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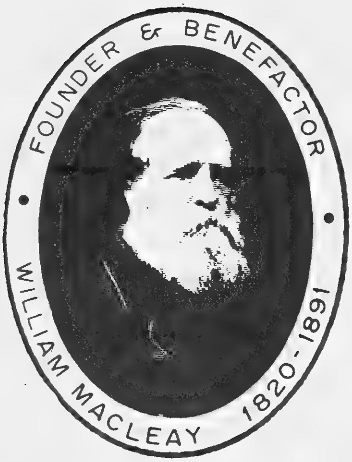
NATURAL HISTORY IN ALL ITS BRANCHES

THE LINNEAN SOCIETY OF NEW SOUTH WALES



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PROCEEDINGS
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William John Macleay — Entomological Lion?

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Macleay Museum A12, University of Sydney, Australia 2006

(Delivered 27 March 1991)

Synopsis

William John Macleay was a well known benefactor to the scientific community in New South Wales in the latter decades of the 1800s. He also devoted much energy to a variety of zoological subjects and published on insects, fish, amphibians, lizards and snakes.

He was well known for his work on Australian insects, primarily beetles. He published 39 papers on insects in four journals in New South Wales, South Australia and Tasmania. His entomological papers in each of the journals are summarized. His entomological contributions are discussed by analyzing the proportion of valid species to synonyms in 5 families of beetles (Buprestidae, Carabidae, Elateridae, Scarabaeidae and Tenebrionidae), accounting for more than 60 per cent of his 1360 new species of beetles. A comparison is outlined of his taxonomic works in these families in relation to those described by Reverend Thomas Blackburn.

KEY WORDS: Reverend Thomas Blackburn, William John Macleay, Buprestidae, Carabidae, Elateridae, Scarabaeidae, Tenebrionidae.

INTRODUCTION

William John Macleay (1820-1891), medical student, squatter, politician, scientist, expedition leader and a benefactor to the scientific community in New South Wales, was an important contributor to neo-colonial science in the latter decades of the 1800s. Much has been written of his life but little of his political and scientific careers has been explored. Macleay was more than a patron of science. He wrote more than 70 reports and papers on entomology, ichthyology and other zoological subjects. He was amongst the first of Australian scientists to publish his works in local journals. His major non-entomological works included the *Descriptive Catalogue of Australian Fishes* (1881) and *Census of Australian Snakes* (1884) (Hoare and Rutledge, 1974). Amongst his many accomplishments, he founded the *Entomological Society of New South Wales*, was a founder of the *Linnean Society of New South Wales* and established a museum of natural history. He provided substantial monies for a variety of scientific enterprises, some of which are still in existence.

So important were his contributions considered to the study of insects that Musgrave (1930) named his third period of Australian entomological history the Macleayan Period (1862-1929). In this address, I wish to restrict myself to his accomplishments in this field. Macleay published 39 papers on Australian insects, primarily beetles, in four journals in New South Wales, South Australia and Tasmania. A summary of his papers in each of the journals is presented (a list of his entomological papers may be found in Musgrave (1932)). His talents as a taxonomist are discussed by analyzing the proportion of his valid species to synonyms he created in five familes of beetles (Buprestidae, Carabidae, Elateridae, Scarabaeidae and Tenebrionidae). This accounts for more that 60 per cent of his 1360 new species of beetles. His colleague, Reverend Thomas Blackburn also published extensively in these five families and his efforts are compared to those of Macleay.

THE ENTOMOLOGICAL SOCIETY OF NEW SOUTH WALES

The awakening of William John Macleay's love of entomology (as early as 1858) is well documented by Fletcher (1929: 211-215). By 1862, as well as collecting in the Sydney area, he received insect collections from at least Mr E. Dämel (King George Sound, Western Australia, 1860-1861), George Masters (Port Denison area, Queensland, 1861-1862) and W. S. Wall (Rockhampton, Queensland, 1861-1862).

By 1862 Macleay had an extensive collection and, working with the earlier Macleays' collections and William Sharp's library, began to describe new species of Coleoptera — his special interest. There were no appropriate Australian journals as an outlet for local entomologists. To rectify the situation, he encouraged his colleagues to form a Society. Seven people met with him at his Macquarie Street residence on 7 April 1862, with the purpose of establishing the *Entomological Society of New South Wales*. It was resolved that William John take the chair, that a Society be formed and that William Sharp Macleay be appointed as Honorary President. He subsequently declined because of his poor health but was prepared to become a member. Fletcher (1929: 217) stated:

> The record of this first Meeting ends with the unpublished statement (from the Minute Book of the Society) that — 'A vote of thanks was unanimously given to Mr. William McLeay for his duties as Chairman, and for having been the originator of the Society.' From this it is evident that William Macleay was behind the enterprise and was the moving spirit. The Rev. R. L. King and Mr. A. W. Scott, on whose co-operation he was relying, were unavoidably absent, as they lived out of Sydney, but he was relying upon their assistance, which was forthcoming at a later stage when wanted.

The Society was instituted for the improvement and diffusion of entomological science. It consisted of Ordinary and Honorary Members and the Honorary Membership was to be conferred only on distinguished naturalists not resident in Australia.

In the resultant *Transactions*, two volumes, each of five parts, were published between 1863 and 1873. There were 37 papers and all but three were about insects and nearly all contained descriptions of new species. Six authors contributed 710 printed pages. Macleay wrote 14 papers with 524 pages (74 per cent of all pages) and King authored 12 papers with 105 pages (15 per cent). So together they accounted for 89% of the content of both volumes.

Volume 1

William John Macleay read his first entomological paper to the *Entomological Society of New South Wales* on 4 August 1862. He stated:

> The following Paper contains descriptions of Twenty hitherto undescribed species of *Coleoptera*, principally selected from a large collection of Insects, which, as I mentioned at the last meeting of this Society, I have lately received from Port Denison. I have not, however, confined myself to Insects from that locality, but have included several species from other parts of Australia, which I believe to be undescribed.

At the previous meeting (7 July 1862), he had introduced George Masters to the members of the Society and indicated that Masters had collected the Port Denison insects. Of the 20 species of tiger beetles and scarabs described in the paper, six (30 per cent) are now synonyms. This percentage of synonymy carried through most of his treatment of insect taxonomy papers of the families I have reviewed.

His next paper (read 1 September 1862) was the description of 20 new species of Buprestidae and 16 species were from Port Denison, apparently collected by George Masters. His third paper newly described 13 species of Carabidae and recorded a further 24 species. This paper showed he had a very reasonable command of the knowledge and literature of this family and he stated:

> I propose in the following Paper to describe all the new species of the family which I have been enabled to procure, and at the same time, for the convenience of the Student, to recapitulate, and give the specific descriptions of all those previously known.

He also described a new genus but it was later placed in synonomy by T. G. Sloane in 1896.

In the *Proceedings* read on 30 January 1863, he gave his first presidential address and stated:

> The advantages which the promoters of the Institution anticipated were of a two-fold character. They wished to give all who were interested in the Science of Entomology opportunities of social intercourse; and they also wished to be the means of assisting in the publication of such Papers connected with the Science as might be deemed worthy of their sanction.
>
> Viewing these as the main objects of the Society, I think I am justified in saying, that it has already been as successful as its most sanguine promoter could have desired.

In his next paper (read on 2 March 1863), also in the *Proceedings*, he described three new species of scarab beetles from Port Denison, north Queensland.

His second presidential address was read on 7 March 1864 and he laid before the Society a brief summary of the earlier history of Australian entomology. His second paper in 1864 contained 17 new species of scarabs and recorded 9 additional species. Once again, this paper shows that he had a good knowledge of the family, possibly based on the fact that Scarabaeidae was the family that William Sharp Macleay had extensively studied. He made an interesting comment on his cousin's Quinary Theory.

> Without attempting to explain the very ingenious system of classification which Mr. MacLeay has the merit of originating, I will merely refer to the "*Horae Entomologicae*" in so far as it may be necessary to show the relative positions of the *Glaphyridae* and *Melolonthidae*.

Two new genera were proposed, one is still valid, the other is now in synonomy.

His third paper in 1864 contained new descriptions of 50 species of beetles. This was the first time that he covered Coleoptera in a broad sense, describing beetles in seven families. All species but one were collected from the Port Denison area by George Masters more than a year earlier. He proposed four new genera in the family Carabidae and two are still valid and two are now in synonomy, one of which was synonymized with a William Sharp Macleay genus by Chaudoir in 1878. This paper also contained his first plate containing four figures of mouthparts of carabid beetles.

In the fourth 1864 paper Macleay showed his continued interest in Carabidae. Some 27 species were newly described from a collection received from Mr E. P. Ramsay, sent by Mr T. G. Waterhouse of South Australia. This paper contained his first key (to the genus *Carenum*) and was written both in Latin and English.

Macleay's first 1865 paper (read 6 June 1864) described a new genus and species (both names are still valid) of a minute apterous carabid. He and George Masters collected five specimens a few weeks before near Wollongong. This was the first species of blind beetle known from Australia. He named it after his friend W. J. Stephens, the Treasurer of the Society. His roughly drawn second plate included a drawing of the whole insect, mouthparts, fore leg and antenna. This was the last illustration in his insect papers.

The second paper in 1865 contained descriptions of 31 new species of carabids from various localities in Australia with many specimens coming from F. G. Waterhouse, South Australia. It included a new genus, still valid, and had a revised key to *Carenum* with a complete catalogue of Australian Scaritidae (now = Scaritinae, Carabidae).

His next 1865 paper (read 7 August 1865) was by far his longest (100 pages) to this time and completely switched from his beloved carabids to weevils Amycteridae (now = Amycterinae, Curculionidae). He described 135 new species and recorded another 40. It is surprising that he would have worked on such a difficult group, considering his friend F. P. Pascoe, London, was studying this family extensively. But he relied extensively on William Sharp's collection and stated:

> I am aware that in undertaking the task of describing and rearranging this large sub-family, I labour under the disadvantage of being unable to refer to and in some cases to identify, the

> many species described by Schönherr and Boisduval, a disadvantage difficult to overcome in the case of the last named author, as most of his descriptions are utterly useless for the identification of the species.
>
> On the other hand, I may lay claim to advantages superior to those of any other person, in the possession of the magnificent collection of the late W. Sharp MacLeay, Esq., which contains nearly 200 species allied to *Amycterus*.

This was the first time that William Macleay offered an opinion on the ability of a fellow insect taxonomist.

His next three efforts were notes published in the *Proceedings*. The first (read 2 October 1865) was a subjoined list of Lepidoptera from Cape York, presented to the Australian Museum by Mr Moore of H.M.S. *Salamander*, and which had been exhibited by Mr Gerard Krefft at a previous meeting of the Society. The list contained 24 species of butterflies and moths of which seven were newly described by Macleay. In a note directly following this one, he described two new species of carabids, both of which are still valid. In the third of these notes (read on 4 June 1866), Macleay exhibited four species of butterflies and moths from a Port Denison collection sent to him by Mr E. Dämel. He also exhibited and described four new species of carabids; only one of these is now in synonomy.

The last paper he published in the first volume of the *Transactions* was a continuation of his previous Amycteridae paper. The 29 new species were based on collections made at Port Lincoln and King George Sound by George Masters.

Volume 2

There was a three year break between the last part of volume 1 and the first part of volume 2. Macleay described 20 new carabid species in the seventh paper in volume two; he also took two colleagues to task for their apparent misinterpretations of genera and species in this family.

The next two papers he published were a radical departure from previous efforts because a broad spectrum of families were covered. These are the two very large papers of the insects from Gayndah (Queensland), based on material collected by George Masters. In the first of these papers he stated:

> I have always hitherto in describing new genera and species, adopted the system most usual with English Entomologists of giving these descriptions in Latin. On this occasion I intend to depart from that rule, as I believe that many of those who take an interest in Australian Entomology, will infinitely prefer the descriptions given in plain and intelligible English.

This departure from the usual species description format must have been a significant contribution to entomology, especially amateurs. In these two papers, he recorded 697 species and newly described 554 of them in 49 families. It is quite surprising that he described 20 new species in Anthicidae, Pselaphidae and Scydmaenidae because his good friend, Reverend R. L. King from Parramatta, was actively describing species in these families of very small beetles.

In the last paper in the *Transactions*, entitled *Miscellanea Entomologica*, Macleay newly described 81 beetles in 4 familes and one ant. The paper was appropriately titled because it represented a mixture of disassociated notes. But it contained more biological and collection information than any of his previous papers. It is interesting that he reverted to the English style of describing species, including a Latin description before the English description. Perhaps he felt the inclusion of Latin descriptions for his two Gayndah papers published previously was too daunting a task. But this was the last insect paper in which he included Latin descriptions.

THE LINNEAN SOCIETY OF NEW SOUTH WALES

William Macleay was a founder of this Society, established in 1874 for 'the cultivation and study of the science of Natural History in all its branches.' (Walkom, 1925). It was during this year that Macleay decided to retire from active politics, enlarge his collections to all branches of natural history and hired George Masters as his curator. The establishment of the *Proceedings* in 1877 created a venue for his interests other than insects. But he did publish 18 insect papers (307 printed pages) between 1881 and 1888.

Macleay's first Australian insect paper in *Proceedings of the Linnean Society of New South Wales* was published in 1878; five years had elapsed since his last insect paper in the defunct *Entomological Society of New South Wales*. He described four species of carabids, returning to his favourite family of beetles. He stated:

> . . . I received from Mr Spalding a large and valuable collection of Mammals, Birds, Reptiles, Fishes, Mollusks, Crustacea, Insects, and other animals, both terrestrial and marine, from Port Darwin . . .
>
> I propose to undertake, on my own part, an account of the Fishes, Lizards, and Snakes, but want of time makes me limit myself in the present Paper to a short notice of the Coleoptera in the collection belonging to the Family *Carabidae*. I select this Family, not only because it is to me the most interesting, . . .

This verifies his interest in carabids and is a published reference to his interests in vertebrates. I believe these interests took him away from his intensive study of insects for the rest of his life.

His next two papers were interesting deviations from his usual style of solely describing insects. Though a new species of leaf-feeding stick insect was described in the first paper, he also provided an extensive discussion on the biology of this stick insect family. In addition he gave a potential method for control of these possible pests — the first time that he had entered the arena of economic entomology:

> If it should be found that the ravages of this or any other species of the *Phasmatidae* are the causes of the wide-spread destruction of trees now going on in many parts of the colony, it will, I think, be a simple matter to limit, where the timber is of sufficient value, the extent of the injury by clearing a wide belt round infested areas.

Even at that early date, defoliation of timber-trees was of concern. The new stick insect was found in amazing numbers near the Binda Caves by C. S. Wilkinson, Government Geologist. The trees for miles around were completely denuded of leaves, and dead and dying insects were lying beneath the trees in heaps.

The second of these 'economically-oriented' papers concerned the havoc wreaked on grape-vines by a weevil. The larvae of this beetle caused extensive damage to the young wood of the vines, but also ate into the old wood and roots. He offered a practical means of control that is still used today:

> There can, I should say, be very little difficulty under such circumstances, in keeping down the number of these insects, a little care in the pruning season in cutting out all the infected branches, and the immediate burning of them, would almost ensure the complete destruction of the pest, if their ravages were confined to the Grape Vine, but as I mentioned before, there may be other plants or trees liable to their attack, and to ascertain what these are, must necessarily accompany any effort to clear an orchard of the insects.

All but one of the remaining Macleay papers in the *Proceedings* reverted to his traditional style of describing species. His 1883 paper described some species of Coleoptera in the Brisbane Museum, sent to him by Mr De Vis. There was quite a problem associated with this collection (one that I am confronted with even today with the Macleay collections):

> . . . sent me lately some hundreds of species of Coleoptera (which he had picked out of the Museum collection), without name, and in most instances without any indication of locality or even country. He sent them in the hope that I might be able, by reference to my very large collection in that branch of Natural history to furnish him with the names of some of them at least. This, I am glad to say, I shall be enabled to do, to a very considerable extent, but it is a work that demands time, and it will probably be weeks before I shall have got entirely through the collection.

He described only nine species of carabids and four scarab beetles from this collection.

Macleay's three 1885 entomological papers in the *Proceedings* tackled a very difficult group — the stag-horn beetles of the genera *Lamprima* and *Neolamprima* (Lucanidae). In the first paper, he described 7 species, five of which are now synonyms. Even today, these genera remain in taxonomic chaos because of the apparent extreme variability shown in the species. His second paper was more successful; he described one new genus and two new species, all of which are valid today. The third paper created a new genus for one species described earlier in the year. His original description was based on a female but Mr C. French of the Botanical Museum of Melbourne, later sent him a male and a new genus had to be created. The sexes are dimorphic in the stag-horn beetles and the generic classification is generally based on males. Britton (1970) stated that this species, *Phalacrognathus muelleri*, is the most attractive of all Australian Coleoptera.

Macleay's next three papers in the *Proceedings* were all entitled *Miscellanea Entomologica*. The reason for the title of these papers was stated by Macleay:

> It is now within a few months of thirteen years, since I published in the Transactions of the Entomological Society of New South Wales, a paper under the above title. I adopt the same prefix now, because my intention and objects are the same as on that occasion. It was my wish then as now, to describe from time to time such new or little known species of insects as I came across in my collection, and, to render such descriptions more interesting and instructive to the Entomologist, to accompany them with a review or revision of the genus or group to which each species belongs.

But two of these three papers differed markedly from his first 'miscellanea' paper because he discussed all known species in the genera *Diphucephala and Liparetrus* (Melolonthinae: Scarabaeidae). His coverage was thorough and his work would be most acceptable today if keys and illustrations had been included. The third paper in this series reverted back to his favourite carabids. He attempted to better define genera in Scaratinae and stated:

> I have been compelled in my effort to make my revision of the group as distinct and intelligible as it is in my power to make it, to add considerably to the number of genera, so that by my present proposed arrangement the genus *Carenum* of Bonelli, yields material for 14 genera. My definition of these, given below, is short and not very definite, but that I find unavoidable, as there are very few marked distinguishing features in the group, and even these run into one another in the most puzzling manner.

He listed species included in each genus but provided no key or illustrations, leaving this group in a much better condition than he found it but still in a confused state.

The next two papers reverted to the style of the Gayndah papers. He described insects in 14 families; they were from Cairns and its neighbourhood (Barron River, Mossman River, Mulgrave River and Russell River) and collected by W. W. Froggatt.

Then followed two *Miscellanea Entomologica* papers on Tenebrionidae. Macleay treated 132 species but only described 41 species. As in his two previous papers on Melolonothinae, he was most careful to survey and summarize the literature of the '*Helaeides*', contributing to a better understanding of part of this large family. I believe these four *Miscellanea Entomologica* papers are the best that he published on Australian insects.

The last four papers published in 1888 were based on several collections sent to him. The first were some of carabids (Scaritinae) brought to him by Mr George Barnard, of Coomooboolaroo, Upper Dawson River. He identified 11 species and described two new species. The last three papers reported on the Froggatt collections:

> Mr. Froggatt, the well-known New Guinea Explorer, left Sydney in March last, in making a collection for the Macleay Museum of the zoological productions of that part of Australia.

In the first of these three papers, no new species were described. It was a summary of zoological specimens collected by Mr Froggatt and how they related to the fauna of the rest of Australia. The last two papers included the descriptions of 108 species in 6 families of beetles. Thus closed the Australian entomological career of William John Macleay.

OTHER JOURNALS

Transactions and Proceedings of the Royal Society of South Australia

In 1885, Macleay published 3 short notes in *Miscellaneous Contributions To The Natural History Of South Australia*, edited by Professor R. Tate. This was a curious mixture of insects: a scarab, a weevil and a stag-horn beetle. Each note is only 3-6 lines long and contains references to their possible economic significance. What prompted him to make these nearly insignificant contributions remains a mystery. There is no known correspondence of Macleay in either the archives of the Royal Society of South Australia or the South Australian Museum to shed light on this question.

Papers and Proceedings of the Royal Society of Tasmania

His 1886 paper in this journal was entitled *Zoology of Australia*. It contained no species descriptions and was a totally different paper from any other that he wrote. He used A. R. Wallace's definition of the Australian Region, 'The Islands of New Holland and Tasmania' as a basis of his review of the known knowledge of most animal groups. His classification of the vertebrates and invertebrates was indeed quaint. He divided these groups into sub-kingdoms. He started with sub-kingdom Vertebrata which included the mammals and marsupials, followed by birds, reptiles, and amphibians. There was a very long review (more than seven pages) on the fishes, which is not surprising since this group was his principle interest at the time.

The sub-kingdom Mollusca was not treated in depth because he felt:

> There is less, however, in the Mollusca than in any other sub-kingdom of the Animalia of a peculiarly Australian character to be observed, — in fact, except in one or two not very important peculiarities, there is nothing to separate the region from the rest of the world.

His third sub-kingdom, the Arthropoda, included an interesting mixture of groups. The insects were reviewed in depth, particularly Coleoptera. He believed there were 'quite 10,000' species and believed that 'in a few years' time thousands may be added to that estimate'. But by 1970, there were only 19 219 species known from Australia (Britton, 1970: 517). So discovery of additional species did not increase at the rate that Macleay anticipated. The knowledge of the spiders, mites, ticks and millipedes and Crustacea were dispensed with in two short paragraphs. His fourth sub-kingdom, the Vermes and rotifers, were also dealt with summarily.

The introductory remarks given for his fifth sub-kingdom, Echinodermata, are interesting:

> . . . are exclusively Marine Animals, and in a country with an extensive seaboard and a favourable climate like Australia, might be expected to hold a predominating position, and they do so.

Yet for the Mollusca he held the opposite view (quoted above).

His comments for his last sub-kingdom, Protozoa,

> . . . may be passed over: they are much the same everywhere. The Australian representatives of the various classes comprising the Sub-kingdom have never been investigated.

What prompted Macleay to write this review is unclear, but I believe that it was the influence of Reverend Tenison-Woods. The Reverend Tenison-Woods spent the years 1874-1876 in Tasmania. O'Neil (1929) stated '. . . Mr, afterwards Sir William, Macleay — a scientific colleague of Father Woods, who became his devoted friend.' In 1878, Reverend Tenison-Woods joined the *Linnean Society of New South Wales* and the Union

Club at Sydney, remaining a member of this Club until his death in 1889. So there were ample opportunities for these two gentlemen to meet.

WILLIAM JOHN MACLEAY AUSTRALIAN INSECT SPECIES

Macleay described 1360 new species of beetles in 52 families (as known in his day): Carabidae (339 species), Scarabaeidae (274), Curculionidae (164), Tenebrionidae (105), Elateridae (71), Buprestidae (63), Staphylinidae (60) and 29 or fewer species in each of the remaining families. Five of the larger families (Buprestidae, Carabidae, Elateridae, Scarabaeidae and Tenebrionidae) are discussed to give a partial idea of his success as a taxonomist by determining how many of his species are now synonyms. The taxonomic efforts of one of his colleagues, Reverend Thomas Blackburn (1844-1912), are compared to Sir William's to give a very general idea of the accuracy of taxonomic decisions of both entomologists in these five families. Their efforts are summarized in Tables 1 and 2.

The Curculionidae (weevils) is the largest family of organisms (plant or animal) and there are no recent catalogues to bring his species names up to date. The catalogue situation is similar for the very large family Staphylinidae (rove beetles), hence these two families unfortunately cannot be discussed.

Coleoptera

Buprestidae

Commonly known as jewel beetles, there are about 850 species in Australia. Many of the species are brilliantly coloured and are eagerly sought after by collectors world-wide. Large specimens of *Castiarina*, *Temognatha* and *Stigmodera*, particularly from Western Australia, are very popular (Macleay described 14 species from that state). The adults are usually found on flowers, seeking nectar. The larvae of most species feed in recently dead wood, producing characteristic flattened burrows, hence they are sometimes called flat-headed wood boring beetles.

Macleay described 63 species in this family. Of his synonyms (32 per cent of his described species), 18 were described by authors other than Macleay; two species are synonyms of Macleay's previously described species (Barker, 1988; Carter, 1929; Gardner, 1990). Blackburn faired little better — 32 per cent synonyms with four of Macleay's previously described species and three of his own.

Carabidae

There are more than 1700 species of ground beetles described from Australia. They are found under rocks, logs and bark and in leaf litter. Most species are nocturnal and some are attracted to lights. Nearly all predate on other invertebrates and can be very beneficial in controlling pest insects in crops. The larvae are also predacious and occur in soil, under bark or in debris.

Between 1862 and 1888, Macleay described 339 species of Australian carabids. Of his synonyms (36 per cent), 85 were described by authors other than Macleay and 38 species (31 per cent) are synonyms of Macleay's previously described species (Moore *et al.*, 1987). This is a very high number of his own synonyms, considering that he would most likely have had specimens of his previously described species in his collection. He had particular trouble with *Carenum*. Of the 76 species Macleay described in this genus, 33 (43 per cent) are now synonyms. He created seven unnecessary names for *Carenum scaritodes* Westwood, 1843 and seven for *Carenum tinctilatum* (Newman, 1838) alone! He also erected four unnecessary names for one of his own species, *Carenum interruptum* Macleay, 1865. Blackburn newly redescribed ten of Macleay's species and three of his own. There appears to have been little or no exchange of type specimens for study

TABLE 1

Species described in five families of Coleoptera by William John Macleay

	Buprestidae	**Carabidae**	**Elateridae**	**Scarabaeidae**	**Tenebrionidae**
Number of species described	63	339	71	274	105
Number unchanged	18	130	24	133	47
Number transferred to other genera	25	87	35	51	33
Number of synonyms	20	122	12	90	25
Per cent synonyms	32	36	17	33	24

TABLE 2

Species described in five families of Coleoptera by Reverend Thomas Blackburn

	Buprestidae	**Carabidae**	**Elateridae**	**Scarabaeidae**	**Tenebrionidae**
Number of species described	124	165	49	632	211
Number unchanged	33	80	25	442	138
Number transferred to other genera	46	50	20	95	20
Number of synonyms	45	35	4	95	53
Per cent synonyms	36	21	8	15	25

between these two entomologists. I have been unable to find any correspondence between them but it may exist. Macleay's species descriptions were abbreviated and there were few remarks comparing his new species with previously described species. Perhaps this led Blackburn to create so many synonyms of Macleay's species.

Elateridae

The adults of this family have a unique click mechanism which enables them to right themselves if disturbed. Hence they are known as click beetles. There are more than 600 described species of this family in Australia. Adults are phytophagous and may be found on flowers, under bark or on vegetation. Larvae are mostly root feeders but some are carnivorous. Included are the well-known wireworms which are pests of vegetable crops, cereals and grasses.

Macleay described 71 species of click beetles. According to Neboiss (1956), six of his synonyms were previously described by Candèze in his four part *Monographie des Élatérides.* Macleay had these works (his personal copies are now in the rare book section of the Fisher Library). However there are no known exchanges of specimens or correspondence between Macleay and the Belgian entomologist who described many Australian click beetles. Both Blackburn and Macleay had low numbers of synonyms in this family. Blackburn created only one synonym from a Macleay species and none of his own.

Scarabaeidae

These are commonly known as Christmas, dung, or scarab beetles and more than 2200 species have been described from Australia. They have a great diversity of habits; many are on dung, decaying plant material, carrion, and roots. Some live in ant or termite nests and a few feed on fungi. Most feed on grasses, foliage, fruits and flowers and some larvae are serious pests of lawns and agricultural crops.

Macleay described 274 species of scarabs. According to Cassis *et al* (1992) and Houston *et al* (1992), 133 of his species names are unchanged, 51 have been transferred to other genera and 90 are synonyms. These numbers most likely will change when several large genera are revised: *Diphucephala* (22 Macleay species), *Heteronyx* (21 Macleay species), *Liparetrus* (79 Macleay species) and *Onthophagus* (37 Macleay species). Of the synonyms (33 per cent of his described scarabs), 60 were described by other authors (including two by William Sharp Macleay and three by George Masters); 30 species are Macleay's previously described species. This is a very high number of his own synonyms indeed. Blackburn created synonyms for 18 of Macleay's species and 31 of his own!

Tenebrionidae

In this very large world-wide family, commonly known as darkling or stink beetles, there are nearly 1300 species described from Australia. They are particularly well adapted to arid areas and most feed on plant materials of many kinds. A few are common pests of stored grains and their products and can be very destructive. A most interesting group in Australia is the 'pie-dish' beetles, especially *Helea* and *Pterohelaeus*. They are remarkably flattened with a broad flange around the outer margins of the fused elytra. Macleay described 31 species in these two genera.

Altogether, he described 105 species of Tenebrionidae (the family as understood in his day). (Recently Alleculidae and Lagriidae have been included as subfamilies in Tenebrionidae and are not discussed here). According to Carter (1926) and Doyen *et al* (1989) 47 of his species names are unchanged, 33 have been transferred to other genera and 25 are synonyms. These numbers will undoubtedly change when the large number of *Pterohelaeus* are revised (28 Macleay species). Of the synonyms (24 per cent of his described species), 23 were described by authors other than Macleay; two species are synonyms of Macleay's previously described species. Of the 23 previously described species, 11 were described by Pascoe. Macleay and Pascoe (in London) corresponded and exchanged specimens and papers extensively. In fact Macleay established five Pascoe patronyms in Tenebrionidae. It is a wonder that Macleay re-described so many of Pascoe's species. Blackburn redescribed five of Macleay's species and 13 of his own.

Hymenoptera

Surprisingly, Macleay (1873) described one species of ant. It was collected in the spring of 1872 while he and Masters were on an entomological excursion to the Murrumbidgee. They found a new species of a very small beetle (Pselaphidae) which was frequently found in the society of a small red ant. He stated:

> So invariably was the association that whenever on turning over a log we found some of the ants we knew that a search in their passages would certainly lead to the discovery of some of these attendant beetles.
>
> The ant answers very nearly to the genus Ectatomma of F. Smith. It is undescribed, I give it therefore a name and description.

But unfortunately it did not prove to be a new species and Taylor and Brown (1985) synonymized it with *Brachyponera lutea lutea* (Mayr, 1862).

Lepidoptera

In 1866, Macleay published his only paper on skippers, butterflies and moths. He described seven species: Hesperiidae (skippers), 1 species; Lycaenidae (copper and blue butterflies), 1 species; Nymphalidae (brush-footed or four-footed butterflies), 2 species; Noctuidae, Agaristinae (forester moths), 2 species; Sphingidae (hawk moths) 1 species. One species retains its original name, three species are now subspecies, transferred to genera differing from those to which they were originally designated when described and three species are synonyms (T. Weir, pers. comm., 1991).

Phasmatodea

Macleay (1881) described one species of a stick insect, *Podocanthus wilkinsoni.* Vickery (1983) listed it as a valid species and the male lectotype (designated by Key, 1960) is in the Australian National Insect Collection, Canberra.

REFLECTIONS

Macleay published 33 taxonomically oriented papers. He described 1360 species of beetles and the number of synonyms he created was high, especially of species he had previously described. If he had taken more time and care, the synonyms of his species should have been very low, if not absent altogether, because he retained representatives of most of the species he had previously described. A very high number of his species have been transferred to genera other than those to which he first assigned the species. This apparently shows that he did not have a good command of the higher classification of Coleoptera. Though he concentrated on species in seven families (1080 species), he also described species in 45 other familes. Perhaps it would have been better for him not to have been an entomological polyhistor but to have concentrated on one family, particularly Carabidae, his pronounced favourite group. He did describe new genera but many of these were later synonymized. He had no apparent desire to delve into the higher classification of insects as did his cousin William Sharp Macleay. Only three of his taxonomic papers had keys to species or illustrations. This would have severely hampered others who did not have access to his collections.

In comparison with Blackburn's taxonomic works, Macleay faired less well (Tables 1 and 2). But at least Macleay provided a foundation for others to follow. Later entomologists who were influenced by Macleay, such as H. J. Carter and A. M. Lea, were more accurate in their taxonomic decisions. This trend continues today with better techniques available such as the greater use of genitalia to separate species and better microscope techniques. Furthermore, there is now better communication between scientists and regular exchange of type specimens between taxonomists.

It is not common for insect taxonomists to criticize their fellow workers. But Fauvel (1877: 170-171) took Macleay to task for not publishing his descriptions in Latin and commented on his taxonomy (my translation of his French text):

> . . . However, single works published by these authors have the character and importance of a local fauna. Such a one is M^{r} William Mac Leay who published in English in volume II of the *Transactions of the Entomological Society of New South Wales* (read 3 April 1871) with the title: *Notes on a collection of Insects from Gayndah,* a town on the Burnett River, in northern Australia (Queensland). Unfortunately the new species descriptions in this paper, at least for Staphylinidae, are inadequate, obscure and never comparative, and they will come to be synonyms almost without exception when one understands the types to which they apply. The genera are not, however, better treated than the species, and the two the author indicates as new: *Myrmecocephalus* and *Pinobius,* are synonyms of *Falagria* and *Dolicaon.* So what confidence can we give to an author who describes Staphylinidae and does not recognise even one of the genera most characteristic and most common of the family, the *Falagria.* It is sad to have to register this work among the deplorable which seem to date from the 18th century.
>
> Of the few I have been able to examine the types of M^{r} W. Mac Leay, I have given a new description in Latin: but it is not easy to obtain insects from Gayndah and the collection made by M^{r} Masters from this locality are nearly all in Australia. . . .

Fauvel obtained his few Macleay type specimens from 'M^{r} De Castelnau' from Melbourne.

On the brighter side, his four *Miscellanea Entomologica* papers of 1886-1888 are examples of well-written and detailed treatises on the groups covered. In my opinion, they were so good that they would be very acceptable by today's standards if keys and illustrations were provided. Macleay's founding of the *Entomological Society of New South Wales*, his financial and editorial support and his entomological contributions to the journal were of considerable value. His resolve, stated in one of the papers in this journal, not to include Latin descriptions with his new species surely had a beneficial effect on entomologists following in his footsteps (at least in Australia).

Macleay's interest, especially his financial support, in establishing and maintaining the *Linnean Society of New South Wales* was of estimable value. Though most of his written contributions in the *Proceedings* of the Society were non-entomological, he still contributed to the knowledge of Australian insects.

Macleay actively encouraged others to study insects. He seemingly was always available to give advice and support, and his collections were freely available for study. Perhaps these were amongst his most worthy accomplishments because there were several successful entomologists that followed in his footsteps such as Blackburn, Carter and Lea and were influenced by him. In my opinion, he was not a particularly noteworthy insect taxonomist, but in reviewing all of his accomplishments in the entomological field, he was most certainly an entomological lion.

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Host Range, Distribution and Importance of the Fungus *Pyrenophora semeniperda* (Brittlebank & Adam) Shoemaker (Ascomycotina: Pyrenomycetes) in Australia

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A field survey of *Pyrenophora semeniperda* (Brittlebank & Adam) Shoemaker, undertaken throughout southern Australia from 1984 to 1986, confirmed its widespread and common occurrence and provided additional information on the host range, geographic distribution and economic importance. The fungus was isolated from 12 of the 26 previously known host genera and an additional seven new genera, all in the family Poaceae. The survey extended the known geographic range of the organism northward and eastward in Western Australia besides adding many new location records within the known range in south-eastern Australia. In New South Wales, the fungus was found only south of Lat. 32°S. Some implications of its wide host range and geographic distribution are discussed together with factors which indicate that the fungus is of negligible economic importance on winter cereals, particularly wheat, either as a leaf spotting or seedling blight organism or as a seed pathogen.

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INTRODUCTION

Pyrenophora semeniperda (Brittlebank & Adam) Shoemaker, the teleomorph of *Drechslera campanulata* (Lév.) Sutton (see Sivanesan, 1987 for synonymy) was described originally as *Angiopoma campanulatum* Lév., from seed of *Bromus sterilis* L. collected at Versailles, France (Léveillé, 1841). Brittlebank and Adam (1924) gave a detailed description of the fungus and of early Australian records, noting that it had been isolated from *Bromus sterilis* in 1899, from wheat in 1913 and that the anamorph had been found on seed of *Avena fatua* L. collected at Ardmona in 1898. Since 1924 the fungus has been recorded throughout southern regions of the continent on a wide range of grasses, including wheat, oats, rye and barley, and some dicotyledonous species (Butler, 1961; Smith, 1965; Walker, 1967; Khan *et al.*, 1968; Shivas, 1989). The fungus also occurs in North America, New Zealand, South Africa and has been recorded once from Europe, as detailed in an annotated checklist of its worldwide host range compiled by Medd (1992).

The fungus is known as a seed pathogen (O'Gara, 1915; Wallace, 1959; Shoemaker, 1966), and has been implicated in seedling blight of a range of grasses including the winter cereals. In addition it has been associated with leaf spotting (Drechsler, 1923; Carne, 1927; Smith, 1965) and leaf stripe symptoms (Carne, 1927) on several grasses.

This paper reports the findings of a survey in Australia undertaken to provide an updated account of the host range and geographic distribution of the disease, and discusses its economic significance.

MATERIALS AND METHODS

Between 1984 and 1986 areas throughout most wheat growing regions in southern Australia were surveyed during late winter and spring for the disease. The survey extended throughout Western Australia (W.A.), South Australia (S.A.), Victoria (Vic.) and New South Wales (N.S.W.), but did not include Tasmania (Tas.) or Queensland (Qld.) since the disease has not been recorded in those states (Sampson, 1989 pers. comm.; Alcorn, 1983 pers. comm.). Grass plants on roadsides and in adjacent crops displaying leaf spot lesions were collected, dried in plant presses and recorded along with physiographical data for the location. Seed or litter material was not generally collected, although some isolates emanated from submissions of such material to our laboratory. Dicotyledonous species were not surveyed.

Host specimens were identified, where necessary, by the National Herbarium of N.S.W. and are held at our laboratory. A number of immature plant specimens lacking reproductive structures remain unidentified.

Leaf spot lesions caused by *P. semeniperda* are non-specific so the fungus must be identified by isolation. Senescent or green leaves (when available) were surface sterilized by immersing for about 5 seconds in a 1% solution of sodium hypochlorite and then washed for approx. two minutes in sterile distilled water. The fungus was isolated by placing sections containing lesions onto the surface of potato dextrose agar (PDA) in petri dishes and incubated at 20°C under fluorescent light. Isolations were purified by subculturing onto fresh plates of PDA, incubated as above, identified and maintained on slopes in screw-capped bottles under refrigeration. A selection of *P. semeniperda* isolates has been lodged as dried cultures with the NSW Agriculture Plant Pathology Branch Herbarium (DAR), Rydalmere. Details of collections, which have been recorded in a computer data base, are outlined in the Appendix.

RESULTS AND DISCUSSION

Host Range

P. semeniperda has a wide host range in Australia, having previously been recorded on 24 grass genera (Table 1). The incidence on twenty of these genera is thus far confined to Australia, and it is known to occur on *Avena*, *Bromus*, *Danthonia* and *Triticum* in other countries as well as Australia. In addition, it has been recorded on *Agropyron* and *Trisetum* in North America and on the dicotyledonous genera *Daucus*, *Goodenia*, *Hedypnois* and *Hypochoeris* in Australia (Smith, 1965) and *Tragopogon* in N. America (Cooke and Shaw, 1952).

The field survey of 635 grass samples collected throughout W.A., S.A., Vic. and N.S.W. yielded 176 isolates of *P. semeniperda*, ranging over 19 genera in all five sub-families of Poaceae plus seven isolates from unidentified hosts (Table 1). Isolations spanned 12 of the 26 grass genera known to be hosts prior to this survey, and an additional seven new genera, *Brachypodium*, *Chloris*, *Cynodon*, *Cynosurus*, *Dichelachne*, *Panicum* and *Paspalum*. One of the specimens, isolated from *Agropyron*, represented the first Australian record for that genus.

Host grasses encompassed a number of summer growing perennials and many natives. The most frequently encountered hosts, however, were exotic winter annual species within the sub-family Pooideae, which includes the winter cereals. This result is biased because the survey concentrated on crops and their associated flora. Consequently, higher incidence on particular genera cannot be construed as an indication of preferred hosts. However, there tended to be agreement between the frequency of isolations made from *Avena*, *Bromus*, *Danthonia*, *Hordeum*, *Lolium*, *Phalaris* and *Triticum* in the survey, and its previous incidence on those hosts. The fungus had continental distribution on most host genera examined, but was only isolated from plants of *Danthonia* collected from south-eastern regions (Table 1, Fig. 1).

In the field there were circumstantial indications that host specific adaptations occurred within the fungus, and in some instances these appeared to be absolute. For example, healthy susceptible hosts often coexisted within infected crops; in another instance, unaffected wheat plants grew adjacent to a heavily infected rogue barley plant. Also, crops often remained uninfected despite being adjacent to a mix of infected annual grasses. Variation in the extent of the disease even existed among cohabiting species encountered on the margin of infected crops. Whilst these observations indicated that pathogenic variation in the fungus may occur, more detailed host range studies with a selection of isolates is needed before this can be demonstrated.

Geographic Distribution

This survey, which concentrated on wheat growing areas, confirmed the widespread distribution of the fungus in all major temperate cropping regions throughout mainland Australia except northern N.S.W. and Qld. (Fig. 1). Some of the new and existing records from coastal and arid regions show, however, that the organism is not confined to the wheat belt. In W.A., the known range of the fungus was extended northward and eastward of previous records. The survey also verified the widespread occurrence of the fungus in S.A., where it was reputedly common but where few validated records existed. Within Vic. and N.S.W., additional records from the survey coincided with the known range of the fungus.

The fungus was not isolated from any of the 143 leaf spotted plant samples collected north of Dubbo/Narromine (Lat. approx. 32°S.) in the eastern wheat belt (Fig. 1), indicating a possible limit to its distribution. This proposition is supported by previous accession records; these reveal that the fungus has only once been recorded from just north of that zone — from near Quirindi, on *Festuca arundinacea* Schreb. In contrast to these findings, Murray and Brown (1987) subjectively assessed that *P. semeniperda* occurs in localized areas on wheat in most seasons in northern N.S.W. Considering that only one record from the southern part of the region exists and that no specimens resulted from the present survey, Murray and Brown's report must be questioned.

Given that the fungus is common throughout the southern wheat belt, it is highly unlikely for inoculum not to have been spread north of the purported boundary. Host availability is likewise unlikely to be limiting distribution since there is considerable overlap in the range of known host species across these regions. Furthermore, delimitation of the fungus cannot be attributed to simple climatic variables. For instance, the organism occurs over a wide range of rainfall zones, from cool temperate regions e.g. Orange, N.S.W. with around 1000 mm annual rainfall to semi-arid regions such as Wilpena, S.A. and Kalgoorlie, W.A. with an annual rainfall of 378 mm and 250 mm respectively. Any suggestion of the north-eastern boundary being defined by day length can probably also be discounted since the organism occurs at more northerly latitudes (Lat. 27°42′S) in the west of the continent. However, the distribution depicted in Fig. 1 does coincide closely with that of the predominately winter-spring rainfall or Mediterranean-type climatic zone (Dell *et al.*, 1986). The north-eastern boundary falls roughly west of the < 350 mm winter, and east of the > 300 mm summer rainfall isohyets calculated by Nix (1975). Temperature, like absolute rainfall or seasonal rainfall patterns, is by itself unlikely to determine distribution; but all three factors probably combine to subtly influence seasonal dew periods, or the synchronization of fungal and plant life cycles critical for complete disease development.

The dichotomy in distribution between northern and southern N.S.W. is not unique to *P. semeniperda*, or indeed to fungi. *Mycosphaerella graminicola* (Fuckel) Schroeter, and *Leptosphaeria nodorum* Muller, for example, are important wheat diseases of southern Australia that are uncommon in the north-eastern wheat belt, whereas it is the reverse for the nematode *Pratylenchus thornei* Sher & Allen (Murray and Brown, 1987).

TABLE 1

Incidence of Pyrenophora semeniperda *on members of Poaceae surveyed in Australia along with all previous records, organized by sub-families and tribes (Wheeler* et al., *1982)*

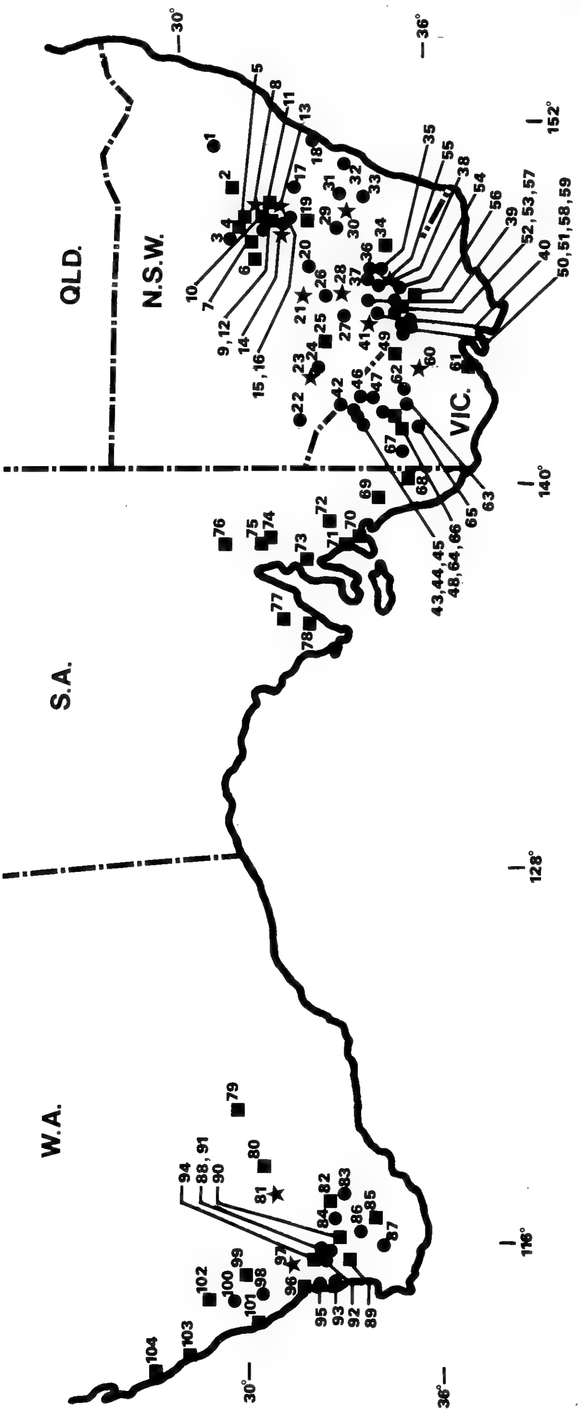
SUB-FAMILY	TRIBE	[1]GENERA	FREQUENCY		PREVIOUS RECORDS		LOCATIONS
			Sampled	Isolated	Australia	Elsewhere	(See Fig. 1)
Panicoideae							
	Paniceae	*Echinochloa*	0	0	1	0	Vic.
	”	*Paspalum*	7	1	0	0	41
	”	*Panicum*	2	1	0	0	64
Eragrostoideae							
	Chlorideae	*Chloris*	4	2	0	0	28, 94
	”	*Cynodon*	7	1	0	0	60
	Sporoboleae	*Astrebla*	0	0	1	0	Vic
Arundinoideae							
	Arundineae	[2]*Cortaderia*	0	0	2	0	18
	”	*Danthonia*	24	11	6	7	19, 22, 27, 28, 30, 49, 55, 60, 61, 64, Vic.
Pooideae							
	Agrosteae	*Deyeuxia*	0	0	1	0	Vic.
	”	*Dichelachne*	1	1	0	0	34
		Polypogon	1	0	1	0	91
	Poeae	[2]*Cynosurus*	2	1	0	0	55
	”	[2]*Dactylis*	0	0	2	0	17, 37
	”	[2]*Festuca*	0	0	1	0	1
	”	[2]*Lolium*	73	32	6	0	5, 6, 11, 12, 13, 28, 36, 49, 55, 60, 64, 68, 69, 71, 72, 74, 75, 76, 77, 78, 80, 81, 82, 92, 93, 94, 97, 99, 100, 103, Vic.
	”	[2]*Vulpia*	7	2	3	0	12, 21, 27, 38, 72
	Aveneae	[2]*Aira*	0	0	1	0	Vic.
	”	[2]*Avena*	132	19	11	1	4, 5, 8, 9, 10, 11, 14, 20, 24, 31, 50, 64, 68, 69, 72, 77, 78, 81, 82, 84, 86, 91, 92, 99, 103, S.A., Vic., W.A.
	”	[2]*Koeleria*	0	0	2	0	Vic.
	”	*Trisetum*	0	0	0	1	
	Phalarideae	[2]*Anthoxanthum*	6	0	1	0	Vic.
	”	[2]*Phalaris*	11	4	7	0	34, 35, 37, 56, 59, 64, 81, 98

TABLE 1 (continued)

SUB-FAMILY	TRIBE	[1]GENERA	FREQUENCY		PREVIOUS RECORDS		LOCATIONS
			Sampled	Isolated	Australia	Elsewhere	(See Fig. 1)
Pooideae (continued)	Triticeae	*Agropyron*	2	1	0	1	34
	"	[2]*Brachypodium*	2	1	0	0	73
	"	[2]*Briza*	4	2	4	0	15, 30, 55, 56, 88, Vic.
	"	*Bromus*	82	29	18	9	3, 5, 15, 16, 21, 23, 25, 27, 32, 36, 38, 50, 55, 56, 59, 64, 68, 71, 72, 75, 76, 77, 78, 81, 82, 90, 91, 100, 101, 104, S.A., Vic.
	Triticeae	[2]*Hordeum*	73	39	18	0	5, 6, 11, 12, 14, 21, 25, 27, 28, 30, 41, 49, 59, 60, 64, 66, 68, 69, 70, 71, 72, 77, 78, 79, 80, 81, 82, 83, 85, 89, 91, 92, 94, 97, 99, 102, 103, 104, S.A., Vic.
	"	[2]*Secale*	0	0	2	0	38, W.A.
	"	[2]*Triticum*	54	23	48	3	4, 5, 6, 7, 8, 12, 13, 14, 15, 16, 18, 21, 26, 28, 30, 33, 36, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 51, 52, 53, 54, 55, 57, 58, 59, 60, 62, 63, 64, 65, 67, 69, 72, 77, 78, 80, 81, 82, 87, 96, 97, Vic., W.A.
Bambusoideae							
	Ehrharteae	[2]*Ehrharta*	6	4	1	0	69, 90, 95, 100, 104
	"	*Microlaena*	0	0	1	0	Vic.
	Stipeae	*Stipa*	14	2	1	0	27, 30, 56
	Oryzeae	*Oryza*	0	0	1	0	26
Unclassified	—	—	89	7	—	—	2, 5, 29, 30, 59, 61, 82

[1] Other genera collected in the survey yielding negative results were: *Agrostis* (5), *Amphibromus* (1), *Dicanthium* (2), *Enteropogon* (1), *Holcus* (16), *Poa* (2), *Setaria* (1) and *Themeda* (1). Numbers of samples collected in parentheses.

[2] Genera which are entirely exotic to Australia.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Why the fungus has not been recorded from Tasmania is perplexing. Failure to observe the fungus is an unlikely possibility since it produces conspicuous stroma when present in germinating seed. Geographic isolation from a source of inoculum is a further unlikely explanation given that there are no quarantine restrictions on the importation of seed or other plant matter contaminated with the fungus. Climatic factors are also unlikely to be limiting its occurrence. Being at more southerly latitudes, the island's temperate climate differs, but not too dissimilarly, from parts of the mainland and is akin to areas of New Zealand where the fungus occurs (Sheridan, 1977; Hampton and Matthews, 1978).

Economic Significance

No serious losses from the fungus have been reported in Australia from any of the types of damage it may cause. The various manifestations of the fungus could cause either poor crop establishment, through effects on germination or seedling vigour, or reduce grain yields through damage to leaves.

The first reports of *P. semeniperda* causing a problem involved destruction of seeds along with seedling blight of wheat in North America and Australia (O'Gara, 1915; Brittlebank and Adam, 1924). This was of particular importance at that time since

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Fig. 1. Locations (numbered in the key below) from where *Pyrenophora semeniperda* had previously been recorded (•), was newly recorded in this survey (■) or had previously been recorded with additional records from this survey (*).

1. Quirindi
2. Dunedoo
3. Trangie
4. Narromine
5. Dubbo
6. Condobolin
7. Trundle
8. Wellington
9. Parkes
10. Cumnock
11. Molong
12. Manildra
13. Orange
14. Forbes
15. Murga
16. Canowindra
17. Bathurst
18. Sydney-Dural, Kenthurst
19. Cowra
20. West Wyalong
21. Weethalle
22. Pooncarie
23. Oxley
24. Maude
25. Hay
26. Leeton
27. Coleambally
28. Narrandera
29. Binalong
30. Yass
31. Gurrundah
32. Kangaroo Valley
33. Bungendore
34. Tumbarumba
35. Holbrook
36. Cookardinia
37. Culcairn
38. Walla Walla
39. Oaklands
40. Berrigan
41. Finley
42. Manangatang
43. Sea Lake
44. Banyan
45. Hopetoun
46. Quambatook
47. Glenloth
48. Corack
49. Echuca
50. Ardmona
51. Pine Lodge
52. Tungamah
53. Esmond
54. Rutherglen
55. Albury
56. Milawa
57. Cosgrove
58. Goomalibee
59. Shepparton
60. Bendigo
61. Geelong
62. Inglewood
63. Bears Lagoon
64. Donald
65. Horsham
66. Dimboola
67. Winiam
68. Bordertown
69. Coonalpyn
70. Strathalbyn
71. Adelaide-Glen Osmond
72. Angaston
73. Crystal Brook
74. Peterborough
75. Orroroo
76. Wilpena
77. Kimba
78. Cleve
79. Kalgoorlie
80. Southern Cross
81. Merredin
82. Corrigin
83. Kulin
84. Bullaring
85. Katanning
86. Wagin
87. Muradup
88. Dale
89. Boddington
90. Brookton
91. Beverley
92. Avondale
93. Serpentine
94. York
95. Perth-Carlisle
96. Muchea
97. Goomalling
98. Moora
99. Caron
100. Cervantes
101. Three Springs
102. Morawa
103. Northampton
104. Kalbarri

continuous cropping relied on the voluntary re-establishment of wheat. The seed rot problem apparently persisted in N. America, albeit rarely, at least until the late 1940's, presumably because the fungus was unaffected by organic mercury seed dressing (Wallace, 1959).

There are indications that the incidence of the fungus as a seed borne pathogen may be related to localized seasonal influences. For example, Shipton and Chambers (1966) found infestations as high as 36% among 277 samples from wheat grain silos in W.A.; the state average being approx. 3%. In contrast a survey of N.S.W. wheat grain by Shaw and Valder (1952) found little evidence of the fungus. A later study by Murray and Kuiper (1988) reported 2 to 4% incidence in weather-damaged wheat seed from southern N.S.W., although in this case its incidence may have been affected by the application of fungicidal dressings. It is unclear, however, if seed infection can be controlled with fungicides. Khan and Young (1989), for instance, found no difference between seedling emergence of untreated barley seed and that treated with a range of fungicidal dressings at a contaminated site in W.A. Damage due to seedling blight, which may likewise be suppressed by seed dressings, also appears to be of little importance. For example, plant pathogens were not implicated in the retarded early growth of wheat plants studied over several seasons in southern N.S.W. (Cornish and Lymbery, 1987), where the fungus is common. The lack of concern from industry with regard to crop establishment is a further indication that seed borne diseases, in general, cause insignificant problems in most years. However, susceptibility of the fungus to fungicidal dressings needs to be clarified to ensure that routine seed treatment practices provide adequate protection.

Farmers in southern N.S.W., Vic. and S.A. occasionally report leaf mottling of crops during early growth stages. Notwithstanding that such outbreaks have been attributed to leaf spot symptoms of *P. semeniperda*, the smallness and sparseness of lesions mostly cause insufficient leaf damage to affect later growth and grain yield (Brown, 1975; Murray and Brown, 1987; Khan, 1988; Brennan and Murray, 1989). This apparent status of the fungus as a foliar disease accords with the conclusion reached by Drechsler (1923), the first to describe leaf spots, who remarked 'The possible damage resulting to the host from the leaf spots would appear quite insignificant'.

Although the fungus currently has limited apparent importance, this may not be the case if more virulent forms appear and spread as a result of the possible host specific adaptations mentioned earlier. Given the lack of quarantine restrictions, it is also possible for more potent material to be imported. Furthermore, the fungus could become more prevalent as a result of recent changes in the cultural practices used in crop production. Burning of stubble is now discouraged and there has been a substitution of herbicides for tillage as a method of managing vegetation during fallowing. With the retention of stubble and other vegetative matter providing a more abundant source of inoculum, the fungus could proliferate. This has already occurred with other foliar (Rees, 1987) and root diseases (Rovira, 1987) of winter cereals.

CONCLUSION

On the basis of existing records and those of this survey, it is evident that *P. semeniperda* is a common and widespread fungus which infects a diverse range of grasses existing throughout southern Australia. It was frequently isolated from leaf spot lesions on many exotic winter annual species including winter cereal crops in the sub-family Pooideae. The fungus was not detected in northern N.S.W., and it is argued that its range in eastern Australia might be restricted by a combination of climatic factors and not by geographic isolation from inoculum or host species. Despite its apparent ubiquity throughout the wheat belt, there is little indication that the fungus is of more than minor economic importance as a seed pathogen, seedling blight or leaf spotting disease of wheat. Should the disease become more important due to a change in its virulence or levels of inoculum it is more likely to impact as a seed/seedling blight pathogen than as a leaf disease. For this reason it is desirable to establish how susceptible the fungus is to fungicides used for dressing seeds.

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APPENDIX

Material obtained during the field survey of Pyrenophora semeniperda

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List of Specimens

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[1]580469 ([2]DAR 64984), *Agropyron scabrum* var. *scabrum*, Tumbarumba NSW, 29/11/84, K. Jones; 580124, *Avena barbata*, Angaston SA, 8/11/84, R. Medd & A. Nikandrow; 580151, Bordertown SA, 9/11/84, R. Medd & A. Nikandrow; 580111, Cleve SA, 7/11/84, R. Medd & A. Nikandrow; 580143 & 580149 (DAR 62310), Coonalpyn SA, 9/11/84, R. Medd & A. Nikandrow; 580100 (DAR 62332) & 580101, Kimba SA, 7/11/84, R. Medd & A. Nikandrow; 580553, Caron WA, 19/8/86, R. Medd; 580531, Corrigin WA, 15/8/86, R. Medd; 580547, Northampton WA, 20/8/86, R. Medd; 580064 (DAR 62291), *Avena fatua*, Dubbo NSW, 17/10/84, K. Jones; 580516 (DAR 62302), Wellington NSW, 19/10/84, R. Medd; 580167, Donald SA, 9/11/84, R. Medd & A. Nikandrow; 580043, *Avena sativa*, Cumnock NSW, 17/10/84, K. Jones; 580148, Coonalpyn SA, 9/11/84, R. Medd & A. Nikandrow; 580567, Merredin WA, 19/8/86, R. Medd; 580421, *Avena* sp., Narromine NSW, 6/9/85, K. Jones; 580556, Caron WA, 19/8/86, R. Medd; 580119, *Brachypodium distachyon*, Crystal Brook SA, 7/11/84, R. Medd & A. Nikandrow; 580490 (DAR 64987), *Briza maxima*, Yass NSW, 30/11/84, K. Jones; 580448, Milawa Vic., 29/11/84, K. Jones; 580012, ex seed *Bromus arenarius*, Oxley NSW, 30/8/83, B. Semple; 580047, 580050 (DAR 62292) & 580068 (DAR 64978), *Bromus diandrus*, Dubbo NSW, 17/10/84, K. Jones; 580130, Adelaide SA, 8/11/84, R. Medd & A. Nikandrow; 580122, Angaston SA, 8/11/84, R. Medd & A. Nikandrow; 580112, Cleve SA, 7/11/84, R. Medd & A. Nikandrow; 580097, Kimba SA, 7/11/84, R. Medd & A. Nikandrow; 580087 (DAR 58948), Orroroo SA, 6/11/84, R. Medd & A. Nikandrow; 580088 (DAR 62304) & 580092, Wilpena SA, 6/11/84, R. Medd & A. Nikandrow; 580156, Bordertown Vic., 9/11/84, R. Medd & A. Nikandrow; 580163, Donald Vic., 9/11/84, R. Medd & A. Nikandrow; 580447, Milawa Vic., 29/11/84, K. Jones; 580211 & 580212 (DAR 62336), Shepparton Vic., 26/11/84, K. Jones; 580450, *Bromus hordeaceus* ssp. *hordeaceus*, Milawa Vic., 29/11/84, K. Jones; 580132, *Bromus hordeaceus* ssp. *molliformis*, Adelaide SA, 8/11/84, R. Medd & A. Nikandrow; 580127, Angaston SA, 8/11/84, R. Medd & A. Nikandrow; 580222 (DAR 62293), Shepparton Vic., 26/11/84, K. Jones; 580011, *Bromus rubens*, Hay NSW, 20/8/83, B. Semple; 580585, *Bromus* sp., Cervantes WA, 22/8/86, R. Medd; 580527 (DAR 62338) & 580538, Corrigin WA, 15/8/86, R. Medd; 580574, Merredin WA, 19/8/86, R. Medd; 580575, *Bromus sterilis*, Kalbarri WA, 21/8/86, R. Medd; 580048 (DAR 64977), *Bromus catharticus*, Dubbo NSW, 17/10/84, K. Jones; 580083, Orroroo SA, 6/11/84, R. Medd & A. Nikandrow; 580215, Shepparton Vic., 26/11/84, K. Jones; 580189 (DAR 62334), *Chloris acicularis*, Narrandera NSW, 10/11/84, R. Medd & A. Nikandrow; 580520, *Chloris truncata*, York WA, 15/8/86, R. Medd; 580246, *Cynodon dactylon*, Bendigo Vic., 27/11/84, K. Jones; 580207, *Cynosurus echinatus*, Shepparton Vic., 26/11/84, K. Jones; 580188 (DAR 64983), *Danthonia caespitosa*, Narrandera NSW, 10/11/84, R. Medd & A. Nikandrow; 580165, Donald Vic., 9/11/84, R. Medd & A. Nikandrow; 580172 (DAR 62313) & 580173 (DAR

64979), Echuca Vic., 10/11/84, R. Medd & A. Nikandrow; 580280, Geelong Vic., 27/11/84, K. Jones; 580242 & 580260, *Danthonia duttoniana*, Bendigo Vic., 27/11/84, K. Jones; 580205 (DAR 62328) & 580208, *Danthonia linkii*, Albury NSW, 26/11/84, K. Jones; 580502, Cowra NSW, 30/11/84, K. Jones; 580491 (DAR 64988), Yass NSW, 30/11/84, K. Jones; 580474 (DAR 64985), *Dichelachne micrantha*, Tumbarumba NSW, 29/11/84, K. Jones; 580150, *Ehrharta calycina*, Coonalpyn SA, 9/11/84, R. Medd & A. Nikandrow; 580526, Brookton WA, 15/8/86, R. Medd; 580582, *Ehrharta longiflora*, Cervantes WA, 22/8/86, R. Medd; 580577, Kalbarri WA, 21/8/86, R. Medd; 580554, *Hordeum glaucum*, Caron WA, 19/8/86, R. Medd; 580540, Kalgoorlie WA, 18/8/86, R. Medd; 580598, Katanning WA, 4/9/86, R. Medd; 580552, Morawa WA, 19/8/86, R.Medd; 580544 (DAR 62339), Southern Cross WA, 18/8/86, R. Medd; 580601, York WA, 4/9/86, R. Medd; 580193 (DAR 58952), *Hordeum hystrix*, Narrandera NSW, 10/11/84, R. Medd & A. Nikandrow; 580254, Bendigo Vic., 27/11/84, K. Jones; 580174 (DAR 64980), Echuca Vic., 10/11/84, R. Medd & A. Nikandrow; 580218 & 580231, Shepparton Vic., 27/11/84, K. Jones; 580017 (DAR 65002), *Hordeum leporinum*, Condobolin NSW, 19/9/84, A. Nikandrow & N. Fettell; 580052, Dubbo NSW, 17/10/84, K. Jones; 580180 (DAR 62306), Finley NSW, 10/11/84, R. Medd & A. Nikandrow; 580013 (DAR 64973), Hay NSW, 18/6/83, B. Semple; 580022 (DAR 64975), Manildra NSW, 5/10/84, R. Medd & A. Nikandrow; 580036 (DAR 64976), Molong NSW, 5/10/84, R. Medd & A. Nikandrow; 580496, Yass NSW, 30/11/84, K. Jones; 580133, Adelaide SA, 8/11/84, R. Medd & A. Nikandrow; 580128, Angaston SA, 8/11/84, R. Medd & A. Nikandrow; 580110, Cleve SA, 7/11/84, R. Medd & A. Nikandrow; 580142, Coonalpyn SA, 9/11/84, R. Medd & A. Nikandrow; 580099 (DAR 62314), Kimba SA, 7/11/84, R. Medd & A. Nikandrow; 580158, Dimboola Vic., 9/11/84, R. Medd & A. Nikandrow; 580161 (DAR 62307), Donald Vic., 9/11/84, R. Medd & A. Nikandrow; 580576, Kalbarri WA, 21/8/86, R. Medd; 580566 (DAR 62312), Merredin WA, 19/8/86, R. Medd; 580549, Northampton WA, 20/8/86, R. Medd; 580533, *Hordeum* sp., Corrigin WA, 15/8/86, R. Medd; 580565, Merredin WA, 19/8/86, R. Medd; 580155 (DAR 62308), *Hordeum vulgare*, Bordertown SA, 9/11/84, R. Medd & A. Nikandrow; 580104 & 580106, Kimba SA, 7/11/84, R. Medd & A. Nikandrow; 580139, Strathalbyn SA, 9/11/84, R. Medd & A. Nikandrow; 580170 & 580171, Donald Vic., 9/11/84, R. Medd & A. Nikandrow; 580006, Boddington WA, 23/9/83, Unknown collector; 580536, Corrigin WA, 15/8/86, R. Medd; 580564, Goomalling WA, 19/8/86, R. Medd; 580152 (DAR 62309), ex seed *Lolium loliaceum*, Bordertown SA, 9/11/84, R. Medd & A. Nikandrow; 580131 (DAR 62333), *Lolium perenne*, Adelaide SA, 8/11/84, R. Medd & A. Nikandrow; 580157, Bordertown SA, 9/11/84, R. Medd & A. Nikandrow; 580079, Peterborough SA, 6/11/84, R. Medd & A. Nikandrow; 580555, Caron WA, 19/8/86, R. Medd; 580550, Northampton WA, 20/8/86, R. Medd; 580569, *Lolium perenne* x *Lolium multiflorum*, Merredin WA, 19/8/86, R. Medd; 580542, Southern Cross WA, 18/8/86, R. Medd; 580602, York WA, 4/9/86, R. Medd; 580057, 580058 (DAR 62330) & 580063, *Lolium perenne* x *Lolium rigidum*, Dubbo, 17/10/84, K. Jones; 580194 (DAR 62335), Narrandera NSW, 10/11/84, R. Medd & A. Nikandrow; 580125, Angaston SA, 8/11/84, R. Medd & A. Nikandrow; 580102, Kimba SA, 7/11/84, R. Medd & A. Nikandrow; 580084, Orroroo SA, 6/11/84, R. Medd & A. Nikandrow; 580162, Donald Vic., 9/11/84, R. Medd & A. Nikandrow; 580018 (DAR 64974), *Lolium rigidum*, Condobolin NSW, 19/9/84, A. Nikandrow & N. Fettell; 580005 (DAR 65001), ex seed, Orange NSW, 16/12/83, K. Jones; 580116, Cleve SA, 7/11/84, R. Medd & A. Nikandrow; 580240 (DAR 62298), Bendigo Vic., 27/11/84, K. Jones; 580176 (DAR 65006), Echuca Vic., 10/11/84, R. Medd & A. Nikandrow; 580053 (DAR 65005), *Lolium rigidum* x *Lolium multiflorum*, Dubbo NSW, 17/10/84, K. Jones; 580066, *Lolium* sp., Dubbo NSW, 17/10/84, K. Jones; 580020 (DAR 62303), Manildra NSW, 5/10/84, R. Medd & A. Nikandrow; 580037, Molong NSW, 5/8/84, R. Medd & A. Nikandrow; 580147, Coonalpyn SA, 9/11/84, R. Medd & A. Nikandrow; 580107, Kimba SA, 7/11/84, R. Medd & A. Nikandrow; 580089 (DAR 62331), Wilpena SA, 6/11/84, R. Medd & A. Nikandrow; 580584, Cervantes WA, 22/8/86, R. Medd; 580532 (DAR 62311), Corrigin WA, 15/8/86, R. Medd; 580561, Goomalling WA, 19/8/86, R. Medd; 580159, *Panicum prolutum*, Donald Vic., 9/11/84, R. Medd & A. Nikandrow; 580179 (DAR 64982), *Paspalum* sp., Finley NSW, 10/11/84, R. Medd & A. Nikandrow; 580475 (DAR 64986), *Phalaris aquatica*, Tumbarumba NSW, 29/11/84, K. Jones; 580459 (DAR 62301), Milawa Vic., 29/11/84, K. Jones; 580223 (DAR 62337), Shepparton Vic., 26/11/84, K. Jones; 580164, *Phalaris minor*, Donald Vic., 9/11/84, R. Medd & A. Nikandrow; 580460, *Stipa neesiana*, Milawa Vic, 29/11/84, K. Jones; 580495, *Stipa scabra*, Yass NSW, 30/11/84, K. Jones; 580016, *Triticum aestivum*, Condobolin NSW, 19/6/84, A. Nikandrow & N. Fettell; 580046, Dubbo NSW, 17/10/84, K. Jones; 580178 (DAR 64981), Finley NSW, 10/11/84, R. Medd & A. Nikandrow; 580004, Forbes NSW, 14/9/83, G. Stovold; 580009 ex seed, 580010 (DAR 62290) ex seed & 580019 (DAR 62329), Manildra NSW, 6/1/84, K. Jones; 580423, Narromine NSW, 6/9/85, K. Jones; 580007, ex seed, Trundle NSW, 15/12/83, B. Milne; 580008, ex seed, Weethalle NSW, 8/12/83, N. Markham; 580126, Angaston SA, 8/11/84, R. Medd & A. Nikandrow; 580113, Cleve SA, 7/11/84, R. Medd & A. Nikandrow; 580144, Coonalpyn SA, 9/11/84, R. Medd & A. Nikandrow; 580098, Kimba SA, 7/11/84, R. Medd & A. Nikandrow; 580241, Bendigo Vic., 27/11/84, K. Jones; 580166, Donald Vic., 9/11/84, R. Medd & A. Nikandrow; 580216, Shepparton Vic., 26/11/84, K. Jones; 580534, Corrigin WA, 15/8/86, R. Medd; 580563 (DAR 62305), Goomalling WA, 19/8/86, R. Medd; 580568 & 580572, Merredin WA, 19/8/86, R. Medd; 580579, Muchea WA, 22/8/86, R. Medd; 580545, Southern Cross WA, 18/8/86, R. Medd; 580061 & 580062, Unknown grasses, Dubbo NSW, 17/10/84, K. Jones; 580305, Dunedoo NSW, 2/9/85, K.Jones; 580422, Narromine NSW, 6/9/85, K. Jones; 580498, Yass NSW, 30/11/84, K. Jones; 580279 (DAR 62299), Geelong

Vic., 27/11/84, K. Jones; 580227, Shepparton Vic., 27/11/84, K. Jones; 580585, Cervantes WA, 22/8/86, R. Medd; 580526 & 580607, Corrigin WA, 15/8/86, R. Medd; 580129 (DAR 58949), *Vulpia bromoides*, Angaston SA, 8/11/84, R. Medd & A. Nikandrow; 580023 (DAR 65003), *Vulpia* sp., Manildra NSW, 5/10/84, R. Medd & A. Nikandrow

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[1] Laboratory accession number

[2] NSW Agriculture Plant Pathology Branch Herbarium (DAR) accession number

A Study of Physicochemical Conditions, Phytoplankton and Microcrustacean Zooplankton in Wallerawang Reservoir, New South Wales

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Wallerawang Reservoir is shallow (mean depth 3.4 m), mesotrophic and lacks persistent summer thermal stratification. During the period from April 1986 to September 1987, the depth-averaged temperature range was 7.6-23.4°C, oxygen 4.8-10.2 mgL^{-1}, pH 6.7-7.7 and total phosphorus less than 0.01-0.09 mgL^{-1}.

Dominant phytoplankton genera found in this reservoir (*Chroococcus*, *Asterionella*, *Attheya*, *Cyclotella*, *Stephanodiscus*, *Melosira* and *Dinobryon*) are generally characteristic of those in other unstratified, mesotrophic lakes of the region; the summer propagation of *Melosira* is attributed to increased temperature, lack of persistent thermal stratification, and moderately high silica during the period.

The common microcrustacean zooplankton species identified (*Bosmina meridionalis*, *Ceriodaphnia* sp., *Daphnia carinata*, *Calamoecia lucasi*, *Boeckella minuta*, and *Boeckella triarticulata*) are ubiquitous in south-eastern Australia.

The gut contents of the dominant microcrustacean zooplankton species reflect the reservoir phytoplankton composition; diatoms are generally better digested than the gelatinous blue-green algae ingested.

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INTRODUCTION

Wallerawang Reservoir, on Cox's River near Lithgow, was first filled in 1979. The reservoir provides water to the cooling tower of the adjacent power station.

A blue-green alga, *Microcystis aeruginosa* Kutz., an indicator of eutrophication (May, 1972; Okino, 1973), occasionally blooms in the reservoir in late summer and early autumn; some two thousand goldfish (*Carassius auratus*) died in Wallerawang Reservoir during a bloom of *Microcystis* in late summer 1983. However, it is not known if *Microcystis* caused the deaths or if some unknown pathogen caused mass mortality (J. Harris, B. Hodgson, 1988, pers. comm.).

A study of physicochemical conditions (transparency, temperature, oxygen, pH, phosphorus, nitrogen and silica) of the reservoir was conducted by the Electricity Commission (Elcom) of New South Wales, to assess the trophic status and possible eutrophication of the reservoir (Hodgson, 1987). There was no detailed study of the biological processes occurring within the reservoir which apparently governed the abundance of phytoplankton (particularly *Microcystis*). Therefore, there was a need to gain fundamental biological information, especially on plankton, to better manage reservoir water quality.

This paper presents the results of a study of physicochemical conditions, phytoplankton and microcrustacean zooplankton in Wallerawang Reservoir between April 1986 and September 1987. Features of particular interest are: the composition and seasonal abundance of dominant phytoplankton; the composition and seasonal abundance of dominant microcrustacean zooplankton (cladocerans and calanoid copepods); diet (gut contents) of the microcrustacean zooplankton. These data display basic limnological data parameters of the reservoir.

STUDY AREA

The characteristics of Wallerawang Reservoir are summarized in Table 1. It is shallow, with short retention time. Cox's River, erratic precipitation and to a lesser extent recirculated water from Lyell Reservoir 16 km downstream, are the major sources of water inflow. Reservoir spill, discharge to the power station and release dominate the outflow. Each month about 18% of the reservoir volume is withdrawn and evaporated through the power station cooling tower (Hodgson, 1988, pers. comm.).

The reservoir is inhabited by six species of fish including rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*), although their density has not been measured (Harris, 1988, pers. comm.). A pond weed (*Potamogeton pectinatus*) is conspicuous in summer.

TABLE 1

Characteristics of Wallerawang Reservoir

Location	150°05′E., 33°25′S.
Elevation (above sea level)	870 m
Maximum length (l)	3.5 km
Maximum width (b)	1.4 km
Area (A)	124.7×10^4 m^2
Volume (V)	4.3×10^4 m^3
Maximum depth (z_{max})	8.0 m
Mean depth (z)	3.4 m
Shore line (L)	10.7 km
Shoreline development (D_L)*	2.7
Mean turnover rate	6.4 year^{-1}

* Hutchinson (1957).

METHODS

Physicochemical Parameters

To measure the water transparency, a 25 cm Secchi disc was lowered at station A (Fig. 1). Downward irradiance in the photosynthetically available radiation or PAR (400-700 nm waveband) was measured at station A as described by Kirk (1977). The instruments used were a Li-185A lightmeter (Lamda Instruments Corp., U.S.A.) and Li-192S underwater quantum sensor (L.I.C., U.S.A.: quantum response in 400-700 nm; sensor output in μEinst m^{-2} sec^{-1}). The depth-averaged vertical attenuation coefficient for downward irradiance (Kd(PAR)) (Kirk, 1986) was calculated by the least squares regression method (Zar, 1974).

Water temperature (°C) and dissolved oxygen (mg l^{-1}) were measured at station A at 1 m intervals to the bottom, using a portable dissolved oxygen/temperature meter (Model 603, Yeo-Kal Electronics Pty., N.S.W.) to the nearest 0.1°C and 0.1 mg l^{-1}, respectively.

Monthly data on pH, total phosphorus (TP as mg l^{-1}), nitrate plus nitrite (NO_3-N plus NO_2-N), ammonia (NH_4-N), and silica (SiO_2-Si) were provided by Elcom, N.S.W. All the data were collected near the surface at station A during daytime. Data on monthly rainfall in the Lithgow area was provided by the Bureau of Meteorology, N.S.W.

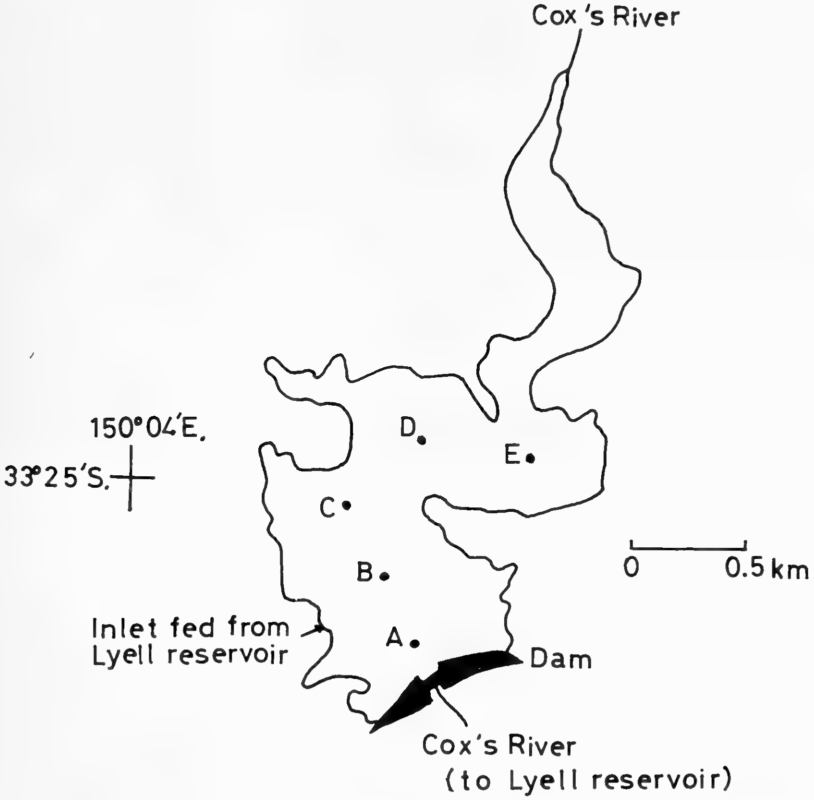

Fig. 1. Sampling stations in Wallerawang Reservoir.

Phytoplankton

Phytoplankton was collected monthly at stations A to E at 0.5 m depth between August 1986 and September 1987, using a 2-L Van Dorn water sampler. A single 500 ml subsample was measured out in a graduated cylinder, and preserved with 0.4 ml Lugol's iodine solution at each sampling station. Identification and counts of phytoplankton were conducted using a Prior inverted microscope at a magnification of 100 x to 420 x. Most phytoplankters were identified only to genus level, but some were taken to species. A maximum of 100 cells or colonies of each genus were counted (Lund *et al.*, 1958). The density of a phytoplankton genus (cells ml^{-1} or colonies l^{-1}) in the reservoir was calculated as the arithmetic mean of the densities of the genus at each sampling station.

Microcrustacean Zooplankton

Microcrustacean zooplankton was collected monthly at stations A to E. A weighted plankton net (mouth diameter 25 cm; mesh size 250 μm; filtration coefficient 0.63) was towed from the bottom to the surface at each station, at a tow speed of 1 m sec^{-1}. A single tow was conducted at each station. Microcrustacean zooplankton was preserved with 5% buffered formalin. Some 200 to 350 zooplankters were counted and identified using a Wild M5A stereo microscope at magnifications of 6x or 12x. The counts included juvenile and adult cladocerans and adult calanoid copepods. The density of a species (individuals l^{-1}) in the reservoir was calculated as the arithmetic mean of the densities of the species at each sampling station.

Microcrustacean Zooplankton Gut Contents

Microcrustacean zooplankton samples were collected monthly from 0.5-1.0 m depth between station B and D, with a conical plankton net (mouth diameter 45 cm; mesh size 200 μm), at a tow speed of 1 m sec^{-1}. The samples were preserved with 10% buffered formalin. From each sample, a maximum of 20 individuals of each cladoceran species and calanoid copepods were selected randomly. The animals were cleared, using sodium hypochlorite (Infante, 1978b) and analysis of gut contents followed Gliwicz (1969). Phase contrast illumination revealed ingested phytoplankton. Proportional occurrence of the ingested phytoplankton was calculated as described by Nadin-Hurley and Duncan (1976).

RESULTS

Physicochemical Parameters

Total monthly rainfall was erratic ranging from 5 to 374 mm month^{-1} with a maximum causing a flood in August 1986 (Fig. 2). Secchi disc measurements ranged from 0.2 to 2.7 m.

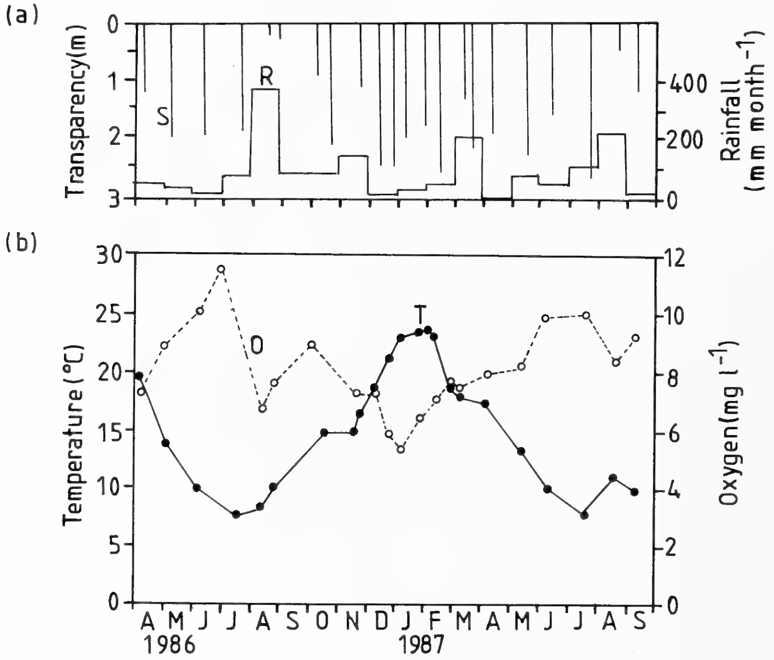

Fig. 2. Physicochemical conditions in Wallerawang Reservoir: (**a**) Secchi disc transparency (S) and rainfall (R); (**b**) depth-averaged temperature (T) and Oxygen (O).

The depth-averaged Kd(PAR) ranged from 0.82 to 6.63 ln units m^{-1} (minimum on 25 July 1987; maximum on 28 August 1986) (Table 2). The depth of 1% PAR ranged from 0.7 to 5.4 m, suggesting considerable seasonal fluctuations in euphotic depth.

The strong correlation between this depth and water transparency ($r=0.95$, $n=10$, $p<0.001$: $y=0.24 + 2.02x$ where y=depth of 1% PAR in metres and x=depth of transparency in metres) indicated that light penetration was controlled not by water colour but by suspended solids (Geddes, 1984a).

TABLE 2

Light penetration at station A in Wallerawang Reservoir: Ed(O), downward irradiance just below the surface; Kd, vertical attenuation coefficient for downward irradiance; 1% level, euphotic depth

Date	**Time** hrs	**Ed(O)** $\mu Em^{-2}s^{-1}$	**Kd** m^{-1}	**1% level** m
11 June 1986	1500	250	1.19	5.3
28 Aug.	1600	280	6.63	0.7
20 Nov.	1400	100	1.92	2.5
31 Jan. 1987	1700	300	1.29	3.5
20 Mar.	1000	60	0.87	5.4
12 Apr.	1450	300	1.23	3.7
19 May	1400	380	1.08	4.2
25 July	1400	300	0.82	5.4
23 Aug.	1420	350	3.98	1.1
13 Sept.	1200	530	1.56	2.8
Mean	—	—	2.06	3.5

The depth-averaged water temperature ranged from 7.6 to 23.4°C (Fig. 2). A minimum of 7.3°C was recorded at 6 m depth on 25 July 1986 and a surface maximum of 27.4°C on 10 January 1987. In summer the surface and bottom temperature differed (up to 8.2°C on 10 January 1987). The reservoir was isothermal in other seasons.

The depth-averaged dissolved oxygen ranged from 4.8 to 10.2 mg l^{-1} (Fig. 2). Saturation of the surface water with oxygen ranged from 78 to 124% (minimum on 28 August 1986; maximum on 31 January 1987). Surface supersaturation and bottom depletion occurred in summer.

The pH was slightly alkaline, ranging from 6.7 to 7.7 (Table 3). Total phosphorus (TP) ranged from 0.01 to 0.09 mg l^{-1} during the period except on 4 August 1986 and 13 April 1987 when TP was below the detectable level (<0.01 mg l^{-1}). NO_3-N plus NO_2-N was often below the detectable level (<0.01 mg l^{-1}). Otherwise, NO_3-N plus NO_2-N ranged sevenfold from 0.10 to 0.73 mg l^{-1}. NH_4-N also ranged sevenfold from 0.01 to 0.07 mg l^{-1} except on 7 October 1986 and 9 March 1987 when NH_4-N was below the detectable level (<0.01 mg l^{-1}). SiO_2-Si ranged from 0.9 to 8.0 mg l^{-1} during the period.

Phytoplankton

A total of 43 phytoplankton taxa were identified (Table 4). Of these, *Chroococcus* (Cyanophyta), *Asterionella*, *Attheya*, *Cyclotella*, *Stephanodiscus*, and *Melosira* (Bacillariophyta), and *Dinobryon* (Chrysophyta) were the dominant genera. Unidentified flagellates were also a major component.

Asterionella displayed a sharp population peak in spring 1986 (Fig. 3). A maximum of 6080 cells ml^{-1} was recorded in October; it then declined, but again increased moderately in autumn 1987 (maximum 90 cells ml^{-1} in May 1987). *Cyclotella* and *Stephanodiscus* displayed two growth peaks. The first peak, which coincided with that of *Asterionella*, occurred in spring 1986, with a maximum of 330 cells ml^{-1}. The second high peak occurred in late autumn 1987, with a maximum of 9980 cells ml^{-1} in June 1987. *Chroococcus* increased in early summer 1986 to a December maximum of 900 cells ml^{-1}.

TABLE 3

Nutrients and pH at surface at station A in Wallerawang Reservoir: pH: total phosphorus (TP); nitrate plus nitrite (NO_3-N + NO_2-N); ammonia (NH_4-N) and silica (SiO_2-Si). Data are from the Electricity Commission of New South Wales

Date	**pH**	**TP (mg l^{-1})**	**NO_3-N + NO_2-N (mg l^{-1})**	**NH_4-N (mg l^{-1})**	**SiO_2-Si (mg l^{-1})**
14 Apr. 1986	7.5	0.05	0.00	0.05	4.0
12 May	7.5	0.04	0.00	0.01	2.4
10 June	7.7	0.02	0.00	0.02	1.9
01 July	7.6	0.03	0.00	0.04	0.9
04 Aug.	7.7	0.00	0.10	0.02	0.9
01 Sept.	6.7	0.06	0.66	0.04	6.2
07 Oct.	7.4	0.01	0.24	0.00	5.2
03 Nov.	7.5	0.08	0.11	0.01	3.1
08 Dec.	—	0.08	—	—	—
09 Feb. 1987	7.6	0.03	0.00	0.07	8.0
09 Mar.	7.2	0.05	0.00	0.00	6.6
13 Apr.	7.4	0.00	0.45	0.06	6.5
18 May	7.2	0.02	0.73	0.03	4.5
15 June	7.4	0.02	0.00	0.01	1.9
13 July	7.5	0.06	0.59	0.01	2.0
10 Aug.	—	0.09	—	—	—
14 Sept.	—	0.03	—	—	—
Mean	7.4	0.04	0.21	0.03	3.9

TABLE 4

Phytoplankton in Wallerawang Reservoir between August 1986 and September 1987

Cyanophyta
Chroococcus spp.
Dactylococcopsis spp.
Oscillatoria sp.
Anabaena sp.

Chlorophyta
Volvox spp.
Botryococcus sp.
Pediastrum spp.
Oocystis spp.
Selenastrum ?minutum (Naeg.) Collins
Closteriopsis longissima Lemmermann
Schroederia ?setigera (Shroeder) Lemmermann
Scenedesmus spp.
Closterium sp.
Cosmarium spp.
Quadrigula spp.
Staurastrum spp.

Euglenophyta
Trachelomonas sp.

Chrysophyta
Dinobryon divergens Imhof
Dinobryon cylindricum Imhof

Bacillariophyta
Melosira granulata (Ehrenb.) Ralfs
Melosira granulata var. *angustissima* Muller
Melosira italica (Ehrenb.) Kutz.
Melosira varians Agardh
Cyclotella spp.
Stephanodiscus spp.
Attheya sp.
Tabellaria sp.
Fragilaria sp.
Asterionella spp.
Synedra pulchella Kutz.
Synedra sp.
Navicula spp.
Pinnularia sp.
Gomphonema acuminatum var. *coronatum* (Ehrenb.) Babenhorst
Gomphonema constricutum Ehrenberg
Gyrosigma sp.
Cymbella spp.
Nitzschia sp.
Surirella spp.

Pyrrhophyta
Peridinium sp.
Ceratium hirundinella O. F. Muller

Unidentified flagellates
Unidentified algae

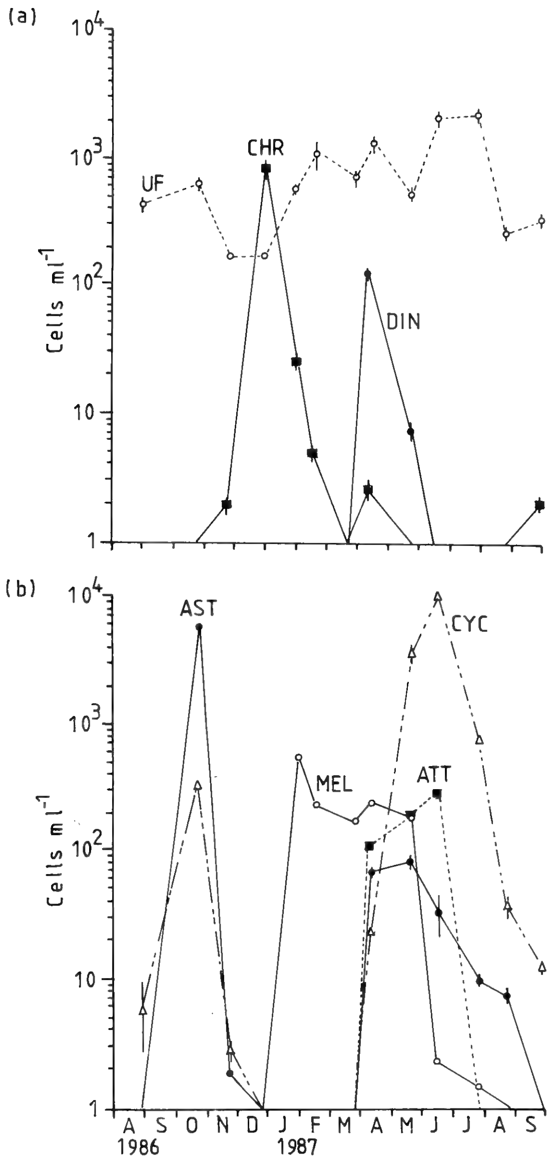

Fig. 3. Density of phytoplankton in Wallerawang Reservoir: (**a**) *Chroococcus* (CHR), *Dinobryon* (DIN) and unidentified flagellates (UF); (**b**) diatoms *Asterionella* (AST), *Attheya* (ATT), *Cyclotella/Stephanodiscus* (CYC) and *Melosira* (MEL). Mean ± SE is shown: n = 5 except 29 August and 23 October 1986 when n = 4.

Melosira (mostly *M. granulata*) became abundant from summer to autumn (maximum 540 cells ml^{-1} in January 1987). In autumn 1987, *Dinobryon* (mostly *D. divergens*) produced a weak growth peak of 130 cells ml^{-1} in late autumn (June) 1987. The unidentified flagellates (probably three species in total; maximum cell width 3-20 μm) occurred throughout the study; their density fluctuated irregularly from 160 to 2240 cells ml^{-1} (minimum in December 1986; maximum in July 1987).

Microcrustacean Zooplankton

A total of 12 cladoceran and 3 calanoid species were identified (Table 5). Of these, the dominant cladocerans were *Bosmina meridionalis*, *Ceriodaphnia* sp., and *Daphnia carinata*, while the dominant calanoid copepods were *Calamoecia lucasi*, *Boeckella minuta*, and *Boeckella triarticulata*.

B. meridionalis occurred scarcely throughout the study except in January 1987 (Fig. 4). The density of this small cladoceran species may be greatly underestimated by the large mesh (250 μm), used in the sampling. *Ceriodaphnia* was a spring-early summer species. A maximum of 5.5 l^{-1} was recorded in November 1986. *D. carinata* was a spring-summer species in 1986, but also increased in winter 1987. During the first growth period (July 1986 to March 1987), *D. carinata* reached a maximum of 21.1 l^{-1} in December 1986. The second growth period commenced in July 1987, with a maximum of 22.3 l^{-1} in August.

C. lucasi was perennial, though its abundance fluctuated. A sharp decline was observed after the August 1986 flood. A minimum of 0.1 l^{-1} and a maximum of 30.4 l^{-1} were recorded in August 1986 and in July 1987, respectively. *B. minuta* was also perennial. Its abundance fluctuated like *C. lucasi*. A minimum of 0.3 l^{-1} and a maximum of 45.9 l^{-1} were recorded in August 1986 and in July 1987, respectively. *B. triarticulata* occurred from spring to early summer. A maximum of 4.2 l^{-1} was recorded in December 1986.

Microcrustacean Zooplankton Gut contents

A total of 240 *Bosmina*, 80 *Ceriodaphnia*, 160 *Daphnia*, 330 *Calamoecia*, 340 *B. minuta*, and 80 *B. triarticulata* guts were examined, yielding 11, 10, 15, 18, 29 and 21 phytoplankton components, respectively (Table 6). Most phytoplankton genera in Wallerawang Reservoir were represented, except *Anabaena*, *Volvox*, *Closterium*, *Shroederia*, *Gyrosigma* and flagellates which were not detected in the zooplankton guts.

TABLE 5

Cladocerans and calanoid copepods in Wallerawang Reservoir between April 1986 and September 1987

Cladocerans
- *Diaphanosoma unguiculatum* Gurney
- *Pleuroxus* cf. *inermis* Sars
- *Chydorus sphaericus* s.l. (Muller)
- *Pseudochydorus* cf. *globosus* (Baird)
- *Alona diaphana* King
- *Leydigia leydigi* (Schoedier)
- *Ilyocryptus sordidus* (Lieven)
- *Bosmina meridionalis* Sars
- *Daphnia carinata* s.l. King
- *Simocephalus vetulus elisabethae* (King)
- *Ceriodaphnia cornuta* Sars
- *Ceriodaphnia* sp.

Calanoid copepods
- *Boeckella triarticulata* Thomson
- *Boeckella minuta* Sars
- *Calamoecia lucasi* Brady

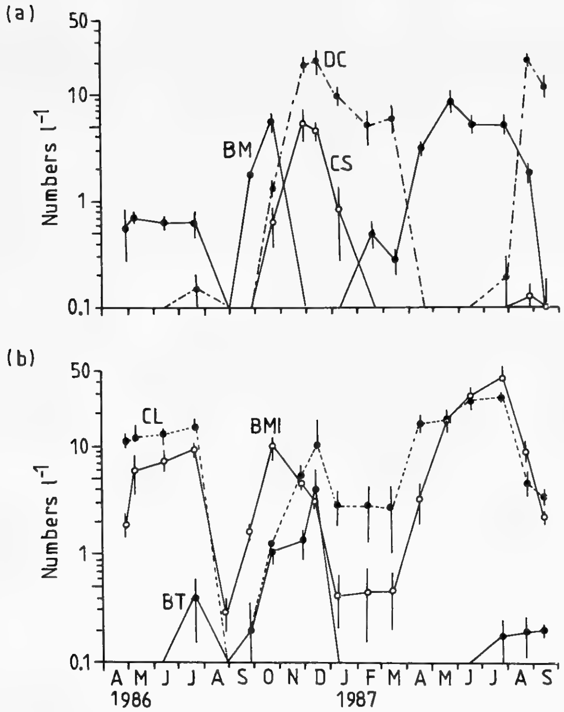

Fig. 4. Density of microcrustacean zooplankton in Wallerawang Reservoir: (**a**) cladocerans *Bosmina meridionalis* (BM), *Ceriodaphnia* sp. (CS) and *Daphnia carinata* (DC); (**b**) calanoid copepods *Calamoecia lucasi* (CL), *Boeckella minuta* (BMI) and *Boeckella triarticulata* (BT). Mean ± SE is shown: n = 5.

(a) *Bosmina meridionalis*

The dominant diet components were *Cyclotella* and *Stephanodiscus* (32%), *Chroococcus* (16%) and *Oocystis* (16%) (see Kobayashi, 1990 for full data). There was a significant positive correlation between the proportional occurrence of centric diatoms (*Cyclotella* and *Stephanodiscus*) in the *Bosmina* guts and their density in the plankton (Spearman's rank correlation coefficient or $r_s = 0.92$, $n = 7$, $p < 0.05$). *Cyclotella* and *Stephanodiscus* were well digested. Ingested *Chroococcus* and *Oocystis* were often unicellular and intact.

(b) *Ceriodaphnia* sp.

Chroococcus (41%) and *Oocystis* (25%) dominated the components. *Chroococcus* was abundant in the *Ceriodaphnia* guts in January 1987 when this blue-green alga also peaked in the plankton. Most of the ingested *Chroococcus* were intact in the *Ceriodaphnia* guts.

(c) *Daphnia carinata*

The dominant components were *Chroococcus* (62%), *Oocystis* (44%), *Botryococcus* (25%) and centric diatoms (*Cyclotella* and *Stephanodiscus* (20%). *Chroococcus* constituted the main dietary phytoplankton component for *Daphnia* in summer 1986 to 1987, as observed in *Ceriodaphnia*. Ten to 80 colonies (800 to 6000 cells) of *Chroococcus* were found in each gut of *Daphnia* in December 1986 when *Chroococcus* propagated in the reservoir. *Chroococcus* cells were mostly intact in the *Daphnia* guts. Of other algae, *Trachelomonas* was detected in 14%; the ingested brown shells and cell tissues inside the shells often remained intact. Large *Staurastrum* and *Ceratium* were fragmented in the guts.

TABLE 6

Dietary phytoplankton components in the guts of microcrustacean zooplankton in Wallerawang Reservoir between April 1986 and September 1987: Bosmina meridionalis (BM); Ceriodaphnia *sp.* (CS); Daphnia carinata (DC); Calamoecia lucasi (CL); Boeckella minuta (BMI); Boeckella triarticulata (BT).
Occurrence symbols are: p — present, x — absent

Taxonomic Grouping	**BM**	**CS**	**DC**	**CL**	**BMI**	**BT**
Cyanophyta						
Chroococcus	p	p	p	p	p	p
Dactylococcopsis	p	x	x	x	p	p
Oscillatoria	x	x	x	x	p	x
Chlorophyta						
Botryococcus	x	x	p	x	x	x
Closteriopsis	x	x	x	x	p	p
Cosmarium	p	x	p	p	p	x
Mougeotia	x	x	x	p	x	p
Oocystis	p	p	p	p	p	p
Pediastrum	x	x	x	x	x	p
Quadrigula	p	x	p	p	p	p
Scenedesmus	p	p	p	p	p	p
Selenastrum	p	x	x	p	p	x
Staurastrum	x	x	p	x	p	p
Euglenophyta						
Trachelomonas	x	p	p	x	p	p
Chrysophyta						
Dinobryon	x	x	x	x	p	p
Bacillariophyta						
Asterionella	x	p	p	p	p	p
Attheya	x	x	x	x	p	x
Cocconeis	x	x	x	x	p	x
Cyclotella/Stephanodiscus	p	p	p	p	p	p
Cymbella	p	p	p	p	p	p
Fragilaria	x	x	x	x	p	x
Frustulia	x	x	x	p	p	x
Gomphonema	x	x	x	p	p	p
Melosira	p	x	p	p	p	p
Navicula	x	p	x	p	p	p
Nitzschia	x	x	x	x	p	x
Pinnularia	x	x	x	p	p	x
Surirella	x	x	x	x	p	x
Synedra	x	p	p	p	p	p
Tabellaria	x	x	x	x	p	p
Pyrrhophyta						
Ceratium	x	x	p	x	x	x
Peridinium	x	x	x	p	p	p
Unidentified algae	p	p	p	p	p	p

(d) *Calamoecia lucasi*

The dominant components were *Oocystis* (41%), *Cyclotella* and *Stephanodiscus* (37%), and *Chroococcus* (20%). The unicellular *Oocystis* was occasionally digested, while the colonial form was mostly intact in the *Calamoecia* guts. The proportional occurrence of centric diatoms and *Chroococcus* in the *Calamoecia* guts was significantly correlated with the algal density in the plankton ($r_s = 0.74$ and 0.84, $n = 12$, $p < 0.05$ and < 0.001, respectively).

(e) *Boeckella minuta*

The dominant components were *Cyclotella* and *Stephanodiscus* (55%), *Oocystis* (49%), *Chroococcus* (33%), *Melosira* (21%), and *Asterionella* (21%). There was a significant positive correlation between the proportional occurrence of *Cyclotella* and *Stephanodiscus*, and *Chroococcus* in the guts of *B. minuta* and their density in the plankton ($r_s = 0.83$ and 0.63, $n=12$, $p<0.001$ and <0.01, respectively). *Oocystis* was abundant in early autumn 1986 and 1987. Large *Asterionella* was abundant in the guts of *B. minuta* in spring 1986 and in autumn 1987. *Melosira* was abundant in autumn 1986 and 1987. Of other algae, *Synedra* was detected in 14%.

(f) *Boeckella triarticulata*

The dominant components were *Chroococcus* (53%), *Oocystis* (49%), *Asterionella* (49%), and centric diatoms (*Cyclotella* and *Stephanodiscus*) (34%). *Chroococcus* and *Oocystis* predominated in early summer 1986, and *Asterionella* in spring 1986 when it was abundant in the plankton. Large *Staurastrum* and *Pediastrum* were fragmented in the guts of *B. triarticulata*.

DISCUSSION

Physicochemical Parameters

Fluctuations in water transparency of Wallerawang Reservoir mainly followed rainfall. The Secchi disc depth of 0.2 to 2.7 m and depth-averaged Kd(PAR) of 0.82 to 6.63 ln units m^{-1} were within the values recorded in other Australian inland waters (Kirk, 1986). In that reservoir mean depth is 3.4 m, the depth of 1% PAR (euphotic depth) of 0.7 to 5.4 m (mean 3.5 m) suggests that light is not a limiting factor for algal growth except after floods.

Persistent thermal stratification did not develop in summer. Since the reservoir is relatively shallow, wind action prevents stratification and development of a thermocline (Hergenrader and Hammer, 1973). The depletion of summer bottom oxygen was also temporary.

The pH values were generally stable in the range 7.2-7.7, except that in September 1986 (pH 6.7). Lowered pH then was probably due to a flow of low-pH flood water (Timms, 1969).

TP was generally within the mesotrophic to eutrophic level (Sakamoto, 1966). The mean TP (0.04 mg l^{-1}) is lower than that of Australian eutrophic waters: 0.089 mg l^{-1} in Lake Daylesford, Victoria (Bales *et al.*, 1980, calculated from their Table 1) and 233 mg m^{-3} in Lake Alexandrina, South Australia (Geddes, 1984a). It is possible that phosphorus may limit algal growth in Wallerawang when nitrogen is high. However, this situation does not occur very often at Wallerawang. Dissolved inorganic nitrogen (NO_3-N plus NO_2-N and NH_4-N) reached relatively high concentrations in spring 1986 and 1987 (maximum 0.76 mg l^{-1} in May 1987), but was mostly low to depleted (<0.10 mg l^{-1}) during the rest of the period studied. NO_3-N and NH_4-N are readily used for algal growth (Golterman, 1975). Thus relatively high dissolved inorganic nitrogen in spring 1986 and 1987, coupled with increasing water temperature, provided the growth of phytoplankton. SiO_2-Si (mean 4.6 mg l^{-1}) was sufficient for the growth of diatoms, particularly from late winter 1986 to autumn 1987 when SiO_2-Si was over 3 mg l^{-1} (Lund, 1965).

Phytoplankton

Phytoplankton in Wallerawang Reservoir followed a seasonal succession of the dominant genera characteristic of other unstratified, mesotrophic lakes (Reynolds, 1980): *Asterionella*, *Cyclotella* and *Stephanodiscus* (spring), *Chroococcus* (early summer), *Melosira* (summer to autumn), *Dinobryon* and *Asterionella* (autumn), *Attheya* and again *Cyclotella* and *Stephanodiscus* (late autumn). In addition, the unidentified flagellates were abundant throughout the study.

Asterionella, a common diatom in the spring bloom (Goldman and Horne, 1983) and centric diatoms (*Cyclotella*, *Stephanodiscus*) were the first phytoplankton to increase after the August 1986 flood. These diatoms tolerate low light availability (Wetzel, 1975). The summer blooms of *Chroococcus* and *Melosira* (mostly *M. granulata*) are characteristic of mesotrophic to eutrophic waters (Hutchinson, 1967; Reynolds, 1980). The increase in water temperature during summer was important for the growth of *Melosira*; its density was significantly correlated with surface water temperature ($r=0.68$, $n=13$, $F=9.63$, $p<0.01$). It is also abundant in Warragamba, Cataract and Prospect Reservoirs, N.S.W. (Thomasson, 1973), and the lower River Murray, South Australia (Shiel *et al.*, 1982). The propagation of *Dinobryon* in early autumn was correlated with low phosphorus with $TP<0.02\ mg\ l^{-1}$ (Hutchinson, 1967).

Microcystis, recorded by Elcom, N.S.W. in 1983 and 1984, was not recorded in Wallerawang phytoplankton during this study. Its absence was probably due to lack of persistent thermal stratification (Reynolds, 1980) and depleted dissolved inorganic nitrogen (Gerloff and Skoog, 1954, 1957; Takahashi *et al.*, 1981) in late summer. However, these conditions, coupled with moderately high silica during the period (SiO_2-Si 6.6 to 8.0 mg l^{-1}), should have supported the abundance of *Melosira* in the reservoir (cf. Lund, 1954; Kilham, 1971; Reynolds, 1980).

Microcrustacean Zooplankton

The dominant cladocerans and calanoid copepods in Wallerawang Reservoir are ubiquitous species in south-eastern Australia (Mitchell, 1986; Timms, 1970a, 1970b, 1987).

Small-bodied *B. meridionalis*, which is often a perennial species (Timms, 1970b; Shiel *et al.*, 1982; Geddes, 1984b), diminished during summer 1986 when the medium-bodied *Ceriodaphnia* and the large-bodied *D. carinata* increased. However, *B. meridionalis* again increased during autumn 1987, with decreasing *Ceriodaphnia* and *D. carinata*. Although zooplankton competitive ability is a complex interplay between size-selective vertebrate and invertebrate predation, reproductive rate, and growth rate (Mitchell and Williams, 1982), the shift from small- to large-bodied cladoceran species in Wallerawang Reservoir may be explained by the size-efficiency hypothesis (Brooks and Dodson, 1965).

To date, there is insufficient information available on the effects of vertebrate and invertebrate predation on zooplankton. The author has observed small flathead gudgeon (*Philypnodon grandiceps*) preying on small-bodied chydorids, *Bosmina* and cyclopoids in Wallerawang Reservoir, but the contribution of larger fish species is unknown.

The highest abundance of *D. carinata* around 11 to 19°C was consistent with Hebert (1977), Mitchell and Williams (1982), who described the species as a cold- to cool-water form. No individuals of *D. carinata* developed crests throughout the study, suggesting low notonectid predation (Grant and Bayly, 1981).

The coexisting and perennial occurrence of small-bodied *C. lucasi*, and medium-bodied *B. minuta* was consistent with Timms (1970a, 1970b). A significant positive correlation between their densities ($r_s=0.73$, $n=18$, $p<0.01$) indicates that competition between these two calanoid copepods is weak or absent.

The densities of microcrustacean zooplankton (cladocerans plus calanoid copepods) in Wallerawang Reservoir, ranging from 0.5 to 82.1 l^{-1} (mean 27.2 l^{-1}), are lower than those in Lake Alexandrina (35 to 123 l^{-1}; mean 66 l^{-1}) (Geddes, 1984b), but similar to those in Lake Hume (10 to 60 l^{-1}) (Walker and Hillman, 1977 as quoted in Geddes, 1984b). In turbid Lake Alexandrina, the high zooplankton population biomass is believed to be maintained by the constant availability of abundant detrital particles and bacteria (Geddes, 1984b). Floods may temporarily produce similar food conditions for microcrustacean zooplankton in Wallerawang Reservoir.

Large Flood Influence (August 1986)

This flood resulted in the lowest transparency, highest depth-averaged Kd(PAR) value and therefore, shallowest euphotic depth found in the reservoir. Jolly (1966) reported similar erratic optical properties of flooded reservoirs in eastern N.S.W. The drop in pH and increase in nutrients were also probably flood-induced (Timms, 1969; Geddes, 1988).

Phytoplankton populations were very scarce except unidentified flagellates which may have come from Cox's River or have been resuspended from sediments. Holoplanktonic *Asterionella* and the small unicellular centric diatoms dominated phytoplankton two months after the flood. Increased silica and moderately improved light availability appeared to have supported the growth of these diatoms (Goldman and Horne, 1983).

The flood also lowered microcrustacean zooplankton density in Wallerawang Reservoir. It took one to two months for cladocerans and calanoid copepods (except *C. lucasi*) to recover after the flood (Jolly, 1966; Timms, 1970b).

Microcrustacean Zooplankton Gut Contents

Comparing the detritus and/or bacteria based zooplankton in the Alligator Rivers region (Tait *et al.*, 1984) and Lake Alexandrina (Geddes, 1984b, 1988), the frequent presence of phytoplankton in the guts of Wallerawang zooplankton is significant; diatoms (*Asterionella*, *Cyclotella*, *Melosira*, and *Stephanodiscus*) were particularly abundant, and were well digested in the zooplankton guts during the study. However, this does not necessarily imply that they should also constitute an important energy pass between phytoplankton and zooplankton in the reservoir. Rapid consumption but with poor assimilation efficiency of *Asterionella* by *Diaptomus* is reported by Schindler (1971). The food value of *Melosira* is species-dependent, but *Stephanodiscus* supports high growth rate and reproduction of zooplankton (Infante and Litt, 1983). The gelatinous blue-green alga *Chroococcus* and the green alga *Oocystis* were also frequently ingested, but were mostly intact. They passed probably unharmed through zooplankton guts (Porter, 1975; Infante, 1978a; Sarnelle, 1986), showing no significant response to grazing (Merrick and Ganf, 1988).

Burns *et al.* (1989) reported that the calanoid *Boeckella* ingested *Anabaena* in some New Zealand lakes, however no *Anabaena* was found in the guts of *B. minuta* and *B. triarticulata* in Wallerawang Reservoir. *Oscillatoria* was found only once in the guts of *B. minuta* during the study. *Volvox*, *Closterium*, and *Gyrosigma* were absent in the zooplankton guts; they were too big for the zooplankton (Burns, 1968). Flagellates, which are generally of high food value (Schindler, 1971; Sarnelle, 1986), were also never detected in the zooplankton gut contents, even though they were abundant in the plankton, and were within the ingestible cell size for the zooplankton. Perhaps they were ingested, but were disrupted and rendered unrecognizable (Infante, 1978a).

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Gonadal Structure in *Arius graeffei* Kner & Steindachner (Pisces: Ariidae) from the Clarence River, New South Wales

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(Communicated by J. R. MERRICK)

RIMMER, M. A. Gonadal structure in *Arius graeffei* Kner & Steindachner (Pisces: Ariidae) from the Clarence River, New South Wales. *Proc. Linn. Soc. N.S.W.* 113 (1), 1992: 43-55.

The small paired testes of the mouthbrooding catfish *A. graeffei* showed limited seasonal macroscopic changes, with spermatogenic activity reaching a peak in November. The ovaries of *A. graeffei* contain yolky oocytes in the anterior region, and small hyaline oocytes thoughout the ovary. Yolky and hyaline oocytes exhibit differential development from 300 μm in diameter. There is no vitellogenesis in hyaline oocytes, but there is a secondary centrifugal proliferation of yolk vesicles. Possible roles for the infertile hyaline oocytes are discussed.

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INTRODUCTION

Arius graeffei Kner & Steindachner is a common inhabitant of estuarine and freshwater habitats in the coastal drainages of northern Australia and south-eastern New Guinea (Kailola, 1983). *A. graeffei* from the Clarence River in northern New South Wales breed annually from early November to early December. Mature oocyte diameters range from 11.0-13.7 mm; fecundity ranges from 40-122 (Rimmer, 1985a). This species, like other ariids, is a mouthbrooder; males carry up to 123 eggs in the mouth for 6-8 weeks, releasing the young as juveniles (Rimmer and Merrick, 1983; Rimmer, 1985b).

Reproduction and development in the family Ariidae has been reviewed by Rimmer and Merrick (1983), who noted that ariid ovaries generally contain three size classes of oocytes: large yolky oocytes which are the group fertilized at spawning, smaller yolky oocytes, and small (c. 1-2 mm) non-functional hyaline oocytes. Yolky oocytes are limited to the anterior part of the ovary, while hyaline oocytes are found throughout the ovary in vast numbers (Rimmer and Merrick, 1983). Gabaeva and Ermolina (1972) noted that the hyaline oocytes of *A. thalassinus* differed considerably from the larger yolky oocytes in the cell structure of the follicular epithelium during the later stages of oogenesis.

The gonadal structure in *A. graeffei* from the Clarence River was investigated in order to document the processes of spermatogenesis and oogenesis, to examine seasonal changes in gonadal activity and to determine structural differences between hyaline and yolky oocytes.

MATERIALS AND METHODS

A. graeffei were captured from the Clarence River using gillnets (Rimmer, 1985a). Gonads used for histology were fixed in Bouin's fixative and stored in 70% ethanol; selected ovaries and testes were frozen and stored at -20°C for cryotome sectioning.

Ovaries and testes were embedded in paraffin and sectioned at 5-8 μm. Due to the

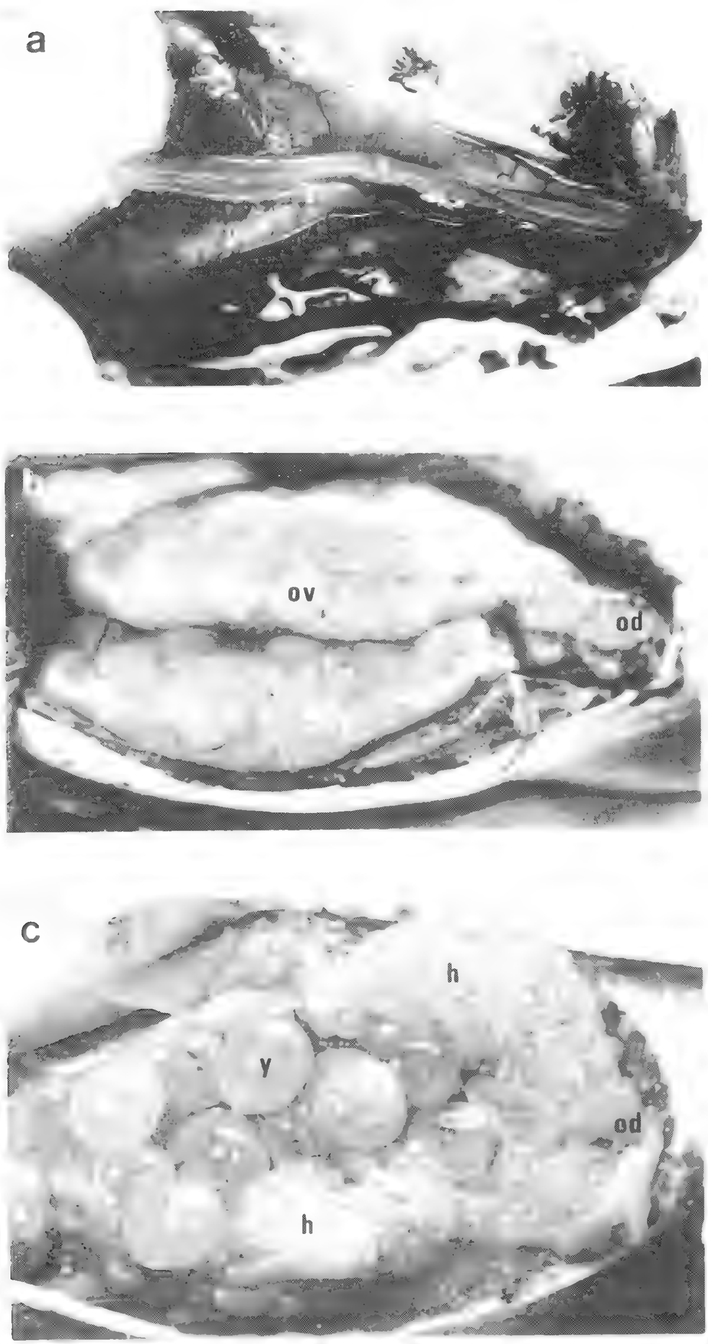

Fig. 1. Gonadal structure in *A. graeffei*: (**a**) male *A. graeffei* dissected to show position and structure of testes; (**b**) female *A. graeffei* dissected to show ovaries; (**c**) female *A. graeffei* shown in (b) with left ovary dissected to show yolky and hyaline oocytes.
Key to abbreviations: h = hyaline oocytes; od = oviduct; ov = ovary; t = testis; y = yolky oocytes.

loss of yolk from large oocytes during sectioning, several techniques were attempted in sectioning mature ovaries, including paraffin embedding, double embedding (Humason, 1972) and celloidin painting (Davis, 1977). The most successful technique involved sectioning frozen material at 6-10 μm on a cryotome at -19°C. As the quality of these sections was inferior to paraffin sections they were used only to examine the structure of the yolk during the later stages of oogenesis. All sections were stained with haematoxylin and eosin.

The sequence of oocyte development was based on Lehri's (1968) modified version of the scheme proposed by Yamamoto (1956a), which reduces the number of later stages of yolk formation to more closely fit the sequence seen in large yolky oocytes. In addition, several new stages for hyaline oocyte development are described since these stages have not been previously described. Cytological data were measured using the procedures adopted by Pollard (1972).

RESULTS

Macroscopic Structure

The testes of *A. graeffei* are small paired organs which are fused along their inner margins with only the rounded anterior tips free (Fig. 1**a**). The dorso-medial sperm ducts continue posterodorsally from the testes, then join to form a common duct which opens at the urogenital pore posterior to the anus.

The ovaries are short paired tubular organs which unite posteriorly to form a short oviduct (Fig. 1**b**). They are suspended from the body wall by a thick mesovarium. Three groups of oocytes are apparent in maturing and ripe ovaries:

I: large (up to 13.7 mm diameter) yolky oocytes which are ovulated and fertilized at spawning;
II: small (1.3 to 3.9 mm diameter) yolky oocytes which are retained at spawning;
III: hyaline oocytes: small (up to 3.3 mm diameter) non-functional oocytes which are ovulated at spawning but which are not fertilized.

Two major regions of oogenesis are found in maturing and ripe ovaries: the anterior 70% of the ovary contains both large and small yolky oocytes with numerous hyaline oocytes (up to 3.3 mm in diameter), while the posterior 30%, including oviduct, contains large numbers of hyaline oocytes up to 2.0 mm in diameter (Fig. 1**c**). Within the oviduct these oocytes are orientated along numerous longitudinal plicae.

Histology of the Testes

Each testis is enclosed by a tunica albuginea formed by connective tissue, which is in turn bounded by a thin peritoneal membrane. The tunica divides internally to form the basement membranes of the seminiferous lobules, which carry the blood vessels that permeate the testes (Fig. 2**a**). The lobules of each testis are arranged approximately dorsoventrally, converging on the dorso-medial sperm duct. Lobules vary in width from 60 to 300 μm in mature testes. All lobules within mature testes show spermatogenic activity, and the majority of lobules within each testis are at the same spermatogenic stage. The lobules of the testes of immature *A. graeffei* show little or no development of lumens (Fig. 2**b**).

Five stages of spermatogenesis were recognized:

1. Spermatogonia (Fig. 2**c**,**d**). Spermatogonia are normally found adjacent to the basement membrane of the lobule. The nucleus (mean diameter 8.6 μm) is lightly staining with a prominent nucleolus and a reticulum of chromatin threads.

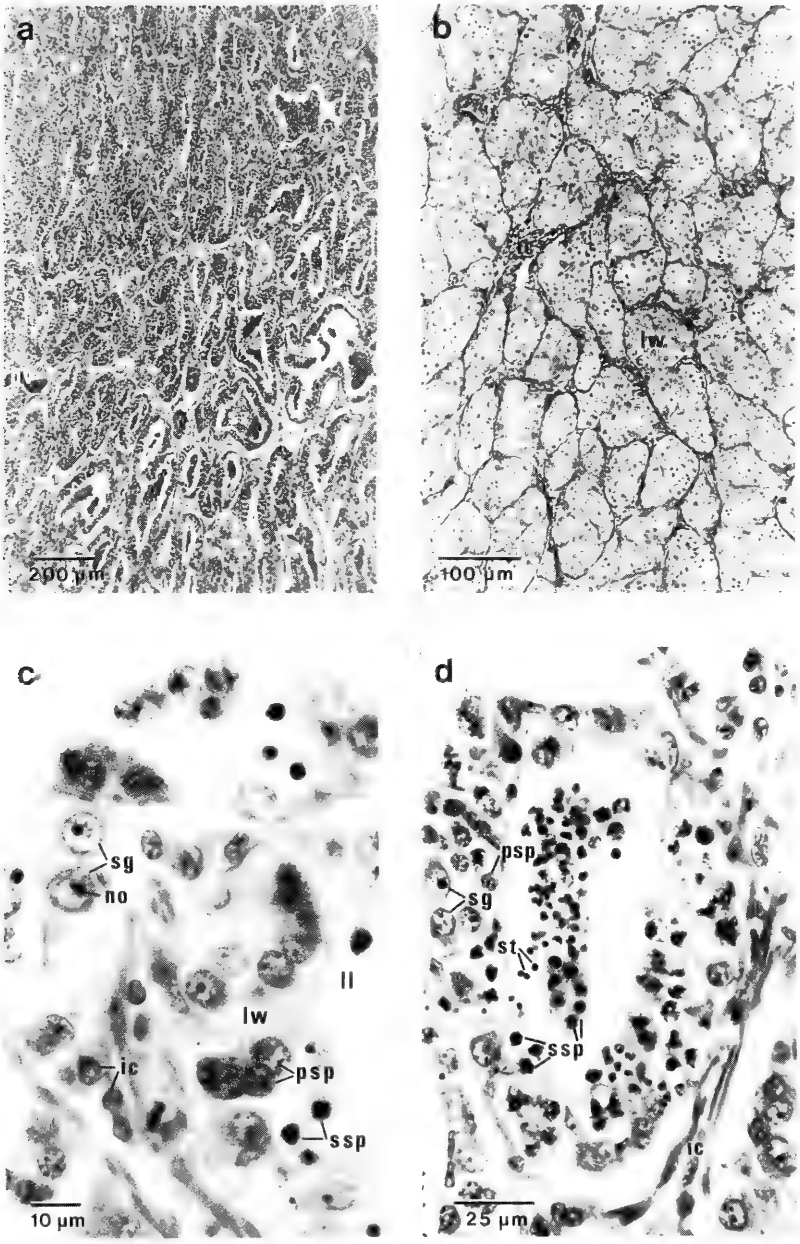

Fig. 2. Stages of spermatogenesis in *A. graeffei*: (**a**) transverse section through a spent testis showing the lobular structure and residual spermatozoa; (**b**) transverse section through an immature testis. Although the lobular structure is apparent, no lumens have yet developed; (**c**) portion of a lobule showing early spermatogenic stages; (**d**) portion of the lobule shown in (b) showing spermatogenic stages and interstitial tissue.
Key to abbreviations (Figs 2, 3): bv = blood vessel; ic = interstitial cell; ll = lobule lumen; lw = lobule wall; no = nucleolus; psp = primary spermatocyte; sg = spermatogonia; ssp = secondary spermatocyte; st = spermatid; sz = spermatozoa.
All sections stained with haematoxylin and eosin.

2. Primary spermatocytes (Fig. 2**c**,**d**). These cells are formed by mitotic division of spermatogonia and occur in nests within the lobule wall. The nuclei have a mean diameter of 5.9 μm and contain a dense reticulum of chromatin material and several small nucleoli.
3. Secondary spermatocytes (Fig. 2**c**,**d**). These cells, formed by meiotic division of primary spermatocytes, occur in nests in the lobule wall. The small nuclei (mean diameter 4.1 μm) are darkly staining due to the very dense chromatin present.
4. Spermatids (Fig. 3**a**). Spermatids are formed by mitotic division of secondary spermatocytes, and are found in dense clusters within the lobule lumen. The small nuclei (mean diameter 2.5 μm) contain dense chromatin and no cytoplasm is distinguishable.
5. Spermatozoa (Fig. 3**a**). Spermiogenesis occurs within the lobule lumen, the resulting spermatozoa having pear-shaped heads of mean diameter 1.6 μm. Spermatozoa have no distinct orientation within the lobule lumen.

Although lobules within the testis may vary slightly in the stage of spermatogenic activity, little lateral or longitudinal differentiation is apparent. Spermatogenesis in *A. graeffei* commenced in October each year and reached a peak in November and December (Fig. 3**b**). Following spawning, the testes entered a quiescent phase until the following season. No structural differences were found between the testes of brooding or non-brooding males (Fig. 3**c**,**d**).

In addition to spermatogenic cells, interstitial (Leydig) cells were found in clusters in the interstices of adjacent lobules, and singly in lobule walls (Fig. 2, 3). Development of the interstitial tissue followed a similar seasonal pattern to spermatogenic activity and reached a maximum at spawning.

Histology of the Ovaries

The ovary wall is composed of thick connective tissue, the tunica albuginea, containing elastic tissue, smooth muscle and an extensive network of blood vessels. Ovigerous folds of the tunica albuginea project into the ovarian lumen, and these folds carry the developing oocytes (Fig. 4**a**,**b**).

Nine stages of oocyte development were recognized:

1. Chromatin-nucleolus stage (Fig. 4**c**). Oocytes at this stage corresponded to the post-synaptic stage described by Yamamoto (1956b). These oocytes have a distinct nucleus (mean diameter 14 μm) with a single large nucleolus and a reticulum of chromatin threads. The cell boundary is indistinct. These oocytes occur singly or in nests of two or three.
2. Early perinucleolus stage (Fig. 4**c**). These oocytes range in diameter from 58 to 140 μm and vary in shape due to compression by developing oocytes. The large nucleus (26 to 50 μm in diameter) contains numerous basophilic nucleoli of varying sizes, and some chromatin material. The basophilic cytoplasm contains a dark-staining area adjacent to the nucleus. A thin unicellular follicle layer envelopes the oocyte. These oocytes are found throughout the ovary, but are far more numerous in the posterior region, particularly the oviduct.
3. Late perinucleolus stage (Fig. 4**d**). These oocytes range from 140 to 900 μm in diameter, and are generally irregular in shape due to compression by other oocytes. The nucleus is 50 to 160 μm in diameter and contains 18 to 32 basophilic nucleoli per section, distributed peripherally. Little or no chromatin material is apparent. The cytoplasm increases in size and becomes eosinophilic. Towards the end of this stage the granulosa layer (< 5 μm thick) forms from the follicle cells, and an outer

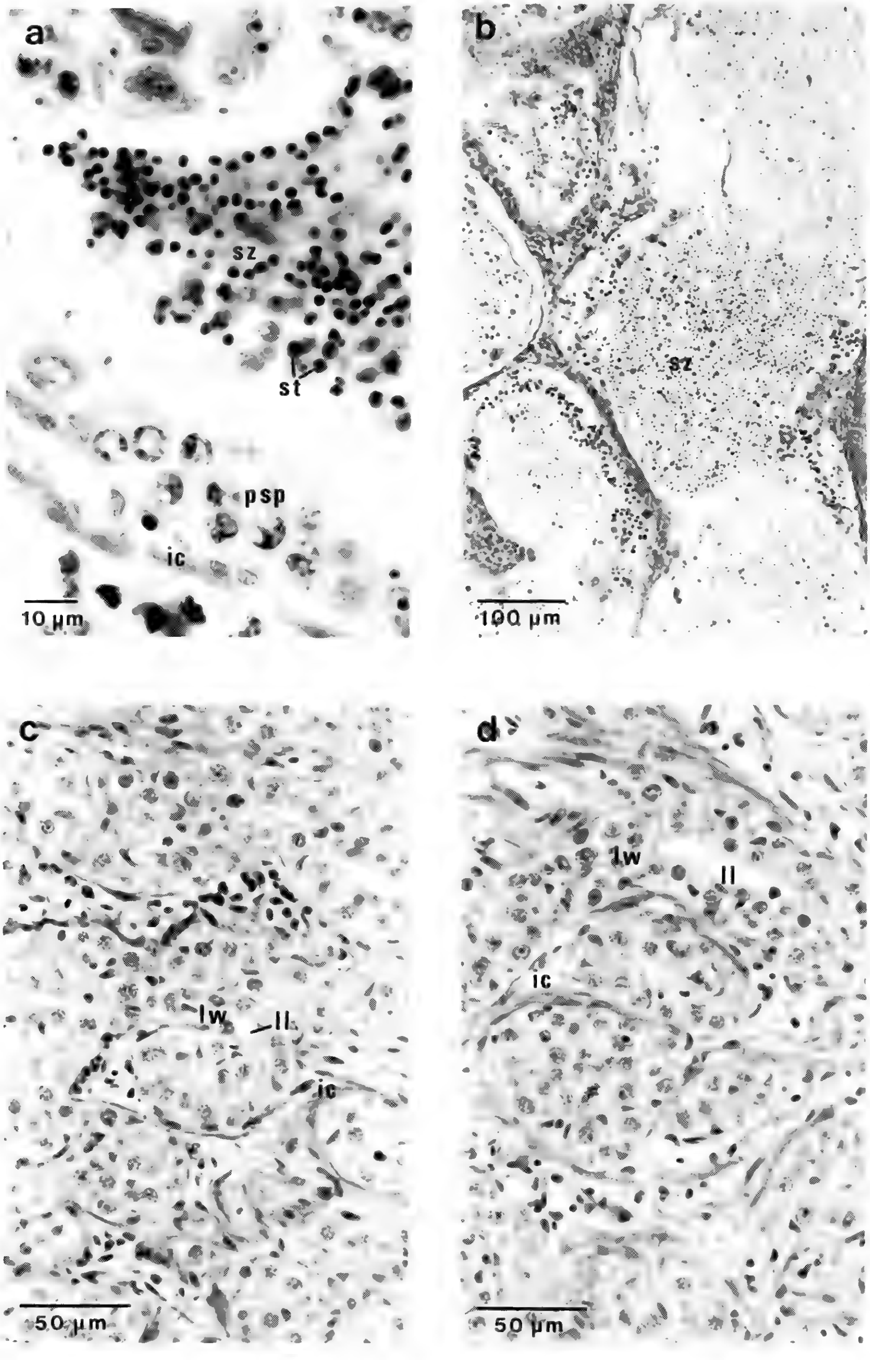

Fig. 3. Stages of spermatogenesis in *A. graeffei*: (**a**) portion of a lobule showing spermatids and spermatozoa in the lumen; (**b**) transverse section of a mature male testis sampled in November showing massed spermatozoa in the lobule lumen; (**c**) transverse section of the testis of a brooding male sampled in January; (**d**) transverse section of the testis of a non-brooding male sampled in January.

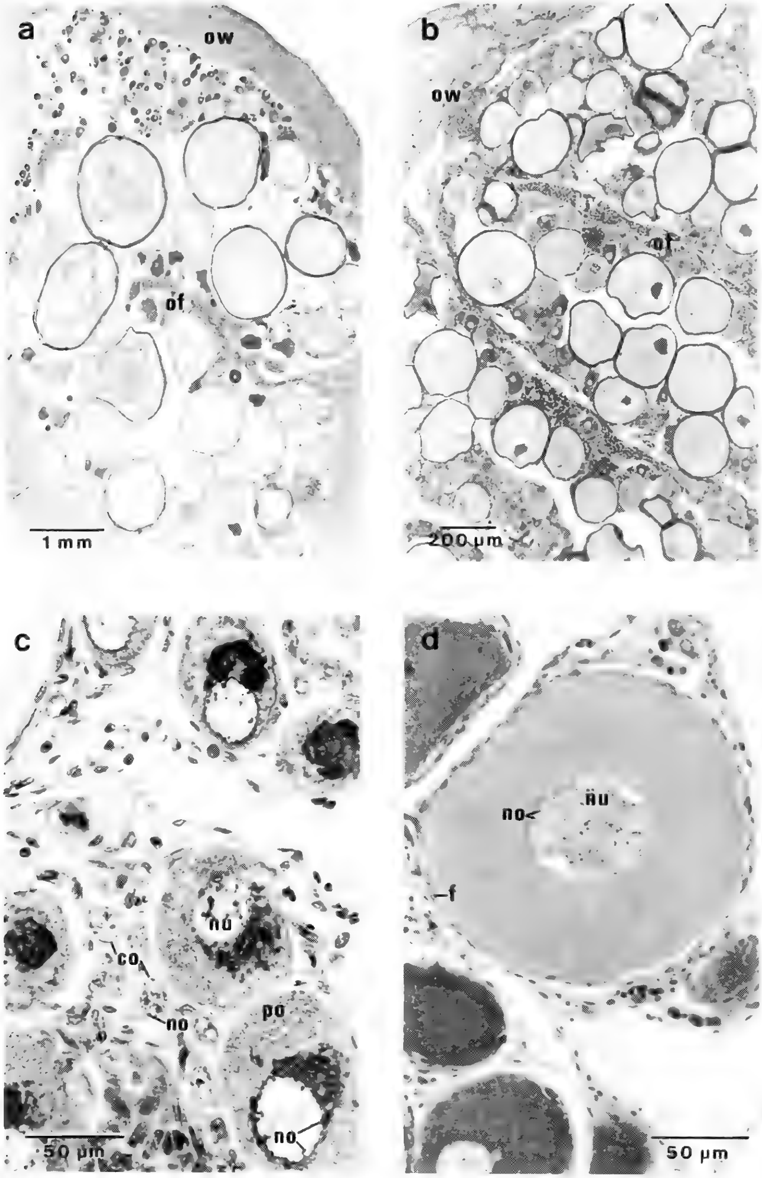

Fig. 4. Stages of oocyte development in *A. graeffei*: (**a**) transverse section through the anterior portion of a spent ovary showing the numerous small Group III oocytes and small numbers of larger Group II oocytes; (**b**) transverse section through the oviduct of a developing ovary showing early and late perinucleolus oocytes arranged on the folds of the tunica albuginea; (**c**) chromatin nucleolus oocytes and early perinucleolus oocytes from the anterior portion of a developing ovary; (**d**) late perinucleolus oocyte from the anterior portion of a resting ovary.
Key to abbreviations (Figs 4, 5, 6): bv = blood vessel; cl = corpus luteum; co = chromatin nucleolus oocyte; f = follicle; fl = follicle lumen; gr = granulosa; mvo = mature yolk vesicle oocyte; no = nucleolus; nu = nucleus; of = ovigerous fold; ow = ovary wall; po = perinucleolus oocyte; pyv = primary yolk vesicle; svo = secondary yolk vesicle oocyte; syv = secondary yolk vesicle; th = theca; yg = yolk granule; zp = zona pellucida; zr = zona radiata.
All sections stained with haematoxylin and eosin.

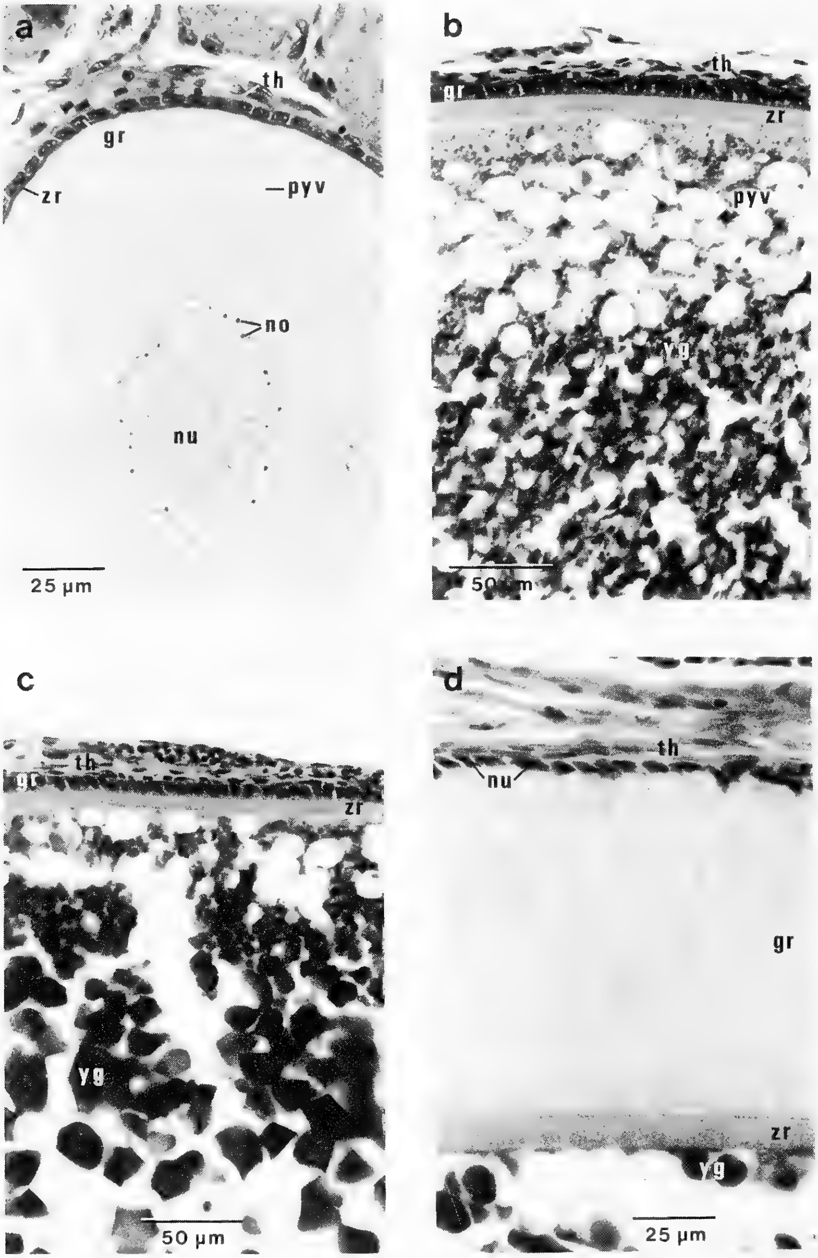

Fig. 5. Stages of yolky oocyte development in *A. graeffei*: (**a**) primary yolk vesicle oocyte from the anterior portion of a resting ovary; (**b**) primary yolk oocyte from the anterior portion of a developing ovary showing formation of yolk granules; (**c**) advanced yolk oocyte from the anterior portion of a developing ovary showing coalescence of yolk granules. Yolk vesicles have been compressed by continuing yolk formation; (**d**) ripe egg from the anterior portion of a ripe ovary. The granulosa has greatly increased in thickness and the cells have become syncytial. Radial banding is apparent in the zona radiata.

layer of connective tissue, the theca, is formed from the connective tissue of the ovary. An eosinophilic non-cellular membrane (< 2 μm thick) forms between the granulosa and the oocyte; this is the zona radiata.

4. Primary yolk vesicle stage (Fig. 5**a**). It is at this stage that the differentiation of oocytes into yolky and hyaline types becomes apparent. Oocytes at this stage range from 190 to 1300 μm, although those in the oviduct range from 190 to only 260 μm. The smaller oocytes of this stage (< 260 μm in diameter) are found in large numbers in the oviduct, while the larger ones are found in smaller numbers further forward in the ovary. This distribution parallels the distribution of yolky and hyaline oocytes in mature ovaries. The nuclei of these oocytes are weakly basophilic and range from 40 to 160 μm in diameter (40 to 70 μm diameter in the oviduct). The nucleoli (3 to 31 per section) are basophilic and are generally arranged peripherally in the nucleus. Yolk vesicles (7 to 12 μm in diameter) form centripetally in the cytoplasm. The granulosa is 5 to 10 μm thick and the zona radiata is 2 to 10 μm thick. Blood vessels are visible in the theca.
5. Primary yolk stage (Fig. 5**b**). Only the larger primary yolk vesicle stage oocytes in the body of the ovary develop to primary yolk stage. Oocytes at this stage range from 1.3 to 3.1 mm in diameter and are characterized by the presence of small yolk granules in the cytoplasm. Yolk vesicles do not change in size or distribution. The granulosa increases in thickness (10 to 12 μm) as does the zona radiata (10 to 12 μm).
6. Advanced yolk stage (Fig. 5**c**). Secondary yolk development commences in oocytes from 1.7 mm in diameter. The yolk granules coalesce to form larger granules (up to 50 μm) and an irregular yolk mass. The cells of the granulosa become columnar with distally arranged nuclei and vacuolated cytoplasm. The granulosa increases in thickness up to 110 μm, and in the final stages of development the granulosa cells become syncytial. The zona radiata ranges from 7 to 12 μm in width and shows distinct radial banding.
7. Ripe egg stage (Fig. 5**d**). Oocytes at this stage range from 11.0 to 13.7 mm in diameter in formalin fixed material. Ripe eggs are demersal, translucent yellow in colour and spherical to elliptical in shape. A network of blood vessels permeates the theca.
8. Secondary yolk vesicle stage (Fig. 6**a,b**). Hyaline oocytes alone proceed to this stage from primary yolk vesicle stage. Oocytes at secondary yolk vesicle stage range from 320 to 440 μm in diameter. The darkly staining nucleus (50 to 80 μm in diameter) is irregular in shape and contains 10 to 29 basophilic nucleoli per section, arranged peripherally. Secondary yolk vesicle formation is centrifugal — the area of secondary development, which is bounded by a distinct membrane, proceeds outward from the nucleus until it reaches the edge of the ooplasm. Secondary yolk vesicles range from 10 to 24 μm in width. The granulosa of oocytes at this stage is 17 to 24 μm in width. The granulosa cells develop from cuboidal to columnar with distally arranged nuclei. A thin zona radiata (< 2 μm) is present.
9. Mature yolk vesicle stage (Fig. 6**c,d**). These oocytes range from 460 to 3300 μm in diameter and represent the final stage of development of hyaline oocytes before ovulation. This stage is characterized by the proliferation of secondary yolk vesicles which occupy the entire ooplasm. The nucleus is weakly basophilic (60 to 90 μm in diameter) and contains 25 to 30 large nucleoli per section arranged peripherally, as well as numerous smaller nucleoli and chromatin material distributed throughout the nucleus. The peripheral yolk vesicles remain distinct, but the inner vesicles show a disorganized appearance, suggesting that they may coalesce. The granulosa increases in width from 24 to 110 μm and the cells become syncytial; the nuclei are distally arranged and the cytoplasm is heavily vacuolated. A zona pellucida (< 2 μm

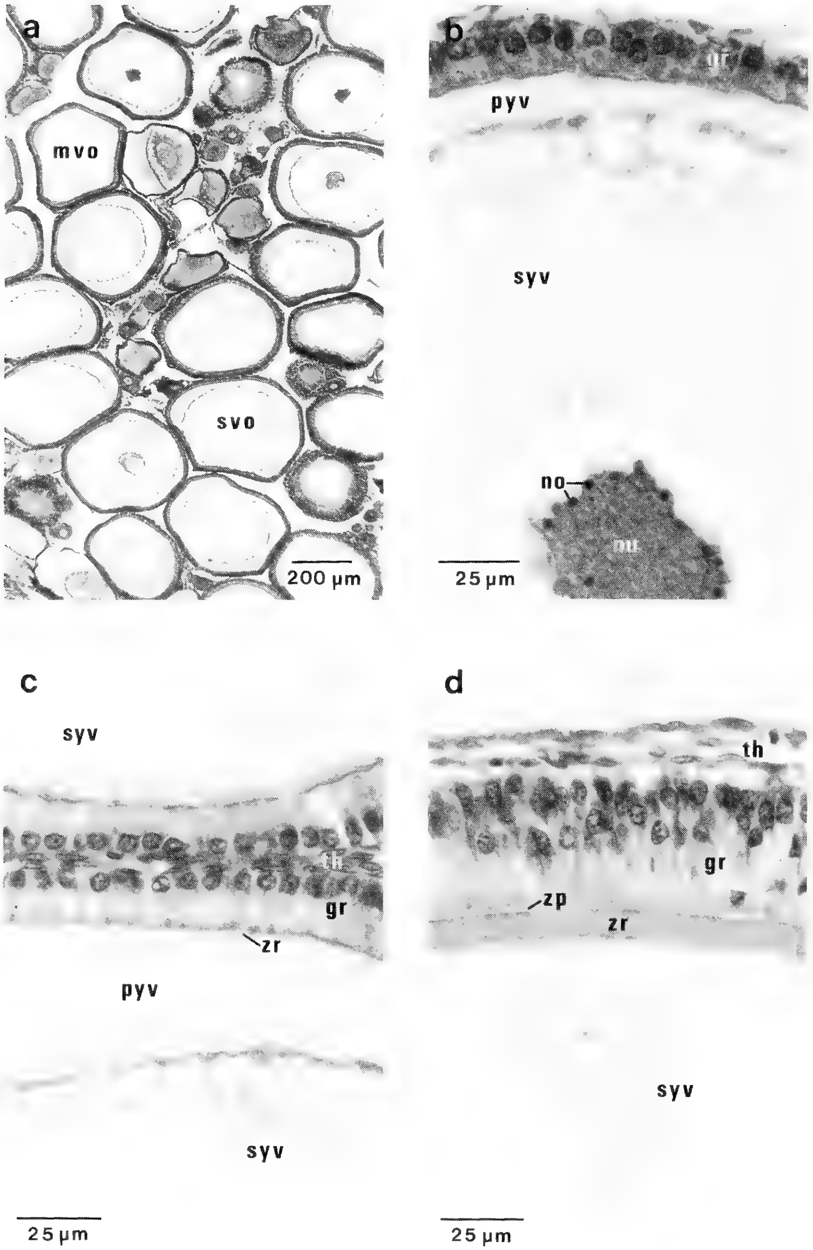

Fig. 6. Stages of hyaline oocyte development in *A. graeffei*: (**a**) transverse section of the oviduct of a developing ovary, showing the arrangement of secondary and mature yolk vesicle oocytes; (**b**) secondary yolk vesicle oocyte from the posterior portion of a ripe ovary, showing the columnar granulosa cells with distally arranged nuclei; (**c**) mature yolk vesicle oocyte (above) and secondary yolk vesicle oocyte (below) from the posterior portion of a ripe ovary, showing the delineation between the areas of primary and secondary yolk vesicles; (**d**) mature yolk vesicle oocyte from the posterior portion of a ripe ovary. The zona radiata has increased greatly in thickness and the zona pellucida is visible.

in thickness) forms between the granulosa and the zona radiata, which is up to 12 μm in thickness.

Both yolky and hyaline oocytes of *A. graeffei* followed an annual pattern of development. Oocyte development reached a peak in November, when spawning occurred (Rimmer, 1985a). The follicles of ovulated yolky and hyaline oocytes are retained after ovulation. The cells of the granulosa and theca form a compact mass which is generally termed the (post-ovulatory) corpus luteum. In resting ovaries the corpus luteum becomes pigmented with a yellow pigment which is retained through histological processing. The corpora lutea are resorbed during the resting stage (March to June) and are not present in developing ovaries.

Spent ovaries of *A. graeffei* contained oocytes up to late primary yolk stage in the body of the ovary (Fig. 4**a**), while large numbers of oocytes up to early primary yolk vesicle stage were retained in the oviduct region (Fig. 4**b**). The ovaries of immature *A. graeffei* contained oocytes up to primary yolk vesicle stage, while the oviducts contained oocytes up to the stage of initial secondary yolk vesicle formation.

DISCUSSION

Testes

Spermatogenesis in *A. graeffei* followed the pattern seen in other teleosts (Lehri, 1967; Davis, 1977; Nagahama, 1983), but the structure of the testes in *A. graeffei*, and in other ariids, is far simpler than in many siluroids (Loir *et al.*, 1989). The testes of the freshwater plotosid *Tandanus tandanus* have specialized spermatogenic and sperm storage regions (Davis, 1977), while the testes of many siluroid families have accessory structures, spermatic vesicles, which show seasonal changes concomitant with those of the testes (Nawar, 1959; Sircar, 1966; Lehri, 1967; Nayyar and Sundararaj, 1969, 1970; Loir *et al.*, 1989). In *A. graeffei*, the testicular structure is homogeneous throughout the testis and all regions function as both spermatogenic and sperm storage areas.

Spermatogenic activity followed the same annual pattern as seen in gravimetric changes in the testes (Rimmer, 1985a). However, the higher gonadosomatic ratios of brooding males, compared with non-brooding males, in January (Rimmer, 1985a) were not associated with the proliferation of a particular cell type in the testes. Testes from both brooding and non-brooding males from January samples had similar distribution of spermatogenic and interstitial tissue (Fig. 3**c**,**d**).

Ovaries

The structure of the ovaries in *A. graeffei* is generally similar to that described for other ariids (Rimmer and Merrick, 1983). The sequence of oocyte development observed histologically in *A. graeffei* can be used to identify the three groups of oocytes evident in macroscopic examination of maturing and ripe oocytes. Group I oocytes are at advanced yolk and ripe egg stages; these are the oocytes which are fertilized at spawning. Group II comprises yolky oocytes at primary yolk stage which are retained at spawning and develop into the Group I oocytes of the following season. Group III oocytes are hyaline oocytes at mature yolk vesicle stage which are ovulated at spawning. Hyaline oocytes form part of the spawned egg mass but are not fertilized (Rimmer and Merrick, 1983); they apparently decompose or are washed out of the male's mouth in the water flow (Rimmer, 1985b).

The sequence of development of yolky oocytes in *A. graeffei* followed, with minor differences, the pattern seen in other teleosts (Nagahama, 1983). In contrast, the development of hyaline oocytes in *A. graeffei* differed markedly. This phenomenon has also been reported in *A. thalassinus*, where hyaline and yolky oocytes differentiated from 500 μm diameter (Gabaeva and Ermolina, 1972); this differential development in oocytes of *A. graeffei* was evident from about 300 μm diameter.

Yolk vesicle formation in teleost oocytes generally follows a centripetal sequence of development (Yamamoto, 1956a; Lehri, 1968; Ginzburg, 1972; Guraya *et al.*, 1975; Davis, 1977). This was observed in primary yolk vesicle formation in oocytes of *A. graeffei*, but secondary yolk vesicle formation followed a centrifugal sequence. Golgi bodies in the ooplasm have been implicated in the formation of yolk vesicles in teleosts (Yamamoto, 1956c; Ginzburg, 1972). In *A. graeffei*, the centrifugal development of secondary yolk vesicles bounded by a membrane apparently originating from the nuclear region of the oocyte suggests that the oocyte nucleus is closely involved in secondary yolk vesicle formation. Although the primary yolk vesicle stages of hyaline and yolky oocytes were initially identical in structure, yolky oocytes grew larger than hyaline oocytes. Yolk vesicles of yolky oocytes were soon restricted to a narrow cortical zone by the formation of yolk granules. In hyaline oocytes of primary yolk vesicle stage, the yolk vesicles remained *in situ* until obliterated by secondary yolk vesicle formation. In the secondary yolk vesicle stage of hyaline oocyte development, secondary yolk vesicles were distributed throughout the oocyte.

Yolk formation in yolky oocytes of *A. graeffei* followed the pattern described for other teleosts (Yamamoto, 1957, 1958; Lehri, 1968; Guraya *et al.*, 1975; Davis, 1977; Nagahama, 1983). Yolk granules initially formed near the yolk vesicles and proliferated centripetally to eventually occupy the entire cytoplasm. Extensive fusion of yolk granules formed a large yolk mass with large granules (up to 50 μm) embedded in it. There was no yolk formation in hyaline oocytes of *A. graeffei*. Similarly, Gabaeva and Ermolina (1972) noted that the hyaline oocytes of *A. thalassinus* did not undergo vitellogenesis.

Hyaline oocytes of the type seen in *A. graeffei* have only been described in the Ariidae. Although many ariid genera are poorly known, gonadal structure, including the presence of hyaline oocytes, appears to be consistent throughout the family (Rimmer and Merrick, 1983). Several possible roles have been suggested for the hyaline oocytes of ariids. Gunter (1947) suggested that they were swallowed by the male to provide a nutritious meal before the long fast during buccal incubation, but it is unlikely that the male could remove the small hyaline eggs without damaging the larger fertilized eggs. Dmitrenko (1970) suggested that the positively buoyant hyaline eggs of *A. thalassinus* prevented the egg mass from sinking into the substrate before it could be fertilized and then ingested by the male. However, the hyaline oocytes of *A. graeffei* sink in freshwater, and the success of many ariid species in freshwater habitats suggests that the flotation role of these oocytes is of little functional significance.

Le Bail *et al.* (1984) suggested a number of possible roles for these oocytes, including the attraction of males, adhesion of oocytes, blockage of the oesophageal opening of the male and nutrition of the incubated juveniles. A further suggestion was that these are relic oocytes which were rendered non-functional during the evolution of the reproductive strategy of buccal incubation, with the concomitant reduction in fecundity and increase in oocyte size.

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The Lichens of Norfolk Island
2: The Genera *Cladonia*, *Pertusaria*, *Pseudocyphellaria* and *Ramalina*

JOHN A. ELIX, HEINAR STREIMANN and ALAN W. ARCHER

ELIX, J. A., STREIMANN, H., & ARCHER, A. W. The lichens of Norfolk Island. 2: The genera *Cladonia*, *Pertusaria*, *Pseudocyphellaria* and *Ramalina*. *Proc. Linn. Soc. N.S.W.* 113 (1), 1992: 57-76.

Twenty-four species in the genera *Cladonia*, *Pertusaria*, *Pseudocyphellaria* and *Ramalina* which currently grow on Norfolk Island are examined critically. Each species is described fully (including chemistry) and its distribution is recorded. *Pertusaria montpittensis* A. W. Archer, *Pertusaria nebulosa* A. W. Archer, *Pertusaria norfolkensis* A. W. Archer and *Pertusaria verdonii* A. W. Archer are described as new to science.

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KEY WORDS: Cladoniaceae, chemotaxonomy, Norfolk Island, lichens.

INTRODUCTION

This paper is a continuation of a series on the lichens of Norfolk Island (Elix and Streimann, 1989). The fruticose genera *Cladonia* and *Ramalina* are cosmopolitan in distribution. *Cladonia* is more common on soil and dead wood in cooler or temperate areas and thus is relatively rare in Norfolk Island (7 species). *Ramalina* is widely distributed in warm temperate and tropical regions (particularly in maritime and hinterland environments) and so is a very common corticolous genus on the island with 6 species, one of which is endemic. On the other hand representatives of the genus *Pseudocyphellaria* are found mainly in the Southern Hemisphere, and three of the four species observed on Norfolk Island have restricted Australasian distributions. *Pertusaria*, the fourth genus dealt with here, is a large genus of cosmopolitan lichens in which the species characteristically produce crustose thalli in which the apothecial development takes place within thalline protruberances. As in many subtropical areas, the genus is common on Norfolk Island, being represented by 7 species, three of which are endemic.

COLLECTIONS AND SITES

Specimens Examined

Collectors and lodgement of specimens examined are as follows: *JAE* were collected by *J. A. Elix* and *H. Streimann* and are held in ANUC: *HS* were collected by *H. Streimann* and are held in CBG with duplicates distributed as indicated.

Twenty five collecting sites were reported previously (Elix and Streimann, 1989) and a further nine are recorded here together with corrected details for S16 (Fig. 1 shows the location of the 34 sites):

S16: *Psidium* and *Olea* infested lowland forest, Duncombe Bay Road, near entrance to Mt Pitt Reserve, 29°00′30″S, 167°56′E, 50 m, 7.xii. 1984.

S26: mixed subtropical rainforest, near Broken Pine, Mt Pitt Reserve, 29°01′30″S, 167°56′20″E, 220 m, 1.xii.1984.

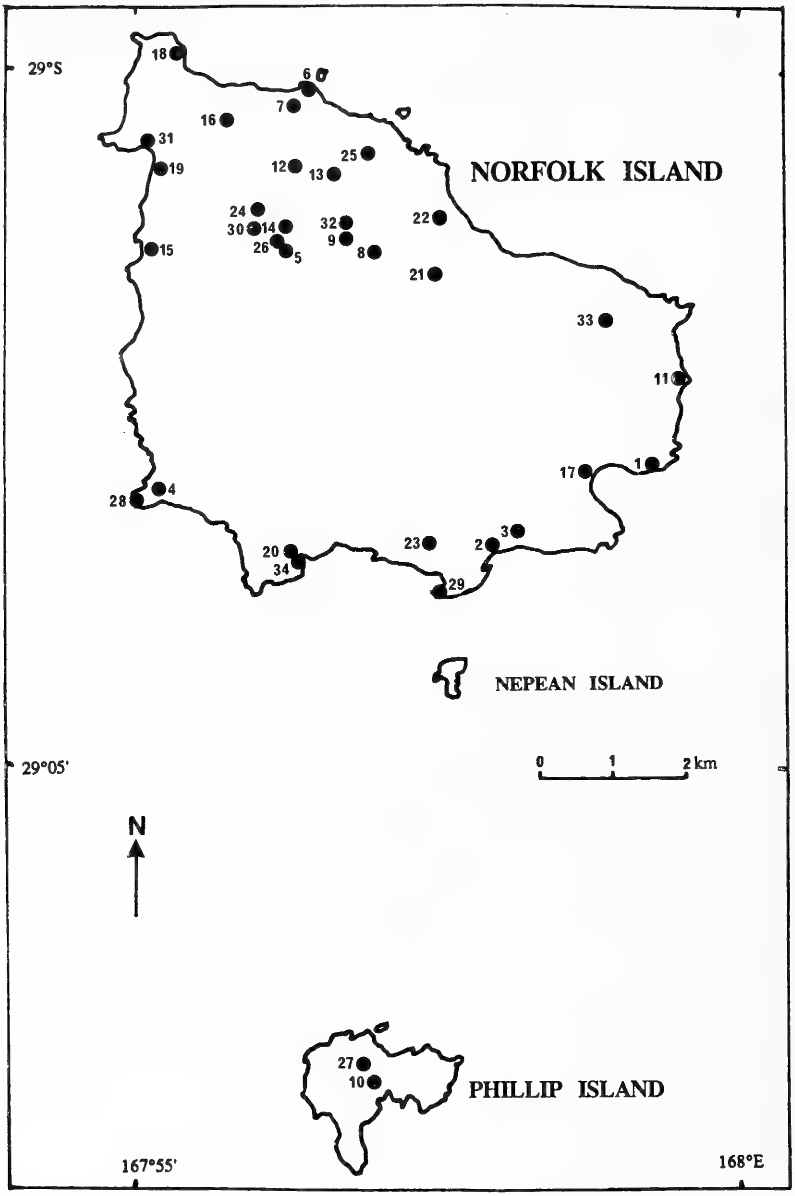

Fig. 1. Collection Sites on Norfolk Island.

S27: barren hillside with remnant *Araucaria heterophylla*, Red Road Valley, Phillip Island, 29°07′S, 167°56′45″E, 60 m, 4.xii.1984.

S28: rocky headland with mixed exotic and *Araucaria* woodland, Rocky Point Reserve, 29°03′S, 167°55′20″E, 40 m, 5.xii.1984.

S29: rocky foreshore and bay, Point Hunter and Emily Bay, 29°04′S, 167°58′E, 3 m, 5.xii.1984.

S30: open woodland, slopes of Mt Bates, above the road opposite King Fern Valley trail, Mt Pitt Reserve, 29°01′S, 167°56′20″E, 280 m, 7.xii.1984.
S31: grassland with scattered *Araucaria heterophylla*, Anson Bay Reserve, 29°00′30″S, 167°55′E, 40 m, 7.xii.1984.
S32: mixed subtropical rainforest with open areas, track at end of Selwyn Pine Road, 29°01′S, 167°56′30″E, 200 m, 8.xii.1984.
S33: open woodland, end of Stockyard Road, 29°01′30″S, 167°59′E, 65 m, 10.xii.1984.
S34: rocks in grassland and along foreshore, Bumboras Reserve, 29°03′30″S, 167°56′20″E, 10 m, 10.xii.1984.

CLADONIA Hill ex Browne

Artificial Key to *Cladonia* in Norfolk Island

1. Apothecia or pycnidia red 2
1. Apothecia brown or lacking 3

2. Podetia ecorticate, farinose sorediate .... *C. bacillaris*
2. Podetia mainly corticate, ± granular sorediate .... *C. floerkeana*

3. Podetia esorediate, squamulose, with thamnolic acid .... *C. acuta*
3. Podetia sorediate at least in part, lacking thamnolic acid 4

4. Medulla P+ orange, containing psoromic acid .... *C. subpityrea*
4. Medulla P+ red, containing fumarprotocetraric acid 5

5. Podetia mainly corticate, sorediate below margins of scyphi only ... *C. fruticulosa*
5. Podetia ecorticate and sorediate towards apices 6

6. Podetia containing fumarprotocetraric acid and homosekikaic acid .. *C. adspersa*
6. Podetia containing atranorin and fumarprotocetraric acid .... *C. praetermissa*

Cladonia acuta (Taylor) Nyl. ex Hue, *Nouv. Arch. Mus. Hist. Nat. Paris*, ser. 3,**2**: 32 (1890).
Cenomyce acuta Taylor, *Hooker's London J. Bot.* **6**: 186 (1847).
Cladonia squamosa var. *acuta* (Taylor) Müll. Arg., *Flora, Regensburg* **71**: 19 (1888).
Cladonia rigida var. *acuta* (Taylor) A. W. Archer, *Muelleria* **7**: 175 (1990).
Type: 'Islands of the Pacific' ('Pacific' on label), Hb. Hooker (FH-holotype, H-isotype); contains thamnolic, decarboxythamnolic and homosekikaic acids (Stenroos, 1988).
Cladonia squamosula Müll. Arg. var. *subsquamosula* A. W. Archer, *Muelleria* **6**: 384 (1987).
Type: Australia, New South Wales, Wentworth Falls, 90 km west of Sydney, 150°22′E, 33°45′S, alt. *ca* 900 m, 1.vi.1985, *Archer 1751* (MEL 1048970 — holotype, NSW — isotype).

Primary thallus of persistent squamules, 1-3 mm long, 0.5-1.0 mm wide, subpalmately lobed, margins crenate to incised. ***Podetia*** arising from the upper surface of the primary squamules, simple or rarely branched, cylindrical or tapering towards the apices, 10-20 mm tall (rarely to 25 mm), 0.5-1.5 mm diam., escyphose, sterile podetia acute; podetia ecorticate and squamulose, squamules *ca.* 0.3 mm long near the base of the podetia, becoming smaller and isidioid, 0.1 mm long, near the apices. ***Apothecia*** brown to dark brown, clustered, 0.5-1.5 mm diam., terminal on podetia, the tips of fertile podetia often open to the interior; spores eight per ascus, colourless, simple, ellipsoid, 12-15 x 3-4 μm. ***Pycnidia*** not seen.

Chemistry: Thallus K+ yellow, KC-, P+ orange; containing thamnolic acid (major), homosekikaic acid (major), sekikaic acid (trace), hyperhomosekikaic acid (trace) and barbatic acid (in the apothecia).

Cladonia acuta is an Australasian species growing on dead wood in moist, semi-shaded positions. It is widespread in southern Australia (W.A., S.A., Tas., Vic., N.S.W.) but rare in Norfolk Island. A previous report of *Cladonia squamosa* (Scop.) Hoffm. from Norfolk Island (Riedl, 1988) may well refer to *C. acuta*, but the chemistry of the specimen was not reported and it was unavailable for examination.

Specimen Examined:
NORFOLK ISLAND. On stump of *Cyathea brownii*, Mt Pitt, *R. Goldsack*, 27.xii.1981 (NSW).

Cladonia adspersa Mont. & v. d. Bosch, in Miquel, *Pl. Jungh.* **4**: 456. 1855 (1857).
Type: Indonesia, Java, ad terram muscosam, ad basin truncorum, *Junghuhn & Teysmann* (PC, here selected as lectotype); contains fumarprotocetraric, protocetraric and homosekikaic acids and the substance Cph-2 (Stenroos, 1988).

Primary thallus of small, thick squamules, squamules persistent or evanescent, 1.0-3.0 mm long, 0.5-1.0 mm wide, incised, occasionally sorediate on the margins or densely granular-sorediate. ***Podetia*** arising from the upper surface of the primary squamules, very variable, cylindrical or tapering towards the apices, 10-30 mm tall (rarely to 50 mm), 0.5-1.5 (2.5) mm diam., axils closed; tips subulate, blunt or provided with shallow, narrow scyphi 1.0-2.0 mm wide, sometimes proliferating from margins; surface of podetia corticate, or corticate at base and lower portion of podetia, cortex continuous or areolate, ecorticate areas often brown, coarsely granular-sorediate, or with corticate granules or squamules, squamules thick, roundish to somewhat elongated, often projecting downwards, easily eroded and exposing the pellucid sterome. ***Apothecia*** convex, pale brown to mid-brown, 2.0-2.5 mm diam., terminal on podetia or on short, corticate proliferations on the margins of the scyphi; spores eight per ascus, colourless, simple, ellipsoid, 7-10 x 3-4 μm. ***Pycnidia*** on apices of podetia, on short marginal proliferations of the scyphi or on basal squamules, conidia 5-6 x 1 μm, slightly arcuate.

Chemistry: Thallus K-, P+ brick red; containing fumarprotocetraric acid, protocetraric acid (trace), homosekikaic acid, sekikaic acid (trace), 4′-*O*-methylnorhomosekikaic acid (trace) and ± unknowns Cph-1 and Cph-2 (traces).

This species has been synonymized with *Cladonia ramulosa* (With.) Laundon by Stenroos (1988) but *C. adspersa* differs chemically, containing medullary homosekikaic acid in addition to fumarprotocetraric acid. These two species also exhibit quite distinctive geographic distributions — *C. ramulosa* is cosmopolitan but *C. adspersa* is restricted to eastern Asia and Australasia. Furthermore Yoshimura (1967) distinguished *C. adspersa* from *C. ramulosa* by the presence of a pellucid sterome (this being semi-pellucid in *C. ramulosa*).

C. adspersa is an Asian-Australasian species growing on moist soil banks, rocks and dead wood in moist, semi-shaded positions. It is widespread in Australia (all States) and also occurs in Malaysia, Indonesia, Papua New Guinea, New Zealand, Solomon Islands and Fiji. Common in Norfolk Island.

Specimens Examined:
NORFOLK ISLAND. On soil bank, S9, *JAE 18456*; on *Cyathea* stump, S12, *JAE 18593,*

HS 34369, 34384; on soil of road bank, S24, *JAE 18832, HS 34850*; on rocks, S32, *JAE 18740, HS 34689.*

Cladonia bacillaris Nyl., *Not. Sällsk. Fauna Fl. Fenn. Förh.* **8**: 179 (1866).
Type: not designated.

Primary thallus of small, persistent squamules, 0.5-1.0 mm wide, 0.5-1.5 mm long, margins with or without soredia. ***Podetia*** growing from the basal squamules, pale green, simple or rarely branched near the apices, escyphose, 0.8-1.5 mm tall, 0.5-1.5 mm diam., ecorticate and completely covered with farinose soredia, rarely with a short, smooth corticate area at the base, with a slight swelling below the apothecium; sterile podetia blunt or rarely subulate, rarely squamulose from the basal corticate areas. ***Apothecia*** and **pycnidia** not seen in Norfolk Island material. Nowak and Tobolewski (1975) report apothecia that are red, convex, terminal, 0.5-1.0 mm diam.; spores 8 per ascus, colourless, simple, ellipsoid, 9-11 x 2-3 μm.

Chemistry: Thallus K-, KC-, P-; containing barbatic acid (major), 4-*O*-demethylbarbatic acid (trace), unknown (trace). This was the only chemotype observed on Norfolk Island but didymic acid and condidymic acid are common accessory compounds in *C. bacillaris* from other areas.

This species recently was reported to be conspecific with *Cladonia macilenta* Hoffm. (Christensen, 1987), but as the two taxa differ chemically (*C. macilenta* contains thamnolic acid) and in our opinion morphologically (*C. bacillaris* has pale green-grey, somewhat blunt, unbranched podetia while *C. macilenta* brown-white, subulate, sparingly branched podetia) the name *C. bacillaris* is retained here.

C. bacillaris is a cosmopolitan species growing on dead wood or on soil. It is widespread in both cool-temperate and tropical regions of the world and relatively common in unpolluted, moist coastal and hinterland habitats. In Australasia it is known from southern and eastern Australia, New Zealand and Papua New Guinea. Rare in Norfolk Island.

Specimen Examined:
NORFOLK ISLAND. On soil of semi-shaded roadside, S24, *HS 34849.*

Cladonia floerkeana (Fr.) Flörke, *Clad. Comment.*: 99 (1828).
Cenomyce floerkeana Fr., *Lich. Suec. Exsicc.*: 82 (1824).
Type: (Sweden) not designated.

Primary thallus of small, inconspicuous basal squamules, 0.5-1.0 mm wide, 1.0-2.0 mm long. ***Podetia*** growing from the basal squamules, simple or sparingly branched near the apices, escyphose, sterile podetia subulate, 5-10 mm tall, 0.5-1.0 mm diam., the major part of the podetia and the area below the apothecia corticate, the cortex scabrose to subverrucose, the remainder ecorticate and minutely squamulose or granular-sorediate, or the podetia completely corticate. ***Apothecia*** common, red, convex, terminal, 1-3 mm diam.; spores eight per ascus, colourless, simple, ellipsoid, 8-10 x 2.5-4 μm. ***Pycnidia*** red, minute, urceolate, on apices of podetia, conidia not seen.

Chemistry: Thallus K+ yellow or K-, KC-, P+ yellow or P-; containing barbatic acid (major), 4-*O*-demethylbarbatic acid (trace), didymic acid (major), thamnolic acid (± major) and condidymic acid (trace).

C. floerkeana is a cosmopolitan species growing on dead or burnt wood or on soil. It is widespread in both cool-temperate and tropical regions of the world and relatively common in unpolluted, moist coastal and hinterland habitats. In Australasia it is known from Australia (all States except W.A., N.T.), New Zealand, Papua New Guinea and New Caledonia. Rare in Norfolk Island.

Specimens Examined:
NORFOLK ISLAND. On old post, S12, *JAE 18555*; Norfolk Island, *J. & T. Gilbert*, s.n. (HO 53167).

Cladonia fruticulosa Krempelh., *Verh. zool.-bot. Ges. Wien* **30**: 331 (1882) ('1881').
Type: Australia. Rockinghams Bay [Rockingham Bay], Queensland, *J. Dallachy* s.n. (M — lectotype, MEL, NSW, REN-Abb — isolectotypes); contains fumarprotocetraric acid (Archer, 1986).

Primary thallus of persistent squamules, 1.5-5.0 mm long, 1.0-2.0 mm wide, slightly to deeply laciniate, often incurved, green above, white, cottony to partly granular-sorediate below. ***Podetia*** arising centrally or more often marginally from the primary squamules, simple or branched by scyphus formation or by podetial squamules which may become elongated and producing new podetia (especially in the apical parts of the podetia), frequently flexuose or somewhat deformed; 10-30 mm tall (rarely to 50 mm), 0.5-1.5 (2.5) mm diam., axils closed; tips blunt or scyphose, scyphi 0.5-4.0 mm wide, shallow, rather abruptly flaring, often slightly deformed; surface of podetia varying from smooth or roughly corticate to partly sorediate, with occasional podetial squamules; soredia granular, ± in well-defined soralia, frequently eroded and exposing the semi-pellucid sterome. ***Apothecia*** pale brown to mid-brown, 1.0-2.0 mm diam., stipitate or marginal on the scyphi or on basal squamules; spores eight per ascus, colourless, simple, ellipsoid, 7-8 x 3-4 μm. ***Pycnidia*** dark brown, urceolate, on apices of podetia, marginal on the scyphi or on basal squamules, conidia 7-8 x 1 μm, slightly arcuate.

Chemistry: Thallus K-, P+ red; containing fumarprotocetraric acid (major), protocetraric acid (trace).

This species has been synonymized with *Cladonia subpityrea* Sandst. by Stenroos (1988) but *C. fruticulosa* differs chemically, containing medullary fumarprotocetraric and protocetraric acids rather than the psoromic and 2′-*O*-demethylpsoromic acids present in *C. subpityrea*. *C. fruticulosa* has been reported to produce smaller, more powdery soredia than does *C. subpityrea* (Stenroos, 1988), but too few specimens were available in the present work to enable valid comparisons.

C. fruticulosa is a circum-Pacific species commonly growing on moist soil banks in open areas, but also occurring on rocks, the base of trees and dead wood. It is widespread in Japan, Taiwan, India, Malaysia, Indonesia, Papua New Guinea, eastern Australia (Qld., northern N.S.W.), Solomon Islands, Fiji, Hawaii, the Society Islands and Central America. Uncommon in Norfolk Island.

Specimens Examined:
NORFOLK ISLAND. On moist soil bank, S17, *JAE 18754, HS 34696.*

Cladonia praetermissa A. W. Archer, *Muelleria* **5**: 273 (1984).
Type: Australia, New South Wales, Epping, near track by side of Devlin's Creek, 151°05′E, 33°45′S, alt. *ca* 80 m, 18.vii.1982, *Archer 1376* (MEL 1036220-holotype, H, NSW-isotypes).

Primary thallus of conspicuous and persistent squamules, 6-10 mm long, 2-5 mm wide, pale green above, sometimes with soredia fallen from the podetia, white below, the margins crenate or somewhat incised. ***Podetia*** arising from the basal squamules, simple or rarely branched near the apices, subulate or somewhat cylindrical, 5-15 mm tall (rarely to 20 mm), 0.3-0.7 mm diam., corticate at the base and becoming ecorticate and granular-sorediate at the tip; sometimes squamulose near the base. ***Apothecia*** rare, pale brown to brown, terminal on the branches, convex, 0.2-0.6 mm diam.; spores eight per ascus, colourless, simple, ellipsoid, 7-10 x 3-4 µm. ***Pycnidia*** not seen.

Chemistry: Thallus K+ pale yellow, KC-, P+ red; containing atranorin (major), fumarprotocetraric acid (major), protocetraric acid (trace).

C. praetermissa is a widespread Australasian species growing on sandy soil in moist, semi-shaded positions. It is known from Australia (all States except N.T.) and the North Island of New Zealand. Common in Norfolk Island.

Specimens Examined:
NORFOLK ISLAND. On charred stump, S4, *JAE 18206*; on soil bank, S9, *JAE 18453, 18454*; on soil at edge of large pit, S12, *HS 34234*; on soil over volcanic rocks, S18, *JAE 18763*; on soil, Mt. Pitt Reserve, 167°56′E, 29°04′S, 130 m, *R. Goldsack*, 25.xii.1981 (A. Archer 1226, NSW).

Cladonia subpityrea Sandst. in Keissler, *Ann. Naturhist. Mus. Wien* **42**: 61 (1928); in Zahlbr., *Krypt. exs. Vindob.* 3056 (1928) (printed label).
Type: The Philippines. Luzon. Manila: Dumulmog, alt. c. 1500 m, *Merrill*, Krypt. exs. Vindob.3056 (W — lectotype, H, GB — isolectotypes); contains usnic and psoromic acids (Stenroos, 1988). For further synonymy see Stenroos (1988).

Primary thallus of persistent squamules, 1.5-5.0 mm long, 1.0-2.0 mm wide, slightly to deeply laciniate, often incurved, green above, white, cottony to partly granular-sorediate below. ***Podetia*** arising centrally or more often marginally from the primary squamules, simple or branched by scyphus formation or by podetial squamules which may become elongated and produce new podetia (especially in the apical parts of the podetia), frequently flexuose or somewhat deformed; 10-30 mm tall (rarely to 50 mm), 0.5-1.5 (2.5) mm diam., axils closed; tips blunt or scyphose, scyphi 0.5-4.0 mm wide, shallow, rather abruptly flaring, often slightly deformed; surface of podetia varying from smooth or roughly corticate to partly sorediate, with occasional podetial squamules; soredia granular, ± in well defined soralia, frequently eroded and exposing the semi-pellucid sterome. ***Apothecia*** pale brown to mid-brown, 1.0-2.0 mm diam., stipitate or marginal on the scyphi; spores eight per ascus, colourless, simple, ellipsoid, 7-8 x 3-4 µm. ***Pycnidia*** dark brown, urceolate, on apices of podetia, marginal on the scyphi or on basal squamules, conidia 7-8 x 1 µm, slightly arcuate.

Chemistry: Thallus K-, P+ intense yellow. Containing psoromic acid (major), 2′-*O*-demethylpsoromic acid (minor) and ± usnic acid or isousnic acid (major).

This species has been synonymized with *Cladonia fruticulosa* Krempelh. by Stenroos (1988) but *C. subpityrea* differs chemically, containing medullary psoromic and 2′-*O*-demethylpsoromic acids rather than the fumarprotocetraric and protocetraric acids present in *C. fruticulosa. C. subpityrea* has been reported to produce larger, less powdery soredia than does *C. fruticulosa* (Stenroos, 1988), but too few specimens were available in the present work to enable valid comparisons.

C. subpityrea is an Asian-Australasian species commonly growing on moist soil banks in open areas, but also occurring on rocks, the base of trees and dead wood. It is widespread in Japan, Taiwan, India, Réunion Is., Malaysia, Indonesia, Papua New Guinea, eastern Australia (Qld., northern N.S.W.), Solomon Islands, Fiji, Hawaii and the Society Islands. Uncommon in Norfolk Island.

Specimens Examined:
NORFOLK ISLAND. On soil bank, S9, *JAE 18455*; on shaded road cutting, S5, *HS 31964.*

PERTUSARIA de Candolle

Artificial Key to *Pertusaria* in Norfolk Island

1. Saxicolous, dull or pale yellow, sorediate, lacking verrucae and spores . . . . *P. persulphurata*
1. Corticolous, variously coloured, with or without fertile verrucae, soredia present or absent 2

2. Thallus lacking verrucae, isidiate or sorediate 3
2. Thallus with verrucae, lacking isidia and soredia 4

3. Thallus sorediate, pale greenish-grey, with scattered soralia; KC+ violet, picrolichenic acid present . . . . *P. verdonii*
3. Thallus isidiate, pale olive-green; KC-, stictic acid present . . . . *P. montpittensis*

4. Thallus yellow, 2 spores per ascus, thiophaninic acid present . . . . *P. thiospoda*
4. Thallus pale green, off-white or pale grey, 4 or 8 spores per ascus, thiophaninic acid absent 5

5. Spores 4 per ascus, thallus pale grey . . . . *P. nebulosa*
5. Spores 8 per ascus; thallus pale green to off-white 6

6. Thallus off-white, K+ red, norstictic acid present; spores ellipsoid, 45-55 x 16-20 μm . . . . *P. norfolkensis*
6. Thallus pale green, K-, stictic acid present; spores fusiform, 100-140 x 35-50 μm . . . . *P. dehiscens*

Pertusaria dehiscens Müll. Arg., *Flora*, Regensburg 67: 286 (1884).
Type: Brazil, Apiahy [Apiai, c. 250 km SW of Sao Paulo], July 1882, *Puiggari 499* (G-lectotype).

Thallus pale to dark olive-green, wrinkled and cracked, lacking isidia and soredia, surface dull, corticolous. ***Apothecia*** verruciform, conspicuous, numerous, concolorous with the thallus, flattened-hemispherical, 0.8-1.5 mm diam., often constricted at the base; ostioles uncommon, black, punctiform, 2-5 per verruca in a hyaline zone, the zone becoming conspicuous, deeply concave and almost disciform, to 0.8 mm diam.; ***spores*** eight per ascus, biseriate, smooth, fusiform, 100-140 (-150) x 35-50 μm.

Chemistry: K-, KC-, C-, Pd-; containing lichexanthone, stictic acid and norstictic acid (trace).

P. dehiscens is characterized by the eight-spored asci with biseriate fusiform spores, and the presence of lichexanthone and stictic acid. *P. dehiscens* resembles the New Zealand endemic *P. theochroa* Krempelh. (Galloway, 1985) which also has eight biseriate spores, but is distinguished from that species by the chemistry, and the appearance of the ostioles. *P. theochroa* contains 4,5-dichlorolichexanthone and 2′-*O*-methylperlatolic acid and has inconspicuous, minute black ostioles which lack the outer hyaline zone present in *P. dehiscens*. *P. dehiscens* also occurs in Australia (Qld., N.S.W.) and Brazil. Uncommon in Norfolk Island.

Specimens Examined:
NORFOLK ISLAND. On palm, S14, *JAE 18682*; on *Citrus limon*, S24, *JAE 18809*.

Pertusaria montpittensis A. W. Archer sp. nov. (Fig. 2**A**)
Thallus corticola, olivaceus vel stramineus, tenuis, continuous, superficies laevis et nitida, sorediis destitutus, copiose isidiata praeter marginem; isidia thallo concoloria, subclaviformia, simplicia vel ramosa et demum coralliformia fiunt, 0.4-1 mm alta, 0.2-0.5 mm diam.; apothecia ignota. Thallus 4,5-dichlorolichexanthone et acidum sticticum continens.
Type: Norfolk Island. On *Elaeodendron* in mixed sub-tropical rainforest, Mt Bates summit trail, Mt Pitt Reserve, 29°00′S, 167°56′30″E, 300 m, *J. A. Elix 18641 and H. Streimann*, 7.xii.1984 (CBG-holotype).

Thallus pale olive-green to pale yellow-grey, thin, continuous, surface smooth and shiny, copiously isidiate away from the margin, corticolous; ***isidia*** concolorous with the thallus, simple, branched or becoming coralloid, narrow at the base and swelling somewhat at the tip, 0.4-1.0 mm tall, 0.2-0.5 mm diam.; verrucae, ostioles, apothecia, asci and spores not seen.

Chemistry: K-, KC-, C-, Pd-; containing 4,5-dichlorolichexanthone and stictic acid.

P. montpittensis is distinguished from other sterile, isidiate, corticolous Australian species of *Pertusaria* by its chemistry. The medullary constituents also distinguish this new species from the corticolous, isidiate Hawaiian species, *P. ramulifera* Magn. (Magnusson & Zahlbruckner, 1944), which contains norstictic acid. *P. montpittensis* grows on *Araucaria*, *Elaeodendron*, *Callistemon* and mangroves, and is so far known only from Norfolk Island and two locations in eastern Queensland. Riedl (1988) described in detail an unnamed sterile *Pertusaria* from Norfolk Island that corresponds to *P. montpittensis* but the chemistry of his specimen was not reported. Common in Norfolk Island.

Specimens Examined:
NORFOLK ISLAND. On truck of *Araucaria heterophylla*, S1, *JAE 18158*; on tree trunk, S5, *JAE 18292, 18313, 18346, 18348*; on *Elaeodendron*, S7, *JAE 18336*; on *Elaeodendron*, S12, *JAE 18630* (topotype); on trunk of *Araucaria heterophylla*, S19, *JAE 18780*.
AUSTRALIA. Queensland, Ingham-Kangaroo Hills road, Seaview Range, 30 km south-west of Ingham, *J. A. Elix 20413*, 19.vi.1986 (ANUC); Springbrook, near N.S.W./Queensland border, *H. Lumbsch 5391h*, 11.vii.1987 (herb. LUMBSCH).

Pertusaria nebulosa A. W. Archer sp. nov. (Fig. 2**B**)
Thallus subolivaceus, parum tuberculatus, corticola, superficies laevis et nitida, isidiis et sorediis destitutus; apothecia numerosa, verruciformia, conspicua, complanata hemisphaerica, basibus constrictis, raro confluentia, 0.8-1.5 mm diam.; ostiola conspicua, nigra, in verrucas 1-4na; sporae 4nae, uniseriatae, ellipsoideae, laeves, 95-115 x 30-35 μm. Thallus vestigia substantiarum incognitarum continens.

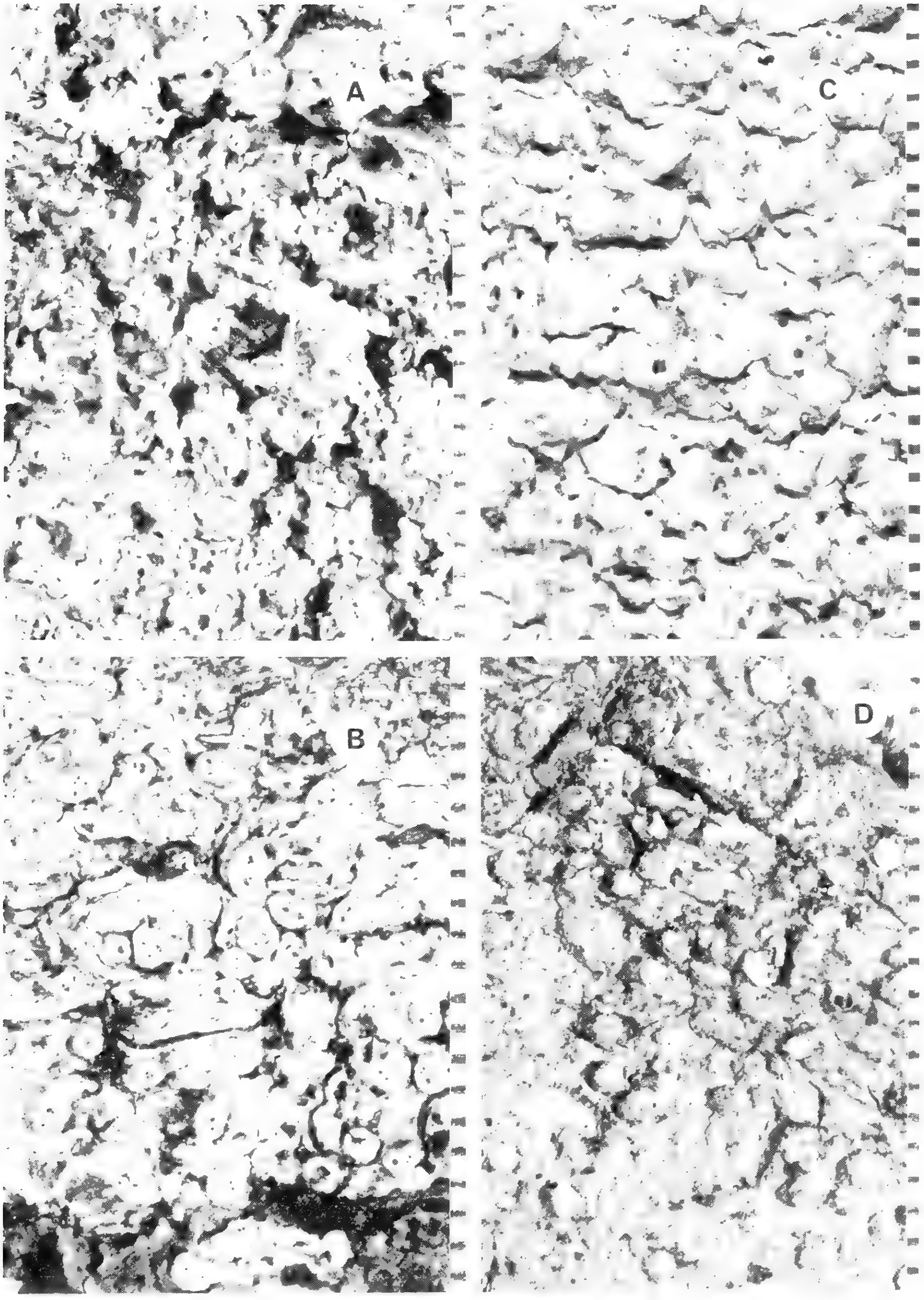

Fig. 2. Lichen types: **A**, holotype of *Pertusaria montpittensis*; **B**, holotype of *Pertusaria nebulosa*; **C**, holotype of *Pertusaria norfolkensis*; **D**, holotype of *Pertusaria verdonii*.
Scales in millimetres.

Type: Norfolk Island. On *Elaeodendron* in regrowth forest, just south of the Captain Cook Memorial, Duncombe Bay, 29°00′20″S,; 167°57′30″E, 100 m, *J. A. Elix 18389 and H. Streimann*, 3.xii.1984 (CBG-holotype).

Thallus pale olive-green, slightly tuberculate, surface smooth and shiny, lacking isidia and soredia, corticolous. ***Apothecia*** verruciform, conspicuous, numerous, rarely confluent, flattened hemispherical, becoming constricted at the base, 0.8-1.5(-2.0) mm diam.; ostioles conspicuous, black, lacking a hyaline margin, 1-4 per verruca; ***spores*** 4 per ascus, uniseriate, ellipsoid, smooth, 95-115 x 30-35 μm.

Chemistry: K-, KC-, C-, Pd-; unidentified traces only found by thin layer chromatography,

This new species superficially resembles *P. javanica* Müll. Arg. (Müller Arg., 1884) as both taxa have numerous, conspicuous black ostioles on each verruca. However, *P. javanica* has spores which are rough and larger, 87-137(-165) x 40-47 μm, and contains stictic acid. This species is known only from the type specimen and apparently is rare in Norfolk Island.

Pertusaria norfolkensis A. W. Archer sp. nov. (Fig. 2C)
Thallus albidus vel flavido-albus, areolatus et rimosus, asper et tuberculatus, corticola, isidiis et sorediis destitutus; apothecia verruciformia, inconspicua, thallo concoloria, irregulariter hemisphaerica, basibus non constrictis, interdum confluentia, 1-2 mm diam.; ostiola conspicua, nigra, depressa, in verrucas 1-4na; sporae 8nae, biseriatae, ellipsoideae, laeves, 45-55 μm longae, 16-20 μm latae. Thallus acidum norsticticum continens.
Type: Norfolk Island. On treelet stem in poor forest on gentle slope, Mt Pitt, Mt Pitt Reserve, 29°01′S, 167°56″E, 300 m, *H. Streimann 34845*, 10.xii.1984 (CBG-holotype; B-isotype).

Thallus off-white to pale yellowish-white, areolate and cracked, rough and tuberculate, surface dull, lacking isidia and soredia, corticolous. ***Apothecia*** verruciform, inconspicuous, concolorous with the thallus, irregularly hemispherical, not constricted at the base, sometimes confluent, 1-2 mm diam.; ostioles conspicuous, black, sunken, 1-4 per verruca; ***spores*** 8 per ascus, biseriate, ellipsoid, smooth, 45-55 x 16-20 μm.

Chemistry: K+ red, C-, Pd+ orange; containing norstictic acid.

P. norfolkensis is distinguished from other corticolous Australian *Pertusaria* containing norstictic acid by its eight small biseriate spores. It resembles the corticolous South American species *P. syngenetica* Müll. Arg. (Müller Arg., 1884), which also has eight biseriate spores (45-52 x 20-25 μm), but lacks norstictic acid. The new species is known only from the type specimen and apparently is rare in Norfolk Island.

Pertusaria persulphurata Müll. Arg., *Nuovo Giorn. Bot. Ital.* 23: 391 (1891).
Type: Australia [Queensland], Brisbane, *Bailey s.n.* (G-holotype).

Thallus variable, usually thin, rarely thick, pale, bright or dull yellow, areolate and cracked, surface smooth and dull, sorediate, saxicolous; soralia sparse to numerous, scattered, 0.3-0.5 mm diam.; verrucae, asci and spores absent.

Chemistry: K-, KC+ orange-red, C+ orange, P-; containing thiophaninic acid, lichexanthone (±), stictic acid (±). The chemistry of *P. persulphurata* (as *P. sulphurata*) has been reported in detail (Elix *et al.*, 1978).

P. persulphurata also occurs in eastern Queensland and New South Wales where it is common on exposed sandstone. Specimens from mainland Australia are usually bright yellow whereas the Norfolk Island specimens are a dull yellow-brown (*JAE 18186, 18494*) or a pale yellowish brown (*JAE 18479, 18505*); all four specimens contain lichexanthone plus thiophaninic and stictic acids, and the slight differences in colour may be due to the different substrate (volcanic rock). Common in Phillip Island but scattered in Norfolk Island.

Specimens Examined:
NORFOLK ISLAND. On volcanic rocks, S2, *JAE 18186*; on volcanic rocks, S10, *JAE 18479, 18494, 18505.*

Pertusaria thiospoda Knight, *Trans. Linn. Soc. London, Bot.* 2: 47 (1882).
Type: Australia, New South Wales [neighbourhood of Sydney, *fide* Filson 1986], *Knight 20* (WELT-holotype).

Thallus pale yellowish white to pale yellow, thin, margin effuse, slightly cracked, surface smooth and dull, lacking isidia and soredia, corticolous. ***Apothecia*** verruciform, inconspicuous, scattered to crowded, sometimes confluent, not constricted at the base, concolorous with the thallus, 0.5-1.0 mm diam.; ostioles pale brown to black, 1 per verruca; **spores** 2 per ascus, uniseriate, ellipsoid, smooth, 80-100(-120) x 30-40 μm.

Chemistry: K-, KC+ yellow-orange, C+ yellow-orange, Pd-; containing thiophaninic and stictic acids.

P. thiospoda is a common corticolous Australasian *Pertusaria* found in Queensland, New South Wales, Tasmania and Lord Howe Island. It is characterized by the pale yellow thallus, the two ellipsoid spores and the presence of thiophaninic and stictic acids. Uncommon in Norfolk Island.

Specimens Examined:
NORFOLK ISLAND. On *Melia*, S4, *JAE 18318*; sine loco, *J. H. Maiden and J. L. Boorman s.n.*, xi. 1902 (NSW L4431).

Pertusaria verdonii Archer sp. nov. (Fig. 2**D**)
Thallus olivaceus, rugosus et rimosus, corticola, superficies laevis et hebetata, isidiis destitutus, sorediata; soralia conspicua, dispersa, thallo concoloria, subhemisphaerica, 1.0-1.5 mm diam.; apothecia ignota. Thallus lichexanthone continens.
Type: Norfolk Island. On *Elaeodendron* in mixed subtropical rainforest, near Broken Pine, Mt Pitt Reserve, 29°01′30″S, 167°56′20″E, 240 m, *J. A. Elix 18283 and H. Streimann*, 2.xii.1984 (CBG-holotype).

Thallus olive-green, wrinkled and cracked, surface smooth and dull, lacking isidia, sorediate, corticolous; ***soralia*** conspicuous, scattered, hemispherical, concolorous with the thallus, 1.0-1.5 mm diam.; verrucae, asci and spores absent.

Chemistry: K-, KC+ violet, C-, Pd-; lichexanthone, picrolichenic acid and a picrolichenic acid homologue.

This new species is distinguished from other sterile Australian, corticolous, sorediate species of *Pertusaria* by its chemistry. Similarly it differs from the common Northern Hemisphere species, *P. amara* (Ach.) Nyl. by the presence of lichexanthone and the absence of protocetraric acid. This species is known only from the type specimen and apparently is rare on Norfolk Island. It is named in honour of the Australian lichenologist Mr Douglas Verdon.

PSEUDOCYPHELLARIA Vainio

Artificial Key to *Pseudocyphellaria* in Norfolk Island

1. Photobiont blue-green 2
1. Photobiont green 3

2. Pseudocyphellae yellow .... *P. crocata*
2. Pseudocyphellae white .... *P. haywardiorum*

3. Isidia granular-coralloid, eroding, yellow .... *P. poculifera*
3. Isidia squamiform, corticate, green to brown .... *P. pickeringii*

Pseudocyphellaria crocata (L.) Vainio, *Hedwigia* 37: 34 (1898).
Lichen crocatus L., *Mantissa Pl.*: 310 (1771).
Type: India, sine loco, *König* (LINN 1273. 137-holotype).
For further synonymy see Galloway (1988).

Thallus corticolous, muscicolous or saxicolous, loosely adnate, undulate at the margins, grey-blue when moist, yellow-brown to dark red-brown when dry, forming rosettes or irregularly spreading, 5-20 cm in diam. ***Lobes*** irregular, 5-15 mm wide, ± rotund at the apices to deeply laciniate, discrete at margins to imbricate centrally, margins sinuous, ± subascending to ragged, incised, sorediate. ***Upper surface*** shallowly and irregularly wrinkled to densely faveolate, ridged or pitted, dull to shiny, maculate, maculae more obvious in faveolate specimens, white, distinctly reticulate, following ridges and in faveolae, lacking isidia, phyllidia and pseudocyphellae, sorediate; **soredia** yellow, marginal and laminal, variable, in scattered erose soralia to linear-elongate marginal soralia with densely farinose yellow soredia, or erupting from pseudoisidiate warts on margins and laminal ridges where the central parts erode and form yellow granular soredia; medulla white. ***Photobiont*** blue-green (*Nostoc*). ***Lower surface*** pale yellow at margins to dark brown-black centrally, tomentose, tomentum short, variable, buff to dark red-brown or black. ***Pseudocyphellae*** yellow, occasional to numerous, punctiform at margins, sunk into the tomentum or ± projecting above, 0.1-1.2 mm diam. ***Apothecia*** rare, marginal or laminal, solitary or grouped, subpedicellate, concave, 0.5-3.0 mm diam., disc red-brown, margin pale pink, often overlapping disc at first, ultimately dentate-irregular, amphithecium verrucose-areolate, ± tomentose towards base; spores olive-brown to dark brown, 1-3 septate, broad-ellipsoid, straight or slightly curved, 22-28 x 8-9 μm. ***Pycnidia*** not seen.

Chemistry: K+ yellow, C-, P+ orange; containing pulvinic acid, pulvinic dilactone, 6α-acetoxyohopane-7β,22-diol (trace), 7β-acetoxyhopane-6α,22-diol (trace), hopane-7β,22-diol (trace), hopane-6α,7β,22-triol, tenuiorin, methyl gyrophorate, gyrophoric acid (trace), physciosporin (± trace), norstictic acid (trace), stictic acid, cryptostictic acid (trace), constictic acid (trace), salazinic acid (±).

P. crocata is a cosmopolitan species widely distributed in both hemispheres. In Australasia it is known from Australia, New Zealand, Papua New Guinea and Fiji. Uncommon in Norfolk Island.

Specimens Examined:
NORFOLK ISLAND. On mossy rocks, S32, *JAE 18732, JAE 18734 (Lich. Australasici Exsicc.* Fasc. 4: 92); on tree trunk, S32, *HS 34633* (B, H, US).

Pseudocyphellaria haywardiorum D. Galloway, *Bull. Br. Mus. nat. Hist. (Bot.)* 17: 159 (1988).
Type: New Zealand. North Island, South Auckland, Red Mercury Island, on tea tree *(Leptospermum)* bark, August 1971, *B. W. & G. C. Hayward H 40.4* (AK 161261-holotype).

Thallus corticolous, loosely adnate to adnate, ± ascending at the margins, dark grey-blue to blue-black when moist, olive-brown to yellow-grey when dry, ± orbicular, 3-7 cm in diam. **Lobes** irregular, 2-10 mm wide, discrete, deeply laciniate, barely imbricate, margins sinuous, ± ascending, irregular, crenate-lacerate, sorediate. ***Upper surface*** plane or shallowly undulate, ± wrinkled-faveolate at the apices, elsewhere punctate-impressed, maculate, maculae minute, whitish, more obvious in reticulate pattern towards the apices, lacking isidia, phyllidia and pseudocyphellae, sorediate; ***soredia*** dark blue-grey, coarsely granular to pseudoisidiate, marginal and laminal, variable, in scattered round to irregular laminal soralia to linear-elongate soralia at the margins or coalescing and forming broad areas of sorediate to pseudoisidiate crust; medulla white. ***Photobiont*** blue-green *(Nostoc).* ***Lower surface*** pale buff at margins, densely tomentose, tomentum buff to red-brown or dark brown centrally. ***Pseudocyphellae*** white, conspicuous, well delimited from the tomentum, rare at margins, common centrally, 0.1-2.0 mm diam. ***Apothecia*** not seen in Norfolk Island specimens. According to Galloway (1985), apothecia rare, marginal or laminal, solitary or grouped, sessile to subpedicellate, concave at first to convex at maturity, 0.5-2.5 mm in diam., disc yellow to dark red-brown, margin pale buff to brownish, amphithecium scabrid-verrucose; spores yellow-brown, 1-septate, fusiform-ellipsoid, apices pointed, 30-32 x 6-7 μm. ***Pycnidia*** not seen.

Chemistry: K-, C-, KC-, P-; containing 7β-acetoxyhopane-22-ol, hopane-15α,22-diol, hopane-7β,22-diol (trace).

P. haywardiorum is a relatively rare Australasian species known also from the north of the North Island of New Zealand. Uncommon in Norfolk Island.

Specimens Examined:
NORFOLK ISLAND. On base of *Araucaria heterophylla* and treefern stem, S12, *JAE 18594, 18598, HS 34386* (H).

Pseudocyphellaria pickeringii (Tuck.) D. Galloway, *Bull. Br. Mus. nat. Hist. (Bot.)* 17: 218 (1988).
Sticta pickeringii Tuck., *U.S. Exploring Exped.* 17 (Bot.): 1138 (pl. 1, fig. VI, 1 & 2) (1874).
Type: New Zealand. Bay of Islands, Wilkes Exped., sine collectoribus nomine (FH-holotype).

Thallus corticolous or saxicolous, tightly to loosely adnate centrally, thin and brittle to ± coriaceous, bright emerald-green to glaucous-green when moist, pale yellow-green to yellow-brown when dry, 5-10(-20) cm diam. ***Lobes*** irregular, 5-15 mm wide, ± rotund at the apices, rarely entire, usually notched and incised, rather ragged, imbricate or subascending at the margins. ***Upper surface*** shallowly wrinkled or pitted, dull, emaculate, continuous, smooth or minutely scabrid in parts, isidiate-phyllidiate; ***isidia*** mainly marginal but also spreading laminally, simple and terete at first but becoming coralloid, flattened, squamiform or phyllidiate, occasionally forming a dense crust obscuring the thallus; medulla yellow. ***Photobiont*** green. ***Lower surface*** pale yellow to brown centrally, tomentose, tomentum rather short, velvety, buff to red-brown. ***Pseudocyphellae*** yellow, flat to papillate, scattered, fleck-like, 0.05-0.50 mm diam., often obscured, sunk into the tomentum. ***Apothecia*** very rare, adnate, concave at first but becoming undulate-distorted, to 5 mm diam., disc red-brown, margin involute then excluded at maturity, amphithecium roughened to coarsely verrucose-areolate; spores 1-3(5) septate, fusiform-ellipsoid, apices pointed, 25-30 x 6.5-7.0 μm. ***Pycnidia*** scattered, laminal, minute, *ca.* 0.1 mm diam., ostiole red-brown to black.

Chemistry: K-, C-, KC-, P-, containing pulvic dilactone, calycin, $2\alpha,3\beta,22\alpha$-triacetoxystictane, $2\alpha,3\beta$-diacetoxystictane-22α-ol, 2α-acetoxystictane-$3\beta,22\alpha$-diol, 3β-acetoxystictane-$2\alpha,22\alpha$-diol, stictane-$3\beta,22\alpha$-diol, stictane-$2\alpha,3\beta,22\alpha$-triol, $3\beta,22\alpha$-diacetoxystictane, 3β-acetoxystictane-22α-ol, pseudocyphellarin A, isopseudocyphellarin A, nephroarctin, phenarctin, $2'$-*O*-methylphenarctin, $1'$-chloronephroarctin, $2'$-*O*-methylisopseudocyphellarin A, $2'$-*O*-methylpseudocyphellarin A.

P. pickeringii is particularly common and widespread in New Zealand (from the Three Kings Islands to Stewart Island) and also known from the Chatham Islands and Fiji. Common in Norfolk Island.

Specimens Examined:
NORFOLK ISLAND. On sapling, S5, *JAE 18289, 18295, 18297*; on *Elaeodendron*, S7, *JAE 18370*; on mossy trunk, S24, *JAE 18819*; on *Elaeodendron*, S8, *HS 32197.*

Pseudocyphellaria poculifera (Müll. Arg.) D. Galloway & P. James, *Lichenologist* 12: 301 (1980).
Sticta poculifera Müll. Arg, *Flora*, Regensburg 65: 304 (1882).
Type: Lord Howe Island, Mt Gower, *F. v. Mueller* (G 002123-holotype; BM, MEL-isotypes).

Thallus corticolous or rarely saxicolous, loosely adnate, undulate at the margins, more tightly adnate in the centre, bright lettuce-green to glaucous-green when moist, pale yellow-grey to yellow-brown when dry but becoming reddish on storage, forming rosettes or irregularly spreading, 4-10 cm in diam. ***Lobes*** irregular, 4-10 mm wide, discrete at margins, irregularly laciniate, contiguous centrally but rarely imbricate; margins subascending, undulate, sinuous, often torn and ragged, ± coralloid-isidiate or white-tomentose. ***Upper surface*** shallowly ridged or pitted dull, minutely white-tomentose in parts, isidiate; ***isidia*** yellow, mainly marginal, rarely spreading to laminal cracks, clustered, minutely coralloid, in part corticate but soon eroding and appearing sorediate; medulla yellow. ***Photobiont*** green. ***Lower surface*** pale yellow or buff to brown centrally, irregularly tomentose, tomentum thin and variable, white to buff, elsewhere entirely glabrous, coarsely to finely wrinkled. ***Pseudocyphellae*** yellow, numerous, conspicuous, punctiform at margins, often confluent centrally, 0.5-1.5 mm diam. ***Apothecia*** moderately common, submarginal, most common at lobe apices, pedicellate, concave, 2-6 mm diam., disc red-brown, margin ragged, granular-isidiate, often eroding and appearing yellow-sorediate, often overlapping disc, amphithecium minutely white-tomentose at first then areolate-scabrid; spores pale to dark red-brown, 3-septate at maturity, fusiform-ellipsoid, apices pointed, 20-23 x 5.5-7.5 μm. ***Pycnidia*** common on lower surface, hemispherical, 0.2-0.5 mm diam., ostiole black.

Chemistry: K-, C-, KC-, P-; containing pulvinic acid, pulvinic dilactone, calycin, 3β-

acetoxyfern-9(11)-en-12-one, fern-9(11)en-3β,12β-ol, 3β-hydroxyfern-9(11)-en-12-one, 3β-acetoxyfern-9(11)-en-12β-ol, 3β-acetoxyfern-9(11)-en-19β-ol, unknown triterpenes.

P. poculifera is an Australasian species known from Australia (Qld.), New Zealand, New Caledonia, Fiji and Lord Howe Island. Common in Norfolk Island. Several previous reports of *Pseudocyphellaria aurata* (Sm.) Vainio from Norfolk Island (Elix, 1985; Riedl, 1988) refer in fact to *P. poculifera*.

Specimens Examined:
NORFOLK ISLAND. On *Cyathea* trunk, S5, *JAE 18315 (Lich. Australasici Exsicc.* Fasc. 4: 91), on vine, *HS 31943* (H, US); on *Elaeodendron*, S7, *JAE 18364, HS 32045* (H, US); on mossy trunk, S8, *JAE 18407, HS 32159* (H, US); on *Campsis grandiflora*, S9, *JAE 18457*; on *Citrus limon*, S12, *JAE 18571, 18576, 18577, HS 34300* (H); on mossy trunk, S24, *JAE 18820, 18823*; on shaded rock, S32, *HS 34648* (H).

RAMALINA Acharius

Artificial Key to *Ramalina* in Norfolk Island

1. Thallus sorediate 2
1. Thallus lacking soredia 3

2. Branching intricate, medulla K-, sekikaic acid present .... *R. peruviana*
2. Branching dichotomous, medulla K+ red, salazinic acid present .... *R. pacifica*

3. Thallus caespitose, less than 4 cm high 4
3. Thallus subpendulous, more than 4 cm long 5

4. Thallus usually more than 2 cm high, divaricatic acid present .... *R. stevensii*
4. Thallus less than 1.5 cm high, divaricatic acid absent .... *R. exiguella*

5. Branches broad, 2-4 mm wide, medulla K-, boninic acid present .... *R. leoidea*
5. Branches narrow, 1-2 mm wide, medulla K+ red, norstictic acid present .... *R. arabum*

Ramalina arabum (Dill. ex Ach.) Meyen ex Flotow, *Nova Acta Akad. Leopold. Carolin.* **19** Suppl.: 212 (1843).
Alectoria arabum Dill. ex Ach., *Lich. Univ.*: 596 (1810).
Type: India (not designated).

Thallus fruticose, corticolous or saxicolous, erect to pendulous, yellow-green to grey-green, 3-10(-20) cm long; branching predominantly dichotomous, sparse to moderate, branch width (0.5-)1.0-2.0 mm, branches rigid, angular-terete to slightly flattened, lateral branches narrower, irregularly divided, apices finely flexed or bent; cortex matt, smooth, with linear ***pseudocyphellae***, occasionally white-striate or longitudinally striate-nervose; holdfast delimited; lacking soredia. ***Apothecia*** common, lateral to subterminal; disc 1.0-1.5 mm diam., concave to plane; margin thin, entire; spores eight per ascus, colourless, 1-septate, oblong, 12-15(-16) x 5-8 μm.

Chemistry: Thallus K+ yellow-red, P+ orange; containing usnic acid, norstictic acid (major), connorstictic acid (minor).

R. arabum is a pantropical-subtropical maritime species, widely distributed among islands of the Mediterranean Sea, and the Indian, South Atlantic and Pacific Oceans. In Australasia it occurs in northern New Zealand and New Caledonia. Very common in Norfolk Island.

Specimens Examined:
NORFOLK ISLAND. On base of *Araucaria heterophylla*, S1, *JAE 18132, 18146, 18147, 18159, 18165, 18166 (Lich. Australasici Exsicc.* Fasc. 4: 95); on volcanic rocks, S2, *JAE 18185*; on exposed *Araucaria* roots and rocks, S3, *HS 31757* (B, H, NY), *31763, 31764*; on *Quercus suber*, S4, *JAE 18194*, on trunk of *Araucaria heterophylla*, S4, *JAE 18209*; on base of *Araucaria heterophylla*, S6, *JAE 18357, HS 32020* (B, H), on dead olive branch, *HS 32038* (B, H, US, NY); on branches of *Araucaria heterophylla*, S11, *JAE 18508*; on old fence posts, S15, *JAE 18709*; on branches of *Araucaria heterophylla*, S16, *JAE 18721 (Lich. Australasici Exsicc.* Fasc. 4: 96); on volcanic rocks, S17, *JAE 18743*; on volcanic rocks, S18, *JAE 18783*; on tree trunk, S25, *HS 34879* (B, LSU); on *Araucaria heterophylla*, S27, *HS 32248*; on truck of *Araucaria heterophylla*, S31, *JAE 18714*.

Ramalina exiguella Stirton, *Trans. Proc. R. Soc. Vict.* **17**: 68 (1881).
Type: Australia. Queensland, Brisbane, *Bailey 91* (BRI-holotype; BM-isotype); contains usnic acid (Stevens, 1987).
For further synonymy see Stevens (Stevens, 1987).

Thallus fruticose, corticolous, caespitose, erect, rigid, grey-green, to 2 cm high; branching mainly from the base, squarrose branchlets sometimes present on main branches; branch width 0.3-1.0 mm, branches subterete, narrow, apices attenuate, sometimes black-tipped; cortex shiny, longitudinally grooved giving a striate appearance; holdfast delimited; ***pseudocyphellae*** linear; lacking soredia. ***Apothecia*** common, usually marginal along the branches and/or subterminal causing the apex of the branch to become geniculate with a long, attenuate spur; disc 0.2-2.0 mm diam., concave, plane to convex; margin entire, thick on immature apothecia; spores eight per ascus, colourless, 1-septate, ovoid to ellipsoid or gibbous and slightly curved, (12-)14-16 x (5-)6-8 μm.

Chemistry: Thallus K-, KC-, P-; containing usnic acid.

R. exiguella is a coastal species, widely distributed in warm temperate to tropical coastal areas of east Africa, eastern Australia (Qld., N.S.W.) and New Zealand. Rare in Norfolk Island.

Specimens Examined:
NORFOLK ISLAND. On dead shrub twigs, S21, *HS 34794* (B, H, LSU).

Ramalina leiodea (Nyl.) Nyl., *Lich. Nov. Zel.*: 22 (1888).
Ramalina subfraxinea ssp. *leiodea* Nyl., *Bull. Soc. linn. Normandie II*, **4**: 141 (1870).
Type: New Caledonia, 'Donné par le Musée Colonial', 1861, *Deplanche* s.n. (PC-lectotype); contains boninic acid aggregate (Stevens, 1987).

Ramalina boninensis Asahina, *J. Jap. Bot.* **14**: 253 (1938).
Type: Bonin Islands, Ogasawara Island, Hahajima, 1836, *Kusaka* s.n. (TNS-lectotype); contains boninic acid aggregate (Stevens, 1987).

Thallus fruticose, corticolous or rarely saxicolous, caespitose, erect to subpendulous, rigid, grey-green, from 4-9 cm high; branching subdichotomous, sparse to moderate; branch width (0.5-)2.0-4.0 mm, branches compressed, flat or canaliculate when narrow, apices attenuate; cortex matt, smooth to rugose, lacking soredia, short linear ***pseudocyphellae*** sometimes present; holdfast delimited. ***Apothecia*** common, marginal to subterminal, rarely laminal, small thalli producing subterminal apothecia subtended by a spur; disc 2.0-3.0 mm diam., concave to plane; margin entire or incised at maturity;

spores eight per ascus, colourless, 1-septate, ellipsoid, straight or slightly curved, 10-12(-16) x 4-5 μm.

Chemistry: Thallus K-, KC-, P-; containing usnic acid, boninic acid (major), 2-*O*-methylsekikaic acid (minor), 2,4′-di-*O*-methylnorsekikaic acid (minor), 4′-*O*-methylpaludosic acid (minor), 4,4′-di-*O*-methylcryptochlorophaeic acid (minor).

R. leiodea is a maritime species, widely distributed among the tropical and subtropical islands of the Pacific (Bonin, Marianas, Lord Howe, New Caledonia, Raratonga, Vanuatu, Hawaii) and Indian Oceans (Mauritius, Réunion), and in eastern Australia (Qld., N.S.W.). Common in Norfolk Island.

Specimens Examined:
NORFOLK ISLAND. On base of *Araucaria heterophylla*, S1, *JAE 18142, 18145, HS 31711, 31737, 31738*; on *Melia*, S4, *JAE 18199, 18247, 18248, 18249, HS 31850*; on shaded rock, S7, *HS 32004* (B); on shaded rock, S18, *HS 34744*; on twigs of *Eucalyptus*, S28, *JAE 18527 (Lich. Australasici Exsicc.* Fasc. 4: 97).

Ramalina pacifica Asahina, *J. Jap. Bot.* **15**: 213 (1939).
Type: Micronesia. Marianas, Saipan Island, 1925, *Kimura* s.n. (TNS-lectotype); contains salazinic acid, usnic acid (Stevens, 1987).

Ramalina insularum H. Magn., *Ark. Bot.* **3**: 361 (1956).
Type: Fiji Islands, 1862, *Daemel* s.n. (H-lectotype); contains salazinic acid, usnic acid (Stevens, 1987).

Thallus fruticose, corticolous or rarely saxicolous, tufted, pendulous to subpendulous, pale yellow-green to grey-green, 2-6(-12) cm long; branching dichotomous, sparse to moderately dense but very variable; branch width (0.5-)1.0-5.0 mm, branches flat, compressed, sometimes splitting along the margins; broad in the basal region but gradually narrowing towards the apices or narrow in the basal region and continuing uniformly to the apices; apices attenuate, mostly forked; cortex matt or shiny, smooth or with linear ***pseudocyphellae*** slightly or strongly developed, sorediate; holdfast delimited and rounded; ***soralia*** marginal or laminal, round to ellipsoid, often coalescing, the edges revolute. ***Apothecia*** rare, marginal, disc 1.0-3.0 mm diam., concave, plane to convex, margin often incised at maturity; spores eight per ascus, colourless, 1-septate, fusiform to ellipsoid, straight or slightly curved, 12-16(-20) x 4-7 μm.

Chemistry: Thallus K+ yellow-red, P+ orange; containing salazinic acid (major), protocetraric acid (trace) and usnic acid (minor/trace).

P. pacifica is widely distributed in warm temperate to subtropical regions surrounding the Indian and eastern Pacific Oceans, including South Africa, Burma, Bangladesh, Indonesia (Java), Japan, Australasia and the Marianas. In Australasia it is known from eastern Australia (Qld, NSW), the Cook Islands, Fiji, New Zealand and Vanuatu. Very common in Norfolk Island.

Specimens Examined:
NORFOLK ISLAND. On base of *Araucaria heterophylla*, S1, *JAE 18134, 18136, 18141, 18160, HS 31712* (B, H, LSU, US); on fence post, *Grevillea* and *Pinus*, S4, *JAE 18204, 18220, 18251, HS 31798* (B), *31846* (B, H, US); on *Melia*, S4, *JAE 18240 (Lich. Australasici Exsicc.* Fasc. 4: 98), *HS 31802* (H, US); on shrub and *Lagunaria*, S7, *JAE 18359, HS 32006* (B, H, NY, US); on old fence post, S15, *JAE 18704*; on twigs of *Eucalyptus* and

volcanic rocks, S28, *JAE 18526, 18528*; on *Lagunaria*, S10, *HS 32214*; on *Araucaria* trunk, S15, *HS 34579*; on tree trunk, S25, *HS 34878* (B, LSU); on stem of *Araucaria heterophylla*, S34, *HS 34862*; on *Elaeodendron curtipendulum*, 300 m west of Steeles Point, 29°02′S, 167°59′E, 100 m, *M. M. Richardson & G. Plant 106* (CBG).

Ramalina peruviana Ach., *Lich. Univ.*, 599 (1810).
Type: South America, Peru, *Lagasta* s.n. (H-ACH-holotype; BM, UPS-isotypes); contains sekikaic acid aggregate, usnic acid (Stevens, 1987).
For further synonymy see Stevens (1987).

Thallus fruticose, corticolous, tufted, erect to subpendulous, pale green to grey-green, up to 6 cm long; branching subdichotomous to irregular, often intricate with the production of dense fragile branchlets; branch width 0.1-0.9(-1.5) mm, branches flat, compressed but becoming angularly subterete to terete towards the apices, branches often slightly twisted, apices sharp to blunt, often broken; surface matt, rarely shiny, smooth to rugose, weakly ***pseudocyphellate*** either basally or along the entire length, appearing weakly striate or ridged or subfenestrate in basal parts, sorediate; holdfast delimited or diffuse; ***soralia*** punctiform, numerous, marginal or lateral, sometimes apical, mounds of soredia often producing small fibrils. ***Apothecia*** rare, marginal, lateral, 0.5-2.0 mm diam., concave, margin thick, often crenate; spores eight per ascus, colourless, 1-septate, narrow, fusiform, straight or rarely curved, 14-16(-18) x 3.5-4.5 μm.

Chemistry: Thallus K+ yellow, P-; containing homosekikaic acid acid (major), sekikaic acid (major), ramalinolic acid (trace), 4′-*O*-demethylsekikaic acid (trace), 4′-*O*-methylnorsekikaic acid (trace) and usnic acid (minor/trace).

R. peruviana is widely distributed in warm temperate to subtropical regions of the Southern Hemisphere. In Australasia it is known from eastern Australia (Qld., N.S.W.), New Zealand and New Caledonia. Uncommon in Norfolk Island.

Specimens Examined:
NORFOLK ISLAND. On *Melia* and *Grevillea robusta*, S4, *JAE 18242, HS 31853*; on *Pinus*, S4, *JAE 18252 (Lich. Australasici Exsicc.* Fasc. 4: 99), *HS 31815* (B, H, US); on *Citrus limon*, S12, *JAE 18586, 18587*; on *Melia*, S22, *JAE 18803*; on roadside tree, S26, *JAE 18126*; on tree trunk, S32, *HS 34933.*

Ramalina stevensiae Elix, *Mycotaxon* 40: 42 (1991).
Type: Norfolk Island. On *Citrus limon* in subtropical rainforest, summit trail to Mt Bates, 29°00′30″S, 167°56′30″E, 300 m, *J. A. Elix 18582 & H. Streimann*, 6.xii.1984 (CBG-holotype; MEL-isotype).

Thallus fruticose, corticolous, caespitose, erect or subpendulous, pale grey-green to pale yellow, often with a paler lower surface, 2-8 cm high, lacking soredia; branching subdichotomous to irregular, moderate to dense, with fragile branchlets towards the apices; branches (0.2-)0.5-1.0(-3.0) mm wide, compressed, flat to subcanaliculate, with attenuate apices, rarely with rounded laminal perforations to 0.5 mm diam.; cortex shiny, smooth, lacking soredia and pseudocyphellae; holdfast delimited or diffuse. ***Apothecia*** sparse to common, subterminal on geniculate branches or terminal on main and short lateral branches, spurred, or in the axils of bifurcating branches; disc 1.0-2.5 mm diam., concave to plane; margin entire; spores eight per ascus, colourless, 1-septate, ellipsoid, straight or often slightly curved, 10-13(-15) x 4-5 μm.

Chemistry: Thallus K-, KC-, C-, P-; containing usnic acid, divaricatic acid (major), nordivaricatic acid (minor/trace), unknown terpenes (traces).

This species is characterized by compressed, narrow, intricately branched lobes and medullary divaricatic acid. *R. stevensiae* appears to be endemic to Norfolk Island and is quite common on forest trees at higher elevations.

Specimens Examined:
NORFOLK ISLAND. On canopy of fallen tree, S8, *JAE 18415*; on mossy trunk, S24, *JAE 18821*; on fallen twigs, S26, *JAE 18122*; on dead wood, sin. loc., *J. & J. Gilbert*, 24-27.viii.1975 (HO); on *Citrus limon*, S12, *HS 34301* (B); on treelet stem, S14, *HS 34571* (B, CBG, H); on tree trunk, S22, *HS 36481* (B, CBG); on dead shrub, S24, *HS 34811*.

Previous reference to *Ramalina australiensis* Nyl., *R. canariensis* J. Stein., *R. celastri* (Spreng.) Krog & Swinsc. and *R. glaucescens* Krempelh. in Norfolk Island (Riedl, 1988) could not be verified as the specimens were not available for examination.

ACKNOWLEDGEMENTS

We thank the Australian National Parks and Wildlife Service for generous financial support for our field work on Norfolk Island, Ms Jen Johnston who determined the chemistry of many specimens and for many constructive suggestions concerning the manuscript and to Mr Douglas Verdon for assistance with the Latin descriptions.

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An Historic Collection of Fleas (Siphonaptera) in the Macleay Museum, Sydney, Australia

R. L. C. PILGRIM

(Communicated by D. S. HORNING, JR)

PILGRIM, R. L. C. An historic collection of fleas (Siphonaptera) in the Macleay Museum, Sydney, Australia. *Proc. Linn. Soc. N.S.W.* 113 (1), 1992: 77-86.

Specimens of 58 fleas, representing 12 genera, 15 species and subspecies, together with 2 larvae, obtained by collecting, purchase or exchange, are identified and listed according to current taxonomic practice. They had been collected in Australia, Cuba, Europe, South Africa, and South America.

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INTRODUCTION

The Macleay Museum, University of Sydney, has an insect collection of about 500 000 specimens (Horning, 1984: 172). Many of these specimens were collected during the early to mid 1800's, and so constitute irreplaceable and historically valuable records. The collection was virtually inaccessible from 1912 to 1982 but the appointment of a curator had made the material available for re-examination. The historic flea collection, of 58 adults and 2 larvae, was sent to me for preparation and identification.

Much of the collection, as received, was in a superficially poor condition: most specimens were glued to card or paper, or to mica slips; some were entirely obscured by fungal hyphae and a great deal of accumulated dust; five adults were pinned.

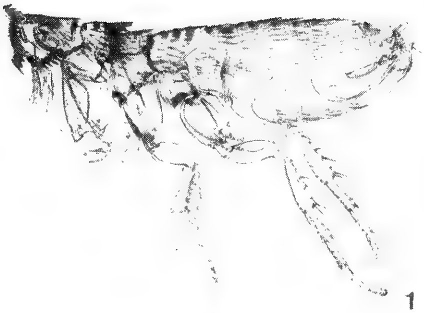
Preparation involved soaking the specimens from the card/paper/mica mounts and the shellac fortunately dissolved readily. Those that were pinned had been removed prior to receipt by me: they had been relaxed for 1-1½ days in a thymol crystal/water relaxing chamber at 40°C., the lower end of the corroded pin scraped clean with forceps, and the flea then slid off the pin. The pins had been thrust through the mid-abdomen, consequently the genitalia and the diagnostically critical posterior segments were retained almost intact. Inevitably many setae were lost, as were some portions of legs and maxillae; nevertheless, surprisingly good results were obtained using a standard slide preparatory technique (Smit, 1957), such that the specimens presented few taxonomic problems attributable to the condition of the material. Some abdomens were badly broken open and occasionally spermathecae became exteriorized on the slide or lost.

The original labels were kept and glued to the microscope slide (right side); where more than one species was present on the original labelled mount, a full replicate of the data has been placed in the corresponding position on the additional slide(s).

SYSTEMATICS

The species present in the collection are listed below. Higher taxonomy of the fleas follows Smit (1982); the subfamilies and tribes of Pygiopsyllidae are those of Mardon (1981) and the subgenera of *Ceratophyllus* those of Smit (1983). Nomenclature of the hosts follows Ride (1970) for Australian, and Hall and Kelson (1959) for North American and Cuban hosts.

Entries are arranged as follows: number, for ease of reference; current name of flea species, with author and date; number of specimens of each sex; number of slides



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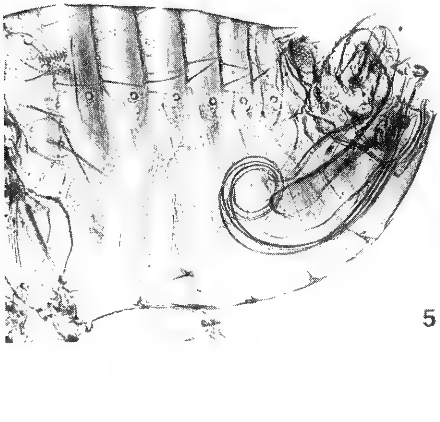

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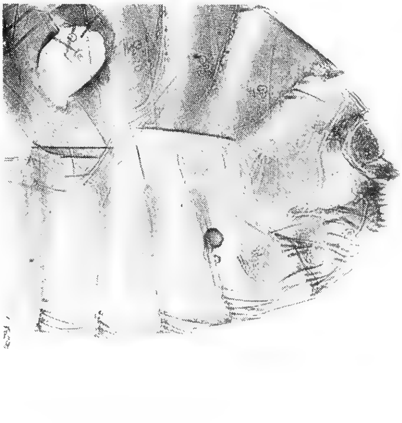

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Fig. 1. Stephanocircus dasyuri Skuse, male (entry 2).
Fig. 2. Bradiopsylla echidnae (Denny), female (entry 3).
Fig. 3. Phthiropsylla agenoris (Rothschild), female (entry 9).
Fig. 4. Pariodontis riggenbachi riggenbachi (Rothschild), female (entry 10).
Fig. 5. Pulex simulans Baker, male, abdomen (entry 14.5).
Fig. 6. Pulex simulans Baker, female, abdomen (entry 14.7).

prepared; original state of mounting of specimens; transcript of original labels (in quotation marks).

Conditions of specimens as now slide-mounted.

Remarks on fleas and/or host(s) and/or localities.

My remarks, corrections or other comments on the original data are interpolated in square brackets [ ].

* denotes specimen(s) of Australian provenance.

** denotes specimen(s) endemic or native to Australia.

In many cases, no host was stated on the original label(s); additionally some labels lacked any locality data, but in a few instances deductions are offered as to probable sites of collection.

HYSTRICHOPSYLLOIDEA

HYSTRICHOPSYLLIDAE

Hystrichopsyllinae — Hystrichopsyllini

1. ***Hystrichopsylla (Hystrichopsylla) talpae (?talpae)*** (Curtis, 1826)
1 female, containing egg, remounted from card. 'Mole Flea female. J. J. Walker Oxford [England] 1908' [W. W. Froggatt's handwriting]. 'From Mr Froggett [*sic*] April 17.1918' [John Shewan's handwriting].
Condition: excellent.
Remarks: subspecies of *talpae* are indistinguishable in the absence of males; the subspecies *t. talpae* is assumed from the locality, since only *t. talpae* is known from England (Hopkins and Rothschild, 1962: 45; Beaucournu and Launay, 1979: 499).

STEPHANOCIRCIDAE

Stephanocircinae

2. ***Stephanocircus dasyuri* Skuse, 1893. Fig. 1.
2 males on 1 slide, remounted from same piece of mica. 'Perameles nasutus' [=*P. nasuta* Geoffroy, 1804] [W. S. Macleay's handwriting, pre-1865]. No locality stated, but host known to occur in eastern parts of Queensland, New South Wales and Victoria (Ride, 1970: 100).
Condition: excellent; 1 abdomen burst open but genitalia retained.
Remarks: the species is very common, and has been recorded from a wide range of macropods, peramelids, large dasyurids and native rodents in Australia (including Tasmania), mainly in coastal regions (Dunnet and Mardon, 1974: 105).

PYGIOPSYLLIDAE

Lycopsyllinae — Bradiopsyllini

3. ***Bradiopsylla echidnae* (Denny, 1843). Fig. 2.
2 females on 2 slides, remounted from 1 card. 'Pulex echidnae Denny and larvae from Echidna hystrix' [=*Tachyglossus aculeatus* (Shaw, 1792)]. 'N.S.W.' [New South Wales].
Condition: very good.
Remarks: specimens known to have been obtained by W. S. Macleay between 1839 and 1860 (*teste* D. S. Horning, Jr). The two associated larvae from the same card have been prepared and mounted independently, and will be referred to in a subsequent paper by me. The genus *Bradiopsylla* is monotypic and endemic to Australia; it has been taken almost exclusively from echidnas of which *T. aculeatus* is the typical host (Dunnet and Mardon, 1974: 55).

Pygiopsyllinae

4. ***Pygiopsylla phiola* Smit, 1979.
1 male, 1 female on 1 slide, remounted from same piece of mica. 'Perameles' [W. S. Macleay's handwriting, pre-1865]. No locality stated, but Smit (1979: 172) recorded the species from a number of hosts, including *Perameles nasuta* in Queensland and New South Wales.
Condition: very good; male abdomen burst open, but genitalia retained.
Remarks: Smit (1979: 173) regarded this species as belonging to Australia, whence it has spread with *Rattus* spp. to New Zealand and its outlying islands.

CTENOPHTHALMIDAE

Ctenophthalminae — Ctenophthalmini

5. ***Palaeopsylla minor*** (Dale, 1878)
2 females on 1 slide, remounted from 1 card. 'Talpa' [?C. L. Nitzsch's handwriting]. No locality stated, but the species is very common on *Talpa europaea* Linnaeus, 1758 throughout Europe, including England (Smit, 1957: 37).
Condition: very good; 1 specimen has lost the spermatheca.
Remarks: specimens probably purchased or exchanged.

CERATOPHYLLOIDEA

CERATOPHYLLIDAE

Ceratophyllinae

6. ***Ceratophyllus (Ceratophyllus) gallinae*** (Schrank, 1803)
1 male, remounted from card. 'Pulex gallinae' [W. S. Macleay's handwriting]. No host or locality stated; the species is very host-promiscuous on birds, especially poultry, and has been accidentally introduced to most parts of the world. Australian records are not common (Dunnet and Mardon, 1974: 130).
Condition: excellent.
Remarks: specimen known to have been derived from the Latreille collection (*teste* D. S. Horning, Jr); thus not of Australian origin.

7. ***Ceratophyllus (Monopsyllus) sciurorum sciurorum*** (Schrank, 1803)
1 male, remounted from card. 'Pulex sciuri' [W. S. Macleay's handwriting]. No host or locality stated; regular hosts are sciurids and glirids throughout much of the Palaearctic Region (Haddow *et al.*, 1983: 76, maps 41, 167).
Condition: very good, but extreme tip of sternum VIII broken off.
Remarks: specimen known to have been derived from the Latreille collection (*teste* D. S. Horning, Jr).

ISCHNOPSYLLIDAE

Ischnopsyllinae

8. ***Ischnopsyllus (Hexactenopsylla) hexactenus*** (Kolenati, 1856)
2 females on 1 slide, remounted from 1 card. 'Pulex vespertilionis' [W. S. Macleay's handwriting]. No host or locality stated; occurs on bats throughout much of European sub-region of the Palaearctic Region (Hopkins and Rothschild, 1956: 305).
Condition: excellent.
Remarks: specimens known to have been derived from the Latreille collection (*teste* D. S. Horning, Jr). *Pulex vespertilionis* Bouché, 1835 is a synonym of *I. hexactenus* (Hopkins and Rothschild, 1956: 306).

MALACOPSYLLOIDEA

MALACOPSYLLIDAE

9. ***Phthiropsylla agenoris*** (Rothschild, 1904). Fig. 3.

1 female, remounted from pin. 'Flea on Dasypus minutus Bahia Blanca N. Patagonia Darwin.' [W. S. Macleay's handwriting].

Condition: very good; scarcely any damage from pinning.

Remarks: this specimen is of exceptional interest — it is listed in Smith (1987: 43, entry 376) as one of the missing specimens from 'Darwin's Insects'. The original label was attached to the slide by Ricardo Palma, National Museum of New Zealand. It is sealed between two layers of 'Mylar' R (a polyester film used to conserve paper), glued to each other with a frame of '3M' R No. 415 double-sided adhesive tape.

The species of this monotypic genus is typically found on armadillos in the Neotropical Region (Smit, 1987: 20).

PULICOIDEA

PULICIDAE

Xenopsyllinae

10. ***Pariodontis riggenbachi riggenbachi*** (Rothschild, 1904). Fig. 4.

1 female, remounted from pin. '2814' on green paper label. No locality stated, but specimen is known to have been collected at the Cape of Good Hope, South Africa (*teste* D. S. Horning, Jr).

Condition: very good; hole in abdomen almost closed over by manipulation of flaps of cuticle; spermatheca floated out of the opening during maceration but was coaxed back inside the abdomen before slide-mounting. One hind leg is detached.

Remarks: specimen is derived from the Verreaux collection 1825-1830 (*teste* D. S. Horning, Jr). Jules Pierre Verreaux lived at the Cape of Good Hope from 1825-1830, where he made collections of invertebrates. Subsequently the collections made in Africa and his manuscript notes were lost in the wreck of the *Lucullus* in 1838 (Musgrave, 1932: 333). But Macleay (1838: 1) wrote 'It may be well that I should mention here my having lately acquired, by purchase, the very extensive collection of *Annulosa* made by M. Verreaux during his long residence at the Cape, and also his manuscript notes on the species collected.' The specimens are readily recognized by the small numbered green labels. Unfortunately the location of the manuscript notes is unknown.

The species occurs on porcupines (*Hystrix* spp.) and is widespread through much of Africa (Hopkins and Rothschild, 1953: 234).

Archaeopsyllinae

11. ***Ctenocephalides felis felis*** (Bouché, 1835)

11.1 2 females on 2 slides, remounted from 2 pins. 'Cuba'.

Condition: good.

Remarks: these and all subsequent 'Cuba' labels in this genus are in W. S. Macleay's handwriting and all are derived from collections made during his stay in Cuba between 1826 and 1836 (Horning, 1984: 173).

11.2 1 female, remounted from card. 'Cuba".

Condition: good, but spermatheca lost during maceration.

Remarks: same card originally bore a very damaged unidentified mite, which was stained with Carbol Fuchsin and remounted on a separate slide.

11.3 2 males on 1 slide, remounted from 1 card. 'Cat. Cuba'.
Condition: excellent.

11.4 1 female, remounted from card. 'Cuba'.
Condition: good; slight fracture in frons.

11.5 2 males, 3 females on 4 slides, remounted from 4 separate cards. 'Cuba'.
Condition: excellent; 1 male failed to macerate thoroughly.
Remarks: 2 females originally on same card with 1 female *Pulex* (?*simulans*), see entry 14.6.

11.6 4 males, 1 female on 3 slides, remounted from 1 card. 'On Capromys Fournieri' [origin of handwriting unknown]. No locality stated.
Condition: excellent; 1 female has genal spines broken and spermatheca missing.
Remarks: originally on the same card with 1 male *Pulex simulans*, see entry 14.5. *Capromys fournieri* Desmarest, 1822 was synonymized with *C. p. pilorides* (Say, 1822) according to Hall and Kelson (1959: 794) in which the type locality of *C. fournieri* is Cuba. However, Walker *et al.* (1964: 1035) further circumscribed the host locality as Isla da Piños, Cuba.

11.7 1 female, remounted from card. 'Dog'. No locality stated but 'Cuba' on separate pin alongside specimen label.
Condition: fair; many genal spines, pronotal spines and body setae broken short.
Remarks: originally on same card with 4 female *Ctenocephalides canis*, see entry 12. It is not unusual for *Ct. f. felis* (cat flea) to be taken from dogs, and another instance from Cuba is reported in Hopkins and Rothschild (1953: 153).

12. ***Ctenocephalides canis*** (Curtis, 1826).
4 females on 2 slides, remounted from 1 card. 'Dog'. No locality stated, see entry 11.7.
Condition: good; some genal spines broken short.
Remarks: originally on same card with 1 female *Ctenocephalides f. felis*, see entry 11.7. *Ct. canis* (dog flea) is not reported from Cuba (Hopkins and Rothschild, 1953: 169; García Avila, 1976).

Occurrence of *Ctenocephalides* spp. in the Collection

Taxonomic separation of the two species of *Ctenocephalides* most commonly found, virtually world-wide, on domestic cats and dogs relies on a combination of characters (Holland, 1949; Hopkins and Rothschild, 1953; Smit, 1957). None of these features is alone absolutely reliable since variations may be found especially in the number of setae on the metepisterna or on the hind tibiae, even on the two sides of a specimen.

In view of the fact that no records of *Ct. canis* in Cuba appear in either Hopkins and Rothschild (1953: 169) or García Avila (1976), despite the presence of dogs as flea hosts (Hopkins and Rothschild, 1953: 153; and see entry 11.7), a very detailed inspection of the specimens was undertaken. As well as reference to standard literature, examination of each male and female was made using a Zeiss 'Comparison Eyepiece Bridge' to compare the Cuban specimens against authenticated *Ct. f felis* and *Ct. canis* material.

Of those specimens identified here as *Ct. f. felis* (entries 11.1-11.7), the eight males all possess only two metepisternal setae on each side (or their alveoli where setae are lost); head shape, and length of the first genal spine agree well with Holland's fig. 14 (1949); the hind tibiae show only one major seta between the postmedian and the apical long setae (Hopkins and Rothschild, 1953: 136, fig. 157) (= seta A in Smit, 1957: fig. 39); setation and shape of the manubrium and of the movable process of the clasper agree with Holland's fig. 16, and Smit's fig. 41: the nine females also possess only two metepisternal setae (or alveoli) on each side; head shape, and length of the first genal spine (except in three instances where the spines are broken short on one side) agree well with Holland's fig. 15; the hind tibiae show only 1 major seta (or its alveolus) agreeing with Hopkins and Rothschild's fig. 157 and Smit's seta A.

Of those specimens identified here as *Ct. canis* (entry 12), three of the four females possess three metepisternal setae on each side, one has three on the right and two on the left side; head shape, and length of the first genal spine agree well with Holland's fig. 12; the hind tibiae all show two major setae between the postmedian and the apical long setae as in Hopkins and Rothschild's fig. 158 (= setae A and B in Smit: fig. 34).

The validity of the identifications is thus held to be as shown under entries 11 and 12. The presence of both these species of *Ctenocephalides* on the (presumed) single host dog (entries 11.7 and 12) is not remarkable; it is not unusual for both to be found together on the same host cat or dog.

Pulicinae

13. ***Pulex irritans*** Linnaeus, 1758

13.1 1 male, remounted from card. 'Pavon [*recte* Pavón = peacock] Pulgas [fleas] Spain' [origin of handwriting unknown].

Condition: excellent.

Remarks: this species (human flea) is now distributed virtually world-wide; its occurrence on peacock (*Pavo cristatus* Linnaeus, 1758) is no doubt accidental. The Spanish 'Pulgas' is plural, but only 1 specimen was present on the card mount as received by me.

*13.2 1 female, remounted from card. 'Opossum NSW' [New South Wales] [W. S. Macleay's handwriting].

Condition: excellent.

Remarks: the occurrence on 'opossum' (=*Trichosurus vulpecula* (Kerr, 1792)) is no doubt accidental; Dunnet and Mardon (1974: 34) include only one record of the species on that host.

*13.3 3 females on 3 slides, remounted from 3 cards. 'NSW' [New South Wales] [W. S. Macleay's handwriting].

Condition: excellent.

Remarks: no indication of host.

13.4 4 males on 2 slides, remounted from 1 card. 'Portugal' [very small type-set label].

Condition: excellent; some damage to legs of 1 specimen.

Remarks: no indication of host or date. Sir William John Macleay had hundreds of world-wide locality labels typeset after the 1874 *Chevert* expedition to New Guinea. In the Macleay Museum today, there are 156 small boxes, containing thousands of very small, hand cut labels, including 'Portugal'.

14. ***Pulex simulans*** Baker, 1895.

14.1 1 male, 1 female on 1 slide, remounted from 1 card. 'Cuba'.

Condition: fair; both specimens failed to macerate adequately, and some legs are broken short or missing completely; female abdomen badly damaged.

14.2 2 males on 1 slide, remounted from 1 card. 'Negro hut in Cuba'.

Condition: fair; both abdomens damaged, and legs broken short or missing completely, but genitalia quite discernible.

Remarks: obtained by W. S. Macleay between 1826 and 1836 [*teste* D. S. Horning, Jr].

14.3 2 males on 2 slides, remounted from 2 cards. 'Cuba'.

Condition: very good.

14.4 1 female, remounted from card. 'Cuba'.

Condition: fair; spermatheca exteriorized. (Species identification uncertain.)

14.5 1 male, remounted from card. 'On Capromys Fournieri.'. Fig. 5.
Condition: excellent; left hind tibia lacks 3 podomeres.
Remarks: originally on same card with 4 males and 1 female *Ctenocephalides f. felis*; see entry 11.6 for remarks on host and locality. *Capromys* spp. are not specifically mentioned as hosts of *P. simulans* by either Smit (1958) or Hopla (1980).
14.6 1 female, remounted from card. 'Cuba'.
Condition: very good.
Remarks: originally on same card with 2 female *Ctenocephalides f. felis*, see entry 11.5.
14.7 2 females on 2 slides, remounted from separate pins. 'Cuba'. Fig 6.
Condition: very good; some legs broken short, but damage to abdomens is minimal.

15. ***Pulex*** sp. indet.
1 female, remounted from card. 'Cuba'.
Condition: poor; very badly damaged (by chewing insects?) prior to receipt by me.

Pulex simulans was, for many years, synonymized with *P. irritans* by Jordan and Rothschild, 1908, following its reduction to a variety by the original describer, Baker, (1904: 379) but was re-established as a separate species by Smit (1958), who included Cuba (as cited in Hopkins and Rothschild, 1953: 115 'from rats') among the sites of natural occurrence. Hopla (1980) gave a wide range of hosts for this species in the United States, but burrowing rodents appear to be the preferred hosts; *Capromys fournieri* [= *Capromys p. pilorides*] is described as 'arboreal' (Burton, 1970: 91).

TUNGIDAE

16. ***Tunga penetrans*** (Linnaeus, 1758)
1 female (undistended), remounted from card. 'nigua' [= chigoe, sand-flea] [origin of handwriting unknown]. 'Cuba' [W. S. Macleay's handwriting].
Condition: good, but both hind legs broken off at femoro-tibial joint.
Remarks: the state of the abdomen corresponds approximately to that depicted in Hopkins and Rothschild, 1953, fig. 21A. The usual host is man, and the species is widespread in tropical parts of Neotropical and Ethiopian Regions; it was recorded from Cuba by García Avila (1976: 13).

MISCELLANEOUS

17. One label was unaccompanied by any specimen. It reads '*Pulex hirundinis*', without further data. This species, now *Ceratophyllus* (*Ceratophyllus*) *hirundinis* (Curtis, 1826), is widespread on passerine birds in the European and west Siberian subregions of the Palaearctic Region (Smit, 1983: 62, maps 24, 172).

DISCUSSION

Few specimens in the collection were taken in Australia: two endemic species (four specimens, entries 2, 3); one species (2 specimens, entry 4) native to Australia though now found elsewhere; a few specimens of 'human flea' (entries 13.2, 13.3) introduced to the continent probably from Europe. These specimens of Australian origin are of value in the history of Australian entomology and they do not appear to have been recorded previously.

The 'Darwin Flea' (entry 9) is of great interest as it represents a hitherto presumed lost specimen (Smith, 1987); its reappearance goes some way towards completing the record of Darwin's entomological relicts.

The remainder of the material comprises: some specimens collected from Europe (entries 1, 5-8, 10, 13.1, 13.4) no doubt obtained by W. S. Macleay by exchange, gift or purchase; the rest are from Cuba, reflecting Macleay's interests during his residency there. The flea fauna of Cuba and vicinity seems to be relatively unexplored. García Avila (1976) recorded only *Ctenocephalides felis* and *Tunga penetrans*, both of which are here confirmed. *Ct. canis*, whose usual host is dogs, may have been overlooked by García Avila or he may have failed to separate the species from *Ct. felis*. His failure to report any species of *Pulex* is surprising, as *P. irritans* at least is widespread. Most of the species referred to in this paragraph are not uncommon; their importance lies chiefly in their historical aspect in that they reveal transactions of collecting, purchasing and exchanging among the persons referred to in the text.

ACKNOWLEDGEMENTS

I wish to thank Dr D. S. Horning Jr, for the opportunity to examine the collection and for much assistance in deciphering records, including the identification of handwriting on the labels. Authenticated specimens of *Pulex simulans*, used for comparison, were kindly provided by Mrs Annette Seccombe and the Trustees of the Natural History Museum, London; by Professor Robert Traub, Smithsonian Institution, Washington, D.C.; and by Drs E. C. Greiner and C. B. Beard, University of Florida, Gainesville. I am indebted to Mr T. P. Williams, University of Canterbury, Christchurch for photographic services.

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PROCEEDINGS
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NEW SOUTH WALES

VOLUME 113
NUMBER 2

The Geology of an Area North-east of Cudgegong, New South Wales

B. D. MILLSTEED
(Communicated by A. J. WRIGHT)

MILLSTEED, B. D. The geology of an area north-east of Cudgegong, New South Wales. *Proc. Linn. Soc. N.S.W.* 113 (2), 1992: 89-107.

In an area to the north-east of Cudgegong, N.S.W. a strip of Early and Late Devonian sediments and volcanics is faulted to the west against Late Silurian strata, mostly of the dacitic and rhyolitic Windamere Volcanics. To the east the Devonian strata are unconformably overlain by the Permian Rylstone Tuff and Megalong Conglomerate.

The Devonian consists of two portions with an unconformable contact. The Early Devonian sequence consists of the Yellowman's Creek beds (new name, oldest Devonian unit), Roxburgh Formation, Riversdale Volcanics and Carwell Creek beds. The brachiopod fauna present in the Yellowman's Creek beds is indicative of a Lochkovian age whereas *Buchanathyris* suggests a Zlichovian age for the Carwell Creek beds; the intervening beds are interpreted as being Lochkovian to Pragian. Late Devonian strata are represented by the Buckaroo Conglomerate (oldest), Bumberra Formation and Lawsons Creek Shale (youngest).

The region was affected by the Mid-Devonian Tabberabberan Orogeny, producing an angular unconformity between Early and Late Devonian strata. The Carboniferous Kanimblan Orogeny produced NW-SE trending faults and folds. Permian strata are undeformed.

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INTRODUCTION

Late Silurian to Permian strata crop out in an area to the immediate NE of the former site of the township of Cudgegong, in the Central Tablelands of N.S.W. Cudgegong, now becoming submerged beneath the waters of Lake Windamere, was located approximately 35 km to the SE of Mudgee and about 260 km NW of Sydney (Fig. 1).

The stratigraphic sequence of the study area is listed in Fig. 2 and includes extensive units of both Early and Late Devonian age as well as subordinate Late Silurian and Permian units.

The pre-Permian rocks were deposited on the Capertee Geanticline of Packham (1960), where Silurian and Devonian strata 'occur *inter alia* in fold structures trending to approximately 140°' (Wright, 1967). As can be observed in Fig. 3, the strata within the study area occupy the easternmost of two fault-bounded blocks in the Mudgee region, whereas the Silurian Windamere Volcanics are part of the belt of strata separating the two fault blocks. These strata are overlain unconformably by the Permian Rylstone Tuff and Megalong Conglomerate of the Sydney Basin sequence.

STRATIGRAPHY

Windamere Volcanics

The only Silurian unit cropping out in the study area is the Late Silurian Windamere Volcanics of Pemberton (1980b). This unit occupies a very minor portion of the study area, cropping out in the extreme west (see Fig. 2) but extending to the NW for approximately 30 km along strike (Pemberton, 1980b). In the study area this unit abuts an extensive suite of Devonian sediments, the contact being a NNW-SSE trending fault (the Cudgegong Fault of Game, 1934).

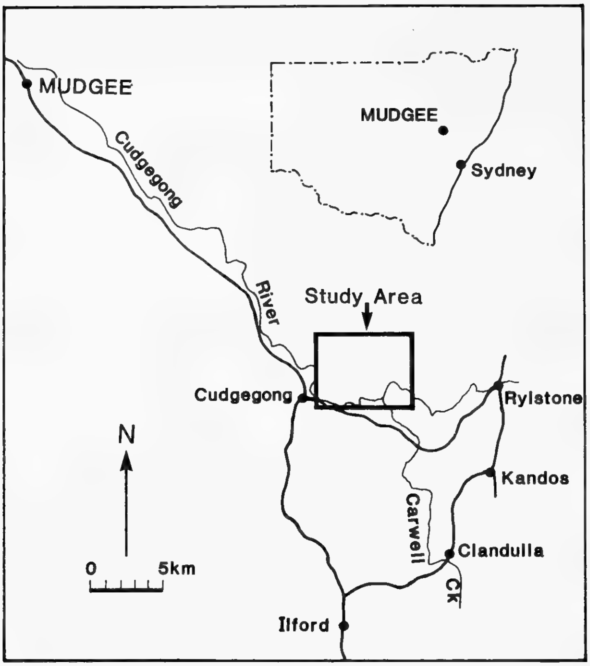


Fig. 1. Locality map showing position of the study area in relation to Mudgee (modified from Offenburg *et al.*, 1971).

Petrography

In the study area the Windamere Volcanics consist of a lower blue-green, massive, fine grained, porphyritic dacite with up to 4.3% embayed quartz and 5.7% albite phenocrysts set in a cherty matrix. Occasional bands of angular to subrounded dacite clasts occur throughout, indicating phases of reworking of the sequence.

Overlying the lower horizon is a white, flow-layered, porphyritic rhyolite lava. Most of the quartz phenocrysts are anhedral to subhedral and up to 2.5 mm in size. Phenocrysts of orthoclase up to 0.9 mm are also present but in trace amounts. The phenocrysts are set in a cherty matrix of probable quartzo-feldspathic composition. Pemberton (1980b) has reported the presence of similar horizons at varying stratigraphic levels elsewhere in the Windamere Volcanics.

Yellowman's Creek Beds

The name Yellowman's Creek beds is introduced for poorly outcropping greenish-brown coloured shale and subordinate grey, dolomitic micritic limestone, outcropping between GR 654 662 and GR 658 696 (see Fig. 2), with a thickness exceeding 165 m. The base of the unit is not exposed in the study area, the unit abutting the Windamere Volcanics further to the west along the Cudgegong Fault. The upper contact of the unit with the Roxburgh Formation is apparently conformable but not well exposed. The representative section of this unit is between GR 657 677 and GR 657 672. This section represents the best outcrop of the Yellowman's Creek beds (but unfortunately consists entirely of shale, the limestone constituting only a very minor proportion of the unit and being restricted to very poorly exposed areas at GR 656 675, see Fig. 2), and passes sharply southwards into the sandstones of the Roxburgh Formation.

Petrography

Shales of the Yellowman's Creek beds are brownish-green in colour and are composed predominantly of chlorite, muscovite, quartz and hematite, with minor detrital biotite. Grain sizes range up to 0.07 mm, the majority being much smaller, with the larger size range being almost entirely quartz grains.

Limestones are dark grey, strongly stylotized, pellet-bearing, packed biomicrite (after the terminology of Folk, 1962), consisting dominantly of ferroan calcite with abundant patches of late diagenetic ferroan dolomite. Areas of silicification are restricted to the cores of the diagenetic dolomite patches and to a lesser extent the shells of brachiopods.

Environment of Deposition

Very little information can be gained about the environment of deposition of this unit due to poor outcrop. The presence of a marine fauna, micritic limestones and the dominance of shale is however indicative of a very quiet water, marine environment.

Fauna and Age

The only fauna recovered from the Yellowman's Creek beds is from the isolated limestone pods, and includes the silicified brachiopods *Atrypa* sp., *Cyrtina* sp., *Howellella* sp., *Eoschuchertella* sp., *Skenidioides* sp., *Dolerorthis* sp., *Anastrophia* sp., *Dicaelosia* sp., as well as pentamerids, other dalmanellids, chonetids and the coral *Rhizophyllum* sp. Identifications were made by Dr A. J. Wright who states that the presence of *Cyrtina* is indicative of a Devonian age. *Eoschuchertella*, *Anastrophia*, and *Skenidioides* have been reported in Lochkovian (Early Devonian) sediments elsewhere in N.S.W. (Savage, 1971), and these indicate this age for the Yellowman's Creek beds.

Roxburgh Formation

The Roxburgh Formation (Pemberton, 1980a) is developed as a northerly-thinning wedge dominated by quartzarenite, sublitharenite and litharenite with minor conglomerate and rare limestone, with a total thickness of 625 m.

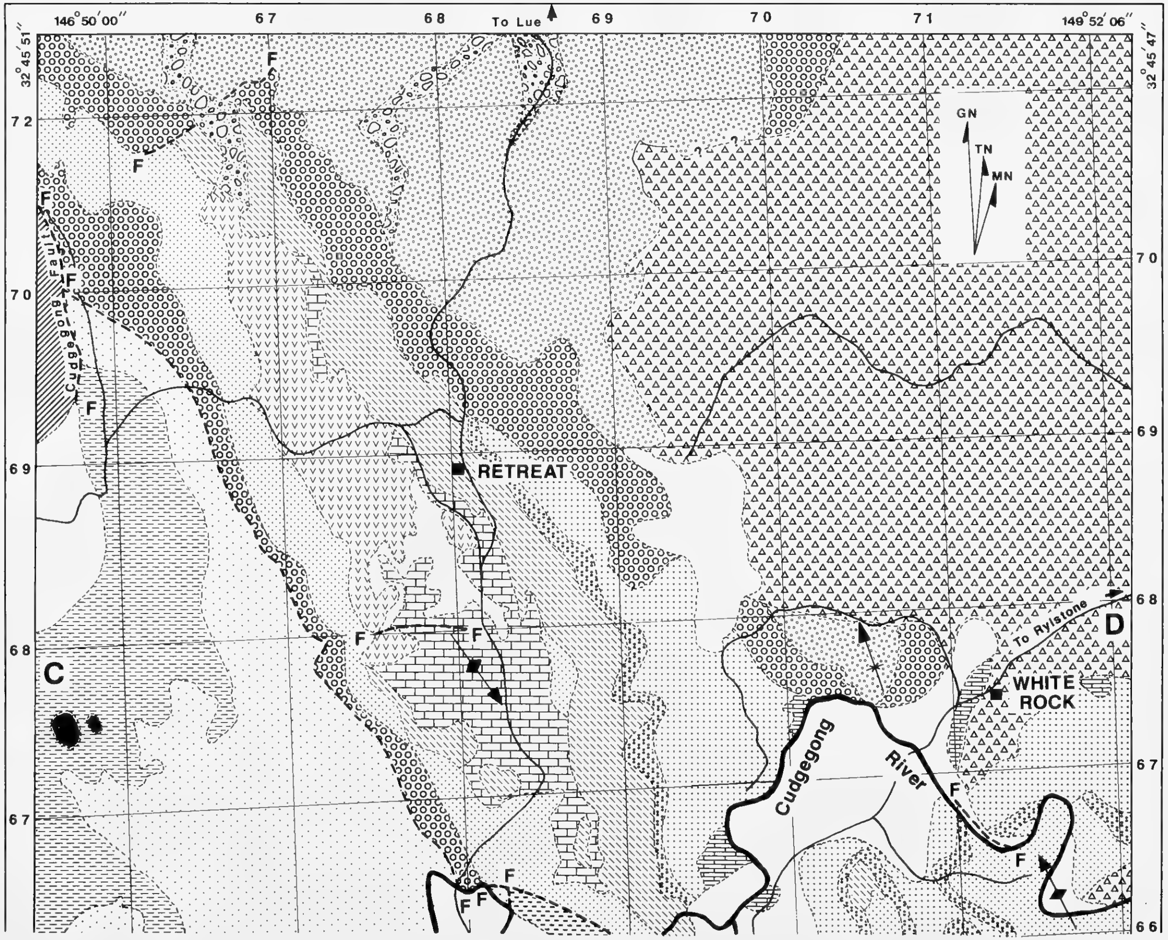
The lower contact of the Roxburgh Formation is best exposed in the vicinity of GR 657 672 where it is apparently conformable with the Yellowman's Creek beds. However, whereas the contact is quite sharp in the given area it is generally poorly exposed in the remainder of the study area. The Roxburgh Formation is conformably overlain by acid volcanics and volcarenites of the Riversdale Volcanics. The nature of this boundary has been described from better outcrops to the south by Pemberton (1980a). In the vicinity of GR 673 661 the Roxburgh Formation passes directly into the Carwell Creek beds, the Riversdale Volcanics being absent. However due to a paucity of outcrop in this area the incomplete stratigraphic sequence remains unexplained.

Petrography

In the Roxburgh Formation the dominant lithology is very fine- to medium-grained, quartzarenite/sublitharenite containing up to 90% quartz grains with cherty acid volcanic rock fragments being the other major component. These lithologies are predominantly moderately to poorly sorted, texturally submature and display abundant quartz overgrowths.

The conglomerates within the sequence are coarse granule-sized, containing abundant pebble-sized clasts dominated by cherty acid volcanics (up to 73%) as well as up to 11.3% angular quartz grains. Texturally the conglomerates are loosely packed, poorly sorted, texturally immature and extensively silica cemented.

The limestone is fine-grained, predominantly grey-coloured, and unfossiliferous with abundant red veins of hematite. The lithology shows extensive growth of neo-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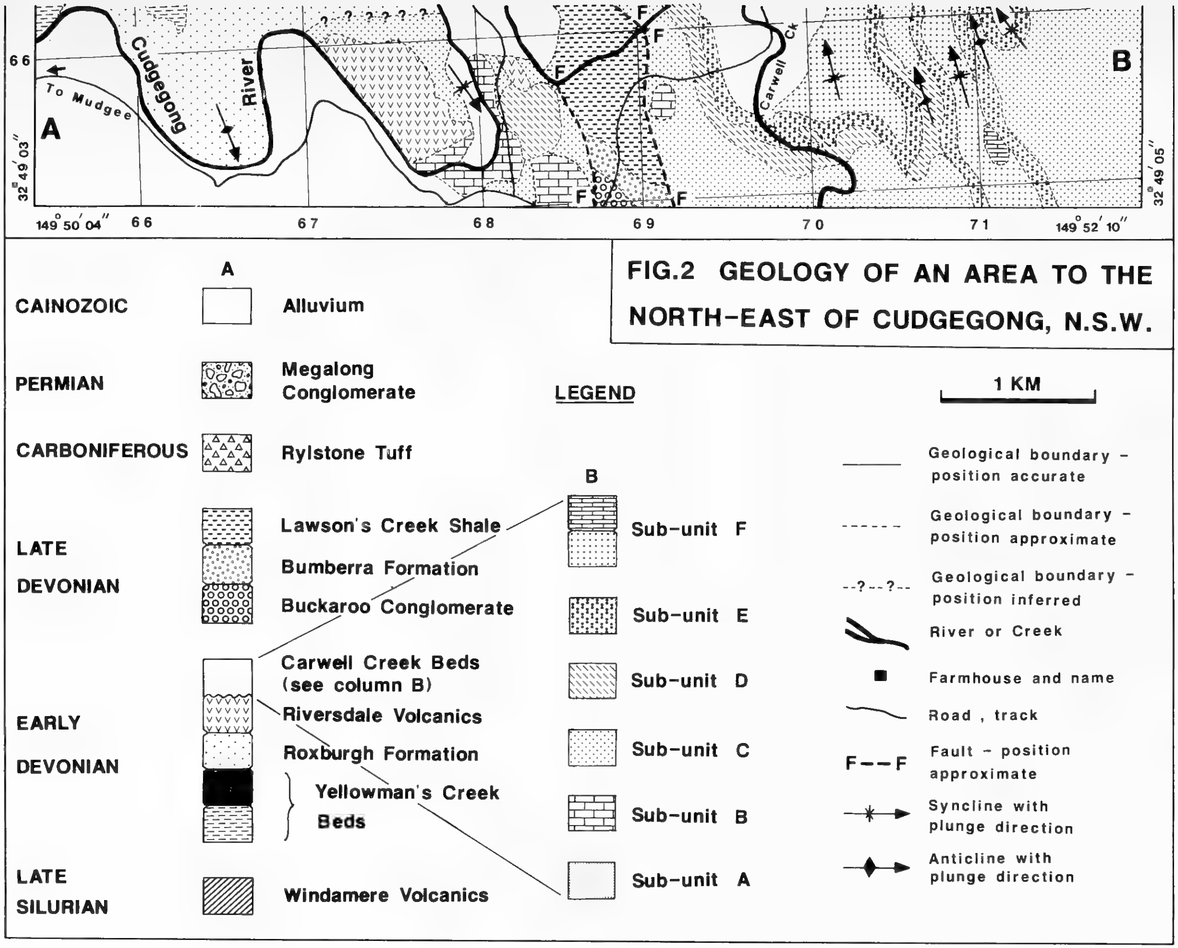

FIG.2 GEOLOGY OF AN AREA TO THE NORTH-EAST OF CUDGEGONG, N.S.W.

morphic spar due to diagenesis. It has been heavily dolomitized, being up to 98% late diagenetic dolomite. The dolomitization postdates the neomorphic recrystallization.

Environment of Deposition

The Roxburgh Formation is subdivided into three main lithotypes; these are A) thinly parallel laminated to rarely cross-bedded sandstone beds up to 40 cm thick, B) massive sandstones up to 40 cm thick, with occasional angular shale clasts, C) rare, thin, lenticular shales. Conybeare and Crook (1982) suggested that the prsence of shale clasts is indicative of several depositional environments, these being fluvial, tidal flats and channels, neritic, and the bathyal-abyssal environments. A marine environment is indicated by the presence of fragments of crinoids and bryozoans. Tidal flat/channel environments are rejected due to the absence of desiccation features, bioturbation, and channel structures, as well as the dominance of sand in the sequence. Similarly the bathyal-abyssal alternatives can be discounted as neither turbidites nor laterally extensive muds are present. A neritic environment is therefore proposed for the Roxburgh Formation, its sediments most closely resembling the sandy facies of Reineck and Singh (1980). This would indicate a lower shore face environment, with maximum water depths of 15-20 m, as Reading (1978) suggested that above this depth the deposition of shales is affected by fair weather wave activity. The change from the shales and micrites of the Yellowman's Creek beds to the sandstones of the Roxburgh Formation therefore probably represents a shallowing of water depths.

Fauna and Age

The fauna of the Roxburgh Formation is very sparse. However, Pemberton (1980a) reported the presence of brachiopods, including *Iridistrophia*, *Howellella*, and *Delthyris*, that are indicative of an Early Devonian age. As the underlying unit is Lochkovian and the overlying Carwell Creek beds Zlichovian, an approximate Pragian age is inferred for this unit.

Riversdale Volcanics

Conformably overlying the sediments of the Roxburgh Formation is a suite of rhyolitic and dacitic lava, tuff and volcarenite, up to 320 m thick. The unit was first described by Wright (1966) as the Riversdale Rhyolite but was later designated by Offenburg *et al.* (1971) as the Riversdale Volcanics.

Petrography

The Riversdale Volcanics can be subdivided into a number of distinct lithologies. The oldest is white flow-layered rhyolite containing up to 45.2% anhedral quartz grains (commonly embayed), 1.6% euhedral orthoclase and 4.8% euhedral Na-plagioclase phenocrysts, set in a very fine-grained quartzo-feldspathic groundmass.

The overlying lithology varies from pink to green, is massive, porphyritic and very fine-grained. In the green (chloritic) lithology anhedral to euhedral quartz grains vary in abundance up to 4.7% and up to 3.5 mm in size; subhedral to euhedral plagioclase phenocrysts up to 2.5 mm in size comprise up to 10.3% of the lithology, while orthoclase as subhedral to euhedral grains up to 2 mm in size can constitute up to 12.7% of the rock. The pink (hematitic) lithology is a lateral equivalent of the green rock type and contains up to 3.5% anhedral quartz phenocrysts which vary in size up to 2.5 mm. The other major phenocryst phase is anhedral orthoclase grains up to 0.6 mm in size. The groundmass contains abundant devitrified glass shards. A reworked horizon at the top of the Riversdale Volcanics consists of tightly-packed, poorly-sorted sandstone and conglomerate with clasts generally in the pebble to cobble size range. The lithology is massive and varies between white and purple in colour, with abundant cherty silica cement.

Age

The Riversdale Volcanics are underlain and overlain by inferred Pragian and Zlichovian rocks respectively. The presence of an unconformity between the Riversdale Volcanics and the overlying Carwell Creek beds is suggested by a discontinuous, apparently reworked volcarenite at the top of the volcanics. This would tend to favour the Riversdale Volcanics being assigned a Pragian age.

Carwell Creek Beds

The Carwell Creek beds (Offenburg *et al.*, 1971) are the youngest and most areally extensive of the Devonian units, occurring over the majority of the central and southeastern portions of the area (between GR 656 712 and 710 650). In the NE of the study area the unit thins in outcrop, being unconformably overlain, to both the east and west, by the Buckaroo Conglomerate.

The Carwell Creek beds are over 1250 m of limestone, litharenite, and conglomerate that can be divided into a number of informal sub-units, as is shown in Fig. 2. The lowermost sub-unit or member (unit A) unconformably overlies the Riversdale Volcanics, often being underlain by discontinuous volcarenite of the volcanic sequence. The upper contact of the Carwell Creek beds is not exposed in the study area, being faulted out in the vicinity of GR 691 652, and overlain with angular unconformity by the southernmost outcrops of Late Devonian strata occupying the major syncline appearing in the NE portion of Fig. 2.

Petrography

Lithologically the Carwell Creek beds are quite varied. These lithologies can be generally grouped into sub-units (see Fig. 2), although each can itself be quite variable, especially the limestones. The following therefore is only a brief summary of the lithologies present, rather than a more detailed description of each.

Sub-unit A is fine- to very fine-grained, buff to cream coloured sandstone with occasional grey limy pods and lenses, especially near the contact with sub-unit B. Scattered throughout are fragments of bryozoans and crinoid ossicles varying between 0.5-1.0 mm in size. The unit is developed at GR 677 685.

Sub-unit B (cropping out between GR 680 679 and 685 672) is dominated by fine-grained, greenish-brown limestone occurring in massive beds up to 15 cm thick. The unit is strongly recrystallized, with primary structures destroyed by the growth of neomorphic spar, the grains varying between 0.09 and 0.22 mm in size. This recrystallized limestone occasionally contains beds of dark grey, fossiliferous, micritic limestone, which appears to be the original texture of the limestones as it lacks neomorphic calcite. Some of these micritic horizons are distinctive in that they contain abundant sericite, giving them a distinctive yellowish coloration, and also in that they contain abundant solitary corals up to 10 cm in size. Discontinuous pods of grey coloured, coarse intrasparrudite also occur in sub-unit B, being present in beds up to 5 m thick. These intrasparrudites are dominated by angular micritic intraclasts with some volcanic rock fragments and occasional fossils. Also present within this sub-unit is a red-brown coloured, highly discontinuous pebble- to boulder-sized conglomerate which is tightly packed, with rounded to subrounded clasts of cherty acid volcanics (very similar to the Riversdale Volcanics), up to 25 cm in size, set in a cherty matrix. A biostromal limestone, present near the base of sub-unit B, contains abundant bulbous stromatoporoids set in a buff coloured, recrystallized matrix.

Sub-unit C is composed of fossiliferous biosparite, and crops out particularly well between GR 688 680 and GR 690 670. It is distinguished by abundant, densely-packed crinoid ossicles and stem segments (up to 3 cm in size) and small to large scale cross-bedded crinoid bearing sandstone. Apart from the crinoid fragments, the rest of the lithology consists dominantly of quartz grains (15.2-22.0%) which are often embayed.

Sub-unit D is composed of grey to brown, fine- to medium-grained litharenite, quartzarenite and sublitharenite, cropping out at GR 682 666, with a maximum thickness of 495 m. The sub-unit is dominated by quartz (40.0-80.3%) with cherty acid volcanic rock fragments constituting up to 45.0%, and is silica cemented.

Cropping out at GR 691 672 is sub-unit E, which is massive to poorly cross-bedded, reddish-purple, tightly packed, poorly sorted conglomerate with cherty acid volcanic rock fragments set in a coarse matrix. The lithology has a maximum thickness of 45 m.

Massive, light grey, fine- to medium-grained, massive to finely plane-laminated litharenites and well-bedded limestones cropping out at GR 695 674 are referred to here as sub-unit F and have a minimum thickness of 700 m. The litharenites contain lithic clasts dominated by cherty acid volcanics, contain very minor metaquartzite and traces of shale, and are strongly silica cemented. Interbedded within sub-unit F is a discontinuous limestone with a maximum thickness of 18 m, that occurs approximately 140 m above the base of the sub-unit. It is composed of a lower horizon of Folk's (1974) type II limestone with dolomitized micrite, fossiliferous micrite, biomicrite, biopelmicrite and pelmicrite present as well as interbedded shales. Fossils include corals and brachiopods. Above this horizon is a sequence of interbedded, dolomitized biolithite beds (dominated by bulbous stromatoporoids) and unfossiliferous, dolomitized, medium-crystalline carbonate. These two (the lower micritic horizon and the upper biolithite/ medium-crystalline horizon) can also be distinguished in that the former is dark grey while the latter is very light grey in colour.

Environment of Deposition

The poor exposure and lack of sedimentary structures in sub-unit A make interpretation of its environment of deposition difficult. However, the presence of bryozoan fragments is indicative of marine conditions, while the calcareous lenses suggest periods of quiet water deposition.

Sub-unit B is lithologically varied, containing extensive, massively bedded micritic limestones, lenses of intrasparrudite, biolithite and conglomerate. The biolithite, the lowermost facies of the sub-unit, is dominated by bulbous stromatoporoids. Wilson (1975) stated that a bulbous shape is an adaptation to prevent fine sediment settling out on the surface of the stromatoporoid; as forms with such a shape are usually found in quiet water, below wave base or in shallow protected back reef areas. The lensoidal intrasparrudite horizons contain abundant, angular, pellet-sized micrite clasts. Intraclasts are deposited either on supratidal flats or in subtidal channels (Shinn, 1983). Intraclasts originating from subtidal and intratidal environments are usually composed of grapestone, individual pellets, mudsized particles or fossils (Flugel, 1982), and the micrites present in the sequence lack evidence of exposure. The intraclasts therefore represent material eroded from supratidal flats during storm activity, and deposited into subtidal channels. The co-occurrence of the micrites and intrasparrudite lenses is indicative of water depths less than 20 m (Flugel, 1982; fig. 70) as their association represents deposition above fair weather wave base. The association of the biolithite with these two lithologies would indicate that it too was deposited above wave base, restricting its environment of deposition to either back reef or back bank, indicating a maximum water depth of 5 m (Enos, 1983). The irregular outcrop and highly variable thickness of the conglomerate suggests that it infills hollows in the underlying carbonate, the coarsest material occurring in the thickest section. It is generally poorly sorted, but in the thickest section the largest clasts are restricted to the top and sides of the outcrop,

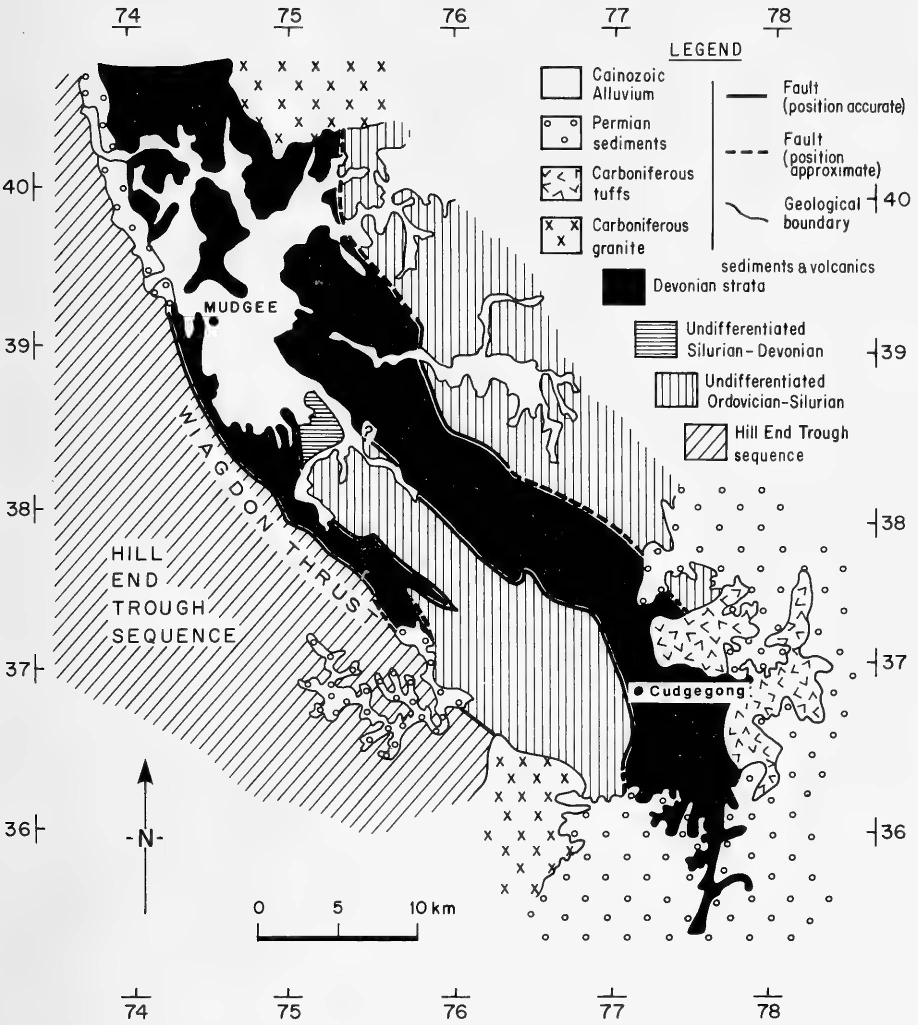

Fig. 3. Regional geology of the Mudgee-Cudgegong area (modified from Offenburg *et al.*, 1971, and Pemberton, 1977, 1980a, and 1980b) illustrating the presence of two faulted blocks of Devonian strata. The grid system appearing on the map is the Australian metric map grid.

suggesting that it is a mass flow deposit derived from an acid volcanic source. The most probable source of this would have been exposed Riversdale Volcanics. A near shore origin for the conglomerate is preferred due to the difficulty in getting clasts up to 25 cm in size into offshore environments.

The sediments of sub-unit C can be divided into three groups on the basis of their sedimentary structures; these being massive beds containing stringers of crinoid ossicles, beds showing fining-upward sequences of crinoidal detritus and thick, cross-bedded horizons composed predominantly of crinoid stem segments up to 3 cm long. The cross-bedded horizons are interpreted as representing nearshore bars, while the sandstones exhibiting fining-upward structures can be explained by pumping of the sediments by storm waves. This association of environments would restrict sub-unit C to the upper shore face.

Sub-unit D is an interbedded sequence of very fine- to medium-grained sandstone beds up to 60 cm thick; either massive (with occasional flat, angular shale clasts up to 4 cm in size) or finely, internally laminated. Rarely interbedded shale horizons up to 5 cm thick are also present. These sediments are almost identical with those of the Roxburgh Formation, and as with that formation the relative lack of cross-bedding, lack of desiccation features, dominance of sand and absence of Bouma sequences indicates a shallow neritic environment. The angular shale clasts within massive beds are interpreted as having been ripped up and deposited during storm activity, the storm waves also disrupting and obliterating sedimentary structures. The plane laminated horizons therefore represent periods of normal sedimentation, while the shale beds indicate that deposition occurred below fair weather wave base, as in the lower shoreface environment of Reineck and Singh (1980).

Sub-unit E is a sequence of poorly bedded and sorted, rarely cross-bedded pebble conglomerates and pebbly sandstones. Collinson and Thompson (1982) indicated several environments in which significant amounts of gravel accumulate, these being river channels, fan deltas, alluvial fans and steep slopes, shorelines, glacial environments and areas associated with volcanoes. Although there is no direct fossil evidence to suggest a marine environment of deposition the association of the unit with marine sediments would suggest a similar origin. There is also no evidence of either Devonian glaciation in the region, or of volcanism contemporaneous with the deposition of the conglomerate. The sheet-like nature of the conglomerate and the absence of fining-upward sequences would then suggest a shoreline deposit, although the presence of tabular cross-bedding and the poorly sorted nature of the sediment preclude a beach environment.

Sub-unit F is primarily a sequence of thickly bedded, massive to finely laminated sandstones (rarely cross-bedded), that are almost identical in appearance with the sandstones of the Roxburgh Formation and sub-unit D of the Carwell Creek beds. Accordingly a lower shoreface environment of deposition is proposed for the sandstones. Interbedded with the siliciclastic sediments of sub-unit F is a discontinuous limestone horizon that is divisible into two sections. The lower 6-7 m consists of thick bedded, micritic limestone interbedded with thin, up to 12 cm thick, shale horizons indicating deposition in quiet water conditions and the abundance of pellets indicating pronounced infaunal activity. It is apparent from the criteria stipulated by Enos (1983) that these lithologies were deposited in a lagoonal environment. The upper section of the limestones contains abundant bulbous stromatoporoids forming biostromal beds up to 2 m thick, the stromatoporoids indicating deposition of fine-grained sediments (Wilson, 1975). Flugel (1982) stated that in the Devonian bulbous stromatoporoids were prominent in back reef and back bank environments. In the absence of any indication of reefal fabrics in the carbonates, it is interpreted that these sediments were deposited in a back bank environment. The limestones interbedded in sub-unit F represent therefore a shoaling upward sequence from quiet lagoonal to a more active, wave-influenced environment. Enos (1983) suggested that the wave base in lagoonal settings is 4-5 m; the stromatoporoid-bearing sediments must therefore have been deposited above this depth.

Fauna and Age

The age of sub-unit F is based on the brachiopod *Buchanathyris* (GR 701 674 — identified by Dr A. J. Wright); *Spinella*, *Atrypa*, several unidentified spiriferids, a gastropod, bulbous stromatoporoids, *Favosites*, solitary corals, bryozoans, crinoid ossicles and at least one species of trilobite are also present. *Buchanathyris* is suggestive of a Zlichovian age (Wright, 1985, pers. comm.).

Buckaroo Conglomerate

The Buckaroo Conglomerate (Wright, 1966) is the oldest Late Devonian unit in this area, overlying Early Devonian strata with angular unconformity. The upper part of this unit is gradational with the Bumberra Formation, the contact being marked by a rapid decrease in the abundance of pebble- and granule-sized lithic fragments. The Buckaroo Conglomerate is distinguished by its dominance of a coarse sandy matrix and patchy reddish coloration, due to abundant hematite in the matrix. The unit crops out in two areas, a western block running between GR 660 700 and GR 690 650 and in a prominant syncline in the NE of the area (e.g. at GR 680 695), where it has an average thickness of 150 m.

Petrography

The dominant lithology of this unit is pebbly sandstone with minor conglomeratic bands, as well as subordinate sandstone and shale. The coarser horizons tend to be tightly packed, very poorly sorted, texturally mature and contain sub-angular to sub-rounded acid volcanic clasts and subordinate metaquartzite fragments in a coarse to very coarse sand matrix. As with the other siliciclastic units in the study area, the Buckaroo Conglomerate is strongly silica cemented.

Environment of Deposition

The presence of medium-scale (up to 0.5 m) tabular cross-stratified pebbly sandstone with clasts up to several centimetres in size is indicative of high energy conditions, and may be generated in either a fluviatile or near shore marine environment. However, the intense bioturbation commonly exhibited by shallow marine shales (Reading, 1978) is not evident in the shales of the Buckaroo Conglomerate; nor would the massive beds of shale (up to several metres thick) be expected to be preserved in the high energy environment necessary to produce a near shore conglomerate.

The presence of large scale, up to 2 m, fining-upward sequences is indicative of a fluvial depositional environment. These sequences begin with a basal, densely packed conglomerate and proceed upward into cross-bedded pebbly sandstone, then coarse sandstone. The sequences may occasionally be capped by a thin shale. The dominance and coarseness of the bed-load sediment, as well as the presence of the fining-upward sequences suggests that the Buckaroo Conglomerate was deposited in a braided fluviatile environment. Similar braided fluviatile sequences have been described by Rust (1984). Relatively few palaeoflow measurements were collected; they are reasonably uniform however, and indicate a northerly flow for the palaeoriver.

Fauna and Age

The Buckaroo Conglomerate has been considered Late Devonian (Wright, 1966) as it is conformably overlain by the Bumberra Formation, which near Mudgee contains *Cyrtospirifer*. However, no fossils were found in this unit in the area of study and the existing age is accepted.

Bumberra Formation

The Bumberra Formation (Wright, 1966) conformably overlies the Buckaroo Conglomerate, the gradational boundary between the two only being able to be placed to within 10 m. The unit is a sequence of buff to light grey, fine-grained sublitharenite up to 1060 m thick, which crops out in two separate areas; one is about GR 690 650 forming part of a faulted block of Late Devonian strata, while near GR 690 710 the second forms part of a large syncline composed only of Late Devonian units.

Petrography

The unit is composed of tightly packed, poorly sorted, texturally mature to submature with subrounded to rounded grains averaging in size from fine to medium sand. However, occasional lithic clasts up to 1.5 cm are scattered throughout the unit, especially near the base. Quartz grains constitute up to 81% of this lithology, while lithic clasts, dominated by cherty acid volcanics vary between 6.0 and 13.0% of the rock. These grains and clasts are set in a sericite-rich, silica cement. Flattened, angular mud flakes up to 3 cm in size are also found throughout the unit.

Environment of Deposition

The presence of marine brachiopods near the base of the Bumberra Formation indicates marine conditions existed during deposition of the unit. The gradational nature of the contact with the fluviatile Buckaroo Conglomerate would also indicate a gradation from fluvial to marine conditions. As such the Bumberra Formation, at least near its base, must have been deposited in very near shore conditions.

The formation consists of basically two lithologies. The first is massive, fine-grained sandstone beds up to 20 cm thick. The second is fine-grained, finely internally laminated sandstone, the laminae defined by thin layers of hematite and tourmaline. The second lithotype occasionally exhibits medium-scale cross-bedding and low (up to 2 cm high) ripples on bedding planes. This latter lithology is interpreted as representing periods of low energy, with long shore drift currents occasionally becoming sufficiently strong to produce the ripples and cross-bedding. The massive beds are the result of wave generated disruption of the laminated horizons. The absence of shale in the sequence would indicate that this disruption occurred very near shore, and was the result of fair weather wave activity.

Fauna and Age

The fauna of the Bumberra Formation in this area is extremely limited, containing bryozoans, bivalves and *Cyrtospirifer*. The presence of *Cyrtospirifer* indicates a Late Devonian age for the unit (Wright, 1985, pers. comm.).

Lawsons Creek Shale

The Lawsons Creek Shale was proposed by Wright (1966), for a sequence of 'thinly interbedded grey or buff shales and siltstones which crop out about Lawsons Creek between Mt. Frome and Mt. Knowles'. In the study area the unit crops out at GR 687 660, where it occurs in a NW-SE trending belt that forms part of a Late Devonian fault block. This unit consists of over 225 m of thinly bedded, coarse silts and shales. Beds vary in thickness from 2 mm to several centimetres.

The unit appears to conformably overlie the Bumberra Formation, as it does elsewhere. The contact however is not exposed. Wright (1966) reported that the Lawsons Creek Shale is overlain by the Derale Sandstone to the north of the study area.

Petrography

This unit consists of two main lithologies, the first being an immature, very finely laminated, coarse, silty quartzarenite with a buff to reddish colour. The dominant component of the lithology is sub-rounded to rounded quartz grains up to 0.07 mm, the remainder consisting of sericite and hematite, the latter forming thin stringers and lineations defining bedding. The second lithology is a very thinly bedded, greenish coloured shale. The dominant and largest component of the shales is sub-rounded to rounded quartz grains in the coarse silt range. These quartz grains are set in a matrix dominated by sericitic mica showing a preferred orientation parallel to bedding. Scattered amongst the sericite are larger (up to 0.05 mm) grains of detrital biotite.

Environment of Deposition

The brachiopod fauna described from this unit by Wright (1966) is indicative of a marine environment of deposition. Reading (1978) stated that most extensive muds are only preserved in water depths in excess of 30 m, due to the effects of wave action. The presence of silty horizons within the shale (this study and Wright, 1966) is probably due to mobilization of the silt by storm wave activity, its transport and subsequent deposition in the shelf muds that represent the majority of the Lawsons Creek Shale. Wright (1966) suggested that the unit becomes increasingly sandy and considerably thicker to the south of Cudgegong, suggesting that this probably reflects increasing proximity to the palaeoshoreline.

Fauna and Age

Although no fossils were found in this area, Wright (1966) identified brachiopods in this unit in the Mudgee area, of which *Mucrospirifer* and *Cyrtospirifer* are indicative of a Late Devonian age.

Rylstone Tuff

The Rylstone Tuff was named after a series of rhyolites and dacites cropping out near the township of Rylstone. The unit crops out extensively in the NE corner of the study area, between GR 710 670 and GR 710 713, continuing well to the east.

The tuff, while exhibiting a slight dip to the NE on its western margin, is generally flat lying. It overlies the Devonian with a pronounced angular unconformity best exposed between GR 693 704 and GR 695 707. The Rylstone Tuff is overlain by Permian sediments of the Sydney Basin elsewhere in the Mudgee region (Day, 1961; Offenburg *et al.*, 1971). However, in the study area this relationship cannot be confirmed as the two sequences do not come into contact. Day (1961) suggested a maximum thickness of 300 ft (100 m) for the unit, but only approximately 50-60 m of section is exposed in the study area.

The sequence is lithologicaly varied, a well-bedded, discontinuous, 1 m thick air-fall tuff (lithology B of Fig. 4) near its base (at GR 699 702), while near the top of the section (GR 692 707) a laterally discontinuous, distinctive, 2 m thick conglomerate containing trough cross-beds up to 6 m across is present. The combination of large scale trough cross-beds, rounded nature of the composite clasts and high content of sandstone and shale clasts suggests that the conglomerate originated from fluvial reworking of the tuff. The bulk of the sequence is composed of massive, very loosely packed, lithic rich tuff, containing very angular, rhyolitic clasts. This lithology is interpreted as a stacked sequence of ash-flow deposits.

Petrography

The fluvially reworked conglomerate is cream to greenish, very poorly sorted, loosely packed and texturally submature with clasts dominantly in the granule to boulder size range, set in a greenish cherty silica matrix. The clasts are mostly angular to sub-angular in shape and rhyolitic, although abundant sub-angular quartz sandstone and shale clasts are also present.

The massive, lithic-rich tuff (lithology A of Fig. 4) is white, poor to very poorly sorted, containing abundant loosely packed, angular clasts of rhyolite and quartzite set in an abundant devitrified glassy matrix. The air-fall tuff (lithology B of Fig. 4) on the other hand is a white, well bedded rock, mostly composed of glass, occasional glass shards and quartz grains and thin horizons (1-2 mm thick) of densely packed quartz grains.

Age and Origin

The Rylstone Tuff has been dated radiometrically by Shaw *et al.* (1989) at 292 Ma. If the 286 Ma. age assigned to the Carboniferous-Permian boundary by Harland *et al.* (1982) is accepted then the Rylstone Tuff is Stephanian in age. However, recently both Lippolt *et al.* (1984) and Gulson *et al.* (1990) have suggested 300 Ma. and 299 Ma. respectively as the age of the boundary. The latter authors are followed here, with an age of ca 300 Ma. being adopted for the Carboniferous-Permian boundary, making the Rylstone Tuff basal Permian.

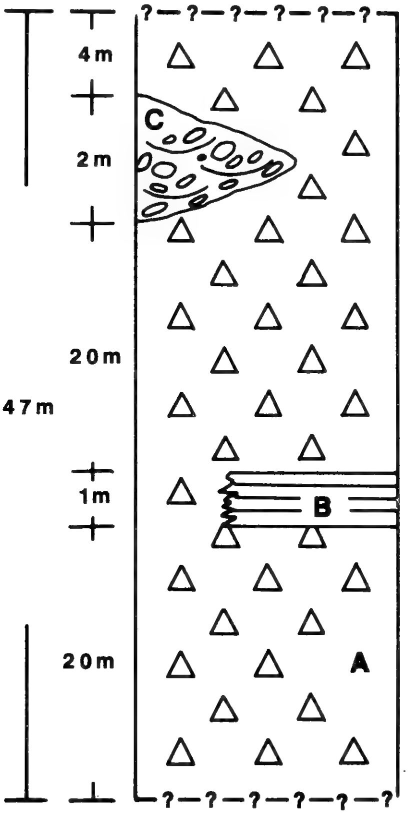

Fig. 4. Generalized stratigraphic section (diagrammatic) through the Rylstone Tuff; in the vicinity of GR 692 707 to GR 700 702. (A) Possible ash-flow tuffs, (B) Air-fall tuff, (C) Fluvially reworked conglomerate.

There appear to have been several periods of plutonism during the Late Carboniferous and Early Permian of eastern Australia. The first was associated with a phase of plutonism that lasted from approximately 325-310 Ma. (Powell, 1984: fig. 204), and resulted in the emplacement of granites such as the Gulgong Granite (312 Ma.; Evernden and Richards, 1962) and Aarons Pass Granite (320-322 Ma.; Vicary, 1983). The second, and younger, major period of volcanism was associated with the initiation of the Bowen-Sydney Foreland Basin in the Permian. Shaw *et al.* (1989) suggested that the origins of the Rylstone Tuff lay with this period of volcanism. Veevers (1984: 239) however suggested that the oldest volcanics associated with the onset of this basin development are the Hillgrove Suite (289 Ma.) and Bundarra Suite (286 Ma.), post-dating the tuff by ca 3-6 Ma. Veevers (1984) also mentioned an intermediate transitional phase of volcanism represented by the Bulganunna Volcanics (297 Ma.) and coeval granites (296 Ma. on average), pre-dating the Rylstone tuff by ca 4-5 Ma. Due to the error margins implicit in these radiometric dates, and the similarity in the age obtained for the Rylstone Tuff with those of both the intermediate and basin initiation phases of volcanism it remains unclear with which of these two phases of volcanism the tuff is associated. It is evident that the origins of the Rylstone Tuff are more closely associated with the inception of the development of the Bowen-Sydney Basin than with the Kanimblan Orogeny, as has been suggested in the past.

Megalong Conglomerate

Flat-lying erosional remnants of Permian conglomerate crop out very poorly in the study area, being best developed further to the east (near Rylstone) and to the south of Cudgegong. The unit forms the base of the Early Permian Shoalhaven Group. The sequence is exposed at GR 665 710 as well as between GR 677 703 and GR 686 711, but is best developed at GR 686 716. At GR 686 716 the unit reaches a thickness of 2-3 m, but in other areas it occurs only as scattered lag deposits on the tops of hills above 650-680 m above sea level. The unit overlies the older Palaeozoic sequence with angular discordance, on an undulatory erosional base.

The unit is dominated by polymictic conglomerate and pebbly sandstone with abundant rounded, cherty and rarer sandstone clasts up to 5 cm in size. Many of the clasts have been derived from older strata exposed in the Mudgee region, *Cyrtospirifer*-bearing clasts being abundant elsewhere in the conglomerate.

STRUCTURE

Folding

Folds in Devonian strata in the study area are shallowly plunging (<30°), with axes trending NW-SE between 129° and 174°. Although there does not appear to be a consistent difference in the trend of folds deforming only Early Devonian strata and those deforming Late Devonian strata, examination of the style of macroscopic folds may distinguish two groups of folds. The folds deforming Early Devonian units tend to be tight to moderately tight, concentric and asymmetrical with rounded to square hinge domains (best developed in the SE of the area). Those folds deforming Late Devonian strata are similar to those deforming the Early Devonian, except that their hinges are rounded and the folds appear to be symmetrical. However, the only macroscopic example of this fold style is exhibited by the Late Devonian syncline occupying the NE part of the study area. The style of deformation described above is illustrated in a series of cross-sections (see Fig. 5).

Faulting

Two separate sets of faults can be recognized. The older and more extensive set has approximately NW-SE trends; parallel to major fold axes, and the same orientation as the major faults in the Mudgee region. The younger group has SW-NE to approximately east-west trends, and can dislocate the previously mentioned faults, as well as apparently being of smaller scale.

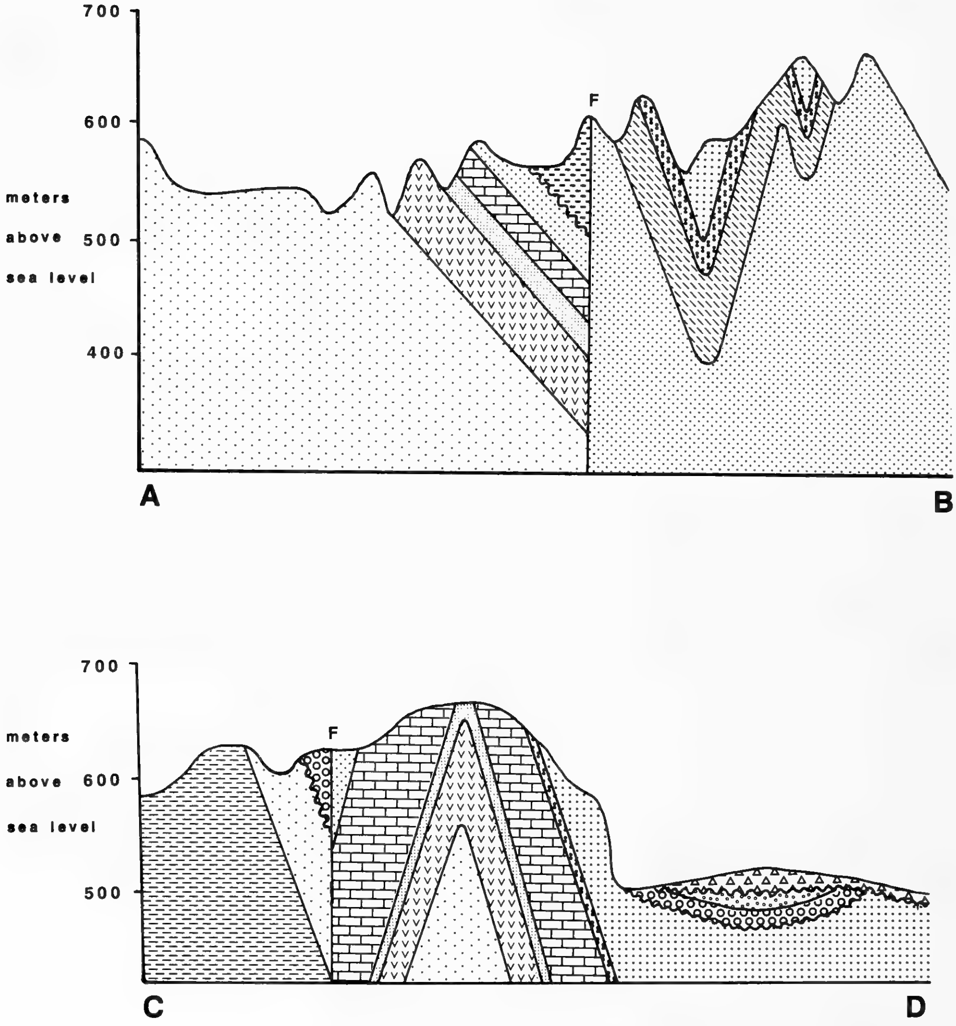

Fig. 5. Cross-sections through the study area, showing structural relationships. See Fig. 2 for the locations of sections.

The most important of the older set of faults exposed in the study area is the Cudgegong Fault. This structure is important because it forms the western margin of the easternmost fault block in Fig. 3. The Cudgegong Fault is a westerly dipping structure, as is shown by the relationship of its trace to the topography (this study) and the occurrence of westerly dipping slickensides to the south of Cudgegong (Pemberton, 1977).

The major faults in the region dislocate Late Devonian strata but are overlain by Permian sediments (the Megalong Conglomerate). It is therefore suggested that their formation was associated with the Carboniferous Kanimblan Orogeny. The age of the second, east-west to NE-SW trending, group of faults is similarly constrained as they dislocate the NW-SE trending faults but are overlain by the Megalong Conglomerate.

GEOLOGICAL HISTORY

During the Mid-Silurian (Wenlockian) the Capertee High was initiated as part of the horst and graben system that also formed the Cowra Trough, Hill End Trough and Molong High (Powell, 1984). This was followed by a period of shallow marine to terrestrial carbonate and clastic sequences (Wright, 1966, 1967, 1969; Packham, 1968).

The area underwent a period of tectonism during the Late Silurian to Early Devonian, this being the Bowning Orogeny (Cas, 1983). Associated with this tectonism (during the Pridolian to Lochkovian) a line of volcanoes developed along the Capertee High (Powell, 1984). These erupted dacitic and rhyolitic material into shallow marine conditions, and gave rise to the Windamere Volcanics.

The Lochkovian Yellowman's Creek beds and younger (?Pragian) Roxburgh Formation were also deposited in very shallow marine conditions, with water depths mostly between 4-5 m and 15-20 m.

Deposition of the Riversdale Volcanics in the ?Pragian represents renewed volcanicity on the Capertee High. Following sedimentation of the Riversdale Volcanics, the Carwell Creek beds were deposited in shallow marine conditions with water depths varying between 5 and 30 m, with the majority deposited in water less than 20 m deep.

The inferred environments of deposition of Early Devonian strata suggest water depths less than 30 m, with no evidence of sub-aerial exposure. This would indicate that during the Early Devonian the area was undergoing either transgression or subsidence, with a rate equal to that of sedimentation.

The angular unconformity between the Carwell Creek beds and the Late Devonian strata proves that the area was affected by the Middle Devonian Tabberabberan Orogeny (see Packham, 1960; Webby, 1972; Scheibner, 1973; Matson, 1975; Powell and Edgecombe, 1978). The low angle of discordance between the two sets of strata suggests that the effects of the orogeny were only mild in the study area. Wright (1967, 1969) found no evidence at Mt Frome, near Mudgee, of an unconformable relationship between Middle and Late Devonian strata, and concluded that the Tabberabberan Orogeny had not affected the Mudgee area.

The Late Devonian sequence represents a marine transgressional period following the Tabberabberan Orogeny, indicating either subsequent subsidence of the palaeohigh following cessation of the uplift associated with the mid-Devonian orogeny or a rise in sea level. This transgression is marked by the progressive change from terrestrial to lower shoreface facies and finally to a transitional (neritic) facies.

The Devonian and older strata were deformed into NW-SE trending folds by the Carboniferous Kanimblan Orogeny, which also produced the major fault structures observed, as well as cratonizing the Lachlan Fold Belt.

Following the Kanimblan Orogeny in the Early Carboniferous (Powell, 1984) there was emplacement of granitic bodies such as the Aaron's Pass Granite. This was followed in the earliest Permian by deposition of the Rylstone Tuff, approximately coinciding with the initiation of the Sydney Basin development. Later in the Early Permian, the deposition of the Megalong Conglomerate occurred on the edge of the Sydney Basin, in response to the subsidence of that basin (Matson, 1975).

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Distribution Patterns, Dispersal, Seasonal Abundance and Reproduction of *Chrysomya rufifacies* (Macquart) (Diptera: Calliphoridae) in the Arid Zone of New South Wales

L. J. McLEOD and J. M. E. ANDERSON

McLEOD, L. J., & ANDERSON, J. M. E. Distribution patterns, dispersal, seasonal abundance and reproduction of *Chrysomya rufifacies* (Macquart) (Diptera: Calliphoridae) in the arid zone of New South Wales. *Proc. Linn. Soc. N.S.W.* 113 (2), 1992: 109-120.

The seasonal abundance, local distribution and dispersal of *Chrysomya rufifacies* (Macq.) were studied at the University of New South Wales Fowler's Gap Arid Zone Research Station. This species is abundant from late spring through to mid-autumn and is trapped in greatest numbers at the homestead and in the creek lines, and will disperse throughout these areas if conditions are suitable. The life cycle of *C. rufifacies* from egg to adult takes 9 to 13 days at 27-29°C. It is confirmed that this blowfly produces unisexual offspring.

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INTRODUCTION

Chrysomya rufifacies, the hairy maggot blowfly, is regarded as the most widespread, abundant and harmful secondary fly in Australia (Mackerras, 1933). A species native to the Australasian and Oriental regions (Holdaway, 1933), it has been reported as far north as Japan (Kano, 1958) and during the last decade has spread into Central America and the southern parts of the United States (Guimarães *et al.*, 1979; Gagné, 1981; Baumgartner and Greenberg, 1984; Greenberg, 1988). The hairy maggot blowfly is a subtropical-temperate species and can be found all year round in northern Australia, but it is restricted to the warmer months in its southern range (Waterhouse, 1947; Norris, 1959; Barton, 1982; Monzu, 1979; O'Flynn and Moorhouse, 1979; Anderson *et al.*, 1984a). Dispersal within Australia and local distribution patterns have not been studied.

Adult *C. rufifacies* are metallic green or blue in colour and grossly resemble *Lucilia cuprina* (Wied.), but are distinguishable to the naked eye by dark bands on the abdominal tergites. The larvae average 14 mm in length and are a dirty yellow colour (Fuller, 1934). The second and third instar maggots possess body papillae giving them a characteristic 'hairy' appearance. This tough, 'spiny' skin is thought to protect the maggots from predators (Fuller, 1934).

Chrysomya rufifacies breeds chiefly as a secondary carrion fly (Norris, 1965; O'Flynn, 1983) but may act as a primary carrion fly under some circumstances (O'Flynn and Moorhouse, 1979; Anderson *et al.*, 1984a). The reason for this change in roles is not fully understood. Adult flies can be seen visiting the carcass before decomposition but oviposition does not occur until the primary flies have become established (Fuller, 1934).

The first instar maggots are necrophagous while those of the second and third instars develop piercing mouth hooks and become predacious, feeding both on the carrion and primary larvae already on the carcass (Fuller, 1934; Waterhouse, 1947). *Chrysomya rufifacies* maggots are considered a major competitor of primary fly species on carrion, particularly *L. cuprina* (Fuller, 1934; Waterhouse, 1947; Anderson *et al.*, 1988). Waterhouse (1947) suggested that the high temperatures generated by the overcrowded maggots exert a repellent effect on the primary larvae, forcing them to leave the carcass even before they have finished feeding.

The life cycle of *C. rufifacies* is briefer than any other carrion species. Pupation occurs in or on the carcass, or on the soil surface, but rarely underground — leaving the pupae vulnerable to predation and parasitization (Fuller, 1934; Norris, 1959). A cold resistant stage has not been recorded for *C. rufifacies* (Norris, 1965). Mackerras (1933) found that *C. rufifacies* could survive as pupae during mild winters in the subtropical areas but it is unclear if this species overwinters in the colder southern parts of its range (Barton, 1982). Norris (1959) suggested that *C. rufifacies* may migrate from the north every spring.

Chrysomya rufifacies was first found to be associated with blowfly strike in Australia in 1912 (Holdaway, 1933). In the majority of cases this species combines with a primary species such as *L. cuprina*, often exacerbating these strikes and increasing the chance of mortality. These combination strikes account for 1 to 10% of strikes in Australia (Fuller, 1934; Mackerras and Fuller, 1937; Monzu, 1979) with 5% being recorded at Fowler's Gap (Anderson *et al.*, 1989).

The aim of this paper is to provide details of the seasonal and local distribution of *C. rufifacies* in an arid, sheep grazing area of New South Wales. Aspects of the reproductive biology of this species are also documented.

MATERIALS AND METHODS

Study Area

This study covers part of a programme being conducted at the University of New South Wales' Fowler's Gap Arid Zone Research Station, 110 km north of Broken Hill. The station covers an area of 39200 ha and is climatically representative of much of southern Australia's arid zone (Mabbutt *et al.*, 1972), with an average annual rainfall of approximately 200 mm, evenly distributed over the summer and winter period.

An extension of the Barrier Ranges separates the station into two major areas, the 'hills' and the 'flats or plains'. Several ephemeral creeks run through the area, the main one being Fowler's Gap Creek. The vegetation is classified as chenopod shrubland. During summer, grasses become prominent and in winter, ephemeral forbs. River red gums (*Eucalyptus camaldulensis*) are restricted to the creek line while clumps of *Acacia victoriae* (prickly wattle) are common over the plains.

Fowler's Gap Station increased its merino sheep flock from 5200 in 1984 to 6500 in early 1990. This has been mainly due to the exceptional seasons experienced from 1987 to 1989. The station also runs small numbers of cattle and horses. The red kangaroo is a common inhabitant of the plains along with small populations of both the western and eastern grey kangaroos which concentrate along the creek lines. The euro is restricted mainly to the hills. Introduced species such as rabbits, feral goats, foxes and pigs proliferate in the area.

Sheep blowflies have been studied at Fowler's Gap since 1981. Trapping data collected over the past eight years are available but for the purposes of this paper we use only the periods from May 1984-June 1985 (dry/normal conditions) and January 1989-March 1990 (exceptional/wet conditions). Only the plains population will be discussed.

Weather Data

Rainfall and monthly temperatures were recorded at the Fowler's Gap meteorological station. A hygrothermograph placed in a Stevensons Screen at the meteorological station took hourly temperature readings throughout the blowfly trap runs. This temperature information was used to standardize the trap catches using the method of Vogt (1988).

Seasonal Abundance and Local Distribution

Flies were trapped every two to three weeks using a Western Australian (WA) style trap (Vogt and Havenstein, 1974). Six permanent trapping sites that have been established on the flats (Fig. 1) incorporate different vegetation and landform types (Table 1). The traps were set for twenty-four hours using fresh baits for each run to reduce the possibility of variation in attractiveness of the bait (Vogt *et al.*, 1983). The bait consisted of 500g of lamb liver, 1L of water and 40g of sodium sulphide (A.R.).

TABLE 1

Description of trap sites (Anderson, 1984)

Trap Site No.	Description
10	Flood out plain, prickly wattle in vicinity, in Mandleman Pdk.
12	Banks of F. Gap Ck, Mandleman Pdk. River red gums and prickly wattle, frequented by stock when fodder growth in channels (after rain).
13	Mandleman bore, permanent water supply, dense shrubs and taller *Eucalyptus* sp., stock yards, regular watering point for sheep and kangaroos.
14	Plains in Saloon Pdk, sparse vegetation no permanent water nearby.
20	Banks of F. Gap Creek in Saloon Pdk, similar vegetation to site 12, water trough 1 km away.
17	Homestead, near killing shed and offal pit, in vicinity of shearing shed, sheep yard, pigpen, dog kennels, rubbish dump, horse stalls and houses. Permanent water, various native trees (mostly *Eucalyptus* spp.), flowers and grasses in gardens.

Local distribution was also studied with mark/release experiments. The blowflies were marked with fluorescent dust using the method of Norris (1957) and released after dusk to minimize handling problems (Vogt *et al.*, 1981). A grid of fifteen Williams traps (Williams, 1984), 500m apart, was set up around the release site and checked every twenty-four hours for three days. The six permanent WA trap sites were set twenty-four hours after release and checked for three days.

Life Cycle and Reproduction Experiments

These experiments were conducted in laboratories at the Centre for Entomological Research and Insecticide Technology (CERIT) and Fowler's Gap. At CERIT flies were kept in constant temperature (CT) rooms at 27°C ±1.5°C, with a light regime of LD12:12 and uncontrolled humidity (water was allowed to evaporate naturally from uncovered containers in the room). In the CT room at Fowler's Gap the temperature ranged between 25°C and 30°C, with similar photoperiod and humidity conditions.

The flies were kept in cloth cages and given water and sugar cubes *ad libitum*. Females were allowed two protein feeds in the form of sponge soaked with lamb's blood and the larvae were raised on a mixture of beef mince and bran. The prepupae were encouraged to leave the beef mixture by gradually wetting it, so they would pupate on or in the sand provided.

The females were 'egged' in individual 20 mL glass tubes, in which a moist piece of sponge and a small amount of minced beef was placed. The number of eggs each female laid was determined by first immersing the egg mass in water so they could be separated and counted.

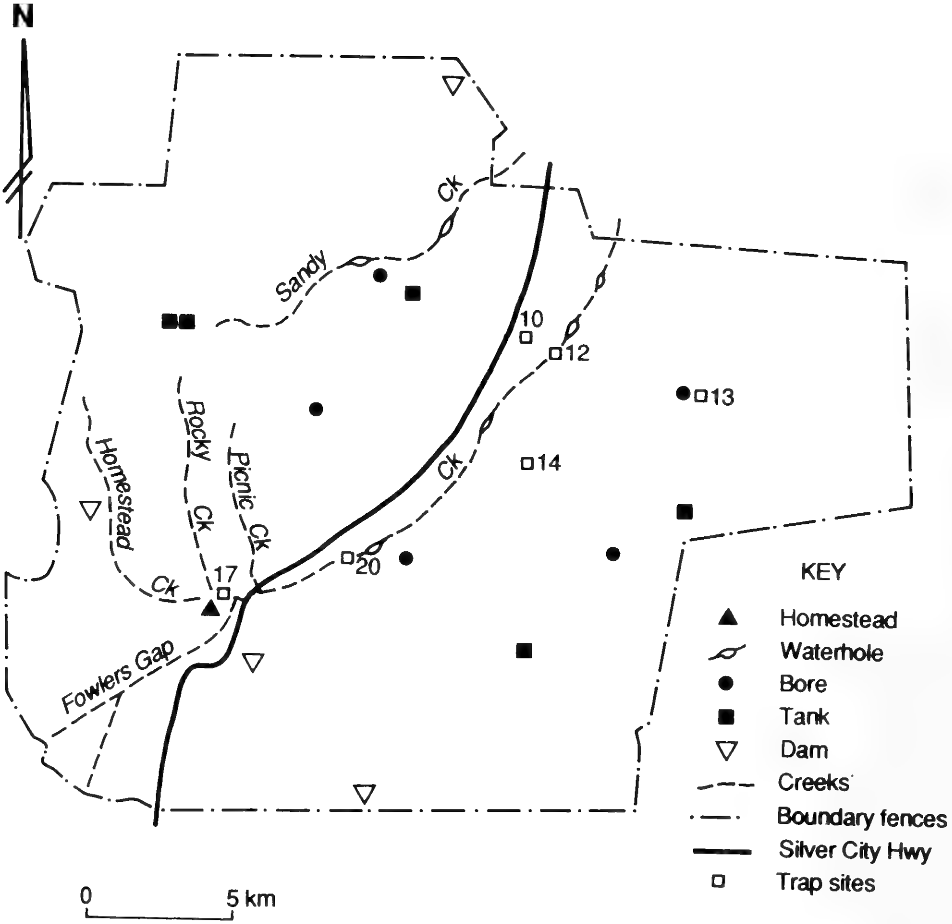

Fig. 1. Map of the Fowler's Gap Research Station showing the main creek lines, water supplies and location of blowfly trap sites.

Statistical Analysis

All fly trapping data were converted to an hourly catch rate (HCR) per trap. For the analysis of seasonal catch variability, an average HCR for the six trap sites (a 'trap run') was calculated. The distribution of trap catches was found to be non-normal so the data were analyzed using the Kruskall and Wallace nonparametric analysis of variance and the nonparametric multiple comparisons test by STP (Sokal and Rohlf, 1981). The average HCR between seasons was compared to establish if there was a seasonal trend, with each trap run as a replicate. The HCR's at each of the trap sites within a season were compared to establish if there was a preference for certain trap sites (i.e. habitat preference).

RESULTS

Weather Data

Fowler's Gap was extremely dry in 1982 (annual rainfall 94 mm) and for the first nine months of 1983 (rainfall 139.3 mm). Heavy rains fell in late spring and summer of 1983/84 (Oct.-Feb. 238.9 mm) which provided excellent vegetation growth. Only a further 120 mm fell throughout 1984, with the last two months of the year becoming very dry (Nov.-Dec. 7.5 mm). The dry conditions continued into 1985 until late autumn (Fig. 2).

Rainfall was above average in 1988 (273.2 mm) and 1989 (336.1 mm) resulting in exceptional vegetation growth. Temporary water holes in creeks and paddocks were present for a large part of the time. Winter 1989 was the coldest on record since 1982, with the average ground minimum dropping below 0°C in August (Fig. 3). Only light rain fell in spring and summer 1989/90 (Sep.-Feb. 76.7 mm) and by autumn 1990 the vegetation had dried off and surface waters had significantly decreased.

Seasonal Abundance

The general pattern of *C. rufifacies* population size is an increase in spring rising to a peak in late spring or early summer, followed by a decline in late summer recovering slightly with a smaller peak in autumn, and then virtually disappearing over winter. This pattern is evident in both the raw and standardized trap data. Although more females were trapped than males, both sexes follow a similar pattern.

The distribution of *C. rufifacies* caught in traps in 1984/85 is shown in Fig. 4. From low numbers throughout winter 1984, the population increased in spring reaching a major peak in early summer then decreased rapidly in late summer. The population recovered in mid-autumn only to decline again in winter 1985. The average HCR was nearly significantly different between seasons ($\chi^2 = 7.815$, $P < 0.07$).

The pattern for 1989/90 was similar (Fig. 5). In mid-autumn there was a small peak in the *C. rufifacies* population but the species was not trapped in winter 1989. The population did not increase until mid-spring and reached a major peak in late spring. The fly numbers trapped at this time were much higher than those of spring 1984. Throughout summer and early autumn the *C. rufifacies* population gradually declined. The average HCR was significantly different between seasons ($\chi^2 = 10.337$, $P < 0.05$).

Local Distribution

In 1984/85 there was a significant difference in HCR between sites in winter ($\chi^2 = 13.796$, $n = 3$, $P < 0.01$) and spring ($\chi^2 = 8.998$, $n = 4$, $P < 0.06$), but not in autumn or summer. *Chrysomya rufifacies* was caught in greatest numbers at site 17 (homestead) and site 12 (creek bed) during winter and spring (Table 2). In 1989/90 there was a significant difference in HCR between trap sites in autumn ($\chi^2 = 11.901$, $n = 3$, $P < 0.05$) and summer ($\chi^2 = 11.600$, $n = 4$, $P < 0.05$) and again the flies were caught in greatest numbers at the homestead and creek areas (sites 17, 12 and 20). Only two *C. rufifacies* individuals were trapped in winter 1990 and they were caught early in the season (Table 2).

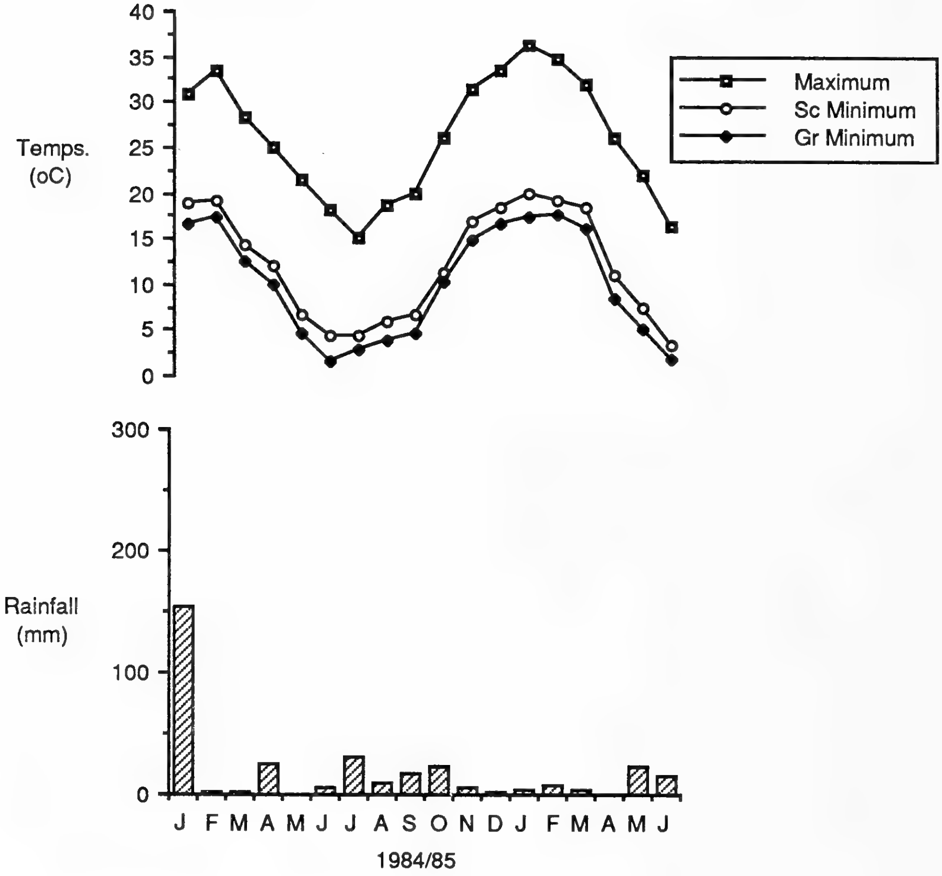

Fig. 2. Monthly rainfall and average monthly temperatures, 1984/June 1985.

Four mark/release trials were conducted (two in autumn, and one each in late winter and mid spring). In all trials the flies were released from site 20, a creek site. In the autumn trials, *C. rufifacies* were mainly trapped at creek sites; the one exception, a female trapped at site 13 (Mandleman bore, 6km from creek) four days after release. Several individuals were caught at site 17 (homestead), five kilometres downstream, after twenty four hours. In the winter and spring releases, individuals were only trapped at the site of release.

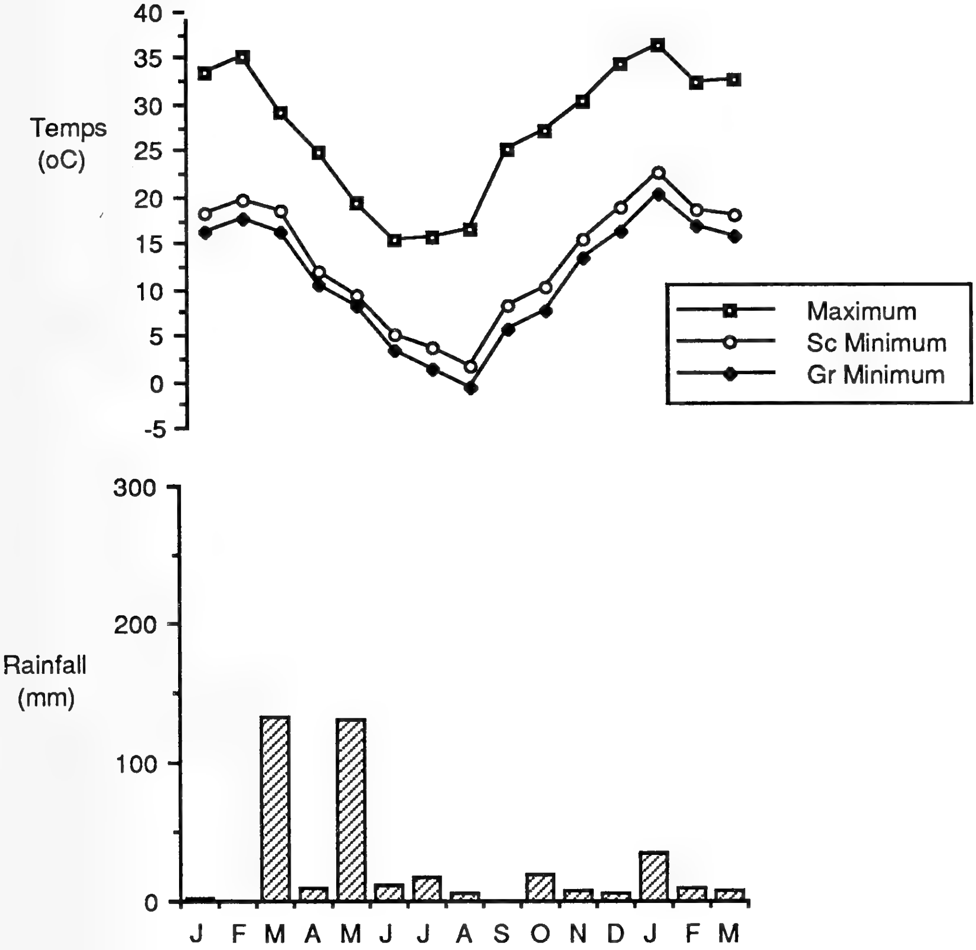

Fig. 3. Monthly rainfall and average monthly temperatures, 1989/90.

Life Cycle and Reproduction

The life cycle of *C. rufifacies* from egg to adult was 9-13 days at 27-29°C. Oviposition took place after 5-6 days but after approximately 28 days females failed to oviposit even though after dissection, many were found to contain fully developed eggs. The results of these experiments are set out in Table 3, with a summary of results from comparable studies.

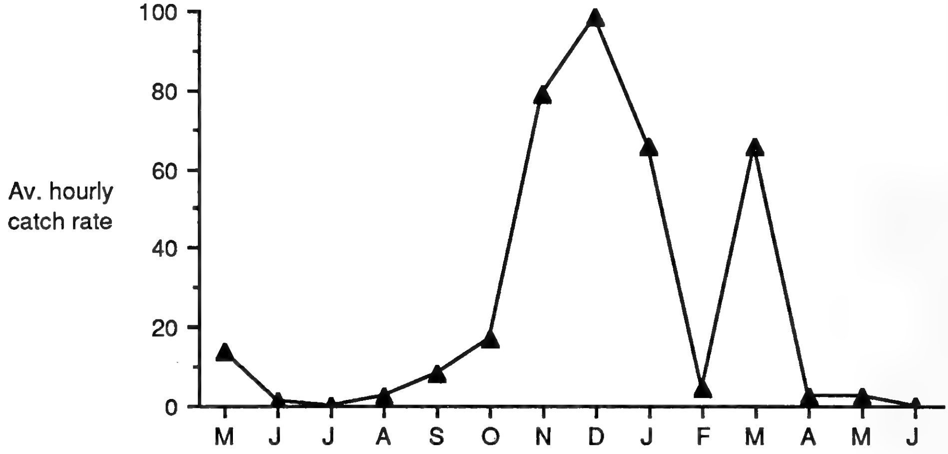

Fig. 4. Chrysomya rufifacies caught between May 1984 and June 1985.

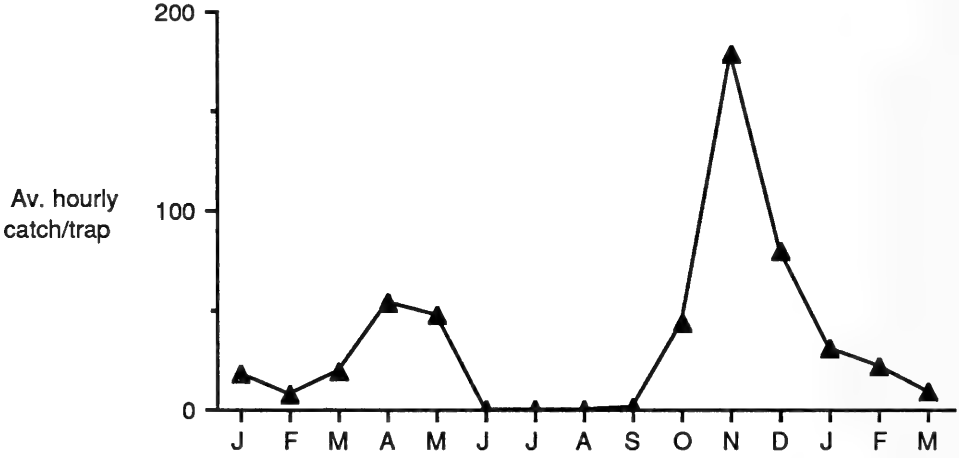

Fig. 5. Chrysomya rufifacies caught between January 1989 and March 1990.

Females tested in the laboratory were able to lay at least three egg batches from one mating. The average number of eggs for the first batch was 205 (range 139-264: n=20) and the second batch was 187 (range 120-243: n=10). Batches laid later were not counted.

As already reported *C. rufifacies* has previously been shown to be monogenic, females always producing unisexual offspring. Our results confirm this with each successive batch of eggs deposited by an individual female always producing the same sex offspring as the first batch.

TABLE 2

Banking of trap catches of C. rufifacies

Catch Period	**Season** **Winter**	**Spring**	**Summer**	**Autumn**
(a) 1984/85				
Site numbers	10 12 13 14 17	14 10 13 12 17	14 13 10 12 17	20 14 13 10 12 17
Test*	$P<0.01$	$P<0.06$	N.S.	N.S.
(b) 1989/90				
Site numbers	12 13 14 20 10 17	10 14 20 13 12 17	10 14 13 20 12 17	13 14 10 12 20 17
Test*	N.S. (low catch)	N.S.	$P<0.05$	$P<0.05$

* Kruskal and Wallace one-way analysis of variance.

TABLE 3

Results of C. rufifacies *life cycle experiments*

Temp (°C)	**Egg (Hrs)**	**Larval Stage (Days)**	**Pupal Stage (Days)**	**Egg to Adult (Days)**	**Oviposition (Days)**	**No. of Eggs Average (range)**
27-29	<12	5-8	3-5	9-13	5-6	1st: 205 (139-264)* 2nd: 187 (120-243)
24-33	8-12	5	4	9.5	5	210 (153-386)#
25.6	10-12	3.5	3	7	–	max. 268†
27-29	<12	6	2-4	9-12	5-6	178 (107-257)^{x}

References: * = this study; # = Roy & Siddons (1939); † = Subramanian & Mohan (1980); x = Schmidt & Kunz (1985).

DISCUSSION

Seasonal Abundance

The seasonal distribution of *C. rufifacies* in this arid, sheep grazing area of New South Wales differs slightly from that described in other parts of Australia. Large numbers are present from September to May, while a small population may survive throughout the year. The population numbers of *C. rufifacies* at Fowler's Gap vary with the temperature and other seasonal conditions. Rainfall is a major dominating factor and it is closely linked to vegetation biomass. Vegetation is important for shelter, food and moisture and is closely related to large animal density and abundance of predators and competitors of *C. rufifacies*.

Mild conditions allowed *C. rufifacies* to breed in carcasses throughout winter 1984 (Anderson, 1984) when usually there are insufficient adults to allow breeding and the temperatures are too cold for successful larval development. Population numbers were severely depressed during winter 1989 and *C. rufifacies* did not breed on carcasses during this winter. Only future studies will show whether *C. rufifacies* overwinters at Fowler's Gap or whether it survives in small numbers by breeding on carcasses in protected areas. The migration and movement of this species at Fowler's Gap is also unknown.

Local Distribution

Distribution of blowflies within a habitat is irregular and aggregations of flies are not readily explained (Norris, 1965), although factors such as food, water and shelter would be important (Braack and Retief, 1986). Most flies require water and carbohydrate (Norris, 1959) and *C. rufifacies* females need protein for maturation of their ovaries (Roy and Siddons, 1939). At Fowler's Gap, the sources of carbohydrate would include nectar from flowers and honeydew produced by hemipterans (Anderson, 1984). Protein would be readily available in carcasses, offal and animal faeces. Water is available from stock watering points and waterholes, as well as sweat and saliva of the larger animals and occasionally as dew on vegetation.

Anderson *et al.*, (1984b) found that *L. cuprina* was trapped in greatest numbers at the homestead and creek areas at Fowler's Gap, and *C. rufifacies* also follows this pattern. When a significant difference occurred between trap sites, the homestead (site 17) and the creek areas (sites 12 and 20) always recorded the highest catches of *C. rufifacies*, indicating a preference for these areas. These sites offer a concentration of food resources and protection. Many larger animals are also attracted to these areas to feed and shelter, increasing the potential food resources for the flies. Adult flies are more active in the shade than in direct sunlight (Braack and Retief, 1986), so the flies can spend more time searching for food and mates in the creek beds than in other exposed areas. As shown from the mark/release trials *C. rufifacies* disperse chiefly throughout the creek lines.

As already discussed, the seasonal distribution and abundance of *C. rufifacies* at Fowler's Gap is linked to the seasonal conditions. The local distribution within a season could also be influenced by the number of individuals in the population. The resources in preferred areas would be limited, so once population numbers reach a level at which additional members cannot be sustained (the preferred area population threshold), individuals would be forced into other areas to search for available resources (food, water, shelter or breeding areas).

$$\text{Threshold value} = \frac{\text{population number when individuals begin to disperse}}{\text{quantity of available resources in the preferred area}}$$

The local distribution in seasons with abundant resources differed from those with limited resources. Heavy autumn rains in 1989 generated heavy vegetation growth which survived until early summer. In late spring and early summer 1989 the preferred areas were able to sustain a higher population number of *C. rufifacies* than for the same period in 1984 when conditions were drier, and the vegetation was still recovering from major drought in 1982/83.

Reproduction

Chrysomya rufifacies is the dominant blowfly species from late spring to early autumn at Fowler's Gap. This species is more tolerant of hot and dry conditions than *L. cuprina* or *Calliphora* spp. (Anderson, 1984) because adults can grow and reproduce normally up to 40°C (Waterhouse, 1947) and larvae can tolerate higher temperatures than primary larvae (Fuller, 1934). *Chrysomya rufifacies* is restricted by cold temperature. Eggs fail to hatch at 9°C and larvae fail to pupate at 15°C (O'Flynn, 1983).

The life cycle results obtained are similar to other studies (Table 3) indicating that *Chrysomya rufifacies* has a shorter life cycle than other calliphorids. Larval development time is variable and can be influenced by several factors such as temperature, humidity, breeding media and density of larvae.

Chrysomya rufifacies is unusual in that it produces monogenic offspring. Ullerich (1984) found that the sex determination in *C. rufifacies* is controlled by a non sex-linked dominant gene, named the female sex realiser (F). The female-producing females are heterozygous for this dominant allele, while male-producing females and males are homozygous for the recessive allele (f). The sex realiser is synthesized by the germ-line cells and is expressed during oogenesis.

The proportion of male-producing females to female-producing females in the wild population is not known, nor whether this proportion changes to take advantage of seasonal conditions. Further work is needed in this area.

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Holocene Vegetation History from the Hawkesbury Valley, New South Wales

J. R. DODSON and B. G. THOM

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Pollen and charcoal records from core sections at sites near the junction of Mill Creek and the Hawkesbury River for three periods, around 9100 B.P., between about 8400 and 8000 B.P. and from 6000 until about 2500 B.P., show a vegetation record dominated by *Eucalyptus* — Casuarinaceae forest and heath not unlike that of the present day. Rainforest elements are restricted today to the upper and more dissected part of the valley; however two of the records indicate that rainforest extended further down the valley earlier in the Holocene. Since rainforest pollen production is low, compared to sclerophyll, the component of rainforest may have been quite significant. Fire and very high sedimentation rates have characterized the valley environment throughout the records; and repeated fires may have been instrumental in periodically reducing the extent of rainforest. The reduction of rainforest in each of the cases identified was probably quite abrupt. High charcoal abundance suggests either evidence of human impact right through the Holocene or abundant wildfires. The results suggest that fire has been important in controlling the distribution of rainforest.

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INTRODUCTION

The view that native vegetation was quite stable until modern human impact has been shown time and again, from fossil records, to be untrue for many areas of the world. This raises questions, especially in areas with highly endemic floras, as to how and in what form they survived the great global climate changes of the recent geological past.

While the direct impact of ice was minimal in Australia during the last glacial maximum, much of the southern part of the continent experienced enhanced aridity (Bowler *et al.*, 1976). Forest was much reduced in area as the central Australian dune-fields extended coastwards; and a grassland steppe dominated large areas of the south-east (Dodson, 1975; Hope, 1989). At the same time sea-level was 120 m lower than present (Chappell, 1974; Thom and Chappell, 1975; Thom and Roy, 1983) and a broad swampy plain occupied part of the land-bridge extending south to Tasmania (Jennings, 1971).

Such change raises questions as to the form in which vegetation now regarded as characteristic of various regions survived the severe aridity. The Pilliga Sandstone vegetation for example is quite distinctive, but in the Mendooran area, on the North West Slopes of New South Wales, it was replaced by a chenopod shrubland between 25,000 B.P. and 10,000 B.P. (Dodson and Wright, 1989). Clearly its recovery in much the same form after 15,000 years absence suggests its integrity survived, perhaps in a reduced area in the same region or more probably east of its present location. Whatever happened it is clear that its present pattern of occurrence has applied for at least the last 10,000 years. This raises the question of whether a similar history holds true elsewhere; for example, the highly endemic and rich sandstone flora of the Central Coast region of New South Wales, and how warm temperate rainforest taxa recovered from the late Pleistocene.

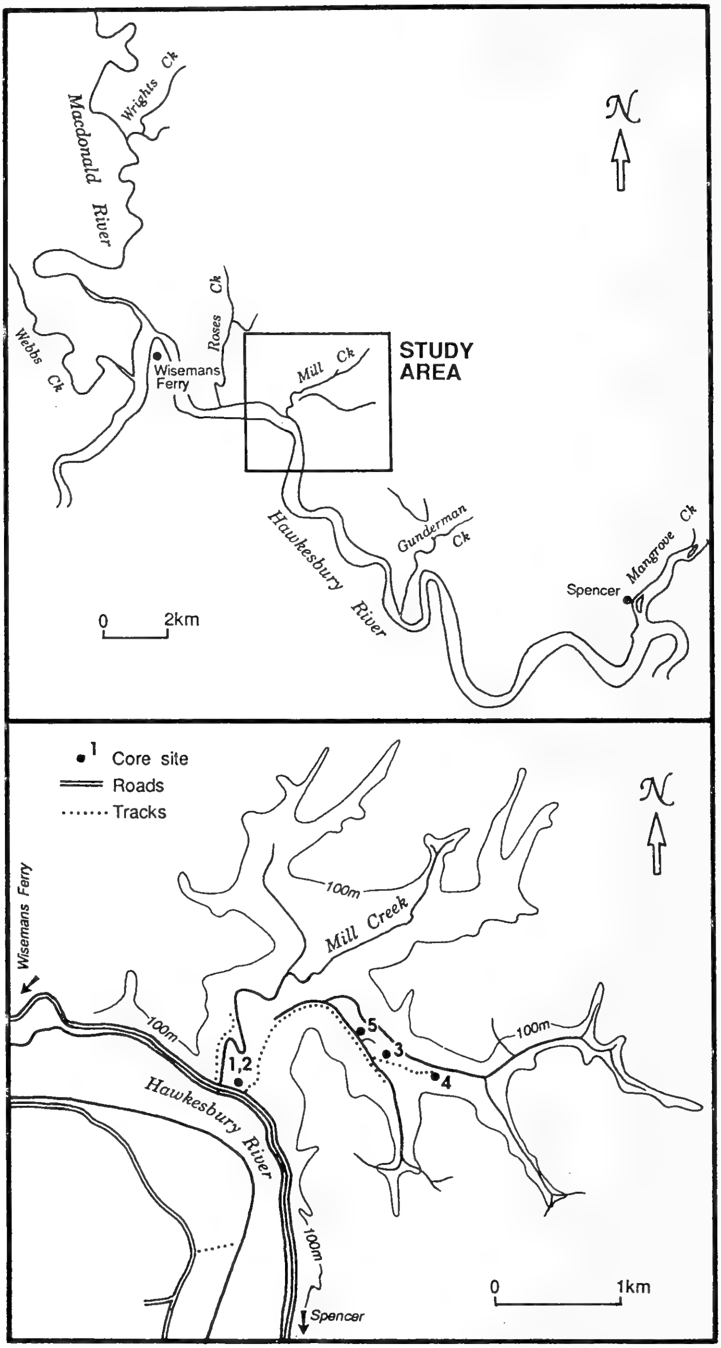

Fig. 1. Study area and location diagram of core sites.

The general patterns of vegetation of the Sydney area are described by Fairley and Moore (1989). The dominant vegetation of the Triassic Hawkesbury Sandstone and Narrabeen Group of sediments is a variety of *Eucalyptus* woodlands and forests with heathland or shrubland understorey. Areas with shallow soils or prone to water-logging support heathlands and wetlands; and sheltered regions, or those on volcanics, support closed forest. Striking features of the vegetation include its richness and high level of endemism suggesting a long history. Vegetation on Wianamatta Shale includes some species in common with those on the sandstones, but it tends to have more open woodlands and forests with grassland as dominant understorey, and lower levels of diversity and endemism.

The land-sea interface, including estuarine areas, supports mangrove systems, saltmarsh, and *Casuarina glauca* forests. The histories of the vegetation types on the different substrata are likely to show strong differences. In particular it could be hypothesized that the nutrient and fire regimes on sandstone exert such a strong influence that climatic change, unless severe, has only a secondary influence on vegetation dynamics. The same may not be so for areas on volcanic or shale soils.

Vegetation histories from Hawkesbury Sandstone are in their infancy. Studies by Chalson (1983) and Kodela and Dodson (1988) provide records that date from as far back as about 6000 B.P. They clearly show that the integrity of the vegetation has remained the same for this length of time with a conspicuous history of burning and the possibility of a recent decline in *Eucalyptus* abundance, which has yet to be explained. The last 6000 years include the end of the mid-Holocene optimum (Bowler *et al.*, 1976), and possibly a late Holocene minor cooling which had some implications for vegetation patterns in upland areas (Dodson *et al.*, 1986; Dodson, 1987). But no major climatic shift has occurred against which the sandstone flora responses to greater climatic stresses can be tested. This would require examination of the pre-Holocene record.

The aim of this paper is to examine the history of the sandstone flora beyond the presently known record, from the Mill Creek Valley in the Hawkesbury River region. It provides an opportunity to measure vegetation change on a longer perspective than that currently available, and to extend the known fire record.

STUDY AREA

Mill Creek is a tributary of the Hawkesbury River some 6 km downstream of Wisemans Ferry (Fig. 1). The lower end is estuarine. The area is dominated by Hawkesbury Sandstone which forms the main ridges and plateaux but the deeper gullies, like Mill Creek, are cut into the underlying Narrabeen Group of softer sandstones and shales. Deep Quaternary age alluvium, estuarine clays and shallow peats occur along the river and creek valleys (New South Wales Department of Mines, 1966).

The present climate is mild. The nearest climate station is some 15 km south at Glenorie (168 m a.s.l.), which has mean maximum temperatures of 27.5°C and 16.4°C for January and July and mean minima of 16.2°C and 5.1°C for the same months. Mean annual precipitation is 973 mm with the wettest month January (107 mm) and the driest September (52 mm) (Bureau of Meteorology, 1975). Since Mill Creek is near sea-level and in a deep valley these values would be locally modified; the microclimate would be more humid and conducive to mesic vegetation, such as rainforest elements.

The major vegetation units are *Avicennia marina* open scrub and *Casuarina glauca* open forest on the estuarine mudflats. Poorly drained soils subject to waterlogging, on the Quaternary alluvial areas, support *Phragmites australis* sedgeland, *Melaleuca ericifolia — Gahnia clarkei* closed scrub and *M. quinquenervia — C. glauca* open forest (Benson, 1986). Open forest of *Eucalyptus deanei — Syncarpia glomulifera — Angophora floribunda — E.*

punctata occurs on Narrabeen Group sediments, and a mix of open forest and woodlands with heath or scrub understorey on Hawkesbury Sandstone, including *E. piperita — A. costata* open forest as well as *E. gummifera — E. eximia — E. punctata* woodland (Benson, 1986). Rainforest elements occur along drainage lines and in fire shadow areas. In addition there are a number of areas previously cleared, but since the inclusion of the area within Dharug National Park these are showing signs of shrub and forest regeneration (Benson, 1986).

METHODS

Four percussion drill cores were collected in August 1989 and May 1990 while a core using a Russian sampler (Jowsey, 1966) was collected in April of 1990 (Fig. 1). The drilling for Core 1 (to about 37 m depth) at the present junction of Mill Creek and the Hawkesbury River was carried out in 3 m sections but recovery was rarely complete.

The stratigraphy will be described in detail elsewhere but consisted of a variety of organic stained sands, clays and peats overlying an oxidized and mottled clay presumed to be of Pleistocene age. Above this boundary was a section of peat and organic clay. The top end of this section contained a piece of wood recovered at 33.60 m depth. A sample of wood and of peat overlying the Pleistocene clay were submitted for radiocarbon dating. Core 4 was taken from the same site as Core 1, using a different coring technique to enhance recovery. Core 2 (to 17 m depth) was taken about 2 km upstream from the Hawkesbury River junction and was collected in shorter sections than Core 1; nevertheless recovery was still incomplete. The sediment consisted of organic and charcoal stained clays, sands and peats. Five organic-clay samples from cores 4 and 2 were submitted for radiocarbon dating.

Mill Creek Core 3 has not been examined at this time. The core taken with the Russian Sampler (Core 5) consisted of peat overlying a sand layer and peaty clays. Radiocarbon dates were obtained to establish the length of time involved in the deposition of the sand lens.

Pollen preparations on about 1 cm^3 of sediment were made using the standard procedures of heavy liquid floatation of organic matter, filtering, acetolysis, dehydration, and mounting of residues in silicone oil (Moore and Webb, 1978). Samples were spiked with a solution containing known quantities of *Alnus rugosa* pollen to help estimate pollen and charcoal concentrations. Pollen counts were made until at least 200 grains of terrestrial taxa had been identified. Charcoal was counted using the point count method (Clark, 1982).

Three samples of surface materials were collected to analyse the broad features of pollen representation in low closed forest, open forest and closed swamp forest. Four sub-samples of moss cushion were collected and combined from a stand of low closed forest in the upper end of the valley. The vegetation was dominated by *Syncarpia glomulifera*, *Backhousia myrtifolia*, *Glochidion ferdinandi*, *Acmena smithii*, *Ficus rubiginosa*, and an understorey of *Trochocarpa laurina*, *Rhodamnia rubescens*, and *Eupomatia laurina* (Benson, 1986). Four sub-samples were also collected from a nearby stand of open forest which was dominated by *Eucalyptus punctata*, *E. eximia*, *Allocasuarina littoralis*, *A. torulosa* and a heathy understorey containing *Astrotricha lanceolata*, and *Xanthorrhoea arborea*.

A peaty sediment sample was collected from the closed forest at the lower end of the valley. This was dominated by *Casuarina glauca* and there was a sparse spread of *Avicennia marina* var. *australasica*, *Melaleuca styphelioides*, *M. ericifolia*, and an open understorey containing patchy areas of *Phragmites australis*, *Gahnia* sp., *Goodenia ovata*, *Cotula australis*, *Triglochin procera*, *Viola hederacea*, *Juncus kraussii*, *Typha orientalis* and several species of low-growing Cyperaceae.

To examine any relationship between sand deposition and fire, sediments were examined in Core 5. For this, 5 cm^3 sediment samples were removed from the lower levels of the sand lens and underlying clays; these were 10 contiguous samples, each covering a 1 cm depth range. Samples were boiled in 10% NaOH for 10 minutes and washed through a 63 μm mesh sieve. Material caught on the sieve was dried and examined for charcoal and sand.

RESULTS

The stratigraphy of the cores shows that the depositional history in the valley has included periods when peat and organic clays predominated, and these were disrupted from time to time by higher energy environments when pulses of sand entered.

Table 1 shows the results of the radiocarbon analyses. The date results for Beta 32,449 and Beta 33,774 overlap within two standard deviations indicating they are not significantly different. Since Beta 32,449 was a wood sample possibly caught in the drill sample and displaced stratigraphically the age of 9180 ± 100 B.P. for the sample at 37.20 m is taken as the definitive result from Core 1. For Core 1 a pollen analysis covering the sediment sections from 33.60 to 33.66 m and from 36.16 to 36.56 m depth was carried out. The missing section resulted from lack of core recovery. Sediments immediately above this section were too sandy for pollen preservation and the presumed Pleistocene material below was oxidized and mottled clay. On examination a sample of this clay yielded only a few weathered eucalypt grains; as the pollen was too sparse for meaningful quantitative analysis, it is not considered further here.

TABLE 1

Radiocarbon date results

Sample Depth (m)	Material	Date Number	Result (yrs B.P.)
i. **Core 1**			
33-36	wood	Beta 32,449	9310 ± 90
37.20	peaty clay	Beta 33,774	9180 ± 100
ii. **Core 4**			
10.60	clay	SUA 2935	4450 ± 250
14.60	clay	Beta 40,393	8390 ± 70
20.20	clay	Beta 37,273	8030 ± 80
iii. **Core 2**			
3.10	clay	Beta 37,776	2610 ± 90
4.25	clay	SUA 2879	2950 ± 70
6.25	clay	Beta 37,777	5540 ± 100
15.12	clay	Beta 37,775	8920 ± 110
iv. **Core 5**			
0.35-0.40	clay	SUA 2561	390 ± 70
0.65-0.70	clay	SUA 2862	390 ± 70

Core 4 was examined between 10.6 and 17.6 m depth. It consisted of mixes of clay and silt and some sand interspersed with several layers of sand. Adding the radiocarbon results from cores 1 and 4 together (Fig. 2) indicates that the sedimentation rate at this site is very high and has varied considerably during the Holocene. Radiocarbon ages from 14.6 and 20.2 m depth dated at 8390 ± 70 and 8030 ± 80 B.P. respectively. These dates are reversed and significantly different but nevertheless indicate a rapid rate of sedimentation until at least 14.6 m depth, after which the rate may have slowed. The second core had a series of clayey peats and sands between 2.9 and 6.7 m depth which

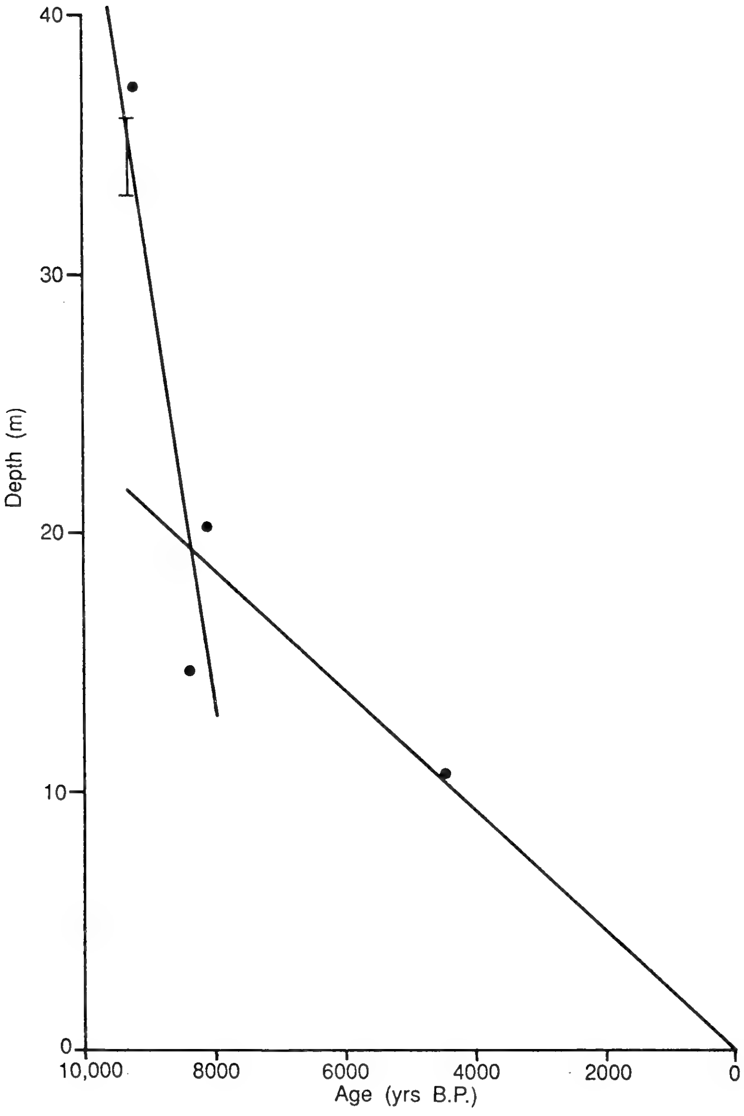

Fig. 2. Radiocarbon and depth relationships from Cores 1 and 4, Mill Creek Valley. The lines are shown to demonstrate the change in mean sedimentation rate.

were sub-sampled for pollen analysis. The section between 4.1 and 5.9 m depth was very sandy and core recovery and hence pollen analysis was incomplete.

Core 5 was a peat underlain by a humic stained sand between 0.40 and 0.65 m, below this was a peaty clay gradually becoming less organic with depth. Samples above and below the sand were dated at 390 ± 70 and 390 ± 70 B.P. respectively. These are of course indistinguishable in age and indicate that deposition of the sand layer was rapid.

The results of the surface sample analyses are given in Table 2. Casuarinaceae pollen formed the largest component in all three samples. The closed swamp forest was dominated by pollen of Casuarinaceae almost to the exclusion of other taxa. The low closed forest sample was distinguished by having a high Myrtaceae count (26%) and small but significant numbers of Apocynaceae, *Synoum*, and Euphorbiaceae pollen. The open forest sample was distinguishable mainly by a relatively high *Eucalyptus* value (30%) and small numbers of pollen from a variety of sclerophyllous shrubs. Both the high representation of many taxa occurring in the surrounding sclerophyllous open forest and the higher values of *Pinus* pollen which has travelled from outside the valley into the samples indicated that the low closed forest was dominated by generally poor pollen producers.

TABLE 2

Pollen representation (shown as percentages of total terrestrial pollen sum sources) in surface sample analyses. + indicates presence less than 1%.

Taxon	**Closed swamp forest**	**Low closed forest**	**Open forest**
Eucalyptus	2	19	30
Eucalyptus (bloodwood type)	+	9	9
Myrtaceae	1	26	12
Leptospermum	+	+	2
Casuarinaceae	93	31	35
Dodonaea triquetra		2	1
Pinus	+	3	1
Avicennia	+		
Moraceae/Urticaceae		1	+
Astrotricha		4	2
Poaceae	2	1	2
Other pollen sum elements	1	4	5
Non-pollen sum elements			
Cyperaceae	4		+
Pteridium	2		
Histiopteris	+	1	
Microsorium		+	+
Cyathea	1		
Other fern spores	3	+	

Core 1

For ease of discussion the pollen diagram (Fig. 3) is sub-divided into two sections.

Section 1.1: depth 36.16 to 36.56 m; assumed age about 9100 B.P.

Eucalyptus, including bloodwood species, and *Casuarina* dominate the pollen of tree taxa. Relatively high values of shrub taxa including, *Monotoca*, *Persoonia/Lomatia* and *Acacia*, plus herbaceous taxa such as Poaceae, Apiaceae and Cyperaceae also occur but

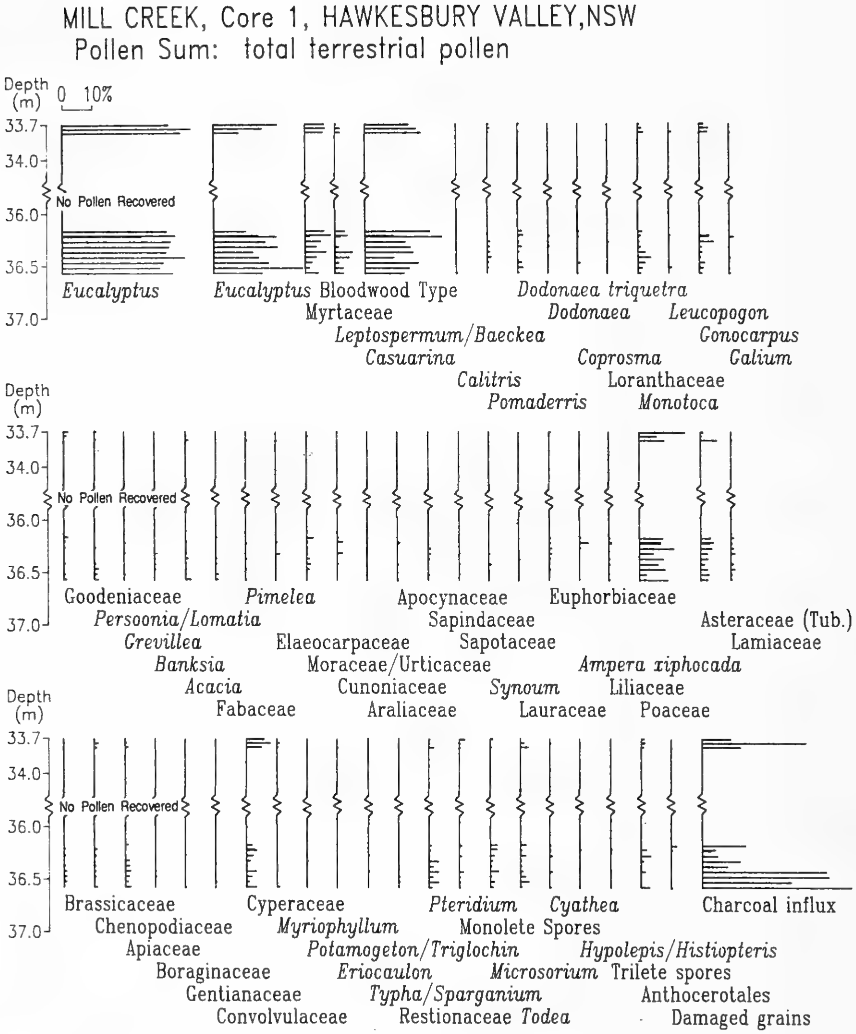

Fig. 3. Pollen diagram for Core 1.

these may have been restricted to the swamp surface. There are small quantities of pollen from Moraceae/Urticaceae, *Synoum*, Cunoniaceae, *Astrotricha*, Apocynaceae, Sapindaceae, Sapotaceae, and Elaeocarpaceae and *Cyathea*, *Microsorium*, *Todea* and other fern spores. This spectrum is somewhere between the low closed and open forest modern pollen surface samples (Table 2) and therefore suggests a sclerophyll forest with heath understorey and a strong presence of rainforest. Charcoal was found in abundance but generally decreased up the profile.

Section 1.2: depth 33.66 m to 33.74 m; assumed age about 9000 B.P.

This section is separated from Section 1.1 by some 2.5 m of unrecovered sediment. The mix of sclerophyll and herbaceous taxa is much the same but the rainforest taxa are absent and the fern spore values are decreased. Hence it appears that the vegetation in this period is largely sclerophyll woodland but of the same character as in Section 1.1. Charcoal values were moderately high throughout.

To test for any differences in the mean abundance a t-test was run for all taxa in the two sections. Since many of the taxa tend to occur in low values and thus may be absent from a relatively low pollen count means were accepted to be significantly different at the 0.10 probability level. A test of differences in the variance for all of these taxa showed no significant differences at the 0.10 level thus all differences are due to differences in means. The t-test results are given in Table 3. Given that the sedimentation rate in this region is very high the loss of rainforest taxa from the core area must have been abrupt.

TABLE 3

Comparison of mean abundance of pollen taxa between Section 1 and 2 in Core 1

Taxon	**Means** **Sect. 1**	 **Sect. 2**	**t-value**	**Two-tail probability**
Myrtaceae	13.7	9.2	2.65	0.023
Leptospermum	3.0	6.0	1.96	0.086
Dodonaea triquetra	0.7	2.1	2.53	0.031
Grevillea	0.0	0.3	1.96	0.081
Banksia	0.0	0.5	2.24	0.052
Fabaceae	0.0	0.7	2.69	0.025
Moraceae/Urticaceae	0.3	1.5	1.94	0.081
Cunoniaceae	0.0	1.0	1.94	0.085
Apocynaceae	0.0	0.5	2.24	0.052
Sapindaceae	0.0	0.6	2.25	0.051
Sapotaceae	0.0	0.3	1.96	0.081
Lamiaceae	0.3	1.5	2.44	0.046
Cyperaceae	13.7	4.5	3.97	0.040
Microsorium	1.0	2.8	2.11	0.071

Core 4

The pollen record from Core 4 has also been subdivided into two sections for ease of discussion (Fig. 4).

Section 4.1: depth 17.6 m to 14.6 m; inferred age about 8400 to 8000 B.P.

Casuarinaceae and *Eucalyptus* pollen dominate the record and there are relatively high values for monolete and trilete spores indicating a substantial fern component. There are also several heath taxa including *Monotoca*, *Gonocarpus*, and *Acacia*. Prominent within the record are *Astrotricha* and *Dodonaea triquetra*. Poaceae and open ground taxa values are relatively low. This taxa mix indicates a wet sclerophyll forest with a possible occurrence nearby of an upper estuarine *Casuarina glauca* forest. Charcoal values are relatively high throughout indicating a significant number of local fires.

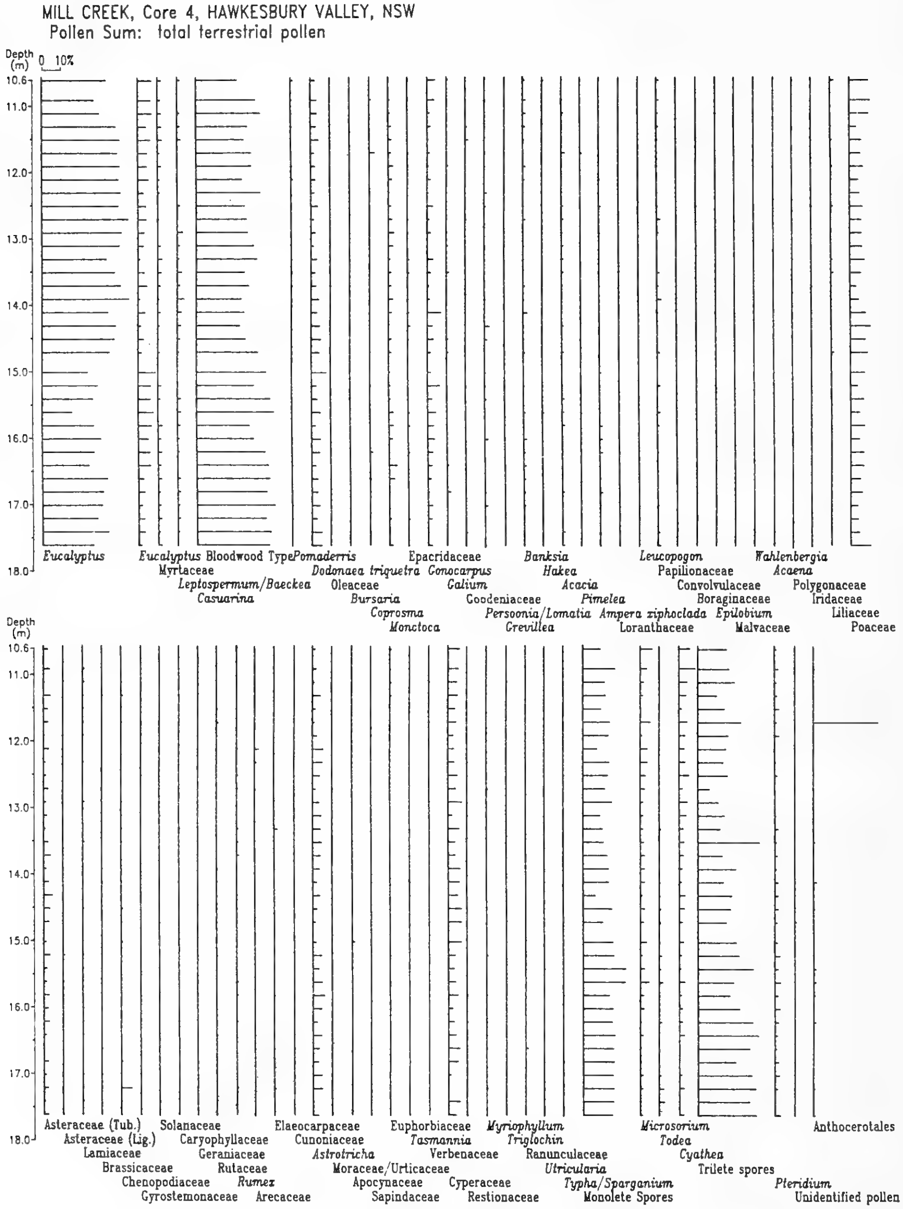

Fig. 4. Pollen diagram for Core 4.

Section 4.2: depth 14.6 m to 10.6 m; inferred age from 8400 B.P. to 4450 B.P.

The species mix is similar to that in Section 4.1 except that there is a decline in Casuarinaceae and a relative increase in *Eucalyptus* pollen. This could be interpreted as either a change in canopy composition, within a wet sclerophyll mix, or a decline in the abundance of *Casuarina glauca* dominated upper estuarine forest in the vicinity of the core. Charcoal values are generally lower in this section, especially above 12.5 m depth.

Core 2

The pollen diagram for Core 2 is shown in Fig. 5. It was likewise sub-divided into two sections for ease of interpretation.

Section 2.1: depth 6.7 m to 3.9 m; assumed age 6000 B.P. to 2800 B.P.

Eucalyptus and Casuarinaceae pollen dominate the spectra and there are several rainforest taxa represented. Fern spores are also abundant. Since there are small but significant amounts of *Monotoca*, *Acacia*, *Persoonia/Lomatia* and *Banksia* pollen, and low values for Poaceae, the pollen mix suggests a vegetation dominated by sclerophyll forest with heath and a strong rainforest component. Charcoal values are relatively high throughout the section suggesting fire may have played a significant role in maintaining the vegetation mix.

Section 2.2: depth 3.8 m to 2.9 m; assumed age 2800 B.P. to 2500 B.P.

Eucalyptus and *Eucalyptus* bloodwood type pollen values begin relatively high then decline. Casuarinaceae values are initially low. Rainforest elements are relatively poorly represented and increases in Poaceae, *Pteridium* and Cyperaceae suggest that the forest is much more open than in Section 2.1. and the rainforest elements have, locally at least, declined. Charcoal values are relatively low throughout.

Core 5

The results of the sand and charcoal abundance estimates are shown in Table 4. Fine charcoal was abundant in all samples and large pieces were absent from the lowermost sand lens samples (levels 62 to 65 cm). Large pieces of charcoal were however conspicuous in the layers below the sand, but not for the sample immediately underlying the sand. Providing deposition was rapid across this sequence it is impossible to rule out the possibility that a series of destructive forest fires destabilized surface cover and led to the sand deposition.

TABLE 4

Abundance of sand and charcoal in sediment from a sand lens and underlying clay in Core 5.
A = abundant, C = common, Nil = absent from sample

Sample depth (cm)	Sand	Charcoal pieces by size > 0.5 cm	 0.5-0.2 cm	 < 0.2 cm
62-3	A	Nil	C	A
63-4	A	Nil	Nil	A
64-5	A	Nil	C	A
65-6	C	C	C	A
66-7	C	A	C	A
67-8	C	A	C	A
68-9	C	A	C	A
69-70	C	A	C	A
70-1	C	A	C	A
71-2	C	C	C	A

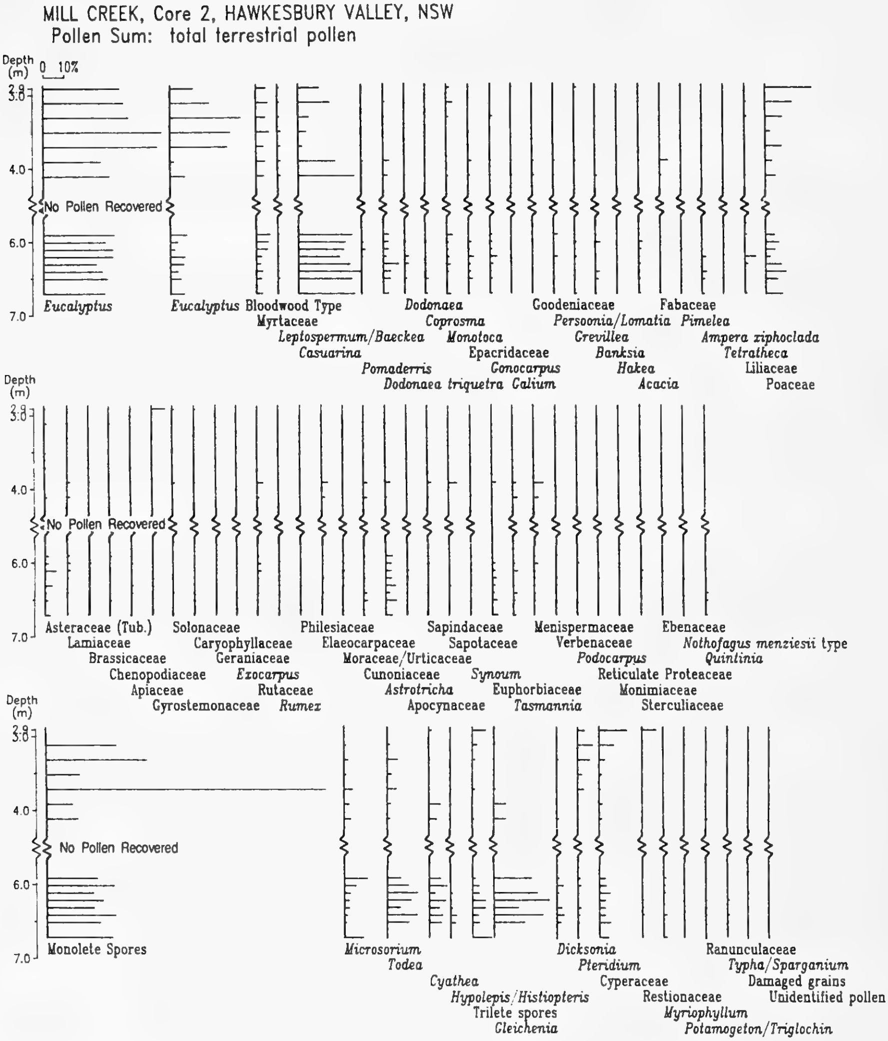

Fig. 5. Pollen diagram for Core 2.

DISCUSSION

The fossil pollen record shows the terrestrial vegetation of the Mill Creek Valley for a time when the sea-level was below its present position; plus for part of the mid-late Holocene when the sea-level was about its present position. The early record is from a freshwater swamp somehow ponded in the junction between the Mill Creek and Hawkesbury River channels, a ponding that was apparently maintained even as sea-level rose to its present position during the Holocene. The changes in vegetation identified have several biogeographic implications for the coastal sandstone region.

Aridity gripped southern Australia during the last glacial maximum and the first signs of vegetation recovery are generally found to be around 10,000 B.P. For sites with records of this age nearest the Hawkesbury Valley, it has been shown that around this time: forest developed over lightly wooded grassland on the Barrington Tops Plateau (Dodson *et al.*, 1986); woodland replaced chenopod shrubland at Ulungra Springs (Dodson and Wright, 1989); and woodland replaced a semi-arid grassland steppe around Lake George (Singh and Geissler, 1985).

The Mill Creek vegetation record shows that a eucalypt forest with a strong component of bloodwood species was present from as early as 9100 B.P., and furthermore, initially at least, had a rainforest component. Samples described here and work by Kodela (1990) show that most rainforest trees are very low pollen producers. Thus small amounts of pollen could represent substantial amounts of rainforest. The variety of rainforest pollen indicates the occurrence of a relatively diverse assemblage of warm temperate forest elements in the vegetation. Since this record comes from a steep-sided valley, located some 36 m below present sea-level, it was unquestionably within a well-protected gully. This could explain the occurrence of rainforest, especially since the site had a southerly aspect. The sclerophyll taxa present suggest a vegetation similar to that growing on Narrabeen Group sediments in the valley today, although Casuarinaceae and *Astrotricha* may have been less common than at present.

It has been hypothesized that the survival of rainforest species during the aridity of the last glacial maximum was in protected refuges not far from the present distribution of rainforest. This explanation is thought to be required to account for the lack of evidence of extinctions and the widespread yet discontinuous nature of rainforest at present, given the slow rates of migration of many of these taxa (Dodson, 1989).

The Core 1 record extends the known fire history of the sandstone flora back some 3000 years further than that in Chalson (1983) and Kodela and Dodson (1989). Fire may have been confined to sclerophyll areas as charcoal is in much the same abundance whether rainforest is present or not; however it may have played a role in restricting the occurrence of any extensive stands of closed forest.

The mid-late Holocene record likewise shows a trend from rainforest to more sclerophyll dominated forest. However the greatest charcoal concentration occurs in the section containing rainforest elements. There is no independent evidence of the source of the charcoal in this instance; there was certainly a different fire regime between the sclerophyll plus rainforest and the sclerophyll forest zones, making it tempting to suggest that the decline in rainforest was in part due to fire. This could suggest that increased occurrences of anthropogenic or natural fires may have been at least partly responsible for the loss in rainforest, and the development of more open vegetation. The lower values of charcoal input to the sediment could then have been due to more frequent and a lower intensity burning regime.

Jones (1991, pers. comm.) is currently working on a Holocene vegetation history from Wrights Creek (see Fig. 1), but has found few rainforest taxa represented. Macphail (1991, pers. comm.) has examined 8 samples of Holocene age which have been recovered from bore holes on the Hawkesbury and Colo rivers. Rainforest elements and charcoal are present in some of these samples. While none of these samples are dated they do show a degree of change and indicate, along with the present study, that rainforest elements were more widespread in the past.

Where the rainforest elements decline in the Mill Creek sites it could be related to rapid sedimentation, seen to be as much as 30 cm in a single or few closely related events, possibly due to fire, at the Core 5 site. The cover of sand would be seen as favouring sclerophyll taxa over the slower responding strategies usually followed by rainforest taxa. Of course, from the records presented it is not possible to rule out fire as a significant causal agent in the high sedimentation environment.

Clearly it is important that more sites be examined to test the distribution of rainforest taxa further back in time and these data suggest that the deeply incised valleys of the Central Coast of New South Wales probably provided refuges for rainforest and sclerophyll species. Ecologists must appreciate however that there is a growing body of evidence showing that much of the vegetation of eastern Australia, including rainforest, has a considerable history of fire; and this must be taken into account when considering the nature and resilience of these communities.

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The Biology and Population Ecology of Two Species of *Cardiaspina* (Hemiptera: Psyllidae) in Plague Numbers on *Eucalyptus grandis* in New South Wales

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CAMPBELL, K. G. The biology and population ecology of two species of *Cardiaspina* (Hemiptera: Psyllidae) in plague numbers on *Eucalyptus grandis* in New South Wales. *Proc. Linn. Soc. N.S.W.* 113 (2), 1992: 135-150.

The genus *Cardiaspina* contains at least five species whose populations increase to very high numbers from time to time. Three species investigated have all caused severe defoliation of prized economic forest tree species of *Eucalyptus*. Historic occurrences are recorded as far as possible but it is probable that such outbreaks also happened long before man's intervention in Australian forests.

In this paper the two species *Cardiaspina fiscella* Taylor and *Cardiaspina maniformis* Taylor have been studied in some detail as they have a common host in the tree *Eucalyptus grandis* Hill & Maiden (the rose or flooded gum) and because of their peculiar and unusual behaviour. Their biology and population ecology is examined and the influence of various biological factors on fluctuations in their numbers discussed. Various aspects of tree and leaf conditions and the possible effects of weather on their populations are also considered. An hypothesis of psyllid outbreak release is presented for consideration.

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INTRODUCTION

There are many species of *Cardiaspina* having *Eucalyptus* spp. as hosts but so far only five species are known to have caused significant or widespread defoliation of trees in south-eastern Australia.

The earliest record of *Cardiaspina* species causing widespread defoliation in New South Wales was in the summer of 1910 in the then Forestry District of Taree (Forestry Commission of N.S.W., unpublished data). Stands of *Eucalyptus paniculata* Smith (grey ironbark) were reported as being severely defoliated. In March 1916 the insects responsible were reported as still infesting the trees and increasing in number; in May W. W. Froggatt visited the area and later described the insect responsible as *C. vittaformis* (Froggatt, 1923). The outbreaks continued until 1936.

High numbers of *C. albitextura* Taylor occurring on *E. blakelyi* Maiden (red gum) in the Australian Capital Territory and Southern Tablelands and south-west slopes of eastern Australia have been studied in detail by Clark (1962, 1963 a, b, c, d, 1964 a, b, c) these papers provided an excellent and comprehensive study of the population ecology of this insect.

C. densitexta Taylor, which occurred in epidemic numbers on *Eucalyptus fasciculosa* F. Muell in parts of South Australia from 1914-22 and also in 1956-63, has been intensively studied by White (1966, 1968a, b, 1969, 1970). These papers dealt with many aspects of the biology and population ecology of this insect/tree relationship and provided a comprehensive understanding of this complex interaction.

In 1938 a species of *Cardiaspina* was found to be defoliating *E. botryoides* Smith (bangalay) at Narrabeen (Sydney, New South Wales). This and another *Cardiaspina* species were defoliating *Eucalyptus grandis* Hill & Maiden (rose or flooded gum) in the Boambee-Coffs Harbour area in the 1960's and these outbreaks have occurred sporadically since. In 1961 defoliation of *E. grandis* in the Boambee area was severe and a study of the outbreak was commenced by the author in the same year. The two species involved were *Cardiaspina maniformis* and *C. fiscella* and were described and named by Taylor (1962). This paper gives an account of the biology and behaviour of these two insects, various controlling factors and some of their population dynamics. Records of past plagues of *Cardiaspina vittaformis* are also included; the life history of this species was described by Froggatt (1923).

PLAGUE RECORDS

Cardiaspina vittaformis *Froggatt*

Infestations of this insect were first reported (Forestry Commission of N.S.W., 1910, unpublished data) in the southern part of the then Taree Forestry District near Dungog and Clarencetown on ironbarks (mainly *E. paniculata* Smith). In the Caincross and Kiwarrak State Forests trees were severely defoliated and outbreaks extended as far north as the Hastings River. It was reported that the ironbarks usually recovered from initial defoliation, but repeated attacks caused a great amount of 'die-back' of the crowns and a number of trees died. Outbreaks continued during 1917-18, and in 1919 the insect was in very high numbers in the northern part of the district in the Maria River, Tanban and Yessabah State Forests (Kempsey Forestry District). In 1920 it was reported only from Trevor State Forest and Froggatt (1923) mentioned it as present but not doing much damage.

In 1924-25 the psyllid was again present in high numbers, this time in Ingalba and Collombatti State Forests; it gradually extended northwards in 1926-27. Saplings and pole-sized trees were killed. The insect was less active in the Taree District but did considerable damage in the Kempsey District. In 1928-34 defoliation caused by *C. vittaformis* was severe in Kiwarrak, Broken Bay, Caincross and Bullengarra State Forests. In the Taree and Wauchope Districts, the heaviest damage occurred between 1924-30, only scattered attacks being noted in 1932-33. The insect was present in high numbers again on *E. paniculata* in 1936 in Olney State Forest between Martinsdale and Olney plantation as well as in the Taree and Wauchope Districts at Broken Bay, Bull's Ground, Keri, Lorne, and Cowarra State Forests; however, the outbreaks were brief and numbers diminished again within the year.

Large numbers of ironbarks were felled and logged as a result of the 1916-30 outbreaks, the practice being to mark for felling and removal trees with their larger branches dead. In almost all cases the upper part of the main trunk of the trees felled (0.6-0.9 m down) showed heart 'doze' (decay due to wood-rotting fungus). This is most unusual in ironbark and was attributed to the psyllid attack killing major parts of the crown and permitting fungal infection of the large branches and the upper trunk.

The remnant ironbark stands at Beecroft and West Pennant Hills (New South Wales) were severely defoliated by *C. vittaformis* in the 1960-64 period but no outbreaks occurred in the areas previously affected in the lower north coast. Another ironbark, *Eucalyptus siderophloia* Benth., was hardly affected by this psyllid.

Cardiaspina fiscella

Although no doubt occurring in high numbers earlier, *C. fiscella* was first reported to cause defoliation, of *Eucalyptus botryoides* Smith (bangalay) at Narrabeen and on the closely related *Eucalyptus grandis* (near Coff's Harbour), in 1938. In 1944 the outbreaks were widespread and *Eucalyptus saligna* Smith (Sydney blue gum) was also reported as being defoliated at Barengarry Mountain and between Bulli and Nowra as well as in the Kangaroo Valley.

This species also defoliated *E. grandis* around Coff's Harbour, especially in Mooball State Forest on the lower slopes of the southern approach to the Burringar Range. Lighter attacks occurred further north in the Tweed area. *E. botryoides* at Narrabeen and around the foreshores of Port Jackson was also attacked in 1944. Outbreaks continued throughout 1945-47 in the Coff's Harbour, Bonville, Korora and Boambee State Forests and near the Pine Creek State Forest nursery; other infestations occurred between Murwillumbah and Mullumbimby.

In Boambee State Forest natural regeneration was severely defoliated, but planted trees were only slightly affected. Some defoliation of the bangalay occurred at Collaroy in 1946. No further outbreaks were recorded until 1954 when *E. botryoides* at Narrabeen and the Royal National Park were defoliated.

In 1957 *E. grandis* at Korora was defoliated and this continued in 1958. In 1959 *Eucalyptus botryoides* at Gosford was attacked. Early in 1961 defoliation of flooded gum was severe in compartments 101 and 102 of the Boambee State Forest and was widespread, extending from South Boambee in a roughly east-west line through South Korora to Mt. Brown, south of Karangi. However, the insects were not present in high numbers in any of the areas of Pine Creek (Whian Whian) State Forest affected in 1946 or further south. In 1948 the *E. grandis* plantations in Whian Whian State Forest were defoliated (Taylor, 1990, pers. comm.), the '80 acre', was severely defoliated — *C. maniformis* was also present. In compartment 16 the insects were present but defoliation was not severe. In No. 1 and Seaview only light defoliation was noted. The natural regeneration of *E. grandis* west of the nursery was the most severely affected.

A detailed study of this latter series of outbreaks in the Boambee area was commenced and it was soon established that two species of *Cardiaspina* were involved. *C. maniformis* was, no doubt, present in all the earlier recorded outbreaks on the lower north coast, but it was not described or named by Taylor until 1962.

LIFE HISTORIES AND BEHAVIOUR

Cardiaspina maniformis

This psyllid occurs on *Eucalyptus grandis* in association with *C. fiscella*. Very often both species are present in the same leaf; the leaves of *E. grandis* are dorsiventral and the dorsal surface of the leaf has few stomatal apertures, most being on the ventral surface.

The eggs are deposited on the dorsal surface of the leaf. After eclosion, the nymph establishes itself, also on the dorsal surface, begins to feed and constructs its covering or 'lerp'. There are five nymphal instars (Fig. 1**a**) and after each moult the perimeter of the lerp is increased to accommodate the insect's greater bulk. Eventually the shell-like lerp characteristic of the species is attained at full growth (Taylor, 1962). The nymphs may be parasitized by small endoparasitic or hyperparasitic wasps. In this case a black nymphal 'mummy', instead of a healthy full-grown nymph results.

After emergence and copulation, the female actively seeks oviposition sites, although adult feeding does not cause significant damage to the leaves as the insect seldom remains in any spot for any time. It is probable that this is the way she also determines whether a leaf is suitable for oviposition and probably as a feeding site for a nymph. Males and females are winged and very mobile, jumping away backwards if threatened. Tender new leaves are not favoured for oviposition, nor are the dead or dried portions damaged by former nymphal feeding; mature and healthy leaves are chosen where possible. Intensive investigation of the mating and oviposition behaviour of *C.*

densitexta on *E. fasciculosa* has shown that the nature and condition of the leaves is critical (White, 1970).

The eggs are a little larger than a first instar nymph and are laid singly but usually adjacent to one another. They are affixed to the leaf surface by a small stalk (illustrated in Froggatt, 1923). *C. maniformis* has four generations a year; all of these may overlap to some extent as indicated in Fig. 1**a**.

Cardiaspina fiscella

Soon after emergence the adults of this psyllid oviposit on either surface of the *Eucalyptus* leaf, but more frequently on the dorsal surface — often at sites adjoining those of *C. maniformis*. However, the first instar nymph practically always establishes its feeding position on the ventral side of the leaf, as they are capable of walking from a crowded or unsuitable site to one more favourable. If they do not find a suitable site within a few hours they will die from exhaustion. Later instars appear incapable of changing their feeding positions. There are five nymphal instars (Fig. 1**b**) and at each moult the insect adds to its lerp covering until, at the last instar, the lerp attains its characteristic shape (Taylor, 1962).

Oviposition

The presence of two species of insects of the same genus on the same host would seem to pose a paradox. However, the obvious ability of these two species to coexist on the same leaf of the host plant, even at very high population densities is seemingly explained by their nymphal behaviour.

Although eggs are laid by *C. maniformis* only on the dorsal leaf surface, those of *C. fiscella* are laid on either surface but it also prefers the dorsal surface. However, when the nymphs eclode, those of *C. maniformis* almost invariably choose feeding sites on the dorsal surface, but *C. fiscella* nymphs seek theirs on the ventral surface.

Selection of Nymph Feeding Sites

In order to determine why nymphs of each species choose their respective feeding sites on the same leaf, a number of leaves with eggs of both species were artificially inverted and held in this position while still living and affixed to their twigs on the tree. Thus the ventral surfaces of the dorsiventral leaves faced upwards and toward the sun and the dorsal surfaces faced downward toward the ground. All the leaves chosen were wholesome and good feeding sites.

After eclosion in every instance the *C. maniformis* nymphs established themselves on the now downward facing dorsal surfaces and *C. fiscella* on the upward facing ventral surfaces, precisely as they would if the leaves were oriented naturally. Many of the nymphs successfully completed their stages. Their behaviour seemed to be neither geotactic or phototactic.

Microscopic examination of nymphs in place on leaves revealed that the stylets of *C. maniformis* readily penetrate the dorsal cuticle. However, *C. fiscella* seems to be unable to achieve this and the nymphal stylets of this insect penetrated through the stomatal apertures, which are mainly on the ventral surfaces of leaves. White (1970) recorded that *C. densitexta* nymphs also fed through the stomates of *E. fasciculosa*. When *C. fiscella* nymphs were gently removed from their feeding sites they had great difficulty in re-establishing themselves, whereas *C. maniformis* did so without much trouble.

As feeding destroys leaf tissue and a well established nymph does not move from its site (not even when attacked by a ferocious syrphid larva), necrotic patches on the leaf surface slowly enlarge. If these patches overlap some interspecific and intraspecific competition does occur, but it is usually only when the insect population is dense that

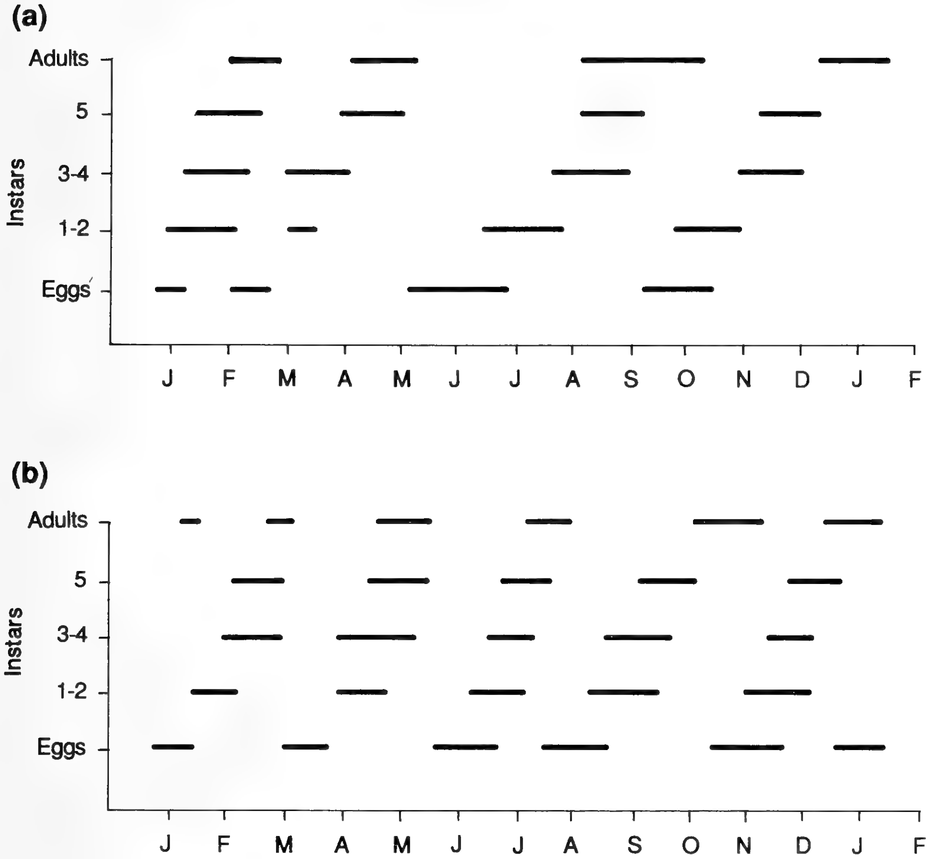

Fig. 1. Occurrence of psyllid life cycle stages over a 15 month period: (**a**) *Cardiaspina maniformis*; (**b**) *C. fiscella.*

nymphal mortality follows. If damage is too great the leaf is shed by the host tree. At the end of a nymphal stage damage to leaves can be so great even at reasonably low population densities that severe defoliation can ensue. The consequences of this will be discussed later (see also Clark, 1963a). Clark (1963b) gave a good account of the behaviour of *C. albitextura* on *E. blakelyi.* White (1970) provided comprehensive descriptions of behaviour patterns in adults of *C. densitexta.*

The males of each species produce distinctive calls, different for each species and are probably used to attract appropriate females (Campbell, 1964). This ability may be critical when numbers are low and the finding of suitable mates important. A comparison of the sounds produced by *C. maniformis, C. fiscella* and *C. densitexta* would be informative.

Mortality Factors

A number of mortality factors which affect psyllid numbers are considered below. These include: endoparasitic wasps; predatory insects; predatory birds; foliage and tree conditions.

Endoparasities

The larvae of several species of *Psyllaephagus* Riek and *Quaylea* (Hymenoptera: Encyrtidae) are parasitic on psyllid nymphs. Species recorded include: *P. gemitus*, *P. cornuatus*, *P. bliteus*, *P. discretus*, *P. facilis*, *P. funiculus*, *P. brachiatus* and *P.* nr *dignus* and *P. clarus* (Riek, 1962, 1970). At Boambee, three species were most prevalent, *P. gemitus* Riek, *P. clarus* Riek and *Q. psyllae*. The relative abundances of these from 1961-63 is shown in Fig. 2.

Numbers of the primary parasite, *P. gemitus*, were low and insignificant compared to those of the hyperparasites during the periods of high psyllid numbers in 1961-62. This suggests that comparative failure of the primary parasite contributed to favourable conditions for psyllid population outbreak (see Fig. 3)

A parasitized nymph does not emerge as an adult but is eaten inside its case by the wasp larva; a black 'mummy' results from which the adult wasp emerges. These can be readily detected on close examination during a census (Clark, 1964a). Many parasitoids are attacked by hyperparasites; this does not alter the mortality as far as the psyllids are concerned but may alter the longer term effects of parasitizm.

Predators

Larvae of the hover fly, *Syrphus viridiceps*, (Diptera: Syrphidae) are voracious predators of nymphs (Fig. 3), though less during winter; however, they are relatively rare and their total effect is uncertain — see Clark (1963d, 1964a). An occasional lacewing (Neuroptera) larva was observed to predate on psyllid nymphs.

Some small birds, such as the weebill (*Smicornis brevirostris*) and the pardalotes (*Pardalotus* spp.) were observed feeding on the nymphs. No doubt these birds also feed on adult psyllids (see Clark, 1964b).

The effect of insectivorous birds on any insect population is very complex, as the bird is just as likely to eat parasites or predators of the insect as the insect itself (Campbell and Moore, 1957; Ward and Neumann, 1982). There is the possibility that this may increase survival rather than mortality of the psyllids and actually increase population numbers, as has been observed in the case of the plague phasmatids (Readshaw, 1964). The actual effect of birds on psyllid numbers requires further study (Ward and Neumann, 1982).

Host Conditions/Interactions

All recorded outbreaks of these psyllids have occurred in areas of good 'site quality' (S.Q.). This is a forestry estimate of the total effect of all growth factors of a particular site on tree growth and health: S.Q.1 is very good, whereas S.Q.7 is extremely poor. The trees considered in these studies were mostly over five years old and not far from the sea. The favoured condition of leaves for oviposition by the psyllid adults has already been stated.

Feeding by the nymphs (sucking the sap from a leaf) ultimately results in a small portion of the leaf being killed. The initial amount of a leaf's tissue killed depends on the number of nymphs feeding in one generation. If numbers are low and only a small amount of tissue is necrotic, reinfestation of that leaf may occur and the feeding and necrosis will continue and spread. When this damage reaches a point where the leaf requires more energy to maintain it than it is returning to the tree, by photosynthesis, it

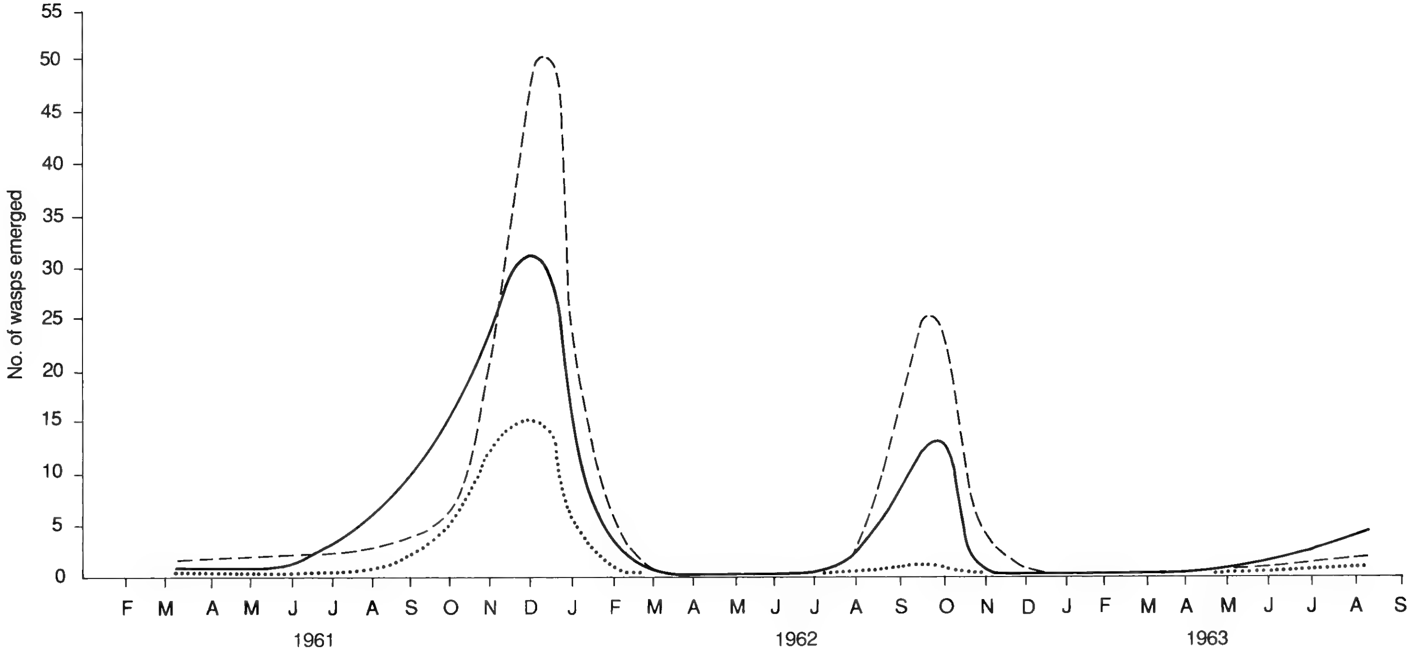

Fig. 2. Relative abundances of 3 parasitic wasps that emerge from 'mummies' of *C. maniformis* and *C. fiscella*; *Psyllaephagus gemitus* (_____), *P. clarus* (----), *Quaylea psyllae* (....).

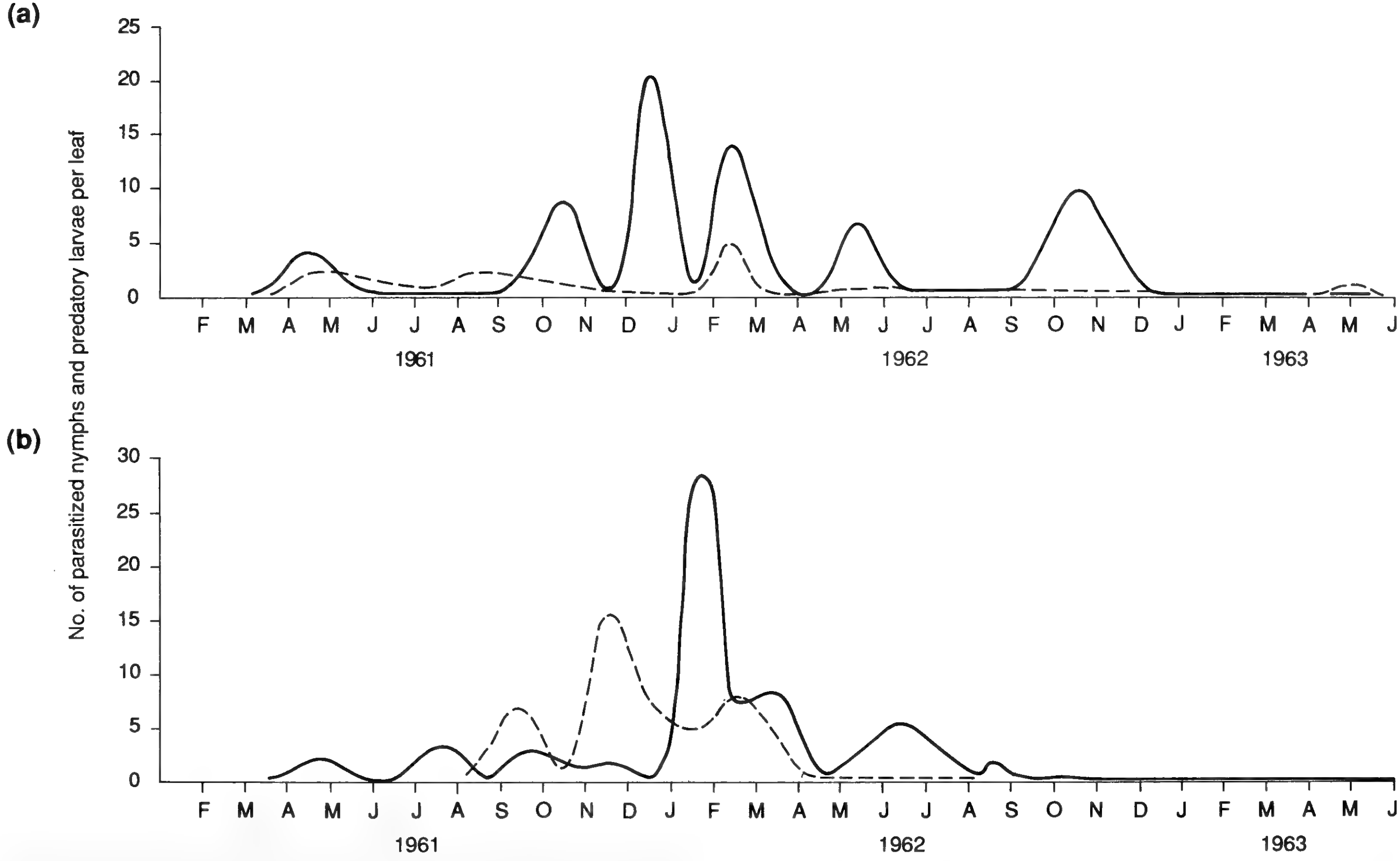

Fig. 3. Parasitizm and predation of *Cardiaspina fiscella* and *C. maniformis*; parasitized nymphs (_____), predatory larvae (----). (**a**) Boambee Plantation, (**b**) South Boambee (6 *C. fiscella*: 1 *C. maniformis*).

is shed and all the nymphs feeding on it, unless they are fully fed and ready to metamorphose, perish.

Leaves are also shed, although they may be still functional, if they become redundant to the tree; this happens when a 'flush' of growth occurs in eucalypts as a result of good growing conditions. This type of leaf loss can also be disastrous to eggs or nymphs present on such leaves.

When population numbers of psyllids increase to the extent that most or all the leaves reach this critical damaged condition at much the same time then a large part of the foliage will be shed, sometimes over quite a large area of forest. This causes a short-term setback for the trees as stored reserves must be channelled immediately into leaf production instead of into progressive growth, normal leaf replacement or wound repair. For a vigorous tree like *E. grandis* growing on a good site this is not a disaster, although it could be to trees growing on poorer sites with less stored reserves (cf. *E. paniculata*, *E. blakelyi*, and *E. fasciculosa*).

The shedding of foliage usually causes a reduction in growth, particularly in wood production; this is of serious concern for forest managers. Prolonged plague numbers can virtually stop tree growth for several years as the tree puts all its energy into maintenance and replacement. Trees can actually be reduced in diameter if all the foliage is damaged (Mazanec, 1966). Also, a tree weakened in this way is subject to 'die-back'.

For high numbers of psyllids to be maintained an ample supply of good oviposition sites in the first case and enough good leaf tissue for nymphal establishment, feeding and survival to full growth is necessary. In the initial stage of a population increase these conditions are abundant and the adults can lay their full quota of eggs. Most of these will survive as will the ecloding nymphs and an explosion in numbers results. If the trees can maintain an adequate supply of suitable leaves to meet this increase in the psyllids, plague conditions will be maintained.

This situation can change quite rapidly if the defoliation of the trees outstrips their ability to refoliate. New and immature leaves are not favoured oviposition sites or feeding sites for the nymphs, so that the psyllid population can then diminish as quickly as it has increased (see Fig. 4). Recovery can occur when the foliage conditions become favourable again.

In the case of *E. grandis* which is very vigorous, probably the fastest growing of all the *Eucalyptus* species, a tree can cope with high psyllid numbers for quite some time. Repeated defoliation, however, will ultimately use up its energy and stored reserves more rapidly than they can be replaced by photosynthesis. The increase in psyllid numbers is thus closely related to the ability of the host tree to sustain the insect population. Thus, it is possible for a host tree to 'regulate' a psyllid plague either by not maintaining enough suitable foliage or by producing too much (new and immature) foliage which is unsuitable. A similar interaction between insect and host has been noted with *C. albitextura* and *E. blakelyi* (Clark, 1963a,b), as well as *C. densitexta* and *E. fasciculosa* (White, 1966, 1970).

Population Studies

Sites and Samples

From early 1961 to mid 1963 a census of the psyllid populations was taken each month at five different sites. These are listed and described below.

1) Inside Boambee State Forest Plantation — in an area previously seriously defoliated.
2) Inside the Boambee Plantation — in an area only moderately defoliated previously.

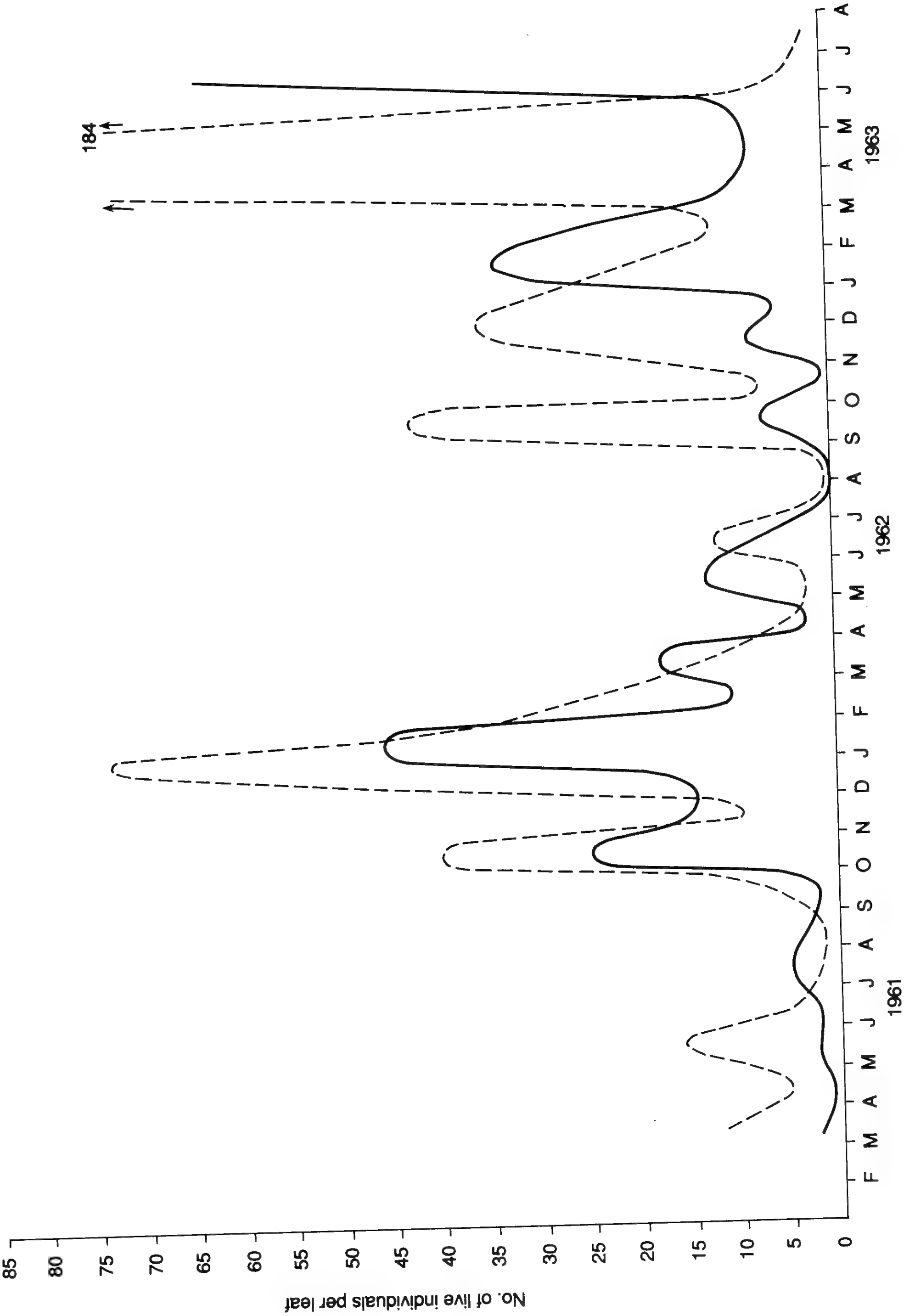

Fig. 4. Population trends of psyllids at South Boambee; *Cardiaspina fiscella* predominates, 6:1. Eggs (----); nymphs (——).

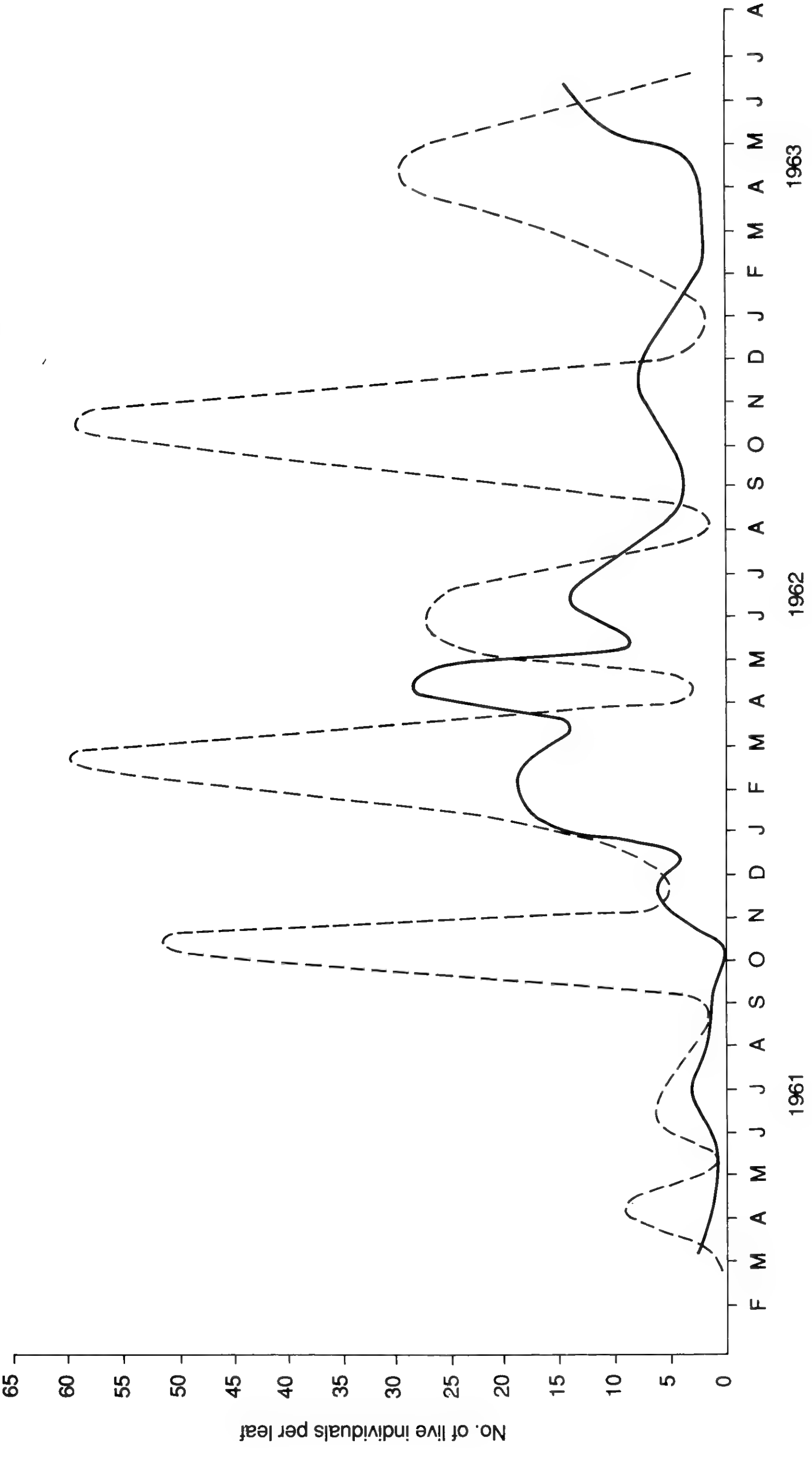

Fig. 5. Population trends of *Cardiaspina maniformis* at Boambee Plantation. Eggs (- - -), nymphs (——).

At 1) and 2) two trees were sampled on each occasion. Five branchlets approximately 23 centimetres long (10 leaves) were taken from (a) the top, (b) the middle and (c) the bottom of the crown (i.e. 15 branchlets from each tree).

3) Outside Boambee Plantation — open grown natural regeneration on private property.
4) Middle Boambee, as in 3).
5) South Boambee.

At 3), 4) and 5), 10 branchlets each of 10 leaves were taken at random from one tree at each site (reduced to 5 branchlets each after 5 June, 1962).

From each leaf, counts of eggs, nymphs — live and dead (lerps without live nymphs) and parasitized nymphs were made; *C. maniformis* and *C. fiscella* were recorded separately. Each psyllid species has a quite characteristic and easily recognized lerp (Taylor, 1962). Counts of numbers of predators and observations and notes of host leaf conditions were also made. Thus the numbers per leaf given in the figures are an average of 150 leaves per tree on sites 1 and 2 and 100 (later 50) leaves at sites 3, 4 and 5.

Figs 2 to 6 illustrate population trends in two different localities. The biotic mortality factors (wasp endoparasites and predators) are shown in Figs 2 and 3; Figs 4, 5 and 6 demonstrate the variation in psyllid populations.

C. maniformis was predominant in the Boambee State Forest Plantation, where the trees are artificially regenerated and the trunks close together with dense tight crowns; both species were present, often on the same leaf. *C. fiscella* predominated in the more open crowned, naturally regenerated area at South Boambee. Again both species were present (often on the same leaf) in the ratio of 6 *C.f*: 1 *C.m*). Despite this the fluctuations in numbers of the various life stages and generations of both insects at each site were synchronized.

Cardiaspina maniformis

In the case of *C. maniformis* in Boambee State Forest Plantation the foliage was not so badly damaged in 1961 and few new leaves were produced by the host in March. Numbers of psyllid nymphs reached their peak numbers in April, 1962, but at a much lower level than those of *C. fiscella* had at South Boambee earlier in January (Figs 5 and 6). Damage to the leaves was not then severe and these leaves were retained by the trees well into 1963.

Parasitizm was also generally higher in nymphs of *C. maniformis* and the tiny wasps were active to the end of 1962, but few were in evidence in 1963, when numbers of psyllids again began to increase (Fig. 3). The syrphid larvae also appeared less active in the plantation area. In 1964 the population of both psyllid species fell to very low numbers.

Cardiaspina fiscella

In the fourth generation of 1961 and first generation of 1962 the feeding of high numbers of nymphs of the *C. fiscella* dominated population caused severe damage to leaves of the host trees. Although new leaves were beginning to be produced, refoliation was not complete until about September 1962, when another build-up to high numbers culminated in the second and third generation in 1963 (Fig. 4). Parasites and predators were common and no doubt helped to reduce numbers in 1962; but after August 1962 they were less significant and psyllid numbers again began to increase to the very high levels recorded in mid 1963.

Predation effects were difficult to assess; the main predators were syrphid fly larvae, some neuropterans and birds. No doubt a syrphid larva eats many psyllid nymphs during its lifetime but it is also readily taken by insectivorous birds (Campbell and Moore, 1957). For example, in January 1962, of 77 lerps on a leaf (1st and 3rd instar) 31 had the nymph removed and in February 1962, of 97 lerps, 87 lerps had the nymph removed. The lerps were undamaged and the only predators present capable of removing the small nymph without doing this were the syrphid larvae, of which there were quite a number present. Birds damage the lerp considerably when seeking the nymph beneath; see Clark (1964b) for the effects of syrphids and birds on *C. albitextura.*

In the Sydney area *C. fiscella* was in high numbers on *E. botryoides* (bangalay) on the northern shore of Narrabeen Lake near and around the mouth of Deep Creek at about the same time as at Boambee. The trees were all natural regeneration, open grown and mainly small (up to 11 metres high).

The eggs were laid mostly on the dorsal surface (*E. botryoides* also has dorsiventral leaves) and the nymphs all established themselves on the ventral surfaces. The population in this area was kept under observation until 1968. The population numbers were high until September, 1967 but very rapidly diminished. After November 1967 it was difficult to find any of the insects; they are still present but in low numbers.

In November 1973 there was evidence of severe damage on *E. saligna* at Bulli Pass; no eggs or nymphs were seen but the remnant lerps of fully grown nymphs were observed. Damage to the foliage was so severe that probably only a relict population was present.

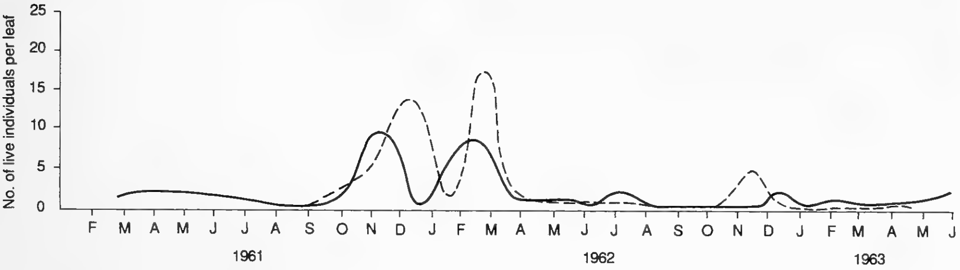

Fig. 6. Population trends of *Cardiaspina fiscella* at Boambee Plantation. Eggs (----), nymphs (____).

Discussion

Sites

All the areas where outbreaks of these psyllids occurred in the 1960-63 period had several characteristics in common. These are listed below.

(i) The trees were at least five years old and therefore producing mature foliage.

(ii) They all grow in 'valley bottom' conditions with abundant soil moisture and nutrients.

(iii) None of the areas had suffered from wildfire or controlled burning since they were established.

Weather

There appears to be a connection between 'wet' years and psyllid outbreaks. In the Boambee area the greater part of the rain usually falls in the summer and a 'dry' year means below average rainfall in this season; 'dry' years were recorded in 1932, 41, 46, 48, 57 and 60. The summers of 1961/2 and 1962/3 were both 'wet' years and cyclonic conditions caused above average rainfall in both these seasons. Some data for recent years are summarized below.

Wet Years: 1942, 43, 44, 45, 47, 49/50, 58/59, 61/62/63

Psyllid Outbreaks Recorded: 1944, 45, 47, 48, 57, 61,62

However, before this apparent correlation can be established many more data are necessary. The direct and indirect effects of weather on insect populations have been discussed by Nicholson (1954) and de Bach (1958). Clark (1962) also discussed the effects of weather-induced breakdowns of the host and parasite synchronization in *C. albitextura*, as well as the reduction of parasite effectiveness in weather conditions unfavourable to them. White (1969) has studied in detail the effects of weather on outbreaks of psyllids and their host trees, particularly *C. densitexta* and *E. fasciculosa* and has evolved a 'stress index' to explain the complex interactions of this important factor.

Life Histories and Behaviour

The concept of one species-one niche appears to be negated by the two distinct species of closely related insects occupying the same host. *C. maniformis* and *C. fiscella* co-exist on the same part of the same host, the dorsiventral leaf of *E. grandis*.

Studies have revealed that although adult females may oviposit on the same leaf surface, after eclosion the nymphs choose quite different feeding sites though often on the same leaves. *C. maniformis* establishes itself on the dorsal surface of a leaf and remains there throughout its nymphal life, whereas *C. fiscella* lives and feeds on the ventral surface, commonly of the same leaf. Interspecific competition is minimized by this difference in feeding site preference. The two species indeed do occupy different niches even though they are otherwise subject to similar habitat conditions. This behaviour does not appear to be unfavourable to either species, as they are able to attain high numbers on the same host at the same site at the same time.

It was notable that *C. maniformis* predominated over *C. fiscella* in the Boambee Plantation where the crowns of the trees are very close together; in this closed canopy situation sunlight would be limiting. In the natural regeneration area, where the crowns were not touching and sunlight was abundant, *C. fiscella* predominated in numbers in the proportion of about 6:1. It appears that lower light intensity is less favourable to *C. fiscella* nymphs. A dorsiventral leaf presents its dorsal surface incident to the light so that a shaded leaf, not so actively photosynthesizing and transpiring less will tend to have more of its stomatal apertures closed than one in full sunlight. This may restrict the nymphal stylets and reduce the food supply to a psyllid feeding on the ventral surface. Of course, the physiological reactions of tree leaves with regard to the ambient humidity, $C0_2$ concentration, sunlight and soil moisture are quite complex and effects of these factors in leaf sap-sucking insects of trees are little known.

There is no doubt that this interaction between nymphal feeding and leaf condition is important both to the tree and the insect. As suggested previously, it is possible for a forest stand (or a single tree) to more or less regulate a psyllid plague in the following way. The adult and nymph both need a sufficient supply of healthy and appropriate leaf tissue, but damage to a leaf to a critical stage will without exception result in shedding of that leaf. If plague numbers are present, damage to a great number of leaves will occur and defoliation of many trees will result.

If sufficient refoliation does not occur (or enough suitable foliage remain), when the surviving adults of the previous generation emerge and require ample oviposition sites, then eggs will be laid on sites which give the nymphs little chance of survival. Too few will reach full growth to maintain high population numbers and consequently the population will decline. Some psyllids will usually survive and other mortality factors may hold them at low levels for some time until another favourable situation occurs to permit another increase in numbers.

The ability of *E. grandis* trees to withstand leaf damage and to refoliate rapidly and successfully depends on their energy reserves built up in periods when they are not under stress (from insect attack or drought). Vegetative growth is considered to be encouraged by a plentiful supply of available nitrogen. The apparent connection between 'wet' years and psyllid outbreak release may be due to the increased availability of atmospheric nitrogen to trees, because of increased thunderstorm activity in such years. In the case of flooded gum, soil moisture and light are not limiting and the ready production of healthy leaves essential for high psyllid numbers is also enhanced by the high levels of available nitrogen.

Other factors affecting the incidence of psyllids are parasites and predators. The primary wasp endoparasites (*P. gemitus* and others) caused considerable mortality of the psyllid nymphs of both species in several generations in 1961-62, though their longer term effect was reduced by the hyperparasitizm by *P. clarus* and *Quaylea psyllae*. Clark (1964a) also discussed the effects of parasites on *C. albitextura* in some detail.

The predatory larvae of the syrphid fly accounted for the deaths of many psyllid nymphs, but more so in the open grown trees of South Boambee, presumably more favourable for the adult flies. The syrphid is an important controlling factor, but in turn is a favourite food of insectivorous birds.

The several insectivorous birds present also accounted for many insects present in the habitat, but these predators were not selecting for particular groups of insect prey. In eating an insect, the bird directly reduces its numbers, but if the parasites or predators of the insect are also eaten a net increase in the insects' numbers may result. The interactions are extremely complex and findings of studies done so far, controversial (Campbell and Moore, 1957; Clark, 1964b; Readshaw, 1964; Ward and Neumann, 1982).

Causes of Psyllid Outbreaks

Drawing together the available information the following hypothesis has been developed to explain the processes that lead to a psyllid outbreak. It is presented here for consideration.

In years when above average summer rainfall occurs, increased thunderstorm activity makes more atmospheric nitrogen available to trees during the growing season; the trees then produce more than adequate high quality foliage. The psyllids, already present in low numbers, are able to take advantage of plentiful and favourable oviposition and nymphal feeding sites and large numbers will survive to adulthood. The biotic mortality factors (endoparasitic wasps, predatory fly larvae, birds), previously maintaining the psyllids at low numbers, cannot now cope with this rapid increase in numbers. Increased numbers of well nourished and vigorous psyllid adults survive and are able to lay many more viable eggs, with many more nymphs surviving to maturity. An exponential increase of the population to plague numbers results.

At this stage the condition of the foliage may become a limiting factor. If damage caused by nymphal feeding is great enough, severe defoliation of the trees will adversely affect survival and reduce numbers of the psyllids. If the biotic mortality factors or overcrowding can limit the psyllid numbers below this level of damage the defoliation may only be partial, giving some respite to the trees so that new leaves can be produced. If the new leaves are produced in time for them to mature and become suitable oviposition sites and feeding sites for the next generation of psyllids, then the population will be maintained at a high level. If not, psyllid numbers must decrease and the biotic mortality factors can again limit psyllid numbers at a lower level. This may continue until another favourable cycle of conditions for outbreak release occurs.

The author considers that the weather, as manifested in below average summer rainfall, is the major 'legislative' factor in maintaining these psyllid populations at low numbers; but it is still not clear whether or not it is the 'governing' factor (Nicholson, 1954).

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Thanks are due to Mrs N. J. Campbell, who typed the manuscript. I am grateful to Mr C. E. Chadwick, who constructively criticized the paper; Dr D. S. Fleming was most helpful with the manuscript and figures.

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Two New Species of *Armadilloniscus* (Isopoda: Oniscidea: Scyphacidae) from Northern Queensland

FIONA LEWIS

(Communicated by N. N. TAIT)

LEWIS, F. Two new species of *Armadilloniscus* (Isopoda: Oniscidea: Scyphacidae) from northern Queensland. *Proc. Linn. Soc. N.S.W.* 113 (2), 1992: 151-155.

Two species of *Armadilloniscus* have been collected from two Queensland beaches. They differ from other species in ornamentation and, in spite of the sexual dimorphism characteristic of this genus, they are considered to be from different species and are described as *Armadilloniscus binodulus* sp. nov. from Karumba and *Armadilloniscus ornatocephalus* sp. nov. from Cardwell.

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manuscript received 21 November 1990, accepted for publication 24 July 1991.

INTRODUCTION

The Scyphacidae has representatives in both hemispheres and is one of the five supralittoral families recorded from Australia (Green, 1966; Vandel, 1973; Lewis and Bishop, 1990), where it is represented by *Deto* and *Alloniscus* (Vandel, 1973), two of the seven described genera. Two species of *Armadilloniscus*, are now described from Queensland.

There have been many changes in the taxonomic position of *Armadilloniscus* since its creation by Uljanin in 1875. The genus was placed in a new subfamily Armadilloniscinae of the Oniscidae by Verhoeff (1916). Then Blake (1930) moved the Armadilloniscinae to the Scyphacidae (Chilton, 1901), distinct from other scyphacid genera which he placed in Scyphacinae. Vandel (1962) listed *Armadilloniscus* in Scyphacinae; however, Menzies (1950), Schultz (1972) and Green (1989, pers. comm.) include *Armadilloniscus* as one of the genera of Scyphacidae — a family with no subfamilies.

Diagnoses of *Armadilloniscus* have been written by both Arcangeli (1957) and Vandel (1962). *Armadilloniscus* is separated from the other genera by the flattened and expanded uropod bases (protopods), with the rami extending to or slightly beyond the body margin (Schultz, 1972).

Sexual dimorphism is common in, if not characteristic of, this genus (Taiti and Ferrara, 1989). Females are larger and in some cases have different, or simply more distinct, tubercular ornamentation than males. The tergal ornamentation provides the best criterion for distinguishing species (Vandel, 1970).

An unidentified species of *Armadilloniscus* has been collected from two islands of the Furneaux Group, Tasmania, but is different in ornamentation from the species described here, and can enroll, although imperfectly (Green, 1988, pers. comm.). Neither of the two new species appears able to enroll although other species have been described as enrolling (Blake, 1930; Schultz, 1972).

Only one specimen of each new species was found — a male of one and a female of the other. Their main distinction is in the eyes, 3 ommatidia in one and 7 in the other. In none of the species described by Taiti and Ferrara (1989) was any disparity in numbers of ommatidia noted between the sexes of the same species; so the Queensland specimens are considered to be from different species.

SYSTEMATIC DESCRIPTIONS

Armadilloniscus binodulus sp. nov.
(Figs 1**a**-1**b**)

Holotype: Male, Australian Museum, Sydney (P39140).
Type Locality: Karumba, (Gulf of Carpentaria), Queensland, 17°29′S, 140°50′E. under compacted shell blocks on beach, August 1988, F. Lewis.
Size: 6 mm long and 3 mm broad. **Cephalon** (Fig. 1**a**) lateral lobes subquadrangular, median lobe triangular; 2 slightly raised elongated tubercles running forwards from just anterior and medial to the eye, to behind the medial cephalic lobe; small pointed tubercle anterior to each eye and close to corresponding lateral lobe; eye of 3 ommatidia in line. **Second antenna** (Fig. 1**a**) 4 articled flagellum terminates in tuft of setae. **Pereon** (Figs. 1**a**, 1**b**) tergites each with 3 pairs elongated dorsal tubercles medial to epimera. **Pereopods** large spine on distal end of carpus, dactylar organ present on all. **Pleon** (Fig. 1**b**) second segment extended laterally into 2 large, round tubercles, 2 small tubercles, on each side of midline on each of segments 2-5; telson trapezoidal with slightly concave lateral margins, 2 small medial tubercles, slightly curved posterior border. **Pleopod 1** endopod angled sharply at tip. **Uropod** (Fig. 1**b**) protopod broad, flat, longer than dorsally inserted exopod. The tergite area is flattened with the epimera angled sharply downwards.

Armadilloniscus ornatocephalus sp. nov.
(Figs 2**a**-2**b**)

Holotype: Female, Australian Museum, Sydney (P39141).
Type Locality: Cardwell beach, east Queensland coast, 18°10′S, 146°01′E, under debris along high water mark, August 1988, F. Lewis.
Size: 3 mm long and 1.5 mm broad. **Cephalon** (Fig. 2**a**) 3 lobed, median lobe triangular, lateral lobes subquadrangular; eye of 7 ocelli in 2 rows; 4 rectangular tubercles in semi-circle on vertex, 2 small tubercles posterior to median lobe, 2 more on midline posterior to semi-circular ornamentation. **Second antenna** (Fig. 2**a**) 4 articled flagellum terminating in tuft of sensory setae; peduncle joints with thick fringe of setae anteriorly. **Pereon** (Figs 2**a**, 2**b**) segments 1-6 each with small median tubercle near anterior border which decreases in size posteriorly and is absent on segment 7; lateral to this is one elongated tubercle on segments 1-5 and 2 small tubercles on segments 6-7; lateral to each tergite are small and elongated tubercles, 4 on segment 1 and 3 on segments 2-7. **Pereopods** all have large spine on distal end of carpus; propodus of pereopod 1 has long spine at each end; all have dactylar organ. **Pleon** (Fig. 2**b**) 2 small paramedial tubercles on each segment, segment 2 with 2 lateral tubercles; telson trapezoidal, lateral margins slightly convex. **Uropod** (Fig. 2**b**) protopod flat, expanded, curving inwards; long exopod attached dorsally in concavity near medial margin. The tergite area is flattened with epimera angled sharply downwards.

DISCUSSION

A. binodulus might be expected to be most similar to species from the Indian and Pacific oceans (Taiti and Ferrara, 1989) or Japan (Nunomura, 1984). It differs however, from *Armadilloniscus amakusaensis* (Nunomura, 1984) in the cephalon tubercles and from the other four Japanese species by the trapezoidal telson. It also differs in many characteristics from the six new Indian and Pacific Ocean species (Taiti and Ferrara, 1989). *A. binodulus* is similar to *Armadilloniscus quadricornis* from the Solomon Islands in having the exopod shorter than the protopod, but differs in (1) the absence of a central boss on

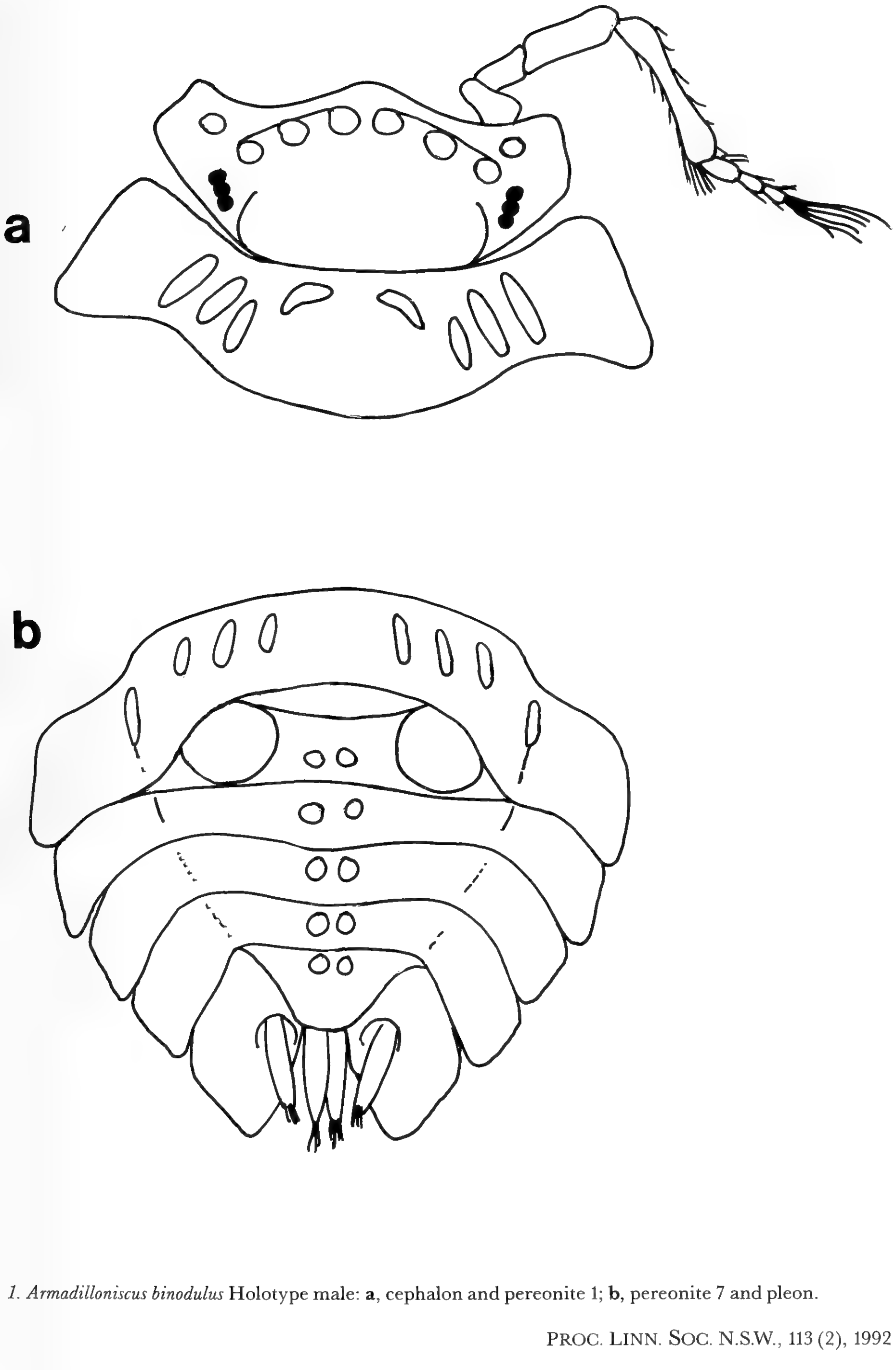

Fig. 1. Armadilloniscus binodulus Holotype male: **a**, cephalon and pereonite 1; **b**, pereonite 7 and pleon.

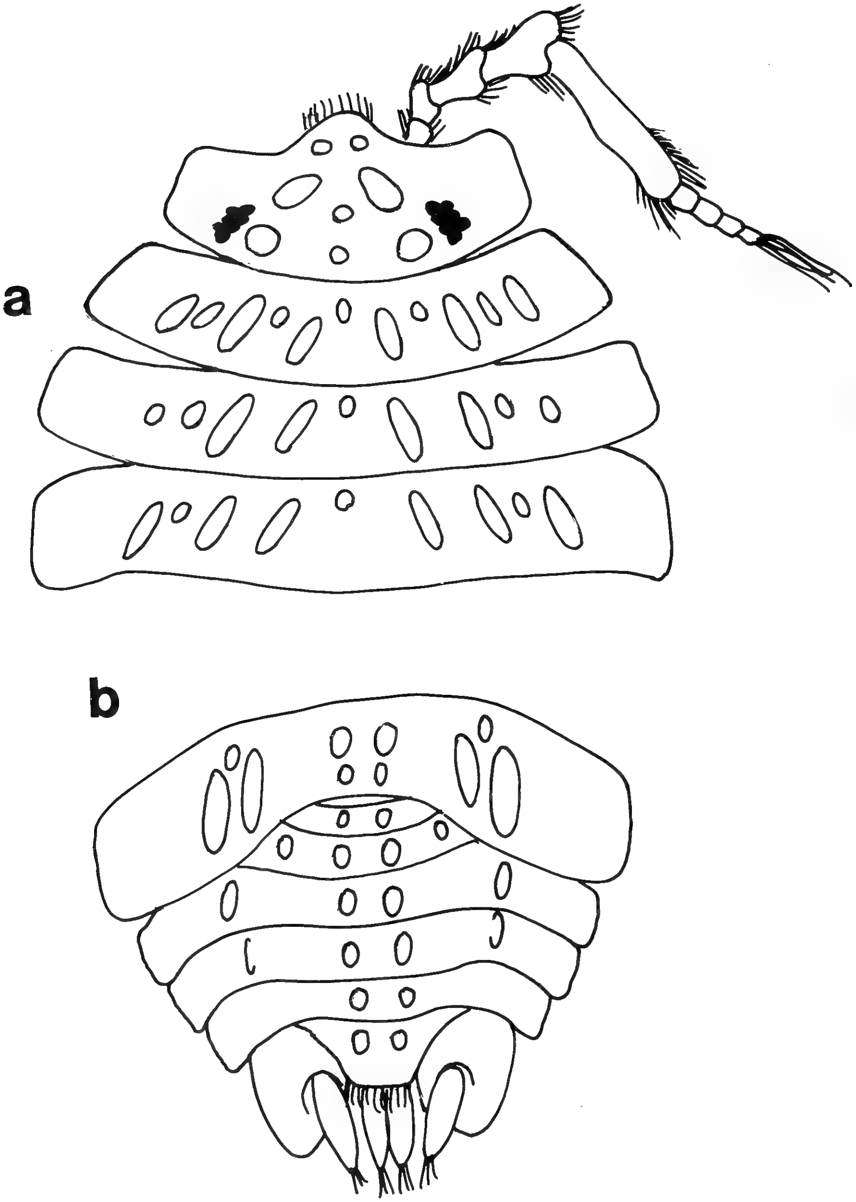

Fig. 2. Armadilloniscus ornatocephalus Holotype female: **a**, cephalon and pereonites 1-3; **b**, pereonite 7 and pleon.

pereonite 1; (2) the absence of tubercles on pleonite 1; (3) the presence of only 3 ommatidia while *A. quadricornis* has 4-5.

Armadilloniscus ornatocephalus differs from the Japanese species in the same features as *A. binodulus*. It is similar to *A. quadricornis* in the presence of a central boss on pereonite 1 and the 2 tubercles on pleonite 1 but differs in (1) the greater number of ommatidia; (2) the exopod being longer than the protopod and (3) the presence of a thick fringe of setae on the joints of the peduncle.

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Revolutus spinosus: A New Genus and Species of Akermaninae (Isopoda: Oniscidea: Armadillidae) from Queensland

FIONA LEWIS

(Communicated by N. N. TAIT)

LEWIS, F. *Revolutus spinosus:* a new genus and species of Akermaninae (Isopoda: Oniscidea: Armadillidae) from Queensland. *Proc. Linn. Soc. N.S.W.* 113 (2), 1992: 157-161.

Specimens of a new species of Akermaninae have been found in two localities of Queensland. They show some similarities to *Laureola* and *Echinodillo* but do not totally agree with the diagnoses of these or any other genera. A new genus, *Revolutus* is proposed for a new species, *Revolutus spinosus* sp. nov.

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INTRODUCTION

Nine genera are presently assigned to the Akermaninae: *Akermania* (Collinge, 1919); *Calmanesia* (Collinge, 1922); *Diploexochus* (Brandt, 1833); *Echinodillo* (Jackson, 1933); *Globarmadillo* (Richardson, 1910); *Laureola* (Barnard, 1960); *Parakermania* (Vandel, 1973); *Pseudolaureola* (Schmalfuss and Ferrara, 1983, *nom. nud*) and *Tridentodillo* (Jackson, 1933) (Green, 1989, pers. comm.).

Australia has representatives from only three of these, *Pseudolaureola* and *Laureola* (Vandel, 1973) — amended by Schmalfuss and Ferrara in 1983 — and *Echinodillo* (Green, 1963). Schmalfuss and Ferrara (1983), also suggest that *Laureola* (Barnard, 1960), may be a synonym of *Echinodillo* (Jackson, 1933).

The new species is an interesting addition to the Australian oniscid fauna requiring the erection of a new genus.

SYSTEMATIC DESCRIPTION

Revolutus gen. nov.

Type species: *Revolutus spinosus* sp. nov.

Diagnosis: Frontal ridge of cephalon cleft medially; eye composed of 13-15 ommatidia; telson cleft posteriorly; 2nd to 7th epimera subquadrate in shape; very small and shallow articulating lobes on 1st and 2nd epimera; tubercles on cephalon and on anterior pereonal segments extended into spines on 4th to 7th pereon and 2nd to 5th pleon segments with those on the pereon being the longest; no median spines or tubercles; telson, uropod protopod and all epimera except 1st recurve strongly upwards in males but less so in females.

The name derives from the shape of the epimera and the tergal ornamentation; revolutus (L) = recurving, spinosus (L) = spiny.

Revolutus spinosus sp. nov.
(Figs 1-3)

Holotype: Male, Australian Museum, Sydney (P39123).

Type Locality: Atherton, Queensland, 17°165′S, 145°29′E; under tree roots on bank of dry creek, September 1988, F. Lewis.

Paratypes: Male and female. Australian Museum, Sydney (P39124); Queensland Museum, (QMW 15791), collection and locality data as for holotype; Tasmanian Museum (G3303), Goldsborough Forest Road/Mulgrave River crossing, near Bellenden Ker, Queensland; in moist leaf litter on river bank, September 1988, F. Lewis.
Size: Length 7 mm, breadth 4 mm. **Colour** (live): pale cream with dark bands along midline and lateral margins of epimera and midline of pleon; antennae dark. **Cephalon:** eye of 13 ommatidia; frontal line of vertex cleft medially and extended laterally into rounded angles; 4 tubercles near midline, 3 larger on each side near eye; posterior margin raised medially. **Second antenna:** short, slender, with scattered setae, 1 large seta on anterior side at distal end of last peduncular article; two articled flagellum shorter than last peduncular article; 2nd flagellar article 3 times longer than 1st, ending in group of long setae joined for most of length. **First maxilla:** bilobed, outer lobe longer, terminating in 9 curved teeth of varying size, 4 largest outer teeth heavily chitinized, inner lobe terminating in 2 short, stout, setose pencils. **Maxilliped:** endite terminating in 3 long tufts of setae with tooth on inner side; the endopod with large pencil and 2 long spines on inner side, 1 spine on outer side at base. **Pereon** pereonites lightly granulated, small rounded scales cover dorsal surface; tergites distinctly decorated with tubercles extended into long spines on segments 4-7. Epimera without tubercles, increasingly upturned posteriorly, lateral borders thin; all except 1st subrectangular; epimeron 1 extends anteriorly below eyes with posterior angle extended into rounded point; lateral border not thickened, small, shallow, articulating lobes on ventral surfaces of first 2 epimera. **Pereopods:** merus, carpus and propodus, shorter and stouter on pereopods 1-2, all have fine scattered setae and large spines on inner margins, dactylus terminating in chitinous claw with 2 spines on inner side on all pereopods. **Pleon:** pleonites 1 and 2 visible dorsally; epimera 3-4 squarely truncated and upturned; epimera 5 narrow, produced into rounded point also upturned; pleonites 2-5 with 2 tubercles extended into spines on posterior borders. Lateral margins of telson indented, posterior margin deeply cleft forming 2 upturned, pointed lobes; 2 tubercles near anterior border of telson. **First pleopod:** exopod approximately oval; posterior margin slightly produced into 3 lobes; endopod apex slightly upturned. Tracheal area on outer part of all exopods. **Second pleopod:** exopod with medial border extended posteriorly to point, spines along convex lateral border; endopod longer, very slender. **Third pleopod:** exopod with medial border slightly extended posteriorly; this extension decreases progressively in pleopods 4-5 which are otherwise similar to pleopod 3. **Uropod:** protopod extended into long lobe with concave lateral margin; exopod ½ length of lobe, inserted dorsally, terminates in bunch of long setae; endopod longer than exopod, shorter than lobe; terminating in bunch of long setae.

Remarks

Females differ from the above description as follows: the epimera are less upturned and the spines are shorter (Figs 3**b**, 3**c**). Breeding specimens have a triple branching broodpouch cotyledon centrally positioned on each of segments 2-5. The number and position of cotyledons has been found to be characteristic of a species (Lewis, 1991).

The species diagnosis is the same as the generic diagnosis.

DISCUSSION

The oniscids from Atherton and Bellenden Ker represent a new species which cannot be placed in any of the nine existing genera, according to the generic diagnoses which are current (Green, 1989, pers. comm.).

They have some characters diagnostic of the three Australian genera but the subquadrate shape of the 2nd to 7th epimera and the cleft cephalon and telson exclude

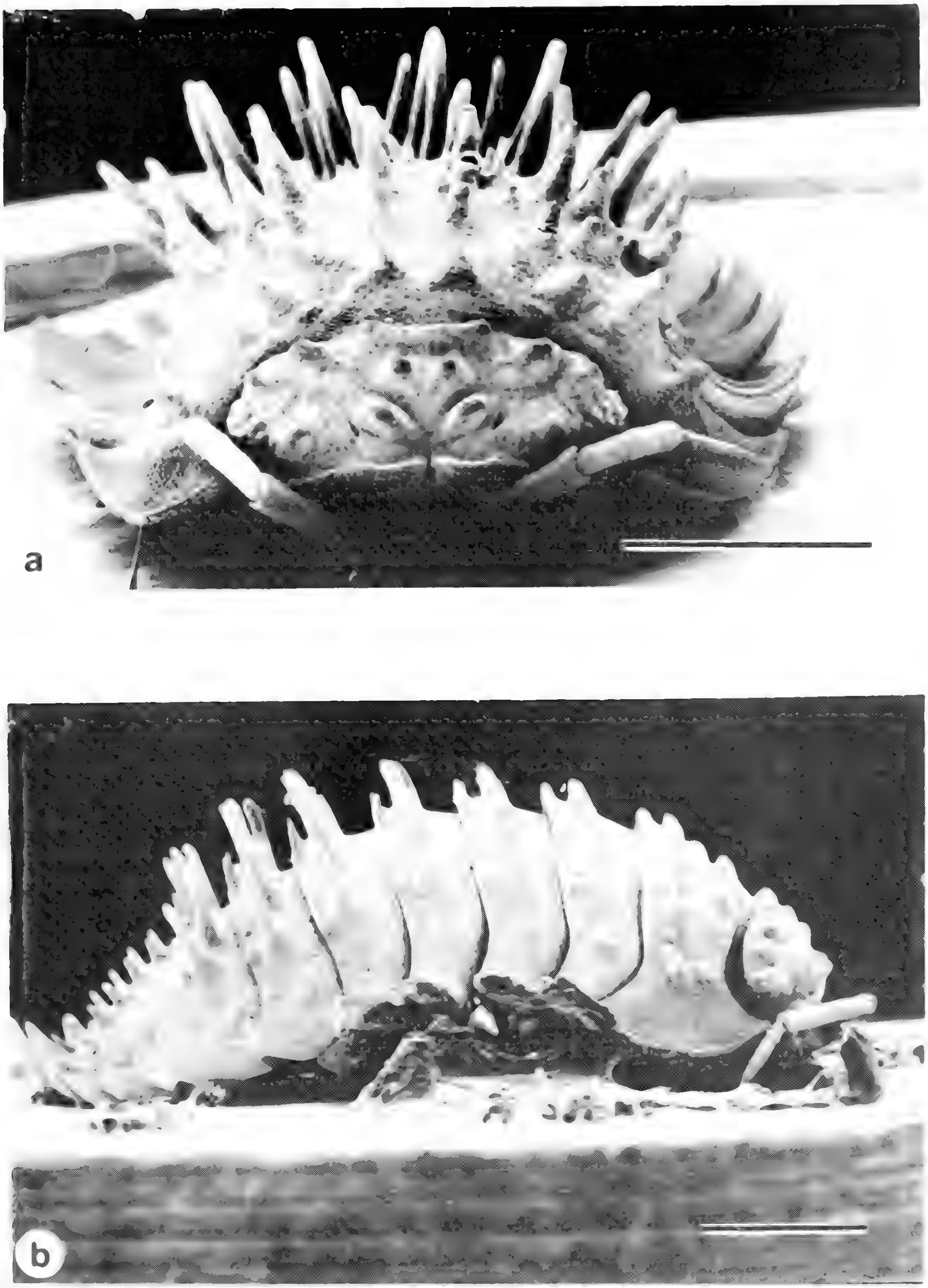

Fig. 1. Revolutus spinosus sp. nov.: **a**, anterior view of whole animal (Scale bar = 1 mm); **b**, lateral view of whole animal (Scale bar = 1 mm).

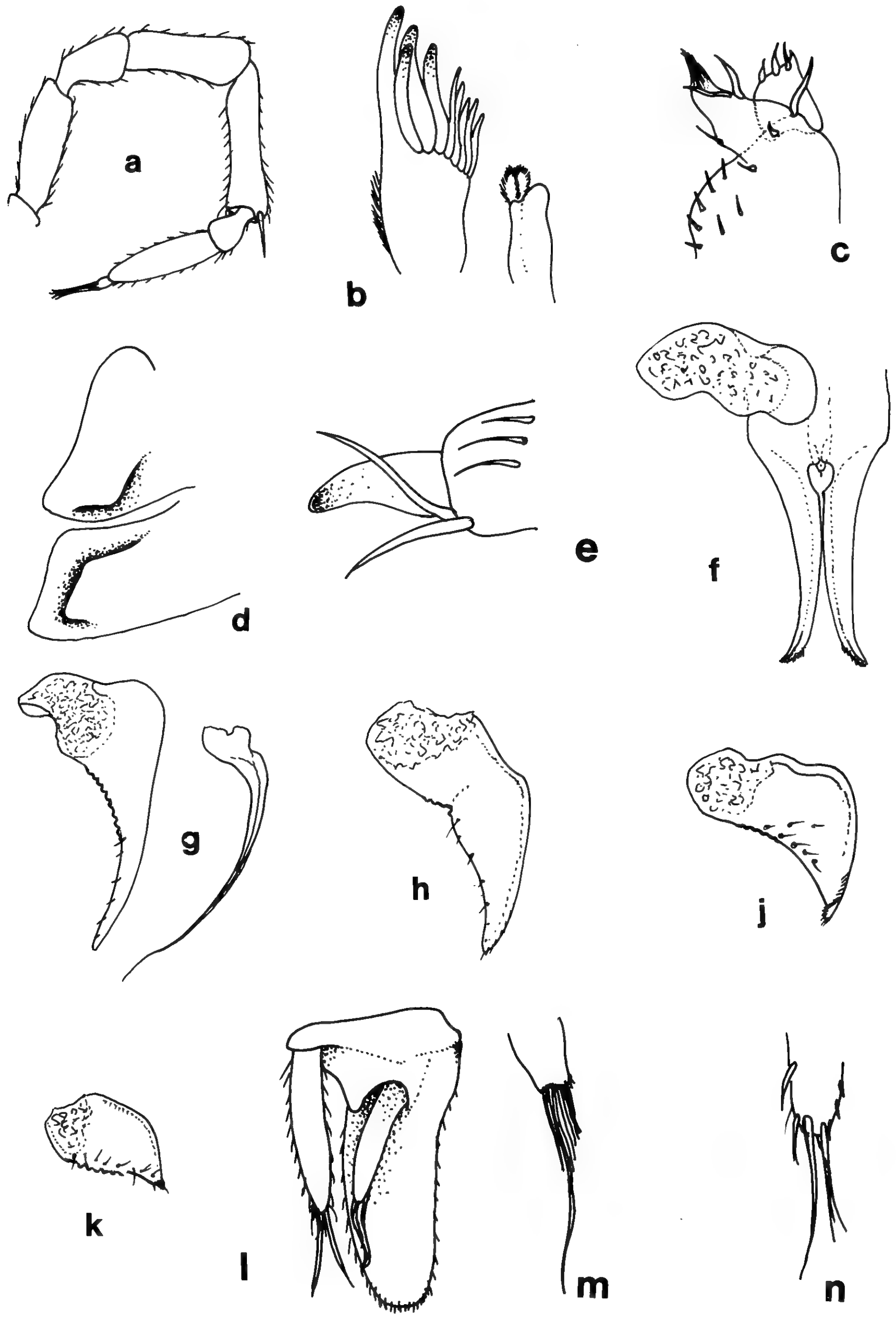

Fig. 2. Revolutus spinosus sp. nov.: **a**, antenna 2; **b**, maxilla 1; **c**, maxilliped; **d**, ventral surface of epimera 1 and 2; **e**, pereopod 1 dactylus; **f**, pleopod 1, exopod and endopod; **g**, pleopod 2, exopod and endopod; **h**, pleopod 3, exopod; **j**, pleopod 4, exopod; **k**, pleopod 5, exopod; **1**, left uropod; **m**, tip of uropod exopod; **n**, tip of uropod endopod.

them from all three genera, while the presence of uropod exopods excludes them from *Pseudolaureola*.

A new genus is therefore proposed with the type species *Revolutus spinosus* sp. nov.

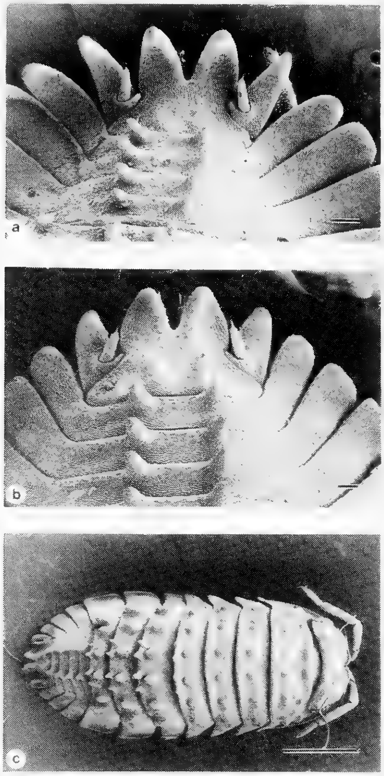

Fig. 3. Revolutus spinosus sp. nov.: **a**, pleon of male (Scale bar = 100 μmm); **b**, pleon of female (Scale bar = 100 μm); **c**, dorsal view of female (Scale bar = 1 mm).

ACKNOWLEDGEMENTS

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The Troglobitic Spider Genus *Tartarus* Gray with a Cladistic Analysis of *Tartarus* and *Baiami* Lehtinen (Araneae: Stiphidiidae)

M. R. GRAY

GRAY, M. R. The troglobitic spider genus *Tartarus* Gray with a cladistic analysis of *Tartarus* and *Baiami* Lehtinen (Araneae: Stiphidiidae). *Proc. Linn. Soc. N.S.W.* 113 (3), 1992: 165-173.

The troglobitic spider genus *Tartarus* Gray is reinstated for four species of spiders from caves on the Nullarbor Plain, W.A. They are *T. mullamullangensis* Gray 1973, *T. nurinensis* sp. nov., *T. murdochensis* sp. nov., and *T. thampannensis* sp. nov. A cladistic analysis of the genera *Tartarus* and *Baiami* Lehtinen is presented. Prey catching behaviour of *T. nurinensis* is recorded.

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INTRODUCTION

Gray (1981) redefined the genus *Baiami* Lehtinen 1967, which limited its distribution to southern Australia. This redefinition included the placement of the monotypic genus *Tartarus* Gray 1973 as a junior synonym of *Baiami*; *T. mullamullangensis* Gray 1973 was regarded as a troglobitic species of *Baiami* with some aberrant characters. These characters included the web structure, cheliceral tooth pattern (3-5 retrolateral teeth in *Tartarus* but only 2 widely separated in *Baiami*) and the fovea shape. The discovery of additional troglobitic species sharing these characters has acted as an argument for the validation of the genus *Tartarus* Gray. The shift in web structure/prey capture behaviour is the clearest synapomorphy for the species comprising this genus. *Baiami* is here limited to south-western and south-eastern Australia with the Nullarbor karst discontinuity being occupied by *Tartarus*.

Three species of troglobitic spiders have been described from caves on the Hampton Tableland area of the Nullarbor Plain. These comprise: a mygalomorph, *Troglodiplura lowryi* Main 1969; a ctenid hunter, *Janusia muiri* Gray 1973 (tentatively reallocated to the Ctenidae from the Miturgidae by Gray, 1990); and *Tartarus mullamullangensis*, a sedentary web builder. The new species described in *Tartarus* were collected in caves on both the Hampton Tableland and the adjacent Roe Plains. It is notable that the most diverse troglobitic fauna of the Nullarbor region occurs on the Roe Plains in Nurina Cave (6N46). This diversity may be associated with the prevalence of more mesic surface conditions on the coastal Roe Plains during much of its Quaternary history, compared with the older (mid-Tertiary) but dryer Hampton Tableland to the north.

SYSTEMATIC DESCRIPTIONS

Abbreviations for institutions are as follows: AM, Australian Museum, Sydney; SAM, South Australian Museum, Adelaide; WAM, Western Australian Museum, Perth. Spine counts are designated in the following way: prolateral, p; retrolateral, r; dorsal, d; ventral, v.

FAMILY STIPHIDIIDAE

Genus **Tartarus** Gray 1973

Tartarus Gray 1973: 210. Type species *T. mullamullangensis* Gray 1973.

Diagnosis: Eyeless, unpigmented, cavernicolous spiders. Legs very long, tarsi curved. Retro-margin of fang groove with 3-5 teeth. Fovea pitlike. Web with the form of a wide, suspended funnel ('lampshade' shaped).

Description: Medium-sized, long legged troglobitic spiders closely related to the genus *Baiami* Lehtinen. Eyes and pigmentation absent (cephalothorax and legs pale amber, abdomen white with off-white mid-dorsal heart stripe). Caput prominent, narrow, with frontal ridge in ocular area. Fovea pit-like. Cheliceral groove with 4-6 prolateral and 3-5 retrolateral teeth. Plumose hairs numerous. Legs slender with curved tarsi and variably reduced spination. Calamistrum placed in third quarter of metatarsus, about one-sixth of metatarsus length. Cymbium of male palp with a basal process. Median apophysis absent. Embolus thin and marginal with a wide semi-circular membraneous conductor. Palpal tibia with 2 retrolateral processes. Epigynum with a deep central fossa. Internal genitalia with short coiled ducts and a pair of ovoid receptacula, bluntly pointed anteriorly. Web a broad funnel narrower basally ('lampshade shaped'), inside which the spider sits upon the substrate attachment.

Included Species: *Tartarus mullamullangensis* Gray, *T. nurinensis* sp. nov., *T. murdochensis* sp. nov., *T. thampannensis* sp. nov.

Distribution: Caves of the Hampton Tablelands and Roe Plains in the Madura-Mundrabilla region, Nullarbor Plain, Western Australia.

Tartarus mullamullangensis Gray 1973

(Figs 1, 2)

Tartarus mullamullangensis Gray 1973: 211, figs 6, 9, pl. 1.
Baiami mullamullangensis (Gray): Gray 1981: 792, figs 22, 27, 45, 46.

Types: Holotype male (SAM, BS1860), Dome Chamber, Mullamullang Cave (6N37), Hampton Tableland, Nullarbor Plain, Western Australia, 10.1.1969, P. Hawkes. Paratypes, 2 juveniles (AM, KS5 and KS6), 4.1.1972, G. Sjoberg and M. Gray (KS5), 25.12.1969, M. Gray and B. Muir (KS6); other data as above.

Diagnosis: Legs 1243 (male). Leg spines fewer compared with *Baiami* spp. and *T. murdochensis*. Spines small in size in juveniles (and, by inference, in females). Carapace length ca 5.6, caput long, narrow. Fovea an elongate pit, widest anteriorly. Male palp as in Figs 1, 2.

Distribution: Type locality only, Hampton Tableland, Western Australia. The type specimens were taken in the most remote part of Mullamullang Cave (Dome Chamber, ca 4 km from entrance), but remains of a male spider and traces of silk were found near The Sail, a rock feature ca 2 km from entrance.

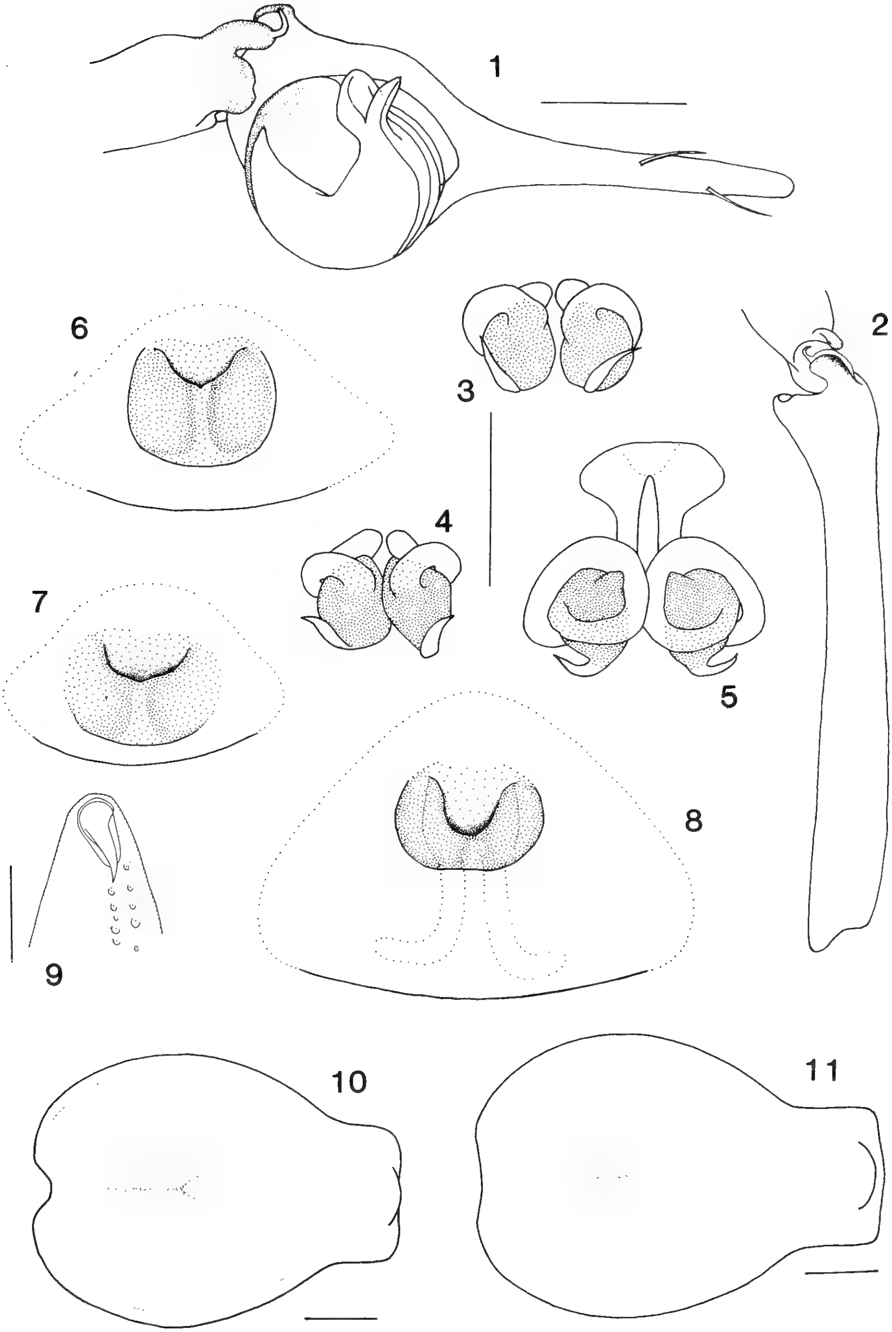
Tartarus nurinensis sp. nov.

(Figs 5, 8, 9)

Types: Holotype female (WAM, 85/1275), Nurina Cave (6N46), Roe Plains, Western Australia, 2.9.1985, N. Poulter.

Diagnosis: Legs 1243 (female). Spination reduced compared with *T. murdochensis*, ventral tibial spines absent. Spines long, slender. Caput long. Posterior margin of epigynal fossa deeply procurved. Copulatory ducts straight proximally, coiled distally once around receptacula.

Description: Female. Carapace length 6.35, width 4.50; (abdomen damaged). Caput long, narrow. Chelicerae with 5-6 promarginal and 4-5 retromarginal teeth. Fovea a longitudinal pit. Carapace posterior margin weakly indented. Legs 1243.



Figs 1-11. Tartarus spp. **1**, **2**, *T. mullamullangensis* male palp: **1**, bulb, ventral; **2**, tibia, retrolateral. **3-5**, female internal genitalia: **3**, **4**, *T. murdochensis* — **3**, Murdoch Sink, **4**, Cave 6N194; **5**, *T. nurinensis*. **6-8**, epigyne: **6**, **7**, *T. murdochensis* — **6**, Murdoch Sink, **7**, Cave 6N194; **8**, *T. nurinensis*, cheliceral tooth pattern. **10**, **11**, carapace: **10**, *T. thampannensis*; **11**, *T. murdochensis*. Scale lines: Figs 1-9, 0.5 mm.; Figs 10 and 11, 1.0 mm.

	1	2	3	4	Palps
Femur	18.50	14.65	12.45	14.75	3.50
Patella	2.53	2.50	2.30	2.35	0.96
Tibia	18.85	15.20	12.05	13.50	1.71
Metatarsus	20.50	17.20	14.00	17.10	—
Tarsus	9.00	7.20	5.15	5.90	2.59
	69.38	56.75	45.95	53.60	8.76

Spination. Spines long. Tibial ventral spines absent. Leg 1, femur p01010 r101101 d1101000; tibia p10110 r11110; metatarsus p1101 r1010101 v001001. Leg 2, femur p11101 r11111 d111010; tibia p0110 r111110; metatarsus p11001 r101001 v11010101. Leg 3, femur p11101 r11101 d110100; tibia p1110 r11110; metatarsus p10101 r1111 v20201. Leg 4, femur p1100 r0011 d111100; tibia p01110 r11110; metatarsus p111101 r100101 v020121. Female genitalia, Figs 5, 8. Posterior margin of epigynal fossa deeply procurved, U-shaped. Copulatory ducts straight proximally, coiled once around receptacula distally and inserted laterally.

Distribution: Type locality only, Roe Plains, Western Australia.

Tartarus murdochensis sp. nov.

(Figs 3, 4, 6, 7, 11)

Types: Holotype female (AM, KS 18430), Phyllistine Flattener Cave (6N194), Hampton Tableland. Nullarbor Plain, Western Australia, 11.7.1985, D. Mitchell. Paratype female (AM, KS 18431), Murdoch Sink (uncatalogued cave), 2 km from 6N194, other data as above.

Diagnosis: Legs 1423 (female). Legs strongly spined. Caput shorter than in other species. Fovea elongate. Epigynal fossa with shallowly procurved posterior margin, copulatory ducts short.

Description: Female. Carapace length 4.55 (3.73), width 3.58 (2.75). Abdomen length 4.94 (4.15), width 3.33 (3.10) (paratype female in parenthesis). Caput normal (not elongate). Chelicerae with 4-6 promarginal and 3-4 retromarginal teeth. Fovea an elongate, narrow pit. Carapace posterior margin strongly indented. Legs 1423.

	1	2	3	4	Palp
Femur	14.30	10.75	9.50	11.80	2.87
Patella	1.90	1.65	1.60	1.60	0.79
Tibia	15.60	11.10	9.25	11.30	1.39
Metatarsus	15.80	11.10	9.65	12.50	—
Tarsus	—	4.90	3.95	5.50	2.12
	>47.6	39.50	33.95	42.70	7.18

Spination: Leg 1, femur p11101 r0111 d21100; tibia p01110 r11110 v1220; metatarsus p11000 r10100 v20202. Leg 2, femur p1111 r1111 d11100; tibia p01110 r11110 v2220; metatarsus p1101 r10101 v11113. Leg 3, femur p1111 r1011 d11100; tibia p01010 r01110 d10000 v2110; metatarsus p1102 r1102 v2011. Leg 4, femur p01001 r01111 d11100; tibia p00010 r01010 d10000 v10000; metatarsus p1112 r10012 v0111. Posterior margin of epigynal fossa shallowly procurved. Copulatory ducts short, curved over anterolateral receptacula surfaces to ventral insertions.

Distribution: Type locality and Murdoch Sink, Hampton Tableland, Western Australia.

Tartarus thampannensis sp. nov.

(Fig. 10)

Types: Holotype juvenile female, penultimate instar (AM, KS16918), Thampanna Cave (6N206), Mundrabilla Station, Hampton Tableland, Nullarbor Plain, Western Australia, II.9.1985, J. Geehan.

Diagnosis: Like *T. mullamullangensis* but fovea much wider. Caput long. Legs 1243. Leg spination sparse and spines reduced in size.

Description: Female (juvenile). Carapace length 4.77, width 3.35. Abdomen length 7.8, width 3.9. Chelicerae with 6 promarginal and 4 retromarginal teeth. Carapace with long narrow caput, not deeply indented posteriorly. Fovea very open, half as wide as long. Legs 1243.

	1	2	3	4	Palp
Femur	13.68	11.11	9.07	11.01	3.30
Patella	1.99	1.94	1.89	1.89	0.97
Tibia	14.70	10.72	9.36	11.16	1.94
Metatarsus	15.04	12.84	10.67	12.90	—
Tarsus	7.08	5.63	4.32	4.75	2.91
	52.49	42.24	35.31	41.71	9.12

Spination: Spines few and small. Leg 1, femur p0001000, d1101000; tibia p0001010, r10101010; metatarsus p1010001, r1010001, v0000100. Leg 2, femur p010100, r100000, d110000; tibia p0101010, r1010110; metatarsus p101001, r1010101, v001100. Leg 3, femur p111000, r100000, d111000; tibia p01010, r111010; metatarsus p1010101, r101101, v0200211. Leg 4, femur p100000, r(1)00000, d111000; tibia p10010, r01010; metatarsus p10101101, r1000101, v0000201.

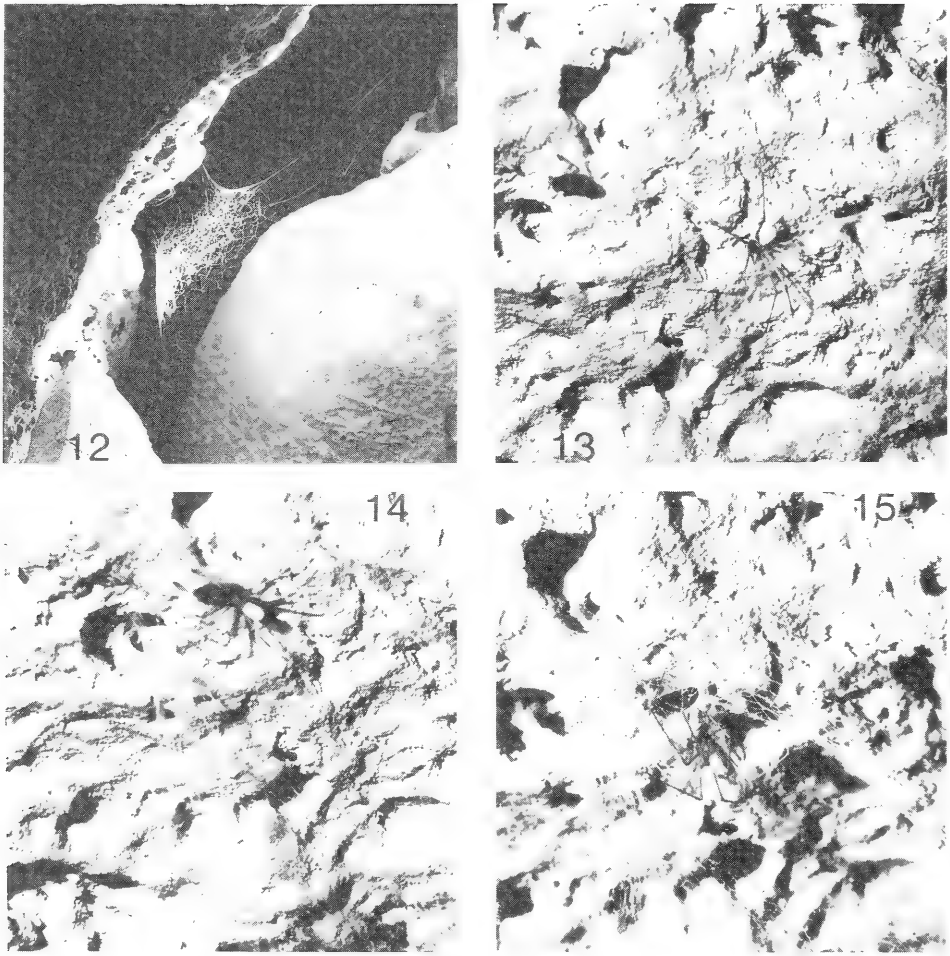
Distribution: Type locality only, Hampton Tableland, Western Australia.

Note on Material: Description of species from juvenile material is not desirable but is justified here because: unique characters are demonstrable; ecophysiological constraints mean that species distributions in this genus are extremely localized — as demonstrated here isolated cave systems on the Nullarbor Plain can harbour unique species of *Tartarus*, whether through *in situ* genetic isolation or attenuated underground dispersal; material from these caves is both rare and rarely collected.

PREY CAPTURE IN *TARTARUS*

The general structure of the web of *T. mullamullangensis* with its distinctive broad, funnel-like structure was noted by Gray (1973, 1981). Webs noted in Thampanna and Nurina Caves were of similar structure. The basal half of the web funnel consists of longitudinal support lines attached to the rock wall and connected by irregularly placed cross lines. These form a protective and prey sensing palisade within which the spider sits head down and motionless on the rock wall, its tarsi touching the web perimeter. The lace-like cribellar catching silk is confined to the wider proximal half of the funnel (Fig. 12).

Winged invertebrates do not occur in the deep regions of the Nullarbor caves so that it can be assumed that the *Tartarus* snare is adapted for the capture of ambulatory prey. Its large circular basal wall attachment may maximize the chances of substrate wandering prey coming into contact with the web from any direction. In Nurina Cave four troglobitic arthropods are potential prey animals: a carabid beetle, a cockroach, a centipede and an isopod. One abandoned web had a cockroach cuticle hanging from it (no prey wrapping was evident).



Figs 12-15. T. nurinensis, web and prey capture: **12**, lateral view of 'lampshade' web, spider on rock wall at base of web; **13**, spider in hunting position at base of web, tarsi on web perimeter, cockroach prey approaching web from left; **14**, spider seizing prey and pulling silk down over it; **15**, prey being dragged into web.

To observe prey capture, a juvenile cockroach (about 2 cm body length) was captured and released on a rock wall some 5 cm from the base of a *T. nurinensis* web (the web measured approximately 10 and 21 cm across its basal attached and apical open ends respectively, with a funnel length of 15 cm; the female spider was about 1 cm body length).

After release the cockroach ran towards the web, coming into contact with its attached margin opposite the spiders third leg (Fig. 13). The spider, immobile until then, immediately lunged sideways towards the disturbance. In doing this both pairs of long front legs dragged down the upper skirt of cribellate silk on that side over the cockroach and rapidly enswathed it. The front legs and palps were then used to drag the swathed and struggling prey further into the web resulting in greater entanglement. The cockroach was then bitten twice, for 2-3 seconds each time, on the soft lateral abdominal tergal membrane (Fig. 14, 15). After this its movements abruptly ceased. The entire capture process took about 10 seconds.

The spider then hung below the inert cockroach cleaning its jaws and palps. No attempt at prey wrapping was observed and the cockroach was simply left in the damaged web for the remainder of the observation period. The spider moved to the undamaged side of the web and began leg grooming (I and IV especially) combined with periods of alternating waving of each palp for 2-3 seconds. These activities continued for about 10 minutes after which the spider resumed its usual position at the base of the web. Neither feeding nor web repair was observed.

A similar immediate lunge/swathe response was elicited from another spider when the base of its web was briefly touched with a pen tip. Subsequently the spider spent several minutes separating the adherent areas of silk from inside the funnel until the original web shape was restored.

CLADISTIC ANALYSIS OF *BAIMI* AND *TARTARUS*

The species data from which the cladogram (Fig. 16) is derived were analysed with the Hennig '86 program. Data on *Baiami* comes from Gray (1981). Character polarity was determined by outgroup comparison with stiphidiid and desid genera.

Troglobionty is so well established in *Tartarus* that many obvious features are a direct consequence of it (e.g. loss of eyes and pigment, leg elongation). Characters that are not of general occurrence in cave adapted spiders constitute more reliable apomorphies. These include the characteristic *Tartarus* web, a unique adaptation for prey capture in a low energy environment. Other characters, such as leg spine number and size, caput length and fovea width vary markedly between *Tartarus* species and so clearly are not solely consequences of troglobionty.

The characters used in the construction of the cladogram are given below.

1. Fovea shape. The wide, pit-like form of the fovea in *Tartarus* is apomorphic. The plesiomorphic condition is a narrow slit.
2. Web structure. The sheet webs of *Baiami* and desid spiders are plesiomorphic. The funnel or 'lampshade' web of *Tartarus* is apomorphic, perhaps derived by enlargement of the narrow funnel-like retreat area of many sheet web builders. It differs significantly, especially basally, from the 'sombrero web' of *Stiphidium* Simon (Main, 1976).
3. Retrolateral cheliceral teeth. The presence of several retrolateral teeth in *Tartarus* is considered plesiomorphic. The two widely spaced teeth found in *Baiami* are apomorphic (independently present in two desid genera). This reductive trend is supported by the presence of only a single apical retrolateral tooth in some individuals of *B. brockmani* Gray.

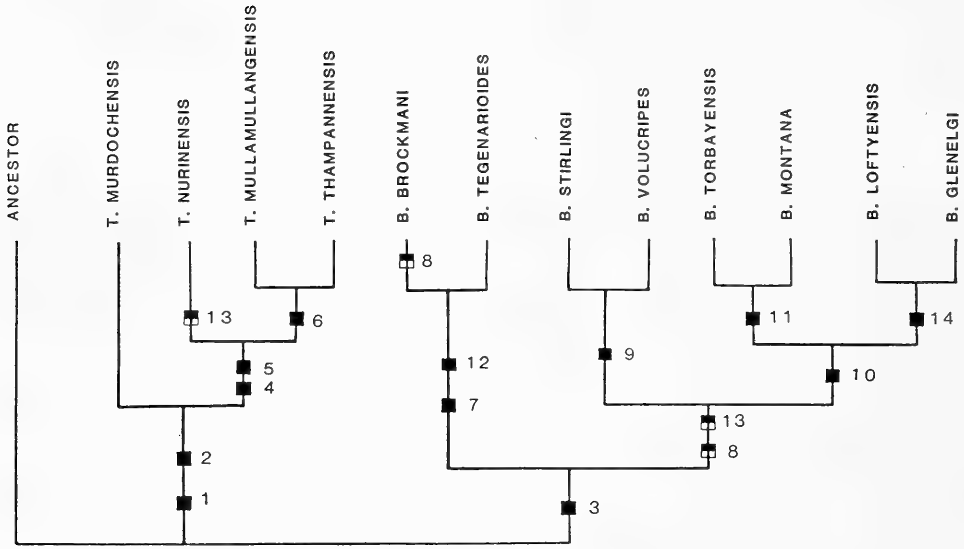


Fig. 16. Cladistic relationships of *Tartarus* and *Baiami* species (Hennig 86; one tree, c.i. 87, r.i. 92).

4. Caput shape. The narrow, long head area or caput seen in some species of *Tartarus* is apomorphic. The presence of a relatively shorter, broader caput in *T. murdochensis* and *Baiami*, the plesiomorphic condition, suggests that the apomorphic condition is not a necessary result of troglobionty.
5. Leg spine frequency. Reduction in the number of spines on all leg surfaces including the absence of ventral tibial spines in some *Tartarus* species is apomorphic.
6. Leg spine size. The very small size of all leg spines in some *Tartarus* species is apomorphic.
7. Cymbium apex. A strongly dorsally reflexed (rather than straight) apical part of the cymbium is apomorphic.
8. Cymbial processes. The presence of cymbial processes is unusual in stiphidiid and desid spiders. A large retrobasal process occurs in *T. mullamullangensis* and *B. tegenarioides* (a smaller additional process also occurs in the latter species). Outgroup comparison suggests apomorphy for presence of processes, requiring independent origin in those species if their respective genera are real. An alternative is that those processes were present in the ancestor of *Tartarus* and *Baiami* and have been secondarily lost (the apomorphic condition) in all but one species in *Baiami*. Both alternatives have been tested and neither alters the structure of the cladogram. The latter alternative is preferred here.
9. Male palpal tibia shape. A very short palpal tibia is apomorphic in stiphidiid spiders.
10. Anterior conductor process. Outgroup comparison indicates that marked attenuation of this process, particularly evident in some *Baiami* spp., is apomorphic.
11. Epigynal fossa. A small external opening into the fossa is apomorphic. Outgroup and ingroup comparison indicate that a broadly open fossa is plesiomorphic.

12. A strongly sclerotized epigynum is apomorphic. Weakly sclerotized epigyna are widespread in the Stiphidiidae and are regarded as plesiomorphic.
13. Copulatory ducts. In some *Baiami* spp. elongate ducts run longitudinally away from the epigynal fossa (apomorphic) rather than curving laterally (a parallel development occurs in *T. nurinensis*).
14. Epigynal atrium. Extension of the epigynal fossa to form a deep posterior atrium (from which the copulatory ducts arise) is apomorphic. A shallow atrium is regarded as the plesiomorphic state.

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Larval Development of the Megabalanine Balanomorph *Megabalanus rosa* (Pilsbry) (Cirripedia, Balanidae)

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CHOI, K. H., ANDERSON, D. T., & KIM, C. H. Larval development of the megabalanine balanomorph *Megabalanus rosa* (Pilsbry) (Cirripedia, Balanidae). *Proc. Linn. Soc. N.S.W.* 113 (3), 1992: 175-184.

The larvae of *Megabalanus rosa* were reared in the laboratory. Naupliar development is planktotrophic, reaching the cyprid stage in 14-16 days at 20°C. Diagnostic features of the stages, including limb setation, are described. The relatively large nauplii, with a smooth, globular dorsal shield, resemble those of *M. tintinnabulum*, but differ from the spinose larvae of *Austromegabalanus nigrescens*. Larval evidence is used to discuss interrelationships of three megabalanine genera.

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INTRODUCTION

Megabalanus rosa (Pilsbry, 1916) has a relatively limited geographical range in the northwest Pacific, being found in the inshore waters of Korea, Japan and Taiwan, with a depth range from the lower littoral to 300 m (Newman and Ross, 1976; Kim, 1985). The species is prominent among the lower littoral fauna of the Korea Strait and East China Sea. Fouling has led to the sporadic spread of *M. rosa* to port waters in other localities such as eastern and western Australia (Jones *et al.*, 1990).

The larval development of *M. rosa* has not been described. Among the megabalanine Balanidae, larval development is known for only one species of the warm water genus *Megabalanus*, *M. tintinnabulum*, and two austral species, *Notomegabalanus agricola* and *Austromegabalanus nigrescens* (Sandison, 1954; Daniel, 1958; Egan and Anderson, 1987). On the basis of this limited evidence, each genus has a distinctive pattern of larval development (Egan and Anderson, 1987), but the account by Daniel (1958) for *M. tintinnabulum* indicates that development in this widespread species is specialized in a number of ways (e.g. very rapid succession of non-feeding naupliar stages; unusually large cyprid) and may not be typical of other species of *Megabalanus*. The present work provides an opportunity to test this question and to extend the comparison of larval development in the megabalanines.

MATERIALS AND METHODS

Megabalanus rosa was collected from rocks and bivalve shells (*Mytilus coruscus*) of the lower littoral of Kadǒck Island, Kyǒngsangnam-do, South Korea. Adults were maintained in the laboratory at 20°C in filtered sea water and fed on *Artemia* nauplii. Release of larvae was observed in February, 1988. Adults were then opened to obtain egg lamellae containing late stage embryos. When transferred to filtered sea water, these lamellae provided a source of newly hatched larvae (Egan and Anderson, 1985).

Some larvae were fixed immediately after hatching. Others were transferred to bowls of filtered sea water at 20°C and fed on *Nitzschia closterium*. Development through six naupliar stages to the cyprid took 14-16 days. Exuviae and specimens of each developmental stage were fixed in 5% neutral formalin.

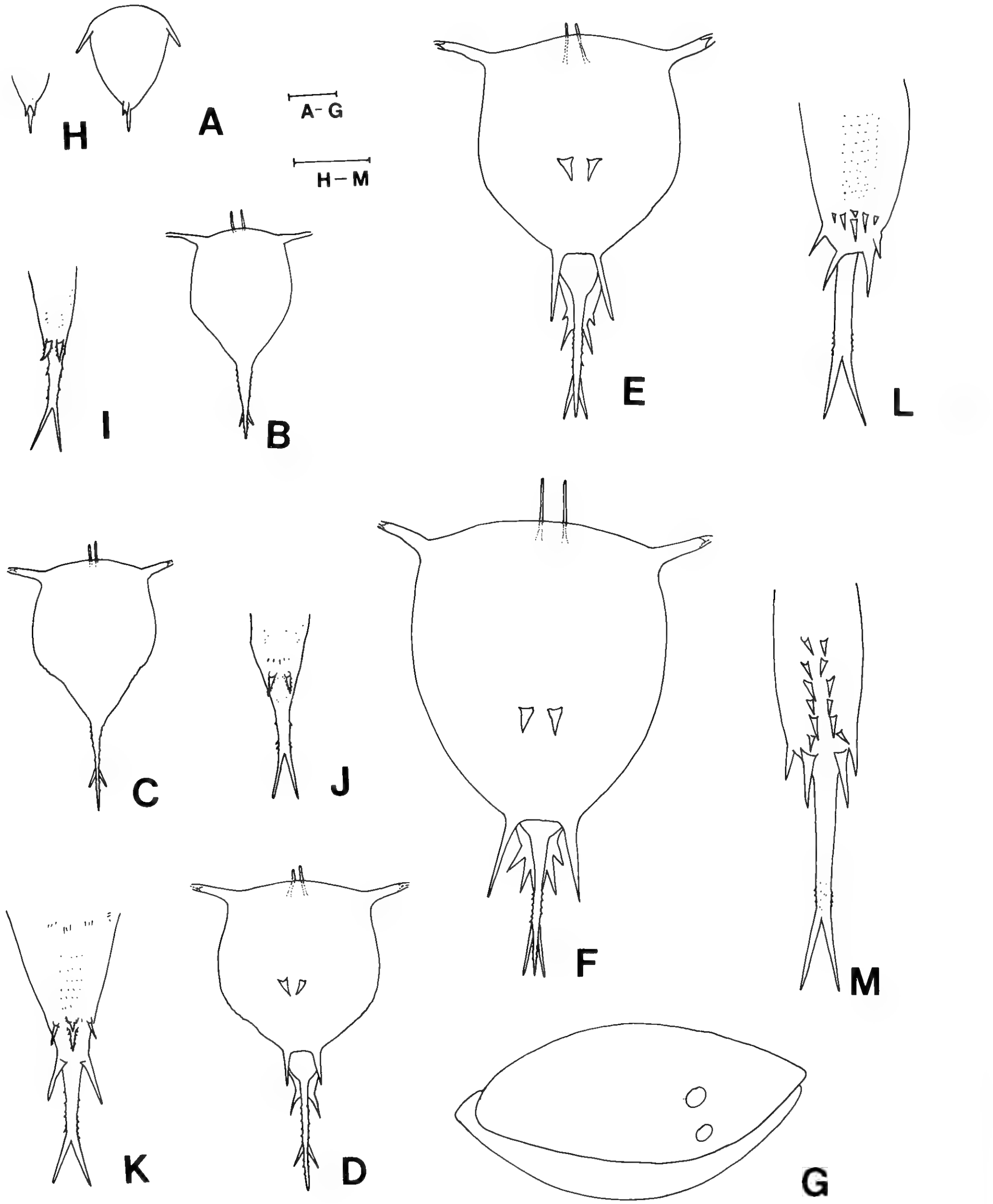

Fig. 1. Megabalanus rosa. Shield outline (dorsal view) of naupliar stages I-VI (**A-F**); thoraco-abdominal process (ventral view) of naupliar stages I-VI (**H-M**); cyprid carapace (lateral view) (**G**). Scale = 0.1 mm.

At least ten specimens of each developmental stage were examined by dissection in a mixture of 70% ethanol:30% glycerine, using fine needles. Either 1% Methyl Blue or 1% Gentian Violet were used for staining. Drawings were prepared using a camera lucida. The developmental stages were distinguished according to the system of Lang (1979). The setal formula and terminology applied to each stage were those of Bassindale (1936) and Branscomb and Vedder (1982).

RESULTS

Larval Morphology

The mean sizes of the larval stages are given in Table 1 and the nauplii are illustrated in Figs 1 and 2. The nauplii of *M. rosa* are relatively large and globular. The body length from the anterior shield margin to the tip of the dorsal thoracic spine is only 1.65-2.0 times the width of the shield. The frontolateral horns are of moderate length, showing a relative increase in length and a development of simple terminal spination in stages IV-VI. The shield margin is smooth in all stages. A single pair of dorsal shield spines is prominent in stages IV-VI, together with a pair of long, smooth posterior shield spines. The dorsal thoracic spine and thoraco-abdominal process are weakly barbed. Furcal spines are typically balanid. The tip of the labrum is square in outline, with a prominent median lobe. The distal margin of the median lobe has serrate setae and small spines in naupliar stages IV-VI.

TABLE 1

Mean size of cultured larval stages of M. rosa.
Abbreviations: n, sample number; TL, total length; SL, shield length; W or D, shield width or cyprid depth.

Stage	n	TL (mm)	SL (mm)	W or D (mm)
Egg	9	0.21		0.15
Nauplius I	11	0.27		0.16
Nauplius II	20	0.47		0.23
Nauplius III	15	0.53		0.29
Nauplius IV	13	0.61	0.37	0.35
Nauplius V	10	0.76	0.46	0.46
Nauplius VI	10	0.98	0.70	0.56
Cyprid	10	0.70		0.35

The diagnostic features of each larval stage can be summarised as follows:

Nauplius I (Figs 1**A**, 1**H**, 2**A**)

Body globular, but generally typical of stage I balanid larvae. Lateral shield margin smooth; dorsal thoracic spine and furcal spines smooth.

Nauplius II (Figs 1**B**, 1**I**, 2**B**, 2**G**)

Shield margin smooth, frontal filaments short, frontolateral horns of moderate length; dorsal thoracic spine barbed, longer than thoraco-abdominal process; smooth series-1 spines present.

Nauplius III (Figs 1**C**, 1**J**, 2**C**, 2**H**)

Morphologically similar to stage II except in size, but with incipient spination at tips of frontolateral horns; first rudiments of maxillae on thoraco-abdominal process; small spines medially between series-1 spines.

Nauplius IV (Figs 1**D**, 1**K**, 2**D**, 2**I**)

Shield with smooth margin; paired, smooth dorsal shield spines and posterior shield spines; frontolateral horns prominent, divided at tips; barbed dorsal thoracic

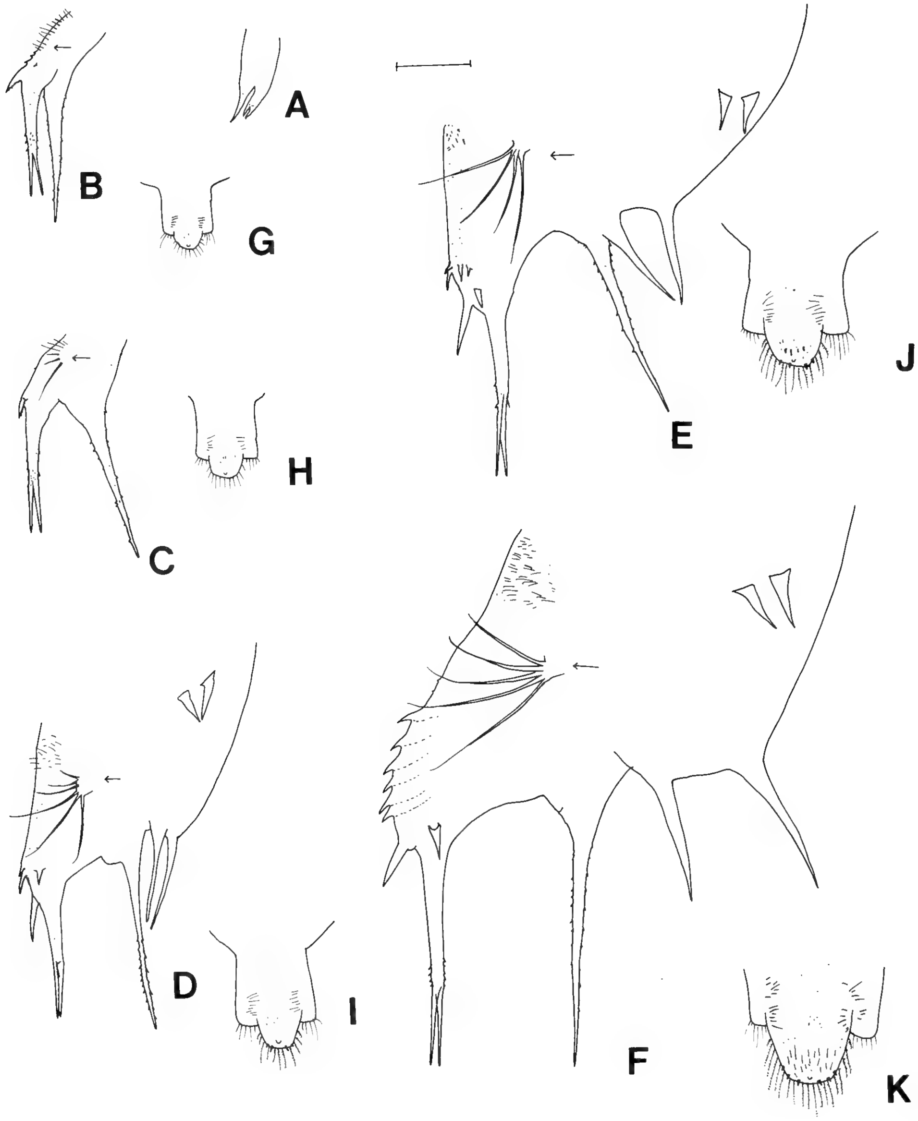

Fig. 2. Megabalanus rosa. Thoraco-abdominal process (lateral view) of naupliar stages I-VI (**A**-**F**); shape of labrum of naupliar stages I-VI (**G**-**K**). Arrow indicates position of maxilla for each naupliar stage. Scale = 0.1 mm.

spine longer than thoraco-abdominal process. Four series-2 spines anterior to long series-1 spines, arranged as paired lateral spines and two median spines in antero-posterior sequence.

Nauplius V (Figs 1**E**, 1**L**, 2**E**, 2**J**)

Morphologically similar to stage IV except in size, but with dorsal thoracic spine now equal in length to thoraco-abdominal process. Long, smooth series-1 spines flanked by a similar pair of series-3 spines; series-2 spines with an additional small pair laterally. Anterior to the series-2 spines, several rows of small spines parallel to the long axis.

Nauplius VI (Figs 1**F**, 1**M**, 2**F**, 2**K**)

Morphologically similar to stage V except in size, but with prominent frontal filaments, and series-1, 2 and 3 spines of thoraco-abdominal process in usual balanoid stage VI pattern. Developing compound eyes conspicuous in older larvae.

Cyprid (Fig 1**G**)

Fusiform, pointed anteriorly and posteriorly, sculptured externally.

Setation of the Appendages

The setal formulae of the antennules, antennae and mandibles of the six naupliar stages of *M. rosa* are given in Table 2 and illustrated in Figs 3**A**-3**F**, 4**A**-4**F** and 5**A**-5**F**. There was almost no variation in setal number among individuals at each naupliar stage. Plumodenticulate setae were present on the endopod of the antennae of stages II-VI, but not on the mandibular endopod of the same stages. A spine was found proximally on the mandibular endopod in stages II-VI.

DISCUSSION

The egg of *Megabalanus rosa* is of greater than average size for a balanid (210 x 150 μm), but larval growth after hatching is dependent on planktotrophy in the normal balanid manner. At 20°C the duration of larval development to the cyprid is 14-16 days, yielding a cyprid of 0.70 mm average length. Larval size and mode of development in *M. rosa* thus conform to the general balanid pattern, but are at the larger end of the size range for planktotrophic larvae of this group.

On the basis of these observations, it seems likely that the development of *M. rosa* represents a generalized condition for *Megabalanus*, and that the unusual features reported by Daniel (1958) for the development of *Megabalanus tintinnabulum* are specializations. *M. tintinnabulum* has a much larger egg (300 x 130 μm), which may account for its ability to develop to the cyprid stage in 26-48 hours without feeding and to produce a large cyprid, 0.82-0.89 mm long.

Egan and Anderson (1987) showed that the three genera of megabalanines represented by *Austromegabalanus nigrescens*, *Notomegabalanus agricola* and *Megabalanus tintinnabulum* each have a distinctive pattern of larval development in respect of naupliar shield shape, marginal shield spines, dorsal shield spines, rate of development, food requirements and size of cyprid (Table 3). When the development of *Megabalanus rosa* is drawn into the comparison, these distinctions remain, in spite of the fact that *M. rosa* has a much more typical larval development than *M. tintinnabulum.* It thus becomes possible to examine, on the basis of larval data, the interrelationships of the three megabalanine genera.

The larval development of *Notomegabalanus agricola*, with an egg size and hatching size similar to those of typical *Balanus* species such as *B. amphitrite* and *B. variegatus* (Egan

TABLE 2

Setal formulae for the nauplii of M. Rosa.

Abbreviations: S, simple; P, plumose; D, plumodenticulate; C, cuspidate; G. gnathobase; sp, spine; S^p*, simple, sometimes plumose; st, setal stub.*

Naupliar stage	**Antennule**	**Antenna**		**Mandible**	
		Exopod	**Endopod**	**Exopod**	**Endopod**
I	SSSS:SS:S:S	S:4S	SSS:SS:SS:SS:G	S:S:S:S	SSS:SS:SS:SS:G
II	SSPS:SP:P:S	SP:4P:S	PPS:SP:PD:SPC:G	P:P:P:P:st	SSS:SP:PCS:spPC:G
III	S:PSPP:SP:P:S	PP:5P	PPP:SP:PD:SPCS:G	P:P:P:P:S	SSS:SPS:PCP:spPPC:G
IV	S:P:PSPP:SP:P:S	PPP:6P	PPPSS:SPS:PD:SPCP:G	P:P:P:P:S^P	SSSS:SPP:PSCP:spPCP:G
V	S:P:P:PSPP:SP:S:P:S	PPP:7PS^P	PPPSP:SPP:PD:SDCP:G	P:P:P:P:P:S	SSSS:SPSP:SPCP:spPPC:G
VI	S:P:P:PSPP:SP:P:PS:S	PPPP:8P	PPPSP:SPP:PD:SPCP:G	P:P:P:P:P:P	SSSS:SPSP:PSCP:spPCP:G

TABLE 3

Larval features of megabalanine genera

Feature	***Austromegabalanus nigrescens***	***Notomegabalanus agricola***	***Megabalanus rosa***	***Megabalanus tintinnabulum***
Feeding	Planktotrophic	Planktotrophic	Planktotrophic	Lecithotrophic
Egg diameters (mm)	0.21 x 0.11	0.15 x 0.11	0.21 x 0.15	0.30 x 0.13
Length/width ratio of nauplius	2.00-2.50	2.00	1.65-2.00	1.20-1.48
Dorsal shield shape	Elongate pentagonal	Elongate globular	Globular	Globular (fat)
Marginal spines	Prominent	Absent	Absent	Absent
Dorsal spines	2, increasing to 4	Absent	2	Absent
Stage VI shield length x width (mm)	0.44 x 0.38	0.46 x 0.38	0.98 x 0.56	0.46 x 0.42 (fat)
Cyprid, length (mm)	0.49	0.50	0.70	0.85
Rate of development	to cyprid, 13-23 days	Not known	to cyprid, 14-16 days	to cyprid, 26-48 hours

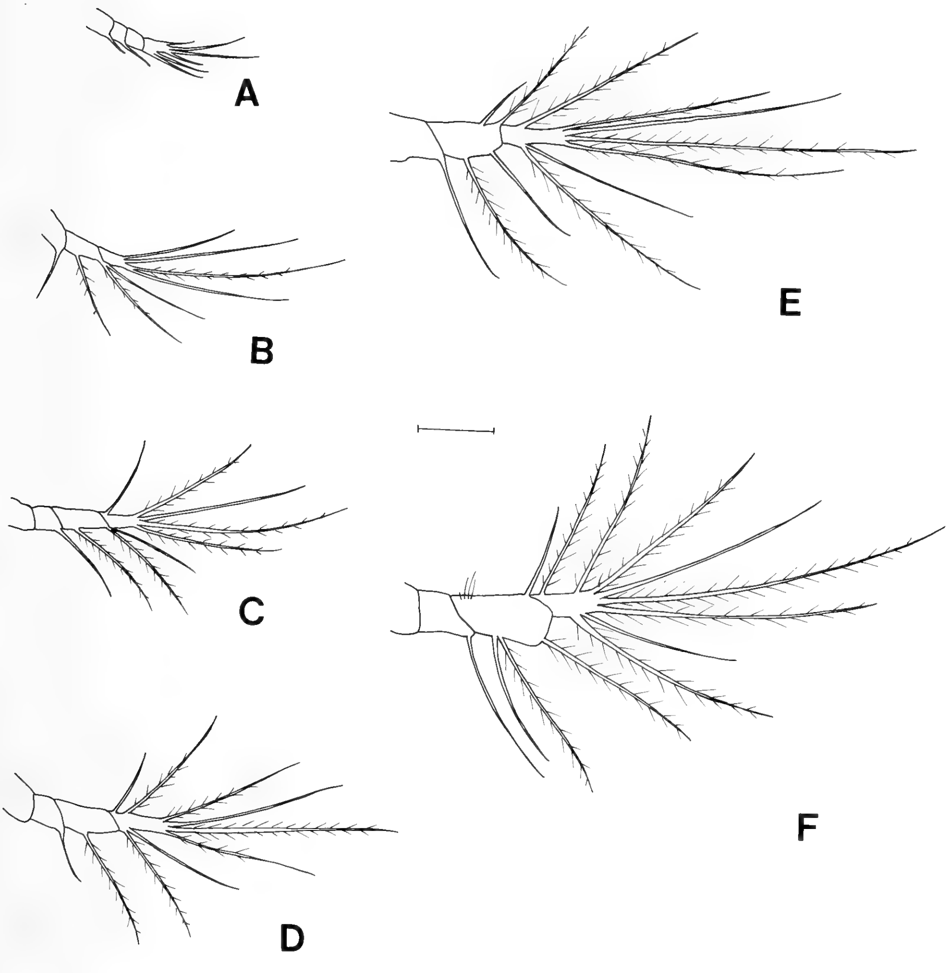

Fig. 3. Megabalanus rosa. Antennule of naupliar stages I-VI (**A-F**). Scale = 0.1 mm.

and Anderson, 1986), differs little from that of the two latter species. The development of *Austromegabalanus nigrescens*, from a larger egg, is distinctive in several ways. The nauplius, although relatively large, is long and narrow, with prominent marginal spines and four dorsal spines on the shield. The resulting cyprid, on the other hand, is no larger than that of *Balanus variegatus*. A better model for the development of *A. nigrescens* may be that of the archaeobalanid genera *Hexaminius and Conopea*, also with a spiny dorsal shield. *Megabalanus rosa*, developing from a somewhat more voluminous egg than that of *A. nigrescens*, presents a sharp contrast. The larvae are more globular, with a smooth shield margin, although they do develop a pair of dorsal shield spines. The emergent cyprid is also larger. These features are further exaggerated in the development of *Megabalanus*

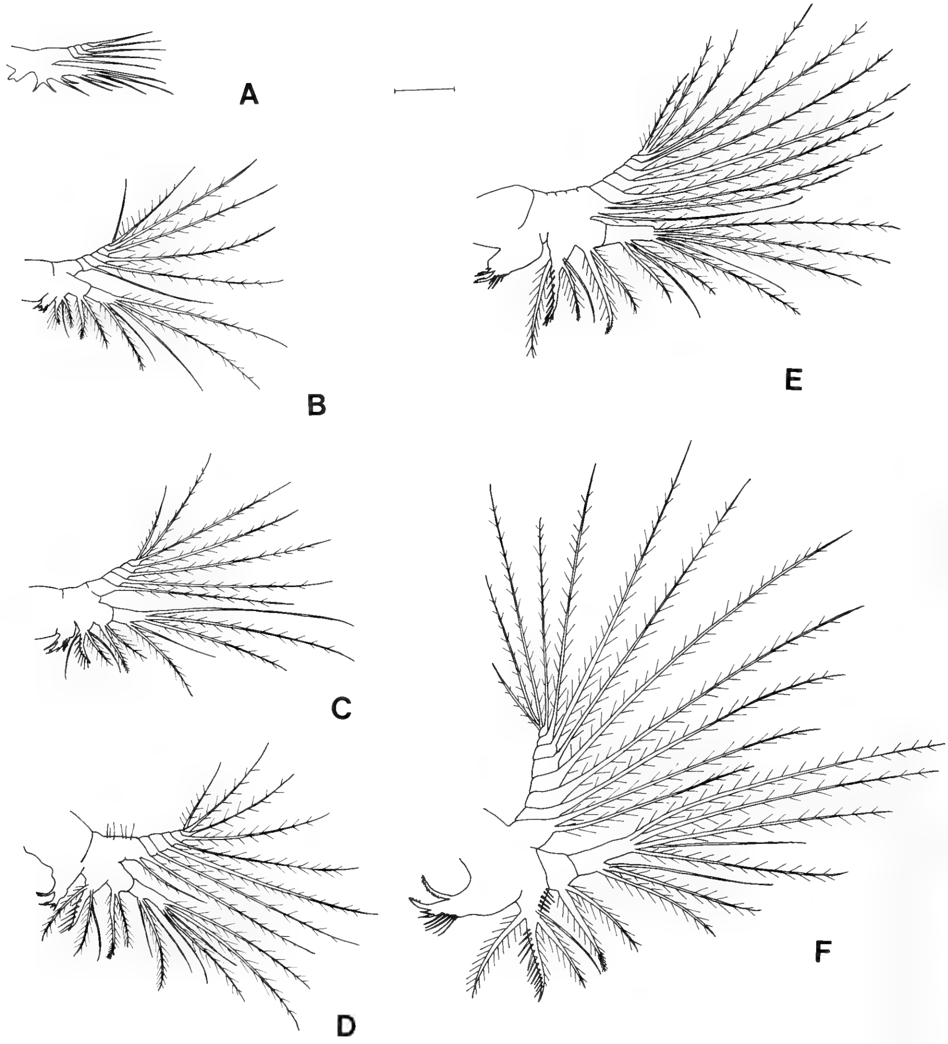

Fig. 4. Megabalanus rosa. Antenna of naupliar stages I-VI (**A-F**). Scale = 0.1 mm.

tintinnabulum, with its large egg, short, fat nauplii, smooth shield lacking dorsal spines, rapid development and large cyprid.

Recent data on sperm ultrastructure (Healy and Anderson, 1990) raised the possibility that *Megabalanus* and *Austromegabalanus* may have had separate origins. The contrasting larval developments of the two genera give further weight to this possibility. The presence of dorsal shield spines on the older nauplii of *M. rosa* seems likely to be a convergent feature, in view of the occurrence of these spines in the unrelated *Balanus venustus* and in the Lepadomorpha (Lang, 1979; Dalley, 1984; Moyse, 1987).

A detailed comparison of larval setation between the two megabalanine species for which sufficient detail is now available, *A. nigrescens* and *M. rosa*, reveals minor differences in the setation of the endopod of the antenna and mandible. The antennal endopod of *M. rosa* has an additional simple seta terminally in nauplius IV-VI. The

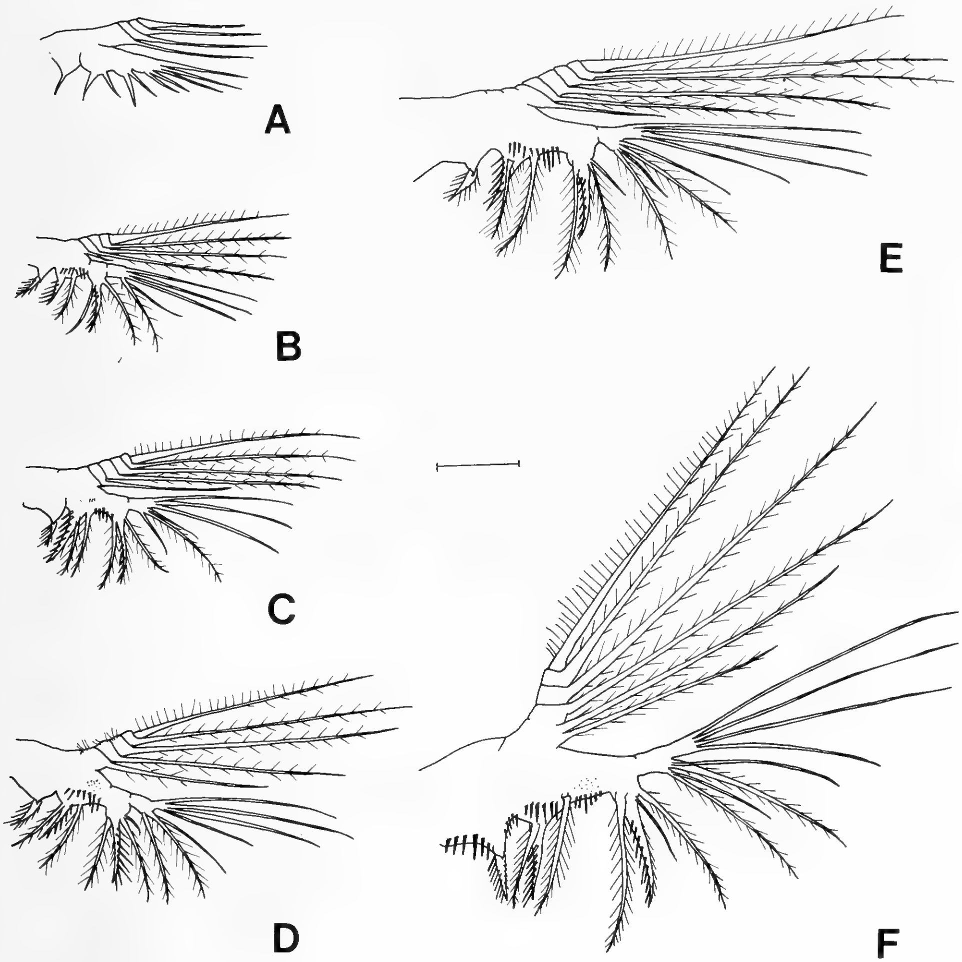

Fig. 5. Megabalanus rosa. Mandible of naupliar stages I-VI (**A-F**). Scale = 0.1 mm.

mandibular endopod of *A. nigrescens* has two plumodenticulate setae in the subterminal group, where *M. rosa* has plumose setae, and sometimes shows a similar replacement of one of the four plumose setae by a plumodenticulate seta in the next most proximal group. In the absence of knowledge of the larvae of other megabalanine species, the significance of these setal differences cannot be fully assessed.

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Lycopodium australianum (Herter) Allan on Subantarctic Macquarie Island

P. M. SELKIRK and R. D. SEPPELT

SELKIRK, P. M., & SEPPELT, R. D. *Lycopodium australianum* (Herter) Allan on subantarctic Macquarie Island. *Proc. Linn. Soc. N.S.W.* 113 (3), 1992: 185-191.

The species of *Lycopodium* on subantarctic Macquarie Island has been variously ascribed to *L. selago, L. varium, L. saururus, L. australianum.* From a careful consideration of the growth habit, general and spore morphology of these species, it is clear that the plant should most appropriately be referred to *L. australianum.*

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INTRODUCTION

Macquarie Island (54° 30′S, 158° 57′E) is an isolated subantarctic island situated about 1580 km SSE of Tasmania, 1130 km SW of New Zealand and 1530km N of the Antarctic continent. The island is approximately 34 km long, 2.5-5 km in width, and 120 km^2 in area. Steep cliffs bound a lake-dotted plateau of about 250 m altitude with peaks to 433 m. The climate is extremely equable, cold, wet and windy. The island lies close to, but north of, the Antarctic convergence.

Vegetation formations have been described by Taylor (1955), with further recent discussion by Seppelt, Copson and Brown (1984), Smith (1984) and Selkirk, Seppelt and Selkirk (1990). Tall tussock grassland predominates on beach terraces and steep coastal slopes. Herbfield occurs on the wetter raised beach terraces and in some upland areas. Short grassland (sub-glacial herbfield of Taylor, 1955) and feldmark, typically with much less than 50% vegetation cover, are widespread on the plateau uplands. The vegetation in much of the feldmark is dominated by bryophytes and cushion plants such as *Azorella macquariensis*. Vegetation patterning in stripes or terraces is common (Selkirk and Seppelt, 1984; Selkirk, Adamson and Seppelt, 1988). There are many ecotonal associations between short grassland and feldmark.

RECORDS OF *LYCOPODIUM* FROM MACQUARIE ISLAND

Since the species was first collected in 1824, the *Lycopodium* from Macquarie Island has been ascribed to *L. selago* (Anon., 1894), *L. billardieri* var. *varium* (Hamilton, 1894), *L. varium* (Cheeseman, 1919), *L. saururus* (Taylor, 1955) and *L. australianum* (Given, 1978). The first recorded collection of plants from the island was made by sealers and forwarded in 1824 by J. H. Fraser, Superintendent of the Sydney Botanic Gardens, to W. J. Hooker at Kew. Attached to a sheet of *Azorella selago* (now *A. macquariensis* Orchard, 1989) was a specimen named *Lycopodium selago* (Anon., 1894).

In 1894 A. Hamilton collected specimens of *Lycopodium* about which he later remarked: 'The habit is like that of *L. selago*, but denser; the leaves are much broader. Seedling plants growing amongst the stems have distant oblong leaves.' (Hamilton, 1894: 569). Kirk identified these specimens as *L. billardieri* Spreng. var *varium* (Hamilton, 1894), equivalent to *L. varium* R. Br. (Cheeseman, 1919). Cheeseman (1919: 41), in examining collections made in 1911-14 by H. Hamilton, stated that the specimens were of the '. . . habit and appearance of *L. selago*, from which they differ mainly in forming dense much-branched compact tufts, often with an even surface at the top. The leaves are larger, broader, and more coriaceous . . . numerous gemmae occur among the leaves . . . the fructification is much more like that of *L. selago* than that of the usual state of *L. varium*, for in most cases the sporangia are produced for a considerable distance down the branches in the axils of unaltered leaves.'

Nomenclatural confusion has persisted in the austral lycopod flora. J. D. Hooker (1864) remarked that Tasmanian specimens of *L. varium* passed confusedly into *L. selago* on the one hand and *L. billardieri* on the other. According to B. Øllgaard (pers. comm.) *L. billardieri* is very closely allied to or even doubtfully distinct from *L. varium*.

Cheeseman (1919) noted that 'true *L. selago* has not yet been definitely recorded from any of the southern circumpolar islands; but the closely allied *L. saururus* Lam. exists in the Falkland Islands, Kerguelen Island, Marion Island, and Tristan d'Acunha.' He considered it possible that the Macquarie Island plant might be referable to *L. saururus*, but that *L. saururus* had stouter stems, and larger and narrower leaves. Cheeseman identified the Macquarie Island specimens as *L. varium*.

Holloway (1919: 167) commented that despite the narrowing of some branch apices (a characteristic of *L. varium*) and leaves that are larger, broader, and more coriaceous than those found on 'typical' *L. selago*, '. . . the presence of bulbils would seem to be an argument in favour of relating this species to *L. selago*.' Taylor (1955) referred Macquarie Island specimens to *L. saururus* on the basis that specimens examined by the Australian National Herbarium were considered identical with specimens of that species from Kerguelen. Jenkin (1972) followed Taylor in applying this name.

In his *Flora of New Zealand*, Allan (1961), in supplementary notes on *L. varium* in New Zealand, equates *L. varium* (*sensu* Cheeseman, 1919) with *L. saururus* (*sensu* Taylor, 1955). However, using his key to species, the Macquarie Island specimens are without question referable to *L. australianum* (Herter) Allan.

Godley (1969: 337) reported a *Lycopodium* sp. from the Auckland Islands with '. . . no differentiated sporophylls, and sporangia were found in one or two whorls about 1 cm below the tips of branches. The specimens match closely the "tussock-country form" or "xerophytic variety" . . . discussed under *L. selago* by Holloway (1919).' Godley (1969: 338) hesitated to name the Auckland Islands plant pending a '. . . detailed study of the status of the "xerophytic" and "mesophytic" (shade) varieties of Holloway, and the relation of the "xerophytic" variety to the lycopod on Macquarie Island, now classified (Taylor 1955) as *L. saururus*.' Johnson and Campbell (1975), in their annotated checklist of the Auckland Islands vascular flora, concurred with Godley (1969) but indicated a relationship to *L. australianum*.

Meurck (1975) reported *Lycopodium* cf. *australianum* from Campbell Island and considered this to match the Auckland Islands *Lycopodium* sp. of Godley (1969). A connection with the *L. saururus* of Macquarie Island (Taylor, 1955) was suggested by the presence of axillary bulbils.

Given (1978: 551) discussed the taxonomic, nomenclatural and morphological relationships of the *L. australianum-varium-selago* group of names in New Zealand thus:

'Meurck (1975) referred to the (Campbell Island) species as cf. *australianum* and suggested that the presence of bulbils in the axils of some leaves might indicate a connection with the Macquarie Island specimens identified by Taylor (1955) as *L. saururus* Lam. Cheeseman (1919) placed all Macquarie Island specimens in *L. varium* and later cited Macquarie, Auckland and Campbell Islands as localities for that species (Cheeseman 1925). However, on Auckland and Campbell Islands there are clearly two entities, the true *L. varium* and a very much scarcer species which I consider to be *L. australianum*. I have not seen specimens from Macquarie Island but descriptions and Fig. 2b of Holloway (1919) suggest that it is very similar to, if not identical with, plants seen on Campbell Island and the *Lycopodium* sp. found on Adams Island, of the Auckland group (Godley 1969). These are almost identical with *L. australianum* of the New Zealand mainland, differing chiefly in having shorter stems. Until Australian mainland and subantarctic collections can be critically compared with authentic specimens of *L. saururus*, it seems best to regard specimens from Campbell, Auckland and Macquarie Islands as belonging to *L. australianum*.'

Greene and Greene (1963), in the checklist of the subantarctic and Antarctic vascular flora, list two species of *Lycopodium* in the subantarctic zone. Greene and Walton (1975) published a revised and annotated checklist, including records of both *L. magellanicum* and *L. saururus* for Prince Edward Island and replacing *L. saururus* by *L. varium* for Macquarie Island. Nomenclatural uncertainty makes it difficult to evaluate the distribution of *Lycopodium* species in the subantarctic region but it appears that three species occur there (Table 1).

TABLE 1

Distribution of Lycopodium *species on subantarctic islands.*
Data sources are as follows: x *Greene and Greene (1963);* + Greene and Walton, (1975); * (this paper).

Species	South Georgia	Prince Edward Is.	Marion Is.	Iles Croz.	Iles Kerg.	Macquarie Is.
L. australianum						*
L. magellanicum	x	+	x	x	x	
L. saururus		+	x	x	x	

DESCRIPTION AND STATUS OF *LYCOPODIUM* ON MACQUARIE ISLAND

On Macquarie Island, the *Lycopodium* grows as small clumps of upright stems to about 10 cm tall (Fig. 1). Branches arising from the erect stems appear whorled. Leaves are up to about 6 mm long, 2-3 mm broad, tapering to a point, stiff, crowded on branches. Sporangia occur singly, in the axils of unaltered leaves, borne towards the apex of stems but not aggregated into a distinct strobilus. Numerous axillary bulbils are found near the tips of stems.

Although sporangia and spores are produced, reproduction appears most commonly to be vegetative, via the abundant deciduous bulbils, or gemmae. Lateral spread of these propagules from a parent plant appears to be limited to a few centimetres, with the propagules dropping off the shoots into the surrounding vegetation. On sprouting, propagules produce a strong tap root (Fig. 2) which quickly develops into a dense fibrous root system. No horizontal rhizome system is produced.

This *Lycopodium* has been a component of the Macquarie Island flora throughout the Holocene: fossil spores (Fig. 3) are abundant in a lacustrine deposit, Palaeolake Nuggets, in strata which have been dated at up to 9400 ± 220 radiocarbon years B.P. (Selkirk *et al.*, 1988).

Our recent field surveys confirm that *Lycopodium* deserves its rare status (Copson, 1984) on Macquarie Island although it is more widespread and locally abundant than previously thought (Fig. 4). Taylor (1955) indicated that *Lycopodium* occurred only in his *Azorella selago* alliance and was 'never found in other communities'. He observed the species in only a dozen localities on the island. 'Where it does grow, two or more plants are generally close together. Of 100 plants seen in the whole of 1950-51, over half were in a small area a few yards in diameter.' In our surveys only one area near Pyramid Lake supported any reasonable number of plants with 96 separate plants in an area 5 x 3m. Most localities contained single or less than ten separate plants.

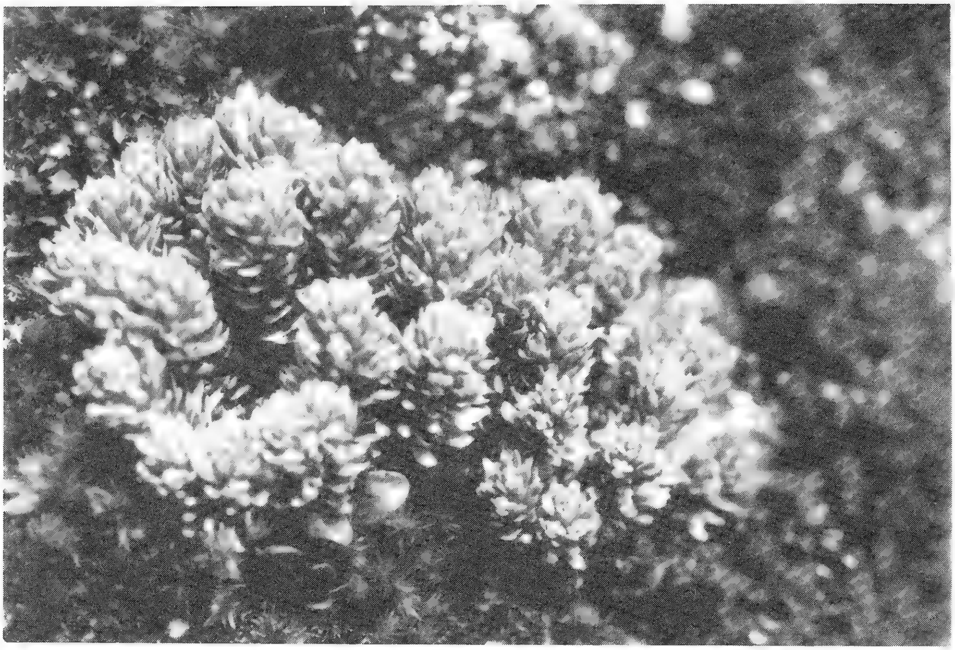

Fig. 1. Clump of *Lycopodium australianum* growing in feldmark with *Grammitis poeppigeana*, *Rhacomitrium crispulum*. Stems in this clump up to 3 cm tall.

Contrary to Taylor's (1955) assertion that the species is restricted to the *Azorella selago* alliance we have found the *Lycopodium* to be more widespread in the short grassland and in ecotonal associations between short grassland and feldmark. We have only occasionally found *Lycopodium* plants growing amongst *Azorella* cushions in feldmark. The Macquarie Island plants clearly belong to the *L. selago* group: development of gemmae from amongst the leaves is restricted to this group. However, *L. selago* is apparently restricted to the Northern Hemisphere (Øllgaard, pers. comm.).

Gemmae do not occur in *L. varium* or *L. saururus*. Both these latter species are quite different in details of growth habit and spore morphology from the Macquarie Island species (Øllgaard, pers. comm.). The position of its sporangia and absence of a distinct strobilus are quite unlike *L. varium* (Brownsey, pers. comm.). The spores of the *L. selago* group have characteristically truncated corners and distinctly pitted proximal faces. Both *L. varium* and *L. saururus* have flattened, smooth proximal faces without, or with shallow, marginal pits and they do not have truncated corners (Fig. 5).

In general growth habit, presence of bulbils, position of sporangia and absence of a distinct strobilus the plant resembles *L. australianum* (Brownsey and Smith-Dodsworth, 1989). The *L. selago* group is a complex one, consisting of a number of closely related taxa with very poor distinguishing characters. Until a thorough taxonomic revision of this group of species has been undertaken, we believe *L. australianum* is the most appropriate name to apply to the Macquarie Island material.

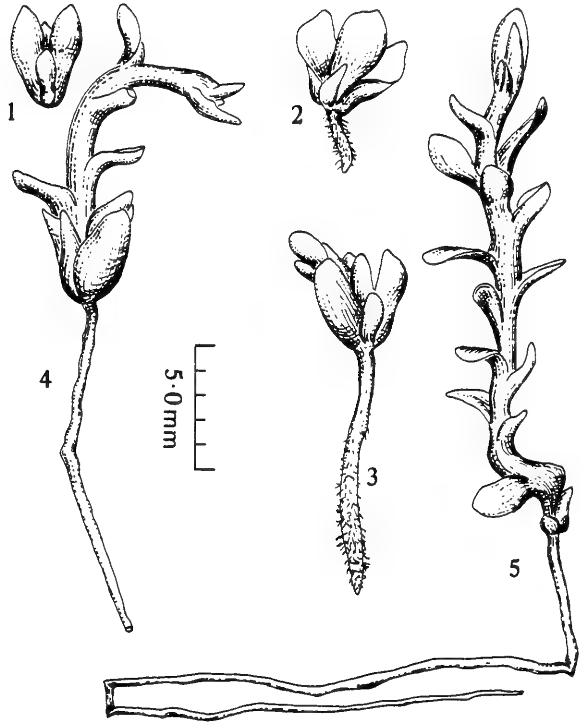

Fig. 2. Lycopodium australianum gemma as shed from parent plant (1), with developing tap root (2, 3), with elongating stem and developing leaves (4, 5).

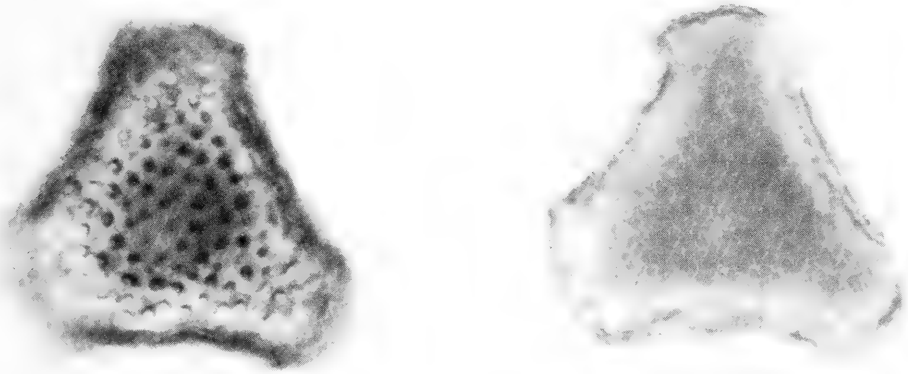

Fig. 3. Lycopodium spores from Palaeolake Nuggets deposit, layer 290 cm below present surface, approximately 10 000 years old. (**a**) distal face, (**b**) optical section, x420.

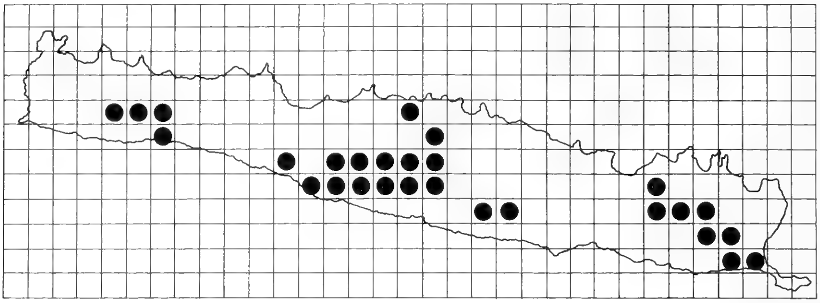

Fig. 4. Presence of *Lycopodium australianum* recorded in 1 km grid squares on Macquarie Island.

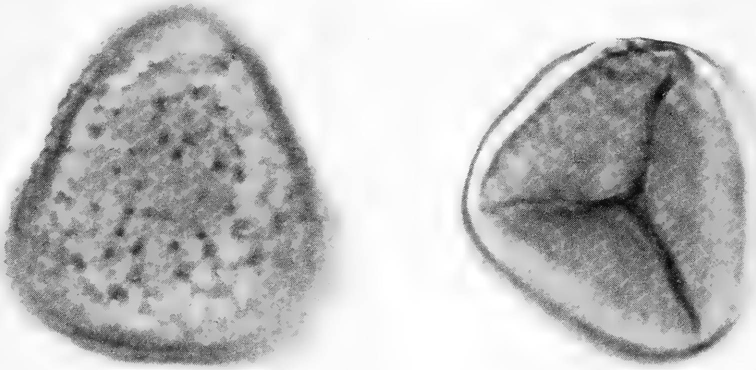

Fig. 5. Spores of (**a**) *Lycopodium varium* (distal face) and (**b**) *L. saururus* (optical section, x420) from Tristan da Cunha. Spore preparations loaned by N. Wace and J. Guppy.

ACKNOWLEDGEMENTS

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Diet and Feeding of Murray Cod (*Maccullochella peelii*) Larvae

STUART J. ROWLAND

ROWLAND, S. J. Diet and feeding of Murray cod (*Maccullochella peelii*) larvae. *Proc. Linn. Soc. N.S.W.* 113 (3), 1992: 193-201.

Murray cod, *Maccullochella peelii*, larvae commence feeding on zooplankton at the completion of yolk sac absorption, 9 to 11 days after hatching at water temperatures of 20-22°C; zooplankters ranged in length from 180-450 μm. In earthen ponds, larvae fed mainly on the calanoid copepods, *Boeckella fluvialis* and *Calamoecia lucasi* and the cladocerans, *Moina micrura* and *Daphnia carinata* for two weeks; then chironomid larvae and aquatic insects became the major components of their diet. The density of zooplankton at the commencement of feeding did not affect survival in 70-L aquaria; but when initial feeding was delayed for five or more days, survival was significantly lower ($P<0.01$) at 250 zooplankters/L compared to 3000/L. A delay of 13 days resulted in high mortality irrespective of zooplankton density. These findings are briefly discussed in relation to the reduced abundance of *M. peelii* in the wild, and the development of artificial breeding techniques.

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INTRODUCTION

Little is known about the larvae of Australian native freshwater fishes, despite the importance of this stage of the life cycle. The survival of the larvae of many fish species, both in the wild and under culture conditions, is affected by the availability of food during a 'critical period' after yolk sac absorption is completed (May, 1974). Laboratory studies have shown that survival of the larvae of some species is dependent on the presence of high densities of food when exogenous feeding commences (O'Connell and Raymond, 1970; Saksena and Houde, 1972; Houde, 1975) and that a delay in the initial feeding may result in reduced survival (Houde, 1974; Laurence, 1974; Roberts *et al.*, 1978).

The successful propagation of fish requires the development of techniques for rearing the larvae. Research into the diet and factors affecting larval survival often produces biological information which, besides enabling the rearing of larvae, provides a better understanding of the life cycle and population dynamics of the species.

The Murray cod, *Maccullochella peelii* (Mitchell, 1838) is Australia's largest and most famous inland fish; it is keenly sought by commercial and recreational fishermen. There has been a dramatic decline in the abundance of Murray cod during the 1900's (Rowland, 1989a) and despite the importance of this species, little is known of its life history. There is no record of Murray cod eggs or larvae being sampled from the wild. Techniques have now been developed for the artificial spawning of *M. peelii* (Cadwallader and Gooley, 1985; Rowland, 1985, 1988). As part of studies on the biology and artificial breeding of *M. peelii*, experiments were conducted to determine the diet of larvae and effects of food density and delayed feeding on survival. The results of this research are presented and discussed below.

MATERIALS AND METHODS

Experiments were conducted in the laboratory and earthen ponds at the Inland Fisheries Research Station, Narrandera, N.S.W., using larvae from both hormone-induced breeding trials and natural spawnings in ponds (Rowland, 1983, 1988). In all

Fig. 1. Murray cod larva prior to feeding — note the large yolk sac still present.

experiments, day 1 refers to the tenth day after the completion of hatching. Water from the Murrumbidgee River was used in all rearing facilities.

Laboratory Experiments

The 70-L rectangular, glass aquaria used in feeding experiments contained subgravel filtration and two airstones to provide gentle circulation and aeration. The back and sides of each aquarium were covered with black polythene sheeting. The water temperature was maintained at 20-22°C. Aquaria were subject to natural photoperiod with additional overhead fluorescent lighting for 8-10 h during daylight hours. Dead plankton and debris were siphoned from each aquarium daily, and larvae and fry were given a prophylactic NaCl bath (5 g/L) for 1 h every five days to prevent infestations of protozoan parasites (Rowland and Ingram, 1991).

Larvae in aquaria were fed wild zooplankton collected from ponds on the research station using a 100 μm-mesh plankton net. The plankton was washed through Endecott sieves of mesh sizes 1000 and 500 μm. For the first two days larvae were offered only zooplankton that passed through the 500 μm sieve; from the third day all sizes of zooplankton were offered to the larvae. The density of zooplankton in each aquarium was estimated and adjusted twice daily during the first week and then daily until the experiments were terminated. The contents of the aquarium were gently stirred to ensure that the zooplankton was evenly distributed and then two, 20 ml samples were collected. Formalin was added to each sample and all crustacean zooplankton, including the various copepodite stages but not nauplii, were counted. The mean number of zooplankters per 20 ml was used to estimate the number of zooplankters remaining in each aquarium. The same method was used to estimate the density of zooplankton in the stock solution collected from the pond. The required number of zooplankters were then placed into each aquarium by adding a known volume of the stock solution.

Diet at First Feed

Two hundred larvae were placed into each of three aquaria. From the eighth day after the completion of hatching, zooplankton which passed through a 1000 μm mesh were added daily to provide a density of 1000 zooplankters/L. Ten larvae were sampled daily for five days from each aquarium. The gut of each specimen was removed and dissected with the aid of a microscope and the number, type and length of food items present were recorded.

Zooplankton Density and Delayed Feeding

Same-age larvae from three females that had been induced to spawn were placed together in a trough and from these, 200 larvae were counted into each of 34 aquaria on the eighth day after the completion of hatching. Ten of the aquaria were used to determine the effect of zooplankton density on the survival of Murray cod larvae. Five densities of zooplankton were offered to the larvae in the aquaria from day 1 (10 days post-hatching): 250, 500, 1000, 3000, 5000 zooplankters/L. Each treatment was duplicated. The experiment was terminated on day 24 and the mean survival rate of fry from each treatment determined.

Twenty aquaria were used to determine the effect on survival of delayed feeding at two different densities of zooplankton. Larvae were kept without food until days 5, 8, 11, 13 or 15 and then offered zooplankton at densities of 250 or 3000 zooplankters/L. The remaining four aquaria were used as a control treatment, where larvae were offered zooplankton at the two densities commencing on day 1. Each treatment was duplicated. The experiment was terminated on day 17 and the mean survival rate of larvae from each treatment was determined.

The effect of zooplankton density on larval survival rate in aquaria was analysed using a one-way analysis of variance; the effect of delayed feeding, at the two zooplankton densities, on survival rate was analysed using a two-way analysis of variance. Percentage data were normalized using an arcsin transformation.

Pond Experiment

Ponds 1 and 2 were filled and fertilized 5 and 10 days before stocking, respectively. Pond 1 was fertilized with inorganic fertilizer only, and pond 2 with inorganic fertilizer plus lucerne hay as recommended by Rowland (1989b). Larvae were stocked on day 1 into the ponds at densities of 3 and 19/m^2. The diets of cod larvae and fry were analysed using the frequency of occurrence and the percent composition by estimated volume methods. The ponds were drained 40 and 34 days after stocking; all fry harvested were counted.

RESULTS

Laboratory Experiments

At water temperatures of 20-22°C, Murray cod eggs generally complete hatching on the eighth day after fertilization and larvae remain clumped together in a single layer on the bottom of troughs for another six or seven days before gradually dispersing; yolk sac absorption is complete nine to 11 days after the completion of hatching (Rowland, 1985, 1988).

Diet at First Feed

Many Murray cod larvae in aquaria commenced feeding on copepodids, copepods and cladocerans (length 220-370 μm) nine and ten days after the completion of hatching; all larvae sampled on the eleventh day contained zooplankton up to 450 μm in length (Table 1). The zooplankton consumed by the larvae were predominantly the copepods, *Boeckella fluvialis* and *Calamoecia lucasi* and the cladocerans, *Moina micrura* and *Daphnia carinata*. Although large numbers of rotifers (*Keratella* spp. and *Brachionus* spp.) were also present in all aquaria, only four of the larvae sampled contained rotifers, suggesting that cod larvae feed selectively on the crustacean zooplankton.

Zooplankton Density and Delayed Feeding

Results of the experiments to determine the effects of zooplankton density and delayed feeding on the survival of Murray cod larvae are presented in Table 2 and Fig. 2.

TABLE 1

Diet of Murray cod larvae held in 70-L aquaria and offered zooplankton collected from ponds and passed through a 1000 μm sieve. 30 larvae were sampled each day

Days after completion of hatching	**Larvae with food in gut (%)**	**Range of food types in number and length (μm) per larva**			
		Copepoda[a]	**Cladocera[b]**	**Rotifer**	**Other**
8	0	—	—	—	—
9	37	1-2 (220-290)	—	—	—
10	87	1-4 (220-350)	1-2 (290-370)	—	—
11	100	0-7 (250-370)	1-3 (300-450)	0-3 (80-120)	1[c]
12	90	2-19 (250-450)	0-7 (270-520)	0-2 (100-160)	—

a including copepodids; predominantly *Boeckella fluvialis* and *Calamoecia lucasi*.

b predominantly *Moina micrura* and *Daphnia carinata*.

c *Volvox*; probably ingested unintentionally.

If feeding commenced on day 1, there was no significant difference ($F_{4,5}$ = 1.78, $P > 0.05$) between the survival of larvae offered zooplankton at densities of 250-5000 zooplankters/L (Table 2). However a delay in the commencement of feeding resulted in significantly reduced survival ($F_{4,15}$ = 74.02, $P < 0.01$), and there was high mortality of cod larvae not fed until day 13. Zooplankton density did have a significant effect (F = 11.98, $P < 0.01$) when initial feeding was delayed, and the survival of larvae offered 250 zooplankters/L commencing on days 5, 8, 11 or 13 was lower than the survival of larvae offered 3000 zooplankters/L (Fig. 2).

TABLE 2

Survival of Murray cod larvae offered different densities of zooplankton commencing on the tenth day after the completion of hatching (day 1); experiment terminated on day 24

Density of zooplankton (no./L)	250	500	1000	3000	5000
Mean survival ± S.D. (%)	80.7 ± 7.5	83.0 ± 3.5	88.7 ± 5.3	89.5 ± 3.5	89.9 ± 3.4

From day 7, unfed larvae appeared weaker and less active than larvae that were being fed. By day 12 most unfed larvae were moribund and floated with the gentle current and most of these larvae appeared too weak to capture zooplankton when it was first offered on day 13. Unfed larvae were all dead by day 15.

Diets of Larvae and Fry in Ponds

Summaries of the diets of Murray cod sampled from the ponds are given in Table 3. Larvae sampled from the ponds two days after stocking were feeding predominantly on the copepods *Boeckella fluvialis* and *Calamoecia lucasi* and on the cladoceran *Moina micrura*; these prey items ranged in length from 180 to 450 μm. By day 7, larvae were eating zooplankton, including *Daphnia carinata* up to 2200 μm in length. Chironomid larvae and aquatic insects (mainly notonectids and corixids) were major components of the diet of fry from the third week after stocking until harvest. This shift in diet may have been partly due to the decrease in availability of larger zooplankton in these two ponds.

A total of 42,870 fry were harvested, with survival rates of 62 and 74% in ponds 1 and 2 respectively (Table 4).

TABLE 3

Diet of Murray cod larvae and fry in earthen ponds. Length range of food type in parentheses; zooplankton µm, chironomid larvae and aquatic insects mm

Pond	Days post-stocking	Mean length of 5 larvae/fry (mm)	Frequency of occurrence; percent composition by volume					
			Copepoda	Cladocera	Unidentified zooplankton	Chironomid larvae	Aquatic insects	Unidentified
1	2	13.9	0.8; 64 (180-350)	0.8; 36 (250-450)	—	—	—	—
	7	16.3	1.0; 70 (350-2000)	1.0; 30 (450-2200)	—	—	—	—
	14	20.7	0.8; 40 (500-1800)	0.6; 30 (600-1800)	0.2; 18 —	0.2; 12 (7)	—	—
	21	23.2	0.8; 28 (1800-2900)	0.4; 15 (2200-3200)	0.4; 15 —	0.6; 42 (4-9.5)	—	—
	30	30.1	0.2; 5 (2000)	0.4; 5 (2000-3000)	—	0.8; 60 (3.8-11)	0.4; 20 (4-12)	0.6; 20 —
	40	38.9	—	—	—	0.6; 34 (6-10)	0.6; 46 (9-12)	0.8; 20 —
2	2	13.1	1.0; 70 (220-350)	0.8; 30 (300-450)	—	—	—	—
	7	15.3	0.8; 50 (400-950)	0.4; 10 (550-1400)	0.4; 20 —	0.4; 20 (2.5-5.5)	—	—
	14	20.4	0.8;30 (450-1500)	0.2; 1 (1500)	0.4; 10 —	0.8; 41 (4-9)	0.4; 18 (3-5.5)	—
	21	22.5	0.8; 18 (700-2800)	0.4; 4 (2800-4000)	—	1.0; 60 (4-11)	0.2; 4 (9-12)	0.4; 14 —
	28	26.5	0.6; 18 (650-2100)	0.4; 6 (600-1900)	—	1.0; 46 (4-11.8)	0.6; 20 (10-14)	0.6; 10 —
	34	31.0	0.2; 4 (1200-2100)	0.2; 6 (1800-2500)	—	1.0; 70 (6.5-12.8)	0.4; 10 (11-14)	0.4; 10 —

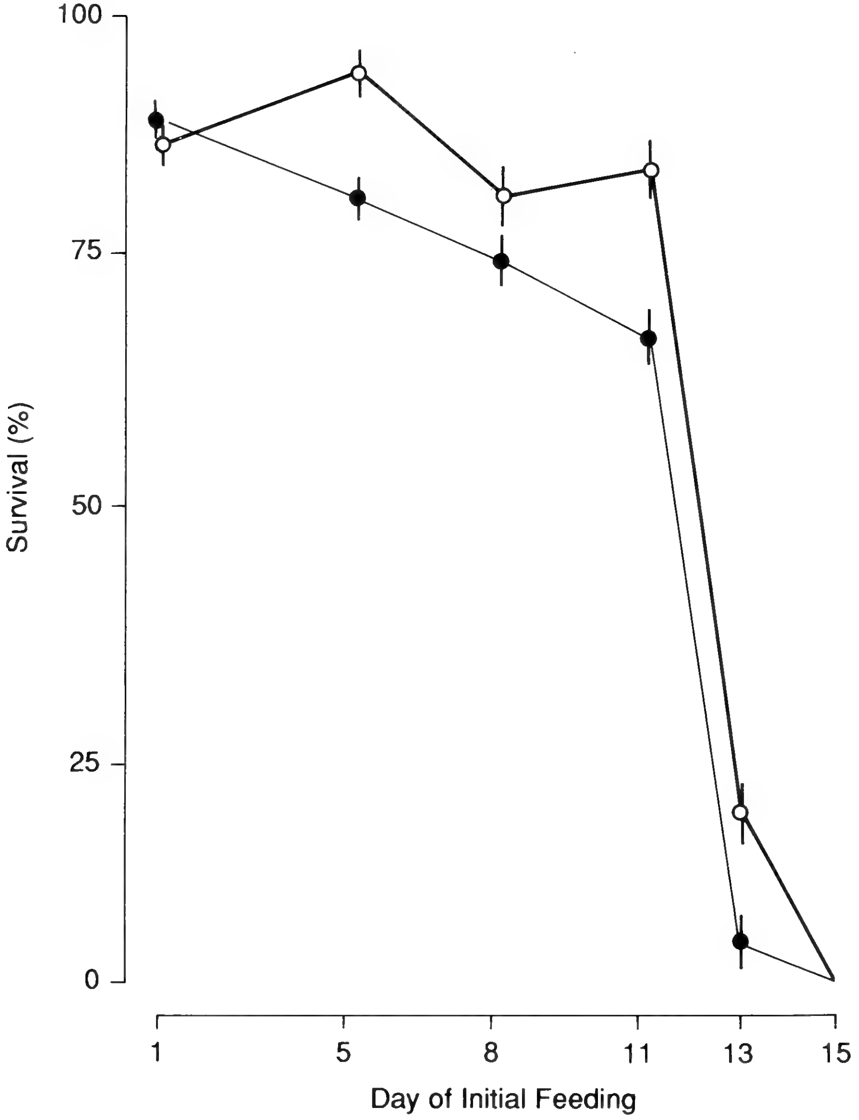

Fig. 2. Effect of delayed feeding at two densities of zooplankton on the survival of Murray cod larvae. Experiment terminated on day 17. mean survival ± S.D. at zooplankton density of 3000/L; mean survival ± S.D. at zooplankton density of 250/L.

TABLE 4

Details of Murray cod stocked in ponds

Pond	Surface area (m^2)	No. of larvae	Stocking density (no./m^2)	No. of fry harvested	Survival (%)	Stocking period (days)
1	3,000	59,000	19	36,580	62	40
2	2,800	8,500	3	6,290	74	34

DISCUSSION

In contrast to the larvae of some other fishes which require densities of zooplankton of 1000/L or greater for survival under intensive rearing conditions (May, 1974), densities of 250-5000 zooplankters/L did not affect the survival of Murray cod larvae. The larvae of *M. peelii* are relatively large (total length, 12-13 mm) and well developed at the completion of yolk sac absorption, and they can swim strongly and effectively capture food items even at the low density of 250 zooplankters/L. However, if initial feeding is delayed for five or more days, survival is significantly affected by food density and a delay of 13 days in initial feeding results in high mortality irrespective of zooplankton density.

Most fish larvae show a rapid increase in feeding efficiency as they grow (May, 1974), but if sufficient food (of suitable size) is not encountered, swimming ability will decline (Laurence, 1972). This was observed in unfed Murray cod larvae from day 7; by day 12 most unfed larvae were moribund. Because fish larvae do not have lipid reserves, protein metabolism results in degeneration of the pancreas in starved or poorly fed larvae (O'Connell, 1976) and this can lead to a loss of ability to digest food even if it is encountered and eaten (Dabrowski, 1982; Pitcher and Hart, 1982).

The results of this study suggest that the availability of zooplankton within two weeks of the completion of yolk sac absorption is an important factor influencing survival in *M. peelii*. Rising water levels and floods in the Murray-Darling river system are followed by an increase in plankton and aquatic insects, particularly chironomid larvae (Frith, 1959; Shiel, 1980; Maher and Carpenter, 1984) and these are the major food items of Murray cod larvae and fry in earthen ponds at the Inland Fisheries Research Station. Consequently floods, besides increasing the available habitat for fishes, also probably provide optimum feeding conditions for *M. peelii* larvae and fry in the wild.

The construction of dams, high-level weirs and levee banks on the major tributaries of the Murray-Darling river system has altered the natural flow and temperature regimes and dramatically reduced the frequency, extent and duration of flooding (Reynolds, 1976; Cadwallader, 1978; Walker *et al.*, 1978; Walker, 1979). Consequently optimum conditions for the high survival of Murray cod larvae now rarely occur and poor larval recruitment may be a reason for the dramatic decline of *M. peelii* since the 1950's (Rowland, 1989a).

In ponds at the Inland Fisheries Research Station, Murray cod larvae fed selectively on crustacean zooplankton, particularly the calanoid copepods *Boeckella fluvialis* and *Calamoecia lucasi* and the cladocerans *Moina micrura* and *Daphnia carinata*, in preference to the abundant rotifers. The larvae of another large, native, percichthyid the golden perch (*Macquaria ambigua*) also feed selectively on crustacean zooplankton (Arumugam, 1986; Rowland, 1986). Rotifers generally dominate the zooplankton communities of the Darling River and at times, the Murray River; whereas limnetic zooplankters such as calanoid copepods and cladocerans dominate habitats such as billabongs, backwaters and impoundments (Shiel, 1978, 1979, 1980; Geddes, 1984). The apparent selectivity of the larvae of both *M. peelii* and *M. ambigua* for crustacean zooplankton suggests that billabongs and backwaters in the Murray-Darling river system play an important role in the survival of larvae of these native fishes.

In fish culture, the larval rearing phase is often a 'bottle neck' in production, because of the high mortality that is encountered soon after the commencement of exogenous feeding; particularly in species with very small (<5 mm) larvae. In contrast, Murray cod larvae are relatively easy to feed under culture conditions because they are large and well developed at the completion of yolk sac absorption. Within 7 days larvae can consume copepods and cladocerans as long as 2200 μm (Table 3).

Murray cod larvae can be reared in intensive facilities using newly-hatched brine shrimp (*Artemia*) as the only food item (Cadwallader and Gooley, 1985). Rowland (1985) compared the survival and growth of larvae feeding on natural zooplankton in a pond, troughs and aquaria, and found that although survival rates were similar (83%, 93% and 89% respectively), the growth rate was significantly faster ($P < 0.01$) in ponds. It was suggested that lower stocking density, the presence of cover, natural light intensities and the availability of different food types, such as chironomid larvae and aquatic insects for older larvae and fry, were contributing factors. In the current study, Murray cod grew rapidly and reached mean lengths of 31.0 and 38.9 mm in 34 and 40 days respectively (Table 3).

Techniques for the preparation and management of earthen ponds for rearing larvae of some Australian native fishes were recommended by Rowland (1989b). These procedures, plus supplementary feeding with wild zooplankton and/or brine shrimp in intensive facilities for three to five days prior to stocking, are now used to achieve high survival and growth rates of Murray cod at commercial native fish hatcheries (Bruce Malcolm, Ray Mepham, 1990, pers. comm.).

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Vegetation of the Coastal Lowlands of Tweed Shire, Northern New South Wales: Plant Communities, Species and Conservation

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(Communicated by J. R. MERRICK)

PRESSEY, R. L., & GRIFFITH, S. J. Vegetation of the coastal lowlands of Tweed Shire, northern New South Wales: plant communities, species and conservation. *Proc. Linn. Soc. N.S.W.* 113 (3), 1992: 203-243.

Plant communities of the coastal lowlands of Tweed Shire, on the far north coast of New South Wales, are described. The communities are grouped into three broad categories: floodplain wetlands which are not further subdivided; estuarine wetlands in four communities; and floodplain forest and the vegetation of dunal areas with 16 sampled communities and brief descriptions of alluvial forest, foredune formations and additional emergent wetland communities. The occurrences of 505 plant taxa in relation to the sampled communities are listed.

Natural vegetation in the study area occupied about 3,300 ha at the time of mapping in 1985. This represents a decline of over 87% from its original extent. The formal reserves in the study area fail to represent much of its natural diversity. The coverage and level of protection provided by less secure conservation measures should be extended.

Increased efforts at conservation planning are needed, particularly because of the biogeographic significance of the area, the significance of some habitats for the mobile fauna of a region much larger than the Shire, the many rare, threatened or otherwise significant species, and the inevitable limitations of available data as a basis for ensuring the adequate protection of the area's species.

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KEY WORDS: Tweed lowlands, plant communities, taxa, conservation.

INTRODUCTION

The coastal wetlands and associated vegetation types of Tweed Shire were surveyed in 1985 as part of a series of consultancy studies funded by the National Parks and Wildlife Service. The studies were intended to provide information on the wetlands of areas which were not well known and were under pressure from development. The survey of coastal Tweed Shire was preceded by surveys of the Hunter, Clarence and Macleay floodplains (Pressey, 1981a, 1989a,b).

Information from the surveys was intended to be used in determining conservation priorities and for responding to proposals for developments which could adversely affect wetlands. In the case of the Tweed survey, attention was not restricted to the wetlands of the floodplain, which is very limited in extent compared to those of the other rivers included in the series, but directed also to estuarine and dunal wetlands. These other wetland types were poorly known and under significant threat from agricultural expansion and clearing for housing and tourist developments. Because the dunal wetlands occur in a matrix of heathland and forest, the Tweed survey was further extended to the remaining naturally vegetated areas of the dunal formations.

Several studies of wetlands and other coastal vegetation types in Tweed Shire preceded the survey reported here but these were either limited in geographical scope or lacked the detail required for decisions on the conservation priorities of particular areas. Hannah (1968) mapped and provided general descriptions of landforms, vegetation, land systems and land use of the coastal strip. Goodrick (1970) mapped and broadly

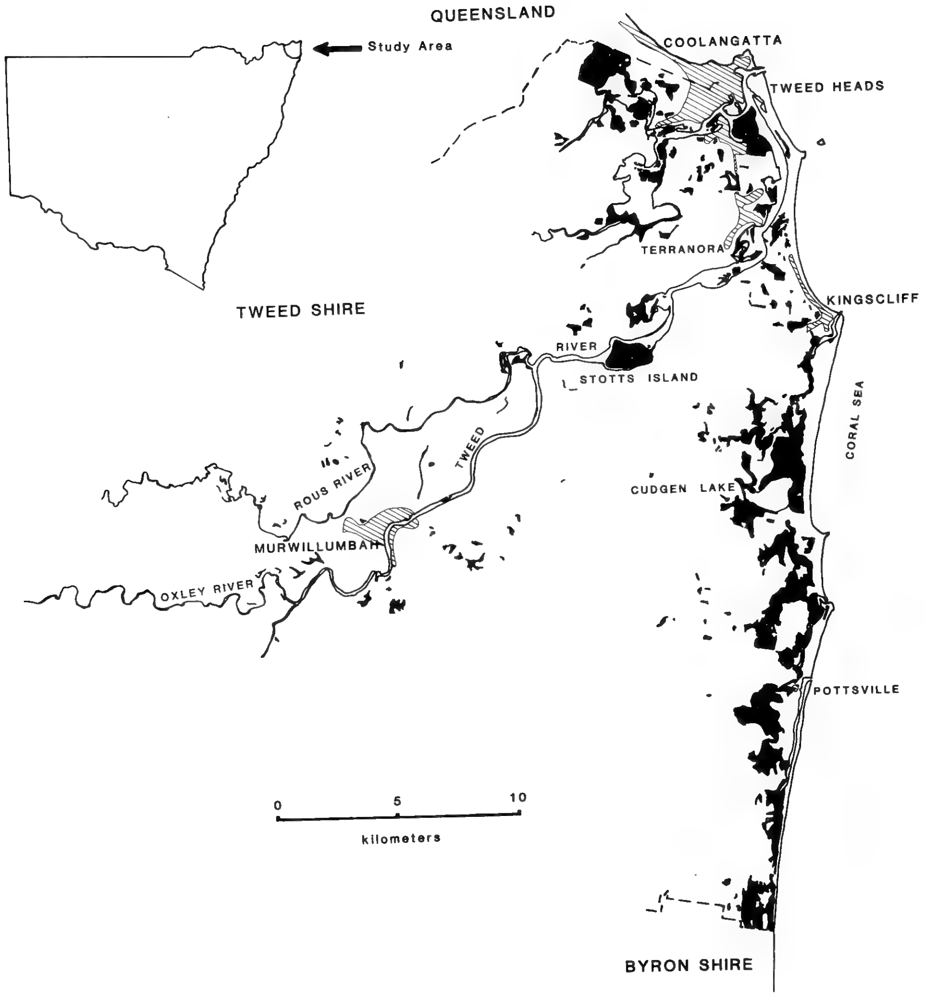

Fig. 1. The study area. Black areas show the remaining extent of wetlands and other communities on the coastal lowlands.

classified the major wetlands of the Tweed region along with those of the remainder of the state's coast. Some of the Tweed wetlands were covered generally by Bell and Edwards (1980) in their inventory of the state's coastal lagoons and their catchments.

The Planning and Environment Commission (1978) undertook a broad-scale study of the Shire's coastal plant communities. The draft plan of management for Stotts Island Nature Reserve (National Parks and Wildlife Service, 1979), a remnant of the original floodplain forest, contains a compilation of information on flora and discussed management issues. Investigation reports by the National Parks and Wildlife Service (Meehan, 1981; Hunter, 1982) provided detailed information on parts of the coastal lowlands and Gilmore (1983) compiled information on significant vegetation in the area in a submission to the Tweed Shire Local Environmental Study.

More recently, West *et al.* (1985) mapped and classified the estuarine wetlands of the state and listed species of mangroves and seagrass for each estuary. In the same year, the Coastal Council of New South Wales (1985) delineated wetlands, without descriptions, for the purposes of development controls under State Environmental Planning Policy No. 14. The other biophysical literature on the coastal parts of Tweed Shire listed by Pressey (1981b) deals with the geomorphology, soils and avifauna of limited areas.

Several detailed surveys of the vegetation of parts of coastal Tweed Shire followed or were concurrent with the study reported here and make a significant contribution to the knowledge of the plant communities and floristics of the region. Gilmore *et al.* (1985) produced a comprehensive report on the hydrology, vegetation, fauna and conservation needs of wetland and associated habitats in the Pottsville area. Detailed surveys of vegetation and vertebrate fauna have also been completed by Murray (1987a) for a small wetland on the Fingal Peninsula, near Tweed Heads, Murray (1987b) for an area adjoining the Cobaki Broadwater and Murray (1989) for land north of Cudgen Lake.

This paper summarizes the inventory and description sections of the 1985 survey of coastal Tweed Shire which was designed to be both comprehensive and detailed in its coverage of wetlands and associated dunal environments, to provide new information on floristics and vegetation formations and to compile information already gathered. Information on sampling sites, detailed maps and the results of conservation evaluation are given in the original survey report (Pressey and Griffith, 1987). Some of the information from the four concurrent or later studies mentioned above has also been summarized in this paper.

STUDY AREA

The study area includes the northernmost part of the New South Wales coastline, about 650 km north of Sydney (Fig. 1). Tweed Shire has the Queensland border to the north and Byron Shire to the south. The areas surveyed and described all lie below the 10 m contour and are mainly on the dunal formations of the immediate coastal strip, although they also include the floodplains and estuaries of the Tweed River and minor streams.

Agricultural and urban development of the Tweed Valley began in about 1865 with the settlement of the first farms, although cedar-getting preceded farming by about 20 years (Soros-Longworth and McKenzie Pty. Ltd., 1981). The Tweed floodplain has been almost entirely cleared for sugar cane cultivation and pastoral use, as have the minor floodplains of the Cobaki and Terranora Broadwaters and those of the small coastal streams such as Cudgen and Cudgera Creeks. More recently, urban expansion has been significant and rapid (Soros-Longworth and McKenzie Pty. Ltd., 1981) due to the tourist potential of the region and annual population increases of 4-5% in the period 1976-1986 (Tweed Shire Council, 1987).

This rapid growth has been sustained. In June 1990, Tweed Shire had the highest estimated population and the highest population growth rate for the previous five years (4.3%) of any local government area on the north coast (Department of Planning, 1990). The estimated 1991 population in the northern coastal strip of Tweed Shire was about 33,500, some 58% of the Shire's total, and the increase in population in this area from 1986 to 1991 was 40% (Tweed Shire Council, 1991). Population increase and associated developments therefore represent a serious threat to the remaining natural habitats on the Tweed coastal lowlands. Planning for population growth in the region to minimize or avoid further impacts on the coastal habitats is a major challenge for the State Government and Tweed Shire Council.

METHODS

The floodplain wetlands of the study area were treated as a floristic complex, but the vegetation of the estuarine and dunal areas was subdivided into communites. Assuming one 'does not insist upon quantitative uniformity of the dominants, which rarely occurs' (Beadle and Costin, 1952), then most of the communities recognized in the present study could be considered associations after Beadle (1981): 'the association is defined as a community in which the dominant stratum exhibits uniform floristic composition, the community exhibiting uniform structure'.

Wetlands and other communities were initially mapped on aerial photographs from two series: Murwillumbah 1:41,000 black and white (March 1979) and NSW Coastal Wetlands 1:25,000 colour (July 1981). Floodplain wetlands were simply delineated without any attempt at classification. Estuarine wetlands were mapped as either mangrove or saltmarsh. Although distinct plant communities were identified in saltmarsh areas during field work, these could not be reliably distinguished on aerial photographs because of lack of photo signature and small, irregular size. Remnant patches of floodplain forest and most of the plant communities identified in the dunal areas were mapped together as either a forest complex or an emergent wetland complex. Detailed photo-interpretation would have allowed mapping of separate communities in these areas but constraints on the time for the study did not allow the field work necessary to accurately locate boundaries.

Most of the field work for the estuarine and dunal areas was completed during May 1985 when 55 sites were systematically sampled and described. Sampling sites were generally 400 sq. m, although 100 sq. m quadrats were used for floristically simple communities such as sedgeland. The information collected for each site included a list of species observed, an assessment of species abundance, structural information (after Walker and Hopkins, 1984), physiographic details, inferred relationships to other communities, and notes on any forms of disturbance. The precise locations of these sampling sites and another 84 descriptive sites were recorded to assist mapping for this and subsequent studies. Additional sampling of plants and truthing of aerial photograph interpretation in the estuarine and dunal areas was carried out in October 1985.

Floodplain wetlands were each visited once in October 1985 and plant species and other information recorded after the procedure outlined by Pressey (1989a). Altered boundaries of wetlands and other communities due to clearing since the dates of aerial photographs were noted during field work and the preliminary mapping of estuarine wetlands was checked against that of West *et al.* (1985). Mapping information was transferred from aerial photographs to 1:25,000 topo-cadastral maps using a zoom transfer scope and then copied onto transparent overlays of the base maps.

RESULTS AND DETAILED DISCUSSION

Plant Community Definitions in Relation to Other Studies

The classification of vegetation into the communities listed is based on the previous experience of one of the authors (SJG). It is intuitively derived and based on dominants, but has been consistently used over much of the north coast of New South Wales for mapping at 1:12,500 and 1:25,000 (Griffith, 1991).

Most of the communities identified in this study have also been recognized by others in south-eastern Queensland. Other intensive studies of small parts of Tweed Shire have produced similar but finer-scale classifications. The intensive survey of low-lying coastal vegetation near Pottsville by Gilmore *et al.* (1985) covered an area of about 370 ha and recognized 22 associations and other units at 1:4000, some of which were confined to bedrock with others ecotonal or resulting from disturbance. Similarly, Murray (1987a) has produced a very detailed vegetation map of a small wetland and its surrounds near Fingal Head, identifying 11 vegetation types over an area of about 20 ha, five of which are estuarine wetland associations. Murray (1987b) identified ten non-estuarine units near the Cobaki Broadwater, three of which were on bedrock, and Murray (1989) mapped 12 units over about 700 ha to the north of Cudgen Lake. Despite the more detailed subdivisions of the vegetation in these studies and the recognition of units not covered by sampled sites for the present study, these other classifications are generally comparable to the one used here.

Floodplain Wetlands

The coastal floodplain wetlands of Tweed Shire were defined as those on alluvium below the 10 m contour and not associated with dune formations or significantly influenced by tidal action. They are basins which occasionally or regularly hold water and which occur on the lower floodplain of the Tweed River upstream of Stotts Island and along the tributaries of the Cobaki and Terranora Broadwaters. Stands of trees in these areas without wetland plants in the understorey were included in a separate category of vegetation (floodplain forest and vegetation of dunal areas, see below) as were forested areas with or without wetland plants in the understorey in areas fringing the estuaries and on the minor alluvial flats of the coastal strip.

The survey covered 48 floodplain wetlands with a total area of 144 ha (Table 1), a much smaller number and area than on any of the large floodplains of the Hunter, Clarence or Macleay. Most of the wetlands are smaller than 5 ha and the largest is only about 19 ha. Two of the wetlands with a combined area of 7 ha were identified on Stotts Island from aerial photographs but not visited on the ground.

Eighty-five plant taxa were recorded during the survey (Appendix 1) to which a herbarium record was added of *Eleocharis dulcis*, collected from a drainage channel near Murwillumbah. Of the total of 86 taxa, one is a liverwort, five are ferns, 61 are monocots and 29 are dicots. Families with the most taxa were Cyperaceae (29 taxa), Poaceae (8) and Polygonaceae (8). The most extensive taxa were *Cyperus lucidus* (17.7% of total area), *Persicaria hydropiper* (15.9%) and *Melaleuca quinquenervia* (10.1%). *Cyperus lucidus*, extensive stands of which were characteristic of the Tweed floodplain wetlands, was not recorded at all during surveys of the Hunter, Macleay and Clarence floodplains, even though it occurs in most of the botanical regions in New South Wales (Jacobs and Pickard, 1981). Other species found in the Tweed floodplain wetlands but not in surveys of other floodplains to the south were *Acacia maidenii*, *Gahnia clarkei*, *Lophostemon suaveolens*, *Ludwigia octovalvis*, *Persicaria dichotoma* and *Rhynchospora corymbosa*.

Apart from occasional floodwaters from the river, eleven of the wetlands receive only local runoff from the surrounding alluvial flats. Of the other 35 which have catchments on nearby land above the 10 m contour, only five are fed by catchments larger than 100 ha.

Forty-two wetlands are grazed and 20 wetlands with a total area of 63 ha have been directly affected by drainage. It is possible that the wetlands which have not been directly drained have also been altered hydrologically by changed patterns of flooding and drainage following flood mitigation works. Other alterations include impoundment, excavation and filling for urban development. The pre-European extent and nature of the floodplain wetlands is difficult to assess but it is likely that some of the original wetlands have been completely destroyed due to structural flood mitigation works. Much of the sugar cane land which now takes up virtually the whole floodplain downstream of Murwillumbah is reclaimed wetland subjected to drainage by local drainage unions and with reduced flooding frequency due to construction of levees (Soros-Longworth and McKenzie Pty. Ltd., 1981). The extensive destruction of shallow wetlands on the main floodplain is also suggested by their present confinement to narrow tributary valleys of the bedrock margins. The remaining wetlands on the broad alluvial flats are deep channels which could not be completely drained or converted to agriculture.

TABLE 1

Original and 1985 extent of vegetation associations or complexes in coastal Tweed Shire
(Bracketed figures indicate percentage decline)

Association/Complex	1985 (ha)	Original (ha)
FLOODPLAIN		
Floodplain wetlands	144	
Floodplain forest	194	
Floodplain total	338	11,460 (97%)
ESTUARINE WETLANDS		
Mangroves	371	
Saltmarsh	55	
DUNAL AREAS		
Forest complex	2298	
Shrubland	10	
Dry heath	56	
Wet heath	46	
Emergent complex	131	
Estuarine and dunal total	2967	14,990 (80%)
OVERALL TOTAL	3305	26,450 (87.5%)

The floodplain wetlands of Tweed Shire are poorly represented in reserves, with only 7 ha of wetland within Stotts Island Nature Reserve. The two within the nature reserve are unusual in having their natural context of surrounding vegetation types, a very rare situation in coastal New South Wales. Poor representation in reserves is typical of other floodplain wetlands on the north coast (Pressey, 1981a, 1989a,b).

Other protection measures are available for wetlands, although of limited value in some cases. Under State Environmental Planning Policy 14 (SEPP 14), clearing, filling, drainage and construction of levees in wetlands delineated on planning maps are now designated developments. They require development applications and environmental impact statements and can only proceed after the consent of local government and the concurrence of the Department of Planning. However, SEPP 14 is only a potential protection measure for the wetlands on the Tweed floodplain, many of which are outside the limits of the Policy's mapping, with the remainder not identified under the Policy, despite their apparent distinctiveness in a state context.

Estuarine Wetlands

For the purposes of this survey, estuarine wetlands were defined only as saltmarsh and mangroves. West *et al.* (1985) have also mapped areas of seagrass in the estuaries of Tweed Shire and elsewhere in the state. The intertidal mudflats and sandflats of the state's estuaries have apparently not been included in any surveys.

Most of the mangrove area in the Shire occurs in the estuary of the Tweed River (Table 2) with relatively small areas in Cudgen Lake and Creek, Cudgera Creek and Mooball Creek. The Tweed estuary is the only estuary in the Shire which contains all five species known to occur in New South Wales: *Aegiceras corniculatum*, *Avicennia marina*, *Bruguiera gymnorrhiza*, *Excoecaria agallocha* and *Rhizophora stylosa*. Only one other estuary in the state, that of the Brunswick River, is known to have all these species together (West *et al.*, 1984) although they each extend well southward. Mangroves in the Shire are in places associated with *Hibiscus tiliaceus* which occurs at the upper limit of tidal influence. Hunter (1982) also reported that *Dendrobium monophyllum* is a common epiphyte on *Bruguiera* on Caddys Island in the Terranora Inlet. In addition, there is an unconfirmed report of *Ceriops tagal* from Cudgera Creek (Shine *et al.*, 1973). This species is not otherwise known from the state and was not found during surveys by West *et al.* (1984).

Saltmarsh is considerably more restricted in extent in Tweed Shire than mangroves and distributed differently between estuaries (Table 2). About half the total area of saltmarsh in the Shire occurs in each of the Tweed and Cudgen estuaries if the stands of *Schoenoplectus litoralis* mapped by West *et al.* (1985) in Cudgen Lake are not considered as typical saltmarsh vegetation. The extensive (about 35 ha) area of *S. litoralis* is significant, however, at least in the context of Tweed Shire, and could be one of the biggest occurrences in the state (Adam, 1991, pers. comm.).

TABLE 2

Extent of estuarine wetlands in Tweed Shire (ha). Data from West et al. *(1985)*

System	Mangrove	Saltmarsh #	Seagrass
Tweed River *	309	21	33
Cudgen Lake	9	56(31)	—
Cudgera Creek	14	2	2
Mooball Creek	5	—	1
Total Area	337	79(44)	36

\# bracketed figures represent areas after subtracting 35 ha of *Schoenoplectus litoralis* mapped by West *et al.* (1985) as saltmarsh in Cudgen Lake.
* includes the Cobaki and Terranora Broadwaters.

Estimates for this study of total areas of mangrove and saltmarsh in Tweed Shire differ from those of West *et al.* (1985). Our estimates of mangrove and saltmarsh extent are 371 ha and 55 ha respectively (Table 1) as opposed to 337 ha and 44 ha respectively (excluding *Schoenoplectus litoralis* in Cudgen Lake) in Table 2. The disparities are presumably due to differences in interpretation of aerial photographs, production of final maps and estimation of areas.

The saltmarsh vegetation seen during field work was divided into three communities on the basis of dominant species and structure, all on interbedded estuarine sediments:

S1. *Sporobolus virginicus — Sarcocornia quinqueflora* dwarf to mid-high closed tussock grassland/chenopod shrubland. Inundated by spring high tides; grades sharply, or occasionally diffusely, into mangrove vegetation downslope; grades diffusely into S2 or S3 upslope where seldom inundated by high tides.

S2. *Juncus kraussii* tall to very tall closed rushland. Grades sharply or diffusely into S1 downslope with more inundation from spring high tides; grades sharply or diffusely into S3 or *Casuarina glauca* (with or without *Melaleuca quinquenervia*) swamp forest higher above the level of tidal influence.

S3. *Baumea juncea* tall to very tall closed sedgeland. Grades sharply or diffusely into S1 or S2 where occasionally subject to tidal inundation; often grades diffusely into swamp forest further upslope.

The communities recognized here are very similar to those derived from more detailed studies of estuarine wetlands in Tweed Shire. After a survey of a small wetland on the Fingal Peninsula, Murray (1987a) was able to map two mangrove units, *Avicennia* and *Excoecaria*, although his saltmarsh associations were virtually identical. In the Cobaki area, Murray (1987b) recognized an *Avicennia* unit, a *Casuarina* — *Excoecaria* unit and a saltmarsh association equivalent to S1. The units defined in the present study translate readily into the communities described by Adam *et al.* (1988) and are similar or equivalent to those recognized in south-eastern Queensland. S1 was described from Moreton Island (Durrington, 1977) and a *Sporobolus virginicus* saltmarsh was listed by McDonald and Elsol (1984). S2 is known from Moreton Island (Durrington, 1977) and from the Sunshine Coast (Batianoff and Elsol, 1989) and was listed by McDonald and Elsol (1984). S3 also occurs in south-eastern Queensland (McDonald, 1991, pers. comm.).

Twenty-two species were recorded in these three communities (Appendix 1). Most of these are native, non-woody plants typical of saltmarshes elsewhere. *Avicennia marina*, *Melaleuca quinquenervia* and *Bruguiera gymnorrhiza* were recorded as scattered emergents. Two species, *Aster subulatus* and *Baccharis halimifolia*, are introduced.

The only estuarine reserve in Tweed Shire, Ukerebagh Nature Reserve, contains 15% of the Shire's mangroves and 33% of its saltmarsh. Elsewhere on the far north coast, limited areas of saltmarsh occur in Broadwater, Bundjalung and Yuraygir National Parks (Griffith, 1983,1984, 1985). In a state context, the *Sporobolus virginicus* — *Sarcocornia quinqueflora* and *Juncus kraussii* communities are inadequately represented in reserves (Benson, 1989) and the reservation of *Baumea juncea* sedgeland is fair. All three saltmarsh communities are covered by SEPP 14.

The estuarine wetlands of the Shire have been subject to a variety of disturbances. Structural flood mitigation works in the Tweed Valley have included floodgates on tidal creeks (Soros-Longworth and McKenzie Pty. Ltd., 1981) which can seriously affect estuarine wetlands (Pressey and Middleton, 1982; Middleton *et al.*, 1985). Clearing and filling for canal estates and other developments are often directly adjacent to mangroves and have in some places extended into estuarine wetlands. Some reductions in the extent of mangroves since the 1981 aerial photography were evident in several areas during field work in 1985. The mangrove islands in the Tweed estuary and some other mangroves fringing the mainland remain relatively undisturbed, although there have been proposals for potentially damaging developments in these areas. Mapping of estuarine wetlands in the Tweed estuary over the period 1947 to 1986 shows a reduction of 20 ha (6%) in the extent of mangroves, a more substantial proportional reduction of saltmarsh from 70 to 21 ha (70%) and a reduction in the extent of seagrass of 72% (Walford, 1991, pers. comm.).

Grazing has affected some saltmarsh areas. One of the introduced plants, *Baccharis halimifolia*, which was recorded at one site is a potential invader of other areas. Another potential impact on estuarine wetlands comes from the control of biting midges which breed in intertidal areas. Watson and Watson (1984) believed that control measures were necessary in the Tweed area and that larviciding was probably the best approach. These views are still held strongly by scientists and urban planners (e.g. Allaway and Reye, 1990; Kettle, 1990). The effects of larvicide on non-target organisms are poorly understood, although limited experiments suggest they could be significant (West, 1990) and the impacts are not necessarily restricted to intertidal organisms. Species of rare and threatened butterflies inhabiting mangroves could be affected as well (Sands, 1991 pers. comm.). Control of insects in Queensland saltmarshes is also attempted by runnelling (construction of shallow drainage channels); however, the effects of this on other organisms are not well known (Adam, 1991, pers. comm.).

Floodplain Forest and Vegetation of Dunal Areas

This broad category of vegetation refers to low-lying coastal vegetation in four main physiographic positions, although there is considerable overlap of plant communities between these:

- the dune formations along the coastal strip and inland to the north and west of the Cobaki Broadwater;
- the small coastal floodplains associated with dune formations south of Kingscliff, occurring between bedrock spurs and derived from both marine and fluvial material (Roy, 1975);
- the alluvial and marine deposits surrounding mangroves and saltmarsh of the lower Tweed River such as those around Banora Point and Tweed Heads South;
- remnant areas of floodplain forest without wetland understorey near the floodplain wetlands.

Sixteen plant communities occurring in these areas were identified. The ten forest communities and the three emergent wetland communities were mapped as forest and emergent complexes, respectively. In the following descriptions, information on geology and geomorphology has been taken from Roy (1982).

F1. Littoral rainforest (low to tall simple notophyll-microphyll forest). Floristic composition variable but falls within the *Cupaniopsis anacardioides* and *Syzygium luehmannii — Acmena hemilampra* suballiances of Floyd (1990). Occupies sheltered aspects of Holocene outer barrier dunes where the soils are siliceous sands. Grades into *Banksia integrifolia* var. *integrifolia* forest where exposure to prevailing winds increases; often grades into *Melaleuca quinquenervia* (with or without *Archontophoenix cunninghamiana*) swamp forest downslope as soils become waterlogged. Both suballiances extend into south-eastern Queensland (Floyd, McDonald, 1991, pers. comm.). Conservation: the *C. anacardioides* suballiance is very well reserved over its range but the *S. luehmannii — A. hemilampra* suballiance is inadequately reserved over the southern part of its range in the Bellinger, Nambucca and Macleay Valleys (Floyd, 1990); extensive areas of both suballiances have been destroyed by mineral sand mining; in Tweed Shire, a limited area of each suballiance occurs in Ukerebagh Nature Reserve; remaining areas outside reserves are protected by State Environmental Planning Policy 26 which defines types of developments affecting designated areas of littoral rainforest and surrounding buffer zones for which the consent of local councils and the concurrence of the Director (private proponents) or Minister (Crown proponents) for Planning is required; despite this protection, many areas of the *Cupaniopsis* suballiance are excessively disturbed (Adam, 1991, pers. comm.).

F2. *Lophostemon confertus* tall to very tall closed forest (grading into mallee forest where multi-stemmed due to past fire), usually with an understorey of subtropical rainforest shrubs and small trees. Occurs on Pleistocene barrier sands of marine-aeolian origin but also extends onto sheltered bedrock slopes. Grades diffusely into *Melaleuca quinquenervia* or *Casuarina glauca* swamp forest downslope as soil waterlogging increases. Reported for sand soils in south-eastern Queensland by

Durrington (1977) and McDonald and Elsol (1984). Conservation: inadequately conserved on bedrock soils (Benson, 1989) and those derived from sand; limited areas occur on sand soils in Bundjalung and Broadwater National Parks (Griffith, 1983, 1985).

F3. *Eucalyptus pilularis* very tall open forest. Occurs on freely draining Pleistocene barrier sands of marine-aeolian origin. Grades into *Melaleuca quinquenervia* swamp forest downslope where soil waterlogging occurs. Reported in south-eastern Queensland by Durrington (1977) and McDonald and Elsol (1984). Conservation: a widespread community on the north coast in which the species *Eucalyptus gummifera*, *E. planchoniana* and *Angophora costata* can be present as associates of *E. pilularis*; well represented in reserves including Bundjalung, Yuraygir, Crowdy Head and Myall Lakes National Parks (Griffith, 1983; 1984, Myerscough and Carolin, 1986).

F4. *Callitris columellaris* tall open to closed forest. Occurs on Pleistocene barrier sands of marine-aeolian origin. Grades into *Melaleuca quinquenervia* swamp forest downslope as soil waterlogging increases; *Eucalyptus signata* is an associate in places. Reported for south-eastern Queensland by Batianoff and Elsol (1989) and Durrington (1977). Conservation: very limited areas are reserved over its range on the New South Wales north coast in Broadwater, Bundjalung and Yuraygir National Parks (Griffith, 1983, 1984, 1985); Benson (1989) considers the association to be vulnerable in a state context.

F5. *Eucalyptus tereticornis-E. intermedia-Lophostemon suaveolens* tall to very tall open forest. Typically occurs on Pleistocene backbarrier deposits of estuarine origin. Grades into *Melaleuca quinquenervia* (with or without *Casuarina glauca*) swamp forest downslope as soil waterlogging increases. Reported from south-eastern Queensland by Batianoff and Elsol (1989) while McDonald and Elsol (1984) describe similar, related communities. Conservation: apart from some 200 ha in Yuraygir National Park (Griffith, 1984), only small areas are in reserves on the north coast of the state; examples are occurrences in Ukerebagh Nature Reserve, within Tweed Shire, and in Limeburners Creek Nature Reserve in the Hastings Valley.

F6. *Eucalyptus signata* mid-high to tall open forest and woodland (grading into open mallee forest and woodland on less favourable sites). On poorly drained Pleistocene barrier sands of marine-aeolian origin. Grades into *Eucalyptus robusta* forest or wet heath downslope as soil waterlogging increases. Reported for south-eastern Queensland by Durrington (1977) and McDonald and Elsol (1984). Conservation: overall, adequately reserved in north-eastern New South Wales (Benson, 1989) but, north of the Clarence River, represented on Pleistocene sands only as tiny patches (<2 ha) in Broadwater and Bundjalung National Parks (Griffith, 1983, 1985).

F7. *Eucalyptus robusta* mid-high to very tall open forest (grading into mallee forest and woodland on less favourable sites). Occurs in low-lying, open depressions on Pleistocene backbarrier deposits of estuarine origin. Grades diffusely into *Melaleuca quinquenervia* swamp forest and borders wet heath at some locations. Reported for south-eastern Queensland by Durrington (1977) and McDonald and Elsol (1984). Conservation: considered by Benson (1989) to be adequately reserved state-wide; however, only limited areas are reserved on the far north coast in, for example, Broadwater and Bundjalung National Parks (Griffith, 1983, 1985); *E. robusta* is very poorly reserved in the southern part of its range (Adam, 1991, pers. comm.).

F8. *Melaleuca quinquenervia* tall to very tall open to closed forest (grading into woodland on less favourable sites). Occurs in low-lying open depressions, commonly on

Pleistocene backbarrier deposits of estuarine origin. Grades diffusely into *Eucalyptus robusta* and *Casuarina glauca* swamp forests; commonly borders areas of sedgeland or open water. Reported for south-eastern Queensland by Batianoff and Elsol (1989), Durrington (1977) and McDonald and Elsol (1984). Conservation: adequately reserved state-wide (Benson, 1989) but only as a small proportion of its original extent which has been largely cleared; poorly reserved in Tweed Shire with only very small areas in Stotts Island and Ukerabagh Nature Reserves; extensive in other north coast reserves including Bundjalung, Yuraygir, Crowdy Bay and Myall Lakes National Parks (Griffith, 1983, 1984; Myerscough and Carolin, 1986); most unreserved stands are protected under SEPP 14.

F9. *Archontophoenix cunninghamiana-Melaleuca quinquenervia* very tall feather palm swamp forest. Occurs in areas of impeded drainage at the base of bedrock spurs on colluvial material. Grades into *Melaleuca quinquenervia* swamp forest on sandier soils; formerly graded into moist eucalypt forest and subtropical rainforest upslope on bedrock soils before clearing of these areas. Conservation: the community falls within Floyd's (1990) *Archontophoenix-Livistona* subtropical rainforest suballiance which extends into southern Queensland (Floyd, 1991, pers. comm.) and in which *M. quinquenervia* is a common associate; Floyd (1990) rates the statewide conservation status of this suballiance as good and records that the largest single remaining stand in the state (77 ha) is in Stotts Island Nature Reserve in Tweed Shire.

F10. *Casuarina glauca* tall to very tall open to closed forest. Occurs on Holocene intertidal sediments where soils are saline or sub-saline. Grades into saltmarsh communities downslope towards high tide level and into *Melaleuca quinquenervia* and *Eucalyptus robusta* swamp forests under less saline conditions. Reported for south-eastern Queensland by Batianoff and Elsol (1989) and McDonald and Elsol (1984). Conservation: inadequately reserved state-wide (Benson, 1989); only minor areas reserved in Tweed Shire in Ukerebagh and Stotts Island Nature Reserves; limited areas reserved elsewhere on the north coast, for example in Bundjalung, Yuraygir and Crowdy Bay National Parks (Griffith, 1983, 1984); many unreserved stands are protected under SEPP 14.

Sh. *Banksia aemula* very tall (dry) shrubland to open shrubland. Occurs on Pleistocene barrier sands of marine-aeolian origin, typically on well-drained sand podzol soils. Reduced in stature to a heathland formation (community H1) on aspects exposed to prevailing onshore winds; grades into wet heathland (community H2) where soils become waterlogged. Reported for south-eastern Queensland by Batianoff and Elsol (1989), Durrington (1977) and McDonald and Elsol (1984). Conservation: unreserved in Tweed Shire but well reserved elsewhere on the north coast in, for example, Broadwater, Bundjalung, Yuraygir and Crowdy Bay National Parks (Griffith, 1983, 1984, 1985).

H1. *Banksia aemula* mid-high to tall closed (dry) heathland. Occurs on sand podzol soils derived from Pleistocene barrier sands of marine-aeolian origin. Increases in height to form a shrubland formation (community Sh) where less exposed to prevailing onshore winds; grades into wet heathland (community H2) downslope as soil waterlogging increases. Reported for south-eastern Queensland by Batianoff and Elsol (1989), Durrington (1977) and McDonald and Elsol (1984). Conservation: as for *B. aemula* shrubland.

H2. *Banksia oblongifolia-Leptospermum liversidgei-Lepyrodia interrupta-Sprengelia sprengelioides-Xanthorrhoea fulva* mid-high to tall closed (wet) heathland. Occurs in low-lying open depressions on humus podzol soils derived from Pleistocene barrier sands of marine-aeolian origin. A floristically variable community in which the species by which it is named are characteristic but not always present together. Grades into *Banksia aemula* heathland or *Eucalyptus signata* forest/mallee forest upslope as soil drainage improves; also grades into *Eucalyptus robusta* swamp forest; replaced by sedgeland where soil waterlogging increases. Equivalent, equally variable communities have been recognized for south-eastern Queensland by Batianoff and Elsol (1989) and Durrington (1977). Conservation: as for *B. aemula* shrubland and heathland.

E1. *Baumea rubiginosa* tall closed sedgeland. Occurs in low-lying open depressions on acid peat soils derived from Pleistocene backbarrier deposits of estuarine origin. Grades into *Melaleuca quinquenervia* swamp forest upslope as drainage improves; also grades into *Triglochin procera* forbland. Conservation: unreserved in Tweed Shire but well reserved elsewhere on the north coast in, for example, Bundjalung, Yuraygir and Crowdy Bay National Parks (Griffith 1983, 1984); many near-coastal occurrences would be protected under SEPP 14 although some could occur inland of the limit of SEPP 14 mapping (Adam, 1991, pers. comm.).

E2. *Eleocharis equisetina* tall closed sedgeland. Occurs in open depressions on Holocene tidal delta sand of estuarine origin. Adjacent land has been converted to pasture but formerly probably dominated by *Casuarina glauca* swamp forest. Conservation: only known to be reserved in Hat Head National Park (Pressey, 1989b); very extensive on the floodplains of the north coast (Pressey, 1989a,b) and, although not well conserved there, unlikely to be further affected by flood mitigation or other developments.

E3. *Triglochin procera* tall forbland to tall open forbland. Occurs in open depressions on acid peat soils derived from Pleistocene backbarrier deposits of estuarine origin. Grades into *Melaleuca quinquenervia* swamp forest upslope as drainage improves; also grades into *Baumea rubiginosa* sedgeland. Conservation: a very small area occurs in Yuraygir National Park (Griffith, 1984); present over very small areas on the floodplains of the north coast (Pressey, 1989a,b).

Some vegetation types occur in coastal Tweed Shire which were not sampled during field work. One of these is a significant area of alluvial forest in Stotts Island Nature Reserve. Stotts Island supports the only substantial remnant of lowland floodplain subtropical rainforest in the state and gives an indication of the vegetation which once covered the Tweed floodplain — stands of rainforest on the higher, better-drained soils grading down into *Melaleuca quinquenervia* forest with rainforest understorey, then palm glades and finally treeless swamps (National Parks and Wildlife Service, 1979). Floyd (1990) has identified three suballiances of subtropical rainforest on Stotts Island, one of which, the *Toona-Flindersia* spp. suballiance, is one of two remaining stands of any significance in New South Wales.

Foredune vegetation was not sampled for the present study and includes the following communities, often in a complex mosaic:

- *Spinifex sericeus* low to mid-high tussock grassland of variable crown cover; also reported for south-eastern Queensland by Batianoff and Elsol (1989), Durrington (1977) and McDonald and Elsol (1984).
- *Acacia longifolia* var. *sophorae* low to tall closed shrubland; reported for south-eastern Queensland by W. McDonald (1991, pers. comm.) but reaches northern limit at Coolum;
- *Banksia integrifolia* var. *integrifolia* mid-high to tall open to closed forest (grading into shrubland on more exposed positions); *Eucalyptus intermedia* and *Lophostemon confertus* are occasional associates; reported for south-eastern Queensland by Batianoff and Elsol (1989) and Durrington (1977) and as a *B. integrifolia* — *Melaleuca quinquenervia* map unit by McDonald and Elsol (1984).

The vegetation of a small area of coastal dune on the Fingal Peninsula has also been mapped and described by Murray (1987a). Much of the foredune vegetation in Tweed Shire is regrowth following sand mining and contains non-indigenous taxa such as *Acacia saligna*, *Chrysanthemoides monilifera* ssp. *rotundata* (bitou bush) and *Leptospermum laevigatum*. Extensive stands of *Casuarina equisetifolia* var. *incana* have also been established. Tweed Shire is within the geographic range of this plant but the extent to which it occurred naturally before sand mining is uncertain. Nevertheless, it has been used to characterize a community in south-eastern Queensland (Batianoff and Elsol, 1989; Durrington, 1977; McDonald and Elsol, 1984). Statewide, foredune communities are considered to be adequately conserved (Benson, 1989) but, on the north coast, all are subject to ongoing displacement by bitou bush.

The emergent wetland complex of the dunal areas also includes stands of three unsampled vegetation types to the north of Cudgen Lake:

- *Lepironia articulata* tall closed sedgeland in low-lying open depressions on acid peat soils derived from backbarrier deposits of estuarine origin; reported for south-eastern Queensland by Batianoff and Elsol (1989) and Durrington (1977); unreserved in Tweed Shire although reasonably well represented in reserves elsewhere on the north coast, for example Bundjalung, Yuraygir, Crowdy Bay and Myall Lakes National Parks (Griffith, 1983, 1984; Myerscough and Carolin, 1986); many occurrences outside existing reserves are protected by SEPP 14 although there are some notable exceptions (Adam, 1991, pers. comm.); this association has been sampled in Tweed Shire by Murray (1989);
- *Phragmites australis* rushland;
- *Typha orientalis* rushland.

The *Phragmites* and *Typha* communities have been combined and described for the Cobaki Broadwater area by Murray (1987a), where they were mixed with *Cyperus lucidus*, and for dunal wetlands north of Cudgen Lake by Murray (1989). Benson (1989) lists both communities as adequately conserved and not threatened in coastal New South Wales but only very small areas appear to be in reserves on the north coast.

Another, somewhat variable, sedgeland community is characterized by species such as *Baumea teretifolia*, *Chorizandra sphaerocephala*, *Leptocarpus tenax*, *Restio pallens* and *Schoenus brevifolius*. It is widespread on the north coast in open depressions inundated to a lesser degree than those supporting, for example, *Lepironia articulata* or *Baumea rubiginosa* (E1). The community is equivalent to Goodrick's (1970) 'coastal bog' and, although not observed during this study of the Tweed, is likely to be present as dunal remnants. Indeed, Gilmore *et al.* (1985) reported four of the characteristic species to be conspicuous elements of some sedgelands in the Pottsville area. The community is not known to be reserved in Tweed Shire but is well conserved elsewhere on the north coast in, for example, Bundjalung, Yuraygir and Crowdy Bay National Parks and Booti Booti State Recreation Area (de Castro Lopo, 1980; Griffith, 1983, 1984). Sedgelands of comparable composition have been reported for south-eastern Queensland by Batianoff and Elsol (1989).

Estimates were made of the extent of each of the mapped communities or complexes in the floodplain forest and dunal areas at the time of the field survey in October 1985 (Table 1). The total extent of the forest complex was 2492 ha, shrubland 10 ha, dry heath 56 ha, wet heath 46 ha and the emergent complex 131 ha with an overall total area of natural or near-natural plant associations of 2735 ha remaining at that time. Within the forest complex, the forest remnants on the Tweed floodplain covered only 194 ha — 135 ha in Stotts Island Nature Reserve and 59 ha of small remnants elsewhere on the floodplain. About 92% of the remaining extent of the forest complex in the Shire was therefore adjacent to the estuaries and on the dunal and minor floodplain formations of the narrow coastal strip.

Four hundred and twenty-three plant taxa were recorded from sampling sites within the sixteen communities listed above (Appendix 1). A further 25 taxa were recorded incidentally at other sites. Of the total 448 taxa recorded for the floodplain forest and vegetation of dunal areas, inadequate specimens allowed eight to be identified only to generic level and five to be tentatively identified. The remaining taxa were identified at least to species level. One of the recorded plants is a moss, one a clubmoss, one a selaginella, 21 are ferns, two are conifers, 110 monocotyledons and 312 dicotyledons. Families represented by the most taxa are Fabaceae (40 taxa: Caesalpinioideae 3, Fabiodeae 27, Mimosoideae 10), Poaceae (38 taxa), Myrtaceae (36), Cyperaceae (28), Asteraceae (19), Epacridaceae (16), Rutaceae (12), Euphorbiaceae (11), Lauraceae (11), Proteaceae (10) and Sapindaceae (10).

More sampling would certainly enlarge this list of taxa. The list of bryophytes, in particular, would be considerably enlarged if the less conspicuous forms were collected and recorded. Other recent surveys in Tweed Shire have provided additional locations for the taxa listed and added species to those in Appendix 1. A list of 115 plant species has been compiled for Stotts Island Nature Reserve with indices of abundance in each of several vegetation types (National Parks and Wildlife Service, 1979). Investigation reports by Meehan (1981) and Hunter (1982) listed species for particular localities in and around the Tweed estuary.

Gilmore's (1983) submission to the Tweed Shire Local Environmental Study contains the localities of significant sites for flora and fauna including the names of plants of particular interest. The very detailed survey by Gilmore *et al.* (1985) lists about 340 taxa for an area near Pottsville, many of which were not recorded in the survey reported in this paper. The inclusion of bedrock sites by Gilmore *et al.* (1985) would be an important reason for the many records additional to the present study. Murray (1987a) recorded about 160 taxa from the Wommin Lagoon area on the Fingal Peninsula, Murray (1987b) recorded about 300 taxa near the Cobaki Broadwater, including bedrock areas, and Murray (1989) listed 260 taxa for an area north of Cudgen Lake.

Of the 41 plant species in the study area considered to have particular significance for conservation (Appendix 2), 20 are listed by Briggs and Leigh (1988) as rare or threatened in a national context. Eleven species are significant because of very few records in the state, localities in Tweed Shire near their distributional limits or disjunct occurrences. Another ten are generally rare or uncommon in New South Wales. Thirty-one of the species in Appendix 2 occur on the coastal lowlands surveyed for this study and the other ten occur on adjacent bedrock areas which must be considered in co-ordinated conservation planning for these areas. Of the 20 species listed by Briggs and Leigh (1988), one is considered to be adequately reserved, six to be inadequately reserved while the adequacy of reservation of eleven is not known. The remaining two are listed as unknown from reserves, although another source (Floyd, 1990) indicates that one of these is reserved. The extent of reservation of many of the other species in Appendix 2 is also inadequate or unknown.

Floodplain forest and the vegetation of the dunal areas is highly fragmented and greatly reduced from its original extent due to clearing for agriculture and other activities. Recent clearing for canal estates and other housing developments is widespread and has significantly reduced the extent of some associations since the 1981 aerial photography. A large area of *Eucalyptus signata*, wet heath and other vegetation was cleared in 1985 on the western side of the Cobaki Broadwater. Extensive recent clearing has also affected natural vegetation on Cobaki Creek, *Melaleuca quinquenervia* near Banora Point and *Lophostemon suaveolens* south of Pottsville. Smaller, recent intrusions into stands of vegetation from existing developments are common in the coastal parts of the Shire. Clearing for cane growing in the catchments of the coastal creeks has been accompanied by drainage which has caused settlement of the peaty soils and lowering of ground levels (Soros-Longworth and McKenzie, 1981).

Previous sand mining has greatly modified the vegetation of the immediate coastal strip. Sand dunes adjacent to Cudgen Creek underwent at least three episodes of mining before the mid-seventies (Roy, 1975). Clearing prior to sand mining has removed very extensive areas of littoral rainforest in sheltered areas behind the frontal dune. Littoral rainforest originally occurred in a nearly continuous strip south of the Queensland border to at least the Richmond River (Floyd, 1990). Sand mining has significantly modified the soil profile of areas near Pottsville (Gilmore *et al.*, 1985). Extractive industries also operate inland from the coast. Several sites in old dune deposits were being worked in 1985 near the Cobaki Broadwater and around Coolangatta Airport where vegetation was being cleared.

In many cases, the areas of remaining vegetation have been altered by various activities. Disturbance seen at or near sampling sites includes logging, burning, grazing, drainage, ringbarking and harvesting of paperbark. Gilmore *et al.* (1985) observed a local lowering of the watertable near Pottsville due to canal construction. Clearing in the catchment of Cudgen Lake is probably increasing the rate of sedimentation in this body of water (Roy, 1975). Other wetlands with catchments on the coastal bedrock slopes could also be affected.

The remaining vegetation also contains a large number of introduced species. Forty-three exotic species were recorded during the survey for the present study, 32 exotics were recorded by Gilmore *et al.* (1985), 46 by Murray (1987a), 46 by Murray (1987b) and 31 by Murray (1989). Some of these are particularly troublesome. Groundsel bush, *Baccharis halimifolia*, is a declared noxious weed and occurs in the dunal areas near Pottsville along with lantana, *Lantana camara*, bitou bush, *Chrysanthemoides monilifera*, and other species capable of invading natural vegetation (Gilmore *et al.*, 1985). Bitou bush occurs commonly in the coastal dunes disturbed by sand mining and, in the long-term, could displace littoral rainforest.

GENERAL DISCUSSION

Extent, Decline and Conservation Status

The survey reported here has mapped and described plant communities which occupy a total area of some 3305 ha — 144 ha of floodplain wetlands, 426 ha of mangrove and saltmarsh, and 2735 ha of floodplain forest and vegetation on the dunal formations. The original extent of these communities, as estimated from the total land area below the 10 m contour in the region surveyed, was 26,450 ha. Up until 1985, the plant communities described in this paper had therefore been reduced in extent by over 87%, 97% on the Tweed River floodplain and 80% around the estuaries and along the immediate coastal strip (Table 1).

The extent of clearing would now be somewhat greater. By far the greatest reduction has been in the extent of plant communities grouped here as floodplain forest and vegetation of the dunal areas. Within this broad category, most of the forest of the Tweed floodplain has been cleared. Widespread clearing has also affected the vegetation communities of coastal south-eastern Queensland with which the communities of Tweed Shire have much in common floristically (McDonald and Elsol, 1984).

The plant communities of the low-lying coastal parts of Tweed Shire have not only been greatly reduced in extent but the remaining areas have been fragmented and altered from their original condition by a variety of factors. To these past impacts is added the ongoing pressure for development of the coastal strip where most of the natural vegetation of the survey area remains. Moreover, this small, altered and steadily disappearing resource of native vegetation on the coastal lowlands of Tweed Shire is poorly represented in formal conservation reserves.

Stotts Island Nature Reserve contains the only significant remnant (135 ha) of alluvial forest left in Tweed Shire and 7 ha of floodplain wetland, 5% of the total remaining. The other reserve in the Shire, Ukerebagh Nature Reserve, has a total area of 120 ha and contains about 57 ha of mangroves, 18 ha of saltmarsh and 34 ha of forest complex, including examples of F2 (*Lophostemon confertus*) and F10 (*Casuarina glauca*) and a small patch of littoral rainforest. Overall, the 270 ha in these two reserves represents only 8% of the remaining vegetation on the coastal lowlands of the Shire and 1% of the original vegetation of the same area.

These reserves are far from representative of the plant communities in coastal Tweed Shire. Only alluvial forest, mangroves and saltmarsh are well represented in terms of percentage area. All the sampled forest and emergent wetland communities are either under-represented or completely unrepresented. This situation could be substantially improved by the dedication of two proposed reserves in Tweed Shire, one on the Fingal Peninsula and one in the Cudgen-Mooball area.

Other planning measures in coastal Tweed Shire afford less secure protection than formal reserves but have been effective in slowing the destruction and alteration of native habitats. SEPP 14 covers large areas of wetland, although it has missed some important wetlands. SEPP 26 protects significant areas of littoral rainforest. Mapping of protected lands under the New South Wales Soil Conservation Act, 1938 mainly covers areas with slopes greater than 18 degrees but does identify some parts of the lowlands as environmentally sensitive, including a large area to the north of the Cobaki Broadwater and the coastal dunes of the Fingal Peninsula. There is additional coverage by environmental protection zonings under the Tweed Shire Local Environmental Plan, although these miss floodplain wetlands and some significant patches of vegetation in the dunal areas. Aside from area coverage, these measures provide incomplete protection and have the potential to be removed. There is a clear case for expanding the network of protected areas in the Shire with formal reserves and the more widespread and stringent application of other protection measures.

The location of the new protected areas must be selected and their representativeness judged with criteria additional to the occurrence of plant communities. Four other considerations are important: the general biogeographic significance of the area, the importance of the low-lying coastal vegetation of Tweed Shire to the fauna of a much wider geographical area, the occurrence of rare or threatened plants and animals, and the more general problem of conserving species with limited information on their localities and requirements. These issues are discussed in turn below.

Biogeographical Significance of Tweed Shire

Biogeographically, Tweed Shire lies within a region which Burbidge (1960) called the MacPherson-Macleay Overlap, extending from the MacPherson Range in southern Queensland to the Macleay River in northern New South Wales, in which many of the plant genera of her tropical and temperate zones intermingle. Burbidge also identified many genera endemic to the Overlap.

More recently, the MacPherson-Macleay Overlap has been shown to be a region where several rainforest floristic alliances are interspersed (Webb *et al.*, 1984) and where there is a zone of overlap between megatherm and mesotherm environments with relatively high growth indices, indicating a region where plants with relatively distinct growth response curves to temperature co-occur (Nix, 1982). The biogeographic importance of the MacPherson-Macleay Overlap has also been reinforced by McDonald and Elsol (1984) with their comprehensive analysis of plant species' distributions in coastal regions between Gladstone and Newcastle. They showed that many species reach their northern or southern limits of distribution in this broad region and in the smaller region of south-eastern Queensland and north-eastern New South Wales in which Tweed Shire lies. In another distributional analysis, Turner (1981) estimated that about 25% of the 370 species of rainforest trees and shrubs which extend southward into New South Wales reach their southern distributional limits within one degree of latitude of the border. Many of these have their southern limits in Tweed Shire (Gilmore *et al.*, 1985). The present study and that of Gilmore *et al.* (1985) showed that several non-rainforest plant species also have their southern limits in Tweed Shire or on the far north coast.

Tweed Shire also lies in a region with a diversity of terrestrial vertebrates much higher than most of the Australian land mass (Pianka and Schall, 1981) and where animal, as well as plant, species approach their southern or northern limits of distribution. Among the vertebrate fauna of Tweed and neighbouring Byron Shire are five mammal, 12 bird and one reptile species approaching their southern breeding or distributional limits, four bird, two reptile and two frog species approaching their northern distributional limits and two frogs with a restricted distribution in north-eastern New South Wales and south-eastern Queensland (Gilmore *et al.*, 1985; Milledge, 1986, 1988).

These considerations also apply to invertebrates. Several species of rare and threatened butterflies are near their southern limits in Tweed Shire (Sands, 1979, 1991, pers. comm.; Common and Waterhouse, 1981; Samson, 1989). The mangrove butterfly, *Acrodipsas illidgei*, is very rare and endangered in New South Wales with a range only from Bribie Island south to Brunswick Heads and is confined to old stands of *Avicennia marina*. *Hypochrisops apelles* is endangered, has its southern limit at the Richmond River and is also confined to mangroves. Both species would be at risk in areas which are treated chemically for midges or mosquitoes. *Pseudodipsas cephanes* occurs only in coastal lowland rainforest as far south as Iluka but is rare and becoming rarer and *Hypochrisops digglesii* is now known from only one locality in the state, in dry eucalypt forest fringing rainforest at Broken Head. The New South Wales form of *H. digglesii* is quite distinct morphologically from Queensland specimens.

The biogeographic position of Tweed Shire therefore contributes to the area's conservation significance in three ways: species at or near the ends of their geographic ranges warrant protection because of the likelihood of genetic distinctiveness and the possibility of further adaptation and extension into new habitats; the few known localities of species near the southern limits of their distributions present the only opportunities for retaining these elements of natural diversity in New South Wales; and some species have limited total ranges in and around Tweed Shire.

Wide Faunal Significance of the Tweed Shire Coastal Lowlands

Another reason for the biological significance of Tweed Shire in a broad context is that the coastal lowlands of north-eastern New South Wales and south-eastern Queensland serve as an overwintering area for bats and birds which migrate latitudinally and altitudinally (Porter, 1982; Gilmore *et al.*, 1985; Milledge, 1986; Eby, 1990). This is attributable to two factors. First, the far north coast of New South Wales has higher growth indices for primary production in all seasons than the remainder of south-eastern Australia, a difference which is particularly pronounced in winter when there is a great reduction of plant growth and associated insect activity throughout the south-east (Nix, 1976). Birds and bats are sufficiently mobile to move to the region, and to other regions further north, when resources become limiting elsewhere. Second, extensive stands of winter-flowering trees and shrubs in the region provide a source of nectar and associated insect food for birds and bats. Of the most common trees and shrubs on the Tweed coastal lowlands, *Eucalyptus tereticornis*, *E. robusta*, *Melaleuca quinquenervia*, *Banksia aemula*, *B. integrifolia* and *B. oblongifolia* are known to flower during winter (Clifford and Specht, 1979; Clemson, 1985; Gilmore *et al.*, 1985; Milledge, 1986), as are other species recorded in the study area. Coastal heaths on the far north coast are a very valuable over-wintering resource for the apiary industry (Stace, 1988), indicating their importance for native fauna as well.

The coastal lowlands of Tweed Shire therefore play an important role in maintaining faunal populations over a much larger area. Destruction of this vegetation has wide implications which will become more serious while clearing continues for rural and urban development. Gilmore *et al.* (1985) have also suggested that further reduction of this vegetation could create a gap in the sequence of nectar availability provided by the full suite of plant species, with adverse consequences for the dependent fauna.

The estuarine wetlands of Tweed Shire also have a wider significance for fauna. Research over the last decade has established the importance of estuarine wetlands in New South Wales as feeding and nursery areas for fish, including commercial species and many others which spend their adult stages offshore (Pollard, 1976, 1984).

Rare and Threatened Species

In addition to the biogeographic considerations above, the Shire contains plant species which are listed by Briggs and Leigh (1988) as rare or threatened nationally. Of the 111 rainforest plant species, subspecies or varieties in New South Wales which are rare or threatened nationally, all but ten occur in the north coast subdivision (region 56 of Briggs and Leigh, 1988) and 21% of these are endemic to the region (Floyd, 1990).

The broader region also has a relatively high number of mammals and birds which are rare or threatened in a national context (Woinarski and Braithwaite, 1990). Other species are at risk in a state context. For example, two species of butterflies occurring on the Tweed coast warrant particular attention: *Hypochrisops epicurus*, which is confined to mangroves, and *Ogyris amaryllis*, which is associated with mangroves, *Casuarina glauca*, and certain mistletoes. The first is at risk in New South Wales and the second was locally common but is becoming scarce (Sands, 1991, pers. comm.).

By their nature, these species are difficult to find in a biological survey, even for a single development on one portion of land. They tend to be sparsely distributed locally as well as regionally and some are cryptic or only occasionally present. Continued new findings indicate that unrecorded occurrences of many of the species listed are likely in coastal Tweed Shire. This fact, and the inadequate or uncertain protection of many of these species in reserves, calls for great caution in approving additional developments in the Shire. It also emphasizes the need for detailed surveys and impact assessments to strongly influence the feasibility and design of developments.

Problems of Conserving Species

More species can be at risk in a rapidly developing region than just the ones which have been formally listed as rare or threatened. In such a region, the species not contained in formal reserves or other protected areas in the near future have an uncertain fate. The problem for species conservation is to gather enough information to ensure that a population of each is protected. In reality, a complete data base on all the species in a region is never available. Some will go unrecorded and none will be fully understood in terms of all its occurrences, variations in density or habitat requirements.

For these reasons, conservation planning relies heavily on subdivisions of regions into land classes of some sort, commonly on the basis of vegetation types. These provide the only way of seeing natural variation across the whole region, rather than through the tiny, and often unclear, windows provided by sampling sites. Even in well sampled regions, samples of the biota make up only a fraction of one percent of the landscape (Margules and Stein, 1989).

Although vegetation types or any other land classes are a necessary basis for conservation planning they are not sufficient. Land classes function as surrogates for detailed information on species and as a basis for spatial extension of data collected at some sites. However, no matter how meaningful the land classification used to judge the adequacy of and need for reserves in a region, land classes are always heterogeneous units. Representation of all land classes in a reserve system does not therefore guarantee the protection of all the region's species. Recognition of this limitation underlies the dual approach to reserve selection by the United States Nature Conservancy: a 'coarse filter' approach based on land classes and a 'fine filter' approach based on the species still in need of protection (Noss, 1987).

Intuitively, the species most likely to be missed or under-represented by land class reservation are the ones with the smallest and most patchy distributions. Other species which are threatened because of sensitivity to changes wrought by European settlement also warrant particular attention in a conservation strategy. Close attention to rare and threatened species in planning the land use of a region is therefore a logical complement to the protection of samples of each land class, a 'fine filter' approach to increase the likelihood of all species being protected.

Although logical, this complementary approach to conservation planning has an important limitation. It assumes that the only species which will slip through the 'coarse filter' and need special attention are the ones on an *a priori* list of rare or threatened plants and animals. The number of species missed by land class reservation can be large (Pressey and Bedward, 1991) and little work has been done on the characteristics of species most likely to require 'fine filter' strategies. There is thus no way to guarantee complete representation of species in a region's reserves unless sites where each species is known to occur and persist in the required numbers are included in the reserve network. Not only is this information seldom available for any significant number of species in a region but the reserve area required to achieve such a coverage would generally be prohibitively large.

Another limitation of plant communities as a basis for conservation planning is that they are incomplete reflections of faunal habitat (Pressey and Bedward, 1992). *A priori* vegetation types or other land classes are not necessarily the best descriptors of faunal habitat. In addition, plant communities do not necessarily delineate or highlight areas of critical resources such as drought refuges and overwintering areas and some animal species require combinations of vegetation types, often poorly defined, to satisfy all their needs. Without specific information on the habitat requirements of each species, some areas of particular importance to fauna might be overlooked in a conservation strategy. For example, some parts of estuarine wetlands and other areas fringing intertidal mudflats of the lower Tweed River are important as high tide roosts for wading birds. Martindale (1987) identified ten such roosts in the Tweed estuary and stressed that destruction or disturbance of these areas will adversely affect the ability of the wading birds to exploit food resources. Hunter (1982) recorded that Womgin Island in the Terranora Broadwater supported a camp of about 1200-1500 black fruit bats (*Pteropus alecto*), although the bats are known to move from one island to another periodically. Such information is impossible to glean from a classification of the landscape and stresses the importance of autecological data. The problems of temporal variation in species occurrence and habitat suitability add an extra layer of complexity to the problem.

All these examples demonstrate the difficulty of conserving species in a relatively well-studied region because of the inevitably limited information on distributions, densities and requirements of plants and animals. Species and their particular needs can be overlooked, even by a comprehensive conservation strategy which delineates large areas for environmental protection. The limitations of available information and planning call for extreme caution in making decisions which permanently alienate natural habitat in a region such as the Tweed.

The Future

The remaining natural vegetation on the coastal lowlands of Tweed Shire is diverse in terms of communities, plant species and animal habitat and contains many species which are rare, threatened or geographically significant. The area of the plant communities mapped in 1985 represented only about 12% of the original vegetation of the coastal lowlands. Perhaps less than 10% now remains. Formal reserves in the study area total 270 ha, about one percent of the original area, and fail to represent much of the natural diversity described and mapped, although additional natural diversity is protected by less secure means.

Decisions on land use planning by local and state government have had and will continue to have serious ecological implications, not only for the biota of the Shire but also in a much wider context. The coastal parts of Tweed Shire are nationally significant biogeographically and because of the rare and threatened species present. The fauna of a large section of south-eastern Australia relies on the study area and the surrounding region as an over-wintering resource. Finally, as in any region, there are many limitations on adequately protecting species which call for a highly conservative approach to planning.

These facts put a weighty responsibility on the relevant planning authorities. They indicate the urgent need for more extensive and stringent application of existing measures for protection and challenge the justification for any further clearing of the study area. A sound basis for adequate planning and management of the remaining habitats requires four things:

- a comprehensive compilation of the data available on natural environments and species, regularly updated as new information becomes available;
- further surveys of the area, designed to fill the geographical gaps in the existing data base and to provide information on the requirements of selected species;
- immediate controls on further clearing and degradation of the remaining naturally vegetated parts of the lowlands with the onus resting on proponents of developments to demonstrate no significant impacts on the natural features of the area;
- delineation of a comprehensive network of protected areas, considering the needs for formal reservation and complementary zonings, which is regularly updated as conservation goals, data and information on the condition and extent of natural areas are refined.

The conservation of habitats and species in New South Wales, as elsewhere, is an understaffed and underfunded enterprise, reflecting the relatively low priority placed on conservation by the electorate and, therefore, by politicians. Environmental planning in coastal Tweed Shire and in many other regions is therefore beset, not only by lack of political commitment, but by lack of information. The way to adequately protect the area's natural diversity is only dimly perceived at present. A clear view and a real chance to conserve that diversity need more from planning authorities than has been given so far.

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APPENDIX 1

*Plant species list for the study area. Plant community codes — FL: floodplain wetland complex; S: saltmarsh complex (three communities); F: forest complex (ten communities); Sh: shrubland; H1: dry heath; H2: wet heath; E: emergent wetland complex of the dunal areas (three communities). Other symbols — * indicates introduced species; ?* indicates possibly introduced; ? and *? indicate tentative identification; (Hb) indicates herbarium record; (D) indicates recorded in dunal areas but not during systematic sampling. Unless otherwise indicated, authorities for plant names are those in Harden (1990) or, for families not included in this publication, in Jacobs and Pickard (1981) as amended by Jacobs and Lapinpuro (1986)*

Taxa	**Plant Community Codes**																				
	FL	S1	S2	S3	M	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	Sh	H1	H2	E1	E2	E3
MOSSES																					
SPAGNACEAE																					
Sphagnum sp.																		H2			
LIVERWORTS																					
RICCIACEAE																					
Ricciocarpus natans (L.) Corda	FL																				
CLUBMOSSES																					
LYCOPODIACEAE																					
Lycopodium cernuum (D)																					
SELAGINELLAS																					
SELAGINELLACEAE																					
Selaginella uliginosa																		H2			
FERNS																					
ASPLENIACEAE																					
Asplenium australasicum						F1			F4												
AZOLLACEAE																					
Azolla filiculoides var. *rubra*	FL																			E2	
A. pinnata	FL																				
BLECHNACEAE																					
Blechnum cartilagineum							F2						F8	F9							
B. indicum	FL						F2	F3				F7	F8	F9					E1		

Taxa	Plant Community Codes																				
	FL	S1	S2	S3	M	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	Sh	H1	H2	E1	E2	E3
CYATHEACEAE																					
Cyathea cooperi														F9							
DENNSTAEDTIACEAE																					
Histiopteris incisa												F7	F8								
Hypolepis muelleri	FL					F1	F2					F7	F8	F9							
Pteridium esculentum						F1	F2	F3	F4	F5	F6	F7	F8			Sh	H1				
DICKSONIACEAE																					
Calochlaena dubia							F2			F5											
GLEICHENIACEAE																					
Gleichenia dicarpa													F8								
LINDSAEACEAE																					
Lindsaea fraseri (D)																					
L. linearis (D)																					
OSMUNDACEAE																					
Todea barbara						F1															
POLYPODIACEAE																					
Platycerium bifurcatum						F1	F2		F4				F8								
Pyrrosia rupestris									F4												
PTERIDACEAE																					
Acrostichum speciosum			S2																		
Pteris vittata							F2														
SCHIZAEACEAE																					
Lygodium microphyllum						F1	F2						F8	F9	F10						
SINOPTERIDACEAE																					
Pellaea falcata						F1															
P. paradoxa						F1															
THELYPTERIDACEAE																					
Christella dentata														F9							
Cyclosorus interruptus	FL												F8	F9	F10						
CONIFERS																					
ARAUCARIACEAE																					
Araucaria cunninghamii						F1								F9							
CUPRESSACEAE																					
Callitris columellaris									F4												
ANGIOSPERMS – MONOCOTYLEDONS																					
AGAVACEAE																					
Cordyline congesta (Sweet) Steudel						F1	F2			F5		F7	F8	F9							
AMARYLLIDACEAE																					
Crinum pedunculatum													F8	F9	F10						
ARACEAE																					
Alocasia macrorrhizos														F9							
* *Colocasia esculenta*	FL																				
Pothos longipes														F9							
ARECACEAE																					
Archontophoenix cunninghamiana						F1	F2						F8	F9							
Linospadix monostachya							F2														
Livistona australis						F1							F8								
COMMELINACEAE																					
Commelina cyanea	FL					F1	F2		F4	F5			F8		F10						
CYPERACEAE																					
Baumea articulata	FL												F8		F10						
B. juncea				S3											F10						
B. muelleri																		H2			
B. rubiginosa	FL												F8						E1		E3

Taxa	**Plant Community Codes**																				
	FL	S1	S2	S3	M	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	Sh	H1	H2	E1	E2	E3
Bolboschoenus caldwellii	FL																				
B. fluviatilis	FL																				
Bulbostylis barbata																	H1				
Carex appressa	FL													F9							
C. fascicularis	FL																				
C. gaudichaudiana	FL																				
C. neurochlamys	FL																				
C. sp.													F8								
Caustis recurvata											F6					Sh	H1				
Chorizandra cymbaria													F8								
Cladium procerum (D)																					
?* *Cyperus brevifolius*	FL																				
C. elatus L.															F10						
C. enervis							F2		F4	F5											
* *C. eragrostis*	FL																				
C. exaltatus	FL																				
C. haspan	FL												F8								
C. lucidus	FL												F8							E2	
C. pilosus	FL																				
?* *C. polystachyos*	FL														F10						
C. sanguinolentus	FL																				
C. sphaeroideus															F10						
C. sp.						F1	F2		F4	F5			F8	F9	F10						
(Hb) *Eleocharis dulcis*	FL																				
E. equisetina	FL																			E2	
?* *E. minuta*	FL																				
E. sphacelata	FL																				
Fimbristylis ferruginea		S1		S3											F10						
Gahnia clarkei	FL						F2			F5		F7									
G. sieberana																		H2	E1		
G. sp.										F5		F7	F8								
Isolepis inundata	FL												F8								
* *I. prolifera*	FL																				
Lepidosperma laterale R. Br.								F3													
Lepironia articulata	FL												F8								
Rhynchospora corymbosa	FL																				
?* *Schoenoplectus litoralis* (D)	FL																				
S. mucronatus	FL																				
S. validus	FL																				
Schoenus brevifolius				S3									F8					H2	E1		
S. ericetorum																	H1				
S. nitens	FL																				
DIOSCOREACEAE																					
Dioscorea transversa						F1	F2														
FLAGELLARIACEAE																					
Flagellaria indica						F1	F2							F9	F10						
HYDROCHARITACEAE																					
Ottelia ovalifolia	FL																			E2	
IRIDACEAE																					
Patersonia sericea																Sh	H1				
JUNCACEAE																					
Juncus kraussii		S1	S2	S3																	
J. polyanthemus	FL																				
J. polyanthemus x *usitatus*	FL																				
J. prismatocarpus	FL																				
J. usitatus	FL																				

Taxa	Plant Community Codes																				
	FL	S1	S2	S3	M	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	Sh	H1	H2	E1	E2	E3
JUNCAGINACEAE																					
Triglochin procera																					E3
T. striata	FL	S1													F10						
LEMNACEAE																					
Lemna minor	FL																				
Spirodela oligorrhiza	FL																				
S. sp.																				E2	
LILIACEAE																					
* *Asparagus densiflorus*						F1															
Dianella caerulea						F1	F2	F3	F4	F5		F7	F8		F10						
D. revoluta										F5	F6										
* *Gloriosa superba*						F1															
Tricoryne elatior (D)																					
ORCHIDACEAE																					
Acianthus fornicatus											F6										
Cryptostylis sp.							F2	F3													
Cymbidium suave							F2			F5		F7									
Pterostylis sp.							F2						F8								
PANDANACEAE																					
Pandanus pedunculatus						F1															
PHILESIACEAE																					
Eustrephus latifolius							F2			F5		F7	F8								
Geitonoplesium cymosum						F1	F2		F4	F5		F7	F8	F9	F10						
PHILYDRACEAE																					
Philydrum lanuginosum	FL												F8								
POACEAE																					
Agrostis avenacea var. *avenacea*	FL																				
* *Andropogon virginicus*										F5		F7	F8								
Aristida warburgii (D)																					
* *Axonopus affinis*						F1				F5		F7			F10						
* *Chloris gayana* (D)																					
Cymbopogon refractus										F5											
Cynodon dactylon										F5											
Digitaria parviflora							F2			F5											
? *D.* sp.	FL																				
Diplachne fusca															F10						
Entolasia marginata												F7	F8		F10						
E. stricta							F2	F3				F7	F8					H2			
Eragrostis interrupta (D)																					
Eriochloa procera															F10						
Hemarthria uncinata				S3									F8								
Imperata cylindrica var. *major*						F1	F2	F3		F5	F6	F7	F8								
Isachne globosa (D)																					
Ischaemum australe				S3									F8		F10						
Leersia hexandra	FL												F8	F9							
* *Melinis minutiflorus*										F5											
Microlaena stipoides var. *stipoides*								F3													
Oplismenus aemulus						F1	F2							F9							
O. imbecillis						F1	F2						F8								
O. sp.												F7		F9							
Ottochloa gracillima						F1									F10						
Panicum obseptum	FL																				
P. simile							F2				F6						H1				
Paspalidium distans																	H1				
P. ? gausum										F5											

Taxa	Plant Community Codes																				
	FL	S1	S2	S3	M	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	Sh	H1	H2	E1	E2	E3
* *Paspalum conjugatum*														F9	F10						
P. distichum	FL																			E2	
P. orbiculare										F5			F8								
* *P. urvillei*															F10						
P. vaginatum	FL														F10						
Phragmites australis	FL												F8	F9	F10						
* *Rhynchelytrum repens*										F5											
Sacciolepis indica										F5			F8		F10						
* *Setaria sphacelata*	FL																				
* *Sporobolus africanus*										F5											
S. virginicus		S1	S2	S3																	
Stenotaphrum secundatum						F1															
Themeda australis										F5	F6						H1				
Zoysia macrantha (D)																					
POTAMOGETONACEAE																					
Potamogeton javanicus	FL																				
RESTIONACEAE																					
Hypolaena fastigiata																	H1				
Leptocarpus tenax																		H2			
Lepyrodia interrupta																Sh		H2			
L. muelleri																			E1		
Restio pallens													F8					H2	E1		
R. tetraphyllus ssp. *meiostachyus*											F6	F7						H2			
SMILACACEAE																					
Ripogonum album							F2			F5				F9							
Smilax australis						F1	F2		F4	F5		F7	F8	F9	F10						
S. glycipylla						F1	F2	F3		F5	F6	F7		F9							
SPARGANIACEAE																					
Sparganium antipodum	FL																				
TYPHACEAE																					
Typha orientalis (D)	FL																				
XANTHORRHOEACEAE																					
Lomandra elongata																Sh					
L. longifolia						F1	F2	F3	F4	F5	F6	F7	F8								
Xanthorrhoea fulva (A. Lee) Bedford																		H2			
X. johnsonii																Sh	H1				
X. macronema								F3			F6										
ZINGIBERACEAE																					
Alpinia caerulea						F1	F2			F5		F7		F9							
ANGIOSPERMS — DICOTYLEDONS																					
AIZOACEAE																					
Carpobrotus glaucescens (D)																					
Macarthuria neocambrica (D)																					
Sesuvium portulacastrum		S1																			
AMARANTHACEAE																					
Alternanthera denticulata	FL													F9	F10						
Deeringia amaranthoides						F1															
ANACARDIACEAE																					
Euroschinus falcata var. *falcata*						F1				F5											
ANNONACEAE																					
Ancana stenopetala						F1															
Polyalthia nitidissima						F1	F2														

Taxa	**Plant Community Codes**																				
	FL	S1	S2	S3	M	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	Sh	H1	H2	E1	E2	E3
APIACEAE																					
Apium prostratum ssp. *prostratum*				S3											F10						
Hydrocotyle acutiloba (F. Muell.) N. A. Wakef.						F1															
* *H. bonariensis*	FL																				
H. verticillata															F10						
Platysace ericoides											F6						H1				
Trachymene sp.												F7									
APOCYNACEAE																					
Alyxia ruscifolia						F1															
Melodinus australis														F9							
Parsonsia straminea var. *straminea*				S3		F1	F2			F5			F8	F9	F10						
ARALIACEAE																					
Astrotricha latifolia								F3			F6	F7									
Polyscias elegans						F1			F4	F5											
* *Schefflera actinophylla* (Endl.) Harms						F1	F2			F5		F7									
ARISTOLOCHIACEAE																					
Aristolochia praevenosa						F1															
ASCLEPIADACEAE																					
Cynanchum carnosum			S2	S3											F10						
Hoya australis						F1															
Marsdenia fraseri (D)																					
M. rostrata													F8								
Tylophora crebriflora						F1															
ASTERACEAE																					
* *Ageratina adenophora*													F8	F9							
* *A. riparia*	FL													F9							
* *Ageratum houstonianum*	FL																				
* *Ambrosia tenuifolia*										F5											
* *Aster subulatus*				S3									F8		F10						
* *Baccharis halimifolia*				S3						F5			F8	F9	F10					E2	
?* *Bidens pilosa*										F5											
* *Chrysanthemoides monilifera* ssp. *rotundata*						F1				F5											
* *Conyza bonariensis*								F3		F5											
* *C. parva*								F3		F5											
* *Coreopsis lanceolata* (D)																					
* *Crassocephalum crepidioides*														F9	F10						
Eclipta platyglossa															F10						
E. prostrata														F9	F10					E2	
Enydra fluctuans													F8		F10						
Helichrysum apiculatum																	H1				
* *Hypochoeris radicata*						F1															
Senecio lautus ssp. *lanceolatus*										F5											
Sigesbeckia orientalis							F2			F5											
Vernonia cinerea							F2	F3		F5			F8								
AVICENNIACEAE																					
Avicennia marina var. *australasica*		S1	S2		M																
BAUERACEAE																					
Bauera capitata																		H2			
BIGNONIACEAE																					
Pandorea jasminoides						F1															
P. pandorana ssp. *pandorana*						F1						F7									

Taxa	**Plant Community Codes**																			
	FL	S1	S2	S3	M	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	Sh	H1	H2	E1	E2	E3
BRASSICACEAE																				
Cardamine paucijuga	FL																			
?* *Rorippa* sp.	FL																			
CARYOPHYLLACEAE																				
Drymaria cordata ssp. *diandra*	FL																			
CASUARINACEAE																				
Allocasuarina littoralis										F5						Sh				
Casuarina equisetifolia (D)																				
C. glauca	FL		S2	S3		F1	F2						F8		F10					E2	
CELASTRACEAE																				
Cassine australis (Vent.) Kuntze var. *australis*						F1														
Denhamia celastroides (F. Muell.)						F1	F2							F9						
Loeseneriella barbata						F1														
CHENOPODIACEAE																				
Einadia nutans ssp. *linifolia*												F7								
Sarcocornia quinqueflora		S1																		
Suaeda australis		S1													F10					
CONVOLULACEAE																				
Convolvulus erubescens										F5										
Dichondra repens													F8							
* *Ipomoea cairica*						F1	F2			F5			F8	F9	F10					E2	
CUCURBITACEAE																				
Diplocyclos palmatus						F1														
DILLENIACEAE																				
Adrastaea salicifolia																		H2		
Hibbertia aspera (D)																				
H. dentata													F8							
H. fasciculata																Sh	H1			
H. linearis											F6									
H. scandens						F1	F2	F3		F5			F8	F9						
DROSERACEAE																				
Drosera auriculata																		H2		
D. spathulata																		H2		
EBENACEAE																				
Diospyros fasciculosa						F1														
D. pentamera						F1														
ELAEOCARPACEAE																				
Elaeocarpus grandis						F1														
E. obovatus						F1	F2					F7								
E. reticulatus						F1	F2	F3		F5	F6	F7	F8							
EPACRIDACEAE																				
Brachyloma daphnoides																	H1			
B. scortechinii											F6									
Epacris microphylla																		H2		
E. obtusifolia																		H2		
E. pulchella																Sh	H1	H2		
Leucopogon deformis																	H1			
L. ericoides											F6						H1			
L. lanceolatus var. *gracilis*						F1				F5	F6	F7								
L. leptospermoides									F4		F6	F7				Sh	H1	H2		
L. margarodes								F3	F4	F5	F6	F7								
L. virgatus																	H1			
Monotoca elliptica						F1			F4	F5	F6					Sh				
M. scoparia											F6					Sh	H1			
Sprengelia sprengelioides																		H2		

Taxa	Plant Community Codes																				
	FL	S1	S2	S3	M	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	Sh	H1	H2	E1	E2	E3
Styphelia viridis											F6					Sh					
Trochocarpa laurina						F1	F2			F5				F9							
EUPHORBIACEAE																					
Actephila lindleyi						F1															
Breynia oblongifolia						F1	F2		F4	F5		F7	F8	F9							
Drypetes australasica						F1	F2			F5				F9							
Excoecaria agallocha					M										F10						
Glochidion ferdinandi						F1	F2	F3		F5		F7	F8	F9							
G. sumatranum						F1	F2	F3		F5		F7	F8	F9	F10						
Macaranga tanarius						F1	F2			F5		F7		F9							
Mallotus discolor						F1															
Omalanthus populifolius						F1	F2					F7		F9							
Pseudanthus orientalis																					
Ricinocarpos pinifolius																	H1				
EUPOMATIACEAE																					
Eupomatia laurina						F1	F2														
FABACEAE																					
Sub-Family CAESALPINIOIDEAE																					
Caesalpinia scortechinii							F2														
* *Cassia coluteoides*						F1	F2														
* *C. floribunda*						F1							F8								
Sub-Family FABOIDEAE																					
Aotus ericoides											F6	F7				Sh	H1	H2			
A. lanigera																		H2			
Bossiaea ensata																	H1				
B. heterophylla																Sh					
Chorizema parviflorum (D)																					
?* *Crotalaria incana*										F5											
Daviesia arborea									F4												
D. umbellulata (D)																					
Desmodium nemorosum													F8								
D. rhytidophyllum						F1				F5											
* *D. uncinatum* (Jacq.) DC.														F9							
D. varians									F4												
Dillwynia floribunda var. *floribunda*																		H2			
D. retorta											F6					Sh					
Glycine clandestina										F5											
Gompholobium virgatum											F6					Sh	H1				
Hovea acutifolia							F2	F3	F4	F5		F7									
Indigofera australis										F5											
Jacksonia scoparia																	H1				
Kennedia rubicunda						F1	F2	F3	F4	F5	F6	F7									
Kunstleria blackii														F9							
* *Macroptilium atropurpureum* (D)																					
Millettia megasperma														F9							
Mucuna gigantea						F1															
Oxylobium robustum								F3	F4			F7									
Phyllota phylicoides																		H2			
Pultenaea villosa								F3													
Sub-Family MIMOSOIDEAE																					
Acacia aulacocarpa									F4	F5	F6										
A. baueri ssp. *baueri*																	H1				
A. longifolia var. *sophorae*						F1							F8				H1				

Taxa	**Plant Community Codes**																				
	FL	S1	S2	S3	M	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	Sh	H1	H2	E1	E2	E3
A. longissima								F3													
A. maidenii	FL																				
A. melanoxylon						F1	F2					F7	F8								
A. obtusifolia											F6	F7									
A. saligna (D)																					
A. suaveolens											F6					Sh	H1				
A. ulicifolia									F4		F6	F7				Sh	H1				
Archidendron hendersonii (F. Muell.)						F1	F2														
GOODENIACEAE																					
Dampiera stricta																	H1				
HALORAGACEAE																					
Gonocarpus micranthus ssp. *ramosissimus*																		H2			
G. tetragynus								F3													
* *Myriophyllum aquaticum*	FL																				
LAURACEAE																					
Cassytha glabella																Sh	H1	H2			
C. pubescens											F6	F7				Sh	H1	H2			
* *Cinnamomum camphora*						F1	F2			F5		F7	F8	F9							
Cryptocarya foetida						F1	F2														
C. microneura						F1	F2						F8	F9							
C. triplinervis						F1	F2			F5				F9							
Endiandra discolor						F1	F2			F5			F8	F9							
E. globosa														F9							
E. sieberi							F2	F3		F5		F7									
Litsea australis						F1	F2							F9							
Neolitsea dealbata													F8	F9							
LENTIBULARIACEAE																					
Utricularia australis																				E2	
U. lateriflora																		H2			
LOBELIACEAE																					
Lobelia alata															F10						
L. trigonocaulis						F1															
Pratia purpurascens										F5			F8								
LORANTHACEAE																					
Dendrophthoe vitellina													F8								
MALVACEAE																					
Hibiscus diversifolius						F1							F8		F10						
H. splendens													F8								
H. tiliaceus					M										F10						
MELASTOMATACEAE																					
Melastoma affine						F1		F3		F5			F8								
MELIACEAE																					
Dysoxylum rufum						F1															
Synoum glandulosum							F2							F9							
MENISPERMACEAE																					
Hypserpa decumbens						F1															
Stephania japonica						F1	F2			F5		F7	F8	F9							
MENYANTHACEAE																					
Villarsia exaltata													F8		F10						
MONIMIACEAE																					
Wilkiea heugeliana														F9							
MORACEAE																					
Ficus coronata						F1							F8	F9							
F. fraseri						F1															
F. obliqua						F1															

Taxa	Plant Community Codes																				
	FL	S1	S2	S3	M	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	Sh	H1	H2	E1	E2	E3
F. rubiginosa						F1			F4												
F. superba var. *henneana*														F9							
F. virens														F9							
F. watkinsiana						F1															
Maclura cochinchinensis						F1	F2			F5			F8	F9	F10						
Malaisia scandens						F1	F2														
MYRSINACEAE																					
Aegiceras corniculatum					M																
Embelia australiana														F9							
Rapanea howittiana														F9	F10						
R. subsessilis						F1															
R. variabilis						F1				F5											
MYRTACEAE																					
Acmena hemilampra						F1															
A. smithii						F1	F2	F3		F5		F7	F8	F9	F10						
Archirhodomyrtus beckleri														F9							
Austromyrtus dulcis						F1	F2	F3	F4	F5	F6	F7				Sh					
Baeckea linearis																Sh	H1				
B. stenophylla									F4									H2			
Callistemon pachyphyllus													F8					H2	E1		E3
C. salignus	FL					F1	F2	F3		F5		F7	F8	F9	F10						
Eucalyptus grandis							F2							F9							
E. gummifera								F3			F6										
E. intermedia							F2		F4	F5		F7				Sh					
E. pilularis								F3													
E. propinqua													F8								
E. robusta	FL										F6	F7	F8					H2			
E. signata									F4		F6										
E. tereticornis										F5											
Homoranthus virgatus											F6					Sh	H1				
Leptospermum attenuatum											F6										
L. flavescens								F3			F6	F7				Sh					
L. juniperinum													F8								
L. laevigatum																	H1				
L. liversidgei																		H2	E1		
L. semibaccatum																	H1				
L. whitei								F3			F6	F7				Sh		H2			
Lophostemon confertus							F2	F3		F5	F6	F7	F8			Sh					
L. suaveolens	FL						F2	F3		F5			F8								
Melaleuca linariifolia	FL												F8								
M. quinquenervia	FL			S3		F1	F2	F3		F5		F7	F8	F9	F10			H2	E1		E3
M. thymifolia																		H2			
Pilidiostigma glabrum							F2														
Rhodomyrtus psidioides						F1															
Syzygium coolminianum							F2			F5											
S. francisii														F9							
S. luehmannii						F1	F2														
S. oleosum (F. Muell.) B. Hyland						F1	F2			F5			F8								
Tristaniopsis laurina						F1															
NYCTAGINACEAE																					
* *Bougainvillaea spectabilis* Willd.										F5											
NYMPHAEACEAE																					
* *Nymphaea capensis*	FL																				
OCHNACEAE																					
* *Ochna serrulata*						F1	F2						F8	F9							

Taxa	**Plant Community Codes**																				
	FL	S1	S2	S3	M	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	Sh	H1	H2	E1	E2	E3
OLACACEAE																					
Olax retusa																		H2			
OLEACEAE																					
Jasminum volubile						F1															
* *Ligustrum sinense*							F2						F8								
Notelaea longifolia						F1	F2			F5											
ONAGRACEAE																					
Ludwigia octovalvis (D)	FL																				
L. peploides ssp. *montevidensis*	FL																			E2	
* *L. peruviana*															F10						
PASSIFLORACEAE																					
* *Passiflora edulis*						F1	F2					F7									
P. herbertiana										F5											
* *P. suberosa*												F7									
* *P. subpeltata*						F1	F2			F5			F8	F9							
PITTOSPORACEAE																					
Pittosporum revolutum						F1	F2		F4	F5		F7			F10						
POLYGALACEAE																					
Comesperma defoliatum																		H2			
POLYGONACEAE																					
Persicaria attenuata	FL																			E2	
P. decipiens	FL																			E2	
P. dichotoma	FL																				
P. hydropiper	FL														F10					E2	
P. orientalis	FL																				
P. strigosa													F8	F9						E2	
P. strigosa/praetermissa	FL																				
P. subsessilis	FL																				
* *Rumex crispus*	FL																				
PRIMULACEAE																					
Samolus repens		S1																			
PROTEACEAE																					
Banksia aemula											F6					Sh	H1				
B. integrifolia						F1	F2		F4	F5											
B. oblongifolia																	H1	H2			
B. robur								F3					F8					H2			
Conospermum taxifolium																	H1				
Lomatia silaifolia (D)																					
Persoonia attenuata						F1															
P. cornifolia						F1		F3	F4	F5						Sh					
P. virgata											F6					Sh		H2			
Strangea linearis																Sh	H1				
RANUNCULACEAE																					
Clematis glycinoides						F1															
Ranunculus inundatus	FL													F9	F10					E2	
R. plebius	FL																				
RHAMNACEAE																					
Alphitonia excelsa						F1	F2			F5		F7	F8								
RHIZOPHORACEAE																					
Bruguiera gymnorrhiza			S2		M																
Rhizophora stylosa					M																
ROSACEAE																					
Rubus hillii														F9							
R. parvifolius						F1				F5											
R. rosifolius														F9							

Taxa	Plant Community Codes																				
	FL	S1	S2	S3	M	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	Sh	H1	H2	E1	E2	E3
RUBIACEAE																					
Canthium odoratum						F1															
Coelospermum paniculatum						F1	F2														
Hodgkinsonia ovatiflora						F1															
Morinda jasminoides						F1	F2														
Pomax umbellata								F3	F4	F5	F6		F8								
Psychotria loniceroides						F1	F2														
RUTACEAE																					
Acronychia imperforata						F1	F2		F4	F5		F7									
A. littoralis T. Hartley & J. Williams						F1			F4												
A. wilcoxiana						F1	F2														
Boronia falcifolia																		H2			
B. parviflora													F8								
B. rosmarinifolia											F6										
Euodia elleryana						F1	F2						F8								
Flindersia bennettiana						F1	F2														
F. schottiana						F1															
Halfordia kendack						F1	F2														
Zieria laevigata											F6					Sh	H1				
Z. smithii							F2					F7	F8								
SANTALACEAE																					
Exocarpos latifolius						F1	F2														
Lepotomeria acida											F6							H2			
SAPINDACEAE																					
Alectryon coriaceus						F1															
Arytera divaricata						F1															
Cupaniopsis anacardioides						F1	F2			F5			F8		F10						
Dodonaea triquetra									F4	F5	F6		F8			Sh					
Guioa semiglauca						F1	F2						F8	F9							
Harpullia hillii						F1															
Jagera pseudorhus						F1	F2						F8	F9							
Lepiderema pulchella Radlk. (D)																					
Mischocarpus pyriformis						F1	F2		F4	F5				F9							
Sarcopteryx stipitata													F8								
SAPOTACEAE																					
Planchonella chartacea						F1	F2							F9							
P. laurifolia						F1															
SCROPHULARIACEAE																					
Bacopa monnieri	FL														F10						
SIMAROUBACEAE																					
Ailanthus triphysa						F1															
SOLANACEAE																					
Duboisia myoporoides						F1						F7									
* *Solanum mauritianum*							F2					F7	F8	F9	F10						
* *S. nigrum*														F9	F10						
* *S. seaforthianum*						F1															
STERCULIACEAE																					
Commersonia bartramia						F1	F2														
Sterculia quadrifida						F1															
SYMPLOCACEAE																					
Symplocos stawellii						F1	F2							F9							
THYMELAEACEAE																					
Pimelia linifolia											F6						H1	H2			
Wikstroemia indica										F5											

Taxa	**Plant Community Codes**																				
	FL	S1	S2	S3	M	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	Sh	H1	H2	E1	E2	E3
TREMANDRACEAE																					
Tetratheca thymifolia																	H1				
ULMACEAE																					
Aphananthe philippinensis														F9							
Celtis paniculata						F1															
Trema aspera						F1	F2														
URTICACEAE																					
Dendrocnide moroides						F1															
D. photinophylla						F1															
VERBENACEAE																					
Clerodendrum floribundum						F1	F2			F5											
Gmelina leichhardtii						F1															
* *Lantana camara*						F1	F2		F4	F5		F7	F8	F9	F10						
VIOLACEAE																					
Viola hederacea						F1	F2			F5		F7	F8		F10						
VITACEAE																					
Cayratia clematidea							F2														
C. eurynema B. L. Burtt						F1															
Cissus antarctica						F1								F9							
C. hypoglauca						F1	F2			F5			F8								
C. sterculiifolia						F1	F2														
WINTERACEAE																					
Tasmannia insipida							F2														

APPENDIX 2

Plant species of particular conservation significance. Numbers of sites refer to sampling sites for this study; locality information also includes some areas of bedrock on Round Mountain and adjacent to extensive wetlands south of Pottsville and south of the Cobaki Broadwater because of the need to consider these jointly with low-lying lands in conservation planning; authorities given only for species not in Appendix 1 or not covered by sources for Appendix 1

Species (Family)	Status, Distribution, Comments
Acacia bakeri (Fabaceae).	Listed by Briggs and Leigh (1988) as 3VC-: range over 100 km, vulnerable, reserved but adequacy of reservation unknown. Southern limit of distribution is Brunswick Heads (Floyd, 1989). Recorded by Murray (1987b) from a bedrock spur near wetlands south of the Cobaki Broadwater and from other specific sites in Tweed Shire.
Acacia baueri ssp. ***baueri*** (Fabaceae).	This plant is very rare on the north coast of New South Wales (Griffith, 1983, 1984, 1985; Pressey and Griffith, 1987) and has been described as rare and in danger of extinction over its range in the extreme south-east of Queensland (Stanley and Ross, 1983). The National Herbarium of New South Wales has north coast collections from Port Stephens, (1 plant in 1912), Myall Lakes (1 in 1987), Nabiac (subject to past and present sand mining), Crowdy Bay and South West Rocks. Recorded in disturbed dry heathland north of Kingscliff.
Acronychia littoralis (Rutaceae).	Rare (Williams *et al.*, 1984). Listed by Briggs and Leigh (1988) and Leigh and Briggs (1992) as 3ECi: range over 100 km, endangered, inadequately reserved. Communities: F1 (one site); a few trees on roadside close to sampling site in F4 — possibly present in the community as it occurs in similar habitat in Bundjalung National Park.
Amorphospermum antilogum (Sapotaceae).	Range extends from the Tweed River to the Olive River in northern Queensland (Floyd, 1989) over which it has a number of disjunct occurrences (Hunter, 1991, pers. comm.). Occurs in lowland subtropical rainforest on stony slopes (Floyd, 1989). Known from four records in the Tweed including a gully to the south of Round Mountain (Floyd, 1989; Hunter, 1991, pers. comm.).
Angiopteris evecta (Angiopteridaceae).	Listed by Leigh and Briggs (1988) as 3RC-: range over 100 km, rare, reserved but adequacy of reservation unknown. Confined to the Tweed Valley and listed as very rare in New South Wales by Harden (1990) but extends into eastern Queensland and the Carnarvon Range (Andrews, 1990). The only specimen known for the state occurs on the edge of the floodplain of a tributary of Cudgera Creek (Hunter, 1991, pers. comm.).
Archidendron hendersonii (Fabaceae).	An uncommon species reduced in abundance because of clearing and sand mining; southern limit of distribution is the Richmond River. Communities: F1 (one site); F2 (two sites). Occurs in Ukerebagh Nature Reserve. Also recorded by Gilmore *et al.* (1985) on bedrock and floodplain south of Pottsville, by Murray (1987a) from littoral rainforest near Wommin Lagoon on the Fingal Peninsula, by Murray (1987b) from the margin of *Melaleuca quinquenervia* forest near the Cobaki Broadwater and by Hunter (1991, pers. comm.) from the northern edge of the Tweed River next to McAuleys Road. Records for Tweed Shire listed by Floyd (1989) are from Stotts Island Nature Reserve, Wooyung, Terranora, Tweed Heads, Mooball State Forest and Murwillumbah.
Archidendron muellerianum (Maiden and R. Barker) Nielsen (Fabaceae).	Listed by Briggs and Leigh (1988) as 3RCa: range over 100 km, rare, adequately reserved. Limited distribution from Tallebudgera Creek in far south-eastern Queensland to the Richmond River. Recorded by Murray (1987b) from *Melaleuca quinquenervia* forest south of the Cobaki Broadwater. Other records for Tweed Shire are listed by Floyd (1989).
Baumea nuda (Cyperaceae).	Collection from sedgeland near Pottsville in 1985 was the third record for the state (Gilmore *et al.*, 1985).
Banksia robur (Proteaceae).	Of regional significance because of disjunct distribution in coastal New South Wales. Considered by George (1981) to occur in two principal areas: one from Kempsey to Wollongong in New South Wales and another from Coolangatta to Shoalwater Bay in Queensland. Records in Tweed Shire

Species (Family)	Status, Distribution, Comments
	are therefore extensions of the previously known northern population. Absent from Broadwater National Park in the Richmond River region and from Bundjalung and Yuraygir National Parks in the Clarence River region although present southwards from Hat Head National Park in the Macleay River region. Communities: F3 (one site); F8 (one site and reported by Hunter, 1982, from elsewhere in this association); H2 (one site). Also reported from the Cudgen Lake area by Murray (1989) and from forested land near Pottsville (Gilmore *et al.*, 1985) which is probably the southern limit of the north coast disjunction.
Boronia rosmarinifolia (Rutaceae).	Apparently rare over its range on the north coast of New South Wales and only known to be reserved at one location in the Sandon area of Yuraygir National Park (Griffith, 1984); confined to the north coast of New South Wales but extends into Queensland where it is reported to be locally common in coastal heathland (Stanley and Ross, 1983); status requires investigation. Communities: F6 (one site).
Bosistoa transversa (Rutaceae).	Listed by Briggs and Leigh (1988) as 3VC-: range greater than 100 km, vulnerable, reserved but adequacy of reservation unknown. Distribution from Mullumbimby to Maryborough in Queensland (Floyd, 1989). Recorded for Stotts Island Nature Reserve by Briggs and Leigh (1988). Other Tweed records listed by Floyd (1989).
Caesalpinia scortechinii (Fabaceae).	Occurs in subtropical and dry rainforest north of Lismore and extends into Queensland (Williams and Harden, 1988); uncommon in New South Wales (Williams, 1985, pers. comm.). Communities: F2 (one site).
Cassia marksiana (Fabaceae).	Listed by Briggs and Leigh (1988) as 3VCi: range over 100 km, vulnerable, inadequately reserved. Known from very few specimens and over a very restricted range from Crabbes Creek to Currumbin. Hunter (1991, pers. comm.) reports it as occurring only as scattered populations or single specimens in New South Wales and generally on alluvial flats and adjacent bedrock margins. Found on the lower edge of a bedrock spur to the south of the Cobaki Broadwater by Murray (1987b) and listed by Floyd (1989, 1990) from several localities including Stotts Island Nature Reserve.
Cayratia acris (Vitaceae).	Considered to be uncommon in New South Wales (Williams, 1985, pers. comm.; Floyd, 1990). Reported from Round Mountain (Hunter, 1985, pers. comm.; Floyd, 1990).
Cordyline congesta (Agavaceae).	Listed by Briggs and Leigh (1988) as 2RC-: range less than 100 km, rare, reserved but adequacy of reservation unknown. Occurs in extreme south-eastern Queensland and in north-eastern New South Wales (Pedley, 1986, and see Williams *et al.*, 1984 who listed it as *Cordyline* sp. aff. *stricta*). In New South Wales, extends south to Ballina and is generally confined to near-coastal areas where it can be locally common (Hunter, 1991, pers. comm.). Communities: F1 (one site); F2 (three sites); F5 (one site); F7 (one site); F8 (one site); F9 (two sites). Occurs in Ukerebagh Nature Reserve.
Cryptocarya foetida (Lauraceae).	Listed by Briggs and Leigh (1988) as 3VCi: range greater than 100 km, vulnerable, inadequately reserved; occurs in littoral rainforest from Ballina to Fraser Island. Very few fertile specimens known and recent records from higher altitude rainforest on basalt (Hunter, 1991, pers. comm.). Communities: F1 (two sites); F2 (one site). Two good populations with fruiting specimens occur at Fingal Head and on the northern side of Terranora Lake at the foot of a bedrock slope (Hunter, 1991, pers. comm.). Also recorded by Murray (1987b) from the margin of a bedrock spur to the south of the Cobaki Broadwater. Floyd (1989) and Hunter (1991, pers. comm.) have listed additional records for the Tweed region.
Cupaniopsis newmanii S. Reyn. (Sapindaceae).	Limited range from Mullumbimby to Mount Tambourine (Williams *et al.*, 1984; Floyd, 1989). Recorded by Gilmore *et al.* (1985) on bedrock near Pottsville. Additional Tweed records listed by Floyd (1989).
Cyperus haspan ssp. ***juncoides*** (Lam.) Kuk. (Cyperaceae).	Collection from dune near Pottsville in 1985 was the third record for the state (Gilmore *et al.*, 1985).

Species (Family)	Status, Distribution, Comments
Dendrocnide moroides (Urticaceae).	Extremely rare in New South Wales but more common in Queensland (Williams *et al.*, 1984). Known present locations of the species are all in the Tweed region (Hunter, 1991, pers. comm.). Communities: F1 (one site — Camp Wollumbin). Other records include Round Mountain near Cudgen Lake (Gilmore, 1983; Hunter, 1991, pers. comm.; Floyd, 1990), Murwillumbah (Floyd, 1989) and Reserve Creek, near Round Mountain (Floyd, 1990; Hunter, 1991, pers. comm.).
Desmodium acanthocladum (Fabaceae).	Listed by Briggs and Leigh (1988) as 2V: range less than 100 km, vulnerable, not known to be reserved (although Floyd, 1990, lists it as reserved). A shrub occurring only on the north coast of New South Wales, between the Clarence and Tweed Rivers, where it has been recorded from the margins of subtropical and dry rainforests (Williams *et al.*, 1984). Only two records for the Tweed, from the Eungella Dip area on the Oxley River and Wollumbin Wildlife Refuge (Hunter, 1991, pers. comm.).
Diospyros mabacea (Ebenaceae).	Listed by Briggs and Leigh (1988) and Leigh and Briggs (1992) as 2ECi: range less than 100 km, endangered, inadequately reserved. Restricted to the Tweed River Valley (Williams *et al.*, 1984; Floyd, 1989) and recorded for Stotts Island Nature Reserve (Floyd, 1989).
Diploglottis campbellii (Sapindaceae).	Listed by Briggs and Leigh (1988) and Leigh and Briggs (1992) as 2E: range less than 100 km, endangered, not known to be reserved. Occurs in riverine rainforest from Tintenbar, on the Richmond River, to upper Tallebudgera Creek in south-eastern Queensland (Floyd, 1989). The best remaining population in the Tweed is on the floodplain of the Oxley River at Eungella Dip (Hunter, 1991, pers. comm.). Other Tweed records listed by Floyd (1989).
Eleocharis dulcis (Cyperaceae).	A herbarium record of this species, from a drain near Murwillumbah, represents its known southern limit, although it is widespread in northern Australia (K. Wilson, Nat. Herb. NSW, 1985, pers. comm.). The species could be present in wetlands on the floodplain or in the dunal areas.
Endiandra globosa (Lauraceae).	Listed by Briggs and Leigh (1988) as 2RC-: range less than 100 km, rare, reserved but adequacy of reservation not known; restricted to lowlands between Mullumbimby and the Gold Coast hinterland (Floyd, 1990). Locally common on metasediments and alluvials in the Tweed-Brunswick region (Hunter, 1991, pers. comm.). Communities: F9 (seen near one site). Also reported on Round Mountain near Cudgen Lake (Gilmore, 1983; Floyd, 1990; Hunter, 1991, pers. comm.), from bedrock and swamp margin south of Pottsville (Gilmore *et al.*, 1985), from the footslopes of a ridge to the south of the Cobaki Broadwater (Murray, 1987b) and from Tanglewood, west of Bogangar, and floodplain margins east of Mooball by Hunter (1991, pers. comm.). Floyd (1989) lists other Tweed records.
Endiandra hayesii (Lauraceae).	Listed by Briggs and Leigh (1988) as 3VC-: range greater than 100 km, vulnerable, reserved but adequacy of reservation unknown. Ranges from the Richmond River to Burleigh Heads in Queensland (Floyd, 1989). Reported from bedrock areas adjacent to coastal wetlands south of Pottsville (Gilmore *et al.*, 1985). Additional Tweed records listed by Floyd (1989).
Geodorum densiflorum (Orchidaceae).	In New South Wales, confined to the coastal region north from the Macleay River (Metcalfe in Beadle, 1987); considered to be uncommon in the state (B. Wallace, Nat. Herb. NSW, 1986, pers. comm.), although apparently common in Queensland. Recorded from bedrock ridges 2 km south of Norries Head, Bogangar (Griffith, 1986).
Hypserpa decumbens (Menispermaceae).	Very rare in New South Wales, known only from Brunswick Heads and Cudgen Lake (Williams, 1991, pers. comm.) and one site in community F1 at Mooball Creek. Extends into south-eastern Queensland.
Lepiderema pulchella (Sapindaceae).	A rare plant occurring from the Brunswick River to Tallebudgera Creek in southern Queensland (Williams *et al.*, 1984; Floyd, 1989). Listed by Briggs and Leigh (1988) as 2RC-: range less than 100 km, rare, reserved but adequacy of reservation unknown. One shrub seen in a highly disturbed area at the end of Mahers Lane, Terranora (D24). Hunter (1991, pers. comm.) reports the species scattered throughout the foothills immediately

Species (Family)	Status, Distribution, Comments
	south of Terranora Road and McAuleys Road and on the north side of Terranora Lake. Not reserved in this area but recorded from Stotts Island Nature Reserve (Floyd, 1989, who lists other Tweed records).
Lindsaea fraseri (Lindsaeaceae).	Locally common in an area of swamp forest-dry sclerophyll forest ecotone 2 km south of Norries Head, Bogangar (Griffith, 1986). This is one of four records for the state, the others coming from the same general locality (Nat. Herb. NSW, 1986, pers. comm.). Extends into southern Queensland.
Macadamia tetraphylla (Proteaceae).	Listed by Briggs and Leigh (1988) as 2VC-: range less than 100 km, vulnerable, reserved but adequacy of reservation not known. According to Floyd (1989), confined chiefly to the Tweed and Richmond Rivers in New South Wales, extending into the Numinbah Valley and Coomera River in south-eastern Queensland and occurring in subtropical rainforest near the coast. Although more common at higher altitudes, found occasionally on toeslopes adjoining the coastal plain, for example east of Mooball on the Pottsville Road (Hunter, 1991, pers. comm.). Floyd (1989) lists other Tweed records.
Maundia triglochinoides (Juncaginaceae).	Limited range between far south-eastern Queensland and about Wyong in New South Wales; status poorly known but thought to be rare (Pressey, 1989a,b). Collected in wetland habitat near Pottsville by Gilmore *et al.* (1985).
Ochrosia moorei (Apocynaceae).	Listed by Leigh and Briggs (1988) as 2RC-: range less than 100 km, rare, reserved but adequacy of reservation unknown. Occurs in riverine and lowland subtropical rainforest from the Richmond River to Springbrook and Currumbin Creek in south-eastern Queensland (Floyd, 1989) who lists Tweed records. One specimen occurs in a small remnant of floodplain rainforest on Cudgera Creek, about 5 km south-west of Pottsville (Hunter, 1991, pers. comm.).
Planchonella laurifolia (Sapotaceae).	Tweed records are close to the southern limit of distribution at the Brunswick River. Habitat is littoral and dry rainforest (Floyd, 1990) and is mostly now cleared (Hunter, 1991, pers. comm.). Communities: F1 (one site). Also recorded from swamp forest and palm forest along gullies to the south of Round Mountain (Gilmore, 1983) and on Round Mountain (Hunter, 1985, pers. comm.). Most records listed by Floyd (1990) are from the Tweed, including several from the area covered by the present study.
Polyalthia nitidissima (Annonaceae).	Rare in New South Wales; recorded from Iluka, Cudgen Lake and Terranora (Floyd, 1989). Occurs in Ukerebagh Nature Reserve. Communities: F1 (one site); F2 (one site).
Potamogeton javanicus (Potamogetonaceae).	Known only from the central and north coast botanical subdivisions of the state (Sainty and Jacobs, 1981) and recorded very rarely over this range although it is widespread in northern Australia and overseas (Aston, 1973). Recorded in one floodplain wetland.
Rhodamnia maideniana (Myrtaceae).	Listed by Briggs and Leigh (1988) as 2RC-: range less than 100 km, rare, population reserved but adequacy of reservation unknown; occurs in occasional populations from Tallebudgera Creek in far south-eastern Queensland to the Richmond River (Williams *et al.*, 1984), more commonly above the coastal lowlands (Hunter, 1991, pers. comm.). Recorded on Round Mountain (Hunter, 1985, pers. comm.) and from the margin of a bedrock spur to the south of the Cobaki Broadwater (Murray, 1987b).
Sterculia quadrifida (Sterculiaceae).	Uncommon to rare (Williams *et al.*, 1984; Floyd, 1990). Occurs as far south as Coraki in New South Wales (Floyd 1989). Communities: F1 (one site). Floyd (1989) records it from Stotts Island Nature Reserve, Round Mountain and other sites in the Tweed region. Also recorded from Ukerabagh Nature Reserve (Hunter, 1991, pers. comm.).
Strangea linearis (Proteaceae).	Confined to the sandmasses of the far north coast of New South Wales and south-eastern Queensland. Formerly considered to be rare or threatened nationally (Leigh *et al.*, 1981) but not listed by Briggs and Leigh (1988). Nevertheless, only reserved at one place in the state, in Tyagarah Nature Reserve south of Brunswick Heads (Hunter, 1991, pers. comm.). Communities: Sh (one site); H1 (one site); also recorded by Murray (1989) in dry heath and tall shrubland near Cudgen Lake.

Species (Family)	Status, Distribution, Comments
Syzygium moorei (Myrtaceae).	Listed by Briggs and Leigh (1988) as 2VCi: range less than 100 km, vulnerable, population inadequately reserved. Recorded on bedrock areas adjacent to extensive wetlands south of Pottsville (Gilmore *et al.*, 1985). Other records by Hunter (1991, pers. comm.) are on the northern side of the Terranora Broadwater, on a toeslope adjacent to littoral rainforest at Fingal Head, on alluvium between Fingal and Kingscliffe, in palm rainforest at the eastern base of Round Mountain, at Tanglewood, and on floodplain east of Mooball.
Thozetia racemosa (Asclepiadaceae).	Listed by Briggs and Leigh (1988) as 3VC-: range over 100 km, vulnerable, adequacy of reservation unknown. Occurs north from Iluka, on the Clarence River (Williams, 1984) and into southern Queensland. Recorded from Round Mountain (Hunter, 1985, pers. comm.).
Xeromphis sp. (Syn. ***Randia moorei***). (Rubiaceae).	Listed by Briggs and Leigh (1988) and Leigh and Briggs (1992) as 3ECi: range over 100 km, endangered, inadequately reserved; considered to be rare by Floyd (1990). Extends from Broken Head to the Logan River in southern Queensland (Floyd, 1989). Listed by Floyd (1989) from Stotts Island Nature Reserve and other Tweed localities and by Hunter (1991, pers. comm.) from Round Mountain.

Plankton of Lyell Reservoir, New South Wales

T. KOBAYASHI

(Communicated by R. J. KING)

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From August 1986 to September 1987, the plankton of Lyell Reservoir near Lithgow, N.S.W. was studied with special reference to species composition, seasonal changes, interaction between phytoplankton and zooplankton, and the effect of artificial aeration.

Forty-five taxa of phytoplankton were identified with species of *Cyclotella*, *Stephanodiscus*, *Melosira*, *Volvox* and *Microcystis* dominant. Among the zooplankton 10 rotifers, 5 copepods and 12 cladocerans were recorded, dominated by *Ceriodaphnia* sp., *Daphnia lumholtzi*, *Boeckella triarticulata* and *Calamoecia lucasi*. Two morphs of *D. carinata* coexisted.

The microcrustacean zooplankton fed mainly on *Chroococcus*, *Oocystis*, *Melosira* and unicellular centric diatoms: diatoms were well digested, but gelatinous algae remained intact. *Microcystis* was ingested by *B. triarticulata*.

Artificial aeration did not prevent a bloom of *Microcystis*, and a concomitant change in the abundance of cladocerans was not necessarily causally related.

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INTRODUCTION

Lyell Reservoir, on the Cox's River at its junction with Farmer's Creek and approximately 10 km southwest of Lithgow, was first filled in 1982. The reservoir provides water storage for pumping 16 km upstream to Wallerawang Reservoir in dry periods, and also for the proposed Mount Piper Power Station.

Lyell Reservoir became anaerobic at times within 5 m of the water surface, leading to disagreeable H_2S odours, high algal levels (*Microcystis* regularly exceeded 50 cells ml^{-1}), and water of highly variable quality entering the cooling water treatment plant (McAuliffe and Rosich, 1989). An aeration system was installed in 1986 so that the reservoir could be artificially mixed, and dissolved oxygen levels at the bottom of the reservoir maintained at or above 1 mg l^{-1} (Hodgson, 1987a, 1987b; 1988, pers. comm.).

Physicochemical conditions and phytoplankton of Lyell Reservoir, monitored by the Electricity Commission of New South Wales (ELCOM), were reviewed and summarized by Bek and Martin (1990) to assess the suitability of water quality for recreational use. This paper presents the seasonal patterns of dominant phytoplankton and microcrustacean zooplankton, the effect of aeration on them, and the dietary phytoplankton for the microcrustacean zooplankton between April 1986 and September 1987. During the study, a major flood occurred in August 1986 (total rainfall 374 mm) (Kobayashi, 1992), so the effect of the flood on plankton is noted. The results of this study are discussed in comparison with the adjacent Wallerawang Reservoir (Kobayashi, 1992).

STUDY AREA

The morphology of Lyell Reservoir is summarized in Table 1. It is relatively large and deep, with a dendritic shoreline. The major sources of water for Lyell Reservoir are Cox's River, Farmer's Creek (containing Lithgow's sewage), and erratic rainfall. Evaporation and reservoir spill dominate the outflow. In dry periods, Lyell water is recirculated to Wallerawang Reservoir via a pipeline.

TABLE 1

Morphology of Lyell Reservoir

Location	150°05′E., 33°30′S.
Elevation (above sea level)	780 m
Maximum length (l)	4.3 km
Maximum width (b)	1.3 km
Area (A)	194.5×10^4 m^2
Volume (V)	26.07×10^6 m^3
Maximum depth (Z_{max})	32 m
Mean depth (z)	13.4 m
Shore line (L)	22.2 km
Shoreline development (D_L)	4.5
Mean turnover rate	2.4 year^{-1}

In 1986 plastic diffuser pipes with an aeration capacity of 120 ls^{-1} were installed at 25 m depth near the dam wall (Hodgson, 1987a; 1988, pers. comm.). During this study, the aeration was conducted from 12 November to 30 December 1986, and 5 January through to February 1987.

Reservoir fish include flatheaded gudgeon (*Philypnodon grandiceps*), gold fish (*Carassius auratus*), rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) (Harris, 1988, pers. comm.).

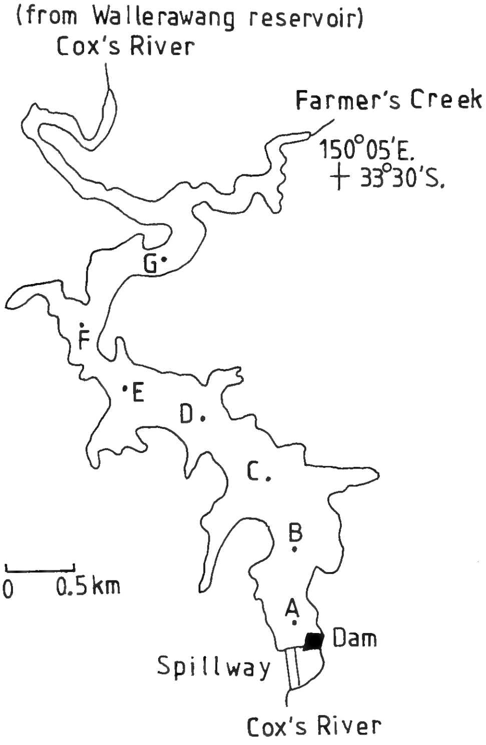

Fig. 1. Sampling stations in Lyell Reservoir.

METHODS

A detailed account of methods is given in Kobayashi (1992). Quantitative phytoplankton and zooplankton samples were collected monthly with a 2-L Van Dorn water sampler and by a vertical haul (250 μm mesh net) at stations A to G (Fig. 1) between August 1986 and September 1987, and between April 1986 and September 1987, respectively. Phytoplankton were identified and counted using a Prior inverted microscope. A Wild M5A stereomicroscope was used to identify and count zooplankton. The densities of phytoplankton and zooplankton were expressed as cells ml^{-1} or colonies l^{-1}, and individuals l^{-1}, respectively. Analysis of the gut contents of zooplankton followed Gliwicz (1969) and Infante (1978b). Proportional occurrences of dietary phytoplankton in the zooplankton guts were calculated by the method of Nadin-Hurley and Duncan (1976).

In addition to plankton samples, sediment-core samples were collected at stations D to G on 26 July and stations A to C on 2 August 1987 (winter) to examine whether viable *Microcystis* colonies existed in Lyell sediments. The upper 2 cm-sediment samples (n=8 at each sampling station) were collected using a modified Satake's handy corer (Satake, 1983), equipped with a 16 mm-inner-diameter sampling tube. The physiological condition of *Microcystis* was assessed by chlorophyll epifluorescence (Reynolds *et al.*, 1981). The density of *Microcystis* in sediments was expressed as colonies cm^{-3}.

RESULTS

Phytoplankton

A total of 45 phytoplankton taxa was identified (Table 2). The dominant genera were *Microcystis* (Cyanophyta), *Volvox* (Chlorophyta), *Cyclotella*, *Stephanodiscus*, and *Melosira* (Bacillariophyta). Unidentified flagellates were also a major component of the plankton.

Volvox occurred throughout the study except between August and November 1986 (Fig. 2). *Volvox* exhibited two growth peaks: December 1986 (490 colonies l^{-1}) and August 1987 (90 colonies l^{-1}). *Microcystis* displayed a single growth peak in summer 1987, with a maximum of 12200 colonies l^{-1} in February. *Melosira* occurred throughout the study except between August and October 1986. *Melosira* displayed two growth peaks: one (mainly *M. granulata*) with a maximum of 6700 cells ml^{-1} in March 1987 and a second (mainly *M. italica*) with 880 cells ml^{-1} in August 1987. *Cyclotella* and *Stephanodiscus* also occurred throughout the study, except during the August 1986 flood. A maximum of 110 cells ml^{-1} was recorded in August 1987. Unidentified flagellates (probably three species, cell width 3-25 μm) were perennial. It was the only abundant phytoplankton group occurring immediately after the August 1986 flood. A maximum of 3390 cells ml^{-1} and a minimum of 3 cells ml^{-1} was recorded in August 1986 and in May 1987, respectively.

Microcystis in Sediments

Microcystis colonies were collected from sediments at all sampling stations (Fig. 3), with a significant difference in the density among sampling stations (Kruskal-Wallis 1-way ANOVA: $H=36.8$, $p < 0.001$). A nonparametric multiple comparison test provided the following overall conclusion at the 5% significance level: $\mu B = \mu C \neq \mu D \neq \mu A = \mu E \neq \mu F \neq \mu G$. Namely, the density of the benthic *Microcystis* was highest at station G, and decreased towards the dam wall and spillway. Eighty percent of the colonies (n=219) contained healthy bright yellow-green cells (4-6 μm diameter), with intense chlorophyll fluorescence.

TABLE 2

Phytoplankton in Lyell Reservoir between August 1986 and September 1987

Cyanophyta

- *Chroococcus* spp.
- *Dactylococcopsis* spp.
- *Microcystis aeruginosa* Kutz.
  - *M.* sp.
- *Oscillatoria* sp.
- *Anabaena* sp.

Chlorophyta

- *Volvox* spp.
- *Botryococcus* sp.
- *Pediastrum* spp.
- *Oocystis* spp.
- *Closteriopsis longissima* Lemmermann
- *Shroederia ?setigera* (Shroeder) Lemmermann
- *Selenastrum ?minutam* (Naeg.) Collins
- *Scenedesmus* spp.
- *Mougeotia* spp.
- *Closterium* sp.
- *Cosmarium* spp.
- *Quadrigula* spp.
- *Actinastrum* sp.
- *Staurastrum* spp.

Euglenophyta

- *Trachelomonas* sp.

Chrysophyta

- *Dinobryon divergens* Imhof
  - *D. cylindricum* Imhof

Bacillariophyta

- *Melosira granulata* (Ehrenb.) Ralfs
  - *M. granulata* var. *angustissima* Muller
  - *M. italica* (Ehrenb.) Kutz.
  - *M. varians* Agardh
- *Cyclotella* spp.
- *Stephanodiscus* spp.
- *Tabellaria* sp.
- *Fragilaria* sp.
- *Asterionella* spp.
- *Synedra pulchella* Kutz.
  - *S.* sp.
- *Navicula* sp.
- *Pinnularia* sp.
- *Gyrosigma* sp.
- *Gomphonema constrictum* Ehrenberg
- *Cymbella* spp.
- *Nitzschia* sp.
- *Surirella* spp.

Pyrrhophyta

- *Peridinium* sp.
- *Ceratium hirundinella* O. F. Muller

Unidentified flagellates
Unidentified algae

Microcrustacean Zooplankton

Twelve cladoceran and 3 calanoid copepod species were identified (Table 3). The rotifers and cyclopoid copepods collected during the study are also listed in Table 3, though species numbers are thought to be underestimates due to the large mesh used in the net samples. The dominant cladocerans were *Ceriodaphnia* sp., *Daphnia lumholtzi* and *Daphnia carinata.* The dominant calanoid copepods were *Calamoecia lucasi* and *Boeckella triarticulata.*

Ceriodaphnia was perennial, increasing towards spring, with a maximum of 28.4 l^{-1} in September 1987 (Fig. 4). *Daphnia lumholtzi* occurred mainly in January to May 1987 and also in July 1986 but was rare or absent at other times. An autumn maximum of 13.5 l^{-1} was recorded in April 1987. *Daphnia carinata* was scarce, and was a spring-early summer form. A maximum of 4.4 l^{-1} was recorded in December 1986.

Calamoecia lucasi and *Boeckella triarticulata* were both perennial. Their density remained low throughout the study, with a maximum of 7.5 l^{-1} and 2.9 l^{-1}, respectively.

Morphs of *Daphnia carinata*

Two morphs of *D. carinata* coexisted (Fig. 5). For females, morph I was characterized by a relatively short rostrum, oval body, and short tail spine, often less than half of the carapace — morph II possessed a long rostrum and tail spine, with a relatively slender body. The postabdomen of morph I had a slight indentation, while in morph II it was straight. Both morphs lacked helmets. Seasonally, morph II became relatively abundant towards February 1987. It was difficult to visually separate juveniles of the two morphs.

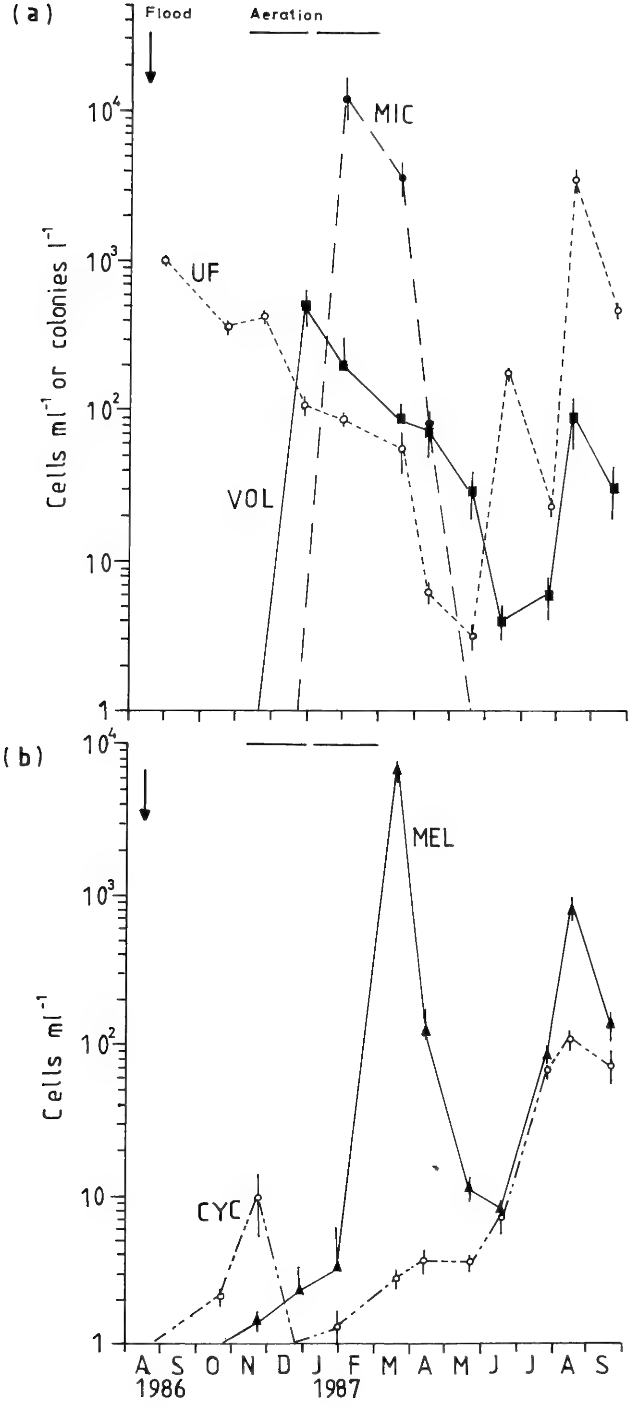

Fig. 2. Density of phytoplankton in Lyell Reservoir: (**a**) *Microcystis* (MIC), *Volvox* (VOL), and unidentified flagellates (UF); (**b**) diatoms *Cyclotella* and *Stephanodiscus* (CYC), and *Melosira* (MEL). Mean ± SE is shown: n=7.

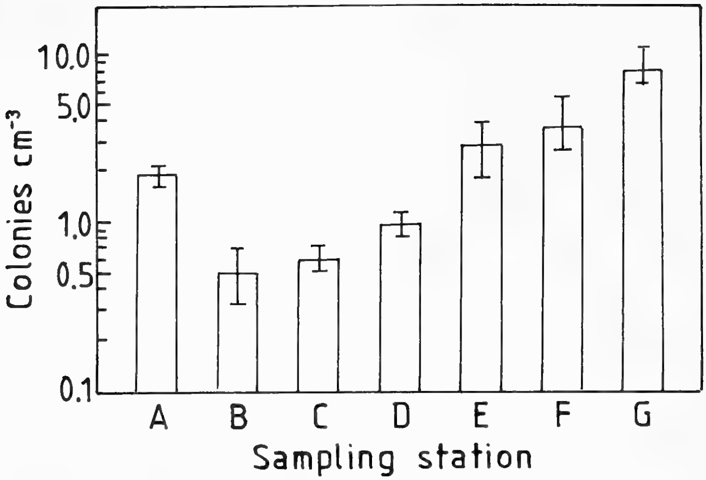

Fig. 3. Density of colonial *Microcystis* in upper 2-cm sediments in Lyell Reservoir. Samples were collected on 26 July (stations D to G) and on 2 August 1987 (stations A to C). Mean ± SE is shown: n=8 at each sampling station.

TABLE 3

Zooplankton in Lyell Reservoir between April 1986 and September 1987

Rotifers
- *Lacinularia* sp.
- *Brachionus novaezealandia* (Morris)
- *Lecane bulla* Gosse
  - *L.* sp.
- *Asplanchna priodonta* Gosse
  - *A. sieboldi* (Leydig)
- *Keratella cochlearis* (Gosse)
  - *K. procurva* (Thorpe)
  - *K. tropica* (Apstein)
  - *K. valga* (Ehrenberg)

Cladocerans
- *Diaphanosoma unguiculatum* Gurney
- *Pleuroxus* cf. *inermis* Sars
- *Chydorus sphaericus* s.l. (Muller)
- *Alona diaphana* King
- *Leydigia leydigi* (Shoedler)
- *Macrothrix spinosa* King
- *Neothrix armata* Gurney
- *Bosmina meridionalis* Sars
- *Daphnia carinata* s.l. King
  - *D. lumholtzi* Sars
- *Simocephalus vetulus elisabethae* (King)
- *Ceriodaphnia* sp.

Calanoid copepods
- *Boeckella triarticulata* Thomson
  - *B. minuta* Sars
- *Calamoecia lucasi* Brady

Cyclopoid copepods
- *Mesocyclops* sp.
- *Tropocyclops* sp.

Lengths of the rostrum, tail-spine, and ventral antenna branch (Fig. 5) of morphs I and II (ovigerous female) on 1 February 1987 were plotted against the carapace length on that date (Fig. 6). Clutch sizes were not plotted due to an inestimable loss of eggs. Simple linear regression models (Table 4) and analysis of covariance (Table 5) showed that two morphs could be separated by the development of those three morphological characteristics.

Plankton During Aeration

The phytoplankton was dominated by the green alga *Volvox* and the blue-green alga *Microcystis*. No obvious change was observed in the dominant calanoid copepods. However, the dominant cladoceran species shifted from *Ceriodaphnia* and *Daphnia carinata* to *D. lumholtzi* and *Bosmina meridionalis* towards February 1987 (the end of aeration).

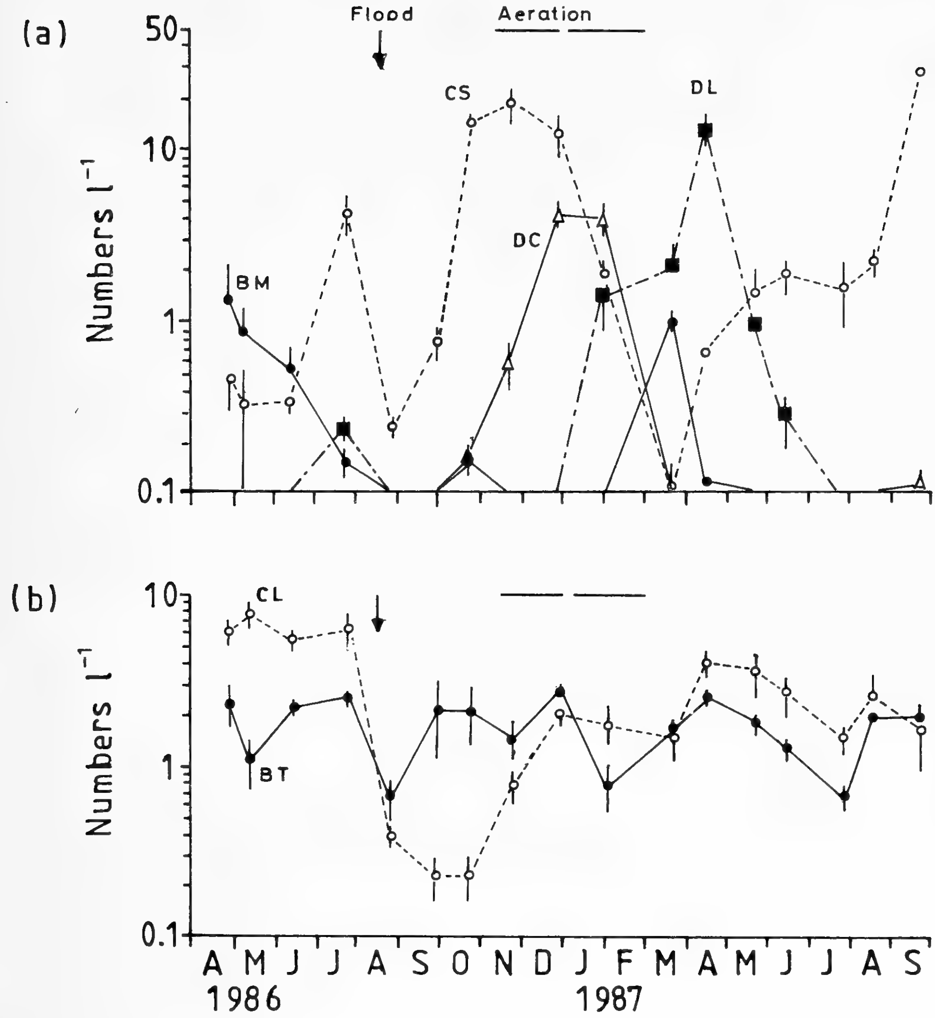

Fig. 4. Density of microcrustacean zooplankton in Lyell Reservoir: (**a**) cladocerans *Bosmina meridionalis* (BM), *Ceriodaphnia* sp. (CS), *Daphnia lumholtzi* (DL), and *Daphnia carinata* (DC); (**b**) calanoid copepods *Calamoecia lucasi* (CL), and *Boeckella triarticulata* (BT). Mean ± SE is shown: n = 7.

Microcrustacean Zooplankton Gut Contents

A total of 140 *Bosmina meridionalis*, 310 *Ceriodaphnia*, 120 *Daphnia lumholtzi*, 90 *D. carinata*, 340 *Calamoecia lucasi*, and 340 *Boeckella triarticulata* guts were examined. Their total diet comprised 11, 18, 13, 10, 17 and 34 phytoplankton taxa, respectively (Table 6). Of these, 20 taxa were detected from more than one zooplankton species, while 14 taxa were detected only in the guts of *B. triarticulata.* The following six reservoir phytoplankton taxa were never detected in the zooplankton guts examined throughout the study: *Anabaena*, *Volvox*, *Closteriopsis*, *Closterium*, *Actinastrum* and flagellates.

Chroococcus, *Oocystis*, *Melosira*, *Cyclotella* and *Stephanodiscus* were the main dietary phytoplankton taxa for the Lyell zooplankton. *Oocystis* and *Chroococcus* were often intact in the zooplankton guts, while most of the ingested *Cyclotella*, *Stephanodiscus* and *Melosira* were digested.

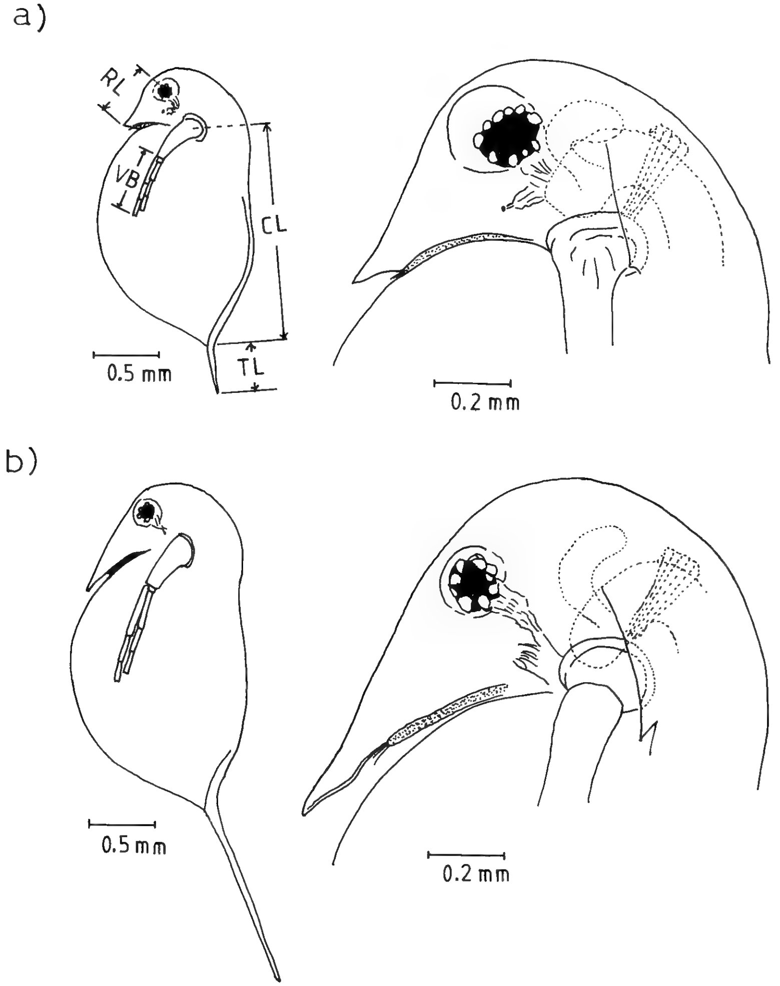

Fig. 5. Two morphs of *Daphnia carinata* s.l. (ovigerous female) in Lyell Reservoir on 1 February 1987: (**a**) Morph I; (**b**) Morph II. Morphological characteristics measured are: carapace (CL); rostrum (RL); tail spine (TL); ventral antenna branch (VB).

The proportional occurrences of *Cyclotella/Stephanodiscus*, and *Melosira* in the *Ceriodaphnia* gut were significantly positively correlated with their density in the plankton (Spearman's rank correlation coefficient $r_s = 0.70$ and 0.74, $n = 11$, $p < 0.05$, respectively). The frequent ingestion of *Trachelomonas* was characteristic of *Daphnia lumholtzi* and, to a lesser extent, of *D. carinata*. Large phytoplankton cells such as *Pediastrum*, *Staurastrum*, and *Ceratium* were fragmented in the guts of *Boeckella triarticulata*. The blue-green alga *Microcystis* was detected only from *B. triarticulata* on 13 April 1987. On this date, 15% of the *B. triarticulata* guts contained small colonial *Microcystis* (50-300 cells colony^{-1}) which were all intact.

TABLE 4

Summary of simple linear regression models for three morphological characteristics (mm) of two morphs of Daphnia carinata *s.l. (ovigerous female) in Lyell Reservoir on 1 February 1987, using carapace (mm) as an independent variable. For each regression, n* = 60

Dependent Variable	Intercept (SE)	Slope (SE)	r^2	t for Ho: Slope = 0	P
Morph I					
Rostrum	0.084 (0.051)	0.214 (0.029)	0.60	7.36	<0.0001
Tail spine	0.188 (0.199)	0.233 (0.114)	0.06	2.05	0.0429
Ventral antenna branch	0.094 (0.050)	0.251 (0.028)	0.59	9.02	<0.0001
Morph II					
Rostrum	–0.076 (0.045)	0.442 (0.024)	0.81	18.57	<0.0001
Tail spine	–0.163 (0.175)	0.947 (0.093)	0.66	10.17	<0.0001
Ventral antenna branch	0.040 (0.044)	0.413 (0.023)	0.84	17.76	<0.0001

DISCUSSION

Phytoplankton

Seasonal succession of dominant Lyell phytoplankton is characteristic of that in deep, eutrophic lakes (Reynolds, 1980): *Volvox* (early summer to autumn 1986), *Microcystis* (summer 1987), *Melosira* (late summer) and again *Volvox*, *Cyclotella*, *Stephanodiscus* and *Melosira* (winter). The unidentified flagellates were also abundant from winter to spring 1986 and in winter 1987.

Volvox, common in N.S.W. (Playfair, 1913; Timms, 1970b; Thomasson, 1973), was the first genus (except flagellates) to increase greatly after the August 1986 flood. Two species of *Volvox* co-occurred. There was no evidence of parasites in *Volvox* as reported from South Australia (Ganf *et al.*, 1983).

The summer bloom of *Microcystis* (mainly *M. aeruginosa*) is consistent with other regions (May, 1970; Reynolds, 1980). *Microcystis* is a eutrophic genus (Hutchinson, 1967), and produces an endotoxin (Falconer *et al.*, 1981) which often causes fish and stock kills (May, 1972). No fish kills were observed in Lyell Reservoir during the 1986/87 summer bloom.

Overwintering of *Microcystis* colonies in lake and reservoir sediments has also been observed by Fallon and Brock (1980), Reynolds *et al.* (1981) and Takamura *et al.* (1984). The benthic form of *Microcystis* which settles after planktonic blooms, remains photosynthetically active for long periods, and may form a new growth cycle in the following season (Fallon and Brock, 1980). The wide distribution of viable benthic *Microcystis* colonies in Lyell sediments allows for the future reappearance in the plankton.

The seasonal behaviour of *Melosira* in Lyell Reservoir is consistent with Lund (1965) and Reynolds (1973); the first peak followed the autumn destratification period and the second during winter unstratified conditions, because *Melosira* is a heavy diatom, which needs mixing to remain in the plankton (Goldman and Horne, 1983).

Microcrustacean Zooplankton

The dominant cladocerans and calanoid copepods in Lyell Reservoir are common in south-eastern Australia (Mitchell, 1986; Timms, 1970a, 1970b). Since zooplankton community composition stabilizes one or two years after impoundment (Timms, 1987), Lyell Reservoir should have stable annual plankton composition.

The mid-summer (1987) decline of the large *Daphnia carinata* indicates a cool-water preference (Herbert, 1977; Mitchell and Williams, 1982), but it was followed by the

TABLE 5

Analysis of covariance for testing for significant difference between slopes of simple linear regression models for three morphological characteristics of two morphs of Daphnia carinata *s.l. (ovigerous female) in Lyell Reservoir on 1 February 1987*

Characteristic	x^2	xy	y^2	n	Slope	Residual SS	Residual DF
Rostrum							
Morph I	1.0983	0.2360	0.0851	60	0.214	0.03441	58
Morph II	1.6459	0.7285	0.3965	60	0.442	0.07409	58
"Pooled" regression						0.10850	116
"Common" regression	2.7442	0.9645	0.4816			0.14261	117
"Total" regression	3.3221	2.3388	3.1717			1.52516	118
Ho: Slope of morph I = slope of morph II, F = 36.5 Since $F_{0.05(1),1,116} \cong 3.94$, reject Ho. $p<0.0005$							
Tail spine							
Morph I	1.0983	0.2562	0.9482	60	0.233	0.88840	58
Morph II	1.6459	1.5588	2.2420	60	0.947	0.76580	58
"Pooled" regression						1.65420	116
"Common" regression	2.7442	1.8150	3.1902			1.98977	117
"Total" regression	3.3206	6.1571	34.7274			23.31082	118
Ho: Slope of morph I = slope of morph II, F = 23.5 Since $F_{0.05(1),1,116} \cong 3.94$, reject Ho. $p<0.0005$							
Ventral antenna branch							
Morph I	1.0983	0.2823	0.1234	60	0.251	0.05086	58
Morph II	1.6459	0.6803	0.3338	60	0.413	0.05258	58
"Pooled" regression						0.10344	116
"Common" regression	2.7442	0.9626	0.4572			0.11954	117
"Total" regression	3.3421	2.1345	2.7544			1.39116	118
Ho: Slope of morph I = slope of morph II, F = 18.1 Since $F_{0.05(1),1,116} \cong 3.94$, reject Ho. $p<0.0005$							

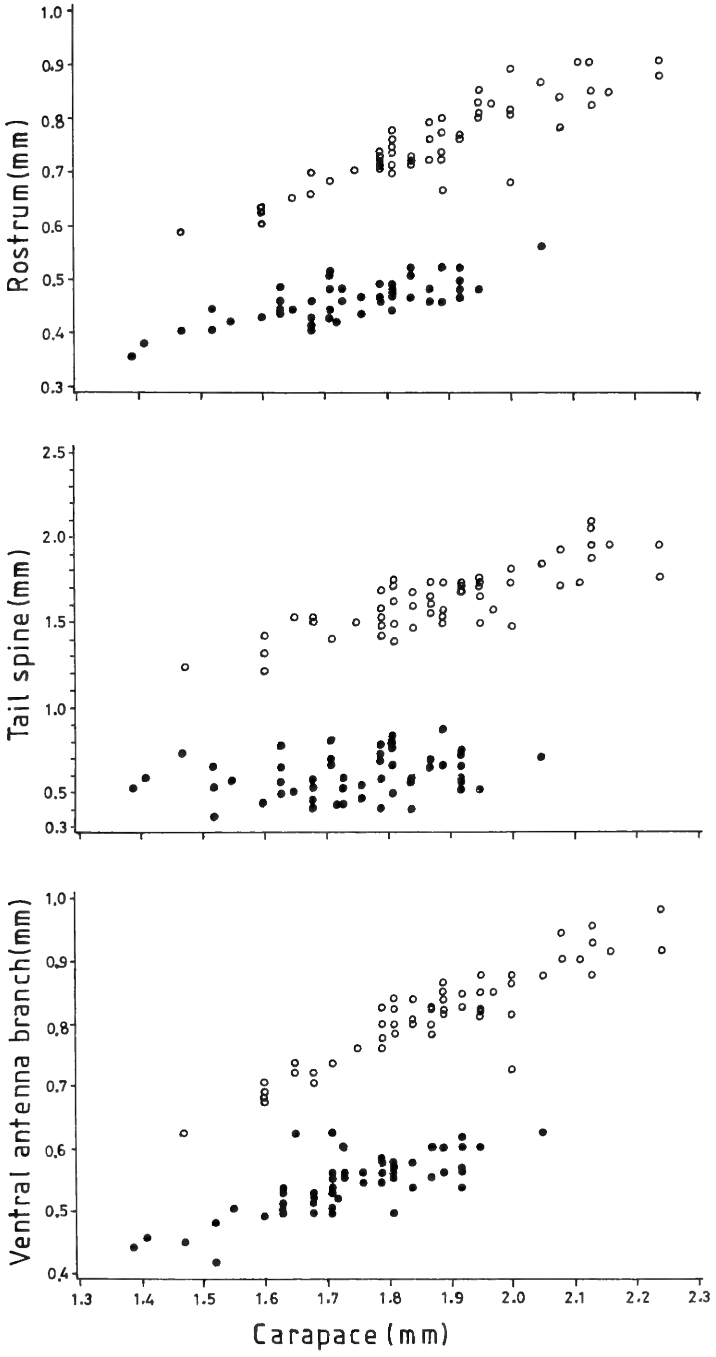

Fig. 6. Morphological characteristics of two morphs of *Daphnia carinata* s.l. (ovigerous female) in Lyell Reservoir on 1 February 1987. Morph I (solid symbols): morph II (open symbols).

TABLE 6

Dietary phytoplankton components in the guts of microcrustacean zooplankton in Lyell Reservoir between April 1986 and September 1987: Bosmina meridionalis *(BM),* Ceriodaphnia *sp. (CS),* Daphnia lumholtzi *(DL),* Daphnia carinata *(DC),* Calamoecia lucasi *(CL), and* Boeckella triarticulata *(BT). Occurrence symbols are p-present, and x-absent. The values in brackets are the relative abundances (%) (Nadin-Hurley and Duncan, 1976) of the guts containing the food item; values less than 20% are not shown*

Taxonomic Grouping	*BM*	*CS*	*DL*	*DC*	*CL*	*BT*
Cyanophyta						
Chroococcus	p(21)	p	p(28)	p(23)	p	p(47)
Dactylococcopsis	p	p	x	p	p	p
Microcystis	x	x	x	x	x	p
Oscillatoria	x	x	x	x	x	p
Chlorophyta						
Botryococcus	x	x	x	p	x	p
Cosmarium	p	p	p	x	p	p
Eudorina	x	x	x	x	x	p
Mougeotia	x	x	x	x	x	p
Oocystis	p(48)	p(36)	p(68)	p(23)	p(50)	p(56)
Pediastrum	x	x	x	x	x	p
Quadrigula	p	p	p	x	p	p(22)
Scenedesmus	x	p	p	p	p	p
Schroederia	x	x	x	x	x	p
Selenastrum	p	p	p	x	p	p
Staurastrum	x	p	p	x	x	p
Euglenophyta						
Trachelomonas	p	p	p(37)	p(22)	p	p
Chrysophyta						
Dinobryon	x	x	x	x	x	p
Bacillariophyta						
Asterionella	x	p	x	x	x	p
Cyclotella/Stephanodiscus	p(44)	p(47)	p(35)	p	p(34)	p(62)
Cymbella	x	p	p	p	p	p
Eunotia	x	p	x	x	p	p
Fragilaria	x	x	x	x	x	p
Frustulia	x	p	x	x	p	p
Gomphonema	x	x	x	x	x	p
Gyrosigma	x	x	x	x	x	p
Melosira	p	p(28)	p(28)	p	p	p(59)
Navicula	p	p	p	x	p	p
Nitzschia	x	x	x	x	p	p
Surirella	x	x	x	x	x	p
Synedra	x	x	x	x	x	p
Tabellaria	x	x	x	x	x	p
Pyrrhophyta						
Ceratium	x	x	x	x	x	p
Peridinium	x	p	x	x	p	p
Unidentified algae	p	p	p(36)	p	p(30)	p(34)

increasing medium-sized *Daphnia lumholtzi* and the small-sized *Bosmina meridionalis*, and the blue-green alga *Microcystis*.

A shift from larger to smaller cladoceran species during summer has been observed in other Australian and overseas water bodies and is often attributed to the reduction or elimination of large species by size-selective fish predation (Brooks and Dodson, 1965; Geddes, 1986). Furthermore, where a bloom of blue-green algae occurs, large-bodied cladocerans (e.g. *Daphnia*) may be excluded through mechanical interference with the filtering mechanism as well as toxins of the blue-green algae (Porter and McDonough, 1984; Lampert, 1987). It is not clear yet whether the observed shift in the summer cladoceran species in Lyell Reservoir was due to size-selective predation or inhibitory effects of the blue-green alga *Microcystis*, although both factors could act concurrently.

Unlike cladocerans, the species composition of the dominant calanoid copepods of *Calamoecia lucasi* and *Boeckella triarticulata* remained unchanged before and after the *Microcystis* bloom. The coexistence of these two different-sized calanoids has already been reported in other N.S.W. reservoirs (Timms, 1970a).

Daphnia carinata Morphs

The general characteristics of morphs I and II of *Daphnia carinata* in Lyell Reservoir resemble *D. thomsoni* Sars (Hebert, 1977, Figs. 85, 86), and *D. carinata* in Lake Alexandrina (Geddes, 1984, Fig. 2(d)), respectively. *Daphnia thomsoni* is quite distinct from *D. carinata*, because in Australia the two species cohabit without interbreeding (Hebert, 1977), though in recent years this species has been regarded as conspecific with *D. carinata* (Hebert, 1977). Furthermore, Benzies (1988a, 1988b) recognized only three groups within the *D. carinata* complex, based on multivariate morphometric studies and electrophoretic data. These were *D. nivalis*, *D. cephalata* and a conglomerate of all other taxa described from the complex, *D. carinata* sensu lato.

With this finding of two distinct morphs of *D. carinata* cohabiting Lyell Reservoir, perhaps further study on the systematics of the *D. carinata* complex is warranted.

Aeration Effects

The 1986/87 summer aeration in Lyell Reservoir did not prevent algal blooms. The large *Volvox* and *Microcystis* colonies, both of which are said to require thermal stability to form a surface scum (Reynolds, 1980), proliferated during aeration, which failed to destratify the reservoir.

The effectiveness of artificial destratification in controlling biological and chemical aspects of Australian water storages is reviewed by McAuliffe and Rosich (1989). In the successful cases, algal blooms were reduced in frequency (Carcoar Dam), or dominance shifted to green algae (Hinze Dam). However, most destratification applications of algal control have failed.

In Happy Valley Reservoir, South Australia, where destratification was used to control zooplankton numbers by reducing water temperature, the anticipated decline did not eventuate (Burch, 1987). It is unlikely that the decline of *Daphnia carinata* reflected low temperatures through destratification in Lyell, as destratification did not occur; *D. carinata* is known as a cool- to cold-water form (Hebert, 1977). The 1986/87 summer aeration appears to have had little effect on the structure of the plankton community in Lyell Reservoir.

Microcrustacean Zooplankton Gut Contents

The cladocerans and calanoid copepods ingested a variety of phytoplankton. *Boeckella triarticulata* consumed more taxa than the other zooplankton species, displaying an advantage in resource competition over other zooplankton. Large-bodied *Daphnia carinata* ingested one-third of the components of the *Boeckella triarticulata* diet, perhaps, due to its limited season in the reservoir. Perennial *Ceriodaphnia* ingested 18 taxa, as did *Calamoecia lucasi* (17 taxa).

Some of the dominant dietary phytoplankton consisted of the dominant reservoir phytoplankton. However, *Volvox* which abounded in the plankton was absent in the zooplankton guts; it was too big (Kobayashi, 1991). Neither were the abundant, small flagellates ever detected in the zooplankton gut contents. Perhaps they were ingested but were rapidly digested. On the other hand, *Chroococcus* and *Oocystis* were of low density in the plankton throughout the study, but were frequently found in the zooplankton guts.

The well digested unicellular centric diatoms such as *Cyclotella*, *Stephanodiscus* and chain-forming *Melosira*, and the intact gelatinous algae such as *Chroococcus* and *Oocystis* in the zooplankton guts are consistent with the observations by Nadin-Hurley and Duncan (1976), and Infante (1978a). Gelatinous sheaths appear to prevent digestion (Porter, 1975).

There was a weak link between the blue-green alga *Microcystis* and zooplankton in Lyell; *Boeckella triarticulata* consumed small *Microcystis* colonies.

Control of blue-green algae is a prime water quality criterion (Hodgson, 1987a). The possibility of using zooplankton to control blue-green algae (particularly *Microcystis*) was studied by De Bernardi *et al.* (1981), Jarvis (1986), and many other workers who highlighted problems: blue-green algae are nutritionally poor (Arnold, 1971; Hanazono and Yasuno, 1987); may be toxic (Lampert, 1981); and form large gelatinous colonies which prevent both ingestion and digestion (Porter, 1975). In natural conditions, grazers do not fully control blue-green algae, and are either excluded (*Daphnia carinata* and *Ceriodaphnia* sp. in Lyell) or coexist with them (*Daphnia lumholtzi*, *Calamoecia lucasi*, and *Boeckella triarticulata* in Lyell).

Comparison between Lyell and Wallerawang Reservoirs

The dominant summer phytoplankton were *Chroococcus* and *Melosira* in Wallerawang (Kobayashi, 1992). *Volvox* and *Microcystis* dominated in Lyell. This reflects their different trophic status: Wallerawang is mesotrophic and Lyell is eutrophic. On an abundance basis, however, all Lyell phytoplankton (except *Microcystis*) lie within the mesotrophic definition (Landner, 1976).

The dominant zooplankton differs between reservoirs by the presence of *Daphnia lumholtzi* and the absence of *Bosmina meridionalis* and *Boeckella minuta* in Lyell; *Ceriodaphnia* and *Boeckella triarticulata* are early-summer forms in Wallerawang, but are perennial in Lyell.

The large August 1986 flood caused high turbidity, increased nutrients, and temporarily reduced plankton density, except of flagellates, in both reservoirs. However, there were some different responses to the flood: *B. triarticulata* did not decline markedly in Lyell, and the recovery of phytoplankton in Lyell was much later than in Wallerawang.

To date, there is insufficient information available on fish predation on zooplankton in both reservoirs (Kobayashi, 1992). Because Lyell and Wallerawang Reservoirs support planktivorous fish such as brown trout and rainbow trout, substantial amounts of zooplankton, especially large forms such as *Daphnia carinata* and *Boeckella triarticulata*, may have been removed by fish predation (Brooks and Dodson, 1965; Geddes, 1986; Evans, 1990). This may be important if the ability of large-bodied zooplankton to limit phytoplankton abundance is restricted by fish predation (Gophen, 1990). The effect of fish predation on the reservoir zooplankton populations needs study.

Analysis of zooplankton gut contents revealed similar main diets and their digestibility among dominant microcrustacean zooplankton between the reservoirs. Zooplankton variety of diet increases with increasing body size of the species. The large, perennial *Boeckella triarticulata* has the most varied diet (including *Microcystis*) in Lyell. *Boeckella triarticulata* ingests filamentous blue-green algae such as *Anabaena* and *Nostoc* in

New Zealand lakes (Burns and Xu, 1990), displaying its adaptability to blue-green algae.

In conclusion, Lyell and Wallerawang Reservoirs are geographically proximate and hydrologically interactive, but support distinctive plankton communities. As Lyell Reservoir shows some eutrophic conditions (Bek and Martin, 1990), the monitoring of physicochemical conditions and plankton communities needs to be continued, especially when the industrial and recreational use of the reservoir are considered.

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PROCEEDINGS
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NUMBER 4

Fossil Flowers of *Ceratopetalum* Sm. (Family Cunoniaceae) from the Tertiary of Eastern Australia

W. B. K. HOLMES and F. M. HOLMES

HOLMES, W. B. K., & HOLMES, F. M. Fossil flowers of *Ceratopetalum* Sm. (family Cunoniaceae) from the Tertiary of eastern Australia, *Proc. Linn. Soc. N.S.W.* 113 (4), 1992: 265-270.

A fossil flower, preserved as an impression in the diatomite of the Middle Miocene Chalk Mountain Formation of the Warrumbungle Mountains, is described as *Ceratopetalum priscum* Holmes and Holmes sp. nov. The presence of petals in the fossil suggests an affinity with the extant *C. gummiferum* Sm. The flower from the Late Eocene-Early Oligocene Vegetable Creek Deep Leads of Northern New South Wales, described by Ettingshausen (1888) as *Getonites wilkinsonii*, is re-assigned to the genus *Ceratopetalum* on the basis of similarity of sepal venation to that of the extant *C. virchowii* F. Mueller. An undescribed flower from the Middle Eocene Maslin Bay flora (Christophel and Blackburn, 1978) probably represents an even earlier occurrence of *Ceratopetalum*.

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INTRODUCTION

The genus *Ceratopetalum* Sm. includes six extant species (Hoogland, 1960, 1981) which range in size from large shrubs to tall trees. At present, the genus has a disjunct distribution in eastern Australia. The type species *C. gummiferum* Sm. is common in rainforests and sclerophyll forests on the eastern side of the Great Dividing Range in New South Wales. *C. apetalum* D. Don is restricted to rainforests in eastern New South Wales and south-eastern Queensland. The remaining four species are rainforest trees in far north-eastern Queensland. *C. succirubrum* C. T. White occurs also in New Guinea where it has a wide distribution.

The genus is characterized primarily by the enlarged and lignified sepals which radiate around the half-inferior ovary. With the exception of *C. gummiferum* which has furcate petals, all extant species are apetalous and show few differences in their floral characters.

In the past, the presence of *Ceratopetalum* in the fossil record was based on leaf impressions which bore varying degrees of similarity in gross morphology to leaves of extant species (Ettingshausen, 1883, 1886, 1888, 1894; White, 1978). Examination of the types or photographs of specimens that could be located, showed that most of the fossil leaves had a gross morphology superficially resembling *C. apetalum* or *C. gummiferum*. However, none agreed exactly with any living species. Although the flowers of extant species are, in the main, very similar, there are considerable differences in leaf morphology, so that identification of species in the field is usually based on leaf characters (R. W. Johnson, pers. comm.). Assuming that leaf form has been variable throughout the evolution of the genus, some at least of the fossil leaf species may prove to belong to *Ceratopetalum*. However, on phytogeographical grounds (Burbidge, 1960), the leaves attributed to *Ceratopetalum* from Tertiary deposits of the Northern Hemisphere (referred to in Ettingshausen, 1888) are certainly misidentifications.

Fossil pollen compared with *Ceratopetalum* has been recorded from the brown coals of the Middle Miocene Yallourn Seam in the Gippsland Basin of Victoria (Luly *et al.*, 1980).

The fossil specimens described below are detached flowers with enlarged sepals. Their identification as *Ceratopetalum* is based essentially on the gross morphology of the 5-merous form, half-inferior ovary and particularly of the venation pattern of the sepals which bears a close similarity to that of some extant species.

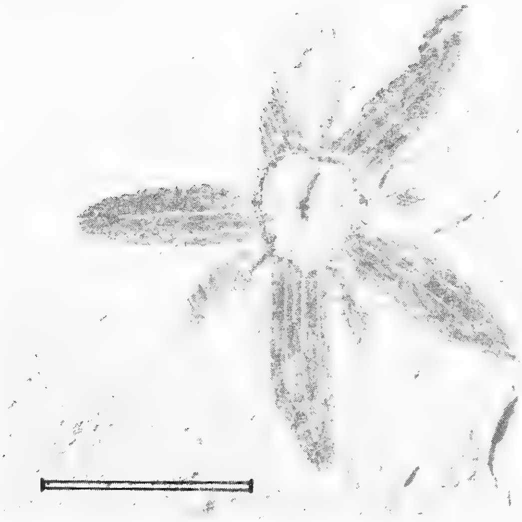
DESCRIPTIONS AND RELATIONSHIPS

Family CUNONIACEAE

Genus ***Ceratopetalum*** Sm.

Ceratopetalum priscum Holmes and Holmes sp. nov.

(Fig 1)



1.

Fig. 1. Ceratopetalum priscum Holmes and Holmes sp. nov. Holotype MMF25501. x2.8. Scale bar equals 10 mm.

Diagnosis: Flower with sepals narrow-oblong, apices, obtuse, bases not contracted. Petals sometimes present but incomplete, with a single vein trifurcating distally.

Description: Limonite impressions or colourless moulds of dorsal and ventral surfaces of mature flowers preserved in diatomite. Ovary 3-5 mm in diameter; style 0.5 mm in diameter; no stamens preserved. Sepals 7-10 mm in length, 3-4 mm in width , narrow-oblong, not contracted at the base; apex obtuse. Sepal venation consists of three major parallel veins; a less prominent vein runs between each of the major veins and between the sepal margin and the outer veins. A few divergent secondary veins link the longitudinal veins to form a long and narrow mesh. Petals preserved only on the holotype, all with distal portion missing, 0.6-1.0 mm in width. A single vein enters the base of each petal. On the type specimen one petal expands in width as the midvein divides into three. No cuticle is preserved.

Name derivation: From the Latin *priscus* — belonging to former times.

Material: Holotype — MMF25501, Mining and Geological Museum, Sydney. From Quarry H (Griffin, 1961), Chalk Mountain Formation, Bugaldie, Warrumbungle Mountains, New South Wales. Paratypes — AMF3975 (illustrated in White, 1990, p. 197); AMF78245 and its counterpart AMF78246, Australian Museum, Sydney. From Quarry A (Griffin, 1961), Chalk Mountain Formation, Bugaldie, Warrumbungle Mountains, New South Wales.

Geological Age: Holmes *et al.* (1983) suggested a Middle Miocene age for the Chalk Mountain Formation. This was based on radiometric dates for volcanic rocks from other areas of the Warrumbungle Volcano Complex. The Chalk Mountain Formation is a lacustrine deposit interbedded between two basalt flows. Subsequent dating of these basalts, carried out by Dr A. Ewart in the Department of Geology and Mineralogy at the University of Queensland, has yielded and age of 17.2 million years for the underlying basalt and 13.7 million years for the overlying flow, both ages ± 2% standard deviation. The Middle Miocene age is thus confirmed.

Discussion: *Ceratopetalum priscum* differs from all previously described species by its uncontracted sepal bases. *C. succirubrum* has sepals which are only slightly contracted at the base but differs by its 4-merous form. The branching venation preserved in one petal on the holotype suggests that, when complete, the petals may have been trifurcate. The presence of petals indicates an affinity with *C. gummiferum* which has furcate petals. All other extant species are apetalous. The venation of the sepals is also similar to that of *C. gummiferum* (Fig. 2). A small undescribed flower from the Middle Eocene Maslin Bay flora (Christophel and Blackburn, 1978, Fig. 2c) may be a species of *Ceratopetalum*. The illustration of the flower shows no petals but appears to be closely similar to *C. priscum* in venation and shape of the sepals. Although less than half the size of *C. priscum*, it would fall within the range of size variation exhibited by flowers of extant *Ceratopetalum* spp. The flower described below as *C. wilkinsonii* comb. nov. differs from *C. priscum* by the shape and venation of the sepals.

Fig. 2. Ceratopetalum gummiferum Sm. Cleared sepal. x5.6.

The flora of the Chalk Mountain Formation is a mixture of rainforest and sclerophyllous elements (Holmes *et al.*, 1983). By analogy with extant species of *Ceratopetalum*, which, with the exception of *C. gummiferum*, are restricted to rainforests, it is likely that *C. priscum* was also a rainforest plant. However, it is not known at what time in the past species of *Ceratopetalum* may have adapted to non-rainforest habitats. Although *C. gummiferum* occurs in sclerophyll forests, Sanders (1983), in a study of the vegetation associated with basalt dykes near the Hawkesbury River, north of Sydney, noted that the species was more abundant in the more fertile soils derived from the dykes than in the adjacent sandy soils. This may indicate a relic preference by *C. gummiferum* for growth in an environment more favourable for rainforest vegetation.

Ceratopetalum wilkinsonii
(Ettingshausen) Holmes and Holmes comb. nov.
(Fig 3)

Getonites wilkinsonii; Ettingshausen, 1888: 167-168, fig. 12 only.

Ettingshausen's original diagnosis was based on the creation of a new genus, *Getonites*. The diagnosis of specific characters included a description of a *Getonia*-like leaf (Ettingshausen, 1888, figs. 11, 11a) but there is no basis whatsoever for this inferred association of the leaf and flower.

3.

Fig. 3. Ceratopetalum wilkinsonii (Ettingshausen) Holmes and Holmes comb. nov. Holotype MMF8812. x2.8. Scale bar equals 10 mm.

Emended Diagnosis: *Ceretopetalum* flower, with sepals ovate-elliptical, apices obtuse. Sepal venation comparable with *C. virchowii.*

Description: This is based on the type and only specimen, MMF8812, which is housed in the Geological and Mining Museum, Sydney. The fossil is an impression of the ventral surface of a mature flower in a matrix of white claystone. Sepal margins and veins have been replaced by limonite. The ovary, 6.5 mm in diameter, is a structureless mass of dark material. The five sepals are ca 10 mm in length, 4 mm in width at the base, increasing to 5.5 mm at half their length and then contracting to an obtuse apex. Fig. 3 clearly shows the pattern of the venation. The incomplete reticulum may be due to the loss of vein material during preservation. Small fragments of limonite are visible between some of the sepals. Ettingshausen regarded these fragments as stamens. Perhaps they are the remains of petals.

Geological Age: The type locality is between Hill and Watson's shafts, Old Rose Valley Lead, near Emmaville in northern New South Wales. Based on palynological evidence and radiometric dating of overlying basalts, the age is Late Eocene — Early Oligocene (Pickett *et al.*, 1990).

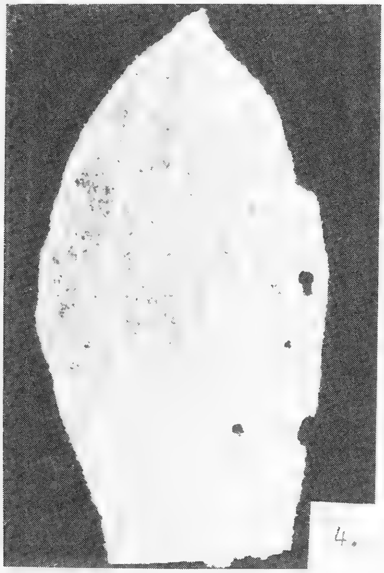


Fig. 4. Calycopteris floribunda (Roxb.) Lam. Cleared sepal. x11.2.

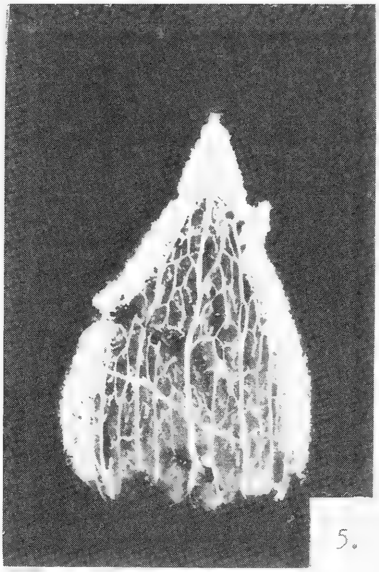


Fig. 5. Ceratopetalum virchowii F. Mueller. Cleared sepal. x11.2.

Discussion: Due to the superficial resemblance of the fossil flower to *Getonia floribunda*, Ettingshausen placed it in a new genus *Getonites* in the family Combretaceae. *Getonia floribunda* (now *Calycopteris floribunda* (Roxb) Lam.) family Combretaceae, occurs from India through south-east Asia to the Malayan Peninsula. This family is represented in Australia only north of latitude 24°S (Byrnes, 1977). Although some species in the genera *Terminalia* and *Macropteranthes* are endemic to Australia, the family is essentially of pantropic occurrence. On phytogeographic evidence (Burbidge, 1960; Johnson and Briggs, 1984) it is unlikely that representatives of the family entered Australia before the Late Tertiary. The pattern of venation on the sepals of *Calycopteris floribunda* (Fig. 4) is significantly different from the venation on the sepals of the fossil flower. However, the venation of the sepals of the fossil is closely similar to that in the sepals of the extant

Ceratopetalum virchowii F. Mueller (Fig. 5). On the basis of this close similarity in venation we believe the fossil is more satisfactorily placed in *Ceratopetalum.*

CONCLUSION

The presence of *Ceratopetalum* flowers in the Middle Miocene and Late Eocene-Early Oligocene and *Ceratopetalum*-like flowers as early as the Middle Eocene (Christophel and Blackburn, 1978) confirms the belief of Burbidge (1960) that the genus is of ancient Australian origin.

ACKNOWLEDGEMENTS

The authors wish to thank Dr L. A. S. Johnson for access to the material in the National Herbarium of New South Wales, Royal Botanic Gardens, Sydney; Ms J. Everett for preparation of sepals of *Ceratopetalum* spp. and *Calycopteris floribunda*; Dr R. W. Johnson for information on extant *Ceratopetalum* spp.; Dr J. W. Pickett, Mining and Geological Museum, Sydney for the loan of specimens; Mr D. Barnes for the *Ceratopetalum (Getonites) wilkinsonii* photograph; Dr A. Ewart, University of Queensland, for radiometric dating of basalts associated with the Chalk Mountain Formation; Dr M. Crawley, British Museum, and staff of the Palaeontology Department of the Australian Museum, Sydney; Dr. S. Forsythe, Tasmanian Geological Survey, for help in locating Ettingshausen's specimens and Tania Large, typist. W. B. K. Holmes is assisted by a grant from the C.S.I.R.O. Science and Industry Endowment Fund.

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Spatial and Temporal Variation in a Perched Headwater Valley in the Blue Mountains: Geology, Geomorphology, Vegetation, Soils and Hydrology

W. N. HOLLAND, D. H. BENSON and R. H. D. MCRAE

HOLLAND, W. N., BENSON, D. H., & MCRAE, R. H. D. Spatial and temporal variation in a perched headwater valley in the Blue Mountains: geology, geomorphology, vegetation, soils and hydrology *Proc. Linn. Soc. N.S.W.* 113 (4), 1992: 271-295.

Geology, geomorphology, vegetation, soils and hydrology were examined in an eight year study of spatial and temporal variation in a perched headwater valley in the Blue Mountains, New South Wales, Australia. Data were collected at a series of fixed sites.

Geology is important in the development of the valley form and landscape. The dominantly sandstone rocks have intercalated claystones which act as aquicludes. The claystones control the valley-in-valley segmentation and the movement of groundwater which in turn results in the development of swamps.

Geomorphic features identified included valley asymmetry, fill-incision transition zone, oversteepened reach, understeepened reach and amphitheatre. Other features defined and described for the first time in the Blue Mountains are alluvial bulges, ephemeral and perennial swamps, and valley-side knickpoints.

Three vegetation units were identified and aligned with a drainage related gradient. These are woodland dominated by trees of *Eucalyptus piperita* and *E. sclerophylla*, ephemeral swamp with sedges of *Lepyrodia scariosa* and perennial swamp with clumps of *Gymnoschoenus sphaerocephalus*. Aspect differences were measured for tree basal area and understorey diversity. Post-fire trends in cover and diversity were measured.

Soil depth was shown to vary with aspect, as was ground water depth, which also varied with vegetation type. Valley asymmetry is evident in the soils, vegetation and hydrology.

Hydrology (surface flow and groundwater movement) varies in response to rainfall regimes, and to differences in evaporation on a yearly, seasonal, daily and hourly basis. The amount and direction of groundwater flow is largely controlled by the claystones. Hydrological patterns in the woodland and ephemeral swamps differ markedly from those in the perennial swamp.

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INTRODUCTION

Because of the complexity of natural systems, landform studies either emphasize individual elements or generalize on a range of aspects using limited data. There is rarely the opportunity to study a wide range of aspects of a natural system in depth. Holland (1974) related the geomorphology of the upper Blue Mountains of New South Wales to the underlying stratigraphy and drew attention to the importance of headwater valleys — renamed here 'perched headwater valleys' — as small, discrete and easily identifiable landforms. This provides a firm base for the further exploration of spatial and temporal variations in a typical perched headwater valley.

The study area chosen, Cold Foot Creek (lat. 33°40′S, long. 150°21′E., 11.3 ha, 900 m elevation) (Fig. 1) is a typical perched headwater valley with undisturbed natural vegetation and east-west oriented drainage which allows ready comparison of aspect differences. It includes a major swamp surrounded by woodland. There are no obvious signs of human disturbance other than Mt Hay Road and a disused side track.

This paper attempts to integrate various aspects of the geology, geomorphology, soils, vegetation, and hydrology in terms of spatial and temporal patterns. A further study (Holland *et al.*, 1992) looks at the influence of solar radiation and temperature on the valley environment.

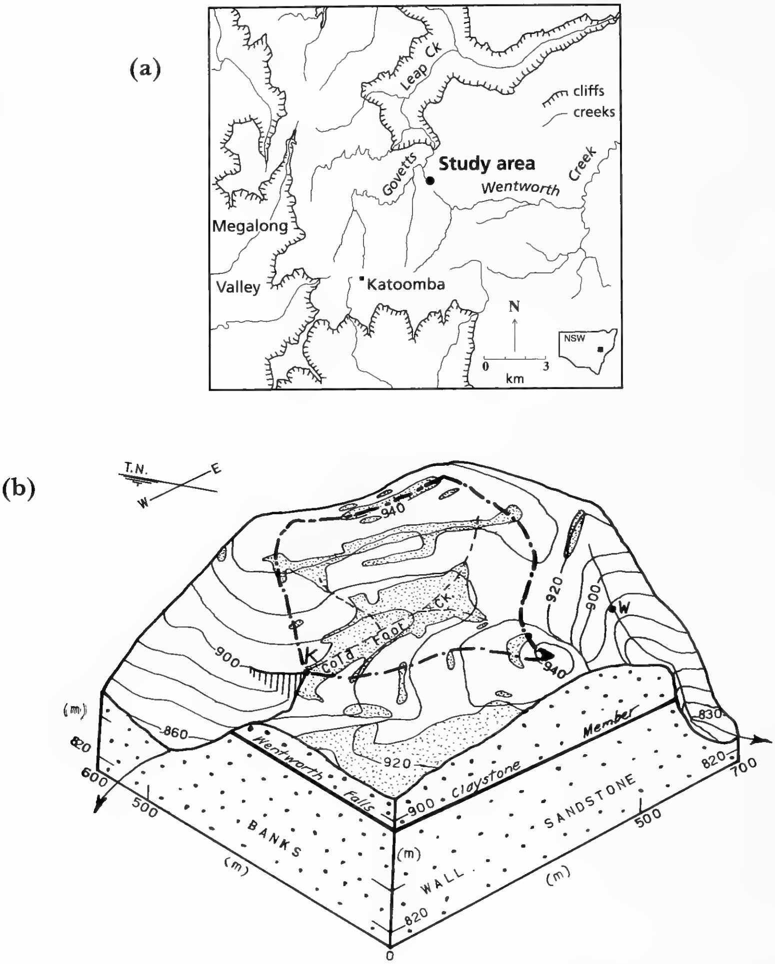

Fig. 1. Study area: (**a**) Location in Blue Mountains; (**b**) block diagram of Cold Foot Creek area (enclosed by dash dot line) showing 10 m contours, swamps (fine stipple), location of measurement of stream flow on Wentworth Creek (W), stepped knickpoint (K) and associated cliff line (vertical hachures).

UPPER BLUE MOUNTAINS SETTING

The Blue Mountains is a dissected plateau with a maximum elevation of about 1100 m a.s.l. The uplands comprise well jointed sandstones of the Banks Wall Sandstone with intercalated shales and claystones (Goldbery, 1966; Goldbery and Holland, 1973). Regional dip is generally easterly at about 1° and primary joints bear 175° (true north) with a secondary direction of 65° (Holland, 1974).

Valley width/depth ratio decreases downstream for all the valleys i.e. they tend to deepen rather than widen, many becoming slots (Holland, 1977). Creek incision includes the development of stepped knickpoints which form in response to differential erosion of the rocks and migrate upstream along individual claystone beds. Their rate of headward erosion slows upstream as drainage basin area diminishes and the amount of water available for erosion becomes less.

Perched headwater valleys are upstream of the first stepped knickpoint below a basin divide. These upland valleys have smooth, gentle slopes and minimal cliff development and contrast with a small number of other valleys in the headwaters without stepped knickpoints but with steep valley sides and cliffs extending close to the divide.

Holland (1974) noted that knickpoints occur where claystone outcrops on the valley sides. They mark the limits of individual valley segments which together form a valley-in-valley landscape. There is usually ferruginized sandstone above a claystone outcrop which obscures it. The hard ironstone probably results from long term movement and evaporation of iron-rich water. Slopes above the claystone are generally less steep than below it. The resistant ironstone facilitates a decrease in the upper slopes while allowing the lower slopes to steepen by slowing the rate of horizontal retreat of the knickpoint. The upper margins of swamps lie along the tops of the claystone beds. These swamps have sedgeland vegetation, part of the 'Blue Mountains Sedge Swamps' unit (all vegetation units are as in Keith and Benson, 1988). The swamps in the perched headwater valleys contain sandy-peaty soils which average 1.2-1.5 m in depth (Holland, 1974). Above a claystone outcrop the ground is usually dry, with woodland cover of the 'Blue Mountains Sandstone Plateau Forest' unit and has trees of *Eucalyptus sclerophylla*, *E. sieberi* and *E. piperita*. These swamps, whose upper edges are controlled by the claystones should not be confused with the dells identified by Young (1982) which have no such geologic control.

Perched headwater valleys tend to have longitudinal profiles which are understeepened compared to headwater valleys with no stepped knickpoints and to a model profile developed by Holland (1974). Slopes facing slightly east of north tend to be less steep than those facing west of south (Holland, 1968, 1974; Stockton and Holland, 1974). Such valley asymmetry has been widely observed elsewhere (Thornbury, 1954).

METHODS

Cold Foot Creek Study

A range of geomorphic features were sampled at 31 sites (Fig. 2**a**, **b**) between September 1980 and December 1988. The sites were connected by a traverse and height, aspect and slope were recorded. Slopes were measured below each site and along selected contours on both valley sides, equally high above the creek. Joints were measured near the stepped knickpoint, at the end of the valley. Identification and measurement of ground features was aided by mapping one metre contours using photogrammetric and stadia methods.

Vegetation data were collected from sites 1-30. The girth of trees in 20 x 20 m plots at each site was recorded in December 1980. Also at this time the plant species in each quarter of a 2 x 2 m sampling site at the centre of each 20 x 20 m plot, were recorded. The species sampling included an estimate of the projective foliage cover of each species.

A bushfire burnt the entire valley in December 1982 and the species were re-recorded twice in the manner outlined above, in February 1984 and September 1985. The data from the pre-fire recording (95 species from 30 sites) were analysed using a TWINSPAN classification (two way indicator species analysis) and DECORANA ordination (detrended correspondence analysis and reciprocal averaging) (Gauch, 1982).

Soil samples were taken by augering to bedrock at each site. Additional soil depths

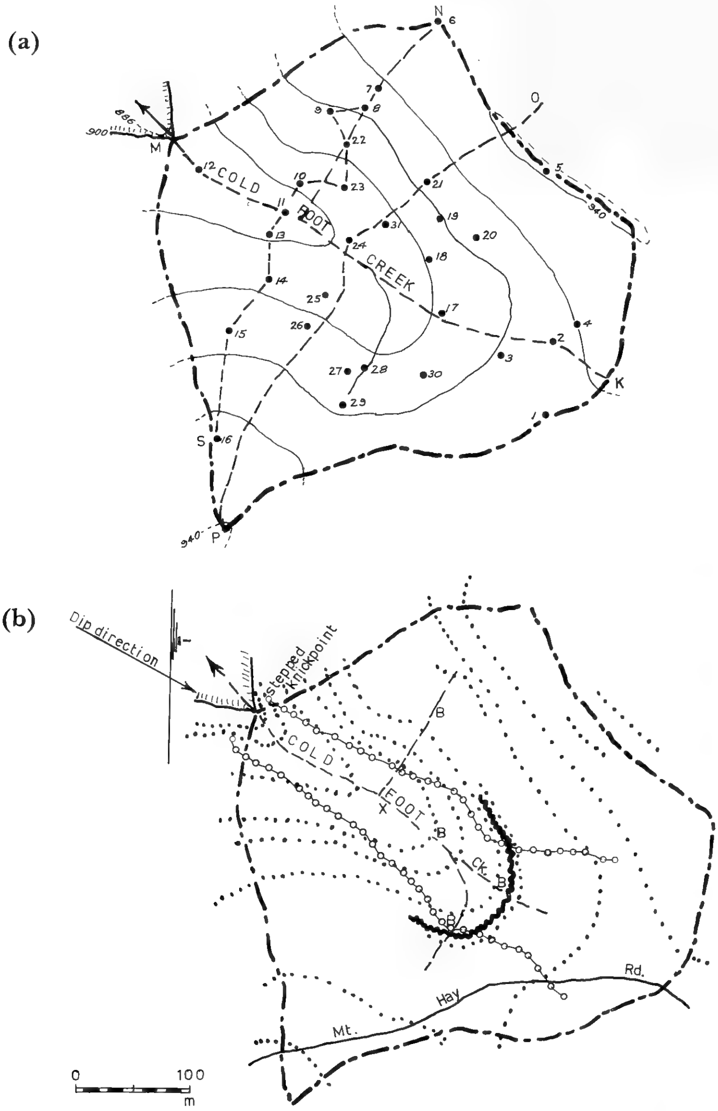

Fig. 2. Study area (dash/dot line) showing: (**a**) contours (8 m interval), sections K-M, S-N, P-O (dashed lines) and sites (numbered solid circles); (**b**) important geomorphic features — valley-side knickpoints along inferred claystone beds (line of dots), valley width/depth (points taken 3 m above, and normal to thalweg) (line of open circles), alluvial bulge (B), understeepened reach (X) and amphitheatre (wavy line).

were measured using 15 mm and 30 mm diameter pointed mild steel bars along sections K-M (Fig. 3**a**) and P-O (Fig. 3**b**). Surface moisture for each site was compared using a horticultural soil tester. Precise values of the units are unknown and were not needed since comparisons only are required. Data were recorded at about monthly intervals (September 1985-December 1987). Additional hourly records were made during several days in June and December of 1987 and 1988.

Stream discharges were recorded at the stepped knickpoint (September 1980-

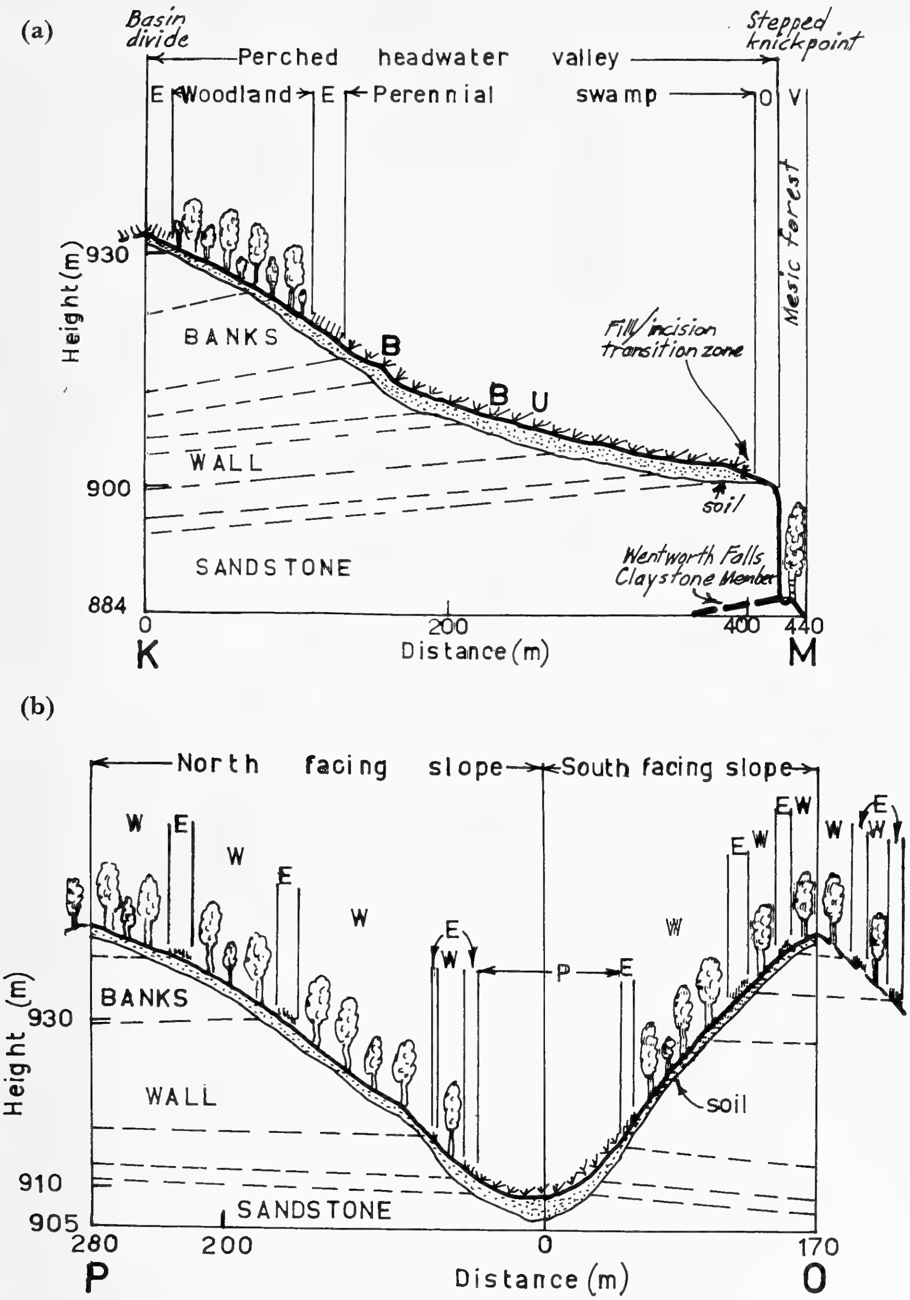

Fig. 3. Sections of valley: (**a**) longitudinal profile of Cold Foot Creek (K-M, Fig. 2**a**) showing stratigraphic, geomorphic and vegetation features (E = ephemeral swamp, B = alluvial bulge, U = understeepened reach, O = oversteepened reach, V = entrenched valley) — inferred claystone beds shown by dashed lines; (**b**) cross section (P-O, Fig. 2**a**) showing stratigraphic, geomorphic and vegetation features (W = woodland, E = ephemeral swamp and P = perennial swamp).

December 1988) at about monthly intervals. Discharges were measured by diverting the flow at the lip of the knickpoint where it flows over bare rock. Sand filled plastic tubes diverted the water into a container where the flow was timed. Additional continuous records of flow, extending over several days, were obtained with a mechanical recorder.

Groundwater movement was measured in a 45 mm dia. perforated plastic pipe — a single pipe was sunk to bedrock at each site (except 3, 27 and 30). Water levels were recorded at about monthly intervals from March 1982 to December 1987. Additional records of hourly measurements were made during surveys in June and December 1987. Continuous records extending over several days, were made at site 10 with an automatic recorder in December, 1987.

RESULTS

Geology and Geomorphology

Spatial Variation

Rock is not visible, apart from ferruginized sandstone less than a metre high, exposed at some valley-side knickpoints and at the stepped knickpoint. Claystone is seen only in road cuttings. Additional beds are inferred from the known relationship between the tops of swamps and claystone beds (Fig. 3**b**). Regional dip, calculated from planes of best fit on the tops of the swamps, varies from 0.8° to 1.6° and the direction of dip from 91° to 119° (based on true meridian). These results are consistent with findings of Holland (1974).

Primary joints near the stepped knickpoint averaged 160° with a secondary set averaging 70°. The joints are numerous and deep.

The valley has smooth, gentle slopes which are generally concave on the valley floor and convex further upslope. There are no cliffs, apart from the characteristic stepped knickpoint (Holland and Pickup, 1976), developed on the Wentworth Falls Claystone Member, at the end of the valley. The mean slope of south-facing sites is significantly greater than those facing north (Table 1). As significant differences are evident in woodland and swamps, slope differences are independent of vegetation cover.

The longitudinal profile traverses the thalweg since the creek is largely unformed. The grade changes where inferred claystones crop out along the thalweg — below these points it is steeper than above them. They could be relict stepped knickpoints smoothed by erosion.

An oversteepened reach (i.e. steeper than Holland's (1974) model profile of Blue Mountain creeks) of 11 m length (Fig. 4), occurs immediately above the stepped knickpoint where bare rock is exposed (Holland and Pickup, 1976).

A fill-incision transition zone is the interface between the upstream limit of erosion of bedrock at the knickpoint (oversteepened reach) and the creek flowing in fill upstream of it. Both field observations (Holland, 1974) and experiments (Holland and Pickup, 1976) have demonstrated that the position of the zone can fluctuate. As the soil here is thinner than further upstream the zone is vulnerable to climatic factors which alter the binding vegetation and roots or to hydrologic factors which affect the erodibility.

An understeepened reach (Fig. 4), results from processes balancing rates of valley widening and deepening above the knickpoint. The concave profile here also incises a number of claystones whereas the claystones further downstream are more widely spaced because of the gentle creek gradient. Thus subsurface water emerges at a number of points on the understeepened reach, possibly aiding bedrock corrosion (Bunting, 1960).

New features on the longitudinal profile are called here *alluvial bulges* (e.g. at sites 8, 17 and 24). These occur below abundant supplies of subsurface water from claystone bed outcrops. The emerging water increases the plasticity of the soil and over a long period adds sediment in suspension to supplement that transported from further upstream. The net result is a bulge in the profile, slumping downstream and ridges and swales normal to the ground slope. The swamps have numerous sediment traps of vegetation and soil up to 0.2 m high and ridges and swales, similar to those described by McElroy (1952), up to 0.5 m deep. These ridges, of living *Gymnoschoenus* tussocks and trapped sediment, are normal to the slope. These features divert the flowline, dispersing water over a wide area and protecting the valley floor from erosion.

An amphitheatre is formed at the head of the swamp (near site 17). Factors affecting the development include headward retreat of the knickpoints and valley-side knickpoints, junction of two thalwegs, oversteepening of the valley sides below valley-side knickpoints and understeepening of the valley floor.

Width/depth values for 3 m above the valley floor are consistent with Holland's (1974) regression equation ($w/d = 94.85 - 30.22 \log D$, where valley width (w) is 3 m above the creek, valley depth (d) is 3 m, distance (D) below the interfluve is in metres, number of observations (n) is 15, and coefficient of determination (r^2) is 0.95). Valley width (w) also narrows downstream.

TABLE 1

Mean Slope (°) ± s.e.m., showing comparison of north and south-facing slopes

	N-facing	n	S-facing	n		
All sites	6.2 ± 0.55	14	9.7 ± 0.79	17	$t = 3.4$	$P<0.005$
***Woodland**	7.7 ± 0.13	19	11.4 ± 0.96	19	$t = 3.7$	$P<0.001$
***Ephemeral swamp**	12.4 ± 0.57	17	16.8 ± 0.58	23	$t = 5.1$	$P<0.001$
***Perennial swamp**	6.6 ± 0.64	17	8.8 ± 0.94	21	$t = 5.5$	$P<0.001$

* Slopes taken opposite each other and equally high above the creek for each vegetation area.

Temporal Changes

Landforms generally are the end result of long-continuing and distant processes. Recognition of time differences is often largely speculative. Alternatively, testing small-scale differences is complex and time-consuming. This study has not examined these differences.

Vegetation and Soils

Spatial Variation

The most notable feature of the vegetation is the distinction between the eucalypt woodland and the treeless sedgeland and shrubby heath of the swamps (Fig. 5). The contrasting vegetation areas are clearly apparent in aerial photography and in most cases the transition from woodland to swamp is abrupt. The major swamp, Cold Foot Swamp, of about 1.7 ha, extends above the stepped knickpoint for some 280 m with a maximum width of 100 m. At the beginning of the study the sedgeland, was dominated by sedges and small shrubs, particularly by *Gymnoschoenus sphaerocephalus* (Button Grass) and *Xyris operculata*. Around the margins was a fringe of *Hakea teretifolia*. The woodland has trees of *Eucalyptus sclerophylla*, *E. sieberi* and *E. piperita*.

The pre-fire TWINSPAN classification identified three species groups (Fig. 6). A group characterized by *Gymnoschoenus sphaerocephalus*, *Baeckea linifolia* and *Empodisma minus*, associated with the wettest swamp sites, a second group characterized by *Lepyrodia scariosa*, associated with marginal swamp conditions, and a third group with *Lambertia*

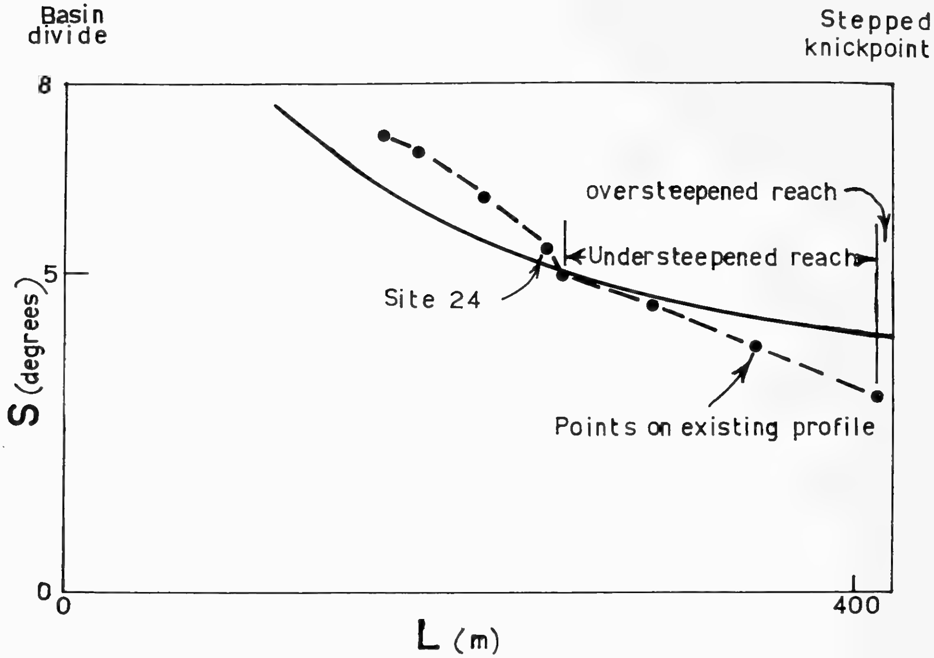

Fig. 4. Longitudinal profile of Cold Foot Creek (dotted line) compared to model profile of Holland (1974) $S = 2.11\ (0.006\ L)^{-0.474}$ (solid line) where S = slope (°) and L = distance from the basin divide (m).

formosa, *Daviesia ulicifolia* and *Patersonia glabrata* was indicative of woodland sites.

The DECORANA ordination showed the three groups to be aligned strongly with the first axis which appears to indicate increasingly better drainage conditions from Group 1 swamp species to Group 3 woodland species.

Soils are shallow, sandy, and contain organic material from rotting vegetation and charcoal from bushfires. Woodland soils are generally yellowish in colour with little contained organic material; ephemeral swamp soils tend to be grey/brown with some organic material in the profile; while the soils in perennial swamps are usually grey/black and contain large amounts of organic material throughout the profile. Soil depth means are higher for the perennial swamps than for the ephemeral swamps and the results are significant (Table 2**a**). The means are also higher for the perennial swamps than the woodland and these results are significant.

Floristic differences between vegetation on the north and south-facing slopes were evident in data collected from the woodland sites (Table 3). Total tree basal area is highest on south-facing slopes. Of the tree species, *Eucalyptus piperita* makes up about half basal area on both north and south-facing slopes, on north-facing slopes *Eucalyptus sclerophylla* is the other major species, on south-facing slopes dominance is shared between *E. sclerophylla* and *E. sieberi* (Table 4).

In comparison with tree predominance on the south-facing slopes, the shrub and ground species flora is richer on the north-facing slopes and has greater total cover (Fig.

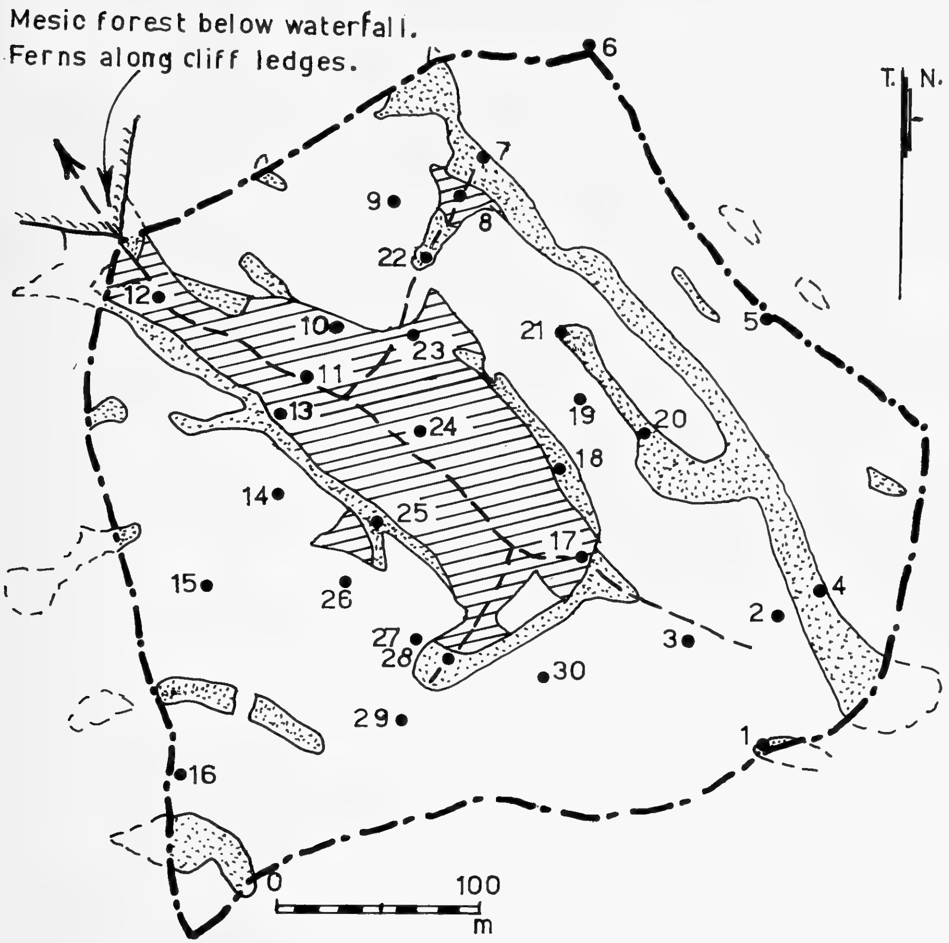

Fig. 5. Vegetation map showing woodland dominated by *Eucalyptus* (unshaded), ephemeral swamp by *Lepyrodia* (stippled) and perennial swamp by *Gymnoschoenus* (hatched), together with vegetation sampling sites.

TABLE 2

Mean soil depth (m) (± s.e.m.), along section P-O (Fig. 3)

(a)	All Sites	n
Woodland	1.06 ± 0.053	16
Ephemeral swamp	1.17 ± 0.165	12
Perennial swamp	1.91 ± 0.233	5

For difference between woodland and perennial swamp $t = 5.0$, $P<0.001$ and between ephemeral and perennial swamps $t = 2.3$, $P<0.05$.

(b) Woodland and Ephemeral Swamp Sites

N-facing	n	S-facing		n	
1.1 ± 0.06	15	0.8 ± 0.09	$t = 3.1$	9	$P<0.01$

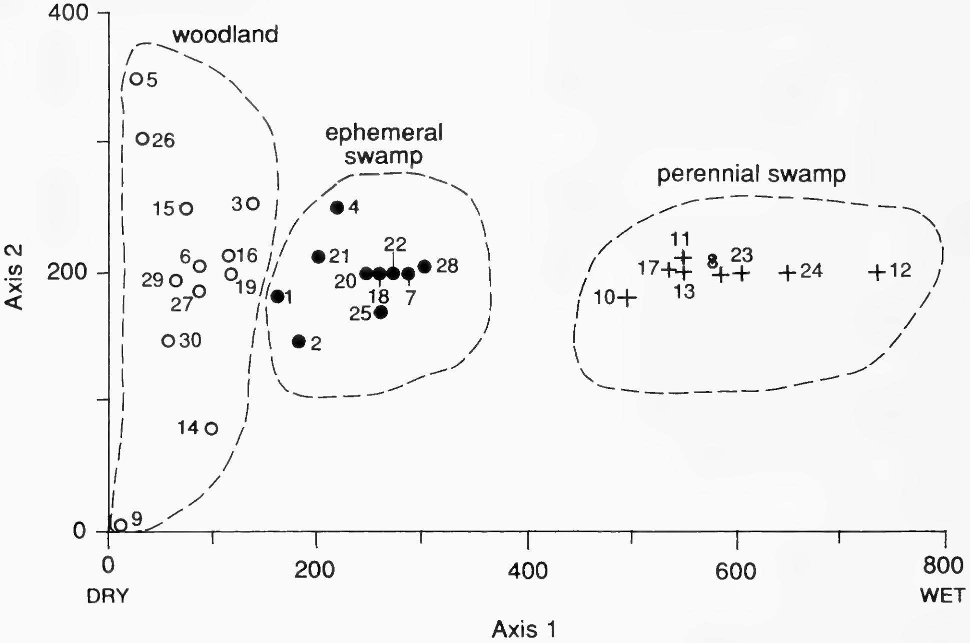

Fig. 6. Ordination of vegetation site data on axes 1 and 2 of DECORANA analysis; woodland (open circle), ephemeral swamp (closed circle) and perennial swamp (cross). Axis 1 is interpreted as a moisture/drainage gradient.

7). After the 1982 fire, species richness increased on both aspects but the relative differences became apparent 3 years after the fire. Ground cover on south-facing slopes reached pre-fire levels 3 years after the fire, but only to half the pre-fire north-facing levels (Table 4, Fig. 7). Some species were noted only at north or south facing sites (Table 3).

Soils were deeper on north-facing slopes than on the south-facing slopes along section P-O (Table 2**b**) and the means are significantly different. From using bars to penetrate the soil to bedrock, the north-facing holes were found to be less compact (i.e. easier to penetrate) than those facing south.

The inclination of ten trees recorded for each woodland site showed a tendency for the trees to lean downslope, presumably in response to soil creep (60% to 90% of the total observations for each station, gave readings within ±90° of the ground slope bearing). The dominant westerly winds also appear to have influenced the trunks since many trees were inclined towards the east. The sun also seems to play a part in the direction of lean as a number of trees on south-facing slopes were observed to reverse their direction (i.e. head towards the north), above two metres from the ground.

Holland (1974) proposed the terms valley-side and valley-floor swamps, differentiated by their depth of fill and location, but new terminologies, based on hydrology and vegetation, are proposed here: *perennial swamp*, where the water supply is virtually constant and vegetation is dominated by *Gymnoschoenus*; *ephemeral swamp*, where the water supply is irregular and vegetation is characterized by *Lepyrodia*.

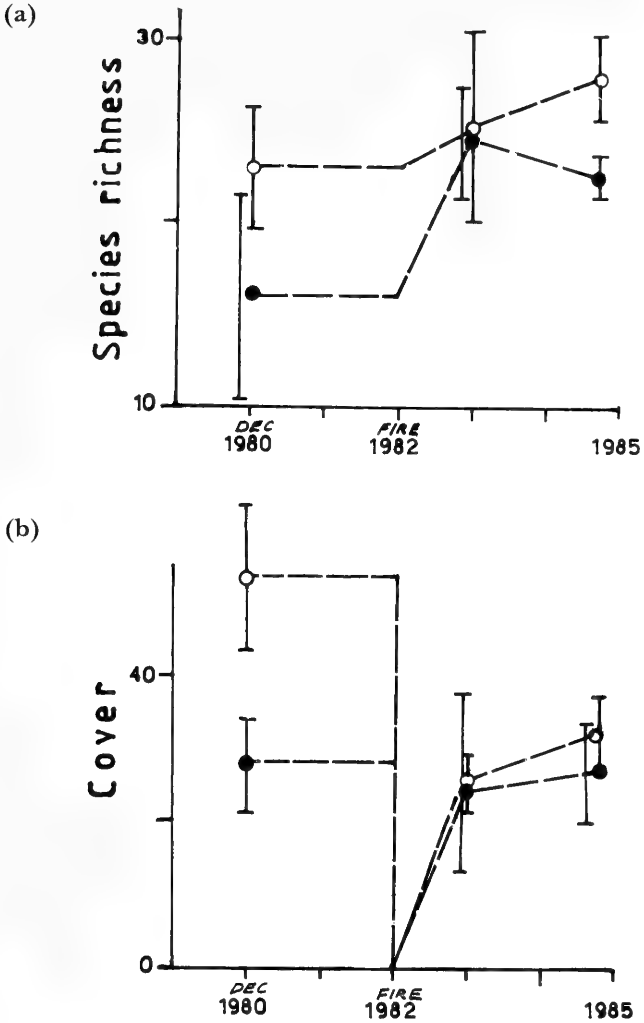

Fig. 7. Woodland understorey species richness (species/$4m^2$) and cover (%) for north (open circle) and south (closed circle) facing slopes before and after fire. Bars indicate 95% confidence intervals with south-facing site offset to left.

Temporal Changes

The major change in the vegetation during the period of the study resulted from the 1982 bushfire that burnt the entire valley, scorching the crowns of the tallest trees and blackening the swamp to ground level. Many species resprouted after the fire and the major pre-fire patterns appeared to quickly re-establish. Some species previously unrecorded during the study were noted, while some other species occupied a wider range of sites. In particular *Hakea teretifolia* seedlings appeared in the perennial swamp where adults had previously been absent. The longer term effects of the fire have not been followed up at this stage.

As with landforms, temporal changes to soils, which are complex and difficult to determine, are not included in this study.

TABLE 3

Plant species and frequencies in three habitats: woodland (12 sites), ephemeral swamp (10 sites) and perennial swamp (8 sites); and occurrence on north/south aspects. Nomenclature follows Jacobs and Pickard (1981)

Species	**Perennial swamp**	**Ephemeral swamp**	**Woodland**	**Aspect**
Acacia obtusifolia			8	S
Acacia terminalis			42	N S
Actinotus minor		20	8	N S
Amperea xiphoclada		10	8	S
Baeckea linifolia	100			N S
Banksia spinulosa			33	N
Baumea gunnii	25			N S
Billardiera procumbens			17	N S
Boronia ledifolia			67	N S
Boronia microphylla			8	N S
Bossiaea ensata			17	N
Bossiaea heterophylla		40	67	N S
Cassytha pubescens		50	67	N S
Caustis flexuosa			42	N
Caustis pentandra			8	N
Chionochloa pallida		10	17	N S
Conospermum taxifolium		20		S
Conospermum tenuiflorum		20	25	N S
Dampiera stricta		90	58	N S
Danthonia sp.			8	N
Daviesia ulicifolia		50	92	N S
Dillwynia sericea		10		S
Empodisma minus	100	10		N S
Entolasia stricta		10		N S
Epacris microphylla		50		S
Epacris obtusifolia	38	20		N S
Epacris pulchella			8	S
Eucalyptus piperita			42	N
Eucalyptus sclerophylla			50	N S
Eucalyptus sieberi			8	S
Eucalyptus stricta		10		S
Gahnia microstachya			17	N S
Gahnia sp.			42	N S
Gompholobium latifolium			8	S
Gonocarpus tetragynus		20	25	N S
Gonocarpus teucrioides	13	40	8	N S
Goodenia belledifolia	13	70	50	N S
Grevillea laurifolia			8	N S
Grevillea sericea		30	58	N S
Gymnoschoenus sphaerocephalus	88			N S
Haemodorum planifolium		10	17	N S
Hakea dactyloides		40	25	N S
Hakea teretifolia	38	50	8	N S
Hibbertia cistiflora		10		N S
Hibbertia empetrifolia		10	25	N S
Isopogon anemonifolius		30	25	N S
Kunzea capitata	25			N S
Lambertia formosa		10	58	N S
Lepidosperma limicola	75			N S
Lepidosperma viscidum		30		N S
Leptospermum attenuatum		80	50	N S
Leptospermum flavescens		10		S
Leptospermum lanigerum	13			S
Leptospermum squarrosum	38	20		N S

TABLE 3 (Cont'd.)

Species	Perennial swamp	Ephemeral swamp	Woodland	Aspect
Lepyrodia scariosa	13	100	17	N S
Lindsaea linearis		50	50	N S
Lomandra cylindrica		40		N S
Lomandra filiformis		10	50	N S
Lomandra glauca		20	58	N S
Lomandra gracilis		10	17	N S
Lomandra longifolia			8	S
Lomandra obliqua		20	75	N S
Lomatia silaifolia			33	N S
Mirbelia rubiifolia		60		S
Monotoca scoparia			8	N
Mitrasacme polymorpha		10		S
Patersonia glabrata		10	75	N S
Patersonia sericea		40	75	N S
Persoonia laurina			8	N
Petrophile pulchella		10	25	N S
Phyllota squarrosa			50	N
Pimelea linifolia			58	N
Platysace linearifolia		40	75	N S
Plinthantheca paradoxa		20		S
Poranthera microphylla			17	N S
Pteridium esculentum			8	S
Ptilanthelium deustum		80	25	N S
Pultenaea divaricata	50			N S
Pultenaea elliptica			25	N
Pultenaea incurvata	13			N S
Schoenus brevifolius		50	17	N S
Schoenus villosus		60	25	N S
Schoenus sp.			8	N S
Selaginella uliginosa	13	10	8	N S
Sowerbaea juncea		10		S
Symphionema montanum		10		S
Tetrarrhena juncea	25	90	50	N S
Tetratheca rupicola			8	N
Thysanotus juncifolius		10		N
Thysanotus tuberosus		10		S
Viola sieberiana			8	N
Xanthorrhoea resinosa			8	N S
Xanthosia pilosa		10	58	N S
Xyris ustulata	63			N S

Hydrology

Spatial Variation

(i) Surface Flow

Perennial creek flow is along a 60 m length above the stepped knickpoint. Elsewhere creeks appear only after heavy rain.

(ii) Groundwater

Height of groundwater table above bedrock increases downslope and downvalley with maximum saturation at site 24 (2.6 m), in the centre of the swamp (Figs. 5, 8, 9). Surface moisture readings show a similar trend (Fig. 10).

Height of groundwater table above bedrock under the woodland is less than for the

TABLE 4

Prefire basal area of tree species

(a) Mean basal area (m^2ha^{-1}), (± s.e.m.)

	N-facing	**n**	**S-facing**	**n**
Eucalyptus piperita	26 ± 10.3	9	34 ± 9.8	3
Eucalyptus sclerophylla	22 ± 6.0	9	18 ± 13.8	3
Eucalyptus sieberi	7 ± 3.3	9	21 ± 7.5	3
Total basal area	55 ± 7.3	9	73 ± 5.2	3

(b) % total basal area

	N-facing	**S-facing**
Eucalyptus piperita	47	46
Eucalyptus sclerophylla	40	25
Eucalyptus sieberi	12	28
Total	100	100

ephemeral swamp which in turn is less than for the perennial swamp, in each season (Table 5**a**). Surface moisture readings show a similar trend (Table 6**a**).

A difference in groundwater behaviour for woodland and ephemeral swamps on one hand and perennial swamps on the other is revealed in the relationship between the mean watertable height above bedrock and the range of readings for each site, in all seasons.

Comparing the mean with the range in the woodland and ephemeral swamps, there is a trend that as the mean increases the range also increases. Means for north-facing woodland sites vary from .005 m to .037 m and for south-facing swamp sites from .06 m to .63 m (Fig. 11**a**). The low number of sites preclude testing of the south-facing woodland and north-facing swamp sites. The results suggest that groundwater is free to move within the soil down the valley side within each vegetation unit. At the same time there is likely to be increasing groundwater available from runoff in the downslope direction. No correlation was found between groundwater depth and surface area draining to each site but it is thought that the segmentation of slopes by the claystones and the effect on local groundwater movements could influence this result. The groundwater drains away fairly rapidly, so the greater the resulting water depth from a rain event, the greater the variation or range.

For south-facing perennial swamp sites there is a trend that as the mean increases the range decreases (Fig. 11**b**). The low number of sites precludes testing of the north-facing sites. The swamps tend to accumulate water, particularly on the understeepened reach, and tend to dry out from the periphery. Factors contributing to impedence of drainage include geomorphology (understeepened reach, alluvial bulge, ridges and swales and decreasing valley width downstream), vegetation (closely spaced sedge clumps) and soil (a fibrous peaty texture acts like a sponge). These conclusions on the three separate vegetation units are supported by watertable heights above bedrock measured on 29 November, 1982 during a dry summer period where rainfall for the preceding 30 days was 13 mm and the temperature on the preceding day was 23°C. All the woodland and ephemeral sites had zero water in the holes while in the perennial swamp only site 10 had zero water depth. There was no flow out of the valley and the knickpoint had zero flow. At the same time the watertable height at site 24, in the centre of the perennial swamp, was 2.4 m.

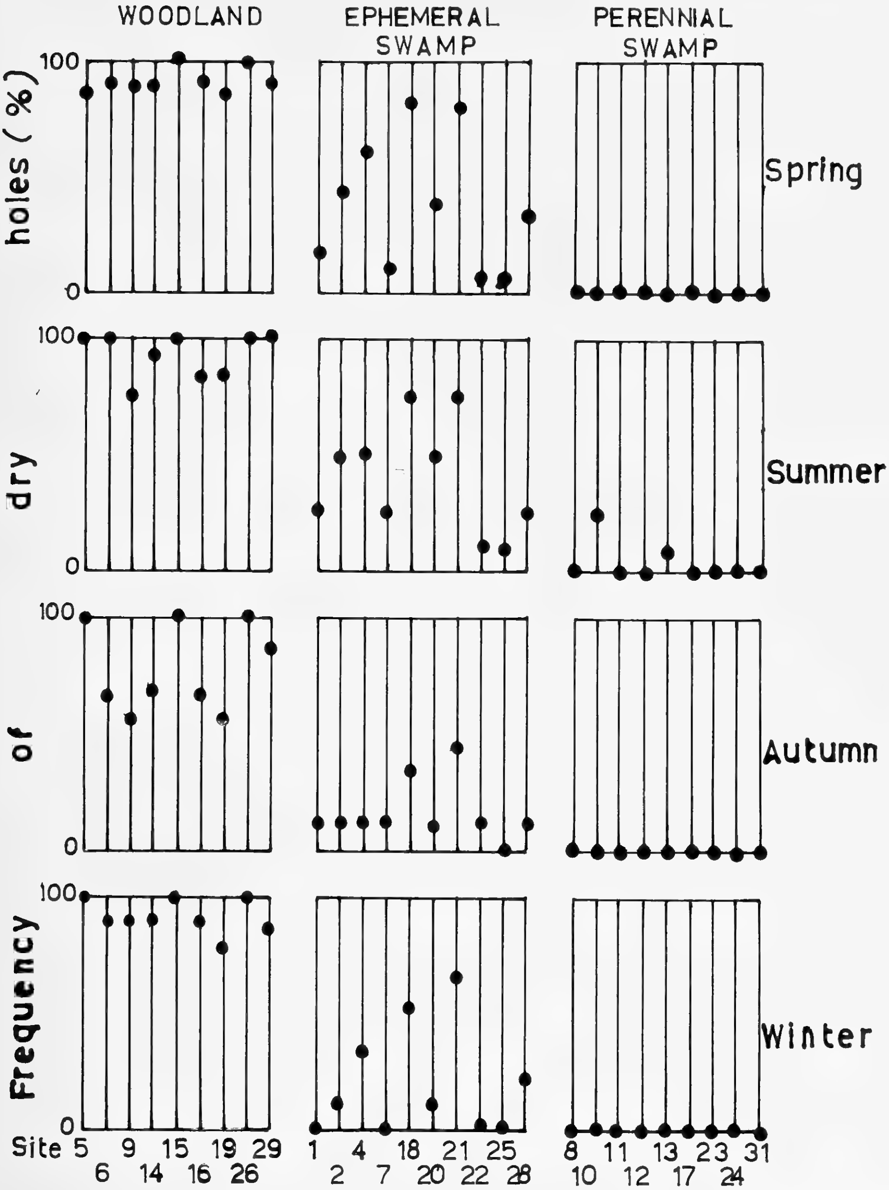

Fig. 8. Frequency that each hole was dry (%) between March, 1982 and December, 1987 for all sites by season and for woodland, ephemeral swamp and perennial swamp.

The maximum height of the groundwater table above bedrock for all woodland sites in each separate season was greater for south-facing sites than for north-facing sites (Table 5**b**). In the perennial swamp the range of groundwater table heights for site 13 (north-facing) was greater than for site 10 (south-facing), in each season (Table 7). Surface moisture on a woodland south-facing site (9) was significantly greater than for a woodland north-facing site (15), sites equally high above the creek (Table 6**b**). Further

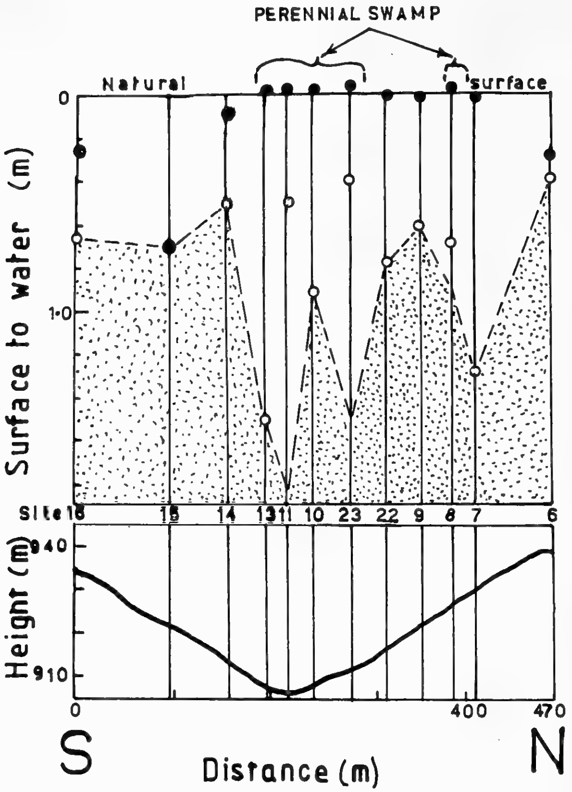

Fig. 9. Sites on section S-N (Fig. 2a) showing ground height (firm line), maximum (closed circle) and minimum (open circle) distance from ground surface to groundwater table level, and distance from ground surface to bedrock (dashed line), all in metres.

TABLE 5

Maximum height of groundwater table above bedrock (m) for vegetation types, March 1982-December 1987:
(**a**) by season, for all sites; (**b**) by season and aspect (woodland sites only)

(a)	**Spring**	**Summer**	**Autumn**	**Winter**
Woodland	0.6	0.5	0.5	0.6
Ephemeral Swamp	1.9	1.6	1.9	1.9
Perennial Swamp	2.6	2.6	2.6	2.6

(b)	**N**	**S**	**N**	**S**	**N**	**S**	**N**	**S**
Woodland	0.4	0.6	0.2	0.5	0.4	0.5	0.4	0.6

evidence for moist south-facing slopes is that there are numerous south-facing ephemeral swamps but few face north. This probably results from greater evaporation on the north-facing sites which have higher temperatures than south-facing sites (Holland *et al.*, 1992). Further, woodland north-facing sites 15 and 26 were always dry as water drains rapidly away from them. This may be a function of the relative soil compaction of north and south-facing sites referred to above.

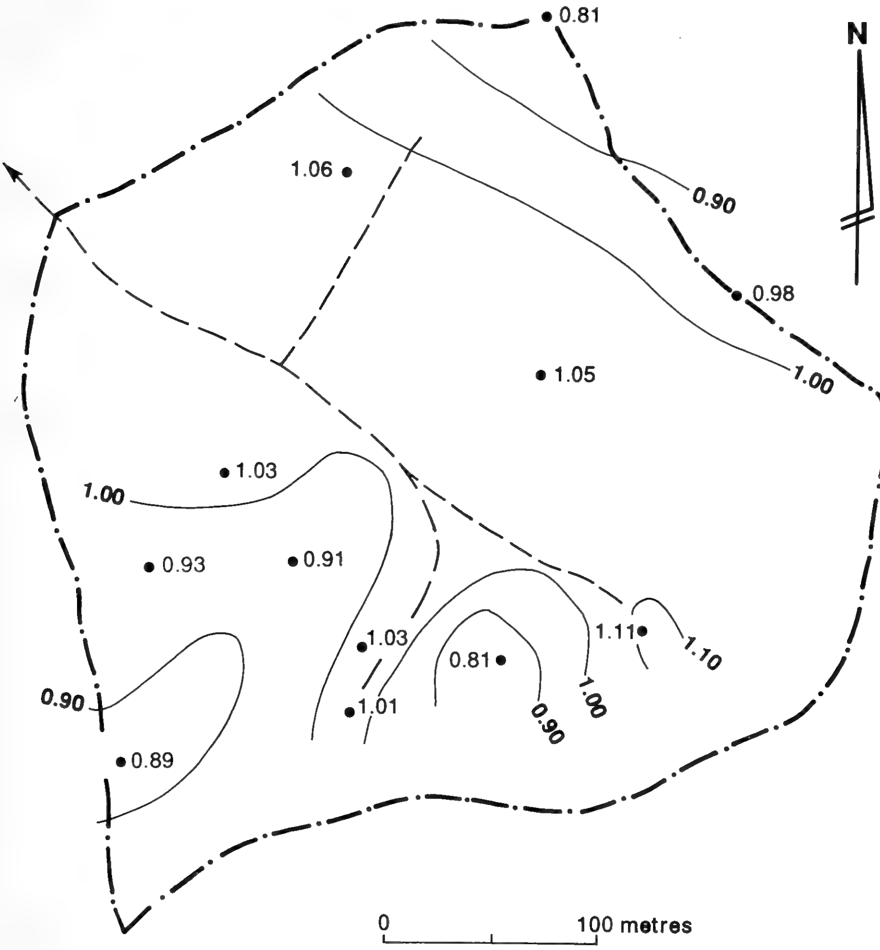

Fig. 10. Morning surface moisture (arbitrary meter units where the lower the reading, the drier the conditions). Iso lines from means of measurements.

TABLE 6

Comparison of mean surface moisture (arbitrary meter units, where lower readings indicate drier conditions) (± s.e.m.) for vegetation type in summer and winter

(a) All sites	Summer	n	Winter	n
Woodland	0.7 ± 0.11	12	0.8 ± 0.10	12
	$t = 3.3$, $P<0.005$		$t = 2.8$, $P<0.01$	
Ephemeral Swamp	1.6 ± 0.25	10	1.5 ±0.77	10
	$t = 7.3$, $P<0.001$		$t = 5.3$, $P<0.001$	
Perennial Swamp	7.0 ± 0.69	9	5.1 ±0.63	9
(b) Sites 9 and 15				
S-facing (9)	0.9 ± 0.11	12	1.0 ± 0.13	13
N-facing (15)	0.3 ± 0.05	12	0.4 ± 0.09	13
	$t = 4.4$, $P<0.001$		$t = 3.2$, $P<0.005$	

TABLE 7

Range of groundwater table height above bedrock (m), by season, for two sites

	Spring	Summer	Autumn	Winter
Site 13 (N-facing)	1.2	1.5	1.1	1.1
Site 10 (S-facing)	0.9	0.9	0.8	1.0

Groundwater movement is influenced by lithological variations and structural features of the rock sequence. Beneath the soil the water seeps through joints, bedding planes or other lines of weakness in the rocks until it reaches a claystone bed. The claystones are aquicludes, but where they pinch out or are breached by joints, water enters the underlying sandstone. Water above an aquiclude emerges on the valley side as springs or as lateral seepage along a valley side knickpoint. These aquicludes control the upper edge of the ephemeral and perennial swamps. The lower edges of the swamps are not subject to such geological controls. Cliffs near the study area reveal that water flows down the joints etc. and where water is not visible ferns and other mesic plants confirm its presence.

From the disposition of Blue Mountain swamps it is clear that water emerges above an aquiclude not only in the dip direction but in any other direction as well. However, there is a tendency for swamps to form most frequently on the sides of the valleys below a dipping claystone (Holland, 1974). The study valley dips to the east, though it drains to the west, so some of its groundwater probably seeps eastwards out of the valley. This was tested by measuring creek flow simultaneously at the stepped knickpoint and on the Wentworth Creek tributary to the east of Cold Foot Creek (Fig. 1). The flow in Cold Foot Creek on 8 December, 1987 at 1100 hours was 0.27 Ls^{-1} and at W 0.16 Ls^{-1}. The Cold Foot Creek catchment is 11.3 ha while the area above W is 3.6 ha. Given the disparate catchment sizes the flow at W is higher than expected suggesting that water enters the catchment from the study area. Furthermore, the vegetation upstream from W supports species indicative of moist conditions (*Callicoma*, *Gahnia*, *Blechnum*), though species on the interfluve of Cold Foot Creek indicate much drier conditions. Also, a swamp near W is perennial while swamps at the same elevation in Cold Foot Creek are ephemeral.

Seasonal Changes

(i) Surface Flow

Flow at the knickpoint ranged from 8.62 Ls^{-1} (28 October 1985) to zero (28 September 1980, 4 January 1981 and 29 November 1982) (Table 8). The highest discharge was when rainfall was high and temperature low. There were zero discharges on three occasions, each associated with high temperature and low rainfall. Except in high flows the water is clear since swamp vegetation effectively sieves the water. Water at the knickpoint, on 30 September 1985, at 1100 hours (flow 0.66 Ls^{-1}) contained less than 1 mgL^{-1} f sediment. The highest seasonal discharge was in spring and lowest in summer (Table 8). The low summer discharge is related to a low rainfall figure but high temperature. Much of the perennial swamp surface is ponded and susceptible to evaporation with high temperature.

Another factor affecting discharge rates is the emergence of spring water (sites 8, 23) after possibly long periods under the surface. There were substantial flows at these springs whenever they were observed.

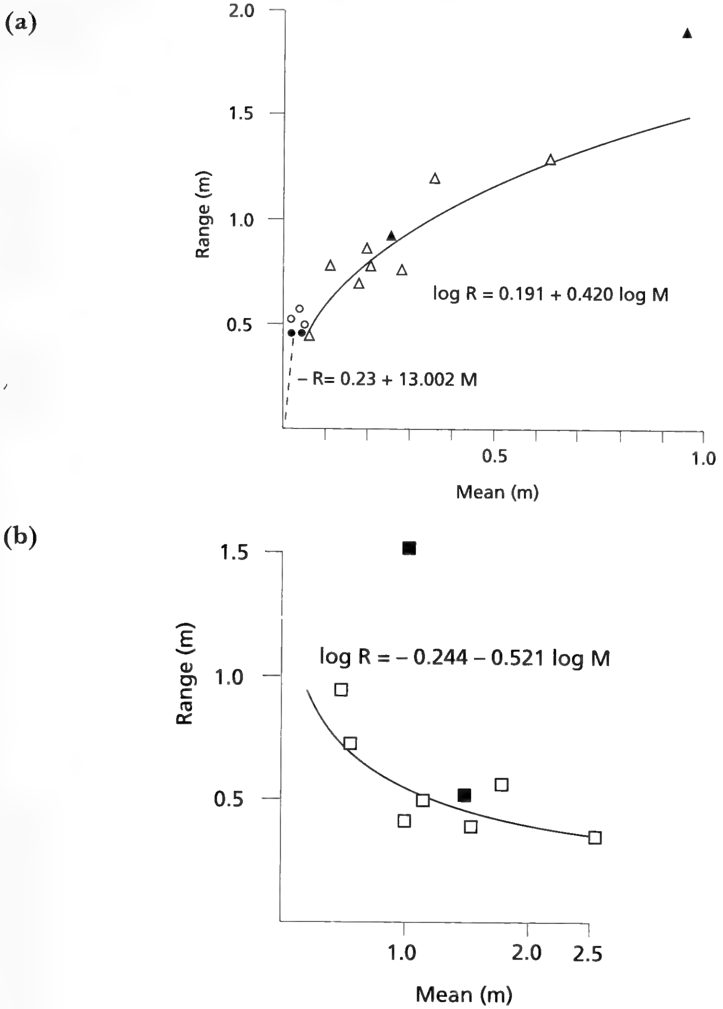

Fig. 11. Regressions of range of watertable height above bedrock (m) on mean watertable height above bedrock (m), in all seasons. (**a**) for north-facing woodland sites (closed circles and dashed line), where range = .023 + 13.002 mean, n = 6 and r^2 = .96; and south-facing ephemeral swamp sites (open triangles and firm line), where log range = .191 + .420 log mean, n = 8, and r^2 = .80. (**b**) for south-facing perennial swamp sites (open squares and firm line), where log range = -.244 + -.521 log mean, n = 7 and r^2 = .70.

Open circles are south-facing woodland sites, closed triangles north-facing ephemeral swamp sites and closed squares north-facing perennial swamp sites.

(ii) Groundwater

Woodland sites usually contain groundwater only after heavy rain (Fig. 8). They were dry over 70% of the time if figures for autumn (wettest season) are excluded (Table 9). In the ephemeral swamps the groundwater table rises rapidly after rain but soon soaks away. Perennial swamp sites were always wet (with the exception of 10 which was dry twice in spring and five times in summer, and 13 which was dry twice in summer).

The effect of evaporation, related to high summer temperatures is clear. Minimum mean groundwater table height above bedrock is in summer, even though the mean summer rainfall is higher than in winter (Table 9). The highest mean groundwater table heights occurred in autumn, coinciding with maximum seasonal rainfall. There is a similar result in the woodland, ephemeral swamp and perennial swamp.

TABLE 8

*Knickpoint discharges (Ls^{-1}): (**a**) overall highest and lowest recorded, with rainfall (mm) for the preceding 30 days and maximum daily temperature (° C) for the previous day (Katoomba meteorological station); (**b**) highest seasonal values*

(a)	**Highest**	**Lowest**		
Discharge (Ls^{-1})	8.7	0	0	0
Rainfall (mm)	420	9	13	84
Temperature (°C)	12.4	21.2	23.3	27.6

(b)	**Discharge (Ls^{-1})**	**Rainfall (mm)**	**Temperature (°C)**
Spring	8.7	420	12.4
Summer	4.8	110	25.0
Autumn	7.0	338	14.9
Winter	5.0	187	5.1

TABLE 9

Frequency of dry holes (%) between March, 1982 and December, 1987 for all sites, by season and for woodland, ephemeral swamp and perennial swamp together with mean monthly rainfall (R) (mm) at Katoomba meteorological station

Season	**Woodland**	**Ephemeral Swamp**	**Perennial Swamp**	**R (mm)**
Spring	91.5	43.3	1.1	133
Summer	93.9	49.3	5.3	110
Autumn	82.9	18.5	0	145
Winter	93.5	35.0	1.0	106

Daily Changes

(i) Surface Flow

Discharges at the knickpoint fell during the day and rose at night. Because of the low flows from the small drainage basin, these minute changes are easily detected where water flows over bare rock. The changes are demonstrated using measurements taken over several days, during rainless periods, when discharges were steadily decreasing (Table 10, Fig. 13). The falls during the day clearly related to evaporation, particularly in the ponded swamp. At night the discharge rose as the evaporation rate declined but groundwater continued to enter the creek. After sunrise there was a delay of about 3 hours before the discharge rate fell. It rose again about sunset (Fig. 13).

(ii) Groundwater

Groundwater table levels tended to fall during the day and rise at night. This is demonstrated by levels for site 10 measured over several rainless days in summer and winter. Here the daily peaks fell throughout the period of measurement but the levels oscillated each day and night and the difference between the means of the day and night fluctuations were significant (Fig. 12, Table 11). The precise mechanism is not known but clearly results from a balance between gains of water from above the aquiclude and losses from evaporation of surface and underground water, together with loss of water by downslope drainage. The changes occurred even when groundwater table level was 0.7 m below the surface. Maximum changes were noted in the swamp sites below the woodland margin e.g. 10, 13 and 31.

TABLE 10

Knickpoint discharge (Ls^{-1}) 1987, during rainless periods of several days, when discharges were steadily decreasing

(a) Overall Variation	**Summer**		**Winter**	
Sunrise	3 December	0.6	22 June	1.9
Sunrise	9 December	0.2	1 July	0.3

(b) Daily and Nightly Variation, means (± s.e.m.)		**n**		**n**
DAY (sunrise-sunset)	-0.18 ± 0.035	9	-0.10 ± 0.026	7
NIGHT (sunset-sunrise)	+0.12 ± 0.030	10	+0.07 ± 0.024	8
	t = 6.2, $P<0.001$		t = 4.2, $P<0.001$	

There was a correlation between groundwater table levels and diurnal fluctuations in weather, as indicated by temperature. This is demonstrated by comparing changes in groundwater table level for site 10 with temperature changes over several days (Fig. 12), and during the course of one 24-hour period (Fig. 13). Note also that surface moisture also falls in response to evaporation during the day. Groundwater table levels rose during the night but started to fall again about three hours after sunrise i.e. when the temperature reached 13°C and relative humidity was 95%. Surface moisture fell during the night until midnight then rose again until three hours after sunrise, when it fell again. Also, falls were greater in summer than in winter (Table 11). Regressions of distance below the surface to groundwater table level, on surface temperature for one summer day for a south-facing site (10) and a north-facing site (13) are each statistically significant. They show differences between these sites (Fig. 14**a**, **b**). Temperatures at site 13 are generally higher than for site 10 (Holland *et al.*, 1992) and the rate of fall of groundwater table level for 13 is generally greater than for site 10, probably from high evaporation on site 13. A significant difference was found when paired readings were taken on 23 December, 1987 (mean = 0.22 $mday^{-1}$ ± s.e.m. 0.027, n = 6, t = 8.1 & $P<0.001$).

TABLE 11

Mean rise (+) and fall (−) of groundwater table level ($mday^{-1}$) at site 10, (± s.e.m.) in June/July and December 1987. Rates taken in summer between nightly peaks and daily lows, in winter between sunrise and sunset. Temperature (°C) is daily maximum recorded on first day of sampling

	Day	**n**	**Night**	**n**		**Temp (°C)**
Summer	− 0.18 ± 0.023	5	+ 0.11 ± 0.011	5	t = 3.9, $P<0.005$	26
	t = 5.6, $P<0.001$		t = 9.4, $P<0.001$			
Winter	− 0.03 ± 0.006	5	− 0.01 ± 0.002	5	t = 2.9, $P<0.027$	7

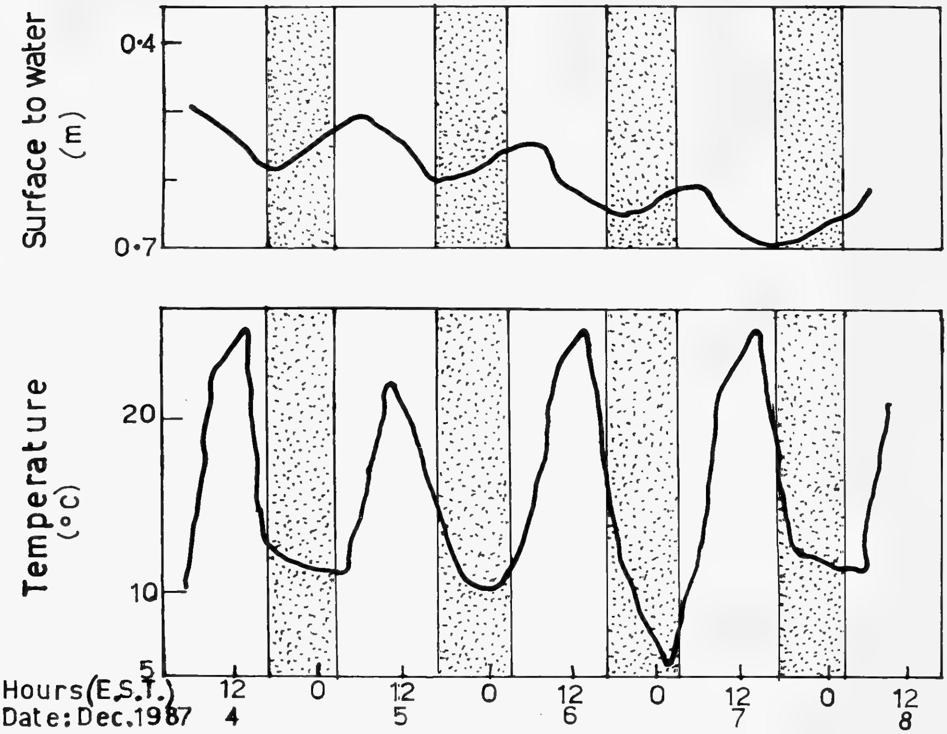

Fig. 12. Groundwater table depth (m) and surface temperature (°C), for day/night (hatched) in December 1987 at site 10. Day/night defined by sunrise and sunset.

DISCUSSION

Studying differences between individual components across a range of factors is a useful tool for investigating complex environmental relationships. This study has examined spatial and temporal variation in geology, geomorphology, vegetation, soils and hydrology.

Spatial differences reveal the gross shape of the present landform, which is being continually modified. The landform is largely a response to surface erosion over a long period, probably extending back at least to the last uplift in the Blue Mountains. This has resulted in a gentle upland valley. However, geologic controls modify many of the surface features, for example claystone beds result in the valley side knickpoints which segment the valley into its valley-in-valley form. These beds also influence the landforms by controlling the amount and movement of groundwater at each site. Examples of this are the swamps, the alluvial bulges and the diversion of water into adjoining Wentworth Creek.

This study has not examined temporal changes in the landforms, though Holland (1974) found that the shallow valley fill of a perched headwater valley could be up to 17,000 years old and that erosion of the fill may have proceeded upstream from the

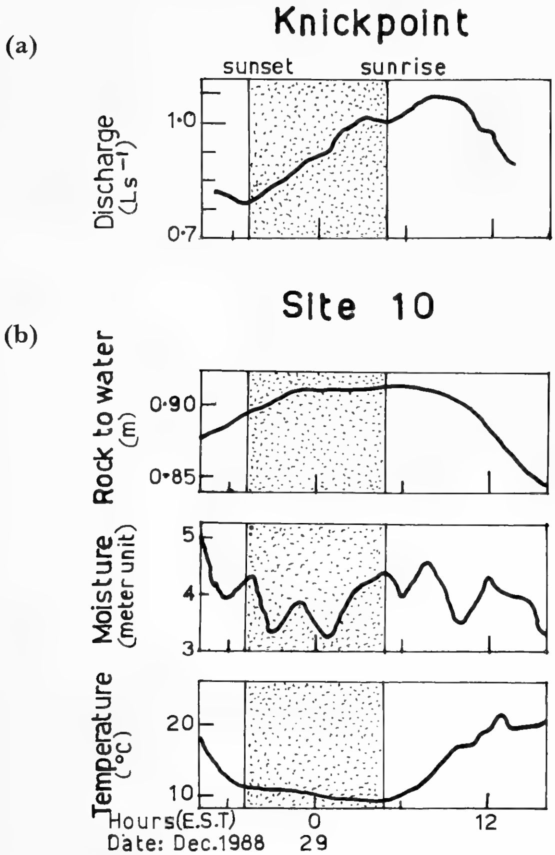

Fig. 13. Events during 24-hour rainless period (28-29 December 1988) when flow falling: (**a**) discharge at stepped knickpoint; (**b**) heights of groundwater table above bedrock, surface moisture (arbitrary meter units where the lower the reading the drier the conditions) and surface temperature at site 10.

stepped knickpoints with subsequent infilling of sediment. It is conceivable that these valleys could have a history of similar cuts and fills prior to 17,000 years ago.

Spatial patterns of vegetation are largely controlled by geology and hydrology. The woodland, ephemeral swamp and perennial swamp are partially delineated by claystone beds and floristic and structural differences can be related to the amount and movement of groundwater. Temporal changes are more difficult to document. Short-term changes, over days and weeks have not been examined. Hydrologic changes occur not only daily but hourly, in response to changing weather conditions.

The study found that groundwater table levels fell during the day as a function of increasing temperature. Further, it was established that different sites had different rates of water movement, related to the individual temperature characteristics of each site.

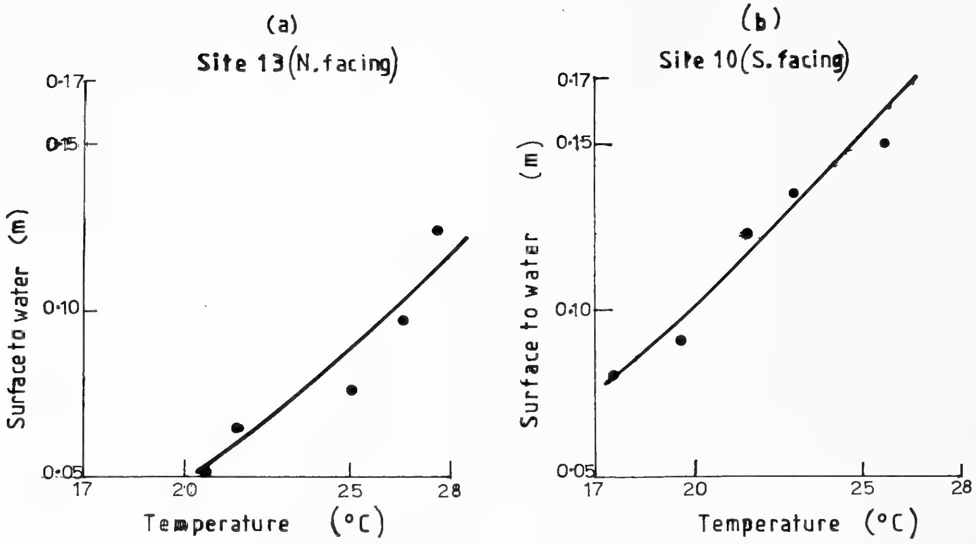

Fig. 14. Regressions of distance between the surface and groundwater table level (m) on surface temperature (°C), in summer (23 December 1987): (**a**) for sites facing north (13); (**b**) for sites facing south (10).

Seasonal changes affect evaporation rates which probably influence erosion. Seasonal vegetation changes include the flowering of species and annual growth cycles. Periodic events include phenomena such as bushfires which can affect vegetation, soils and landform (Selkirk and Adamson, 1981).

North-facing slopes are generally less steep than south-facing slopes. There is some evidence that soils are deeper, less compact, and dry out faster on north-facing slopes. Geological structure appears to play no part, since the beds dip to the east. Asymmetry is found in both swamps and the woodland so is independent of vegetation cover. Within the woodland north and south-facing slopes show differences in tree growth (greater basal area on south-facing) and ground cover (greater species richness on north-facing slopes). As the result of soil creep most trees lean downhill, though the upper trunks of some trees on south-facing slopes curve back towards the north. Some differences were also noted in daily groundwater table heights and on seasonal surface moisture and groundwater table heights on north or south-facing slopes. Because of the wide ranging nature of these north/south differences, it is assumed that solar radiation is the main factor responsible for the asymmetry.

Our other paper (Holland *et al.*, 1992) extends the present findings by examining calculated solar radiation and temperature variations in the valley and relates these to long-term changes in the landscape.

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Spatial and Temporal Variation in a Perched Headwater Valley in the Blue Mountains: Solar Radiation and Temperature

W. N. HOLLAND, D. H. BENSON and R. H. D. MCRAE

HOLLAND, W. N., BENSON, D. H., & MCRAE, R. H. D. Spatial and temporal variation in a perched headwater valley in the Blue Mountains: solar radiation and temperature. *Proc. Linn. Soc. N.S.W.* 113 (4), 1992: 297-309.

Solar radiation in a perched headwater valley in the Blue Mountains is calculated using slope and aspect and the results are compared with measured temperature variations. The calculated solar radiation and temperature values are each examined for spatial and temporal variations within the valley. The model predicts some spatial and temporal relationships, particularly differences between north and south-facing slopes but also between east and west-facing slopes. Solar radiation appears to be the main factor in valley asymmetry although the precise mechanisms at work are not known. This explanation provides a unifying framework to cover the whole period of valley development.

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INTRODUCTION

In a typical perched headwater valley in the Blue Mountains — Cold Foot Creek (lat. 33°40′S, long. 150°21′E) — landforms, vegetation, soils and hydrology are affected by the underlying rock strata (Holland *et al.*, 1992). But there are other significant spatial and temporal variations not related to rock strata, including valley asymmetry, in the geomorphology, vegetation, soils and hydrology. Holland (1974) speculated that differential solar insolation could account for asymmetric north/south valley slopes in the Blue Mountains. He found that rock structure was not a consideration since regional dip is easterly. Furthermore, asymmetry also occurs in the Carboniferous rocks of Megalong Valley (20 km south west of Cold Foot Creek) which have no regular rock structure.

In this study we consider the effects of solar radiation and temperature in the Cold Foot Creek perched headwater valley. Solar radiation values are calculated to establish relative spatial differences across the valley and for various time zones. These results are compared with observed temperatures, to test the validity of the calculated solar radiation findings and to gain insights into the nature and extent of temperature variations.

METHODS

Solar radiation for the summer and winter solstices was calculated for each of the 31 sites (Fig. 1**a**) used by Holland *et al.* (1992), at 1200 h solar time. Tables (Philips 1983; Loewe, 1962), depending on aspect, slope, latitude and longitude were used. The calculations assume a cloudless sky and are for solar radiation falling on a surface at right angles to the solar beam. Solar time is used exclusively. For the summer solstice, 1200 h equals about 1157 h Eastern Standard Time, while for the winter solstice the correction is less than one minute. The calculations give values of solar radiation at sea level though Cold Foot Creek is at 930 m a.s.l. However, these assumptions are acceptable as the aim was to examine relative position and time differences. Variations resulting from latitude and longitude differences within the study area have been disregarded as they are less than the order of accuracy achieved.

Values were also calculated throughout the day on each of the summer and winter solstices for sites 10 and 13. Further values, at 1200 h were calculated for selected sites, for the autumn equinox. Additional values at 1200 h were calculated for selected sites, for 11 days in December 1987.

Temperature is difficult to measure since it varies so much from place to place and over time. Continuous monitoring for long periods and concurrently at numerous sites was impractical so selected measurements were made at critical times to scan the various sites and time zones for trends. Comparisons are made on a relative basis and assume simultaneous recording and other conditions being equal. Measurements between September 1980 and December 1988 allowed sampling of a wide range of temperatures.

Surface temperatures for selected sites were measured over 15 days in summer (1987) and 13 days in winter (1987). Maximum/minimum thermometers were placed 50 mm above the surface, in the shade, and open to the air. Readings were taken throughout the day for sites 19 and 29 in June 1981, and for sites 10 and 13 in June and December 1987.

Additional temperatures were measured with thermometers 0.4 m below the surface at selected sites, for 11 days in summer (1987). These were measured inside 45 mm diameter perforated plastic pipes sunk to bedrock. The pipes were capped and further insulated from air temperature with foam within the pipes.

Relative humidity readings were calculated for sites 10 and 13, in June 1988 using a sling psychrometer held 1 m above the surface.

Wind readings about 1.6 m above the surface were taken for sites 10 and 13 in June 1988. A compass measured the direction of a blown woollen thread while speed was read from a device described by Linacre and Barrero (1975).

RESULTS

Calculated Solar Radiation

Spatial Variation

Values of calculated solar radiation of each individual site are a function of the angle of incidence of the sun's rays. Thus they are also a function of the geomorphology (i.e. they depend on aspect and slope). On north-facing sites the calculated solar radiation mean is significantly higher than the mean for south-facing sites on the summer and winter solstices (Table 1**a**). Because of the southern latitude of the study area, the sun always crosses the meridian in the northern sky. Thus the angle of incidence of the sun's rays is generally more on north-facing slopes than on those facing south. The range of calculated solar radiation values for all the north-facing sites is less than the range for the sites facing south (Table 1**b**). Since the ranges are functions of the aspect and slope of each site chosen for study they will vary from area to area.

There are also considerable differences in calculated solar radiation on east and west-facing slopes, depending on the season and time of day. This is discussed below, under daily changes.

Seasonal Changes

The mean value of calculated solar radiation in midsummer for all sites is significantly greater than the mean for midwinter. (Table 1**a**, Fig. 1). The range of values of calculated solar radiation for all the sites is less in midsummer than in midwinter (Table

1b). Again, this is a function of the high angles of incidence of the sun's rays in midsummer.

Calculated solar radiation values for some sites in a north/south trending section across the valley (S-N, Fig. 2**a**) show that the highest value for midsummer is at site 13 and for midwinter at site 14 (Table 3). Each of these sites are on the convex north-facing slope. The lowest value is for site 9 on the convex south-facing slope, in both midsummer and midwinter.

TABLE 1

Calculated solar radiation (Wm^{-2}) for all sites, at 1200 h solar time, for summer and winter solstices, and comparison of north and south-facing sites

(a) Means (± s.e.m.)

	Summer	n	Winter	n
All sites	26.3 ±0.12	31	11.1 ± 0.37	31
N-facing	26.9 ± 0.03	13	13.3 ± 0.18	13
S-facing	25.9 ± 0.12	18	9.6 ± 0.31	18
	t = 7.3 P<0.001		t = 8.9 P <0.001	

(b) Range of values

	Summer	Winter
All sites	1.9	6.6
N-facing	0.3	2.4
S-facing	1.6	4.5

Daily Changes

During the day, the calculated radiation value for each site increases as the sun rises to its maximum elevation on the meridian, at midday. Solar radiation decreases as the sun's elevation diminishes in the afternoon. These changes are shown for sites facing north (13) and south (10), in midsummer and midwinter (Fig. 3).

Calculated solar radiation is greater on east-facing sites than on west-facing sites in the morning but in the afternoon the reverse applies. This is demonstrated by comparing morning and afternoon values for sites facing east (27) and west (30) in midsummer and midwinter (Table 2).

Calculated Solar Radiation and Temperature

The calculated radiations do not take into account the masking effects of vegetation, soil type, ground moisture, cloudiness or other physical features affecting surface temperatures (Rosenberg *et al.*, 1983). Nevertheless, there is a close relationship between calculated radiation and surface temperature. Separate regressions of the daily mean surface temperature on calculated radiation for selected sites in summer, winter and autumn for woodland and perennial swamp sites, are each statistically significant (Fig. 4). A regression of daily mean temperature below the surface against calculated radiation for selected sites, in summer at midday, is also significant (Fig. 5). Thus, even beneath the surface, differences related to calculated solar radiation are evident in temperature variations.

Temperature

Spatial Variation

A comparison of sites along section S-N (Fig. 2) reveals a number of significant correlations in surface temperature. The highest mean daily maximum temperature is on the convex north-facing slope (Table 4**a**). The lowest mean daily maximum temperature is on the convex south-facing slope. These results are compatible with the findings for calculated solar radiation values.

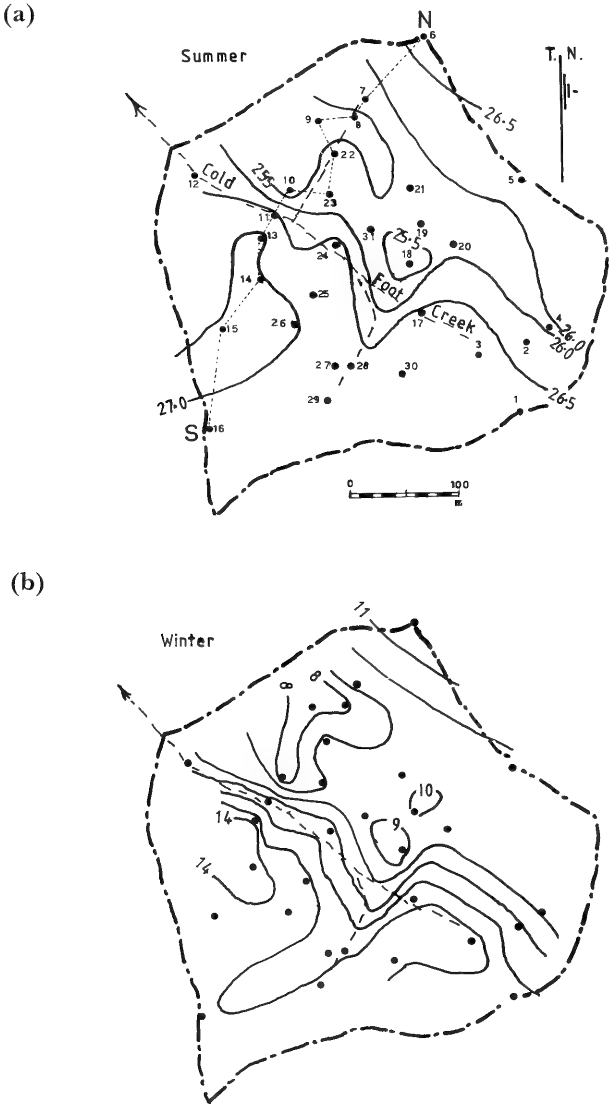

Fig. 1. Cold Foot Creek study area (enclosed by dash dot line) showing calculated solar radiation (Wm^{-2}) isolines at 1200 h solar time on: (**a**) the summer solstice; (**b**) the winter solstice. Also showing sites (numbered closed circles) and section S-N across the valley.

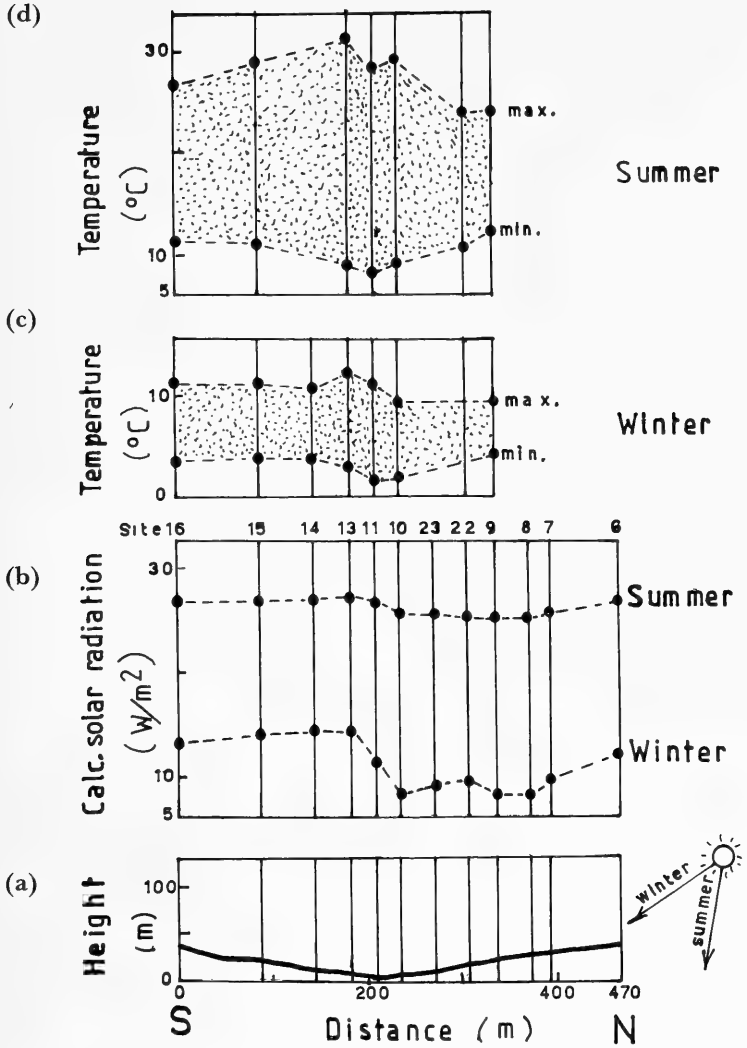

Fig. 2. Sites along section S-N (Fig. 1a) showing: (**a**) heights (m) and elevation of sun at 1200 h on the summer and winter solstices; (**b**) calculated solar radiation (Wm^{-2}) values at 1200 h solar time on the summer and winter solstices; (**c**) temperature (°C), daily maximum and minimum means, in winter (n=13 days), 16 June-6 July 1987; (**d**) temperature (°C), daily maximum and minimum means in summer (n=15 days), 2 December-28 December 1987.

TABLE 2

Calculated solar radiation (Wm^{-2}), at 0800 and 1600 h solar time, for east-facing site 27 (aspect 66°) and west-facing site 30 (aspect 337°), on summer and winter solstices

Site, Aspect	Summer 0800	Summer 1600	Winter 0800	Winter 1600
27 (E-facing)	15.4	11.9	3.3	1.1
30 (W-facing)	13.0	14.3	2.2	2.6
	+ 2.4	-2.4	+ 1.1	−1.5

The highest mean daily minimum temperature is on the convex north-facing slope. The lowest mean daily minimum temperature is on the convex south-facing slope in midsummer (site 9) but on the valley floor in midwinter (site 11). By contrast the lowest value of calculated solar radiation was for site 9 on the convex south-facing slope (Table 3**b**). Probably a physical factor such as cold air drainage lowers temperatures on the valley floor. This is supported by the finding that the daily mean difference between maximum and minimum temperatures is greater for site 11 than for site 9 in midsummer and midwinter (Table 4**c**).

North-facing slopes generally have higher temperatures than slopes facing south (Table 4**b**). However, the range of values between maximum and minimum is greater for south-facing slopes than for those facing north. These results are compatible with the findings for calculated solar radiation. Higher values on north-facing sites are found in both woodland and perennial swamp sites (Table 4**d**).

Daily mean minimum temperatures were higher in the woodland than in the perennial swamp (Table 4**e**). This circumstance is clearly influenced by cold air

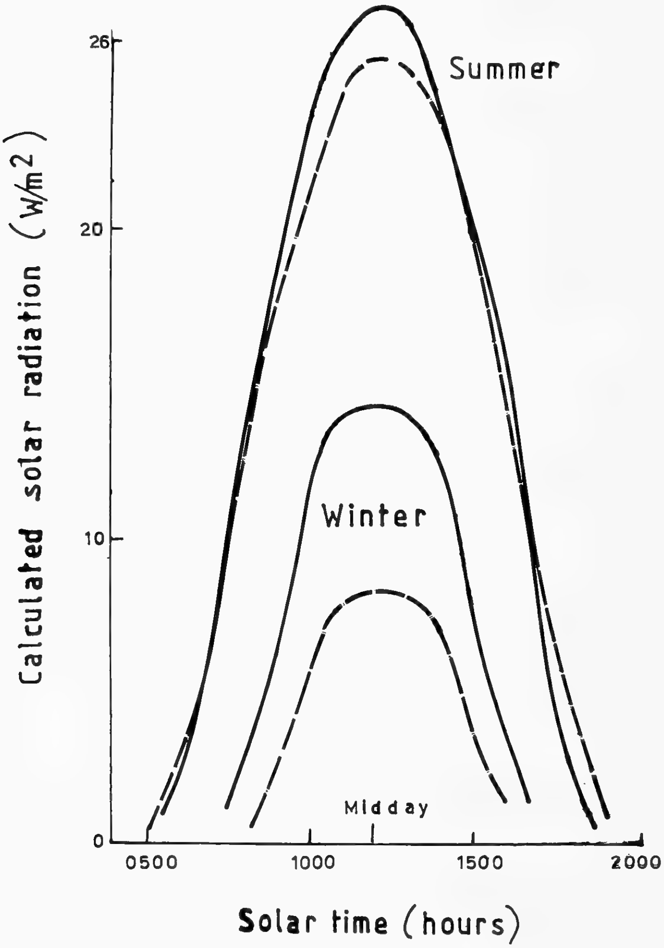

Fig. 3. Calculated solar radiation (Wm^{-2}) for site 13 (north-facing, shown by firm line) and 10 (south-facing, shown by dashed line) on the summer (longest day) and winter (shortest day) solstices.

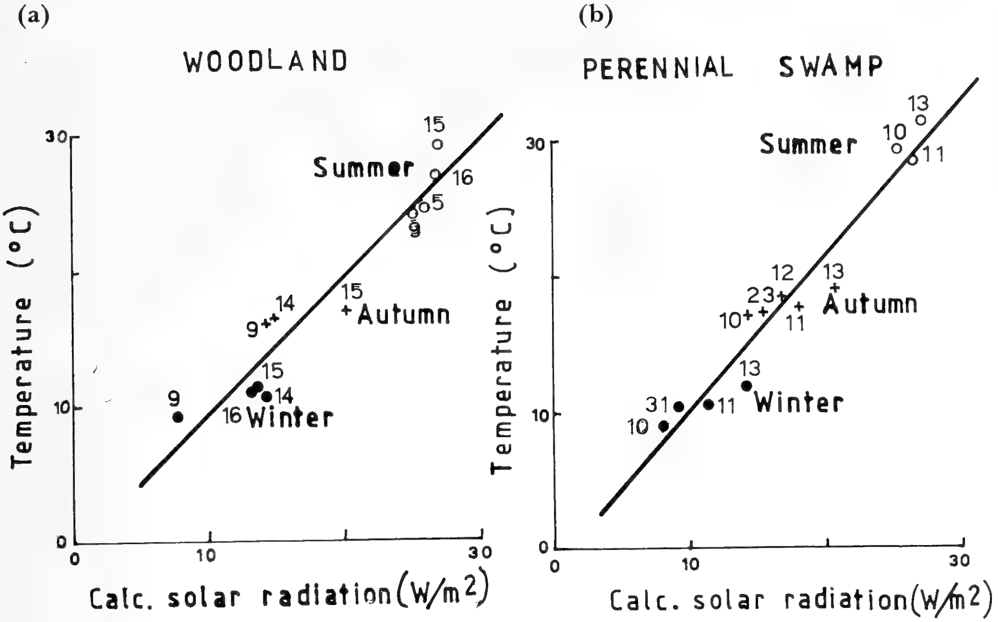

Fig. 4. Regressions of daily mean maximum surface temperature (°C) on calculated solar radiation (Wm^{-2}), at 1200 h solar time, for selected sites on the summer and winter solstices and autumn equinox: (**a**) woodland sites, where temperature = 0.053 calculated solar radiation — 0.795, coefficient of determination = 0.911, n = 11, and $P < 0.001$; (**b**) perennial swamp sites, where temperature = 0.060 calculated solar radiation — 1.277, coefficient of determination = 0.944, n = 12 and $P < 0.001$.

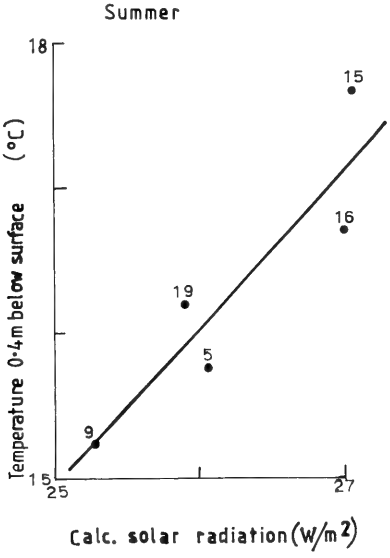

Fig. 5. Regression of daily mean maximum temperature (°C) 0.4 m below the surface on calculated solar radiation (Wm^{-2}), at 1200 h solar time, for selected woodland sites, for 11 days in summer (2-17 December 1987) where log temperature, 0.4 m below the surface = 1.746 log calculated solar radiation — 1.265, r^2 = 0.81, n = 5 and $P < 0.05$.

drainage and other physical factors which may include the relative insulation effects of different vegetation cover.

In readings taken 0.4 m below the surface north-facing slopes had significantly higher temperatures than south-facing slopes (Table 5).

Temperature differences between east and west-facing sites are discussed below.

Seasonal Changes

The daily mean temperature range (daily mean difference between maximum and minimum) was significantly greater in midsummer than midwinter (Table 4**f**). The daily mean maximum and minimum temperature ranges (i.e. between highest and lowest daily readings) were both significantly greater in midsummer than in midwinter (Table 4**g**, 4**h**).

Daily Changes

Daily variations in midsummer and midwinter temperatures (Fig. 6) demonstrate the lag between peak solar radiation and surface temperature. This results from the balance between net incoming and outgoing radiation, and the effect on temperatures of shielding by topography and vegetation. (We cannot explain the lowering of the temperatures at noon, for site 13, in winter (Fig. 6). The only other changes noted between 1100 and 1200 hours were an increase in cloud cover from 30% to 60%, a decrease in relative humidity from 11.4% to 8.2% and an increase in wind speed (from 3 to 5 kmh^{-1}).

Daily temperatures measured 0.4 m below the surface are less variable than surface temperatures as the direct effect of solar radiation is damped down by vegetation cover and soil. Measurements in summer, (sites 9 and 15) show significant regressions of the difference between mean maximum surface temperature and temperature 0.4 m below the surface on mean maximum surface temperature (Fig. 7).

There is also a contrast (albeit of smaller magnitude to north/south asymmetry) between east and west-facing slopes. The morning sun warms east-facing slopes more than those facing west. In the afternoon this is reversed (Fig. 8, Table 2). Site 29 (aspect 249°) shows higher temperatures all day than site 19 (aspect 46°) as expected from their respective north/south orientations. However, because they also face respectively east and west, site 29 heats up more rapidly than 19 in the morning and cools off more rapidly in the afternoon. Site 29 also maintains its midday peak longer than site 19 from the additional warming in the morning.

TABLE 3

Calculated solar radiation (Wm^{-2}) for sites along section S-N (Fig. 2), on summer and winter solstices, and comparison of north and south-facing sites

(a) Means (± s.e.m.)

	Summer	n	Winter	n
N-facing	27.0 ± 0.05	5	13.4 ± 0.40	7
S-facing	25.7 ± 0.16	5	8.9 ± 0.43	7
	$t = 6.1$ P<0.001		$t = 6.9$ P<0.001	

(b) Range of values

	Summer		Winter	
	N-facing	S-facing	N-facing	S-facing
Highest	27.1 (13)	26.6 (11)	14.3 (14)	11.3 (11)
Lowest	26.8 (6)	25.3 (6)	11.9 (6)	7.7 (9)

TABLE 4

Daily maximum and minimum surface temperature (° C), means (± s.e.m.), and individual temperature (° C) values for sites on section S-N (Fig. 2), over 19 days in summer (2 December-28 December 1987) and 15 days in winter (16 June-6 July 1987)

(a) Range of individual daily max. and range of individual daily min. temperatures for both summer and winter

	Summer		Winter	
	Max.	**Min.**	**Max.**	**Min.**
Highest	37.8 (site 13)	26.3 (13)	15.5 (15)	9.5 (15)
Lowest	6.5 (9)	3.5 (9)	6.0 (9)	-4.5 (11)
Range	31.3	22.8	9.5	14.0

(b) Range of individual daily max. temperatures for summer and winter, and for north and south-facing sites

	Summer		Winter	
	N-facing	**S-facing**	**N-facing**	**S-facing**
Highest	37.8 (site 13)	34.5 (9)	15.5 (15)	14.0 (11)
Lowest	13.8 (13)	6.5 (9)	8.0 (15)	6.0 (9)
Range	24.0	28.0	7.5	8.0

(c) Comparison of daily mean difference between max. and min. temperatures for a south-facing site (9) and a valley floor site (11), in summer and winter.

	Summer	**n**	**Winter**	**n**
Site 11 (valley floor)	17.8 ± 1.3	19	9.1 ±0.8	13
Site 9 (S-facing)	10.8 ± 1.0	18	5.4 ± 0.4	13
	$t = 4.0$ $P<0.001$		$t = 3.9$ $P<0.001$	

(d) Daily mean difference between max. temperatures for paired sites

	Summer				**Winter**			
		n	**t**	**P<**		**n**	**t**	**P<**
Perennial swamp (13N-10S)	2.8 ± 0.4	17	6.9	0.001	2.8 ± 0.3	12	8.1	0.001
Woodland (15 N-9S)	4.5 ± 0.6	19	7.0	0.001	1.8 ± 0.3	13	6.6	0.001

(e) Daily mean min. temperatures for summer and winter

	Summer	**n**	**Winter**	**n**
Woodland	11.6 ± 0.4	3	3.6 ± 0.1	4
Perennial swamp	8.6 ± 0.3	3	2.0 ± 0.4	3
	$t = 6.2$ $P<0.005$		$t = 3.9$ $P<0.02$	

(f) Daily mean temperature range (daily mean difference between max. and min. temperatures).

Summer	**n**	**Winter**	**n**	**t**	
16.8 ± 1.3	8	7.7 ± 0.4	8	6.1	$P<0.001$

TABLE 4 (Cont'd)

(g) Daily mean maximum temperature range in summer and winter

	Summer	n	Winter	n
Highest	31.4 ± 1.1	15	11.8 ± 0.5	13
Lowest	23.9 ± 1.1	15	9.0 ± 0.6	13
	$t = 14.6$ $P<0.001$		$t = 3.5$ $P<0.005$	

(h) Daily mean minimum temperature range in summer and winter

	Summer	n	Winter	n
Highest	12.2 ± 0.8	15	3.8 ± 0.7	13
Lowest	7.9 ± 1.0	15	1.5 ± 1.0	13
	$t = 3.3$ $P<0.005$		$t = 1.8$ $P<0.10$	

TABLE 5

Daily temperature (°C), means (± s.e.m.),
0.4 m below the surface at sites 9 and 15,
about 0800 h solar time (30 November-28 December, 1987

Site, Aspect	Temperature	n
15 (N-facing)	17.7 ± 0.3	20
9 (S-facing)	15.9 ± 0.2	20
	$t = 4.2$ $P<0.001$	

DISCUSSION

It is surprising that the differential amounts of solar radiation received at individual sites, as a result of the movement of the sun, has received scant attention in geomorphology textbooks. Treatment of the subject is usually on a broad brush approach (Thornbury, 1954; Selby, 1982). Selby, for example, notes that the sun is the prime energy source but does not pursue the matter of differences which occur from place to place and over time.

This study, together with our other investigation (Holland *et al.*, 1992) has revealed significant differences between the environments of north and south-facing sites. These differences include slopes (north-facing less steep), temperatures (north-facing generally warmer but south-facing sites having a greater range of temperatures), hydrology (greatest fluctuation of water depths on north-facing swamp sites) and vegetation (some differentiation in species and degree of species richness).

It would be dubious science to conclude that any of the differences demonstrated result in solar radiation effects which 'stress' the environment. However, most of the differences detected will always be in the one direction e.g. north-facing slopes will always tend to be warmer than south-facing slopes because of the sun's position relative to the earth. Further, the sun has moved in its path continuously for a long time. The differences are incremental and have occurred over a long period of time. It is not unrealistic to speculate that subtle changes could occur in the micro-environments in response to the differences noted, and of any other undetected differences f n varying solar radiation intensity. In any event all the differences noted warrant seric consideration in studies of geomorphology or vegetation. Further, if these differer s do affect (say) slope, then at some point in time there is probably a feedback sit ion where alteration of a slope results in a new set of solar radiation criteria. Sim feedback mechanisms apply to the vegetation and other aspects of the environmer Our study

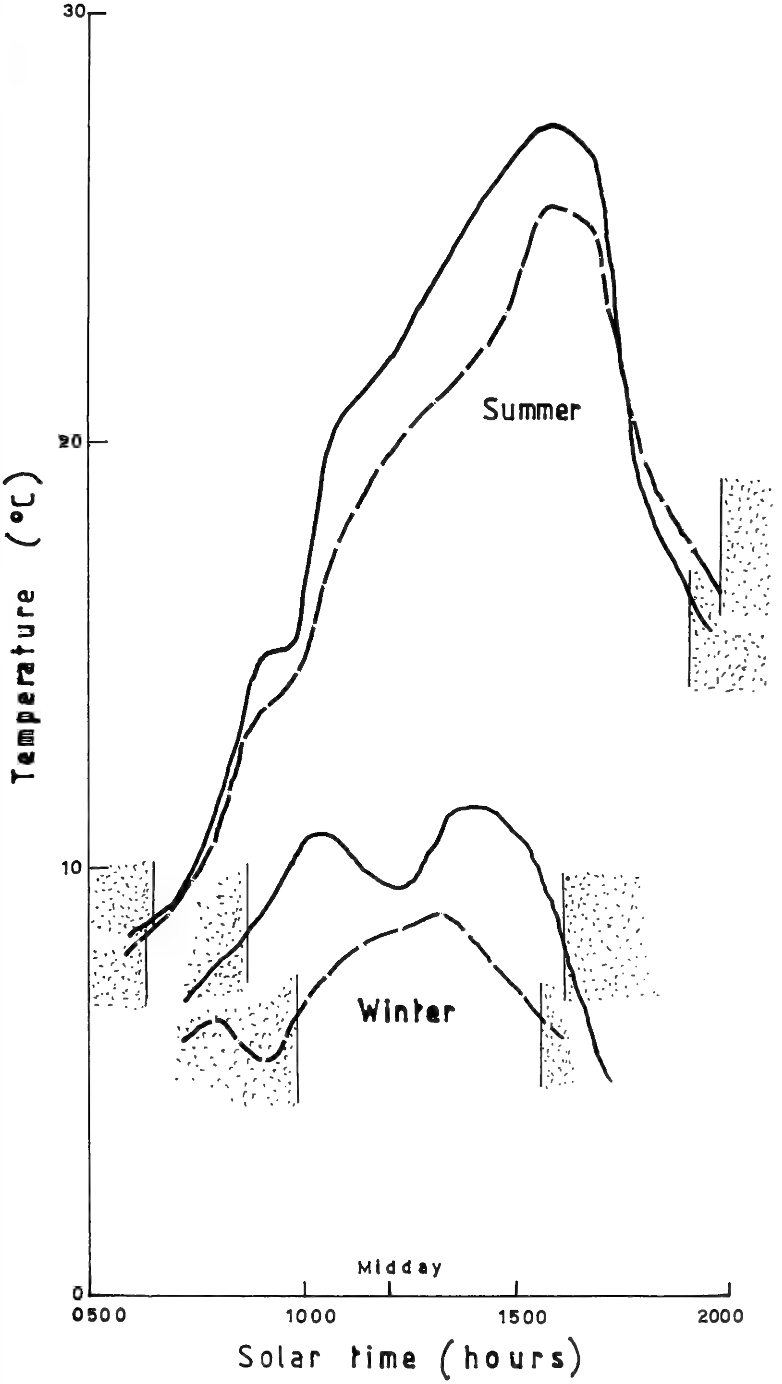

Fig. 6. Daily surface temperature (°C) range for sites 13 (north-facing, shown by solid line) and 10 (south-facing, shown by dashed line), in summer (23 December 1987) and winter (21 June 1988). Dotted areas show periods when the sun's rays were blocked by physical objects.

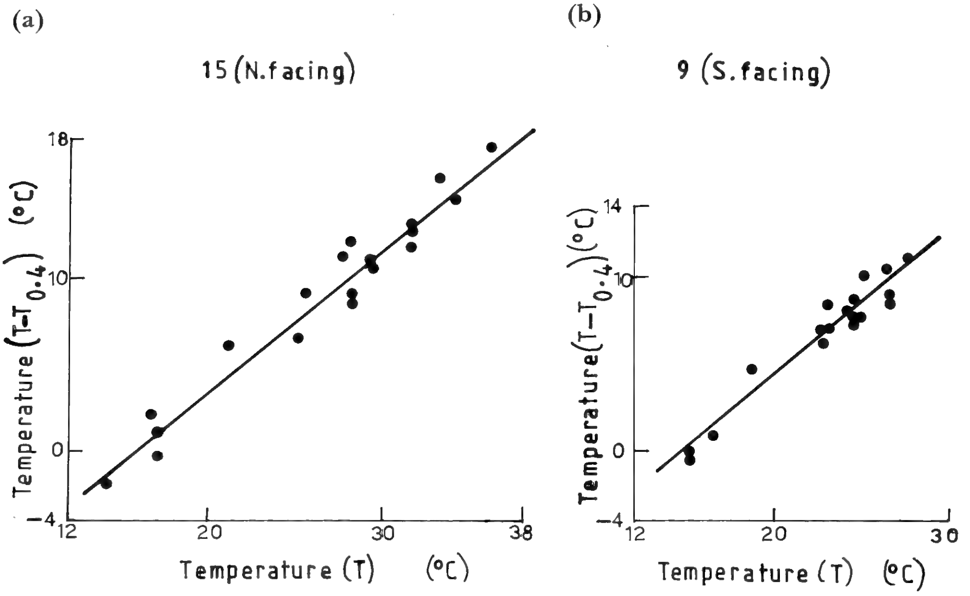

Fig. 7. Regressions of the difference between daily maximum surface temperature (T) and temperature 0.4 m below the surface ($T_{0.4}$), on T between 2 December and 28 December 1987: (**a**) site 15 (north-facing) where $T_{0.4} = 0.823\,T - 13.016$, $r^2 = 0.956$, $n = 19$ and $P < 0.001$; (**b**) site 9 (south-facing) where $T_{0.4} = 0.841\,T - 12.421$, $r^2 = 0.943$, $n = 18$, and $P < 0.001$.

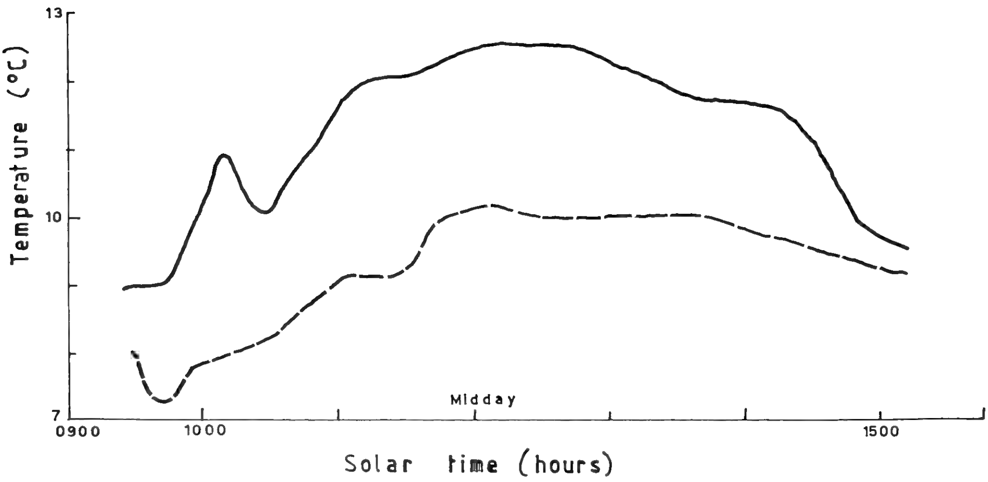

Fig. 8. Surface temperature (°C) for site 29 (E-facing, shown by solid line) and 19 (W-facing, shown by dashed line), on 28 June 1981.

has already established some such relationships e.g. the daily movement of groundwater levels which depend largely on evaporation from the sun's rays.

Calculated solar radiation using only aspect and slope measurements, has yielded useful correlations with temperature. These correlations concern differences in both position and time. From this it is possible to rank sites, with respect to expected radiation intensity and from this to anticipate temperature variations. When tested against temperature the results correlate well, suggesting that the model could be used for studying other environmental aspects. In practice, differences relating to aspect have long been recognized and incorporated in mapping vegetation areas, for example Keith and Benson (1988). Use of the calculated solar radiation model provides a means of easily ranking each site. Since micro-climates change so continuously and unpredictably, computer control is needed to handle the voluminous spatial and temporal data needed. This thinking also applies to soil analysis and mapping. From a research viewpoint, the demonstrated differences in solar radiation indicate the likely extent of radiation on a particular slope. It could enable research to be directed to comparing numerous factors such as soil texture or any other aspect of the soil profile which could be modified by variations in solar radiation from site to site and over different time zones. One key question which could be addressed is the precise mechanism which makes one slope greater than another one nearby.

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Descriptions of the Pupae of Nine Genera of Australian Paropsine Chrysomelinae (Coleoptera: Chrysomelidae)

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(Communicated by C. N. SMITHERS)

REID, C. A. M. Descriptions of the pupae of nine genera of Australian paropsine Chrysomelinae (Coleoptera: Chrysomelidae). *Proc. Linn. Soc. N.S.W.* 113 (4), 1992: 311-337.

The pupae of 18 species of 9 genera of Paropsina and Dicranosternina are described, including species of *Chrysophtharta* Weise, *Dicranosterna* Motschulsky, *Novacastria* Selman, *Paropsides* Motschulsky, *Paropsis* Olivier, *Paropsisterna* Motschulsky, *Pyrgoides* Aslam, *Trachymela* Weise and *Trochalodes* Weise. The contribution of pupal morphology to the interrelationships of these genera and to related Chrysomelinae is discussed. Pupal characters support discrimination of the subtribes Dicranosternina and Paropsina, established on adult characters.

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INTRODUCTION

The term paropsine is generally used in Australia to refer to members of two subtribes, Paropsina and Dicranosternina, of the leaf-beetle tribe Chrysomelini (Daccordi, 1982). Most paropsine genera are endemic to Australia, but *Paropsides* Motschulsky reaches China and Japan (Ohno, 1958) and other genera are present in New Guinea (Gressitt, 1963).

Paropsine larvae and adults are important pests of *Acacia* in Tasmania (Elliott and de Little, 1985), and plantation *Eucalyptus* in Australia (Greaves, 1966; Ohmart and Edwards, 1991) and abroad (Tribe and Cillie, 1985). The identification of paropsines represents a major problem for Australian insect ecologists because most genera are weakly defined. Adults of the Paropsina and Dicranosternina are defined by usually (!) having toothed claws and the edge of the elytral dorsal surface completely obscuring the epipleura in lateral view (Weise, 1915). Their larvae show similarities to *Gonioctena* (Gonioctenina; Takizawa, 1976) and their pupae have not been characterized. Studies of the phylogeny of the genera are confined to unpublished theses (de Little, 1979b; Reid, 1983; Daccordi, 1986). There are no recent published descriptions of the adults, except for revisions of the Tasmanian species of *Paropsis* (de Little, 1979a; Selman, 1983). Eggs and larvae are known to show good taxonomic characters at species level (Cumpston, 1939; de Little, 1979a,b; Reid, 1983; Selman, 1985) but pupae of Australian paropsines have only been superficially described (Cumpston, 1939). Here the pupae of nine genera, including the recently described paropsine-like *Novacastria* Selman (Selman and Lowman, 1983), are described and compared with other, non-paropsine, genera.

This study was undertaken to find pupal character states which may indicate relationships between genera or species groups of Paropsina and Dicranosternina and help clarify the position of *Novacastria*.

MATERIALS AND METHODS

The pupae were associated with identifiable adults in three ways: by rearing from eggs laid by identified adults, by rearing other members of a larval population into adults, or, in species with unusual hosts, by rearing from young larvae collected with adults. The sample described includes all such pupae in the Australian National Insect Collection (ANIC), CSIRO Division of Entomology, Canberra. The adults were determined by comparison with named material in the ANIC, or comparison with a colour photograph collection named by B. J. Selman, or from the published keys to species of *Pyrgoides* Aslam (Blackburn, 1897b, 1899, 1900). Plant hosts were identified using Costermans' (1981) guide to trees and shrubs. The specimens, fixed in KAA or 70% ethanol, were drawn with the aid of a drawing tube attached to a Wild M8 stereomicroscope. Fixing in KAA causes the elytra and wing thecae to spread out lateral to the body and the drawings have been made of this artificial state. All specimens are held in the ANIC unless otherwise indicated.

DESCRIPTIONS OF PUPAE

Nomenclature for the setae has been partly modified from the curculionid system of May (1978), in which regions of the head and abdomen are named to distinguish what appear to be homologous groups of setae. Setal groups on the head are identified according to Fig. 2. The great variability in number and position of setae obviates the need to name each seta. Because of the prevalence of asymmetric variation, all counts of setae on the head and thoracic segments in the following descriptions refer to the setae on one side of a pupa only, unless otherwise specified. Numbers of setae in brackets represent unique scores in the larger samples. In the example given (Fig. 2) the setae are scored as follows: 1 upper vertex, 3-4 vertex, 1 ocular, 1 upper frons, 2 lateral frons, 0 inner frons. Short spine-like setae are referred to as spinulose. Each of abdominal segments I-VI may have one or two pairs of lateral knob-like or condyliform setose projections.

The pupae described here have the following combination of characters: *Body* closely resembling form of adult in size and shape, and proportion of cephalic and thoracic appendages (except wings). Colour usually yellow or orange, with characteristic pattern of setae. *Head* bent downwards so that mouthparts are directed posteriorly; antennae extend as far as mesothorax (terminating between front and mid-femora); labrum with 4 minute setae. *Legs* with subapical setae on femora. *Abdomen* with 9 movable segments, segments IX and X telescoped within segment VIII; tergite IX terminating in paired and adjacent, or fused, urogomphi (apical processes). *Spiracles* present on first 6 abdominal segments and well developed. *Sexual dimorphism.* There may be a small difference in size (♀ larger on average) but in most species the sexes differ only in the structure of the apical abdominal sternites (Reid and Ohmart, 1989). Sternite VIII of the ♀ is deeply divided in the large species, but only slightly grooved in the small species and therefore difficult to see. Sternite VIII of the ♂ is not grooved or divided. All species pupate in soil and have the long setae typical of this type of chrysomeline pupa (Paterson, 1931).

KEY TO PUPAE OF PAROPSINE GENERA IN AUSTRALIA

1. Urogomphi, in dorsal view, widely separated and incurved at tip; 6 functional (well-developed) spiracles . . . . (Phyllocharina; Reid 1991)

— Urogomphi, in dorsal view, fused into a single process, or narrowly separated and not incurved; 5 apparently functional spiracles 2

2(1). Urogomphi either separated or completely fused into a short blunt or slightly bifid process; sides of tergites without lateral tubercles and tergites without dense bands of setae . . . (Australian Gonioctenina; not treated further)

— Urogomphi either completely fused into a long sharply acute or deeply bifid process or dorsally fused but with each urogomphus distinguishable ventrally and apex of process deeply bifid; dense transverse bands of setae present if tergites with reduced lateral tubercles .... (Paropsina and Dicranosternina) 3

3(2). Abdominal tergites I-VI with two pairs of condyliform tubercles, at lateral margin and posterior to spiracle (Figs 1, 11); lateral tubercles of tergite VI with >10 setae; apical margin of sternite VII thickened and spinulose (Figs 3, 13) (size >5 mm; apex of urogomphus bifid) 4

— Abdominal tergites I-VI with only a pair of simple or condyliform lateral tubercles; lateral tubercles of tergite VI with <10 setae; apical margin of sternite VII not thickened, rarely spinulose 5

4(3). Abdominal tergites between spiracular tubercles with two pairs of setal patches, central tergal setae therefore in longitudinal rows (Fig. 11); outer patch of setae on a tubercle on tergites II-V; >10 vertical setae, each side; apices of femora with 3 setae .... *Paropsisterna*

— Abdominal tergites with central setae in an irregular lateral row, without additional tubercles (Fig. 1); <10 vertical setae, each side; apices of femora with at least 4 setae .... *Paropsis*

5(3). Metanotal and tergal setae in dense transverse bands (Figs 26, 31); lateral tergal tubercles feebly developed (length >8.5 mm; apex of urogomphus bifid) 6

— Metanotal and tergal setae scattered or in irregular single rows (Figs 4, 14); lateral tubercles more strongly developed 7

6(5). Dorsal setae set on small tubercles (Fig. 31); apex of tibia without setae; upper vertex with >5 setae each side (Fig. 32) .... *Trochalodes*

— Dorsal setae simple (Fig. 26); apex of tibia setose (Fig. 28); upper vertex with 1 seta each side (Fig. 27) .... *Dicranosterna*

7(5). Apex of urogomphus bifid (Figs 4, 14); size larger, >5 mm 8

— Apex of urogomphus acutely pointed (Figs 18, 34); size smaller, <5 mm 11

8(7). Pronotum with >80 relatively short setae (Fig. 4); lateral tubercles condyliform, mostly with >3 setae 9

— Pronotum with <70 long setae (Fig. 14); lateral tubercles simple, with 2-3 setae 10

9(8). >2 vertical and <3 upper vertical setae each side (Fig. 5) ...... *Chrysophtharta*

— 2 vertical and >3 upper vertical setae each side (Figs 23-24) .... *Trachymela*

10(8). Apex of sternites VII and VIII with sclerotized spinules (Figs 9-10); tergite VI with >15 setae between spiracles (Fig. 7) .... *Paropsides*

— Apex of sternites VII and VIII simple (Figs 16-17); tergite VI with <15 setae between spiracles (Fig. 14) .... *Pyrgoides* partim (*rubiginosa*)

11(7). Meso- and metanotum each with 4 setae (Fig. 18); tergites I-VI with 6 setae between spiracles; upper vertex setae absent (Fig. 19) .... *Pyrgoides* partim (*hamadryas* and allies)

— Mesonotum with 3-5 setae, metanotum with 5-7 setae (Fig. 34); tergites I-VI with 6-12 setae between spiracles; 1-2 upper vertex setae (Fig. 35) .... *Novacastria*

SPECIES DESCRIPTIONS

Remarks: The pupa of the type species of *Paropsis*, *P. atomaria* Olivier, is described first. Full descriptions are given of *P. atomaria*, *Chrysophtharta* sp. nr *amoena* (Clark), *Pyrgoides*

TABLE 1

Summary of lengths (in mm.) and setal scores (all other figures) for pupae of Paropsina and Dicranosternina. Chry = Chrysophtharta; *Pard* = Paropsides; *Parp* = Paropsis; *Parn* = Paropsisterna; *Pyrh* = Pyrgoides hamadryas *and allies; Pyrr* = Pyrgoides rubiginosa; *Trac* = Trachymela; *Nova* = Novacastria; *Dicr* = Dicranosterna; *Troc* = Trochalodes. *Number in brackets is number of species. Number in brackets after femoral score is modal value.*

	Chry (2)	Pard (1)	Parp (4)	Parn (2)	Pyrh (3)	Pyrr (1)	Trac (1)	Nova (1)	Dicr (1)	Troc (1)
Length (mm.)	6.3-9.4	5.8-6.4	9.8-16.3	12.0	3.2-5.0	5.9-6.4	10.2-11.0	4.2-4.4	13.0-14.8	8.6-8.7
HEAD										
Upper vertex	0-2	1	0-1	3-4	0	0	4-6	1-2	1-2	6-9
Vertex	3-7	2-3	3-9	11-20	2	2	2	2	2-4	5-7
Upper frons	1	1	1-2	2-5	0-1	0-1	0-1	0-1	0-2	2-3
Ocular	1	1	1-4	1-5	1	1	1-2	1	1-3	1-2
Lateral frons	2	2	2-3	2	0-2	2-3	1-2	2	3-8	2-3
Inner frons	0	0	0-1	0	0	0	0-1	0	0-1	2-3
PRONOTUM	80-105	75-90	90-120	100-110	16-21	25-32	100-120	25-31	125-145	100-110
MESONOTUM	4-8	2-6	5-15	19-26	2	2-3	7-9	3-5	3-10	7-18
METANOTUM	4-12	4-6	6-16	18-28	1-2	2-4	9-13	5-7	25-33	21-31
LEGS										
Femur	0-4 (4)	0-3 (3)	4-7 (5)	3	3	3	3-4 (3)	3	8-14	2-6 (4)
Tibia	0	0	0	0	0	0	0	0	1-3	0
TERGITE I										
Central	2-8	3-6	10-17	4-20	2	2-5	11-12	2-5	22-40	
Spiracular	1-3	1-2	3-6	5-13	1	1		1-2	2-8	17-22
Lateral	0-4	2	5-8	8-11	1	2-3	3-5	1-2	4-7	1-2
TERGITE VI										
Central	5-12	6	14-24	21-29	2	2-5	16-20	2-5	27-36	
Spiracular	1-4	1-2	6-12	15-17	1	1-2		1-2	4-9	22-36
Lateral	1-9	2-3	14-20	12-25	2	2-3	4-8	1-2	5-8	2-7
TERGITE VII										
Central + spir.	16-27	6-8	29-37				17-21			34-42
Lateral	1-8	3	8-14	35-49	2-3	6-7	6-8	5-6	28-42	1-3
TERGITE VIII	4-13	6-10	17-25	27-32	3	3-4	11-12	4-5	18-28	17-23

rubiginosa (Chapuis), *Trachymela* sp. nr *tincticollis* (Blackburn) and *Dicranosterna immaculata* Motschulsky, and the other species are compared with these. At least one species of each genus is illustrated. The distributions of setae and measurements of all species in each genus are summarized in Table 1. Colour of the living pupa is various shades of yellow, with brown setae.

SUBTRIBE PAROPSINA Motschulsky, 1860

Paropsis Olivier, 1807

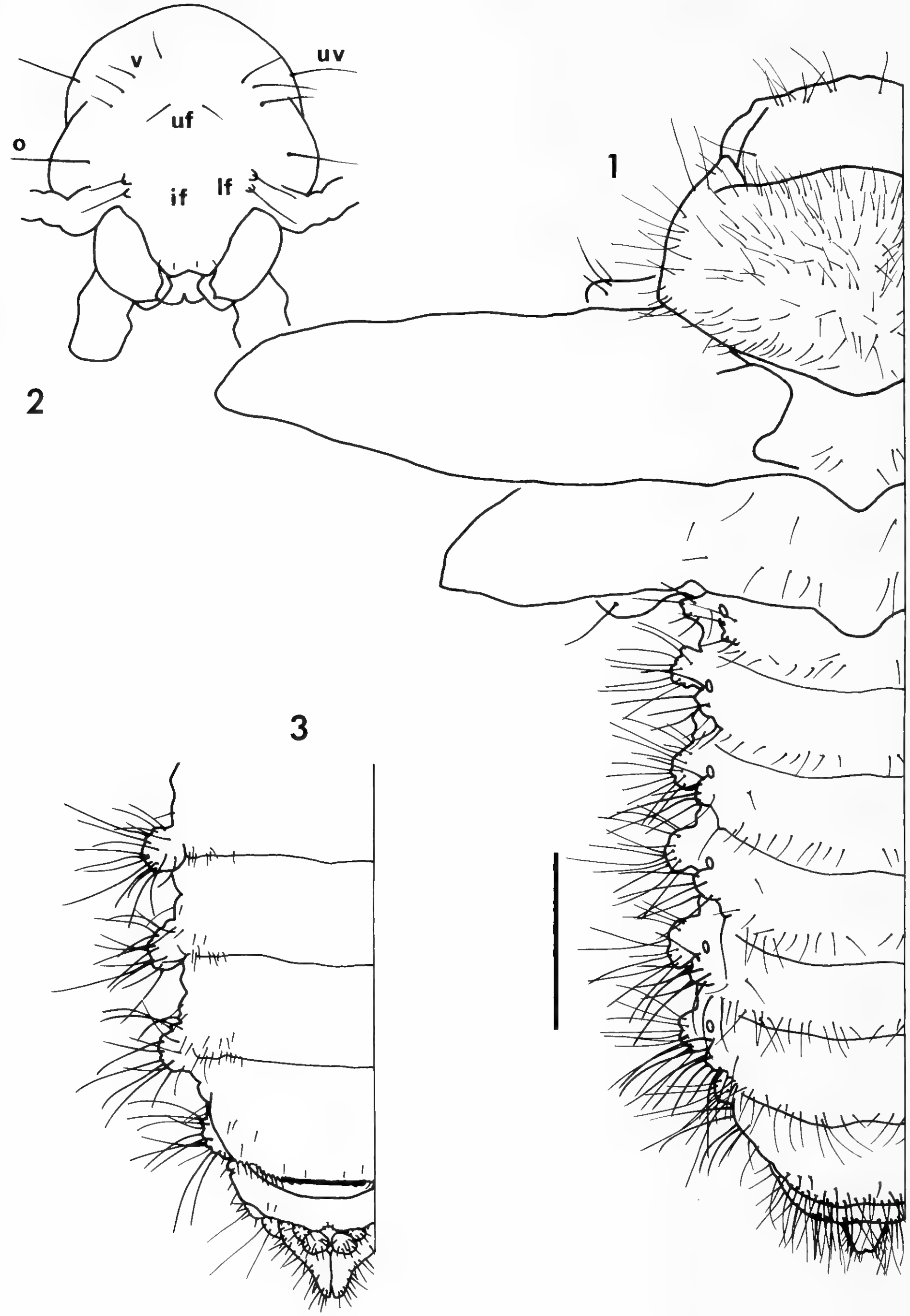
Type species: *Paropsis atomaria* Olivier (Selman, 1963)

Diagnosis: Pupae of *Paropsis* may be distinguished from all other genera except *Paropsisterna* by the possession of strongly developed spiracular tubercles, patches of small setae at the sides of sternite VI, and the strongly sclerotized apex of sternite VII. Pupae of *Paropsis* may be separated from those of *Paropsisterna* by the fewer setae on the vertex and metanotum, the transverse band of central abdominal setae, the fewer apical spinuliform setae on sternite VII and the presence of 4-7 subapical setae on each femur.

Paropsis atomaria Olivier, 1807
(Figs 1-3)

Material examined: AUSTRALIAN CAPITAL TERRITORY: 10♂ 10♀, ex culture, originally collected Canberra, 1984, C. P. Ohmart.

Description: *Measurements* (mm.): length, ♂ 13.2-15.3, ♀13.4-16.3; head width, ♂ 2.8-3.3, ♀3.0-3.6; pronotal width, ♂ 4.6-5.3, ♀4.7-5.5. *Head.* Setae: (0)-1 upper vertex, 3-9 vertex, 1-(2) ocular, 1-(2) upper frons, 2-(3) lateral frons. Mandibular thecae conspicuously toothed. *Thorax.* Pronotum with 90-110 scattered setae, greatest density in anterior half, near midline. Mesonotum: setae in 2 groups, outer 1-3, inner 4-12. Metanotum: 6-16, scattered in transverse row, or almost in 2 or 3 groups. Legs: each femur with 4-7 preapical setae, 5 most frequent (64%). *Abdomen* (see Reid and Ohmart, 1988, figs 1-2): tergites I-VI with irregular transverse row of setae along posterior margin (central setae) increasing from 10-17 each side on tergite I, to 14-24 on tergite VI; usually 1-2 small, subsidiary setae on each side of tergites I-VII, anterior to central row; tergites I-VI with two setose globular prominences, lateral to central row, smaller one posterior to spiracle (spiracular tubercle), larger on posterior half of lateral margin (lateral tubercle); spiracular tubercle small with 3-6 setae on tergite I, larger with 6-12 setae on tergites II-VI; lateral tubercle small with 5-8 setae on tergite I, larger with 14-20 setae on tergites II-VI; tergite VII central and spiracular tubercle setae merged, 29-37, lateral tubercle reduced, 8-14; tergite VIII without obvious tubercles, largely enclosed within tergite VII, 17-25; tergite IX projecting from within tergite VIII as a blunt posterio-dorsally directed process with a bifid sclerotized apex; sternites II-VI with a scattered patch of small setae on posterior margin near lateral tubercle, otherwise glabrous; posterior margin of sternite VII thickened centrally into a dark brown ridge, with 7-13 dark brown spinuliform setae (actually very short setae on sclerotized conical tubercles) between this and lateral margin; sternite VIII of ♂ with a small incision on posterior margin and 14-23 dark brown spinuliform setae each side of margin; sternite VIII of ♀ deeply cleft along midline from base to apex, with 11-15 dark brown marginal spinuliform setae each side; venter of tergite IX represented by 2 brown sclerotized lobes with sinuate lateral margins, the lobes contiguous from hemitergites X to their apices, with many short setulose setae; sternite IX divided, lobes ovate, separated by their diameter in ♂, lobes transverse, contiguous in ♀; tergite X divided, lobes ovate, contiguous in both sexes; lobes of sternites IX and X with scattered spinulose setae; spiracles distinct, dark brown and sclerotized, slightly raised, on tergites I-V, small, pale and presumably functionless on tergite VI.



Figs 1-3. ⊙ *Paropsis atomaria.* **1**, left side, dorsal (lateral tubercle setae omitted). **2**, head, anterior; setae; lf = lateral frons, if = inner frons, o = ocular, uv = upper vertex, uf = upper fronts, v = vertex. **3**, right side abdomen, ventral. Scale = 2mm.

Paropsis obsoleta Olivier, 1807

Material examined: AUSTRALIAN CAPITAL TERRITORY: 1♂, 2♀, Canberra, reared from adults, i.1974, C. P. Whittle.

Description: similar to *P. atomaria*, setal pattern apparently differing only in ocular setae. Only the head setae are described here as the setae of the pronotum, mesonotum, abdomen (including sexual structures) and legs are all within the range of *P. atomaria*. The spinuliform setae and their tubercles are pale and inconspicuous on sternites VII and VIII, but this may be due to bleaching. *Measurements* (mm.): length, ♂ 9.8, ♀ 10.1 mm; head width, ♂2.7, ♀3.1; pronotal width, ♂4.2, ♀4.5. *Head setae:* 1 upper vertex, 3-8 vertex, 2-3 ocular, 1 upper frons, 2-3 lateral frons.

Paropsis porosa Erichson, 1842

Material examined: 1♂, unprovenanced material in vial with larvae and adults (ex Carne).

Description: similar to *P. atomaria*, setal pattern different on meso- and metanotum and with more head setae. Pronotum as *P. atomaria*. Mesonotum and metanotum with setae more or less in 3 groups. Abdomen and legs as *P. atomaria*. *Measurements* (mm.): length (slightly shrivelled) 10.3; head width 2.5; pronotal width 4. *Head setae:* 1 upper vertex, 7-9 vertex, 2-4 ocular, 1-2 upper frons, 2 lateral frons, 1 inner frons.

Paropsis sp. nr. *bella* Blackburn, 1894

Material examined: AUSTRALIAN CAPITAL TERRITORY: 2♂, 1♀, Canberra, reared from adults, 9.ix.1975, C. P. Whittle.

Description: similar to *P. atomaria*, no setal differences detected, except more, denser pronotal setae (c120 each side). *Measurements* (mm.): length, ♂12.1, ♀14.3; head width, ♂2.7, ♀3.0; pronotal width, ♂4.3, ♀4.7. *Head setae:* 1 upper vertex, 3-5 vertex, 1 ocular, 1 upper frons, 2 lateral frons, 0-(1) inner frons.

Chrysophtharta Weise, 1901

Type species: not designated

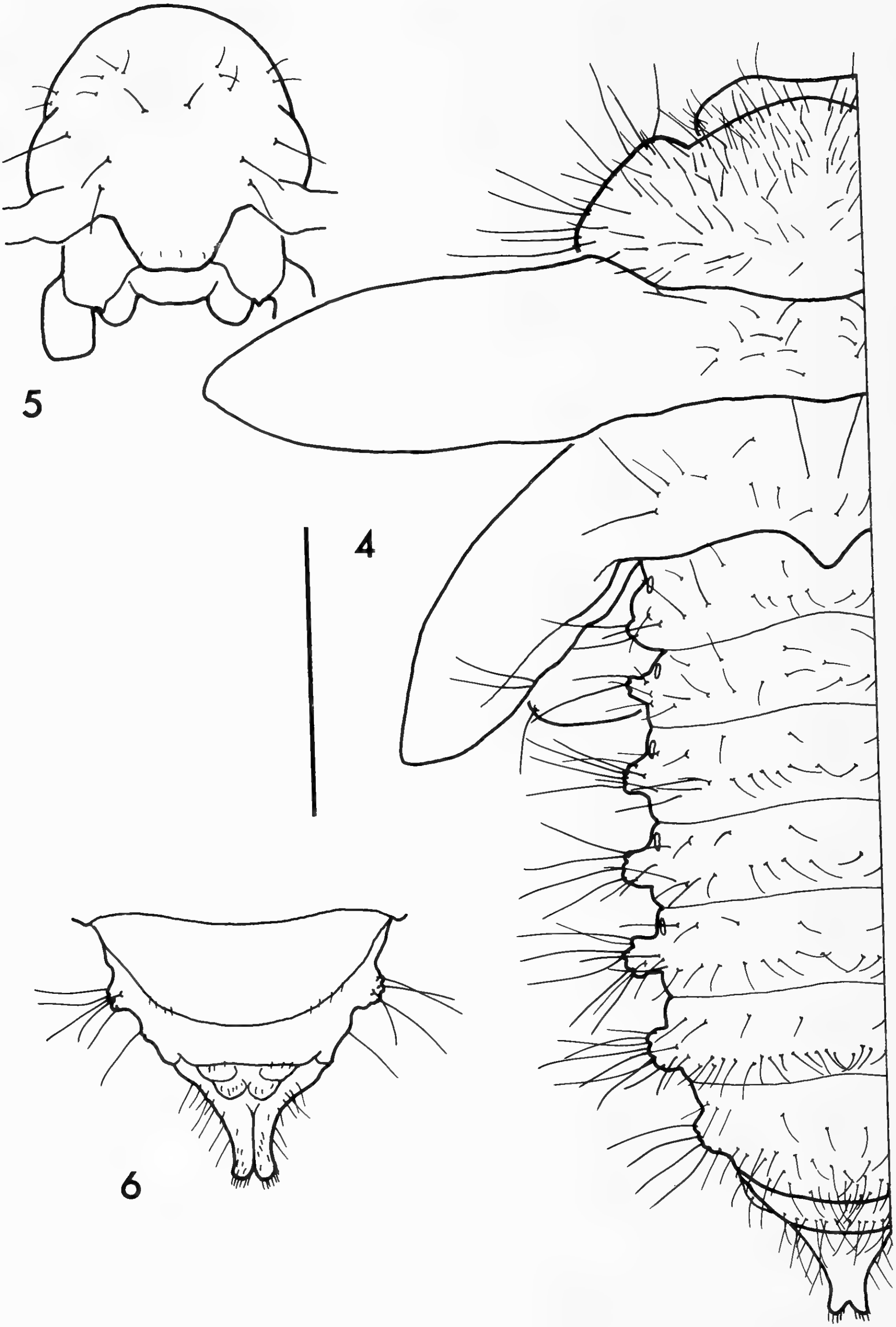
Diagnosis: Pupae of *Chrysophtharta* may be distinguished by the lack of spiracular tubercles, and the presence of moderately setose lateral tubercles, less than 3 upper vertex setae and more than 2 vertex setae.

Chrysophtharta sp. nr *inconstans* (Blackburn, 1900)

(Figs 4-6)

Material examined: AUSTRALIAN CAPITAL TERRITORY: 2♂, 4♀, Shepherd's Lookout, Murrumbidgee R., ex larvae on *Eucalyptus polyanthemos*, 26.xi.1989, C. Reid; pupated 3-5.xii. 1989, 3 adults reared.

Description: *Measurements* (mm.): length, ♂8.6-8.8, ♀8.6-9.4; head width, ♂1.8-1.9, ♀1.9-2.0; pronotal width, ♂3.2-3.3, ♀3.2-3.4. *Head.* Setae: 2 upper vertex, (3)-(7) vertex, 1 ocular, 1 upper frons, 2 lateral frons. Mandibular thecae conspicuously toothed. *Thorax.* Pronotum with 80-95 setae, scattered but more dense towards front and side margins. Mesonotum: 5-8 setae, sometimes in two groups, with 1-2 subsidiary anterior setae. Metanotum: 7-(12) setae in scattered row or two groups plus 1-2 subsidiary anterior setae. Legs: apex of each femur with 3-4 setae, 4 most frequent (97%). *Abdomen:* tergites I-VI with irregular transverse row of setae along posterior margin (central setae) increasing from 5-(8) each side on tergite I, to (7)-12 on tergite VI; 2-5 small, subsidiary setae on each side of tergites I-VII, anterior to central row; spiracular setae on small tubercles, (1)-(3) setae on tergite I, 2-3 setae on tergites II-VI; lateral



Figs. 4-6. ♂ *Chrysophtharta* sp. nr *inconstans*. **4**, left side, dorsal. **5**, head, anterior. **6**, apex abdomen, ventral. Scale = 2 mm.

tubercles of tergites II-VI condyliform, small with 1-(4) setae on tergite I, larger with 5-9 setae on tergites II-VI; tergite VII central and spiracular tubercle setae merged, 22-27, lateral tubercle (5)-8; tergite VIII without obvious tubercles, largely enclosed within tergite VII, 8-(13); tergite IX projecting from within tergite VIII as a posterio-dorsally directed process with a bifid sclerotized apex; sternites IV-VI with 1-2 small setae on posterior margin near lateral tubercle, otherwise glabrous; posterior margin of sternite VII simple, with 3-8 inconspicuous setae each side; sternite VIII of ♂ with straight posterior margin and 5-6 short setae each side of margin; sternite VIII of ♀ deeply emarginate and divided along midline, 3-6 short setae each side; venter of tergite IX represented by 2 lobes sclerotized at tips with sinuate lateral margins, the lobes contiguous from hemitergites X to their apices, with many short setae; sternite IX divided, lobes ovate, separated by their diameter in ♂, lobes transverse, almost contiguous in ♀, tergite X divided, lobes ovate, almost contiguous in both sexes; spiracles dark brown and sclerotized on tergites I-V, not visible on tergite VI.

Chrysophtharta sp. nr *amoena* (Clark, 1865)

Material examined: NEW SOUTH WALES: 3♂, 3♀, reared from adults collected at Mill Post, 8 km. sw. Bungendore, P. Edwards.

Description: similar to *C.* nr *inconstans*, except slightly less setose, especially on the thoracic and abdominal tergites. The lateral tubercles are also slightly less prominent. *Measurements* (mm.): length, ♂6.3-7.2, ♀7.3-8.3; head width, ♂1.9-2.2, ♀2.1-2.3; pronotal width, ♂2.7-3.1, ♀3.2-3.7. *Head.* Setae: 0-2 upper vertex, 3-5 vertex, 1 ocular, 1 upper frons, 2 lateral frons. Mandibular thecae conspicuously toothed. *Thorax.* Pronotum: 80-105 setae, scattered but more dense towards front and side margins. Mesonotum: 4-(8) setae, in roughly two groups, outer 1-3, inner (2)-(6). Metanotum: (4)-(8) setae in scattered row or two groups. Legs: apex of each femur with 0-4 setae, 4 most frequent (62%). *Abdomen:* tergites I-VI with irregular transverse row of setae increasing from (2)-5 each side on tergite I, to (5)-(10) on tergite VI; 0-4 small, subsidiary setae on each side of tergites I-VII, anterior to central row; spiracular setae on small tubercles, 1-2 setae on tergite I, 1-4 setae on tergites II-VI; lateral tubercle small with (0)-2 setae on tergite I, larger and condyliform with (1)-7 setae on tergites II-VI; tergite VII central and spiracular tubercle setae merged, 16-(25), lateral tubercle reduced, (1)-6; posterior margin of sternite VII simple, with 2-5 inconspicuous setae each side; sternite VIII of ♂ with simple posterior margin and 3-5 short spinulose setae each side of margin; sternite VIII of ♀ deeply cleft along midline from base to apex, 3-5 short spinulose setae each side; spiracles dark brown and sclerotized on tergites I-V, small, pale and presumably functionless on tergite VI.

Paropsides Motschulsky, 1860

Type species: *Paropsis duodecimpustulata* Gebler, by original designation (Motschulsky, 1860)

Diagnosis: Pupae of *Paropsides* may be distinguished by the combination of weak lateral tubercles with 2-3 setae, 75+ pronotal setae, and a bifid urogomphus.

Paropsides umbrosa (Chapuis, 1877)
(Figs 7-10)

Material examined: AUSTRALIAN CAPITAL TERRITORY: 5♂, 6♀, Black Mountain, ex larvae with adults of *P. umbrosa* on *Daviesia retorta*, 29.vii.1989, C. Reid; pupated 20-30.viii. 1989.

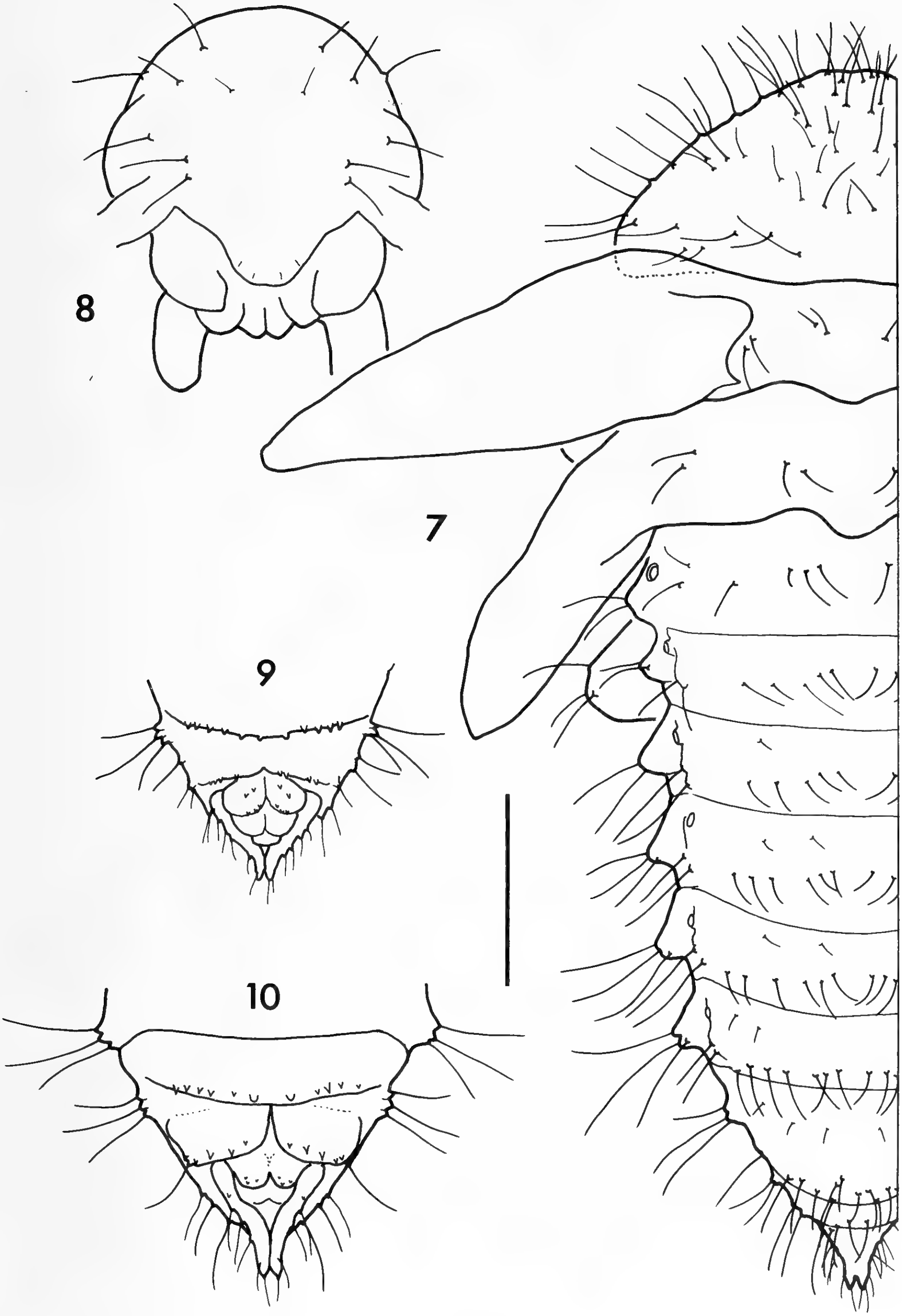
Description: *Measurements* (mm.): length, ♂5.8-6.3, ♀6.0-6.4; head width, ♂1.4-1.5, ♀1.5-1.7; pronotal width, ♂2.2-2.5, ♀2.3-2.5. *Head.* Setae: 1 upper vertex, 2-3 vertex, 1 ocular, 1 upper frons, 2 lateral frons. *Thorax.* Pronotum: 75-90 setae, scattered but more dense towards middle. Mesonotum: setae in two groups, outer (1)-2, inner 1-(4). Metanotum: setae in two groups, outer 2-3, inner 2-3. Legs: apex of each femur with 0-3 setae, 3 most frequent (95%). *Abdomen:* tergites I-VI with irregular transverse central row of setae along posterior margin (central setae) increasing from 3-6 (usually 4) each side on tergite I, to 6 on tergite VI; 0-3 small, subsidiary setae on each side of tergites I-VII, anterior to central row; tergites without condyliform tubercles; 1-2 spiracular setae on tergites I-VI; lateral tubercle small with 2 setae on tergite I, larger with 2-3 setae on tergites II-VI; tergite VII combined central and spiracular setae 6-8, lateral tubercle reduced, 3; tergite VIII largely enclosed within tergite VII, (4)-7, lateral tubercle 2-3; tergite IX projecting from within tergite VIII as a posterio-dorsally directed process with a bifid sclerotized apex; sternites II-IV glabrous, V with 2 small lateral setae, VI with 0-3 small lateral spinules; posterior margin of sternite VII with (4)-(8) dark brown spinuliform setae (actually very short setae on sclerotized conical tubercles) on either side; sternite VIII of ♂ with a shallow median incision and 4-6 dark brown spinuliform setae each side of margin; sternite VIII of ♀ divided along midline from base to apex, with (0)-5 dark brown marginal spiniform setae each side; venter of tergite IX represented by 2 brown sclerotized lobes with sinuate lateral margins, the lobes contiguous for most of their length, with spinules and short setae; separate lobes of sternites IX adjacent in both sexes, with scattered small spiniform setae; spiracles dark brown and sclerotized on tergites I-V, not visible on tergite VI.

Paropsisterna Motschulsky, 1860

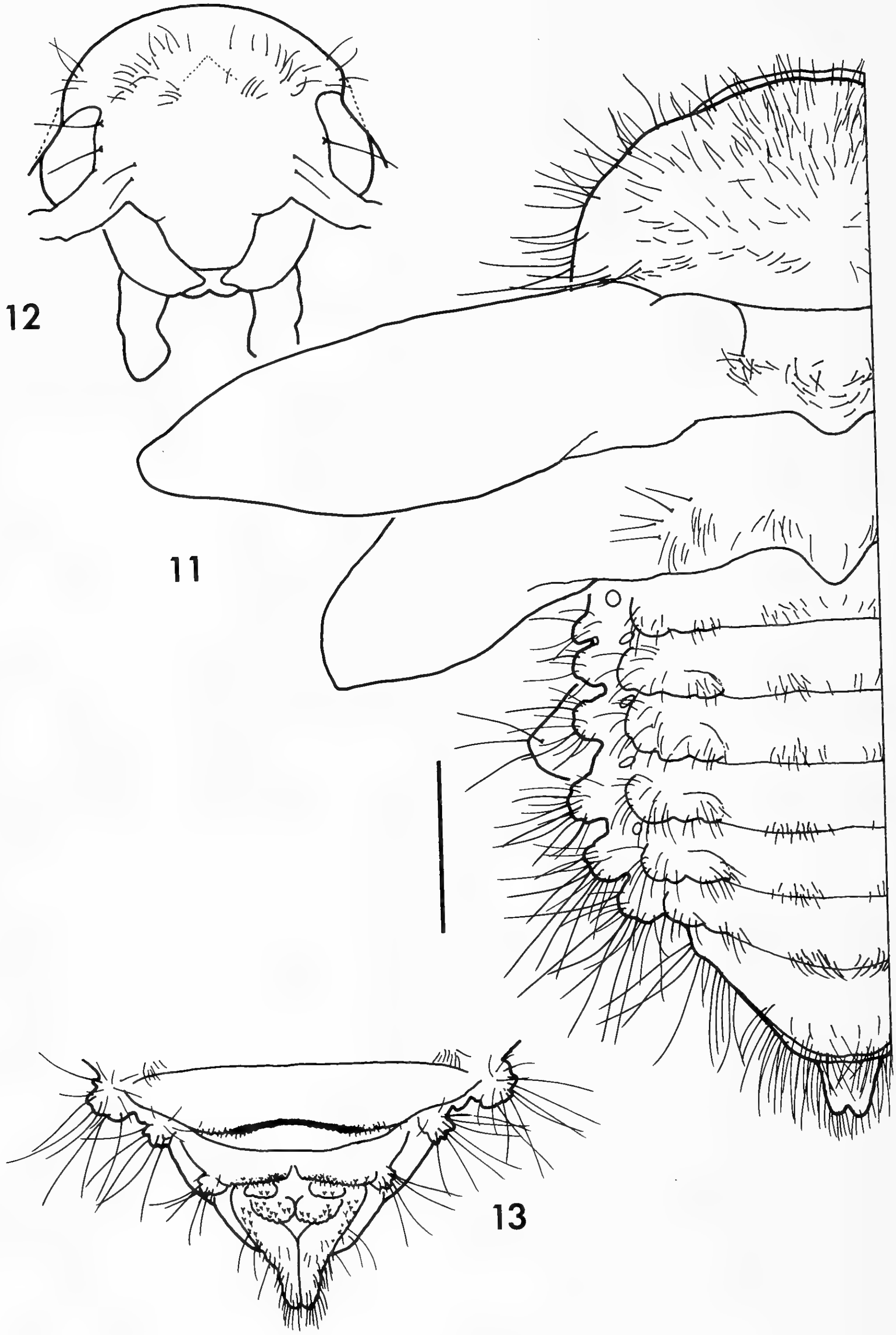
Type species: *Paropsisterna sexpustulata* Motschulsky, by original designation
Diagnosis: Pupae of *Paropsisterna* may be distinguished from all others except *Paropsis* by the possession of strongly developed spiracular tubercles, patches of small setae at the sides of sternite VI, and the strongly sclerotized apex of sternite VII. Pupae of *Paropsisterna* may be separated from those of *Paropsis* by the greater number of setae on the vertex and metanotum, the division of central abdominal setae into 2 groups, the greater number of apical spinuliform setae on sternite VII and the presence of only 3 subapical setae on each femur.

Paropsisterna beata (Newman, 1842)
(Figs 11-13)

Material examined: AUSTRALIAN CAPITAL TERRITORY: 1♀, Glendale Crossing, reared from adult on eucalypt, eggs laid 13.i.1987, hatched 20.i.1987, pupated 12.ii.1987, C. Reid; 1♀, Black Mountain, eggs laid 9.ii.1966, hatched 14.ii.1966, prepupa 4.iii.1966; pupated 7.iii.1966, B. Musik.
Description: *Measurements* (mm.): length 12; head width 3; pronotal width 4.6-4.9. *Head.* Setae: 3-4 upper vertex, 11-20 vertex, 1-4 ocular, 2-5 upper frons, 2 lateral frons. *Thorax.* Pronotum: 110 setae, especially on apical half of disc. Mesonotum: setae in two groups, outer 10-14, inner 9-12. Metanotum: setae in two groups, outer 14-17, inner 9-11. Legs: all femora with 3 preapical setae. *Abdomen:* tergites I-VI with 2 groups of central setae along posterior margin, between spiracular tubercle and midline, outer group on small tubercle; no subsidiary setae in apical half; outer group increasing from 5-7 on tergite I to 9-13 on tergite VI; inner group 11-15 on tergites I-VI; spiracular and lateral tubercles well-developed, condyliform, with long setae; spiracular tubercle with 10-12 setae on tergite I to 15-16 on tergite VI; lateral tubercles with 8-11 on tergite I and 12-17 on tergites II-VI; tergite VII with 35-37 setae each side; tergite VIII with 27-28 setae each side; sternite VII with 21-23 spinuliform setae each side, evenly spaced across posterior margin including ridge; sternite VIII as ♀ *P. atomaria* except 28-30 spinuliform setae



Figs. 7-10. ♂ *Paropsides umbrosa.* **7**, left side, dorsal. **8**, head, anterior. **9**, apex abdomen, ventral. **10**, ♀, apex abdomen, ventral. Scale = 1 mm.



Figs. 11-13. ♂ *Paropsisterna beata*. **11**, left side, dorsal. **12**, head, anterior. **13**, apex abdomen, ventral. Scale = 2 mm.

each side, these larger than in *Paropsis* spp.; segments IX and X as ♀ *P. atomaria*. Spiracles as *P. atomaria*.

Paropsisterna sexpustulata (Marsham, 1808)

Material examined: QUEENSLAND: 1 ♂, Brisbane, reared from adults on *Eucalyptus*, iv-vi. 1978, K. Houston (Department of Primary Industries, Indooroopilly, Queensland).

Description: similar to *P. beata*, with only small differences in the numbers of setae. *Measurements* (mm.): body length not measured due to shrinkage; head width 3.0; pronotal width 4.7. *Head.* Setae: 4 upper vertex, 16-17 vertex, 4-5 ocular, 2-3 upper frons, 2 lateral frons. *Thorax.* Pronotum: 100 setae, distributed as *P. beata.* Mesonotum: setae in 2 groups, outer 8-9, inner 13. Metanotum: setae in 2 groups, outer 9-13, inner 9-11. Legs: all femora with 3 preapical setae. *Abdomen:* tergites I-VI with 2 groups of setae as *P. beata*; outer group increasing from 2-3 on tergite I to 11-14 on tergite VI; inner group increasing from 2-3 on tergite I to 10-15 on tergite VI; no subsidiary setae on apical half; spiracular and lateral tubercles as *P. beata*; spiracular tubercle with 5-7 setae on tergite I, increasing to 16-17 on tergite VI; lateral tubercle with 8-10 setae, segment I, and 17-25 setae segs. II-VI; tergite VII with 46-49 setae; tergite VIII with 27-32 setae; tergite IX and sternites II-VI as *P. beata*; sternite VII with 6 spinuliform setae between ridge and lateral margin, and ridge with 25 minute spinuliform setae along posterior margin; sternite VIII with 26 spinuliform setae each side; segments IX and X and spiracles as *P. beata*.

Pyrgoides Aslam, 1968

Type species: not designated

Diagnosis: Pupae of *Pyrgoides* may be distinguished by ventrally fused urogomphi, lack of upper vertical setae, less than 5 metanotal setae and weakly developed lateral tubercles with 1-3 setae.

Pyrgoides rubiginosa (Chapuis, 1877)

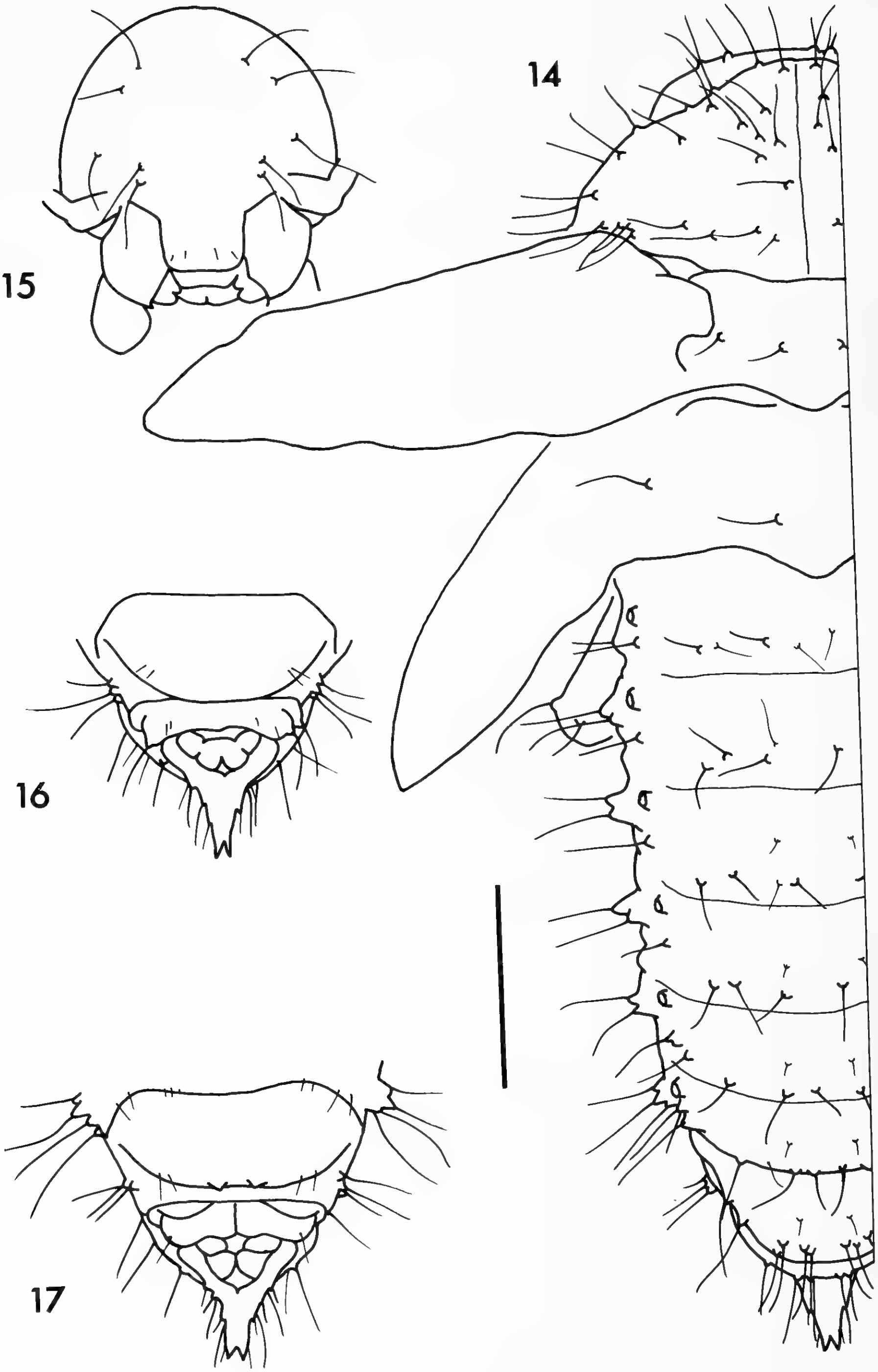
(Figs 14-17)

Material examined: NEW SOUTH WALES: 2 ♂, 1 ♀, Temora, reared from larvae and adults on *Acacia hakeoides* flowers, collected 20.viii.1985, pupated 30.viii.1985, C. Reid.

Description: *Measurements* (mm.): length 5.9-6.4; head width 1.2-1.4; pronotal width 2.1-2.2. *Head.* Setae: 2 vertex, 1 ocular, 2-3 lateral frons, 0-1 upper frons. Mandibular thecae toothed. *Thorax.* Pronotum: 25-32 setae, distributed submarginally and near the midline. Mesonotum: 2-3 setae. Metanotum: 2-4 setae. Legs: all femora with 3 preapical setae. *Abdomen:* each of tergites I-VI with (2)-5 central setae each side, and frequently a small subsidiary seta anterior to these, 1-2 spiracular setae (only 1 on tergite I), and 2-3 setae on lateral tubercle; tergite VII with 6-7 marginal setae plus 1 subsidiary; tergite VIII 3-4; tergite IX represented by an elongate projection, bifid and sclerotized at tip; apical sternites with few minute marginal setae, without spinuliform setae; sternite VIII medially longitudinally grooved in ♀, simple in ♂; sternites VIII-X fused together and hard to distinguish; spiracles distinct and strongly raised on tergites I-VI.

Pyrgoides hamadryas (Stål, 1860)

Material examined: AUSTRALIAN CAPITAL TERRITORY: 3, sex indeterminate, Canberra, reared from adults on *Acacia baileyana* flowers, 13.viii. 1985, C. Reid.



Figs. 14-17. ♀ *Pyrgoides rubiginosa.* **14**, dorsum, left side. **15**, head, anterior. **16**, **17**, apex of venter of ♂ and ♀ respectively. Scale = 1 mm.

Description: similar to *P. rubiginosa*, but less setose. The pupae are almost identical to those of *P.* sp. nr *dryope* (Figs 18-21). *Measurements* (mm.): length 4.8-5.0; head and pronotal width not measured because of distortion. *Head.* Setae: 2 vertex, 1 ocular, 1 upper frons, 2 lateral frons. *Thorax.* Pronotum: 18-19 setae. Mesonotum: 2 setae. Metanotum: 2 setae. Legs: all femora with 3 preapical setae. *Abdomen:* each of tergites I-VI with 2 central, 1 spiracular, setae each side; tergite I with 1 lateral tubercle seta, tergites II-VI with 2 lateral tubercle setae; tergite VII 2-3; tergite VIII 3; tergite IX produced into an elongate triangular process with a single sclerotized apex; sternites as *P. rubiginosa* but sexual characters not distinguished because of poor state of material.

Pyrgoides sp. nr *oenone* (Blackburn, 1899)

Material examined: NEW SOUTH WALES: 1 ♀, 91 km E. Hay, reared from adults and larvae on *Acacia salicina* flowers, 16.v.1986, C. Reid.
Description: similar to *P. hamadryas* except size, and shape of urogomphus. Pronotum with 16-17 setae each side; sternite VIII faintly grooved as in ♀ *P. rubiginosa. Measurements* (mm.): length 3.3; head width 0.8; pronotal width 1.1.

Pyrgoides sp. nr *dryope* (Blackburn, 1900)
(Figs 18-21)

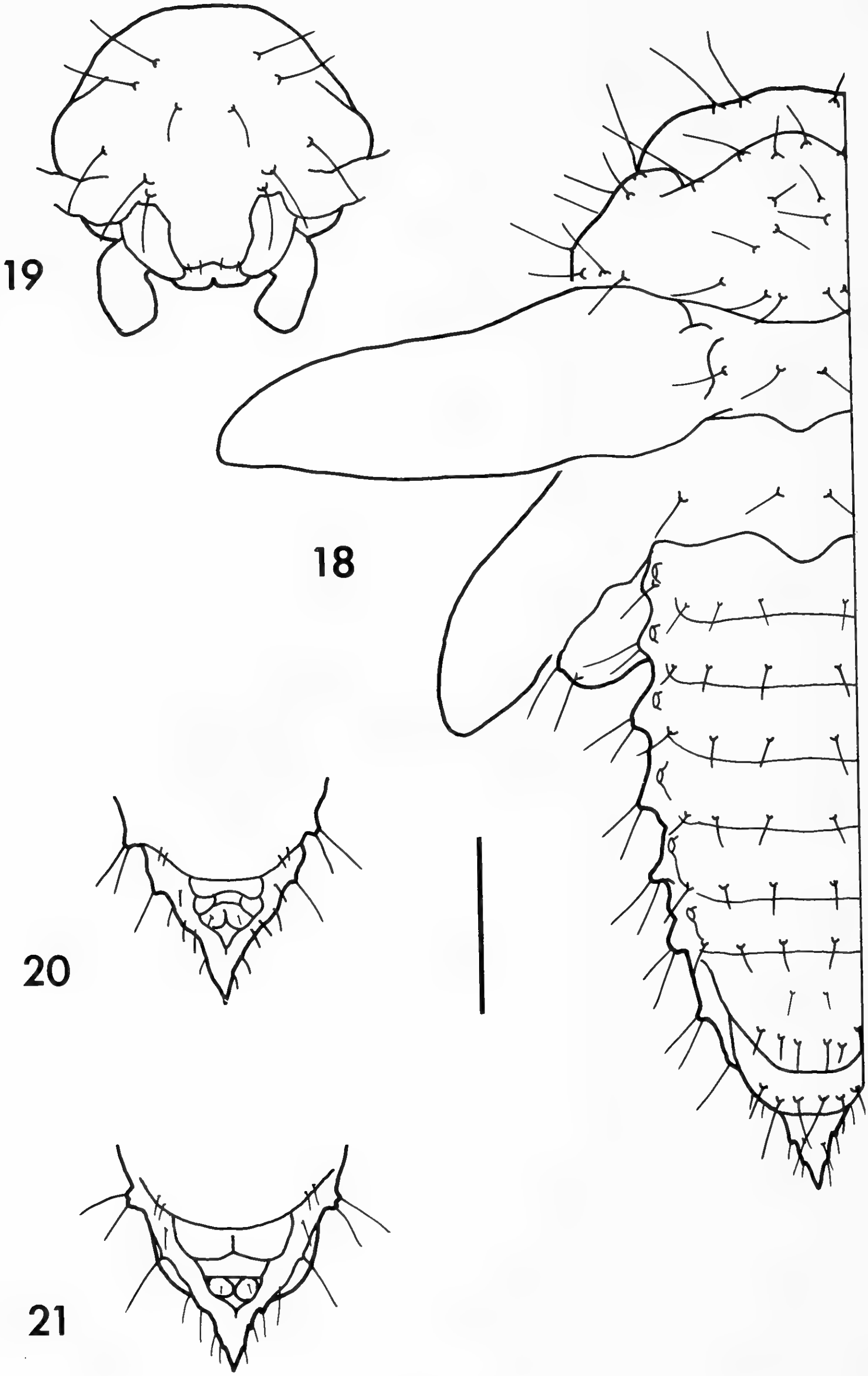
Material examined: AUSTRALIAN CAPITAL TERRITORY: 2♂, 1♀, Canberra, reared from adults on *Acacia baileyana* flowers, 13.viii.1985, C. Reid.
Description: similar to *P. hamadryas*, except in size. *Measurements* (mm.): length 3.2-3.4; head width 0.8; pronotal width 1.3. *Head.* Setae: 2 vertex, 1 ocular, 0-2 lateral frons, 0-1 upper frons. *Thorax.* Pronotum: 17-21 setae, distributed as *P. rubiginosa*. Mesonotum: 2 setae. Metanotum: (1)-2 setae. Legs: all femora with 3 preapical setae. *Abdomen:* setal configuration exactly as in *P. hamadryas* except some lateral tubercles other than tergite I occasionally with 1 seta; sternite VIII of ♀ large with a midline groove, small and simple in ♂; apical sternites fused and difficult to distinguish; spiracles distinct and strongly raised on tergites I-VI.

Trachymela Weise, 1908

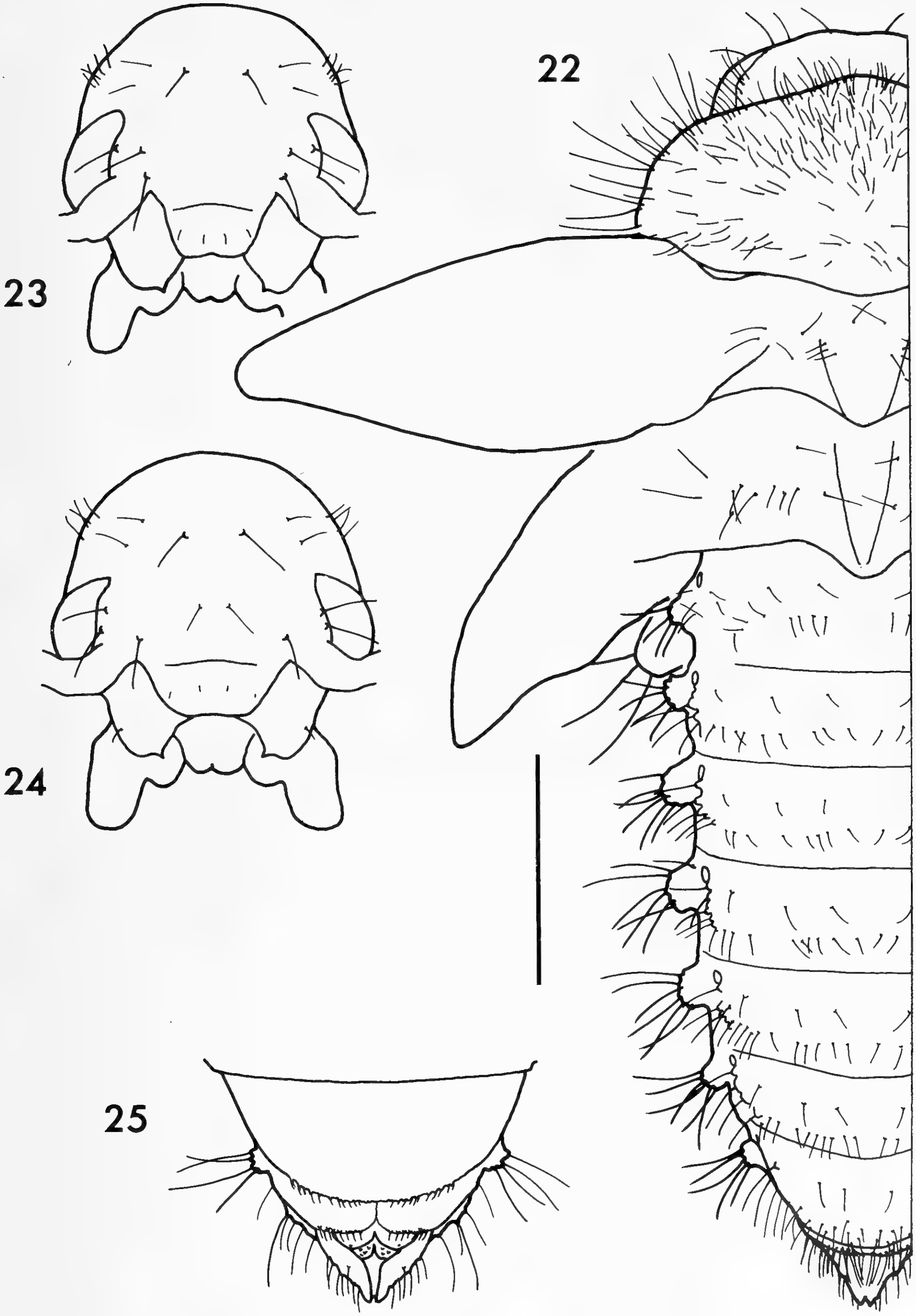
Type species: not designated
Diagnosis: Pupae of *Trachymela* may be distinguished by lack of spiracular tubercles, and presence of moderately setose lateral tubercles, more than 3 upper vertex setae and less than 3 vertex setae.

Trachymela sp. nr *tincticollis* (Blackburn, 1897a)
(Figs 22-25)

Material examined: WESTERN AUSTRALIA, 1♂, 1♀, Kojaneerup, 12k S Bluff Knoll, with larvae and reared adults, ex large secreted tubes (homopteran ?) on stems of *Eucalyptus sargentii*, 9.v.1990, G. P. Hall.
Description: creamy yellow with pale brown setae. *Measurements* (mm.): length, ♂10.2, ♀11.0; head width, ♂2.9, ♀3.0; pronotal width, ♂4.0, ♀3.9. *Head.* Setae: 4-6 upper vertex, 2 vertex, 1-2 ocular, 1 upper frons, 0-1 inner frons, 1-2 lateral frons. Mandibular thecae conspicuously toothed. One specimen with short mandibular setae. *Thorax.* Pronotum: 100-120 setae, scattered but more dense towards front and on disc, and much longer at sides. Mesonotum: 6-9 setae, in roughly two groups, outer 2-3, inner 3-8. Metanotum: 9-13 setae in scattered row, 1-2 setae anteriorly placed. Legs: apex of each femur with 3-4 setae, 3 most frequent (83%). *Abdomen:* tergites I-VI with irregular



Figs. 18-21. ♂ *Pyrgoides* nr. *dryope.* **18**, dorsum, left side. **19**, head, anterior. **20**, **21**, apex of venter of ♂ and ♀. Scale = 0.5 mm.



Figs. 22-25. ♀ *Trachymela* sp. nr *tincticollis*. **22**, left side, dorsal. **23-24**, ♀ and ♂ head, anterior. **25**, apex abdomen, ventral. Scale = 2 mm.

transverse row of setae along posterior margin (central and spiracular setae) increasing from 11-12 each side on tergite I, to 16-20 on tergite VI, spiracular setae on raised tubercles; 3-5 small, subsidiary setae on each side of tergites I-VII, anterior to central row; lateral tubercle small with 3-5 setae on tergite I, larger with 4-11 setae on tergites II-VI; tergite VII central and spiracular tubercle setae merged, 17-21 plus 3 anterior subsidiary setae, lateral tubercle reduced, 6-8; tergite VIII without obvious tubercles, largely enclosed within tergite VII, 11-12 plus 3 anterior subsidiary setae; tergite IX projecting from within tergite VIII as a posterio-dorsally directed process with a bifid sclerotized apex; sternites II-VI with 1-2 small setae on posterior margin near lateral tubercle, otherwise glabrous; posterior margin of sternite VII simple, with 12-15 short setae each side; sternite VIII of ♂ with simple posterior margin and 3-5 short spinulose setae each side of margin; sternite VIII of ♀ deeply cleft along midline from base to apex, 8 short spinulose setae each side; venter of tergite IX represented by 2 elongate brown sclerotized lobes with sinuate lateral margins, the lobes contiguous from hemitergites X to their apices, with a few short spinulose setae; sternite IX divided, lobes ovate, separated by their diameter in ♂, lobes transverse, almost contiguous in ♀, tergite X divided, lobes ovate, almost contiguous in both sexes; spiracles dark brown and sclerotized on tergites I-V, small, pale and presumably functionless on tergites VI-VII.

SUBTRIBE DICRANOSTERNINA Weise, 1915

Dicranosterna Motschulsky, 1860

Type species: *Dicranosterna immaculata* Motschulsky, by monotypy

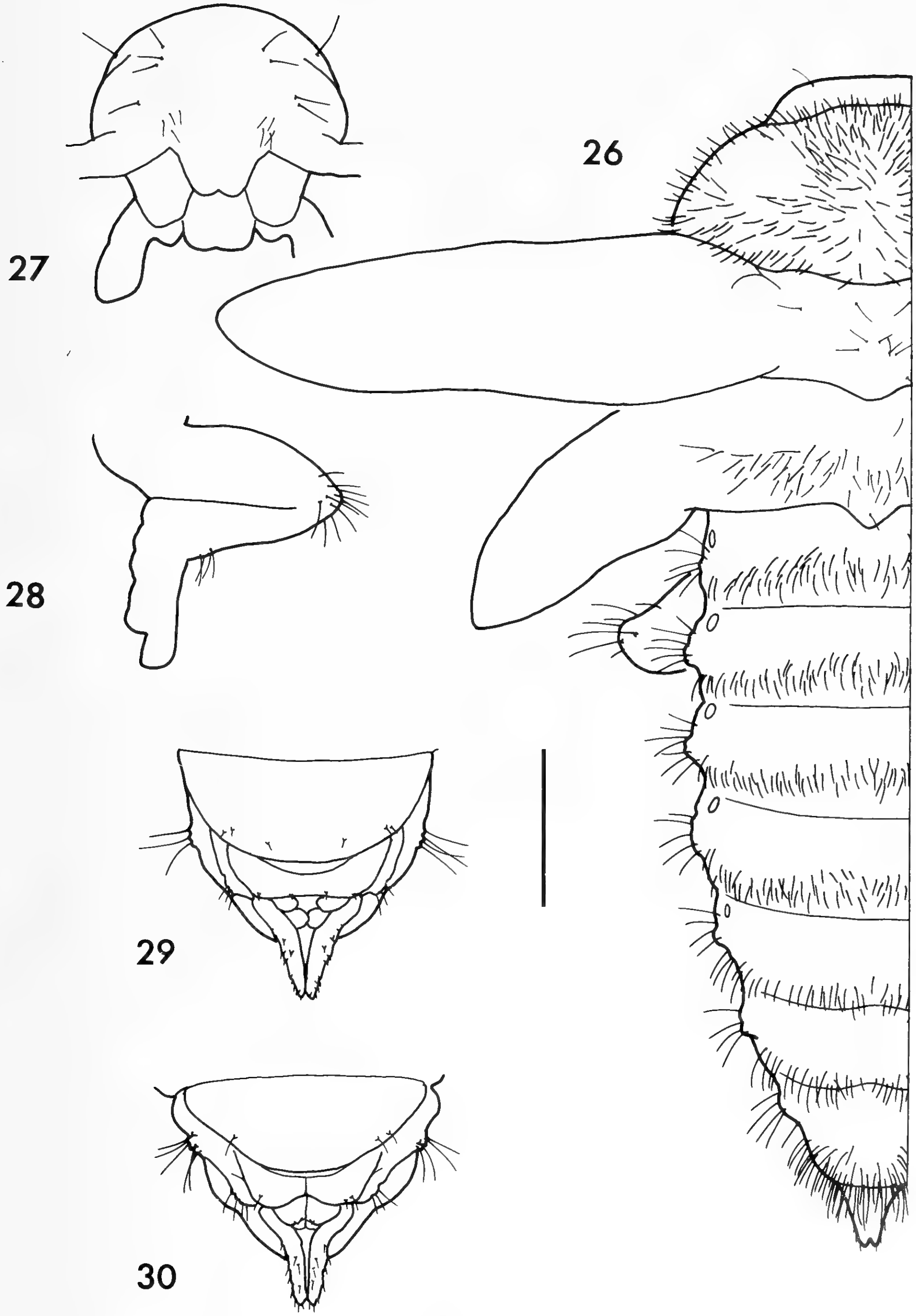
Diagnosis: Pupae of *Dicranosterna* may be distinguished from all others except *Trochalodes* by the combination of dense transverse bands of abdominal setae and very weak or absent lateral tubercles. From *Trochalodes* the pupae are distinguished by having apical tibial setae, less than 3 upper vertical setae and dorsal setae not set on tubercles.

Dicranosterna immaculata Motschulsky, 1860

(Figs 26-30)

Material examined: AUSTRALIAN CAPITAL TERRITORY: 2♂, 5♀, Mount Majura, ex eggs laid by *D. immaculata* on *Acacia mearnsii*, ix.1989, C. Reid; pupated x.1989.

Description: *Measurements* (mm.): length, ♂13.1-14.8, ♀12.1-15.4; head width, ♂2.8, ♀2.8-3.1; pronotal width, ♂ and ♀ 5.2-5.6. *Head.* Setae: 1-2 upper vertex, 2-(4) vertex, 1-(3) ocular, 0-2 upper frons, 3-8 lateral frons, 0-1 inner frons. *Thorax.* Pronotum: 125-145 setae, absent from anterior sides of disc and greatest density in anterior half near midline. Mesonotum: setae in 2 groups, outer 1-2, inner (2)-(8). Metanotum: 50-66 setae in total, in dense transverse row. Legs: each femur with 8-14 preapical setae (11 modal, 29%), fore and mid tibia with 1-2 preapical setae and hind tibia with 1-3 preapical setae. *Abdomen:* tergites I-VI with dense transverse row of setae along posterior margin (central setae) of similar density from tergite I (22-40 each side) to tergite VI (27-36); with occasional small, single setae on each side of tergites I-VII, anterior to central row; tergites I-VI without globular prominences, lateral tubercles small and spiracular setae on weak tubercle separate from central setae; (2)-(8) spiracular setae on tergite I, 4-(9) on tergite VI; 4-(7) lateral tubercle setae on tergite I, (5)-8 setae on tergite VI; tergite VII with 24-36 central and 4-6 spiracular setae; tergite VIII largely enclosed within tergite VII, with apical band of 36-56 setae; tergite IX projecting from within tergite VIII as a blunt posterio-dorsally directed process with a bifid weakly sclerotized apex; sternites II-V glabrous, VI with 2 small lateral apical setae; posterior margin of



Figs. 26-30. ♂ *Dicranosterna immaculata.* **26**, left side, dorsal. **27**, head, anterior. **28**, hind leg. **29-30**, ♂ and ♀ apex abdomen, ventral. Scale = 2 mm.

sternite VII simple, evenly rounded with 2-5 small apical setae set on tubercles; posterior margin of sternite VIII of ♂ slightly concave, with 3-4 setae on tubercles each side; sternite VIII of ♀ completely divided along midline from base to apex, with 2-4 setae each side; venter of tergite IX represented by 2 apically contiguous lobes with sinuate lateral margins with many short setae; sternite IX divided, lobes ovate, separated by their diameter in ♂, contiguous in ♀; tergite X divided, lobes ovate, contiguous in both sexes; spiracles distinct, dark brown and sclerotized, slightly raised, on tergites I-V, not visible on tergite VI.

Trochalodes Weise, 1901

Type species: not designated.
Diagnosis: Pupae of *Trochalodes* may be distinguished from all others except *Dicranosterna* by the combination of dense transverse bands of abdominal setae and very weak or absent lateral tubercles. From *Dicranosterna* the pupae are distinguished by having more than 3 upper vertical setae and dorsal setae set on tubercles and lacking apical tibial setae.

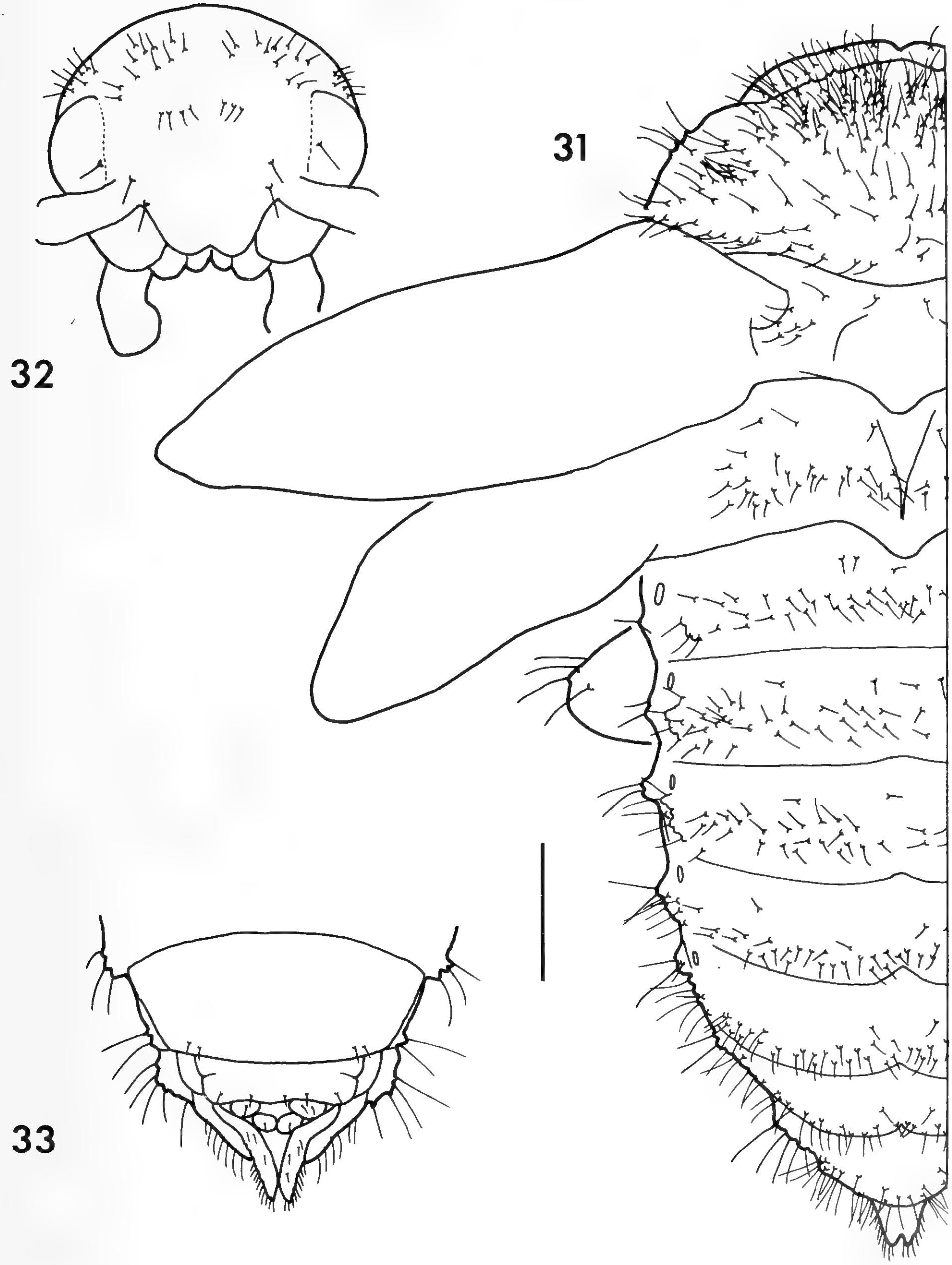
Trochalodes sp. nr *hemisphaerica* (Chapuis, 1877)
(Figs 31-33)

Material examined: WESTERN AUSTRALIA: 3♂, Cervantes, ex larvae with adults on *Acacia rostellifera*, 20-23.viii.1987, C. Reid; pupated 1-3.ix.1987.
Description. *Measurements* (mm.): length, 8.6-8.7; head width, 2.1-2.3; pronotal width, 3.5-3.7. *Head.* Setae: 6-9 upper vertex, 5-7 vertex, 1-2 ocular, 2-4 upper frons, 2-3 lateral frons. *Thorax.* Pronotum: 60-65 scattered setae set on prominent tubercles, greatest density in anterior half, near midline. Mesonotum: setae in 2 groups, outer 7-16, inner 0-2. Metanotum: 21-31 setae, scattered in transverse row, with 2 or 3 basal setae. Legs: each femur with 2-6 preapical setae, 4 most frequent (56%). *Abdomen:* tergites IV-VI emarginate at apex; tergites I-VI with irregular transverse row of setae along posterior margin (central setae and spiracular setae) increasing from 17-22 each side on tergite I, to 22-36 on tergite VI and 1-6 small, subsidiary setae on each side of tergites I-VIII, anterior to central row; tergites I-VI without globular prominences, but slightly tuberculate at sides; setae of spiracular area not distinguishable from central setae; lateral tubercles small, with 1-2 setae on tergite I, 2-7 setae on tergites II-VI; tergite VII central and spiracular tubercle setae merged, 34-42, lateral tubercle, 1-3; tergite VIII largely enclosed within tergite VII, 17-23; tergite IX projecting from within tergite VIII as a blunt posterio-dorsally directed process with a bifid, weakly sclerotized, apex; sternites II-VI glabrous; posterior margin of sternite VII simple, with 1-2 small setae laterally; sternite VIII simple, with 1-2 small setae each side of margin; venter of tergite IX represented by 2 weakly sclerotized lobes with straight lateral margins, the lobes contiguous at their apices, with a few short setae; sternite IX divided, lobes ovate, separated by their diameter; tergite X divided, lobes ovate, contiguous; spiracles distinct, dark brown and sclerotized on tergites I-V, not visible on tergite VI.

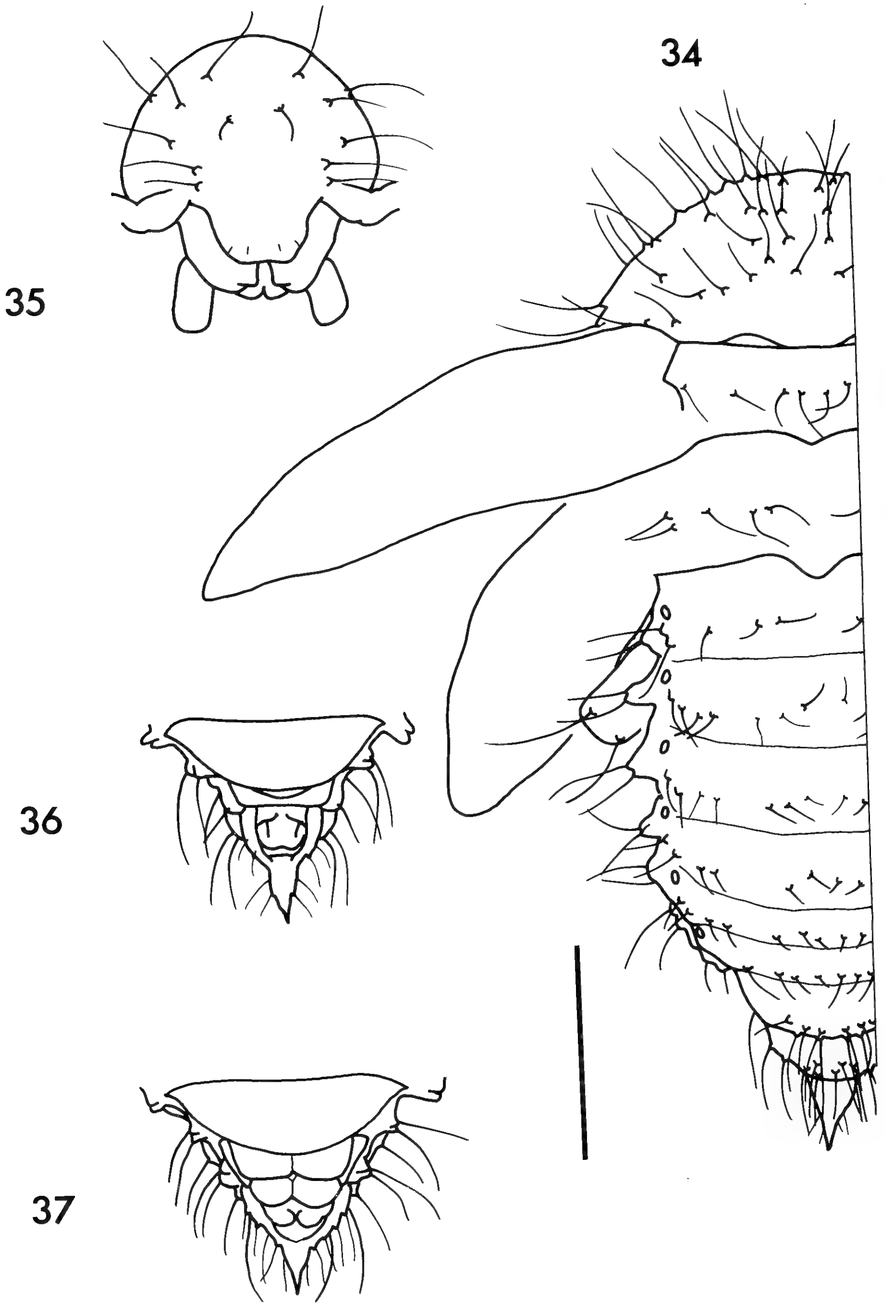
SUBTRIBE UNKNOWN

Novacastria Selman, in Selman and Lowman, 1983

Type species: *Novacastria nothofagi* Selman, in Selman and Lowman, 1983, by original designation and monotypy
Diagnosis: The pupae of *Novacastria* may be distinguished by the combination of ventrally fused urogomphi with a single pointed apex, 1-2 upper vertical setae, more than 4 metanotal setae and weakly developed lateral tubercles with 1-3 setae.



Figs. 31-33. ♂ *Trochalodes* nr *hemisphaerica.* **31**, left side, dorsal. **32**, head, anterior. **33**, apex abdomen, ventral. Scale = 1 mm.



Figs. 34-37. ♂ *Novacastria nothofagi.* **34**, dorsum, left side. **35**, head, anterior. **36-37**, apex of venter of ♂ and ♀. Scale = 1 mm.

Novacastria nothofagi Selman, in Selman and Lowman, 1983
(Figs 34-37)

Material examined: NEW SOUTH WALES: 2♂, 3♀, New England National Park, ix.1980, M. Lowman.

Description: similar to *P. rubiginosa*, but broader and urogomphus simple. *Measurements* (mm.): length 4.2-4.4; head width 1.2-1.3; pronotal width 1.8-2.1. *Head.* Setae: 1-(2) upper vertex, 2 vertex, 1 ocular, 2 lateral frons, (0)-1 upper frons. *Thorax.* Pronotum: 25-31 setae, distributed as *P. rubiginosa.* Mesonotum: 3-5 setae. Metanotum: 5-7 setae. Legs: all femora with 3 preapical setae. *Abdomen:* each of tergites I-VI with (2)-5 central setae each side, without subsidiaries, 1-2 spiracular setae, and 2 lateral tubercle setae (frequently only 1 on tergite I); tergite VII with 5-6 marginal setae; tergite VIII with 4-5 setae; tergite IX produced as an elongate triangular process with a single sclerotized apex; sternite VIII of ♀ large with a midline groove, of ♂ small and simple; spiracles distinct and slightly raised on tergites I-VI.

DISCUSSION

Kimoto (1962a) discovered a correlation between pupal and larval characters of Japanese Chrysomelinae and used this in a new classification of the subfamily. He divided the subfamily into two by the presence or absence of a row of eversible glands in the larvae. Each subdivision was further divided according to characteristics of both larvae and pupae. His pupal types were defined on the basis of urogomphal structure. Only 3 of his genus-groups (all of which belonged to the assemblage of larvae without lateral glands) had pupae with urogomphi on tergite IX: *Chrysolina*-group (Doryphorina + Chrysolinina *sensu* Daccordi, 1982; single projection), *Gonioctena*-group (Gonioctenina + Chrysomelina partim, *sensu* Daccordi, 1982; pair of free-standing projections), and *Potaninia*-group (Entomoscelina, *sensu* Daccordi, 1982; pair bent inwards at the base). The only paropsine pupa to have been associated with this classification belongs to *Paropsides* which Takizawa (1976) placed in the *Paropsis*-group (Paropsina, *sensu* Daccordi, 1982), near the *Gonioctena*-group, using larval characters. Pupae of these 2 groups were distinguished by him by the possession of a single urogomphus in the *Paropsis*-group. However the pupa of *Paropsides* was first described and illustrated by Ohno (1958) who clearly showed that the apex of tergite IX consisted of a pair of contiguous processes. Ohno considered the similarities of the larva and pupa of *Paropsides* to those of *Gonioctena* Chevrolat (= *Phytodecta* Kirby) to be sufficient to negate their placement in separate tribes on the single criterion of elytral epipleuron shape (Weise, 1915).

The only descriptions of Australian paropsine pupae are very brief. Cumpston (1939) noted that the pupa of *Paropsis atomaria* (= *reticulata* auctt.) had a 'ventral bilobed dark brown shield', presumably referring to segment IX. This structure was also recorded for *P. obsoleta* but was not mentioned in her descriptions (of colour) of pupae of *Paropsisterna* Motschulsky and *Chrysophtharta* Weise.

Discrimination of the subtribes Dicranosternina and Paropsina

The combination of large size, feeble development of the lateral tubercles, dense transverse bands of setae and adjacent but apically separated urogomphi distinguishes the pupae of Dicranosternina from Paropsina and other Chrysomelinae. The similarity of the pupa of *Dicranosterna* to *Trochalodes* is not surprising because these two genera are poorly differentiated as adults. They may be synonymous, although from the material to hand they are also distinguishable as larvae, and it is possible that the presence of tibial setae, unique in Chrysomelinae, is a generic characteristic of *Dicranosterna.*

The subtribe Paropsina is not well characterized as a monophyletic group because it is morphologically diverse. For example, the urogomphi are either completely fused or adjacent but ventrally free and separated at tips. The lateral tubercles are prominent, but variably setose. The distribution of setae is variable. Some pupae are similar to those of Dicranosternina (for example in urogomphi), but without an outgroup for comparison it is not known if this similarity is phylogenetically significant. The pupae of Paropsina may be divided into 2 distinct groups, and these are considered further below.

Discrimination of groups of genera in Paropsina

The pupae of the genera of Paropsina considered here appear to show a sequence of progressive setal diversity, from the few, non-spinulose, setae of *Pyrgoides hamadryas* and allies to the numerous secondary, and in the anal region, spinulose, setae of *Paropsisterna.* This sequence is to some extent correlated with both size and development of lateral tubercles, and is negatively correlated with fusion of the 2 urogomphi. However, setal development and fusion of urogomphi are quite different in the similar-sized pupae of *Pyrgoides rubiginosa* and *Paropsides* and this suggests that these attributes are of phylogenetic significance. The primary division of the Paropsina genera may therefore be pupae with: (a) simple setal pattern, no spinulose setae on apical sternites and fused urogomphi (species of *Pyrgoides*); or, (b) numerous secondary setae, spinulose setae on apical sternites and a pair of adjacent but distinct urogomphi (*Chrysophtharta, Paropsides, Paropsis, Paropsisterna* and *Trachymela*).

Pyrgoides species

Two forms of pupa are distinguishable: larger, with incompletely fused urogomphi and a few secondary setae (*P. rubiginosa*), or smaller, with completely fused, apically pointed, urogomphi and simple setal pattern (*P. hamadryas* and allies). These differences may be correlated with size.

Chrysophtharta, Paropsides, Paropsis, Paropsisterna and *Trachyrnela*

In this group, there is a range of variation from the relatively less setose, laterally weakly tuberculate, small pupae of *Paropsides*, to the densely setose, strongly tuberculate, large pupae of *Paropsisterna.* The pupae of *Paropsis* and *Paropsisterna* are distinguished by shared possession of strongly developed spiracular tubercles, patches of small setae at the sides of sternite VI, and the strongly sclerotized apex of sternite VII. The pupae of *Chrysophtharta* and *Trachymela* are morphologically intermediate between *Paropsides* and *Paropsis.*

The features characteristic of this group of genera are also present in *Paropsides duodecimpustulata* Gebler (Ohno 1958, the pupal description appears to be of a ♂), the Asian type species of *Paropsides.* This species differs from its Australian congener by having more numerous setae on the vertex, lateral tubercles and femoral apices, and therefore appears more similar to Australian genera other than the species currently placed in *Paropsides.*

Position of Novacastria

Pupae of *Pyrgoides* and *Novacastria* are similar to each other and are characterized by: small size; few setae, on raised tubercles, including only 2 pairs of vertical setae and less than 6 pairs of central abdominal tergite setae; spiracular tubercles absent and lateral tubercles weakly developed with 3 or less setae; posterior margins of sternites VII and VIII simple, without specialized setae or ridges; abdominal segments VIII-X fused, difficult to distinguish; tergite IX produced into a single process, sclerotized only at tip, sometimes bifid; sexual dimorphism poorly indicated, sternite VIII with a medial groove in ♀ but simple and apparently smaller in ♂.

The pupa of *N. nothofagi* differs from those of all *Pyrgoides* spp. by having upper vertical setae and more metanotal setae. The pupa of *P. rubiginosa* may be distinguished from those of other *Pyrgoides* spp. and *Novacastria* by the bifid urogomphus.

Possession of paired, basally fused urogomphi was regarded by Selman and Lowman (1983) as characteristic of paropsine pupae (e.g. *Paropsisterna*) in contrast to a single urogomphus (*Novacastria*) or a pair of separated urogomphi (*Calomela* Hope). These authors placed *Calomela* in the *Chrysolina*-group and *Novacastria* in the *Gonioctena*-group of Kimoto, although the pupal urogomphi suggest the reverse. They considered the paropsines to be intermediate between these two groups. *Novacastria* was not considered to be a paropsine because of the single pupal urogomphus, which is now shown to be present in *Pyrgoides* species, and the unrecessed epipleurae. In *Novacastria* the epipleurae slope upwards slightly, especially by the humeri. In *P. rubiginosa* and related species the epipleurae slope upwards at no more than 45°. This single character of the epipleuron is the only criterion for the separation of Gonioctenini (*sensu* Weise, 1915) and Paropsini, and was implicitly rejected by Ohno (1958). The larva (Selman and Lowman, 1983), adult and pupa of *N. nothofagi* are similar to various paropsine species. These similarities suggest that the genus *Novacastria* may be better placed in the subtribe Paropsina.

Pupal Characters and Phylogeny

Structure of the urogomphi of tergite IX is a key element in the subdivision of the Chrysomelinae using pupal characters. A pair of separate urogomphi on tergite IX appears to be the plesiomorphic state within the Chrysomeloidea, with wide occurrence in both Cerambycidae (Duffy, 1952) and Chrysomelidae (eg. Takizawa, 1972; LeSage, 1984; Reid, 1991). Urogomphi are absent from the 'glanduliferous' Chrysomelinae (Kimoto, 1962a), but the pupa of the plesiomorphic genus *Timarcha* Latreille (not considered by Kimoto) has a single urogomphus with a bifid apex (Paterson, 1931). The single (ie. completely fused pair) urogomphus of *Pyrgoides* spp. and *N. nothofagi* may not be homologous with the single urogomphus of the *Chrysolina*-subgroup of genera, because in the latter, at least in *Leptinotarsa* Stål (Doryphorina, *sensu* Daccordi, 1982; specimens seen in ANIC), the whole structure is strongly sclerotized and ridged at the base. The form of urogomphi with fusion of the processes dorsally but separation ventrally, as described here for Paropsina and Dicranosternina, appears to be unique to these subtribes.

The toothed and setose mandibular thecae of the pupa of *Johannica* Blackburn was recently considered to be unique to that genus in the Chrysomelinae (Reid, 1991). The mandibular theca is conspicuously toothed in *Chrysophtharta*, *Paropsis* and *Trachymela* and in other genera the tooth is present but less distinct. One pupa of *Trachymela* had a mandibular seta. These possibly plesiomorphic characters are evidently widespread in Chrysomelinae and may have little phylogenetic importance.

The presence of lateral tubercles is widespread in the Chrysomelidae (Paterson, 1931), although absent from the 'glanduliferous' chrysomelines (Kimoto, 1962a). The condyliform type is only known from Paropsina in the Chrysomelidae. Spiracular tubercles are rarely indicated in descriptions but are apparently present in *Gonioctena* (Takizawa, 1976) and *Chrysolina* (Kimoto, 1962b).

The number of apical femoral setae is variable in the sample of genera described here, although each species generally has 3 or less or 4 or more femoral setae. The plesiomorphic number of setae is probably 3, as this occurs widely in Chrysomelidae and Curculionoidea (Takizawa, 1972; Costa, Vanin and Casari-Chen, 1988). However, the variation between individual femora is so high that this character has only limited use in phylogenetic analyses. The derived state of more than 3 femoral setae is found in all genera except *Pyrgoides*, *Paropsides* and *Novacastria*.

The large pupae of the 'non-glanduliferous' genera of Japan (Kimoto, 1962b) are mostly very setose, with setose abdominal tubercles, similar to *Paropsis*. However pupae of the 'glanduliferous' genera (Kimoto, 1962a) always have few setae, similar to *Pyrgoides* and *Novacastria*, despite great variation in size. This reduced setal pattern is widespread in the Chrysomelidae generally (Paterson, 1931; Takizawa, 1972; LeSage, 1984), and may represent the plesiomorphic condition for the paropsines, but it is difficult to be sure that the patterns are homologous.

Pupal sexual dimorphism has been described for pupae of *Paropsis* (Reid and Ohmart, 1989), *Colaphellus* Weise (Brovdii, 1977) and *Johannica* (Reid, 1991) in the Chrysomelinae, and for Cerambycidae (Duffy, 1952). In the three latter examples the female is characterized by sternite IX being represented by two prominent tubercles. The sexually dimorphic structure of the abdominal apex described above for the pupae of Paropsina and Dicranosternina appears to be restricted to these groups.

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TROPICAL SCALLOP FOUND IN JERVIS BAY, NEW SOUTH WALES

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An unusual capture of a tropical saucer scallop *Amusium japonicum balloti* (Bernardi, 1861) has been made by divers, from the Fisheries Research Institute, in the waters of Jervis Bay, New South Wales.

The normal Australian range of saucer scallops is reported as extending from Hervey Bay in southern Queensland, northward around tropical Australia to Esperance on the south coast of Western Australia (Young and Martin, 1989). Commercial fisheries for saucer scallops are located offshore from Townsville and Bundaberg in Queensland, as well as the Abrolhos Islands and Shark Bay in Western Australia.

The collection of *Amusium japonicum balloti* from Jervis Bay is the farthest south that this species has been recorded. The southernmost occurrence of *A. japonicum balloti* was previously recorded as Port Jackson by the Australian Museum (Iredale and McMichael, 1962; Loch, 1990, pers. comm.).

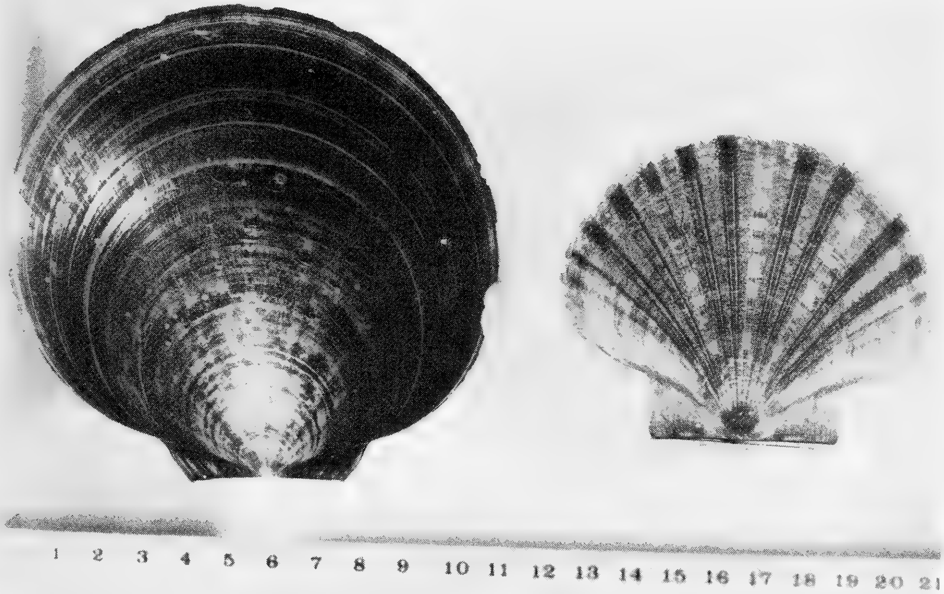

Fig. 1. The saucer scallop *(Amusium japonicum balloti)* on left with a commercial scallop *(Pecten fumatus)* on right — both collected in Jervis Bay, N.S.W.

The saucer scallop was captured in 17 metres of water on 13th November 1990 while SCUBA divers were collecting the commercial scallop *Pecten fumatus* (Reeve, 1852) off Murrays Beach, Jervis Bay (35°07′S, 151°45′E). In this area the substratum is sandy with algae and polychaete hummocks. The shape (Fig. 1) and colour of the scallop was normal for this species. The upper valve was dark reddish brown and the lower valve white flecked with brown. The specimen had a shell height of 103 mm and weighed 110.2 g. Maximum size and weight of this species are reported as 116 mm and 110.0 g, and the maximum age (based on tagging and length frequency) is three years (Heald and Caputi, 1981).

The saucer scallop found at Jervis Bay is 1300 kms south of Hervey Bay. The adult scallop is not capable of moving large distances; however, this occurrence so far from the tropics may be related to current patterns. The pelagic larvae may have been transported down the Queensland and New South Wales coasts by the East Australian Current (EAC). This dispersal is feasible as *Amusium* larvae have a 20 day pelagic phase; an average southward current of 1.7 knots would carry the larvae from Hervey Bay to Jervis Bay in 20 days. The velocity of the EAC and its eddies has been recorded as varying between 0.15 and 4.0 knots (Rochford, 1975). Alternatively, the scallop may have been spawned from an unknown saucer scallop, or bed of saucer scallops, existing in southern Queensland or New South Wales waters. The settlement and survival of a larva to grow into an adult saucer scallop 2-3 years old suggests that favourable environmental conditions have occurred in Jervis Bay in recent years for a tropical species.

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Notes and Discussion

OCCURRENCE OF A NEOSILURID CATFISH (*NEOSILURUS* SP.) IN THE PAROO RIVER, MURRAY-DARLING BASIN

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In April 1991, forty seven plotosid catfish were caught in 40 mm stretch-mesh gill nets in Mullawoolka Basin (143°45′S, 30°30′E), an ephemeral lake on the flood plain of the Paroo River near its junction with the Darling River, in north-western New South Wales (Fig. 1). Specimens of this plotosid were found at all four sites sampled in Mullawoolka Basin, although they were most common at the site in Tongo Creek, where 33 fish were caught. In comparison, ≤4 individuals were caught for the same effort at each of the remaining sites in the lake.

The series collected included a substantial size range; total lengths ranged from 115-195 mm (mean 172 mm, s.e. ±1.9 mm), and weights from 15-58 g (mean 33.2 g, s.e. ±1.3 g). The colouration of these fish was light brown dorsally, with silver sides becoming paler ventrally. All fins were yellow. Four representative specimens were fixed in 10% formalin then preserved in 70% ethanol and lodged in the Western Australian Museum collection (WAM P.30299-001).

On examination this catfish was identified as a member of the genus *Neosilurus*, however, a specific epithet has not been used for two reasons. Firstly, there is considerable confusion about the status of various species of Australian eel-tailed catfish (Plotosidae) — especially the *Neosilurus* group. Secondly, the family is presently under review (Allen, 1991, pers. comm.).

Neosilurids have now been reported from the Condamine system (Lake, 1978; Leggett, 1988), Warrego River (Unmack, 1991, pers. comm.) and an upper Paroo tributary (Leggett, 1991, pers. comm.); however, species identifications have been tentative and few reference specimens retained. This capture marks a range extension for the species group within the Murray-Darling system. The Paroo River is the most north-westerly Darling tributary and only flows periodically into the Darling following major flooding — such as that occurring in 1990 and 1991.

Two *Neosilurus* species have similar broad distributions over the northern Australian drainages (Indian Ocean, Timor Sea, Gulf of Carpentaria, North-east Coast) and from the inland catchment of the Lake Eyre drainage division (Merrick and Schmida, 1984). Neither *Neosilurus hyrtlii* (Steindachner, 1867) nor *N. glencoensis* (Rendahl, 1992) — considered a synonym of *N. hyrtlii* by Allen (1989) — has been positively identified as occurring within the Murray-Darling catchment, although Lake (1978) did report that specimens of a plotosid catfish captured by Hamar Midgley in 1975 from the Condamine River, could have been *N. hyrtlii.*

N. hyrtlii and *Neosilurus ater* in the Ross River, Queensland, were demonstrated to be lithophilic flood-spawners; they migrate upstream into ephemeral rain-fed creeks during periods of high flow to lay demersal eggs freely into a gravel substrate (Orr and Milward, 1984). Tongo Creek, which is usually dry, flowed briefly after rainfall of 55 and 81 mm averaged over the Paroo catchment, which fell during a few days in January and February 1991 (National Climate Centre data). However, this creek had ceased to flow before the sampling period in April.

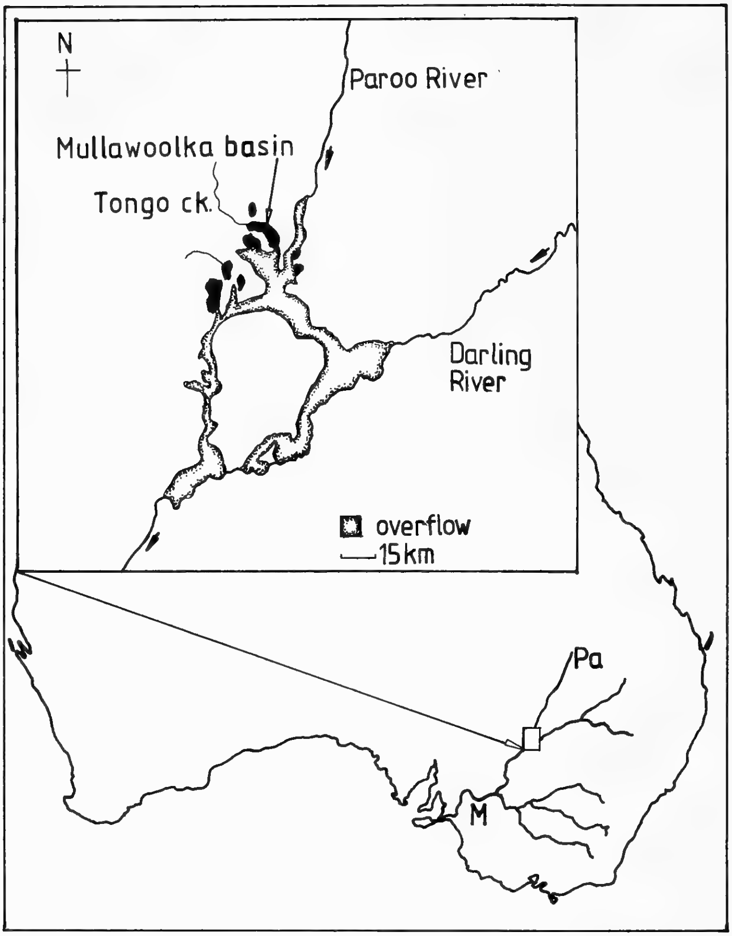

Fig. 1. Collection site for *Neosilurus* sp; the Paroo River (Pa), a second order tributary of the Murray River (M). Inset: Mullawoolka Basin and Tongo Creek showing their relationship with the Paroo River overflow and the Darling River.

Ovaries from the four specimens examined from Tongo Creek were small (gonadosomatic index <1), flaccid, and contained a few large oocytes within a large lumen — a typical post-spawning condition. This evidence suggests that the *Neosilurus* sp. in Tongo Creek may have spawned in response to flood conditions as Orr and Milward (1984) found for the Ross River population of *N. hyrtlii.*

All preserved specimens of *Neosilurus* sp. examined had infestations of a copepod parasite, *Lernaea* sp., as did the sympatric population of golden perch, *Macquaria ambigua*, and spangled perch, *Leiopotherapon unicolor.*

ACKNOWLEDGEMENTS

I am grateful for the practical assistance of Les Rava, and for the help of Dr Gerry Allen of the Western Australian Museum and Sally Reader of the Australian Museum. Thanks also to Dr Peter Gehrke and Dr Dave Pollard for helpful comments during preparation of the manuscript. Ray Leggett (Caboolture, Queensland) and Peter

Unmack (Doncaster, Victoria) are also thanked for unpublished information based on field collecting in the area.

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ADVICE TO AUTHORS

The Linnean Society of New South Wales publishes in its *Proceedings* original papers and review articles dealing with biological and earth sciences. Papers of general significance are preferred but useful works of more limited nature are acceptable.

Manuscripts from non-members must be communicated by a member of the Society and are accepted on the understanding that papers by members may be given priority.

The original and two copies of the manuscript should be sent to the Secretary, Linnean Society of New South Wales, PO Box 457, Milsons Point, New South Wales 2061 Australia.

Member authors are supplied with 25 free offprints. Additional copies may be purchased if ordered when proofs are returned.

Donations to the cost of publication are most welcome and in the case of lengthy papers contributions from authors, especially those who are not members, may be requested by Council.

On publication, a paper and its copyright belong to the Society. Requests to use copyright material must be directed to the Secretary.

PREPARATION OF MANUSCRIPTS

Copy must be typewritten, double-spaced, on one side of A4 (210 x 297 mm) paper with a margin of not less than 25 mm all round. Pages should be numbered in sequence and fastened together. The desired position for figures and tables should be indicated in the margin. The Botanical and Zoological Codes of Nomenclature must be followed. Generic and specific names must be clearly underlined or be in italics and must be given in full with authorities when first used but may be abbreviated subsequently if there is no ambiguity.

Papers should be written in clear, concise English and spelling should conform to that preferred by the *Oxford English Dictionary*.

The general layout of a paper should conform to the following scheme:

1. Title and author's name — all in capitals.
2. A concise Abstract, complete in not more than 200 words.
3. No more than seven key words.
4. Main text. Footnotes should be avoided. Headings and subheadings may be used where they assist in understanding the paper.
5. References. These should be cited in the text by author's name and year of publication, *e.g.* Bullough (1939) or (Bullough, 1939) according to context. Papers should be listed under *References* as follows (giving journal titles in full):

   Bullough, W. S. 1939. A study of the reproductive cycle of the minnow in relation to environment. *Proceedings of the Zoological Society of London, Series A* 109: 79-108.

   If more than one work is published by the same author in the same year, use a, b, *etc* after the year in the text and in the list of references.
   Books should be listed as follows:
   Rees, A. R. 1972. *The Growth of Bulbs*. Academic Press, London.
   Chapters in books should be listed as follows:

   Cocking, E. C. and Evans, P. K. 1977. The isolation of protoplasts. *In:* Street, H. E. (ed.). *Plant Tissue Culture and Cell Structure*. Second edition. Chapter 1, pp. 103-135. Blackwell Press, Oxford.

Illustrations are marked as figures. Legends for illustrations should be typed on separate sheets. The maximum printed dimension for a set of figures and associated legends will normally be 125 x 200 mm. Figures and labels must be designed to give clear images at this size. Where possible, a linear scale, with dimensions clearly marked, should be added rather than making the assumption that a statement of scale in the legend will be correct after plate-making.

All line drawings should be in ink on a suitable surface; high quality laser printed charts and figures are also acceptable. Authors should supply good quality, high-contrast glossy photographs of the illustrations at the scale intended for printing. Each illustration should have the author's name, figure number and orientation indicated in pencil on the back.

Tables should be submitted in clear form on separate sheets and, like illustrations, should be designed to fit on a single page.

Authors should ensure that all omissions and errors that can be checked against original manuscripts are corrected at proof stage. A charge may be made for alterations or errors for which the author is responsible.

Annexure to *Proceedings* Vol. 113

THE LINNEAN SOCIETY OF NEW SOUTH WALES

RECORD OF THE ANNUAL GENERAL MEETING, 1989

The one hundred and fourteenth Annual General Meeting was held in the J. H. Maiden Theatre, Royal Botanic Gardens, Sydney, on Wednesday, 22nd March, 1989, at 6.00 p.m.

The President, Professor T. G. Vallance, occupied the Chair. The minutes of the one hundred and thirteenth Annual General Meeting were taken as read and adopted by the meeting.

REPORT ON THE AFFAIRS OF THE SOCIETY FOR THE YEAR 1988-89

Publications

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

Volume 110, Nos 1 & 2	July, 1988
Volume 110, Nos 3 & 4	January, 1989

During this year, Professor Vallance continued to act as Honorary Editor of the *Proceedings*. After serving the Society in this capacity for the last ten years, Professor Vallance has retired with the beginning of Volume 111. A member of the Society's Council, Dr J. R. Merrick, has agreed to take on the duties of Hon. Editor and will see Volume 111 through the press.

Back issues of the *Proceedings* have been sold at bargain prices throughout the year with a return to the Society of over $10,000. As orders are still being received and some issues are still in stock, we intend to advertize them once more before disposing of the remainder.

Newsletter

Dr Helene Martin continued to produce the quarterly newsletter which is sent to all members. It includes details of our programme, summaries of some lectures, reports of Council resolutions, titles and authors of papers accepted for publication in the *Proceedings*, details of research grants, news of meetings of other organizations with similar concerns and other items of interest to our members.

Membership

On March 21st we had 240 Ordinary Members and 20 Associate Members, making a total of 260 members.

We record with regret the death during the year of the following members:

Dr L. R. Richardson, member since 1967, died on 6th September, 1988.

Professor F. V. Mercer, member since 1944, died on 2nd December, 1988.

Mr T. G. Campbell, member since 1927, died during 1988.

Meetings

All meetings this year were held at the Royal Botanic Gardens, Sydney, by kind permission of the Director, Professor T. C. Chambers.

Our first general meeting for the year, in June, was addressed by Mr Alan Andrews, a member of the Society's Council. His topic was 'Major Mitchell's Map of the Colony of New South Wales'.

In October, Dr Bob Wagner, Visiting Fellow, Department of Geology, University of Newcastle, spoke on the topic 'Carboniferous and Permian Floral Distribution'.

In November, Dr John Cairney, School of Biological Science, University of New South Wales, gave a talk with the intriguing title 'When I grow up, I am going to be a Toadstool . . . I hope'.

Our customary informal luncheon for members and friends was held this year on 15th March, before the Monthly Council Meeting.

The Joyce W. Vickery Scientific Research Fund

Seventeen grants, totalling $6,782, were awarded this year. Details were recorded in Newsletter No. 49, in September.

Linnean Macleay Fellowship

It was decided at the Council meeting held in December, 1988, that Miss Julia Hush be re-appointed as the Fellow for 1989 in view of the recommendation from her Supervisor and our Fellowships Committee.

Office

The Society's office continues to operate from 6/24 Cliff Street, Milson's Point, and is open from 9.30 a.m. every Tuesday. The telephone number is (02) 929 0253.

Linnean Macleay Lectureship in Microbiology

Dr Cho's research project this year was concerned with the lipid metabolism of edible mushrooms. Lipids were shown to stimulate greatly both the yield of mycelium and sporophore. The incorporation of lipids into protein rich slow release mushroom supplement would further enhance mushroom yield. His work was financed by a grant from the Oilseed Research Council and two grants from the Rural Credits Development Fund.

In July, 1989, Dr Cho was invited to speak at an International Symposium on the biotechnology of shiitake cultivation.

PRESIDENTIAL ADDRESS

The President, Professor T. G. Vallance, delivered an address entitled 'Jupiter Botanicus in the Bush: Robert Brown's Australian field-work, 1801-5'.

Synopsis

Every serious student of Nature in Australia knows of Robert Brown (1773-1858), the naturalist with Matthew Flinders on H.M.S. *Investigator.* Some, in particular systematic botanists, will have read his published writings on Australian plants, perhaps even studied his specimens preserved in the British Museum (Natural History). Among those specimens are types of many of our taxa, yet all too frequently with them there arise problems about collecting localities. In short, despite Brown's acknowledged fame in science and the recognized significance of his collections, where he went in Australia and where he collected have been known as a rule in pretty vague terms.

This problem of 'where' in Brown's travels was addressed by the late Nancy Burbidge in our *Proceedings* in 1956 but although her survey was titled 'Robert Brown's Australian Collecting Localities' it embraced only stations visited from *Investigator*, as well, unfortunately, as a number not visited. The Burbidge list is, in fact, simply a key to the geographical notation devised by Flinders during the voyage. There is no detail about routes of shore excursions from the ship or indeed anything about travel after Brown and the artist Ferdinand Bauer were permitted to stay in the colony following the de-commissioning of *Investigator* and Flinders' departure in 1803. To this later period belong Brown's visits to Tasmania and the Hunter River as well as extended work about Sydney, on occasion with George Caley, until he eventually left Australia on a revived *Investigator* 23 May 1805.

Division of the *Investigator* voyage into two quite distinct parts and the equally-unplanned colonial intermission (1803-5) for Brown and Bauer no doubt contributed to the confused record. So also did the death of Brown's loyal assistant, the gardener Peter Good, in June 1803; Good had been a consistently-careful note-taker. But Brown also kept a Diary, of sorts, from the time he left London (14 June 1801) until 4 November 1804. This document, in places cryptic and often hastily compiled, has long been known but a complete reading of it has only recently been achieved. An annotated version is now nearing readiness for publication. Annotation of the work has been certainly necessary; at intervals throughout his record Brown confuses days, even years. Similar vagaries exist among his notes on specimen labels. Fixing Brown's lapses during the time he was with Flinders and Good is usually a straightforward matter. Thereafter, the task of tracing and confirming the naturalist's activities becomes more complex, and more dependent on scattered records. Nevertheless, a chronological scheme for almost all of Brown's time in Australia has been pieced together. With the agreement of my two London colleagues in the Diary work, I propose in this address to draw on our findings and to indicate what we make of Brown's travels in Australia with the aid of maps prepared for the Diary publication.

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 1989-90.

President — Dr P. J. Myerscough
Members of Council — Dr R. J. King
Professor T. C. Chambers
Mr A. E. J. Andrews
Dr P. J. Myerscough
Dr J. R. Merrick
Dr I. G. Percival
Auditor — W. Sinclair & Co.

LINNEAN SOCIETY OF NEW SOUTH WALES

GENERAL ACCOUNT

Balance Sheet as at 31st December, 1988

1987 $		$	$
	Accumulated Funds –		
	Balance 1st January, 1988		255,429.68
	Add: Surplus for Year		1,407.54
			256,837.22
	Less: Transfer to Fellowship Account	15,000.00	
	Decrease in Value of Assets	110.14	15,110.14
255,430	Balance at 31st December, 1988		241,727.08
677	Library Fund		2,177.00
1,142	Reserve – Bookbinding		1,142.66
	Sundry Creditors		1,000.00
$257,249			$246,046.74

1987 $		$	$
	Fixed Assets –		
	Furniture, Fixtures and Fittings – At Cost	1,947.91	
892	*Less* Depreciation written off	1,122.37	825.54
	Office Machines – At Cost	4,943.88	
2,488	*Less* Depreciation written off	2,828.88	2,115.00
3,380	Total Fixed Assets		2,940.54
	Investments –		
20,526	Australian Savings Bonds	20,526.00	
8,000	N.S.W. Treasury Corp. – inscribed stock	8,000.00	
	Debentures –		
5,000	Australian Guarantee Corp. Ltd.	7,390.00	
59,300	Custom Credit	59,300.00	
–	Elders Lensworth Finance Corp.	42,500.00	
13,700	Esanda Ltd	13,700.00	
	Deposits –		
25	Advance Bank Australia Ltd.	26.38	
	Bank of New Zealand	70,359.73	
	Mercantile Mutual Finance Corp.	5,184.68	
118,058	Westpac Banking Corp.	–	
224,609	Total Investments		226,986.79
	Current Assets –		
1,519	Sundry Debtors	1,059.64	
27,591	Cash at Bank	14,909.77	
150	Deposit	150.00	
29,260	Total current assets		16,119.41
$257,249	Total assets		$246,046.74

LINNEAN SOCIETY OF NEW SOUTH WALES

Income & Expenditure Account for the Twelve Months ended 31st December, 1988

1987 $	EXPENDITURE	$	$
950	Audit Fees	1,000.00	
139	Bank Charges	74.10	
503	Depreciation	440.00	
856	General Expenses	203.86	
170	Insurance	278.30	
212	Light and Power	191.98	
227	Newsletter Expenses	—	
1,650	Postage	2,295.56	
7,672	Proceedings — Printing Costs	24,443.27	
1,272	Printing and Stationery	511.01	
4,995	Rent	5,015.00	
60	Photocopying Expenses	—	
6,279	Salaries	12,099.36	
2,927	Secretarial Services	3,043.32	
319	Telephone	310.73	
$28,231	Total Expenditure		$49,906.49
$22,867	Surplus for Year Transferred to Accumulated Funds		$1,407.54

1987 $	INCOME	$	$
	Subscriptions —		
2,387	Members	1,970.50	
6,125	Proceedings	7.740.64	
8,512			9,711.14
23,340	Interest Received		18,969.57
	Fellowships Account —		
10,271	Surplus Income for the year ended 31st December, 1988		16,760.35
	Reprint Sales		
819	General	778.00	
481	Polychaete	175.00	953.00
7,675	Sales — back issues		4,919.97
$51,098	Total Income		$51,314.03

AUDITOR'S REPORT

We have audited the Books and Records of the Linnean Society of New South Wales for the twelve months ended 31st December, 1988 and are of the opinion that the accompanying Balance Sheet and Income and Expenditure Account correctly sets forth the position of the financial affairs as at 31st December, 1988 according to the explanations given to us and as disclosed by the Books of the Society.

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

Dated at Sydney this fourth day of May, 1989.

I. PERCIVAL
Hon. Treasurer.
4th May, 1989.

LINNEAN SOCIETY OF NEW SOUTH WALES

LINNEAN MACLEAY FELLOWSHIPS ACCOUNT

Balance Sheet as at 31st December, 1988

1987 $		$	$	1987 $		$
	Accumulated Funds—				Investments—	
	Balance 1st January, 1988			5,132	Australian Savings Bonds	5,131.50
	Amount bequeathed by Sir William Macleay	7,000.00		55,300	N.S.W. Premier State Bonds	55,300.00
	Transfers from Income Account	59,873.10			Debentures—	
	Increase in Value of Assets	384.32	130,257.42	5,000	Beneficial Finance Corp. Ltd.	5,000.00
	Less Adjustment in Assets Values		1,200.06	200	British Petroleum Co. Aust. Ltd.	200.00
			129,057.36	700	Custom Credit Corp. Ltd.	700.00
129,057				18,800	Esanda Ltd.	18,800.00
	Add Increase in Assets	214.66		35,400	Australian Guarantee Corp. Ltd.	35,400.00
	Transfer from General Account	15,000.00	15,214.66	–	Elders Lensworth Finance Ltd.	5,000.00
$129,057	Balance 31st December, 1988		$144,272.02		Deposits—	
				2,859	St. George Building Soc. Ltd	12,033.30
				666	Advance Bank of Aust. Ltd.	6,707.22
				5,000	Westpac Banking Corp.	–
				$129,057	Total Investments	$144,272.02

Income and Expenditure Account for the Twelve Months ended 31st December, 1988

3,200	Salaries	3,200.04	13,472	Interest Received	19,960.39
$10,272	Surplus for Year Transferred to General Account	$16,760.35			

AUDITOR'S REPORT

We have audited the Books and Records of the Linnean Society of New South Wales for the twelve months ended 31st December, 1988 and are of the opinion that the accompanying Balance Sheet and Income and Expenditure Account correctly sets forth the position of the financial affairs of the Linnean Macleay Fellowships Account as at 31st December, 1988 according to the explanations given to us and as disclosed by the Books of the Society.

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

I. PERCIVAL.
Hon. Treasurer.
4th May, 1989.

Dated at Sydney this fourth day of May, 1989.

LINNEAN SOCIETY OF NEW SOUTH WALES

BACTERIOLOGY ACCOUNT

Balance Sheet as at 31st December, 1988

1987 $		$	$
	Accumulated Funds—		
	Amount bequeathed by Sir William Macleay	24,000.00	
36,900	Transfers from Income Account	12,900.00	36,900.00
	Macleay Lecturer in Microbiology Reserve—		
	Balance 1st January, 1988	5,634.66	
	Add Interest	5,018.00	
5,635	Balance 31st December, 1988		10,652.66
$42,535			$47,552.66

1987 $			$
	Investments—		
	Deposits		
26,900	N.S.W. Premier State Bonds		26,900.00
—	St. George Building Soc. Ltd.		4,500.00
485	Advance Bank Australia Ltd.		484.64
	Debentures—		
8,590	Australian Guarantee Corp. Ltd.		8,590.00
200	British Petroleum Co. Aust. Ltd.		200.00
1,600	Esanda Ltd.		1,600.00
37,775	Total Investments		42,274.64
	Currents Assets—		
4,715	Cash at Bank	5,233.28	
45	Sundry Debtors	44.74	
4,760	Total Current Assets		5,278.02
$42,535			$47,552.66

AUDITOR'S REPORT

We have audited the Books and Records of the Linnean Society of New South Wales for the twelve months ended 31st December, 1988 and are of the opinion that the accompanying Balance Sheet correctly sets forth the position of the financial affairs of the Bacteriology Account as at 31st December, 1988 according to the explanations given to us and as disclosed by the Books of the Society.

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

Dated at Sydney this fourth day of May, 1989.

I. PERCIVAL.
Hon. Treasurer.
4th May, 1989.

LINNEAN SOCIETY OF NEW SOUTH WALES

SCIENTIFIC RESEARCH FUND ACCOUNT

Balance Sheet as at 31st December, 1988

1987 $		$
	Accumulated Funds—	
	Balance 1st January, 1988	92,204.64
	Donation Received	67.00
	Interest Received	13,514.74
	Increase in Value of Assets	929.00
		106,715.38
	Less Research Fund Grants	6,782.00
92,204	Balance at 31st December, 1988	99,933.38

1987 $		$
	Investments—	
5,132	Australian Savings Bonds	5,131.50
20,000	N.S.W. Premier State Bonds	20,000.00
	Debentures—	
17,000	Australian Guarantee Corp. Ltd.	30,529.00
1,200	British Petroleum Aust. Ltd.	1,200.00
18,000	Custom Credit Corp. Ltd.	18,000.00
13,000	Esanda Ltd	13,000.00
—	Elders Lensworth Finance Ltd.	2,500.00
	Deposits—	
15,100	Westpac Banking Corp.	—
165	St. George Building Soc. Ltd.	4,665.29
89,597	Total Investments	95,025.79
	Current Assets—	
2,607	Cash at Bank	4,907.59
$92,204		$99,933.38

AUDITOR'S REPORT

We have audited the Books and Records of the Linnean Society of New South Wales for the twelve months ended 31st December, 1988 and are of the opinion that the accompanying Balance Sheet correctly sets forth the position of the financial affairs of the Scientific Research Fund Account as at 31st December, 1988 according to the explanations given to us and as disclosed by the Books of the Society.

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

I. PERCIVAL.
Hon. Treasurer.
4th May, 1989.

Dated at Sydney this fourth day of May, 1989.

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