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Cover motif: Reconstruction of *Palorchestes* from the paper by B.S. Mackness, page 30 this volume.

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Museum Holdings of the Broad-headed Snake *Hoplocephalus bungaroides* (Squamata: Elapidae)

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The broad-headed snake *Hoplocephalus bungaroides* (Schlegel, 1837) is a highly endangered species endemic to the Sydney basin. We attempted to track down the whereabouts of museum specimens of this snake by contacting mainly Australian, European and North American curators of natural history museums and university herpetological collections. We received replies from 200 institutions, and from these we present details of 159 specimens from 27 museums in 11 countries reported to us as *H. bungaroides*. Countries include Australia (108 specimens), Germany (13), the United States (9), United Kingdom (7), France (4), Belgium (5), the Netherlands (5), Austria (3), Denmark (3), Italy (1), and Switzerland (1). At least 47 specimens are from the 19th Century, and accurate locality records were available for 98 specimens. Obviously, all of the specimens have value insofar as they may provide important biological data that will be useful to researchers working on the future conservation of this snake. Many of these specimens also provide important historical evidence of the species' past distribution.

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KEYWORDS: conservation, distribution, museum, reptile, natural history, Krefft

INTRODUCTION

The broad-headed snake *Hoplocephalus bungaroides* is possibly the most endangered snake in Australia, with research indicating there are serious concerns for its future conservation (Shine and Fitzgerald 1989; Webb and Shine 1997, 1998a,b; Goldingay 1998; Shine et al. 1998; Goldingay and Newell 2000; Webb et al. 2002; Newell and Goldingay 2005). It has a highly restricted distribution within the Sydney basin where it is dependent on habitats characterised by sandstone cliffs, ridges and outcrops (Krefft 1869; Longmore 1989; Cogger 2000; Swan et al. 2004). This species is threatened by habitat loss through urbanisation, removal of bush rock for landscaping and ongoing degradation of rocky habitat caused by hikers and reptile poachers (Hersey 1980; Shine and Fitzgerald 1989; Cogger et al. 1993; Goldingay and Newell 2000; Webb and Shine 1998a, 2000; Newell and Goldingay 2005).

The decline of *H. bungaroides* was noted as early as 1869 by Gerard Krefft (1830-1881), Curator and Secretary of the Australian Museum (Whitley 1961, 1969), in *The Snakes of Australia* (Krefft 1869), the first monograph published on Australian snakes. Krefft (1869) considered *H. bungaroides* (as its junior synonym *Hoplocephalus variegatus*) to be "very local" with specimens found only "in the immediate neighbourhood of Sydney", that is, from Port Jackson to Botany Bay, on the shores of Middle Harbour, and at Lane Cove and Parramatta inlets. Krefft stated that this snake is "not so numerous as they were six or eight years ago" (i.e. around 1861-1863) and the decline was attributed to "their haunts having been invaded by the builder and the gardener". Krefft also stated that "many hundreds" of *H. bungaroides* specimens had been distributed to unnamed "kindred institutions". These statements sparked our curiosity, and subsequently we made considerable effort to locate these specimens. In so doing, we also aimed to gather information on all museum holdings of *H. bungaroides* because this may offer a rich source of data potentially useful to the future conservation of this endangered species.

MATERIALS AND METHODS

We reviewed the annual reports of the Australian Museum for mention of reptile specimens received and exchanged by Krefft during his tenure as Curator and Secretary (1861-1874) (see Appendix 1). We also searched for information in the archives of the Australian Museum, including examination of Krefft's correspondence and the 'Exchange Register' (pre 1874; series 58, Volume 1). Finally, we surveyed other museums and related institutions with herpetological collections, particularly those in Australia, Belgium, Czech Republic, France, Germany, India, Italy, Netherlands, Portugal, Spain, United Kingdom (UK) and the United States (US) since Krefft did send reptile specimens to these countries (Appendix 1). Museums in these and other countries were identified using online directories and also published lists in Leviton et al. (1980, 1985) and Roselaar (2003). Curators or collection managers were asked via email whether there were any *H. bungaroides* (or its synonym *H. variegates*) in their museums. If *H. bungaroides* was present, data were requested on numbers of specimens held; catalogue / registration numbers; collection locality; collector or donor name; collection date; and other details recorded with the specimens. Additionally, photographs of the specimens were requested to confirm that the correct identifications had been made. In relation to photographs, for one museum in France (Musée de Zoologie, Strasbourg) we received reports about two *H. bungaroides* specimens in their collection, but the photographs supplied did not reveal the striking appearance of *H. bungaroides* and we believe they represent the Stephens banded snake *H. stephensii*. We are confident about the identification of all other museum specimens listed, except for those at Zoological Museum, University of Liege (Belgium) because photographs of the five *H. bungaroides* in their collection were not supplied.

RESULTS

The annual reports of the Australian Museum for 1861-1874 did not provide details of "many hundreds" of *H. bungaroides*. Descriptions of species exchanges in these reports lack detail, and indicate, at a minimum, that *H. bungaroides* was definitely sent out to only three places (see Appendix 1). The reports mention that reptiles were shipped to a number of museums and specimen dealers in this period, but the specific composition of the shipments was generally not published. Recipients of Krefft's reptiles included his colleagues in Mauritius (Victor de Robillard) and India (Richard Henry Beddome); one learned society (Royal Society of Tasmania); four specimen 'dealers' - J.C. Puls (Belgium), C.L. Salmin (Hamburg, Germany), Václav Frič (Prague, Czech Republic), and Robert Damon (Weymouth, England); and at least nine museums, i.e. those in Hamburg and Berlin (Germany), Leiden (Netherlands), Madras (=Chennai, India), Milan (Italy), Paris (France), Madrid (Spain), London (UK), and Harvard at Cambridge (US).

The pre-1874 Exchange Register in the Australian Museum archives (series 58, Volume 1) contained some inbound 1860s correspondence addressed to Krefft from dealers such as J.C. Puls and some museums, such as the Muséum National d'Histoire Naturelle, Paris and the Museum of Comparative Zoology, Cambridge. This Register also lists some, but not all, specimens sent on exchange by Krefft and also his predecessor George Bennett. These lists include an entry that a single *H. bungaroides* was sent to the Government Museum at Madras (=Chennai, India) (see Exchange Register p.16). Whilst this list is undated, it was probably the same consignment listed in the annual report for 1864 (see Appendix 1). The Exchange Register also itemised specimens dispatched to the Royal Society of Tasmania and *H. bungaroides* was absent from this list.

By contacting museums directly, we located 159 specimens reported to us as *H. bungaroides* from 28 institutions in 11 countries (Table 1). Most specimens we found are held in Australia (108 specimens), but a considerable number are in Europe (43 specimens) and the US (9 specimens). Negative responses to our email enquiries were received from 174 institutions (see Appendix 2). There were also 74 other institutions that did not respond to our correspondence, despite more than one request (Appendix 2). We have compiled some detailed information on *H. bungaroides* specimens from many institutions in Australia, Europe and the US (see below).

Australian collections

The Australian Museum, Sydney (AM), has 77 *H. bungaroides* specimens (Table 1; Appendix 3) but none of these are designated type specimens (Shea and Sadlier 1999). Eight of these do not have any locality data and another 5 have an imprecise collection locality recorded as "Sydney". There are 18 AM specimens collected at Waterfall, seven at Nowra, five at Long Bay, six at Royal National Park (NP) (including Bundeena), three at the Blue Mountains, three at Woronora Dam and two at La Perouse. Single AM specimen locality records were recorded for 20 locations (Appendix 3). Twenty four (31 %) of the

Table 1: Specimens of *Hoplocephalus bungaroides* held in Australian and overseas museums.

Institution	Code	*n*
Australia		
Australian Museum, Sydney	AM	77
Western Australian Museum, Perth	WAM	3
Museum Victoria, Melbourne	NMV	6
South Australian Museum, Adelaide	SAMA	6
Queensland Museum, Brisbane	QM	4
Northern Territory Museum, Darwin	NTM	4
Australian National Wildlife Collection, Canberra	ANWC	3
Macleay Museum, University of Sydney	MMUS	3
Biological Museum, Australian National University	ANU	2
Austria		
Museum of Natural History, Vienna	NMW	3
Belgium		
Zoological Museum, University of Liege	MZULG	5
Denmark		
Zoological Museum, University of Copenhagen	ZMUC	3
France		
Muséum National d'Histoire Naturelle, Paris	MNHNP	4
Germany		
Museum für Naturkunde, Berlin	ZMB	8
Senckenberg Natural History Museum, Frankfurt	SMF	1
Zoologisches Museum, University of Hamburg	ZMH	2
Zoologische Staatssammlung, Munich	ZSM	2
Italy		
Museo Civico di Storia Naturale, Genoa	MSNG	1
Netherlands		
National Museum of Natural History, Leiden	RHNH	5
Switzerland		
Naturhistorisches Museum, Basel	NMB	1
United Kingdom		
Natural History Museum, London	BMNH	6
Oxford University Museum of Natural History	OUM	1
United States		
Field Museum of Natural History, Chicago	FMNH	2
Museum of Comparative Zoology, Harvard University	MCZ	3
National Museum of Natural History, Smithsonian Institution	USNM	2
San Diego Natural History Museum	SDNHM	1
University of Illinois Museum of Natural History	UIMNH	1
	Total	159

77 AM specimens do not have collection dates, but presumably some of the undated specimens are very old and derive from the late 19th Century (Krefft's era). The collection dates on the remaining 53 range from 1904 to 1996.

The Macleay Museum (MMUS) holds three *H. bungaroides* that all are believed to be from the late 19th Century. One is from "Mount Wilson" but the collector and date are unknown. It was possibly John Anderson or James Cox since both of these zoologists made collections for MMUS in the Mount Wilson area (Fletcher 1929; Stuart Norrington *pers. comm.*). The only information with the two other MMUS specimens is that they were collected on the "coast near Sydney".

Hoplocephalus bungaroides specimens are also held in all other Australian mainland capital cities. The South Australian Museum, Adelaide (SAMA), has 6 specimens recorded on its collection register, but one of these (R00463) is now missing. This misplaced specimen is recorded as collected on 2 June 1915 at La Perouse and donated to the SAMA by the AM. Other SAMA specimens were from Kuringai Chase, Sydney and Woronora River. The Kuringai Chase specimens are reported to us as having been collected by "W. Irvine" in 1967. We enquired with William (Bill) Irvine (a well-known collector who still lives in Sydney) for details about these but he explained that his field notebooks from 40 years ago had now been destroyed. The Queensland Museum, Brisbane (QM), has four specimens: one from Waterfall; one from Nowra that was held in captivity for a period of time (Queensland Reptile Park); one was captive-bred; and another was confiscated by Queensland Parks and Wildlife Service in 1989. In Canberra, three specimens are in the Australian National Wildlife Collection (ANWC): one from about 1963-1964; the other two from around 1978-1980 (J. Wombey *pers. comm.*). Collection localities are not available for any of these. Also in Canberra, the Museum at the Australian National University (ANU) has two specimens: Waterfall and Tiajuara Falls (22 km from Nerriga), although these have no dates or registration numbers. In Darwin, the Northern Territory Museum (NTM) has four specimens all from the 1970s and collected at Heathcote, Jarra Fall (Nowra), and Woronora Dam. In Melbourne, Museum Victoria (NMV) has six specimens. Four of these were registered sometime between 1900 and 1945, but collection dates are not available. Localities are Helensburg, Long Bay, Middle Harbour, and Coast Range at Botany Bay. The Middle Harbour specimen, at least, possibly originated from, or was known to, Krefft because this collection locality was specifically referred to by him (Krefft 1869). Two other specimens in NMV collected in 1975 are from Yal Wal (Nowra) and Royal NP. The Western Australian Museum (WAM) has three specimens, all from Woronora Dam in the 1960s and 70s.

European collections

In Germany, there are four museums with records of 13 *H. bungaroides* specimens. The Museum für Naturkunde, Berlin (ZMB) has eight specimens. Two of these were purchased from "Salmin", a dealer in Hamburg who traded with Krefft. They are undated, but it is known from the Annual Reports that Krefft sent Salmin reptiles in 1866 (see Appendix 1). The ZMB also has three specimens labeled "Krefft" specifically. Another two specimens are from 1867 and donated by Richard Schomburgk (1811-1891). Schomburgk was Director of the Botanical Garden in Adelaide from 1865-1891. None of these seven specimens have specific point localities, i.e. either "Australia", "New South Wales" or "Sydney". The eighth specimen in the ZMB was donated by the Berlin Zoo on 12 September 1913, and the original collector and collection place are unknown. In the Zoologisches Museum, University of Hamburg (ZMH), there are two specimens: one from Krefft; the other with no collector details. These specimens are recorded as from "Sydney" and "Australia" respectively. The single specimen in the Senckenberg Natural History Museum, Frankfurt (SMF), from "eastern Australia" was donated in 1911 by "O. Frank". We have no details on "O. Frank" or any other information on where he found his specimen. The Zoologische Staatssammlung, Munich (ZSM) had two *H. bungaroides* from "New South Wales" registered in 1920 and 1928, but these were destroyed during World War Two (D. Fuchs *pers. comm.*).

Seven specimens were found in the UK. Six are preserved in the Natural History Museum, London (BMNH), and one in the Oxford University Museum of Natural History (OUM). One BMNH specimen was presented by the 'Earl of Derby' in 1847 (see also Günther 1858; Boulenger 1896). This was Edward Smith Stanley (1775-1851), the 13th Earl of Derby. Two specimens in the BMNH derive from 1855. One of these was donated by the Zoological Society of London (ZSL), but the collector of this specimen is unknown. It was possibly John Gould, since he collected many specimens in Australia and also worked for ZSL. The second 1855 specimen is from the "collection of Captain Stokes". This was John Lort Stokes, who was on the *Beagle* surveying expedition to Australia from 1837-1843. There is also a specimen in the BMNH registered 1859 that was presented by

"Dr G. Bennett". This was George Bennett, who was an early Curator of the Australian Museum from 1835-1841, and a Trustee of the Museum from 1853-74. The other two BMNH specimens were purchased from Krefft and were registered on 16 June 1863. The only locality data with these specimens are "New South Wales" or "Australia". The single specimen in the OUM was collected at "Sydney" by Francis Pascoe (1813 - 1893). Pascoe sailed to Australia in the *Buffalo*, captained by John Hindmarsh (first Governor of South Australia). After Pascoe's death his large collection of zoological specimens was presented to the OUM by his daughter in 1909 (M. Nowak-Kemp *pers. comm.*).

In France, the Muséum National d'Histoire Naturelle, Paris (MNHP) has four specimens. One of these (no. 7679) is the type of *Alecto variegata* (a junior synoymn for *H. bungaroides*), with locality given as "Australia", collector/donor as Pierre François Kéraudren. This specimen is referred to by Schlegel (1837), Duméril et al. (1854), and Guibé and Roux-Estève (1972). There is also a specimen from Port Jackson donated by "Quoy and Gaimard" (i.e. Jean René Constant Quoy and Paul Gaimard), collected some time prior to 1829 when these French naturalists visited Australia. The actual location data provided to us are for Middle Head. This specimen is also mentioned by Schlegel (1837), Duméril et al. (1854) and Guibé and Roux-Estève (1972). Another MHNP specimen was collected from "Australia" by the French naturalist/specimen dealer Jules Pierre Verreaux some time in the early 1840s (also in Duméril et al. 1854). According to the MNHP donations book, it was received in December 1846. The fourth MNHP specimen is a skull registered as no. 1991-4163. This specimen has no date, collector or locality details, but it is a different specimen to the above three, and it is believed to be from the same era, i.e. 19th Century (I. Ineich *pers. comm.*).

In Austria, three specimens are preserved in the Museum of Natural History, Vienna (NMW). These are NMW 27699:1-3 and are dated between 1863 and 1877. There are no collector or donor names recorded with any of these, and the original label for these specimens indicates "West Australien" (=Western Australia). Photographs of the specimens supplied to the authors confirmed that the identifications are correct. However, the locality data is certainly erroneous. Other Australian snake specimens in the NMW collection were purchased from the dealer "Gerrard", and it is possible that specimens with confused localities were sold by him, including these three *H. bungaroides* specimens.

In Denmark, three *H. bungaroides* are preserved in the collection of the Zoological Museum, University of Copenhagen (ZMUC). Two of these are dated 1862 and from "Sydney", but no collector details are recorded for either specimen. The third from "Australia" was donated to ZMUC by "Dr Günther" in 1867.

In the Netherlands, the National Museum of Natural History, Leiden (RHNH), has five *H. bungaroides* specimens. One of these from "Nouv. Hollande" (Australia) was donated to RMNH by John Gould. Another two specimens recorded as from "Nouv. Hollande" are dated 1849 and were donated by "Frank". This was probably G.A. Frank, a natural history dealer based in Amsterdam. A specimen from "Botany Head", dated 1862, was received as a gift from the AM. The fifth specimen was also from the AM, but this has no date and no locality.

Naturhistorisches Museum, Basel, Switzerland (NMB), has one specimen of *H. bungaroides* from "Australia". It was donated in 1882 by Dr. Fritz Müller and is registered as no. 2188. Müller apparently contributed many purchased or traded herpetological specimens to the NMB in the years between 1880 and 1890 (R. Winkler *pers. comm.*). Advice received was that in this period, Müller worked voluntarily for the NMB and cared for the reptile, amphibian and fish collections.

At the Zoological Museum, University of Liege, Belgium (MZULG), there are five *H. bungaroides* mentioned in the museum register. All arrived between 1856 and 1875 from specialised natural history shops (C. Michel *pers. comm.*). Three of these do not have localities, but two indicate "Melbourne". If the latter two are truly *H. bungaroides*, then the recorded localities are also incorrect. However, as with the specimens from the NMW further study of MZULG specimens are also required to ascertain whether this is the case.

In Italy, the Museo Civico di Storia Naturale, Genoa (MSNG), has one *H. bungaroides* (8687). The specimen was acquired in 1879 from the Godeffroy Museum of Hamburg (Germany), a private institution founded in 1860 by Johann Cesar Godeffroy (1831-1885). The MSNG acquired specimens from the Godeffroy Museum by means of nine catalogues edited from 1864 till 1884 that listed duplicates put up for sale (G. Doria *pers. comm.*). No locality data are available for the specimen held at MSNG.

North American collections

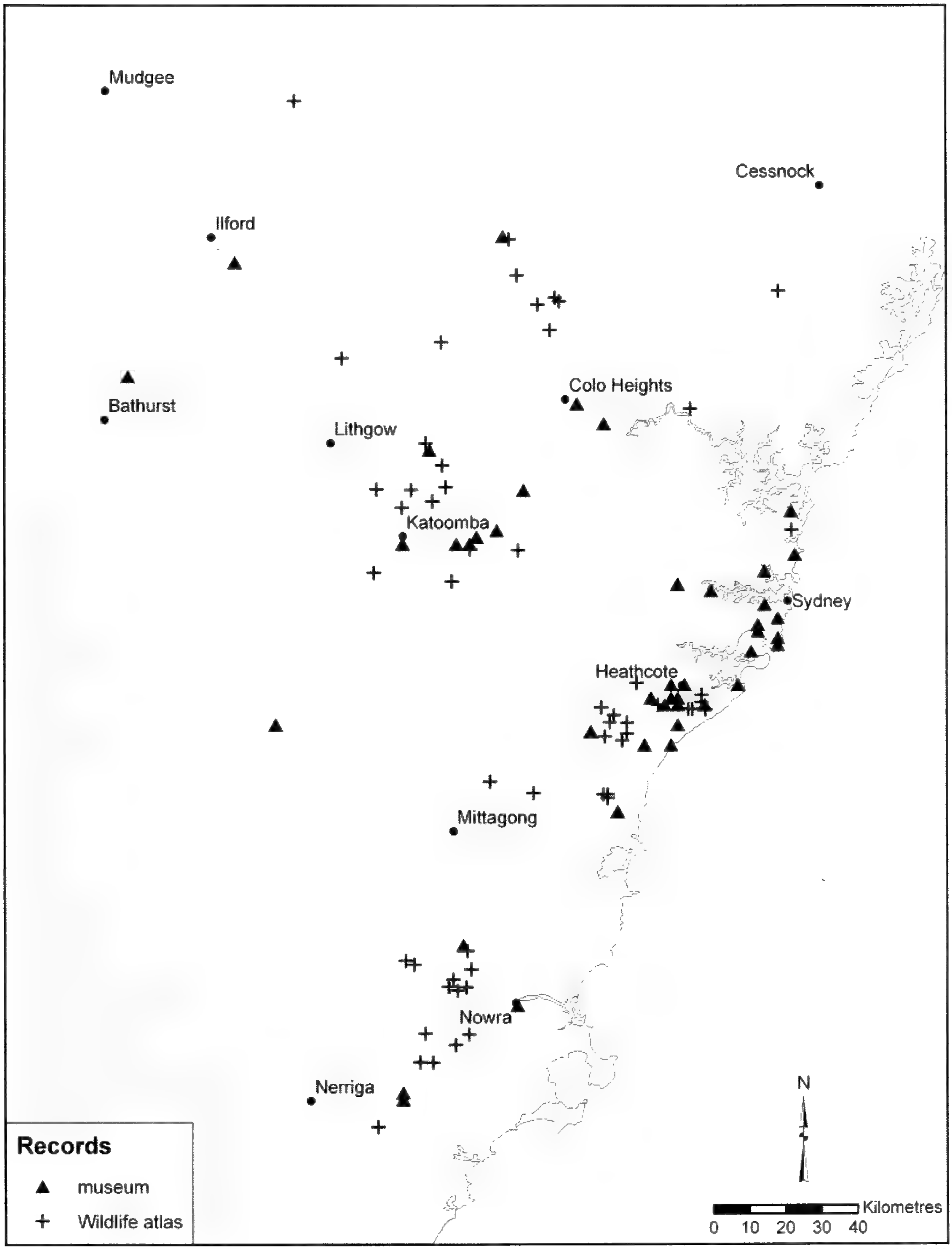
In the US, there are five museums that together hold nine *H. bungaroides* specimens. The Field Museum of Natural History, Chicago (FMNH), has two specimens both collected at "Waterfall" in the 1950s. One was collected by William Hosmer, a well-known herpetologist who worked as a field collector for the FMNH for many years and sold his Australian collection to that museum. It is known that the other FMNH specimen was collected by B Kaspiew, although we have no further information about this person. The Museum of Comparative Zoology, Harvard University (MCZ), has three specimens: one from "New South Wales", received from Krefft in 1876; one from "Australia", received from "W. Keferstein" and registered in 1865; and one from "Gelle, Mt. Wilson, Blue Mountains", received from the AM in 1914 (Loveridge 1934). The National Museum of Natural History, Smithsonian Institution (USNM), has a specimen catalogued in about 1872 with no locality details or collector name. The third from Sydney dated 1911 was received from "Julius Hurter", a Swiss-American naturalist and early Curator of the St. Louis Academy of Sciences. The single specimen in the San Diego Natural History Museum (SDNHM) was originally sent there by the AM on exchange to Van Wallach and Richard Etheridge (San Diego State University) for Wallach's studies on the visceral anatomy of the Australian Elapidae (see also Wallach 1985, 1998). A copy of the "specimen invoice form" shown to the authors was dated 19 January 1982 and indicates that this *H. bungaroides* was a "no data specimen". The single specimen in the University of Illinois Museum of Natural History (UIMNH) has no location recorded with the specimen and was apparently "purchased from the AM" but the date for this transaction is unknown. It was originally catalogued into the very old zoology collection (<1943) and the Curator at the UIMNH suggested that it was probably from the 1920s judging by its very low "Z" catalogue number (006) (C. Philips *pers. comm.*)

DISCUSSION

Of the 159 specimens, accurate locality records were available for only 98 (62 %). The AM contributed 77 while another 25 institutions contributed the remaining 82. Several of the latter (detailed in the notes above) are highly significant: two records for Middle Head (dated <1829; 1935), two for Botany Bay (dated 1862; <1935), one for Long Bay (dated <1935), one for La Perouse (dated 1915), and three for Ku-ring-gai Chase NP (dated 1967). Four of the AM specimens (dated 1904/5) were from the same location at Long Bay as that above and two specimens (undated; 1895) were from the same locations at La Perouse as that above. Significant specimen records from the AM include those from the western side of the Blue Mountains (Bathurst: dated 1979; Ilford: dated ca. 1962), and from Mudgee (<1964). Other significant records are those from within the vicinity of Shoalhaven Formation geological outcropping along the western and north-western rim of the Sydney Geological Basin, the presumed limits of the species' distribution. Whilst perhaps the species is absent there today, it gives a clear indication that some of this otherwise presumed habitat was in fact occupied by *H. bungaroides*. With many of these historical records collectors probably gave locations that covered wider districts or the specimens were allocated names of the centres they were brought to from the field. This is likely to be the case for the western records from Bathurst, north of Bathurst and Mudgee.

The specimen locality data were mapped and contrasted with the 67 records in the Atlas of NSW Wildlife (Fig. 1). Two specimens from the AM (dated 1969) and one from SAMA (dated 1973) had as the locality data a site close to the location of the AM itself. We believe the co-ordinates for these three relatively recent specimens to be incorrect, and so excluded them from the map. The distribution of the museum records shows some concordance with the Atlas data. Both databases show aggregations of records in the Katoomba (Blue Mountains), Waterfall-Heathcote and Nowra (Shoalhaven) areas. Surprisingly, 37% of the records in the museum database are from Royal NP (28) and the adjoining Heathcote NP (8) and Garrawarra SRA (1). One location in Royal NP covering an area with a radius of 2 km contributed 23 specimens with collection dates spanning 1951-72. These observations identify and confirm the currently known 'hotspots' of the distribution. We can also contrast Figure 1 with the only map previously published based on Australian Museum holdings (Longmore 1986; 50 specimens). There are about 15 museum records since 1986 including several for the Blue Mountains area (including Wollemi NP). Including these on our finer detail map gives it greater completeness as it includes Atlas records and non-AM museum records.

Hoplocephalus bungaroides is reported from only a small geographic area, as evidenced from the locality data available from museum specimens (Fig. 1). Krefft (1869) reported *H. bungaroides* from Port Jackson, Botany Bay, Middle Harbour, Lane Cove and Parramatta, although as pointed out by Cogger et al. (1993), there have not been records from these areas for quite some time. These data indicate that the only museum specimen from Port Jackson was collected prior to 1829 by Quoy and Gaimard (MNHP 7678).



Map produced by Greg Luker, SCU GIS Lab, 22/8/2006

Figure 1. Geographic distribution of *Hoplocephalus bungaroides* as indicated by museum records and records in the Atlas of NSW Wildlife.

At Botany Head, a specimen was collected in 1862, and ended up in Leiden, Netherlands, sent there by the AM (i.e. Krefft). There is also an AM specimen from Botany dated 1909 and another in NMV undated, but registered some time between 1900 and 1935. Middle Harbour museum specimens are in the NMV and MNHP. It is likely that the Botany Bay and Middle Harbour specimens were known to Krefft, because these localities were specifically referred to by him (Krefft 1869). Of the 159 *H. bungaroides* specimens located, none had locality details recorded as Lane Cove or Parramatta. Thus, Krefft knew of *H. bungaroides* records from these locations, but it is uncertain whether he collected specimens from there. Krefft did undertake snake collecting in many places in the vicinity of Sydney. Rose Bay, Randwick, Manly, Coogee and Middle Harbour were reportedly principal localities (see correspondence between Krefft and Günther in the archives of the AM).

The annual reports of the AM are unequivocal in reporting that *H. bungaroides* specimens were sent to the Civic Museum, Milan (Italy), in 1865; R.H. Beddome (India) in 1867; and Berlin Museum (Germany) in 1871 (Appendix 1). The Exchange Register also indicates that one *H. bungaroides* was sent to the Madras Museum (now Government Museum, Chennai). In relation to the first of these, we made enquires with the museum in Milan (MSNM; Appendix 2), but *H. bungaroides* could not be found on the shelves or in the collections register. However, we found an *H. bungaroides* in Genoa, Italy (MSNG; Table 1), but this is dated 1879, and it is unknown whether this snake arrived at MSNG via the AM. In relation to Beddome, it is known that he was a naturalist and a British military officer posted to India. His zoological collection together with that of his son-in-law (G. C. Leman) was sold in 1935, and much of this material is now in the National Museums of Scotland (NMS); National Museum of Wales (NMW); and the Natural History Museum, London (BMNH). However, only the latter institution has *H. bungaroides* represented, and these specimens are all dated prior to 1863. Hence, the fate of the AM's 1867 specimen sent to India is also unknown. The AM *H. bungaroides* sent to Berlin in 1871 are still preserved in the ZMB. This museum has three *H. bungaroides* from the AM (Krefft), and another five specimens that arrived via other avenues. Unfortunately we were unable to confirm the presence or absence of *H. bungaroides* at the Government Museum, Chennai, because no advice was received in reply to our correspondence.

The annual reports of the AM were quite vague in terms of the reptiles sent to de Robbillard in Mauritius; dealers Puls, Salmin, Frič and Damon; and museums in Hamburg, Leiden, Madras, Paris, Madrid, London and Harvard (Appendix 1). Of these, we managed to track down *H. bungaroides* specimens collected/donated by Krefft in Hamburg (ZMH), Leiden (RMNH), London (BMNH) and Harvard (MCZ). We can also confirm that Salmin received some *H. bungaroides* specimens (presumably from Krefft) because two from him were located in Berlin (ZMB). We found no evidence that other high-profile dealers such as Frič (Reiling and Spunarová 2005) received *H. bungaroides* from Krefft or anyone else.

This review demonstrates the value of museum specimens as a source of information on species' distribution (see also Shaffer *et al.* 1998). It's widely known that much Australian material has made its way to 19th Century collections overseas, but the details of such holdings are still not easily accessible and so our contribution at least makes such distributional information available for *H. bungaroides*. Collectively, the museum data show specific records for Sydney's urban areas - Botany Head, La Perouse, Long Bay, Botany, Concord West, Randwick, Middle Harbour and Port Jackson. These localities represent part of this species' historical geographic range that has now been eliminated (see also Swan et al. 2004; Shine et al. 1998). Increasing our understanding of the historic distribution of *H. bungaroides* is of considerable importance because continued habitat clearing and fragmentation may eliminate this species from an area and without an historic record may lead to disagreement about whether an area is actually suitable for this species. For example, Hoser (1995) categorically refutes that *H. bungaroides* occurred in Ku-ring-gai Chase NP but three *H. bungaroides* specimens in the SAMA have collection details dated 1967 for that locality and there is no reason to doubt their authenticity. Recent surveys there (1998/9) failed to detect *H. bungaroides* (Newell and Goldingay 2005), suggesting it may now be locally extinct.

The museum specimen localities provide a focus for increasing our understanding of the geographic range of *H. bungaroides*. There are three broad areas with aggregations of records: Katoomba (Blue Mountains), Waterfall-Heathcote and Nowra (Shoalhaven area). These areas also show aggregations of records in the Atlas of New South Wales Wildlife (Fig. 1). These may represent areas of highly suitable habitat for *H. bungaroides*. However, there is likely to be collecting bias evident with these data. For example, a few areas near Waterfall contribute 37% of all specimen locations, though records span a 27-year period. Recent detailed surveys in Royal NP (i.e.

Waterfall) indicate that *H. bungaroides* is uncommon there (Goldingay 1998; Goldingay and Newell 2000; Newell and Goldingay 2005; Goldingay and Newell unpubl. data). The failure to detect *H. bungaroides* in recent surveys of national parks surrounding the Hawkesbury River where there are few historic records (Newell and Goldingay 2005) suggests that the species' distribution is much more patchy than what might be predicted based on the presence of apparently suitable sandstone habitats. Further surveys of suitable habitat in areas without records need to be conducted. Records in the north-west of the species' range (Bathurst: dated 1979; Ilford: ca. 1962) also highlight areas where further surveys need to be conducted. These represent the most western records of the species and a population in this area may show some genetic divergence and be of considerable conservation significance. The identification of museum holdings of *H. bungaroides* may be useful for a range of future research studies. This includes morphological research and further descriptions of diet based on stomach content analysis (e.g. Shine 1981a,b, 1983; Keogh 1999). Furthermore, these specimens may provide a source of tissue samples for genetic studies that could contribute to an understanding of whether *H. bungaroides* has lost genetic diversity over time or if unique genotypes have been lost (see also Keogh 1998; Slowinski and Keogh 2000). Our collation here provides a record that will facilitate the use of specimens in this way.

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Appendix 1: Summary notes taken from the Annual Reports of the Australian Museum 1861-1874 with details of reptile exchanges. The notes place an emphasis on reference to the broad-headed snake *Hoplocephalus bungaroides*.

Year	Notes collated from Annual Reports
1861	Krefft collected reptiles (including 35 snakes, 10 species) for the Australian Museum but specific details were not published.
1862	A Broad-headed Snake (as *Hoplocephalus variegatus*) was donated by a Mr Coleman.
1863	A Broad-headed Snake (*H. variegatus*) was donated by a Miss Caroline F. Parsons.
1864	Reptiles were sent to museums in Hamburg, Leiden and Madras, although *H. bungaroides* was apparently not included.
1865	No *H. bungaroides* were received; but one *H. bungaroides* (as *H. variegatus*) was sent to Civic Museum in Milan. Also in 1865, other reptiles, but not *H. bungaroides*, were sent to the Paris Museum, and to a Mr J.C. Puls (a dealer in Belgium).
1866	A *Hoplocephalus* was received from a Mr. W. Gorman, but it was not stated whether this was *bungaroides* or another species. Reptiles were sent out to various museums but the identity of these reptiles was not given. Reptiles went to the Royal Society of Tasmania (20 reptiles), Royal Museum at Madrid (one reptile), Mr C.L. Salmin, Hamburg (50 reptiles and fishes), Paris Museum (34 reptiles and fishes), Civic Museum in Milan (25 reptiles).
1867	No *H. bungaroides* were received; one specimen (as *Hoplocephalus variegatus*) was reportedly sent to Captain R.H. Beddome, Official Conservator of Forests, Madras (=Chennai, India).
1868	No *H. bungaroides* were received; but a collection of mammals, reptiles and fishes was sent to the Berlin Museum. No indication is provided of the numbers or identity of the species sent.
1869	No *H. bungaroides* were received; and no reptiles were sent out.
1870	No *H. bungaroides* were received; however 25 unspecified reptiles were sent to Museum of Comparative Zoology, Harvard University; 128 specimens of reptiles and fishes sent to British Museum; 27 reptiles (plus 12 tortoises) sent to Mr V. Frič, Prague [a dealer]; and 150 specimens of mammals, reptiles, birds and fishes were sent to Mr Robert Damon, Weymouth [a dealer].
1871	No *H. bungaroides* were received; but a collection of reptiles were sent to “Professor Peters, Director of the Royal Museum in Berlin”, including one or more *H. bungaroides* (as *H. variegatus*).
1872	A collection of living snakes including *H. bungaroides* (as *H. variegatus*) was received from Mr H.H. Bradley. A collection of 29 reptiles was sent to Mr V. de Robillard, Port Louis, Mauritius.
1873	No *H. bungaroides* were received; and no lists of exchanges were provided. The Board of Trustees stated in this annual report that Krefft had lately not been keeping a list of exchanges.
1874	“A variegated black snake *Hoplocephalus variegatus*” (=*H. bungaroides*) was received from Mr Williams, Canterbury; no lists of species sent out

Appendix 2: Institutions in Australia and overseas that do not hold specimens of the broad-headed snake *Hoplocephalus bungaroides* or did not reply to our email correspondence. Entries are listed with Australia first then alphabetically by country and then institution name. R= Reply; Note: institutions marked with a (*) replied that no *H. bungaroides* specimens were held in their museum; institutions with a (-) did not reply despite more than one request.

Institution	R
Australia	
Biological Sciences Museum, Macquarie University	*
Queen Victoria Museum and Art Gallery, Launceston	*
Tasmanian Museum and Art Gallery, Hobart	*
Zoology Museum, University of New England	*
Zoology Museum, University of Queensland	*
Tiegs Museum, University of Melbourne	*
Zoology Collection, Royal Melbourne Institute of Technology	*
Zoology Collection, University of Tasmania	*
Haswell Zoology Museum, University of Sydney	*
Argentina	
Fundación Miguel Lillo	*
Museo Argentino de Ciencias Naturales	-
Museo de La Plata	*
Austria	
Haus der Natur, Salzburg	*
Landesmuseum Joanneum, Graz	*
Oberösterreichisches Landesmuseum, Linz	*
Vorarlberger Naturschau Dornbirn	-
Belgium	
Musée d'Histoire Naturelle, Tournai	*
Muséum de Zoologie, Brussels	*
Museum voor Dierkunde, Gent University	*
Museum Zoölogie, Katholieke Universiteit Leuven	*
Royal Belgium Institute of Natural Sciences, Brussels	*
Bulgaria	
National Museum of Natural History, Sofia	-
Canada	
Canadian Museum of Nature	*
Cowan Vertebrate Museum, University of British Columbia	*
Nova Scotia Museum of Natural History	*
Redpath Museum, McGill University, Montréal, Québec	*
Royal Alberta Museum	*
Royal British Columbia Museum	*
Royal Ontario Museum	*
University of Alberta Museum of Zoology	*
Czech Republic	
Moravian Museum, Brno	*
National Museum, Prague	*
Denmark	
Naturhistorisk Museum, Arhus	-
Lolland-Falsters Stiftsmuseum	-
Estonia	
Museum of Viljandi, Viljandi	-
Estonian Museum of Natural History	-
Finland	
Finnish Museum of Natural History	*
Jyväskylä University Museum	*
Zoological Museum, University of Turku	*
France	
Laboratoire de Zoologie de la Faculté Des Sciences, Nancy	-
Laboratoire Zoologique, Faculté Des Sciences, Dijon	-
Muséum d'Histoire Naturelle, Grenoble	*
Muséum d'Histoire Naturelle, Autun	-
Muséum d'Histoire Naturelle, Lyon	*
Museum d'Histoire Naturelle, Marseilles	*
Muséum d'Histoire Naturelle, Nantes	*
Museum d'Histoire Naturelle, Nice	-
Muséum d'Histoire Naturelle, Rouen	*
Muséum d'Histoire Naturelle, Toulouse	*
Musée de Zoologie, Strasbourg	*
Germany	
Dümmer-Museum, Lembruch	-
Haus der Natur, Cismar	*
Hessisches Landesmuseum, Darmstadt	*
Jura-Museum, Willibaldsburg	-
Museum Alfeld, Langenholzen	-
Museum für Naturkunde, Dortmund	-
Museum Heineanum Halberstadt	-
Museum Koenig, Bonn	*
NABU Lüneburg, Heiligengeiststraße	-
Naturhistorisches Museum, Mainz	*
Naturhistorisches Museum, Rudolstadt	*
Naturkundemuseum Leipzig	-
Naturkunde-Museum, Coburg	*
Naturkundliches Museum Mauritianum, Altenburg	-
Niedersächsisches Landesmuseum, Hannover	-
Staatliches Museum für Naturkunde, Görlitz	*
Staatliches Museum für Naturkunde, Karlsruhe	*
Staatliches Museum für Naturkunde, Stuttgart	*
Staatliches Museum für Tierkunde, Dresden	*
Staatliches Naturhistorisches Museum, Braunschweig	*
Westfälisches Museum für Naturkunde, Münster	-
Wiesbaden Naturwissenschaftliche Sammlung, Wiesbaden	-
Zoological Collection, University of Leipzig	*

Germany continued	
Zoological Collection, University of Rostock	*
Zoological Museum, Christian-Albrechts-University	*
Zoological Museum, Göttingen	*
Zoological Museum, University of Heidelburg	*
Zoologischen Museum, Greifswald	-
Zoologisches Institut, Martin-Luther University	*
Zoologisches und Tiermedizinisches Museum	-
Zoology Museum, Universitat Tubingen	-
Greece	
Zoological Museum, University of Athens	-
Hungary	
Hungarian Natural History Museum, Budapest	*
India	
Bombay Natural History Society Collection, Bombay	*
National Museum of Natural History, New Delhi	*
Zoological Survey of India Collection	-
Government Museum, Chennai	-
Indian Museum, Calcutta	-
Zoological Museum, Andhra University, Waltair	-
Ireland	
Natural History Museum, Dublin	*
Trinity College Dublin	-
Italy	
Bari Zoological Museum, University of Bari	*
Casalnuovo Monterotaro Civic Museum of Natural History	-
Civic Museum of the Salento Natural History, Calimera	-
Civic Museum of Zoology, Rome	-
Florence Natural History Museum, Florence	*
Museo di Storia Naturale e del Territorio, University of Pisa	-
Museo Civico di Storia Naturale di Trieste	-
Museo Civico di Storia Naturale, Milan	*
Museo Civico di Storia Naturale, Venice	*
Museo Civico di Storia Naturale, Verona	-
Museo dell'Instituto Nazionale per la Fauna Selvatica, Bologna	-
Museo di Zoologia, University of Padova	-
Museo di Zoologia, Università di Bologna, Bologna	-
Museo di Zoologia, University of Rome "La Sapienza"	*
Museo Regionale di Scienze Naturali	-
Museo Regionale di Scienze Naturali, Turin	-
Museo Zoologico, Siena	-
Museo Zoologico, Università di Palermo	-
Museo Zoologico, University of Naples	*
Museum of Natural History, Trento	-
Provincial Museum of Natural History, Foggia	-
Zoological Collection, Cagliari University	-

Japan	
Kitakyusyu Natural History Museum	-
Museum of Natural History, Tohoku University	-
Osaka Museum of Natural History	*
Zoology Collection, National Science Museum, Tokyo	*
Latvia	
Natural History Museum of Latvia, Riga	-
Luxembourg	
Musée National d'Histoire Naturelle, Luxembourg	-
Netherlands	
Natuurhistorisch Museum Maastricht	*
Natuurmuseum Rotterdam, Rotterdam	*
Zoological Collection, University of Utrecht	*
Zoological Museum, Amsterdam	*
New Zealand	
Canterbury Museum, Christchurch	*
Auckland Museum, Auckland	*
Otago Museum, Dunedin	*
Norway	
Museum of Natural History and Archaeology, Trondheim	-
Stavanger Museum Zoologisk Avdeling, Stavanger	*
Zoology Collection, University of Bergen	*
Zoology Museum, University of Oslo	*
Poland	
Museum and Institute of Zoology, Warsaw	-
Natural History Museum, University of Wroclaw	*
Polish Academy of Sciences	*
Zoological Museum, Jagiellonian University, Kraków	*
Portugal	
Centro de Zoologia, Lisbon	*
Museu de História Natural, University of Porto	*
Museu Municipal do Funchal, Madeira	-
Museu Nacional de História Natural, University of Lisbon	-
Museu Zoológico e Antropológico, University of Coimbra	-
Natural History Museum, Coimbra	-
Romania	
Brukenthal Museum, Sibiu	*
Natural History Museum, Bucharest	*
Zoological Museum, Babes-Bolyai University	*
Russia	
Museum of Natural History, Kharkov University	-
Siberian Zoological Museum, Russia	*
State Darwin Museum, Moscow	-
Zoological Museum, Moscow State University	-
Zoological Museum, Russian Academy of Sciences	*

Appendix 2 continued

Spain	
Durangaldeko Natur Zientzien Museoa, Durango	*
"Luis Iglesias" Natural History Museum	*
Museo de Zoologica, Barcelona	*
Museo Nacional de Ciencias Naturales, Madrid	*
Slovakia	
Sarisske Museum, Bardejov	*
Slovenia	
Slovenian Museum of Natural History, Ljubljana	*
South Africa	
Albany Museum, Grahamstown	-
Durban Museum, Durban	-
McGregor Museum, Kimberley	*
Natal Museum, Pietermaritzburg	*
National Museum, Bloemfontein	-
Port Elizabeth Museum	*
South African Museum, Cape Town	*
Transvaal Museum, Pretoria	*
Zoological Museum, University of Stellenbosch	*
Zoology Museum, University of Witwatersrand	*
Sweden	
Swedish Museum of Natural History	*
Zoological Museum, Lund University	*
Göteborg Natural History Museum, Göteborg	*
Switzerland	
Muséum d'Histoire Naturelle, Geneva	*
Natural History Museum, Bern	*
Natural History Museum, Fribourg	*
Zoological Museum, University of Zurich	*
Naturmuseum, St. Gallen	*
Musée de Zoologie, Lausanne	*
Musée d'Histoire Naturelle, La Chaux-de-Fonds	*
Naturmuseum, Solothurn	*
United Kingdom	
Bell Pettigrew Museum, University of St Andrews	*
Bolton Museums, Bolton (Manchester)	-
Booth Museum of Natural History, Brighton	*
Bristol City Museum and Art Gallery, Bristol	*
Cole Museum of Zoology, Berkshire	*
Grant Museum of Zoology, University College London	*
Hampshire County Museums Service, Winchester	*
Hancock Museum, Newcastle	*
Hereford Museum and Art Gallery	*
Horniman Museum, London	*
Hunterian Museum and Art Gallery, Glasgow, Scotland	*
Hunterian Museum at the Royal College of Surgeons, London	*
Ipswich Museum, Ipswich	*
John Moore Countryside Museum, Gloucestershire	-
Kendal Museum, Kendal	*
Kings College, London	*
Leeds City Museum, Leeds	*
Linnean Society, London	*
Liverpool Museums	*
Manchester Museum, University of Manchester	*
National Museum of Wales, Cardiff	*
National Museums of Scotland, Edinburgh	*
Natural History Collection, University of Edinburgh	-
Plymouth City Museum and Art Gallery, Plymouth	*
Portsmouth City Museums and Records Service	*
Reading Museum Service	*
Royal Albert Memorial Museum, Exeter	*
Saffron Walden Museum, Essex	*
Ulster Museum in Northern Ireland	-
University Museum of Zoology, Cambridge	*
University of Dundee Zoology Museum	*
Worcester City Museum and Art Gallery	*
Zoological Collection, University of Leeds	*
Zoology Museum, Aberdeen University	*
United States of America	
Academy of Natural Sciences, Philadelphia	*
Alabama Museum of Natural History	-
American Museum of Natural History, New York	-
Arizona State University Herpetology Collection	*
Austin Peay State University Museum	-
Bell Museum of Natural History, University of Minnesota	*
Bishop Museum, Hawaii	*
Burke Museum of Natural History and Culture	*
Burpee Museum of Natural History, Rockford, Illinois	*
California Academy of Science Herpetology Collection	*
Carnegie Museum of Natural History	*
Charles R. Conner Museum, Washington State University	*
Charleston Museum, South Carolina	*
Cleveland Museum of Natural History	*
Cornell University Museum of Vertebrates	*
Dallas Museum of Natural History	*
Fernbank Museum of Natural History, Atlanta	-
Florida Museum of Natural History	*
Georgia Museum of Natural History	*
Great Valley Museum of Natural History, California	-
Houston Museum of Natural Science	*
Idaho Museum of Natural History	*
Joseph Moore Museum, Earlham College, Indiana	*
Kansas University Natural History Museum, Lawrence	*
Life Science Museum, Brigham Young University	-

United States of America continued	
Milwaukee Public Museum	*
Museum of Southwestern Biology, Univ. of New Mexico	*
Museum of Zoology, University of Memphis	-
New Mexico Museum of Natural History	*
New York State Museum	*
North Carolina State Museum of Natural Sciences	*
Oregon State University Museum	*
Peabody Museum of Natural History, Yale University	*
Sam Noble Oklahoma Museum of Natural History	*
Santa Barbara Museum of Natural History	*
Texas Natural History Collections, University of Texas, Austin	*
University of Nebraska State Museum	*
University of Oregon Museum of Natural History	*

Appendix 3: *Hoplocephalus bungaroides* specimens reportedly held in Australian and overseas museums. Note: the authors have not personally confirmed the identification of any of these specimens by examination. Records are arranged alphabetically by museum abbreviation (see Table 1) then numerically by registration number. Abbreviations: Coll. = Collected; Confis. = Confiscated; Don. = Donated; NP = National Park; NSW = New South Wales; QNPWS = Queensland National Parks and Wildlife Service; ZSL = Zoological Society of London.

Collection Date	Museum	Rego. No.	Locality details	Other details
-	AM	R 1440	-	Registered 30/08/1893
-	AM	R 1603	La Perouse	-
-	AM	R 1722	La Perouse	Registered 14/04/1895
6/04/1900	AM	R 2696	Mount Wilson	Registered 10/05/1977
11/10/1904	AM	R 3646	Long Bay	Registered 15/05/1977
12 Apr 1905	AM	R 3675	Long Bay	Registered 15/05/1977
28/04/1905	AM	R 3678	Long Bay	Registered 15/05/1977
26/11/1905	AM	R 3847	Long Bay	Registered 18/05/1977
26/11/1905	AM	R 3848	Long bay	Registered 18/05/1977
16 Dec 1909	AM	R 4619	Botany	Registered 22/05/1977
-	AM	R 11179	Randwick	Registered /04/1934
1/11/1959	AM	R 15676	Waterfall	Registered 27/11/1959
Aug 1959	AM	R 18939	Waterfall	Registered 30/11/1962
-	AM	R 18940	Waterfall	Registered 30/11/1962
Apr 1962	AM	R 18941	Mount Keira	Registered 30/11/1962
-	AM	R 18942	Waterfall	Registered 30/11/1962
-	AM	R 18943	Waterfall	Registered 30/11/1962
-	AM	R 18944	Waterfall	Registered 30/11/1962
-	AM	R 18945	Waterfall	Registered 30/11/1962
-	AM	R 18946	Waterfall	Registered 30/11/1962
-	AM	R 18947	Waterfall	Registered 30/11/1962
-	AM	R 21071	Mudgee	Registered 6/02/1964
2 Mar 1964	AM	R 21219	Concord West	Registered 6/03/1964
Feb 1969	AM	R 30345	Springwood	Registered 1/03/1971
8/09/1973	AM	R 40309	Darkes Forest	Registered 9/10/1973
2 May 1970	AM	R 47415	Waterfall	Registered 25/06/1975
22/10/1967	AM	R 70034	Woodford	Registered 1/02/1978
1966	AM	R 74276	Royal NP	Registered 16/06/1978
1966	AM	R 74277	Royal NP	Registered 16/06/1978
1971	AM	R 74278	Waterfall	Registered 16/06/1978
1971	AM	R 74279	Sydney	Registered 16/06/1978
1969	AM	R 74280	Nowra	Registered 16/06/1978
1969	AM	R 74281	Sydney	Registered 16/06/1978
1970	AM	R 74282	Appin	Registered 16/06/1978
1972	AM	R 74283	Waterfall	Registered 16/06/1978
Apr 1972	AM	R 74284	Woronora Dam	Registered 16/06/1978
2 Oct 1972	AM	R 74285	Nowra	Registered 16/06/1978
2 Oct 1972	AM	R 74286	Nowra	Registered 16/06/1978
2 Oct 1972	AM	R 74287	Nowra	Registered 16/06/1978

2 Oct 1972	AM	R 74288	Nowra	Registered 16/06/1978
2 Oct 1972	AM	R 74289	Nowra	Registered 16/06/1978
2 Oct 1972	AM	R 74290	Nowra	Registered 16/06/1978
1967	AM	R 74291	Helensburgh	Registered 16/06/1978
1968	AM	R 74292	Royal NP	Registered 16/06/1978
1969	AM	R 74293	Royal NP	Registered 16/06/1978
1971	AM	R 74294	Waterfall	Registered 16/06/1978
1971	AM	R 74295	Waterfall	Registered 16/06/1978
1969	AM	R 74296	Sydney Area	Registered 16/06/1978
Oct 1978	AM	R 76338	Colo	Registered 30/10/1978
-	AM	R 82584	-	-
1969	AM	R 84381	Waterfall	Registered 31/05/1979
5 Aug 1978	AM	R 92955	Colo Heights	Registered 14/05/1980
2 Sep 1951	AM	R 103159	Waterfall	Registered 28/10/1981
Jun 1963	AM	R 103162	Heathcote	Registered 28/10/1981
5 Sep 1980	AM	R 103711	Mount Macleod Morgan	Registered 25/12/1981
-	AM	R 107684	Woronora Dam	Registered 7/04/1983
-	AM	R 107685	Bundeena	Registered 7/04/1983
1966	AM	R 107716	Bundeena	Registered 7/04/1983
1966	AM	R 107717	Stanwell Park	Registered 7/04/1983
1969	AM	R 107718	Woronora Dam	Registered 7/04/1983
-	AM	R 107719	Waterfall or Heathcote	Registered 7/04/1983
-	AM	R 107720	Waterfall or Heathcote	Registered 7/04/1983
1979	AM	R 118644	~ 15km NE Bathurst on Road to Sofala	Registered 30/05/1986
17 Oct 1986	AM	R 125335	-	Registered 28/03/1988
-	AM	R 125414	Sydney	Registered 18/04/1988
-	AM	R 128548	Evans Lookout, Blue Mountains	Registered 31/12/1987
-	AM	R 131075	-	Registered 17/05/1988
-	AM	R 131143	-	Registered 19/05/1988
-	AM	R 131144	-	Registered 19/05/1988
-	AM	R 131145	-	Registered 19/05/1988
9 Feb 1996	AM	R 144614	Hazelbrook, Terrace Falls Reserve	-
1/01/1996	AM	R 144720	Kangaroo Valley	Registered 10/05/1996
Jan 1980	AM	R 144876	Captivity	Registered 15/05/1996
Aug 1992	AM	R 147417	Linden, Glossop Road, Blue Mountains	Registered 10/05/1995
Aug 1992	AM	R 147418	Linden, Glossop Rd., Blue Mountains	Registered 10/05/1995
-	AM	R 150348	Sydney	-
Feb 1998	AM	R 151978	Wollemi NP	Registered 24/02/1998
-	ANU	-	Waterfall	-
-	ANU	-	Tiajuara Falls	-
~1963-1964	ANWC	R01868	-	-
~1978-1980	ANWC	R05040	-	Coll. H. Cogger
~1978-1980	ANWC	R05041	-	Coll. Greg Mengden
~1855	BMNH	1855.8.25.??	Australia	Capt. Stokes Collection
~1847	BMNH	1847.7.29.40	Australia; Presented: Earl of Derby	Macgillivray collection

~1863	BMNH	1863.6.16.50	NSW; Purchased from: G. Krefft	Registered 16 Jun 1863
~1863	BMNH	1863.6.16.55	Australia	Krefft
~1855	BMNH	1855.10.16.109	Australia	ZSL
~1859	BMNH	1859.6.30.10	Australia; Presented: Dr G. Bennett	-
~1953-1956	FMNH	75118	Waterfall	B Kaspiew
6 Oct 1951	FMNH	97310	Waterfall	W. Hosmer
1876	MCZ	R2525	New South Wales; received Nov 1870	Krefft
1865	MCZ	R3642	Australia;	W. Keferstein
1914	MCZ	R10282	Gelle, Mt. Wilson, Blue Mountains	AM
-	MMUS	R0501a	Mount Wilson	-
-	MMUS	R0501b1	coast near Sydney	-
-	MMUS	R0501b2	coast near Sydney	-
<1837	MNHP	1991-4163	-	-
Dec 1846	MNHP	3301	Australia	J. Verreaux
-	MNHP	7678	Port Jackson	Quoy and Gaimard
Jun 1836	MNHP	7679	Australia - - type of *Alecto variegata*	Keraudren
-	MSNG	8687	Australia	Acquired 1879
-	NMV	D 4270	Long Bay	Registered 1900-1935
-	NMV	D 4704	Middle Harbour	Registered 1900-1935
1975	NMV	D 51865	Yal Wal, Nowra	-
1975	NMV	D 51866	Royal NP	-
-	NMV	D 65041	Helensburg	Registered 1900-1935
-	NMV	R 12709	Coast Range, Botany Bay	Registered 1900-1935
1856-1875	MZULG	D.R.1883	Melbourne	-
1856-1875	MZULG	R.E. 2657a	-	-
1856-1875	MZULG	R.E. 2657b	-	-
1856-1875	MZULG	R.E. 2657c	-	-
1856-1875	MZULG	R.E. 4221	Melbourne	-
1893	MZUS	626	Queensland	Rolle
1893	MZUS	627	Queensland	Rolle
1882	NMB	2188	Australia	Fritz Müller
2 Aug 1863	NMW	27699:1	Original Label " West Australien"	-
12 Feb 1869	NMW	27699:2	Original Label " West Australien"	-
1877	NMW	27699:3	Original Label " West Australien"	-
~1970s	NTM	R1212	Jarra Fall, Nowra	Coll. Graeme Gow
9 Mar 1975	NTM	R958	Woronora Dam	Coll. Graeme Gow
25 Nov 1972	NTM	R1115	Heathcote	Coll. Graeme Gow
1 Aug 1978	NTM	R1217	Woronora Dam	Coll. Graeme Gow
<1909	OUM	OUM 4641	Sydney	Coll. F.P.Pascoe
6 Jan 1959	QM	J52877	Waterfall	Found under rock
30 Apr 88	QM	J47924	Nowra	Captive specimen
4 Sep 1989	QM	J49761	-	Confis. by QNPWS
-	QM	J61008	-	Captive bred
Aug 1862	RMNH	RMNH 1141	Botany Head, Sydney	gift of AM
No date	RMNH	RMNH 1142	Museum Sydney	-

-	RMNH	RMNH 1335	"Nouv. Hollande" (Australia)	Gould
1849	RMNH	RMNH 1336a	"Nouv. Hollande" (Australia)	Frank
1849	RMNH	RMNH 1336b	"Nouv. Hollande" (Australia)	Frank
2/06/1915	SAMA	R00463	La Perouse	Don. AM; now missing
1967	SAMA	R12099	Kuringai Chase	W. Irvine
1967	SAMA	R12100	Kuringai Chase	W. Irvine
1967	SAMA	R12101	Kuringai Chase	W. Irvine
2/07/1971	SAMA	R13433	Woronora River	H. Ehmann
Sep-73	SAMA	R14116	Sydney	G.N. Coombe
1980s	SDNHM	63864	-	sent on exchange by AM
1911	SMF	20532	eastern Australia	Don. O. Frank
~1920s	UIMNH	95151	-	purchased from AM
<1872	USNM	8050	-	Catalogued about 1872
1911	USNM	56166	Sydney	Coll. Julius Hurter
8 Aug 1964	WAM	R53761	Woronora Dam	G.F. Gow
9 Mar 1975	WAM	R53762	Woronora Dam	G.F. Gow
9 Mar 1975	WAM	R53763	Woronora Dam	G.F. Gow
1860s-1870s	ZMB	4443	Sydney	dealer Salmin
1860s-1870s	ZMB	4444	Sydney	dealer Salmin
1860s-1870s	ZMB	5208	NSW	Krefft
13 Sep 1913	ZMB	63510	Donated by Berlin Zoo	-
1860s-1870s	ZMB	63755	Australia	Krefft
1860s-1870s	ZMB	63756	Australia	Krefft
1867	ZMB	63757	Recorded incorrectly as Adelaide	Schomburgk
1867	ZMB	63847	Sydney	Schomburgk
1868	ZMH	R08213 514	Australia	-
1861	ZMH	R08212 763	Sydney	Krefft
Sep 1862	ZMUC	R65270	Sydney	-
Sep 1862	ZMUC	R65271	Sydney	-
Aug 1867	ZMUC	R65272	Australia	Don. Günther
1920	ZSM	387/1920	NSW	Destroyed in WWII
1928	ZSM	36/1928	NSW	Destroyed in WWII

Reconstructing *Palorchestes* (Marsupialia: Palorchestidae) - from Giant Kangaroo to Marsupial 'Tapir'

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Since their initial description in 1873, palorchestid marsupials have been reconstructed in a variety of ways ranging from giant kangaroos, long-necked llama like-forms, bizarre okapians to their present popular image as quadrupedal marsupial 'tapirs'. These reconstructions have resulted from an improved understanding of the phylogenetic position of *Palorchestes*, more complete fossil material and even the interpolation of supposed Australian Aboriginal renderings of these animals in Arnhem Land rock art. An examination of the timing of these different 'views' of *Palorchestes* has revealed that historical and social factors have also influenced how this animal has been visualized.

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KEYWORDS: history, *Palorchestes*, palorchestid, visual representation

INTRODUCTION

Attempts by vertebrate palaeontologists to reconstruct fossil animals are almost as old as the science that has informed such endeavours. In nineteenth century Europe, the French anatomist, Baron Georges Cuvier, gained a public reputation of being able to complete a "restoration from a single fossil fragment of complete skeletons of creatures long since extinct" (Owen 1894:398). It appears, however, that Cuvier had only a marginal interest in attempting such reconstructions, dismissing them as too speculative (Coleman 1964, Outram 1984). Indeed, Cuvier didn't publish any full reconstructions of prehistoric animals due primarily to his concern that such drawings would impact on his reputation as a scientist (Rudwick 1992). Across the channel, the so-called 'British Cuvier', Sir Richard Owen, earned similar accolades for his ability to reconstruct extinct animals from the most meager of remains. In one instance, Owen was said to have deduced the general form of the giant extinct New Zealand bird *Dinornis* from just "a six inch splint of bone with broken extremities" (Desmond 1975:101).

Not all such palaeontological endeavours were so compelling however. When Cuvier was shown a tooth of the ornithischian dinosaur *Iguanodon*, he identified the fossil as the upper incisor of a rhinoceros and later dismissed the metacarpal bones of the same animal as a species of hippopotamus (Delair and Sarjeant 1975). Owen's work on *Iguanodon* was equally flawed. After being called on to supervise the sculpting of a life-size statue of the dinosaur, for the 1851 Great Exhibition of London, Owen not only posed the bipedal *Iguanodon* on all fours, but also placed its characteristic thumb spike on its nose (Desmond 1975).

Although Cuvier was able to acknowledge his errors in identification before Mantell (1825) formally described *Iguanodon*, Owen was not so fortunate. His anatomical *faux pas* were, and remain, highly visible thanks to the continued presence of the giant *Iguanodon* statue on its artificial island at Sydneham in London (Desmond 1975). In fact, almost a century and a half after its unveiling, Owen is still belittled over the anatomical inaccuracies of this reconstruction (Rudwick 1992) even though Owen was neither the first to reconstruct *Iguanodon* nor the first to incorporate such inaccuracies. Around 1835, for example, Mantell first visualized *Iguanodon* as a type of a hypertrophied iguana (Williams 1991). Three years later, two further *Iguanodon* reconstructions were published in popular books on geology. George Nibbs completed a reconstruction as the frontispiece of George Richardson's 1838 book, 'Sketches in Prose and Verse' while John Martin composed a gothic scene featuring three *Iguanodon* battling each other for Mantell's, 1838 'Wonders of Geology' (Rudwick 1992). Although significantly different from Mantell's original iguana-like reconstruction, both followed his lead by picturing *Iguanodon* as a sprawling reptile with its thumb spike on its nose.

While a paucity of fossil material has historically often been given as the reason for such errors in early reconstructions — in *Iguanodon*'s case nothing more than a "few teeth and isolated bones" (Rudwick 1992:222) — other factors have also been implicated. At the time of *Iguanodon*'s discovery, the very concept of 'dinosaur' had not been formulated and the notion of extinct giant land reptiles was still novel (Delair and Sarjeant 1975:14). Further, given that there was also no demonstrated stratigraphic evidence that the *Iguanodon* fossils were anything older than Quaternary, it is perhaps not surprising that they were, at first, considered to be those of extinct mammals (Delair and Sarjeant 1975). Eventually, the existence of such giant land reptiles came to be accepted by scientists and even enshrined in the appellation *Megalosaurus* or 'great lizard' — the formal name for the first of these creatures to be described (Buckland, 1824). As these giants had no living counterparts, they were understood using modern lizards as analogues and hence reconstructed as quadrupeds (Williams 1991). The first bipedal dinosaurs were not to be discovered for almost another two decades and on a different continent (Leidy 1858). As for the misplaced thumb spike, Mantell had originally indicated that the bone may be a dermal horn or tubercle but was convinced by unnamed authorities that the bone was a lesser horn of a rhinoceros (Delair and Sarjeant 1975). Even when *Iguanodon* was shown to be a giant reptile, it made more sense to place this 'horn' on the nose rather than on the hand given that there were no examples of similar thumb spikes in extant lizards.

Desmond (1979, 1982), however, posits a deeper, political and perhaps even personal motives for Owen's Crystal Palace reconstruction of *Iguanodon* and the establishment of the taxonomic rank of Dinosauria (Owen (1841[1842]). This was to directly challenge the doctrine of Lamarckian transmutation, being espoused by many continental scientists and in England by his *bête noir*, Robert Grant of University College, London. Instead of giving the Crystal Palace statue the typical sprawling posture of all previous reconstructions, Owen stood his *Iguanodon* erect like a mammal (Desmond 1982). By reconstructing it with such a modern stance, Owen hoped to discredit the doctrine of transmutation showing that present-day lizards and snakes represented a *descent* rather than an ascent as the ladder-like progression of the Lamarckian scheme demanded. Rupke (1994:133), however, contends that the establishment of the Dinosauria was nothing more than "the product of contemporary advances in taxonomic practices".

In Australia, the fossils of extinct giant marsupials, not dinosaurs, were the first to be studied and later reconstructed — primarily by overseas experts (Rich et al. 1985, Vickers-Rich and Archbold 1991). Among the earliest was *Palorchestes*, described by Owen (1873:387) as "the largest form of kangaroo hitherto found". Its reconstructed skull was illustrated by Owen (1876) and then again in his seminal two volume work on Australian fossil mammals. In that work, Owen (1877) also provided a reconstruction of the country's largest marsupial *Diprotodon*. As its feet were unknown at the time, the wily professor disguised these missing elements by hiding them in long grass. The foot bones were eventually found and described, almost a quarter of a century later, by Stirling and Zietz (1900). Modern reconstructions of *Diprotodon* differ little from the initial attempt by Owen except, of course, for the addition of the absent feet (Berganini 1964, Ruhen 1976, Quirk and Archer 1983).

Other diprotodontid reconstructions have not been so readily accepted. The lack of recognizable postcranials of *Zygomaturus* meant that Gerard Krefft's illustration of the animal, reproduced in Whitley (1966), was regarded as "curious speculation" by Archer (1984:677) while Lord and Scott's (1924) reconstruction of the same animal was characterized as a "murky misconception" by Murray (1978:77), in spite of it being based on relatively complete fossil material (Scott 1915). The diprotodontoid *Palorchestes*, whilst being one of the first marsupials to be reconstructed, has also had the most varied reconstructions, being variously envisioned as a giant kangaroo (Owen 1876, Fletcher 1945); a gracile llama-like form (Bartholomai 1978); a bizarre okapian (Ford 1982); an elephantine-trunked quadruped (Flannery and Archer 1985); to its most recent guise as a marsupial 'tapir' (Quirk and Archer 1983) or ground-sloth-like creature (Long et al. 2003).

Changes to how an animal has been reconstructed over time have normally been explained by reference to an increase in the availability of fossil material — "scientists of later periods have the benefit of more (and often better) specimens . . . than were available to their predecessors"(Rudwick 1992:220). The fossils of *Palorchestes*, however, are regarded as uncommon (Mackness 1995:606) or rare elements of fossil assemblages (Murray 1991:1106, Black 1997a:183), perhaps representing a solitary habit (Flannery 1983, Flannery and Archer 1985, Black and Mackness 1999). The hypothesis that the extraordinary divergence in how *Palorchestes* has been reconstructed is due solely to changes in the amount of fossil material available has never been tested. Nor does such a suggestion allow for the influence of other factors even though these have been shown to have directly affected the visualization of other animals (Desmond 1979, Bakker 1988, Gould 1991, van Reybrouck 1998).

This paper therefore seeks to systematically examine the major reconstructions of the marsupial 'tapir' *Palorchestes,* executed over the past 130 years, against the corresponding taxonomic understanding and available fossil material of the time in order to test the notion that changes in reconstructions of a particular animal result solely from improved fossil material and phylogenetic understanding and are independent of all other factor/s. The role played by palaeontological reconstructions in science communications is also discussed.

MATERIALS AND METHODS

Published reconstructions of *Palorchestes* from scientific and popular texts were digitally scanned and their main features rendered into line drawings. The taxonomic history of *Palorchestes* was chronologically arranged using summaries provided by Mahoney and Ride (1975) and Rich (1991). Details of fossils elements described were likewise listed in order of their publication following Woods (1958) and Rich et al. (1991), including those misidentifications that were used in the description of anatomical features of *Palorchestes*. Both these factors were compared against the line drawings of *Palorchestes* in order to ascertain whether there was any correlation between them. The possible effects of broader social and historical issues on each reconstruction were also considered.

RESULTS

Owen (1873) erected the genus *Palorchestes* on the basis of the anterior portion of a cranium, which included the rostrum. The holotype, collected by Dr Ludwig Becker from an unspecified deposit in Victoria, was named *P. azael* Owen, 1873. This locality has since been interpreted by Mahoney and Ride (1975) as the River Tambo in Gippsland. Owen assumed the animal was some sort of giant kangaroo as its cheek-teeth had longitudinal links between and in front of the transverse lophs (Archer 1984). These features were later shown to have independently evolved in both palorchestids and kangaroos (Woods 1958). Nevertheless, Owen was convinced at the time that the new animal was a macropodid, a view reflected in his choice of its generic name, a conjunction of two Greek words which literally translate as 'ancient leaper' (Owen 1874:797).

Two years later, Owen (1876) assigned further elements to *P. azael* including a left and right mandibular rami, sacrum, caudal vertebra, innominate bone, femur, tibia, calcaneum and metatarsals, even though there was no field association with the holotype (Woods 1958). This same paper also contained the first published attempt to reconstruct *Palorchestes* in the form of an outline of its skull (Owen 1876, plate 20). The drawing (Fig. 1a), incorporated a realistic rendering of the holotype with a significant amount of the skull being inferred from extant kangaroos. This included the posterior portion of the cranium and the dentary. Surprisingly, although two mandibular fragments were assigned to *Palorchestes* in the same paper, they were not figured as part of the reconstruction but were used to justify the shape of the jaw as being most similar to *Macropus*, based on the changes in the depth of the fossil rami, rather than other extinct kangaroos such as *Sthenurus* and *Protemnodon* (Owen 1876). By reconstructing *Palorchestes* as a macropodid, Owen effectively obfuscated those features that would eventually come to be recognized as unique to palorchestids, such as the reduction of the nasals.

Owen (1880a) described another species, *P. crassus* from fluviatile deposits near Gowrie, south-east Queensland, on the basis of the symphyseal portion of a mandible with an anomalous condition in the molars of the right ramus. Lydekker (1887), however, found the condition absent in the left ramus and therefore synonomized *P. crassus* with *P. azael*. Woods (1958:182), in supporting Lydekker's (1887) synonymy, further noted that the distortion originally described by Owen (1880a) was actually "postmortem fracturing, expansion and cementation with matrix". A palorchestid palate from the Wellington Caves, New South Wales, named *P. rephaim* by Ramsay (1885), was subsequently listed by both De Vis (1895) and Woods (1958) as *P. azael*. Consequently, the second valid palorchestid species to be described was *P. parvus* De Vis, 1895 from south-east Queensland. This new taxon appeared in De Vis's (1895) paper on fossil macropodid jaws leaving no doubt that he shared Owen's opinion that palorchestids were kangaroos. A premolar from Beaumaris Victoria identified by Hall and Pritchard (1897) as *Palorchestes* was later shown to belong to the Diprotodontidae (Stirton 1957).

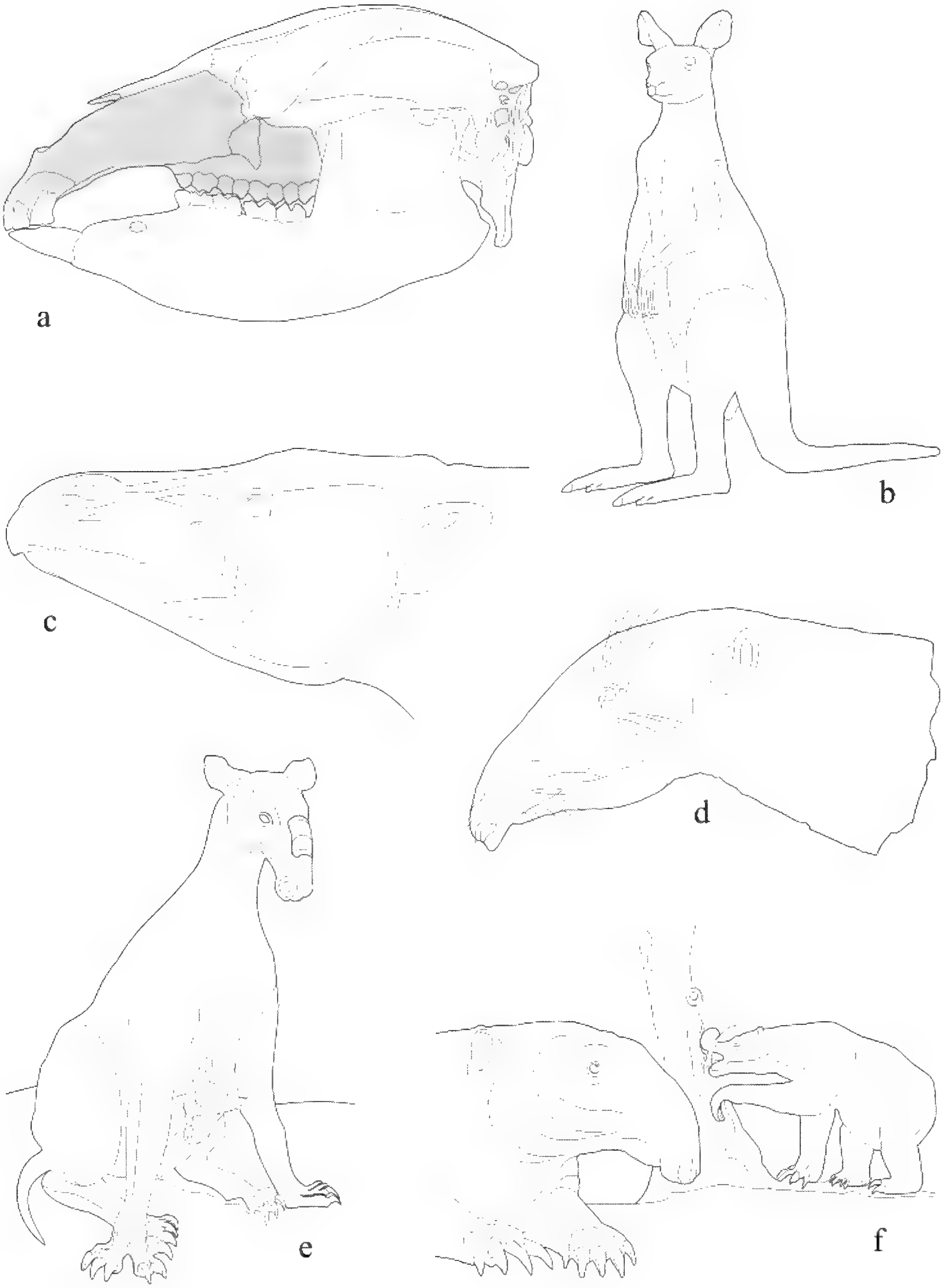

Figure 1. Historical reconstructions of *Palorchestes* from: a. Owen (1876); b. Fletcher (1945); c. Murray (1978); d. Bartholomai (1978); e. Ford (1982); f. Quirk and Archer (1983).

In 1912, the Trustees of the Australian Museum attempted the first three-dimensional reconstruction of *Palorchestes* using measurements from Owen and those from the mounted skins of living kangaroos (Fletcher 1945). The resulting sculpture stood almost three metres in height, even when posed in a resting position. Its imposing stature, when compared to that of living kangaroos, was said to have garnered much attention. This reconstruction was on display in the Museum for thirty-three years (Fletcher 1945).

During the post-wars years, the higher classification of some mammal groups, including palorchestids, was reviewed by several workers. Simpson (1945) placed *Palorchestes* within the subfamily Macropodinae, following Owen's lead, but the following year, Raven and Gregory (1946) moved it to the subfamily Sthenurinae. When Tate (1948) revised the kangaroos, he erected a new subfamily, the Palorchestinae, for *Palorchestes*. This meant that when the Australian Museum undertook a second supposedly more realistic reconstruction, taking into account "additional and important fossil remains" and to adopt "less misleading" assessments of how the animal should be modeled, *Palorchestes* was still thought of as a giant kangaroo (Fletcher 1945:363). The resultant model (Fig. 1b), was around 25% smaller than the 1912 original and photographed as the frontispiece of the Australian Museum Magazine (Fletcher 1945).

Claims that this new museum model was the most accurate possible were somewhat tarnished however by errors in Fletcher's (1945) accompanying text. He stated, for example, that *Palorchestes* was "first described in 1877 by Professor Sir Richard Owen, M.D., from the forepart of a cranium and portions of the jaw-bone with teeth" (Fletcher 1945:362-363) not in 1873 and based solely on a partial cranium as accepted by most other workers (Mahoney and Ride 1975, Mackness 1995, Black 1997a). Further, he interpreted the generic name *Palorchestes* to mean "the ancient dancer" (Fletcher 1945:362), even though Owen (1874a:797) specifically detailed its etymology. The greatest inaccuracies in the model, however, were to be exposed some thirteen years later. These were so significant that an embarrassed Australian Museum was forced to make a hasty and unceremonial disposal of their prized reconstruction (Archer 1984) with rumours still persisting that it is actually buried somewhere under Centennial Park in Sydney (M. Archer pers. comm.).

The catalyst for the Museum's precipitous action was a revision of *Palorchestes* by Woods (1958) who proposed that palorchestids were actually closer to diprotodontids than macropodids. The dentary of all kangaroos possess a large mandibular foramen and masseteric canal. Both of these features were absent or suppressed in *Palorchestes* (Archer 1984). This meant that all the kangaroo-based reconstructions were incorrect and that palorchestids were most probably quadrupedal like other diprotodontids. Further, postcranials that had been attributed to *Palorchestes* in the past (e.g. Owen 1876, Gregory 1902, Scott 1916, Fletcher 1945) were shown by Woods (1958) to belong to either extinct kangaroos or wombats.

The first undisputed palorchestid postcranial material was a series of caudal vertebrae of *P. azael* described by Bartholomai (1962), not in 1975 as claimed by Murray (1978). Five years after their description, a third palorchestid species, *P. painei* Woodburne, 1967, was named from the Miocene Alcoota fauna of central Australia. Significantly, it showed the same extensive modifications to the rostral area that had been observed in *P. azael* and *P. parvus* by Woods (1958). In that same year, Stirton (1967) also formally recognized the Palorchestinae, which included *Ngapakaldia* and *Pitikantia*, as a subfamily within the Diprotodontidae. Archer and Bartholomai (1978) later raised this to familial status — the Palorchestidae.

Further palorchestid postcranials were discovered in the seventies from a cave in the Wee Jasper area of New South Wales (Flannery and Archer 1985). These included a humerus and hindfoot which was subsequently prepared by the Australian Museum (Wells 1978). A humerus of *P. azael* was also reported from Victoria Cave, Naracoorte, South Australia by Wells (1975, 1978) along with phalanges and strange laterally-compressed scimitar-like claws, which Tedford of the American Museum of Natural History opined as being reminiscent of the extinct chalicotheres of the American Miocene. This led Wells (1978:109) to posit a tentative reconstruction of *Palorchestes* as "a large, quadrupedal grazing animal with longish limbs and plantigrade feet".

In the same year that Wells made his textual reconstruction, two new visual attempts were also published (Bartholomai 1978, Murray 1978). Both took account of Woods's (1958) new phylogenetic understanding of palorchestids rejecting the earlier macropodid-based reconstructions. Murray's (1978) sketch of a generalised *Palorchestes* (Fig. 1c), published in the specialist archaeological journal 'The Artefact', was based on the smaller Plio-Pleistocene palorchestid *P. parvus*. The reconstruction was part of a broader attempt to provide images of late Pleistocene fossil marsupials and a monotreme. Murray's (1978, Fig. 12) sketch only included the head and shoulder region, but a partial view of the entire animal was provided as part of a gallery of reconstructions (Murray 1978, Fig. 17). Following Woods's (1958) re-description of *P. parvus*, Murray (1978:88) posited that *Palorchestes* would have had a "mobile upper lip indicated by the prominent pre-maxillary flange in the skull of *P. parvus*". It appears that Murray (1978:88) was also familiar with Fletcher's (1945) article on the second model made by the Australian Museum as he repeated its error of interpreting the generic name of *Palorchestes* to mean 'graceful dancer'.

By contrast, Oakden's scrapper board drawing of *Palorchestes* (Fig. 1d), for Bartholomai's (1978) paper, was based primarily on the Miocene species *P. painei*. The catalyst for this reconstruction was the description of the cranium of *P. painei* by Woodburne (1967); the preparation of further cranial material of the same species collected from the Waite formation during the 1974 Ray E. Lemley expedition of the Queensland Museum; and similar but less complete material of *P. azael* and *P. parvus* held in the Queensland Museum (Bartholomai 1978:145). The reduction of the nasals, the elongation of the anterior of the palate and the presence of very large infraorbital foramina observed in these specimens led Bartholomai (1978) to postulate that all known species of *Palorchestes* probably had an extensive rhinarium or a tapir-like proboscis. Further, Bartholomai (1978) interpreted the narrow, deeply channeled mandibular symphysis as indicative of *Palorchestes* having had a long, flexible tongue.

There were differences between the two reconstructions of *Palorchestes*, however, that could not be explained simply by the fact that they were based on different species. While Murray (1978:88) characterized *Palorchestes* as a 'lightly buil[t] diprotodontid', Bartholomai (1978) reconstruction was even more gracile with the longer neck making the animal look very llama-like. The position of the nares also differed, with those of Murray (1978) placed more posterior and superior to those in Bartholomai (1978). The latter was in line with Bartholomai's (1978:148) assertion that *Palorchestes* may have possessed an "extensive rhinarium with anterodorsally directed nostrils". Bartholomai's (1978) *Palorchestes* was the first to feature a tapir-like trunk and also featured conspicuous vibrissae on the snout.

By 1980, confirmation that the Wee Jasper material was indeed palorchestid came when a partial skeleton in the collection of the National Museum of Victoria was also shown to be that of *Palorchestes* (Flannery and Archer 1985). Although the Museum skeleton had no locality data, its association with some undisputed palorchestid teeth made the specimen very important. Several of the bones in the skeleton had previously been labeled incorrectly by Scott (1916) as a giant species of wombat or wombat-like animal. Subsequently, other bones from Foul Air Cave at Buchan in eastern Victoria were also recognized as palorchestid. Given that the humerus of the Wee Jasper specimen was much smaller than the Buchan material, it was assumed that the Wee Jasper fossils represented *P. parvus* while the Buchan bones were those of the larger *P. azael* (Flannery and Archer 1985).

The identification of this additional postcranial material enabled a full reconstruction of *Palorchestes* as a quadruped. In 1981, Stahel produced a stipple drawing of an entire animal for an article published in a University newsletter (Archer 1981). This illustration was used the following year as the basis of a reconstruction (Fig. 1e) by Ibraham for an article in the science magazine 'Omega Science Digest' titled 'The strange creatures of ancient Australia' (Ford 1982). What is significant about both drawings is that they embodied a rather 'chimeraesque' understanding of *Palorchestes*, demonstrating a concomitant "high coefficient of weirdity" (Archer 1984:670). The overall body outline was rather 'okapian' with the hind-quarters lower than the front and the neck long and giraffid-like. The 'bizarre herbivorous animal' was said to be as "large as a horse . . . [with] a trunk-like structure on its face . . . kangaroo-like teeth . . . [a] long giraffe-like tongue and . . . phenomenally huge sharp claws" (Ford 1982:84-85). These sharp koala-like claws were even thought, for a brief time, to represent an adaptation to climbing in trees like modern-day sloths but the idea was rejected when the huge size of *Palorchestes* became apparent (Archer 1984:670). These speculative views of *Palorchestes* were informed by palaeontologist Mike Archer who, just one year later, was involved in the production of another reconstruction that directly challenged many of the assumptions inherent in the 'okapian' model (Archer 1984).

The rethink of how *Palorchestes* should be reconstructed was prompted by several factors including the identification of additional fossil elements and the opportunity to further refine or challenge aspects of previous reconstructions. The neck length of the Stahel and Ibraham reconstructions, for example, was deemed too long after the discovery that palorchestid cervical vertebrae were not elongate like that of giraffids (Archer 1984:670). Likewise, the size of the trunk was also thought to be over-inflated and consequently reduced with the tail likewise being shortened. These changes were encapsulated in a new rendering of *Palorchestes* which Archer (1984:670) judged to be the "best" to date, acknowledging however that his opinion was biased, given his involvement in its formulation. The reconstruction, executed by Schouten (Fig. 1f), appeared in a book on prehistoric animals published by the Australian Museum (Quirk and Archer 1983). Schouten presented a composite view of the head and front feet of *P. azael* along with a full-view of the animal ripping bark from a tree. Beneath this illustration, a further sketch was provided to demonstrate how *Palorchestes* may have used its tongue to strip vegetation off branches. The body shape of Schouten's *Palorchestes* was much more diprotodontid-like and its size more like that of a bull. The reconstruction also highlighted *Palorchestes*'s massive forearms; its rapier-like claws and tapir-like trunk. The text accompanying the new reconstruction was titled "unique trunked giant" and contained the first explicit connection between *Palorchestes* and Aboriginal people. Flannery (1983:54), who penned the text, suggested that *Palorchestes* may have been the inspiration behind the legend of the bunyip and that newly arrived Aboriginals may have had second thoughts about settling after seeing one of these giant marsupials. Further, Flannery (1983:54) claimed that Aboriginal people and *Palorchestes* had "co-existed in Australia between about 40 000-20 000 years ago".

In 1984, three different reconstructions of *Palorchestes* were executed by Murray, but in very different contexts. The first was a drawing of a generalized palorchestid (Fig. 2a) as part of a family tree of diprotodontoids presented in a children's book 'Australia's prehistoric animals' (Murray 1984a). Both *Palorchestes* and the mid-Miocene *Ngapakaldia* were shown on the same blue branch representing the Palorchestidae (Murray 1984a). In contrast to his 1978 reconstruction of *Palorchestes* (Fig. 1c), however, Murray's new depiction had a much longer tapir-like trunk. This interpretation was justified with the inclusion of a diagram showing the similarities between the skull and trunk of a tapir and that suggested for *Palorchestes*. Murray's illustration differed from Schouten's (Fig. 1f) in having a longer tail but smaller body. Murray was also the first to explicitly use the term "tapir-like marsupial" (Murray 1984a:20).

Murray's second reconstruction was specifically of *P. azael* (Fig. 2b) and was published in a book on Quaternary extinctions. As with Ford's (1982) characterization, *Palorchestes* was once again presented as a composite animal only this time it was said to have "tapir, chalichothere, pantodont and sloth-like features" (Murray 1984b:608). The "large kangaroo-like tail" of *P. azael* was highlighted, citing Bartholomai (1962) and a personal communication from the same author, while Archer and Bartholomai (1978) were quoted as the source of *P. azael* being "equipped with huge, curved, laterally compressed claws" (Murray 1984b:608). The overall body size of Murray's *P. azael* was much more massive than his more generalized drawing (Fig. 2a) and featured a long flexible tongue. Fossil remains of *P. azael* were regarded by Murray (1984b) as not especially common but widely distributed, with specimens of *P. azael* from Pulbeena Swamp in Tasmania, (54 200+11 000 - 4 500 yr BP) listed as a recent occurrence of the taxon (Banks et al. 1976).

Flannery's (1983) suggestion that *Palorchestes* and Aboriginal people lived contemporaneously was seemingly validated in 1984 when a large Aboriginal painting (Fig. 2c) was tentatively identified as a possible representation of the extinct marsupial (Murray and Chaloupka 1984). The painting, discovered in Deaf Adder Gorge, Arnhem Land in 1976, was part of a tradition called the Large Naturalistic Animal Style (sensu Chaloupka 1993), which included depictions of animals now extinct from the Australian mainland such as thylacines and Tasmanian devils (Calaby and Lewis 1977, Lewis 1977, Clegg 1978). Some of the features used by Murray and Chaloupka (1984) to identify the painting as *Palorchestes* included: 1) the considerable attention given to the tongue including small lines which were said to perhaps represent items of food such as leaves or insects; 2) the detail given to the claws and the angled calcaneal joint; and 3) a lack of ears. Two anomalous breast-like projections under the body were explained as "stylised attempts to show a long shoulder mane or shaggy long hair" (Murray and Chaloupka 1984:114). A smaller animal besides the larger painting was said to represent a joey of the extinct marsupial. Murray and Chaloupka (1984) compared the *Palorchestes* painting with those of introduced animals such as those found previously in Cape York (Trezise 1971) as well as a variety of megafaunal species.

In suggesting that the painting represented a *Palorchestes*, Murray and Chaloupka (1984:115) were extremely circumspect however, stating that "maybe it [the painting] represents *Palorchestes*" but "it must be made very clear that the connection at present is of the most tenuous kind". They even suggested that "there may not be much gained by attempting to compare this unique and intriguing painting with perhaps the most poorly known species in the megafaunal assemblages" (Murray and Chaloupka 1984:112). In spite of such tentativeness, however, and in spite of a serious challenge to both the methodology and assumptions used (Lewis

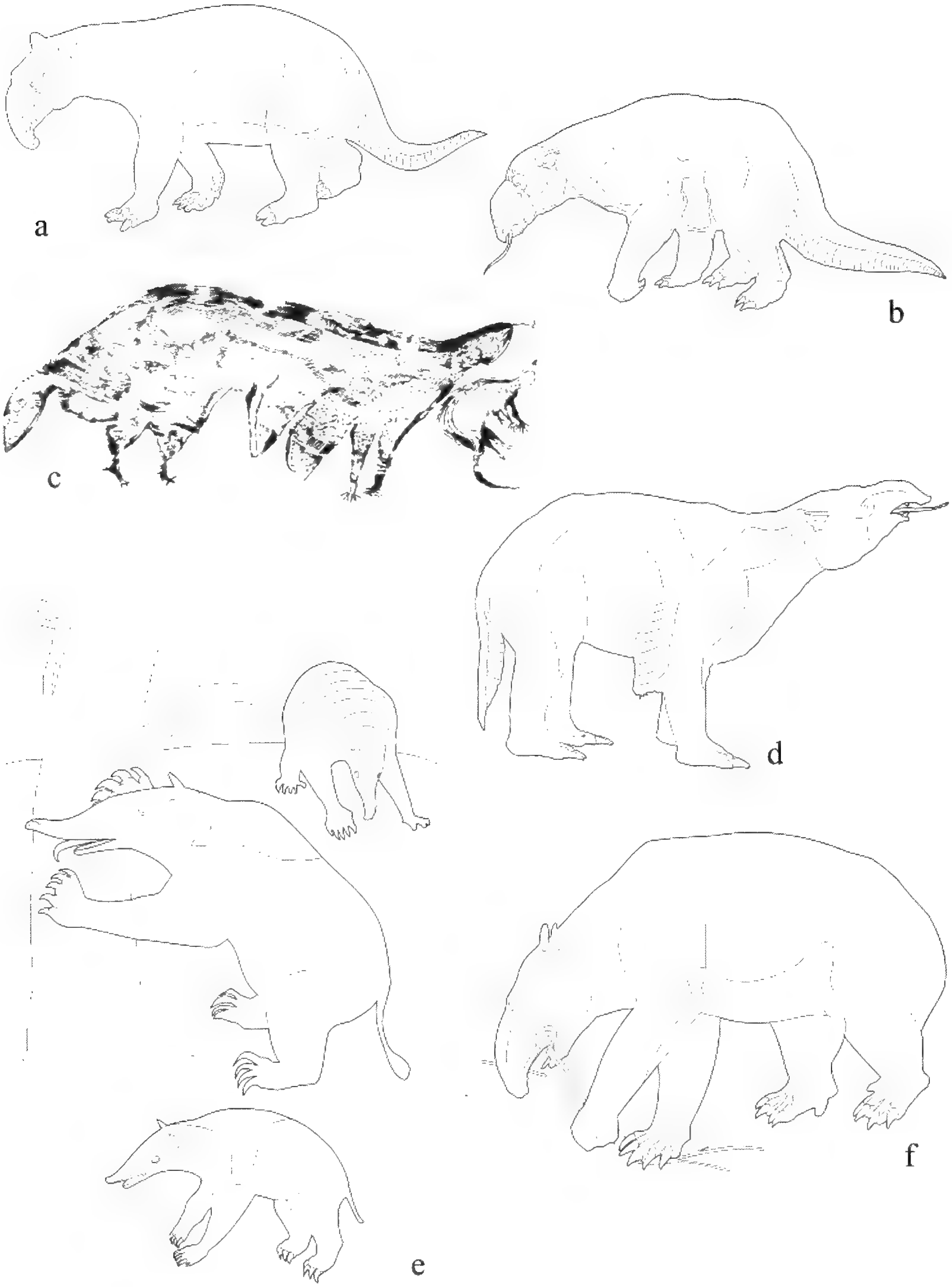

Figure 2. Further reconstructions of *Palorchestes* from: a. Murray 1984a; b. Murray 1984b; c. Arnhem Land 'Palorchestes' from Murray and Chaloupka (1984); d. Murray and Chaloupka (1984); e. Rich et al. (1985), f. Long et al. (2003).

1986, Mackness, unpublsihed data), the painting has been promoted as a credible example of megafauna depiction by Aboriginal artists (Chaloupka 1993, Flood 1997).

A third *Palorchestes* reconstruction (Fig. 2d) by Murray appeared in his joint paper with Chaloupka on rock art. What was unique about the reconstruction was that certain features were specifically added to match the supposed Aboriginal representation of *Palorchestes*. The most obvious of these was a mane of long hair protruding below the line of the abdomen to match the anomalous projections of the painting (Murray and Chaloupka 1984). This feature was not present in any of Murray's previous 1984 reconstructions. The ears were also placed so that they didn't project beyond the outline of the head to likewise match the painting. In Murray's generalised *Palorchestes* (Fig. 1a), the line of the ears was clearly shown projecting above the head. In support of such modifications, the authors restated Clegg's (1981:313) assertion that "if a well executed drawing of potentially great antiquity best matches a good restoration of an extinct species , then that may well have been the target species". While invoking this "Occam's Razor of rock art analysis" as justification for their identification of a *Thylacoleo* drawing, Murray and Chaloupka (1984:115) regarded the evidence for the *Palorchestes* drawing as being "less satisfactory" however.

While the reconstructions of *Palorchestes* by both Schouten and Murray featured relatively short tapir-like trunks and diprotodontid-like bodies, Knight's (Fig. 2e) composite illustration of *P. azael* and *P. parvus*, published in Rich et al. (1985), featured much longer trunks, body shapes more reminiscent of myrmecophagids and rhinoceros-like tails. Knight actually completed the illustration in 1982, around the same time that the Stahel and Ibraham reconstructions were published. The text accompanying the illustration, by Flannery and Archer (1985), provided the first detailed description of palorchestid postcranials along with a sketch of the articulated arm bones and a rear view of the humerus.

Flannery and Archer (1985) argued that the front legs of palorchestids were unusual, relative to other marsupials, because of a greatly enlarged area for the attachment of the pectoralis muscle which formed a high, hooked process. The ulna of both species was said to be almost solid with only a tiny marrow cavity. The nature of the articulation between the lower and upper arm bones in *P. azael* was such that it appeared to indicate an immobile elbow with the front legs being permanently locked in a partly flexed position, strengthening the already massive forearms. The smaller *P. parvus*, however, appeared to have a slightly more flexibility in this joint. The authors also drew attention to the highly mobile fingers that each bore a massive, sharp, laterally-compressed claw similar to that of a koala but far larger. Flannery and Archer (1985) interpreted these claws as suitable for ripping, tearing or climbing but not for digging.

By comparison, the authors considered the hindlimb of *Palorchestes* to be far less robust. The fourth and fifth toes were equipped with the same kind of massive claws seen on the fingers of the hands but toes two and three were reduced in size and syndactylous, perhaps used for grooming. Flannery and Archer (1985) also suggested that *Palorchestes* may have possessed a clawless opposable great toe similar to that seen in possums. Overall they suggested that *Palorchestes* filled a niche similar to that of elephants or the extinct ground sloths of the Americas, using its narrow and elongate tongue in conjunction with its trunk, to strip leaves off trees and bushes. Once again, an explicit connection was made between *Palorchestes* and Aboriginal people with the suggestion that the "exceptionally powerful forearms, massive claws and bizarre head would surely have been enough to have inspired the legend of the bunyip — or at least a few nightmares among Australia's first Aboriginal inhabitants" (Flannery and Archer 1985:236).

The composition of the Palorchestidae was challenged by Murray the following year with the description of the lamb-sized palorchestid *Propalorchestes* from mid-Miocene deposits of Bullock Creek Local Fauna, Northern Territory and several Oligo-Miocene sites at Riversleigh, Queensland. Doubts had previously been cast by Archer and Bartholomai (1978) and Archer (1984) about the monophyly of the Palorchestidae. Aplin and Archer (1987), in their review of marsupial systematics, had placed palorchestids in their present position within the Vombatiformes.

A further reconstruction of *Palorchestes* (Fig. 3) was executed by James Reece for a popular book on prehistoric life by Mackness (1987). Reece combined the reconstructions of Schouten and Knight to produce a hybrid image that adhered to a by now standard formula for illustrating *Palorchestes* with a diprotodontid body, sharp claws and tapir-like trunk. Such visual codification, called conventionalization by Rudwick (1992) enabled those viewing the animal to instantly recognize it as *Palorchestes*.

In 1990, Murray described another species of *Propalorchestes* and concluded that members of that genus were the plesiomorphic sister-taxon of

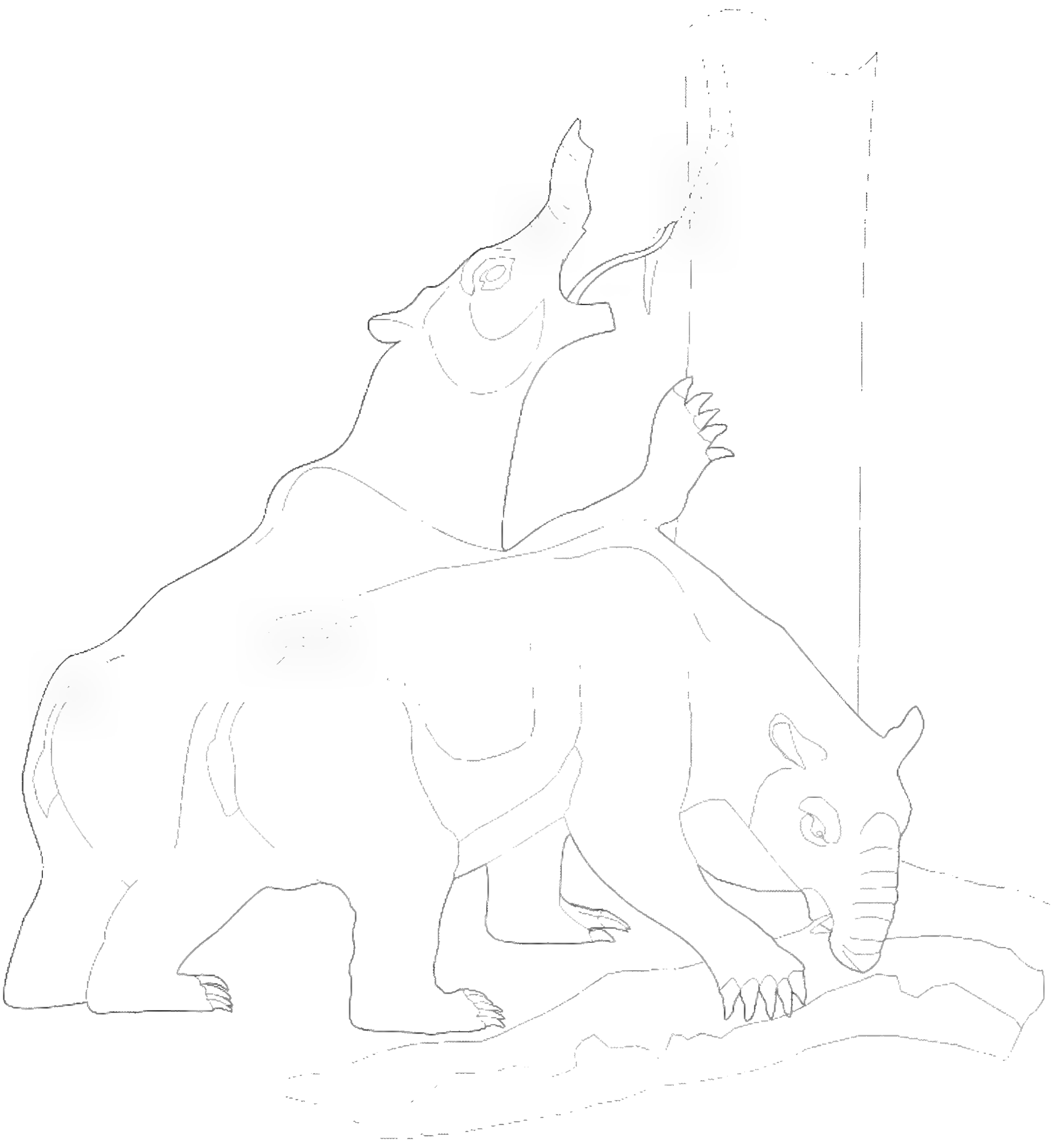

Figure 3. Reconstructions of *Palorchestes* from Mackness (1987).

Palorchestes while *Ngapakaldia* and *Pitikantia* should be regarded as primitive members of the Diprotodontidae (Black 1997a). Five years later, a new species of palorchestid, *Palorchestes selestiae*, was described from the early Pliocene Bluff Downs Local Fauna on the basis on an isolated M^1 (Mackness, 1995) with a fifth species, *P. anulus* described just two years later by Black (1997a) from the early-late Miocene Encore Local Fauna, Riversleigh, again on the basis of an isolated M^1. The most recently described palorchestid, *P. pickeringi*, was recovered by Piper (1996) from Pliocene and early Pleistocene deposits of Victoria. It is represented by a significant amount of fossil material and has also possibly been identified from Queensland (Hocknull et al. 2007).

By the last decade of the twentieth century, the term "marsupial tapir" had become firmly entrenched as the popular name for palorchestids (Murray 1991) even though alternative descriptors such as "marsupial tree-fellers" had been proposed (Flannery 1994). The visual codification of *Palorchestes* reconstructions continued to be refined with the most recent reconstruction of *P. azael* (Fig. 2f), executed by Anne Musser and published in Long et al. (2003), perhaps being the apogee of how the animal should be depicted. Musser's illustration did not show an exaggeratedly long tongue or a trunk capable of being bent back on itself as illustrated by Schouten. The forearms were shown to be immobile following Flannery and Archer (1985), while the tail was more like that proposed by Murray (1984b). The explicit connection between *Palorchestes* and the eutherian *Tapirus* was also being down-played with extinct ground sloths now being the dominant analogue. This suggestion, first raised by Archer (1984) and Murray (1991), was visually encoded by the depiction of *Palorchestes* walking on the sides of its feet or on its knuckles. Long et al. (2003) also included an illustration of the skull of *P. painei* showing its fragmentary nature, linking the real with the inferred in a similar manner to that first employed in Owen's (1876) first reconstruction almost a hundred and thirty years previously.

DISCUSSION

The veracity of palaeontological reconstruction is underpinned by a specific methodology which is supposedly deployed with each attempt to illustrate a prehistoric creature. Murray (1978:77) characterizes "serious" reconstructions as only those that are based on "detailed anatomical build up of soft tissues". This requirement challenges most reconstructions as very few conform to such rigor. Schouten visualized this same process using *Diprotodon* as an example in Quirk and Archer (1983). It should be noted, however, that it would have been singly impossible for any one artist to have the detailed anatomical knowledge required to undertake similar soft tissue build ups of all the other animals illustrated in that work.

Rudwick (1992:221) provided yet another outline of the methodology suggesting it occurs in the following sequence:- 1) the selection of suitable fossil bones for assembly of a partial skeleton of a particular individual; 2) the reconstruction of a complete skeleton representative of the species, based generally on the remains of many individuals; 3) reconstruction of a generalised complete individual body with inferences about the animal's unpreserved muscles and other soft parts, based partly on anatomical analogy with related living forms; 4) and finally inferences about the animal's dynamic mode of life and habits, based partly on functional analysis of its anatomy and on physiological analogy with related living forms. Rudwick (1992:221) posits that the outcome of such a sequence is "a cascade of representations that are progressively bolder—yet still well-founded—reconstructions of the unobservable prehuman past . . . progressing from the observed to the inferred, from the specific and contingent to the general and idealized". Changes in successive attempts to portray the same animal are simply "attributed to the discovery of more and better specimens that are relevant to that reconstruction" (Rudwick 1992:220).

Latour (1986:17), however, from whom Rudwick (1992) derived the notion of "cascade", uses the term in a much different sense. For Latour (1986:17), the sequence of reconstructing a prehistoric animal results in a "cascade of ever simplified inscriptions [visual representations] that allow harder facts to be produced". Therefore, it is the selection of bones from a collection to be used in the description of a new species or the reconstruction of a complete skeleton from bones held in several museums over a wide geographic locality that allow scientists to make "bolder" reconstructions. When a pile of individual elements are coalesced into a published type description or into an articulated form, they became a single entity of "the type of . . ." or "the skeleton of . . ." with all its associated eidetic qualities. This process of accumulation and simplification is only useful however when there is confidence that the meaning of each coalescence has been stabilized (Pinch 1985). If it hasn't, then all subsequent layers that are built upon it risk collapsing like a veritable 'house of cards' should the underlying assumptions prove to be unstable or incorrect.

Such was the case with Owen's (1876, 1877) reconstruction of *Palorchestes* as a macropodid. While in hindsight, it may seem that Owen made a grave error in his classification of the animal, Fyfe and Law (1988:1) caution that " . . . both the processes that lead to the creation of depictions, and the way in which they are subsequently used, have to be studied in their historical specificity". With *Palorchestes,* several factors mitigated against Owen recognizing its 'true' taxonomic affinities. The partial cranium used as the holotype, for example, lacked those features, such as the reduction and retraction of the nasals, which would eventually be regarded as autapomorphies for palorchestines. Indeed, it wasn't until almost a century later, after Woods (1958) had revised the genus and Woodburne (1967) had described *P. painei*, that suitable material became available to elucidate such characters.

The presence of longitudinal links between and in front of the transverse lophs, while used by Owen (1874) to justify *Palorchestes* as a kangaroo, has since been shown to be convergent with at least two zygomaturine genera — *Maokopia* Flannery, 1992 and a new, as yet unnamed, Plio-Pleistocene species from eastern Australia (Black and Mackness

1999. Mackness, unpublished data) possessing similar links. Flannery (1992:325) postulates that the development of "anteroposteriorly directed linking is an adaptation to a more abrasive diet". Similarly, it wasn't until the early part of the twentieth century that Abbie (1939) demonstrated that the presence of the masseteric fossa was a feature that united all macropodids. The fossil rami described by Owen (1876) lacked this relevant portion. Archer (1984) rightly concluded that the absence of such a feature in palorchestids didn't preclude the possibility that they were still a plesiomorphic sister group of kangaroos. It wasn't until Murray's (1986, 1990) description of *Propalorchestes* and detailed biostratigraphical research into the Riversleigh Local Faunas by Black (1997b) that the taxonomy of palorchestids obtained some sort of stability with many authors (e.g. Archer and Bartholomai 1978, Archer 1984, Murray 1990, Mackness 1995) having previously cast doubt about the phylogenetic make-up of the group.

The first major rethink about how *Palorchestes* should be reconstructed was not so much a result of additional and better fossil evidence becoming available as required by Rudwick's (1992) sequence, but rather a reassessment of existing museum material and a consequential re-interpretation of its phylogenetic affinities (Woods 1958). This conforms to Latour's (1986) notion of a 'cascade' with Wood's (1958) coalescence providing a stable platform for harder facts to be produced. When new fossil material was collected by Woodburne (1967) and Bartholomai (1978), it was therefore added to the already stable platform of 'palorchestids as diprotodontoids'. In particular, Bartholomai's (1978) interpretation that the rostral area of palorchestids may have supported a tapir-like proboscis or extensive rhinarium provided the basis for the interpretation of palorchestids as marsupial 'tapirs'. The lack of unequivocal palorchestid postcranials, however, apart from those described by Bartholomai (1962), meant that only the head region was known well enough for Bartholomai (1978) and Murray (1978) to attempt reconstructions — except for one very generalized body view (Murray's 1978, Fig. 17). Even after palorchestid postcranials had been discovered and identified from caves in New South Wales, Victoria and South Australia in the 1970's, their lack of publication meant they were effectively unavailable for use in reconstructions except for those few who had access to the relevant museum collections and the detailed anatomical knowledge to interpret what individual elements represented. To this day, the only description of these fossils is the popular account by Flannery and Archer (1985) in Rich et al. (1995).

The temporal lag of almost a decade between the discovery of these fossils and their incorporation into reconstructions also suggests that the relationship proposed by Rudwick (1992) may not be as straight forward as first thought. While some delay is to be expected, to allow for the preparation, study and publication of fossils, the postcranials of *Palorchestes* were never published in a peer-reviewed journal. Further, the most diverse representations of *Palorchestes* occurred between 1981 and 1983 (acknowledging that Knight's reconstruction was completed in 1982) after the concept of palorchestids as diprotodontoids was stabilized by Woods (1958). The various attempts at reconstruction may, in part, be due to scientists using them as heuristic devices to test various anatomical options. The fact that palaeontologists Archer and Flannery, supervised all these divergent 'views' of *Palorchestes* perhaps bears this out.

Van Reybrouck (1998), in his study of Neanderthal reconstructions, suggests that the intellectual *zeitgeist* may also affect how an organism is visualized. The publication of the various reconstructions of *Palorchestes* coincided with what Tedford (1991:76) characterizes as the "coming of age" of Australian vertebrate palaeontology with many academic institutions launching indigenous study programs at that time. Concomitantly, it was also a time when attempts were being made to raise the profile of the discipline in order to attract new students to the nascent palaeontological programs being offered at Universities (Vickers-Rich and Archbold 1991, Tedford 1991); to raise funds for research; and to mobilize and educate the general public (Quirk and Archer 1983, Rich et al. 1985, Mackness 1987). Perhaps not surprisingly, these popular texts featured creatures with superlative values such as the oldest, the largest or in *Palorchestes*'s case, the weirdest (Archer 1984:670). Part of the reason *Palorchestes* came to be reconstructed in so many guises was its 'weirdness' when compared to other marsupials.

As well as being co-opted as a 'poster child' to demonstrate the uniqueness of Australia's past, *Palorchestes* was included in some seminal debates about Aboriginality concerning the interrelated topics of land rights, environmental management and the extinction of the megafauna. Questions about the antiquity of Aboriginal settlement of the Australian continent had followed the widespread availability of radiocarbon dates (Mulvaney and Kamminga 1999) and in particular the dating of the Lake Mungo burials. A date of more than 40 000 years became a "slogan for indigenous people" (Gillespie 2004:1) and mobilized in legal arguments about rights to land (Yunupingu

1997). The contemporaneity of Aboriginal people and extinct megafauna was another plank in this argument with suggestions that *Palorchestes* was the subject of the bunyip legend (Flannery 1983, Flannery and Archer 1985) and its supposed representations in rock art (Murray and Chaloupka 1984) adding credence to such claims. While Owen (1880b) was amongst the first to implicate Aboriginal people and the extirpation of the Australian megafauna, the early eighties saw the emergence of a full blown debate on the issue (Horton 1979, 1980; Martin and Klein 1984), a subject that continues to provoke controversy two decades later (Flannery 1994, Horton 2000, Roberts et al. 2001, Wroe et al. 2004).

Consequently, while fossil discoveries and reinterpretations of phylogenetic relationships have played an important part in the varied reconstructions of *Palorchestes*, other broader factors have also been implicated. No matter what these influences are, however, they only become relevant if a particular reconstruction continues to be deployed. Corrigan (1988) contends that every time someone reproduces a reconstruction it becomes imbued with power. The context of reproduction can also play an important part in how a reconstruction is judged. Schouten's 1983 reconstruction of *Palorchestes azael* has, until recently, held sway not only because it supposedly best matched the fossil evidence and was the most sophisticated rendition (Archer 1984) but also because it appeared in a book published under the imprimatur of the Australian Museum, one of the nations leading scientific institutions. The most recent reconstruction by Musser in Long et al. (2003) has yet to gain the same widespread exposure of Schouten's effort but it obviously has only been in circulation for a short time. Its eventual hegemony also rests on the acceptance of the ground sloth analogy, explicit in the reconstruction rather than the existing and long-standing marsupial 'tapir' model.

Latour (1987:258) suggests that '. . .to determine the objectivity or subjectivity of a claim [like that made by a scientific illustration] . . . we look not for their intrinsic qualities but all the transformations they undergo later in the hands of others'. Consequently, future reconstructions of *Palorchestes* will not just be judged by whether or not they best fit the palaeontological information available but also whether they are reproduced in wide enough contexts to be accepted.

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A Basal Actinopterygian Fish from the Middle Devonian Bunga Beds of New South Wales, Australia.

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Choo, B. (2009). A basal actinopterygian fish from the Middle Devonian Bunga Beds of New South Wales, Australia. *Proceedings of the Linnean Society of New South Wales* **130**, 37-46.

A partial articulated skeleton of a basal actinopterygian fish is described from the Middle Devonian Bunga Beds of New South Wales. The specimen represents a new species and is questionably assigned as a congener of *Howqualepis rostridens* from the Middle Devonian of central Victoria. This represents the first record of an articulated postrcranium of a Devonian ray-finned fish from New South Wales. The pectoral fin of *Howqualepis* is also redescribed based on a re-examination of Victorian material. The fin is broader in shape and less extensively unsegmented than previously recognised. The close similarity of the new form with contemporaneous taxa from Victoria and the Aztec Siltstone of Antarctica adds to an already wide body of evidence supporting a regionally endemic freshwater vertebrate fauna in the Middle Devonian of Eastern Gondwana.

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KEYWORDS = Actinopterygians, Bunga Beds, Devonian, fish, *Howqualepis*, New South Wales

INTRODUCTION

In stark contrast to their modern abundance and diversity, actinopterygians are a sparse component of most Devonian vertebrate assemblages. Australia is notable in producing some of the finest fossils of Devonian actinopterygians, the best known of which are exceptionally preserved specimens from the Frasnian Gogo Formation of northern Western Australia. Included within the assemblage are *Moythomasia durgaringa* (Gardiner & Bartram 1977, Gardiner 1984), the currently preoccupied *"Mimia" toombsi* (ibid), *Gogosardina coatesi* (Choo et. al, in press) and at least two additional forms (Choo, in prep).

Southeastern Australian fossil sites have also produced a substantial amount of early ray-finned fishes. The first record of Australian Devonian actinopterygians consisted of the isolated scales of *Ligulalepis toombsi* from the Lower Devonian Taemas-Wee Jasper Limestones of New South Wales (Schultze 1968). A subsequently discovered braincase and skull-roof was assigned to this genus (Basden *et al.* 2000, Basden & Young 2001). Long (1988) described *Howqualepis rostridens* based on numerous specimens from the Givetian Mt Howitt fauna of central Victoria (age revised in Young, 1999).

Adding to this Eastern Australian record is an incomplete but articulated fossil that was recently discovered by Gavin Young from the Middle Devonian Bunga Beds, near the shoreline at Bunga Beach in south coastal New South Wales. This represents the first discovery of an articulated Devonian actinopterygian postcranium from New South Wales. Subsequent repeated searches failed to recover additional material of this form (Gavin Young, pers. com.).

GEOLOGICAL SETTING

The Bunga Beds represent a thinly bedded sequence of carbonaceous shale and sandstone that comprises the lowest section of an extensively fossiliferous Devonian sequence (Fergusson et al. 1979, Young 2007). Young (2007, figs 1, 2) provides and up to date account of the lithology, fossil assemblage and possible age of the Bunga Beds. The age of the unit is poorly constrained and probably older than the Late Devonian age stated in recent literature (Cas et al. 2000, Giordano and Cas 2001, Rickard and Love 2000).

The dark shales of the Bunga Beds are highly fossiliferous with abundant plant material and uncommon vertebrate remains (Young 2007, fig. 3), possibly representing a deepwater lacustrine depositional environment. The fossil fish fauna includes ischnacanthid acanthodians (Burrow 1996), several taxa of chondrichthyans including *Antarctilamna prisca* (Young 1982), originally described from the Givetian Aztec Silstone of Antarctica, and a possible tetrapodomorph sarcopterygian (Young 2007, table 1). The fossil ichthyofauna of the Bunga Beds seems impoverished due to the apparent absence of placoderms and dipnoans that are abundant in other southeastern Australian sites of a similar age.

MATERIALS AND METHODS

The fossil was recovered as a natural mould set within a matrix of dark shale. After collection, the specimen was split into part and counterpart and bone remnants removed. Bone margins were exposed with mechanical preparation and the impressions of the fish were examined using a latex rubber cast whitened with ammonium chloride. For comparison, fresh latex casts were made from the following specimens of *Howqualepis rostridens* in Museum Victoria (MV) = P.160745A, P.160782A, P.160788, P.160792B, P.160811, P.160822A, P.160851B, P.160857.

Abbreviations for actinpterygian dermal bones and other structures used in the text and figures are as follows: **an.f**, anal fin; **Br. 1**, 1st branchiostegal ray; **Br. 7**, 7th branchiostegal ray; **c.ful**, caudal (basal) fulcra; **Clav**, clavicle; **Clth**, cleithrum; **cw.lep,** cutwater of short lepidotrichial segments; **d.lep**, probable dorsal lepidotrichia; **f.ful,** fringing fulcra; **nm**, notochordal mass of caudal fin; **Op**, operculum; **Sop**, suboperculum; **pec.f**, pectoral fin; **pel.f**, pelvic fin; **pseg,** segmented posterior lepidotrichia on pectoral fin; **tfr,** terminal fringe of fine branching segments on pectoral fin; **vhl,** ventral hypochordal lobe of caudal fin; **useg.** unsegmented proximal lepidotrichia on pectoral fin.

SYSTEMATIC PALAEONTOLOGY

CLASS OSTEICHTHYES Huxley, 1880
SUBCLASS ACTINOPTERYGII, Cope, 1887
Family Howqualepididae Long, Choo and Young, 2008

Diagnosis (revised)

Basal actinopterygians with an open spiracular slit bordered by the intertemporal, dermosphenotic and supratemporal. Intertemporal is very small (less than 1/3 the size of parietals). Pineal foramen present on anterior half of the median frontal contact. Dermosphenotic is elongate and tripartite. Suboperculum has a prominent anterodorsal process. Body form is elongate and fusiform. Squamation macromeric; scales are rhombic with linear ganoine ornamentation. Fringing fulcra are spine-like terminal sections of the anterior fin rays, lacking median contact between the hemilepidotrichia. Longest anterior pectoral fin rays are proximally unsegmented for over 60% of their length. Median scute series on dorsal and ventral surface do not extend anteriorly to reach the head.

Remarks

Diagnosis slightly modified from Long et. al (2008) to incorporate the revised description of the pectoral fin and fringing fulcra of *Howqualepis* presented below.

Genus *?Howqualepis* Long, 1988
?Howqualepis youngorum sp. nov.

Etymology

After Professor Gavin Young (ANU) who discovered the holotype specimen and Mr Ben Young for conducting both the preparatory work as well as the key photography of the specimen.

Repository

The type and only known specimen is lodged in the collections of the Department of Earth & Marine Sciences, Australian National University, Canberra, represented in the text by the prefix **ANU V**.

Holotype.

ANU V2929a, b, an incomplete, partially articulated fish preserved laterally in part and counterpart. Consists of an incomplete opercular-gular series, cleithrum, clavicle, scales and all fins except the dorsal fin (Figs. 1-4). Collected by Gavin Young (ANU) from the Bunga Beds at Bunga Beach, south of Bermagui, New South Wales.

Diagnosis

A *Howqualepis* with more than 54 primary lepidotrichia on the anal fin and porous ornamentation on the cleithrum and clavicle.

Remarks

Tentatively assigned to the genus *Howqualepis*. The extensive unsegmented pectoral lepidotrichia of *?Howqualepis youngorum* sp.nov separates this taxon from all other Devonian actinopterygians except *Howqualepis rostridens* Long, 1988, *Donnrosenia schaefferi* Long, Choo and Young, 2008, and *Tegeolepis clarki* Newberry, 1888. *?H. youngorum* differs from *Donnrosenia* in that the unsegmented fin-rays account for more than 75% of the total length of the pectoral fin. *?H. youngorum* differs from *Tegeolepis* in possessing macromeric squamation, long-based pelvic fins and a segmented terminal fringe on the pectoral fin. Separable from *H. rostridens* in having porous (as opposed to entirely linear) ornament on the pectoral girdle and in having a larger anal fin (54+ vs 45 primary lepidotrichia).

DESCRIPTION

Overall body form

ANU V2929 is preserved in lateral aspect (Fig. 1). The anterior part of the specimen terminates at an oblique breakage margin, with elements of the opercular-gular series and pectoral girdle preserved along with the pectoral fin (Fig. 2). 2.5 cm behind this is an incomplete pelvic fin with patches of squamation present above and to the rear of the fin (Fig. 3). The largest preserved segment comprises the rear section of the fish, including well preserved anal and caudal fins along with extensive squamation (Fig. 4). The preserved sections suggest a highly elongate, fusiform body form similar to that of *Howqualepis rostridens* (Long 1988) and quite unlike the more compact and robust form of "*Mimia*" or *Moythomasia* (Jessen 1968, Gardiner 1984).

As preserved, the fossil measures slightly less than 12 cm from the anterior preserved edge of the clavicle to the posteriormost caudal scales. Assuming that the missing portions of the fish were of similarly proportions to that of *Howqualepis rostridens*, the complete fish would have measured about 14 cm from snout to caudal peduncle.

Opercular-gular series

A section of the dermal operculo-gular series of ANU V2929 is preserved in articulation and comprises

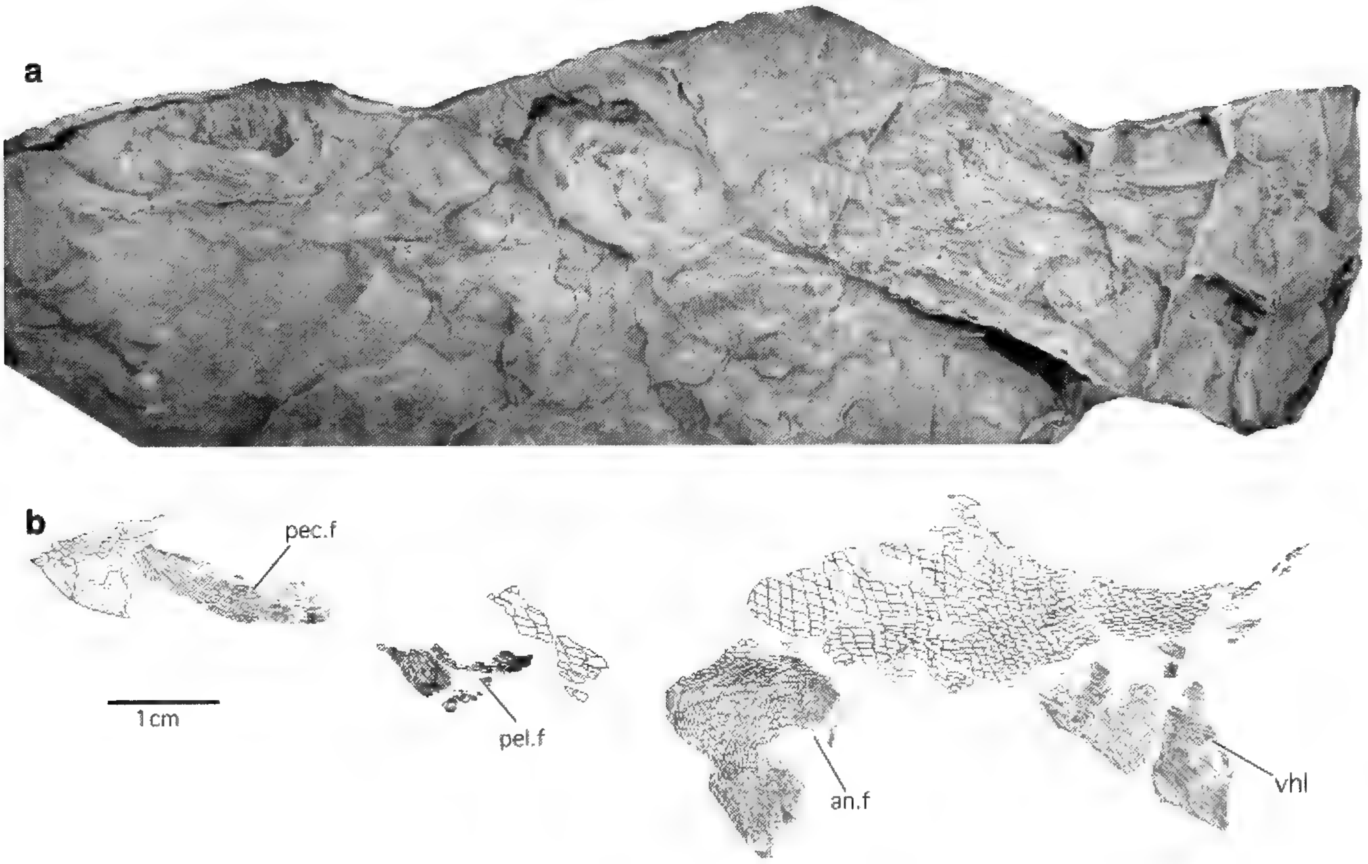

Figure 1. *?Howqualepis youngorum* sp. nov. a. photograph and b. line drawing of holotype (ANU V2929A) showing the entire preserved fossil in lateral view. The specimen is a latex cast whitened with ammonium chloride.

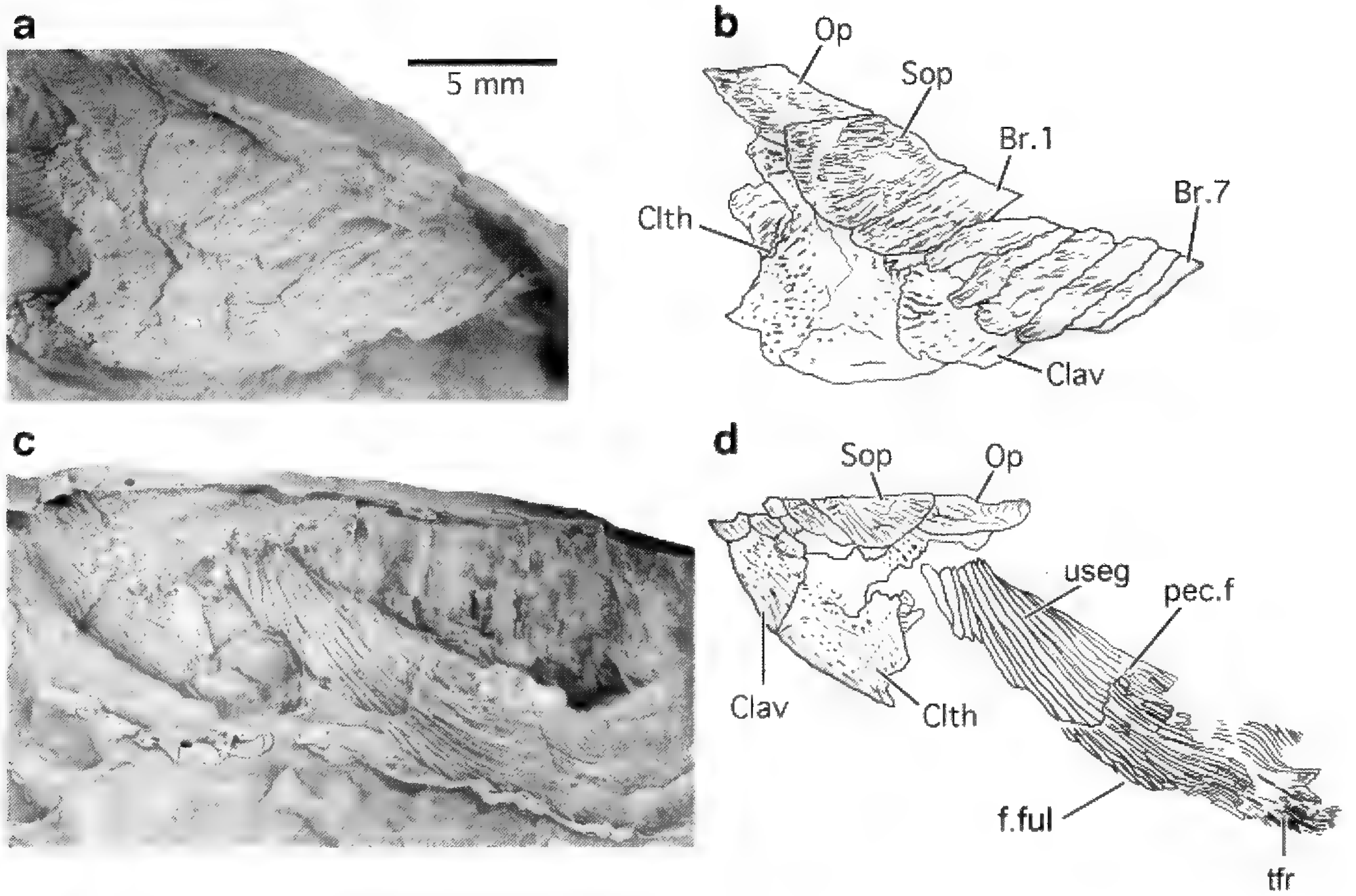

Figure 2. ?*Howqualepis youngorum* sp. nov. a. photograph and b. line drawing of the pectoral girdle and opercular-gular series of the holotype counterpart (ANU V2929B), c. photograph and d. line drawing of pectoral girdle, opercular-gular series and pectoral fin of the holotype (ANU V2929A).

a posteroventral fragment of the operculum, a partial suboperculum, and at least seven branchiostegal rays (Fig.2). The anterior portions of most of these elements are missing, the preserved sections terminating at a margin of clean breakage, suggesting that a substantial portion of the fossil, possibly including the skull, was lost prior to collection due to weathering.

The posterodorsal-most bone in the series is tentatively identified as the posteroventral fragment of an operculum. It is an oblong bone bone, missing the dorsal and anterior margins. The bone surface is ornamented with short, posterolaterally directed linear ridges. The suboperculum is rectangular with a convex posterior margin. Ornament consists of short linear ridges that extend to near the posterior bone margin.

At least seven branchiostegal rays are visible on ANU V2929b (Fig. 2). The first branchiostegal ray, whose dorsal margin is overlapped by the suboperculum, is more than twice as thick dorsoventrally as the other bones in the series. The 2nd ray is poorly preserved while the 3rd is narrower than the following two rays. Rays 6 and 7 are very narrow. Ornament on all bones in this series consists of short rostrocaudally directed ridges with little evidence of the tubercular ornament present on the laterally facing branchiostegals of *Howqualepis rostridens* (Long 1988).

Pectoral girdle

A partial cleithrum and clavicle (Fig. 2) have a similar overall shape to those of most early actinopterygians. The cleithrum consists of an expanded ventral region with a slender vertically directed blade although the dorsal portion of this structure is missing. The bone is convex postiorly with a moderately deep embayment on the posterior margin for the insertion of the pectoral fin, similar to that of *H. rostridens* (Long 1988. Fig.27). The clavicle is triangular and overlaps the cleithrum posteriorly and is itself dorsally overlapped by the branchiostegal rays.

Preserved sections of ornament on both the cleithrum and clavicle consists of limited areas of short ridges, particularly around the posterior margin of the clavicle and the vertical blade of the cleithrum, that are largely replaced by rostrocaudally oriented rows of small pores over most of the remainder of the bone surface. This differs from the condition in *Howqualepis rostridens* where the dermal surface of the corresponding area is covered in a mixture of ridges and raised tubercles with no porous ornamentation (Long, 1988. Fig.15). *Donnrosenia* has very similar ornamentation on the clavicle but has entirely linear ornamentation on the cleithrum (Long, Choo & Young, 2008. Fig.6). *Moythomasia durgaringa* and *M. nitida* also have porous ornamentation on the pectoral girdle, but restricted to the ventral faces of the cleithrum and clavicle (Choo, in prep) whereas pores are also present on the lateral surface in ?*H. youngorum.*

Fins

The pectoral fin (Fig. 2) is incomplete with no traces of the endoskeletal radial although the visible lepidotrichia are well preserved. The fin is elongate and triangular with more than 14 primary lepidotrichia present. As with *H. rostridens* and *Donnrosenia*, the anterior lepidotrichia are unsegmented for most of their length with secondary division restricted to the region near the fin margin. The trailing edge of the fin is not preserved and it is unclear if the posterior fin rays were fully segmented as in *H. rostridens* (see below). The fin reaches its maximum length at about the seventh primary ray, which is unsegmented for more than 75% of its length as in *H. rostridens*, longer than the c.65% unsegmented region in the fin of *Donnrosenia* (Long et.al, 2008). A short section of the leading edge is preserved with spine-like fringing fulcra formed by terminal branching of the leading fin rays. As with *H. rostridens* and *Donnrosenia* (see below) there is no medial contact visible between the distal hemilepidotrichia of each fringing fulcra on any of the fins.

The pelvic fin (Fig. 3) is long-based and triangular. Its preserved lateral aspect and does not appear to be as elongate as in *H. rostridens* although it is unclear if a section of the posterior margin is missing. The fins are located approximately midway along the body between the pectoral and anal fins. Primary lepidotrichia are only preserved for the anterior half of the fin, comprising more than 22 rays suggesting more the 40 primary rays on the entire preserved section. These rays are evenly segmented along their preserved length. Slender spine-like fringing fulcra are present on the leading edge.

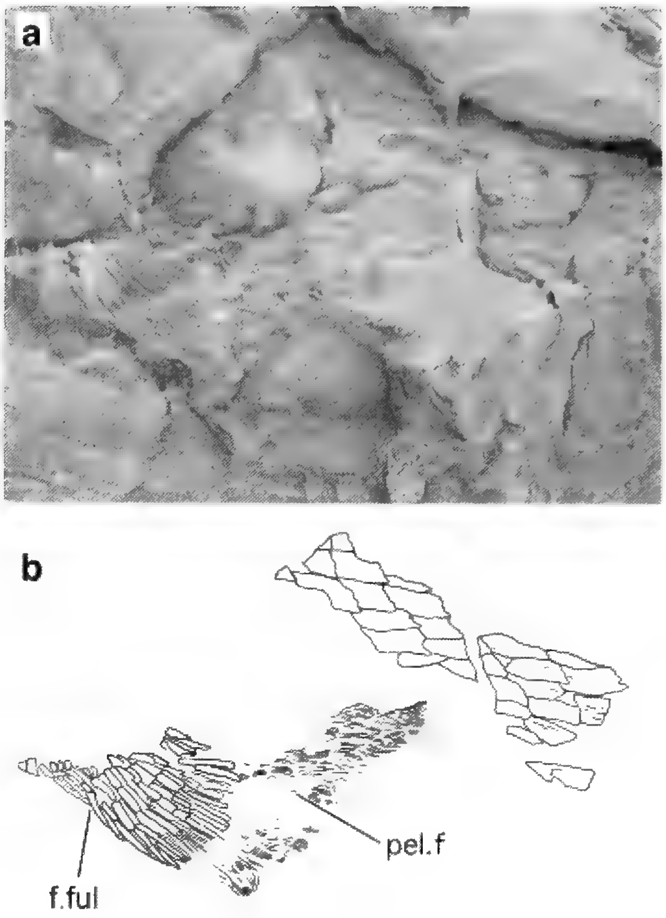

Figure 3. ?*Howqualepis youngorum* sp. nov. a. photograph and b. line drawing of the pelvic fin and associated squamation on ANU V2929A.

The anal fin (Fig. 4a, b) is large and triangular in shape. At least 54 primary segmented lepidotrichia are present as opposed to c.45 fin rays on the anal fin of *H. rostridens.* It is unclear if the fin originally had a short posterior fringe trailing behind the main triangular area of the fin as in *H. rostridens*. If this was the case then the complete fin would have probably had over 60 primary lepidotrichia. As in the other fins, shortened spine-like lepidotrichial segments form a serrated cutwater of fringing fulcra on the leading edge.

As was the case in other known Devonian actinopterygians, the caudal fin (Fig. 4) was heterocercal in structure with a distinct posterior cleft separating the dorsal lobe (notochordal mass of the fin plus the dorsal hypochordal lobe) from the ventral hypochordal lobe. While little of its dorsal counterpart has been preserved, the ventral hypochordal lobe is elongate and triangular with c.40 primary lepidotrichia preserved. Spine-like fringing fulcra are present on the leading edge.

The dorsal fin is not preserved in the holotype although a pair or large, isolated lepidotrichs preserved near the counterpart tail may have originated from that fin (Fig. 4d).

Scales and squamation

Articulated macromeric scales, scutes and basal fulcra are preserved from the caudal fin, extending

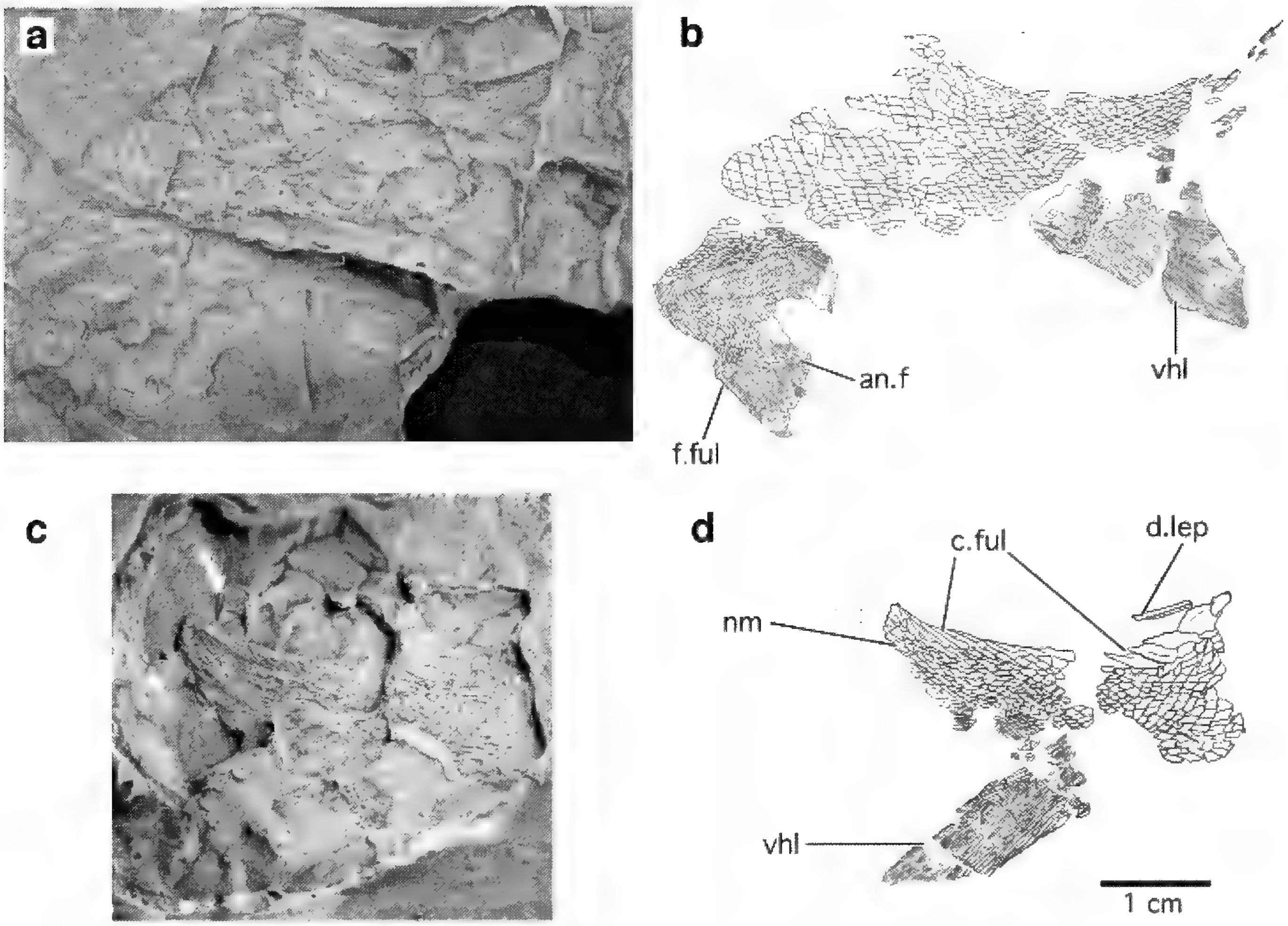

Figure 4. ?*Howqualepis youngorum* sp. nov. a. photograph and b. line drawing of the anal and caudal fins of ANU V2929A, c. photograph and d. line drawing of the caudal fin of the holotype counterpart (ANU V2929B).

forwards to above the anal fin (Fig. 4c, d). There are also isolated patches of scales preserved above and to the rear of the pelvic fins (Fig. 3). Very little of the scale ornamentation has been preserved. The visible scale types are described in accordance with the zonation terminology as proposed in in Esin (1990) and employed in Trinajastic (1999).

Area C = flank scales extending from above the pelvic fins to above the anal fin. Scales are elongate and rectangular, with rostrocaudal length being at least twice the height of the scale. Ventral margin is gently convex. The disposition of the peg and socket articulation is unknown in the scales close to the pelvic fins and absent in the scales near the anal fin. Free field ornamentation is poorly preserved but individual scales show remnants of longitudinal furrows. Scales from near the front and rear of the field seem to have two or three serrations protruding along the caudal edge suggesting little or no rostrocaudal decrease in the number of serrations.

Area D = scales anterior to the caudal fin and on the notochordal mass of the caudal fin.

Scales anterior to the caudal fin are rhombic in form, becoming smaller and increasingly elongate on the notochordal mass of the fin. Scales near area C have a gently convex ventral margin, becoming less prominent towards the caudal fin until the margin is completely straight at those scales near the caudal inversion. Peg and socket articulation is absent. The free field is smooth with no preserved traces of raised ornamentation. Posterior serrations range from two in scales near area C to none on those scales on the caudal fin.

Area H = scales adjacent to the base of the anal fin. These scales are small, elongate rhomboids. Peg and socket articulation is not visible and probably absent. There is no evidence of ornamentation or posterior ridges.

The only dermal scutes that have been preserved are an articulated series visible anterior to the dorsal caudal lobe and extending over the dorsal margin of the caudal fin (Fig 3b, c). Anterior to the caudal fin, the scutes are triangular plates with a caudallydirected apex and are about three times longer than the adjacent flank scales. As the series progresses posteriorly over the notochordal mass of the caudal fin, the scutes narrow and spine-like with extensive overlap between the individual scutes.

Redescription of the pectoral fin of *Howqualepis rostridens*

Long (1988) described the pectoral fin of *Howqualepis rostridens* as consisting of 25 primary lepidotrichia that are unsegmented for most of their extent, save for some secondary division near the fin margin. A complete pectoral fin was not figured and re-examination of this form has revealed the fin to be more extensive than previously recognised (Fig. 5). Additionally, the leading edge of the pectoral and other fins was described as having short, parallel rays similar to fringing fulcra, but not paired (ibid). A similar condition in *Donnrosenia* led to Long et. al (2008) to diagnose the Howqualepididae as possessing short spine-like lepidotrichia in lieu of true fringing fulcra.

The anterior two-thirds of the fin consist of c.25 lepidotrichia that possess extensive proximally unsegmented sections that in some specimens display distal bifurcation. At the lateral margins, these primary rays branch into a fringe of narrow, segments. The relative length of the proximal rays to the segmented fringe is variable, with the unsegmented region accounting for between 75-90% of the length of the fin. There appears to be no correlation between the degree of distal segmentation and the size of the specimen.

Posterior of the unsegmented rays are at more than 10 additional primary lepidotrichia that are segmented from base to margin, again displaying a variable degree of distal branching. The pectoral fin of *H. rostridens* was thus broader in shape and less-extensively unsegmented than has previously been described. In the majority of specimens, the delicate elements of the posterior rays and terminal fringe are scattered or missing, leaving only the thick unsegmented proximal sections in articulation. This configuration of the pectoral fin-rays is similar to that of a number of Carboniferous taxa including *Rhadinichthys* (Moy-Thomas & Bradley Dyne, 1938).

On the leading edge of the pectoral fins of *Howqualepis rostridens*, *?H. youngorum* sp.nov and *Donnrosenia*, the terminal sections of the otherwise unsegmented marginal fin rays branch at least twice, to forming narrow spine-like elements that are not obviously paired. These elements are called "terminal lepidotrichia" in *Cheirolepis* (Pearson and Westoll, 1979) and *Melanecta* (Coates, 1998) or "cutwater lepidotrichia" in the Howqualepididae

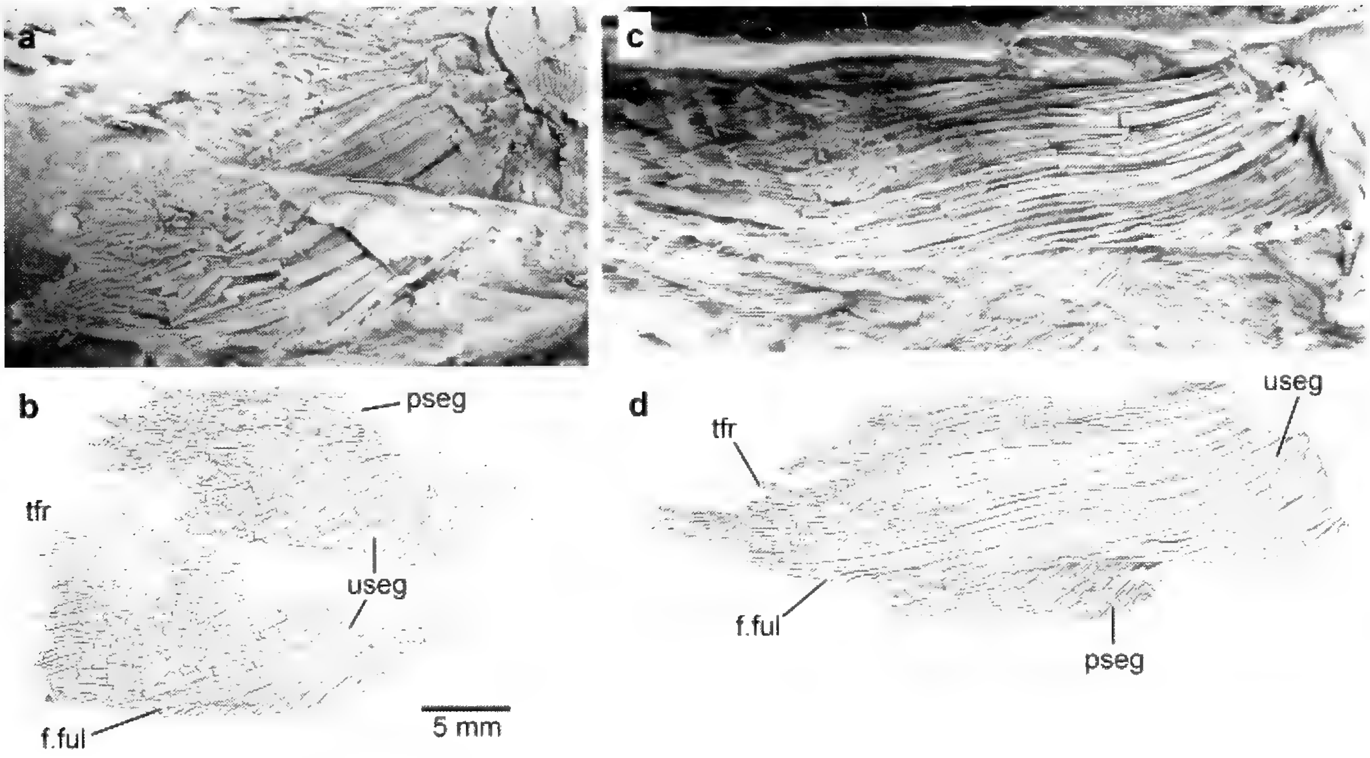

Figure 5. Pectoral fin of *Howqualepis rostridens*. a. photograph and b. line drawing of the fin of MV P.160857. c. photograph and d. line drawing of the fin of MV P.160851B. In this specimen, the posterior section has partially torn off and folded to be visible ventral of the anterior edge of the fin.

(Long, Choo and Young, 2008). In a recent study, such structures fall into Arratia's "Pattern A" class of fringing fulcra, formed from overlapping branched projections of the anteriormost lepidotrichia (Arratia, in press), a condition found in all undisputed Devonian actinopterygians with the exception of *Tegeolepis* which appears to lack any sort of spiny cutwater (Dunkle and Schaeffer, 1973). The fulcra of *Cheirolepis*, which are of similar form to those of the Howqualepididae, comprise distally enlarged hemilepidotrichia that partially enclose their paired counterparts (Arratia, in press). The more obviously paired structures present in *Moythomasia* and "*Mimia*" (also falling within "Pattern A") are the result of the terminal segments being of equal length and in medial contact. Given that the scheme proposed by Arratia (and adopted here) means that all Devonian fringing fulcra are in fact modified spine-like lepidotrichia (merely differing in the nature of contact between the hemilepidotrichia), the diagnosis of Howqualepidiae has been adjusted accordingly in the systematic description.

DISCUSSION

Long, Choo and Young (2008) erected the Howqualepididae, comprising *Howqualepis rostridens* from Mount Howitt, Victoria and *Donnrosenia schaefferi* from the Aztec Siltstone of Antarctica. ANU V2929 appears to represent a third taxon within this clade (Fig. 6). All three fish have an elongate body form with macromeric squamation; long-based pelvic fins; small fringing fulcra without medial contact between the distal hemilepidotrichia, and extensive unsegmented primary lepidotrichia that comprise most of the length of the pectoral fin. Among the other Devonian actinopterygians, only *Tegeolepis clarki* (Dunkle and Schaeffer, 1973) possesses extensive unsegmented pectoral lepidotrichia but is distinguished from the Gondwanan forms in lacking a terminal segmented fringe on the pectoral fins, in possessing micromeric squamation and having small, short-based pelvic fins.

Assigning the Bunga Bed taxon to a genus is rendered difficult owing to the lack of key skull characters that are used to characterise *Howqualepis rostridens* from the similar *Donnrosenia*. For example, *H. rostridens* possesses an extremely long maxillary blade, a dentigerous rostral and small, dorsoventrally compressed premaxillae (Long 1988). *Donnrosenia* displays a short, deep maxillary blade, dorsoventrally prominent premaxillae, a small accessory operculum and much smaller teeth than *Howqualepis* (Long, Choo and Young, 2008).

ANU V2929 is considered to be closer *H.rostridens* in having more extensive unsegmented pectoral lepidotrichia and relatively smaller scales than *Donnrosenia*. The pectoral fins of ANU V2929 are more similar to that of *H. rostridens* in that both forms possess unsegmented lepidotrichia that account for over 75% of the maximum length of the fin. Those of *Donnrosenia* account for less than 70% of the maximum fin length (Long, Choo and Young, 2008. Fig.7).

Based on these anatomical similarities and pending the discovery of skull material for this taxon, ANU V2929 is tentatively assigned to *Howqualepis*. The Bunga Bed form is not conspecific with *H. rostridens* and is distinguished in having a larger anal fin with a greater number of primary lepidotrichia and in possessing porous dermal ornamentation of the pectoral girdle.

The presence of a grade of Devonian actinopterygian so far found exclusively in Middle Devonian freshwater deposits of southeastern Australia and Victoria Land, Antarctica highlights the close biogeographical similarity between the fossil faunas of these two regions. The apparent absence of these ray-finned fishes in Devonian sites outside this area also adds to a growing body of fossil evidence that indicates a regionally endemic freshwater vertebrate fauna within Middle Devonian Eastern Gondwana. Similarities in key taxa of placoderms (Young 1988, Young and Long 2005), acanthodians (Long 1983, Young 1989, Young & Burrow 2004), chondrichthyans (Young 1982, 2007; Long & Young 1995) and dipnoans (Long 1992, 2003) have been well documented.

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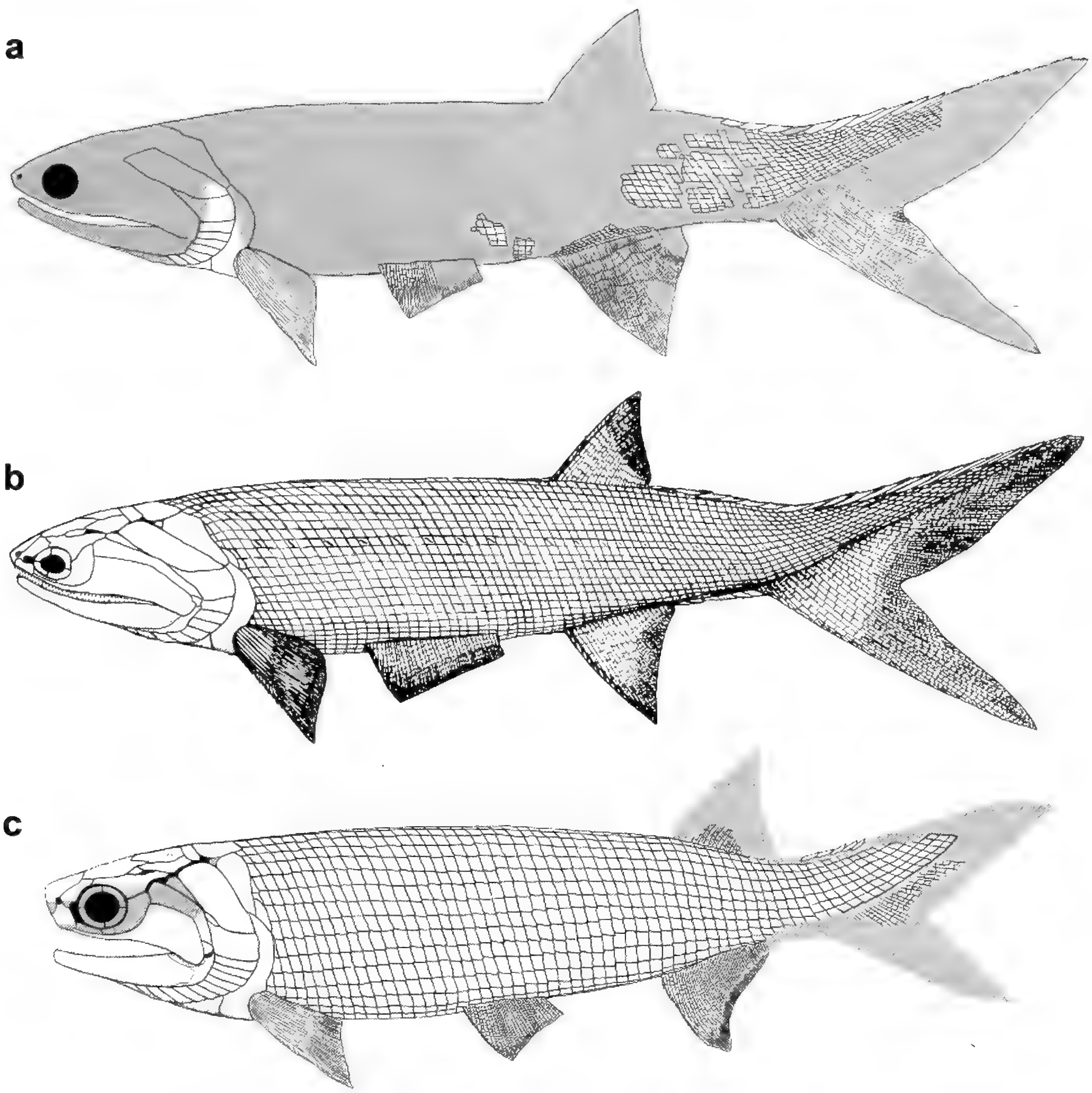

Figure 6. Comparison of the three known species of the Howqualepididae. Reconstructions presented in lateral view and are not to scale. Unknown parts of the anatomy are represented by dark grey areas. a. ?*Howqualepis youngorum* sp.nov., based on the preserved extent of the holotype with outline based on *H. rostridens*, c.14cm long. b. *Howqualepis rostridens* from Mount Howitt, Victoria (modified after Long, 1988). Size of specimens range from 20-50cm. c. *Donnrosenia schaefferi* from the Aztec Siltstone, Southern Victoria Land, Antarctica (from Long et.al, 2008), c. 14cm long.

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Fire and Habitat Interactions in Regeneration, Persistence and Maturation of Obligate-seeding and Resprouting Plant Species in Coastal Heath

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Myerscough, P.J. (2009). Fire and habitat interactions in regeneration, persistence and maturation of obligate-seeding and resprouting plant species in coastal heath. *Proceedings of the Linnean Society of New South Wales* **130**, 47-61.

After a fire in January 1991, populations of two obligate-seeding and two resprouting species were followed from seeds sown in dry heath and wet heath on Pleistocene beach sands in the Myall Lakes area. In each type of heath, there were four plots, each with ninety 25 X 25 cm quadrats in which seeds of the four species had been sown in various combinations and surface soil conditions. All four wet-heath plots burned again in January 1998, as did two of the dry-heath plots. The two obligate-seeding species were confined to their respective habitats early in the life cycle; *Acacia ulicifolia* to dry heath by lack of seeds and suitable conditions for seedling emergence in wet heath; *Dillwynia floribunda* to wet heath by failure of its seedlings to survive in dry heath. The two resprouting species were confined to their respective habitats in different ways; *Banksia oblongifolia* by failure of its seedlings to survive in dry heath; *Banksia aemula* by lack of suitable soil surface in wet heath for establishment of its seedlings. In both species of *Banksia*, seedlings require a lignotuber to survive their first fire, and may persist several years without appreciable growth.

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KEYWORDS: banksias, fire, heath, lignotubers, maturation, oskars, persistence, regeneration, resprouters, seeders

INTRODUCTION

Dispersal, survival and reproduction of individuals underlie patterns of distribution and abundance of species. Fire influences these processes in plant life histories, and moulds patterns evident in fire-prone vegetation across gradients in habitat. In fire-prone vegetation, species of seed plants tend to fall into two groups (Gill 1981), obligate-seeders, those whose adult plants die in fires that destroy their leaf canopies and regenerate after fire solely from seed, and resprouters, some of whose plants survive complete loss of their canopy in intense fires and resprout new canopies after fire from vegetative tissue that is protected from fire. Frequent fires may act selectively and reinforce the respective characteristics of these two groups of plants. In obligate-seeders, high production of seeds, in amount and early availability after fire, would be expected, with the seeds protected from burning, either by being contained in fire-resistant fruits or by dispersal to safe sites in soil and having dormancy that is only readily broken by stimuli connected with the passage of fire. In resprouters, seedlings would be expected to produce at an early stage vegetative parts that survive fire. Pate et al. (1990) showed that seedlings of obligate-seeding species devote much growth to their shoots and early seed production, while seedlings of comparable resprouting species devote a high proportion of their growth to underground tissues including fire-resistant vegetative storage organs. In seedlings of resprouters, production of fire-resistant vegetative tissue typically precedes seed production. In their life histories, seed production is usually considerably delayed compared with related obligate-seeding species.

Obligate seeders probably have simpler relationships linking seed dispersal, germination and seedling establishment in particular environments, their regeneration niches (sensu Grubb 1977), to seed production than do resprouters. Resprouters, while passing through seed dispersal, germination and seedling establishment in particular environments, their regeneration niches, also have periods of persistence as vegetative plants, that though fire-hardy, may or may not become reproductive and produce seed. It is possible that resprouters may simply persist many years as small plants with little net growth. The persistence niche (sensu Bond and Midgley 2001) of resprouters may be wider than conditions under which the plants progress to seed production.

The opportunity arose to observe through time seedlings of obligate-seeding and resprouting species after fire occurred across habitats in fire-prone coastal heath. Such heath occurs in south-eastern Australia on leached siliceous beach sands and dunes deposited during the Pleistocene from South Australia (Specht 1981) to sand islands such as North Stradbroke Island (Clifford and Specht 1979) off the south-eastern coast of Queensland. On the coast of New South Wales, they occur particularly north of Newcastle to the Queensland border (Griffith et al. 2003, Keith 2004). In the Myall Lakes area, heath occurs on a Pleistocene system of beach sands in the Eurunderee Embayment of Thom et al. (1992). On these sands, there is a catenary sequence of soils and vegetation with dry heath on ridges, wet heath on slopes and swamps in periodically waterlogged swales (Carolin 1970, Myerscough and Carolin 1986, Myerscough et al. 1995). Dry heath belongs to the *Banksia serratifolia (aemula)* Alliance of Beadle (1981) and Wallum Sand Heaths of Keith (2004), and wet heath to Beadle's (1981) *Banksia aspleniifolia (oblongifolia)* Alliance and Keith's (2004) Coastal Heath Swamps. Fire has occurred fairly frequently, but over two decades produced no detectable effect in changing the pattern of differentiation of vegetation across the sequence of habitats, though changes with time since fire were clearly evident in the vegetation within habitats (Myerscough and Clarke 2007). Carolin (1970) demonstrated that various species occupy characteristic ranges of habitat in the catenary sequence from the ridges to the swales. Myerscough et al. (1996) and Clarke et al. (1996) investigated in four species how occupancy of their ranges of habitat might arise through dispersal of seed and, after fire, germination and establishment of their seedlings. Seedlings of two species characteristic of wet heath, obligate-seeding *Dillwynia floribunda* and resprouting *Banksia oblongifolia*, did not survive in dry heath, despite their seeds occurring and germinating there (Myerscough et al. 1996). Seed of two species characteristic of dry heath, obligate-seeding *Acacia ulicifolia* and resprouting *Banksia aemula*, were at best rare in wet heath (Myerscough et al. 1996), and, unless the soil surface is artificially disturbed and seeds are buried, germination and seedling establishment did not occur (Clarke et al. 1996). In short, it was largely in regeneration niche (Grubb 1977) that these species appeared to be segregated to their respective habitats, *D. floribunda* and *B. oblongifolia* to wet heath, and *A. ulicifolia* and *B. aemula* to dry heath (Myerscough et al. 1996, Clarke et al. 1996).

Seedlings of the four species were observed beyond the phase of establishment. Establishment of seedlings of *Acacia ulicifolia* and *Banksia aemula* had occurred in wet heath, following experimental manipulation of the soil surface (Clarke et al. 1996). Early survival of seedlings of both obligate-seeding species was related to type of habitat, but in both resprouting species it was related to variation among plots within types of habitat (Clarke et al. 1996). In this paper, ongoing survival of seedlings of the two obligate-seeding species is examined in relation to type of habitat, while in the two resprouting species it is examined in relation to variation among plots within types of habitat.

Fire recurred in six of the eight experimental plots seven years after the fire that immediately preceded the start of the experiment. Survival of seedlings of the two resprouting species through fire could thus be assessed. Benwell (1998) observed lignotubers in seedlings of *Banksia aemula* and *B. oblongifolia* in similar coastal heath and found their growth to be slow seven years after fire. Four years after our experiment started, lignotubers were observed on some seedlings of each of the two species. By using fire-proof tags and measuring sizes and positions of lignotubers, survival of seedlings through their first fire could be assessed in relation to size and position of their lignotubers, if indeed they had been formed. Auld (1987) had found in *Angophora hispida* that seedlings with buried lignotubers survived fire better than those lacking lignotubers or with them exposed above the soil surface.

Ongoing observation of lignotubers and sizes of banksia seedlings was used to try to identify whether they were growing or merely surviving without net growth. One seedling of *Banksia aemula* was observed to flower and set fruit. It was thus possible to see whether a fire-proof stem was required for flowering and seed production as Bradstock and Myerscough (1988) found in juveniles of *Banksia serrata*.

The questions investigated in this paper are:

- Do patterns of early seedling survival in the two obligate-seeding species seen in relation to type of habitat continue into later stages, and how are these patterns related to flowering and seeding?
- How are patterns of seedling survival in the two resprouting species related to characteristics of individual plots?
- What roles do formation, size and position of lignotubers play in the survival through fire of

Table 1. Experimental plot locations and their transect, ridge position relative to coastline, habitat, and fire history since January 1991.

Plots	GDA	Transect	Ridge	Habitat	Fire history	
	32° S 152° E				Jan 1998	Nov 2006
T2W1	29.734'S * 21.125'E	T2	Near	WH	Totally burnt	Totally burnt
T2W3	29.530'S * 21.013'E	T2	Far	WH	Totally burnt	Totally burnt
T3W1	29.162'S * 22.310'E	T3	Near	WH	Totally burnt but some scorched leaves present	Totally burnt
T3W2	29.083'S* 22.250'E	T3	Mid	WH	Totally burnt but some scorched leaves present	Burnt but with some patches unburnt
T2D2	29.594'S* 21.040'E	T2	Mid	DH	Totally burnt	Totally burnt
T2D3	29.500'S 21.026'E	T2	Far	DH	Totally burnt	Totally burnt
T3D1	29.111'S* 22.302'E	T3	Near	DH	Unburnt	Unburnt
T3D2	29.019'S 22.289'E	T3	Mid	DH	Most or less unburnt - one edge slightly scorched	Mostly unburnt – some lightly scorched patches

*, 30 X 5-m plot extends to left of marker post when facing inland; other plots extend to right of post. Dry heath (DH) and wet heath (WH).

seedlings of the two resprouting species?

- Do seedlings of the two resprouting species show appreciable net growth, and under what conditions may they do so?
- Do patterns of seedling growth and survival give evidence of the longterm stability of the patterns observed in the vegetation across habitats of this coastal heath?

METHODS AND MATERIALS

Study area

The heath studied was on sands of a Pleistocene beach system in the Euruderee Embayment of Thom et al. (1992). Twenty-four plots, 3 wet-heath and 3 dry-heath plots in each of 4 transects, were used by Myerscough et al. (1995) to analyse floristic variation in heaths across the system. Each plot was 30 X 5 m with its longer sides parallel to the nearest beach ridge. Eight of the plots, two wet-heath and two dry-heath plots on each of the two central transects, were used in the experiments of Myerscough et al. (1996) and Clarke et al. (1996). Each of these plots (Table 1) was divided into a grid of 150 square-metre cells. Ninety cells were randomly chosen and to each of these cells a 25 X 25 cm quadrat was randomly allocated to a particular experimental treatment. Experimental treatments, including placement of seeds of the four species of this study, are described in Myerscough et al. (1996). These ninety quadrats in each of the 8 plots were the areas in which seedlings that arose in 1991 were observed.

Data collection

Periodic counts of seedlings of *Acacia ulicifolia* and *Dillwynia floribunda* were maintained from 1991 until the fire of January 1998 burned six of the eight plots (Table 1). Between 1995 and 1997, due to the density of stems, especially in wet heath, it became increasingly difficult to count seedlings of *D. floribunda* and *A. ulicifolia* on the small quadrats. Since there was no seedling recruitment apparent during this period, where a greater number of seedlings on a plot was recorded six months after the previous count, the greater number was taken to be correct. After January 1998 until October 2008, individuals of *Acacia ulicifolia* continued to be counted on the unburnt plots T3D1 and T3D2.

In *Banksia aemula* and *B. oblongifolia*, all survivors of the 1991 cohort of seedlings were counted on the eight plots. In November 1995, surviving banksia seedlings were marked with fireproof metallic tags on stainless steel pins placed beside the seedlings. All seedlings of *Banksia aemula* were tagged. In *B. oblongifolia*, many more seedlings were then surviving, and in those quadrats where there was more than one seedling only one seedling in the 25 X 25 cm quadrat was randomly selected and tagged. The proportion of individuals tagged in November 1995 and the number of tagged individuals subsequently surviving were used to estimate the population of surviving seedlings of *B. oblongifolia* in each plot. When no tagged individuals had survived in a plot, it was assumed that the whole cohort of seedlings that had arisen in 1991 in the experimental quadrats of the plot had died.

Lignotuber development was followed on each of the tagged seedlings, noting whether a lignotuber was absent or present. If present, its mean width was recorded from two measurements taken in two directions at right angles, and if it was not entirely buried, the height of its top above the soil surface was measured. After the fire of 1 January 1998, in March 1998 survival of the tagged seedlings was assessed. A seedling was scored as dead if it failed to resprout and live if it had resprouted. Most seedlings that resprouted had done so by March 1998, but a few resprouted later and were identified as alive when scored some months later. In all tagged seedlings, alive or dead, lignotuber presence or absence was noted, and, if present, its mean width was measured and whether its top was buried or exposed. The top was scored as exposed if its height above the soil surface was greater than 1 mm. Survival of seedlings through the fire was assessed in relation to habitat and lignotuber presence and exposure above the soil using 2 X 2 contingency tables and Chi square statistic.

Growth of banksia seedlings between 1995 and 2007 was assessed from lignotuber width and plant height. In *Banksia aemula*, seedlings were deemed to have grown if in October 2007 they were found to have a lignotuber width of over 40 mm or a plant height of greater than 40 cm, while in *Banksia oblongifolia* seedlings with a lignotuber width of over 20 mm were deemed to have grown. Widths of lignotubers of *Banksia aemula* were not easily assessed in a consistent way through time for two reasons. Firstly, although two measurements of width taken at right angles to each other were made on each occasion, not all lignotubers are radially symmetrical. Secondly, the lignotubers form with a thick bark, as in the sister species *Banksia serrata* (Beadle 1940, Bradstock and Myerscough 1988), and this bark may erode so that measured widths of lignotubers may lessen in time. Thus it is possible that some of the seedlings of *Banksia aemula* deemed not to have grown between 1995, or from when their lignotuber formed if it was later than 1995, may actually have grown slightly.

Watertables were observed in the plots between 1991 and 1997, and their depths recorded as described in Myerscough et al. (1996). The fire of January 1998 prevented further observations, destroying tops of the plastic pipes used to observe depths to the watertable on 6 of the 8 plots. The depths given in Table 2 were measured on 23 September 1997, when the watertable was relatively high.

To illustrate key floristic variation observed in 1990 across the plots, the nineteen most abundant species were selected from Appendix II of Myerscough et al. (1995) and listed in Table 2 in the order in which they were sorted in the TWINSPAN analysis given in Appendix I of Myerscough et al. (1995). The nineteen species included *Banksia aemula*, *B. oblongifolia* and *Dillwynia floribunda*. The other species, *Acacia ulicifolia*, whose seedlings were observed on the experimental plots was also included.

The height of the canopy of each of the plots was recorded in September 2005 in ten randomly selected 1 X 1 m cells, except in T2W3 where inadvertently there were only nine cells. In each cell, the species of the tallest plant was noted. At the same time, the degree to which each surviving banksia seedling was shaded by surrounding vegetation was subjectively scored using a five-point scale of shade: 5, >95%; 4, 95-75%; 3, <75-25%; 2, <25% shaded; 1, seedling's canopy unshaded.

Nomenclature

Nomenclature of plant names used follows Harden (1990, 1992, 1993 and 2002).

RESULTS

The plots differed floristically and in depths to the watertable (Table 2). Depths to watertable were greater in dry heath than in wet heath plots ($F_{1,6}$=5.90 (*p* just >0.05)) and differed markedly among plots within habitats ($F_{6,24}$=299.3 (*p*<0.001)). The habitats differed in plant species that provide significant cover. Both habitats had shrubs with appreciable

Table 2. Experimental plots and mean (SE) depth (cm) to watertable and mean cover (%) of twenty species (RS, resprouter; OS, obligate-seeder).

Plot	T2W1	T2W3	T3W1	T3W2	T2D2	T2D3	T3D1	T3D2
Watertable	2.0 (0.7)	10.6 (1.1)	2.8 (1.4)	18.9 (1.2)	43.3 (0.6)	26.3 (0.6)	108.8 (2.4)	38.5 (2.5)
Empodisma minus RS	44							
Gymnoshoenus sphaerocephalus RS	29							
Leptospermum livesidgei RS	29	1	9					
Banksia oblongifolia RS	10	11	8	13				
Dillwynia floribunda OS	14	13	18	15				
Epacris obtusifolia OS	17	10	15	15				
Xanthorrhoea fulva RS	11	15	34	18				
Lepyrodia interrupta RS	32	4	59	36		16		
Darwinia leptantha OS	1	22	2	2		4	2	1
Pseudanthus orientalis RS		5	1	19	1		14	15
Persoonia lanceolata OS	4	20	5	6	1	4	1	3
Kunzea capitata OS	1	19		5		14		1
Dillwynia retorta OS					49		25	3
Leptospermum polygalifolium RS		6			1	3		
Leptospermum trinervium RS					24	5	15	6
Acacia ulicifolia OS					3		2	3
Banksia aemula RS				1	20	52	26	23
Melaleuca nodosa RS		1		2	13	3	20	13
Hypolaena fastigiata RS					10	7	15	4
Epacris pulchella OS						12		8

cover such as the banksias, *Banksia aemula* in dry heath and *B. oblongifolia* in wet heath. Wet heath had more cover from resprouting monocotyledons such as *Xanthorrhoea fulva* than dry heath, and more cover from obligate-seeding shrubs such as *Dillwynia floribunda* and *Epacris obtusifolia* with sparsely branched, elongate ascending stems. Though similar in depth to the watertable, the wet heath plots T2W1 and T3W1 differed in plant cover. T2W1 had high cover of *Empodisma minus* and *Gymnoschoenus sphaerocephalus*.

After the fire of January 1991, and sowing seeds in March 1991 under various treatments across the eight plots, as described in Myerscough et al. (1996), seedlings of *Banksia aemula*, *B. oblongifolia*, *Acacia ulicifolia* and *Dillwynia floribunda* differed in their patterns of survival across the plots (Table 3).

In dry heath plots, seedlings of *Dillwynia floribunda*, though fairly numerous at six months, suffered heavy mortality and were completely absent after four years. They persisted in all wet heath plots with approximately 10% of the population observed at six months present six years later, with some plants observed to have flowered after three and half years. All the plants in the plots were killed by the fire of January 1998. In short, it was only in the wet heath plots that plants of *D. floribunda* survived and reproduced, doing so with little plot to plot variation apparent in their survival (Table 3). Seven and a half years after the fire in January 1998, *D. floribunda* was among emergent species in the canopy of the wet heath plots (Table 4).

Some seedlings of *Acacia ulicifolia* survived from 1991 in each of the eight plots until the fire of January

Table 4. Experimental plots and height (m) of canopy (mean (SE)), emergent species and relative shading (*RSh) of banksia seedlings (numbers in each category) in September 2005.

Plot	T2W1	T2W3	T3W1	T3W2	T2D2	T2D3	T3D1	T3D2
Canopy height	1.50 (0.06)	1.37 (0.06)	1.38 (0.06)	1.09 (0.07)	2.08 (0.14)	1.93 (0.16)	2.15 (0.16)	1.63 (0.08)
@ Emergent species - number of contacts out of 10 (but out of 9 for T2W3)	*D.fl* 3	*D.fl* 2	*D.fl* 1	*D.fl* 2	*B.ae* 3	*B.ae* 4	*B.ae* 4	*B.ae* 1
	L.li 3	*L.li* 1	*L.li* 7	*L.li* 1	*L.tr* 5	*L.tr* 1	*L.tr* 4	*L.tr* 4
	S.in 3	*S.in* 2		*S.sp* 1	*D.re* 2			
		P.la 1				*P.la* 3		*P.la* 3
	A.el 1					*L.po* 1		
		E.mi 1	*E.mi* 1	*E.ob* 2				*E.mi* 1
		B.ob 1	*B.ob* 1	*B.ob* 1		*A.te* 1		
				B.fa 1			*C.te* 1	
				M.n 1			*W.p* 1	
				X.fu 1				*K.ca* 1
B. aemula RSh 5	3		4					
4	3		9	5		2		2
3	3	4	5	31		9		5
2		1	2	10	1	1		5
1		1		1				
B. oblongfolia Rsh 5								
4			2	2				
3		1	1	1				
2		2						
1								

@ A.el – Acacia elongata; A.te – Acacia terminalis; B.ae – Banksia aemula; B. ob – Banksia oblongifolia; B.fa – Boronia falcifolia; C.te – Calytrix tetragona; D.fl – Dillwynia floribunda; D.re – Dillwynia retorta; E.mi – Epacris microphylla; E.ob – Epacris obltusifolia: K.ca - Kunzea capitata; L.li – Leptospermum liversidgei; L.po – Leptospermum polygalifolia; L.tr – Leptospermum trinervium: M.n – Melaleuca nodosa; P.la – Persoonia lanceolata; S.in – Sprengelia incarnata; S.sp – Sprengelia sprengelioides; W.p – Woollsia pungens; X.fu – Xanthorrhoea fulva.

* RSh: 5, >95%; 4, 95-75%; 3, <75-25%; 2, <25% shaded; 1, seedling's canopy unshaded.

Table 3. Number of seedlings surviving on experimental plots through time (years) since sowing in March 1991.

Time	0.47	1.52	2.01	3.41	4.59	5.56	6.56	7.64	8.53	9.68	10.56	11.58	12.69	13.58	14.57	15.64	16.67	17.65
A. ulicifolia																		
T2W1	54	42	33	22	7	5	3											
T2W3	52	39	22	17	10	10	10											
T3W1	70	38	30	14	4	3	3											
T3W2	66	44	22	4	1	1	1											
T2D2	43	14	10	4	2	2	2											
T2D3	43	17	17	13	11	10	10											
T3D1	52	29	25	19	14	14	14	13	13	12	12	11	8	8	8	8	5	5
T3D2	55	15	14	12	5	5	3	3	3	3	3	3	1	1	1	1		
D. floribunda																		
T2W1	407	290	251	107	87	58	48											
T2W3	505	256	175	82	50	39	35											
T3W1	407	230	202	130	90	63	36											
T3W2	960	392	320	127	118	121	90											
T2D2	120	2	1															
T2D3	92	3																
T3D1	85	3	1															
T3D2	223	7	1	1														
B. aemula																		
T2W1	24	25	27	22	22	21	21	13	13	13	12	12	12	10	9	7	5	4
T2W3	47	45	47	10	9	9	9	6	6	6	6	6	6	6	6	6	6	6
T3W1	32	35	30	31	30	30	30	23	23	23	22	21	21	20	20	18	14	12
T3W2	73	65	68	62	61	61	61	51	50	48	48	48	47	47	47	45	44	44
T2D2	52	22	22	17	17	17	15	2	2	2	2	2	1	1	1	1	1	1
T2D3	54	51	54	48	47	46	44	12	12	12	12	12	12	12	12	12	10	10
T3D1	45	16	10	4	3	3	2	1	1	1								
T3D2	59	41	44	17	17	17	17	14	14	14	13	13	12	12	12	12	10	10
B.oblongifolia																		
T2W1	283	277	265	205	171	133	95	15	12	9	9	3						
T2W3	287	276	266	84	60	49	43	10	10	10	10	7	7	7	7	7	7	7
T3W1	284	241	240	182	149	110	86	18	18	18	18	12	12	9	9	9	9	9
T3W2	447	420	439	202	169	135	101	11	11	11	11	11	11	11	11	11	8	8
T2D2	94	16	13															
T2D3	126	73	67	48	40	37	28											
T3D1	65	14	5	4	1													
T3D2	160	50	35	2	1	1	1											

1998 burned six of the plots. Though survival varies considerably with plot, there is no clear pattern in this variation in relation to habitat or other characteristics of plots. In the two plots not burned in 1998, one plant continued to survive in T3D2 until it was fifteen and a half years-old, while in T3D1 five plants were still alive at 17.65 years (Table 3), four of them having fruited in 2008. In this plot, four-year-old plants flowered and fruited, and four-year-old plants were seen flowering on other plots (T2D3 and T2W3).

In *Banksia oblongifolia*, some seedlings survived on each of the eight plots up to two years (Table 3). On dry heath plots, they had died out after 5 years on both plots where the watertable was deep (T2D2 and T3D1) but continued to survive in significant number on T2D3, the dry heath plot with the least depth to the watertable (Table 2). No seedling of *B. oblongifolia* survived the fire of January 1998 on a dry heath plot, but on each of the four wet heath plots some seedlings survived. On T2W1, the plot with high cover of *Gymnoschoenus sphaerocephala* and *Empodisma minus* (Table 2), no seedling survived twelve years, but on the other three wet heath plots some seedlings survived up to seventeen years (Table 3).

In *Banksia aemula*, some seedlings survived on each of the eight plots up to nine and half years, including on the six plots totally burnt in the fire of January 1998. Their numbers were lowest on the two dry heath plots (T2D2 and T3D1) where the watertable was deep and cover of *Leptospermum trinervium* relatively high (Table 2). On T3D1, which had the deepest watertable (Table 2) and which was not burnt in 1998 (Table 1), the last survivor had died after ten years. On each of the other seven plots, at least one plant survived to seventeen years (Table 3). Among wet heath plots, there was heavier mortality of survivors of the fire of January 1998 on T2W1 and T3W1 (see years 7.64 to 17.65 in Table 3), plots with the shallowest watertable and highest cover of resprouting monocots (Table 2), than on T2W3 and T3W2. On T2W3 and T3W2, not only was the watertable deeper and the cover of monocots less (Table 2), but in September 2005 the surviving seedlings of *Banksia aemula* were less shaded (Table 4). There was one seedling of *B. aemula* on each of these plots that was unshaded (Table 4). On T2W3, one plant flowered at fourteen years and formed swollen follicles, and, after the fire in November 2006, six follicles appeared to have opened. This was the only banksia originating from seed in 1991 that was observed on any of the eight plots to have become reproductive.

Across the wet heath plots, mortality from the fire of 1 January 1998 was much higher among seedlings of *Banksia oblongifolia* (83%) than among those of *B. aemula* (23%) ($p<0.001$).

In both species of banksia, survival of seedlings on plots burnt in the fire of 1 January 1998 entirely depended on possessing a lignotuber; without a lignotuber no seedling survived (Table 5). Under comparable conditions in wet heath, the lignotubers of *B. aemula* survived better than those of *B. oblongifolia*. With the top of the lignotuber exposed, only 10% of seedlings of *B. oblongifolia* survived whereas 78% of those of *B. aemula* survived; with the lignotuber buried, 36% survived in *B. oblongifolia* and 95% in *B. aemula*. No tagged seedling of *B. oblongifolia* survived fire in a dry heath plot (Tables 3 and 5), while seedlings of *B. aemula* survived fire in both wet heath (WH) and dry heath (DH). The survival of *B. aemula* seedlings was much lower in DH (24%) than in WH (76%) not only because there was a higher proportion of seedlings without lignotubers in DH (24%) than in WH (7%) ($p<0.001$) but there was higher mortality of seedlings with lignotubers in DH (68%) than in WH (18%) ($p<0.001$). Burial of the lignotuber

Table 5. Number of tagged banksia seedlings live or dead in March 1998 after fire of 1 January 1998 in relation to habitat and lignotubers.

Species	*Banksia aemula*				*Banksia oblongifolia*			
Habitat	Dry heath		Wet heath		Dry heath		Wet heath	
Seedlings	Live	Dead	Live	Dead	Live	Dead	Live	Dead
Lignotuber:								
absent	0	14	0	8	0	5	0	5
present	14	30	93	21	0	10	19	117
Lignotuber top:								
buried	11	21	20	1	0	2	8	14
exposed	3	9	73	20	0	8	11	103

Table 6. Dimensions and relative shading (RSh) of grown tagged banksia seedlings in October 2007.

Species	*Banksia aemula*			*Banksia oblongifolia*		
Dimension	Mean lignotuber width (mm)	Plant height (cm)	Relative shading (RSh)@	Mean lignotuber width (mm)	Plant height (cm)	Relative shading (RSh)@
Dry heath plot T3D2	41	43	3			
Wet heath plots	41	14	2	23	16	2
T2W3	43	31	2	39	28	2
	74*	79*	1			
	53	76	1			
T3W2	37	72	1			

* Plant first flowered in 2005.
@ RSh: 1, seedling's canopy unshaded; 2, <25%; 3, <75-25% shaded

increased the chances of survival of seedlings, particularly in *B. oblongifolia*. In *B. aemula*, the extent of this was mediated by habitat. A higher proportion of lignotubers were buried in DH (73%) than in WH (18%) (p<0.001). Despite this, mortality of seedlings with buried lignotubers was much higher in DH (66%) than in WH (5%) (p<0.001), whereas seedlings with lignotubers exposed above ground suffered 75% mortality in DH and 22% mortality in WH (p<0.001). In short, though burial of their lignotubers enhanced survival of seedlings in both habitats, it was more effective in WH than DH though the proportion of seedlings with buried lignotubers was lower in WH than DH.

Of those tagged banksia seedlings surviving to October 2007, appreciable growth was detected in relatively few (Tables 6 and 7), and most of these seedlings occurred in one wet heath plot, T2W3. Indeed, in this plot, two of the three surviving seedlings of *Banksia oblongifolia,* and four of the six surviving seedlings of *Banksia aemula* had grown, with one of them flowering in 2005 and producing an infructescence with a single swollen follicle. This individual was the only seedling to have had a lignotuber over 40 mm in width by March 1998; no others had achieved this by September 2005. In March 2007, it had four infructescences on which a total of six follicles had opened after the fire in November 2006. This was the only tagged banksia seedling to have reached reproductive maturity. In all the other plots, there were only two tagged banksia seedlings that could be identified as having grown, both *B. aemula*, one on a dry heath plot, T3D2, and the other on a wet heath plot, T3W2. The rest of the surviving tagged banksia seedlings appeared to be simply surviving without net growth, and on the wet heath plot T3W2 such seedlings of *B. aemula* were particularly numerous (Table 7). In October 2007, all seedlings deemed to have grown were unshaded or <25% shaded (Table 6), except for the seedling on T3D2, a plot largely unburnt by the fire of November 2006 (Table 1).

All the tagged banksia seedlings surviving in October 2007 had originated on quadrats sown in March 1991 with seed of their own species, except for three seedlings; a seedling of *Banksia aemula* on T2D3, another on T3W2 and a seedling of *B. oblongifolia* on T3W1 (Table 8). All six seedlings of *B. aemula* that had grown since their lignotubers were first recorded (Table 6) had each originated from seed sown and then shallowly buried (Table 8). In wet heath plot T3W2, the pattern of survival of the relatively numerous seedlings of *B. aemula* in October 2007 appears to reflect reasonably closely the original 4:6:4 ratio in March 1991 of seed buried: seed sown on disturbed surface: seed sown on undisturbed soil surface among the quadrats on the plot (Table 8).

Table 7. Dimensions (mean (S.E.)) of tagged banksia seedlings deemed not to have grown between first recorded presence of lignotuber (in November 1995 unless otherwise indicated) and October 2007.

Species	*Banksia aemula*				*Banksia oblongifolia*			
	Number of plants	Initial lignotuber width (mm)	2007 lignotuber width (mm)	Plant height in 2007 (cm)	Number of plants	Initial lignotuber width (mm)	2007 lignotuber width (mm)	Plant height in 2007 (cm)
Dry heath plots								
T2D2	1	20	33	20				
T2D3	10	15 (2)	19 (2)	20 (2)				
T3D2	9	15 (1)	22 (3)	16 (3)				
Wet heath plots								
T2W1	5	18 (2)	16 (1)	7 (1)				
T2W3	2*	17	15	11	1	17	16	15
T3W1	14	23 (2)	22 (2)	12 (2)	3	14 (1)	12 (3)	13 (3)
T3W2	43@	20 (1)	19 (1)	12 (1)	2*	12	11	8

* 1 plant first record of lignotuber in March1998; @ 4 plants first record of lignotuber in November 1996, and 4 in March 1998.

DISCUSSION

Fire and habitat interaction

Fire and habitat variation interact in different ways across the four species of this study. The interaction is more complex in the two resprouting species than in the two obligate-seeding species.

Of the two obligate-seeding species, *Dillwynia floribunda* has the more straightforward relation with habitat and fire. After fire, seedlings emerge from seeds whose dormancy has been broken by heat, as in *Acacia ulicifolia* (Auld and O'Connell 1991). Though its seedlings can appear in dry heath, they only survived to maturity in wet heath (Table 3). In wet heath, its soil seed-bank was found by Myerscough et al. (1996) to be abundant, survival of plants after six months was high (Table 3), it was seen to be in flower three and a half years after fire and to be one of the emergent species in the canopy seven and a half years after fire (Table 4). It is one of a suite of obligate-seeding species with soil seed banks and similar sparsely branched erect stems with microphyllous leaves that emerge above resprouting monocotyledons characteristic of wet heath. Other such species are the heaths *Epacris microphylla*, *E. obtusifolia*, *Sprengelia incarnata*, *S. sprengelioides*, some of which occur with *D. floribunda* in fire-prone wet heaths on sandstones in the Sydney region (e.g., Keith and Myerscough 1993, Keith 1994, Keith et al. 2007a).

Seedlings of *Acacia ulicifolia* arose in both wet and dry heath particularly after shallow burial of heat-treated seed (Clarke et al. 1996). Survival varied among plots in both wet and dry heath, but there

Table 8. Number of tagged banksia seedlings live in October 2007 (grown: plants deemed to have grown; dwarfs: plants deemed not to have grown since their lignotubers were first recorded) in relation to how their seed was placed in March 1991 on or within the soil.

Species		*Banksia aemula*			*Banksia oblongifolia*	
Seed placed	Buried	Surface disturbed	Surface not disturbed	Buried	Surface disturbed	Surface not disturbed
Dry heath plots						
T2D2 dwarf	1					
T2D3 dwarfs	2	5*	3			
T3D2 dwarfs	1	4	4			
grown	1					
Wet heath plots						
T2W1 dwarfs	1	4				
T2W3 dwarfs	1	1			1	
grown	4			1	1	
T3W1 dwarfs	7	6	1		2*	1
T3W2 dwarfs	12	19	12*			2
grown	1					

* includes one seedling that arose in a quadrat not sown with seed of that species.

was at least one survivor in each plot immediately before the fire in January 1998 burned six of the plots (Table 3). Some plants were observed to flower at about three and a half years old, and, in an unburnt dry heath plot, plants flowered and set fruit until they were at least seventeen years old. The seedlings are, compared to those of *Dillwynia floribunda*, slow to gain in height, and are quickly overtopped in wet heath by resprouting monocotyledons, such as *Gymnoschoenus sphaerocephalus* in T2W1. A modest seed bank of *A.ulicifolia* was shown to occur in dry heath but none was found in wet heath (Myerscough et al. 1996). Thus, in wet heath, lack of seed and, for any seed reaching it, scarcity of conditions for successful seedling emergence appear to exclude *Acacia ulicifolia*, and occurrence of the species is confined to dry heath where it has a soil seed bank, suitable conditions occur after fire for germination of seed and emergence of seedlings, and seedlings are less readily overtopped by other understorey species.

Thus *Dillwynia floribunda* and *Acacia ulicifolia* are excluded from each other's characteristic habitat early in the life cycle, though at different stages; *A. ulicifolia* through lack of available seed and suitable safe sites (sensu Harper 1977) for any rare seeds present in wet heath, and *D. floribunda* apparently by lack of suitable growing conditions for seedlings in dry heath. In short, their respective distributions relate to their regeneration niches (sensu Grubb 1977). Beyond the regeneration stage, they need to reproduce successfully in their respective habitats, which observations in this study, while not detailed, indicate occurs, with some seedlings of each species in their fourth year probably contributing seed to the soil seed-bank.

This study reveals that in this coastal heath the two resprouting species have three critical phases in their life cycle, regeneration, persistence and growth. What happens to individual plants as they enter and pass through each phase and make transition from one stage to the next depends on fire and habitat. This differs between the two species. Transition from seedling to persistent plant is made evident through fire, while that from fire-resistant but merely persistent plants to plants growing toward reproductive capability is more gradual, presumably depending on success in garnering necessary resources.

In the regeneration phase, patterns of seedling establishment between habitats (Myerscough et al. 1996) and among experimental treatments and plots within habitats (Clarke et al. 1996) differed between *Banksia aemula* and *B. oblongifolia*. Seedlings of *B. oblongifolia* that arose in dry heath were fewer and died earlier than on wet heath plots, and, though several survived on T2D3 for six and a half years, none survived the fire in January 1998 (Table 3). In contrast, survival of *Banksia aemula* occurred across both habitats, and on all the wet heath plots and on three of the dry heath plots there was at least one survivor after seventeen years (Table 3). Survival of seedlings of *B. aemula* was least on dry heath plots (T2D2 and T3D1) with low water tables (Tables 2 and 3).

The fire of 1 January 1998 caused mortality among seedlings of both species, but mortality was much greater in *B. oblongifolia* than in *B. aemula*. Overall, in the wet heath plots, 77% of seedlings of *B. aemula* survived the fire while only 17% did in *B. oblongifolia*. In both species, to persist through the fire a lignotuber was essential (Table 5). Lignotubers had formed by four and a half years from the sowing of the seed on most of the seedlings that survived, but some had formed somewhat later (Table 7). One factor in the lower survival of seedlings of *Banksia oblongifolia* is the structure of the lignotubers its seedlings form. They are small and lack the thick corky bark of the larger lignotubers of the seedlings of *B. aemula*. In *B. oblongifolia* many of the unburied lignotubers formed completely above the ground surface while this did not occur in seedlings of *B. aemula*; in them, a lower part was at least in the ground. In both species, as Auld (1987) showed in seedlings of *Angophora hispida*, burial of the lignotuber enhanced survival of the seedlings, though again to a greater extent in *Banksia aemula* than in *B. oblongifolia*. In short, the lignotubers of seedlings of *B. aemula* appear to be better insulated than those of seedlings of *B. oblongifolia*, and the transition of seedlings through fire to the fire-resistant persistent phase is made with much less mortality in *B. aemula* than in *B. oblongifolia*.

In each of the banksia species, very few of the surviving seedlings showed detectable growth between March 1998 and September 2007. Most of them appeared to be simply persisting without detectable net growth. They seem to be in a prolonged "sit-and-wait" state, ageing juvenile plants that Silvertown (1982) called oskars. In many plant communities, growth of such oskars is restricted by lack of sufficient light. Though some shading occurs in the heaths, especially wet heath with abundant monocots in the understorey (Tables 2 and 4), lack of growth in these banksia seedlings is not solely related to light (Table 4). Indeed light was abundant at ground level for several weeks after fire, as occurred when the seedlings arose from seed in 1991 and immediately following their survival through the fire of 1 January 1998. If their growth is resource-limited, the critical resources are those in the soil. Water is probably readily available across the range of habitats, though water stress may be a factor in dry heath with deeper water tables (Table 2). The limiting resources are likely to be one or more of the mineral nutrients needed for plant growth. Previous work (Myerscough and Carolin 1986) has indicated that the sands on which these heaths occur are very low in mineral nutrients. Circumstantial evidence that shortage of mineral nutrients retarded growth of the seedlings comes from the seedlings that grew. All except two were from the wet heath plot T2W3. On this site, when holes were drilled to observe the watertable, a very consolidated coffee rock, B horizon, was reached at c. 0.5 m in three of the four holes. In other wet heath plots, B horizons were deeper and less consolidated. Data of Griffith et al. (2004) indicate that roots of seedlings of both species of banksia, particularly *B. aemula*, may grow down to B horizons fairly rapidly in similar heaths. It is thus possible that banksia seedlings on this plot could reach the B horizon relatively easily and extract nutrients from it. Furthermore, the plant that grew early and reached reproductive maturity was relatively near one of the holes that had pierced the B horizon to observe the watertable; the disturbance of the hole may have released nutrients that accelerated its growth. Incidentally, this individual flowered when it was less than a metre high (Table 6), showing no sign of requiring an elongated stem for flowering, as in *Banksia serrata* (Bradstock and Myerscough 1988). Its inflorescences were produced more or less sessile on a thickened main stem that was merely an upward extension of the thickening of the lignotuber. Other low-growing reproductive individuals of *B. aemula* on this sand system had a similar growth form, while taller growing individuals with trunks occur in sites such as T2D2 and T3D1, and, after fire, produce inflorescences on newly grown stems up to 1 m long.

Growth leading to mature reproductive individuals, persistence of fire-resistant juveniles and regeneration in terms of establishment of seedlings appear as fairly distinct phases in the life cycles of *B. aemula* and *B. oblongifolia*. Each phase has its characteristic relations with habitat and fire that differ between the species. In *B. oblongifolia*, its restriction to wet heath is clearly evident at the regeneration phase (Myerscough et al. 1996), and, as seen in this study, should seedlings survive in a dry heath site they tend to be eliminated in the first fire and thus never enter the phase of fire-resistant juveniles (Tables 3 and 5). Fire-resistant juveniles of *B. oblongifolia* occurred in wet heath plots, but in the plot, T2W1, having survived the fire of 1 January 1998, they were eliminated (Table 3), probably shaded out under the high cover of *Empodisma minus* and *Gymnoschoenus sphaerocephalus* (Table 2). In the other three wet heath plots some continued to survive to seventeen years, but only clearly entering the growth phase in one, T2W3.

In *Banksia aemula*, given availability of seed and modification of the soil surface (Myerscough et al. 1996, Clarke et al. 1996), seedlings arose and survived in all wet and dry heath plots. Ongoing survival was least in the two dry heath plots T2D2 and T3D1 (Table 3) with deep watertables. Transition through the fire of 1 January 1998 on six of the eight plots to persistent fire-resistant juveniles was made with high rates of survival, particularly in the wet heath plots (Table 3). The question arises as to whether the patterns seen at the regeneration stage in seedlings in relation to particular soil treatments applied at sowing of the seeds in March 1991 (see Clarke et al. 1996) were maintained or altered in subsequent survival. In T3W2, the plot with highest number of fire-resistant juveniles persisting at seventeen years, the indication is that the pattern seen in the regeneration phase in relation to soil surface disturbance and seed burial is retained at seventeen years in the persistence phase (Table 8). This plot incidentally was unique among the four wet heath plots in showing little effect of soil treatment and seed burial in numbers of seedlings surviving at the regeneration phase (see Fig. 2 of Clarke et al. 1996); the three other plots all showed that the greatest number of seedings arose from buried seeds. All six of the plants that were deemed to have entered the growth phase had arisen from buried seed (Table 8).

These findings give some insight into the status of populations of the two banksia species on the Eurundereee Pleistocene beach ridges. Firstly, they suggest that their population turn-over is very slow. Indeed, after seventeen years, there is little firm evidence of effective recruitment in either species. In *Banksia aemula*, only one surviving juvenile showed any evidence of growth in dry heath. While, in wet heath plots, there were numbers of persistent fire-resistant juveniles, a few of which grew, it was an artificial situation brought about by firstly unnaturally increased availability of seed, relative to naturally occurring levels of seed (Myerscough et al. 1996), and secondly by burial of seeds which is unlikely to occur readily in nature in wet heath (Clarke et al. 1996). In *Banksia oblongifolia*, very few seedlings survived the fire on 1 January 1998 and persisted as fire-resistant juveniles. The only two that grew arose from seed that in one case had been buried and in the other from seed on a disturbed surface (Table 8). Casual observation of existing mature individuals of either *B. aemula* or *B. oblongifolia* suggests that over the seventeen years there was little if any mortality among them. The picture then is of populations of mature long-lived individuals into which there is little opportunity for recruitment of juveniles. Secondly, it appears that, though juveniles may persist several years in a non-growing state, they are limited by lack of resources for growth to progress to mature plants. It is probable that on most plots, the limiting resources are soil nutrients. In the case of one wet heath site with cover of *Empodisma minus* and *Gymnoschoenus sphaerocephalus,* lack of light may eliminate juveniles of *Banksia oblongifolia*, even though mature plants of the species had appreciable cover (Table 2). This suggests that either the current mature plants recruited as seedlings before *E. minus* and *G. sphaerocephalus* were so abundant in the site, or, if they were present and abundant, fire frequency was so high that shade from them did not eliminate juveniles of *B. oblongifolia.*

Though the evidence indicates that, presently on these Pleistocene sand ridges, niches for effective regeneration, persistence and growth for these two resprouting species are rare, there must be periods when they are in colonising mode and these niches are more common. This would have been so for *B. aemula* when parts of Holocene dunes south of Mungo Brush between the Myall River and the sea were colonised by it. Their winged seeds, dispersed some distance in wind, as in those of *Banksia serrata* observed by Hammill et al. (1998), particularly in willy-willies as were seen to occur in the area of this study on the Pleistocene beach ridges after an intense fire in January 1991, appear well suited for the initial step in colonisation of new habitat.

Selection and mode of regeneration

The contrast is stark between the two obligate-seeding species studied in which in suitable habitat regeneration is followed very quickly by reproductive maturity of individuals, and the two resprouting species where formation of a fire-resistant lignotuber occurs early and fire-resistant individuals enter a period of persistence in which the majority in this study showed no demonstrable growth toward maturity. As Keith et al. (2007b) have pointed out, the resprouters thus show all the characteristics of Grime's (1979) stress-tolerators or Stearns' (1976) K-selected species, while the obligate-seeders are examples of Stearns' r-selected species. Whether, under selection, their breeding systems follow the suggestion of Heslop-Harrison (1964, Table IV, p. 200) that species with short life cycles, exemplified here by obligate-seeders, are more likely to be inbreeders while species with longer life cycles and slowly maturing adults, exemplified by resprouters, are more likely to be out-breeders would be interesting to establish.

It is possible that paths to extinction may differ between obligate-seeders and resprouters. Resprouters may lose effective reproduction through seedlings and reach a terminable state of a few mature long-persisting individuals, perhaps propagating as clones, while high levels of inbreeding may lead to extinction in some obligate-seeders. How far, in fire-prone habitats, general differences exist between obligate-seeders and resprouters in degrees of in and out-breeding, and thus levels of heterozygosity of individuals, is a question that is yet to be investigated.

There is an indication in Table 2 that the species with high cover ten years from fire in both habitats are either strongly obligate-seeding or resprouting, with the possible exception of *Pseudanthus orientalis*. This would support the suggestion that, in vegetation subject to fairly frequent fires, as appears to have been so in these heaths (Myerscough and Clarke 2007), selection is strong for individuals and thus species to be either markedly obligate-seeding or strongly resprouting and against individuals and species that are neither markedly one nor the other. To establish this as a general rule would require further work.

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Late Llandovery (Early Silurian) Dendroid Graptolites from the Cotton Formation near Forbes, New South Wales

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Rickards, R.B., Wright, A.J. and Thomas, G. (2009). Late Llandovery (Early Silurian) dendroid graptolites from the Cotton Formation near Forbes, New South Wales. *Proceedings of the Linnean Society of New South Wales* **130**, 63-76.

A well-preserved dendroid graptolite fauna of Early Silurian (late Llandovery: probable *turriculatus* graptolite zone) age is described from the Cotton Formation near Forbes, New South Wales. A possible rhabdopleuran hemichordate is described from Australia for the first time. The fauna consists of 13 taxa as follows: *Dendrograptus* sp. aff. *D. avonleaensis*, *Dictyonema zalasiewiczi* sp. nov., *Dictyonema* sp. aff. *D. paululum australis*, *Dictyonema paululum australis*, *Dictyonema* sp. aff. *D.* sp. cf. *D. venustus* of Bulman (?ssp. nov.), *Dictyonema venustum*, *Dictyonema* sp. cf. *D. falciferum*, *Callograptus bridgecreekensis*, *Callograptus rigbyae*, *Callograptus* sp. aff. *C. ulahensis*, *Stelechocladia* sp. cf. *S. praeattenuata*, *Acanthograptus praedeckeri* and ?*Rhabdopleura* sp. (? with zooids). The fauna is close in composition (although less diverse) and age to a dendroid fauna recently described from Bridge Creek near Orange, NSW, which was assigned to the slightly younger *griestoniensis* zone.

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KEY WORDS: Cotton Formation, dendroids, Early Silurian, Forbes, graptolites, New South Wales.

INTRODUCTION

The dendroid graptolites described here have been collected over many years by one of us (GT) from a quarry in the Cotton Formation at Cotton Hill near Forbes in western N.S.W. Fossils from these beds have been described by Sherwin (1974: graptolites) and Edgecombe and Sherwin (2001: trilobites). The described trilobite and graptolite faunas are from beds exposed in the quarry high in the upper part of the Cotton Formation (Sherwin 1974) and the graptolite fauna is correlated with the late Llandovery (Early Silurian) *turriculatus* graptolite zone (Edgecombe and Sherwin 2001). Despite the very nature of collections made in an active quarry, there seems little doubt that the bulk of the dendroid fauna and the graptoloids are from the same narrow horizon. The most similar known dendroid fauna was described by Rickards et al. (2003) from the Four Mile Creek district, south of Orange, NSW, and comparisons are made below with that fauna.

AGE OF THE ASSEMBLAGE

Although the Cotton Formation dendroid fauna (13 species and subspecies) is less diverse that described from the Bridge Creek localities in the Four Mile Creek district (24 species and subspecies) by Rickards et al. (2003), there can be little doubt that the two faunas are close in age. The largest assemblage at Bridge Creek, from locality F14, was referred by Rickards et al. (2003) to a horizon low in the *griestoniensis* graptolite Zone. The Cotton Hill fauna is assigned almost certainly to the stratigraphically lower *turriculatus* graptolite zone.

Of the fauna we record here from the Cotton Formation, only *Dictyonema zalasiewiczi* sp. nov. and ?*Rhabdopleura* sp. have not been recorded from Bridge Creek at locality F14. *Callograptus ulahensis* Rickards et al., 2003 was recorded from a lower (*gregarius* Zone) assemblage at locality BF15 on Bridge Creek: the Cotton Hill Quarry species is referred to *Callograptus* sp. cf. *C. ulahensis*.

Stelechocladia praeattenuata Rickards et al., 2003 was not recorded from F14 but occurs below (F19) and above (BF28, BF24 and BF18), ranging from the *gregarius* Zone to the uppermost *griestoniensis* Zone. Sherwin (1973, 1974) referred the strata at Cotton Hill Quarry to the *turriculatus* Zone, with some levels probably earlier than this but without definite faunas. Sherwin (1970, 1973) also recorded *Dictyonema* spp. from the highest band of a group of beds yielding a likely *turriculatus* Zone fauna. Hence the two dendroid assemblages, from Cotton Hill (probable *turriculatus* Zone) and from Bridge Creek (*griestoniensis* Zone), are not dissimilar in age, the Cotton Hill fauna being about one graptolite zone lower.

There is another difference between the two assemblages apart from a possible slight age difference and a diversity range, and that is that the Cotton Hill fauna is almost exclusively of slender, delicate species, often broken. In contrast, most of the species described by Rickards et al. (2003) from Four Mile Creek are robust, and are preserved in poorly bedded siltstone. The only robust form common to the two localities is *Stelechocladia* and at Cotton Hill it is known only from three small fragments showing distal, slender thecae. It is possible that the Cotton Hill assemblage lived in a quieter depositional environment, such as a lagoon, or further offshore. Edgecombe and Sherwin (2001) concluded that the laminated siltstones that dominate the formation were deposited in a 'very calm' environment, 'most likely below storm surge wave base'.

Associated graptoloids. Sherwin (1970, 1973) was the first to identify graptoloid species from the Cotton Beds, following the initial recognition of graptolites from this locality by Packham (1967). Sherwin (1970, 1973) recognised two faunas, an earlier assemblage (his fauna C) and a later assemblage (his fauna D) respectively from the east and west quarries on Cotton Hill: both are in the upper Cotton Formation. Fauna D, from the western, larger quarry, includes *Dictyonema* sp. (Sherwin 1973, fig. 10). Some mixing of faunas possibly occurred because collection was from large blocks on the quarry floor (Sherwin 1974, p. 149). It is this western quarry from which the present collection of dendroids came; the eastern, smaller, quarry has not so far yielded dendroid graptolites.

The graptoloid assemblages were described in detail by Sherwin (1974) and, allowing for some possible mixing of faunas, the overall aspect is of a *turriculatus* Zone fauna, perhaps rather low in that horizon given the presence of *Rastrites linnaei*, *Monograptus halli*, and *Monograptus* sp. cf. *M. sedgwickii*. Thus the Cotton Hill quarry is at a stratigraphically lower level than the Four Mile Creek (F14) locality which was mentioned in the preceding section and which is probably low in the *griestoniensis* Zone.

Graptoloids occurring on the same rocks as the Cotton Hill dendroids described below include: *Parapetalolithus palmeus*, *?Glyptograptus tamariscus*, *Monograptus andrewsi* and *Spirograptus turriculatus* (Fig. 7b). The faunal lists given by Sherwin (1974) are fuller and much more reliable than the graptoloids at our disposal. Here we also record and illustrate (Fig. 7a) *Parapetalothius palmeus* (Barrande, 1850), a form not recorded by Sherwin (1974); its occurrence accords with his age attribution of the *turriculatus* zone. In their revision of *Spirograptus*, Loydell et al. (1993) assigned Sherwin's (1974) *Monograptus turriculatus* (Barrande, 1850) to their new species *Spirograptus guerichi*. They further (Loydell et al. 1993, p. 924, text-fig. 7) stated that *S. guerichi* is "virtually confined to its biozone", whereas *S. turriculatus* ranges through their *turriculatus* biozone into the *crispus* biozone; Sherwin (1974, p. 150) shows that both species occur in his fauna D.

SYSTEMATIC PALAEONTOLOGY

This benthic graptolite fauna has been assembled only by sustained and diligent collecting over many years by one of us (GT), as dendroids are rare at the locality. The preservation is of reddish brown graptolites against a very pale, fine-grained siltstone or mudstone. The specimens are often large but are mostly fragmentary, and there seems to be little in the way of burial distortion or twisting and no obvious tectonic deformation. Some specimens are preserved in three dimensions infilled, probably with goethite: in others the periderm is diagenetically flattened, but with some parts (e.g. stolons) pyritised. It is possible that in some instances pyritised zooids are present. Rarely stolons occur free on the bedding plane, the surrounding periderm having degenerated; this situation has been noted by Chapman et al. (1993) and Rickards et al. (2003). All specimens are deposited in the Australian Museum, Sydney, with numbers AM F123381-123428.

Subphylum Pterobranchia Lankester, 1877 (*nom. trans*. Rickards and Durman 2006)
Class Graptolithina Bronn, 1849
Order Dendroidea Nicholson, 1872
Family Dendrograptidae Roemer *in* Frech 1897

Dendrograptus J. Hall, 1858

Type species

Graptolithus hallianus Prout, 1851, subsequently designated by J. Hall (1862).

Dendrograptus sp. aff. *D. avonleaensis* Rickards et al., 2003

Figures 1a, 3a

Synonymy

aff. 2003 *Dendrograptus avonleaensis* n. sp.; Rickards et al., pp. 312-3, figs 5A, 6A.

Material

AM F123381.

Description

The single specimen shows nine stipes and five

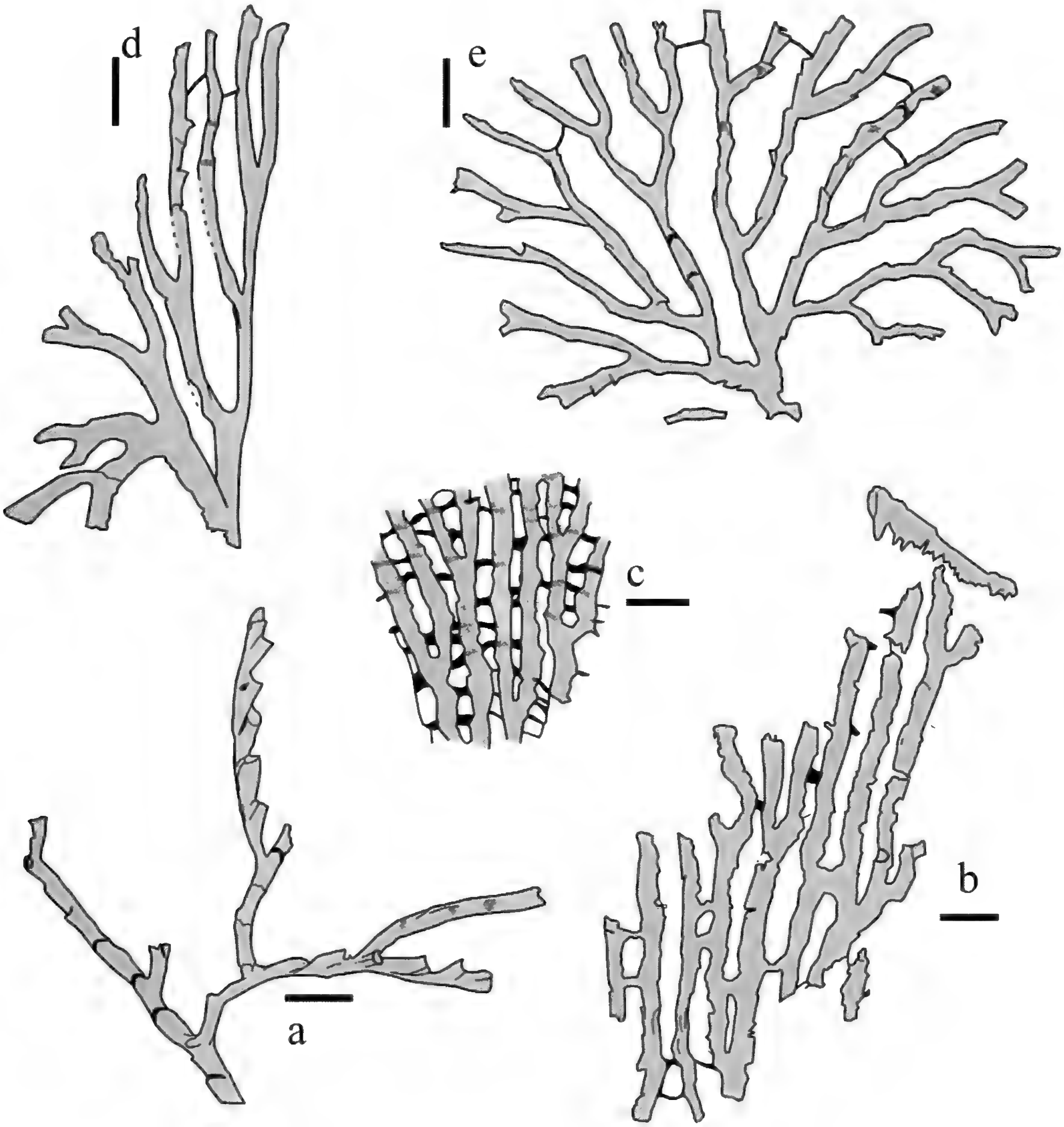

Figure 1. a, *Dendrograptus* sp. aff. *D. avonleaensis* Rickards et al., 2003; AM F123381. b, *Dictyonema* sp. aff. *D.* cf. *venustum* Bulman, 1928; AM F123398. c, *Dictyonema zalasiewiczi* sp. nov., holotype AM F123402; d, *Callograptus bridgecreekensis* Rickards et al., 2003; AM F123403. e, *Callograptus rigbyae* Rickards et al., 2003; AM F123406. Black bars are dissepiments; black rods, arched in ventral views, are autothecal ventral processes. Scale bars 1 mm.

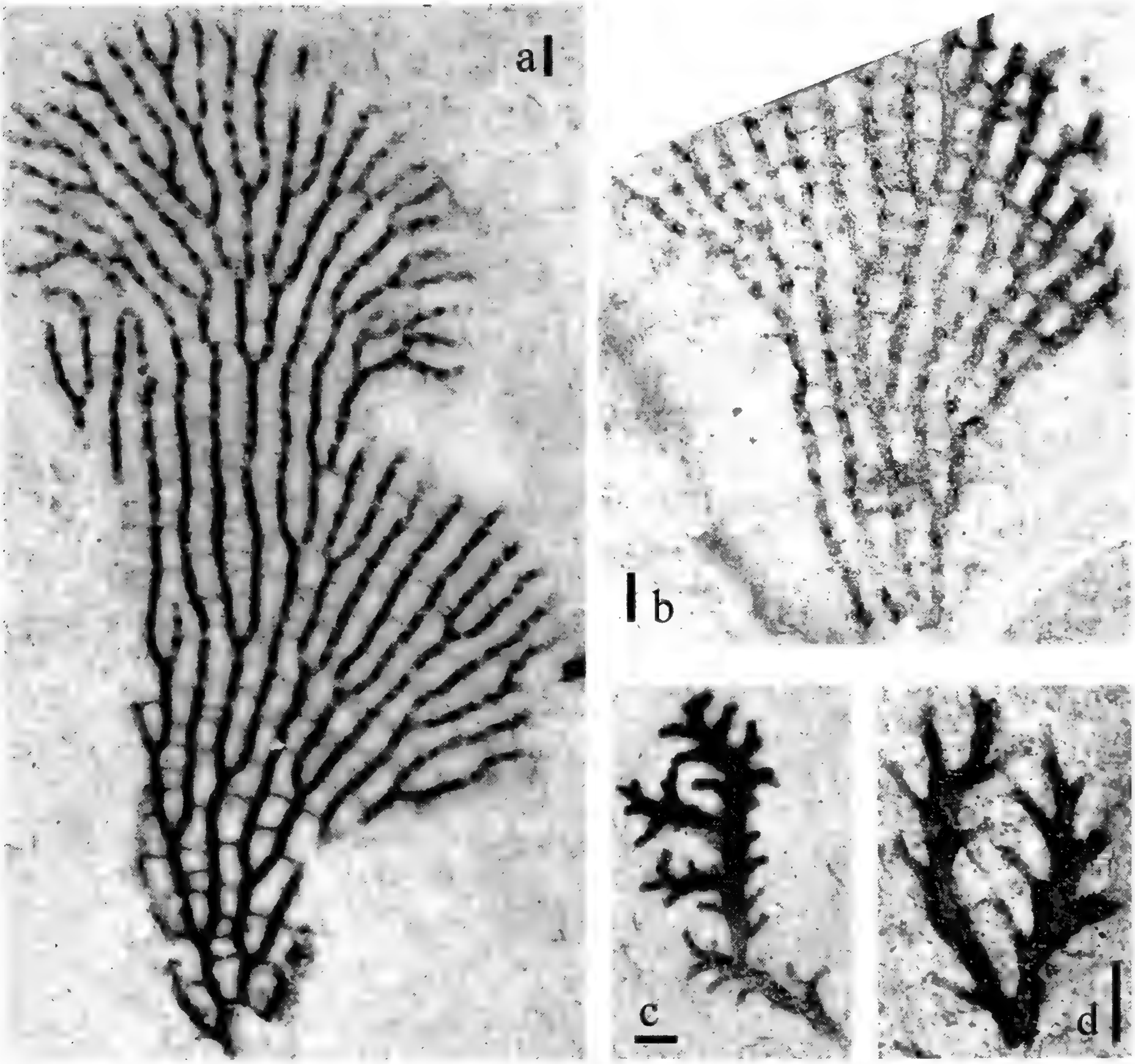

Figure 2. a-b, *Dictyonema paululum australis* Rickards et al., 2003, respectively AM F123382, AM F123383. c-d, *Acanthograptus praedeckeri* Rickards et al., 2003, respectively AM F123411, AM F123410. Scale bars 1 mm.

branching points in mostly ventral view, but also shows autothecal profiles in places. Specimen almost flattened diagenetically, but periderm still slightly transparent. 15-20 autothecae in 10 mm, with a profile width of 0.2 mm, and a fairly simple aperture slightly arched ventrally as seen in the ventral view. Bithecae exceedingly inconspicuous, being tiny tubes opening externally alongside autothecal apertures and alternating along stipe. Branching of stipes may be in zones at 1-3 mm intervals; stipe lateral width 0.30 mm and dorsoventral width 0.40 mm.

Remarks

This specimen, probably representing the distal-most parts of the colony, agrees closely with the type material of *D. avonleaensis* in most characters, especially the roughly zonal branching, autothecal nature and spacing and stipe dimensions. The type specimens from Bridge Creek (Rickards et al. 2003) had much of the proximal region preserved, and this is much more robust than the Cotton Hill material.

Dictyonema J. Hall, 1851

Type species

Gorgonia retiformis J. Hall, 1843, subsequently designated by Miller (1889).

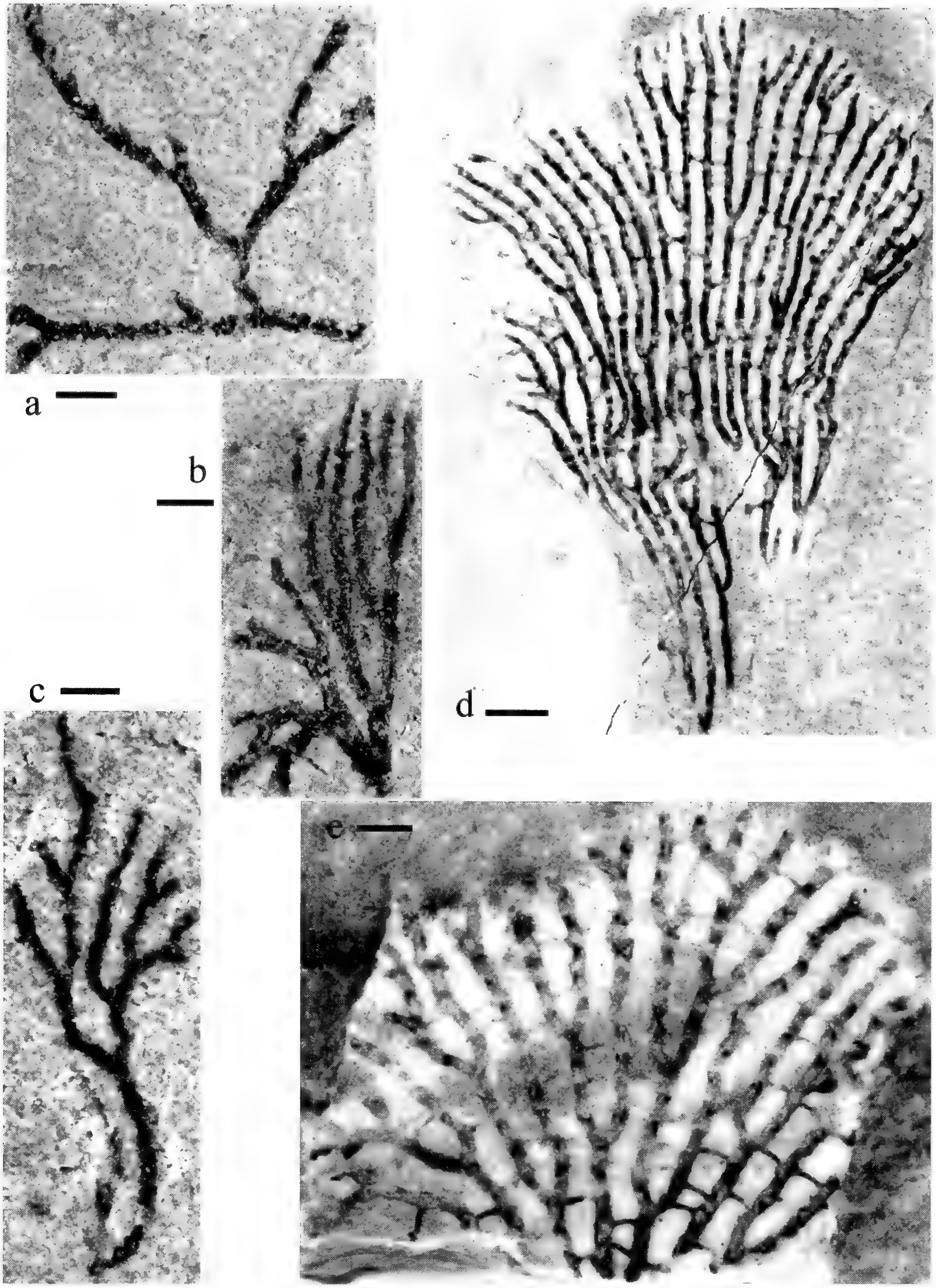

Figure 3. a, *Dendrograptus* sp. aff. *D. avonleaensis* Rickards et al., 2003; AM F123381. b, *Callograptus bridgecreekensis* Rickards et al., 2003; AM F123403. c, *Callograptus* sp. aff. *C. ulahensis* Rickards et al., 2003; AM F123407. d, *Dictyonema* sp. cf. *D. falciferum* Bulman, 1928, AM F123401. e, *Dictyonema paululum australis* Rickards et al., 2003; AM F123386. Scale bars 1 mm.

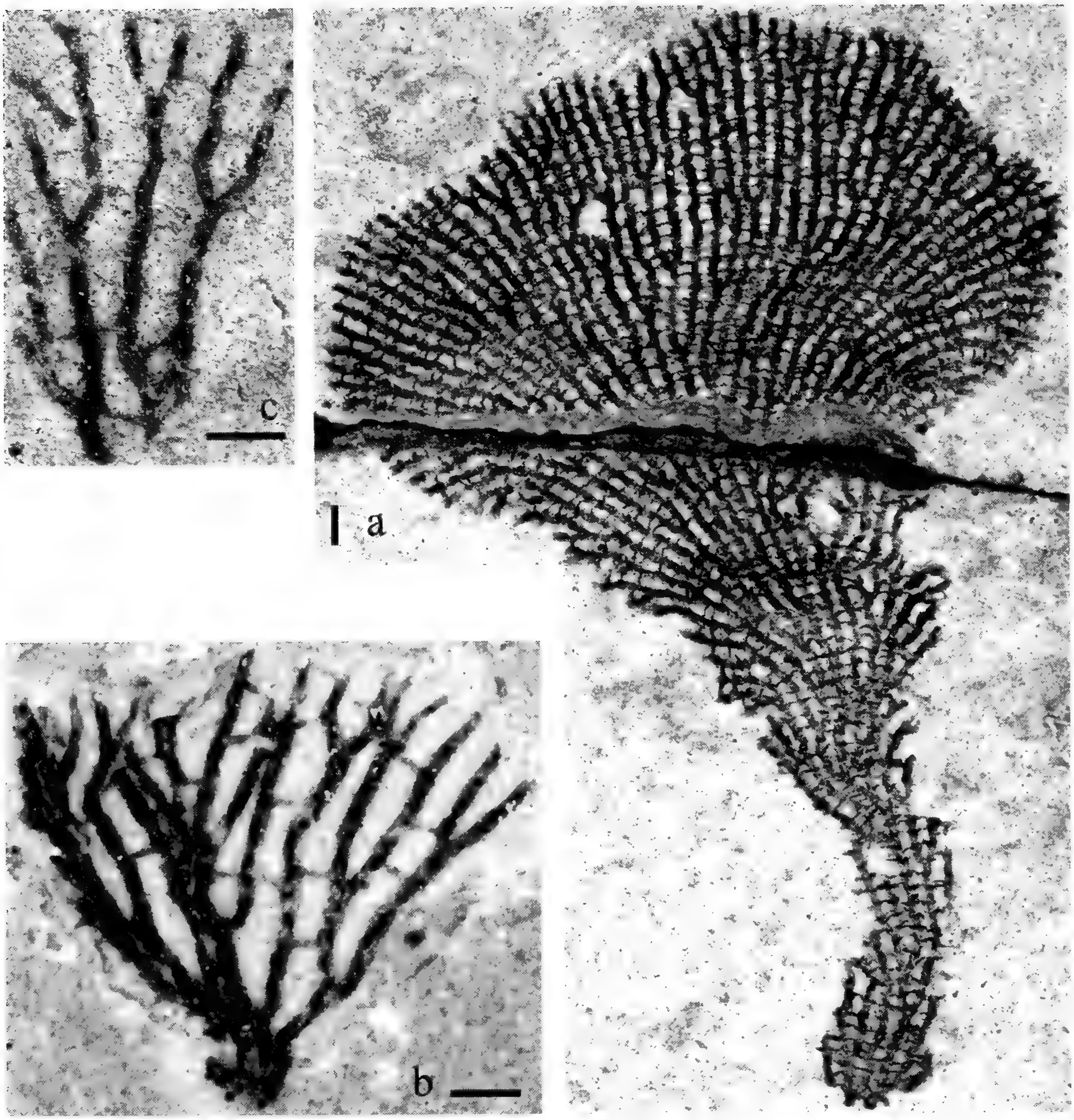

Figure 4. a, *Dictyonema zalasiewiczi*, sp. nov., holotype AM F123402. b, *Dictyonema venustum* Lapworth, 1881; AM F123397. c, *Dictyonema paululum australis* Rickards et al., 2003, respectively AM F123385. Scale bars 1 mm.

Dictyonema paululum australis Rickards et al., 2003

Figures 2a-b, 3e, 4c, 7c

Synonymy

2003 *Dictyonema paululum australis* n. subsp., Rickards et al., p. 316, figs 7F-G, 9E, 12A.

Material

Twelve specimens, AM F123382-93, ranging from small fragments to almost complete colonies.

Description

Probably fan-shaped rhabdosome of slender stipes, no indication of a conical colonial arrangement; colony with slender, parallel stipes, only approximately branching in zones, sometimes fanning out in rapid expansion. Stipes branch at intervals of 1.5-3.0 mm; stipe lateral width 0.20-0.25 mm proximally, 0.15 mm more distally; dorsoventral width 0.50-0.60 mm; stipe spacing 13-16 in 10 mm, stipe interspaces 0.50-0.60 mm. Autothecae denticulate, 18-20 in 10

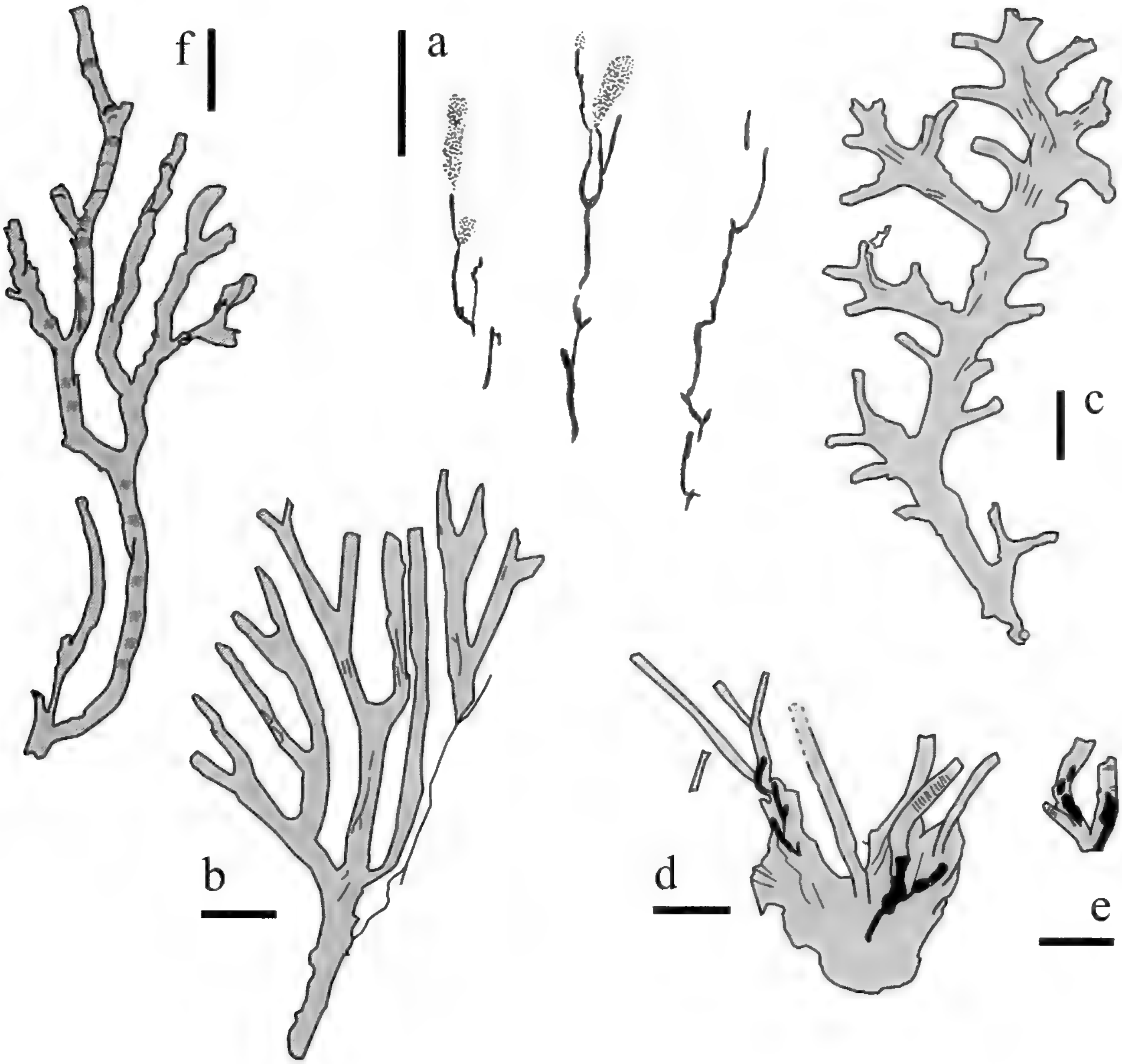

Figure 5. a, *Dictyonema* sp. cf. *D. falciferum* Bulman, 1928, partially preserved stolons in three portions of stipes where periderm is degenerate; AM F123400. b, *Stelechocladia* sp. cf. *S. praeattenuata* Rickards et al., 2003, AM F123408a. c, *Acanthograptus praedeckeri* Rickards et al., 2003, AM F123410. d-e, ?*Rhabdopleura* sp., respectively AM F123412-3; both exhibit stolons with possible preserved soft tissue (encysted zooidal attached). f, *Callograptus* sp. aff. *C. ulahensis* Rickards et al., 2003; AM F123407. Scale bars 1mm; stipple on Fig. a indicates possible attached soft parts. Scale bars 25 mm (a), 1 mm (b-f).

mm; dissepiments slender, 0.05-0.10 mm, 14-20 in 10 mm. Dissepiments conspicuous because of their frequency; proximally they are more robust and perhaps sparser. Bithecal tubes seen in places but their apertural regions are difficult to discern; they may be of the type described by Bulman (1928) in *D. falciferum* where the bithecal apertural region hooks over the dorsal apertural region of the autotheca. Alternatively, they may grow short of the full hook (Fig. 3e); bithecal tubes 0.05 mm wide.

Remarks

Rickards et al. (2003) considered the original material from Four Mile Creek probably had conical rhabdosomes but it seems more likely that they are fan-shaped. Bulman (1928) could not see the nature of the rhabdosome as a whole in the type subspecies, and he was particularly vague about the nature of the bithecae: otherwise the type subspecies is clearly close to the Australian form differing only as outlined by Rickards et al. (2003). *Dictyonema paululum australis* is the most common dendroid at Cotton Hill Quarry

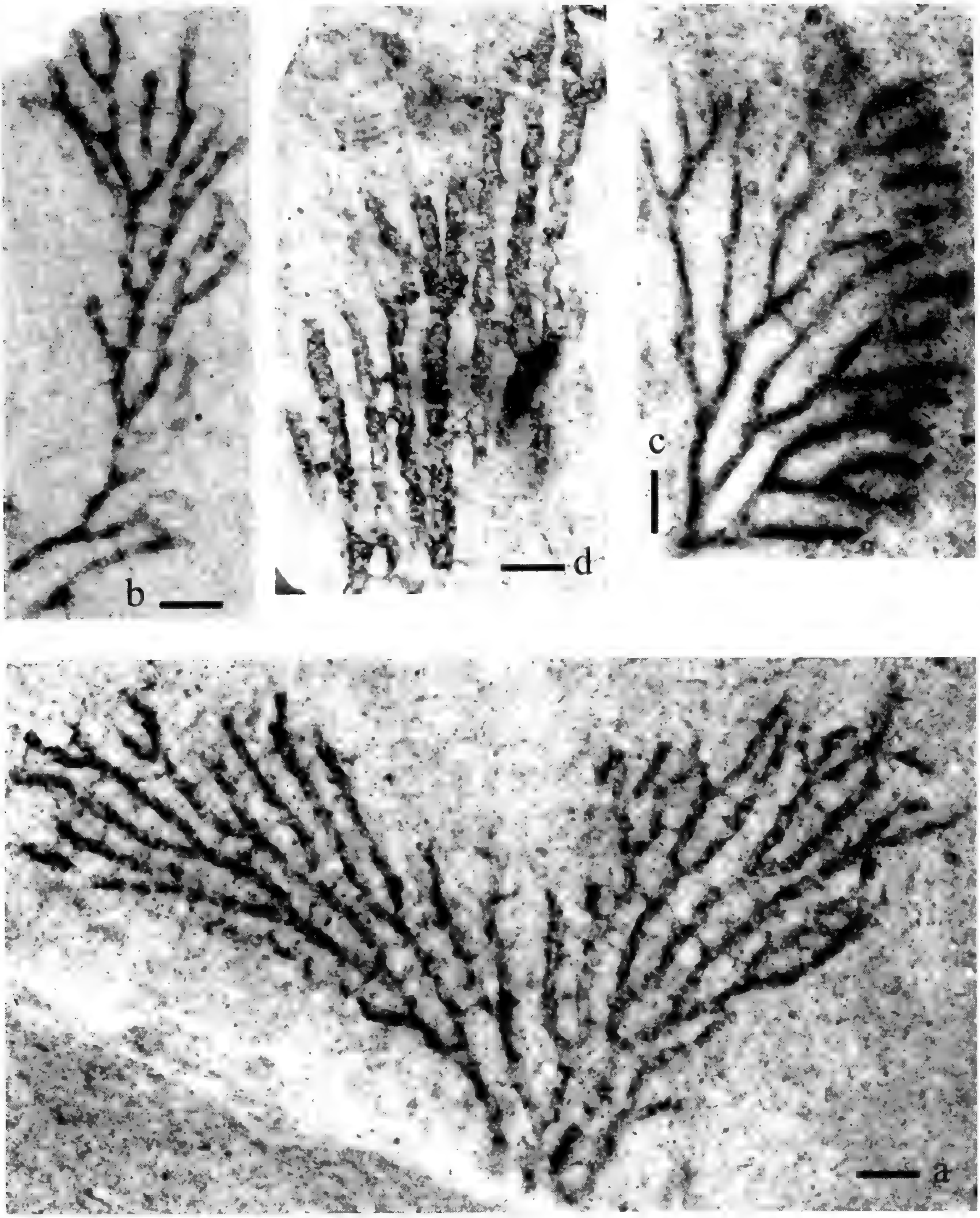

Figure 6. a-b, *Dictyonema* sp. aff. *D. paululum australis* Rickards et al., 2003; respectively AM F123395, AM F123396. c, *Callograptus rigbyae* Rickards et al., 2003; AM F123405. d, *Dictyonema* sp. aff. *D.* sp. cf. *D. venustum* Bulman, 1928; AM F123398. Scale bars 1 mm.

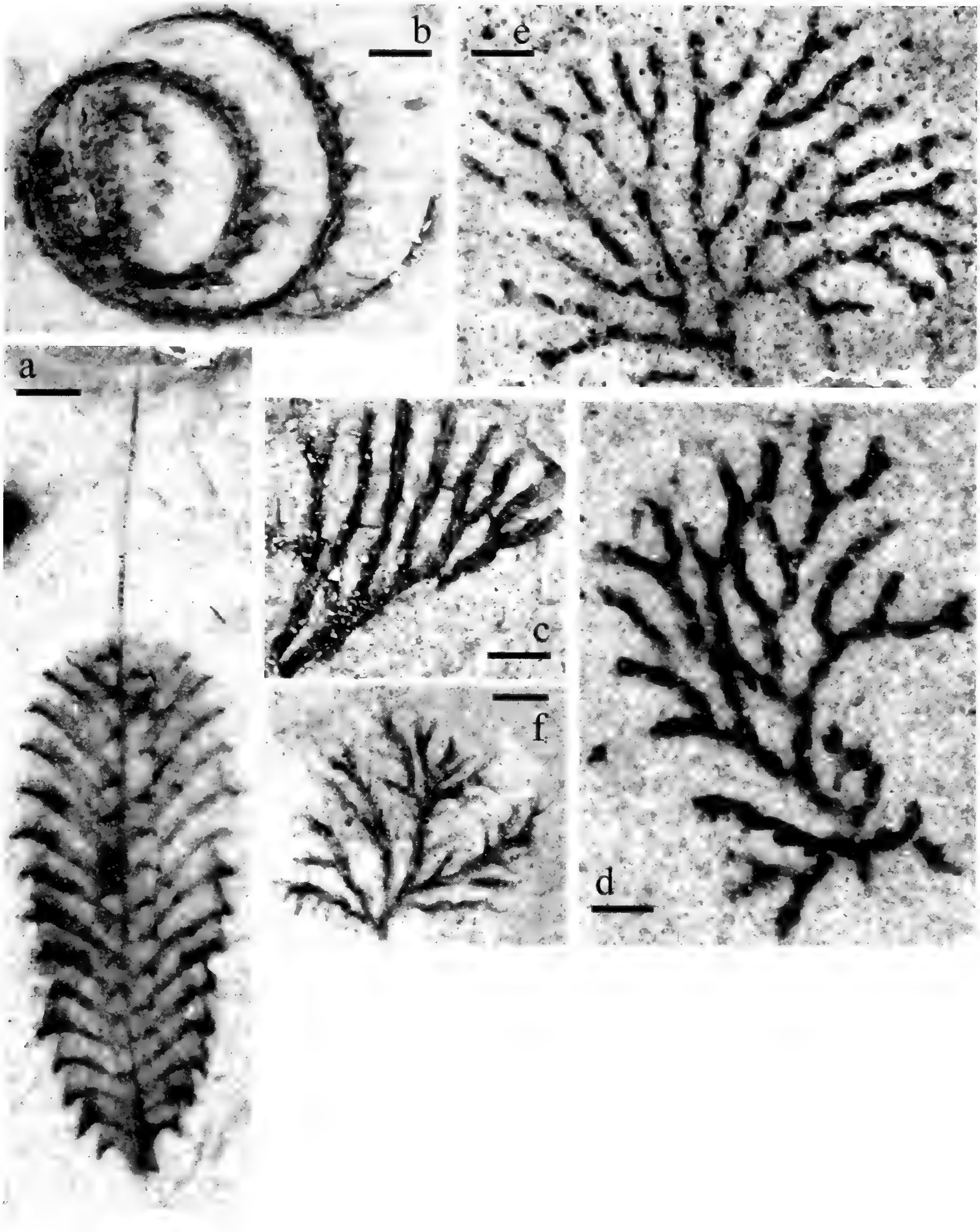

Figure 7. a, *Parapetalolithograptus palmeus* (Barrande, 1850) s.l., AM F123428. b, *Spirograptus turriculatus* (Barrande, 1850), AM F123427. c, *Dictyonema paululum australis* Rickards et al., 2003; AM F123384. d-e, *Callograptus rigbyae* Rickards et al., 2003; respectively AM F123404, AM F 123406. f, *Acanthograptus praedeckeri,* AM F123409. Scale bars 1 mm.

(and see also *D.* sp. aff. *D. p. australis* described below). *Dictyonema paululum hanoverense* Rickards et al., 2005 from the Late Silurian *parultimus* Zone near Neurea, N.S.W. differs in having an autothecal spacing of 28-30 in 10 mm and quite spinose ventral apertures.

Dictyonema sp. aff. *D. paululum australis* Rickards et al., 2003

Figure 6a-b

Synonymy

aff. 2003 *Dictyonema paululum australis* subsp. nov.; Rickards et al., p. 316, figs 7F-G, 9E, 12A.

Material

AM F123394-6, 123415a-b.

Description

Nature of colony uncertain, possibly fan-shaped. Stipes with lateral width of 0.20-0.25 mm, and spaced at 20-22 in 10 mm, more or less parallel, and with interstipe spaces of 0.20-0.40 mm; branching roughly in zones every 1.0-2.5 mm. Autothecae spaced at 19-20 in 10 mm; dorsoventral width uncertain but may be *ca.* 0.50 mm. Bithecae not detected. Dissepiments fine, spaced at *ca.* 20 in 10 mm.

Remarks

These specimens are superficially similar to those of the *D. paululum australis* material described in this paper, except that the stipes are more closely spaced and the interstipe spaces concomitantly narrow. There may be a temporal subspeciation factor involved here as the source level in the quarry for the specimens is uncertain; thus some of the *D. p. australis* specimens may be from older beds and others from the *turriculatus* level.

Dictyonema venustum Lapworth, 1881

Figure 4b

Synonymy

1881 *Dictyonema venustum* sp. nov.; Lapworth, pp. 171-2, pl. 7, fig. 1a-c

1928 *Dictyonema venustum,* Lapworth, emend; Bulman, pp. 61-3, pl. 5, figs 6-7, ?8, text-fig 34.

2003 *Dictyonema venustum* Lapworth, 1881; Rickards et al., pp. 315-6, figs 7A, 9D, 10B-D.

Material

An almost complete rhabdosome, AM F123397, plus AM F123416-7.

Description

Rhabdosome conical, reaching 8 mm x 8 mm; very proximal end missing though part of the holdfast may be present. Stipes with lateral width of 0.25-0.30 mm, dorsoventral width of 0.70 mm, and spaced at 16 in 10 mm. Interstipe spaces rectangular, up to 0.50 mm wide, and are bounded by stipes and dissepiments spaced at 5-8 in 10 mm. Dissepiments relatively robust, up to 0.15 mm thick. Autothecal spacing 16 in 10 mm; thecae appear to be denticulate but otherwise simple. Bithecal tubes present but relationships to autothecal apertures not seen.

Remarks

The specimen is very close to the type material redefined by Bulman (1928), differing only in a slightly closer spacing of the stipes.

Dictyonema sp. aff. *D.* sp. cf. *venustum* Bulman, 1928

Figures 1b, 6d

Synonymy

aff. 1928. *Dictyonema* cf. *venustum* Lapworth, emend.; Bulman, pp. 62-3, pl. 5, fig. 8 (*non* 6-7).

Material

AM F123398; three other specimens (AM F123424-6) questionably assigned here.

Description

The large fragmental rhabdosome (AM F123398) has 12 stipes preserved, spaced at 16 in 10 mm, with interstipe spaces of 0.10-0.40 mm, and spaced at *ca.* 1-6 in 10 mm. Lateral stipe width 0.25 -0.40 mm, usually nearer the latter. Autothecae unclear but may be spaced at *ca.* 20 in 10 mm with dorsoventral width of 0.50 mm.

Remarks

This specimen is very close to that figured by Bulman (1928, pl. 5, fig. 8) which he listed as *D. venustum* but he made it clear in the text that he placed it there only with reserve. As in the Cotton Hill quarry specimen the interstipe spacing is less and the stipes are more robust. The Girvan specimens illustrated by Bulman were said to come from *communis* zone beds (probably *convolutus-sedgwickii* zone in modern terminology); thus they may have come from pre-*turriculatus* Zone strata, and this is also possible in the case of the present specimen.

Dictyonema sp. cf. *D. falciferum* Bulman, 1928

Figures 3d, 5a

Synonymy

cf. 1928 *Dictyonema falciferum* n. sp.; Bulman, pp. 53-6, pl. 5, figs 1-3, text-figs 27-29.

cf. 2003 *Dictyonema falciferum* Bulman, 1928; Rickards et al., p. 315, figs 5I, 8B, 9C, 10A.

Material

AM F123399-123401.

Description

Rhabdosome possibly fan-shaped (?conical), at least 25mm long and 18 mm broad, with numerous parallel stipes spaced at 14 in 10 mm, having stipe interspaces of 0.50-0.60 mm. Rectangular meshes are defined by stipes and conspicuous dissepiments spaced at 8-10 in 10 mm. Autothecal spacing 20 in 10 mm. Lateral stipe width 0.20-0.25 mm, and dorsoventral stipe width 0.50 mm. Autothecae appear to be simple denticulate but not spinose. Bithecal tubes present but their apertural regions unclear. Branching rather irregular, at 0.5-5.0 mm intervals.

Remarks

These specimens are closely similar to the specimens described from Four Mile Creek by Rickards et al. (2003) differing only in having a less regular branching pattern and slightly more parallel stipes. One specimen (AM F123400; Fig. 5a) has traces of preserved stolons.

Dictyonema zalasiewiczi sp. nov.

Figures 1c, 4a

Material

Holotype, AM F123402, an almost complete rhabdosome.

Derivation of name

After Dr. J. Zalasiewicz, University of Leicester, a leading graptolite worker.

Diagnosis

A *Dictyonema* species with 30-40 dissepiments in10 mm; stipes 0.2-0.5 mm wide and spaced at 0.2-0.3 mm.

Description

Fan-shaped rhabdosome more than 30 mm long and over 20 mm wide, typified by its striking number of dissepiments, up to 40 per 10 mm, never less than 30. Dissepiments 0.05-0.10 mm across, often arched distally, and quite frequently branching; commonly angled rather than normal to adjacent stipes, but also occur as closely spaced pairs. Stipes uniformly 0.20-0.25 mm in lateral width, with branching every 2-2.5 mm proximally and more sparse distally, up to 6 mm. Branching occurs in broad zones. Stipes parallel and closely spaced, with interstipe spaces of 0.20-0.30 mm, similar to the lateral width, resulting in a stipe spacing of about 20 in 10 mm. Autothecal spacing difficult to discern in this dorsoventral view, but may be around 20 in 10 mm. Nature of autothecal apertures cannot be seen, except in one area where they appear to be denticulate or spinose. Bithecae not detected.

Remarks

This is a highly unusual and distinctive species because of the huge number of dissepiments. Bulman (1928, table II) gave only two species of Silurian dictyonemids with as many as 20 dissepiments in 10 mm (and none with this frequency in the Ordovician species; Bulman 1928, table I). Of Australian dictyonemids, Rickards and Wright (1997) and Rickards et al. (2003), for example, only once have dissepimental spacings as high as 30 in 10 mm been recorded, and that in some specimens of *Dictyonema delicatulum barnbyensis* from the middle to upper Ludlow; a few other Australian species have as many as 20 in 10 mm. *Dictyonema paululum australis* Rickards et al., 2003 is similar in having conspicuous dissepiments, but their spacing and that of the stipes is quite different. None of Bouček's (1957) dictyonemids has high dissepimental spacings.

Callograptus J. Hall, 1865

Type species

Callograptus elegans J. Hall, 1865, by original designation.

Callograptus bridgecreekensis Rickards et al., 2003

Figures 1d, 3b

Synonymy

2003 *Callograptus bridgecreekensis* n. sp.; Rickards et al., p. 319, figs 14A, 15A-B.

Material

AM F123403.

Description

These 13 or so stipes are towards the distal end of a moderately-sized (8 mm x 5 mm) piece of rhabdosome; lateral stipe width of 0.50 mm most proximally, and 0.20 mm at distal ends of stipes. Branching irregular, stipe spacing over 20 in 10 mm. No dissepiments. Autothecae not detected in this wholly dorsoventral view, but traces of bithecal tubes apparent.

Callograptus rigbyae Rickards et al., 2003

Figures 1e, 6c, 7d-e

Synonymy

2003 *Callograptus rigbyae* n. sp. Rickards et al., p. 319, figs 14B-C.

Material

Four almost complete colonies, AM F123404-6, 123414, plus AM F123419-123421.

Description

Fan-shaped or discoidal colony about 10 mm across, developed from a small holdfast. Up to 6 branching zones may occur in this short distance giving numerous peripheral stipes. Rare anastomosis of stipes. Interstipe spacing 0.50 mm; stipe spacing *ca.* 16 in 10 mm, lateral stipe width 0.20-0.30 mm. Autothecae spaced at 20 in 10 mm, and autothecal apertures bear a ventral spine up to 0.50 mm long. Dissepiments rare, and extremely fine. Bithecae occur, but their nature is unclear.

Remarks

The original specimens from Bridge Creek (Rickards et al. 2003, p. 319) were two colonies preserved in plan view. Two Cotton Hill specimens (Figs 7d-e) are more in profile. One (AM F123404a-b: Fig. 7d) shows the autothecae best and a short spine can be clearly seen. Bithecae were not detected in the original material.

Callograptus sp. aff. *C. ulahensis* Rickards et al., 2003

Figures 3c, 5f

Synonymy

aff. 2003 *Callograptus ulahensis* n. sp.; Rickards et al., pp. 319-20, figs 16A, 17A.

Material

A small fragment of rhabdosome, AM F123407, comprising nine stipes.

Description

The initial two parallel stipes branch after 3 mm, but thereafter branch at 1-1.5 mm intervals resulting in short, parallel stipes with lateral width of 0.20 mm. Interstipe spaces *ca.* 0.50 mm, and stipe spacing *ca.* 20 in 10 mm. Autothecal spacing 20 in 10 mm; dorsoventral width may be 0.40-0.50 mm and thecal aperture may be denticulate. No dissepiments present.

Remarks

This specimen adds a little to the original description which was based upon two specimens (AM F114760 and 114780) from locality BF15, some 100 m S of the junction of Four Mile Creek and its tributary Bridge Creek (Rickards et al. 2003). The autothecae are not so clear in the Cotton Hill Quarry specimen, but the disposition of the stipes is more apparent.

Family Stelechocladiidae Chapman et al., 1993

Stelechocladia Počta, 1894

Type species

Stelechocladia subfruticosa Počta, 1894, subsequently designated by Bouček (1957).

Stelechocladia sp. cf. *S. praeattenuata* Rickards et al., 2003

Figure 5b

Synonymy

cf. 2003 *Stelechocladia praeattenuata* n. sp.; Rickards et al., p. 322, figs 17B, 19A-B.

Material

AM F123408a-b, and AM F123422-3.

Description

AM F123408 is the distal end of a stelechocladiid with stipes spaced at 16 in 10 mm, some apparently laterally derived from nearby dominant stipes. Lateral stipe width from 0.20-0.40 mm, the more robust stipes being more proximal. Branching, where it occurs, is almost every mm, but long, unbranched portions also occur. Autothecae not seen.

Remarks

This form is almost certainly referable to *S. praeattenuata,* having the typical combination of dichotomous and "lateral" branching as well as the dimension of a distal part of that species' rhabdosome. Lack of autothecal presentation, however, urges caution.

Family Acanthograptidae Bulman, 1938

Acanthograptus Spencer, 1878

Type species

Acanthograptus granti Spencer, 1878, by original designation.

Acanthograptus praedeckeri Rickards et al., 2003

Figures 2c-d, 5c, 7f

Synonymy

2003 *Acanthograptus praedeckeri* n. sp.; Rickards et al., pp. 322-5, figs 17C-D, 19C, 20A- (not fig. 18A).

2003 *Dictyonema warrisi*; Rickards et al., fig. 18A (mislabelled).

Material

Three specimens, including one almost entire, small rhabdosome (AM F 123409, Fig. 7f): AM F123409-11.

Description

Twigs arranged at 8-16 in 10 mm, each 0.70-1.00 mm long and comprising two or more thecae. Main stipes 0.40-0.50 mm wide laterally, and their ramifications fill all the space available to form a flabellate or fan-shaped colony. Branching occurs every 0.50-2.0 mm, usually 1.00-1.50 mm. Autothecal tubes 0.10 mm wide and do not seem to expand towards apertures. Bithecae may be not much smaller and may open near bases of twigs or on main stipe.

Remarks

The caption for Rickards et al. (2003, fig. 18A) wrongly states that the illustrated species is *Dictyonema warrisi,* really being *Acanthograptus praedeckeri*.

Class Rhabdopleurina Fowler, 1892
Family Rhadopleuridae Harmer, 1905

Rhabdopleura Allman, 1869

Type species

R. normani Allman, 1869.

?*Rhabdopleura* sp.

Figures 5d-e

Material

AM F1123412-3; the latter has a fragment of *Callograptus rigbyae* on the reverse side (AM F123414).

Description

The larger specimen (AM F123412: Fig. 5d) appears to have a basal thecorhiza from which arise about nine tubes with a diameter of 0.15-0.20 mm. Tubes distally less sclerotised. Suggestion of growth lines in places, especially on AM F123413 (Fig. 5e). In thecorhizal portion there are probably pyritised (non-goethitised) stolons and possibly also attached encysted zooids. Distal parts of tubes (coenecia) unoccupied and may represent free-standing parts of tubes. AM F123413 may also have pyritised stolons and zooidal remains.

Remarks

This form does not resemble tuboids such as *Galeograptus* and *Cyclograptus* which we have previously recorded from Australia (Rickards et al. 1995, 2003). Were it not for the uncertainty about the growth lines we would refer this to *Rhabdopleura* with more confidence. *Rhabdopleura* has not previously been recorded in Australian strata.

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A Holocene History of the Vegetation of the Blue Mountains, New South Wales

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Chalson, J.M. and Martin, H.A. (2009). A Holocene history of the vegetation of the Blue mountains, New South Wales. *Proceedings of the Linnean Society of New South Wales* **130,** 77-109.

The Greater Blue Mountains Area has been inscribed on the World Heritage list for its exceptionally diverse *Eucalyptus* communities. Hanging swamps in this region, listed as 'vulnerable ecological communities', accumulate sediments that contain the palaeoenvironmental record. Seven of these swamps have been studied, revealing a history of the vegetation, climate and fire regimes.

Palynological analysis of each swamp reveals a history of the surrounding vegetation. There are similarities and parallel changes between some of the swamps allowing generalities about the climate of the Holocene to be made. In the early Holocene, about eleven to nine thousand years ago (11-9 ka), the vegetation was more wooded and the climate was probably somewhat warmer and wetter. By the mid Holocene about 6-4 ka, trees were less dominant in the vegetation suggesting that the climate was probably drier. By 3-2 ka, wooded vegetation had mostly returned, and after 2 ka, *Baeckea, Leptospermum, Kunzea* and *Melaleuca* species increased somewhat, with further increases in European settlement time, possibly reflecting a reduction or thinning of the wooded canopy.

Charcoal analysis of the accumulated sediments suggest that there was more fire in the early Holocene when trees increased the biomass. There was less fire through the mid Holocene when the biomass was lower, but it increased with the return to more wooded vegetation in the late Holocene. In particular, the woody shrubs of *Baeckea, Leptospermum, Kunzea* and *Melaleuca* increased with an increase in charcoal, probably because these shrubs benefit from a more open canopy, but they also grew on the swamps hence could deposit charcoal directly into the sediments. Charcoal values are particularly high after European settlement. It is possible that the disruption of Aboriginal burning practices allowed the increased growth of woody shrubs and hence a much greater fuel load.

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KEY WORDS: Blue Mountains, Climate change, Fire history, Palynology, Vegetation history.

INTRODUCTION

The Greater Blue Mountains Area was inscribed on the World Heritage List in December 2000. The Blue Mountains are a deeply incised sandstone plateau rising to over 1,300 m at its highest point. This plateau is thought to have enabled the survival of a rich diversity of plant and animal life by providing a refuge from climatic changes during the recent geological history. It is particularly noted for its wide representation of habitats, from wet and dry sclerophyll, mallee heathlands, as well as localised swamps, wetlands and grassland. Ninety one species of eucalypts are found in the Greater Blue Mountains Area and twelve of these are believed to occur only in the Sydney sandstone region (Australian Government, Department of the Environment and Water Resources, 2007a).

The area has been described as a natural laboratory for studying the evolution of the eucalypts (Australian Government, Department of the Environment and Water Resources, 2007a). The steep terrain and sharp environmental gradients have allowed for major evolutionary change in some taxa, resulting in exceptional biodiversity, particularly within the eucalypt communities that dominate the place. Importantly, the evolutionary processes underpinning this diversity are believed to be ongoing, resulting in an evolutionary 'laboratory' that is exceptional in the world (Australian Government, Department of the Environment and Water Resources, 2007a).

Peat formation on sandstone, the substrate of most of the Blue Mountains, is very unusual. The hanging swamps of the Blue Mountains are especially notable and have lower sediment loads and accumulate organic matter more slowly than valley swamps and swamps along watercourses. They are also easily eroded with any disturbance. The small geographic distribution and demonstrable threat has meant that these hanging swamps are now listed as 'vulnerable ecological communities' under the NSW Threatened Species Conservation Act of 1995 ((Australian Government, Department of the Environment and Water Resources, 2007b; Sullivan, 2007)

Seven swamps in an altitudinal sequence in

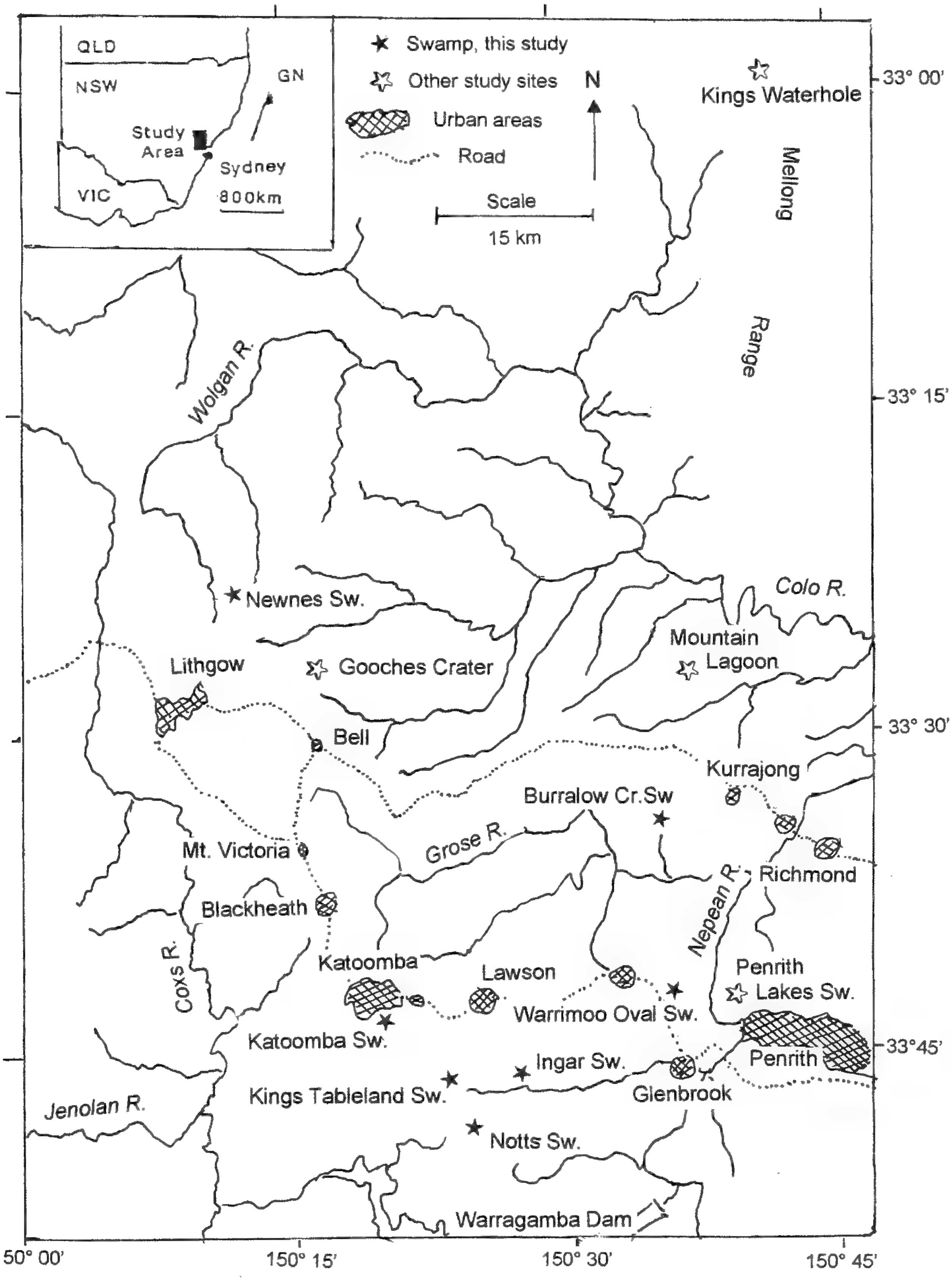


Figure 1. Locality map.

the Blue Mountains (Fig. 1) were chosen for a palynological study and are described in Chalson and Martin (this volume). A method to identify *Eucalyptus* pollen to species was developed (Chalson and Martin, 1995) with the aim of revealing the history of the eucalypt communities of the region. At the beginning of the Holocene, 10,000 years ago, the climate was approaching that of today, but there have been changes through the Holocene (Allan and Lindsay, 1998). The history of the Holocene is thus the history of vegetation very like that of today.

THE ENVIRONMENT

Geology and geomorphology

The Blue Mountains consist of a deeply dissected plateau rising from the Cumberland Plain in the east, along the Lapstone Monocline. Elevation is about 30 m in the east to over 1,000 m in the west. The sedimentary rock units are Triassic in age and curve upwards, from east to west, towards the edge of the Sydney Basin. In the east, Wianamatta Shale outcrops along the side of the Lapstone Monocline. West of the Monocline, the underlying Hawkesbury Sandstone Formation outcrops and further west, underlying the Hawkesbury Sandstone, the Grose Sub-Group of the Narrabeen Group outcrops. The Grose Sub-Group is divided into a number of formations and the ones encountered in this study are as follows: The Banks Wall Sandstone Formation, within which is found the Wentworth Falls Claystone Member, and the basal Burra-Moko Head Sandstone Formation, which is the most prominent cliff-forming unit in the Blue Mountains (Bembrick, 1980).

The plateau surface is undulating with small creeks forming upland valleys. In areas where Hawkesbury Sandstone is the underlying rock type, the upland valleys progressively increase in gradient as they incise below the plateau surface and develop steeply inclined V-shaped gorges with only minor benching in the valley sides. To the west, where the Banks Wall Sandstone formation is the underlying rock type, the valley sides and floors slope gently and the streams do not incise but flow across a series of swamps and sandy peat deposits. Eventually, the streams cut through a sandstone layer into claystone or shale when a nickpoint (often a waterfall) is formed (Langford-Smith, 1976).

The development of the swamps in these two areas varies enormously. The eastern region supports few swamps which are usually associated with large streams that have a central channel and flowing water. In the western region, there are more swamps and they are developed in broad shallow valleys with no marked central stream but rather experience a general slow flow of water across the whole area (Langford-Smith, 1976).

The climate

Maximum temperatures in the Blue Mountains relate strongly to altitude. Average January maxima are highest at the lower altitudes, 29 °C at Richmond and lowest at the higher altitudes, 23 °C at Mt. Victoria. Average minimum temperatures generally decrease from east to west. The July minima range from 3.4 °C at Richmond to –0.8 °C at Lithgow (Table 1). Temperatures as low as –3 °C have been recorded from Katoomba (BoM, 2006; Bureau of Meteorology, 1979).

Rainfall patterns relate to elevation and distance from the coast. The average annual rainfall increases from 806 mm at Richmond to 1424 mm at Newnes (Table 1). The driest months are usually July to September and the wettest are December to March (BoM, 2006; Bureau of Meteorology, 1979).

Winds from the west or northwest dominate all the year, although there are significant easterly and northeasterly winds during the summer months of November to April. Fogs frequently occur on the higher Blue Mountains, with Katoomba and Mt. Victoria recording an average of 55 and 90 fog days per year, respectively (BoM, 2006). Frosts occur on 35 to 40 days of the year, mostly between April and November. Snow falls most frequently in July and August: Katoomba and Mt. Victoria have and average of 3 and 10 snow days per year, respectively (Bureau of Meteorology, 1979).

Soils

The quartz-rich sandstones in the area are low in most nutrients, and thus soil and alluvium derived from sandstones are low in nutrients. The soils are mainly lithosols and yellow podzolics with small areas of red and lateritic podzolic soils and sandy alluvial soils in the valleys. Most of the soils are moderately acidic, with pH values of 4.5 to 5. In rugged terrain, rock commonly lies near or at the surface. The soil fertility in the valleys may be higher because of the accumulation of organic matter (Chalson, 1991)

Vegetation

The vegetation is almost entirely dry sclerophyll woodland and open forest, the ‘Sydney Sandstone Complex’ (Keith and Benson,1988) with localised swamps in the valleys. There are small patches of tall open forest or wet sclerophyll in specially favourable habitats, such as protected gorges. Heathlands are found in the harshest environments.

Table 1. Climatic Averages. Stations are arranged according to altitude.

Station and altitude (m)	Mean max. temp, hottest month, (Jan.) °C	Mean min. temp, coldest month, (June or July) °C	Mean annual rainfall, mm
[1]Richmond, 19-20 [3]	29.5	3.4	806
[2]Penrith, 27	-	-	786
[2]Springwood ~400	-	-	1076
[2]Kurrajong Heights, ~550	-	-	1253
[2]Lawson, 715	-	-	1260
[2]Wentworth Falls, ~900			1409
[1]Lithgow (Birdwood St.), 950	25.5	0.7	860
[1]Katoomba, 1030	23.1	2.5	1398
[1]Mt Victoria, 1064	23.0	1.7	1061
[2]Blackheath PO, 1065	-	-	1145
[1]Lithgow (Newnes Forest Centre), 1050	23.2	-0.8	1072

1 From BoM (2007). 2 From Bureau of Meteorology (1979)
3 Average of Richmond RAAF and Richmond UWS Hawkesbury

Open forest with *Angophora costata*, *Eucalyptus piperita*, *E. agglomerata* and *Syncarpia glomulifera* dominant is found in sheltered gullies with moist, well-drained soils on the Hawkesbury and Narrabeen Group sandstones. The understorey includes small trees of *Allocasuarina torulosa* and *Acacia elata*, with shubs of *Hakea dactyloides*, *Pultenaea flexilis* and *Dodonaea triquetra*. Tall open forest is restricted to the more sheltered gorges and is dominated by *E. deanei* with *Syncarpia glomulifera*, *Acacia elata*, *Ceratopetalum apetalum*, *Callicoma serratifolia* and *Angophora floribunda*. There is a distinctive riparian scrub of *Tristaniopsis laurina* and *Backhousia myrtifolia* along the larger water courses (Keith and Benson,1988),

Woodland and low woodland with *Corymbia gummifera*, *Eucalyptus sclerophylla* and *E. oblongata* dominant is widespread on ridges and open slopes on shallow, well-drained soils of the Hawkesbury and Narrabeen Group sandstones. *E. punctata*, *E. piperita* and *Angophora costata* may be present in the more sheltered sites. *E. sclerophylla* is particularly common on damper soils. The understorey is rich in shrubs of the Proteaceae, Myrtaceae and Fabaceae (Keith and Benson,1988).

There are other woodlands: the 'Tablelands Grassy Woodland Complex' with *Eucalyptus dives*, *E. mannifera*, *E. eugenioides*, *E. pauciflora*, *E. rubida*, *E. aggregata* and *E. stellulata* the common species. The 'Snow Gum Woodland' has *E. pauciflora*, *E. dalrympleana*, *E. rubida* and *E. stellulata* dominant (Keith and Benson,1988).

Open heath communities have *Eucalyptus stricta*, *Allocasuarina nana* and *Leptospermum trinervium, Phyllota squarrosa*, *Eriostemon obovalis*, *Epacris reclinata*, *Dracophyllum secundatum* and *Gleichenia rupestris* dominant. *Phyllota squarrosa* and *Eriostemon obovalis* are common in montane heaths whereas *Phyllota phylicoides* and *Eriostemon hispidula* are common on the Lower Blue Mountains heath. Many other smaller shrubs are found in these heath communities (Keith and Benson,1988).

Closed heath or 'Newnes Shrub Swamps' have *Leptospermum lanigerum*, *Baeckea linifolia*, *Grevillea acanthifolia* and *Xyris ustulata* dominant. They are found in shallow valleys above 1,000 m elevation in swamps, with poorly drained, acid and sandy peat soils. There is a ground cover of sedges including *Baloskion australe*, *Empodisma minus*, *Lepyrodia scariosa*, *L. anathria*, *Lepidosperma limicola* and small shrubs (Keith and Benson,1988).

Closed sedgeland, the 'Blue Mountains Sedge Swamps', have *Gymnoschoenus sphaerocephalus*, *Lepidosperma limicola*, *Xyris ustulata* and *Baeckea linifolia* dominant. These sedge swamps are found at lower altitudes than the closed heath swamps and occupy steep-sided basins (the 'hanging swamps'). They are intermittently waterlogged and have shallow sandy soils. Many sclerophyllous shrubs form an open heath (Keith and Benson,1988).

For a full description of the specific vegetation found at each site, see Chalson and Martin (this volume).

Human Occupation

The Blue Mountains, especially the lower part, was highly favourable to the hunter-gatherer, (Stockton,1993a). Movement was relatively easy on the ridges, water was not scarce while flora and fauna suitable for food were both plentiful and varied. The rivers were also a source of rock types used for tool making.

Campsites with an abundance of worked stone were particularly common in the Lower Blue Mountains. In the Upper Mountains, there were fewer campsites than in the Lower Mountains, but their concentration of flaked stone showed that they have been equally well used. The Central Mountains reveal many rockshelter sites where there were fewer stone artifacts than the Upper and Lower Mountains. However, there was a high concentration of rock art, engravings, paintings and axe grinding grooves. This suggests that the Upper and Lower Mountains were used for survival but the Central Mountains were more of religious and ritual significance (Stockton,1993a).

It is generally presumed that the climate in the Blue Mountains was too severe for year-round occupation during the ice age. However, protected sites such as the rock shelters would have been livable, especially if protected from the bitter westerly winds. (Stockton,1993b).

The oldest signs of occupation in the Blue Mountains were found at Kings Tableland, Wentworth Falls with the oldest date of 22,240 years BP. Walls Cave at Blackheath and Lyre Bird Dell, Leura both yielded dates of more than 12,000 years BP. There were other sites, e.g. Hazelbrook, to 7,200 years BP, Springwood Creek Rock Shelter, from 8,500 years BP up to European times and open sites, e.g. Jamison Creek. Evidence from the Nepean River, at the foot of the Blue Mountains suggests human occupation could go back to 40,000 years BP. In all, there were over 700 Aboriginal sites in the Blue Mountains (Stockton, 1993b; Attenbrow, 2002).

With the coming of Europeans, both Europeans and Aborigines avoided each other and early travelers in the Mountains rarely saw any Aborigines. Settlers followed the first crossing of the Mountains in 1813 by Blaxland, Lawson and Wentworth (Breckell, 1993) After some skirmishes about the land the settlers had taken, Aborigines and Europeans co-existed, though not without racist incidents (Smith, 1993).

METHODS

Seven swamps in an altitudinal sequence were chosen for study and they are described in Chalson and Martin (this volume). A study of the pollen in surface samples from swamps (Chalson and Martin this volume) provides insights that assist in the interpretation of the pollen spectra from the sediments. The description of the vegetation at each site is also presented in Chalson and Martin (this volume).
The swamps were systematically probed to identify the area where accumulating sediments were the deepest, using a Russian D-corer (Birks and Birks, 1980). The sediments and stratigraphy were described using the terminology of Birks and Birks (1980) Samples for radiocarbon dating were taken from a pit where possible, otherwise with repeated use of the D-corer until sufficient sediment was acquired. The standard radiocarbon dates were calibrated using the CalPal (Version March 2007) program.

Samples of sediment were taken from the core every 10 cm, or where it was thought there could be a critical change, every 5 cm. For pollen preparations, the core sediments were spiked with *Alnus* of a known concentration, treated with hydrochloric and hydrofluoric acids to remove siliceous material (Birks and Birks, 1980), oxidised with Schultz solution (a saturated solution of potassium perchlorate in nitric acid), cleared in 10% potassium carbonate and the residue was mounted in glycerine jelly (Brown, 1960). Reference pollen was treated with standard acetolysis (Moore et al., 1991) and also mounted in glycerine jelly.

Pollen was identified by comparing grains from the core with a collection of reference pollen. Special attention was paid to pollen of the family Myrtaceae which may be identified to species following the method in Chalson and Martin (1995).

Pollen was counted along transects across the slides and tests showed that a count of more than 140 grains adequately sampled the residues. The counts were presented as percentages of the total count and pollen concentrations were calculated for the most abundant pollen groups. Percentages are relative and a change in a single pollen group will affect percentages of all the other groups, but presenting both percentages and concentrations will reveal fluctuations in individual pollen groups.

The abundance of charcoal retained on a 150 μm sieve, as part of the palynological preparation, was estimated subjectively on a scale of 0 to 8. Counts of microscopic charcoal for a swamp at Kings Tableland showed that the two methods gave similar results, although the microscopic charcoal was more variable (Chalson, 1991).

RESULTS

Burralow Creek Swamp

Burralow Creek Swamp, at 33° 32'S, 150° 36' 38"E and 310-330 m altitude, is situated in a narrow V-shaped valley and follows the course of the creek for some 3.5 km. The substrate is Hawkesbury Sandstone, but Wiananatta Shale outcrops on the surrounding ridge-tops. The upper reaches of Burralow Creek drain urban areas and farmland areas. An isolated farm adjacent to the swamp was incorporated into the Blue Mountains National Park. Weed growth from this farm is confined to a small area and has not spread into the adjacent bushland.

Stratigraphy: Sediments were recovered to a depth of 310 cm. Clayey peat was found down to 10 cm, humic clay at 15-50 cm and humic sandy clay at 60-70 cm. Sand was encountered at 80-260 cm and clay/sand at 260-310 cm. The radiocarbon dates are presented in Table 2.

Swamp vegetation and surface pollen: Species of *Kunzea* and *Leptospermum* were dominant on the swamp but Restionaceae, Cyperaceae and *Selaginella* species were also present (Chalson and Martin, this volume). Surface sample pollen from the swamp (Chalson and Martin, this volume) showed appreciable *Leptospermum/Baeckea* and a considerable amount of Restionaceae or Cyperaceae in some samples. The fern spore content was low.

The pollen record: The pollen spectra from the sediments is presented in Figs 2A, 2B and has been divided into the following zones:

310 to140 cm, no pollen recovered.

Zone E, 130 cm, age ? > 1,200 cal yr BP (see Fig. 3 for estimated ages). *Angophora floribunda*, *Eucalyptus* spp. and possibly Casuarinaceae pollen were the most abundant of the possible arboreal groups. There was a moderate representation of Poaceae and *Selaginella* (Fig 2A) and other shrubs and herbs were present in low frequencies (Fig 2B).

120-110 cm, no pollen recovered.

Zone D, 100-90 cm, age c. 1,200 –1,000 cal yr BP . This zone had a very high proportion of *Selaginella* spores and low proportions of everything else, including tree pollen. The pollen concentrations showed a similar pattern to that of the percentages which revealed a change in the whole pollen spectrum, not only reflecting the addition of a large number of *Sellaginella* spores to spectra otherwise like that in zone E.

Zone C, 80-60 cm, age c. 1,000-800 cal yr BP The Sellaginella content had decreased considerably when compared with the zone brlow, There was a high proportion of Casuarinaceae and Myrtaceae, including *Eucalyptus* species and the Poaceae content was low.

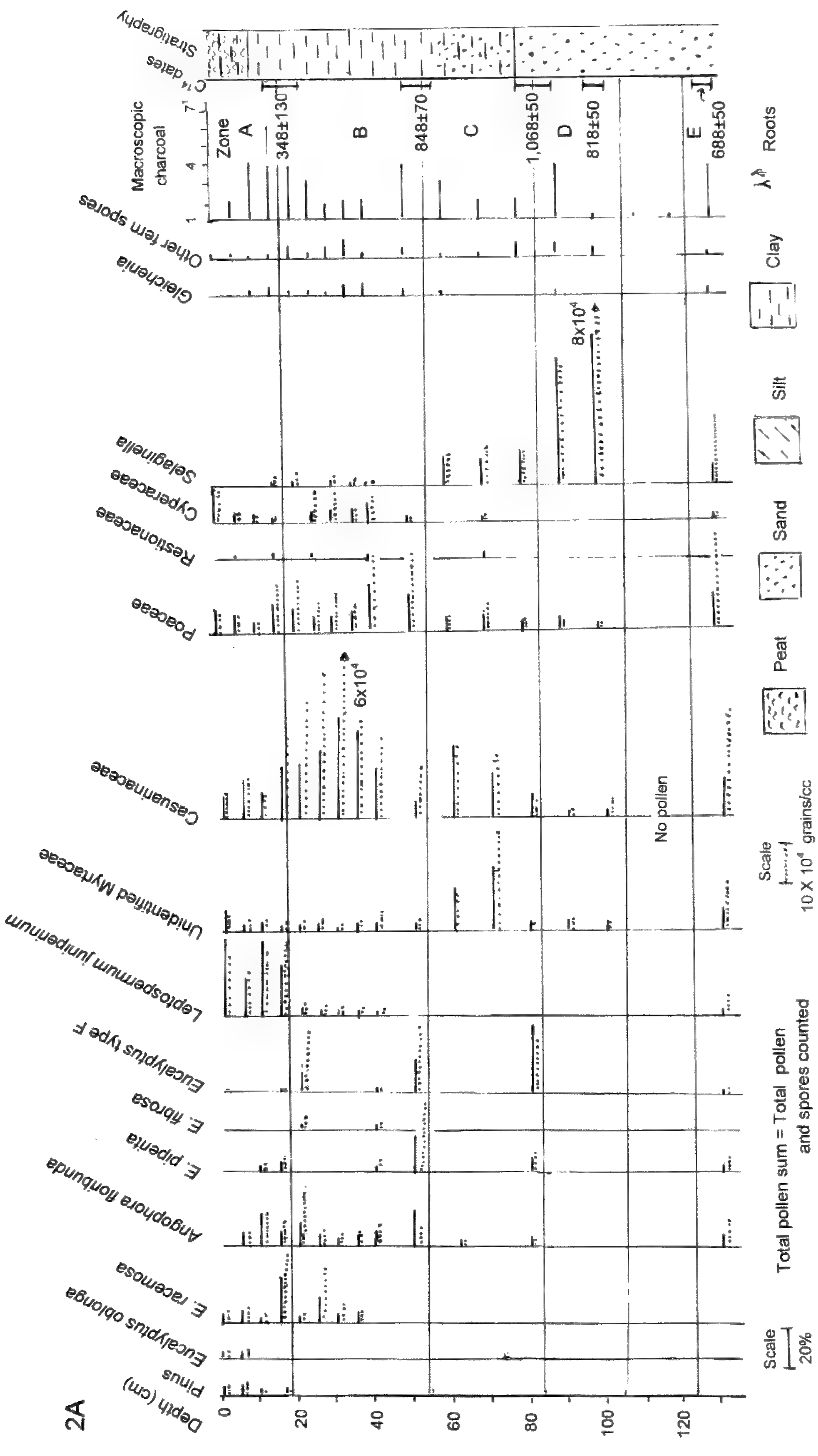
Zone B, 50-20 cm, age c.8700-250 cal yr BP. The Casuarinaceae content had increased and was the highest for the profile. *Eucalyptus* species and *Angophora floribunda* were well represented and *Leptospemum juniperinum* was present in low frequencies. There was a moderate content of Poaceae and Cyperaceae, with a diversity of fern spores. *Sellaginella* content was minimal.

Zone A, 15-0 cm, age c. 250-present, cal yr BP. European *Pinus* was found in this Zone and there was a high content of *L. juniperinum*. There was some change in the *Eucalyptus* species, Casuarinaceae declined. and the Poaceae content was moderate, when compared with the zone below.

Charcoal content was low to moderate through most of the profile, with a somewhat higher content at the base of Zone A, the zone of European influence.

Table 2. Radiocarbon ages for Burralow Creek Swamp

Depth (cm)	Material dated	Laboratory no.	Radiocarbon years (yr BP)	Calibrated age (cal yr BP.)
15-20	Humic clay	SUA-2607	250 ±50	348±130
50-60	Humic sandy clay	SUA-2608	830±60	848±70
80-90	Sand	SUA-2609	1,070±50	1068±50
95-105	Sand	SUA-2610	820±50	818±50
125-135	Sand	SUA-2611	660±55	688±50



Figures 2A, 2B. Burralow Creek Swamp pollen spectra. For probable source of the pollen type in the vegetation, see Appendix.

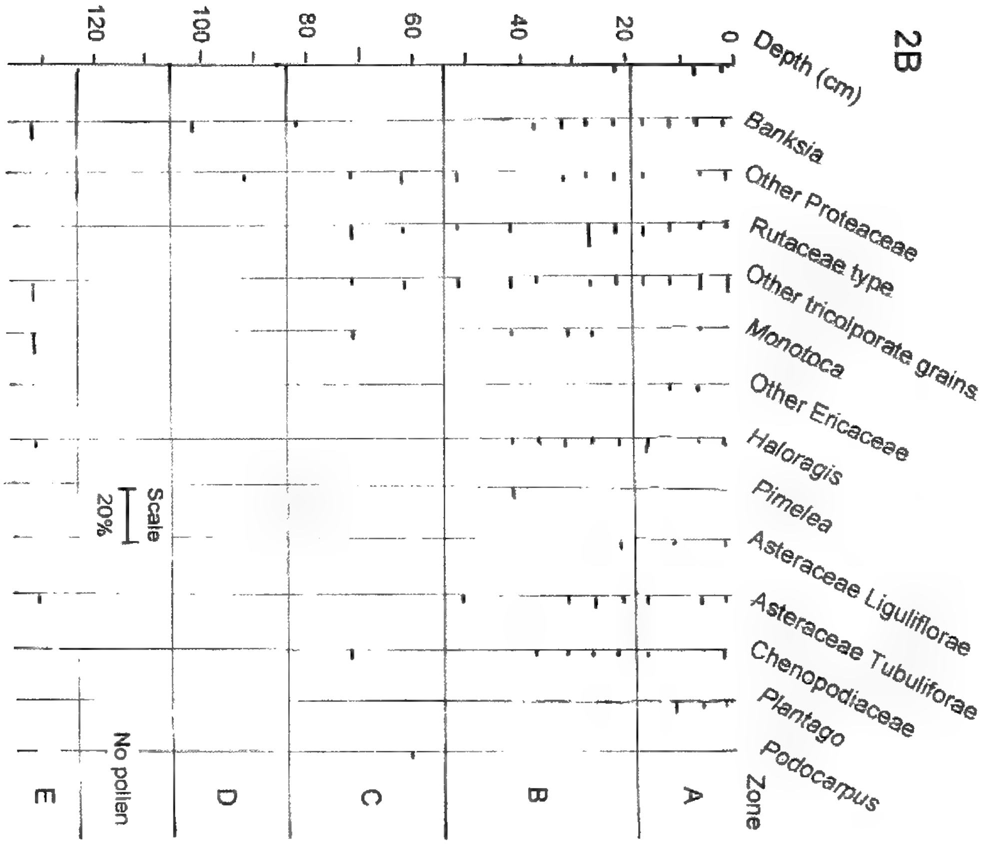


Figure 2 continued

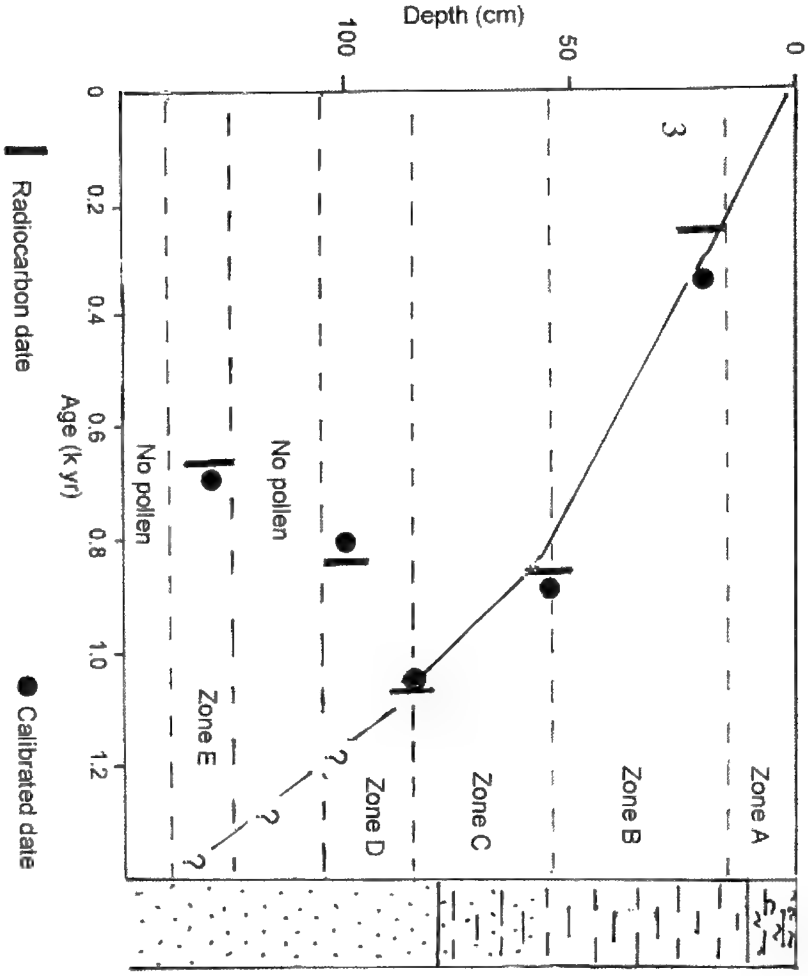


Figure 3. Burralow Creek Swamp summary diagram.

History of the vegetation: Initially, more than 1,200 cal yr BP, there was a mixed tree cover of Myrtaceous species and possibly Casuarinaceae with a moderate Poaceae understorey. *Selaginella*, was prominent on the swamp. A period of possibly a reduced tree cover followed, with an expanded swamp area with abundant *Selaginella* about 1.2-1.0 cal ka. Alternatively, if the swamp area was larger, the trees may have been further away, hence they contributed less pollen to the spectrum. The tree cover increased and *Selaginella* was much reduced by about 1-0.8 cal ka. At this time, the clay content of the sediments increased, perhaps indicating a less energetic water flow. Casuarinaceae became prominent about 0.8-0.25 cal ka with less Myrtaceae, although a diversity of species was identified. Simultaneously, *Sellaginella* decreased while Cyperaceae and Poaceae increased. In the European zone, there was some change in *Eucalyptus* species and a big decline in Casuarinaceae while *Leptospermum juniperinum* became prominent.

Fire was a constant factor in the environment, especially in the early part of the European zone.

Warrimoo Oval Swamp

Warrimoo Oval Swamp, at 33° 43' 21.44"S, 150° 36' 58.35"E and 190-200 m altitude, is situated in a V-shaped valley with a stream flowing through it. The substrate is Hawkesbury Sandstone, but Wiananatta shale outcrops on the surrounding ridge-tops. Substantial urban areas occur within a kilometre from the swamp and weed invasion is considerable.

Stratigraphy: Total depth recovered was 250 cm. The top 20 cm was peat, then sandy peat down to 50 cm. A layer of sand was found between 50 and 90 cm, then sandy silt down to 200 cm, then sand down to 250 cm when coring stopped (Fig. 4A). The radiocarbon dates are given in Table 3.

Swamp vegetation and surface pollen: Species of *Baeckea, Kunzea* and *Leptospermum* were dominant on the swamp. Cyperaceae, Juncaceae and *Gleichenia* species were also present (Chalson and Martin, this volume). The pollen spectra from the surface samples (Chalson and Martin, this volume) contained appreciable *Melaleuca*, *Baeckea/Leptospermum* and *Gleichenia* species.

The pollen record: The pollen spectra from the sediments are shown in Figs 4A, 4B.

Zone B, 250-130 cm, c. 4,700-2,200 cal yr BP (for estimated ages, see Fig. 5). Abundant *Gleichenia* denoted this zone, The Myrtaceae content was low, with some of the pollen identifiable to genus/species. There was a consistent content of Casuarinaceae and *Haloragis,* and Poaceae was almost entirely absent.

Zone A, 120 cm to surface, c. 2,200-present cal yr BP. There was very little *Gleichenia*,, together with an increase in the Myrtaceae and Casuarinaceae content, when compared with the zone below. The Poaceae, Cyperaceae and Restionaceae content was higher and the pollen flora considerably more diverse when compared the preceding zone. *Pinus* was found down to a depth of 20 cm, thus denoting the European influence, where *Baeckea/Leptospermum* species increased and Casuarinaceae decreased.

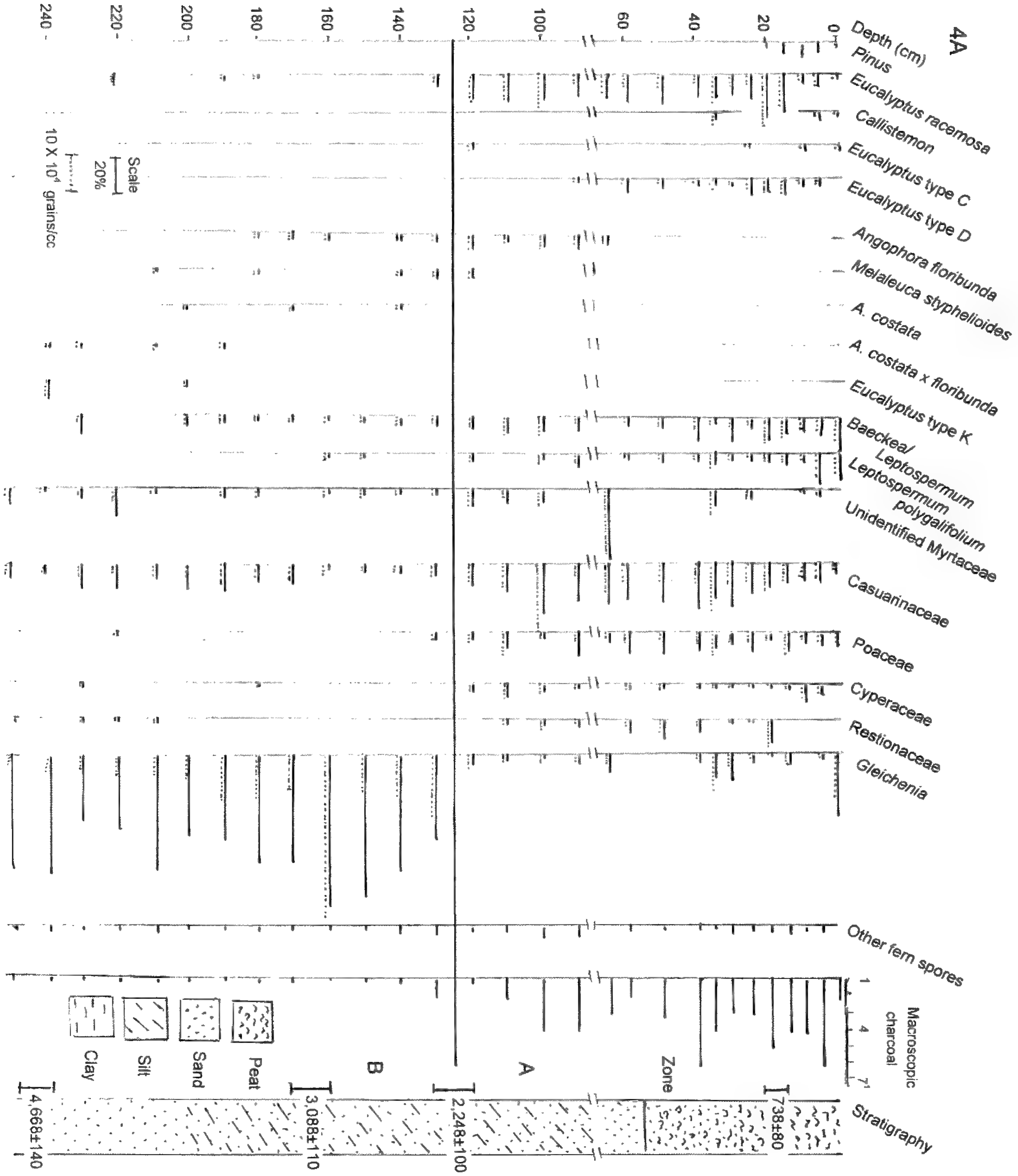
The charcoal content was consistently very low in zone B (4.7-2.2 cal ka) and higher in zone A (2.2 cal ka to present).

History of the vegetation: From about 4.7-2.2 cal ka, myrtaceous species and Casuarinaceae dominated open vegetation communities. The swamp supported abundant *Gleichenia*. About 2.2 cal ka, the tree cover of the dryland vegetation increased, with *Eucalyptus* spp and *Leptospermum* spp. becoming more diverse and abundant. Casuarinaceae was also more abundant. *Gleichenia* declined dramatically, but this change was not accompanied by any visible change in the sediments.

Fire appears to have been a rare feature of the environment when *Gleichenia* was dominant. With the change to a more diverse flora and increase of *Leptospemum* in the swamp community after 2.2 cal ka, fire was more common, particularly in the

Table 3. Radiocarbon ages for Warrimoo Oval Swamp

Depth (cm)	Material dated	Laboratory no.	Radiocarbon years (yr BP)	Calibrated age (cal yr BP)
15-25	Peat	SUA-2603	730±80	738±80
120-130	Sandy silt	SUA-2604	2,190±80	2,248±100
160-170	Sandy silt	SUA-2605	2,880±70	3,088±110
240-250	Sand	SUA-2606	4,060±80	4,668±140



Figures 4A, 4B. Warrimoo Oval Swamp pollen spectra. For probable source of the pollen type in the vegetation, see Appendix.

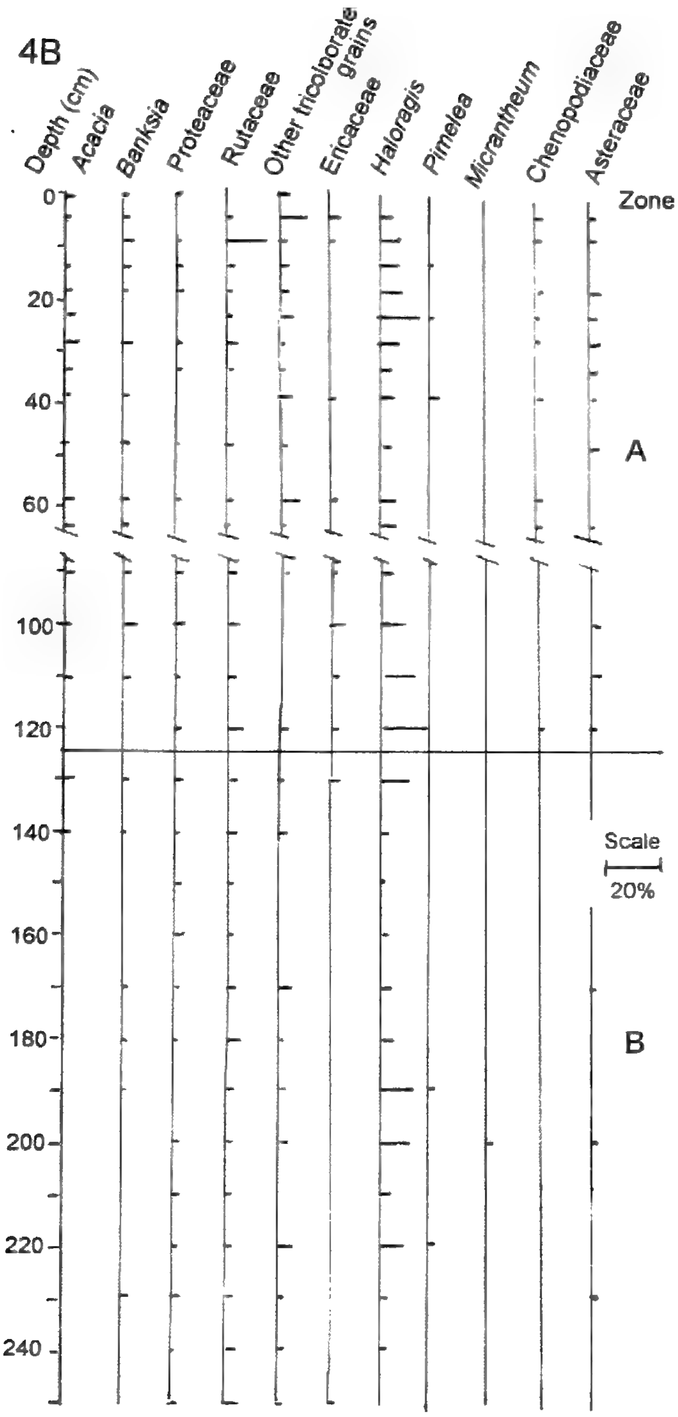


Figure 4 continued

European part at the top of the profile. There would have been a greater biomass after 2 cal ka, hence more fuel to burn, particularly on the swamp itself.

Notts Swamp

Notts Swamp, at 33° 48' 35.44" S, 150° 24' 27.66" E and about 682 m altitude is located in a shallow hanging valley. Below the swamp, Reedy Creek flows over a small cliff and follows a steep, narrow valley into the Kedumba Valley. The Wentworth Falls Claystone Member outcrops near the base of the swamp.

The lower third of the swamp is used for a market garden, but there is no sign of disturbance or weed invasion on the upper part of the swamp used for this study. There is no indication of European activities in the catchment upstream of the study site and the nearest settlement is some 7 km to the north-northeast.

Stratigraphy: The core recovered 130 cm of sediment. There was dark brown and greyish brown peat with roots down to 50 cm, then black or very dark greyish brown clay at 60-100 cm, with dark grey or light grey sandy silt at 110-130 cm. Pollen was recovered throughout the sequence, sometimes in very high concentrations. Radiocarbon ages are given in Table 4.

The swamp vegetation and surface pollen: Species of *Kunzea, Gahnia* and *Leptocarpus tenax* were dominant on the swamp. Species of *Gleichenia, Selaginella, Leptospermum,* Cyperaaceae, Juncaceae and a number of sclerophyllous shrubs were also present (Chalson and Martin, this volume). In the surface samples, Myrtaceae, Casuarinaceae and Restionaceae were well represented. There was appreciable *Pinus* pollen also. (Chalson and Martin, this volume).

The pollen record: The pollen spectra from the sediments are presented in Fig. 6A, 6B and is zoned thus:

Zone D, 110-130 cm, c. ?7,300-4,500 cal yr BP (for estimated ages, see Fig. 7). Myrtaceae pollen content was low and Casuarinaceae moderate. The *Selaginella* spore content was appreciable at the base, decreasing through the zone. The Restionaceae and Poaceae content was moderate and the lowest for the profile.

Zone C, 100-80 cm, c. 4,500-2,400 cal yr BP. The Myrtaceae, Restionaceae and Poaceae representation increased but the *Selaginella* content was much reduced when compared with the zone below, and this change coincided with a change in sediments to clay. *Gleichenia* and other fern spores increased somewhat when compared with the zone below.

Zone B, 70-30 cm, c. 2,400 cal yr BP. to ?modern. There were more identifications of the mytaceous pollen, an increase in Restionaceae and few *Gleichenia* and other fern spores when compared with the zone below. The *Selaginalla* and Cyperaceae content was minimal.

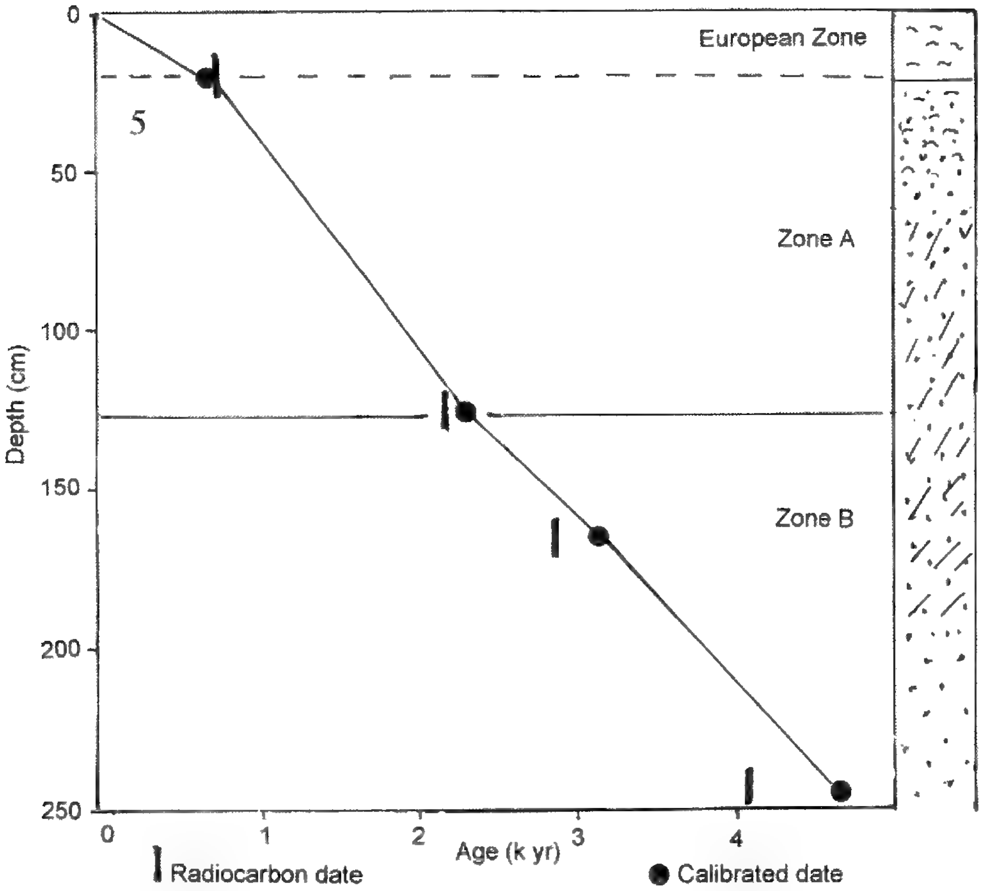


Figure 5. Warrimoo Oval Swamp summary diagram.

Zone A, 20-0 cm, modern. *Pinus* was found throughout the zone, indicating post European settlement. The Myrtaceae and Casuarinaceae pollen content was maintained. Restionaceae decreased towards the top and the Cyperaceae content, although low, is the greatest for the profile, when compared with the zones below

The charcoal content was very low at the base of the profile when *Selaginella* was prominent on the swamp, then increased after the decline in *Selagiella* and was consistently high in the European zone.

History of the Vegetation: About 7-4.5 cal ka, *Selaginella* was common on the swamp and the surrounding vegetation was an open woodland, with Casuarinaceae prominent. Fire was not common then. After about 4.5 cal ka, *Selaginella* was replaced by Restionaceae, the tree cover increased somewhat and fire became more common. The vegetation remained relatively stable until modern times when there was a slight decrease in Restionaceae and an increase in Cyperaceae. Charcoal abundance was higher when the tree cover was greater.

Ingar Swamp

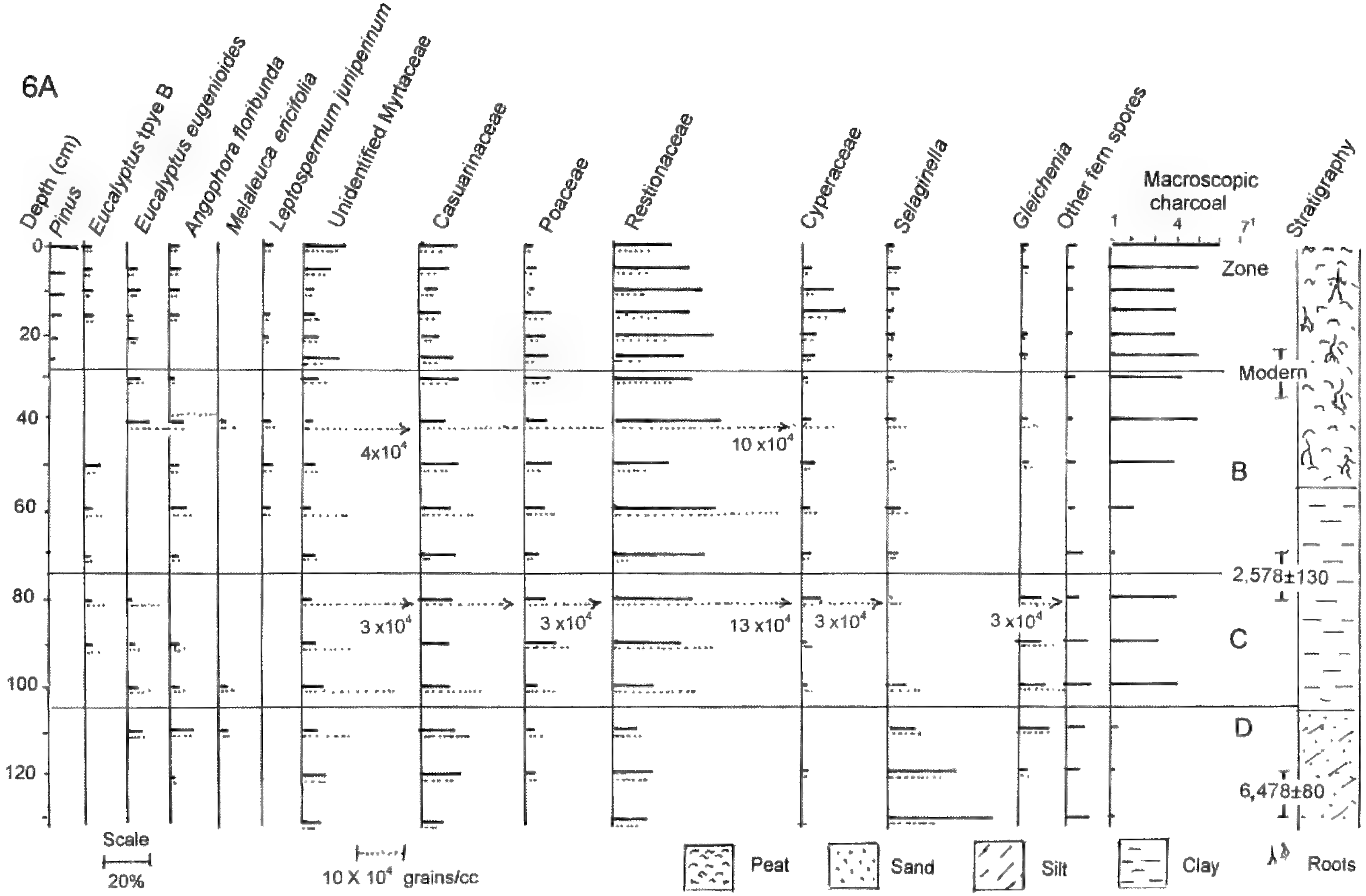
Ingar Swamp, at 33° 46' 11.65" S, 150° 27' 22.92" E and 584m altitude, is broad with many channels and hummocks of Cyperaceae forming ridges. The Banks Wall Sandstone Formation underlies the swamp and there are outcrops of the Wentworth Falls Claystone Member near the lower margin of the swamp. The swamp occupies the floor of a shallow hanging valley on the plateau surface. Below the swamp, Ingar Creek forms a waterfall where the valley gradient steepens.

Stratigraphy: The core recovered 155 cm of sediment. Peat with roots was found at 0-20 cm, then humic clay with roots at 25-110 cm, sandy humic clay at 120-130 cm, then sandy clay at 135-145cm, and silty clay at 150-155 cm. The radiocarbon ages are given in Table 5.

The swamp vegetation and surface pollen: Species of *Leptospermum*, Cyperaceae and Restionaceae were dominant on the swamp. *Gleichenia* and some sclerophyllous shrubs were also present (Chalson and Martin, this volume). The surface samples (Chalson and Martin, this volume) showed that most of the Myrtaceae pollen was

Table 4. Radiocarbon ages for Notts Swamp

Depth (cm)	Material dated	Laboratory no.	Radiocarbon years (yr BP.)	Calibrated age (cal. yr BP.)
25-35	Peat with roots	SUA 2653	1.O13±O.OO8x modern	Modern (<33)
75-85	Clay	SUA 2654	2,400±70	2,578±130
120-130	Sandy silt	SUA 2655	5,630±70	6,478±80



Fiuress 6A, 6B. Notts swamp pollen spectra. For probable source of the pollen type in the vegetation, see Appendix.

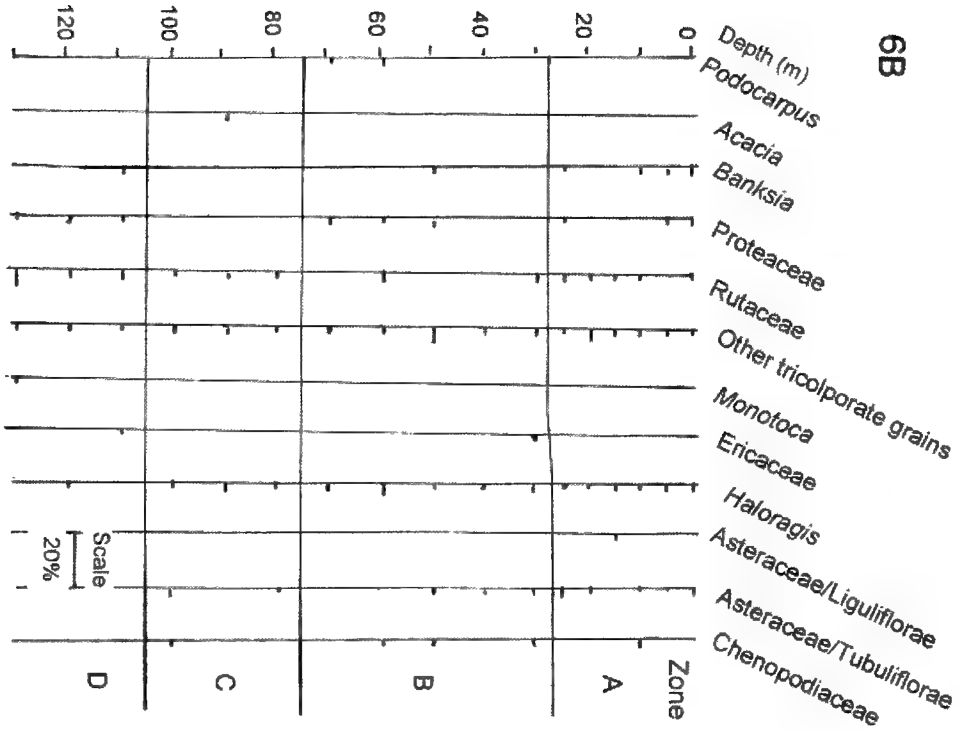


Figure 6 continued

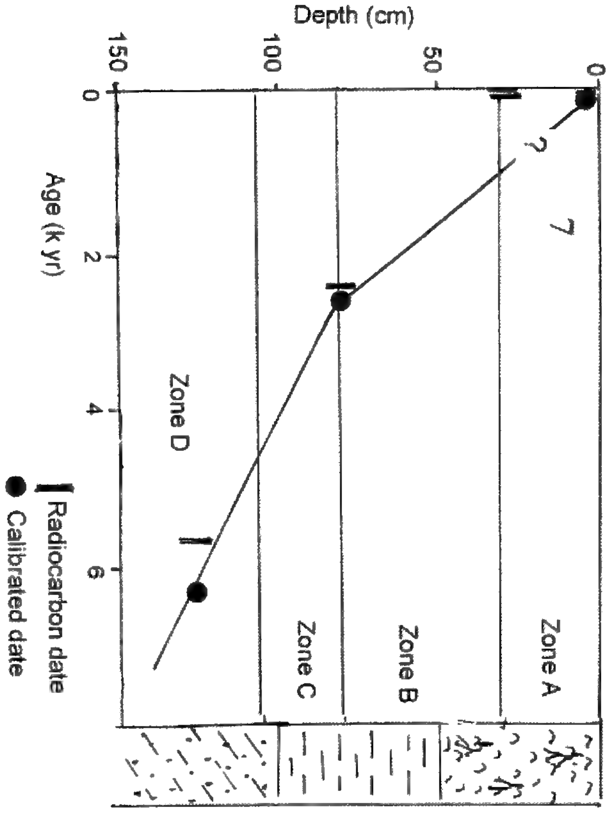


Figure 7. Notts swamp summary diagram.

Table 5. Radiocarbon ages for Ingar Swamp

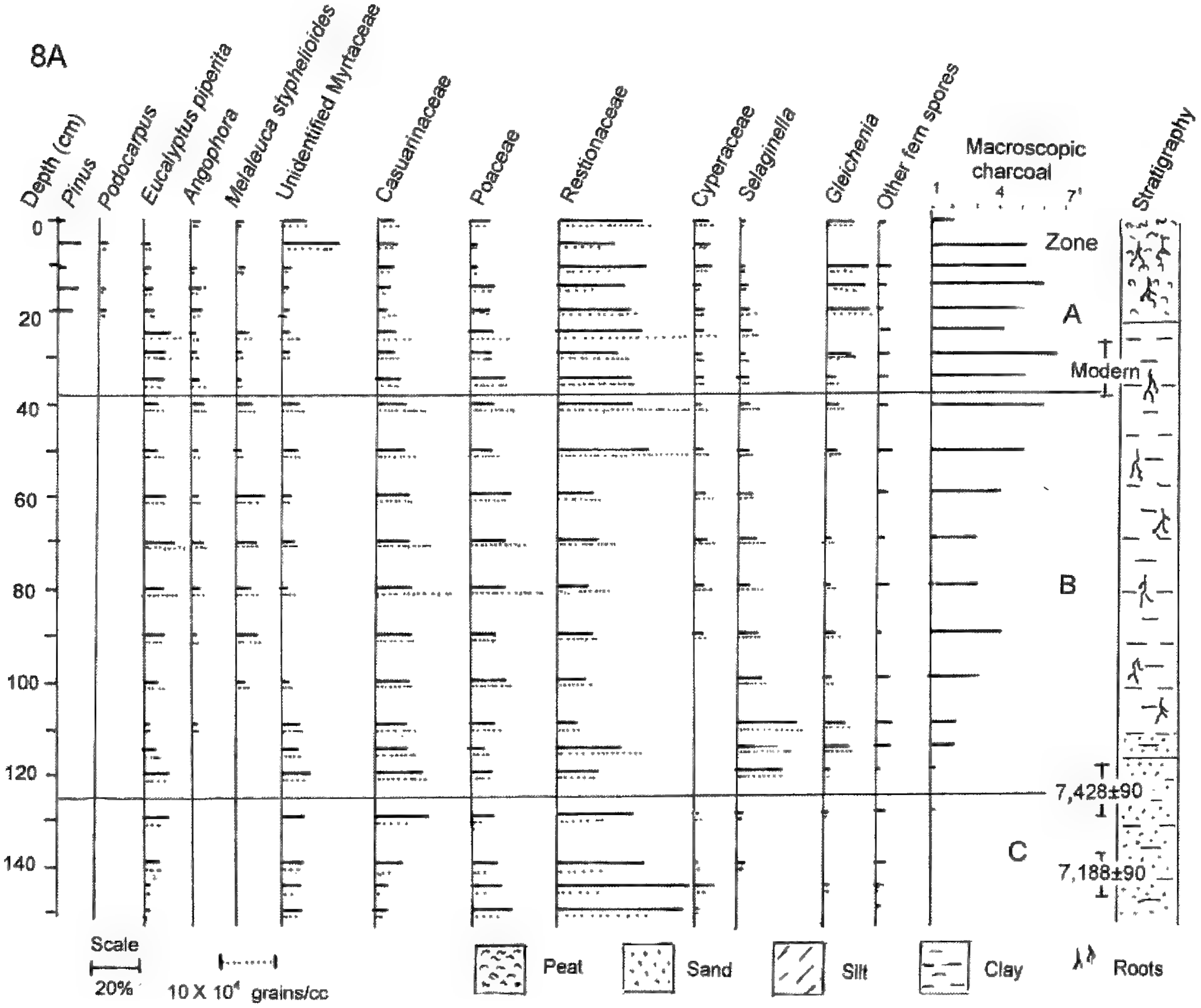
Depth (cm)	Material dated	Laboratory no.	Radiocarbon years (yr BP.)	Calibrated age (cal. yr BP.)
30-40	Humic clay with roots	BETA 20942	105.1±0.8% modern	Modern (<43)
120-130	Sandy humic clay	BETA 20943	6,460±100	7,428±90
140-150	Sandy clay	BETA 20944	6,220±100	7,188±90

unidentifiable. There was moderate Casuarinaceae and Poaceae.

The pollen record: The pollen spectra from the sediments is shown in Fig. 8A, 8B and has been zoned thus:

Zone C, 150-130 cm, c. 7,000 cal yr BP (see Fig. 9 for estimated ages). Abundant Restionaceae marked this zone. *Eucalyptus piperita*, other Myrtaceae and Casuarinaceae were prominent and there was a moderate content of Poaceae.

Zone B, 120-40 cm, c. 7,000-?2,200 cal yr BP. There was greater diversity here and more of tree/large shrub pollen, viz. *E. piperita*, *Angophora*, *Melaleuca*



Figures 8A 8B. Ingar swamp pollen spectra. For probable source of the pollen type in the vegetation, see Appendix.

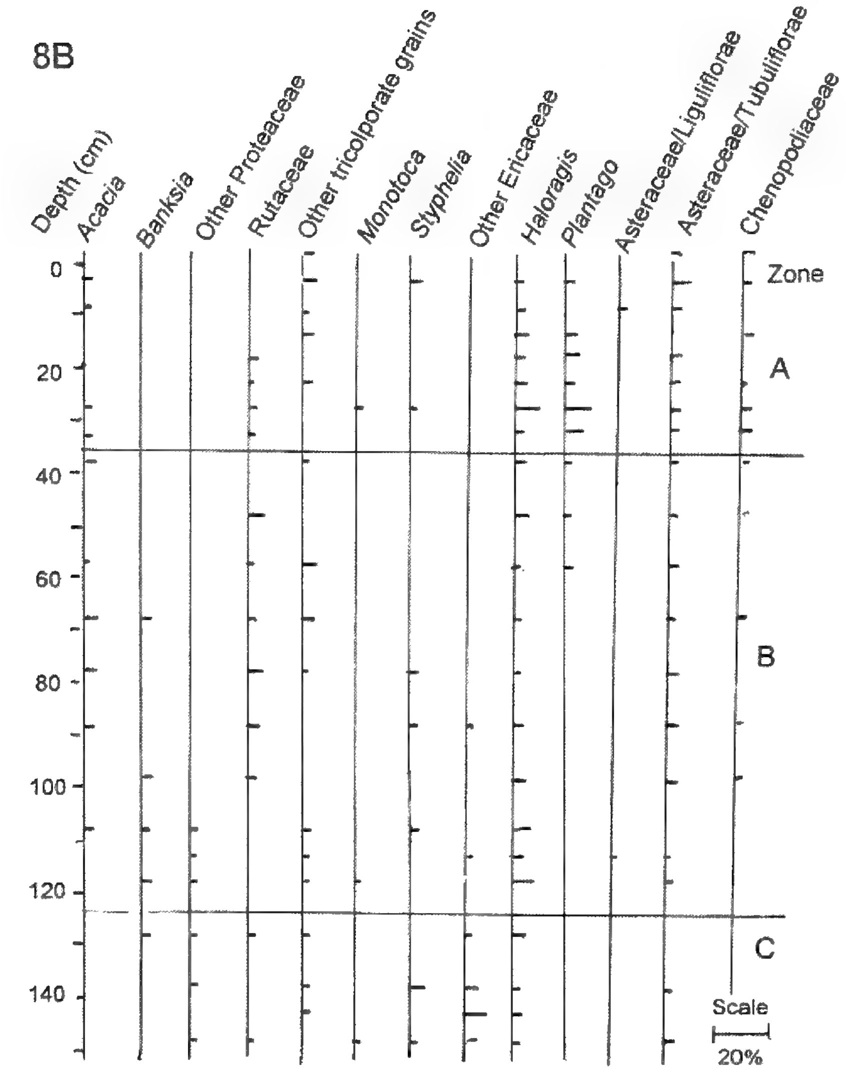


Figure 8 continued

styphelioides and Casuarinaceae, when compared with the zone below. There was a little more Poaceae but less Restionaceae than in the zone below. *Selaginella*, and to a lesser extent, *Gleichenia*, were moderate in the base of the zone.

Zone A, 40-0 cm, c. 2,200-0 cal yr BP to modern. *Pinus* was found down to 20 cm, marking European settlement. The dryland flora was similar to the zone below, but tree species declined with European influence. Restionaceae and *Gleichenia* were more abundant than in the zone below.

There was very little charcoal in the basal zone C, increasing in zone B and reaching a maximum in the European zone A.

History of the vegetation: Before 7 cal ka , the vegetation was relatively open, but after about 6 cal ka, the tree cover increased, especially Casuarinaceae. On the swamp, Restionaceae decreased but Cyperaceae, *Selagiella* and *Gleichenia* increased slightly. In the European zone, there was a slight decline in Casuarinaceae and an increase in the swamp species of Restionaceae and *Gleichenia.* Fire was relatively rare about 6 cal ka, but increased through time, to a peak in the European period.

Kings Tableland Swamp

Kings Tableland Swamp, at 33° 45' 47" S, 150° 22' 43" E and about 780-790 m altitude, is located in the floor of a steeply sloping small valley off Queen Victoria Creek. The valley floor steepens abruptly below the swamp and a waterfall cascades over a small cliff. The Banks Wall Sandstone Formation underlies the swamp and the Wentworth Falls Claystone outcrops near the base of the swamp. An area of development is found less than 1 km to the west where exotic conifers have been planted in the gardens.

Stratigraphy: The core sampled 220 cm of sediments which were peat down to 10 cm, then peaty sand at 15–20 cm, humic sand at 30-40 cm, peaty silt at 50 cm, humic sand at 60-90 cm, clay/sand at 100-120 cm and sand at 130-220 cm. Radiocarbon dates are given in Table 6.

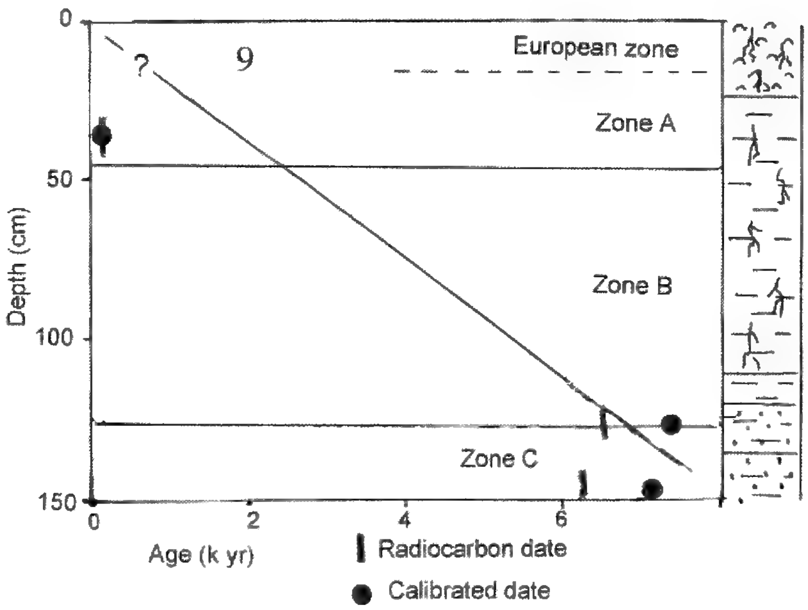


Figure 9. Ingar Swamp summary diagram

Table 6. Radiocarbon ages for Kings Tablelands Swamp

Depth (cm)	Material dated	Laboratory no.	Radiocarbon years (yr BP.)	Calibrated age (cal. yr BP.)
15-20	Peaty sand	SUA 2656	1.045±0.008 x modern	Modern (< 33)
50-60	Humic sand	SUA 2657	1,210±70	1,208±90
80-90	Humic sand	SUA 2658	2,410±70	2,578±130
155-160	Fine sand	SUA 2659	9,040±80	10,208±130

The swamp vegetation and surface pollen: *Leptospermum* species were dominant, but *Gleichenia* and sclerophyllous shrubs were also found on the swamp (Chalson and Martin, this volume). In the surface samples, the Myrtaceae content was low but Casuarinaceae was well represented (Chalson and Martin, this volume). The swamp taxa Restionaceae, *Selaginella* and *Gleichenia* were also well represented and the introduced *Pinus* was abundant.

The pollen record: The pollen spectra from the sediments (Figs 10A, 10B) have been zoned thus:

Zone C, 200-90 cm, c. ?>12,000-3,800 cal yr B P (see Fig. 11 for estimated ages). The Myrtaceae content was low and Casuarinaceae content moderate (Fig. 10A). Sclerophyllous shrubs and Restionaceae were well represented (Fig. 10B). *Gleichenia* and other fern spores were moderate. *Eucalyptus deanei* was found in the basal part of the zone and *Banksia* in the upper part.

Zone B, 80-30 cm, c. 3,800 cal yr BP to modern. This zone had some very high pollen concentrations which mirrored the spectra of the percentages, suggesting that the high concentrations result from slow sediment accumulation rather than the increased input of any one (or more) particular pollen type(s).

The Myrtaceae pollen proportion remained low but the Casuarinaceae representation had increased, when compared with the zone below. The proportion of Restionaceae and *Gleichenia* had decreased, but Cyperaceae and *Selagiella* had increased, in comparison with the zone below. Sclerophyllous shrubs were also well represented in this zone.

Zone A, 0-25 cm, modern. *Pinus* was found here, delimiting the European zone. The myrtaceous content had increased a little, especially *Melaleuca*. Casuarinaceae and Restionaceae decreased somewhat but *Gleichenia* increased considerably, when compared with the zone below.
The charcoal content was low to moderate in zones C and B, and increasing in the modern zone A.

History of the vegetation: The dearth of myrtaceous taxa, predominance of Casuarinaceae and the diversity and relative abundance of the shrubby taxa suggests a heathland, given that the two species of Casuarinaceae found in the region today, *Allocasuarina distyla* and *A. nana*, are shrubs/small trees. The swamp flora was dominated by Restionaceae throughout, with *Gleichenia* becoming prominent in modern times. Myrtaceae remains low until modern times, suggesting the surrounding vegetation remained relatively open. The charcoal content was relatively low until modern times, suggesting less fire activity, or lesser fuel to burn, until European times.

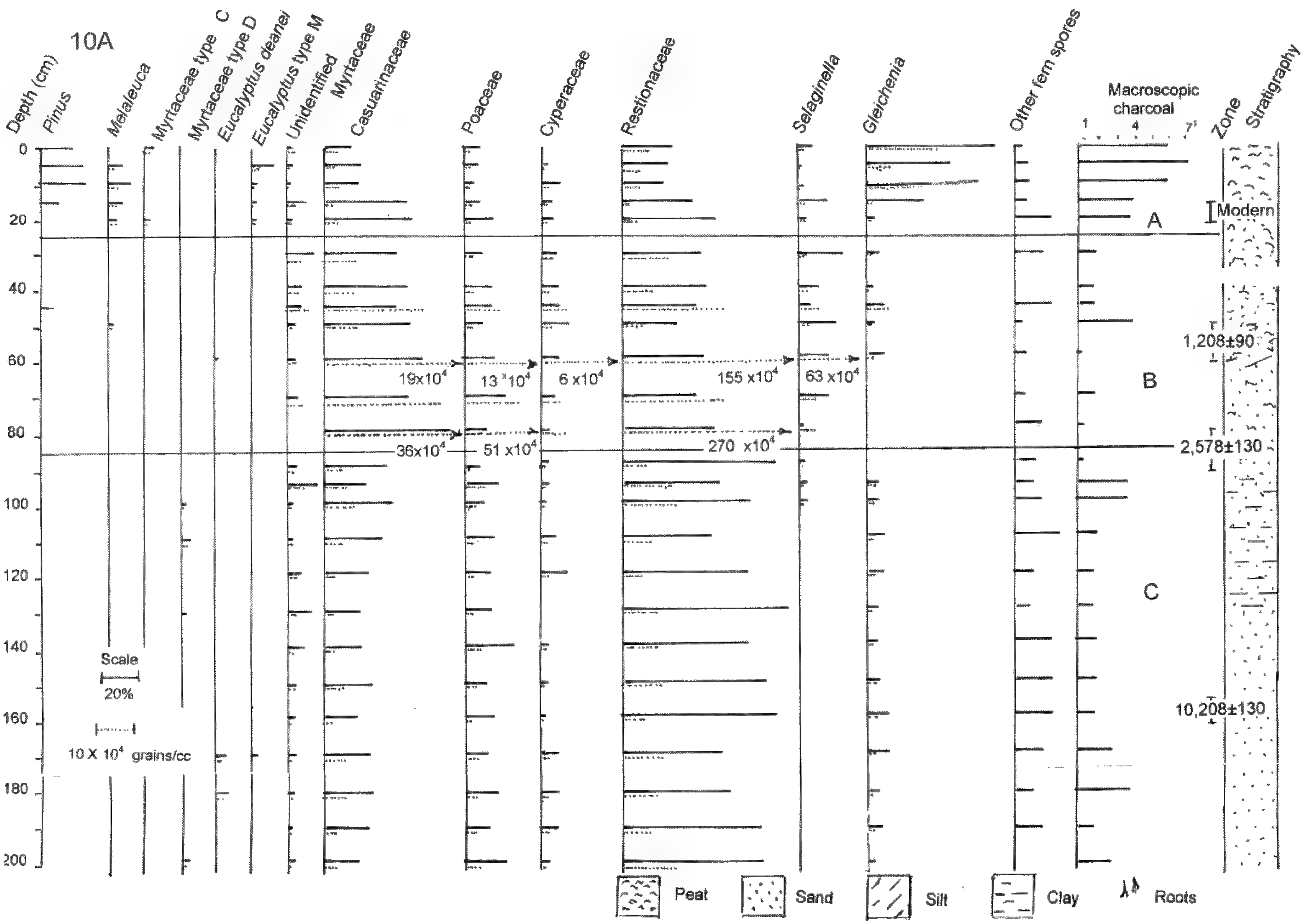
Katoomba Swamp

Katoomba Swamp, at 33° 43' 03" S, 150° 19' 18" E and 950 m altitude, is located in a small, shallow valley which is a tributary of Gordon Creek (Chalson and Martin, this volume). The Banks Wall Sandstone Formation underlies the swamp and the Wentworth Claystone Member outcrops near the base of the swamp, probably impeding drainage.

This swamp is surrounded by urban development. There is evidence of drainage ditches and a sealed road runs across the swamp. Much of it is (or has been) used for yards for light industry and horse paddocks. Housing extends to the edge of the swamp.

Stratigraphy: Two cores were necessary to recover sediments spanning the whole of the Holocene. Core 1 consisted of (1) dark greyish brown or dark brown silty clay/humic clay/clay with roots, 0-20 cm, then (2) dark greyish brown, black, or dark grey silty or sandy clay at 25-80 cm, followed by (3) dark grey sand at 85 cm, (4) dark grey clay at 90 cm, (5) dark greyish brown or dark grey sandy or silty clay at 95-115 cm, (6) dark grey sand at 120 cm and (7) dark grey sandy clay at 125-130 cm.

The stratigraphy of core 2 consisted of (1) dark greyish brown, dark grey or dark brown silty clay at 0-30 cm, then (2) dark grey or dark brown sandy clay,



Figures 10A, 10B. Kings Tableland Swamp pollen spectra. For probable source of the pollen type in the vegetation, see Appendix.

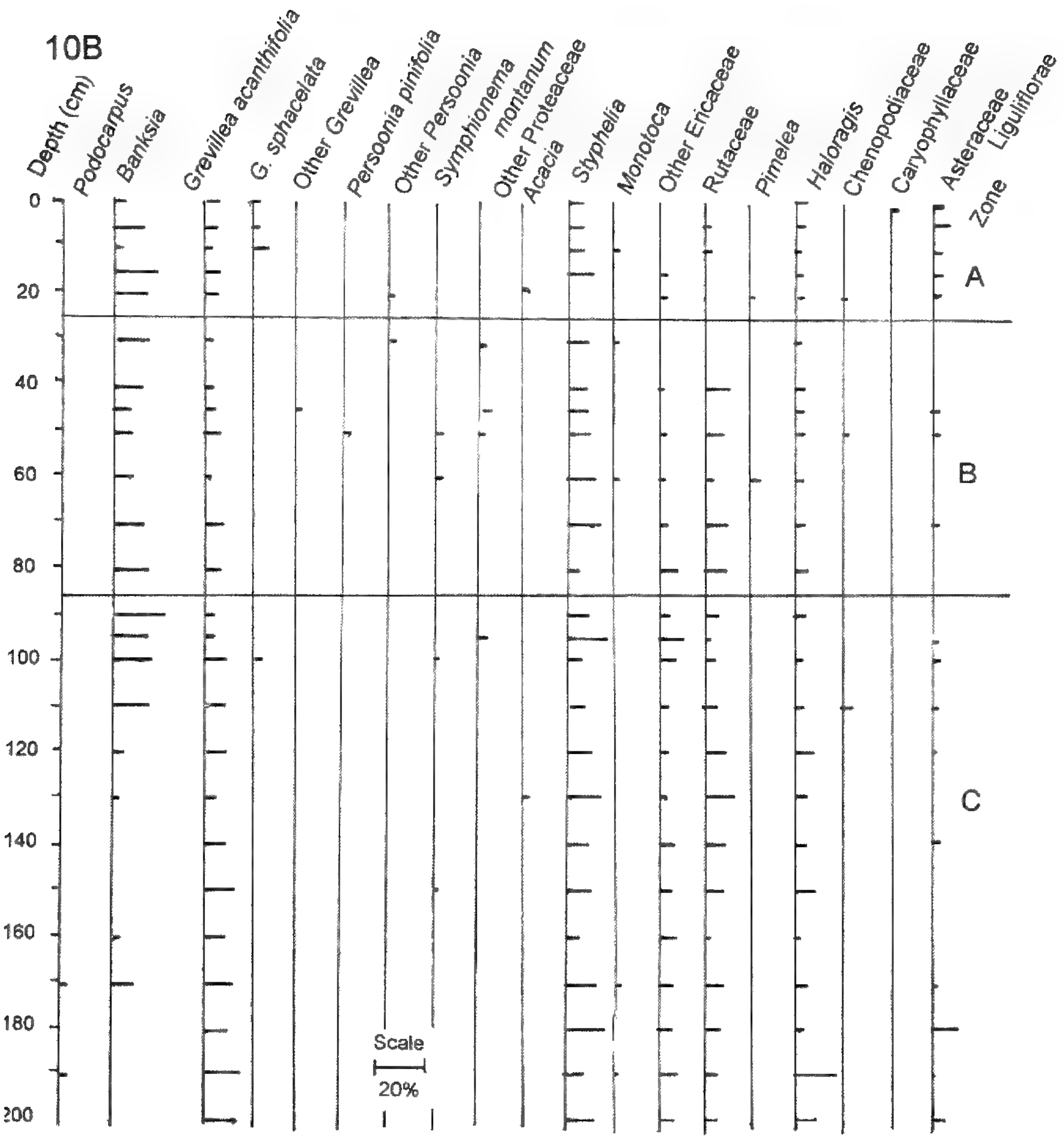


Figure 10 continued

35-40 cm, followed by (3) dark greyish brown sand at 42-48 cm and (4) dark grey clay or sandy clay at 50-55 cm. Radiocarbon dates are presented in Table 7.

The swamp vegetation and surface pollen: The moss *Dawsonia*, and species of Cyperaceae and Juncaceae were dominant on the swamp. *Kunzea* and *Leptospermum* species were also dominant and many sclerophyllous shrubs were found on the edge of the swamp, but the natural vegetation was highly disturbed here (Chalson and Martin, this volume). Poaceae (both native and introduced species) was the dominant pollen type in the surface samples, reflecting the urbanisation and the disturbance at the site. *Pinus* pollen was also present in appreciable amounts. Total Myrtaceae pollen was moderate and Casuarinaceae pollen was low. The swamp taxa, Restionaceae, Cyperaceae, *Selaginella* and *Gleichenia* were present in low proportions (Chalson and Martin, this volume).

The pollen record: Pollen recovery from the cores was good and some very high concentrations were found, especially in the clay (Figs 12A, 12B). The cores were zoned thus:

Core 2, Zone D, 55-0 cm, c. 12-11,000 cal yr BP (see Fig. 13 for estimated ages). The Myrtaceae content was low but *Eucalyptus oreades* and *E. pauciflora* had been identified. Casuarinaceae and Poaceae representation was moderate and Restionaceae was high (Fig. 12A). Asteraceae/Tubuliflorae and Ericaceae were prominent amongst the herbs and shrubs (Fig. 12B). The charcoal content was moderate throughout.

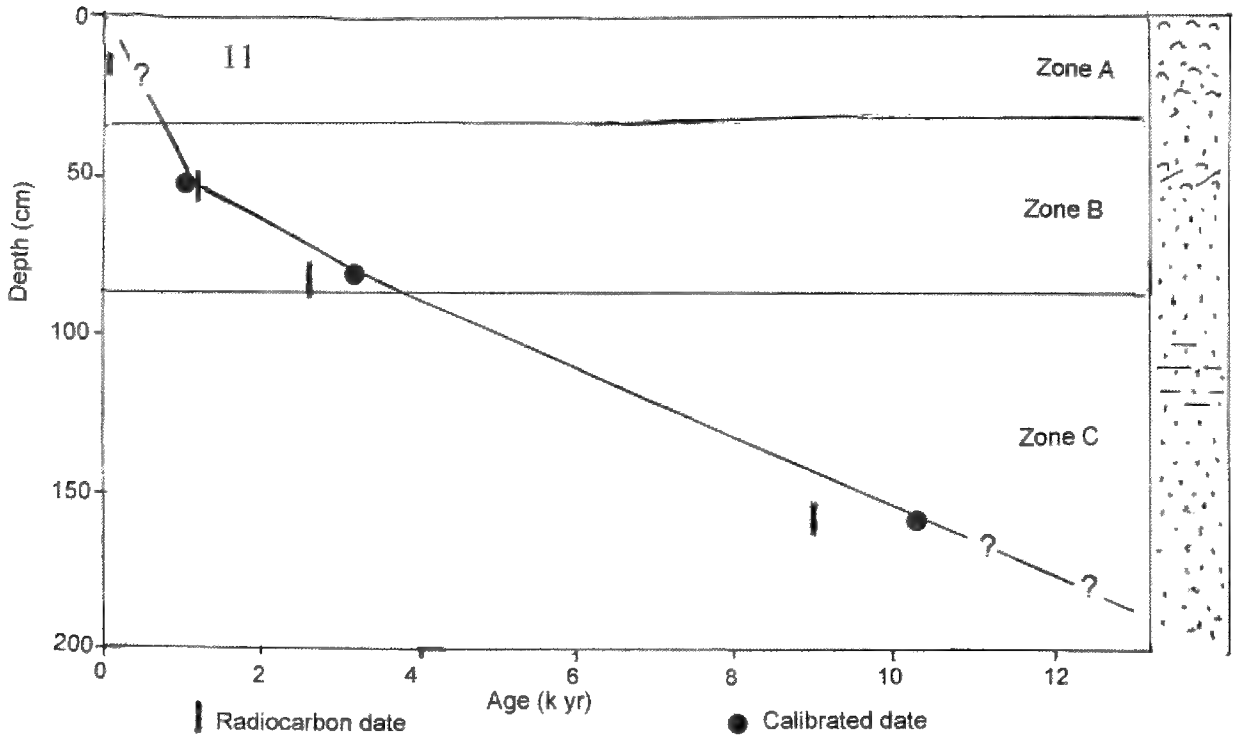


Figure 11. Kings Tableland Swamp summary diagram.

Core 1, zone C, 130-75 cm, c. 6,200-4,000 cal yr BP (for estimated ages, see Fig 13). The Myrtaceae representation was very low, lower than in the zone below, and *Eucalyptus* species were not recorded from most samples. Casuarinaceae representation was low also, Poaceae was moderate and Restionaceae high, all fairly similar to the zone below.

Core 1, zone B, 70-30 cm, c. 3,100-?1,500 cal yr BP. The Myrtaceae content had increased and *Eucalyptus oreades* was present through the zone, and this was the most notable difference when compared with the zone below. Casuarinaceae abundance was moderate and the Poaceae representation had decreased when compared to the zone below. Restionaceae abundance was a little less than in the zone below, decreasing further towards the top of the zone. *Haloragis* and *Grevillea acanthifolia* were prominent amongst the herbs and shrubs.

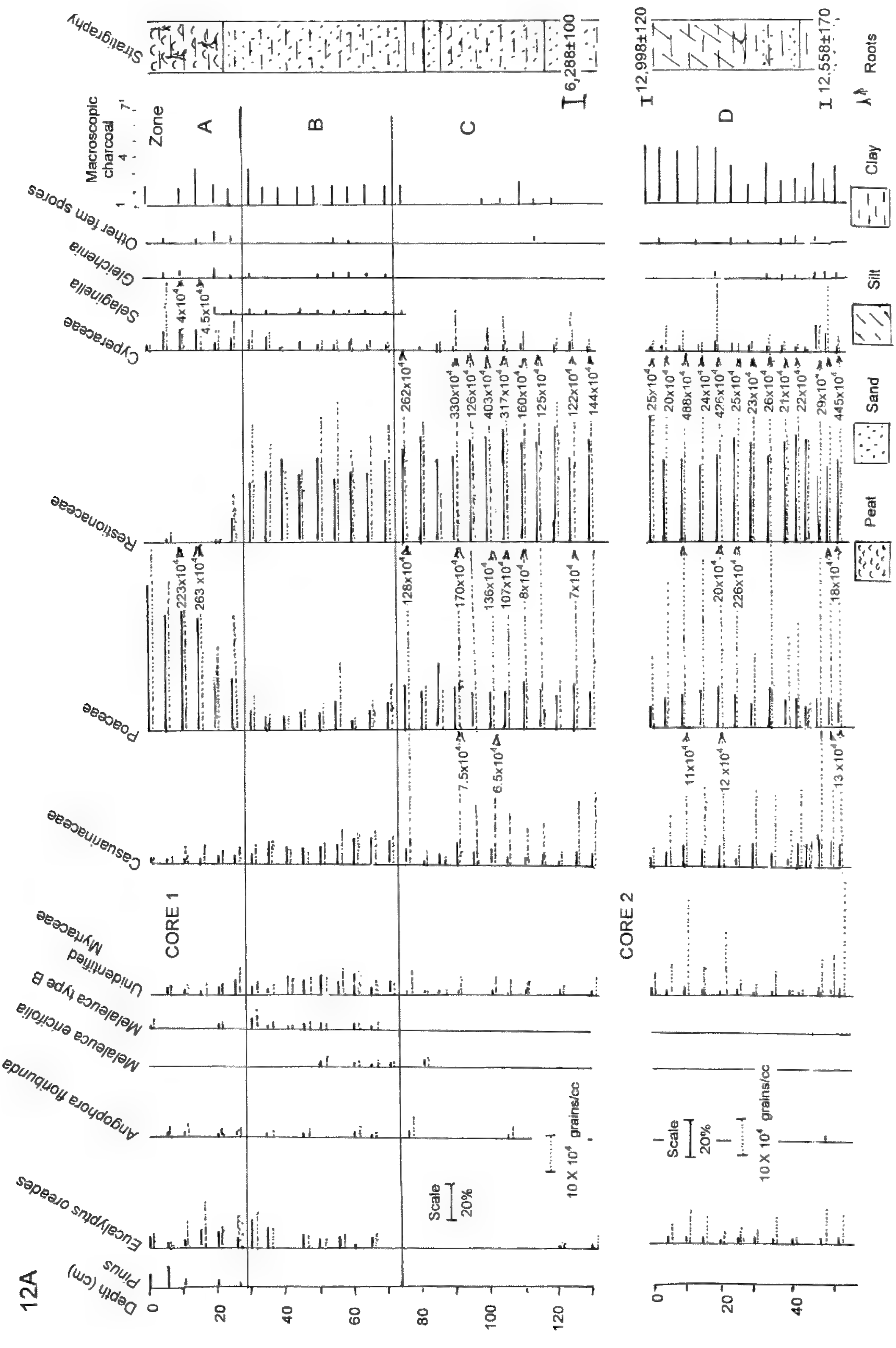
Core 1, zone A, 25-0 cm, c. ?1,500 cal yr BP to present. *Pinus* was consistently present, denoting the European zone. Total Myrtaceae and Casuarinaceae representation were low, decreasing somewhat from the base, but *E. oreades* and *A. floribunda* were found throughout the zone. Poaceae pollen increased markedly from the base of the zone but Restionaceae was very low at the very base, then virtually absent from the rest of the zone. Cyperaceae increased a little and Asteraceae/Liguliflorae was present throughout the zone.

The charcoal content was very low in zone C, then low through the rest of the core, with an occasional moderate value.

History of the vegetation: There was an open or sparse tree cover about 11-12 cal ka. By 6-5 cal ka, the site appears to have been almost treeless. About 4 cal ka, *E. oreades* returned to the site which became wooded once again. Restionaceae was dominant on the swamp and Poaceae was moderately common until 3 kyr BP, after which, both declined. In the European zone, Poaceae increased dramatically, no doubt reflecting urbanisation. At the same time Restionaceae decreased and almost vanished from the swamp. *E. oreades* remained dominant but it

Table 7. Radiocarbon ages for Katoomba Swamp

Depth (cm)	Material dated	Laboratory no.	Radiocarbon years (yr BP)	Calibrated age (cal. yr BP)
Core 1,125-130	Sandy clay	Beta 24545	5,450±80	6,288±100
Core 2, 0-5	Silty Clay	Beta 24547	11,030±130	12,998±120
Core 2, 50-55	Sandy Clay	Beta 24546	10,570±100	12,558±170



Figures 12A, 12B. Katoomba Swamp pollen spectra. For probable source of the pollen type in the vegetation, see Appendix.

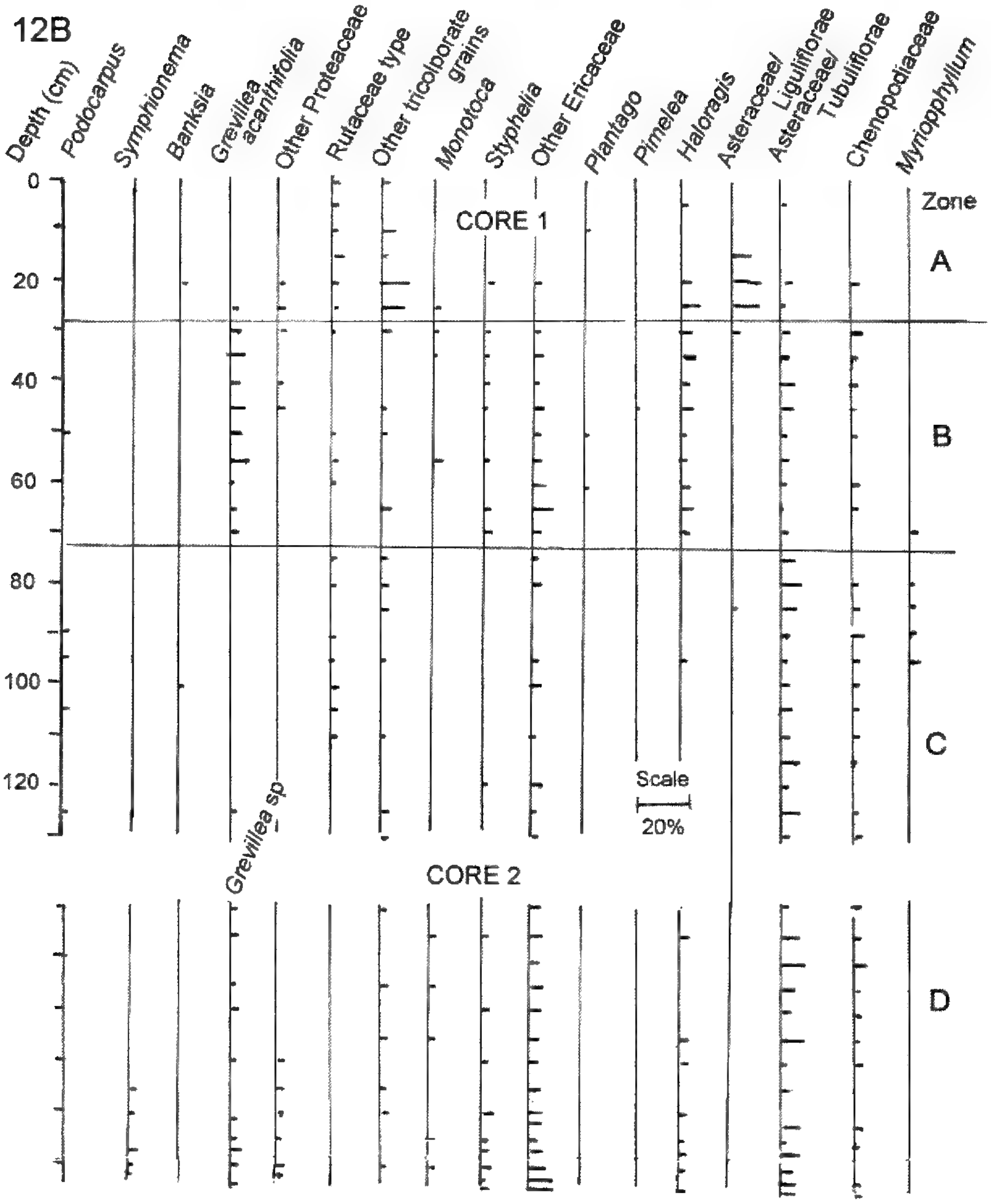


Figure 12 continued

decreased, along with Casuarinaceae in the time of the Europeans. Fire activity was low to moderate through most of the time.

Newnes Swamp

Newnes Swamp, at 33° 22’ 57” S, 150° 13’ 20” E and 1,060 m altitude, is located in a shallow hanging valley with pine plantations in close proximity. Regular burning maintains fire breaks for the young pine plantations. The swamp is underlain by the Burra-Moko Head Sandstone Member of the Banks Wall Sandstone Formation which has thin claystone interbeds, and it is likely that one of these clay layers impedes drainage and hence maintains the swamp.

Swamp stratigraphy: The core sampled 90 cm of sediment. Clay or peat with roots was found down to 20 cm, then sandy clay down to 35 cm, followed by sand to 55 cm, then sandy clay with roots down to 65 cm, then silty clay to 75 cm, and finally sand or sandy clay in layers to 90 cm. Radiocarbon dates are presented in Table 8.

The swamp vegetation and surface pollen: *Banksia* and *Kunzea* were dominant and *Baeckea*, *Leptospermum*, other sclerophyllous shrubs, Cyperaceae and Poaceae were also present on the swamp (Chalson and Martin, this volume). There was appreciable Myrtaceae pollen in the surface samples, but Restionaceae and *Gleichenia* were dominant in the surface pollen spectra. *Pinus* was present but not abundant. (Chalson and Martin, this volume).

The pollen record: Pollen recovery from the core

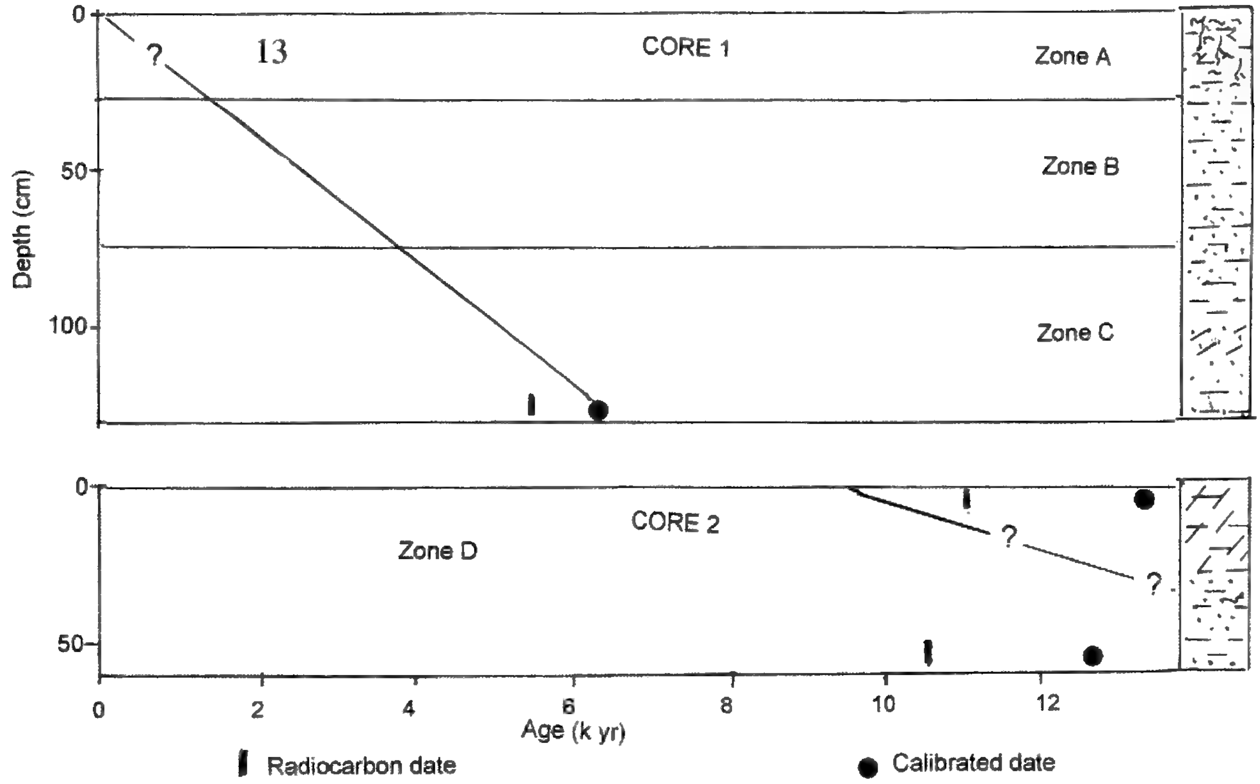


Figure 13. Katoomba Swamp summary diagram.

was good and there was some exceptionally high concentrations, especially in the clay at 60-70 cm. The core was zoned thus (Figs 14A, 14B):

Zone D, 90-55 cm, c. 11,000-7,5 00 cal yr BP (see Fig. 15 for estimated ages). Myrtaceae pollen was low, but *Eucalyptus pauciflora/rubida* had been identified. Casuarinaceae was also low at the base of the zone, increasing upwards (Fig 2A). Asteraceae/Tubuliflorae and Chenopodiaceae were prominent amongst the herbs and shrubs (Fig. 14B). Poaceae and Restionaceae were well represented.

Zone C, 50-40 cm, c. 7,500-1,800 cal yr BP There was very little Myrtaceae pollen, with only one record of a *Eucalyptus* species. Casuarinaceae pollen increased, *Haloragis* was moderate and Poaceae and Restionaceae were reduced when compared with the preceding zone.

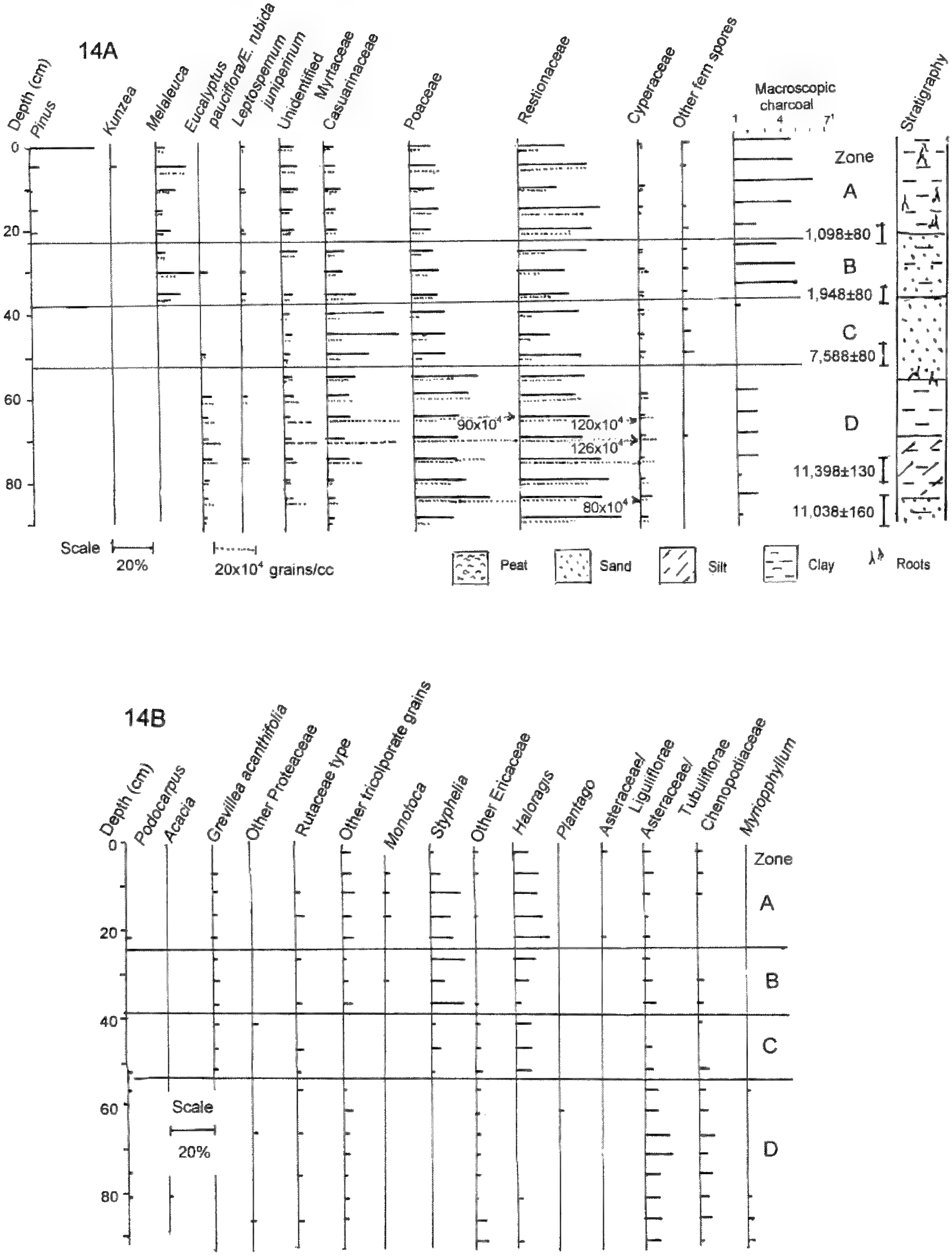
Zone B, 35-25 cm, c. 1,800-?1,000 cal yr BP. *Melaleuca* representation was significant, Casuarinaceae had decreased, the shrubs were well represented, and Poaceae and Restionaceae remained low when compared with the previous zone.

Zone A, 20-0 cm, ?1,000 cal yr BP to present. *Melaleuca* continued to be the most significant of the Myrtaceae, *Styphelia* and *Haloragis* were appreciable, Poaceae remained low and Restionaceae was somewhat greater than the zone below. *Pinus* was present throughout the zone, denoting European activity.

The charcoal content was moderate in zone D, extremely low in zone C, and moderate to high in zones B and A.

Table 8. Radiocarbon ages for Newnes Swamp

Depth (cm)	Material dated	Laboratory no.	Radiocarbon years (yr BP)	Calibrated age (cal. yr BP)
20-25	Sandy clay	SUA 2648	1,090±70	1,098±80
35-40	Sandy clay	SUA 2649	1,930±70	1,948±80
50-55	Sand	SUA 2650	6,650±100	7,588±80
77-83	Silty clay	SUA 2651	9,820±90	11,398±130
87-93	Sand	SUA 2652	9,640±80	11,038±160



Figures 14A, 14B. Newnes Swamp pollen spectra. For probable source of the pollen type in the vegetation, see Appendix.

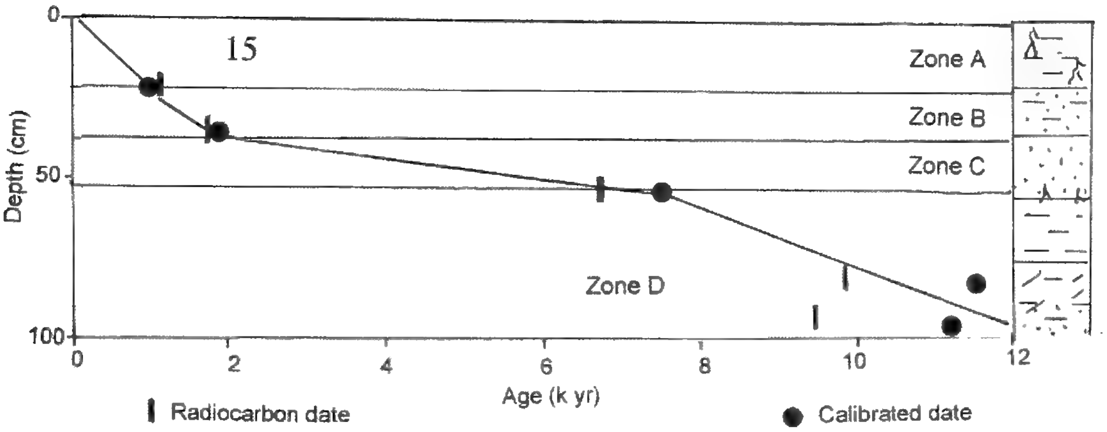


Figure 15. Newnes Swamp summary diagram.

History of the vegetation: The vegetation was open *Eucalyptus* woodland at 11 cal ka, but by about 7.5 cal ka, *Eucalyptus* species had disappeared, Casuarinaceae and the sclerophyllous shrubs increased, suggesting a heathland. After 2 ka, *Melaleuca* became prominent, possibly around or on the swamp. Burning was moderate to low in the early Holocene, very low in the mid Holocene when the vegetation was a shrubland or heath and after 2 ka, it was moderate to high, when *Melaleuca* had colonised the swamp.

DISCUSSION

Stratigraphy

All of the swamps chosen for this study are found associated with small streams in valleys of the rugged terrain of the Blue Mountains. While such sites may not be the first preference for palynology, they allow study in an area where the more favoured sites are rare. These small valley swamps rely on some barrier, often a clay substrate, to impede drainage and maintain the swampy conditions. The root mats of the vegetation stabilise the sediments and slow down the water flow, but if the vegetation is disturbed, then the sediments are prone to erosion. The swamps dry out occasionally but not seasonally. The vegetation can withstand mild or short droughts, but prolonged, severe droughts such as has been experienced in recent years destabilise the communities as some species die and others replace them. The swamps then become very vulnerable to fire, human trampling or even the next major rainfall event. Elimination of the vegetation cover over even a small area of the swamp leaves it vulnerable to subsequent erosion.

If the vegetation is destroyed and there is erosion, channelised water and higher energy flows deposit coarser grained sediment, such as sand. Eventually the vegetation re-establishes and stream flow slows down and finer particles, such as silt and clay are deposited.

It has been assumed that the sediments were deposited at a uniform rate: however, the resolution of dating does not allow this to be tested. Uniform rates of sedimentation are probably not the case at finer scales of resolution.

The peat layer at the top of the swamp is usually only 20 cm or less in thickness. While roots of the present vegetation may penetrate to a considerable depth, a discrete layer with roots at depth in some profiles suggests former peat or vegetation layers that have been buried, and the decay of most of the organic matter as the sediments accumulated. Also, there may be an appreciable humic content of the sediments at depths in the profile, a further indication of decayed vegetation.

Using the above description of the dynamics of the swamps, the sediments are interpreted as follows:

Burralow Swamp: There is only some 1.2 cal ka represented here, with sand at depth, then grading to clay and peat at the top. The rate of accumulation of the sand was rapid, with the clay and peat accumulating much slower (from Fig. 3). It is likely that the whole of this profile post-dates an erosive event.

The two basal two dates are puzzling, given that they do not conform to the uniform sedimentation rate discussed above. They are within the sand layer, which was carbon poor, and it is possible that groundwater carrying humic acids could have contaminated the sediments with younger organic matter, overwhelming the small quantities of older carbon.

Warrimoo Oval Swamp: A basal sand layer dating to about 4.7 cal ka grades into sandy silt, then another sand layer at about 1.2-1.5 cal ka. The sediments then became increasingly peaty towards the top. Deposition of the basal sand layer probably followed an erosive event, and the sand layer at 50-90 cm probably represents another erosive event. This latter layer may correlate with the basal sand layer in Burralow Creek (from Figs 3 and 5), but this hypothesis requires additional dating control to test it.

Notts Swamp: About 7 cal ka are recorded here (Fig. 7). The basal sandy silt layer is overlain by clay, with peat with roots above it. The profile appears to reflect a low energy depositional environment throughout. The stratigraphy suggests that the lower and upper layers may have accumulated at a somewhat faster rate than the clay in the middle.

Ingar Swamp: This profile also represents about 7 cal ka (Fig. 9). Sandy clay formed the basal sediments, with clay with roots above it, then peat with roots forming the top most layer.

Kings Tableland. Over 10 cal ka, the majority of the Holocene is represented here (Fig. 11). There is a basal sand layer, then a complex stratigraphy of clay, sand, silty peat, sand and sandy peat above it. This suggests that conditions of deposition would have fluctuated, and in which case is unlikely that the sequence is continuous.

Katoomba Swamp. Over 6 cal ka are represented in core 1 and 10-12 cal ka in core 2 (Fig. 13). There are no large sand layers similar to those seen in sediments at some of the other sites, but a complex stratigraphy of finer sediments, often with a sandy component.

Newnes Swamp. About 12 cal ka is recorded here (Fig. 15). The sediments are sand then sandy or silty clay in a complex stratigraphy at the base of the profile. Above this, there is a prominent sand layer, then sandy clay and peat with roots at the top. Superficially, it appears that the sand layer in the middle of the profile accumulated very slowly (Fig. 15), but another interpretation is possible. The date at the top of this sand layer is about 1.3 ka, which approximates the date of the top of the sand layers seen in Warrimoo Oval Swamp and Burralow Creek Swamp. If the sand layer does represent the aftermath of an erosive event, then a section of the sediment profile is likely to have been lost. The roots in the sandy clay at the base of the sand layer may indicate the base of a peat or vegetation layer that was buried by the accumulating sand.

Each swamp thus has its own history of sedimentation. Sandy layers in three of the swamps suggest erosion after disruption of the vegetation, sand deposition, then stabilisation sometime about 1.2-1.6 ka, with subsequent re-establishment of the vegetation and deposition of fine-grained sediments.

If fire was the cause of this erosion, then we could expect evidence of it in the charcoal record, but there is no evidence of increased charcoal at this time. Absence of charcoal cannot be taken as evidence of no fire, as erosion may well have removed the charcoal, along with some of the sediments. Fire is not the only likely cause: as discussed, prolonged drought could also destabilise these systems. Minor tectonics along fault lines in the Blue Mountains (Bembrick et al, 1980) would also accelerate erosion.

The three swamps which have this sand body are Newnes, Burralow Creek and Warrimoo Oval. Newnes and Burralow Creek are the two most northerly swamps and Burralow Creek and Warrimoo Oval are the two most easterly swamps. Whatever the cause of this disturbance, it seems to have come from or been concentrated in the north east (see Fig. 1). That Burralow Creek Swamp has only 1 ka of sediment suggests that it may have suffered the greatest disturbance and erosion.

History of the vegetation

The swamp vegetation. The survey of the vegetation (Chalson and Martin, this volume), shows that species of Restionaceae, Cyperaceae, *Gleichenia*, *Selaginella*, *Baeckea*, *Kunzea* and *Leptospermum* dominate the vegetation cover of these swamps. Many of the common sclerophyllous shrubs have been recorded on the swamps, though not dominant, as well as in the dryland vegetation (Chalson and Martin, this volume). Poaceae has both dryland and swamp species (Sainty and Jacobs, 1981).

In the pollen diagrams, *Gleichenia* and *Selaginella* are found predominantly where the sediments are sandy and Restionaceae is dominant on the clayey sediments. There is very little Cyperaceae here, unlike other sites, e.g Lake Baraba (Black et al., 2007), Dry Lake, (Rose and Martin, 2007), Mountain Lagoon (Robbie and Martin, 2007) and Penrith Lakes (Chalson and Martin, 2008) which have more Cyperaceae than Restionaceae. The swamps of this study, however, are more ephemeral and unlike the others with more Cyperaceae, which are lakes or lagoons where the water would be more permanent. Indeed, there are many species of Cyperaceae that are aquatic (Sainty and Jacobs, 1981) whereas species of

Restionaceae are found more in damp and swampy places. Thus Cyperaceae flourishes in the more permanently wet swamps and Restionaceae is more abundant in these swamps subjected to irregular drying. Species of both families may be found in the dryland vegetation but the pollen record is heavily dominated by the wetland species.

Baeckea, Kuzea and *Leptospermum* species are present in the pollen diagrams of the swamps, but mainly towards the top and especially in the European zone. There is very little pollen of these taxa at depths in the profiles. Some *Melaleuca* pollen is present and it shows much the same trends. Although the trend to more of these shrubs started before European settlement, it appears that these woody shrubs, which are often dominant on the swamps today, have probably been further encouraged by European activity, probably by the altered fire regime (Kohen, 1995).

The swamp vegetation thus reflects the sediment substrate and hydrological conditions, with some changes due to European activity.

The dryland vegetation. The sites are examined in a time sequence to determine if there has been any synchronous changes in the vegetation across the Blue Mountains.

Three sites record the early Holocene of 10 ka to 6 ka: Kings Tableland, Katoomba and Newnes Swamps. About 10 cal ka, *Eucalyptus* species were present at all three sites, but there was very little at Kings Tableland. Casuarinaceae, the other group which could be either trees or shrubs was present also. Thus all three sites appear to have been wooded in the early Holocene, with Kings Tableland probably more open than the other sites. By 6-4 cal ka, the mid Holocene, there were virtually no *Eucalyptus* in any of the sites. The vegetation had become more open and probably more of a sclerophyllous shrubland or heath. *Eucalyptus* returned to the Katoomba site about 3 cal ka, but very little is recorded in Newnes and Kings Tableland up to the present. The Katoomba swamp is located in a narrower and steeper valley than the other two sites, and this shelter may have produced better moisture retention and hence tree regeneration. *Melaleuca* became established at Newnes about 1.3 cal ka.

Two sites date from about 6 cal ka, the mid-Holocene: Notts and Ingar Swamps. Species of *Eucalyptus* and *Angophora* were present at both sites, hence they were probably wooded at the time that Kings Tableland, Katoomba and Newnes were dominated by shrubs. Warrimoo Oval dates from about 4 cal ka, and the relatively low frequencies of *Eucalyptus* and *Angophora* indicate it was an open woodland at that time.

In the period 4-2 cal ka, there was little change from the previous period at Notts and Ingar Swamps. At Kings Tableland, Casuarinaceae increased but there was still no *Eucalyptus*. At Katoomba, *Eucalyptus* and *Angophora* species reappeared, as this site probably gained an overstorey of trees again. At Newnes, the 4-2 cal ka period was similar to that before, with very little *Eucalyptus*. Burralow Swamp dated from 1 cal ka was initially very open, with the tree cover increasing about 0.8 cal ka. Except for an increase in *Melaleuca* or *Leptospermum* species in some of the swamps, there was relatively few changes after 2 cal ka until the European period,

In the European zone, there was minimal or no decline in the *Eucalyptus* and *Angophora* content. Casuarinaceae content declined noticeably at all the sites. At Burralow, Warrimoo Oval and Kings Tableland, the woody shrubs *Callistemon*, *Baeckia, Leptospemum* and *Melaleuca* increased. The Poaceae content remains unchanged in all swamps except for Katoomba, where there is a dramatic increase.

There is thus relatively little change in the palynology after European settlement in all of the sites, except at Katoomba. This perhaps reflects the relatively minor European changes to the sites, with the exception of Katoomba where the swamp itself has a history of use for various urban activities. Agricultural development has been minimal, reflecting the poor soils. The general lack of decline in tree species is unexpected, but European development has largely been confined to the ridgetops and extensive natural vegetation is a feature of the Blue Mountains. The wood of Casuarinaceae was prized by Europeans as the firewood of choice for bakeries and the timber had many uses (Entwisle 2005), hence it may have been sought out more than the *Eucalyptus* species.

Each site has its own distinctive history, as are the dominant *Eucalyptus* species at each site (Chalson and Martin, this volume). There is limited synchronicity of change between the swamps. The three swamps at the highest altitude are the oldest, dating to the beginning of the Holocene. They were wooded in the early Holocene, but became very open or almost treeless by the mid-Holocene. The sites at the lower altitudes, however, were wooded during the mid-Holocene. By the late Holocene, all of the sites had become wooded, although the tree layer may have been very open in some of them. Clearly, the interplay of many environmental factors, not the least of which is altitude, have influenced the vegetation at each site.

Other sites in the Blue Mountains also present unique histories when compared with those of this study. At Mountain Lagoon (Robbie and Martin, 2007), the proportion of Casuarinaceae pollen is substantial at the beginning of the Holocene, then declines throughout the Holocene. *Allocasuarina torulosa* is more common at Mountain Lagoon than at any of the sites of this study. Pollen of swamp plants increase through the Holocene at Mountain Lagoon as the site developed from a lake in the early Holocene to a peat swamp in the mid-late Holocene. The Myrtaceae species identified are mainly different to the species of this study and the proportion of pollen remains much the same throughout the Holocene and only declines after European settlement. The species identified at Mountain Lagoon are often prized for timber (Robbie and Martin, 2007). The physical environment of Mountain Lagoon is totally different to that of the Blue Mountain sites: it is a small basin on Wainamatta Shale, in a particularly sheltered location.

Kings Waterhole, part of the Mellong Swamps in the Wollemi National Park, at 280 m altitude, has a 6 ka history (Black and Mooney, 2007). Myrtaceae (excluding *Melaleuca* spp.) and Casuarinaceae are prominent until about 4-3 ka, when Casuarinaceae begins to deline. At the same time, Restionaceae increases. After 3 ka, there is minimal Casuarinaceae and Restionaceae declines, but *Melaleuca* and Poaceae increase. After 1 ka, Myrtaceae decreases somwhat and Poaceae is prominent (Black and Mooney, 2007). This decline of Casuarinaceae after 3 ka is not seen in any of the sites of this study.

At Gooches Crater Swamp on the Newnes Plateau, between 900 and 1,200 m altitude (Black and Mooney, 2006), there is a 14 ka history of the vegetation. There is a moderate level of variability in the pollen assemblages, and the swamp vegetation varied from a wet heath with semi-permanent to permanent water to a fern swamp. The Myrtaceae and Casuarinaceae content is appreciable and continuously variable. The Asteraceae content is considerable (Black and Mooney, 2006), unlike the sites of this study, although the Newnes site has the greatest Asteraceae content of all the sites of this study.

Penrith Lakes on the Cumberland Plain just east of the Lapstone Monocline has 6 ka of Holocene history. The tree cover was very open in the mid Holocene, becoming somewhat more wooded in the late Holocene (Chalson and Martin, 2008), mirroring the findings of this study.

The rugged terrain of the Blue Mountains would have provided some isolation to each site so that each has its own sedimentary and vegetation history. Any climatic change or other regional event should imprint in these deposits, especially in the more environmentally sensitive sites.

Climatic change

The decline of the trees from the early Holocene to the mid Holocene in the sites at the higher altitudes, *viz*. Newnes, Katoomba and Kings Tableland, suggests that the climate had become drier. A detailed analysis of the climatic requirements of the *Eucalyptus* species also suggests a wetter early Holocene (Chalson, 1991).

Climatic trends in the mid Holocene are uncertain, for while the sites at higher altitudes were not wooded, sites at lower altitudes, i.e. Notts and Ingar Swamps, were wooded at this time. Trees returned to Katoomba about 3k yr, suggesting that the climate had become wetter. As discussed previously, the Katoomba catchment is narrower and steeper-sided, hence the most sheltered of the three higher altitude sites. Newnes and Kings Tableland, however, remained open with few trees, suggesting that if there was an improvement in the rainfall, it had not returned to the early Holocene levels. These uncertain trends continued into the late Holocene. About 2 kyr, there was an increase in the wooded vegetation, with more *Eucalyptus* at Warrimoo, more Casuainaceae at Kings Tableland and more *Melaleuca* at Newnes. The other sites, however, remained much the same. There probably was an increase in rainfall, but it was slight. The detailed analysis by Chalson (1991) came to similar conclusions: climatic changes in the mid and late Holocene are equivocal.

The climatic changes deduced from the this study are in general agreement with other sites in the Blue Mountains. The early Holocene is regarded as a climatic optimum when it was warmer and wetter (Allen and Lindesay, 1998). Evidence for the mid and late Holocene is variable, some indicating wetter, some drier conditions. Evidence suggests that the El Niño-Southern Oscillation (ENSO) phenomenon came into operation about 5 ka, with increasing seasonality. Thus from the mid Holocene, the climate became more like that of today, with more variability (Allen and Lindesay, 1998; Moy et al., 2002; Donders et al., 2007).

Fire history

Charcoal has been found in all of the sites and throughout all of the profiles. In the early Holocene, the charcoal content was low to moderate in Kings Tableland, Katoomba and Newnes. By mid Holocene, the quantity of the charcoal had declined in Katoomba and Newnes: there had been a change in the vegetation from more wooded in the early Holocene to less wooded in the mid Holocene, hence there may have been less fuel to burn.

In the mid Holocene at Notts, Ingar and Warrimoo Swamps, there is very little charcoal. All of the sites would have been wooded to some degree but not as much as in the late Holocene. The charcoal content increases at each site as the tree cover increased. In the late Holocene, charcoal content is variable, but mainly greater than in the mid Holocene. In the European zone, charcoal content is consistently high and the highest for the profile, with the exception of Katoomba. It may be that because of urban use of the swamp at Katoomba, fire was excluded. Within these trends, there may be the occasional single high value, but they do not form any pattern.

The interpretation of a charcoal record is problematical because so many factors are involved, e.g. fire frequency, intensity and transport of charcoal. The results of this study suggest that the greater the biomass, the more fuel there is to burn hence the more charcoal in the sediments.

The higher charcoal content of the European period suggests that fire regimes were changed with settlement. If Aboriginal people regularly burnt off the undergrowth and suppressed the shrubs, then the fuel load would be kept down. With European settlement and the cessation of traditional fire practices, it is possible that the woody shrubs became more common (Kohen, 1995; Ward et al., 2001). Under these conditions, the fuel load would increase. Today, species of *Baeckia, Kunzea* and *Leptospemum* are dominant on all of the swamps (Chalson and Martin, this volume). There is a trend for *Leptospermum* and *Kunzea* species to increase slightly in the late Holocene, with a further increase in the European Zone. These woody species would have had the capacity to produce more charcoal when burnt and be incorporated in the sediments, especially when growing on the swamp, when compared with the smaller sedges and reeds.

At Mountain Lagoon (Robbie and Martin, 2007), fire activity was low through the Holocene, until about 3-2 ka, when it increased. This pattern is similar to those of this study.

At Gooches Crater the charcoal content and hence fire activity fluctuates between 14 ka and 9 ka, then follows a period of low fire activity until about 6 ka, then a period of dramatic increase in fire activity in the late Holocene (Black and Mooney, 2006). Fire activity reaches unprecedented levels in the post-European period (Black and Mooney, 2006). The increase in fire activity in the mid Holocene is attributed to climate, in particular to the greater seasonality associated with the onset of the El Niño-Southern Oscillation (ENSO) phenomenon (Black et al., 2007). This pattern of fire activity is similar to that seen in the sites of this study.

At Kings Waterhole Swamp (Black and Mooney, 2007), the fire activity was low about 6 ka, then increased between 5-3 ka, after which it decreased to low levels to the present. This pattern of fire activity is quite unlike that of this study. It is thought that the decline in fire activity after 3 ka represented an alteration to Aboriginal management strategies associated with increasing population and/or the increased risk of conflagration in an ENSO-dominated climate (Black and Mooney, 2007).

Black et al. (2007) examined the charcoal record together with the archaeological record in an attempt to assess the likely effect of Aboriginal burning on the ecosystem. At Gooches Crater Swamp, the charcoal content appeared to be most influenced by climate, with an abrupt increase in the mid Holocene, perhaps associated with the onset of the modern ENSO-dominated conditions. Kings Waterhole also showed the abrupt increase in the mid Holocene, but there was a marked decrease in charcoal from about 3 ka. Lake Baraba also showed similar low levels of charcoal in the late Holocene. The archaeological records of all three regions showed increased activity/habitation in the late Holocene. It is thus possible that Aborigines strongly influenced fire activity in some places in the Sydney Basin during the late Holocene to prevent the risk of large intense fires as the ENSO-dominated climate became more prevalent (Black et al., 2007)

CONCLUSIONS

Seven swamps were studied and each had its own distinctive history. Where the *Eucalyptus* species were identified, the dominant species were different at each site, as they are today.

Similarities in the histories could be seen between some of the sites and are as follows:

In the early Holocene, the vegetation was more wooded, i.e. woodland or forest, which suggests a warmer wetter climate. Only the three sites at the highest altitudes had sediments of early Holocene age.

In the mid Holocene, the vegetation was less wooded in the three highest sites when the vegetation was probably shrublands and heaths, and this suggests a drier climate. Other sites at lower elevations were wooded in the mid Holocene.

The *Eucalyptus* species return to the less wooded sites towards the late Holocene. There is also a tendency for an increase in *Baeckea, Kunzea,* *Leptospermum* and *Melaleuca*, the woody shrubs. These woody shrubs are dominant on the swamps today.

There is some decline in Casuarinaceae in the European period but the *Eucalyptus* species are maintained at about the same level as in the late Holocene. The woody swamp shrubs increase in the late Holocene and European period.

The charcoal levels suggest that there was moderate fire activity in the early Holocene when the vegetation was more wooded, decreased fire in the mid Holocene when the vegetation was more open, with increased fire in the late Holocene and a further increase in the European period.

It is thought that the altered fire regime under European settlement encouraged the increase in woody shrubs on the swamps (and elsewhere) which in turn produced more charcoal.

These swamps on sandstone are highly erodable and a sand body at about 1.2-1.6 ka in the three most northerly and easterly swamps suggests they may have suffered an erosive event about that time. The destabilising event(s) which triggered this erosion is uncertain.

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APPENDIX A

Pollen type name on the pollen diagrams and the probable source in the vegetation.

Name of pollen type. Major pollen groups (A diagram)	Probable source in the vegetation and ecological inference. From PlantNet (2007)
Podocarpus	Probably *Podocarpus spinulosus*: sclerophyllous shrub/small tree
Pinus	*Pinus* sp(p). Introduced: Pollen input from urban/forestry areas.
Angophora/Corymbia	Species within the two genera: sclerophyll woodland
Eucalyptus/Melaleuca	Species within the two genera sclerophyll woodland/forest
Melaleuca styphelioides	*Melaleuca styphelioides*: moist stream bank habitat
Leptospermum/Baeckea	Species within the two genera: ?mainly swamp communities
Tristaniopsis	*Tristaniopsis* spp : moist habitats in sclerophyll communities
Unidetified Myrtaceae	All pollen types not identifiable further
Casuarinaceae	*Casuarina, Allocasuarina* sp(p): *A. distyla* and *A. nana* in this study
Poaceae	Native and exotic species in the family: open situations, dryland and swamp species
Restionaceae	All species in the family: swamp and dry land species
Cyperaceae	All species in the family: swamp and dry land species
Selaginella	All species in the genus: damp sites, edge of swamp
Gleichenia	*Gleichenia* sp(p): damp sites, edge of swamp
Other fern spores	Other ferns: many possible species
Names of shrubs and herbs (B diagrams)	
Grevillea acanthifolia	Shrub: swampy areas, sand or peat
G. sphacelata	Shrub: heath, dry sclerophyll forest
Grevillea	*Grevillea* sp(p): sclerophyllous understorey
Hakea	*Hakea* sp(p): sclerophyllous understorey
Persoonia pinifolia	Shrub: heath, dry sclerophyll forest
Persoonia	*Persoonia* sp(p): sclerophyllous understorey
Symphionema montanum	Shrub: heath or dry sclerophyll forest, wet or dry situations
Banksia	*Banksia* sp(p): sclerophyllous understorey
Other Proteaceae	Other taxa in the family: sclerophyllous understorey
Acacia	All species in the genus
Styphelia	*Styphelia* sp(p): sclerophyllous understorey
Monotoca	*Monotoca* sp(p): sclerophyllous understorey
Other Ericaceae	Other taxa in the family: sclerophyllous understorey
Rutaceae type	All taxa in the family sclerophyllous understorey
Pimelea	*Pimelea* sp(p): sclerophyllous understorey
Plantago	*Plantago* sp(p): native and introduced herbs
Haloragis	*Haloragis/Gonocarpus* sp(p): Damp sites, sclerophyllous understorey
Other tricolporate grains	Probably shrubs and herbs
Podocarpus	Probably *Podocarpus spinulosus*: sclerophyllous shrub/small tree
Micrantheum	Shrub: heath and dry sclerophyll forest, sandy infertile soils
Myriophyllum	Mainly aquatic herbs, also on damp ground around water bodies
Asteraceae/Liguliflorae	Fenestrate-grained taxa in the subfamily Liguliflorae: herbs
Asteraceae/Tubuliflorae	Echinate-grained taxa in the subfam. Tubuliflorae: shrubs and herbs
Chenopodiaceae	Ruderals, salt tolerant

APPENDIX B

Myrtaceae Pollen type name on the pollen diagrams and the probable source in the vegetation.

Name on the pollen diagrams	Probable source in the vegetation and ecological inference. From PlantNet (2007)
Angophora costata	Deep sandy soils on sandstone
Angophora floribunda	Usually on deep alluvial soils
A. costata x floribunda	-
Angophora	-
Baeckea/Leptospermum	Some species in swamp/moist habitats, also dryland species
Callistemon	Dry sclerophyll communities, some swamp species
Eucalyptus deanei	Tall wet forest, sheltered valleys, deep sandy alluvial soils
E. eugenioides	Dry sclerophyll or grassy forest, on deep soils
E. fibrosa	Wet or dry sclerophyll forest, on shallower, somewhat infertile soils
E. oblonga	Dry sclerophyll woodland, on extremely infertile, sandy soils
E. oreades	Wet or dry scleropnhyll forest, on poor skeletal or sandy soils
E. pauciflora/E. rubida	Grassy or dry sclerophyll woodland, on cold flats.
E. piperita	Dry sclerophyll forest/woodland, moderately fertile, often alluvial sandy soils
E. racemosa	Dry sclerophyll woodland, on shallow infertile soils
Eucalyptus type B	)
Eucalyptus type C	)
Eucalyptus type D	) For definition of Eucalyptus pollen types, see Chalson (1991)
Eucalyptus type K	)
Eucalyptus type M	)
Eucalyptus/Melaleuca	Species within the two genera: sclerophyll woodland/forest
Kunzea	Understorey sclerophyll forest, moist depressions
Leptospermum juniperinum	Swamp, heath and sedgeland, on sandy peat soils
L. polygalifolium	Dryland habitats and moist depressions
Melaleuca ericifolia	Heath and dry sclerophyll forest, streambanks and coastal swamps
M. styphelioides	Moist situations, often stream bank habitats
Melaleuca type B	)
Melaleuca type C	) For definition of pollen type, see Chalson (1991)
Melaleuca	For definition of *Melaleuca* pollen types, see Chalson (1991)
Myrtaceae type C	)
Myrtaceae type D	) For definition of pollen types, see Chalson (1991)
Unidentified Myrtaceae	All myrtaceous pollen types not identifiable further

Modern Pollen Deposition Under Vegetation of the Blue Mountains, New South Wales

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Pollen was extracted from surface samples of swamp sediments and soils under various types of vegetation in the catchments of these swamps. The pollen assemblages in these surface samples were compared with the floristic composition of the vegetation to provide a means of interpreting the assemblages of fossil pollen retrieved from the swamp sediments.

The surface pollen assemblages reflected the local vegetation, indicating more/less tree cover, swamp and/ or adjacent dryland environment and local flora diversity. All the evidence pointed to very local deposition and little long distance dispersal of pollen. A number of different units may be defined within the one major vegetation type, dry sclerophyll forest/woodland in this case, but the floristics of the units are too similar to allow discrimination of them from their modern pollen assemblages.

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KEYWORDS: Blue Mountains, local pollen deposition, long distance pollen dispersal, modern pollen deposition, pollen spectra.

INTRODUCTION

Pollen is deposited in sediments by the contemporaneous vegetation, but a number of factors affect the representation of each taxon in the sediments so that it is not possible to relate a fossil pollen assemblage in a deposit directly to the vegetation that produced it. Pollen productivity, dispersal and preservation are the main factors that influence representation of a taxon, and each of these factors are in turn influenced by the local environmental conditions. Pollen deposited from under known plant communities, however, may be used to characterize that community and hence assist in the interpretation of pollen spectra recovered from swamp sediments. The nature of pollen deposition of individual taxa may also be deduced from the surface pollen spectra.

Sites for a study of the history of the vegetation were chosen from swamps in an altitudinal sequence in the Blue Mountains (Fig. 1). These sites are situated on a relatively uniform substrate, sandstone, within dry sclerophyll woodland/open forest. Observations of modern pollen deposition are reported in this paper, and the Holocene history of the vegetation from the swamps is reported in Chalson and Martin (this volume).

THE STUDY SITES

The Blue Mountains are a deeply dissected plateau rising from the Cumberland Plain in the east. The plateau surface is undulating and small creeks form upland valleys. Where the underlying rock type is Hawkesbury Sandstone, the upland valleys become incised and develop into V-shaped gorges. In the west where rock type is Banks Wall sandstone, the valley sides and floors slope gently and the streams flow through a series of swamps (Chalson, 1991).

The swamps chosen for study are as follows (see Fig. 1) and the species found at each site are listed in Appendix 1:

Burralow Creek Swamp, at 33° 32'S, 150° 38'E and 310-330 m altitude, is a narrow swamp that follows the creek for some 3.5 km. The upper end of the swamp is 2 km southeast of Kurrajong Heights. The core site is 1 km downstream from the northern end. There are few cleared areas near the swamp, the nearest being over 2 km away.

The vegetation around Burralow Creek is open forest, woodland and swamps (Keith and Benson,

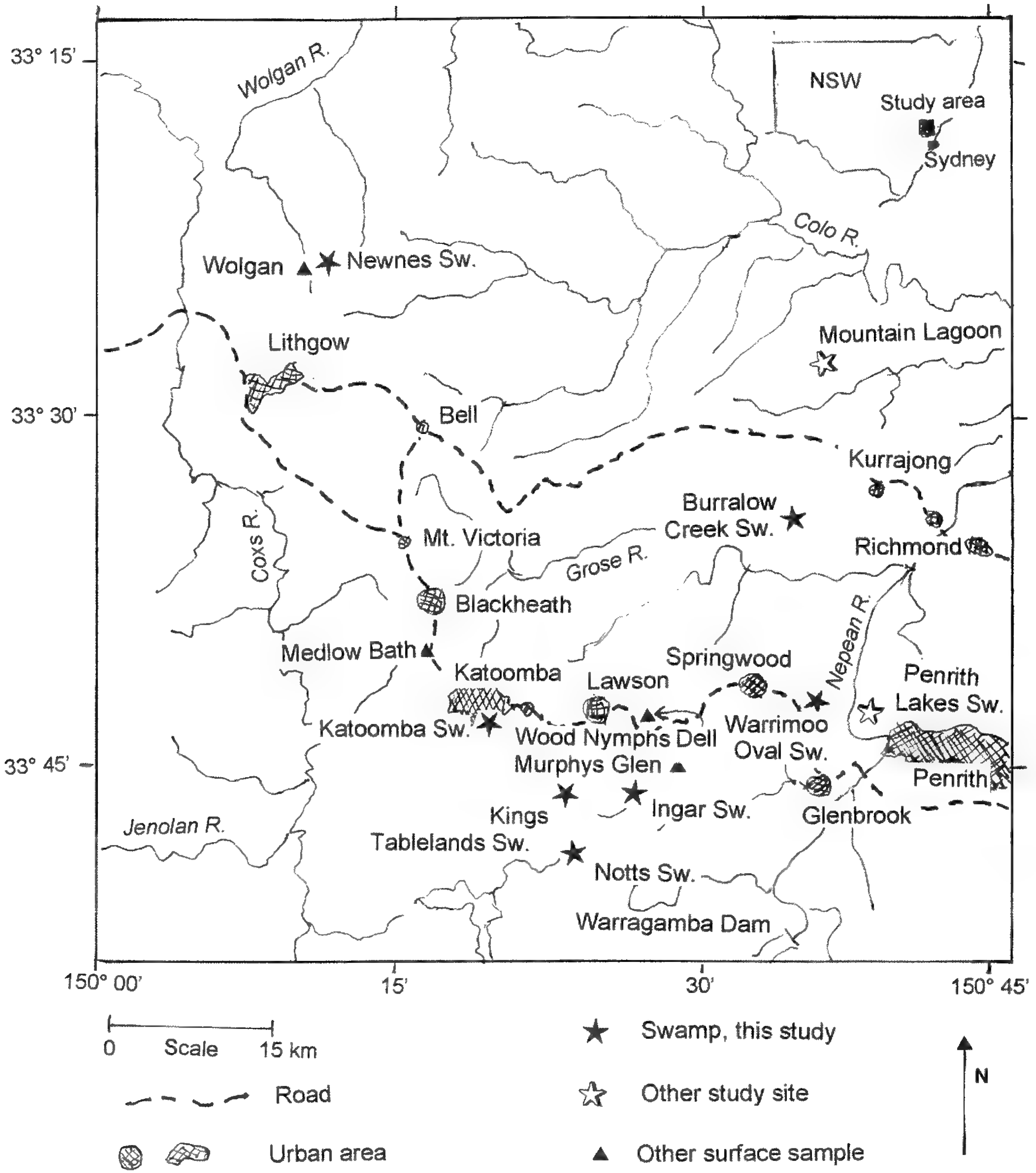

Figure 1. Locality map

1988). *Angophora bakeri*, *A. costata*, *Corymbia eximia*, *Eucalyptus eugenioides*, *E. multicaulis*, *E. pauciflora* and *E. radiata* are locally dominant with a few kilometers of the swamp. The surface of the swamp supports an open heathland of *Leptospermum polygalifolium*, *L. trinervium* and *Eleocharis sphacelata*. Nomenclature follows Harden (1992; 1993; 2000; 2002) and PlantNet (2006)

Warrimoo Oval Swamp, at 33° 43' 21.44"S, 150° 36' 58.35"E and 190-200 m altitude, is approximately 1.5 km east of Warrimoo Post office and 0.4 km south of Warrimoo Oval. There are substantial urban areas within a kilometer of the swamp and weed invasion is considerable.

The vegetation is mainly woodland with some open forest and swamp communities (Keith and Benson, 1988). Locally, *Angophora bakeri*, *Eucalyptus pauciflora* and *E. radiata* are dominant. The swamp surface supports an open heathland with *Leptospermum* spp.

Notts Swamp, at 33° 48' 35.44" S, 150° 24' 27.66" E and about 682 m altitude is approximately 12 km south-southeast of Wentworth Falls and to the west of Notts Hill. The lower third of the swamp is used as a market garden, but there is no sign of disturbance or weed invasion at the study site. There is no indication of European activities in the catchment upstream of the study site and the nearest settlement is some 7 km to the north-northeast.

The major plant community is open woodland and there is a little open forest and some swamps (Keith and Benson 1988). *Eucalyptus eugenioides, E. multicaulis, E. piperita, E. racemosa* and *E. sieberi* are locally dominant. The swamp supports a closed sedgeland of *Gymnoschoenus sphaerocephalus, Leptospermum trinervium* and *Baloskion australe.*

Ingar Swamp, at 33° 46' 11.65" S, 150° 27' 22.92" E and 584m altitude, is approximately 8 km southeast of Lawson. European settlement is some five km to the northeast, along the highway, and includes some very large, old conifer trees.

The vegetation is mainly woodland with *Corymbia gummifera, Eucalyptus oblongata, E. piperita, E. pauciflora,* and *Angophora costata* dominant locally. Open forest in gorges along the creeks is dominated by *E. eugenioides, E. sclerophylla, Tristania neriifolia* and *Angophora costata.* The swamp community is a closed sedgeland of *Gymnoschoenus sphaerocephalus, Leptocarpus tenax, Baumea* sp., *Chorizandra* sp., *Baloskion australe* and, towards the edge, *Hakea teretifolia, H. dactyloides* and *Leptospermum lanigerum.*

Kings Tablelands, at 33° 45' 47" S, 150° 22' 43" E and about 780-790 m altitude, is located in small valley off Queen Victoria Creek. It is about 0.6 km east of Queen Victoria Memorial Hospital near Wentworth Falls. An urban area is found less than 1 km to the west where exotic conifers have been planted in the gardens.

The vegetation is mainly open forest around the study site, with woodland on the ridges and closed sedgelands in the swamps (Keith and Benson, 1988). Locally, *Eucalyptus dives, E. oreades, E. sieberi* and *E. piperita* are dominant in the open forest and *Corymbia gummifera, E. racemosa* and *E. sieberi* are dominant in the woodland. On the exposed plateau to the northeast, the dominants in an open heathland are *Allocasuarina distyla, E. ligustrina, E. stricta, Banksia serrata* and *Hakea teretifolia.* The dominants on the swamp are *Leptospermum juniperinum* and *L. grandiflorum.*

Katoomba Swamp, at 33° 43' 03" S, 150° 19' 18" E and 950 m altitude, is 1 km east northeast of Katoomba Post Office and 1 km west of Leura Post Office. This swamp is surrounded by urban activity, with drainage ditches and a sealed road running across the swamp. Much of the swamp is (or has been) used for yards for light industry and horse paddocks. Housing extends to the edge of the swamp.

Most of the area around the swamp has been cleared but there are a few remnant pockets of Sandstone Plateau Forest (Keith and Benson, 1988) remaining. *Eucalyptus acmenoides, E. oreades, E. stellulata, E. oblongata* and *E. sieberi* are dominant. The understorey is problematic as the remnant stands are heavily weed infested.

Little remains of the original vegetation over the swamp surface and species of Poaceae are predominant. A small patch of swamp edge vegetation forms a dense thicket of *Leptospermum juniperinum* and *L. scoparium.*

Newnes Swamp, at 33° 22' 57" S,150° 13' 20" E and 1,060 m altitude, is within a forestry area with pine plantations. Regular burning maintains fire breaks.

Woodland communities are found around the swamp (Benson and Keith, 1990) but the shrub layer has been much reduced by frequent burning. Shrubs remaining on the swamp include *Leptospermum trinervium* and *Grevillea acanthifolia.* A ground cover of grasses is found in all but the wettest areas where Juncaceae and Restionaceae are dominant.

METHODS

The vegetation units at each site were determined from maps in Benson (1992), Keith and Benson (1988) and Benson and Keith (1990). Each site was visited, the vegetation checked with the maps and as many species as possible were identified in each of the vegetation units. Since palynology cannot reveal the structure of the vegetation, the focus of survey was on the species list. Dominance was determined subjectively from the abundance of the species

Samples from the surface of the soil, or where possible, from moss polsters, were collected from the centre of the swamp, the swamp edge and the plant communities adjacent or local to, the swamp sites. Samples were taken from at least 100 m away from community boundaries where possible. The sample types and vegetation are listed in Table 1 and the

Table 1 Surface samples used for pollen spectra presented in Figs 2 and 3. Codes for vegetation map units are from Keith and Benson (1988).

Surface sample no.	Vegetation	Vegetation map unit	Sample material
	Burralow Creek		
1	Open sedgeland mid-swamp	28a	Soil
2	Open sedgeland mid-swamp	28a	0 cm core
3	Swamp fringe	28a	Soil
4	Low Woodland	10ar	Soil
5	Open forest	10ag	Soil
	Warrimoo Oval		
6	Closed sedgeland mid-swamp	26a	Soil
7	Closed sedgeland mid-swamp	26a	0 cm core
8	Closed sedgeland swamp fringe	26a	Soil
9	Low woodland	10ar	Soil
	Notts		
10	Closed sedgeland mid-swamp	26a	Soil
11	Closed sedgeland swamp fringe	26a	Soil
	Ingar		
12	Closed sedgeland mid-swamp	26a	Soil
13	Closed sedgeland swamp fringe	26a	Soil
14	Low woodland	10ar	Soil
15	Low woodland	10ar	Soil
	Kings Tableland		
16	Closed sedgeland mid-swamp	26a	0 cm core
17	Closed sedgeland swamp fringe	26a	Soil
18	Low woodland	10ar	Soil
19	Low woodland	10ar	Soil
20	Open forest	9i	Soil
21	Open forest	9i	Soil
22	Open heath	21f	Soil
	Katoomba		
23	Closed sedgeland mid-swamp	26a	Soil
24	Closed sedgeland swamp fringe	26a	Soil
25	Open forest	9i	Soil
26	Open forest	9i	Soil
	Newnes		
27	Closed heath mid-swamp	20a	Moss
28	Closed heath swamp fringe	20a	Moss
29	Woodland	10f/11a	Moss
30	Woodland	10f/11a	Moss
31	Woodland	10f/11a	Soil
32	Woodland	10f/11a	Soil
33	Open heath	21d	Soil
34	Open heath	21c	Soil
35	Forest	10f	Soil
36	Forest	10f	Soil
	Murphys Glen		
37	Tall open forest	6c	Soil
38	Tall open forest	6c	Soil
	Wolgan		
39	Open woodland	11a	Soil
40	Open woodland	11a	Soil
	Wood Nymphs Dell		
41	Open forest	10ag	Soil
	Medlow Bath		
42	Open forest	9i	Soil

study sites are shown in Fig. 1

Six to ten sub-samples were taken from each plant community over a transect of approximately 20 m. The sub-samples were mixed together to reduce the possible over-representation of any one species due to close proximity to an individual plant (Chalson, 1991).

The samples were treated with hydrochloric and hydrofluoric acids to remove siliceous material (Birks and Birks, 1980), oxidised with Schultz solution (a saturated solution of potassium perchlorate in nitric acid), cleared in 10% potassium carbonate and the residue was mounted in glycerine jelly (Brown, 1960).

Pollen was identified by comparing the grains with reference pollen treated with standard acetolysis (Moore et al., 1991). Grains were counted along transects across the slides and tests showed that a count of 140 grains adequately sampled the residues. The counts of each pollen type were presented as percentages of the total count on the pollen diagrams.

RESULTS

Fig. 2 presents the pollen spectra from vegetation on the swamp surface and at the edge of the swamp, and Fig 3. presents spectra from the dry-land communities in the surrounding vegetation. Table 2 presents the name on the pollen diagram, the probable source of the pollen in the vegetation and ecological inference.

Preservation, although adequate, was not good enough for the identification of *Eucalyptus* species beyond broad groups (Chalson and Martin, 1995). The pollen from moss polsters may be better preserved than that from the soil, but moss polsters were not common and usually dried out severely in the forest environment, hence soil samples were usually collected in all but the dampest areas.

Exotic *Pinus* is present in all samples (Figs 2A, 3B) and values are highest at sites near urban areas (Kings Tableland, Katoomba). Surprisingly, *Pinus* values are not high at Newnes, in the forestry area with pine plantations, but the pines were very young at the time of this study.

Angophora/Corymbia and *Eucalyptus/Melaleuca* have been identified in low frequencies in some of the samples which were better preserved. *Melaleuca styphelioides* has been identified in some of the swamp samples (Fig. 2A) where counts may be high. *M. styphelioides* was not found during the survey of the vegetation, but it may be grown in gardens. The highest count at Warimoo Oval Swamp is close to substantial urban areas. *Leptospermum/Baeckea* has been identified from some swamp samples (Fig. 2A) where counts may be considerable. *Leptospermum* spp. are often dominant in the swamp communities (see Appendix 1)

The unidentified Myrtaceae group is larger than the other groups of Mytaceae and counts from the swamp samples are the lowest of all. The woodland or forest samples from the borders of the swamp (Fig. 2A) all have higher counts than the swamp samples. Frequencies in samples from the dry-land vegetation (3A) are much higher than those from swamps. Lack of specific identification was generally due to poor preservation.

Casuarinaceae frequencies are usually low, with a few higher values. The highest value (Fig. 3A) comes from heathland vegetation.

Poaceae frequencies are generally low and the high values are associated with urbanisation and disturbance (Katoomba, Fig. 2A).

Restionaceae frequencies are variable but most of the high values are found in the swamp samples. Cyperaceae has not been recorded from many samples, and where it is present, frequencies are generally low, with the few higher frequencies being found in the swamp samples.

Selaginella is present in a few samples and appreciable frequencies may be recorded in some swamp samples. *Gleichenia* may be present in appreciable frequencies in some swamp samples also. Other fern spores are usually recorded in low frequencies and are more common in the dry-land samples.

Table 2 also lists the likely environmental indication of the pollen groups on the diagrams, but this is difficult, given that a group may include many possible species. For example, the families Restionaceae and Cyperaceae include both swamp and dry-land species, but the species in the vegetation and patterns of high pollen frequencies on the diagrams may indicate the nature of the environment when considered together. Thus the species of Restionaceae and Cyperaceae found in the local vegetation (Appendix 1) are almost entirely species of swamps or damp places (Table 2).

DISCUSSION

There are many indications that the pollen recovered from the surface samples was produced mainly by the local vegetation and thus the pollen spectra can indicate the type of

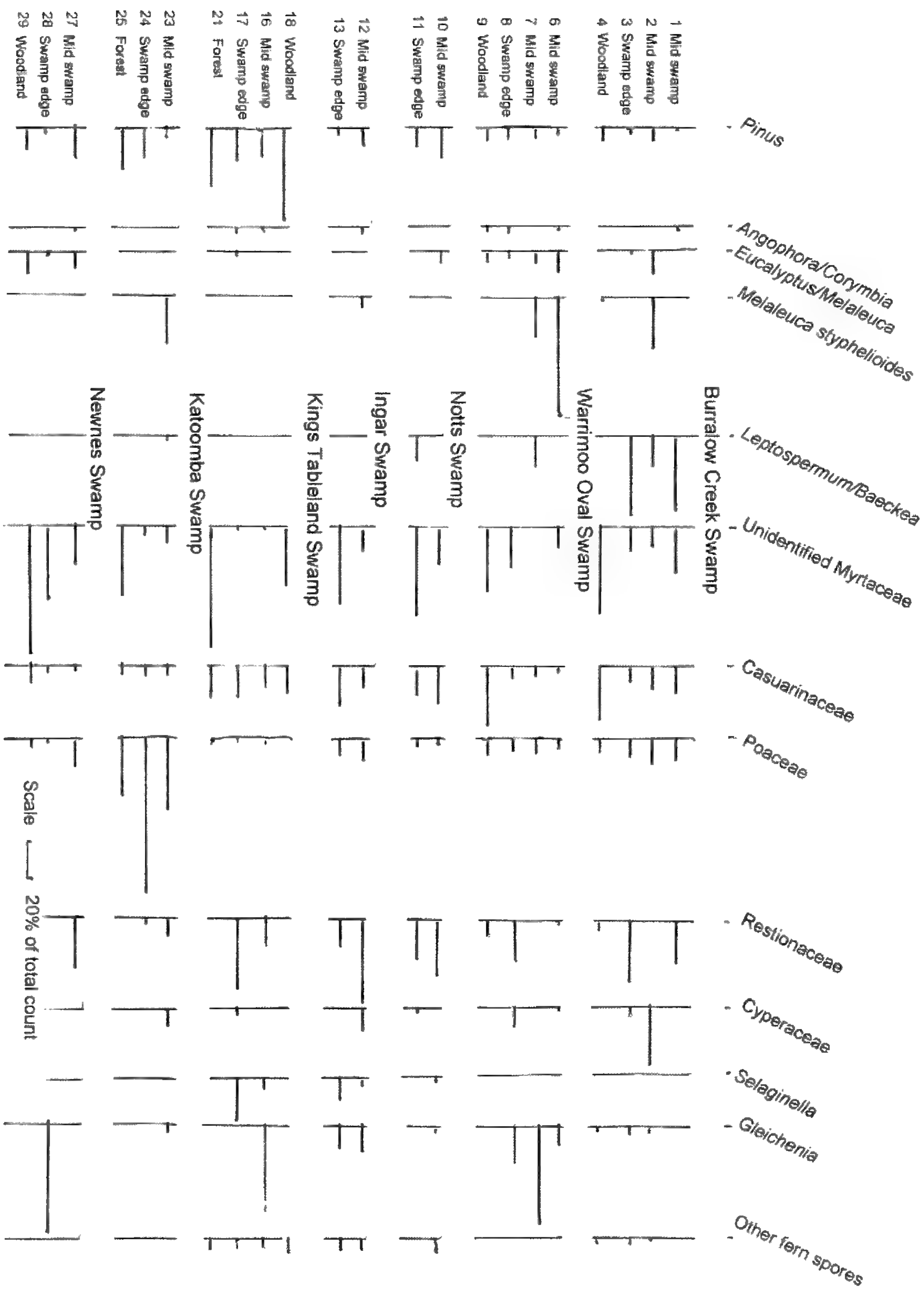

Figure 2A. The pollen spectra from plant communities associated with swamps within major pollen groups. The Sample number (extreme left hand side) refers to the sample in Table 1.

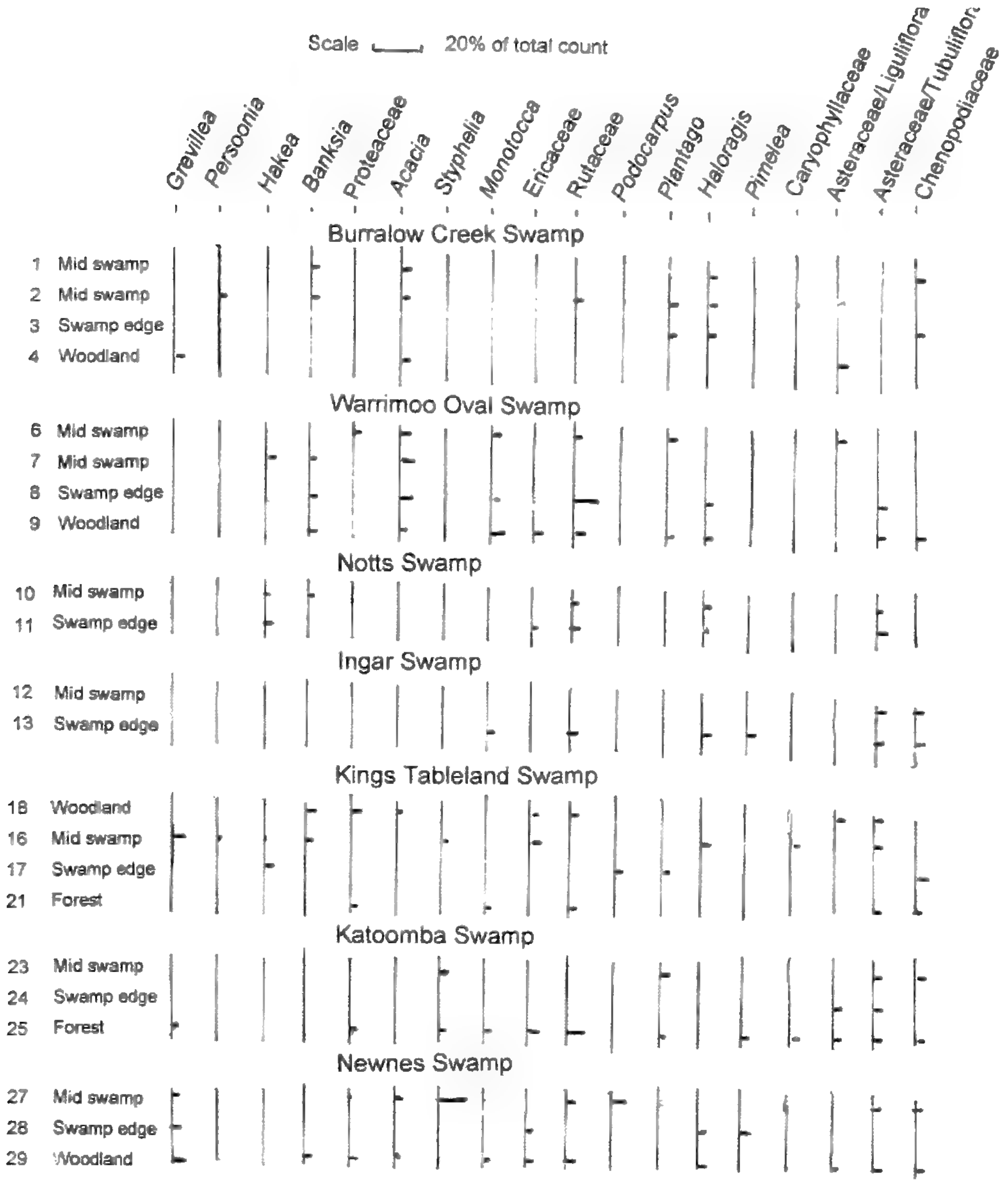

Figure 2B. The pollen spectra from plant communities associated with swamps within low frequency taxa. The Sample number (extreme left hand side) refers to the sample in Table 1

vegetation from which it came. For example, the Myrtaceae pollen content (Figs. 2A, 3A), is lowest from swamp sites, intermediate from the dry-land communities bordering the swamps and highest from the woodland and forest sites away from the swamps, thus inferring a parallel approximate tree cover.

Swamp samples contain much higher pollen frequencies of Restionaceae and/or Cyperaceae than the dry-land sites, although both of these families contain swamp and dry-land species. The species of Restionaceae recorded in the vegetation (Appendix 1) are found on wet and poorly drained soils and in damp to wet heaths (PlantNet, 2007). Most of the species of Cyperaceae, on the other hand, are found in fresh water swamps and swampy areas (Sainty and Jacobs, 1981; PlantNet, 2007), although one dry-land species is also recorded (Appendix 1). Thus high frequencies of Cyperaceae probably indicate swamps which are more permanently waterlogged than swamps with high frequencies of Restionaceae. Both *Selaginella* and *Gleichenia* are found in wet places, on the edge of swamps and streams (PlantNet, 2007).

The pollen of sclerophyllous shrub taxa (Figs 2B, 3B) are usually found sporadically and in very low frequencies, indicating under-representation and very localised distribution.

These findings are in accord with other studies of surface pollen assemblages which indicate very localised distribution of pollen (Dodson, 1983; Kodela, 1990). Kershaw and Strickland (1990) found that, in a 10 year pollen trapping experiment, most pollen came from within 10 m of the trap.

These study sites are all contained within small valleys where some barrier impedes drainage of the

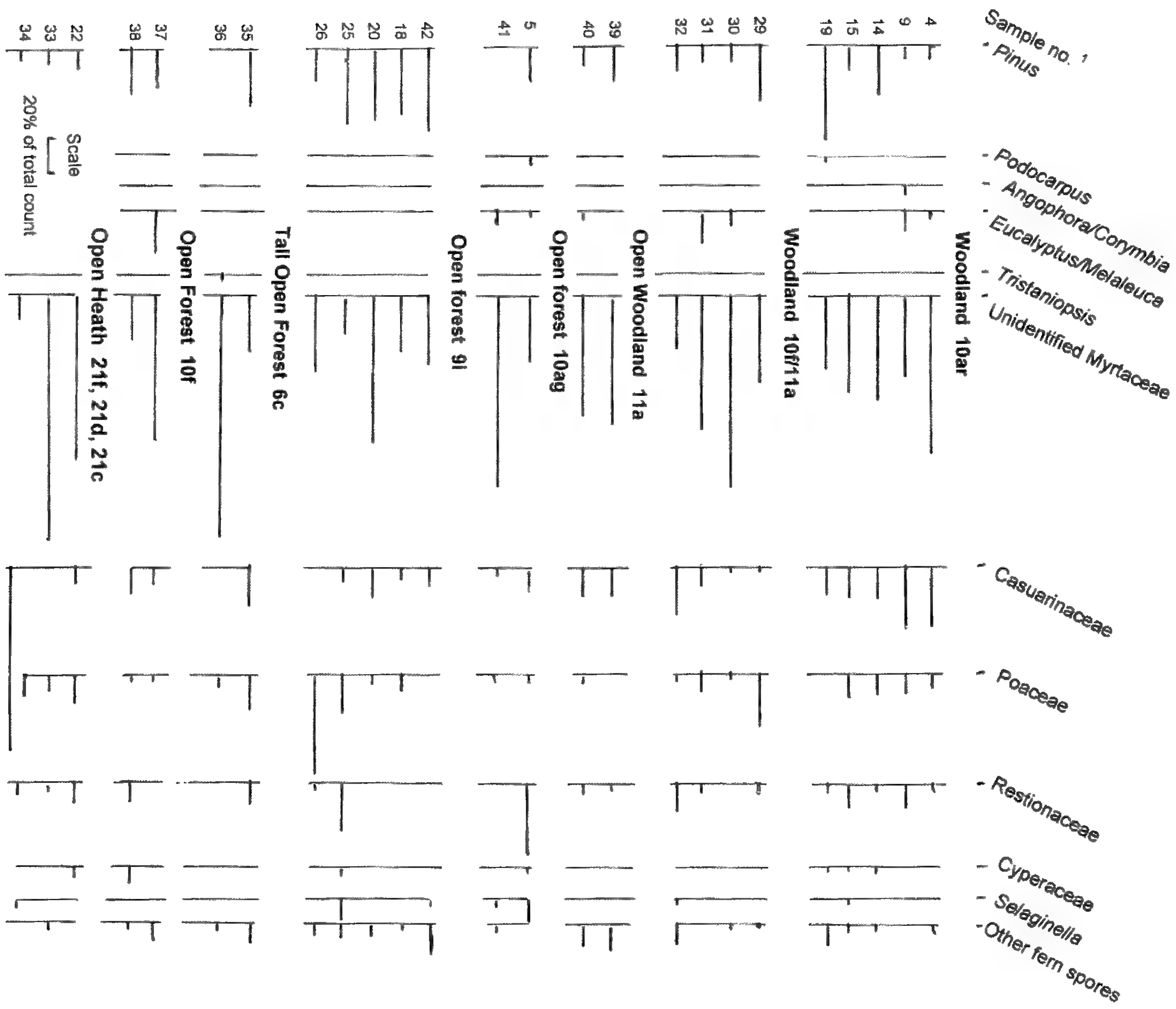

Figure 3A. Pollen spectra associated with dry-land plant communities within major pollen groups. 1 The sample number refers to the sample in Table 1. Codes for the vegetation map units are from Keith and Benson (1988)

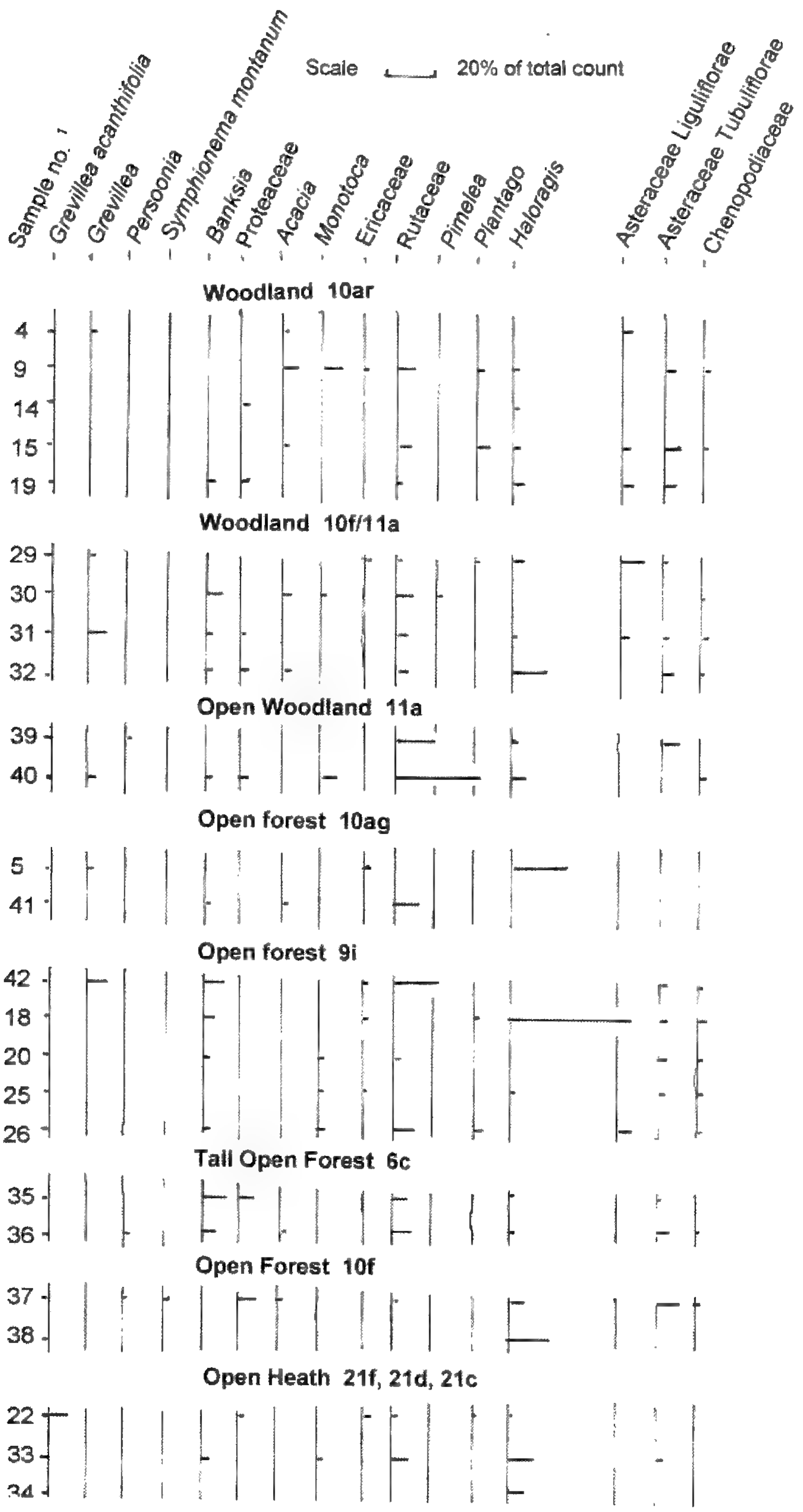

Figure 3B. Pollen spectra associated with dry-land plant communities within low frequency taxa. 1 The sample number refers to the sample in Table 1. Codes for the vegetation map units are from Keith and Benson (1988)

stream and maintains the swamp (for a full description of the sites, see Chalson and Martin, this volume). It may be argued that pollen can be transported a long distance by a stream, to be deposited with the local assemblage. While this may happen, it has been found that very little pollen is transported into the site so that the assemblage truly reflects the local vegetation (Chmura and Liu, 1990).

Table 2. Pollen type name on the pollen diagrams (Figs 2, 3) and the probable source in the vegetation.

Name on the pollen diagrams 2A and 3A	Probable source in the vegetation and ecological inference. From Plantnet (2007)
Podocarpus	Probably *Podocarpus spinulosus*: sclerophyllous shrub/small tree
Pinus	*Pinus* sp(p), Introduced: Pollen input from urban/forestry areas.
Angophora/Corymbia	Species within the two genera: sclerophyll woodland
Eucalyptus/Melaleuca	Species within the two genera : sclerophyll woodland/forest
Melaleuca styphelioides	*Melaleuca styphelioides*: moist stream bank habitat
Leptospermum/Baeckea	Species within the two genera: ?mainly swamp communities
Tristaniopsis	*Tristaniopsis* spp : moist habitats in sclerophyll communities
Unindetified Myrtaceae	All pollen types not identifiable further
Casuarinaceae	*Casuarina, Allocasuarina* sp(p): *A distyla* and *A. nana* in this study
Poaceae	Native and exotic species in the family: open situations, dryland and swamp species
Restionaceae	All species in the family: swamp and dry land species
Cyperaceae	All species in the family: swamp and dry land species
Selaginella	All species in the genus: damp sites, edge of swamp
Gleichenia	*Gleichenia* sp(p): damp sites, edge of swamp
Other fern spores	Other ferns: many possible species
Names on 2B and 3B	
Grevillea acanthifolia	*G. acanthifolia*: sclerophyllous understorey
Grevillea	*Grevillea* sp(p): sclerophyllous understorey
Hakea	*Hakea* sp(p): sclerophyllous understorey
Persoonia	*Persoonia* sp(p): sclerophyllous understorey
Symphionema montanum	*S. montanum*: heath or dry sclerophyll forest
Banksia	*Banksia* sp(p): sclerophyllous understorey
Proteaceae	Other taxa in the family sclerophyllous understorey
Acacia	All species in the genus
Styphelia	*Styphelia* sp(p): sclerophyllous understorey
Monotoca	*Monotoca* sp(p): sclerophyllous understorey
Ericaceae	Other taxa in the family: sclerophyllous understorey
Rutaceae	All taxa in the family: sclerophyllous understorey
Pimelea	*Pimelea* sp(p): sclerophyllous understorey
Plantago	*Plantago* sp(p): native and introduced herbs
Haloragis	*Haloragis/Gonocarpus* sp(p): Damp sites, sclerophyllous understorey
Asteraceae/Liguliflorae	Fenestrate-grained taxa in the subfamily Liguliflorae: herbs
Asteraceae/Tubuliflorae	Echinate-grained taxa in the subfam. Tubuliflorae: shrubs and herbs
Chenopodiaceae	Ruderals, salt tolerant

It is unfortunate that the Myrtaceae species cannot be identified in most cases, since the vegetation units are defined on their species of Myrtaceae. Most Myrtaceae grains are small and thin-walled (Chalson, 1991; Chalson and Martin, 1995) and the preservation may not be good enough to preserve this fine detail which would distinguish the species. The result is that there are large counts of unidentified Myrtaceae. The alternate wetting and drying at the soil surface in these sclerophyll forests are not ideal conditions for pollen preservation.

The forests, woodlands and heaths defined by Benson (1992), Keith and Benson (1988) and Benson and Keith (1990) are structural units within one major vegetation formation and share many species, although the abundance of a particular species may vary. The pollen assemblages cannot denote structure of the vegetation and the floristics of these units are too similar to allow any differentiation, especially as the Myrtaceae pollen is so poorly preserved. For practical purposes, the surface pollen assemblages can denote major vegetation formations (Birks and Birks, 1980; Moore et al., 1991), more/less catchment tree cover, swamp and/or adjacent dry-land environments and local floral diversity.

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APPENDIX. Species found in the vegetation on and around the swamps. Nomenclature follows Harden (1992; 1993; 2000; 2002) and Plantnet (2006). Vegetation map units are from Keith and Benson (1988) D, dominant. *, introduced species.

BURRALOW CREEK SWAMP Species	Open forest 10ar	Wood-land 10ag	Edge swamp 28a	Mid swamp 28a
BRYOPHYTES				
Sphagnaceae				
Sphagnum sp.			+	
PTERIDOPHYTES AND ALLIES				
Adiantaceae				
Adiantum aethiopicum	+	+		
Blechnaceae				
Blechnum ambiguum			+	
B. cartilaginum		+		
Dennstaediaceae				
Pteridium esculentum		+	+	+
Gleicheniaceae				
Gleichenia dicarpa			+	
G. microphylla	+			
Osmundaceae				
Todea barbara		+		
Selaginellaceae				
Selaginella uliginosa			+	
ANGIOSPERMS, DICOTYLEDONS				
Apiaceae				
Platysace ericoides	+			
P. lanceolata				+
P linearifolia	+			+
Xanthosia pilosa	+	+		
Apocynaceae				
Parsonsia straminea	+			
Araliaceae				
Polyscias sambucifolia	+	+		
Asteraceae				
Cassinia aculeata	+			
C. aureonitens	+			
Casuarinaceae				
Allocasuarina nana			+	
Ceratophyllaceae				
Ceratophyllum demersum	+			
Cunoniaceae				
Callicoma serratifolia	+			
Dilleniaceae				
Hibbertia acicularis			+	
H. bracteata		+		

Elaeocarpaceae				
Elaeocarpus reticulatus	+			
Tetratheca thymifolia		+		
Ericaceae				
Epacris paludosa	+			
E. pulchella	+	+		
Leucopogon hookeri	+	+		
Euphorbiaceae				
Ampera xiphoclada	+			
Phyllanthus hirtellus	+			+
Fabaceae, Faboideae				
Bossiaea obcordata	+			
Dillwynia floribunda	+		+	+
D. retorta	+			
Gompholobium huegelii		+	+	
Pultenaea tuberculata	+			
Fabaceae, Mimosoideae				
Acacia falciformis	+			
A. myrtifolia	+			
A. obtusata	+			+
A. ptychoclada			+	+
A. terminalis	+		+	
Goodeniaceae				
Dampiera stricta	+		+	
Goodenia dimorpha			+	
G. heterophylla	+			
G. ovata	+			
Lamiaceae				
Prostanthera violacea		+		
Lauraceae				
Cassytha melantha	+			
Lobeliaceae				
Pratia purpurascens			+	
Loganiaceae				
Mitrasacme pilosa				+
Meliaceae				
**Melia azedarach* var. *australasica*	+			
Menyanthaceae				
Villarsia exaltata				+
Myrsinaceae				
Rapanea howittiana	+	+		
Myrtacae				
Angophora bakeri			D	
A. costata	D			
A. floribunda	+	+		

Baeckea linifolia			+	
Corymbia eximia			D	
Eucalyptus eugenioides			D	
E. multicaulis			D	
E. pauciflora	D	D		
E. radiata		D		
Kunzea capitata	+			D
Leptospermum polygalifolium			+	
L. trinervium				D
Melaleuca linariifolia	D	D		
Tristania neriifolia	D			
Oleaceae				
**Ligustrum sinense*	+			
Notelaea longifolia	+	+		
Pittosporaceae				
Billardiera scandens	+			
Proteaceae				
Banksia ericifolia	+			
B. serrata				+
Hakea teretifolia	+		+	
Lambertia formosa	+	+		
Persoonia laurina			+	
P. levis	+			
P. linearis	+			
P. mollis				+
P. oblongata	+			
Petrophile pulchella		+		
Ranunculaceae				
Clematis aristata		+		
Rhamnaceae				
Cryptandra amara		+		
Rutaceae				
Eriostemon hispidulus	+	+		
Sapindaceae				
Dodonaea pinnata	+			
D. triquetra	+			
Stackhousiaceae				
Stackhousia viminea	+			
Thymelaeaceae				
Pimelea ligustrina	+			
Violaceae				
Viola hederacea		+		
ANGIOSPERMS, MONOCOTYLEDONS				
Cyperaceae				
Baumea juncea				+

Baumea sp.			+	+
Chorizandra sp.	+			+
Eleocharis sphacelata		+	+	
Lepidosperma longitudinale			+	
Schoenus sp.			+	
Lomandraceae				
Lomandra glauca		+		
L. longifolia				+
Phormiaceae				
Dianella caerulea	+			
Restionaceae				
Leptocarpus tenax				+
Baloskion fimbriatum		+		
Smilacaceae				
Smilax australis	+			
S. glyciphylla	+			

WARRIMOO OVAL SWAMP Species	Open forest 10ar	Edge swamp 26a	Mid swamp 26a
PTERIDOPHYTES AND ALLIES			
Adiantaceae			
Adiantum diaphanum	+		
Dennstaediaceae			
Pteridium esculentum	+	+	
Gleicheniaceae			
Gleichenia dicarpa		+	+
ANGIOSPERMS, DICOTYLEDONS			
Apiaceae			
Actinotus minor	+		
Platysace lanceolata	+	+	
P linearifolia	+		
Ericaceae			
Brachyloma daphnoides	+		
Dracophyllum secundum		+	
Epacris paludosa	+	+	
Fabaceae, Faboideae			
Bossiaea heterophylla	+	+	
**Cytisus scoparius*	+		
Daviesia ulicifolia	+	+	
Dillwynia phylicoides		+	
Gompholobium huegelii	+	+	
G. latifolium	+		
Hovea linearis		+	

Mirbelia rubifolia	+		
Fabaceae, Mimosoideae			
Acacia falciformis	+		
A. ptychoclada		+	
A. rubida			+
A. terminalis	+		
Goodeniaceae			
Dampiera stricta	+	+	
G. ovata	+		
Lobeliaceae			
Pratia purpurascens	+		
Myrtacae			
Angophora bakeri	D	D	
Baeckea linifolia	+		+
Eucalyptus notabilis		D	
E. pauciflora	D		
E. radiata	D		
Kunzea capitata	+		D
Leptospermum grandifolium			D
L. polygalifolium	+		D
L. trinervium	+	+	
Polygalaceae			
Comesperma defoliatum	+		
C. ericinium	+		
Proteaceae			
Banksia ericifolia	+	+	
B. oblongifolia	+		
B. serrata	+	+	
Grevillea laurifolia	+	+	
G. mucronulata	+		
G. phylicoides	+	+	
Hakea salicifolia	+	+	
Isopogon anethifolius	+	+	
I. prostratus	+	+	
Persoonia laurina	+		
P. myrtilloides	+		
P. pinifolia	+		
Rutaceae			
Boronia microphylla	+	+	
Thymelaeaceae			
Pimelea glauca			+
P. ligustrina	+		
Violaceae			
Viola hederacea			

ANGIOSPERMS, MONOCOTYLEDONS			
Cyperaceae			
Baumea juncea			+
Eleocharis sphacelata			+
Juncaceae			
Juncus remotiflorus			+
Lomandraceae			
Lomandra filiformis ssp *coriacea*		+	
L. longifolia	+		
L. obliqua	+		
Phormiaceae			
Dianella caerulea		+	
Restionaceae			
Leptocarpus tenax	+	+	

NOTTS SWAMP Species	Open forest 10ar	Mid swamp 26a
PTERIDOPHYTES AND ALLIES		
Dennstaediaceae		
Pteridium esculentum	+	
Gleicheniaceae		
Gleichenia dicarpa		+
Selaginellaceae		
Selaginella uliginosa		+
ANGIOSPERMS, DICOTYLEDONS		
Apiaceae		
Actinotus forsythii	+	
Platysace lanceolata	+	
P linearifolia	+	
Ericaceae		
Epacris paludosa	+	
Lissanthe sapida	+	
Euphorbiaceae		
Poranthera microphylla		+
Fabaceae, Faboideae		
Bossiaea heterophylla	+	
Phyllota squarrosa		+
Platylobium formosum		+
Fabaceae, Mimosoideae		
Acacia melanoxylon	+	
A. obtusata	+	
A. obtusifolia		+
A. stricta	+	

Myrtacae		
Eucalyptus aggregata		+
E. dives	D	
E. ligustrina	D	
E. pauciflora	D	
E. piperita	D	
E. sclerophylla	D	
Kunzea capitata		D
Leptospermum juniperinum		+
Proteaceae		
Banksia oblongifolia	+	
B. serrata	+	
Grevillea phylicoides	+	
Hakea teretifolia	+	
Isopogon prostratus	+	
Persoonia laurina	+	
P. linearis	+	
Petrophile pedunculata	+	
Rutaceae		
Boronia microphylla	+	+
ANGIOSPERMS, MONOCOTYLEDONS		
Cyperaceae		
Baumea rubiginosa		+
Carex sp.	+	
Gahnia sp.		D
Iridaceae		
Patersonia sericea	+	
Juncaceae		
Juncus remotiformis		+
Phormiaceae		
Dianella caerulea	+	
Poaceae		
Entolasia marginata	+	
Poa sp.	+	
Restionaceae		
Baloskion australe		+
Leptocarpus tenax (Labill.)		D

INGAR SWAMP Species	Open forest 10ar	Wood-land 10ag	6c Tall open forest	Edge swamp 26a	Mid swamp 26a
PTERIDOPHYTES AND ALLIES					
Adiantaceae					
Adiantum aethiopicum				+	

Dennstaediaceae					
Pteridium esculentum	+		+		
Dicksoniaceae					
Calochlaena dubia			+		
Gleicheniaceae					
Gleichenia dicarpa		+			+
G. microphylla		+			
Osmundaceae					
Todea barbara		+			
Selaginellaceae					
Selaginella uliginosa				+	
ANGIOSPERMS, DICOTYLEDONS					
Apiaceae					
Actinotus forsythii	+			+	
Platysace lanceolata	+	+	+		
P. linearifolia	+			+	
Casuarinaceae					
Allocasuarina distyla		+			
Cunoniaceae					
Bauera rubioides		+			
Callicoma serratifolia		+	+		
Ceratopetalum apetalum		+			
Dilleniaceae					
Hibbertia acicularis	+				
Elaeocarpaceae					
Elaeocarpus reticulatus			+		
Ericaceae					
Brachyloma daphnoides		+			
Dracophyllum secundum				+	
Epacris paludosa	+	+			
Leucopogon esquamatus				+	
L. hookeri		+			
L. lanceolatus		+			
Lissanthe sapida	+				
Euphorbiaceae					
Ampera xiphoclada	+				
Fabaceae, Faboideae					
Bossiaea heterophylla	+				
B. obcordata		+			
Daviesis alata	+	+			
D. ulicifolia	+				
Dillwynia philicoides		+			
D. retorta	+				
Glycine clandestina	+				
Hovea linearis				+	

Phyllota phylicoides	+				
P. squarrosa		+			
Platylobium formosum					+
Pultenaea divaricata		+			
P. flexilis				+	
P. incurvata		+			
P. tuberculata		+	+		
Fabaceae, Mimosoideae					
Acacia echinula	+	+	+		
A. melanoxylon	+				
A. obliquinervia	+				
A. obtusata	+		+		
A. obtusifolia				+	+
A. stricta	+			+	+
A. suaveolens		+	+		
Goodeniaceae					
Dampiera stricta				+	
Goodenia bellidifolia				+	
G. dimorpha				+	
G. ovata				+	
Haloragaceae					
Gonocarpus chinensis ssp *verrucosus*				+	
G. longifolius			+	+	
Myrtacae					
Angophora bakeri	D	D	+		
Backhousia myrtifolia				+	
Baeckea diosmifolia		+			
Corymbia eximia	D				
Eucalyptus agglomerata		D			
E. dalrympleana			D		
E. dives		D			
E. obliqua	D				
E. oreades	D				
E. pauciflora	D	D			
E. radiata		D			
E. sieberi	+				
Kunzea capitata	+	+			
Leptospermum grandifolium			+		
L. juniperinum					D
L. polygalifolium		+			+
L. scoparium			+		
L. trinervium			+		
Melaleuca linariifolia			D		
Syncarpia glomulifera		D			

Proteaceae					
Banksia ericifolia				+	
B. oblongifolia	+	+			
B. serrata	+	+	+		
Grevillea aspleniifolia		+			
G. laurifolia			+		
G. phylicoides	+			D	
Hakea propinqua			+		
H. sericea		+		D	
H. teretifolia	+	+		+	
Isopogon prostratus	+	+			
Lambertia formosa		+			
Lomatia myricoides			+		
Persoonia acerosa		+			
P. laurina	+				
P. levis		+			
P. linearis	+	+	+		
P. pinifolia		+			
Petrophile pedunculata	+				
Ranunculaceae					
Clematis aristata			+		
Rhamnaceae					
Cryptandra amara			+		
Rutaceae					
Boronia microphylla	+				
Thymelaeaceae					
Pimelea ligustrina				+	
ANGIOSPERMS, MONOCOTYLEDONS					
Cyperaceae					
Baumea rubiginosa					D
Carex sp.	+	+			+
Chorizandra cymbaria				D	
Eleocharis sphacelata		+			
Gahnia sieberana		+	+		
Gahnia sp.					D
Gymnoschoenus sphaerocephalus				+	
Lepidosperma longitudinale				D	
Iridaceae					
Patersonia sericea	+				
Juncaceae					
Juncus remotiformis			+		
Luzuriagaceae					
Eustrephus latifolius			+		
Phormiaceae					
Dianella caerulea	+				

Poaceae					
Entolasia marginata	+				
Poa sp.				+	
Restionaceae					
Baloskion australe					+
Empodisma minus				D	
Leptocarpus tenax				D	D
Smilacaceae					
Smilax australis				+	

KINGS TABLELAND SWAMP Species	Woodland 10ar	Open forest 9i	Open heath 21f	Edge swamp 26a	Mid swamp 26a
PTERIDOPHYTES AND ALLIES					
Dennstaediaceae					
Pteridium esculentum		+			
Gleicheniaceae					
Gleichenia dicarpa					+
GYMNOSPERMS					
Cupressaceae					
Callitris muelleri			+		
ANGIOSPERMS, DICOTYLEDONS					
Apiaceae					
Actinotus forsythii			+		
Platysace lanceolata	+	+	+		
Casuarinaceae					
Allocasuarina distyla		+	D		
Allocasuarina nana			+		
Ericaceae					
Dracophyllum secundum					+
Epacris paludosa			+		
Fabaceae, Faboideae					
Bossiaea heterophylla		+	+		
Daviesia alata	+		+		
D. ulicifolia		+			
Hovea linearis			+		
Phyllota squarrosa	+				
Pultenaea divaricata	+				
Fabaceae, Mimosoideae					
Acacia obtusata		+			
A. stricta		+			
A. suaveolens	+	+			
A. terminalis			+		

Myrtacae					
Corymbia eximia	D				
C. gummifera			D		
Eucalyptus deanei		D			
E. oblonga		D			
E. pauciflora		D			
E. piperita	D				
E. sclerophylla	D	D			
E. stellulata			D		
E. stricta			+		
Kunzea capitata	+	+			
K. ericoides			+		
Leptospermum grandifolium			+		
L. juniperinum					D
L. polygalifolium			+		D
Olacaceae					
Olax stricta			+		
Proteaceae					
Banksia ericifolia	+		+		+
B. oblongifolia		+	D		
B. serrata	+	+	+		
B. spinulosa					+
Grevillea phylicoides	+	+	+		
Hakea dactyloides			+		
H. salicifolia	+	+			
H. sericea			D		+
Isopogon anemonifolius		+			
I. prostratus	+	+	+		
Lomatia silaifolia			+		
Persoonia laurina	+	+			
Petrophile pedunculata	+		+		
Thymelaeaceae					
Pimelea ligustrina					+
ANGIOSPERMS, MONOCOTYLEDONS					
Lomandraceae					
Lomandra glauca		+			

KATOOMBA SWAMP Species	Open forest Upper 9i	Open forest Lower 9i	Edge swamp 26a	Mid swamp 26a
BRYOPHYTES				
Dawsoniineae				
Dawsonia sp.				D

PTERIDOPHYTES AND ALLIES			
Blechnaceae			
Blechnum cartilaginum			+
Dennstaediaceae			
Pteridium esculentum	+	+	
Gleicheniaceae			
Gleichenia dicarpa			+
Lycopodiaceae			
Lycopodium deuterodensum	+		
ANGIOSPERMS, DICOTYLEDONS			
Araliaceae			
Polyscias sambucifolia	+	+	
Asteraceae			
Arrhenechthites mixta	+		
Bracteantha bracteata		+	
Cunoniaceae			
Callicoma serratifolia	+		
Ericaceae			
Epacris paludosa		+	
Fabaceae, Faboideae			
Bossiaea rhombifolia	+	+	+
Daviesia latifolia		+	
Fabaceae, Mimosoideae			
Acacia obtusata	+		
A. suaveolens		+	
Myrtacae			
Callistemon citrinus	D		
Eucalyptus obliqua		D	
E. oblonga	D		
E. sclerophylla		D	
E. squamosa	D		
Kunzea capitata	+	+	
K. ericoides			D
Leptospermum polygalifolium			D
L. trinervium		+	
Oleaceae			
**Ligustrum sinense*	+	+	
Polygonaceae			
**Acetosella vulgaris*			+
**Rumex obtusifolius*			+
Proteaceae			
Banksia spinulosa			+
Grevillea mucronata		+	
Isopogon prostratus		+	
Lomatia myricoides		+	

Persoonia laurina		+		
Petrophile pedunculata		+		
Rutaceae				
Boronia microphylla		+		
ANGIOSPERMS, MONOCOTYLEDONS				
Cyperaceae				
Caustis flexuosa				D
Juncaceae				
Juncus remotiformis			+	D
Lomandraceae				
Lomandra obliqua		+		
Phormiaceae				
Dianella caerulea	+			
Poaceae				
Poa sp.			+	

NEWNES SWAMP Species	Open forest 9i	Wood-land 11a	Edge swamp 20a	Mid swamp 2oa
PTERIDOPHYTES AND ALLIES				
Blechnaceae				
Blechnum cartilaginum	+			
Dennstaediaceae				
Pteridium esculentum	+			
Gleicheniaceae				
Gleichenia dicarpa	+		+	
ANGIOSPERMS, DICOTYLEDONS				
Apiaceae				
Platysace lanceolata	+			
Asteraceae				
Arrhenechthites mixta	+			
Helichrysum scorpioides	+	+		
Olearia sp. aff. *chrysophyplla*	+			
Casuarinaceae				
Allocasuarina nana		+		
Dilleniaceae				
Hibbertia dentata	+			
Ericaceae				
Brachyloma daphnoides			+	
Epacris obtusifolia			+	
E. paludosa	+		+	
Lissanthe sapida	+	+		
Monotoca scoparia				+

Euphorbiaceae				
Ampera xiphoclada	+			
Fabaceae, Faboideae				
Daviesis corymbosa	+			
D. ulicifolia	+			
Gompholobium grandiflorum		+		
G. latifolium		+		
Phyllota phylicoides		+		
P. squarrosa	+	+		
Platylobium formosum			+	
Fabaceae, Mimosoideae				
Acacia elata	+			
A. linifolia	+			
A. longifolia		+		
A. melanoxylon		+		
A. suaveolens	+			
Goodeniaceae				
Dampiera stricta	+		+	
Myrtacae				
Baeckea diosmifolia			+	+
Eucalyptus acmenoides		D		
E. aggregata		D		
E. deanei		D		
E. notabilis	D	D		
E. oreades	D	D		
E. racemosa	D			
E. sclerophylla		D		
Kunzea capitata	+		D	
Leptospermum juniperinum			+	+
L. polygalifolium	+			
Proteaceae				
Banksia spinulosa			+	D
Grevillea acanthifolia	+			
G. aspleniifolia	+	+		
G. phylicoides		+		
Hakea salicifolia	+			
H. teretifolia	+			
Petrophile pedunculata	+	+		
Ranunculaceae				
Clematis aristata	+			
Rhamnaceae				
Cryptandra amara		+		
Rutaceae				
Boronia microphylla		+		

Santalaceae				
Exocarpos strictus		+		
Thymelaeaceae				
Pimelea glauca	+			
P. ligustrina	+			
ANGIOSPERMS, MONOCOTYLEDONS				
Cyperaceae				
Lepidosperma laterale	+			+
Iridaceae				
Patersonia sericea	+	+		
Juncaceae				
Juncus remotiformis			+	
Lomandraceae				
Lomandra filiformis ssp *coriacea*	+	+		
L. filiformis ssp *filiformis*		+		
L. glauca Ewart	+			
Phormiaceae				
Dianella caerulea		+		
Poaceae				
Entolasia marginata				+
Poa sp.		+		
Restionaceae				
Empodisma minus				+
Leptocarpus tenax		+	+	

Silurian Rhynchonellide Brachiopods from Yass, New South Wales

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Rhynchonellide brachiopods are rare in the Silurian sequence at Yass. In this paper two species are described, one new species *Agarhynchus australe* being abundant at just one locality in the late Wenlock or earliest Ludlow Yass Formation. The other species, tentatively assigned to *Tuvaerhynchus*, is known from only a few specimens of late Wenlock to Ludfordian age.

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KEYWORDS: *Agarhyncha australe*, Ludlow, rhynchonellide, Silurian, *Tuvaerhynchus*, Wenlock, Yass

INTRODUCTION

Rhynchonellide brachiopods were recognised in early accounts of the stratigraphy of the Yass Syncline, but none has ever been described. Jenkins (1879, p. 26) recorded *Rhynchonella* from what (using modern terminology) was probably the basal Bowspring Limestone at locality GOU57, and Mitchell (1887, p. 1201) listed the same genus from pebbles in the Sharpeningstone Conglomerate at Bowning (two specimens, described in this paper). Shearsby (1912, pp. 110-112) in his more detailed account of the succession north of Yass then noted the presence of possible *Rhynchotreta* and *Camarotoechia* at two localities, one within the Douro Volcanics, the other in the Yass Formation. The latter is in the same area along Derringullen Creek from which both of the species described in this paper were collected by Dr R.S. Nicoll and myself in 1982. However, other than at that locality, rhynchonellides are rare (only six usable specimens) in the Yass sequence.

Only two taxa can be recognised. The first, *Agarhyncha australe* n. sp., occurs at only the one locality (on Derringullen Creek), just below the Cliftonwood Limestone Member of the Yass Formation, but is there in some numbers. *Agarhyncha* Havlíček, 1982, is otherwise known from the Wenlock and Ludlow of the Czech Republic. The other Yass rhynchonellide occurs in very low numbers at a few localities from the Yass Formation to the Yarwood Siltstone Member of the Black Bog Shale, and in pebbles in the Sharpeningstone Conglomerate. It is tentatively referred to the genus *Tuvaerhynchus* Kul'kov, 1985, from the Wenlock of Tuva. This raises some problems concerning provinciality which cannot be properly assessed until better material from Yass becomes available, enabling more confident identification.

For a diagrammatic representation of Yass stratigraphy and ages, refer to Strusz (2002, fig. 1). Localities are detailed in that publication, with additions in Strusz (2003, 2005).

SYSTEMATIC PALAEONTOLOGY

Classification

The classification followed is that of Savage et al. (2002).

Measurements and symbols

All linear measurements are in millimetres, and unless otherwise specified are as defined by Williams and Brunton (1997); the following symbols are used for these measurements:

Ls, Ws, Ts – maximum shell length, width, thickness.

Wh – hinge width.

L(Wmax) – length to widest part of shell.

Repositories

The repositories for the specimens studied are shown by the following prefixes to their catalogue numbers:

AMF - macrofossil collection, Australian Museum, Sydney.

ANU - Department of Earth and Marine Sciences (Research School of Earth Sciences), Australian National University, Canberra.

CPC - Commonwealth Palaeontological Collection, Geoscience Australia, Canberra.

Phylum BRACHIOPODA
Class RHYNCHONELLATA Williams, Carlson, Brunton, Holmer and Popov, 1996
Order RHYNCHONELLIDA Kuhn, 1949
Superfamily RHYNCHOTREMATOIDEA Schuchert, 1913
Family TRIGONIRHYNCHIIDAE Schmidt, 1965
Subfamily TRIGONIRHYNCHIINAE Schmidt, 1965
Genus *Agarhyncha* Havlíček, 1982

Type species

Terebratula famula Barrande, 1847, by original designation; Ludlow, Bohemia.

Diagnosis

Subpentagonal to subcircular outline; biconvex to globose profile. Beak suberect to erect; foramen with minute deltidial plates. Fold and sulcus well defined, broad, anterior commissure uniplicate; tongue rectangular, serrate. Costae coarse, rounded, simple, but umbones smooth. Dental plates very short. Dorsal median septum thin; septalium with cover plate anteriorly; crura close to septum posteriorly (Savage p. 1052 in Savage et al. 2002).

Agarhyncha australe sp. nov.
Figs 1-5, Table 1

Diagnosis

Relatively large biconvex species of *Agarhyncha* with smooth non-sulcate umbones, sulcus often weak anteriorly, ribs only moderately developed, medially concave dental plates, impressed ventral muscle field, raduliform crura, long dorsal median septum.

Material

Holotype CPC39529, paratypes CPC39530-39592, all from locality GOU49.

Horizon

Topmost O'Briens Creek Member, Yass Formation.

Age

Probably Homerian (late Wenlock), possibly earliest Gorstian (early Ludlow).

Description

Juvenile shells (taken as Ws ≤6.0 mm - see Fig. 4b) lenticular, biconvex to ventribiconvex, elongate lacriform to lozenge-shaped (mean juvenile Ls/Ws 1.10, mostly 1.0-1.2), generally relatively thin (mean juvenile Ts/Ws 0.43, mostly 0.35-0.50). Adult shells (Ws >6 mm) subtriangular to subpentagonal, biconvex to slightly ventribiconvex, largest shells globose (mean adult Ts/Ws 0.55, max. 0.85). Maximum observed width 12.2 mm; length about equal to width (mean adult Ls/Ws 1.01, mostly 0.9 - 1.1). Dorsal fold and ventral sulcus appear at lengths of 3-4 mm, generally shallow, but variably developed anteriorly in larger shells; tongue when developed trapezoidal. Ventral beak suberect, sharp (especially in juveniles), usually small but in some shells extended posteriorly. Foramen mesothyrid (Fig. 1h), delthyrium wide, deltidial plates narrow, disjunct. Umbones smooth, ribs appearing at Ls from 2.5 to 5 mm, initially faint. Ribs anteriorly rounded-angular, simple, generally low (especially laterally); margins of sulcus defined by pair of relatively well developed ribs, sulcus contains 1-3 ribs (2-4 on fold); 2-5 ribs on each flank.

Shell generally thin-walled. Dental plates short, upright to gently convergent ventrally, somewhat concave medially. Ventral muscle field elongate, moderately impressed into slightly medially thickened shell, may be divided by very low myophragm. Dorsal median septum long (at least Ls/2), posteriorly supports small V-shaped septalium (Fig. 3) which is open posteriorly, covered mid-length to anteriorly (see Fig. 2, especially CPC39544, sections 1.2 to 1.8 mm). Outer hinge plates wide, flat in narrow zones between crural bases and inner socket ridges, moderately thick medially and generally strongly thickened beneath sockets. Sockets widely divergent, large; inner socket ridges robust, outer socket ridges merged with valve walls. Crural bases strong, triangular; crura calciform, curved somewhat towards ventral valve. No cardinal process.

Remarks

This form differs from leiorhynchids in its generally thin-walled shell which is mostly not globose, in its only moderately impressed ventral

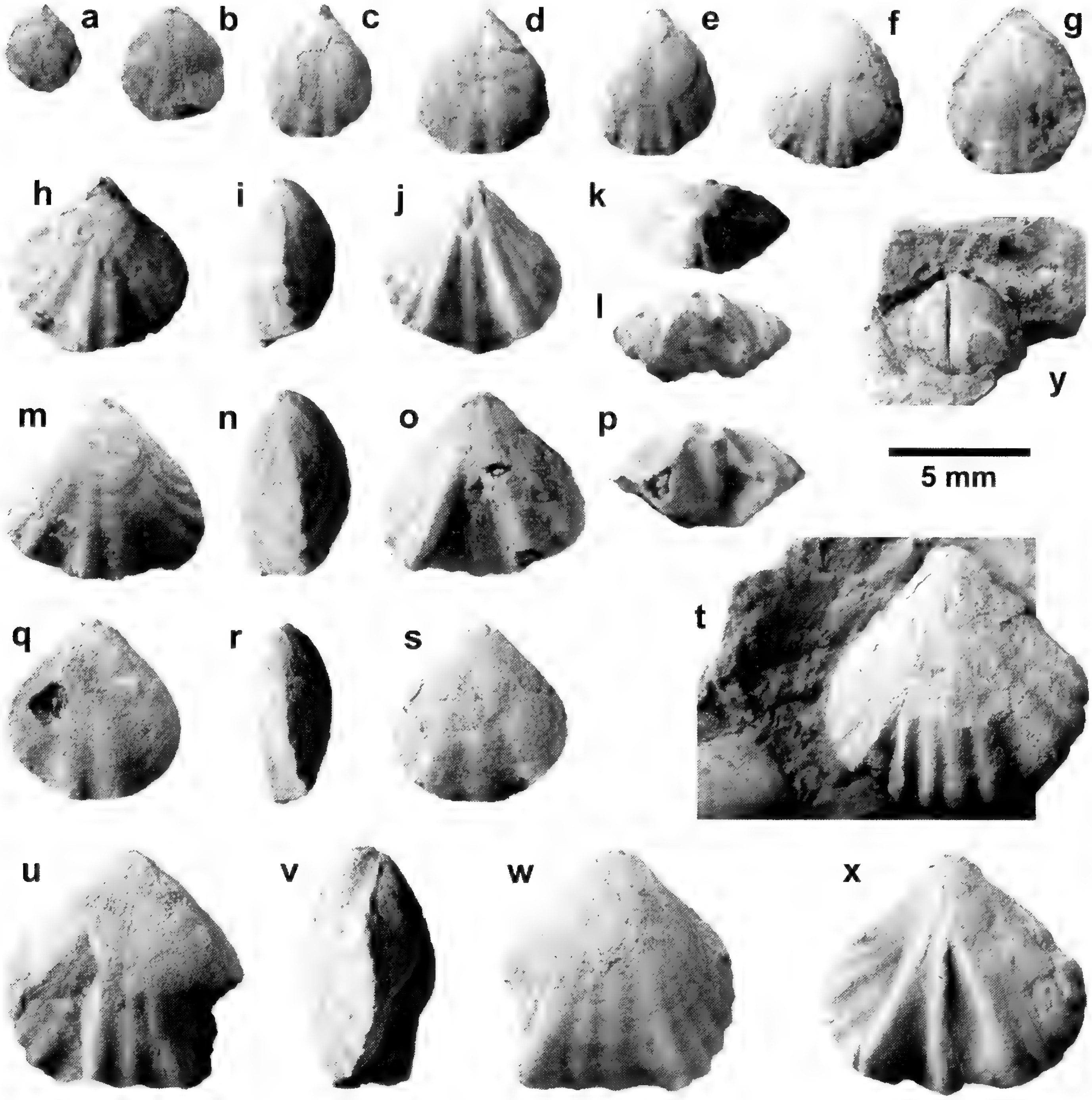

Figure 1. ***Agarhyncha australe*****; a-g, growth series of paratype shells in dorsal aspect, CPC39535, 39536, 39537, 39540, 39539, 39541, 39538; h-l, holotype CPC39529 in dorsal, lateral, ventral, posterior and anterior aspects; m-p, paratype CPC39532 in dorsal, lateral, ventral and anterior aspects, a partly decorticated relatively wide shell with anteriorly well developed fold; q-s, paratype CPC39533 in dorsal, lateral and ventral aspects, a posteriorly decorticated shell with low convexity, few subdued ribs; t, paratype CPC39543, a large shell in ventral aspect, with 4 anteriorly strong ribs in sulcus; u-w, paratype CPC 39534 in dorsal, lateral and ventral aspects, a posteriorly decorticated large shell showing local crushing, presumably before lithification of the enclosing sediment; x, paratype CPC 39542, a large relatively wide shell in ventral aspect; y, paratype CPC39592, a dorsal internal mould (see Fig. 3). All x4, scale bar 5 mm. Locality GOU49, Yass Formation, O'Briens Creek Member immediately below Cliftonwood Limestone; probably Late Wenlock.**

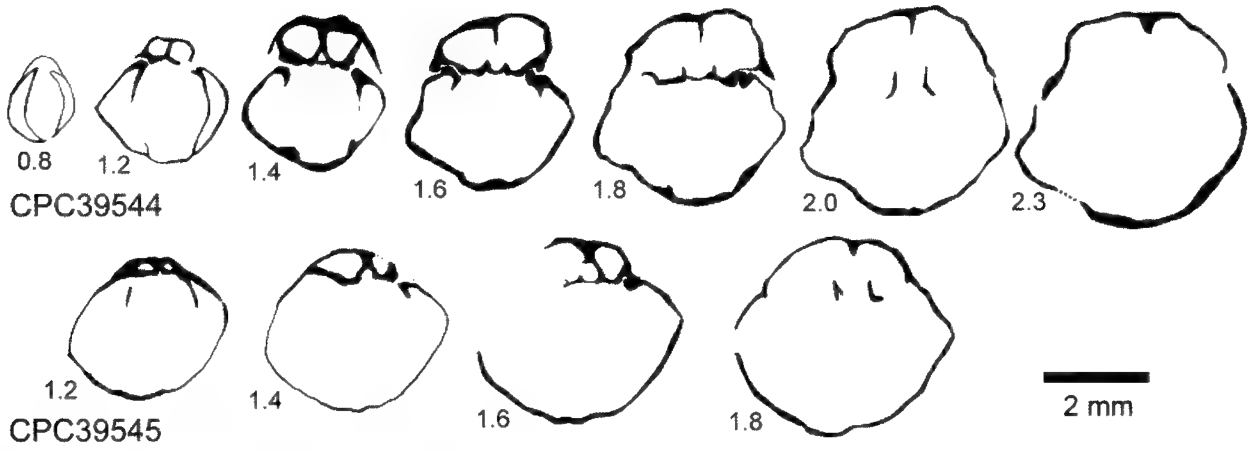

Figure 2. ***Agarhyncha australe*; selected serial sections of paratypes CPC39544, 39545; distances from posterior ends in millimetres. Scale bar 2 mm.**

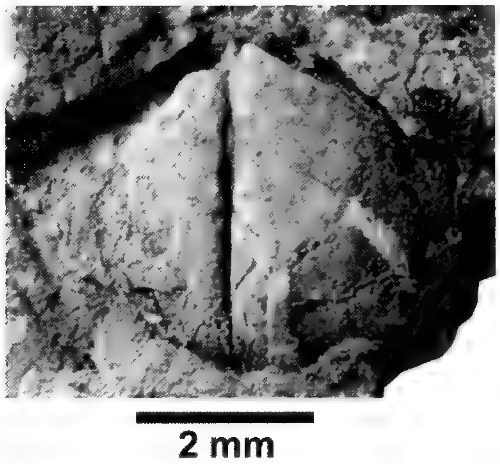

Figure 3. ***Agarhyncha australe*; paratype dorsal internal mould CPC39592 enlarged to show septalium and long but low median septum. Scale bar 2 mm.**

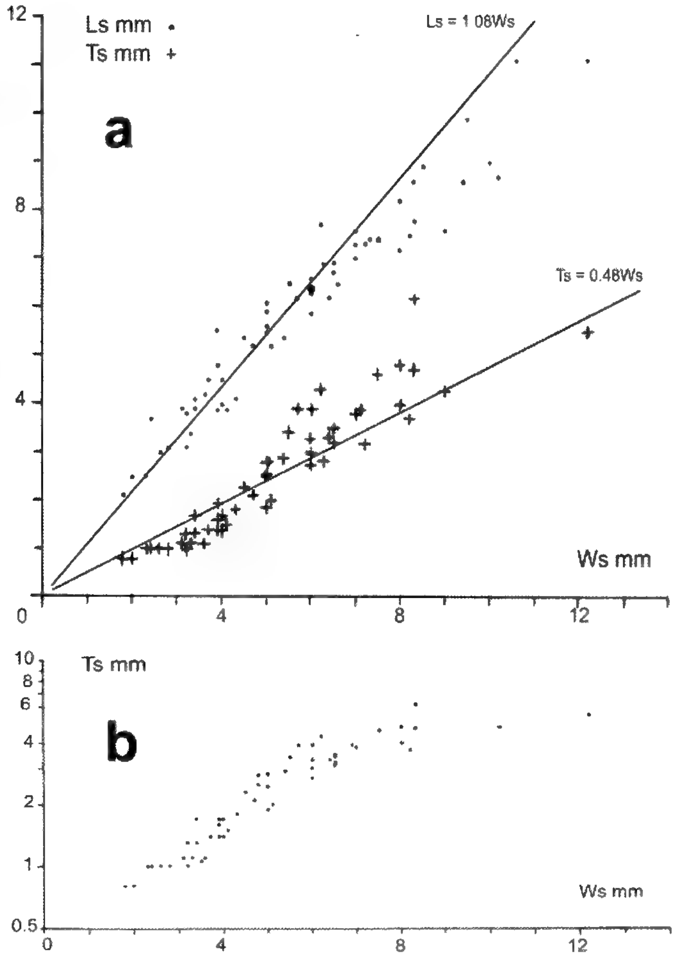

Figure 4. ***Agarhyncha australe*; a, length (Ls) and thickness (Ts) plotted against width (Ws). The divergence from the overall means at widths above 6 mm is just noticeable on these plots; b, thickness (Ts) plotted against width (Ws) on log-normal coordinates; in this plot the change in growth parameters at a width of about 6 mm is quite clear.**

muscle field, and a cover plate on the septalium. From rhynchotrematids it differs in its smooth umbones, distinct dental plates and lack of a cardinal process. It shares important features with the Trigonirhynchiidae. Among trigonirhynchiids *Astua* Havlíček, 1992 (Lochkovian, Bohemia and central Asia) differs in stronger ribs, fold and sulcus, an emarginate anterior commissure, and internally in lacking a cover-plate on the septalium. *Oxypleurorhynchia* Plodowski, 1973 (Přídolí, Carnic Alps) is dorsibiconvex, with coarse ribs and pronounced fold and sulcus extending from the umbones. *Virginiata* Amsden, 1968 (Llandovery to Ludlow, N. America, China and Siberia) lacks fold and sulcus, but its ribs extend from the beaks; it also differs in being more elongate, having a posterior cover-plate on the very small septalium, robust cardinalia, and a short dorsal median septum. The new species is referred to the Bohemian Wenlock to Ludlow genus *Agarhyncha* on the basis of its smooth umbones, short dental plates, and medially to anteriorly covered septalium.

The Ludlow-age type species, *Agarhyncha famula* (Barrande, 1847) is smaller (Ws to c. 9.6

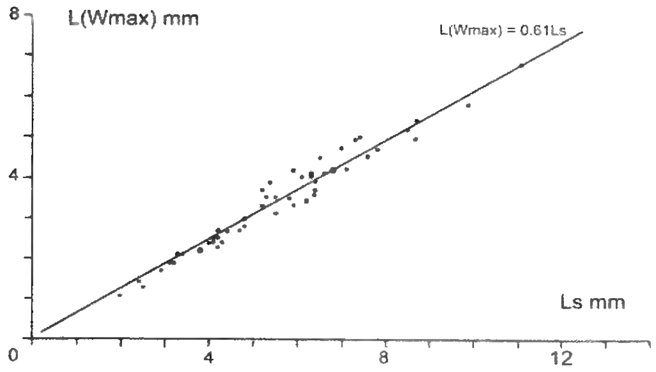

Figure 5. *Agarhyncha australe*; plot of length to greatest width (L(Wmax)) against length (Ls), showing only weak variability.

mm), more globose, with in some cases anteriorly truncated margins, often posteriorly elongate ventral beak, stronger ribs which may be flattened and grooved marginally, shallower sulcus, ribs at least faintly developed umbonally, high dorsal median septum, and rod-like crura. The Wenlock species *A. agason* Havlíček in Havlíček and Štorch, 1990 is of comparable size and outline, but has more and stronger, more angular ribs, especially medially. The other Bohemian Ludlow species, *A. chuchlensis* Havlíček in Havlíček and Štorch, 1990 is wider (Ls/Ws 0.83-0.95), with generally subpentagonal outline, low, rounded beak, weakly ribbed umbones, anteriorly well developed fold and sulcus, more ribs, ventral muscle field not impressed but dorsal adductor field with fine lateral bounding ridges, rod-like crura, and somewhat shorter dorsal median septum. None of the Bohemian species shows medially concave dental plates.

Family ORTHORHYNCHULIDAE Cooper, 1956

Genus *Tuvaerhynchus* Kulkov, 1985

Type species

Tuvaerhynchus khalfini Kul'kov in Kul'kov et al., 1985, by original designation; Wenlock, Tuva.

Diagnosis

Small with subpentagonal to subrectangular outline and dorsibiconvex profile. Beak suberect; delthyrium with disjunct deltidial plates. Fold and sulcus strong, narrow, well defined, from umbones; anterior commissure uniplicate; tongue high, trapezoid, dentate. Costae numerous, simple, angular. Dental plates short, vertical, close to valve wall. Septalium short, wide; hinge plates concave, slope medially; cardinal process septiform, thin; crura short, curved sharply ventrally (Savage p. 1081 in Savage et al. 2002).

Tuvaerhynchus? sp.

Fig. 6, Table 2

Material

Yass Formation: GOU47, CPC 39595 and 1 very uncertain fragment; GOU49, CPC 39596. *Barrandella* Shale Member, Silverdale Formation: GOU2a, CPC 39593. Lower Black Bog Shale: KF, ANU46537. Yarwood Siltstone Member, Black Bog Shale: GOU28, CPC 39594. Horizon uncertain: Bowning, "Upper Conglomerate", Mitchell Collection AMF28588, 133959 - presumably (following Mitchell 1887) from pebbles in the Sharpeningstone Conglomerate, derived from an older horizon.

Stratigraphic distribution

Yass Formation to Yarwood Siltstone Member, Black Bog Shale

Age

Late Wenlock? to early Ludfordian

Description

Available specimens are few, and mostly poorly preserved. Best are a steinkern from the Mitchell Collection, and a small shell from GOU47. Both are dorsibiconvex, with rounded outline; the small shell (CPC 39595, Ws 6.2 mm) is longer than wide (Ls/Ws ca 1.16), the steinkern (AMF28588, Ws ca 12 mm) transversely oval (Ls/Ws ca 0.8). They are globose - in both cases Ts/Ls is about 0.7. They are strongly ribbed, the ribs starting at the beaks. CPC 39595 has a shallow ventral sulcus with 3 ribs, there being 5 ribs on each flank. AMF28588 has a well developed fold and sulcus, forming a high trapezoidal tongue anteriorly; the sulcus contains 3 ribs, the flanks 5 ribs each, and the fold is formed of 2 ribs which split once. The other Mitchell Collection specimen, AMF133959, is an incomplete flattened internal mould with 4 ribs in the sulcus, 6 on each flank. Inter-rib furrows extend as short marginal spines. None of the specimens shows clear details of the ventral beak, and so the presence and nature of a delthyrium cannot be demonstrated.

Large teeth are supported by fairly short but distinct dental plates which are somewhat convergent towards the valve floor. Details of the ventral muscle field are not known. Dorsal median septum long, low, fine, continuous with linear cardinal process which arises from a shallow septalium which is either sessile or nearly so. Crural bases robust, crura unknown.

Discussion

Among Silurian rhynchonellides, the general

	Ls	Ld	Ws	Ts	L(Wmax)	Ls/Ws	Ts/Ws
CPC39529*	6.2	5.6	6.4	3.3	3.4	0.97	0.52
CPC39530	5.9	5.5	6.0	3.9	3.3	0.98	0.65
CPC39534	*9.0*	-	*8.9*	5.0	*5.2*	*1.01*	0.56
CPC39538	5.9	5.4	5.0	2.5	4.0	1.18	0.50
CPC39543	9.9	-	9.6	-	5.5	1.03	-

Table 1: *Agarhyncha australe*: dimensions in mm and proportions of holotype (*) and selected paratypes. Measurements in italics are best estimates for damaged specimens.

	Ls	Ws	Ts	L(Wmax)	Ls/Ws	Ts/Ws
AMF28588	9.7	12.0	7.0	*4.8*	0.81	0.58
CPC39593	*10.5*	*9.5*	5.3	*5.5*	*1.11*	*0.56*
CPC39595	*7.2*	6.2	5.1	*4.0*	*1.16*	*0.82*
ANU46537	*7.5*	*8.0*	-	*5.5*	*0.94*	-

Table 2. *Tuvaerhynchus*? sp.: dimensions in mm and proportions of selected specimens. Measurements in italics are best estimates for damaged specimens.

shell form and strong simple ribbing of this form, coupled with distinct but short dental plates and a linear cardinal process on a sessile or near-sessile septalium, points to the Orthorhynchulidae (whose genera are also united by possessing an open or near-open delthyrium). *Orthorhynchula* Hall and Clarke, 1893, has dental plates fused to the valve walls, and a low fold. The Tasmanian Ordovician *Tasmanella* Laurie, 1991, has a high fold, but differs in its fused dental plates, and a short, high dorsal median septum supporting a raised septalium. *Tuvaerhynchus* is closest morphologically, but in the absence of details of delthyrium, deltidial plates, and crura, generic identity cannot be certain. In the absence of that certainty, palaeobiogeographic speculation on this possible link between the *Tuvaella* and *Retziella* Faunas of Rong et al. (1995), and thus the Mongolo-Okhotsk and Sino-Australian Provinces of the Uralian-Cordilleran Region, is pointless.

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I thank Ian Percival and Norman Savage for reviewing this paper, and Prof. Brian Kennett, Director of the ANU Research School of Earth Sciences, for continuing provision of facilities in the Department of Earth and Marine Sciences within that School. Serial sectioning was made possible by the loan of a Croft Parallel Grinder from the Geological Survey of New South Wales. Photography by H.M. Doyle (formerly of Geoscience Australia) and the author.

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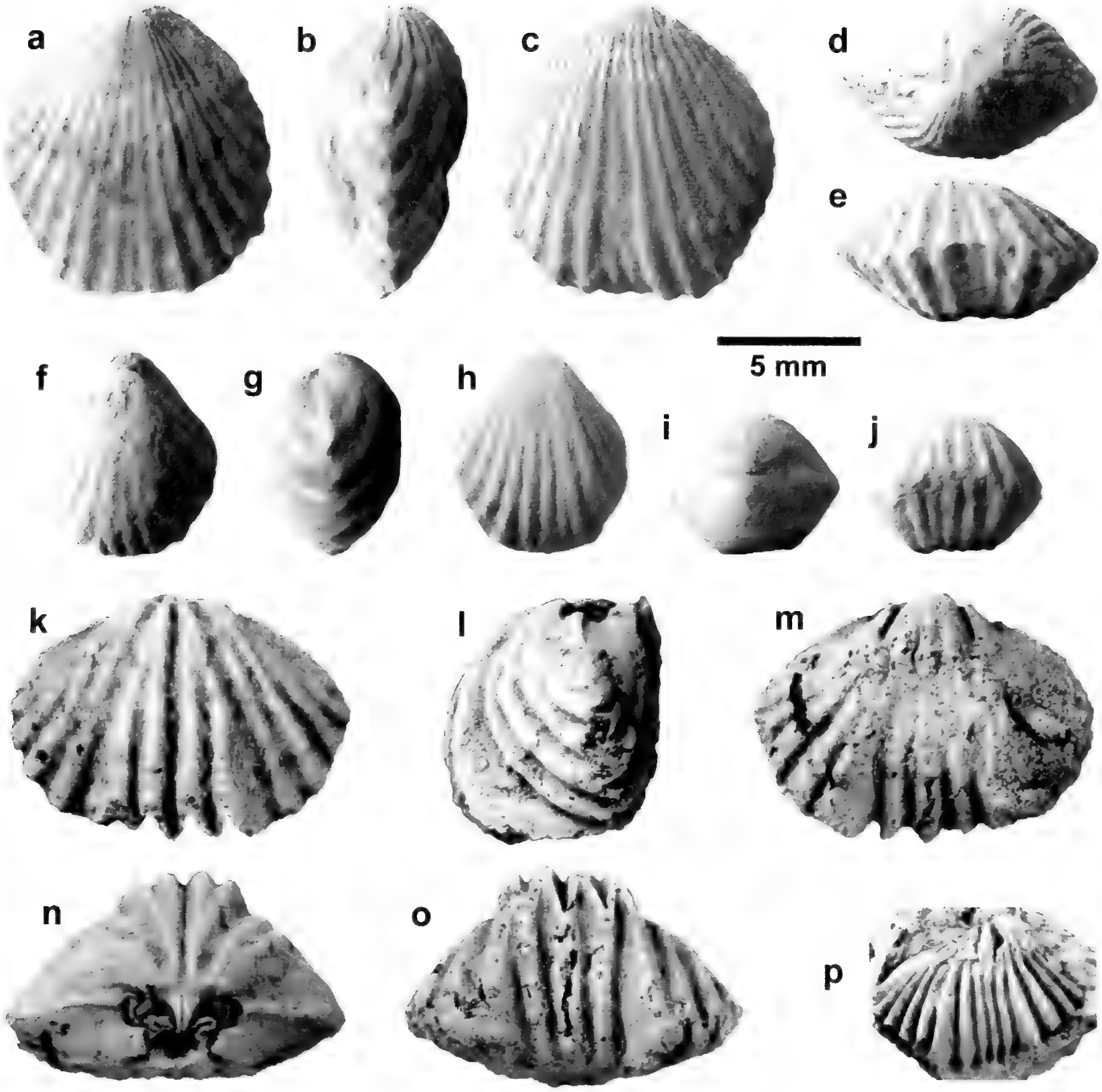

Figure 6. ***Tuvaerhynchus*? sp.; a-e, CPC39593, a slightly crushed lenticular shell in dorsal, lateral, ventral, posterior and anterior aspects (locality GOU2a, Barrandella Shale Member, Silverdale Fm, late Gorstian); f-j, CPC39595, a shell in dorsal, lateral, ventral, posterior and anterior aspects, the dorsal umbo worn and revealing the median septum (locality GOU47, topmost O'Briens Creek Member, Yass Fm, probably Late Wenlock); k-o, AMF28588, a wide and very globose steinkern in dorsal, lateral, ventral, posterior and anterior aspects, the ventral beak broken (Mitchell Collection, from pebble in Sharpeningstone Creek Conglomerate); p, AMF133959, somewhat crushed ventral internal mould (source as AMF28588). All x4, scale bar 5 mm.**

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Cortinarius Fr. Subgenus *Cortinarius* in Australia

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Wood, A.E. (2009). *Cortinarius* Fr. subgenus *Cortinarius* in Australia. *Proceedings of the Linnean Society of New South Wales* **130,** 147-155.

Three new species within *Cortinarius* subgenus *Cortinarius* from Australia are described, each belonging near a different species, but differing significantly from the type variety in all cases. They represent distinct species – *C. jenolanensis, C. kioloensis and C. hallowellensis.*

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Keywords: agarics, *Cortinarius,* distribution, mushrooms, new varieties, toadstools

INTRODUCTION

Cortinarius subgenus *Cortinarius* is characterised by the presence of fleshy carpophores, with a cap that is frequently squamulose, large conspicuous cheilocystidia and vacuolar, mostly violet, pigments. The spores show both a suprapilar plage, usually flattened and often more or less smooth.

There have been scattered records of this subgenus, particularly *C. violaceus* from Australia. This species was reported from Victoria by Cooke (1892) and this report was carried forward by McAlpine (1895) and Brittlebank (1940). Cleland (1933, 1934) did not record the species, nor did Grgurinovic (1997) record it from South Australia. Shepherd and Totterdell (1988) recorded the species from the Australian Capital Territory, New South Wales and Victoria. Young (1994) also recorded the species from New South Wales and Victoria. This species was also recorded from Western Australia by Griffiths (1985), Hilton (1988) and Syme (1992) and more recently was fully described by Bougher and Syme (1998). All these records are for *C. violaceus*, in some cases with uncertainty being expressed as to whether the collections are identical with the European species. Recently a new species, *Cortinarius austroviolaceus* has been described from Tasmania by Gasparini (2001).

There have been some recent studies on *C. violaceus* in Europe and now two species are widely recognised, *C. violaceus* and *C. hercynicus* (Brandrud 1983; Brandrud *et al.* 1989-1998). The study by Moser (1986) of some collections from the SW-Pacific area has added four more species to the subgenus *C. atroviolaceus, C. subcalyptrosporus, C. atrolazulinus* and *C. paraviolaceus*. In view of the diversity of taxa of the subgenus in the SW Pacific, the suggestion has been made that they represent the descendants of a Gondwanan species of possibly ancient origin (Gasparini, 2001). However the subgenus has not been reported from Tierra del Fuego (Horak 1979) or in other areas of South America (Moser and Horak 1975). *Cortinarius violaceus* s.s. Montagne, (from Chile, see Horak, 1979) is a different, unrelated species, *Cortinarius gayii* Horak (see Horak, 1979, p. 396 with full description).

There has been considerable discussion over many years as to whether *Cortinarius violaceus* is a single species in Europe or whether several taxa at some close level (species, subspecies or variety) are involved. Some claim that over a large number of collections, a continuous variation can be found between the two main forms. However many now recognise two distinct forms, though the level at which they should be considered is also disputed. The view taken here (following Moser (1983), Horak (2005), Breitenbach & Kranzlin (2000) and Knudsen &Vesterholt (2008)) is to recognise two separate species from Europe as follows :

Cortinarius violaceus with spores (12)13-16(17) x 7-8(8.5) µm, elliptic to amygdaliform, verrucose, cap mostly 6-14 cm, under deciduous woods;

Cortinarius hercynicus with spores (12)13-16(17) x 7-8(8.5) µm, broadly ellipsoid to subglobose, strongly verrucose, cap mostly 5-10 cm, under coniferous woods (spruce, pine, sometimes mixed woods).

Most records are only from the latter part of the twentieth century (May and Wood, 1997). The records are probably accurate because of the distinctive characteristics of *Cortinarius violaceus* s.l., but they give no information as to which of the currently reported species are intended. Later records indicate that the subgenus is widespread throughout most of Australia, but that it is not collected frequently.

Studies of DNA sequences of various species of *Cortinarius* concluded that there were grounds for considering the creation of two separate genera (Hoiland and Holst-Jensen, 2000). A later study of DNA sequences for a large range of *Cortinarius* species (Garnica et al, 2005) supported the *Cortinarius* clade, without any further additions of any closely related groups or species. Bougher and Syme (1998) used the epithet *C. violaceus* with some reservations for their local collections. Chambers et al. (1999) compared DNA from New South Wales material with reported sequences from Northern Hemisphere collections of *Cortinarius violaceus,* and reported that the local material while close, belonged to a different taxon and noted 'a careful revision of Australian *Cortinarius violaceus* collections is clearly required'. Unfortunately, voucher material of these collections has not yet been available.

Examination of material from mainland Australia has demonstrated close similarities to the European species but with some clear differences. All the Australian material does not belong to a single species but represents four different taxa of which three are new. The differences described below clearly indicate three distinct taxa, related to previously described species. The differences are sufficient to require the creation of three new species.

MATERIAL AND METHODS

Material was mounted in 5% KOH solution and stained with Congo Red. Specimens are housed in the J.T.Waterhouse Herbarium, University of New South Wales (UNSW), except for Western Australian material, which is in the Western Australian Herbarium (PERTH). The collections at UNSW all have extensive field notes and colour photographs taken under standard conditions.

Spore measurements indicate the range of sizes found in the various collections. Where spore sizes are included in brackets, they indicate that the spore sizes were more than one measuring unit (0.3 µm) beyond the range for all other spores. The value Q represents the mean length:breadth ratio of the spores. Measurements of Q were averaged for a collection and where a range is quoted it represents the range across collections. Measurements of the spores exclude the apiculus and the ornamentation. Measurements of cystidia indicate length and maximum width. Measurements of the basidia exclude the sterigmata.

Colours are usually followed by an annotation from Maerz and Paul (1950) and have a format such as 10D3. All colour comparisons were made under natural light.

The figures show the microscopic features at standard magnification: spores x2000, cystidia and basidia x1000. The scale bar represents 10 µm at x2000 magnification.

Key to the SW-Pacific species of C*ortinarius* subgenus *Cortinarius*

1. Average basidiospore length less than 10 µm, cheilocystidia not capitate..............................2
1* Average basidiospore length more than 10 µm 3
2. Cheilocystidia 50-140 x 10-25 µm, pleurocystidia scarce, 40-100 x 10-18 µm, lanceolate.........................*C. atroviolaceus*
2* Cheilocystidia 30-48 x 4-7 µm, pleurocystidia absent..............................1.*C. jenolanensis*
3. Cheilocystidia capitate..........*C.austroviolaceus*
3* Cheilocystidia not capitate or absent..............4
4. Spores with visible perispore ....*C. subcalyptrosporus*
4* Spores without visible perispore....................5
5. Cheilocystidia absent, pleurocystidia rare...... ....*C. paraviolaceus*
5* Cheilocystidia present....................................6
6. Spores large, at least up to 12 µm long, mostly up to 16 µm in length.......................................7
6* Spores smaller, at most up to 12 µm long, slender, Q 1.86, cheilocystidia lageniform, 45-70 x 12-20...............................*C. atrolazulinus*
7. Spores ellipsoid to amygdaliform..................8
7* Spores broadly ellipsoid to subglobose...........9
8. Spores elongate Q=1.87, width narrow, 6.3-7.5 µm; cheilocystidia 50-60 x 10-12 µm, pleurocystidia frequent, similar................. ....2.*C. hallowellensis*
8* Spores shorter Q=1.56, width broader 7.5-8.5 µm; cheilocystidia 35-80 x 15-25 µm, pleurocystidia frequent, similar..... *C. violaceus*
9. Spores 11-13 x 8-9 µm, Q=1.45; cheilocystidia 55-80 x 14-19 µm, lageniform............................*C. hercynicus*

9* Spores 11-14 x 8.1- 9.3 µm, Q=1.40; cheilocystidia 45 – 120 x 14-17 µm, lageniform ……………………..…………..3.*C. kioloensis*

1. *Cortinarius jenolanensis* Wood, sp. nov. (Fig. 1: a-d)

Pileo usque ad 4 cm lato, convexo, demum plano, obscure violaceo, sicco, subtiliter fibrillo-squamoso. Lamellis obscure violaceis, brunnescentibus. Stipite 5-6 cm longo, 5-8 mm crasso, sicco, appresse fibrilloso, pallidiori violacea. Sporis 8.4 – 10.2 x 5.7-6.9 µm, Q=1.55, ellipsoideis, subtiliter verrucosis, cheilocystidiis sparsis, lageniformis 30-48 x 10-14 µm, absentibus pleurocystidiis, absentibus pileocystidiis. Hyphis fibuligeris. Habitato in humo in silvis *Eucalyptus* mixtis.

Pileus to 4 cm, hemispherical at first, then convex to flat convex and finally plane, very finely to a little coarsely radially fibrillose, deep violet, dry, not

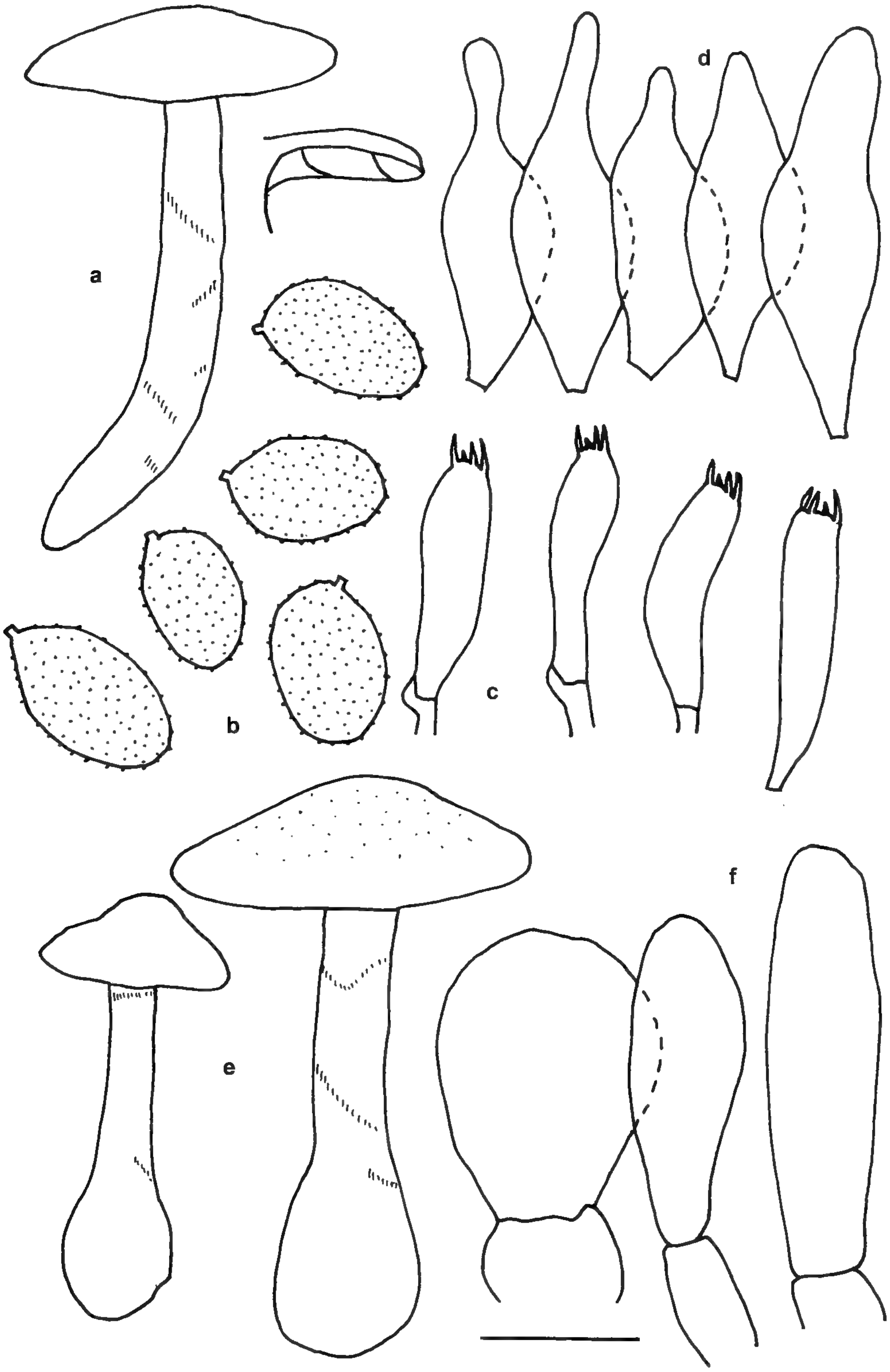

Figure 1. ***Cortinarius jenolanensis*** **(UNSW 88/107) : a. basidiome (x 1); b.spores; c.basidia; d. cheilocystidia;** ***Cortinarius kioloensis*** **(UNSW 83/781) e. basidiome(x 1) f. pileocystidia.**

hygrophanous. Lamellae broadly adnate to slightly decurrent, thin, crowded, with one to two series of lamellulae, deep violet then deep ferruginous, margin concolorous. Stipe 50-60 x 5-8 mm, central, firm to tough, equal to slightly swollen below, sometimes slightly tapering at the base, upper part cap coloured or slightly paler, lower part a little paler with base pale violet, with no obvious basal mycelium, and no clear zone of velar remains. The only velar remains were a few scattered appressed fibrils throughout with only small areas or groups.

Aroma

There is no apparent aroma.

Spores

8.4-10.2 x 5.7-6.9 μm, mean 9.44 x 6.09 μm, mean Q = 1.55, oval, suprahilar depression not clearly present and not clearly smooth, ornamentation low to very low, a little blunt, not anastomosing. Basidia 25-32 x 11-14 μm, clavate, four-spored; clamp connections present. Cheilocystidia fairly sparse, variously lageniform (some somewhat irregular) 30-48 x 10-14 μm, pleurocystidia absent. Pileal cuticle a loose layer of narrow hyphae, each 4-7 μm diameter, not encrusted with pigment, mainly radially arranged and repent, a few a little irregularly loose and more or less upright with rounded terminal cells but not specialised as pileocystidia. Below this layer was a densely packed layer of parallel hyphae, the layer about 40-50 μm thick with individual hyphae of 4-10 μm diameter. Below this layer was a layer of interwoven hyphae, somewhat compact, of pale golden hyphae with individual hyphae of 5-8 μm diameter.

Habitat

On soil in eucalypt sclerophyll forest.

Commentary

This species is different from all the species described by Moser (1987) because of the smooth pileus, different structure of the cuticle, absence of pleurocystidia, without amorphous deposits and also by being of smaller general size and lacking aroma.

It is close to the typical forms of *Cortinarius atroviolaceus* but differs in having slightly smaller spores which are more finely rough and lack a clearly visible plage, the complete absence of pleurocystidia and smaller cheilocystidia. It may be that Corner Collection RSNBB 5258B, noted by Moser(1987), which has finer ornamentation on the spores and smaller cheilocystidia, also represents this species. *Cortinarius austroviolaceus* is also close, but that species has cheilocystidia that are regularly slightly capitate and are more variable otherwise, and it also has a different cuticle with occasional lanceolate (lageniform) terminal cells. (See Moser 1987, pp 139,140).

Material Examined

NSW : Jenolan Caves, Binda Cabins, Eucalypt woodland, 30.4.88, A.E.Wood et al. (UNSW 88/107) Holotype; ACT, Canberra, Tidbinbilla Nature Reserve, Eucalypt woodland, 16.5.92, A. E. Wood et al. (UNSW 92/121).

2. Cortinarius kioloensis Wood, sp. nov. (Fig. 1: e,f; 2: a-c)

Pileo usque ad 6 cm lato, convexo, demum plano, obscure violaceo, sicco, fibrilloso-squamoso. Lamellis obscure violaceis, brunnescentibus. Stipite 8-12 cm longo, 15 mm crasso, basi clavatus usque ad 30 mm crasso, sicco, appresse fibrilloso, pallidiori violacea. Sporis 11.1 - 13.5 x 8.1 – 9.3 (10.5) μm ellipsoideis. verrucosis, cheilocystidiis lageniformis, 45-120 x 14 –19 μm, pleurocystidiis sparsis, lageniformis 45 –113 x 15 –26 μm, pileocystidiis cylindricis vel fusiformis 35-60 x 13 –28 μm. Hyphis fibuligeris. Habitato in humo silvis *Eucalyptus* mixtis.

Pileus to 6 cm diam., rounded convex at first, then rounded umbonate to convex, finally almost plane with age, strongly fibrillose to a little tomentose to finely squamulose, more adpressed with age, deep violet (48H11–12), becoming blackish with age, dry, not hygrophanous. Lamellae narrowly to broadly adnate to slightly sinuate, thin to moderately thick, somewhat spaced, one or two sets of lamellulae, dark violet at first, then gradually deep ferruginous, margin concolorous. Stipe central, firm, solid, bulbous at base, 8–12 x 1.5 cm, base 3 cm, dry, mostly with clear fibrillar velar zone and scattered fibrils below, violet above, somewhat paler than cap, a little paler below (to 46E6 - 17E4), basal bulb globose, concolorous. Flesh whitish to pale violet, outer layer of stem dark violet, deep violet at apex of stipe.

KOH (5%) on cap bright red.

Aroma

Clearly absent even when quite young and fresh; one collection with slight aroma of wood shavings (but not camphor wood).

Spores

11.1–13.5 x 8.1–9.3 (10.5) μm, mean 12.5 x 8.8 μm, Q = 1.37–1.46, grand mean Q = 1.42,

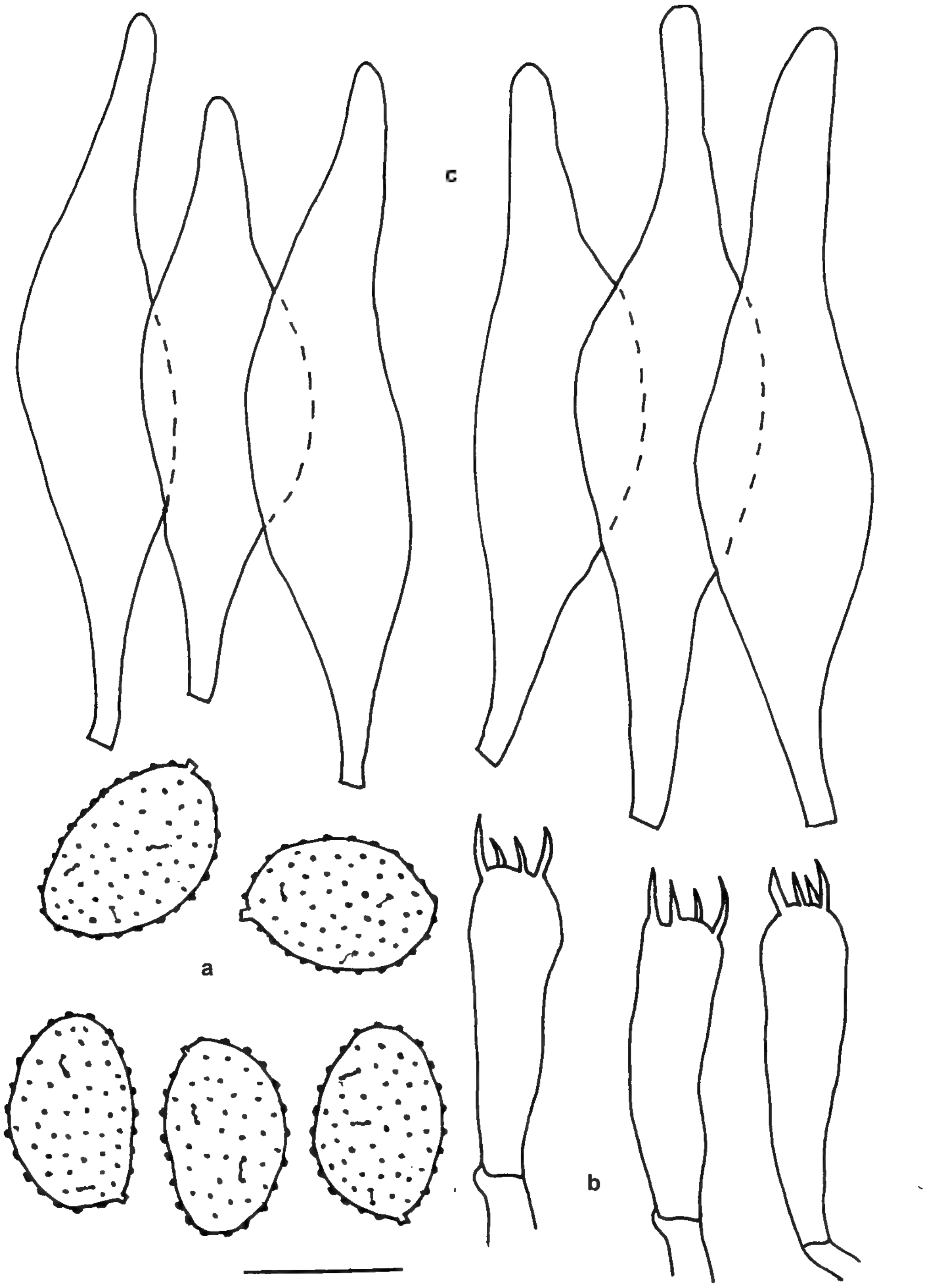

Figure 2. ***Cortinariu kioloensis*** **(UNSW (83/781) : a. spores; b. basidia; c. cheilocystidia**

ovoid to elliptic, suprahilar depression not marked but present in some cases, but not clearly smooth, ornamentation moderate, coarse, blunt, with some slight anastomosing. Basidia 35–50 x 10–12 µm, four-spored; clamp connections present. Cheilocystidia abundant, ventricose to lageniform, 45–120 x 14–19 µm; pleurocystidia sparse but clearly present, similar to cheilocystidia, but with some a little fusoid, 45–113 x 15–26 µm. Pileal cuticle a layer of loose hyphae with upturned terminal cells which are somewhat inflated, swollen or cylindrical, 35–60 x 13–28 µm; subcuticular layer of subcellular cells, 30–40 µm diameter, walls not coloured, below this a narrow layer of somewhat inflated, closely packed hyphae, 20–25 µm diameter, with coloured contents, below this the context was of loosely arranged somewhat inflated hyaline hyphae, 15–25 µm diameter.

Habitat

On soil in eucalypt sclerophyll forest.

Commentary

This species is different from the typical forms of *Cortinarius violaceus* and *C. hercynicus* and from all the other species described by Moser (1986). It is distinct because of the different habit, absence of aroma, relative scarcity of pleurocystidia, presence of pileocystidia and spores which are without a well-differentiated plage and have less well developed wall ornamentation. There are also some slight differences in the size and shape of the spores. In this species, the size and shape are nearer to that found in *Cortinarius hercynicus* rather than that found in *Cortinarius violaceus* but the shape seems distinctly different from that of spores of *Cortinarius hercynicus* in that the spores are broadly ellipsoid rather than distinctly amygdaliform. Because of all these features it is regarded as a distinct taxon and is described as a new species of *Cortinarius* near to C. *hercynicus.*

Material Examined

NSW: Sydney, Scotland Island, Eucalypt woodland, 22.6.80, S. Lowry, (UNSW 80/268); Batemans Bay, Kioloa State Forest, Eucalypt woodland, 19.5.83, A. E. Wood & J. J.Bruhl, (UNSW 83/781) Holotype; Sydney, Royal National Park, Eucalypt woodland, 5.6.83, F. K. Taeker, (UNSW 83/923);Batemans Bay, Kioloa State Forest, Higgins Creek, Eucalypt woodland, 15.5.84, A. E. Wood & N. B. Gartrell, (UNSW 84/495); Sydney, Royal National Park, Couranga Track, Eucalypt woodland, 28.5.86, F. K. Taeker, (UNSW 86/254); Sydney, Boronia Park, Eucalypt woodland, 27.5.90, R. Kearney, (UNSW 90/197); Hazelbrook, James Park, Eucalypt woodland, 30.5.92, A.E.Wood et al., (UNSW 92/206); Springwood, Sassafras Gully, Eucalypt woodland, 16.4.94, A. E. Wood et al.,(UNSW 94/47); Sydney, Sydney Harbour National Park, Bradleys Head, 7.6.98, B. J.& N. W. Rees, (UNSW 98/25); Sydney, Lane Cove Bushland Park, Gore Creek, Eucalypt woodland, 7.6.98, B. J. & N.W. Rees, (UNSW 98/28).

Authentic material from Sweden (Femsjo) was collected and at first was identified as *Cortinarius violaceus*. However later detailed examination clearly showed that it was a typical example of *Cortinarius hercynicus* and the following microscopic details are added for this collection (as *Cortinarius hercynicus var hercynicus*)

Spores

12.6-15.0 x 8.4-9.3 µm, mean 13.47 x 8.94 µm, Q = 1.51, spores elliptic, only vaguely amygdaliform, with only some spores showing a slightly flatter supra-hilar depression, but that mostly not smooth, ornamentation moderate, a little broad and only slightly blunt. Cheilocystidia frequent 75-85 x 13-19 µm, narrowly lageniform, pleurocystidia sparse but clearly present, lageniform, somewhat more variable, 50-90 x 12-20 µm. Pileal cuticle of closely packed and interwoven hyphae, layer 100-200µm deep, individual hyphae 5-7 µm diameter, without any terminal cystidia (Fig. 3).

Material Examined :

SWEDEN: Femsjo, woodland, 2.9.79, M.M.Moser & A.E.Wood, in UNSW(UNSW 79/29).

3. *Cortinarius hallowellensis* Wood, sp. nov. (Fig. 4)

Pileo usque ad 6 cm lato, convexo, demum plano, obscure violaceo, sicco, subtiliter fibrilloso-squamoso. Lamellis obscure violaceis, brunnescentibus. Stipite cylindrico vel clavato, 4-7 cm longo, 10-15 mm crasso, basi leviter, sicco, fibrilloso violacea. Sporis 11.1-12.0 x 6.3-7.5 µm, ovoideo-ellipsoideis, verrucosis, cheilocystidiis fusiformis vel lageniformis, 50-60 x 9-13 µm, pleurocystidiis fusiformis, 50-60 x 9-13 µm, absentibus pileocystidiis. Hyphis fibuligeris.

Habitato in humo in silvis *Eucalyptus* mixtis.

Pileus to 3.4-6.0 cm, rounded convex at first, flattening at maturity, finely radially fibrillose, very dark violet brown (16F4), not hygrophanous. Lamellae broadly adnate to adnate, thin, a little spaced, dark violet (16B5), more rusty with age, with two series of lamellulae. Stipe cylindrical to clavate, with a swollen base 3.7-7.0 x 1.0-1.5 cm, solid, dry, dark violet (16B4) with fine cobweb veil, rapidly disappearing (after Bougher & Syme 1988, colours from Kornerup & Wanscher, 1978).

Spores

11.1-12.0 x 6.3-7.5 µm, mean 11.49 x 6.81 µm, mean Q = 1.69, oval to elliptic, occasionally vaguely amygdaliform, with occasionally a slight supra-hilar depression, but not visibly smooth, ornamentation moderate, coarse, blunt. Basidia cylindrical to clavate, 40-55 x 10-12 µm, four-spored, clamp connections present. Cheilocystidia plentiful, narrow lageniform to fusoid, 50-60 x 9-13 µm, pleurocystidia sparse, but clearly present, similar to cheilocystidia, but mostly fusiform 50-60 x 10-12 µm. Pileal cuticle with a surface layer 35 -50(80) µm deep, a thin layer of loosely arranged hyphae, individual hyphae 2.5-5 µm diameter, mainly repent, with no erect hyphae and no differentiated terminal cells, without wall encrustation, some walls with pale golden walls; below this a layer of closely packed cylindrical hyphae of the trama (35-50 x 7-10 µm, some a little larger and a few pseudoparenchymatous cells present).

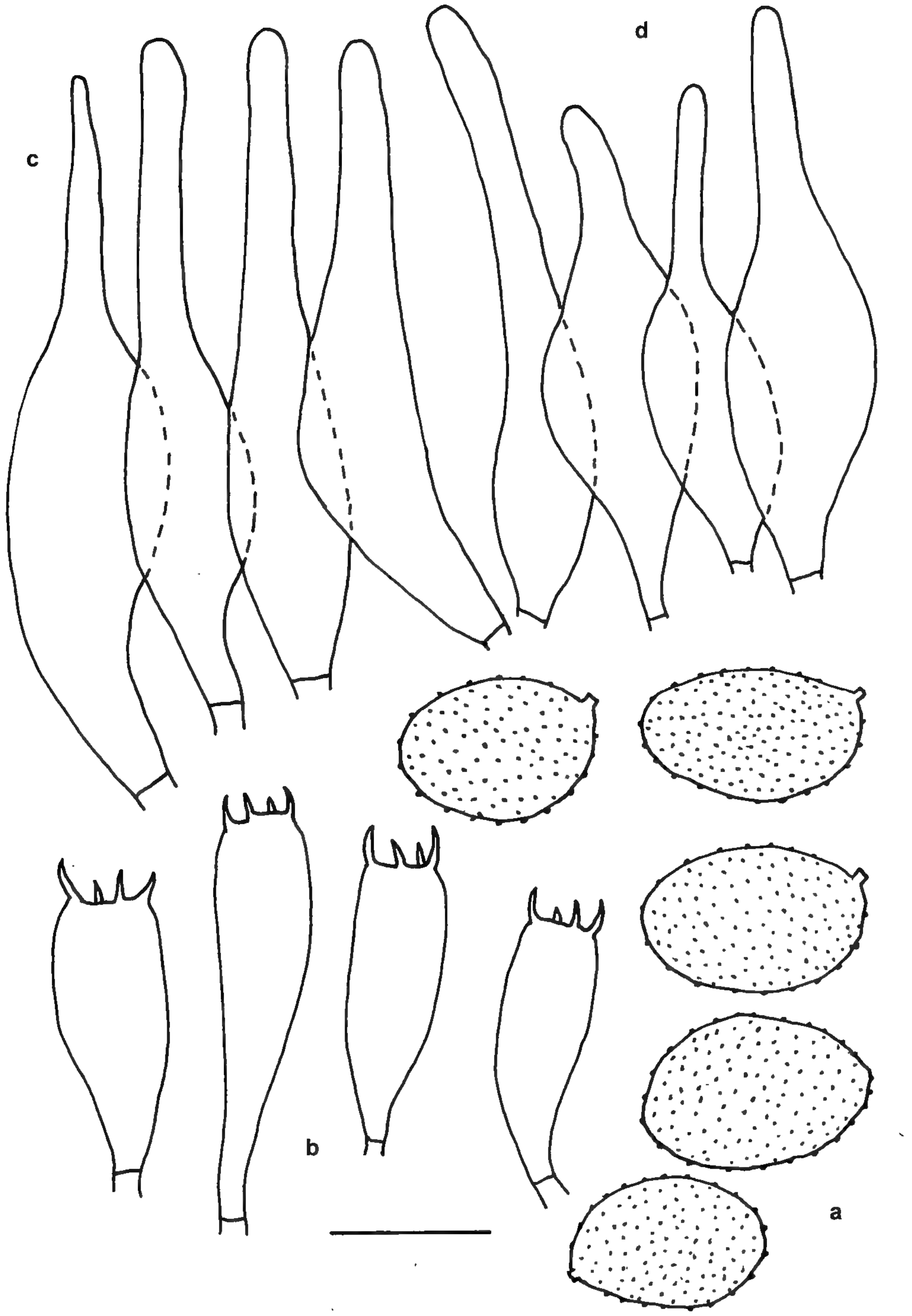

Figure 3. ***Cortinarius herycynicus*** **(UNSW 79/29) : a. spores; b. basidia; c. cheilocystidia; d. pleurocystidia**

Commentary

This species is different from the typical *Cortinarius violaceus* in that this species has oval to elliptic spores (Q = 1.69), rather than amygdaliform spores, the cuticle does not produce pileocystida, the cheilocystidia are narrower to fusiform and the general habit is much smaller. Hence it is regarded as a close, but distinct species.

Material Examined

WA: Denmark, Mount Hallowell Reserve, Eucalypt woodland, 22.5.93, K. Syme. (PERTH 0550 6794), Holotype.

Collection PERTH007775665 also seems to be this species. However it was collected in a *Pinus radiata* plantation. It has spores with size 12-13.8 x 6.6-7.5 µm, mean 13.14 x 7.02 µm, Q = 1.87, spores ovoid to elliptic, some vaguely amygdaliform, supra-hilar depression sometimes slightly present, but never clearly smooth. Cheilocystidia abundant, narrow lageniform to narrow fusiform 85-110 x 10-

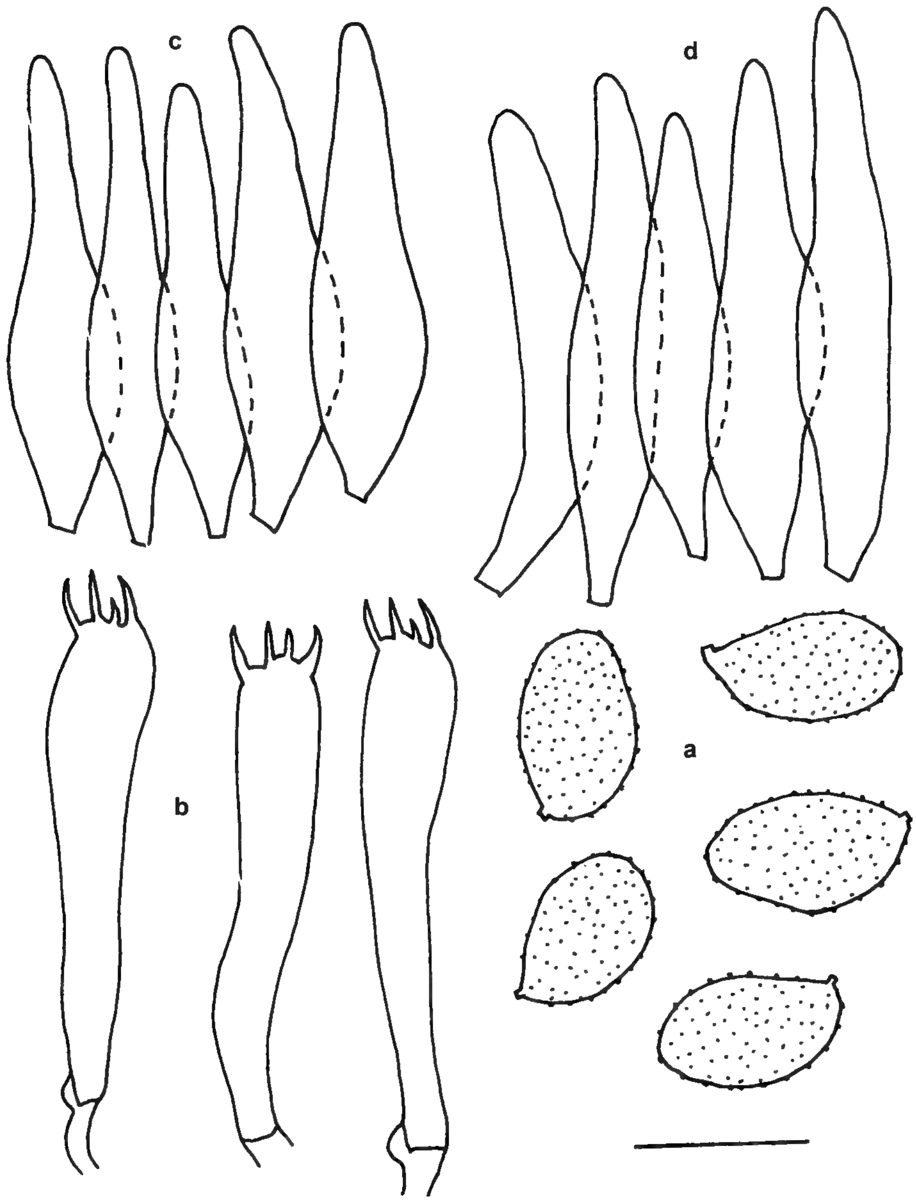

Figure 4. ***Cortinarius hallowellensis*** **(PERTH 0550 6794) : a. spores; b. basidia; c. cheilocystidia; d. pleurocystidia.**

12 µm, pleurocystidia abundant, narrow fusiform of the same dimensions. Pileal cuticle a thin, scarcely differentiated layer 20-30 µm deep, composed of narrow hyphae, 2-5 µm diameter, the surface slightly more loosely arranged, but with no special terminal cells and no upturned cystidia and then the underlying tissues gradually becoming more densely packed. This collection has slightly larger spores and slightly longer cystidia, but does not otherwise differ from the previous collection. In the absence of further collections, this is left as another collection of *Cortinarius hallowellensis.* This leaves the question as to whether this form is a local form which has transferred to the introduced host or whether it was introduced with the exotic species, and may occur elsewhere. Much more extensive collecting may allow this question to be answered.

Material Examined

WA:. North of Jarrahdale, *Pinus radiata* plantation, 2.6.76, M. Durack. (PERTH 00775665).

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Late Ordovician Strophomenide and Pentameride Brachiopods from Central New South Wales

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Percival, I.G. 2009. Late Ordovician Strophomenide and Pentameride Brachiopods from central New South Wales. *Proceedings of the Linnean Society of New South Wales* **130**, 157-178.

Strophomenide and pentameride brachiopods are described from shelfal environments (BA 3) flanking islands of the Macquarie Arc during the Late Ordovician (latest Sandbian to early Katian stages). Most of the strophomenoid genera recognized are new, monotypic, and hence endemic, although the occurrence of a new species of *Shlyginia* is indicative of affinities with Kazakhstan. Taxa described include the strophomenid *Geniculomena barnesi* gen. et sp. nov., the rafinesquinid *Testaprica rhodesi* gen. et sp. nov., glyptomenids *Resupinsculpta cuprafodina* gen. et sp. nov., *Paromalomena zheni* sp. nov., and *Platymena*? sp., and the plectambonitoid *Shlyginia rectangularis* sp. nov. Review of the generic assignment of *Oepikina*? *walliensis* Percival, 1991 suggests that this species is better placed in *Murinella* Cooper, 1956. Relatively rare pentameride brachiopods are represented by only a few specimens, including an unnamed species of *Parastrophina*, and a species tentatively referred to *Eoanastrophia*.

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KEYWORDS: brachiopod, Late Ordovician, Macquarie Arc, new genera, pentameride, strophomenide

INTRODUCTION

Late Ordovician strophomenide brachiopods are well-represented in limestones and sandstones deposited around volcanic islands forming the Macquarie Arc in central New South Wales, with most of the fauna having previously been described over the past three decades (Percival 1979a, 1979b, 1991; Percival et al. 2001). For various reasons (including rarity of specimens, and insufficient knowledge of morphological features needed to characterize new species), several additional strophomenide taxa have remained undocumented. This paper aims to address this deficiency in order to present a more complete picture of the fauna to underpin future analyses of biogeographic relationships. In addition, species of Late Ordovician strophomenides previously tentatively ascribed to *Oepikina* by Percival (1979b) from the vicinity of Gunningbland, and Percival (1991) from the Licking Hole Creek area, near Cliefden Caves (Figure 1), are reassessed in order to clarify their systematic position.

The opportunity is also taken to describe some rare examples (represented by just a handful of specimens) of Late Ordovician pentameride brachiopods. Both genera recognized are left in open nomenclature as all specimens are incomplete. However, the presence in the fauna of two additional camerelloids is significant and worthy of documentation as only one species of pentameride brachiopod, *Didymelasma inconspicua* Percival, 1991, had previously been described from contemporaneous rocks of the region.

Except for specimens of *Testaprica rhodesi* gen. et sp. nov. and *Platymena*? sp. which were found in fine-grained sandstone in the upper Gunningbland Formation of late Eastonian (Ea3-4) age, the brachiopods described here are silicified, having been recovered from residues of limestones dissolved in dilute hydrochloric acid. These limestones are of early Eastonian age, equivalent to the latest Sandbian or earliest Katian of international usage. Details of the stratigraphic succession and tectonic context within the Macquarie Arc in central NSW are provided by Percival and Glen (2007), and only a brief summary of the age and correlation of these strata (Figure 2) is given here.

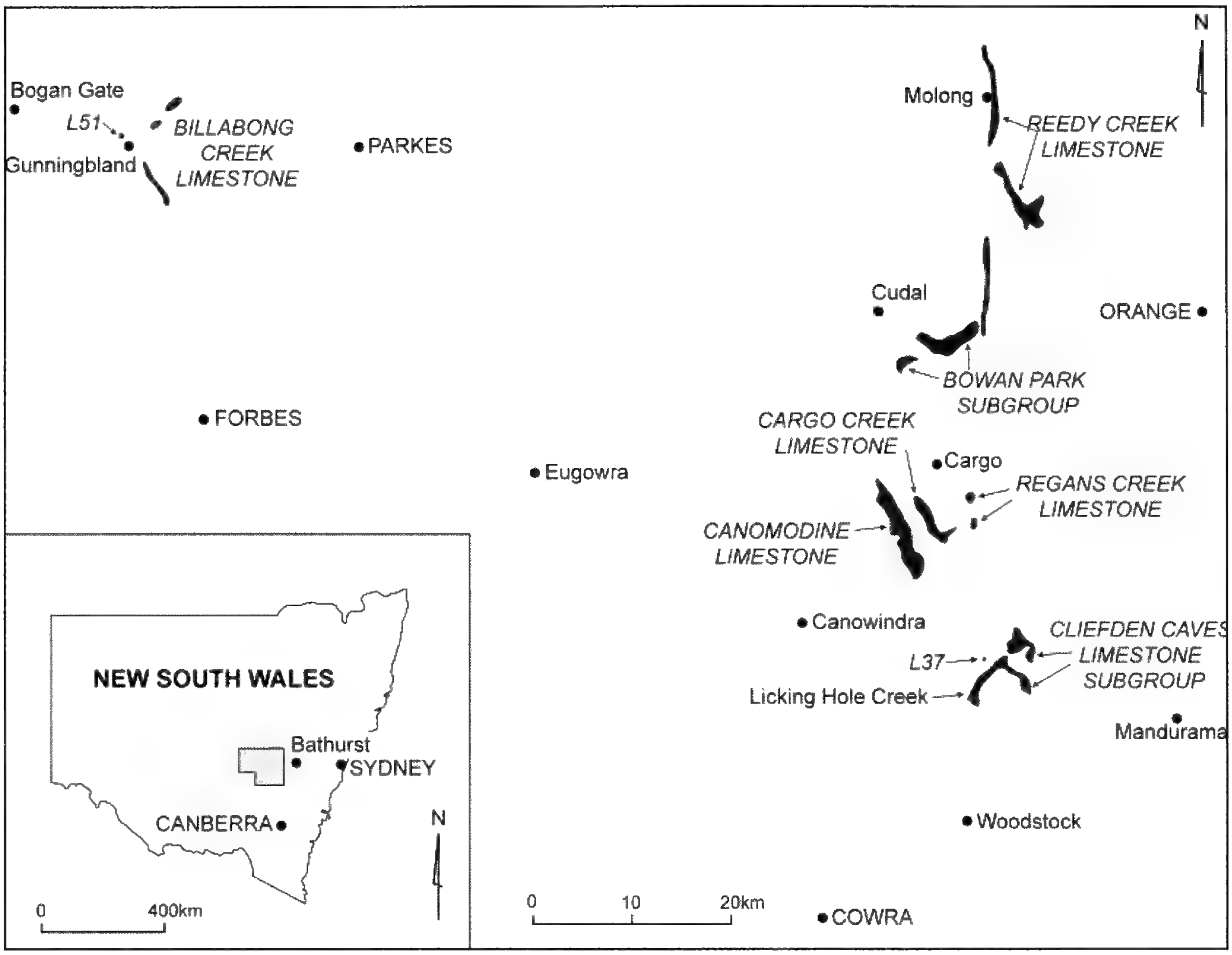

Figure 1. Locality map showing sites in central New South Wales yielding Late Ordovician brachiopods described in this paper. Outcrop of main Upper Ordovician limestone units shown in black; localities (L37, L51) in overlying Upper Ordovician clastic-dominated units are shown by spots.

Stratigraphic setting

Cliefden Caves and Licking Hole Creek areas, east flank of Molong Volcanic Belt

In the Cliefden Caves area of central New South Wales (Webby and Packham 1982) and the Licking Hole Creek area adjacent to the west (Percival 1976), a well preserved Late Ordovician carbonate-dominated sedimentary succession formed on an eroded volcanic island setting, represented by the Walli Volcanics. The Cliefden Caves Limestone Subgroup includes the Fossil Hill Limestone at the base, succeeded by the massive Belubula Limestone which is itself overlain by the Vandon Limestone. Biostratigraphic evidence from conodonts, trilobites, corals and stromatoporoids, and brachiopods, demonstrates that the Fossil Hill Limestone (and equivalents in the Licking Hole Creek area), and the lower part of the Belubula Limestone, were deposited in the earliest Eastonian (Ea1); the remainder of the limestone succession is of Eastonian 2 age, which corresponds to the basal Katian stage.

The strophomenide biofacies characterizes Benthic Assemblage 3 (BA 3) throughout these limestone deposits, which is interpreted as occupying open shelf environments in well-circulated shallow to moderate water depths (Percival and Webby 1996). Representative brachiopods of this biofacies have been largely documented by Percival (1991); further species described herein include *Geniculomena barnesi*, *Resupinsculpta cuprafodina*, *Paromalomena zheni*, *Shlyginia rectangularis*, and *Parastrophina* sp. Additionally *Oepikina walliensis* Percival, 1991, described from the basal Belubula Limestone in the Licking Hole Creek area, is reassessed and assigned to *Murinella*.

Regans Creek Limestone, southeast of Cargo, east flank of Molong Volcanic Belt

The Regans Creek Limestone, mapped by McLean (1974), is a relatively small exposure of limestone that is contemporaneous with the Cliefden Caves Limestone Subgroup.

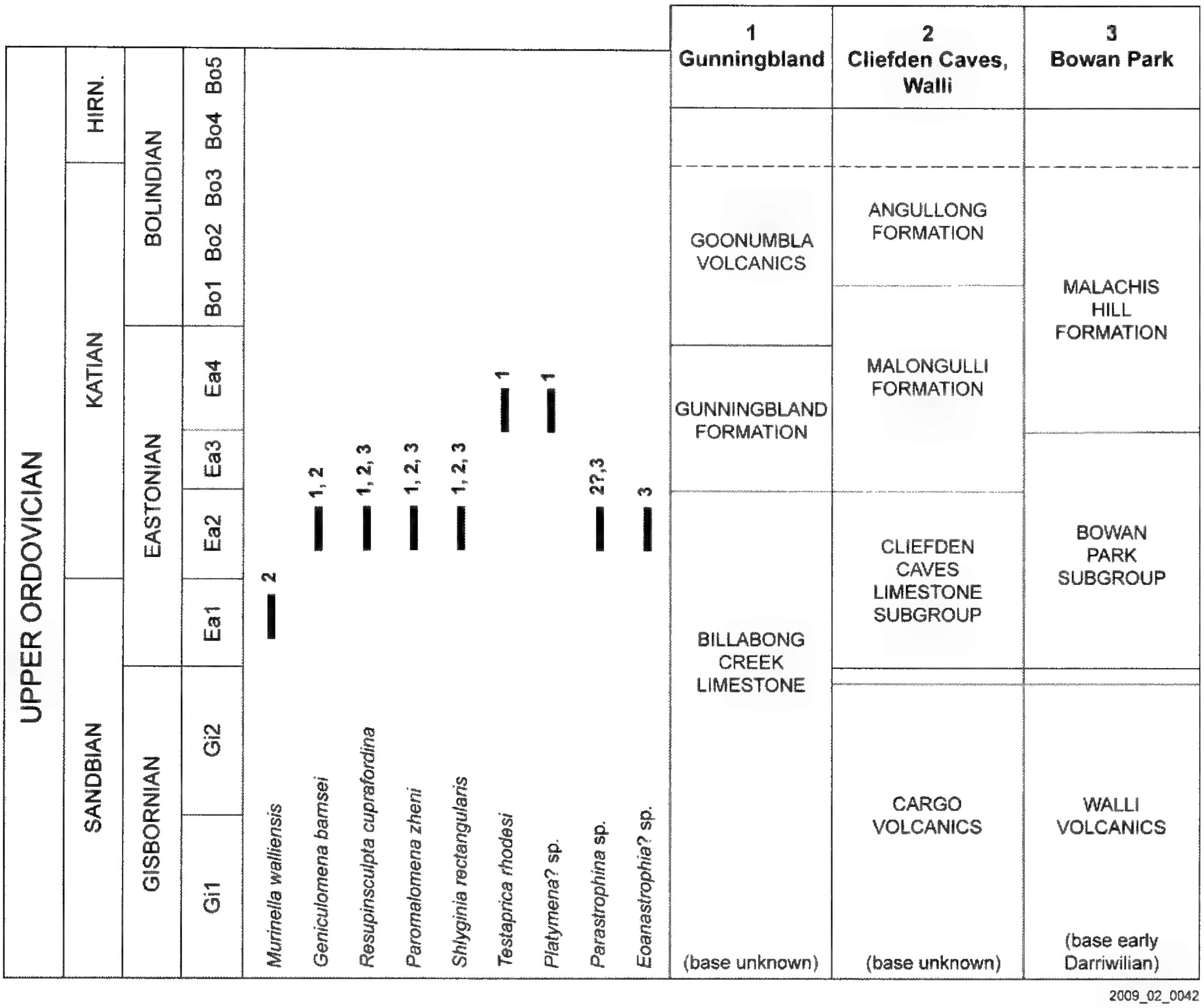

Figure 2. Stratigraphic levels at which Late Ordovician brachiopods described in this paper occur in central New South Wales. Numerals associated with approximate ranges refer to numbered stratigraphic columns to the right. Note that *Parastrophina* sp. also occurs in the Checkers Member in the upper Regans Creek Limestone (not shown on this diagram). HIRN. = Hirnantian stage.

The Checkers Member in the upper part of the Regans Creek Limestone yields a silicified fauna comparable to that in the Trilobite Hill Limestone Member of the Vandon Limestone at Cliefden Caves, although diversities are considerably lower. To the brachiopods described from this level by Percival (1991) can now be added *Parastrophina* sp.

Bowan Park area, west flank of Molong Volcanic Belt

The geology of the Bowan Park area has been described in detail by Semeniuk (1970, 1973). Limestones of the Bowan Park Subgroup (including in ascending order, the Daylesford Limestone, Quondong Limestone, and Ballingoole Limestone) overlie the Cargo Volcanics, and are in turn overlain by the Malachis Hill Formation (Fig. 2). The succession at Bowan Park differs from that on the southwestern MVB (in the Cliefden Caves area) where late Eastonian (Ea3) age sediments are represented by the graptolitic Malongulli Formation above the Cliefden Caves Limestone Subgroup, whereas carbonate deposition (Ballingoole Limestone) occupied this interval in the Bowan Park area.

The Quondong Limestone contains abundant marine invertebrate faunas of the strophomenide biofacies (Percival 1991), comparable in age and diversity with those in the Trilobite Hill Member of the Vandon Limestone (Cliefden Caves Limestone Subgroup) and like that unit clearly belongs to BA 3 (i.e. shelfal). Additional species described herein from the Quondong Limestone include *Resupinsculpta* *cuprafodina*, *Paromalomena zheni*, *Shlyginia rectangularis*, *Parastrophina* sp. and *Eoanastrophia*? sp.

Gunningbland area, Junee-Narromine Volcanic Belt

The Billabong Creek Limestone was shown by Pickett and Percival (2001) to extend from southeast of Gunningbland in a broad arcuate band trending northwestwards to north of the Parkes-Broken Hill railway, then northeast to exposures on "Kirkup" property (Figure 1). Conodonts from the "Kirkup" section, of early Darriwilian (Da2) age (Zhen and Pickett 2008), are the oldest dated fossils in the Billabong Creek Limestone. Younger conodont and coral assemblages from the type section of the formation on "Nelungaloo" property, southeast of Gunningbland, range in age through the late Darriwilian, Gisbornian and earliest Eastonian (Pickett and Percival 2001). Outcrops in and adjacent to Billabong Creek at the southern extremity of the limestone belt are rich in silicified fossils, particularly brachiopods (including *Geniculomena barnesi*, *Resupinsculpta cuprafodina*, *Paromalomena zheni* and *Shlyginia rectangularis*, described herein, and a diverse fauna documented by Percival 1991) and trilobites (Webby 1973, 1974), of Eastonian 2 age (Pickett and Percival 2001). These upper beds of the Billabong Creek Limestone correlate with the Quondong Limestone at Bowan Park, and the Trilobite Hill Limestone Member of the Vandon Limestone in the Cliefden Caves Limestone Subgroup (Figure 2).

The Billabong Creek Limestone is apparently conformably overlain by the Gunningbland Formation, although the actual boundary is unexposed. The outcrop belt of the Gunningbland Formation consistently lies immediately west of the arcuate trend of the Billabong Creek Limestone exposures (Pickett and Percival 2001). Shallow excavations and exposures in ploughed fields on "Currajong Park", "Sunnyside" and "New Durran" properties in the Gunningbland district reveal that the Gunningbland Formation predominantly consists of siltstone, shale, and fine- to medium-grained sandstone, together with minor fossiliferous limestones.

Most of the Gunningbland Formation is of late Eastonian (Ea3) age, determined from graptolites in siltstones, and conodonts including *Taoqupognathus tumidus* in limestone lenses. The limestones also contain a coral-stromatoporoid assemblage corresponding to the contemporaneous Fauna III (McLean and Webby 1976, Webby and Morris 1976). Two brachiopod faunas, elements of which were described by Percival (1978, 1979a, 1979b), are recognised. Brachiopod Fauna C, of Ea3 age, is present in the lower part of the formation on "New Durran" property. The presumed latest Eastonian age of Fauna D (Percival 1992), occurring in strata on "Currajong Park" property, was confirmed by the presence of graptolites of Ea4 age in the uppermost beds of this section (Pickett and Percival 2001). A diverse trilobite fauna has recently been described from this upper part of the unit (Edgecombe and Webby 2006, 2007), associated with the brachiopods *Testaprica rhodesi* gen. et sp. nov. and *Platymena*? sp. which are documented herein. This completes description of the brachiopod fauna collected from the Gunningbland Formation over more than three decades; two other genera (*Christiania* sp., *Ptychopleurella*? sp.) are represented in the upper part of this unit by single specimens of ventral valves, which do not warrant description until further material is forthcoming.

Systematic palaeontology

Type material (designated MMF), comprising specimens described and illustrated or listed herein, is curated in the palaeontological collections of the Geological Survey of New South Wales held at Londonderry in western Sydney. Some specimens labeled SUP, including material of *Murinella walliensis* and an external mould of the ventral valve of *Testaprica rhodesi*, were transferred from the Geology Department of the University of Sydney to the Australian Museum, Sydney in the mid-1980s (these are awaiting renumbering). For brevity, authorship of taxonomic hierarchy above genus level is not cited in the References; these bibliographic sources are listed in the revised (2nd edition) Treatise of Invertebrate Paleontology, Part H: Brachiopoda Volume 3 (Williams et al. 2000).

Phylum Brachiopoda Duméril, 1806
Subphylum Rhynchonelliformea Williams, Carlson, Brunton, Holmer and Popov, 1996
Class Strophomenata Williams, Carlson, Brunton, Holmer and Popov, 1996
Order Strophomenida Öpik, 1934
Superfamily Strophomenoidea King, 1846
Family Strophomenidae King, 1846
Subfamily Furcitellinae Williams, 1965

Geniculomena gen. nov.

Type species (by monotypy): *Geniculomena barnesi* gen. et sp. nov.

Diagnosis

Dorsally geniculate planoconvex to weakly concavoconvex furcitellin with unequally parvicostellate ornament lacking rugae; teeth and sockets without crenulations; dorsal myophragm absent; septa associated with dorsal muscle field are less strongly developed than single continuous median ridge.

Geniculomena barnesi gen. et sp. nov.
Fig. 3 A-N

Diagnosis

As for genus.

Etymology

Genus name in reference to geniculate dorsal valve profile and broadly crescent-like shell outline; species name honours David Barnes, photographer in the NSW Department of Primary Industries, in appreciation of the assistance he has provided to me

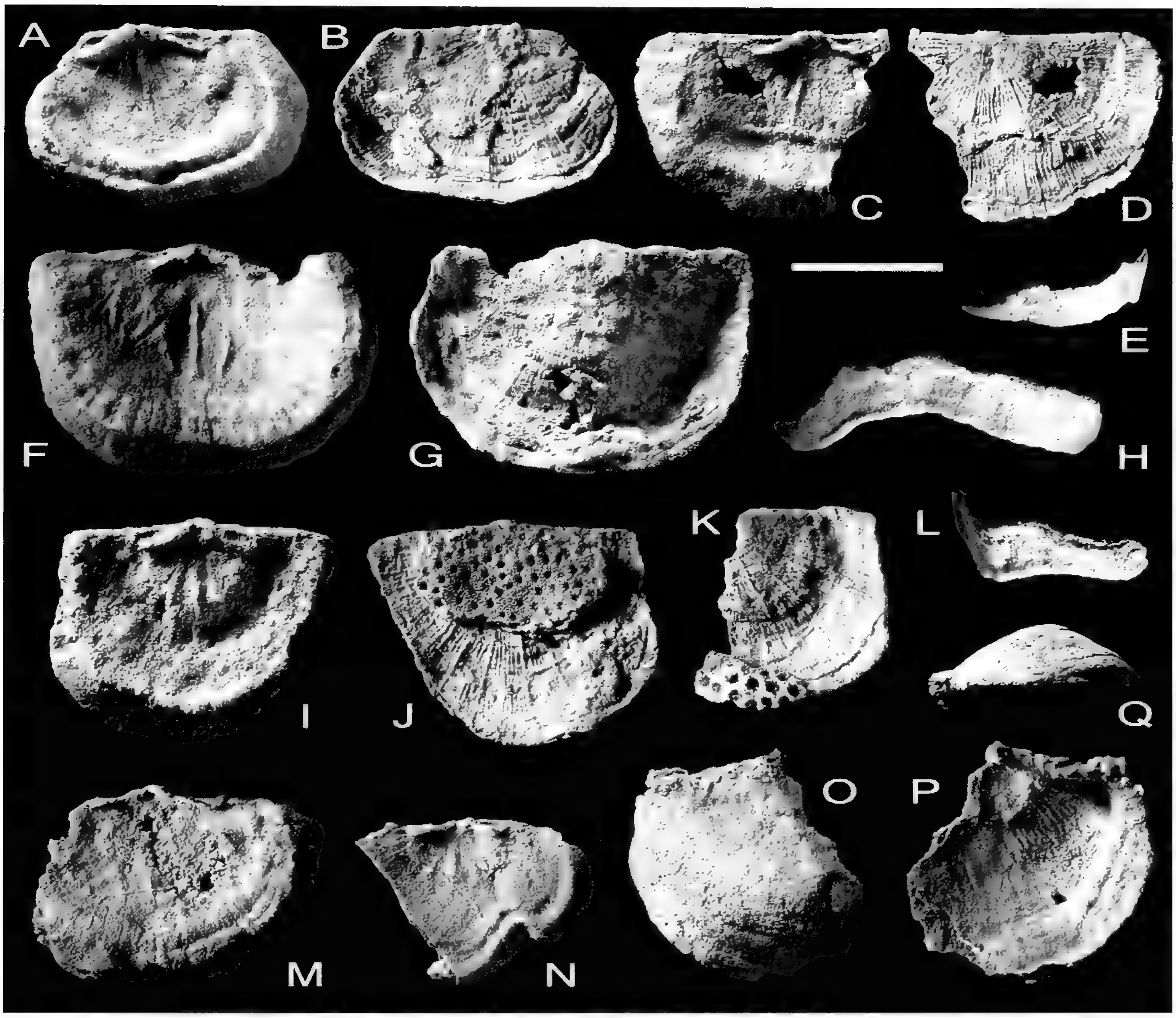

Figure 3. *Geniculomena barnesi* gen. et sp. nov. A – B: interior and exterior of dorsal valve, holotype MMF 44915. C – E: interior, exterior and lateral profile (dorsal side uppermost) of dorsal valve, MMF 44916. F – H: interior, exterior and anterior profile (dorsal side uppermost) of dorsal valve, MMF 44919. I – J: interior and exterior (bearing heliolitid coral) of dorsal valve, MMF 44917. K – L, O – Q: one incomplete individual shell, which disarticulated during acid dissolution of limestone matrix; K – L: exterior and lateral profile (dorsal side uppermost) of dorsal valve, MMF 44918a; O – Q: exterior, interior and lateral profile (ventral side uppermost) of ventral valve, MMF 44918b. M: interior of dorsal valve, MMF 44920. N: interior of dorsal valve, MMF 44921; note distortion on anterolateral margin, probably indicating repaired injury. Scale bar below C represents one cm. A – E, I – L, O – Q from L24, Trilobite Hill Limestone Member of Vandon Limestone, upper Cliefden Caves Limestone Subgroup at Licking Hole Creek near Walli; F – H from L135 (east of Copper Mine Creek, near Cliefden Caves) in Trilobite Hill Limestone Member of Vandon Limestone, upper Cliefden Caves Limestone Subgroup; M – N from L143, upper Billabong Creek Limestone at Billabong Creek road crossing south of Gunningbland.

over the past decade in preparing many illustrations of fossils for publication.

Material

Five dorsal valves, mostly entire, and one partial ventral valve with corresponding partial dorsal valve (disarticulated), all material silicified. Holotype is dorsal valve MMF 44915; paratypes include dorsal valves MMF 44916, MMF 44917, MMF 44919, MMF 44920 and 44921, and ventral valve MMF 44918a and corresponding dorsal valve 44918b.

Localities

Type locality is L24 (Licking Hole Creek area), in Trilobite Hill Limestone Member of Vandon Limestone, upper Cliefden Caves Limestone Subgroup; also found in same stratigraphic unit at L135 (east of Copper Mine Creek, near Cliefden Caves); also occurs at L143 in upper Billabong Creek Limestone, at Billabong Creek road crossing south of Gunningbland [full details of these localities are given by Percival 1991].

Description

Shell planoconvex to very weakly concavoconvex (rarely ventribiconvex, e.g. Fig. 3G), becoming dorsally geniculate when fully grown; transversely subquadrate with maximum width either at, or immediately anterior to, hingeline; lateral and anterior margins broadly curved. Shell of moderate size, ranging in length from 12 to 16 mm, and in width from 23 to 29 mm in largest specimens; length to width ratio 0.55 -0.80. Ornament unequally parvicostellate, with every fourth or fifth rib accentuated; rugae lacking; exterior of the sole ventral valve assigned to this species is almost entirely devoid of ornament, but this may have been eroded prior to fossilization.

Ventral interior (described from an incomplete valve) shows robust oblique teeth supported by low plates for approximately three-quarters length; dental plates extend anteriorly to bound triangular diductor scars flanking (but not enclosing) narrower median pair of adductor scars separated by low median ridge not extending forward of muscle field which occupies three-eighths valve length. Mantle canals prominent, of lemniscate type with anteriorly divergent *vascula media* not enclosing *vascula genitalia*. A distinct but low subperipheral rim defines a dorsally-deflected marginal band approximately one-seventh of valve length extending around entire lateral and anterior valve margin. Details of interarea and delthyrium not known.

Dorsal interior with Type A strophomenoidean cardinalia consisting of twin cardinal process lobes extending just posterior to hingeline and convergent above a hollow, with narrow, widely divergent socket ridges recurved posterolaterally at extremities; sockets short but deep; no crenulations visible on socket ridges. Notothyrial platform poorly developed, lacking myophragm; low median septum extends from immediately in front of cardinal process lobes to terminate at about half valve length, separating moderately conspicuous pair of adductor scars which are bounded by weaker side septa; short transmuscle septa barely visible or lacking. Mantle canals apparently lemniscate, poorly expressed, except for *vascula genitalia* in largest specimen. A variably defined subperipheral ridge is sometimes developed slightly posterior to dorsally-directed geniculation of marginal band.

Dimensions

Holotype MMF 44915: length 12.0 mm, width 19.0 mm; paratypes MMF 44916: length 13.1 mm, estimated width 23 mm; MMF 44917: length 15.5 mm, width of specimen (incomplete) 18.8 mm; MMF 44919: length 16.0 mm, width 23.5 mm; MMF 44920: length 13.5 mm, estimated width 22.5 mm; MMF 44918a (vv): length 15.9 mm, estimated width 29 mm.

Discussion

Geniculomena is assigned to the subfamily Furcitellinae, rather than the Strophomeninae, due to the presence of a moderately well-defined dorsal muscle field in some specimens, although muscle bounding ridges, side septa and transmuscle septa are somewhat variably developed and may be barely discernible in other examples depending on degree of silicification. Dorsally geniculate genera similar to *Geniculomena* are more typical of furcitellins rather than strophomenins. *Dactylogonia* Ulrich and Cooper, 1936 (and its synonym *Cyphomena* Cooper, 1956) appears to closely resemble *Geniculomena* in general morphology, but *Dactylogonia* is readily distinguished by its much stronger development of transmuscle and side septa in the dorsal valve. The new genus lacks the characteristic rugate ornament of *Bellimurina* Cooper, 1956, and differs internally in absence of a forked anterior termination to the dorsal median ridge.

Although *Geniculina* Rõõmusoks, 1993, from the latest Ordovician (Hirnantian) of the Baltic region, is broadly similar to *Geniculomena*, the new genus apparently lacks the prominent posterolateral oblique rugae developed on the ventral valve of *Geniculina*. Nor have crenulations been observed on the teeth and socket ridges of *Geniculomena*, whereas these are characteristic of at least four species of *Geniculina* (e.g., Rõõmusoks 2004, pl. IX fig. 12, pl. XI fig. 6). The median septum in *Geniculomena* is a single ridge that extends from the cardinal process and is rather more prominent than the side septa, unlike the arrangement in *Geniculina* that has strong side septa and a stout myophragm which bifurcates at its anterior extremity.

The multicostellate ornament of *Maakina* Andreeva, 1961 (in Nikiforova and Andreeva 1961), from the early Katian of the Siberian Platform, is quite different from that of *Geniculomena*. Internally, the absence of a dorsal median septum and presence of crenulations on the socket ridges in *Maakina* are additional features clearly distinguishing these two genera.

Distribution

Early Eastonian (Ea2), equivalent to basal Katian; presently monotypic and known only from limestones of the Macquarie Arc in central NSW.

Murinella Cooper, 1956

Type species: *Murinella partita* Cooper, 1956

Murinella walliensis (Percival, 1991)

Fig. 4 A-G

Synonymy

Oepikina? *walliensis* Percival, 1991: p.147, fig. 14.20-28.

Discussion

Two species with *Oepikina*-like morphology have previously been described from the Late Ordovician of central NSW. One form from the Gunningbland Formation was tentatively referred to *Oepikina*? sp. by Percival (1979b), and a new species *Oepikina*? *walliensis* was described by Percival (1991) from the Licking Hole Creek area, occurring in strata equivalent to the basal Belubula Limestone. In their revision of the superfamily Strophomenoidea, Rong and Cocks (1994, p.694) noted that the cardinalia of *O*? *walliensis* was "of the *Strophomena* group", presumably implying that in their view the species was a strophomenin rather than a furcitellin. Zhan *et al.* (2008) observed that these two subfamilies are difficult to separate using the revised Treatise classification (Cocks and Rong 2000). Rong and Cocks (1994, text-fig. 3) also presented a well-illustrated comparison between the dorsal cardinalia of the type species of *Strophomena* and *Murinella*. Although a reclassification of *O*? *walliensis* on the basis of cardinalia alone might therefore be superfluous, the comments by Rong and Cocks (1994) have prompted a reassessment of other possible generic affinities of

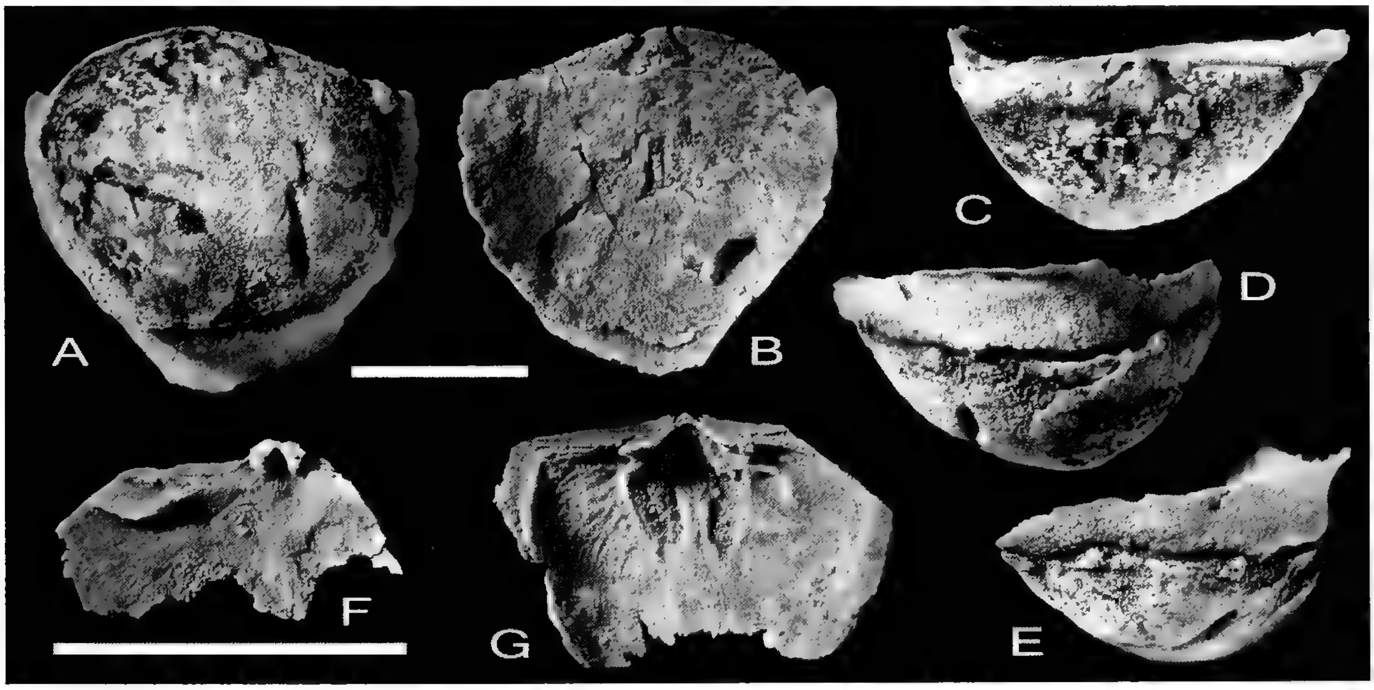

Figure 4. *Murinella walliensis* (Percival, 1991). A – E: Holotype SUP 68516, exterior of conjoined valves, dorsal, ventral, posterior profile, anterior profile and lateral profile respectively. F: fragment of dorsal valve interior showing cardinalia, SUP 68523. G: interior of ventral valve, SUP 68518. Both scale bars represent 1 cm (that beneath F pertains only to this specimen; the shorter scale bar applies to specimens A-E and G). All specimens from basal Belubula Limestone at Licking Hole Creek, near Walli.

this species.

The holotype of *O*? *walliensis* is here refigured, together with a paratype fragment showing the cardinalia and a ventral valve interior. Reasons given by Percival (1991) for provisionally assigning this species to *Oepikina* include poorly developed septa in the dorsal valve, and presence of a relatively small ventral muscle field enclosed by low bounding ridges. Both these features are atypical of *Oepikina*, whereas they are characteristic of the similar genus *Murinella* Cooper, 1956. Although a distinguishing feature of the type species of *Murinella*, *M. partita* Cooper, 1956, is the extension of the median septum anterior to the ventral muscle field, not all species show this (e.g. *M. muralis* Cooper, 1956 and *M. semireducta* Cooper, 1956). In retrospect, *O*? *walliensis* accords best with *Murinella*, and it is here designated *M. walliensis* (Percival, 1991). Other features supporting this reassignment include the relatively large pseudodeltidium and prominent subperipheral rim in the dorsal valve of *M. walliensis*. Furthermore, the cardinalia definitely conform to the *Murinella* model.

A species of *Murinella* has also been described from the lower limestone member of the Benjamin Limestone in Tasmania by Laurie (1991). That species, *M. magna*, is distinguished by its much larger dimensions, and in having a median septum extending forward of the ventral muscle field, compared to *M. walliensis*.

Oepikina? sp from Gunningbland is known only from one specimen (Percival 1979b, fig. 1.12), which clearly shows the presence of Type A cardinalia (*sensu* Rong and Cocks 1994). In all other features this dorsal valve is definitely *Oepikina*-like, with strong side septa, but the absence of a corresponding ventral valve continues to prevent a confident assignment to that genus. The external mould supposedly of a dorsal valve (SUP 62569), mentioned but not figured by Percival (1979b, p.183), is now considered to be a ventral valve of *Testaprica rhodesi* (see below) rather than being related to *Oepikina*.

Family Rafinesquinidae Schuchert, 1893
Subfamily Rafinesquininae Schuchert, 1893

Testaprica gen. nov.

Type species (by monotypy): *Testaprica rhodesi* gen. et sp. nov.

Diagnosis

Convexo-concave to convexo-planar rafinesquinin similar to *Rhipidomena* but with prominent subparallel side septa in dorsal valve; other septa and median ridge subdued or lacking.

Testaprica rhodesi gen. et sp. nov.

Fig. 5 A-H

Diagnosis

As for genus.

Etymology

Genus name derived from testa (Latin): shell, and apricum (Latin): a sunny spot, in reference to the occurrence of this brachiopod adjacent to "Sunnyside" property; species named in honour of Julie and John Rhodes, former owners of "Sunnyside" and "Currajong Park" properties at Gunningbland, who kindly provided access to collect on their land, and who also recognised and donated several important brachiopods and trilobites for scientific description.

Material

Holotype: MMF 36806a and b, dorsal valve internal mould and external mould of corresponding ventral valve. Paratypes: MMF 36798a and b, dorsal valve internal and external moulds; MMF 36801 and MMF 36805, both external moulds of dorsal valves; MMF 36813, dorsal valve internal mould; SUP 62569 ventral valve external mould.

Localities

All specimens from upper Gunningbland Formation on "Currajong Park", Gunningbland at locality L51 [see Percival 1979a for full details] with exception of MMF 36813, collected from locality L48 situated in immediately underlying beds in the same formation on this property.

Description

Large convexo-concave to convexo-planar shells up to 40 mm wide and 30 mm long, with maximum width attained at or immediately anterior to hingeline; anterolateral and anterior margins very broadly rounded. Length to width ratio varies between two-thirds and almost three-quarters. Ornament finely and evenly multicostellate, lacking rugae; costellae slightly curved on lateral flanks; occasional concentric growth discontinuities may be present, but concentric filae lacking.

Ventral valve weakly concave, becoming almost planar anteriorly; interarea low, catacline to weakly apsacline, with small pseudodeltidium. Details of interior unknown.

Dorsal valve strongly convex; interarea very low with delicate chilidial plates (poorly preserved on

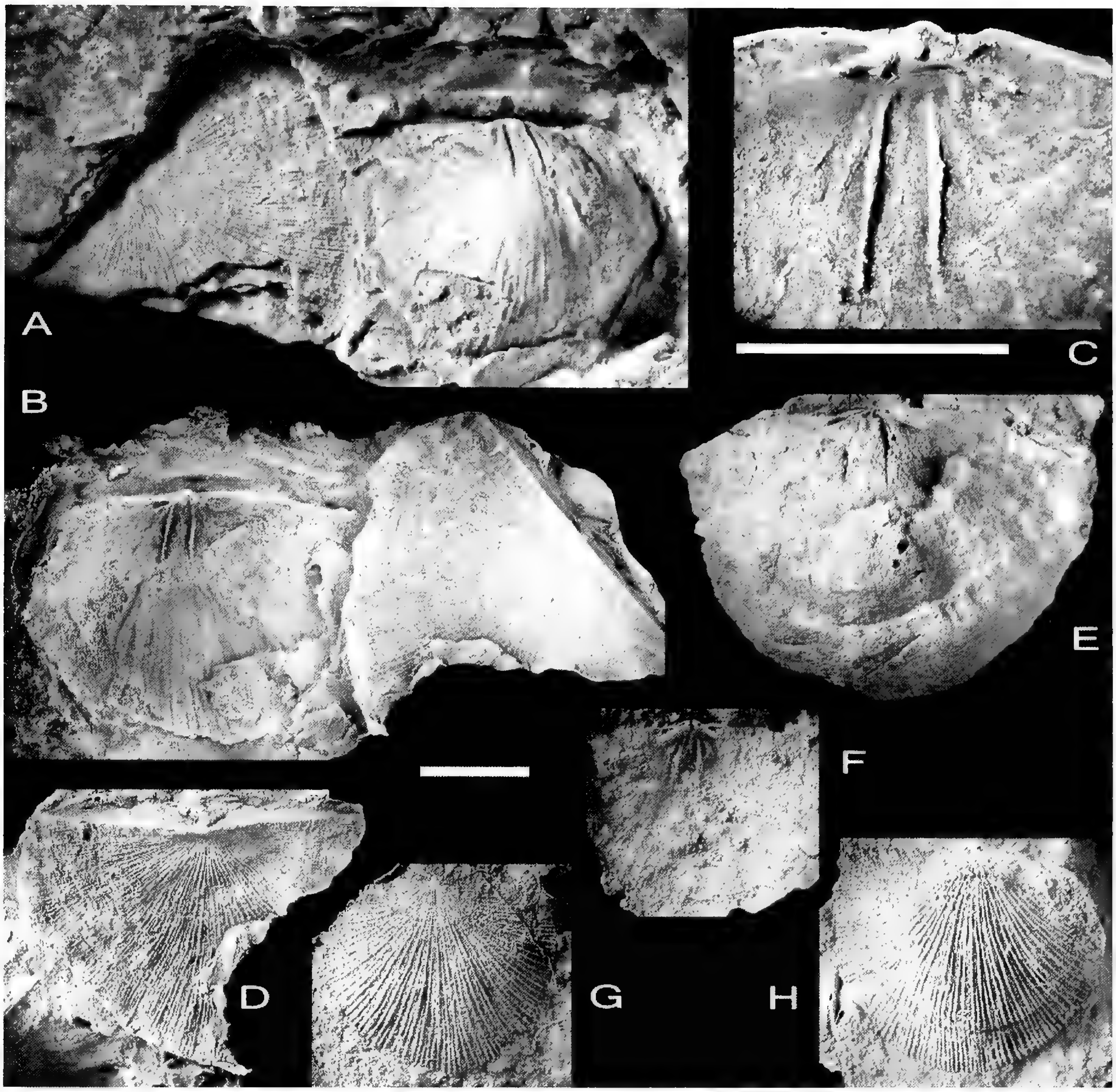

Figure 5. *Testaprica rhodesi* gen. et sp. nov. All specimens from upper beds of the Gunningbland Formation on "Currajong Park", Gunningbland. A – D: Holotype, MMF 36806a and b; A: exterior mould of ventral valve (on left, 36806a) and interior mould of corresponding dorsal valve (on right, 36806b); B: latex replica taken from this specimen; C: enlargement of posterior region of latex replica of dorsal valve; D: latex replica of exterior of ventral valve, tilted to better show ornament and interarea. E: interior mould of dorsal valve, MMF 36798a. F: latex replica of dorsal valve, MMF 36813. G: latex replica of exterior of dorsal valve, MMF 36805. H: latex replica of exterior of dorsal valve, MMF 36801. Both scale bars represent 1 cm (that below C pertains only to this enlargement).

available specimens). Cardinalia consisting of small cardinal process with pair of discrete peg-like lobes above low notothyrial platform, with very short, straight socket ridges extending obliquely; median ridge either very short or not developed; prominent subparallel pair of side septa, low and thin, extend to between one quarter and one third valve length; transmuscle septa barely visible; muscle bounding ridges not present and muscle field not impressed. Mantle canals not discernible.

Dimensions

MMF 36806a, b (holotype): DV internal mould and VV external mould L= 26.3 mm, hinge W= 39.3 mm;

MMF 36798a, b: DV internal and external moulds L= 28.4 mm, W= 39.3 mm;

MMF 36801: DV external mould L= 22.4 mm, spec W= 25.3 mm, W= 29.6 mm;

MMF 36805: DV external mould L= 16.0 mm, W= 22.0 mm;

MMF 36813: DV internal mould L= 17.6 mm;

SUP 62569: VV external mould L= 13.5 mm, W= 17.5 mm.

Discussion

This monotypic genus has cardinalia of Type B (*sensu* Rong and Cocks 1994), with small discrete cardinal process lobes that are not continuous with a median ridge, and which are also definitely disjunct from the socket ridges (the latter being straight and oblique, rather than recurved laterally towards the hingeline as in strophomenids). Clearly then, its affinities lie with the rafinesquinids. The only previously described rafinesquinin brachiopod with a convexo-concave valve profile is *Rhipidomena*, which is of generally comparable size. However, dorsal valves of the 5-6 species of this genus known from North America (Cooper 1956), are never quite as convex as is *Testaprica*, and the latter is not resupinate as is commonly the case with *Rhipidomena*. In possessing prominent side septa *T. rhodesi* differs from all North American *Rhipidomena* species, and is further distinguished by its relatively poorly developed median ridge and transmuscle septa (although there is some variation in the strength of these features). These distinctions in total appear to be of generic significance, so that despite the absence of ventral interiors the establishment of a new genus is warranted.

Equally prominent side septa are also characteristic of *Lateriseptomena* Zhan, Jin, Rong, Chen and Yu, 2008, known from two species of late Katian age from Zhejiang Province, south-east China. However, *Lateriseptomena* has Type C (glyptomenid) cardinalia, and furthermore has a planoconvex to biconvex profile, so is apparently not closely related to *Testaprica*. The concavo-convex profile of *Dirafinesquina* Cocks and Zhan, 1998, from Upper Naungkangyi Group equivalent strata (probable Katian age) in the Southern Shan States of Burma, readily distinguishes this genus from *Testaprica*; the few known dorsal interiors of *Dirafinesquina* also lack the characteristic side septa of the new genus.

Distribution

Presently known only from the Gunningbland Formation (upper part) in vicinity of Gunningbland village, between Parkes and Bogan Gate, central west NSW; late Eastonian (Ea3-4) i.e. Katian.

Family Glyptomenidae Williams, 1965
Subfamily Glyptomeninae Williams, 1965

Resupinsculpta gen. nov.

Type species (by monotypy): *Resupinsculpta cuprafodina* gen. et sp. nov.

Diagnosis

Resupinate glyptomenin displaying weak rugation on exterior of both valves; teeth and socket ridges occasionally crenulate.

Resupinsculpta cuprafodina gen. et sp. nov.

Fig. 6 A-P

Diagnosis

As for genus.

Etymology

Genus name in reference to resupinate profile and finely engraved appearance of ornament (resupinus: L bent back; insculptus: L engraved); species name in reference to Copper Mine Creek, the type locality (cuprum: L copper; fodina: L mine or pit).

Material

Holotype MMF 44923 (conjoined valves); paratypes include MMF 44924 (ventral valve), MMF 44925 (dorsal valve), MMF 44926 (ventral valve), MMF 44927 (dorsal valve), MMF 44928 (ventral valve), and MMF 44929 (conjoined valves). All specimens are silicified.

Localities

Type locality L135 (east of Copper Mine Creek, near Cliefden Caves), in Trilobite Hill Limestone Member of Vandon Limestone, upper Cliefden Caves Limestone Subgroup; also found at L138 (“Quondong”, Bowan Park, east of Cudal) in Quondong Limestone, Bowan Park Subgroup; and at L144 in upper Billabong Creek Limestone beside the road crossing Billabong Creek, south of Gunningbland [full details of these localities are given by Percival 1991].

Description

Shell relatively small, length up to 12 mm and width to approximately 18 mm; outline subquadrate initially, becoming transverse and slightly auriculate when fully grown with maximum width at hinge line; length two-thirds width in these largest specimens.

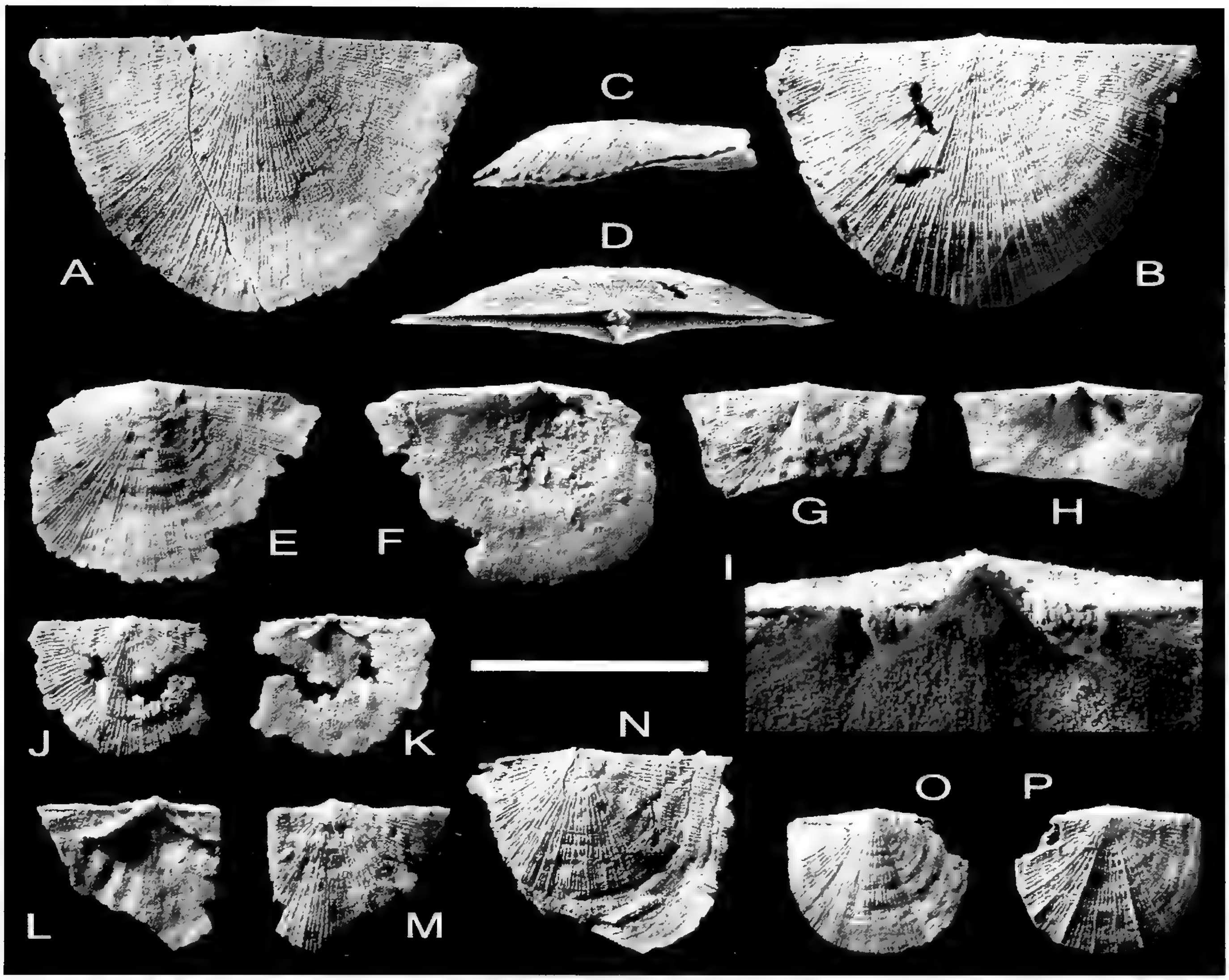

Figure 6. *Resupinsculpta cuprafodina* gen. et sp. nov. A – D: Holotype conjoined valves, MMF 44923; A: exterior of ventral valve; B: exterior of dorsal valve; C: lateral profile (dorsal valve uppermost); D: posterior profile (dorsal valve uppermost). E – F: exterior and interior of ventral valve, MMF 44924. G – I: exterior and interior of ventral valve, and enlargement of delthyrium to show crenulated teeth, MMF 44926. J – K: exterior and interior of dorsal valve, MMF 44925. L – M: interior and exterior of dorsal valve, MMF 44927. N: exterior of ventral valve, MMF 44928. O – P: conjoined valves, ventral and dorsal exteriors respectively, MMF 44929. Scale bar represents 1 cm for whole figure (except I, which is a five-times enlargement of H). A – F, J – K from L135 (east of Copper Mine Creek, near Cliefden Caves): in Trilobite Hill Limestone Member of Vandon Limestone, upper Cliefden Caves Limestone Subgroup; G – I, N – P from L138 (“Quondong”, Bowan Park, east of Cudal) Quondong Limestone, Bowan Park Subgroup.

Ventral valve with sharply pointed beak; profile initially weakly convex, becoming resupinate in largest specimens; dorsal valve planar posteriorly, gently to moderately convex anteriorly in adults; whole shell very compressed dorsoventrally. Ornament unequally parvicostellate, commonly with 3-4 finer costellae between accentuated ribs, with indistinct rugae developed posteriorly.

Ventral interarea low, apsacline, with wide delthyrium covered apically by pseudodeltidium. Delicate teeth, crenulated in one specimen (Fig. 6I), supported by thin subparallel dental plates that terminate immediately in front of teeth. Muscle field indistinct, apparently very short, not enclosed by ridges. A weak subperipheral rim is present in one specimen. Mantle canals not visible.

Dorsal interarea very low, orthocline to weakly anacline; notothyrium entirely occupied by cardinal process lobes; chilidial plates either lacking or extremely weakly developed. Cardinalia consist of small paired cardinal process lobes fused to long, straight, widely divergent socket ridges (which are finely crenulated in at least one specimen, Fig. 6L) with slightly curved terminations; cardinal process lobes extend very slightly posteriorly of hingeline and anteriorly overhang a concavity in place of notothyrial platform; median ridge short, very low; side and transmuscle septa absent. Muscle field and mantle canals not visible.

Dimensions

Nearly all specimens are incomplete; a juvenile conjoined shell MMF 44929 is 6.2 mm long and 7.7 mm wide; the largest shell (holotype, MMF 44923) is 11.6 mm long and 18.5 mm wide.

Discussion

The new species presents a conundrum as regards its generic affinities. It has Type C (glyptomenin) cardinalia, and conforms in almost all respects with the characteristics of *Glyptomena*, except for the resupinate profile of larger shells. Smaller shells are planoconvex and thus more similar to the typical concavoconvex profile of *Glyptomena*. As shell profile is often used to distinguish genera in strophomenides, it seems reasonable to establish a new genus within the glyptomenines based on the resupinate character. Furthermore, crenulated teeth and socket ridges as seen in *Resupinsculpta cuprafodina* are apparently rare in glyptomenines; Rong and Cocks (1994) only mentioned their occurrence in *Mjoesina*, which was doubtfully assigned to the family (Cocks and Rong 2000), but is now regarded more likely to be a rafinesquinid (Cocks 2005). The indistinct rugae present in the posterior region of the exterior of both valves of *R. cuprafodina* are lacking in species of *Glyptomena*, but the distinctively dorsally geniculate *Glyptomenoides* Popov and Cocks, 2006 (which is otherwise generally similar to *Glyptomena*) also displays irregular rugae. Most comparable of other strophomenids is possibly *Longvillia* Bancroft, 1933, which also is resupinate; however, *Longvillia* has Type A cardinalia and is therefore not closely related to the new genus.

Distribution

Only known from limestones of early Eastonian (Ea2) age, equivalent to the earliest Katian Stage, in the Macquarie Arc, central NSW.

Paromalomena Rong, 1984

Type species: *Platymena polonica* Temple, 1965

Paromalomena zheni sp. nov.

Fig. 7 A-V

Diagnosis

A species of *Paromalomena* distinguished by its prominent pseudodeltidium with a minute foramen at the apex, and lacking conspicuous external rugae.

Etymology

This species is named in honour of my colleague Dr Yong-Yi Zhen, in recognition of his extensive palaeontological studies in the Ordovician of both Australia and China.

Material

Holotype is MMF 44932 (ventral valve); paratypes include MMF 44930 (dorsal valve), MMF 44931 (ventral valve), MMF 44933 (ventral valve), MMF 44934 (conjoined valves), MMF 44935 (dorsal valve), MMF 44936 (ventral valve), MMF 44937 (conjoined valves), MMF 44938 (dorsal valve), MMF 44939 (dorsal valve), MMF 44940 (dorsal valve), MMF 44941 (dorsal valve), MMF 44942 (dorsal valve), MMF 44943 (ventral valve), MMF 44944 (ventral valve), MMF 44945 (ventral valve), and MMF 44946 (conjoined valves). All specimens are silicified.

Localities

Type locality is L138 ("Quondong", Bowan Park, east of Cudal) in Quondong Limestone, Bowan Park Subgroup; also occurs at L24 (Licking Hole Creek area, Walli) in Trilobite Hill Limestone Member of Vandon Limestone, upper Cliefden Caves Limestone Subgroup; and at localities L143 and L144 in upper Billabong Creek Limestone, in vicinity of Billabong Creek road crossing, south of Gunningbland [full details of these localities are given by Percival 1991].

Description

Shells generally small and thin, not exceeding 7.5 mm in length and 9.2 mm in width, with subquadrate to subrectangular outline; hingeline straight and wide, in all but one specimen just slightly narrower than maximum valve width which is approximately coincident with midlength, anterior margin broadly rounded; length:width ratio ranges from 0.65 to 0.88, with average of 0.77 for 18 specimens. Profile generally planoconvex, to weakly concavoconvex with tendency to geniculation dorsally in largest specimens; a subtle sulcus may develop in anteromedian sector of dorsal valve, with corresponding weak fold in ventral valve. Ornament finely and equally parvicostellate, lacking rugae; occasional concentric growth discontinuities may be present. Ventral interarea apsacline, with relatively wide delthyrium at least half

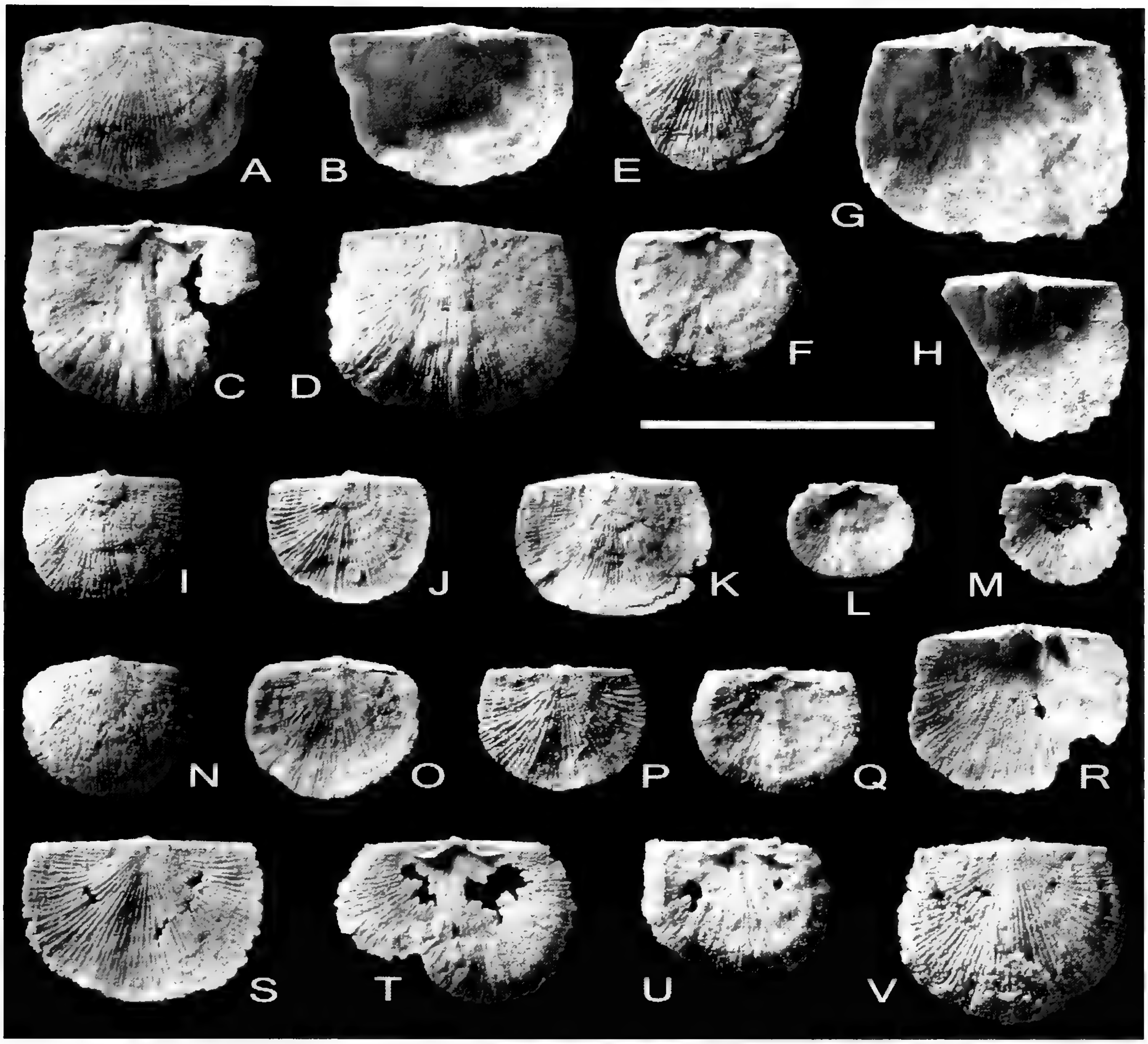

Figure 7. ***Paromalomena zheni*** **sp. nov. A – B: exterior and interior of ventral valve, MMF 44931. C: interior of dorsal valve, MMF 44935. D: exterior of ventral valve, MMF 44936. E – F: exterior and interior of dorsal valve, MMF 44930. G: interior of ventral valve, holotype MMF 44932. H: interior of ventral valve, MMF 44933. I – J: conjoined valves, ventral and dorsal exteriors respectively, MMF 44934. K: dorsal exterior of conjoined valves, MMF 44937. L: interior of juvenile dorsal valve, MMF 44938. M: interior of juvenile ventral valve, MMF 44944. N – O: conjoined valves, ventral and dorsal exteriors respectively, MMF 44946. P – Q: exterior and interior of dorsal valve, MMF 44939. R: interior of ventral valve, MMF 44945. S: exterior of dorsal valve, MMF 44940. T: interior of dorsal valve, MMF 44941. U: interior of dorsal valve, MMF 44942. V: exterior of ventral valve, MMF 44943. Scale bar represents 1 cm. A – L from L138 ("Quondong", Bowan Park, east of Cudal) Quondong Limestone, Bowan Park Subgroup; M, Q – V from L143, upper Billabong Creek Limestone at Billabong Creek road crossing south of Gunningbland; N – O from L24, Trilobite Hill Limestone Member of Vandon Limestone, upper Cliefden Caves Limestone Subgroup at Licking Hole Creek near Walli.**

to three-quarters covered by prominent high convex pseudodeltidium; a minute pedicle foramen is present at apex of pseudodeltidium. Dorsal interarea barely evident, considerably lower than that of ventral valve; chilidial plates (if present) extremely delicate.

Ventral interior: Pedicle foramen about pinhole size, encased in callus at extreme posterior of delthyrial cavity. Small teeth supported by receding dental plates, below which extend anteriorly divergent, subparallel or slightly convergent lateral muscle bounding ridges that rapidly decline in height and do not enclose muscle field anteriorly; diductors surround adductors that are embedded in shallow subcircular pit on low median ridge. Muscle field occupies approximately one-third valve length and less than one-quarter width. Mantle canals not observed.

Dorsal interior: Cardinalia of glyptomenin type (Type C), with very delicate cardinal process lobes joined to fine, short socket ridges that diverge and curve to extend subparallel to hingeline; notothyrial platform absent; low, broad median ridge is barely developed in some larger specimens, otherwise lacking; side and transmuscle septa never developed; muscle scars not clearly defined. Mantle canals not discernible, due to thinness of shell material that reflects external costellae.

Dimensions

Valve length ranges from 3.2 mm to 7.5 mm, and valve width ranges from 4.3 mm to 9.2 mm (measurements from 18 individuals; no significant difference between ventral and dorsal valves). Holotype (ventral valve MMF 44932) is 7.5 mm long and 9.2 mm wide; majority of specimens cluster in the range of 5.0-6.5 mm long, and 5.5-8.5 mm wide.

Discussion

This new species shares many morphological characteristics with the cosmopolitan Late Ordovician (late Katian – Hirnantian) genus *Paromalomena* including shell profile and ornament, development of fold and sulcus anteriorly, and in most internal details. It differs from described species mainly in having a conspicuous pseudodeltidium, and in lacking a large chilidium and external rugae. *Paromalomena* typically occurs in deepwater settings (BA 4-6) in distinctive faunal associations such as the *Foliomena* fauna (e.g. Neuman 1994) and the younger *Hirnantia* fauna (e.g. Temple 1965). Like these species, *P. zheni* is quite thin-shelled, but unlike them it occurs in considerably shallower environments (BA 3) and is somewhat older (earliest Katian).

Unlike species of *Glyptomena*, the new species has a furcitellin-like ornament (i.e. equally parvicostellate), and is generally planoconvex rather than concavo-convex, except in largest specimens. *P. zheni* is readily distinguished from *Resupinsculpta cuprafodina*, the other glyptomenin with which it is associated in the same strata in central NSW, by the latter's resupinate profile, unequally parvicostellate ornament and presence of rugae.

Glyptomenoides species differ in having an unequally parvicostellate ornament with rugae developed, and furthermore are quite distinct internally from *P. zheni* which lacks a stout myophragm and transmuscle septa.

Distribution

Limestones of early Eastonian (Ea2) age, equivalent to the earliest Katian Stage, in the Macquarie Arc, central NSW.

Platymena Cooper, 1956

Type species: *Platymena plana* Cooper, 1956

Platymena? sp.

Fig. 8 A-D

Material

MMF 36804, external mould of ventral valve; MMF 36810, internal mould of dorsal valve; MMF 44968, internal mould of dorsal valve (not figured).

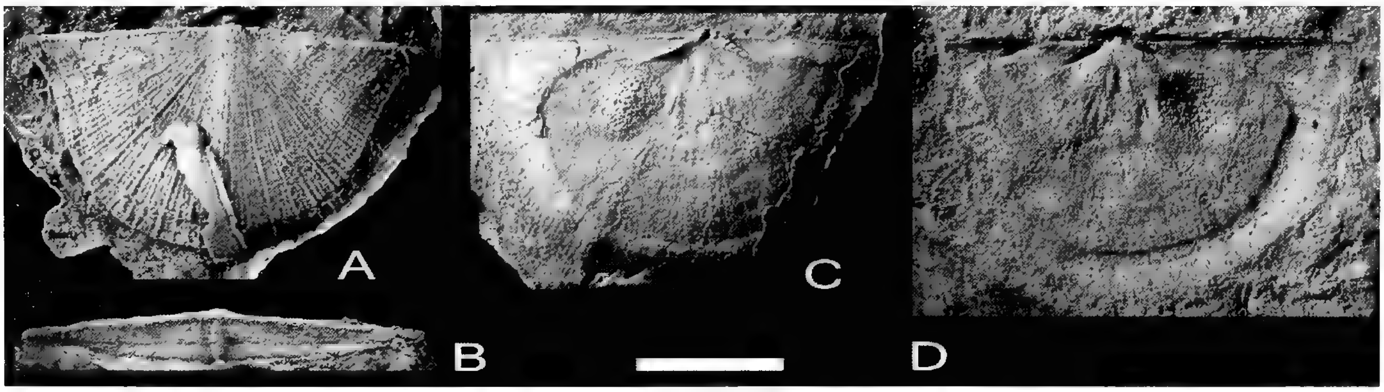

Figure 8. *Platymena*? sp. A – B: latex replica of ventral valve exterior and interarea of conjoined valves, MMF 36804. C – D: latex replica and corresponding internal mould of dorsal valve, MMF 36810. All specimens from upper beds of the Gunningbland Formation on "Currajong Park", Gunningbland. Scale bar represents 1 cm.

Locality

All three known specimens from sandstones in upper Gunningbland Formation on "Currajong Park", Gunningbland at locality L51 [see Percival 1979a for full details].

Description

Transverse auriculate shell with maximum width at hingeline; lateral and anterior margins broadly rounded; profile apparently weakly concavo-convex, with median ventral fold; periphery of both valves dorsally geniculated. Length:width ratio 0.53 (ventral valve), 0.56 (dorsal valve). Ornament unequally parvicostellate, with 2-3 finer costellae separating relatively strongly accentuated costellae; very fine crowded concentric filae are just visible interstitially between costellae; three faint oblique rugae developed on posterolateral flanks.

Ventral valve with low apsacline interarea, and narrow pseudodeltidium extending entire height of interarea. Interior details of ventral valve unknown.

Dorsal valve interarea very low, orthocline to weakly anacline, with small, apparently complete chilidium. Delicate cardinal process lobes are continuous laterally with fine, broadly divergent socket ridges; notothyrial platform beneath cardinal process is barely thickened above valve floor, extending anteriorly as a short, low median ridge; transmuscle septa very poorly developed. Musculature and mantle canals not deeply impressed; muscle field extends no more than one-third valve length. Broadly rounded subperipheral rim slightly raised above dorsal valve floor, geniculate dorsally in anterior portion; width of subperipheral rim greatest in posterolateral corner of valve.

Dimensions

MMF 36804 (VV): length 14.8 mm, width 27.7 mm;

MMF 36810 (DV): length 17.1 mm, specimen width 26.8 mm; estimated complete width 30.8 mm;

MMF 44968 (DV): length 18.6 mm, width 28.8 mm.

Discussion

Lack of knowledge about interior details of the ventral valve prevents conclusive identification of this species as either *Platymena* or *Glyptomena*. In establishing both genera, Cooper (1956, p.882) commented upon differences between them, remarking on the flatness of the dorsal valve and thickened marginal region in *Platymena*. The delicate cardinalia and socket ridges, and weakly developed to barely perceptible septa in the dorsal muscle field are more reminiscent of *Glyptomena*, and although no dorsal valve exteriors are known for the Gunningbland species, the sole internal mould seems to suggest a weakly concave (rather than planar) profile. However, the presence of a relatively prominent subperipheral rim is more characteristic of *Platymena*, to which this species is tentatively assigned.

Distribution

Gunningbland Formation (upper part) in vicinity of Gunningbland village, between Parkes and Bogan Gate, central west NSW; late Eastonian (Ea3-4) i.e. Katian.

Superfamily Plectambonitoidea Jones, 1928
Family Leptellinidae Ulrich and Cooper, 1936
Subfamily Leptellininae Ulrich and Cooper, 1936

Shlyginia Nikitin and Popov, 1983

Type species: *Shlyginia declivis* Nikitin and Popov, 1983

Remarks

In addition to describing *S. printhiensis* from Molong, NSW, the first species of *Shlyginia* known from outside Kazakhstan, Percival (in Percival et al., 2001) reviewed all six species previously attributed to this genus. All are similar with respect to general characteristics of the dorsal valve interior, whereas there is a wide variation in the size and disposition of the ventral muscle field. The type species, *S. declivis*, has a widely divergent ventral muscle field extending to about one-third valve length (Nikitin and Popov 1983, pl. 3, fig. 4; Cocks and Rong 2000, fig. 208, 3b – same specimen). In *Shlyginia fragilis* (Rukavishnikova, 1956) the ventral muscle field extends for about one-third valve length (Rukavishnikova 1956, pl. 2, fig. 18; Popov *et al.* 2002, pl. 6, figs 22, 25). *Shlyginia extraordinaria* (Rukavishnikova, 1956) has a very large ventral muscle field extending beyond mid valve length, in which the muscle impressions are conjoined medially for much of their length (Popov *et al.* 2000 pl. 3, fig. 19; Popov and Cocks 2006, pl. 4 figs 22-23). The ventral muscle field of *S. perplexa* Nikitin and Popov, 1996 is much reduced, occupying no more than one-quarter to one-fifth valve length (Nikitin and Popov 1996, fig. 4 F-G). The NSW species *S. printhiensis* has a ventral muscle scar confined to the posterior third of the valve, whereas in the new species described below, the ventral muscle field just reaches (but never exceeds) half valve length.

Excluded from *Shlyginia* is *S. solida* Nikitin and Popov, 1984; the sturdy, apparently tubular dorsal median septum of this species indicates that it belongs in *Mabella* Klenina, 1984. Also referred to *Mabella* on this same criterion is *Dulankarella namasensis* Klenina, 1984 (and its synonym *D. subquadrata* Klenina, 1984), previously assigned to *Shlyginia* by Nikitin and Popov (1996).

***Shlyginia rectangularis* sp. nov.**

Fig. 9 A-X

Diagnosis

Transversely rectangular, dorsoventrally compressed *Shlyginia* with distinctive V-shaped incision at posterolateral extremities of ventral valve; muscle scar extending to midlength of ventral valve; 2-3 pairs of discrete nodes present on platform of dorsal valve laterally between muscle field and peripheral rim.

Etymology

Referring to rectangular outline.

Material

Holotype MMF 44959 (ventral valve); paratypes include MMF 44947 (conjoined valves), MMF 44948 (ventral valve), MMF 44949 (dorsal valve), MMF 44950 (dorsal valve), MMF 44951 (conjoined valves), MMF 44952 (ventral valve), MMF 44953 (ventral valve), MMF 44954 (ventral valve), MMF 44955 (dorsal valve), MMF 44956 (dorsal valve), MMF 44957 (ventral valve), MMF 44958 (dorsal valve), MMF 44960 (dorsal valve), and MMF 44961 (dorsal valve). All specimens are silicified.

Localities

Type locality is L142 (Paling Yards Creek section at "The Ranch", Bowan Park), in Quondong Limestone, Bowan Park Subgroup; also found in same horizon at L138 ("Quondong", Bowan Park, east of Cudal); occurs also at L24 (Licking Hole Creek area, Walli) in Trilobite Hill Limestone Member of Vandon Limestone, upper Cliefden Caves Limestone Subgroup; and at L143 in upper Billabong Creek Limestone, from outcrop in Billabong Creek at road crossing, south of Gunningbland [full details of these localities are given by Percival 1991].

Description

Transversely rectangular shells with long, straight hingeline, lateral margins nearly straight and parallel to slightly convergent anteriorly, with broadly rounded anterior margin. Dorsoventrally compressed, planoconvex profile; maximum convexity close to anterior margin; ventral valve flattened medially, becoming broadly sulcate anteromedially in largest specimens. Valve length between 4.4 and 8.8 mm, width 5.7 to 13.7 mm; length:width ratios in 13 specimens ranging from 0.55-0.69, with average of 0.61; maximum width at hingeline with slightly auriculate, posterolateral extremities in best preserved specimens, otherwise widest in posterior third of shell. Ornament finely unequally parvicostellate, very faintly impressed except for accentuated costellae, rarely lamellose peripherally in largest specimens. Ventral interarea low, apsacline, with upper third of delthyrium covered by small deltidium; dorsal interarea much lower, anacline, with very fine, paired chilidial plates flanking trifid cardinal process.

Ventral valve interior: teeth small, unsupported by dental plates. Muscle field moderately to deeply impressed, adductor scars confined to a small median depression deep within delthyrium; diductors much larger, moderately divergent anteriorly, distinctly separated medially by fine ridge, and extending to mid valve length. Mantle canals of lemniscate type, with moderately strongly impressed *vascula media* and weaker *vascula genitalia* (sometimes not visible). Narrow, linear median depression extending from muscle field nearly to anterior margin of valve appears to exactly coincide with dorsal median septum.

Dorsal valve interior: Anterior edge of hingeline thickened towards lateral extremities. Cardinalia typically leptellinine, trifid with prominent central ridge flanked by finer oblique lateral ridges, supported on a low thickened notothyrial platform. Socket ridges short, bladelike and pointed oblique to hingeline. Muscle field well defined by bounding ridges extending anteriorly from ends of socket ridges; muscle field bisected obliquely by low ridges that may represent proximal traces of *vascula media*. Solid ridge-like median septum, not expanding anteriorly, is separated from front of notothyrial platform by shallow depression; septum rises sharply and extends to approximately 0.8-0.85 valve length to merge with edge of barely undercut platform margin. Two to three pairs of discrete nodes are present on platform lateral to muscle field. Mantle canals beyond muscle field rarely impressed, possibly saccate.

Dimensions

Holotype MMF 44959 (ventral valve) is 7.2 mm long and 11.5 mm wide. Paratype MMF 44947 (conjoined valves) measures 7.4 mm in length, 12.1 mm in width, and 2.0 mm in thickness. Lengths of 12 other paratypes range from 4.4 mm to 8.8 mm, with most between 5.0-7.5 mm long; widths of 13 paratypes range from 5.7 mm to 13.7 mm, most are 9-12 mm wide. There is no appreciable difference

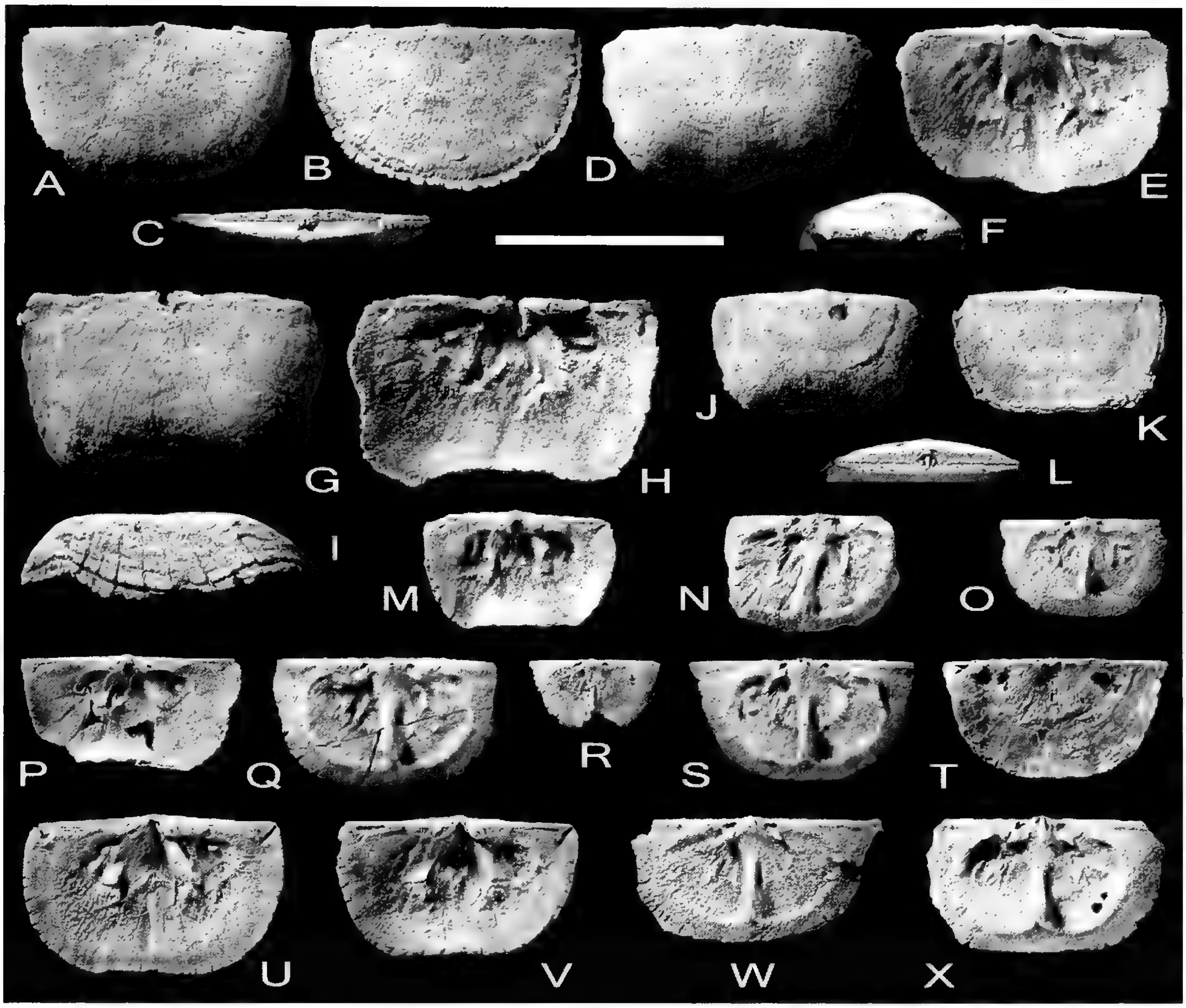

Figure 9. *Shlyginia rectangularis* sp. nov. A – C: exterior of conjoined valves, ventral and dorsal respectively, and posterior profile (dorsal valve uppermost), MMF 44947. D – F: exterior, interior and lateral profile (posterior to left) of ventral valve, MMF 44952. G – I: exterior, interior and anterior profile of ventral valve, MMF 44948. J – L: conjoined valves, ventral and dorsal exteriors and posterior profile (ventral valve uppermost) respectively, MMF 44951. M: interior of ventral valve, MMF 44953. N: interior of dorsal valve, MMF 44950. O: interior of dorsal valve, MMF 44955. P: interior of ventral valve, MMF 44954. Q: interior of dorsal valve, MMF 44958. R: interior of juvenile dorsal valve, MMF 44956. S – T: interior and exterior of dorsal valve, MMF 44960. U: interior of ventral valve, holotype MMF 44959. V: interior of ventral valve, MMF 44957. W: interior of dorsal valve, MMF 44961. X: interior of dorsal valve, MMF 44949. Scale bar represents 1 cm. A – C, G – I, N, X from L24, Trilobite Hill Limestone Member of Vandon Limestone, upper Cliefden Caves Limestone Subgroup at Licking Hole Creek near Walli; D – F, J – L, M, O, P, R from L135 (east of Copper Mine Creek, near Cliefden Caves), in Trilobite Hill Limestone Member of Vandon Limestone, upper Cliefden Caves Limestone Subgroup; Q, U, V from L142 (Paling Yards Creek section at "The Ranch", Bowan Park), in Quondong Limestone, Bowan Park Subgroup; S – T from L138 ("Quondong", Bowan Park, east of Cudal), Quondong Limestone, Bowan Park Subgroup; W from L143, upper Billabong Creek Limestone at Billabong Creek road crossing south of Gunningbland.

between measurements of dorsal and ventral valves.

Discussion

Two distinctive morphological features – the V-shaped incisions at the posterolateral extremities of the ventral valve interior, and the presence of nodes on the platform lateral to the dorsal muscle field – serve to distinguish *S. rectangularis* from all other known species of *Shlyginia*. The function of the V-shaped incisions is not clear, although one likely explanation is that they interlock with corresponding thickened parts of the hingeline in the dorsal valve to strengthen articulation of the valves when open. Containment of the dorsal muscle field by bounding ridges is another characteristic feature of *S. rectangularis*. The large ventral muscle field of the new species is comparable only with that of *S. extraordinaria* which also has a similar trapezoidal outline, being noticeably widest at the hingeline. However, the dorsal interior of *S. extraordinaria*, illustrated by Popov *et al.* (2000, pl. 3, figs 18-20) and Popov and Cocks (2006, pl. 4, figs 25-26), exhibits a much less robust median septum than does *S. rectangularis*. Unlike both *S. extraordinaria* and the other NSW species *S. printhiensis*, the new species lacks a well-defined marginal rim in the ventral valve; the median septum of *S. rectangularis* is also relatively much longer than that of *S. printhiensis*.

Distribution

Limestones of mid-Eastonian (Ea2) age, equivalent to basal Katian, throughout the Macquarie Arc in central NSW.

Order Pentamerida Schuchert and Cooper, 1931

Suborder Syntrophiidina Ulrich and Cooper, 1936

Superfamily Camerelloidea Hall and Clarke, 1895

Family Parastrophinidae Schuchert and LeVene, 1929

Parastrophina Schuchert and LeVene, 1929

Type species: *Atrypa hemiplicata* Hall, 1847

Parastrophina sp.

Fig. 10 A-G

Material

One fragmentary dorsal valve (MMF 44962) from L147, three ventral valves (all incomplete) MMF 44963-44965 from L24, and one partial ventral valve (MMF 44966) from L138 (doubtfully attributed).

Localities

Vandon Limestone (Trilobite Hill Limestone Member), Cliefden Caves Limestone Subgroup at locality L24, Licking Hole Creek, Walli; Checkers Member of Regans Creek Limestone at locality L147, "Red East", Regans Creek southeast of Cargo; ventral valve from Quondong Limestone, Bowan Park Subgroup at locality L138, "Quondong", Bowan Park, east of Cudal is doubtfully attributed [full details of localities given by Percival (1991)].

Description

Ventral valve: convex, smooth externally on posterior and lateral flanks, with shallow sulcus developed anteriorly, bearing 2-3 costae to form a weakly plicate anterior margin; internally with large subparallel dental plates extending to valve floor, bounding narrow, deep, parallel-sided sessile spondylium extending to approximately two-thirds valve length, supported anteriorly by very short median septum which barely extends beyond anterior edge of spondylium.

Dorsal valve: smooth, convex posteriorly with prominent umbo (anterior part of valve not preserved); cardinal process lacking; deep narrow septalium present bounded by thin walls anteriorly convergent on to low thin median septum that extends anteriorly for an unknown distance; alate plates present.

Dimensions

Dorsal valve MMF 44962 L= 7.5 mm (incomplete), width estimated at 20 mm.

Ventral valve MMF 44963 L= 4.5 mm, full width unknown.

Ventral valve MMF 44966 W= 12.5 mm (incomplete), estimated width about 20 mm.

Discussion

The available material, although incomplete, is assigned to *Parastrophina* rather than to the externally similar *Camerella* on the basis of the presence of alate plates in the sole dorsal valve. The ventral valve from the Quondong Formation at Bowan Park has the same smooth exterior, at least posteriorly, and similar dimensions to the other specimens. However, it is only doubtfully attributed to the same species, as evidence that the spondylium is supported above the valve floor at the front is lacking (this part of the shell being broken away). Alternatively, if the dental plates rest unsupported on the valve floor then this specimen may be better placed in *Stenocamara* Cooper, 1956.

Numerous species of *Parastrophina* have been described, from North America (Cooper, 1956), Kazakhstan (Sapelnikov and Rukavishnikova 1975; Nikitin et al. 1996; Popov et al. 2002; Nikitin et al. 2006) and elsewhere, but it is difficult to make accurate comparisons between those (particularly when described from serial sections) and the sparse and incomplete silicified material from NSW.

Distribution

Rare in limestones of early Eastonian (Ea2) age, equivalent to earliest Katian, in the Macquarie Arc of central NSW.

Eoanastrophia Nikiforova and Sapelnikov, 1973

Type species: *Eoanastrophia antiquata* Nikiforova and Sapelnikov, 1973

Eoanastrophia? sp.

Fig. 10 H-I

Material

One specimen, an incomplete dorsal valve, MMF 44967.

Locality

Quondong Limestone, Bowan Park Subgroup at locality L138, "Quondong", Bowan Park, east of Cudal [full details of locality given by Percival (1991)].

Description

Dorsal valve entirely costate with angular ribs, occasionally with intercalated costellae; internally with short septalium supported on long high median septum; very small sockets; crura present (preserved only on left-hand side of specimen); no cardinal process. Ventral valve not available for description.

Dimensions

Specimen 11.4 mm long and 9.4 mm wide (both dimensions incomplete).

Discussion

Similarly strongly costate parastrophinid genera include *Eoanastrophia* Nikiforova and Sapelnikov, 1973 and *Maydenella* Laurie, 1991. The latter genus, from the late Middle Ordovician Upper Cashions Creek Limestone in Tasmania, has a sessile septalium resting on the valve floor that is bounded by long subparallel hinge plates, whereas in *Eoanastrophia* the hinge plates converge onto a septum which

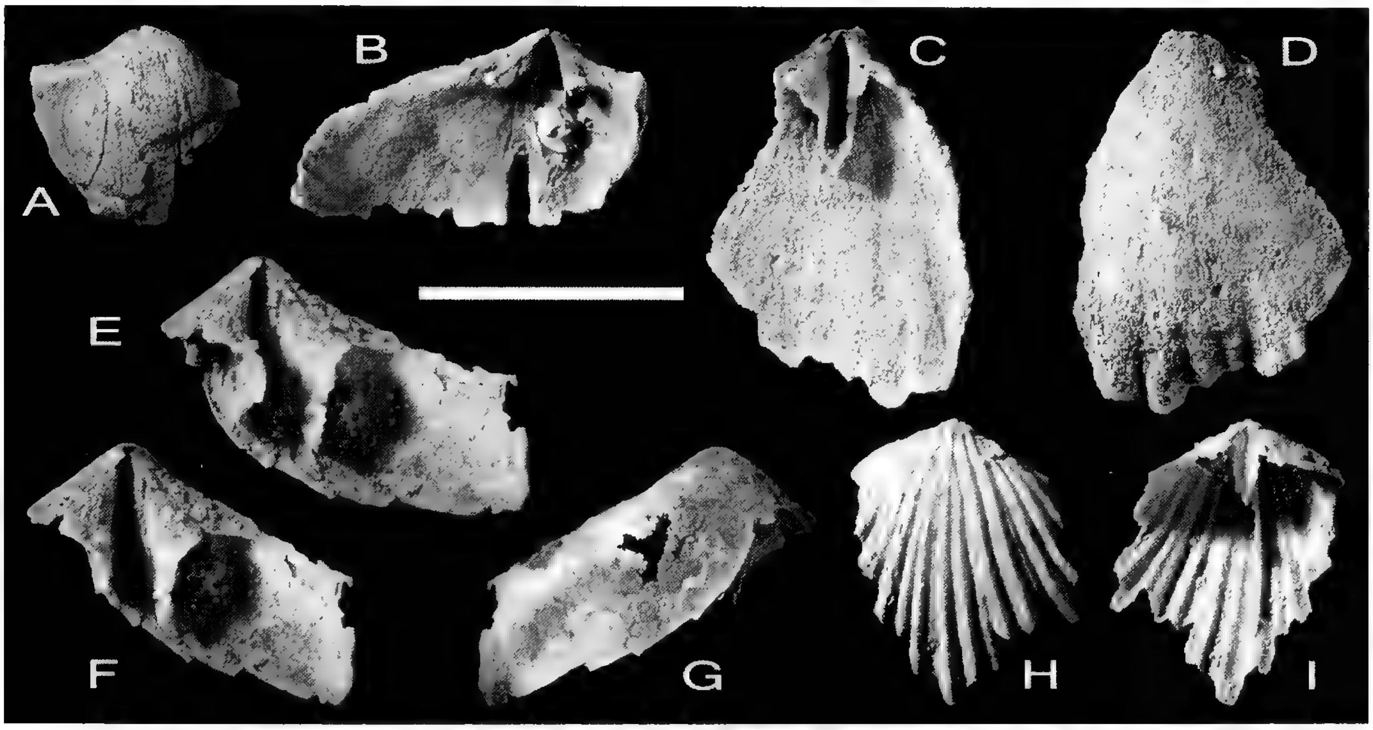

Figure 10. A – G: *Parastrophina* sp. A – B: exterior and interior of partial dorsal valve, MMF 44962, specimen broken during photography; from Checkers Member of Regans Creek Limestone at locality L147, "Red East", Regans Creek southeast of Cargo. C – D: interior and exterior of partial ventral valve, MMF 44963; from Vandon Limestone (Trilobite Hill Limestone Member), Cliefden Caves Limestone Subgroup at locality L24, Licking Hole Creek, Walli. E – G: two interior views (the first slightly tilted to show dental plates extending to valve floor) and exterior of ventral valve, MMF 44966, doubtfully attributed to this species; from Quondong Limestone, Bowan Park Subgroup at locality L138, "Quondong", Bowan Park, east of Cudal. Scale bar representing 1 cm applies to all specimens in this figure.
H – I: *Eoanastrophia*? sp., exterior and interior of dorsal valve (interior view slightly tilted to better show septum supporting septalium), MMF 44967, from Quondong Limestone, Bowan Park Subgroup at locality L138, "Quondong", Bowan Park, east of Cudal.

supports the septalium (Laurie 1991, p. 85; Carlson 2002, p. 955-958). On this basis, the NSW specimen is most like *Eoanastrophia*, although as only one valve is known, the generic assignment is necessarily tentative.

Distribution

Presently known only from the one locality in the Quondong Limestone.

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Rare Fossils (Conulata; Rostroconchia; Nautiloidea) from the Late Ordovician of Central New South Wales

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Percival, I.G. 2009. Rare fossils (Conulata; Rostroconchia; Nautiloidea) from the Late Ordovician of central New South Wales. *Proceedings of the Linnean Society of New South Wales* **130**, 179-191.

Four decades of detailed palaeontological investigations into highly fossiliferous Upper Ordovician strata of the Macquarie Arc in central New South Wales has revealed several unique specimens which in some instances represent the only known examples of phyla or subphyla in this region. Conulariids have not previously been reported from Ordovician rocks in NSW; here is documented *Conularia* sp., known from one specimen found in the Fossil Hill Limestone, and several microscopic specimens of different genera (including *Metaconularia*? sp., and the new genus and species *Microconularia fragilis*) from deep water allochthonous limestones (Malongulli Formation, and Downderry Limestone Member of the Ballingoole Limestone). The first Ordovician rostroconch mollusc from NSW is described from a solitary individual of *Eopteria*, from the top of the Malongulli Formation. A coiled nautiloid tentatively identified as *Plectoceras* from the Gunningbland Formation, again represented by a single specimen, is also described and illustrated.

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KEYWORDS: Conulariid, Late Ordovician, Macquarie Arc, Nautiloid, Rostroconch

INTRODUCTION

Rare fossils, often represented by unique specimens, can sometimes be overlooked in systematic documentation of a fauna, particularly if they are not spectacular in appearance or preservation. Yet such fossils, even when fragmentary or incomplete, by their very presence can be quite significant biogeographically. Despite intensive collecting over more than thirty years (and in some cases around four decades), the examples described in this paper are the only known specimens of conulariids, a rostroconch mollusc, and a genus of tarphyceratid nautiloid that have been found in Upper Ordovician rocks of the Macquarie Arc in central New South Wales. Their uniqueness well qualifies them to be described and illustrated for the first time.

Stratigraphic setting

The Cliefden Caves Limestone Subgroup and the overlying Malongulli Formation occur in the Walli area, between Mandurama and Canowindra in central NSW (Figure 1). Outcrop of these units has been mapped in detail south of the Belubula River by Webby and Packham (1982) in the vicinity of Cliefden Caves, and by Percival (1976) in the Licking Hole Creek area, adjoining to the west. Webby and Packham (1982) established the stratigraphic nomenclature of the Cliefden Caves Limestone Subgroup, comprising three formations (in ascending order: Fossil Hill Limestone, Belubula Limestone, Vandon Limestone), with the first and last of these subdivided into a number of members.

Conularia sp. is represented by a single specimen (described herein) collected by G.H. Packham in the late 1960s from the Taplow Limestone Member of the Fossil Hill Limestone in the section west of the "Boonderoo" shearing shed (Webby and Packham 1982, fig. 3, p.302). No other material of this species has been found in this or any other level in the Cliefden Caves Limestone Subgroup, despite intensive palaeontological investigation of the area over the past four decades. The age of the Fossil Hill Limestone is early Eastonian (Ea1), equivalent to latest Sandbian in the middle Late Ordovician. The Taplow Limestone Member was deposited in shallow

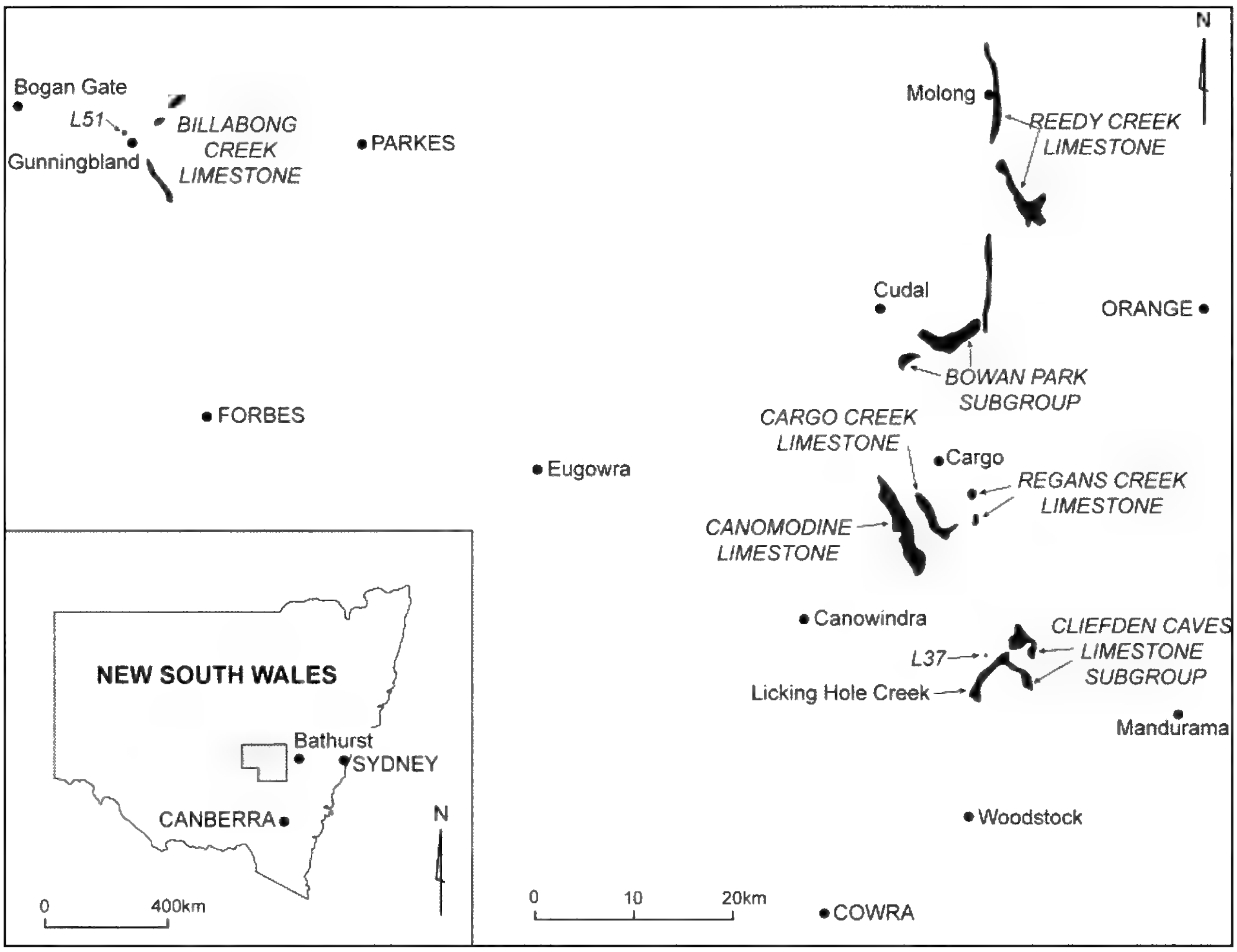


Figure 1. Locality map showing sites in central New South Wales yielding the Late Ordovician fossils described in this paper. Outcrop of main Upper Ordovician limestone units shown in black; localities (L37, L51) in overlying Upper Ordovician clastic-dominated units are shown by spots.

turbulent water interpreted as Benthic Assemblage (BA) 2 in depth (Percival and Webby 1996); the conulariid was obtained from skeletal grainstones in the middle to upper part of the member, overlying *Tetradium cribriforme* coral banks.

A solitary outcrop of allochthonous limestone at the top of the Malongulli Formation on the north-east flank of Malongulli Trig (Percival 1976) directly overlies graptolitic shale of early Bolindian age (Bo1, Zone of *Climacograptus uncinatus*), equivalent to the latest Katian stage of the Late Ordovician. A very diverse fauna – including stromatoporoids (Webby and Morris 1976), radiolaria (Webby and Blom 1986), sponge spicules (Webby and Trotter 1993), and brachiopods including lingulates (Percival et al. 1999), strophomenoids and orthoids (Percival 2005), accompanied by numerous fragments of the nautiloid *Bactroceras latisiphonatum* Glenister, 1952 (Stait et al. 1985) – is known from acid-processed residues of the limestone. Also present in the residues are extremely rare conulariid remains, including a single microscopic conulariid specimen designated as *Microconularia fragilis* gen. et sp. nov. and fragments of a separate conulariid with distinctive pustulose ornamentation, and a unique specimen of an articulated rostroconch identified as *Eopteria* sp. which, although fragmentary, is recognizable as the first (and only) known example of this Class in the Upper Ordovician of NSW. The conulariid material and the rostroconch are described herein. The allochthonous limestone is interpreted as having been initially deposited as periplatformal ooze on the upper slope (Webby 1992) in BA 4 water depths, prior to being displaced (after lithification) downslope to its present BA 5 setting. Thus the conulariids occurring at this level lived at considerably greater depths than the larger *Conularia* sp. from the Taplow Limestone Member.

The Bowan Park Limestone Subgroup in the area east of Cudal (Fig. 1) spans a similar age range to the Cliefden Caves Limestone Subgroup and the lower part of the Malongulli Formation, i.e. early (Ea1) to late (Ea 3-4) Eastonian, as indicated by conodonts studied by Zhen et al. (1999). The Bowan Park area was mapped in detail by Semeniuk (1973) who established the internal stratigraphy of formations and members in use today. One specimen of *Microconularia fragilis* gen. et sp. nov. is known from residues of the Downderry Limestone Member (of the Ballingoole Limestone at the top of the Bowan Park Subgroup), which is interpreted as a submarine channel-fill deposit emplaced at water depths approximating BA 4 environments. The Downderry conulariid therefore occupied a comparable habitat to that of the conspecific example from allochthonous limestone at the top of the Malongulli Formation.

Upper Ordovician rocks in the Gunningbland area, west of Parkes on the western side of the Macquarie Arc (Pickett and Percival 2001), include the Billabong Creek Limestone (the upper part of which is correlative with the Cliefden Caves Limestone Subgroup), and the overlying clastic-dominated Gunningbland Formation which was deposited contemporaneously with the Malongulli Formation, though in slightly lesser water depths. Faunas of the Gunningbland Formation are dominated by trilobites (Edgecombe and Webby 2006, 2007) and brachiopods (Percival 1978, 1979a, 1979b, 2009). Stait et al. (1985) previously described two coiled nautiloids from this formation, including a single specimen each of *Paradiscoceras dissitum* and an indeterminate tarphyceratid. The specimen of *Plectoceras*? sp. described herein is the best preserved tarphyceratid nautiloid known from this level (a further fragmentary coiled nautiloid is documented by illustration only). These specimens, of late Eastonian (Ea3) age, equivalent to early Katian, are externally similar to slightly younger tarphyceratids documented by Percival et al. (2006).

Systematic palaeontology

Type material, comprising specimens described and illustrated or listed herein, is curated in the palaeontological collections of the Geological Survey of New South Wales (designated MMMC for microfossil specimens, and MMF for macrofossils). For brevity, authorship of taxonomic hierarchy above genus level is not cited in the References; these bibliographic sources are listed in Leme et al. (2008) for conulariids, Pojeta and Runnegar (1976) for rostroconchs, and Furnish and Glenister (1964) for tarphyceratid nautiloids.

Phylum Cnidaria
Class Scyphozoa Goette, 1887
Subclass Conulata Moore and Harrington, 1956
Order Conulariida Miller and Gurley, 1896
Suborder Conulariina Miller and Gurley, 1896
Family Conulariidae Walcott, 1886

***Conularia* Miller, in Sowerby 1821**
Type species: *Conularia quadrisulcata* Miller, 1821

***Conularia* sp.**
Fig. 2

Material

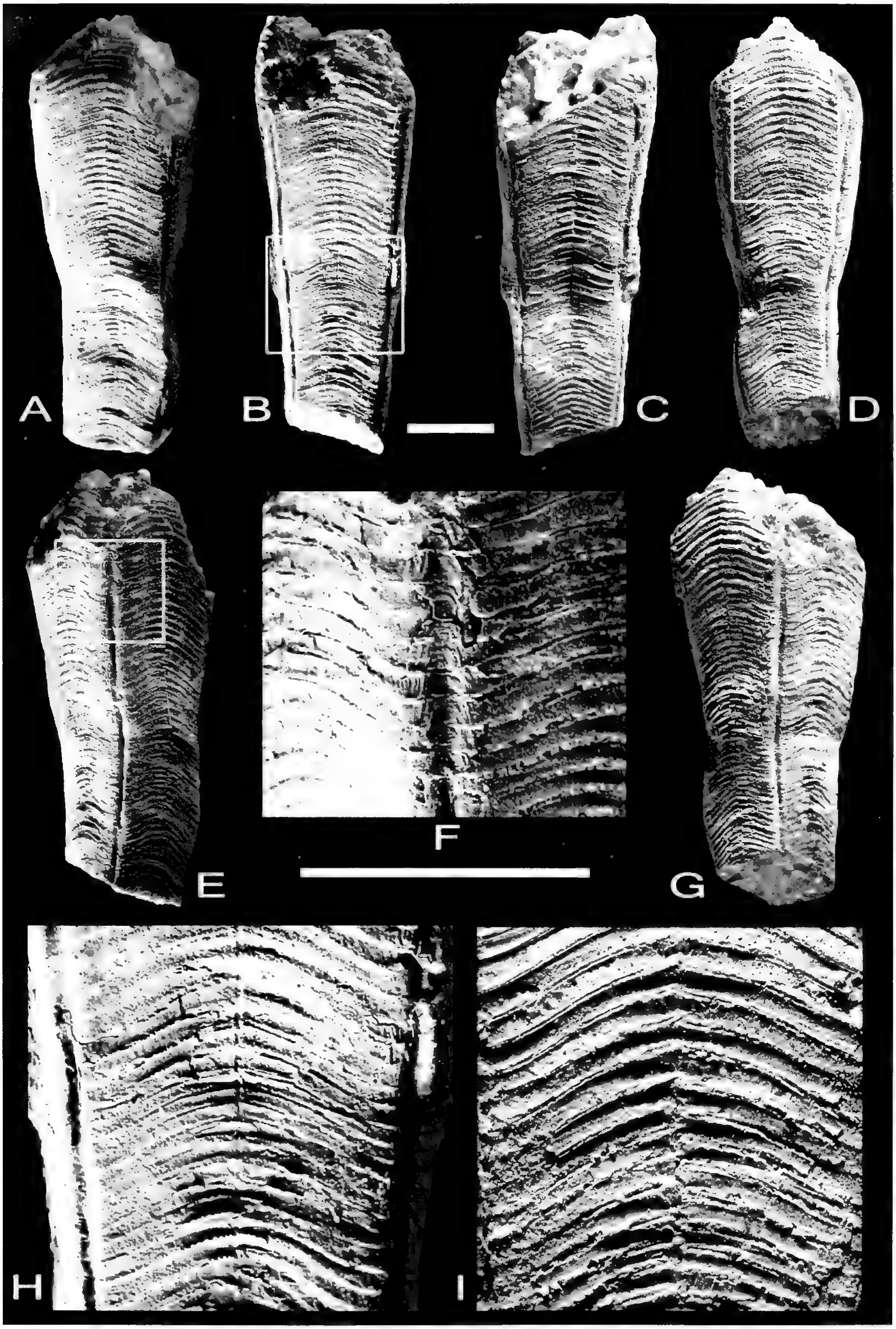
A single incomplete specimen, MMF 44969a-b, represented by a natural cast and an associated partial external mould.

Description

The sole specimen includes the upper two-thirds (approximately) of one individual, extending 25.1 mm in length from the top of the apertural lobes; maximum width immediately below aperture is 9.1 mm. Cross-section quadrate, profile steeply pyramidal with planar to very slightly convex faces (slightly distorted in preservation) that gently taper apically, with apical angle estimated to be 8°; apex not preserved. Ornament consists of narrow, gently arched transverse ribs (23 per cm) that are defined by pair of closely-spaced parallel ridges, separated by interspaces up to three times as broad as the ribs; interspace ridges barely visible on one face (Fig. 2I). Midline variably expressed, either as a very narrow ridge (suggestive of an internal carina) across which the transverse ribs meet in opposition (Fig. 2H), or a vertical discontinuity across which ribs alternate (Fig. 2I). Transverse ribs are almost everywhere non-tuberculate except for isolated section of one face (Fig. 2H). Corner sulcus flat-bottomed, with transverse ribs continuous between adjacent faces. Apertural lobes triangular in outline and broadly convex in profile, with continuation of midline; individual lobes are near vertical in orientation, surrounding a large open aperture. No internal features preserved.

Discussion

Conulariids are very rare in the Ordovician of Australia; only a single species has previously been described from Tasmania by Parfrey (1982), who established a new genus and species, *Tasmanoconularia tuberosa*, based on a solitary partially fragmented specimen (nevertheless with excellent surface detail) preserved in the Westfield Sandstone of the Florentine Valley. The brachiopod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fauna of this unit (Laurie 1991; age revised by Rong et al. 1994) contains species of *Hirnantia*, *Kinnella*, *Eospirifer*, *Cryptospira*, *Onniella*? and *Isorthis* (*Ovalella*), which are representative of the *Hirnantia* fauna of Hirnantian (latest Ordovician) age.

Parfrey (1982) distinguished *Tasmanoconularia* from *Conularia* and other genera included in the subfamily Conulariinae Walcott, 1886, by virtue of the Tasmanian conulariid having a distinct corner furrow which interrupted the continuity of the majority of transverse furrows between adjacent faces. This characteristic suggested affinities with the Paraconulariinae Sinclair, 1952. Subsequent opinion (Van Iten and Vyhlasová 2004) and cladistic analysis (Leme et al. 2008, page 652) has concluded that *Tasmanoconularia* is most likely identical with *Conularia*, with Leme et al. (2008) advocating that all previously-proposed families and subfamilies of conulariids (with the exception of the Conulariidae Walcott, 1886) be regarded as invalid.

Comparison of *C. tuberosa* (Parfrey, 1982) with *C.* sp. reveals significant differences in size and ornamentation, sufficient to easily distinguish the two forms. The Tasmanian species is considerably wider, attaining a width estimated at 15 mm in an incomplete specimen, and is much more sharply tapering towards the apex than is the NSW species. The ribs of *C. tuberosa* are crowded together (35-38 per cm) whereas those of *C.* sp. are considerably less crowded (23 per cm). Both species are finely tuberculate, *C. tuberosa* conspicuously so; although *C.* sp. appears to be almost exclusively devoid of tubercles, this is most likely an artifact of preservation, as they are present in one small area (Fig. 2H) of a face that is less weathered.

Conularia is a long-ranging cosmopolitan genus with numerous species; furthermore, the cladistic analysis of Leme et al. (2008) suggests that several other genera should probably be regarded as synonyms of *Conularia*. Comparison of the NSW species with others assigned to *Conularia* or its synonyms seems to be of doubtful value until the genus as a whole is revised. Coarsely crystalline calcite infilling the sole specimen of *C.* sp. has destroyed definitive evidence of carinae and ridges internal to the corners and midline (although it is possible the midline is strengthened internally by a carina – see Fig. 2H). Such features are significant criteria distinguishing genera and species of conulariids (Van Iten 1992, Jerre 1994, Leme et al. 2008), and their absence hinders comparisons with established taxa.

It is appropriate here to compare *C.* sp. with Late Silurian conulariids revised or newly described from central NSW by Sherwin (1970), as these forms are closest in age and geography. *Mesoconularia webbyi* Sherwin, 1970 has an identical apical angle of 8° and generally comparable dimensions; however, transverse ribs on this species are more than twice as crowded as are those on the Late Ordovician *C.* sp., and are always offset across the midline. *Paraconularia packhami* Sherwin, 1970, has a very similar apical angle and spacing of transverse ribs compared to the older *Conularia* sp., but in *P. packhami* the arched transverse ribs are disjunct and apically depressed at the midline, whereas in *Conularia* sp. the transverse ridges are evenly convex toward the aperture and may be both continuous and alternating across the midline.

Distribution

Only known from the Taplow Limestone Member of the Fossil Hill Limestone, Cliefden Caves Limestone Subgroup; early Eastonian (Ea1) age, equivalent to latest Sandbian.

Microconularia gen. nov.

Type species (by monotypy): *Microconularia fragilis* gen. et sp. nov.

Diagnosis

A microscopic conulariid with non-tuberculate widely-spaced transverse ribs, lacking a midline; corners rounded, without furrows.

Discussion

Most Ordovician conulariids are more than 25 mm in length, with only two previously-described species being less than one-tenth this (Leme et al. 2003, fig. 5). Size would not normally be considered

Figure 2 (LEFT). *Conularia* sp. A – D: Four faces of internal cast, MMF 44969; E, G, views of corners of this specimen; F, detail of area of corner outlined on E, showing continuation of transverse ridges across corner sulcus; H, detail of area of face outlined on B, note minute nodes present on four transverse ridges adjacent to midline in lower part of enlargement, and continuation of majority of transverse ridges across midline; I, detail of area of face outlined on D, showing disjunct transverse ridges at midline, and suggestion of interspace ridges in upper part of enlargement. Scale bar in centre of upper row applies to A-E and G; scale bar beneath F applies only to the three enlargements. In both instances the scale bar represents five mm. From Taplow Limestone Member of Fossil Hill Limestone, near Cliefden Caves.

as a distinguishing generic character, but in the case of conulariids there seems to be a clear dichotomy between those forms commonly found in inner and outer shelf environments in a variety of lithologies (where the overwhelming majority are macrofossils), and other taxa that are generally known only from fragmentary remains or microfossils recovered in acid-insoluble residues of limestones. The latter may range from relatively shallow to moderate water depths (BA 2-3), such as those described from Silurian limestones of central NSW (Bischoff 1973) and the island of Gotland, Sweden (Jerre 1993), to deep water (BA 4) settings as interpreted for the forms described here. One genus is less than 2 mm long, and appears to be quite distinct from many described macrofossil conulariids in lacking a definite midline, and in not developing furrows along the corners. Certainly these characteristics seem to qualify for differentiation at genus level, and hence the new genus *Microconularia* is proposed.

Teresconularia Leme et al., 2003, from the Lower Ordovician Santa Victoria Group of the Cordillera Oriental, northwestern Argentina, shares with *Microconularia* the attributes of minute size (length 1.4 mm) and rounded corners lacking a sulcus. However, the Argentine genus is considerably more widely expanding than is *Microconularia*, and the latter genus bears much coarser transverse ribs with strongly angular profiles. The ornament of *Teresconularia* is very fine and crowded by comparison. There is no evidence of a midline on the faces of *Microconularia*, whereas in *Teresconularia* a midline is present, albeit very faintly, being marked by a slight deflection of the otherwise confluent transverse ribs.

Climacoconus pumilus (Ladd, 1929), most recently described and illustrated from the Upper Ordovician Maquoketa Formation of northeastern Iowa by Van Iten et al. (1996), is another unusually tiny conulariid up to 2.5 mm in length. Although it resembles *Microconularia* in its low apical angle and coarse transverse ribs, the two genera are readily distinguished by the pronounced midline and corner sulcus of *C. pumilus*.

The maximum length of *Eoconularia loculata* (Wiman, 1895), from the Silurian Hemse Beds of Gotland, is estimated by Jerre (1994) at 10 mm, approximately 6-7 times as large as *Microconularia*. It resembles the new genus in lacking a midline, and has a similar gradually tapering shape and coarse transverse ribs. However, the presence of a corner sulcus in *E. loculata* distinguishes it from *Microconularia*. The distinctive internal septa of *E. loculata* have not been observed in the two known specimens of the new genus.

Microconularia fragilis gen. et sp. nov.

Fig. 3

Diagnosis

As for genus.

Etymology

Genus name in reference to the microscopic size of the test; species name in reference to the thin and fragile nature of the specimens.

Material

Holotype MMMC 4388 from L37, allochthonous limestone at top of Malongulli Formation, head of Sugarloaf Creek on northeast flank of Malongulli Trig, near Cliefden Caves; paratype MMMC 4389, a fragmentary specimen from the same locality as the holotype; paratype MMMC 4390 from Downderry Limestone Member of the Ballingoole Limestone, Bowan Park Subgroup, near Malachis Hill at Bowan Park.

Description

Test minute, less than 2 mm in length, very gradually tapering with apical angle of the order of 1-3°; cross-section quadrate, with flat to slightly concave faces ornamented with relatively coarse

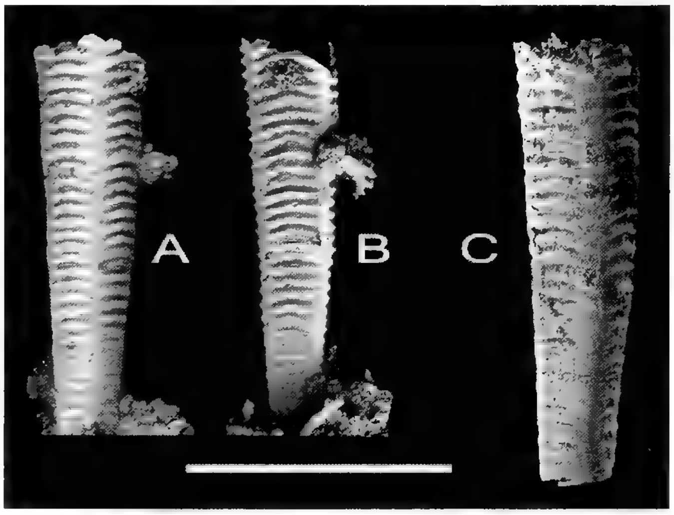

Figure 3. A – C. *Microconularia fragilis* gen. et sp. nov. A – B: Holotype, MMMC 4388, view showing corner, and lateral view of face. C: Paratype MMMC 4390. Scale bar represents one mm. Holotype from locality L37, allochthonous limestone at top of Malongulli Formation on flank of Malongulli Trig; earliest Bolindian (Bo1) age. Specimen C from Downderry Limestone Member of the Ballingoole Limestone, Bowan Park Subgroup, near Malachis Hill at Bowan Park, late Eastonian (Ea3) age.

widely and evenly spaced transverse ribs separated by interspaces of similar length; 14-19 ribs per mm; ribs have angular profile (where not eroded) and are gently and evenly arched; midline lacking. Corners of test rounded without any furrow; transverse ribs from adjacent faces are not continuous around corners, but appear to be offset and alternate so that a rib passes abruptly into an adjacent interspace. Apertural lobes and apex not preserved in available specimens. Internal features unknown.

Dimensions

Holotype MMMC 4388: length 1.5 mm, maximum width 0.3 mm.

Paratype MMMC 4390: length 1.7 mm, maximum width 0.4 mm

Discussion

This exceptionally rare conulariid is represented in two localities, both in allochthonous limestones of BA 4 original depositional depth (inferred on the basis of associated faunas) that have been redeposited downslope. Age of these horizons is reasonably contemporaneous (late Eastonian to early Bolindian).

Distribution

Deepwater strata of late Eastonian (Ea3-4) to earliest Bolindian (Bo1) age, equivalent to Katian Stage, in central NSW.

***Metaconularia* Foerste, 1928**

Type species: *Conularia aspersa* Lindström, 1884

***Metaconularia*? sp.**

Fig. 4

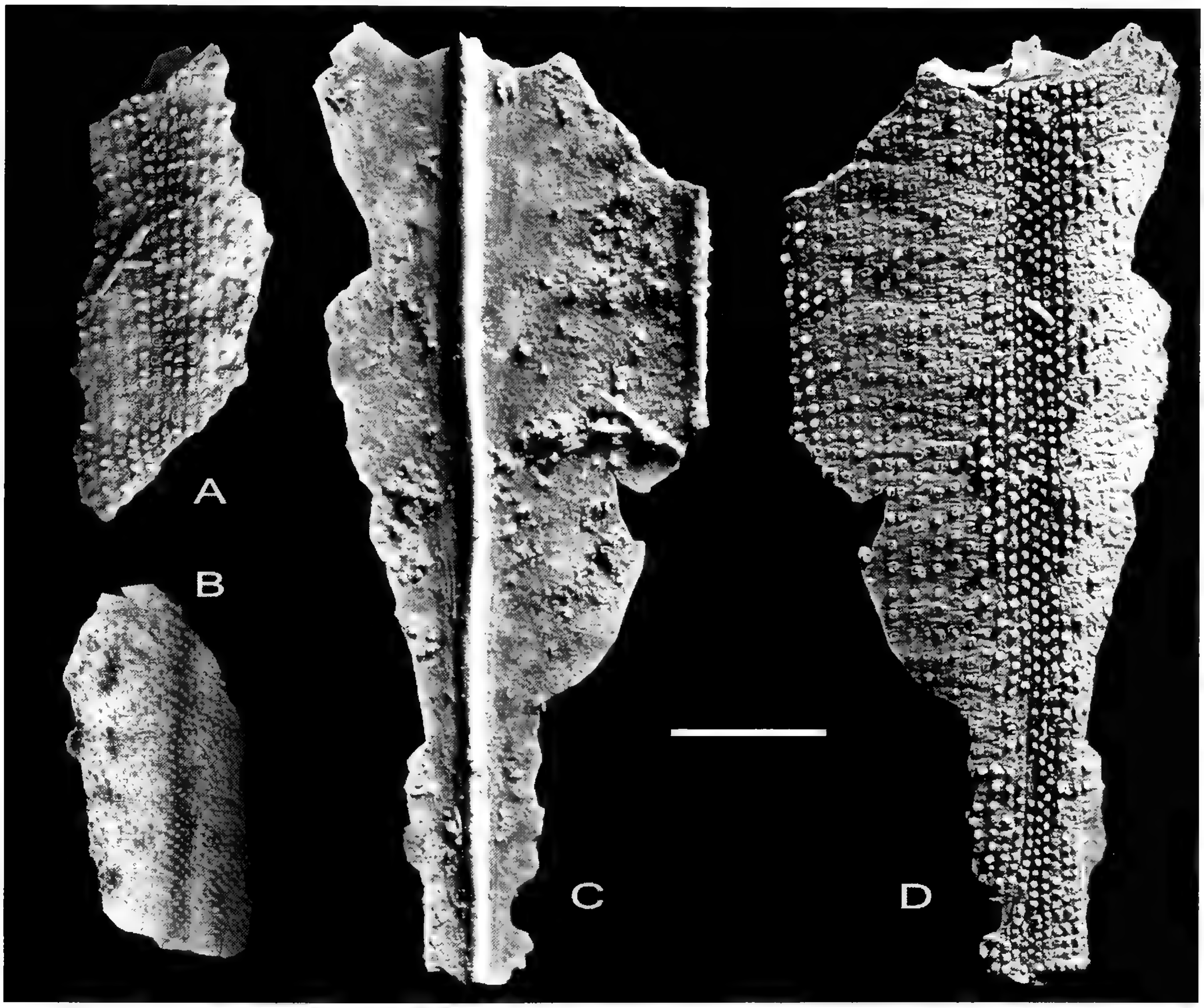

Figure 4. A – D *Metaconularia*? sp. A: exterior fragment, MMMC 4391. B: exterior fragment, MMMC 4392. C – D: interior and exterior of fragment, MMMC 4393. Scale bar represents one mm. All specimens from locality L37, allochthonous limestone at top of Malongulli Formation on flank of Malongulli Trig; earliest Bolindian (Bo1) age.

Material

Fragments with tuberculate ornamentation are uncommon in residues of acid-etched limestones at locality L37, allochthonous limestone at top of the Malongulli Formation, head of Sugarloaf Creek on northeast flank of Malongulli Trig, near Cliefden Caves. Three representative specimens, MMMC 4391 – 4393, are illustrated.

Description

All material consists of incomplete fragments of the test, displaying distinctive coarse and fine tuberculate ornamentation on the exterior surface. The fragments are flat to gently convex, sometimes bearing shallow sulci or furrows, and presumably represent portions of the faces of the theca. Largest fragment observed is 6.3 mm in length. Tubercles are irregularly distributed, generally crowded along shallow furrows in the shell surface (occasionally, a furrow is underlain by a septum on the interior surface of the test) and more scattered on the flanks adjacent to the furrows. A subtle to moderately strongly expressed longitudinal and transverse arrangement of the tubercles into columns and rows is often discernable; the rows may be oblique (Fig. 4B) or perpendicular (Fig. 4D) to the main axis of the specimen. Many (if not all) of the tubercles are hollow, observable where the tips have been eroded. Transverse ridges and interrods are lacking, and sharply defined midlines are not present. Corners between faces are unknown in the available material. Internal septa are low narrow linear features, not twinned; remainder of interior surface is smooth.

Discussion

The tuberculate ornament and absence of transverse ridges on the faces readily distinguishes these fragments from specimens of *Microconularia* with which they are associated in the acid-etched residues. Where septa are present internally, their surficial expression is a crowding of tubercles along a shallow linear depression or furrow; there is no development of a deep narrow midline such as is seen in conulariid fragments from the Silurian age Boree Creek Formation of central NSW (Bischoff 1978, pl. 1, fig. 11a-b).

Jerre (1993) discussed and figured several conulariid fragments with comparable tuberculate ornamentation that he referred to *Metaconularia aspersa* (Lindström, 1884) from the Silurian of Gotland. Bischoff (1973) also recognized similar fragments from both Silurian (Bischoff 1973, pl. 2, figs. 15 and 17) and Ordovician (pl. 3, fig. 11) horizons, but did not attribute these to genera. *Metaconularia* ranges from the Middle and Late Ordovician (Van Iten and Vyhlasová 2004, fig. 14.1) through the Silurian (Leme et al. 2008). The specimens from NSW are too incomplete for definitive identification, so they are tentatively assigned to *Metaconularia* pending collection of more entire material.

Distribution

Recovered only in residues of allochthonous limestone at top of Malongulli Formation; earliest Bolindian (Bo1) age, equivalent to Katian.

Phylum Mollusca Cuvier, 1797
Class Rostroconchia Pojeta, Runnegar, Morris and Newell, 1972
Order Conocardioidea Neumayr, 1891
Superfamily Eopterioidea Miller, 1889
Family Eopteriidae Miller, 1889

***Eopteria* Billings, 1865**
Type species: *Eopteria typica* Billings, 1865

Diagnosis

Eopteriid with a prominent anterior snout that lacks radial ribs (Pojeta et al. 1977, p. 26).

***Eopteria* sp.**
Fig. 5

Material

Figured specimen MMF 44970a, comprising a fragmentary pair of silicified conjoined valves. Several shell fragments definitely attributable to this specimen were also picked from the same limestone residue, as was the isolated posterior extremity MMF 44970b here figured (Fig. 5C). Although the latter cannot with certainty be assigned to the main specimen due to absence of intervening shell, there is a very high probability that it was broken from that specimen.

Description

Valves moderately biconvex, maximum length at hingeline; inflated medial third of valves extends from prominent umbo to ventral margin, and bears about a dozen rounded radial ribs spaced 2-3 per mm; raised ribs not present on snout, which instead bears shallow radial grooves becoming more widely spaced towards anterior extremity. Posterior third of valves also marked with shallow radial grooves. Faint closely spaced concentric growth lines are present on anterior and posterior flanks. Few internal features visible due to fragmentary preservation; however, a prominent

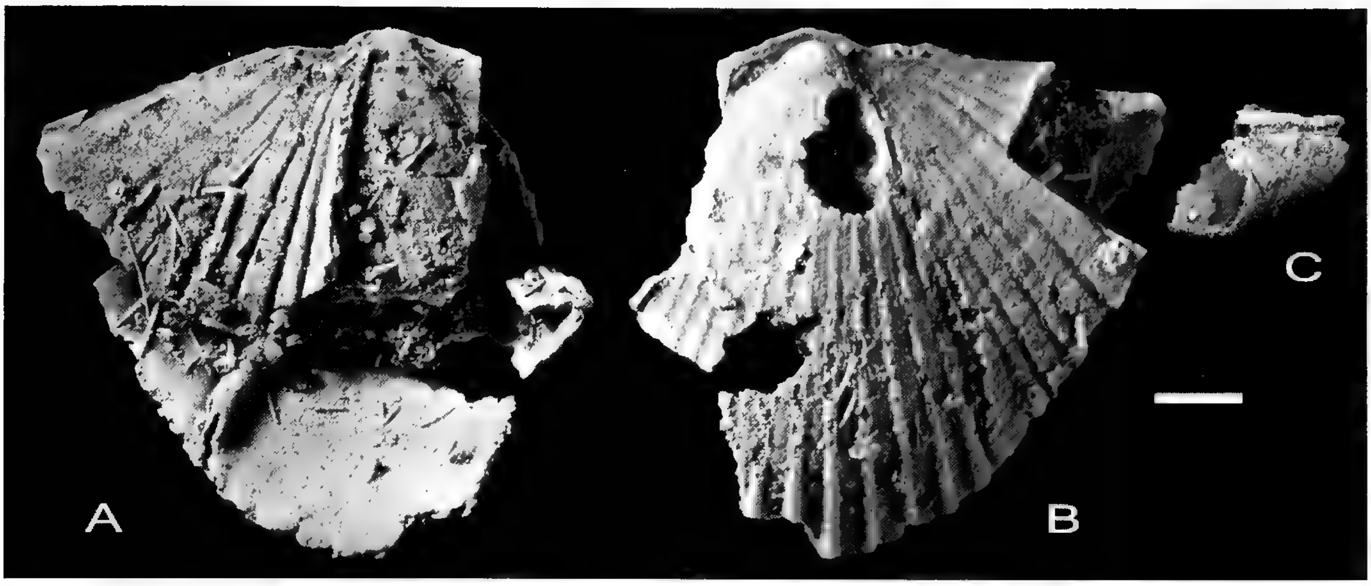

Figure 5. A – C *Eopteria* sp., conjoined specimen MMF 44970. A: left valve; B: right valve; C: fragment of posterior, viewed slightly obliquely. Scale bar represents one mm. Specimen from locality L37, allochthonous limestone at top of Malongulli Formation on flank of Malongulli Trig.

internal ridge is present on the interior of the right valve, trending anteroventrally to intersect the valve margin. Internal shell surface smooth. Presence of pegma not verifiable.

Dimensions

The specimen is incomplete, with length of 6.7 mm, and height of 6.0 mm. The separate posterior extremity is 2.1 mm in length. Estimated maximum dimensions of the complete individual would be 6-7 mm in height, and at least 9-10 mm in length.

Discussion

This was the specimen from NSW referred to by Popov et al. (2003, p.177, pers. comm. by I.G. Percival), in discussion of the palaeogeographic setting of their new species *Eopteria aiteneria* from the Late Ordovician (Hirnantian) Angrensor Formation of north-eastern central Kazakhstan. That species was also described from a single damaged shell, though it is more complete than the NSW specimen which is of almost identical dimensions. However, the two are not conspecific, the most significant point of difference between them being the characteristic lunulate comarginal ornament developed on the anterior snout of *E. aiteneria*. The anterior snout of the NSW species instead bears several shallow radial grooves that possibly define a series of flattened wide ribs progressively decreasing in amplitude away from the inflated umbo. The medial strongly ribbed part of *E. aiteneria* is sharply bounded by carinae, particularly posteriorly, whereas the NSW species is more evenly rounded with a relatively gradual change in slope from the median region to the adjacent flanks. The presence of an internal ridge in the right valve of *E. aiteneria* cannot be verified as the interior of this species is unknown.

The only other known Late Ordovician species of *Eopteria* is *E. conocardiformis* Pojeta and Runnegar, 1976 from the Little Oak Formation of Alabama and the High Bridge Group of Kentucky, which is characterized by an elongation of the anterior snout. It also appears to be considerably more inflated than the species from NSW. Cope (2004) assigns an early Late Ordovician (Sandbian equivalent) age to this species. Thus *Eopteria* sp. from NSW, of late Katian age, is significant in partly bridging the gap between the Laurentian and Kazakhstan occurrences, where previously no species referable to this genus were known (Cope 2004, fig. 20).

Although *Eopteria* sp. can be readily distinguished from these Late Ordovician (and older) species, it would be unwise to establish a new species based on such fragmentary material, and so the specimen is left in open nomenclature.

Distribution

Recovered only in residues of allochthonous limestone at top of Malongulli Formation at locality L37; earliest Bolindian (Bo1) age, equivalent to late Katian.

Class Cephalopoda Cuvier, 1797
Subclass Nautiloidea Agassiz, 1847
Order Tarphycerida Flower, in Flower and Kummel, 1950
Family Plectoceratidae Hyatt, 1894

Genus *Plectoceras* Hyatt, 1894

Type species: *Nautilus jason* Billings, 1859

Plectoceras? sp.

Fig. 6

Material

Specimen MMF 44971, represented by a composite cast, mostly decorticated; this specimen was longitudinally sectioned for study.

Description

Conch exogastric, planispiral, tightly coiled with three whorls all in contact, gently expanding from 6-7 mm height in inner whorls to attain 16.5 mm in height at body chamber which is approximately 21 mm in length; whorl expansion rate (WER) 1.78. Exterior with moderately coarse rounded ribs directed apicad and forming a wide V-shape at midline; 3-4 ribs in 10 mm. Chambers are rounded subquadrate in cross section, moderately inflated and gently impressed

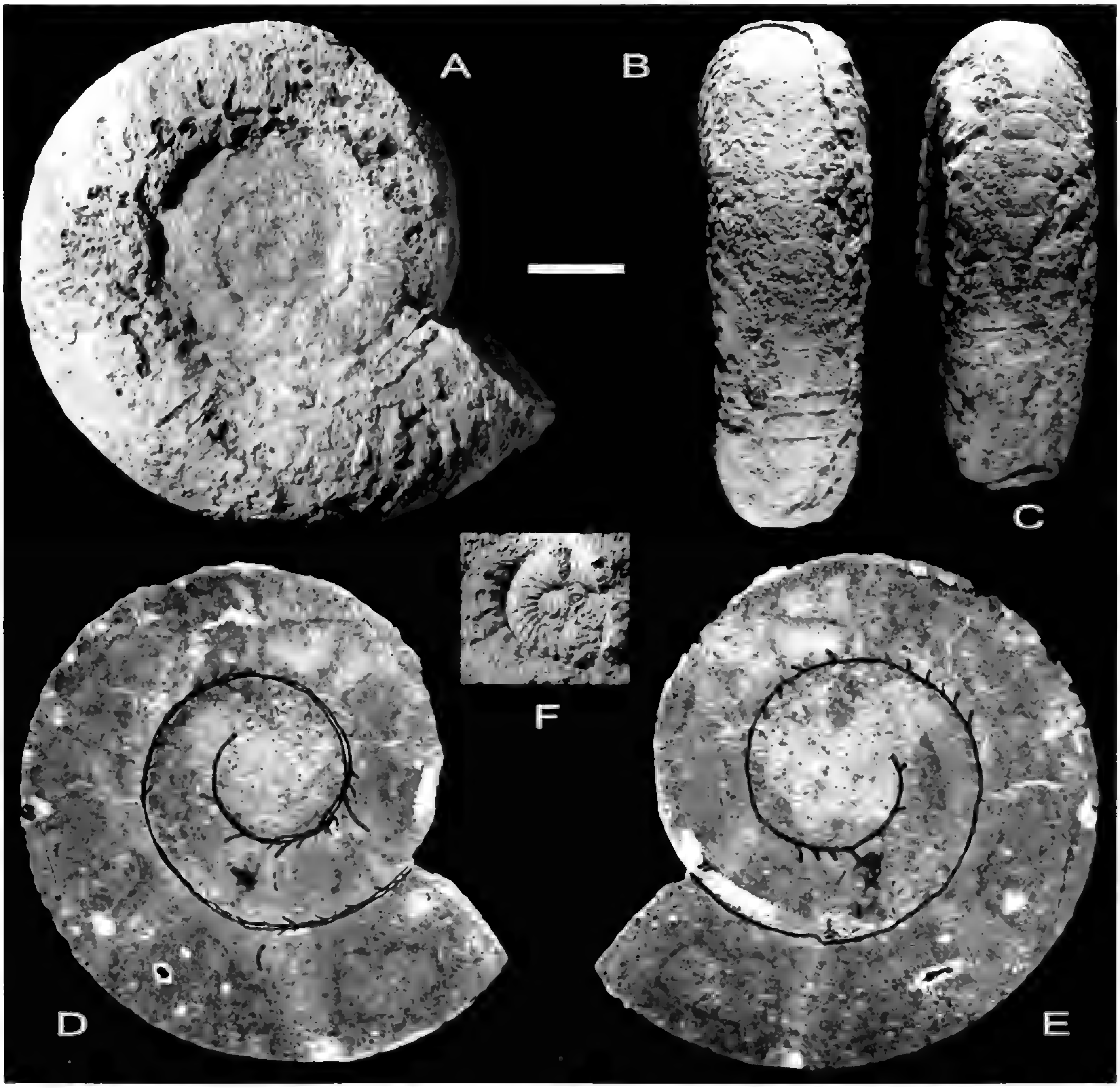

Figure 6. A – E *Plectoceras*? sp., MMF 44971. A – C: conch (prior to sectioning) in lateral view, and two whorl profiles (slightly rotated) showing ornament and camerae; D – E: longitudinal section through conch, D off-centre, and E sagittal, with internal features inked-in for clarity. Note in E, remains of siphuncle (ventral in position) infilled with calcite immediately above body chamber. F. fragment of exterior of indeterminate tarphyceratid nautiloid, MMF 44972. Scale bar represents one cm. Both specimens from Gunningbland Formation at locality L51, "Currajong Park", Gunningbland.

dorsally. Camerae behind body chamber gently flexed towards aperture and spaced up to 4.3 mm apart, narrowing to about 2 mm apart in inner whorls where they extend straight across venter. Siphuncle only partly visible as a calcite-filled tube with diameter of 2.4 mm, ventral and marginal in position; septal necks and connecting rings not preserved.

Dimensions

Maximum diameter of conch 60 mm; width of body chamber 20.0 mm.

Discussion

Due to its poor internal preservation, with septal necks absent and the siphuncle inadequately preserved, identification of this specimen to genus level remains tentative at this time pending the discovery of additional better-preserved material. The ventral position of the siphuncle and strongly ribbed coiled conch invites comparisons with tarphyceratids. Of Middle to Late Ordovician genera, the most similar to the Gunningbland specimen appears to be *Plectoceras*, which is represented by numerous species in North America. Frey (1995) observed that these species fell into two major groups, one comprising forms that are generally smaller in diameter in which the whorls remain in contact, contrasting with the second group of generally larger conchs (including the type species) in which the final whorls became disjunct. Affinities of the Gunningbland species lie with the first of these species groups.

The relatively low WER is also similar to that of *Tarphyceras*, but that predominantly Early Ordovician genus is typically nearly smooth externally (B. Kröger, pers. comm.). Two species of ribbed coiled nautiloids of latest Ordovician (Hirnantian) age from the Morkoka River region of the Siberian Platform were identified as *Tarphyceras*? by Balashov (1962). Illustrations of one of these, *T*? *morkokense* Balashov, 1955, clearly show a ventral submarginal siphuncle. Dimensions of the type specimen (Balashov 1955, pl. XLIII fig. 3a-b; refigured by Balashov 1962, pl. XLVI fig. 3) are very similar to those of *Plectoceras*? from Gunningbland.

Stait et al. (1985, fig. 10) documented an incomplete external cast of a strongly ribbed coiled nautiloid from immediately overlying beds in the Gunningbland Formation, which, in the absence of any internal features, could only be referred to an indeterminate tarphyceratid. This specimen is very possibly congeneric with the one described here as *Plectoceras*? as it shares comparable dimensions and external features. An additional fragmentary exterior of a similar unidentified coiled nautiloid with coarse ribbing is illustrated (Fig. 6F). Slightly younger tarphyceratids, again with prominent ribs, have been found in the Jingerangle Formation (of early Bolindian age, i.e. latest Katian) near Quandialla, about 95 km south of Gunningbland (Percival et al. 2006), but as all are preserved as moulds the position of the siphuncle and other internal features is unknown.

Distribution

Gunningbland Formation (upper part), "Currajong Park" property at Gunningbland; late Eastonian (Ea3-4), equivalent to early Katian.

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Devonian Marine Invertebrate Fossils from the Port Macquarie Block, New South Wales

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Two assemblages of rugose and tabulate corals, with accessory stromatoporoids and chaetetids, are described from the Touchwood and Mile Road Formations of the Wauchope – Port Macquarie district of northeastern New South Wales. Both assemblages are derived from allochthonous limestone clasts, except that the Mile Road fauna is accompanied at the same level by branching tabulate corals occurring in the matrix, indicating probable contemporaneity. The fauna from the Touchwood Formation indicates an Early Devonian (Emsian) age. Macrofossils from the Mile Road Formation indicate a broad Middle Devonian, probably Givetian age; conodonts accompanying the coral assemblage yield a precise age in the upper part of the early Givetian *varcus* Zone. Geographic affinities of the assemblages are typically eastern Australian, so that if terranes are represented in the block, these were not remote. Stratigraphic and structural relationships of the units are discussed. The name Mile Road Formation is formally defined.

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Key words: chaetetids, conodonts, Devonian, Emsian, Givetian, Mile Road Formation, Port Macquarie Block, Rugosa, stromatoporoids, Tabulata, Touchwood Formation.

INTRODUCTION

Immediately west of Port Macquarie, some 350 km north of Sydney, Palaeozoic units of the New England Fold Belt are exposed in a series of narrow belts delimited by NNE-striking faults (Fig.1) (Leitch, 1980; Roberts et al., 1995). Stratigraphic relationships between the units and their relative ages are not clear, so indications of age are particularly important in geological interpretations of the area. The ages of these rocks have been little constrained by published biostratigraphic data, with the only firm determinations those yielded by conodonts of Middle-Late Ordovician age from chert in the structurally dismembered Watonga Formation (Och et al., 2007), earlier attributed a Silurian or Devonian age on the basis of meagre conodont and radiolarian faunas (Ishiga et al., 1988). Unpublished reports by Pickett (1985, 1991) presented evidence for the Devonian age of limestone from two other units, the Touchwood Formation (Leitch, 1980) and the Mile Road Formation (Taylor, 1984, unpublished; Roberts et al., 1995). The present article is principally based on the re-examination of material described by Pickett, augmented by additional collecting. This has led to some refinement of the initial results, tectonically valuable biogeographic information, and a new stratigraphic interpretation. A formal description of the Mile Road Formation is included as Appendix 1.

STRATIGRAPHIC UNITS

The *Mile Road Formation* has only been recognized in the southern part of the wedge of rocks bounded by the Sancrox, Cowarra and Sapling Creek faults (Fig. 1) where it comprises interbedded fossiliferous siltstone and sandstone, containing blocks of coralline limestone and silicic tuff. The rocks form a sequence at least 1500 m thick, dipping steeply

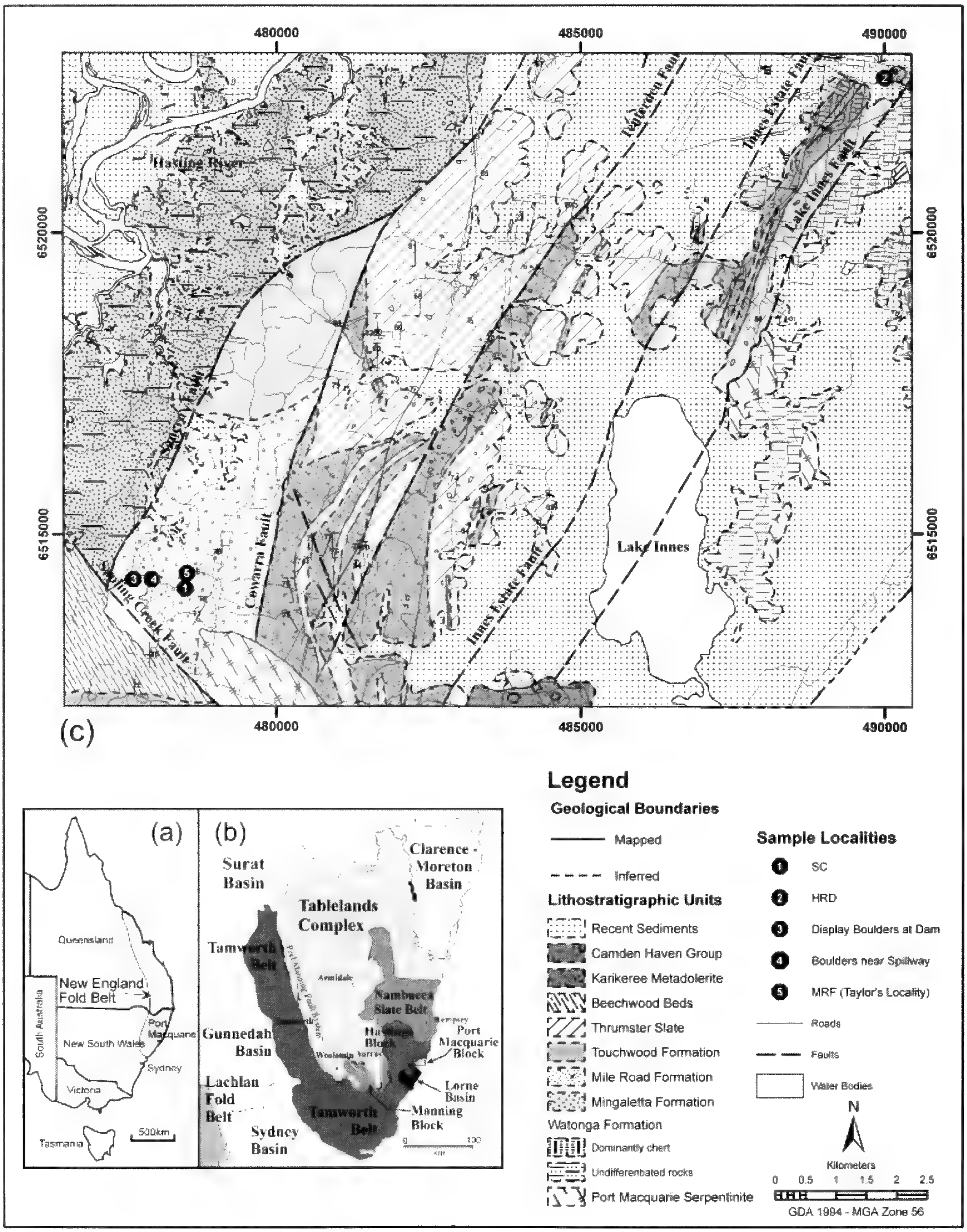


Figure 1. Geological map of Wauchope – Port Macquarie area.

mostly to the west, and younging in this direction, based on meagre data from near the intersection of Cowarra Access Road and the Mile Road (GR 478900 6514400, Grants Head 1:25 000 sheet). Strike ranges from northeast away from the Cowarra Fault to almost north close to the fault. Sandstone is volcaniclastic and of silicic, probably dacitic, provenance, with abundant detrital plagioclase and vitric and felsitic lithic grains, and uncommon monocrystalline quartz grains. Many grains are angular and little abraded suggesting the rocks include abundant little modified ash. Finer grained rocks are of similar composition. Scattered coral, brachiopod and crinoid fossils are locally prominent in the clastic rocks some of which are extensively bioturbated (cf. Fig. 7C). Coralline limestone occurs as blocks embedded in fossiliferous sandstone and siltstone and locally (GR 478400 6514100) as weathered-out boulders up to about 1 m across that may originally have been derived from autochthonous lenses beyond the outcrop area. Silicic tuff is prominent in the lower part of the formation where it forms hard grey beds up to at least 0.25 m thick. It is of similar composition to the sandstones but distinguished by the presence of well-preserved shard structures in which the original glass has been replaced by fine-grained quartzofeldspthic aggregate. Euhedral plagioclase grains are widespread although broken angular grains are also common.

The *Touchwood Formation* is exposed between the Lake Innes and Innes Estate faults (Fig.1) from where it was described by Leitch (1980) as consisting of a sequence of siltstone, sandstone, paraconglomerate, basalt breccias and andesite at least 600 m thick. Much of the stratigraphically lower sedimentary part of the formation here is thin-bedded and consists predominantly of simply graded grey sandstone and darker horizontally laminated siltstone. Rare paraconglomerate beds, up to at least 20 m thick and the upper part of which are simply graded, contain clasts of basalt and andesite, slabs of bedded intraformational material and cobbles of coralline limestone.

Further west, between the converging Sancrox and Cowarra faults north of the Mile Road Formation, Taylor (1984) mapped thin bedded siltstone, some radiolarian-bearing, graded and massive sandstone, chert and andesitic breccia as Touchwood Formation. He considered these rocks were faulted against the Mile Road Formation, an interpretation followed by Roberts et al. (1995). The contact between the two units is unexposed and occurs in a region of very little outcrop. Although it may be a fault, on the basis of structural and younging indications in both units, we favour interpretation as a stratigraphic contact, with Touchwood overlying the Mile Road (but see below under Discussion).

Like those of the Mile Road Formation, Touchwood sandstones are volcaniclastic but differ in being of more mafic provenance. Abundant detrital components are lathwork and microlitic lithic grains and plagioclase; felsitic and vitric grains and quartz are uncommon, and calcic clinopyroxene is widespread but mostly only in small amounts.

FOSSIL LOCALITIES

The fossils described in this article come from three localities. The first (HRD) lies within the Touchwood Formation in its type section (Leitch, 1980), the material coming from a disused quarry on the eastern side of Aston Street, north of the Hibbard – Port Macquarie road (Hastings River Drive) at GR 490000 6522560 (m), Port Macquarie 1:25,000 sheet (9435-2S). The material was originally collected by Erwin Scheibner, and is supplemented by samples taken by the present authors; Leitch's (1980, p. 278) first mention of fossils is restricted to reporting rugose and tabulate corals. The second (MRF) is within the informally named "Mile Road Formation" of Taylor (1984) in a creek-bed in wooded country west of Forest Road at GR 478400 6514100 (m), Grants Head 1:25,000 sheet. The material was originally collected by Michael Taylor, and his formation name is formalised herein.

Locality MRF could not be re-located using the information supplied by Taylor, but a general search led to a third locality (SC) in the bed of Sarahs Creek south of the ford on an unnamed forestry track at GR 478500 6514100 on the Grants Head 1:250,000 sheet (9434-1N). Here the mudstones of the Mile Road Formation dip 65° to 145°, and contain abundant fragments of the branching tabulate coral *Thamnopora* over a stratigraphic interval of possibly 30 m; near the middle of this interval there are also larger blocks of limestone made up of large colonies of massive favositid and heliolitid corals, the largest with maximum dimensions of c. 700 x 450 mm. The broken fragments of *Thamnopora* which occur in the matrix indicate that the larger blocks were derived penecontemporaneously.

During the construction of Cowarra Dam a number of large blocks of allochthonous limestone were uncovered, the largest of which are now on display at the picnic area near the dam wall. The assemblages in these blocks indicate that their source is the same as that of the blocks originally collected by Taylor, but the assemblages they contain are much richer. In addition to the small assemblage originally reported by Pickett (1985) and supplemented herein, the blocks include large colonies of a large species of *Spongophyllum*, *Syringopora* sp., *Heliolites* sp., a cystiphyllid, a large solitary rugosan and *Squameofavosites* sp., as well as brachiopods. Because of the display situation, none of this material could be collected. The display boulders were obtained from a locality now covered by the dam wall at GR 477650 6514250 (Grants Head sheet), and more material near the spillway at GR 477950 6514250. All these localities within the Mile Road Formation are roughly aligned in a WNW

– ESE direction, suggesting an episode of slumping of limy material during deposition of what is probably the older part of the formation.

The environmental setting of all localities is similar, in that the fossils are allochthonous, being derived from clasts in slump deposits. At locality HRD the limestone clasts are small, the largest observed being about 35 cm in maximum dimension; some of the soft-sediment clasts in this deposit exceed a metre in maximum dimension. All the limestone and fossil clasts from the Mile Road Formation however are considerably larger, suggesting that their source lay much closer than in the case of the Touchwood Formation.

AGES OF THE OCCURRENCES

The occurrences of coralliform taxa are listed in Table 1. Those forms only identified in the field (marked with an asterisk) are not used for age determination. Detailed discussion is supplied in the Systematics section, under "Remarks" for each of the relevant taxa.

Touchwood Formation. Significant for the age of this unit are *Xystriphyllum* cf. *mitchelli minus*, known only from the mid-Emsian *perbonus-gronbergi* Zone, *Acanthophyllum* sp., whose congeners are restricted to the Emsian in eastern Australia, and *Sterictophyllum* sp., whose genus is typically Pragian. *Phillipsastrea*

Table 1. Occurrences of coral taxa in the Mile Road and Touchwood Formations.

	HRD **Ashton St Quarry** **Touchwood Fm**	**MRF** **Cowarra Dam** **Mile Road Fm**	**SC** **Sarahs Creek** **Mile Road Fm**
Chaetetes sp.	x		
Coenostroma sp.	x		
Endophyllum cf. *columna* Hill		x	
Acanthophyllum sp	x		
Xystriphyllum cf. *mitchelli minus* Parker	x		
Phillipsastrea cf. *maculosa* Hill	x		
Sterictophyllum sp.	x		
Favosites salebrosa Etheridge fil.			x
Pachyfavosites sp.	x		
Squameofavosites squamuliferus Etheridge fil.	x		
Cladopora sp.	x		
Thamnopora randsi Jell & Hill			x
Alveolites sp. A	x		
Alveolites sp. B		x	
Heliolites daintreei group IV Jones & Hill			x
**Spongophyllum* sp.		x	
**Syringopora* sp.		x	
*?*Squameofavosites* sp.		x	
**Heliolites* sp.		x	
*cystiphyllid		x	
*large solitary rugosan		x	

maculosa is known from Pragian and Emsian strata, and the *Squameofavosites squamuliferus* group is typically Early Devonian, although it does range down into the uppermost Silurian. Some further slight support for an Emsian age is indicated by the occurrence of the stromatoporoid *Coenostroma*. In summary, the assemblage is taken to indicate a later Early Devonian age, with a high probability of its being Emsian.

Mile Road Formation. The coral assemblages from this unit are less reliably indicative of age than those of the Touchwood Formation. The best indicator is probably *Endophyllum* cf. *columna*, which suggests a mid-Givetian age. *Thamnopora randsi*, on the other hand, is only known reliably from the mid-Emsian, whereas *Favosites salebrosa* is apparently more typical of Eifelian strata. A small amount of material, offcuts from the original collection of Michael Taylor, was digested in acetic acid (Geological Survey of NSW sample C880), and yielded material of conodont species which indicate a precise age: *Polygnathus linguiformis klapperi* Clausen et al., 1979, *Polygnathus linguiformis weddigei* Clausen et al., 1979, *Polygnathus hemiansatus* Bultynck, 1987 and *Icriodus difficilis* Ziegler et al., 1976. The area of overlap of the ranges of these species, as given by Bultynck (1987, fig. 9) lies in the upper part of the lower *varcus* Zone, of early Givetian age. These taxa are illustrated in Fig. 2.

DISCUSSION

In the Touchwood Formation the dated material all occurs as clasts, and in the Mile Road Formation at least some of the dated material occurs as blocks embedded in a clastic matrix, and none has been shown unequivocally to be autochthonous. Thus the dates provide a maximum age for the units. The presence of fossils in the matrix as well as in blocks in the Mile Road Formation suggests the blocks are penecontemporaneous and hence the Givetian age is taken as that of at least part of the Mile Road Formation. For the Touchwood Formation the interpretation is more equivocal. The limestone here occurs only as clasts which are restricted to a single bed that is a debris flow or the product of a high density turbidity current. Fossils are absent from the surrounding rocks. There is no record of Devonian limestone clasts in any of the Carboniferous or Permian units in this region, and the rocks are of a more mafic provenance than any of the latter units but similar to those of the Frasnian Birdwood Formation of the Yarras district some 25 km further west (Roberts et al., 1995). This suggests the age of the formation lies within the Emsian - Frasnian range, and on the basis of its stratigraphically overlying the Mile Road Formation can be further restricted to Givetian - Frasnian. However, the rocks north of Cowarra Dam mapped as Touchwood Formation have so far yielded no fossils, and the age suggested by the assemblage from the type area is older (Emsian) than that of the possibly underlying Mile Road Formation (early Givetian). Thus either the assemblage from the Touchwood formation in its type area does not yield a true age for the formation or, as originally interpreted by Taylor (1984), the contact between Mile Road Formation and Touchwood Formation north of Cowarra Dam is faulted.

It is noteworthy that the aspect of all fossil

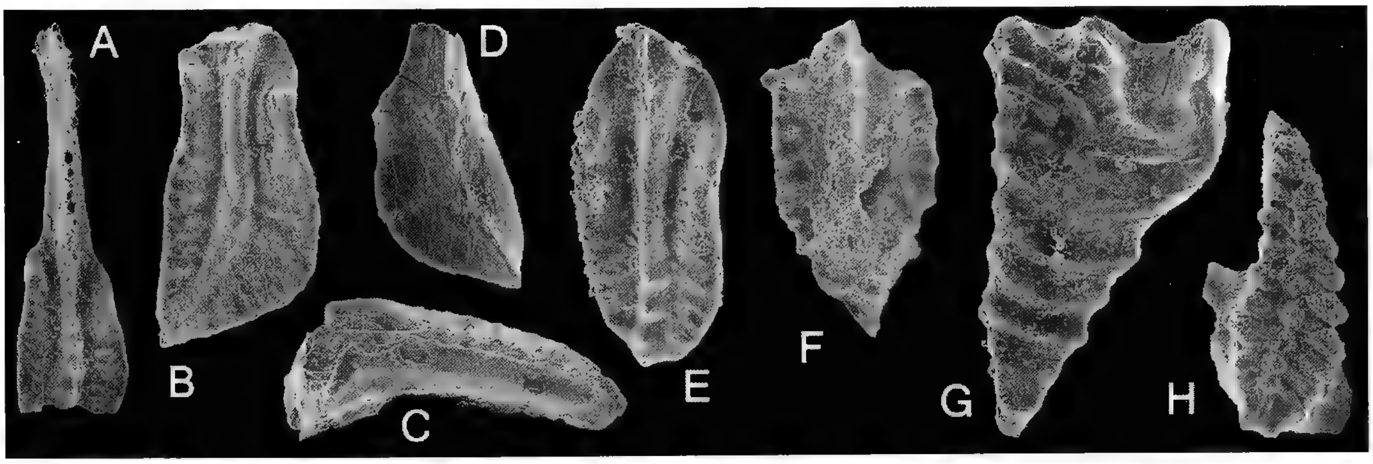


Figure 2. Conodonts from the Mile Road Formation, all x10 except A, x7.5, and E, x20. A–E, Pa elements of *Polygnathus hemiansatus* Bultynck, 1987, B and C are oral and oblique views of the same specimen; E is a juvenile. F, Pa element of *Polygnathus linguiformis weddigei* Clausen et al., 1979. G, Pa element of *Polygnathus linguiformis klapperi* Clausen et al., 1979. H, icriodiform element of *Icriodus difficilis* Ziegler et al., 1976.

assemblages is typically Australian. Several taxa are ascribed to Australian species (*Endophyllum* cf. *columna*, *Xystriphyllum* cf. *mitchelli minus*, *Phillipsastrea* cf. *maculosa*, *Favosites salebrosa*, *Thamnopora randsi*), and the *Squameofavosites squamuliferus* group is very common in Early Devonian assemblages throughout eastern Australia. The genus *Sterictophyllum* is not known outside Australia. Thus although the rocks have been displaced along with the rest of the Hastings Block (e.g. Cawood and Leitch, 1985) their original location was well within the Australian province, probably from a southern continuation of the Tamworth Belt (Roberts and Geeve, 1999). It is also worth noting that in the latter a change in sediment provenance from a region in which intermediate and silicic volcanism was widespread to one dominated by mafic volcanic occurred in the Middle Devonian (Cawood, 1983), a change similar to that which occurred between deposition of the Mile Road and Touchwood Formations.

SYSTEMATIC PALAEONTOLOGY

The material discussed below is held in the collections of the Geological Survey of NSW, indicated by the prefix MMF. Specimens prefixed AM or AMF are held in the Australian Museum, Sydney. Literature citations for authors of taxa above the family level are not cited in the references; they may be found in Hill (1981).

Phylum PORIFERA Grant, 1836
Class ?DEMOSPONGIAE Sollas, 1885
Order uncertain
Family CHAETETIDAE Milne-Edwards & Haime, 1850

Genus *Chaetetes* Fischer von Waldheim in Eichwald, 1829

Type species

Chaetetes cylindraceus Fischer von Waldheim, 1829.

Remarks

The taxonomy of the fossil group informally known as chaetetids has been in a state of flux since the recognition that certain Recent sponges have a chaetetid morphology, although their spicular morphology indicates that they are demosponges (e.g. *Ceratoporella*: Hartman & Goreau, 1972; *Acanthochaetetes*: van Soest, 1984). In the last overview of chaetetids as a taxonomic group (Hill, 1981) they were regarded as tabulate corals; in recent treatises on Porifera (Hooper & Van Soest, 2002; Finks et al., 2004) they have been largely ignored, at least in terms of updated taxonomy: of the twenty-nine available generic names given by Hill (1981) in her review of the "Order" Chaetetida, only two are mentioned in Finks et al. (2004) and three in Hooper & Van Soest (2002). On the other hand, modern genera of "sclerosponges" with chaetetid morphology receive more exhaustive treatment. It is clear from Hill's (1981) introductory remarks that she regarded the group as polyphyletic, but she has also rendered the service of bringing together those names relating to a particular group of morphologies.

In the past, the vertical tubes of chaetetids have usually been referred to as corallites. In view of their highly probably sponge nature this seems inappropriate, so they are here referred to as calicles, the term favoured for similar features in *Ceratoporella* (e.g. Hartman & Goreau, 1972).

Chaetetes sp.

Figure 3 D-G

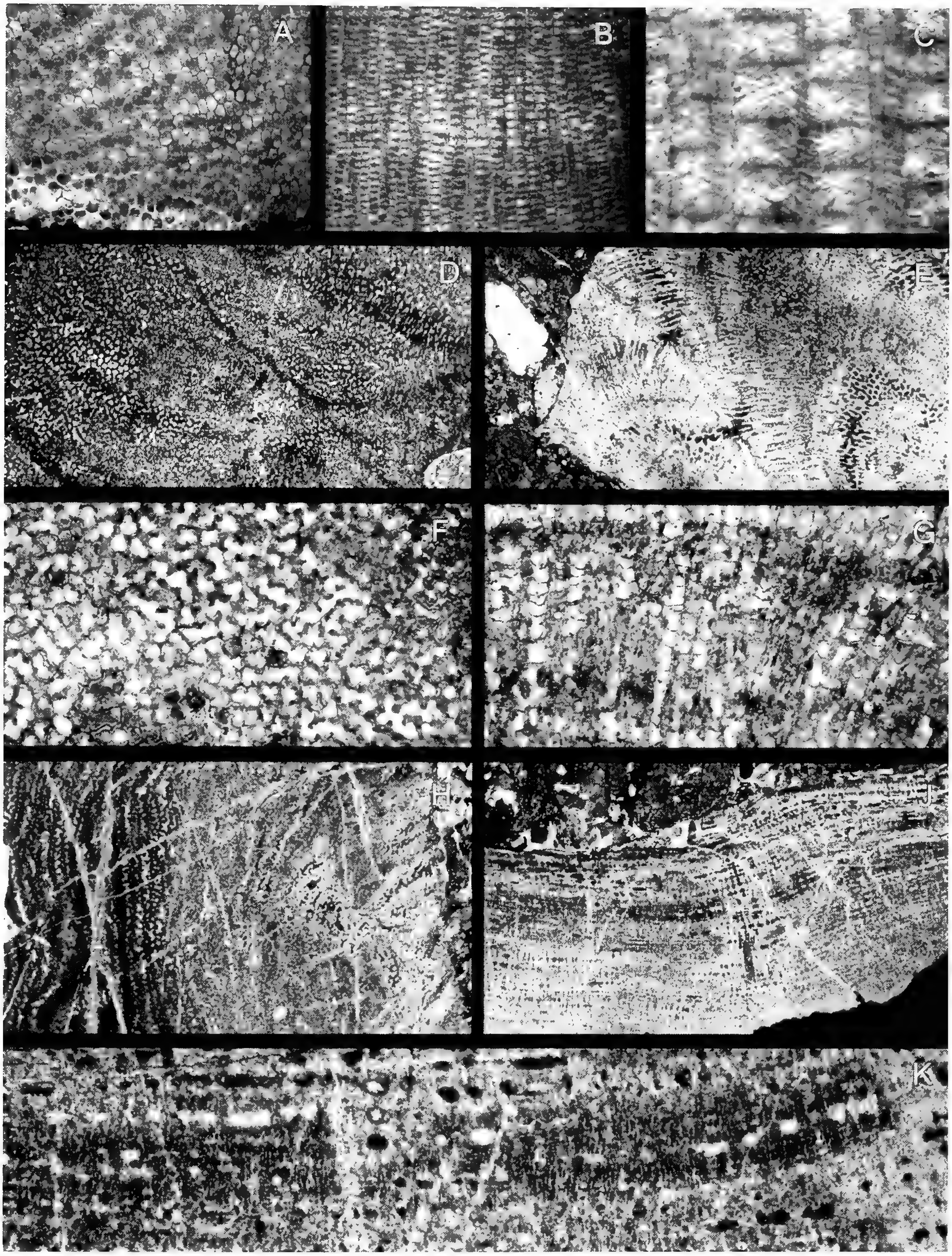
Material

Two specimens, MMF 32039 and 32040, with six thin sections. Locality HRD, probably Emsian.

Description

The species forms small, compact masses reaching at least 5 cm in diameter and 3 cm in height. The shape appears to have been more or less hemispherical, but some thin sections show a surface which bears low mamelons about 7 mm in diameter,

Figure 3 (RIGHT). Spongiomorphs. A-C, topotype specimen of *Litophyllum konincki* (Etheridge & Foord, 1894), MMF884, Reid River Limestone, Reid Gap, S of Townsville, Queensland. A, B, transverse and longitudinal sections, x6; C, detail of B showing vertical trabeculae, x20 approx. D-G, *Chaetetes* sp., Touchwood Formation, locality HRD. D, transverse section, MMF32039b, x 3; E, longitudinal section of specimen with irregular surface, MMF32040a, x3; F, transverse section, MMF32039a, x10; G, longitudinal section, MMF32039c, x10. H-K, *Coenostroma* sp., Touchwood Formation, locality HRD. H, K, tangential and longitudinal sections, MMF44850, x4.5; J, detail of K showing microstructure of micropillars, x15.



whereas others have a smooth surface.

The skeleton is for the most part recrystallised, but some areas reveal it to have been composed of fine, near-vertical monacanthine trabeculae about 0.05 mm in diameter (Fig. 3G). The trabeculae are united to form walls defining subrounded calicles about 0.2 mm in internal diameter; wall thickness at the mid-point is 0.1 – 0.15 mm. In some areas the calicles are interconnected uniserially, but in a rather meandering pattern (Fig. 3F); in longitudinal section these appear as pores in the walls. The calicles are traversed by fine, rather sagging tabulae c. 0.02 mm thick, generally separated by a distance greater than the width of the calicle, though this is not always the case; they number about eleven in 5 mm. The tabulae display a marked tendency to occur at similar levels in adjacent calicles, and may even be continuous through the mural pores.

Remarks

Chaetetids have been reported from Australia in a number of publications. Etheridge & Foord (1884) described *Amplexopora konincki* from Reid Gap, south of Townsville, north Queensland (Reid River Limestone, Emsian); Etheridge (1899) reported the species from Tamworth in NSW and erected for it the genus *Litophyllum*. Etheridge's specimen of *L. konincki* from Tamworth (Australian Museum specimens AM3940, 3941, Moore Creek, near Tamworth, presumably from the Eifelian Moore Creek Limestone) is too recrystallised to show details of wall structure; it is impossible to recognise whether or not there were trabeculae. It does show rare connections between calicles. A topotype specimen (MMF884), rather recrystallised, shows a microstructure of vertical trabeculae similar to those of the Port Macquarie material and of other species of chaetetids (Fig. 3C). However, the tabulae are crowded (23 in 5 mm) and the spaces between them always less than the calicle diameter. Connections between the calicles are rare. I can see no reason for separating *Litophyllum* from *Chaetetes* itself.

Chapman (1918) described *Ch. stelliformis* from Early Devonian Loomberah Limestone of the Tamworth area and, in 1920, *Ch. spinuliferus* from an Early Carboniferous Limestone in the Parish of Mooroowarra, i.e. near Somerton, NSW. Most of the material reported with this locality information derives from the hill known as Watts, Babbinboon (Visean; cf. Campbell, 1957; Pickett, 1967; Moore and Roberts, 1976), but, in spite of intensive collecting, the species has not been found there again. The type specimen in the Museum of Victoria (P73813, with a longitudinal section; the transverse section is apparently lost) is clearly a favositid of the *squamuliferus* group, revised by Philip (1960), though not included in his revision; the age of the specimen is therefore most probably Early Devonian, and the locality data given by Chapman erroneous, since there are no outcrops of Early Devonian rocks within the Parish of Mooroowarra. The species *stelliformis* is now considered a tabulate coral, *Squameofavosites* (Hill, 1950; Philip 1960). Pohler (1998) reported *Pachytheca* cf. *abdita* Yanet, 1972 (in Breyvel' et al., 1972) from a stromatoporoid bioherm in the Moore Creek Limestone Member of the Yarrimie Formation (Eifelian), but the material was not illustrated or described. It may be that this is the same form as Etheridge's (1899) *Litophyllum konincki*.

Material of *Chaetetes* (MMF44896-7) from the Uglovka Formation in Uglovka quarry, Russia (upper Serpukhovian) is interesting in that one of the specimens grew with a smooth surface, while the other bore abundant mamelons, just as in the Port Macquarie material, suggesting that this apparent dimorphism was a regular feature of chaetetids.

Hill (1981) also included desmidoporids and lichenariids in the order Chaetetida, and the genera *Desmidopora* and *Lichenaria* have both been reported from Australia (Etheridge, 1902; Fitzgerald, 1955; Hill, 1955, 1957). These occurrences are either Ordovician or Silurian; they differ considerably from the present material, and their taxonomic status is not discussed here.

Class STROMATOPOROIDEA Nicholson and Murie, 1878
Order SYRINGOSTROMATIDA Bogoyavlenskaya, 1969
Family COENOSTROMATIDAE Waagen and Wentzel, 1887
Genus *Coenostroma* Winchell, 1867

Type species

Stromatopora monticulifera Winchell, 1866.

Coenostroma sp.

Figure 3 H-K

Material

MMF44860 from locality HRD.

Description

Specimen fragmentary, but in excess of 32 mm wide and 9 mm high. Surface apparently smooth and undulose. Coenostromes dominant, varying widely in thickness from 0.05 to 0.25 mm 8 – 11 in 2 mm, separating galleries 0.07 – 0.13 mm high, and which are subrounded to rather wider than high, consistently on the same level, generally discrete in longitudinal section, but occasionally joined laterally over six or more adjacent galleries. The transverse section shows a single walled tube 0.6 mm in diameter which may be a syringoporellid corallite. Coenosteles strongly superimposed, up to 20 observed in a vertical series, appearing rather meandrine in tangential section. Microstructure reticulate, of clearly defined micropillars which are normal to the surface, appearing as dark spots in tangential section.

Remarks

Coenostroma species do not form a conspicuous element of eastern Australian Early and Middle Devonian faunas, as far as they are known (e.g. Webby et al., 1993; Webby & Zhen, 1993, 1997), the only published report being *Coenostroma* sp. from the Early Emsian (*dehiscens* Zone) Buchan Caves Limestone and Heath's Quarry, Buchan, Victoria (Webby et al., 1993). The present material differs from this in its more crowded coenostromes, coenosteles which are more strongly superposed, and apparently also in the prominent micropillars of the coenosteles.

Phylum COELENTERATA Frey and Leuckart, 1847
Class ANTHOZOA Ehrenberg, 1834
Subclass RUGOSA Milne Edwards and Haime, 1850
Order STAURIIDA Verrill, 1865
Family ENDOPHYLLIDAE Torley, 1933

Genus *Endophyllum* Milne-Edwards & Haime, 1851

Type species

Endophyllum bowerbanki Milne-Edwards & Haime 1951.

Endophyllum cf. *columna* Hill, 1942a

Figures 4 A-B, 5A

Material

MMF29212a, 29213a, with two thin sections. Locality MRF.

Description

Corallum cerioid, exceeding 10 cm in diameter. Epitheca 0.4 – 0.5 mm thick, showing strong median dark line. Maximum corallite diameters are 7 – 10 mm. Septa 18 – 22 in each order, the major septa extending well into the tabularium and sometimes almost reaching the axis. Minor septa also enter the tabularium but inside the presepiments are only about half as long as the major septa. Even in young corallites both orders are interrupted peripherally by up to four rows of steep to almost horizontal presepiments, some of the inner ones bearing septal crests corresponding to both orders of septa. Tabularium 4.5 – 6.0 mm wide, with tabulae which are flat or slightly concave near the axis, but turned strongly down and then back up again in the outer tabularium; 9 or 10 tabulae in 5 mm.

Remarks

The Queensland species *Endophyllum columna* Hill most nearly approaches the present material in corallite dimensions, though it is generally slightly larger, in both corallite diameter (10 – 22 mm) and tabularium diameter (6 – 9 mm), and the wall thickness is rather less (0.05 – 0.15 mm). Of the other Australian species of *Endophyllum* still referred to that genus, *E. jelli* Zhen, 1994 has a much wider tabularium (10 mm), *E. giganteum* Zhen & Jell, 1996 has much larger corallites (24 – 40 mm), and *E. banksi* Jell & Hill, 1970a has much larger corallites and more than twice as many septa.

Endophyllum columna occurs in the upper part of the Burdekin Formation and the lower beds of the Cultivation Gully Formation, and is ascribed a mid-Givetian age by Zhen and Jell (1996).

Family PTENOPHYLLIDAE Wedekind, 1923

Genus *Acanthophyllum* Dybowski, 1873

Type species

Cyathophyllum heterophyllum Milne-Edwards & Haime, 1851.

Acanthophyllum sp.

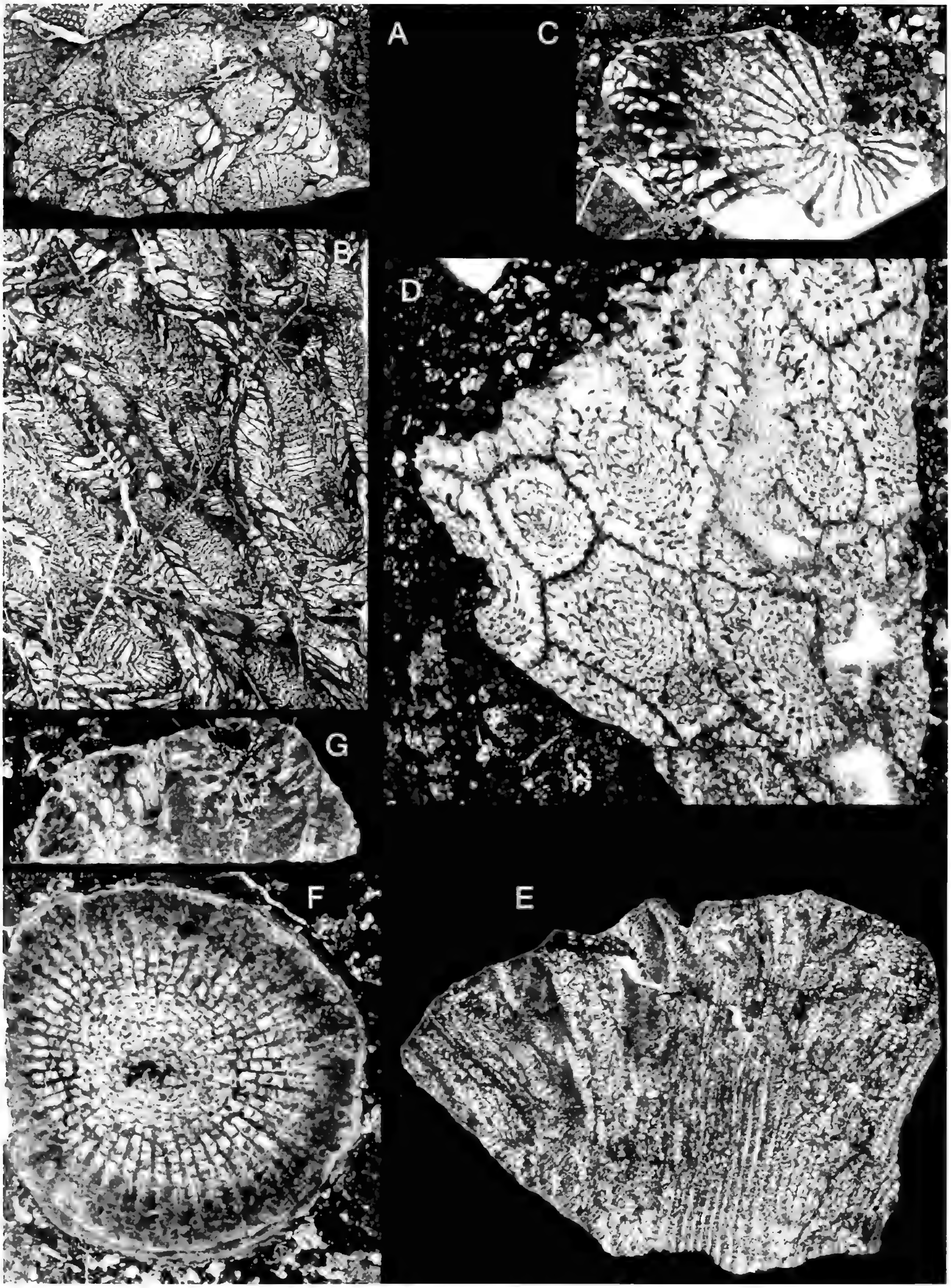
Figure 4C

Material

MMF32041, locality HRD.

Description

The single specimen is a somewhat oblique thin section of an eroded corallite near 10 mm in diameter. In spite of the obliquity of the section the tabularium appears to be oval rather than round. There are an estimated 28 major septa; both orders of septa are thickened in the dissepimentarium, being thickest in its central part. Near the epitheca they are quite thin. Minor septa only just reach the tabularium. Septa are smooth and strongly trabeculate and in their thickest parts they show a clear zone of trabecular divergence. Major septa extend almost to the axis; they are straight in the dissepimentarium but become wavy in the tabularium. There is a degree of bilaterality of septa coinciding with the long axis of the section, and at its margin, on this axis, lies a very short septum, possibly the counter septum, situated between a major septum on one side and a minor septum on the other. The dissepimentarium accounts for about half the radius of the corallite, the estimated diameter of the tabularium being 6 mm.



Remarks

Most acanthophyllids described from Australia have a calyx which is either bell-shaped or inverted conical. Strusz (1966) took these two calical shapes as the distinguishing character between the subgenera *Acanthophyllum* and *Neostringophyllum*, although this differentiation has not always been supported (e.g. Hill, 1981). The only material showing pronounced fusiform dilatation of the septa in the dissepimentarium has been referred to the related species *Acanthophyllum clermontense* (Etheridge, 1911) and *A. kennediense* Yu & Jell 1990, both of which are much larger than the present specimen, which is not necessarily a fully grown individual. If the smaller size is a reliable indication, it comes closest to the material from the Garra Formation referred to *A.* aff. *clermontense* by Strusz (1966). The Queensland reports of *A. clermontense* are from the Emsian (*perbonus* to *inversus* Zones; Mawson & Talent, 2003) Douglas Creek Limestone and the late Emsian Mount Podge Limestone (Zhen, 1995); *A. kennediense* is from the older, Lochkovian to Pragian Shield Creek Formation (Yu & Jell, 1990). Most of Struzs's material from the Garra Formation comes from the upper levels, so the age is probably late Emsian (Mawson & Talent, 2000).

Genus *Xystriphyllum* Hill, 1939

Type species

Cyathophyllum dunstani Etheridge, 1911.

Xystriphyllum cf. *mitchelli minus* Pedder, 1970a (in Pedder et al., 1970a)

Figure 4D

Material

MMF32042, MMF44865 from locality HRD.

Description

One specimen is a small piece of a cerioid colony which is too thin to permit preparation of a thin section, but the other has yielded a transverse section. The weathered surface shows about 20 corallites more or less in cross section. Corallites range in diameter from 4.2 mm to 5.8 mm and have 16 – 18 septa in each order. The major septa reach or almost reach the axis, but do not appear to interdigitate.

Remarks

In size and septal number the specimen falls within the ranges of the three smallest species of *Xystriphyllum* known from Australia. *Xystriphyllum insigne* Hill, 1940a, from Limestone Siding, Silverwood, Queensland, has diameters in the range 2 – 4 mm with 12 – 13 septa of each order; the corallites of *X. mitchelli minus* Pedder, 1970 (in Pedder et al., 1970a), from the Taemas Limestone, Wee Jasper, N.S.W. (mid-Emsian) are less than 6 mm in diameter, with no more than 20 septa of each order; and *X. parvum* Yu & Jell, 1990 has 12 – 15 septa and diameters of 4 – 4.5 mm. Yu & Jell (1990) indicate a Lochkovian to Pragian age for *X. parvum*; Mawson & Talent (1989, fig. 2) suggest an age in the *pesavis* – *sulcatus* Zones, which is in direct agreement with that of Yu & Jell.

If weight is given to the septal number in determining the species, then the present material comes closest to *X. mitchelli minus*. This form is known only from the Emsian Taemas Limestone, from a level within the *perbonus-gronbergi* Zone (Pedder et al., 1970a; Mawson & Talent, 2000).

Family PHILLIPSASTREIDAE Hill, 1954

Genus *Phillipsastrea* d'Orbigny, 1849

Type species

Astrea (Siderastrea) hennahi Lonsdale, 1840.

Phillipastrea cf. *maculosa* Hill, 1942c

Figures 4E, 5B

Material

MMF44866, a single fragment from locality HRD, from which only a longitudinal section could be prepared.

Description

The slide shows longitudinal sections of one tabularium of an astraeoid or thamnastraeoid coral, 5 mm in diameter and bounded on either side by strongly thickened, trabecular fans of a septal stereozone and its associated ring of horseshoe dissepiments. The fans are 1.5 – 2.0 mm wide. Septa are robust even in the outer dissepimentarium, and the dissepimentarial profile indicates that the everted calyces were raised

Figure 4 (LEFT). Rugose corals from the Touchwood and Mile Road Formations. A, B, *Endophyllum* cf. *columna* Hill, 1942, Mile Road Formation, locality MRF, transverse and oblique longitudinal sections, MMF29213a and 29212a respectively, x1.6. C, *Acanthophyllum* sp., Touchwood Formation, locality HRD, oblique section, MMF32041, x3.5. D, *Xystriphyllum* cf. *mitchelli minus* Pedder, 1970, Touchwood Formation, locality HRD, transverse section MMF44865, x4.3. E, *Phillipsastrea* cf. *maculosa* Hill, 1942, Touchwood Formation, locality HRD, longitudinal section, MMF44866, x3. F, G, *Sterictophyllum* sp., Touchwood Formation, locality HRD, transverse and longitudinal sections, MMF44861, x4.5.

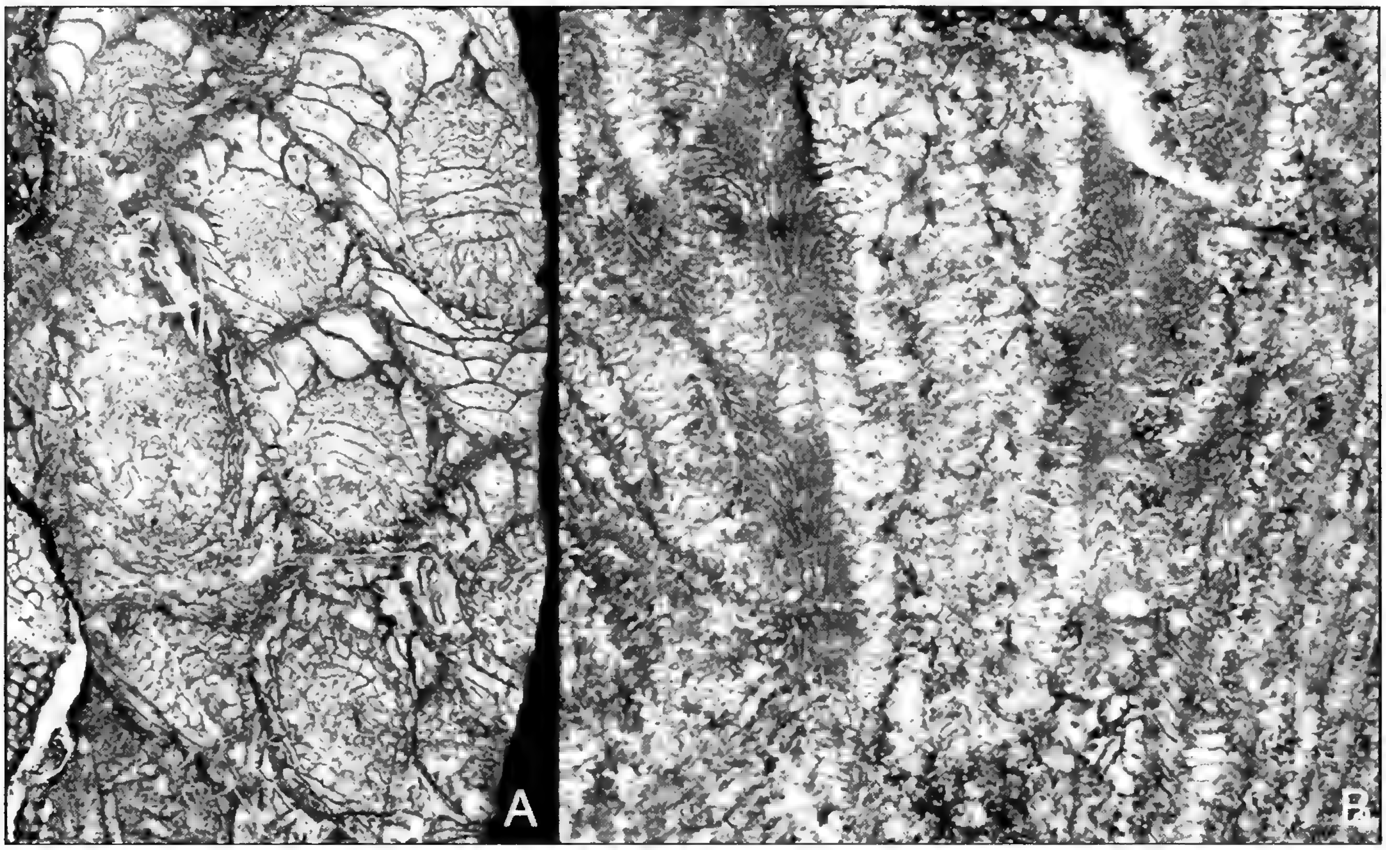


Figure 5. Detail of material from Figure 4. A, *Endophyllum* cf. *columna* Hill, 1942, Mile Road Formation, locality MRF, showing details of septa and budding corallite (centre) MMF29213a, x 2.8. B, *Phillipsastrea* cf. *maculosa* Hill, 1942, Touchwood Formation, locality HRD, MMF44866, showing long major septa and details of traabecular fans and horseshoe dissepiments, x 8.8.

only a millimetre or so above the general level of the dissepimentarium. Trabeculae stout, 0.1 – 0.45 mm in diameter. Tabulae incomplete, the tabularial floor more or less flat or somewhat raised axially, the rather confused nature of the section suggesting that the major septa extend close to the axis.

Remarks

Tabularia are rather larger than those of the type material ("about 3 mm"), but in its general robustness the specimen is much closer to *P. maculosa* than any other Australian species currently referred to the genus. The tabularia of *Bensonastraea praetor* Pedder, 1966 are similar in dimensions, but that genus has strongly vepreculate septa, of which the present material gives no indication; the septa of *B. praetor* are also less robust than those of the Port Macquarie specimen. The tabularia of *P. carinata* Hill, 1942a are only 3 mm wide and, as the name implies, the septa are strongly carinate. *P. oculoides* Hill, 1942d, from the Garra Formation, has tabularia similar in width to those of the present specimen, but the septa of that species are so short that major and minor septa are of nearly the same length, and the tabulae are concave or nearly horizontal (see also Wright, 2008). *Phillipsastrea currani* Etheridge, 1892, as redescribed by Pedder (in Pedder et al., 1970a), has tabularia up to 4 mm in diameter, short major septa and horseshoe dissepiments which are not continuously developed. Finally, the recently described *P. scotti* Wright, 2008, is also close to the present form, but the Port Macquarie material is too scant for confident attribution to either this species or *P. maculosa*.

Phillipsastrea maculosa is known from its type locality in the Sulcor Limestone (Emsian, *serotinus* Zone, Mawson & Talent, 2000), from the Liptrap Formation at Waratah Bay (Hill, 1954; Emsian, *perbonus-gronbergi* Zone, Mawson & Talent, 2000), the Coopers Creek Limestone at Tyers in Victoria (Philip, 1962; Pragian, *sulcatus* to *pireneae* Zones, Mawson & Talent, 1994b) and the Late Emsian (*serotinus* Zone) Mount Podge Limestone Zhen, 1995). *Phillipsastrea scotti* is also of *serotinus* Zone age.

Suborder CYATHOPHYLLINA Nicholson, 1889
Family CYATHOPHYLLIDAE Dana, 1846
Genus *Sterictophyllum* Pedder, 1965

Type species

Cyathophyllum cresswelli Chapman, 1925.

Sterictophyllum sp.

Figure 4 F-G

Material

A single specimen MMF44861 from locality HRD, with a transverse and a partial longitudinal section.

Description

Corallum solitary, apparently cylindrical, with a maximum diameter of 14.7 mm. Septa long, strongly radial, of two orders, forming a marginal stereozone about 3 mm wide, in which the trabeculae are clearly visible. Septa 25 in each order, the major septa reaching the axis, where they are carinate; minor septa long, entering the tabularium. Septa of both orders taper abruptly after leaving the stereozone.

The imperfect longitudinal section shows no details of the tabulae, but shows the numerous, steeply inclined dissepiments inside the stereozone, and the carinate septa near the axis. The tabularium is 5.5 mm wide. Within the stereozone sections of laterally-growing trabeculae appear as dark spots; in the inner dissepimentarium they are only slightly inclined towards the axis.

Remarks

The present specimen is smaller than the maximum diameters quoted for any of the Australian species referred to *Sterictophyllum*, although a single specimen cannot give any impression of the range of variation. The stereozone is thicker than in the other species (*S. creswelli* (Chapman, 1925) – 2 mm; *S. vallatum* Pedder, 1965 – 2.5 mm; *S. pridianum* (Philip, 1962) – 1.5 – 2.5 mm); in *S. vallatum*, however, the major septa do not reach the axis. On the basis of its relative dimensions, the present form appears to be closest to *S. pridianum*. (A fourth species, *Mictophyllum trochoides* Hill, 1940b, type species of *Cavanophyllum* Pedder, 1964, has been included in the genus by Jell & Hill, 1969, but has major septa which are somewhat contorted at the axis, lacks the pronounced stereozone, and is much larger than all the others. It is not further considered here).

All these species are Early Devonian in age. The type species (sensu stricto) is known only from its type locality in the Lilydale Limestone at Lilydale, Victoria (Pragian, *kindlei – pireneae* Zones; Mawson & Talent, 2000); both the other species come from the Limestone phase of the Coopers Creek Formation (Pragian, *sulcatus* to possibly *dehiscens* Zones; Mawson & Talent, 2000).

Subclass TABULATA Milne-Edwards & Haime, 1850

Family FAVOSITIDAE Dana, 1846

Genus *Favosites* Lamarck, 1816

Type species

Favosites gothlandicus Milne-Edwards and Haime, 1850.

Favosites salebrosa Etheridge, 1899

Figure 6 A-B

Synonymy

1899 *Favosites basaltica* var. *salebrosa* Etheridge, p. 166, pl. 21 figs 3-5, pl 27, figs 1-2.

1937 *Favosites salebrosa* Etheridge; Jones, p. 95, pl. 14, figs 2-6.

1940 *Favosites salebrosus* Etheridge; Hill and Jones, p. 197.

2002 *Favosites* sp. aff. *F. salebrosus* Etheridge; Pohler, p. 19, figs 5A-D

Material

MMF 44857 from the Mile Road Formation, locality SC.

Description

The material is from fragments of a large, massive colony, exceeding 70 x 45 cm in original dimensions. Corallites range in diameter from 0.65 to 0.83 mm, with a mean at 0.73. Wall thickness ranges from 0.05 to 0.14, mean 0.06. Mural pores are 0.2 – 0.3 mm in diameter and at least 0.6 mm apart. Septal spines are neither conspicuous nor frequent, projecting 0.2 mm from the wall. There are 14 – 18 complete tabulae in 10 mm.

Remarks

The material accords well with the sections of the lectotype (AMF 4288. sections AM 47A, B) from the Woolomol Limestone, in portion 38, parish of Woolomol, northwest of Tamworth, N.S.W., in which I have measured rare corallites with a diameter of as much as 0.9 mm. Jones (1937) reports the species from what is probably the Cavan Bluff Limestone at Taemas, without illustration or nomination of material; this equates to the middle part of the Cavan Formation of Pedder et al. (1970a), of early Emsian (*dehiscens* Zone) age. For the type locality, neither Hill (1942c), Brown (1942) nor any of the publications of the Macquarie University group (e.g. Mawson and Talent, 1994a; Pohler, 2001) provides information which helps age determination. However, this limestone outcrop,

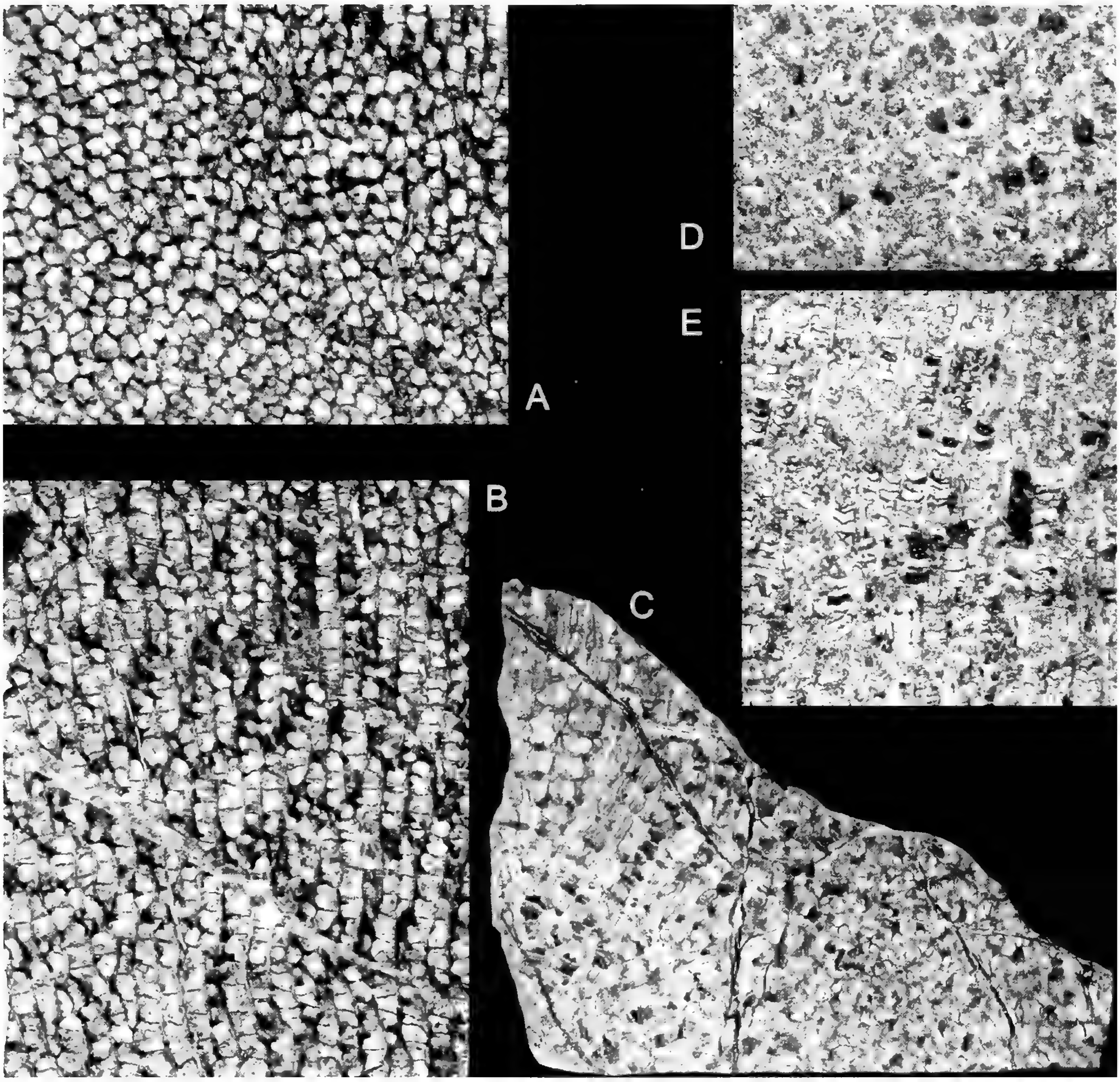


Figure 6. Tabulate corals from the Touchwood and Mile Road Formations. A, B, *Favosites salebrosa* Etheridge, 1899, Mile Road Formation, locality SC, transverse and longitudinal sections, MMF44857, x5. C, ?*Pachyfavosites* sp., Touchwood Formation, locality HRD, predominantly longitudinal section, MMF44863, x4. D, E, *Squameofavosites squamuliferus* (Etheridge, 1899), transverse and longitudinal sections, MMF32037, x3.7.

in adjacent portions, is the type locality for some of the sponges described by Pickett (1969), which are also characteristic of the lowermost beds of the Timor Limestone to the southeast. For this interval Pedder et al. (1970a) have determined an earliest Eifelian age, so it is probable that the so-called Woolomol Limestone is more or less coeval. On the other hand, Pohler (2001, p. 96) indicates that all favositids from the Tamworth district examined by her are Emsian in age, and later (Pohler, 2002) describes *Favosites* aff. *F. salebrosus* from the Emsian Sulcor Limestone, but her material forms cylindrical branches of at least 3 cm diameter, in contrast to the type material, which is massive, and certainly the present material, which forms large masses.

Genus *Pachyfavosites* Sokolov, 1952

Type species

Calamopora polymorpha var. *tuberosa* Goldfuss, 1826.

?Pachyfavosites sp.

Figure 6C

Material

A single specimen, MMF 44863, from locality HRD, with two thin sections.

Description

Corallum massive, original form unknown. Surface possibly with raised areas. Corallites four to six sided, 1 – 1.3 mm in diameter. Walls immensely thickened, so that the lumen diameter is 0.2 – 0.7 mm, and composed of large bundles of calcite fibres. Mural pores prominent, about 0.2 mm in diameter. Tabulae complete, more or less horizontal, irregularly spaced, possibly reach as many as 14 in 5 mm.

Remarks

This species is much more thickened than the type, or any other species referred to the genus by the Russian school, such as *P. markovskyi* (fide Sokolov, 1962), as the lumen may be all but occluded. In this respect it is similar to the mature stages of *Riphaeolites* Yanet in Sokolov, 1955 (tentatively included in the family Cleistoporidae by Hill, 1981), but the present material shows no indication of the early, less thickened favositid stage characteristic of that genus .

Pachyfavosites has been reported from Australia by Pohler (2002), who illustrates both *P. rariporosus* Dubatolov, 1963 and *P. tumulosus* Yanet, 1965 from the Emsian Sulcor Limestone Member of the Yarrimie Formation near Tamworth, NSW; neither of these species has the intense thickening of the Port Macquarie material. *Riphaeolites* is restricted to a single doubtful record from an unspecified Emsian limestone (Sulcor?) from the Tamworth area (Pohler, 1998), unaccompanied by either description or illustration.

Genus *Squameofavosites* Chernyshev, 1941

Type species

Favosites hemisphericus var. *bohemica* Počta, 1902.

Squameofavosites squamuliferus (Etheridge 1899)

Figure 6 D-E

Material

MMF32027, with three thin sections; locality HRD.

Description

The single specimen is a fragment of a cerioid colony 30 x 15 mm in diameter and c. 30 mm high. Corallite diameter ranges from 1.0 to 1.25 mm, diameters in the lower range being more common. Wall thickness is variable, from 0.1 to as much as 0.27 mm. Squamulae, though present, are not obvious, the longest one observed being only 0.1 mm in length. There are 33 – 40 tabulae per cm. Mural pores have a diameter close to 0.2 mm, but the preservation is such that measurements are imprecise. The vertical distance between their centres is 0.7 – 0.9 mm.

Remarks

Forms which may be referred to the *squamuliferus* group in Australia make a fairly homogeneous assortment (cf. Philip, 1960). The range of variation described by Philip (1960, notably figs 2, 3) suggests continuous variation between most of these forms.

All of the material described by Philip (1960), and the type material of the various taxa involved, derives from strata of Early Devonian age; in central western New South Wales the group ranges down into Late Silurian strata (Pickett & Ingpen, 1990; Pickett & McClatchie, 1991).

Philip (1960) referred the taxa in this group either to *Squameofavosites grandiporus* (Etheridge, 1890) or to "formae" within *Squameofavosites squamuliferus* (Etheridge, 1899), these latter comprising some eight subspecific units designated by the first eight Greek letters, and for the first five of which names in the species category are available (*bryani* Jones, 1937; *nitidus* Chapman, 1914; *stelliformis* Chapman, 1918; *australis* Chapman, 1907; *ovatiporus* Hill & Jones, 1940). The present specimen fits within the range reported for forma *bryani* (Jones, 1937), the type locality of which is in the Taemas Limestone at Good Hope, NSW, and which Philip reports from the "Tyers River Limestone"; both these localities are Emsian, though the lack of precise localities makes it difficult to assess the age more accurately.

Family PACHYPORIDAE Gerth, 1921

Genus *Cladopora* Hall, 1851

Type species

Cladopora seriata Hall, 1851.

Remarks

Following a revision of the type species by Oliver (1963), Hill (1981) restricts the genus to those species whose calices are lozenge-shaped in their mature portion. This definition excludes most of the Australian species previously included in the genus. Since the restricted material of this study does not allow the observations necessary for more rigorous treatment, forms with a consistently rounded calyx are also treated here.

Cladopora sp.

Figure 7 A-B

Material

MMF 23038, a single fragment of a branching colony, with one oblique thin section; locality HRD.

Description

The colony is cerioid and branching, the branch 4 mm in diameter. Corallites very small, many in

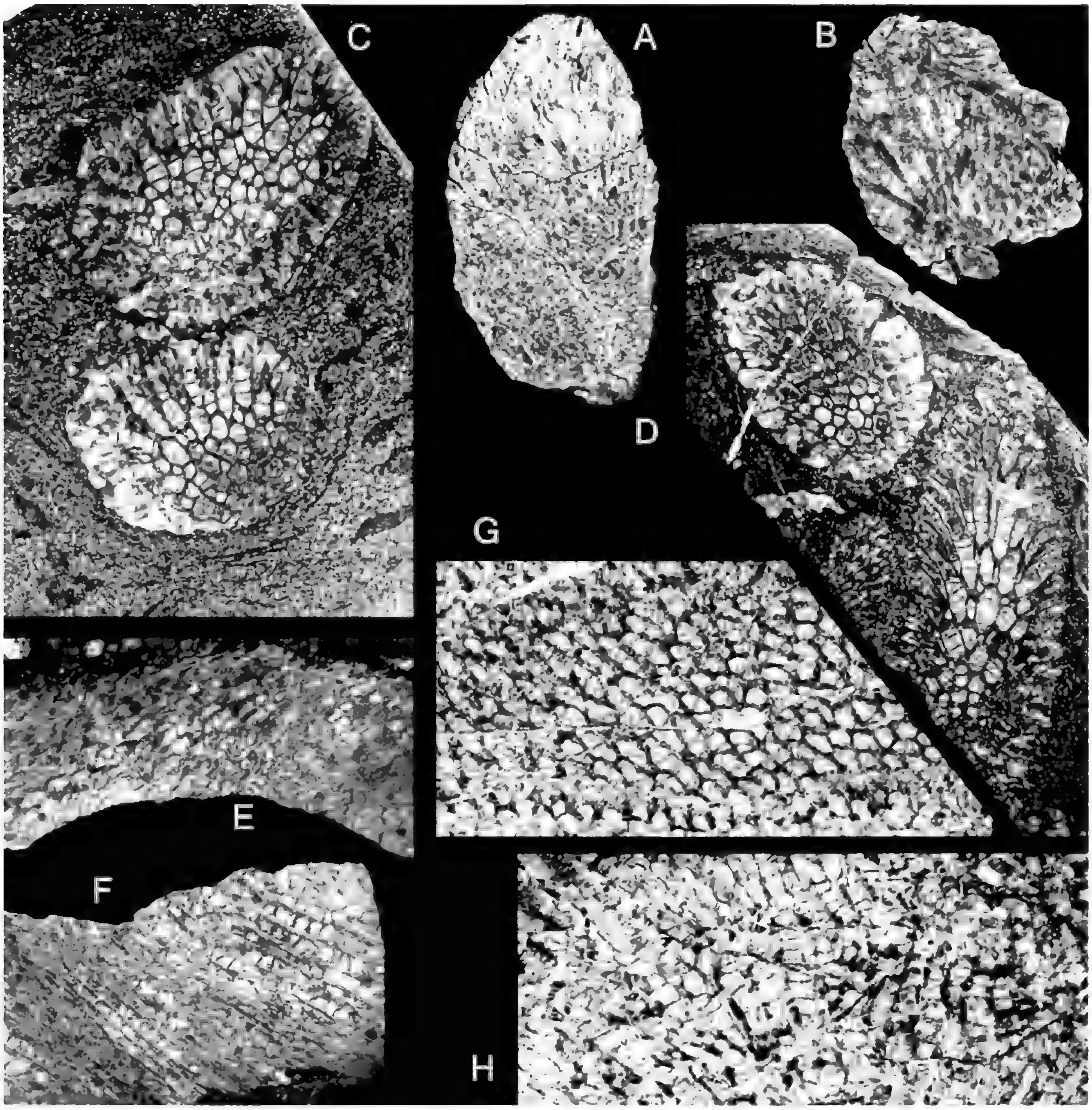


Figure 7. Tabulate corals from the Touchwood and Mile Road Formations. A, B, *Cladopora* sp., Touchwood Formation, locality HRD, oblique sections of branches. A, MMF32028d, x7.5; B, MMF32038b, x7.8. C, D, *Thamnopora randsi* Jell & Hill, 1970. Mile Road Formation, locality SC, random sections, MMF44858, x2.5. Note bioturbation burrows in C. E, F, *Alveolites* sp. A., Touchwood Formation, locality HRD. E, transverse section, MMF32038c, x4.8; F, longitudinal section MMF32038a, x5. G, H, *Alveolites* sp. B, Mile Road Formation, locality MRF, portions of large specimen MMF29213a with areas of transverse (G) and longitudinal (H) orientation, x5.

the cross-section of a branch (at least 18 along a diameter), rounded in transverse section axially, but lozenge-shaped towards the margin, 0.35 – 0.4 mm in maximum diameter, vertical at the axis and curved gradually towards the surface, which they reach at an acute angle. Walls thick relative to size of corallites, without any obvious thickening towards the surface. Tabulae not observed; there is some indication that the calices were back-filled with lamellar calcite rather than by tabulae. Septal spines not observed.

Remarks

Among the Australian species referred to *Cladopora*, *C. foliata* (Jones,1941) is encrusting; *C. gippslandica* (Chapman, 1907), originally described as a bryozoan, and redescribed by Philip (1962), does not appear to have the lozenge-shaped calices of the present form; three species from Victoria (Talent, 1963) (*lemaitreae, corrigia, surculus*) are all described as having rounded apertures. I have examined the type specimen of *Cladopora mirabilis* (Etheridge, 1917) (AMF899; 4 thin sections) from the Reid River Limestone at Reid Gap, south of Townsville, Queensland. This species forms branches 2 – 3 mm in diameter in which the axial corallites are subrounded, becoming lozenge-shaped only towards the periphery. In longitudinal section they curve gently towards the periphery, without geniculation. There are 6 – 7 corallites along a diameter. Mural pores are common, tabulae rare, and the wall displays a prominent median dark line. The present material differs markedly from *C. mirabilis* in the much smaller and more crowded corallites.

Genus *Thamnopora* Steininger, 1831

Type species

Thamnopora madreporacea Steininger, 1831 (= *Alveolites cervicornis* de Blainville, 1830).

Thamnopora randsi Jell and Hill, 1970b

Figure 7 C-D

Material

Two large blocks of mudstone containing abundantly branching coralla, MMF 44858 (2 thin sections), MMF 44869, Mile Road Formation, locality SC.

Description

Corallum branching, bifurcating, branches cylindrical, 6 – 14 mm in diameter, mature branches being generally in the upper range. In transverse section there are 8 – 10 corallites along the median plane of a mature branch. Diameter of mature corallites 1.2 – 1.5 mm, their combined walls about 0.2 mm in thickness near the axis, and 0.6 – 0.8 mm in the outer stereozone, which is 2.5 – 3 mm wide. In the inner parts of the branches the walls show a conspicuous median dark line, but this becomes much more diffuse in the outer stereozone, where the stereome may show a lamination parallel to the surface. Near the axis the corallites are parallel to the branch, but turn outwards without geniculation to reach the sides of the branch at about 45°. Mural pores have a diameter of 0.2 – 0.3 mm, and are rather funnel-shaped in the stereozone. They occur in a single series on the faces of the corallites. Calices are 3 – 4 mm deep. Septal spines are rare, < 0.1 mm in length, conical, not trabeculate, and occur both at the axis and in the stereozone. Latex replicas from natural moulds show no sign of septal ridges in the calyces. Tabulae are complete, lie closer together than the width of the corallite, usually 4 in 2 mm.

Remarks

The present material accords well with that described by Jell and Hill (1970b), though the branches are slightly thinner (14 mm as against 15 mm in the types), and the corallites open slightly more obliquely to the sides of the branches. A significant similarity is the way the median dark line becomes less obvious towards the exterior, and the presence of growth lamination in these areas. *Thamnopora plumosa* Jones, 1941 has much stouter branches with nearly twice as many corallites across the median plane, and the thickening is less conspicuous. *Thamnopora foliata* Jones, 1941 is laminate; *T. meridionalis* (Nicholson and Etheridge, 1879) is more delicately branched; *T. crummeri* (Etheridge, 1899) is closer, but has fewer corallites across the median plane and the difference in the amount of thickening between the axial and outer zones is less pronounced (I have examined the sections of the holotype, AM 3981 and 4687). The Victorian species, *T. alterivalis* (Chapman, 1914), *T. angulata* Hill, 1950 and *T. tumulosa* Hill, 1950 all have significantly thinner branches, the largest reaching only 7 mm.

Thamnopora randsi is known so far only from its type area, the Douglas Creek Limestone, of Clermont, Queensland (mid-Emsian, *perbonus* to *inversus* Zones; Mawson & Talent, 2003).

Family ALVEOLITIDAE Duncan, 1872

Genus *Alveolites* Lamarck, 1801

Type species

Alveolites suborbicularis Lamarck, 1801.

Alveolites sp. A

Figure 7 E-F

Material

Four indifferently preserved specimens, MMF32038, 44862, 44867 and 44868, with six thin sections, all from locality HRD.

Description

All the material is of small fragments, the largest being less than 2 cm in maximum diameter. Corallites usually crescentic, apparently reclined, up to 0.4 mm high and 0.8 – 1.0 mm wide. Squamulae, septal spines and mural pores not observed. Tabulae 0.25 – 0.4 mm apart.

Alveolites sp. B

Figure 7 G-H

Material

Three specimens, MMF 29213 – 29315, with three thin sections, all from locality MRF.

Description

Corallum moderately large, exceeding 10 cm in maximum dimension. Corallites generally crescentic, but occasionally polygonal, 0.3 – 0.5 mm high and 0.5 – 0.7 mm wide. Occasional short septal spines occur on the side of the corallite away from the curved surface. The wall thickness varies considerably within the corallum, some areas having corallites whose walls reach only 0.02 mm, but for the most part the walls are thickened, reaching 0.1 or even 0.2 mm in extreme cases. The non-thickened areas pass rather abruptly into thickened areas, and individual corallites may lie partly in each of the two. There are occasional mural pores. Tabulae are at right angles to the direction of growth of the corallite, thin even in the thickened parts of the corallum, complete, and 0.2 – 0.6 mm apart.

Remarks

For all that the Australian literature refers to some twenty species of *Alveolites* (Pickett, 1999), the genus is not well documented in this country, either morphologically or stratigraphically. Six species (*caudatus* Hill, 1954; *intermixtus* Lecompte, 1939; *multiperforatus* Salée, 1916 (in Lecompte, 1933); *saleei* Lecompte, 1933; *suborbicularis* Lamarck, 1801; *tumida* Hinde, 1890) are known from Late Devonian strata in Western Australia. A further two were established by de Koninck (1876; *obscurus*, *rapa*) and, as the type material was destroyed by fire and details of the type localities are vague, it is probably better that the names be allowed to languish; his other three reports are unillustrated and, based as they are on external features alone, should be regarded as dubious. Chapman's (1921) species *regularis* and *victoriae* were regarded as species of *Favosites* by Philip (1960).

The status of the remaining eight taxa is not necessarily sound. The holotype of the only Silurian species, *Alveolites piriformalis* Etheridge, 1921 from the Yass district, has never been traced, and its internal structure is inadequately known. The holotype of *A. queenslandensis* Etheridge & Foord, 1884, from the Emsian Reid River Limestone at Reid Gap, south of Townsville, has not been traced and the species has not been redescribed since the original publication. Hill et al. (1967) illustrated, without description, forms referred to *A.* sp. ex gr. *fecundus* (Salée, 1916) and *A.* sp. nov. aff. *lemniscus* Smith, 1933, of which the first has a branching corallum and the second does not show the areas of thin- and thick-walled corallites of *A.* sp. B. from locality MRF. *Alveolites stamineus* Hill, 1950 from the Emsian Murrindal Limestone at Buchan, Victoria, is a distinctive, thinly encrusting form. Neither of the forms referred to *A. suborbicularis* Lamarck, 1801 or *A.* sp. nov. aff. *A. hemisphericus* (Chernyshev, 1937) by Brühl & Pohler (1999) shows areas of thin- and thick-walled corallites, apart from the thinner-walled basal layer of *A. suborbicularis*. Finally, the material referred to *A.* sp. aff. *A. taenioformis* Schlüter, 1899 by Philip (1962) forms encrusting layers no more than 4 mm in thickness.

The material described here as *Alveolites* sp. A is too scant for proper identification, and that described as *Alveolites* sp. B does not appear to be the same as any Australian forms so far reported.

Order HELIOLITIDA Frech, 1897

Family HELIOLITIDAE Lindström, 1876

Genus *Heliolites* Dana, 1846

Type species

Astraea porosa Goldfuss, 1826.

Heliolites daintreei Nicholson & Etheridge, 1879 group IV Jones & Hill, 1940

Figure 8

Material

Two specimens, fragments of much larger

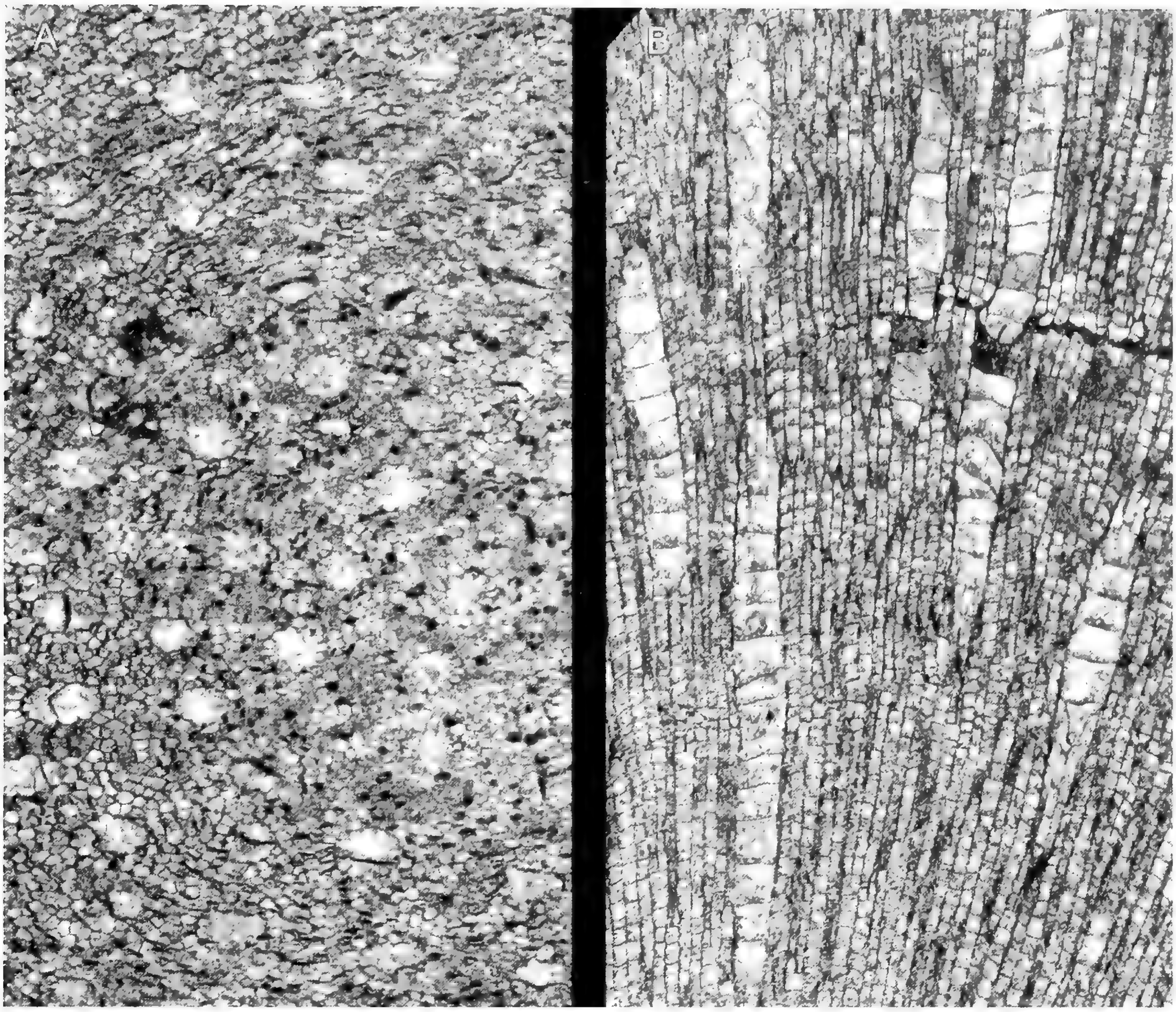


Figure 8. Tabulate corals from the Mile Road Formation, locality SC. A, B, *Heliolites daintreei* Nicholson & Etheridge, 1879, group IV Jones & Hill, 1940. A, transverse section MMF44856, x5.3; B, longitudinal section MMF44859, x5.7.

colonies, MMF 44856, 44859, from locality Sarahs Creek.

Description

Corallum massive, large. Tabularia consistently 1.2 mm in diameter, but ranging up to 1.5 mm. No areola is developed, but the tabularia are surrounded by 19 – 20 tubules of varying size; tubules throughout the coenenchyme range from 0.2 to 0.5 mm in diameter. Tabularia separated by 3 – 10 tubules. Septa 12, laminar, apparently without axial spines, reaching about halfway to the axis. There are thin horizontal zones in which the skeleton is slightly thicker; these are about 2 mm thick and 7 – 9 mm apart. The tabulae are 0.6 – 1.1 mm apart, and the diaphragms about 11 in 5 mm.

Remarks

Since the review of Australian Silurian and Devonian heliolitids by Jones and Hill (1940) no other overview of the group has been attempted. There is a clear need for any proper study of the group to be based on extensive material, allowing population studies. Here we simply follow the work of Jones and Hill.

Heliolites daintreei, as conceived by Jones and Hill (1940), is an enormously variable species ranging from the Late Silurian to the Early Devonian, even the four informal "groups" not demonstrating reliable stratigraphic range. The present material, as it appears to lack axial spines on the septa, does not fit comfortably in any of the taxa recognised by them.

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APPENDIX 1.

Mile Road Formation

Definition: The name Mile Road Formation is applied to interbedded fossiliferous siltstone and sandstone, containing blocks of coralline limestone and possibly autochthonous limestone lenses, and silicic tuff, mapped as stratigraphically underlying the Touchwood Formation in the eastern part of the Hastings Block.

Synonymy: The unit was first recognised by Taylor (1984) who termed it the Mile Road Formation. The unit was referred to as the Mile Road beds by Roberts et al. (1995).

Derivation of name: Named from the Mile Road that traverses part of the unit in the Cowarra State Forest (GR 478700 6514700 Grants Head 1:25 000 sheet).

Distribution: The Mile Road Formation is known only from the eastern Hastings Block where it has been recognised in the southern part of a slender wedge bounded by the Cowarra, Sapling Creek and Sancrox faults. It is mapped over an area of about 7 km^2.

Type section: Neither Taylor (1984) nor Roberts et al. (1995) designated a type section although the latter authors specified a type locality on the Cowarra Access Road (GR 479000 6514800 to 478900 6513100, Grants Head 1:25 000 sheet). This locality lies nearly along strike and encompasses only the lower part of the formation. We suggest that the type section be that extending northwest from the Cowarra Access Road at GR 478800 6513800 (base) along a tributary of Sarah Creek to GR 478300 6514300 (top) (Grants Head 1:25 000 sheet).

Stratigraphic relationships: Neither base nor top of the unit is exposed. It is truncated downwards by the Cowarra Fault and is here interpreted as being stratigraphically overlain by the Touchwood Formation 1 – 2 km south of the Oxley Highway.

Thickness: A maximum preserved thickness of between 1500 and 2000 m is estimated based on the mapped width of the unit and the assumption of an overall steep northwest dip and consistent northwest direction of younging.

Content: Medium to thick bedded volcaniclastic siltstone and sandstone of intermediate-silicic provenance, locally bioturbated and/or fossiliferous with crinoids, brachiopods and corals. Widespread breccias/conglomerates with coralline limestone clasts to c. 1 m set in a coarse sandy matrix. Grey hard massive silicic tuff interstratified with epiclastic rocks.

Age and correlation: A small conodont assemblage from probably penecontemporaneously derived allochthonous blocks gives a precise age of the upper part of the lower *varcus* Zone, early Givetian. Significant taxa are *Polygnathus linguiformis klapperi* Clausen et al., 1979, *Polygnathus linguiformis weddigei* Clausen et al., 1979, *Polygnathus hemiansatus* Bultynck, 1987 and *Icriodus difficilis* Ziegler et al., 1976. Additionally the blocks contain an abundant macrofauna of rugose and tabulate corals, spongiomorphs and brachiopods; the branching tabulate coral *Thamnopora*, occurring in the bioturbated matrix, suggests strongly that the blocks are penecontemporaneous, and that the conodont assemblage indicates a real age, at least for that part of the Formation.

Age Determination and Growth in the Male South African Fur Seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae) Using External Body Measurements

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Stewardson, C.L., Prvan, T., Meÿer, M.A. and Ritchie, R.J. (2009). Age determination and growth in the male South African fur seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae) using external body measurements. *Proceedings of the Linnean Society of New SouthWales* **130**, 219-244.

Morphology, relative size and growth of the South African fur seal or Cape fur seal, *Arctocephalus pusillus pusillus*, from the coast of southern Africa are described and comparisons made to data available on the closely related Australian fur seal (*Arctocephalus pusillus doriferus*) and the New Zealand fur seal (*Arctocephalus forsteri*). Useful information can be gained from body measurements of seal carcasses provided canine teeth are extracted for aging. External body measurements (12 linear variables) were examined in relation to standard body length (**SBL**) and chronological age (y) using linear regression and non-linear least squares fitting as appropriate. Animals ranged from < 1 month to ≥ 12 y. Of the 149 animals in the study, 39 were animals of known-age based on tagging; 34 were aged from highly reproducible counts of incremental lines observed in the dentine of upper canines (i.e., range 1–10 y); 10 were identified as adults ≥ 12 y (i.e., pulp cavity of the upper canine closed); and 66 were not aged. At birth, male South African fur seals are 35% (*c.* 69 cm) of their mean adult size. At puberty, they are 57% (*c.* 113 cm). The foreflippers measure 25–26% (*c.* 18 cm) of standard body length (**SBL**) in pups, and 24% (*c.* 48 cm) of **SBL** in adults. The hind flippers are considerably shorter, measuring 19% (*c.* 13 cm) in pups, and 14.5% (*c.* 29 cm) in adults. Axillary girth is usually about 57–67% of **SBL**. Growth of **SBL** was rapid during the early postnatal period with a significant growth spurt occurring at the onset of puberty (2–3 y). The rate of growth slowed significantly between 6 and 7 y. Social maturity was reached at about 9 to 10 y. Growth slowed thereafter. The mean **SBL** for aged males >10 y and unaged animals > 200 cm was 199 cm. Relative to **SBL**, facial variables and the fore/hind limbs scaled with negative slope relative to **SBL** or were negatively allometric; tip of snout to genital opening scaled with positive slope; and tip of snout to anterior insertion of the foreflipper was positively allometric. Relative to age, body variables scaled were negatively allometric. **SBL** was found to be a 'rough indicator' of age and age group. The growth kinetics of juvenile and adult the South African fur seal and the Australian fur seal are best described by the logistic and double exponential (Gompertz) models rather than the exponential von Bertalanffy model. Australian fur seals grow at a faster rate but asymptotic maximum sizes are similar in South African and Australian fur seals.

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Key words: Allometry, *Arctocephalus pusillus doriferus*, *Arctocephalus pusillus pusillus*, Australian fur seal, body, growth, growth curve modelling, pinnipeds, South African fur seal.

INTRODUCTION

Data on the physical growth of pinnipeds is important to understanding the biology, ecology and evolutionary links within and between populations of the same species and between species. Growth and body-size estimates can be used for monitoring the effects of population pressures and changes in the quality of the habitat of marine mammals (Bester and Van Jaarsveld, 1994). Within the Otariidae (fur seals and sea lions) quantitative descriptions of growth in body length based on animals aged from tooth structure, or on animals of known-age (i.e., animals tagged or branded as pups), are available for several species of fur seals and sea lions including the Australian fur seal (*Arctocephalus pusillus doriferus*) (Arnould and Warneke, 2002) which is very closely related to the South African fur seal (Wynen et al., 2001); the New Zealand fur seal (*Arctocephalus forsteri*) (Dickie and Dawson, 2003; McKenzie et al., 2007), the subantarctic fur seal (*Arctocephalus tropicalis*) (Bester and Van Jaarsveld, 1994), the Antarctic fur seal (*Arctocephalus gazella*) (Payne, 1979; Krylov and Popov, 1980; McLaren, 1993), the Northern fur seal (*Callorhinus ursinus*) (Scheffer and Wilke, 1953; Bychkov, 1971; Bigg, 1979; Lander, 1979; McLaren, 1993; Trites and Bigg, 1992, 1996) and the sea lions, *Eumetopias jubatus*, the Steller sea lion (Fiscus, 1961; Thorsteinson and Lensink, 1962; Calkins and Pitcher, 1983; Loughlin and Nelson, 1986; McLaren, 1993; Winship et al., 2001), and *Otaria byronia*, the South American sea lion (Rosas et al., 1993).

Physical growth in the northern fur seal and Steller sea lion have been studied in the most detail and is based on the largest number of animals of known age. The general growth curve for the Northern fur seal and the Steller sea lion is presumably representative of all highly polygynous male otariids. Male pups of Northern sea lions measure *c.* 66 cm at birth and grow at a steady rate (Scheffer and Wilke, 1953; Trites and Bigg, 1992, 1996). Growth is claimed to increase suddenly at 3–4 y (puberty) and slows soon after attainment of social maturity (McLaren, 1993). Estimated asymptotic length is about 189 cm for males > 4 y, and is reached by *c.* 12 y in most animals (McLaren, 1993). Growth curves of the Steller sea lion are basically similar in shape and also claimed to best fit a logistic rather than exponential saturation curve (Winship et al., 2001). Asymptotic maximum size of the Steller sea lion is much larger than fur seals: maximum size of males is about 3 m and 700 kg at about 12 y.

The limited information on growth in body size available for South African fur seals was based on measurements that were aged physiologically (cranial suture age) rather than chronologically (y) (Rand, 1956). Unfortunately, in South African fur seals cranial sutures are not a very reliable guide to age (Stewardson, 2001; Stewardson et al., 2008). Comparisons will be made to data available on the Australian fur seal (Arnould and Warneke, 2002), the New Zealand fur seal (Dickie and Dawson, 2003; McKenzie et al., 2007) and the subantarctic fur seal (Bester and Van Jaarsveld, 1994). Apart from studies by Scheffer and Wilke (1953) and Payne (1979) information on the relative growth of external body measurements of other fur seals is scant, e.g., axillary girth vs. standard body length, length of limbs vs. standard body length.

Here we examine the body measurements of 149 male South African fur seals, *Arctocephalus pusillus pusillus*, from Southern Africa. Specific objectives were to: (i) describe the general morphology of the animal; (ii) quantify growth of body measurements (12 variables) relative to standard body length (n = 134 animals) and chronological age (n = 83 animals), (iii) determine if standard body length (**SBL**) is a useful indicator of age, (iv) compare three commonly used models for the growth kinetics of South African fur seals compared to Australian fur seals (exponential saturation curve or von Bertalanffy curve, Logistic curve and the double exponential or Gompertz curve) (Zullinger et al., 1984; Zeide, 1993).

MATERIALS AND METHODS

Collection of specimens

South African fur seals were collected along the Eastern Cape coast of South Africa between Plettenberg Bay (34° 03'S, 23° 24'E) and East London (33° 03'S, 27° 54'E), from August 1978 to December 1995, and accessioned at the Port Elizabeth Museum (PEM). From this collection, 110 males were selected for examination. Apart from specimens collected before May 1992 (n = 38), all specimens were collected by the first author. PEM animals were aged based on dentition (n = 32), some PEM animals were aged using dentition growth rings, animals designated ≥12 y (n = 10) were animals with 12 growth rings in their teeth but their pulp cavities were closed and so no more growth rings could be deposited and so were at least 12 y old but could have been older. One animal (PEM2238) was collected NE of the study area, at Durban.

Measurements from 39 males from Marine and Coastal Management (MCM), Department of Environment Affairs and Tourism, Cape Town were also available. These measurements were from animals that had been tagged as pups, and were therefore of known-age (1–13 y). MCM seal specimens are accessioned as MCM followed by a number. The accession numbers of all the animals used in the present study are listed in Appendix 1. The full data set is accessible in the public domain (Stewardson, 2001).

Body measurements

Standard necropsies were performed and biological parameters recorded, based on recommendations of the Committee on Marine Mammals, American Society of Mammalogists (1967). Upper canines were collected for age determination. The skull is probably the most useful part of a seal carcass to retain for later study but it is not always possible to arrange for the skull of a dead seal to be retained. Nuisance seals are sometimes culled to satisfy the concerns of aquaculture and fisheries interests. From humane considerations, permits for such culls usually specify that the animals are fatally shot in the head, which ruins the skulls for morphological studies, but teeth for aging can usually be retrieved (Thorsteinson and Lensink, 1962; Pemperton et al., 1993; Winship et al., 2001; Arnould and Warneke, 2002; McKenzie et al., 2007). Body measurements of seal carcasses are most useful if canine teeth are extracted for aging.

Measurements (12 variables) were taken to the nearest 5 mm (0.5 cm) using a flexible tape measure or vernier callipers as appropriate (Figure 1). Although body weight and blubber thickness were recorded, these measurements were not included in the analysis because they can vary according to physiological condition, e.g., body condition is influenced by seasonal fluctuations in food supply, illness or injury, and breeding condition. The blubber of Australian fur seals is known to vary seasonally with a maximum in late austral spring (Arnould and Warneke, 2002). Apart from specimens collected before May 1992, all PEM measurements were recorded by the first author. The majority of MCM measurements were recorded by the third author.

Age determination

The age of animals was estimated from counts of Growth Layer Groups (GLGs) observed in the dentine of thin tooth sections (Payne, 1978; Oosthuizen, 1997; Oosthuizen and Bester, 1997; Stewardson et al., 2008). Upper canines were sectioned longitudinally using a circular diamond saw. Sections were ground down to 280–320 µm, dehydrated, embedded in resin and viewed under a stereomicroscope in polarised light (Oosthuizen, 1997; Oosthuizen and Bester, 1997). Each section was read by one individual five times, without knowledge of which animal was being examined (repeated blind counts) similar to Payne (1978). Ages were rounded off to the nearest birth date. The median date of birth was assumed to be 1 December (Shaughnessy and Best, 1975), which is similar to the mean date of birth for Antarctic fur seals (Payne, 1978). The median of the five readings was used as an estimate of age. Outliers were discarded as reading errors.

Currently, examination of tooth structure is the most precise method of age determination in pinnipeds (McCann, 1993), including South African fur seals (Oosthuizen, 1997; Oosthuizen and Bester, 1997). However, this method can only be used in South African fur seals ≤ 12 y. At about 12 y of age, closure of the pulp cavity terminates tooth growth and no further growth rings are formed. Arnould and Warneke (2002) claim that growth rings could be distinguished in male Australian fur seals up to 16 y and a similar upper limit of about 15 y was found in the Antarctic fur seal by Payne (1978). Payne (1978, 1979) also found that useful ages could be estimated from growth lines in the cementum of the teeth of Antarctic fur seals (*A. gazella*) but this method was not attempted in the present study.

Of the 149 animals in the study: (i) 39 were known-age MCM animals; (ii) 34 were aged from counts of incremental lines observed in the dentine of upper canines, i.e., range 1–11 y; (iii) 10 were identified as adults ≥ 12 y (pulp cavity of the upper canine closed); (iv) 66 were not aged but could be classified into subadults and adults based upon **SBL**; allowing for (i), (ii) and the problem animals mentioned in (iii) above, there was a total of 73 animals of known age available for modelling of growth vs. age.

For this study, the following age groups were used: pup (< 1 month to 6 months); yearling (7 months to 1 y 6 months); subadult (1 y 7 months to 7 y 6 months); and adult (≥ 7 y 7 months) (Table 1). Very old animals of known-age were not available for examination. Estimated longevity is *c.* 20 y, based upon the lifespan of zoo animals and known life-spans of other fur seals (Wickens, 1993). Australian male fur seals (*A. pusillus doriferus*) have a lifespan of about 20 years but female Australian fur seals are known to live to over 20 y (Arnould and Warneke, 2002). The New Zealand fur seal (*A. forsteri*) (McKenzie et al., 2007) and the Steller sea lion (*Eumetopias jubatus*) (Winship et al., 2001) both have similar lifespans of about 20 y for males and well in excess of 20 y for females.

Australian Material

The South African fur seal data on **SBL** vs. age were compared to published material from Arnould and Warneke (2002) on Australian fur seals. Data were read off the graphs in their published paper (Arnould and Warneke, 2002) with an accuracy of the **SBL** readings of about ± 1 cm. Fits of their data were then compared to similar data for South African fur seals from the present study using the same statistical software.

1

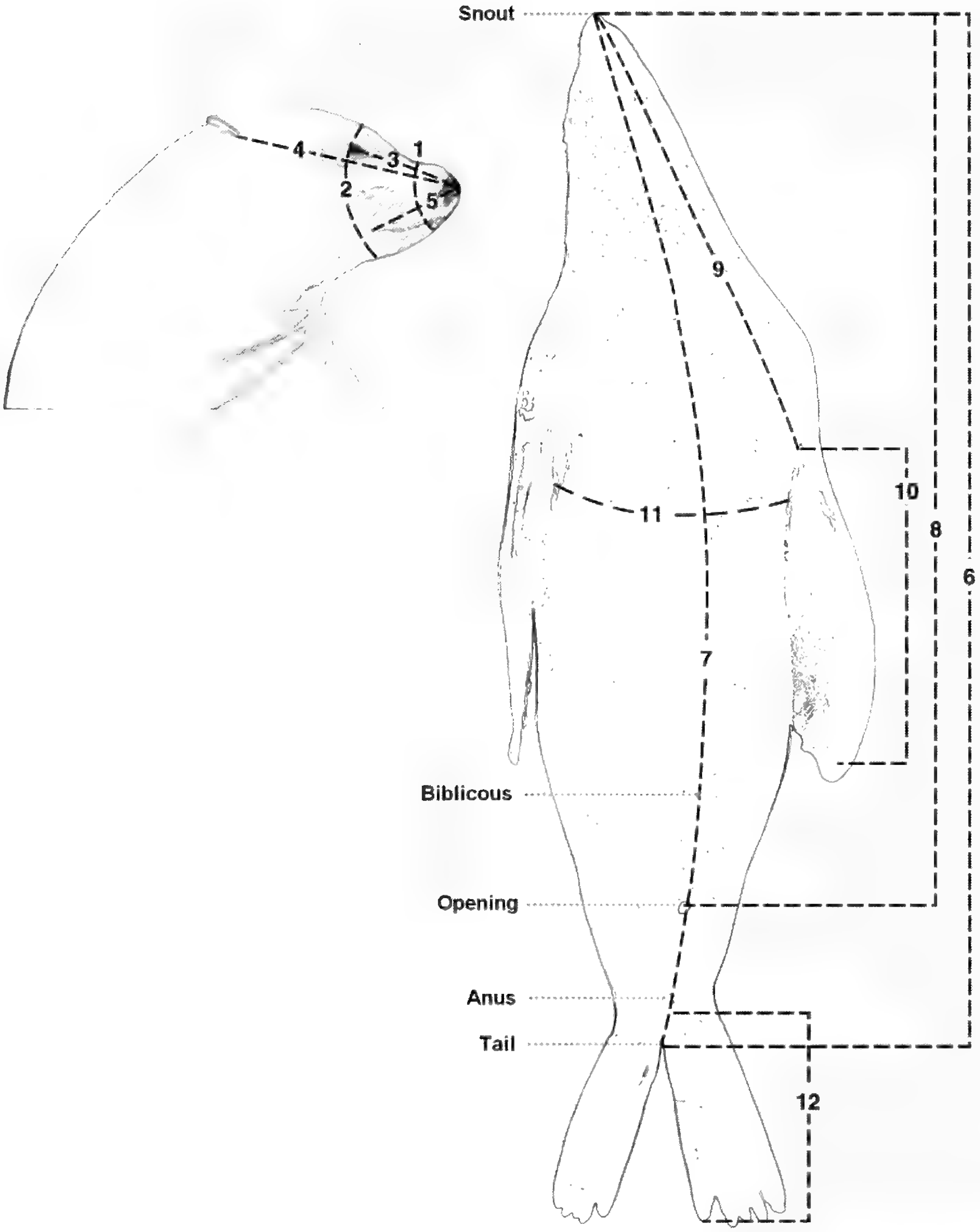


Figure 1: Diagram of a male South African Fur Seal showing how individual body measurements were taken. All measurements were taken with the animal lying on its back.

B1, Circumference of head at canine; B2, circumference of head at eye; B3, tip of snout to centre of eye; B4, tip of snout to centre of ear; B5, tip of snout to angle of gape; B6, standard body length or SBL (straight line from tip of snout to tip of tail with animal lying on its back); B7, ventral curvilinear length (tip of snout to tip of tail over body curve); B8, tip of snout to genital opening; B9, tip of snout to anterior insertion of the foreflipper; B10, length of foreflipper (anterior insertion to tip of first claw); B11, axillary girth; and B12, length of hind flipper (anterior insertion to tip of first claw). All body measurements were made in cm.

Table 1: The age distribution of Male South African Fur Seals. Pups were defined as animals < 1 month old. Animals 1–10 y: 37 MCM animals were of known-age; 34 PEM animals were aged from counts of incremental lines observed in the dentine of upper canines. Animals > 12 y: 2 MCM animals were 13 y; 10 PEM males were > 12 y, i.e., the pulp cavity of the upper canine was closed.

Age group	Age (y)	Frequency	Percentage
Pup	0	3	3.6
Yearling	1	10	12.0
Subadult	2	5	6.0
	3	4	4.8
	4	7	8.4
	5	6	7.2
	6	6	7.2
	7	15	18.1
Adult	8	4	4.8
	9	4	4.8
	10	6	7.2
	12	1	1.2
	13	2	2.4
	> 12	10	12.0
Total		83	100

Statistical analysis

Body variable expressed in relation to standard body length

Growth in body measurement, relative to standard body length (**SBL**), was calculated as follows:

body measurement (cm)/**SBL** (cm) x 100%

As the variance of the ratio estimate is difficult to validly estimate, particularly on small samples, percentages must be interpreted with caution, i.e., both *y* and *x* vary from sample to sample (Cochran, 1977, p. 153).

Body length as an indicator of age

The degree of linear relationship between log body measurement (log **SBL)** and age (y) was calculated using the Spearman rank-order correlation coefficient.

Linear discriminant analysis can be used to classify individual seals into mutually exclusive age groups based on seal body length. The dependent variable (y) is the age group and the independent variable seal body length (x) is the feature that might describe the age group. For each age group we can determine the mean of seal body length ($\bar{x}_i$) and for each seal we compute the Mahalanobis distances of the body length (x) to the mean seal body length of age group i:

EQUATION 1

$$D_i^2(x) = -2\left[\bar{x}_i^T S^{-1} x - \frac{1}{2}\bar{x}_i^T S^{-1}\bar{x}_i\right] + x^T S^{-1} x$$

where, S is the pooled sample variance matrix. Since we are dealing with univariate data we have $\bar{x}_i^T = \bar{x}_i$, $x^1 = x$ and S being the pooled sample covariance. The term in square brackets is the linear discriminant function. We allocate an observation (x) to the age group (pup, yearling, sub adult, adult), which gives the smallest calculated Mahalanobis distance. This is equivalent to allocating the observation (x) to the age group which has the largest linear discriminant function value (Anderson, 1984).

Growth Models

The most commonly used growth models (**SBL** vs. age) for post-natal growth of marine mammals are the exponential saturation curve, known as the von Bertalanffy model, the logistic `curve and the double exponential or Gompertz model (Zullinger et al., 1984; Trites and Bigg, 1992, 1996; Zeide, 1993; Winship et al., 2001; Arnould and Warneke, 2002; McKenzie et al., 2007). In most cases where these equations have been used, a time base adjustment (moving the x-axis) has been used to optimise the fit but this is not a good statistical procedure. No attempt is usually made to estimate the errors of the fitted parameters. In the present study, the models have been expressed in forms where the unknowns were the asymptotic maximum size, the apparent pup size (P) and an exponential constant. Models are for post-natal growth; they are not intended to model the growth of suckling pups and the apparent pup size (P) does not necessarily reflect the actual birth size:

EXPONENTIAL SATURATION OR VON BERTALANFFY CURVE
EQUATION 2

$$Y = (E_\infty - P).(1 - e^{kt}) + P$$

$$\text{or } Y = E_\infty - E_\infty e^{kt} + Pe^{kt}$$

where, E_∞ is the asymptotic maximum size,
P is the apparent pup size,
k is an exponential growth constant
t is time.

LOGISTIC EQUATION
EQUATION 3

$$Y = \frac{E_\infty}{\left(1 + \left(\frac{E_\infty}{P} - 1\right)e^{kt}\right)}$$

where, E_∞ is the asymptotic maximum size,
$\left(\frac{E_\infty}{P} - 1\right)$ is a scaling constant,
P is the apparent pup size,
k is an exponential constant,
t is time.

DOUBLE EXPONENTIAL OR GOMPERTZ EQUATION - EQUATION 4

$$Y = E_\infty . e^{[Ln(P) - Ln(E_\infty)]e^{kt}}$$

where, E_∞ is the asymptotic maximum size,
$[Ln(P) - Ln(E_\infty)]$ is a scaling constant
P is the apparent pup size,
k is an exponential constant,
t is time.

For Equations 2, 3 and 4 the incremental component of growth (E_{growth}) is;

EQUATION 5

$$E_{growth} = E_\infty - P$$

The approximate error for E_{growth} (ΔE_{growth}) is,

$$\Delta E_{growth} \approx \sqrt{(\Delta E_\infty)^2 + (\Delta P)^2}$$

where, ΔE_∞ is the error of the maximum body size,
ΔP is the error of the apparent pup size.

The growth of suckling pups would be expected to be governed by a different growth curve and so the apparent pup size (P) is an abstraction. There are also statistical limitations of the models. Three (3) unknowns have to be fitted. It is much more difficult to fit an equation with 3 unknowns than one with 2 unknowns. The characteristics of the underlying function can also give rise to difficulties; the logistic equation, in particular, is notoriously difficult to fit (Zullinger et al., 1984). The equations cannot be adequately fitted if there is an insufficient amount of data to clearly indicate curvature towards an asymptotic maximum.

The errors of the fitted parameters can be estimated using matrix inversion methods (Johnson and Faunt, 1992). However, most attempts to use such growth curves on mammals and growth of trees have not used enough data points, resulting in the asymptotic errors being so large that the estimates of the fitted parameters are not useful (Zullinger et al., 1984; Zeide, 1993).

Most previous attempts to fit various types of exponential saturation curves have used data where the equations have been simplified by using a fixed estimate of the initial condition at t = 0 (the apparent pup size), hence simplifying the equations to equations with only two unknowns (Australian fur seals - Arnould and Warneke, 2002; New Zealand fur seals – McKenzie et al., 2007; Steller sea lion – Winship et al., 2001).

Least squares fitting routines assume that the error in the dependent variable is normally distributed and independent of the magnitude of the independent variable. In many biological situations this assumption is not valid because the error of the dependent variable increases with increasing magnitude of the independent variable. A constant relative error is often a more realistic assumption to make for biological data. The usual procedure to deal with situations is to log/log transform the data and then use a least squares fitting procedure on the transformed data. In the present study, we found no great improvement in the curve fits (in terms of correlation r) using log/log transformed data. Plots of residuals vs. predicted Y-values did not indicate a systematic increase in the size of the residuals as the predicted Y-value increased. No log/log transform was needed.

Bivariate allometric regression

The relationship between value of body measurement and: (i) **SBL** and (ii) age (y), was investigated using the logarithmic (base e) transformation of the allometric equation,

$y = ax^b$, which may equivalently be written as $\log y = \log a + b \log x$. 'Robust' regression (Huber M-Regression) was used to fit straight lines to the transformed data. The degree of linear relationship between the variables was calculated using the Spearman rank-order correlation coefficient, r (Gibbons and Chakraborti, 1992). This is a non-parametric procedure. Since the log-transformation is monotonic you get the same value for r on transformed or untransformed data. It is important to note that the regression equations relating to overall growth are not used on body measurements that are likely to vary with seasonal variations in body condition that are known to occur in this species (e.g. Rand, 1956). For example, body girth or weight would be inappropriate parameters to use in such analyses.

Statistical tests of hypotheses about model parameters are only valid if the model assumptions hold (i.e., errors are independently and identically normally distributed, with zero mean and with a variance (σ^2) (Weisberg, 1985, p. 24, 156). The standard approach is to first examine the residual values versus fitted plot. If this is a random scatter about zero then it is valid to assume the model is adequate and proceed to check the normality assumption. In the present study, the following tests for checking for normality were used: (i) Anderson-Darling, (ii) Ryan-Joiner and (iii) Kolmogorov-Smirnov (Cochran, 1977).

We used the following test statistic to test one of the hypotheses given below about the slopes of the fitted lines:

EQUATION 6

$$T = \frac{\hat{b} - 1}{SE(\hat{b})}$$

where, $\hat{b}$ is our estimate of the slope using robust regression and SE ($\hat{b}$) is the standard error of $\hat{b}$. Under the null hypothesis the test statistic T has a t distribution with $n - 2$ degrees of freedom (df).

The following hypotheses were tested: H_0: $b = 1$ (isometric) versus H_1: $b \neq 1$ (either positively or negatively allometric); H_1: $b > 1$ (positively allometric); H_1: $b < 1$ (negatively allometric).

Statistical Software

Statistical analysis and graphics were implemented in Minitab (Minitab Inc., State College, 1999, 12.23), Microsoft Excel 97 (Microsoft Corp., Seattle, 1997) and S-PLUS (MathSoft, Inc., Seattle, 1999, 5.1). The EXCEL 97 routines for non-linear least squares fits and calculation of the asymptotic errors of the fitted parameters for the von Bertalanffy, Logistic and Gompertz equations (Equations 2, 3 and 4) are available from Dr R.J. Ritchie (rrit3143@usyd.edu.au) upon request.

Terminology

A juvenile is a weaned pup that has not yet achieved adult size. Puberty is when reproduction first becomes possible (production of sperm in quantity), and social maturity is the age when the animal reaches full reproductive capacity (physically able to establish and maintain a harem). Sexual development of male South African fur seals is discussed elsewhere (Stewardson et al., 1998).

RESULTS

Age determination based on dentition (intra-observer variability)

Counts of GLGs (growth layer groups) in canine teeth were found to be highly reproducible. Of the 34 PEM animals for which GLGs were counted, 14 (41%) had all five readings equal; 16 (47%) had one reading out of 5 different from the mode; and 4 (12%) had 2 readings out of 5 different from the mode.

Age determination (variability between known-age and canine aged animals)

Standard body length (**SBL**) was selected to investigate whether MCM (animals of known-age) and PEM (canine aged animals) animals were similar with respect to age. When comparing the (robust) regression line for **SBL** on age for MCM animals with **SBL** on age for PEM animals, partial t-tests indicate that age is important ($t = 7.07$, $p < 0.001$), even after adjusting for group and age-group interaction; but they provide little information on group ($t = -0.82$, $p = 0.42$) and age group interaction ($t = 0.87$, $p = 0.58$), hence one straight line can be fitted to the data. These statistical conclusions were verified by examining graphical displays of fitted values and residuals. Thus PEM and MCM animals were not significantly different with respect to age distribution.

This conclusion is supported by the sequential F test, provided the sequence of terms added sequentially (first to last) was: (i) none (i.e., fitting a line parallel to the x axis); (ii) age ($F = 817.69$, $p < 0.001$) (one straight line); (iii) museum (i.e., MCM and PEM) ($F = 0.0659$, $p = 0.7984$) (two parallel lines); (iv) age ×

museum interaction (F = 0.1883, p = 0.6661) (two lines not necessarily parallel).

Bivariate allometric regression

Regression statistics for body measurements on **SBL** and age (1–10 y) are given in Appendix 3 and 4. Overall, correlation coefficients were moderately to strongly positive, i.e., most points on the scatter plot approximated a straight line with positive slope, $r \geq 0.70$. Exceptions included tip of snout to centre of eye **(B3)** with age and **SBL** (r = -0.008 and r = 0.15 respectively); tip of snout to angle of gape **(B5)** with age (r = 0.56); circumference of head at canine **(B1)** with age (r = 0.59). Although correlation coefficients indicate that linearity was reasonably well approximated for most variables by log-log transformations, a linear relationship did not necessarily best describe the relationship. In the present study, we have attempted to fit more complex models in the case of **SBL** vs. age with the specific aim of comparing our growth curves with those found for the Australian fur seal (Arnould and Warneke, 2002)(see below).

Growth of body variables

Most variables were significantly positively correlated with each other, $r \geq 0.68$ (Appendix 2). Exceptions were: (i) tip of snout to centre of eye (**B3**) with all variables; (ii) circumference of head at eye (**B2**) with tip of snout to angle of gape (**B5**) (r = 0.61); and (iii) circumference of head at canine (**B1**) with tip of snout to angle of gape (**B5**) (r = 0.63).

Circumference of head at canine (B1)

Growth of circumference of head at canine **(B1)** was variable relative to age, r = 0.59 (Appendix 4). Overall growth expressed negative allometry relative to **SBL** and age (Appendix 3, 4), increasing by 57% at 10 y relative to pups (**RTP**) (Table 2). Growth increment decreased with increasing **SBL** until about 7 y (*c*. 15% of **SBL**) (Table 3). The mean **B1** of males > 10 y (including unaged animals > 200 cm and of indeterminate age ≥ 12 y) was 31.8 ± 1.2 cm (n = 5). The maximum-recorded value was 35.0 cm (animal MCM3017, **SBL** 209 cm, 12 y 11 months).

Circumference of head at eye (B2)

Growth of circumference of head at eye **(B2)** was rapid during the early postnatal period and continued to increase until at least 13 y. Overall growth expressed negative allometry relative to **SBL** and scaled with negative slope relative to age (b = 0.12) (Figures 2a, b; Appendix 3, 4), increasing by 65% at 10 y (**RTP**) (Table 3). Growth increment decreased with increasing **SBL** until about 7 y (*c*. 22% of **SBL**) (Table 2). Mean **B2** of males > 10 y (including unaged animals > 200 cm and of indeterminate age ≥ 12 y) was 45.8 ± 1.8 cm (n = 6). Maximum recorded value was 53.0 cm (animal PEM676, **SBL** 197 cm).

Tip of snout to centre of eye (B3)

Growth of tip of snout to centre of eye **(B3)** was highly variable relative to age, r = -0.008, and **SBL**, r = 0.15 (Appendix 3, 4). Growth increment decreased with increasing **SBL** until about 9 y (*c*. 5% of **SBL**) (Table 2). Mean **B3** of all males > 10 y (including unaged animals > 200 cm and of indeterminate age ≥ 12 y) was 10.4 ± 0.6 cm (n = 10). Maximum recorded value was 14.4 cm (animal PEM2194, **SBL** 194 cm).

Table 2 (Pages 227-228): Summary statistics for body variables (B1–B12), according to age (y) and age group of male South African Fur seals.

Data presented as mean body measurement in cm ± S.E., followed by coefficient of variation in round brackets, and body variable expressed as a percentage of SBL. Maximum value of each variable (males of unknown-age) is also presented.

Variables: B1, Circumference of head at canine; B2, circumference of head at eye; B3, tip of snout to centre of eye; B4, tip of snout to centre of ear; B5, tip of snout to angle of gape; B6, standard body length (SBL); B7, ventral curvilinear length; B8, tip of snout to genital opening; B9, tip of snout to anterior insertion of the foreflipper; B10, length of foreflipper; B11, axillary girth; B12, length of hind flipper. Variable B3 was poorly correlated with body variables and age (Appendices 1, 2, 3 and 4), therefore has been excluded from further analysis. B7 was shown to be a poor indicator of SBL, therefore was excluded from further analysis. B11 may be influenced by seasonal change and illness, therefore was excluded from further analysis. Sample size (n) is the number of dentition-aged and known-age (tagged) animals. Sample size given in square brackets where this does not equal total sample size. The data summary includes calculations of the mean of each variable ± S.E. for the 7 largest males (> 200 cm) of known or unknown-age; maximum value in square brackets, followed by sample size.

Age group	Age (y)	Sample size (n)	B1	B2	B3	B4	B5	B6
Pup	< 1	3	16.9 ± 1.1 (11.3) 24.4%	24.1 ± 1.4 (10.3) 34.7%	9.1 ± 0.9 (16.4) 13.1%	11.8 ± 0.1 (2.1) 17.0%	7.1 ± 0.7 (16.5) 10.3%	69.3 ± 2.8 (7.1) –
Yearling	1	8	19.6 ± 0.9 (12.5) 21.6%	27.9 ± 1.4 [7] (13.2) 30.9%	8.3 ± 0.6 [7] (18.2) 9.0%	13.7 ± 0.4 (7.6) 15.1%	7.7 ± 0.3 (12.3) 8.4%	90.8 ± 2.4 (7.4) –
Subadult	2	5	21.1 ± 1.1 (12.1) 22.5%	30.8 ± 1.6 (11.7) 32.8%	10.2 ± 1.3 [4] (25.5) 10.8%	14.9 ± 0.5 (7.7) 15.9%	7.8 ± 0.4 (11.4) 8.3%	93.8 ± 1.9 (4.5) –
	3	5	22.2 ± 0.5 (4.8) 19.7%	32.2 ± 0.8 (5.3) 28.5%	10.7 ± 1.2 [4] (23.2) 9.6%	17.1 ± 0.4 (5.8) 15.2%	8.6 ± 0.6 (14.3) 7.6%	112.8 ± 4.0 (8.0) –
	4	9	24.1 ± 0.6 (7.6) 19.6%	34.3 ± 0.5 (4.8) 27.7%	9.1 ± 0.5 (17.7) 7.6%	18.3 ± 0.5 (7.9) 14.8%	9.9 ± 0.3 (7.8) 7.9%	124.3 ± 5.0 [8] (11.4) –
	5	5	24.0 ± 0.4 [4] (3.4) 17.9%	34.8 ± 1.4 [4] (7.9) 26.8%	9.9 ± 0.7 (15.4) 6.6%	18.8 ± 0.9 (11.3) 13.4%	8.6 ± 0.7 [3] (14.7) 6.8%	136.5 ± 2.5 [2] (2.6) –
	6	10	24.9 ± 0.6 (7.8) 17.0%	37.1 ± 0.8 (7.0) 25.3%	10.4 ± 0.5 [8] (14.6) 7.2%	19.3 ± 0.5 (8.2) 13.0%	10.2 ± 0.3 [9] (7.6) 7.0%	145.8 ± 1.4 [9] (2.8) –
	7	11	23.7 ± 0.8 [10] (10.6) 15.1%	34.7 ± 0.8 [10] (7.2) 22.3%	9.0 ± 0.6 [7] (18.6) 6.2%	18.2 ± 0.4 (7.7) 11.5%	9.3 ± 0.5 (16.7) 6.3%	157.5 ± 3.4 [8] (6.2) –
	2–7	45	23.6 ± 0.3 [43] (9.5) 17.9%	34.5 ± 0.5 [43] (8.9) 26.2%	9.8 ± 0.3 [37] (18.5) 7.7%	18.0 ± 0.3 (10.5) 13.6%	9.3 ± 0.2 [42] (14.1) 7.2%	131.7 ± 3.8 [37] (17.5) –
Adult	8	6	24.2 ± 1.0 [5] (9.6) 14.8%	38.6 ± 1.8 [5] (10.5) 21.4%	8.8 ± 0.6 (16.2) 5.7%	18.9 ± 0.7 (9.2) 11.7%	9.9 ± 0.8 [5] (19.0) 6.8%	161.0 ± 3.5 [3] (3.8) –
	9	5	26.0 ± 0.5 [4] (4.2) 15.2%	37.4 ± 1.0 (5.8) 21.6%	8.1 ± 0.7 [4] (18.1) 4.6%	20.5 ± 0.8 (9.1) 12.0%	10.7 ± 0.4 (8.8) 6.4%	170.8 ± 2.3 [4] (2.7) –
	10	4	26.6 ± 1.1 [3] (7.4) 14.7%	39.7 ± 1.8 [3] (7.7) 21.9%	9.5 ± 1.1 [3] (20.7) 5.2%	20.0 ± 0.2 (1.9) 10.9%	11.1 ± 0.4 (6.7) 6.0%	182.9 ± 6.0 (6.6) –
	13	2	31.5 ± 3.5 (15.7) 15.3%	44.5 ± 5.5 (17.5) 21.5%	11.1 ± 0.9 (11.5) 5.3%	24.6 ± 0.6 (3.4) 11.9%	13.5 ± 0.5 (5.2) 6.5%	206.5 ± 2.5 (1.7) –
	8–13	17	26.3 ± 0.9 [14] (12.2) 15.0%	39.2 ± 1.1 [15] (10.5) 21.6%	9.1 ± 0.4 [15] (18.4) 5.2%	20.3 ± 0.5 (11.0) 11.6%	10.9 ± 0.4 [16] (14.7) 6.4%	177.7 ± 4.7 [13] (9.4) –
Total		**73**	**68**	**68**	**62**	**73**	**69**	**61**
Mean for all males > 200 cm	31.3 ± 2.0	44.3 ± 3.2	11.8 ± 0.6	24.4 ± 0.4	14.0 ± 0.5	210.7 ± 5.7	211.8	172.0 ± 5.9
[max. value in brackets]	[35.0] n = 3	[50.0] n = 3	[13.0] n = 4	[25.2] n = 3	[14.9] n = 3	[243.0] n = 7	n = 1	[182.0] n = 4

Table 2 continued

Age group	Age (y)	Sample size (n)	B7	B8	B9	B10	B11	B12
Pup	< 1	3	70.9 ± 3.6 (8.7) –	55.6 ± 1.7 (5.3) 80.2%	31.7 ± 0.9 (4.8) 45.7%	17.6 ± 1.6 (16.2) 25.4%	39.6 ± 3.5 (15.5) 57.1%	13.3 ± 0.7 (9.4) 19.2%
Yearling	1	8	95.3 ± 3.9 [3] (7.1) –	75.9 ± 2.2 (8.1) 83.7%	41.1 ± 1.7 (11.6) 45.3%	22.4 ± 1.2 (15.0) 24.7%	53.1 ± 4.6 (24.4) 58.5%	15.1 ± 0.4 (8.0) 16.6%
Subadult	2	5	– [0]	79.6 ± 2.4 (6.8) 84.9%	37.7 ± 0.8 (4.6) 40.2%	23.5 ± 0.4 (4.3) 25.1%	58.2 ± 3.1 (11.8) 62.0%	16.0 ± 0.6 (8.3) 17.0%
	3	5	– [0]	98.1 ± 2.1 (4.9) 87.0%	48.9 ± 2.1 (9.5) 43.3%	27.4 ± 1.4 (11.2) 24.3%	73.9 ± 2.0 (6.2) 65.5%	18.1 ± 0.8 (9.3) 16.0%
	4	9	– [0]	107.2 ± 3.6 [8] (9.5) 86.2%	52.5 ± 1.7 (9.8) 42.6%	30.1 ± 1.1 (11.0) 24.5%	80.2 ± 2.3 (8.5) 64.7%	18.6 ± 0.5 (8.8) 15.2%
	5	5	149.7 ± 2.7 [3] (3.2) –	124.5 ± 4.8 (8.7) 84.4%	62.7 ± 4.2 (14.9) 40.5%	35.7 ± 1.4 (9.0) 23.9%	85.8 ± 0.8 [2] (1.2) 62.8%	21.7 ± 1.3 [3] (10.1) 15.0%
	6	10	155.3 ± 5.2 [3] (5.8) –	126.7 ± 1.7 (4.2) 87.2%	65.5 ± 3.4 (16.3) 43.6%	33.6 ± 0.9 [9] (7.7) 23.0%	91.4 ± 2.1 [9] (6.8) 62.7%	21.2 ± 0.4 [9] (5.9) 14.5%
	7	11	158.5 ± 4.3 [5] (6.0) –	132.5 ± 2.5 (6.3) 84.9%	71.8 ± 2.1 (9.6) 45.8%	34.7 ± 1.1 (10.1) 22.4%	100.2 ± 3.1 [7] (8.3) 64.4%	23.6 ± 0.7 [10] (9.1) 15.2%
	2–7	45	155.2 ± 2.6 [11] (5.5) –	115.7 ± 2.9 [44] (16.5) 86.0%	59.2 ± 2.0 (22.2) 43.4%	31.6 ± 0.7 [44] (15.3) 23.6%	83.2 ± 2.4 [37] (17.5) 63.8%	20.2 ± 0.5 [41] (15.0) 15.3%
Adult	8	6	166.0 ± 2.1 [5] (2.8) –	136.6 ± 3.1 (5.5) 85.8%	76.6 ± 2.2 (7.1) 50.1%	35.2 ± 1.6 (11.5) 21.3%	90.6 ± 4.6 [2] (7.2) 57.5%	26.0 ± 1.0 (9.7) 15.8%
	9	5	185.8 ± 3.4 [4] (3.7) –	152.6 ± 2.6 (3.8) 89.6%	83.8 ± 5.8 (15.6) 48.4%	40.6 ± 0.9 (5.0) 24.1%	114.5 ± 2.9 [4] (5.1) 67.0%	28.2 ± 1.3 (10.1) 16.5%
	10	4	203.7 ± 4.9 [3] (4.2) –	159.3 ± 5.4 (6.8) 87.1%	87.8 ± 8.5 (19.5) 48.1%	40.3 ± 2.1 [3] (10.2) 22.0%	111.9 ± 6.9 (12.2) 61.2%	27.1 ± 1.6 (11.7) 14.8%
	13	2	– [0]	178.5 ± 3.5 (2.8) 86.4%	91.5 ± 3.5 (5.4) 44.3%	48.4 ± 3.6 (10.5) 23.4%	– [0]	27.7 ± 1.5 (7.7) 13.4%
	8–13	17	182.0 ± 4.9 [12] (9.2) –	151.6 ± 3.8 (10.2) 87.4%	83.1 ± 2.9 (14.1) 47.9%	39.5 ± 1.3 [16] (13.5) 22.7%	108.7 ± 4.1 [10] (12.0) 62.8%	27.1 ± 0.46 (9.8) 15.3%
Total		**73**	**29**	**72**	**73**	**72**	**58**	**69**
Mean for males > 200 cm [max. value in brackets]	31.3 ± 2.0 [35.0] n = 3	44.3 ± 3.2 [50.0] n = 3	91.0 ± 3.4 [98.0] n = 4	49.0 ± 2.7 [55.0] n = 4	135.0 ± 34.0 [169.0] n = 2	28.8 ± 1.4 [29.2] n = 3		

Table 3: Growth in body variables (B1–B12) relative to the mean value of body measurement of male South African Fur seals: (i) at age zero, RGR y_0; and (ii) from the previous year, RGR$_{yt-1}$. All measurements are in cm ± S.E. with a coefficient of variation in brackets. Maximum value of each variable (males of unknown-age) is also presented.

Variables (B1-B12) as for Table 2. Variables B3, B7 and B11 were excluded from analysis (see Table 2). Sample size (n) is the number of dentition-aged and known-age (tagged) animals. For animals measured at sea (by-catch) it was not always possible to record SBL because of rough conditions, i.e., SBLs for 12 of these animals were not recorded. Values for growth relative to age zero are presented on the left hand side of the relevant columns, i.e., $[(y_t - y_0)/y_0] \times 100\%$ where t = 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 13 and y0 is the known size as a pup. Values for growth relative to the previous year (age = t-1), are presented on the right hand side of the relevant columns, i.e., $[(y_t - y_{t-1})/y_{t-1}] \times 100\%$. Sample size given in square brackets [n] where this does not equal total sample size due to the exclusion of some animals from the analysis.

Age group	Age (y)	Sample size (n)	B1	B2	B4	B5	B6 (SBL)	B8	B9	B10	B12
Pup	< 1	3	–	–	–	–	–	–	–	–	–
Yearling	1	8	15.7; 15.7	16.1; 16.1 [7]	16.5; 16.5	7.1; 7.1	30.9; 30.9	36.5; 36.5	29.9; 29.9	27.1; 27.1	13.3; 13.3
Subadult	2	5	24.6; 7.7	28.0; 10.2	26.7; 8.8	9.2; 2.0	35.3; 3.4	43.2; 4.9	19.1; -8.3	33.6; 5.1	19.7; 5.7
	3	5	31.0; 5.1	33.7; 4.5	45.7; 15.0	20.7; 10.5	62.7; 20.3	76.4; 23.2	54.3; 29.6	55.8; 16.6	35.5; 13.2
	4	9	42.6; 8.9	42.7; 6.7	55.4; 6.6	38.1; 14.5	79.3; 10.2 [8]	92.7; 9.2 [8]	65.8; 7.4	71.2; 9.9	39.5; 3.0
	5	5	41.7; -0.6 [4]	44.6; 1.3 [4]	59.5; 2.6	20.9; -12.5 [3]	96.9; 9.8 [2]	124.0; 16.2	98.0; 19.4	103.0; 18.5	63.0; 16.8 [3]
	6	10	47.1; 3.8	54.3; 6.7	64.0; 2.8	42.3; 17.8 [9]	110.3; 6.8 [9]	127.8; 1.7	106.8; 4.5	90.9; -5.9 [9]	58.9; -2.5 [9]
	7	11	40.0; -4.9 [10]	44.3; -6.5 [10]	54.8; -5.7	29.9; -8.7	127.2; 8.1 [8]	138.3; 4.6	126.7; 9.6	97.3; 3.3	76.8; 11.3 [10]
Adult	8	6	42.8; 2.0 [5]	60.2; 11.0 [5]	61.0; 4.0	38.6; 6.7 [5]	132.2; 2.2 [3]	145.7; 3.1	142.0; 6.8	99.7; 1.2	95.1; 10.4
	9	5	53.5; 7.5 [4]	55.2; -3.1	74.0; 8.1	50.1; 8.3	146.3; 6.1 [4]	174.5; 11.7	164.6; 9.3	130.5; 15.4	111.4; 8.3
	10	4	57.3; 2.4 [3]	64.8; 6.2 [3]	69.9; -2.4	54.7; 3.1	163.7; 7.1	186.4; 4.4	177.3; 4.8	128.7; -0.8	103.4; -3.7
	13	2	86.0; –	84.9; –	109.2; –	89.0; –	197.8; –	221.0; –	188.9; –	175.0; –	107.8; –
Total		73	68	68	73	69	61	72	73	72	69

Tip of snout to centre of ear (B4)

Growth of tip of snout to centre of ear **(B4)** was rapid during the early postnatal period and continued to increase until at least 13 y (Table 2 and 3). Overall growth expressed negative allometry relative to **SBL** and scaled with negative slope relative to age ($b = 0.04$) (Figures 3a, b; Appendix 3, 4), increasing by 70% at 10 y **RTP** (Table 3). Growth increment decreased with increasing **SBL** until about 7 y (*c.* 12% of **SBL**) (Table 2). The mean **B4** of all males > 10 y (including unaged animals > 200 cm and of indeterminate age ≥ 12 y) was 22.7 ± 0.8 cm ($n = 7$). The maximum-recorded value was 25.2 cm (animal MCM3125, **SBL** 204 cm, 13 y).

Tip of snout to angle of gape (B5)

Growth of tip of snout to angle of gape **(B5)** was variable relative to age, $r = 0.56$ (Appendix 4). Overall growth scaled with negative slope relative to **SBL** ($b = 0.64$) and expressed negative allometry relative to age (Appendix 3, 4), increasing by 55% at 10 y **RTP** (Table 3). Growth increment decreased with increasing **SBL** until about 7 y (*c.* 6% of **SBL**) (Table 2). The mean **B5** of all males > 10 y (including unaged animals > 200 cm and of indeterminate age ≥ 12 y) was 13.2 ± 0.7 cm ($n = 7$). The maximum recorded value was 15.0 cm (animal PEM676, **SBL** 197 cm).

Standard body length (B6 or SBL)

Growth of **SBL (B6)** was rapid during the early postnatal period with a significant growth spurt between 2 and 3 y (two sample t test: p-value = 0.008; df = 5). The rate of growth slowed significantly between 6 and 7 y (two sample t test assuming unequal variances: p-value = 0.011; df = 9). A weak growth spurt was observed at 9 and 10 y but could not be examined statistically, i.e., this secondary growth spurt may be attributed to sampling error. Growth increased by 164% at 10 y **RTP** (Table 3). Considering that the 13 y old males measured 206.5 ± 2.5 cm ($n = 2$), and mean **SBL** of all males > 10 y and/or unaged animals > 200 cm was 197 ± 4.1 cm ($n = 15$), growth appears to slow after attainment of social maturity (Table 2).

Tip of snout to genital opening (B8)

Growth of tip of snout to genital opening **(B8)** was rapid during the early postnatal period and continued to increase until at least 13 y (Table 2 and 3). Growth increased by 186% at 10 y **RTP** (Table 3). In subadults and adults, mean value remained at about 86% of **SBL** (Table 2). Overall growth scaled with weak positive slope relative to **SBL** ($b = 1.04$) and negative slope relative to age ($b = 0.02$). The maximum recorded value for parameter **B8** was 184.0 cm (animal PEM2256, **SBL** 198 cm). The mean **B8** of all males > 10 y, including unaged animals > 200 cm) was 171.1 ± 3.4 cm ($n = 7$).

Tip of snout to anterior insertion of the foreflipper (B9)

Growth of tip of snout to anterior insertion of the foreflipper (**B9**) was rapid during the early postnatal period and continued to increase until at least 10 y (Table 2 and 3). Overall growth expressed positive allometry relative to **SBL**, and negative allometry relative to age (Figure 4a, b; Appendix 3, 4). Growth increased by 177% at 10 y **RTP** (Table 3). Mean **SBL** of all males > 10 y, including unaged animals > 200 cm was 94.2 ± 3.1 cm ($n = 7$). Maximum recorded value for **B9** was 110.0 cm (animal PEM2374, **SBL** 186 cm).

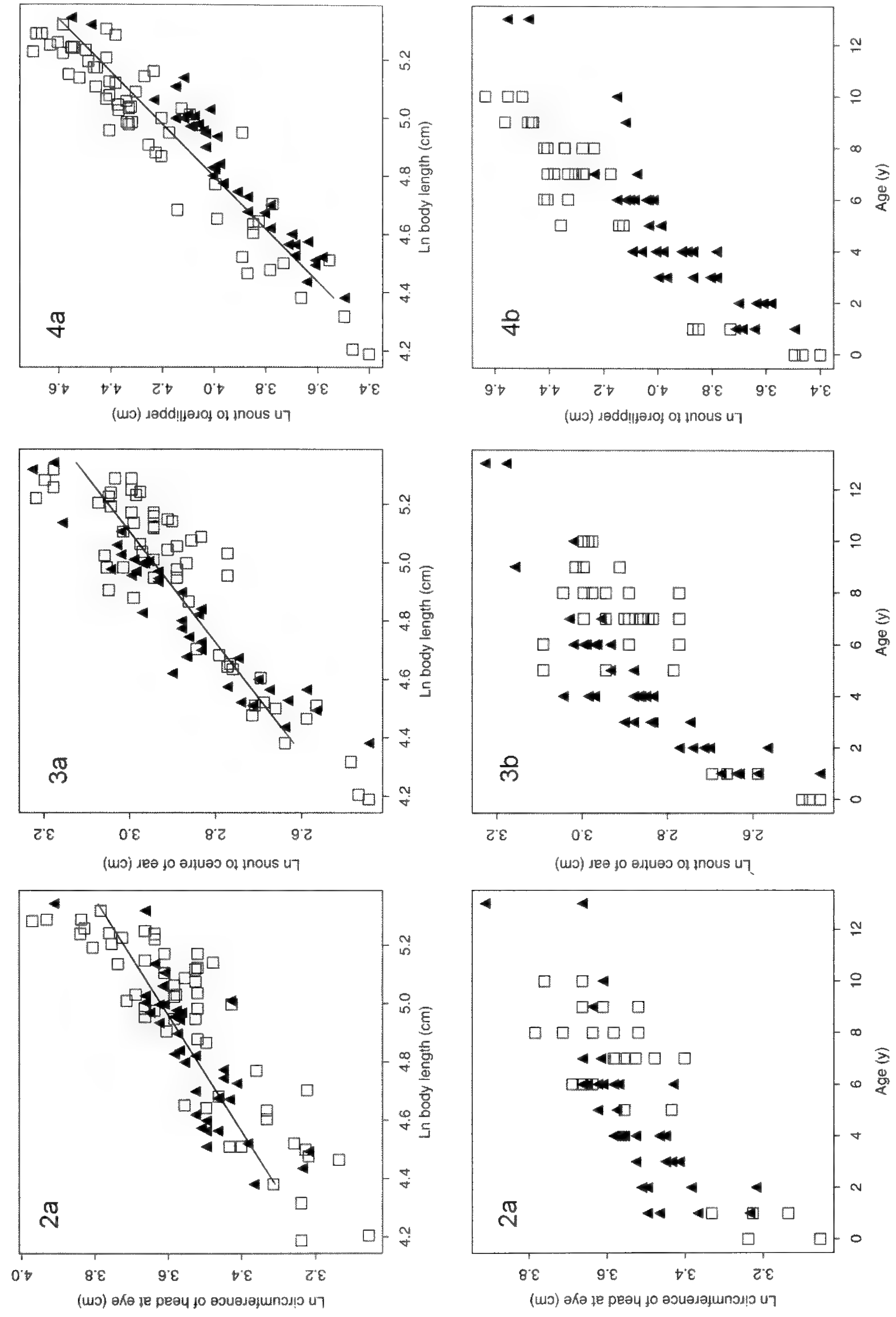
Length of foreflipper (B10)

Growth of length of foreflipper **(B10)** was rapid during the early postnatal period and continued to increase until at least 13 y (Table 2 and 3). A significant growth increment was evident between 4 and 5 y (two sample t test: p-value = 0.015; df = 8). Overall growth scaled with negative slope relative to **SBL** ($b = 0.89$) and age ($b = 0.07$). Growth increased by 129% at 10 y RTP (Table 3). Growth increment decreased with increasing **SBL** until about 6 y (*c.* 23% of **SBL**) (Table 2). The mean length of flipper **(B10)** of all males > 10 y, including unaged animals > 200 cm was 47.2 ± 1.9

Figure 2a, b (right): Bivariate plot of log circumference of head at canine (cm) on: (a) log SBL length of seal (cm) and (b) age (y). PEM animals, open squares; MSM animals, closed triangles.

Figure 3a, b (right: Bivariate plot of log tip of snout to centre of ear (cm) on: (a) log length of seal (cm) and (b) age (y). PEM animals, open squares; MCM animals, closed triangles.

Figure 4a, b (right): Bivariate plot of log tip of snout to anterior insertion of the foreflipper (cm) on: (a) log length of seal (cm) and (b) age (y). PEM animals, open squares; MCM animals, closed triangles.


4a
3a
2a
4b
3b
2a
Ln body length (cm)
4.2
4.4
4.6
4.8
5.0
5.2
Age (y)
0
2
4
6
8
10
12
Ln snout to foreflipper (cm)
3.4
3.6
3.8
4.0
4.2
4.4
4.6
Ln snout to centre of ear (cm)
2.6
2.8
3.0
3.2
Ln circumference of head at eye (cm)
3.2
3.4
3.6
3.8
4.0

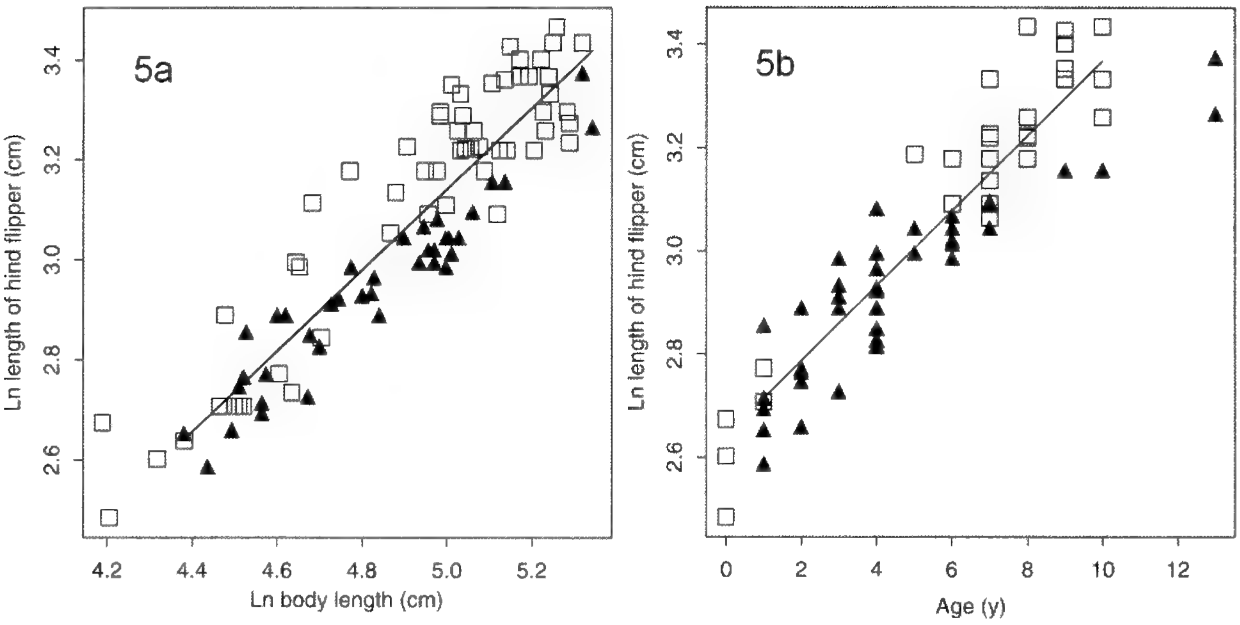


Figure 5a, b: Bivariate plot of log length of hind flipper (cm) on: (a) log length of seal (cm) and (b) age (y). PEM animals, open squares; MCM animals, closed triangles.

cm (*n* = 8). The maximum recorded value for **B10** was 55.0 cm (animal PEM1560, **SBL** 201 cm).

Length of hind flipper (B12)

Growth of length of hind flipper **(B12)** was rapid during the early postnatal period and continued to increase until at least 8–9 y (Table 2 and 3). Overall growth scaled with negative slope relative to **SBL** ($b = 0.81$) and expressed negative allometry relative to age (Figures 5a, b; Appendix 3, 4), increasing by 103% at 10 y RTP (Table 3). Growth increment decreased with increasing **SBL** until about 4 y (*c*. 15% of **SBL**) (Table 2). The mean **B12** of all males > 10 y, including unaged animals > 200 cm was 28.7 ± 0.9 cm (*n* = 7). The maximum recorded value was 32.0 cm (animal PEM1890, **SBL** 192 cm, ≥ 12 y).

Body length as an indicator of age

In animals 1–10 y, growth in **SBL** was highly positively correlated with age (y) ($r = 0.96$, $n = 56$) (Appendix 4). After fitting the (robust) straight line model of age on standard body length, graphical displays of residuals and fitted values were examined, and the straight line model was found to be adequate. Thus, the following equation can be used as a 'rough indicator' of absolute age for animals 1–10 y.

$$\text{Age} = -6.54 + 0.0087 \times \mathbf{SBL},\ n = 56$$

The coefficient of variation ($100 \times s/\bar{x}$) in **SBL** for young males 1–5 y (17.2%) was considerably higher than in older males (8–10 y, 6.9%; ≥ 12 y, 5.3%).

Body length as an indicator of age group

Linear discriminant analysis was used to classify seals of unknown age into one of the four age groups (pup, yearling, subadult, adult) based on body length. Performing linear discriminant analysis using the body length data where the age group is known we get the following four linear discriminant functions of the form y = mx+b:

$$\begin{array}{lll} y_1 = 0.19 \times \text{SBL} - 6.5 & & \text{(pup)} \\ y_2 = 0.25 \times \text{SBL} - 11.14 & & \text{(yearling)} \\ y_3 = 0.36 \times \text{SBL} - 23.46 & & \text{(subadult)} \\ y_4 = 0.50 \times \text{SBL} - 45.28 & & \text{(adult)} \end{array}$$

where, **SBL** is in cm. A seal with known **SBL** but unknown age is classified into the age group which gives the largest value for the associated linear discriminant function. For example, an animal 150 cm long would have linear discriminant function values of $y_1 = 22$, $y_2 = 26.36$, $y_3 = 30.54$ and $y_4 = 29.72$ and so would be classified as a subadult. Animals over 180 cm would be automatically classified as adults.

Table 4 shows that when the method was used on animals of known age it was highly successful in classifying animals into the correct categories. All 3 pups were correctly classified and nearly all the yearlings (7/8) were correctly classified but one was classified as a pup. There were some difficulties in distinguishing yearlings with subadults and subadults with adults but only one adult out of 22 was incorrectly

Table 4: Discriminant analysis for seal age group (pup, yearling, subadult, adult) inferred from body length of male South African Fur seals.

Size (i) is at age zero, RGR y0; and size (ii) from the previous year, RGR yt–1. All measurements are in cm. Sample size (n) is the number of seals of known-age (MCM animals tagged as pups), and aged from counts of incremental lines observed in the dentine of upper canines (PEM animals), n = 70 (of the 73 animals of known age, three animals had insufficient data for this analysis to be carried out). Includes animals ≥ 12 y (known to be at least 12 y but could not be aged more definitively due to the limitations of the dentition aging method). Percentage of animals correctly classified into age group is given in brackets. The overall percentage correctly classified: (3+7+23+21)/70 x 100% = 77.14%. Pups: All 3 pups have been correctly classified. Yearlings or juveniles: 1 yearling was incorrectly classified as a pup and the rest of the juveniles (7) have been correctly classified. Subadults: 9 subadults were classified as yearlings, 23 subadults were correctly classified and 5 subadults were classified as adults. Adults: one (1) adult was incorrectly classified as being subadult and the rest (n = 21) were correctly classified.

	True Group				
Predicted Group	**Pup**(< 1 mo)	**Juvenile or Yearling**(7 mo to 1 y 6 mo)	**Subadult**(1y 7 mo to 7 y 6 mo)	**Adult**(≥ 7 y 7 mo)	**Total**
Pup	3 (100%)	1 (12.5%)	0	0	**4**
Juvenile or Yearling	0	7 (87.5%)	9 (24.3%)	0	**16**
Subadult	0	0	23 (62.2%)	1 (4.5%)	**24**
Adult	0	0	5 (13.5%)	21 (95.5%)	**26**
Total	**3**	**8**	**37**	**22**	**70**

classified as a subadult. The overall percentage correctly classified was calculated from adding up all the correctly classified animals and then dividing by the total number of animals multiplied by 100%; that is, (3+7+23+21)/70 x 100% = 77.14%. Body length is therefore useful in discriminating between different age groups but some groups such as yearlings and subadults can be difficult to correctly classify.

Curvilinear Body length as an indicator of SBL

Curvilinear body length **(CBL)** was found to be approximately 10.0 cm longer than **SBL** (**SBL**: 146.7 ± 5.6; CBL: 157.1 ± 6.2, $n = 50$ using paired samples only). However, **CBL** was greatly influenced by the quantity of food in the stomach and by the degree of post-mortem bloating. For example, **CBL** was 20–25 cm longer than **SBL** in 5 animals that had been dead for several days, or had consumed large quantities of fish; therefore, **CBL** was not considered to be a useful substitute for **SBL**.

Growth Curve Models

Figure 6 shows a non-linear least squares fit of the Logistic model (Equation 3) to **SBL** vs. age for male South African fur seals compared to curve fits on data from a previously published study on the Australian fur seal (Arnould and Warneke, 2002). Non-linear fits were also made using the exponential saturation + constant or von Bertalanffy model (Equation 2), and the Gompertz or double exponential equation (Equation 4). Table 5 shows the statistics of the curve fits. The correlations for all three models are very high ($r > 0.94$). Tests for significant differences in the fitted parameters were done using t-tests assuming equal variances or assuming unequal variances as appropriate (Cochran, 1977).

The Australian fur seal data fits to the von Bertalanffy model quite well (Table 5), however the model does not appear to be suitable for the South African fur seal data. The fit for the South African fur seal data gives a fitted curve that is very close to linear and gives an unrealistically high estimate of the asymptotic **SBL** of over 270 cm. South African fur seals have a lower apparent pup size and exponential constant and the growth rate is lower than for the Australian fur seals (Table 5).

The fits using the logistic (Equation 3) and the Gompertz (Equation 4) equations are more similar to

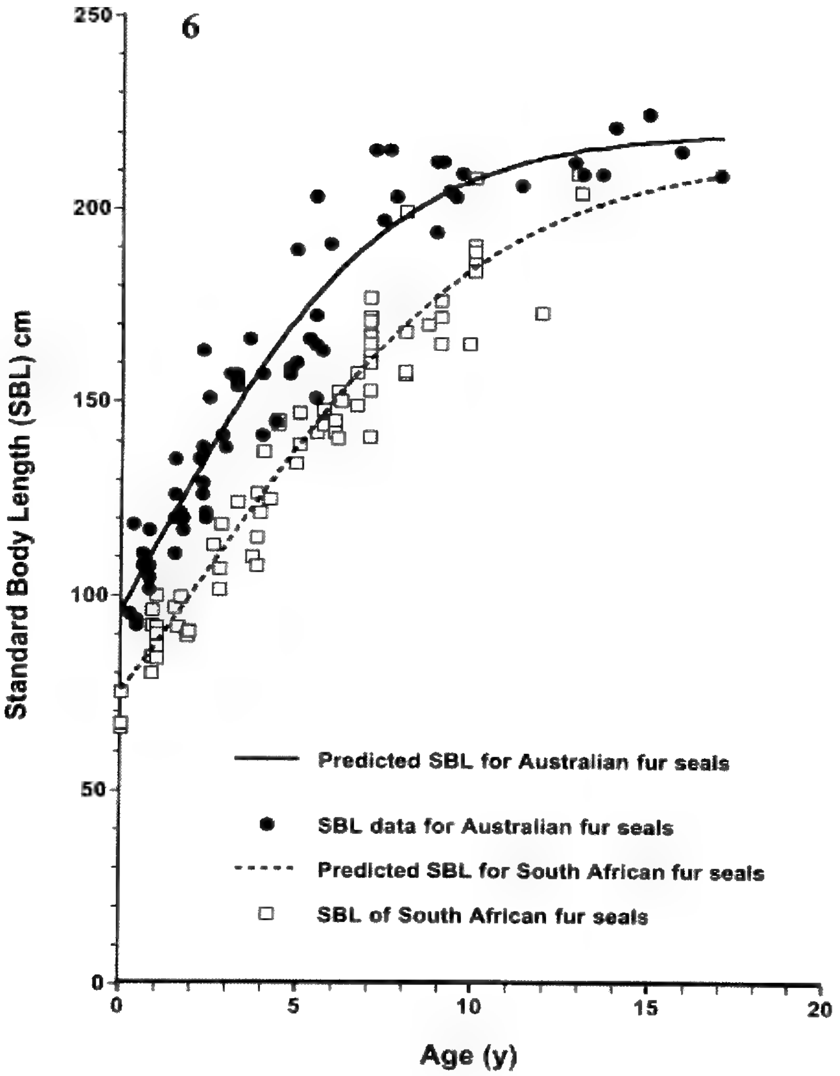


Figure 6: Growth kinetics of male South African fur seals (Arctocephalus pusillus pusillus) (closed circles) compared to male Australian fur seals (A. pusillus doriferus) (open squares). Age in y and SBL in cm. Curves fitted using the logistic model (Equation 3).

each other than those made using the von Bertalanffy model (Equation 2) and both models give more realistic estimates of asymptotic maximum size for both the Australian and South African fur seals. Table 5 shows that the significant differences in the model parameters between the South African and Australian fur seals are the apparent pup size (P) and the exponential constant (k). The significant differences in (k) values reflect a slower growth rate from a lower initial (P) in South African fur seals.

The asymptotic maximum **SBL** is about 214-232 cm based on the logistic and Gompertz models. These two models agree that the asymptotic maximum **SBL** is not significantly different in South African and Australian fur seals. Overall, the logistic curve (Figure 6, Equation 3) seems to be the most satisfactory growth model, based upon the high correlation coefficients of least-squares fits to the data and the lowest relative errors of the fitted parameters.

DISCUSSION

Age determination

Dentition-age estimates of the South African fur seals were considered to be reliable, with inconsistencies among readings mitigated by repeated estimates, following a set protocol of procedures and double-blind tests (Payne, 1978, 1979; Doubleday and Bowen, 1980; Arnbom et al., 1992; McCann, 1993; Oosthuizen, 1997; Oosthuizen and Bester, 1997; Arnould and Warneke, 2002). Nevertheless, the limitations of dentition-based estimates of the ages of seals are apparent, particularly for old animals where the pulp-cavity has filled and they can no longer be aged by growth rings. There is a need for more life-history and morphometric data based on animals tagged as pups.

Body size

Arctocephalus pusillus is the largest of the fur seals with the South African subspecies (*A. pusillus pusillus*) tending to be slightly smaller than the Australian subspecies (*A. pusillus doriferus*) (Stewardson et al., 2008). Comparison of growth curves for the two populations show that the Australian fur seal grows at a faster rate than the South African variety but asymptotic maximum sizes are very similar (Table 5). Male **SBL** ranged from 66 to 243 cm. The largest animal in the collection (PEM952) was measured in 1980 at Kings Beach, Port Elizabeth, by V. Cockcroft and A. Bachelor. This is of similar length to an unusually large male (**SBL** 241 cm) measured by Rand in 1946 (Rand, 1949). The largest animal measured by the first author was 203 cm in 1994 (PEM2201). The largest individual in the data set used by Arnould and Warneke (2002) for the Australian fur seal was a 15 y old bull 224 cm long (close to the asymptotic maximum sizes estimated using the Logistic and Gompertz models for the Australian fur seal). The slightly larger mean size reached by male Australian vs. the South African populations of *Arctocephalus pusillus* may or may not be genetically based. Stewardson et al. (2008) pointed out that the present South African population has largely recovered to pre-exploitation levels,

Table 5: Growth Kinetics Models of Male South African fur seals (Arctocephalus pusillus pusillus) compared to Male Australian fur seals (A. pusillus doriferus).

The SBL vs. age data were fitted to the exponential saturation model (Equation 2), the Logistic model (Equation 3, Figure 6) and the double exponential of Gompertz model (Equation 4). Student's t-tests were performed to test if the fitted parameters for the South African and Australian fur seals were significantly different (Cochran, 1977). Preliminary F-tests showed that in most cases the variances could be assumed to be equal ($p > 0.05$). This assumption could not be accepted in the cases of the asymptotic maximum sizes and incremental growths determined using the exponential saturation model. The t-test for the case of unequal variances was used for comparing the asymptotic maximum size and incremental growth of the two varieties of fur seal estimated using the exponential saturation model. Growth curve fits for the South African fur seal are based on 73 animals of definitive age (dentition-aged animals with an undefined age ≥12 y are excluded). The data for the Australian seals (n = 69) were redigitized from Arnould and Warneke (2002).

5a. Exponential saturation growth model

Population	Maximum SBL (cm)	Growth k (y^{-1})	Pup Size at Birth (cm)	Lifetime Incremental Growth (cm)
Australian fur seal n = 69, r = 0.9423	230.6 ± 7.592	-0.1703 ± 0.0223	91.26 ± 3.92	139.4 ± 8.54
South African fur seal n = 73, r = 0.9524	275.6 ± 33.4	-0.0799 ± 0.0197	72.12 ± 3.17	203.5 ± 33.55
Significance	P = 0.1928 n.s.	P < 0.001	P < 0.001	P = 0.0678 n.s.

5b. Logistic growth model

Population	Maximum SBL (cm)	Growth k (y^{-1})	Pup Size at Birth (cm)	Lifetime Incremental Growth (cm)
Australian fur seal n = 69, r = 0.9443	220.5 ± 4.806	-0.3023 ± 0.0268	96.32 ± 3.088	124.2 ± 5.713
South African fur seal n = 73, r = 0.9495	215.3 ± 9.342	-0.2409 ± 0.0223	75.61 ± 2.600	139.6 ± 9.697
Significance	p = 0.6273 n.s.	p < 0.001	p < 0.001	p = 0.1796 n.s.

5c. Double exponential or Gompertz growth model

Population	Maximum SBL (cm)	Growth k (y^{-1})	Pup Size at Birth (cm)	Lifetime Incremental Growth (cm)
Australian fur seal n = 69, r = 0.9437	224.2 ± 5.738	-0.2352 ± 0.0242	94.04 ± 3.197	130.2 ± 6.569
South African fur seal n = 73, r = 0.9528	232.3 ± 14.48	-0.1599 ± 0.0207	74.01 ± 3.844	158.3 ± 14.99
Significance	p = 0.6115 n.s.	p = 0.019	p < 0.001	p = 0.0954 n.s.

whereas the Australian population is still rapidly increasing and have not yet reached a steady population.

At birth, male South African fur seals are about 35% (*c*. 70-80 cm) of their mean adult size which is about 197 cm based upon the mean adult size, **SBL** for animals >10 y including unaged animals > 200 cm. At puberty they are about 57% (*c*. 112.8 cm at 3 y) of their mean adult size. Although axillary girth varies with body condition, it is usually about 57–67% of **SBL**. The foreflippers are relatively long measuring 25–26% (*c*. 18 cm) of **SBL** in pups, and 24% (*c*. 48 cm) of **SBL** in adults. The hind flippers are considerably shorter measuring 19% (*c*. 13 cm) of **SBL** in pups, and 14.5% (*c*. 29 cm) of **SBL** in adults.

Body shape

Male South African fur seals are exceptional swimmers and divers, and haul out on land to rest, moult and breed. Body shape and general physiology have been modified to accommodate the demands of both marine and terrestrial environments (Bryden, 1972). For example, bulls spend most of their life at sea, hauling out to moult (predominantly February and March), rest, and reproduce (establish territories and breed from late October to late December/early January).

The body is streamlined with a rounded head and a relatively short snout; small external ear pinnae (narrow and pointed); a small tail positioned between the hind flippers; a retractable penis that can be withdrawn into a cutaneous pouch; and modified fore/hind limbs (flippers).

The strong fore limbs have been modified into elongated flippers for propulsion through the water (forceful strokes towards the body) and terrestrial locomotion (palm extends laterally with the flipper bending between the two rows of carpal bones). Characteristic features include predigital cartilage, a long first digit, reduced fifth digit, rudimentary nails and hairless palms.

Unlike the foreflippers, which are the primary appendage used for propulsion through the water, the smaller hind flippers have been modified for terrestrial locomotion (soles extend laterally with the flipper bending forward at the ankle). Characteristic features include predigital cartilage; long grooming claws on digits 2–4; enlargement of digits one and five; and hairless soles.

Function and growth

Overall growth in **SBL** was similar to that of other highly polygynous male otariids including *Arctocephalus gazella* and *Callorhinus ursinus*, with rapid early postnatal growth; a sudden increase in body size at puberty; and a reduced rate of growth soon after attainment of social maturity (McLaren, 1993).

South African fur seals pups are born on land between October and late December (Rand, 1956; Rand, 1967; Shaughnessy and Best, 1975). Newborn pups are 70-80 cm long at birth (*c*. 35% of mean adult length), which agrees with the apparent pup size estimates from the present study shown in Table 5. In November (when the majority of pups are born), mean length and weight is about 76 cm and 5.986 kg for males, and 73 cm and 5.487 kg for females (Rand, 1956). By April, mean length and weight is about 82.0 cm and 19.183 kg for males, and 84 cm and 15.147 kg for females (Rand, 1956). Table 5 shows that the estimated pup size at birth derived from the exponential and logistic growth curve models are not significantly different from the actual measurements given by Rand (1956).

When juveniles gain their permanent teeth (June) they disperse to deeper water for short periods, supplementing their milk diet with solids (Rand, 1956). During this period they learn foraging skills while accompanying their lactating mothers to sea. Most animals feed independently at 9–11 months (Rand, 1956). There is a decline in body weight soon after weaning (Rand, 1956).

Most males attain puberty between 3–4 y, as evidenced by the presence of sperm in the epididymis of some animals at 2 y 10 months (Stewardson et al., 1998). The onset of puberty (2–3 y) is associated with a sudden increase in body size (present study). It is thought that puberty is attained when seals reach a certain threshold size in body weight, with slower-growing animals reaching puberty later than faster-growing animals (Laws and Sinha, 1993). Although pubertal males produce sperm, they do not have the ability to acquire and maintain a harem (Stewardson et al., 1998). Small body size and inexperience prevents young males from gaining the high social status required for a breeding male.

Growth in **SBL** continues to increase steadily until about 6 y. In animals ≥ 7 y, growth continues to increase but at a slower rate (Tables 5 and 6, Figure 6). Social maturity is attained at about 9–10 y and appears to be associated with a weak secondary growth spurt in body size (present study). At this age, large body size has a direct advantage in competitive interactions with rival males, including intimidatory display without actual fighting, and an indirect effect through the presence of large stores of fat which enable large males to remain on territory for up to 40 days (Rand, 1967; Wartzok, 1991). Successful bulls may hold harems multiple times over a two to three year period but are likely to die before reaching reproductive senescence (see Stewardson et al., 1998). Growth in body size slows soon after attainment of social maturity (present study).

Growth of length of the foreflippers continued to increase until at least 13 y, with a significant increase in length at 4–5 y (present study). This increase may partially reflect changes in swimming and/or diving behaviour, with older animals presumably diving to deeper depths in search of prey. Growth of the smaller hind flippers slowed much earlier (8–9 y) than growth of the foreflippers (as is also found in the case of the Australian fur seal; Arnould and Warneke, 2002). The maximum sizes of the fore and hind flippers found in the present study for the South African fur seal are similar to the asymptotic sizes found in the fore and hind flippers of the Australian fur seal (Arnould and Warneke, 2002). No special development of the foreflippers or hind flippers associated with locomotion was reported in *Arctocephalus gazella*, i.e., a more or less constant rate of growth from age one to 7 (Payne, 1979).

Body length as an indicator of age

SBL could not be used reliably to assign a seal to a particular age because there was considerable overlap between year classes, especially among middle-aged animals. Similar findings have been reported in other species of pinnipeds (e.g., Laws, 1953; Bryden, 1972; Bengston and Sniff, 1981). However, **SBL** was found to be a 'rough indicator' of age for animals 1–10 y, and of age group (Table 4). The curvilinear models (von Bertalanffy, logistic and Gompertz models) shown in Table 5 could also be used to estimate age from **SBL** but inspection of Figure 6 clearly shows that they would not be reliable for estimating the age of animals greater than about 10 y.

In male South African fur seals, postnatal growth is rapid with a significant growth spurt at the onset of puberty (2–3 y) and a weak growth spurt at social maturity (9–10 y). Body size continues to increase but at a slower rate between 6 and 7 y, and then growth slows soon after the attainment of social maturity. Growth was a differential process and not simply an enlargement of overall size. Relative to **SBL**, facial variables and the fore/hind limbs scaled with negative slope relative to **SBL** or were negatively allometric; tip of snout to genital opening scaled with positive slope; and tip of snout to anterior insertion of the foreflipper was positively allometric. Relative to age, body variables scaled with negative slope or were negatively allometric. **SBL** was found to be a 'rough indicator' of age and of age group.

Model Growth Curves for Male South African and Australian fur seals

Further information is needed on older animals of known-age in order to more accurately estimate asymptotic maximum size (see Figure 6 and Table 5). In the present study, low sample size at the intermediate ages, and the absence of very old animals of known-age (15–20 y), made it difficult to determine a more exact shape of the growth curve. Published growth curves are also available on the male Australian fur seal (Arnould and Warneke, 2002, n = 69), male and female New Zealand fur seals (Dickie and Dawson 2003, males n = 64), male New Zealand fur seals (McKenzie et al., 2007, n = 86), subantarctic fur seals (Bester and Van Jaarsveld, 1994) and the male Steller sea lion (Winship et al., 2001, n = 203). The breeding/non-breeding status of the animals in the present study was not known. Breeding bulls are thought to be larger in size than non-breeding bulls of the same age; therefore, the growth pattern of male fur seals may be more complex than implied by the models used in the present study. For example, the data of Arnould and Warneke (2002) is based on males shot at a breeding colony and so has many large males of breeding status. The males in the present study are mainly based on dead or dying animals found stranded on the coastline and incidental drownings from trawling. The study area of the present study was a seal feeding area rather than a breeding colony.

Figure 6 and Table 5 show that the von Bertalanffy, Logistic and Gompertz models suggest that the kinetics of growth in **SBL** vs. age is different in the two subspecies. South African fur seals seem to have a smaller apparent pup size and a slower growth rate than the Australian fur seal once living independently. The skulls of male Australian fur seals are significantly larger than South African male seal skulls (Stewardson et al., 2008), however the often repeated statement that Australian fur seals are consistently larger in body size than the South African variety (Pemperton et al., 1993; Arnould and Warneke, 2002; Stewardson et al., 2008) is not supported by the values for the asymptotic maxima of the logistic and Gompertz curve fits shown in Table 5 and by inspection of Figure 6. However, for our South African material, the average **SBL** of all males > 10 y and/or **SBL** > 200 cm was 197 ± 4.1 cm (n = 15) is significantly smaller than a similar calculation for Australian males (211 ± 1.5 cm, n = 17) using the data of Arnould and Warneke (2002). This might more accurately reflect differences in the types of populations sampled in the study by Arnould and Warneke (2002) – a breeding colony, and in the present study – a feeding population probably with many non-breeding males. In any case, more data on age-tagged old males is needed to better define the growth kinetics of the species.

After weaning, the Australian variety seems to grow faster and reaches maturity earlier than the South African variety. For example, the data of Arnould and Warneke (2002) includes one individual that exceeded 200 cm when only 5 and a half years old.

Such growth kinetics are consistent with what would be expected of a rapidly increasing population, not limited by natural resources, recovering from severe depletion. The Australian population has not yet reached pre-exploitation population size whereas the South African population is today close to pre-exploitation levels (Pemperton et al., 1993; Arnould and Warneke, 2002). Differences between the two varieties might therefore reflect differences between a well-fed expanding population and a population in steady-state with limited resources (Stewardson et al., 2008), rather than a genetic difference. Such a proposition would predict that as the Australian fur seal population approaches the carrying capacity of its niche, a reduction in the average pup size, growth rate of the pups and the growth rate of independent animals would be expected.

Winship et al. (2001) working with a data set of 203 aged male Steller sea lions were also able to show that the Logistic and Gompertz models were better (in terms of sum of squares residuals and correlation r) than the von Bertalanffy model for describing the growth kinetics of seals. The logistic and Gompertz models are also a very good fit to the growth kinetics of male New Zealand fur seals (Dickie and Dawson 2003; McKenzie et al., 2007). The Logistic and Gompertz exponential constants found for the New Zealand fur seal are comparable to those found in the Australian fur seal due to a similar lifespan and similar relative sizes of the pup to the adult.

A great deal of effort has been spent in discussing the relative merits of growth curves in biology but often the data sets are too small for this time and effort to be justifiable (Zeide, 1993). The von Bertalanffy model was not a satisfactory fit for the South African fur seal data because it gave an unrealistically high estimate of the asymptotic maximum size of 276 cm, which is well above the largest recorded **SBL** of 241 cm for a South African fur seal. The fitted equation shows very little curvature, due to a lack of accurately aged very old animals (Figure 6). Previous attempts to model the growth kinetics of seals have generally reached the conclusion that the von Bertalanffy model tends to give imprecise overestimates of the asymptotic maximum size (Zullinger et al., 1984; Trites and Bigg, 1992; Bester and Van Jaarsveld, 1994; Winship et al., 2001; Arnould and Warneke, 2002; McKenzie et al., 2007).

The logistic and Gompertz models are both more realistic than the von Bertalanffy model for post-natal mammalian growth because they both have a point of inflection: mammals grow exponentially while pups and juveniles, then linearly as a subadult and finally growth decreases asymptotically when reaching maturity. Both are very popular for modelling growth in mammals but Zullinger et al. (1984) points out that both models tend to both underestimate and imprecisely estimate the maximum body size of mammals. Plots of the fit to the Gompertz model are almost identical to those made using the Logistic model but Table 5 and Figure 6 show that the asymptotic body size is not as precisely defined as in the case of the Logistic model (Equation 4). This is particularly the case for the South African fur seal data, due to the lack of very old animals in the data set.

The growth models suggest there are significant differences in how the maximum size is achieved in the two populations; independent juvenile and adult Australian fur seals have a very significantly higher growth rate than in the case of South African fur seals. Thus the Australian fur seal achieves maximum size earlier than the South African fur seal and tends to grow larger, at least under current population densities.

Caution is needed in interpreting changes in growth kinetics of seals over time or differences between different species or populations. The population history of the Northern fur seal is similar to that of most fur seals: extreme depletion by the beginning of the 20th century, followed by recovery but for reasons that are not clear-cut population numbers and growth kinetics have varied considerably since their initial recovery in about 1940. Trites and Bigg (1992, 1996) have found that the growth kinetics of the Northern fur seal (*Callorhinus ursinus*) has varied over time on the Pribilof Islands off Alaska but were cautious about attributing it to changes in population pressure on resources or other environmental effects. Trites and Bigg (1992) state that higher growth rates and body size seem to correlate with lower total densities of animals but migration effects between different colonies could be a complicating factor.

Conclusion

The classification criteria for age and age group developed in this study will be particularly useful when canines are not available for age determination, e.g. behavioural studies, census counts and where animals are drugged for mark/recapture studies.

Removing postcanines for aging live animals as done by Payne (1978, 1979) might not be possible under some jurisdictions. Tagging of live animals, should be encouraged wherever possible, because of the lack of data on development and longevity of most species of fur seal impacts on the development of rational management policies. Information presented in this study contributes to earlier descriptions of the South African fur seal (Rand, 1956), and provides new information on body growth according to age (y) that is useful for comparisons with the Australian fur seal.

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APPENDIX 1

South African fur seals (n = 149) examined in this study. Animals were collected from the coast of southern Africa between August 1978 and September 1997.

Accession Numbers of Specimens used in the Present Study.

Port Elizabeth Museum (PEM), Port Elizabeth, South Africa

PEM603 PEM605 PEM607 PEM608 PEM658 PEM661 PEM670
PEM676 PEM824 PEM828 PEM834 PEM852 PEM874 PEM875
PEM877 PEM886 PEM888 PEM889 PEM898 PEM916 PEM917
PEM928 PEM951 PEM952a PEM958 PEM975 PEM1073 PEM1135
PEM1159 PEM1453 PEM1507 PEM1560 PEM1587 PEM1696 PEM1697
PEM1698 PEM1706 PEM1879 PEM1882 PEM1885 PEM1890 PEM1892
PEM1895 PEM1999 PEM2000 PEM2002 PEM2003 PEM2004 PEM2006
PEM2007 PEM2008 PEM2009 PEM2010 PEM2013 PEM2014 PEM2015
PEM2020 PEM2021 PEM2036 PEM2045 PEM2046 PEM2047 PEM2048
PEM2049 PEM2051 PEM2052 PEM2053 PEM2054 PEM2081 PEM2082
PEM2087 PEM2131 PEM2132 PEM2137 PEM2140 PEM2141 PEM2143
PEM2186 PEM2188 PEM2191 PEM2194 PEM2197 PEM2198 PEM2201
PEM2203 PEM2238 PEM2248 PEM2252 PEM2253 PEM2254 PEM2256
PEM2257 PEM2257 PEM2348 PEM2359 PEM2374 PEM2379 PEM2400
PEM2401 PEM2403 PEM2404 PEM2405 PEM2406 PEM2409 PEM2411
PEM2414 PEM2415 PEM2454 PEM2455 PEM2458

Marine and Coastal Management (MCM), Dept of Environment Affairs and Tourism, Cape Town, South Africa

MCM1565 MCM1786 MCM2763 MCM2795 MCM3017 MCM3125 MCM3582
MCM3586 MCM3587 PEM3589 MCM3636 MCM4023 MCM4365 MCM4388
MCM4577 MCM4584 MCM4585 MCM4595 MCM4597 MCM4985 MCM4987
MCM4989 MCM4991 MCM4992 MCM4996 MCM4998 MCM4999 MCM5000
MCM5001 MCM5002 MCM5005 MCM5021 MCM5022 MCM5133 MCM5134
MCM5135 MCM5136 MCM5142 MCM5145

APPENDIX 2

Spearman rank-order correlation coefficients for log body variables of male South African Fur seals. Variables are as for Appendix 1. Pups were excluded from the analysis. $p < 0.001$ unless otherwise stated in square brackets. * Significant at 2% level (2-tailed). ** Significant at 1% (2-tailed).
Sample size (n) in brackets.

	B1	**B2**	**B3**	**B4**	**B5**	**B6**	**B7**	**B8**	**B9**	**B10**	**B11**	**B12**
B1	1	0.82*	0.12	0.74*	0.63*	0.77*	0.84*	0.76*	0.71*	0.71*	0.82*	0.72*
	-99	-98	[0.27]	-97	-94	-87	-54	-96	-98	-96	-81	-93
			-85									
B2	0.82*	1	0.17	0.76*	0.61*	0.62*	0.81*	0.78*	0.73*	0.74*	0.86*	0.72*
	-98	-102	[0.11]	-100	-97	-90	-57	-97	-101	-99	-83	-96
			-87									
B3	0.12	0.17	1	0.25**	0.25**	0.15	0.002	0.08	0.17	0.12	0.07	0.15
	[0.27]	[0.11]	-101	[0.02]	[0.02]	[0.17]	[0.99]	[0.46]	[0.10]	[0.26]	[0.54]	[0.16]
	-85	-87		-93	-89	-87	-54	-90	-92	-90	-71	-87
B4	0.74*	0.76*	0.25**	1	0.85*	0.84*	0.68*	0.79*	0.74*	0.85*	0.79*	0.76*
	-97	-100	[0.02]	-108	-104	-93	-61	-103	-106	-104	-85	-101
			-93									
B5	0.63*	0.61*	0.25**	0.85*	1	0.78*	0.68*	0.69*	0.68*	0.72*	0.71*	0.68*
	-94	-97	[0.02]	-104	-105	-94	-57	-100	-103	-102	-86	-101
			-89									
B6	0.77*	0.82*	0.15	0.84*	0.78*	1	0.96*	0.99*	0.93*	0.92*	0.94*	0.90*
	-87	-90	[0.17]	-93	-94	-131	-51	-94	-95	-93	-86	-92
			-87									
B7	0.84*	0.81*	0.002	0.68*	0.68*	0.96*	1	0.97*	0.92*	0.74*	0.92*	0.82*
	-54	-57	-54	-61	-57	-51	-65	-60	-61	-59	-45	-57
B8	0.76*	0.78*	0.08	0.79*	0.69*	0.99*	0.97*	1	0.93*	0.89*	0.94*	0.90*
	-96	-97	[0.46]	-103	-100	-94	-60	-107	-104	-102	-84	-99
			-90									
B9	0.71*	0.73*	0.17	0.74*	0.68*	0.93*	0.92*	0.93*	1	0.82*	0.89*	0.91*
	-98	-101	[0.10]	-106	-103	-95	-61	-104	-109	-105	-87	-102
			-92									
B10	0.71*	0.74*	0.12	0.85*	0.72*	0.92*	0.74*	0.89*	0.82*	1	0.88*	0.87*
	-96	-99	[0.26]	-104	-102	-93	-59	-102	-105	-107	-85	-101
			-90									
B11	0.82*	0.86*	0.07	0.79*	0.71*	0.94*	0.92*	0.94*	0.89*	0.88*	1	0.85*
	-81	-83	[0.54]	-85	-86	-86	-45	-84	-87	-85	-87	-86
			-71									
B12	0.72*	0.72*	0.15	0.76*	0.68*	0.90*	0.82*	0.90*	0.91*	0.87*	0.85*	1
	-93	-96	[0.16]	-101	-101	-92	-57	-99	-102	-101	-86	-103
			-87									
Total	**99**	**102**	**101**	**108**	**105**	**131**	**65**	**107**	**109**	**107**	**87**	**103**

APPENDIX 3

'Robust' least squares straight line equations, Spearman rank-order correlation coefficients, and allometry for log body measurement (cm) on log seal body length (cm) of male South African Fur seals.

Sample size (n) is for aged and unaged animals with SBL recorded (pups were excluded from analysis, and SBLs from 15 aged/unaged males were not recorded, i.e., n = 116). r, Spearman rank-order correlation coefficient. All correlations are significant at the 1% level (2-tailed) apart from B3. Model assumptions for variable B3 were met; however, linear regression not significant. NA, model assumptions required to test hypotheses about the slope of the line (b) were not met, i.e., test not applicable. Variables B7 and B11 excluded from analysis (see footnotes in Table 2).

		Linear regression			**Allometry**		
Dependent variable	Sample size (n)	Intercept ± S.E.	Slope ± S.E.	r (p)	Alternative hypothesis	df	Probability (p)
Circumference of head at canine **(B1)**	87	0.89 ± 0.18	0.47 ± 0.04	0.77 ($p < 0.01$)	$H_1 : b < 1$	85	$p < 0.01$
Circumference of head at eye **(B2)**	90	1.09 ± 0.18	0.50 ± 0.04	0.82 ($p < 0.01$)	$H_1 : b < 1$	88	$p < 0.01$
Tip of snout to centre of eye **(B3)**	87	–	–	0.15 ($p = 0.16$) ns	–	–	–
Tip of snout to centre of ear **(B4)**	93	0.30 ± 0.14	0.53 ± 0.03	0.84 ($p < 0.01$)	$H_1 : b < 1$	91	$p < 0.01$
Tip of snout to angle of gape **(B5)**	94	-0.82 ± 0.22	0.64 ± 0.04	0.78 ($p < 0.01$)	NA	NA	NA
Tip of snout to genital opening **(B8)**	94	-0.35 ± 0.07	1.04 ± 0.01	0.99 ($p < 0.01$)	NA	NA	NA
Tip of snout to anterior insertion of the foreflipper **(B9)**	95	-1.33 ± 0.22	1.11 ± 0.05	0.93 ($p < 0.01$)	$H_1 : b > 1$	93	$p = 0.007$
Length of foreflipper **(B10)**	93	-0.91 ± 0.18	0.89 ± 0.04	0.92 ($p < 0.01$)	NA	NA	NA
Length of hind flipper **(B12)**	92	-0.91 ± 0.19	0.81 ± 0.04	0.90 ($p < 0.01$)	NA	NA	NA
Total	**116**						

APPENDIX 4

‘Robust’ least squares straight-line equations, Spearman rank-order correlation coefficients, and allometry for log body measurement (cm) on age (y) of male South African Fur seals.

Sample size (n) is the number of skulls with body variable and age recorded (only animals 1–10 y were included in analysis, i.e., n = 68). r, Spearman rank-order correlation coefficient. All correlations are significant at the 1% level (2-tailed), except for B3. Model assumptions were met for variable B3; however, linear regression not significant. NA, model assumptions required to test hypotheses about the slope of the line (b) were not met, i.e., test not applicable. Variables B7 and B11 excluded form analysis (see footnotes in Table 2).

Dependent variable (B)			**Linear regression**		**Allometry**		
	Sample size (n)	Intercept ± S.E.	Slope ± S.E.	r (p)	Alternative hypothesis	df	Probability (p)
Circumference of head at canine **(B1)**	63	-2.59 ± 0.50	0.17 ± 0.021	0.59 ($p < 0.01$)	$H_1 : \beta < 1$	61	$p < 0.01$
Circumference of head at eye **(B2)**	63	-2.63 ± 0.43	0.12 ± 0.01	0.69 ($p < 0.01$)	NA	NA	NA
Tip of snout to centre of eye **(B3)**	57	–	–	-0.008 ($p = 0.95$) ns	–	–	–
Tip of snout to centre of ear **(B4)**	68	2.67 ± 0.02	0.04 ± 0.004	0.69 ($p < 0.01$)	NA	NA	NA
Tip of snout to angle of gape **(B5)**	64	2.03 ± 0.03	0.04 ± 0.005	0.56 ($p < 0.01$)	$H_1 : \beta < 1$	62	$p < 0.01$
Standard body length **(B6)**	56	4.45 ± 0.02	0.08 ± 0.003	0.96 ($p < 0.01$)	NA	NA	NA
Tip of snout to genital opening **(B8)**	67	-1.28 ± 0.14	0.02 ± 0.001	0.93 ($p < 0.01$)	NA	NA	NA
Tip of snout to anterior insertion of the foreflipper **(B9)**	68	3.56 ± 0.03	0.10 ± 0.005	0.90 ($p < 0.01$)	$H_1 : \beta < 1$	66	$p < 0.01$
Length of foreflipper **(B10)**	67	3.10 ± 0.03	0.07 ± 0.005	0.82 ($p < 0.01$)	NA	NA	NA
Length of hind flipper **(B12)**	64	2.64 ± 0.02	0.07 ± 0.004	0.93 ($p < 0.01$)	$H_1 : \beta < 1$	62	$p < 0.01$
Total	**68**						

Linnaeus: King of Natural History

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Linnaeus' legacy was far more encompassing than taxonomic. We argue that, while the systematic recording of species remains fundamental to modern ecological concerns, Linnaeus also laid the foundation for other major areas of ecology, including comparative biogeography, plant demography, and comparative anatomy.

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KEYWORDS: Biodiversity, Linnaeus, natural history, natural philosophy, taxonomy.

INTRODUCTION

Linnaeus is one of the towering figures in the history of biological science. He is remembered today chiefly for his introduction of the binomial system of nomenclature and for his taxonomy. However, if we consider his skill as an observer of the relationships between the plants and animals he classified, and their environment, he should also be regarded as one of the earliest practicing ecologists. He passed on these skills to his many students, including those who travelled the world collecting and classifying organisms and became known as the 'apostles'.

In eighteenth-century Sweden, Linnaeus was accorded high status, and this great respect continued to hold internationally until the twentieth century. Lord Rutherford's throw-away comment that '(a)ll science is either physics or stamp collecting' reflected the marginalization of taxonomy and natural history within science as technological advances in physics, chemistry and engineering attracted funding and support. These advances also revolutionised biology, permitting breakthroughs in physiology, biochemistry and the molecular sciences, but in this brave new world the diversity and distribution of organisms lost their attraction as fields of study. It was only towards the end of the twentieth century when environmental issues became such a major theme in politics and with the public that there was renewed interest in the study of biodiversity, and a need to bring new techniques and approaches to 'old fields'. By then, many of the essential skills underpinning the study of biodiversity were already in decline. (Biodiversity itself is a word of recent origin – first coming to the fore with the publication of Wilson [1988].)

The taxonomic side of Linnaeus' achievements was outstanding. While his sexual system did not long survive as a basis for plant classification, Linneaus had grasped the potential for classification to be predictive and 'natural', even if his particular approach had its limitations. He had recognized the importance of the hierarchical approach and provided a nomenclatural system that was functional and, importantly, had practical application to the large number of new species that were being discovered outside Europe. It was the first classification system that was accessible to the non-specialist, with the work encapsulated in handbooks that were 'small enough to be carried into the field' (Koerner, 1999, p40).

In the year 2007, we celebrated the tercentenary of Linnaeus' birth. It also happens to be the anniversary of Georges-Louis Leclerc, Comte de Buffon, the author of the *Histoire Naturelle*. Conniff (2007), in his article aptly titled *Happy Birthday, Linnaeus*, argues that Buffon should be regarded as at least the equal of Linnaeus, and in particular suggests that Buffon had a superior understanding of habitat, anticipating the development of ecology as a science. Linnaeus and Buffon were mutually fierce critics, and Buffon was undoubtedly also a major figure in the history of science: he had better geological insight than Linnaeus, and was closer to having an evolutionary perspective. However, to suggest that Linnaeus' natural history was not ecologically focused is far from accurate. A major part of Linnaeus' teaching was based on field excursions: he had a very comprehensive knowledge of the local flora of southern Sweden, and while his sexual system was not appropriate for higher taxonomic ranks, Linneaus' species concepts have largely stood the test of time.

We would argue that Linnaeus' taxonomic work was firmly underpinned by a deep understanding of natural history and that natural history in turn provided the basis for ecology (Mayr, 1997; Blunt, 1971). The ecological insights of Linnaeus are clearly seen in his botanical 'text book', *Philosophia Botanica* (Linnaeus, 1751). Koerner (1999) notes that '...he described many of the mechanisms of species interdependence, as Charles Darwin noted on reading his *Oeconomia naturae* of 1749' (p15).

LINNAEUS AND NATURAL HISTORY

'Natural history', the advancement of which is the prime objective of the various Linnean Societies around the world, has a very long history. Early hunter-gatherer societies could not have survived unless members possessed what we might consider to be an innate understanding of natural history, including the ability to recognise different sorts of food and to distinguish between the edible, the toxic and the dangerous. Cave paintings provide, in a tangible form, evidence for knowledge of natural history. In classical times, plants and animals were seen as sources of medicines or as an element in a broader natural philosophy, and the Greeks and Romans left a documentary record which at least in part survives to this day and that would have been known to Linnaeus. Knowledge of natural history would have been current amongst the broader population, the majority of which lived in rural environments and were intimately dependent on the natural world for survival, but in 'academic' circles natural history was increasingly associated with medicine. For hundreds of years herbalists recycled the writings of classical authors, without making original observations and with the claims becoming more fanciful on each retelling. The Renaissance then brought a new curiosity about the world and more organized scientific inquiry, although the importance of the links to medicine continued, and old myths still retained currency. Linnaeus himself was Professor of Medicine and Botany at Uppsala University, and in some institutions close links between the two disciplines survived until the twentieth century. The recent growth of interest in alternative medicine suggests a need for revitalizing the links to scientific botany, and ethnobotany has been given a new impetus as a field of study by the regime for rewarding traditional owners of knowledge and resources, which was established by the United Nations Convention on Biological Diversity 1992.

From the late 16th century onwards there was a considerable interest in collecting and studying 'curiosities' of all kinds, and some of the collections of natural history objects that were assembled were large. Some of the more academic natural historians associated with these collections were distinguished scientists whose work has stood the test of time. An example is John Ray, who was the first to draw a distinction between Monocots and Dicots and who is commemorated in the still existing Ray Society and in the name of the herbarium at the University of Sydney. Some of the impetus for collecting was stimulated by the increasing numbers of exotic specimens being sent back to Europe from wider exploration. Linnaeus was very much part of this natural history tradition and although he did not travel beyond Europe, he actively encouraged his students to do so, and he was familiar with non-European plants both in the form of herbarium specimens and in gardens. The non-European species he described famously included bananas, which would then have been regarded as very exotic.

Linnaeus' own exploration was closer to home and included his early expedition to Lapland. Although there are suggestions that his account of his travels is somewhat exaggerated[1] (Koerner, 1999), it established his reputation as an explorer and natural historian. Lapland in the eighteenth century was at the edge of the world and for many Europeans would have been regarded with as much trepidation as Africa. Even today it remains one of the few wilderness areas in Europe (Ratcliffe 2006).

Once he was established as a senior academic in Uppsala, field teaching became an essential and popular part of Linneaus' teaching. His excursions attracted large numbers of students and were organized with almost military precision (Blunt 1971). Most attention was paid to the flora, although any matter of natural history interest was open for study and comment. Many of the localities around Uppsala that were visited on excursions still support the same species today, so that it requires no great stretch of the imagination to visit sites today and see what Linneaus' students would have seen, and to experience the same excitement of first encountering a wet meadow full of snakeshead fritillaries (*Fritillaria meleagris*) or a dry calcareous esker with a spring abundance of Pasque flowers (*Anemone pulsatilla*).

LINNAEUS AND ECOLOGY

William Stearn (in Appendix I of Blunt, 1971) recognised that Linnaeus has been variously declared 'a pioneer ecologist, a pioneer plant-geographer, a pioneer dendrochronologist, a pioneer evolutionist…' but considered that the 'most influential and useful of his contributions to biology undoubtedly is his successful introduction of consistent binomial specific nomenclature'.

It is true that Linneaus' contribution to ecology and plant geography is rarely acknowledged within these disciplines, and the recognized founding fathers were all much more recent. Nevertheless his *Philosophia Botanica* contains many ecological insights, which were in the published literature and were dormant seeds for many decades. Given the very large number of students who attended Linneaus' classes, and the wide circulation of his publications, the ecological perspective he developed must have been assimilated into the perceived wisdom of the day, and when ecology and plant geography developed as separate disciplines, Linneaus' ideas would have been part of the assumed background.

Today the major concerns of ecology include the identification and evaluation of biodiversity. Of the three generally accepted levels of biodiversity, Linneaus was ignorant of genes, but he clearly recognized the need to document species, and recognized that species occupied habitats. In fact, he devotes part of the *Philosophia* to discussing the main habitats (communities) in Sweden. He also indicated what notes should be made on field excursions.

Unfortunately, the details on many herbarium labels in current collections fail to provide any ecological information. Linnaeus' advocacy of the systematic recording of habitat data was part of his approach to cataloguing information and these features are easily accommodated in modern databases. If Linnaeus were alive today, he would undoubtedly be active in the development of bioinformatics and the creation and manipulation of databases. The omissions of the past cannot be corrected but today's collectors should be encouraged to record much more than is often the case. Regrettably, ecologists are often amongst the worst offenders when it comes to a lack of detail associated with voucher specimens.

Linneaus was well aware of the variability displayed by some species and devoted Chapter IX of the *Philosophia* to a discussion of 'Varieties'. He urged against giving taxonomic recognition to environmentally determined phenotypic variation, as he recognized that a variety of diseases and insect attack could cause abnormalities in plants (*Philosophia* section 312), displaying evidence of very careful observation. He also pointed out that variation could be correlated with soil conditions and microclimate and advocated an experimental approach (*Philosophia* section 316: 'Cultivation is the mother of very many varieties and is the best means of testing varieties'), foreshadowing by a century and a half experimental taxonomy (genecology), which enjoyed its heyday in the second half of the 20th century.

Chapter XI of *Philosophia* (entitled 'Sketches') contains much ecological material. Section 334 'The native locations of plants relate to *region, climate, soil* and *ground*' contains a very succinct introduction to ecology and biogeography (as well as some rather strange views about geology). The discussion about the relationship between latitude and flora gives hints of the ideas subsequently developed in greater detail by Alexander von Humboldt. The relationships between soil types and the plants they support also introduce topics that formed a major part of ecological research in the twentieth century. Section 335 provides an overview of phenology and indicates that Linnaeus was well aware that factors such as temperature and day length were involved in controlling flowering, although it was to be many years before physiological understanding of the mechanisms involved was achieved. Even on botanical excursions students recorded the plant species eaten by particular animal species 'while watching the botanical specimens disappear at the moment they realized that they needed to identify them' (Koerner 1999 p49).

Chapter V of *Philosophia* (Sex) includes observations on annual seed production of individual plants, probably the first scientific exploration of plant demography. The essential feature of the *Philosophia* is the importance of observation, and it is remarkable how much was achieved using lenses and microscopes that today would be regarded as woefully inadequate.

While Linnaeus was a creationist, the recognition of variation suggests that he was not as rigidly so as he is usually portrayed - he certainly recognized that the appearance of species could change. A synthesis of Buffon's and Linnaeus' ideas could have accelerated the development of evolutionary theories, well ahead of the publications of Darwin and Wallace in the mid 19th century.

The *Philosophia* is also strongly focused on the utilisation of plants, not just as medicines but for a whole range of purposes. The 365th (and final) article states: 'The economic use of plants is of great utility to the human race.' (Linnaeus, 1751). One of the major justifications for biodiversity conservation is the maintenance of the ecosystem services that biodiversity supports. This is a concept that would clearly have found favour with Linneaus, and the sorts of observations he advocated are needed to document ecosystem processes. He recorded details of the trophic interactions between organisms and had an appreciation of the recycling of materials, noting people used churchyard soil for growing cabbages, hence 'human heads ... turn into cabbage heads' (Koerner, 1999, p83).

Robert MacArthur (1972) famously wrote that 'to do science is to search for repeated patterns' and stressed the importance of natural history as the starting point for ecological research. MacArthur pointed out that not every natural historian was a scientist (in terms of approach and method, not necessarily profession) and not all ecologists were natural historians, but we would agree with him that most of ecology has its roots in natural history: even theoretical mathematical ecology starts with ideas that are ultimately based on field observation. Underwood (2007) has recently observed 'one of the great joys of experimental ecology is that natural history is so important in the development of explanatory models'.

COLLECTING BIODIVERSITY: PRESERVING BIODIVERSITY?

In the eighteenth, nineteenth and early twentieth century much natural history involved collections; and many large collections of, for example, insects, bird eggs, or plants were made both by, or for, major institutions and individual collectors. Many people who subsequently became famous scientists in other fields (for example Macfarlane Burnet - Sexton 1999) were avid collectors in their youth. Charles Darwin himself was an avid beetle collector in his college days (preferring 'beetling' to mathematics - Desmond and Moore 1991). (Another suggestion for Linnaeus' mis-representation of his travels in Lappland was mis-calculation (Selander, 1947 in Koerner, 1999). Perhaps he shared Darwin's aversion to mathematics?). The making of collections taught the need for careful observation, systematic recording of data, and provided in-depth understanding of particular groups of organisms.

Collectors and recorders were not just the clergy and the landed gentry (or their spinster siblings); there was, at least in the United Kingdom, a very strong working class element of miners and factory workers, who, in their very limited free time, spent many hours completing arduous hikes and making major finds of often taxonomically-challenging organisms. This tradition of the extremely skilled amateur was never as strong in New South Wales as it was in the United Kingdom (for reasons that perhaps require the attention of a social historian). Certainly, there have been some very gifted amateurs, but their interests tended to be restricted to groups such as birds or flowering plants; there was not the same interest or expertise shown in, for example, cryptogamic plants as was the case in the United Kingdom. Given the dearth of professionals in Australia, this means that there are major components of biodiversity about which we remain still basically ignorant.

Today collection is frowned upon, and in many cases (such as the collecting of bird eggs) it is properly illegal. The shift away from collection partly reflects lack of opportunity given an increasingly urbanized population, rejection of a 'stamp collecting' approach to science and greater concern for conservation. Certainly, it would not be possible to condone egg-collecting or capturing and killing native vertebrates outside specially-approved scientific licences, but nevertheless it is probable that both school and university students are missing out on what previously had been important educational experiences.

The old collections remain of continuing value, providing comparative material for taxonomic studies, as well as evidence of changing distributions or of environmental change. For example, the ability to measure long-term trends in thickness of the shells of raptor eggs was extremely important in drawing attention to the effects of the new post-war organic agricultural chemicals (Ratcliffe 1967, 1970; Olsen and Olsen 1979). Sadly, curation of historical collections in some of our greatest museums is being eroded as funding for the care of collections, in the management schemes of modern-day directors, is coming a distant second behind promotion of exhibitions for entertainment's sake without the underlying scholarship being obvious.

Even in the absence of collections, skilled amateurs in the United Kingdom have been able to systematically record distributions of large numbers of taxa at the national scale. These spatially explicit data are of enormous value for monitoring environmental change. Data of this sort would be very difficult to collect (and inordinately expensive) if we had to rely on professionals, yet they will be crucial to our monitoring of biodiversity. In Australia the ornithologists have pioneered systematic recording of species distribution at the continental scale, harnessing the skills and enthusiasm of amateurs and professionals. The differences in distribution and abundance between the two editions of the Bird Atlas (Blakers et al. 1984; Barrett et al. 2003) provides compelling evidence for the impacts of environmental change, and the recording program will continue into the future. Other areas of natural history have not been so well served.

Teaching in the field is still a component of many University courses but is under great pressure because of cost, occupational health and safety issues (which can create bureaucratic nightmares), the large number of students with part-time jobs who find it difficult to attend courses at weekends or during vacations, and because of the decline in the number of academic staff with knowledge of many groups of organisms. The long-term future of field teaching is very uncertain and this will have major consequences for our ability to produce graduates capable of addressing biodiversity issues.

Peter Marren (2002, 2005) has written on a number of occasions, pointing out the loss of expertise in UK institutions and the decline in the numbers of skilled amateurs. At the same time there is an increase in the membership of NGO conservation societies, indicating wide support for natural history, but the deep engagement with some particular field within natural history is less common. There may be many and varied reasons for this, but Marren suggests one may be that, with the modern pressures on many people, and the absence of time, natural history had become a spectator rather than participant sport. The quality and expertise shown in recent TV natural history programs is such that rather than encouraging participation they suggest that we already know everything. This is an idea that needs further exploration.

The achievements of Linneaus and his students were remarkable and the detail of their observations made with minimal technological aids, was particularly remarkable. Few students today would have the capacity or patience to make similar investigations. Experimental science needs to be underpinned by substantial bodies of observation in order that appropriate hypotheses can be generated and tested. Linnaeus' legacy of observation has been built upon for the last 250 years, but the capacity to continue to do so is being lost.

Contrary to the impression left by Conniff, we would argue that Linnaeus also laid the foundation for other major areas of ecology, including comparative biogeography (long before van Humbolt), plant demography, and comparative anatomy. His legacy was far more encompassing than taxonomic, even though the systematic recording of species remains absolutely fundamental to modern ecological concerns.

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(Endnotes)

[1] *He variously reported traveling up to three times further than he really did and spoke of long periods spent with the native Sami, when in fact it was a few weeks. The fact that he was being paid by the mile for his journey by the Science Society of Uppsala is cited by way of partial explanation (Koerner 1999).*

Erratum

Wright, A.J. (2008). Emsian (Early Devonian) tetracorals (Cnidaria) from Grattai Creek, New South Wales. *Proceedings of the Linnean Society of New South Wales* **128**, 83-96.

Figure 4 on page 92 of the above paper was published without scale bars. It is reproduced here:

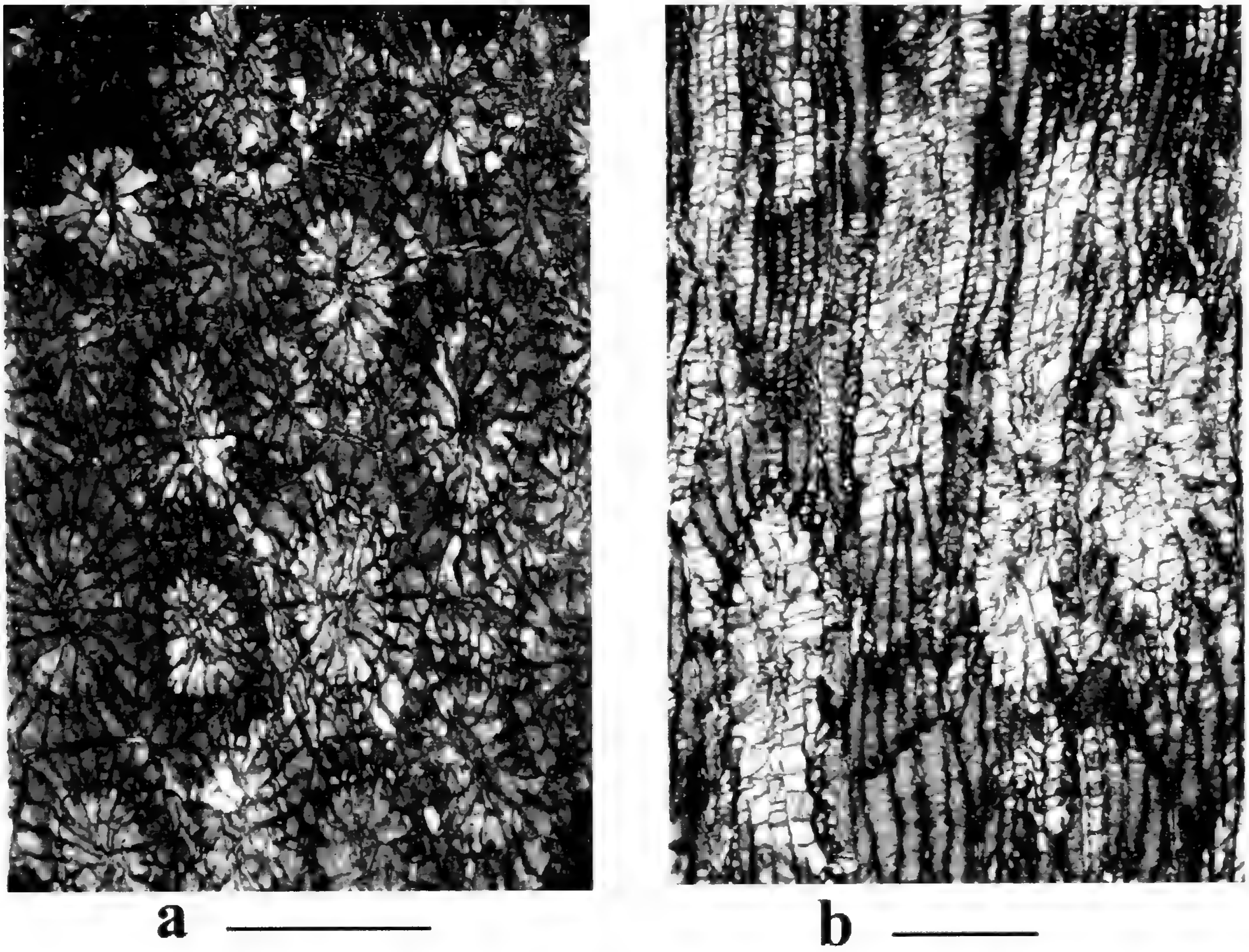

Figure 4a-b. *Trapezophyllum grattaiensis* sp. nov., holotype. a, MMF 34186b, transverse view ; b, MMF 34186a, longitudinal view. Bar scales = 5 mm.

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Ralph, P.H. (2001). The use of ethanol in field studies. In 'Field techniques' (Eds. K. Thurstle and P.J. Green) pp. 34-41. (Northwood Press, Sydney).

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