



## Feeding currents: a limiting factor for disparity of Palaeozoic fenestrate bryozoans



Juan L. Suárez Andrés <sup>a,\*</sup>, Patrick N. Wyse Jackson <sup>b</sup>

<sup>a</sup> SONINGEO, S.L., PCTCAN, C/ Isabel Torres, 9, 39011 Santander, Spain

<sup>b</sup> Department of Geology, Trinity College, Dublin 2, Ireland

### ARTICLE INFO

#### Article history:

Received 11 December 2014

Received in revised form 22 April 2015

Accepted 19 May 2015

Available online 28 May 2015

#### Keywords:

Palaeobiology

Fenestrata

Bryozoa

Growth habits

Functional morphology

Evolution

### ABSTRACT

The Palaeozoic bryozoan Order Fenestrata is represented almost exclusively by erect unilaminar forms, most of which consist of a fan-shaped, conical or spiral reticulate meshwork. Fewer taxa developed pinnate or branching growth habits, and encrusting or bifoliate colonies occurred only exceptionally. Fenestrate disparity apparently peaked and then declined within the Devonian with the appearance of singular encrusting, bifoliate and large branching-conical morphologies in the Emsian and their decline in diversity in the Eifelian, together with the proliferation and morphological diversification of superstructures lying above the meshwork. In contrast, conventional reticulate and pinnate growth habits show a wider stratigraphical range and geographical distribution. Colony shapes are interpreted in terms of zooid-generated feeding currents; the most common morphologies are inferred to have developed more effective unidirectional feeding currents. The ephemeral Devonian encrusting, bifoliate and branching-conical fenestrates, all of them with superstructures, have features that hindered or prevented unidirectional water flow. Except for the subcolonies of *Ernstipora*, there is no evidence of chimneys or maculae in fenestrates such as those commonly present in other bryozoan groups with these habits, so it can be concluded that these fenestrate forms did not develop bidirectional currents that would have enhanced the efficiency of feeding activity. Unidirectional feeding currents were universal in Palaeozoic fenestrates; optimization of colony shape for colony-wide currents was a major factor limiting the morphological disparity within this group of bryozoans.

© 2015 Elsevier B.V. All rights reserved.

### 1. Introduction

The Order Fenestrata Elias and Condra, 1957 comprises about 140 genera of bryozoans that ranged from the Ordovician to the end of the Permian, characterised by erect, unilaminar colonies except for only two Devonian genera, *Schischcatella Waschurowa*, 1964, with a wide encrusting base and a low-standing bifoliate habit, and *Ernstipora* Suárez Andrés and Wyse Jackson, 2014, which developed clusters of small encrusting subcolonies. This restricted diversity in zoarial morphology is similar to that of esthonioporine trepostomes or timanodictyine, rhabdomesine and ptilodictyine cryptostomes, and contrasts greatly with the wide variety of growth habits exhibited by cystoporates and amplexoporine or halloporine trepostomes.

Most fenestrates developed either reticulate or pinnate meshworks, both morphologies appearing early in the geological history of the order, and a minority of genera are characterised by dendroid colonies composed of bifurcating branches. A few exceptional genera such as those mentioned above represent adaptations of the fenestrate mode of growth to substantially different habits, such as erect bifoliate or encrusting. Some common, conical reticulate taxa have been reported

to grow in a particularly complex way, so as to form rather large colonies composed of long, narrow branching cones (Suárez Andrés and McKinney, 2010).

Recent studies (Suárez Andrés and McKinney, 2010; Suárez Andrés and Wyse Jackson, 2014; Suárez Andrés et al., 2014; Suárez Andrés and Ernst, 2015) have documented a number of unusual fenestrate growth morphologies that seem to have originated and gone extinct during the Devonian. These morphologies represent additional evidence of novel diversification in zoarial form in the Order Fenestrata during this period, as distinct to the radiation of new taxa documented by Ernst (2013). The aim of this paper is to discuss and interpret the significance of the various growth forms within the history of bryozoans of the Order Fenestrata, particularly with regard to the generation of colony-wide feeding currents. Comparison with the feeding-habits and current flow of extant bryozoans shows some analogues, but conversely some patterns of fluid-flow apparently are not considered to have been present in extinct fenestrate forms.

### 2. Material and methods

This study is based on the Lower–Middle Devonian fenestrate bryozoans of NW Spain, as well as on analysis of the published literature on Palaeozoic fenestrates worldwide and an assessment of the collections

\* Corresponding author.

E-mail address: [juanl\\_suarez@yahoo.es](mailto:juanl_suarez@yahoo.es) (J.L. Suárez Andrés).

housed at the Natural History Museum, London (NHMUK). Specimens collected by the senior author from the Lower–Middle Devonian of Spain have been deposited in the Department of Geology, University of Oviedo, Oviedo, Spain (accession numbers with prefix DGO).

Morphological data were collected from relevant literature describing Ordovician to Permian fenestrate species worldwide. 363 fenestrate species representing all growth habits within this order have been considered in this survey. Mean values of branch width were recorded for all selected species; mean branch spacing has also been recorded from reticulate and pinnate species. Branch width and spacing in 330 species have been plotted in a bivariate morphospace in order to determine if there is any correlation between these characters, which would provide indirect evidence of genetically induced constraints for colony shape disparity in the Order Fenestrata. Accession numbers are indicated in figure captions; abbreviations for each institutional repositories and corresponding figures are: AMNH: American Museum of Natural History, New York, USA (Fig. 3G); DGO: Department of Geology, University of Oviedo, Spain (Figs. 3F, 4D, I); GIT: Geological Institute, Tallin, Estonia (Fig. 3D); JMM: James Mitchell Museum, University College, Galway, Ireland (Fig. 3I); NHMUK: Natural History Museum, London, UK (Figs. 3A, B, 4C, H); NMING: National Museum of Ireland, Dublin, Ireland (Fig. 4F); NGS: Nebraska Geological Survey, Lincoln, NE, USA (Figs. 4A, B); SMF: Senckenberg Museum, Frankfurt, Germany (Fig. 4E); TCD: Geological Museum, Trinity College, Dublin, Ireland (Fig. 3C); and USNM: United States National Museum, Washington DC, USA (Figs. 3H, 4J).

### 3. Water current patterns in extant bryozoans

The interrelationships between the generation of water currents, the removal of waste products and the methods of feeding in fossil and Recent bryozoans are complex. Examination of mechanisms of feeding and water-flow regimes in living bryozoans may facilitate interpretation of skeletal morphology in members of the extinct Order Fenestrata.

Bryozoans feed on materials extracted from inhalant water currents generated by the beating of cilia on the tentacles of the cone-, bell-shaped or asymmetrical lophophores (Cowen and Ryder, 1972; Cook, 1977; Taylor, 1979; Cook and Chimonides, 1980; Nielsen and Riisgård, 1998). This mode of feeding has been regarded by some authors as being a major factor in determining the architectural form of the zoarium (McKinney and Jackson, 1989).

Zoarial form can be plastic and different energy regimes and environmental factors can be reflected in differences in zoarial form within the same taxon (Wyse Jackson et al., 1991; Hageman and Sawyer, 2006). Where ambient water flow is elevated some modern taxa react by producing a higher density of spines than seen in colonies that have grown under average or normal conditions (Grünbaum, 1997).

#### 3.1. Polypide and lophophore morphology, pumping, and feeding ability

The position and integration of polypides within the colony can affect water hydrodynamics. Larsen et al. (1998) through flume studies have shown that inhalant currents are distorted with increased numbers of lines of zooids, and consequently their feeding efficiency is impaired. Grünbaum (1995) has demonstrated that in large encrusting colonies interference in the fluid or viscous flow is due to high shear beneath lophophores—this produces high pressures that act most strongly on the lophophores in the interior portions of these colonies and these individuals are less efficient in terms of pumping water than are laterally-placed individuals.

The problems caused by large size and zooidal packing in both encrusting and large branch diameter ramose colonies can be reduced through the development of maculae or 'chimneys' from which currents exit the colony surface at regularly spaced intervals across the colony (Banta et al., 1974; Taylor, 1979; Lidgard, 1981; Larsen and Riisgård, 2001; Key et al., 2011). These maculae may be monticulate (i.e. elevated

above the general zoarial surface) which may serve to enhance excurrent velocity (Wyse Jackson et al., 2014). In *Membranipora membranacea* (L.) chimneys developed when the feeding efficiency dropped to 30% of expected values (Larsen et al., 1998).

Efficiency may also be enhanced through the directed placement of lophophores. In some cystoporate genera the everted lophophores were inferred to bend in a particular direction as determined by the development of hoods over zoecial apertures or by lunaria. Anstey (1981) interpreted that water flow in large colonies of the cystoporate *Fistulipora* M'Coy, 1849 was centripetally directed towards monticulae. Similar centripetal flow is hypothesized in the cystoporate *Constellaria* Dana, 1846 where star-shaped maculae direct exhalant water towards the centres, but is less obvious in some very large colonies of the trepostome *Tabulipora* Young, 1883 where large stellate maculae are present (Key et al., 2011).

Within bryozoans, polypide and lophophore morphology is rather varied from symmetrical cone- or bell-shaped to strongly asymmetrical (Winston, 1979), whereas the number of tentacles can vary from eight to thirty-one and size also varies (Winston, 1978). Environmental factors such as temperature and salinity impact on the number of tentacles: in *Membranipora membranacea* (L.) the number increased (from 14 to 18) with temperature rise, but showed the opposite effect with higher levels of salinity (Amui-Vedel et al., 2011). In some fenestrates tentacle number is as low as eight (McKinney and Jackson, 1989), but this is determined by the development of zoecial tentacles and does not present a measure of palaeotemperature or palaeosalinity.

Cilia generate inhalant currents that vary in velocity from 1 to 3 mm/s but also increase from water above the tentacles towards the mouth (Nielsen and Riisgård, 1998; von Dassow, 2005a, 2005b; von Dassow, 2006). The height of eversion of the tentacle crown (McKinney, 1988; Nielsen and Riisgård, 1998), as well as pumping volume and other factors such as tentacle flicking, affect the ability of individual polypides to capture particles (Riisgård and Manriquez, 1997; Riisgård et al., 2010), and thus their efficiency of feeding. Zooids of *Bugula* Oken, 1815 increase tentacle flicking as the diameter of food particles and ambient water volume increase (Okamura, 1990). Some living bryozoans coordinate their tentacles in a wrapping movement to entrap particles that cannot be moved by the activity of a single tentacle (Winston, 1978).

### 4. Inference of feeding currents in fenestrate bryozoans

The patterns of feeding currents in Palaeozoic fenestrates can only be inferred from direct observation of morphologically similar living bryozoans, of which some exhibit remarkable similarities in terms of gross zoarial form and meshwork dimensions (see Taylor and Gordon, 1997; McGhee and McKinney, 2000; Starcher and McGhee, 2000, 2002, 2013; McKinney et al., in preparation). These patterns are inevitably founded on assumptions that involve considering that the feeding behaviours of extinct and morphologically equivalent living bryozoans are alike.

Borg (1923) stated that the beating cilia of an autozooid create currents that drive nutrients down to the mouth and evacuate water between the tentacles. Banta et al. (1974) demonstrated the existence of coordinated colony-wide water currents and inferred the role of maculae as excurrent water outlets from the observation of feeding colonies of *Membranipora*. Cook (1977) described and analysed feeding currents in living colonies of erect and encrusting bryozoans. She observed water flow passing from the obverse to the barren reverse surface through the fenestrules of the funnel-shaped reticulate cheilostome *Sertella* Jullien in Jullien and Calvet, 1903, thus producing two opposite patterns depending on the position of zooidal apertures on the outer or inner surface of the funnel. As stated by Cook (1977) and Winston (1978, 1979), observed feeding behaviour in different bryozoans ranges from isolated individual currents to highly organized colony-wide zooid-

Download English Version:

<https://daneshyari.com/en/article/4465930>

Download Persian Version:

<https://daneshyari.com/article/4465930>

[Daneshyari.com](https://daneshyari.com)