A NEW GENUS OF INADUNATE CRINOID WITH UNIQUE STEM MORPHOLOGY FROM THE ASHGILL OF SWEDEN

by STEPHEN K. DONOVAN

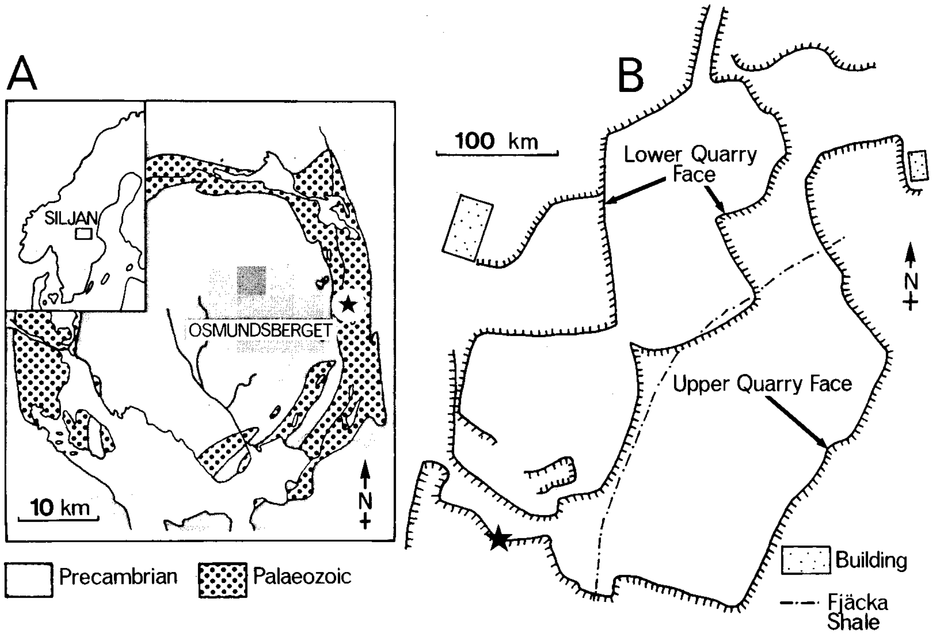
ABSTRACT. *Bodacrinus columnus* gen. et sp. nov. from the Ashgill Boda Limestone of Sweden is described on the basis of dissociated stem material only. The column is unusual, being trimeric, and trilobate to sub-trapezoid in outline. *Bodacrinus* is presumed to be closely related to the disparid inadunate crinoid *Ectenocrinus*, the only other pelmatozoan known to have had a trimeric stalk. Relative stratigraphic positions indicate that *Ectenocrinus* may have been the ancestor of *Bodacrinus*. The stem of *Bodacrinus* is functionally adapted to articulate about an axis which is at 90° to the directions of movement in other bilaterally symmetrical columns such as those of myelodactylids.

THE upper Ordovician rocks of the Siljan district, Dalarna, Sweden (text-fig. 1A) contain an abundant shelly fauna, principally of pelmatozoan columnals, cystoids, crinoid cups, orthocones, bivalves, gastropods, bryozoans, brachiopods, ostracods, trilobites, tabulates, and rugose corals. Echinoderms, particularly their columnals, form the dominant part of this fauna and are very abundant in the flank beds of the Kullsberg (Caradoc) and younger Boda (Ashgill) Reef Limestones. Only two species of crinoid cup have so far been described from these rocks; *Cornucrinus mirus* Regnéll, 1948 (both Kullsberg and Boda Limestones) and *C. longicornis* Regnéll, 1948 (Boda Limestone only). Additionally, *Grypocrinus genuinus* Strimple, 1963 has tentatively been identified from the Boda Limestone and seventeen further crinoid species have been identified from cups (Jobson 1983). From columnal evidence it is estimated that over fifty crinoid species are present in the Boda Limestone flank beds. So far only two inadunate crinoids from the Boda Limestone have been identified on the basis of columnals: the iocrinid *Ristnacrinus* sp. and the myelodactylid *Musicrinus bodae* Donovan, 1985. A third inadunate with distinctive columnals is described herein, from the Boda Limestone in Osmundsberget quarry (text-fig. 1B).

The new species is unusual both in its outline, which varies from trilobate (Pl. 23, figs. 1, 3, 6) to almost trapeziform (Pl. 23, fig. 5), and in being trimeric. Meric columnals are limited almost exclusively to the inadunate crinoids and the rhombiferan superfamily Caryocystitida, apart from the camerate crinoids *Cleiocrinus* (Ubaghs 1978, p. T65) and *Colpodecrinus* (Sprinkle and Kolata 1982), and the flexible (?)*Archaeotaxocrinus* (Lewis 1981). Trimeric columns are particularly rare and unusual, and have hitherto only been reported from the inadunate genus *Ectenocrinus* S. A. Miller, although not all members of this taxon have a tripartite stem (Warn and Strimple 1977, p. 89). Even when trimeric columnals are present, the column appears to be holomeric in the dististele, unlike *Bodacrinus*. The proxistele of the type species, *Ectenocrinus simplex* (Hall), is circular, trimeric, with a central pentagonal lumen and radiating crenularium. This is obviously quite different from the specimen described herein. Unfortunately the crown of the new species is unknown but the column and distal attachment are represented by numerous specimens. It is most probable that these columnals represent a new species closely related to *E. simplex* but with a stem that is functionally unusual. For these reasons, although the columnals represent a homocrinid close to *Ectenocrinus*, they are interpreted as representing a new genus.

Crinoid columnal terminology used in this paper follows Moore *et al.* (1968), Ubaghs (1978), and Webster (1974).

[Palaeontology, Vol. 29, Part 2, 1986, pp. 235–242, pl. 23.]



TEXT-FIG. 1. A, generalized geological map of the Siljan district of Dalarna, Sweden. The inset map shows the position of Siljan. The circular outcrop pattern was produced following meteorite impact (Thorslund and Auton 1975). B, plan of Osmundsberget quarry, with the position of the *Bodacrinus columnus* horizon marked by a star. Dip is to the north-west. Both figures after Jobson (1983, figs. 1, 3, respectively). The Fjäcka Shale marks the approximate boundary between the Kullsberg and Boda Limestones.

SYSTEMATIC PALAEONTOLOGY

Class CRINOIDEA J. S. Miller, 1821
Subclass INADUNATA Wachsmuth and Springer, 1885
Order DISPARIDA Moore and Laudon, 1943
Family HOMOCRINIDAE Kirk, 1914
Genus BODACRINUS gen. nov.

Type species. Bodacrinus columnus sp. nov.

Derivation of generic name. After the Boda Limestone.

Diagnosis. A genus of crinoid based on columnals only. Columnals trimeric, low, trilobate to subtrapezoid in outline, with a keyhole-shaped lumen and long, subparallel crenulae on the articular facet of the outer mere only.

Bodacrinus columnus sp. nov.

Plate 23; text-figs. 2A, 3, 4

Derivation of trivial name. After the Latin *columna* = column.

Types. Holotype, British Museum (Natural History) specimen BMNH E69536. Thirty-three paratypes, BMHN E69535, E69537–E69565 (E69547 refers to two columnals, E69564 to three columnals). All are either dissociated columnals, pluricolumnals, or distal terminations of columns with or without cirri.

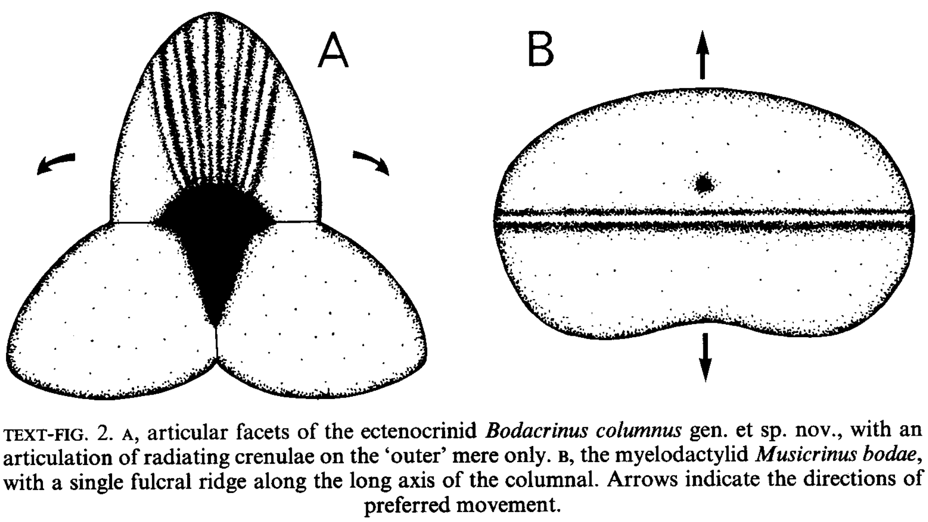
Locality and horizon. All specimens are from the upper Ordovician (Harjuan Series; Ashgill in terms of the British succession) Boda Limestone of Osmundsberget quarry, north of Boda, Siljan district, Dalarna, Sweden (text-fig. 1B).

Diagnosis. As for the genus.

Description. Columnal outline trilobate (Pl. 23, figs. 1, 3), triangular (Pl. 23, fig. 6), or sub-trapezoid (Pl. 23, fig. 5). Columnals trimeric, with an uneven but symmetrical development of the meres. A larger 'outer' mere (*sensu* Willink 1980; text-fig. 3A) is supported by two smaller, lateral meres. The articulum of the outer mere bears three to five crenulae which radiate from the lumen towards the circumference of the facet and may be slightly curved. The articular facet is otherwise unsculptured. The lumen is 'keyhole'-shaped, triangular, with the 'outer' side curved outwards and the two lateral sides curved inwards. Meric sutures correspond to the lumen angles and are apparent on both the articula and on the latus (Pl. 23, fig. 7). Columnals lower than wide. Latera are planar or slightly convex (Pl. 23, figs. 2, 4, 8–10), and unsculptured, except in the distal termination of the column. The latus may be slightly bevelled adjacent to the articula (Pl. 23, figs. 9, 10). The column generally appears to be homeomorphic, although some specimens may be heteromorphic based on slight variations in columnal height (e.g. BMNH E69553, where the order of columnals appears to be 11NN1). Distally the column tapers (Pl. 23, figs. 4, 8), although no actual terminal columnal (presumably conical) is preserved. Cirrus scars on the latus appear circular with a circular lumen and synostosial articulation (Pl. 23, fig. 2). Cirri circular, wider than high, with planar, unsculptured latera (Pl. 23, fig. 4).

Discussion. From this sample of only thirty-four specimens, two are distal attachment structures and a further pluricolumnal shows a definite taper at one end (Pl. 23, fig. 10), presumably related to the distal column. This apparently high frequency of distal stem fragments suggests that the complete column of *B. columnus* was short, perhaps with, say, less than 100 columnals.

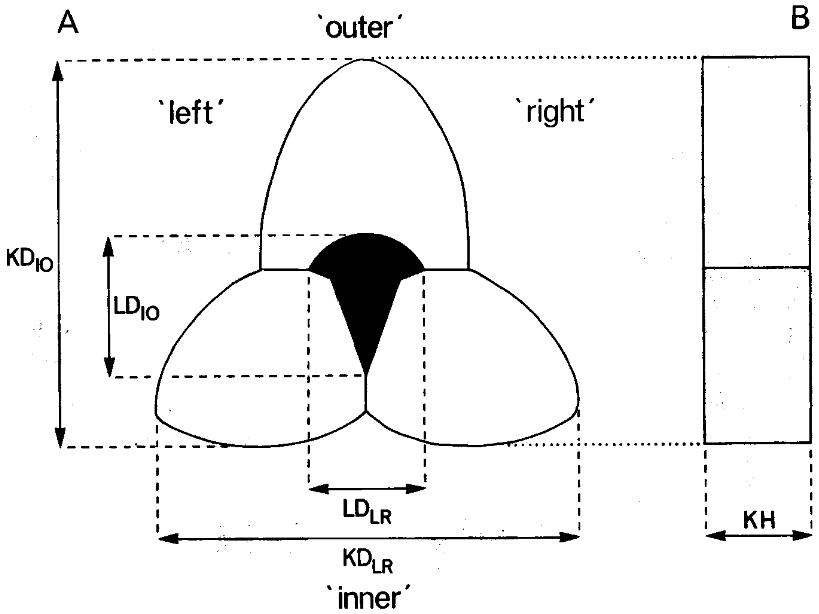
Functionally, the stem of *Bodacrinus* is unlike that of other crinoids with a bilaterally symmetrical stem such as the myelodactylids, platycrinitids, camptocrinids, and *Ristnacrinus*. The column of the myelodactylid *Musicrinus*, for example (text-fig. 2B), has a synarthrial fulcral ridge corresponding to the longest axis of the articular facet, which enabled the column to coil in a plane and individual columnals to rock towards their outer and inner surfaces in a see-saw manner. The unusual arrangement of the crenularium in *Bodacrinus* would have prevented such movement (text-fig. 2A)



TEXT-FIG. 2. A, articular facets of the ectenocrinid *Bodacrinus columnus* gen. et sp. nov., with an articulation of radiating crenulae on the 'outer' mere only. B, the myelodactylid *Musicrinus bodae*, with a single fulcral ridge along the long axis of the columnal. Arrows indicate the directions of preferred movement.

and made the stem less flexible. Because of the slightly fanning configuration of the crenulae it is thought that any movement would have been laterally but with a component of twisting towards the 'inner' surface (although 'outer' and 'inner' are used to describe different sides of the column, these terms do not necessarily have the same functional significance in *Bodacrinus* as they do in *Neocamptocrinus* Willink, 1980). The slight bevel of the latus seen adjacent to the articula on the lateral (and, to a lesser extent, the 'outer') surfaces in some specimens (Pl. 23, figs. 9, 10) may have aided stem flexibility, allowing more movement in the regions where this would have been greatest.

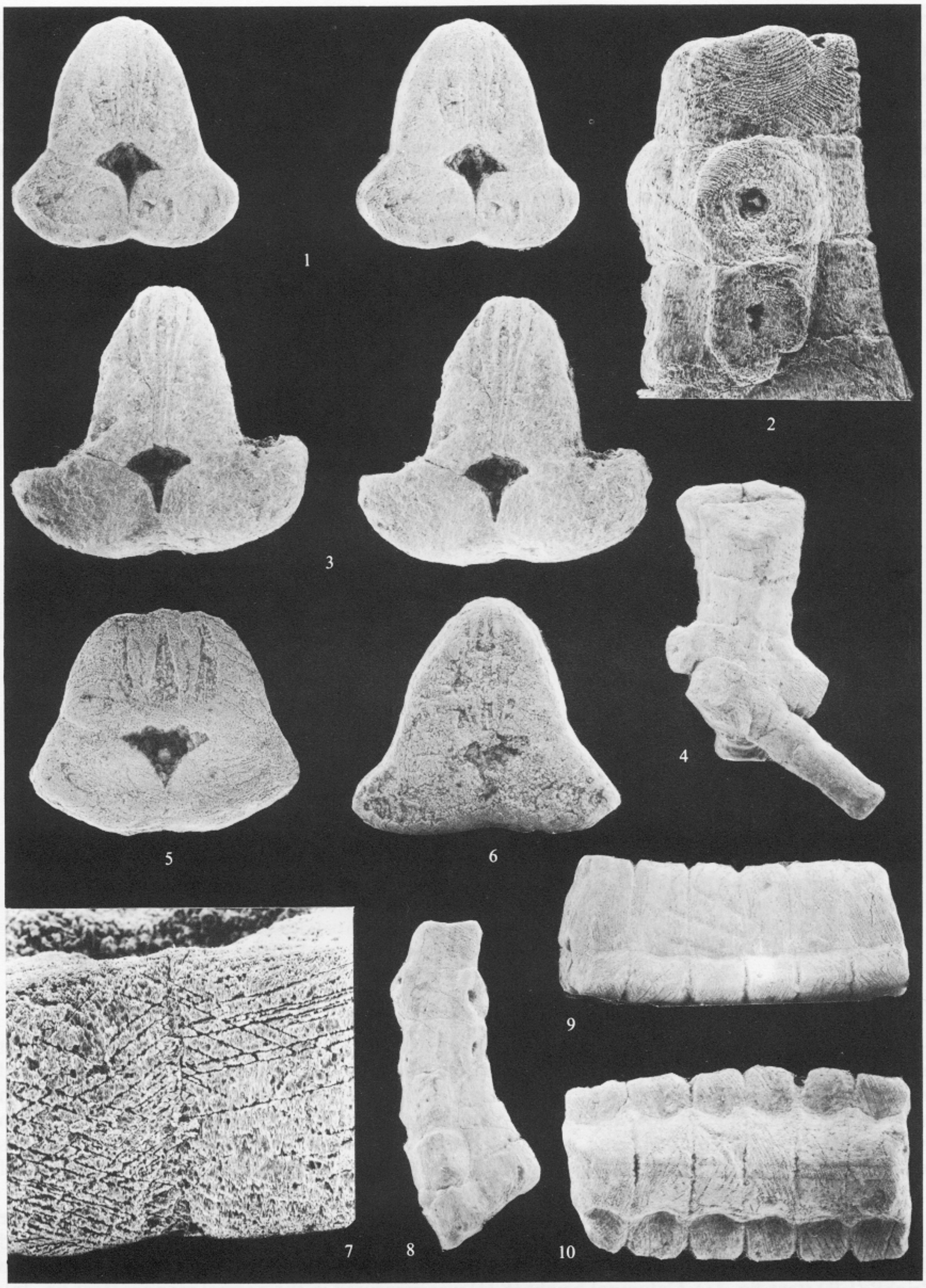
Bodacrinus was anchored to the substrate by cirri. Cirrus scars are limited to pluricolumnals from the (presumed) tapering dististele (Pl. 23, figs. 2, 4, 8) and arise on adjacent columnals



TEXT-FIG. 3. Measurements taken from columnals of *Bodacrinus columnus* gen. et sp. nov. A, articular facet. B, latus. LD = lumen 'diameter', KD = columnal 'diameter', KH = columnal height, IO = inner to outer, LR = left to right. 'Left' and 'right' are decided arbitrarily, 'outer' and 'inner' are used *sensu* Willink (1980), although the function of this stem is somewhat different to that of the camptocrinids to which the latter terms were originally applied.

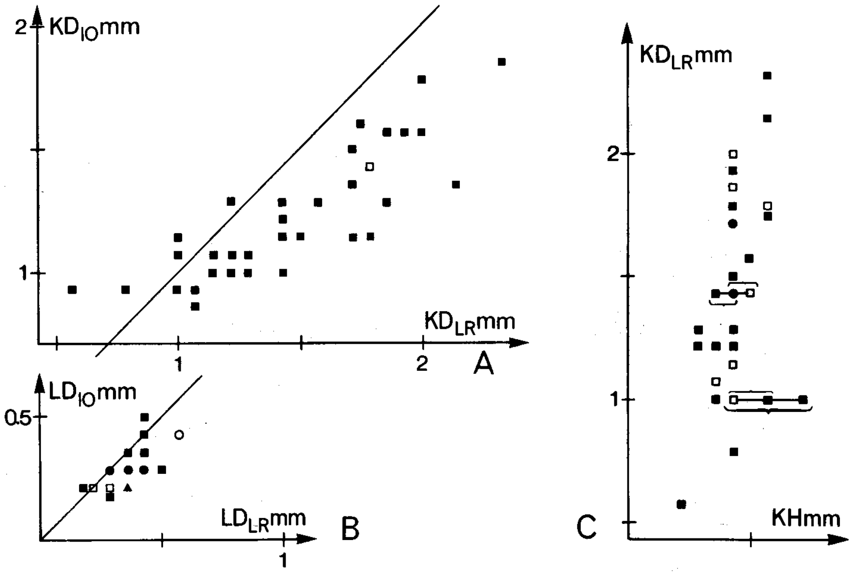
EXPLANATION OF PLATE 23

Figs. 1–10. *Bodacrinus columnus* gen. et sp. nov. All SEMs of specimens coated in gold. Figs. 2–10 show paratypes. Figs. 1, 3, 5, 6 orientated with 'outer' meres towards top of the page. 1, BMNH E69536, holotype. Stereo pair of the articular facet, ×30. 2, 8, BMNH E69540. Distal termination of the column. 2, lateral view of distal part of pluricolumnal showing cirrus scars, ×42. 8, lateral view of complete specimen. ×18. 3, BMNH E69535. Stereo pair of the articular facet, ×24. 4, BMNH E69542. Distal termination of the column retaining some cirral ossicles, ×21. 5, BMNH E69541. Articular facet with sub-trapezoid outline, ×42. 6, BMNH E69539. Articular facet with triangular outline, ×24. 7, BMNH E69537. Lateral view of meric suture, ×120. 9, 10, BMNH E69538, pluricolumnal, ×21. 9, lateral view. 10, 'outer' surface.



DONOVAN, *Bodacrinus columnus* gen. et sp. nov.

(cirrinodals). These scars do not show a fixed pattern of distribution (cf. Pl. 23, figs. 4, 8). Cirral ossicles have a synostosial articulation and are round, indicating inflexibility in all directions (Lewis 1980). The longest cirrus preserved (Pl. 23, fig. 4) is certainly very rod-like, although this may merely be an artefact of preservation. Cirri were orientated in a number of directions relative to the stem, which would favour their insertion into a soft substrate as a tree-like root, anchoring either an upright or, more probably, a recumbent stem. No specimen of *Bodacrinus* is known that was attached to a hard substrate. All have been collected from calcareous mudstones and shales, although columnals may be present in the associated limestone beds from which the recovery of fossils is more difficult. It is, therefore, concluded that *Bodacrinus* was most probably attached with the tapering dististele inserted directly into soft sediment, in which it was anchored by relatively few, stiff, rod-like cirri.



TEXT-FIG. 4. Graphical analysis of data from type specimens of *Bodacrinus columnus* gen. et sp. nov. A, KD_{IO}/KD_{LR}. B, LD_{IO}/LD_{LR}. C, KD_{LR}/KH. The reference lines in A and B have a slope of 1. Brackets in C group represent variations within heteromorphic columns. Black squares = 1 columnal, open squares = 2, black circles = 3, open circles = 4, black triangles = 5.

The 'inner' face of columnals is consistently flattened (Pl. 23, figs. 1, 3, 5, 6). If the attachment structure was inserted into the substrate at a low angle to the sediment surface, this flattened surface may have rested directly on the sediment. In this position the stem would only have been able to move from side-to-side, and slightly into, the sediment. This may have been an adaptation which prevented the column being swept back and snapped in strong currents. However, it is emphasized that this is merely conjecture and we really need to know the form of the crown of *Bodacrinus* before a more confident functional analysis can be made.

Graphical analysis of the columnals of *B. columnus* is more difficult than for ossicles of a more regular outline. In consequence of the unusual columnal outline the columnal 'diameter' (KD) and lumen 'diameter' (LD) were both measured in two directions, 'inner' to 'outer' (IO) and 'left' to 'right' (LR) (text-fig. 3A). Columnal height (KH) was measured in the normal manner (text-fig. 3B).

Both KD_{IO}/KD_{LR} and LD_{IO}/LD_{LR} plots (text-fig. 4A, B, respectively) show that these columnals are generally slightly wider than long. Presumably a very wide column ($KD_{LR} \gg KD_{IO}$) would be less flexible than a stem composed of very long ossicles ($KD_{LR} \ll KD_{IO}$), because the former would allow only comparatively little movement at its lateral extremities. Therefore, the measured parameters do not suggest the stem was very flexible. KH is generally low (text-fig. 4C), increasing slightly with increase in KD_{LR}.

The genus *Ectenocrinus* has a stratigraphic range from the Kirkfieldian or Shermanian to the Richmondian (Warn and Strimple 1977), i.e. approximately mid-Caradoc to Rawtheyan in terms of the British sequence (Ross *et al.* 1982). The stratigraphic position of *Bodacrinus* approximates to the upper limit of the range of *Ectenocrinus*, from which it is assumed to have evolved. This is one of the first records of an ectenocrinid in Europe, although the author has found rare trimeric columnals in the Ashgill of Ireland and north Wales. Also, Jobson (1983, p. 28) has recorded an *Ectenocrinus*-like cup from the Boda Limestone, although this is considerably smaller than most columnals of *Bodacrinus*.

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