

Morphology and systematics of some interior-walled cheilostome Bryozoa

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Synopsis

The colony structure and zooidal morphology found in two cryptocystidean cheilostome bryozoan Families, the Euthyrisellidae and the Didymosellidae are described. All calcified walls are interior, and colony-wide (extrazoooidal) basal coeloms are present in nearly all species. In the Family Euthyrisellidae, interzooidal visceral-to-hypostegal communication complements or even replaces the more usual, intrazooidal kind, which is that found in the Family Didymosellidae. In the Euthyrisellidae an extension of the hypostegal coelom on the basal side of the calcified frontal shield is present in most species. One new species, *Tropidozoum burrowsi*, is introduced. The Family Didymosellidae has a fossil record extending from the Middle Eocene to the Recent, and a wide Tertiary-to-Recent distribution. One new Recent species, *Didymosella pluma*, is introduced, and *Tubiporella boninensis* Borg is redefined. *Tubiporella levinseni* Borg is redescribed and assigned to the umbonuloid ascophoran genus *Reptadeonella*.

Introduction

The calcified and uncalcified body walls defining the member zooids of bryozoan colonies may conveniently be regarded as belonging to two kinds. The first is the exterior, limiting or boundary wall, which is primarily cuticular and which, if calcified, almost invariably has an outermost layer of cuticle throughout ontogeny. This kind of wall is actually or potentially capable of dividing the internal coelomic tissues of zooids from the environment. Zooids delimited by this kind of wall develop as uncalcified buds by expansion and extension of coelomic tissue through septulae in the calcified wall of an existing zooid. The boundary wall of cuticle and epidermis expands intussusceptively as growth proceeds. The earliest known, Late Jurassic cheilostomes had zooidal walls almost entirely of this kind (see Boardman & Cheetham, 1973), and large numbers of species now living have the same, or similar zooidal structure and budding pattern. Many lateral vertical walls of contiguous

zooids in expanses of more integrated species are also exterior walls, even though they may appear to be 'inside' the colony. The second kind of wall is the interior wall, which may or may not possess any cuticular element, and which partitions existing coeloms and is not directly in contact with the environment. Zooids with interior walls are differentiated from a colony-wide expansion of coelom bounded by intussusceptively expanding cuticle and epidermis, by growth of a calcified lamina which, in earlier stages of ontogeny at least, is surrounded by coelom (see Boardman & Cheetham, 1973). Both kinds of wall have arisen several times in the long evolutionary history of the Bryozoa, and both kinds are usually to be found in any cheilostome colony. In some colonies, the distinction between the two kinds of wall is not clear cut. However, the astogenetic and ontogenetic sequences reflected by interior and exterior walls, and the intrazooidal and interzooidal communications associated with them, are important in the study of colony structure, of integration, and of systematic relationships through time.

Colonies with a high proportion of their calcified walls of the interior kind are well known among the 'free-living' anascan cheilostomes (Håkansson, 1973, Chimonides & Cook, 1981). Like these, several ascophoran Families, such as the Conescharellinidae, and genera such as *Sphaeropora*, as well as the Euthyrisellidae and Didymosellidae, have virtually no exterior calcified walls at all (Cook & Lagaaij, 1976, and Cook & Chimonides, 1981). The ascophoran forms show a much larger range of colony morphotypes than the anascan forms.

The species of Euthyrisellidae and Didymosellidae have cryptocystidean frontal shields (see Banta, 1970). These frontally placed parts of zooids in which the orifice is situated, are interior calcified walls which partition the visceral from the hypostegal coelom. The exterior frontal wall above the hypostegal coelom is completely cuticular, with underlying epidermal cells. In some species (e.g. *Pleurotoichus clathratus*) the frontal, cuticular wall is a continuous, colony-wide expanse, connected only intermittently with the vertical walls and the frontal shields. The lateral and distal vertical calcified walls are also interior walls, which partition a colony-wide coelom at the growing edge or tip of an expanse or branch. Basal calcified walls are also interior walls in the majority of species described here. These too, have communication with an extrazooidal basal coelom, which is protected from the environment by a cuticular and epidermal wall.

Intrazooidal, interzooidal and extrazooidal communication is an important feature in these colonies (Figs 1A, B) and its skeletal expression, in the form of septulae, and often in subsequent thickening of calcification, enables inferences to be made for fossil and Recent specimens in which the cuticular walls and coelomic tissues are no longer present.

Material and methods

The possibility of restoring recognizable structures, including muscles and viscera, in previously dried material, and the advantages of study of epoxy-resin mounted thin-sections of 'hard' and 'soft' tissues *in situ* have been demonstrated (Cook, 1975). Dried specimens were previously soaked in 10% trisodium phosphate solution for 48 hours, gently cleaned in detergent solution, and rinsed in water before staining. The accession of fixed, well-preserved material of *Pleurotoichus*, *Tropidozoum*, *Neo euthyris* and *Didymosella* has enabled us to make sections which may be compared with those made from restored material. This comparison has tested the inferences drawn previously, and will allow further inferences to be made with greater confidence in the future.

Specimens for scanning electron microscopy were treated with sodium hypochlorite, rinsed and coated with gold-palladium. Specimens to be thin-sectioned were heavily stained in borax carmine or safranin, impregnated with epoxy-resin, cut and polished attached to 3" × 1" microscope slides.

Early attempts at embedding followed Nye *et al* (1972) and Sandberg (1971). Three resin types were available: Reichold Epotuf 37 128 with hardener 37 614, Shell Epon 812 and

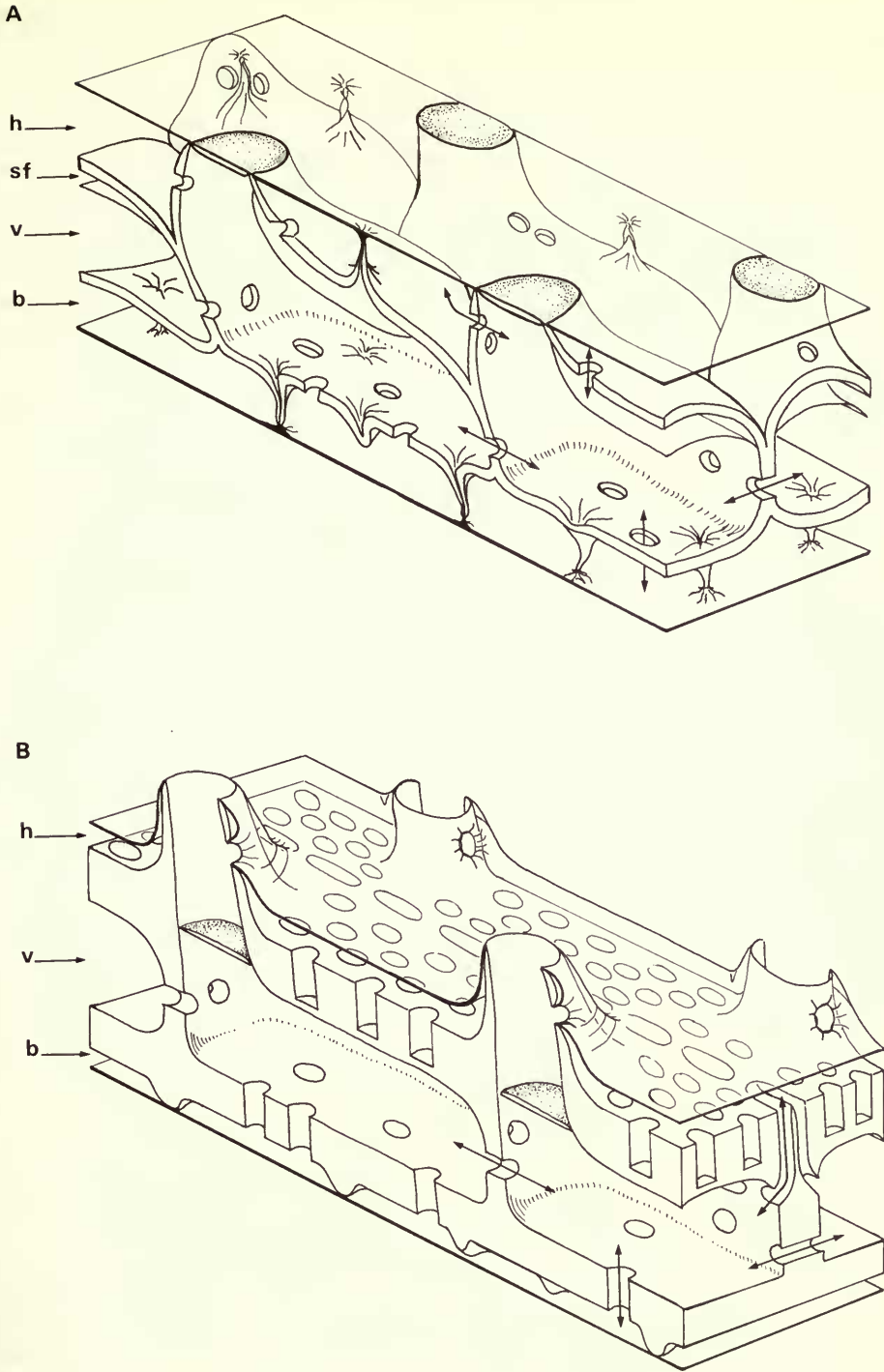


Fig. 1 Generalized diagrams to show residual communication after development of interior calcified walls in: (A) Euthyrisellidae; (B) Didymosellidae. Intercoelomic communications arrowed: *h* hypostegal coelom, *sf* subfrontal hypostegal coelom, *v* visceral coelom, *b* basal coelom.

Ciba Araldite CY212 with their complementary additives MNA, DDSA, BDMA, DMP 30 etc.

The Reichold resin, well tested by Nye *et al* (1972) was found to be difficult to use. The high viscosity of the components hindered obtaining the intended ratio of 4 parts resin to 1 part hardener and their subsequent mixing. The mix was found to be sensitive to heat and U.V. light (e.g. sunlight) and there was a tendency for thermal runaway to occur. This reaction was more readily provoked if the mix contained slightly excess hardener, even though the plug size was only 30 cm³ and curing was initiated at room temperature, 20°C. It was found that surface temperatures in excess of 80°C were reached, coupled with emission of phenol-smelling fumes, bubbling and volumetric expansion. When curing could be controlled by refrigeration a volumetric contraction, estimated as 8% total, was noted. No significant change in behaviour was noted with prolonged storage of the components at 5–10°C. The recommended life of hardener 37 614 is given as 6–12 months in a tightly closed container at room temperature or less. Denaturing is characterized by progressive discolouration to a dark brown colour. Epon 812 was used as described by Sandberg (1971) using only MNA as hardener. DMP 30 and BDMA (Glauert, 1965, 1974) were used as accelerators in parallel series. Araldite CY212 was used in the same way. The preferred ratios of the components were: resin 54%, hardener 44% and accelerator 2%. Both resins were found to have tolerant curing temperatures of 50–80°C. Epon 812, with its low viscosity and production of relatively clear and hard plugs promised to be the ideal medium. It was found, however, that as lapping of thin-sections progressed, small, granular particles of resin (and sometimes of specimen) would break away leaving score marks on the polished surface. This was more noticeable as the thickness of the preparation reached 40 μ or less. It was almost impossible to produce an intact section below 20 μ. Freeman & Spurlock (1962), in electron microscopical studies, reported Epon 812 as being inherently granular. This suggests that thin-section disintegration may be a larger scale manifestation of the same characteristic. The disintegration problem was more pronounced at the lower curing temperatures. In addition, it was found that the resin in sections became 'milky' in aqueous solutions (even without the aquon component), or in the lapping lubricant used, Engis Hyprez type W. The resin would also accept stains which were difficult to remove. Further, as the section was thinned, it would distort and lift from the slide. These effects were noted regardless of resin and additive batch and of precautions to ensure uniform mixing of components and cleanliness of the glass slides. A noticeable volumetric contraction (of about 6–7%) was again found, regardless of recipe and of curing procedure.

Araldite CY212, in spite of its high viscosity, was found to be the most suitable resin. Its total curing contraction was estimated as 1–2%, regardless of recipe. Stability during lapping was high, and it was possible to obtain sections in the order of 3 μ thickness. One disadvantage was that xylene affected the cured resin and coverslides mounted with Canada balsam were therefore avoided. Where required, coverslides were mounted using more epoxy-resin.

In all cases propylene oxide was used as the antemedium. Final embedding was vacuum assisted after first soaking the specimens in an equal mixture of propylene oxide and accelerated resin mix. One well known advantage of the use of propylene oxide is that any residual quantities trapped in the specimen should polymerize with the resin.

In all resins used, behaviour appeared equally divided between pre- and post-gel contraction. Reichold Chemicals Inc. (*pers. comm.* 16.2.1977) suggested that a more typical contraction behaviour of their resin would be approximately 5% total, distributed as 3% pre-gel and 2% post-gel phase. Potter (1970 : 171) identified post-gel shrinkage as the phase at which stresses may be introduced which can lead to damage, although his account relates to electrical component encapsulation and is without reference to scale. It was indicated that post-gel contraction for epoxy resins is normally in the region of 2–3% and that contraction overall is affected primarily by the accelerator used.

In making thin-sections the effects of resin contraction were most apparent when attaching preparations to microscope slides, when bowing of the glass, and in many cases, even

breaking was noted. The amount of resin was therefore kept to a minimum, and Araldite resin obviously showed to advantage.

Within the specimen itself, shrinkage should have little effect providing that complete penetration by the resin has been achieved. Although penetration may appear to be complete, it has been found, during cutting and polishing stages, that calcified walls may drop out of the section completely, as opposed to partial fracturing and partial loss. This indicates a lack of specimen support.

If a final surface stain was applied, there was a tendency for the stain to delineate the boundary of the calcification, although it should be borne in mind that the micro-relief produced by lapping may have been a contributory factor. In sections of 10 μ thickness or more, the stain sometimes soaked into the boundary irregularly. Support failure and staining characteristics suggest an unpredictable penetration of the resin into the calcification, together with a degree of incomplete adhesion which may be exacerbated by resin shrinkage. The evidence is at present considered to be inconclusive, especially as the effects were observed most often when using the structurally unsatisfactory Epon 812 resin. For these reasons staining before embedding was preferred.

Measurements and abbreviations used

The value of comparative measurements among, for example fossil and Recent colonies of the same or different species, varies considerably among bryozoans, both with the structures measured and with the species groups being investigated. For example, some species retain recognizable traces in frontal view, of structures such as the tops of vertical walls, throughout ontogeny and in spite of wear. In such species comparisons of zooidal length and width among colonies are easily made and are significant. Primary calcified orifices with distinct boundaries are also capable of yielding reasonably accurate measurements. In the species considered here, one family, the Euthyrisellidae, which has no fossil record, retains throughout ontogeny recognizable features which allow morphometric analysis. The Didymosellidae, on the other hand, includes species in which continuous ontogenetic changes throughout colony life obscure zooidal boundaries and primary orifices, which in themselves are not easily definable. Fossil (and some Recent) specimens, which have been damaged or are worn, are therefore not strictly comparable with well preserved colonies. Other micro-environmental effects, such as those influencing the length of peristomes, may sometimes be recognized, but are difficult to quantify.

Abbreviations

Measurements in millimetres

Length of autozooid	Lz	Width of autozooid	lz
Length of brooding zooid	Lbz	Width of brooding zooid	lbz
Length of primary orifice	Lo	Width of primary orifice	lo
Length of brooding z. orifice	Lbo	Width of brooding z. orifice	lbo
Length of rostrum	Lr	Width secondary orifice	l2o
Length of mandible	Lm		

BMNH British Museum (Natural History)
 NMV National Museum of Victoria
 ZMA Zoological Museum, Amsterdam

MM Manchester Museum
 AM Australian Museum, Sydney.
 SAM South African Museum, Cape Town.

Key to species described

- 1 Raised peristomes absent, opercula well-developed, often with two layers and with complex sclerites. Frontal pores and septulae absent or rare; large frontal foramina present or absent. Avicularia and ovicells usually absent. Secondary calcification slight. Brooding zooids strongly dimorphic **EUTHYRISELLIDAE** 2
- Raised peristomes present, opercula simple, not usually visible. Frontal pores and septulae numerous. Avicularia and ovicells present. Secondary calcification extensive. Dimorphic zooids not obvious **DIDYMOSELLIDAE** 6
- 2 Colonies encrusting, avicularia and ovicells present, basal coelom absent
Neoeuthyris woosteri p. 67
- Colonies erect. Avicularia and ovicells absent, basal coeloms present 3
- 3 Colonies flustriform, unilaminar, with lateral and basal coeloms 4
- Colonies cellariiform, with kenozooidal nodes. Internodes with zooids in curved, laterally contiguous series. Basal coelom forming a central column **Tropidozoum** 5
- 4 Frontal shield complete, smooth. Lateral coeloms with series of calcified plates
Euthyrisella obtecta p. 60
- Frontal shield with calcified bars and large, slit-like foramina. Lateral coeloms without series of calcified plates
Pleurotoichus clathratus p. 63
- 5 Autozooidal orifices not sinuate, frontal shield with large foramina
Tropidozoum cellariiforme p. 64
- Autozooidal orifices with a deep, triangular sinus, frontal shield with small foramina
T. burrowsi sp. nov. p. 65
- 6 Peristomes with large, paired proximal foramina, spiramen absent **Didymosella** 7
- Peristomes with one, or no foramen, spiramen present **Tubiporella** 13
- 7 Colonies erect, ligulate, unilaminar. Zooids in 2–5 transverse rows. Basal pores present 8
- Colonies encrusting, semi-encrusting or repent, or bilaminar or cylindrical 9
- 8 Branches flat, 4–5 zooids wide, basal pores numerous
Didymosella porosa p. 72
- Branches laterally curved towards the basal side, 2–3 zooids wide, basal pores rare
D. clypeata p. 72
- 9 Colonies bilaminar or cylindrical
D. larvalis-complex (fossil populations) p. 73
- Colonies unilaminar or semi-encrusting, with large basal foramina, or basal pores and/or calcified processes 10
- 10 Colonies encrusting or semi-encrusting. No coelom basally, but zooid walls uncalcified or with a large, central foramen. Peristomes deficient distally, raised proximally
D. larvalis-complex (Recent populations) p. 73
- Colonies repent. with basal pores and/or long calcified processes. Peristomes tubular 11
- 11 Zooids large (Lz > 0.70 mm), avicularian rostra with an open channel terminally 12
- Zooids smaller (Lz < 0.70 mm), avicularian rostra very small and acute
parviporosa p. 75
- 12 Zooids with more than 25 frontal pores. Basal surface with pores (fossil) *D. crassa* p. 71
- Zooids with less than 25 frontal pores. Basal surface with long, calcified processes. Avicularian mandible expanded laterally (Recent) *D. pluma* sp. nov. p. 76
- 13 Colonies forming broad, repent expansions. Peristomes with a single foramen early in ontogeny. Avicularia with acute, hooked mandibles
Tubiporella magnirostris p. 77
- Colonies ligulate, 4–7 zooids wide, repent. Peristomes entire, very long and tubular. Avicularia elongated, with laterally expanded mandibles *T. boninensis* p. 79

Systematic Section

EUTHYRISELLIDAE Bassler

Euthyrisellidae Bassler, 1953 : G226.

TYPE GENUS. *Euthyrisella* Bassler, 1936.

DESCRIPTION. Interior walled cryptocystidean ascophorans, usually with extrazooidal, cuticle-bounded basal coeloms. Colonies encrusting algae, or erect, flexible, rooted. Zooids

Table 1 Average measurement (mm) of zooids of Euthyrisellidae.

	Lz	lz	Lbz	lbz	Lo	lo	Lbo	lbo
<i>E. oblecta</i>	0.55	0.35	0.73	0.52	0.15	0.19	0.20	0.27
<i>P. clathratus</i>	0.55	0.37	0.60	0.51	0.24	0.24	0.24	0.31
<i>T. cellariiforme</i>	0.65	0.34	0.73	0.38	0.21	0.18	0.24	0.19
<i>T. burrowsi</i>	0.67	0.36	0.67	0.50	0.21	0.15	0.15	0.20
<i>N. woosteri</i>	0.90	0.41	1.60	0.50	0.23	0.17	0.26	0.31

with relatively little secondary calcification frontally, frontal septulae restricted or absent. Hypostegal coeloms extensive, often extending basally to the calcified frontal shield, and communicating interzooidally with visceral coeloms of zooids of the previous astogenetic generation. Externally obvious brooding structures and avicularia usually, but not exclusively absent. Orifices of brooding zooids enlarged, dimorphic.

REMARKS. The family was introduced by Bassler (1953) for the genera *Euthyrisella*, *Pleurotoichus*, *Neo euthyris* and *Urceolipora*. The relationships among these genera have been discussed by Levinsen (1909), Harmer (1957) and Hastings (1964). *Urceolipora* shows many characteristics in common with *Euthyrisella* and *Neo euthyris* on the one hand, and with the genera *Calwellia* and *Ichthyaria* on the other. These generic groups, together with others which have some similarities in their colony organization, such as *Onchoporella* and *Euthyroides* all require detailed analysis, but are beyond the scope of this paper. *Urceolipora* is therefore excluded here, but the genus *Tropidozoum* is included in the family.

ONTOGENY OF ZOOID WALLS. In all species, the primary ontogenetic changes in calcification of the zooid walls and formation of the orifice, operculum and ascus, appear to be very rapid, as few intermediate stages between undifferentiated buds and complete zooids are present. In addition, growth appears to proceed in distinct episodes, alternating with periods of astogenetic quiescence, as many colonies show little evidence of any zones of developing zooids at the growing edges or tips, and some colonies show distinct 'growth lines' (see below).

Where present, the growing zones consist of an undifferentiated area of coelomic tissue bounded by thin cuticle. The calcification of interior walls proceeds distally, and the lateral walls become intermittently attached to the frontal cuticle. At the same time the opercular cuticle becomes thickened and differentiated. Where there is a basal coelom, the calcified lateral walls converge, forming a basal zooid wall which may be linear, or merely a curved continuation of the lateral walls. Contact with the cuticular, basal colony-wide wall occurs later in ontogeny in some species. The development of the lophophore and viscera is complete 2-3 zooid generations from the growing zone, just in advance of the final stages of ascus development (see also Harmer, 1902).

In *Tropidozoum*, particularly *T. burrowsi* (see p. 65, there is some subsequent thickening of the calcification of the frontal shield and basal walls. In *Euthyrisella*, *Pleurotoichus* and *Neo euthyris*, thickening is confined to the development of processes attaching the cuticle to the frontal shields, or to the development of calcification within the lateral extrazooidal coeloms, when present.

Coelomic systems and communication

The intercommunication among the hypostegal, visceral and extrazooidal coeloms is considerable, and reflects the varying extent and patterning of these coeloms throughout the colony (Fig. 1A). The virtual isolation of the hypostegal coelom, particularly in *Tropidozoum*, is a direct result of the rarity of the frontal septulae (areolae) usually found in cryptocystidean ascophorans, and is accompanied in most species by an extension of this coelom beneath the calcified frontal shield (see also Cook, 1975). Transfer of nutrients in

coelomic fluids is inferred by the presence of communication pores in the distal-terminal or distal-lateral calcified walls, which connect the visceral coelom of one zooid with the hypostegal coelom of the next successive, distal zooid. This system, too, is unusual in cheilostomes, although it probably occurs in the genera *Urceolipora*, *Calwellia* and *Onchoporella* as well (see above). The basal and lateral extrazoooidal coeloms are extensive in all the erect genera, but absent in *Neoeuthyris*, which is encrusting. Where present, they are inferred to function connectively and, as their cuticular walls thicken with ontogeny, to become involved in the anchoring and support of the colony.

Opercula

The opercula are large and double layered, with strengthening sclerites in most species. The morphology of the complex opercula of *Euthyrisella* and *Pleurotoichus* has been fully described by Harmer (1902). Those of *Tropidozoum* and *Neoeuthyris* are simpler in construction, but also have strong sclerite systems.

Brooding zooids

All species show dimorphism of brooding zooids, the larger dimorphs having enlarged orifices and, in the erect species, swollen basal walls. Embryos have now been observed in all species and without exception, are associated with the larger dimorphs. They are not readily seen except by transmitted light (cf. Harmer, 1902), but when present, usually fill the central and proximal parts of the cystid and are presumably contained in ovisacs.

The ovicells of *Neoeuthyris* differ considerably in appearance from the brooding zooids of the other genera. However, the brooding cavity may be regarded as a displacement of the swollen basal cavity in a distal and frontal direction. This is correlated with the encrusting mode of life, which does not allow basally directed expansion.

EUTHYRISELLA Bassler

Euthyrisella Bassler, 1936 : 161 (for *Euthyris* Hincks *preocc.*)

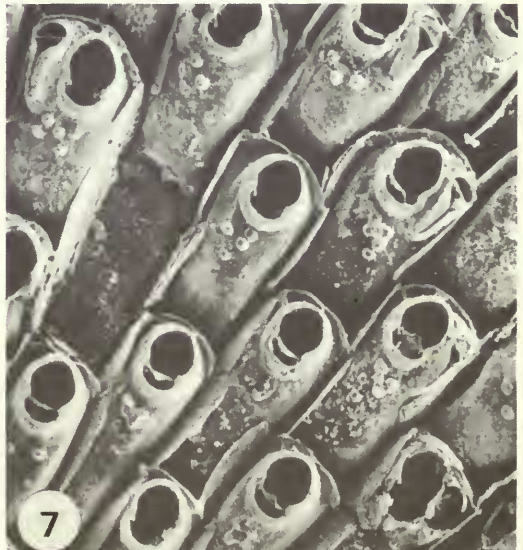
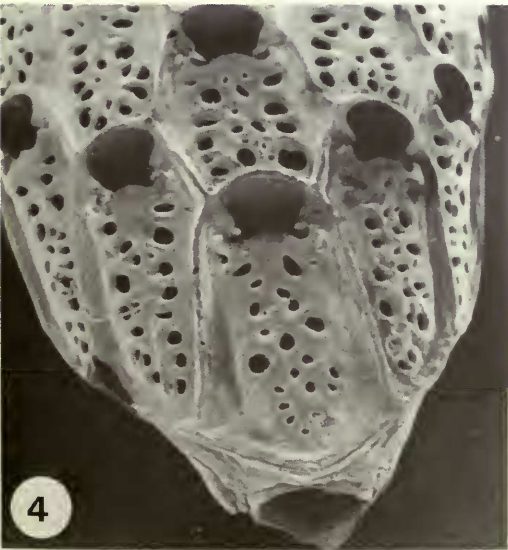
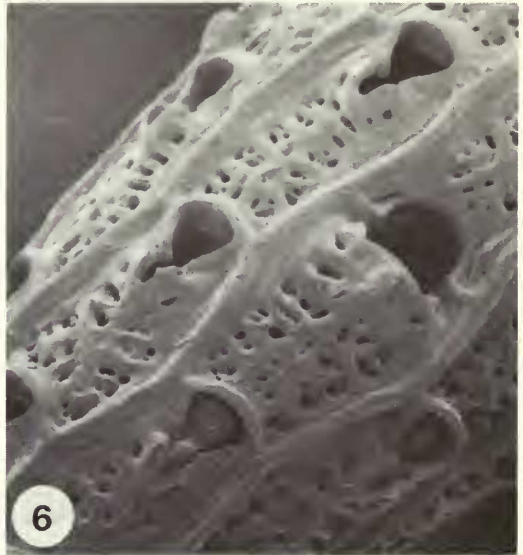
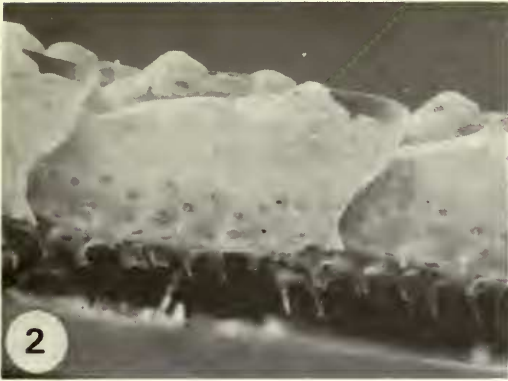
TYPE SPECIES. *Euthyris obtecta* Hincks, 1882.

DESCRIPTION. Colony flustriform, branching, multiserial and unilaminar, with basal and marginal extrazoooidal coeloms bounded by cuticular walls, which become thickened to form anchoring, rooting structures, with internal calcified plates late in ontogeny. Zooids with depressed, curved, thinly calcified frontal shields, with few pores. Lateral walls converge basally and are attached to the basal cuticular wall by intermittent calcified processes. Dimorphic brooding zooids inflated basally, with enlarged orifices and opercula.

Euthyrisella obtecta (Hincks)

Euthyris obtecta Hincks, 1882 : 164, pl. 7, fig. 3, 1893 : 177. Harmer, 1902 : 277, pl. 16, figs. 32–37. Levensen, 1909 : 272, pl. 15, figs 2a–f. Canu & Bassler, 1929 : 464, Figs 199 A–M.

Figs 2–7 Scanning electron micrographs of Euthyrisellidae: (2) *Euthyrisella obtecta* (Hincks) BMNH 1890.3.24.22, Torres Straits, lateral view of zooids showing lateral and oral septulae and basal processes $\times 65$; (3) *E. obtecta*, zooids viewed from distal end, showing distal septulae (arrowed) and frontal processes $\times 120$; (4) *Tropidozoum cellariiforme* Harmer BMNH 1964.3.10.1, Celebes, frontal view of primary zooids of internode, showing calcified tube at distal end of nodal kenozooid $\times 72$; (5) *T. burrowsi* sp. nov. BMNH 1975.1.4.1, Madagascar, basal view of proximal part of internode, showing autozooids and basal coelomic column, with basal septulae and bars of calcification $\times 30$; (6) *T. burrowsi*, frontal view of autozooids and brooding zooid $\times 53$; (7) *Neoeuthyris woosteri* (MacGillivray) BMNH 1979.2.1.1, Western Australia, frontal view of autozooids and avicularia $\times 30$.



SPECIMENS EXAMINED. BMNH. North Australia, 1897.5.1.445 (possibly type material); Broughton Id., New South Wales, 1883.11.29.3; Port Denison, East Queensland, 1883.11.29.43; Murray Id., Torres Straits, 1890.3.24.22, 16–36 metres; 1890.7.23.38, 17–36 metres; 1916.8.23.115, 9–36 metres; Baleine Bank, Northwest Australia, 1892.1.28.34A, 17–22 metres; Holothuria Bank, Northwest Australia, 1892.1.28.61A, 22 metres; Long Reef, 5 miles North of Sydney, New South Wales, 1975.1.2.3, 101 metres.

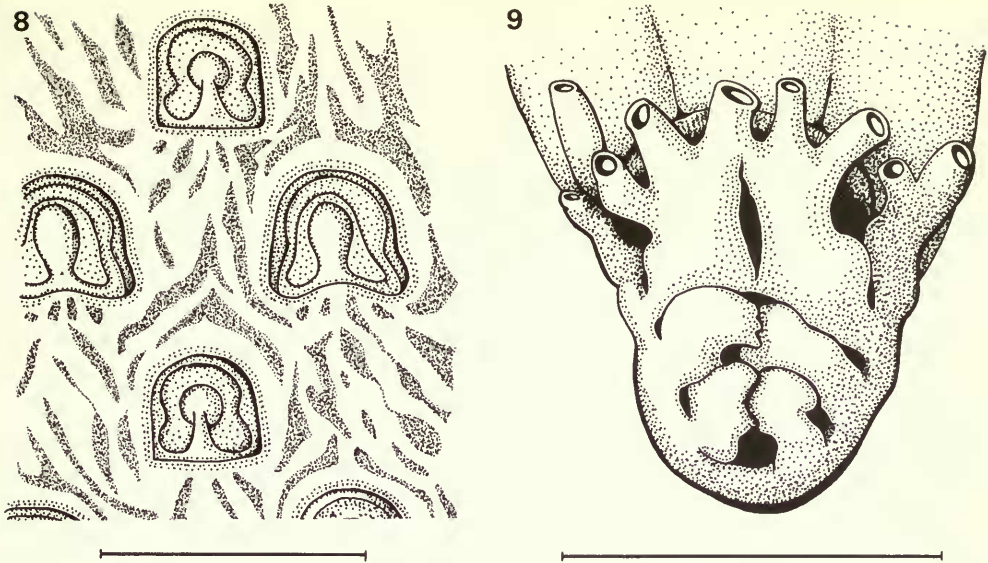
DESCRIPTION (Figs 2, 3, 33, 35). *Euthyrisella* with zooids intercommunicating by 6–8 lateral septulae (8–10 in brooding zooids) and 5–6 distal septulae. Zooids with 12–20 basal septulae (45–50 in brooding zooids) and 2–8 septulae distal to the orifice, which communicate with the hypostegal coelom of the next distal zooid. Frontal shield thinly calcified, with 2–5 pores proximal to the orifice (10–15 in brooding zooids), some of which are septulae communicating with the part of the hypostegal coelom basal to the frontal shield. Orifices with small lateral condyles. Dimorphic (brooding) zooids about twice the size of the autozooids.

REMARKS. The hypostegal coelom beneath the frontal shield is not nearly as extensive as in *Pleurotoichus* and *Tropidozoum* (see below), but forms a small expansion proximally to the orifice (Fig. 35). The dimorphic brooding zooids occur in a proportion of approximately 1:20 autozooids. Large embryos are present in one colony from Torres Straits (1890.7.23.38).

The colonies are profusely branched and reach a height of 150 mm. The branches are 2–3 mm wide and are usually formed by simple bifurcation, but some, astogenetically late, lateral branches occur. Before a bifurcation the width increases to 4 mm, and the number of zooids in a transverse series from 3–4 to 5–6. There is a tendency for one branch of a bifurcation to include more zooids than its pair. At irregular intervals there is an increase in the width which does not result in a bifurcation, but a sudden decrease in zooid numbers between successive generations. This seems to be associated with a period of cessation of growth, as the basal cuticle is much thicker on the proximal side of the interruption.

The early astogeny has been inferred from one colony (1883.11.29.3). A single, erect kenozooid is followed by a distal zooid which itself buds one distal and paired distal-lateral zooids. Thereafter, increase in zooid rows originates from bifurcations of series distal to marginal zooids. At the base of fronds zooids have the series: Lz 0.50, 0.50, 0.67, 0.50, 0.53, 0.58, 0.60 mm. The only other astogenetic changes are confined to brooding zooids which do not appear until the branch is 100 mm in length (300 zooid generations). Brooding zooids are central and often paired in the same transverse series.

The extrazoooidal marginal coelomic systems are extensive and resemble those formed by lateral kenozooids in several anascan, flustriform genera and the ascophoran species *Euthyroides episcopalis* and *Onchoporella buskii*. The changes during colony growth may be regarded as ontogenetic, in that they occur within the bounding walls of an existing structure. The primary changes are found 40 zooid generations back from the growing tip. The lateral cuticle expands intussusceptively and thickens considerably. About 150 zooid generations back, calcareous spicules derived from the lateral walls of the marginal zooids expand and form a series of plates within the lateral coeloms. Subsequent series of plates, alternating with cuticle, are formed at the base of the colony, and the investing cuticular wall continues to expand and thicken (see Harmer, 1902). At the earliest astogenetic level there are 9–12 series of thickened plates on each side of the branch. The growth of anchoring rootlets is also an ontogenetic rather than an astogenetic change. The marginal elements extend basally and divide into rhizoids which penetrate the substratum, incorporating particles of sediment within a meshwork. Some calcification occurs so that the rhizoids are not only flexible but adherent. It is possible that further extensions are astogenetic and consist of kenozooids budded from the extrazoooidal coeloms. It is interesting that an almost identical series of calcareous plates occurs in the kenozooidal, lateral rooting systems of *O. buskii*. The rooting system of the colony (1883.11.29.3) has incorporated the substratum of shell fragments, sand grains, foraminiferans and dead bryozoans. Although these last are worn, and may have been transported, it is interesting that they comprise



Figs 8 and 9 (8) *Pleurotoichus clathratus* (Harmer) BMNH 1976.1.2.1, Heron Island, sketch of frontal surface of autozooids and brooding zooids, showing opercula and irregular bars of calcification of frontal shield beneath the cuticular frontal wall; (9) *Didymosella larvalis* (MacGillivray) BMNH 1890.4.17.1-10pt., Spencer Gulf, sketch of ancestrula. Scale bars = 0.50 mm.

rooted 'sand fauna' species (see Cook, 1965, 1966, 1979*b*). They include colonies of *Conescharellina* sp., the internodes of jointed species of cyclostomes and of the cheilostome anascan, *Exostesia didomatia* (see Brown, 1948 : 111). Other epizoic forms include a ramifying hydroid and numerous egg sacs of some unknown animal.

PLEUROTOICHUS Levinsen

Pleurotoichus Levinsen, 1909 : 270.

TYPE SPECIES. *Euthyris clathrata* Harmer, 1902.

DESCRIPTION. Colony flustriform, branching, multiserial, unilaminar, with marginal and basal extrazoooidal coeloms. Zooids with flat, depressed frontal calcified shields consisting of irregular bars and foramina, each bar surrounded by cuticle. Lateral walls curved and converging, basal walls linear, reaching the extrazoooidal basal wall in discontinuous series. Dimorphic zooids slightly larger than autozooids, with larger opercula, inflated basally. Lateral coeloms slightly calcified late in ontogeny.

Pleurotoichus clathratus (Harmer)

Euthyris clathrata Harmer, 1902 : 266, pl. 16, figs 18-31.

Pleurotoichus clathratus : Levinsen, 1909 : 270. Canu & Bassler, 1929 : 464, Figs 200 A-N.

SPECIMENS EXAMINED. BMNH. Australia, 1899.7.1.2606; Port Jackson, New South Wales, 1903.5.1.2, sublittoral; Swan River, South Australia, 1935.10.18.1; Middle Harbour, Port Jackson, 1975.8.1.7; Watsons Bay, 1975.8.1.8.9, under rock ledges, low tide; Heron Id., Queensland, 1976.1.2.1.

DESCRIPTION (Figs 8, 34). *Pleurotoichus* with zooids communicating by 7-9 lateral and 7-10 distal septulae. Zooids with 12-15 basal septulae, and 3-5 distal to the orifice,

communicating with the hypostegal coelom of the next distal zooid. The frontal shield is formed by irregular cuticle-covered bars, which anastomose, leaving large slit-like foramina. The hypostegal coelom is extensive both above and below the shield. The dimorphic brooding zooids are only slightly larger than the autozooids; they are inflated basally, and occur in larger numbers than in *E. obtecta*, in a proportion of 1 : 5 autozooids.

REMARKS. The presence of cuticle surrounding the bars of calcification of the frontal shield, and the layers of cuticle on either side of the lateral and distal calcified walls, together with the general delicacy of the interior structures, makes it almost impossible to prepare calcified skeletons of *P. clathratus* for scanning electron microscopy. Investigation of specimens has therefore been almost entirely confined to examination of thin-sections. The hypostegal coelom, both frontal and basal to the calcified shield is very extensive. The convergent lateral walls reach the basal cuticular extrazoooidal wall in one short, linear insertion. The calcified processes are cuticular terminally at the point of contact. Zooids are thus almost suspended from the circum-orificial region in a bag of tough, flexible cuticle. This flexibility is probably correlated with the turbulence of the very shallow waters in which the species lives. The growth form is analogous to that of *Chartella papyracea* (see Ryland & Hayward, 1977 : 80), which also inhabits rocky ledges in the sublittoral region.

Colonies may reach a height of 185 mm (Harmer, 1902 : 268). The specimens examined have a maximum height of 50 mm, and have very few bifurcations. A few lateral sub-branches occur late in astogeny. The earliest stages are missing, but may be inferred from a colony from Port Jackson (1975.8.1.7), which has 4 zooids in a transverse row at its base. Extrapolating from this, the early astogeny is probably similar to that of *E. obtecta*, and the zooids show a similar series of increase in size. Interruptions of growth, involving a sudden decrease in the number of zooids in transverse series from 6-7 to 3-4, occur frequently, between 6 and 10 zooid generations apart.

Dimorphic zooids are frequent (Fig. 2), and are first found 25 generations from the base of the colony. They are placed in the central zooid series, and large embryos are present in the colony from Heron Island (1976.1.2.1.).

The marginal coeloms become inflated with ontogeny, and the cuticular walls become thickened. Small calcified processes develop from the lateral walls of adjacent zooid series, but calcified plates do not occur.

The colony from Heron Island has a large number of epizoid forms, particularly colonies of hydroids. On the basal cuticle there are small colonies of jointed cyclostome bryozoans and of *Cellaria* sp. The lower part of the colony is completely invested by a colonial ascidian.

TROPIDOZOUM Harmer

Tropidozoum Harmer, 1957 : 1106. Cook, 1975.

TYPE SPECIES. *T. cellariiforme* Harmer, 1957.

DESCRIPTION. Colony cellariiform, internodes connected by complex nodes of partially calcified kenozooids and investing extrazoooidal basal coelom. Basal coelomic channel confluent among internodes. Central zooids of internodes with extended basal calcification forming a keel. Zooids with depressed frontal shields, with large foramina. Hypostegal coelom extensive, frontal septulae absent. Brooding zooids large, inflated basally, with dimorphic orifices.

Tropidozoum cellariiforme Harmer

Tropidozoum cellariiforme Harmer, 1957 : 1106, pl. 67, figs 15-17, 20. Cook, 1975 : 162, pl. 2, pl. 3, Figs 2A, 3 (explanation of plates 1 and 3 transposed). Cook, 1979a : 200, pl. 1, fig. 1.

SPECIMENS EXAMINED. BMNH. Siboga Stn 144, South of Halmaheira, Djilolo, East Celebes, 0-45 metres, coral and lithothamnion bottom, 1964.3.10.1 and 1979.1.4.1.

ZMA, as above, TYPE and other material.

DESCRIPTION (Figs 4, 11, 30). *Tropidozoum* with internodes 8 mm long and 1.6 mm wide, comprising 70 zooids. Longest, usually the central series, of 12 zooids; widest, usually the penultimate transverse series, of 6 zooids. Zooids occupying an arc of 240° in section. The proximal zooid of each internode is wider (Lz 0.37 mm), and the ultimate zooids shorter and narrower (Lz 0.50, lz 0.30 mm), than other zooids. Orifice rounded distally with large complex condyles delimiting a proximal part which is straight or curved distally. Frontal shield with up to 30 large, irregular foramina. Hypostegal coelom extending beneath the frontal shield. Communication between the visceral coelom of one zooid and the hypostegal coelom of the next distal zooid inferred to be through a pair of minute pores passing through the distal-lateral calcification of the orifice (Fig. 30). Communication with the basal coelom through numerous pores in the confluent lateral and basal walls. Brooding zooids dimorphic, large, inflated basally, placed in the central zooid series, occurring in the proportion of 1 : 10 autozooids. Brooding zooid orifices larger, but similar to those of autozooids.

REMARKS. The earliest astogenetic stages are missing from the colonies examined, but it is inferred that they are similar to those of *T. burrowsi* (see below). The cuticle of the basal coelom becomes increasingly thickened and inflated with ontogeny, and eventually forms a supportive and rooting structure.

The septulae connecting the visceral and hypostegal coeloms of sequential zooids are very small, and apparently pass through the thick calcification distal and lateral to the orifice. The tubular communication traces a curved path, at an angle to the longitudinal axes of the zooids, and is impossible to expose in its entirety in either longitudinal-lateral or in tangential thin-section. The pattern of other zooidal and extrazooidal communications has been described by Cook (1975).

A few, small embryos have been seen in the brooding zooids. The distal part of the orifice of these zooids appears to be formed by the proximal calcification of the next distal zooid (see Fig. 30).

Epizoid forms include other erect, jointed bryozoans such as *Cellaria* sp., small colonies of a *Bowerbankia*-like ctenostome, encrusting colonies of *Robertsonidra argentea* (Hincks), and foraminiferans belonging to the informal 'Homotrema' group.

Tropidozoum burrowsi sp. nov.

Tropidozoum sp. Cook, 1975 : 165, pl. 1, figs A-C, Fig. 2B (explanation of Plates 1 and 3 transposed).
Hayward & Cook (in press).

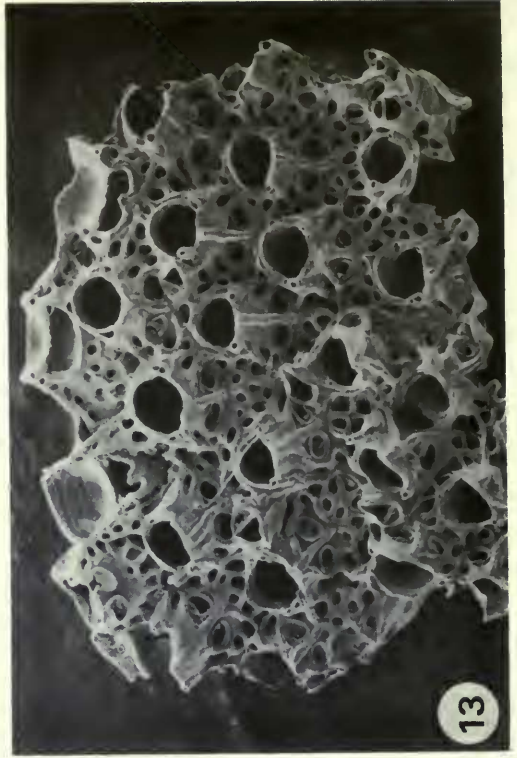
SPECIMENS EXAMINED. BMNH. HOLOTYPE, Tuléar, TU 24, Madagascar, extérieur Grande Vasque, 23.9.69, 15 metres, 1975.1.4.2. Paratypes, Tuléar, Pichon D25, 1975.1.4.1; other material: South of Durban, Umtwalume River mouth North by West 7 miles, 12271, shell fragment bottom, 90 metres, 1949.11.10.184, and 12272, 1949.11.10.250, transported, dead internodes.

SAM. 'Meiring Naude', Southeast Africa, Stn 131, 780 metres, Stn 151, 900 metres, transported, dead internodes.

ETYMOLOGY. Named after Mr H. W. Burrows, whose manuscript notes and drawings on the Gilchrist Collection from South Africa are stored at the BMNH.

DESCRIPTION (Figs 5, 6, 10). *Tropidozoum* with internodes 7 mm long and 1.1 mm wide, comprising 70 zooids. Longest longitudinal series of 16 zooids; widest, penultimate transverse series of 6 zooids. Zooids occupying an arc of 300° in section. Proximal and ultimate zooids wider than other zooids. Central basal keel thickened by base of calcification during ontogeny. Orifices rounded distally, with large condyles delimiting a deep, triangular sinus. Frontal shield with 30 small, irregular foramina, occluded during ontogeny. Dimorphic brooding zooids inflated basally, larger than autozooids, with wide, non-sinuate orifices.

REMARKS. The early stages in astogeny of erect branches arise from a confused mass of



rooting kenozooids, and it is not known if these represent one, or a large number of colonies. Some kenozooids are rootlets, others are shorter, and from these small erect internodes originate. The maximum number of internodes in an erect branch is 15, reaching a height of 130 mm. The primary internodes are nearly all small, including only 3 zooids, and are rounded in shape. Later internodes become progressively more elongated and include more zooids; a typical sequence has 3, 6, 25, and 36 zooids. Occasionally, a small internode occurs later in astogeny, between two longer internodes. Zooid length at the base of an internode forms a series Lz 0.55, 0.47, 0.60, 0.55, 0.62, 0.58, 0.60 mm (cf. *E. obtecta*).

Brooding zooids appear by the fifth internode and are placed in the centre of a transverse zooidal series; a maximum of 10 occur in one internode. *T. burrowsi* is known from direct observation (Dr J.-G. Harmelin, *pers. comm.* 1974), to be a shallow-shelf species, and all the deep water records given above are of worn, dead internodes found in sediments which had been transported. The colonies from Madagascar were observed alive *in situ*; they have several epizoic and epiphytic forms, including sponges, small gorgonians, hydroids, serpulids, the bryozoan *Cellaria* sp. and small algae. The coelomic pigment of living colonies was bright red, and they were found growing together with gorgonians etc., and forming patches 20–40 cm across on calcareous accretions covered by sand.

NEOEUTHYRIS Bretnall

Neoeuthyris Bretnall, 1921 : 157.

TYPE SPECIES. *Euthyris woosteri* MacGillivray, 1891.

DESCRIPTION. Colonies encrusting, basal walls of zooids uncalcified except at the margins. Frontal shields curved, hyaline. Lateral walls prominent. Orifices with a wide sinus and paired condyles. Avicularia unilateral and oral, mandible hinged on a complete bar. Brooding zooids with large, dimorphic orifices and a brood chamber formed by a large endozooidal ovicell, closed by the operculum.

REMARKS. The characters of *N. woosteri*, the only species, differ from those of other genera of Euthyrisellidae in the encrusting habit, lack of basal coelom, and presence of ovicells and avicularia. The essential structure of the colony, the nature of the frontal shield, the interzooidal communications and the dimorphism of brooding zooids, are, however, all similar to those found in the other genera.

Neoeuthyris woosteri (MacGillivray)

Euthyris woosteri MacGillivray, 1891 : 77, pl. 9, fig. 2.

Neoeuthyris woosteri: Bretnall, 1921 : 158, Fig. 1. Hastings, 1960; 1964 : 245, figs 1, 2.

SPECIMENS EXAMINED. BMNH. Fremantle, Western Australia, 1948.3.12.1; Western Australia, 1938.8.10.1; Cosy Corner, Torbay Head, Western Australia, 1979.2.1.1.

AM and NMV: U875 HOLOTYPE (see Hastings, 1964 : 246).

DESCRIPTION (Figs 7, 12, 28, 29, 31, 32). *Neoeuthyris* encrusting algae (usually *Metamastophora flabellata*), zooid basal walls uncalcified. Zooids communicating by 3–5 lateral and 2–3 distal septulae placed at the base of the vertical walls. Visceral-to-hypostegal communication by paired groups of 4–5 septulae in the upper part of the distal

Figs 10–13 Scanning electron micrographs of brooding zooids of Euthyrisellidae and Didymosellidae: (10) *Tropidozoum burrowsi* sp. nov. BMNH 1975.1.4.1, Madagascar $\times 103$; (11) *T. cellariiforme* Harmer BMNH 1964.3.10.1, Celebes $\times 127$; (12) *Neoeuthyris woosteri* (MacGillivray) BMNH 1979.2.1.1, Western Australia $\times 50$; (13) *Didymosella larvalis* (MacGillivray) BMNH 1979.7.5.2, near Melbourne, showing partially formed ovicells at growing edge $\times 35$.

wall behind the orifice (Fig. 32). Frontal shield smooth, very thinly calcified, with small protuberances, but no suboral septulae, and with no extension of hypostegal coelom basally. Two pairs of frontal septulae beside the orifice, one pair giving rise to an avicularium (Fig. 28). Avicularia with acute mandibles, directed proximally. Brooding zooids large, with dimorphic orifices, ovicell apparently formed by an expansion of the lateral and distal walls, protruding into the cavity of the next zooid, which is very short (Lz 0.45 mm).

REMARKS. Avicularia on the right hand side of a lobe tend to occur on the right hand side of the zooids (viewed frontally), and *vice versa*. The algal substratum is influenced during growth by the presence of the bryozoan (see Hastings, 1964).

The extreme fragility of the colonies makes investigation very difficult. Scanning electron microscopy of small fragments, and thin sections, have enabled us to reconstruct the interzooidal and intrazooidal communication systems, which are hardly visible in whole preparations using a light microscope.

N. woosteri has rarely been reported, and the ancestrula and early astogeny is unknown. Most specimens are known to have encrusted *M. flabellata* which had been washed up on the shore, and both species probably occur together in deeper water. Nearly all records are from Western Australia, but MacGillivray (1891) reported specimens from Cooktown, Queensland.

Table 2 Measurements (mm) of autozooids and avicularia of Didymosellidae

	Lz	lz	12o (av.)	Lr	Lm	No. of frontal pores
<i>Didymosella</i> sp. (Labracherie)	0.33-0.50	0.25-0.37	0.15	0.15-0.23	-	4
<i>D. irregularis</i>	0.58-0.73	0.34-0.37	0.22	0.14-0.22	-	10
<i>D. acutirostris</i>	0.50-0.60	0.50-0.60	0.16	-	-	-
<i>D. crassa</i>	0.68-1.00	0.69-0.90	0.27	0.22-0.27	-	30
<i>D. porosa</i>	0.50-0.75	0.33-0.44	0.15	0.08-0.13	-	10
<i>D. clypeata</i>	0.88-0.96	0.46-0.57	0.23	0.12-0.15	-	15
<i>D. 'larvalis'</i> -fossil (New Zealand)	0.50-0.60	0.45-0.48	0.16	0.20-0.30	-	9
<i>D. 'larvalis'</i> -fossil (Australia)	0.60-0.65	0.48-0.50	0.19	0.20-0.30	-	10
<i>D. larvalis</i> -Recent	0.55-0.70	0.40-0.50	0.18	0.20-0.30	0.15-0.25	10
<i>D. parviporosa</i>	0.55-0.75	0.35-0.65	0.16	0.13-0.20	-	20
<i>D. pluma</i>	0.65-0.80	0.64-0.90	0.22	0.28-0.32	0.70-0.80	20
<i>T. magnirostris</i>	0.80-1.00	0.60-0.80	0.15	0.25-0.28	0.23-0.30	20
<i>T. magna</i>	0.65-0.70	0.65-0.70	0.27	0.30-0.35	-	5
<i>T. boninensis</i>	0.60-0.90	0.50-0.70	0.20	0.15-0.20	0.50-0.75	15

DIDYMOSELLIDAE Brown

Didymosellidae Brown, 1952 : 194.

TYPE GENUS. *Didymosella* Canu & Bassler, 1917.

DESCRIPTION. Interior-walled cryptocystidean ascophorans, usually with extrazooidal basal coeloms, and considerable basal calcification. Zooid frontal shields with pores and marginal frontal septulae, becoming thickly calcified during ontogeny, obscuring the lateral walls.

Peristomes elongated, with or without foramina and/or spiramina frontally. Primary calcified orifice not well defined, operculum a flap-like extension of the distal part of the ascus wall. Septulae in vertical and basal zooid walls numerous. Avicularia adventitious,

arising from oral frontal septulae, usually unilateral, with large subrostral chambers and acute rostra. Mandibles orientated laterally, hinged on a complete bar. Brood chambers formed by an expansion of the distal part of the peristome wall, opening above the operculum.

Ontogeny of zooid walls

As in the Euthyrisellidae, ontogenetic changes in the Didymosellidae are apparently rapid. Few colonies show complete series of frontal shield development, and partially uncalcified buds are contiguous proximally with fully formed zooids in which secondary calcification is well advanced (see Fig. 21). For a brief period, the prominent lateral walls and depressed cryptocystal shield resemble those of *Pleurotoichus* or *Tropidozoum*. The presence of numerous frontal marginal septulae, however, means that the frontal calcification soon thickens, obscuring all zooidal boundaries. Funnels in the calcification common to tubular extensions above septulae of adjacent zooids are developed, as in the umbonuloid genus *Tremogasterina* (see Cook, 1977).

The calcification of the primary orifice merges into the development of the peristome and no clear-out boundary is obvious. Avicularia are formed as lateral-oral frontal buds, their subrostral chambers deriving from a flattened plate of the frontal shield, bordered by 3–8 marginal septulae (see Fig. 20). In *D. pluma* particularly, funnels derived from these septulae, and frontal pores, remain prominent features of the large avicularian chambers quite late in ontogeny (see Fig. 21).

Coelomic systems and communication

The presence of frontal septulae is correlated both with the absence of interzooidal visceral-to hypostegal communication (Fig. 1B), and with the massive calcification of the frontal shields. In nearly all species, basal septulae, which communicate with a thin extrazooidal coelom, have been observed. Basal calcification, too, is considerable, and forms processes or massive pillars, which contact the substratum, allowing a semi-repent mode of life, or strengthening erect branches. The nature of the porous basal calcification has long been noted by authors (Stoliczka, 1865, MacGillivray, 1895, Waters, 1885, Levinsen, 1909, and Brown, 1952), who have either compared it to that of *Selenaria* (which also has an extrazooidal, basal coelom, see Chimonides & Cook, 1981), or have suggested a radicular function for the pores.

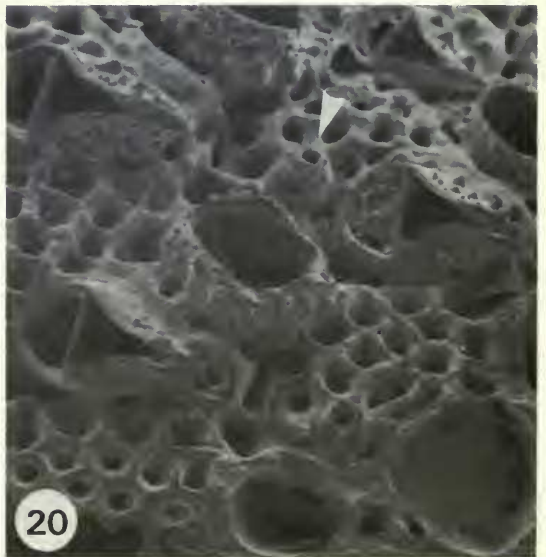
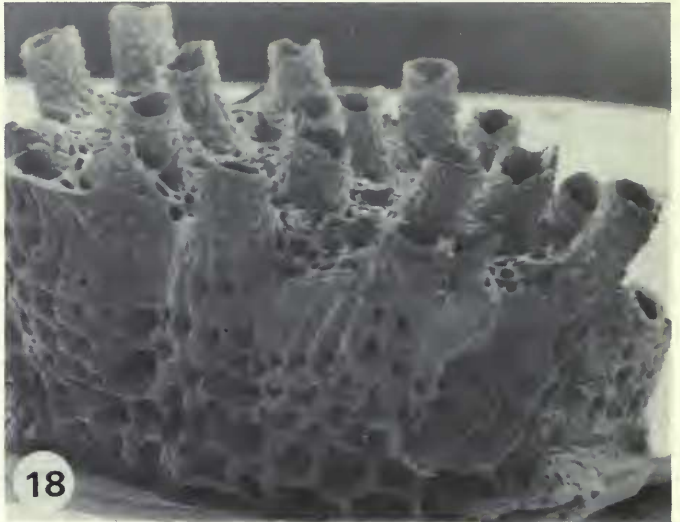
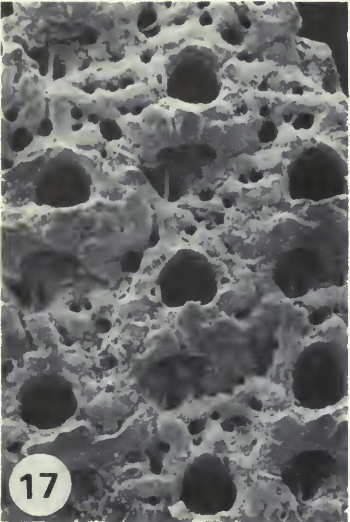
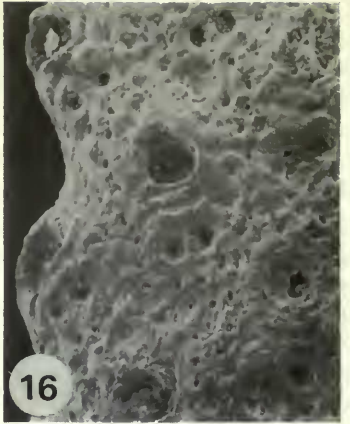
Opercula, mandibles and peristomes

In correlation with the elongated peristomes (see Harmer, 1957 : 652), and in contrast to the Euthyrisellidae, opercula are hardly differentiated, and are flap-like expansions of the ascus wall. Mandibles are acute, and hooked in *D. larvalis* and *T. magnirostris*. Those of *D. pluma* and *T. boninensis* are elongated and resemble the mandibles of the anascan genus *Smittipora* (see Harmer, 1926), in having a central rachis, and expanded wings of cuticle.

Brooding zooids

In some species, brooding zooids and their orifices are larger than those of autozooids, but there seems little evidence of dimorphism in other characters. In some species, the brooding zooids may have smaller avicularia, or none, and there is evidence of patterning of the avicularia of surrounding zooids.

Unlike the Euthyrisellidae, the family Didymosellidae has an extensive fossil record (see below).



***DIDYMOSELLA* Canu and Bassler**

Didymosella Canu & Bassler, 1917 : 43.

TYPE SPECIES. *Lepralia larvalis* MacGillivray, 1869.

DESCRIPTION. Zooidal peristomes with large, paired foramina, spiramina absent.

REMARKS. *Didymosella* was included in the family Escharellidae by Canu & Bassler (1929 : 33), and in the Exochellidae by Bassler (1953 : G205). The distinctive characters of the genus were discussed by Brown (1952 : 194), who noted that the Italian fossil species *Porina bioculata* Waters (1891 : 26, pl. 3, fig. 15), the type species of *Bimicroporella* Canu (1904 : 12), was not closely related to *Didymosella*. *B. bioculata* (Waters), *B. ventricosa* Canu (1904) and *B. watersi* Brown (1958) all have some superficial similarity with *Didymosella*, but have no suggestion of a basal coelom, and have hyperstomial ovicells.

Didymosella has an extensive fossil record. The earliest known species is an undescribed form listed by Labracherie (1972 : 44), from the Middle Eocene of North Aquitaine, France. Specimens of this species have been examined (Bazas-rural, 200 metres, Labracherie Coll.). The material is fragmentary and comprises only 30 zooids. Most of the fragments appear to have been encrusting, but some have basal grooves and a few have minute pores, which together with the thick, basal calcification are interpreted to indicate the former presence of a basal coelom. The frontal shields have 3–6 pores and 7–9 funnels indicating frontal septulae. Zooids communicate through 1–2 distal, and 2–3 lateral septulae. The paired peristomial foramina are distinct, as are the avicularian rostra, some of which have a complete bar. The rostra are open terminally which, by analogy with *D. pluma* (see p. 76) probably indicates that the mandibles were elongated.

Another fossil species, *D. irregularis*, was described from the Upper Eocene (Lower Jacksonian) of north-western Florida by Cheetham 1963 : 66, pl. 2, fig. 13). This had unilaminar colonies and larger zooids with up to 20 frontal pores and very small, acute avicularia. The orifices of the brooding zooids; which had broken peristomes exposing the ovicells, were slightly dimorphic.

In view of Labracherie's (1972) records, it appears that *D. acutirostris* Faura y Sans & Canu (1917 : 90, pl. 7, figs 3–5), from the Upper Eocene of Monresa, Barcelona, is also attributable to *Didymosella*. The illustration is not conclusive, but the species was described with paired, peristomial foramina and peristomial ovicells. The zooids were larger than those of Labracherie's species.

The wide Eocene distribution of *Didymosella* continued during the Oligocene and Miocene (see below), and is maintained in Recent seas.

***Didymosella crassa* Canu and Bassler**

Didymosella crassa Canu & Bassler, 1920 : 116, pl. 88, figs 1–7.

SPECIMENS EXAMINED. BMNH. Oligocene (Vicksburgian), west bank of Conecuh River, Escambia Co., Alabama. Canu & Bassler Coll.

Figs 14–20 Scanning electron micrographs of fossil and Recent Didymosellidae: (14) *Didymosella clypeata* Canu & Bassler BMNH Lower Miocene, Victoria, basal side of branch, showing septulae $\times 31$; (15) *D. clypeata*, frontal side of branch $\times 34$; (16) *D. porosa* (Stoliczka) BMNH D 36784–92, Middle Oligocene, New Zealand, part of frontal margin of branch $\times 21$; (17) *D. 'larvalis'* BMNH D36783–7, Miocene, New Zealand, $\times 40$; (18) *Tubiporella boninensis* Borg BMNH 1889.8.21.105, Recent, China Sea, lateral view of young colony, ancestrula at right, showing basal extrazooidal calcification $\times 25$; (19) *T. boninensis* zooids at growing edge, showing spiramina, frontal pores and avicularian rostra $\times 57$; (20) *T. magnirostris* (MacGillivray) BMNH 1899.7.1.2686, Recent, Victoria, zooids viewed from distal end, showing spiramen (arrowed) and base of avicularian subrostral chamber (bottom right) $\times 57$.

DESCRIPTION (Fig. 23). *Didymosella* with large zooids and tubular peristomes. Zooids with 25–35 frontal pores and 6–8 marginal septulae. Avicularia large, with channelled rostra open terminally. Basal surface thickened, with grooves and pores.

REMARKS. In all respects *D. crassa* and *D. pluma* (see p. 76) are so alike that it is possible to postulate a direct genetic link between the Oligocene and Recent populations from the central West Atlantic. The skeletal characters differ from those of *D. pluma* only in the larger number of frontal pores and in the absence of elongated calcified basal processes, which last may be due to wear during preservation. The open channel at the terminal end of the avicularian rostrum allows the inference that the mandible was elongated, and may have even been expanded laterally like that of *D. pluma* (see p. 78).

Didymosella porosa (Stoliczka)

Semiescharipora porosa Stoliczka, 1865 : 128, pl. 19, figs 10–13.

Didymosella porosa : Canu & Bassler, 1929 : 328.

Didymosella aff. *porosa* : Brown, 1952 : 198, Figs 139, 140.

SPECIMENS EXAMINED. BMNH. Middle Oligocene, Pareora, Tarahoke Quarry, N.W. tip of South Island, New Zealand, D36788-92.

DESCRIPTION (Figs 16, 27). *Didymosella* with erect, ligulate branches, with 4–5 transverse zooid series. Branches flat and bifurcated. Lateral marginal zooids curved outward, their peristomes forming serrations. Secondary orifices with paired spine bases. Marginal avicularia large. Basal calcification with numerous pores.

REMARKS. Branches are composed of 20 sequentially distal zooid series. The marginal zooids are curved so that their orifices are at an angle of over 45° to those of the central series. At the same time, the orifices are curved towards the frontal side of the branch. The paired peristomial foramina are separated from the proximal edge of the peristome by a distance greater than 0.20 mm.

Stoliczka (1865) mentioned the thickening of the basal calcification and the porous surface, which was also noted by Brown (1952), who suggested that the pores might have a radicular function. In spite of Brown's doubtful assignment of his material to *D. porosa*, it is so close in general characters, age and locality to Stoliczka's specimens (which were from the Lower Miocene of Orakei (Hauraki) Bay, North Island), that it may be confidently included in the species.

Didymosella clypeata Canu & Bassler

Didymosella clypeata Canu & Bassler, 1935 : 32, pl. 9, figs 7, 8.

SPECIMENS EXAMINED. BMNH. Lower Miocene, Mount Martha, Victoria. Anticline Creek (Janjukian), Dartmoor, Victoria D34200-01.

DESCRIPTION (Figs 14, 15). *Didymosella* with erect ligulate branches, with 2–3 transverse series of zooids. Branches curved towards the basal side so that orifices of the marginal series are at an angle of 70° to those of the central series. The marginal zooids also curve outwards slightly at about 15° to the central axis. Secondary orifices with paired spine bases. Frontal pores are stellate (in basal view) and the paired peristomial foramina are close to the proximal edge of the peristome, at a distance of 0.10–0.15 mm. Basal calcification thickened, with a few irregularly spaced pores.

REMARKS. The marginal avicularia are large, and occur about half way up the zooids.

Although very similar to *D. porosa*, *D. clypeata* differs in the number of zooids in a transverse series, the curvature of the branches and the placing of the peristomial foramina.

The combination *Porina clypeata* Waters (1881 : 332, pl. 17, fig. 67, 1882a : 268) was used for an entirely different species from the Miocene of Mount Gambier, Victoria.

The *Didymosella larvalis*-complex

The Recent species *D. larvalis* is here confined to algal-associated, encrusting colonies, with no evidence of basal coeloms. Two fossil populations, one from the Australian Miocene, the other from the Oligocene to Miocene of New Zealand, have been ascribed by several authors to *D. larvalis*. Neither of these populations is assignable to *D. clypeata* or *D. porosa*, and they differ considerably from Recent *D. larvalis* in their colony forms.

A. *Didymosella* aff. *larvalis* (fossil specimens)

Porina larvalis: MacGillivray, 1895 : 104, pl. 14, fig. 26, Waters, 1882a : 269, pl. 8, fig. 19; 1882b : 509; 1887 : 189, pl. 6, fig. 8.

Didymosella larvalis: Brown, 1952, part: 195, Figs 135-138; 1958 : 56.

SPECIMENS EXAMINED. BMNH. Oligocene, Tarakohe Quarry, Waitapu, New Zealand, D36787; Miocene, Weka Pass, New Zealand, D36783-6, D36938, D36961-2; Miocene Muddy Creek, Victoria, Australia, D34255; Mount Gambier, Victoria, D32981-3 (Waters Coll.).

MM. Bairnsdale, Victoria, T42 (figured Waters, 1882a, pl. 8, fig. 19).

DESCRIPTION (Fig. 17). *Didymosella* with erect colonies with bilaminar expansions or cylindrical branches. Peristome slightly raised, thickened proximally forming a transverse ridge which overhangs the paired, peristomial foramina. Frontal pores stellate.

REMARKS. The bilaminar colonies (from Weka Pass, New Zealand), have basal walls forming a double layer. No pores connecting the layers can be seen. The erect fragments also have complete basal walls, and have a central cavity. One fragment (D36786) has a very long avicularium with a channelled rostrum which is open terminally. In general, the specimens are poorly preserved and worn. The calcification is, however, considerably thicker than that of Recent specimens. The stellate frontal pores can be seen from the inner surface of broken zooids.

B. *Didymosella larvalis* (MacGillivray)

Lepralia larvalis MacGillivray, 1869 : 134. 1879 : 30, pl. 37, fig. 5.

Escharoides larvalis: Levinsen, 1909 : 318. Livingstone, 1926 : 170, pl. 11.

Didymosella larvalis Brown, 1952, part: 195.

SPECIMENS EXAMINED. BMNH. Spencer Gulf, 1890. 4.17.10pt. Australia, 1897.5.1.883, 1963.4.18.16; Port Phillip Heads, 1897.5.1.881.882; Adelaide, 1899.7.1.5036A; Cowes Phillipps Id., 20 miles S.E. Melbourne, beach sand, 1979.7.5.2; No locality, 1963.2.12.63.

DESCRIPTION (Figs 9, 13, 36). *Didymosella* with colonies encrusting algae, sometimes rising into small, unilaminar expansions. Zooids communicating by 2 distal and 2-3 lateral multiporous septulae, surrounded by chambers of calcification. Basal wall uncalcified in encrusting zooids, peripherally calcified, or with a large, uncalcified, cuticle covered window in erect zooids. Proximal side of peristome elongated, calcification thin and hyaline. Distal side of peristome deficient. Lateral peristome with spinous processes. Frontal pores stellate, frontal septulae numerous. Avicularia large, with acute mandibles, hooked terminally. Ancestrula with a complex frontal shield of spinous processes.

REMARKS. The thin frontal calcification and lack of basal calcification are similar to that of



the algal-associated *Neoeuthyris woosteri* (see p. 67), and are also usually present in numerous other cheilostome species which are specific to this type of substratum. In erect zooids, the uncalcified basal area is progressively decreased with astogeny, eventually becoming confined to a window in the basal wall. No evidence of a basal coelom or of radicular expansions has been seen.

Specimens are small, but a few parts of colonies (1897.5.1.882) comprising more than 100 zooids, on narrow fronds of algae, show a distinct central zone of brooding zooids which have minute, paired avicularia. They are flanked by lateral series of autozooids in which most of the avicularia are placed with the closed mandible directed medially (cf. *T. magnirostris*, p. 77). In other colonies, there is no obvious patterning of brooding zooids or of avicularia.

Ancestrulae (1890.4.17.1.–10 pt., 1963.2.12.63) are large (La 0.52 mm, la 0.40 mm), and distinctly 'cribrimorph' in character. There is a well developed gymnocyst and large, oval opesia, overarched by 4 robust lateral spines. The oral shield is formed by a pair of large, spinous processes, which are fused centrally, leaving an open foramen. The shield terminates distally in 5 spines, and a further, laterally placed pair of bifurcated spines is closely apposed to the lateral walls of the ancestrula and the distal-lateral primary zooids of the post-ancestular triad (see Fig. 9). The systematic significance, if any, of 'cribrimorph' ancestrulae in ascophoran species is unknown. The ancestrulae of other species of *Didymosella* have not been found, and that of *Tubiporella boninensis* (see below) is not 'cribrimorph', but resembles subsequent zooids. Most cribrimorph species have anasciform, 'tata' ancestrulae, but 'cribrimorph' ancestrulae are known in the umbonuloid ascophorans *Triporella bidenticulata* (Canu & Bassler), see Cook (1967: 341) and *Romancheina asymmetrica* Moyano (1975: 63, Figs 1–8). *Temachia opulenta* Jullien (1883: 509, pl. 14, figs 26–29) also has a 'cribrimorph' ancestrula and is so similar to *R. asymmetrica* that it too may be postulated to have umbonuloid ontogeny. Apart from *D. larvalis*, the only cryptocystidean species with 'cribrimorph' ancestrulae known at present is *Schizoporella kiiensis* (Okada & Mawatari), see Mawatari (1952: 279, fig. 13).

Didymosella parviporosa Canu & Bassler

Didymosella parviporosa Canu & Bassler, 1929: 327, pl. 39, fig. 1.

Didymosella costulata Canu & Bassler, 1929: 327, pl. 39, fig. 2.

SPECIMENS EXAMINED. BMNH. Philippines, Albatross Stn D5145, 42 metres, 1931.12.30.119 (*D. parviporosa*); Stn D55141, 53 metres, 1931.12.30.120. (*D. costulata*).

DESCRIPTION. *Didymosella* with small, narrow zooids, each with an average of 20 frontal pores. Secondary thickening forming interzooidal funnels, with bars of calcification. Basal calcified wall with furrows and a few scattered pores. Avicularia, small, with acute rostra.

REMARKS. The specimens include one fragment of *D. costulata* and three of *D. parviporosa*, together comprising only 40 zooids. Both species were described from the same region and *D. costulata* appears to be a slightly worn, ontogenetically thickened stage of development of *D. parviporosa*. This conclusion is strengthened by the locality data of the BMNH specimens, which were labelled by Bassler. One, labelled *D. parviporosa*, is from Stn 5145, the original locality for *D. costulata*; the other labelled *D. costulata*, is from Stn 5141, one of the original localities for *D. parviporosa*.

Figs 21–24 Scanning electron micrographs of fossil and Recent Didymosellidae: (21)

Didymosella pluma sp. nov. BMNH 1899.7.1.5324, Recent, off Brazil, zooids at growing edge, showing raised lateral walls, frontal pores and channelled avicularian rostra $\times 71$; (22) *D. pluma*, lateral view of zooids showing lateral septulae and basal calcified processes $\times 62$; (23) *D. crassa* Canu & Bassler BMNH Oligocene, Alabama, showing channelled avicularian rostra $\times 59$; (24) *Tubiporella magnirostris* (MacGillivray) BMNH 1899.7.1.2686, Recent, Victoria, growing edge viewed from distal end of zooids, showing distal and basal septulae and basal calcified processes $\times 75$.

D. parviporosa differs from *D. larvalis* in the presence of a basal coelom, and its small, narrow zooids. It differs from *D. pluma* in its much smaller zooid size, and in its avicularian mandibles, which may be inferred to have been acute.

Didymosella pluma sp. nov.

Didymosella sp. Brown, 1952 : 198. Cook, 1981 (in press).

SPECIMENS EXAMINED. BMNH. HOLOTYPE, John Adams Bank (=Victoria Bank, off Brazil, Approx. 21°S, 37°W, depth less than 183 metres), 1899.7.1.5322. Paratypes, 1899.7.1.5323, 5324, 4476, 4477, 176; Havana, 1911.10.1.1702, 146 metres.

ETYMOLOGY. *Pluma* (L)—a feather, referring to the expanded avicularian mandible. The name was given as a manuscript label by Busk.

DESCRIPTION (Figs 21, 22, 25). *Didymosella* with semi-repent colonies forming irregular expansions. Frontal shield with 15–23 pores and 6–8 marginal septulae, the distal pair enlarged. Zooids communicating by 2–4 distal and lateral septulae. Peristomes raised, tubular, with paired, marginal spinous processes. Basal calcified wall becoming extrazoooidal with septulae and long, calcified extensions. Avicularian subrostral chambers very large, rostra with a channel open terminally. Mandible very long, expanded and fimbriated laterally.

REMARKS. The thickening of the frontal calcification above and around the distal pair of frontal septulae forms large, slit like foramina, one either side of the orifice. Two large lobes of about 300 zooids each, show areas in which groups of zooids with 'left-handed' avicularia are opposed to groups with 'right-handed' avicularia. Unlike the colonies of *T. magnirostris* (see p. 79), these groups are not obviously associated with the presence of brooding zooids. The avicularian rostra have pores which are visible late in ontogeny. The remarkable mandibles resemble those of *Smittipora* (see Cook, 1964), but are fimbriated marginally. When open, each mandible covers the frontal foramina of the zooid; when closed, it usually covers the foramina of the adjacent, lateral zooid (see Fig. 25). Presumably the mandibles ensure that the foramina do not become blocked by detritus, which would restrict water flow into the ascus, and the laterally directed water currents produced by mandibular movement may assist in clearing deposits from the frontal surface of the zooids (see Cook, 1981). Expanded mandibles are also present in *Tubiporella boninensis* (see below).

D. pluma is so similar to *D. crassa* that it is highly probable that Miocene-to-Pliocene specimens, linking the two forms may eventually be found from sediments in the Gulf of Mexico region.

TUBIPORELLA Levinsen

Tubiporella Levinsen, 1909 : 304.

TYPE SPECIES. *Lepralia magnirostris* MacGillivray, 1883.

DESCRIPTION. Colonies semi-encrusting, with free expansions. Zooids with long, tubular peristomes and a frontal spiramen. Frontal and basal septulae numerous, and extrazoooidal calcification considerable. Avicularia lateral, arising from several frontal septulae, subrostral chambers large. Rostra acute, directed laterally, mandible slung on a complete bar. Brooding zooids with a slightly enlarged orifice.

REMARKS. *Tubiporella* was introduced with no formal description. Levinsen (1909 : 304) listed it as 'n.g.' in a key to the family Tubucellariidae; *T. magnirostris* was the only species included. Species of *Tubucellaria* (or *Margaretta*, see Harmer, 1957 : 824), have an ascopore, not a peristomial spiramen, and have erect, jointed colonies. *Tubiporella* was assigned to the Tubucellariidae by Bassler (1953 : G210), and to the Porinidae by Harmer

(1957 : 844). Finally, Brown (1952 : 194) recognized its close affinities with *Didymosella* and included it in the family Didymosellidae.

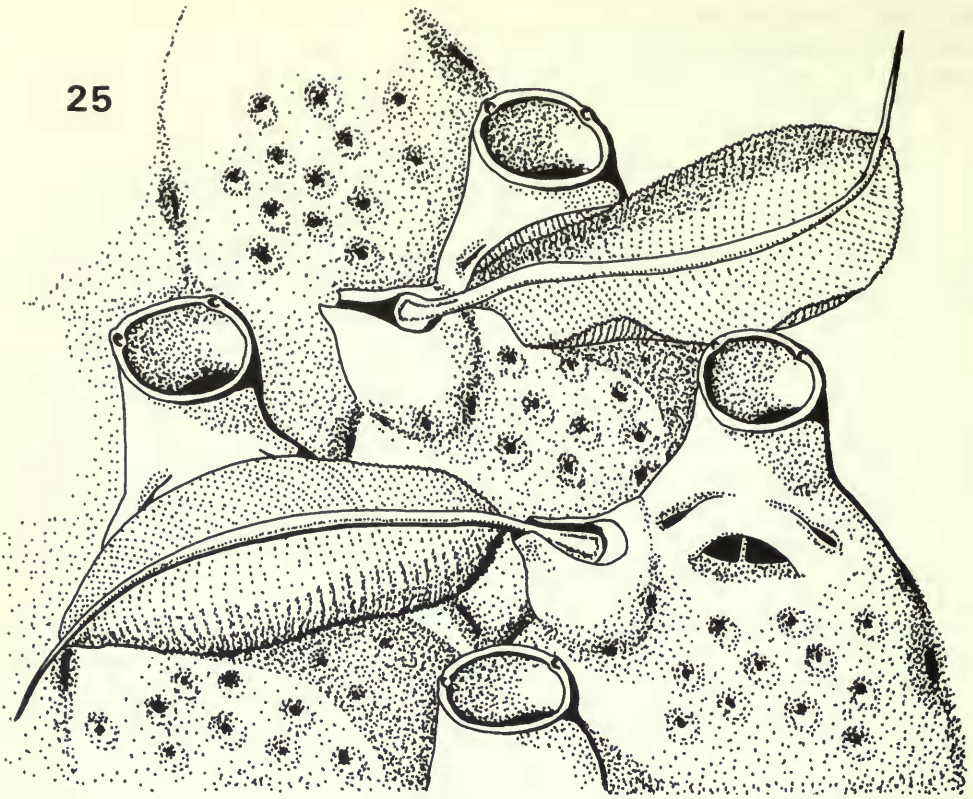
Tubiporella, like *Didymosella*, has an Australian Tertiary record, although this extends only to Miocene deposits. The characters of fossil specimens are very similar to those of Recent *T. magnirostris*, but there are some doubts in accepting the identity of these forms without examination of type specimens. Brown (1952) noted that Recent colonies had the larger zooidal dimensions (see Table 2), and in view of the degree of difference between Recent and fossil populations of the *D. larvalis*-complex, it seems advisable at present to regard the Tertiary forms as distinct taxa. Several fossil forms have been described. Waters (1882a : 268, pl. 9, figs 33, 34) introduced *Micropella introversa* from the Miocene of Mount Gambier, Australia with two drawings which he stated were magnified at $\times 12$ and $\times 25$ respectively. The (secondary) orifice measurements he gave on p. 268 were: Lo 0.16 mm, lo 0.20 mm. Using the magnifications given, the average dimension of zooids for Fig. 33 would be: Lz 1.75 mm, lz 1.00, Lo 0.25 mm, lo 0.33 mm. These are obviously too large; very few cheilostome zooids are more than 1.5 mm in length, and Waters did not mention that the zooids of *M. introversa* were particularly large. A magnification of $\times 20$ would give Lz 0.90 mm, lz 0.60 mm, Lo 0.15 mm, lo 0.20 mm, which is not only in accordance with the given orifice measurements, but is more feasible. The spiramen, which Waters regarded as 'microporellid' ascopore, was described and figured as being very close to the proximal border of the secondary orifice. When describing further fossil specimens from the River Murray Cliffs, Waters (1885 : 296) called this a 'central pore'. In a still later paper, Waters (1887 : 55) included *M. introversa* in the synonymy of *T. magnirostris* although the species had originally been described by him a year before MacGillivray's species. Waters (1885 : 295, pl. 7, fig. 7) also described, as *Microporella magna*, fossil specimens from Aldinga and Mount Gambier, and identified them with *Lunulites magna* Tenison Woods (1880), which he stated was 'very closely allied' to *T. magnirostris*. Tenison Woods (1880 : 7, pl. 1, figs 6 a-d), had described an irregularly domed, hollow, almost circular colony. His figure (6c) shows zooids with raised peristomes, numerous frontal pores and acute, laterally directed avicularia with a complete bar. This species is obviously ascophoran, and is in no way referable to the free-living, anascan genus *Lunulites*. Two specimens in the British Museum Collections confirm the existence of this species in the Australian Tertiary. The first (labelled '*Lunulites magna*'. D33050, Janjukian, Aldinga) has a domed colony 25 mm in diameter and 10 mm high, somewhat larger than Tenison Woods' colonies. The zooids have raised peristomes, extrazoooidal frontal thickening with funnels and pores, and a distinct proximal pore which may be a spiramen. The avicularia are directed almost distally, and are much larger than those figured by Tenison Woods (1880, pl. 1, fig. 6c). They have a complete bar, and the rostra are acute, with a terminal channel which may indicate that the mandibles were elongated. The basal surface of the colony is obscured by matrix. The second colony (D31940, River Murray Cliffs) forms an almost truncated cone 20 mm in diameter and 13 mm high, but the zooids are not arranged in regular radial series. They are very worn, but the peristomial orifices and avicularia can be seen. The hollow basal side of the colony has numerous pores and irregular masses of calcification and may be inferred to have possessed an extrazoooidal coelom in life.

Pachystomaria parvipuncta MacGillivray (1895 : 97, pl. 8, fig. 24), another Miocene Australian form, appears to be a further species belonging to this complex. MacGillivray noted that the porous basal surface was similar to that of *Selenaria*, an observation also made by Waters (1885) when describing *M. magnirostris*. At present it is not known whether any or all of these nominal species are synonymous, or if they are conspecific with Recent *T. magnirostris*.

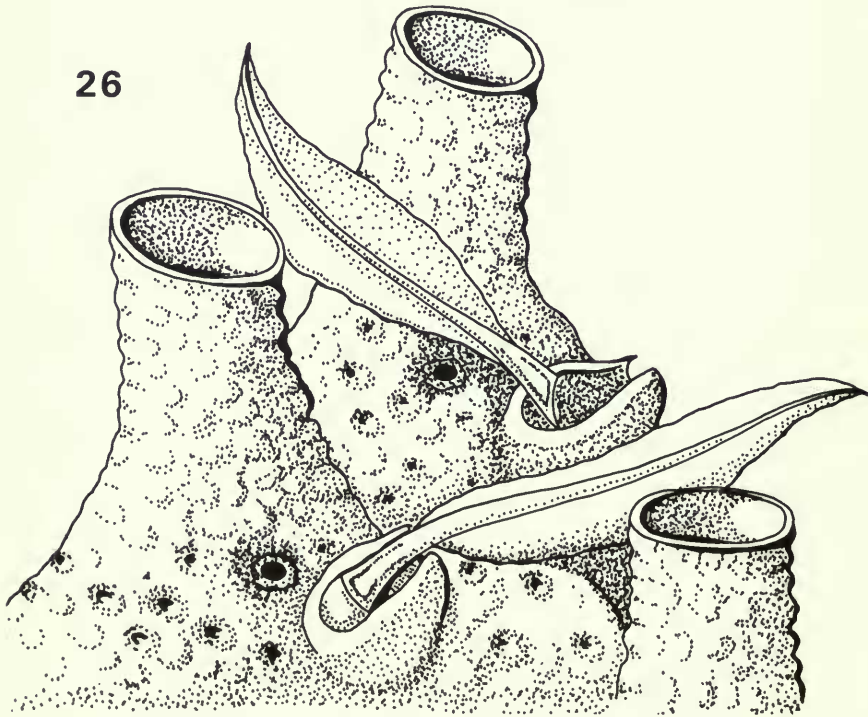
Tubiporella magnirostris (MacGillivray)

Lepralia magnirostris MacGillivray, 1883 : 134, pl. 1, fig. 6.

25



26



Tessaradoma magnirostris: MacGillivray, 1889 : 211, pl. 175, fig. 1.

Porina magnirostris: Hincks, 1884 : 279 (sep. p. 129), pl. 9, fig. 6.

Tubiporella magnirostris: Levinsen, 1909 : 307, pl. 16, figs 5a–d. Canu & Bassler, 1920 : 549, Figs 161 A–D.

Tubiporella magnirostris part, 'f. *victoriensis*': Borg, 1940 : 416, Figs 1–3.

SPECIMENS EXAMINED. BMNH. Port Phillip Heads, Victoria, Australia, 1887.6.27.1, 1887.12.10.120, 1893.8.11.17, 46 metres; 1927.8.4.24, 1979.1.12.3. Port Phillip, 1899.5.1.1214, 1899.7.1.5409, 5410, 5411, 2333, 2338, 2686, 2687, Victoria, 1979.7.2.1. Amirante Islands, 64 metres, 1936.12.30.199.

NMV. Port Phillip, 63876.

DESCRIPTION (Figs 20, 24). *Tubiporella* with colonies forming broad, foliaceous expansions attached above the substratum by thick, extrazoooidal, columns of porous calcification. Zooidal peristomes tubular, but not very prominent, with a small proximal, cuticle-covered foramen early in ontogeny. Spiramen originating on the proximal edge of the base of the peristome, apparently migrating proximally with thickening calcification. Avicularian subrostral chambers without pores, mandible hooked but not greatly elongated. Lateral frontal septulae surrounded by large uncalcified areas, which increase in size with calcification. Brooding zooids with larger secondary orifices than autozooids, with no avicularia, or paired, small avicularia. Avicularian mandibles of autozooids surrounding brooding zooids are directed away from brooding zooid when closed.

REMARKS. The primary orifice can be seen early in ontogeny, and the developing peristome has a small foramen which rapidly becomes obscured. The 'migration' of the spiramen with thickening of the frontal shield is similar to that described in the umbonuloid family Adeonidae (see Cook, 1973). The patterning of brooding zooids and avicularia is similar to that found in *D. pluma*. The peristomial orifices of the brooding zooids are slightly larger than those of the autozooids, and the distal expansion of the ovicell can be seen. The lateral frontal septulae of the brooding zooids remain visible at the base of the funnels in the calcification, resulting in wide lacunae beneath the investing cuticle (cf. *D. pluma*). Levinsen (1909 : 308) mentioned that the 'very thick basal wall of the colony . . . is . . . perforated by pore canals' which he noted were derived from multiporous basal septulae. Harmer (1957 : 1012) described a colony of *Emballothecha subimmersa* (MacGillivray) which encrusted the basal wall of a large specimen of *T. magnirostris*.

Tubiporella boninensis Borg

Tubiporella magnirostris part, 'f. *boninensis*': Borg, 1940 : 420, Fig. 4, (operculum).

SPECIMENS EXAMINED. BMNH. Tizard Reef, 64 metres, 1889.21.27; 68 metres, 1892.8.8.26; Macclesfield Bank, China Sea, 66 metres, 1889.8.21.95,105; 64–79 metres, 1934.11.6.23; 46 metres, 1893. 8.11.17; China Sea, 66 metres, 1979.1.6.2; S. of Bua Bua passage, Falafuti, 264 metres, 1903.1.29.60. Fuafatu, 109 metres, 1903.1.29.61.

DESCRIPTION (Figs. 18, 19, 26). *Tubiporella* with narrow, ligulate, semi-erect colonies, with zooids in 4–7 transverse series. Zooids with long, tubular peristomes, imperforate early in astogeny. Spiramen at the base of the peristome, migrating only slightly with ontogeny. Basal calcification produced into a massive, central keel in erect specimens, which produce branched, supporting pillars of extrazoooidal, porous calcification 5–7 mm deep. Avicularian subrostral chambers large, imperforate. Rostra acute, with an open channel terminally.

Figs 25 and 26 (25) *Didymosella pluma* sp. nov. BMNH 1899.7.1.5322, off Brazil, sketch of four zooids and two avicularia with open (upper) and closed (lower) mandibles. Scale bar = 0.50 mm; (26) *Tubiporella boninensis* Borg BMNH 1893.8.11.17, China Sea, sketch of three zooids and two avicularia with open (upper) and closed (lower) mandibles Scale bar = 0.50 mm.

Mandibles elongated, directed laterally towards the margins of the colony; expanded laterally, with notched, fimbriated edges.

REMARKS. Although Borg (1940) did not consider that his specimens were specifically distinct from *T. magnirostris* and did not formally introduce the name '*boninensis*' for them, the name is available and is therefore used here. Borg noted that the operculum was hardly differentiated from the ascus wall, and that the avicularian mandible was 'distinctly broader than that of the Australian colonies and nearly straight, but with its tip rather sharply bent'. He also described the cuticular expansions and noted that 'this border is often broader on one side'. The mandibles are similar to those of *D. pluma*; when open they cover the area above the frontal spiramen. (see Fig. 26).

The ancestrula resembles later-budded zooids and is unusual in having a lateral avicularium.

Generally, *T. boninensis* differs from *T. magnirostris* in its colony form, shorter, more erect zooids, longer peristomes, and avicularian mandibles.

Note on *Tubiporella levinseni* Borg, 1940

In his description of the genus *Tubiporella*, Borg (1940) described a new species, *T. levinseni*, which had large, encrusting zooids with long, tubular peristomes, multiserial marginal pores and a proximal spiramen. The centrally placed avicularium had an elongated, almost setiform mandible. Borg mentioned that he had shown his specimens to Sir Sidney Harmer, who had recognized them as belonging to the same species as specimens from the Paternoster Islands which were present in the Siboga Expedition Collections. Harmer was not aware of Borg's description, which was subsequently published in Sweden during the 1939–1946 war (see Explanatory Note by Dr A. B. Hastings in Harmer, 1957: xiv). The specimens from the Paternoster Islands were described as *Reptadeonella flagellifera* by Harmer (1957), who, however, had provisionally labelled them as '*Tubiporella*'.

The structure and relationships of *T. levinseni* differ from those of *Tubiporella* as represented by the type species, *T. magnirostris*, and by *T. boninensis*. The specimens examined by Harmer from the Siboga Collections, together with one large, additional colony without locality, but comprising more than 2000 zooids (which was found fortuitously in the unnamed collections of the BMNH, and was not seen by Harmer), have been examined. A few zooids show a cuticular frontal wall with operculum, which is overarched by calcification, indicating that the ontogeny of the frontal shield is umbonuloid. There are no frontal pores, and the frontal septulae are multiserial and extend round the distal side of the orifice (see also Borg, 1940). The long tubular peristome is thus subterminal, and the primary orifice is well defined, with minute condyles and distinct operculum (see also Borg, 1940: 422, Fig. 8). The avicularium is central in position and is derived from one lateral-oral septula. The subrostral chamber is small, and the rostrum is acute and directed distally and laterally. The mandible is elongated, setiform and slung between condyles. Zooids communicate through septulae at the base of the vertical walls, but there is no basal coelom and the basal wall is completely calcified. The zooids are nearly all encrusting, but where they stretch across irregularities in the substratum, have produced small, peg-like expansions. There are however, no extrazoooidal pillars as in *Tubiporella*.

All the character correlations are similar to those found in the umbonuloid family Adeonidae (see Cook, 1973), and they confirm that Harmer (1957) was correct in attributing his specimens to the genus *Reptadeonella*, which has encrusting colonies.

Both Borg (1940) and Harmer (1957) mentioned that some zooids with short peristomes may have been brooding zooids. A few zooids have wide, rather slit-like orifices, but their peristomes do not differ from those of other zooids. Generally, brooding zooids in the Adeonidae are strongly dimorphic, and it is probable that as yet, no brooding zooids have

been found in this species. The synonymy, distribution and measurements of *R. levinseni* (Borg) are as follows:

Reptadeonella levinseni (Borg)

Tubiporella levinseni Borg, 1940 : 420, pl. 1 and Figs 5–8.

Reptadeonella flagellifera Harmer, 1957 : 817, pl. 54, figs 4–7.

SPECIMENS EXAMINED. BMNH. Siboga Stn 315, N. of Sumbawa, Paternoster Islands, 0–36 metres, 1979.1.2.1; no locality, 1979.1.2.2.

ZMA. Stn 315 and Stn 60, 303, Hangsisi, Samau Islands, W. Timor, 0–36 metres.

DISTRIBUTION. Jaluit, Marshall Islands, 2 metres (Borg), Paternoster Islands and West Timor.

MEASUREMENTS (in mm). Lz 0.80–1.30 lz 0.50–0.90 Lo 0.13 lo 0.16–0.20 Lr 0.16–0.25 Lm 0.30–0.50.

Discussion

Study of Bryozoa emphasizing the concept of colonies as entities composed of cooperative members has increased during recent years as a result of observation of living colonies and the application of new techniques. Species show many kinds and degrees of structural and functional integration. Colonies may be composed of almost autonomous member zooids, or have various correlations of morphology and behaviour which in some cases amount to virtual colony control (see Cook, 1979*a*, and Ryland 1979). The relationships of zooid body walls, intercommunications, zooidal and extrazooidal coeloms, astogenetic and ontogenetic changes, polymorphism and the patterning of polymorphs, all express the degree of such colony control and may be analysed and arranged in series of increasing integration (see Boardman & Cheetham, 1973 and Cook, 1979*a*).

Expressed in terms of such series, the degree of integration of the families Euthyrisellidae and Didymosellidae is considerable. It is reflected in the zonation and polymorphism of brooding and avicularian zooids, and in the supporting and attachment structures of colonies. Most significantly, it is expressed in the preponderance of interior calcified walls, and in the various combinations of intrazooidal, interzooidal and extrazooidal coelomic communications.

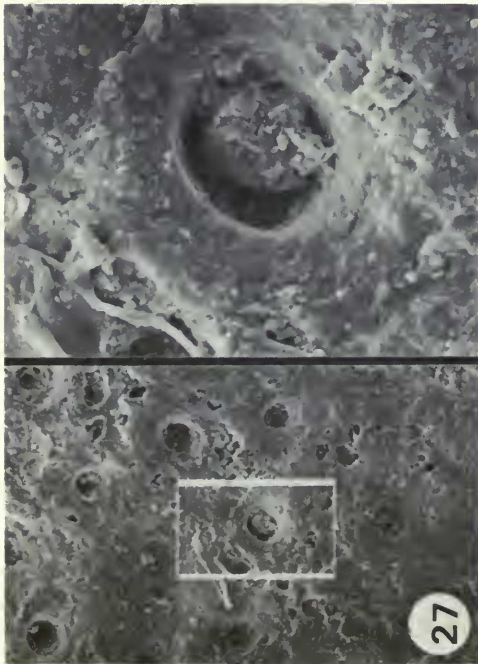
Relationships both between the Euthyrisellidae and the Didymosellidae, and between them and other ascophoran groups are hard to evaluate. Although they share cryptocystidean frontal shield ontogeny, the differences between the two kinds of shield suggest that these structures have arisen more than once in cheilostome evolutionary history. The appearance through time of more than one kind of frontal shield in the 'catenicellid' genera (see Banta and Wass, 1979), indicates that many more cryptocystidean families will require detailed investigation before the degrees and kinds of relationships among apparently similar groups are established.

The presence of extrazooidal basal coelom and of interior basal zooid walls is another shared character. However, these structures are also known in such diverse systematic groups as the lunulitiform, free-living anascan Selenariidae (see Chimonides & Cook, 1981) and the cryptocystidean Petraliidae. *Petralia undata* has erect, reteporiform, rooted colonies with a high degree of organization and an extensive basal coelom.

The lateral and basal rooting coelomic systems of the Euthyrisellidae have very close parallels among the many erect, flustriform genera, especially *Onchoporella* (see p. 59).

Peristomal spiramina, too, are found in a diversity of Recent and fossil ascophoran genera; for example, *Adeonella* (see Cook, 1973), *Gigantopora* (see Harmer, 1957), and compare *Pachyderma rarepunctata* Voigt (1967 : 67, pl. 24, figs 1, 2, from the Upper Cretaceous of West Kasachstan, USSR).

Within the Euthyrisellidae, there is great diversity in frontal shield calcification and in



orifice shape which is not strongly correlated with colony form. This diversity suggests that the family has a long evolutionary history, but unfortunately, no fossil species are known. Internodes of *Tropidozoum* are fairly robust, and have been found in transported deposits; they might be expected to be recognizable in Tertiary sediments. Even the thinly calcified zooids of *Euthyrisella* could be preserved, by analogy with the equally fragile fragments of *Selenariopsis*, which have been found, albeit rarely, in the fine fractions of Australian Miocene sediments (see Cook & Chimonides, 1981). Lagaaij (1968, 1973) has documented records of similar fragile species, several of which were not previously known as fossils. It is perhaps possible that the ancestral forms of Euthyrisellidae had more heavily calcified colonies, which have not yet been recognized as being systematically related to the Recent species.

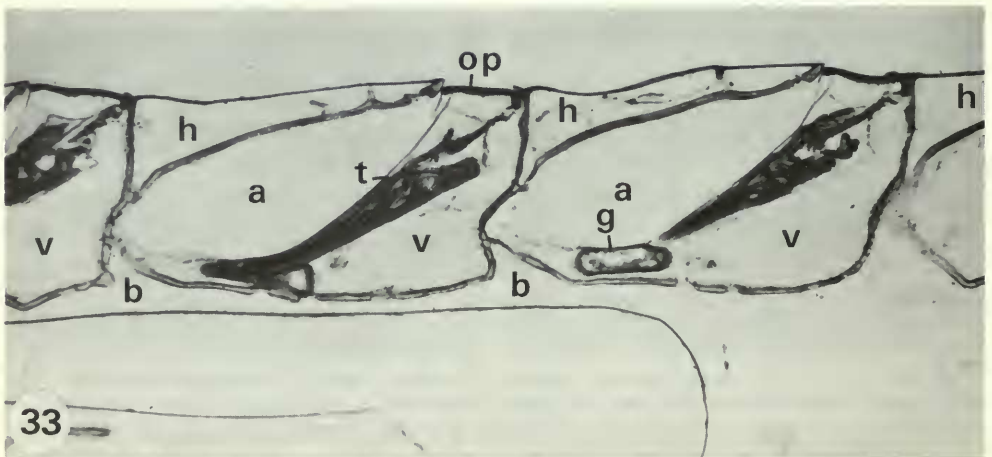
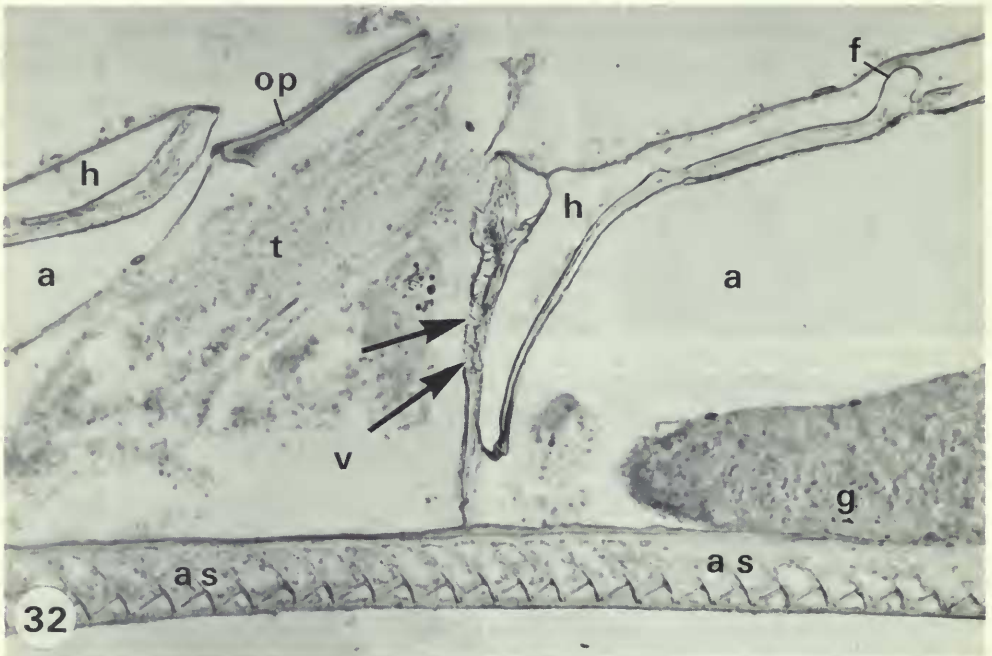
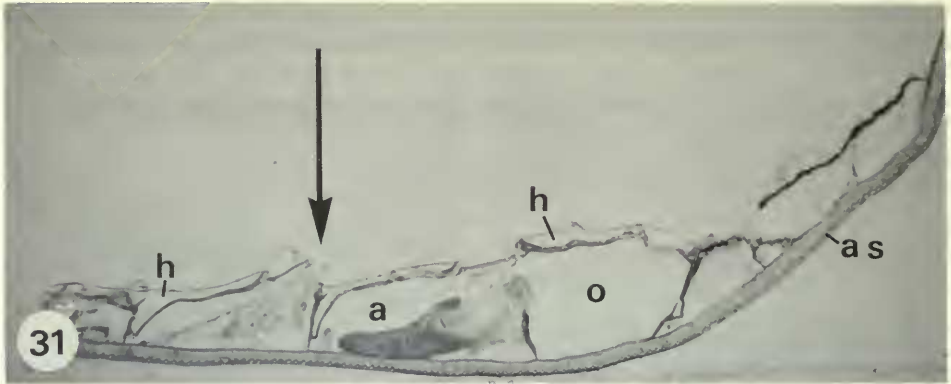
In contrast, the long fossil record of the Didymosellidae might be expected to provide some evidence of evolutionary trends and relationships. Diversity among the known species, both in zooidal morphology and colony form is, however, far lower than that found in the Euthyrisellidae. Generally, the species have very similar patterning of avicularia and autozooids, and the repent or semi-encrusting colony form is known in both Eocene and Recent species. The erect, branching colonies of *D. porosa* and *D. clypeata* are not found among Recent species, and the algal association of *D. larvalis* (like that of *Neoeuthyris woosteri*), may have been evolved fairly recently.

To a certain extent, the distribution of species in time and space shows strong collection bias, and reflects the large number of faunal descriptions of the abundant bryozoan sediments of the Tertiary-to-Recent of the Gulf of Mexico and Australasian regions. The Euthyrisellidae seems to have a purely Indo-West Pacific and Australian range. Most species are from shallow shelf or sublittoral waters, and several are rooted in sediments. The Didymosellidae are also shallow shelf species, although *D. pluma* and *T. boninensis* are found from the deeper end of the range. All species are from warm waters. Labracherie (1972) noted that the occurrence of *Didymosella* (together with other species) allowed the inference of warm marine conditions in the Middle Eocene of south Western France. The general pattern of distribution of the family in time and space follows that illustrated by Lagaaij & Cook (1973) for other warm water, shallow shelf species, and even for some deeper water forms (see Cook & Lagaaij, 1976). This comprises a very wide (sometimes circumtropical) distribution during the Eocene and Oligocene followed by a progressive restriction of range in a south-easterly direction through time. The occurrence of Recent *D. pluma* off Brazil and in the Gulf of Mexico is of importance, as it indicates that, like the genus *Adeonellopsis* (see Cook, 1973), groups which are supposed to be 'extinct' in the western Atlantic may be found to be still living in this area.

Summaries in French and German

Nous décrivons la structure de la colonie et la morphologie zooidale trouvées dans les deux familles cheilostome-cryptocystidiennes des Bryozoaires, la Euthyrisellidae et la Didymosellidae. Tous les murs calcifiés sont internes, at les coelomes basals (extra-zooidales) sont présents dans presque toutes les espèces. Dans la famille Euthyrisellidae, la communication interzooidale viscerale- à hypostigienne complémente ou meme remplace

Figs 27–30 Scanning electron micrographs of communication septulae: (27) *Didymosella porosa* (Stoliczka) BMNH D36788–92, Middle Oligocene, New Zealand, basal septulae (left) $\times 100$ (right) $\times 600$; (28) *Neoeuthyris woosteri* (MacGillivray) BMNH 1979.2.1.1, Recent, Western Australia, lateral frontal septulae at base of developing avicularian subrostral chamber $\times 315$; (29) *N. woosteri*, visceral-to-hypostegal septulae (arrowed) viewed from distal side $\times 197$; (30) *Tropidozoum cellariiforme* Harmer BMNH 1964.3.10.1, Recent, Celebes, visceral-to-hypostegal septula in distal-lateral wall of brooding zooid, viewed from proximal side. Note suture in wall showing contribution of distal zooid calcification to brooding zooid orifice $\times 368$.



la sorte intrazoidale la plus commune, cells qu'on trouve dans la Didymosellidae. Dans la Euthyrisellidae, une extension du coelome hypostigienne au-dessous du coté basal de la paroi frontale cacifiée, est présente dans la majorité des espèces. Une espèce nouvelle est introduite, *Tropidozoum burrowsi*. La famille Didymosellidae possède un record fossil qui s'étend d'Eocène Moyen et a une distribution très grande du Tertiaire au Récent. Nous introduisons une nouvelle espèce Recente, *Didymosella pluma*. *Tubiporella boninensis* Borg a été redefinie. *Tubiporella levinseni* Borg a été redécrite et attribué au genre umbonuloide *Reptadeonella*.

Die Koloniestruktur und Morphologie der Zooide der Euthyrisellidae und Didymosellidae, zweier cryptocystider Familien der Bryozoa Cheilostomata, werden beschrieben. Alle verkalkten Wände sind intern, und kolonieweite (extrazoidale) Basalcoelome finden sich bei fast allen Arten. Bei den Euthyrisellidae ergänzt oder sogar ersetzt die interzoidale (viscerale bis hypostegale) Kommunikation die gewöhnlichere intrazoidale, die sich bei den Didymosellidae findet. Bei den meisten Arten der Euthyrisellidae ist eine Verlängerung des hypostegalen Coeloms an der Basalseite des verkalkten Frontalschildes zu beobachten. Eine neue Art, *Tropidozoum burrowsi*, wird eingeführt. Die Familie Didymosellidae ist fossil seit dem mittleren Eozän nachgewiesen und ist vom Tertiär bis zur Gegenwart weit verbreitet. Eine neue recente Art, *Didymosella pluma*, wird eingeführt und *Tubiporella boninensis* Borg neu definiert. *Tubiporella levinseni* Borg wird wiederbeschrieben und in die umbonuloide Gattung *Reptadeonella* verwiesen.

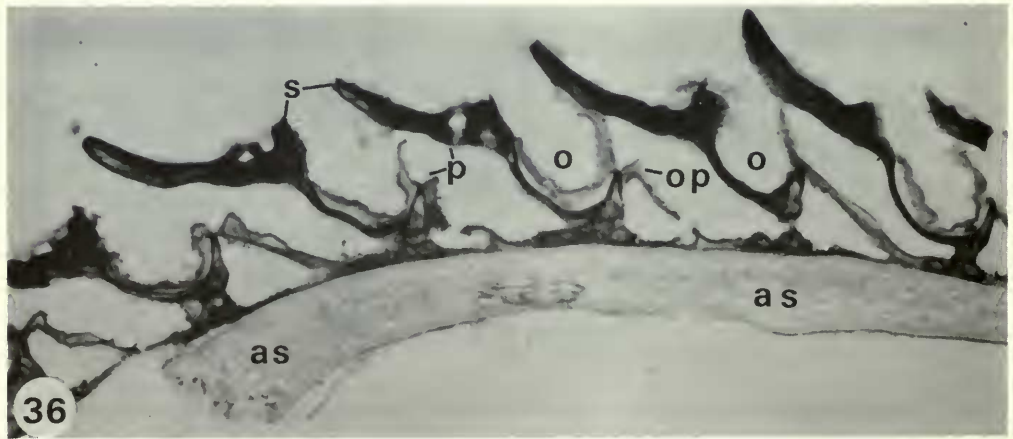
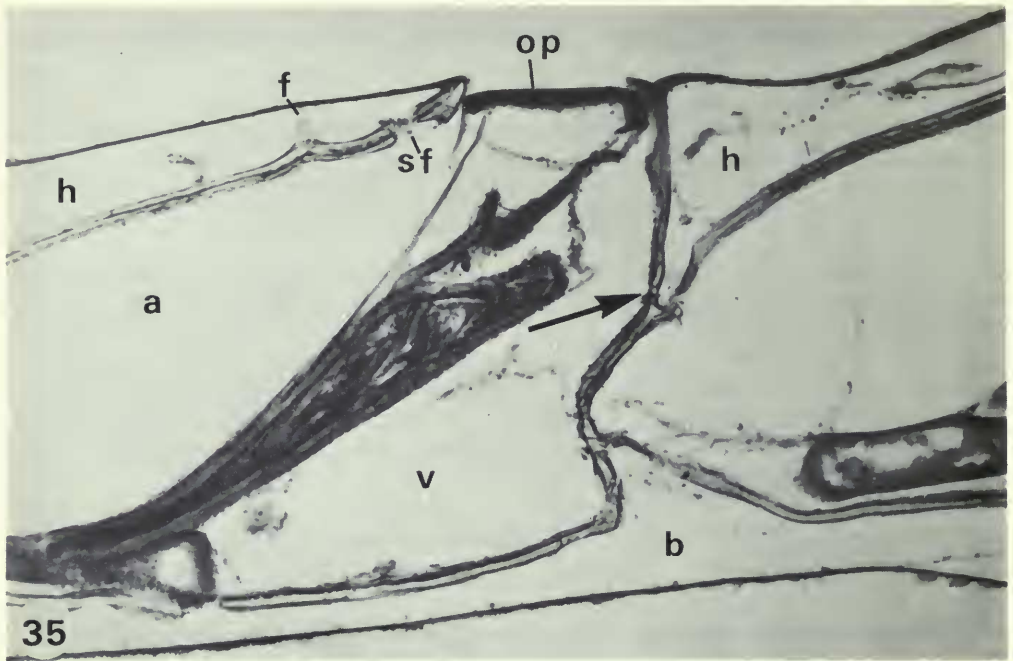
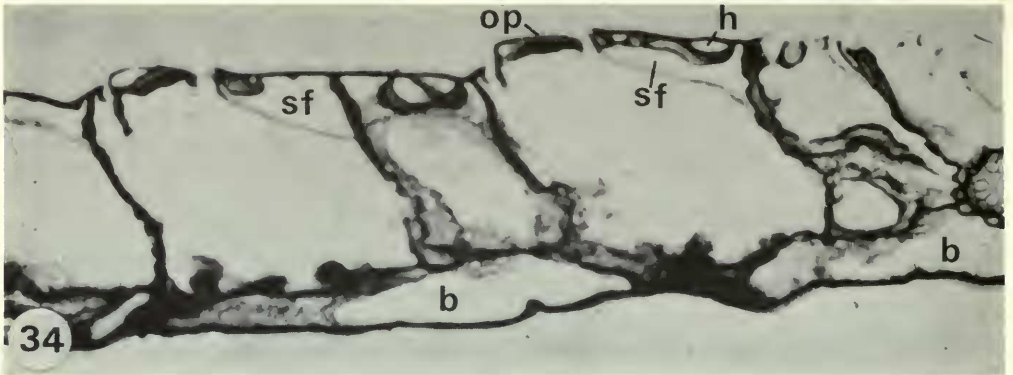
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Figs 31-33 Micrographs of longitudinal thin-sections of epoxy resin embedded specimens of Euthyrisellidae: (31) *Neo euthyris woosteri* (MacGillivray) BMNH 1979.2.1.1, Western Australia, zooids with cuticular basal walls encrusting algae, autozoid (left) and brooding zooid with large ovicell (centre), arrow indicates area enlarged in Fig. 32 $\times 30$; (32) *N. woosteri* visceral-to-hypostegal communications (arrowed) $\times 165$; (33) *Euthyrisella obtecta* (Hincks) BMNH 1890.7.23.38, Torres Straits, brooding zooids (without ova), cuticular basal wall detached at right $\times 70$. *a* ascus, *o* ovicell, *op operculum*, *f* frontal process, *t* tentacles, *g* gut, *h* hypostegal coelom, *v* visceral coelom, *b* basal coelom, *as* algal substratum.



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Figs 34–36 Micrographs of longitudinal thin-sections of epoxy resin embedded specimens of Euthyrisellidae and Didymosellidae: (34) *Pleurotoichus clathratus* (Harmer) BMNH 1976.1.2.1, Queensland, showing large subfrontal hypostegal coeloms $\times 60$; (35) *Euthyrisell obiecta* (Hincks) BMNH 1890.7.23.38, Torres Straits, visceral-to-hypostegal communication (arrowed) and minute subfrontal hypostegal coelom $\times 170$; (36) *Didymosella larvalis* (MacGillivray) BMNH 1890.4.17.1–10pt., Spencer Gulf, zooids with cuticular basal walls encrusting algae $\times 40$. *a* ascus, *o* ovicell, *op* operculum, *f* frontal process, *p* primary orifice, *s* secondary orifice, *h* hypostegal coelom, *sf* subfrontal hypostegal coelom, *v* visceral coelom, *b* basal coelom, *as* algal substratum.

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