

BIOIMMURED CTENOSTOMES FROM THE JURASSIC AND THE ORIGIN OF THE CHEILOSTOME BRYOZOA

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ABSTRACT. Soft-bodied ctenostome bryozoans, preserved as bioimmurations following overgrowth by encrusting organisms with hard skeletons, are described from the Middle and Upper Jurassic of England and Normandy. They include one new genus, *Cardoarachnidium*, and three new species, *C. bantai*, *C. voighti* and *Arachnidella abusensis*. These and new bioimmured specimens of *Arachnidium smithii* (Phillips) show fine-scale details of original morphology as well as artefacts caused by partial collapse of zooids during overgrowth. The D-shaped zooidal orifices present in *Cardoarachnidium* probably indicate that the zooids were operculate. Opercula are one of the two apomorphies of the closely-related cheilostomes, and therefore the Oxfordian *Cardoarachnidium* is placed in the stem-group of the Cheilostomata, which first appear in the Tithonian.

CTENOSTOMES are unique among marine bryozoan orders in lacking a calcified skeleton. Accordingly, they are less well-represented in the fossil record than groups such as trepostomes, fenestrates, cyclostomes and cheilostomes, more familiar to palaeontologists. Fossil ctenostomes, however, can be preserved as borings (see Pohowsky 1978) and as bioimmurations, i.e. natural moulds and casts formed as a result of overgrowth by organisms with mineralized skeletons (see Taylor 1990). Boring ctenostomes, first known from the Upper Ordovician, are generally regarded as a specialized group or groups. In contrast, bioimmured fossil ctenostomes include several uniserial encrusting species which have many features apparently primitive among marine Bryozoa.

During recent years, bioimmured ctenostomes have been discovered with increasing frequency in the Jurassic and Cretaceous, mainly through the work of Voigt (1966, 1968, 1972, 1977, 1979, 1980). The present paper utilizes an uncoated SEM technique (Taylor 1986) to describe some finds and redescribe earlier finds from the Jurassic. The quality of preservation of some of the new specimens exceeds that previously known and has revealed hitherto unknown morphological features. Artefacts formed during the process of bioimmuration process are also illustrated.

Jurassic bioimmured ctenostomes have special significance because they almost certainly include representatives of the stem-group of the order Cheilostomata. Cheilostomes, the dominant bryozoans of present-day faunas, first appear in deposits of latest Jurassic age. Comparative anatomical studies have led to the belief that the ancestor of the cheilostomes was a ctenostome or, more strictly, that living ctenostomes are the primitive sister-group of living cheilostomes. The description here of a new bioimmured Upper Jurassic ctenostome which apparently possesses one of the two apomorphic features characteristic of the Cheilostomata supports this hypothesis of cheilostome origins and gives the sequence of appearance of the two apomorphies.

SYSTEMATIC PALAEOLOGY

Material. Specimen repositories are abbreviated as follows: BMNH, British Museum (Natural History); YM, Yorkshire Museum, York; VH, Voigt Collection, Universität Hamburg.

Order CTENOSTOMATA Busk, 1852
Suborder CARNOSA Gray, 1841
Family ARACHNIDIIDAE Hincks, 1877
Genus ARACHNIDIUM Hincks, 1859

Type species. Arachnidium hipphooides Hincks, 1859.

Discussion. *Arachnidium* Hincks is founded on a comparatively rare present-day type species which has been redescribed recently by Hayward (1985, p. 78). D'Hondt (1983) included five living species in the genus, all possessing uniserial branching colonies with zooids pyriform or ovoidal in outline shape. In common with many ctenostomes, the surface morphology of species of *Arachnidium* is comparatively simple, and descriptions of living species generally include only a small number of external morphological characters (notably size, shape and ornamentation of the zooids). These characters are equally available in bioimmured fossil *Arachnidium*. Not available in fossil *Arachnidium* are aspects of polypide morphology (e.g. tentacle number) which have been used in species descriptions.

The difference between *Arachnidium* and *Arachnoidella* d'Hondt, 1983 (see p. 26) is rather slight, the latter possessing rather longer peristomes and sometimes developing lateral crenulations close to the substratum. However, pending further study of living species, the two genera are retained.

Range. Jurassic (Aalenian) to Recent.

Arachnidium smithii (Phillips, 1829)

Plate 1, figs. 1–6; Plate 2, figs. 1 and 2; text-figs. 1, 2A, B, 3A, B.

- 1829 *Cellaria smithii* Phillips, p. 143, pl. 7, fig. 8.
- 1875 *Hippochoa smithii* (Phillips); Phillips, p. 242, pl. 7, fig. 8.
- 1892 *Stomatopora phillipsii* Vine, p. 250, pl. 12, figs. 1–3.
- 1894 *Stomatopora smithi* (Phillips); Gregory, p. 58, fig. 1.
- 1895 *Stomatopora smithi* (Phillips); Gregory, p. 226.
- 1896 *Stomatopora smithi* (Phillips); Gregory, p. 56, fig. 8.
- 1907 *Stomatopora phillipsi* Vine; Lang, fig. 6.
- 1911 *Corynotrypa smithi* (Phillips); Bassler, p. 521, fig. 22.
- 1935 *Stomatopora smithi* (Phillips); Melmore, p. 1, test-figs. 1 and 2.
- 1977 *Arachnidium jurassicum* Voigt, p. 172, figs. 1–4.
- 1978 *Arachnidium smithii* (Phillips); Taylor, p. 214, pl. 7, figs. 1–4.
- 1980 *Arachnidium smithii* (Phillips); Voigt, fig. 4a.
- 1980 *Arachnidium jurassicum* Voigt; Voigt, fig. 4b.

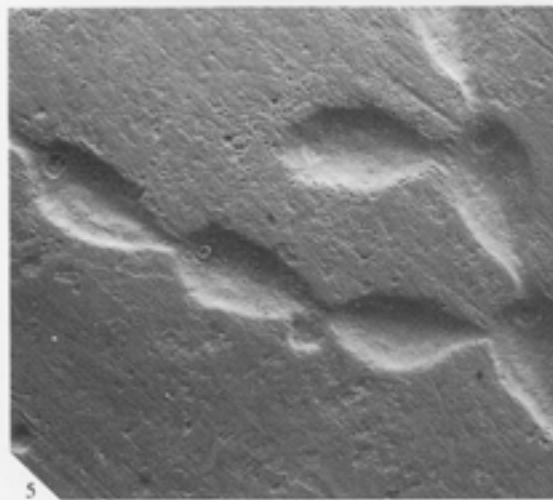
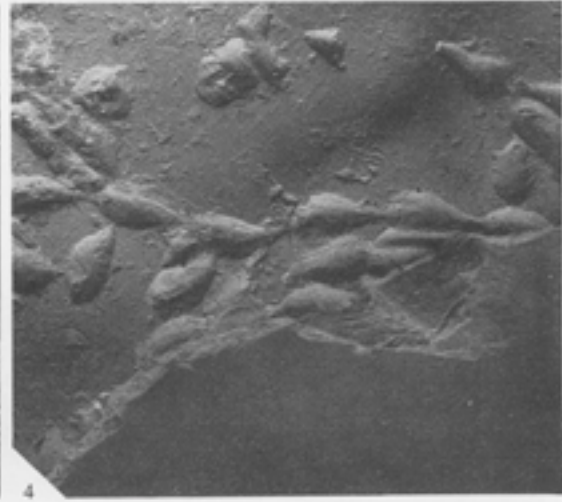
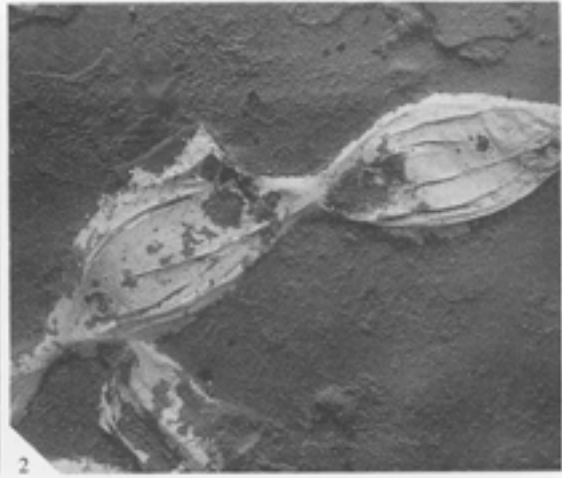
Holotype. YM 78, Cornbrash, Scarborough, Yorkshire. This specimen (Pl. 1, figs. 1 and 3; text-fig. 1), a cast bioimmuration attached to the type specimen of the bivalve *Cardium citrinoideum* Phillips, is almost certainly of Callovian age (*macrocephalus* Zone).

Other material. BMNH D 31144, Cornbrash, Thrapston, Northamptonshire; the holotype of *Stomatopora phillipsi* Vine, 1892; a cast bioimmuration attached to the brachiopod *Obovothyris* and undoubtedly originating from the Bathonian (*discus* Zone). BMNH D 53156, Bathonian, Bradford Clay (*discus* Zone), Cirencester, Gloucestershire, J. P. Woodward Collection; a mould bioimmuration on the attachment area of

EXPLANATION OF PLATE 1

Figs. 1–6. *Arachnidium smithii* (Phillips, 1829). 1, 3, holotype, YM 78, natural cast bioimmuration, Scarborough, Cornbrash (Callovian). 1, crowded zooids with overgrowing branches, $\times 28$. 3, partly collapsed zooid (with well-preserved orifice) overgrown by another zooid, $\times 100$. 2, 4, BMNH D 57497, natural cast bioimmuration, South Ferriby, Kimmeridgian. 2, collapsed zooids cast in pyrite, $\times 50$. 4, calcite cast zooids emerging from beneath the cover of the bioimmuring bivalve (bottom), $\times 16$. 5 and 6, BMNH D 57492, mould bioimmuration, Villers-sur-mer, Oxfordian. 5, uniserial chain of zooids $\times 35$. 6, orifice, $\times 240$.

All illustrations are back-scattered electron micrographs of uncoated specimens.





TEXT-FIG. 1. *Arachnidium smithii* (Phillips, 1829), holotype, YM 78, Scarborough, Cornbrash (Callovian). Extensive colony preserved as a natural cast attached to the surface of a bivalve shell. Back-scattered scanning electron micrograph of an uncoated specimen, $\times 19$.

a small *Praeoxoira*. BMNH D 57492, 4–5, D 58002, Oxfordian, float probably from the 'Couches à *Myophorella huddlestoni* et *Lopha gregaria*' (*plicatilis* Zone), Vaches-Noires, Villers-sur-mer, Normandy, collected by P. D. Taylor, 1985; apart from D 58002, all are mould bioimmurations on the attachment areas of gryphaeate oysters; D 58002 is a partially exposed, partly infilled cast bioimmuration. BMNH D 57496, Kimmeridgian, Bed M8 of Birkelund *et al.* (1983) (mid *mutabilis* Zone), Westbury, Wiltshire, collected by P. Wignall, 1986; mould bioimmuration, partly infilled by pyrite, on the attachment area of a small oyster. BMNH D 57497, Kimmeridgian, Bed 9 of Birkelund and Calloman (1985) (lower *baylei* Zone), South Ferriby, Humberside, collected by M. Simms, 1986; a cast bioimmuration (Pl. 1, figs. 2 and 4; Pl. 2, figs. 1–2), partly calcitic and partly pyritic, attached to *Delloideum delta* (Sowerby).

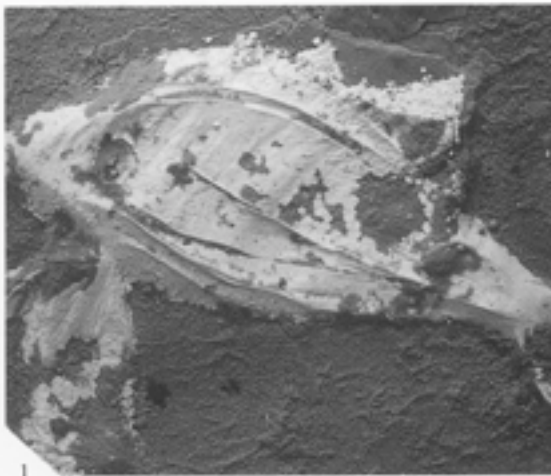
The holotype of *Arachnidium jurassicum* Voigt, 1977, unavailable for study during 1987, is VH 1899, Middle Dogger (*Polyplocus*-Schichten, Dogger γ), Goslar, West Germany; this is a cast bioimmuration attached to a guard of *Metateuthis*.

Description. Colony adnate, consisting of ramifying, uniserial branches of zooids (text-figs. 1 and 2). Branches often gently curved, new branches arising with variable frequency, sometimes in pairs but sometimes singly, by distolateral budding at an angle of between about 45° and 90° to the parent branch. Crowding of zooids

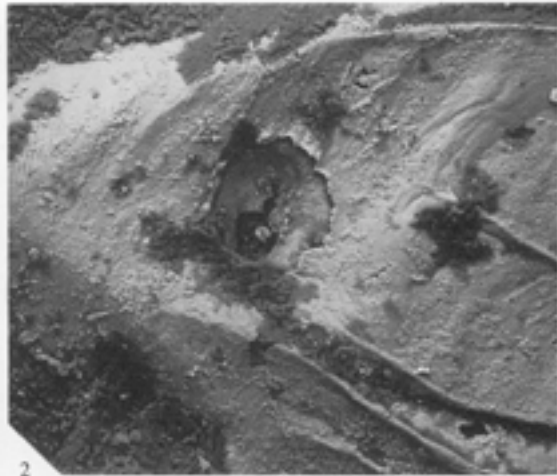
EXPLANATION OF PLATE 2

Figs. 1 and 2. *Arachnidium smithii* (Phillips, 1829), BMNH D 57497, South Ferriby, Kimmeridgian. 1, pyritic cast of collapsed zooid with wrinkled frontal membrane, $\times 100$. 2, orifice of the same zooid, $\times 270$.

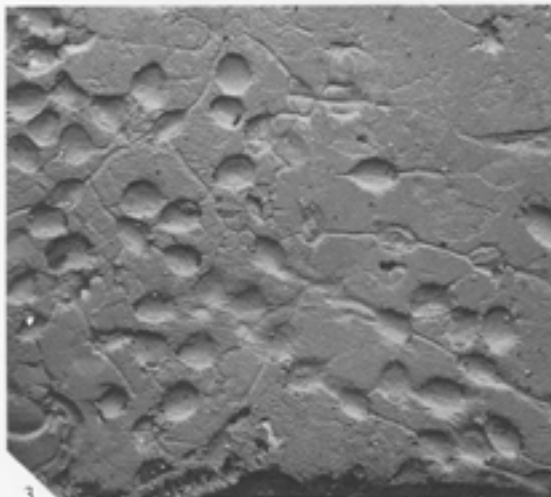
Figs. 3–6. *Arachnoidella abusensis* sp. nov., holotype, BMNH D 57637, South Ferriby, Kimmeridgian. 3, crowded zooids moulded on the underside of the bioimmuring bivalve, $\times 15$. 4, astogenetic increase in zooid length along a branch originating as a lateral bud from the zooid on the left, $\times 28$. 5, mould of zooid showing marginal processes; note lack of visible orifice which is located on a distally-directed peristome hidden in the shadow at the distal end of the zooid, $\times 93$. 6, marginal processes in zooid preserved as a calcitic cast $\times 136$. All illustrations are back-scattered electron micrographs of uncoated specimens.



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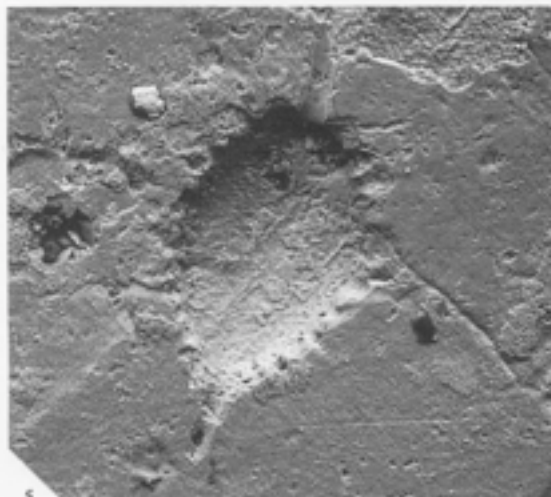
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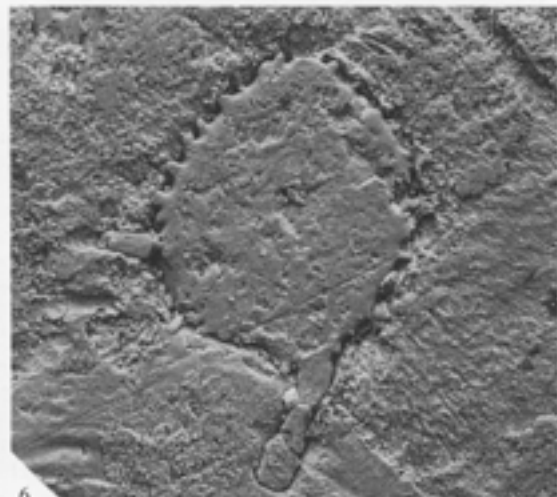
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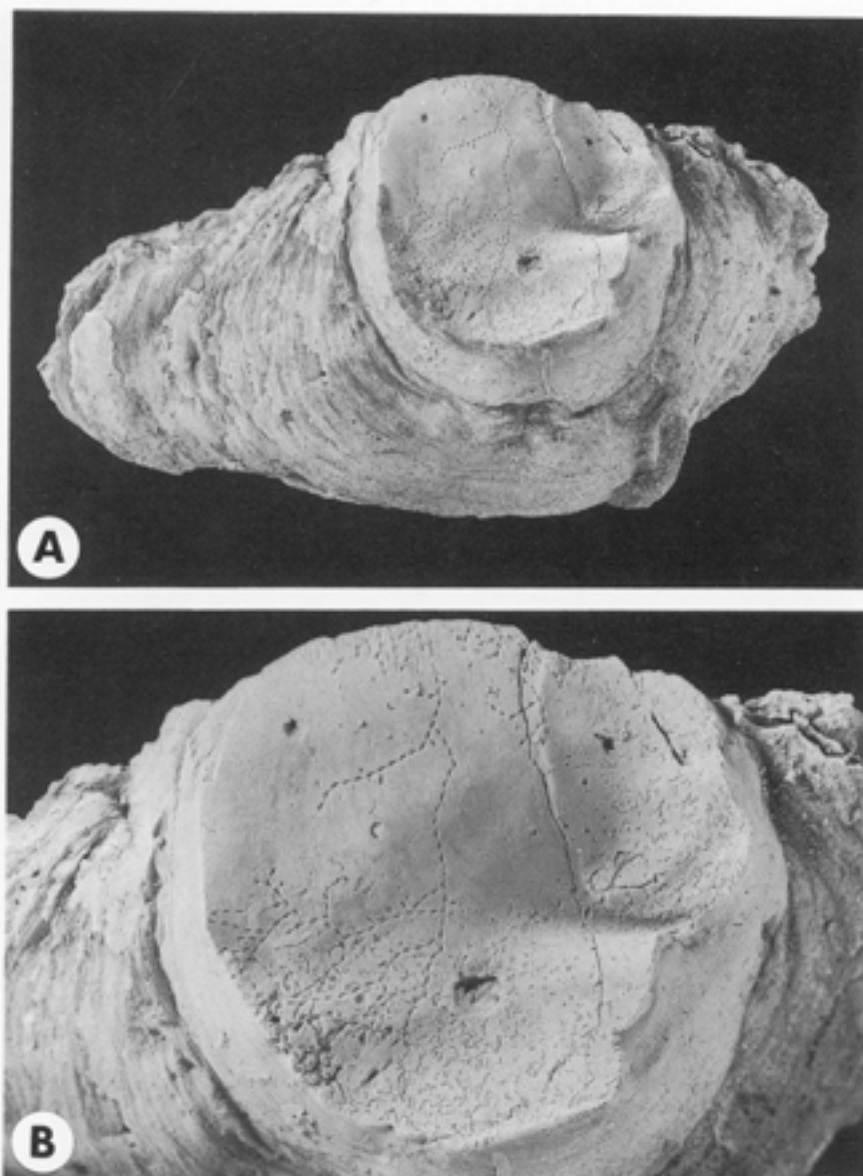
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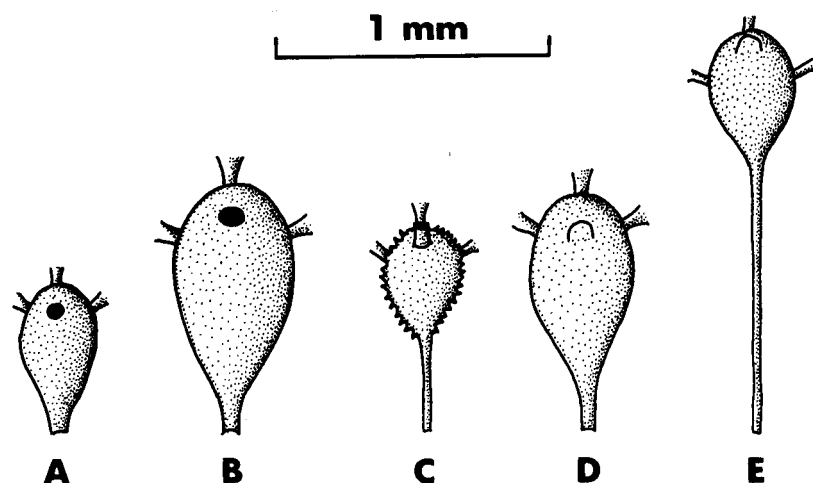
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TEXT-FIG. 2. Mould bioimmuration of *Arachnidium smithii* (Phillips, 1829) visible on the large attachment area of the bivalve *Gryphaea* from the Oxfordian of Villers-sur-mer, BMNH D 57492. A, general view of the bioimmuring *Gryphaea*, $\times 1.2$ B, attachment area showing prominent branch of zooids running from top to bottom, and dense settlement of the foraminifer *Nubeculinella* on the younger, peripheral parts of the attachment area, $\times 2.1$.

may occur in colonies with a high frequency of branching, and can be accompanied by branch overgrowths (Pl. 1, fig. 3) and/or abutment of growing branches against existing branches. In early astogeny (visible only in D 57495), the ancestrula apparently buds proximal and distal periancestrular zooids which initiate two primary colony branches growing in opposite directions. A brief primary zone of astogenetic change is marked by an increase in zooid size with generation. Putative ancestrula about 0.23 mm long by 0.17 mm wide.

Autozooids moderately pyriform in frontal outline shape, narrow proximally, achieving maximum width about or a little distally of mid-length, and with rounded distal ends. Length and width of autozooids is very variable between colonies, measured length ranging from 0.47 to 1.00 mm, width from 0.25 to 0.45 mm, with



TEXT-FIG. 3. Zooid morphology in Jurassic arachnidiids. A and B, *Arachnidium smithii* (Phillips, 1829) showing variation in zooid size (A is based on YM 78, B on BMNH D 57497). C, *Arachnoidella abusensis* sp. nov. D, *Cardoarachnidium bantai* sp. nov. E, *C. voighti* sp. nov.

zooids generally about twice as long as wide. Frontal wall gently convex, often preserved with flattened lateral margins flanking a raised median area which includes the orifice. Longitudinal wrinkles and folds (Pl. 1, fig. 2; Pl. 2, fig. 1) developed on frontal walls of zooids cast by pyrite in BMNH D 57497. In BMNH D 58002, the casting mineral near an autozooidal orifice contains shallow pits which may perhaps represent original pits on the frontal wall. Orifice simple, subterminal, located opposite or a little distal to origins of lateral buds, subcircular to transversely elliptical in shape (Pl. 1, fig. 6), about 0.04–0.08 mm in diameter, occasionally with a slightly raised rim. An eccentrically perforated structure partly occludes the orifice of one zooid of BMNH D 57497 (Pl. 2, fig. 2).

Kenozooids may develop in regions of crowding as small subtriangular-shaped buds (?aborted autozooids) lacking an orifice (text-fig. 1).

Dimensions (mm).

| | \bar{x} autozooid length (range) | \bar{x} autozooid width (range) |
|-----------------------------------|---------------------------------------|--------------------------------------|
| YM 78 (holotype) | 0.59 (0.50–0.68) | 0.31 (0.26–0.36) |
| BMNH D 31144 | 0.52 (0.47–0.59) | 0.30 (0.26–0.36) |
| VH 1899 (<i>vide</i> Voigt 1977) | 0.72 (0.63–0.84) | 0.33 (0.25–0.41) |
| BMNH D 57492 | 0.74 (0.63–0.90) | 0.32 (0.27–0.36) |
| BMNH D 57494 | 0.66 (0.54–0.74) | 0.38 (0.30–0.45) |
| BMNH D 57495 | 0.62 (0.53–0.71) | 0.32 (0.30–0.38) |
| BMNH D 57496 | 0.76 (0.62–0.90) | 0.38 (0.32–0.42) |
| BMNH D 57497 | 0.88 (0.80–1.00) | 0.40 (0.38–0.45) |

Discussion. The present concept of *Arachnidium smithii* (Phillips) encompasses colonies exhibiting a wide range of variation in autozoid length and width (compare text-figs. 3A and B). It seems possible that *A. smithii* may represent a species complex. However, the overlapping dimensions of colonies from different stratigraphical horizons prohibit convenient splitting into two or more putative species. Furthermore, there are no obvious differences in zoid shape, budding pattern etc. which might be used for this purpose. Accordingly, *Stomatopora phillipsii* Vine and *Arachnidium jurassicum* Voigt are taken into synonymy with *A. smithii*. It should be noted that the ctenostome nature of *A. smithii* and *S. phillipsii* were unknown when Voigt (1977) erected *A. jurassicum*; neither species was revised until Taylor (1978) and both were presumed to be cyclostomes of the common Jurassic genus *Stomatopora* Bronn.

The Barremain species *A. brandesi* Voigt strongly resembles *A. smithii* but has considerably larger zooids; according to Voigt (1968), zoid length ranges from 1.65 to 1.75 mm.

The appearance of the zooids within colonies of *A. smithii* may vary according to the extent of their collapse during overgrowth. Uncollapsed zooids have evenly convex frontal walls (Pl. 1, fig. 5), whereas partially collapsed zooids generally have flattened lateral margins flanking a raised median area (Pl. 1, fig. 3). The pattern of collapse undoubtedly reflects some aspect of original zooidal morphology. Dried zooids of the Recent species *Arachnoidea annosciae* figured by d'Hondt and Geraci (1976, fig. 4) show a similar collapsed structure. Banta (1975, fig. 22), in a drawing of bioimmured *A. brandesi*, labels the margins of the zooids as 'gymnocyst' and the median area as 'opesium', suggesting an organization like that of anascan cheilostomes in which the frontal membrane is attached to rigid lateral walls and stretches over the opesium (see Taylor 1981). The parietal muscle (whose contraction depresses the frontal membrane and brings about polypide eversion) were possibly attached to the frontal membrane along the well-defined lines between flattened lateral margins and raised median area. Wrinkling and folding of the frontal wall in pyrite casts of zooids in BMNH D 57497 (Pl. 1, fig. 2; Pl. 2, fig. 1) is a further indication of partial collapse during overgrowth. Transverse contraction of the zoid resulted in the relatively non-elastic cuticle being thrown into a series of folds and wrinkles running subparallel to the length of the zoid.

Stratigraphical range. Aalenian (*polylocus* Zone) to Kimmeridgian (*baylei* Zone).

Genus ARACHNOIDELLA d'Hondt, 1983

Type species. *Arachnoidea annosciae* d'Hondt and Geraci, 1976.

Discussion. *Arachnoidella* was originally proposed by d'Hondt (1983) as a subspecies of *Arachnoidea* Moore, 1903. However, Gordon (1986) elevated *Arachnoidella* to genus rank because the type species of *Arachnoidea* (*A. raylankesteri* Moore) is a freshwater species in which the zooids are interconnected by anastomosing filaments, absent in marine *Arachnoidella*. As noted on p. 20, the distinction between *Arachnoidella* and *Arachnidium* is not great, and the former may eventually prove to be a junior subjective synonym of the latter. D'Hondt (1983) recognized eight Recent species of *Arachnoidella*. The genus has not been previously recorded as a fossil.

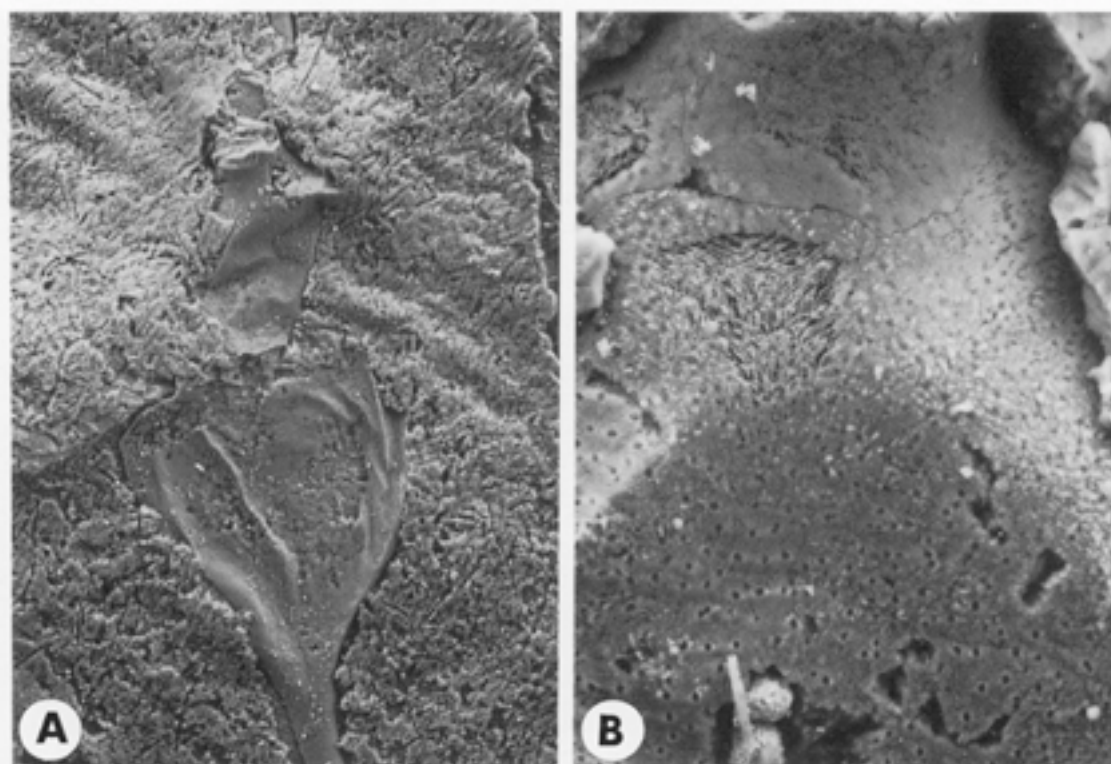
Range. Jurassic (Kimmeridgian) to Recent.

Arachnoidella abusensis sp. nov.

Plate 2, figs. 3–6; text-fig. 3C; text-fig. 4

Holotype. BMNH D 57637, Kimmeridgian, Bed 9 of Birkelund and Calloman (1985) (lower *baylei* Zone), South Ferriby, Humberside, collected by P. D. Taylor, 1987; predominantly a mould bioimmuration (Pl. 2, figs. 3–5) but with a few zooids cast by calcite (Pl. 2, fig. 6) on the attachment area of the bivalve *Deltoideum delta* (Sowerby).

Paratype. BMNH D 57602, details as for holotype; a cast bioimmuration (text-fig. 4) partly exposed by abrasion of the thin overgrowing organism which encrusts a bivalve shell fragment.



TEXT-FIG. 4. *Arachnoidella abusensis* sp. nov., partly collapsed zooids preserved as natural casts, BMNH D 57602, South Ferriby, Kimmeridgian. A, zooid with distally-directed peristome exposed by abrasion of the bioimmuring organism, $\times 162$. B, distal part of frontal membrane of another zooid showing minute pores which are absent from the peristome base at the top of the figure; note presence of 3 sets of fibres in corroded frontal membrane left of centre, $\times 890$. Back-scattered scanning electron micrographs of an uncoated specimen.

Derivation of name. From *Abus*, Roman name for the River Humber which is close to the type locality of South Ferriby.

Diagnosis. *Arachnoidella* with small zooids having about 30 marginal processes; orifice situated terminally on a distally orientated peristome; caudae account for half or more of total zooid length and increase in length during early branch astogeny.

Description. Colony adnate, consisting of branches of uniserially-arranged zooids. New branches arise as lateral buds and diverge from the parent branch at an angle averaging about 60° . Frequent branch ramification results in areas of zooid crowding and branch overgrowth (Pl. 2, fig. 3). Ancestrula unknown. Secondary zones of astogenetic change occur in the early parts of new branches: caudal length increases progressively for the first three or four generations of zooids (Pl. 2, fig. 4).

Autozooids pyriform with a cauda of variable length, generally accounting for half or more of the total length of the zooid, succeeded distally by a longitudinally elliptical dilated frontal wall. Autozooid length variable within colonies, observed range 0.42–1.26 mm ($\bar{x} = 0.92$ mm); width ranging from 0.21–0.27 mm ($\bar{x} = 0.25$ mm). Distal frontal wall gently convex (Pl. 2, fig. 5) or flattened (text-fig. 4A) as a result of overgrowth, and bearing minute pores which are absent from the cauda and peristome (text-fig. 4B). Lateral buds arise a little distally of the level of maximum width on the distal frontal wall. Marginal processes visible around the distal frontal walls of some zooids, numbering about 30 per zooid (Pl. 2, figs. 5 and 6). Orifice situated at the extreme

distal end of the zooid on a peristome (text-fig 4A) which is directed distally and is about 0.05 mm wide at its base.

Discussion. This species is distinguished from previously described Jurassic arachnidiids by the extreme distal location of the orifice. Secondary zones of astogenetic change, manifested by progressive increase in zooid length along new branches, are considerably better developed than in other species. In comparison with Recent species of *Arachnoidella*, *A. abusensis* zooids have fewer marginal processes than *A. annosciae* (c. 30 versus 60) but more than all the other species tabulated by d'Hondt (1983).

The preservation of the paratype (text-fig. 4) deserves comment. Naturally-cast zooids are partially visible beneath the thin basal layer of the overgrowing organism. The casting is of a very high quality, and shows clearly the presence of minute pores on the frontal wall and their absence on the cauda and peristome. Although the identity of the casting material is unknown, an abraded area of the cast of one zooid has a fibrous structure (text-fig. 4B). Fibres are arranged in 3 conjugate sets orientated at 120° to one another. One of the sets exactly parallels the long axis of the zooid. This suggests that the fibres may reflect some aspect of the original structure of the zooidal frontal wall. Possibly they are pseudomorphs of one of the organic components of the zooid body wall.

Stratigraphical range. Kimmeridgian (*baylei* Zone).

Genus CARDOARACHNIDIUM gen. nov.

Type species. *Cardoarachnidium bantai* sp. nov.

Derivation of name. *Cardo-*, Latin for hinge, in reference to the apparent presence of a hinged operculum.

Diagnosis. Arachnidiidae in which the autozooidal orifice is D-shaped with a straight proximal edge and a curved distal/lateral edge.

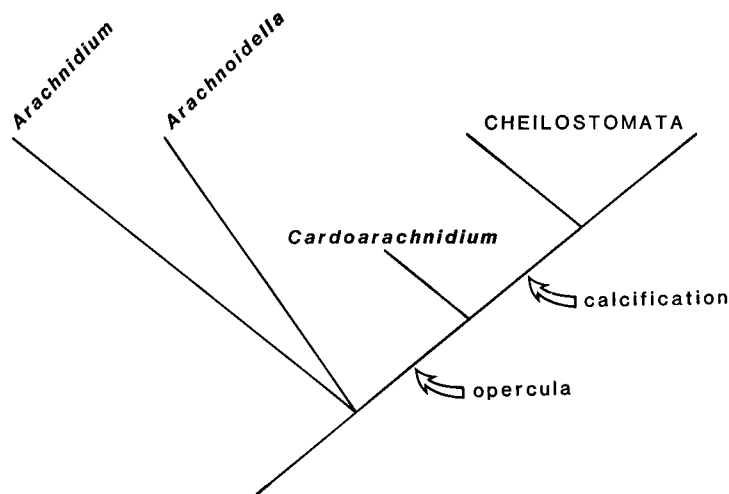
Discussion. This new genus is established for two new species of Jurassic bioimmured ctenostomes which differ from species of *Arachnidium* and *Arachnidiella* in having a D-shaped autozooidal orifice suggesting the presence of a hinged operculum during life. Opercula are generally regarded as being absent in ctenostome bryozoans. However, Banta (1975) notes that structures 'virtually indistinguishable from opercula' occur in the living ctenostome genera *Flustrellidra*, *Elzerina* and *Hislopia*, and d'Hondt (1983) describes the lip of the orifice in *Haywardozoon* as 'simulating an operculum'. An important difference between *Cardoarachnidium* and these Recent genera is that the operculum of *Cardoarachnidium* is a well-defined, univalved structure, whereas those of the Recent genera are bivalved – they are commonly described as bilabiate – with a distal hinged flap as well as a generally larger proximal hinged flap.

Although the phylogenetic significance of the inferred operculum in *Cardoarachnidium* is discussed fully on page 32, it is appropriate to note here that its presence allows *Cardoarachnidium* to be placed within the stem-group of the Cheilostomata. If correct, *Cardoarachnidium* is more closely related (in cladistic terms) to the Cheilostomata than it is to other genera of the Arachnidiidae. The latter family as understood here and by previous authors is almost certainly paraphyletic, and demands future division into its constituent monophyletic clades. Until this is accomplished *Cardoarachnidium* is assigned to the Arachnidiidae.

Cardoarachnidium bantai sp. nov.

Plate 3, figs. 1–3; text-fig. 3D

Holotype. BMNH D 57499 (a), Sandsfoot Clay (sandy top), Upper Oxfordian (*serratum* or *regulare* Zones), below Sandsfoot Castle, Weymouth, Dorset, collected by W. J. Kennedy, N. J. Morris and C. P. Palmer, 1971.



TEXT-FIG. 5. Simplified cladogram showing inferred phylogenetic relationships between genera of arachnidiid ctenostomes present in the Jurassic and the Cheilostomata. *Cardioarachnidium* is depicted as a stem-group cheilostome because it apparently possesses one (opercula) but not the second (calcification) apomorphic feature of the crown-group cheilostomes. The trichotomy between *Arachnidium*, *Arachnoidella* and *Cardioarachnidium* + the Cheilostomata is unresolved.

A mould bioimmuration on the attachment scar of the bivalve *Deltoideum delta* (Sowerby), and intergrown with the holotype of *Cardioarachnidium voighti* sp. nov. (see p. 30).

Derivation of name. In recognition of the bryozoological research of Dr W. C. Banta (The American University, Washington).

Diagnosis. *Cardioarachnidium* with pyriform zooids lacking significant caudae; orifice located subterminally.

Description. Colony adnate, consisting of uniserial branches, often slightly curved, from which daughter branches arise sporadically as lateral buds and diverge at angles of 60–90° to the parent branch (Pl. 3, fig. 1). Ancestrula budding a proximal periancestrular zooid only; no distal periancestrular zooid visible (Pl. 3, fig. 2). Ancestrula of similar shape but smaller than the periancestrular zooid and later zooids, with a length of 0.30 mm, width 0.17 mm and D-shaped orifice 0.06 mm wide.

Autozooids moderately pyriform in outline shape, narrow proximally, rounded distally, achieving maximum width rather distal of mid-length. Length of autozooid about 2.5 times the width, length averaging 0.76 mm (range 0.63–0.93 mm), width averaging 0.32 mm (range 0.27–0.39 mm). Frontal wall gently convex, sometimes with slightly flattened lateral margins. Close to the orifice in one autozooid, the basal layer of the bioimmuring bivalve is penetrated by small pores which may represent a negative impression of an originally spinose or pustulose frontal wall and operculum. Orifice when visible is D-shaped (Pl. 3, fig. 3), wider than long, small, about 0.05 × 0.08 mm in size, situated more-or-less opposite sites of lateral bud origin. The straight proximal edge is less well-defined than the crescentic lateral/distal edge which, together with the shape of the orifice, suggests that an operculum was hinged on the proximal edge of the orifice. In many zooids the orifice cannot be seen, possibly because of poor quality bioimmuration.

Discussion. Colony-form and autozooid shape and size are very similar to *A. smithii*, although the length:width ratio of the autozooids is a little greater in *C. bantai*. However, the D-shaped orifice serves to distinguish *C. bantai* from *A. smithii*.

Stratigraphical range. Oxfordian (*serratum* or *regulare* Zones).

Cardoarachnidium voighti sp. nov.

(Plate 3, figs. 4–6; text-fig. 3E)

Holotype. BMNH D 57499 (b), Sandsfoot Clay (sandy top), Upper Oxfordian (*serratum* or *regulare* Zones), below Sandsfoot Castle, Weymouth, Dorset, collected by W. J. Kennedy, N. J. Morris and C. P. Palmer, 1971. A mould bioimmuration on the attachment scar of the bivalve *Deltoideum delta* (Sowerby), and intergrown with the holotype of *C. bantai* sp. nov. (see p. 28).

Derivation of name. In honour of Professor E. Voigt (Universität Hamburg).

Diagnosis. *Cardoarachnidium* with slender, caudate zooids; orifice located terminally.

Description. Colony adnate, consisting of uniserial branches from which daughter branches arise as lateral buds at an angle of about 45–90° to the parent branch (Pl. 3, fig. 4). Branch ramification occurs frequently, most zooids producing two lateral buds. Growing branches generally terminate on meeting established branches, giving an anastomosing network in some areas of the colony. Ancestrula unknown.

Autozooids slender (Pl. 3, fig. 5), 0.74–1.65 mm long (\bar{x} 1.20 mm), a narrow proximal cauda accounting for a third to three quarters of their length and succeeded distally by a dilated part the shape of a longitudinally elongate ellipse 0.32–0.45 mm long (\bar{x} 0.37 mm) by 0.20–0.29 mm wide (\bar{x} 0.22 mm). Distal frontal wall gently convex or flat-topped; ornamentation not apparent. Laterally-budded daughter zooids often rather shorter than their parental zooids, but clearly-defined secondary zones of astogenetic change not obvious. Lateral budding loci situated a little distally of mid-length on the distal frontal wall. Orifice terminal (Pl. 3, fig. 6), small, slightly raised, a poorly-defined D-shape, about 0.07 mm wide.

Discussion. This species is immediately distinguished from most other Jurassic bioimmured ctenostomes by the long length of the caudae. In this feature it most closely resembles the Maastrichtian *Arachnidium longicauda* Voigt, 1980 which has a roughly circular distal frontal wall, and subcircular orifice situated much further proximally than that of *C. voighti*. Although the caudae of *Arachnoidella abusensis* (see p. 26) may also be long, the orifice of this species is more terminally situated and the zooids often possess marginal processes.

None of the autozooidal orifices are as well-preserved as those of *C. bantai* which shares the same substratum. Nevertheless, *C. voighti* also appears to have a D-shaped orifice suggesting the presence of an operculum hinged on the straight proximal edge of the orifice. This D-shape is apparently not an artefact caused by the overgrowing organism pushing over short peristomes in a distal direction; if it were the D-shape would be better developed in zooids orientated parallel to the growth direction of the overgrowing organism, which is not the case.

Stratigraphical range. Oxfordian (*serratum* or *regulare* Zones).

DISCUSSION

Present-day bryozoan faunas are dominated by species belonging to the order Cheilostomata. For example, in a survey of seven regional faunas (Taylor 1981), the percentage contribution of cheilostome species ranged from 69 to 91. However, cheilostomes are a geologically young order,

EXPLANATION OF PLATE 3

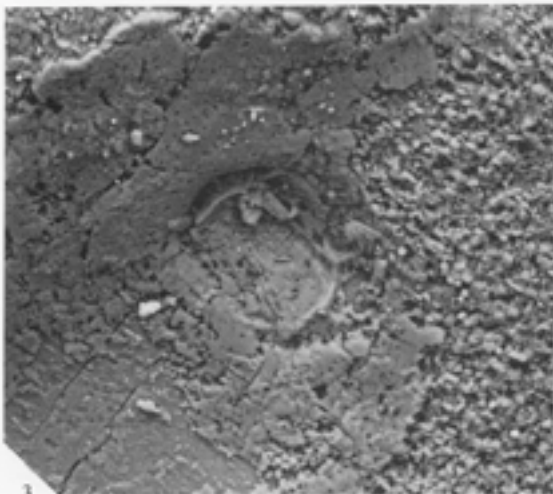
Figs. 1–3. *Cardoarachnidium bantai* sp. nov., holotype, BMNH D 57499 (a), mould bioimmuration, Weymouth, Oxfordian. 1, uniserial branch, $\times 14$. 2, ancestrula (lower left) with proximal ancestrular bud (centre) and its distal bud, $\times 55$. 3, D-shaped orifice of proximal periancestrular zooid, $\times 15$.
Figs. 4–6. *Cardoarachnidium voighti* sp. nov., holotype, BMNH D 57499 (b), mould bioimmuration, Weymouth, Oxfordian. 4, $\times 16$. 5, caudate zooids, $\times 38$. 6, distal part of zooid showing terminal orifice, $\times 120$.
All illustrations are back-scattered electron micrographs of uncoated specimens.



1



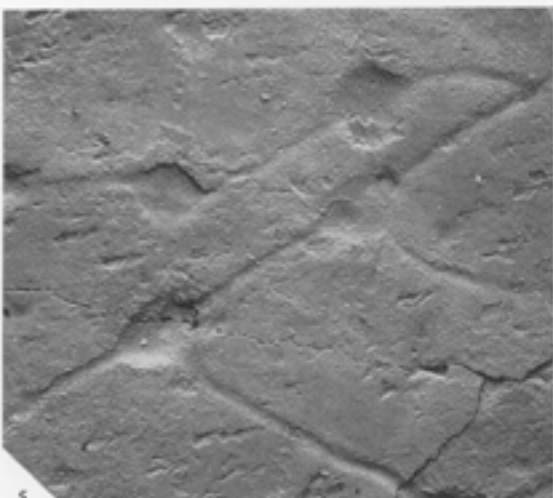
2



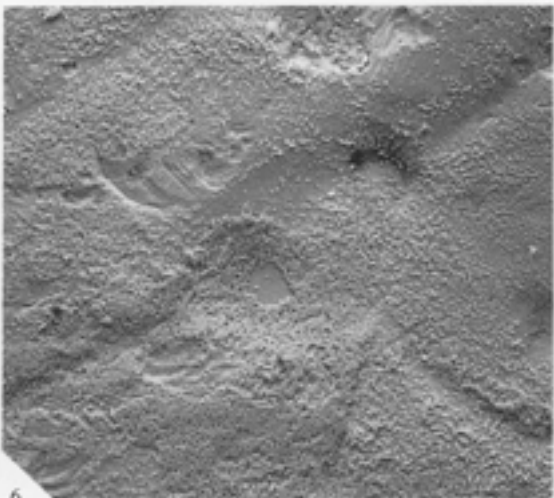
3



4



5



6

first appearing at the end of the Jurassic (Pohowsky 1973) and not diversifying appreciably until the late Cretaceous (see Taylor 1988). Several hypotheses have been proposed to account for the phylogenetic origin of cheilostomes (Banta 1975). Cheilostome ancestry has been sought in the Fenestrata (Ulrich 1890), Cyclostomata (Dzik 1975) and Ctenostomata (e.g. Banta 1975; Cheetham and Cook in Boardman *et al.* 1983). There are severe difficulties with hypotheses which propose an origin from either of the first two orders which are stenolaemate bryozoans. Similarities do exist between some cheilostome species and fenestrates (which may share box-shaped zooecia), and between other cheilostome species and stomatopod or corynotrypid cyclostomes (which can both have uniserial colonies with pyriform zooecia), but these are best explained by homoplasy in the first case (Tavener-Smith 1971) and plesiomorphy in the second. Comparative anatomical studies of living bryozoans support the theory of a ctenostome ancestry for the cheilostomes, or more strictly, that 'ctenostomes' (a primitive, paraphyletic grouping of marine bryozoans) include the sister-group of cheilostomes. As Banta (1975) points out, there are extremely few differences between many carnosan ctenostomes and primitive cheilostomes.

The Cheilostomata are very probably a monophyletic clade which can be distinguished from their sister group ctenostomes by two apomorphic characters; calcification of parts of the zooid body walls, and the possession of an operculum to close the orifice on retraction on the tentacles. All living cheilostomes have some degree of calcification, although in certain genera (e.g. *Membranipora*, *Flustra*) this is slight. Most cheilostomes possess opercula; absence of the operculum in the feeding zooids of a few genera (e.g. *Bugula*) is undoubtedly a result of their secondary loss, as shown by the presence in the same colonies of polymorphic zooids (avicularia) which retain opercula. Extinct cheilostomes for which adequate information is available also possess the two apomorphies. Indeed, they are present even in the oldest known cheilostome, *Pyriporopsis portlandensis* from the Tithonian (Portlandian) of southern England, which has thickly-calcified zooid vertical walls, and in which the past presence of a non-calcified operculum can be inferred confidently from impressions on the closure plates of degenerated zooids (Pohowsky 1973; Banta 1975; Taylor 1987). Therefore, current knowledge of living and fossil cheilostomes provides no information on the order of appearance of the two apomorphies; did calcification predate opercula or vice-versa?

The new genus *Cardoarachnidium* is important because it apparently has one of the two apomorphies of the Cheilostomata. The simple D-shaped opercula of *Cardoarachnidium* closely resemble the opercula of primitive anascan cheilostomes. However, *Cardoarachnidium* clearly did not have calcified zooids and therefore lacked the second apomorphy of the Cheilostomata; bioimmured colonies show no trace of calcified zooid walls, and distortion of the zooids during overgrowth, typical of that seen in other bioimmured ctenostomes, implies that the zooids were soft-bodied.

The stem-group concept in phylogenetics has been explained recently by Jefferies *et al.* (1987). Stem-groups are the paraphyletic ancestral groupings of extinct taxa remaining when the crown groups have been subtracted from the total group. They are distinguished by possessing some but not all of the apomorphies that separate any two monophyletic clades with extant representatives (crown groups). By this criterion, *Cardoarachnidium* can be included in the stem-group of the Cheilostomata. This inferred relationship is expressed in the cladogram depicted in text-fig. 5. Stratigraphical sequence is consistent with the cladogram; arachnidiids date back at least to the Aalenian, *Cardoarachnidium* occurs in the Oxfordian, and the first cheilostome in the Tithonian. The discovery and phylogenetic placement of *Cardoarachnidium* solves the problem of the order in which the two apomorphies of cheilostomes appeared; opercula apparently predate calcification.

As the most crownward known representative of the stem-group of the Cheilostomata, *Cardoarachnidium* is a useful outgroup for inferring character polarities (plesiomorphic versus apomorphic) during studies of phylogenetic relationships within the cheilostomes. Unfortunately, however, relatively few morphological characters are available in bioimmured *Cardoarachnidium* and these do not, of course, include characters of the calcified skeleton which are generally emphasized during studies of cheilostomes. Nevertheless, *Cardoarachnidium* does suggest the following plesiomorphic character states in cheilostomes: uniserial pattern of colony growth with

the potential for each zooid to produce a distal and two lateral buds; pyriform zooid shape; and the budding of a proximal periancestrular zooid from the ancestrula. *Pyriporopsis*, *Pyripora* and *Herpetopora* among primitive 'malacostegan' cheilostomes (see Taylor 1987) retain all of these characters, although there is a tendency towards pluriserial growth in *Pyriporopsis*.

Knowledge of Jurassic bryozoans is strongly geographically constrained; very few Jurassic bryozoans have been described outside Europe, and modern studies are mostly concerned with faunas from France and southern England. Within this limited geographical region, however, an interesting pattern of stratigraphical distribution is apparent. Rich cyclostome bryozoan faunas occur locally in the Middle Jurassic (e.g. Gloucestershire Aalenian, Normandy Bathonian), with assemblages containing encrusting and erect tubuliporine and cerioporine cyclostomes. Few ctenostomes are evident, either as borers in the abundant shelly substrata, or as encrusters preserved by bioimmuration. Upper Jurassic bryozoan faunas from southern England and France contain assemblages of encrusting tubuloporine cyclostomes greatly reduced in diversity and abundance. However, ctenostomes are much more prominent than in the Middle Jurassic. They include shell borers as well as the bioimmured encrusters described herein. Considering the fairly low probability of preservation of soft-bodied arachnidiids, their abundance and diversity in the late Jurassic epicontinental sea of north-west Europe may have been substantial, quite possibly exceeding arachnidiid abundance and diversity at the present-day. The origin of the Cheilostomata should be viewed within the context of this time of comparative arachnidiid prevalence.

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