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 autozoocelial chambers, proximity of autozoocelia, and the number of autozoocelial rows on branches and disseptions. Type A oovicells from large globose distentions to gonozoocelia, are intra-colonially few in number and occur in *Fenestella*, *Hemitrypa*, and *Penniretepora*; Type B oovicells occur in *Septatapora*, and form shallow hemispherical depressions at the proximal rims of autozoocelial apertures and are connected to the lower vestibular regions of adjacent gonozoocelia by an auxiliary tube; Type C oovicells occur in *Synoctalia*, *Acanthoecladia*, and *Thamniscus*, and form hemispherical depressions at the proximal rims of autozoocelial apertures and are intra-colonially very abundant; Type D oovicells are extrazooidal and occur in *Polypora*, oovicells are located on disseptions and are linked to gonozoocelia by a system of canal-like structures traversing branches and disseptions, several gonozoocelia shared an oovicell. 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 gonozoocelia prior to their release into the sea. It is only recently that oovicells 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 oovicells and that they constitute the most diverse form of polymorphism in the Fenestrata.

Fenestrate oovicells 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 oovicells 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 oovicells in taxa known to possess oovicells, it seems probable that oovicells 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 autozoocelial chamber, similar to oovicells described in chelostome gymnoelaenates, and the dilated parts of gonozoocelia in cyclostome stenolaenates (Borg 1926; Ryland 1970). In fenestrates oovicells belong to a single zooid (the gonozooid), with one exception where oovicells may be regarded as extrazooidal 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 autozoocelial chambers and the proximity and number of rows of autozoocelia 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 autozoocodial chambers which they interpreted as ovicells in the fenestellids *Fenestella* Lonsdale and *Hemiprypa* Phillips. Tavener-Smith first described this type of ovicell in three species: *H. hibernica* McCoy, *F. cf. fanata* Whidborne, and *F. cf. delicatula* Ulrich from Lower Carboniferous (Ashian) 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 gonozoocoeium is directly connected, by a short vestibular region, to the ovicell above which forms a large globose distention of the gonozoocoeial 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 oovicells 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 oovicells in *Fenestella* and *Hemiprypa* species, with an opening (oociopore) in the crests through which the larvae were presumably liberated (Pl. 19, fig. 2; text-fig. 1a). In most of Tavener-Smith’s material the oovicells are partly weathered with the fragile roof of the oovicell missing revealing the smooth and well-rounded interior (Pl. 19, fig. 1). The basal area of these oovicells 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 oovicells commonly affect the development of adjacent autozoocia 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 oovicells is very low compared to the number of normal autozoocia, 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 oovicells in *Fenestella* and *Hemiprypa* species bears a strong resemblance to Recent cyclostome gonozoociae described by Borg (1926). This resemblance, together with the relatively large size of oovicells 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 oovicells: Figs. 1 and 5, *Hemiprypa hibernica* McCoy, BMNH PD.4493, 1, showing oovicells forming distentions on top of gonozoocoeial vestibular regions (one vestibule is arrowed), ×29. 5, distribution of oovicells on colony fragment, ×12.

Figs. 2, 3, 4, *Fenestella cf. fanata* Whidborne. 2, BMNH PD.4487, oociopores in the crest of two oovicells, ×52, 3, BMNH PD.4486, increase in branch height due to oovicell, ×66. 4, BMNH PD.4486, distribution of oovicells on colony fragment, ×15.

Figs. 6 and 7, *Pennireteta spinosa* (Young and Young) BMNH PD.6280. 6, obverse surface detail and showing oovicell on top left lateral branch, ×30. 7, detail of oovicell, ×140.

Figs. 8 and 9, *Pennireteta* sp. BMNH PD.6281. 8, obverse surface detail and showing oovicells, ×22. 9, detail of oovicell on mainstem, also showing top of vestibular region of gonozoocoeium (arrowed) at base of oovicell, ×150.

SEMs.
BANCROFT, bryozoan ovicells
species of the acanthocladiiid 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 *Hemitrype*.

**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 *Glaucome stellipora* Young and Young (1874), but it is proposed to elevate the variety to species level.

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

**Ovicell Description:** One small colony fragment has been found on which a single oviscell is situated on a lateral branch (Pl. 19, figs. 6 and 7). The oviscell 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 oviscell does not disturb the disposition of adjacent apertures. The base of the oviscell is depressed relative to the obverse branch surface and is situated centrally over the vestibular region of the gonozoocoeum. 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 autozoocoeal 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 oviscell as a calcified cover during life. Ovicells are situated centrally above the vestibular region of gonozoocoea (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*,

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**TEXT-FIG. 1.** Type A ovicells: A (redrawn from Tavener-Smith 1966, text-fig. 1A), *Fenestella* cf. *fanata* Whidborne, showing gonozoocoeum with large cyst-like oviscell, ×26. B (redrawn from Stratton 1975, fig. 3), transverse section through a branch in *Fenestella* sp. showing oviscell with ooeiopore, ×230. C (redrawn from Engel 1975, text-fig. 1A), *Septatopora acarinata* (Crockford), showing oviscell at proximal extremity of autozoocoeal aperture, ×60. D (redrawn from Engel 1975, text-fig. 1A), *Septatopora flemingi* Engel, detail as for C, ×75.

Type C oovicells F, *Syno cladia virgulacea* (Phillips) (redrawn from Southwood 1985, fig. 5a, b). F, oblique tangential section through a branch, points 1-5 correspond to the level in the branch shown in F, ×50. R, longitudinal section through an autozoocoeum with oviscell, ×50.

Type D oovicells: G, *Polypora shamardii* Prout, showing canal pathways meandering over the branch surface and oviscell situated on dissepiment, ×60.
and in all fenestellids type A ovoids 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 ovoids 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, ovoids described in three taxa by Tavener-Smith (1966) all came from the same locality, and secondly, ovoid bearing zoaria are quite common in these taxa from this locality.

Type B
Engel (1975) described hemispherical ovoidular depressions situated at the proximal rims of autozoocoeal apertures in two species of the Carboniferous fenestrate Septatopora Engel, from eastern Australia. The ovoids form very shallow, well-rounded depressions and are relatively small, being about 0.1 mm in diameter in S. acarinita (Crockford) and 0.2 mm in diameter in S. flemingi Engel. They are connected to the lower vestibular regions of adjacent gonozoocoeal chambers by an auxiliary tube which is present in every autozoocoeum (text-fig. 1c, d). Ovoids are quite common in zoaria of S. acarinita, but are scarcer in S. flemingi and are of a similar abundance to type A ovoids.

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

The method of transfer of fertilized eggs from the gonozoocoeum through the auxiliary tube is conjectural. In some Recent cheilostome gymnolaemate the transfer of fertilized eggs to distally positioned brooding cavities requires considerable movement and manipulation by the tentacle crown of the autozooid. 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 auxiliary tube was combined with an alimentary function. Autozoocoeal 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 zoocoeal 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 auxiliary tube had a sanitary function in providing an outlet for faces. The fact that every autozoocoeum, including those lacking ovoids, in all species of Septatopora possesses an auxiliary 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 ovoids in three Upper Permian taxa from the Middle Magnesian Limestone reef facies of north-east England, the acanthocladids Synochladia virgulacea (Phillips) and Acanthocladia sp., and the thamniscid Thaniscus sp. The ovoids are morphologically alike in all three taxa. They form small rounded cavities as distal extensions of autozoocoeal vestibules and are possibly contained within branches according to Southwood. Some of Southwood’s material is dolomitized with autozoocoeal chambers and ovoidcicular 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 autozoocoeal vestibular regions. While deeper tangential sections show a line of skeletal material separating the cavity from the vestibular region of autozoocoeia, in shallow sections this line disappears and the ovoidicular cavity and vestibular spaces are continuous (text-fig. 1a, f). Although
TEXT-FIG. 2. Type C ovi cells: A, B, Synoecelia virgulacea (Phillips), DUGD, SC, MP.18 (reproduced from Southwood 1985, fig. 6). A, cast preservation of abundant ovi cells (one ovi cell is arrowed), ×13. B, detail of ovi cells, ×52. C, D, Thamniscus octonarius Ulrich (reproduced from Ulrich 1890, pl. 62). C, arrangement of autozoocel apertures on obverse surface, ×9. D, obverse surface detail showing rounded ovi cellular depressions at proximal extremity of every autozoocel aperture; some depressions have low elevated rims, ×35.

Type D ovi cells: E, Polypropora shumardii Prout (reproduced from Stratton 1981, pl. 1). FMNH UCI4016 F15–16, showing canal pathways traversing branches(a) and ovi cells situated on disseipents(b), ×5.

All figures except C and D are SEMs.

Longitudinal sections show a small rounded concave depression proximal to autozoocel 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 ovi cells formed features on the zoarial surface, and are morphologically similar to type B ovi cells 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 ovi cells. On the obverse surface, the peristomial rim of autozoocel 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 autozoocel apertures (text-fig. 2C, D).
Identical structures to these have been found recently in an Upper Permian species of *Acantho cladia* from the Lower Magnesian Limestone of County Durham (Southwood, pers. comm.). In *T. octonarius* and *Acantho cladia* although a low rim-like structure occurs around the perimeter of many ovoicells there is no indication of this rim having extended in life to form a roof over cavities. Roofs of type C ovoicells were possibly uncalcified during life, as were those of type B ovoicells.

Ovoicells in most of these taxa are of fairly similar diameter; those of *T. octonarius* being approximately 0·20 mm, while those in *Synocladia virgulacea, Acantho cladia* sp., and *Thamniscus* sp. are about 0·16 mm in diameter. This is comparable in size to type B ovoicells in *Septatopora fl e m ing i* (0·20 mm).

The striking feature of ovoicells in *Synocladia virgulacea* is their abundance (Southwood 1985). They can be found in every autozoosccium 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* ovoicells are also very abundant with every autozoosccium figured by Ulrich (1890) possessing one, while in *Acantho cladia* sp. and *Thamniscus* sp. ovoicells are possibly less abundant though still more abundant than in *Septatopora* species.

Type B and C ovoicells are very different from type A ovoicells in their morphology, size, and within-colony abundance. Southwood (1986) suggested that if Tavener-Smith’s (1966) conclusions are valid about the large size of ovoicells in *Fenestella* and *Hemitorypa* being evidence of polyembryony, then it is possible that polyembryony did not occur in the small sized ovoicells of *Synocladia virgulacea*. Southwood also suggested that because almost every autozoosccium in *S. virgulacea* has an ovoicell 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 ovoicell at the same time as the zooid was feeding. Southwood made particular reference to the aspect of these ovoicells being reminiscent of entozooidal ovoicells in some chelostome 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 disseipments. The canals lead from autozoosccia interpreted to be gonozoosccia, to inflated bowl-like depressions located on the disseipments, interpreted as ovoicells (text-figs. 1G, 2E). Several autozoosccia may be situated alongside each meandering canal (text-fig. 1G). Autozoosccial 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. Ovoicells 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 ovoicells may not have been enclosed by a calcitic cover during life. Stratton suggested that the canals provided a pathway from gonozoosccia to ovoicells, enabling the transport of embryonic products to ovoicells. He also suggested that because of the reduced peristomes of several autozoosccia along a canal, the canals served more than one gonozoosccium. This is a unique phenomenon in fenestrate reproductive strategy, in that this type of ovoicell may be regarded as extrazooidal.

Canal and ovoicell 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 autozoosccia on canal-bearing zoaria to be gonozoosccia 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 ovoicells on disseipments without significantly disturbing adjacent autozoosccia. Considering the close proximity and number of autozoosccial rows on branches severe disruption would have occurred if the zoosccial 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 autozoocodial chamber morphology, proximity of autozoocia, and the number of autozoocodial rows on branches.

In the type A ovicells of *Fenestella*, *Hemitrypa*, and *Penniretepora* with only two rows of autozoocia on branches there was ample space for the development of relatively large cyst-like ovicellular structures, incorporating the distal portion of vestibular regions of gonozoocia, on the obverse surface of branches. In taxa with several rows of autozoocia on branches and disseipments the development of such structures would have severely interfered with the feeding function of autozoocia because of their closer proximity and greater number of autozoocodial rows. Different types of incubation structures were developed in some forms. Type B ovicells in *Septatopora* and type C ovicells in *Synocladia*, *Acanthocladia*, and *Thammiscus* form small hemispherical depressions situated on the zoarial surface at the proximal extremities of autozoocodial 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 disseipments with gonozoocia linked to ovicells by a system of canal pathways at the zoarial surface, and several gonozoocia seemingly shared a single ovicell.

Only type A ovicells described in *Fenestella*, *Hemitrypa*, and *Penniretepora* bear close resemblance to living cyclostome gonozoocia. 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 gonozoocia 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 polymbryony in fenestrates on the grounds of ovicell morphology alone, for it has yet to be investigated whether all large gonozooids in living cyclostomes undergo polymbryony 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 polymbryony. Sounder basis for regarding fenestrates as having been polymbryous is provided by the phylogenetically closer affinities of fenestrates with cyclostomes than with cheilostomes, and by the occurrence of inter-colony fusion (homosyndrome) in fenestrates, suggesting that genetically identical larvae resulting from polymbryony 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 fenestellids *Fenestella* and *Hemitrypa* and the acanthocladiids *Penniretepora* while both autozoocodial chamber and ovicell morphology are nearly identical in the acanthocladiids *Synocladia* and *Acanthocladia* and the thammisciid *Thammiscus*. If
these similarities are important phylogenetically then conventional taxonomic arrangements of the fenestrae may require some revision.

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