

# MYELODACTYLID CRINOIDS FROM THE SILURIAN OF THE BRITISH ISLES

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**ABSTRACT.** Crinoids of the disparid family Myelodactylidae are distinctive in having a bilaterally symmetrical distal column which was coiled in life, and a slender proxistele that is doubly recurved. Seven genera of myelodactylid have been described. Of these, *Herpetocrinus* is regarded as a junior synonym of *Myelodactylus*. Six species of myelodactylid are definitely recognized from the Silurian of Britain and Ireland: *Myelodactylus ammonis* (Bather), *Myelodactylus fletcheri* (Salter), *Myelodactylus parvispinifer* (Brower), *Myelodactylus hibernicus* sp. nov., *Myelodactylus penkillensis* sp. nov., and *Myelodactylus* sp. A. *Myelodactylus convolutus* Hall is not found in the Wenlock Limestone, despite reports to the contrary. Most myelodactylids, apart from the genus *Crinobrachiatus*, probably lay on the substrate on their sides.

MOORE and Teichert (1978) diagnosed all families of Palaeozoic crinoids, except one, on features of the crown, with plating of the dorsal cup usually being regarded as the most important character. The single exception is the unusual family Myelodactylidae, which comprises six genera, all of which possess a distinctive, bilaterally symmetrical, coiled stem. In those myelodactylid genera in which the proximal portion of the stem is known, it is doubly recurved. These features of the stem define the family. Stem symmetry is an important character because the crown is not known in three of the six myelodactylid genera that we recognize. In most other families, characters of the stem are not considered as reliable criteria for distinguishing different genera.

The purpose of this paper is to discuss the taxonomy, palaeoautecology and phylogeny of the myelodactylids, and to describe the species of this family found in Britain and Ireland. The terminology used follows Moore, Jeffords and Miller (1968), Webster (1974), and Ubaghs (1978). The following abbreviations are used in the text: AMNH, American Museum of Natural History; BCM, City of Bristol Museum; BGS, British Geological Survey; BM(NH), British Museum (Natural History); BU, Birmingham University Museum; RM, Naturhistoriska Riksmuseet, Sektionen for Paleozoologi, Stockholm; OUM, Oxford University Museum; RSM, Royal Scottish Museum, Edinburgh; SM, Sedgwick Museum, Cambridge; TCD, Trinity College, Dublin.

## GENERA OF THE MYELODACTYLIDAE

The type genus of the family Myelodactylidae, *Myelodactylus*, was erected by James Hall in 1852 (p. 191), although he mistakenly believed that he was describing a crinoid arm rather than a stem. The type species by monotypy, *M. convolutus*, is characterized by having a long pair of cirri, formed of long slender cirral ossicles, directed inwardly ('inner' and 'outer' are used *sensu* Willink 1980) from each columnal (nodal) of the dististele. *Ophiocrinus* Charlesworth (Anon. 1865) is a junior synonym of *Myelodactylus* (Moore *et al.* 1978, p. T552). Salter (1873, p. 118) did not accept that *Myelodactylus*, 'based on false ideas', was valid and proposed the new name *Herpetocrinus* when he described the species *H. fletcheri*. However, as Nicholson and Etheridge (1880, p. 332) pointed out, Hall's generic name is not invalidated because it was based on a misconception of the nature of the fossil. Nevertheless, Bather (1893, p. 36) rejected *Myelodactylus* and maintained *Herpetocrinus*; Foerster (1919) regarded the two names as synonyms; and Springer (1926*a, b*) rejected *Herpetocrinus*. The status of *Herpetocrinus* is discussed below.

*Brachiocrinus* Hall (Anon. 1858, p. 278, *nomen nudum*; Hall 1861, pp. 118–119, pl. 5, figs. 5–7;

pl. 6, figs. 1–3) has been accepted by later authors as a valid myelodactylid genus (Moore 1962, p. 43; Moore *et al.* 1978, p. T552), even though only the distal termination of the column is known. The stem is heteromorphic, with nodals supporting forward-pointing cirri. The cirral ossicles are larger than the columnals of the associated stem, a unique feature. Hall (1861, pl. 6, fig. 3a) illustrated a columnal of *Brachiocrinus* in section, which is similar to that of *M. convolutus*. The column has a bulbous termination.

The crown of the coiled genus *Eomyelodactylus* Foerste (1919, pp. 19–21, pl. 1, fig. 8; pl. 2, fig. 3) is also unknown, but the figured specimens show a constriction, as in other genera in this family, in the transition zone between the stout dististele and slender proxistele. Foerste regarded *Eomyelodactylus* as a subgenus of *Myelodactylus* (1919, p. 19) but gave it generic status in the plate captions. Its column is pentameric and very similar to that of *Macnamaratylus* Bolton (1970). The latter genus is cirriferous, unlike *Eomyelodactylus*, and in the type specimen the proxistele and a crown with five rays are preserved. The cirri are composed of low ossicles, similar to those of *Myelodactylus fletcheri* (Salter).

Moore (1962, p. 43) proposed the genus *Crinobrachiatus*, based on the unusual species *Myelodactylus brachiatus* Hall. Well-preserved specimens of this species are not uncommon in the Rochester Formation (Wenlock) of New York and Ontario but often lack a crown (Springer 1926a, p. 18; Eckert and Brett 1985). Cirri are few and are concentrated in the distal part of the column. This is the only myelodactylid genus in which branching cirri are known.

The oldest known myelodactylid, *Musocrinus* Donovan, 1985, from the Ashgill of Sweden, is based on dissociated stem material only. The known column (dististele?) lacks cirri and is composed of holomeric ossicles.

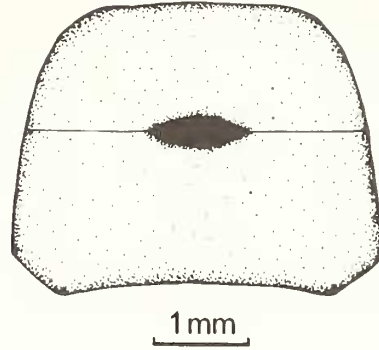
#### TAXONOMIC STATUS OF *MYELODACTYLUS* AND *HERPETOCRINUS*

Moore (1962, p. 41) proposed the following criteria for distinguishing between *Myelodactylus* and *Herpetocrinus*: '*Myelodactylus* is distinguished from *Herpetocrinus*... by the presence of five rays (instead of four) in the dorsal cup and crown, by weak development or lack of longitudinal divisions of distal columnals, and notably elongate, rather than short, beaded cirrals'. Moore considered the two genera to be separate, even though Salter (1873) had proposed *Herpetocrinus* as a name to replace *Myelodactylus*.

Although the dorsal cup of myelodactylids is rarely seen, that of *Myelodactylus* has been shown to have five rays (for instance, by Springer 1926a, pl. 6, fig. 10). In *Herpetocrinus* only four rays have been recognized. Bather (1893, pl. 1, fig. 38) noted this feature in *H. fletcheri*, the type species. Springer (1926a, pl. 1, fig. 12c) illustrated a four-rayed cup of *H. fletcheri* but referred it to *Myelodactylus*. Ramsbottom (1954, p. 83) concluded that this four-rayed specimen was abnormal, because other specimens (which cannot, however, be viewed from every angle) appear to have five rays. We agree with Ramsbottom that both *Herpetocrinus* and *Myelodactylus* have five-rayed cups. The holotype of *H. fletcheri* (Pl. 81, fig. 7) is too poorly prepared for an accurate count to be made of the number of rays present. However, it seems probable that four rays are exposed with a fifth concealed. BU Holcroft Collection 509 (Pl. 81, figs. 1 and 2) has three rays exposed, and it is likely that a further two rays are concealed. If only a single ray is hidden it would have to be very broad. RM Ec 8909 (specimen k of Bather 1893, pl. 1, figs. 36–49; Moore *et al.* 1978, fig. 345, l, j, k), from Gotland, has three rays exposed. The proxistele of the stem is elliptical in section and there are undoubtedly two rays, or a single remarkably broad ray, concealed. From this accumulated evidence, we conclude that *H. fletcheri* Salter does indeed have five rays and that *Herpetocrinus* typically has five, and not four, rays.

It is more difficult to comment on Moore's second criterion for separating *Herpetocrinus* and *Myelodactylus*. In small specimens of *H. fletcheri*, such as the holotype, the distal stem generally appears holomeric, that is, each columnal is composed of a single calcite plate. However, in a small *H. fletcheri* (BU Holcroft Collection 462), a plurimere from the outer surface of the dististele is missing, indicating that this stem is undoubtedly bimeric. In large specimens, such as RM Ec 8904,

TEXT-FIG. 1. Bimerism in myelodactylid stems. Schematic diagram of section through the stem of *Myelodactylus fletcheri* (Salter), based on RM Ec 8904, 8908 and 8909. 'Outer' surface (*sensu* Willink 1980) towards the top of the page.



8908 and 8909 (all from Gotland), the dististele (and, where preserved, the proxistele) is undoubtedly bimeric (text-fig. 1), with a transverse meric suture at the level of the axial canal separating a smaller 'outer' plate (*sensu* Willink 1980) from a larger 'inner' plate. Good articulation surfaces between meres can be seen on RM Ec 8909. The columns of almost all specimens of *Myelodactylus* that we have examined appear to be holomeric, but none of them has been thin sectioned. However, one specimen of *M. ammonis* (BGS PL 3684) certainly has a bimeric distal columnal (Pl. 80, figs. 1 and 2). The incidence of bimeric and holomeric columnals in myelodactylids requires further study, particularly of thin sections and polished surfaces of columnals. However, it is clear that there is no consistent difference in the structure of the column in *Myelodactylus* and *Herpetocrinus fletcheri*.

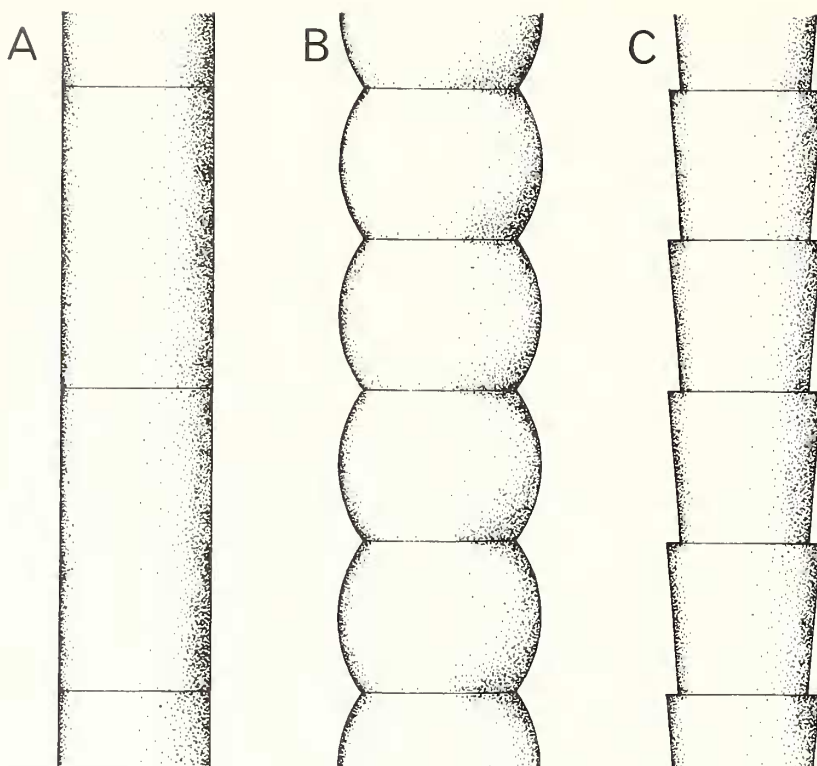
Moore's third criterion was based on the shape of the cirri. There is no doubt that the cirri of species assigned to *Myelodactylus* and those of *Herpetocrinus fletcheri* differ morphologically. Unfortunately, Hall's original cirriferous specimen of *M. convolutus* is lost, although two syntype pluricolumnals (minus cirri) are preserved (AMNH 1708, 31370; Pl. 80, fig. 10). However, it is clear from various specimens and published figures that the cirral ossicles of *Myelodactylus* are slender, elongate, perhaps two or three times as long as broad, and with planar or slightly concave latera (text-fig. 2A). In contrast, the cirri of *Herpetocrinus fletcheri* are generally about as high as wide, 'bead-like', and with convex latera (text-fig. 2B). *Herpetocrinus parvispinifer* Brower and the new species from Lettershanbally, County Galway, Ireland, described below, each have cirral ossicles (text-fig. 2C) that differ from those of both *Myelodactylus convolutus* and *Herpetocrinus fletcheri*. The ossicles are truncated cones, the 'base' of the cone forming the distal facet, and a plane parallel to the base, the proximal facet. Each ossicle is thus broader distally than proximally and is about as high as wide, with planar latera.

At what taxonomic level are these differences in shape of the cirral ossicles important? The myelodactylids are the only group of Palaeozoic crinoids for which the morphology of the cirrals has been claimed to be a feature of major significance. On the other hand, one could counter that the cirri of Palaeozoic crinoids have been poorly described in general, so that the variation between taxa (other than within the myelodactylids) is not known. Turning to post-Palaeozoic crinoids, it appears that cirral ossicles of the isocrinids are of value in differentiating between species (M. J. Simms pers. comm.). We conclude that cirral morphology is probably not a good taxobase to use on its own in discriminating genera of myelodactylids.

It seems, therefore, that there are only minor differences between species assigned to *Myelodactylus* and those that have been assigned to *Herpetocrinus*. We thus consider *Herpetocrinus* to be a junior synonym of *Myelodactylus*.

#### PALAEOAUTECOLOGY

The first restoration of a myelodactylid in life position was the original figure of *Herpetocrinus* (Salter 1873, p. 118). This shows the stem recumbent and loosely coiled in a planar spiral. The



TEXT-FIG. 2. Schematic diagrams of short lengths of cirri, to illustrate morphology of differing cirral ossicle within *Myelodactylus*. A, based on *M. convolutus* Hall; B, based on *M. fletcheri* (Salter); C, based on *M. parvispinifer* (Brower).

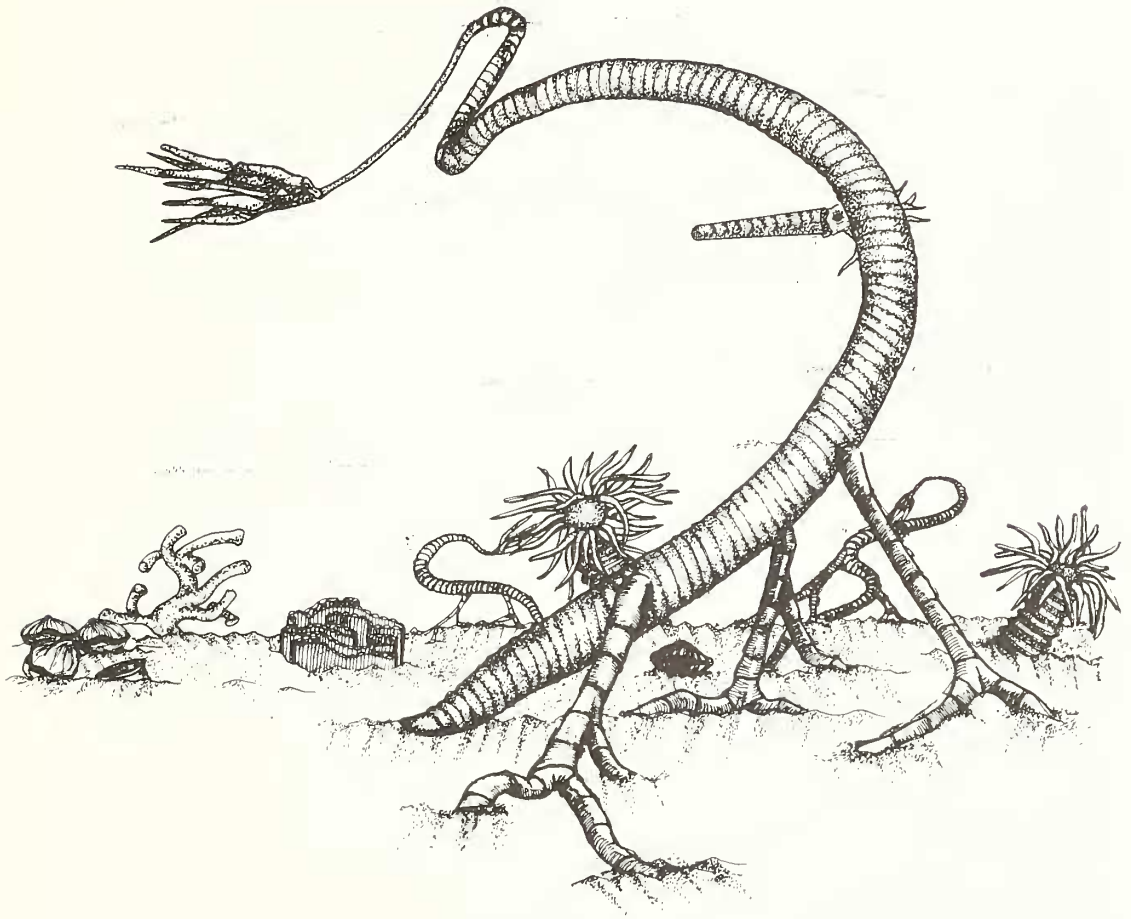
crown is held vertically aloft in the centre of the spiral (there is no indication of any double recurvature of the stem) with the arms arrayed in a cone to catch falling detritus. The cirri are also shown held aloft.

Bather (1893, p. 45) suggested that myelodactylids may have been mobile nektonic organisms that used their cirri to grasp corals. Springer (1926*a*, p. 7) also considered the cirri to be prehensile. Breimer (1978, p. T340) interpreted the coiled myelodactylid configuration to be a resting and hiding position for the crinoid when lying on the sea bottom. During 'activity', the stem uncoiled, exposing the crown. The cirri could grasp adjacent objects for temporary fixation, could be used to crawl over the sea floor or could even function as oars for short swims.

The most convincing arguments presented to date for the life habit of a myelodactylid are in Eckert and Brett's (1985) restoration of *Crinobrachiatus*. This is similar to an independent reconstruction by S. K. D. (text-fig. 3). The stem is supported at an acute angle to the substrate by the branching cirri. The cirri are shortest distally, that is, nearest the sea floor, and become longer proximally. The proximal stem may be enrolled to protect the crown within the cage of cirri.

*Crinobrachiatus* is unusual amongst the myelodactylids in having branched cirri. In *Myelodactylus* the cirri are unbranched and tend to be of approximately equal length within an individual. They also tend to be distributed along the length of the dististele, whereas in *Crinobrachiatus* they are concentrated in the distal 20% of the column, so that the mesistele is non-cirriforous. The stem of *Myelodactylus* was thus not adapted for a life habit similar to that of *Crinobrachiatus*.

There are some features of *Myelodactylus* which are unusual for crinoids. There are no reports of species having been found with a distal attachment. The distal part of a stem that is apparently



TEXT-FIG. 3. Restoration of *Crinobrachiatus brachiatus* (Hall) to life position. Drawing by Mrs Elaine Cullen.

attached to a shell or shells (SM A.12610; Wenlock Limestone, Dudley) is one of the syntypes of *Myelodactylus* [*Herpetocrinus*] *fletcheri* (Salter, 1873) but it is doubtful that the stem is that of a myelodactylid. In many specimens, the stem is tapered distally (Springer 1926a; Pl. 81, fig. 1), a feature also seen in *Crinobrachiatus*, which has, however, been found attached to a hard substrate. In *Myelodactylus*, the cirri, although common, are directed inwardly and are clearly not adapted to function as components of a cirriferous runner. Specimens are normally found more (Pl. 80, figs. 3–5) or less (Pl. 81, figs. 1, 4, 7, 9) enrolled. The cirri usually form a dense curtain behind which, because of the coiled column, the crown was concealed (Pl. 80, figs. 3–5; Pl. 81, figs. 2 and 6). Some of the better-preserved crowns of myelodactylids have been exposed by removing these enclosing cirri. The crown, where found, is always fully developed, with relatively long arms. Most of the previous hypotheses for the mode of life of myelodactylids imply that the stem could have been actively moved. However, the stems of modern crinoids are almost certainly incapable of active

movement because the columnals are linked by ligaments and there is no evidence of muscles (Grimmer *et al.* 1985). Slender contractile fibres have been detected in the cirri of comatulids (Holland and Grimmer 1981) and of the stalked *Metacrinus* (Grimmer *et al.* 1985) but these are of minute diameter and almost certainly of minimal mechanical significance. Thus, there is no support from the study of Recent crinoids for the intuitively attractive hypothesis that some ancient crinoids were actively able to move their columns. In the myelodactylids, in particular, Donovan and Franzén-Bengtson (1988) could find no signs of sites of muscle attachment on dissociated columnals from Gotland. We therefore believe that the coiled attitude of myelodactylids was their life position: the animals lay on their sides on the sea floor. The enclosing envelope of cirri would have protected the crown from the sediment below and against predation from above, and the stem would have encircled the crown as a sort of armoured skirt.

The reason for the double recurvature of the proxistele now becomes clear. If the stem had a simple spiral form, the crown would have faced into the centre of the coil. The double recurvature reorientated the crown so that it was parallel with the dististele and pointed backwards towards the opening of the envelope at the distal end of the column, where the stem and cirri would have enclosed an oblong slot. The crinoid would have fed by filtering water either drawn down from the opening of this slot and expelled through the cirri or *vice versa*.

The advantages of this concealed mode of life are obvious. The cup, and consequently the bulk of the soft tissues, would have been protected. In most crinoids the stem is primarily an organ of elevation for the crown, anchoring the whole animal to the substrate by the holdfast. In *Myelodactylus* both the stem and cirri ('holdfast') were adapted as organs of protection for the crown. However, this was at the expense of having an elevated feeding position. *Myelodactylus* was thus in competition with other benthonic epifaunal elements such as brachiopods. Unfortunately, there were no myelodactylids in the crinoid faunas from the Wenlock Limestone of Dudley which were discussed by Watkins and Hurst (1977). The relationship of *Myelodactylus* to the other elements of the Silurian fauna is therefore still largely unknown.

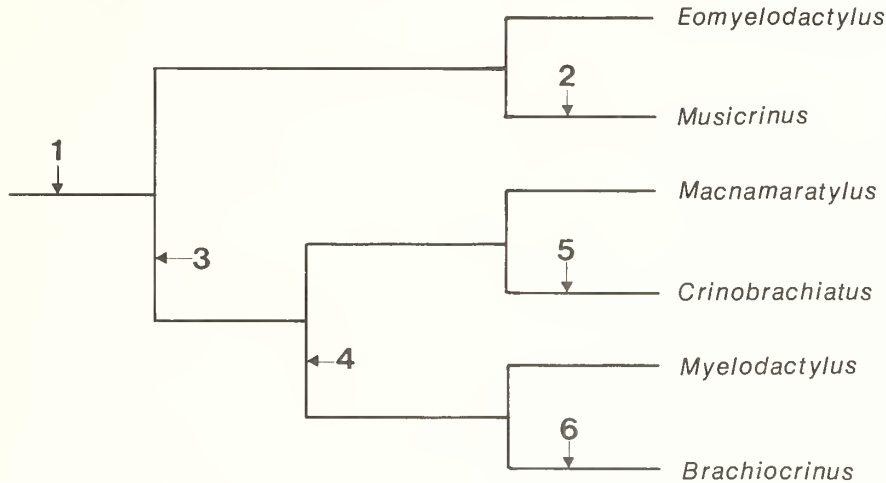
#### PHYLOGENY

Any analysis of the relationships between the myelodactylid genera is hampered by the lack of critical information. *Crinobrachiatus* Moore (Eckert and Brett 1985) is the only genus which has been redescribed recently and for which there are new observations on the crown. Indeed, the crown is unknown in *Brachiocrinus*, *Eomyelodactylus*, and *Musocrinus*. All other genera are now recognized to have five-rayed crowns.

The C-ray radial in myelodactylids has generally been considered to be compound (Moore *et al.* 1978, p. T551). However, Eckert and Brett (1985) have shown that the C-ray aniradial of *Crinobrachiatus* is undivided. *Macnamaratylus* (Bolton 1970, pp. 64–65) has five undivided radials. Springer's illustrations of the cup plating of *Myelodactylus* (1926*a*, pl. 1, fig. 12*c*, an aberrant four-rayed specimen; and pl. 6, fig. 1*c*) do not show any division of the C-ray radial. The latter specimen shows the C-ray radial to be larger than the B- and D-ray radials, which in turn are larger than the A- and E-ray radials; however, there is no suggestion in the illustration that the C-ray radial is compound. Springer (1926*a*, p. 7) considered the crown of myelodactylids to be '... of the type of the Heterocrinidae; without compound radials...' and certainly we have been unable to determine a divided C-ray radial in any of the specimens that we have examined. We therefore consider the presence of a compound C-ray radial plate in the myelodactylids as unproven. This must throw doubt on the supposed close relationship of myelodactylids, iocrinids and eustenocrinids.

Where known, the dorsal cup in myelodactylids seems to have essentially the same structure. The arrangement of the arms and anal tube is poorly known and will be of little use in taxonomy until more well-preserved specimens are available. Thus, with so many features of the crown poorly known, or not known at all, it is necessary to base any interpretation of the relationships between the myelodactylid taxa on the features of the stem and cirri. This was regarded as acceptable by Brower (1975, p. 649) but not by Eckert and Brett (1985, p. 4), who pointed out the potential pitfalls

of including myelodactylid-like homeomorphs within this family. However, although a number of other crinoids have a bilateral stem symmetry (for example, *Camptocrinus* and *Ammonocrinus*) which is loosely similar to that of myelodactylids, sufficient differences exist to make the recognition of members of each family relatively simple. For example, compare the figures of myelodactylid stems herein with those of Springer (1926*a*, pl. 6, fig. 6: *Ammonocrinus*) and Willink (1980, text-fig. 3: *Neocamptocrinus*).



TEXT-FIG. 4. Cladogram showing the inferred relationships between myelodactylid genera. Synapomorphies/autapomorphies (1–6) as follows: 1, stem attains bilateral symmetry and becomes coiled, proxistele becomes double recurved; 2, holomerism; 3, development of cirri; 4, fusion of pentameres; 5, development of branching cirri and holomeric dististele; 6, hypertrophy of cirral ossicles.

Our interpretation of the phylogenetic relationships of the myelodactylid genera is shown in text-fig. 4. We speculate that the six genera that we recognize form a monophyletic group, defined by the following synapomorphy (synapomorphy 1 in text-fig. 4): a coiled stem with bilaterally symmetrical ossicles in the dististele and a doubly recurved proximal portion. The latter character has been confirmed only in *Crinobrachiatus*, *Macnamaratylus* and *Myelodactylus*, but can reasonably be inferred in *Eomyelodactylus*. *Musicrinus* is known only from dissociated stem ossicles and *Brachiocrinus* from the distal part of the stem. The following characters of the stem offer some prospect of resolving the relationships within the family. Three genera have pentameric stems: *Crinobrachiatus*, in which only the proxistele was reported to be meric by Eckert and Brett (1985), *Eomyelodactylus* and *Macnamaratylus*. By analogy with other crinoids (Sprinkle 1973; Paul and Smith 1984), the pentameric stem is likely to be a plesiomorphic character and the bimeric and holomeric stem, apomorphic. Two genera, *Eomyelodactylus* and *Musicrinus* lack cirri, a plesiomorphic character. The other four bear cirri; in *Brachiocrinus* the cirral ossicles are hypertrophied, an autapomorphy; and in *Crinobrachiatus* the cirri are branched, also an autapomorphy. If the acquisition of cirri is regarded as a unique synapomorphy within the myelodactylids (synapomorphy 3 in text-fig. 4), then the holomeric condition may have been achieved more than once (in *Musicrinus* and possibly in some species of *Myelodactylus*). Within the genera that bear cirri, the fusion of pentameres is regarded as a synapomorphy (synapomorphy 4).

The known stratigraphical distribution of the myelodactylid genera is broadly consistent with the relationships depicted in text-fig. 4. One anomaly is that *Musicrinus*, the oldest genus (from the Ashgill), has a holomeric stem. This implies that the oldest myelodactylids must occur earlier in the Ordovician. *Eomyelodactylus*, whose pentameric stem lacks cirri, is known only from the early Llandovery (probably late Rhuddanian or Aeronian) of Ohio, USA (Sevastopulo *et al.* 1989).

*Macnamaratylus* occurs in the late Llandovery (probably Telychian) of Quebec, Canada (stratigraphical information interpreted from Bolton 1970; and Berry and Boucot 1970). *Crinobrachiatus* is known only from the Wenlock of New York, USA. The oldest known *Myelodactylus* is *M. penkillensis* sp. nov. from the Fronian or early Telychian of southern Scotland. The genus certainly ranges into the Lower Devonian and possibly higher. *Brachiocrinus* is known only from the Lower Devonian of New York, USA.

#### SYSTEMATIC PALAEOLOGY

Class CRINOIDEA J. S. Miller, 1821

Order DISPARIDA Moore and Laudon, 1943

Family MYELODACTYLIDAE S. A. Miller, 1883

*Diagnosis.* A family of disparid crinoids with distinctive, bilaterally symmetrical columns which are either oval (pentameric) or broadly U-shaped (holomeric or bimeric) in section. Proxistele much more slender than the dististele. Stem doubly recurved in the region of the proxistele–dististele transition. Cirri, where present, adapted for attachment or, more usually, for protection of the crown in coiled, recumbent forms. Crown monocyclic, five-rayed, all radials simple. Anal tube long, arising in the C-ray. Arms slender, branching isotomously or heterotomously.

*Remarks.* The following myelodactylid species have previously been reported from the Silurian of Britain: *Myelodactylus convolutus* Hall, 1852; *Myelodactylus* sp. Nicholson and Etheridge, 1880; *Myelodactylus* [*Herpetocrinus*] *fletcheri* (Salter, 1873); *Myelodactylus* [*Herpetocrinus*] *ammonis* (Bather, 1893); and *Myelodactylus* [*Herpetocrinus*] *parvispinifer* (Brower, 1975).

#### Genus MYELODACTYLUS Hall, 1852

= *Ophiocrinus* Charlesworth *nom. nud.* (Anon. 1865)

= *Herpetocrinus* Salter, 1873, p. 118 (Type species *Herpetocrinus fletcheri*).

*Type species.* *Myelodactylus convolutus* Hall, 1852, p. 191, by the subsequent designation of Springer (1926*a*, p. 8).

*Diagnosis.* A genus of myelodactylid crinoid with numerous unbranched cirri arising from the closely spaced nodals of the proximal portion of the dististele. Columnals of the dististele may be holomeric or bimeric.

#### *Myelodactylus convolutus* Hall, 1852

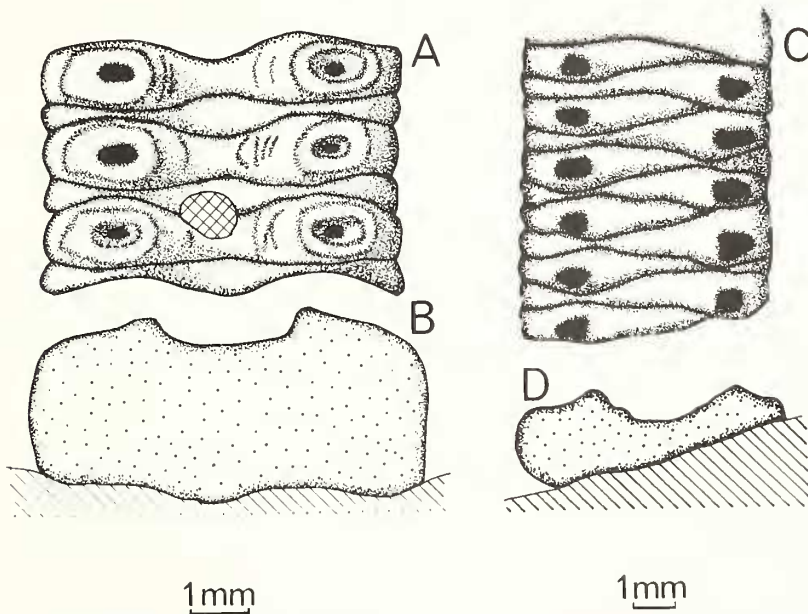
Plate 80, fig. 10

- |               |   |
|---------------|---|
| 1852          | <i>Myelodactylus convolutus</i> sp. nov., Hall, p. 191, pl. 45, figs. 5 and 6.  |
| 1893          | <i>Herpetocrinus convolutus</i> (Hall); Bather, p. 48, pl. 2, figs. 50–53.  |
| 1926 <i>a</i> | <i>Myelodactylus convolutus</i> Hall; Springer, pp. 8–10, pl. 1, figs. 1–8.   |
| 1926 <i>b</i> | <i>Myelodactylus convolutus</i> Hall; Springer, p. 86, pl. 27, figs. 6–8.   |
| 1930          | <i>Herpetocrinus</i> ( <i>Myelodactylus</i> ) <i>convolutus</i> (Hall); Ehrenberg, p. 322, pl. 16, fig. 1, table opposite p. 324. |
| 1943          | <i>Myelodactylus convolutus</i> Hall; Bassler and Moodey, p. 568.   |
| 1944          | <i>Myelodactylus convolutus</i> Hall; Moore and Laudon, p. 143, pl. 54, fig. 26.  |
| 1952          | <i>Myelodactylus convolutus</i> Hall; Moore <i>et al.</i> , figs. 15 <i>A</i> , 18–19.  |
| 1954          | <i>Myelodactylus convolutus</i> Hall; Ramsbottom, pp. 86, 87.   |
| 1962          | <i>Myelodactylus convolutus</i> Hall; Moore, p. 41, pl. 4, fig. 2.  |
| 1971          | <i>Myelodactylus convolutus</i> Hall; Dubatolova, p. 15.  |
| 1978          | <i>Myelodactylus convolutus</i> Hall; Moore <i>et al.</i> , pp. T551, T552, fig. 344, 1 <i>a–d</i> .                              |
| 1988          | <i>Myelodactylus convolutus</i> Hall; Donovan and Franzén-Bengtson, p. 70.  |



*Remarks.* Springer (1926a, pp. 8, 10) reported *M. convolutus* from the Wenlock Limestone of Dudley. However, Ramsbottom (1954, p. 87) did not find specimens of *M. convolutus* in any of the major British collections. At our request, Dr F. J. Collier of the Smithsonian Institution examined Springer's collection and could find no specimens of *M. convolutus* from Britain; however, *M. fletcheri* and *M. extensus* (= *M. ammonis*) were both present.

The two surviving syntypes of *M. convolutus*, AMNH 1708 and 31370 (Pl. 80, fig. 10), were borrowed for comparison with the British material. Cirri are not preserved on either pluricolumnal (but see Hall 1852, pl. 45, fig. 5). Columnals have parallel articular facets and are not wedge-shaped. The column is homeomorphic, holomeric, each nodal bearing a pair of cirral scars, one at either side of the inner surface, each angled slightly away from the depressed central groove. Cirral scars are elongate but the lumina of the scars are circular. This is outside the range of morphologies noted for British myelodactylids. We therefore confirm Ramsbottom's earlier observation and suggest that Springer's original identification of *M. convolutus* from the Wenlock Limestone was erroneous.



TEXT-FIG. 5. *Myelodactylus ammonis* (Bather, 1893). A, B, BMNH E356, 'var. *bijugicirrus*'. A, inner surface showing cirral scars and heteromorphy N1; B, pluricolumnal in section; C, D, 'var. *alternicirrus*': C, inner surface; D, pluricolumnal in section. Camera lucida drawings.

*Myelodactylus ammonis* (Bather, 1893)

Plate 80, figs. 1-9, 11, 12; text-fig. 5

- 1893 *Herpetocrinus ammonis* sp. nov., Bather, p. 49, pl. 2, figs. 54-63.
- 1922a *Herpetocrinus ammonis* Bather; Ehrenberg, p. 188, figs. 7, 14, 16.
- 1926a *Myelodactylus ammonis* (Bather); Springer, pp. 10-14, pl. 2, figs. 1-9.
- 1926a *Myelodactylus brevis* sp. nov., Springer, p. 10, pl. 1, figs. 9, 9a.
- 1926a *Myelodactylus extensus* sp. nov., Springer, pp. 14, 15, pl. 3, figs. 1-13a.
- 1926b *Myelodactylus ammonis* (Bather); Springer, p. 86, pl. 27, figs. 1-5a.
- 1926b *Myelodactylus brevis* Springer; Springer, p. 86, pl. 27, figs. 9 and 9a.
- 1926b *Myelodactylus extensus* Springer; p. 87, pl. 27, figs. 11-18.
- 1926 *Herpetocrinus* (*Myelodactylus*) *ammonis* Bather; Ehrenberg, p. 256, fig. 3.
- 1930 *Herpetocrinus* (*Myelodactylus*) *ammonis* Bather; Ehrenberg, p. 322, pl. 16, fig. 5.

- 1943 *Myelodactylus ammonis* (Bather); Bassler and Moodey, p. 567.  
 1954 *Myelodactylus ammonis* (Bather); Ramsbottom, pp. 84, 85, pl. 16, figs. 6–10.  
 1968 *Myelodactylus ammonis* (Bather); Moore and Jeffords, pp. 32, 33, pl. 1, figs. 1 and 2.  
 1978 *Myelodactylus ammonis* (Bather); Ubaghs, p. T78, fig. 57.2.  
 1988 *Myelodactylus ammonis* (Bather); Donovan and Franzén-Bengtson, pp. 70–71.

*Material, localities and horizon.* The majority of specimens of this species have the simple locality information 'Wenlock Limestone, Dudley'. Specimens that come from different localities are identified in the following list: OUM C17249, C17254, C17476 and C18094 (all from Malvern Tunnel, Wenlock Shale), C18093 (Wenlock Limestone, locality unknown), C18095 (Wenlock Series, locality unknown); BCM Cc902 and 903 (Wenlock Series, Malvern Tunnel tip heap at Colwall Station, Herefordshire), Cc906 to 910 (Wenlock Limestone, old quarries at Dormington Wood, a quarter of a mile east of Wooton, near Woolhope, Herefordshire; NGR SO 598391), Cc911 and 912 (Wenlock Limestone, quarry 290 yards east of Pentaloe Cottage, Little Hill, near Woolhope, Herefordshire); BGS PI 3684 (old quarry, 100 yards south of Brown Works, Canal Bridge, Daw End, Walsall); BGS GSM91777, 91778 (Wenlock Edge); BU Holcroft Collection 376, 377, 379, 381, 384, 386; BU Ketley Collection 176; BMNH 47827 (Upper Shale above Wenlock Limestone, Dudley Tunnel), BMNH E70710, 70711 (Road cutting on the west side of the B4378 road at Farley, about 2 km north of Much Wenlock and about 200 m north of the 'Rock House' public house (NGR SJ 632022), Wenlock Limestone), 57434 (identification uncertain) E1326, E1410 *a, b*, E6336, E6660 (Wenlock Shale, Ledbury), E22562, E22563, E22576, E22583 (identification uncertain), E25584. BMNH E1326, E1410 *b*, E22562 and E22563 are syntypes for *M. ammonis* 'var. *bijugicirrus*'; E14 is a syntype for *M. ammonis* 'var. *alternicirrus*'. The 'Upper Shale above the Wenlock Limestone, Dudley Tunnel' could be the Upper Quarried Limestone (Watkins and Hurst 1977, fig. 2), in which laterally discontinuous limestone horizons alternate with thin marl bands. However, it could also represent the overlying Lower Ludlow Shales (Cocks *et al.* 1971, p. 115), although this is considered unlikely. The Malvern Tunnel and Ledbury localities are both within the Malvern Inlier of the Welsh Borderland. The Wenlock Shales in this area span most of the Wenlock Series (the *Cyrtograptus purchisoni* Subbiozone to the early *Pristiograptus ludensis* Biozone; Ziegler *et al.* 1974, fig. 1). In view of the known occurrence of this species within the Wenlock Limestone, it is suggested that *M. ammonis* may be limited to the younger part of the Wenlock Shale.

*Diagnosis.* A species of *Myelodactylus* in which the crown is concealed by closely spaced, elongate cirri. The dististele is composed of two configurations of pluricolumnal: either heteromorphic N1, with each nodal bearing a pair of cirri, one on either side of the inner surface; or homeomorphic, with wedge-shaped nodals which alternate in orientation to give a zigzag appearance to the inner surface and which bear a single cirral scar towards the wider lateral surface. Cirral scars elongate parallel to the plane of the columnal. Cirral ossicles elliptical in section proximally, becoming more circular distally; longer than wide, with planar to slightly concave latera.

*Description* Crown: not seen. In Bather's type specimen (1893, pl. 2, fig. 54), from Gotland, both the crown and the proxistele are concealed by cirri. This is also the case with the better preserved British specimens,

#### EXPLANATION OF PLATE 80

Figs. 1–9, 11, 12. *Myelodactylus ammonis* (Bather, 1893). 1 and 2, BGS PI 3684. 1, oblique lateral view,  $\times 2.5$ . 2, view of articular surface of most distal columnal, demonstrating the meric character of the stem,  $\times 3.5$ . 3, 6, 7, BU Holcroft Collection 384. 3, lateral view of entire specimen showing the tight enrolment which conceals the crown,  $\times 2$ . 6, view of the outer surface of the enrolled specimen, showing the prominent central groove,  $\times 3$ . 7, enlargement of the cirri in the area concealing the crown,  $\times 4.5$ . 4 and 8, OUM C18094. 4, lateral view of entire specimen,  $\times 2.5$ . 8, enlargement of the cirri and part of the column,  $\times 5$ . 5, OUM C17254, lateral view of entire specimen,  $\times 2.25$ . 9, BU Holcroft Collection 376, 'var. *bijugicirrus*', enlargement of the cirral scars on one side of the specimen,  $\times 6$ . 11 and 12, OUM C18095. 11, part of the pluricolumnal to show the unusual reverse curvature and consistent orientation of the cirri,  $\times 3$ . 12, detail of the cirri,  $\times 9$ .

Fig. 10. *Myelodactylus convolutus* Hall, 1852. AMNH 31370, syntype. Articular facet,  $\times 8$ . All specimens whitened with ammonium chloride.



including BU Holcroft Collection 377, 379, 381, 384 (Pl. 1, figs. 3 and 7), BU Ketley Collection 176, OUM C17254 (Pl. 80, fig. 5), C17476, C18094 (Pl. 80, figs. 4 and 8), BMNH 47827, 57434, E6660, E22576, E22582 and E22583. By analogy with other species of *Myelodactylus*, we expect that the crown will be found to be five-rayed. Confirmation and further comment must await specimens becoming available for sectioning and dissection.

Dististele: more or less coiled in a planar spiral (Pl. 80, figs. 1–5), either terminating in a distal taper (Springer's 1926*a*, p. 11) or elongate and extending away from the spiral (Springer's *M. extensus* 1926*a*, pl. 3; Pl. 80; fig. 9 herein). Lengths of stem occasionally show a 'reverse' curvature with respect to the proximal coil (Pl. 80, figs. 11 and 12). Columnals robust and holomeric or bimeric (Pl. 80, figs. 1 and 2), with a broad U-shaped section (text-fig. 5B, D). Axial canal elliptical. Column either 'homeomorphic' or heteromorphic, N1. Both forms of stem may be found in the same column (Bather 1893, pl. 2, fig. 59; Springer 1926*a*, p. 12; see comments below). 'Homeomorphic' form with wedge-shaped columnals, the 'var. *alternicirrus*' of Bather (1893; Pl. 80, fig. 9 and text-fig. C, D herein). Column appears regularly homeomorphic on the outer surface but nodals wedge alternately to 'left' and 'right' sides on the inner surface to produce a zigzag pattern (text-fig. 5C). One scar per nodal, at the taller side. Cirral scars are offset and arranged in two columns at the edges of the inner surface. The heteromorphic column (text-fig. 5A, B), the 'var. *bijugicirrus*' of Bather (1893), has alternating low priminternodals and tall nodals. Each nodal bears two cirral scars, one on either side of the inner surface, so that the scars are arranged in two columns at the edges of the inner surface. The outer surface of the column may be slightly ridged (Pl. 80, fig. 4) or grooved (Pl. 80, fig. 6). Latera unsculptured, planar or slightly convex. Cirral scars elliptical with elliptical lumina (Pl. 80, fig. 9; text-fig. 5A). Scars and cirral ossicles articulate synostosially. Cirral ossicles elliptical proximally, becoming circular distally. Ossicles taller than high, with planar or slightly concave latera. Terminal cirral ossicles conical. The double row of cirri are arranged so that they enclose the crown.

*Remarks.* Springer (1926*a*) erected two species of *Myelodactylus* which we consider to be synonymous with *M. ammonis*. *M. brevis* has a short column and was based on a single specimen. *M. extensus* has a stem whose coil is open distally, extending away from the crown region. We do not consider these features to be taxonomically significant. In all other respects Springer's specimens are undoubtedly *M. ammonis*.

Bather's varieties, var. *alternicirrus* and var. *bijugicirrus*, have no standing in taxonomy. As pointed out by Moore and Jeffords (1968, p. 32), Bather figured a pluricolumnal in which both 'varieties' occur in the same stem (1893, pl. 2, fig. 59). The terms 'alternicirrus' and 'bijugicirrus' are regarded as descriptive terms useful in separating the two column morphologies found in the xenomorphic dististele. The precise mutual relationship of these two morphologies within the stem is unknown.

### *Myelodactylus fletcheri* (Salter, 1873)

Plate 81; text-fig. 1

- 1873 *Herpetocrinus fletcheri* sp. nov., Salter, p. 118.
- 1878 *Myelodactylus heterocrinus*; Angelin, p. 11, pl. 10, figs. 24 and 25.
- 1880 *Herpetocrinus fletcheri* Salter; Nicholson and Etheridge, p. 332.
- 1893 *Herpetocrinus fletcheri* Salter; Bather, p. 46, pl. 1, figs. 24–49.
- 1922*a* *Herpetocrinus fletcheri* Salter; Ehrenberg, p. 184, figs. 1–5, 8.
- 1922*b* *Herpetocrinus fletcheri* Salter; Ehrenberg, p. 282, fig. 13.
- 1926*a* *Myelodactylus fletcheri* (Salter); Springer, p. 569.
- 1926*b* *Myelodactylus fletcheri* (Salter); Springer, p. 86, pl. 27, figs. 10 and 10*b*.
- 1926 *Herpetocrinus fletcheri* Salter; Robertson, p. 171.
- 1943 *Myelodactylus fletcheri* (Salter); Bassler and Moodey, p. 569.
- 1953 *Myelodactylus fletcheri* (Salter); Ubaghs, p. 730, figs. 125–127.
- 1954 *Myelodactylus fletcheri* (Salter); Ramsbottom, pp. 82, 83, pl. 16, figs. 12 and 13.
- 1962 *Herpetocrinus fletcheri* Salter; Moore, p. 42, pl. 4, fig. 3.
- 1964 *Myelodactylus fletcheri* (Salter); Yakovlev, p. 69, fig. 106.
- 1975 *Herpetocrinus fletcheri* Salter; Brower, p. 650.
- 1978 *Herpetocrinus fletcheri* Salter; Moore *et al.*, p. T552, fig. 345.
- 1988 *Herpetocrinus fletcheri* Salter; Donovan and Franzén-Bengtson, p. 71.

*Material, localities and horizons.* As with *M. ammonis*, the majority of specimens have the simple locality information 'Wenlock Limestone, Dudley'. It is not known whether the type is from the famous Wren's Nest or from one of the other localities of Wenlock Limestone at Dudley. Specimens that have different locality information are identified in the following list: SM A12609, the holotype; OUM C83 (Wenlock Limestone, Dudley?), C17255, C17475 (Wenlock Shale, Malvern Tunnel); BCM Ce904 and 905 (Wenlock Series, Malvern Tunnel tip heap at Colwall Station, Herefordshire); BU Holcroft Collection 380, 457, 462, 509, 551 (Sedgley), 578; BU Ketley Collection 181; BMNH 47859, 57239, E415, E1067 (Wenlock Limestone, Dudley Tunnel), E1327 (plaster cast of the holotype), E5616, E22571, E22573 and E22579. The Malvern Tunnel localities are discussed under *M. ammonis*.

*Diagnosis.* A species of *Myelodactylus* with very slender, elongate arms and a prominent anal tube. The column is usually only loosely coiled and is bimeric. Cirri arise irregularly proximally but occur in pairs on every nodal distally. Columnals of the dististele have a 'cottage loaf' section.

*Description.* In contrast to *M. ammonis*, the crown of *H. fletcheri* is often well exposed (Pl. 81, figs. 1, 2, 4, 7). Unfortunately, the holotype has been very poorly prepared, presumably by Salter, but in many specimens it is well preserved, especially BU Holcroft Collection 509 (Pl. 81, figs. 1 and 2) and RM Ec 8909 from Gotland (Bather 1893, pl. 1, figs. 36–38). However, there are some specimens in which a well-preserved column, retaining the proxistele, still showing the double recurvature of the stem and also retaining the cirri, no longer has the crown attached, for example, OUM C83, C17255 (Pl. 81, figs. 6 and 9), C17475 (Pl. 81, fig. 5), BU Holcroft Collection 380, 578, and from Gotland RM Ec 8903 (Bather 1893, pl. 1, fig. 29).

Crown: five-rayed, or four-rayed in some aberrant individuals (Springer 1926*a*, p. 10, pl. 1, figs. 12*a–c*). Cup monocyclic, with simple radials in all five rays. Latera of cup unsculptured. The transverse section of the cup is approximately pentagonal, becoming elliptical in larger specimens. Anal tube supported by the posterior part of the C-ray radial. Five rays, one supported by each radial. Arms long, slender, non-pinnulate, branching heterotomously.

Stem: xenomorphic, divided into a short, slender proxistele and a more elongate, robust dististele. Stem doubly recurved proximally in the region of the proxistele–dististele transition (Pl. 81, figs. 1, 4, 5, 7, 9). No distal attachment is known. The proxistele is homeomorphic (except immediately beneath the cup, where it is heteromorphic, N1?) and non-cirriiferous, apparently of circular cross-section but becoming elliptical in the largest specimens. The articulation between columnals of the proxistele is symplectial. The proxistele appears to be holomeric in most British specimens, but in OUM C17255 (Pl. 81, fig. 6) a weak bimeric suture is present.

The coiling of the stem in *H. fletcheri* is much looser than that of *M. ammonis*. In some specimens the proxistele is in contact with the inner surface of the dististele (Pl. 81, figs. 1 and 2), whereas in others there is a perceptible gap between the two (Pl. 81, figs. 4–7, 9). The development of cirri is also weak in the more proximal part of the dististele, so that any protection that they may have given the crown was poorer than in *M. ammonis*.

Dististele bilaterally symmetrical in section, with a distinct 'cottage loaf' outline (text-fig. 1). Undoubtedly bimeric in large specimens but possibly holomeric in some small individuals such as the holotype. Flexible due to synarthrial articulation and capable of forming loose spirals, but often preserved with long, straight sections in the more distal parts of the stem (Pl. 81, fig. 8). Crenularium marginal, limited to the outer surface only. Lumen elliptical. Homeomorphic, with nudinodals predominating more proximally. More distal part of the stem bears two cirri per nodal, one on either side of the inner surface. In the intervening region nodals bear two, one, or no, cirri.

Cirri elongate, unbranched, composed of short, barrel-like cirral ossicles of circular section. Latera convex and cirral ossicles generally about as wide, or wider, than high. Articulation between cirral ossicles synostiosal, with a central, circular axial canal. Cirri are generally perpendicular (Pl. 81, fig. 8) or nearly perpendicular (Pl. 81, fig. 3) to the column, although they are sometimes preserved depressed towards the region of the crown (Pl. 81, fig. 6).

*Remarks.* The weak proximal coiling of *H. fletcheri* and the relatively poor proximal development of cirri suggests that the crown of this species was not so completely enclosed in life as those of *M. ammonis* and *M. convolutus*. The crown was well developed and, possibly of necessity, the proximal coil was more open than in *M. ammonis*. However, we have not seen the crown in the latter species; on the basis of the external morphology, it is probable that it was generally smaller and simpler than that of *H. fletcheri*.

The absence of a crown in many otherwise well-preserved specimens of *M. fletcheri* is a phenomenon similar to that described by Springer (1926*a*, p. 18) from *Crinobrachiatus brachiatus* (Hall). In a collection of thirty-four otherwise well-preserved specimens of *C. brachiatus*, only one individual had a crown. It is possible that in *Crinobrachiatus* the crown could have become disarticulated and the ossicles dispersed during a short period of exposure on the sea floor between death and burial (see discussion of the biostratigraphy of this species in Eckert and Brett 1985, pp. 6–7). However, the cirri of myelodactylids probably became disarticulated soon after death, whereas many pluricolumnals remained on the sea floor long enough to become encrusted with bryozoans. It therefore seems unlikely that the crown could have become totally disarticulated and had its ossicles winnowed away while the stem retained many relatively complete cirri. Some specimens of *M. fletcheri* such as OUM C17255 have lost the crown without the cirri being appreciably disturbed (Pl. 81, figs. 6 and 9). In cases like this it is more likely that the severance between stem and crown occurred during life, by autotomy, as in Recent crinoids.

Meric sutures in the dististele may be cryptic and often impossible to detect except in thin section or on a polished surface. For example, BU Holcroft Collection 462 appears to have a holomeric dististele but there is a prominent groove in the centre of the outer surface which appears to be the result of a plurimere becoming dissociated.

*Myelodactylus parvispinifer* (Brower, 1975)

Plate 82, fig. 2

1975 *Herpetocrinus parvispinifer* sp. nov., Brower, pp. 649, 650, pl. 73, figs. 3 and 5.

*Material, locality and horizon.* A holotype, RSM 1897.32.285 (Pl. 82, fig. 2), and four paratypes, RSM 1885.26.78*e*, 1897.32.286, 1897.32.287 and 1897.32.288 (all paratypes have a part and counterpart). All from the Gutterford Burn Starfish Bed, Gutterford Burn Flagstones, North Esk Inlier, Pentland Hills, Scotland. Llandoverly, C6 (late Telyehian).

*Diagnosis.* A species of *Myelodactylus* with sparsely developed cirri and a very open proximal coil (Pl. 82, fig. 2), with the crown relatively exposed and the more distal part of the dististele uncoiled. Cirral ossicles are truncate conical in shape.

*Remarks.* We have nothing to add to the very thorough description of this species by Brower (1975, p. 650). It differs from *M. hibernicus* sp. nov. in having relatively few cirri on the column. The holotype has lost its crown (unknown in this species), despite the perfection of the preservation of the proximal column. This is similar to the crown loss in *M. fletcheri* and *Crinobrachiatus brachiatus*, discussed above.

*Myelodactylus hibernicus* sp. nov.

Plate 82, figs. 1, 3, 4; text-fig. 6

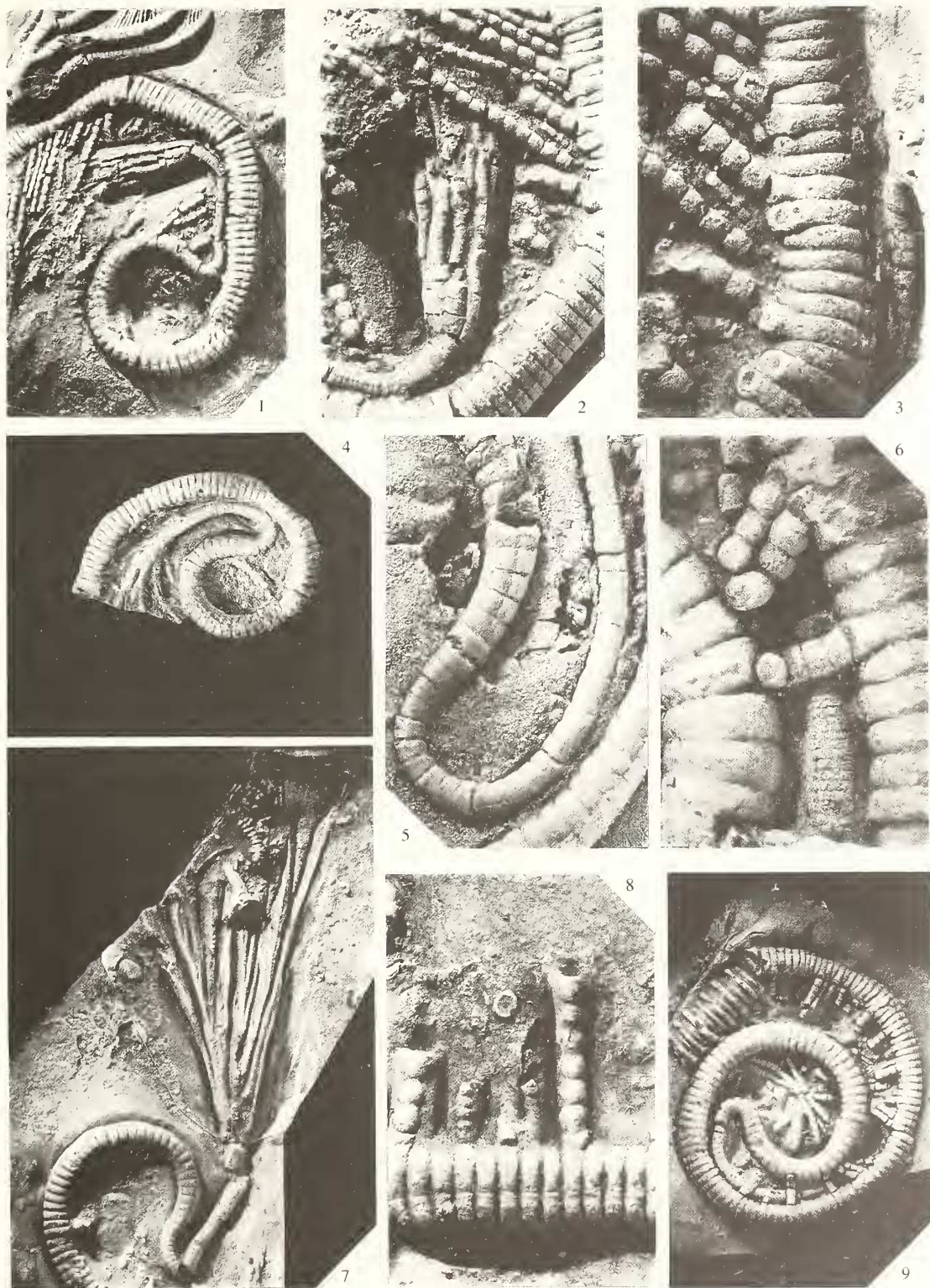
*Derivation of the trivial name.* From the Latin *Hibernia*, Ireland.

*Material, locality and horizon.* A unique holotype specimen, a crown and column preserved as a mould in sandstone (TCD 17381). The specimen label reads 'Lettershanbally, Maume'. Mr N. Monaghan of the

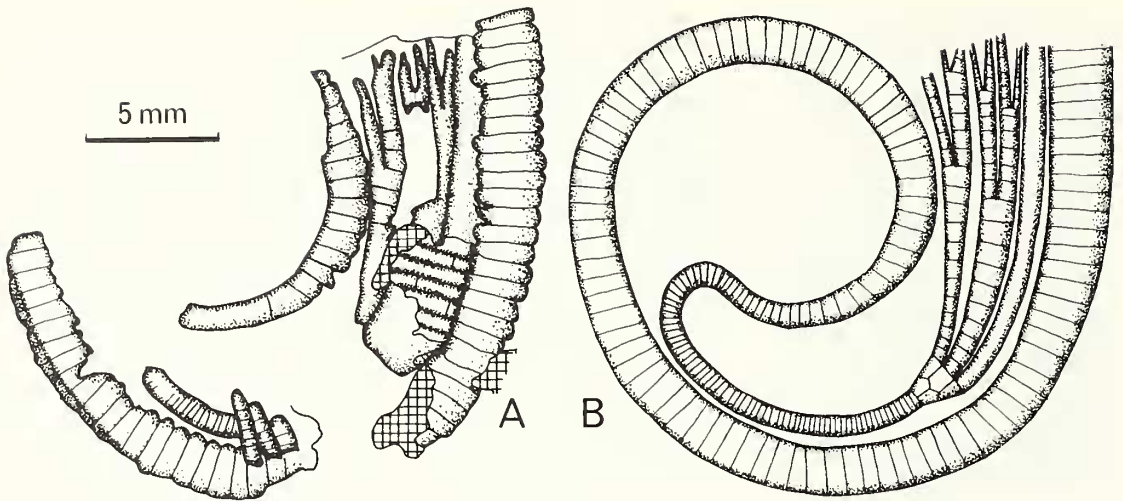
EXPLANATION OF PLATE 81

Figs. 1–9. *Myelodactylus fletcheri* (Salter, 1873). 1–3, BU Holcroft Collection 509. 1, complete specimen,  $\times 2$ . 2, crown (showing three rays) partially concealed by cirri,  $\times 4.5$ . 3, cirri, cirrus scars and part of the column,  $\times 9$ . 4, BU Holcroft Collection 457, specimen preserving only a single cirrus,  $\times 2$ . 5, OUM C17475, detail of the proxistele–dististele transition,  $\times 3.5$ . 6 and 9, OUM C17255. 6, the top of the column (the crown is missing), with protective, downcurved cirri (curvature of cirri probably postmortem),  $\times 10$ . 9, complete specimen,  $\times 2$ . 7 and 8, SM A12609, holotype. 7, crown and proximal part of the stem,  $\times 2$ . 8, part of the dististele retaining cirri,  $\times 5$ .

All specimens whitened with ammonium chloride.



DONOVAN and SEVASTOPULO, *Myelodactylus*



TEXT-FIG. 6. *Myelodactylus hibernicus* sp. nov., holotype, TCD 17381. The crown and proximal region of the stem. A, camera lucida drawing from a latex cast; B, restoration of the same (cirri omitted). Anal tube adjacent to the dististele.

National Museum of Ireland, Dublin, has kindly provided the following information. The label on the specimen of *Myelodactylus* identifies it as having been part of the Griffith Collection. Griffith (1855) showed two asterisks against Lettershanbally, Maam, County Galway (Irish Grid Reference L 965 537), which indicates that there were two collecting localities there. The lithostratigraphical unit which crops out at these localities is Griffith's Eb division, which corresponds to the Kilbride Sandstone Formation of Llandoverly (Telychian) age (Piper 1972).

*Diagnosis.* A species of *Myelodactylus* in which the crown and proximal stem are tightly coiled with cirri closely spaced, concealing the crown, the more distal part of the stem being straight but still cirriferous. Cirral ossicles are truncate conical in shape.

*Description.* Crown: the dorsal cup is concealed (Pl. 82, figs. 1 and 3; text-fig. 6), but was small. The branches of two apinnulate arms are poorly preserved (Pl. 82, fig. 3; text-fig. 6A). The anal tube is preserved adjacent to the inner surface of the dististele and, in consequence, the two arms are interpreted as being the D- and E-rays. The D-ray arm appears to branch isotomously twice; the E-ray arm branches heterotomously. It is difficult to discern individual ossicles in the anal tube, but they appear to be approximately as high as wide. They are not shown in text-fig. 6.

Stem: xenomorphic, divided into a short proxistele and a much longer dististele (the distal termination of the column is not seen). The proxistele is about 12 mm long, uncirriferous and homeomorphic, composed of low, ?circular columnals with convex latera. It is seen near the arms but not attached to the crown or the dististele (text-fig. 9A). The dististele is homeomorphic. Columnals are bilaterally symmetrical with a section similar to a 'cottage loaf'. Columnals of the dististele are about twice the diameter of those in the proxistele. Nodals bear

#### EXPLANATION OF PLATE 82

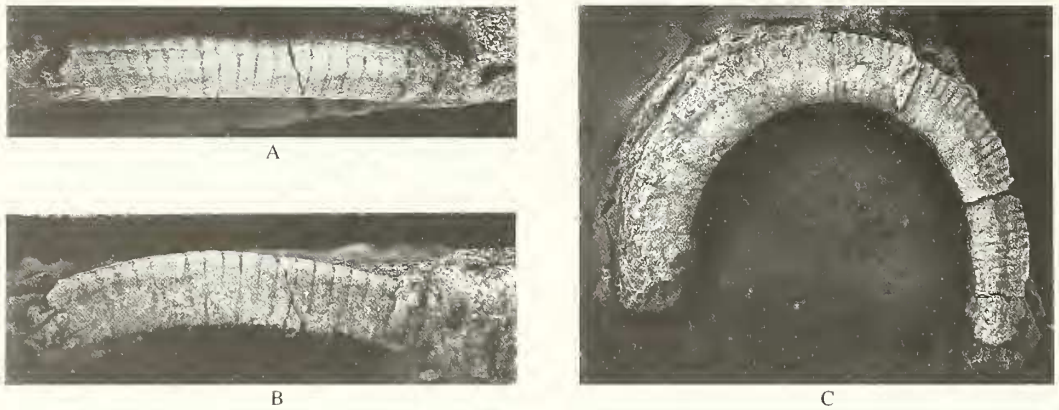
Figs. 1, 3, 4. *Myelodactylus hibernicus* sp. nov. Silicone rubber cast of the holotype, TCD 17381. 1, Crown and stem,  $\times 1.5$ . 3, detail of the crown, showing, from right to left, the anal tube, and arms in the D and E ray,  $\times 4$ . 4, Detail of the cirri attached to the dististele,  $\times 4$ .

Fig. 2 *Myelodactylus parvispinifer* (Brower). Latex rubber cast of the holotype RSM 1897.32.285,  $\times 1$ . Both specimens whitened with ammonium chloride.

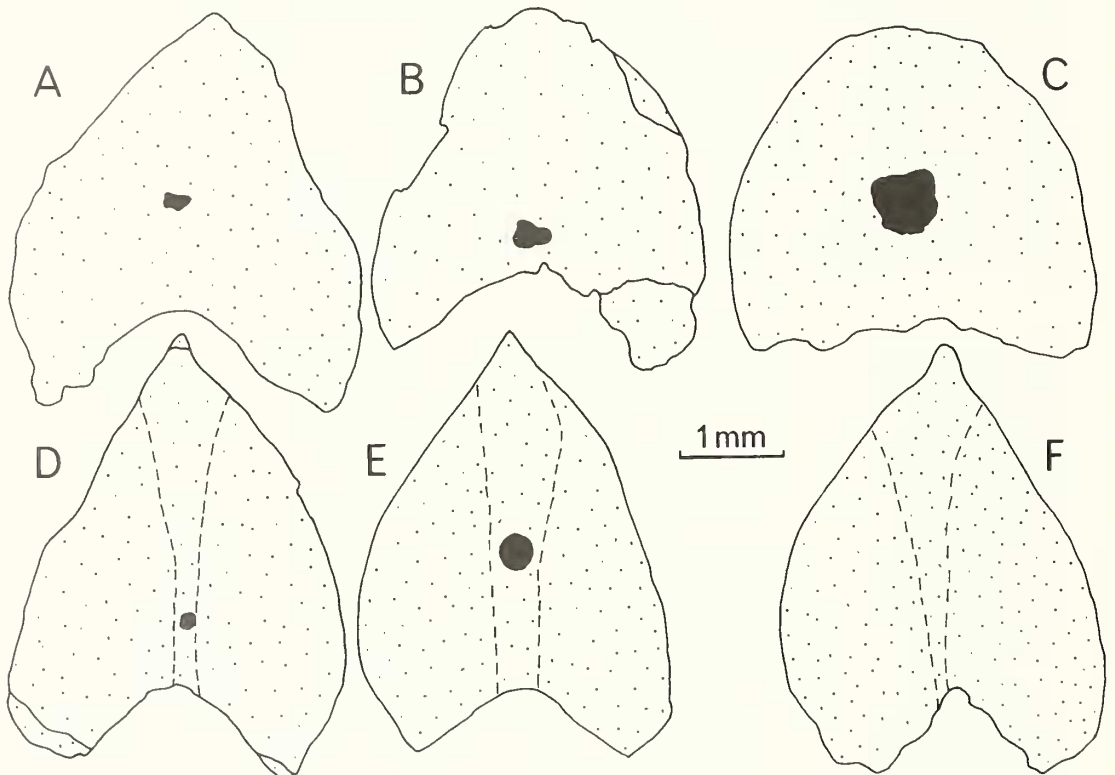




DONOVAN and SEVASTOPULO, *Myelodactylus*



TEXT-FIG. 7. A-C. *Myelodactylus penkillensis* sp. nov. A and B, outer and lateral view of the holotype, BMNH E49931,  $\times 2$ ; C, lateral view of paratype, BMNH E68010b,  $\times 2.5$ . Both specimens whitened with ammonium chloride.



TEXT-FIG. 8. *Myelodactylus penkillensis* sp. nov. Camera lucida drawings of four loose fragments of paratype BMNH E49930. A and B, D and E, represent the ends of two pluricolumnals, respectively; C and F, each represent an end from two further pluricolumnals. All fractured surfaces.

a pair of cirri, one at each edge of the inner surface, angled slightly away from the mid-line of the column. Nodal latera are convex. About 120 mm of the dististele is preserved. The articular facets are not visible.

Cirri arise in pairs from each nodal of the dististele. Cirri unbranched, slender, circular in section and composed of cirral ossicles which are slightly higher than wide. Cirral ossicles slightly conical with a truncated apex, tapering towards the proximal end. No distal termination of a cirrus is seen. Apparently forty or more cirral ossicles per cirral. The facet at the distal end of each cirral ossicle is fringed with short spines.

*Remarks.* The truncate conical cirral ossicles serve to distinguish this species from all other described species of *Myelodactylus* except *M. parvispinifer*. The latter has much less closely spaced cirri along the dististele than *M. hibernicus*.

*Myelodactylus penkillensis* sp. nov.

Text-figs. 7 and 8

1880 *Myelodactylus* sp.; Nicholson and Etheridge, pp. 330–334, pl. 21, figs 11 and 12.

1954 *Myelodactylus* sp.; Ramsbottom p. 87.

*Derivation of the trivial name.* After the type locality.

*Material, localities and horizon.* A holotype specimen, BMNH E49931 (text-fig. 7A, B), plus eight paratypes; BMNH E49930 (external mould with four associated fragments of column; text-fig. 8), E49932, E49933, E68009a, c (not counterparts), E68010a, b (text-fig. 7C) and E68013. All are pluricolumnals. The specimen labels state 'Silurian (Upper Llandovery). Penkill, Girvan, Ayrshire'. This is probably the locality in Penkill Burn that was mentioned by Lapworth (1882, p. 648; Ramsbottom 1954, p. 87), although Nicholson and Etheridge (1880, p. 332) mentioned two localities, '...the grey fossiliferous mudstone of Penkill; in the dark greenish-blue mudstone of Balclatchie'. Cocks *et al.* (1971, fig. 2) indicated that the Penkill Flags of the Girvan district correspond approximately to the *turriculatus-crispus* graptolite Biozones (late Fronian to early Telychian).

*Diagnosis.* A species of *Myelodactylus* known only from the dististele. The column has a unique section, similar in outline to a gothic arch.

*Description.* Crown: unknown.

Dististele: homeomorphic and curved to a lesser or greater extent. Columnals low, slightly wedge-shaped, with convex latera. Articular facet not seen. Axial canal appears circular in outline and lies in the plane of symmetry of the column (text-fig. 8A–E). In section the outer surface of the column is shaped like a gothic arch, sometimes with a prominent groove on either side of the angled crest (text-fig. 8A, B, D–E), which becomes more rounded in some specimens (text-fig. 8C). The inner surface of all columnals is more gently curved than the outer. Each nodal bears a pair of circular cirral scars at the edges of the inner surface.

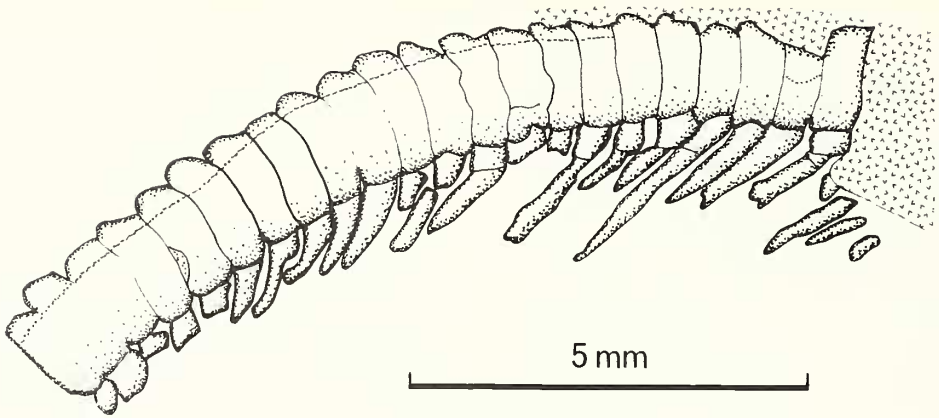
*Remarks.* By analogy with other species of myelodactylid these columnals represent part of the dististele. Pluricolumnals of this species are preserved as short, curved fragments, sometimes semicircular (text-fig. 7C) but never coiled. The distinctive columnal section differentiates this species from other British and Irish myelodactylids.

*Myelodactylus* sp. A

Text-fig. 9

*Material, locality and horizon.* A single specimen, BCM Cc913a, b, preserved as part and counterpart external moulds. Collected from Beds 10–18, Buckover section, near Tortworth, Gloucestershire: Tortworth Inlier. Wenlock Series (Curtis and Cave 1964).

*Description.* A homeomorphic pluricolumnal approximately 17 mm long, composed of thirty-three columnals. There are slight variations in columnal height but all are nodals. Sutures between columnals slightly curved. Latera gently convex. Articular facet not seen. Columnals probably about as long as wide. All cirri straight,



TEXT-FIG. 9. *Myelodactylus* sp. A. BCM Cc913B. Camera lucida drawing of a latex cast.

parallel and angled to the long axis of the column. Cirri taper towards the pointed tip and are short, composed of about four ossicles. Cirral ossicles have planar latera. Cirral facets cannot be seen.

*Remarks.* This species differs from *M. ammonis* in having a homeomorphic column composed of columnals with parallel articularia, rather than wedge-shaped columnals of the 'var. *alternicirrus*' type. The cirri are shorter than those found in *M. convolutus* and the column is relatively much narrower. This pluricolumnal is only slightly curved, suggesting that it was not part of the tightly coiled region of the stem.

*Acknowledgements.* We thank the following for allowing us to study the collections in their care: P. R. Crowther and M. L. K. Curtis, City of Bristol Museum; S. P. Tunnicliff, British Geological Survey; R. P. S. Jefferies, D. N. Lewis and A. B. Smith, British Museum (Natural History); A. Hallam, Birmingham University; C. Franzén-Bengtson, Naturhistoriska Riksmuseet, Sektionen for Paleozoologi, Stockholm; H. P. Powell, Oxford University Museum; W. D. I. Rolfe and C. D. Waterston, Royal Scottish Museum, Edinburgh; D. Price and R. B. Rickards, Sedgwick Museum, Cambridge; J. R. Nudds, Trinity College, Dublin. N. Monaghan, National Museum of Ireland, kindly gave us information about a specimen from the Griffith Collection; and F. Collier and P. Kier examined specimens in the Springer collection in the U.S. National Museum for us.

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Typescript received 20 April 1988

Revised typescript received 18 January 1989