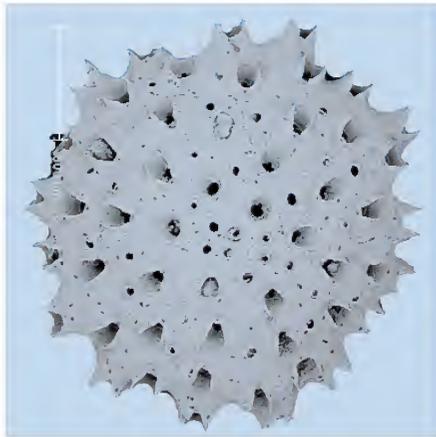
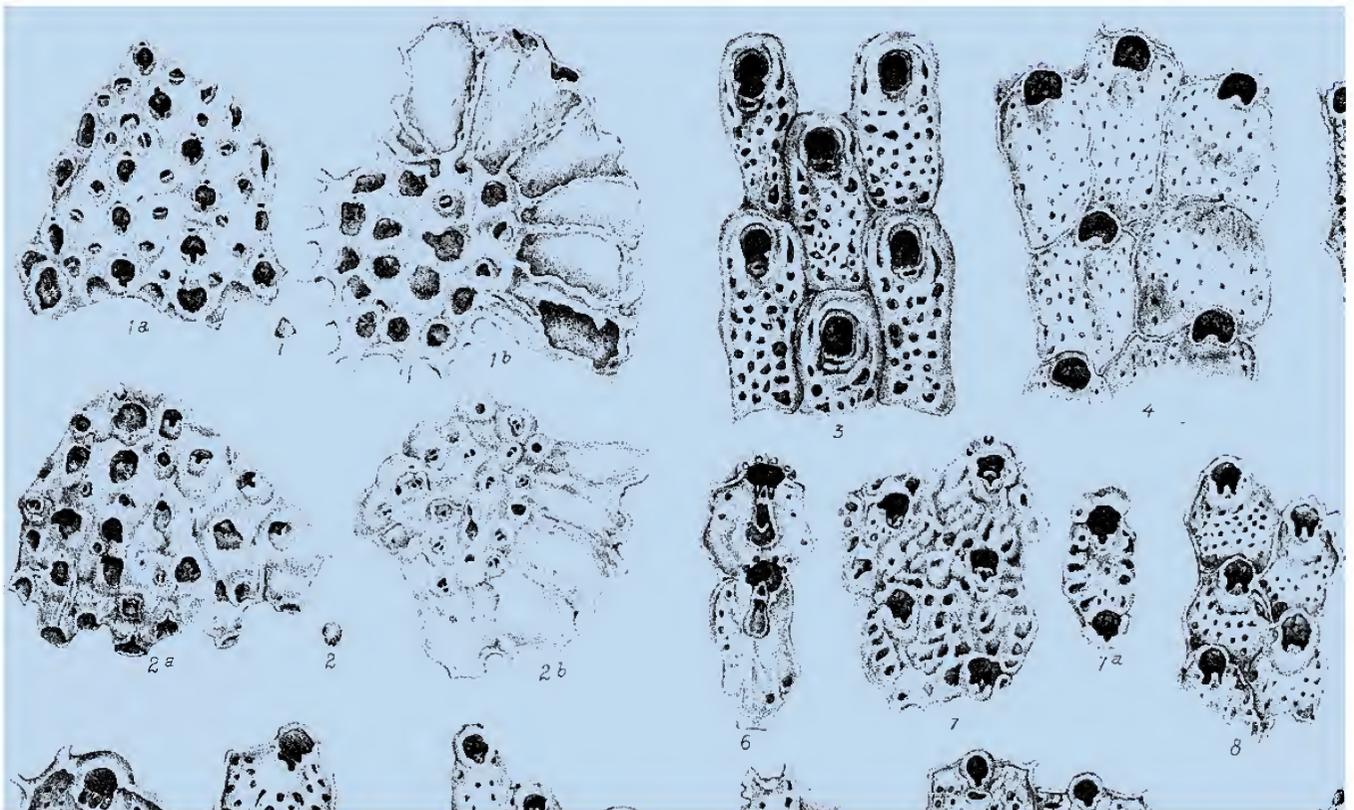


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*Front cover* Top left: Scanning electron micrographs of two species of bryozoans of the genus *Conescharellina* from southern Australia described as new by Philip Bock and Patricia Cook in this volume.

Bottom: part of the original plate published by P. H. MacGillivray in 1895 in *Transactions of the Royal Society of Victoria* in which the same two species are illustrated.

## Mitochondrial 12S rRNA sequences support the existence of a third species of freshwater blackfish (Percichthyidae: *Gadopsis*) from south-eastern Australia

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### Abstract

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Fish of the genus *Gadopsis* are a distinctive component of the freshwater fish fauna of south-eastern Australia. *Gadopsis marmoratus* and *G. bispinosus* are the only two species recognised within the genus, with the former of uncertain taxonomic status, as it is thought to be composed of at least two distinct geographical forms based on morphological and allozyme data. The objective of this study was to investigate DNA sequence divergence in *Gadopsis*, especially in the western portion of its distribution, using an approximately 400 base pair fragment of the mitochondrial small subunit 12S rRNA gene region in order to reassess the taxonomy of the genus. Individuals from 11 locations were sequenced and confirm that *G. marmoratus* and *G. bispinosus* are genetically distinct, and further that the *G. marmoratus* complex consists of two divergent clades representing the previously identified northern and southern forms. The degree of divergence between the three *Gadopsis* clades was similar (5–6% nucleotide substitutions), suggesting that they diverged from a common ancestor at approximately the same period in geological time. These results are consistent with previous allozyme studies and highlight the usefulness of mitochondrial DNA data coupled with allozyme information for clarifying taxonomic boundaries in morphologically conservative aquatic organisms.

### Keywords

Mitochondrial rRNA, taxonomy, blackfish, Percichthyidae, *Gadopsis*, Australia

### Introduction

Fish of the genus *Gadopsis*, commonly known as the river or freshwater blackfish, are endemic to south-eastern Australia (including Tasmania), and carry out their entire life cycle in freshwater (Jackson et al., 1996). The genus is phylogenetically distinct and its evolutionary origins remain uncertain as it may have either evolved from a marine ancestor some 15 million years ago or had a more ancient Gondwanan freshwater origin (Sanger, 1984; Jerry et al., 2001).

*Gadopsis* belongs to the family Percichthyidae and contains two currently recognised species, *G. marmoratus* (Richardson, 1848) and *G. bispinosus* (Sanger, 1984). Sanger (1986) suggested, based on morphological and allozyme evidence, that *G. marmoratus* potentially consists of a northern and a southern species. However, Sanger (1986) did not formally recognise the northern and southern forms of *G. marmoratus* as these putative species were not found in sympatry and because the taxonomic significance of the genetic and morphological divergence between the two forms was uncertain.

*Gadopsis marmoratus* has a large geographic range that includes tributaries of the Murray–Darling river system, as far north as the Condamine River in southern Queensland. The species is also found in Tasmania with endemic populations in the north and translocated populations in the Huon River and elsewhere in the south. Sanger (1986), assuming that *G. marmoratus* is in fact a complex of two species, suggested that these taxa evolved in allopatry following the isolation of Tasmania from mainland Australia. According to this scenario ancestral gadopsids are thought to have been originally widespread throughout Victoria and northern Tasmania and that the formation of the two species may have occurred during periods of raised sea levels which isolated Tasmanian from mainland populations. Subsequently, when sea levels were lower during the Pleistocene glaciation and land connections re-established with the mainland, the Tasmanian form of *G. marmoratus* invaded southern Victoria, consequently displacing the northern *G. marmoratus* (Ovenden et al., 1988).

Sanger's (1986) biogeographical hypothesis assumes that the two forms of *G. marmoratus* behave as independent

species. This hypothesis also suggests that the two forms have come into contact in the past and therefore it may still be possible to find locations where both the northern and southern forms coexist in Victoria (KoeHN and O'Connor, 1990). Sanger (1986) suggested that the two forms may occur in sympatry in the state's southwest, an area encompassing the Gellibrand and Glenelg river systems. An allozyme study by Ryan et al. (in press) was unsuccessful in finding evidence supporting the existence of sympatric populations of northern and southern *G. marmoratus* in south-western Victoria. However, their findings were consistent with Sanger's (1986) results indicating genetic divergence between the two forms inhabiting adjacent river systems in this region.

In addition to Sanger's and Ryan's allozyme studies there have been several studies of blackfish using DNA-based techniques (Ovenden et al., 1988; Waters et al., 1994; Jerry et al., 2001). These studies, however, are limited by minimal sampling of the northern form of *G. marmoratus*, especially in the western portion of its distribution. This study therefore extends these studies by using Polymerase Chain Reaction (PCR) amplification of an approximately 400 base pair fragment of the mitochondrial 12S rRNA gene region coupled with direct DNA sequencing, in order to further evaluate the taxonomic status of the northern and southern forms of *G. marmoratus* with emphasis on its western distributions. This approach was chosen because mitochondrial DNA (mtDNA) has been found to be very useful for inferring phylogenetic and taxonomic relationships in groups of organisms where the protein-based techniques of allozyme electrophoresis have lacked resolution or produced ambiguous results (Hillis et al., 1996).

## Methods and materials

**Gadopsis samples.** Tissue samples were obtained from specimens previously collected by Ryan et al. (in press). Sample selection was based on the results of Ryan et al. (in press) together with three reference sites based on previous studies by Sanger (1984) and Ovenden et al. (1988). These three sites consisted of the MacDonald River (Murray-Darling catchment, northern *G. marmoratus*), the Gellibrand River (south-west Victoria, southern *G. marmoratus*) and Cudgewa Creek (north-east Victoria, *G. bispinosus*). The other samples obtained by Ryan et al. (in press) included specimens of the *G. marmoratus* complex from eight additional sites. These sites included Darlot Creek, Brucknell Creek, the Wimmera River, and the Wannon River. In addition DNA sequences were provided by D. Jerry, James Cook University, Queensland, for samples from Stony Creek, Victoria, representing both *G. bispinosus* (GenBank accession number: AF294459) and *G. marmoratus* and Little Forester Creek (Tasmania) also representing *G. marmoratus* (AF294452). The remaining specimens were from Eight Mile Creek and Mosquito Creek (South Australia) (Fig. 1). Samples of *Maccullochella peelii peelii* (Murray cod) and *Bostockia porosa* (Western Australia nightfish) were included as outgroups (sequences derived from GenBank, accession numbers: AF295060 and AF295048).

**DNA extraction and amplification of mtDNA.** Total DNA was extracted from muscle tissue using an extraction protocol developed by Crandall et al. (1999). A fragment of the 12S mtDNA gene region (approximately 400 bp) was amplified via PCR using the 12S c/d primers described in Jerry et al. (2001). Double stranded PCR amplifications were performed in 50 ml volumes consisting of: 1x PCR

buffer, 2.0  $\mu$ M MgCl<sub>2</sub>, 0.2 mM dNTPs, 1 mM of each primer and 2 units *Taq* DNA polymerase. PCR amplifications were performed in a Corbett PC-960 Microplate Thermal Sequencer and consisted of 30 cycles of denaturation at 94°C for 30 sec, annealing at 55°C for 30 sec, and extension at 72°C for 30 sec. An initial denaturation cycle of 3 min at 94°C was used and the program terminated with a 5 min cycle at 72°C. The PCR products were visualised in 1% agarose / TAE gels stained with ethidium bromide under UV light.

**Purification and sequencing.** PCR products were purified using a QIAquick PCR purification kit (QIAGEN) according to the manufacturers instructions. Purified DNA was quantified via direct comparison with DNA marker (Promega DNA / HAE III marker) of known concentration, again visualized under UV light in a 1% agarose / TAE gel containing ethidium bromide. Purified DNA was then sequenced according to Australian Genome Research Facility (AGRF), University of Queensland, protocols.

**Data analysis.** Sequence chromatograms were viewed using EditView and edited using SeqPup software (Gilbert, 1997). Sequences were aligned using the Clustal X program (Thomson et al., 1997) with alignment-ambiguous regions excised prior to phylogenetic reconstruction (Gatesy et al., 1993). Phylogenetic analyses were conducted using a range of approaches implemented by the PAUP\* software package (Swofford, 1998). Phylogenetic signal within the data set was assessed using the *g*<sub>1</sub> statistic from the random tree length-frequency distribution (Hillis and Huelsenbeck, 1992). Phylogenetic relationships were estimated using maximum parsimony, neighbour-joining and maximum likelihood approaches. The most parsimonious tree was identified using a full exhaustive search with support for branches evaluated by 1,000 bootstrap replicates. Distance analysis was performed using the Tajima-Nei model of evolution and the neighbour-joining option with the number of bootstrap replicates set at 1,000. The most appropriate model of evolution for the maximum likelihood (ML) analyses was obtained via testing alternative modes of evolution using Modeltest (Posada and Crandall, 1998).

## Results

Approximately 400 bp of the mitochondrial 12S rRNA coding region were sequenced for 12 individuals of *Gadopsis* from 11 locations. After sequence editing, 290 bp were used for subsequent analysis (GenBank accession numbers: AF505866 - AF505872). The random tree distribution based on the entire data set including both the outgroup taxa is significantly skewed to the left with *g*<sub>1</sub> = -0.899, *P* < 0.01, indicating significant phylogenetic information (Hillis and Huelsenbeck, 1992). The random tree distribution within the ingroup taxa was also significantly skewed (*g*<sub>1</sub> = -0.686, *P* < 0.01).

Percentage sequence divergences and the number of nucleotide substitutions among individuals (Table 1) indicate the existence of three equally distinct groups within *Gadopsis*. The individuals representing southern *G. marmoratus* (samples 9-12, Table 1) differ at 14-18 base positions (5-6% sequence divergence) in comparison with northern *G. marmoratus* individuals (samples 3-8), and 15-16 base positions (5-6% sequence divergence) compared to *G. bispinosus* (samples 1 and 2). *Gadopsis marmoratus* (northern) and *G. bispinosus* differed at 15-20 base positions (5-7% sequence divergence). In contrast, comparison between samples within each of these groups revealed much lower levels of divergence with *G. marmoratus* (southern), *G. marmoratus* (northern) and

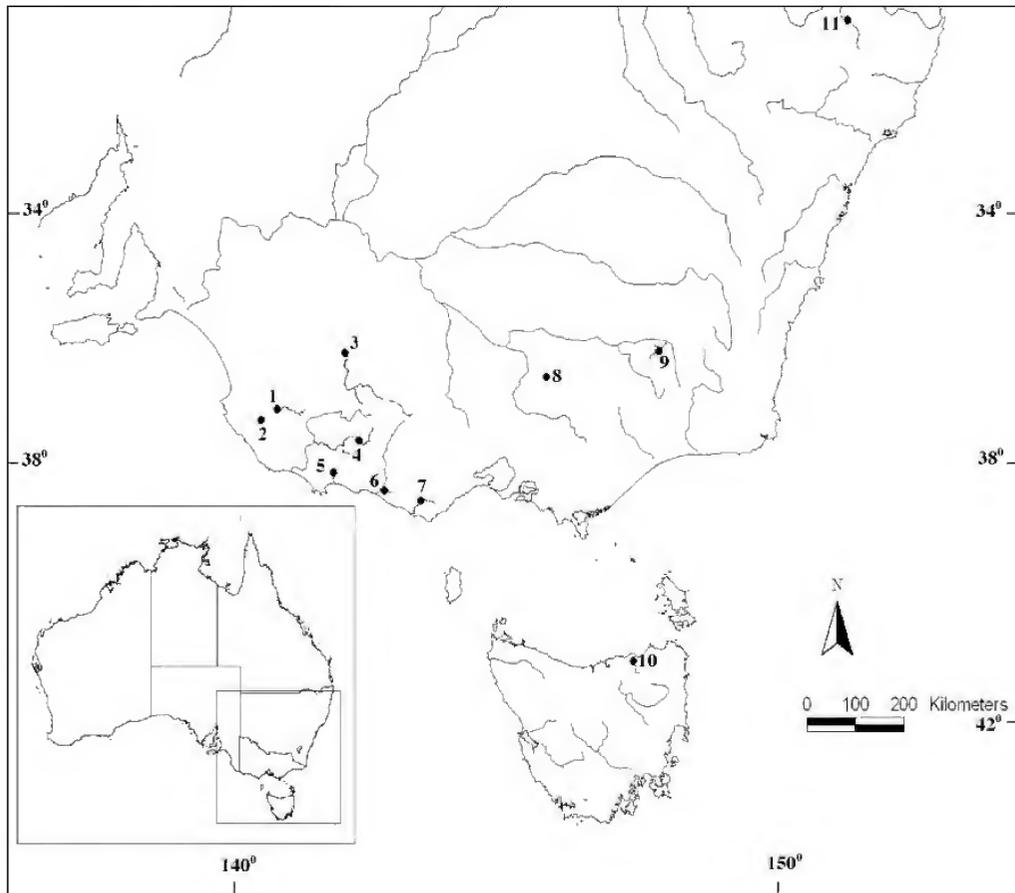


Figure 1. Sample locations: 1. Mosquito Creek, 2. Eight Mile Creek, 3. Wimmera River, 4. Wannon River, 5. Darlot Creek, 6. Brucknell Creek, 7. Gellibrand River, 8. Stony Creek, 9. Cudgewa Creek (*G. bispinosus*), 10. Little Forester Creek (Tasmania), 11. MacDonald River (New South Wales).

*G. bispinosus* showing differences at 0–1 bp positions (0.00–0.03%), 0–8 bp positions (0–3% sequence divergence) and 4 bp positions (1% sequence divergence) respectively. Nevertheless, geographic variation was apparent within the northern form of *G. marmoratus*. Blackfish samples from western Victoria and south-eastern South Australia (sites 1–4) differ by 7–8 base positions from the two samples from the Murray–Darling River system (the sites 8–11). Variation within each of these groups was minimal with haplotypes either being identical or differing at only a single base position.

The degree of divergence between the outgroup taxa, *B. porosa* and *M. peeli peeli*, and blackfish samples was substantial ranging between 12 and 16% (34–45 bp differences). This was also similar to the difference between the two outgroup taxa (10% sequence divergence) (Fig. 2). The maximum parsimony, distance and maximum likelihood methods gave similar tree topologies. The Tamura–Nei model was chosen for the maximum likelihood analysis, involving a full heuristic

search with support for branches evaluated by 100 bootstrap replicates and the application of a gamma distribution shape parameter value equal to 0.2293 and calculated base frequency and substitutional rate matrix values. The significant feature of the trees is the clustering of *Gadopsis* into three distinct clades, representing the two putative northern and southern species of *G. marmoratus* and *G. bispinosus*. These three clades are supported by high confidence values in each method of analysis (66–100% bootstrap). Especially noteworthy is that the analyses do not necessarily indicate that the northern and southern forms are each other's closest relative. While maximum parsimony and maximum likelihood methods indicate an unresolved trichotomy for the relationship between the three clades, the distance approach suggests the northern *G. marmoratus* may in fact be more closely related to *G. bispinosus* than to the southern *G. marmoratus*, although the bootstrap support for this relationship is low. The maximum likelihood and distance analyses also highlight phylogenetic patterns within the

Table 1. Percentage sequence divergence and number of nucleotide substitutions among individuals of *Gadopsis* (specimens 1–4, southern *G. marmoratus*; 5 and 6, *G. bispitosus*; 7–12, northern *G. marmoratus*) and outgroup taxa (13, *Bostockia porosa* and 14, *Maccullochella peeli peeli*) based on 290 bp of the mitochondrial 12S rRNA gene. Below diagonal: total character differences; above diagonal: mean character differences (adjusted for missing data).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 Gellibrand R.	*	0.003	0.000	0.000	0.052	0.052	0.048	0.048	0.048	0.052	0.059	0.059	0.126	0.152
2 Brucknell Ck	1	*	0.003	0.003	0.055	0.055	0.052	0.052	0.052	0.055	0.062	0.062	0.129	0.156
3 L. Forester Ck	0	1	*	0.000	0.052	0.052	0.048	0.048	0.048	0.052	0.059	0.059	0.126	0.152
4 Darlot Ck	0	1	0	*	0.052	0.052	0.048	0.048	0.048	0.052	0.059	0.059	0.126	0.152
5 Stony Ck	15	16	15	15	*	0.014	0.052	0.052	0.052	0.055	0.069	0.069	0.136	0.149
6 Cudgewa Ck	15	16	15	15	4	*	0.052	0.052	0.052	0.005	0.062	0.062	0.133	0.145
7 Wimmera R.	14	15	14	14	15	15	*	0.000	0.000	0.003	0.024	0.024	0.147	0.138
8 Wannon R.	14	15	14	14	15	15	0	*	0.000	0.003	0.024	0.024	0.147	0.138
9 Mosquito Ck	14	15	14	14	15	15	0	0	*	0.003	0.024	0.024	0.147	0.138
10 Eight Mile Ck	15	16	15	15	16	16	1	1	1	*	0.028	0.028	0.143	0.135
11 MacDonald R.	17	18	17	17	20	18	7	7	7	8	*	0.000	0.150	0.149
12 Stony Ck	17	18	17	17	20	18	7	7	7	8	0	*	0.150	0.149
13 <i>Bostockia porosa</i>	36	37	36	36	39	38	42	42	42	41	43	43	*	0.126
14 <i>Maccullochella peeli peeli</i>	44	45	44	44	43	42	40	40	40	39	43	43	36	*

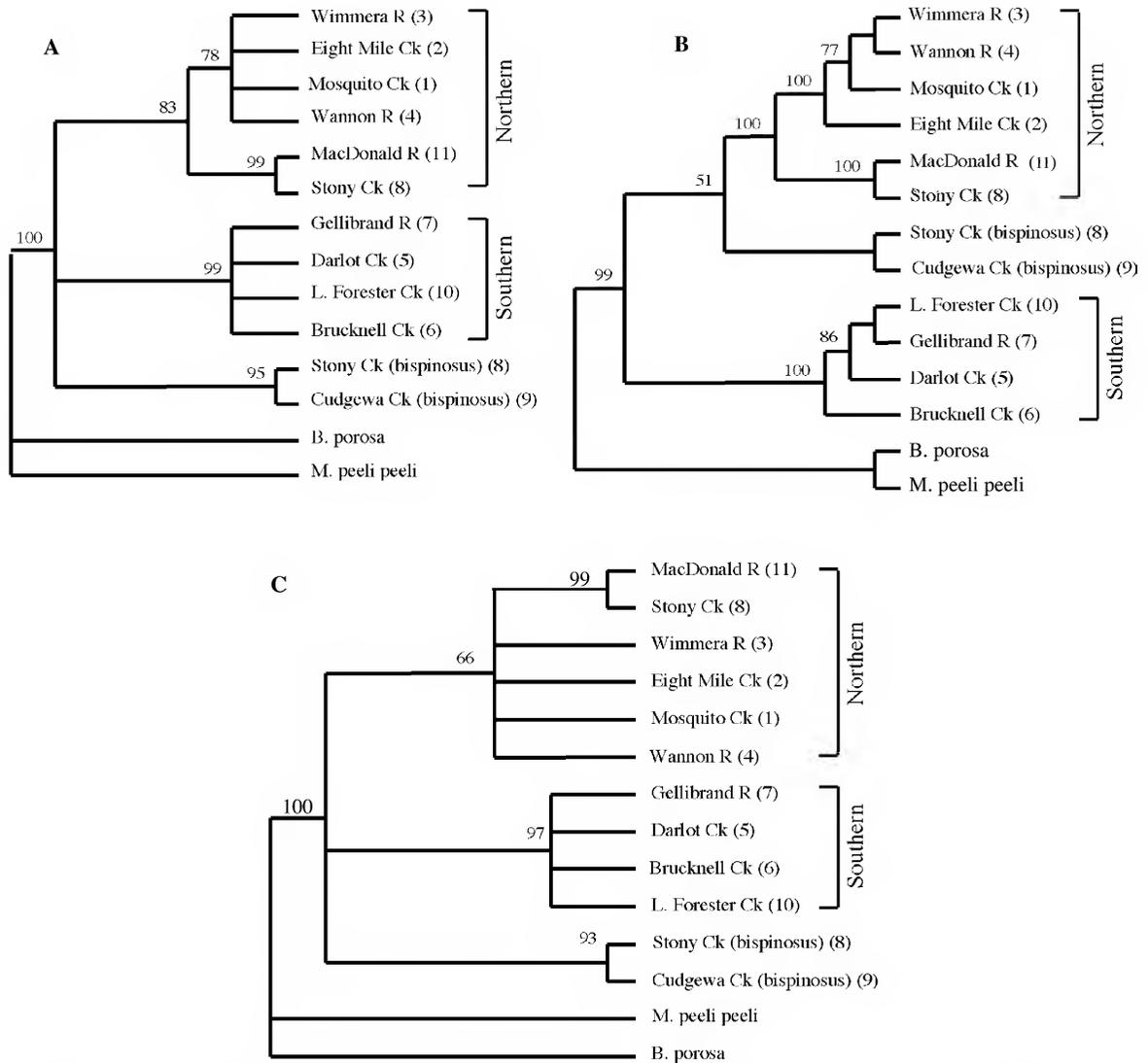


Figure 2. Phylogenetic trees, using the PAUP software package (Swofford, 1998). A, Maximum parsimony, using a full exhaustive search with 1000 bootstrap replicates. B, Distance analysis, using the neighbour-joining option, bootstrap replicates set at 1000. C, Maximum likelihood, using the Tamura-Nei model with 100 bootstrap replicates.

northern form of *G. marmoratus*. The samples from south-eastern South Australia and western Victoria (sites 1–4) form a well supported clade (78–100% bootstrap support) as do the individuals from Stony Creek and the MacDonalld River from the Murray–Darling River system (99–100% bootstrap support) (Fig 2.)

### Discussion

The taxonomic value of molecular genetic data is widely appreciated (Hillis et al., 1996) and they can be used in essentially

the same way as other data to address issues concerning the identification of taxonomic boundaries. Thus, finding that the degree of nucleotide divergence between *G. bispinosus* and the northern form of *G. marmoratus* is similar to that between *G. bispinosus* and the southern form (5–7%), and substantially greater than that observed within these groupings (0–3%), strongly suggests that each represents a distinct taxonomic entity.

The degree of divergence between the northern and southern forms of *G. marmoratus* and *G. bispinosus* is very similar to those reported by Jerry et al. (2001). These authors examined a

560 bp fragment of the 12S gene region for a single individual representing each of the three genetic forms of blackfish as part of phylogenetic study on Australian members of the family Percichthyidae. It is also noteworthy that Jerry et al. (2001) reported divergence levels of a similar or smaller magnitude for a number of congeneric percichthyid species that are considered good biological species. This together with the fact that *G. bispinosus* and *G. marmoratus* are known to behave as good biological species based on their maintenance of genetic differences in sympatry (Sanger 1986), suggests that the northern and southern forms of *G. marmoratus* also represent distinct biological species.

Additional support for the validity of northern and southern forms of *G. marmoratus* as discrete species derives from an examination of intra- and interspecific levels of divergence. Overall, the intraspecific comparisons average was 1.2%, compared with an average of 5.2% divergence for interspecific comparisons. The largest intraspecific comparison is 2.8% divergence between samples of northern *G. marmoratus* from Eight-Mile Creek in South Australia and the MacDonald River in New South Wales. Finding this degree of intraspecific divergence is not surprising given that the samples come from independent drainages over 1000 km apart. Conversely, finding that the Wannon River sample differs from the Darlot creek sample by 14 base positions (6%) and are less than 100 km apart strongly suggests that either a biological or geographical barrier has limited or completely impeded migration of blackfish between the two adjacent drainages. Decoupling of genetic divergence and geographic separation between samples indicates that the two forms represent good biological species and suggests that if they do come into contact they are unlikely to interbreed.

The application of the biological species concept to allopatric populations has, however, been widely criticized and is considered a persistent problem for taxonomic studies of freshwater fish (McDowell, 1972). Some authors have called for the abandonment of the biological species concept and its replacement with lineage or genealogically-based concepts such as the phylogenetic species concept (Claridge et al., 1997; Avise and Walker, 1999; Shaw, 2001). An advantage of the phylogenetic and related species concepts is that they allow recognition of species in sympatry or allopatry because genealogical relationships can be determined independently of geographical status (Shaw, 2001). While there are also operational difficulties in the application of lineage-based species concepts (Avise and Wollenberg, 1997; Sites and Crandall, 1997), the three distinct clades of blackfish identified in this study, via all three methods of phylogenetic analysis, would qualify for recognition as distinct species when applying a lineage-based species concept.

It is unwise to base the determination of species boundaries on a single source of information such as mitochondrial sequences from a single gene region. Support for the taxonomic conclusions of this study comes from studies of allozyme and morphological variation (Sanger, 1986; Ryan et al., in press) and restriction digests of the whole mitochondrial genome (Ovenden et al., 1988). Allozyme data indicated substantial differences between *G. marmoratus* and *G. bispinosus*

(22% fixed differences) and between the northern and the southern forms of *G. marmoratus* (11% fixed differences) (Ryan et al., in press). It is noteworthy that while the allozyme variation between the northern and southern forms is low relative to that between *G. marmoratus* and *G. bispinosus*, the extent of these differences are far greater than that detected between samples within the northern and southern groupings. Significantly, finding the same pattern of geographically abrupt genetic discontinuity between samples of blackfish from western Victoria in both mitochondrial DNA and allozymes (Ryan et al., in press), provides substantial support for the recognition of distinct northern and southern species. Further, results reported by Ovenden et al. (1988) are entirely consistent with the findings of this study based upon restriction digest of the whole mitochondrial genome.

An outcome of this study, which was not apparent from allozyme analyses or Ovenden's study (1988), is the finding of geographic variation in mitochondrial 12S rRNA sequences within the northern form of *G. marmoratus*. Specifically, based upon the six samples analysed, it appears that *Gadopsis* from western Victoria and south-eastern South Australia (sites 1–4) form a monophyletic group distinct from those of the Murray–Darling drainage system (sites 8 and 11). While the degree of divergence among these two groups is considerably less than that seen among the northern and southern *G. marmoratus* and *G. bispinosus*, they nevertheless represent distinct diagnosable lineages. It is noteworthy that Jackson et al. (1996), without going into any great detail expressed the view that blackfish from south-eastern South Australia may possibly be taxonomically distinct, therefore it will be important to investigate this pattern of variation in greater detail and determine if blackfish from this region may deserve taxonomic recognition.

Independent of the consideration of taxonomic status of *Gadopsis* spp., it is apparent that four evolutionary significant units (Waples, 1995) can be recognised in Victoria. If supported by additional sampling, each of these units will require the development of appropriate management strategies if the blackfish biodiversity is to be conserved and protected. In addition to loss of populations due to habitat deterioration, translocations associated with aquaculture, stocking of private water bodies and the use of *Gadopsis* as live bait, are factors that could threaten the integrity of local blackfish stocks. The genetic hazards of local translocations are well illustrated by the rapid genetic displacement of a freshwater crayfish species in the south-west of Western Australia as a result of an inadvertent translocation of a closely related species (Austin and Ryan, 2002).

The major difference between the results of this and previous allozyme studies is that the allozyme data appear to underestimate the degree of divergence between the northern and southern forms. In fact, the relationships among the three putative *Gadopsis* species remain an open question. The parsimony and maximum likelihood analyses suggest an unresolved trichotomy (see also Ovenden et al., 1988), the distance analysis suggests that the northern form of *G. marmoratus* is more closely related to *G. bispinosus*, although with poor bootstrap support, Jerry et al. (2001) supports a closer relationship

between the southern form and *G. bispinosus*, and the allozyme data suggests that the northern and southern *G. marmoratus* species are the most closely related. These inconsistencies leave the phylogenetic relationships among these species unresolved, and therefore also their possible evolution and biogeographic history (Sanger, 1986).

Given the vulnerability of *Gadopsis* from a conservation perspective, the relatively high degree of genetic diversity found in this study, and the unresolved phylogenetic relationships among the three major *Gadopsis* lineages, it becomes apparent that further research is important. Given the relatively slow evolutionary rate of the mitochondrial 12S rRNA gene region, it is suggested that genetic variation within and between *Gadopsis* populations using more rapidly evolving gene regions is determined to fully resolve geographical patterns of genetic diversity in these taxonomically distinct groups and the phylogenetic relationships among them. Further, the geographic sampling of *Gadopsis* for taxonomic and population genetic analysis needs to be expanded, especially with respect to populations in the eastern part of Victoria for which our genetic knowledge is limited.

#### Acknowledgments

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#### References

- Austin, C.M., and Ryan, S.G. 2002. Allozyme evidence for a new species of freshwater crayfish of the genus *Cherax* Erichson (Decapoda: Parastacidae) from the south-west of Western Australia. *Invertebrate Systematics* 16: 357–367.
- Avise, J.C., and Walker, D. 1999. Species realities and numbers in sexual vertebrates: perspectives from an asexually transmitted genome. *Proceedings of the National Academy of Science* 96: 992–995.
- Avise, J.C., and Wollenberg, K. 1997. Phylogenetics and the origin of species. *Proceedings of the National Academy of Sciences* 94: 7748–7755.
- Claridge, M.F., Dawah, H.A., and Wilson, M.R. 1997. Practical approaches to species concepts for living organisms. Pp 1–13 in: *Species: The Units of Biodiversity*. Chapman and Hall Publishers: New York.
- Crandall, K.A., Fetzner, J.W., Lawler, S.H., Kinnersley, M., and Austin, C.M. 1999. Phylogenetic relationships among the Australian and New Zealand genera of freshwater crayfishes (Decapoda: Parastacidae). *Australian Journal of Zoology* 47: 199–214.
- Gatesy, J., DeSalle, R., and Wheeler, W. 1993. Alignment-ambiguous nucleotide sites and the exclusion of systematic data. *Molecular Phylogenetics and Evolution* 2(2): 152–157.
- Gilbert, D.G. 1997. *SeqPup software*. Indiana University.
- Hillis, D.M., and Huelsenbeck, J. P. 1992. Signal, noise, and reliability in molecular phylogenetic analyses. *Journal of Heredity* 83: 189–195.
- Hillis, D.M., Mable, B.K., Larson, A., Davis, S.K., and Zimmer, E.A. 1996. Nucleic acids IV: sequencing and cloning. Pp. 336–339 in: Hillis, D.M., Moritz, C., and Mable, B.K. (eds), *Molecular systematics* (2nd edn). Sinauer Associates: Sunderland.
- Jackson, P.D., Koehn, J.D., Lintermans, M., and Sanger, A.C. 1996. Family Gadopsidae, freshwater blackfishes. Pp. 186–190 in: McDowall, R.M. (ed.), *Freshwater fishes of south-eastern Australia*. A.H. and A.W. Reed Publishing: Sydney.
- Jerry, D.R., Elphinstone, M.S., and Baverstock, P.R. 2001. Phylogenetic relationships of Australian members of the family Percichthyidae inferred from mitochondrial 12S rRNA sequence data. *Molecular Phylogenetics and Evolution* 18(3): 335–347.
- Koehn, J.D., and O'Connor, W.G. 1990. *Biological information for the management of native freshwater fish in Victoria*. Victorian Government Printer: Melbourne. 165 pp.
- McDowall, R.M. 1972. The species problem in freshwater fishes and the taxonomy of diadromous and lacustrine populations of *Galaxiias maculatus* (Jenyns). *Journal of the Royal Society of New Zealand* 2(3): 325–367.
- Ovenden, J.R., White, R.W.G., and Sanger, A.C. 1988. Evolutionary relationships of *Gadopsis* spp. inferred from restriction enzyme analysis of their mitochondrial DNA. *Journal of Fish Biology* 32: 137–148.
- Posada, D., and Crandall, K.A. 1998. MODELTEST: testing the model of DNA substitution. *Bioinformatics* 14: 817–818.
- Ryan, S.G., Miller, A.D., and Austin, C.M. in press. Allozyme variation and taxonomy of the river blackfish, *Gadopsis marmoratus* Richardson, in western Victoria. *Proceedings of the Royal Society of Victoria*.
- Richardson, J. 1848. Ichthyology. In: *Zoology of the Voyage of H.M.S. Erebus and Terror, Under the Command of Capt. Sir J. C. Ross, R.N. During the Years 1839 to 1843*. Longman, Brown and Longmans: London.
- Sanger, A.C. 1984. Description of a new species of *Gadopsis* (Pisces: Gadopsidae) from Victoria. *Proceedings of the Royal Society of Victoria* 96: 93–97.
- Sanger, A.C. 1986. The evolution and ecology of the *Gadopsis marmoratus* complex. Ph.D. thesis, The University of Melbourne, Melbourne.
- Shaw, K.L. 2001. The genealogical view of speciation. *Journal of Evolutionary Biology* 14: 880–882.
- Sites, J.W., and Crandall, K.A. 1997. Testing species boundaries in biodiversity studies. *Conservation Biology* 11(6): 1289–1297.
- Swofford, D.L. 1998. *PAUP\*. Phylogenetic analysis using parsimony (\*and other methods)*. Version 4. Sinauer Associates: Sunderland. 128 pp.
- Thomson, J.D., Gibson, T.J., Plewniak F., Jeanmougin, F., and Higgins, D.G. 1997. The Clustal X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* 24: 4876–4882.
- Waples, R.S. 1995. Evolutionary significant units and the conservation of biological diversity under the Endangered Species Act. *American Fisheries Society Symposium* 17: 8–27.
- Waters, J.M., Lintermans, M., and White, R.W.G. 1994. Mitochondrial-DNA variation suggests river capture as a source of vicariance in *Gadopsis bispinosus* (Pisces: Gadopsidae). *Journal of Fish Biology* 44(3): 549–551.



## Dimorphic brooding zooids in the genus *Adeona* Lamouroux from Australia (Bryozoa: Cheilostomata)

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### Abstract

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The genus *Adeona* is a characteristic and common part of the Australian shelf fauna, extending to the tropical Indo-West Pacific. The genus first appears in the fossil record of the Miocene of south-eastern Australia. Zooid dimorphism has been recognised initially from subtle differences in the external appearance, which have not been described previously. Detailed examination has shown enlarged brooding zooids with marked differences from autozooids in the internal structure of the peristomes and in the occurrence of a primary calcified orifice.

### Keywords

Bryozoa, bryozoans, Cheilostomata, Adeonidae, Recent, Australia, brooding, dimorphism

### Introduction

The Family Adeonidae includes genera with colonies which are mainly erect and bilaminar, and some which are encrusting. Frontal wall development is umbonuloid as demonstrated in a study of a range of Recent material (Cook, 1973). Further analysis of skeletal structures in a number of Australian and New Zealand examples was done by Lidgard (1996). Enlarged brooding zooids are well-known in the genera *Adeonellopsis* MacGillivray, 1886, *Reptadeonella* Busk, 1884 (Hayward and Ryland, 1999), and *Dimorphocella* Maplestone, 1903. Brooding dimorphs are also characteristic in *Adeonella* Maplestone, 1903 and *Laminopora* Michelin, 1842, which display schizoporelloid frontal wall development. For that reason these latter genera are considered to belong to a distinct family, the Adeonellidae (although there is disagreement on this issue, see Lidgard, 1996). In the genus *Adeona* Lamouroux, 1812, enlarged brooding zooids (“ooecial cells”) were first identified by Busk (1884: 181) in the species *A. appendiculata* Busk, 1884 from Twofold Bay, off Eden, NSW. His illustration (pl. 33, fig. 6) shows two zooids with slightly larger secondary orifice dimensions. He also figured the opercula of brooding and non-brooding dimorphs (fig. 47). Cook (1973: 249, 250) inferred the presence of brooding zooids in unidentified material from the collection of the Natural History Museum, but these were not described or illustrated. A study of skeletal regeneration in a specimen of *Adeona* (Wass, 1983), included illustrations of early ontogenetic stages of regenerating zooids.

These show dimorphism in the size of the secondary calcified orifices but no comment was made about this dimorphism. Wass (1991) illustrated zooidal variation in *Adeona*, and remarked on the larger size of inferred brooding zooids, and the porous distal plate in the calcified orifice of these zooids.

At least 15 species of *Adeona* have been described, mainly from the Recent of Australia, with some from Indonesia, Japan and South Africa, and one from Brazil. A thorough revision of this group is badly needed; it is expected that some of these species will be better placed in other genera, while it is also believed that detailed study will reveal more undescribed species from Australia. The type species, *Adeona grisea* Lamouroux, 1812 was collected from Australia by the Baudin expedition: the exact locality is not known. It is assumed that the type material of Lamouroux was largely destroyed but material in the Nice Museum may be relevant (Tillier, 1977).

Most of the specimens collected from southern Australia are of folded and branching bilaminar fenestrate sheets, often forming colonies 150–250 mm wide and high. These large colonies are attached to the sea floor by a complex articulated stem built of porous calcareous segments joined by cuticular tubes, forming a stout trunk (Bock and Cook, 2000). The original illustration of Lamouroux (1816) shows a single fenestrate sheet but it is uncertain if this is a specific character or if it represents an early stage of colony development. Colonies with a lanceolate, non-fenestrate form are known from Indonesia and Western Australia as *Adeona foliifera* Lamarck, 1816 (= *Adeona foliacea* Lamouroux, 1816).

**Material and methods.** The collection of Museum Victoria includes a large amount of material of the family Adeonidae from southern Australia, including very large colonies collected from near Port Phillip heads in the late nineteenth and early twentieth centuries. This has been supplemented by colonies dredged from Bass Strait in the 1980s, and from the Great Australian Bight in 1995. The latter material was sampled using the CSIRO Marine Laboratories vessel, RV *Franklin*. The taxonomic revision of this collection is a major project which has been barely commenced.

The material examined is from three samples: stations GAB-033, GAB-113, BSS-119 (locality details given in explanation of figures). Four colonies were used, apparently belonging to four distinct species, although species identification has not been attempted in this preliminary study. These species appear to be neither *Adeona cellulosa* (MacGillivray, 1869) nor *A. wilsoni* (MacGillivray, 1881). It is possible that the material may be identified as one or more of the four species and one variety defined by Kirchenpauer, 1880 (*Adeona albida*, *A. arborescens*, *A. intermedia*, *A. macrothyris* and *A. foliacea* var. *fascialis*) but the type material of these has not been seen.

In order to prepare the interior of the frontal shield for examination, dry colony fragments were cemented to a glass slide with domestic cyanoacrylate adhesive ('Superglue'). After polymerization, the entire upper layer of zooids, together with the basal wall of the lower layer, was removed by abrasion. After dissolving the adhesive with acetone, the remaining material was cleaned of organic tissue using bleach. The resulting preparation clearly shows details of the internal skeletal structures, as revealed in the illustrations.

## Observations

The genus *Adeona* includes several species, with the most common colony form composed of a boxwork of branching bilaminar fenestrate sheets. Some species form simple sheets, or branches without fenestrae. Colonies of the complex types are up to 30 cm in diameter; the age of these colonies is unknown but is suspected to be of the order of some tens of years. Colonies are attached, usually to solid substrates, by a slightly flexible stem composed of calcareous stem joints with cuticular connecting tubes (Bock and Cook, 2000).

The systematically important characters of *Adeona* are considered to include gross colony morphology, fenestra size, type of heterozooids on the fenestral rim and the zooidal skeletal characters. Zooidal appearance changes greatly and rapidly with ontogeny, so that young zooids at the growing edge of the colony should be more reliable for identification than older zooids with thick secondary calcification. Internal characters of the zooid skeleton should also reveal useful characters, particularly in the shape of the orifice, although no information on this has been published previously.

Specimens of a number of species of the genus have been examined externally after removal of tissue using bleach, revealing that zooid dimorphism is common. The four examples illustrated here differ in the zooid and orifice proportions, the relative position of frontal avicularia and foramen opening, and the presence or absence of avicularia on brooding zooids.

It is inferred that the dimorphs with larger secondary orifices are brooding zooids. The calcified external opening of the orifice is generally larger in the brooding zooids. This is best seen in zooids near the growing edge of the colony where secondary calcification is less well-developed (Figs 1, 4). Examination of the interior of the frontal shield has revealed considerable

differences between brooding and non-brooding zooids (Fig. 2). The interior opening of the brooding zooid peristome is much larger and leads to a distal peristomial chamber with smooth calcification. This space contained large single embryos which were observed during the process of sectioning the colony. The smooth calcification of the brood chamber terminates proximally at a line that is continuous with the ring scar of the body chamber of the zooid (Fig. 3). The lateral and distal walls peripheral to the ring scar are perforated with numerous pores leading to tubes communicating with the septular pores on the exterior surface of the calcified skeleton. The porous distal plate observed by Wass (1991) is the frontal surface of the peristomial brood chamber (Figs 5, 8).

Observations on the fairly small sample which has been examined in detail shows that brooding zooids may occur in clusters of up to at least 20 zooids (Fig. 6). These clusters do not appear to be closely related to colony margins or to be proximal to colony fenestrae. However, in other colonies brooding zooids appear to be scattered with no obvious clustering.

Other differences between brooding zooids and non-brooding zooids are relatively subtle. Brooding zooids tend to be larger (Fig. 4) but not greatly (Fig. 1). In one example the brooding zooids lack avicularia (Fig. 5) but the significance of this character is not known. In many examples, a thin laminar plate is seen on each side of the orifice at the position where the hinge of the operculum would be articulated (Fig. 3). These are considered to be paired condyles, which have not been noted in this genus previously. These are also present in non-brooding zooids (Fig. 2).

The illustrations show the complexity of the frontal shield in *Adeona*. The wall over the epistegal space is clearly multi-layered (Figs 4, 8). A thin layer forms immediately above the epistegal space and an overlying porous layer develops by secondary thickening, beneath the hypostegal coelom (Fig. 7). The rapid thickening of the outer layer of secondary calcification on the colony surface obscures such relationships except at the growing margin. The pores seen in the outer layer (Fig. 8) are conventionally termed areolae; they are assumed to be for communication between the hypostegal coelom and the main zooid. However, the complexity of these pores suggests that the complete account of their function is yet to be elucidated. Additional work needs to be done using thin sections, together with methods of reconstructing the paths of communication pores. Further investigation should also examine the relationship between the tubes communicating between the zooid interior and the hypostegal coelom and those communicating with adjacent zooids.

Previous accounts, subsequent to Cook (1973), have described the external opening to the epistegal space as a spiramen rather than as an ascopore as this opening does not lead to a true compensation sac in the interior of the zooid. However, this terminology is ambiguous as the term spiramen normally applies to an opening leading from the frontal surface into a peristome, as in the genus *Porina*. The frontal openings in *Adeona* and *Adeonellopsis* are more closely analogous to frontal wall foramina in the families Arachnopsiidae and Exechonellidae, and preferably should be termed foramina. In the material examined, the foramen initially develops in the

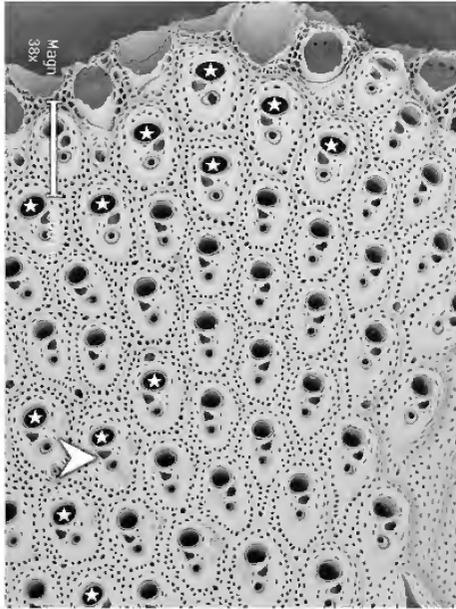


Figure 1. Growing edge of colony of *Adeona* species 1 (stn GAB-113, Great Australian Bight, depth 106 m, 34°36'S, 119°55'E). Starred zooids are inferred brooding dimorphs. Arrow indicates zooid also arrowed in Fig. 2. Scale = 500  $\mu$ m.

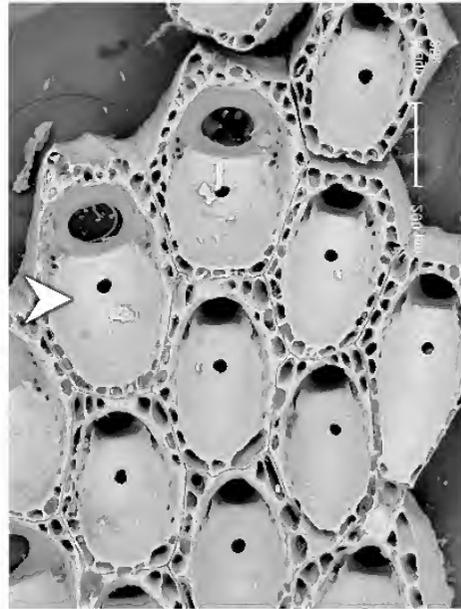


Figure 2. Interior of part of material shown in Fig. 1. Image is reversed left to right for comparison of zooid positions in the fragment. Arrow indicates zooid also arrowed in Figure 1. Two brooding dimorphs showing enlarged orifice and peristomial brood chamber. Scale = 200  $\mu$ m.

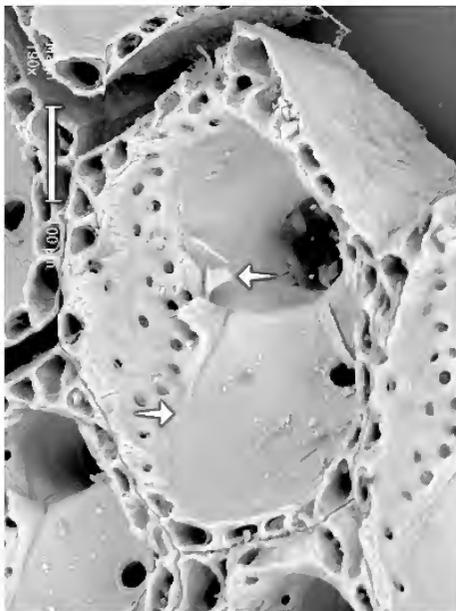


Figure 3. Detail of the distalmost of the two brooding zooids in Fig. 2 (not reversed). Shows ring scar at margin of epistegal space (arrow), plate-like condyle (arrow), and numerous communication pores lateral to orifice and brood chamber, leading to hypostegal coelom. Scale = 100  $\mu$ m.

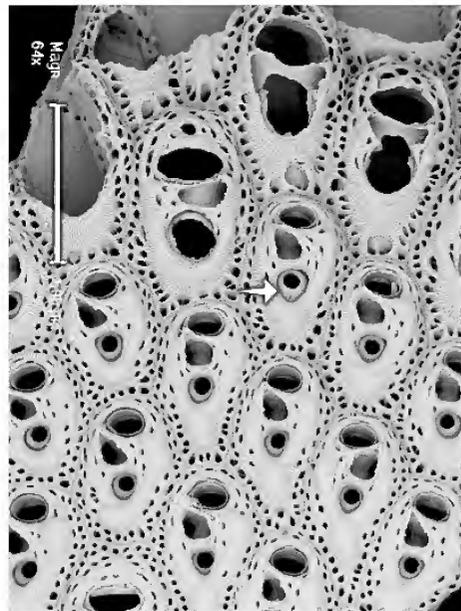


Figure 4. Growing edge of colony of *Adeona* species 2 (stn GAB-113 as in Fig. 1). Ontogenetic thickening of secondary calcification and development of avicularia. Distalmost three zooids are brooding dimorphs, as well as orifice in left proximal margin. Arrow marks calcification around foramen. Scale = 500  $\mu$ m.

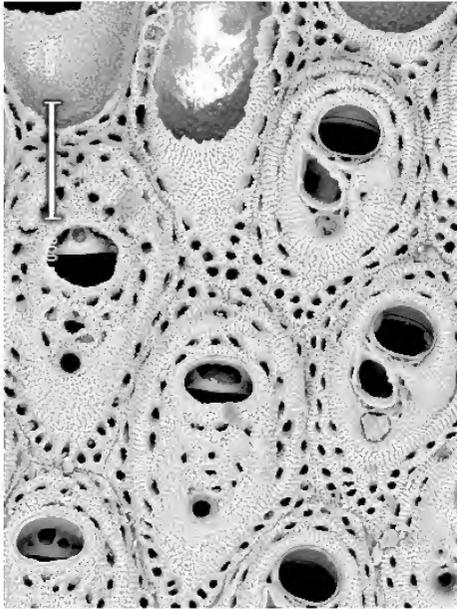


Figure 5. Same colony as Fig. 4. Proximal zooid and left zooid are brooding dimorphs, with well-defined 'distal plate' in orifice, and with no avicularium, having communication pores in its place. Distal and right zooids are non-brooding zooids. Scale = 200  $\mu$ m.

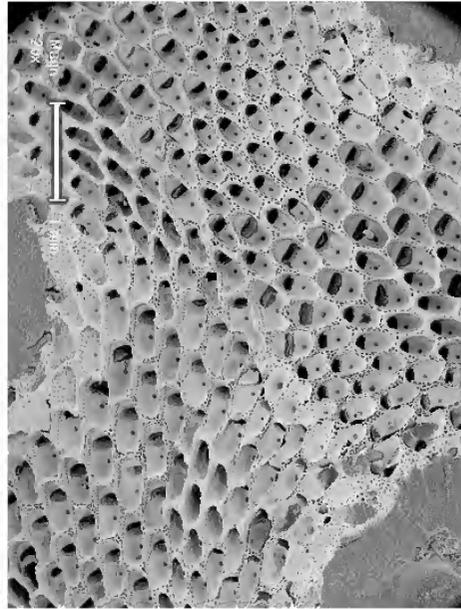


Figure 6. *Adeona* species 3 (stn BSS-119, Bass Strait, depth 92 m, 39°6.7'S, 143°28.7'E). Interior of colony section between three fenestrae, showing clusters of brooding dimorphs at top left, bottom left, and centre right. Scale = 1 mm.



Figure 7. Same specimen as Fig. 6. Detail of single non-brooding zooid. Showing multi-layered frontal calcification, with communication pores in outer layer. Scale = 200  $\mu$ m.

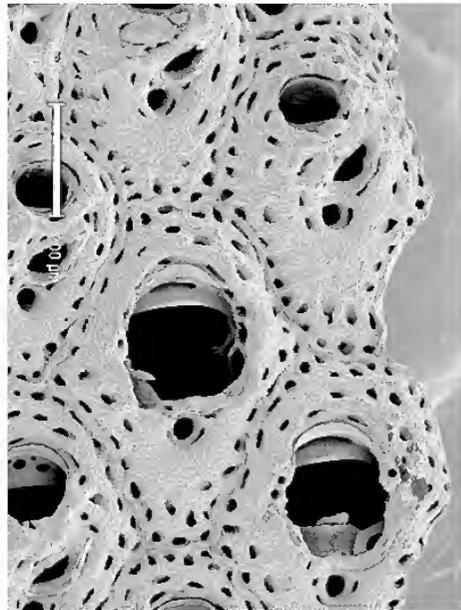


Figure 8. *Adeona* species 4 (stn GAB-033, Great Australian Bight, depth 106 m, 34°36'S, 119°55'E). Two brooding zooids with partly broken frontal walls, showing distal plate and condyle in calcified orifice. Scale = 200  $\mu$ m.

lower layer of calcification, and the secondary layer progressively thickens above it (Fig. 4).

### Acknowledgments

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### References

- Bock, P. E. and Cook, P. L. 2000. Early astogeny of *Adeona* colonies. Pp. 161–167 in: Herrera Cubilla, A., and Jackson, J.B.C. (eds), *Proceedings of the 11th International Bryozoology Association Conference*. Smithsonian Tropical Research Institute: Balboa.
- Cook, P.L. 1973. Preliminary notes on the ontogeny of the frontal body wall in the Adeonidae and Adeonellidae (Bryozoa, Cheilostomata). *Bulletin of the British Museum of Natural History (Zoology)* 25: 243–263.
- Busk, G. 1884. Report on the Polyzoa collected by H.M.S. *Challenger* during the years 1873–1876. Part 1. The Cheilostomata. *Report on the Scientific Results of the Voyage of the H.M.S. "Challenger"*, *Zoology* 10: 1–216.
- Hayward, P.J., and Ryland, J.S. 1999. Cheilostomatous Bryozoa. Part 2. Hippothoidea – Celleporoidea. (2nd edn) In: Barnes, R.S.K., and Crothers, J.H. (eds), *Synopses of the British Fauna (New Series)* 14. The Linnean Society of London and Estuarine and Coastal Sciences Association, Field Studies Council: Shrewsbury.
- Kirchenpauer, G. H. 1880. Über die Bryozoen-Gattung *Adeona*. *Abhandlungen aus dem Gebiete der Naturwissenschaften, Herausgegeben von dem naturwissenschaftlichen Verein in Hamburg* 7: 1–24.
- Lamarck, J.B.P.A. de M. de 1816. *Histoire naturelle des Animaux sans Vertèbres ... précédée d'une introduction offrant la détermination des caractères essentiels de l'animal, sa distinction du végétal et des autres corps naturels, enfin, exposition des principes fondamentaux de la zoologie*. Verdier: Paris. 568 pp.
- Lamouroux, J.V.F. 1812. Extrait d'un mémoire sur la classification des Polypiers coralligènes non entièrement pierreux. *Nouveau Bulletin Scientifique de la Société Philosophique* 3: 181–188.
- Lamouroux, J.V.F. 1816., *Histoire des polypiers Coralligènes Flexibles, vulgairement nommés Zoophytes*. F. Poisson: Caen. 559 pp.
- Lidgard, S. 1996. Zooidal skeletal morphogenesis of some Australian and New Zealand *Adeonellopsis* (Cheilostomatida). Pp. 167–177 in: Gordon, D.P., Smith, A.M., and Grant-Mackie, J.A. (eds), *Bryozoans in Space and Time*. NIWA: Wellington.
- MacGillivray, P.H. 1869. Descriptions of some new genera and species of Australian Polyzoa; to which is added a list of species found in Victoria. *Transactions and Proceedings of the Royal Society of Victoria* 9: 126–148.
- MacGillivray, P.H. 1881. On some new species of *Catenicella* and *Dictyopora*; and on *Urceolipora*, a new genus of Polyzoa. *Transactions and Proceedings of the Royal Society of Victoria* 17: 84–87.
- Maplestone, C. M. 1903. Further descriptions of the Tertiary Polyzoa of Victoria. 9. *Proceedings of the Royal Society of Victoria (new series)* 16: 140–147.
- Michelin, J. H. L. 1840–1847. *Iconographie zoophytologique, description par localités et terrains des Polypiers fossiles de France et pays environnants etc.* P. Bertrand: Paris. 348 pp. (1842, pp. 41–72).
- Tillier, S. 1977. Les types de bryozoaires de la collection Risso. *Annales du Muséum d'Histoire Naturelle de Nice* 5: 153–154.
- Wass, R.E. 1983. Regeneration of calcification in the Adeonidae (Bryozoa: Cheilostomata). *Memoir of the Association of Australasian Palaeontologists* 1: 305–310.
- Wass, R.E. 1991. Intracolony variation in the cheilostome genera, *Adeona* and *Adeonellopsis*. In: Bigey, F.P., and d'Hondt, J.-L. (eds), *Bryozoaires Actuels et Fossiles: Bryozoa Living and Fossil*. *Bulletin de la Société des Sciences Naturelles de l'Ouest de la France, Mémoire hors serie* 1: 523–529.



## A review of Australian Conescharellinidae (Bryozoa: Cheilostomata)

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### Abstract

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The family Conescharellinidae Levinsen is defined and is regarded as comprising seven cheilostome genera (*Conescharellina*, *Bipora*, *Trochosodon*, *Flabellopora*, *Zeuglopora*, *Crucesharellina* and *Proboroa*). The astogeny of colonies, that consists of frontally budded zooids with “reversed” orientation, is briefly described and compared between genera. The morphology of zooids and heterozooids is defined and keys to genera and Australian species are provided. Taxa that were first described from Australia or from reliable subsequent records are redescribed and illustrated where possible. Australian specimens that have been identified as non-Australian species, have generally been found to be distinct and are here redescribed as new species. Some non-Australian records of specimens previously assigned to Australian species have also been re-examined. These are described and sometimes referred to other taxa. Altogether, eight previously described species that have not been found in the present material are discussed and 27 taxa are described from collections, principally from the eastern and southern coasts of Australia and from the Tertiary of Victoria. Eighteen of these are considered to be new species. Where possible, type or at least topotype material of previously described species has been examined. Colonies from the collections of Museum Victoria (NMV) and the Natural History Museum, London (BMNH), have been examined. New species from Australia described here are: *Conescharellina cognata*, *C. ecstasis*, *C. diffusa*, *C. obscura*, *C. stellata*, *C. plana*, *C. perculata*, *C. pustulosa*, *C. ocellata*, *C. macgillivrayi*, *C. humerus*; *Trochosodon fecundus*, *T. asymmetricus*, *T. diommatus*, *T. aster*, *T. anomalus*, *T. praecox* and *Crucesharellina australis*. In addition, the New Zealand bryozoan *Trochosodon multiarmatus* (Gordon, 1989) (not *Bipora multiarmata* Maplestone, 1909) is described as *Trochosodon gordonii* sp. nov.

### Keywords

Bryozoa, bryozoans, Cheilostomata, Conescharellinidae, fossil, Recent, Australia, new taxa

### Introduction

The Bryozoa sorted from dredge samples offshore from south-eastern and south-western Australia in the past 25 years have revealed a wide diversity of species, with many apparently undescribed. The present study is of the family Conescharellinidae. The principal collection programs were the Bass Strait Survey by the Victorian Institute of Marine Science and the National Museum of Victoria (now Museum Victoria) (stations with BSS prefix), Museum Victoria’s South-eastern Australian Slope Survey (SLOPE prefix), and the RV *Franklin* 1995 shelf survey of the Great Australian Bight including areas to the west by Dr Y. Bone (University of Adelaide) (GAB prefix). Further collections were made by Gary C.B. Poore on an expedition with the Western Australian Museum to the Dampier Archipelago, north-western Australia in 1999 (DA-02 prefix). All these surveys used epibenthic sleds and grabs to collect sediments. Sampling of sandy sea-floor sediments, followed by careful sorting, yields examples from a wide range of

groups adapted to loose sediments (Hayward and Cook 1979, Bock and Cook, in press). In view of the unexpected diversity from the scattered survey stations, it is to be expected that yet more species remain undiscovered.

In addition, an interesting series of partially sorted specimens, labelled in C.M. Maplestone’s hand, from the NMV collection, includes some boxes labelled “S.A.” (i.e. South Australia) and others with no locality. These last are labelled with the names of Maplestone’s species from New South Wales, described by him in 1909 and include specimens of species that have not been reported again. They do not occur in any other collections except as “types” in the Australian Museum, and as “cotypes” that are held in the Natural History Museum (London) (BMNH), that were originally sent to London by Maplestone and were registered in 1909. Among others, these include examples of five species of Conescharellinidae, labelled as *Bipora biarmata*, *B. multiarmata*, *B. magniarmata* (all now referred to *Conescharellina*), *Bipora* (= *Trochosodon*) *ampulla* and *Zeuglopora lanceolata*.

The Appendix includes full data on station locations and species occurrences.

A further collection from the Natural History Museum (London) was originally one of the sediment samples collected by H.M.S. *Challenger*. These were stored in the Mineralogy Department and remained uninvestigated until the 1970s. One sample, from *Challenger* stn 185 (11°25'35"S, 144°2'0"E, 249–286 m, near Raine Island, on the outer rim of the Great Barrier Reef, Cape York, Queensland), was first examined in 1972–73. This sample included foraminiferans and minute bryozoan colonies, some of which were figured by Cook and Lagaaij (1976). Cook (1981) later emphasised and illustrated the striking similarities in size and general appearance of these two different components of the sample. Further examination of the numerous bryozoan colonies has revealed that three species of *Trochosodon* and one of *Crucesharellina* are present. Busk (1884) did not include stn 185 in his Report as its bryozoan component was undiscovered. Similarly, a specimen of *Crucesharellina* sp. from *Challenger* stn 169 (37°34'0"S, 179°22'0"E, 1295 m, off New Zealand) also remained unreported although a preparation of the single colony is preserved in the BMNH collection.

Colonies of fossils *Crucesharellina* from the Miocene of Victoria are also included in this study (see Appendix).

*Colonial development.* The group of conescharellinids discussed below construct small colonies that are anchored into the soft-sediment substratum by one or several cuticular roots. The colony may develop and grow below the water-sediment interface or live slightly above the sea-floor. Colonies are conical or lenticular except in the genus *Crucesharellina* which branches into several horizontal arms.

*Notes on astogeny of colonies.* The astogeny of "conescharellinids", like that of "batoporids" (Batoporidae), has been the subject of a considerable amount of theoretical discussion that was reviewed by Waters (1919) and Harmer (1957: 722). Full explanation had to await the description of concepts of frontal budding (Banta, 1972) and reversed frontal budding (Cook and Lagaaij, 1976). The type of astogeny generally known as "reversed frontal budding" occurs in all genera of Conescharellinidae and Batoporidae but is not unique to these families. A closely similar form of budding occurs in the orbicular, flattened colonies of Orbituliporidae. In addition the rounded and lenticular colonies of the numerous species of the genus *Sphaeropora* have a similar type of budding. This genus, however, is closely related to *Celleporaria*; both genera are referable to the family Lepraliellidae.

Frontal budding was first described by Banta (1972) in encrusting colonies of *Schizoporella*; different sequences were also illustrated by Cook (1985). Essentially, a frontal bud is formed by enlargement of an existing hypostegal coelom, bounded frontally by an intussusceptive expansion of frontal cuticle. The nutrients necessary to support the growth of the bud are derived from the pre-existing zooid or zooids, via the frontal septular pores in the calcified frontal shield. Frontal buds often have an orientation closely similar to that of the "parent" zooid but in some mammilliform growths where buds are derived from more than one "parent" zooid, the orientation

may be random, the orifices occurring with no reference to the position or direction of the originating zooids.

These forms of frontal budding occur frequently in ascophoran cheilostomes, particularly among "schizoporellid" and "celleporid" genera. However, different types of frontal budding may occur among "anascan" and "cribrimorph" genera. For example, new branches in the erect "anascan" *Rhabdozoum* develop from an elongated frontal bud that arises from extended calcification surrounding the opesia of a single zooid (Cook and Bock, 1994). In the cribrimorph *Anaskopora*, interzooidal frontal buds arise from uncalcified "windows" in the chambered pores surrounding each zooid and the resultant colonies may resemble those of conescharellinids in organisation (Arnold and Cook, 1997). In *Corbulipora*, buds arise from the uncalcified pelmatidia in the spines of the frontal shield (Bock and Cook, 2001). Encrusting colonies of *Trematooecia* and *Fatullina* exhibit a reversal of polarity of orifice within zooids but new buds arise from vertical interior walls (Grischenko et al, 1998 (1999)). In the Conescharellinidae all zooid orifices are reversed with respect to the direction of growth and all zooids are interzooidal frontal buds.

In "reversed frontal budding" the buds arise regularly between or among the series of frontal septular pores of two or more neighbouring zooids. The orientation of the primary orifice is with the "distal" border directed towards the ancestrular or adapical region. In nearly all the colonies considered here, most of the frontal shield of a zooid is overgrown and concealed by the next generation of zooids at the growing edge (see Cook and Lagaaij, 1976; Pizzaferrri and Braga, 2000). The remaining frontal regions surrounding the orifices (exposed frontal shields) form the exterior surface of the colony except for the proliferal region. An analogous arrangement occurs in the leaf-like colonies of *Flabellopora* and *Zeuglopora* where the zooids of either surface interdigitate, forming a superficially "bilaminate" erect colony (see p. 175).

*Mode of life.* All living colonies of Conescharellinidae are known or inferred to be anchored to a substratum by one or more cuticular roots or extrazooidal rhizoid systems. Generally, the majority of roots, or the greater part of rhizoid systems, is located at or near the adapical region of earliest astogeny. There is evidence from living specimens that metamorphosis of the larva produces a binary complex consisting of a pair of ancestrular and root elements (Cook and Chimonides, 1985). Roots were first described in living colonies of *Crucesharellina* by Whitelegge (1887); they have also been illustrated by Silén (1947), Harmer (1957) and Cook (1979, 1981). The mode of life of small, conescharelliniform and flabelloporiform colonies, especially early in astogeny, appears to be interstitial, almost without exception. The minute colonies exist within the upper centimetres of the sediment surrounded by sand grains and shell fragments. The colonies are anchored randomly to minute particles with no particular orientation with regard to gravity. Colonies are robust and are preserved in the sediment samples after death. These samples include associations of several species, with each species showing colonies at different growth stages. The function of the roots seems to be purely one

of anchorage in most genera, not of support, in contrast to the turgid, extrazoidal rhizoid systems of *Sphaeropora* and *Parmularia* (Cook and Chimonides, 1981, 1985; Brown et al., 2002). In some species of *Flabellopora*, however, the more numerous and larger roots may have a supportive function. Roots may extend up to 10 mm or more from the colony surface (Silén, 1947). They are usually thin and delicate, as illustrated by Cook (1981, pl. A fig. 1) in *Trochosodon optatus* Harmer, 1957. They arise from special pores that are formed in the outer walls of frontally budded, interzoidal kenozooids. These are quite small and are in communication with the surrounding zooids and kenozooids through small septular pores, that were described by Levinsen (1909), Livingstone (1925) and Cook and Lagaaij (1976). In the Conescharellinidae, many of the root pores that have been reported have a lunate shape, although others are circular. Both types have been reported to occur in a single colony; it has been suggested that the circular pores may be an early ontogenetic stage of the lunate pores (Harmer, 1957). No colony has been observed here to develop both kinds of root pore. The lunate shape has given rise to a terminology that has included “lunoecia”, “semilunar pores” and “semilunar slits”. Root pores are frequent in the earlier stages of astogeny, occurring amongst both the autozooid orifices and the avicularian series. Lunate pores often possess a pair of lateral avicularia, whereas circular pores may be surrounded by a circlet of avicularia.

The association of a solitary coral, *Dunocyathus parasiticus* T. Woods, with colonies of *Conescharellina* was documented by Maplestone (1910) in specimens from New South Wales and South Australia. He considered that the position of the coral, that usually occupies the entire antapical region of the bryozoan colony, was evidence of the orientation in life of *Conescharellina*, because “the delicate tentacles of the coral would be crushed” if they rested on the substratum. Harmer (1957: 724, text-fig. 69) examined a specimen from Maplestone in the collections of Cambridge Museum. He concluded that Maplestone’s theoretical orientation was probably correct, as the adapical region of the bryozoan colony was usually without feeding zooids but was the origin of roots. Of course, as the actual, interstitial mode of life does not involve a hard substratum, and as the anchoring, not supportive, nature of roots, together with the minute size of colonies, is unaffected by gravity, these theories are of historical interest only. It appears possible that the coral component of the association did not live interstitially. A total of 22 bryozoan-coral associations has been found among the specimens examined here. Two of these involve *Conescharellina multiarmata*, seven *C. magniarmata*, ten *C. cognata*, and three *C.* species (Figs 1D, 2F). Although the majority of coral specimens grow from the antapical surface of the bryozoan colony, three are asymmetrically developed and one occurs at the adapical end of a small colony. The adjustment of the growth of both organisms seems to be mutually advantageous. There is no evidence of the bryozoan occluding the coral, although calcification has developed laterally, that appears to originate from the bryozoan (Figs 1D). The large avicularian mandibles of *C. magniarmata* probably discouraged settlement on any other but the antapical region but *C. multiarmata* has only very small avicularia. One

significant correlation may be that all the colonies showing the association have a “high” conical shape and few or no antapical cancelli.

**Abundance and diversity.** The very strong correlation between the occurrence of minute colonies and fine-grained sediments was noted by Harmer (1957) and was also emphasised by Cook (1981). The paucity of earlier records and of numbers of specimens from each sample is almost certainly an effect of collection bias. Strikingly different observations have resulted where samples of the sediments themselves have been examined (Hayward and Cook, 1979; Cook, 1981). The Australian specimens described by Maplestone (1909), from a single dredge haul in 146 m off New South Wales, also illustrate this difference, as no fewer than 145 specimens were found, that belonged to eight nominal species, now known to be referable to four genera. A total of 79 specimens of Conescharellinidae were reported by Harmer (1957) from 16 *Siboga* stations from the East Indies. These were described as belonging to 18 nominal species and five genera. Silén (1947) also listed 79 specimens, that he referred to nine species and three genera, from eight stations that overlapped both the *Siboga* area and the “Philippines” region reported by Canu and Bassler (1929). Canu and Bassler included 25 stations with conescharellinids, identifying 32 nominal species belonging to four genera. Analysis of sediments from south-eastern Africa revealed 31 specimens belonging to two genera from six stations (Hayward and Cook 1979). In contrast, Gordon (1985) listed only eight colonies, belonging to two species, from five stations in the Kermadec region. Unfortunately, other reports on collections have not always included consistently the total number of specimens of species from each locality. Gordon (1989) described six species from 41 stations from southern New Zealand; Gordon and d’Hondt (1997) also reported six species from 18 New Caledonian stations but gave no estimate of abundance. Lu (1991) described 24 species referred to Conescharellinidae from the South China Sea and tabulated estimates of colony abundance from each of 27 stations. As noted above, Harmer (1957) was the first to remark on the correlation of sediment type with the presence of minute, rooted colony forms. Apart from Gordon and d’Hondt (1997), all the above-mentioned authors give some indication of sediment type at each collecting station. With hardly any exception, these are of sand, mud, or ooze, depending on the depths at which they occurred. Conescharelliniform colonies belonging to the Conescharellinidae are often associated with slope (200 to 1000 m), or even abyssal depths. Several records given by Harmer (1957), Gordon (1989) and Gordon and d’Hondt (1997) are from depths in excess of 1000 m or even 4000 m.

#### Morphology of structures with characters used in specific determination

**Colony shape and structure.** The genera of Conescharellinidae are characterised to a large extent by shape, that reflects the arrangement and proportion of autozooids, kenozooids and avicularia. The principal axis of most colonies extends from the ancestrular or adapical region to the proliferal or antapical region. In *Conescharellina*, autozooids are arranged with their

orifices in apparent radial or in quincuncial series and alternate frequently with series of avicularia. They often surround a core of small kenozooids (cancelli). These are budded centrally from the frontal septular pores on the inner edge of the autozoid walls and occupy a variable area on the antapical surface. The successive whorls of autozooids, in fact, always alternate radially in the antapical direction (quincuncial). The distance between whorls varies, so that the orifices may appear to form almost continuous radial chains in colonies with a "high" conical shape, but are obviously quincuncially arranged in colonies with a "low" cone. In *Trochosodon*, the conical autozoid arrangement is very similar but there is little or no central kenozooidal core resulting in a more obvious quincuncial arrangement. In *Ptoboroa*, that does not occur from Australia, the colonies are stellate with a prominent central root kenozooid. In *Bipora*, the radial axes occurring in *Conescharellina* are greatly reduced in one dimension; the kenozooidal core is flattened producing an intervening layer of cancelli and a fan-shaped colony. In *Flabellopora* and *Zeuglopora*, the reduction of all but two of the radial axes is complete. The autozooids are budded in alternating and interdigitating series with no intervening kenozooids. Colonies are elongated and leaf-like or occasionally trilobate. In *Crucescharellina*, it is the adapical to antapical axis that is completely reduced and the radial axes elongated, discrete and often branched. This produces a cruciform colony with only one series of zooid orifices on one face and an antapical, "non-zooidal" series on the other (see also Silén 1947). The colonies of *Crucescharellina* and trilobate *Flabellopora* have the potential to grow far larger than those of the more conical genera such as *Conescharellina*, *Trochosodon* and *Bipora*. In *Conescharellina*, the shape of the cone appears to be decided early in astogeny and is often apparently species-specific. For example, the cones of *C. biarmata*, *C. multiarmata* and *C. diffusa* are usually higher than wide, whereas those of *C. eburnea* and *C. obscura* are wider than high. The angle of the frontal surface to the vertical axis also affects the extent and nature of the kenozooidal core. This forms an interior cone, or cylinder, completely filling the antapical surface, or lines a shallow concavity (see *C. cognata*, Figs 3F, G). Most colonies of the conical genera have a mature growth stage antapically in that there is no further budding of autozooids but in that the "cancellated" kenozooidal core is itself covered by a smooth extrazooidal lamina with small, intervening avicularia (*C. eburnea*, Fig. 1G; *C. plana*, Fig. 10D). These are often derived from the frontal septular pores of the exposed shields of the most proliferal of the antapical whorls. Later development of cancelli may include alternating series of kenozooids and small avicularia.

For some species, examination of large samples has shown that they may exhibit a wide range of colony shape and of avicularian size, although in other species variation appears minor. Particularly in early astogenetic stages, orifices tend to be quincuncial and the small colonies dome-shaped. In later astogeny, the orifices may appear radially arranged and the colonies conical (see *C. ecstasis*, Figs 5A, B). Ontogenetic changes affect both the adapical and antapical regions, with the development of secondary calcification that obscures zooidal characteristics. In all colonies, zooid orifice and avicularian

dimensions increase with astogenetic age and there is no distinct zone of astogenetic repetition. Usually, root pores and other kenozooids remain almost constant in size, although they may become surrounded by extrazooidal calcification or by groups of secondary avicularia, forming specific patterns. Variation in colony shape and in the astogenetic timing of "mature" characteristics often reduce the value of past taxonomic descriptions, such as those of Canu and Bassler (1929).

The earliest astogenetic stages have not been observed in any genus but may be inferred from analogous structures in other "sand fauna" colonies and from study of minute stages that infrequently occur in samples. It is inferred that the ancestrula is anchored to a sand grain or similar object within the upper layers of sediment, as has been observed in *Conescharellina*, *Sphaeropora* and *Parmularia* (Cook and Chimonides, 1981, 1985). The position and orientation of the first zooidal buds relative to the ancestrula indicate the eventual mode of growth and structure of the subsequent colony. For example, Harmer (1957) illustrated very young colonies of *Trochosodon linearis* and *T. optatus* and analysed their budding patterns. The ancestrula and paired primary buds formed a radially directed triad, followed by "cycles" (whorls) of alternating zooids, increasing in size and number. Kenozooids and small avicularia were budded on the adapical surface. Almost exactly the same series of astogenetic changes may be traced in very young colonies of *Conescharellina*. Cook (1981: pl. A fig. 6) illustrated a young colony of *Crucescharellina* (as *Agalmatozoum* sp.) showing a central adapical area of rhizoid pores (probably overlying the ancestrular region), with four autozooids forming the earliest stages of a cruciform colony. Gordon and d'Hondt (1997) illustrated a slightly older colony with five arms and a central, adapical area of rhizoid pores and avicularia, very similar in appearance.

**Primary orifice.** The primary orifice is invariably sinuate, the sinus defined by a pair of condyles, that may be prominent or minute. The dimensions of all primary orifices increase with astogeny but the proportions appear to remain virtually the same within species. Although the differences among species are minute and are usually only observable in scanning electron micrographs, they are constant and correlated and therefore taxonomically valid. The shape of the sinus varies from rounded to subtriangular and is species-specific but it may vary slightly among populations.

**Secondary orifice.** Secondary orifices are variable, usually being confined to raised lappets of lateral peristome. In apparently radial series, these produce an appearance described as "costulate" (Canu and Bassler, 1929). Sometimes peristomes are tubular and very prominent marginally (e.g. in *Trochosodon* and *Ptoboroa*) but may be elongated without being prominent at the colony surface (e.g. *Conescharellina plana*).

**Ovicell.** Ovicells are known in two of the genera described here, *Conescharellina* and *Trochosodon*. They are globular, hyperstomial and often extremely delicately calcified, with an exposed, frontal entoecium. Ovicells apparently originate from the small, adapical pore placed close to the border of the maternal zooid orifice. Gordon (1985) clearly illustrated the

early stages of ovicell ontogeny in *Conescharellina*, showing the ectoocial and entoocial calcified layers developing from the adapical and antapical sides of this pore respectively. Colonies of *C. diffusa* and *T. fecundus* also show traces of both layers, associated with the adapical pore (Figs 6B, 17C). Harmer (1957) described ovicells as peristomial but, although they are closely associated with the adapical edge of the peristome, they are not derived from it nor do they normally include any part of it (see *Trochosodon praecox*). Ovicells have also been illustrated by Maplestone (1910) and by Livingstone (1925b). Silén (1947) illustrated asymmetrically placed ovicells; these may be inferred to occur in *T. asymmetricus*, from the asymmetric position of the adapical pore, although ovicells have not been found (Fig. 19A). Harmer (1957) also described asymmetrically placed ovicells, and noted their fragility in some species. Lu (1991, pl. 17 fig. 5C) illustrated part of an ovicell, in a species he called "*Conescharellina radicata*" from the South China Sea. No ovicells were mentioned in the description, that apparently refers to *C. radiata* Canu and Bassler (1929: 493, pl. 67 figs 1–3). Although the majority of recorded ovicells is from the later astogenetic stages of growth, ovicells have been found very early in astogeny in *Conescharellina africana* (see Cook 1966, 1981; Hayward and Cook, 1979) and in *Trochosodon praecox* sp. nov. (as *Trochosodon* sp. in Cook and Lagaaij, 1976; Cook, 1981). Colonies of *Conescharellina* with embryos in their ovicells were found within a rhizoid and sediment mass belonging to *Parmularia* from off Townsville, Queensland, in 1982. These too, were very fragile, and often became detached when colonies were moved. The mature colonies occurred together with very young specimens that were anchored by means of a minute, turgid ancestrular rhizoid element. Embryos were released from the mature colonies, that apparently spent their entire life interstitially (Cook and Chimonides, 1985). The roots of adult colonies were not turgid or supportive but anchored the colonies with random orientations with regard to gravity, within the rhizoid mass of *Parmularia*. Ovicells, sometimes with embryos in situ, have been found in the present collection in colonies of *Conescharellina plana* (stn BSS-167), *C. diffusa* (Dampier, N.W. Australia), *C. stellata* (stn GAB-019), *C. obscura* (stn GAB-048), *Trochosodon fecundus* (Dampier, N.W. Australia), and *T. praecox* (Cape York, Queensland). Study of these examples strongly suggests that in many cases the basal wall of the ovicell, that is formed by ectoocium developing from the adapical side of the pore, is covered by cuticle that is in contact with the frontal shield only at the point of origin. This explains the ease of detachment of ovicells in many specimens (see Figs 9H–I). The entoocium may be ridged and occasionally is porous. The ridges appear to form pores marginally where the entoocial layer meets the ectoocium. Ovicells are distinctive as there is no contribution to their structure by any zooid other than the maternal zooid. This is a result of the reversed nature of the frontal astogeny.

**Avicularia.** Avicularia vary considerably in size, distribution and orientation but may provide some distinguishing character states among species. The great majority has small, rounded rostra, that may be minute (*Conescharellina multiarmata*).

Some species have large avicularia; in *Crucescharellina* and *Zeuglopora* these may be spatulate. Those near the orifices appear to be adventitious in most cases, derived from frontal septular pores of zooids at the proliferal region, becoming slightly immersed as the next whorl of zooids is budded. Larger avicularia appear to be budded interzooidally (Fig. 3D). Avicularia on the antapical surface are often derived from cancelli and may alternate with them. Cancelli are kenozooids originating from septular pores in the antapical part of the frontal shield in the proliferal region. In some colonies of *Conescharellina* that have only just reached a mature astogenetic stage, the avicularia follow the radial rows of frontal septular pores of the last-budded, proliferal whorl, and may not be accompanied by any cancelli (see Fig. 3F). Avicularia have a bar that often bears one or more calcareous spinous processes (ligulae) on the palatal side. In one species, *C. diffusa*, small spinous processes are present on the non-palatal side of the bar (Figs 6A, B); in another, *C. stellata*, the non-palatal area is sometimes occupied by a thin lamina that may be perforate (Figs 9B, E). Generally, the palates are without any expanded cryptocystal margin but this occurs in *C. magniarmata* (see Fig. 3B). Large, acute avicularia also occur in *C. ecstasis* (Fig. 4) and were seen in the living specimens of *Conescharellina* sp. from Queensland mentioned above. These last were very active, snapping shut and holding any surrounding objects in the sediment. Whether their function is one of stabilization or defence, or perhaps both, is unknown, as is that of small avicularia.

#### Superfamily *Conescharellinoidea* Levinsen, 1909

D'Hondt (1985: 11) stated that the diagnosis was "confondue avec celle des Conescharellinidae publiée par Ryland (1982)". He included only the family Conescharellinidae Levinsen, 1909.

#### Family *Conescharellinidae* Levinsen, 1909

*Type genus.* *Conescharellina* d'Orbigny, 1852.

**Description.** Free-living Cheilostomata attached to small particles by cuticular roots originating from kenozooidal pores. All autozooids with reversed frontal budding; ancestrular region adapical, with root pores and avicularia. Zooids elongated; frontal wall composed of two parts; "exposed", surrounding the primary orifice, and "concealed", only visible completely in the antapical region of the colony. Primary orifice usually sinuate, often with paired condyles, almost terminal, in the centre of the exposed frontal wall. Avicularia adventitious or interzooidal, often in patterns among autozooids. Antapical regions often occupied by kenozooids (cancelli), originally budded from the septular pores of the frontal walls of zooids of the proliferal region. Extrazooidal calcification and/or secondary kenozooids and avicularia often budded from the primary cancelli. Other avicularia budded directly from the proliferal zooids. Ovicells hyperstomial, originating from an adapical pore, globular, not closed by the operculum, entoocium and ectoocium often delicate and fragile; usually distinct from the peristome but occasionally associated with it through a foramen.

*Remarks.* The family includes closely related groups of species with distinctive colony forms that define genera. The typical growth pattern of each genus restricts variation of the colony form; minor differences in astogenetic pattern and zooid morphology may be important in distinguishing species. All known species have in common: small size (usually less than 10 mm in maximum dimension), anchorage to sediment particles by roots arising from special kenozooids, and a strong association with fine-particle sediments, often from continental slope and lower slope depths. All species have sinuate primary orifices, often with condyles. Most species have interzooidal or adventitious, frontally budded avicularia, that form patterns among the autozooid orifices. Special pores, derived from kenozooids, are the origin of roots. These may be generally distributed or confined to the regions of earliest astogeny. The family resembles the Batoporidae and the Orbituliporidae in its reversed frontal budding pattern but differs in the structure of the primary orifice and the few known ovicells. It also resembles the Lekythoporidae, another group including several closely related genera that have erect branching colonies with a type of reversed frontal budding (Bock and Cook, 2000). These last genera, however, have zooidal and ovicellular characters that show stronger links with the family Celleporidae. Gordon (1989) has suggested that the Conescharellinidae and Orbituliporidae should be included with the Lekythoporidae in a single superfamily. This view was not accepted by Bock and Cook (2000) who noted that *Sphaeropora* Haswell, 1881, that also has globular to lenticular colonies formed by reversed frontal budding, anchored by supportive, turgid, extrazooidal rhizoids, is closely related to *Celleporaria*, and is therefore assignable to the family Lepraliellidae. Reversed frontal budding itself may not therefore reflect any close systematic relationships.

Six of the seven genera of Conescharellinidae are represented in Australia, often by several species. However, the type species of *Conescharellina*, *C. angustata* d'Orbigny, 1852, was described from the Philippines, and that of *Flabellopora*, *F. elegans* d'Orbigny, 1852, from the China Sea. The type species of *Trochosodon*, *T. linearis* Canu and Bassler, 1927, occurred from Borneo, and the type species of *Crucescharellina*, *C. japonica* Silén, 1947, from Japan. Two of the remaining genera, *Bipora* and *Zeuglopora*, have Australian type species: *Bipora flabellaris* Levinsen, 1909, and *Zeuglopora lanceolata* Maplestone, 1909 respectively. The type species of *Ptoboroa*, *Trochosodon pulchrior* Gordon, 1989, occurs from New Zealand.

No attempt has been made here to review or revise the numerous species of *Conescharellina*, *Trochosodon* and *Flabellopora* introduced and described by Canu and Bassler (1929) from the Philippine region. Similarly, the synonymies of these species, and of further new taxa introduced from the same region by Silén (1947), from the East Indies by Harmer (1957), and the South China Sea by Lu (1991), cannot be assessed without examination of all relevant material. It is possible that some of the species from eastern and south-eastern Australia described by Tenison Woods (1880), Whitelegge (1887) and Maplestone (1909), may be synonymous with some, or part, of the nominal species described by later authors from the west

Pacific region. Similarly, it is possible that some taxa, introduced here as new, may have been described earlier by these authors, or even later by Gordon (1989), or Gordon and d'Hondt (1997) from the New Zealand and New Caledonian regions.

There is no unequivocal record of a member of the Conescharellinidae, as defined here, from the European Tertiary. *Conescharellinopsis* Labracherie, 1975, described from the Lower Eocene of Aquitaine, has the type species *C. vignauxi* Labracherie, 1975 (p. 151, pl. 4 figs 4–11). This species appears to be similar to species of *Atactoporida*, as described by Cook and Lagaaij (1976), with which it was associated and is not referred to the Conescharellinidae here.

*Conescharellina perfecta* Accordi (1947), from the Upper Eocene of northern Italy, has been demonstrated to belong to the genus *Lacrimula* (Batoporidae) by Cook and Lagaaij (1976) and more recently by Zágoršek and Kázmér (2001) who gave a full synonymy. *Lacrimula perfecta* also appears to be congeneric with another north Italian Eocene species, *Conescharellina ecoena* Neviani, 1895. Cook and Lagaaij (1976) suggested that it seems possible that all fossil records of *Conescharellina* from western Europe may “prove to belong to one species complex, attributable to *Lacrimula*.” The Conescharellinidae therefore seems to have an Indo-west-Pacific and Australasian distribution only, perhaps extending from the Eocene (Labracherie and Sigal, 1975), to the present day.

*Notes on the use of the name “Biporidae”.* Zágoršek (2001: 558) and Zágoršek and Kázmér (2001: 73) introduced a superfamily “Biporidae Gregory, 1893” but no mention was made of the genus *Bipora* Whitelegge, 1887. The superfamily was described to include the family “Batoporoidae” (sic) Neviani, 1901 and the genera *Lacrimula* Cook, 1966 and *Orbitulipora* Stoliczka, 1862. Neviani (1901) had, however, included in his family “Batoporoidae” [sic] only the genera *Batopora* Reuss (for *B. rosula*) and *Conescharellina* d'Orbigny (for *C. conica*, a manuscript name, almost certainly referable to *Lacrimula perfecta*; see Cook and Lagaaij, 1976 for discussion).

Gregory (1893: 223) suggested a classification of Cheilostomata that included five Suborders. Two of these included the “ascophorine” forms and consisted of the Suborders Schizothyriata and Holothyriata. Gregory's treatment of families and subfamilies was not consistent but among the Schizothyriata the family Schizoporellidae and subfamily Schizoporellinae were provided (p. 239) with an informal designation of *Schizoporella* as type genus, and a reference to its diagnosis by Hincks (1880). In a similar manner, the type genus *Schizoretepora* was designated in a footnote for the family Schizoreteporinae. The type genus *Schismoporina* was also designated for the subfamily Schismoporinae in another footnote. The treatment of the subfamily Biporinae was completely different. No generic names were included but the description given was “Schizoporellidae with a patelliform unilaminar zoarium, with vibracularia systematically arranged”. This is a parallel of the description of a subfamily of Microporidae included in Gregory's suborder Athyriata, called the Selenarinae, similarly described as “Microporidae with

patelliform zoaria and vibraculata systematically arranged". The Biporineae may even have been introduced to provide a form of symmetrical concept between the Athyriata and Schizothyriata. Presumably, Gregory had in mind some lunulitiform ascophoran genus or genera that would be included in his Biporineae but he did not mention the subfamily again, or describe *Bipora*, or any other genus as belonging to it. In addition, although Whitelegge's (1887) paper and its reprint (1888) were both listed in Gregory's bibliography (on p. 274), no mention of either was made anywhere in his text. Both Whitelegge and Jelly (1889), whose Synonymic Catalogue was also listed by Gregory in his bibliography, gave *Conescharellina* in the synonymies of several species assigned to *Bipora*. In fact, Jelly (1889: 20) referred to Whitelegge's paper under her entry for *B. umbonata* (Haswell), and again (on p. 64) under *Conescharellina cancellata* and *C. elegans*, where *Bipora* was given in synonymy.

Gregory must therefore have been aware that other, earlier authors had described a relationship between the two genera. Any Conescharellinidae were, however, tacitly excluded from the subfamily Biporineae by Gregory (1893: 225, 251), as the genus *Conescharellina* was listed as belonging to the family Celleporidae, a member of his suborder Holothyriata. Gregory regarded *Conescharellina* as a senior synonym of *Batopora* and described one species from the British Eocene, *Conescharellina clithridiata*, that is, in fact, referable to the Batoporidae. This species was illustrated as *Batopora* by Cook and Lagaaij (1976, pl. 2 fig. 1, pl. 5 fig. 5) and by Cook (1981, pl. B fig. 4). One other species, *B. glandiformis*, was erroneously referred to the cyclostome genus *Heteropora* by Gregory (1893) but was briefly discussed and assigned to *Batopora* by Cheetham (1966) and subsequently was assigned to *Atactoporida* by Cook and Lagaaij (1976). Waters (1904: 96) made the illuminating remark, with reference to Gregory's "undoubted abilities" that "sometimes angel visits stir up all that has been done without establishing order" and "classification has been left in a much more hopeless condition than it was before . . . made by those who have swooped down on the Bryozoa for a short visit".

It seems that Biporineae is not a synonym of Conescharellinoidea and there is no necessity to use any emended suprafamilial name such as "Biporidae Gregory" to include the "Batoporoidae" as used by Zágöršek and Kázmér (2001), or the Conescharellinidae as used by Levinsen (1909). "Biporinae" Maplestone (1910) was an informal usage of a name and is a junior "synonym" of Levinsen's (1909) name Conescharellinidae. As Conescharellinidae has been in common usage, the rule of priority can be ignored, as in ICZN Rule 35.5.

**Key to genera of Conescharellinidae**

- 1. Colonies conical with circular cross section, or stellate 2
- Colonies not as above . . . . . 4
- 2. Autozooids and avicularia frequently in antapically directed, alternating series. Autozooids not very prominent marginally; kenozooids forming a central core or as antapical layers . . . . . *Conescharellina*

- Colonies stellate, without central core of kenozooids, autozooid orifices often arranged quincuncially, marginal zooids prominent; avicularia often absent . . . . . 3
- 3. Colonies with elongated peripheral peristomes; antapical avicularia and cancelli rare . . . . . *Trochosodon*
- Colonies with prominent central root kenozooid *Ptoboroa*
- 4. Colonies compressed laterally in one plane . . . . . 5
- Colonies compressed antapically in one plane, often branching . . . . . *Crucescharellina*
- 5. Colonies with a laterally compressed cone, becoming fan-shaped, zooids on each face separated by a narrow band of kenozooids. . . . . *Bipora*
- Colonies leaf-like, with no intervening kenozooids between two interdigitating, frontally budded series of zooids . . . . . 6
- 6. Lateral margins of colonies serrated, often with groups of prominent zooids or enlarged avicularia . . . . *Zeuglopora*
- Lateral margins not serrated, colonies sometimes trilobate . . . . . *Flabellopora*

**Key to Australian species of *Conescharellina***

- 1. Avicularian rostra acute, longer than orifice . . . . . 2
- Avicularian rostra rounded, smaller than orifice . . . . . 6
- 2. Colonies domed, height and/ or width > 3mm . . . . . 3
- Colonies small, distinctly conical, higher than wide. Avicularia paired, lateral oral, orientated laterally . . . . . *C. biarmata*
- 3. Avicularia lateral oral, single . . . . . 4
- Avicularia lateral oral paired, orientated laterally and adapically . . . . . *C. ecstasis*
- 4. Avicularia randomly orientated . . . . . *C. angulopora*
- Avicularia orientated laterally and adapically . . . . . 5
- 5. Colonies domed, width and height subequal. Solid antapically. Avicularia with lateral cryptocyst lamina, and 3 large ligulae . . . . . *C. magniarmata*
- Colonies becoming very large, wider than high, diameter 10 mm. Antapical surface hollow, covered by cancelli . . . . . *C. cognata*
- 6. Colonies large, height and / or width > 4mm . . . . . 7
- Colonies small, height and / or width < 3mm . . . . . 10
- 7. Root pores circular, surrounded by avicularia . . . . . 8
- Root pores lunate, with paired avicularia . . . . . 9
- 8. Colonies with patent orifices; avicularia lateral and adapical, visible on antapical surface of marginal zooids . . . . . *C. eburnea*
- Orifices at the base of a long peristome, that is not raised at the colony surface; avicularia minute, scattered and paired, adapical . . . . . *C. plana*
- 9. Colonies conical, higher than wide, height up to 5 mm; avicularia and root pores in series alternating with orifices; root pores without small avicularia; rostra with non-palatal spinules . . . . . *C. diffusa*
- Colonies flat, up to 13 mm diameter, or small and discoidal; avicularia scattered or single, antapical and peristomial; root pores with paired avicularia . . . . . *C. obscura*
- 10. Colonies with lunate root pores with paired avicularia 11

- Colonies with circular root pores surrounded by avicularia ..... 12
- 11. Colonies domed, orifices in radial series alternating with avicularia, root pores adapical (fossil) . . . . . *C. aff. diffusa*
- Colonies conical, higher than wide, orifices with minute lateral and antapical avicularia . . . . . *C. multiarmata*
- Colonies stellate, marginal peristomes bilabiate or spout-like; avicularia with non-palatal lamina . . . . . *C. stellata*
- Colonies with pustular calcification adapically and antapically; avicularia minute, one peristomial and antapical, others scattered . . . . . *C. pustulosa*
- 12. Colonies with prominent spout-like marginal peristomes and numerous pairs of avicularia, some visible on the antapical surface marginally . . . . . *C. perculata*
- Colonies not as above . . . . . 13
- 13. Colonies slightly domed, or raised centrally; orifices with a long subtriangular sinus, peristomes raised laterally; avicularia paired lateral-oral, visible on the antapical surface of marginal zooids; cancelli absent . . . . . *C. ocellata*
- Colonies fairly flat, with bilabiate marginal peristomes; orifice with a small rounded sinus; avicularia rare, antapical surface with large cancelli . . . . . *C. macgillivrayi*
- Colonies slightly raised centrally; orifices with a rounded sinus and laterally raised peristome, with paired lateral avicularia that form prominent “shoulders” on marginal zooids . . . . . *C. humerus*

**Key to Australian species of *Trochosodon***

- 1. Colonies large, diameter 3–4.7 mm ..... 2
- Colonies smaller ..... 3
- 2. Colonies fairly flat, domed centrally, with numerous tubular marginal peristomes . . . . . *T. ampulla*
- Colonies lenticular, with prominent radial rows of peristomes with paired avicularia on the antapical surface; root pores lunate . . . . . *T. diommatus*
- 3. Colony diameter 2–3 mm ..... 4
- Colony diameter <2 mm ..... 5
- 4. Colonies with bilabiate marginal peristomes, orifices quincuncial with wide, shallow sinus; ovicells symmetrical, root pores lunate . . . . . *T. secundus*
- Colonies with short, tubular peristomes, orifices radial, sinus rounded; adapical pores asymmetric, root pores circular . . . . . *T. asymmetricus*
- 5. Colonies conical, higher than wide; zooid peristomes prominent and curved; root pores rare, lunate *T. anomalus*
- Colonies as wide as high, or wider ..... 6
- 6. Colonies very small, fairly flat, stellate; peristomes tubular, with paired lateral avicularia; root pores lunate . . . *T. aster*
- Colonies minute, with an antapical dome of mamillate calcification; peristomes tubular, with paired lateral avicularia; ovicells small, robust, symmetrical; root pores rounded . . . . . *T. praecox*

***Conescharellina* d’Orbigny 1852**

*Conescharellina* [sic] d’Orbigny 1852: 447.

*Conescharellina*.—Canu and Bassler, 1917.—Waters, 1919: 93.—Canu and Bassler, 1929: 480.—Silén, 1947: 33.—Harmer, 1957: 726.—Gordon, 1989: 81.

*Type species. Conescharellina angustata* d’Orbigny, 1852, subsequent designation by Waters, 1919: 93. [Canu and Bassler (1917) had earlier incorrectly indicated *C. cancellata* (Busk, 1884), see Harmer (1957: 726)]. The mis-spelling of the name as *Conescharellina* occurs only in the genus heading of d’Orbigny (1852: 447); all other spellings of the name are as *Conescharellina*. *Conescharellina angustata* was included in *Batopora* by Reuss (1867: 224).

*Description.* Colony conical, with autozooids appearing to be in radial series, either placed in rows alternating with avicularia, or in quincunx with intervening avicularia. Cuticular roots arise from circular or crescentic skeletal pores, concentrated in the adapical region in some species. Orifices with an antapical sinus, often with raised lateral peristomes. Avicularia adventitious and interzooidal, usually budded in distinct patterns, with acute or rounded mandibles, slung on a bar, that often has one or more palatal ligulae. Ovicells hyperstomial, prominent, derived from an adapical pore, with thinly calcified ectooecium and entoecium. Central part of colony cone occupied by a core of small kenozooids (cancelli), often accompanied by avicularia, that may cover the antapical surface late in as togeny.

*Remarks.* *C. angustata* was described by d’Orbigny (1852: 447, pl. 714 figs 14–16) from the Philippine island of Basilan (approx. 6°50’N, 122°E, in the Celebes Sea). The figured colony (fig. 15) was an elongated cone with 8–9 apparently radial series of zooids forming costules. The orifices are raised, circular-to-oval, each with an asymmetrically arranged pair of pores adapically, and a single series of “special” pores alternating with the zooid orifices in a radial depression. D’Orbigny noted that the orifices were in quincunx, and figured the antapical surface (fig. 16) showing five alternating series of proliferal and subproliferal zooids, with no central cancelli. D’Orbigny noted this particularly, comparing it with the antapical side of *C. dilatata* (see below). In view of the relatively large size and possible maturity of the type colony (height approximately 2.5 mm), it is unusual in *Conescharellina* for cancelli to be absent. In fact, this is characteristic of *Trochosodon*.

A scanning electron micrograph of the putative type specimen, from the Muséum Nationale d’Histoire Naturelle, Paris, has been provided by Drs D.P. Gordon and P.D. Taylor. It resembles d’Orbigny’s figure 15 in its elongated conical shape and radial series of zooid orifices. The adapical region is less regular than the figure, and there are fewer zooid series but this may be the result of damage. The rounded secondary orifices, almost all of which have an adapical pore, are similar to those figured but the additional pores shown near the orifices are not present. D’Orbigny figured a radial series of pores in the depression between zooid series, that were lateral to the adapical edge of the adjacent orifices. Avicularia occupy a similar position in the micrograph of the specimen but are far larger and twice as frequent. These avicularia are small and rounded with a delicate, simple bar. The orifices of fig. 15 are secondary and show a slightly raised peristomial rim; a few of those in the micrograph also show a sunken primary orifice with a rounded sinus. The specimen of *C. angustata* resembles some

of the more elongated colonies of *C. diffusa*. These differ in their proportionally larger avicularia and the presence of numerous lunate root pores, that are absent from *C. angustata*. Waters (1905: 9, pl. 1 fig. 7) examined the type material of *C. angustata* and gave a figure of the specimen from Basilan. This does not show the entire colony but only a formalised representation of four oval orifices and a single antapical avicularium. Later, Waters (1919: 93) indicated *C. angustata* as type species of *Conescharellina*, without comment. He also (1921: 419, pl. 30 fig. 18) figured but did not describe a specimen “from China, sent to me thus named by Jullien” as *C. angustata*. This colony was also conical and very elongated, with raised “costules” of radial rows of oval secondary orifices separated by adapically placed pores. One elongated sinuate, perhaps primary, orifice was figured, and small scattered pores among the orifices may have represented avicularia. Unlike the type specimen, the adapical region was occupied by extra-zooidal or kenozooidal calcification. The figure is otherwise similar to that of d’Orbigny’s *C. angustata*, with “costules” of secondary orifices that are more elongated and with “pores” less regularly spaced. Harmer (1957) was doubtful that the three *Siboga* collection specimens from East Java, that he nevertheless assigned to *C. angustata*, were identical with d’Orbigny’s species. These colonies were not elongated; the primary orifices were patent, with little or no peristome, and were relatively wide with a rounded sinus. These specimens do not appear to be conspecific with the type specimen. D’Orbigny (1852: 447) also introduced but did not figure *Conescharellina dilatata* from “Manille et détroit de Malacca” [sic]. It differed from *C. angustata* in its greater width (“ensemble plus large”) and in the presence of “un espace poreux” (presumably of cancelli) on the antapical surface. Waters (1905: 9, pl. 1 fig. 6) gave a semidiagrammatical figure of two zooid orifices from a specimen of *C. dilatata* from d’Orbigny’s collection from Manila. There were “two species in the tube” but he did not indicate which of these he regarded as *C. dilatata*. As before, only examination of the type material can elucidate fully the characters and relationships of this species. However, it is obvious that d’Orbigny’s *C. angustata* is closely similar to, and congeneric with, many of the other taxa subsequently referred to *Conescharellina* but description of its specific characters must await examination of the type specimen.

*Species recorded from Australia but not recognised in the material examined here*

*Conescharellina philippinensis* (Busk, 1854) and *C. cancellata* (Busk, 1854)

*Lunulites philippinensis* Busk, 1854 and *L. cancellata* Busk, 1854 were described and figured by Busk (1854: 101, pl. 113 figs 1–3 and 4–7 respectively) from the Philippines. They are obviously species of *Conescharellina* but the characters described and figured are not sufficiently clear to allow their recognition and identification with other material with any certainty. It has been possible to examine specimens from the “type suites” of *L. philippinensis* and *L. cancellata* but it must be emphasised that until all Busk’s specimen suites have been

revised, little may be concluded as to the nature and the identity of specimens later reported under these names. According to Waters (1921: 419), Busk’s specimens in the British Museum collection confused both species and included at least two additional species. Harmer (1957: 742) did not, however, agree with all Waters’ conclusions. The “type” slide of *L. philippinensis* (BMNH 1854.11.15. 150) originally included five colonies. Two of these have been lost in the past; one was remounted as an additional slide and labelled in Kirkpatrick’s hand. This very worn, separated colony may be the original of Busk’s figure (1854: pl. 113 fig. 2). The other specimens do not appear to have been figured, although all three seem to be conspecific. The specimens are all worn and show little detail. Two are flat and are less than 2 mm in diameter. They include approximately five quincuncial generations of zooids and each whorl has nine to ten zooid orifices. The marginal peristomes are slightly prominent and tubular; the primary orifices cannot be seen. Small rounded pores, inferred to have been avicularia, are interspersed randomly among the zooid orifices and the antapical surface has a central cancellate area. In both the larger colonies, the centre of the adapical surface has two prominent rounded “bosses”, that are illustrated in Busk’s pl. 113, fig. 2. It is not possible to recognise this species, either among those described from the Philippines by Canu and Bassler (1929) or in the Australian material examined here. The “type” slide of *L. cancellata* (BMNH 1854.11.15.151) includes four specimens that are in a better state of preservation. The originals of Busk’s pl. 113, figs 4–7 are recognisable; an additional large, worn, unfigured colony, that does not seem to be conspecific, is present (Brown, 1958: 82). The figured colonies are distinctly domed; the largest, that is less than 2 mm in diameter, includes approximately seven quincuncial zooid generations and nine to ten zooids per whorl. The peristomes are only slightly raised and circular; the primary orifices are visible and are rounded with a short, wide, almost semicircular sinus. Traces of an adapical pore are present in a few zooids. Small oval avicularia, with a delicate, simple bar, occur somewhat irregularly among the zooid orifices. No root pores are visible; the antapical surface has a central cancellate area. This species was apparently not among the other Philippine forms described by Canu and Bassler (1929) and has certainly not been recognised among the Australian specimens examined here.

Waters’ (1921) account of *L. cancellata* is not at all clear. He remarked “specimens from Busk’s own collection so named are *C. angustata* d’Orb.” Harmer (1957: 742), when discussing *C. crassa*, seems to have mistaken Waters’ (1921) reference to *C. angustata*, as describing part of the type material of *L. cancellata*. A specimen in Busk’s collection from the Sea of Japan (BMNH 1899.7.1.1276 labelled *Lunularia cancellata*) is narrowly conical, with seven to eight radial series of orifices and five to six zooid whorls. Zig-zag series of small oval avicularia alternate with the orifice series; these also occur on the antapical surface. The colony somewhat resembles d’Orbigny’s *C. angustata* and may be the one mentioned by Waters. Waters (1921) also stated that the specimens he described “from New South Wales” (i.e. in 1887) “then called *cancellata* by me are seen to be *philippinensis*.” Both names have been used for

several Australian records; references to Recent material assigned to these species are discussed below under *C. diffusa* and *C. obscura*.

It is unfortunate that little of the previously described Tertiary material is extant. Various combinations and spellings of *C. cancellata* having been quoted, particularly for specimens from the Tertiary, by Waters (1881; 1882a; 1882b) and by MacGillivray (1895). Maplestone (1904) tabulated several additional fossil localities, including Campbells Point, Mitchell River and Lake Gnotuk, together with his own observations of material from Mornington. Unfortunately, Maplestone's specimens are not extant, and therefore his concept of fossil *B. cancellata* and *B. philippinensis* must remain unknown. He also listed *B. elegans* Waters (= *Bipora flabellaris*), from Jimmys Point, that has otherwise not been reported as a fossil, and therefore seems unlikely to be this species. MacGillivray (1895: 89, pl. 12 fig. 2) reported "*Bipora philippinensis*" from the Tertiary of Schnapper Point and Muddy Creek, Victoria. His specimen from Muddy Creek is extant (NMV P27728). It is a fairly flat colony, with quincuncial zooid orifices with a small sinus and scattered avicularia. The antapical surface has a large cancellated area. This specimen appears to be referable to the fossil species described here as *Conescharellina macgillivrayi* sp. nov. Waters (1881) mentioned Recent specimens of *B. cancellata* from Torres Strait but no fossil examples. However, he appears to have believed that he had specimens from the "Curdies Creek" locality, as he mentioned them (Waters, 1882a) in connection with the "better preserved" material he had from Bairnsdale, Victoria (Waters, 1882b: 512, pl. 22 figs 10, 11, as *Lunulites cancellatus*), that he figured showing the orifice and surrounding avicularia. These illustrations suggest that the species may also have been *Conescharellina macgillivrayi*. Whitelegge (1887: 341) listed *C. cancellata*, remarking that he had several fossil examples from Muddy Creek, Victoria, that might be identical with the species recorded by Waters (1882b) but that in *C. cancellata* and *C. philippinensis* "the identity can only be definitely settled by comparison with the types". *Bipora cancellata* was recorded by MacGillivray (1895: 89, pl. 12 fig. 1) from Bairnsdale; he noted that it was often difficult to distinguish it from *B. philippinensis*. His specimen (NMV P22727) is a conical colony with orifices arranged in radial series. The primary orifice has a fairly wide, rounded sinus and is flanked antapically by a pair of small, rounded avicularia. The antapical surface has very few cancelli. His specimen resembles others from Bairnsdale, and is discussed here under Maplestone's Recent colonies of *C. diffusa*. Colonies from the Miocene of Victoria and South Australia are numerous and diverse; four species, *C. ocellata*, *C. macgillivrayi*, *C. humerus* and *C. aff. diffusa* are described below.

The ovicells of *C. cancellata* were mentioned, in passing, by Levinsen (1909: 310, pl. 23 figs 8a, b), who illustrated small, globular ovicells with marginal pores and an oval zooid orifice with an adapical pore. Three small rounded avicularia surrounded the ovicelled zooid orifice. Levinsen did not give any details of the provenance of the specimens illustrated and the information given is insufficient for identification of the species.

### *Conescharellina angulopora* (Tenison Woods, 1880)

*Lunulites angulopora* Tenison Woods, 1880: 7, pl. 1 figs 3a–c.

?*Lunulites conica* Haswell, 1881: 42, pl. 3 figs 7, 8.

?*Conescharellina incisa* Hincks, 1881: 127 (sep. p. 68), pl. 4 figs 1–3.

?*Bipora angulopora*.—Whitelegge, 1887 (1888): 18.

not ?*Lunulites angulopora*.—MacGillivray, 1895: 46, pl. 8 fig. 1 (= *Selenariopsis macgillivrayi* Bock and Cook, 1996).

?*Conescharellina angulopora*.—Levinsen, 1909: 311, pl. 23 figs 7a–f.

not *Conescharellina angulopora*.—Gordon, 1985: 173, figs 20–23; Gordon, 1989: 81, pl. 48B (see *C. cognata*).

**Remarks.** Search for type material of Tenison Woods has been unsuccessful; consequently the characters of this species remain somewhat doubtful. The colony was figured as a distinct cone and the autozooids and avicularia occurred in apparent alternating radial series. However, the description of the orifice as "divided into two portions; one half triangular constricted in the middle; the other semicircular", taken together with the illustration, indicates that Tenison Woods had confused the avicularia with the secondary orifices. The illustration shows at least one triangular avicularium accompanied by a typical lunate root pore that he did not recognise as distinct structures. His later remark "the cells are obliquely placed; sometimes in contrary directions alternately", also appears to refer to avicularia, that have been described in other material assigned to this species as having alternating orientations. The description of "the vibracular pores" as "long and narrow, and in a depressed area" and the illustration, showing irregularly ovoid openings, apparently refers, in fact, to the secondary autozooid orifices. Waters (1887: 199), describing specimens he assigned to *C. incisa* (Hincks), remarked "This may be *Lunulites angulopora* T. Woods, but apparently the avicularia were mistaken for zoecial cells, and the zoecia for vibracula". Tenison Woods had only two specimens from Port Stephens, New South Wales, that he noted were "worn"; his type material has not been found. It seems unlikely that his species is recognisable. Livingstone (1924) regarded *C. conica* Haswell (1881), *Lunulites incisa* Hincks (1881, 1892), *Bipora biarmata*, and *B. magniarmata* Maplestone (1909), all as junior synonyms of *L. angulopora* Tenison Woods (1880). Both Livingstone (1928) and Hageman et al. (1996) reported *C. angulopora* from South Australia, and specimens labelled *Bipora angulopora* occur in Maplestone's collection from this area. These specimens belong to at least two other taxa (see *C. cognata* and *C. diffusa*) but specimens in Maplestone's collection (NMV), inferred to have been from New South Wales, are described below as *C. species* (*C. angulopora* sensu Maplestone not T. Woods). Haswell (1881) gave an illustration of his *C. conica* showing the orifices "upside down", so that the apparent antapical primary sinuses are in fact, adapical parts of the peristome. He did not label his types or conserve entire specimens (Livingstone, 1924). Hincks' (1881) type specimens of *L. incisa* are not available, so that the identity of these species and their possible synonyms remains in doubt, in spite of the superficial similarity of his figure of *L. incisa* with that of *C. conica* (see below).

*Conescharellina crassa* (Tenison Woods, 1880)

*Lunulites* (*Cupularia*) *crassa* Tenison Woods, 1880: 5, pl. 1 figs 1a–c.

*Bipora crassa*.—Whitelegge, 1887: 343 [reprinted 1888: 18].

*Conescharellina crassa*.—Livingstone, 1924: 212.—Livingstone, 1925: 301, pl. 46 figs 1–5, text-fig. 1.

**Description.** (modified in part from Livingstone's 1925 account). Colony a large, shallow cone, maximum diameter 10 mm, height 5 mm. Zooids arranged in quincunx. Primary orifice elongated, with a fairly narrow but rounded sinus; lateral peristomes raised, marginal peristomes prominent. Adapical pore ("special pore") large, on the edge of the peristome, forming a tube. Root pores rounded, not lunate. Avicularia small and rounded; with a bar and one ligula; one (possibly the "vibracular pore") placed adapically to the orifice; others minute, sometimes paired, antapical and lateral, or irregularly scattered among orifices, rounded. Antapical surface "spongy", (inferred to have consisted of cancelli), and "solid".

**Remarks.** Tenison Woods (1880) mentioned "about a dozen specimens" from Cape Three Points and Port Stephens, New South Wales. They were collected from depths of approximately 130–150 metres. Whitelegge (1887, 1888) examined these, the type specimens of *C. crassa*, that were then in the Macleay Museum, Sydney. He remarked on the raised lateral peristomes, the primary orifice, the subcircular avicularian mandibles and the large, antapically placed pore (inferred by Harmer (1957) to have been an avicularium) but did not mention the antapical surface or the form of root pore. Whitelegge (1887) noted that Tenison Woods' figure was "the first published figure which exhibits the form of the true operculum-bearing aperture". This was narrow and elongated, with a rounded sinus. Livingstone (1925) also examined the type specimens, and other colonies from New South Wales. He redescribed *C. crassa*, noting that some of the "vibracular pores" were "filament pores", i.e. root pores. These were rounded, not lunate. The raised lateral peristomes obscured the orifice, with its fairly elongated, narrow sinus. The adapical pore ("special pore") was figured on the edge of the peristome, forming a tube, very similar to the pore illustrated here in *C. multiarmata* (Fig. 2D). Livingstone (1925) was the first to suggest that "lunoecia" and "filament pores" had the same function.

Harmer (1957: 740, pl. 48 figs 1–6, text-figs 70, I, 73) described specimens from West Timor, the Arafura Sea and Holothuria Bank (north-west Australia) as *C. crassa*. The colonies resembled those reported from eastern Australia in size and shape, having a concave antapical surface lined by cancelli, and bordered by prominent zooids; they were, however, not solid antapically. The orifices had an elongated sinus but were arranged in quincunx, not in apparently radial series. Harmer noted that both the "vibracular pore" of Tenison Woods (1880) and the "filament pore" of Livingstone (1925) might have been avicularia. A small adapical pore ("proximal pore") was sometimes present in his material but the circular root pores were found scattered among the orifices, not directly associated with the peristomes. Three of Harmer's preparations have been examined (BMNH *Siboga* stn 59, West Timor, 390

m, 1964.3.2.8 part, and from Murray Island, Torres Strait, from Haddon, 1890.3.24.17). The latter was mentioned by Kirkpatrick (1890) who described the operculum as "broadly pyriform". They are large colonies, ranging from 10 to 12 mm in diameter but are all very worn. Only one primary orifice is clearly visible: it is wide, with a rounded sinus, unlike Tenison Woods' figure. Otherwise, Harmer's *C. crassa* resembles the original description but only examination of Tenison Woods' type material, and comparison with that seen by Haswell from Queensland, can decide if any of them are conspecific.

Livingstone (1925: fig. 1) described ovicells in the "smallest specimen" of a group of colonies of *C. crassa* from north-east of Port Jackson, at 137–146 m. These were "bean-shaped", wider than long, flattened frontally. They appear to have had an ectoocelial rim bordered by "a row of elongated pores". The figure of the ovicells depicts these pores as minute and certainly not elongated. Curiously, Livingstone (1925: 303) noted the absence of "special pores" in the smallest colony that bore the ovicells. His illustration (pl. 46 fig. 3) leaves no doubt that the adapical pore is depicted. As its presence is a necessary part of ovicell development, his observation requires explanation. The illustration of the ovicells in *C. crassa* given by Livingstone (1925: Fig. 1) is remarkably similar to that of the ovicells of "*Batopora pulchrior*" Gordon (1989: 81, pls 47F, G, 48A) from very deep water (914–3347 m) off New Zealand. The ovicells of *B. pulchrior* lack marginal pores. *B. pulchrior* is the type species of *Ptoboroa* Gordon and d'Hondt (1997), a genus that appears to have closer links with *Trochosodon* than with *Batopora* (see below).

Although specimens of *C. crassa* should be recognisable from the descriptions of authors mentioned above, no colony in the collections examined here appears to be assignable to this species. Two species described here with large, relatively flattened colonies are *C. cognata* and *C. obscura*.

*Conescharellina depressa* Haswell, 1881

*Conescharellina?* *depressa* Haswell, 1881: 41, pl. 3 fig. 4.

*Conescharellina depressa*.—Livingstone, 1924: 212.

**Description.** Colony forming a low cone, concave antapically, with prominent marginal zooids. Orifices with raised peristomes, arranged in apparent radial series, alternating with large avicularia with elongated, rounded, or semicircular mandibles. Lunate root pores occur among the avicularia. Antapical cancelli lining the concave surface (based on Livingstone, 1924).

**Remarks.** *C. depressa* was originally described from Port Denison, Queensland. Whitelegge (1887) mentioned "5 or 6 specimens" but these do not seem to have been part of the type material, although he mentioned no locality other than Haswell's. Livingstone (1924: 205) noted that Whitelegge had informed him that Haswell did not label his type specimens, and that he himself had seen only small fragments of each species. The orifice was described with a sinus "about half the diameter of the mouth; or ovate with a sub-triangular denticle on each side near the base". Harmer (1957: 743) regarded *C. depressa* it as "nearly allied" to his *C. crassa* but the wide

primary orifice and lunate root pores suggest that it may be distinct. Until type material can be examined, the characters of this species must remain uncertain; no colony resembling it has been found in the present material.

***Conescharellina conica* Haswell, 1881**

*Conescharellina conica* Haswell, 1881: 43, pl. 3 figs 7, 8.  
 ?*Lunulites incisa* Hincks, 1881: 68 (sep. p. 127), pl. 4 figs 1–3.

**Description.** Colony conical, distinctly higher than wide. Zooid orifices apparently in radial rows, peristome raised laterally. Primary orifice elongated, with a minute sinus. Avicularia large, in raised rows, mandibles acute, orientated laterodistally, in both directions; bar with well developed ligula.

**Remarks.** Haswell's material was from Holborn Island, Queensland, from 37 m, and Hincks' specimens were from Bass Strait (from less than 73 m) but their illustrations of the primary orifices and avicularia appear to be closely similar. Haswell's figure, however, does not illustrate the primary orifice, as the antapical side is uppermost. Hincks' figure has a reversed orientation and the apparent similarity in orifice shape is accidental. Hincks (1892: 331, sep. p. 194), however, regarded his species as synonymous with *C. conica* Whitelegge (1887). Livingstone (1924) placed both species in the synonymy of *Conescharellina angulopora*, see above. Without examination of type material, the relationships of these three nominal taxa remains uncertain.

**Descriptions of species present in the material examined**

***Conescharellina* sp.**

Figures 1A–D.

*Bipora angulopora*.—Maplestone 1909: 268 (not *Conescharellina angulopora* Tenison Woods).

**Specimens examined.** NMV F98977, F98978, F101878. 13 specimens, all somewhat worn, labelled "*Bipora angulopora*" are present in the Maplestone material, inferred to be from New South Wales.

**Description.** Colonies conical, slightly wider than high; zooid orifices in apparent radial series, elongated, with prominent condyles and a subtriangular sinus. Peristomes deep, worn, not raised, with an adapical pore present. Avicularia very elongated and narrow, usually occurring antapically and laterally, sometimes paired, usually alternating with zooid orifices, orientation lateral or random, bar with a ligula. Small lunate root pores adapical, with paired avicularia. Antapical surface solid, with rows of small avicularia but no cancelli.

Height of colony up to 2.1 mm, width 2.6 mm, number of whorls 9–10, number of zooids per whorl 10–12.

**Remarks.** Maplestone (1909: 268) listed "*Bipora angulopora*" from the "Miner" dredgings from New South Wales but did not describe his specimens. His labelled material agrees in part with Livingstone's (1924) description of some colonies of *C. angulopora*. These were conical and had elongated avicularia orientated in several directions. The colonies examined are very worn, have adapical lunate root pores; the avicularia have

a ligulate bar. Generally, the orientation of the avicularia is random but some colonies tend to have a pair of laterally directed avicularia, somewhat similar to those of *C. ecstasis* (compare Fig. 1B with 5B), from which they are distinguished by their orifice shape and the presence of a ligulate bar. The peristomes are worn but a few show an adapical pore on their outer edge. The antapical surface is smooth and thickly calcified, with no sign of cancelli but with radial series of minute avicularia. These colonies may be assigned to a general category of "*C. angulopora*" but, without examination of type material of that species, it is not possible to be certain of their identification, other than that they represent Maplestone's (1909) concept of the species. Three of the colonies have associated antapical solitary corals, one of which is figured (Fig. 1D).

Specimens from South Australia in the NMV Collection, identified and labelled as "*Bipora angulopora*" by Maplestone but never described, belong to two additional species, *C. cognata* and *C. diffusa* (see below).

***Conescharellina eburnea* (Maplestone, 1909)**

Figures 1E–H

*Bipora (Conescharellina?) eburnea* Maplestone, 1909: 270, pl. 72 figs 6a, b.

*Conescharellina eburnea*.—Livingstone, 1924: 212.

**Specimens examined.** BMNH 2000.2.23.3, New South Wales (2 colonies, part of material sent by Maplestone to the BMNH, labelled "cotypes"); NMV F101879, stn SLOPE-2 (3 colonies).

**Description.** Colonies discoid, wider than high; slightly raised centrally, marginal zooids prominent. Calcification finely mamillate. Orifices in quincunx, patent, wide, with a rounded sinus and distinct condyles. Peristome not raised, with a rounded adapical pore on its edge. Root pores round, with a circlet of 3–4 minute avicularia, tending to occur near the adapical region only. Other avicularia paired, small, rounded, closely distolateral to the adapical margin of the orifice, orientated distolaterally, with a minute ligula. At the proliferal margin, these avicularia appear on the antapical surface of the zooids and closely resemble the paired avicularia of *C. ocellata*, *C. perculata*, and *Trochosodon diommatus* (see also Figs 11B, 13C, 21B). There are only a few cancelli on the solid antapical surface but a regularly distributed series of small, rounded avicularia.

Colony diameter 4–5 mm, height 1 mm, number of whorls 8, number of zooids per whorl 10.

**Remarks.** Maplestone's specimens were from 22 miles east of Port Jackson, from 146 m; he did not give details of the number of colonies. There are few records of this species, all from New South Wales. The distinctive features are the patent orifices, that possess hardly any peristomial rim, the rounded sinus, and the paired, antapical peristomial avicularia. The circular root pores, each surrounded by small avicularia, resemble those of several other species of *Conescharellina* (see *C. plana* sp. nov., *C. ocellata* sp. nov.) and of *Crucesharellina australis* sp. nov.

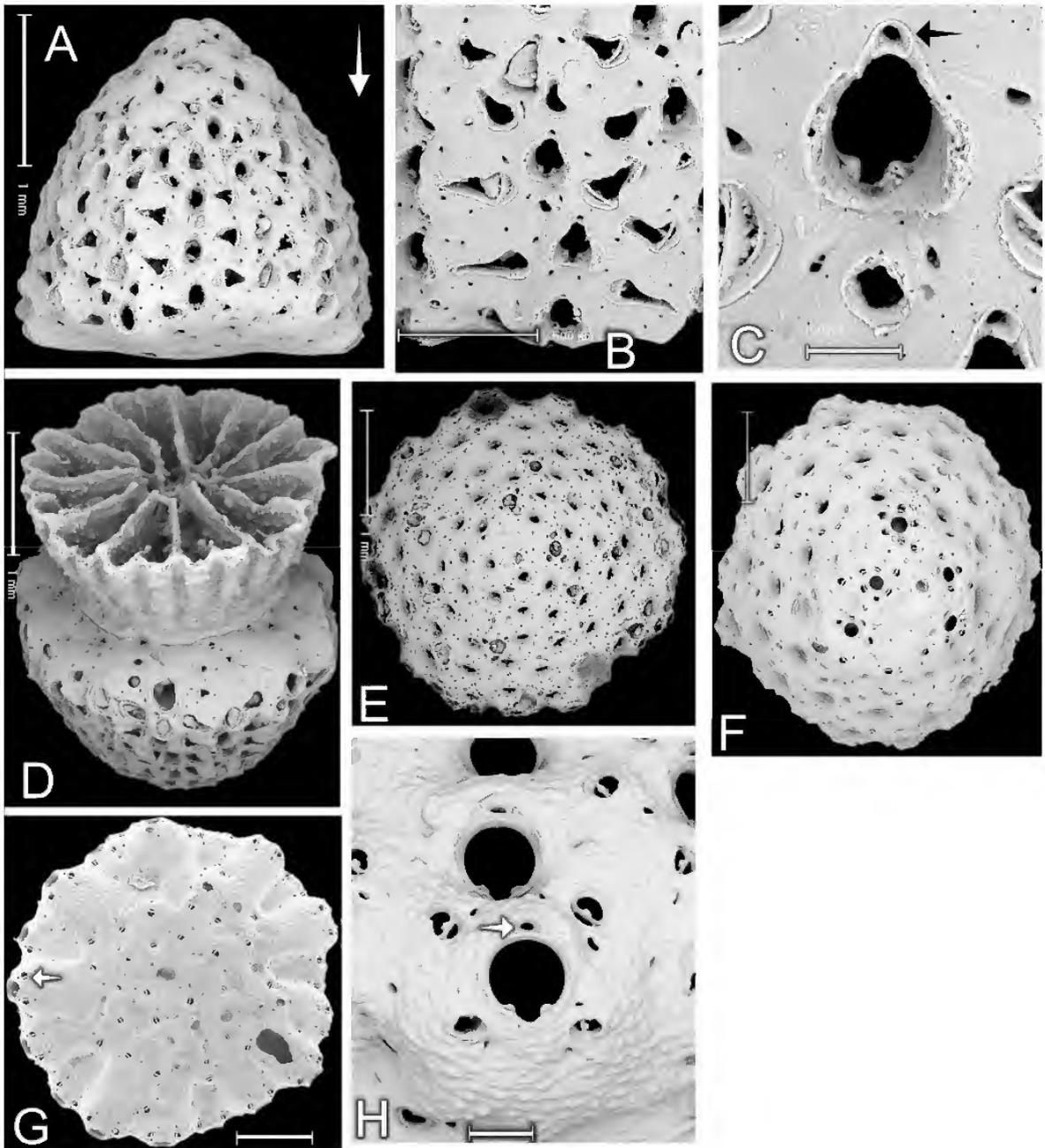


Figure 1. A–D, *Conescharellina* sp. A–C, NMV F98977, colony; direction of growth arrowed; scale=1 mm, B, detail of orifices and avicularia, scale = 500  $\mu$ m, C, detail of orifice with adapical pore (arrow), scale=100  $\mu$ m. D, NMV F98978, colony from antapical surface with commensal coral, scale = 1 mm. E–H, *Conescharellina eburnea* (Maplestone, 1909). E, BMNH 2000.2.3.33, adapical view of colony, scale=1 mm. F–H, NMV F98979. F, adapical view of colony showing root pores, scale = 500  $\mu$ m. G, antapical view of colony with small, central and paired marginal peristomial avicularia (arrow), scale=500  $\mu$ m. H, detail of orifices and avicularia, adapical pore arrowed, scale= 100 $\mu$ m.

*Conescharellina biarmata* (Maplestone, 1909).

Figures 2A, B

*Bipora biarmata* Maplestone, 1909: 268, pl. 75 figs 1a, b.  
*Conescharellina biarmata*.—Harmer, 1957: 729.

*Specimens examined.* BMNH 2000.2.23.2, (4 colonies, part of material sent by Maplestone to BMNH, labelled “cotypes”); NMV F98980, no locality (89 colonies, labelled by Maplestone, probably part of type material); NMV F101880, South Australia, (9 colonies, from Maplestone, with “S.A.” on box); NMV F101881, stn SLOPE-19 (2 colonies); NMV F101882, stn BSS-170 (1 colony); NMV F101883, no locality, slide labelled E3195, suspected material from “Endeavour” (New South Wales) but no other information (2 colonies).

*Description.* Colonies very small, conical, distinctly higher than wide. Calcification smooth. Orifices in radial series, patent, with little raised peristome, elongated oval, with a very small sinus formed by paired condyles. Frontal septular pores slit-like. Adapical pore placed just outside the edge of the peristome. Avicularia regularly paired, proximolateral to the orifical sinus, small, elongated, narrow, triangular, with a ligulate bar, orientated laterally and slightly antapically. Lunate root pores adapical, uncommon. Antapical surface with small avicularia in mature specimens, adapical surface solid with kenozooidal calcification and scattered avicularia.

Specimens 2.0–2.3 mm high, 1.4–1.6 mm wide, and comprise approximately 10–13 astogenetic generations arranged in radial rows. The number of zooids in each whorl, 6–8.

*Remarks.* Livingstone (1924) placed *C. biarmata* in the synonymy of *C. angulopora*. Maplestone’s material differs from Livingstone’s concept of this species in the consistently small colonies, and the characters of orifices and avicularian orientation. Harmer (1957) did not describe *C. biarmata* but treated it as a distinct species. Maplestone’s specimens are numerous and very consistent in characters that are shared by the specimens from stn SLOPE-19 and the slide E3195. Other specimens with elongated, triangular, paired avicularia from the SLOPE stations differ in several respects and are here described as *Conescharellina ecstasis* (see below).

*Conescharellina multiarmata* (Maplestone, 1909)

Figures 2C–F

*Bipora multiarmata* Maplestone, 1909: 268, pl. 75 figs 2a, b.  
*Conescharellina multiarmata*.—Livingstone, 1924: 212.  
 not *Trochosodon multiarmatus*.—Gordon, 1989: 83, pl. 49 D–F (= *Trochosodon gordonii* sp. nov., see below).

*Specimens examined.* BMNH 2000.2.23.4; (3 colonies, part of material sent by Maplestone to the BMNH, labelled “cotypes”); NMV F98981, probably NSW (31 small colonies from two boxes labelled by Maplestone, probably part of type material); NMV F101884, stn BSS-169 (1 colony); NMV F101885, stn BSS-170 (1 colony); NMV F98982, F98983, stn SLOPE-2 (20 colonies, 4 with roots, 2 with corals on antapical side); NMV F101886, stn SLOPE-7 (1 colony); NMV F101887 stn SLOPE-39 (2 colonies); NMV F101888, stn SLOPE-40 (47 colonies); NMV F101889, stn SLOPE-48 (1 colony); NMV F101890, stn GAB-030 (1 colony).

*Description.* Colony conical, higher than wide. Calcification smooth to finely mamillate. Orifices in radial series, small,

elongated, with a small sinus flanked by distinct condyles, and a raised lateral peristome. Adapical pore obviously tubular, opening on the inside of the peristome edge. Avicularia very small, rounded, 4 placed laterally and 1 proximolaterally near the orifice sinus; bar with a minute ligula. Frontal pores minute, forming a pattern among the orifices. Antapical surface solid with pores and small avicularia at maturity; marginal peristome with small paired avicularia. Lunate root pores in radial series with the zooid orifices, present towards the adapical region of the colony.

Colonies 1.9–2.2 mm in height and 1.8–2.2 mms wide. They comprise approximately 4–12 or more astogenetic generations, arranged radially, and include 8–10 zooids per whorl. The numerous colonies from the SLOPE stations are wider than those from Maplestone’s collection, inferred to be from New South Wales. Mature colonies may show a small central area of cancelli on the antapical surface.

*Remarks.* *C. multiarmata* differs from *C. biarmata*, that also has very small colonies, in the details of the primary orifice and character and distribution of the minute avicularia. These alternate with minute frontal pores and have a rounded rostrum; the bar has a single small ligula. Paired avicularia are visible on the antapical surface of marginal zooids but are not as prominent as those of *C. eburnea*. In some zooids, the adapical pore is prominent and a tubular extension of its calcification can be seen to descend into the peristome, like that of *Trochosodon asymmetricus* (Fig. 2D). The colonies from the SLOPE stations are generally larger than those from the Maplestone collection. A colony from stn SLOPE-2 has an incorporated antapical solitary coral present (Fig. 2F).

Gordon (1989) identified specimens from New Zealand as Maplestone’s species and assigned them all to *Trochosodon*. The New Zealand material appears to be referable to *Trochosodon* but certainly not to *Conescharellina multiarmata*: it is here renamed *Trochosodon gordonii* sp. nov.

*Conescharellina magniarmata* (Maplestone, 1909)

Figures 3A, B

*Bipora magniarmata* Maplestone, 1909: 269, pl. 75 figs 3a, b.  
*Conescharellina magniarmata*.—Harmer, 1957: 729.

*Specimens examined.* BMNH 2000.2.23.5 (2 colonies, part of material sent by Maplestone to the BMNH, labelled “cotypes”); NMV F98984 (12 colonies, labelled in Maplestone’s hand, inferred to be from NSW); NMV F101891, South Australia (1 colony, Maplestone’s specimens, no other information); NMV F101892, stn BSS-167 (4 colonies with roots and antapical corals); NMV F101893, stn BSS-170 (2 colonies with antapical corals); NMV F101894, stn BSS-171 (1 colony); NMV F101895, stn GAB-015 (1 colony); NMV F101896, stn GAB-020 (1 colony); NMV F101897, stn GAB-056 (1 colony).

*Description.* Colony conical, becoming large, broader than previous species, with adapical extrazooidal, kenozooidal and avicularian growth forming a prominent “lump” quite early in astogeny. Orifices in 6–8 radial series, slightly elongate, with an extended sinus; secondary orifices with laterally raised peristomes, forming “costules”. Adapical pore outside the peristome. Avicularia very large, originating beside the orifice,

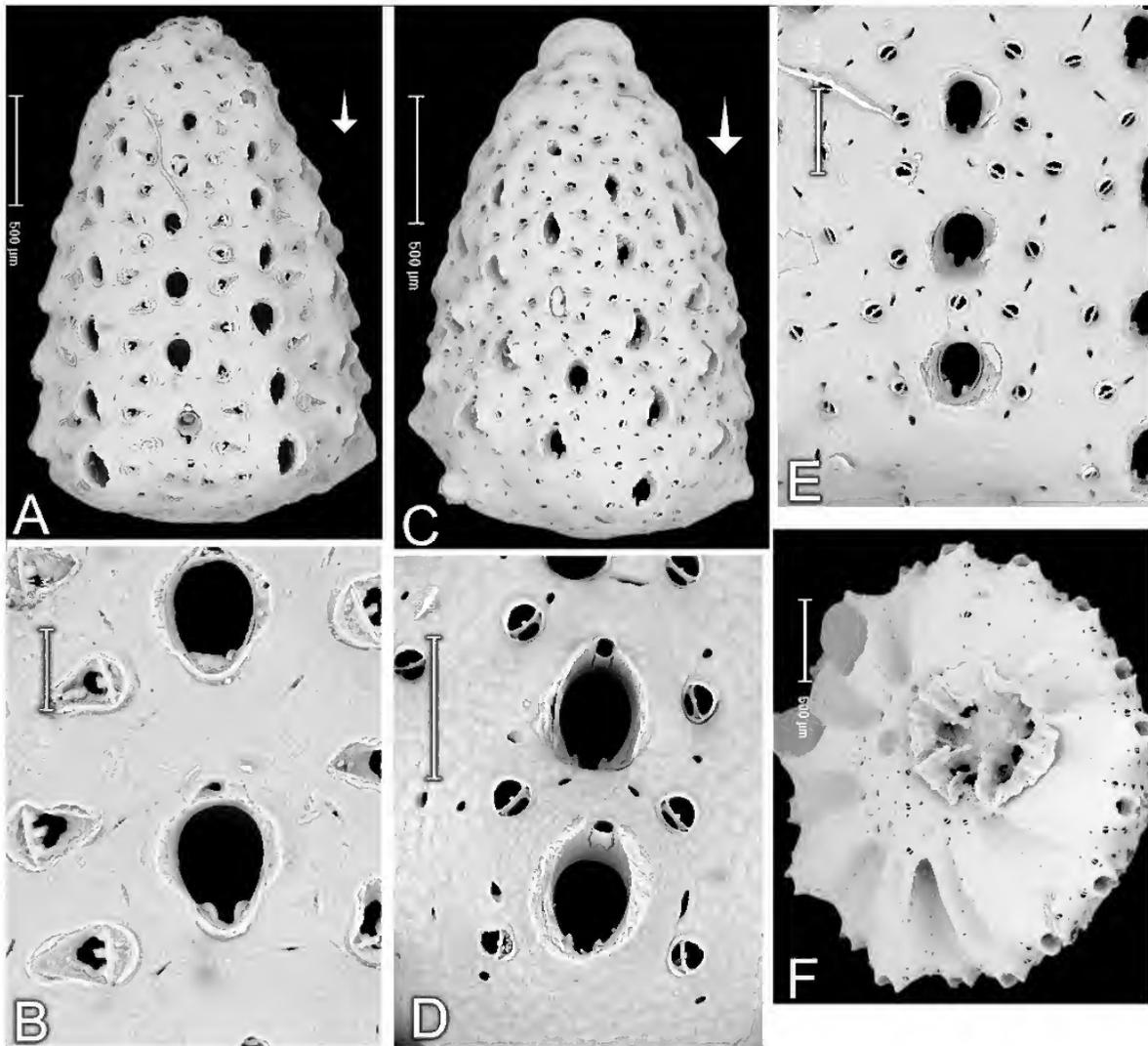


Figure 2. A–B, *Conescharellina biamata* (Maplestone, 1909). NMV F98980. A, lateral view of colony, growth direction arrowed, scale=1 mm. B, detail of orifices with adapical pore, avicularia and slit-like frontal septular pores, scale= 100 µm. C–D, *Conescharellina multiarmata* Maplestone, NMV F98981. C, Lateral view of colony, growth direction arrowed, scale=500 µm, D, detail of orifices from slightly antapical view, showing tubular adapical pores, avicularia and minute frontal septular pores, scale = 200 µm. E–F, *Conescharellina multiarmata* (Maplestone, 1909). E, NMV F98983, orifices and avicularia; note pattern of septular pores, scale= 200 µm. F, NMV F98982, Antapical view of colony showing small solitary coral. Note paired, marginal peristomial avicularia, scale= 500 µm.

acute, orientated distolaterally, with a wide, curved, palatal flange surrounding an opesia, and a bar with at least 3 large ligulae. Lunate root pores present, each with a pair of small lateral avicularia. Mature colonies with solid antapical extrazoidial calcification and avicularia.

Height of colonies 3.0 mm, diameter 3.0 mm, number of zooid whorls 8–9, number of zooids per whorl 8.

*Remarks.* Livingstone (1924) regarded *C. magniarmata* as a synonym of his "*C. angulopora*" but Harmer (1957) was

doubtful of the identity of the two forms. The avicularia certainly distinguish *C. magniarmata*. Few of the colonies assigned here to *C. cognata* show any intermediate characters, although the two forms are obviously very closely related. All the specimens from eastern Australia have elongated conical colonies but one from south-western Australia (stn GAB-015) is very small and domed. However, it has typical "*magniarmata*"-type avicularia, with a wide palatal flange and is therefore referred to this species.

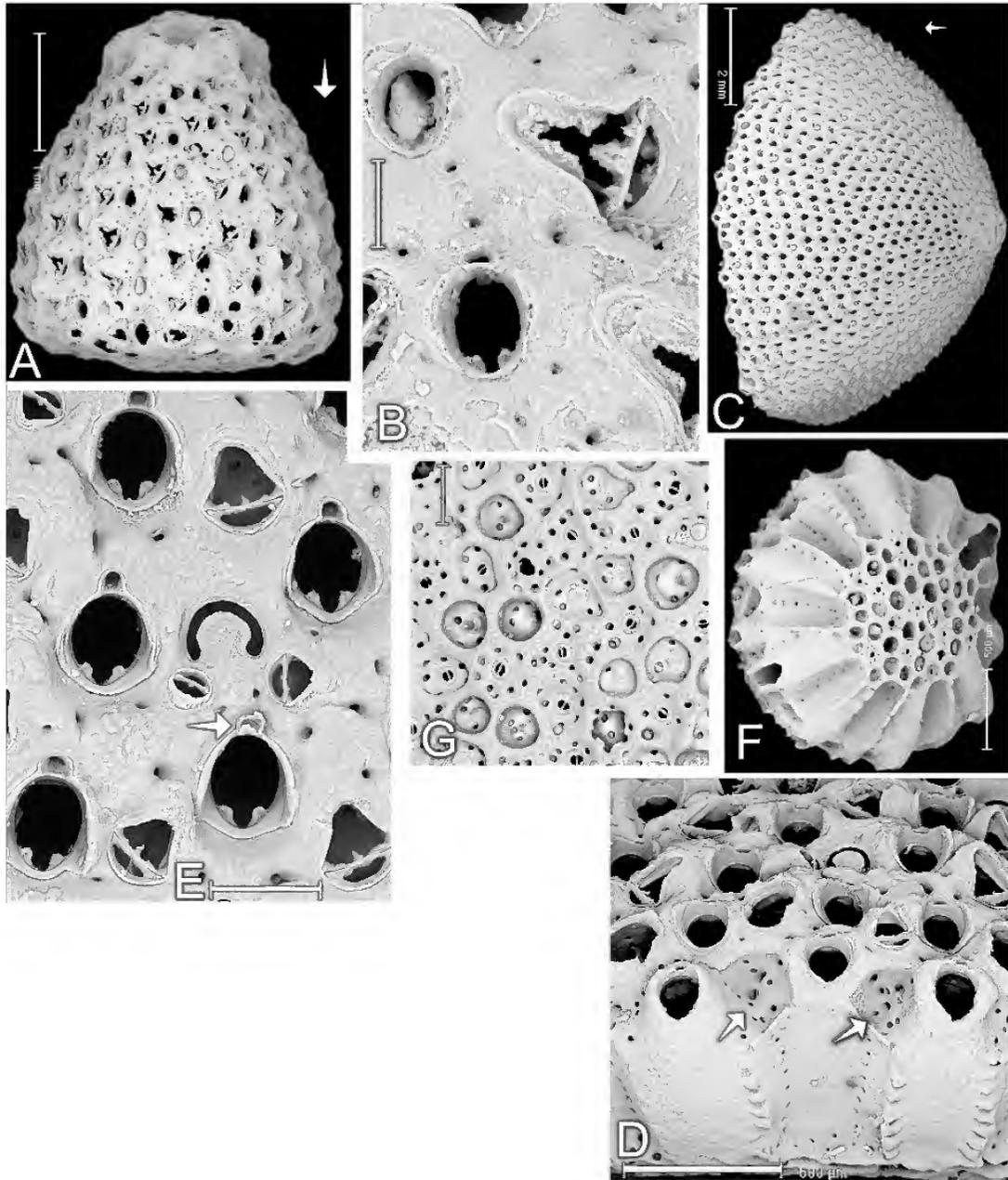


Fig. 3. A–B, *Magniarmata magniarmata* Maplestone, NMV F98984. A, Lateral view of colony, growth direction arrowed, note adapical secondary calcification, scale= 1 mm. B, detail of orifice with adapical pore and avicularium, scale= 100  $\mu$ m. C–G, *Conescharellina cognata* sp. nov. C–E, NMV F98985, holotype. C, lateral view of large colony, growth direction arrowed, scale = 2 mm. D, margin of proliferal region in antapical view, showing zooid orifices with adapical pores and “concealed” frontal shields with marginal septular pores. Chambers of alternating developing interzooidal avicularia arrowed, scale = 500  $\mu$ m. E, detail of orifices with adapical pores, one with entoocelial and ectoocelial laminae of developing ovicell (arrow); large, interzooidal avicularia and lunate root pore with small paired avicularia, scale = 200  $\mu$ m. F, NMV F98986, antapical view of small colony, showing central area of cancelli and alternating “concealed” zooids with marginal septular pores, scale = 500  $\mu$ m. G, NMV F98985, holotype, detail of antapical surface of large colony, showing alternating series of cancelli, minute avicularia and extensions of septular pores, scale = 200  $\mu$ m.

*Conescharellina cognata* sp. nov.

Figures 3C–G

*Holotype.* NMV F98985, Maplestone collection, Kangaroo Island, South Australia, labelled “*Bipora angulopora*”.

*Paratypes.* NMV F101898, locality as above (23 colonies).

*Other specimens.* NMV F101899, Maplestone collection, South Australia (no details) (23 colonies); NMV F101900, stn BSS-55 (1 colony); NMV F101901, stn BSS-65 (1 colony); NMV F101902, stn BSS-117 (4 colonies with roots); NMV F101903, stn BSS-127 (1 colony); NMV F101904, stn BSS-130 (4 colonies); NMV F101905, stn BSS-132 (1 colony); NMV F101906, stn BSS-138 (1 colony); NMV F98986, stn BSS-155 (34 colonies); NMV F101907, stn BSS-158 (12 colonies); NMV F101908, stn BSS-159 (12 colonies); NMV F101909, stn BSS-161 (11 colonies); NMV F101910, stn BSS-162 (3 colonies); NMV F101911, stn BSS-170 (2 colonies); NMV F101912, stn BSS-171 (8 colonies); NMV F101913, stn BSS-176 (6 colonies); NMV F101914, stn BSS-194 (3 colonies); NMV F101915, stn GAB-019 (1 colony); NMV F101916, stn GAB-020 (5 colonies); NMV F101917, stn GAB-030 (3 colonies); NMV F101918, stn GAB-045 (2 colonies, one with root); NMV F101919, stn GAB-049 (1 colony with root and antapical coral); NMV F101920, stn GAB-067 (1 colony); NMV F101921, stn GAB-098 (2 colonies); NMV F101922, stn GAB-101 (1 colony).

*Etymology.* *cognatus* (L.) – related, referring to the similarities of the species with some descriptions of “*C. angulopora*”.

*Diagnosis.* *Conescharellina* with large, often flattened colonies; antapical surface flat or hollow, with large cancelli. Zooid orifices with a narrow sinus and large condyles. Avicularia large, lateral, interzooidal, with subtriangular rostrum orientated adapically and laterally. Root pores frequent, lunate.

*Description.* Colonies very large, usually flattened, occasionally conical, particularly early in astogeny. Calcification smooth. Zooids in irregular quincuncial series, tending to appear radial in very large colonies. Primary orifice an elongated oval with a narrow sinus and prominent condyles, peristome raised laterally and antapically but only a little adapically; adapical pore just outside, or on edge of the peristome. Avicularia interzooidal, lateral and adapical, large, rostrum subtriangular, directed adapically and laterally (usually in the same direction); bar with 1–3 ligulae. Lunate root pores frequent among orifices, apparently replacing avicularia, each with a pair of small lateral avicularia with a ligulate bar. Antapical surface with large, central cancelli, or hollow, covered by series of cancelli and minute avicularia. Proliferal region growing edge with prominent frontal shields visible at all stages of growth.

Colony diameter up to 10 mm, height 3 mm, number of whorls (radial) 18, number of zooids per whorl, at least 10.

*Remarks.* *C. cognata* differs from the accepted character of Maplestone’s concept of *C. angulopora* (see above) that it resembles in several features: its colony shape and the variable but generally slightly wider primary orifice. There is a variation in orifice shape between colonies from Bass Strait, where they are very narrow, and those from Southern Australia. The large avicularia can be seen at the growing edge to be interzooidal (Fig. 3D) and are usually consistently orientated in one direction within a single colony, although they vary within samples.

The pair associated with each root pore is orientated laterally. Root pores are abundant, apparently replacing avicularia. In the larger colonies, the hollow antapical surface is completely covered by series of cancelli, interspersed with minute, rounded avicularia, totally unlike the solid surface of the conical colonies of *C. angulopora* (sensu Maplestone).

*C. cognata* is common among the samples from GAB and BSS stations and in the Maplestone collection from South Australia. Gordon (1985, 1989) described and figured specimens from the Kermadec region and from New Zealand, that he assigned to *C. angulopora*. The colonies were not conical but flat. The antapical surface had no avicularia and a small central cancellate area. Gordon used an identical description for both sets of specimens and figured developing ovicells in one of the colonies from the Kermadec region (1985: fig. 23). Although closely similar to the colonies from South Australia, these specimens differ in the more elongated shape of the primary orifices and the characters of the antapical surface.

*Conescharellina ecstasis* sp. nov.

Figures 4, 5A–D.

*Holotype.* NMV F98987, stn SLOPE-6.

*Paratypes.* NMV F101923, stn SLOPE-6 (45 colonies, many with roots and opercula and mandibles).

*Other specimens.* NMV F101924, stn SLOPE-2 (7 colonies, 4 with roots); NMV F98988, stn SLOPE-7 (10 colonies, 2 with roots); NMV

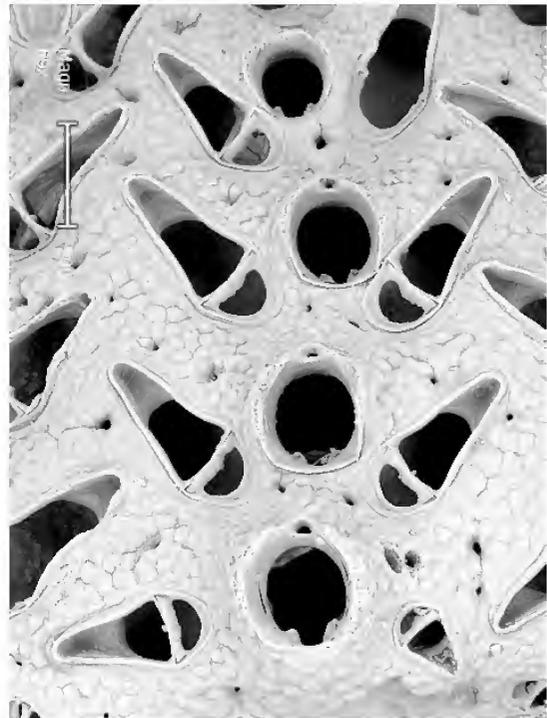


Figure 4. *Conescharellina ecstasis* sp. nov. NMV 98987, holotype. Radial series of zooid orifices with adapical pores and large avicularia, scale = 200µm.

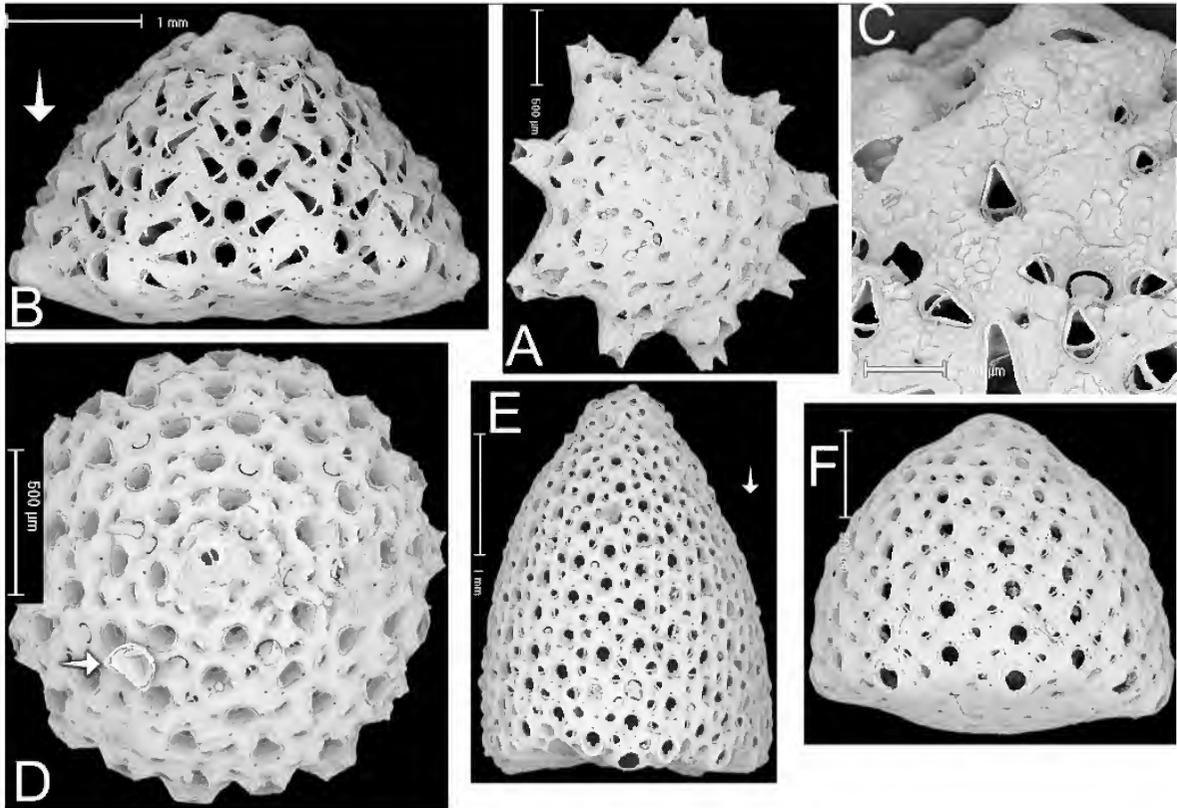


Figure 5. A–C, *Conescharellina ecstasis* sp. nov. A, NMV 98988. Adapical view, scale = 500 µm. B–C, NMV 98987, holotype. B, lateral view of colony, growth direction arrowed, scale = 1 mm. C, detail of adapical surface showing secondary calcification, avicularia and lunate root pore with three small avicularia, scale = 200 µm. D–F, *Conescharellina diffusa* sp. nov. D, NMV F98990. Adapical view of colony showing lunate root pores and broken ovicell (arrow), scale = 500 µm. E, NMV F98989, holotype. Lateral view of large colony, growth direction arrowed, scale = 1 mm. F, *Conescharellina* aff. *diffusa* sp. nov. NMV P311803, Bairnsdale, Victoria, Miocene. Lateral view of colony, scale = 500 µm.

F101925, stn SLOPE-39 (1 colony with root); NMV F101926, stn SLOPE-40 (2 colonies); NMV F101927, stn SLOPE-45 (1 colony); NMV F101928, stn SLOPE-48 (1 colony); NMV F101929, stn SLOPE-53 (3 colonies).

**Etymology.** *ecstasis* (L.) – joy, with reference to the appearance of the orifice and paired lateral avicularia.

**Diagnosis.** *Conescharellina* with large, conical colonies, solid antapically. Zooid orifices in radial series, primary orifice with a rounded sinus. Avicularia very large, paired, elongated, lateral to orifice, orientated laterally and adapically. Root pores lunate.

**Description.** Colonies large, conical, wider than high, domed and stellate in early astogeny. Calcification finely mamillate. Zooids in apparently radial series, peristomes prominent marginally, particularly in young, stellate colonies. Primary orifice with a distinct, rounded sinus and paired condyles, adapical pore on the edge of the peristome. Avicularia paired, lateral, very large, with acutely triangular rostra, nearly always directed laterally and adapically; bar without a ligula. Adapical region with large avicularia and lunate root pores, each with a

pair of small lateral avicularia. Antapical region solid, with radiating series of small avicularia and a few cancelli.

Colony diameter up to 4.7 mm, height 2.3 mm, number of whorls 6, number of zooids per whorl 8.

**Remarks.** The colonies of *C. ecstasis* sp. nov. are recognisable immediately, even to the naked eye, by the pairs of large avicularia, with mandibles of dark brown cuticle. The orientation of the rostra varies a little; those of the one specimen from stn SLOPE-45 being almost horizontal, like the rostra of *C. biarmata*. In contrast, one of the two colonies from stn SLOPE-7 has rostra directed almost adapically. Young colonies are stellate, with prominent peristomes, especially marginally, giving the colony a “*Trochosodon*-like” appearance (Fig. 5A). *C. ecstasis* differs completely from *C. biarmata* in colony shape and size, the characters of the primary orifice, and lack of avicularian ligulae. Except for stn SLOPE-6, only a few specimens of *C. ecstasis* were present at each of the eight SLOPE stations. The two colonies of *C. biarmata* sensu stricto from stn SLOPE-19 were easily distinguished by their much

smaller dimensions and orientation of avicularia. All records of *C. ecstasis* are from deep water. The SLOPE stations range from south-eastern New South Wales, to eastern Victoria and Tasmania. The bathymetric range of records is from 400 m to 1096 m.

*Conescharellina diffusa* sp. nov.

Figures 5D–F, 6A–B

*Holotype*. NMV F98989, South Australia (no other details), from box labelled “*Bipora philippinensis*” in Maplestone’s hand.

*Paratypes*. NMV F101930, South Australia, as above (3 colonies).

*Other specimens*. NMV F101931, South Australia, Maplestone Collection (55 colonies); NMV F101932, Kangaroo Island, South Australia, Maplestone Collection (1 colony); NMV F101933, probably NSW, Maplestone Collection (3 colonies); NMV F101934, stn BSS-065 (8 colonies, 5 with roots); NMV F101935, stn BSS-171 (1 colony); NMV F101936, stn SLOPE-49, (2 colonies); NMV F101937, stn GAB-020 (1 colony); NMV F101938, stn GAB-067 (1 colony); NMV F101939, stn GAB-069 (1 colony); NMV F101940, stn GAB-118 (3 colonies); NMV F101941, stn GAB-129 (2 colonies); NMV F98990, Dampier DA-2-37-01, North-western Australia (2 colonies, one with 8 ovicells, both with roots); NMV F101942, *Dmitri Mendeleev* collection, Tasmania (1 colony).

*C. aff. diffusa*: Specimens from the Tertiary of Victoria with very similar but not identical characters: Bairnsdale, NMV P311803 (Fig. 5F), P311804, plus 20 additional colonies; Muddy Creek (three colonies).

*Etymology*. *diffusus* (L.) – extended, dispersed, with reference to the wide distribution of this species.

*Diagnosis*. *Conescharellina* with large, often elongated, conical colonies, zooid orifices radial, surrounded by a rim of peristome. Root pores frequent, lunate, without avicularia. Avicularia in series alternating with orifices, small, rounded to subtriangular, bar without a ligula; non-palatal area with spinous processes. Ovicells fragile, with a wide ectoocelial rim, with a wide ectoocelial rim.

*Description*. Colony often large, conical, very narrow or domed, higher than wide. Zooid orifices apparently radial, alternating with radial series of rounded avicularia. Calcification smooth. Primary orifice with a fairly deep, rounded sinus and paired condyles, surrounded by a peristome rim; adapical pore outside peristome. Ovicells fragile, with a wide ectoocelial rim and a semitransparent entoocelial frontal area. Avicularia paired, lateral and slightly adapical, or in series alternating with orifices. Orientation lateral and adapical; rostrum rounded to subtriangular, bar without ligula, but with 3 or more very fine, spinous processes on the non-palatal side. Antapical surface solid, with a small, central cancellate area. Lunate pores frequent, occurring in series with the avicularia but without any accompanying small avicularia.

Recent colonies with up to 28 zooid whorls and more than 14 zooids per whorl, height up to 5.0 mm, diameter 3.5 mm. Fossil colonies rounded, height 2.5 mm, diameter 3 mm.

*Remarks*. The Recent colonies are among the largest and most widely distributed of the Australian species examined. The avicularia appear to be unique in possessing small calcareous spine-like structures on the non-palatal side of the bar. Some

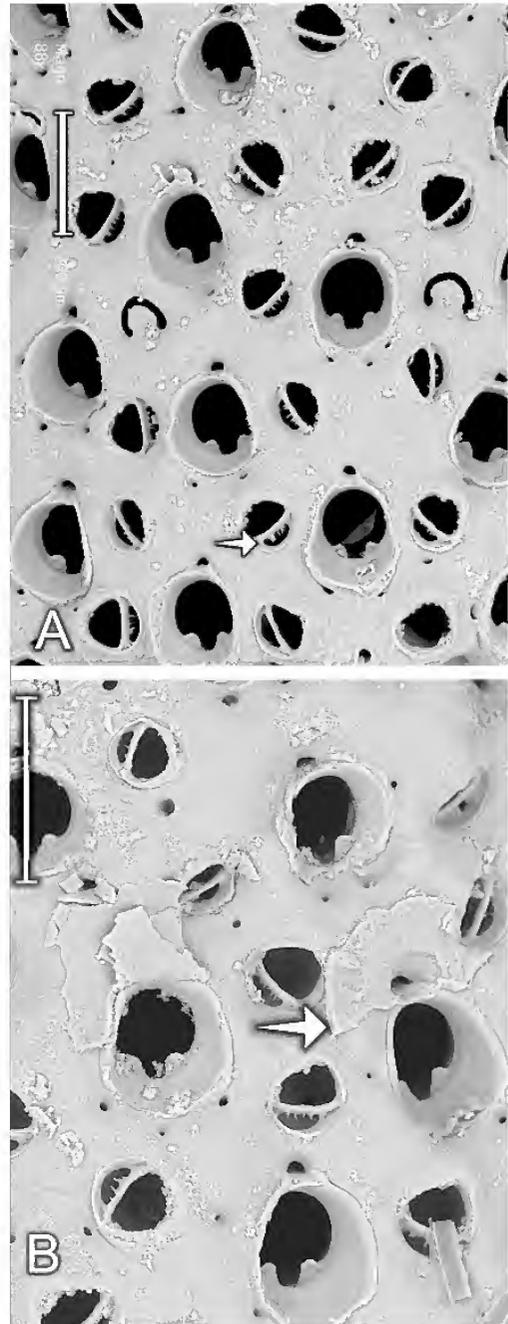


Figure 6. *Conescharellina diffusa* sp. nov. NMV F98989, holotype. A, detail of zooid orifices with adapical pores, lunate root pores and avicularia with non-palatal spinules (arrow), scale = 200 µm. B, detail of orifices with adapical pores; orifice at left shows broken laminae of ectoocium and overlying entoocium of developing ovicell; orifice at right shows adapical pore surrounded by ectoocelial lamina of ovicell (arrow). Note non-palatal spinules of avicularia, scale = 200 µm.

zooids show evidence of the development of an ectooecial lamina surrounding the adapical pore; others appear to have also developed an entoecial layer above the pore (Fig. 6B). Usually, colonies are distinctly higher than wide but five of eight from Bass Strait (stn 64) are shorter and more rounded in outline. All five have long roots, in one case, anchored terminally to a fragment of a "scrupocellariid" bryozoan. The two colonies from north-western Australia are also conical but somewhat rounded; their avicularia show non-palatal spinous processes. One colony has eight fragile and only partially complete ovicells (Fig. 5D), showing that these have a very thinly calcified entoecium and a wider ectooecium than those of *Trochosodon fecundus* sp. nov. and *C. stellata* sp. nov.

Records of *C. diffusa* are widely separated. It ranges from north-west Australia to New South Wales, the west and central Australian Bight, South Australia, Bass Strait, and Tasmania, from 15 m. (north-west Australia) to 200 m. (Tasmania).

The fossil colonies are much smaller and domed; their avicularia do not possess any non-palatal projections and it appears probable that, although closely related, they are not referable to *C. diffusa* sensu stricto (Fig. 5F). The specimen of "*Bipora cancellata*" from Bairnsdale described by MacGillivray (1895: 89, pl. 12 fig. 1; NMV P22727) appears to be conspecific with those listed here from Bairnsdale and Muddy Creek.

***Conescharellina obscura* sp. nov.**

Figures 7, 8A–C

*Bipora philippinensis*.—Maplestone, 1910: 6, pl. 1 figs 2, 2a (not Busk, 1854).

*Holotype* NMV F98991, stn BSS-155.

*Paratype* NMV F98992, stn BSS-155.

*Other specimens*. BMNH as *C. philippinensis*, 1909.11.12.12 and 13, Green Point, Port Jackson, NSW (Maplestone Collection, possibly from Whitelegge's material, 2 colonies with ovicells); BMNH 1899.5.1.1148, Port Jackson (Hincks Collection, 5 colonies); BMNH,

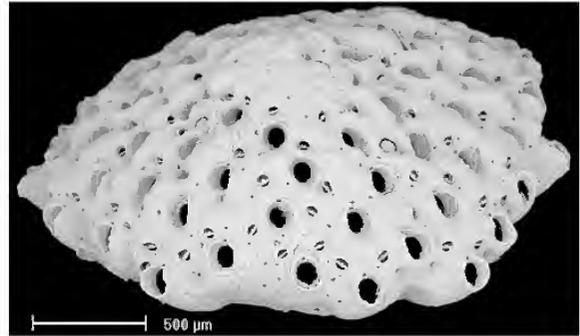


Figure 7. *Conescharellina obscura* sp. nov. A, NMV F98991, holotype. Lateral and adapical view of large colony, scale= 500  $\mu$ m.

as *L. cancellatus*, 1934.10.20.88, Port Stephens, NSW (Vine Collection, 2 colonies); NMV F101943, stn GAB-048; (1 colony with ovicells); NMV F101944, stn GAB-074; (3 colonies); NMV F101945, stn GAB-108 (1 colony); NMV F101946, stn GAB-113 (2 colonies); NMV F101947, stn GAB-118 (2 colonies); NMV F101948, stn GAB-131 (1 colony); NMV F101949, Dampier DA-2-09-02 (1 colony with root); NMV F101950, Dampier DA-2-73-01 (2 colonies with roots).

*Etymology*. *obscura* (L.) – hidden, referring to the confusion of records with those of *C. cognata*, *C. stellata* and *C. philippinensis*.

*Diagnosis*. *Conescharellina* with flat, often large colonies. Zooid orifices oval with a short sinus, peristomes not prominent. Avicularia rounded, lateral and antapical, near the orifice, bar with 1–3 ligulae. Root pores lunate. Ovicells globular, very fragile, with an extensive area of entoecium frontally.

*Description*. Colony fairly flat, even lenticular, distinctly wider than high. Zooid orifices quincuncial, sunken in surrounding peristome, that is not prominent. Orifice oval, with a short,

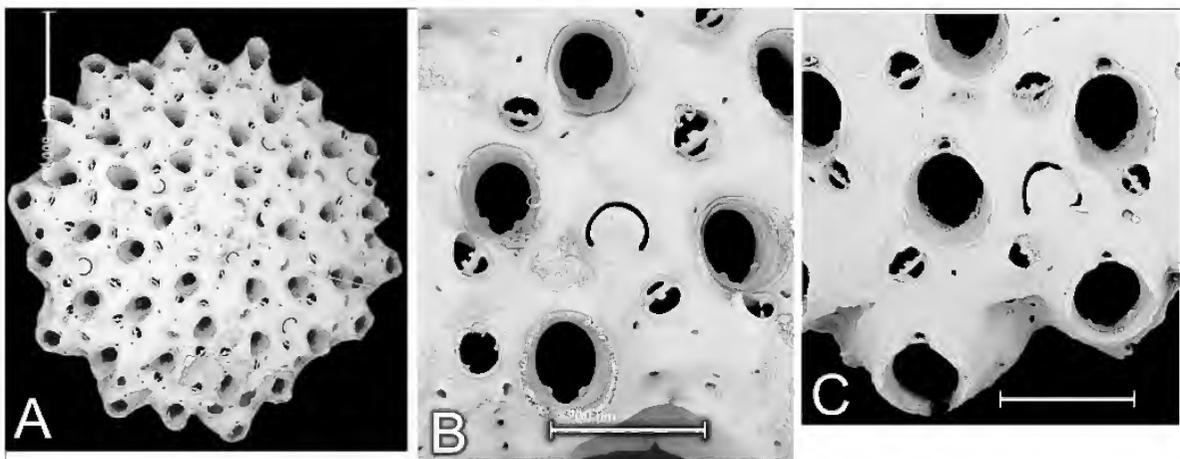


Figure 8. *Conescharellina obscura* sp. nov. A–B, NMV P98992. A, adapical view of small colony, showing lunate root pores, scale = 500  $\mu$ m. B, detail of zooid orifices, avicularia, and one lunate root pore, scale = 200  $\mu$ m. C, BMNH 1899.5.1.1148, Hincks Collection, Port Jackson, New South Wales. Detail of zooid orifices with adapical pores, avicularia and one lunate root pore. Note the wide orifice sinuses, scale = 200  $\mu$ m.

rounded sinus and small condyles. Adapical pore within peristome calcification. Avicularia rounded, lateral and antapical near the orifice, bar with 1–3 ligulae. Lunate root pores frequent adapically, with 1, occasionally 2, lateral avicularia. Antapical surface covered with small cancelli.

Colonies up to 14 mm in diameter but usually much smaller, maximum number of zooid whorls estimated as 15, and zooids per whorl 20.

*Remarks.* The close but superficial similarity in colony form means that records of this species were originally confused with those of *C. cognata*, that also has large, flat colonies with numerous antapical cancelli. The colonies from the GAB stations are very large, ranging from 9 to 12 mm in diameter and are hollow antapically; those from stns GAB-074 and GAB-118 are more domed and nearly solid antapically. In the smaller colonies from stn BSS-155, the lunate root pores are present but they are very rare or absent from the large colonies. Again, this is in contrast to *C. cognata*, where they are common throughout colony growth. Although the large, flat colonies resemble those described in “*C. crassa*” by Tenison Woods (1880), they differ in orifice shape and the types of avicularia and root pores present. Antapical oral avicularia are also found only in *C. pustulosa*, from which *C. obscura* differs in colony shape and size, orifice shape and form of the antapical cancelli. Whitelegge (1887) described specimens from Port Jackson as *Bipora philippinensis*, with a depressed conical shape and orifices with a wide sinus. Avicularia with subcircular mandibles occurred in pairs and sometimes on the antapical side of each orifice. The antapical surface had cancelli and avicularia. Ovicells were present and were “globose and smooth, with a faint fimbriated stigma in front.”

Colonies referred to this species were observed alive by Whitelegge (1887: 347) for three days. He noted pairs of “tubular filaments” attached to annelid tubes and to fragments of shell. He thought that these roots originated from avicularia and did not recognise the function of the lunate root pore that he also reported. Maplestone (1910: 6, pl. 1, fig. 2) illustrated ovicells in specimens of Whitelegge’s material that he also referred to *C. philippinensis* but noted that he could see no frontal stigma. Maplestone’s specimens from Port Jackson, in the BMNH collection, are probably part of Whitelegge’s material and are here referred to *C. obscura* sp. nov., whereas those in the NMV collection from South Australia, also labelled *Bipora philippinensis*, are here assigned to another new species, *C. diffusa*. The two slides from Green Point (1909.11.12.12 and 13) each contain a single, fairly flat colony, less than 2.5 mm in diameter, with most of the opercula and mandibles intact. They each include two fragile ovicells and up to eight partially developed ovicells. These are globular, like those figured by Maplestone (1910). They appear to have an extensive area of frontal ectoecial calcification and a series of minute pores close to the ovicell base, that may mark the limit of the ectoecium. There is no sign of any striations or a “stigma”. The other, smaller specimens from the BMNH collections are obviously conspecific but have no ovicells. They too, have most of the opercula and mandibles present; only one

preparation shows the primary orifice clearly. One of the five specimens from Port Jackson (Fig. 8C, Hincks collection, BMNH 1899.5.1.1148) is similar in characters to specimens from Bass Strait (Fig. 8B, stn BSS-155) except for the greater width of the orifice sinus. *C. obscura* occurs from north-west Australia and across the Great Australian Bight to New South Wales, from a depth range of 12 to 125 metres.

### *Conescharellina stellata* sp. nov.

Figures 9A–I

*Holotype.* NMV F98993, stn GAB-019.

*Paratypes.* NMV F98994, stn GAB-019 (8 colonies).

*Other specimens.* NMV F98995, stn GAB-128 (1 colony).

*Etymology.* *stellata* (L.) – starry, referring to the appearance of the colonies from the adapical side.

*Diagnosis.* *Conescharellina* with small, domed colonies. Orifices with rounded sinus and distinct condyles, surrounded by a raised peristome laterally and sometimes antapically. Avicularia lateral, rounded; bar without a ligula, non-palatal area sometimes filled by a lamina. Ovicells fragile, with a depressed, marginally striated ectoecium.

*Description.* Colony small, domed, wider than high; zooid orifices quincuncial. Calcification smooth and slightly tuberculate, adapical region sometimes with small, secondarily thickened mamillae. Peristomes raised laterally, forming a prominent, stellate pattern, especially at the colony margin; sometimes extended adapically and very prominent. Primary orifices rounded with a fairly wide sinus and small to distinct condyles. Adapical pore large, on the edge or outer face of the peristome, surrounded by a rim of calcification, sometimes slightly asymmetrically placed. Avicularia rounded, lateral and paired, widely separated from the peristomes; bar without a ligula, non-palatal side sometimes with a thin lamina, occasionally pierced by a pore. Lunate root pores tending to occur adapically, each with a pair of closely apposed, rounded lateral avicularia. Ovicells present on subperipheral zooids, very fragile, with a raised, smooth, transparent ectoecium and a depressed ectoecium, striated marginally, forming pores at the ectoecial junction. Antapical surface with a small central cancellate area.

Colony diameter 1–1.5 mm, height 1 mm, number of alternating whorls 6, number of zooids per whorl 6–8.

*Remarks.* The colonies have a very regular, stellate appearance from the adapical side. The peristomes are usually well developed laterally but, in one colony (from stn GAB-128), they are also extensive antapically, forming a funnel. The ovicells are extremely fragile and were detached soon after initial scanning electron microscopy. The lower face of the ectoecium shows that it was almost certainly covered by cuticle and apposed but not attached to the surface of the zooid adapically (Figs 9H, I). Although closely similar to the smaller colonies of *C. obscura* in several features, *C. stellata* differs in the form and distribution of the avicularia, that do not include a solitary one on the antapical side of the peristome. The avicularia also differ in the lack of ligulae and the presence of a lamina filling the non-

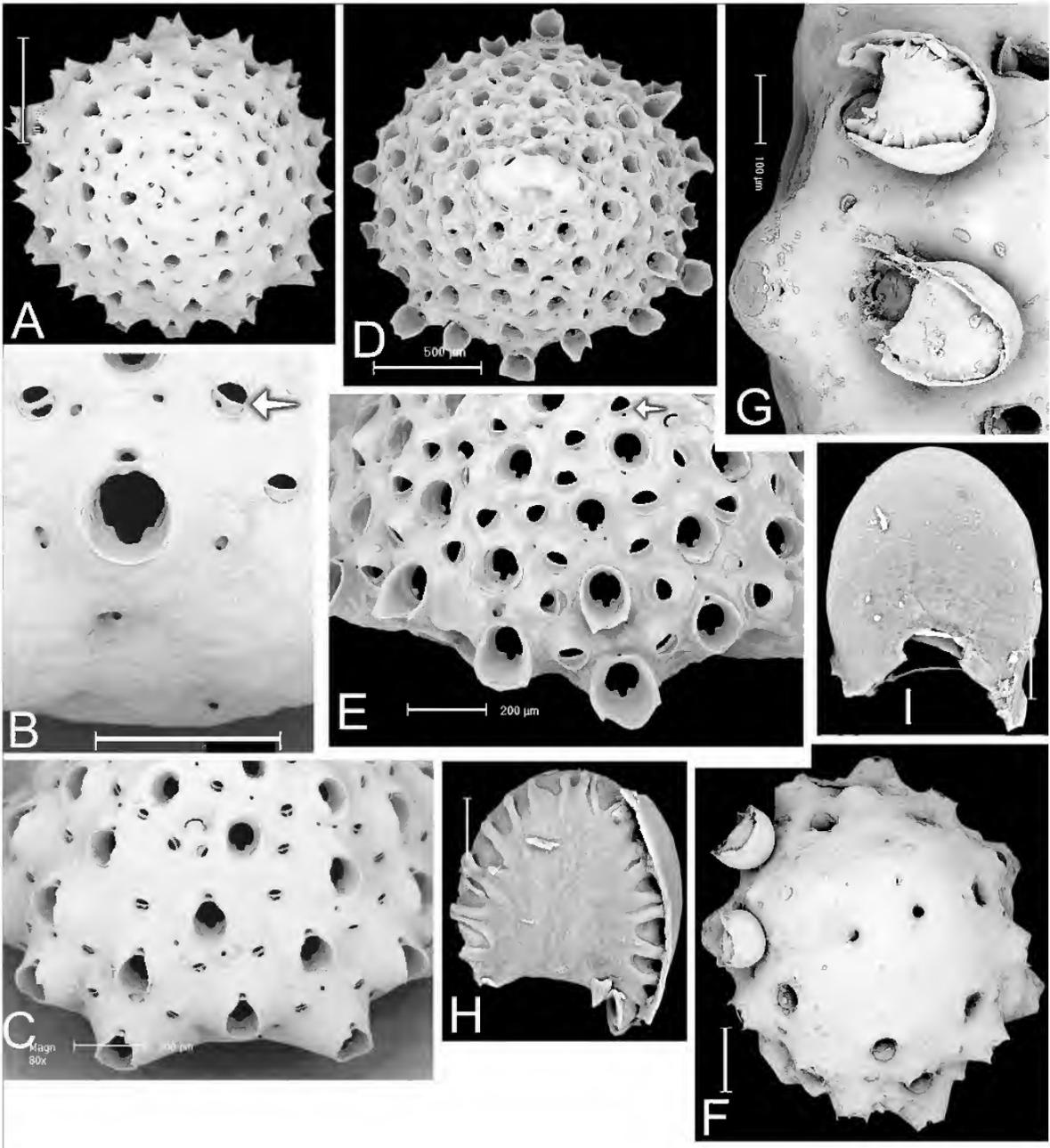


Figure 9. *Conescharellina stellata* sp. nov. A–C NMV F98993, holotype. A, adapical view of colony showing prominent bilabiate marginal peristomes and lunate root pores, scale = 500  $\mu$ m. B, detail of marginal zooid orifice with adapical pore. Avicularium with porous non-palatal lamina (arrow), compare Figure 9E, scale = 200  $\mu$ m. C, lateral view of colony showing lunate root pore, avicularia, scale = 200  $\mu$ m. D–E, NMV F98995. D, adapical view of colony with prominent, rounded, funnel-shaped marginal peristomes, scale = 500  $\mu$ m. E, marginal view showing extended peristomes, orifices and avicularia with non-palatal laminae, one with pore (arrow), compare Figure 9B, scale = 200  $\mu$ m. F–I, NMV P98994. F, Colony with cuticle in situ and two ovicells near margin, scale = 100  $\mu$ m. G, detail of ovicells, scale = 100  $\mu$ m. H, I, frontal and basal surfaces of detached ovicell. H, showing ridges in margin of entoecium, forming pores at junction with ectoecium, with basal smooth ectoecium. I, with fracture at original margin of adapical pore, scales = 50  $\mu$ m.

palatal area. This is not always developed in the specimens from stn GAB-019 but is constantly present in the distinctly larger, more prominent avicularia of the colony from stn GAB-128. The lamina may be pierced by a pore in both populations. *C. stellata* has been found from the western end of the Great Australian Bight at a depth of 59 m and from the central region at a depth of 304 m. Although these two populations show differences in detail, the number of colonies does not allow any estimate of its significance.

*Conescharellina plana* sp. nov.

Figures 10A–D

*Holotype.* NMV F98996, stn SLOPE-2.

*Paratypes.* NMV F98997, stn SLOPE-2 (26 colonies).

*Other specimens.* NMV F101951, stn BSS-167 (4 colonies, 1

with root and ovicells); NMV F101952, stn BSS-169; 3 colonies, 1 with root); NMV F101953, stn SLOPE-6 (5 colonies); NMV F101954, stn SLOPE-7 (1 colony); NMV F101955, stn SLOPE-40 (57 colonies, 2 with roots); NMV F101956, stn SLOPE-56 (13 colonies); NMV F101957, stn GAB-020 (6 colonies); NMV F101958, stn GAB-030 (2 colonies, 1 with root); NMV F101959, stn GAB-044 (1 colony with root); NMV F101960, stn GAB-049 (1 colony).

*Etymology.* *plana* (L.) – smooth, with reference to the lack of raised peristomes above the colony surface.

*Diagnosis.* *Conescharellina* with large, slightly flattened colonies, solid antapically. Zooid orifices in radial rows, deeply sunken within a circular peristome, that is not raised above the colony surface. Avicularia paired, small, with a minute ligula. Root pores numerous, circular, surrounded by avicularia. Ovicells fragile with a fairly wide ectoecial rim.

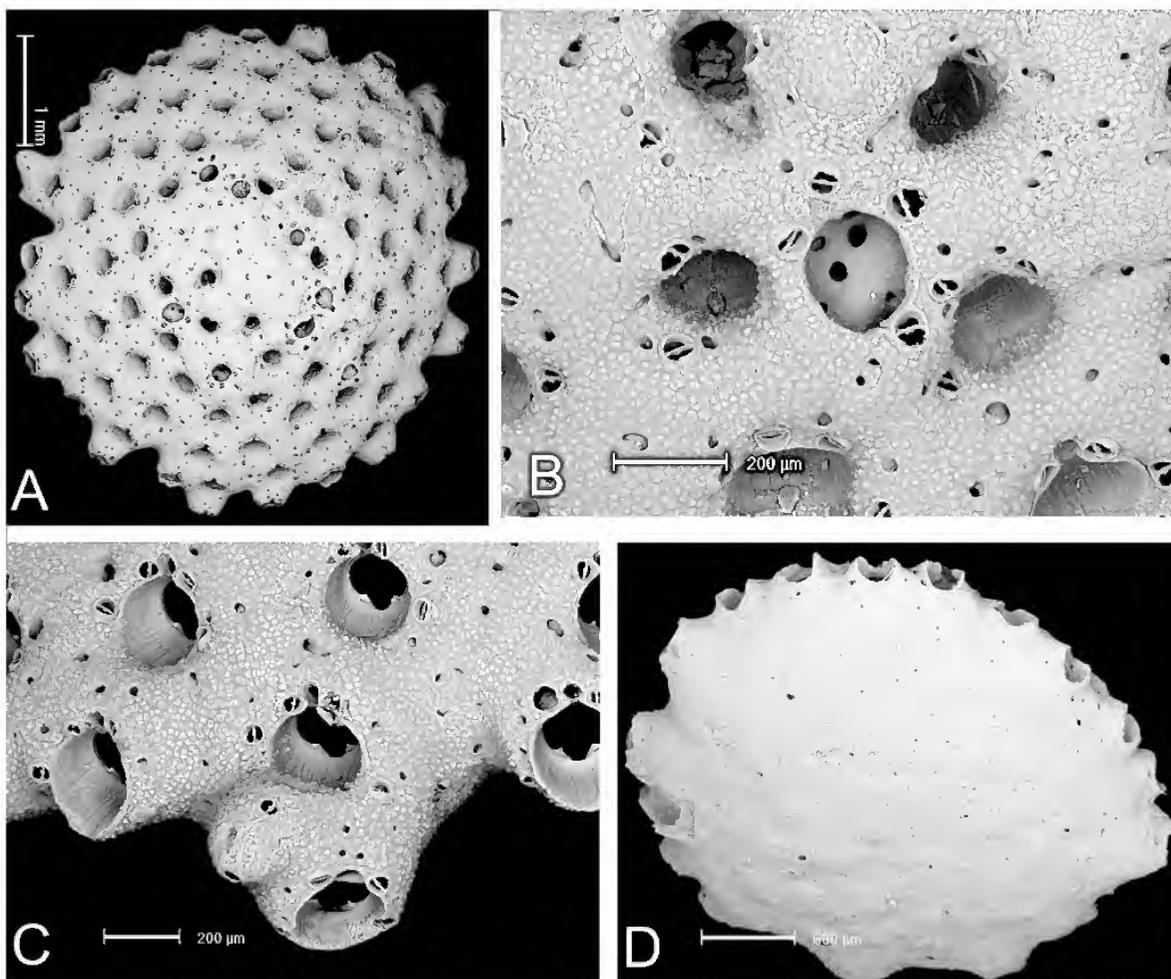


Figure 10. *Conescharellina plana* sp. nov. A–C, NMV F98996, holotype. A, adapical view of colony, scale = 1 mm. B, detail of root pore with surrounding avicularia, scale = 200 µm. C, detail of colony margin showing orifices, peristomes, and avicularia, scale = 200 µm. D, NMV F98997, paratype, antapical surface of colony, scale = 500 µm.

*Description.* Colonies large, slightly flattened, wider than high. Zooid orifices in marked, apparently radial series, peristomes tubular, deep but not prominent at the surface. Calcification smooth to finely tuberculate. Primary orifice with a small, rounded sinus, deeply hidden at the base of the circular peristome, adapical pore just outside the edge of the peristome. Ovicells fragile, with a fairly wide ectoocelial rim and a semi-transparent entoocelial frontal area. Avicularia paired, close to the edge of the peristome, adapical and antapical, very small, rounded, with a minute ligula. Root pores numerous, large, circular, surrounded by a cirlet of 3–4 small avicularia. Antapical surface solid and flat, with small, scattered avicularia.

Colony diameter 4.5 mm, height 2 mm. Number of whorls 5, number of zooids per whorl 8.

*Remarks.* The large, circular root pores of *C. plana* are similar in appearance to those of *Conescharellina eburnea*, *C. perculata*, *C. humerus* and *Crucescharellina australis* that are also surrounded by a cirlet of small, rounded avicularia. The peristomes of *C. plana* are unusual in being elongated but not prominent and the colony surface is smooth. Two colonies exhibit a single, marginal zooid each, with a prominent peristomial avicularium (Fig. 10C). Only one of the two ovicells present in the colony from stn BSS-167 is complete; a deeply pigmented embryo is visible through the thin frontal calcification. Colonies of *C. plana* are widely distributed off the southern and eastern coasts of Australia occurring from the western Australian Bight to the eastern border of Victoria, through Bass Strait, from depths ranging from 80 to 1096 m.

*Conescharellina perculata* sp. nov.

Figures 11A–D

*Holotype.* NMV F98998, slide labelled E3195 (Locality unknown, probably off New South Wales).

*Paratypes.* NMV F98999, locality as above.

*Etymology.* *perculus* (L.) – highly adorned, with reference to the patterning of the numerous avicularia and colony calcification.

*Diagnosis and description.* Colonies small, discoid, distinctly wider than high, with a mamillate centre and prominent marginal peristomes, calcification delicate and finely tuberculate. Orifices quincuncial, becoming radial. Primary orifice with a rounded sinus. Peristomes elongated and tubular, raised antapically and prolonged into a spout, prominent at the colony margin. Adapical pore present on outer face of the peristomes. Root pores circular, surrounded by up to 5 small avicularia. All avicularia small, rostrum rounded, bar with a minute ligula. Each orifice with 1 adapical, 1 lateral and 1 antapical pair of avicularia. Further pairs of lateral and antapically placed avicularia, that are visible from the antapical surface, are accompanied by pairs of pores.

Largest colony about 2.3 mm wide and 0.5 mm high, with 6 astogenetic generations and probably up to 11–12 zooids per whorl at margin.

*Remarks.* The locality from that the three small colonies of were collected also provided two well preserved colonies of

*C. biarmata* and therefore is inferred to have been collected from New South Wales. *C. perculata* is distinguished by its delicate, semitransparent, finely tuberculate calcification, with numerous avicularia surrounding the spout-shaped peristomial orifices. As in *C. eburnea*, *C. ocellata* and *T. diommatas*, the marginal peristomes can be recognised from the antapical surface by the pattern or outline of the associated paired avicularia. In many other respects, such as the depth of the peristome, the distribution of circum-oral avicularia, and type of root pore, *C. perculata* greatly resembles *C. plana*, from which it differs principally in colony size, the patterning and shape of the orifices, and nature of the antapical surface, including the peristomes. The circular root pores, with their surrounding avicularia, resemble those of *C. eburnea*, *C. plana* and *C. humerus*, as well as those of *Crucescharellina australis*.

*Conescharellina pustulosa* sp. nov.

Figures 12A–D

*Holotype.* NMV F99000, stn SLOPE-2.

*Paratypes.* NMV F99001, stn SLOPE-2 (9 colonies).

*Other specimens.* NMV F99002, unlabelled Mapstone specimens, probably from NSW (5 colonies); NMV F101961, stn BSS-158 (1 colony); NMV F101962, stn BSS-169 (1 colony); NMV F101963, stn SLOPE-40 (14 colonies); NMV F101964, stn SLOPE-45 (1 colony); NMV F101965, stn GAB-049 (1 colony).

*Etymology.* *pustula* (L) - a bubble or blister, with reference to the calcification of the zooid surfaces.

*Diagnosis.* *Conescharellina* with small, domed colonies. Zooids orifices with a subtriangular sinus; surrounded by raised, pustular secondary calcification, that also covers the antapical surface. Avicularia antapical, peristomial, raised, bar without a ligula.

*Description.* Colonies small, domed. Surface irregular, formed by raised, pustular secondary calcification. Zooids in quincuncial series, peristomes raised laterally, prominent only at colony margins. Primary orifice with a wide subtriangular sinus and minute condyles. Adapical pore outside the peristome rim. One small peristomial avicularium lateral and antapical, nearly vertical to the rim of the peristome, rostrum rounded, bar without a ligula; other occasional avicularia scattered among the zooids. Adapical region with a few, lunate root pores; antapical region with more pustular secondary calcification, cancelli and avicularia.

Colony diameter 2.2 mm, height 1.2 mm, number of whorls 6, number of zooids per whorl 8.

*Remarks.* The pustular calcification occurs among the zooid orifices and is a prominent feature of the antapical surface of the small colonies. The only other species in the samples examined that possesses an antapical peristomial avicularium is *C. obscura*, but this is not placed on the edge of the peristome as in *C. pustulosa*. *C. pustulosa* bears a close but superficial similarity to *C. papulifera* Harmer (1957: 734, pl. 47 figs 7–9, text-fig. 70C). Harmer did not describe or figure the primary orifice, that he was not certain was visible. He mentioned

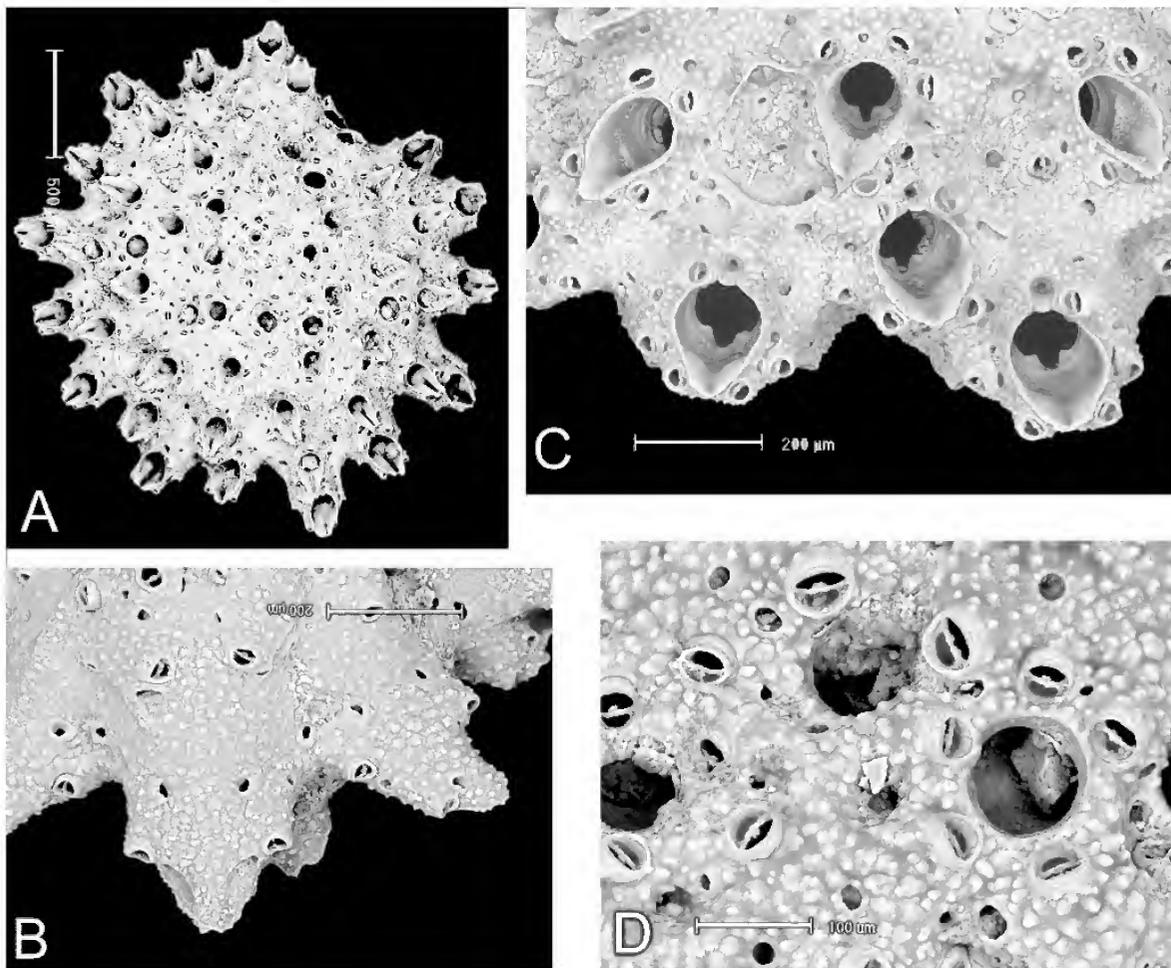


Figure 11. *Conescharellina perculata* sp. nov. A, NMV F98998, holotype. A, adapical view of colony, scale = 200 µm. B, NMV P98999, antapical view of marginal peristomes, scale = 200 µm. C–D, NMV F98998, holotype. C, detail of orifices, peristomes, and avicularia, scale = 200 µm. D, detail of root pore, scale = 200 µm.

paired avicularia and radially costulate zooid orifices but did not figure them. Specimens of *C. papulifera* (BMNH, 1964.3.2.3, paratype?, Java Sea and 1964.3.2.2, *Siboga* stn 77, Borneo Bank, 59 m) have been examined. They are minute; their dimensions being less than half of those of *C. pustulosa* at the same astogenetic stage. The peristomes are raised and tubular, arranged in radial series; the primary orifices are not visible. Minute avicularia alternate with the zooid orifices and none are antapical and peristomial.

*C. pustulosa* is distributed from the coasts of New South Wales to Bass Strait and the Great Australian Bight, from a wide depth range of 36 to 800 m. There is, however, little variation in the characters of the colonies from the different populations.

#### *Conescharellina ocellata* sp. nov.

Figures 13A–D

*Holotype*. NMV P311805; Miocene, Balcombe Bay, Victoria (see appendix).

*Paratype*. NMV P311806; Balcombe Bay, Victoria.

*Other specimens*. Victoria, Balcombe Bay (55 colonies); Batesford Quarry (see appendix) (45 colonies).

*Etymology*. *ocellata* (L.) – having little eyes, with reference to the appearance of the antapical peristomial avicularia.

*Diagnosis*. *Conescharellina* with minute, slightly domed colonies. Zooid orifices radial. Avicularia small, paired, lateral, with a minute ligula. Paired avicularia visible on the antapical side of the marginal peristomes.

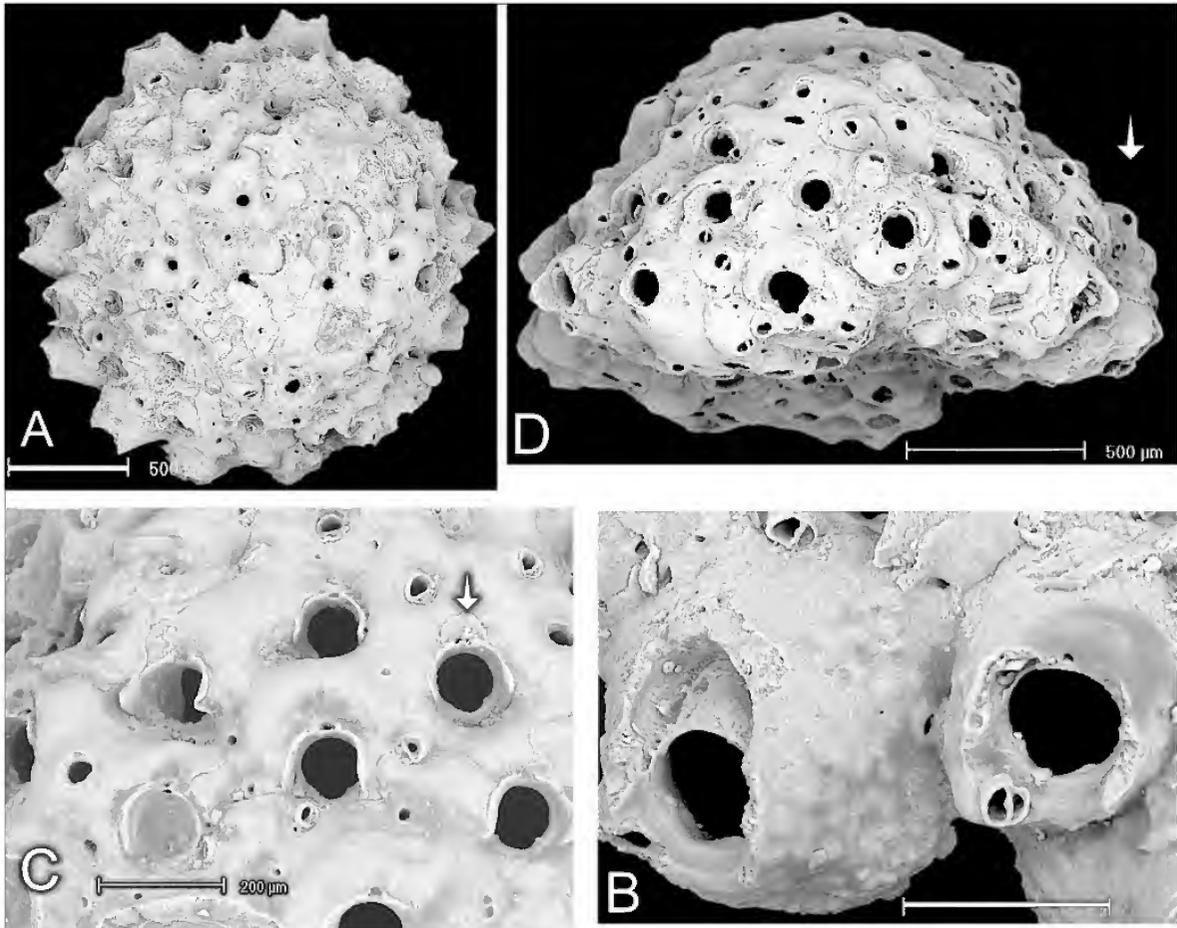


Figure 12. *Conescharellina pustulosa* sp. nov. A–B, NMV F99000, holotype. A, adapical view of colony, scale = 500 µm. B, detail of two marginal orifices, showing thick secondary calcification and peristomial avicularia, scale = 200 µm. C, NMV F99001, paratype, group of orifices, adapical pores with developing ectoecial lamina arrowed, scale = 200 µm. D, NMV F99002, colony lateral view, growth direction (antapical) arrowed, scale = 500 µm.

**Description.** Colonies very small, domed, orifices appearing to be in radial series. Primary orifice with a short, narrow sinus and distinct paired condyles, with a laterally and antapically raised peristome. Adapical pore on the edge of the peristome. Avicularia small, rounded, paired and antapical, lateral to the sinus, bar with a minute ligula, orientated laterally and adapically. Adapical region with a few rounded pores, inferred to be root pores, with 2–3 small adjacent avicularia. Antapical region with a few avicularia and central cancelli; and with prominent, paired avicularia present on the antapical side of the peristome of marginal zooids.

Diameter of colony 2.4 mm, height 1.6 mm, up to 6 radial whorls, 5–7 zooids per whorl.

**Remarks.** *C. ocellata* is easily recognisable in unworn colonies by the paired antapical avicularia on the marginal peristomes. *C. ocellata* resembles *C. eburnea* and *Trochosodon diammotos*

in this character but differs in all its dimensions and in the shape of the primary orifice. It differs from *C. macgillivrayi* in its domed colonies, radially arranged orifices, shape of the primary orifice, and rarity of antapical cancelli. It differs from *C. humerus* in the position and shape of the primary orifice and position of the lateral avicularia, especially in antapical view.

***Conescharellina macgillivrayi* sp. nov.**

Figs 13E–F, 14A

*Bipora philippinensis*.—MacGillivray, 1895: 89, pl. 12 fig. 2.

**Holotype.** NMV P311810, Miocene, Balcombe Bay, Victoria.

**Paratypes.** NMV P311811, Balcombe Bay.

**Other specimens,** Miocene, Balcombe Bay (approximately 209 colonies); Miocene, Bairnsdale (12 colonies); Miocene, Batesford Quarry (22 colonies); Miocene, Heywood Bore (approximately 63 worn colonies); Miocene, Muddy Creek (13 colonies), Miocene,

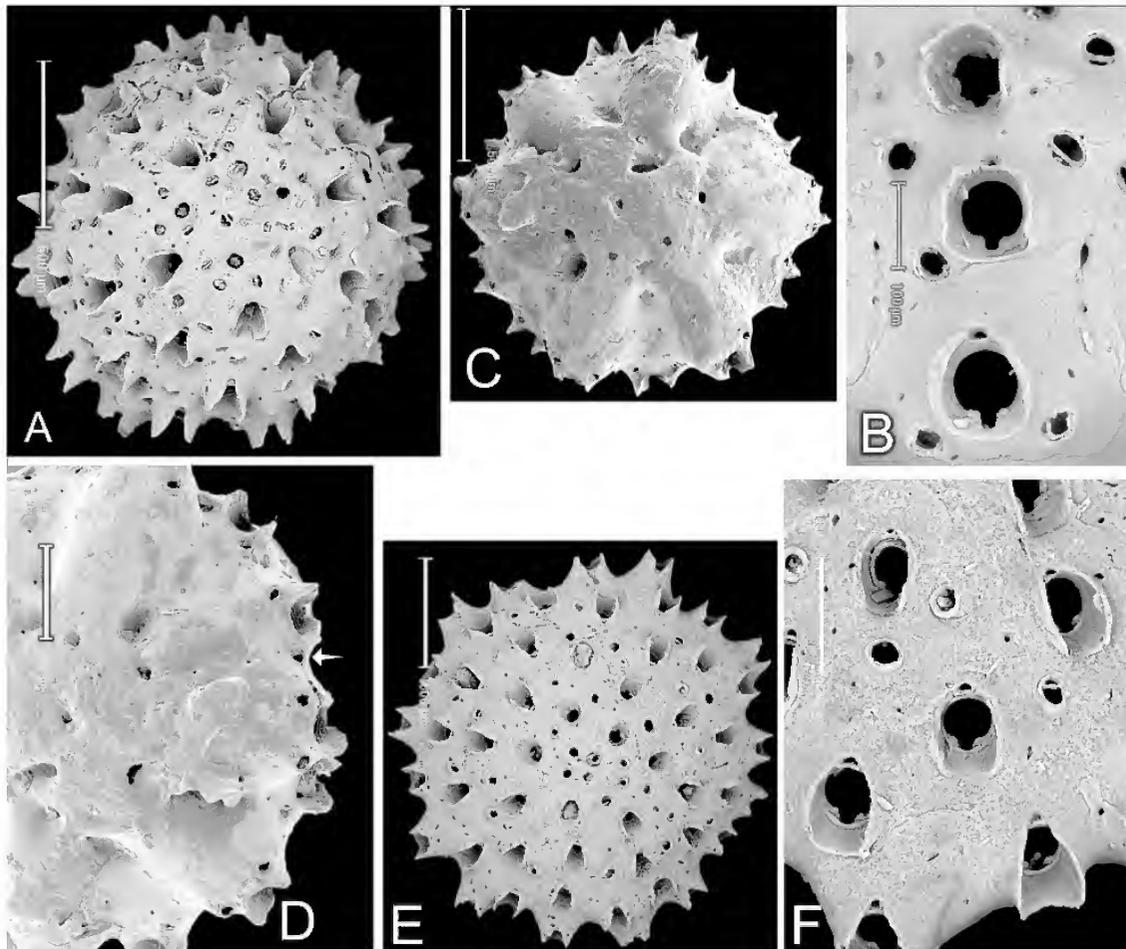


Figure 13. A–D, *Conescharellina ocellata* sp. nov. A–B, NMV P311805. A, adapical view of colony, scale = 500  $\mu$ m. B, detail of orifices, avicularia and septular pores, scale = 200  $\mu$ m. C–D, NMV P311806. C, antapical view, scale = 500  $\mu$ m. D, marginal view showing peristomes and paired avicularia (arrow), scale = 200  $\mu$ m. E–F, *Conescharellina macgillivrayi* sp. nov. NMV P311810. E, adapical view of colony, scale = 500  $\mu$ m. F, detail of orifices with adapical pores, peristomes and avicularia, scale = 200  $\mu$ m.

Puebla Clay, Torquay (16 colonies); Miocene, Mount Schanck, South Australia (approximately 100 colonies).

*Etymology.* Named for P.H. MacGillivray.

*Diagnosis.* *Conescharellina* with fairly flat, small colonies. Zooid orifices arranged quincuncially, marginal peristomes prominent. Avicularia rare. Root pores circular. Antapical surface with cancelli.

*Description.* Colonies fairly flat, distinctly wider than high, peristomes prominent marginally. Calcification finely tuberculate. Zooid orifices obviously quincuncial, sinus short and rounded, with paired condyles. Peristomes raised laterally and antapically; adapical pore outside the peristome. Root pores round, small, adapical. Avicularia rare, lateral or antapical,

rounded, bar with a minute ligula. Antapical surface with large cancelli and minute avicularia.

Colony diameter 1.9 mm, height 1.25 mm, number of whorls 6, zooids per whorl 8.

*Remarks.* Colonies of *C. macgillivrayi* are the most numerous of the fossils found in the Victorian and South Australian Tertiary samples, although many colonies are worn and their identity has had to be inferred from their proportions and orifice pattern. Comparison of the colonies with MacGillivray's (1895) specimen of "*Bipora philippinensis*" (NMV P 27728) indicates that they are conspecific and it is also possible that this species is the "*Lunulites cancellatus*" of Waters (1882b: 512, pl. 22 figs 10, 11) from Bairnsdale, although this was figured with more numerous avicularia. None of his specimens has been examined.

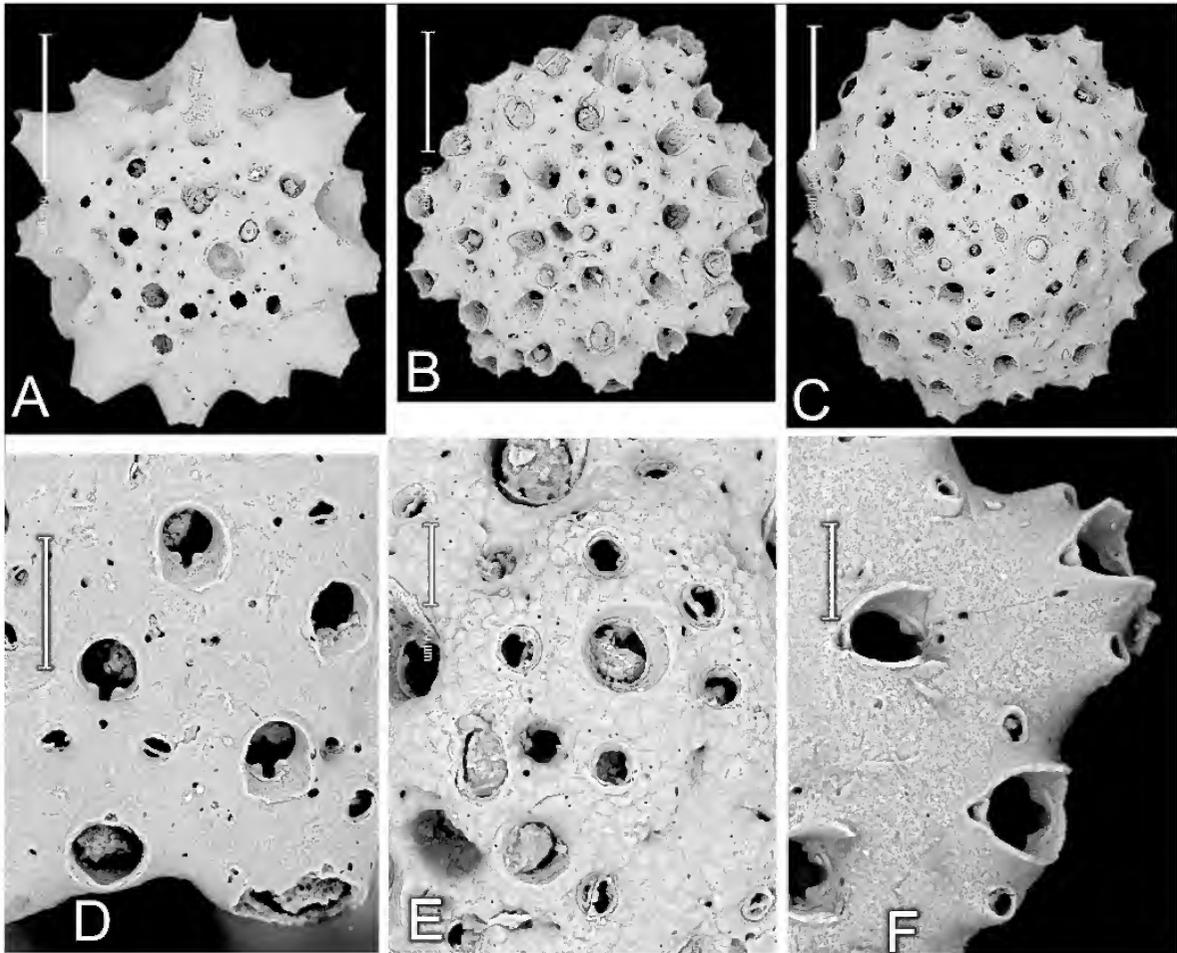


Figure 14. *Conescharellina macgillivrayi* sp. nov. and *C. humerus* sp. nov. A, *C. macgillivrayi* NMV P311811, antapical view of colony, showing cancelli, scale = 500  $\mu$ m. B–F. *C. humerus*. B, NMV P311814, adapical view of colony, showing root pore, scale = 500  $\mu$ m. C–D. NMV P311812. C, Adapical view of colony, scale = 500  $\mu$ m. D, detail of orifices and avicularia, scale = 200  $\mu$ m. E, NMV P311814, detail of root pore (see Figure 14B), scale = 100  $\mu$ m. F, NMV P311813, detail of marginal zooids, showing profiles of peristomes and avicularia, scale = 100  $\mu$ m.

*Conescharellina humerus* sp. nov.

Figures 14B–F

*Holotype*. NMV P311812, Miocene, Balcombe Bay, Victoria.

*Paratypes*. NMV P311813, P311814, Miocene, Balcombe Bay.

*Other specimens*. Miocene, Balcombe Bay (43 colonies); Miocene, Batesford Quarry (170 colonies); Miocene, Muddy Creek (7 colonies); Miocene, Paraatte Bore (8 colonies); Miocene, Puebla Clay, Torquay (16 colonies); Miocene, Mount Schanck, South Australia (approximately 125 colonies).

*Etymology*. *humerus* (L.) – a shoulder, with reference to the outline of the lateral avicularia and peristome from antapical view.

*Diagnosis*. *Conescharellina* with slightly domed colonies. Zooid orifices radial. Avicularia small, lateral, forming a

“shoulder” visible on marginal peristomes. Round root pore near the centre adapically, surrounded by small avicularia.

*Description*. Colonies small, slightly domed, distinctly wider than high. Orifices radially arranged towards the margin of the colony. Primary orifices with a distinct, deep, rounded sinus and paired condyles, peristome raised laterally, adapical pore outside peristome. Avicularia small, paired, rounded, lateral and antapical, directed inwardly, bar with ligula, subrostral chamber prominent, visible as a lateral “shoulder” in marginal zooids. A fairly large, rounded root pore near the centre of the adapical region, surrounded by a circlet of six avicularia. Antapical surface cancellate centrally, otherwise smooth, with small avicularia.

Colony diameter 3.3 mm, height 1.5 mm, number of whorls 4, number of zooids per whorl 7.

*Remarks.* The colonies of *C. humerus* are widely distributed in the Victorian Tertiary but are not as numerous as those of *C. macgillivrayi*. *C. humerus* is immediately recognisable by the profile of the marginal peristomes formed by the prominent lateral avicularian rostra. The rounded root pore with circler of avicularia is reminiscent of those found in *C. eburnea*, *C. plana*, *C. perculata* and in *Crucescharellina australis*.

#### *Bipora* Whitelegge, 1887

*Bipora* Whitelegge, 1887: 340 (part).—Levinsen, 1909: 312.—Harmer, 1957: 754.

*Type species.* *Flabellipora* [sic] *flabellaris* Levinsen, 1909 (subsequent designation by Levinsen, 1909).

*Description.* Colony fan-shaped, laterally flattened, zooids arranged in 2 apposing, frontally budded expanses, separated by a series of cancelli, visible antapically. Orifices sinuate, with paired condyles, surrounded by a peristome that is not prominent. Avicularia small and rounded, with a bar but no ligula. Root pores lunate, paired, adapical. Ovicells not known, but adapical pore present.

*Remarks.* Whitelegge (1887) described seven species that he assigned to *Bipora* but did not indicate a type species. He assigned specimens from Port Jackson to "*Bipora* (?) *elegans*" of d'Orbigny (1852) somewhat doubtfully, remarking "if this species proves to be different (as I think it will) from the fossil form described by d'Orbigny as *Flabellopora elegans*, it can remain as *B. elegans* Waters". D'Orbigny's species was not a fossil: Whitelegge's reference was to a remark by Waters (1887a: 71) who mentioned receiving a specimen of "*Flabellopora elegans*" from New South Wales that grew in an "irregular subcrescentic form with two layers of zoecia separated by a cellular structure formed of avicularian cells". This specimen was apparently from Brazier, as Waters (1887: 200) listed specimens from Port Stephens (from approximately 13–15 m depth), collected by him, some of which had "between the layers a cancellous structure". Waters' figures (pl. 5 figs 13–17) leave no doubt that they represent "*Bipora flabellaris*", even though Waters (1889) remarked that Whitelegge had "favoured me with further specimens of *Flabellopora elegans*, d'Orb., and I feel no doubt as to the correctness of my identification". However, Waters later (1905, 1921) amended this view and stated that he had adopted Levinsen's name. Levinsen (1909) had somewhat informally and irregularly designated *Flabellipora* [sic] *elegans* Waters (1887) not d'Orbigny (1852), that he then renamed *Flabellipora flabellaris*, as the type species of *Bipora*. Harmer (1957: 755) remarked that "*Bipora* is a genus of uncertain validity" but that *B. flabellaris* was the only species mentioned by Whitelegge (1887: 346), as *Bipora* (?) *elegans*, that would be available as type species, as all the other species had subsequently been referred either to *Conescharellina* or *Flabellopora*. Presumably, the type specimens of *B. flabellaris* are among those figured by Waters (1887). Harmer (1957: 755) incorrectly listed the registration numbers of some specimens in the collections of the Natural History Museum. The numbers should read "99.5.1.1147" indicating Hincks' material and "97.5.1.807" indicating

Bracebridge Wilson material. Harmer concluded that there seemed to be "sufficient reason for regarding *Bipora*, with this genotype" (i.e. *B. flabellaris*) "as a distinct genus of Conescharellinidae". Lu (1991) described three species of *Zeuglopora* from the South China Sea as *Bipora*.

Maplestone (1904: 209) listed specimens of "*Bipora elegans*" among his own collection of fossils from Jimmy's Point, Victoria. No specimens of Maplestone's material are extant and it cannot be established whether or not this is the only fossil record of *Bipora*.

#### *Bipora flabellaris* Levinsen, 1909

Figures 15A–E

*Bipora* (?) *elegans*.—Whitelegge, 1887 (not d'Orbigny, 1852).

*Flabellopora elegans*.—Waters, 1887: 200.

*Flabellipora flabellaris* Levinsen, 1909.—Livingstone, 1924: 211.

*Specimens examined.* NMV F99003, stn GAB-020 (2 colonies); NMV F101966, stn GAB-030 (2 colonies); NMV F99004, stn GAB-116 (1 colony); NMV F101967, stn GAB-118 (1 colony).

*Description.* Colony fan-shaped, composed of 2 apposed zooidal faces, separated by an intervening cancellated and avicularian layer. Adapical region often extrazoidally thickened, with rhizoids arising from small lunate pores. Zooid primary orifice with a subtriangular sinus and paired condyles. Adapical pore present outside peristome. Peristome raised laterally. Avicularia paired, lateral and antapical, rostrum rounded, directed adapically, bar without ligula.

Colonies up to 10 mm wide, 8 mm deep.

*Remarks.* Many of the specimens examined here are worn. Only one, from stn GAB-020, has three long roots (width 0.25 mm, length 2.0 mm), that arise from the adapical region of a large colony from 155 m depth.

*B. flabellaris* is obviously very closely related to species of *Conescharellina*. The early growth stages are hardly distinguishable, except for the slight flattening of the colony. Later stages, however, emphasise the cancellated region, that curves round the antapical edge and protrudes beyond the orifices of the zooidal series of each face, producing the typical fan-shaped colony. All the specimens examined here appear to belong to one species but it is possible that other forms of *Bipora* may eventually be found from the Australian region.

#### *Trochosodon* Canu and Bassler, 1927

*Trochosodon* Canu and Bassler, 1927: 11.—Canu and Bassler, 1929: 493.—Harmer, 1957: 744.

*Type species.* *Trochosodon linearis* Canu and Bassler, 1927 (original designation).

*Description.* Colonies forming a low cone, orifices both radial and quincuncially arranged, antapical marginal series of zooids tubular, projecting, often prominent; frequently without avicularia. Adapical pores and kenozooids present, among large rounded root pores; lunate pores also reported to be present. Avicularia and ovicells present. Antapical cancelli usually rare or absent.

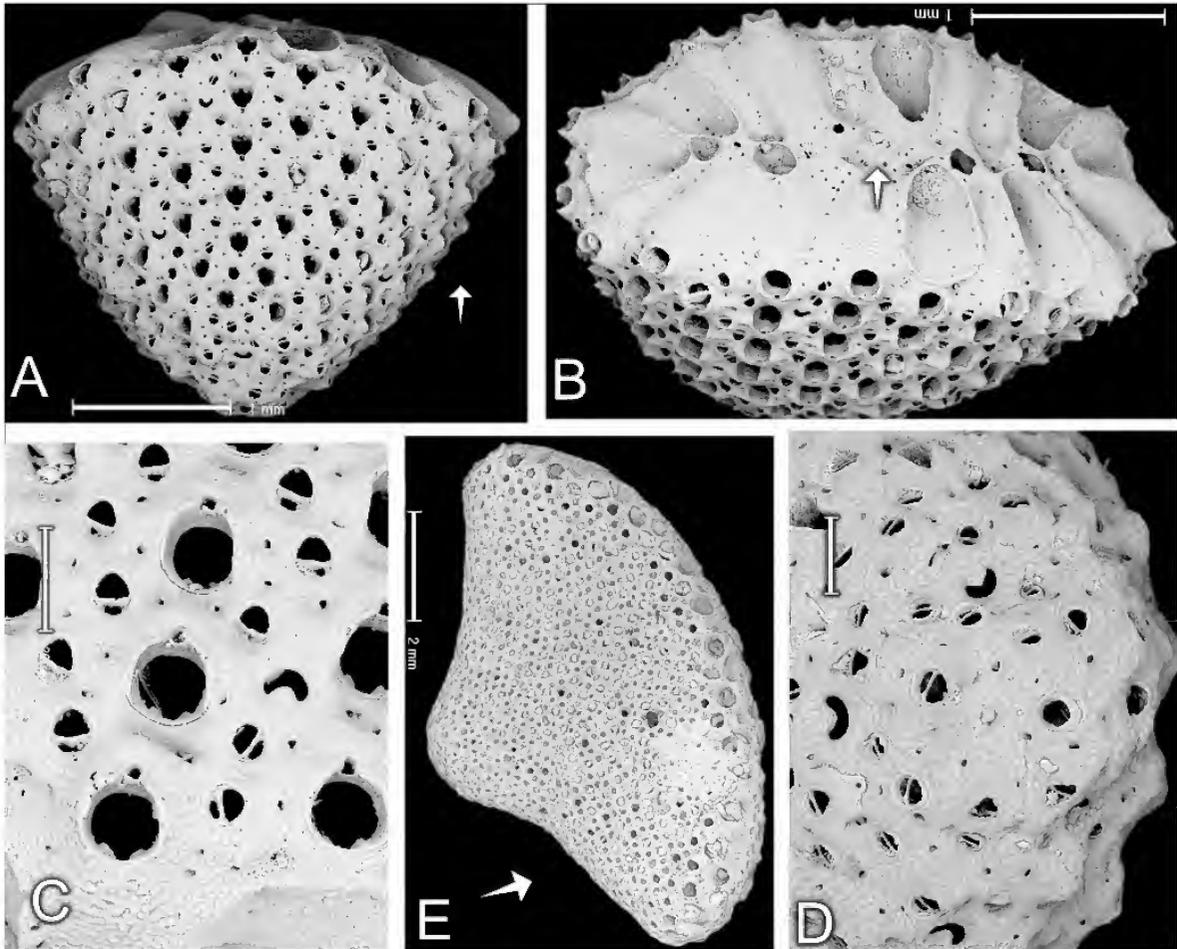


Figure 15. *Bipora flabellaris* (Levinsen, 1909). A–D, NMV F99003. A, young colony, direction of growth arrowed, scale = 100 µm. B, antapical view of colony, showing narrow kenozooidal region (arrowed), scale = 1 mm. C, detail of orifices with adapical pores, and avicularia, scale = 200 µm. D, adapical region, showing lunate root pores, scale = 200 µm. E, NMV F99004, large worn colony at late growth stage, showing flabelliform shape and everted antapical region, direction of growth arrowed, scale = 2 mm.

*Remarks.* Canu and Bassler (1927, 1929) considered that *Trochosodon* was characterised by the absence of avicularia. The type species, *T. linearis* (Canu and Bassler, 1927: 11, 42, pl. 1 fig. 12; 1929: 493, pl. 1 figs 11–13), was from Sibuko Bay, Borneo (*Albatross* stn 5586), from a depth of 247 fathoms (625 m). The unique figured colony was 2.5 mm in diameter, with approximately 6–8 zooids per whorl and a strong tendency for the orifices to be arranged radially. The marginal peristomes were prominent and the antapical surface was convex, with little structure except some scattered pores, that may have been minute avicularia. No avicularia appear to have occurred on the adapical surface near the peristomes. Canu and Bassler (1929: 494, pl. 70 figs 7–10) also described *T. quincuncialis* from the same station. It was distinguished by its quincuncially arranged orifices but pl. 70, fig. 10 clearly shows some series to be

radially arranged; it is probable that the two species are synonymous. Canu and Bassler (1927, 1929) gave no details of the primary orifices except that they were sinuate. Their figures were all retouched but pl. 70 fig. 12 perhaps shows a few adapical pores. Harmer (1957: 744) noted difficulties in defining *Trochosodon*, remarking “it is not easy to establish a clear distinction between this genus and *Conescharella*”, maintaining that all the abyssal species, including *T. linearis* that he assigned to the genus, possessed avicularia. However, he could not have examined the unique type specimen of *T. linearis* *sensu stricto* and it seems possible that his *Siboga* specimens belonged to a distinct species (see below). Generally, the distinguishing features of *Trochosodon* include prominent, tubular marginal peristomes and virtual or complete absence of antapical cancelli. Gordon (1989) introduced several abyssal

species from the New Zealand region but the only authentic past records from Australia appear to be those of *T. ampulla* (Maplestone), described below and three hitherto unnamed species from Cape York, Queensland, figured by Cook and Lagaaij (1976) and Cook (1981), from *Challenger* stn 185, from 279 m, a locality that was not mentioned by Busk (1884). These colonies are here referred to *T. aster* sp. nov., *T. anomalus* sp. nov. and *T. praecox* sp. nov., bringing the total of species described from Australia to seven. Ovicells were described by Harmer (1957) in *T. optatus* (see below). These appear to be asymmetrical and have ridged frontals, resembling those of specimens of *T. fecundus* sp. nov. from north-western Australia, that are, however, symmetrically developed. Similarly ridged ovicells were reported in *C. striata* by Silén (1947) but these were also asymmetrically developed, like those of *C. catella*, as described by Harmer (1957), and almost certainly of *T. asymmetricus* sp. nov. A suite of independent character states distinguishing "*Trochosodon*" from "*Conescharellina*" is thus far from complete or consistent. However, the wide diversity of species assigned to *Conescharellina* itself, suggests that this genus will certainly require eventual revision, including a definition of its type species and a review of all other taxa referred to it (see Silén, 1947: 34). Until this is accomplished, it is probably wisest to maintain *Trochosodon* for a group of species that are fairly consistent and differ slightly from most other forms assigned to *Conescharellina*. Australian species are introduced here from New South Wales, Victoria, north-west Australia and Queensland. Although they exhibit a mosaic of characteristics some of which can be regarded as "typical" of *Conescharellina*, they are considered here to be distinct enough to be assigned provisionally to a generic group and referred to *Trochosodon*. Harmer (1957) considered this to be mainly an abyssal genus but material included here also derives from shallow depth.

***Trochosodon ampulla* (Maplestone, 1909)**

Figures 16A–C

*Bipora ampulla* Maplestone, 1909: 269, pl. 76 figs 4a, b, 5a, b.

*Conescharellina ampulla*.—Livingstone, 1924: 212.

*Trochosodon ampulla*.—Canu and Bassler, 1929: 493.—Harmer, 1957: 744.

*Specimens examined*. BMNH 2000.2.23.1 (part of material sent by Maplestone to the Natural History Museum, 1 colony). NMV F99005, F99006, labelled by Maplestone, almost certainly part of the type material from NSW; and NMV F101968, same collection (6 additional colonies).

*Description*. Colony forming a very low dome, distinctly wider than high. Orifices quincuncially arranged, rapidly obscured by extrazoooidal and kenozoooidal calcification. Prominent, flask shaped, marginal zooids with elongated, tubular peristomes. Primary orifice slightly elongated, with a small pointed sinus. Adapical pore present outside peristome. A few scattered pores (root pores?) present adapically. Avicularia small, often paired, placed laterally and adapically beside each peristome, rostrum almost semicircular, bar with a minute ligula. Antapical surface with a small central region of cancelli.

Colonies up to 4.7 mm in diameter and 1.6 mm in height; with approximately 8 whorls, each with 10 zooids.

*Remarks*. The specimens examined are somewhat worn and show few primary orifices, deeply hidden by the elongated peristome. The peristomes of the marginal zooids are tubular and prominent, the calcification is thickened and there are only one or two apparent adapical pores. Antapical cancelli are usually confined to a small, central area, although a much larger area was figured by Maplestone (1909). The species is distinguished by large size and stellate colony form with very prominent tubular marginal peristomes.

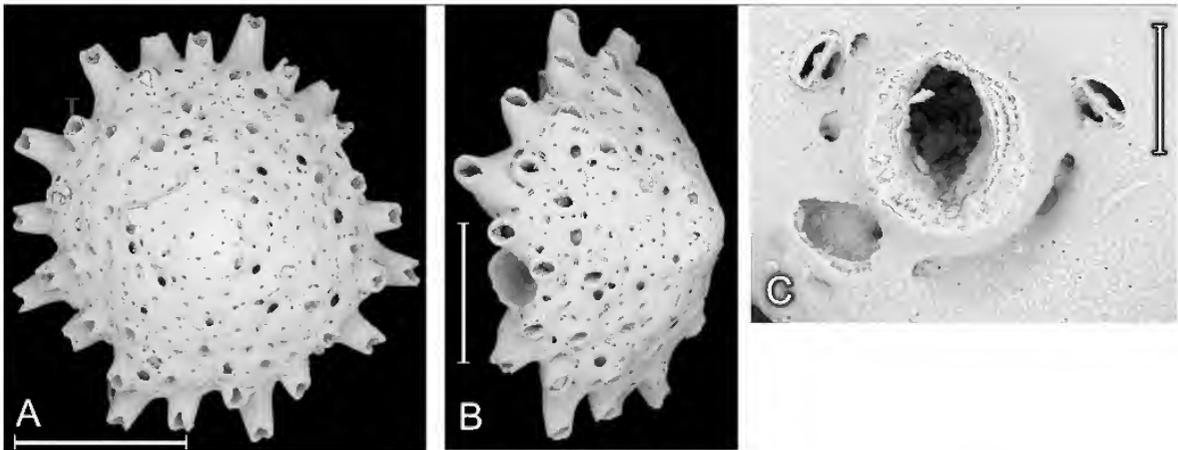


Figure 16. *Trochosodon ampulla* (Maplestone, 1909). A, NMV F99005, adapical view of colony, scale = 1 mm. B–C, NMV F99006. B, lateral view of larger colony, scale = 1 mm. C, detail of orifice and avicularia, scale = 100  $\mu$ m.

Specimens additional to the types suites of *T. ampulla* have not been reported since its first description. This, taken together with Maplestone's labelling of the NMV specimens and the occurrence in this collection of other, apparently unique records from New South Wales, of *Zeugltopora lanceolata* etc., strongly suggests that these specimens are part of the original type suite.

***Trochosodon fecundus* sp. nov.**

Figures 17A–F

*Holotype.* NMV F99007, Dampier Archipelago, stn DA-2-75-02.

*Paratypes.* NMV F99008, F99009, Dampier Archipelago, stn DA-2-75-02.

*Etymology.* *fecundus* (L.) – fertile, prolific, with reference to the numerous ovicells present in the specimens.

*Diagnosis.* *Trochosodon* with peristomes raised laterally and arranged quincuncially. Zooid orifices concealed, with a very wide, shallow sinus. Avicularia rounded. Ovicells prominent, symmetrical, with a thin marginal ectooecium. Root pores lunate.

*Description.* Colony forming a low cone, wider than high, with prominent peristomes, particularly at the margin. Calcification smooth to finely mamillate. Orifices in irregular, quincuncial series, oval, with a pair of minute condyles that delineate a broad, very shallow sinus. Peristomes raised laterally and antapically, forming a partial, shallow tube. One avicularium near and lateral to each orifice, rostrum semicircular, often orientated adapically, with a bar but no ligula. Adapical pore symmetrically placed. Ovicells fragile, symmetrical, prominent, with an ectooecial layer visible marginally, that extends laterally to form paired leaflike lobes above the orifice and the lateral part of the peristomes. Entooecium flat and smooth frontally, with raised marginal striations forming a series of pores where it meets the edge of the ectooecium. Small lunate root pores present. Antapical surface with large cancelli.

Colonies with maximum diameter 2.25 mm and height 0.75 mm, number of whorls 6–7, number of zooids per whorl 10–12.

*Remarks.* The extreme fragility of the ovicell calcification makes it impossible to treat specimens with bleach before electron microscopy. The striated ovicells are similar to those

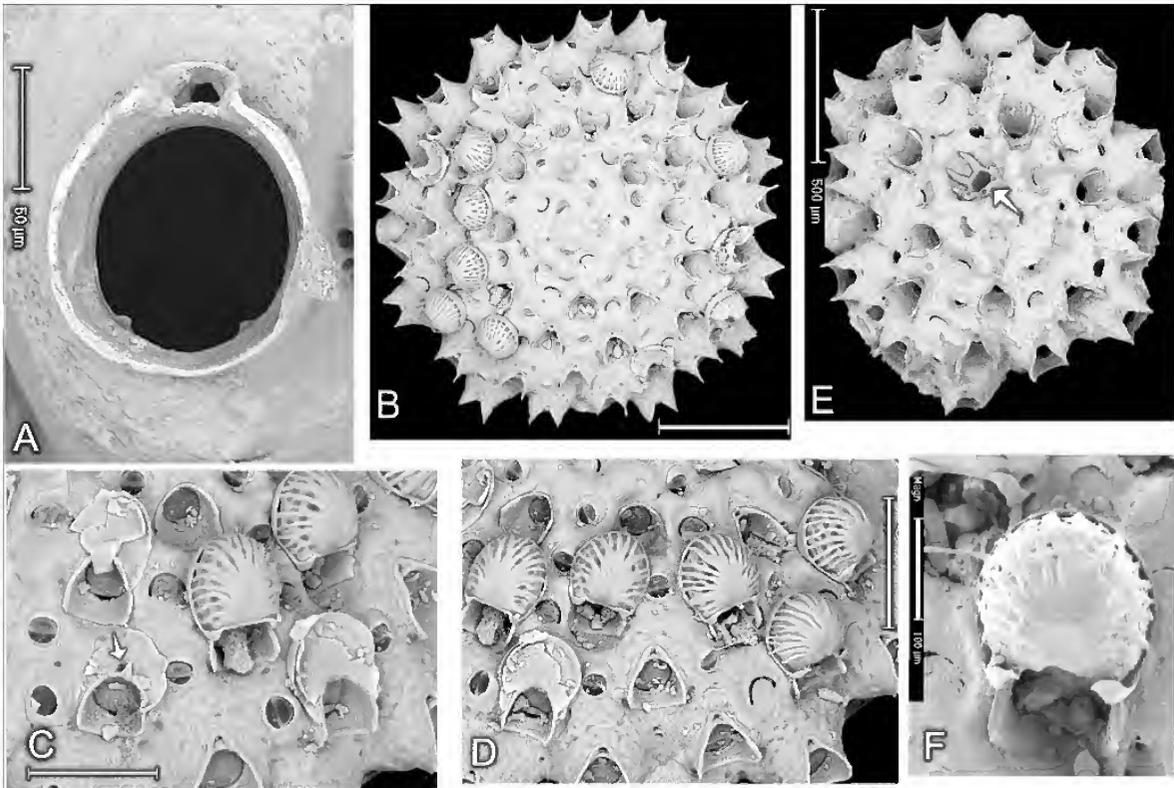


Figure 17. *T. fecundus* sp. nov. A, NMV F99009, paratype. Detail of orifice and adapical pore, scale = 50 µm. B–D, NMV F99007, holotype. B, Adapical view of colony with ovicells and lunate root pores, scale = 500 µm. C, detail of orifices and avicularia, note one adapical pore with developing ectooecial lamina (arrowed), scale = 200 µm. D, ovicells, orifices and lunate root pore, scale = 200 µm. E, NMV F99009, paratype. Adapical view of small colony with associated “anascan” ancestrula (arrowed), scale = 500 µm. F, NMV 99008, paratype, detail of ovicell, showing marginal ectooecium with lateral lappets and ridged entooecium, scale = 100 µm.

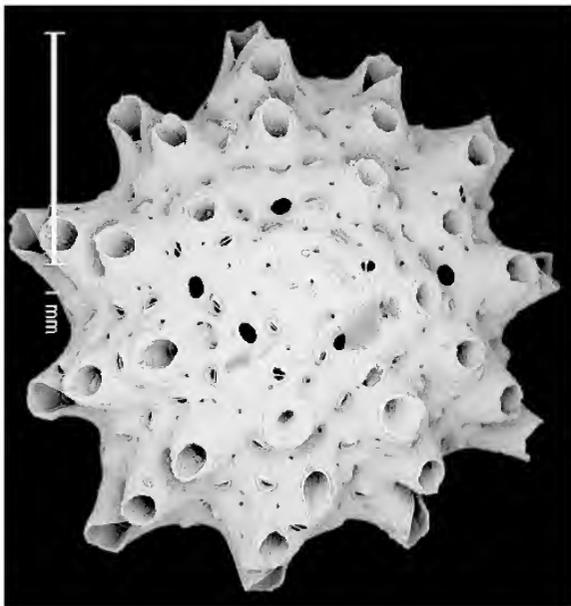


Figure 18. *Trochosodon asymmetricus* sp. nov. NMV F99011, paratype. Adapical view of colony, scale = 1 mm.

figured in *Trochosodon optatus* by Harmer (1957: 747, pl. 48 figs 16–18, text-figs 77, 78). As the locality from that these colonies were collected is off the north-west coast of Australia, it is therefore not very remote from the type locality of *T. optatus*, from the coast of Java (*Siboga* stn 318, Kangeang Island, 88 m). However, examination of two of the colonies

from this station (BMNH 1964.3.2.12 part), shows that they differ in having raised, radial series of zooid orifices, minute avicularia, and only rare, adapical, lunate root pores. The principal differences occur in the relationships and position of the ovicells, that are not exactly as described by Harmer (1957). They are, in fact, asymmetrically developed, like the ovicells of *C. striata* Silén (1947) but, unlike that and other similar species, have no obvious orifice. Instead, the ovicell opens into the base of the peristome through a laterally placed foramen. The peristome is long and tubular and completely obscures the ovicell opening. The frontal entoecium is striated, as figured by Harmer, and resembles that of *C. striata* and *T. fecundus*. The ectoecial wall of the ovicell of *T. optatus* is closely apposed to the walls of both the neighbouring peristomes; the ovicells are wedged in between them and difficult to observe. The only other species observed in that the ovicell orifice opens into the peristome is *T. praecox* (see below), and that has symmetrical ovicells.

The occurrence of an ancestrula with seven marginal spines (Fig. 17E) on the adapical centre of two colonies is unique. They are not referable to *Trochosodon*; this suggests that they are extraneous and belong to another, possibly “anaskan” species.

*T. fecundus* is known only from north-western Australia from 20 m.

***Trochosodon asymmetricus* sp. nov.**

Figures 18, 19A–C

*Holotype*. NMV F99010, stn SLOPE-6 (colony with root).

*Paratypes*. NMV F99011 (figured), stn SLOPE-6 (1 worn colony).

*Other specimens*. NMV F101969, stn SLOPE-7 (1 colony).

*Etymology*. *asymmetros* (Gr.) – without symmetry, referring to the position of the adapical pore.

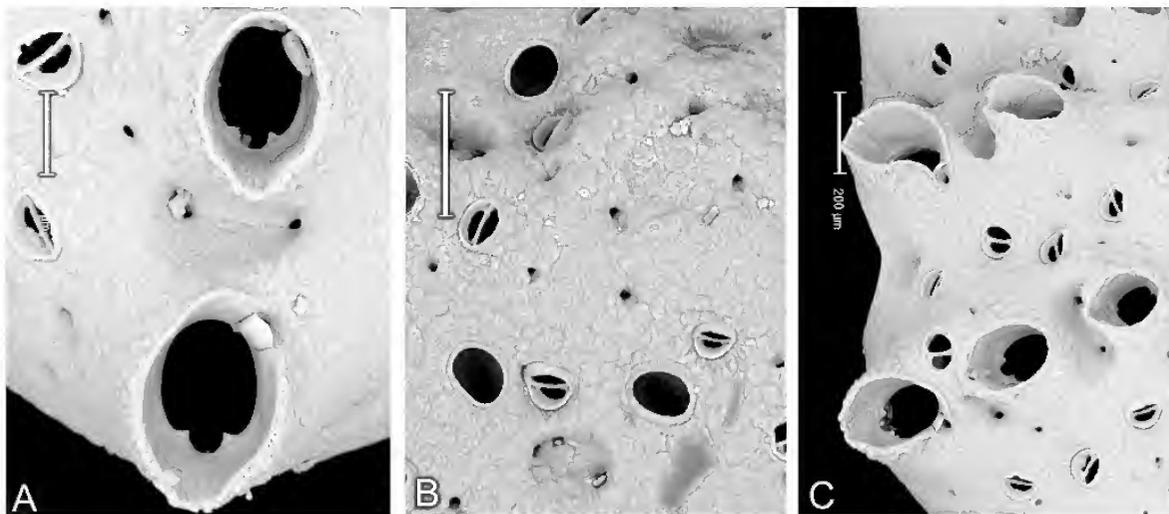


Figure 19. *Trochosodon asymmetricus* sp. nov. NMV F99011, paratype. A, detail of orifices and asymmetrically placed, tubular adapical pores, scale = 100 µm. B, adapical region showing rounded root pores and avicularia, scale = 200 µm. C, detail of marginal peristomes, orifices, adapical pores, and avicularia, scale = 200 µm.

**Diagnosis.** *Trochosodon* with radial series of peristomes, alternating with minute, rounded avicularia. Zooid orifices deeply concealed. Adapical pore asymmetrically placed. Root pores circular.

**Description.** Colony domed, very small, wider than high; orifices apparently arranged radially; calcification granular. Peristomes raised, tubular, with intervening radial series of minute, rounded avicularia; occasional, asymmetrically placed adapical avicularia; bar without ligula. Primary orifice oval, deeply concealed, with a short, rounded sinus. Adapical pore tubular, present in peripheral and subperipheral zooids, asymmetrically placed inside the margin of the peristome. Ovicells inferred to be asymmetrical. Root pores adapical, circular, with a rim and 1 adjacent avicularium. Antapical surface with occasional short radial series of isolated cancelli, derived from the frontal septular pores of the antapical surface of the zooids.

Colony diameter 2.5 mm, height 1.5 mm, 5 whorls of 8–9 zooids per whorl.

**Remarks.** *T. asymmetricus* is the only species among those examined (except *T. optatus*, see above, and a few zooids of *C. stellata*), that exhibits an asymmetrically placed adapical pore. No ovicells have been found but it may be inferred that these, too, would be in an asymmetrical position between the rows of zooid orifices, as are the ovicells of *T. optatus* Harmer (1957), together with those of *C. striata*, *C. brevirostris* and *C. longirostris* of Silén (1947), as well as the specimens described by Harmer (1957) assigned to *C. catella* Canu and Bassler (1929). The tubular appearance of the adapical pore resembles that figured by Livingstone (1925) in "*C. crassa*". There are more zooids per whorl than in *Trochosodon anomalus* but there are several closely similar characters shared by these two species. Both have finely tuberculate calcification and similar radial series of avicularia alternating with the orifices. The primary orifice is also almost identical in appearance (compare Figs 19A, 24F). However, the adapical pores are completely different in position, so it is inferred that the types of ovicells would be an important distinction between the two taxa. *T. asymmetricus* occurs from two adjacent stations from the New South Wales slope, from 770 to 1096 m.

***Trochosodon diommatus* sp. nov.**

Figures 20, 21A–C

**Holotype.** NMV F99012, figured specimen, stn SLOPE-7.

**Paratype.** NMV F99013, F99014, figured specimens, stn SLOPE-7.

**Other specimens.** NMV F101970, stn SLOPE-6 (4 colonies, 3 very young); NMV F101971, stn SLOPE-7 (22 colonies, 10 with roots); NMV F101972, stn SLOPE-45 (1 colony with root).

**Etymology.** *di* – two and *ommatos* – an eye (Gr.), referring to the paired antapical peristomial avicularia.

**Diagnosis.** *Trochosodon* with stellate, radial peristomes, calcification smooth to finely tuberculate. Zooid orifices deeply concealed, with a narrow sinus. Frontal avicularia minute; a prominent pair on the antapical surface of the marginal peristomes.

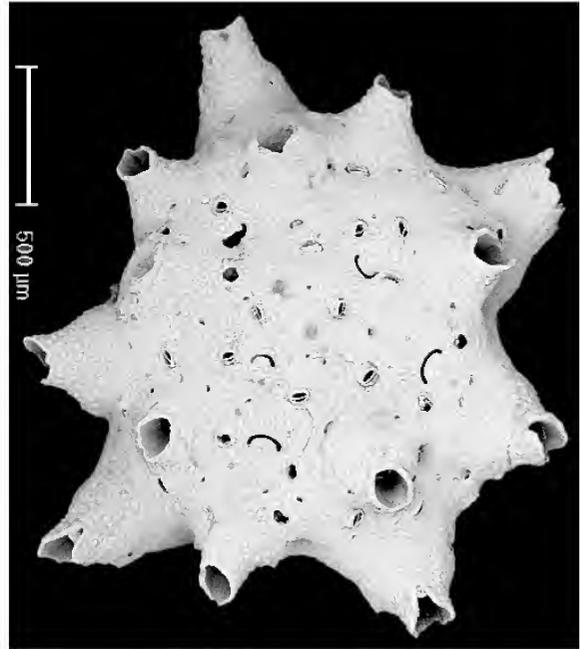


Figure 20. *Trochosodon diommatus* sp. nov. NMV F99012, holotype. adapical view of colony showing lunate root pores, scale = 500  $\mu$ m.

**Description.** Colony stellate, fairly flat, distinctly wider than high, with prominent marginal peristomes. Orifices quincuncial at first, becoming radial. Primary orifice at the base of the long, tubular but not prominent peristome, with an elongate, fairly narrow sinus and large, paired condyles. An adapical pore present on the edge of the peristome of some peripheral zooids. Avicularia single, lateral and antapical between the peristomes, rostrum semicircular, with a bar but no ligula; other small avicularia scattered. Lunate root pores frequent in the adapical region, each with a pair of avicularia laterally. Antapical surface with marginal pores and avicularia; a pair of avicularia on the antapical surface of each peristome (cf. *C. ocellata* and *C. eburnea*).

Colony with up to 4 whorls and 4–5 zooids per whorl. Diameter up to 4.7 mm, height up to 1.5 mm.

**Remarks.** Ovicells have not been seen in *T. diommatus* but the central position of the adapical pore suggests that they would be symmetrical, like those of *T. fecundus*, rather than asymmetrical, as in *T. asymmetricus*. Several colonies from stn SLOPE-7 have roots present; these are 0.5–1.0 mm long. *T. diommatus* is easily distinguished by the presence of the pair of minute avicularia on the antapical side of the marginal zooid peristomes. It resembles two other species in the presence of antapical peristomial avicularia. It differs completely from fossil *C. ocellata* in dimensions and arrangement of the zooid orifices, that have a longer, more acutely subtriangular sinus. It differs from *C. eburnea* in its long peristomes and narrow orificial sinus, as well as the form of its root pores. *T. diommatus*

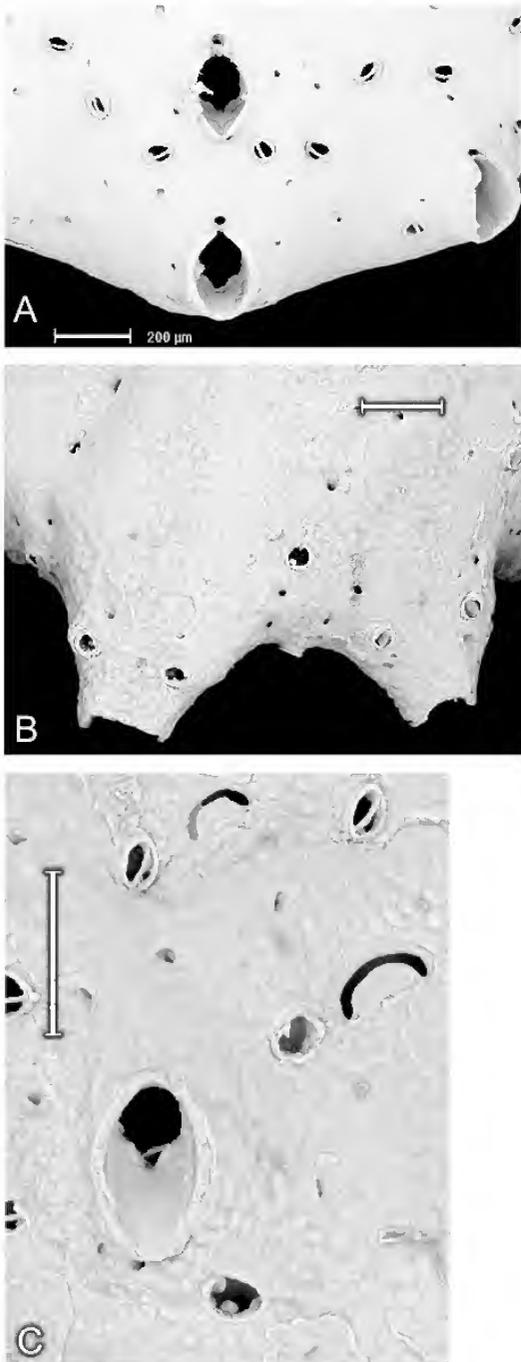


Figure 21. *Trochosodon diommatus* sp. nov. A. NMV F99012, holotype. Detail of orifices and adapical pores, scale = 200 µm. B. NMV F99013, paratype, antapical view of marginal peristomes, showing paired avicularia, scale = 200 µm. C. NMV F99014, paratype, detail of peristome, orifice, and lunate root pores, scale = 200 µm.

has a similar distribution to *T. asymmetricus*, with the addition of a record from 800 m depth off Tasmania.

*Trochosodon aster* sp. nov.

Figures 22A–C, 23

*Trochosodon* sp. 1.—Cook and Lagaaij, 1976, pl. 1 figs 3, 4.

*Holotype*. BMNH 1976.1.6.2 part, *Challenger* stn 185, Cape York, Queensland, 279 m.

*Paratypes*. BMNH 1976.1.6.2. part (20 colonies) and BMNH 1969.1.2.2 (7 colonies). NMV F99015, F99016, F99017, and F101973, same locality (7 colonies).

*Etymology*. *aster* (L.) – a star, referring to the budding pattern.

*Diagnosis and description*. Colonies very small, stellate, budded in alternating zooid triads early in astogeny, orifices becoming radial later, fairly flat, but mamillate and raised centrally. Primary orifice almost circular, with a wide sinus, usually obscured by the elongated peristome, that has a pair of small, rounded, lateral avicularia. Adapical pores present, root pores lunate, rare. Calcification mamillate, on adapical and antapical surfaces.

Colony diameter up to 2 mm, height 0.3 mm, number of whorls up to 4 and 3–4 zooids per whorl.

*Remarks*. The colonies from Cape York are heavily calcified and often somewhat worn. They range in size from 0.25 mm to nearly 2 mm in diameter and have long marginal peristomes that bear small avicularia laterally. One colony, figured by Cook and Lagaaij (1976), shows lunate root pores among the adapical mamillae. *T. aster* resembles *T. pacificum* Lu (1991: 74, pl. 21 fig. 4) from the South China Sea but differs in the presence of lunate root pores and minute lateral peristomial avicularia. *T. aster* also has some characteristics similar to those described for *T. linearis* from the East Indies by Harmer (1957). Two of his specimens have been examined (BMNH 1964.3.2.10, Strait of Makassar, *Siboga* stn 88, 1301 m, and 1964.3.2.11, the Banda Sea, stn 227, 2081 m). These are proportionally larger than *T. aster*, with bilabiate peristomes. One colony was figured by Harmer (1964.3.2.11, p1. 48 fig. 14, text-fig.75), who gave a very detailed description of the early astogeny. The colony has a central, rounded root pore. Canu and Bassler's (1929) unique type specimen of *T. linearis* was dredged from 635 m depth, from Borneo. The description is not adequate to decide its synonymy with Harmer's specimens, that he could not have compared with the type.

*Trochosodon anomalus* sp. nov.

Figures 24A–F

*Holotype*. NMV F99018 stn SLOPE-7.

*Paratypes*. NMV F99019, stn SLOPE-7 (2 colonies).

*Other specimens*. BMNH 1976.1.6.2, *Challenger* stn 185, Cape York, Australia, 279 m (26 colonies); NMV F101974, *Challenger* stn 185 (10 colonies).

*Etymology*. From *anomalos* (Gr.) – irregular, inconsistent, deviating, with reference to the combination of character states found in several genera, that are uniquely possessed by this species.

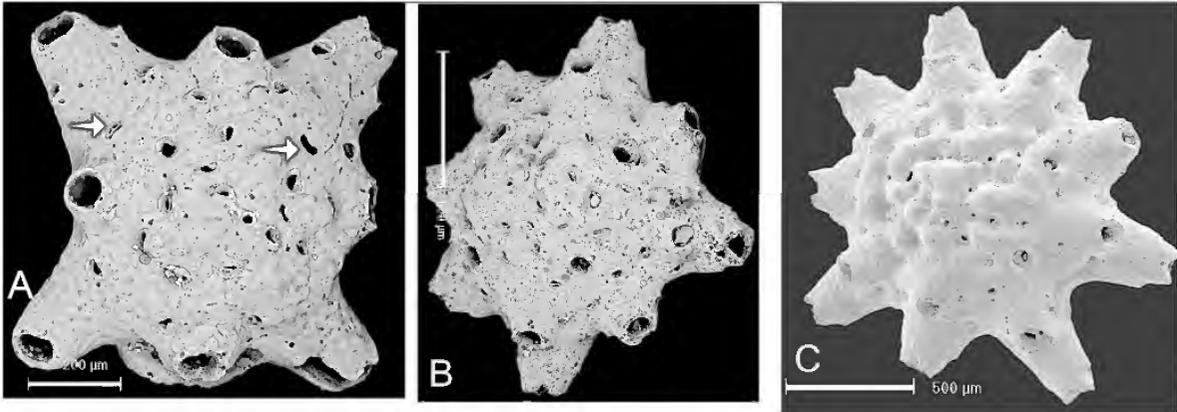


Figure 22. A–D *Trochosodon aster* sp. nov. A, NMV F99015, paratype, young colony showing alternating triad structure; root pores and avicularia arrowed, scale = 200 µm. B, NMV 99016, paratype, older colony, scale = 500 µm. C, NMV P99017, paratype, colony showing adapical calcification, scale = 500 µm.



Figure 23. *Trochosodon aster* sp. nov. NMV F99015, paratype, Detail of orifice and avicularia, scale = 100 µm.

**Diagnosis and description.** Colonies very small, less than 2 mm in height and diameter but appearing to be higher than wide. Calcification mamillate. Zooids arranged in alternating whorls, each of 3 zooids, appearing to be in radial series; peristomes elongated and prominent. Primary orifice with a shallow, rounded sinus and paired condyles, adapical pore symmetrically placed on the edge of the peristome. Avicularia paired, lateral, widely separated from the orifices, alternating in radial series; rostra rounded, bar without a ligula. Adapical region with avicularia and small rounded pores; antapical region with a few avicularia only.

Colony diameter 0.5–1.5 mm, height 0.5–1.5 mm, number of whorls 2–4, number of zooids per whorl 3.

**Remarks.** Specimens of *T. anomalus* are of great interest as they include characteristics “typical” of both *Trochosodon* and *Conescharellina*; in some features they even resemble species of *Batopora*, from which they are readily distinguished by the presence of an adapical pore. The arrangement of the radial series of avicularia suggests assignment to *Conescharellina* but the lack of basal cancelli and the presence of prominent, tubular peristomes allow its inclusion here with other species of *Trochosodon*.

The numerous colonies from Cape York indicate that the distribution of this tiny species extends from Queensland to New South Wales, from lower shelf to slope depths. The similarities between *T. anomalus* and *T. asymmetricus* are described above.

***Trochosodon praecox* sp. nov.**

Figures 25A–F

*Trochosodon* sp. 2.—Cook and Lagaaij, 1976, pl. 1 figs 5, 6.

*Trochosodon* sp.—Cook, 1981, pl. C fig. 4.

**Holotype.** BMNH 2003.11.27.1 (specimen figured by Cook and Lagaaij, 1976 and Cook, 1981), *Challenger* stn 185, Cape York, Queensland, Australia, 279 m.

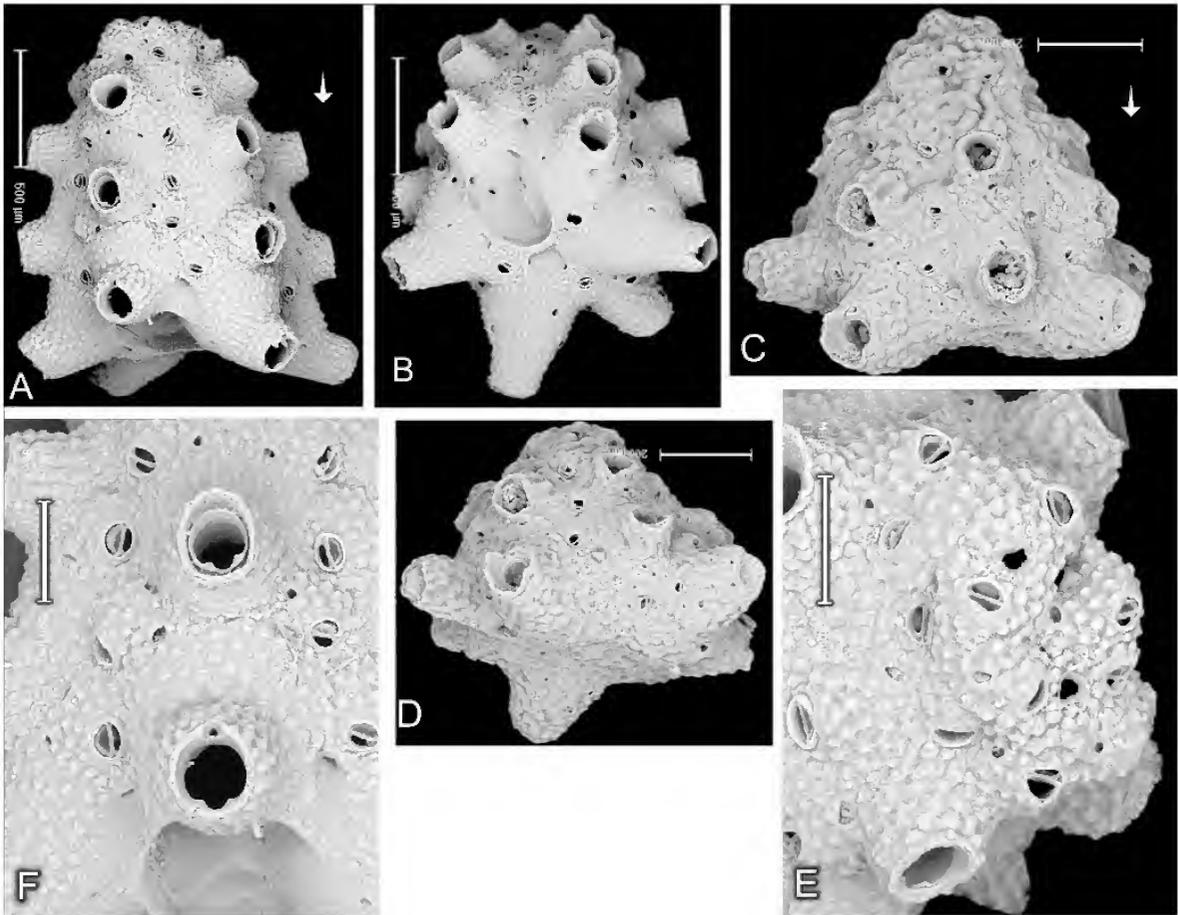


Figure 24. *Trochosodon anomalus* sp.nov. A–B, NMV F99018, holotype. A, lateral view of colony, direction of growth arrowed, scale = 500  $\mu$ m. B, antapical view showing developing zooid, scale = 500  $\mu$ m. C–D, BMNH 2003.11.27.2. C, lateral view of colony, growth direction arrowed, scale = 500  $\mu$ m. D, antapical view, scale = 500  $\mu$ m. E–F, NMV F99018, holotype. E, adapical region showing root pores and avicularia, scale = 200  $\mu$ m. F, detail of orifices and avicularia, scale = 200  $\mu$ m.

*Paratypes*. BMNH 2003.11.27.4 (as above), 1969.1.2.1, 1976.1.6.2 (part); NMV F99020–F99022. (67 colonies in total).

*Etymology*. *praecox* (L.) – precocious, immature, referring to the production of ovicells at the earliest astogenetic stages in these minute colonies.

*Diagnosis and description*. Colonies minute, domed, with mamillate calcification, that forms a raised mound adapically and covers the antapical surface. Primary orifice obscure, with a rounded sinus. Peristomes elongated; tubular and marginally prominent. Root pores adapical, rare, rounded. Lateral peristomial avicularia paired, very small, rostrum rounded. Ovicells developed on zooids of the second and third whorls, symmetrical, globular, very well calcified, opening into the peristome through a foramen. Ectoecium narrow, marginal; entoecium with frontal and marginal pores. Antapical surface granular and mamillate.

Colony diameter 0.50–0.80 mm, height 0.25–0.50 mm, number of whorls 2, number of zooids per whorl 3.

*Remarks*. *T. praecox* is known from more than 60 specimens, retrieved from one of the unstudied sediment samples from the *Challenger* collection, stored in the the Natural History Museum Mineralogy Department. Busk (1884) reported no bryozoan specimens from stn 185 from Cape York. Like *T. optatus*, *T. praecox* has ovicells that open into a tubular peristome but are symmetrical in development. They resemble those of *C. africana* Cook, 1966 (also Cook, 1981), that also has ovicells that differ from the ovicells observed in most other species in their relatively robust calcification. Of the 68 specimens examined, 17 have at least one completely developed ovicell. Some of the smallest colonies have two or three ovicells, developed on second or third astogenetic zooid generations. Although the specimens are all worn, scanning electron

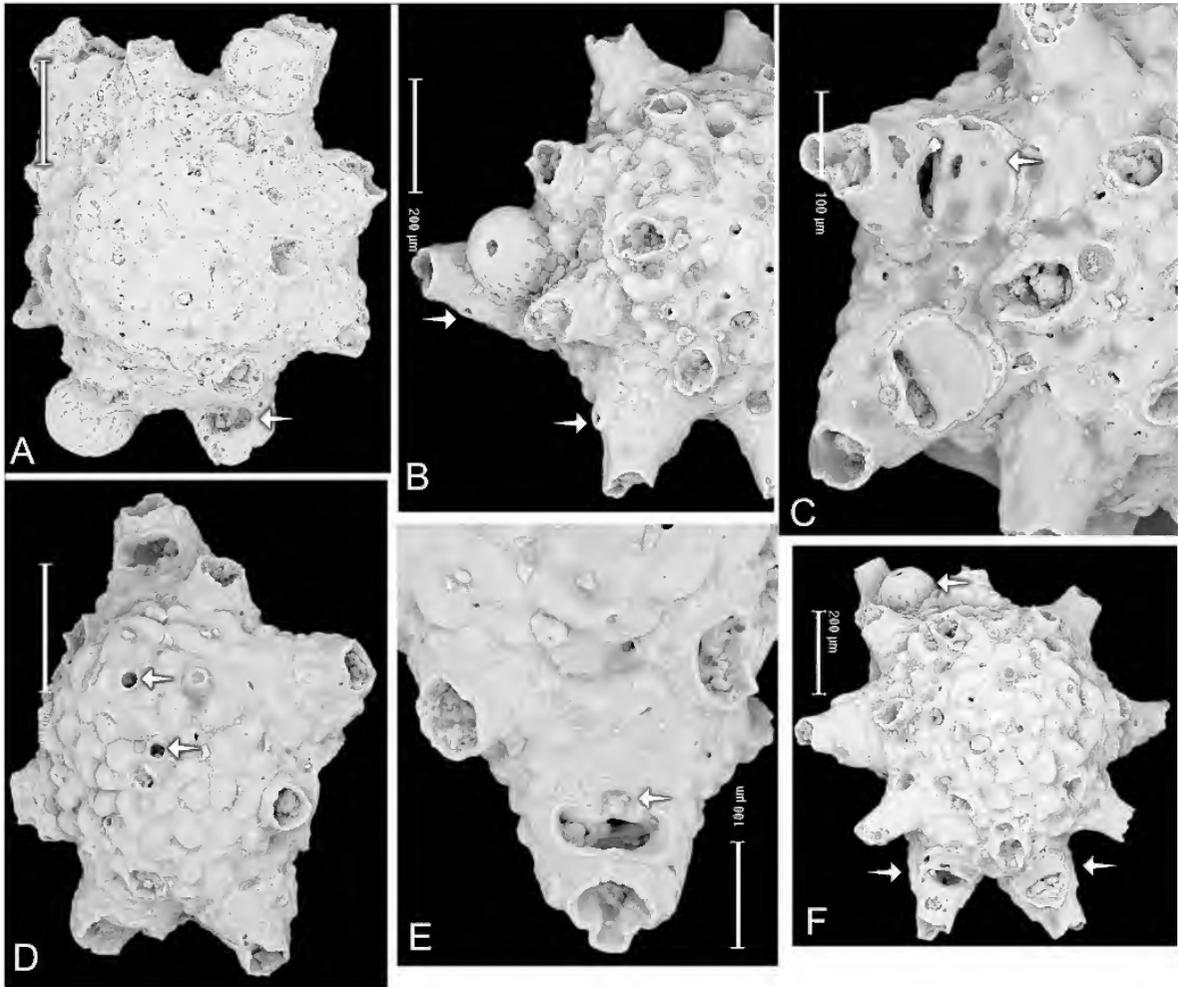


Figure 25. *T. praecox* sp. nov., Cape York, NMV F99020, paratype, detail of orifices and avicularia. with two complete ovicells and one peristomial foramen (arrowed), scale = 200 µm. B–C, NMV F99022, paratype, B, marginal zooids of colony with complete ovicell, avicularia arrowed, scale = 200 µm. C, detail of ovicells, showing ectooecial margin and central foramina of entoecium (arrowed); note avicularia, scale = 100 µm. D–E, NMV F99021, paratype. D, young colony with one peristomial foramen, root pores arrowed, scale = 200 µm. E, detail of foramen and adapical pore (arrowed), scale = 100 µm. F, NMV P99022, paratype. Colony with one complete and two developing ovicells (arrowed), scale = 200 µm.

microscopy has revealed details of ovicell development. Zooids apparently develop an elongated peristome, with a foramen on its adapical surface. This is in contact with an adapical pore (Fig. 25E) at its edge. An ectooecial and an entoecial lamina then grow together, one “below” the other, from the adapical pore in the adapical direction (Fig. 25C). The two laminae then curve in an antapical direction, forming a capsule. The fusion of the laminae with the lateral and antapical edges of the foramen finally closes it, forming the complete ovicell (Fig. 25B). It should be noted that this does not produce a peristomial ovicell, the walls of which are expansions of the frontal shield. The

ovicells of *T. praecox* comprise a separate development of ectooecium and entoecium. Other characteristics that are distinct enough for colonies to be recognised from additional, better preserved material, should it ever become available, are also revealed by scanning electron microscopy. The minute size of the colonies of *T. praecox* is comparable to those of accompanying foraminiferans; Cook (1981) noted the close similarity in appearance among them.

The occurrence of reproductive precocity in interstitial bryozoans with very small colonies has been described and discussed by Winston and Håkansson (1986: 43).

*Trochosodon gordonii* sp. nov.

*Trochosodon multiarmatus*.—Gordon, 1989: 83, pl. 49 figs D–F (not *Bipora multiarmata* Maplestone, 1909: 268).

*Etymology*. Named for Dr Dennis P. Gordon.

*Description*. Colony domed, wider than high, calcification finely mamillate. Zooid orifices in quincunx, sinus rounded, peristomes raised slightly marginally. Rounded avicularia and large frontal septular pores scattered among orifices. Circular root pores adapical. Antapical surface with a few avicularia.

*Remarks*. Gordon (1989) identified specimens from New Zealand as Maplestone's species and assigned them all to *Trochosodon*. He appears to have confused the dimensions of his colonies with those of *Conescharellina multiarmata*, that are always "higher than wide", not "typically wider than high", as he described. The broad orifice sinus of the New Zealand species is also quite unlike that of *C. multiarmata*. Gordon's species lacks any basal cancelli and has one or two large, circular, central rhizoid pores adapically. It appears to be referable to *Trochosodon* but certainly not to *Conescharellina multiarmata*. Gordon figured a specimen from Station P927 (40°50.1'S, 168°14.8'E, 1005–1009 m, western South Island, New Zealand) and reported it from numerous other localities from southern New Zealand, from a range of 540 to 1676 m depth.

*Crucescharellina* Silén, 1947

*Crucescharellina* Silén, 1947: 44.

*Agalmatozoum* Harmer, 1957: 757.

*Type species*. *Crucescharellina japonica* Silén, 1947 (original designation).

*Description*. Colonies are cruciform or star-shaped and may have branches that bifurcate terminally. The adapical zooid orifices are sinuate and interspersed with lunate or rounded root pores. The antapical growing edges are positioned at the limits of the branches but an antapical surface, that is the equivalent of the exposed frontal wall of conescharelliniform colonies, is also continuous and present on the "lower, non-orificial side" of colonies. It is inferred that the colonies live, in fact, with this antapical surface upward with the orifices directed downward, because the rhizoids that occur among them are inferred to anchor the colonies above or into the surface of the bottom sediments. Rounded or acute avicularia occur, that are occasionally large and spatulate. The orifices possess an adapical pore but ovicells have not been seen. Roots were figured in *C. japonica* by Silén (1947: pl. 1 fig. 11) and the position of the root pores suggests that the mode of life is similar to that inferred for the genus *Euginoma* (Hayward 1978), that also occurs from abyssal depths (d'Hondt and Schopf, 1984).

*Remarks*. *Crucescharellina* was introduced by Silén (1947) for *C. japonica* from near the Goto Islands, Japan, from a depth of 175 m. Only one colony was found; it was stellate but each branch originated from a narrow neck, one or two zooids in width. The branches rapidly expanded and then bifurcated, each subbranch starting with one or two zooids. The

subbranches also expanded rapidly, so that within two as togenetic generations, the segments were 4 zooids wide. Lunate root pores were present but these were not associated with branch bifurcations and no large, spatulate avicularia were described. Gordon and d'Hondt (1997: 73, figs 221–223) described "*C. japonica*" from the Philippines from 640–668 m. They too, had only one colony. It differed in having much less expanded branches, regular lunate root pores, and rare large axillary avicularia. The primary orifice had a shallow sinus and paired condyles. Silén (1947: 44) stated that he referred *Trochosodon decussis* Canu and Bassler (1929: 495, pl. 71 figs 7–10, from 456 m, east of Mindanao in the Philippines) to his genus *Crucescharellina*. Harmer (1957) was unaware of Silén's work, that was not available to him during the war of 1939–1945, and introduced *Agalmatozoum* for *Trochosodon decussis* Canu and Bassler (1929). Colonies of this species were cruciform, with triserial branches, and were described with lunate root pores and an elliptical secondary orifice. Avicularia or small pores were present antapically but no large avicularia were mentioned in the original description. Harmer (1957) listed more than ten colonies of *A. decussis* from seven localities in the Sulu, Banda, and Celebes Seas. The depths were nearly all abyssal, ranging from 535 to 3112 m. The branches of the colonies were mostly biserial and the root pores were circular, placed regularly at bifurcations, and surrounded by a ring of small avicularia. In addition, large, axillary spatulate avicularia sometimes occurred on the lateral sides of branches. The species from the *Siboga* area described by Harmer (1957) as *A. decussis* strongly resembles *Crucescharellina australis* from Australia described below, not the original form from the Philippines described by Canu and Bassler (1929). Gordon and d'Hondt (1997: 74, figs 224–227) introduced another very similar stellate species, *C. aster*, with biserial branches, from several New Caledonian and New Zealand localities at a depth range of 760 to 1573 m. The root pores were central and rounded but no large avicularia were present. Their material included numerous colonies, that they noted resembled "clusters of snowflakes". A single preparation of a colony in the Natural History Museum collection (BMNH 1963.8.18.18) closely resembles the description of *C. aster* but has slightly more extended, spiny peristomes. The specimen is from *Challenger* stn 169, off New Zealand (37°34'S, 179°22'E, 1295 m), a station that was not mentioned by Busk (1884). Gordon (1989: 84, pl. 1E figs 50B–E) described another biserial species, *C. jugalis*, from northern New Zealand, from a depth range of 1217–1357 m. The colonies were irregularly branched but had circular root pores very similar to those of the Australian *C. australis* and *A. decussis* sensu Harmer (1957).

Although there is no doubt of the synonymy of the two genera *Crucescharellina* and *Agalmatozoum*, there are uncertainties as to the identity of the various taxa referred to them in these previous descriptions. Among other records, Cook (1981) figured one of two very young, cruciform colonies from Cape York, from 279 m (BMNH 1976.1.6.2, part), as *Agalmatozoum* species. These, with the specimens of *C. australis* described here from Point Hicks, Victoria and from eastern Tasmania, remain the only records of *Crucescharellina* from Australian waters to date.

Labracherie and Sigal (1975) mentioned a form similar to *Crucescharellina* obtained from Lower Eocene samples collected from a deep-sea drilling south of Madagascar (33°37.21'S, 45°09.60'E, 1030 m). This was not described further but is not too remote from the Recent south-west Indo-Pacific records and, unlike the European Eocene species mentioned above, may represent an early form of Conescharellinidae.

***Crucescharellina australis* sp. nov.**

Figures 26A–E

*Holotype.* NMV F99024, stn SLOPE-27.

*Paratypes.* NMV F99025, stn SLOPE-27 (8 colonies).

*Other specimens.* NMV F101975, stn SOELA-S03/84/74, E. Tasmania, 320 m.

*Etymology.* *australis* (L.) – southern, referring to the distribution of the species.

*Diagnosis.* *Crucescharellina* with biserial branches; zooid orifice with a shallow sinus. Avicularia small and rounded; occasionally large, axillary spatulate. Root pores circular, placed at branch bifurcations.

*Description.* Colonies probably cruciform, present material with four branches. Branches biserial, bifurcating at each fourth to fifth astogenetic generation. Primary orifice with a wide, shallow sinus, and minute condyles; obscured at the base of a long peristome. These are sometimes raised antapically (i.e. towards the end of a branch) and may have 4–5 small, spinous processes on their margins. Avicularia small, rounded, near each peristome, bar without a ligula. Rare enlarged, spatulate avicularia placed in the axils between branches. Root pores regular.

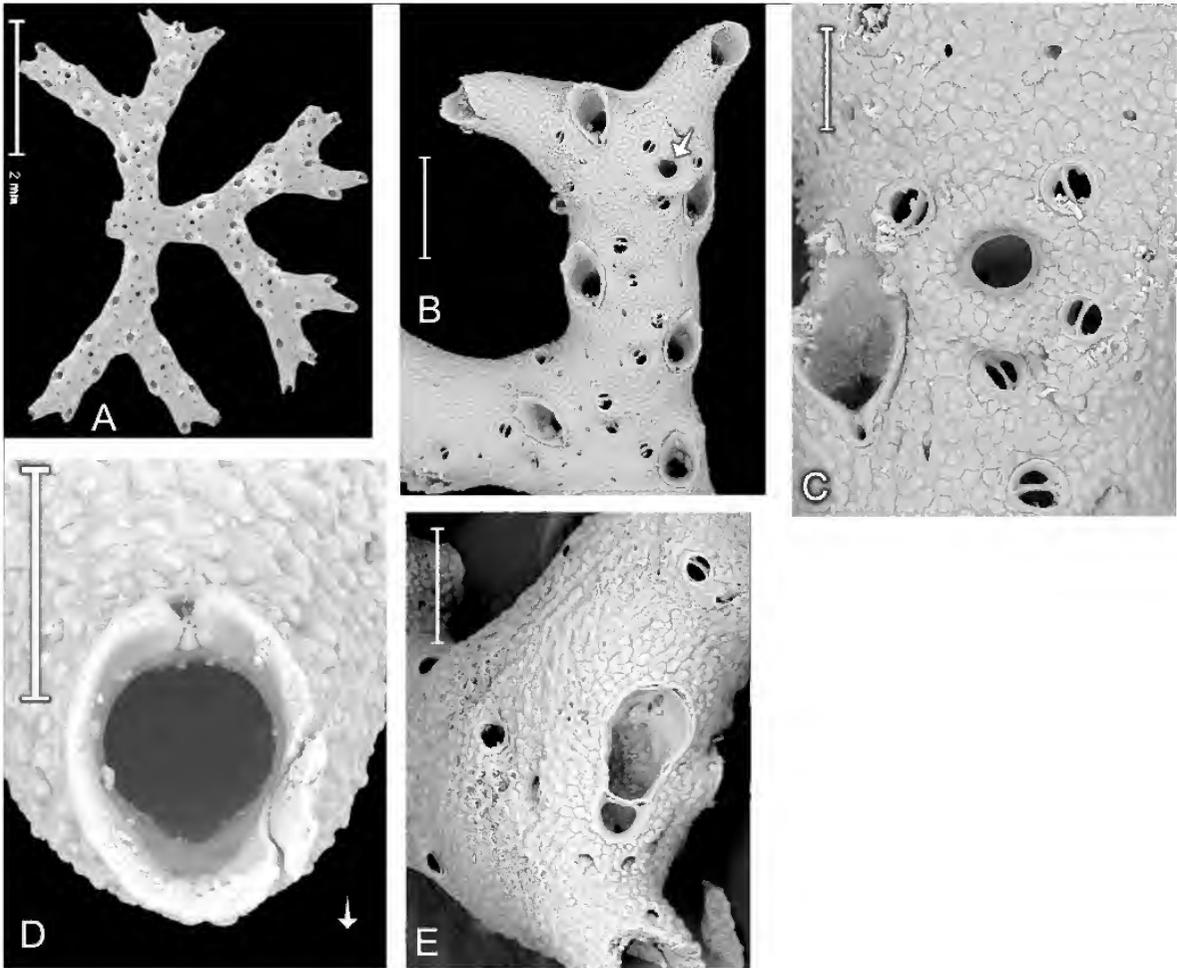


Figure 26. *Crucescharellina australis* sp. nov. A–D, NMV F99024, holotype. A, colony from adapical surface, scale = 2 mm. B, detail of branch showing orifices, avicularia and root pore (arrowed), scale = 500 µm. C, detail of root pore, scale = 200 µm. D, detail of orifice with adapical pore, direction of growth arrowed, scale = 100 µm. E, NMV F99025, paratype, large spatulate axillary avicularium, scale = 100 µm.

ularly placed at bifurcation of branches; circular, with a distinct rim, surrounded by 3–4 small avicularia. Adapical pore within the calcification of the edge of the peristome, present in many zooids, but no ovicells seen. Antapical surface finely granular, with approximately one small rounded avicularium per zooid.

Branches 0.6 mm width, length 6 mm.

**Remarks.** The specimens from stn SLOPE-27 comprise nine colony fragments. The largest show evidence of having once been cruciform but only four complete branches are now present. Two colonies have enlarged, spatulate avicularia in the axil between two branches, very similar to that shown in his “*A. decussis*” by Harmer (1957, pl. 49 fig. 13). The colony structure, type and distribution of root pores, and the large avicularia of *C. australis* make it virtually certain that it is conspecific with some specimens of *A. decussis* sensu Harmer but it is distinct from *T. decussis* Canu and Bassler (1929) and the other species mentioned above. Some fragmentary preparations of Harmers’ *Siboga* material, labelled *A. decussis*, from the BMNH collection, have been examined. The specimens are all slightly worn, and none possesses large avicularia. A cruciform colony and fragments from *Siboga* stn 211 (BMNH 1964.3.2.21, south of Celebes, 1158 m.), most closely resembles *C. australis*. Other fragments from *Siboga* stn 102 (BMNH 1964.3.2.23, Sulu Archipelago, 535 m.) differ in having triseriate branches and distinctly elongated avicularia near the zooid orifices. Some partially decalcified fragments from *Siboga* stn 221 (BMNH 1964.3.2.25, Banda Sea, 2798–3112 m.) also resemble *C. australis* but have raised peristomes on the antapical side of the orifices. They possess three long roots (over 20 mm), that emanate from the root pores. It is possible that Harmer’s material, identified as *A. decussis*, may belong to more than one species. Circular root pores surrounded by small avicularia also occur in *Conescharellina eburnea*, *C. plana*, *C. perculata* and *C. humerus*.

### *Zeuglopora* Maplestone, 1909

*Zeuglopora* Maplestone, 1909: 272.—Canu and Bassler, 1929: 510.—Harmer, 1957: 755.

**Type species.** *Zeuglopora lanceolata* Maplestone, 1909 (original designation).

**Description.** Colony similar to *Flabellopora*, ligulate, apparently composed of 2 laminae but in fact consisting of a pair of alternating and interdigitating expanses of frontally budded zooid series. Single or small groups of marginal zooids enlarged and prominent, forming a serrated edge, occasionally with enlarged avicularia. Orifices oval, with paired condyles forming a subtriangular antapical sinus; peristome tubular. A rounded adapical pore is present but ovicells are unknown. Avicularia usually small, rounded, with a bar but no ligula. Colony anchored by 1 or 2 roots, arising from lunate pores in the adapical region.

**Remarks.** Both Canu and Bassler (1929) and Harmer (1957) analysed the colony structure of *Zeuglopora* and maintained its distinction from *Flabellopora*.

### *Zeuglopora lanceolata* Maplestone, 1909

Figures 27, 28A–C

*Zeuglopora lanceolata* Maplestone, 1909: 272, pl. 78, fig. 11.—Harmer, 1957: 757.

*Bipora lanceolata*.—Livingstone, 1924: 211.

**Specimens examined.** NMV F99026, 1 colony labelled by Maplestone, probably part of the type material from NSW.

**Diagnosis and description.** As for the genus, serrated edges of colony formed by prominent zooids, that occur in alternating unequal pairs. Primary orifice with a subtriangular sinus and well developed paired condyles; obscured at the base of a tubular peristome, that is most prominent adapically. A rounded adapical pore, at a little distance from the edge of the peristome, is present in some central and antapical zooid orifices. Surface of zooids mammilate, interspersed with minute, rounded avicularia, with a bar but no ligula. Root pores lunate, adapical, paired, large and surrounded by extrazooical calcification.

Colony length 7 mm, breadth 2.25 mm. Number of astogenetic generations 12–13, number of zooids per generation 10.

**Remarks.** The single colony from New South Wales resembles Maplestone’s (1909) description. The orifices of the enlarged marginal zooids are surrounded by up to five small avicularia and resemble the root pores of *C. eburnea* and *C. plana*. However, the adapical end of the colony shows that the actual root pores resemble those of *Flabellopora* and consist of large lunate pores surrounded by massive, secondary extrazooical calcification. The adapical pore is large and a little offset in position towards the colony margin. It seems probable that any ovicell would be slightly asymmetrically placed. Harmer (1957: 737) examined a colony that was part of Maplestone’s (1909) type material in the BMNH collection (BMNH 1909.11.12.3). It has a large adapical foramen that was filled with detritus. It seems almost certain that this colony actually possessed paired, lunate adapical root pores like other specimens (Fig. 28C). There are no additional records of *Z. lanceolata* from Australia but Canu and Bassler (1929: 511, pl. 75, fig. 6) described a very similar colony from deep water (630 m) north-east of Borneo as *Z. lanceolata*, an identification accepted by Harmer (1957). The locality was remote from Australia; the figured colony is slightly narrower than those from Australia, with more prominent marginal zooids than the type specimens. The character of the primary orifices, root pores and avicularia are uncertain. Harmer (1957) also described a new species, *Z. arctata*, from two minute colonies from 82 m off Java, where the bottom sediment consisted of fine grey mud. Each colony had large marginal avicularia, and a long single root emanating from the adapical region. Cadée (1987: 52) noted the occurrence of several hundred colonies of *Z. arctata* together with an undescribed species from soft-bottom sediments in the Banda Sea but gave no detailed descriptions. Lu (1991) described several species of *Zeuglopora* (as *Bipora*) from the South China Sea. His *B. pagoda* (p. 70, pl. 18 fig. 2) and *B. trinodata* (p. 71, pl. 18 fig. 3) both resemble the unnamed species mentioned by Cadée (1987).

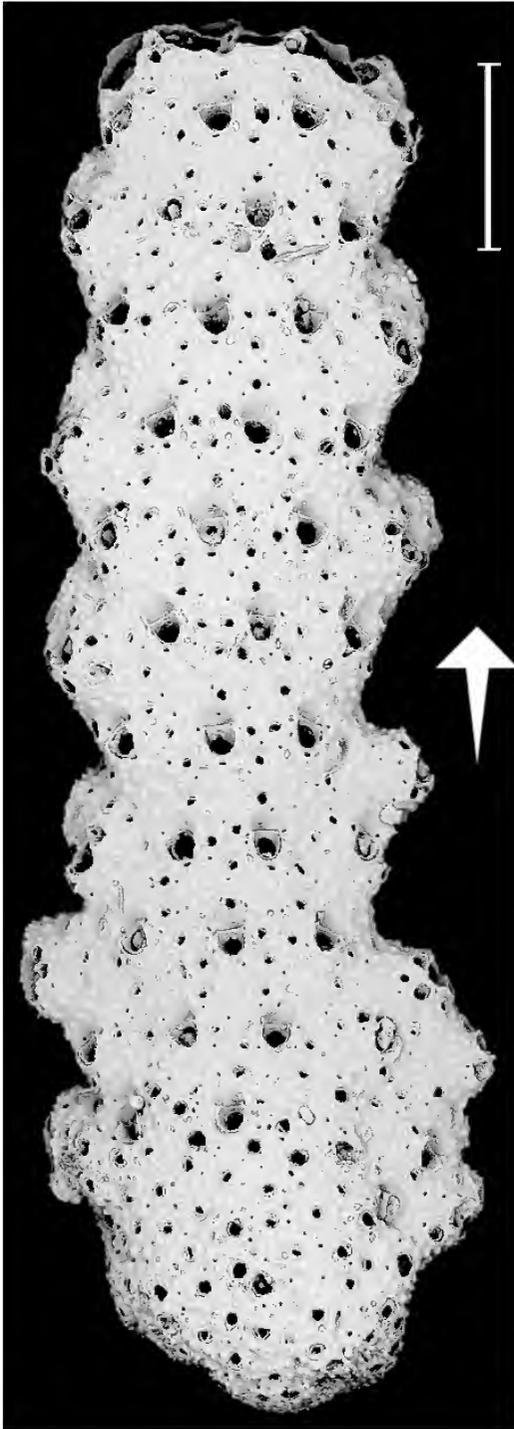


Figure 27. *Zeuglopora lanceolata* Maplestone, 1909. NMV F99026. Lateral view of colony, direction of growth arrowed, scale = 1 mm.

*Flabellopora* d'Orbigny, 1851

*Flabellopora* d'Orbigny, 1851: 52.

*Flabillopora*, d'Orbigny, 1852: 186 (bis) (lapsus).—Canu and Bassler, 1929: 495.—Harmer, 1957: 749.—Silén, 1947: 47.—Lu, 1991: 72.

*Type species. Flabellopora elegans* d'Orbigny, 1851 (monotypy).

*Description.* Colony leaf-like or trilobed, superficially appearing to be bilaminar, anchored by root systems originating from lunate pores on the adapical edge. Zooids in alternating and interdigitating frontally budded series, orifices sinuate, the sinuses orientated antapically towards the growing edge. A small adapical pore sometimes present. Avicularia in patterns among orifices, usually small and rounded, with a bar but no ligula. Ovicells unknown but presumably originating from adapical pores.

*Remarks.* *F. elegans* was recorded by d'Orbigny (1851: 53) from about 20 m. "près de Quantang et d'Hainan" in the China Sea. Later, d'Orbigny (1852: 186 bis) mentioned additional specimens from "dans le détroit de Malaca et à Manille" [sic]. Harmer (1957: 751) noted that Waters' (1905: 9, pl. 1 fig. 5) figured specimen from the d'Orbigny collection was from Malacca. It was therefore certainly not of the type specimen and may not even have been of the same species. Waters' figure, like those of *Conescharella* from the d'Orbigny collection (see above), was semidiagrammatical and included only three zooid orifices. A photograph of the type specimen (Taylor and Gordon, 2002, fig.3D) closely resembles d'Orbigny's 1852 illustration but provides no details of the primary orifices or distribution of avicularia. As in the case of *Conescharella*, the generic characters of d'Orbigny's descriptions and illustrations are unmistakable but the details of specific characters are obscure and require examination and redescription of the type specimen.

Delicate roots up to 25 mm in length were described by Harmer (1957), who noted their origin from lunate pores. In one of the trilobed colonies he illustrated, as *F. irregularis* (pl. 49 fig. 6), thirteen roots occur along the adapical edge of the colony. Ovicells are unknown in *Flabellopora* although d'Orbigny (1852: 186 bis) mentioned the presence of a "pore ovarien". It is not known if this is the equivalent of the "proximal pore" of Harmer (1957) or the adapical pore, that is now known to be the origin of ovicells in *Conescharella* and *Trochosodon*. Harmer (1957: 749, text-fig. 79) illustrated the central region of a colony expanse, that showed hemispherical areas of calcification adapically to zooid orifices. The surrounding calcification was raised into "lozenge-shaped" areas, a term used by Canu and Bassler (1929). Harmer suggested that each hemispherical calcification might represent the basal part (i.e. the ectoecium) of an ovicell. He figured and mentioned the presence of "proximal pores" but did not appear to associate them with ovicells. Adapical pores have been found frequently in the specimens examined here but they are usually associated with zooids that are marginal in position; they are not distributed in the centre of colony expanses, or surrounded by raised "lozenges".

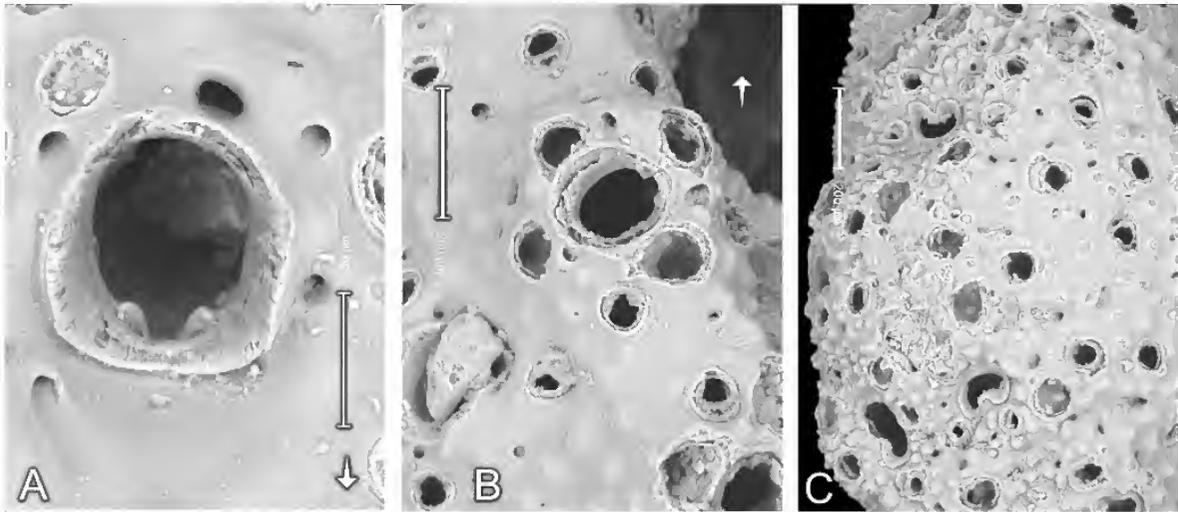


Figure 28. *Zeuglopora lanceolata* Maplestone, 1909. NMV F99026. A, detail of orifice with adapical pore, scale = 100  $\mu$ m. B, detail of large, marginal zooid orifice with surrounding avicularia, direction of growth arrowed, scale = 200  $\mu$ m. C, adapical region showing lunate root pores, scale = 200  $\mu$ m.

***Flabellopora umbonata*** (Haswell, 1881)

Figures 29A–C

*Eschara umbonata* Haswell, 1881: 41, pl. 2 figs 5, 6.

*Bipora umbonata*.—Whitelegge, 1887: 345.—Livingstone, 1924: 209.—Livingstone, 1926: 98, pl. 5 figs 4, 5.

*Bipora mamillata* Maplestone, 1909: 270, pl. 77 fig. 7.

*Conescharellina mamillata*.—Bretnall, 1922: 191.

*Specimens examined*. NMV F99395, stn SLOPE-40 (1 colony); NMV F101976, stn GAB-020 (2 young and 1 trilobed colony with roots, plus fragments); NMV F101977, stn GAB-030 (2 young and 2 trilobed colonies with roots, plus fragments); NMV F101978, stn GAB-045 (1 trilobed colony with roots, plus fragments); NMV F101979, stn GAB-056 (1 colony with fragments); NMV F101980, stn GAB-067 (1 trilobed colony); NMV F101981, stn GAB-074 (5 fragments); NMV F101982, stn GAB-084 (2 trilobed colonies plus fragments); NMV F101983, stn GAB-088 (1 colony plus fragments); NMV F101984, stn GAB-093 (1 large colony); NMV F101985, stn GAB-112 (1 colony); NMV F101986, stn GAB-117 (1 trilobed colony plus fragments); NMV F101987, stn GAB-119 (2 young and 3 trilobed colonies); NMV F101988, stn GAB-128 (1 trilobed colony); NMV F101989, stn SOELA-S03/84/74, E. Tasmania, 320 m (1 colony).

*Description*. Colony leaf-shaped, sometimes trilobed. Zooid frontal shield continuous, without zooid borders; calcification smooth with umbonate mamillae occurring among the orifices and the avicularia. Orifices almost circular, patent, with a rounded sinus, peristomial rim raised, narrow; adapical pores present. Avicularia small, rostra subtriangular or rounded, bar without a ligula. Septular pores rare, scattered. Root pores lunate, on the adapical edge, surrounded by thickened calcification.

*Remarks*. Livingstone (1924, 1926) and Harmer (1957) examined specimens from Queensland that were reported to be from Haswell's original material, although only fragments of this were preserved. Maplestone's (1909) type specimen of *Bipora mamillata* was unique but Livingstone (1924) mentioned "types" that may have had a different provenance. Both Livingstone and Harmer were convinced that *F. umbonata* was identical with *B. mamillata*, Maplestone (1909) however had noted some differences, both within Haswell's suite of specimens and between them and his colonies from New South Wales.

The numerous specimens examined here are often slightly worn and very few possess roots. There are small differences among specimens but these seem to be the result of astogenetic position, ontogenetic thickening and wear. Some specimens have larger umbonate mamillae among orifices than others and some have larger avicularia but none of these differences is correlated with locality. The specimens from stations GAB-020, GAB-030 and GAB-119 include several very young colonies. These are lanceolate and consist principally of parallel series of antapically directed zooids with few laterally inclined series. Later growth illustrated the development of paired lateral laminae, giving the typically trilobed shape. One regenerated colony from station GAB-093 has a diameter of 28 mm and has developed nine thickened rays from an irregular central area. It is possible that other species of *Flabellopora* occur in Australian waters but have not yet been recognised.

***Ptoboroa*** Gordon and d'Hondt, 1997

*Ptoboroa* Gordon and d'Hondt, 1997: 70, pl. 47F, G, 48A.

*Type species*. *Trochosodon pulchrior* Gordon, 1989: 81 (original designation).

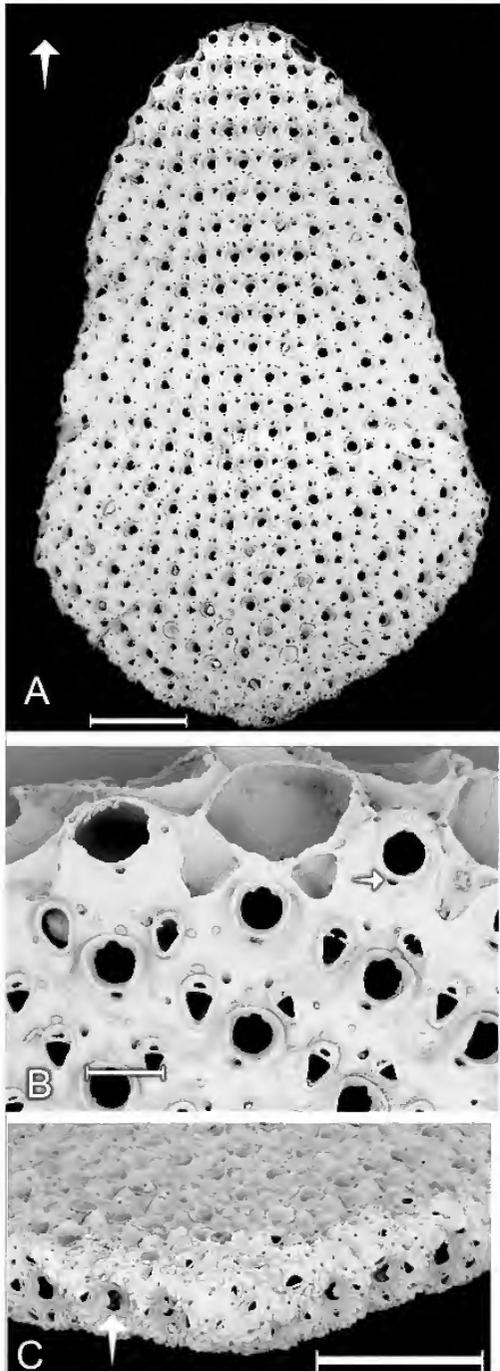


Figure 29. A–C, *Flabellopora umbonata* (Haswell, 1881). NMV F99395, stn GAB-056. A. Colony, growth direction arrowed, scale = 1 mm. B. Antapical region showing orifices and avicularia, adapical pore arrowed, scale = 200  $\mu$ m. C. Adapical region, root pore arrowed, scale = 1 mm.

*Remarks.* No species of *Ptoboroa* has been found in the present collections. *P. pulchrior* from New Zealand is strikingly similar to a species of *Batopora* from stations SLOPE-6 and SLOPE-7 but differs in the possession of an adapical pore, indicating its closer association with the Conescharellinidae, particularly *Trochosodon*, in the development and form of its ovicells (Bock and Cook, in press).

#### Summary and discussion

Six of the seven genera of Conescharellinidae (*Conescharellina*, *Bipora*, *Trochosodon*, *Zeuglopora*, *Crucescharellina* and *Flabellopora*) are represented in Australian waters (see Appendix). The seventh genus, *Ptoboroa*, is at present known only from New Zealand and New Caledonia (Bock and Cook, in press). Records occur from north-west Australia, Cape York, Queensland, the coasts of New South Wales and Victoria, and Western Australia to Tasmania. Numerous Tertiary samples from Victoria and South Australia have been examined.

Although many species, particularly of *Conescharellina*, have been described from the western Pacific region by Canu and Bassler (1929), Silén (1947) and Harmer (1957), the present collections include an unexpectedly high proportion (approximately 66%) of new taxa. There are apparently several explanations for this diversity. First, the number of colonies examined is greatly in excess of any other named collection. The total number is more than 1940, of which 52% are Recent specimens. A few species are represented by only one to three colonies, occurring from a single locality (for example *Conescharellina perculata*, *Trochosodon ampulla*, *T. fecundus* and *Zeuglopora lanceolata*), and 30 localities provided specimens of only one species. In contrast, seven taxa are represented by more than 60 colonies (for example *C. cognata* (177), *C. plana* (120), *C. biarmata* (98), *C. multiarmata* (85), *C. diffusa* (82), *C. ecstasis* (71) and *T. praecox* (67), while stn SLOPE-7 and stn GAB-020 include specimens of six species each). The Tertiary accumulations of colonies include 438 of *C. macgillivrayi* from seven localities, 360 of *C. humerus* from five localities and 102 of *C. ocellata* from two localities. The large number of specimens allows comparisons among and within populations, and subsequent definition of taxa with confidence, within a range of variation. Second, the reports of Australian species made in the nineteenth and early twentieth centuries were from fairly restricted geographical and bathymetrical localities, mostly from New South Wales. The extensive geographic range of species examined here has revealed new taxa and also allowed investigation of their variation. For example, there are differences between populations of *C. diffusa*, that has a range from north-west Australia to Tasmania but its essential characteristics are consistent. Third, the interstitial or semi-interstitial mode of life, particularly at very deep localities, may reduce the possibility of wide dispersal of some larvae but the distribution of *C. ecstasis*, from New South Wales to Tasmania from a depth range of 400 to 1096 m, suggests that some other factors are involved. Fourth, examination of colonies using the scanning electron microscope, often for the first time, has refined definitions of previously described species and has revealed characters and character states essential for future investigations.

The Australian fauna of Conescharellinidae appears to be quite distinct from the Indo-West-Pacific fauna to the north and the New Zealand fauna to the east. Further investigations may show similarities among the deeper water faunas of New Caledonia and the eastern Australian coast, for example, among species of *Crucesharellina*. There are also some tenuous links with New Zealand illustrated by populations of *C. cognata*. Little is known of fossil populations of Conescharellinidae; only *Conescharellina* has an established fossil record. The three most abundant fossil species are not only very similar to one another in characters, they appear to have little in common with any of the Recent forms. All have very small colonies that are apparently astogenetically mature; all have rounded root pores with a cirlet of avicularia. *C. ocellata* resembles *C. eburnea* in possessing a pair of antapical avicularia on marginal peristomes but there is no evidence of any descendant sequence among the specimens examined.

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### References

- Accordi, B. 1947. Nuove forme di Briozoi eocenici. *Studi Trentini di Scienze Naturali Acta Geologica* 25: 103–110.
- Arnold, P., and Cook, P.L. 1997. Some Recent species of the genus *Anaskopora* Wass., 1975 (Bryozoa: Cribriomorpha) from Queensland. *Memoirs of the Queensland Museum* 42: 1–11.
- Banta, W.C. 1972. The body wall of cheilostome Bryozoa, V. Frontal budding in *Schizoporella unicornis floridana*. *Marine Biology* 14: 63–71.
- Bock, P.E., and Cook, P.L. 1996. The genus *Selenariopsis* Maplestone, 1913 (Bryozoa, Ascophorina). *Records of the South Australian Museum* 29: 23–31.
- Bock, P.E., and Cook, P.L. 2000. Lekythoporidae (Bryozoa, Cheilostomata) from the Tertiary and Recent of southeastern Australia. *Memorie di Scienze Geologiche* 52: 167–174.
- Bock, P.E., and Cook, P.L. 2001. Revision of the multiphased genus *Corbulipora* MacGillivray (Bryozoa: Cribriomorpha). *Memoirs of Museum Victoria* 58: 191–213.
- Bock, P.E., and Cook, P.L., in press. New species of the bryozoan genera *Batopora* and *Lacrimula* (Batoporidae) from Australia. *Proceedings of the Royal Society of Victoria*.
- Brettnall, R.W. 1922. Studies on Bryozoa 2. 1. On a collection of Bryozoa from 26–38 fathoms off Norah Head. *Records of the Australian Museum* 13: 189–192.
- Brown, D.A. 1958. Fossil cheilostomatous Polyzoa from south-west Victoria. *Memoirs of the Geological Survey of Victoria* 10: 1–90.
- Brown, K.M., Schmidt, R., and Bone, Y. 2002. Observations on ecological adaptations of *Lanceopora smeatoni* (MacGillivray), from West Island, South Australia. Pp. 61–65 in: Wyse Jackson, P.N., Butler, C.J., and Spencer-Jones, M. (eds), *Bryozoan Studies 2001*. A.A. Balkema Publishers: Lisse, Abingdon, Exton, Tokyo.
- Busk, G. 1854. *Catalogue of marine Polyzoa in the collection of the British Museum, II. Cheilostomata (part)*. Trustees of the British Museum (Natural History): London. pp. viii, 55–120.
- Busk, G. 1884. Report on the Polyzoa collected by H.M.S. *Challenger* during the years 1873–1876. Part 1. The Cheilostomata. *Report on the Scientific Results of the Voyage of the H.M.S. "Challenger"*, *Zoology* 10: 1–216.
- Cadée, G.C. 1987. The shallow soft-bottom faunas of the Java Sea and Banda Sea. Pp. 49–56 in: Ross, J.R.P. (ed.), *Bryozoa: Present and Past*. Western Washington University: Bellingham.
- Canu, F., and Bassler, R.S. 1917. A synopsis of American Early Tertiary Cheilostome Bryozoa. *United States National Museum Bulletin* 96: 1–87.
- Canu, F., and Bassler, R.S. 1927. Classification of the cheilostomatous Bryozoa. *Proceedings of the United States National Museum* 69: 1–42.
- Canu, F., and Bassler, R.S. 1929. Bryozoa of the Philippine region. *United States National Museum Bulletin* 100: 1–685.
- Cheetham, A.H. 1966. Cheilostomatous Polyzoa from the Upper Bracklesham Beds (Eocene) of Sussex. *Bulletin of the British Museum (Natural History) (Geology)* 13: 1–115.
- Cook, P.L. 1966. Some "sand fauna" Polyzoa (Bryozoa) from Eastern Africa and the northern Indian Ocean. *Cahiers de Biologie Marine* 7: 207–223.
- Cook, P.L. 1979. Mode of life of small, rooted "sand fauna" colonies of Bryozoa. Pp. 269–281 in: Larwood, G.P., and Abbott, M.B. (eds), *Advances in Bryozoology*. Academic Press: London.
- Cook, P.L. 1981. The potential of minute bryozoan colonies in the analysis of deep sea sediments. *Cahiers de Biologie Marine* 22: 89–106.
- Cook, P.L. 1985. Bryozoa from Ghana. A preliminary survey. *Annales Musee Royale de l'Afrique Centrale, Sciences Zoologiques, Tervuren* 238: 1–315.
- Cook, P.L., and Bock, P.E. 1994. The astogeny and morphology of *Rhabdozoum wilsoni* Hincks (Anasca, Buguloidea). Pp. 47–50 in: Hayward, P. J., Ryland, J.S., and Taylor, P.D., (eds), *Biology and Palaeobiology of Bryozoans*. Olsen and Olsen: Fredensborg.
- Cook, P.L., and Chimonides, P.J. 1981. Morphology and systematics of some rooted cheilostome Bryozoa. *Journal of Natural History* 15: 97–134.
- Cook, P.L., and Chimonides, P.J. 1985. Larval settlement and early astogeny of *Parmularia* (Cheilostomata). Pp. 71–78 in: Nielsen, C., and Larwood, G.P. (eds), *Bryozoa: Ordovician to Recent*. Olsen and Olsen: Fredensborg.
- Cook, P.L., and Chimonides, P.J. 1987. Recent and fossil Lunulitidae (Bryozoa, Cheilostomata), 7. *Selenaria maculata* (Busk) and allied species from Australasia. *Journal of Natural History* 21: 933–966.
- Cook, P.L., and Lagaaij, R. 1976. Some Tertiary and Recent conescharelliniform Bryozoa. *Bulletin of the British Museum (Natural History), Zoology* 29: 317–376.
- Gordon, D.P. 1984. The marine fauna of New Zealand: Bryozoa: Gymnolaemata from the Kermadec Ridge. *New Zealand Oceanographic Institute Memoir* 91: 1–198.
- Gordon, D.P. 1985. Additional species and records of Gymnolaemate Bryozoa from the Kermadec region. *Records of the New Zealand Oceanographic Institute* 4: 160–183.
- Gordon, D.P. 1989. The marine fauna of New Zealand: Bryozoa: Gymnolaemata (Cheilostomida Ascophorina) from the western south Island continental shelf and slope. *New Zealand Oceanographic Institute Memoir* 97: 1–158.

- Gordon, D.P., and d'Hondt, J.-L. 1997. Bryozoa: Lepraliomorpha and other Ascophorina from New Caledonian waters. *Mémoires du Muséum National d'Histoire Naturelle, Paris* 176: 9–124.
- Gregory, J.W. 1893. On the British Palaeogene Bryozoa. *Transactions of the Zoological Society of London* 13: 219–279.
- Grischenko, A.V., Gordon, D.P., and Taylor, P.D. 1998 (1999). A unique new genus of cheilostomate bryozoan with reversed-polarity zooidal budding. *Asian Marine Biology* 15: 105–117.
- Hageman, S.J., Bone, Y., McGowran, B., and James, N.P. 1996. Bryozoan species distributions on the cool-water Lacedpede Shelf, southern Australia. Pp. 109–116 in: Gordon, D.P., Smith, A.M., and Grant-Mackie, J.A. (eds), *Bryozoans in Space and Time*. NIWA: Wellington.
- Harmer, S.F. 1957. The Polyzoa of the *Siboga* Expedition, Part 4. Cheilostomata Ascophora II. *Siboga Expedition Reports* 28d: 641–1147.
- Haswell, W.A. 1881. On some Polyzoa from the Queensland Coast. *Proceedings of the Linnean Society of New South Wales* 5: 33–44.
- Hayward, P.J. 1978. The morphology of *Euginoma vermiformis* Jullien (Bryozoa, Cheilostomata). *Journal of Natural History* 12: 97–106.
- Hayward, P.J., and Cook, P.L. 1979. The South African Museum's Meiring Naude Cruises. Part 9, Bryozoa. *Annals of the South African Museum* 79: 43–130.
- Hincks, T. 1880. *A history of the British Marine Polyzoa*. Van Voorst: London. cxli + 601 pp.
- Hincks, T. 1881. Contributions towards a general history of the marine Polyzoa. (Part VI. Polyzoa from Bass's Straits continued, no title). *Annals and Magazine of Natural History* (5) 8: 122–129 (separate pp. 63–70).
- Hincks, T. 1892. Contributions towards a general history of the marine Polyzoa. Appendix. *Annals and Magazine of Natural History* (6) 9: 327–334 (separate pp. 190–197).
- d'Hondt, J.-L. 1985. Contribution à la systématique des Bryozoaires Eurystomes. Apports récents et nouvelles propositions. *Annales des Sciences Naturelles, Zoologie et Biologie Animale* (13) 7: 1–12.
- d'Hondt, J.-L., and Schopf, T.J.M. 1984. Bryozoaires des grandes profondeurs recueillis lors des campagnes océanographiques de la Woods Hole Oceanographic Institution de 1961 à 1968. *Bulletin du Muséum National d'Histoire Naturelle, Paris* (4) 6A (4): 907–973.
- Jelly, E.C. 1889. *A synonymic catalogue of the Recent marine Bryozoa*. Dulau and Company: London. 322 pp.
- Kirkpatrick, R. 1890. Reports on the zoological collections made in Torres Straits by Professor A.C.Haddon, 1888–1889. Hydroida and Polyzoa. *Scientific Proceedings of the Royal Dublin Society, new series* 6: 603–626.
- Labracherie, M. 1975. Sur quelques bryozoaires de l'Eocene inférieur nord-aquitain. *Revista Española de Micropaleontología* 7: 127–164.
- Labracherie, M., and Sigal, J. 1975. Les Bryozoaires cheilostomes des formations Eocene Inférieur du Site 246 (croisière 25, Deep Dea Drilling Project). Pp. 449–466 in: Pouyet, S. (ed.), *Bryozoa 1974 (Documents de Laboratoires de Géologie Faculté de sciences de Lyon, HS 3)* Université Claude Bernard: Lyon.
- Levinsen, G.M.R. 1909. *Morphological and systematic studies on the cheilostomatous Bryozoa*. Nationale Forfatterers Forlag: Copenhagen. 431 pp.
- Livingstone, A.A. 1924. Studies on Australian Bryozoa. No. 1. *Records of the Australian Museum* 14: 189–212.
- Livingstone, A.A. 1925. Studies on Australian Bryozoa. No. 2. *Records of the Australian Museum* 14: 301–305.
- Livingstone, A.A. 1926. Studies on Australian Bryozoa. No. 3. *Records of the Australian Museum* 15: 79–99.
- Livingstone, A.A. 1928. Bryozoa from South Australia. *Records of the South Australian Museum* 4: 111–124.
- Lu Linhuang 1991. Holocene bryozoans from the Nansha sea area. Pp. 11–81, 473–486 in: Multidisciplinary Oceanographic Expedition Team of Academia Sinica to the Nansha Islands (eds), *Quaternary Biological Groups of the Nansha Islands and the Neighbouring Waters*. Zhongshan University Publishing House: Guangzhou.
- MacGillivray, P.H. 1895. A monograph of the Tertiary Polyzoa of Victoria. *Transactions of the Royal Society of Victoria* 4: 1–166.
- Maplestone, C.M. 1904. Tabulated list of the fossil cheilostomatous Polyzoa in the Victorian Tertiary deposits. *Proceedings of the Royal Society of Victoria (new series)* 17: 182–219.
- Maplestone, C.M. 1909. The results of deep-sea investigations in the Tasman Sea. The expedition of the H.M.C.S. "Miner", 5. The Polyzoa. *Records of the Australian Museum* 7: 267–273.
- Maplestone, C.M. 1910. On the growth and habits of the Biporae. *Proceedings of the Royal Society of Victoria (new series)* 23: 1–7.
- Neviani, A. 1895. Briozoi Eocenici del calcare nummulitico di Mosciano presso Firenze. *Bolletino della Società Geologica Italiana* 14: 119–129.
- Neviani, A. 1901. Briozoi neogenici delle Calabrie. *Palaeontographia Italica* 6 (1900), 115–266.
- d'Orbigny, A. 1851–1854. *Paléontologie française, Terrains Crétacés, V. Bryozoaires*. Victor Masson: Paris (1851: 1–188; 1852, 185 bis–472; 1853, 473–984; 1854, 985–1192).
- Pizzaferrri, C., and Braga, G. 2000. Nuove osservazioni sullo sviluppo astogenetico di *Batopora rosula* (Reuss), Bryozoa Cheilostomatida del Miocene del Pedeaappennino Parmense. *Annali dei Museo Civico – Rovereto* 14 (1998): 55–88.
- Reuss, A.E. 1867. Über einige Bryozoen aus dem deutschen Unteroligozän. *Sitzungsberichte der Akademie der Wissenschaften in Wien (Abt. 1)* 55: 216–234.
- Ryland, J.S. 1982. Bryozoa. Pp. 743–769 in: Parker, S.P. (ed.), *Synopsis and classification of living organisms*. McGraw-Hill: New York.
- Silén, L. 1947. Conescharellinidae (Bryozoa Gymnolaemata) collected by Prof. Dr Sixten Bock's expedition to Japan and the Bonin Islands 1914. *Arkiv för Zoologi* 39A: 1–59.
- Stoliczka, F. 1862. Oligocäne Bryozoen van Latdorf in Bernburg. *Sitzungsberichte der Kaiserlichen Akademie Wissenschaften Wien* 45, Abt. 1: 71–94.
- Taylor, P.D., and Gordon, D.P. 2002. Alcide d'Orbigny's work on Recent and fossil bryozoans. *Comptes Rendus Palevol* 1 (7): 533–547.
- Tenison Woods, J.E. 1880. On some Recent and fossil species of Australian Selenariidae (Polyzoa). *Transactions of the Royal Society of South Australia* 3: 1–12.
- Waters, A.W. 1881. On fossil chilostomatous Bryozoa from south-west Victoria, Australia. *Quarterly journal of the geological society (London)* 37: 309–347.
- Waters, A.W. 1882a. On fossil Chilostomatous Bryozoa from Mount Gambier, South Australia. *Quarterly Journal of the Geological Society (London)* 38: 257–276.
- Waters, A.W. 1882b. On fossil chilostomatous Bryozoa from Bairnsdale, (Gippsland). *Quarterly Journal of the Geological Society (London)* 38: 502–513.
- Waters, A.W. 1887. Bryozoa from New South Wales, North Australia, etc. Part II. *Annals and Magazine of Natural History* (5) 20: 181–203.
- Waters, A.W. 1889. Bryozoa from New South Wales, North Australia, etc. Part IV. *Annals and Magazine of Natural History* (6) 4: 1–24.
- Waters, A.W. 1904. Bryozoa. Résultats du Voyage du S.V. "Belgica", Zoologie. *Expedition Antarctique Belge* 4: 1–114.
- Waters, A.W. 1905. Notes on some Recent Bryozoa in d'Orbigny's collection. *Annals and Magazine of Natural History* (7) 15: 1–16.

- Waters, A.W. 1919. On *Batopora* and its allies. *Annals and Magazine of Natural History* (9) 3: 79–94.
- Waters, A.W. 1921. Observations on the relationships of the (Bryozoa) Selenariidae, Conescharellinidae, etc., fossil and Recent. *Journal of the Linnean Society (Zoology) London* 34: 399–427.
- Whitelegge, T. 1887. Notes on some Australian Polyzoa. *Proceedings of the Linnean Society of New South Wales* 2: 337–347.
- Whitelegge, T. 1888. Notes on some Australian Polyzoa. *Annals and Magazine of Natural History* (6) 1: 13–22.
- Winston, J.E., and Håkansson, E. 1986. The interstitial fauna of the Capron Shoals, Florida. *American Museum Novitates* 2865: 1–98.
- Zágoršek, K. 2001. Upper Eocene Bryozoa from the Alpine Foreland Basin in Salzburg, Austria (Borehole Helmsberg-1). *Österreichische Akademie der Wissenschaften, Schriftenreihe der Erdwissenschaftlichen Kommissionen* Band 14: 509–609.
- Zágoršek, K., and Kázmér, M. 2001. Eocene Bryozoa from Hungary. *Courier Forschungsinstitut Senckenberg* 231: 1–159.

#### Appendix. Station numbers, details of localities, latitude, longitude, depth, with distribution of species

##### Maplestone specimens

South Australia, *C. biarmata*, *C. magniarmata*, *C. cognata*, *C. diffusa*

Kangaroo I., South Australia, *C. cognata*.

Locality assumed to be NSW and includes part of type material described by Maplestone (1909). “*C. angulopora*” sensu Maplestone, *C. biarmata*, *C. magniarmata*, *C. cognata*, *C. diffusa*, *C. pustulosa*, *Trochosodon ampulla*, *Zeuglopora lanceolata* BMNH 1976.1.6.2, Cape York, Queensland, *Challenger* stn 185, 279 m, *Trochosodon fecundus*, *T. anomalus*, *T. praecox*

##### Museum Victoria Bass Strait Survey

BSS-055, 39°9'S, 143°26', 85 m, *C. cognata*.

BSS-065, 39°5'S, 142°33' 207 m, *C. cognata*.

BSS-117, 40°38'S, 145°23'E 36 m, *C. pustulosa*.

BSS-130, 39°38'S, 145°5.01'E 66 m, *C. cognata*.

BSS-155, 38°24'S, 144°54.03'E, 70 m, *C. cognata*.

BSS-158, 38°34'S, 144°54.03'E, 82 m, *C. cognata*, *C. pustulosa*.

BSS-159, 39°46'S, 146°18'E, 80 m, *C. cognata*.

BSS-161, 39°47'S, 147°19.3'E, 60 m, *C. cognata*.

BSS-162, 40°9.4'S, 147°32'E, 51 m, *C. cognata*.

BSS-167, 39°44.8'S, 148°40.6'E, 124 m, *C. magniarmata*; *C. plana*.

BSS-169, 39°2.4'S, 148°30.6'E, 120 m, *C. multiarmata*; *C. plana*, *C. pustulosa*.

BSS-170, 38°52.6'S, 148°25.2'E, 140 m, *C. biarmata*, *C. multiarmata*, *C. magniarmata*, *C. cognata*.

BSS-171, 38°53.7'S, 147°55.2'E, 71 m, *C. magniarmata*, *C. cognata*, *C. diffusa*.

BSS-176, 38°54.3'S, 147°13.4'E, 58 m, *C. cognata*.

##### Museum Victoria eastern Australian continental slope, RV *Franklin*, 1986

SLOPE-2, off Nowra, NSW, 34°57.90'S, 151°8'E, 503 m, *C. eburnea*, *C. multiarmata*, *C. ecstasis*, *C. plana*, *C. pustulosa*

SLOPE-6, off Nowra, NSW, 34°51.90'S, 151°12.60'E, 770 m, *C. ecstasis*, *C. plana*, *T. asymmetricus*, *T. diommatius*

SLOPE-7, off Nowra, NSW, 34°52.29'S, 151°15.02'E, 1096 m, *C. multiarmata*, *C. ecstasis*, *C. plana*, *T. asymmetricus*, *T. diommatius*, *T. anomalus*

SLOPE-19, off Eden, NSW, 37°07.3'S, 15°20.2'E, 520 m, *C. biarmata*

SLOPE-27, S of Point Hicks, Vic., 38°25'S, 149°E, 1500 m, *Crucscharellina australis*

SLOPE-39, S of Point Hicks, Vic., 38°19.1'S, 149°14.3'E, 600 m, *C. multiarmata*, *C. ecstasis*, *C. pustulosa*

SLOPE-40, S of Point Hicks, Vic., 38°17.7'S, 149°11.3'E, 400 m, *C. multiarmata*, *C. ecstasis*, *C. plana*, *C. pustulosa*, *Flabellopora umbonata*

SLOPE-45, off Freycinet Peninsula, Tas., 42°02.2'S, 148°38.7'E, 800 m *C. ecstasis*, *C. pustulosa*, *T. diommatius*

SLOPE-48, off Freycinet Peninsula, Tas., 41°57.5'S, 148°37.9'E, 400 m, *C. multiarmata*, *C. ecstasis*

SLOPE-49, off Freycinet Peninsula, Tas., 41°56.5'S, 148°37.9'E, 200 m, *C. diffusa*

SLOPE-53, 54 km ESE, of Nowra, NSW, from 34°52.77'S, 151°15.04'E, 996 m to 34°54.03' 151°19.05'E, 990 m, *C. ecstasis*.

SLOPE-56, 44 km E, of Nowra, NSW, from 34°55.79'S, 151°08.06'E, 429 m to 34°56.06'S, 151°07.86'E, 466 m, *C. plana*.

##### Great Australian Bight, Y. Bone collection, RV *Franklin*, 1995

GAB-015, 33°20'S, 130°00'E, 203 m, *C. magniarmata*

GAB-019, 33°22'S, 129°19'E, 301 m, *C. cognata*, *C. stellata*

GAB-020, 33°20'S, 129°18'E, 157 m, *C. magniarmata*, *C. cognata*, *C. diffusa*, *C. plana*, *Bipora flabellaris*, *Flabellopora umbonata*

GAB-030, 33°13'S, 128°29'E, 137 m, *C. multiarmata*, *C. cognata*, *C. plana*, *Bipora flabellaris*, *Flabellopora umbonata*

GAB-044, 33°25'S, 125°58'E, 163 m, *C. plana*

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**Appendix.** Continued

GAB-045, 33°25'S, 125°58'E, 143.5 m, *C. cognata*, *Flabellopora umbonata*  
 GAB-048, 33°53'S, 125°22'E, 182 m, *C. obscura*  
 GAB-049, 33°53'S, 125°22'E, 156 m, *C. cognata*, *C. plana*, *C. pustulosa*  
 GAB-056, 33°19'S, 125°43'E, 72.5 m, *C. magniarmata*, *Flabellopora umbonata*  
 GAB-067, 33°22'S, 124°23'E, 50 m, *C. cognata*, *C. diffusa*, *Flabellopora umbonata*  
 GAB-069, 33°43'S, 124°23'E, 65.5 m, *C. diffusa*  
 GAB-074, 34°15'S, 124°24'E, 117–125 m, *C. obscura*, *Flabellopora umbonata*  
 GAB-084, 34°20'S, 124°08'E, 96 m, *Flabellopora umbonata*  
 GAB-088, 34°35'S, 123°38'E, 98 m, *Flabellopora umbonata*  
 GAB-093, 34°32'S, 122°58'E, 95 m, *Flabellopora umbonata*  
 GAB-098, 34°39'S, 122°26'E, 156 m, *C. cognata*  
 GAB-101, 34°33'S, 121°33'E, 236 m, *C. cognata*  
 GAB-108, 34°29'S, 121°32'E, 101 m, *C. obscura*  
 GAB-112, 34°20'S, 119°55'E, 65 m, *Flabellopora umbonata*  
 GAB-113, 34°36'S, 119°55'E, 106 m, *C. obscura*  
 GAB-116, 34°37'S, 119°21'E, 66 m, *Bipora flabellaris*  
 GAB-117, 34°35'S, 119°00'E, 65.5 m, *Flabellopora umbonata*  
 GAB-118, 34°59'S, 119°00'E, 87 m, *C. diffusa*, *C. obscura*, *Bipora flabellaris*  
 GAB-119, 35°00'S, 119°00'E, 149 m, *Flabellopora umbonata*  
 GAB-128, 35°07'S, 116°52'E, 59 m, *C. stellata*, *Flabellopora umbonata*  
 GAB-129, 35°07'S, 116°20'E, 70 m, *C. diffusa*  
 GAB-131, 35°07'S, 115°51'E, 160 m, *C. obscura*

**Dampier Archipelago, north-western WA, G.C. B. Poore collection, 1999**

DA-2-09-02, 20°20.5'S, 117°05.4'E, 33 m, off Delambre I., *C. obscura*  
 DA-2-75-02, 20°32.17'S, 116°33.63'E, 20.5 m, off Goodwyn I., *T. fecundus*  
 DA-2-73-01, 20°40.0'S, 116°27.7'E, 12.5 m, off Eaglehawk I., *C. obscura*  
 DA-2-37-01, 20°36.5'S, 116°35.0'E, 15 m, off Enderby I., *C. diffusa*

**Other Museum Victoria collections**

Off Tasmania?, RV *Dmitri Mendeleev*, *C. diffusa*  
 S03/84/74, off eastern Tas., RV *Soela*, 42°41'S, 148°25.0'E, 320 m, *Flabellopora umbonata*, *Crucescharellina australis*

**Fossil localities from Victoria and South Australia**

Bairnsdale (Skinner's): Mitchell River bank, about 12 km W of Bairnsdale, Vic., 37°47.9'S, 147°29.5'E. *C. macgillivrayi*, *C. aff. diffusa*  
 Balcombe Bay: also known as Fossil Beach, Mornington, Mount Martha and possibly "Schnapper Point" (MacGillivray); on coast of Port Phillip Bay, about 3 km S of Mornington, Vic., 38°14.5'S, 145°01.7'E. Fyansford Clay. Age: Balcombian; Middle Miocene, (Langhian). *C. ocellata*, *C. macgillivrayi*, *C. humerus*  
 Batesford Quarry: upper levels of Batesford Limestone Quarry, 7 km W of Geelong, Vic., 38°06.5'S, 144°17.3'E. Fyansford Clay. Age: Balcombian; Middle Miocene, (Langhian). *C. ocellata*, *C. macgillivrayi*, *C. humerus*  
 Heywood No. 10 Bore, Mines Department of Victoria, 38°07.9'S, 141°37.6'E. Age: Miocene. *C. macgillivrayi*.  
 Mount Schanck: limestone quarry about 1 km W of Mount Schanck, about 15 km S of Mount Gambier, SA, 37°57'S, 140°43.2'E. Gambier Limestone. Age: Early Miocene, (Longfordian). *C. macgillivrayi*, *C. humerus*  
 Muddy Creek: Clifton Bank, Muddy Creek, 8 km W of Hamilton, Vic., 37°44.6'S, 141°56.4'E. Muddy Creek Marl (= Gellibrand Marl). Age: Balcombian. *C. macgillivrayi*, *C. humerus*, *C. aff. diffusa*  
 Paaratte No.1 Bore. Mines Department bore in the Parish of Paaratte, located in the village of Port Campbell, Vic., 38°36.8'S, 143°00.0'E. Age: Middle Miocene. *C. humerus*  
 Puebla: coastal section, about 3 km W of Torquay, Vic., 38°21.4'S, 144°17.8'E. Jan Juc Formation. Age: Longfordian; Early Miocene, (Aquitanian). *C. macgillivrayi*, *C. humerus*

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## A review of the Tertiary fossil Cetacea (Mammalia) localities in Australia

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### Abstract

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The stratigraphy, age, lithology, and vertebrate fauna of all 56 pre-Pleistocene fossil Cetacea-bearing localities in Australia are reviewed. The majority of these localities occur in the state of Victoria, and are Miocene in age. The most complete cetacean fossils have been recovered from coastal exposures of the Upper Oligocene Jan Juc Formation, south-west of Torquay in the Torquay Basin (Victoria). The inadequately known fossil record of cetaceans in Australia is due to a lack of research, and not a lack of potentially fossiliferous rock outcrop.

### Keywords

Cetacea, Archaeoceti, Mysticeti, Odontoceti, Australia, localities, fossil record, Tertiary, Oligocene, Miocene, Pliocene

### Introduction

Australia has an incompletely known fossil record of cetaceans (whales, dolphins, and porpoises; Order Cetacea). The oldest fossil cetaceans from Australia are Early Oligocene, with the fossil record being best known from the Late Miocene–Early Pliocene (Fig. 1 for correlation of cetacean-bearing stratigraphic units). The majority of Australian fossil cetaceans described (but not necessarily published) have been derived from only a few locations. These fossil sites occur within the Paleogene–Neogene marine sedimentary basins along the southern margin of Victoria. Other described fossil cetaceans have been collected from South Australia and Tasmania, although fossil cetaceans from these states are less well represented in museums.

Mahoney and Ride (1975) provided a synopsis of fossil cetacean genera and species described from Australia with information on the history of collection and study. They did not include all cetaceans in institutional palaeontology collections. Fordyce (1982a, 1982b) published important taxonomic reviews of Australian fossil cetaceans based on museum collections. Bearlin (1987, 1988) continued studies on Australian fossil Cetacea, with analyses of Neogene mysticete specimens and their provenance. In all of these studies, research was conducted primarily on specimens in Museum Victoria, Melbourne (NMV), and to a lesser extent on fossils in the South Australian Museum and the School of Earth Sciences, University of Melbourne. The fossil cetaceans in the palaeontology collections of the Tasmanian Museum, Hobart and Queen Victoria Museum, Launceston remain largely unknown.

The Australian fossil record of cetaceans is so poorly known because little systematic prospecting has been carried out. All significant fossil cetaceans have been discovered by accident, often by amateur palaeontologists or members of the public. Initial steps to advance research are: 1, to identify where fossil cetaceans have previously been discovered in Australia; 2, determine the faunal compositions of these localities based on fossils in museum and other collections; 3, conduct a census of the sedimentary geology of these localities; and 4, determine the geological age of the fossil-bearing localities.

This review aims to document localities in Australia from which pre-Pleistocene fossil cetaceans have been recovered. Because this review is principally based on museum and university collections, it is unlikely that all localities have been recognised. Several large private collections exist that include significant material. If accurate locality and stratigraphic data occur with these specimens, it is likely that the real number of fossil cetacean localities is much larger. This review is intended to serve as a companion to Rich and co-workers' (1991) review of Tertiary terrestrial mammal localities.

### Overview of localities and the fossil record

The fossiliferous localities in Australia that have yielded cetaceans occur within the offshore and onshore marine, and in one case freshwater, sedimentary basins in south-eastern and southern central Australia. These areas of Paleogene–Neogene sedimentation correspond to the: Otway, Torquay, Port Phillip, and Gippsland basins in Victoria; St Vincent, Murray, Gambier and Lake Eyre basins in South Australia; and the Bass Basin in

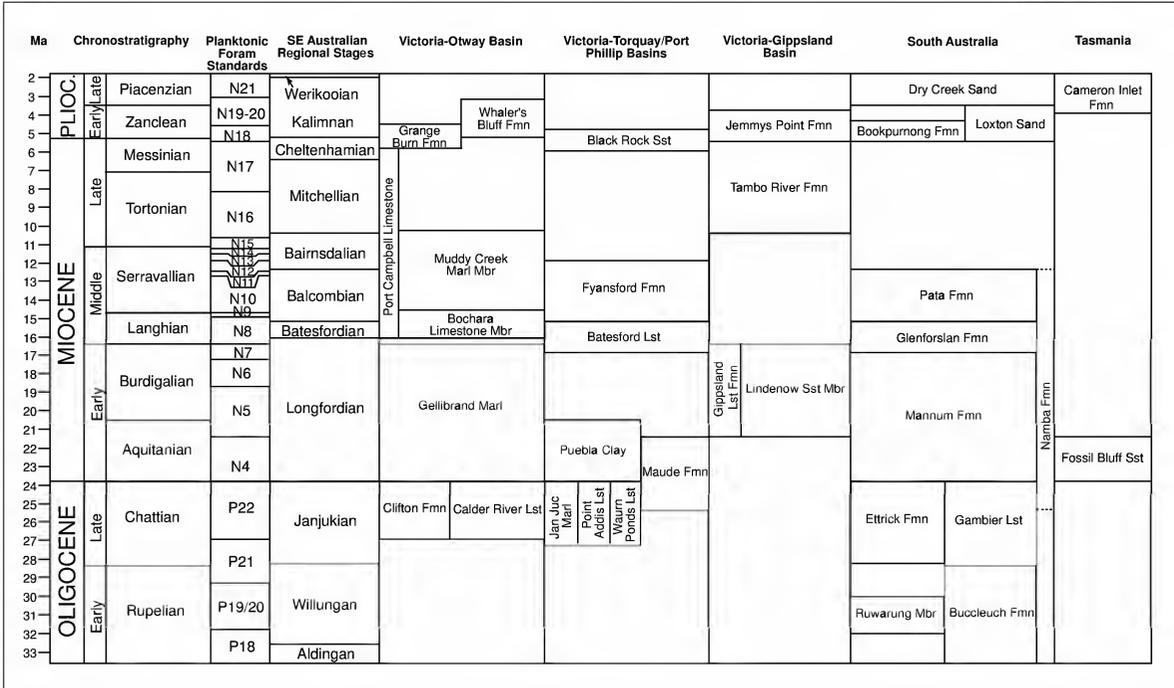


Figure 1. Correlation chart of Oligocene–Pliocene Australian fossil cetacean-bearing stratigraphic units. Abbreviations: Fmn=Formation; Lst=Limestone; Mbr=Member; Sst=Sandstone. Broken lines indicate uncertain maximum and minimum age ranges of stratigraphic units. Ages, chronostratigraphy, and planktonic foram zones modified from Alley et al. (1995) and Holdgate and Gallagher (2003).

Tasmania (Figs 2, 3). The most abundant and diverse fossil records of cetaceans occur in the Otway, Torquay, and Port Phillip basins of Victoria. However, the most complete and best-preserved fossil cetacean material is derived from the Torquay Basin in central coastal Victoria.

The most northern localities are those in the Lake Frome area in north-eastern South Australia (31°S), whereas the most southern localities occur offshore southern Tasmania (45°S). The stratigraphic record of cetaceans is most complete for the Miocene, with several localities in South Australia, Victoria, and Tasmania representing the Early, Middle, and Late Miocene (see below). However, most Miocene sites are either Middle or Late Miocene in age. The Late Oligocene record is becoming better known, with a higher diversity of cetaceans than previously recognised (Fitzgerald, 2003, 2004). It is important to note that most of the Late Oligocene fossil cetaceans can probably be referred to Mammalodontidae, and a new undescribed group of archaic toothed mysticetes. No fossil cetaceans have been recorded from the Eocene of Australia (Fordyce, 1982a, 1991). Other poorly documented stratigraphic intervals are the Early Oligocene, early Early Miocene and Late Pliocene.

In Australia, the fossil record of mysticetes is much better known than that for odontocetes (Bearlin, 1987; Fitzgerald, 2004). The Australian Late Oligocene–Late Pliocene record of Mysticeti is particularly informative because it documents

stem-group toothed mysticetes (Berta et al., 2003), the archaic baleen-bearing “cetotheres” in the Miocene, early records of Balaenopteridae in the Mid–Late Miocene (Bearlin, 1988), and the transition to a relatively modern mysticete fauna composed of balaenids and balaenopterids in the Late Miocene–early Pliocene (Bearlin, 1987, 1988; Fordyce, 1991).

The Australian fossil record of Odontoceti is known only in broad outlines. This reflects the paucity of complete skulls, preserving diagnostic features, in museum and university collections. There are only two records of fairly complete and diagnostic fossil odontocete skulls in Australia: an undescribed squalodontid from Victoria (Bearlin, 1982), and *Prosqualodon davidis* (Flynn, 1923, 1948) from Tasmania. The skull of the latter specimen is now lost (Mahoney and Ride, 1975) and the former skull lacks the rostrum and most of the dorsal surface of the cranium. However, the remainder of the holotype specimen of *P. davidis*, consisting of much of the postcranial skeleton and mandibles, is still extant in the collection of the Department of Geology, University of Tasmania. Most odontocete fossils are represented by isolated mandibles, teeth, periotics and tympanic bullae. An exception is an incompletely prepared, partially articulated, postcranial skeleton from the Late Oligocene of Victoria (NMV P48861). Although lacking cranial elements (apart from several teeth), the morphology of the scapula indicates that this specimen may represent a primitive eurhinodelphinid odontocete.

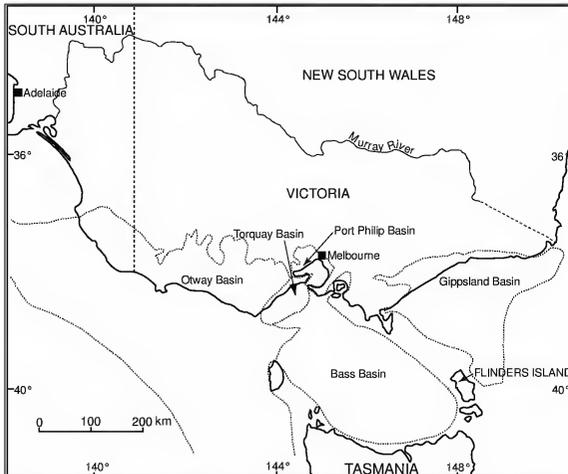


Figure 2. Tertiary sedimentary basins with fossil Cetacea localities in Victoria and Tasmania. Modified from Abele et al. (1988) and Holdgate and Gallagher (2003).

### Taxonomy

Systematic biologists have yet to reach a consensus on cetacean systematics and taxonomy. This is largely due to the publication of numerous divergent phylogenetic hypotheses, utilising both molecular and morphological data sets, over the last two decades (e.g., Arnason and Gullberg, 1994; Geisler and Luo, 1996; Heyning, 1989, 1997; Messenger and McGuire, 1998; Milinkovitch et al., 1993; Zhou, 1982). Higher classification schemes were reassessed by Geisler and Sanders (2003) but the more conventional classification of Fordyce and Muizon (2001) is followed herein. The classification of non-cetacean mammals follows McKenna and Bell (1997). For non-mammalian tetrapods, osteichthyans, and most chondrichthyans, the classification of Carroll (1988) is used. Some modifications to chondrichthyan taxonomy presented in Carroll (1988) and Kemp (1991) have been made following a recent review by Purdy and colleagues (2001). Fossil species of great-toothed sharks are referred to the genus *Carcharodon*, and not *Carcharocles*, following Gottfried and Fordyce (2001).

### Faunal lists

Few Australian workers have studied Cainozoic marine vertebrate faunas in detail, with notable exceptions being Bearlin (1987), Chapman and Cudmore (1924), Chapman and Pritchard (1904, 1907), Fordyce (1984, 1991), Kemp (1970, 1982, 1991), and Pledge (1985). Kemp (1991) outlined the various biases affecting the taxonomic compositions of chondrichthyan faunas in Australia, and his conclusions may be applied to cetaceans. Most of the substantial Tertiary marine vertebrate holdings of Museum Victoria were obtained prior to 1980. Indeed, most of the collection of Cainozoic marine vertebrate fossils dates from the first half of the twentieth century. It is, therefore, inevitable that identifications and alpha taxonomic

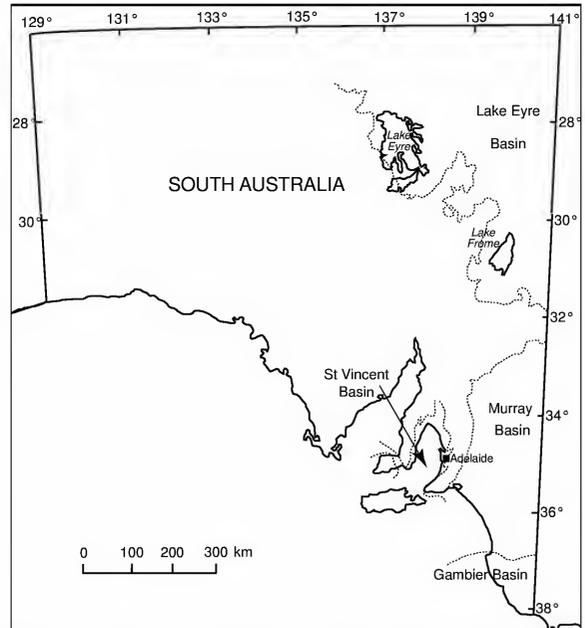


Figure 3. Tertiary sedimentary basins with fossil Cetacea localities in South Australia. Modified from Alley et al. (1995).

studies were influenced by the taxonomic references of the time and contemporary philosophical approaches to systematics. The faunal lists presented herein reflect these biases. However, given the paucity of new material (apart from cetaceans) added to museum collections over the last 30 years, it is unlikely that the taxonomy requires major reassessment. Of more singular importance is the incomplete nature of the faunal lists, due to the lack of identification of many specimens. It is highly probable that the faunal lists represent artificially impoverished faunas, particularly of marine tetrapods and osteichthyan fish.

For cetaceans and other marine tetrapods, faunal lists have been compiled from my personal observations and consultation of published (Bearlin, 1988; Fordyce, 1982a, 1984, 1991; Pledge, 1985) and unpublished (Bearlin, 1987) studies. Terrestrial and freshwater vertebrate faunas were adopted from Rich and others (1991), and unpublished data provided by K. Piper. Chondrichthyan and osteichthyan faunas were adapted from information in Kemp (1978, 1991), Pledge (1985) and Stinton (1958, 1963) as well as my own observations. Although Pledge (1967) reviewed South Australian Tertiary chondrichthyans, his published localities for chondrichthyans cannot be correlated with South Australian cetacean localities. Many of the identifications of marine tetrapods, and their taxonomic affinities, are preliminary.

Information on the Australian Cainozoic fossil record of marine birds may be found in: Finlayson (1938), Glaessner (1955), Jenkins (1974, 1990), Simpson (1957, 1959, 1965, 1970), Rich (1975), Vickers-Rich (1991), Vickers-Rich and Rich (1993) and Wilkinson (1969). For more detailed informa-

tion on Cainozoic fossil marine fish see Chapman (1913, 1917a, 1930), Chapman and Cudmore (1924), Chapman and Pritchard (1904, 1907) and Kemp (1991).

### Localities

For the purposes of this review, a locality is defined as a limited area where fossils have been derived from one particular stratigraphic unit. However, there is some variation in the use of the term “locality” when applied to sites that have yielded fossil cetaceans. For example, cetacean fossils have been recovered from an area around Bird Rock, Torquay, which encompasses outcrop in the shore platform, and in the cliff sections, at varying heights above the base of the cliff. Furthermore, fossils may have been derived from an area in the immediate vicinity of the Bird Rock stack, or up to 150 m south-west of Bird Rock. This contrasts with localities such as Clifton Bank, along Muddy Creek, where there is only a small area of outcrop within a limited area. In most cases, field collection data for specimens is not detailed enough to enable precise limits to be placed on the area of a locality. Hence, these localities have a relatively broad definition.

### Stratigraphy

Unless otherwise indicated, stratigraphic nomenclature follows that of Abele and colleagues (1988) and Holdgate and Gallagher (2003) for Victoria, and Alley and co-workers (1995) for South Australia. Determination of the stratigraphic position of most localities was based on work in Abele and colleagues (1988, and references therein), data presented by Alley and others (1995), and Lukasik and James (1998).

### Australian fossil Cetacea localities

#### VICTORIA (Fig. 4)

##### 1. The Otway Basin (Fig.5)

###### 1.1 Dutton Way, Portland

**Geographic location.** This site consists of several disjunct points along south-south-east facing sea cliffs and beach on the north-west side of Portland Bay, north of Portland (38°19'S, 141°38'E). Fragmentary material has also been collected from reefs and the seafloor in Portland Bay, in water depths of up to 100 m.

**Stratigraphic position.** The fossiliferous horizon that has yielded fossil cetaceans has been identified as a phosphatic nodule bed at the base of the Whaler's Bluff Formation.

**Age.** Early Pliocene. The onshore Whaler's Bluff Formation has been dated to zones N18-N19 (Mallett, 1977). Dating of the offshore deposits of the Whaler's Bluff Formation indicate that sedimentation continued into the mid-Pliocene (zones N19-N21) (Holdgate and Gallagher, 2003). It is likely that most of the fossil cetacean material was derived from the nodule horizon and therefore has a maximum age of earliest Pliocene.

**Lithology.** The main lithologies present include a basal phosphatic nodule bed, fossiliferous clays, oyster beds, and sandy limestones (Holdgate and Gallagher, 2003).

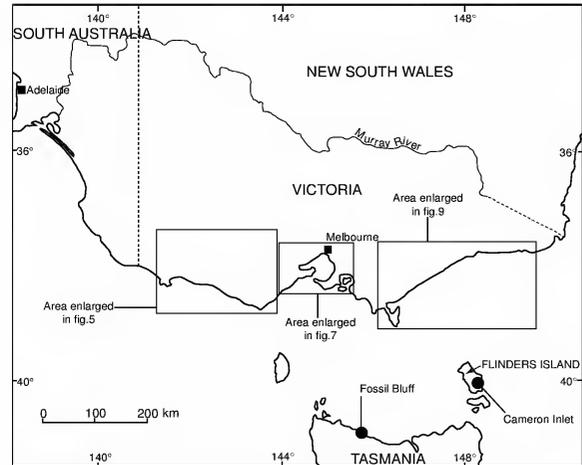


Figure 4. Areas with fossil cetacean-bearing localities in Victoria and Tasmania. Solid circles represent fossil Cetacea localities. Modified from Abele et al. (1988) and Holdgate and Gallagher (2003).

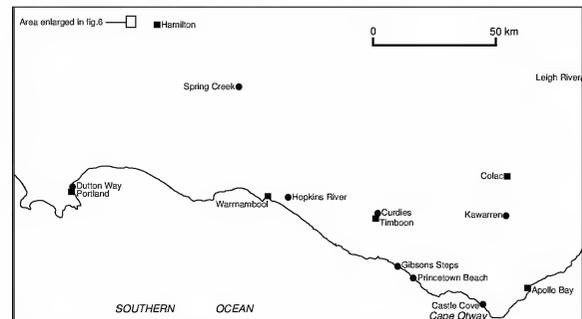


Figure 5. Fossil Cetacea localities in the Otway Basin, western Victoria. Solid circles represent fossil Cetacea localities.

**Material.** All worn, isolated elements: cranial fragments, periotics, tympanics, teeth, vertebrae, rib fragments.

**Fauna.** *Carcharodon megalodon*, *Carcharodon carcharias*, *Isurus hastalis*, *Isurus* sp., Palorchestidae, Vombatidae, Macropodidae, Ektopodontidae, ?Phocidae, Balaenidae, *Balaenoptera* sp., *Megaptera* sp., Physteridae, Ziphiidae, Delphinidae: 2 species.

###### 1.2 Arch Site, Grange Burn (Fig.6 for localities 1.2–1.4)

**Geographic location.** Resting on a quartz porphyry bar at the base of a low cliff on the southern bank of Grange Burn, opposite a natural arch, immediately north of “The Caves” property, 8 km west of Hamilton, western Victoria (near 37°43'30"S, 141°56'0"E) (Bearlin, 1987).

**Stratigraphic position.** Bochara Limestone Member, Port Campbell Limestone, unconformably overlying Devonian Rocklands Rhyolite.

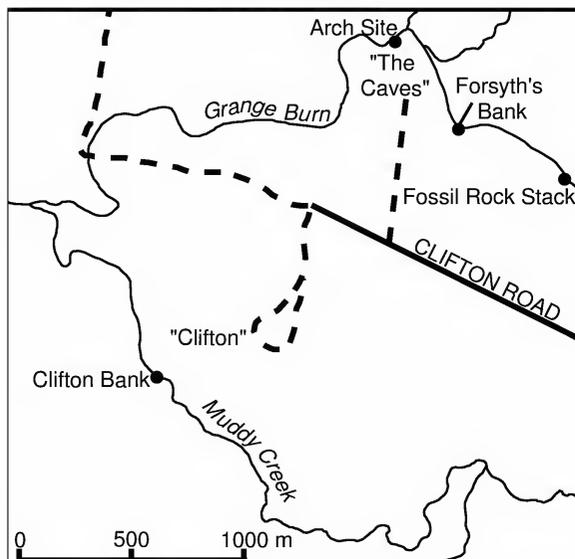


Figure 6. Fossil Cetacea localities in the Grange Burn area, west of Hamilton in western Victoria. Solid circles represent fossil Cetacea localities.

**Age.** Early Middle Miocene. The foraminifera *Lepidocyclina howchini* in the matrix suggests a zone N8–N9 (Batesfordian) age for the cetacean fossils from this locality (Bearlin, 1987).

**Lithology.** Yellow-brown bryozoal calcarenite.

**Material.** One partial skeleton.

**Fauna.** *Carcharodon megalodon*, *Isurus hastalis*, *Pelocetus* sp.

### 1.3 Clifton Bank

**Geographic location.** Low cliffs above the riverbank on the western and eastern sides of Muddy Creek (south of the junction of Grange Burn and Muddy Creek), and due west of the “Clifton” property, located 8 km west of Hamilton (near 37°43'30"S, 141°56'0"E).

**Stratigraphic position.** Muddy Creek Marl Member, Port Campbell Limestone. In more complete sections along Grange Burn, e.g. at Pat's Gully (see Gill, 1957), the Muddy Creek Marl is conformably underlain by the Bochara Limestone (Gill, 1957), and disconformably overlain by the Grange Burn Formation.

**Age.** Middle Middle Miocene to early Late Miocene. Sr/Sr dating of shells from 1 m below the base of the Grange Burn Formation, within the Muddy Creek Marl, yielded an age of 10.8 Ma (Dickinson et al., 2002). The presence of the foraminiferan *Orbulina suturalis* indicates a zone N10 age (Middle Miocene, Serravallian, 12–14 Ma) (Abele et al., 1988). However, the Muddy Creek Marl can range as high as zone N16 (up to ~8 Ma) (Singleton et al., 1976). *Acacia* pollen have

been recorded from the base of the Muddy Creek Marl, at Clifton Bank, which indicate that this member lies above the top of the *Cyatheacidites annulatus* Zone (Harris, 1971); this suggests that the Muddy Creek Marl Member is younger than 15 Ma. Gill (1957) suggested a Middle or Lower Miocene age (Balcombian) for the Muddy Creek Marl.

**Lithology.** Richly fossiliferous grey silty marl.

**Material.** Fossil cetacean elements are generally very well preserved, although no articulated skulls and skeletons have yet been recovered from this unit. Elements preserved include vertebrae, ribs, and periotics.

**Fauna.** *Carcharias* sp., *Carcharias taurus*, *Odontaspis acutissima*, *Isurus hastalis*, *Isurus retroflexus*, *Isurus desori*, *Isurus planus*, *Isurus* cf. *paucus*, *Isurus* sp., *Carcharodon megalodon*, *Carcharodon* sp., *Galeocerdo aduncus*, *Notorynchus primigenius*, *Dasyatidae*, *Heterenchelys regularis*, *Muraenesox obrutus*, *Hypomesus glaber*, *Merluccius fimbriatus*, *Trachichthodes salebrosus*, *Sebastes fissicostatus*, *Sillago pliccaenica*, *Diodon formosus*, *Balaenidae*, *Scaldicetus lodgei*, cf. *Physeter* sp., *Odontoceti* indet.

### 1.4 Forsyth's Bank to Fossil Rock Stack

**Geographic location.** River bank and river bed exposures along and in Grange Burn, south-east of “The Caves” homestead, 8 km west of Hamilton (37°43'42±03"S, 141°56'40±04"E).

**Stratigraphic position.** Grange Burn Formation, unconformably overlying the Muddy Creek Marl. The base of the Grange Burn Formation is marked by a phosphatic nodule bed horizon (Gill, 1957; Dickinson et al., 2002; Holdgate and Gallagher, 2003). In most sections where the top of the Grange Burn Formation is exposed, a basalt layer disconformably overlies the marine sediments (Gill, 1957). Further to the south-east along the Grange Burn, a terrestrial palaeosol facies is present between the Grange Burn Formation and the basalt.

**Age.** The Grange Burn Formation has generally been considered as Kalimnan (Early Pliocene) in age, due to the composition of the rich invertebrate macrofauna (Gill, 1957). Foraminifera dates indicate a zone N17 age (Mallett, 1977). The basalt above the Grange Burn Formation has been dated to 4.35 Ma using K-Ar (Turnbull et al., 1965). More recently, Sr/Sr dates from the base of the Grange Burn Formation indicated a 4.0–5.0 Ma maximum age for the formation (Dickinson et al., 2002). These data indicate an earliest Early Pliocene age for the Grange Burn Formation.

**Lithology.** Shelly marl and sandy to pebbly limestone (Holdgate and Gallagher, 2003).

**Material.** As is typical of most Mio-Pliocene nodule bed fossil vertebrate material in Victoria, fossils are often rolled, polished, and broken. Almost all specimens represent isolated elements, with associated material being very rare. Typically preserved elements include partial rostra, cranial fragments, isolated periotics and tympanic bullae, teeth, incomplete mandibles, vertebrae, and ribs.

*Fauna.* *Heterodontus cainozoicus*, *Carcharodon megalodon*, *Carcharodon carcharias*, *Isurus escheri*, *Isurus hastalis*, *Myliobatis* sp., *Edaphodon sweeti*, *Ischyodus* cf. *dolloi*, *Kurrabi* sp., Phocidae, “Cetotheriidae”, *Balaenoptera* sp., cf. *Scaldicetus* sp., cf. *Physeter* sp., cf. *Mesoplodon* sp., ?Delphinidae.

### 1.5 Spring Creek

*Geographic location.* Bed of Spring Creek, near Minhamite, 40 km south-east of Hamilton (near 37°59'S, 142°20'E).

*Stratigraphic position.* Unnamed unit (Abele et al., 1988). This unit is probably laterally equivalent to the Grange Burn Formation. Gill (1957) mentioned a Kalimnan-aged location “from Goodwood station near Minhamite Railway Station 25 miles (40.2 km) SE of Hamilton” (p. 152).

*Age.* Presumed Late Miocene–Early Pliocene. T.A. Darragh (pers. comm. to G.G. Simpson, cited in Simpson (1970)) has suggested a Cheltenhamian (Upper Miocene) or older age for the Spring Creek beds near Minhamite. Simpson (1970) suggested that the Spring Creek locality was equivalent in age to the Black Rock Sandstone at Beaumaris.

*Lithology.* Fossiliferous green-grey marly fine sand approximately 1 m thick (Abele et al., 1988).

*Material.* Worn and polished isolated elements: periotics and indeterminate bone fragments.

*Fauna.* *Pseudaptenodytes macraei*, *Balaenoptera* sp.

### 1.6 Kawarren

*Geographic location.* Old “Alkemade’s Quarry”, slightly north of Kawarren railway station, on the steep north bank of Loves Creek, Kawarren, about 19 km south of Colac (near 38°29'S, 143°35'E).

*Stratigraphic position.* Clifton Formation (Abele et al., 1988; McHaffie and Inan, 1988).

*Age.* In the north-east margins of the Port Campbell Embayment, the Clifton Formation is Late Oligocene (Abele et al., 1988).

*Lithology.* The Clifton Formation is generally a medium-coarse-grained calcarenite, with about 10% quartz and limonite sand (Tickell et al., 1992). At the Kawarren Quarry, this unit consists of friable, pale yellow limestone interbedded with harder crystalline bands (McHaffie and Inan, 1988). All of the vertebrate fossils have been recovered from the more friable calcarenite layers.

*Material.* Generally well-preserved isolated elements, exhibiting a low degree of rolling. Elements preserved include teeth, ribs and bone fragments.

*Fauna.* *Carcharias* sp., *Isurus* sp., *Isurus desori*, *Carcharoides* sp., *Carcharoides totuserratus*, *Carcharodon angustidens*, ?Mysticeti new family.

### 1.7 Leigh River

*Geographic location.* Outcrop on the eastern bank of the Leigh River, about 5 km north of Shelford, 46 km north-east of Geelong (near 38°00'S, 143°58'E).

*Stratigraphic position.* Middle section of the Gellibrand Marl (Abele et al., 1988; Dickinson et al., 2002).

*Age.* Probably Early Miocene. In the north-east part of the Port Campbell Embayment, the Gellibrand Marl ranges in age from Late Oligocene to Middle Miocene (Abele et al., 1988). Outcrop along the Leigh River is Early Miocene in age, as the Late Oligocene-aged base of the formation is not exposed, and the youngest Middle Miocene (Bairnsdalian) section has probably been eroded, or not deposited, due to the Leigh River locality being at the embayment margin (Abele et al., 1988).

*Lithology.* Marl, calcareous silt, clay, and sand with minor calcarenite layers.

*Material.* One well-preserved isolated tooth.

*Fauna.* *Isurus* sp., Cetacea indet.

### 1.8 Hopkins River

*Geographic location.* North end of outcrop in a quarry on the west bank of the Hopkins River, 150 m south of the Princes Highway bridge over the Hopkins River, near Allansford, about 10 km east of Warrnambool (near 38°23'S, 142°35'E).

*Stratigraphic position.* Port Campbell Limestone sensu stricto (Abele et al., 1988; Tickell et al., 1992).

*Age.* Middle–Late Miocene, zones N11–N17 (Holdgate and Gallagher, 2003).

*Lithology.* Yellow fine-grained calcarenite.

*Material.* A fairly well-preserved posterior part of mandible with two large conical teeth in place.

*Fauna.* cf. *Scaldicetus* sp.

### 1.9 Gibson’s Steps

*Geographic location.* Cliff at Gibson’s Steps, approximately 12 km east of Port Campbell, western Victoria (near 38°40'S, 143°07'E).

*Stratigraphic position.* Port Campbell Limestone (Bearlin, 1987; Abele et al., 1988; Tickell et al., 1992).

*Age.* Bairnsdalian, Middle Miocene, zone N10 (Bearlin, 1987).

*Lithology.* Yellow-grey fine-grained calcarenite.

*Material.* One partial skeleton

*Fauna.* “Cetotheriidae”.

### 1.10 Curdie

*Geographic location.* “Kurdeez” Quarry (Victorian Agricultural Lime Ltd), 5 km north-north-west of Curdie, near Timboon (approximately 38°27'S, 142°56'E).

*Stratigraphic position.* Port Campbell Limestone.

*Age.* Balcombian, correlated with zone N10, Serravallian, Middle Miocene (Bearlin, 1987).

*Lithology.* Calcarenites.

*Material.* One partial skeleton.

*Fauna.* ?Balaenopteridae.

### 1.11 Princetown Beach

*Geographic location.* Near Point Ronald, Princetown, 18 km east of Port Campbell, western Victoria (38°42'S, 143°09'E).

*Stratigraphic position.* Nodule bed within the Clifton Formation.

*Age.* Late Oligocene. Below the unnamed nodule horizon, shells have given Sr/Sr dates of 27.4 Ma (Holdgate and Gallagher, 2003). Immediately above the nodule bed Sr/Sr dates average ~24.0 Ma. Foraminifera from the Clifton Formation indicate a zone P21b-P22 age (Late Oligocene).

*Lithology.* Thin horizon of phosphate and limonite nodules within limestone-sandy limestone matrix.

*Material.* One worn and polished incomplete rib.

*Fauna.* *Odontaspis* sp., Cetacea indet.

### 1.12 Castle Cove

*Geographic location.* One of two possible locations: (1) type locality for the Calder River Limestone along the south-eastern bank of the Calder River, north-west of Hordern Vale, or (2) on the coast 1.7 km south-east of Castle Cove. Both sites are on the western side of Cape Otway, and east of Point Reginald, in the Aire district (near 38°47'S, 143°25'E). Etheridge (1878) noted that the holotype tooth of *Parasqualodon wilkinsoni* was found west of the Aire River.

*Stratigraphic position.* Calder River Limestone. Fordyce (1982a) suggested that the holotype specimen of *Parasqualodon wilkinsoni* was derived from the Calder River Limestone, despite the fact that there is no direct evidence that would indicate such a derivation. However, there are two lines of evidence that indirectly suggest the provenance of the holotype of *Parasqualodon wilkinsoni*: (1) the holotype tooth preserves distinctive features suggesting affinities with *Prosqualodon davidis* (indeed, this isolated tooth may be congeneric with *P. davidis*, or even conspecific); the Prosqualodontidae is only known from Late Oligocene–earliest Miocene deposits; (2) McCoy (1867a) stated that the holotype tooth was collected from sandy beds at Castle Cove on the Cape Otway coast; the only fossiliferous marine sediments in this area, which are of suitable age to yield a prosqualodontid tooth, are those of the Calder River Limestone.

*Age.* Late Oligocene.

*Lithology.* Sandy bryozoal calcarenite with a thin discontinuous basal layer of phosphatic nodules and quartz pebbles (Abele et al., 1988).

*Material.* One tooth.

*Fauna.* *Prosqualodon* sp. (= *Parasqualodon wilkinsoni*).

## 2. The Torquay Basin (Fig.7)

### 2.1 Split Point (Fig.8 for localities 2.1–2.7)

*Geographic location.* Towards lighthouse, at Split Point, near Aireys Inlet, 49 km south-west of Geelong (near 38°28'S, 144°06'E).

*Stratigraphic position.* Point Addis Limestone Member (Webb, 1995).

*Age.* Late Oligocene.

*Lithology.* Yellow sandy bryozoal calcarenite.

*Material.* One incomplete anterior caudal vertebra, and one worn tooth.

*Fauna.* *Carcharias macrotus*, *Carcharoides totuserratus*, Cetacea indet.

### 2.2 Point Addis

*Geographic location.* Cliffs on southern side of Point Addis, south-west of Torquay, central coastal Victoria (38°23'S, 144°15'E).

*Stratigraphic position.* Point Addis Limestone. Most vertebrate fossils have been collected from the base of the upper member of the Point Addis Limestone (Nicolaidis and Wallace, 1997; Webb, 1995).

*Age.* Late Oligocene (Abele et al., 1988; Holdgate and Gallagher, 2003).

*Lithology.* Ferruginous intraclastic conglomerate with abraded shelly and vertebrate skeletal components (Nicolaidis and Wallace, 1997; Webb, 1995). This horizon directly overlies a regionally extensive hardground (Nicolaidis and Wallace, 1997; Webb, 1995).

*Material.* Isolated elements: teeth, tympanic bullae, rare postcranial remains. The material is usually broken and worn.

*Fauna.* Mammalodontidae.

### 2.3 Bells Headland

*Geographic location.* 300 m south-west of Bells Beach, south-west of Torquay (near 38°22'S, 144°16'E).

*Stratigraphic position.* Lower beds of the Point Addis Limestone (Abele et al., 1988).

*Age.* Late Oligocene.

*Lithology.* Sandy bryozoal calcarenite (Abele et al., 1988).

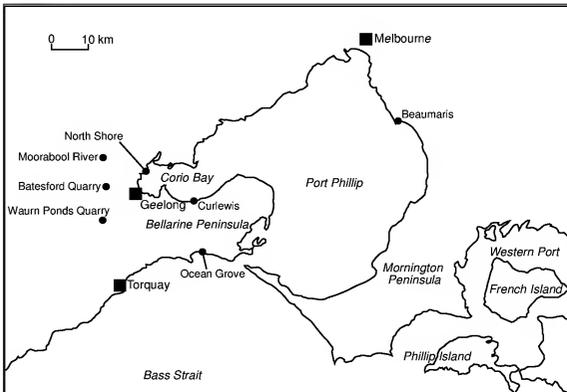


Figure 7. Fossil Cetacea localities in the Torquay and Port Phillip basins, central coastal Victoria. Solid circles represent fossil Cetacea localities. Modified from Holdgate and Gallagher (2003).

**Material.** Fossil preservation is generally very good. Cetacean material consists of: one skull and associated ear bones; associated vertebrae, and bone fragments.

**Fauna.** Mysticeti new family; genus and species 2.

#### 2.4 Bells Beach

**Geographic location.** On shore platform, low tide mark, base of low cliffs at north-east end of Bells Beach, south-west of Torquay, central coastal Victoria (38°22'S, 144°17'E).

**Stratigraphic position.** Point Addis Limestone

**Age.** Late Oligocene

**Lithology.** Yellow bryozoal calcarenite (Abele et al., 1988).

**Material.** One partially articulated incomplete skeleton, isolated periotics, and vertebrae.

**Fauna.** *Carcharodon angustidens*, Mammalodontidae genus and species indet 1.

#### 2.5 Rocky Point

**Geographic location.** Low cliffs at Rocky Point, small headland at northern-most end of Bells Beach, about 250 m NE of Bells Beach, south-west of Torquay (near 38°22'S, 144°17'E).

**Stratigraphic position.** ?Lower Jan Juc Marl.

**Age.** ?Late Oligocene.

**Lithology.** Yellow-orange silty and sandy marls.

**Material.** Indeterminate bone fragments.

**Fauna.** Cetacea indet.

#### 2.6 Deadman's Gully

**Geographic location.** Cliff exposures 600 m south-west of Fishermans Steps, near Deadman's Gully, south-west of Torquay, central coastal Victoria (near 38°20'S, 144°18'E).

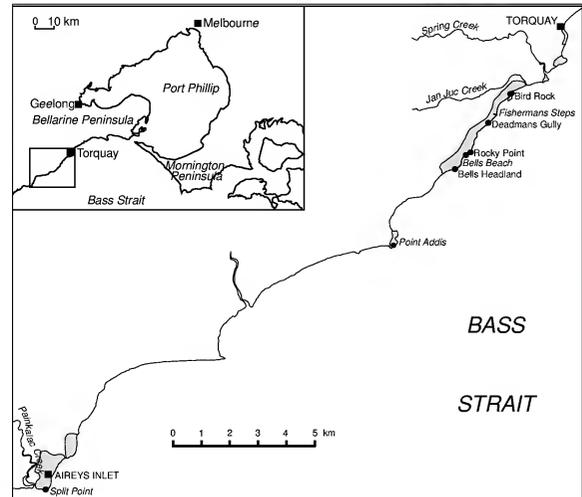


Figure 8. Late Oligocene fossil Cetacea localities on the coast south-west of Torquay, in central coastal Victoria. Shaded areas represent coastal outcrop of the Oligocene–Miocene Torquay Group. Solid circles represent fossil Cetacea localities.

**Stratigraphic position.** Jan Juc Marl, based on the presence of the molluscs *Liratomina intertexta* and *Chione halli* (which are restricted to the Jan Juc Marl, T.A. Darragh, pers. comm.).

**Age.** Late Oligocene.

**Lithology.** Grey-yellow glauconitic and pyritic carbonate-cemented calcarenite.

**Material.** One partially articulated incomplete skeleton: skull, mandibles, teeth, tympanics, thyrohyal, atlas, axis, cervical vertebra, ribs, scapulae, radius.

**Faunal.** Mysticeti new family, genus and species 1.

#### 2.7 Bird Rock

**Geographic location.** Bluff adjacent to Bird Rock stack and cliffs to the south-west, and shore platform exposures from Bird Rock in the north-east, extending 250 m to the south-west; south-west of Torquay, central coastal Victoria (38°20'54"S, 144°18'35"E).

**Stratigraphic position.** Upper Jan Juc Marl (Holdgate and Gallagher, 2003; Webb, 1995).

**Age.** Late Oligocene. Siesser (1979) suggested that the Oligocene–Miocene boundary occurs 2.5 m below the Jan Juc Marl–Puebla Clay contact. Li and colleagues (1999) noted that the local nannoplankton datum used by Siesser (1979) to estimate the position of the Oligocene–Miocene boundary, is no longer valid because the age of this datum is ~24.5 Ma, while the recognised date of the Oligocene–Miocene boundary is 23.8–23.9 Ma (Berggren et al., 1995). Li and others (1999) provided foraminiferal biofacies evidence indicating that the top of the Jan Juc Marl corresponded to the Late Oligocene–Early

Miocene boundary. Furthermore, the Jan Juc Marl–Puebla Clay contact has yielded Sr/Sr dates of  $23 \pm 1$  Ma (Kelly et al., 2001), consistent with the Oligo–Miocene boundary occurring at the Jan Juc Marl–Puebla Clay contact, and not within the Jan Juc Marl. Foraminifera from the Jan Juc Marl correlate this formation with international foram zones P21–P22, and therefore indicate a Late Oligocene age (Holdgate and Gallagher, 2003). Sr/Sr dates have yielded an age of 23.9–27.4 Ma for the Jan Juc Marl exposed at Bird Rock (Dickinson, 2002; Holdgate and Gallagher, 2003). These data support a Late Oligocene (Chatian) age for the Jan Juc Marl, and indicate that the beginning of the Early Miocene occurs immediately above the top of the Jan Juc Marl, in the Puebla Clay.

**Lithology.** Silty glauconitic marl and clayey sandy glauconitic calcarenite (Abele, 1979; Glover, 1955; Holdgate and Gallagher, 2003; Raggatt and Crespin, 1955; Webb, 1995).

**Material.** Fossil preservation is generally fairly good, however fossils from the upper beds exposed in the bluff are often corroded. Typical elements preserved include ribs, vertebrae, teeth, tympanics, and periotics. Less common are skulls and partially articulated skeletons.

**Fauna.** *Heterodontus cainozoicus*, *Carcharias elegans*, *Carcharias taurus*, *Carcharias* sp., *Odontaspis incurva*, *Carcharoides totuserratus*, *Carcharodon angustidens*, *Isurus desori*, *Isurus planus*, *Isurus* sp., *Dasyatis* sp., *Myliobatis* sp., *Megalops lissa* (Stinton, 1958), *Pterothrissus pervetustus* (Stinton, 1958), *Heterenchelys regularis* (Stinton, 1963), *Astroconger rostratus* (Stinton, 1958), *Urconger rectus* (Stinton, 1963), *Merluccius fimbriatus*, *Gadus referus* (Stinton, 1958), *Ophidion granosum* (Stinton, 1963), *Trachichthodes salebrosus* (Stinton, 1958), *Cleidopus carvernosus* (Stinton, 1963), *Sillago pliocaenica* (Stinton, 1958), *Coelorhynchus elevatus*, *Xiphias* sp., Aves indet., Mysticeti family indet., *Mammalodon colliveri* (Pritchard, 1939), *Mammalodon* sp., *Mammalodon* new species 1, Mysticeti new family, *Prosqualodon* sp., ?Eurhinodelphinidae.

## 2.8 Waurm Ponds Quarry

**Geographic location.** Waurm Ponds Quarry, operated by Blue Circle Southern Cement Ltd, south of Waurm Ponds (near 38°12'S, 144°16'E).

**Stratigraphic position.** Waurm Ponds Limestone Member of the Jan Juc Formation; a lateral equivalent of the lower part of the Point Addis Limestone (Holdgate and Gallagher, 2003; Nicolaides and Wallace, 1997).

**Age.** Late Oligocene (~24–27 Ma) (Abele et al., 1988; Holdgate and Gallagher, 2003; Nicolaides and Wallace, 1997).

**Lithology.** Bryozoal calcarenite with some interbedded marls. These sediments are capped by a subaerial exposure surface that is laterally equivalent to a similar horizon at Point Addis. At Waurm Ponds Quarry, this horizon is heavily cemented (Abele et al., 1988; Holdgate and Gallagher, 2003; Nicolaides and Wallace, 1997; Webb, 1995).

**Material.** The completeness and quality of preservation of fossil cetacean material varies. However, the vast majority of cetacean fossils consist of disarticulated and isolated elements. Some fossils preserve fine surface detail on bones and teeth, whereas others are highly polished and worn with no surface detail present.

**Fauna.** *Carcharias taurus*, *Carcharias macrotus*, *Carcharoides totuserratus*, *Carcharodon angustidens*, *Isurus desori*, *Isurus* sp., ?*Lamna cattica*, *Lamna* sp., *Carcharhinus* sp., *Galeocerdo* sp., *Notorynchus cepedianus*, *Myliobatis* sp., Diprotodontidae (D. Pickering and T. Rich pers. comm.), cf. *Mammalodon colliveri*, *Mammalodon* sp., Mammalodontidae sp. indet., “Cetotheriidae”, Mysticeti new genus, Mysticeti family indet., cf. Squalodontidae indet., Odontoceti family indet.

## 2.9 Ocean Grove

**Geographic location.** Near Ocean Grove, on the Bass Strait side of the Bellarine Peninsula (near 38°15'S, 144°31'E).

**Stratigraphic position.** Puebla Clay (Abele et al., 1988).

**Age.** Early Longfordian (Early Miocene).

**Lithology.** Calcareous sand (Abele et al., 1988).

**Material.** Bone fragments.

**Fauna.** Cetacea indet.

## 3. The Port Phillip Basin (Fig.7)

### 3.1 Batesford Quarry

**Geographic location.** Australian Cement Company quarry south of Batesford, on the western bank of the Moorabool River, west of Geelong (38°06'S, 144°17'E).

**Stratigraphic position.** Batesford Limestone; unconformably overlies Palaeozoic granite, and grades conformably up into the overlying Pyansford Formation (Abele et al., 1988; Holdgate and Gallagher, 2003; Webb, 1995).

**Age.** The lower 21 m of the Batesford Limestone is Longfordian (Lower Miocene) in age, whereas the upper 12 m of the formation is the *Lepidocyclina*-bearing type section of the uppermost Lower to lower Middle Miocene Batesfordian local marine stage (Holdgate and Gallagher, 2003).

**Lithology.** Fossil cetaceans have been recovered from the basal beds, which are composed of calcareous sand and gravel. The upper Batesfordian part of the formation consists of biocalcarene (Abele et al., 1988; Bowler, 1963; Webb, 1995).

**Material.** In both upper and lower parts of the Batesford Limestone, cetacean fossils are generally well preserved with only slight mineralisation of original bone. The majority of cetacean fossils have been found in the Batesfordian-age upper beds. Rib fragments and vertebrae are the most commonly represented elements, with tympanic bullae being poorly represented. Elements of the appendicular skeleton and cranial remains are very rare. Only two skeletons represented by associated elements have been recovered from Batesford Quarry.

*Fauna.* *Orectolobus* sp., *Carcharias taurus*, *Carcharodon megalodon*, *Isurus desori*, *Isurus hastalis*, *Isurus oxyrinchus*, *Isurus* cf. *oxyrinchus*, *Isurus planus*, *Isurus retroflexus*, *Isurus* cf. *paucus*, *Isurus* sp., Lamnidae incerta sedis, *Carcharhinus* cf. *brachyurus*, *Carcharhinus* sp., *Galeocerdo aduncus*, *Sphyrna* sp., *Notorynchus primigenius*, *Pristiophorus lanceolatus*, *Labrodon* sp., Spheniscidae, Diprotodontidae indet., “Cetotheriidae” indet., Physeteridae, ?Squalodontidae new genus and new species.

### 3.2 Moorabool River

*Geographic location.* North-west of Geelong (near 37°56'S, 144°09'E).

*Stratigraphic position.* Lower Maude Formation (Abele et al., 1988).

*Age.* Latest Late Oligocene–earliest Miocene (zones P22-N4) (Abele et al., 1988; Holdgate and Gallagher, 2003).

*Lithology.* Shelly bryozoal calcarenite.

*Material.* Cetacean material consists of one tympanic bulla and bone fragments.

*Fauna.* *Heterodontus cainozoicus*, *Carcharias* sp., *Isurus* sp., cf. Mammalodontidae.

### 3.3 North Shore, Corio Bay

*Geographic location.* Outcrop along north shore of Corio Bay, near Geelong (near 38°06'S, 144°24'E).

*Stratigraphic position.* Fyansford Formation (Abele et al., 1988).

*Age.* Youngest part of the Fyansford Formation, representing zone N12 (Bairnsdalian, Middle Miocene) (Abele et al., 1988).

*Lithology.* Basal sandy calcarenite passing upwards into calcareous silt and clay with sandy calcarenite interbeds (Abele et al., 1988).

*Material.* Bone fragments.

*Fauna.* *Lamna* sp., Cetacea indet.

### 3.4 Curlewis

*Geographic location.* Cliff sections along the northern side of the Bellarine Peninsula, near Curlewis (near 38°11'S, 144°30'E).

*Stratigraphic position.* Fyansford Formation (Abele et al., 1988).

*Age.* Early Middle Miocene (Abele et al., 1988).

*Lithology.* Calcareous clay and marl with thin bryozoal calcarenite interbeds (Abele et al., 1988).

*Material.* Bone fragments.

*Fauna.* *Heterodontus cainozoicus*, *Isurus hastalis*, *Trachichthodes salebrosus* (Stinton, 1958), *Diodon* sp., Cetacea indet.

### 3.5 Beaumaris

*Geographic location.* Coastal exposures located east of Rickett's Point on the west shore of Beaumaris Bay, north-east shore of Port Phillip Bay (37°59'S, 145°03'E).

*Stratigraphic position.* Basal Black Rock Sandstone (Abele et al., 1988; Holdgate and Gallagher, 2003).

*Age.* Cheltenhamian to Kalimnan (latest Late Miocene–earliest Early Pliocene) (Abele et al., 1988; Dickinson et al., 2002; Gill, 1957; Holdgate and Gallagher, 2003; Mallett, 1977).

*Lithology.* Most fossil vertebrates have been recovered from a layer of ferruginous and phosphatic nodules in a matrix of quartz sand and gravel. This nodule bed occurs at the base of the Black Rock Sandstone. Less abundant fossil vertebrates occur in the sediments immediately above the nodule horizon, this layer consisting of calcareous sandstone and sandy marl (Abele et al., 1988; Gill, 1957; Singleton, 1941).

*Material.* Cetacean fossils derived from the nodule bed consist of fragmentary, isolated elements that are usually highly worn and polished, having undergone significant post-mortem transport. These fossils include indeterminate bone fragments, ribs, vertebrae, forelimb elements, teeth, rostral and cranial fragments, periotics, tympanic bullae, and incomplete mandibles. Vertebrate fossils from the sandy beds overlying the nodule horizon are better preserved than the nodule material, with a lesser degree of replacement of bone by secondary mineralisation. The sandy bed material includes ribs, vertebrae, teeth, mandibles, periotics, tympanic bullae, middle-ear ossicles, and rare partially articulated skeletons.

*Fauna.* *Heterodontus cainozoicus*, *Carcharias taurus*, *Carcharodon megalodon*, *Parotodus benedenii*, *Isurus desori*, *Isurus hastalis*, *Isurus retroflexus*, ?*Lamna*, *Megascyliorhinus* sp., *Carcharhinus* cf. *brachyurus*, *Carcharhinus* sp., *Galeocerdo aduncus*, *Pristiophorus lanceolatus*, *Myliobatis* sp., *Edaphodon mirabilis*, *Edaphodon* cf. *mirabilis*, *Edaphodon sweeti*, *Ischyodus* cf. *dolloi*, *Sillago pliocaenica* (Stinton, 1958), *Lactarius tumulatus* (Stinton, 1963), ?Trionychidae, *Pseudaptenodytes macraei*, ?*Pseudaptenodytes minor*, Spheniscidae, *Diomedea thyridata* (Wilkinson, 1969), *Zygomaturus gilli* (Woodburne, 1969; Stirton, 1967), *Kolopsis* sp. cf. *K. torus* (Rich et al., 2003), Phocidae (Fordey and Flannery, 1983), “Cetotheriidae” indet., cf. *Balaena*, Balaenidae indet., *Balaenoptera* sp., *Megaptera* sp., *Physetodon baileyi* (probably Physeteridae indet.), *Scaldicetus macgeei*, Physeteridae indet., Ziphiidae, Delphinidae indet.

## 4. Gippsland Basin (Fig 9)

### 4.1 Merrimans Creek

*Geographic location.* Approximately 25 m from the surface, in the Gippsland Cement Quarry on Merrimans Creek, about 19 km south-east of Rosedale, Gippsland, Victoria (near 38°15'S, 146°51'E).

*Stratigraphic position.* Gippsland Limestone Formation (Holdgate and Gallagher, 2003).

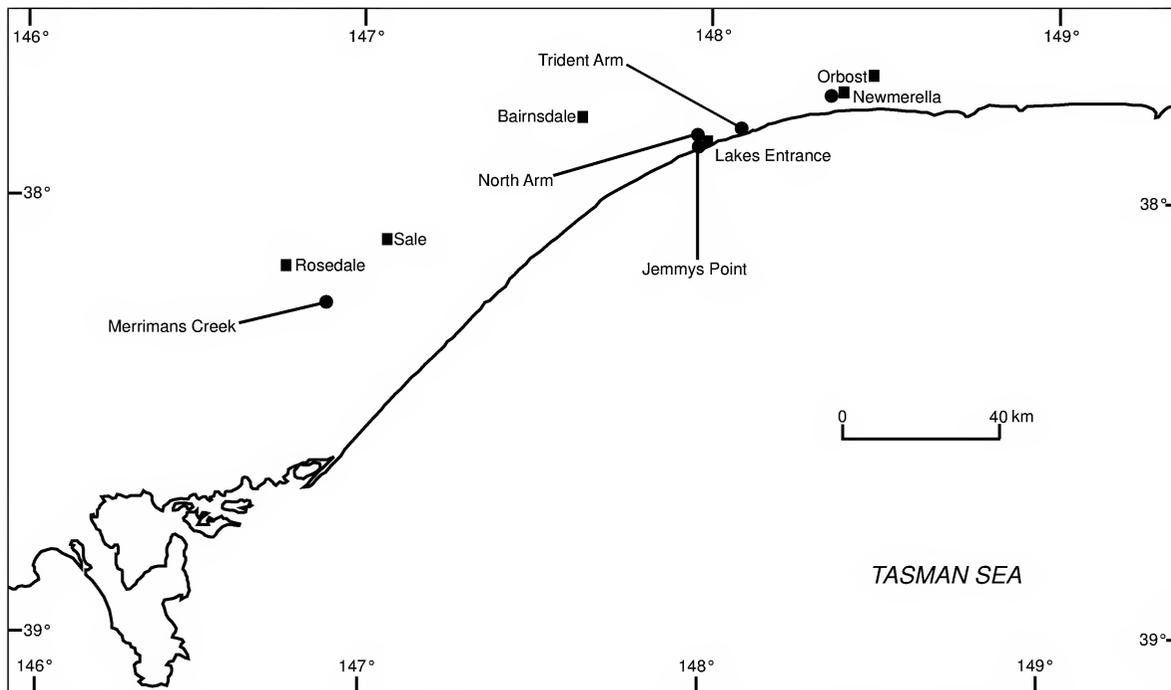


Figure 9. Fossil Cetacea localities in the Gippsland Basin, eastern Victoria. Solid circles represent fossil Cetacea localities.

*Age.* Longfordian; Early Miocene (planktonic foraminiferal zones N5-N7).

*Lithology.* Light grey fossiliferous marly limestone and interbedded limestone and marl.

*Material.* Fragmentary mandible and probable vertebrae.

*Fauna.* *Isurus hastalis*, Mysticeti.

#### 4.2 Rose Hill

*Geographic location.* On Mitchell River, near Bairnsdale, East Gippsland, Victoria (near 37°49'S, 147°36'E).

*Stratigraphic position.* Tambo River Formation.

*Age.* Mitchellian (Late Miocene), representing planktonic foraminiferal zones N16-N17. Dickinson (2002) recorded Sr/Sr dates averaging 6.0 Ma for the top of the type section of the Tambo River Formation at Swan Reach.

*Lithology.* Uniform marl and marly limestone, and glauconitic sandy coquinas (Abele et al., 1988).

*Material.* Bone fragments.

*Fauna.* Cetacea indet.

#### 4.3 Jemmys Point

*Geographic location.* Low cliffs at Jemmys Point, between the south-east end of "The Narrows", and the confluence of North

Arm and Cunningham Arm, west of Lakes Entrance, East Gippsland (37°53'S, 147°58'E).

*Stratigraphic position.* Jemmys Point Formation (Abele et al., 1988; Singleton, 1941; Wilkins, 1963).

*Age.* Kalimnan (Early Pliocene); planktonic foraminiferal zones N18-N19 (Holdgate and Gallagher, 2003).

*Lithology.* Sandy clay with shell beds (Abele et al., 1988; Carter, 1985; Holdgate and Gallagher, 2003; Wilkins, 1963).

*Material.* Isolated bone fragments, vertebrae, and one incomplete skull.

*Fauna.* *Carcharodon carcharias*, *Notorynchus cepedianus*, *Mesoplodon longirostris*.

#### 4.4 North Arm

*Geographic location.* "Golden Point" property, North Arm, Lake King, near Lakes Entrance, East Gippsland (close to 37°51'S, 148°58'E) (Bearlin, 1987).

*Stratigraphic position.* Jemmys Point Formation.

*Age.* Kalimnan (Early Pliocene); planktonic foraminiferal zones N18-N19 (Holdgate and Gallagher, 2003).

*Lithology.* Calcareous shelly sand, with phosphorite concretions (Abele et al., 1988; Carter, 1985).

**Material.** One incomplete skeleton comprising: almost complete skull, mandibles, periotics, tympanic bullae, complete series of cervical vertebrae, isolated thoracic and lumbar vertebrae, and ribs.

**Fauna.** *Megaptera* new species 1.

**4.5 Trident Arm**

**Geographic location.** Trident Arm of Lake Tyers, east of Lakes Entrance, East Gippsland, Victoria (near 37°49'S, 148°08'E).

**Stratigraphic position.** Phosphatic horizon at the base of the Jemmys Point Formation (M. Wallace, pers. comm.).

**Age.** Kalimnan (Early Pliocene); planktonic foraminiferal zones N18-N19 (Carter, 1985; Holdgate and Gallagher, 2003).

**Lithology.** Cemented phosphatic and glauconitic calcarenite with *Ostrea* shells.

**Material.** One partial cranium.

**Fauna.** ?*Balaenidae*.

**4.6 Newmerella**

**Geographic location.** Railway cutting 3 km west of Newmerella, Orbost district, East Gippsland, Victoria (near 37°45'S, 148°24'E).

**Stratigraphic position.** Probably the Lindenow Sandstone Member, Gippsland Limestone Formation.

**Age.** Longfordian (Early Miocene), planktonic foraminiferal zones N5-N7 (Holdgate and Gallagher, 2003).

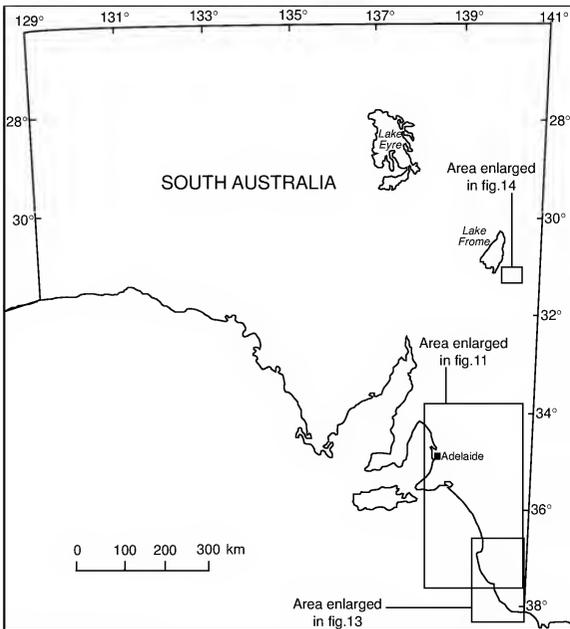


Figure 10. Areas with fossil cetacean-bearing localities in South Australia. Modified from Alley et al. (1995).

**Lithology.** Ferruginised fine quartz sandstone (Abele et al., 1988)

**Material.** Cetacean fossils are relatively well preserved. The most significant specimens occur in private collections and these include a mysticete skull and mandibles, and postcranial elements (Bearlin, 1987). Material in Museum Victoria includes the posterior part of a large mandible, and one large vertebra.

**Fauna.** *Carcharodon megalodon*, ?"Cetotheriidae".

**South Australia (Fig.10)**

**5. St Vincent Basin (Fig.11)**

**5.1 Port Willunga**

**Geographic location.** 300–400 m south of the old jetty, Port Willunga Beach, approximately 45 km south of Adelaide (this is the locality data for the cranium; the exact location for the radius is unknown, but it was collected in the vicinity of Port Willunga) (Pledge, 1994; N. Pledge, pers. comm.) (near 35°19'S, 138°27'E).

**Stratigraphic position.** Ruwaring Member, Port Willunga Formation (N. Pledge, pers. comm.).

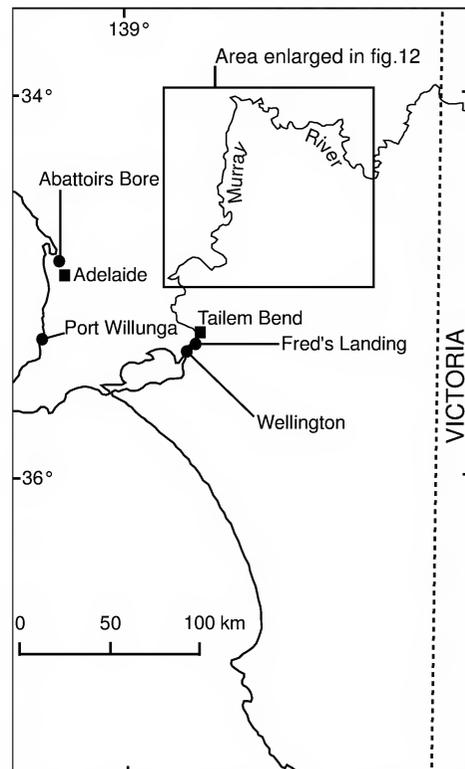


Figure 11. Fossil Cetacea localities in the St Vincent and Murray basins in south-east South Australia. Solid circles represent fossil Cetacea localities. Modified from Alley et al. (1995).

*Age.* Willungan (Early Oligocene; Rupelian), 30–32 Ma (Alley et al., 1995; Holdgate and Gallagher, 2003).

*Lithology.* Bryozoal marl limestone containing chert nodules (Alley et al., 1995; N. Pledge pers. comm.).

*Material.* One right radius (Pledge, 1994) and one incomplete cranium.

*Fauna.* Cetacea indet., cf. Aetiocetidae (N. Pledge, pers. comm.).

## 5.2 Abattoirs Bore

*Geographic location.* Abattoirs Bore, Dry Creek, about 10 km north of Adelaide (34°50'00"S, 138°36'35"E) (Howchin, 1919; Bearlin, 1987).

*Stratigraphic position.* Dry Creek Sand.

*Age.* Late Pliocene (Alley et al., 1995).

*Lithology.* Shelly sand.

*Material.* One isolated periotic.

*Fauna.* *Carcharodon carcharias*, Balaenidae (Howchin, 1919).

## 6. Murray Basin (Figs 11, 12)

### 6.1 Fred's Landing

*Geographic location.* Boat launching area about 3 km downstream from Tailem Bend, on the east bank of the Murray River (35°17'S, 139°27'E) (Pledge, 1994).

*Stratigraphic position.* Upper Buccleuch Formation (Pledge, 1994).

*Age.* Early Oligocene.

*Lithology.* Green and slightly glauconitic fine-grained limestone (Pledge, 1994; Alley et al., 1995).

*Material.* One heterodont tooth.

*Fauna.* Cetacea indet.

### 6.2 Wellington

*Geographic location.* Near Wellington, on the Murray River, south-east of Adelaide (Pledge and Rothausen, 1977) (near 35°19'S, 139°23'E).

*Stratigraphic position.* Etrick Formation (Pledge and Rothausen, 1977).

*Age.* Late Oligocene (Alley et al., 1995).

*Lithology.* Glauconitic marl, calcareous clay, and mudstone, with silt and sand (Pledge and Rothausen, 1977; Alley et al., 1995).

*Material.* Several heterodont teeth (possibly associated).

*Fauna.* *Hexanchus agassizi*, Cetacea indet. (= *Metasqualodon harwoodi*).

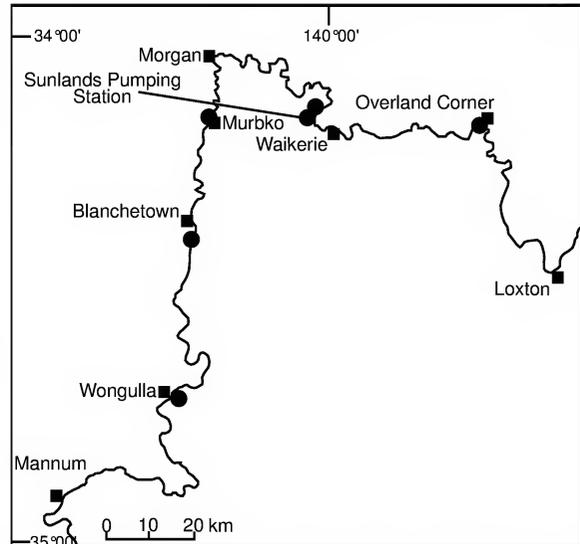


Figure 12. Fossil Cetacea localities along the Murray River north-east of Adelaide. Solid circles represent fossil Cetacea localities. Modified from Lukasik and James (1998).

### 6.3 Wongulla

*Geographic location.* Cliffs on east bank of Murray River opposite Wongulla, approximately 5 km south of Devon Downs (near 34°41'S, 139°35'E).

*Stratigraphic position.* Upper Member, Mannum Formation.

*Age.* Early Miocene (Lukasik and James, 1998).

*Lithology.* Yellow-orange calcarenite.

*Material.* Anterior portions of two large mandibles and associated incomplete vertebrae.

*Fauna.* Mysticeti.

### 6.4 Blanchetown

*Geographic location.* Close to the north end of the channel between Notts Island and Murray River cliffs, about 4 km south of Blanchetown Bridge, north-east of Adelaide (N. Pledge, pers. comm.) (near 34°28'S, 139°36'E).

*Stratigraphic position.* Upper Member, Mannum Formation (Lukasik and James, 1998).

*Age.* Cetacean fossils were recovered about 3–4 m below the *Lepidocyclina* Zone (N. Pledge, pers. comm.), and therefore, pre-Batesfordian. The minimum age of the upper Mannum Formation is earliest Longfordian, based on the presence of *Operculina victoriensis* at the base of this unit. The Upper Member of the Mannum Formation is overall no younger than Early Miocene (Lukasik and James, 1998).

*Lithology.* Fine-grained calcarenite.

*Material.* One mandible with two posterior teeth in situ and four associated vertebrae. These fossils represent one individual, and other bones remain unprepared at the South Australian Museum.

*Fauna.* ?Squalodontidae.

### 6.5 MacBean's Pound

*Geographic location.* About 6.5 km from Blanchetown, Murray River (near 34°25'20"S, 139°37'05"E).

*Stratigraphic position.* Upper Member, Mannum Formation.

*Age.* Early Miocene.

*Lithology.* Bryozoal calcarenite.

*Material.* Mandibles.

*Fauna.* ?"Cetotheriidae".

### 6.6 Murbko

*Geographic location.* Murray River cliffs near Murbko Homestead, 22.5 km north-east of Blanchetown (34°07'55"S, 139°39'05"E).

*Stratigraphic position.* Glenforlan Formation (sensu Lukasik and James, 1998).

*Age.* The presence of *Lepidocyclina howchini* indicates a Batesfordian (early Middle Miocene) age (Lukasik and James, 1998).

*Lithology.* Bryozoal calcarenite.

*Material.* One almost complete cranium.

*Fauna.* cf. *Parietobalaena* sp.

### 6.7 Waikerie

*Geographic location.* 100 m downstream from the Sunlands Pumping Station, 8 km west of Waikerie, Murray River (near 34°09'S, 139°55'E).

*Stratigraphic position.* Pata Formation.

*Age.* Balcombian (Middle Miocene) (Lukasik and James, 1998).

*Lithology.* Yellow-orange fine calcarenite with muddy bands.

*Material.* One incomplete scapula.

*Fauna.* Mysticeti indet.

### 6.8 Winkie

*Geographic location.* Riverbed, Murray River, Gerard Mission, near Winkie (near 34°22'45"S, 140°28'30"E).

*Stratigraphic position.* ?Bookpurnong Formation (Bearlin, 1987).

*Age.* ?Mio-Pliocene.

*Lithology.* ?Marl, silty clay and minor fine sand (Alley et al., 1995).

*Material.* Incomplete cranium and mandible (Bearlin, 1987).

*Fauna.* Balaenopteridae.

### 6.9 Sunlands Pumping Station

*Geographic location.* Beds immediately above a hardground of cemented sand and oyster shells, 3–4 m above the base of the cliffs, Sunlands Pumping Station, 8 km west-north-west of Waikerie, Murray River (near 34°09'S, 139°55'E) (Pledge, 1985).

*Stratigraphic position.* Loxton Sand (Alley et al., 1995; Pledge, 1985).

*Age.* Early Pliocene.

*Lithology.* Poorly sorted coarse sand containing pebbles.

*Material.* Isolated elements comprising vertebrae and teeth (Pledge, 1985).

*Fauna.* *Heterodontus* cf. *cainozoicus*, *Orectolobus gippslandicus*, *Carcharias* sp., *Carcharodon* cf. *megalodon*, *Isurus hastalis*, *Lamna* cf. *cattica*, *Mustelus* sp., *Carcharhinus* cf. *brachyurus*, *Galeocerdo aduncus*, *Galeorhinus* cf. *australis*, *Sphyrna* sp., *Pristiophorus lanceolatus*, cf. *Myliobatis* sp., Labroidei indet., Monacanthidae indet., *Diodon formosus*, cf. *Zygomaturus*, *Phascolarctos maris*, *Dorcopsis* sp., cf. *Dugong* sp. (Pledge, 1992; Domning, 1996), Mysticeti indet., ?Delphinidae indet.

### 6.10 Overland Corner

*Geographic location.* Near Overland Corner, Murray River, about 10 km north-west of Lake Bonney (near 34°09'20"S, 140°20'E).

*Stratigraphic position.* ?Glenforlan Formation.

*Age.* ?Batesfordian (early Middle Miocene).

*Lithology.* Bryozoal calcarenite.

*Material.* One incomplete cranium.

*Fauna.* Mysticeti.

## 7. Gambier Basin

### 7.1 Mount Gambier (Fig. 13)

*Geographic location.* The old "Knights and Pritchard's" dimension stone quarry, near Marte, 10 km west of Mount Gambier (near 37°48'S, 140°09'E).

*Stratigraphic position.* Camelback Member, Gambier Limestone (Alley et al., 1995).

*Age.* Late Oligocene (planktonic foraminiferal zones P21-P22) (Li et al., 2000).

*Lithology.* Pale cream-white porous bryozoal calcarenite.

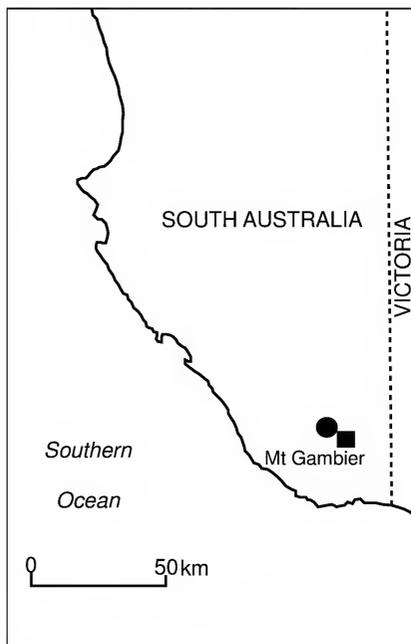


Figure 13. Fossil Cetacea locality in the Gambier Basin, extreme south-east of South Australia. Solid circles represent fossil Cetacea localities. Modified from Alley et al. (1995).

**Material.** Fossil preservation is generally very good. Cetaceans are represented by isolated teeth, vertebrae, and cranial fragments.

**Fauna.** *Carcharodon angustidens*, Spheniscidae, “*Squalodon gambierensis*, Mysticeti indet., Prosqualodontidae.

## 8. Lake Eyre Basin (Fig. 14)

### 8.1 Lake Namba

**Geographic location.** 4 km south of Ericmas Quarry, which occurs at the base of low bluffs just south of track to Billeroo Waterhole on western side of Lake Namba, Lake Frome area, South Australia (31°14'S, 140°14'E) (Fordyce, 1983; T.Rich, pers. comm.).

**Stratigraphic position.** Ericmas Fauna, base of upper member, Namba Formation, equivalent to unit 4 of Namba Formation at Lake Pinpa.

**Age.** Late Oligocene–Middle Miocene (Callen and Tedford, 1976). Palynofloras suggest a Miocene–Pliocene age range for the Namba Formation (Alley et al., 1995). Fordyce (1983) suggested that the Namba Formation was Middle Miocene in age, and no older than Batesfordian–Balcombian. Recently, Woodburne and colleagues (1993) have indicated that the Etadunna Formation (a correlate of the Namba Formation) is perhaps 24–28 Ma. If the latter dates are accurate, they would imply that the Namba Formation is Late Oligocene in age. However, due to the inconsistent results of various dating

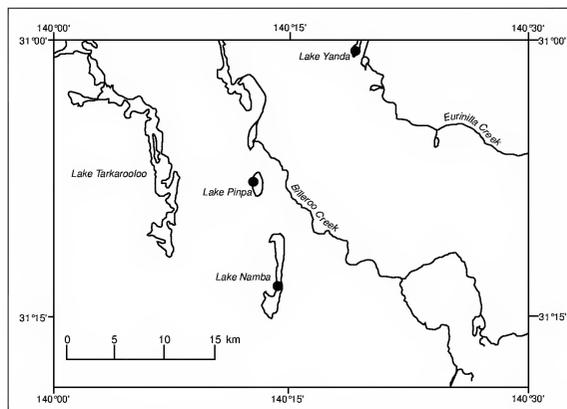


Figure 14. Fossil Cetacea localities east of Lake Frome, in the Lake Eyre Basin, north-east South Australia. Solid circles represent fossil Cetacea localities. Modified from Tedford et al. (1977).

methods, the Namba Formation is considered herein as Late Oligocene–Middle Miocene in age.

**Lithology.** Illite and kaolinite clays (Alley et al., 1995).

**Material.** One right periotic.

**Fauna.** *Neoceratodus djelleh*, *Neoceratodus eyrensis*, *Neoceratodus gregoryi*, *Neoceratodus* sp. 1, *Neoceratodus* sp. 4, Osteichthyes indet., Chelidae, Crocodylia, Columbidae, Anseriformes, *Obdurodon insignis*, Dasyuridae, *Raemotherium yatkolai*, *Madakoala devisi*, *Madakoala wellsii*, *Pildra antiquus*, *Pildra secundus*, Petauridae, Eurhinodelphinidae.

### 8.2 Lake Pinpa

**Geographic location.** Western margin and floor of Lake Pinpa (31°10'S, 140°14'E) (Fordyce, 1983).

**Stratigraphic position.** At top of unnamed member 1, Namba Formation (Fordyce, 1983).

**Age.** Late Oligocene–Middle Miocene (Alley et al., 1995; Callen and Tedford, 1976; Woodburne et al., 1993).

**Lithology.** Illite and kaolinite clays.

**Material.** One incomplete associated skeleton, and isolated left periotics and radius.

**Fauna.** *Neoceratodus djelleh*, *Neoceratodus forsteri*, *Neoceratodus eyrensis*, *Neoceratodus gregoryi*, *Neoceratodus nargun*, *Neoceratodus* sp. 1, *Neoceratodus* sp. 2, *Neoceratodus* sp. 3, *Neoceratodus* sp. 4, Osteichthyes indet., *Emydura* sp., Meioliidae, Crocodylia, Passeriformes, Rallidae, Podicipedidae, Burhinidae, Phoenicopteridae, Anatidae, *Pelecanus tirarensis*, Phalacrocoracidae, *Obdurodon insignis*, *Muramura* sp., *Ilaria illumidens*, Ilariidae indet., *Madakoala devisi*, ?Potoroidae, ?Macropodidae, Petauridae, *Pildra antiquus*, *Chunia* cf. *illuminata*, *Pilkipildra handae*, *Miralina* cf. *minor*, Eurhinodelphinidae.

### 8.3 Lake Yanda

*Geographic location.* Western side of Lake Yanda, Lake Frome area, South Australia (31°01'S, 140°19'E).

*Stratigraphic position.* Yanda Fauna, near the contact between the two unnamed members of the Namba Formation (Rich et al., 1991).

*Age.* Late Oligocene–Middle Miocene (Alley et al., 1995; Callen and Tedford, 1976; Woodburne et al., 1993).

*Lithology.* Illite and kaolinite clays (Alley et al., 1995).

*Material.* One incomplete tympanic bulla.

*Fauna.* *Neoceratodus djelleh*, *Neoceratodus eyrensis*, *Neoceratodus gregoryi*, *Neoceratodus* sp. 1, *Neoceratodus* sp. 4, Osteichthyes indet., Crocodylia, Phoenicopteridae, Anatidae, *Dasylyrinja kokuminola*, *Ilaria* sp., *Djilgaringa thompsonae*, *Miralina* cf. *minor*, Eurhinodelphinidae.

## Tasmania

### 9. Bass Basin

#### 9.1 Fossil Bluff (Fig.4)

*Geographic location.* Coastal cliff section at Fossil Bluff, Table Cape, near Wynyard, north-east of Launceston, Bass Strait coast of Tasmania (40°58.8'S, 145°43.9'E). Strictly speaking, the Fossil Bluff locality is situated approximately 40–50 km south of the southern margin of the Bass Basin (N. Kemp, pers. comm.).

*Stratigraphic position.* Fossil Bluff Sandstone.

*Age.* Longfordian (Early Miocene). The Fossil Bluff Sandstone has a planktonic foraminiferal fauna which corresponds to zone N4 (earliest Early Miocene; Aquitanian = 21–23.9 Ma) (Quilty, 1980). Fordyce (2003) indicated that the Aquitanian in south-east Australia is comparable to the Chattian (Late Oligocene) in New Zealand. The odontocete genus *Prosqualodon* occurs in the Waitakian (latest Oligocene–earliest Miocene) of New Zealand (Fordyce, 1984, 1991), the Late Oligocene of Victoria and perhaps South Australia (Fitzgerald, 2004, and herein), the Early Miocene of Tasmania (Flynn, 1923; Fitzgerald, 2004), and the Early Miocene of Patagonia, Argentina (Lydekker, 1899; Cabrera, 1926; Fordyce, 2002b; Muizon, 2002).

*Lithology.* Fine siltstones and shales, and glauconitic calcareous sandstone (Kemp, 1991).

*Material.* Isolated teeth, vertebrae, ribs, partially articulated postcranial skeletons, and one associated skeleton comprising: skull, mandibles, teeth, almost complete right forelimb, ribs, 2+ thoracic vertebrae, 4+ lumbar vertebrae, and other elements. The latter specimens represent the holotype of *Prosqualodon davidis*. Unfortunately the skull is now lost (see Mahoney and Ride (1975) for details). Isolated teeth from Fossil Bluff, that represent prosqualodontids congeneric, and perhaps conspecific, with *Prosqualodon davidis*, are present in Museum Victoria and the South Australian Museum.

*Fauna.* *Heterodontus cainozoicus*, *Carcharias taurus*, *Ischyodus mortoni*, *Wynyardia bassiana*, *Prosqualodon davidis*, *Prosqualodon* cf. *davidis*. The holotype of *Scaptodon lodderi* was discovered near this locality.

#### 9.2 Cameron Inlet (Fig.4)

*Geographic location.* Excavations of drains around Memana, near Cameron Inlet, east coast of Flinders Island, Bass Strait, Tasmania (near 39°59'S, 148°05'E).

*Stratigraphic position.* Cameron Inlet Formation (Sutherland and Kershaw, 1971).

*Age.* Late Early–Late Pliocene (Sutherland and Kershaw, 1971).

*Lithology.* Fine silty coquina limestones and sands (Sutherland and Kershaw, 1971).

*Material.* Vertebrae, ribs, incomplete skulls, partial mandibles, teeth, periotics, and tympanic bullae.

*Fauna.* *Carcharodon megalodon*, *Carcharodon carcharias*, *Isurus hastalis*, *Isurus oxyrinchus*, *Carcharhinus* sp., cf. *Balaenoptera*, cf. *Megaptera*, *Physeter* sp., Ziphiidae indet., ?Delphinidae.

### 10. South Tasman Rise (Fig.15)

#### 10.1 Tasman Fracture Zone

*Geographic location.* Pipe dredge 147DR013, 2700–3900 m depth, northern end of eastern Tasman Fracture Zone, south-west of Tasmania (45°07'S, 144°31'E) (Exon et al., 1995).

*Stratigraphic position.* Unnamed lithological unit.

*Age.* Late Neogene (Exon et al., 1995). The one cetacean from this site (a probably indeterminate ziphiid) may indicate a maximum age for these sediments of Late Miocene. Exon and others (1995) suggested that fossil ziphiids from the South Tasman Rise represented a similar fauna to that of Cameron Inlet, which has a mid-Late Pliocene age (Sutherland and Kershaw, 1971).

*Lithology.* ?Silicified limestones (Exon et al., 1995).

*Material.* One incomplete rostrum.

*Fauna.* Ziphiidae indet.

#### 10.2 Seamount east of South Tasman Rise

*Geographic location.* Dredge 147DR038, 2050–2300 m depth, on a seamount east of South Tasman Rise (near 45°43.0'S, 149°00'E) (Exon et al., 1995).

*Stratigraphic position.* Unnamed lithological unit.

*Age.* Late Neogene (Exon et al., 1995).

*Lithology.* ?Silicified limestones (Exon et al., 1995).

*Material.* One incomplete rostrum.

*Fauna.* Ziphiidae indet.

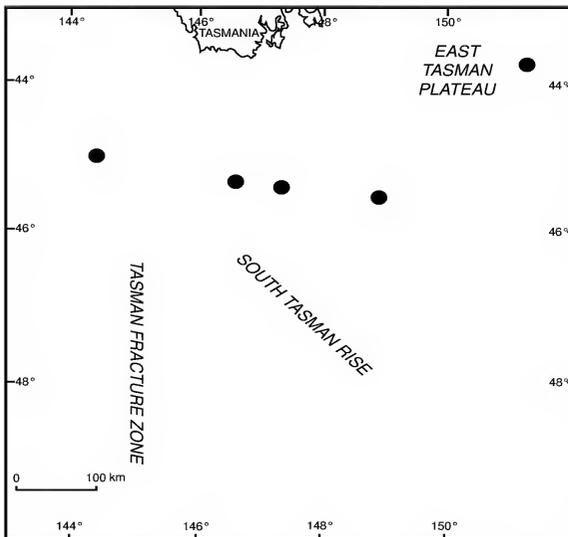


Figure 15. Fossil Cetacea localities offshore southern Tasmania. Solid circles represent fossil Cetacea localities. Modified from Exon et al. (1997).

### 10.3 Eastern South Tasman Rise

*Geographic location.* Dredge site 147DR50, 2050–2300 m depth, east-west trending high on the eastern side of the South Tasman Rise (near 45°30'S, 147°20'E) (Exon et al., 1995).

*Stratigraphic position.* Unnamed lithological unit.

*Age.* Late Neogene (Exon et al., 1995).

*Lithology.* ?Silicified limestones (Exon et al., 1995).

*Material.* One incomplete rostrum, and one skull.

*Fauna.* ?Mysticeti, Ziphiidae.

### 10.4 North-east South Tasman Rise

*Geographic location.* Dredge site 147DR052, 2200–2370 m depth, north-east South Tasman Rise, south-west of Tasmania (near 45°38.1'S, 146°24.5'E) (Exon et al., 1995).

*Stratigraphic position.* Unnamed lithological unit.

*Age.* Late Neogene (Exon et al., 1995).

*Lithology.* ?Silicified limestones (Exon et al., 1995).

*Material.* One small periotic.

*Fauna.* Odontoceti.

### 10.5 East Tasman Rise

*Geographic location.* Dredge site 147DR043, 3030–3600 m depth, eastern scarp of East Tasman Rise, south of Tasmania (near 43°54'S, 151°18'E) (Exon et al., 1995).

*Stratigraphic position.* Unnamed lithological unit.

*Age.* Late Neogene (Exon et al., 1995).

*Lithology.* ?Silicified limestones (Exon et al., 1995).

*Material.* One incomplete tympanic bulla (Exon et al., 1995).

*Fauna.* ?Mysticeti indet.

## 11. East Tasman Plateau (Fig.15)

### 11.1 Eastern Scarp

*Geographic location.* Dredge 147DR043, 3030–3600 m depth, eastern scarp of East Tasman Plateau, south-east of Tasmania (near 43°54'S, 151°18'E) (Exon et al., 1995).

*Stratigraphic position.* Unnamed lithological unit.

*Age.* Late Neogene (Exon et al., 1995).

*Lithology.* ?Silicified limestones (Exon et al., 1995).

*Material.* One incomplete skull.

*Fauna.* cf. *Mesoplodon* sp.

## Discussion

Fordyce (1984) identified 21 and Fitzgerald (2004) 26 fossil Cetacea localities in Australia. Further discoveries, and more study of museum collections has resulted in the recognition of 56 Tertiary fossil Cetacea localities in Australia. Thirty-two of these localities occur in Victoria, 16 in South Australia, and eight in and around Tasmania. All are geographically distinct and generally include only one stratigraphic unit that has yielded fossil cetaceans. The number of recognised Australian fossil Cetacea localities compares with approximately 58–60 recognised Australian Tertiary terrestrial mammal localities (Rich et al., 1991; pers. obs.). That almost all the fossil cetacean-bearing localities occur in the south-east of the continent, while extensive areas of Cainozoic marine sedimentary rock outcrop occur outside this region, points to a potentially rich record of fossil cetaceans in unexplored areas. Moreover, it is highly probable that many localities in south-east Australia remain unrecognised. This is suggested by the broad distribution of cetacean-bearing localities within marine sedimentary basins. However, a perhaps less fortuitous aspect of this locality distribution and the faunal lists and material derived from these localities is the lack of cetacean fossil density at these localities.

Few localities have yielded diagnostic, reasonably complete skulls and/or skeletons. These localities are: Victoria; Arch Site (Grange Burn), Gibson's Steps, Curdie, Bells Headland, Bells Beach, Deadman's Gully, Bird Rock, Batesford Quarry, North Arm, Newmerella; South Australia; Murbko, Lake Pinpa; and Tasmania; Fossil Bluff. The source stratigraphic units (and lithologies) at the latter localities occur elsewhere, and it may be expected that more reasonably complete specimens will be discovered at these localities in future. The most important general area for fossil cetaceans in Australia is the coastline south-west of Torquay, in the Torquay Basin, Victoria. Eight skulls/skeletons have been collected from this area, with all derived from the Upper Oligocene Jan Juc Marl and its lateral

equivalents. Limitations to conducting fieldwork to prospect for, and recover, fossil cetaceans in this area include: extreme rarity of shore platforms being scoured by storm tides to remove sand and algae, thus uncovering larger areas of accessible outcrop; and dangerously unstable, steep, and high cliff sections. Despite these limitations, systematic prospecting of the coastline in this area will likely yield more important fossil cetaceans.

The Australian pre-Pleistocene fossil record of cetaceans, as currently understood, can be summarised thus: Eocene – not present; Early Oligocene – poorly known, but great potential; Late Oligocene – poorly known at present but will probably be the second-best known period of cetacean evolution in Australian waters; Early Miocene – poorly known, but great potential; Middle Miocene – poorly known, but great potential; Late Miocene – reasonably well-known; Early Pliocene – best known period of cetacean evolution in Australian waters; and Late Pliocene – poorly known.

Although the fossil record of Cetacea in Australia is known only in the broadest of terms, the identification of 56 recognised pre-Pleistocene fossil cetacean-bearing localities emphasises the wide distribution of cetacean fossils, and the potential for the elucidation of the details of this fossil record. These localities indicate geographic areas that may be fruitful for future discoveries, as well as stratigraphic horizons that are known to produce fossil cetaceans. Fossil cetaceans have arguably received the least attention of all groups of Australian fossil vertebrates, and yet they have, potentially, the richest pre-Pleistocene fossil record of all mammalian taxa in Australia.

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### References

- Abele, C. 1979. Geology of the Anglesea area, central coastal Victoria. *Geological Survey of Victoria Memoir* 31: 1–73.
- Abele, C., Gloe, C.S., Hocking, J.B., Holdgate, G., Kenley, P.R., Lawrence, C.R., Ripper, D., Threlfall, W.F., and Bolger, P.F. 1988. Tertiary. Pp. 251–350 in: Douglas, J.G. and Ferguson, J.A. (eds), *Geology of Victoria*. Victorian Division, Geological Society of Australia Incorporated: Melbourne.
- Alley, N.F., Lindsay, J.M., Barnett, S.R., Benbow, M.C., Callen, R.A., Cowley, W.M., Greenwood, D., Kwitko, G., Lablack, K.L., Lindsay, J.M., Rogers, P.A., Smith, P.C., and White, M.R. 1995. Tertiary. Pp. 151–218 in: Drexel, J.F., and Preiss, W.V. (eds), *The geology of South Australia. Volume 2. The Phanerozoic*. Bulletin of the Geological Survey of South Australia 54.
- Anonymous. 1939. A fossil whale from Australia. *Nature* 143: 525.
- Arnason, U., and Gullberg, A. 1994. Relationships of baleen whales established by cytochrome b gene sequence comparison. *Nature* 367: 726–728.
- Barnes, L.G., and Mitchell, E.D. 1978. Cetacea. Pp. 582–602 in: Maglio, V.J., and Cooke, H.B.S. (eds), *Evolution of African Mammals*. Harvard University Press: Cambridge.
- Bearlin, R.K. 1982. A new “shark-toothed dolphin” (Order Cetacea, Family Squalodontidae) from Batesford, Victoria, Australia. B.Sc. (Honours) Thesis, Monash University: Clayton. 133 pp.
- Bearlin, R.K. 1987. The morphology and systematics of Neogene Mysticeti from Australia and New Zealand. Ph.D. Thesis, University of Otago: Dunedin. 212 pp.
- Bearlin, R.K. 1988. The morphology and systematics of Neogene Mysticeti from Australia and New Zealand (abstract of Ph.D. Thesis, University of Otago, Dunedin). *New Zealand Journal of Geology and Geophysics* 31: 257.
- Berggren, W.A., Kent, D.V., Swisher, C.C. III, and Aubry, M.-P. 1995. A revised Cenozoic geochronology and chronostratigraphy. Pp. 129–212 in: Berggren, W.A., Kent, D.V., Aubry, M.-P., and Hardenbol, J. (eds), *Geochronology, Time Scales and Global Stratigraphic Correlation*. SEPM Special Publication 54.
- Berta, A., Deméré, T., and Gatesy, J. 2003. Systematics and evolution of the Mysticeti. *Journal of Vertebrate Paleontology* 23 (Supplement to Number 3): 33A–34A.
- Bowler, J.M. 1963. Tertiary stratigraphy and sedimentation in the Geelong-Maude area, Victoria. *Proceedings of the Royal Society of Victoria* 76: 69–137.
- Cabrera, A. 1926. Cetáceos fósiles del Museo de La Plata. *Revista del Museo de La Plata* 29: 363–411.
- Callen, R.A., and Tedford, R.H. 1976. New late Cainozoic rock units and depositional environments, Lake Frome area, South Australia. *Transactions of the Royal Society of South Australia* 100: 125–167.
- Camp, C.L., Taylor, D.N., and Welles, S.P. 1942. Bibliography of fossil vertebrates 1934–1938. *Geological Society of America Special Paper* 42: 1–663.
- Carroll, R.L. 1988. *Vertebrate Paleontology and Evolution*. W.H. Freeman and Company: New York. 698 pp.
- Carter, A.N. 1985. A model for depositional sequences in the Late Tertiary of southeastern Australia. *Special Publication, South Australian Department of Mines and Energy* 5: 13–27.
- Chapman, F. 1912. On the occurrence of *Scaldicetus* in Victoria. *Records of the Geological Survey of Victoria* 3: 236–238.
- Chapman, F. 1913. Note on the occurrence of the Cainozoic shark, *Carcharoides*, in Victoria. *Victorian Naturalist* 30: 142–143.
- Chapman, F. 1917a. New or little-known Victorian fossils in the National Museum. Part XX.—Some Tertiary fish-teeth. *Proceedings of the Royal Society of Victoria* 29: 134–141.

- Chapman, F. 1917b. New or little-known Victorian fossils in the National Museum. Part XXI.—Some Tertiary cetacean remains. *Proceedings of the Royal Society of Victoria* 30: 32–43.
- Chapman, F. 1918. On an apparently new type of cetacean tooth from the Tertiary of Tasmania. *Proceedings of the Royal Society of Victoria* 30: 149–152.
- Chapman, F. 1929. *Illustrated Guide to the Collection of Fossils Exhibited in the National Museum of Victoria*. H.J. Green, Government Printer: Melbourne. 55 pp.
- Chapman, F. 1930. Note on chimaeroid fish remains from the Australian Tertiaries. *Annals and Magazine of Natural History Series* 10, 8: 139.
- Chapman, F., and Cudmore, F.A. 1924. New or little-known fossils in the National Museum. Part XXVII.—Some Cainozoic fish remains, with a revision of the group. *Proceedings of the Royal Society of Victoria* 36: 107–162.
- Chapman, F., and Pritchard, G.B. 1904. Fossil fish remains from the Tertiaries of Australia. Part I. *Proceedings of the Royal Society of Victoria* 17: 267–297.
- Chapman, F., and Pritchard, G.B. 1907. Fossil fish remains from the Tertiaries of Australia. Part II. *Proceedings of the Royal Society of Victoria* 20: 59–75.
- Cozzuol, M.A. 1996. The record of the aquatic mammals in southern South America. Pp. 321–342 in: Arratia, G. (ed.), *Contributions of Southern South America to Vertebrate Paleontology*. Münchner Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Paläontologie, 30.
- Dickinson, J.A. 2002. Neogene tectonism and phosphogenesis across the SE Australian margin. Ph.D. Thesis, University of Melbourne: Melbourne. 229 pp.
- Dickinson, J.A., Wallace, M.W., Holdgate, G.R., Gallagher, S.J., and Thomas, L. 2002. Origin and timing of the Miocene–Pliocene unconformity in south-east Australia. *Journal of Sedimentary Research* 72: 288–303.
- Domning, D.P. 1996. Bibliography and index of the Sirenia and Desmostylia. *Smithsonian Contributions to Paleobiology* 80: 1–611.
- Etheridge, R., Jr. 1878. *A catalogue of Australian Fossils (Including Tasmania and the Island of Timor) Stratigraphically and Zoologically Arranged*. Cambridge University Press: Cambridge. 232 pp.
- Exon, N.F., Marshall, J.F., McCorkle, D.C., Alcock, M., Chaproniere, G.C.H., Connell, R., Dutton, S.J., Elmes, M., Findlay, C., Robertson, L., Rollet, N., Samson, C., Shafik, S., and Whitmore, G.P. 1995. AGSO Cruise 147 report: Tasman Rises geological sampling cruise of *Rig Seismic*: stratigraphy, tectonic history and palaeoclimate of the offshore Tasmanian region. *Australian Geological Survey Organisation Record* 1995/56.
- Exon, N.F., Moore, A.M.G., and Hill, P.J. 1997. Geological framework of the South Tasman Rise, south of Tasmania, and its sedimentary basins. *Australian Journal of Earth Sciences* 44: 561–577.
- Finlayson, H.H. 1938. On the occurrence of a fossil penguin in Miocene beds in South Australia. *Transactions of the Royal Society of South Australia* 62: 14–17.
- Fitzgerald, E.M.G. 2003. Oligocene Cetacea (Mammalia) from the southern margin of Australia. *Geological Society of Australia Abstracts* 70: 17.
- Fitzgerald, E.M.G. 2004. The fossil record of cetaceans (Mammalia) on the Australian continent. *Fossil Collector Bulletin* 72: 5–32.
- Flynn, T.T. 1920. Squalodont remains from the Tertiary strata of Tasmania. *Nature* 106: 406–407.
- Flynn, T.T. 1923. A whale of bygone days. *Australian Museum Magazine* 1: 266–272.
- Flynn, T.T. 1932. A new species of fossil cetacean from Tasmania. *Geological Magazine* 69: 327–329.
- Flynn, T.T. 1948. Description of *Prosqalodon davidi* Flynn, a fossil cetacean from Tasmania. *Transactions of the Zoological Society of London* 26: 153–197.
- Fordyce, R.E. 1978 (1979). A review of austral archaeocete whales [Abstract]. *New Zealand Geological Society Miscellaneous Publication* 23A: [unpaginated].
- Fordyce, R.E. 1982a. A review of Australian fossil Cetacea. *Memoirs of the National Museum of Victoria* 43: 43–58.
- Fordyce, R.E. 1982b. The Australasian marine vertebrate record and its climatic and geographic implications. Pp. 595–627 in: Rich, P.V., and Thompson, E.M. (eds), *The Fossil Vertebrate Record of Australasia*. Monash University Offset Printing Unit: Clayton.
- Fordyce, R.E. 1983. Rhabdosteid dolphins (Mammalia: Cetacea) from the Middle Miocene, Lake Frome area, South Australia. *Alcheringa* 7: 27–40.
- Fordyce, R.E. 1984. Evolution and zoogeography of cetaceans in Australia. Pp. 929–948 in: Archer, M., and Clayton, G. (eds), *Vertebrate Zoogeography and Evolution and Zoogeography in Australasia*. Hesperian Press: Perth.
- Fordyce, R.E. 1988. Taxonomic status of Victorian fossil whales assigned to the genus *Cetotolites* McCoy, 1879. *Memoirs of the Museum of Victoria* 49: 59–65.
- Fordyce, R.E. 1991. The Australasian marine vertebrate record and its climatic and geographic implications. Pp. 1165–1190 in: Vickers-Rich, P., Monaghan, J.M., Baird, R.F., and Rich, T.H. (eds), *Vertebrate Palaeontology of Australasia*. Pioneer Design Studio in cooperation with the Monash University Publications Committee: Melbourne.
- Fordyce, R.E. 2002a. Oligocene archaeocetes and toothed mysticetes: Cetacea from times of transition. Pp. 16–17 in: Fordyce, R.E., and Walker, M. (eds), *Abstracts, Third Conference on Secondary Adaptation to Life in Water*. Geological Society of New Zealand Miscellaneous Publication 114A.
- Fordyce, R.E. 2002b. Fossil sites. Pp. 471–482 in: Perrin, W.F., Würsig, B., and Thewissen, J.G.M. (eds), *Encyclopedia of Marine Mammals*. Academic Press: San Diego.
- Fordyce, R.E. 2003. Cetacean evolution and Eocene–Oligocene oceans revisited. Pp. 154–170 in: Prothero, D.R., Ivany, L.C., and Nesbitt, E.A. (eds), *From Greenhouse to Icehouse: the Marine Eocene–Oligocene Transition*. Columbia University Press: New York.
- Fordyce, R.E., and Flannery, T.F. 1983. Fossil phocid seals from the late Tertiary of Victoria. *Proceedings of the Royal Society of Victoria* 95: 99–100.
- Fordyce, R.E., and Muizon, C. de. 2001. Evolutionary history of cetaceans: a review. Pp. 169–233 in: Mazin, J.M., and Buffrénil, V. de. (eds), *Secondary Adaptation of Tetrapods to Life in Water*. Verlag Dr. Friedrich Pfeil: München.
- Geisler, J.H., and Luo, Z. 1996. The petrosal and inner ear of *Herpetocetus* sp. (Mammalia: Cetacea) and their implications for the phylogeny and hearing of archaic mysticetes. *Journal of Paleontology* 70: 1045–1066.
- Geisler, J.H., and Sanders, A.E. 2003. Morphological evidence for the phylogeny of Cetacea. *Journal of Mammalian Evolution* 10: 23–129.
- Gill, E.D. 1957. The stratigraphical occurrence and palaeoecology of some Australian Tertiary marsupials. *Memoirs of the National Museum of Victoria* 21: 135–203.
- Glaessner, M.F. 1947. A fossil beaked whale from Lakes Entrance, Victoria. *Proceedings of the Royal Society of Victoria* 58: 25–34.

- Glaessner, M.F. 1955. Pelagic fossils (*Aturia*, penguins, whales) from the Tertiary of South Australia. *Records of the South Australian Museum* 11: 353–372.
- Glover, J.E. 1955. Petrographical study of rock samples from the coastal section between Torquay and Airey's Inlet, Victoria. *Proceedings of the Royal Society of Victoria* 67: 149–164.
- Gottfried, M.D., and Fordyce, R.E. 2001. An associated specimen of *Carcharodon angustidens* (Chondrichthyes, Lamnidae) from the Late Oligocene of New Zealand, with comments on *Carcharodon* interrelationships. *Journal of Vertebrate Paleontology* 21: 730–739.
- Hall, T.S. 1911. On the systematic position of the species of *Squalodon* and *Zeuglodon* described from Australia and New Zealand. *Proceedings of the Royal Society of Victoria* 23: 257–265.
- Harris, W.K. 1971. Tertiary stratigraphic palynology, Otway Basin. Pp. 67–87 in: Wopfner, H., and Douglas, J.G. (eds), *The Otway Basin of Southeastern Australia*. Special Bulletin, Geological Surveys of South Australia and Victoria.
- Heyning, J.E. 1989. Comparative facial anatomy of beaked whales (Ziphiidae) and a systematic revision among the families of extant Odontoceti. *Natural History Museum of Los Angeles County, Contributions in Science* 405: 1–64.
- Heyning, J.E. 1997. Sperm whale phylogeny revisited: analysis of the morphological evidence. *Marine Mammal Science* 13: 596–613.
- Holdgate, G.R., and Gallagher, S.J. 2003. Tertiary: a period of transition to marine basin environments. Pp. 289–335 in: Birch, W.D. (ed.), *Geology of Victoria*. Geological Society of Australia Special Publication 23, Geological Society of Australia (Victoria Division): Melbourne.
- Howchin, W. 1919. [Tympenic bone of *Balaena* from the Pliocene of South Australia.] *Transactions and Proceedings of the Royal Society of South Australia* 43: 430.
- Jenkins, R.F. 1974. A new giant penguin from the Eocene of Australia. *Palaeontology* 17: 291–310.
- Jenkins, R.F. 1990. *Anthropornis nordenskjoldi* Nordenskjöld's giant penguin. Pp. 183–187 in: Rich, P.V. and van Tets, G.F. (eds), *Kadimakara: Extinct Vertebrates of Australia*. Princeton University Press: Princeton.
- Kelly, J.C., Webb, J.A., and Maas, R. 2001. Isotopic constraints on the genesis and age of autochthonous glaucony in the Oligo–Miocene Torquay Group, south-eastern Australia. *Sedimentology* 48: 325–338.
- Kemp, N.R. 1970. Studies on the dentition of Australian Tertiary and Recent sharks. M.Sc. Thesis, University of Melbourne: Melbourne. 354 pp.
- Kemp, N.R. 1978. Detailed comparisons of the dentitions of extant hexanchid sharks and Tertiary hexanchid teeth from South Australia and Victoria, Australia (Selachii: Hexanchidae). *Memoirs of the National Museum of Victoria* 39: 61–83.
- Kemp, N.R. 1982. Chondrichthyans in the Tertiary of Australia. Pp. 88–117 in: Rich, P.V., and Thompson, E.M. (eds), *The Fossil Vertebrate Record of Australasia*. Monash University Offset Printing Unit: Clayton.
- Kemp, N.R. 1991. Chondrichthyans in the Cretaceous and Tertiary of Australia. Pp. 497–568 in: Vickers-Rich, P., Monaghan, J.M., Baird, R.F., and Rich, T.H. (eds), *Vertebrate Palaeontology of Australasia*. Pioneer Design Studio in cooperation with the Monash University Publications Committee: Melbourne.
- Köhler, R., and Fordyce, R.E. 1997. An archaeocete whale (Cetacea: Archaeoceti) from the Eocene Waihao Greensand, New Zealand. *Journal of Vertebrate Paleontology* 17: 574–583.
- Li, Q., Davies, P.J., and McGowran, B. 1999. Foraminiferal sequence biostratigraphy of the Oligo–Miocene Janjukian strata from Torquay, southeastern Australia. *Australian Journal of Earth Sciences* 46: 261–273.
- Li, Q., McGowran, B., and White, M.R. 2000. Sequence and biofacies packages in the mid-Cenozoic Gambier Limestone, South Australia: reappraisal of foraminiferal evidence. *Australian Journal of Earth Sciences* 47: 955–970.
- Lukasik, J.J., and James, N.P. 1998. Lithostratigraphic revision and correlation of the Oligo–Miocene Murray Supergroup, western Murray Basin, South Australia. *Australian Journal of Earth Sciences* 45: 889–902.
- Lydekker, R. 1899. On the skull of a shark-toothed dolphin from Patagonia. *Proceedings of the Zoological Society of London* 1899: 919–922.
- Mahoney, J.A., and Ride, W.D.L. 1975. Index to the genera and species of fossil Mammalia described from Australia and New Guinea between 1838 and 1968. *Western Australian Museum Special Publication* 6: 1–250.
- Mallett, C.W. 1977. Studies in Victorian Tertiary Foraminifera: Neogene planktonic faunas. Ph.D. Thesis, University of Melbourne: Melbourne. 381 pp.
- McCoy, F. 1866. *Notes sur la zoologie et la palaeontologie de Victoria, par Frederick M'Coy*. Traduit de l'anglais par E. Lissignol. Masterman: Melbourne. 35 pp.
- McCoy, F. 1867a. On the occurrence of the genus *Squalodon* in the Tertiary strata of Victoria. *Geological Magazine* 4: 145.
- McCoy, F. 1867b. On the recent zoology and palaeontology of Victoria. *Annals and Magazine of Natural History* 20: 175–202.
- McCoy, F. 1875. *Squalodon wilkinsoni* (McCoy). *Prodromus of the palaeontology of Victoria; or, figures and descriptions of the Victorian organic remains*. Decade 2: 7, 8. Geological Survey of Victoria: Melbourne.
- McCoy, F. 1879a. *Cetotolites*. *Prodromus of the palaeontology of Victoria; or, figures and descriptions of the Victorian organic remains*. Decade 6: 13–17. Geological Survey of Victoria: Melbourne.
- McCoy, F. 1879b. *Physetodon baileyi* (McCoy). *Prodromus of the palaeontology of Victoria; or, figures and descriptions of the Victorian organic remains*. Decade 6: 19–21. Geological Survey of Victoria: Melbourne.
- McHaffie, I.W., and Inan, K. 1988. Limestone. Pp. 572–579 in: Douglas, J.G., and Ferguson, J.A. (eds), *Geology of Victoria*. Victorian Division, Geological Society of Australia Incorporated: Melbourne.
- McKenna, M.C., and Bell, S.K. 1997. *Classification of mammals above the species level*. Columbia University Press: New York. 631 pp.
- Messenger, S.L., and McGuire, J.A. 1998. Morphology, molecules, and the phylogenetics of cetaceans. *Systematic Biology* 47: 90–124.
- Milinkovitch, M.C., Ortí, G., and Meyer, A. 1993. Revised phylogeny of whales suggested by mitochondrial ribosomal DNA sequences. *Nature* 361: 346–348.
- Mitchell, E.D. 1989. A new cetacean from the Late Eocene La Meseta Formation, Seymour Island, Antarctic Peninsula. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 2219–2235.
- Muizon, C. de. 2002. River dolphins, evolutionary history. Pp. 1043–1049 in: Perrin, W.F., Würsig, B., and Thewissen, J.G.M. (eds), *Encyclopedia of Marine Mammals*. Academic Press: San Diego.
- Nicolaidis, S., and Wallace, M.W. 1997. Submarine cementation and subaerial exposure in Oligo–Miocene temperate carbonates, Torquay Basin, Australia. *Journal of Sedimentary Research* 67: 397–410.

- Pledge, N.S. 1967. Fossil elasmobranch teeth of South Australia and their stratigraphic distribution. *Transactions of the Royal Society of South Australia* 91: 135–160.
- Pledge, N.S. 1985. An Early Pliocene shark tooth assemblage in South Australia. *Special Publication, South Australian Department of Mines and Energy* 5: 287–299.
- Pledge, N.S. 1992. First record of fossil sirenians in southern Australia. *Fossil Collector Bulletin* 37: 6.
- Pledge, N.S. 1994. Cetacean fossils from the Lower Oligocene of South Australia. *Records of the South Australian Museum* 27: 117–123.
- Pledge, N.S., and Rothausen, K. 1977. *Metasqualodon harwoodi* (Sanger, 1881)—a redescription. *Records of the South Australian Museum* 17: 285–297.
- Pritchard, G.B. 1939. On the discovery of a fossil whale in the older Tertiaries of Torquay, Victoria. *Victorian Naturalist* 55: 151–159.
- Purdy, R.W., Schneider, V.P., Applegate, S.P., McLellan, J.H., Meyer, R.L., and Slaughter, B.H. 2001. The Neogene sharks, rays, and bony fishes from Lee Creek Mine, Aurora, North Carolina. Pp. 71–202 in: Ray, C.E., and Bohaska, D.J. (eds), *Geology and Paleontology of the Lee Creek Mine, North Carolina, III*. Smithsonian Contributions to Paleobiology 90.
- Quilty, P. 1980. New rotalid foraminiferids from the Oligo–Miocene of Tasmania. *Alcheringa* 4: 299–311.
- Raggatt, H.G., and Crespin, I. 1955. Stratigraphy of Tertiary rocks between Torquay and Eastern View, Victoria. *Proceedings of the Royal Society of Victoria* 67: 75–142.
- Rich, P.V. 1975. Antarctic dispersal routes, wandering continents, and the origin of Australia's non-passeriform avifauna. *Memoirs of the National Museum of Victoria* 36: 63–125.
- Rich, T.H., Archer, M., Hand, S.J., Godthelp, H., Muirhead, J., Pledge, N.S., Flannery, T.F., Woodburne, M.O., Case, J.A., Tedford, R.H., Turnbull, W.D., Lundelius, E.L., Jr., Rich, L.S.V., Whitelaw, M.J., Kemp, A., and Rich, P.V. 1991. Appendix 1. Australian Mesozoic and Tertiary terrestrial mammal localities. Pp. 1005–1058 in: Vickers-Rich, P., Monaghan, J.M., Baird, R.F., and Rich, T.H. (eds), *Vertebrate Palaeontology of Australasia*. Pioneer Design Studio in cooperation with the Monash University Publications Committee: Melbourne.
- Rich, T.H., Darragh, T.A., and Vickers-Rich, P. 2003. The strange case of the wandering fossil. *Bulletin of the American Museum of Natural History* 13: 556–567.
- Romer, A.S. 1966. *Vertebrate Paleontology*. Third Edition. University of Chicago Press: Chicago. 468 pp.
- Sanger, E.B. 1881. On a molar tooth of *Zeuglodon* from the Tertiary beds on the Murray River near Wellington, S.A. *Proceedings of the Linnean Society of New South Wales* 5: 298–300.
- Siesser, W.G. 1979. Oligocene–Miocene calcareous nanofossils from the Torquay Basin, Victoria, Australia. *Alcheringa* 3: 159–170.
- Simpson, G.G. 1957. Australian fossil penguins, with remarks on penguin evolution and distribution. *Records of the South Australian Museum* 13: 51–70.
- Simpson, G.G. 1959. A new fossil penguin from Australia. *Proceedings of the Royal Society of Victoria* 71: 113–119.
- Simpson, G.G. 1965. New record of a fossil penguin in Australia. *Proceedings of the Royal Society of Victoria* 79: 91–93.
- Simpson, G.G. 1970. Miocene penguins from Victoria, Australia, and Chubut, Argentina. *Memoirs of the National Museum of Victoria* 31: 17–23.
- Singleton, F.A. 1941. The Tertiary geology of Australia. *Proceedings of the Royal Society of Victoria* 53: 1–125.
- Singleton, O.P., McDougall, I., and Mallett, C.W. 1976. The Pliocene–Pleistocene boundary in southeastern Australia. *Journal of the Geological Society of Australia* 23: 299–311.
- Stinton, F.C. 1958. Fish otoliths from the Tertiary strata of Victoria, Australia. *Proceedings of the Royal Society of Victoria* 70: 81–93.
- Stinton, F.C. 1963. Further studies of the Tertiary otoliths of Victoria, Australia. *Proceedings of the Royal Society of Victoria* 76: 13–22.
- Stirton, R.A. 1967. New species of *Zygomaturus* and additional observations on *Meniscolophus*, Pliocene Palankarinna fauna, South Australia. *Australian Bureau of Mineral Resources, Geology and Geophysics Bulletin* 85: 129–147.
- Sutherland, F.L., and Kershaw, R.C. 1971. The Cainozoic geology of Flinders Island, Bass Strait. *Papers and Proceedings of the Royal Society of Tasmania* 105: 151–175.
- Tate, R. 1892. [*Zeuglodon* tooth from Tasmania.] *Transactions of the Royal Society of South Australia* 15: 265.
- Tedford, R.H., Archer, M., Bartholomai, A., Plane, M., Pledge, N.S., Rich, T., Rich, P., and Wells, R.T. 1977. The discovery of Miocene vertebrates, Lake Frome area, South Australia. *BMR Journal of Geology and Geophysics* 2: 53–57.
- Tickell, S.J., Edwards, J., and Abele, C. 1992. Port Campbell Embayment 1:100 000 map geological report. *Geological Survey of Victoria Report* 95.
- Turnbull, W.D., Lundelius, E.L., and McDougall, I. 1965. A potassium–argon dated Pliocene marsupial fauna from Victoria, Australia. *Nature* 206: 816.
- Uhen, M.D. 1998. Middle to Late Eocene basilosaurines, and dorodontines. Pp. 29–61 in: Thewissen, J.G.M. (ed), *The Emergence of Whales*. Plenum Press: New York.
- Vickers-Rich, P. 1991. The Mesozoic and Tertiary history of birds on the Australian plate. Pp. 721–808 in: Vickers-Rich, P., Monaghan, J.M., Baird, R.F., and Rich, T.H. (eds), *Vertebrate Palaeontology of Australasia*. Pioneer Design Studio in cooperation with the Monash University Publications Committee: Melbourne.
- Vickers-Rich, P., and Rich, T.H. 1993. *Wildlife of Gondwana*. Reed: Chatswood. 276 pp.
- Webb, J.A. (ed). 1995. Cool-water carbonates of the north-eastern Otway Basin, southeastern Australia. Australasian Sedimentologists Group Field Guide Series No. 6. Geological Society of Australia: Sydney. 56 pp.
- Wilkins, R.W.T. 1963. Relationships between the Mitchellian, Cheltenhamian and Kalimnan Stages in the Australian Tertiary. *Proceedings of the Royal Society of Victoria* 76: 39–59.
- Wilkinson, H.E. 1969. Description of an Upper Miocene albatross from Beaumaris, Victoria, Australia, and a review of fossil Diomedidae. *Memoirs of the National Museum of Victoria* 29: 41–51.
- Woodburne, M.O. 1969. A lower mandible of *Zygomaturus gilli* from the Sandringham Sands, Beaumaris, Victoria, Australia. *Memoirs of the National Museum of Victoria* 29: 29–39.
- Woodburne, M.O., MacFadden, B.J., Case, J.A., Springer, M.S., Pledge, N.S., Power, J.D., Woodburne, J.M., and Springer, K.B. 1993. Land mammal biostratigraphy and magnetostratigraphy of the Etadunna Formation (Late Oligocene) of South Australia. *Journal of Vertebrate Paleontology* 13: 483–515.
- Zhou, K. 1982. Classification and phylogeny of the Superfamily Platanistoidea, with notes on evidence of the monophyly of the Cetacea. *Scientific Reports of the Whales Research Institute* 34: 93–108.

Table 1. Taxonomy of vertebrates from Tertiary fossil cetacean-bearing localities. \* indicates provisional classification.

Class	Order	Suborder	Family	Genus and species		
Chondrichthyes	Galeomorpha	Heterodontoidea	Heterodontidae	<i>Heterodontus cainozoicus</i> Chapman and Pritchard, 1904		
		Orectoloboidea	Orectolobidae	<i>Orectolobus gippslandicus</i> Chapman and Cudmore, 1924		
		Lamnaidea	Lamnaidea	Odontaspidae	<i>Carcharias elegans</i> Agassiz, 1843	
					<i>Carcharias taurus</i> Rafinesque, 1810	
					<i>Carcharias macrotus</i> Agassiz, 1843	
					<i>Odontaspis acutissima</i> Agassiz, 1843	
					<i>Odontaspis incurva</i> Davis, 1888	
					Lamnidae	<i>Carcharodon angustidens</i> Agassiz, 1843
					<i>Carcharodon megalodon</i> Agassiz, 1835	
					<i>Carcharodon carcharias</i> Linnaeus, 1758	
	<i>Isurus hastalis</i> Agassiz, 1838					
	<i>Isurus retroflexus</i> Agassiz, 1843					
	<i>Isurus desori</i> Agassiz, 1843					
	<i>Isurus escheri</i> Agassiz, 1843					
	<i>Isurus planus</i> Agassiz, 1843					
	<i>Isurus oxyrinchus</i> Rafinesque, 1810					
	<i>Isurus paucus</i> Guitart-Monday, 1966					
	<i>Parotodus benedenii</i> Le Hon, 1871					
	<i>Carcharoides totuserratus</i> Ameghino, 1901					
	<i>Lamna cattica</i> Philippi, 1846					
Carcharhinoidea	Carcharhinoidea	Carcharhinoidea	Parascylidae	<i>Megascyliorhinus</i> sp.		
			Triakidae	<i>Mustelus</i> sp.		
			Carcharhinidae	<i>Galeorhinus australis</i> Macleay, 1881		
				<i>Carcharhinus brachyurus</i> Günther, 1870		
				<i>Galeocerdo aduncus</i> Agassiz, 1843		
			Sphyrnidae	<i>Sphyrna</i> sp.		
			Hexanchoidae	Hexanchidae	<i>Hexanchus agassizi</i> Cappetta, 1976	
					<i>Notorynchus primigenius</i> Agassiz, 1843	
			<i>Notorynchus cepedianus</i> Peron, 1807			
			Squalomorpha	Pristiophoroidea	Pristiophoridae	<i>Pristiophorus lanceolatus</i> Davis, 1888
Batoidea	Myliobatoidae	Myliobatidae				<i>Myliobatis</i> sp.
		Dasyatidae	<i>Dasyatis</i> sp.			
Chimaeriformes	Chimaeroidei	Chimaeridae	<i>Edaphodon sweeti</i> Chapman and Pritchard, 1907			
			<i>Edaphodon mirabilis</i> Chapman and Cudmore, 1924			
<i>Ischyodus dolloi</i> Leriche, 1902						
<i>Ischyodus mortoni</i> Chapman and Pritchard, 1907						
Osteichthyes	Elopiformes	Elopoidei	Megalopidae	<i>Megalops lissa</i> Stinton, 1958		
			Pterothrissidae	<i>Pterothrissus pervetus</i> Stinton, 1958		
	Anguilliformes	Albuloidei	Heterenchelyidae	<i>Heterenchelys regularis</i> Stinton, 1958		
			Muraenesocidae	<i>Muraenesox obrutus</i> Stinton, 1958		
			Congridae	<i>Astroconger rostratus</i> Stinton, 1958		
	<i>Urconger rectus</i> Frost, 1928					
	Salmoniformes	Argentinoidei	Argentidae	<i>Hypomesus glaber</i> Stinton, 1963		
	Gadiformes	Gadoidei	Merluccidae	<i>Merluccius fimbriatus</i> Stinton, 1958		
			Gadidae	<i>Gadus refertus</i> Stinton, 1958		
	Ophidiiformes	Berycoidei	Ophidiidae	<i>Ophidion granosum</i> Stinton, 1958		
	Beryciformes		Trachichthyidae	<i>Trachichthodes salebrosus</i> Stinton, 1958		
	<i>Cleidopus carvernosus</i> Stinton, 1958					
	Scorpaeniformes	Scorpaenoidei	Scorpaenidae	<i>Sebastes fissicostatus</i> Stinton, 1963		
	Perciformes	Percoidei	Sillaginidae	<i>Sillago pliocaenica</i> Stinton, 1952		
			Lactariidae	<i>Lactarius tumulatus</i> Stinton, 1958		
	Labroidei	Labridae	<i>Labrodon</i> sp.			
			Scombroidei	<i>Coelorhynchus elevatus</i> Stinton, 1956		
			Xiphiidae	<i>Xiphias</i> sp.		
	Tetraodontiformes	Balistoidei	Monacanthidae	<i>Diodon formosus</i> Chapman and Pritchard, 1907		
	Dipnoi	Tetraodontoidei	Diodontidae	<i>Neoceratodus djelleh</i> Kemp, 1982		
Neoceratodontidae			<i>Neoceratodus eyrensis</i> White, 1925			
<i>Neoceratodus gregoryi</i> White, 1925						
<i>Neoceratodus forsteri</i> Krefft, 1870						
<i>Neoceratodus nargun</i> Kemp, 1983						



Table 2. Classification of formally described Australian fossil Cetacea.

Taxon	Previous classification
Suborder Archaeoceti	
Family Basilosauridae	
“ <i>Squalodon</i> ” <i>gambierensis</i> Glaessner, 1955	Odontoceti: Squalodontidae, Glaessner, 1955; Odontoceti: Squalodontidae, Pledge and Rothausen, 1977; Archaeoceti: Basilosauridae, Fordyce 2002a; Archaeoceti: Basilosauridae, Fitzgerald 2004
Suborder incerta sedis	
<i>Metasqualodon harwoodi</i> Sanger, 1881	Archaeoceti: Basilosauridae, Sanger, 1881; Odontoceti: Squalodontidae Hall, 1911; Odontoceti: Physeteridae, Chapman, 1929; Odontoceti: Squalodontidae, Pledge and Rothausen, 1977; Odontoceti: ?Squalodontidae, Fordyce, 1991; Autoceta: incertae sedis, Fitzgerald 2004
<i>Cetotolites leggei</i> McCoy, 1879a (nomen dubium; Fordyce, 1988)	Odontoceti: Ziphiidae, McCoy, 1879a
<i>Cetotolites nelsoni</i> McCoy, 1879a (nomen dubium; Fordyce, 1988)	Odontoceti: Ziphiidae, McCoy, 1879a
<i>Cetotolites pricei</i> McCoy, 1879a (nomen dubium; Fordyce, 1988)	Odontoceti: Ziphiidae, McCoy, 1879a
<i>Cetotolites rugosa</i> McCoy, 1879a (nomen dubium; Fordyce, 1988)	Odontoceti: Ziphiidae, McCoy, 1879a
Suborder Mysticeti	
Family Mammalodontidae	
<i>Mammalodon colliveri</i> Pritchard, 1939	Archaeoceti: Basilosauridae, Anonymous, 1939; Cetacea: incertae sedis, Camp et al., 1942; Archaeoceti: Basilosauridae, Romer, 1966; Odontoceti: Squalodontidae, Pledge and Rothausen, 1977; Archaeoceti: Dorudontidae (=Basilosauridae: Dorudontinae of Barnes and Mitchell, 1978; Uhen, 1998), Fordyce, 1979; Mysticeti: incertae sedis, Fordyce, 1982a; Mysticeti: Mammalodontidae, Mitchell, 1989; Mysticeti: incertae sedis, Fordyce, 1991
Suborder Odontoceti	
Family Physeteridae	
<i>Physetodon baileyi</i> McCoy, 1879b	Odontoceti: Physeteridae, McCoy, 1879b; Odontoceti: Physeteridae, Fordyce, 1982a
<i>Scaptodon lodderi</i> Chapman, 1918	Odontoceti: Physeteridae, Chapman, 1918; Odontoceti: Physeteridae, Fordyce, 1982a
<i>Scaldicetus lodgei</i> Chapman, 1917b	Odontoceti: Physeteridae, Chapman, 1917b; Odontoceti: Physeteridae, Fordyce, 1982a
<i>Scaldicetus macgeei</i> Chapman, 1912	Odontoceti: Physeteridae, Chapman, 1912; Odontoceti: Physeteridae, Fordyce, 1982a
Family Prosqualodontidae	
<i>Prosqualodon davidis</i> Flynn, 1923	Odontoceti: Squalodontidae, Flynn, 1920, 1923, 1932, 1948; Odontoceti: Prosqualodontidae: <i>Prosqualodon australis</i> , Cozzuol, 1996; Odontoceti: Prosqualodontidae, Muizon 2002
<i>Prosqualodon</i> sp. McCoy, 1866	Odontoceti: Squalodontidae: <i>Phocodon wilkinsoni</i> , McCoy, 1866; Odontoceti: Squalodontidae: <i>Squalodon wilkinsoni</i> , McCoy, 1867a, 1875; Odontoceti: Squalodontidae: <i>Parasqualodon wilkinsoni</i> , Hall, 1911; Odontoceti: Squalodontidae: <i>Prosqualodon</i> sp., Pledge and Rothausen, 1977; Odontoceti: Squalodontidae: ? <i>Prosqualodon davidis</i> , Fordyce, 1982a; Odontoceti: Squalodontidae: <i>Prosqualodon davidis</i> , Fitzgerald 2004
Family Delphinidae	
Gen. et sp. indet. Chapman, 1917b	Odontoceti: Delphinidae: <i>Steno cudmorei</i> , Chapman, 1917b; Odontoceti: Delphinidae: Gen. et sp. indet., Fordyce, 1982a

Table 3. Summary of Australian Tertiary aquatic mammal taxa, localities, stratigraphy, ages, and references. Abbreviations: SA, South Australia; Tas., Tasmania; Vic., Victoria; Fmn, Formation; Lst, Limestone; Sst, Sandstone; M, Miocene; O, Oligocene; P, Pliocene. \* indicates provisional classification.

Taxa	Locality	Stratigraphy	Age	References
CETACEA				
ARCHAEOCETI				
Basilosauridae*				
<i>"Squalodon" gambierensis</i>	Mount Gambier; SA	Gambier Lst	Late O	Glaessner, 1955; Pledge and Rothausen, 1977; Fordyce, 2002a
MYSTICETI				
Mammalodontidae				
<i>Mammalodon colliveri</i>	Bird Rock; Vic.	Jan Juc Marl	Late O	Pritchard, 1939; Fordyce, 1982a, 1984; Mitchell, 1989; Fitzgerald, 2004
<i>Mammalodon</i> sp. indet.	Bird Rock, Waurm Ponds Quarry; Vic.	Jan Juc Marl; Waurm Ponds Lst	Late O	Fordyce, 1982a, 1988
<i>Mammalodon</i> sp. nov. 1	Bird Rock; Vic.	Jan Juc Marl	Late O	
Gen. et sp. indet. 1	Bells Beach; Vic.	Point Addis Lst	Late O	Pledge, 1994
Gen. et sp. indet.	Point Addis, Waurm Ponds Quarry; Vic.	Point Addis Lst; Waurm Ponds Lst	Late O	Fordyce, 1982a, 1988
cf. Mammalodontidae	Moorabool River; Vic.	Maude Fmn	Late O-Early M	
?Aetiocetidae*				
Gen. et sp. nov.	Port Willunga; SA	Port Willunga Fmn	Early O	
Cetotheriidae				
Gen. et sp. indet.	Forsyth's Bank to Fossil Rock Stack, Gibson's Steps, Waurm Ponds Quarry, Batesford Quarry, Beaumaris, Newmerella; Vic.; MacBean's Pound; SA Arch Site, Grange Burn; Vic Murbko; SA	Grange Burn Fmn; Port Campbell Lst; Waurm Ponds Lst, Batesford Lst; Black Rock Sst; Gippsland Lst; Fmn; Mannum Fmn	Early P; Middle M; Late O; Middle M; Late M-Early P; Early M; Early M	Bearlin, 1987, 1988; Fitzgerald, 2004
<i>Pelocetus</i> sp.		Bochara Lst	Middle M	Bearlin, 1987, 1988
cf. <i>Parietobalaena</i> sp.		Glenforslan Fmn	Middle M	Bearlin, 1987, 1988
Balaenidae				
Gen. et sp. indet.	Dutton Way (Portland), Clifton Bank, Forsyth's Bank to Fossil Rock Stack, Beaumaris, Trident Arm; Vic.; Abattoirs Bore; SA	Whalers Bluff Fmn; Muddy Creek Marl; Grange Burn Fmn; Black Rock Sst; Jemmys Point Fmn; Dry Creek Sand	P; Middle-Late M; Early P; Late M-Early P; Early P; Late P	Howchin, 1919; Fordyce, 1982a, 1984; Bearlin, 1987
cf. <i>Balaena</i> sp.	Beaumaris; Vic.	Black Rock Sst	Late M-Early P	Gill, 1957; Fordyce, 1982a
Balaenopteridae				
Gen. et sp. indet.	Curdie; Vic.; Winkie; SA	Port Campbell Lst; ?Bookpurnong Fmn	Middle M; ? M-P;	Bearlin, 1987, 1988
<i>Balaenoptera</i> sp.	Dutton Way (Portland), Forsyth's Bank to Fossil Rock Stack, Spring Creek, Beaumaris; Vic.	Whalers Bluff Fmn; Grange Burn Fmn; Unnamed unit; Black Rock Sst	P; Early P; Late M-Early P; Late M-Early P	Fordyce, 1982a; Bearlin, 1987
cf. <i>Balaenoptera</i> sp.	Cameron Inlet; Tas.	Cameron Inlet Fmn	P	Fordyce, 1982a
<i>Megaptera</i> sp.	Dutton Way (Portland), Beaumaris; Vic	Whalers Bluff Fmn; Black Rock Sst; Jemmys Point Fmn	P; Late M-Early P	Bearlin, 1987
<i>Megaptera</i> sp. nov. 1	North Arm; Vic.	Jemmys Point Fmn	Early P	Bearlin, 1987, 1988; Fitzgerald, 2004
cf. <i>Megaptera</i> sp.	Cameron Inlet; Tas.	Cameron Inlet Fmn	P	
Family nov.				
Gen. et sp. nov. 1	Deadman's Gully; Vic.	Jan Juc Marl	Late O	Fitzgerald, 2004
Gen. et sp. nov. 2	Bells Headland; Vic.	Point Addis Lst	Late O	Köhler and Fordyce, 1997
ODONTOCETI				
Physeteridae				
Gen. et sp. indet.	Dutton Way (Portland), Forsyth's Bank to Fossil Rock Stack, Batesford Quarry, Beaumaris; Vic.	Whalers Bluff Fmn; Grange Burn Fmn; Batesford Lst; Black Rock Sst	P; Early P; Middle M; Late M-Early P	Fordyce, 1982a, 1984
<i>Physeter</i> sp.	Cameron Inlet; Tas.	Cameron Inlet Fmn	P	Fitzgerald, 2004

Table 3. continued.

Taxa	Locality	Stratigraphy	Age	References
cf. <i>Physeter</i> sp.	Clifton Bank, Forsyth's Bank to Fossil Rock Stack; Vic.	Muddy Creek Marl; Grange Burn Fmn	Middle-Late M; Early P	Fordyce, 1982a; Fitzgerald, 2004
cf. <i>Scaldicetus</i> sp.	Forsyth's Bank to Fossil Rock Stack, Hopkins River Beaumaris; Vic.	Grange Burn Fmn; Port Campbell Lst; Black Rock Sst	Early P; Middle-Late M; Late M-Early P	Fitzgerald, 2004
Ziphiidae Gen. et sp. indet.	Dutton Way (Portland),  Beaumaris; Vic.; Cameron Inlet, Tasman Fracture Zone, Seamount East of South Tasman Rise, Eastern South Tasman Rise; Tas.	Whalers Bluff Fmn;  Black Rock Sst; Cameron Inlet Fmn; Unnamed unit	P; Late M-  Early P; P; Late Neogene	Sutherland and Kershaw, 1971; Exon et al. 1995; Fitzgerald, 2004
cf. <i>Mesoplodon</i> sp.	Forsyth's Bank to Fossil Rock Stack; Vic.; Eastern Scarp; Tas.	Grange Burn Fmn; Unnamed unit	Early P; Late Neogene	Chapman, 1917b; Fordyce, 1982a; Exon et al., 1995
<i>Mesoplodon longirostris</i> Squalodontidae* Gen. et sp. indet.	Jemmys Point; Vic.	Jemmys Point Fmn	Early P	Glaessner, 1947; Fordyce, 1982a
?Gen. et sp. nov.	Waurm Ponds Quarry; Vic.; Blanchetown; SA Batesford Quarry; Vic.	Waurm Ponds Lst; Mannum Fmn Batesford Lst	Late O; Early M Middle M	Bearlin, 1982; Fordyce, 1982a, 1984; Fitzgerald, 2004
Prosqualodontidae <i>Prosqualodon davidis</i>	Fossil Bluff; Tas.	Fossil Bluff Sst;	Early M;	Flynn, 1920, 1923, 1932, 1948; Mahoney and Ride, 1975
<i>Prosqualodon</i> sp.	Castle Cove, Bird Rock; Vic.; Fossil Bluff; Tas.	Calder River Lst; Jan Juc Marl; Fossil Bluff Sst	Late O; Late O; Early M	McCoy, 1866, 1867a, 1867b, 1875; Tate, 1892; Hall, 1911; Flynn, 1948; Fordyce, 1982a, 1982b, 1984; Fitzgerald, 2003, 2004 Hall, 1911; Fordyce, 1984
Gen. et sp. indet. Eurhinodelphinidae Gen. et sp. nov.	Mount Gambier; SA Lake Namba, Lake Pinpa, Lake Yanda; SA	Gambier Lst Namba Fmn	Late O Late O-Middle M	Hall, 1911; Fordyce, 1984 Tedford et al., 1977; Fordyce, 1982a, 1982b, 1983, 1984
?Gen. et sp. indet. Delphinidae Gen. et sp. indet.	Bird Rock; Vic.	Jan Juc Marl	Late O	
?Gen. et sp. indet.	Dutton Way (Portland), Beaumaris; Vic.	Whalers Bluff Fmn; Black Rock Sst	P; Late M -Early P	Chapman, 1917; Fordyce, 1982a; Fitzgerald, 2004
?Gen. et sp. indet.	Forsyth's Bank to Fossil Rock Stack; Vic.; Sunlands Pumping Station; SA; Cameron Inlet; Tas.	Grange Burn Fmn; Loxton Sand; Cameron Inlet Fmn	Early P; Early P; P	Fordyce, 1982a; Pledge, 1985
<b>CARNIVORA</b>				
Phocidae ?Gen. et sp. indet.	Dutton Way (Portland), Forsyth's Bank to Fossil Rock Stack, Beaumaris; Vic.	Whalers Bluff Fmn; Grange Burn Fmn; Black Rock Sst	P; Early P; Late M-Early P	Fordyce and Flannery, 1983
<b>SIRENIA</b>				
Dugongidae cf. <i>Dugong</i> sp.	Sunlands Pumping Station; SA	Loxton Sand	Early P	Pledge, 1992; Domning, 1996

## A new Late Eocene cassiduloid (Echinoidea) from Yorke Peninsula, South Australia

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### Abstract

Holmes, F.C. 2004. A new Late Eocene cassiduloid (Echinoidea) from Yorke Peninsula, South Australia. *Memoirs of Museum Victoria* 61(2): 209–216

A new species of cassiduloid, from the Muloowurtie Formation on the east coast of Yorke Peninsula, is described and tentatively assigned to the genus *Rhynchopygus*. *R? janchrisorum* sp. nov. is the first record of the genus, as redefined by Smith and Jeffery (2000), to occur outside Europe, and the first confirmed from the Cainozoic. The history of species previously assigned to *Rhynchopygus* is briefly discussed and details of further occurrences of the type species, *R. marmini*, listed.

### Keywords

Echinoidea, Cassiduloida, *Rhynchopygus*, Late Eocene, South Australia, new species

### Introduction

Australian Tertiary echinoids, donated to Museum Victoria by R.J. Foster in 1996, included a single specimen of a cassiduloid quite distinct from any other species of this order so far recorded from Australia. The specimen was collected in the 1970s from “Sliding Rocks” (Fig. 1), the type section of the Muloowurtie Formation (redefined by Stuart, 1970), 9.9 km SSW of Ardrossan and 1.1 km NNE of Muloowurtie Point, on the east coast of Yorke Peninsula, South Australia [MV locality PL3497].

*Materials and methods.* Specimen numbers prefixed P, on which this study is based, are housed in the Invertebrate Palaeontology Collection, Museum Victoria (NMV). Measurements were made with a dial calliper to an accuracy of 0.1 mm. Parameters are expressed as a percentage of test length (%TL) or test width (%TW).

### Age and stratigraphy

The early to middle Late Eocene Muloowurtie Formation at “Sliding Rocks” consists of a 12 m thick sequence of biogenic calcarinites, quartz sands, calcareous and glauconitic quartz sands and sandstones with minor thin conglomerates, silts and clays, disconformably overlying the Lower Cambrian Kalpara Formation. While it is unclear from which specific horizon Foster collected his specimen (the holotype), three additional specimens were found by C. Ah Yee and J. Krause during 2002, in the uppermost bed of the formation about 800 m north of

“Sliding Rocks”. This latter horizon, consisting of variegated argillaceous quartz sands interbedded with arenaceous clays, lies immediately below the disconformity separating the Muloowurtie Formation from the overlying Throoka Silts.

The fossiliferous beds of the Muloowurtie Formation are generally considered to be Aldingan (Priabonian) in age lying within planktonic foraminiferal zones P15 and P16, although the base of the formation is probably late Middle Eocene (P14). In general, the Muloowurtie Formation is contemporaneous with the Tortachilla Limestone at Maslin Bay on the south-east side of the Basin, both having been deposited during the Tortachilla and Tuketja transgressions. However, the uppermost beds of the formation are currently considered to be equivalent to the upper middle part of the Blanche Point Formation, which overlies the Tortachilla Limestone, a time of relatively high sea level preceding the onset of the Chinamans Gully regression.

### Associated fauna

Stuart (1970) recorded the echinoids *Fibularia gregarta* Tate, 1885, *Salenidia tertiaria* (Tate, 1877) and *Eupatagus* sp. (?), together with crinoid plates, brachiopods, bivalves, the bryozoans *Retopora* and *Cellopora*, ostracods and foraminifera from richly fossiliferous sands in the lower part of the Muloowurtie Formation at “Sliding Rocks”. In addition to the new cassiduloid, a typical Australian Late Eocene echinoid fauna consisting of *Australanthus longianus* (Gregory, 1890),

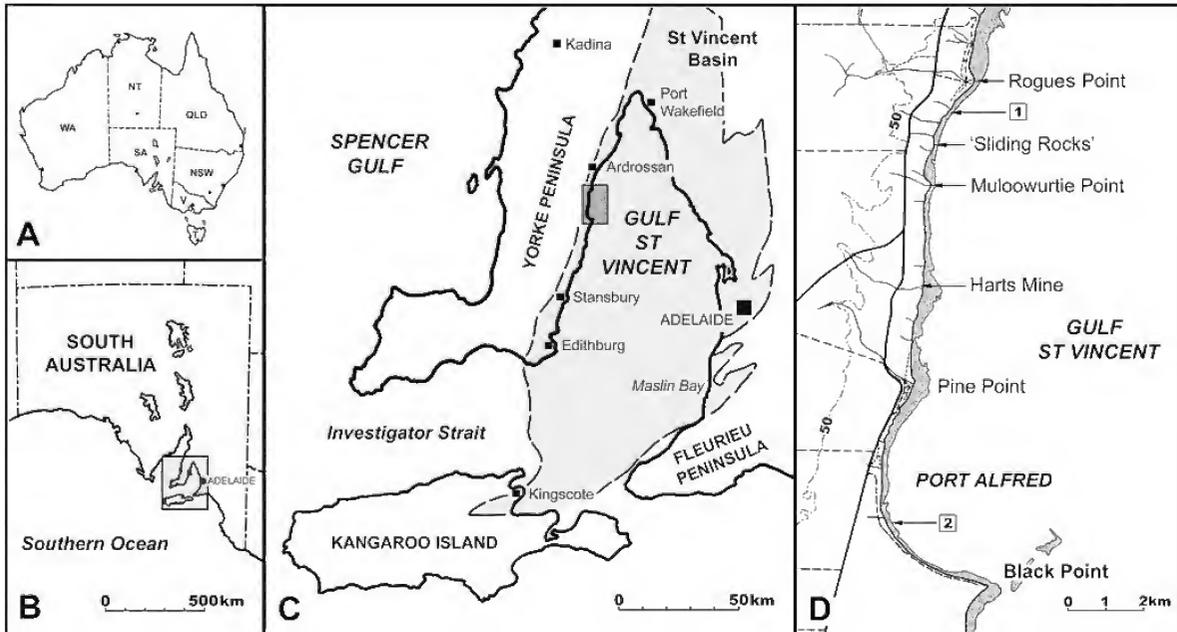


Figure 1. A and B, general location maps; C, map of St Vincent Basin in relation to Yorke Peninsula, Kangaroo Island and the Fleurieu Peninsula (Maslin Bay), South Australia; D, location of the northernmost exposure (1), and southernmost exposure (2), of the Muloowurtie Formation, west side of Gulf St Vincent.

*Eurhodia australiae* (Duncan, 1877), *Gillechinus cudmorei* Fell, 1963, and *Schizaster (Paraster) tatei* McNamara and Philip, 1980, have been found in the same general area. Two of these, *Gillechinus cudmorei* and *Salenidia tertiaris* occur with *Hemiaster (Bolbaster) cf. subidus* McNamara, 1987 and the new cassiduloid in the uppermost bed of the Formation. *Apatopygus vincentinus* (Tate, 1891) was recorded from "Muloowurtie", near Ardrossan, although no specific localities were given with Tate's syntypes of this species. The neolampadoid *Pisolampas concinna* Philip, 1963, is also found in the Formation in the vicinity of Harts Mine, approximately 3.8 km south of "Sliding Rocks".

A list of echinoid species recorded from the three major Late Eocene formations in the St Vincent Basin, the Tortachilla Limestone, Kingscote Limestone (lowest unit) and Muloowurtie Formation, is given in the Appendix.

The difference in the number of species recorded from each of these formations is no doubt primarily due to collecting bias; the Tortachilla Limestone in the coastal cliffs along Maslin Bay being well exposed and easily accessible from Adelaide. Although the Kingscote (Kangaroo Island) and Muloowurtie (Yorke Peninsula) deposits have been known for over 120 years (Tepper, 1879; Tate, 1883), virtually no systematic study of their echinoid fauna has been carried out. It is only in comparatively recent times that detailed stratigraphic information relating to these deposits has been published (Kingscote Limestone, Milnes et al., 1985; Muloowurtie Formation, Stuart, 1970). The variation in sedimentary lithology within the Basin, a consequence of small basin size, narrow basin width, and the

paralic nature of deposition (Cooper, 1985), rather than any minor age difference, must also be considered in relation to species distribution and difference in size, preservation, and number of specimens of individual species found in the three formations. As well as the apparent unique occurrence of the new cassiduloid in the Muloowurtie Formation, the lack of *Echinolampas posterocrassa posterocrassa* Gregory, 1890, one of the most common species in the Kingscote and Tortachilla Limestones, may, in this context, be quite significant.

### Systematic Palaeontology

Order **Cassiduloida** Claus, 1880

Family **Faujasiidae** Lambert, 1905

*Rhynchopygus* d'Orbigny, 1856

*Type species. Cassidulus marmini* Agassiz, in Agassiz and Desor, 1847, by monotypy.

*Diagnosis.* See Smith and Jeffery (2000: 191)

*Remarks.* Because of its monobasal apical system (Fig. 3) and lack of known phyllode detail, the new Late Eocene species from South Australia can only tentatively be assigned to the genus; although Smith and Jeffery (2000: 192) suggested that the apical system of *Rhynchopygus donetzensis* Faas, 1918, may indeed be monobasal or at least have very reduced genital plates. *Rhynchopygus*, has been used in the past 150 years as a genus or subgenus to accommodate nearly 40 species, ranging

in age from early Late Cretaceous (Turonian) to Recent. Virtually all of these species have subsequently been reassigned to other genera, namely *Cassidulus* Lamarck, 1801, *Eurhodia* Haime, 1853, *Procassidulus* Lambert, 1918, *Rhyncholampas* Agassiz, 1869, and even the holasteroid *Corystus* Pomel, 1883. The type species of all these genera, except *Eurhodia*, have at some time been assigned to *Rhynchopygus*. The most recent review of *Rhynchopygus* (Smith and Jeffery, 2000) noted that the differently shaped and positioned periprocts of three species included in the genus by Kier (1962), the type species *R. marmini*, *R. lapiscancris* (Leske, 1778) and *R. macari* (Smiser, 1935), preclude uniting them into a single genus-level taxon; referring only to *R. marmini* and *R. donetzensis* as belonging to the genus. Although *R. donetzensis* was listed by Lambert and Thiéry (1925: 588), no reference to this important species was made by Kier (1962). *R. lapiscancris* has since been assigned by van der Ham et al. (1987) to *Procassidulus* and *R. macari* by Smith and Jeffery (2000) to *Rhyncholampas*. Without comment the latter authors also assigned both *Rhynchopygus* and *Procassidulus* to the Faujasidae, rather than the Cassidulidae.

Both Mortensen (1948: 201) and Kier (1962:161) blame the inaccurate illustrations of d'Orbigny (1856: pl. 927) for the early taxonomic problems in defining *Rhynchopygus*. While this is unquestionably true, d'Orbigny (1856) and Desor (1855–1858) did illustrate and refer to the prominent lip-like projection of the test that occurs in interambulacrum 5 adjacent to the periproct; the main feature now considered to distinguish *Rhynchopygus* from genera which have many other characteristics in common. However, Mortensen (1948) considered this projection to be of no generic value and Kier (1962) did not even mention it in his generic diagnosis, but added to the confusion by describing the periproct opening as either transverse or longitudinal, presumably to accommodate other species then assigned to the genus.

Mortensen (1948) considered *Rhynchopygus* a synonym of *Cassidulus* while Kier (1962) regarded the tetrabasal apical system as a major feature separating the two genera. In addition he deemed *Procassidulus*, a genus retained by Mortensen, to be a synonym of *Rhynchopygus*.

### *Rhynchopygus? janchrisorum* sp. nov.

Figures 2A–F, 3A, B, 4A–C, 5, 6A

**Type material.** Holotype, NMV P145616 from Late Eocene (Aldingan, Priabonian) Muloowurtie Formation, “Sliding Rocks”, Yorke Peninsula, South Australia. Paratypes, NMV P312113 to P312115 from the uppermost bed of the same formation, NNE of “Sliding Rocks” at approximately 34°34.17'S, 137°53.40'E (Fig. 1).

**Description.** Test moderately small, oval in outline at the ambitus, anterior and posterior evenly rounded, widest point central. Aboral surface moderately inflated, except for a depression posterior to the periproct, with the apex just anterior of the apical disk at the proximal end of slightly swollen ambulacrum III. Adoral surface slightly depressed around peristome and along the posterior paired ambulacra I and V.

Aboral tubercles very small, about 0.15 mm diameter, and closely spaced with a density of about 12–15 tubercles per

mm<sup>2</sup>. Adoral tubercles, where visible near the margin, are also closely spaced but larger, about 0.6 mm diameter. Naked granular zone in ambulacrum III and interambulacrum 5.

Apical system monobasal, centre of disk 42–45% TL from anterior margin, with 4 gonopores in contact with the apical disk but extending into the first pair of interambulacral plates, anterior pair closer together than posterior pair. Ocular plates relatively small and about equal in size. Approximately 80 hydropores (Fig. 3).

Petals moderately short, broad and unequal in length. Longest in ambulacrum III (approx. 62% radius with about 30 pores per tract) and shortest in anterior pair II and IV (approx. 50% radius with about 20 pores per tract). Inner pores of pore pairs oval, outer pores slot like, with alignment noticeably oblique in ambulacra II and IV. At widest point interporiferous zone in ambulacra II, III and IV about equal in width to zones of pore pairs, parallel sided and open ended in ambulacrum III and narrowing distally in II and IV. Posterior pair of petals have narrower poriferous zones curving outwards distally with poriferous zones Ib and Va noticeably wider than Ia and Vb. Poriferous zones in individual petals equal in length. Anterior pair of petals diverge between 134° and 140°, posterior pair between 306° and 310°. The aboral swelling in ambulacrum III forms a low ridge along line of perradial suture for full length of petal.

Periproct supramarginal, transverse, situated at the anterior end of a pronounced posterior anal depression in interambulacrum 5, beneath a wide semi-circular projecting lip (about 19% TW) extending to nearly 20% TL from the posterior margin. The anal depression diminishes posteriorly and barely reaches the margin.

Peristome small, pentagonal, centre of opening situated 37–40% TL from the anterior margin, Floscelle well developed with very pronounced pointed and inflated bourrelets, anterior pair wide and wedge-shaped, posterior single and pair elongated and near parallel sided. Phyllodes deeply sunken proximally but with pronounced ridge between bourrelets at edge of peristomal opening. Detail of phyllode pores unknown.

**Etymology.** For Janice Krause and Christopher Ah Yee of Hamilton, Victoria.

**Remarks.** The description is based on four specimens, all of which have been subject to diagenetic compression resulting in radial cracks along adradial and interradial sutures. In the case of the holotype these cracks extend between half and two-thirds distance between ambitus and distal end of petals. Compared with a similarly compressed specimen of *Australanthus longianus* from the same locality, it is estimated that the holotype of *Rhynchopygus? janchrisorum* sp. nov. would have been about 24.0 mm long, 20.5 mm (85.5% TL) wide and a minimum of 10.5 mm (44% TL) high compared with the 26.8 mm long, 22.9 mm wide and 7.8 mm high dimensions of the compressed fossil test (Fig. 4). *Rhynchopygus? janchrisorum* is easily distinguished from the type species of the genus, *R. marmini*, in having a larger, less elongated and less inflated test, a monobasal apical disk, far more pronounced and broader petals, and prominent bourrelets. It differs from *R. donetzensis*, based on the illustrations in Smith and Jeffery (2000),

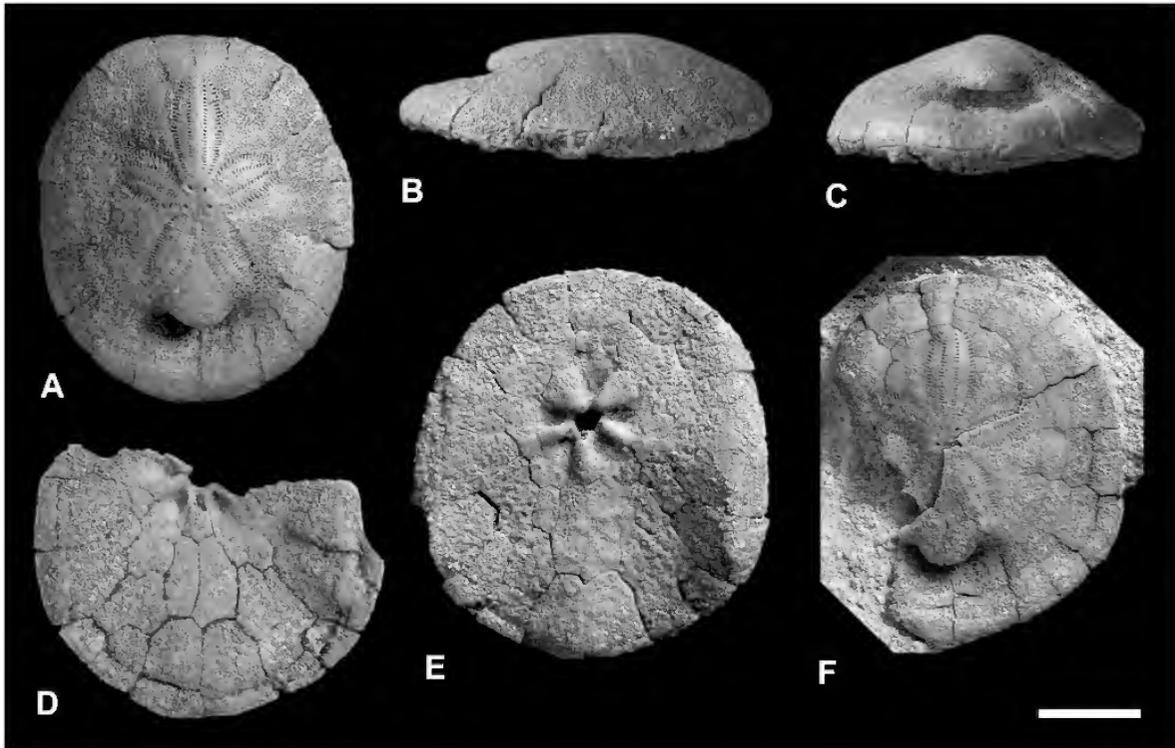


Figure 2. *Rhynchopygus? janchrisorum* sp. nov. A–C, adapical, right lateral and posterior views of holotype NMV P145616; D, adoral view of paratype NMV P312115; E, adoral view of paratype NMV P312114; F, adapical view of paratype NMV P312113. All specimens form the Late Eocene Muloowurtie Formation, Yorke Peninsula, South Australia. Scale bar 10 mm.

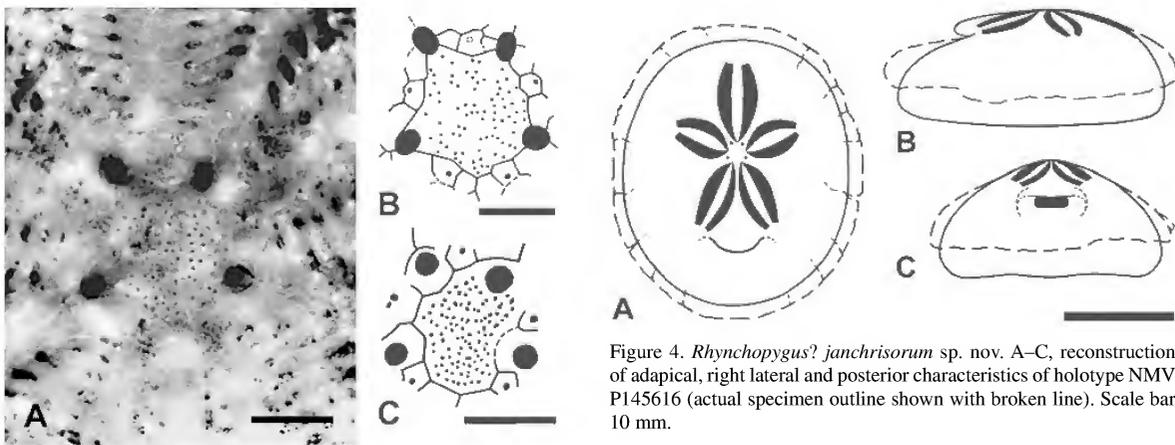


Figure 3. Apical plate structure. A and B, *Rhynchopygus? janchrisorum* sp. nov., Late Eocene holotype NMV P145616; C, *R. marmini*, Late Cretaceous USNM 19559 from Port Brechay, La Manche, France (drawing adapted from Kier, 1962). Scale bars 1mm.

Figure 4. *Rhynchopygus? janchrisorum* sp. nov. A–C, reconstruction of adapical, right lateral and posterior characteristics of holotype NMV P145616 (actual specimen outline shown with broken line). Scale bar 10 mm.

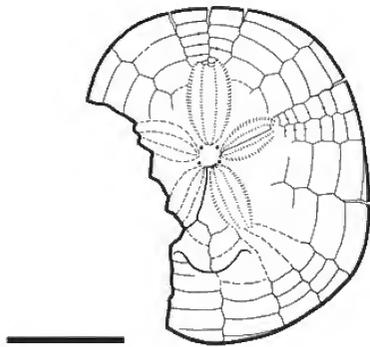


Figure 5. *Rhynchopygus? janchrisorum* sp. nov. Drawing of adapical surface of NMV P312113 showing plate structure distal to petals. Scale bar 10 mm.

primarily in being far less tumid and having a longer and broader petal in ambulacrum III, shorter posterior petals and considerably wider ambulacral plates at the ambitus (Fig. 5). The test of *R.? janchrisorum* is longer and proportionately wider than the other two species and has a more anterior periproct and projecting lip.

The occurrence of a similar but much less pronounced canopy above the periproct is also present in *Hardouinia (Fauraster) priscus* Lambert, in Lambert and Thiéry, 1924. Kier (1962: 143), in his description of the poorly preserved and compressed test, noted that the periproct is very wide and low; however, Smith and Jeffery (2000: 205) referred to this as an external feature that funnels into an opening only a little wider than tall and list *Hardouinia waageni* Holland and Feldman, 1967, and *Hardouinia nuratensis* Moskvina, 1984, as synonyms of this species. Apart from this feature, *H. (F.) priscus* differs from *R.? janchrisorum* in its near circular outline with slightly truncated posterior, its tetrabasal apical system and smaller and equal sized petals with narrower poriferous tracts and much wider interporiferous zone

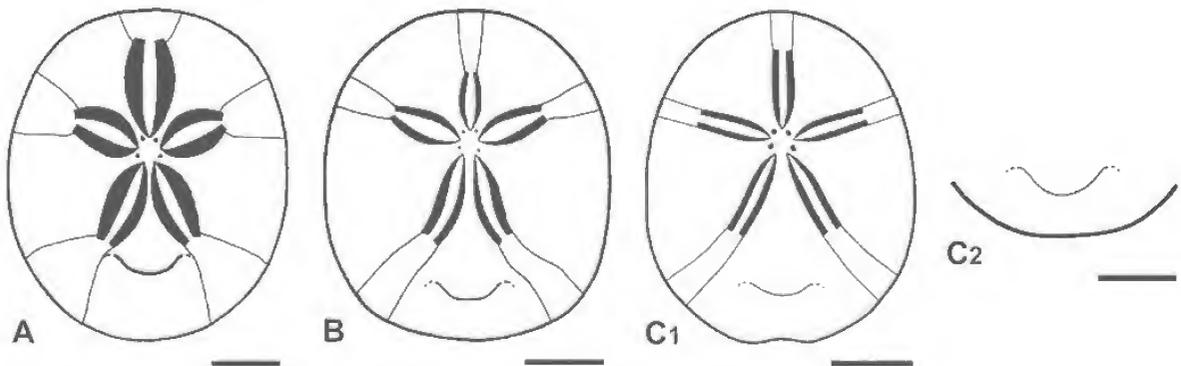


Figure 6. Comparative drawings of A, Late Eocene *Rhynchopygus? janchrisorum* sp. nov. from Yorke Peninsula, South Australia; B, Late Cretaceous (Late Maastrichtian) *R. donetzensis* from the Severny Donetz Basin, Ukraine (adapted from Smith and Jeffery, 2000); C1, Late Cretaceous (Late? Santonian) *R. marmini* from La Richardière, Dissay, France; C2, posterior profile of Late Cretaceous (Late Campanian) *R. marmini* from near Royan and St Palais-sur-Mer, France. Based on published illustrations, latter profile typical of Maastrichtian *R. marmini* specimens in general. Scale bars 5 mm.

### Distribution and age of *Rhynchopygus*

The type species *R. marmini* recorded from France, Belgium, and The Netherlands, has until now been considered to occur only in the Late Maastrichtian, becoming extinct at the Cretaceous/Tertiary boundary (Smith et al., 1999: 136). Recent investigations (Philippe Mercier, pers. comm., 2004) showed that *R. marmini* occurs in the Late? Santonian Calcarénite de la Bouchardière, Craie de Villedieu, at La Richardière, Dissay (Sarthe), France; and that three specimens (NMV P311748) from cliffs on the right bank of the Gironde Estuary, between the south side of Pointe Suzac northwards to Pointe de Vallières, Royan and St Palais-sur-Mer, France, are Late Campanian. In the southeast Netherlands and northeast Belgium, *R. marmini* has so far been recorded only from the Nekum and Meerssen members of the Maastricht Formation (Jagt, 2000: 263).

A partial specimen, *R. sp.*, is recorded from the Maastrichtian section, west of Cabo Major, near Santander (Cantabria), Spain (Smith et al., 1999: 105), and the Muséum national d'Histoire naturelle, Paris, holds a single specimen preserved in flint, labelled as originating from the Danian of St Christophe (*sic*), Loire et Cher, France, which Smith and Jeffery (2000) suspected to be reworked Maastrichtian. Philippe Mercier (pers. comm.) suggested this latter locality is probably St Christophe in Eure et Loire (near Loire et Cher) but is uncertain of the local stratigraphy.

The second species, *R. donetzensis*, is recorded from the Maastrichtian (Cretacé Supérieur) of the Donetz Basin, in the vicinity of Krymskoïé and Sérébrianka, Ukraine (Faas, 1918). Savchinskaya (1974) referred to the species occurring in the Maastrichtian of the Don Basin, Russia. As with *R. marmini*, Smith and Jeffery (2000: 192) did not show this species crossing the K/T boundary.

The additional information on French localities and the discovery of *R.? janchrisorum*, extends the range of *Rhynchopygus* from the Late? Santonian to the Late Eocene, an interval of approximately 85 million years (Table 1).

Table 1. Currently known distribution and age of *Rhynchopygus marmini* (1); *R. sp.* (2); *R. donetzensis* (3); and *R? janchrisorum* sp. nov. (4). Triangle (▲) indicates occurrence in Late (Upper) section of Stage; inverted triangle, Early (Lower) section (▼); and square (■), non specific. Spain (Sp), France (Fr), Belgium (Bel), The Netherlands (Net), Ukraine (Ukr). Australia (Aus).

Epoch	Stage	Est. Age	Sp	Fr	Bel	Net	Ukr	Aus
Eocene	Priabonian	33.0ma						■ 4
	Bartonian	37.0						
	Lutetian	41.3						
		49.0						
	Ypresian							
Paleocene	Thanetian	54.8						
		57.9						
	Selandian	60.9						
	Danian			?				
Late Cretaceous	Maastrichtian	65.0	▲ 2	▲ 1	▲ 1	▲ 1		■ 3
		73.0						
	Campanian	83.0		▲ 1				
	Santonian	87.0		▲ 1				
	Coniacian	89.0						
	Turonian	91.0						
	Cenomanian	97.5						

Found with *R? janchrisorum* (see Appendix), *Australanthus* Bittner, 1892, from the Middle/Late Eocene of southern Australia is the only member of the Faujasiidae previously recorded from this continent. Kier (1962: 18) considered *Australanthus* a possible descendant of *Hardouinia* Haime, in d'Archiac and Haime, 1853.

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I am indebted to Christopher Ah Yee and Janice Krause (Hamilton, Victoria) for collecting and donating the paratypes; Andrew Smith (Natural History Museum, London) for sketches and details of *Rhynchopygus donetzensis*; and Zang Wenlong (Primary Industries and Resources, South Australia) for stratigraphic information on the Muloowurtie Formation. I thank Museum Victoria staff, David Holloway and Thomas Darragh (Invertebrate Palaeontology) for continuous help and encouragement; and Frank Job and Sandra Winchester (Library) for access to references. I also thank Philippe Mercier (St Rimay, France) for photographs, measurements, locality information, and age of *R. marmini* specimens used for comparative purposes; and John Jagt (Nationaal Natuurhistorisch

Museum Maastricht, The Netherlands) for current information on Maastricht Formation specimens from The Netherlands and Belgium.

### References

- Agassiz, A. 1869. Preliminary report on the Echini and starfishes dredged in deep water between Cuba and the Florida Reef by L. F. De Pourtalès. *Bulletin of the Museum of Comparative Anatomy, Harvard University* 1(9): 253–308.
- Agassiz, L., in Agassiz, L. and Desor, E. 1847. Catalogue raisonné des familles, des genres et des espèces de la classe des échinodermes. *Annales des Sciences Naturelles* 7: 129–168.
- Bitner, A. 1892. Über echiniden des Tertiärs von Australien. *Sitzungsberichte der kaiserlichen Akademie der Wissenschaften zu Wien (math. Naturw. Classe)* 101(1): 331–371, pls 1–4.
- Claus, C.F.W. 1880. *Grundzüge der Zoologie* (4 edn) vol. 2. N.G. Elwert: Margburg and Leipzig. 552 pp.
- Cooper, B.J. 1985. The Cainozoic St Vincent Basin – tectonics, structure, stratigraphy. Pp. 35–49 in: Lindsay, J.M. (ed.), *Stratigraphy, palaeontology, malacology: papers in honour of Dr Nell Ludbrook. Department of Mines and Energy, South Australia, Special Publication* 5.
- Desor, E. 1855–1858. *Synopsis des échinides fossiles*. Ch. Reinwald: Paris. Kriedel and Niedner: Weisbaden. lxiii + 490 pp., 44 pls.
- Duncan, P.M. 1877. On the Echinodermata of the Australian Cenozoic (Tertiary) deposits. *Quarterly Journal of the Geological Society of London* 33(1): 43–73, pls 3, 4.
- Faas, A. 1918. *Rhynchopygus donetzensis* n. sp. des dépôts crétacés supérieurs du bassin de la rivière Severny Donetz. *Annuaire de la Société Paleontologique de Russie* 2: 65–84, pl. 3 [In Russian with French summary].
- Fell, H.B. 1963. New genera of Tertiary echinoids from Victoria, Australia. *Memoirs of the National Museum of Victoria* 26: 211–217.
- Gregory, J.W. 1890. Some additions to the Australian Tertiary Echinoidea. *The Geological Magazine* 27: 481–492. pls 13, 14.
- Haime, J., in d'Archiac, V. D. and Haime, J. 1853. *Descriptions des animaux fossiles du groupe nummulitique de l'Inde*. Gide and Baudry: Paris. 373 pp, 36 pls.
- Ham, R.W.J.M. van der Wit, W. de, Zuidema, G., and Birgelen, M. van, 1987. Zeeëgels uit het Krijt en Tertiair van Maastricht, Luik en Aken. *Publicaties van het Natuurhistorisch Genootschap in Limberg* 36: 1–91, 24 pls.
- Holland, F.D., and Feldman, R.M. 1967. A new species of cassiduloid echinoid from the Fox Hills Formation (Upper Cretaceous) of North Dakota. *Journal of Paleontology* 41: 252–255.
- Holmes, F.C. 1993. Australian fossil echinoids: annotated bibliography and list of genera and species. *Occasional Papers of the Museum of Victoria* 6: 27–53.
- Jagt, J. W. M. 2000. Late Cretaceous–Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium – Part 4: Echinoids. *Scripta Geologica* 121: 181–375.
- Kier, P.M. 1962. Revision of the cassiduloid echinoids. *Smithsonian Miscellaneous Collections* 144(3): 1–262, pls 1–44.
- Lamarck, J.B. 1801. *Système des animaux sans vertèbres, ou, Tableau general des classes, des ordres, et des genres de ces animaux*. Chez Deterville: Paris. viii + 432 pp.
- Lambert, J., in Doncieux, L. 1905. Catalogue descriptif des fossiles nummulitiques de l'Aube et de l' Hérault. *Annales de l' Université de Lyon* 17: 129–164, pl. 5.
- Lambert, J. 1918. Considérations sur la classification des Echinides Atélostomes. 1. Brachygnata (sic) et Procassiduloida. *Mémoire*

- Société Académique, d'agriculture, des sciences, arts et belle lettres du département de l'Aube* 82: 1–48.
- Lambert, J., and Thiéry, P. 1910–1925. *Essai de nomenclature raisonnée des Échinides*. Vols. 1–9. Librairie L. Ferrière: Charmont. 607 pp., 15 pls.
- Leske, N.G. 1778. *Jacobi Theodori Klein Naturalis dispositio Echinodermatum. Edita et descriptionibus novisque inventis et synonymis auctorum aucta*. Officina Gleditschiana: Lipis. xxii + 278 pp., 54 pls.
- McNamara, K.J. 1987. Taxonomy, evolution and functional morphology of southern Australian Tertiary hemiasterid echinoids. *Palaeontology* 30(2): 319–352.
- McNamara, K.J., and Philip, G. M. 1980. Australian Tertiary schizasterid echinoids. *Alcheringa* 4(1): 47–65.
- Milnes, A.R., Ludbrook, N.H., Lindsay, J.M., and Cooper, B.J. 1985. The succession of Cainozoic marine sediments on Kangaroo Island, South Australia. *Transactions of the Royal Society of South Australia* 107(1): 1–35.
- Moskvin, M.M. 1984. [Echinoids *Domechinus* and *Hardouinia* (Echinoidea) from the Upper Cretaceous of Middle Asia]. *Paleontologicheskii Sbornik* 21, 63–68, 1 pl. [In Russian].
- Mortensen, T. 1948. *A monograph of the Echinoidea* 4(1). *Holactypoida, Cassiduloida*. C. A. Reitzel: Copenhagen. 371 pp., 14 pls.
- d'Orbigny, A. 1856. Echinoïdes irréguliers. *Paléontologie Française: descriptions zoologique et géologique de tous les Animaux Mollusques at Rayonnés fossiles de France. Terrain Crétace* 6. Maisson: Paris. 596 pp., pls 801–1005.
- Philip, G.M. 1963. Two Australian Tertiary neolampadids, and the classification of cassiduloid echinoids. *Palaeontology* 6(4): 718–726. pls 106–107.
- Pomel, N.A. 1883. *Classification méthodique et genera des échinides vivants et fossiles*. Adolphe Jourdan: Alger. 131 pp., 36 pls.
- Savchinskaya, G.Y. 1974. [Atlas of the Upper Cretaceous fauna of the Don Basin]. Nidra Press: Moscow. 639 pp., 128 pls [In Russian].
- Smiser, J.S. 1935. A monograph of the Belgian Cretaceous echinoids. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique* 68: 1–98, pls 1–9.
- Smith, A.B., Gallemí, J., Jeffery, C.H., Ernst, G., and Ward, P. D. 1999. Late Cretaceous–early Tertiary echinoids from northern Spain: implications for the Cretaceous–Tertiary extinction event. *Bulletin of the Natural History museum, London (Geology)*, 55(2): 81–137.
- Smith, A.B., and Jeffery, C. H., 2000. Maastrichtian and Palaeocene echinoids: a key to world faunas. *Special papers in palaeontology* 63. The Palaeontological Association: London. 406 pp.
- Stuart, W.J. Jnr 1970. The Cainozoic stratigraphy of the eastern coastal area of Yorke Peninsula, South Australia. *Transactions of the Royal Society of South Australia* 94: 151–178, figs 2–4.
- Tate, R. 1877. On a new species of *Belemnites* and *Salenia* from the Middle Tertiaries of South Australia. *Quarterly Journal of the Geological Society of London* 33(2): 256–259.
- Tate, R. 1883. The botany of Kangaroo Island. *Transactions and Proceedings of the Royal Society of South Australia* 6, 116–171.
- Tate, R. 1885. Miscellaneous contributions to the palaeontology of the older rocks of Australia. *Southern Science Record* (n.s.) 1: 1–5.
- Tate, R. 1891. A bibliography and revised list of the described echinoids of the Australian Eocene, with descriptions of some new species. *Transactions and Proceedings and Report of the Royal Society of South Australia* 14: 270–282.
- Tepper, O. 1879. Introduction to the cliffs and rocks at Ardrossan, Yorke's Peninsula. *Transactions and Proceedings and Report of the Philosophical Society of Adelaide, South Australia* 2: 71–79.

## Appendix

South Australian Middle?–Late Eocene echinoids recorded from the Tortachilla Limestone, Maslin Bay (TL), lowest unit of the Kingscote Limestone, Kangaroo Island (KL), and the Muloowurtie Formation, Yorke Peninsula (MF). Named species confirmed from all three formations are marked ▶. Information based on published literature and specimens housed in Museum Victoria Invertebrate Palaeontology collection or privately owned. References to authors cited but not listed in the main text references can be found in Holmes (1993)

		TL	KL	MF
Cidaroida	Cidaridae sp.	● <sup>1</sup>	● <sup>1</sup>	
	<i>Stereocidaris cudmorei</i> Philip, 1964	●		
	<i>S. fosteri</i> Philip, 1964	●		
	<i>S. inermis</i> Philip, 1964	●		
	<i>S. sp.</i> 'C' Philip, 1964	●		
	<i>S. sp.</i> [unidentified]			● <sup>4</sup>
	<i>S. (?) hispida</i> Philip, 1964	●		
	<i>S. (?) intricata</i> Philip, 1964	●		
Salenoida	▶ <i>Salenidia tertiaria</i> (Tate, 1877)	●	●	●
Temnopleuroidea	<i>Tatechinus nudus</i> Philip, 1969	●		
	Temnopleuridae sp.	● <sup>1</sup>	● <sup>1</sup>	● <sup>1</sup>
	<i>Ortholophus bittneri</i> Philip, 1969	●		
Clypeasteroida	<i>Fibularia. sp.</i> 'A' [Irwin pers. com.]	●		
	<i>F. sp.</i> 'B' [Irwin pers. com.]	●		
	<i>F. sp.</i> 'C' [Irwin pers. com.]		●	
	<i>F. sp.</i> [unidentified, non. <i>F. gregata</i> of Stuart, 1970]			● <sup>1</sup>
	<i>Monostychia sp.</i> 'A' [small undescribed species]		● <sup>4</sup>	
	<i>M. sp.</i> 'B' [medium sized undescribed (?) species]		● <sup>4</sup>	
Cassiduloida	▶ <i>Apatopygus vincentinus</i> (Tate, 1891)	●	●	●
	▶ <i>Australanthus longianus</i> (Gregory, 1891)	●	●	● <sup>4</sup>
	<i>Echinolampas posterocrassa</i> Gregory, 1890	●	●	● <sup>4</sup>
	▶ <i>Eurhodia australiae</i> (Duncan, 1877)	●	●	
	<i>Rhyncopygus? janchrisorum sp. nov.</i>			●
Neolampadoida	<i>Aphanopora? bassoris</i> Holmes, 1995	● <sup>4</sup>	●	
	▶ <i>Pisolampas concinna</i> Philip, 1963	●	●	●
Holasteroida	<i>Corystus dysasteroides</i> (Duncan, 1877)	● <sup>2</sup>	● <sup>2</sup>	
	<i>Giraliaster bellissae</i> Foster and Philip, 1978	●		
	<i>G. sulcatus</i> (Hutton, 1873)	●		
	<i>G. tertiaria</i> (Gregory, 1890)	●		
Spatangoida	<i>Eupatagus sp.</i>		● <sup>3</sup>	● <sup>3</sup>
	▶ <i>Gillechinus cudmorei</i> Fell, 1963	●	●	● <sup>4</sup>
	<i>Hemiaster (Bolbaster) subidus</i> McNamara, 1987	●		● <sup>4</sup>
	<i>Linthia pulchra</i> McNamara, 1985	●		
	<i>Prenaster aldingensis</i> Hall, 1907	●		
	<i>Protenaster preaustralis</i> McNamara, 1985	●		
	<i>Psephoaster lissos</i> McNamara, 1987	●		
	<i>Schizaster (Paraster) tatei</i> McNamara and Philip, 1980	●		● <sup>4</sup>
Total	37	27+3?	11+4?	10+3?

<sup>1</sup> Not specifically identified, may belong to one of the listed species

<sup>2</sup> Although almost certainly Late Eocene, occurrence of species in the formation requires confirmation

<sup>3</sup> No reference to occurrence of species in taxonomic literature: may have been incorrectly identified or come from an overlying stratigraphic unit

<sup>4</sup> Previously unpublished identification

## A new species of *Quinquelaophonte* (Crustacea: Copepoda: Harpacticoida: Laophontidae) from Port Phillip Bay, Victoria, Australia

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### Abstract

Walker-Smith, G.K. 2004. A new species of *Quinquelaophonte* (Crustacea: Copepoda: Harpacticoida: Laophontidae) from Port Phillip Bay, Victoria, Australia. *Memoirs of Museum Victoria* 61(2): 217–227.

A new species of *Quinquelaophonte* Wells, Hicks and Coull, 1982 from Port Phillip Bay, is separated from its congeners by the presence of five elongate setae on P1 exopod-2. The P1 exopod-2 of all other species of *Quinquelaophonte* has two long setae and three shorter spines. In addition, the P1 endopod-2 of the new species has an accessory seta that is longer than the terminal claw. This condition is also present in *Q. wellsi*, the only other species of *Quinquelaophonte* described from Australia. The new species brings the total number of species of *Quinquelaophonte* to ten.

### Keywords

*Quinquelaophonte*, Laophontidae, Harpacticoida, marine Copepoda, Port Phillip Bay, Victoria, Australia

### Introduction

Australia's harpacticoid fauna is diverse. In a recent survey of harpacticoids from Port Phillip Bay more than 50 species were identified from the shallow subtidal seagrass and surrounding sandy areas (Walker-Smith, 2003). It is estimated that only a small percentage of Australian harpacticoid species has been described; 94 species have been described from marine, estuarine and brackish water ecosystems, although worldwide there are in excess of 3000 species (Giere, 1993; Huys et al., 1996). Sixty-four of the species found in Australia are considered endemic.

Nine species of *Quinquelaophonte* Wells, Hicks and Coull, 1982 have been described from around the world (Lee, 2003), including *Q. wellsi* (Hamond, 1973), which was described from a saline lake in South Australia. During a survey of Harpacticoida in Port Phillip Bay, a new species of *Quinquelaophonte* common on the surface of the unvegetated sediment adjacent to the subtidal seagrass, *Heterozostera tasmanica* (Martens ex Ascherson) den Hartog, was discovered. This new species was rarely found among the seagrass itself (Walker-Smith, 2003). Several other species of *Quinquelaophonte* are considered to be sediment-surface dwellers; *Q. wellsi*, *Q. candelabrum* Wells, Hicks and Coull, 1982 and *Q. longifurcata* (Lang, 1965) (Hamond, 1973; Wells et al., 1982; Lang, 1965).

Seagrass and sediment samples were collected by hand (Walker-Smith, 2003) and fixed in 4% buffered formalin in sea-water. After (at least) 48 hours samples were washed over a 63- $\mu$ m mesh sieve and retained material was transferred to 70% ethanol. Samples were examined under a Zeiss Stemi SV 11 or a Wild M8 stereomicroscope and harpacticoids were extracted using fine forceps. Harpacticoids were dissected in a drop of glycerol on a microslide, using electrolytically-sharpened tungsten needles. Appendages were mounted in glycerol. Microslides were examined using three microscopes (Olympus BX50 and Leica DMR compound microscopes with Nomarski interference contrast, Leitz Dialux 22 compound microscope). Illustrations were made with the aid of a camera lucida. Once appendages were illustrated, they were permanently mounted in Gurr's Aquamount and coverslips were sealed with clear nail varnish. Scanning electron micrographs were taken using a Philips XL20 scanning electron microscope (KV=10, spot size 3).

Terminology used follows that of Huys and Boxshall (1991). Abbreviations used are: A1, antennules or first antennae; A2, antennae or second antennae; Mx1, maxillules; Mx, maxillae; P1–P4, swimming legs 1–4. Individual segments of P1–P4 rami are written (for example) as P1 exopod-3, which refers to the third or terminal segment of the P1 exopod. P5 and P6 refer to the fifth and sixth legs. Total length measurements are from the base of the rostrum to the posterior margin of the caudal rami (caudal setae are excluded). Armature formulae (also known as the setal formulae) for swimming legs are constructed following the methods of Lang (1934) (also see Huys and Boxshall, 1991: 29). The term "armature" is used to refer collectively to setae and spines. Type material is held in Museum Victoria (NMV) and the South Australian Museum (SAM).

Table 1. Distribution of *Quinquelaophonte* species

Species	Distribution	Reference
<i>Q. brevicornis</i> (T. Scott, 1894)	Ghana	T. Scott, 1894
<i>Q. quinquespinosa</i> (Sewell, 1924)	India: Chilka Lake, Orissa	Sewell, 1924
	Egypt: Lake Menzaleh	Gurney, 1927
	Bermuda	Willey, 1930; Lang, 1948
	Tunisia: Goulette	Monard, 1935
	Réunion	Chappuis et al., 1956
	Angola: Benguela	Candeias, 1959
	USA: Puget Sound, Seattle, Washington State	Wieser, 1959
	France: Marseilles	Bodin, 1964; Hamond, 1973
	Mozambique: Inhaca Island	Wells, 1967
	Seychelles: Aldabra	Wells and McKenzie, 1973
	Andaman Islands	Wells and Rao, 1987
<i>Q. capillata</i> (Wilson, 1932)	USA: Katama Bay, Marthas Vineyard, Massachusetts;	Wilson, 1932; Coull, 1976, 1986
	North Inlet, Georgetown, South Carolina	Coull, 1986
	Bahamas: Eleuthera; Crooked Island	Fiers, 1986
<i>Q. longifurcata</i> (Lang, 1965)	USA: California	Lang, 1965
<i>Q. parasigmoides</i> (Božić, 1969)	Réunion: St Phillippe	Božić, 1969
<i>Q. wellsi</i> (Hamond, 1973)	Australia: Robe and Beachport, South Australia	Hamond, 1973
<i>Q. candelabrum</i> Wells, Hicks and Coull, 1982	New Zealand: Raion Point, Pauatahanui Inlet, Porirua Harbour, Wellington; Papanui Inlet, Otago Peninsula; Whangateau Harbour, Northland; Avon-Heathcote Estuary, Christchurch; Hobson's Bay, Waitemata Harbour, Auckland	Wells, Hicks and Coull, 1982
<i>Q. bunakenensis</i> Mielke, 1997	Indonesia: Sulawesi	Mielke, 1997
<i>Q. koreana</i> Lee, 2003	Korea: Taean	Lee, 2003
<i>Q. prolixasetae</i> sp. nov.	Australia: Port Phillip Bay, Victoria	present study

***Quinquelaophonte*** Wells, Hicks and Coull, 1982

*Quinquelaophonte* Wells, Hicks and Coull, 1982: 178–179.

*Type species. Laophonte quinquespinosa* Sewell, 1924.

**Diagnosis.** A1 of female with 5 or 6 segments; A2 exopod reduced, 1-segmented; P2–P4 exopods of male strongly modified; P2 endopod of male not modified (same as for female); P5 of male reduced to 4–5 setae arising from the somite margin; caudal rami with 3 terminal setae, only one of which is well developed (seta V).

**Species.** *Quinquelaophonte brevicornis* (T. Scott, 1894); *Q. quinquespinosa* (Sewell, 1924); *Q. capillata* (Wilson, 1932); *Q. longifurcata* (Lang, 1965); *Q. parasigmoides* (Božić, 1969); *Q. wellsi* (Hamond, 1973); *Q. candelabrum* Wells, Hicks and Coull, 1982; *Q. bunakenensis* Mielke, 1997; *Q. koreana* Lee, 2003; *Q. prolixasetae* sp. nov.

**Distribution.** See Table 1.

**Habitat.** Marine, intertidal and shallow subtidal; in saline lakes; sand and mud. Frequently recorded in detritus-rich habitats.

**Remarks.** Fiers (1986) discovered specimens of *Q. quinquespinosa* (from the West Indies) and noted the specimens had an “interesting feature”: the inner distal edge of P3 endopod-1 with a few “long and fragile hairs” (Fiers, 1986: 142). Because Fiers (1986) believed these “hairs” resembled the inner seta of *Q. parasigmoides*, he suggested *Q. parasigmoides* was within the range of variability of *Q. quinquespinosa* and therefore

should be considered synonymous with it. However, Lee (2003) rejected this, instead believing confirmation of the synonymy required examination of more specimens, from more localities and I agree.

In his catalogue of marine harpacticoids, Bodin (1997) listed *Paronychocamptus wilsoni* Coull, 1976 as a junior synonym of *Q. capillata* but Lee and Huys (1999) recognized *P. wilsoni* as a valid species and I support this. Inspection of Coull's (1976) illustrations of *P. wilsoni* revealed distinct differences between this species and *Q. capillata*. Firstly, the P3 endopod-2 of male *P. wilsoni* is modified and has a spine-like distal outgrowth and this modification does not occur in *Q. capillata*. Secondly, the P5 exopod of the male is well developed and has four setae in *P. wilsoni* but is reduced and represented by five setae in *Q. capillata*. For all other species of *Quinquelaophonte* the P5 exopod of male is reduced. The P5 of female *P. wilsoni* has only four setae on the baseoendopod and five setae on the exopod, while in *Q. capillata* there are five setae on the baseoendopod and six setae on the exopod. The caudal setae of the two species also differ; *P. wilsoni* has two well developed terminal setae but *Q. capillata* has only one well developed terminal seta (seta V) — the possession of only one well developed caudal seta is a character state defining *Quinquelaophonte*. The setal formula for the swimming legs also varies between these species (Table 2). Lastly, when Coull (1986) re-examined Wilson's type material he discovered the A2 exopod of *Q. capillata* had three setae, and not two as originally reported. The A2 exopod of *P. wilsoni* has only two setae.

Table 2. Comparison of the setal formulae of *Quinquelaophonte capillata* and *Paronychocamptus wilsoni*. Endp = endopod; exp = exopod.

	Segments of swimming legs				
	P2 endp-2	P3 exp-3	P3 endp-3	P4 exp-3	P4 endp-2
<i>Q. capillata</i>	1.2.0	1.2.3	2.2.1	1.2.3	1.1.1
<i>P. wilsoni</i>	2.2.0	2.2.3	3.2.1	1.2.2	1.2.0

*Quinquelaophonte prolixasetae* sp. nov.

Figures 1–8

**Material examined.** Holotype. NMV J52388 (ovigerous female, on 8 slides). Australia, Victoria, Port Phillip Bay: at the end of Grand Scenic Drive, in front of the Sands Caravan Park, Moolap (38°09.92'S 144°28.42'E). Collected from the surface of unvegetated sediments, adjacent to subtidal seagrass beds of *Heterozostera tasmanica* (water depth approximately 1 m), G. K. Walker-Smith, 17 Nov 1997.

Paratypes. NMV J52389 (1 male, allotype, on 6 slides), NMV J53020 (1 female on 5 slides), NMV J53110 (1 female on 5 slides), NMV J53111 (1 female on 1 slide), NMV J53112 (1 male on 1 slide), NMV J53021 (20 adult females and 2 juveniles), NMV J53022 (9 males), SAM C6096 (20 females, including 2 ovigerous and 4 juveniles), SAM C6097 (9 males), SAM C6098 (8 females on a SEM stub), SAM C6099 (4 males on a SEM stub). All paratypes collected with the holotype.

Other material. NMV J48528 (13 specimens), NMV J48529 (3 specimens), NMV 48530 (5 specimens), NMV J48531 (12 specimens), NMV J48532 (29 specimens), NMV J48533 (3 specimens), NMV J48535 (103 specimens). Collection data as for holotype.

**Diagnosis.** A1 of female 6-segmented; A2 exopod with 3 setae; P1 exopod-2 with 5 thin, elongate setae; P1 endopod-2 accessory setae longer than terminal claw; P3 exopod-3 of female with 1 inner seta; P3 endopod-2 of female with 5 setae; P4 exopod-3 of female without inner seta; P4 endopod-2 with 3 setae; P5 exopod of female with 6 setae; P5 of male with 5 setae.

**Adult dimensions.** Females: mean length 0.85 mm ± 0.05 mm (n = 22). Males: mean length 0.82 mm ± 0.03 mm (n = 21).

**Description of female.** Body tapering posteriorly (Fig. 1A–B). Rostrum fused to cephalothorax, with 2 sensillae. Clear delineation of body somites. Somite margins with setules. Hyaline frill present on somite preceding anal somite. Anal somite with anal operculum (Figs 3D, 8D). Caudal rami length 3 times width (Fig. 3D); 3 setae on lateral margin (Figs 3D, 8C), seta I minute (difficult to see under compound microscope), seta IV reduced, seta V well developed and covered with minute spinules (only visible via SEM) (Figs 3D, 8C), terminal accessory seta (VI) on inner subdistal corner, dorsal seta (VII) triarticulate at the base.

Antennule 6-segmented (Fig. 2A), aesthetasc fused basally to seta on segment 4, terminal segment with smaller aesthetasc fused basally to 2 setae (i.e. tritheck). Antenna with allobasis (Fig. 2B), abexopodal seta reduced to a small spine no different from the surrounding spines, exopod reduced to single segment with 3 setae. Endopod with 2 pinnate spines

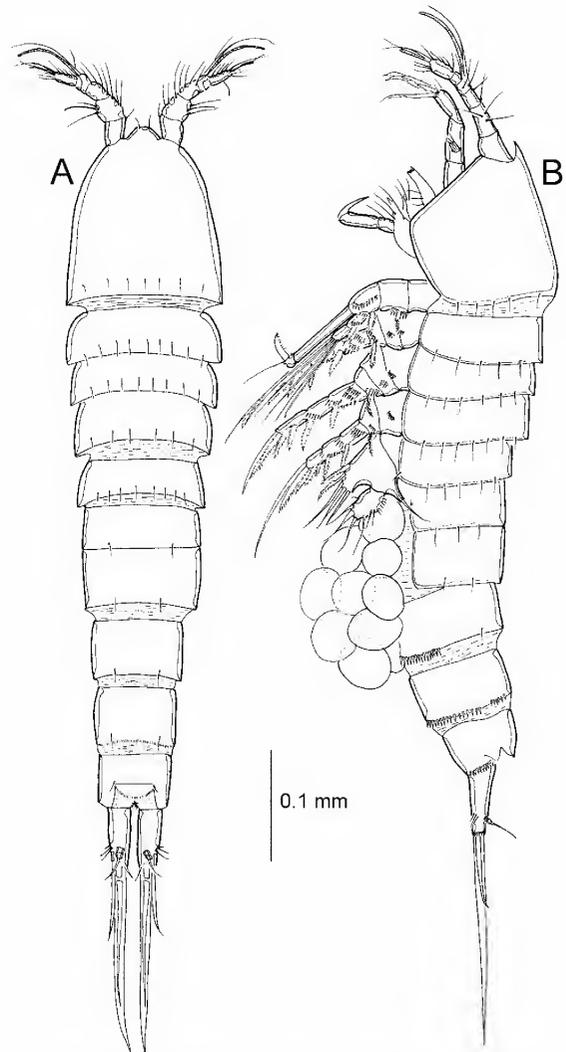


Figure 1. *Quinquelaophonte prolixasetae* sp. nov., female, paratype (NMV J53020): A, habitus, dorsal view; B, habitus, lateral view.

laterally and 3 geniculate setae and 2 pinnate spines terminally. Endopod also with spinules laterally and a subapical hyaline frill.

**Mouthparts.** Labrum with setules along anterior margin (Figs 2G, 7A). Paragnaths as in figures 2H and 7A. Mandible with well developed gnathobase (Fig. 2C), palp 1-segmented and with 4 setae (endopod and exopod fused to basis), endopod represented by 3 setae, exopod represented by 1 seta, basal armature represented by a larger pinnate seta. Maxillule (Figs 2D, 7A) arthrite with 6 spines and a row of setae on the posterior surface, also with 1 seta on lateral margin; coxa with 1 smooth seta, 1 long spine and a row of spinules on upper surface; endopod and basis fused, endopod represented by

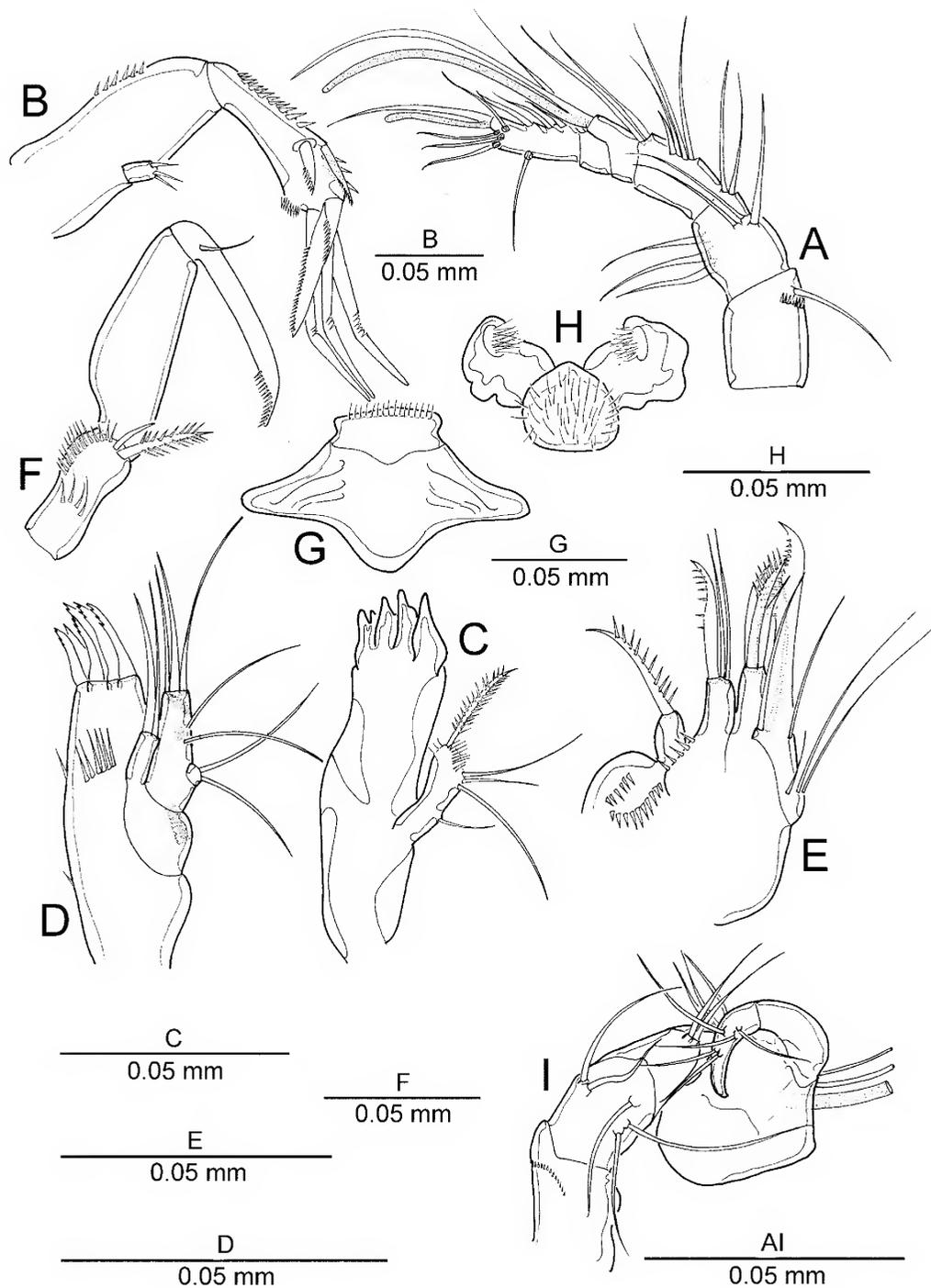


Figure 2. *Quinquelaophonte prolixasetae* sp. nov., female, holotype (NMV J52388): A, A1, ventral view; B, A2. Female, paratype (NMV J53110); C, mandible; D, maxillule. Female, paratype (NMV J53020): E, maxilla; F, maxilliped; G, labrum; H, paragnaths. Male, paratype (NMV J52389): I, A1, dorsal view.

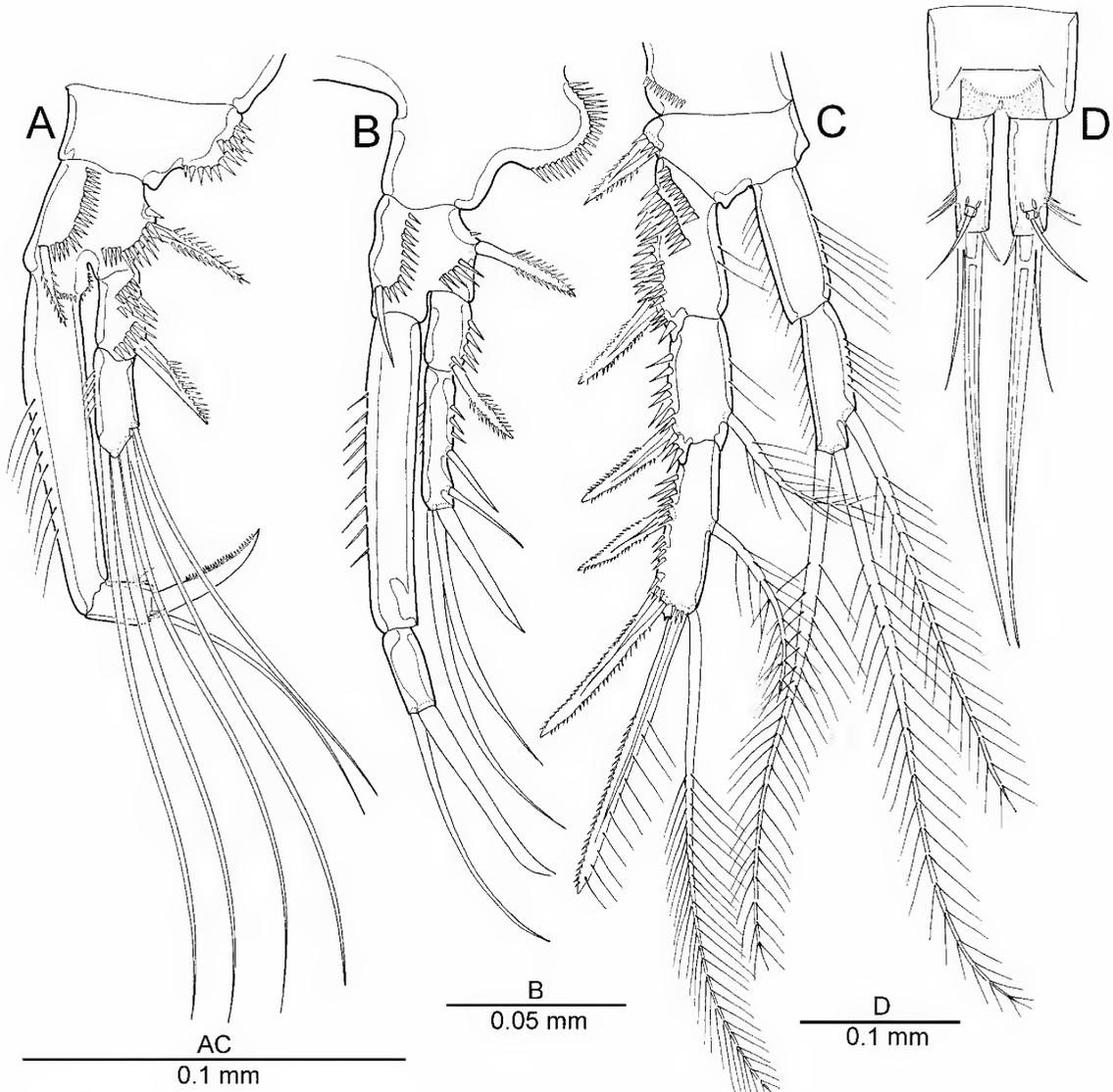


Figure 3. *Quinquelaophonte prolixasetae* sp. nov., female, holotype (NMV J52388): A, P1; C, P2. B, P2 *Q. wellsi* (redrawn from Hamond, 1973). Female, paratype (NMV J53020): D, caudal rami and anal somite.

2 setae, basis endite with 2 smooth setae and 1 long spine; exopod 1-segmented and with 2 smooth setae. Maxilla (Figs 2E, 7B) syncoxa with 3 endites, first endite with 1 spinose seta, middle endite with 2 setae and 1 pinnate spine, distal endite with 1 pinnate spine and 2 setae; allobasis with a pinnate claw and 2 smooth setae inserted at the base of the claw, also with 3 lateral setae that are remnants of the endopod. Maxilliped (Fig. 2F), prehensile, syncoxa with 2 setae, basis without ornamentation, endopod represented by terminal claw with 1 seta and some distal spinules.

P1 (Figs 3A, 8A–B) coxa with spinules on outer margin.

Basis with 2 rows of spinules and 2 spinulose spines. Exopod 2-segmented, exopod-1 with 3 rows of spinules and 1 unipinnate spine, exopod-2 with 5 elongate, smooth setae. Endopod 2-segmented, endopod-1 with fine setules along inner margin, endopod-2 with 1 spinulose claw, 3 setae on lateral margin and 2 short setae at the base of the claw, terminal accessory seta is more than twice the length of the claw.

P2–P4 exopod 3-segmented, endopod 2-segmented (Figs 3C, 4A–B). P2 endopod reaching just beyond distal margin of P2 exopod-2 (Fig. 3C). P3 endopod not reaching beyond distal margin of P3 exopod-2 (Fig. 4A). P4 endopod not reaching

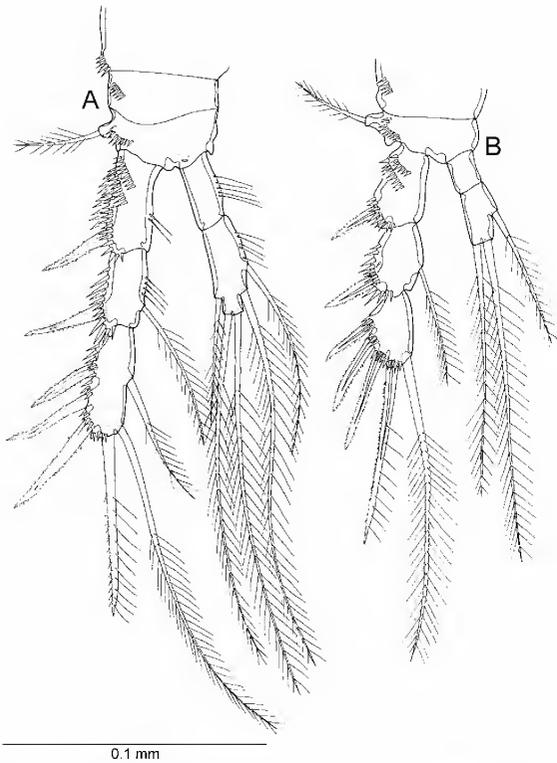


Figure 4. *Quinquelaophonte prolixasetae* sp. nov., female, holotype (NMV J52388): A, P3; B, P4.

beyond distal margin of P4 exopod-2 (Fig. 4B). P3 and P4 endopod-2 without tube pore.

Armature formulae for swimming legs:

Exopod	Endopod	
P2	0.1.123	0.120
P3	0.1.123	0.221
P4	0.1.023	0.120

P5 baseoendopod (Fig. 5C), outer setophore with 1 seta, endopodal lobe with 2 serrate spines and 3 smooth setae, endopodal lobe not reaching to distal margin on exopod. Exopod longer than wide, with 3 pinnate setae and 3 smooth setae, as well as some spinules.

**Description of male.** Male same as for female except for the following: A1 subchirocer and without seta on segment-1 (Figs 2I, 7C–F); P2–P4 larger and more chitinised (Figs 5B, 6A–B), lateral spines longer, exopod-3 almost at right angles to exopod-2. P4 endopod-2 more than 2 times length of endopod-1. P5 reduced to 5 setae (Fig. 5D).

**Etymology.** *Prolixus* (Latin): stretched out, long; plus *setae* (Latin): bristles; referring to the five elongate setae on P1 exopod-2.

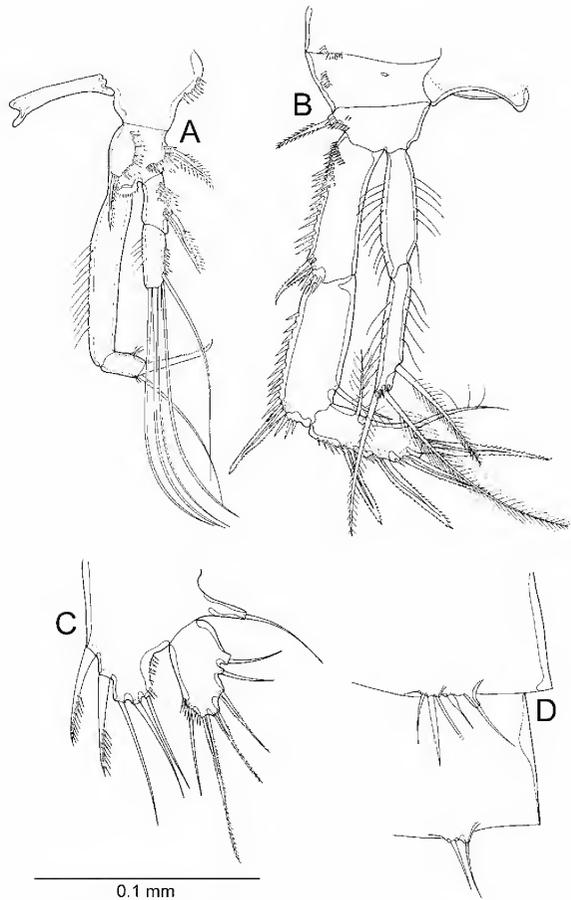


Figure 5. *Quinquelaophonte prolixasetae* sp. nov. male, paratype (NMV J52389): A, P1 and intercoxal sclerite; B, P2 and intercoxal sclerite; D, section of urosome, ventral view showing P5 and P6. Female, holotype (NMV J52388): C, P5.

**Distribution.** Australia, Victoria, Port Phillip Bay, specifically: Blairgowrie, St Leonards, Grassy Point, Point Richards, Clifton Springs and Moolap.

**Remarks.** Although all appendages of the holotype have been mounted on microscope slides, the orientation of the mouthparts did not allow for clear illustration, thus mouthparts have been illustrated using paratypes. Careful comparison of the holotype and paratypes were made.

## Discussion

*Quinquelaophonte prolixasetae* is the second species of the genus described from Australia and is distinguished from its congeners by the presence of five elongate setae on the P1 exopod-2. All other species of *Quinquelaophonte* have two long setae and three spines on P1 exopod-2 (Fig. 3B).

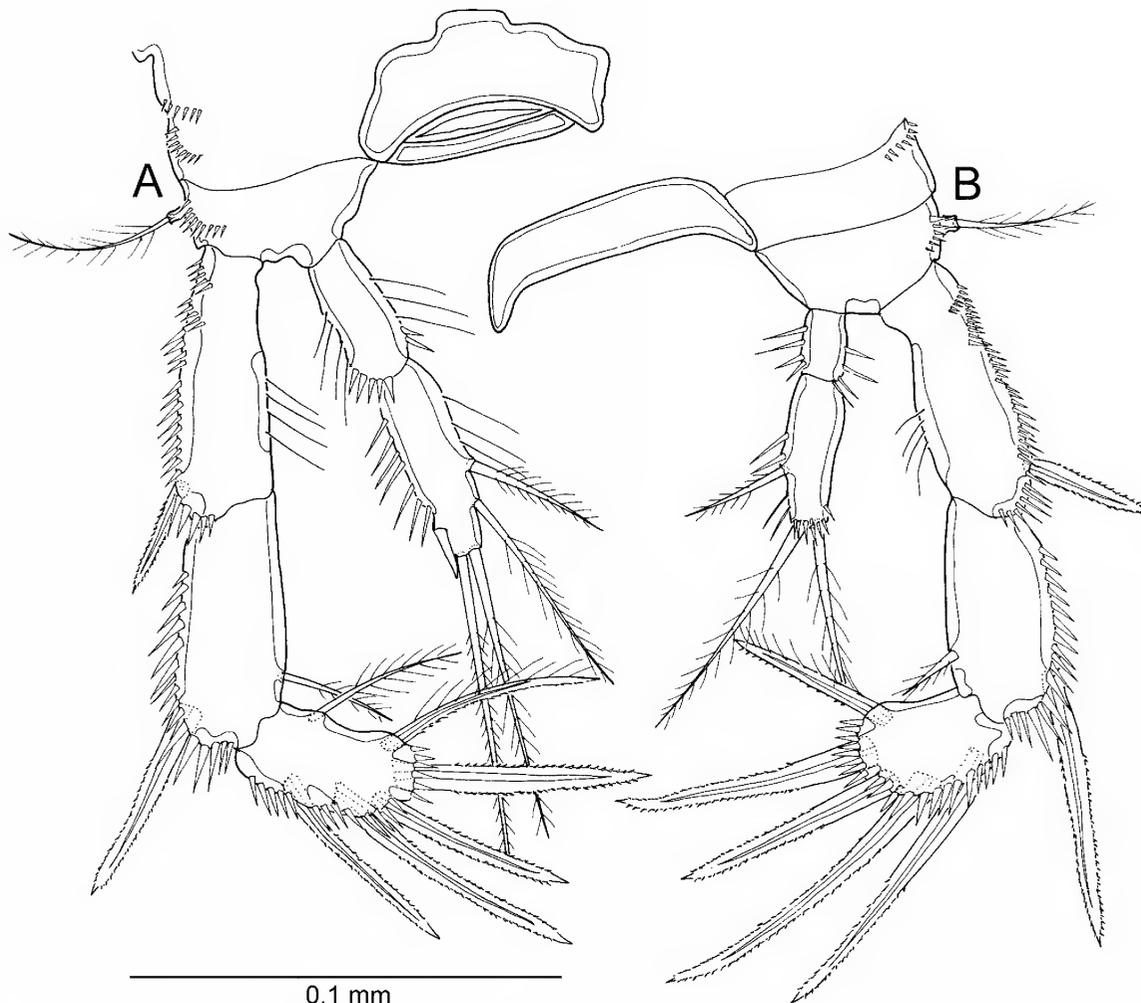


Figure 6. *Quinquelaophonte prolixasetae* sp. nov. male, paratype (NMV J52389): A, P3 and intercoxal sclerite; B, P4 and intercoxal sclerite.

*Quinquelaophonte prolixasetae* is most closely related to *Q. wellsii* (the other Australian species) sharing the unusual character of the P1 endopod-2 accessory seta longer than the terminal claw. Character states separating *Q. prolixasetae* from *Q. wellsii* are: P3 exopod-3 with one inner seta (two in *Q. wellsii*), P4 exopod-3 without an inner seta (with one in *Q. wellsii*) and the setation of P1 exopod-2 as mentioned above.

Many illustrations of species of *Quinquelaophonte* lack fine detail, however, in a recent paper (Lee, 2003) several smaller features, possibly omitted by previous authors, were illustrated. Lee (2003) noted the abexopodal seta on the A2 of *Q. koreana* was a “tiny . . . pinnate seta”. In most illustrations of the A2 (of other *Quinquelaophonte* species) no distinction has been made between the abexopodal seta and the other spinules on the allobasis. This lack of distinction may be because the difference went unnoticed or it may simply be that the abexopodal seta

appears exactly like the other allobasis spinules. I was unable to distinguish the abexopodal seta of *Q. prolixasetae* from the other spinules on the ventral margin of the allobasis. The abexopodal seta of *Q. bunakenensis*, *Q. candelabrum* and *Q. wellsii* is longer than the neighbouring allobasis spinules (Mielke, 1997; Wells et al., 1982; Hamond, 1973). The maxillule of *Q. prolixasetae* also differed from that of *Q. koreana* having a short lateral seta on the lateral margin of the arthrite instead of a long one, as found in *Q. koreana*. The illustration of the maxillule arthrite of *Q. wellsii* did not include a lateral seta (Hamond, 1973). *Quinquelaophonte bunakenensis* and *Q. parasigmoides* both have a long seta on the distal end of the maxillule arthrite (Mielke, 1997; Božić, 1969). Lee (2003) noted P3 and P4 endopod-2 of *Q. koreana* possessed a tube pore. This character state was not observed in *Q. prolixasetae* and has not been illustrated for any other species of

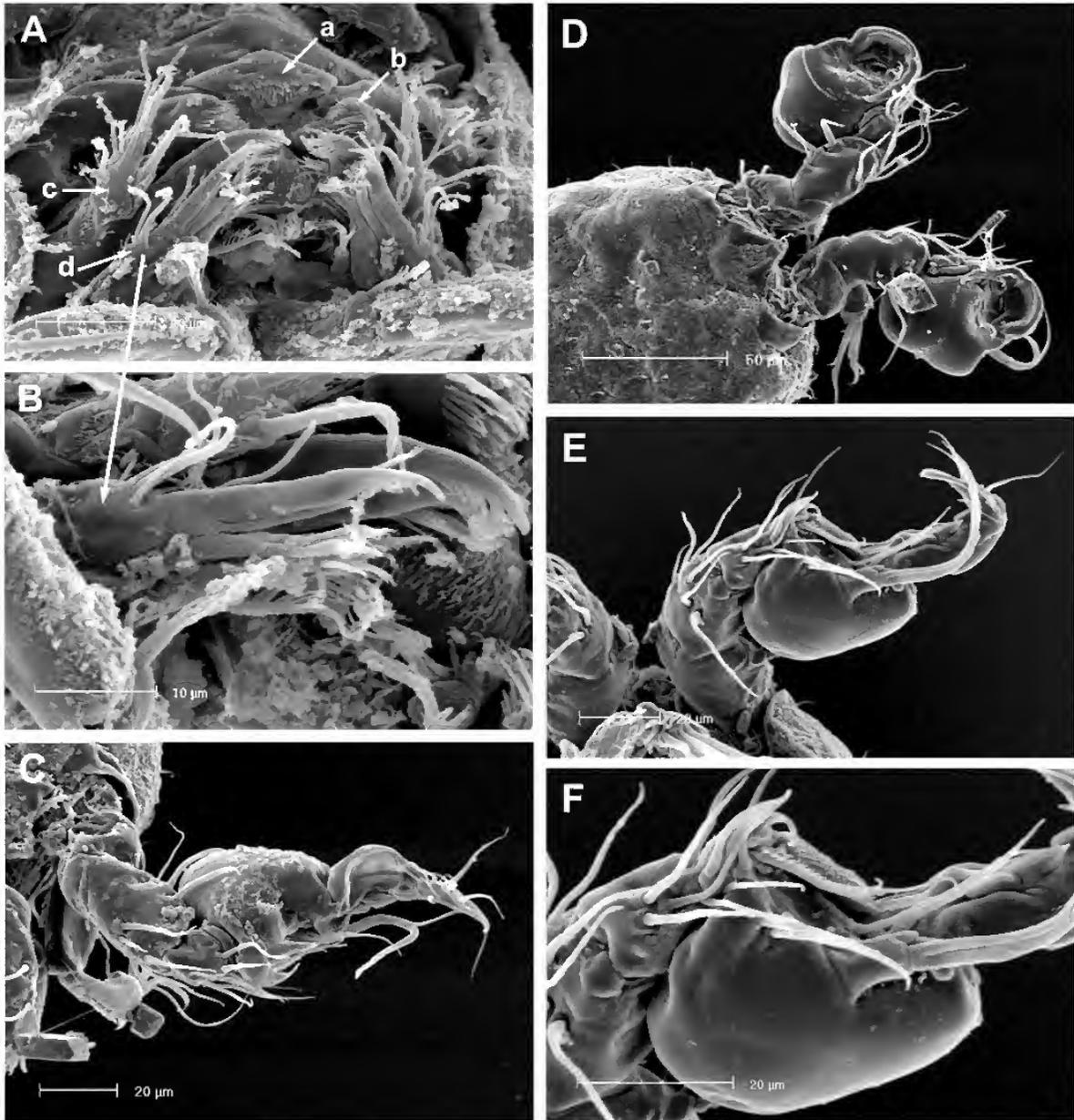


Figure 7. *Quinquelaophonte prolixasetae* sp. nov. Female (SAM C6098): A, mouthparts: a, labrum; b, paragnath; c, MxI; Mx; B, Mx. Male (SAM C6099): C, A1 (open) dorsal view; D, A1 dorsal view; E, A1 ventral view; F, A1 ventral view close up.

*Quinquelaophonte*. The possession a single well developed terminal seta (V) on the caudal rami is a diagnostic feature of *Quinquelaophonte*. Seta V and seta IV are fused basally in *Q. koreana* but are not fused in *Q. prolixasetae*. The distal half of seta V of *Q. koreana* has tiny spinules covering the surface but the entire length of seta V of *Q. prolixasetae*, is covered with minute spinules.

Some of the character states distinguishing *Q. prolixasetae* from all other species of *Quinquelaophonte* are listed in table 3.

#### Acknowledgements

This work was supported (in part) by a grant from the Australian Biological Resources Study. I would like to thank

Table 3. Some morphological differences between *Q. proluxasetae* and the other species of *Quinquelaophonte*.

	<i>proluxasetae</i>	<i>brevicornis</i>	<i>quinquespinosa</i>	<i>capillata</i>	<i>longifurcata</i>	<i>parasigmoides</i>	<i>wellsi</i>	<i>candelabrum</i>	<i>bunakenensis</i>	<i>koreana</i>
P1 exp-2	5 elongate setae	2 long setae and 3 shorter spines								
A1 ♀	6-segmented	6-segmented	6-segmented	6-segmented	6-segmented	6-segmented	6-segmented	6-segmented	6-segmented	6-segmented
A2 exopod	3 setae	4 setae	2-4 setae	2 setae	3 setae	3 setae	3 setae	2 setae	3 setae	2 setae
P1 endp-2	longer than terminal claw	?	shorter than terminal claw	shorter than terminal claw	shorter than terminal claw	?	longer than terminal claw	shorter than terminal claw	shorter than terminal claw	shorter than terminal claw
accessory seta	6 setae	6 setae	6-7 setae	6 setae	6 setae	6 setae	6 setae	5 setae	6 setae	6 setae
P5 exopod †	5 setae	?	5 setae	4 setae	5 setae	5 setae				
P3 exp-3 ‡ no. of setae	1.2.3	?	2.2.3	1.2.3	0.2.3, or 1.2.3	1.2.3	2.2.3	2.2.3	2.2.3	2.2.3
P3 endp-2 ‡ no. of setae	2.2.1	?	2.2.1	2.2.1	2.2.1	3.2.1	2.2.1	2.2.1	2.2.0	2.2.1
P4 exp-3 ‡ no. of setae	0.2.3	1.2.3	1.2.3 or 2.2.3	1.2.3	0.2.3	1.2.3	1.2.3	1.2.3	1.2.3	1.2.3
P4 endp-2 no. of setae	1.2.0	1.2.1	1.2.0 or 1.2.1	1.1.1	1.2.1	1.2.0	1.2.0	1.2.0 or 1.2.1	1.2.0	1.2.1

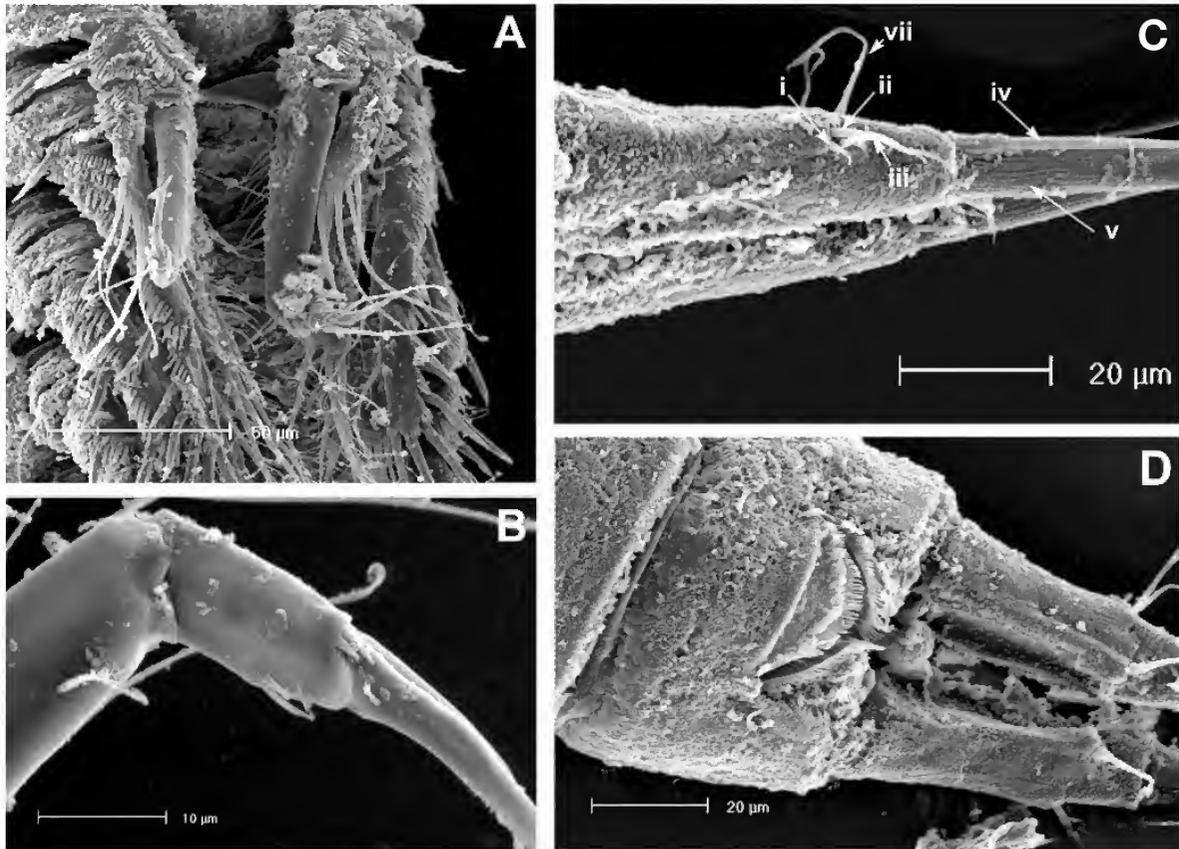


Figure 8. *Quinquelaophonte prolixasetae* sp. nov. female (SAM C6098): A, P1 dorsal view; B, P1 endopod-2 and claw; C, caudal rami, ventro-lateral view; D, anal operculum and caudal rami, dorsal view.

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## References

- Bodin, P. 1964. Recherches sur la systématique et la distribution des Copépodes Harpacticoides des substrates meubles des environs de Marseille. *Recueil des travaux de la Station marine d'Endoume. Faculté des Sciences de Marseille* 51(35): 107–183.
- Bodin, P. 1997. *Catalogue of the new marine harpacticoid copepods*. L'Institut Royal des Sciences Naturelles de Belgique: Brussels. 304 pp.
- Božić, B. 1969. Copépodes Harpacticoides de la Réunion. *Bulletin du Muséum National d'Histoire Naturelle* 41(4): 867–882.
- Candeias, A. 1959. Contribution to the knowledge of the harpacticoids (Crustacea, Copepoda) from the littoral of Angola. *Publicações Culturais da Companhia de Diamantes de Angola* 45: 77–104.
- Chappuis, P.A., Delamare Deboutteville, C., and Paulian, R. 1956. Crustacés des eaux souterraines littorales d'une resurgence d'eau douce à la Réunion. *Mémoires de l'Institut Scientifique de Madagascar* 11A: 51–78.
- Coull, B.C. 1976. On the two laophontid harpacticoid copepods described by Wilson as *Laophonte capillata*, with keys to the genus *Paronychocamptus*. *Transactions of the American Microscopical Society* 95(1): 35–45.
- Coull, B.C. 1986. A new species of *Pseudobradya* and the rediscovery and correction of *Quinquelaophonte capillata* (Copepoda: Harpacticoida). *Transactions of the American Microscopical Society* 105(2): 121–129.
- Fiers, F. 1986. Harpacticoid Copepoda from the West Indian islands: Laophontidae (Copepoda, Harpacticoida). *Bijdragen tot de Dierkunde* 55(2): 331–426.
- Giere, O. 1993. *Meiobenthology: the microscopic fauna in aquatic sediments*. Springer-Verlag: Berlin. 328 pp.
- Gurney, R. 1927. Zoological results of the Cambridge expedition to the Suez Canal, 1924. 23. Report on the Crustacea-Copepoda (littoral and semi-parasitic). *Transactions of the Zoological Society of London* 22: 451–577.
- Hamond, R. 1973. The harpacticoid copepods (Crustacea) of the saline lakes in southeast Australia, with special reference to the Laophontidae. *Records of the Australian Museum* 28(17): 393–420.

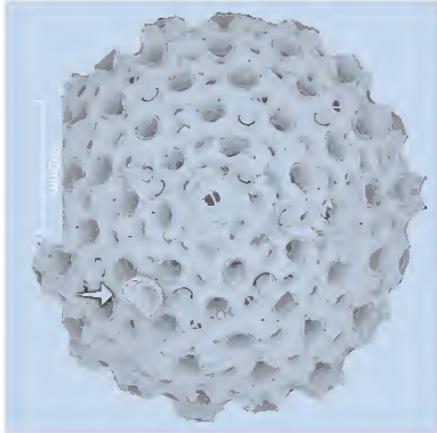
- Huys, R., and Boxshall, G.A. 1991. *Copepod Evolution*. The Ray Society: London. 468 pp.
- Huys, R., Gee, J.M., Moore, C.G., and Hamond, R. 1996. *Marine and brackish water harpacticoid copepods, part 1*. Field Studies Council: Shrewsbury. 352 pp.
- Lang, K. 1934. Marine Harpacticiden von der Campbell-Insel und einigen anderen südlichen Inseln. *Acta Universitatis Lundensis, New Series*, Avd. 2, 30:1–56.
- Lang, K. 1948. *Monographie der Harpacticiden*. Håkan Ohlsson's Bøkttryckeri: Lund and Nordiska Bøkhandeln: Stockholm. 2 vols, 1682 pp.
- Lang, K. 1965. Copepoda Harpacticoida from the Californian Pacific coast. *Kungliga Svenska Vetenskapsakademiens Handlingar* (series 4) 10(2): 1–560.
- Lee, W. 2003. A marine harpacticoid, *Quinquelaophonte koreana* sp. nov. from a sandy beach in Korea (Crustacea: Copepoda). *Zoological Science* 20: 657–668.
- Lee, W. and Huys, R. 1999. *Bathylaophonte* gen. nov. from deep-sea hydrothermal vents and the polyphyly of *Paronychocamptus* (Copepoda: Harpacticoida). *Cahiers de Biologie Marine* 40: 293–328.
- Mielke, W. 1997. On a small collection of Laophontidae (Copepoda) from Sulawesi, Indonesia. *Microfauna Marina* 11: 223–250.
- Monard, A. 1935. Les Harpacticoides marins de la region de Salammbô. *Bulletin de la Station Océanographique de Salammbô* 34: 1–94.
- Scott, T. 1894. Report on Entomostraca from the Gulf of Guinea, collected by John Rattray, B.Sc. *Transactions of the Linnean Society of London* (Series 2), *Zoology* 6(1): 1–161.
- Sewell, R.B.S. 1924. Fauna of the Chilka Lake. *Crustacea Copepoda. Memoirs of the Indian Museum* 5: 771–851.
- Walker-Smith, G.K. 2003. The harpacticoid copepod fauna of Port Phillip Bay (Victoria, Australia) and their contribution to the diet of juvenile King George whiting (*Sillaginoides punctata*: Sillaginidae). PhD thesis, Department of Zoology, The University of Melbourne: Victoria, Australia. 278 pp.
- Wells, J.B.J. 1967. The littoral Copepoda (Crustacea) of Inhaca Island, Mozambique. *Transactions of the Royal Society of Edinburgh* 67: 189–358.
- Wells, J.B.J., Hicks, G.R.F., and Coull, B.C. 1982. Common harpacticoid copepods from New Zealand harbours and estuaries. *New Zealand Journal of Zoology* 9: 151–184.
- Wells, J.B.J., and McKenzie, K.G. 1973. Report on a small collection of benthic copepods from marine and brackish waters of Aldabra, Indian Ocean. *Crustaceana* 25(2): 133–146.
- Wells, J.B.J., and Rao, G.C. 1987. Littoral Harpacticoida (Crustacea, Copepoda) from Andaman and Nicobar Islands. *Memoirs of the Zoological Survey of India* 16(4): 1–385.
- Wieser, W. 1959. Free-living nematodes and other small invertebrates of Puget Sound beaches. *University of Washington Publication in Biology* 19: 1–79.
- Willey, A. 1930. Copepod phenology — Observations based on new material from Canada and Bermuda. *Archivio Zoologico Italiano* 16: 601–617.
- Wilson, C. B. 1932. The copepods of the Woods Hole region Massachusetts. *Bulletin of the United States National Museum* 158: 1–365.







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