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

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

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

Introduction

The Family Adeonidae includes genera with colonies which are mainly erect and bilaminar, and some which are encrusting. Frontal wall development is umbonuloid as demonstrated in a study of a range of Recent material (Cook, 1973). Further analysis of skeletal structures in a number of Australian and New Zealand examples was done by Lidgard (1996). Enlarged brooding zooids are well-known in the genera *Adeonellopsis* MacGillivray, 1886, *Reptadeonella* Busk, 1884 (Hayward and Ryland, 1999), and *Dimorphocella* Maplestone, 1903. Brooding dimorphs are also characteristic in *Adeonella* Maplestone, 1903 and *Laminopora* Michelin, 1842, which display schizoporelloid frontal wall development. For that reason these latter genera are considered to belong to a distinct family, the Adeonellidae (although there is disagreement on this issue, see Lidgard, 1996). In the genus *Adeona* Lamouroux, 1812, enlarged brooding zooids ("ooecial cells") were first identified by Busk (1884: 181) in the species *A. appendiculata* Busk, 1884 from Twofold Bay, off Eden, NSW. His illustration (pl. 33, fig. 6) shows two zooids with slightly larger secondary orifice dimensions. He also figured the opercula of brooding and non-brooding dimorphs (fig. 47). Cook (1973: 249, 250) inferred the presence of brooding zooids in unidentified material from the collection of the Natural History Museum, but these were not described or illustrated. A study of skeletal regeneration in a specimen of *Adeona* (Wass, 1983), included illustrations of early ontogenetic stages of regenerating zooids. These show dimorphism in the size of the secondary calcified orifices but no comment was made about this dimorphism. Wass (1991) illustrated zooidal variation in *Adeona*, and remarked on the larger size of inferred brooding zooids, and the porous distal plate in the calcified orifice of these zooids.

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

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

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

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

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

Observations

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

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

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

It is inferred that the dimorphs with larger secondary orifices are brooding zooids. The calcified external opening of the orifice is generally larger in the brooding zooids. This is best seen in zooids near the growing edge of the colony where secondary calcification is less well-developed (Figs 1, 4). Examination of the interior of the frontal shield has revealed considerable differences between brooding and non-brooding zooids (Fig. 2). The interior opening of the brooding zooid peristome is much larger and leads to a distal peristomial chamber with smooth calcification. This space contained large single embryos which were observed during the process of sectioning the colony. The smooth calcification of the brood chamber terminates proximally at a line that is continuous with the ring scar of the body chamber of the zooid (Fig. 3). The lateral and distal walls peripheral to the ring scar are perforated with numerous pores leading to tubes communicating with the septular pores on the exterior surface of the calcified skeleton. The porous distal plate observed by Wass (1991) is the frontal surface of the peristomial brood chamber (Figs 5, 8).

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

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

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

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

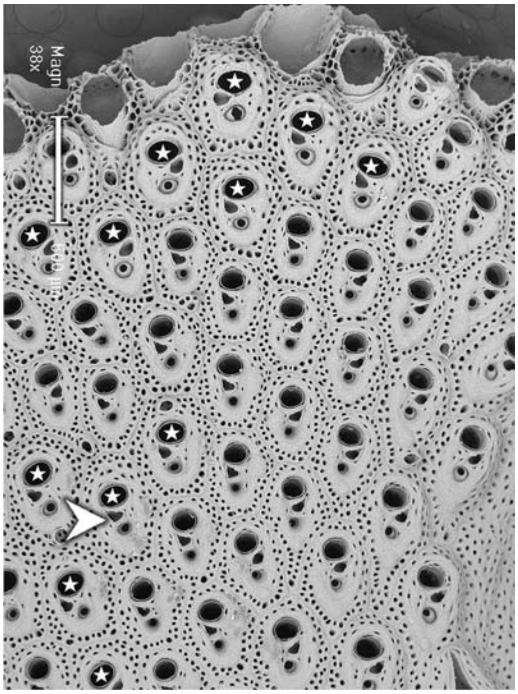

Figure 1. Growing edge of colony of *Adeona* species 1 (stn GAB-113, Great Australian Bight, depth 106 m, 34º36'S, 119º55'E). Starred zooids are inferred brooding dimorphs. Arrow indicates zooid also arrowed in Fig. 2. Scale = 500 µm.

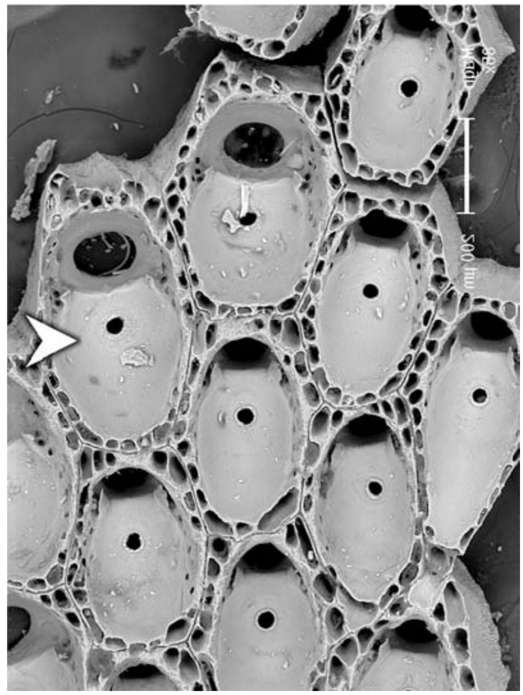

Figure 2. Interior of part of material shown in Fig. 1. Image is reversed left to right for comparison of zooid positions in the fragment. Arrow indicates zooid also arrowed in Figure 1. Two brooding dimorphs showing enlarged orifice and peristomial brood chamber. Scale = 200 µm.

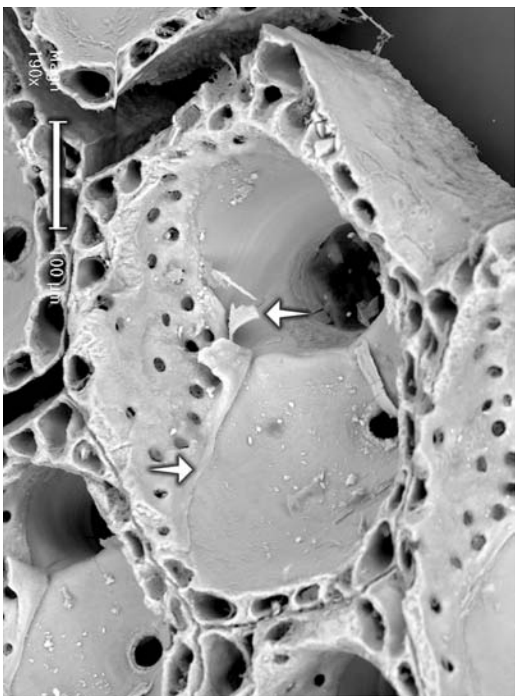

Figure 3. Detail of the distalmost of the two brooding zooids in Fig. 2 (not reversed). Shows ring scar at margin of epistegal space (arrow), plate-like condyle (arrow), and numerous communication pores lateral to orifice and brood chamber, leading to hypostegal coelom. Scale = 100 µm.

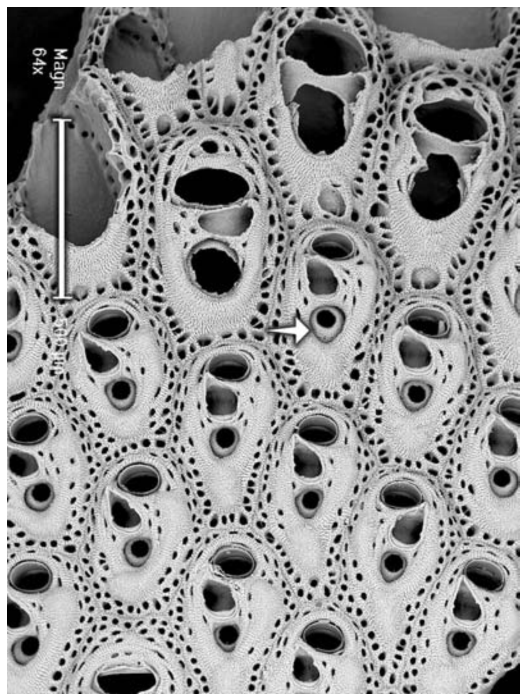

Figure 4. Growing edge of colony of *Adeona* species 2 (stn GAB-113 as in Fig. 1). Ontogenetic thickening of secondary calcification and development of avicularia. Distalmost three zooids are brooding dimorphs, as well as orifice in left proximal margin. Arrow marks calcification around foramen. Scale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

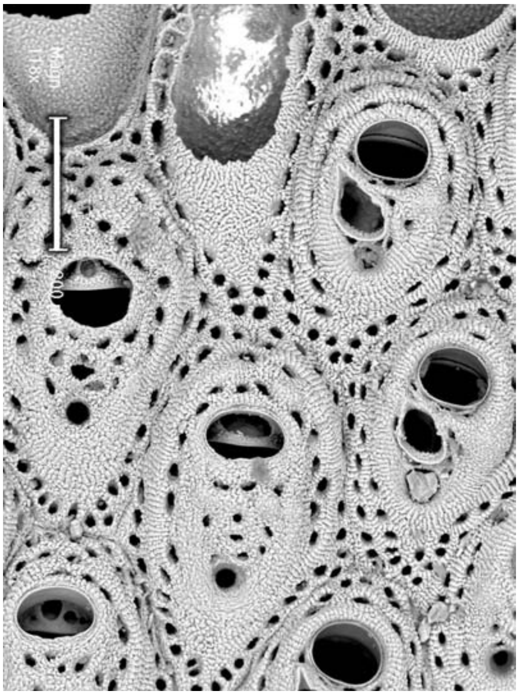

Figure 5. Same colony as Fig. 4. Proximal zooid and left zooid are brooding dimorphs, with well-defined 'distal plate' in orifice, and with no avicularium, having communication pores in its place. Distal and right zooids are non-brooding zooids. Scale = 200 µm.

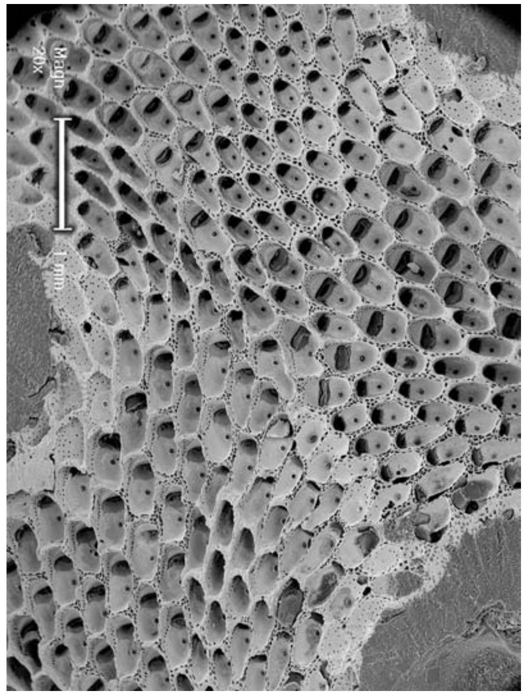

Figure 6. *Adeona* species 3 (stn BSS-119, Bass Strait, depth 92 m, 39º6.7'S, 143º28.7'E). Interior of colony section between three fenestrae, showing clusters of brooding dimorphs at top left, bottom left, and centre right. Scale = 1 mm.

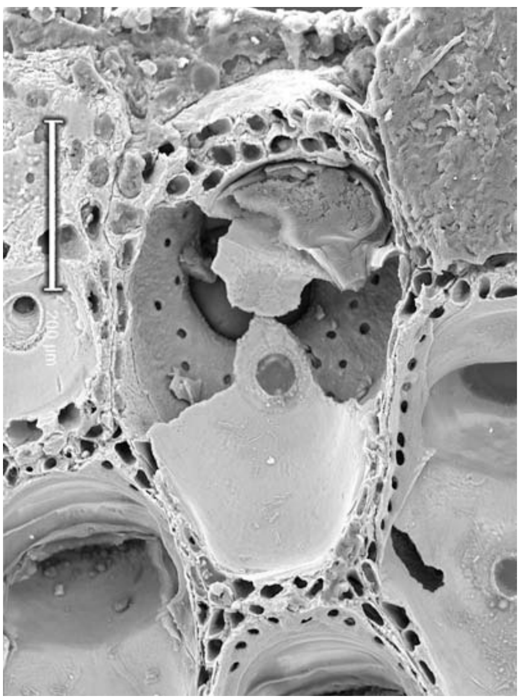

Figure 7. Same specimen as Fig. 6. Detail of single non-brooding zooid. Showing multi-layered frontal calcification, with communication pores in outer layer. Scale = 200 µm.

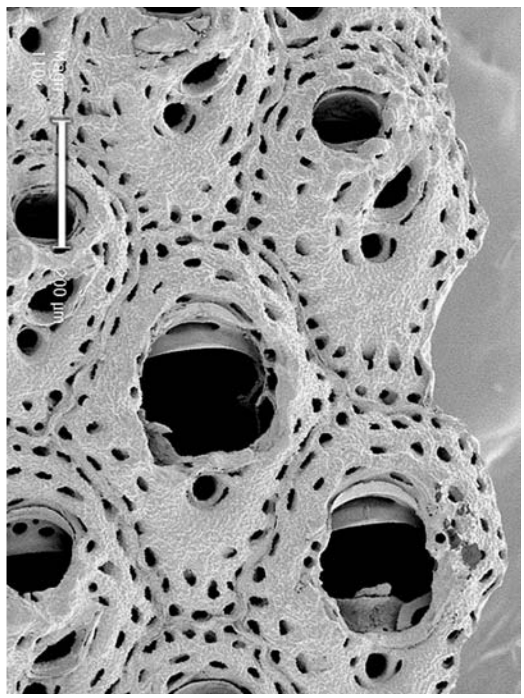

Figure 8. *Adeona* species 4 (stn GAB-033, Great Australian Bight, depth 106 m, 34º36'S, 119º55'E). Two brooding zooids with partly broken frontal walls, showing distal plate and condyle in calcified orifice. Scale = 200 µm.

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

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