

OVICELLS IN THE PALAEOZOIC BRYOZOAN ORDER FENESTRATA

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ABSTRACT. The occurrence and morphology of fenestrate ovicells is reviewed and ovicells are described for the first time in *Penniretepora*. Four ovicell types are recognized and the considerable variation in morphology, size, position, and intra-colonial abundance of ovicells at generic level is related to variation in the morphology of autozooeccial chambers, proximity of autozooeccia, and the number of autozooeccial rows on branches and dissepiments. Type A ovicells from large globose distentions to gonozooeccia, are intra-colonially few in number and occur in *Fenestella*, *Hemirypa*, and *Penniretepora*; Type B ovicells occur in *Septatopora*, and form shallow hemispherical depressions at the proximal rims of autozooeccial apertures and are connected to the lower vestibular regions of adjacent gonozooeccia by an auxillary tube; Type C ovicells occur in *Synocladia*, *Acanthocladia*, and *Thamniscus*, and form hemispherical depressions at the proximal rims of autozooeccial apertures and are intra-colonially very abundant; Type D ovicells are extrazooecial and occur in *Polypora*, ovicells are located on dissepiments and are linked to gonozooeccia by a system of canal-like structures traversing branches and dissepiments, several gonozooeccia shared an ovicell. Ovicell morphology may be of phylogenetic significance and of value at higher taxonomic rank in fenestrates.

OVICELLS are chambers for the brooding of embryonic products from gonozooeccia prior to their release into the sea. It is only recently that ovicells have been recognized and described in Palaeozoic fenestrate Bryozoa (Class Stenolaemata Borg 1926; Order Fenestrata Elias and Condra 1957). Tavener-Smith (1966), Engel (1975), Stratton (1975, 1981), and Southwood (1985) have shown that a considerable variety exists in the morphology of ovicells and that they constitute the most diverse form of polymorphism in the Fenestrata.

Fenestrate ovicells are rare and Stratton (1975, 1981) suggested that in the majority of taxa embryonic products were either immediately discharged into the sea, or else brooded internally in the coelom or in external organic ovisacs which are not preserved fossil. He also partly attributed the paucity of fenestrate ovicells to low preservation potential. However, their paucity may be also explained by the fact that many taxa have been established on the basis of single, small, often poorly preserved colony fragments. Considering the rarity of zoaria containing ovicells in taxa known to possess ovicells, it seems probable that ovicells will be discovered in a number of these poorly described forms when additional comparative material becomes available.

The repositories of all the cited and figured material are: British Museum (Natural History), BMNH; Durham University Geology Department, Southwood Collection, DUGD, SC; Field Museum of Natural History, Chicago, Illinois, USA, FMNH.

FENESTRATE OVICELLS

The fenestrate ovicell is distal to the autozooeccial chamber, similar to ovicells described in cheilostome gymnolaemates, and the dilated parts of gonozooeccia in cyclostome stenolaemates (Borg 1926; Ryland 1970). In fenestrates ovicells belong to a single zooid (the gonozooid), with one exception where ovicells may be regarded as extrazooecial and apparently served more than one zooid.

Four different types of ovicellular structures are recognized in fenestrates and these correlate with variations in the morphology of autozooeccial chambers and the proximity and number of rows of autozooeccia on branches. More than one genus may possess the same ovicell morphology. For ease of description and comparison the different types are here designated A, B, C, and D.

Type A

Tavener-Smith (1966) and Stratton (1975) described inflated calcified structures incorporating the distal portions of autozooeical chambers which they interpreted as ovicells in the fenestellids *Fenestella* Lonsdale and *Hemitrypa* Phillips. Tavener-Smith first described this type of ovicell in three species: *H. hibernica* M'Coy, *F. cf. fanata* Whidborne, and *F. cf. delicatula* Ulrich from Lower Carboniferous (Asbian) limestones of Carrick Lough, County Fermanagh, Northern Ireland. Stratton described similar structures in *Fenestella* sp. from the Middle Devonian (Eifelian), North Vernon Limestone, Indiana, USA. Earlier workers have also described comparable structures in *Fenestella* (e.g. Hall and Simpson 1887, p. 105, pl. 45, fig. 23, pl. 47, fig. 24; Nikiforova 1938, pp. 245, 248, 251; Elias and Condra 1957, p. 131).

In all these forms the gonozoecium is directly connected, by a short vestibular region, to the ovicell above which forms a large globose distention of the gonozooeical chamber (Pl. 19, fig. 1; text-fig. 1A, B). In *H. hibernica* ovicells range in diameter from 0.46 mm to 0.50 mm (Tavener-Smith 1966, p. 195 stated that ovicells in *H. hibernica* have an average diameter of 0.28 mm, this is presumably a typographical error), and in *F. cf. fanata* the average dimensions of ovicells are length 0.67 mm and width 0.58 mm (Tavener-Smith 1966, p. 191). The ovicells described in *Fenestella* sp. by Stratton (1975) are significantly smaller, with an average diameter of 0.29 mm.

Tavener-Smith (1966) also described the occurrence of partially preserved fragile calcified roofs to ovicells in *Fenestella* and *Hemitrypa* species, with an opening (oeciopore) in the crests through which the larvae were presumably liberated (Pl. 19, fig. 2; text-fig. 1B). In most of Tavener-Smith's material the ovicells are partly weathered with the fragile roof of the ovicell missing revealing the smooth and well-rounded interior (Pl. 19, fig. 1). The basal area of these ovicells is usually depressed into the obverse branch surface and their cyst-like character locally increases the height of the branch (Pl. 19, fig. 3; text-fig. 1A). Because of their large size ovicells commonly affect the development of adjacent autozooeia and they may even extend across the entire width of a branch causing its margins to bulge (Pl. 19, fig. 1).

The intra-colonial abundance of ovicells is very low compared to the number of normal autozooeia, and they commonly occur in isolation and are apparently randomly positioned (Pl. 19, figs. 4 and 5). As Tavener-Smith (1966) noted the morphology of ovicells in *Fenestella* and *Hemitrypa* species bears a strong resemblance to Recent cyclostome gonozooeia described by Borg (1926). This resemblance, together with the relatively large size of ovicells in fenestellids, suggested to Tavener-Smith that polyembryony which occurs in the gonozooids of Recent cyclostomes may also have occurred in fenestellids. (Polyembryony or embryonic fission is the asexual division of the primary embryo into secondary embryos or even tertiary embryos, all presumably with the same genetic make-up.)

During a recent revision of British and Irish Carboniferous fenestrate Bryozoa, study of several

EXPLANATION OF PLATE 19

(Specimens figured 1-5 were also figured by Tavener-Smith 1966, pl. 25.)

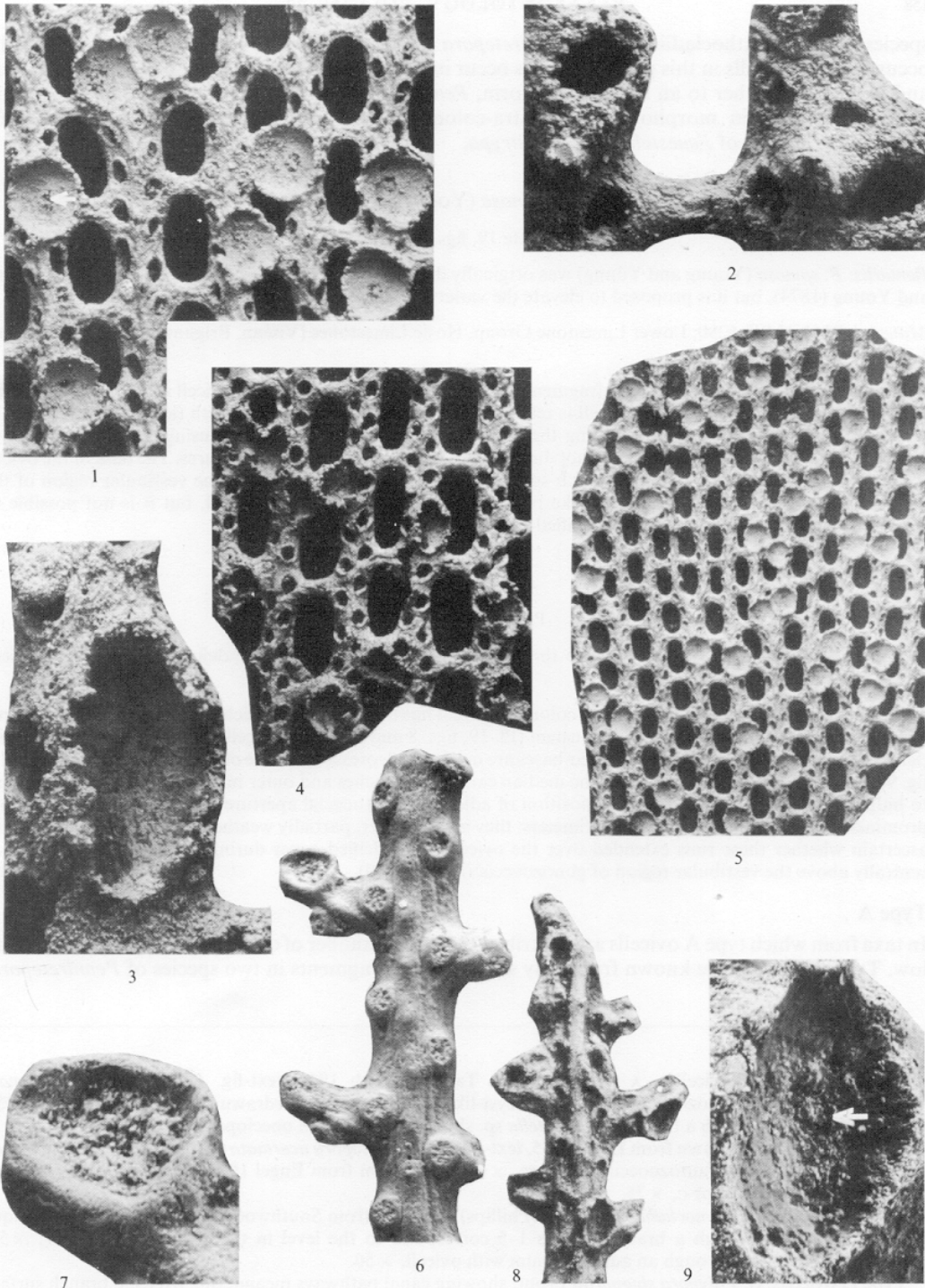
Type A ovicells: Figs. 1 and 5, *Hemitrypa hibernica* M'Coy, BMNH PD.4493, 1, showing ovicells forming distentions on top of gonozooeical vestibular regions (one vestibule is arrowed), $\times 29$. 5, distribution of ovicells on colony fragment, $\times 12$.

Figs. 2, 3, 4, *Fenestella cf. fanata* Whidborne. 2, BMNH PD.4487, oeciopores in the crest of two ovicells, $\times 52$, 3, BMNH PD.4486, increase in branch height due to ovicell, $\times 66$. 4, BMNH PD.4486, distribution of ovicells on colony fragment, $\times 15$.

Figs. 6 and 7, *Penniretepora spinosa* (Young and Young) BMNH PD.6280. 6, obverse surface detail and showing ovicell on top left lateral branch, $\times 30$. 7, detail of ovicell, $\times 140$.

Figs. 8 and 9, *Penniretepora* sp. BMNH PD.6281. 8, obverse surface detail and showing ovicells, $\times 22$. 9, detail of ovicell on mainstem, also showing top of vestibular region of gonozoecium (arrowed) at base of ovicell, $\times 150$.

SEMs.



BANCROFT, *bryozoan ovicells*

species of the acanthocladid genus *Penniretepora* d'Orbigny has, for the first time, revealed the occurrence of ovicells in this genus. Ovicells occur in two species, one assigned to *P. spinosa* (Young and Young), the other to an undescribed form, *Penniretepora* sp. The ovicells in *Penniretepora* are comparable both in morphology and intra-colonial abundance to type A ovicells previously described in species of *Fenestella* and *Hemitrypa*.

Penniretepora spinosa (Young and Young, 1874)

Plate 19, figs. 6 and 7

Remarks: *P. spinosa* (Young and Young) was originally described as a variety of *Glauconome stellipora* Young and Young (1874), but it is proposed to elevate the variety to species level.

Material: BMNH PD.6280; Lower Limestone Group, Hosie Limestones (Viséan, Brigantian), Hairmyres, East Kilbride, Scotland.

Ovicell Description: One small colony fragment has been found on which a single ovicell is situated on a lateral branch (Pl. 19, figs. 6 and 7). The ovicell is relatively large compared to branch width (length 0.21 mm, width 0.16 mm), with its inner margin abutting the median carina and outer margin causing the branch to bulge considerably. However, the ovicell does not disturb the disposition of adjacent apertures. The base of the ovicell is depressed relative to the obverse branch surface and is situated centrally over the vestibular region of the gonozooecium. It also has a thick rim-like perimeter which is partially weathered, but it is not possible to determine whether this extended as a calcified cover during life.

Penniretepora sp.

Plate 19, figs. 8 and 9

Material: BMNH PD.6281; shales above the Main Limestone (Namurian, Pendelian-Arnsbergian), Hurst, North Yorkshire.

Ovicell Description: Again only one small colony fragment has been found on which five ovicells occur randomly situated on lateral branches and the mainstem (Pl. 19, figs. 8 and 9). These ovicells form fairly large oval cysts (length 0.30 mm, width 0.20 mm) and their bases are markedly depressed into the obverse branch surface (Pl. 19, fig. 9). Their inner margins abut on to the median carina of branches and outer margins cause branch margins to bulge, but they do not affect the disposition of adjacent autozooeical apertures. The ovicells have low but prominent, slightly elevated rim-like perimeters; they are, however, partially weathered and it is not possible to ascertain whether these rims extended over the ovicell as a calcified cover during life. Ovicells are situated centrally above the vestibular region of gonozooecia (Pl. 19, fig. 9).

Type A

In taxa from which type A ovicells are described the actual number of colonies possessing them is very low. Type A ovicells are known from only single colony fragments in two species of *Penniretepora*,

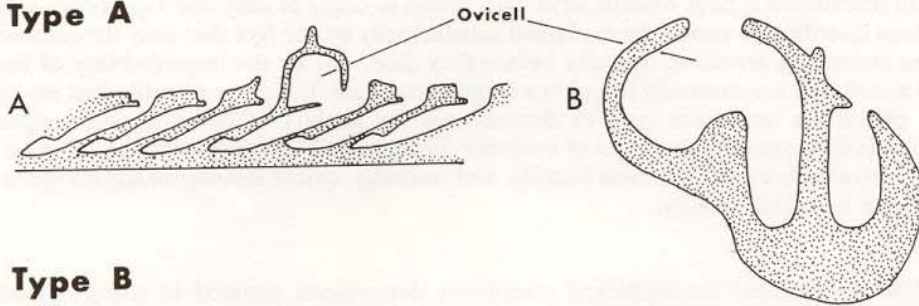
TEXT-FIG. 1. Type A ovicells: A (redrawn from Tavener-Smith 1966, text-fig. 1A), *Fenestella* cf. *fanata* Whidborne, showing gonozooecium with large cyst-like ovicell, $\times 26$. B (redrawn from Stratton 1975, fig. 3), transverse section through a branch in *Fenestella* sp. showing ovicell with ooeciopore, $\times 230$.

Type B ovicells: C (redrawn from Engel 1975, text-fig. 1B), *Septatopora acarinata* (Crockford), showing ovicell at proximal extremity of autozooeical aperture, $\times 60$. D (redrawn from Engel 1975, text-fig. 1A), *Septatopora flemingi* Engel, detail as for C, $\times 75$.

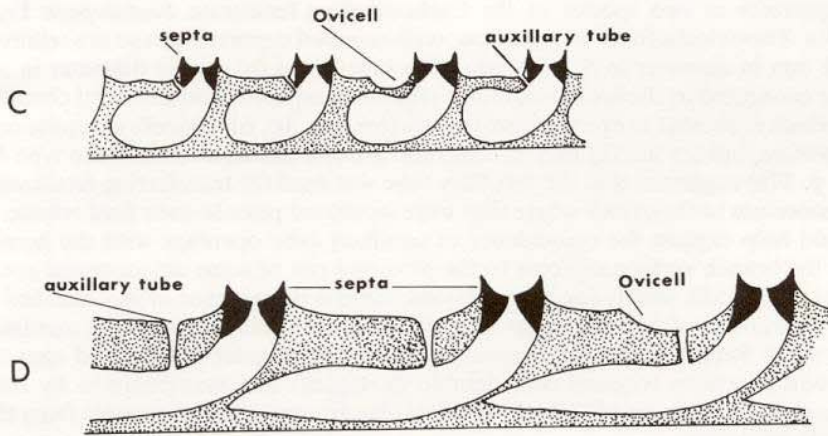
Type C ovicells E, F, *Synocladia virgulacea* (Phillips) (redrawn from Southwood 1985, fig. 5a, b). E, oblique tangential section through a branch, points 1-5 correspond to the level in the branch shown in F, $\times 50$. F, longitudinal section through an autozooeium with ovicell, $\times 50$.

Type D ovicells: G, *Polypora shumardii* Prout, showing canal pathways meandering over the branch surface and ovicell situated on dissepiment, $\times 60$.

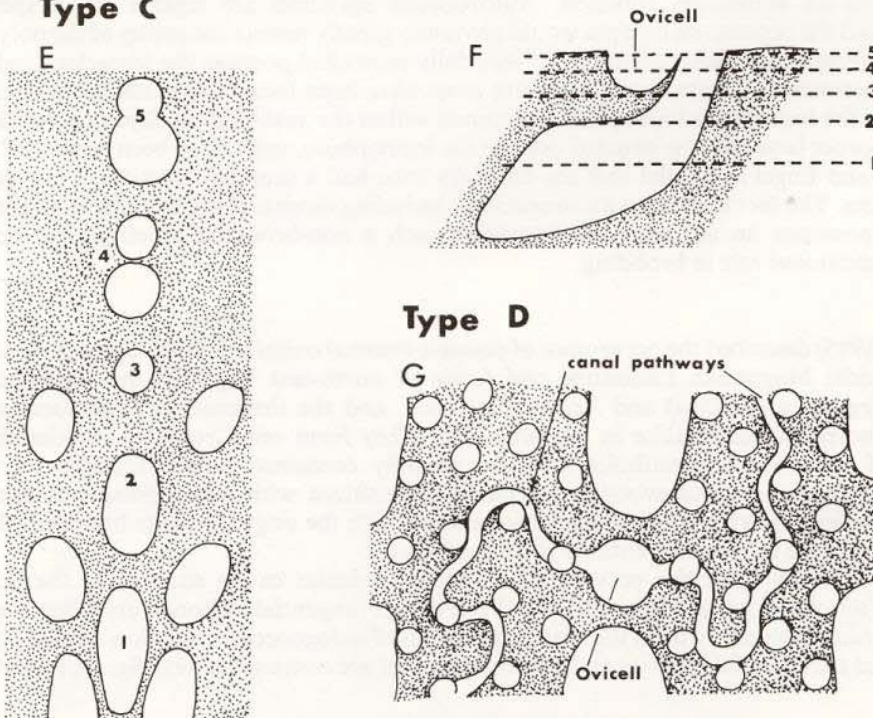
Type A



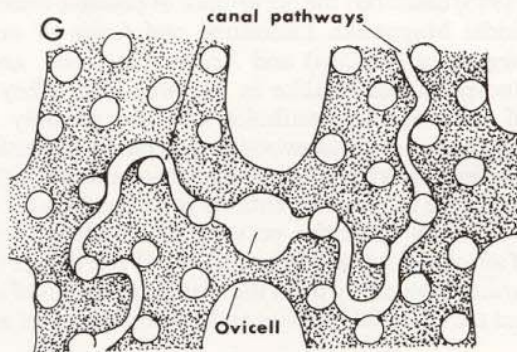
Type B



Type C



Type D



and in all fenestellids type A ovicells have been found to occur at only one locality per species. This anomalous distribution cannot be explained satisfactorily by the fact that only the colonies at these localities attained a brooding capacity before they died, nor by the improbability of finding rare ovicells as colonies are normally found in a fragmented state. It may be possible that environmental factors played an important part in determining the fertility of colonies within species. This suggestion is supported by two lines of evidence. First, ovicells described in three taxa by Tavener-Smith (1966) all came from the same locality, and secondly, ovicell bearing zoaria are quite common in these taxa from this locality.

Type B

Engel (1975) described hemispherical ovicellular depressions situated at the proximal rims of autozooeical apertures in two species of the Carboniferous fenestrate *Septatopora* Engel, from eastern Australia. The ovicells form very shallow, well-rounded depressions and are relatively small, being about 0.1 mm in diameter in *S. acarinata* (Crockford) and 0.2 mm in diameter in *S. flemingi* Engel. They are connected to the lower vestibular regions of adjacent gonozooeical chambers by an auxillary tube which is present in every autozooeicum (text-fig. 1C, D). Ovicells are quite common in zoaria of *S. acarinata*, but are scarcer in *S. flemingi* and are of a similar abundance to type A ovicells.

Engel (1975, p. 576) suggested that the auxillary tube was used for transferring fertilized embryos from the gonozooeicum to the ovicell where they were incubated prior to their final release. As Engel stated this would help explain the coincidence of auxillary tube openings with the hemispherical depressions on the branch surface adjacent to the proximal rim of some autozooeical apertures. In Engel's material the ovicells simply form depressions; there is no evidence of any calcified roof.

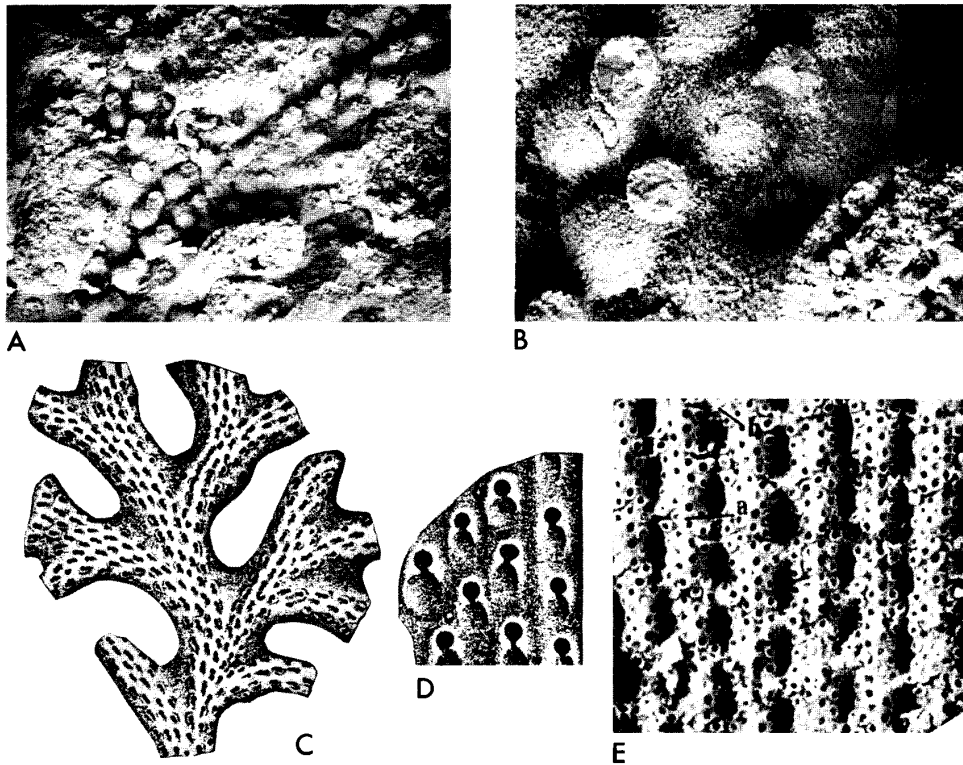
The method of transfer of fertilized eggs from the gonozooeicum through the auxillary tube is conjectural. In some Recent cheilostome gymnolaemates the transfer of fertilized eggs to distally positioned brooding cavities requires considerable movement and manipulation by the tentacle crown of the autozoooid. As Engel (1975) stated this is clearly a process not possible from the base of the vestibule in *Septatopora*.

Engel (1975, p. 576) also suggested that the reproductive function of the auxillary tube was combined with an alimentary function. Autozooeical apertures are septate in all species of *Septatopora* and the occurrence of septa would obviously greatly restrict the ability of the polypide to be protruded from the zooeical chamber. In their fully protruded position the tentacles would have been placed between the septa, and the mouth must have been located beneath the small central opening, with the base of the lophophore contained within the vestibule. In *Septatopora* the anus, which in ectoproct bryozoans is situated outside the lophophore, must have been contained within the vestibule and Engel suggested that the auxillary tube had a sanitary function in providing an outlet for faeces. The fact that every autozooeicum, including those lacking ovicells, in all species of *Septatopora* possesses an auxillary tube supports such a non-brooding function, but does not preclude an additional role in brooding.

Type C

Southwood (1985) described the occurrence of possible internal ovicells in three Upper Permian taxa from the Middle Magnesian Limestone reef facies of north-east England, the acanthocladiids *Synocladia virgulacea* (Phillips) and *Acanthocladia* sp., and the thamnisciid *Thamniscus* sp. The ovicells are morphologically alike in all three taxa. They form small rounded cavities as distal extensions of autozooeical vestibules and are possibly contained within branches according to Southwood. Some of Southwood's material is dolomitized with autozooeical chambers and ovicellular cavities preserved as three dimensional casts with the original calcite bryozoan skeleton replaced by dolomite or removed entirely (text-fig. 2A, B).

Tangential sections show the occurrence of a small circular cavity situated at the proximal extremities of autozooeical vestibular regions. While deeper tangential sections show a line of skeletal material separating the cavity from the vestibular region of autozooeica, in shallow sections this line disappears and the ovicellular cavity and vestibular spaces are continuous (text-fig. 1E, F). Although



TEXT-FIG. 2. Type C ovicells: A, B, *Synocladia virgulacea* (Phillips), DUGD, SC. MP.18 (reproduced from Southwood 1985, fig.6). A, cast preservation of abundant ovicells (one ovicell is arrowed), $\times 13$, B, detail of ovicells, $\times 52$. C, D, *Thamniscus octonarius* Ulrich (reproduced from Ulrich 1890, pl. 62). C, arrangement of autozoecial apertures on obverse surface, $\times 9$. D, obverse surface detail showing rounded ovicellular depressions at proximal extremity of every autozoecial aperture; some depressions have low elevated rims, $\times 35$.

Type D ovicells: E, *Polypora shumardii* Prout (reproduced from Stratton 1981, pl. 1). FMNH UC14016 F15-16, showing canal pathways traversing branches(a) and ovicells situated on dissepiments(b), $\times 5$. All figures except C and D are SEMs.

longitudinal sections show a small rounded concave depression proximal to autozoecial apertures, these are not well defined and Southwood suggested that their occurrence at the zoarial surface may be due to the removal of some of the bryozoan skeleton. However, it may be possible that these ovicells formed features on the zoarial surface, and are morphologically similar to type B ovicells in *Septatopora* which also form shallow rounded depressions at the zoarial surface.

Ulrich (1890, p. 611, pl. 62, fig. 7a, b) described and figured comparable structures in the American Carboniferous fenestrate *T. octonarius* Ulrich. These are definitely external features and may also be interpreted as ovicells. On the obverse surface the peristomial rim of autozoecial apertures is incomplete, and from this a very shallow depression emanates. In some cases a low rim-like structure extends around the perimeter of the depressions from the incomplete proximal extremities of autozoecial apertures (text-fig. 2C, D).

Identical structures to these have been found recently in an Upper Permian species of *Acanthocladia* from the Lower Magnesian Limestone of County Durham (Southwood, pers. comm.). In *T. octonarius* and *Acanthocladia* although a low rim-like structure occurs around the perimeter of many ovicells there is no indication of this rim having extended in life to form a roof over cavities. Roofs of type C ovicells were possibly uncalcified during life, as were those of type B ovicells.

Ovicells in most of these taxa are of fairly similar diameter; those of *T. octonarius* being approximately 0.20 mm, while those in *Synocladia virgulacea*, *Acanthocladia* sp., and *Thamniscus* sp. are about 0.16 mm in diameter. This is comparable in size to type B ovicells in *Septatopora flemingi* (0.20 mm).

The striking feature of ovicells in *Synocladia virgulacea* is their abundance (Southwood 1985). They can be found in every autozoecium of some colony fragments but their distribution can also be sparse and irregular and they may show a weak clustering into groups (text-fig. 2A). In *T. octonarius* ovicells are also very abundant with every autozoecium figured by Ulrich (1890) possessing one, while in *Acanthocladia* sp. and *Thamniscus* sp. ovicells are possibly less abundant though still more abundant than in *Septatopora* species.

Type B and C ovicells are very different from type A ovicells in their morphology, size, and within-colony abundance. Southwood (1985) suggested that if Tavener-Smith's (1966) conclusions are valid about the large size of ovicells in *Fenestella* and *Hemitrypa* being evidence of polyembryony, then it is possible that polyembryony did not occur in the small sized ovicells of *Synocladia virgulacea*. Southwood also suggested that because almost every autozoecium in *S. virgulacea* has an ovicell the zooid was an autozooid that did not degenerate during brooding (unlike gonozooids of Recent cyclostomes) and that it may have been possible for an embryo to develop in an ovicell at the same time as the zooid was feeding. Southwood made particular reference to the aspect of these ovicells being reminiscent of entozooidal ovicells in some cheilostome Bryozoa (Ryland 1970).

Type D

These were described by Stratton (1981) in *Polypora shumardii* Prout from the Jefferson Limestone (Mid Devonian) Falls of Ohio, Indiana-Kentucky, USA. Stratton described a system of canal-like structures traversing branches and dissepiments. The canals lead from autozoecia interpreted to be gonozoecia, to inflated bowl-like depressions located on the dissepiments, interpreted as ovicells (text-figs. 1G, 2E). Several autozoecia may be situated alongside each meandering canal (text-fig. 1G). Autozoecial apertures bordering canals have normally developed peristomes on their margins opposite the canals but reduced peristomes within the canals. Apertures situated entirely within canals have very poorly developed peristomes. Ovicells are of moderate size, about 0.30 mm in diameter, and open towards fenestrules.

Stratton's material was silicified, and although he observed that some of the canals were partly covered by a thin silicified layer he concluded that the canals and ovicells may not have been enclosed by a calcitic cover during life. Stratton suggested that the canals provided a pathway from gonozoecia to ovicells, enabling the transport of embryonic products to ovicells. He also suggested that because of the reduced peristomes of several autozoecia along a canal, the canals served more than one gonozoecium. This is a unique phenomenon in fenestrate reproductive strategy, in that this type of ovicell may be regarded as extrazooidal.

Canal and ovicell bearing zoaria were fairly common in Stratton's material with approximately half of the total population examined possessing them. Stratton considered about 20% of the total number of autozoecia on canal-bearing zoaria to be gonozoecia on the basis of their position in relation to the canals and the presence of a reduced peristome. As he stated it is conjecture whether or not all gonozooids along a single canal were active at one time, but the presence of reduced peristomes and their location along canals may suggest that each gonozooid was probably active at least once. The canals would have enabled the transportation of fertilized eggs to ovicells on dissepiments without significantly disturbing adjacent autozoecia. Considering the close proximity and number of autozoecial rows on branches severe disruption would have occurred if the zoecial walls had

expanded for brooding in situ, i.e. if large cyst-like ovicellular structures had developed on branch surfaces.

CONCLUSIONS

The diverse morphological variation exhibited at generic level by fenestrate ovicells in their size, position, and intra-colonial abundance is related to variations in autozooeccial chamber morphology, proximity of autozooeccia, and the number of autozooeccial rows on branches.

In the type A ovicells of *Fenestella*, *Hemitrypa*, and *Penniretepora* with only two rows of autozooeccia on branches there was ample space for the development of relatively large cyst-like ovicellular structures, incorporating the distal portion of vestibular regions of gonozooeccia, on the obverse surface of branches. In taxa with several rows of autozooeccia on branches and dissepiments the development of such structures would have severely interfered with the feeding function of autozooeccia because of their closer proximity and greater number of autozooeccial rows. Different types of incubation structures were developed in some forms. Type B ovicells in *Septatopora* and type C ovicells in *Synocladia*, *Acanthocladia*, and *Thamniscus* form small hemispherical depressions situated on the zoarial surface at the proximal extremities of autozooeccial apertures and are usually significantly more abundant intra-colonially than type A ovicells. In the type D ovicells of *P. shumardii* a unique strategy was developed. Ovicells are situated on non-poriferous dissepiments with gonozooeccia linked to ovicells by a system of canal pathways at the zoarial surface, and several gonozooeccia seemingly shared a single ovicell.

Only type A ovicells described in *Fenestella*, *Hemitrypa*, and *Penniretepora* bear close resemblance to living cyclostome gonozooeccia. Contrary to Tavener-Smith's (1966, p. 196) and Stratton's (1975, p. 175) suggestion that fenestrate ovicell morphology suggests a close relationship with cyclostome stocks, recent descriptions of fenestrate ovicellular structures by Stratton (1981) and Southwood (1985) show that on the whole the morphological similarity of fenestrate ovicells and cyclostome gonozooeccia is no better than between fenestrate and cheilostome ovicells. Tavener-Smith (1966, p. 196) even noted the superficial resemblance of the external morphology of ovicells in *Fenestella* and *Hemitrypa* with peristomial ovicells in certain cheilostome genera. There is no suggestion, however, that fenestrate ovicells contradict the closer affinities of fenestrates to cyclostomes than to cheilostomes demonstrated by various other morphological evidence.

Stratton (1981, p. 881) stated, without giving reasons, that although the morphology and structure of ovicells he described in *P. shumardii* was different from those described by Tavener-Smith (1966) and Stratton (1975), in *Fenestella* and *Hemitrypa*, the methods of incubation were probably consistent among all these forms. However the morphological variety shown by fenestrate ovicells may suggest that different methods of embryonic development and incubation occurred.

It is not reasonable to infer polyembryony in fenestrates on the grounds of ovicell morphology alone, for it has yet to be investigated whether all large gonozooids in living cyclostomes undergo polyembryony in their reproductive cycles (Boardman *et al.* 1983, p. 108). If this does prove to be the case only then can it be reasonably assumed that fenestrate taxa with comparable ovicellular structures may have undergone polyembryony. Sounder basis for regarding fenestrates as having been polyembryous is provided by the phylogenetically closer affinities of fenestrates with cyclostomes than with cheilostomes, and by the occurrence of inter-colony fusion (homosyndrom) in fenestrates, suggesting that genetically identical larvae resulting from polyembryony may have occurred (see McKinney 1981).

Ovicells can be very useful in bryozoan taxonomy and at species level they are critical to taxonomic determinations in some groups, e.g. many cheilostomes and cyclostomes. The morphology of bryozoan ovicells may also be of phylogenetic significance and of value at high taxonomic rank, though their application is largely uninvestigated (Viskova 1981).

Ovicell morphology is almost identical in the fenestrellids *Fenestella* and *Hemitrypa* and the acanthocladid *Penniretepora* while both autozooeccial chamber and ovicell morphology are nearly identical in the acanthocladids *Synocladia* and *Acanthocladia* and the thamnisciid *Thamniscus*. If

these similarities are important phylogenetically then conventional taxonomic arrangements of the fenestrates may require some revision.

Acknowledgements. I thank Dr G. P. Larwood and Mr D. A. Southwood, Department of Geological Sciences, University of Durham, for critically reading an early draft of this paper, and Dr P. D. Taylor, Department of Palaeontology, British Museum (Natural History), for reviewing a revised draft. This work was carried out during the tenure of a Natural Environment Research Council research studentship at the Department of Geological Sciences, University of Durham.

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Typescript received 22 March 1985