

## A review of Australian *Siphonicytara* Busk (Bryozoa: Cheilostomatida)

Philip E. Bock<sup>1</sup> and Patricia L. Cook<sup>2</sup>

<sup>1</sup>Honorary Fellow, School of Ecology and Environment, Rusden Campus, Deakin University,  
Clayton 3168, Victoria, Australia

<sup>2</sup>Associate, Museum Victoria, Carlton 3053, Victoria, Australia

---

**Abstract** – Until recently, species of the deep-water ascophoran genus *Siphonicytara* have been recorded from only two areas, nearly 10,000 km apart. Three species were known from the East Indies and one from the southwest Indian Ocean. A hitherto unrecognized species is now known from the southern-most Philippine region, and six new species have recently been described from New Caledonia. A further new species from relatively shallow water, *S. occidentalis*, is described here from Western Australia. Examination of fossil specimens from the Tertiary of Victoria and South Australia has shown that specimens attributed to *Porina clypeata* Waters have a close relationship with *Siphonicytara*, and the species is referred here to this genus, as is *Mucronella airensis* Maplestone. Another Tertiary species with a similar distribution, '*Eschara elevata*' Waters not Tenison Woods, is assigned to *Siphonicytara irregularis* (Maplestone). The stratigraphic range for the family extends from the Late Eocene to Recent. *Eschara elevata* Tenison Woods *sensu stricto* is the type species of the genus *Tubitrabecularia* Bassler, and a discussion of the nature and status of this genus is included. A key to the species described is given.

### INTRODUCTION

The genus *Siphonicytara* was introduced by Busk (1884) for *S. serrulata*, a deep-water species from the Celebes Islands (Sulawesi) from a depth of 1508 m. Two other Recent forms, *S. formosa* (from western Irian, 469 m), and *S. cylindrica*, (also from the Celebes, 1901 m), were later described by Harmer (1957). A further species, *S. symetrica*, was introduced from very deep water from southeast of Madagascar in the Indian Ocean, from 4297 m depth, by David and Pouyet (1986). Recently Gordon and d'Hondt (1997) have described six new species from New Caledonia from a range of depths from 435 m to 1980 m. One of these species, *S. armata*, somewhat resembles another new form described here from Western Australia, *S. occidentalis*, which is not found from deep water. These colonies, like *S. formosa*, are anchored by rhizoids.

Gordon and d'Hondt (1997) noted, in passing, the similarities between *S. armata* and a species from the Sulu Archipelago in the southern Philippines region which was described by Canu and Bassler (1929: 154, plate 17, figure 4) as '*Thalamoporella* (?) *insolita*'. Their specimen consisted of one small cylindrical fragment from a depth of 619 m. Canu and Bassler (1929) were obviously very uncertain of the generic attribution of this species. They regarded the frontal shield as a cryptocyst with a distal opesia ('aperture'), and the raised septal

ridges as the mural rims of zooids. The species is obviously referable to *Siphonicytara*, but understandably, was overlooked by Harmer (1957) in his discussion of the genus. *Siphonicytara insolita* is very similar to the Tertiary Australian species *S. clypeata*, described below, but has more robust branches and rounded avicularia.

Study of the numerous Tertiary specimens from Victoria and South Australia has shown that *Siphonicytara cylindrica* Harmer also has some similarities with *S. clypeata* (Waters). The genus is now known to have two further Tertiary Australian representatives, *S. irregularis* (Maplestone) and *S. airensis* (Maplestone). The increase in the number of known species belonging to *Siphonicytara* has necessitated a review of its characters and systematic affinities.

The systematic importance of the ascopore (which passes through the frontal shield calcification and opens into a sealed chamber with one flexible wall – the ascus), as opposed to the spiramen (which passes through peristomial calcification into an open space external to the operculum), has been discussed by Harmer (1957) and Cook (1973). The structure of some ascophorans in which the 'outer' calcified walls (interior walls) were almost all separated from the environment by coelomic tissue bounded by external cuticle, has been discussed by Cook and Chimonides (1981). Some of the species belonging to the family Didymosellidae which they

described (particularly those of the genus *Tubiporella* Levinsen), showed ontogenetic changes which resulted in the peristomial spiramen appearing to open in the centre of the zooid frontal shield. Similar changes occur in the family Adeonidae (Cook, 1973). *Siphonicytara* is of interest because, although it possesses a true ascopore, which often opens very closely to the proximal edge of the primary orifice, the ontogenetic changes involving elongation of the peristome, and the thickening of the calcification of the frontal shield, result in the ascopore appearing to open externally, in the centre, or even at the proximal end of the exposed frontal shield. In addition, as the external calcified walls of *Siphonicytara* are all interior walls, the family Siphonicytaridae provides an interesting analogue with *Tubiporella* and the Didymosellidae in general.

Astogenetic and ontogenetic changes of great complexity occur in some species of *Siphonicytara*. Of the Tertiary species, only one has been redescribed since its introduction during the last 90 years. The majority of these species has never been investigated nor illustrated by scanning electron microscopy. The figures given here therefore trace some of the astogenetic and ontogenetic changes in some detail.

This study is based on the descriptions of type material in the collections of the Museum national d'Histoire naturelle, Paris (MNHN), the Natural History Museum, London (NHM), and the Naturhistorisk Rijksmuseum, Amsterdam (NRA). Specimens from the collections of the Museum of Victoria, Melbourne (MOV), the Queensland Museum, Brisbane (QM), and the Western Australian Museum, Perth (WAM), have been examined and are illustrated here.

## SYSTEMATICS

### Siphonicytaridae Harmer

Siphonicytaridae Harmer, 1957: 892.

#### Diagnosis

Erect cylindrical to flattened branching colonies, with lepralioid frontal wall development. Zooids with extensive frontal calcification, often divided into compartments by septal ridges. Ascopore located centrally within a septal ridge, distant from the secondary orifice. Avicularia adventitious, arising from marginal septular pores. Brooding unknown.

#### Stratigraphic Range

Late Eocene to Recent.

#### Remarks

*Siphonicytara* was assigned to the family

Siphonicytaridae by Harmer (1957); it had previously been referred to the Tubucellariidae by both Busk (1884) and Bassler (1953). The Tubucellariidae includes forms with elongated peristomes, an ascopore and peristomial ovicells, but the colony form is nodal, and neither septal ridges nor avicularia are present. The complex astogenetic and ontogenetic changes typical of *Siphonicytara* do not occur. Cheetham (1972) assigned *S. clypeata* to *Tubitrabecularia*, and placed the genus in the Siphonicytaridae.

#### Key to some species of *Siphonicytara*

1. Some or all peristomial orifices asymmetrical, deflected to one side of the branch surface ....  
..... 2  
Peristomial orifices symmetrical, all facing outward ..... 3
2. Autozooids in whorls of 2; laterally facing zooid with basal ascopore and single basal peristomial avicularium ..... *S. serrulata*  
Autozooids in whorls of 3 or more; avicularia lateral, on basal peristomes only .... *S. formosa*
3. Branches cylindrical; avicularia peristomial .... 4  
Branches slightly flattened to distinctly bilaminar; avicularia peristomial or sutural ...  
..... 7
4. Branches 2- to 4- serial, but no larger, even late in astogeny ..... 5  
Branches rapidly becoming more than 4- serial early in astogeny ..... 6
5. Branches 2-serial. Avicularia rare, single, distolateral, large, with paired condyles. Septal ridges simple, transverse ..... *S. symmetrica*  
Branches 2- to 4-serial. Avicularia paired, distolateral, large, directed medially, with serrated bar. Ascopore in shield-shaped area marked by septal ridges ..... *S. clypeata*
6. Avicularia proximolateral, paired, directed medially .....  
..... *S. irregularis* (early astogenetic stages)  
Avicularia distal, single, directed proximolaterally ..... *S. cylindrica*
7. Avicularia rare, scattered, sutural only .....  
..... *S. occidentalis*  
Avicularia paired, regularly present ..... 8
8. Avicularia peristomial, proximo-lateral, directed medially. Septal ridges profusely developed .....  
..... *S. irregularis* (later astogenetic stages)  
Avicularia sutural, lateral. Septal ridges deficient ..... *S. airensis*

*Siphonicytara* Busk

*Siphonicytara* Busk, 1884: 101, 168.

*Tubitrabecularia* Bassler, 1934: 408 (*sensu lato*, see below).

**Type Species**

*Siphonicytara serrulata* Busk, 1884.

**Diagnosis**

As for the family.

**Description**

Colonies erect, known to be attached by rhizoids in some species. Branches unsegmented, cylindrical or somewhat flattened in cross section. Autozooids arranged in horizontal whorls of alternating longitudinal series; orifices either regularly distributed round the branch and symmetrical, facing outward, or deflected to one face of the branch, asymmetrical. In some species the resulting frontal and basal faces of the branch have zooids of different morphologies. Primary calcified orifices D-shaped or oval, not well defined. Peristomes long, prominent or immersed in calcification, secondary orifices round. Frontal shields lepralioid (cryptocystidean), imperforate centrally, with large marginal septular pores which may develop into areolae of wide extent and great complexity later in ontogeny. Ascopore present, opening in the interior close to the proximal edge of the primary orifice, but, at the exterior, appearing to open at the centre, or even at the proximal end of the exposed frontal shield. Raised calcified septal ridges variously extensive and prominent, sometimes extending round the secondary orifice, from the proximal side of the peristome to the ascopore and beyond, surrounding the ascopore, and from the ascopore to the lateral margins of the frontal shield. Ontogenetic changes considerable, with thickening of frontal calcification, or with calcification of septal ridges extending into the hypostegal coelom and producing a honeycomb-like appearance, with areolae anastomosing and dividing. Primary avicularia present early in ontogeny, arising from lateral frontal septular pores, often placed near the peristome, occasionally lateral and frontal. Subsequent avicularia often sutural, arising late in ontogeny at the margins of the zooids, variously orientated. Mandibles rounded or triangular, hinged on paired condyles or a complete bar, which usually has a protuberance (ligula) on its palatal side, or may be serrated, with several prominences. Ovicells not seen here or described in any species, assumed to be peristomial and immersed. Rhizoids arising from marginal frontal septular pores late in ontogeny in some species.

**Remarks**

The effects of ontogenetic thickening of the

calcification in most species is marked. In some, the early and late states may have virtually no recognisable feature in common. This is particularly the case in *S. irregularis*, where the septal ridges become irregularly convoluted and anastomose, obscuring the outline of the underlying zooid frontals. In addition, the occurrence of large sutural avicularia in this species makes it difficult to trace the position of the ascopores. The raised septal ridges in Recent species were investigated by Harmer (1957), who illustrated and described the astogenetic and ontogenetic changes at the growing tips of the branches. The septal ridges include cuticular traces, and these appear to be derived from the insertion of the frontal cuticle as the septal ridges grow into the extrazoidal coelom and deepen with ontogenetic thickening. In all species other than *S. irregularis* and *S. occidentalis*, the relationship of the septal ridges with secondary orifices and ascopores remains visible, even in late ontogenetic stages. The septal ridges do not all mark the boundaries of zooid frontals, but often resemble the lozenge-shaped areas of the anascan Cellariidae (see Harmer, 1926: 335).

*Siphonicytara serrulata* Busk

*Siphonicytara serrulata* Busk, 1884: 101, plate 15, figures 2, 2b; Canu and Bassler, 1920: 549, figure 162; Harmer, 1957: 893, plate 61, figure 10.

**Type Material***Lectotype*

NHM 1897.12.9.446 [figured by Busk (1884)], Challenger Stn 196, approx. 0°48'S, 126°58'E, east of Celebes, 1508 m (825 fathoms).

*Paralectotype*

NHM 1897.12.9.447, collecting data as above, transverse section, see Harmer (1957).

**Description**

Branches slightly flattened, with alternating whorls of two zooids, one with peristome facing laterally and slightly frontally, the other with the peristome symmetrical and facing frontally. Ascopore of frontally facing zooid is frontal, placed in a distinct area outlined by septal ridges. Ascopore of laterally facing zooid is basal, also placed within an area. Avicularia small, rounded, confined to a single one on the basal side of the peristome of each laterally facing autozooid. Rhizoids arising from above a frontal septular pore of a laterally facing zooid, on the basal side.

**Remarks**

Harmer (1957) redescribed *S. serrulata*, and was the first to note the presence of small avicularia on

the peristome of the laterally facing autozooids. The septal ridges are not very prominent, and outline only the area surrounding the ascopore.

#### Distribution

Celebes (Sulawesi), 1508 m.

#### *Siphonicytara formosa* Harmer

*Siphonicytara formosa* Harmer, 1957: 893, plate 61, figures 1-5, 7.

#### Type Material

##### Lectotype

NRA Siboga Stn 156, approx 0°29.2'S, 130°5.3'E, west of Waigeu Id, Northwest New Guinea (Irian), 469 m.

##### Paralectotype

NHM 1986.1.12.1, collection data as above.

#### Description

Branches slightly flattened, autozooids in alternating whorls of three and four, four and four, or four and five zooids, widest just before a bifurcation. Alternating frontal and latero-frontal zooids respectively with nearly symmetrical or frontally deflected peristomes; ascopores slightly raised, flanked by paired frontal septular pores, avicularia absent. Latero-basal zooids with long, free peristomes directed towards frontal surface; ascopores basal, raised, with a lip, and flanked by paired frontal septular pores. Avicularia peristomial, lateral and basal, variously orientated. Central basal longitudinal series of zooids with very long peristomes deflected alternately to one or the other side, ascopores raised, with a lip; avicularia very large, lateral and peristomial, but subrostral chambers encroaching on frontal shield, surrounded by septular pores. Avicularian mandibles subtriangular to rounded, bar stout, curved, but without ligula. Rhizoids arising on basal surface, from one of the frontal septular pores surrounding an avicularian chamber, sometimes paired, passing downward and becoming apposed to form a supporting stalk.

#### Remarks

According to Harmer (1957), the colony originates as a narrow branch of alternating, uniserial autozooids, supported by rhizoids. Most branches are quadriserial, but in those with alternating series of 3 and 4 autozooids, the basal surface is partially composed only of the frontal surfaces of the latero-basal pair of zooids, without an intervening basal zooid. Septal ridges are prominent early in ontogeny, but become less noticeable as the frontal calcification thickens.

#### Distribution

New Guinea (Irian), 469 m.

#### *Siphonicytara cylindrica* Harmer

*Siphonicytara cylindrica* Harmer, 1957: 895, plate 61, figures 6, 8, 9, 11, 12.

#### Type Material

##### Lectotype

NRA Siboga Stn. 119, approx. 1°33.5'N, 124°41'E, north Celebes (Sulawesi), 1901 m.

##### Paralectotype

NHM 1986.1.12.2, collecting data as above.

#### Description

Branches stout, with orifices regularly distributed in whorls of 4 and 5 autozooids. Free peristomes short, symmetrical, ascopores with tubular orifice flanked by paired frontal septular pores. Avicularia large, arising from a septular pore distal to the peristome; subrostral chamber surrounded by septal ridges at first, with frontal septular pores; mandible subtriangular to rounded; bar with a small ligula. Small rounded sutural avicularia developed late in ontogeny, becoming numerous.

#### Remarks

*Siphonicytara cylindrica* differs from *S. chypeata* in its more robust size, and in the occurrence of only one peristomial avicularium on the distal side of the orifice. It differs from *S. occidentalis* in the cylindrical form of the branches, and the large number of sutural avicularia developed late in ontogeny, and from *S. symetrica* in its much thicker branches and numerous avicularia with ligulate bar. Harmer did not find any rhizoids; it is possible that they occur on all sides of the branch, as in *S. occidentalis* (see p. 317). The septal ridges are prominent early in ontogeny, surrounding both the ascopore area and the avicularian subrostral chamber.

#### Distribution

Celebes (Sulawesi), 1901 m.

#### *Siphonicytara symetrica* David and Pouyet

*Siphonicytara symetrica* David and Pouyet, 1986: 160, plate 3, figures 1-4.

#### Type material

##### Holotype

MNHNP, Safari Stn. I, 88 (CP04), approx. 30°S, 50°E, southeast of Madagascar, 4297 m.

**Description**

Branches cylindrical, autozooids in alternating whorls of two zooids, rising to three before a bifurcation. Free peristomes slightly raised, circular; ascopores with a raised rim; four to seven lateral marginal septular pores, enlarged to form areolae. One undulating septal ridge passing horizontally across the distal end of each zooid, and another passing between the ascopore and the orifice. Avicularia rare, lateral and oral, large, with a swollen subrostral chamber and paired condyles. Peristome next to avicularium deflected to one side.

**Remarks**

*Siphonicytara symetrica* resembles *S. cylindrica* in the regularity of zooid orientation and its oral avicularium, but differs in the rarity of avicularia and in their paired condyles. The occurrence of *S. symetrica* provides yet another example of links between the Recent deeper-water fauna of southeast Africa, and that of the Australasian Tertiary (Hayward and Cook, 1983: 147), and underlines the antiquity of this link.

**Distribution**

Off southeast Madagascar, 4297 m.

***Siphonicytara irregularis* (Maplestone)**

Figures 1A–E, 2A–D

?non *Eschara elevata* Tenison Woods, 1876: 148, figure 10.

*Microporella elevata*: Waters, 1881: 330, plate 17, figures 63,64, plate 18, figure 90; Waters, 1882b: 503, 508 (listed); Waters, 1883: 427, 436 (listed); Waters, 1885: 296, plate 7, figures 6,9.

*Tessaradoma elevata*: MacGillivray, 1895: 66, plate 9, figure 20 (as figure 28 on p. 66).

*Mucronella irregularis* Maplestone, 1902: 21, plate 2, figure 11.

*Tubitrabecularia proditor* Canu and Bassler, 1935:18, plate 4, figure 10.

*Tubitrabecularia elevata*: Brown, 1958:75.

**Material Examined**

*Holotype* of *Mucronella irregularis*

MOV P10200, Mitchell River, near Bairnsdale, Victoria (Miocene), Maplestone Collection.

**Other material**

MOV P27667 locality unknown (MacGillivray); MOV P73195, Allot.1, Parish of Glenaulin (Brown) and see below.

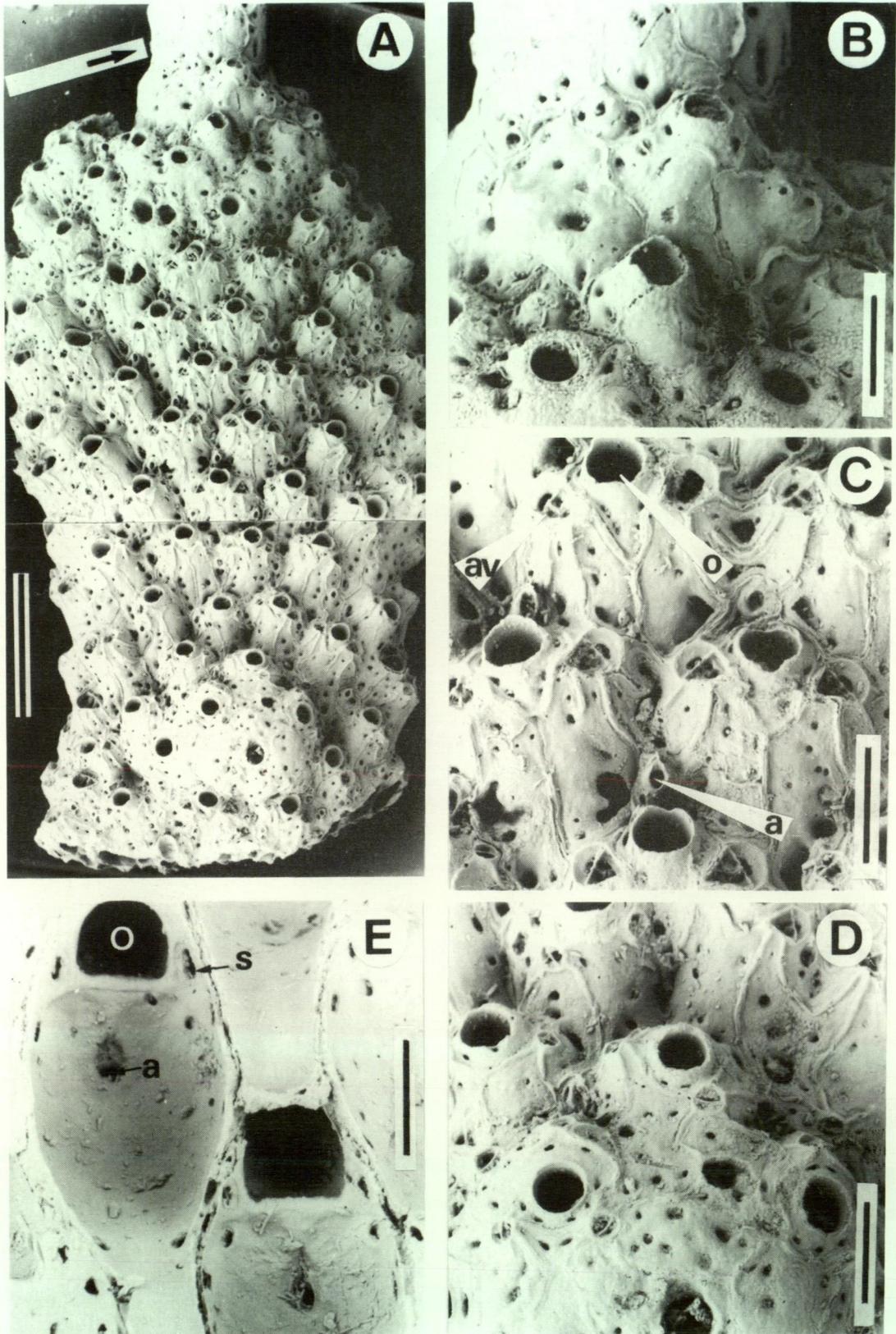
**Description**

Branches cylindrical early in astogeny, becoming wide, flattened, sometimes irregular, thickened, with up to 20 autozooids in a horizontal whorl. Primary orifice D-shaped, ascopore near proximal edge. Free peristomes short, symmetrical, ascopores slightly raised, often flanked by paired frontal septular pores, which become enlarged as areolae. Septal ridges very prominent, becoming irregular with ontogeny, finally obscured by increasing calcification. Primary peristomial avicularia usually paired, arising from lateral septular pores, proximolateral to peristome, orientated medially. Mandible rounded, subtriangular or sometimes enlarged, elongated. Sutural avicularia numerous, often large, bar with a prominent ligula.

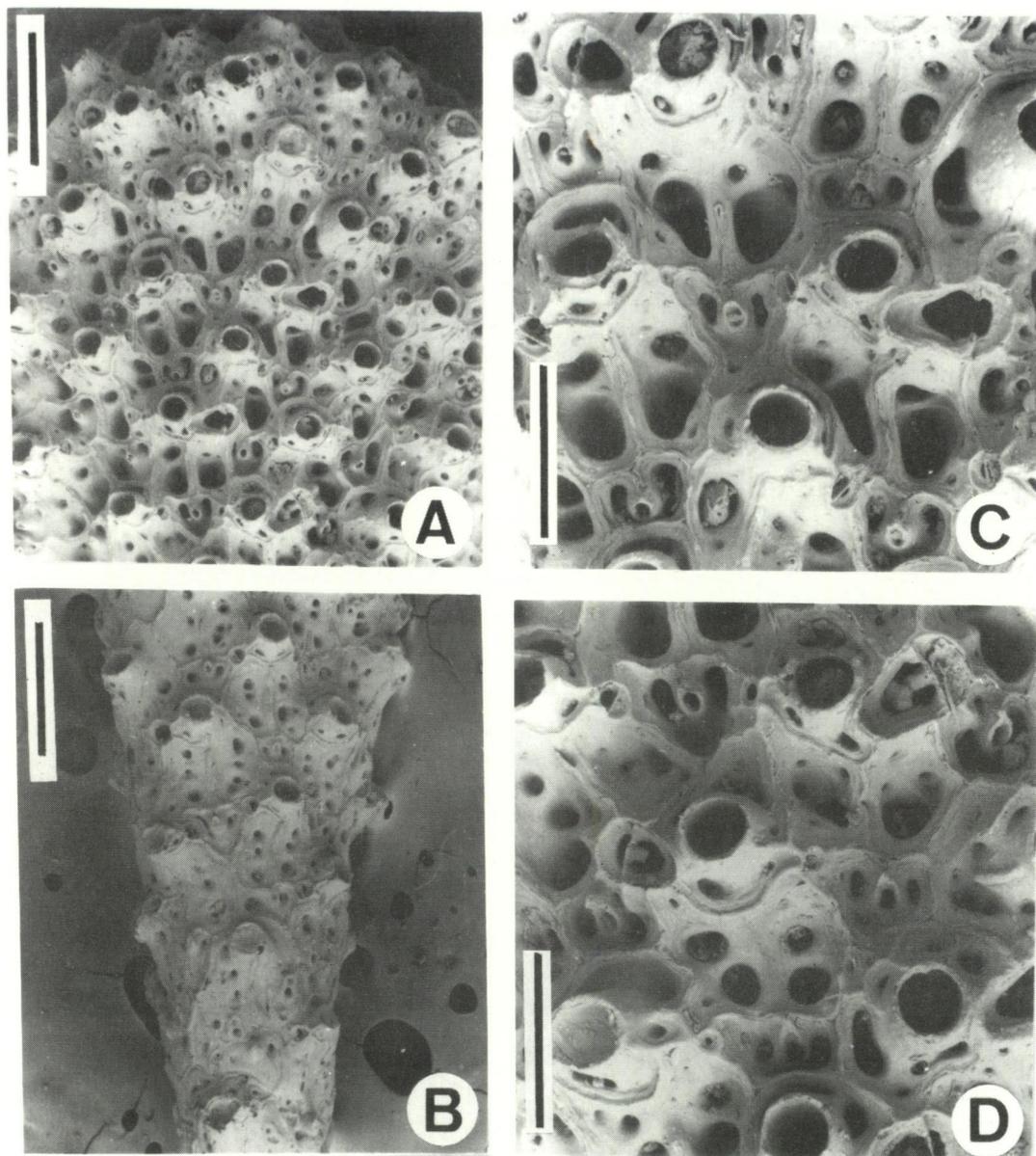
**Remarks**

'*Eschara elevata*' Tenison Woods is not readily recognisable in the absence of type material. The original description does not mention any ascopore or avicularia, and the complete absence of any septal ridges in the figure make it unlikely that the species represented belongs to *Siphonicytara*. The genus *Tubitrabecularia* was introduced by Bassler (1934: 408) for Tenison Woods's *Eschara elevata*. Bassler's diagnosis noted 'The peristomie is strengthened by a trabecular network supporting a more or less thickened epicalcification ... exterior aspect of the zooecia irregular and quite different from the true zooecial form observed in the interior. Ascopore visible with difficulty at the exterior but clearly seen in the interior.' Bassler also mentioned a peristomial ovicell but gave no illustration. The characters ascribed to *Tubitrabecularia* were not those of Tenison Woods's species, but of *Microporella elevata* of Waters (1881, 1885) and *Tessaradoma elevata* MacGillivray (1895). In fact, MacGillivray stated (1895: 67) that he could not 'see any reason for identifying' his material with Tenison-Woods's species, and therefore quoted 'Waters as the authority for the name'. Whatever MacGillivray and Waters may have considered the characters of their species to have been, only '*E. elevata* Tenison Woods' can be the type species of the genus *Tubitrabecularia*, and the other material recognised by this name in the literature requires a new name. *Tubitrabecularia* was ascribed to a non-existent work, namely 'Canu and Bassler, 1934' in Canu and Bassler, 1935 (see also Cheetham, 1972).

Waters (1881, 1885) gave full descriptions of the material he assigned to *M. elevata*, noting particularly the dramatic changes in appearance of colonies at different ontogenetic stages, and illustrating some of them. He also described and illustrated the relationship of the primary orifice to the ascopore and peristome, together with the development of the septal ridges and the areolar spaces between them. MacGillivray (1895) also



**Figure 1** *Siphonicytara irregularis* (Maplestone, 1902), Balcombe Bay, Miocene. (A) Collage of flabelliform branch developed by frontal budding from cylindrical early astogenetic stage (arrowed): Scale=1.0 mm. (B) Distal end of colony showing frontally budded zooids: Scale=0.25 mm. (C) Zooids from central region showing septal ridges becoming obscured by thickening calcification of frontal shield. Note relative positions of secondary orifice (*o*) and its proximal ascopore (*a*), and oral avicularium with ligula (*av*): Scale=0.25 mm. (D) Zooids from proximal region showing development of a mound: Scale=0.25 mm. (E) Interior of frontal shield showing primary orifice (*o*) and ascopore (*a*). Note opening of oral frontal septular pores (*s*) leading to avicularian subrostral chamber: Scale=0.20 mm.



**Figure 2** *Siphonicytara irregularis* (Maplestone, 1902), Balcombe Bay, Miocene. (A) Zooids of the last 6 astogenetic generations of a flabelliform, bilaminar colony, showing small marginal areolae becoming obscured by development of septal ridges and secondary areolar spaces: Scale=1.0 mm. (B) Cylindrical proximal end of the same colony (Compare *S. clypeata*, Figure 3A), Showing earlier astogenetic and ontogenetic states: Scale=1.0 mm. (C) Zooids enlarged from A, showing secondary areolar spaces and large avicularia: Scale=0.50 mm. (D) As above, later ontogenetic stage: Scale=0.50 mm.

described and illustrated the septal ridges and the internal relationships of the ascopore and primary orifice. The attribution of *S. irregularis* to *Tessaradoma* (as *T. elevata*) by MacGillivray was based on the occurrence of an ascopore ('trypa'), and *T. elevata* was included in the genus with *T. magnirostris* (MacGillivray). In his discussion of *Tessaradoma*, Cheetham (1972: E6) implied that all the fossil species assigned to this genus by MacGillivray in 1895 belonged instead to the genus *Tubiporella* Levinsen. It is true that *T. magnirostris* is referable to *Tubiporella* (see Cook and Chimonides, 1981, for discussion), but the second species which MacGillivray described, *T. elevata*, is definitely

assignable to *Siphonicytara irregularis*. This in no way alters Cheetham's later statement that the genus *Tessaradoma* does not occur in Australia (see also Lagaij and Cook, 1973).

Maplestone (1902) described his single specimen of *Mucronella irregularis* as encrusting, and noted that the zooids had a small proximal mucro on the edge of the peristome, with a pore below it. In spite of these characteristics, which do not seem typical of *Siphonicytara*, his description of the surface ridges, which he noted 'do not appear to indicate the margins of the zooecia', and his figure, suggest that his material belongs to the genus. Our examination of the type specimen (MOV P10200)

confirms this. It is probable that the small pore mentioned by Maplestone (1902) was not the ascopore, which he did not recognise, but one of the irregular areolar spaces left between the circum-oral septal ridges and the peristome in a highly calcified, and somewhat worn, specimen.

Canu and Bassler (1935) introduced *Tubitrabecularia proditor* for specimens from the Victorian Miocene which had wide, flattened branches. Neither the description nor the retouched photograph gives any detail of peristomial avicularia, but an ascopore is present. 'Trabeculae' were mentioned in the description: these are the equivalent of septal ridges. Cheetham (1972) assigned *T. proditor* to *Tubitrabecularia clypeata*. His Eocene material may have included more than one species (see p. 315).

As *M. elevata*, *S. irregularis* has been recorded from Mount Gambier, Curdies Creek, Bairnsdale, Muddy Creek, Spring Creek, River-Murray Cliffs, and, as *Tessaradoma elevata*, from Schnapper Point (presumably Balcombe Bay).

The astogenetic and ontogenetic changes occurring in *S. irregularis* are more marked than in any other species of *Siphonicytara*. The early astogenetic changes are rarely preserved; they consist of portions of cylindrical branches with two to eight zooids per whorl, similar to those of *S. clypeata* in general appearance. They differ in being more robust, in having much more prominent septal ridges, and in the more proximal position of the lateral peristomial avicularia. In some colonies, intercalary series of autozooids are rapidly introduced, and within seven generations, a biserial branch has become a bilaminar lobe with eight to ten autozooids in each horizontal whorl (Figures 2 A, B). In other colonies, a similar, quadriserial cylindrical branch is transformed in an entirely different manner. The first change is ontogenetic, with considerable deepening of the septal ridges, and increasing irregularity of the areolar spaces. Subsequent increase of frontal calcification obscures the septal ridges and is followed by an astogenetic change which results in the covering of the primary cylindrical branch by a flattened branch with many more zooids per whorl. This change may be the result of overgrowth by distal budding from a focus of frontally budded zooids at the base of the branch (Figure 1A). This would be similar to mamilliform growth in many encrusting cheilostomes. Alternatively, there may be a series of distally directed episodes of frontal budding from the zooids of the cylindrical part of the branch. In fact, a combination of these processes probably occurs. The large, bilaminar expanses (which may attain 8 x 10 mm in size) may show further thickening of calcification, or deepening of the septal ridges, with production of large sutural avicularia, which are irregularly orientated, all over the surface of the

colony. The final stage consists of the development of clusters of autozooids on the surface of a branch, which becomes greatly thickened, forming mound-like areas of calcification (Figure 1D). The thickening eventually obscures orifices, ascopores and most areolae. In fragmented assemblages, these mounds are less easily fractured than surrounding areas of a branch, and may be preserved in isolation. The mounds are at first extremely difficult to recognize as more than worn bryozoan fragments, and are completely different from the earlier astogenetic and ontogenetic stages of *S. irregularis*. It is possible that some of these mound-like clusters of zooids may be derived from frontal extensions of existing zooids, rather than from interzooidal frontal buds (see *S. occidentalis*, p. 318). Canu and Bassler (1935) suggested that these were ovicelled zooids, but there is no positive evidence of this (see also Cheetham, 1972).

Generally, the range of variation exhibited in specimens from any one locality is very wide. Among the large numbers of colony fragments from Balcombe Bay, a significant proportion have autozooids with one, very large, elongated avicularium, rather than a pair of smaller peristomial avicularia. Well preserved, quadriserial branches from Browns Creek rarely exhibit long peristomes, some with a large avicularium placed on one side.

#### Distribution

Bairnsdale; Balcombe Bay; Batesford; Bird Rock; Browns Creek; Cape Otway; Grices Creek; Mount Gambier; Mount Schanck; Muddy Creek; Narrawaturk Bore 2; Princetown (Also reported from River Murray Cliffs, Curdies Creek, Spring Creek).

#### *Siphonicytara clypeata* (Waters)

Figures 3A-C

*Porina clypeata* Waters, 1881: 332, plate 17, figure 67; Waters, 1882a: 268; Maplestone, 1904: 213 (listed).

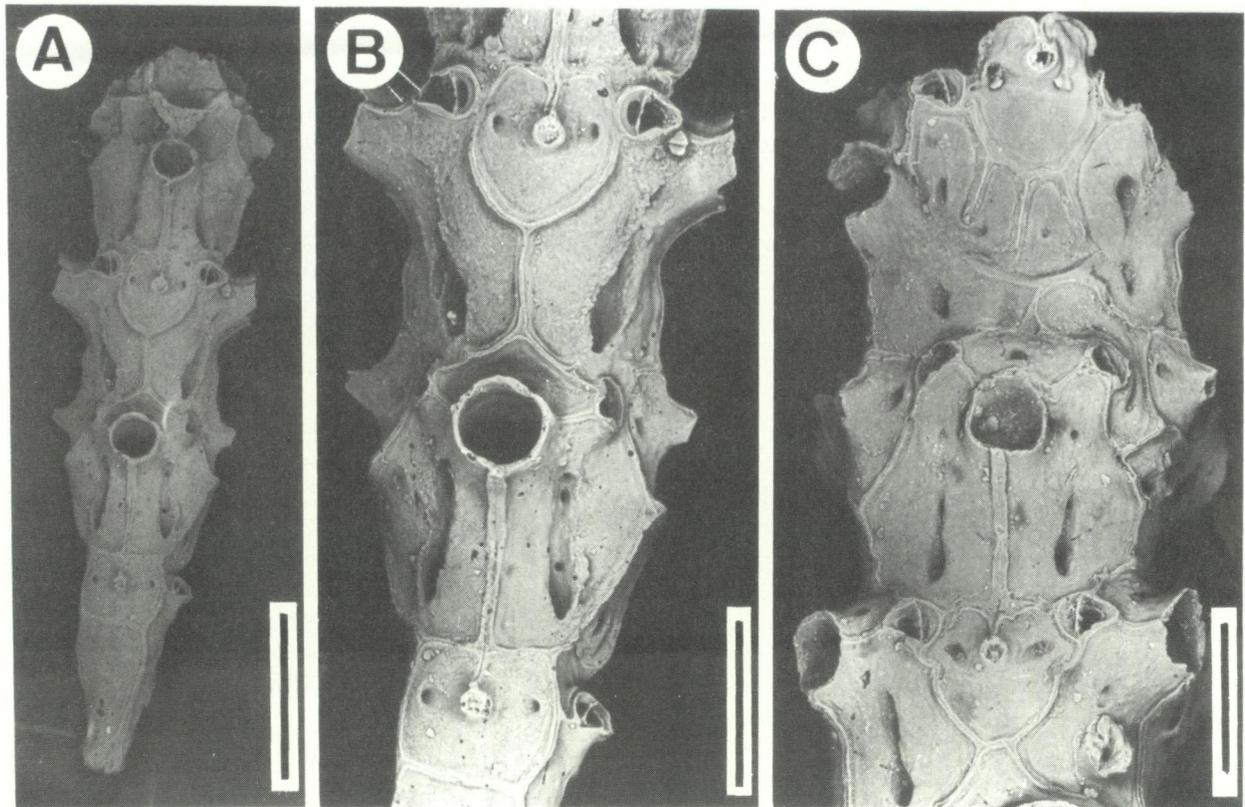
*Tubitrabecularia clypeata* (part): Cheetham, 1972: E17, plate 6, figure 2.

#### Material Examined

Specimens from the Miocene of Victoria; including Balcombe Bay, Cooriemungle, Fyansford, Muddy Creek, Narrawaturk Bore 2, Paaratte Bore (Port Campbell), Princetown, and from South Australia, including Mount Schanck.

#### Description

Branches cylindrical, with whorls of two to four alternating zooids. Free peristomes raised, symmetrical, not very long; ascopore raised and



**Figure 3** *Siphonicytara clypeata* (Waters, 1881), Balcombe Bay, Miocene. (A) Biserial to quadriserial astogenetic stage: Scale=0.50 mm. (B) Zooids at higher magnification, note grooves surrounding frontal septular pores and shield-shaped area of septal ridges surrounding ascopore: Scale=0.25 mm. (C) Growing end of astogenetically older branch: Scale=0.25 mm.

tubular. Septal ridges raised but not prominent, shield-shaped area surrounding ascopore distinct and including a pair of frontal septular pores. Primary peristomial avicularia paired, disto-lateral to peristome, orientated medially; rostra and mandibles subtriangular, bar serrated. Small, paired oval or spatulate avicularia, orientated proximally, occasionally developed above lateral areolae.

#### Remarks

*Siphonicytara clypeata* is a well-marked species, and there is little difference between the specimens described from the Miocene of Victoria by Waters (1881, 1882a), and those illustrated by Cheetham (1972) from the Upper Eocene of Eua, Tonga. *Siphonicytara clypeata* is not common in Australian samples, although it has a wide occurrence among the localities examined. Waters (1881, 1882a) mentioned it only twice, from Curdies Creek, southwest Victoria and from Mount Gambier, South Australia (Miocene), and Maplestone (1904: 213) listed one additional record he had found, from the Mitchell River, west of Bairnsdale, eastern Victoria (Miocene). MacGillivray (1895) gave no description of *S. clypeata*. Some specimens may have been confused with those of young, cylindrical branches of *S. irregularis*. These are more robust, and may be distinguished by the

distinctly more proximal position of the peristomial avicularia, and by the much more prominent septal ridges.

Waters (1881) gave a detailed description which included discussion of the ascopore and septal ridges, and figured the avicularia. Cheetham (1972) included *T. proditor* Canu and Bassler (1935) in the synonymy of his *T. clypeata*. His description mentions specimens with slightly flattened branches with more than four autozooids per whorl. These certainly resemble *T. proditor*, but not *S. clypeata*. It is therefore reasonably certain that Cheetham's (1972) material included more than one species, *S. clypeata*, which was figured, and another species resembling *S. irregularis*.

#### Distribution

See above; also Mitchell River, Victoria; Mount Gambier, South Australia and Eua, Tonga.

#### *Siphonicytara airensis* (Maplestone)

Figures 4A–C

*Mucronella airensis* Maplestone, 1902: 22, plate 2, figure 12; Maplestone, 1904: 212 (listed).

*Bathosella bulbosa* Canu and Bassler, 1935: 31, plate 9, figure 1; Brown, 1958: 69.

*Bathosella laticella* Canu and Bassler, 1935: 31, plate 9, figure 2.

### Material Examined

#### Lectotype

MOV P10201, Aire Coastal Beds, Victoria (exact location not specified, Eocene or Oligocene).

#### Other Material

Browns Creek (Late Eocene).

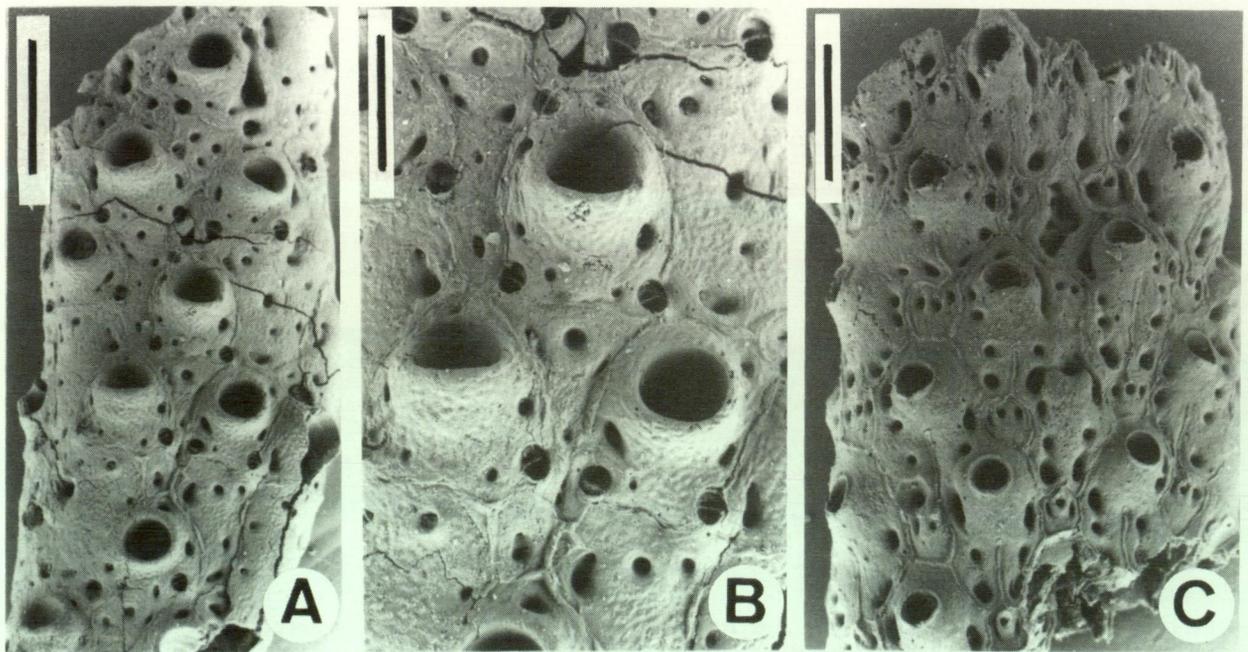
### Description

Branches subcylindrical to bilaminar and slightly flattened; autozooids in lateral series of four to eight, in alternating longitudinal rows, outlined by shallow grooves, septal ridges shallow or virtually absent. Primary orifice large, straight distally and rounded proximally, proximal ascopore subtriangular. Secondary orifice circular or subtriangular and straight proximally, sometimes raised proximally, but not prominent; peristomial calcification very thick. Ascopore in an indistinct proximal area, outlined by a shallow septal ridge late in ontogeny, when it is often flanked by paired areolae derived from frontal septular pores. Marginal septular pores four to six, developing as rounded areolae. Avicularia paired, lateral, small, sutural, rounded and orientated proximo-laterally with a complete bar; other similar avicularia developed above areolae later in ontogeny.

### Remarks

Maplestone's (1902) description of *M. airensis* did not mention the ascopore, which also was not figured. His drawing and the lectotype specimen, however, confirm that *M. airensis* is referable to *Siphonicytara* and identical with material collected from Browns Creek, illustrated here. *Siphonicytara airensis* is distinguished by the virtual lack of raised septal ridges, and by its large, rounded or subtriangular secondary orifices. The dimensions of both primary and secondary orifices are greater than those of *S. irregularis* and *S. clypeata*. The significance of the circular orifices is unknown, and investigation requires additional well preserved specimens. Although there are no raised septal ridges, the ascopore and the zooids in general are outlined by shallow grooves in the calcification, marking the former presence of cuticular insertions. *Siphonicytara airensis* is clearly assignable to *Siphonicytara*, but it also bears some similarity to a species described by Cheetham (1975), as *Tubucella* sp. 2, from Early Eocene deposits in the northwestern Pacific (see p. 320). *Tubucella* sp. 2 differs in its lateral oral avicularia and more porous frontal shield.

The description and illustrations given by Canu and Bassler (1935) for two species from the Aire Coastal Beds, *Bathosella laticella* and *B. bulbosa*, suggest that only one taxon is involved. Both figures have been somewhat heavily retouched, but show a proximal ascopore in several zooids, and paired



**Figure 4** *Siphonicytara airensis* (Maplestone, 1902), Browns Creek, Eocene. (A) Part of a bilaminar branch: Scale=0.50 mm. (B) Three zooids enlarged, note small rounded lateral sutural avicularia and one circular secondary orifice: Scale=0.25 mm. (C) Part of an astogenetically and ontogenetically older fragment, showing slightly raised septal ridges and ascopores with flanking frontal septular pores: Scale=0.50 mm.

lateral avicularia, particularly in the figure of *B. bulbosa*. The genus *Bathosella* was introduced by Canu and Bassler (1917: 43) for *Mucronella aspersa* Ulrich, from the very Early Eocene of Maryland and New Jersey. According to their expanded description (1920: 405, plate 1, figures 27–31), *B. aspersa* was encrusting, the zooid orifice had a proximal tooth, and ovicells with a frontal entoecial area were present. Neither *B. laticella* nor *B. bulbosa* have any of these characters, and both greatly resemble *Siphonicytara airensis*. Without examination of the type or figured material it is not certain that these species are junior synonyms of *S. airensis*, but it is significant that the holotypes of all three forms are from the same locality. Brown (1958: 69) examined the type specimens and placed *B. laticella* in synonymy with *B. bulbosa*.

#### Distribution

Browns Creek; southwestern Victoria, Late Eocene.

#### *Siphonicytara occidentalis* sp. nov.

Figures 5A–C, 6A–D

#### Material Examined

##### Holotype

QM GH3217 CSIRO sample 134/DM4/63, 33°40'S, 114°28'E, southwest of Bunbury, Western Australia, Australia, 137 m.

##### Paratypes

QM GH1022 CSIRO sample 131/DM4/63, 27°40'S, 113°03'E, west of Kalbarri, Western Australia, 128m. QM GH1113 CSIRO sample 134/DM4/63, details as for holotype. QM GH1181 CSIRO sample 144/DM4/63, 32°00'S, 115°08'E, west of Fremantle, Western Australia, 119 m. MOV F52871, part of QM GH1113. WAM, part of QM GH1113.

##### Other material

MOV Locality 'Franklin' GAB128, 35°7'S, 116°52'E, 59 m, GAB130, 35°7'S, 115°59'E, 100m.

#### Description

Branches flattened, bilaminar, with 10–12 autozooids per horizontal whorl, rising to 14–16 before a dichotomy. Primary orifice semicircular, secondary orifice oval, free peristomes symmetrical, moderate. Septal ridges prominent, surrounding the peristome and ascopore, which becomes flanked by paired areolae. Avicularia absent over large areas of the colony, when present, usually small, mandibles and rostra rounded, ligula absent. Rhizoids arising above lateral frontal septular pores of zooids near the base of a branch, from both surfaces, running proximally but not forming a stalk as in *S. formosa* (see p. 310).

#### Remarks

*Siphonicytara occidentalis* resembles *S. irregularis* in

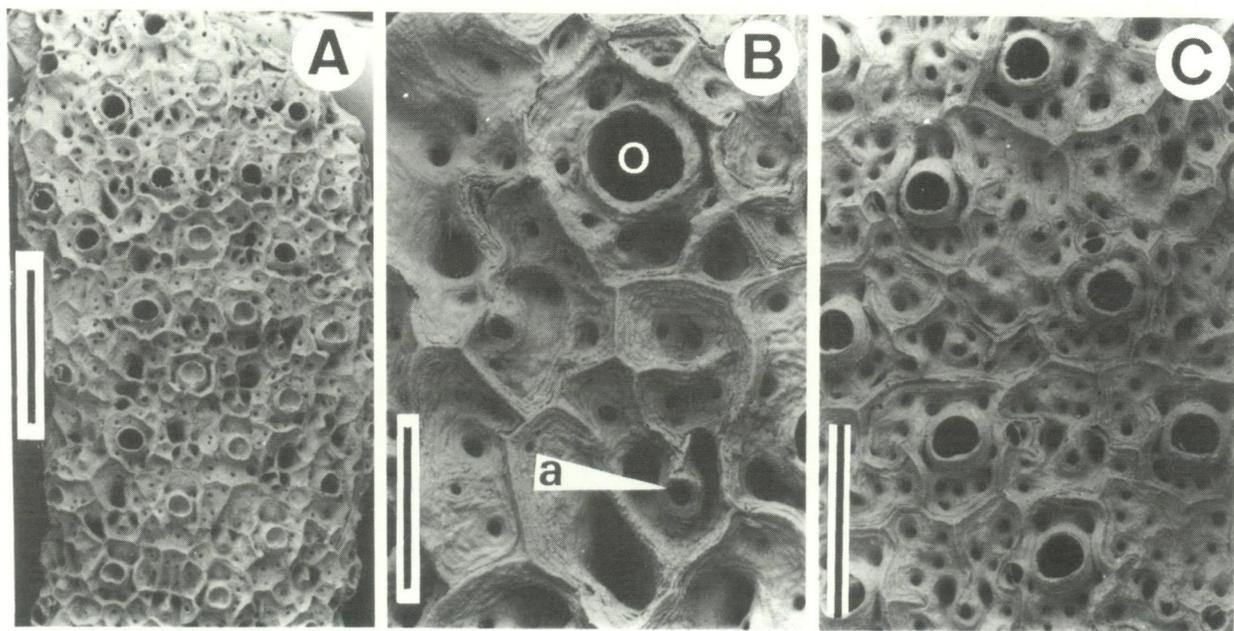
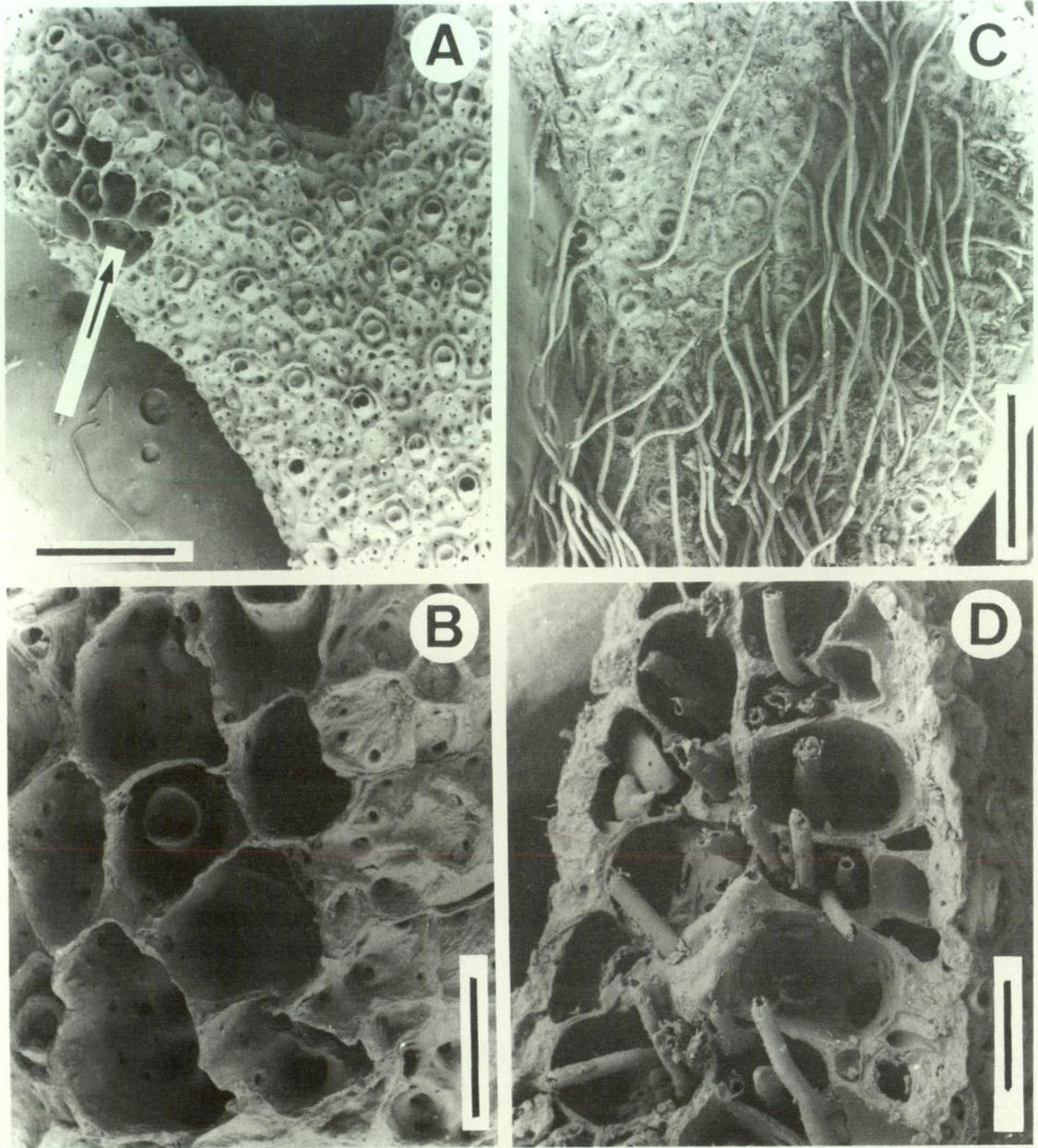


Figure 5 *Siphonicytara occidentalis* sp. nov., Western Australia, Holotype QM GH3217. (A) Part of branch: Scale=2.0 mm. (B) Zooid enlarged to show secondary orifice (o) and ascopore (a), note thickening around areolae and prominence of septal ridges: Scale=0.50 mm. (C) Group of zooids with small oral avicularia: Scale=1.0 mm.



**Figure 6** *Siphonicytara occidentalis* sp. nov., Western Australia, A–B Holotype QM GH3217; C–D Paratype QM G1181. (A) Bifurcation of branch with group of uncalcified frontal buds (arrowed): Scale=2.0 mm. (B) Frontal buds enlarged, showing elongated peristomes and frontal septular pores of underlying zooids: Scale=0.50 mm. (C) Lower part of a branch showing rhizoids: Scale=1.0 mm. (D) Broken end of branch showing developing rhizoids: Scale=0.25 mm.

colony form, and in the prominence of the septal ridges. The material does not show any sign of the massive thickening of calcification occurring in *S. irregularis*, however. The septal ridges are deep and form a network over the entire frontal shields. Avicularia are very rare, scattered and small, and they are sutural, arising late in ontogeny above lateral marginal septular pores. Very rarely one of the avicularia is enlarged, with a subtriangular mandible and a spout-like rostrum. The bars of all avicularia are delicate and lack ligulae. One colony shows a cluster of zooids similar to those found in

*S. irregularis*. In this cluster (Figures 6A, B) the peristomes and surrounding septal ridges have elongated considerably. This suggests that a similar process in *S. irregularis*, followed by an increase in frontal calcification filling in the areolar pores and irregular areolar areas, is the origin of the mound-like clusters of raised zooids (see p. 314).

Some branches have numerous rhizoids, as many as eight originating from each zooid, concentrated in zones surrounding the lower part of the branch. Cuticular zooid linings, similar to rhizoids, are also present at the proximal end of broken branches.

These, together with evidence of regeneration of growing tips of branches suggest that detached fragments and colonies may be able to maintain an independent existence.

#### Distribution

Western Australia, 119–137 m.

#### Etymology

*Occidentalis* (Latin), western, referring to its occurrence from Western Australia.

### DISCUSSION

Fifteen species of *Siphonicytara* are now known. Twelve Recent taxa occur in two speciose groups, four from the East Indian, and six from the New Caledonian regions. There is one isolated record from the western Indian Ocean, and a group of five from Western Australia. Bathymetrically, *S. symetrica* is by far the deepest occurrence, at over 4000 m depth. *Siphonicytara cylindrica*, *S. serrulata* and *S. mosaica* all occur from less than 2000 m, and all other species are from less than 1000 m depth. *Siphonicytara occidentalis*, from Western Australia has the shallowest distribution, less than 150 m depth.

The three fossil species all occur from the Late Eocene, two having a range extending to the Miocene of southeastern Australia.

Colonies are erect, cylindrical or slightly compressed and almost bilaminar, and often branched. Five of the Recent species (*S. serrulata*, *S. formosa*, *S. armata*, *S. vittata* and *S. occidentalis*) are known to be anchored by rhizoids. Many deep-water taxa have a similar mode of growth, but although *S. occidentalis* occurs at relatively shallow depths, its rhizoids presumably reflect the soft, sea-bottom environment in which it lives. Some deep-sea species occur from widely separated regions. For example, the ctenostomes *Pachyzoon atlanticum* and *Aethozoon pellucidum*, both described first from the north Atlantic, have now been found from New Caledonia (see d'Hondt and Gordon, 1996). Hayward (1981) has commented on similar extended ranges in the cheilostomes *Columnella magna*, *C. delicatissima* and *Himantozoon leontodon*. Samples of deep-sea bryozoans are often monospecific, but in spite of the great depth of some of the localities collected, the assemblages containing *Siphonicytara* are all multispecific. The majority of accompanying species has erect, rooted growth. The locality with the least specific diversity is Siboga Stn 119, with only two species, *Siphonicytara cylindrica* and a reteporiform stenolaemate, *Tubulipora cassiformis* (now *Fenestulipora cassiformis*, see Taylor and Gordon, 1997). The latter species also occurs at Siboga Stn 156 accompanying *S. formosa*, together with another

erect stenolaemate, *Hornera spinigera*, and the delicate uniserial, jointed cheilostome, *Chlidoniopsis inflata* (Harmer, 1915, 1957). This station is remarkable in also producing specimens of no fewer than eight species of reteporiform Phidoloporidae (Harmer, 1934). *Siphonicytara serrulata* is accompanied by seven other erect species, including *Cornucopina moluccensis*, *Farciminellum hexagonum*, and *Domosclerus papillatum* (Busk, 1884; Hayward, 1981; Gordon, 1988). The six species of *Siphonicytara* introduced by Gordon and d'Hondt (1997) include three each from only one locality, and three collected at from three to five localities. All are multispecific assemblages, with up to nine species belonging to erect genera such as *Notoplites*, *Cornucopina*, *Himantozoom*, *Chelidozoum*, *Ichthyaria*, *Diplonotos*, *Domosclerus*, *Haswelliporina* and *Tetraplaria*, as well as reteporiform species of *Iodictyum* and *Reteporella* (Gordon and d'Hondt, 1997; Gordon, 1993; d'Hondt and Gordon, 1996). The deepest locality, from southeast of Madagascar, provides a large number of accompanying species, including 16 erect taxa. Species of *Columnella*, *Himantozoom*, *Petalostegus*, *Bifaxaria* and *Tessaradoma* are present, and in addition, specimens of the monoserial stenolaemate *Anguisia verrucosa*, which was previously known only from deep-water in the northeastern Atlantic and the Mediterranean (David and Pouyet, 1986). The largest number of species accompanies the specimens of *S. insolita* from Albatross Stn 5574. Of the 31 species present, 11 are known to be members of 'sand faunas' and are anchored by rhizoids. These include species of *Conescharellina*, *Flabellopora*, *Zeuglopora* and *Parmularia* (see Canu and Bassler, 1929).

The fossil species, too, are found with a similar range of colony forms and are in multispecific assemblages. In the samples from Victoria and South Australia, many species of are known to have occurred on soft, unstable bottom sediments. So many Australian fossil species have very close, or even apparently identical representatives in Recent seas, that their ecological parameters may be inferred with a fair degree of confidence. In complete contrast to nearly every Recent assemblage including *Siphonicytara*, none of these fossil species can be regarded as from deep-water conditions. but resemble those from Western Australia.

Cheetham (1972) considered his Eocene specimens of *S. clypeata* from Tonga to represent part of a shallow-water, allochthonous element of his assemblage. This contained 18 species, five of which (belonging to the genera *Bifaxaria*, *Tessaradoma* and *Spiroporina*) were autochthonous, deep-water forms, which contributed the greater part of his material. In spite of the shallow-water associations of the Western Australian Recent *S.*

*occidentalis*, and of the Victorian fossil specimens, it is possible to regard *S. clypeata* as a cryophilic species (or at least a representative of a cryophilic genus) which descends to deeper water in low latitudes. In this case, the Eocene record from Tonga, from a tropical locality, might instead be regarded as one of the deep-water, autochthonous species in the assemblage.

The Didymosellidae shows some interesting analogues with the Siphonicytaridae, although the two families do not seem to be closely related, and share a long, but distinct, fossil history. Among the erect fossil forms of *Didymosella*, *D. porosa* (Stoliczka) has orifices which are deflected to the frontal side of the branch, whereas those of *D. clypeata* Canu and Bassler are not (Cook and Chimonides, 1981). The frontal thickening of the lepralioid shields in *Didymosella* and *Tubiporella* is considerable, and in *T. magnirostris* consists of a deep network of areolae and intervening calcification, in which the spiramen is difficult to recognise, as is the ascopore in *S. irregularis*. As in the Didymosellidae, almost all the calcified walls in *Siphonicytara* are interior walls, which have an overlying coelom and cuticle separating them from the environment. In *S. irregularis* and *S. occidentalis*, even the free peristomes are in part surrounded by coelom. However, none of the species of *Siphonicytara* develop basal coelomic complexes as in the Didymosellidae.

Two ancient genera which appear to have closest relationships with *Siphonicytara* are *Gastropella* Canu and Bassler, 1917 and *Tubucella* Canu and Bassler, 1917. Both genera have been included in the family Tubucellariidae, but both could be reassigned to the family Siphonicytaridae. *Gastropella* was introduced for *G. ventricosa* (see Canu and Bassler, 1917: 38, plate 4, figure 3, and 1920: 320, plate 6, figures 7–12) from the Midwayan (Early Eocene) of Arkansas and Georgia, U.S.A. It resembles the cylindrical species of *Siphonicytara* in colony form, and in its tubular peristomes, central ascopore, and marginal septular pores which form large areolae. The type species has an umbonuloid frontal shield, and appears to be more closely related to the genus *Tessaradoma* (D.P. Gordon, personal communication).

*Tubucella* was introduced for *T. mamillaris* (Milne-Edwards), a European species ranging from Early Eocene to Miocene. *T. sp. mamillaris* was redescribed by Cheetham (1966: 85, figures 62–64), from the Late Eocene Bracklesham Beds of the United Kingdom. It is closely similar in appearance to *T. monilifera* Canu and Bassler (1917: 63, plate 5, figure 9), from the Late Eocene of North Carolina. The wide Eocene to Miocene distribution of *Tubucella* was discussed by Cheetham (1975, Table 3), who listed all previous records. Colonies of *Tubucella* have cylindrical to compressed, even flabellate

branches. The zooids have numerous frontal pores, many of which may be 'carried up' from marginal areolae (Cheetham, 1975, plate 2, figure 2). Species have raised, circular peristomial orifices, often accompanied by lateral avicularia. The ascopore was noted by Cheetham (1975) to be placed in a distinct region of the frontal shield, divided by a 'presumably cuticular' line from the orifice region. Species of *Gastropella* and *Tubucella* have peristomial ovicells, and in *Tubucella*, the brooding zooids tend to occur in centrally placed rows. They are often enlarged, with distinctive secondary orifices. As mentioned above, *Tubucella* sp. 2 Cheetham (1975: 842, plate 3, figures 1–2, and plate 4, figure 5), from the Early Eocene of the Koko Seamount (approximately 35°N, 172°E), resembles *Siphonicytara airensis*, although it has a more porous frontal shield, and lateral oral paired avicularia. The 'dimorphic' rounded orifices found in *S. airensis* are not placed at the centre of the branch, and require further investigation of well preserved material. It is presumed that all species of *Siphonicytara* have concealed peristomial ovicells, but none have been reported.

There is no evidence of any descendant sequences in *Siphonicytara*. The colonies of *S. clypeata* and *S. irregularis* show that a wide range of growth form already occurred in the Late Eocene. Colonies with a similar diversity in branch structure and zooid arrangement occur in the Recent species *S. insolita* and *S. occidentalis* respectively. One trend which appears to have developed since the Tertiary is the formation of branches with frontal and basal (abfrontal) sides. The differences are slight in *S. excentrica* and *S. mosaica*, but distinct in *S. glabra* and *S. vittata* (Gordon and d'Hondt, 1997), and reach their greatest development in *S. serrulata*.

#### ACKNOWLEDGEMENTS

We would like to thank Dr David Holloway (MOV) for access to collections, and Dr Pat Mather (QM) for the loan of material from which *S. occidentalis* were separated. Mr P.J. Chimonides (NHM) provided information on specimens, and Mr D. McDonald assisted in preparation of the paper.

#### REFERENCES

- Bassler, R.S. (1934). Notes on fossil and Recent Bryozoa. *Journal of the Washington Academy* 24: 404–408.
- Bassler, R.S. (1953). Bryozoa. In R.C. Moore (ed.), *Treatise on invertebrate paleontology, Part G*. Geological Society of America and University of Kansas Press, Lawrence. 253 pp.
- Brown, D.A. (1958). Fossil cheilostomatous Polyzoa from south-west Victoria. *Geological Survey of Victoria Memoir* 20: 1–90.

- Busk, G. (1884). Report on the Polyzoa collected by H.M.S. 'Challenger' during the years 1873-76. Part 1 - The Cheilostomata. *Report on the Scientific Results of the Voyage of the H.M.S. Challenger, Zoology* 10(30): i-xxiv, 1-216.
- Canu, F., and Bassler, R.S. (1917). A synopsis of American Early Tertiary Cheilostome Bryozoa. *Bulletin of the United States National Museum* 94: 1-87.
- Canu, F., and Bassler, R.S. (1920). North American early Tertiary Bryozoa. *Bulletin of the United States National Museum* 106: i-vii, 1-879.
- Canu, F., and Bassler, R.S. (1929). Bryozoa of the Philippine Region. *Bulletin of the United States National Museum* 100: 1-685.
- Canu, F., and Bassler, R.S. (1935). New species of Tertiary Cheilostome Bryozoa from Victoria, Australia. *Smithsonian Miscellaneous Collections* 93(9): 1-54.
- Cheetham, A.H. (1966). Cheilostomatous Polyzoa from the Upper Bracklesham Beds (Eocene) of Sussex. *Bulletin of the British Museum (Natural History). Geology* 13(1): 1-115.
- Cheetham, A.H. (1972). Cheilostome Bryozoa of Late Eocene age from Eua, Tonga. *United States Geological Survey, Professional Paper* 640-E, i-vii, E1-26.
- Cheetham, A.H. (1975). Preliminary report on Early Eocene Cheilostome bryozoans from site 308 - leg 32, deep sea drilling project. *Initial Report of the Deep Sea Drilling Project* 32: 835-851.
- Cook, P.L. (1973). Preliminary notes on the ontogeny of the frontal body wall in the Adeonidae and Adeonellidae (Bryozoa, Cheilostomata). *Bulletin of the British Museum (Natural History). Zoology* 25: 243-263.
- Cook, P.L. and Chimonides, P.J. (1981). Morphology and systematics of some interior-walled cheilostome bryozoans. *Bulletin of the British Museum (Natural History). Zoology series* 41: 53-89.
- David, L., and Pouyet, S. (1986). Bryozoaires abyssaux des campagnes Safari (Océan Indien). *Annales d'Institut Océanographique, n.s.* 62(2): 141-192.
- Gordon, D.P. (1988). The bryozoan families Sclerodomidae, Bifaxariidae, and Urceoliporidae and a novel type of frontal wall. *New Zealand Journal of Zoology* 15: 249-290.
- Gordon, D.P. (1993). Bryozoa: the ascophorine infraorders Cribriomorpha, Hippothoomorpha and Umbonulomorpha mainly from New Caledonian waters. In A. Crosnier (ed.), *Résultats des Campagnes MUSORSTOM 11. Mémoires du Muséum national d'Histoire naturelle* 158: 299-347.
- Gordon, D.P., and d'Hondt, J.-L. (1991). Bryozoa: The Miocene to Recent family Petalostegidae. Systematics, affinities, biogeography. In A. Crosnier (ed.), *Résultats des Campagnes MUSORSTOM 8. Mémoires du Muséum national d'Histoire naturelle* 151: 91-123.
- Gordon, D.P., and d'Hondt, J.-L. (1997). Bryozoa: Lepraliomorpha and other Ascophorina, mainly from New Caledonian waters. In A. Crosnier (ed.), *Résultats des Campagnes MUSORSTOM 18. Mémoires du Muséum national d'Histoire naturelle* 176: 9-124.
- Harmer, S.F. (1915). The Polyzoa of the Siboga Expedition, Part 1. Entoprocta, Ctenostomata and Cyclostomata. *Siboga Expeditie* 28a: 1-180.
- Harmer, S.F. (1926). The Polyzoa of the Siboga Expedition, Part 2. Cheilostomata Anasca. *Siboga Expeditie* 28b: 181-501.
- Harmer, S.F. (1934). The Polyzoa of the Siboga Expedition, Part 3. Cheilostomata - Ascophora I. Family Reteporidae. *Siboga-Expeditie* 28c: 503-640.
- Harmer, S.F. (1957). The Polyzoa of the Siboga Expedition, Part 4. Cheilostomata - Ascophora 2. *Siboga-Expeditie* 28d: 641-1147.
- Hayward, P.J. (1981). The Cheilostomata of the deep sea. *Galathea Report* 15: 21-68.
- Hayward, P.J., and Cook, P.L. (1983). The South African Museum's Meiring Naude Cruises. Part 13, Bryozoa II. *Annals of the South African Museum* 91(1): 1-161.
- d'Hondt, J.-L., and Gordon, D.P. (1996). Bryozoa: Cténostomes et Cheilostomes (Cellularines, Scrupariines et Malacostéges) des campagnes MUSORSTOM autour de la Nouvelle-Calédonie. In A. Crosnier (ed.), *Résultats des Campagnes MUSORSTOM 15. Mémoires du Muséum national d'Histoire naturelle* 168: 55-123.
- Lagaaij, R., and Cook, P.L. (1973). Some Tertiary to Recent Bryozoa. In A. Hallam, *Atlas of palaeobiogeography*, 489-498, Elsevier, Amsterdam.
- 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. (1902). Further descriptions of the Tertiary Polyzoa of Victoria. 8. *Proceedings of the Royal Society of Victoria* 15: 17-27.
- Maplestone, C.M. (1904). Tabulated list of the fossil cheilostomatous Polyzoa in the Victorian Tertiary deposits. *Proceedings of the Royal Society of Victoria* 17: 182-219.
- Taylor, P.D., and Gordon, D.P. (1997). *Fenestulipora*, gen. nov., an unusual cyclostome bryozoan from New Zealand and Indonesia. *Invertebrate Taxonomy* 11: 689-703.
- Tenison Woods, J.E. (1876). On some Tertiary Australian Polyzoa. *Journal and Proceedings of the Royal Society of New South Wales* 10: 147-150.
- Waters, A.W. (1881). On fossil cheilostomatous Bryozoa from South-west Victoria, Australia. *Quarterly Journal of the Geological Society of London* 37: 309-347.
- Waters, A.W. (1882a). On fossil cheilostomatous Bryozoa from Mount Gambier, South Australia. *Quarterly Journal of the Geological Society of London* 38: 257-276.
- Waters, A.W. (1882b). On fossil cheilostomatous Bryozoa from Bairnsdale, (Gippsland). *Quarterly Journal of the Geological Society of London* 38: 502-513.
- Waters, A.W. (1883). On fossil cheilostomatous Bryozoa from Muddy Creek, Victoria. *Quarterly Journal of the Geological Society of London* 39: 423-443.
- Waters, A.W. (1885). Cheilostomatous Bryozoa from Aldinga and the River-Murray Cliffs, South Australia. *Quarterly Journal of the Geological Society of London* 41: 279-310.

## APPENDIX

## Details of Australian Tertiary localities mentioned in the text

- Aire Coastal Beds:** Brown (1958: 29) noted that this locality cannot be more precisely stated, but the evidence from Maplestones's (1904) faunal lists and from the localities quoted by Canu and Bassler (1935), suggests that this is about the same horizon as the beds at Cape Otway. Age: Eocene or Oligocene.
- Bairnsdale (Skinner's):** Mitchell River bank, about 12 km west of Bairnsdale, Victoria. Lat. 37°47.9'S, Long. 147°29.5'E. Age: Miocene.
- Balcombe Bay:** Also known as **Fossil Beach**, **Mornington**, **Mount Martha** and possibly '**Schnapper Point**' (MacGillivray); on coast of Port Phillip Bay, about 3 km south of Mornington, Victoria. Lat. 38°14.5'S, Long. 145°01.7'E. Fyansford Clay. Age: Balcombian; Middle Miocene, (Langhian).
- Batesford Quarry:** Upper levels of Batesford Limestone Quarry, 7 km west of Geelong, Victoria. Lat. 38°06.5'S, Long. 144°17.3'E. Fyansford Clay. Age: Balcombian; Middle Miocene, (Langhian).
- Bird Rock:** Coastal section, about 3 km west of Torquay, Victoria. Lat. 38°21.4'S, Long. 144°17.8'E. Jan Juc Formation. Age Janjukian; Late Oligocene, (Chattian). Also known as **Spring Creek**.
- Browns Creek:** Cliffs just east of the mouth of Johanna River, Victoria. Lat. 38°46'S, Long. 143°22.6'E. Browns Creek Clay. Age: Late Eocene, (Priabonian).
- Cape Otway:** Also **Point Flinders**, Locality AW1. Coastal section 2 km northwest of Cape Otway, Victoria. Lat. 38°51.1'S, Long. 143°29.5'E. Glen Aire Clay. Age: Early Oligocene, (Rupelian/Latdorfian).
- Cooriemungle area:** Road cuttings about 18 km north of Princetown. Lat. 38°32.4'S, Long. 143°08.1'E. Gellibrand Marl. Age: Balcombian, Middle Miocene, (Langhian).
- Curdies Creek:** This is the locality name applied to the bryozoans described by Waters (1881). The original paper mentions 'Yarra Yarra', which is the river on which Melbourne is located, and from which no bryozoan fossil localities have been recorded. Later publications (eg MacGillivray, 1895) have used the locality Curdies Creek for this collection. The coastal section at the mouth of the Curdies River exposes Late Miocene limestone with a sparse bryozoan fauna. Inland sections are generally in limestone, but some of the muddy sediments of the Gellibrand Marl are exposed near Timboon. However, it is believed that the sample is more likely to have come from coastal sections, which were much more accessible at that time. If the sample was obtained from the coastal exposure, it almost certainly was close to the locality listed as '**Princetown**' below.
- Fyansford.** This locality was mentioned by Maplestone (1904), and is almost certainly in the same area as **Batesford Quarry**.
- Glenaulin:** Allotment 2, Parish of Glenaulin, Southwest Victoria, Locality IV of Brown (1958). Glenaulin Clay. Age: Late Oligocene, (Janjukian).
- Grices Creek:** Also known as **Gunyong Creek**; on the coast of Port Phillip Bay, about 8 km north of Mornington, Victoria. Lat. 38°11.9'S, Long. 145°03.9'E. Fyansford Clay. Age Balcombian (some material may be Bairnsdalian); Middle Miocene, (Langhian).
- Mitchell River**, see **Bairnsdale**.
- Mount Gambier:** Abandoned quarry on road to Port MacDonnell, about 7 km south of Mount Gambier, South Australia. Lat. 37°53.5'S, Long. 140°43.2'E. Gambier Limestone. Age: Longfordian(?) Early Miocene.
- Mount Schanck:** Limestone quarry about 1 km west of Mount Schanck, about 15 km south of Mount Gambier, South Australia. Lat. 37°57'S, Long. 140°43.2'E. Gambier Limestone. Age: Early Miocene, (Longfordian).
- Muddy Creek:** Clifton Bank, Muddy Creek, 8 km west of Hamilton, Victoria. Lat. 37°44.6'S, Long. 141°56.4'E. Muddy Creek Marl (= Gellibrand Marl). Age: Balcombian, Middle Miocene, (Langhian).
- Narrawaturk Bore 2:** At Peterborough, Victoria. Lat. 38°36.3'S, Long. 142°52.3'E. Gellibrand Marl. Age: Early Miocene, (Longfordian).
- Paaratte No.1 Bore.** Mines Department bore in the Parish of Paaratte, located in the village of Port Campbell, Victoria. Lat. 38°36.8'S, Long. 143°00.0'E. Age: Middle Miocene.
- Princetown (Gigantocypraea locality):** Coastal section, about 2 km west of Princetown, Victoria. Lat. 38°41.9'S, Long. 143°08.3'E, Gellibrand Marl. Age: Balcombian, Middle Miocene.
- River Murray Cliffs.** A large number of fossil localities are exposed between Tailem Bend and Overland Corner, in South Australia. It is suspected that the material described by Waters (1885) may have come from the region of Murray Bridge. Age: Miocene.
- Schnapper Point;** see **Balcombe Bay**.
- Spring Creek;** see **Bird Rock**.
- Waurm Ponds.** Several quarries and other exposures 10 kilometres southwest of Geelong, Victoria.