

*POLYORA STENOSTOMA*: A CARBONIFEROUS  
BRYOZOAN WITH CHEILOSTOMATOUS  
FEATURES

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ABSTRACT. The morphology of *Polyora stenostoma* sp. nov., a fenestrate cryptostome from the Viséan, is described and discussed. Unusual zooecial features suggest that the frontal surface was substantially uncalcified during the active life of a zooid. It is probable that the soft external coverings on this side were depressed by retraction of the vestibular extensor muscles. The consequent decrease in zooidal volume and increase in body fluid pressure would have facilitated extrusion of the tentacles, as in modern anascan cheilostomes. It is therefore likely that the mechanism for lophophore extrusion now regarded as characteristic of, and peculiar to, the *Anasca* was also present in a much earlier cryptostome stock.

IN bryozoa the extrusion of tentacles, a vital function in these animals, is effected by different means in different groups. The mechanism is always fundamentally the same, however, in that a reduction of bodily volume by muscular contraction causes an increase of body fluid pressure, which promotes the extrusion of the lophophore by hydraulic means. In the order Cheilostomata, which ranges from the Cretaceous to the present day, the basic arrangement is that of muscles acting on a frontal membrane, as seen in the suborder *Anasca*. Although this pattern, and that of the compensation sac which stems from it, are generally accepted as peculiar to the Cheilostomata (Bassler 1953, pp. G147, 149) the frontal morphology of a new species of *Polyora* from Viséan limestone (D<sub>1</sub>) at Carrick Lough, County Fermanagh, Ireland, suggests the presence of an essentially similar mechanism in a much earlier stock. In the following paragraphs the new species is described, and the significance of the unusual frontal characteristics examined.

SYSTEMATIC DESCRIPTION

Order CRYPTOSTOMATA Vine 1883  
Family FENESTELLIDAE King 1850  
Genus POLYORA M'Coy 1844

*Emended diagnosis.* Planar, funnel, or cup-shaped fenestrate expansions of radiating, straight, or gently sinuous branches connected by regularly disposed, transverse dissepiments. Branches bear three or more rows of zooecial apertures on one side only; dissepiments are sterile. Obverse of branch smooth or with low, longitudinal ridges separating rows of apertures. Ridges may bear low nodes. Reverse smooth, or longitudinally striate, with or without nodes.

*Type species.* *P. dendroides* M'Coy 1844. Tournaisian, Ireland.

[*Palaeontology*, Vol. 14, Part 1, 1971, pp. 178-87, pl. 25.]

*Polypora stenostoma* sp. nov.

Plate 25, figs. 1-10

*Type specimens.* Holotype: Specimen PD 4858 in the British Museum (Natural History) collection, London. Paratypes: Specimens PD 4859 to PD 4864 in the same collection.

*Type locality.* Limited exposures along the south shores of Carrick Lough, two miles north-west of Derrygonnelly village, County Fermanagh, Northern Ireland.

*Material.* The following description is based on examination of thirty-three small zoarial fragments. The largest measured 17 × 15 mm.

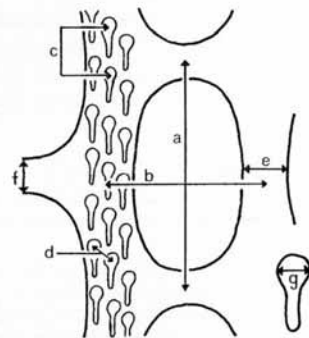
*Measurements.* For every variable listed, twelve measurements were taken from each of fifteen zoarial fragments. Specimen means were then calculated, and the following statistics derived by the method suggested in Tavener-Smith (1966b, pp. 421-2). The dimensions recorded are illustrated in text-fig. 1.

	Range	Mean	Standard deviation	Coeff. of variation
Fenestrule length	1.60-2.20	1.86	0.163	8.76
Fenestrule width	0.90-1.20	1.053	0.089	8.47
Inter-apertural distance (within one row)	0.25-0.32	0.295	0.016	5.51
Inter-apertural distance (measured diagonally)	0.20-0.25	0.235	0.015	6.49
Branch width	0.37-0.50	0.417	0.034	8.16
Zooidal ap. width	0.07-0.10	0.085	0.009	10.88
Dissepiment width	0.25-0.35	0.302	0.030	9.87
Micrometric formula	8-12/4-6//15-18			

*Diagnosis.* *Polypora* with cup-shaped zoarium consisting of strong branches and short, stout dissepiments bounding oval or elliptical fenestrules. There are mostly three rows of elongate, slit-like apertures per branch. No carinal nodes. Dimensions of a sample are as stated above.

*Description.* The proximal parts of colonies are cup-shaped (Pl. 25, fig. 4), with zooecial apertures on the inner side of the meshwork. Complete structures were probably erect, foliaceous, cup-shaped expansions about 5 cm high.

Branches are relatively stout, with a slightly sinuous growth habit (Pl. 25, fig. 1). There is no median ridge on the obverse, nor are carinal nodes present. One row of apertures follows the mid-line and is flanked by a row on either side. Although three rows of apertures per branch are commonest, the number may increase to four or five at bifurcations, and diminish to two immediately thereafter. Branch widths show corresponding adjustment, increasing to as much as 0.7 mm at the point of division, then sharply decreasing to about 0.35 mm. The reverse is broadly



TEXT-FIG 1. *Polypora stenostoma*: dimensional measurements. *a*, fenestrule length; *b*, fenestrule width; *c*, interapertural distance (within a row); *d*, inter-apertural distance (diagonally); *e*, branch width; *f*, dissepiment width; *g*, zooidal aperture width.

rounded (Pl. 25, fig. 3) and may be thickly encrusted with secondary skeletal material. Cross-sections of branches are approximately circular.

Dissepiments are short, stout, and roughly circular in transverse section. They are slightly depressed below branch level on both sides, though in the proximal region secondary accretions may render the underside more or less flush with branch surfaces. Fenestrules are mostly imperfect oval or elliptical shapes, though they may be rectangular with rounded extremities.

This species is characterized by the presence on the frontal side of each zoecium of an elongate opening extending for much of the chamber length, but narrower than the chamber width. This opening is slightly wider and more rounded at its distal end (where the lophophore was extruded) so that the over-all shape may be described as spatulate (Pl. 25, figs. 1, 7). In some cases the proximal part of the opening is narrowed to a slit, while in others this slit is partly closed so that the proximal extremity is isolated as a separate, secondary or accessory aperture, about half the size of the main one (Pl. 25, figs. 8, 9). The last condition results in an alternation of larger and smaller openings in a single row, each pair relating to a single zoecium. In some specimens many of the larger or zooidal apertures (so called to distinguish them from the smaller ones) show prominent collar-like peristomes (Pl. 25, figs. 1, 7) while in others they are sealed by calcite laminae or completely obscured by secondary calcification (Pl. 25, fig. 10).

Zoecial chambers are compact structures with an elongate-hexagonal plan, enabling them to fit closely together in three rows within a branch. There are from four to seven chambers along the side of a fenestrule, though the number is most commonly five, and less commonly six. Average dimensions of six chambers were: length, 0.35 mm; width, 0.15 mm; height, 0.17 mm.

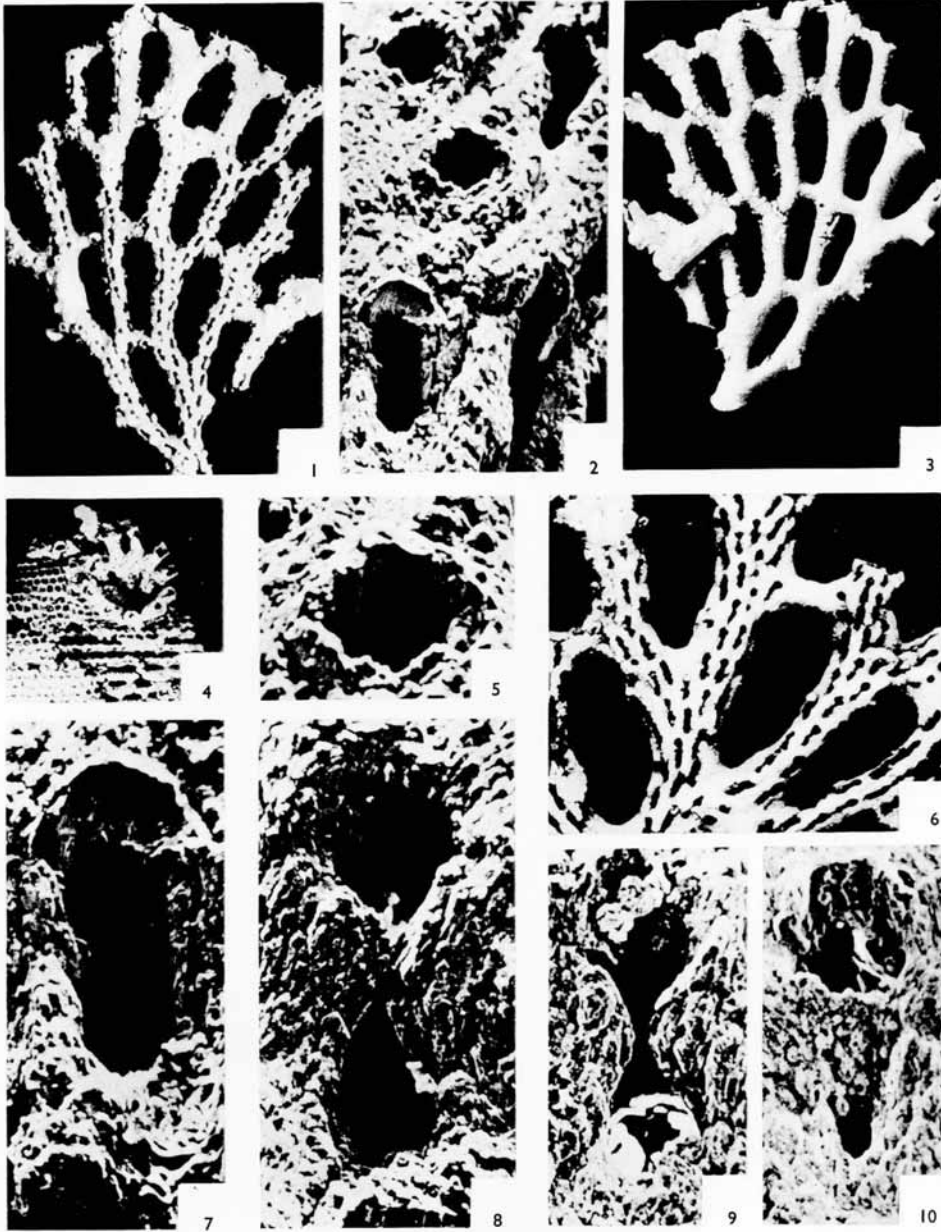
The form, as described above, cannot be assigned to any of the Carboniferous *Polypora* described by M'Coy from Ireland, nor is there a satisfactory correspondence with any other known species in the genus. It is therefore necessary to introduce a new name for these specimens, and *P. stenostoma* (στενόστομος = narrow-mouthed) is proposed for the purpose.

#### DISCUSSION

The peculiarly shaped frontal openings distinguishing this species merit special attention and it is evident that they may have been formed in one of several ways. First, they

#### EXPLANATION OF PLATE 25

Figs. 1–10. *Polypora stenostoma* sp. nov. 1, Obverse of holotype showing elongate frontal openings and localized areas of heavy secondary encrustation, PD 4858,  $\times 10$ . 2, Scanning electron micrograph showing a zoecial aperture of near-maximum size (lower left); one with a proximal slit (upper right) and two with notched outlines (centre and upper left). Small dark patch below notched aperture at upper left denotes position of almost sealed accessory aperture, PD 5312,  $\times 130$ . 3, Reverse of holotype, PD 4858,  $\times 10$ . 4, Cup-like proximal part of a colony attached to obverse of an *Hemitrypa hibernica* fragment, PD 4864,  $\times 6$ . 5, Scanning electron micrograph showing a late stage zoecial aperture with notched outline. Note that the notches persist into the zoecium as grooves, PD 5312,  $\times 280$ . 6, Obverse of zoarial meshwork showing frontal openings with proximal slits, PD 4860,  $\times 21$ . 7, Scanning electron micrograph showing a zoecial aperture at near-maximum size, PD 5312,  $\times 250$ . 8, Scanning electron micrograph showing the stage at which closure of the proximal slit has led to the formation of an accessory aperture, PD 5312,  $\times 285$ . 9, Scanning electron micrograph showing constriction of the proximal slit by lateral growth, PD 5312,  $\times 245$ . 10, Scanning electron micrograph of an example in which separation of zooidal and accessory apertures has been achieved, PD 5312,  $\times 210$ .



TAVENER-SMITH, Carboniferous bryozoan

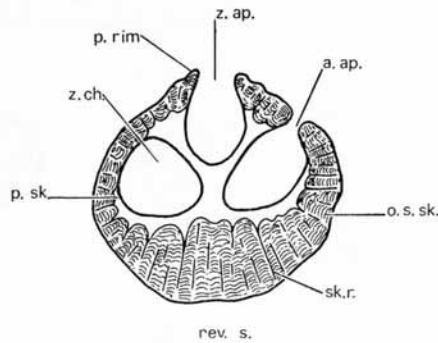
could have resulted from the enlargement of normal zoecial apertures by accidental breakage or abrasion. This presupposes that the present openings were of secondary origin and therefore of no relevance to the life of a colony. Secondly, it is possible that the original condition was that in which larger and smaller apertures alternated in a single zoecial row, and that breakage or abrasion led in many cases to the union of pairs, thus forming elongate openings. If so, it might be thought that during life the smaller apertures gave access to brood chambers, or some kind of kenozooid. Thirdly, it may be that the elongate openings were primary structures communicating directly with the zoecium.

Taking these possibilities serially: the first fails to constitute a satisfactory explanation. Shape variation between frontal openings, though present, is not great, and there is no sign of mechanical breakage or abrasion. Nor is it likely that the smaller openings, where such are seen, gave access to kenozooids, for none of these is present. Finally, the absence of brood chambers makes it improbable that the subsidiary apertures were oeciopores.

Elimination of these possibilities increases the likelihood that the frontal openings communicated directly, and along all their length, with zoecial chambers. This is confirmed by transverse sections which show complete structural continuity between frontal surfaces flanking the opening and the lateral walls of zoecial chambers (text-fig. 2). Where the frontal opening is constricted into two parts, a section through the smaller, proximal, one showed an identical pattern.

In outlining the characteristics of the frontal surface three conditions were mentioned. These were, first, the presence of an elongate opening, slightly wider and more rounded distally. Second, cases where the proximal part of the opening is reduced to a slit. Third, replacement of the slit by a small accessory aperture, quite separate from that of the main zooidal orifice. The second condition predominates in the specimens examined (hence the specific name), though the third is also common. The first condition is restricted to the distal parts of the largest fragments, while the third is associated with areas of heaviest secondary encrustation. These tend also to be the most proximal parts, but are not always so, for the progress of secondary calcification was by no means uniform. Study of the specimens strongly suggests that these three conditions are related stages in a continuum of change; that the first was characteristic of the younger parts of colonies, and that the other two reflect to an increasing degree the effects of declining vigour. Observation indicates the following sequence:

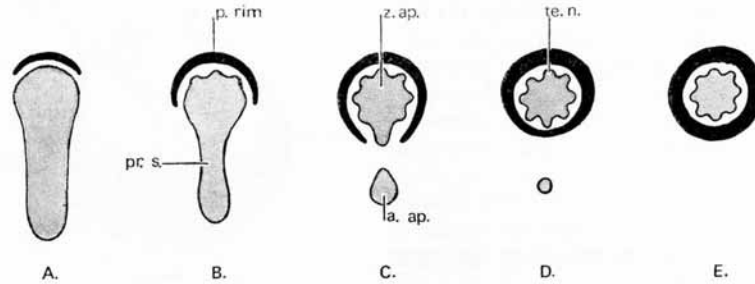
Stage 1. This is envisaged as the condition applicable to normally functioning zooids (text-fig. 3A). The frontal opening is at maximum size, approximating in dimensions to



TEXT-FIG. 2. *Polypora stenostoma*: transverse section across branch; drawn from a cellulose acetate peel. *a.ap.*, accessory aperture; *o.s.sk.*, outer secondary skeleton; *p.rim*, peristome rim; *p.sk.*, primary skeleton; *rev.s.*, reverse surface; *sk.r.*, skeletal rod; *z.ap.*, zoecial aperture; *z.ch.*, zoecial chamber.

the length and width of the zoecial front. The peristome is a low, arcuate ridge confined to the distal side of the apertural region.

Stage 2. With increasing age there appear signs of encroachment by the colonial secondary skeleton. The frontal opening is constricted laterally and, proximal to the zooidal orifice, it is commonly reduced to an elongate slit. The peristome is more strongly developed, and its arc extended (text-fig. 3B). Rounded notches visible on the inner margin of the peristome at this stage probably indicate positions occupied by extended tentacles. Constant extrusion and retraction of these appear to have kept the grooves open, but secondary substance accumulated between them.



TEXT-FIG. 3. *Polypora stenostoma*: plan views showing stages in the reduction of the frontal opening. *a.ap.*, accessory aperture; *p.rim*, peristome rim; *pr.s.*, proximal slit; *te.n.*, tentacular notch; *z.ap.*, zooidal aperture.

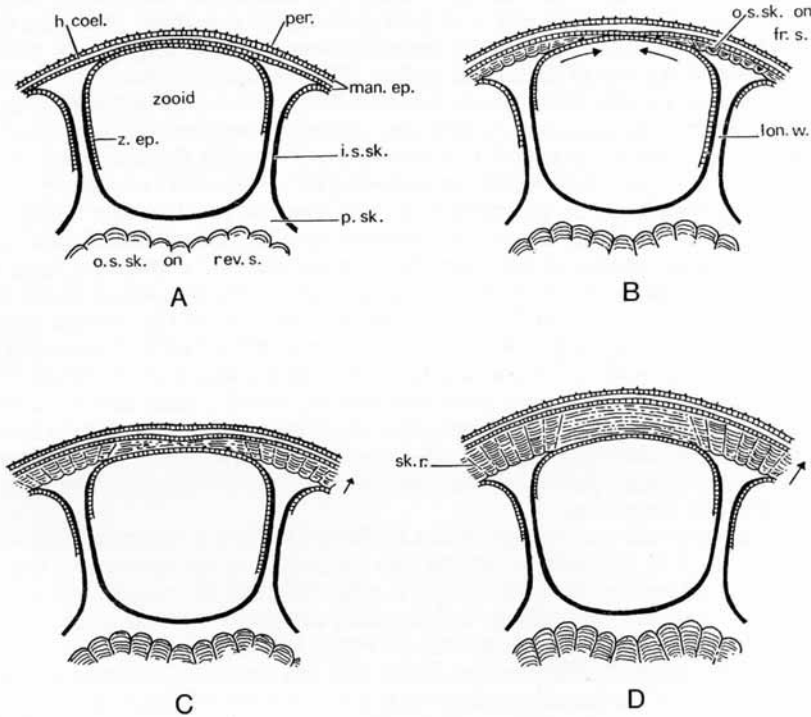
Stage 3. Further constriction of the elongate slit led to its closure except at the proximal end, where an accessory aperture formed. With the closure of the slit extremities of the arcuate peristomial ridge united and continued secondary accretion resulted in the formation of a high, circular collar around the aperture (text-fig. 3C-D). Up to eight symmetrically placed notches are visible on the inner margin of the peristome at this stage. Similar features have been reported by other authors in several fenestellid genera and species. In the writer's opinion the notched, scalloped, or denticulate appearance is an ontogenetic effect without taxonomic significance.

Stage 4. Continued secondary deposition brought about progressive diminution in the size of the accessory aperture, and its eventual occlusion (text-fig. 3 D, E). At this stage the zooidal orifice itself is, in most cases, already significantly reduced, and its subsequent closure and sealing by secondary laminae soon followed.

Stage 5. In the most proximal parts of colonies further skeletal secretion from the exterior eventually led to the complete obliteration of the original frontal structures. A smooth calcite surface resulted, so that the obverse of a branch is indistinguishable from the underside.

The reason for the presence of the enlarged frontal opening in *P. stenostoma* is a matter for conjecture but it is reasonably certain, considering the mode of formation of the fenestellid skeleton (Tavener-Smith 1969) that, except at the zooidal orifice, the opening was covered during life by the soft external mantle of the colony. The presence of the opening must, in fact, have been due to initial calcification in only marginal parts

of the frontal surface. Nevertheless, with the onset of senility the frontal wall progressively encroached upon and eventually sealed the opening. It is natural to inquire why the closure was so long delayed and why, during the active life of a zooid, the opening remained unencumbered by secondary skeletal accretions.



TEXT-FIG. 4. *Polypora stenostoma*: diagrammatic transverse sections of a zooid to show stages in the calcification of the frontal opening. A, The condition in a vigorously functioning zooid. B, Formation of the proximal slit by lateral encroachment of outer secondary tissue. C, Sealing of the frontal opening. D, Late stage thickening of the frontal secondary skeleton. *fr.s.*, frontal surface; *h.coel.*, hypostegal coelom; *i.s.sk.*, inner secondary skeleton; *lon.w.*, longitudinal wall; *man.ep.*, epithelia of external mantle; *o.s.sk.*, outer secondary skeleton; *p.sk.*, primary skeleton; *per.*, periostracum; *rev.s.*, reverse surface; *sk.r.*, skeletal rod; *z.ep.*, zooidal epithelium.

In the Fenestellidae it is inferred (Tavener-Smith 1969, pp. 290–300) that the frontal zooecial wall was deposited partly by the zooidal epithelium, but mainly by the inner mantle epithelium. During early developmental stages it is likely that these layers faced one another close beneath the outer mantle epithelium and colonial periostracum (1969, text-fig. 4A–D). In order to account for the uncalcified frontal opening in *P. stenostoma* it must be supposed that either the secretory epithelia were absent; or that, though



present, they remained non-secretory during the active life of a zooid. The first alternative is unlikely, and the second demands an explanation for the apparent lack of secretory activity. It is possible that the reason for the latter was simply movement.

Within the Fenestellidae there is ample evidence that recurrent movement inhibited the deposition of calcite from normally secretory epithelia. For example, in parts of *Archimedes* and *Lyropora* colonies it is clear that regular movement of the tentacles prevented the formation of secondary material above the aperture, though massive deposits covered the rest of the frontal surface. The formation of peristomial notches (as in the present species) illustrates the same tendency. If it is true that regular movement may inhibit calcification, it would seem logical to suppose that a cessation of movement might permit a resumption of secretory activity. It is therefore possible that in *P. stenostoma* sustained movement, commencing before the onset of primary calcification in the frontal region, prevented wall formation there until a late ontogenetic stage when, due to declining vigour, the movement became retarded. Calcification then resumed its normal course so that secondary skeletal material encroached upon and eventually sealed the frontal zoecial opening (text-fig. 4A-D). Deposition of this kind would have been from the middle epithelial layer (inner side of the external mantle) and therefore of colonial origin. The secretory vigour of this colonial tissue would not have been affected by the declining activity of individual zooids and, on the contrary, observations suggest that physiological controls promoted a high rate of external secondary deposition on the frontal surfaces of moribund zooids so that these became thickly coated and eventually sealed. In *P. stenostoma* the presence of prominent peristomial collars indicates that accelerated secondary deposition preceded the death of a zooid, and not the reverse.

If regular movement was responsible for the failure to form a complete frontal wall in this species, it is pertinent to inquire into the nature of the movement, and the reason why it did not lead to similar results in other *Polypora*. Movements affecting the soft frontal tissues are most likely to have been connected with the extrusion and retraction of the lophophore. Such movements would, with advancing age and declining vigour, become sluggish, and it seems likely that this permitted a recrudescence of calcification around the frontal opening which led to its eventual elimination.

The distinctive frontal morphology of this species differs from that of other *Polypora*, and appears to be unique in the Fenestellidae. It may well have arisen as a result of some genetic accident. A malfunction of physiological co-ordinating mechanisms may, for example, have caused the polypide to become operational prior to the formation of the primary frontal wall instead of immediately afterwards. Movement associated with protrusion and retraction of the lophophore may then have inhibited calcification except in the more static peripheral parts of the frontal area.

At this point it is relevant to consider whether a musculature basically of fenestellid type would, in its operation, have been likely to cause movement of the soft frontal tissues. Although nothing is certainly known of the soft parts of these extinct organisms, deductive reasoning suggests an affirmative answer. This bryozoan group had affinities with the Cyclostomata, and with certain of the Trepostomata also (Bassler 1953, p. G116; Tavener-Smith 1966a, p. 196). Indeed, stratigraphic and phylogenetic considerations suggest that these orders of Palaeozoic bryozoa derived from a common ancestral stock. In attempting to visualize the apparatus for lophophore extrusion in the



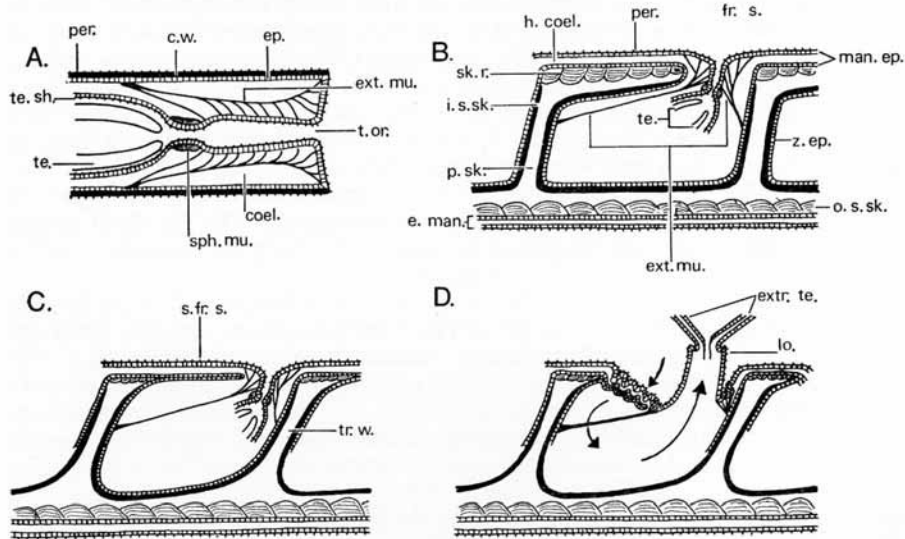
Fenestellidae one cannot, therefore, do better than take as a model Borg's (1926, pp. 241-4) account of corresponding arrangements in modern cyclostomes, the only surviving representatives of these groups. In doing so it must be recalled that typical fenestellid zooecia differ from those of the Cyclostomata in important respects, notably in having roughly box, as opposed to tubular, shapes and in the presence of a frontal rather than a terminal aperture. These differences become less absolute on closer examination for within the Fenestellidae, and even within *Fenestella* itself, there is a great diversity of zooecial shape, and though most chambers are box-like, some are sac- or pear-shaped and a few are tubular. It seems possible that tubular zooecia, perhaps derived from phylloporinid predecessors and well seen in early forms such as *Archaeofenestella* Miller, in general gave way to shorter and more compact shapes. These changes must have been accompanied by a migration of the aperture from a distal to a frontal position, in the same way as has been postulated for the Cheilostomata by Silen (1944, pp. 18-24). It is therefore reasonable to suppose that the apertural region of a box-like fenestellid zooecium corresponds morphologically with the distal surface of a tubular cyclostomatous one. This is important in deducing the arrangement of the musculature concerned with lophophore movement.

In the Cyclostomata muscular effort in lophophore extrusion is directed towards opening the vestibule. To this end the radially arranged extensor muscles, which are attached proximally to the epithelial lining of the tubular zooecium (Borg 1926, p. 189, fig. 1), are inserted at their distal ends not only along the vestibular walls, but also on to the adjacent distal surface of the zooid (text-fig. 5A). This pattern of musculature, efficient in promoting lophophore extrusion in a tubular zooecium, must have undergone some modification and rearrangement in order to ensure continued efficient functioning as the more compact chamber shapes of the Fenestellidae emerged. But it is likely that the basic pattern remained unchanged, for in the fenestellids muscular effort must still have been directed towards opening the vestibule and, as Silen has pointed out (1944, p. 44), the position of muscle insertions is a conservative anatomical feature. Supposing the system to have retained the over-all characteristics of that in the Cyclostomata, but making due allowance for changes in zooecial morphology, it seems reasonable to conclude that the arrangement in orthodox fenestellid zooids was similar to that suggested in text-fig. 5B. In *P. stenostoma*, a form in which the frontal surface was only periphally calcified, it is difficult to see how contraction of muscles of this pattern could have been effected without depressing the soft frontal covers (text-fig. 5C-D). This would have contributed to a diminution in zooidal volume, a rise in body fluid pressure, and the consequent extrusion of the lophophore. It therefore seems likely that there was, in this Palaeozoic species, a mechanism for polypide movement essentially similar to that now regarded as peculiar to, and characteristic of, much later cheilostomes of the sub-order *Anasca*.

It is worth noting that, whereas in the Cyclostomata (and by inference in orthodox cryptostomes also) muscular effort in lophophore extrusion is directed towards expansion of the vestibule, and in anascan cheilostomes towards depressing the frontal membrane, in *P. stenostoma* an hybrid situation probably existed. In that species it seems that a cyclostome-like musculature, acting mainly on vestibular walls and in the presence of a soft frontal surface, caused as an ancillary effect the depression of the frontal cover, thus aiding extrusion of the tentacles. It seems relevant to recall that Borg (1926, p. 231)

considered the vestibular extensor muscles of cyclostomes and the parietal muscles of cheilostomes (which, in the *Anasca*, depress the frontal surface) to be homologous.

Considering further the matter of structural parallels with the Cheilostomata another, and rather obvious, possibility needs examination, namely that the subsidiary aperture of *P. stenostoma* may be equivalent to the similarly situated ascopore of certain cheilostome genera, such as *Microporella*. This resemblance must, however, be dismissed as



TEXT-FIG. 5. Arrangement and operation of vestibular extensor muscles. A, In a typical member of the cyclostomata (after Borg 1926, p. 189, fig. 1). B, Suggested arrangement in a fenestellid. C, Inferred arrangement in *Polypora stenostoma* (muscles relaxed). D, The same, with muscles contracted. *c.w.*, calcareous wall; *coel.*, coelom; *e.man.*, external mantle; *ep.*, epithelium; *ext.mu.*, extensor muscles; *extr.te.*, extruded tentacles; *fr.s.*, frontal surface; *h.coel.*, hypostegal coelom; *i.s.sk.*, inner secondary skeleton; *lo.*, lophophore; *man.ep.*, mantle epithelia; *o.s.sk.*, outer secondary skeleton; *per.*, periostracum; *p.sk.*, primary skeleton; *s.fr.s.*, soft frontal surface; *sk.r.*, skeletal rod; *t.or.*, terminal orifice; *te.*, tentacle; *te.sh.*, tentacular sheath; *tr.w.*, transverse wall; *z.ep.*, zooidal epithelium.

superficial and unimportant, for the accessory aperture of the former represents only a late ontogenetic stage of skeletal development, and was not present in vigorously functioning zooids. The ascopore, on the other hand, is a permanent zoecial feature. Also, the presence of an ascopore implies the presence of an ascus (compensation sac), and there is no reason to believe that such structures existed in *P. stenostoma*. Morphology of the groups concerned suggests that the compensation sac is a specialized modification of a soft frontal surface that was evolved by cheilostomes of the sub-order Ascophora from a more simple condition now seen in the *Anasca*. Thus, there seems to be no justification for comparing anatomical arrangements in *P. stenostoma* with those of the Ascophora, but comparison with the *Anasca* reveals a number of points in common.

Some authors (e.g. Ulrich 1890, p. 333; Bassler 1911, p. 112) have regarded the Cryptostomata as Palaeozoic forerunners of later cheilostomatous bryozoans, and in *P. stenostoma* the architectural similarity is undoubtedly marked. The presence of erect branches with multiple rows of zooecia, box-like chambers and uncalcified parts of the frontal surface are strongly reminiscent of many anascan genera. But these features, and even the presence of an extrusion mechanism of anascan type, do not necessarily indicate a direct phylogenetic relationship with any part of the Cheilostomata. In a comparatively small group like the bryozoa the potential morphological range must be genetically limited, and in a vigorously developing stock the emergent pattern of diversity may already, at an early stage, have covered many of the available possibilities, including some which later reappeared as major themes. In the present case the precocious appearance of an anascan-like extrusion mechanism in *P. stenostoma* apparently exerted no significant influence on cryptostome evolution, and the order became extinct early in the Triassic. It was not until the mid-Cretaceous that anascan cheilostomes with a similar extrusion mechanism appeared, and the long interval devoid of a relevant fossil record presents a serious obstacle to suggestions that the Cheilostomata sprang from cryptostome ancestors. It is more likely, on both morphological and stratigraphic grounds, that early anascan cheilostomes developed from a ctenostome-like stock (Silen 1944). Nevertheless, though the possibility of a simple phylogenetic relationship can be discounted, the probable occurrence of an extrusion mechanism of anascan type in a late Palaeozoic fenestellid species suggests an interesting case of repetitive evolution where none was previously suspected.

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