

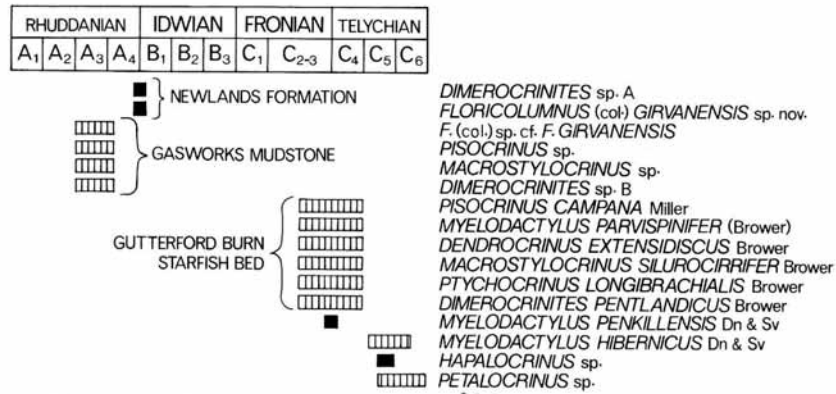
AN UNUSUAL CRINOID COLUMNAL MORPHOSPECIES FROM THE LLANDOVERY OF SCOTLAND AND WALES

by STEPHEN K. DONOVAN and NEIL D. L. CLARK

ABSTRACT. Distinctive crinoid columns with pentastellate to serrate circular nodal epifacets are probably derived from rhodocrinitid diplobathrid camerates and are placed in the morphogenus *Floricolumnus* (col.) gen. nov., which is only known from the Lower Llandovery of the British Isles. The type species, *F. (col.) girvanensis* sp. nov., is known only from the Newlands Formation of the Girvan district (late A₄ to early B₁). Nodals of this species are inflated; epifacet 'rays' are simple, bifid or multilobate; the column is strongly heteromorphic. *F. (col.)* sp. cf. *F. (col.) girvanensis* is from the Gasworks Mudstone of Dyfed (A₃ to early A₄). The presence of this genus in both the North American and South European faunal provinces is compatible with the cosmopolitan distribution of Late Ordovician and Silurian crinoids previously recognized on the basis of complete specimens.

THE Llandovery crinoid fauna is poorly known. For example, only one faunule of this age has been described from the British Isles (Brower 1975). In particular, Lower Llandovery crinoid faunas are rare and only two have, as yet, been documented, from the Cataract Group of Ontario (Eckert 1984) and the Brassfield Formation of Ohio (Ausich 1984a, 1984b, 1985, 1986a, 1986b, 1986c, 1987; Ausich and Dravage 1988). However, there are two British formations from low in the Llandovery which have produced small, but significant, crinoid faunules (Ramsbottom 1954; Text-fig. 1). The Gasworks Mudstone of the Haverfordwest area, Dyfed, of mid Rhuddanian age (A₃ to early A₄; Cocks *et al.* 1971, fig. 2), has yielded three crinoid taxa: *Pisocrinus* sp. (Family Pisocrinidae); *Macrostylocrinus* sp. (family Patelloocrinidae); and *Dimerocrinites* sp. (family Dimerocrinitidae). A further species of *Dimerocrinites* is known from the Newlands Formation of the Girvan district, Strathclyde, which is of Rhuddanian/Idwian boundary age (late A₄ to early B₁; Cocks *et al.* 1971, fig. 2). The Gasworks Mudstone taxa all represent earliest known appearances of their respective families in the British Isles south of the Iapetus Suture. The presence of *Dimerocrinites* at both localities further suggests a possible similarity of the crinoid taxa, at least at the generic level, in the North American and South European faunal provinces in the Lower Llandovery. This is similar to the pattern seen in the Upper Ordovician before the late Ordovician extinctions (Donovan 1989a, table 1), when 100% of crinoid families and 75% of genera occurred in both provinces. Of the taxa known from the Gasworks Mudstone, patelloocrinids and dimerocrinitids are both known from the Cataract Group and the Brassfield Formation, the latter also including a species of pisocrinid (Donovan 1989a, fig. 2). This distribution suggests that, by the Lower Llandovery, the crinoid faunas of the North American and South European faunal provinces may have been nearly cosmopolitan, at least at the family level (but also see comments on Silurian crinoid distributions in Holland 1971, pp. 70–71).

A further crinoid taxon common to both the Gasworks Mudstone and the Newlands Formation has been recognized on the basis of large and distinctive columnals, probably derived from rhodocrinitid camerates. Ramsbottom (1954, p. 264) considered these two occurrences to be conspecific, a deduction with which we broadly concur, although the Gasworks Mudstones specimens are few. We have therefore been cautious in comparing the columnals from the two localities.



TEXT-FIG. 1. Stratigraphic distribution of Llandovery crinoids from the British Isles (based on data derived from Ramsbottom 1954; Brower 1975; Donovan and Sevastopulo 1989). Stratigraphic ranges indicated as closed boxes (species known from a short, well-defined interval) or ruled boxes (species whose range is less precisely known).

Crinoid terminology used herein follows Moore *et al.* (1968), Webster (1974) and Ubaghs (1978). The use of (col.) to denote a columnal morphogenus follows Stukalina (1967).

SYSTEMATIC PALAEOLOGY

Class CRINOIDEA J. S. Miller, 1821
 Subclass CAMERATA Wachsmuth and Springer, 1885
 Order DIPLOBATHRIDA Moore and Laudon, 1943
 ?Family RHODOCRINITIDAE Roemer, 1855 *sensu* Kolata, 1982
 Genus *FLORICOLUMNUS* (col.) gen. nov.

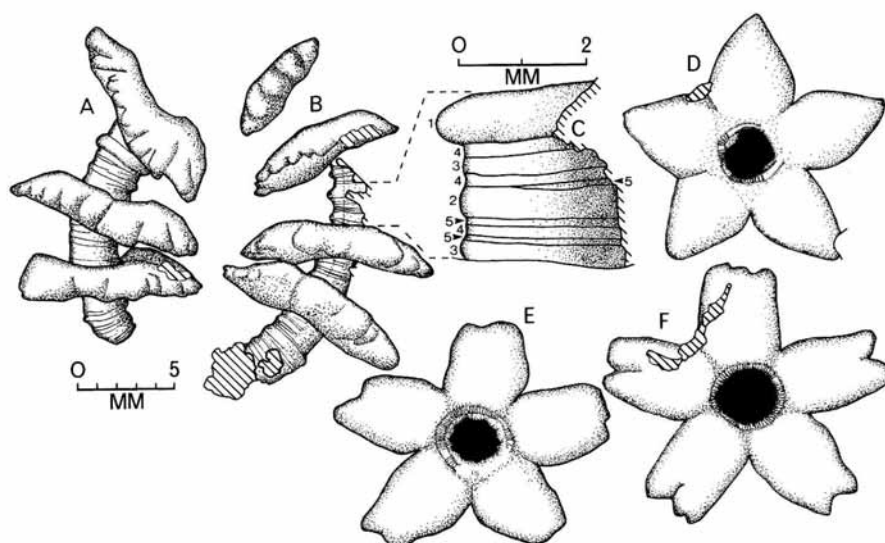
Derivation of name. From the Latin *floris*, blossom and *columna*, column.

Type species. *Floricolumnus* (col.) *girvanensis* sp. nov.

Other species. *F.* (col.) sp. cf. *F.* (col.) *girvanensis* nov.

Diagnosis. A morphogenus of crinoid columnal with broad nodal columnals of pentastellate to serrated circular outline. The 'rays' of the epifacet may have pointed, blunt, bifid or multilobate tips. Epifacet swollen. Lumen central, pentagonal to circular in outline and surrounded by a narrow crenularium of short, unbranched crenulae. Crenularium depressed in nodals. Internodals lack an epifacet.

Remarks. These columnals show a typical rhodocrinitid-type geometry, such as is seen in *Balacrinus* Ramsbottom and *Trochocrinites* Portlock (Donovan 1986). The lumen is central, broad with respect to facet diameter and rounded pentagonal to circular in outline; it is surrounded by a narrow crenularium of unbranched crenulae; a broad, smooth epifacet is developed; and the column is strongly heteromorphic. The nodal outline is particularly distinctive and sets *Floricolumnus* (col.) apart from other rhodocrinitids, which generally have columnals with a pentagonal or circular outline.



TEXT-FIG. 2. *Floricolumnus* (col.) *girvanensis* gen. et sp. nov. A-C, holotype. A, BMNH E49740a, lateral view of pluricolossal. B-C, BMNH E49740b; B, lateral view of pluricolossal; C, enlargement of part of a noditaxis, with internodal orders numbered. D-F, articular facets of paratype nodals, D, BMNH E49741a. E-F, BMNH E49739b and a, respectively (counterparts). All figures are camera lucida drawings of latex casts; all, except C, at the same scale.

Floricolumnus (col.) *girvanensis* sp. nov.

Plate 1, figs 1-2, 5-6; Text-figs 2-4

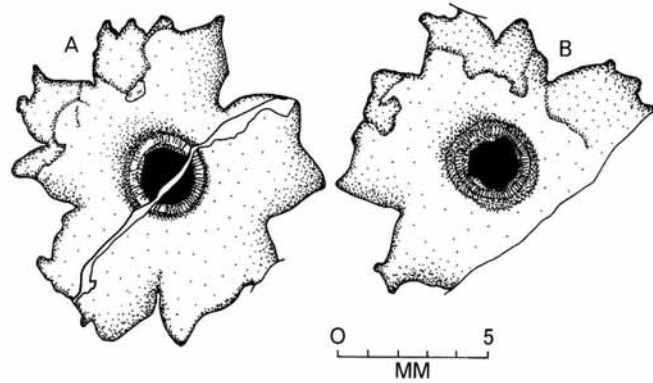
1954 Peculiar crinoid stem (in part); Ramsbottom, p. 264, pl. 12, figs 10-13.

Derivation of trivial name. After Girvan.

Type material, locality and horizon. Holotype, British Museum (Natural History) (BMNH) E49740a-b (counterpart external moulds: Pl. 1, fig. 6; Text-fig. 2A-C); paratypes, BMNH E49739a-b, E49741a-b, Hunterian Museum (HM) E3265/1-5, E3266/1-5, E3481/1-10, E3482/1-23, E3530, E3553/1, E3554-E3556, E3564-E3566, E3643, E3645/1-3, E6062a-b, E6063a-b, E6064a, E6065-E6069, E6071a-b, E6072 (all external moulds with or without counterparts). All specimens are from the Newlands Formation (Llandovery, Rhuddanian/Idwian boundary, late A₁ to early B₁; Cocks *et al.* 1971, fig. 2) of the Girvan district, Strathclyde, Scotland (Cocks and Toghil 1973, pp. 215, 216). It is probable that all specimens come from the type locality, a 'small N-S sandstone ridge on the E side of a small stream 150 m due E of Newlands Farm' (Howells 1982, p. 4), near Dailly, about 11 km ENE of Girvan, Strathclyde, Scotland, GR NS 2775 0434. Howells (1982) considered this locality to be of *Monograptus gregarius* Biozone age (= B₁ to early B₂).

Diagnosis. As for the genus.

Description. Nodals: pentastellate to circular crenulate columnals with a central lumen of pentagonal or circular outline. Lumen surrounded by a conical claustrum (Text-fig. 2E), of pentagonal, circular or crenulate pentagonal outline, which is often partly or completely obscured by sediment. The claustrum of HM E3566 appears to be pentameric, although the epifacet shows no evidence of merism. Claustrum surrounded by a narrow articular facet, of circular or pentagonal outline (Pl. 1, figs 1-2; Text-figs 2D-F, 3-4), comprising



TEXT-FIG. 3. *Floricolumnus* (col.) *girvanensis* gen. et sp. nov. A–B, HM E6062a and b respectively, paratype (counterparts); camera lucida drawings from latex casts.

numerous short, unbranched, fine, radial crenulae. The articular facet is usually conical and continuous with the claustrum (Text-fig. 2E). Where the facet appears to be parallel to the plane of the columnal, it is apparently due to the presence of a low internodal (or internodals) that is still articulated with the nodal (for example, Pl. 1, fig. 2; Text-figs 2F, 4B). Epifacet broad, pentastellate to serrated circular in outline, unsculptured and inflated, so that the crenularium always lies within a depression. The 'rays' of the epifacet vary from being pointed (Pl. 1, fig. 1; Text-fig. 2D) through bifid (Pl. 1, figs 2, ?5; Text-figs 2E–F, 4A) to multilobate (Pl. 1, fig. 6; Text-figs 2A–B, 3, 4B). 'Ray' form is highly variable, but is broadly consistent within any columnal. The outline of the epifacet is often asymmetrical. 'Rays' may be in close contact (Pl. 1, figs 1–2, 6; Text-figs 2–3, 4B) or separated (Pl. 1, fig. 5; Text-fig. 4A). The surface of some epifacets is uneven and coarsely laminar, possibly suggesting secretion of a new stereom layer (Text-fig. 4B).

Internodals: column heteromorphic, with up to five orders of internodals developed and regularly intercalated (Text-fig. 2C). Priminternodals are highest *et seq.* Prim-, secund- and tertinternodals have decreasingly convex latera, while quart- and quintinternodals have planar latera. Articulation is symplectial. An ideal noditaxis of this column would comprise N5453545254535451545354525453545 (notation follows Webster 1974), but is not clearly seen in the available specimens; part of one of the most complete noditaxes from the holotype is illustrated (Text-fig. 2C). HM E3481/10 is poorly preserved, but at least five orders of internodal appear to be regularly intercalated. Columnals are wedge-shaped in the early stages of intercalation (Text-fig. 2C, quintinternodal in middle of figure). The column was obviously highly flexible, as is indicated by the strong curvature of the holotype (Pl. 1, fig. 6; Text-fig. 2A–B). A claustrum is present in the internodals of some pluricolumnals.

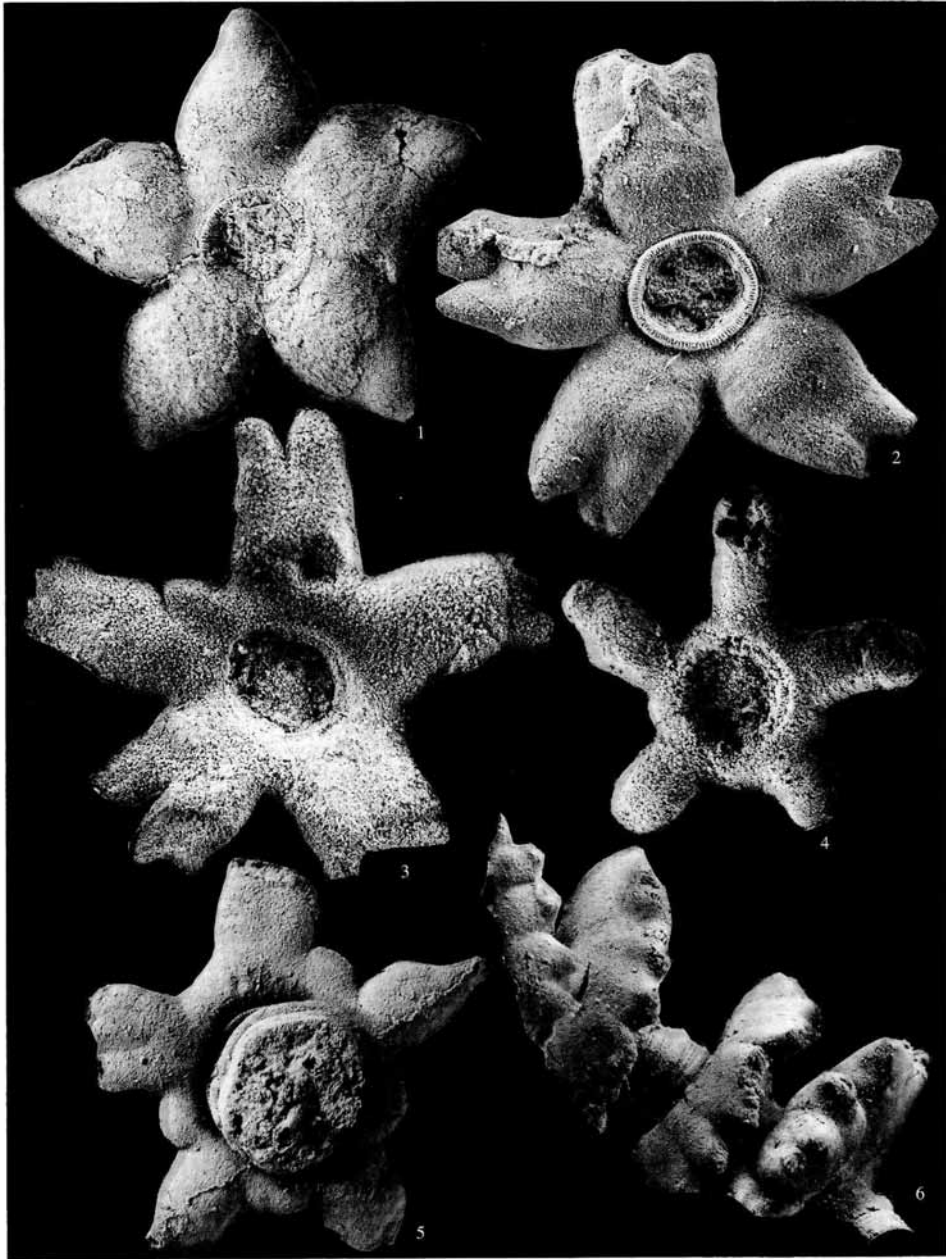
Dimensions. Columnal diameter (KD), articular facet diameter (FD) and lumen diameter (LD) were measured, where possible, from all of the available nodals (measurement of KD followed Moore *et al.* 1968, fig. 5G; lumen diameter includes the width of the claustrum). Graphs of KD/FD and FD/LD (Text-fig. 5) showed close correlations between these parameters at the 99% confidence level.

EXPLANATION OF PLATE I

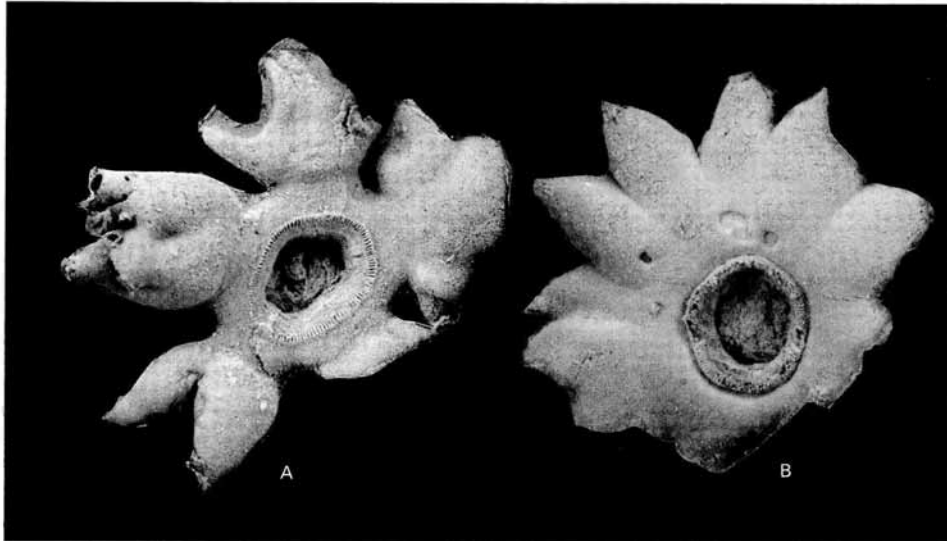
Figs 1–2, 5–6. *Floricolumnus* (col.) *girvanensis* gen. et sp. nov. 1, BMNH E49741a, paratype, $\times 5$. 2, BMNH E49739a, paratype, $\times 5$. 5, HM E6063a, paratype, $\times 5$. 6, BMNH E49740b, holotype, lateral view of pluricolumnal, $\times 4.5$.

Figs 3–4. *Floricolumnus* (col.) sp. cf. *F.* (col.) *girvanensis* gen. et sp. nov. 3, SM A32132, $\times 5$. 4, SM A32131, $\times 4.5$.

All figures illustrate latex casts of natural moulds whitened with ammonium chloride sublimate. All except figure 6 show articular facets (with or without articulated internodals) of nodal columnals.



DONOVAN and CLARK, *Floricolumnus*



TEXT-FIG. 4. *Floricolumnus* (col.) *girvanensis* gen. et sp. nov., paratypes. A, HM E3265/1. B, HM E3482/15. Both figures illustrate latex casts from natural moulds whitened with ammonium chloride. Both $\times 5$.

Floricolumnus (col.) sp. cf. *Floricolumnus* (col.) *girvanensis* sp. nov.

Plate 1, figs 3–4; Text-fig. 6

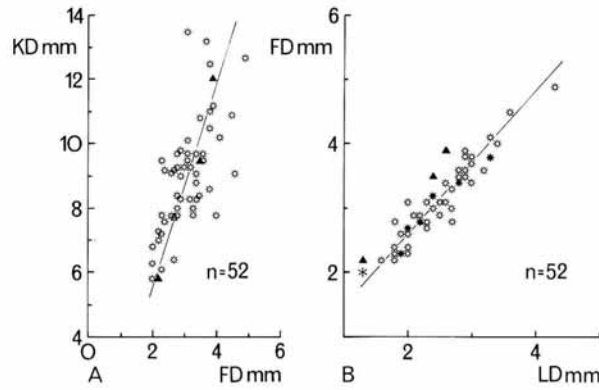
1954 Peculiar crinoid stem (in part); Ramsbottom, p. 264.

Material, locality and horizon. Three specimens, Sedgwick Museum (SM) A32131–A32133, all external moulds without counterparts. All specimens are from the Gasworks Mudstone of Dyfed, southwest Wales (Lower Llandovery, Rhuddanian, A_3 to early A_4 ; Cocks *et al.* 1971, fig. 2), from near the gasworks, Haverfordwest, opposite the entrance to the quay, NGR SM 9585 1540.

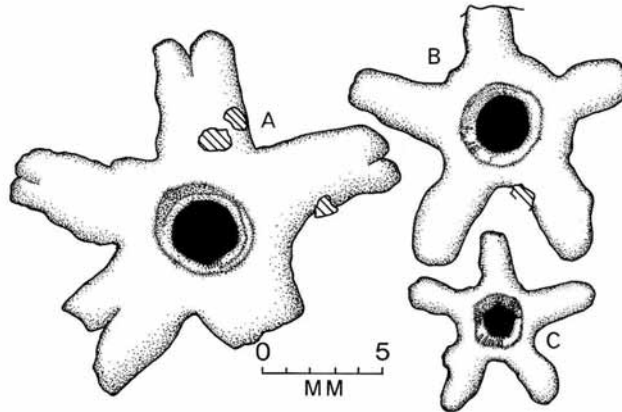
Description. Only known from pentastellate nodal columnals with a central, pentagonal to circular lumen (Pl. 1, figs 3–4; Text-fig. 6). Where the lumen is pentagonal, the lumen angles are rounded. The lumen is surrounded by a crenularium composed of short, fine, unbranched crenulae. The crenularium occurs within a conical depression, with or without a flattened platform adjacent to the lumen. The articular facet is surrounded by a broad, smooth and unsculptured epifacet of pentastellate outline. The 'rays' of the epifacet are blunt and well-rounded, dividing into a pair of blunt projections in the largest columnal (Pl. 1, fig. 3; Text-fig. 6A).

Measurements. These data have been plotted on Text-fig. 5 for comparison with the Girvan specimens. Note that, although the KD/FD data agree well, the FD/LD points consistently plot well to the left of the regression line for *F.* (col.) *girvanensis* s.s.

Discussion. A broad diversity of nodal geometries has been included in *Floricolumnus* (col.) *girvanensis*, but the variation shown is not outside the range of morphologies that might be expected within a single species. It is well known that the majority of crinoid columns show changes in morphology along their length (Moore *et al.* 1968; Ubags 1978; for specific examples, see Donovan 1984; Donovan *et al.* 1986). The range of nodal morphologies in *F.* (col.) *girvanensis* is from strongly pentastellate columnals with elongate 'rays' (Pl. 1, fig. 2), through ossicles with



TEXT-FIG. 5. A, plot of columnal diameter (KD) versus articular facet diameter (FD), and B, plot of FD versus lumen diameter (LD) in *Floricolumnus* (col.) *girvanensis* gen. et sp. nov., based on measurements taken from the type specimens. Where the specimens are deformed, original diameters were estimated. Open star = one specimen, closed star = two specimens, asterisk = three specimens. Regression lines are plotted ($FD = 0.31 + 0.31 KD$; $LD = 0.89 FD - 0.29$). Data for *F.* (col.) sp. cf. *F.* (col.) *girvanensis* are plotted as closed triangles.



TEXT-FIG. 6. *Floricolumnus* (col.) sp. cf. *F.* (col.) *girvanensis* gen. et sp. nov. A, SM A32132. B, SM A32131. C, SM A32133. All figures are camera lucida drawings from latex casts.

broader rays (Pl. 1, fig. 1; Text-fig. 4A), to columnals where the 'rays' are so expanded that the ossicles have become near-circular with a serrated outline (Pl. 1, fig. 6; Text-figs 2A-B, 4B). This progression most logically represents the change in columnal geometry from the proximal to the distal regions of the stem, as it is more likely that calcite would have been secreted, rather than absorbed, to alter the outline of the ossicles. At least some nodals have a coarsely laminar appearance, suggesting secretion of an outer calcitic layer.

This interpretation of column morphology begs two questions: what were the functions of these

unusual nodals, and why was it necessary to change their outline down the length of the stem? Three interpretations are possible and each may have made some contribution to the function of the column: protection from predation; improved hydrodynamic lift; and attachment to the substrate. The nodals are always 'spinose', whether pentastellate or serrated, and may have acted to deter predators. However, none of the columnals shows undoubted signs that they may have been regenerating following unsuccessful predation and it is doubted if a crinoid column would have been particularly nutritious, unless the axial canal contained tissues not found in modern stalked crinoids (cf. Jefferies 1968, fig. 5). This is at least possible, as the axial canal of *F. (col.) girvanensis* is broader than that of any extant crinoid, although the function of these tissues is problematic (they are unlikely to have been muscular: Donovan 1989b).

Perhaps more probably, the broad epifacets may have been an aid to hydrodynamic lift to help raise the crown above the substrate (cf. the kite paradigm of Breimer and Webster 1975). Riddle (1989) has recently demonstrated how an unusual column geometry could influence the behaviour of water currents close to a crinoid and, by analogy, it may have been that broad epifacets were an aid to generating lift. However, the more rounded columnals which we interpret as being distal would probably have performed this function more efficiently than the proximal(?) pentastellate columnals.

Attachment of the distal column is the most probable principal function of these serrated and pentastellate nodals. It is a general observation that, although rhodocrinitid columnals are often very common locally (for example, *Balacrinus basalis* (McCoy) in the Onny Valley, Shropshire; Donovan 1986, p. 48), obvious attachment structures are absent. This may indicate that attachment was by a form of non-cirriiferous runner (analogous to cirriiferous runners: Brett 1981) which relied upon frictional contact to help the crinoid maintain its station. Broad epifacets normal to the axis of the column would have acted as a series of drag anchors to prevent the crinoid being transported by a current, enabling the orientation of the crown to change in response to alterations in current direction (the presence of numerous low columnals would have made the column particularly flexible; Text-fig. 2A–B). The serrated distal epifacets of *F. (col.) girvanensis* may have helped the stem to cut down into the underlying sediment and thus gain a particularly good purchase.

Acknowledgements. We thank David Lewis (BMNH) and David Price (SM) for providing latex casts of specimens in their care.

REFERENCES

- AUSICH, W. I. 1984a. Calceocrinids from the Early Silurian (Llandoveryan) Brassfield Formation of southwestern Ohio. *Journal of Paleontology*, **58**, 1167–1185.
- 1984b. The genus *Clidochirus* from the Early Silurian of Ohio (Crinoidea: Llandoveryan). *Journal of Paleontology*, **58**, 1341–1346.
- 1985. New crinoids and revision of the Superfamily Glyptocrinacea (Early Silurian, Ohio). *Journal of Paleontology*, **59**, 793–808.
- 1986a. Early Silurian rhodocrinitacean crinoids (Brassfield Formation, Ohio). *Journal of Paleontology*, **60**, 84–106.
- 1986b. Early Silurian inadunate crinoids (Brassfield Formation, Ohio). *Journal of Paleontology*, **60**, 719–735.
- 1986c. New camerate crinoids of the Suborder Glyptocrinina from the Lower Silurian Brassfield Formation (southwestern Ohio). *Journal of Paleontology*, **60**, 887–897.
- 1987. Brassfield Compsocrinina (Lower Silurian crinoids) from Ohio. *Journal of Paleontology*, **61**, 552–562.
- and DRAVAGE, P. 1988. Crinoids from the Brassfield Formation of Adams County, Ohio. *Journal of Paleontology*, **62**, 285–289.
- BREIMER, A. and WEBSTER, G. D. 1975. A further contribution to the paleoecology of fossil stalked crinoids. *Proceedings. Koninklijke Nederlandse Akademie van Wetenschappen, Series B (Physical Science)*, **78**, 149–167.
- BRETT, C. E. 1981. Terminology and functional morphology of attachment structures in pelmatozoan echinoderms. *Lethaia*, **14**, 343–370.

- BROWER, J. C. 1975. Silurian crinoids from the Pentland Hills, Scotland. *Palaeontology*, **18**, 631–656.
- COCKS, L. R. M., HOLLAND, C. H., RICKARDS, R. B. and STRACHAN, I. 1971. A correlation of Silurian rocks in the British Isles. *Journal of the Geological Society*, **127**, 103–136.
- and TOGHILL, P. 1973. The biostratigraphy of the Silurian rocks of the Girvan district, Scotland. *Journal of the Geological Society*, **129**, 209–243.
- DONOVAN, S. K. 1984. Stem morphology of the Recent crinoid *Chladocrinus* (*Neocrinus*) *decorus*. *Palaeontology*, **27**, 825–841.
- 1986. Pelmatozoan columnals from the Ordovician of the British Isles, part 1. *Monograph of the Palaeontographical Society*, **138** (568), 1–68.
- 1989a. The significance of the British Ordovician crinoid fauna. *Modern Geology*, **13**, 243–255.
- 1989b. The improbability of a muscular crinoid column. *Lethaia*, **22**, 307–315.
- HOLLINGWORTH, N. T. J. and VELTKAMP, C. J. 1986. The British Permian crinoid ‘*Cyathocrinites*’ *ramosus* (Schlothheim). *Palaeontology*, **29**, 809–825.
- and SEVASTOPULO, G. D. 1989. Myelodactylid crinoids from the Silurian of the British Isles. *Palaeontology*, **32**.
- ECKERT, J. D. 1984. Early Llandovery crinoids and stelleroids from the Cataract Group (Lower Silurian) in southern Ontario, Canada. *Royal Ontario Museum Life Sciences Division, Contributions*, **137**, 1–83.
- HOLLAND, C. H. 1971. Silurian faunal provinces? 61–76. In MIDDLEMISS, F. A., RAWSON, P. F. and NEWELL, G. (eds). *Faunal provinces in time and space*. Seel House Press, Liverpool, 236 pp.
- HOWELLS, Y. 1982. Scottish Silurian trilobites. *Palaeontographical Society Monographs*, **135** (561), 1–76.
- JEFFERIES, R. P. S. 1968. The Subphylum Calcichordata (Jefferies 1967), primitive fossil chordates with echinoderm affinities. *Bulletin of the British Museum (Natural History) (Geology)*, **16**, 241–339.
- KOLATA, D. R. 1982. Camerates. 170–205. In SPRINKLE, J. (ed.). Echinoderm faunas from the Bromide Formation (Middle Ordovician) of Oklahoma. *University of Kansas Paleontological Contributions, Monograph 1*, i–x, 1–369.
- MILLER, J. S. 1821. *A natural history of the Crinoidea or lily-shaped animals, with observation on the genera Asteria, Euryale, Comatula, and Marsupites*. Bryan and Co., Bristol, 150 pp.
- MOORE, R. C., JEFFORDS, R. M. and MILLER, T. H. 1968. Morphological features of crinoid columns. *University of Kansas Paleontological Contributions, Echinodermata, Article 8*, 1–30.
- and LAUDON, L. R. 1943. Evolution and classification of Paleozoic crinoids. *Geological Society of America, Special Paper*, **46**, i–x, 1–153.
- RAMSBOTTOM, W. H. C. 1954. British Lower Palaeozoic Crinoidea. Unpublished Ph.D. thesis, University of London.
- RIDDLE, S. W. 1989. Functional morphology and paleoecological implications of the platycrinoid column (Echinodermata, Crinoidea). *Journal of Paleontology*, **63**, 889–897.
- ROEMER, C. F. 1855. Erste Periode, Kohlen-Gebirge. In BRONN, H. G. (ed.). *Lethaea Geognostica*, 3rd edition, **2**. Schweizerbart, Stuttgart, 788 pp. [Not seen].
- STUKALINA, G. A. 1967. Principles of classification of stems of ancient sea lilies. *International Geological Review*, **9**, 549–555.
- UBAGHS, G. 1978. Camerata. T408–T519. In MOORE, R. C. and TEICHERT, C. (eds). *Treatise on invertebrate paleontology. Part T. Echinodermata 2(2)*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, T403–T812.
- WACHSMUTH, C. and SPRINGER, F. 1885. Revision of the Palaeocrinoidea, part 3, section 1. Discussion of the classification and relations of the brachiote crinoids, and conclusion of the generic descriptions. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **1885**, 223–364.
- WEBSTER, G. D. 1974. Crinoid pluricolumnal noditaxis patterns. *Journal of Paleontology*, **48**, 1283–1288.

STEPHEN K. DONOVAN
Department of Geology
University of the West Indies
Mona, Kingston 7, Jamaica

NEIL D. L. CLARK
Hunterian Museum
The University
Glasgow G12 8QQ

Typescript received 5 December 1989
Revised typescript received 6 June 1991