Memoirs of Museum Victoria 61(2): 135–182 (2004)

ISSN 1447-2546 (Print) 1447-2554 (On-line)
http://www.museum.vic.gov.au/memoirs/index.asp

A review of Australian Conescharellinidae (Bryozoa: Cheilostomata)

PHILIP E. BOCK[1, 2] AND PATRICIA L. COOK[2]

[1] School of Ecology and Environment, Deakin University, Melbourne Campus, Burwood Highway, Burwood, Vic. 3125. (pbock@deakin.edu.au)
[2] Honorary Associate, Marine Biology Section, Museum Victoria, GPO Box 666E, Melbourne, Vic. 3001, Australia

Abstract Bock, P.E. and Cook, P.L. 2004. A review of Australian Conescharellinidae (Bryozoa: Cheilostomata). *Memoirs of Museum Victoria* 61(2): 135–182.

The family Conescharellinidae Levinsen is defined and is regarded as comprising seven cheilostome genera (*Conescharellina, Bipora, Trochosodon, Flabellopora, Zeuglopora, Crucescharellina* and *Ptoboroa*). 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. perculta, C. pustulosa, C. ocellata, C. macgillivrayi, C. humerus; Trochosodon fecundus, T. asymmetricus, T. diommatus, T. aster, T. anomalus, T. praecox and Crucescharellina australis*. In addition, the New Zealand bryozoan *Trochosodon multiarmatus* (Gordon, 1989) (not *Bipora multiarmata* Maplestone, 1909) is described as *Trochosodon gordoni* 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 *Crucescharellina* are present. Busk (1884) did not include stn 185 in his Report as its bryozoan component was undiscovered. Similarly, a specimen of *Crucescharellina* 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 *Conescharellina* 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 *Crucescharellina* 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 *Fatkullina* 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; Pizzaferri 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 *Conescharellina* 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, extrazooidal 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, interzooidal 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 "lunooecia", "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 autozooid 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 autozooid 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 entooecium. 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 ectooecial and entooecial 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 ectooecium 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 entooecium may be ridged and occasionally is porous. The ridges appear to form pores marginally where the entooecial layer meets the ectooecium. 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 spathulate. 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 septupler 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, entooecium and ectooecium 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. vigneauxi* Labracherie, 1975 (p. 151, pl. 4 figs 4–11). This species appears to be similar to species of *Atactoporidra*, 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 eocoena* 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 "Batoporoidea" (sic) Neviani, 1901 and the genera *Lacrimula* Cook, 1966 and *Orbitulipora* Stoliczka, 1862. Neviani (1901) had, however, included in his family "Batoporideae" [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 Schismoporineae in another footnote. The treatment of the subfamily Biporineae was completely different. No generic names were included but the description given was "Schizoporellidae with a patelliform unilaminate 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 vibracularia 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 *Atactoporidra* 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 "Batoporoidea" as used by Zágoršek 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. perculta*
— 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. fecundus*
— 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. praeco*x

Conescharellina d'Orbigny 1852

Conescarellina [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 *Conescarellina* 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 entooecium. 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 extrazooidal 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, 18540 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 zooecial cells, and the zooecia 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 to12 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 ectooecial 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 *Trochos*odon 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. perculta*, 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 *Crucescharellina australis* sp. nov.

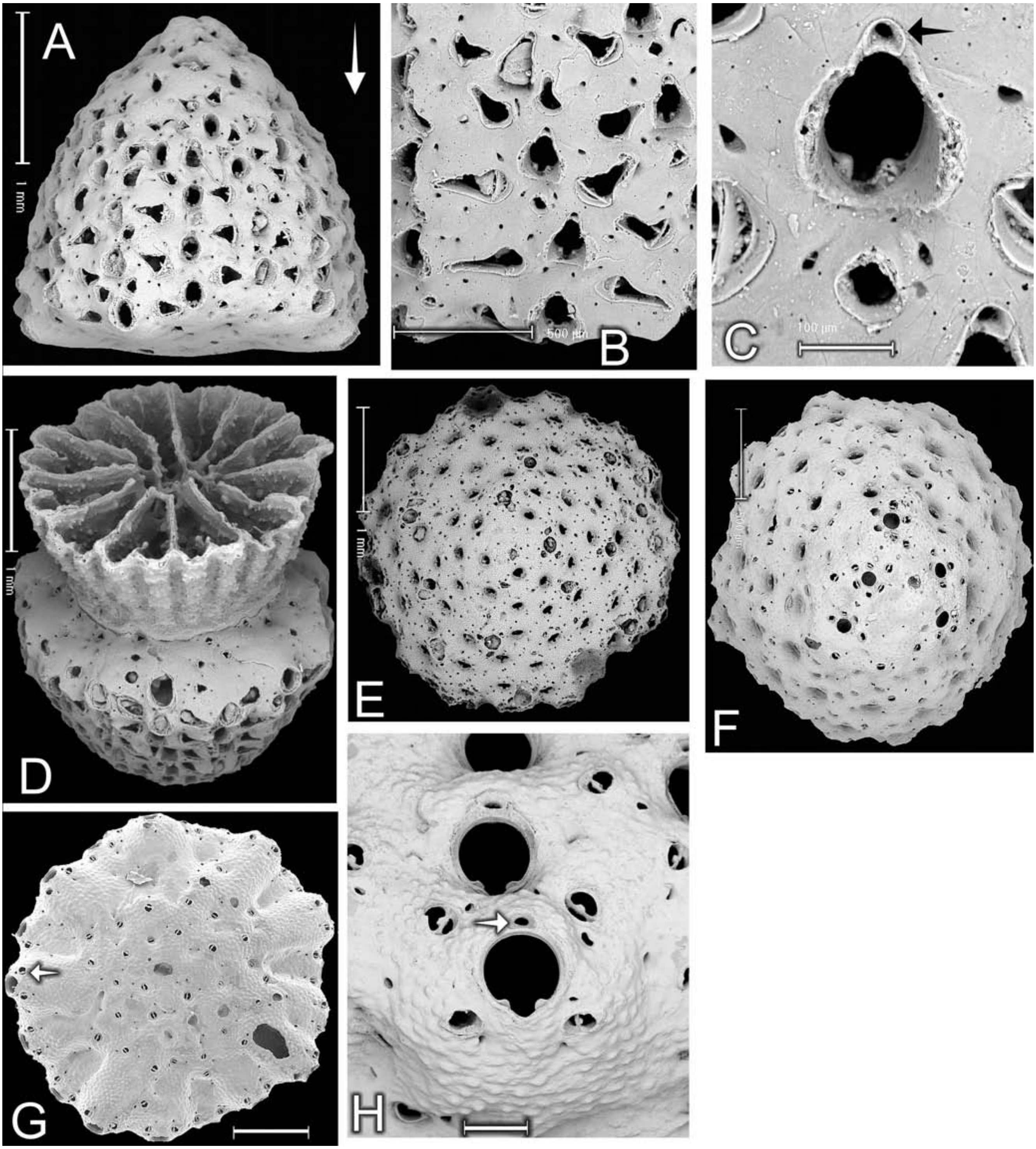

Figure 1. A–D, *Conescharellina* sp. A–C, NMV F98977, colony; direction of growth arrowed; scale=1 mm, B, detail of orifices and avicularia, scale = 500 µm, C, detail of orifice with adapical pore (arrow), scale=100 µm. D, NMV F98978, colony from antapical surface with commensal coral, scale = 1 mm. 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 µm. G, antapical view of colony with small, central and paired marginal peristomial avicularia (arrow), scale=500 µm. H, detail of orifices and avicularia, adapical pore arrowed, scale= 100µm.

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 orificial 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 gordoni* 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 gordoni* 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,

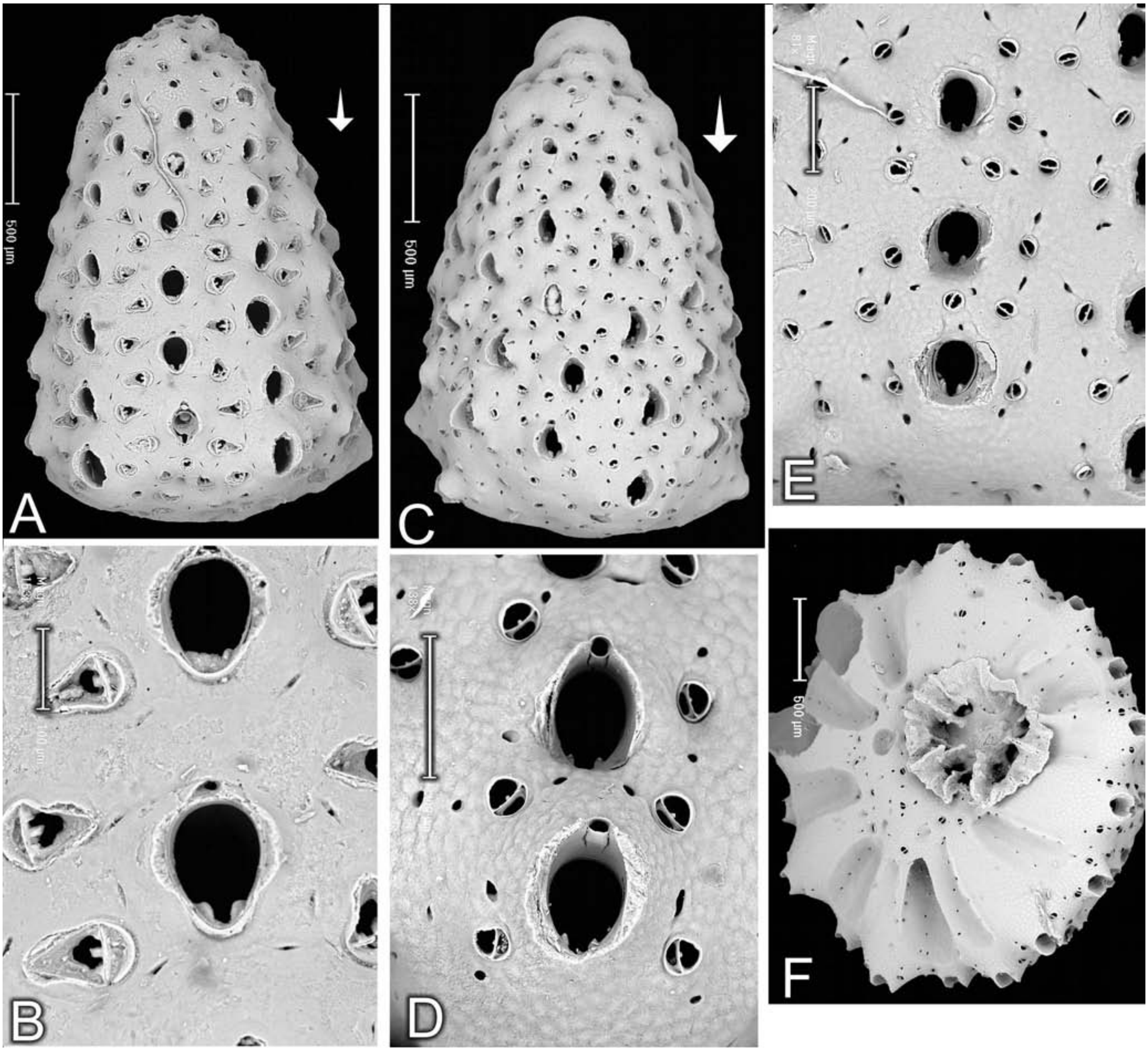

Figure 2. A–B, *Conescharellina biarmata* (Maplestone, 1909). NMV F98980. A, lateral view of colony, growth direction arrowed, scale=1 mm. B, detail of orifices with adapical pore, avicularia and slit-like frontal septular pores, scale= 100 µm. C–D, *Conescharellina multiarmata* Maplestone, NMV F98981. 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 extrazooidal 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.

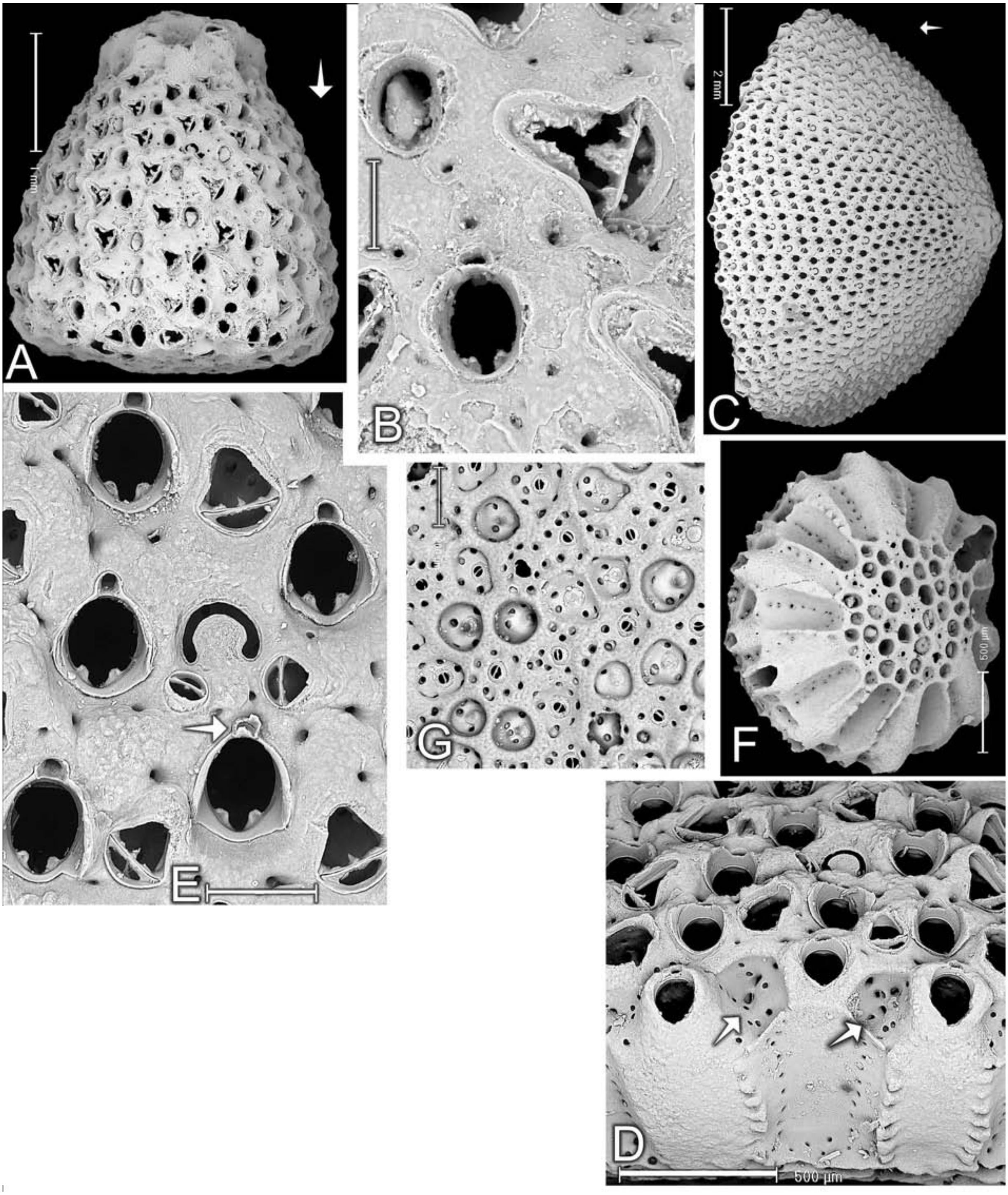

Fig.3. A–B, *C. magniarmata* Maplestone, NMV F98984. A, Lateral view of colony, growth direction arrowed, note adapical secondary calcification, scale= 1 mm. B, detail of orifice with adapical pore and avicularium, scale= 100 µm. C–G, *Conescharellina cognata* sp. nov. C–E. NMV F98985, holotype. C, lateral 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 µm. E, detail of orifices with adapical pores, one with entooecial and ectooecial laminae of developing ovicell (arrow); large, interzooidal avicularia and lunate root pore with small paired avicularia, scale = 200 µm. F, NMV F98986, antapical view of small colony, showing central area of cancelli and alternating "concealed" zooids with marginal septular pores, scale = 500 µm. 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 µm.

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

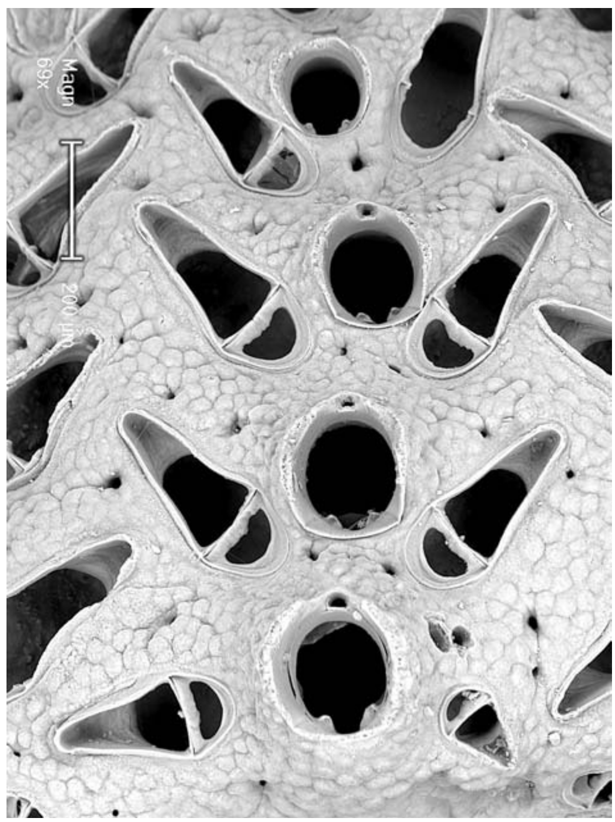

Figure 4. *Conescharellina ecstasis* sp. nov. NMV 98987, holotype. Radial series of zooid orifices with adapical pores and large avicularia, scale = 200µm.

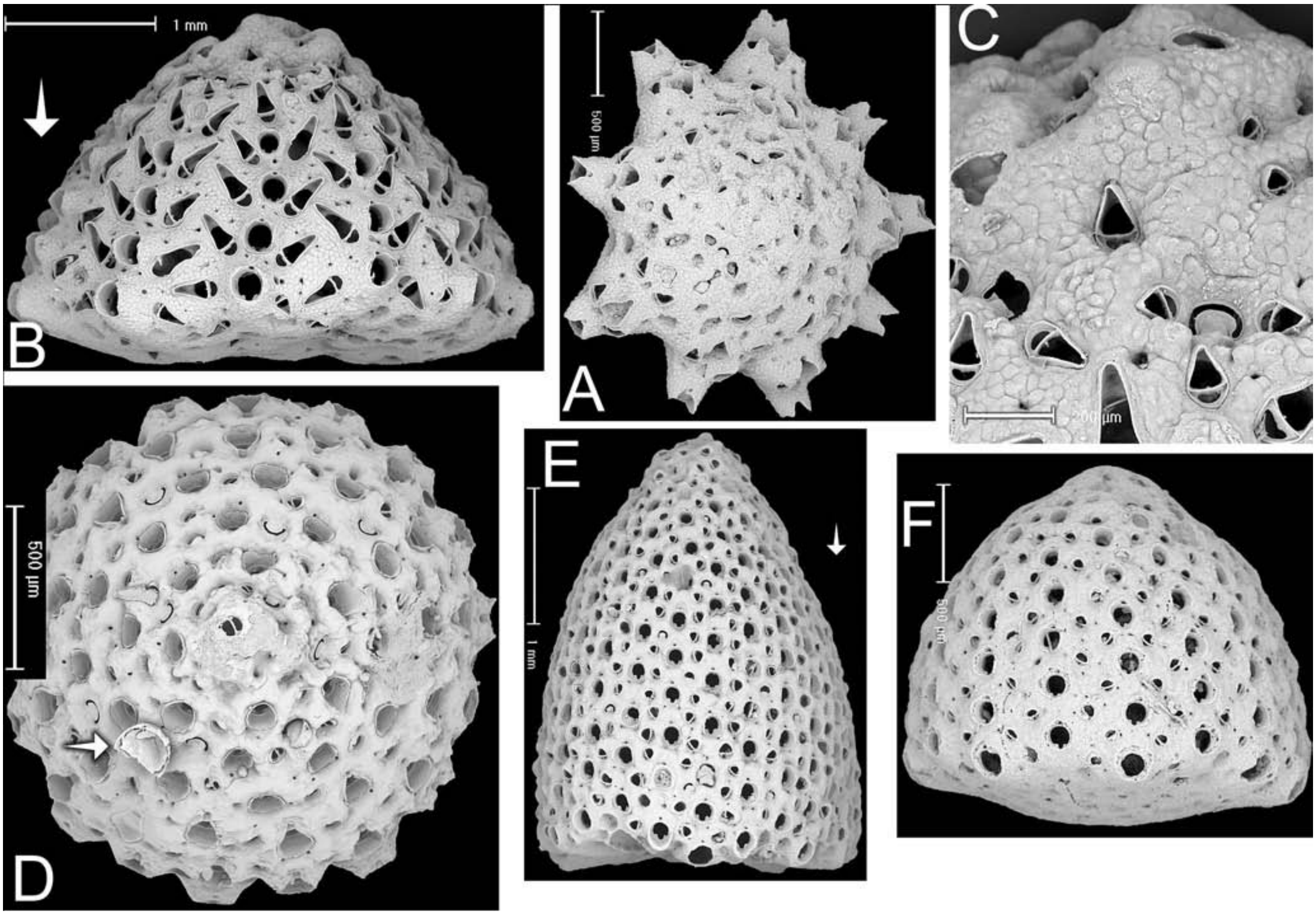

Figure 5. A–C, *Conescharellina ecstasis* sp. nov. A, NMV 98988. Adapical view, scale = 500 µm. B–C, NMV 98987, holotype. B, lateral view of colony, growth direction arrowed, scale = 1 mm. C, detail of adapical surface showing secondary calcification, avicularia and lunate root pore with three small 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 ectooecial 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 ectooecial rim and a semitransparent entooecial 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

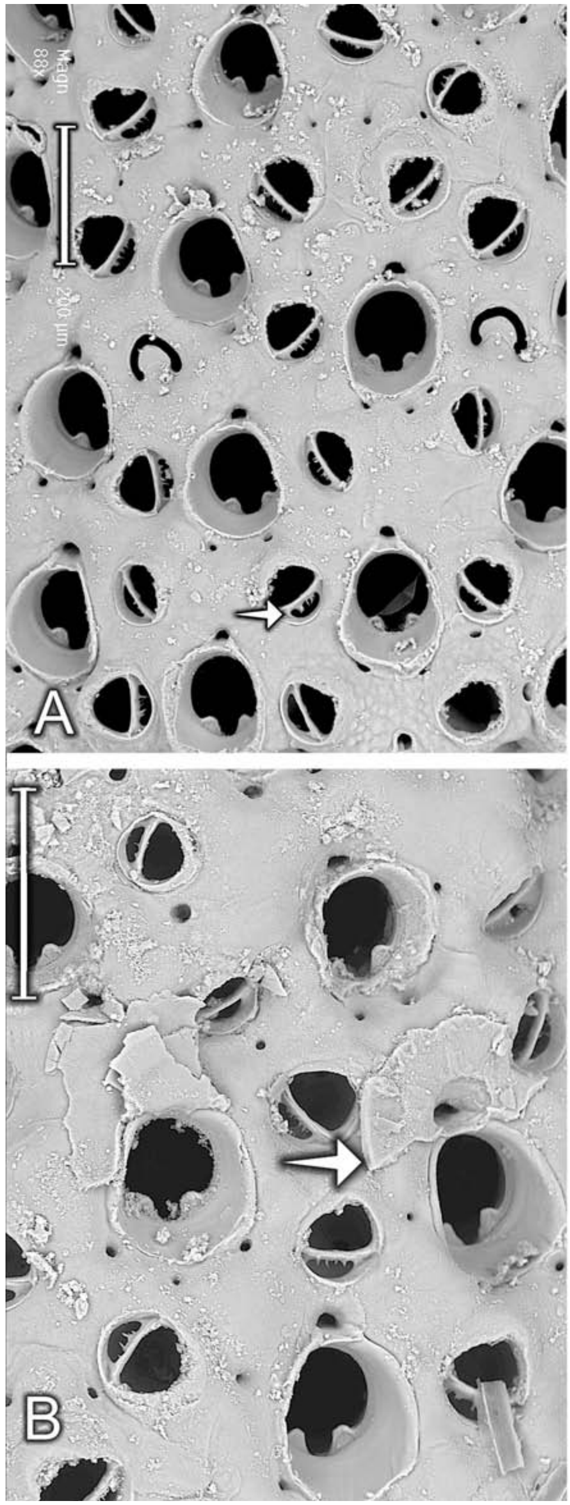

Figure 6. *Conescharellina diffusa* sp. nov. NMV F98989, holotype. A, detail of zooid orifices with adapical pores, lunate root pores and avicularia with non-palatal spinules (arrow), scale = 200 µm. B, detail of orifices with adapical pores; orifice at left shows broken laminae of ectooecium and overlying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

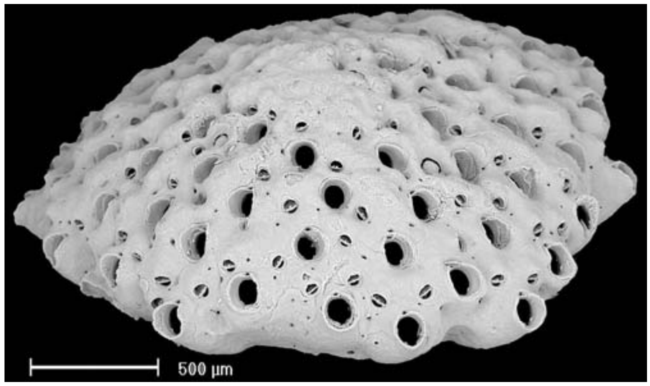

Figure 7. *Conescharellina obscura* sp. nov. A, NMV F98991, holotype. Lateral and adapical view of large colony, scale= 500 µm.

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 entooecium 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,

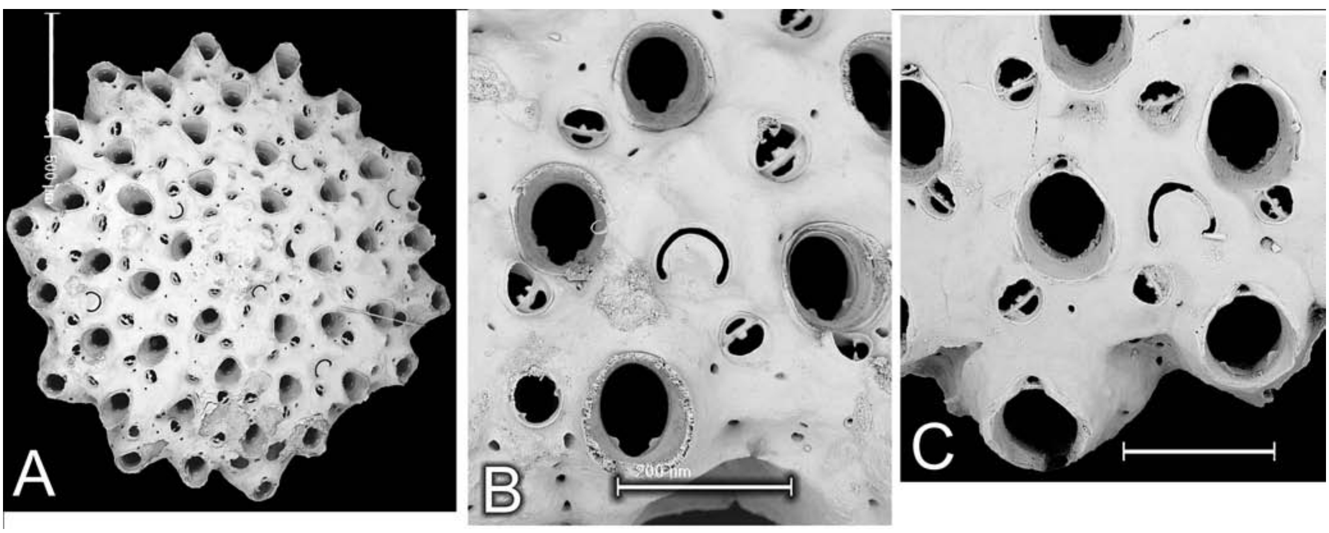

Figure 8. *Conescharellina obscura* sp. nov. A–B, NMV P98992. A, adapical view of small colony, showing lunate root pores, scale = 500 _m. B, detail of zooid orifices, avicularia, and one lunate root pore, scale = 200 µm. C, BMNH 1899.5.1.1148, Hincks Collection, Port Jackson, New South Wales. Detail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

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 philippinensi*s, 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 entooecial calcification and a series of minute pores close to the ovicell base, that may mark the limit of the ectooecium. 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 entooecium.

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 ectooecium and a depressed entooecium, striated marginally, forming pores at the ectooecial 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 ectooecium 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-

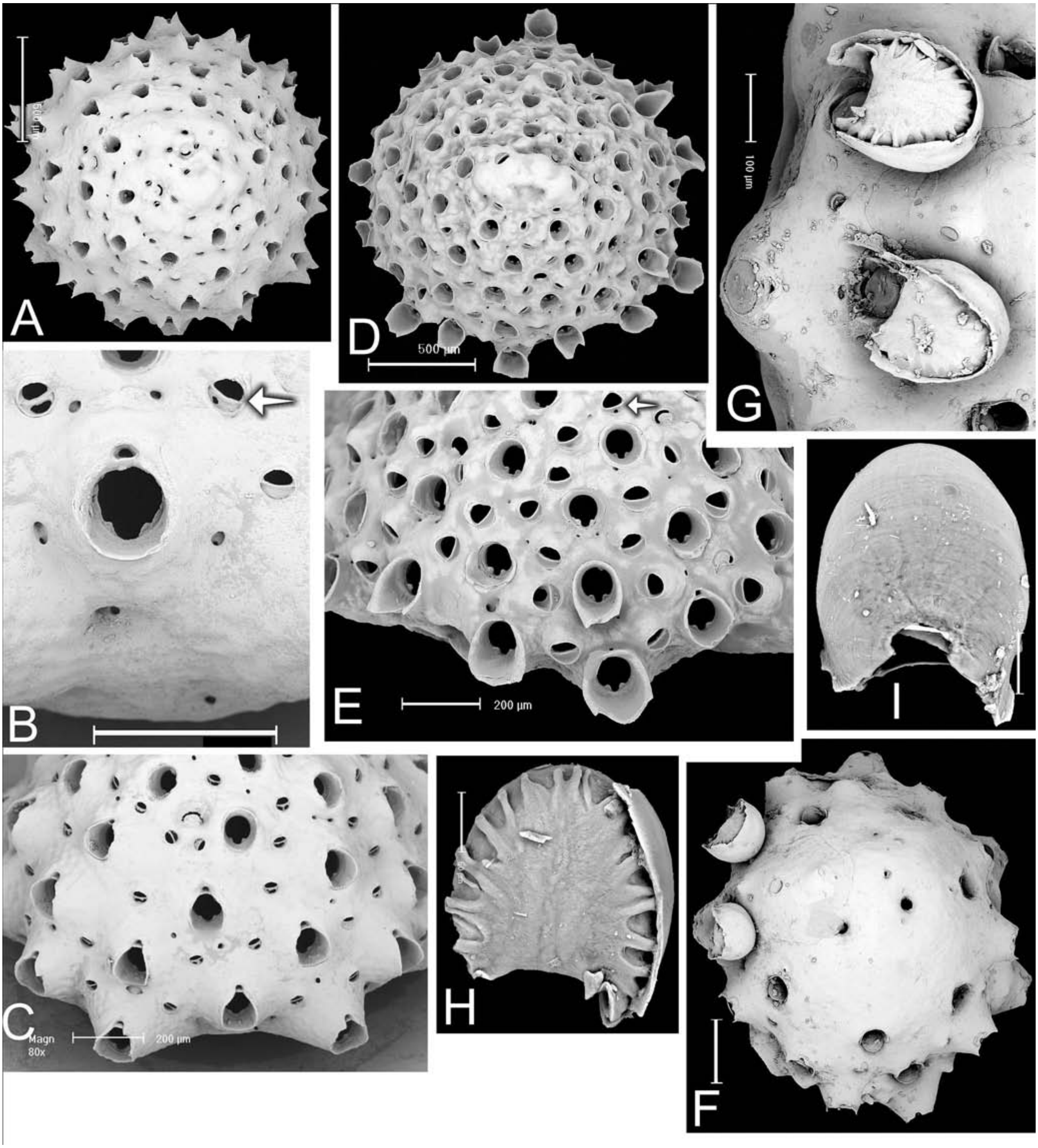

Figure 9. *Conescharellina stellata* sp. nov. A–C NMV F98993, holotype. A, adapical view of colony showing prominent bilabiate marginal peristomes and lunate root pores, scale = 500 µm. B, detail of marginal zooid orifice with adapical pore. Avicularium with porous non-palatal lamina (arrow), compare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

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. planus (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 ectooecial rim.

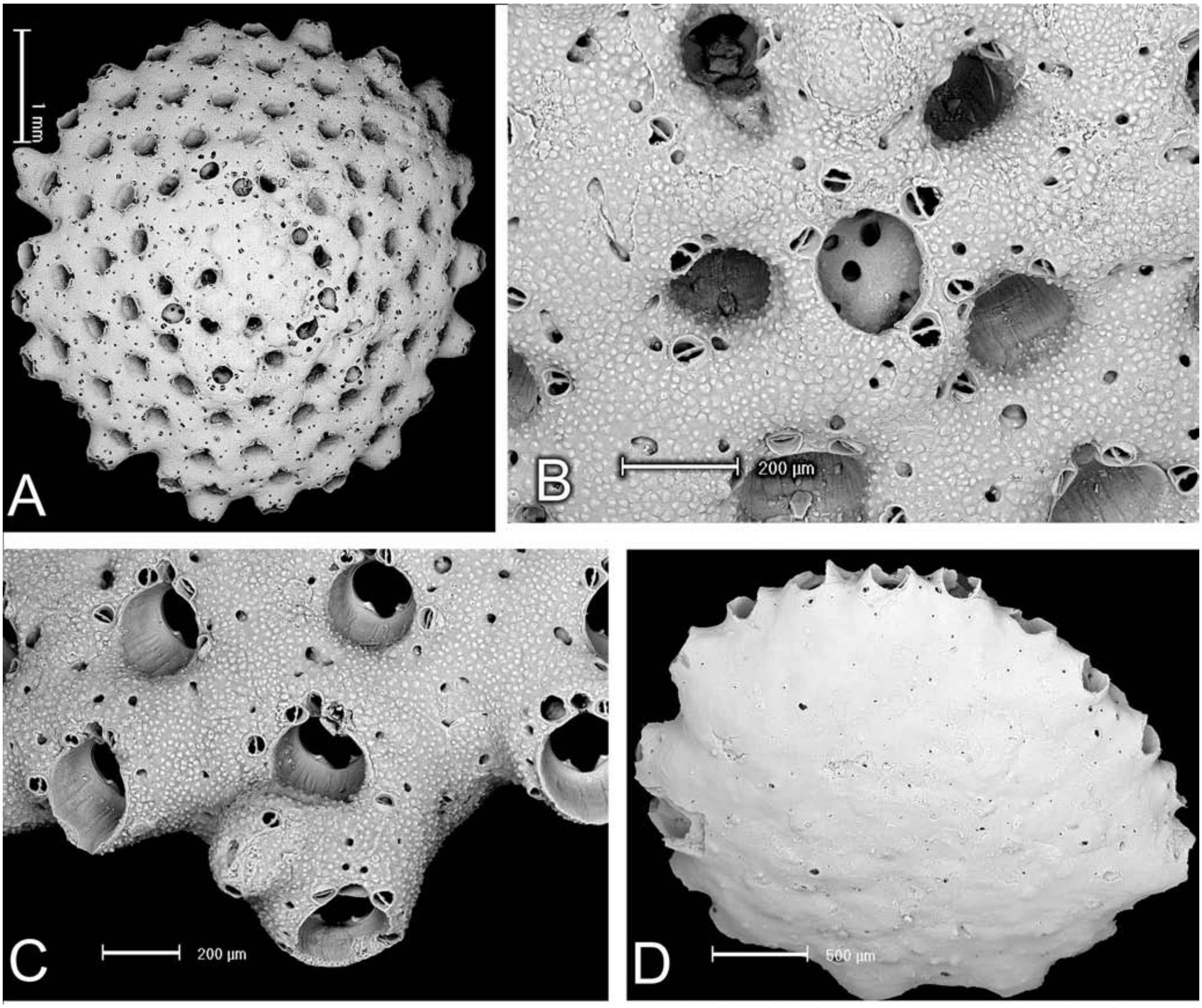

Figure 10. *Conescharellina plana* sp. nov. A–C, NMV F98996, holotype. A, adapical view of colony, scale = 1 mm. B, detail of root pore with surrounding avicularia, scale = 200 µm. C, detail of colony margin showing orifices, peristomes, and avicularia, scale = 200 µm. D, NMV F98997, paratype, antapical 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 ectooecial rim and a semitransparent entooecial 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 circlet 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. perculta*, *C. humerus* and *Crucescharellina australis* that are also surrounded by a circlet 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 perculta 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. percultus (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. perculta* 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. diommatus*, 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. perculta* 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 Maplestone 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

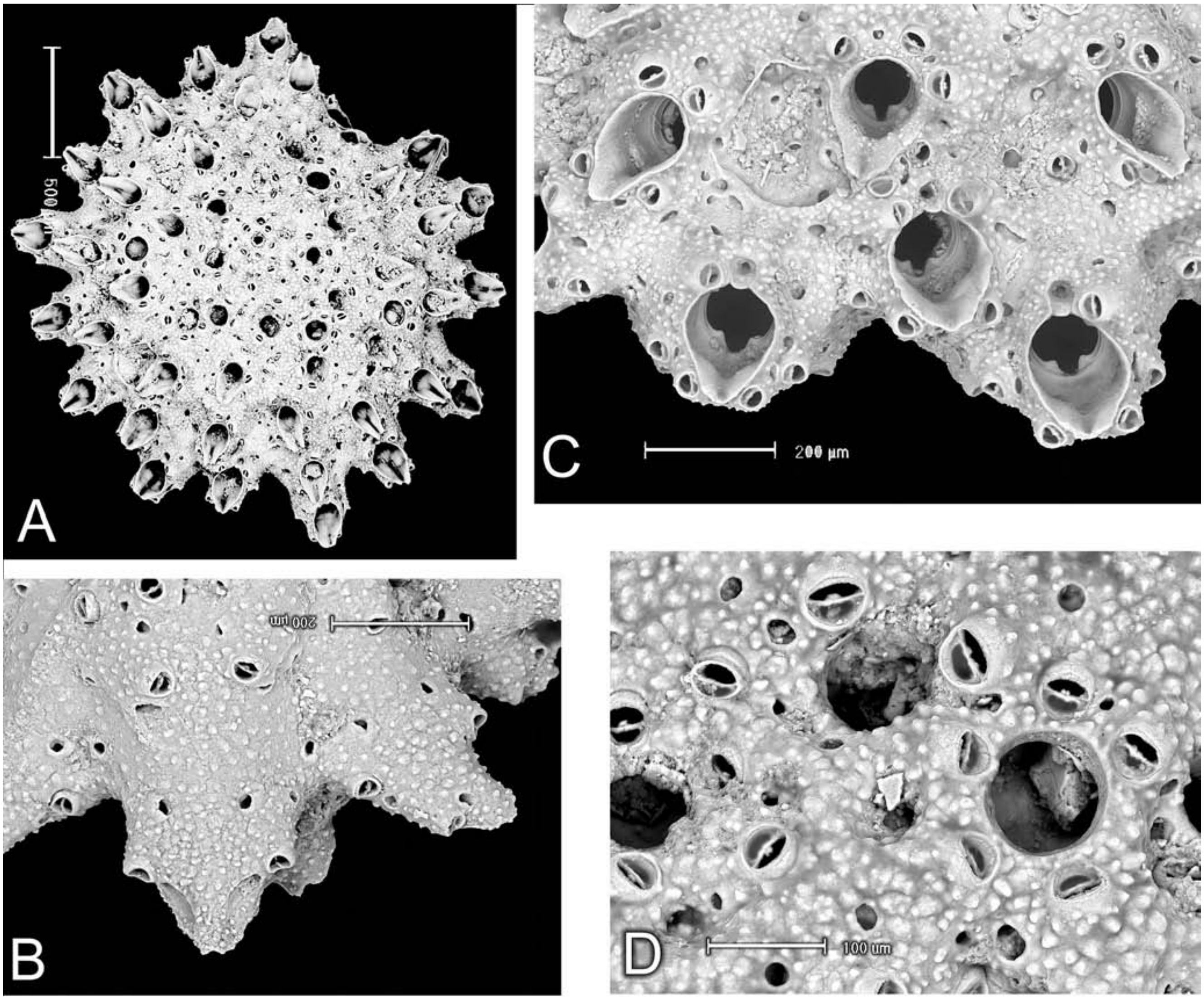

Figure 11. *Conescharellina perculta* sp. nov. A, NMV F98998, holotype. A, adapical view of colony, scale = 200 µm. B, NMV P98999, antapical view of marginal peristomes, scale = 200 µm. C–D, NMV F98998, holotype. C, detail of orifices, peristomes, and avicularia, scale = 200 µm. D, detail of root pore,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

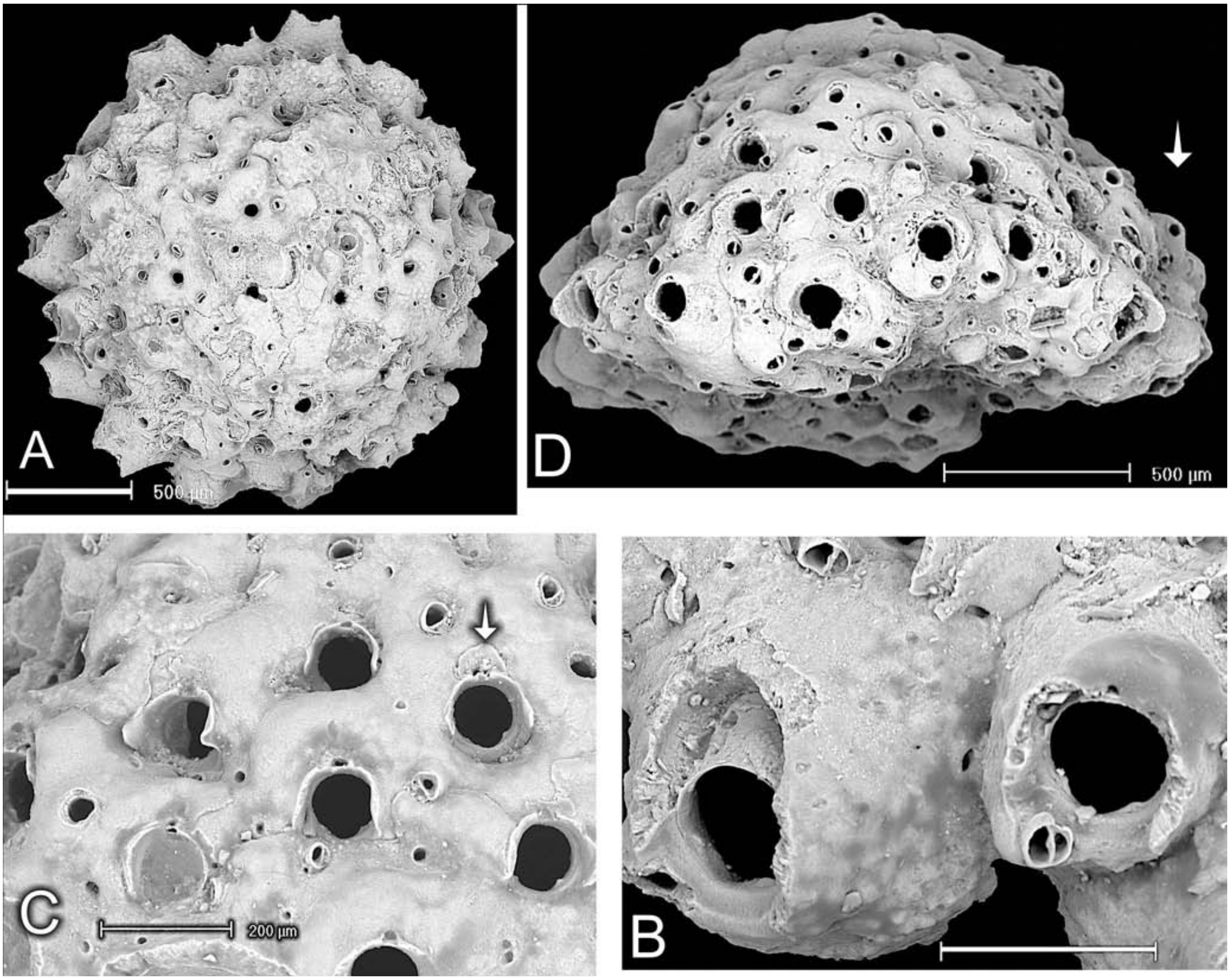

Figure 12. *Conescharellina pustulosa* sp. nov. A–B, NMV F99000, holotype. A, adapical view of colony, scale = 500 µm. B, detail of two marginal orifices, showing thick secondary calcification and peristomial avicularia, scale = 200 µm. C, NMV F99001, paratype, group of orifices, adapical pores with developing ectooecial 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 differes 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,

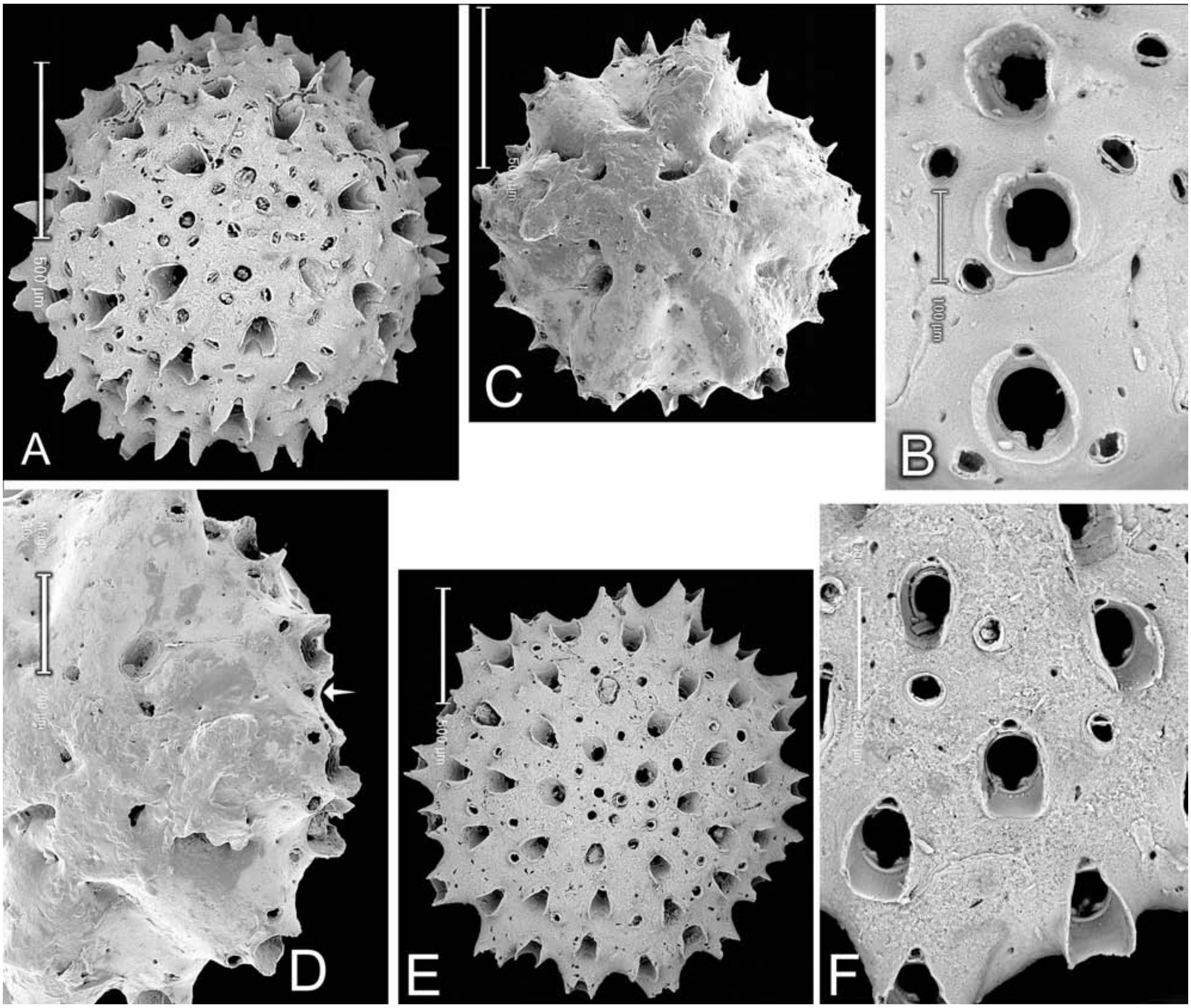

Figure 13. A–D, *Conescharellina ocellata* sp. nov. A–B, NMV P311805. A, adapical view of colony, scale = 500 µm. B, detail of orifices, avicularia and septular pores, scale = 200 µm. C–D, NMV P311806. C, antapical view, scale = 500 µm. D, marginal view showing peristomes and paired avicularia (arrow),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

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.

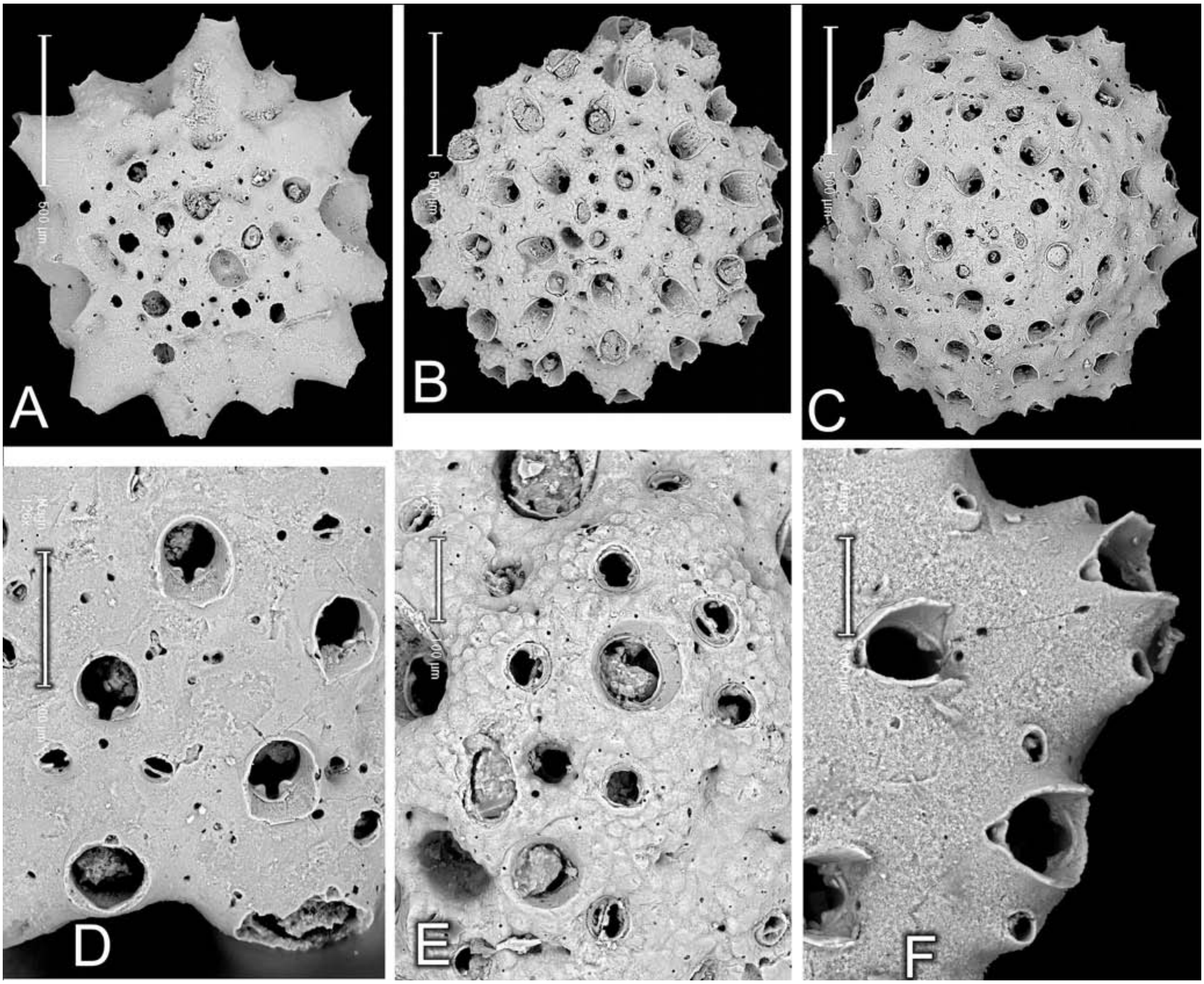

Figure 14. *Conescharellina macgillivrayi* sp. nov. and *C. humerus* sp. nov. A, *C. macgillivrayi* NMV P311811, antapical view of colony, showing cancelli, scale = 500 _m. B–F. *C. humerus*, B, NMV P311814, adapical view of colony, showing root pore, scale = 500 µm. C–D. NMV P311812. C, Adapical view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

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 circlet of avicularia is reminiscent of those found in *C. eburnea, C. plana*, *C. perculta* 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 zooecia 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 extrazooidally 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 radially 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.

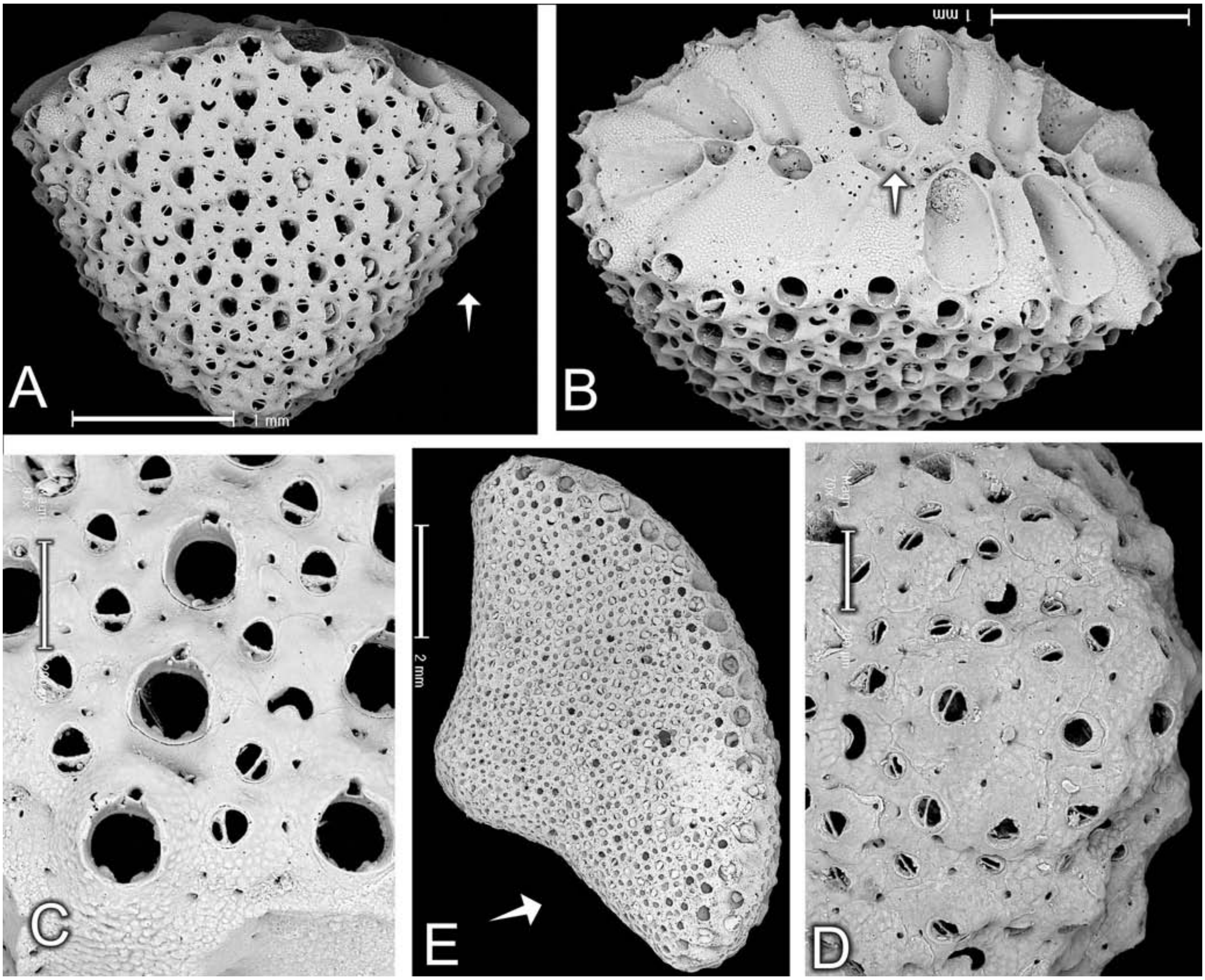

Figure 15. *Bipora flabellaris* (Levinsen, 1909). A–D, NMV F99003. A, young colony, direction of growth arrowed, scale =100 μm. B, antapical view of colony, showing narrow kenozooidal region (arrowed), scale = 1 mm. C, detail of orifices with adapical pores, and avicularia, scale = 200 μm. D, adapical 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 *Conescharellina*", 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 extrazooidal and kenozooidal 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.

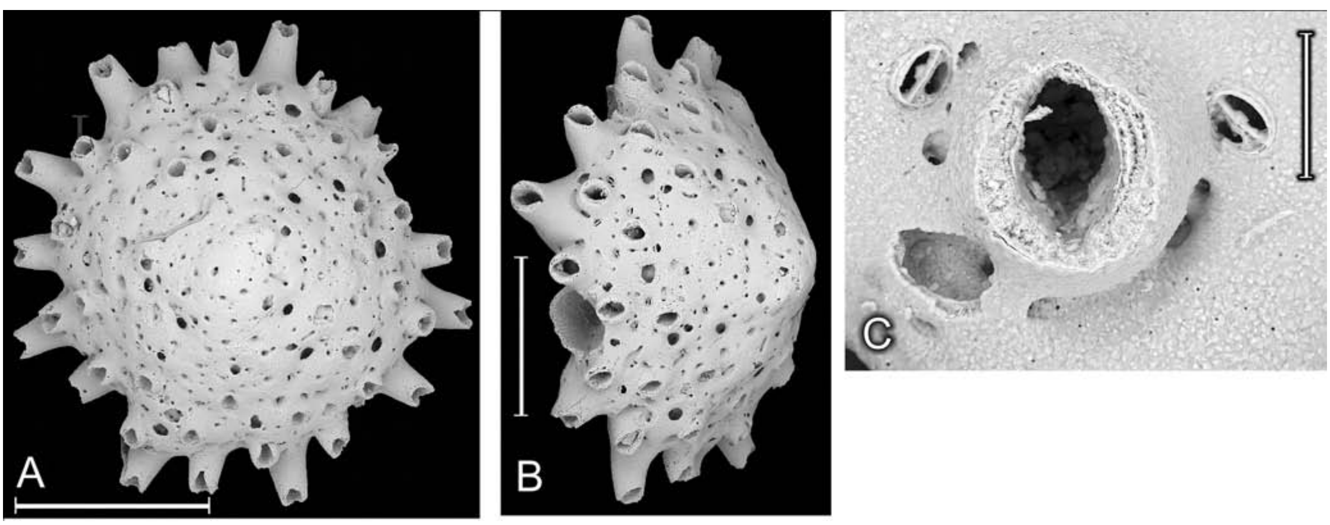

Figure 16. *Trochosodon ampulla* (Maplestone, 1909). A, NMV F99005, adapical view of colony, scale = 1 mm. B–C, NMV F99006. B, lateral view of larger colony, scale = 1 mm. C, detail of orifice and avicularia, scale = 100 µm.

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 *Zeuglopora 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

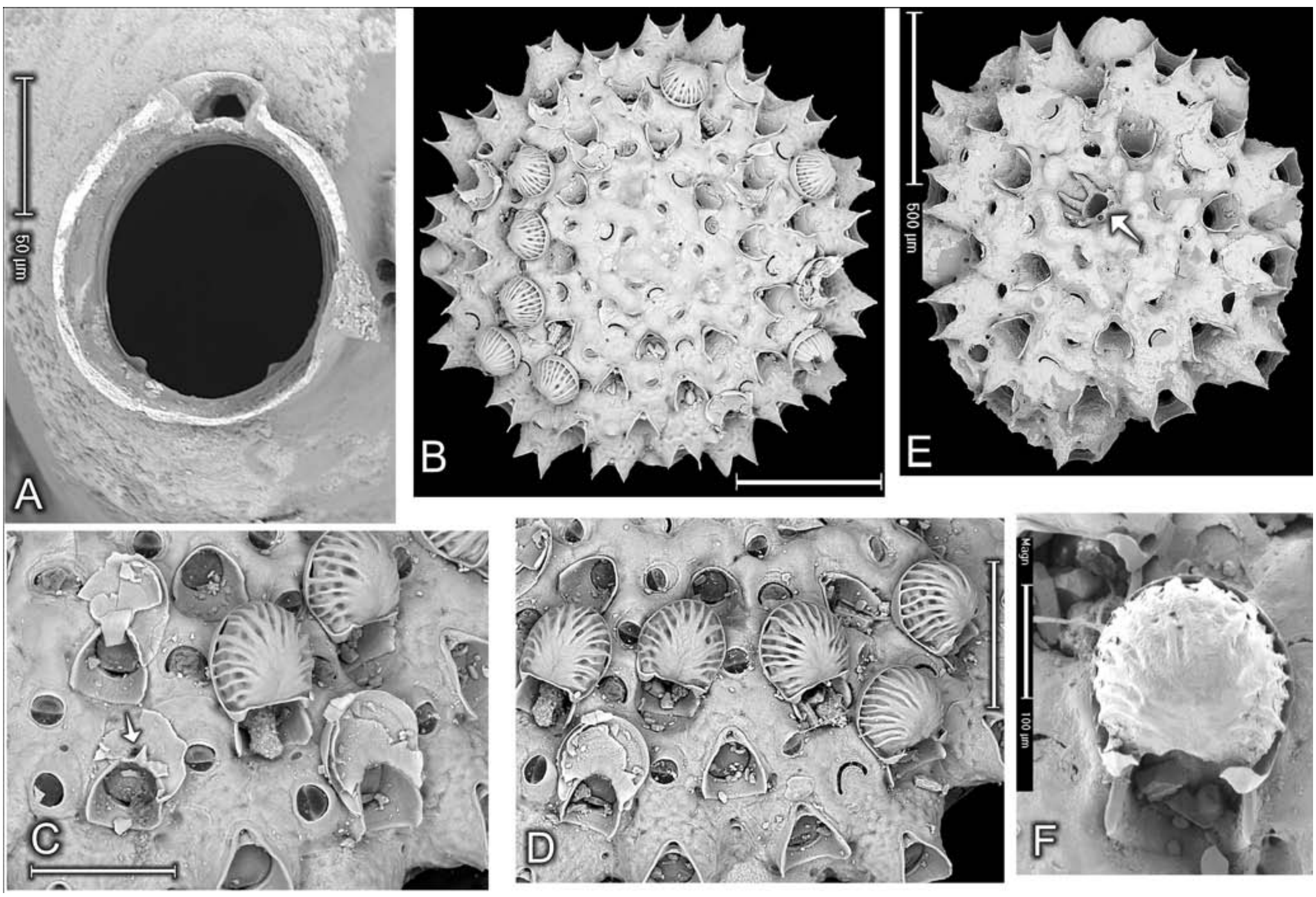

Figure 17. *T. fecundus* sp. nov. A, NMV F99009, paratype. Detail of orifice and adapical pore, scale = 50 µm. B–D, NMV F99007, holotype. B, Adapical view of colony with ovicells and lunate root pores, scale = 500 µm. C. detail of orifices and avicularia, note one adapical pore with developing ectooecial 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.

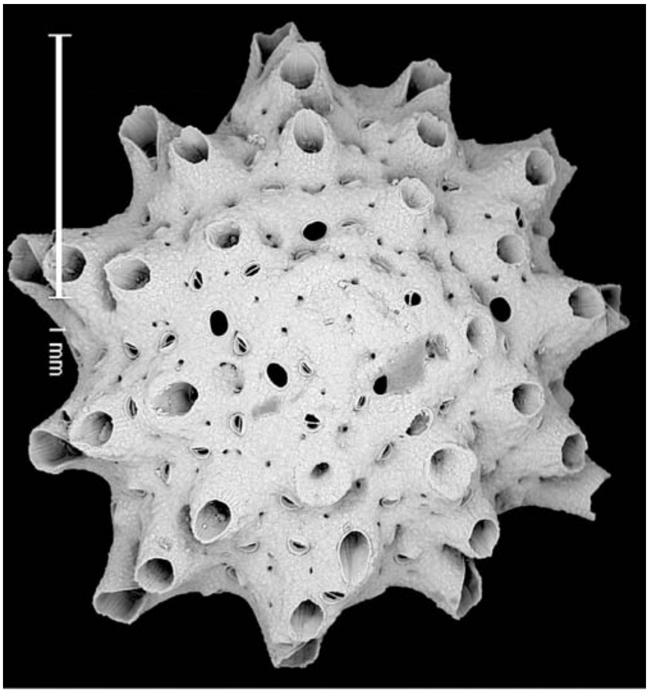

Figure 18. *Trochosodon asymmetricus* sp.nov. NMV F99011, paratype. Adapical view of colony, scale = 1 mm.

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 entooecium is striated, as figured by Harmer, and resembles that of *C. striata* and *T. fecundus*. The ectooecial 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 "anascan" 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.

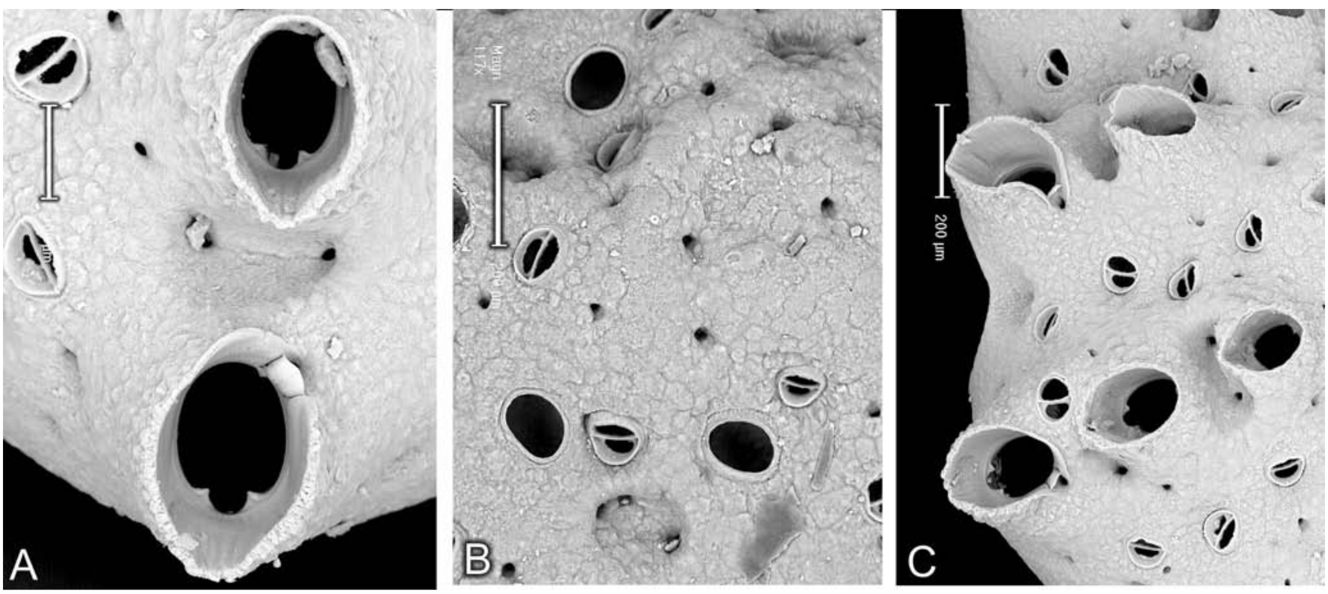

Figure 19. *Trochosodon asymmetricus* sp.nov. NMV F99011, paratype. A, detail of orifices and asymmetrically placed, tubular adapical pores, scale =100 µm. B, adapical region showing rounded root pores and avicularia, scale = 200 µm. C, detail of marginal peristomes, orifices, adapical pores, and avicularia,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

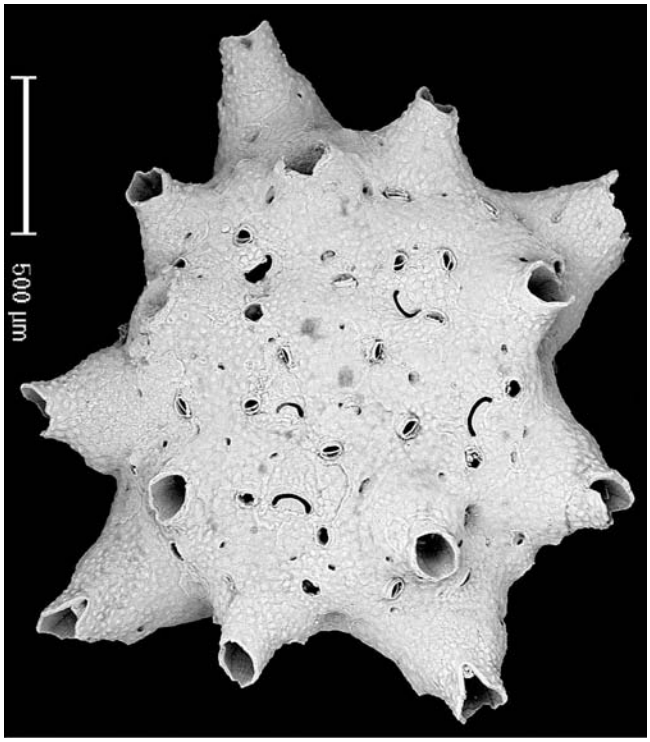

Figure 20. *Trochosodon diommatus* sp. nov. NMV F99012, holotype. adapical view of colony showing lunate root pores, scale = 500 µm.

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*

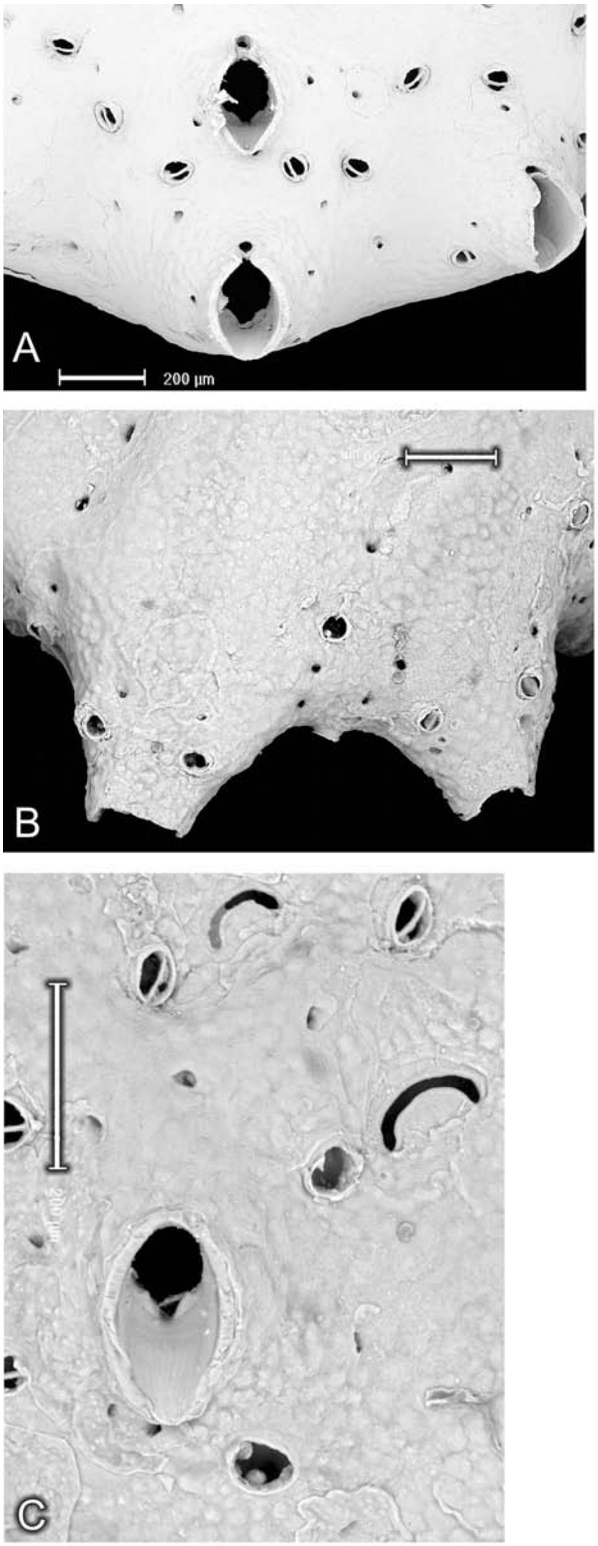

Figure 21. *Trochosodon diommatus* sp. nov. A. NMV F99012, holotype. Detail of orifices and adapical pores, scale = 200 µm. B, NMV F99013, paratype, antapical view of marginal peristomes, showing paired avicularia, scale =200 µm. C. NMV F99014, paratype, detail of peristome, orifice, and lunate root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

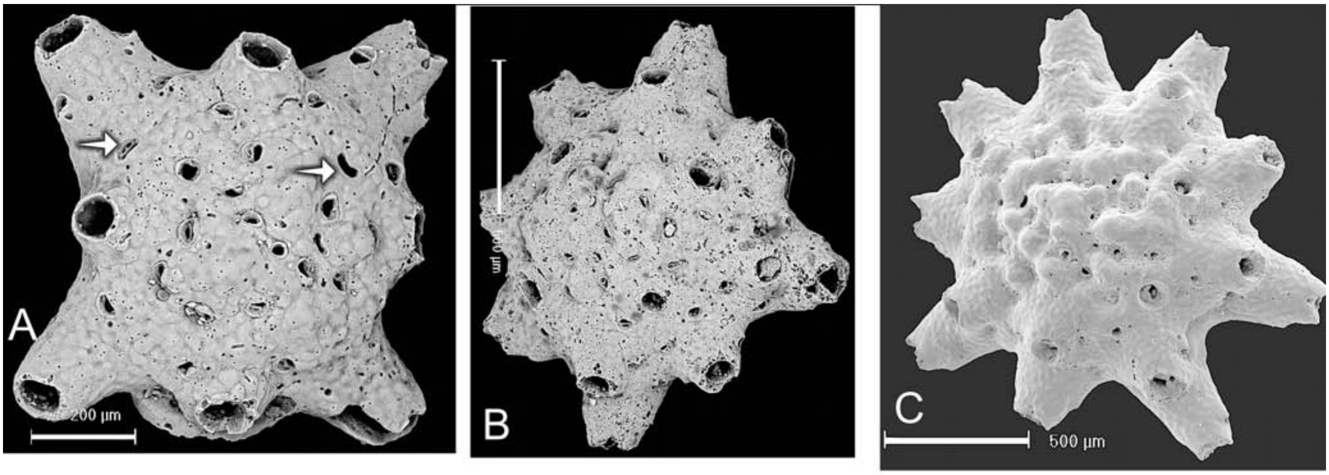

Figure 22. A–D *Trochosodon aster* sp. nov. A, NMV F99015, paratype, young colony showing alternating triad structure; root pores and avicularia arrowed, scale = 200 µm. B, NMV 99016, paratype, older colony, scale = 500µm. C, NMV P99017, paratype, colony showing adapical calcification, scale = 500 µm.

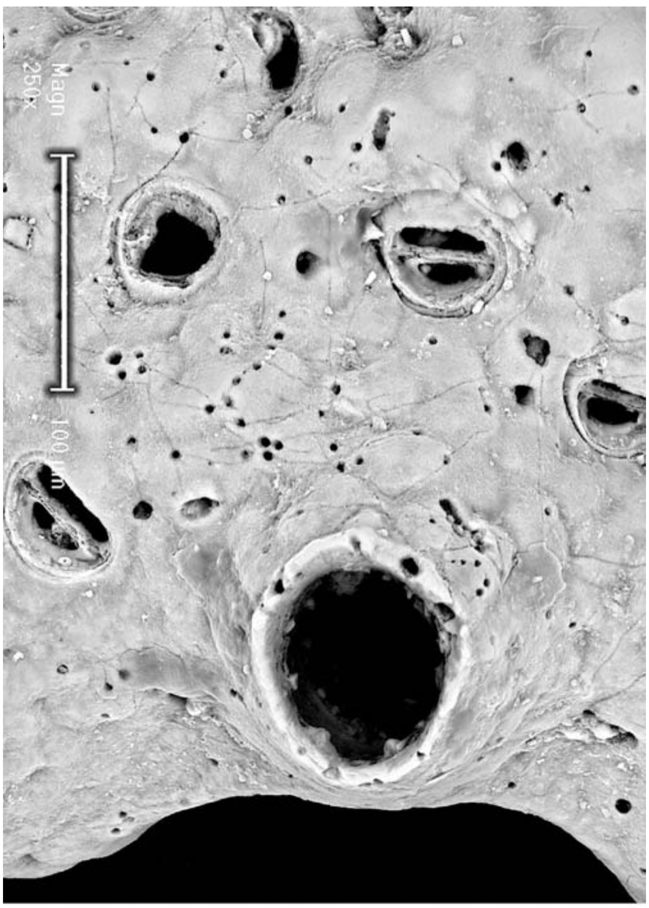

Figure 23. *Trochosodon aster* sp. nov. NMV F99015, paratype, Detail of orifice and avicularia, scale = 100 µm.

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.

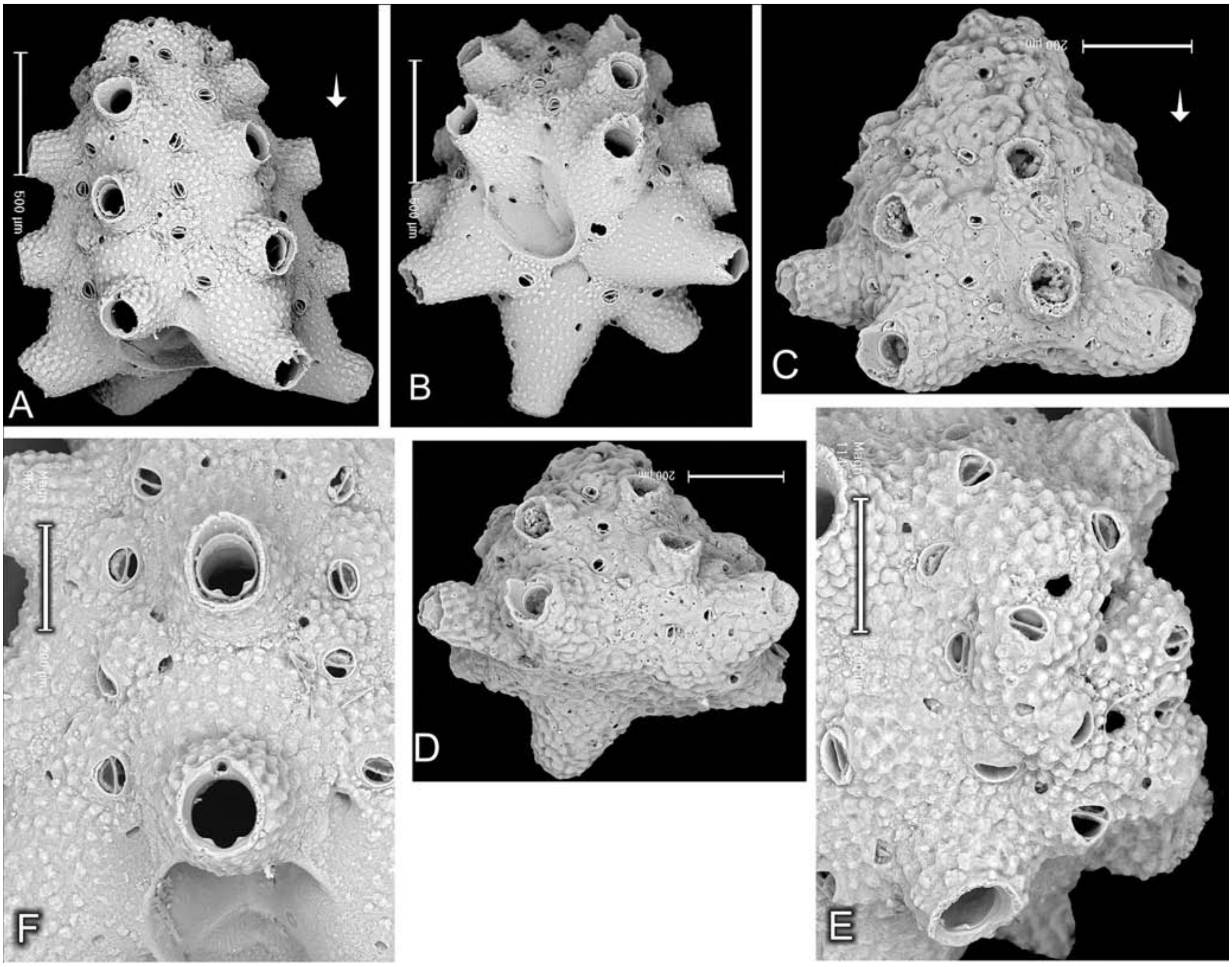

Figure 24. *Trochosodon anomalus* sp.nov. A–B, NMV F99018, holotype. A, lateral view of colony, direction of growth arrowed, scale = 500 _m. B, antapical view showing developing zooid, scale = 500 µm. C–D, BMNH 2003.11.27.2. C, lateral view of colony, growth direction arrowed, scale = 500 µm. D, antapical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

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. Ectooecium narrow, marginal; entooecium 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

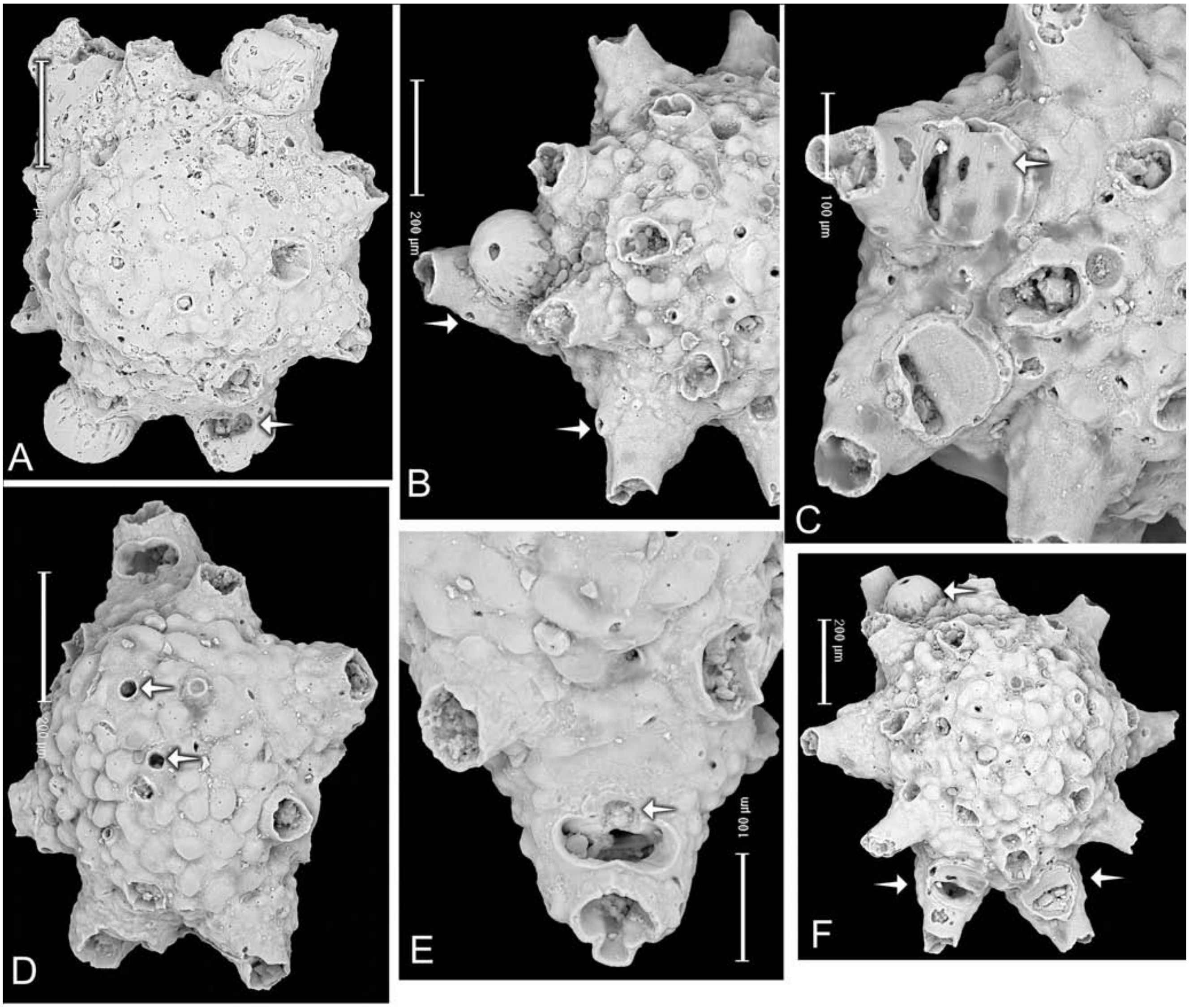

Figure 25. *T. praecox* sp. nov., Cape York. A, NMV F99020, paratype, detail of orifices and avicularia. with two complete ovicells and one peristomial foramen (arrowed), scale = 200 µm. B–C, NMV F99022, paratype, B, marginal zooids of colony with complete ovicell, avicularia arrowed, scale = 200 µm. C, detail of ovicells, showing ectooecial margin and central foramina of entooecium (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 entooecial 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 entooecium. 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 gordoni sp. nov.

Trochosodon multiarmatus.—Gordon, 1989: 83, p1. 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 spathulate. 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 astogenetic generations, the segments were 4 zooids wide. Lunate root pores were present but these were not associated with branch bifurcations and no large, spathulate 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 spathulate 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 spathulate. 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, spathulate avicularia placed in the axils between branches. Root pores reg-

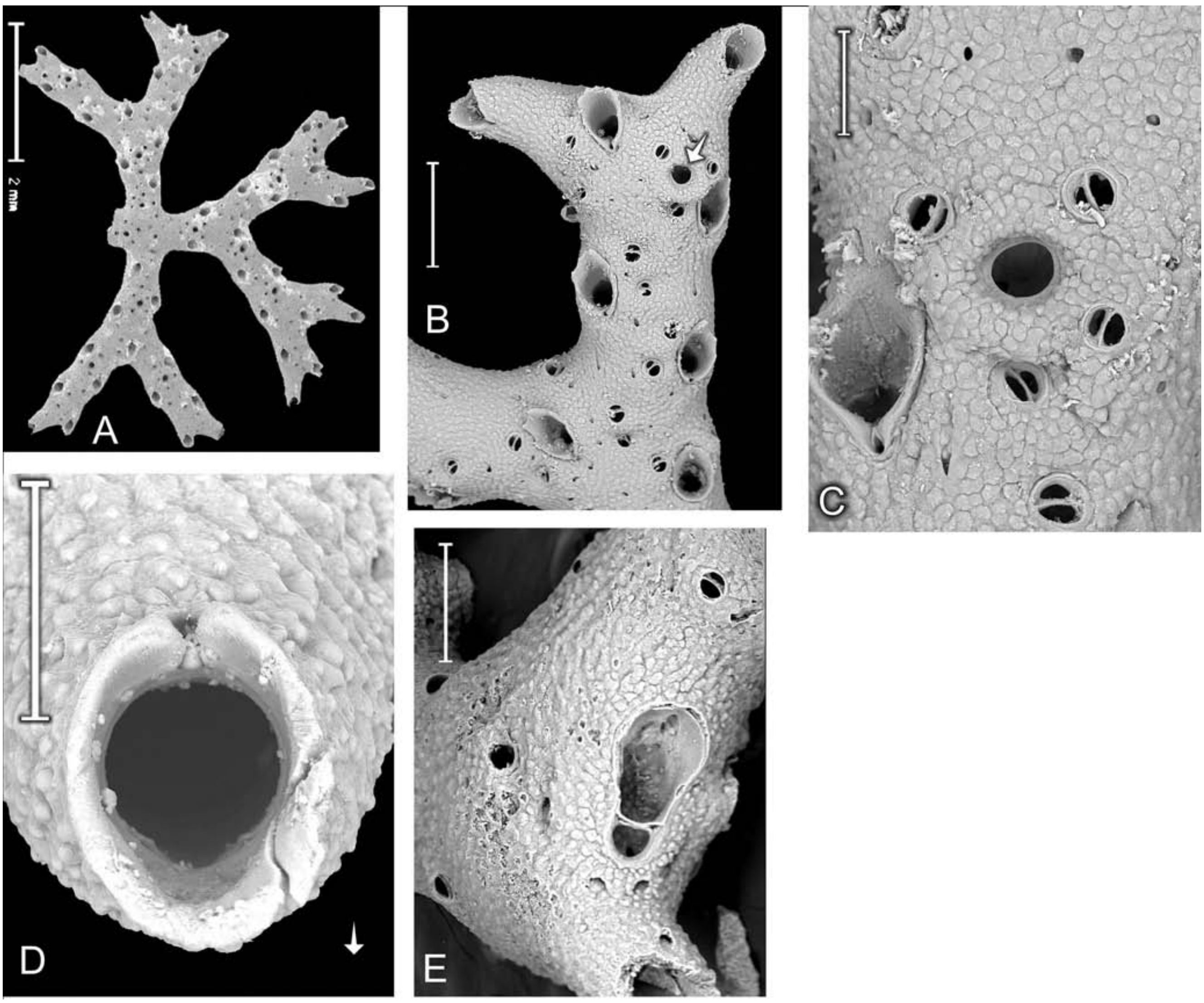

Figure 26. *Crucescharellina australis* sp.nov. A–D, NMV F99024, holotype. A, colony from adapical surface, scale = 2 mm. B, detail of branch showing orifices, avicularia and root pore (arrowed), scale = 500 µm. C, detail of root pore, scale = 200 µm. D, detail of orifice with adapical pore, direction 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, spathulate 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. decussi*s, 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 triserial 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. perculta* 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 extrazooidal 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 extrazooidal 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).

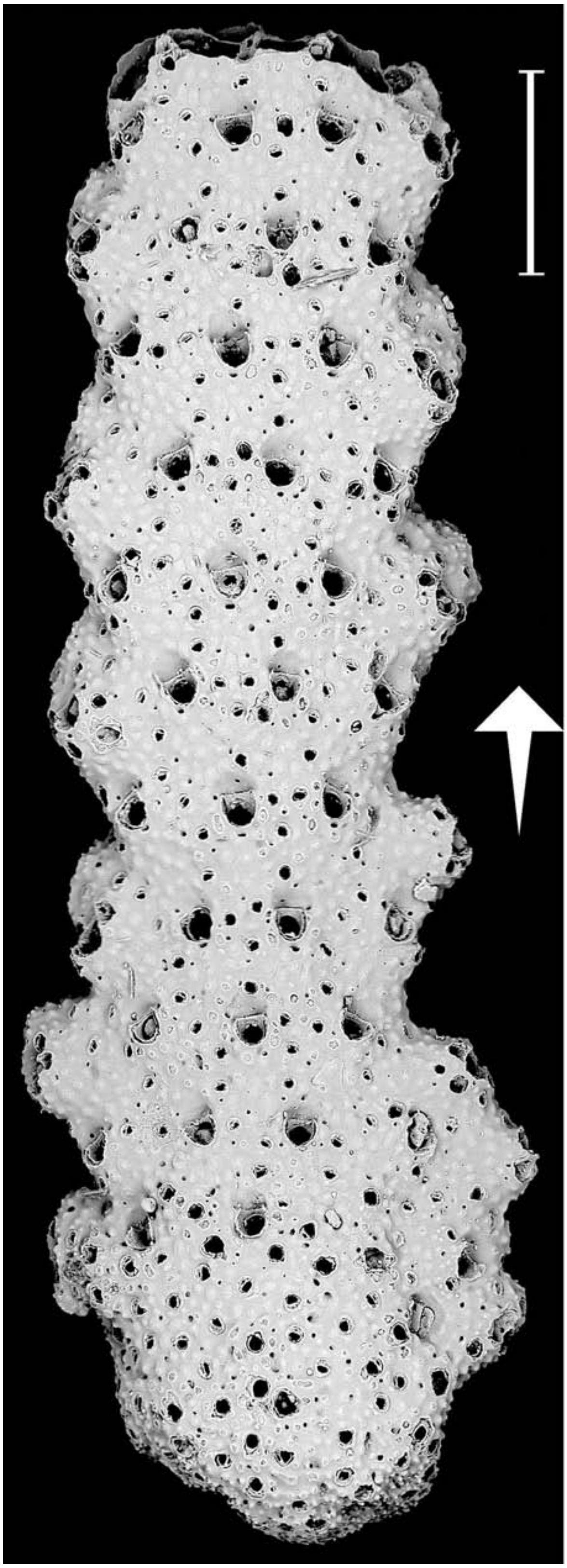

Figure 27. *Zeuglopora lanceolata* Maplestone, 1909. NMV F99026. Lateral view of colony, direction of growth arrowed, scale = 1 mm.

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 Ouantang 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 *Conescharellina* 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 *Conescharellina*, the generic characters of d'Orbigny's descriptions and illustrations are unmistakeable 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 *Conescharellina* 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 ectooecium) 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".

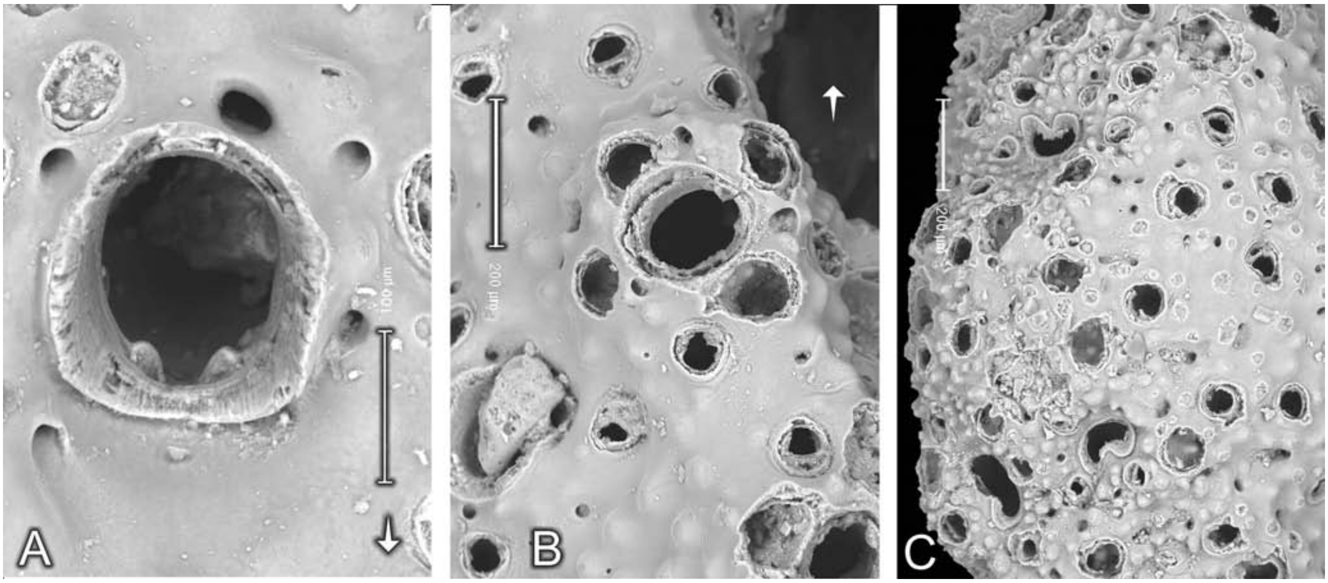

Figure 28. *Zeuglopora lanceolata* Maplestone, 1909. NMV F99026. A, detail of orifice with adapical pore, scale = 100 µm. B, detail of large, marginal zooid orifice with surrounding avicularia, direction of growth arrowed, scale = 200 µm. C. adapical region showing lunate root pores, scale =200 µm.

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).

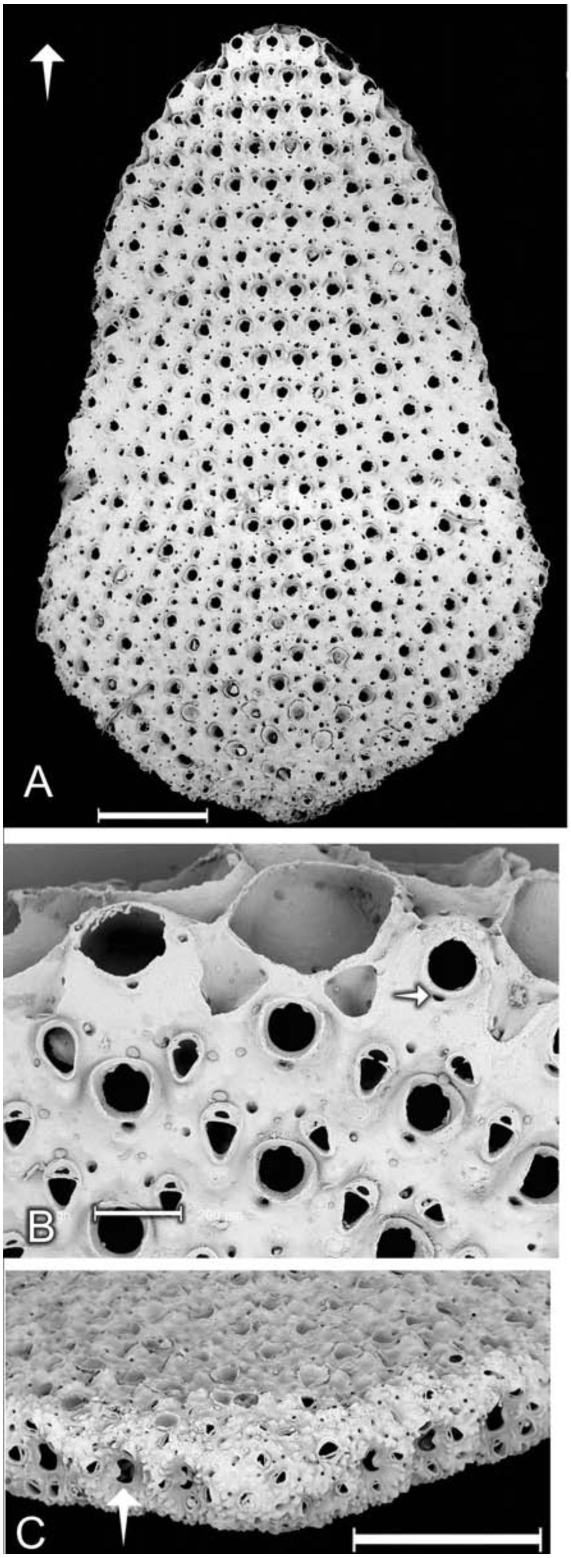

Figure 29. A–C, *Flabellopora umbonata* (Haswell, 1881). NMV F99395, stn GAB-056 . A. Colony, growth direction arrowed, scale = 1 mm. B. Antapical region showing orifices and avicularia, adapical pore arrowed, scale = 200 µm. C. Adapical region, root pore arrowed, scale = 1 mm.

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 perculta, 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 fom 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 *Crucescharellina*. 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 circlet 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.

Acknowledgements

Dr K. J. Tilbrook provided the initial impetus for this study by finding specimens of Maplestone species in the collections of the Natural History Museum, that were kindly lent by Mary Spencer Jones. Chris Rowley, Museum Victoria, has been helpful in facilitating access to that collection. Samples from Dampier were from collections made by Dr Gary Poore. Samples from the GAB series are provided through the activities of Dr Yvonne Bone (University of Adelaide) and the Master and crew of RV *Franklin*. The contribution of CSIRO is gratefully acknowledged.

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.*

Bretnall, 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., Buttler, 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. N*ew 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 Lacepede 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 and 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. S*cientific Proceedings of the Royal Dublin Society, new series* 6: 603–626.

Labracherie, M. 1975. Sur quelques bryozoaires de l'Eocene inferieur nord-aquitain. *Revista Española de Micropaleontología* 7: 127–164.

Labracherie, M., and Sigal, J. 1975. Les Bryozoaires cheilostomes des formations Eocene Inferieur du Site 246 (crosière 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).

Pizzaferri, C., and Braga, G. 2000. Nuove osservazioni sullo sviluppo astogenetico di *Batopora rosula* (Reuss), Bryozoa Cheilostomatida del Miocene del Pedeappennino 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. *Sitzungberichte 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 Helmberg-1). *Österreichische Akademie der Wissenschaften, Schriftenreihe der Erdwissenschäftlichen 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, diommatus*
SLOPE-7, off Nowra, NSW, 34°52.29'S, 151°15.02'E, 1096 m, *C. multiarmata, C. ecstasis, C. plana, T. asymmetricus, T. diommatus, 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, *Crucescharellina 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. diommatus*
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°52.77S, 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*

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°33S, 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 Mendeelev, 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*