Pre-Cenomanian Cheilostome Bryozoa: Current State of Knowledge

Andrew N. Ostrovsky1,2, Paul D. Taylor3,*, Matthew H. Dick4 and Shunsuke F. Mawatari4,5

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

<table>
<thead>
<tr>
<th>genus/species</th>
<th>age</th>
<th>horizon and locality</th>
<th>references</th>
<th>genus range</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>MALACOSTEGINA</strong></td>
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<tr>
<td><em>Pyriporopsis portlandensis</em> Pohowsky, 1973 (Fig. 1A)</td>
<td>Tithonian-Berriasian</td>
<td>Portland and Purbeck Beds. Dorset, Wiltshire and Buckinghamshire, England.</td>
<td>2, 3</td>
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<tr>
<td><em>Wawalia crenulata</em> Dzik, 1975 (Fig. 1B)</td>
<td>Upper Valanginian-Hauterivian</td>
<td>Wawal, Poland</td>
<td>4</td>
<td>Middle Valanginian-?Albian</td>
</tr>
<tr>
<td><em>Wawalia sp.</em> (undescribed species mentioned by Dzik 1975)</td>
<td>Middle Valanginian</td>
<td>Poland</td>
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<tr>
<td><em>Wawalia sp.</em></td>
<td>Hauterivian</td>
<td>Lower Tealby Clay. Nettleton, Lincolnshire, England</td>
<td>22</td>
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<td><em>Wawalia sp.</em></td>
<td>Hauterivian</td>
<td>Speeton Clay (Upper D and C Beds). Speeton, Yorkshire, England</td>
<td>22</td>
<td></td>
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<tr>
<td><em>Wawalia neocomiensis</em> (d’Orbigny, 1853)</td>
<td>‘Neocomian’</td>
<td>Saint-Sauveur, Yonne, France</td>
<td>7</td>
<td></td>
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<tr>
<td><em>Wawalia constricta</em> (d’Orbigny, 1853)</td>
<td>Aptian</td>
<td>Les Croute, France</td>
<td>22</td>
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<td><em>Wawalia sp.</em></td>
<td>Upper Aptian</td>
<td>Upper Greensand (Fullers Earth). Baulking, Oxfordshire, England</td>
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<td>?<em>Wawalia sp.</em> (as ‘Membranipora kiowana’ Scott, 1970)</td>
<td>Albian</td>
<td>Kiowa Fm. Kansas, USA</td>
<td>5, 7</td>
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<td><em>Charixa sp.</em> nov. Taylor, Lazo, Aguirre-Urreta, in review</td>
<td>Upper Hauterivian-?Lower Barremian</td>
<td>Agrio Fm. Neuquen Basin, Argentina</td>
<td>6</td>
<td>Upper Hauterivian-Albian</td>
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<td><em>Charixa? sp.</em> Taylor, 1986</td>
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<td>Makatini Fm. Northern Zululand, South Africa</td>
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<tr>
<td><em>Charixa lindens</em> Taylor, 1986 (Fig. 1C)</td>
<td>Aptian</td>
<td>Tanzania</td>
<td>7</td>
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<tr>
<td><em>Charixa venenensis</em> Lang, 1915</td>
<td>Upper Albion</td>
<td>Cowstones, Upper Greensand. Dorset, England</td>
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<tr>
<td><em>Charixa cryptocauda</em> Taylor, 1986</td>
<td>Albian</td>
<td>Mzizene Fm. Zululand, South Africa</td>
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<td><em>Rhummatopora gaultina</em> (Vine, 1890) (Fig. 1D-E)</td>
<td>Albian</td>
<td>Gault Clay. Cambridgeshire and Kent, England</td>
<td>14–16</td>
<td>Albian</td>
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<td>Glen Rose Fm. Texas, USA</td>
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<td>Aptian-Recent</td>
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<td><em>Pyripora texana</em> Thomas and Larwood, 1956 (Fig. 1F)</td>
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<td>Washita Group. Texas, USA</td>
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<td><em>Pyripora sp.</em></td>
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<td>Alexander Island, Antarctica</td>
<td>13</td>
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<td>‘Conopeum’ s. l. (Fig. 1G)</td>
<td>Upper Aptian - Lower Albion</td>
<td>Glen Rose Fm. Texas, USA</td>
<td>10</td>
<td>Upper Aptian-Recent</td>
</tr>
<tr>
<td>‘?Conopeum’ s. l.</td>
<td>Upper Albian</td>
<td>Upper Greensand, Cherty Beds. Devon, England</td>
<td>22</td>
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cryptocyst is absent. Colonies are uniserial to pluri-
serial encrusters (Fig. 1A) and lack regular bud fu-
sions. Closure plates are often present and may bear
impressions of the uncalcified operculum. Kenozooi-
dal polymorphs occasionally develop where space is
restricted.

Wawalia (Wawaliidae) appeared approximately
20 million years after Pyriporopsis, in the Valangin-
ian of Poland [4]. Younger examples of Wawalia oc-
cur 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 gym-
nocyst 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 pres-
ent on the basal wall near the distolateral corners of
the zooids.

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

Probably related to Charixa is Spinicharixa (Fig.
Fig. 1  Morphology of early cheilostomes. (A) *Pyriporopsis 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 circumpesial 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 circumopesial 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 malacostregan 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 malacostregan 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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