soil is 6.5%, with a seed half-life of 10.7 years (Auld, 1986b). The peak size of the soil seed bank occurs at a population age of about 6 years, and the population self-replacement point (ie. where the number of seeds in the soil equals the initial mature population size) is about 60 years (Auld, 1987).

Dispersal of seeds onto bare rock has also been reported. Five years after an 8-acre [3.2ha] area of Hawkesbury sandstone was cleared of both plant and soil cover to expose the underlying rock, *A. suaveolens* was one of the few species recorded to have become established (Cambage, 1923); and 44 years later plants were reported to be scattered infrequently over the still extremely thin sandy soil (Hannon and Evans, 1963).

VIABILITY OF SEEDS AND GERMINATION

Staining with 2,3,5-triphenyl-tetrazolium chloride reveals that mature seeds heavier than 20mg are more than 98% viable, independent of site or age of the parent plant (Auld, 1986a). Seeds less than this weight have significantly reduced viability (down to 40%). The seeds have a hard impermeable seed coat 180μm thick (Cavanagh, 1980), which means that the seeds are in induced dormancy (*sensu* Harper, 1977). Less than 1% of the mature seeds will germinate spontaneously on release from the fruit, and the remainder enter the soil seed bank (Auld, 1986a). Most of the induced dormancy is acquired during the first 2 weeks after seed release (Auld, 1986a).

The seeds can remain viable in storage for many years. P. J. Myerscough (pers. comm.) found that after 83 months storage 16/23 seeds were still capable of imbibing after scarification and treatment with boiling water, and Ewart (1908) reported that 1/25 seeds stored for 51 years was still capable of imbibing after sulphuric acid treatment.

The seed coat impermeability can be overcome by heating (either by adding boiling water, heating in an oven, or exposure to microwaves), treatment with sulphuric acid and dilute ammonia or lime water, or mechanical chipping or abrading (Ewart, 1908; Clemens *et al.*, 1977; Cavanagh, 1980; Auld, 1986c). Clemens *et al.* (1977) achieved maximum germination of 77% by chipping the seeds, while Auld (1986a) achieved 98% germination by abrading with sandpaper. For mechanical chipping, seeds germinate more rapidly, with a maximum rate of 48.5 seeds/day as opposed to only 2.2 seeds/day for the boiling water treatment (Clemens *et al.*, 1977). Seeds imbibe within 15 hours when mechanically chipped (Clemens *et al.*, 1977). The optimum temperatures for breaking seed dormancy are 60-80°C, for any length of time (Clemens *et al.*, 1977; Auld, 1986c). Below this temperature, germination percentage is low, even if heated for long periods of time, and above this the seeds are killed even if exposed for short periods.

Cavanagh (1980) considers the strophiole to be responsible for overcoming the hard-seededness. He found that, after heating the seeds to 100°C by microwave exposure, the shortened palisade cells covering the vascular bundle at the strophiole broke down, allowing water penetration in this area. The seeds then swelled from this end. Heat-treated seeds that had the strophiole covered with petroleum jelly did not imbibe, and so there is no general water permeability after treatment.

Heat-treated seeds have been observed to germinate and emerge from depths of up to 10-15cm in laboratory trials (Drake, 1981; Auld, 1986c); but in the field, emergence has only been recorded from a maximum depth of 6cm (mean depth 2.4cm) (Auld, 1986c).

SEEDLING MORPHOLOGY

Seedling growth in *A. suaveolens* has been monitored and described in detail by Cambage (1915) (see his fig. 1, fig. 3, plate IX nos 8-10) and more recently by Vassal (1970; 1972).

After germination, the curved upper portion of the hypocotyl appears above the soil first, the cotyledons free themselves from the testa, and then the hypocotyl elongates and becomes erect, pulling the cotyledons out of the soil, where they open out. The hypocotyl is erect, terete, pale reddish-violet, 5-40mm long, thicker than the epicotyl, with their boundary marked by an annular crest. The cotyledons are opposite, shortly (but distinctly) petiolate, oblong, distinctly lobed, sagittate, 6-9mm long, 3-4mm wide, erect at first but becoming horizontal in a few days, reddish-violet on the lower surface, greenish-brown becoming greenish-red then green on the upper surface. They are persistent at least until the production of the 15-16th leaves.

The first leaf produced is pinnate, followed by a succession of alternate, bipinnate leaves, phyllodinization beginning at the 5-8th leaf stage and ending between the 7-12th leaves. The first two leaves are produced at right angles to the plane of the cotyledons, and subsequent leaves appear in two helices. This pattern does not change with the transition to phyllodes. The first leaf is usually 5-7mm long, and is a similar colour to the cotyledons. Subsequent leaves sequentially increase from 1-2cm to 3-4cm long, and are pale green. The early leaves are lyrate, with the number of leaflets sequentially increasing from (2-)3-4 (-5) to 4-6(-7), before phyllodinization. Up to the 4th leaf stage, mixed leaves are sometimes produced, where the proximal pair of leaflets may be replaced by a pair of pinnae which are as large as the distal part of the leaf. The phyllodes appear gradually as the petioles in subsequent leaves become more dilated vertically, with reducing numbers of leaflets at the tips.

MYCORRHIZA

Rhizobial root nodules have been reported on this species in the field in the Sydney region (Carne, 1913a; Benjamin, 1915; Hannon, 1956; Norris, 1959; Barnet *et al.*, 1985) and in Queensland (Bowen, 1956). Thess rhizobia are of the slow-growing *Bradyrhizobium* type (Norris, 1959; Barnet *et al.*, 1985) as well as the fast-growing *Rhyzobium* type (Barnet *et al.*, 1985). The nodules can produce a urea-splitting enzyme (Benjamin, 1915). In cultivation, the bacteria show increased growth with increased Mg in the medium (Norris, 1959); and root nodulation decreases with increasing N levels in the substrate (Groves and Keriatis, 1976), but increases with added P at low N levels (Hannon, 1956; Beadle, 1962).

ANIMAL FEEDERS AND PARASITES

The fruits of *A. suaveolens* are reported to be an important food source for lorikeets, parrots, cockatoos, and native pigeons (Adams, 1980), although evidence has been presented only for crimson rosellas [*Platycercus elegans* (Gmelin)], which cut the edge from the unripe pod to extract the half-ripe seed.

The only invertebrates reported to be associated with *A. suaveolens* are insects. Froggatt (1902) reports that larvae of *Rhinotia hoemoptera* Kirby (Coleoptera: Bruchidae) live inside the branches, while the adults feed in the foliage. Also, *Sextius virescens* (Faimaire) (Homoptera: Membracidae) lay their eggs in slits cut through the bark of young branches (Cookson and New, 1980). New (1983) reports 11 unidentified species of arthropods inhabiting 18-month-old seedlings, 3 of these species being Araneae, 2 Coleoptera, and 1 Lepidoptera.

Morrison (1986) reports unidentified beetles (Coleoptera: Chrysomelidae) and grasshoppers (Orthoptera: Acrididae) consuming flowers.

Auld (1983), Auld (1986d) and Auld and Myerscough (1986) report that larvae of *Melanterius corosus* (Boisduval) (Coleoptera: Curculionidae) feed in developing seeds in the field, as well as consuming whole fruits. Auld (1986d) also reports that adults of *Melanterius maculatus* Lea will oviposit in fruits in the laboratory. Auld (1983) and Auld and Myerscough (1986) report unidentified lepidopterans, hemipterans, and grasshoppers feeding on all or part of developing fruits, while Morrison (1986) lists unidentified species of adult grasshoppers (Orthoptera: Acrididae), sap-suckers (Hemiptera: Psyllidae), and beetles (Coleoptera: Chrysomelidae) doing the same. Morrison (1986) also notes several unidentified species of coleopteran larvae (Coleoptera: Lagriidae, Pythidae, Tenebrionidae, Nitidulae), and five unidentified species of lepidopteran larvae, all eating developing fruits.

Drake (1981) reports *Aphaenogaster longiceps* F. Smith and *Rhytidoponera metallica* F. Smith (Hymenoptera: Formicidae) eating the aril of mature seeds, while Auld (1986b) reports two species of *Pheidole* and one of *Iridomyrmex* to do the same.

PLANT DISEASES AND PARASITES

Weste and Law (1973) and Weste (1981) consider *A. suaveolens* to be a species which is tolerant of *Phytophthora cinnamomi* Rands rather than resistant to it. In their study plots on Wilsons Promontory, the species did not show early signs of becoming affected by the root rot, unlike the majority of the surrounding woodland (Weste and Law, 1973), but did eventually develop mild but fluctuating symptoms (Weste, 1981). While the surrounding community changed from a low shrub woodland to an open sedge woodland, with a reduction in tree density and a loss of susceptible species, *A. suaveolens* was the only species to actually increase in percentage frequency. On the diseased plots, *A. suaveolens* plants showed severe and permanent die-back during periods of high evaporation and low rainfall, while on the control plots no die-back occurred. This behaviour may merely be a response to the opening of the tree canopy.

Fletcher (1920) records that *A. suaveolens* plants are 'particularly liable to fungoid attacks, which sometimes interfere with, or even kill the growing point', but he does not specify the fungi involved. Similarly, Cambage (1917) comments on 'pathological trouble' at the growing points but is not specific.

HISTORY AND CONSERVATION

A. suaveolens was first collected by Joseph Banks and Daniel Solander at Botany Bay in 1770 (Britten, 1905), and it was among the first species to have seeds sent back to Europe from Australia (Lebler, 1980), so that by the end of that century it had been established in a number of the botanical gardens of Britain (Loudon, 1830) and Europe (e.g. Jacquin, 1798). The only report of the direct human exploitation of *A. suaveolens* is the use by the early European settlers of the aromatic leaves in infusions as teas (Nakao, 1976). The prehistory is unknown, as no pollen directly referrable to *A. suaveolens* has been found in the fossil record.

A. suaveolens was apparently common throughout its geographical range when it was first collected by Europeans, as it was readily collected by many of the early exploration parties. However, it is now much more restricted in occurrence in Queensland, Victoria, South Australia, and Tasmania due to human destruction of suitable habitats (Morrison *et al.*, 1983).

In Queensland, populations are now rare, principally because of the many new coastal housing developments that are occupying the available habitats (Morrison *et al.*, 1983). The only areas where this species appears not to be at risk are the less-disturbed parts of the large sand islands.

In Victoria, there are apparently no longer any large coastal populations west of Wilsons Promontory, although this species was frequently collected between there and Melbourne at the turn of the century (Morrison *et al.*, 1983). This appears to be a result of pastures and settlements encroaching on the somewhat restricted habitats.

In South Australia, this species has only been recorded since the early 1960's, and the majority of the known populations are in vacant lots in plantations (Morrison *et al.*, 1983). More recently, the western-most known population was apparently destroyed by roadside vegetation clearing.

In Tasmania, this species is also rarely encountered, principally due to destruction of coastal heathlands. In particular, the species' distribution along the northern and eastern coastlines is now very patchy.

The species is most widespread and common in New South Wales, and it is very easily located along most of the coastal areas. In particular, even in the disturbed urban areas *A. suaveolens* is commonly encountered in the coastal parts, unlike the other states.

The two geographically-restricted morphological forms are each present in conservation areas, the narrow-leaved form in the Myall Lakes National Park, and the Grampians form in the Grampians National Park.

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Multiple Folding of the Ordovician Sequence, Tambo River, eastern Victoria

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FERGUSSON, C. L. Multiple folding of the Ordovician sequence, Tambo River, eastern Victoria. *Proc. Linn. Soc. N.S.W.* 109(4), (1986) 1987: 293-309.

Ordovician quartz-rich clastics of the Tambo River region in the Tabberabbera Belt of eastern Victoria show the effects of four folding episodes. A strong to weak bedding-parallel slaty cleavage is developed throughout the region and predates the earliest folds so far identified. F_1 folds are tight to close with steep easterly trending axial surfaces and large amplitude-to-wavelength ratios. The F_1 folding is thick-skinned and is responsible for major crustal thickening in the area. F_2 folding is only locally developed and is associated with a pervasive stripy cleavage in sandstones. F_3 folds are widespread upright northerly-trending structures with close to open interlimb angles. Superimposition of F_3 on F_1 has caused bending of F_1 fold trends and formed an eye-type interference fold pattern in one instance. F_4 folds consist of warps and kink-like folds.

The east-west F_1 folds extend into the Omeo Metamorphic Complex and predate the Late Silurian volcanic and sedimentary sequence near Benambra. F_3 folds have been traced westwards to Tabberabbera where they are of the Middle Devonian age and are related to east-west compression.

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INTRODUCTION

The Palaeozoic tectonic history of the Lachlan Fold Belt in eastern Victoria is characterized by several intermittent compressional events (VandenBerg and Wilkinson, 1982). The styles and orientations of structures produced by these deformations are known only from some restricted areas (e.g. Beavis, 1967; Fagan, 1979; Wilson *et al.*, 1982). The aim of this paper is to describe the structure of the Ordovician rocks in the Tambo River region of eastern Victoria (Fig. 1) and to relate the two main deformations to the Early-Middle Silurian Benambran and Middle Devonian Tabberabberan deformations respectively.

REGIONAL SETTING

The Ordovician sequence of the Tambo River region lies partly in the southern Omeo Metamorphic Complex and mainly in a belt of very low-grade metamorphosed rocks called the Tabberabbera Sub-zone by VandenBerg (1978) and the Tabberabbera Belt by Fergusson (1985). The eastern boundary of the Tabberabbera Belt is the Kiewa Fault which has a steeply dipping mylonite zone up to 2km in width (Scott, 1985). East of the Kiewa Fault is the Omeo Metamorphic Complex which consists of lower greenschist to upper amphibolite facies metamorphics derived from Ordovician quartzose clastics and intruded by S- and I-type 'granitoids' (Fagan, 1979).

Fagan (1979) has shown that major folds in the metamorphics are upright and easterly trending. This deformation extends throughout the Tabberabbera Belt and is the major folding in the Tambo River region (Fergusson, 1985). North and east of Benambra the Late Silurian volcanic and sedimentary sequence postdates the major metamorphism and deformation in the Omeo Metamorphic Complex (Fig. 1; Bolger, 1982; Bolger *et al.*, 1983). The Silurian sequence was strongly deformed prior to the deposition of the unconformably-overlying Lower Devonian Snowy River Volcanics (VandenBerg and Wilkinson, 1982).

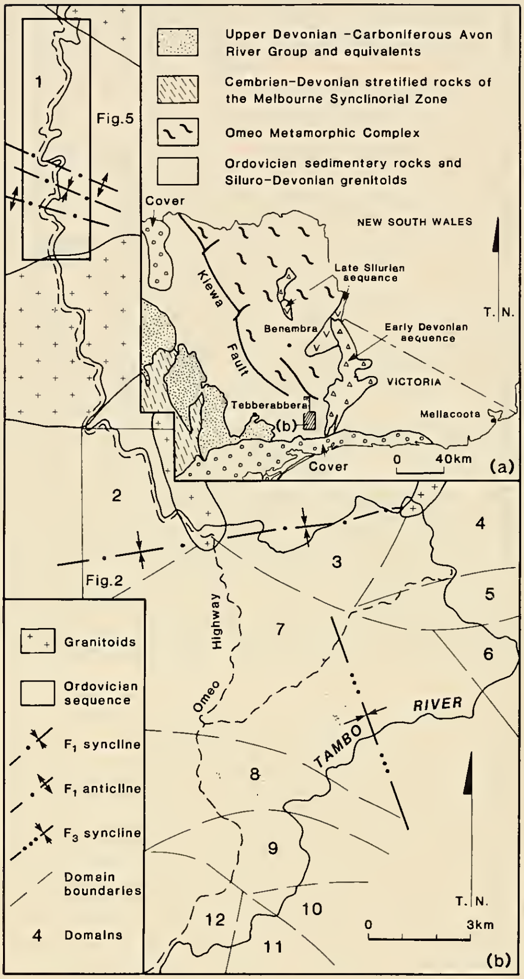

Fig. 1. a. — Geological sketch map of eastern Victoria with the location of the Tambo River region shown by the shaded inset.
b. — Geological map of the Tambo River region showing the locations of Figs 2 and 5 and domains 1 to 12. Note that the Kiewa Fault is not shown as it is cut by the 'granitoid' between domains 1 and 2.

At Tabberabbera the Ordovician sequence is overlain with a high angular unconformity by the Emsian Wentworth Group and both are, in turn, overlain with a high angular unconformity by the Upper Devonian-Lower Carboniferous Avon River Group (Talent, 1963). The latter surface was called the Tabberabberan Unconformity by Harrington *et al.* (1974) and VandenBerg (1977). This was caused by uplift and erosion associated with the deformation that formed a tight northerly-trending syncline in the Wentworth Group. The deformation is commonly referred to as the Tabberabberan Orogeny.

West of the Tabberabbera Belt lies the Melbourne terrane of Fergusson *et al.* (1986). The Melbourne terrane consists of Cambrian mafic volcanics and a conformable Ordovician to Middle Devonian quartzose clastic succession. Structurally the Melbourne terrane is dominated by northerly-trending upright folds with a major fault zone along its eastern margin. The Cambrian rocks occur as slices within the fault zone which is unconformably overlain by Upper Devonian — Lower Carboniferous fluviatile sediments and volcanics. These relations establish that the deformation that affected the Melbourne terrane was the Tabberabberan Orogeny (VandenBerg and Wilkinson, 1982).

STRUCTURE

The Ordovician strata of the Tambo River region consist of a monotonous quartz turbidite succession (Stewart and Fergusson, in preparation). The structure of the region is dominated by two main deformations with two additional deformations of lesser extent and significance. Each deformation is characterized by folds and accordingly each event is labelled F_1, F_2, F_3 and F_4 in order from oldest to youngest. These fold episodes are mapped on the basis of orientation and fold style groups whose age relations have been determined by overprinting criteria. The nature of axial plane foliations associated with each fold generation has been the least useful guide in structural mapping (cf. Williams, 1985). Macroscopic structure is indicated by many sections of homoclinal strata and the abundance of younging criteria (Figs 2, 3, 4, 5 and 6).

The earliest structure developed in the Ordovician sequence is a bedding-parallel slaty cleavage that predates all folding (Fig. 7**d**). A similar fabric has been described from the Ordovician at Mallacoota (Wilson and de Hedouville, 1985). The significance of this fabric will be discussed elsewhere (C. L. Fergusson and D. R. Gray, unpub. data).

F_1 FOLDING

The F_1 folding is the most pervasive structural event developed throughout the Tambo River region. F_1 folds are upright isoclinal to open structures with northeast to southeast trends that were initially easterly trending (Figs 8 and 9). Hinges are narrow and angular with long planar limbs (Fig. 7**a**). Sandstone layers have class 1B and 1C shapes whereas mudstones have class 3 shapes (Fig. 7**a**-**c**). Many of the F_1 folds are flattened chevron folds, and probably formed by flexural slip along bedding planes with accompanying flexural flow in mudstones, and fold flattening.

An S_1 axial surface cleavage is associated with the F_1 folds (Fig. 7**c**). In mudstones the cleavage has formed from microfolding, accompanied by dissolution, of the early bedding-parallel slaty cleavage and forms a zonal crenulation cleavage (Fig. 7**d**). On the limbs of some F_1 folds the angle between S_1 and the early cleavage is low and the two fabrics are indistinguishable. Throughout domains 9-11 (Fig. 1) a pervasive S_1 stripy cleavage is developed in sandstones. The stripy cleavage consists of planar domains of aligned micas and other pressure solution residue up to 0.5cm in width separated by microlithon domains of quartz sandstone up to 2cm in width. The microlithons have abundant chlorite overgrowths (especially on quartz grains) indicating extension within the cleavage plane.

On the map-scale the main F_1 structures are an anticlinorium in domains 1 and 2 and a synclinorium, with a refolded southern limb, in domains 3 to 12 (Fig. 1). These structures are described separately below.

Domains 1 and 2: Domains 1 and 2 lie to the north and south of the Kiewa Fault respectively but as there are no major differences in structure these domains are described together. Domain 1 contains the hinge region and the northern limb of the F_1 anticlinorium (Figs 5 and 6) whereas domain 2 has the relatively planar south-younging limb of the anticlinorium (Figs 2 and 4).

Four orders of folding are developed within the anticlinorium. Fourth order folds are slightly overturned Z-shaped structures, with wavelengths up to 5m, found on the upright limbs of third order S-shaped folds on the steeply dipping to overturned northern limb of the anticlinorium (Fig. 6). Third order folds have wavelengths of 10-20m. The core of the

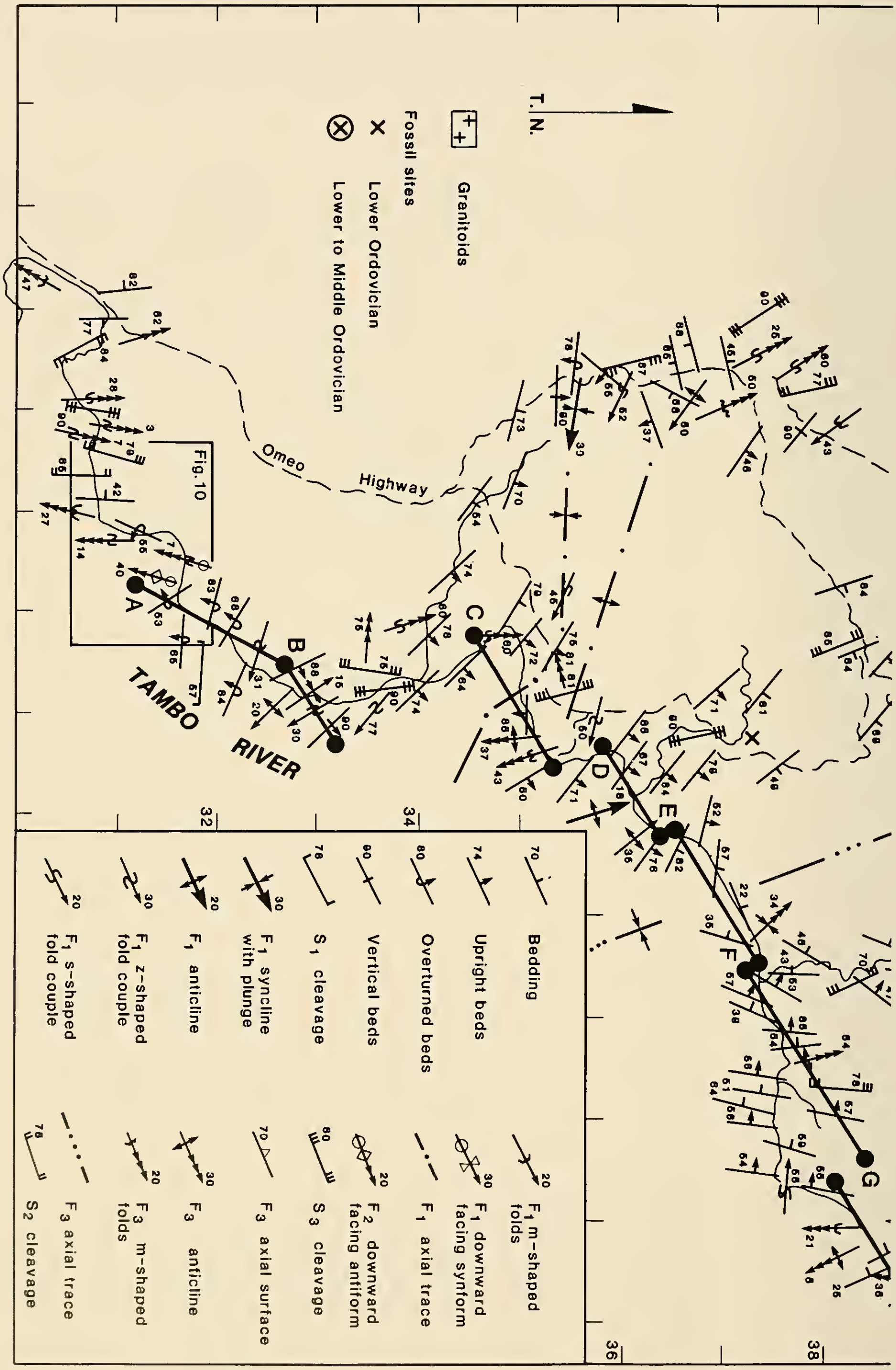

Fig. 2. Geological map of the Ordovician sequence in the southern Tambo River region showing the main structural features and locations of cross sections and Figs 10 and 12. Note the small amount of overlap across the double page.

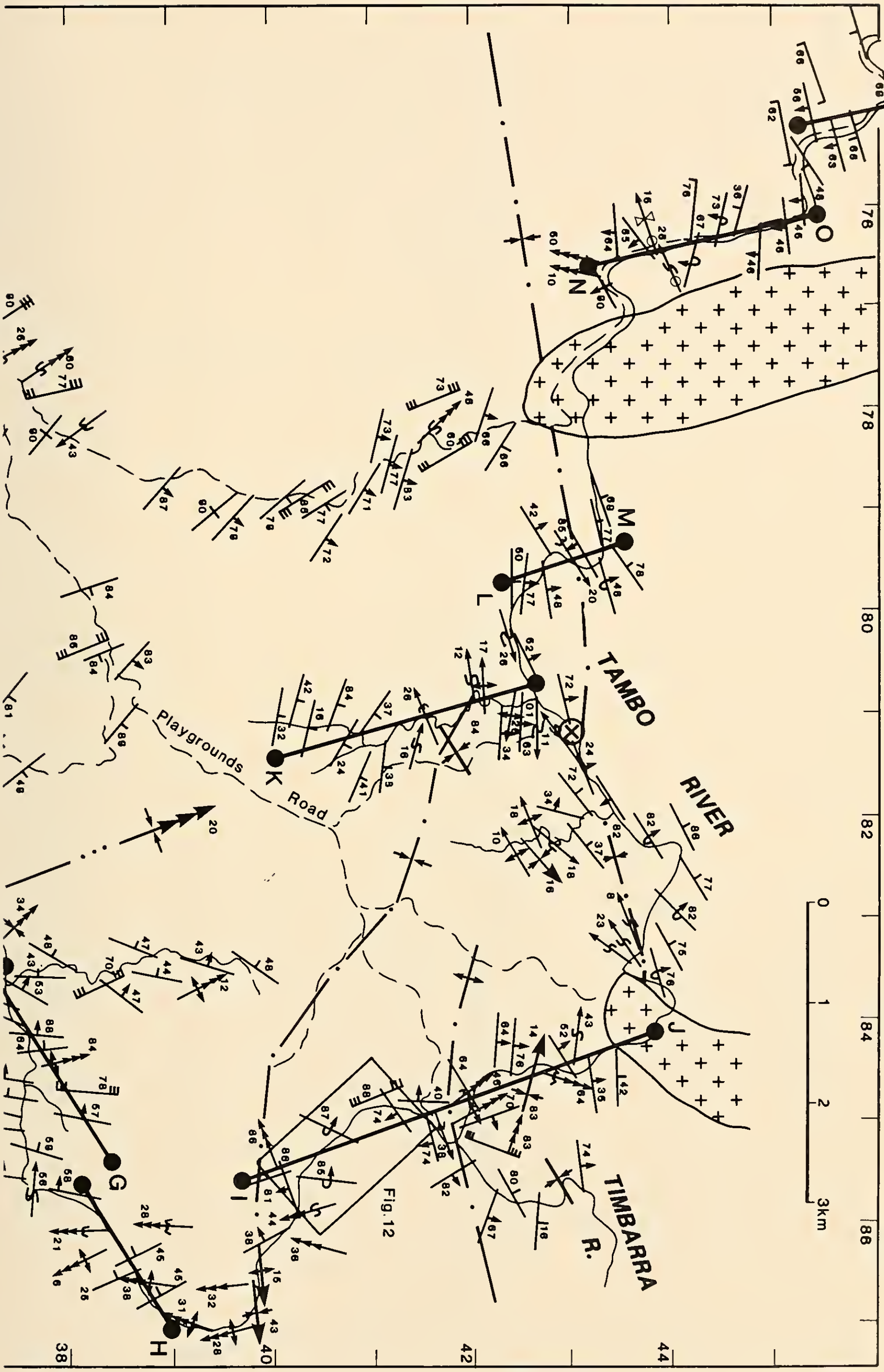

Fig. 2. For explanation see opposite.

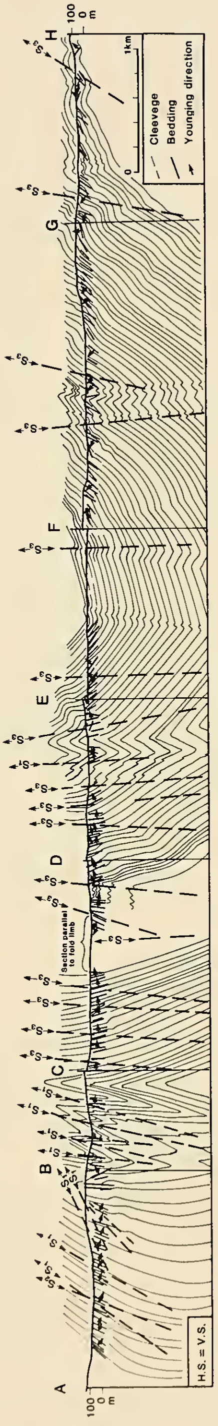

Fig. 3. Regional cross section across the major F_3 syncline in the southern Tambo River region. See Fig. 2 for location.

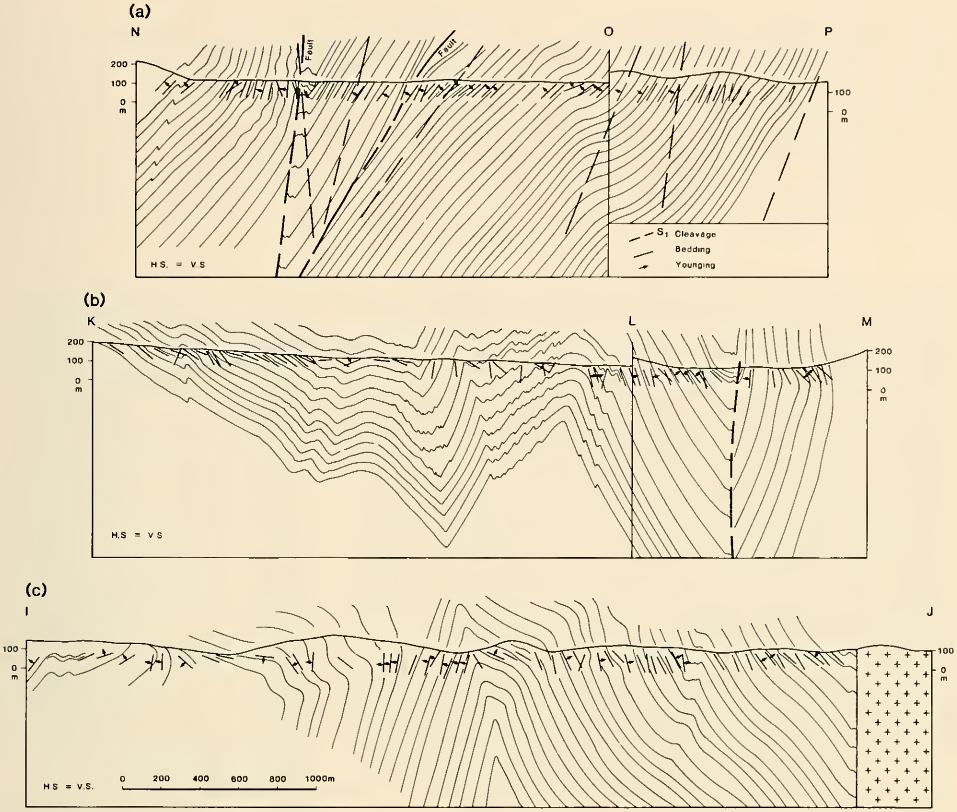

Fig. 4. Cross sections for the southern Tambo River region. See Fig. 2 for location.

anticlinorium consists of three second order folds up to 600m apart. The northernmost hinge contains several third and fourth order mesoscopic folds (Fig. 6).

One stretch of the southern limb in domain 2 consists of approximately 1km of southward dipping overturned beds with some parasitic F_1 downward facing folds (Figs 2, 4 and 7**b**). Along this section the S_1 cleavage dips steeper than overturned bedding and is axial planar to the F_1 folds (Fig. 7**b**). These overturned beds are fault-bounded and projections to depth indicate that they are pinched out at about 1km below the surface (Fig. 4, cross section NOP). This section is unique within the Tambo River region and reflects local deformation prior to the F_1 folding.

The lack of significant younger deformation in domains 1 and 2 provides a clear cross section of the F_1 structures. From cross section QRS (Fig. 6) these folds have narrow hinges and long planar limbs and a fold style characteristic of flattened chevron folds. These folds have a large amplitude-to-wavelength ratio which coupled with the 4-5km of succession indicates a relatively thick-skinned style of deformation.

Domains 3 to 12: The southern Tambo River region is dominated by the north-younging limb of the major F_1 synclinorium (Figs 2, 3, 4, 8, 9 and 10). The axis of the synclinorium occurs along the Tambo River in domain 3 (Figs 1 and 2). The hinge is angular with a planar and locally overturned northern limb (Fig. 4, cross section KLM). Throughout domains 6 and 7 the southern limb of the F_1 synclinorium is shallowly dipping and

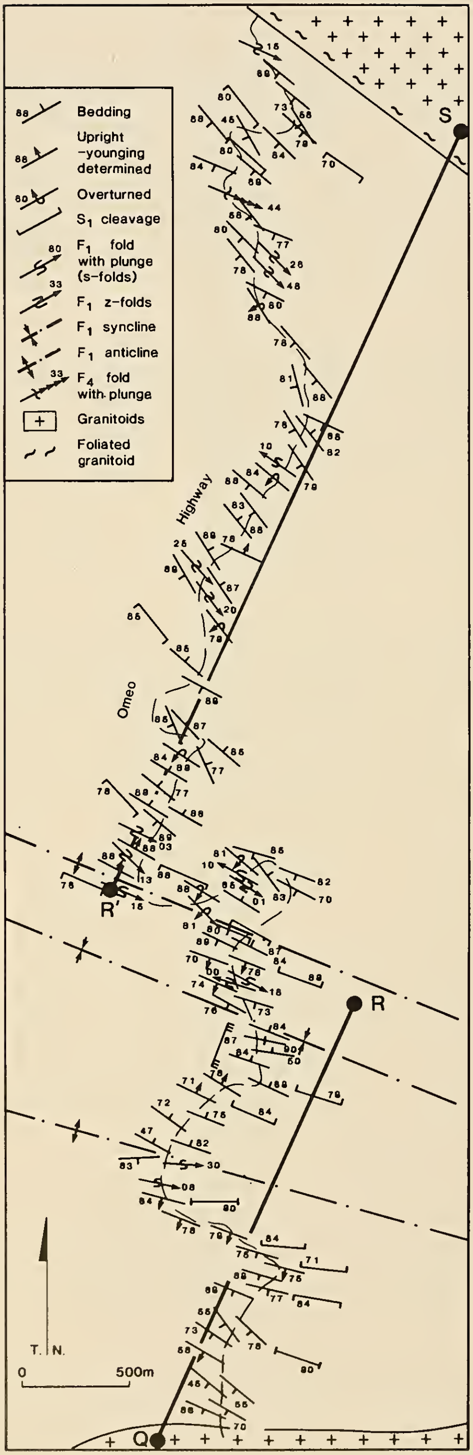

Fig. 5. Structural map of the Ordovician sequence in the northern Tambo River region.

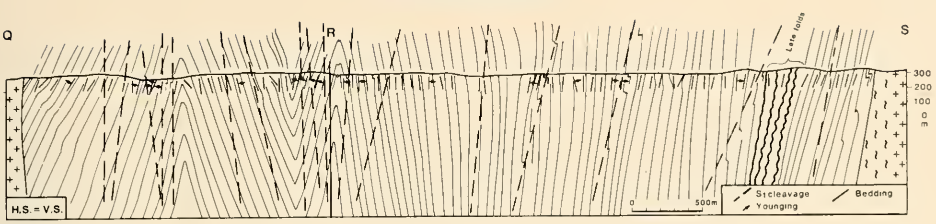

Fig. 6. Cross section for the northern Tambo River region (see Fig. 5 for location).

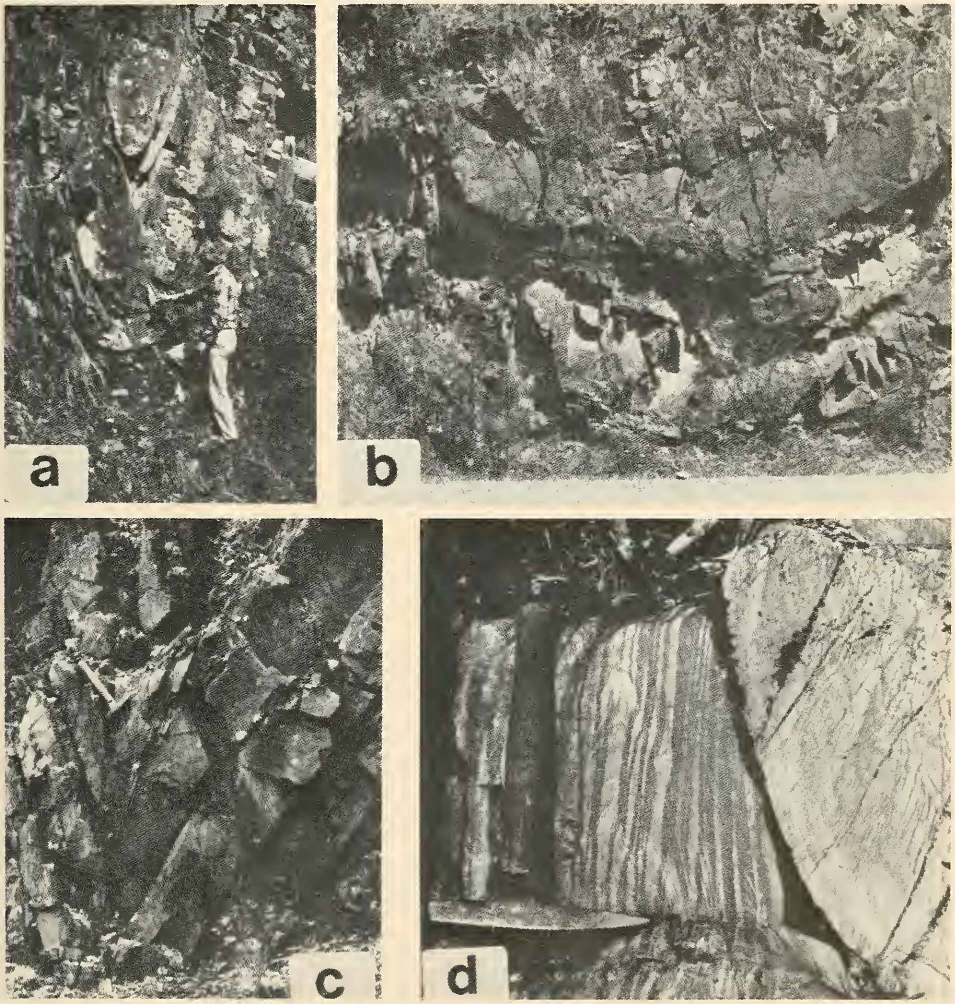

Fig. 7 a. — Tight F_1 syncline from domain 1, Omeo Highway (D. W. Durney for scale). Location — GR 734534 (Grid references from Omeo and Bairnsdale 1:100 000 Topographic Sheets).
b. — Downward facing F_1 synformal anticline from domain 2 (see text), Omeo Highway. Note that the southern limb of the fold is truncated by a steeply dipping fault. Width of view is 6m. Location — GR 764432.
c. — Angular upright F_1 syncline from domain 1. Hammer 33cm in length for scale. Location — GR 734538.
d. — A well-developed S_1 crenulation cleavage from the core of an upright F_1 anticline. Note the S_1 stripy cleavage in the sandstone bed and the cleavage refraction. Hammer is 33cm in length. Location — GR 809333.

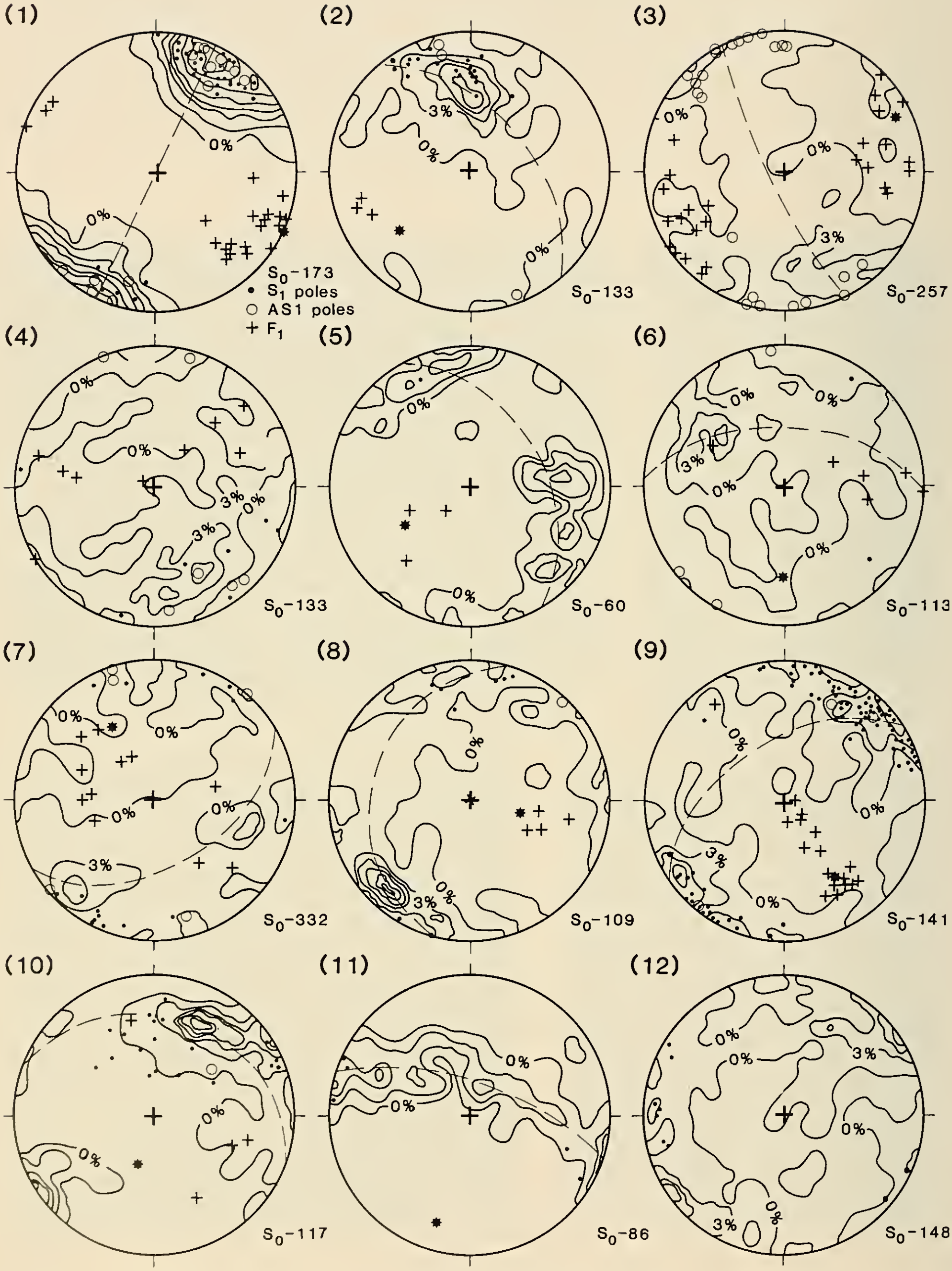

Fig. 8. Lower hemisphere equal-area stereographic projections from the Tambo River region (for domains see Fig. 1). Heavy dot is the calculated fold axis in each stereographic projection. Stereographic projections have bedding poles contoured at: 0, 3 and 6% per 1% area (nets 3, 4, 6 and 7); 0, 3, 6 and 9% per 1% area (nets 5, 9, 11 and 12); 0, 3, 6, 9 and 12% per 1% area (net 2); 0, 3, 6, 9, 12 and 15 per 1% area (nets 8 and 10); and 0, 3, 6, 9, 12, 15, 18 and 21% per 1% area (net 1).

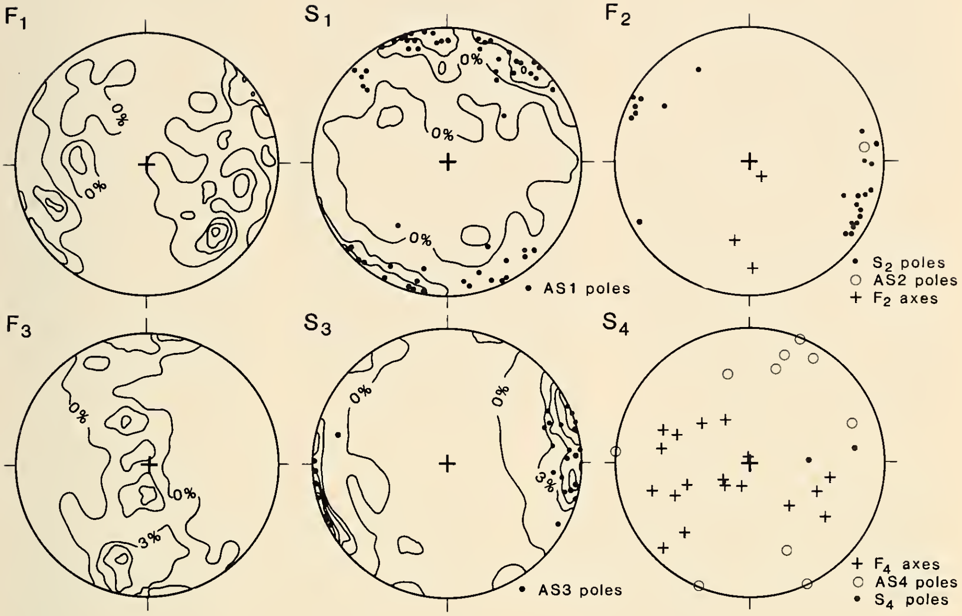

Fig. 9. Summary lower hemisphere equal-area stereographic projections for structural elements in the Tambo River region. Points are contoured at 3% intervals per 1% area. Structural elements include: F_1 fold axes (100); S_1 cleavage (212), F_1 axial surfaces (AS1); F_2 fold axes, S_2 cleavage, F_2 axial surfaces (AS2); F_3 fold axes (137), S_3 cleavage (347), F_3 axial surfaces (AS3); F_4 fold axes, S_4 cleavage and F_4 axial surfaces (AS4).

dominated by abundant F_1 parasitic folds and refolded by F_3. In domains 8 to 10 the southern limb is steeply dipping and becomes overturned farther south (Fig. 3, cross section ABCDEFG and Fig. 10). F_1 parasitic folds are largely restricted to two major Z-shaped fold pairs along cross section BCD (Fig. 3). The northern fold pair consists of F_1 minor folds plunging steeply to moderately to the east (Fig. 8, domain 8) with a faulted axial surface along the major syncline hinge. The southern fold pair (cross section BC, Fig. 3) contains a central limb with abundant upright F_1 folds in contrast to the steep limbs which only have rare Z-shaped parasitic folds. The overturned beds to the south of this fold pair in domains 11 and 12 are strongly refolded by F_2 and F_3 (Fig. 1).

F_2 FOLDING

In domain 10 this deformation formed a discrete hair-like crenulation cleavage that overprints S_1 and is in turn overprinted by S_3 (Figs 10 and 11a). F_2 folding is restricted to domains 11 and 12 (Figs 1 and 10). Throughout domain 11 the overturned limb of the major F_1 synclinorium is refolded by close downward facing F_2 folds with axial surfaces dipping moderately to the east (Fig. 10). The F_2 folds have relatively narrow hinge zones and are extensively refolded by the F_3 folds (Fig. 10). The inset in Fig. 10 shows the shape of the F_2 folds prior to folding by F_3.

Across the boundary between domains 11 and 12 (Fig. 1) the S_2 axial surface cleavage rapidly intensifies and bedding is transposed (with the exception of exposures along the Omeo Highway in domain 12). Throughout domain 12 S_2 is developed as a pervasive stripy cleavage in sandstones (Fig. 11g) and as a strong continuous cleavage in mudstones.

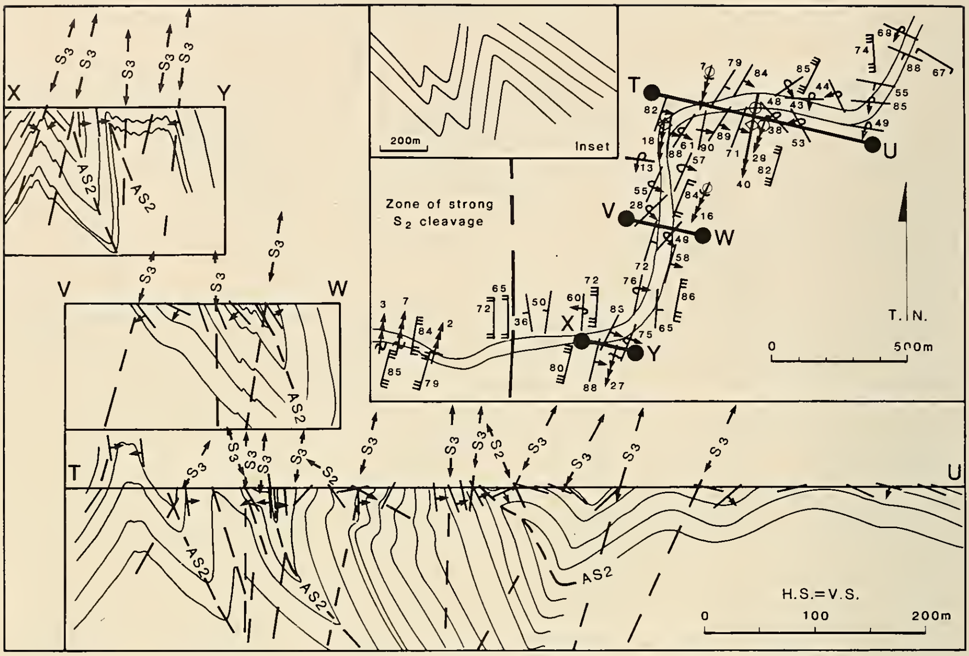

Fig. 10. Map and cross-sections of downward facing F_2 and F_3 folds in domain 11 (see Fig. 1 and Fig. 2 for location). See text for discussion. Inset shows a reconstruction of the F_2 folds in cross section prior to the F_3 folding.

The S_2 stripy cleavage is similar to S_1 cleavage in sandstones except that the former is much more pervasive. F_2 folds have not been found in domain 12 and the S_2 cleavage itself is refolded by younger structures (see below).

F_3 FOLDING

F_3 structures occur throughout the southern Tambo River region (Fig. 2). They are northerly-trending folds with steep axial surfaces and variable plunges (Figs 2, 8, 9 and 11**b-e**). F_3 folds are close to open with slightly rounded hinges and characteristic small amplitude-to-wavelength ratios (<0.5, Fig. 11**b-e**). An axial surface crenulation cleavage is developed in mudstones and occasionally a weak stripy S_3 cleavage is developed in sandstones (Fig. 11**a-d**).

Throughout most of the southern Tambo River region the F_3 folds are upward facing (Figs 2, 3 and 4). In domain 11, however, the F_3 folds are developed on the overturned limbs of the downward facing F_2 folds and are therefore downward facing (Fig. 10). Locally the combination of F_2 and F_3 folding has formed box-fold structures with the western hinge formed by an F_2 fold and the eastern hinge by an F_3 fold (e.g. cross section XY, Fig. 10). F_3 folds are abundant in domain 11 in contrast to the general scarcity of F_2 hinges.

On the map-scale the most obvious F_3 fold is the large open syncline shown in cross section DEFGH (Fig. 3). Along the Tambo River this structure has a hinge zone 800m across with an open conjugate fold style (cross section EF, Fig. 3). The hinges in the conjugate pair plunge shallowly to the north-northwest (Figs 2, 8 and 9) which indicates that they must have developed along a shallowly dipping part of the north-younging limb of the

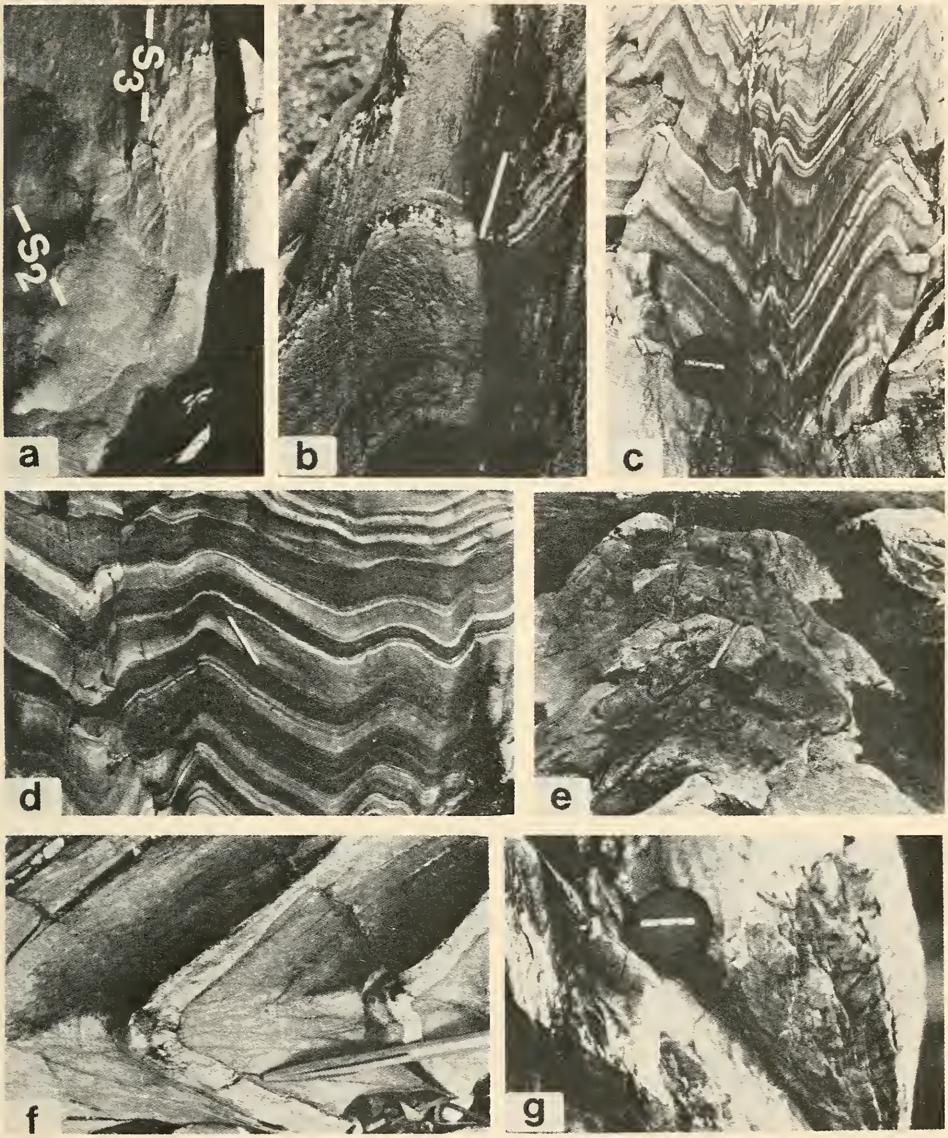

Fig. 11 **a.** — An S_3 crenulation cleavage is shown locally cross-cutting a less steeply dipping S_2 crenulation cleavage. Bedding dips steeply to the east and is overturned. Hammer for scale. Location — GR 793315.

b. — Broad F_3 fold couple with an axial surface S_3 crenulation cleavage. Note an early S_1 crenulation cleavage is folded in the core of the fold. Match stick for scale. Location — GR 808336.

c. — Close F_3 folds with a well-developed axial surface crenulation cleavage. Lens cap is 5.5cm across. Location — same as (b).

d. — Broad to open F_3 folds with S_1 crenulation cleavage oblique to bedding on the limbs and in the fold cores. Match stick for scale. Location — same as (b).

e. — Upright close F_3 fold with a box-shaped hinge. Hammer is 33cm in length. Location — GR 819362.

f. — Steeply plunging close F_3 fold with an axial surface crenulation cleavage. Pen cap is 6.5cm in length. Location — GR 809331.

g. — S_2 stripy cleavage in sandstone in the core of an upright F_3 fold with a steep S_3 axial surface cleavage (in domain 12). Location — GR 783308.

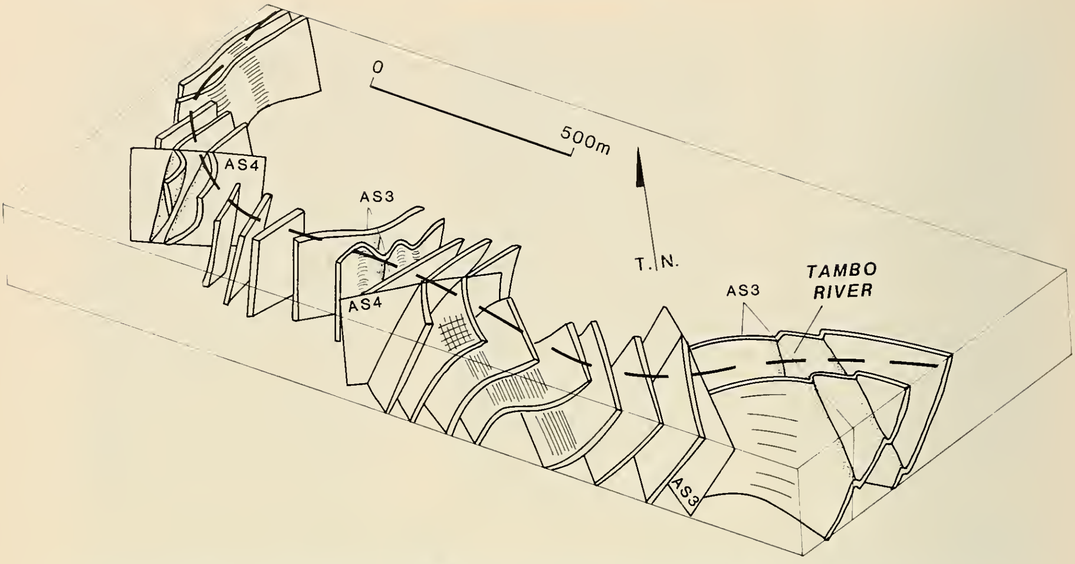

Fig. 12. Schematic block diagram of the F_4 and F_3 folds along the Tambo River in domain 5 (see Fig. 2 for location). Note that the dip of the limb of an F_3 fold has been locally decreased by post F_3 warping.

F_1 synclinorium. On the east limb of the F_3 syncline bedding dips moderately to the west whereas on the western limb it dips steeply to the northeast (Figs 2, 3 and 8, domain 7).

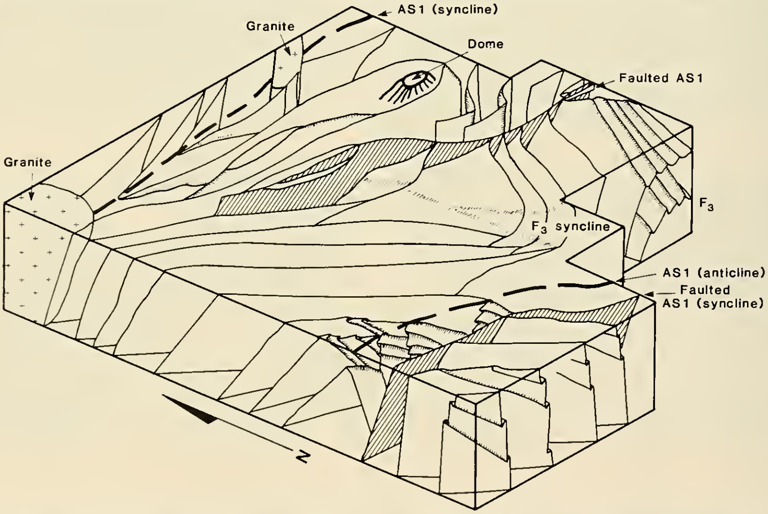

Fig. 13. Schematic block diagram of the structures in the southern Tambo River region (domains 3-10). Note the easterly trending F_1 folds and the large F_3 syncline developed on the shallow limb of the F_1 syncline.

Map-scale F_3 anticlines occur to the east and west of the major F_3 syncline (Fig. 2). The eastern F_3 anticline is partly shown on cross section GH (Fig. 3) and contains abundant M-shaped shallowly plunging F_3 folds (Figs 2 and 11**e**). Farther north the limbs of F_3 folds are extensively refolded by F_4 structures (Fig. 12). At GR 850 417 (Fig. 2) the F_3 anticline is superimposed on an F_1 anticline producing a prominent dome with bedding dipping outward from a central focus (see also Fig. 13). F_1 minor folds show significant plunge variations in this area (domain 4, Fig. 8). North of the dome the F_3 anticline causes the bending of F_1 trends from east-northeast to east-west either side of the 'granitoid' at J (Fig. 2). The western F_3 anticline caused a change in structural trends from southeasterly to easterly from domains 2 to 7 respectively (Figs 1, 2, 8 and 13). Thus the main effect of the F_3 folding on the map-scale is the bending of F_1 structures with only local development of dome and basin type interference fold patterns.

F_4 FOLDING

Local post-F_3 folds, warps and kinks occur throughout the area and these are grouped together as F_4 structures. Some of these structures may belong to different fold generations but these are not distinguished due to the lack of overprinting criteria. In domain 1 there are several moderately-plunging east-southeast trending late-stage mesoscopic folds with rounded open hinges. These late-stage structures are grouped with F_4 for convenience, as their orientations differ from the F_2 and F_3 structures.

Late-stage F_4 folds thoughout Fig. 2 are mainly easterly trending broad to open folds and/or kinks (Fig. 12). Several of these are map-scale F_2 folds (Fig. 12). Rare kink-like folds with rotated limbs up to 50m across occur at GR 806 322 (Fig. 2). In addition to the late-stage folds a number of weak crenulation cleavages and crenulation lineations are developed in the Tambo River region. These structures are not related to other deformations and they reflect only low values of shortening.

DISCUSSION

The F_1 east-west folding event extends throughout the Tabberabbera Belt (Fergusson, 1985) and the Omeo Metamorphic Belt where it is constrained between the Ordovician and Late Silurian. Bolger (1982) has emphasized that the timing of deformation and metamorphism in the Metamorphic Belt is only broadly delimited and is not confined to the Early Silurian as is sometimes implied (e.g. Crook *et al.*, 1973; Powell 1984).

Powell (1983, 1984) has proposed a tectonic model for southeastern Australia relevant to the formation of east—west folds in the Omeo Metamorphic Complex and the Tabberabbera Belt. The basis of his model is that in the Ordovician a back-arc basin (Wagga Marginal Sea) was bordered to the east by a volcanic island arc associated with a westward dipping subduction zone. In the Early and Middle Silurian Chilean-style locking of plates on the subduction zone was accompanied by dextral oblique-slip plate movement and east—west upright folds were formed at several localities in the Lachlan Fold Belt (see Cas *et al.*, 1980). The east—west folds of the Tabberabbera Belt and Omeo Metamorphic Complex are the best examples of this deformation.

The F_1 folding of the Tambo River region caused shortening of 50% or more (calculated from regional cross sections, Fig. 14). Estimates of the thickness of the Ordovician succession obtained from cross sections indicate a minimum of 4-5km. The stratigraphic thickness, fold style and shortening indicate that at least 12km and as much as 20km of the present crustal thickness consists of the folded Ordovician succession. Thus the F_1 folding represents a major episode of crustal thickening in this part of the Lachlan Fold Belt, and was probably associated with closure of the Wagga Marginal Sea.

The F_2 folding is areally restricted and is only constrained in time as post-F_1 and pre-F_3. This folding event reflects localized east-west shortening of unknown tectonic significance.

The F_3 folding is extensive throughout the southern Tambo River region but no constraints on the timing of this deformation exist within this area. Farther west at Tabberabbera, however, similar northerly trending upright folds with low amplitude-to-wavelength ratios and an axial surface crenulation cleavage affect the Ordovician succession (Fergusson, 1985). These structures have been mapped in reconnaissance between

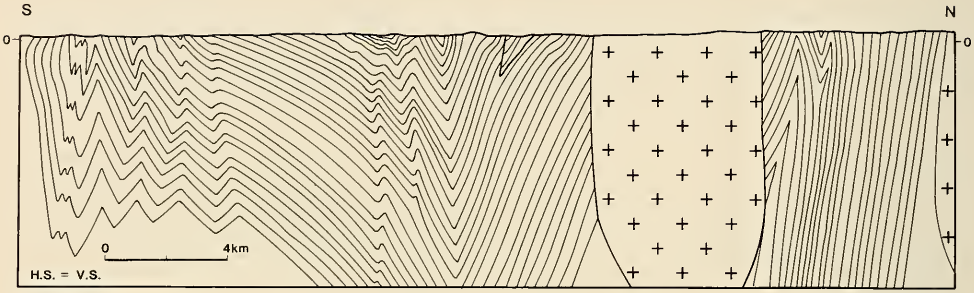

Fig. 14. Regional cross section of the main F_1 structures in the Tambo River region. Note the relatively thick-skinned style of folding.

the two areas. At Tabberabbera they are related to the deformation that strongly affected the overlying Lower Devonian Wentworth Group (Fergusson, unpub. data). Thus the F_3 folding is regarded as a consequence of the Middle Devonian Tabberabberan Orogeny. This event reflects major east—west compression and overthrusting of the Melbourne terrane over the western part of the Tabberabbera Belt (Fergusson *et al.*, 1986).

The F_4 folds must have postdated F_3 and reflect several mild compressions of differing orientations.

CONCLUSIONS

(1) F_1 folding in the Ordovician sequence of the Tambo River region involved the formation of east—west upright folds with a shortening of at least 50%. The major F_1 structures are a anticlinorium—synclinorium pair with a thick-skinned style of deformation. They may have formed due to an episode of regional dextral oblique-slip shear associated with a westward dipping subduction zone in the Early to Middle Silurian. This event was responsible for closure of the Wagga Marginal Sea and caused significant crustal thickening in the area.

(2) The F_3 folding formed due to east-west compression in the Tabberabberan Orogeny. The largest F_3 structure is a box-shaped F_3 syncline that developed on the flat-lying undeformed part of the southern limb of an F_1 synclinorium. Shortening associated with F_3 is variable and this event, though of regional significance, did not result in extensive crustal thickening in this region.

(3) The F_2 and F_4 events consist of locally developed and variably oriented folds that formed during relatively mild compressional events.

ACKNOWLEDGEMENTS

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Geomorphic and physicochemical Features of floodplain Waterbodies of the lower Hunter Valley, N.S.W.

B. V. TIMMS

TIMMS, B. V. Geomorphic and physicochemical features of floodplain waterbodies of the lower Hunter Valley, N.S.W. *Proc. Linn. Soc. N.S.W.* 109(4), (1986) 1987: 311-324.

The lower ends of 42 tributary valleys of the lower Hunter and Paterson Rivers contain floodplain lakes because the tributary outlet has been blocked by alluvial deposits of the main stream. On average these waterbodies are elongated to dendritic in shape, 4.3ha in area, 2m deep and have a Shoreline Development index of 2.13. Typically they fill from local run-off and subsequently their levels are largely determined by fluctuations in the water table.

In the 5 waterbodies studied in detail, mean values for Total Dissolved Solids varied between 215 and 468mg l^{-1}, pH between 7 and 8, turbidity between 26 and 318 FTU's, Secchi disc depth between 30 and 100cm, and nitrates were *c.* 1.4mg l^{-1} and phosphates *c.* 0.4mg l^{-1}. These parameters fluctuated widely as the waterbodies filled and dried according to variable rainfall and evaporation. Water temperatures ranged from 12-32°C with no persistent stratification. Waters were of the sodium chlorocarbonate or sodium chloride types.

Almost all waterbodies are adversely affected by man, mainly via drainage, nutrient accessions and cattle usage.

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KEY WORDS: floodplain lakes, morphometry, water chemistry, turbidity, nutrients, water temperatures, conservation.

INTRODUCTION

Floodplains typically contain areas of ponded water. Such wetlands encompass a wide range in sizes, depths, geomorphic origins, degree of permanence, physicochemical features and aquatic macrophyte communities, so that even reconnaissance classification is difficult (e.g. see Cowardin *et al.*, 1979, for USA and Riley *et al.*, 1984, for NSW). Detailed and long term data sets are needed for each perceived type before such schemes can be much improved. A contribution towards this is made here for a small area of the Hunter Valley in which wetlands are genetically similar.

According to most textbooks, ponded water on floodplains typically lies in oxbow lakes (i.e. cut-off meanders) and in broad depressions (swamps) behind levees. These certainly occur on the Hunter floodplain from about Maitland downstream and on the floodplain of the lower Paterson River (Pressey, 1981). However in the section of the Hunter R. between Singleton and Maitland and also adjacent to the Paterson R. near Paterson, most ponded waters lie in depressions where small tributaries meet the main valley. These form when the main stream 'by deposition of levees and of sediment elsewhere on its flood bed, aggrades its course faster than aggradation can occur in lateral tributary valleys' (Hutchinson, 1957: 115). Hence streams in side valleys tend to become obstructed and water accumulates so they become partly drowned. In many cases the main river, when in flood, flows into the lateral valley and so lengthens the obstruction by reverse delta formation. Hutchinson (1957) uses the term 'lateral lakes' for these waterbodies, but this is unfortunate as it implies relationships to floodplain processes such as lateral migration. The more appropriate term of 'blocked valley lake' (Blake and Ollier, 1971) is used here.

All of the present waterbodies are wetlands in the broad sense (Cowardin *et al.*, 1979) but called 'lagoons' in the local vernacular. Overseas this term is usually used genetically for coastal marine waterbodies, but in Australia it generally refers to shallow, often small, inland waterbodies in any geomorphic situation. This general descriptor is appropriate here though technically those lacking emergent macrophytes are lakes or ponds according to size and depth and those covered with emergent macrophytes are swamps (Bayly and Williams, 1973; Riley *et al.*, 1984). A few lagoons in downstream parts of the study area were included by Pressey (1981) in his inventory, but otherwise little is known of those investigated here.

METHODS

Locations of possible lagoons were ascertained from 1:25,000 topographical maps and aerial photographs and checked first from a light plane and then on the ground. The depth (when full) and siting with respect to local geology and landforms were ascertained in the field for each lagoon. The area and shore length of all except the smallest/shallowest lagoons were determined in the laboratory by planimetry and measurement from enlarged vertical aerial photographs.

Three lagoons, 'Birds' (4), 'Bootlands' (19) and 'Murphys' (21) were sounded at 5m intervals along numerous lines (30, 42 and 26 lines respectively in each lake) stretched between known places on opposite shores. From the resultant bathymetric maps, direct and derived parameters were determined using formulae given in Bayly and Williams (1973) and Hakanson (1981). Altitudes were estimated to ±2m from topographic maps.

Five representative lagoons in the Gosforth series with a wide range in size and degree of permanence were chosen for a study of the physicochemical features of the waters of the 42 floodplain lagoons. A causeway separated 'Bootlands' (19) into two parts on almost all visits, so both parts were sampled separately. Visits were made at monthly intervals for 63 consecutive months commencing in October 1979 and information was collected on water depth, temperature (by a resistance thermometer), light penetration (by a standard 20cm Secchi disc), pH (by a Selbys 800 pH Meter), Total Dissolved Solids (by gravimetry), and on turbidity, phosphate and nitrate (determined on a HACH Environmental Laboratory DR/EL 1). Samples were always taken in the morning between 0800 and 1200hrs and in the same sequence (Lagoons 19 to 23). From water samples collected in February 1981 the major ions were measured — Na and K by flame photometry, Ca and Mg by titration with EDTA, Cl by titration against $AgNO_3$, HCO_3 by titration with 0.01N HCl to an end point of pH 4.5, and SO_4 by the turbidimetric $BaSO_4$ method (Anon, 1975). Accuracy for all physicochemical methods was ±2.5% or better.

Where possible, landowners of each lagoon were interviewed in an attempt to establish the influence of river floods, local heavy rain and droughts on water level fluctuations. Their opinion of the lagoons (e.g. water resource value, nuisance value) and the extent of their (or their predecessor's) modifications, if any, of the lagoons was also canvassed.

RESULTS

(a) GEOMORPHOLOGY

Of the 42 floodplain lagoons in the study area, 31 occur along the Hunter R. and 11 along the Paterson R., giving densities of 0.7km and 1.2km respectively. The lagoons

TABLE 1

Summary of information on 42 floodplain lakes of the Hunter and Paterson Rivers

LAKE	MAP REFERENCE	AREA* (ha)	DEPTH* (m)	PERIMETER LENGTH* (m)	SHORELINE DEVELOP-MENT*	PERMANENCE +	MODIFICATIONS
Dalwood Series							
1. Unnamed	Elderslie 9132-I-N 498902	0.9	?	—	—	semipermanently flooded	none
2. Unnamed	Elderslie 9132-I-N 501903	1.2	3.2	—	—	semipermanently flooded	none
Luskintyre Series							
3. Unnamed	Greta 9132-I-S 503854	<0.5	—	—	—	seasonally flooded	none
4. 'Birds'	Greta 9132-I-S 514854	6.8	2.5	2350	2.55	permanently flooded	partly drained
5. 'Peters'	Greta 9132-I-S 506851	0.7	?	590	2.02	seasonally flooded	none
6. 'Russells'	Greta 9132-I-S 507842	7.1	2.1	2510	2.66	intermittently exposed	partly drained
7. Unnamed	Greta 9132-I-S 508829	<0.5	—	—	—	seasonally flooded	none
8. 'Martins'	Greta 9132-I-S 523823	4.7	2.6	1870	2.44	intermittently exposed	partly drained
9. Windermere	Greta 9132-I-S 538834	1.7	—	—	—	seasonally flooded	drained
10. Unnamed	Greta 9132-I-S 532840	<0.5	—	—	—	seasonally flooded	drained
11. Kaludah	Greta 9132-I-S 531813	10.3	?	2310	2.03	seasonally flooded	drained
12. 'Appledene'	Greta 9132-I-S 530835	1.5	—	—	—	seasonally flooded	drained
13. 'Windella 1'	Greta 9132-I-S 546851	0.8	—	—	—	seasonally flooded	none
14. 'Windella 2'	Greta 9132-I-S 551851	0.9	—	—	—	seasonally flooded	none
Rosebrook Series							
15. 'Rosebrook Sch'	Maitland 9232-IV-S 603860	5.9	2.2	1800	2.08	semipermanently flooded	partly drained
16. 'Rosebrook Sth'	Maitland 9232-IV-S 606841	1.1	?	590	1.56	seasonally flooded	drained
17. 'Dickensens Rd. big'	Maitland 9232-IV-S 617828	4.7	1.8	1690	2.19	semipermanently flooded	drained
18. 'Dickensens Rd. small'	Maitland 9232-IV-S 621831	1.3	?	760	1.88	seasonally flooded	drained
Gosforth Series							
19. 'Bootlands'	Greta 9132-I-S 584868	8.0	3.9	2890	2.87	permanently flooded	none
20. 'Burgess'	Greta 9132-I-S 591862	1.2	1.9	626	1.65	semipermanently flooded	partly drained
21. 'Murphys'	Greta 9132-I-S 592851	7.4	2.4	2170	2.20	intermittently flooded	partly drained
22. Unnamed	Maitland 9132-IV-S 597845	2.4	1.8	900	1.63	semipermanently flooded	partly drained
23. Unnamed	Maitland 9132-IV-S 598843	0.6	?	380	1.32	semipermanently flooded	partly drained
24. 'Birds' Folly'	Greta 9132-I-S 593827	11.0	—	2610	2.22	semipermanently flooded	drained
25. 'Greens'	Greta 9132-I-S 591821	10.7	1.5	2810	2.43	intermittently flooded	partly drained
26. Anambah	Maitland 9132-IV-S 602815	9.9	0.9	2660	2.25	seasonally flooded	drained

TABLE 1 (Continued)

LAKE	MAP REFERENCE	AREA* (ha)	DEPTH* (m)	PERIMETER LENGTH* (m)	SHORELINE DEVELOP-MENT*	PERMANENCE +	MODIFICATIONS
Oakhampton Series							
27. Oakhampton Swamp	Maitland 9132-IV-S 642803	*ca*26	–	–	–	intermittently flooded	partly drained
28. Walka Lagoon	Maitland 9132-IV-S 639793	*ca*20	7 ?	–	–	permanently flooded	damned
Bolwarra Series							
29. Unnamed Far Nth	Maitland 9132-IV-S 664808	2.3	–	920	1.70	seasonally flooded	drained
30. Unnamed Nth	Maitland 9132-IV-S 660797	2.5	–	–	–	semipermanently flooded	drained
31. Unnamed Sth	Maitland 9132-IV-S 659795	1.4	2.0 ?	–	–	intermittently flooded	
Paterson Series							
32. 'Tocal' Sth	Maitland 9132-IV-S 686878	1.9	4.0 ?	810	1.66	intermittently flooded	none
33. 'Tocal' Nth	Maitland 9132-IV-S 687888	0.7	1.5	–	–	intermittently flooded	partly drained
34. 'Tocal' Homestead	Paterson 9232-IV-N 678896	7.6	2.5 ?	2010	2.66	permanently flooded	none
35. 'Orange Grove'	Maitland 9132-IV-S 690884	0.7	–	–	–	semipermanently flooded	partly drained
36. 'Duninald' Sth	Paterson 9232-IV-N 687895	<0.5	–	–	–	semipermanently flooded	partly drained
37. 'Duninald' Nth	Paterson 9232-IV-N 690899	1.1	–	–	–	seasonally flooded	drained
38. 'Bona Vista'	Paterson 9232-IV-N 693907	6.4	2.5 ?	2970	3.30	semipermanently flooded	partly drained
39. Unnamed South of Paterson	Paterson 9232-IV-N 698913	3.7	–	–	–	semipermanently flooded	partly drained
40. Unnamed in Paterson	Paterson 9232-IV-N 701917	<0.5	–	–	–	semipermanently flooded	partly drained
41. 'Brisbane Grove'	Paterson 9232-IV-N 703924	1.3	–	–	–	semipermanently flooded	none
42. 'Valentia'	Paterson 9232-IV-N 696933	<0.5	–	–	–	seasonally flooded	none

* measured at full water level

\+ scheme according to Cowarden *et al.*, (1979) range in size from <0.25ha to *c.* 26ha (Table 1), with the average being 4.3ha. However few approximate the average as size distribution is negatively skewed and somewhat bimodal. There is one peak in the 1.1–1.5ha class and another lesser one in the 5.1–7.5ha class (Fig. 2a). All lagoons stand many metres (*c.* 2-10) above the normal water level of the river. Limited data on maximum depths suggest the lagoons are relatively shallow, with the majority *c.* 2m deep and the deepest only 7m. The latter (No. 28), though, is artificially dammed so that the deepest natural lagoon is only 4m.

Shoreline Development (i.e. the ratio of the length of the shoreline to the length of the circumference of a circle of the same area) lies between 1.3 and 3.3, with an average of 2.13 for the 21 lagoons measured. This indicates these lagoons are either branched or have indented shorelines (see Figs 1,3 and 5). Actually the average for all 42 lagoons is probably a little less than 2.1, because the unmeasured lagoons generally had smoother shorelines than measured ones.

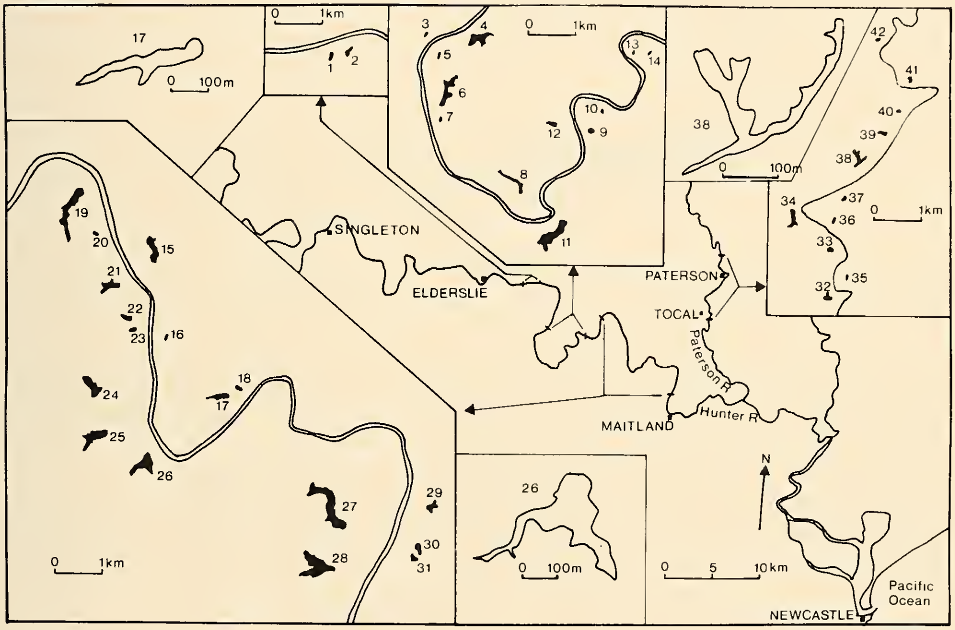

Fig. 1. Map showing location of the 42 lateral lakes studied in the lower Hunter. Three inserts give details of the shape of 3 quite different lagoons — No. 17, a lagoon in an essentially unbranched valley; No. 26, a lagoon in a branched valley and No. 38, a composite lagoon with one part a blocked valley lake and the other a lateral levee lake.

Water regimes vary widely but are accommodated within the four categories of the classification of Cowardin *et al.* (1979). Just four (9.5%) lagoons are *permanently flooded* and even two of these are artifically dammed. A natural example is No. 19 ('Bootlands') which contained water for all 63 months it was studied, even during the 1980 and 1983 droughts (Fig. 4). In a few lagoons (19%) the bottom is *intermittently exposed*, i.e. water is present except during extreme droughts. Examples are No. 21 ('Murphys') which only dried for 5 months during the 1980 drought (Fig. 4) and No. 25 ('Greens') which has dried 3 times during the last 26 years during the final stages of an extended drought (J. Green, personal communication). Many lagoons (35.7%) are *semi-permanently* flooded containing water for 1/3 to 2/3rds of the time. Lagoons 20, 22 and 23 are examples (Fig. 4). There are also many ephemeral lagoons (35.7%) that are *seasonally flooded* for <3 months in most years.

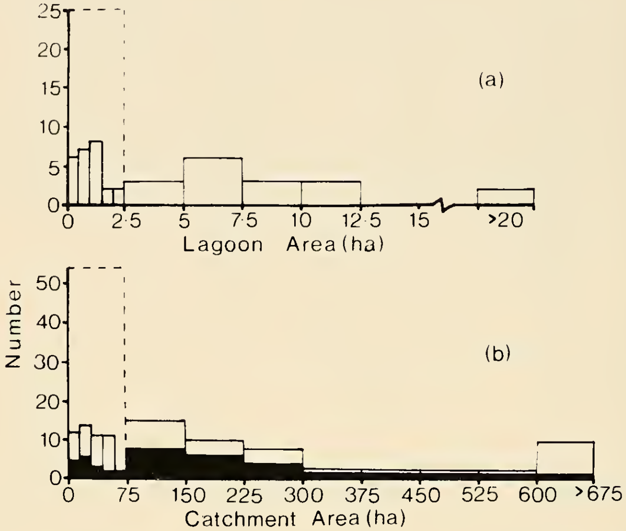

Fig. 2. Histogram showing the distribution of (a) lagoon sizes and (b) catchment sizes. In the latter case the proportion of catchments containing lagoons in each size class is indicated by the solid part of each block.

The relative number in each group of the above classification, especially in the semipermanently flooded and seasonaly flooded groups, has been influenced by drainage programs (Table 1) so that in the past more were in the intermittently exposed and permanently flooded classes. In fact most of the lagoons have been partly or completely drained, so that only a third have natural hydrological regimes.

The three lagoons that were mapped are similar morphometrically (Table 2, Fig. 3). 'Birds' Lagoon with its three distinct arms is the most branched, but 'Bootlands' has a higher S.D. because of its irregular shoreline. Volume development (i.e. ratio of the

TABLE 2

Morphometric Parameters of three lateral lakes of the lower Hunter River

Parameter	'Birds' L.	'Bootlands' L.	'Murphys' L.
Area (ha)	6.79	8.04	7.40
Volume (m^3 ×10^4)	9.10	14.80	8.44
Max Depth (m)	2.5	3.9	2.4
Mean Depth (m)	1.34	1.84	1.14
Shoreline length (m)	2350	2890	2170
Shoreline Development	2.55	2.87	2.20
Volume Development	1.59	1.42	1.42
Length (m)	460	625	655
Width (m)	305	170	205
Altitude (m)	*ca*18	*ca*16	*ca*15

All measurements made at full lake level. See text and Bayly and Williams (1973) for explanation of the parameters Shoreline Development and Volume Development.

volume of a lake to that of a cone of basal area equal to the area of the lake and height equal to the maximum depth of the lake) in each is relatively high in keeping with the steep littoral area and flat floor. In 'Birds' (Fig. 3**a**) and 'Bootlands' the deepest point is well removed from the levee dam, but in 'Murphys' it is close by (Fig. 3**b**).

(b) PHYSICOCHEMICAL PARAMETERS

All physicochemical data refer to the five lagoons (19-23) in the Gosforth series which were studied over a 63-month period from October, 1979 to December, 1984. Rainfall (see Fig. 4) was well below average during 1980 and again in late 1982 — early 1983, so these were drought years. There were some periods of high rainfall (e.g. February 1981, March 1982, Fig. 4) which produced significant local run-off, but there were no river floods during 1979-84.

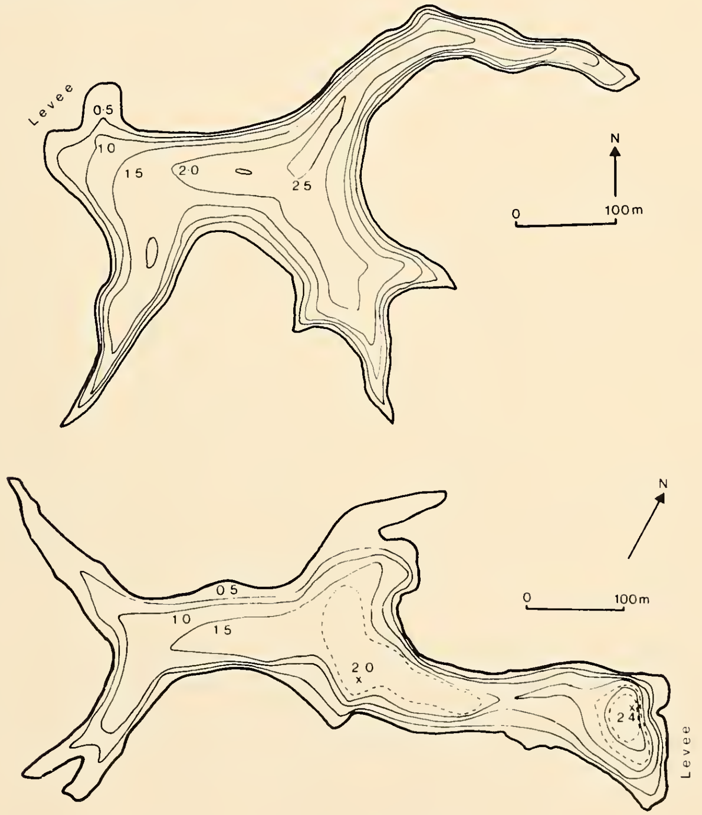

Fig. 3. Bathymetric map of **a** (above) Lagoon No. 4 'Birds' and **b** (below) Lagoon No. 21, 'Murphys'. Contours at 0.5m intervals, with some dashed ones at 0.25m intervals.

Mean TDS for the lagoons varied between 215 to 468mg l^{-1} (Table 3, Fig. 4). The lowest value recorded was 87mg l^{-1} in Lagoon 22 and the highest was 2208mg l^{-1} in Lagoon 21. During the two droughts there were steady increases in TDS to unusually high values, particularly in Lagoons 19b, 21, and 22. Fluctuations were a function of the relative input of run-off and loss by evaporation (Timms, 1970a) as expressed by the significant correlation between the ratio catchment area: lagoon surface area and annual

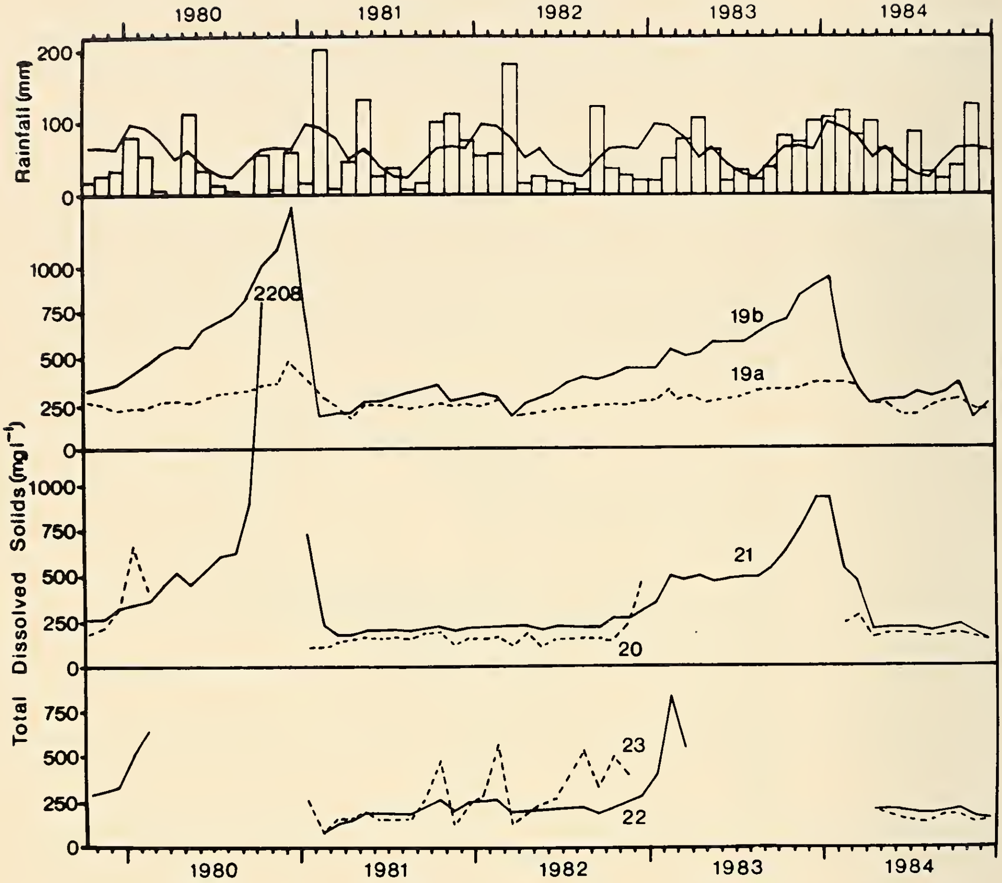

Fig. 4. Monthly rainfall (and long term average) at Singleton (nearest Meteorological Station) and TDS for lagoons 19-23 for period October 1979 to December 1984. Gaps in the TDS curves indicate the lagoons were dry for those periods.

percentage fluctuation in TDS ($r = 0.8239$, $n = 6$, $P < 0.05$). Fluctuations in lagoon 19a were much less than in 19b, yet both are sequentially located in the same valley (Fig. 5) and joined during high water. This is explained in part, by lagoon 19b receiving proportionally more run-off than 19a, but it also has salty springs along its western shore (R. Bootland, personal communication).

Waters in the 5 Gosforth lagoons are of the sodium chlorobicarbonate type. Cationic dominances were $Na > Mg > Ca > K$ in all lakes, but anionic dominances varied between $HCO_3 > Cl > SO_4$, $HCO_3 = Cl > SO_4$ and $Cl > HCO_3 > SO_4$ (Table 4). Generally all 5 lagoons were slightly alkaline with pH's between 7 and 8 (Table 4). No regular pattern of variation was evident. Unusually high pH values of 9.0-9.4 were seen in Lagoons 21 and 22 in low rainfall summers and equally unusual pH values of 6.2-6.8 were measured in Lagoons 19b, 20 and 23 after large inflows.

Water temperatures varied seasonally from late winter lows of *c.* 12-13°C to summer highs of *c.* 27-32°C (Table 3). The extreme range was 10.8°C in Lagoons 19a to 34.4°C in Lagoon 23. All values, especially the maxima, were influenced by the time of measurements. This explains the steady increase in values from 19 to 23, but even so

TABLE 3

Summary of some physicochemical parameters of lakes 19-23

Lake	TDS (mg l^{-1}) mean	TDS (mg l^{-1}) SD	TDS (mg l^{-1}) Fluctuation*	pH mean	pH SD	Temperature (°C) mean min	Temperature (°C) mean max	Turbidity (FTU) mean	Turbidity (FTU) SD	Secchi disc depth (m) mean	Secchi disc depth (m) SD	Nitrate (mg l^{-1}) mean	Nitrate (mg l^{-1}) SD	Phosphate (mg l^{-1}) mean	Phosphate (mg l^{-1}) SD
19a	265	61	90	7.7	0.9	12.2	26.9	52	30	0.63	0.41	1.2	0.8	0.47	0.33
19b	468	256	174	7.8	0.9	12.3	27.3	115	60	0.36	0.25	1.2	1.1	0.30	0.23
20	215	141	155	7.3	0.7	12.0	28.2	48	42	0.76	0.34	1.6	0.7	0.43	0.23
21	400	320	282	8.0	0.9	12.6	28.1	26	25	1.00	0.47	1.2	0.6	0.20	0.14
22	269	150	66	7.6	0.8	12.8	31.0	32	22	0.63	0.38	1.6	0.7	0.31	0.35
23	247	136	294	7.0	0.4	12.1	32.6	318	460	0.30	0.20	1.8	2.0	0.68	0.37

* These are mean figures for the 5 years (October 1979 to December 1984) and are calculated by dividing the difference between the greatest and lowest value each year by the lowest value and expressing as a percentage.

TABLE 4

Ionic composition of the water of lakes 19-23

Lake	Cations meq. l^{-1} Na^+	K^+	Mg^{2+}	Ca^{2+}	Total Ionic Conc. Cations	Total Ionic Conc. Anions	Anions meq. l^{-1} Cl^-	HCO_3^-	SO_4^{2-}
19	1.10	0.07	0.56	0.40	2.03	2.01	0.83	1.02	0.16
20	0.52	0.03	0.44	0.40	1.39	1.30	0.63	0.60	0.07
21	1.20	0.05	0.92	0.66	2.83	2.80	1.35	1.35	0.10
22	0.46	0.02	0.42	0.32	1.22	1.14	0.42	0.70	0.02
23	0.46	0.02	0.34	0.26	1.08	1.14	0.44	0.62	0.08

lagoons 20 and 23 tended to be warmer in summer and colder in winter because of their relative shallowness. During the summer months Lagoons 19a, and to a lesser extent 19b, 21 and 22, were often thermally stratified. In that bottom temperatures were only occasionally constant or slightly elevated from one month to the next, it is likely stratification rarely persisted between visits.

Turbidity also varied between and within the lagoons with mean values between 26 and 318 FTU's (Table 3) and extremes ranging from 0 in Lagoon 21 to 1600 in Lagoon 23. Values in Lagoon 23 were largely unnatural, as cattle trampled in it particularly during low water levels. The high values in Lagoon 19b may also be unnatural as European Carp, which are thought to muddy waters by their feeding activities (Tilzey, 1980), were present. There was little pattern in turbidity variations though, in general, values were highest following intense run-off. Algal blooms only had a noticeable effect in Lagoon 19a where *Oscillatoria* sp. regularly bloomed in late summer.

Light penetration, as measured by Secchi disc depth, varied from a mean value of 30cm to 100cm. The lowest recorded value was 1cm in Lagoon 23 and the highest 190cm in Lagoon 19a. Mean values in Lagoons 20, 21 and 23 should be a little higher as occasionally the disc reached the bottom before becoming obscured. Not surprisingly, turbidity and Secchi disc values were negatively correlated ($r = -0.7756$, $n = 6$, $P > 0.05$).

Nutrients in the 5 lagoons were of the same order of magnitude, averaging *c.* 1.4.mg l^{-1} NO_3-N and *c.* 0.4mg l^{-1} PO_4-P (Table 3). Lagoon 23 had the highest values and Lagoon 21 the lowest, with the former situation easily related to its use by cattle. Values in Lagoon 20 were probably elevated by intermittent agriculture and use of fertilizers in its catchment, and in Lagoon 19a the relatively high phosphates could be due to the 50-100 commercial ducks kept in a partially submerged pen on one bank. Nutrient values fluctuated erratically, but in lagoons which dried nutrients were elevated soon after filling and often during low water periods as well.

Discussion

(*a*) GEOMORPHOLOGY

Almost all of the lagoons studied fit the characteristics of the blocked valley lake type of Blake and Ollier (1971) (= lateral lake type of Hutchinson, 1957). Typically they are contained wholly or largely within small side valleys cut into Permian or Carboniferous sandstones, siltstones and mudstones or into high river terraces (e.g. No. 11) and with their lower ends blocked by natural levees of the Hunter or Paterson Rivers. Many, like Nos. 19 and 21 (Fig. 5) end abruptly at the floodplain — country rock junction, but others project onto the floodplain of the main stream e.g. Nos 6 and 8. There is one, No. 38, that lies partly in a tributary valley and partly between the levee and the scarp defining the edge of the flood plain (Fig. 1). Finally in this continuum, there are a few that lie almost entirely within the alluvium of the floodplain and are dammed by the natural levee of the main stream — embankment lakes of Blake and Ollier (1971).

Alluvium is often deposited in the form of an obvious levee, as it is at Nos 9 and 11 (Kaludah Lagoon), but in many cases the levee is complex, wide and of low uneven slope e.g. along the Hunter River between Nos 19 and 26 (Fig. 5). Reverse delta formation is apparent in some lagoons e.g. No. 4 ('Birds') (Fig. 3a) and in these the deepest point is well away from the dam. In others no such fan of alluvium is present so that the dam front is relatively steep and the deepest part is consequently near the dam e.g. No. 21 ('Murphys') (Fig. 3b).

Lagoon size is correlated significantly with catchment size ($r = 0.7305$, $n = 42$, $P > 0.001$), though catchments >600ha rarely contain lagoons and those below 75ha are

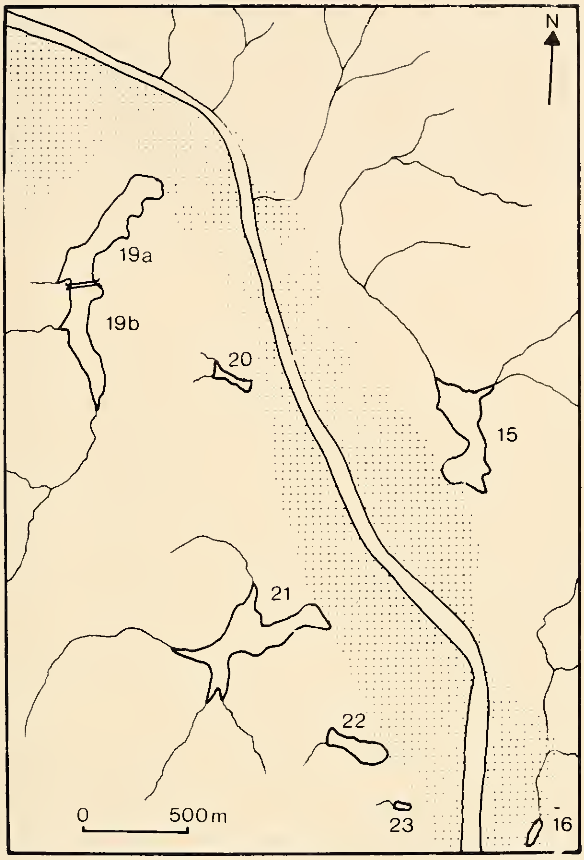

Fig. 5. Position of Lagoons 15-16 and 19-23 with reference to levee alluvium (stippled) of the Hunter River.

less likely too (Fig. 2**b**). This is probably because large catchments generate sufficient run-off to keep the channel to the main river open and very small catchments do not generate enough water to pond or more likely any depression is easily infilled with sediment from the main river.

The geomorphology of the tributary valley substantially influences the depth, shape and size of any lagoon in it. Lagoons in wide shallow valleys are typically shallow, large and with low S.D. values (e.g. Nos 11, 21, and 26), whereas those in narrow steep-sided valleys are usually smaller, deeper and more dendritic (e.g. Nos 19 and 38). The contrast in the two extremes is seen in the one lagoon, No. 4, 'Birds', where the deep northeast arm is in a steep-sided gully while the shallower southeast arm is surrounded by more gentle terrain.

Lagoons usually fill from local run-off following heavy rain, but rarely flood waters from the main stream contribute also. Following such filling, water levels are probably controlled largely by surface evaporation and by exchange with the regional watertable. However, given the great salinity increase as some lagoons dry (see later), perhaps some lagoons are at least partly perched. Although shallower lagoons are the ones most likely to be ephemeral, sediment types and geomorphic setting are also important. Lagoons largely on alluvium of sandy silt are less permanent than those in tributary valleys cut in rock and abutting alluvium.

Major floods may change the alluvial dam and hence the geomorphic and hydrologic features of a lagoon. An example is No. 19 which before the 1955 Flood was a marsh, but with the deposition of 5 to 10m of alluvium on the levee (telephone poles were almost buried) it became a permanent lagoon. Similar episodic changes to floodplain lakes on the Macdonald River near Sydney have been reported by Erskine (1986) and Henry (1977). Artificial drains silt after floods and many landowners redig their drains every few years.

(b) PHYSICOCHEMICAL ENVIRONMENT

Probably the most significant aspect of the physicochemical environment in these lagoons is its variability. Basic to this is the variable hydrologic regime as determined by their geomorphic position. The mean annual fluctuation in TDS of 177% is higher than for most freshwaters in southeast Australia (Bayly and Williams, 1966; Williams, 1967), but is nevertheless typical of small lentic waters such as billabongs of the Murray River around Albury (Shiel, 1980) and farm dams, including those nearby (Timms, 1970b; 1980). In common with these environments, but in contrast to larger reservoirs and lakes (Bayly and Williams, 1973; Powling, 1980; Timms, 1976) there are also great variations in pH, turbidity and nutrient levels. Such variations are influenced more by irregular inflows from the catchment than by within-lake processes and are exacerbated by the shallowness of the lagoons.

Other physicochemical characteristics of these lagoons indicate features typical of Australian freshwaters either countrywide or regionally, or of small shallow lentic waters such as river billabongs and farm dams. These include:

(a) TDS content in all is higher than usual for the region where only 12% of waters exceed 225mg l^{-1} (Timms, 1970c). This is probably due to their closed hydrologic regime for most of the time. Certainly, flushing after heavy local rain reduces TDS levels (Fig. 4) and this happens on average for a few days in wet years. The influence of rare river floods is unknown, but presumably flushing occurs then also.

(b) Ionic composition is typical of Australian waters as a whole (Bayly and Williams, 1973), though HCO_3 levels are relatively high, as is generally the case in northeastern NSW (Timms, 1970c).

(c) pH is generally between 7 and 8 which is usual for most freshwaters in eastern Australia (Bayly and Williams, 1973).

(d) Annual temperature range of surface waters is *c.* 15-20°C which is similar to that reported for other small sites in lowland southern Australia (Shiel, 1980; Timms, 1970b). Minima of 11-12°C are characteristic of low-altitude waters at this latitude (33° S) (Shiel, 1980; Timms, 1970b). The perceived lack of persistent stratification distinguishes these lagoons from many farm dams (Timms, 1980), typical larger reservoirs and lakes (Powling, 1980; Timms, 1976) but not from billabongs (Shiel, 1980). Any stratification in these lagoons is short-lived because of their shallowness and exposure to winds. However, more detailed studies are needed as there are some indications that at least one stratifies for weeks at a time, and given its eutrophic status, extensive deoxygenation could occur.

(e) In common with farm dams (Timms, 1980) and most inland waterbodies (Bayly and Williams, 1973) the waters of these lagoons are turbid. Consequently Secchi disc depths of <1m, often <0.5m are characteristic.

(f) Nutrient levels, particularly phosphate, are higher, than for most freshwaters in Australia (Bayly and Williams, 1973) but similar to values recorded in farm dams (Timms, 1980). As discussed earlier at least some of these nutrients are anthropogenically derived. Despite these high nutrient levels there is no evidence that the lagoons are hypereutrophic; indeed some appear at most to be mesotrophic based on evidence on their planktonic and benthic standing crops (author, in preparation). It seems high turbidity and associated limited light penetration limit production (Williams and Wan, 1972).

In summary then, while the physicochemical environment in these lagoons is typical for Australia, it is distinctive by virtue of its elevated TDS content, high turbidity and nutrient levels. Most charcteristic of all though is the high variability in all parameters.

(c) INFLUENCE OF MAN

Not one of the lagoons is unaffected by man. Indirectly, they are probably being flushed less frequently because of the flood mitigation effect of Glenbawn Dam upstream on the Hunter R. (Erskine, 1985). More directly, most landowners consider the lagoons occupy valuable grazing land, so they endeavour to drain them. Two-thirds of the lagoons are affected in this way (Table 1) with the most drastic changes being seen on the larger lagoons in wide shallow valleys. Other less obvious changes are wrought by (i) cattle wading which increases turbidity in smaller lagoons and in larger lagoons during low water periods and (ii) by use of fertilizers on upstream catchments.

Nutrient levels are probably elevated in all lagoons, particularly in those with discrete sources, e.g. duck pens. The effects of these changes on their ecosystems are unknown. Nevertheless, while some eutrophication may have enhanced waterfowl habitat in many lagoons, their natural value as drought refuges has been further reduced by drainage. Fortunately, should the opinions of landowners change, the river can right wrongs by depositing new alluvial dams or silting drains, so tributary valleys can once more be effectively dammed to become permanent lagoons again.

ACKNOWLEDGEMENT

I wish to thank many of my geomorphology students for help in mapping the lagoons, and in particular Glen King and the late Edu Nerinckx for assisting in the initial survey and interviews as well. I am grateful to numerous landowners who allowed access to their lagoons and spent time talking with us, and to the Director of the Bureau of Meteorology for supplying rainfall data for Singleton. Dr I. A. E. Bayly of Monash University and Wayne Erskine of University of N.S.W. are thanked for reviewing the manuscript.

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Records of *Eudendrium* (Hydrozoa: Hydroida) from New Zealand

JEANETTE E. WATSON

WATSON, J. E. Records of *Eudendrium* (Hydrozoa: Hydroida) from New Zealand. *Proc. Linn. Soc. N.S.W.* 109(4), (1986)1987: 325-330.

Three species of *Eudendrium* are recorded from New Zealand, all from the North Island. These are *E. novaezelandiae* Marktanner-Turneretscher, 1890, *E. terranovae* Watson, 1985 and *E. ritchei* Millard, 1975. The holotype of *E. novaezelandiae* has been re-examined and the description amplified from study of fresh material. The doubtful record of *E. novaezelandiae* from North Cape by Totton (1930) is now known to be *E. terranovae*, while *E. insigne* Hincks, 1861, reported from the east coast (Ralph, 1953), is here referred to *E. ritchei*. This is the first record of the latter species outside South Africa.

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INTRODUCTION

Records of the genus *Eudendrium* are comparatively rare in the New Zealand hydroid literature. The earliest record is of *Eudendrium novaezelandiae* Marktanner-Turneretscher, 1890 from Auckland, the holotype of which is lodged in the Naturhistorisches Museum of Vienna. This species was included by Farquhar (1896) in his checklist of New Zealand hydroids. There are no other references to *Eudendrium* in the literature of early authors (e.g. Hutton, 1873; Coughtrey, 1875; 1876; 1876a; Thompson, 1879; Hilgendorf, 1897; Hartlaub, 1901; Bale, 1924; Trebilcock, 1928).

Totton (1930), doubtfully assigned to *E. novaezelandiae* a specimen collected at North Cape by the Terra Nova Expedition (1910-1913). Comparison of the cnidome of Totton's material with that of the holotype (Watson, 1985) showed the North Cape material not to be *E. novaezelandiae* but a new species of *Eudendrium*. This species, named *E. terranovae* Watson, 1985, is a common oceanic hydroid of the southeastern Australian coast. The systematics, ecology and distribution of *E. terranovae* are fully described by Watson (1985: 189-191).

The remaining reference to *Eudendrium* in the New Zealand literature is a very brief description by Ralph (1953) of a hydroid which she assigned to *E. insigne* Hincks, 1861, from the east coast of New Zealand.

These records are all from the North Island; the genus has not yet been recorded from the South Island. Judging by the number of species of *Eudendrium* now known from comparable latitudes and habitats in Australian waters (Watson, 1985), the New Zealand fauna should, however, include many more species than are known at present.

A small collection of hydroids made by the author, using SCUBA, from the Coromandel Peninsula (37°48′S, 175°30′E) in the North Island in February 1983, yielded two species of *Eudendrium*. One, identified as *Eudendrium novaezelandiae* Marktanner-Turneretscher, 1890, now provides a basis for redescription of that species. The other, referred by Ralph (1953) to *E. insigne* Hincks, 1861, is here identified with *E. ritchei* Millard, 1975. This is the first record of *E. ritchei* outside southern Africa.

Material of each species is lodged in the Museum of Victoria (MVF) and held in the personal collection of the author.

SYSTEMATIC ACCOUNT

Eudendrium novaezelandiae Marktanner-Turneretscher, 1890

Eudendrium novaezelandiae Marktanner-Turneretscher, 1890:201, pl. 3, fig. 21.
non *E. novaezelandiae* Marktanner-Turneretscher. Totton, 1930:141.

Material Examined: Holotype, AN12389, Naturhistorisches Museum of Vienna. Other material, MVF51780, male colony on shell of *Atrina zelandica*, Coromandel, Haurakai Gulf, 8m deep, bottom gravel and mud, coll: J. E. Watson, 20/2/83.

Description: The holotype material comprises an alcohol preserved distal fragment of a larger female colony. The stem is about 6cm in height and is broken into two pieces. The following description of the holotype supplements that of Marktanner-Turneretscher.

The stem is branched irregularly in various planes, the main branches being fascicled almost to their tips, perisarc smooth and shining. The distal branches are roughly alternate, passing upwards at an acute angle, with up to seven indistinct proximal annulations and additional groups of annulations occurring at intervals along the distal branches; hydranth pedicels annulated throughout. There are no remaining hydranths. The gonophores are mature and are borne in groups of up to five scattered along a blastostyle devoid of tentacles. The single egg is enclosed in a thick transparent pellicle.

Nematocysts of three sizes present but poorly preserved; none fully discharged:

(i) microbasic euryteles (probably from tentacles), capsule 5-6 × 2-3μ, abundant in patches in pedicels of hydranths,

(ii) large microbasic euryteles, capsule bean-shaped, 17 × 8μ, abundant in pedicels of gonophores,

(iii) microbasic euryteles, smaller than above, 11-13 × 5-6μ, capsule bean-shaped. Present in the pedicel of the female gonophore and possibly on the gonophore itself.

The colony from Coromandel is 30mm in height, comprising two separate stems arising from the same hydrorhizal plexus. Main stems 0.7mm in proximal width, lightly fascicled to about half the height of colony. Branches alternate, proximal width 0.1-0.13mm, rebranching in the same plane with up to eight distinct annulations at origin of branches, perisarc otherwise smooth and shining. Pedicel of hydranth long, distal width 0.13-0.15mm. Hydranth large, with about 20 tentacles, a nematocyst ring on the lower body, hypostome elongate and clavate, maximum width below tentacles (preserved material) 0.3mm. Male gonophores immature, blastostyle without tentacles.

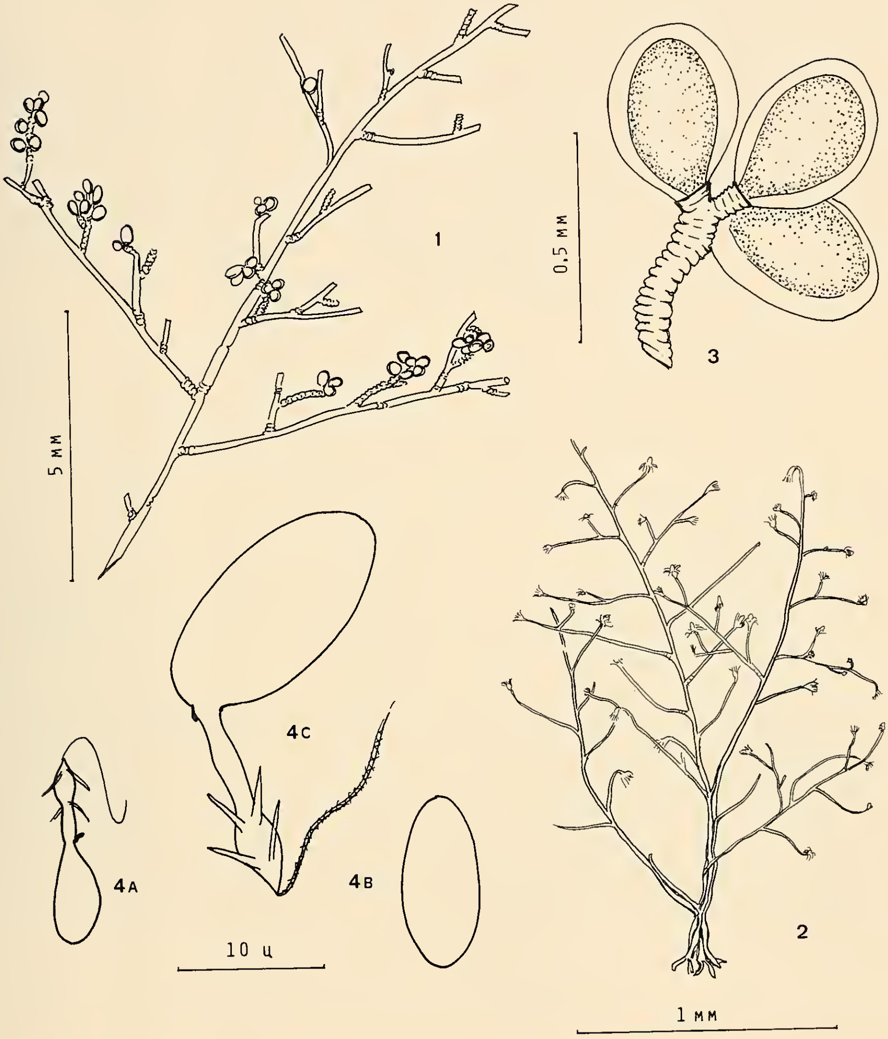
Nematocysts of two sizes present:

(i) small microbasic euryteles, 6-7 × 3μ, shaft 5-6μ long, with a few spines, moderately abundant on tentacles,

(ii) larger microbasic euryteles, capsule 18-19 × 8-10μ, bean-shaped, shaft 11-15μ long, spines not clearly visible, thread with fine bristles. Abundant in nematocyst ring; a few present on the hypostome and on gonophore.

Colour: Living colony cream coloured, stems dark brown proximally, becoming lighter distally.

Remarks: The main differences between the Coromandel material and the holotype of *E. novaezelandiae* are the flatter and more regular branching, the more regular appearance, and the absence from the cnidome of the third, intermediate-sized microbasic eurytele. The larger and smaller microbasic euryteles agree well with those of the holotype. The absence of the intermediate-sized nematocysts from the present specimen may be due to association with the female gonophore only, in a similar manner to that noted in *E. generale* von Lendenfeld, 1885, by Watson (1985). All other characters agree well with those of the holotype.



Figs 1-4. Eudendrium novaezelandiae. 1. — Distal part of branch of holotype colony (AN12389, Naturhistorisches Museum of Vienna) showing clusters of female gonophores. *2.* — Whole stem of specimen from the Hauraki Gulf, New Zealand. *3.* — Cluster of mature female gonophores drawn from holotype. *4.* — Nematocysts: **A**, tentacular microbasic euryteles from holotype; **B**, medium-sized, undischarged microbasic eurytele from female gonophore of holotype; **C**, large microbasic eurytele, discharged, from specimen from the Coromandel Peninsula.

Eudendrium ritchei Millard, 1975

Eudendrium ritchei Millard, 1975:87, fig. 30.
non *E. insigne* Hincks, 1861. Ralph, 1953:63, pl. 1, fig. 2A, 2B.

Material Examined: MVF51781, male colony, MVF51782, female colony; east coast of Coromandel Peninsula, on brown algae, 2m deep, coll: J. E. Watson, 21/2/83. British Museum (Natural History) alcohol preserved specimen 1912.12.21.90 labelled *E. insigne* Hincks, 1861.

Description: Colonies growing luxuriantly on algal holdfast. Stems up to 1cm in height and 0.13-0.18mm in width, unfascicled, irregularly branched, arising from a smooth reticulating hydrorhiza. Stems completely and closely annulated throughout, perisarc very thick. Hydranths terminal on branches, with 20-24 tentacles.

Male and female gonophores borne on different but closely associated colonies on algal substrate. Immature male gonophore with an apical tubercule, mature gonophore 1-2 chambered, distal 5 chamber 0.14-0.2mm in diameter, borne on lower stems of colony in a tight cluster of 20-30 on a blastostyle devoid of tentacles at all stages. Young female gonophore with a strongly bifurcated spadix; gonophores borne in clusters of 4-6 in various stages of development below a hydranth with a reduced number of tentacles. At maturity, the tentacles are completely absent, with 2-5 mature gonophores scattered along the blastostyle. Length of mature female gonophore 0.3mm, width 0.25mm.

Nematocysts of two kinds present:

(i) microbasic euryteles, capsule 6-7 × 2.5μ, shaft 5μ long, abundant in tentacles, few discharged,

(ii) larger microbasic euryteles, capsule bean-shaped, 16.5-18 × 7-8μ, shaft thick, at least 37μ long, spinous, the thread very long and covered with bristles. Abundant on hydranth, spadix of female, and on apical tubercule of male gonophore.

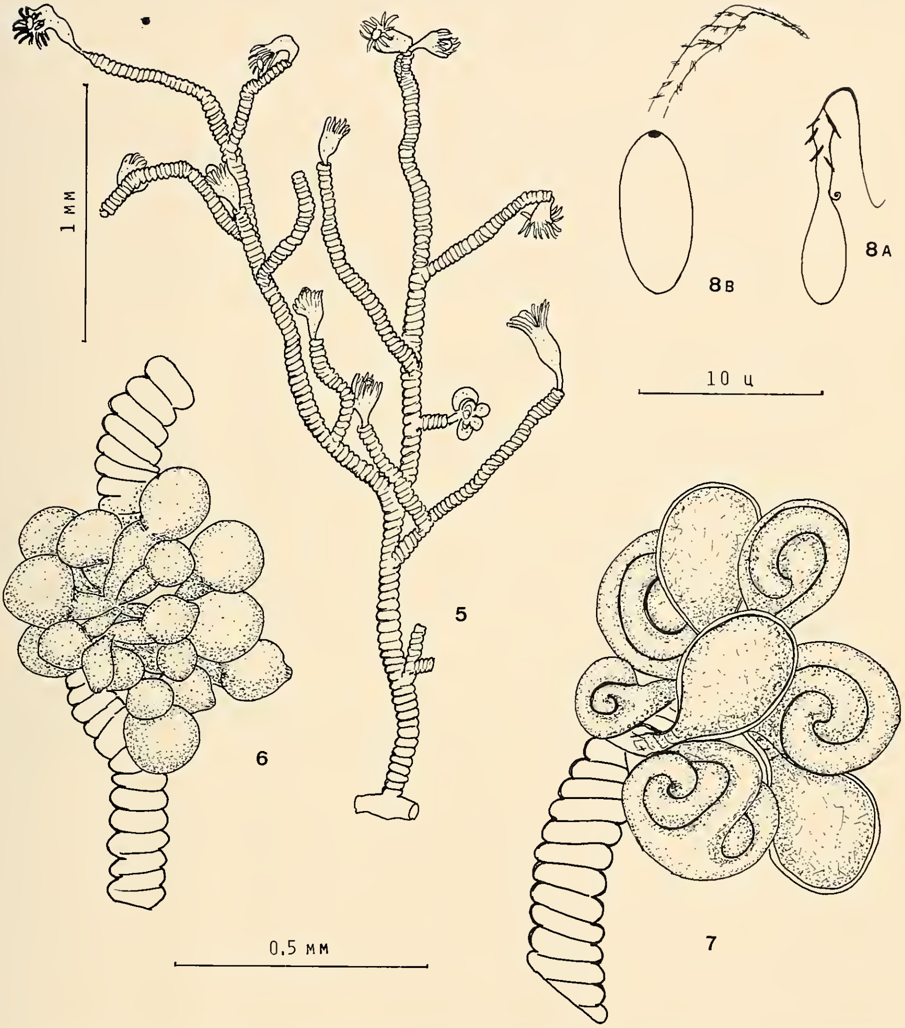
Colour: Hydranths and gonophores cream coloured, perisarc dark shining brown.

Remarks: Although the material upon which Ralph's (1953) identification was based has not been examined, her description, figure and locality notes leave no doubt that specimens collected by the present author on the east coast of the Coromandel Peninsula are identical with those recorded by her as *E. insigne* Hincks, 1861. Comparison of the cnidome of a specimen of fresh material from the Hauraki Gulf with the British Museum material of *E. insigne* shows that Ralph's material is not this species.

The New Zealand specimens collected by the author agree well in colony morphology with Millard's (1975) description of *Eudendrium ritchei*, including important structures such as the bifurcated female spadix and the strongly annulated stems. They differ from the South African species in the smaller size of the mature colony and in having strictly monosiphonic stems. Although the tentacular and supplementary nematocysts (Watson, 1985) of the New Zealand specimens are similar to those described and figured by Millard for *E. ritchei*, there are, however, certain differences, namely the greater length-width (L/W) ratio (Kubota, 1976; Watson, 1985) and the greater ratio of length of shaft to capsule (S/C) in the southern African material. These ratios are compared below:

		New Zealand	S. Africa
Tentacular microbasic euryteles	Capsular L/W ratio	2.8:1	2.7:1
	S/C ratio	0.8:1	0.8:1
Supplementary nematocysts	Capsular L/W ratio	2.3-2.4:1	2.6-2.8:1
	S/C ratio	> 2:1 (not fully discharged)	2.7- 3.2:1

It has been suggested that variations may occur in the relative size and dimensional ratios of nematocysts across the geographical range of a single species of *Eudendrium*



Figs 5-8. Eudendrium ritchei from the east coast of Coromandel Peninsula. *5.* — Single stem from female colony. *6.* — Cluster of mature male gonophores. *7.* — Cluster of female gonophores in various stages of maturity. *8.* — Nematocysts: **A**, tentacular microbasic eurytele, discharged; **B**, microbasic eurytele showing distal end of shaft.

(Kubota, 1976; Watson, 1985). The differences in size between the supplementary nematocysts of the southern African and the New Zealand specimens further support this view. Thus, until the limitations of variability of nematocysts within a species is established, the New Zealand specimens are assigned to *E. ritchei*.

Millard classified the larger (supplementary) nematocysts of *E. ritchei* as macrobasic euryteles. However, according to her definition of nematocysts (Millard, 1975: 21), they should be considered microbasic euryteles since, according to her figure, the shaft is less than four times the length of the capsule. Although no fully discharged shafts were found in the New Zealand material, the S/C ratio would clearly be less than four at full eversion.

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Description of a new Species of freshwater Hardyhead *Craterocephalus kailolae* (Pisces: Atherinidae) from Safia, northeastern Papua New Guinea

W. IVANTSOFF, L. E. L. M. CROWLEY and G. R. ALLEN
(Communicated by P. SELKIRK)

IVANTSOFF, W., CROWLEY, L. E. L. M., & ALLEN, G. R. Description of a new species of freshwater hardyhead *Craterocephalus kailolae* (Pisces: Atherinidae) from Safia, northeastern Papua New Guinea. *Proc. Linn. Soc. N.S.W.* 109(4), (1986) 1987: 331-337.

Craterocephalus kailolae is described from specimens collected in Foasi Creek, Safia, northeastern Papua New Guinea. The new species is considered to be related to members of the *C. eyresii* species group. *C. kailolae* is the only freshwater hardyhead known from the northeastern drainages of Papua New Guinea as well as being the only representative of the *C. eyresii* group known from outside Australia . It can be distinguished from other species of *Craterocephalus* by a spatulate maxilla and other osteological characters and a combination of morphological features. The zoogeography of this group in relation to this distribution is discussed briefly. As no literature exists on the species composition of the genus *Craterocephalus*, its members and their authors are given.

Walter Ivantsoff and L. E. L. M. Crowley, School of Biological Sciences, Macquarie University, North Ryde, Australia 2113, and Gerald R. Allen, Department of Ichthyology, Western Australian Museum, Francis Street, Perth, Australia 6000; *manuscript received 25 November 1986, accepted for publication 20 May 1987.*

INTRODUCTION

The predominantly freshwater genus *Craterocephalus*, is endemic to Australia (Merrick and Schmida, 1984) and Papua New Guinea. In the most recent revision, (Ivantsoff, 1978) divided the genus into two species groups (see also Patten, 1978), '*C. eyresii*' and and '*C. stercusmuscarum*.' Recent work by Crowley and Ivantsoff (unpublished) suggests that a third group, which includes the marine and estuarine species, can also be recognized. The '*C. eyresii*' group comprises *C. eyresii* (Steindachner, 1884). *C. cuneiceps* Whitley 1944, *C. marjoriae* Whitley 1948 as well as two species recently described by Ivantsoff *et al.* (1987). The '*C. stercusmuscarum*' group comprises *C. stercusmuscarum* (Günther, 1867) which includes spotted and unspotted subspecies (Ivantsoff *et al.*, 1987). *C. nouhuysi* (Weber, 1910), *C. randi* Nichols and Raven 1934, *C. lacustris* Trewavas 1940, *C. dalhousiensis* Ivantsoff and Glover (1974) and a new species from northern Australia (Ivantsoff *et al.*, 1987; Allen, 1982). The '*C. honoriae*' or the marine/estuarine group includes the remaining known species: *C. honoriae* (Ogilby, 1912), *C. pauciradiatus* (Günther, 1861) and *C. capreoli* Rendahl 1922 (now regarded as distinct, see Potter *et al.*, 1986).

Two related monotypic genera *Quirichthys* Whitley 1950 and *Allanetta* Whitley 1943 are under review and on present evidence (Crowley and Ivantsoff, unpublished) will probably be included in the synonymy of *Craterocephalus*.

The new species, *C. kailolae*, which is herein described, shows morphological, meristic and osteological characteristics which align it with the '*C. eyresii*' group. It is the only representative of that group to occur in Papua New Guinea.

MATERIALS AND METHODS

The specimens in this study were collected from a quiet backwater using a small seine

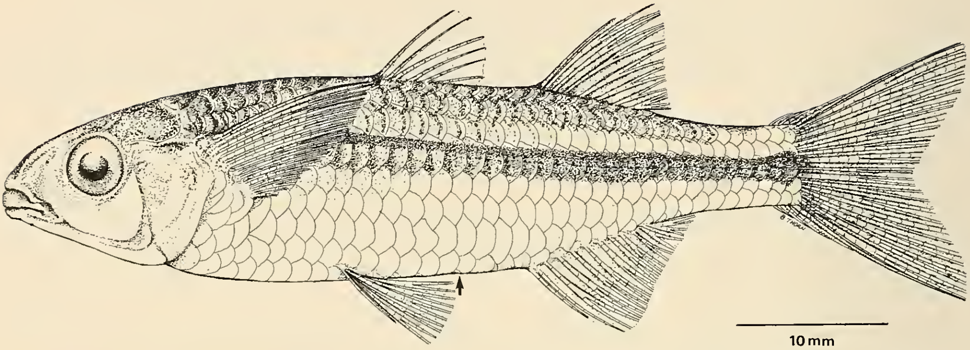


Fig. 1. Holotype *Craterocephalus kailolae*. AMS I.24640-001.

net of about 20mm mesh size which provided an adequate sample in a short time of collecting.

The methods of counting and measuring were modified from Munro (1967) and were as described by Prince *et al.*, (1982) and Patten and Ivantsoff (1983). In *Craterocephalus* species, the second dorsal and anal fins may or may not have an unbranched ray preceding branched rays. For the sake of uniformity, the first ray following the spine is not considered as part of the branched ray count throughout this work. The vertebral counts were obtained by radiography and the osteological studies were made on alizarin specimens prepared using standard techniques developed by Taylor (1967). Morphometric measurements and meristic counts were recorded for 31 specimens, designated holotype and paratypes (Table 1). These specimens are now deposited in The Australian Museum, Sydney. N.S.W. (AMS); Western Australian Museum, Perth, W.A. (WAM); Kanudi Fisheries Research Station, Kanudi, Papua New Guinea, (KFRS); Museum of Zoology, Ann Arbor, Michigan, U.S.A. (UMMZ).

DESCRIPTION

Craterocephalus kailolae sp. nov.

(Fig. 1)

Holotype — AMS 1.24640 - 001. 57.5mm standard length (SL) collected with a small seine; type locality, 3km west of Safia airstrip in still backwater of Foasi Creek , Papua New Guinea 9°36′S, 148°37′E, collected by Walter Ivantsoff and John Paska. September 16. 1985.

Paratypes, 30 (25.2-52.3), locality as for holotype, collected by G. R. Allen using small seine, September 8, 1982.

WAM P27783-001 (11 + 3 alizarin specimens); AMS I.24640-002 (10); KFRS F.5390.01 (3); UMMZ 213857 (3)

Overall size range 25.2-57.5mm SL. Measurements expressed as proportions and counts for the holotype and 30 paratypes are presented in Table 1.

DIAGNOSIS

Distinguished from all other species and subspecies of *Craterocephalus* by the combination of the following characters: small, moderately robust fish with seven rows of transverse scales with two rows above, one covering, and four below midlateral band. Midlateral scales 31-34, interdorsal scales 5-7. Mouth small, gape restricted by labial ligament. Gill rakers in first lower gill arch 8-10, those in angle of first arch (1-2) slightly elongated, others

TABLE 1

Measurements (expressed as proportions) and counts of the holotype and 30 paratypes of Craterocephalus kailolae *from Safia, Papua New Guinea*

	Holotype	30 Paratypes		SD
SL	57.5mm	25.2-52.3mm		
In SL				
		mean	range	
Head	3.8	3.6	(3.3-4.0)	.15
PecL	5.0	4.9	(4.6-6.0)	.35
H max	4.3	4.0	(3.6-4.5)	.21
H min	9.8	9.5	(8.8-10.2)	.31
Sn-OD1	2.0	2.0	(1.9-2.1)	.06
Sn-OD2	1.4	1.4	(1.3-1.5)	.04
Sn-OV	2.3	2.2	(2.1-2.3)	.08
Sn-TV	1.8	1.7	(1.6-1.8)	.05
SN-OA	1.5	1.5	(1.4-1.5)	.05
Sn-TA	1.3	1.3	(1.2-1.3)	.05
In Head				
Eye	3.4	3.3	(3.0-3.8)	.18
Interorbital	2.5	2.6	(2.4-2.8)	.12
Postorbital	2.3	2.3	(1.9-2.5)	.12
In Eye				
Snout	1.0	1.1	(0.9-1.5)	.13
Premaxilla	1.0	1.0	(0.9-1.2)	.07
Dorsal process of premaxilla	1.1	1.2	(1.0-1.5)	.12
Scale counts				
Midlateral	34	33.2	(31-34)	.82
Transverse	7	7.0	—	—
Predorsal	12	12.5	(11-14)	.90
Interdorsal	6	6.0	(5-7)	.26
Fin elements				
First dorsal spines	6	5.6	(4-7)	.63
Second dorsal branched rays	6	6.2	(5-7)	.48
Anal branched rays	8	8.2	(7-9)	.56
Pectoral branched rays	11	12.0	(11-13)	.68
Position of fins				
OD1 to TV	F4.0	F3.3	(F2.5-4.5)	.50
OD1 to TPec	B1.5	B1.4	(0-B2.5)	.57
OV to TPec	F1.0	F1.7	(0-F3)	.68
Other values				
Gill rakes in first lower gill arch	8	8.8	(8-10)	.55
Position of anus to TV	B1.0	B1.0	(0-B3)	.78
Vertebrae	34	34.3*	(33-35)	.69

* 17 specimens.

Abbreviations used in table: SL, standard length; Pec L, length of longest pectoral ray; H max, greatest body depth; H min, least body depth at caudal peduncle; Sn, snout; OD1, origin of first doral fin; OD2, origin of second dorsal fin; OV, origin of ventral fins; TPec, tips of pectoral fins; TV, tips of ventral fins; OA, origin of anal fin; TA, point of last ray insertion of anal fin. Position of fins and anus is expressed as a number of scales in front (F) or behind (B) point of reference. SD, standard deviation.

short, rounded and with spinules. Dorsal process of premaxilla long, extending into interorbital space. Anterior process of maxilla broad, spatulate, almost meeting its opposite at midline (Fig. 2). Palatine cylindrical, without pointed dorsal end. Branchiostegals 5.

Canals tubular and closed on nasals, anterior infraorbitals and postemporals; those on frontals and temporals partially closed.

DESCRIPTION

Meristic counts and morphometric proportions for the holotype and paratypes are presented in Table 1.

Small, moderately robust fish, largest specimen known 57.5mm SL. Dorsal profile somewhat rounded, continuing in unbroken curve from origin of first dorsal to snout. Lips thick, mouthparts protrusible. Premaxilla almost never reaching vertical through anterior margin of orbit. Dorsal process of premaxilla long, reaching into interorbital space. Upper jaw with two rows of teeth pointing posteriorly. Ramus of dentary highly elevated posteriorly. Anteriorly, dentary expanded, forming wide edentulous plate. Other elements of mouth edentulous also. Pharyngeal teeth sharp and fine, never molariform. Body scales moderately large, scalloped and prominent, dorsoventrally elongated with circuli complete. Single large interorbital scale with one smaller scale on either side always present. Preopercle scaled.

Intercalars large. Anterior infraorbitals reduced, sometimes fused (Figs 3, 4). Large dorsal and ventral postcleithra present. Urohyal with well developed dorsal plate, reduced ventral plates, ventral pocket absent. Basihyal bone and cartilage about equal. Other osteological features similar to other members of the '*C. eyresii*' group as described later.

COLOUR

Preserved specimens yellow brown above silvery midlaterlal band and pale yellow below. Scales on dorsal surface and sides outlined with melanophores . Scales in row immediately above midlateral band pigmented only to end of first dorsal fin along side of body. Body below midlateral band unpigmented. Spine and rays of first and second dorsal and caudal fins with rows of melanophores, other fins unpigmented. Dorsum of head, snout and lips peppered with melanophores. Posterior border of orbit outlined with melanophores. Live specimens yellow brown with silvery band, not distinctly different from those preserved.

ETYMOLOGY

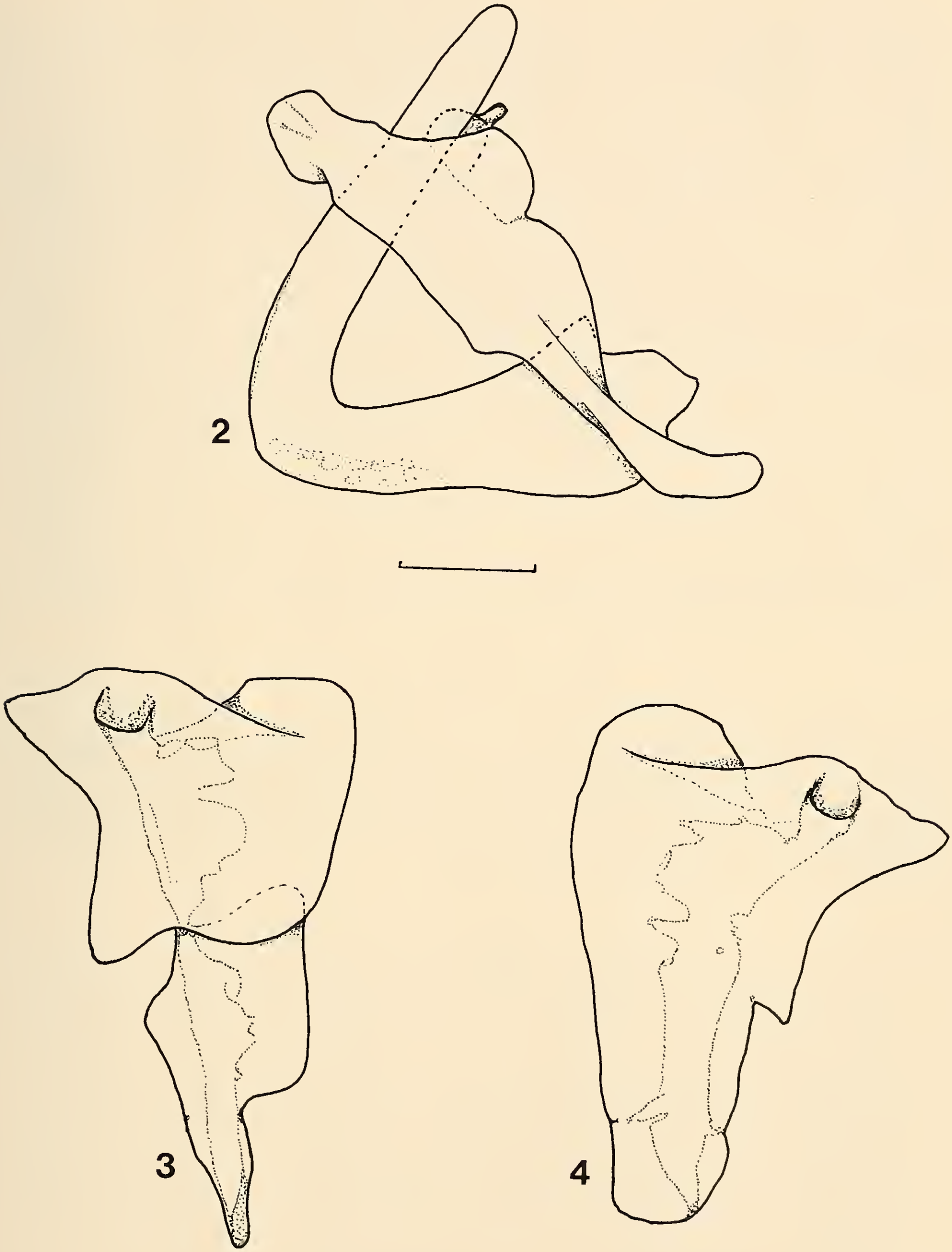
kailolae. Named after Mrs Patricia Kailola, a major contributor to the knowledge of ichthyology of Papua New Guinea. Without her help much of the work on Papua New Guinea species of *Craterocephalus* would have been very difficult.

RELATIONSHIPS WITH OTHER SPECIES OF *CRATEROCEPHALUS*

Craterocephalus kailolae is a member of the '*C. eyresii*' group (Ivantsoff, 1978; Patten, 1978). The group can be identified by the following characters: gut elongate, longer than body length; small finger-like epiotic crest; unbranched posterior myodome extending into basioccipital but without posterior opening; urohyal with ventral plates reduced; lower pharyngeals close but not fused and with sharp non-molariform teeth; mesopterygoid small; posterior edge of coracoid rounded, medial shelf reduced; scapular foramen large: interdorsal pterygiophores usually weakly developed or absent; anal plate small with no anterior elongation. Colour of midlateral band usually silvery in contrast to members of *stercusmuscarum* group where band darkly pigmented.

DISTRIBUTION AND ZOOGEOGRAPHY

Craterocephalus kailolae is at present known only from the type locality in the north-eastern highlands of Papua New Guinea. It appears to be present in relatively large



Figs 2-4. Craterocephalus kailolae — Paratype WAM P27783-001. 2) upper jaw elements; 3) first and second infraorbitals — right side; 4) first and second infraorbitals fused — left side. Scale line represents 1.00mm.

numbers in slower flowing branches of the main stream, in very shallow water, often only several centimetres deep. It also occurs in backwaters which may be shallow or deep, murky or clear.

The location of this species is of great interest since all other hardyhead species from Papua New Guinea occur in southern drainages. These are *C. randi*, extending from the Fly River to the Port Moresby area, *C. lacustris*, at present known only from Lake Kutubu, but possibly also occurring in the Kiori and Wago Rivers draining the lake to the south, and *C. nouhuysi*, occurring in the Lorenz River, Irian Jaya, near the border of Papua New Guinea and possibly in the upper tributaries of the Fly River near Tabubil. These species are all members of the '*C. stercusmuscarum*' group. Their closely related counterparts, *C. stercusmuscarum stercusmuscarum* and *C. species B* (Allen, 1982) occur on the other side of the Arafura Sea and Torres Strait. *C. marjoriae*, *C. marianae* Ivantsoff *et al.*, 1987 and *C. species A* (Allen, 1982) also occur in the northern coastal areas of Australia but there are no known south coast representatives of the '*eyresii*' group in Papua New Guinea.

It appears that speciation of the genus *Craterocephalus* may have been slow, unlike the Melanotaeniidae, another speciose group of freshwater fishes common to both Papua New Guinea and Australia (Allen and Cross, 1982). *C. kailolae* must have been separated from its north Australian relatives 2-5 million years ago, that is, since the uplifting of the highlands in Papua New Guinea during Plio/Pleistocene (Veevers, 1984). The members of the '*C. stercusmuscarum*' group, on the other hand, could still have been sympatric 7-10,000 years ago, prior to the last transgression on Torres Strait, thus allowing for gene flow to continue and maintain similarity. *C. randi* and *C. s. stercusmuscarum* for example are morphologically and osteologically very close. The fact that *C. kailolae* is readily identifiable as a member of the '*C. eyresii*' group (although morphologically distinct from other members) supports the proposal that members of the genus *Craterocephalus* do not speciate rapidly.

ACKNOWLEDGEMENTS

We thank John Paska of Port Moresby who helped us to collect the fish, and Mr Patrick O'Connor, the manager of Bulmacau Station in Safia who gave us shelter and allowed us to collect in Foasi Creek. We also thank Miss Betty Thorn for her drawing of the holotype and Basim Said and John Patten for their help with osteology and comments on the relationships within the genus *Craterocephalus*. Dr D. Hales and Dr J. Bassett are thanked for reading and commenting on the manuscript.

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Index

VOLUME 109

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VOLUME 109

Issued 22nd December, 1987

CONTENTS:

NUMBER 3

NUMBER 4

Contents continued inside

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PROCEEDINGS
OF THE
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VOLUME
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Contents of Proceedings
Volume 110

NUMBER 1 (No. 481)
(Issued 12th July, 1988)

NUMBER 2 (No. 482)
(Issued 12th July, 1988)

NUMBER 3 (No. 483)
(Issued 13th January, 1989)

NUMBER 4 (No. 484)
(Issued 13th January, 1989)