

PALAEOCORYNID-TYPE APPENDAGES IN UPPER PALAEOZOIC FENESTELLID BRYOZOA

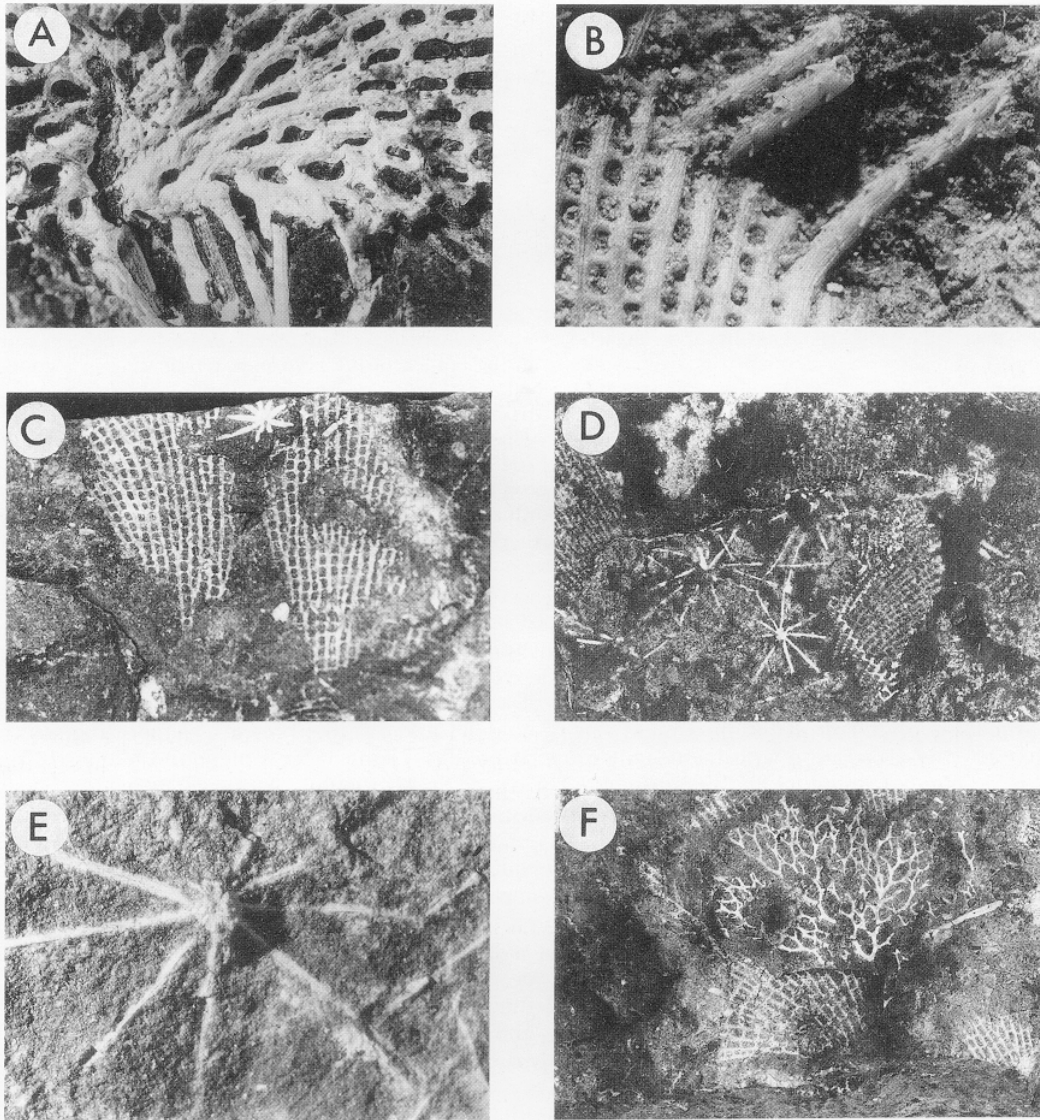
by ADRIAN J. BANCROFT

ABSTRACT. Palaeocorynid-type structures (Family Palaeocorynidae Duncan and Jenkins 1869), currently regarded as being of uncertain zoological affinities, are here interpreted as being a specialized form-appendage of Upper Palaeozoic fenestellid Bryozoa. Palaeocorynid-type appendages are morphologically complex, and consist of a short stem developed at right angles from the branch of the bryozoan, terminating in a cone-shaped body from whose lateral margins a variable number of long slender spines or branchlets emanate at high angles. Spines form simple, distally tapering structures; branchlets are much longer and repeatedly bifurcate, converge and fuse to develop an anastomosing reticulate meshwork. The external ornament and internal microstructure of these structures is identical and continuous with that of the branch of the bryozoan on which they occur. Up to five developments have been found *in situ* on a colony, occurring anywhere over the colony surface, and nearly all are developed from the obverse surface of branches. They are interpreted as having a defensive function, giving a protective covering to feeding autozoecial polypides beneath by providing a surface deterrent to predatory organisms.

CALCIFIED appendages are commonly developed on *Fenestella s.l.* and other fenestrate bryozoan genera from Upper Palaeozoic strata. They generally form slender, distally tapering, cylindrical, unbarbed, or barbed stem-like structures up to several centimetres in length, and can diverge from the lateral margins, obverse or reverse surface of branches in a colony (text-fig. 1A, B). They are particularly abundant in the proximal parts of colonies and are interpreted as supporting struts that acted in association with the heavily calcified holdfast (King 1850; Young and Young 1874; Vine 1879a, b; Cumings 1906; Ferguson 1963; Tavener-Smith 1969).

During ongoing revision of British Carboniferous fenestrate Bryozoa, large numbers of another type of structure occurring on *Fenestella s.l.* have been examined. Morphologically they consist of a short cylindrical stem, attached to the underside of a cone-shaped body from whose lateral margins a number of long slender spines or branchlets project. The base of the stem is directly connected at right angles to the branch of the bryozoan and they nearly always occur on the obverse surface of branches, being developed anywhere over the colony surface.

Although these curious and morphologically complex structures have been the subject of several detailed studies, their zoological affinities and functional significance have remained somewhat enigmatic. They were first described by Duncan and Jenkins (1869), who suggested that they were hollow and represented the trophosomes of a hydroid that attached itself to *Fenestella*. Duncan and Jenkins erected the genus *Palaeocoryne* with two species, within the new family Palaeocorynidae, which they classified within the Order Tubulariidae. In a subsequent paper, Duncan (1873) reiterated the zoological affinities of the Palaeocorynidae. Allman (1872) refuted Duncan and Jenkins's interpretation, and suggested that the group had foraminiferal affinities. Young and Young (1874) stated that the Palaeocorynidae were merely outgrowths of a bryozoan colony, and were solid structures directly connected to the skeletal tissues of the branch on which they occur. Vine (1879a, b) agreed with Young and Young's observations and suggested that these structures had a combined supportive and reproductive function. Barnes (1903) described the body and spines of two specimens of Palaeocorynidae, and assigned them to the phylum Polyzoa under the genus *Evactinopora* Meek and Worthen. Elias and Condra (1957) discarded evidence suggested by G. F. Papenfuss of a relationship between *Palaeocoryne* and the living red alga *Asparagopsis armata*, and regarded the structures as appendages of *Fenestella*. Ferguson (1961) erected the



TEXT-FIG. 1. A, B, morphology of stem-like appendages diverging from branches. A, BOM 25-09-238, *Fenestella plebeia* M'Coy (Visean), Halkyn, Clwyd, $\times 7.0$. B, BM(NH) PD.7794, *F. bicellulata* Etheridge Jun., Fifth Limestone (Asbian), Alston Group, Penruddock, near Penrith, Cumbria; showing occurrence of barbs on stems, $\times 16.0$. C-F, morphology of *in situ* palaeocorynid appendages. C, BH(NH) PD.7795, single spinose development on *F. multispinosa* Ulrich, shales in Upper Fell Top Limestone (Pendleian), Haltwhistle, Northumberland, $\times 2.9$. D, BM(NH) PD.2371, four spinose developments on *F. multispinosa* colony, Carboniferous (Visean), Halkyn, Clwyd, $\times 2.1$. E, detail of one development shown in D, $\times 8.6$. F, BM(NH) PD.2609, reticulate development on *F. plebeia*, Carboniferous, locality and horizon unknown, $\times 2.1$.

new palaeocorynid genus *Claviradix*, and concluded that the Palaeocorynidae were separate organisms from the host bryozoan, using it only as support, and in a following paper (1963) he stated that they probably had bryozoan affinities.

Since Ferguson (1963), no systematic studies have been undertaken on the Palaeocorynidae. The discovery of abundant, well-preserved fragmented and *in situ* material, including significantly larger and more complex developments than hitherto recognized has prompted the present work. This study incorporates a detailed re-examination of the morphology of palaeocorynid-type structures and reassessment of their zoological affinities and functional significance. External and internal details of morphology have been examined under the SEM. Cited material is located in the collections of Bolton Museum (abbreviated BOM) and the British Museum (Natural History), London (abbreviated BM(NH)).

MORPHOLOGY OF PALAEOCORYNID-TYPE STRUCTURES

External

Palaeocorynid-type structures almost exclusively occur on the obverse surface of branches, and may be developed anywhere over the colony surface. Their occurrence has been documented on the reverse surface of branches (Ferguson 1963, p. 156), and one example was found on the reverse side of a colony of *F. frutex* M'Coy during the course of the present study. Palaeocorynid-type developments have been found *in situ* on the obverse surface of the following taxa: *F. plebeia* M'Coy and *F. multispinosa* Ulrich. F. K. McKinney (pers. comm.) has reported their occurrence in the fenestellid genus *Archimedes* Hall.

Stems range between 0.50 mm and 1.80 mm in length, and may be barrel-shaped, expand distally, or be of uniform diameter (Pl. 65, figs. 1, 2, 4). They generally arise at right angles from branches, and their external ornament is continuous with that of the branch on which they occur (Pl. 65, figs. 3 and 4). The disposition, shape, and size of autozooeical apertures is usually not affected by the development of palaeocorynid-type structures (Pl. 65, fig. 4), except where buttress-like features are developed at their bases when apertural shape may be distorted (Pl. 65, fig. 1). These buttress-like structures were interpreted as root-like processes by Ferguson (1961), who established the palaeocorynid genus *Claviradix* on the basis of their occurrence, the taxon being distinguished from *Palaeocoryne* which apparently does not possess them. Stems are longitudinally striate, with a single row of closely spaced, small, pustules situated on ridges (Pl. 65, fig. 4).

In all the described species of *Claviradix* and *Palaeocoryne*, with one exception, stems are single cylindrical structures. The form *C. bifurcata* Ferguson (1961) is apparently unique in that the stem bifurcates. However, only one incomplete fragment of this taxon is known, of which only the bifid stem is preserved, and the recognition of this form as a palaeocorynid-type of development cannot be qualified.

The body of palaeocorynid-type developments varies significantly in shape and size, from small box-like structures, 0.20 mm in diameter, to large high-angle cones, 0.60 mm in diameter (Pl. 65, figs. 5-8). The centre of the bodies upper surface is most commonly depressed or flat, but is occasionally slightly elevated into a dome-like structure and may rarely be developed into a prominent spine up to 0.40 mm in length (Pl. 65, figs. 8-11). The external ornament of the body is continuous with that developed on the stem, with striae being radially arranged (Pl. 65, figs. 4, 7, 11).

Spines are regularly developed and geometrically arranged around the lateral margins of the body, and display considerable variation in their number, shape, and size. Between four and fifteen spines may be developed around the body, and they most commonly project slightly upwards away from it (Pl. 65, figs. 2, 4-6). Spines generally form long, straight, cylindrical, distally tapering structures and are longitudinally striate, their ornamentation being continuous with that of the stem and body (Pl. 65, figs. 4, 6, 7, 11). In all the described species of *Palaeocoryne* and *Claviradix*, spines are equally developed around the body (Pl. 65, figs. 6-9, 11). However, in several specimens recently discovered one spine is significantly more robust and appears to have been longer than

any of the others (Pl. 65, figs. 12 and 13). Spines range from 0.10 mm to 0.20 mm in diameter (measured at their proximal extremities), and the largest spine examined in the present study was 6.0 mm in length (an incomplete example) (text-fig. 1D, E).

Considerable morphological variation exists in the spinose developments occurring on *F. multispinosa* (incorrectly identified as *F. nodulosa* (Phillips) by Ferguson 1963); the number of spines ranges between seven and ten, and the open cone-shaped body ranges between 0.25 mm and 0.40 mm in diameter. While only one palaeocorynid development is usually found preserved on colonies of *F. multispinosa* examined, up to four may be present (text-fig. 1C, D). In one colony where four do occur, some of the spines from individual structures converge and overlap (text-fig. 1D).

Two species of *Claviradix* described by Ferguson (1963) are unusual in that each of the four spines developed from the body bifurcate, once in the case of *C. ashfellensis* and twice in *C. cruciformis*. However, several recently discovered colonies of *F. plebeia* M'Coy exhibit significantly larger and more complex developments of *C. cruciformis* than hitherto described. It is apparent that Ferguson (1963) had only examined incomplete specimens of this particular growth form developed on *F. plebeia* (incorrectly identified by Ferguson as *Parafenestella formosa* (M'Coy)). In these larger developments, individual spines, more appropriately termed branchlets, repeatedly bifurcate at high angles. Individual branchlets also converge and fuse, so that an anastomosing reticulate meshwork is developed around the body (text-figs. 1F, 2A-F, 4A). The largest recorded single development is 40 mm in diameter (measured on an incomplete structure). Extremely thin lateral offsets commonly diverge from branchlets at right angles and are of variable morphology. They may be straight bars that extend fully across the gap between adjacent branchlets or else form short barb-like structures projecting laterally into the gap (text-fig. 2C, E). Branchlets appear to taper distally and range between 0.15 mm and 0.27 mm in diameter (measured away from points of bifurcation and convergence), and are longitudinally striate with an oval cross-section (text-fig. 2F).

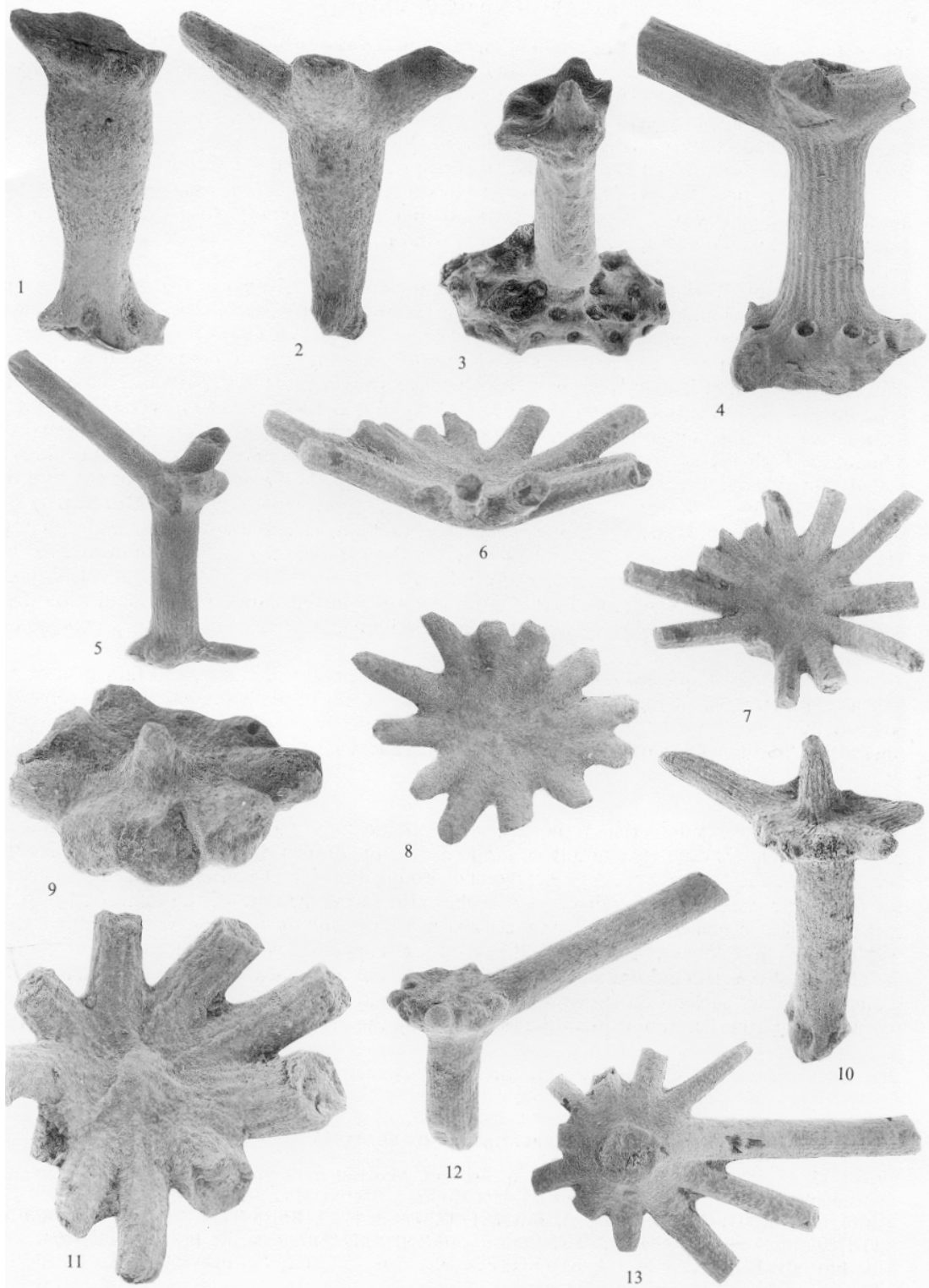
In one colony of *F. plebeia* five such developments are preserved *in situ*, and they overlap and appear to fuse irregularly together. The 'superstructure' is only partially preserved and is somewhat covered by matrix, but it possibly covered the entire obverse surface of the colony fragment (measuring 70 mm × 45 mm), and was developed parallel to it (text-fig. 4A).

Internal

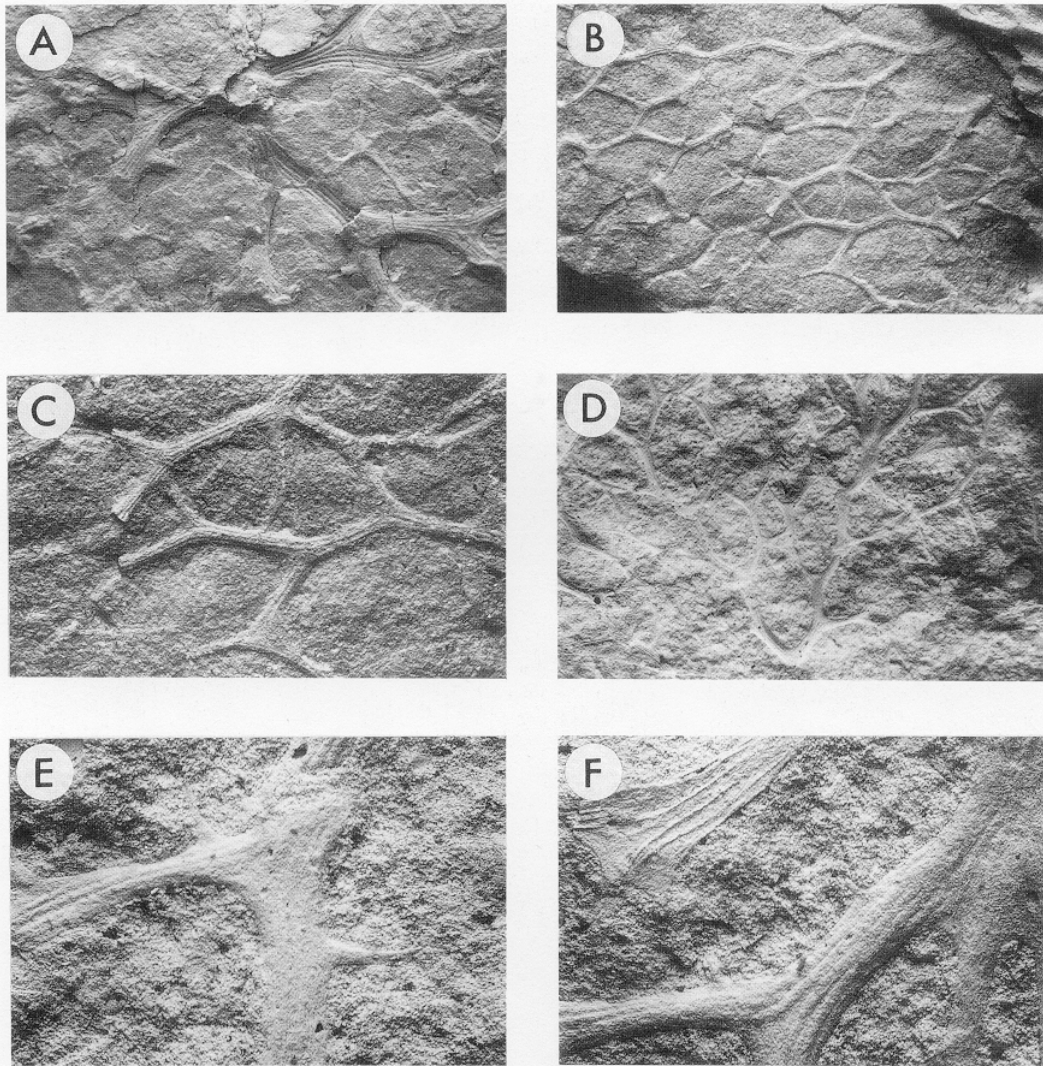
SEM investigations undertaken on the internal ultrastructure of palaeocorynid-type developments have shown that they are structurally continuous with the branch of the bryozoan on which they occur, as originally suggested by Young and Young (1874). The granular primary skeleton surrounding autozoecial chambers on branches also forms the core of the stem, body, spines, and branchlets of palaeocorynid structures (text-figs. 3A-F and 4B-D). This observation contrasts with those made by Elias and Condra (1957) and Ferguson (1963), who concluded that the granular (axial) core of the stem did not join that of the branch but terminated at the base of the stem. The granular primary skeleton in the stem, body, spines, and branchlets is surrounded by laminated secondary skeleton continuous with that surrounding the granular primary skeleton on branches

EXPLANATION OF PLATE 65

Figs. 1-13. Morphology of palaeocorynid appendages. Material from shales above the Main Limestone (Namurian, Pendleian), Hurst, North Yorkshire Moors. 1, BM(NH) PD.7796, × 30. 2, BM(NH) PD.7797, × 24. 3, BM(NH) PD.7798, × 24. 4, BM(NH) PD.7799, × 30. 5, BM(NH) PD.7800, × 21. 6, BM(NH) PD.7802, × 24. 7, BM(NH) PD.7802, × 18. 8, BM(NH) PD.7803, × 24. 9, BM(NH) PD.7804, × 42. 10, BM(NH) PD.7805, × 24. 11, BM(NH) PD.7806, × 48. 12, BM(NH) PD.7807, × 18. 13, BM(NH) PD.7808, × 21. All are SEM photographs.



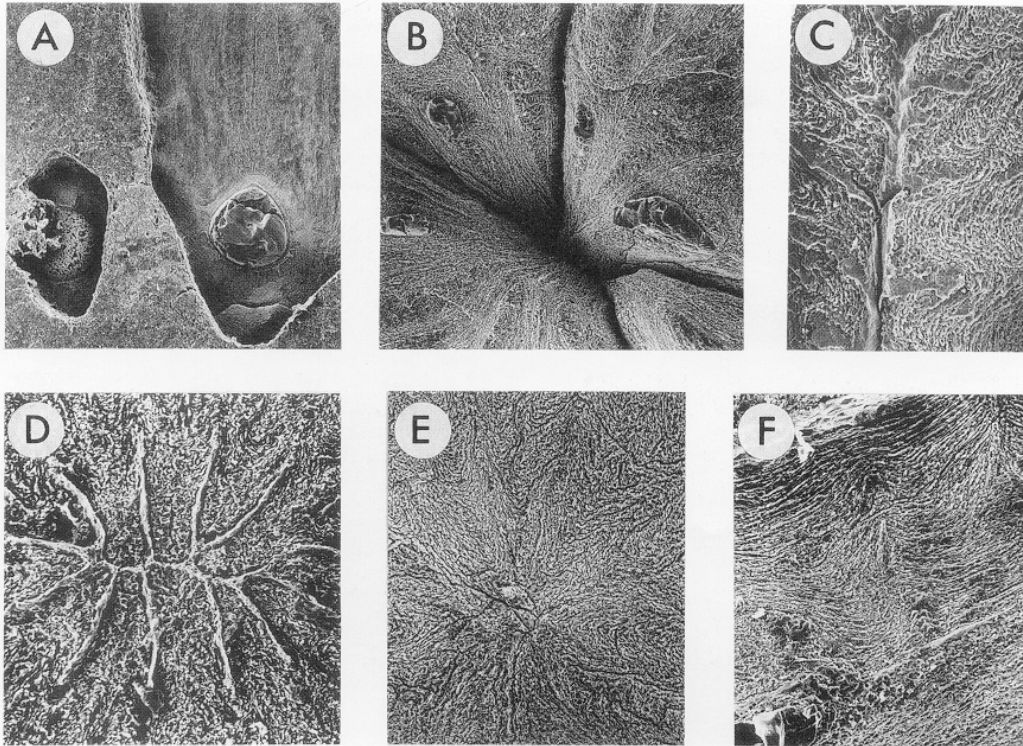
BANCROFT, palaeocorynid Bryozoa



TEXT-FIG. 2. A-F, morphology of reticulate palaeocorynid appendages on *Fenestella plebeia* M'Coy. A, BM(NH) PD.7809, Hardrow shales (Visean, Brigantian), Middle Limestone Group, Mill Gill, Askrigg, North Yorkshire; body of structure and proximal extremities of diverging branchlets with initial bifurcations, $\times 7$. B, C, BM(NH) PD.7810, Carboniferous, Cambeck, locality and horizon unknown. B, $\times 9$; C, detail of branchlets, $\times 19$. D-F, BM(NH) PD.2609, Carboniferous, locality and horizon unknown. D, proximal portion of structure, $\times 4.3$. E, curved barb-like structures developed from lateral margins of branchlets, $\times 42$. F, striated ornamentation of branchlets, $\times 32$. All are SEM photographs.

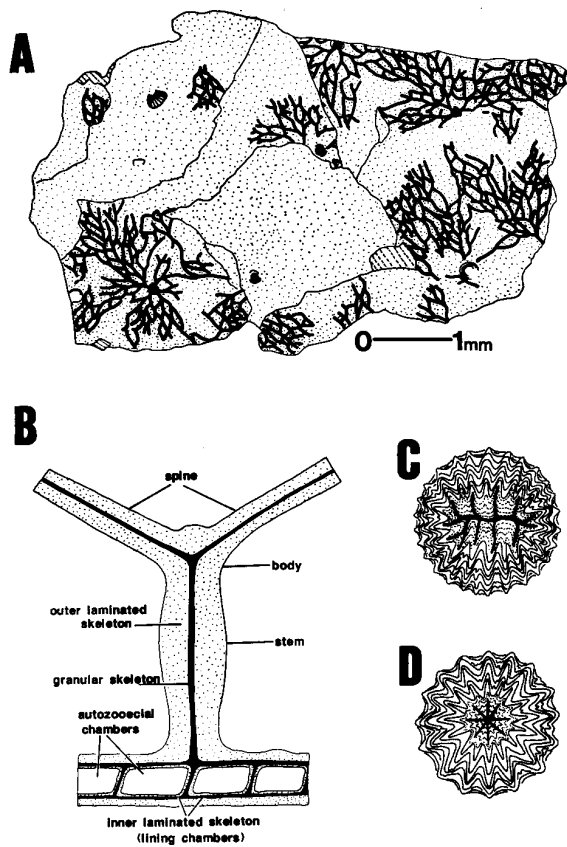
below (text-figs. 3A-D and 4B-D). Although Ferguson (1963) also observed this fact he suggested that the laminated skeleton of *Palaeocoryne* developed after that of the branch of *Fenestella* on which the structure occurs.

The granular core divides in the body of palaeocorynid structures, and the resultant cores



TEXT-FIG. 3. A-F, ultrastructure of palaeocorynid appendages; A, B, E, F of *Fenestella multispinosa* Ulrich and other spinose developments and C-D of reticulate developments in *F. plebeia* M'Coy. Material from shales above the Main Limestone (Namurian, Pendleian), Hurst, North Yorkshire Moors. A, BM(NH) PD.7811, continuation of laminated secondary skeleton around autozooeal chamber and proximal portion of development (right), transverse section through normal branch to left, $\times 90$. B, BM(NH) PD.7812, transverse section through body showing several granular cores diverging away from its centre, $\times 180$. C, BM(NH) PD.7813, slight oblique section of linear granular skeleton with lateral offsets in branchlet, $\times 420$. D, BM(NH) PD.7814, transverse section through stem showing linear arrangement of granular skeleton and zone of poorly defined laminated skeleton between ridges, $\times 300$. E, BM(NH) PD.7815, transverse section through stem showing stellate granular core and radiating stellate arrangement of surrounding laminated skeleton, $\times 360$. F, BM(NH) PD.7818, oblique section through spine, showing granular core (bottom left), granular ridge, and stylets in laminated skeleton, $\times 420$.

developed from the axial cores of spines and branchlets emanating from the lateral extremities of the body (text-figs. 3B and 4B). The morphology of the granular skeleton in the spinose developments of *F. multispinosa* and fragmented specimens of other spinose developments of unknown provenance, is significantly different from that of reticulate developments on *F. plebeia*. The morphology of the granular skeleton in transverse section in the stems and branchlets of *F. plebeia* has a linear structure and it possesses lateral offsets that may bifurcate (text-figs. 3C, D and 4C). The main axis of the granular skeleton in branchlets lies parallel to the plane of the development of the branchlets (text-fig. 4C). In *F. multispinosa*, and fragments of other spinose developments, the granular core in stems and spines has a stellate appearance in transverse section (text-figs. 3E and 4D), and is identical in most respects to the morphology of the granular skeleton in stem-like appendages and disseminants that interconnect branches in fenestellid colonies.



TEXT-FIG. 4. A, BM(NH) PD.7819, *Fenestella plebeia* M'Coy, Hardrow shales (Viséan, Brigantian), Mill Gill, Askrigg, North Yorkshire; showing the occurrence of five, possibly six, *in situ* reticulate palaeocorynid developments on one colony. Thick solid lines indicate location of branchlets, dashed lines indicate areas where obverse surface of colony is visible, and orientation of branches. Scale bar for size. B-D, ultrastructure of palaeocorynid appendages. B, longitudinal section through palaeocorynid development and branch of fenestellid showing arrangement of various skeletal elements, $\times 36$. C, D, transverse sections through stems of palaeocorynid developments. C, linear arrangement of granular skeleton in *F. plebeia* M'Coy, $\times 78$; D, stellate arrangement of granular skeleton in *F. multispinosa* Ulrich, $\times 78$.

The junction between the granular primary skeleton and the laminated secondary skeleton is well defined (text-fig. 3D). The morphology of the laminated secondary skeleton is variable, with no difference in morphology occurring between spinose and reticulate developments. Laminae within the inner portion of this unit are often poorly defined and pass gradually into an outer region where they become well defined (text-figs. 3D and 4C, D). The poorly laminated inner zone probably represents the additional granular layer recognized by Ferguson (1963) between the central granular core and the outer laminated skeleton. Ferguson (1963) distinguished the skeletal structure of *Palaeocoryne* and *Claviradix* from *Fenestella* on the presence of this additional granular layer, and used this feature to support his suggestion that palaeocorynid-type structures were separate organisms.

The laminated secondary skeleton is typically arranged in orally flexed ridges around the ridges of the granular skeleton, with additional ridges commonly developed in between, and has a well-defined radiating stellate appearance in transverse section (text-figs. 3D, E and 4C, D). Close to the outer surface, laminae forming the ridges are commonly arranged in closely spaced orally flexed nests (termed stylets), forming papillae or small pustules on the outer surface (text-fig. 3F; Pl. 65, fig. 11).

The granular core of spines and branchlets continues along their length in all the material examined, and has an identical stellate or linear appearance to that developed on stems, with the

granular core and ridges appearing to thin distally (text-fig. 4B). No bifurcations have been observed in the lateral offsets of the granular skeleton in branchlets (text-fig. 3C).

ZOOLOGICAL AFFINITIES

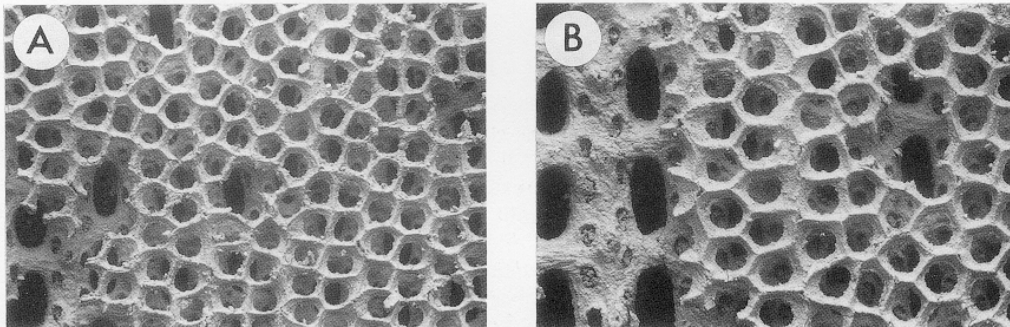
The preceding morphological assessment of palaeocorynid-type structures unequivocally proves that they are not a distinct group of organisms which were parasitic on fenestellid bryozoans, as suggested by some previous workers (Duncan and Jenkins 1869; Duncan 1873; Ferguson 1961, 1963), nor are they of algal origin (Elias and Condra 1957). The fact that their external ornament and internal microstructure is continuous with that of the bryozoan on which they occur proves that palaeocorynid-type developments are merely a form of appendage. In accordance with this conclusion, the generic and specific names applied to individual morphotypes by Duncan and Jenkins (1869), Duncan (1873), and Ferguson (1961, 1963) should perhaps best be regarded as invalid.

Skeletal secretion in fenestrate bryozoans is inferred to have been undertaken by an external epithelial tissue common to the whole colony, comparable to that of some living Bryozoa (Elias and Condra 1957; Tavener-Smith 1969; Gautier 1973). Accordingly, palaeocorynid-type appendages must have been secreted by an epithelium continuous with that covering the rest of the colony.

FUNCTIONAL SIGNIFICANCE

The diverse and complex morphology of palaeocorynid-type appendages, coupled with the fact that they may occur anywhere over the colony surface, suggests that they did not have a supportive function, akin to that interpreted for unbarbed or barbed long stem-like appendages commonly present in the proximal parts of fenestellid colonies.

The discovery of large, anastomosing reticulate meshworks on *F. plebeia* is particularly interesting, and is reminiscent of superstructures developed above the obverse surface of colonies in certain other fenestellid genera, such as *Cyclopelta* Bornemann, *Unitrypa* Hall, and *Hemitrypa* Phillips. These three genera possess colony-wide superstructures that are developed as outgrowths of carinal nodes or the median carina on the obverse surface of branches. *Hemitrypa* possesses the most complex type of superstructure that is developed as geometrically arranged lateral bar-like outgrowths of the crests of elongate carinal nodes, and forms an intricate interlocking, perforate, hexagonal latticework situated at a uniform distance above the main reticulate meshwork below (text-fig. 5A, B). The superstructure in *Hemitrypa* is interpreted to have acted as a protective screen



TEXT-FIG. 5. A, B, *Hemitrypa hibernica* M'Coy. BM(NH) PD.6642, High Glencar Limestone (Viscan, Asbian), Carrick Lough, County Fermanagh, Northern Ireland. Silicified colony fragment with the superstructure *in situ*. A, with almost the entire superstructure intact, $\times 26$. B, showing an area where the superstructure is broken away revealing the obverse surface of the main meshwork below, $\times 26$.

for feeding autozooeical polypides functioning between the branch surface and the superstructure, by providing a surface deterrent to predatory organisms (Tavener-Smith 1973; Bancroft 1986). Such a function may also be inferred for other fenestellid taxa (e.g. *Cyclopelta*) with different and less intricate superstructures, in which the superstructure consists of a vertical extension of the median carina that bifurcates into two lateral wedges at a uniform distance above the meshwork (see McKinney and Kriz 1986).

The reticulate meshworks preserved on *F. plebeia* appear to have covered a relatively large area of the colony surface, and in one large colony fragment where five such developments occur, they may have completely covered it. These facts possibly suggest that these structures had a function analogous to that inferred for the superstructure in *Hemitrypa*. The radiating spine-like structures observed on *F. multispinosa* may also have had a comparable function. Although only one development is usually found on colonies, up to four have been observed (text-fig. 1D).

Although palaeocorynid-type appendages have only been found *in situ* on the obverse surface of two fenestellid taxa, the variety of morphotypes found in fragmented specimens examined that cannot be attributed to either *F. multispinosa* or *F. plebeia* suggests their occurrence in several other taxa. The presence of a palaeocorynid development on the reverse surface of *F. frutex* suggests that this taxon was capable of growing such appendages, but its occurrence on the reverse surface of branches cannot be explained other than as a growth enigma in the light of the preceding discussion.

The rare *in situ* occurrence of palaeocorynid-type appendages, and their apparent intracolony sparsity in taxa known to possess them, is possibly accounted for by their low preservation potential as they are delicate structures. Abundant fragments of spines, bodies, and branchlets have been found at several horizons in association with fenestellid bryozoans, with none being found *in situ*. Their disposition is such that they would have readily broken away on the death of the colony and its subsequent post-mortem fragmentation.

However, the occurrence of palaeocorynid-type appendages does appear to be spatially and temporally intermittent, and at many horizons where fenestellids are abundant (including *F. multispinosa* and *F. plebeia*), no fragments of palaeocorynid developments have been found. Laboratory experiments on the living cheilostome bryozoan *Membranipora membranacea* have shown that colonies exposed to direct predation by slow feeding nudibranch molluscs have the ability to grow protective chitinous and membranous spines around autozooeia to defend them from attack (Harvell 1984). These spines grow rapidly, during the course of predation, and are fully developed within a day or two. They serve to control effectively the pattern of predation, reduce the extent of intracolony mortality and to slow down significantly the rate of predation. The development of palaeocorynid-type appendages in fenestellid bryozoans may also have been predator-induced, their spatial and temporally intermittent occurrence reflecting that of possible molluscan predators.

CONCLUSIONS

1. The external ornament and internal microstructure of palaeocorynid-type structures developed on *Fenestella s.l.* is continuous with that of the branch of the bryozoan colony on which they occur.
2. Palaeocorynid-type structures are almost exclusively developed on the obverse surface of branches and may occur anywhere over the colony surface.
3. They are a specialized form of appendage, and possibly had a defensive function, in that the extensive array of spines or branchlets developed laterally from the distal extremity of stems served to give a protective covering to feeding autozooeical polypides beneath, by providing a surface deterrent to predatory organisms.

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REFERENCES

- ALLMAN, G. J. 1872. A monograph of Gymnoblasic or Tubularian hydroids. Part II. *R. Soc. Publ.* **47**, 155-450.
- BANCROFT, A. J. 1986. Revision of the Carboniferous fenestrate bryozoan *Hemitrypa hibernica* M'Coy. *Ir. J. earth Sci.* **7**, 111-124.
- BARNES, J. 1903. On a fossil Polyzoa from the Mountain Limestone District, Castleton. *Manchr geol. Min. Soc. Trans.* **28**, 243-245.
- CUMINGS, E. R. 1906. Description of the Bryozoa of the Salem Limestone of Southern Indiana. *Ann. Rept. Dept. Geol. nat. Res., Indiana*, **30**, 1274-1296.
- DUNCAN, P. M. 1873. On the genus *Palaecoryne*, Duncan and Jenkins, and its affinities. *Q. Jl geol. Soc. Lond.* **29**, 412-417.
- and JENKINS, H. M. 1869. On *Palaecoryne*, a genus of Tubularine Hydrozoa from the Carboniferous Formation. *Phil. Trans. R. Soc.* **159**, 693-699.
- ELIAS, M. K. and CONDRA, G. E. 1957. *Fenestella* from the Permian of West Texas. *Mem. geol. Soc. Am.* **70**, 1-158.
- FERGUSON, J. 1961. *Claviradix*, a new genus of the Family Palaecorynidae from the Carboniferous rocks of County Durham. *Proc. Yorks. geol. Soc.* **33**, 135-148.
- 1963. British Carboniferous Palaecorynidae. *Trans. nat. Hist. Soc. Northumb.* **14**, 141-162.
- GAUTIER, T. 1973. Growth in bryozoans of the Order Fenestrata. In LARWOOD, G. P. (ed.). *Living and Fossil Bryozoa*, 271-274. Academic Press, London.
- HARVELL, C. D. 1984. Predator-induced defense in a marine Bryozoan. *Science, NY*, **224**, 1357-1359.
- KING, W. 1850. A monograph of the Permian fossils of England. *Palaeontogr. Soc. [Monogr.]*, 258 pp.
- MCKINNEY, F. K. and KRIZ, J. 1986. Lower Devonian Fenestrata (Bryozoa) of the Prague Basin, Barrandian Area, Bohemia, Czechoslovakia. *Fieldiana Geol.* **15**, 1-90.
- TAVENER-SMITH, R. 1969. Skeletal ultrastructure and growth in the Fenestellidae. *Palaeontology*, **12**, 281-309.
- 1973. Fenestrate Bryozoa from the Viséan of County Fermanagh, Ireland. *Bull. Br. Mus. nat. Hist. (Geol.)*, **23**, 389-493.
- VINE, G. R. 1879a. Physiological character of *Fenestella*. *Sci. Gossip.* **15**, 50-54.
- 1879b. On *Palaecoryne*, and the development of *Fenestella*. *Ibid.* 225-229, 247-249.
- YOUNG, J. and YOUNG, J. 1874. On *Palaecoryne* and other polyzoal appendages. *Q. Jl geol. Soc. Lond.* **30**, 684-687.

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