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Pre-Cenomanian Cheilostome Bryozoa: Current State of Knowledge

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ABSTRACT

This paper briefly summarizes published and new data on the occurrences of pre-Cenomanian cheilostome Bryozoa following their first appearance in the Late Jurassic. We tabulate all known taxa chronologically, summarize stratigraphical and geographical distributions, and comment on the main morphological innovations that appeared in pre-Cenomanian times. Most early cheilostomes are classified in the suborder Malacostegina. Early cheilostomes were morphologically simple and low in diversity, but were geographically widespread. These features can be explained by the possession of a long-living planktotrophic larval stage, as in Recent malacostegans. Diversification of the suborder Neocheilostomina, which greatly dominates modern and post-Albian bryozoan faunas, began in the Late Albian and coincided with the origin of brood chambers (ovicells) and a presumably short-lived, non-planktotrophic larva. The presence of Late Albian neocheilostomes in both Europe and North America implies that their brief larval life was not an obstacle to achieving a wide distribution and suggests a role for rafting in their dispersal.

Keywords: Cheilostomata, Bryozoa, Cretaceous, Diversity

INTRODUCTION

The bryozoan order Cheilostomata, which first appeared in the Late Jurassic, subsequently diversified to become the dominant group of Bryozoa in modern seas. For the first third of their history, cheilostomes were characterized by low diversity and morphological simplicity, yet they achieved a wide geographical distribution. All known cheilostomes older than Late Albian are classified in the suborder Malacostegina (Table 1). Recent representatives of this paraphyletic group possess non-brooded planktotrophic larvae. The Late Albian saw the first ap-

pearance of the suborder Neocheilostomina, modern species of which brood non-planktotrophic larvae.

JURASSIC AND EARLY CRETACEOUS CHEILOSTOME GENERA

The earliest cheilostomes belong to the genus *Pyriporopsis* (Electridae) and have been described from the Oxfordian/Kimmeridgian of the Yemen [1] and the Tithonian-Berriasian of England [2, 3]. This genus has a very simple zooidal morphology with oval or pyriform zooids having elliptical opesia that are surrounded by striated mural rims. A pustulose

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Table 1 Generic and species diversity of the pre-Cenomanian cheilostome bryozoans.

genus/species	age	horizon and locality	references	genus range
MALACOSTEGINA				
<i>Pyriporopsis pohowskyi</i> Taylor, 1994	?Oxfordian, ?Kimmeridgian	Madbi Fm. Jebel Sakha, Yemen	1	?Oxfordian, ?Kimmeridgian- Berriasian
<i>Pyriporopsis portlandensis</i> Pohowsky, 1973 (Fig. 1A)	Tithonian-Berriasian	Portland and Purbeck Beds. Dorset, Wiltshire and Buckinghamshire, England.	2, 3	
<i>Wawalia crenulata</i> Dzik, 1975 (Fig. 1B)	Upper Valanginian-Hauterivian	Wawal, Poland	4	Middle Valanginian- ?Albian
<i>Wawalia</i> sp. (undescribed species mentioned by Dzik 1975)	Middle Valanginian	Poland	4	
<i>Wawalia</i> sp.	Hauterivian	Lower Tealby Clay. Nettleton, Lincolnshire, England	22	
<i>Wawalia</i> sp.	Hauterivian	Speeton Clay (Upper D and C Beds). Speeton, Yorkshire, England	22	
<i>Wawalia neocomiensis</i> (d'Orbigny, 1853)	'Neocomian'	Saint-Sauveur, Yonne, France	7	
<i>Wawalia constricta</i> (d'Orbigny, 1853)	Aptian	Les Croute, France	22	
<i>Wawalia?</i> sp.	Aptian	Lower Greensand. Brickhill, Bedfordshire, England	22	
<i>Wawalia</i> sp.	Upper Aptian	Upper Greensand (Fullers Earth). Baulking, Oxfordshire, England	22	
? <i>Wawalia</i> sp. (as ' <i>Membranipora kiowana</i> ' Scott, 1970)	Albian	Kiowa Fm. Kansas, USA	5, 7	
<i>Charixa</i> sp. nov. Taylor, Lazo, Aguirre-Urreta, in review	Upper Hauterivian- ?Lower Barremian	Agrio Fm. Neuquen Basin, Argentina	6	Upper Hauterivian- Albian
<i>Charixa?</i> sp. Taylor, 1986	Barremian	Makatini Fm. Northern Zululand, South Africa	7	
<i>Charixa lhuydi</i> (Pitt, 1976)	Upper Aptian	Faringdon Sponge Gravel. Faringdon, Oxfordshire, England	7, 9	
<i>Charixa?</i> sp.	Aptian	Lower Greensand. Upware, Cambridgeshire, England	22	
<i>Charixa lindiensis</i> Taylor, 1986 (Fig. 1C)	Aptian	Tanzania	7	
<i>Charixa vennensis</i> Lang, 1915	Upper Albian	Cowstones, Upper Greensand. Dorset, England	7, 8	
<i>Charixa cryptocauda</i> Taylor, 1986	Albian	Mzizene Fm. Zululand, South Africa	7	
<i>Rhammatopora gaultina</i> (Vine, 1890) (Fig. 1D-E)	Albian	Gault Clay. Cambridgeshire and Kent, England	14–16	Albian
<i>Pyripora</i> sp.	Upper Aptian - Lower Albian	Glen Rose Fm. Texas, USA	10	Aptian-Recent
<i>Pyripora texana</i> Thomas and Larwood, 1956 (Fig. 1F)	Upper Albian	Washita Group. Texas, USA	11, 12	
<i>Pyripora</i> sp.	Aptian	Alexander Island, Antarctica	13	
' <i>Conopeum</i> ' s. l. (Fig. 1G)	Upper Aptian - Lower Albian	Glen Rose Fm. Texas, USA	10	Upper Aptian-Recent
? <i>Conopeum</i> ' s. l.	Upper Albian	Upper Greensand, Cherty Beds. Devon, England	22	

Table 1 continued

<i>Spinicharixa pittii</i> Taylor, 1986	?Aptian	?Urgoniana Fm., Spain	7	Aptian-Upper Albian
<i>Spinicharixa dimorpha</i> Taylor, 1986 (Fig. 1H-I)	Middle-Upper Albian	Gault Clay. Sussex, Kent and Cambridgeshire, England	7, 16	
cf. <i>Spinicharixa</i> sp.	Upper Aptian - Lower Albian	Glen Rose Fm., Texas, USA	10	
unnamed erect genus (Fig. 1J)	Upper Albian	Upper Greensand (including Blackdown Greensand). Devon and Dorset, England	7, 18, 22	Upper Albian-Cenomanian
' <i>Membranipora</i> ' <i>wilsonensis</i> Etheridge, 1902	Unspecified Lower Cretaceous	New South Wales, Australia	7, 23	
NEOCHEILOSTOMINA				
<i>Wilbertopora mutabilis</i> Cheetham, 1954	Upper Albian	Fort Worth Fm. Oklahoma and Texas, USA	20, 21	Upper Albian-?Maastrichtian
<i>Wilbertopora tappanae</i> Cheetham et al. 2006	Upper Albian	Denton, Weno and Paw Paw Fms. Texas, USA	20	
<i>Wilbertopora hoadleyae</i> Cheetham et al. 2006	Upper Albian	Fort Worth Fm. Texas, USA	20	
<i>Wilbertopora spatulifera</i> Cheetham et al. 2006 (Fig. 1K)	Upper Albian - Lower Cenomanian	Fort Worth, Denton, Weno, Paw Paw, Main Street and Georgetown Fms., Oklahoma and Texas, USA	20	
<i>Wilbertopora attenuata</i> Cheetham et al. 2006	Upper Albian - Lower Cenomanian	Denton and Georgetown Fms. Texas, USA	20	
<i>Wilbertopora improcera</i> Cheetham et al. 2006	Upper Albian - Lower Cenomanian	Fort Worth, Denton, Georgetown Fms. Oklahoma and Texas, USA	20	
<i>Wilbertopora</i> sp.	Albian	Upper Greensand. Wiltshire, England	7, 24	
<i>Wilbertopora</i> sp.	Upper Albian	Upper Greensand, Cherty Beds. Devon, England	22	
? <i>Marginaria</i> sp. (<i>Membranipora elliptica</i> (?) Hagenow of Vine 1890) (Fig. 1L)	Upper Albian	Red Chalk, Hunstanton Fm. Norfolk, England	7, 14, 19	?Albian-Maastrichtian
? <i>Mystripora</i> sp. Dzik, 1975	Upper Albian or Lower Cenomanian	Annapol, Poland	4	Upper Albian-Campanian

cryptocyst is absent. Colonies are uniserial to pluriserial encrusters (Fig. 1A) and lack regular bud fusions. Closure plates are often present and may bear impressions of the uncalcified operculum. Kenozooidal polymorphs occasionally develop where space is restricted.

Wawalia (Wawaliidae) appeared approximately 20 million years after *Pyriporopsis*, in the Valanginian of Poland [4]. Younger examples of *Wawalia* occur in the British Hauterivian and Aptian, the French Aptian, and possibly also the Upper Albian of the USA [5]. Colonies are multiserial with the zooids arranged in a regular quincuncial pattern, perhaps reflecting bud fusion at the growing edge. The gymnocyst may contain irregular pores and cracks and

has a scalloped, ill-defined border with the radially striated cryptocyst (Fig. 1B). Paired attachment scars of the opercular occlusor muscles can be present on the basal wall near the distolateral corners of the zooids.

Charixa (Electridae) is first known from the Upper Hauterivian of Argentina [6] and persisted at least until the Upper Albian (South Africa, Tanzania, England) [7–9]. Colonies are pluriserial with irregularly arranged zooids (Fig. 1C). Paired bases of oral spines may be visible at the distolateral corners of the opesia. Gymnocysts are moderately to well developed, and a pustulose cryptocyst is generally present.

Probably related to *Charixa* is *Spinicharixa* (Fig.

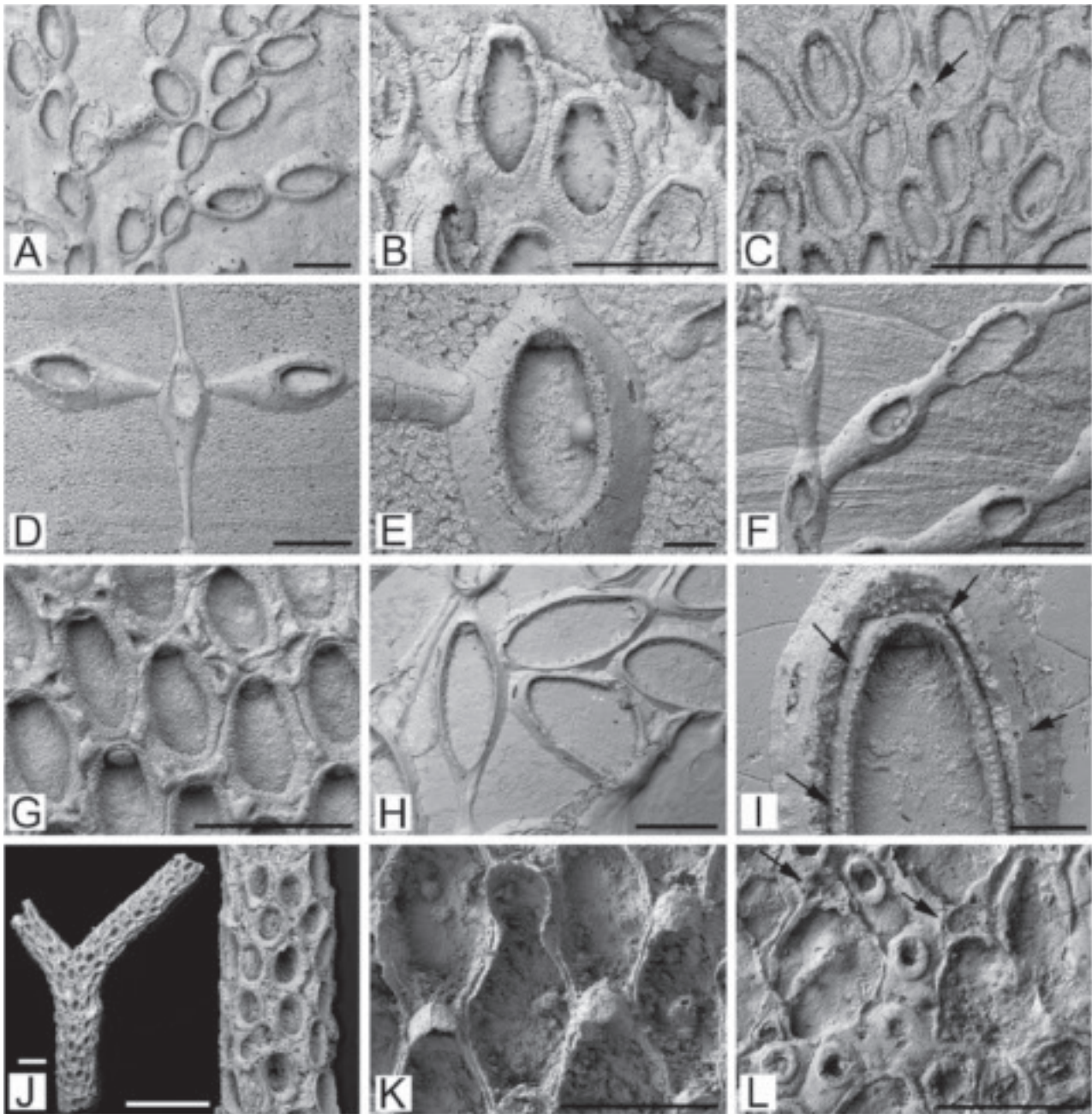


Fig. 1 Morphology of early cheilostomes. (A) *Pyripopsis portlandensis* Pohowsky; Tithonian, Portland Beds, Buckinghamshire, England; NHM D53695. (B) *Wawalia crenulata* Dzik; Upper Valanginian, Wawal, Poland; NHM unregistered. (C) *Charixia lindiensis* Taylor, with kenozooid arrowed; Lower Aptian, Utimbe, Tanzania; NHM D55025. (D-E) *Rhammatopora gaultina* (Vine), showing cruciate budding from zooid with a closure plate (D) and tiny circumopesial spine bases (E); Upper Albian, Burwell, Cambridgeshire, England; NHM D58150. (F) *Pyripora texana* Thomas and Larwood; Upper Albian, Denison, Texas, USA; NHM BZ1353. (G) '*Conopeum*' s. l.; Lower Albian, Hays County, Texas, USA; NHM unregistered. (H-I) *Spinicharixa dimorpha* Taylor; minute spine bases (arrows) are present in an intramural bud and its host zooid in (I); Upper Albian, Burwell, Cambridgeshire, England; NHM D59192. (J) Chiplonkarinidae, undescribed genus, showing bifurcating erect branch (left) and detail of zooids (right); Upper Albian, Blackdown, Devon, England; NHM unregistered. (K) *Wilbertopora spatulifera* Cheetham et al., with spatulate vicarious avicularium (center left) and three ovicellate autozooids; Lower Cenomanian, Fort Worth, Texas, USA; NHM BZ1372. (L) ?*Marginaria* sp., showing small polymorphs and autozooids with worn ovicells (arrows); probably Upper Albian, Hunstanton, Norfolk, England; NHM D2054. Scale bars: 500 µm, except for E and I, which are 100 µm.

1H), which has been recorded from the Upper Aptian of Spain and the Albian Gault Clay of southern England [7]. In this genus, however, spine bases (Fig. 1I) are more numerous and expand onto the proximal part of zooids, forming a circumopesia ring in the type species.

Some undescribed species of cheilostomes from the Upper Aptian-Upper Albian of Texas [10] and southern England resemble the extant malacostegan *Conopeum* and are provisionally assigned to this genus. Colonies are multiserial, lack spine bases, and seemingly do not have bud fusions. In the Texan species, kenozooids are developed at the distolateral corners of the autozooids (Fig. 1G), recalling the so-called reticulozooids of the Recent *Conopeum reticulum*.

Another extant genus, *Pyripora*, has runner-like, uniserial colonies consisting of simple pyriform zooids with long proximal gymnocysts (Fig. 1F). The oldest known examples are from the Aptian or Early Albian of Antarctica and Texas [11–13].

Rhammatopora (Fig. 1D, E), which occurs in the Albian Gault Clay and also the Red Chalk of southern England [14–16], has a similar colony form to *Pyripora*, although zooids tend to be more gracile and very narrow proximally (Fig. 1D). This genus was originally described on the basis of the longitudinal crack (rhamma) present in the proximal gymnocyst (cauda) of many of the zooids, but this feature may be unimportant taxonomically. However, *Rhammatopora* (Fig. 1E) is distinguished from *Pyripora* (Fig. 1F) in having minute spine bases surrounding the opesia. These structures are very difficult to resolve without the benefit of SEM.

An undescribed genus from the Upper Albian and Lower Cenomanian of southern England is the oldest cheilostome known to develop erect growth (Fig. 1J). It resembles the Upper Cretaceous genus *Chiplonkarina* [17], and indeed has recently been placed in a new family, Chiplonkarinidae [18], but has a different endozonal morphology.

Rapid diversification of cheilostomes began in the Late Albian. Important novelties that evolved during this major radiation included chambers (ovicells) for the brooding of non-planktotrophic larvae, and mandibulate zooidal polymorphs (avicularia) [19–20]. The first of these characters is diagnostic of the Neocheilostomina, of which the Calloporidae is the only family represented in the pre-Cenomanian.

The most common pre-Cenomanian neocheilostome is *Wilbertopora* (Fig. 1K), recorded from the Upper Albian of the USA and England [19–21]. Two more calloporid genera - *?Marginaria* (Fig. 1L)

and *?Mystriopora* - have been recorded from the Upper Albian of England [19] and Poland [4], respectively. However their precise taxonomic affinities need to be clarified.

DISCUSSION

For the first approximately 60 million years of cheilostome evolution, only 10 or 11 genera belonging to four families are known (Table 1). In contrast, 30 new genera and five new families appeared during the 6 million years of the succeeding Cenomanian stage [25–26]. It has been proposed that the evolution of a new larval type was the trigger for this major radiation [19].

The wide geographical distribution of malacostegan cheilostomes in pre-Cenomanian times is not surprising given that they probably possessed feeding larvae capable of spending a long time in the plankton. However, it is surprising that neocheilostomes with short-lived larvae and limited powers of dispersal appeared almost simultaneously in the Late Albian deposits of both Europe and North America. The mechanism for achieving this wide geographical distribution is not understood, but it is possible that rafting played an important role [19]. Evidence that cheilostome bryozoans encrusted the shells of living nektonic ammonites and nautiloids would bolster a rafting hypothesis.

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