

SECONDARY NANOZOOECIA IN SOME UPPER PALAEOZOIC FENESTRATE BRYOZOA

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ABSTRACT. Autozooeical apertures sealed by perforate terminal diaphragms have been found in eleven species of British and Irish Carboniferous and Permian fenestrate Bryozoa. In their skeletal morphology, intra-colonial abundance, and distribution they resemble the perforate terminal diaphragms of polymorphs that are termed secondary nanoozoecia in the Recent tubuloporinid cyclostome *Plagioecia* and the lichenopoid cyclostome *Disporella*. The former presence in fenestrates of single-tentacled non-feeding polymorphs comparable to those of *Plagioecia* and *Disporella* is inferred. As in *Plagioecia* and *Disporella*, secondary nanoozoecia of fenestrate bryozoans may represent a late stage of zooidal ontogeny. The function of secondary nanoozoecia in *Plagioecia* and *Disporella* is unknown, but those of fenestrates possibly had a defensive/cleaning function comparable to that suggested for primary nanoozooids in the Recent tubuloporinid cyclostome *Diplosolen obelium*.

FENESTRATE Bryozoa (Class Stenolaemata Borg, 1926; Order Fenestrata Elias and Condra, 1957) were once considered to be monomorphic. However, recent morphological studies have revealed the existence of a variety of skeletal structures which have been interpreted as reflecting the occurrence of several types of polymorphic zooids. Certain types of polymorphic zoecia are reasonably well documented in fenestrates, e.g. brood chambers (Tavener-Smith 1966; Engel 1975; Stratton 1975, 1981; Southwood 1985) and accessory pores (Nikiforova 1938; Shulga-Nesterenko 1941, 1952; Shishova 1970), but inferred secondary nanoozoecia have hitherto been described in only one taxon, *Lyroporella quincuncialis* (Hall), from the Carboniferous of the USA (McKinney 1977).

During a recent revision of British and Irish Carboniferous Bryozoa, skeletal structures that resemble the perforate terminal diaphragms of secondary nanoozoecia in certain Recent Bryozoa (the tubuloporinid cyclostome *Plagioecia*, the lichenopoid cyclostome *Disporella*, and *L. quincuncialis*) have been found to occur in eight species of fenestrate Bryozoa. Identical structures have also been recently found in three species of Upper Permian fenestrate Bryozoa from the Middle Magnesian Limestone (reef facies) of County Durham, England (D. A. Southwood, pers. comm.). The abundance of the material available and the occurrence of these structures in a number of taxa has allowed a detailed analysis of their morphology and interpretation of their functional significance. Cited material is located in the collections of the British Museum (Natural History).

RECENT SECONDARY NANOZOOECIA

Primary nanoozoecia were first described in detail by Borg (1926) in the living cyclostome *Diplosolen* Borg and are morphologically and functionally reasonably well known. Secondary nanoozoecia, however, have only recently been documented by Silén and Harmelin (1974) in the living tubuloporinid cyclostome *Plagioecia* and by Moyano (1982) in the living lichenopoid cyclostome *Disporella*. Although the soft part morphology of primary and secondary nanoozooids is comparable, primary nanoozooids are budded from the outset as polymorphic zooids whereas secondary nanoozooids are intra-zooidal, that is ontogenetic polymorphs developed within the chamber of a degenerated autozooid.

Colonies of *Plagioecia* and *Disporella* are adnate and secondary nanoozoecia are developed in older parts of the colonies. They represent a late stage of ontogenetic development. According to Silén and Harmelin (1974, p. 93) the development of a secondary nanoozooid takes the following path.

Following the degeneration of the autozooeical polypide only the atrial sphincter and the proximal part of the zooid remain unchanged. A perforate terminal diaphragm, with a single small circular secondary aperture, is calcified centripetally over the original autozooeical aperture. The secondary aperture is slightly elevated above the level of the terminal diaphragm by a peristome-like rim (Silén and Harmelin 1974, figs. 16 and 17.). A new polypide with a different morphology is then regenerated. All parts are smaller, the alimentary canal is rudimentary, and there is a single non-ciliated tentacle. When protruded the tentacle is very short and extends vertically from the secondary aperture (Silén and Harmelin 1974, figs. 16–20).

Although these authors made observations on the behaviour and morphology of secondary nanozooids in *Plagioecia*, they did not reach any conclusions as to their functional significance. They did however exclude a feeding function, because of the lack of cilia on the tentacle, and a cleaning function analogous to that of primary nanozooids in *Diplosolen obelium* (Johnston) because the tentacle is too short and inappropriately orientated. They also found no evidence of any male cells, glands, or other special organs.

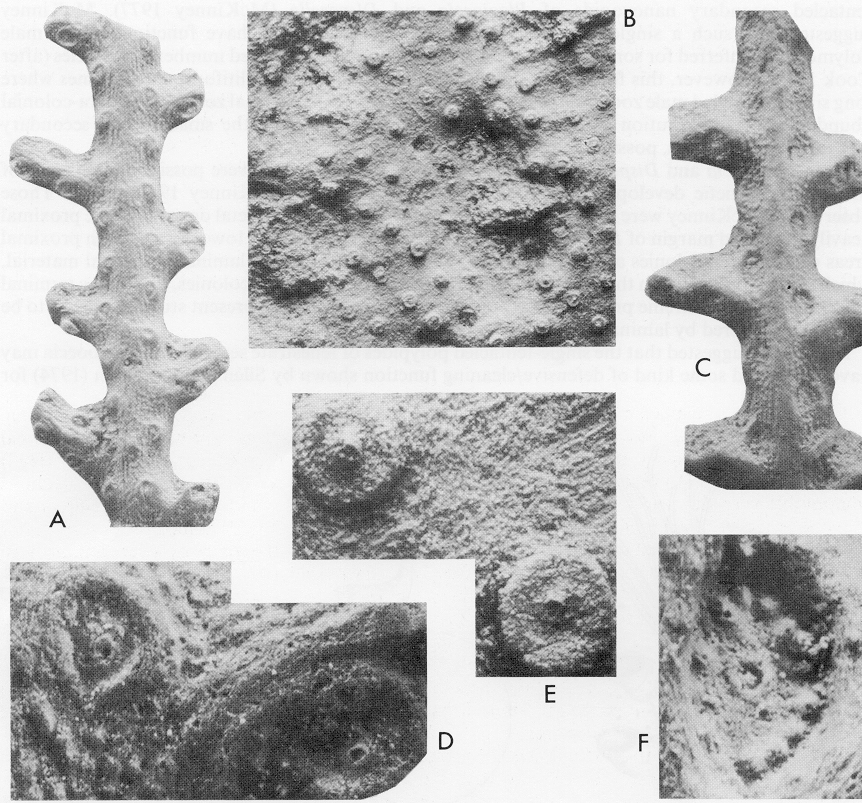
FENESTRATE SECONDARY NANOZOOECIA

In fossil Bryozoa, calcified perforate terminal diaphragms with elevated secondary apertures sealing autozooeical apertures have only been recognized and interpreted as representing the terminal diaphragms of secondary nanozoecia in the Carboniferous fenestrate *L. quincuncialis* (Hall) (McKinney 1977). However, several authors have illustrated and described similar structures comparable with the perforate terminal diaphragms of secondary nanozoecia in *Plagioecia* and *Disporella* in other Carboniferous fenestrate taxa. Young (1879, p. 212) described the occurrence of cell pores covered by a thin calcareous disc or diaphragm pierced in the centre by a very minute pore in *Fenestella plebeia* M'Coy, *F. ejuncida* M'Coy, *Polypora tuberculata* Prout, and *Penniretopora elegans* (Young and Young). He believed that this structure was a condition of the perfectly preserved cell pore in these taxa. Zittel (1895), in diagnosing the Family Fenestellidae King, described the structure of zooeical apertures when perfectly preserved as being covered by centrally perforate closures. Tavener-Smith (1969, pl. 54, figs. 4 and 5; text-fig. 9) illustrated the peristomial funnels of secondary nanozoecia in longitudinal section, in the Carboniferous fenestrates *Lyropora quincuncialis* Hall and *L. subquadrans* (Hall). Most recently Tavener-Smith (1973, p. 459) described autozooeical apertures in some specimens of *F. polyporata* (Phillips) as being sealed by a translucent plate-like deposit, sometimes incomplete and pierced by a small central orifice.

During a recent revision of British and Irish Carboniferous fenestrate Bryozoa (Bancroft 1984) identical structures have been found to occur in another four taxa in addition to those mentioned by Young and Tavener-Smith. These are *Penniretopora flexicarinata* (Young and Young), *P. pulcherrima* (M'Coy), *Ptylopora pluma* M'Coy, and *Polypora dendroides* M'Coy. They have also been found to occur in three Upper Permian fenestrate taxa from the Middle Magnesian Limestone (reef facies) of County Durham, England: *Penniretopora waltheri* (Korn), *Synocladia virgulacea* (Phillips), and *F. retiformis* (Sclotheim) (D. A. Southwood, pers. comm.).

The morphology of perforate terminal diaphragms in all these taxa is comparable and there is only slight morphological variation within a species (text-fig. 1). All consist of a thin lamina sealing the autozooeical aperture, at a level immediately below the crest of the peristomial rim, or the branch surface in taxa without peristomes, and are perforated by a very small approximately centrally positioned secondary aperture. Secondary apertures range between 0.010 mm and 0.021 mm in diameter, and while in *P. pulcherrima* the perimeter of the secondary apertures form low, well-rounded, thick peristomes (text-fig. 1C, F), in all other taxa secondary apertures are elevated above the level of diaphragms by distally narrowing funnel-shaped peristomes (text-fig. 1D). The surface of diaphragms is usually flat and smooth, except in *P. pulcherrima* in which the perimeter of the diaphragm is ornamented by a single row of closely spaced small circular pustules (text-fig. 1F).

Tavener-Smith (1973, p. 459) noted the occurrence of these structures in the proximal parts of colonies of *F. polyporata*. However, while terminal diaphragms appear to be particularly abundant in



TEXT-FIG. 1. SEMs of Upper Palaeozoic Bryozoa showing autozoecial apertures sealed by a perforate terminal diaphragm. A, D, *Penniretepora elegans* (Young and Young), BM(NH) PD.6282. Lower Limestone Group, Hosié Limestones (Viséan, Brigantian), Hairmyres, East Kilbride, Scotland. A, $\times 20$; D, $\times 160$. B, E, *Synocladia virgulacea* (Phillips) BM(NH) PD.6285. Middle Magnesian Limestone, reef facies (Upper Permian), Ryhope, Sunderland, Tyne and Wear, England. B, $\times 28$; E, $\times 178$. C, F, *P. pulcherrima* (M'Coy), BM(NH) PD.6284. Lower Limestone Group, Hosié Limestones (Viséan, Brigantian), Hairmyres, East Kilbride, Scotland. C, $\times 26$, F, $\times 190$.

the extreme proximal parts of fenestrate colonies, in several large colony fragments of *S. virgulacea* they extend further distally: colonies may possess perforate terminal diaphragms sealing autozoecial apertures up to more than 10 cm from the colony origin.

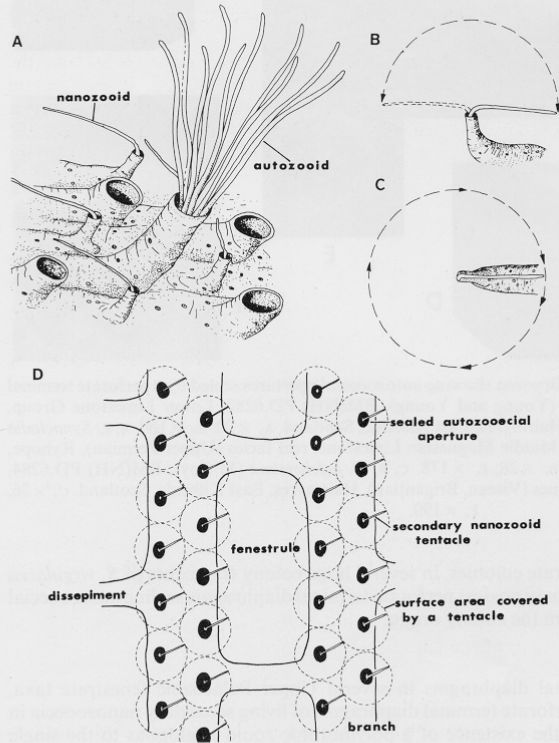
Functional interpretation

The occurrence of perforate terminal diaphragms in several Upper Palaeozoic fenestrate taxa, comparable in morphology to the perforate terminal diaphragms of living secondary nanoozoecia in *Plagioecia* and *Disporella*, suggests the existence of a polymorphic zooid analogous to the single

tentacled secondary nanozooids of *Plagioecia* and *Disporella* (McKinney 1977). McKinney suggested that such a single-tentacled polypide in fenestrates may have functioned as a male polymorph as inferred for some Recent cheilostome zooids with a reduced number of tentacles (after Cook 1968). However, this function is possibly limited to mobile lunulitiform cheilostomes where long single-tentacled male zooids almost appear to copulate with maternal zooids. The intra-colonial abundance and distribution of perforate terminal diaphragms, and the small size of secondary apertures in fenestrates, possibly does not favour such a role.

As in *Plagioecia* and *Disporella*, fenestrate secondary nanozoecia were possibly a late stage of zooidal ontogenetic development (Tavener-Smith 1973, p. 459; McKinney 1977, p. 96). Those observed by McKinney were completely covered over by laminated skeletal deposits in the proximal heavily thickened margin of *Lyroporella* soon after their development. However, although proximal areas of fenestrate colonies are susceptible to additional deposition of laminated skeletal material, which served to strengthen the basal areas of large reticulate or pinnate colonies, only a few terminal diaphragms in the extreme proximal parts of colonies examined in the present study were seen to be completely covered by laminated skeletal deposits.

McKinney suggested that the single-tentacled polypides of fenestrate secondary nanozoecia may have performed some kind of defensive/cleaning function shown by Silén and Harmelin (1974) for



TEXT-FIG. 2. A-C, *Diplosolen obelium* (Johnston), redrawn from Silén and Harmelin (1974). A, autozoid and primary nanozooids with their tentacles extended, $\times 120$. B, C, movement of a nanozooid tentacle, $\times 120$. D, areas covered by the action of fenestrate secondary nanozooid tentacles projected on a colony surface in the fenestrate genus *Fenestella* Lonsdale, $\times 40$.

primary nanozooids of *Diplosolen obelium*. In *D. obelium* colonies the single tentacle protruded from the aperture of the nanozooecium is long. It extends in a horizontal plane and performs a periodic proximal to distal motion or sweeping circular motion (text-fig. 2 A-C). Silén and Harmelin showed that these movements facilitated the clearance of mud particles from the colony surface.

It is quite possible that fenestrate secondary nanozooids had a function comparable to that of primary nanozooids in *D. obelium*, and that they facilitated the removal of sediment particles and prevented the settlement and attachment of larvae of other organisms on the obverse surface of branches. Primary nanozooecia are equidistant in colonies of *D. obelium*, and Silén and Harmelin (1974, fig. 15) showed that the movement of nanozooid tentacles was such that almost the entire surface area of the colony would be situated within reach of them. In fenestrates, autozooecial apertures only open on one side of the meshwork, the obverse or frontal surface, are equidistant and alternately arranged in longitudinal rows on branches. As in *D. obelium* it is possible to envisage that almost the entire obverse surface of branches in the proximal portion of a fenestrate colony would be situated within reach of secondary nanozooid tentacles (text-fig. 2D). The inferred defensive/cleaning function of fenestrate secondary nanozooids may not have been necessary in other parts of the colony where active autozooids created powerful feeding currents that scoured obverse branch surfaces. It is also possible that fenestrate autozooids may have utilized particle rejection mechanisms similar to those of many living gymnolaemates to facilitate the removal of unwanted particles. The action of secondary nanozooids and autozooids possibly explains the reason why the reverse surface of branches are more commonly found encrusted by parasitic organisms, such as serpulids and adnate Bryozoa, than the obverse surface.

The distribution of perforate terminal diaphragms in fenestrate colonies suggests that the morphologic change from autozooid to nanozooid was probably age related as in *Plagioecia* and *Disporella*. In mature colonies of *Plagioecia* and *Disporella* the largest portion of the colony surface is comprised of secondary nanozooecia (Silén and Harmelin 1974; Moyano 1982). Unfortunately, the growth rate of fenestrate bryozoans is undetermined, and it is not possible to tell the relative age of colony fragments solely on the relative abundance of secondary nanozooecia.

CONCLUSIONS

1. Perforate terminal diaphragms sealing autozooecial chambers in fenestrates are comparable in morphology, distribution, and relative abundance to identical structures sealing autozooecial chambers and occupied by non-feeding polymorphs (secondary nanozooids) in the Recent tubuloporinid cyclostome *Plagioecia* and the lichenoporid cyclostome *Disporella*.

2. In fenestrates, autozooecial chambers sealed by such structures may also have been occupied by single-tentacled non-feeding polypides comparable to secondary nanozooids in *Plagioecia* and *Disporella*.

3. As in *Plagioecia* and *Disporella*, fenestrate secondary nanozooecia may represent a late stage of zooidal ontogenetic development.

4. Fenestrate secondary nanozooids possibly had a defensive/cleaning function comparable to primary nanozooids in the Recent tubuloporinid cyclostome *Diplosolen obelium*.

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REFERENCES

- BANCROFT, A. J. 1984. Studies in Carboniferous Bryozoa. Ph.D. thesis (unpubl.), University of Durham.
BORG, F. 1926. Studies on Recent cyclostomatous Bryozoa. *Zool. Bidr. Upps.* **10**, 181-507.

- COOK, P. L. 1968. Observations on living Bryozoa. *Atti. Soc. It. Nat. e Museo Civ. St. Nat. Milano*, **108**, 155–160.
- ELIAS, M. K. and CONDRA, G. E. 1957. *Fenestella* from the Permian of West Texas. *Mem. Geol. Soc. Am.* **70**, 1–158.
- ENGEL, B. A. 1975. A new ?bryozoan from the Carboniferous of Eastern Australia. *Palaeontology*, **18**, 571–605.
- MCKINNEY, F. K. 1977. Functional interpretation of lyre-shaped Bryozoa. *Paleobiology*, **3**, 90–97.
- MOYANO, H. I. 1982. Genus *Disporella* Gray, 1848; Two new Chilean species (Bryozoa, Cyclostomata, Disporellidae). *Bol. Soc. Biol. de Concepción, Chile*, **53**, 71–77.
- NIKIFOROVA, A. I. 1938. Types of Carboniferous Bryozoa of the European part of the U.S.S.R. *In Acad. Sci. U.S.S.R.* 1–290. [In Russian.]
- SHISHOVA, N. A. 1970. Some new Silurian and Devonian bryozoans of Mongolia. *In New species of Paleozoic Bryozoa and corals. Izd-vo. Nauka.* 28–31. [In Russian.]
- SHULGA-NESTERENKO, M. I. 1941. Lower Permian Bryozoa of the Urals. *Akad. Nauk. S.S.S.R. Trudy Paleontol. Inst.* **5**, 1–226. [In Russian.]
- 1952. New Lower Permian bryozoans of Cisuralia. *Akad. Nauk. S.S.S.R. Trudy Paleontol. Inst.* **37**, 1–84. [In Russian.]
- SILÉN, L. and HARMELIN, J. G. 1974. Observations on living Diastoporidae (Bryozoa Cyclostomata) with special regard to polymorphism. *Acta. Zool.* **55**, 81–96.
- SOUTHWOOD, D. A. 1985. Ovicells in some Fenestrata from the Permian of N.E. England. *In NIELSEN, C. and LARWOOD, G. P. (eds.). Bryozoa Ordovician to Recent.* Olsen and Olsen, Fredensborg.
- STRATTON, J. F. 1975. Ovicells in *Fenestella* from the Speed Member, North Vernon Limestone (Eifelian, Middle Devonian) in Southern Indiana, U.S.A. *Doc. Lab. Geol. Sci. Lyon.*, H.S. **3** (Fasc. 1), 169–177.
- 1981. Apparent ovicells and associated structures in the fenestrate bryozoan *Polypora shumardii* Prout. *J. Paleont.* **55**, 880–884.
- TAVENER-SMITH, R. 1966. Ovicells in fenestrate cryptostomes of Viséan age. *Ibid.* **40**, 190–198.
- 1969. Skeletal structure and growth in the Fenestellidae (Bryozoa). *Palaeontology*, **12**, 281–309.
- 1973. Fenestrate Bryozoa from the Viséan of County Fermanagh, Ireland. *Bull. Br. Mus. Nat. Hist. (Geol.)*, **23**, 389–493.
- YOUNG, J. 1879. Notes on the perfect condition of the cell pores and other points of structure in certain species of Carboniferous Polyzoa from Western Scotland. *Trans. Geol. Soc. Glasg.* **6**, 211–217.
- ZITTEL, K. A. 1895. *Textbook on Paleontology* (1927 translation, revised and enlarged edition), 531 pp. Macmillan and Co., London.

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