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Comparative morphology of the stems of the extant bathycrinid *Democrinus* Perrier and the Upper Palaeozoic Platycrinitids (Echinodermata, Crinoidea)

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Abstract

The stems (=columns+attachment structures) of the extant bathycrinid, bourgueticrinine crinoids *Democrinus chuni* (Döderlein) and *Democrinus brevis* (A. H. Clark), from the western Indian and tropical western Atlantic Oceans, respectively, are described. The column is gracile; a short proxistele consists of low columnals that articulate synostosially; a long mesistele is comprised of high columnals that articulate synarthrially and show highly divergent fulcral angles within each columnal; and a distal, radicular attachment structure. The lumen is elliptical throughout most of the stem. Radices grow, in response to tactile stimuli, from paired radice nodes that occur on the latus, one at each end of the fulcrum at the proximal end of the columnals of the distal stem. Regeneration of the arms in bathycrinids following autotomy or predation involves the resorption of calcite from the proximal column. Encrusting epibionts, such as bryozoans, that are limited to single columnals may be indicative of frequent flexure in that part of the column.

The Upper Palaeozoic platycrinitids are the most diverse Palaeozoic crinoid group with stems that articulate synarthrially, that is, like *Democrinus* spp. The platycrinitid column mainly articulated synarthrially with elliptical columnals, apart from proximally, where the columnals were circular and a symplexy was developed. Articular facets within each elliptical columnal usually show divergent fulcral directions. Attachment was by a distal radicular structure. Unlike bourgueticrinines, the platycrinitid stem is usually robust, columnals are usually relatively lower, the features of the articular facet may be different and the pattern of radicular insertion shows differences in detail. Stabilization of the synarthrial ridges between adjacent columnals shows a wider range of morphologies in platycrinitids than in bourgueticrinines.

Key words: Crinoidea, Bathycrinidae, Platycrinitidae, morphology, stem, column, attachment structure, function.

Introduction

The stalked crinoids were a major group of marine invertebrates during the Palaeozoic, particularly in shallow-water environments, but are somewhat less important at the present day, having a reduced diversity and generally being limited to water depths of greater than about 150 m (Lane and Webster, 1980, p. 145). Studies of the functional morphology of Palaeozoic crinoids, while numerous, have nevertheless been hampered by a relative lack of direct observations by palaeontologists of extant stalked species, in both the laboratory and the field. Those studies of the microstructure of extant crinoids that have been published are largely concerned with two groups, the isocrinines and the so-called 'stemless' comatulids; in fact, in adult comatulids, the stem is reduced to one plate, the centrodorsal, from which the cirri (=attachment structures) arise. Important studies include those of Roux (1970, 1974a, 1974b, 1975, 1977b), Macurda and Meyer (1975), Macurda and Roux (1981), Macurda *et al.* (1978), Donovan (1984, 1993), Bourseau and Roux (1989), and Bourseau *et al.* (1991), amongst others. However, two of the other extant groups, the bourgueticrinines and the millericrinids (including the hyocrinids and the cyrtocrinines), have columns (see, for example, Donovan and Pawson, 1994; Roux, 1980) and attachment structures (discussion in Donovan, 1993) that are perhaps closer in morphology to at least some ancient groups (Donovan and Pawson, 1994, p. 1336).

The present study is an examination of the stem (both column and attachment structure) in two species of the bathycrinid bourgueticrinine genus *Democrinus* Perrier, 1883, with a particular emphasis on an analysis by scanning electron microscope (SEM), principally in order to determine their morphology and function. This study of these small, gracile crinoids is intended to complement the recent investigation of the robust phrynocrinid bourgueticrinine *Phrynocrinus nudus* A. H. Clark, 1907 (Donovan and Pawson, 1994). This systematic, descriptive approach is intended to reveal those morphological structures of the column and attachment structure which are peculiar to each, as well as identifying functional patterns in common to more than one, group. The ultimate purpose of the study is to produce data of value in interpreting morphologically similar stems in ancient taxa, such as the Palaeozoic platycrinitids (see below) and fossil bourgueticrinines. Such research is best undertaken on extant, rather than fossil, crinoids for a number of reasons, particularly the ease of disarticulation, the completeness, quality and abundance of specimens, and the absence of diagenetic effects. While well-preserved fossil crinoids are locally common, they cannot be disarticulated from their lithified state without mechanical damage, if at all; disarticulated columnals suitable for SEM analysis may be locally abundant, but they often cannot be related to gross stem morphology (see discussion of platycrinitid columnals below), the producing species being unknown (but exceptions occur: see, for example, Moore, 1967).

Terminology

Crinoid terminology used herein mainly follows Moore *et al.* (1968, 1978), Webster (1974) and Ubaghs (1978). The principal divergences in usage concerns the features used in fixation of the stem. The overall term "attachment structure" *sensu* Brett (1981) is preferred as the name of any pelmatozoan rooting, grasping or adhesion structure, rather than "holdfast", defined by Moore *et al.* (1978, p. T237) as "Any structure at distal extremity of column serving for fixation". This distinction is made as some of the attachments of *Democrinus* spp. and platycrinitids are not holdfasts *sensu stricto*, but are "rhizoidal holdfasts" ("distal stem segments with [radicles]"; Brett, 1981, table 1) approaching "runners" (="column attachments", not "holdfasts", according to Brett, 1981) in morphology. "Runners" are defined (Brett, 1981, table 1) as "usually non-permanent attachments by unmodified main portions of crinoid columns". However, attachments of *Democrinus* spp. and platycrinitids are permanent.

Further, it should be emphasized that the root-like attachments of bathycrinids have been referred to

herein as radicles rather than cirri. As was discussed in Donovan (1993), the cirri of isocrinids and comatulids are morphologically and functionally distinct from the root-like, radicular attachments of other crinoid groups. In brief, cirri articulate synarthrially and may include contractile tissues that enable re-attachment following relocation (Holland and Grimmer, 1981); radicular attachments articulate synostosially or symplectially and lack contractile tissues, precluding relocation. Synostoses in the attachment structures of *Democrinus* spp. indicate that the "roots" are rigid, not flexible. Such a branching attachment is presumably best adapted for penetrating and rooting in unconsolidated sediment; bourgueticrinines that attach to hard substrates do so with a terminal discoidal holdfast (see, for example, Donovan and Pawson, 1994).

The higher classification of crinoids used herein follows Simms (1988) and Simms and Sevastopulo (1993). The terminology of stereom microstructure follows Smith (1980). Recent specimens discussed herein are deposited in the Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Locality data for all of the specimens of *Democrinus* used in the present study are summarized in Appendix 1. Specimens mounted for SE microscopy are given a suffix (particularly in captions to Pls. 1-10) that includes the box number and number of stub with in the box, for example, USNM E99999/box 9/stub 9 (Appendix 2). Fossil platycrinitids are deposited in the Department of Paleobiology, USNM, and the Department of Palaeontology, Natural History Museum, London (BMNH).

Materials and Methods

Specimens of *Democrinus chuni* examined in the present study came from four stations in the Indian Ocean and south Atlantic Ocean between 700 and 2,125 m depth; those of *Democrinus brevis* are from 23 stations in the tropical western Atlantic Ocean from between 30 and 1,574 m depth (Appendix 1). Specimens of *Democrinus* were disarticulated using a solution of "Clorox" bleach diluted about 5 : 1 with tapwater. The process was observed using a Wild binocular microscope, enabling the removal of ossicles as they disarticulated so that they could be selected for examination before complete disaggregation into a mass of plates. Ossicles chosen for SEM examination were then thoroughly washed in tapwater to remove excess bleach, dried on a blotter and mounted on aluminium stubs using double-sided adhesive tape or, with some large fragments, with white "Elmer's Glue-All". Stubs were coated with 60% gold-palladium in the Scanning Electron Microscope Laboratory, National Museum of Natural History, Washington, D.C., and were examined using their Cambridge Stereoscan 250 Mark 2 and Leica 440 SE microscopes. Camera lucida drawings were made using a Wild binocular microscope.

Systematic Descriptions

Class Crinoidea J. S. Miller, 1821
Subclass Cladida Moore and Laudon, 1943
Infraclass Articulata J. S. Miller, 1821
Order Isocrinida Sieverts-Doreck, 1952
Suborder Bourgueticrinina Sieverts-Doreck, 1953

Remarks: The present paper adheres to the classification of Rasmussen (1978, p. T841-T847), who recognized four families of bourgueticrinine crinoids; the Bourgueticrinidae de Loriol, 1882 (Turonian-Eocene), Bathycrinidae Bather, 1899 (Maastrichtian-Recent), Phrynocrinidae A. H. Clark, 1907 (?-Recent), and Porphyrocrinidae A. M. Clark, 1973 (?-Recent). The stem of the extant phrynocrinid *Phrynocrinus nudus* A. H. Clark, 1907, was described in detail by Donovan and Pawson (1994), while Klikushin (1982) has figured numerous columnals derived from various Cretaceous-Palaeogene species of the bourgueticrinid *Bourgueticrinus* d'Orbigny, 1841 (see also Roux, 1978). The most comprehensive SEM analysis of the bourgueticrinine stem was that of Roux (1977a), which considered both phyrnocrinids and bathycrinids.

Macurda and Meyer (1975, p. 4-5, pl. 2, figs. 4-7 ; see also Macurda *et al.*, 1978, fig. 186.5-186.6), in a broad SEM survey of the crinoid endoskeleton, figured and discussed the morphology of a columnal(s) from the

mesistele of the bathycrinid *Democrinus* sp., emphasizing the typical features of the bathycrinid column, particularly details of the synarthrial articulation, while noting that more proximal columnals have a synostosial articulation, resulting in an unequally xenomorphic stem. Roux (1977a) made detailed analyses, including discussion of column ontogeny, in three species of bathycrinid from the Bay of Biscay; *Conocrinus cherbonnieri* Roux, 1976, *Conocrinus cabiochi* Roux, 1976, and *Democrinus parfaiti* Perrier, 1883. Subsequently, Roux (1978, pl. 2, figs. 2-11) figured SE micrographs of columnals of the Eocene *Democrinus londinensis* (Forbes, 1852) and Recent *Conocrinus* spp., both of which showed strong similarities to Recent *Democrinus* (see also Roux, 1976). Macurda and Meyer (1976, p. 648-657, pl. 1, pl. 2, figs. 3-4, 9-10, text-figs. 1B, C, 2-5) also made a particularly detailed SEM study of the skeleton of *Bathycrinus aldrichianus* Wyville Thomson, 1877, supplemented by analysis of column ontogeny using growth curves. Bourseau *et al.* (1991, p. 267-270, pl. 5, figs. 8-11) made a detailed SEM study of *Caledonicrinus vaubani* Avocat and Roux, 1990, including figuring a sequence of columnal morphologies. The soft tissues of Recent *Democrinus conifer* (A. H. Clark, 1909) were examined by TEM by Grimmer *et al.* (1984), who demonstrated that the radicular attachment was not homologous to the cirri of isocrinids and comatulids (also see discussion in Donovan and Pawson, 1994) and that no contractile tissues are identifiable in the stem. SE micrographs of early Pleistocene *Democrinus* sp. or *Monachocrinus* sp. were figured by Donovan (1995, fig. 5).

Family Bathycrinidae Bather, 1899
Genus *Democrinus* Perrier, 1883

Diagnosis: After Rasmussen (1978 : T844) : "Cup variably slender conical, cylindrical or fusiform, composed of 5 very high, slender basals forming greater part of cup and superposed by 5 short radials surrounding narrow central canal. Sutures distinct. Radial articular facets large. Articulation of basal circlet with top of stem smooth and circular, with diameter corresponding to base of cup. Growth of cup mainly affects basal circlet, height increasing more than width, mature specimens attaining slender, more cylindrical form. Interradial nerve canal extends from basals in sutures between radials before dividing. Arms 5, undivided. Every second brachial articulation is synostosial, synarthrial or trifascial. Synostosial articulations may be modified, a short median ridge from axial canal to dorsal edge of proximal articular face fitting into a furrow in distal face of preceding brachial. Few (generally less than 6) low proximal columnals have synostosial articulations. More distal columnals resemble those of other Bathycrinidae."

Range: Maastrichtian to Recent (Rasmussen, 1978 : T844).

Democrinus chuni (Döderlein, 1907)
(Pls. 1-5, Pl. 6, Figs. 1-5 ; Fig. 1)

1900 *Rhizocrinus* sp., Döderlein *in* Chun, p. 487-488, fig.
1907 *Rhizocrinus chuni* Döderlein, p. 14-15, fig. 6, pl. 1, fig. 5, pl. 6, fig. 6.
1908 *Rhizocrinus chuni* Döderlein ; A. H. Clark, p. 204.
1909 *Rhizocrinus chuni* Döderlein ; A. H. Clark, p. 676.
1911 *Rhizocrinus chuni* Döderlein ; A. H. Clark, p. 47.
1912 *Rhizocrinus chuni* Döderlein ; A. H. Clark, p. 279.
1912 *Rhizocrinus* (*Bythocrinus*) *chuni* Döderlein ; Döderlein, p. 14-16, figs. 3a, 5, 6, pl. 3, pl. 5, figs. 3, 4, pl. 7, pl. 8, figs. 1-9.
1912 *Rhizocrinus* (*Bythocrinus*) *braueri* Döerlein, p. 16-18, figs. 3b, 7. pl. 4, figs. 1-6, pl. 5, figs. 2, 5, pl. 6, figs. 1-6, pl. 8, fig. 10.
1917 *Bythocrinus chuni* (Döderlein) ; A. H. Clark, p. 392.
1917 *Bythocrinus braueri* (Döderlein) ; A. H. Clark, p. 392.
1923 *Bythocrinus chuni* (Döderlein) ; H. L. Clark, p. 229.
1924 *Bythocrinus chuni* (Döderlein) ; Gislén, p. 219.
1924 *Bythocrinus braueri* (Döderlein) ; Gislén, p. 219.
1927 *Bythocrinus braueri* (Döderlein) ; Gislén, p. 58.
1938a *Democrinus chuni* (Döderlein) ; Gislén, p. 26-27.
1938b *Democrinus chuni* (Döderlein) ; Gislén, p. 21-22, pl. 2, fig. 8.
1969 *Bythocrinus chuni* (Döderlein) ; Tommasi, p. 2.
1972 *Democrinus chuni* (Döderlein) ; A. M. Clark, p. 146-150, fig. 17, table 15.
1973 *Democrinus chuni* (Döderlein) ; A. M. Clark, p. 286-287.

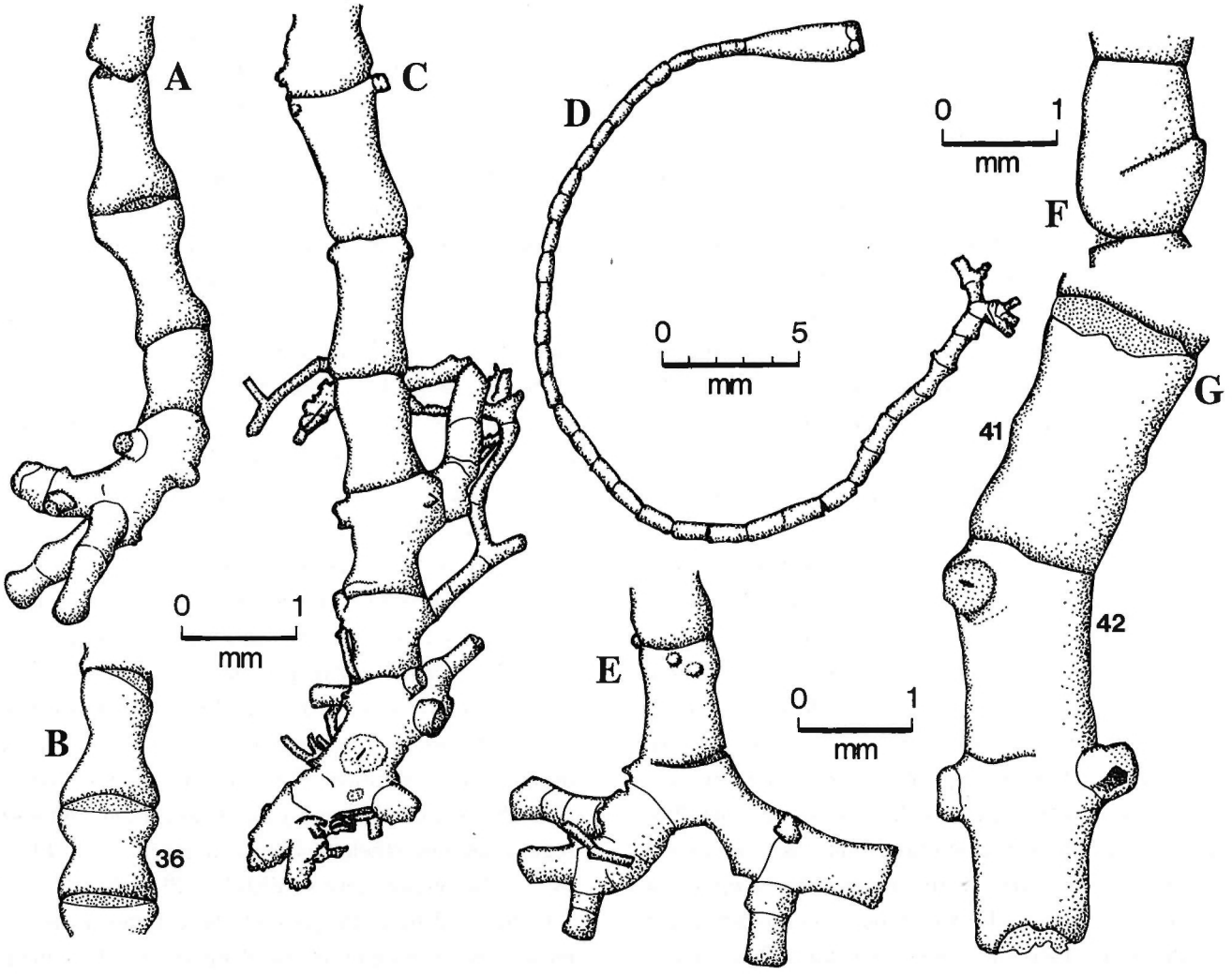


Fig. 1. *Democrinus chuni* (Döderlein, 1907). A, USNM E11616, distal stem with short attachment structure. B, USNM E11708, columnal 36, unusually low and with no relative rotation of the facets. C, USNM E11616, distal stem showing incipient root nodes at the proximal ends of more proximal columnals and the transition to a radicular attachment. D, E, USNM E11616 (=dissected specimen; see Pl. 1, figs. 1-5, Pl. 2, Pl. 3, figs. 1-3, 5, 6), complete specimen lacking only arms distal to $1Br_1$ (D) and Y-shaped attachment (E). F, G, USNM E11705, columnal 15 with swollen growth deformity (F) and columnal 42 (G), which is unusually elongate due to fusion (?) with adjacent, distal columnal. All figures camera lucida drawings of the stem.

1978 *Democrinus chuni* (Döderlein) ; Rasmussen, p. T844.

1997 *Democrinus chuni* (Döderlein) ; Donovan and Pawson.

Material and localities: See Appendix 1.

Description of stem:

Gross morphology: The stem of this species is elongate, slender and much narrower than all but the base of the conical dorsal cup, which is strongly tapered below the oral surface (Pl. 4, fig. 5 ; Fig. 1D). The column is either narrower than (Pl. 1, fig. 6) or as wide as (Pl. 4, fig. 1) the base of the cup. The column varies between being very slender (Pl. 1, fig. 6) to merely narrow (Pl. 4, figs. 1-5), altering in diameter little throughout the length of an individual. The stem varies in length up to at least 70 mm (USNM E11705) and can be composed of up to at least 48 columnals (Table 1), with associated radicles. The attachment structure is either tapered (Pl. 4, figs. 4, 5 ; Fig. 1C) or, more commonly, bifurcated or trifurcated (Pl. 3, fig. 4 ; Pl. 6, figs. 1, 3, 5 ; Figs. 1A, E).

Column: Columns of *D. chuni* are slender (Fig. 1D) and often string-like. Dorsal cups of about the same size have columns of different diameters, varying by a factor of about two. The proxistele may be slightly tapered away from the base of the cup. The proximal column of *D. chuni* consists of cylindrical columnals, lower than, or about as high as, wide, usually with planar latera, that increase in height away from the base of the dorsal cup (Pl. 1, fig. 6; Pl. 4, figs. 1, 5; Fig. 1D) until, within a short distance, they become over twice as high as wide (Pl. 4, fig. 2). The articular facet at the base of the dorsal cup is essentially planar, but with five shallow, regularly spaced, radial grooves that correspond to the sutures between basal plates (Pl. 1, fig. 1). These sutures are perpendicular to the sides of the central, rounded pentagonal lumen. In mature specimens, the proximal facet of columnal 1 has a pattern of raised, radial ridges of stereom trabeculae that interlock with the sutures between basals, forming an immovable, modified synostosial articulation (Pl. 1, fig. 4). In more slender, probably less mature columns this articulation appears to be synostosial (Pl. 1, fig. 6). The lumen of columnal 1 is more rounded than that at the base of the cup. The latus is planar and unsculptured, and this is the lowest columnal in the stem, with the possible exception of some low columnals bearing radicles in the distal part of the attachment structure (see below). The microstructure of columnal 1 is weakly organised galleried, perhaps trending towards labyrinthic, stereom (Pl. 1, fig. 4) ; certainly in slightly more distal columnals the stereom is distinctly galleried in lateral view (Pl. 1, figs. 2, 6). However, more distal columnals loose this organization and become distinctly labyrinthic (see, for example, Pl. 2, figs. 5, 7; Pl. 4, figs. 2-4).

Articulations between columnals in the most proximal part of the column are synostosial (Pl. 1, fig. 3; Pl. 5, fig. 2), with progressively more elliptical lumina. The long axes of these lumina correspond to what become the axes of synarthrial articulation on slightly more distal facets. The most proximal, weakly developed, synarthrial ridges may appear as high in the column as on the distal facet of columnals 2 (Pl. 1, fig. 5) or 3 (Pl. 5, fig. 3). The early synarthrial ridges are little more than concentrations of thicker stereom trabeculae on an essentially planar facet. Although the circumference of the lumen is flush with the articular facet in the most distal synostosis (Pl. 1, fig. 3; Pl. 5, fig. 2), with the appearance of the first synarthry it is slightly sunken (Pl. 1, fig. 5; Pl. 5, fig. 3). In this region the elliptical lumina have divergent orientations of *circa* 80° (compare Pl. 1, figs. 3, 5, mounted in the same relative orientations). The facet also becomes slightly elliptical with the development of a synarthry, the long axis corresponding to the synarthrial ridge (compare with discussion in Donovan, 1988). The greatest proportional increase in columnal height in the proximal stem is between columnals 1 and 2 (compare Pl. 1, figs. 4 and 2, respectively), although columnals become progressively higher until about the region of columnals 3-7 (Pl. 1, fig. 6; Pl. 4, fig. 5; Fig. 1D). In the proximal region of the column latera are essentially planar to gently convex and, with the development of synarthrial ridges that are divergent between the facets of any given columnal, the cylindrical shape of the columnals becomes slightly distorted as the facets become more elliptical. The areolae flanking these synarthries are only weakly depressed, although these regions are nevertheless obvious in lateral view (Pl. 4, fig. 5), becoming more so distally (Pl. 4, fig. 2).

In the mid to distal part of the column, facet ellipticity is far more pronounced and the areola regions much more depressed, giving columnals a more lobate, high 'T'-shaped to vase-like outline in lateral view with prominent, lensoid sutures between them (Pl. 2, fig. 5; Pl. 4, fig. 3). Columnal 15 of USNM E11705 (Fig. 1F), in a specimen consisting of 42 ossicles (Table 1), appears to have a slight, inflated growth deformity, although no evidence of parasitism is apparent. Only rarely do (aberrant?) columnals not show rotations between facets (Fig. 1B); the illustrated example is also unusually low. Otherwise, the angle of offset between fulcra of columnals in the mesistele generally lies in the range 70-80°. For example, in USNM E11616/box I/stubs 5-12, the offset angles for columnals 4 (=C4) through 19 (=C19) are: C4, 88°; C5, 69°; C6, 74°; C7, 75°; C8, 76°; C9, 80°; C10?, 74°; C11?, 88.5°; C12, 64°; C13, not measured; C14, 72°; C15, 76°; C16, 76°; C17, 75.5°; C18, 77°; C19, 76°. Despite

the extreme changes of shape when compared with more proximal columnals, latera in the middle and more distal column are still unsculptured, but are more obviously convex. Articular facets are more (Pl. 2, fig. 6; Pl. 5, fig. 8) or less (Pl. 2, fig. 1) elliptical. The elliptical lumen occurs in a deep depression, shaped like the figure '8', that separates the two parts of the synarthrial fulcrum. A fulcrum corresponds to the long axis of its articular facet. Fulcra are moderately broad (that is, the articular surface of the fulcrum is flattened) with a narrow, longitudinal groove that separates two linear rows of robust crenulae orientated perpendicular to the ridge axis. Crenulae on either side of the longitudinal groove are more or less offset (Pl. 2, figs. 1, 6). Stereom of the articular facet is apparently labyrinthic, or possibly galleried or rectilinear, apart from the crenulae of the fulcra, which are massive and imperforate (see, for example, Pl. 2, figs. 1, 6; Pl. 5, fig. 8).

Attachment structure: The attachment of *D. chuni* is a more or less branched, radicular structure at the distal end of the stem. The first apparent modifications of the column as the attachment is approached (Fig. 1C) occur on the latus on the proximal end of each columnal and adjacent to the ends of the synarthrial ridges (Pl. 2, figs. 3, 4, 7; Pl. 5, figs. 1, 4, 5), where tubercular structures are formed. Initially no more than one such structure is formed at each end of a ridge. These structures, termed radice nodes herein, are initially low domed or low cylindrical in shape, becoming broader and/or longer on more distal columnals. These nodes are perforated by an axial canal (Pl. 2, fig. 3), which must be formed by resorption of stereom calcite. In more distal columnals their facet is broader and more flattened, developing into the synostosial radicular facet upon which the individual radicles articulate (see, for example, Pl. 5, figs. 6, 7). These radice nodes may increase in number per columnal (Pl. 5, figs. 6, 7; Pl. 6, figs. 2, 4) or increase in diameter (Pl. 3, figs. 1, 3; Pl. 5, figs. 6, 7; Pl. 6, figs. 2, 4) or both more distally. New radicular growths in this region are mainly, but not invariably (Pl. 5, fig. 6), concentrated at the proximal ends of the columnals.

Attachment structures vary from having radicles growing from each of a series of columnals as a radicular 'runner'-like structure (Pl. 6, fig. 3; Fig. 1C), analogous to a cirriferous runner *sensu* Brett (1981), to having a distal branching termination (Pl. 3, fig. 4; Pl. 4, fig. 4; Pl. 6, figs. 1, 5; Figs. 1A, E) (=dendritic and virgate radices of Brett, 1981). The synarthrial articulations that are otherwise found throughout most of the column are progressively modified in this region to synostoses, with the lumen becoming rounded and flush with the surface of the planar facet (see sequence Pl. 2, fig. 2 to Pl. 3, figs. 1, 3 to Pl. 6, figs. 2, 4). Articular facet morphology of the most proximal and most distal columnals is thus convergent. The longitudinal groove of the synarthrial ridge, which extends into the periluminar depression (Pl. 3, fig. 3), also becomes branched and more penetrative to form the extensions of the axial canal of the column that project into the radicles (Pl. 3, fig. 1). These canals persist in the more distal columnals that have lost the synarthry (Pl. 6, fig. 4). Columnals in this distal region are about as high as wide, or slightly higher (more proximal) or lower, with a gentle, distal taper (Pl. 5, figs. 6, 7). Some columnals in the region of the attachment structure may at least appear to be fused. The attachment may retain part of a thin, brown, sheath-like cover.

In a typical example (USNM E11616; for others, see Table 1), the first undoubted branch of the attachment structure occurred at the columnal 31. However, radice nodes (=incipient root branches) occur at the proximal ends of columnals 26-30, one at either end of each fulcral ridge. Branching points increase in number more distally, with the first pair of radicular facets on columnal 32. Such columnals have an inverted Y-shaped and are obviously terminal, with numerous radicles on either branch of the Y (Figs. 1D, E).

Radicles vary from being robust to gracile, even within one stem (Fig. 1C). Radicular ossicles are rounded to elliptical in outline, with a synostosial articulation, a central to slightly excentric axial canal that is rounded, elliptical or slot-like in outline, and a facet displaying a coarse labyrinthic stereom with an obvious concentric arrangement (Pl. 3, figs. 5, 6). Radicular ossicles may be higher than wide, particularly in major branches following bifurcation (Pl. 3,

fig. 4; Pl. 6, fig. 1), but are more often about as high as wide or lower.

Columnals 41 and 42 (most distal preserved columnal; Table 1) of USNM E11705 may each be fused from a pair of columnals (Fig. 1G). About the midpoint of 42 is a pair of broken radicular branches, plus there is a radicular facet at the proximal end. No incipient radicular nodes are apparent on any more proximal columnals. Table 1 summarizes data on the occurrence of root structures in this and other specimens.

Table 1. Features of some columns of *Democrinus chuni* (Döderlein, 1907), including number of columnals per column, the columnal on which the first radice node is present and that on which the first radicular facet occurs. Key: *=incomplete; +=possible 49th columnal at base of cup; ~=column slender ('string-like') and presumed juvenile; **=discussed in text.

Specimen number	No. of columnals	First node(s)	First facet(s)
USNM E11616**	32	26	31
USNM E11705**	42*	42	42
USNM E11705	48+	45	48
USNM E11705	44	37	41
USNM E11705	47	36	42
USNM E11705	34*	29	31
USNM E11705~	34	30	31
USNM E11705~	27	27	27

Democrinus brevis (A. H. Clark, 1909)
(Pl. 6, Fig. 6, Pls. 7-10 ; Figs. 2, 3)

1884 *Rhizocrinus rawsoni* Pourtalés (*pars*) ; Carpenter, p.

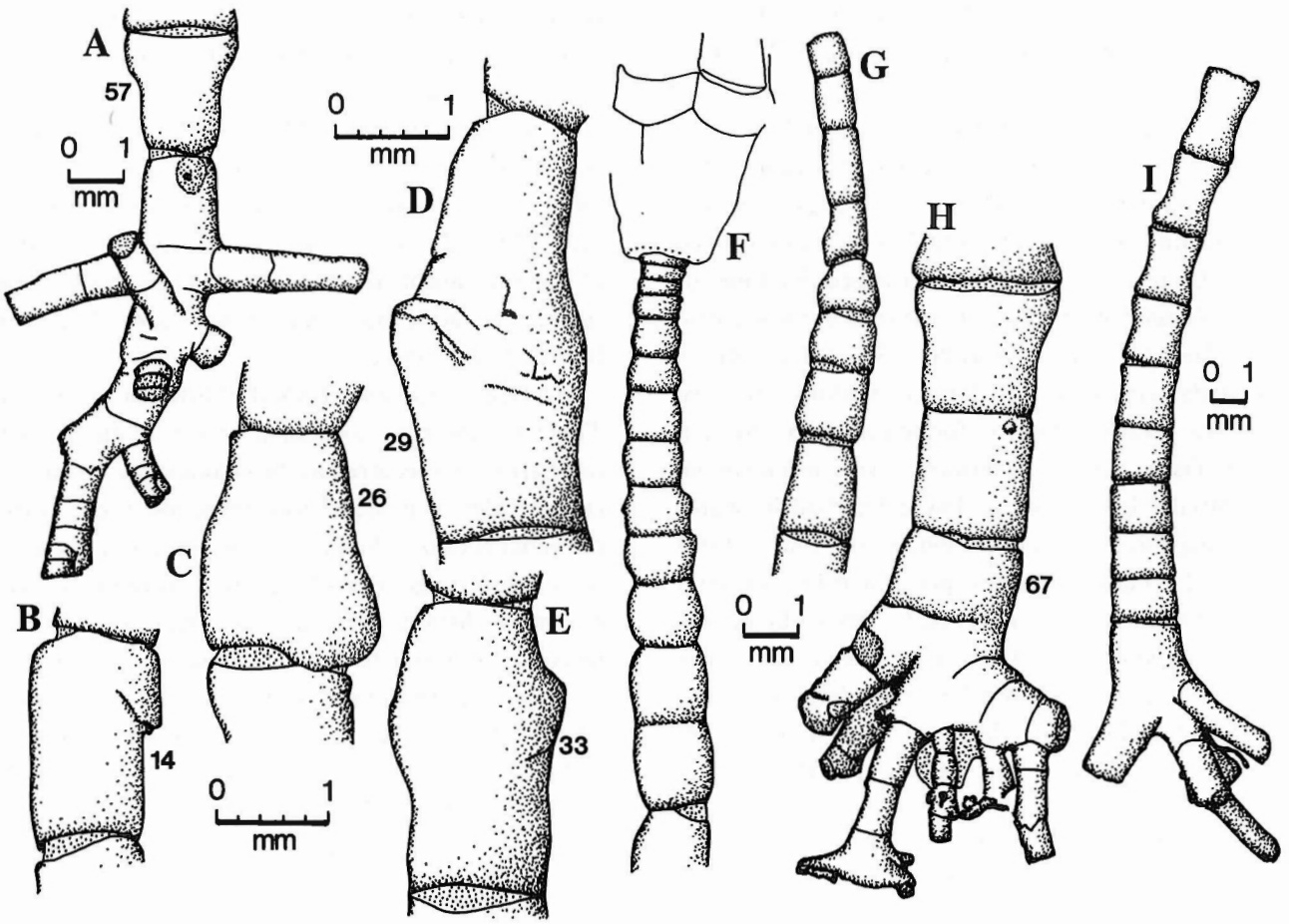


Fig. 2. *Democrinus brevis* (A. H. Clark, 1909). A, USNM E26226, attachment structure. B-E, USNM E26224, columnals with growth deformities in a column 95+ mm in length. F, USNM E17499, specimen with unusual proxistele that is particularly narrow adjacent to the crown. G, USNM E17917, tapering proximal column (crown not preserved). H, USNM E17498, attachment structure (note node on columnal 66). I, USNM E17917, attachment structure. Numbers next to some columnals indicate their position in the stem. All figures camera lucida drawings of the stem.

262, 263, 267, fig. 19.

1892 *Rhizocrinus rawsoni* Pourtalés ; A. Agassiz, p. 66, footnote.

1909 *Rhizocrinus brevis* A. H. Clark, p. 675.

1917 *Bythocrinus brevis* (A. H. Clark) ; A.H. Clark, p. 392.

1928 *Democrinus rawsoni* (Pourtalés) (*pars*) ; Gislén, p. 14.

1938a *Democrinus brevis* (A. H. Clark) ; Gislén, p. 25-26.

1978 *Democrinus brevis* (A. H. Clark) ; Meyer *et al.*, p. 426, 434, table 1, appendix 1.

1990 *Democrinus brevis* (A. H. Clark) ; Messing and Dearborn, p. 22.

1997 *Democrinus brevis* (A. H. Clark) ; Donovan and Pawson.

Synonymy: Note that, although Messing and Dearborn (1990, p. 22) suggested that *D. brevis, Democrinus robustus* (A. H. Clark, 1909) and Democrinus conifer A. H. Clark, 1909 are synonymous (also note comments by Gislén, 1928, p. 15; Meyer *et al.*, 1978, p. 435), no formal revision has been published. The above synonymy list only includes references to *D. brevis*, and not to *D. robustus* or *D. conifer*.

Material and localities: See Appendix 1.

Description of stem:

Gross morphology: The stem of this species is commonly longer than that of *D. chuni* and is composed of more columnals (Table 2). The column is as wide as the base of the cup (Pl. 6, fig. 6) or narrower in presumed juveniles; in at least one specimen the column increases in diameter away from the base of the cup (Fig. 2F). This is a more robust species than *D. chuni* and mature columns tend to be wider. The stem varies in length up to at least about 190 mm (USNM E17498) and can be composed of up to at least 67-68 columnals plus attachment structure, with associated radicles (Fig. 2H; Table 2). The attachment structure is tapered (Fig. 2A), distally branched (Pl. 10, fig. 1; Fig. 2I), densely branched (Pl. 10, fig. 7; Fig. 2H) or may form a radicular runner or rhizoidal holdfast (Pl. 10, figs. 2, 3).

Column: In lateral view the structure of the column is similar to that of *D. chuni*, although some differences of detail occur. The most proximal columnals increase in height away from the cup and have planar

Table 2. Features of some columns of *Democrinus brevis* (A. H. Clark, 1909), including number of columnals per column, the columnal on which the first radice node is present and that on which the first radicular facet occurs. Key: *=incomplete; **= see Figure 2A (overall length about 127 mm); ~=columnal 51 is a multi-branched radicular structure, more proximal columnals not appearing nodose; °=attachment structure distal of columnal 67 (Fig. 2H).

Specimen number	No. of columnals	First node(s)	First facet(s)
USNM E17498	67°	66	'68'
USNM E17992	44	32/33	43(?)
USNM E26223	44*	33	37
USNM E26224	30	28(?)	29
USNM E26226**	64+	??	58
USNM E41938	51~	--	--

latera (Fig. 2F; sequence Pl. 6, fig. 6 to Pl. 7, figs. 1, 2). The first synarthrial articulation obvious in lateral view is between columnals 6 and 7 (Pl. 7, figs. 3, 4; also USNM E26226), although the fulcra are more triangular than elongate (for example, compare Pl. 7, fig. 4 with Pl. 8, fig. 7). Synarthrial ridges are well-developed by columnal 11 (Pl. 7, figs. 5, 6), although distinct crenulae perpendicular to the ridge are only present more distally (Pl. 8, figs. 4, 6, 7). Columnals may not be higher than wide until about columnal 5 (Fig. 2F).

The mesistele is composed of tall columnals that articulate synarthrially. In contrast with *D. chuni*, these may be very tall and the ends of the elliptical articular facets are particularly angular (Pl. 8, figs. 4, 6, 7). Columnal 26 of USNM E17992 is particularly long, with a ridge at mid-height on the latus. Similarly, USNM E41938, which lacks the distal column, has some unusually high, ridged columnals in the proximal part of the mesistele (Fig. 3A) and is best compared with certain tall, juvenile columnals (see below; Pl. 9, figs. 5, 6). One tall columnal has a nodose structure developed on the latus (Figs. 3B, C).

Columnals of the mesistele may show a range of irregular deformations, even within one column (Figs. 2B-E). Although at least one gall-like growth deformity has been noted (USNM E17447; Donovan and Pawson, 1997, fig. 3D), most deformations of the column lack any obvious signs of infestation. How-

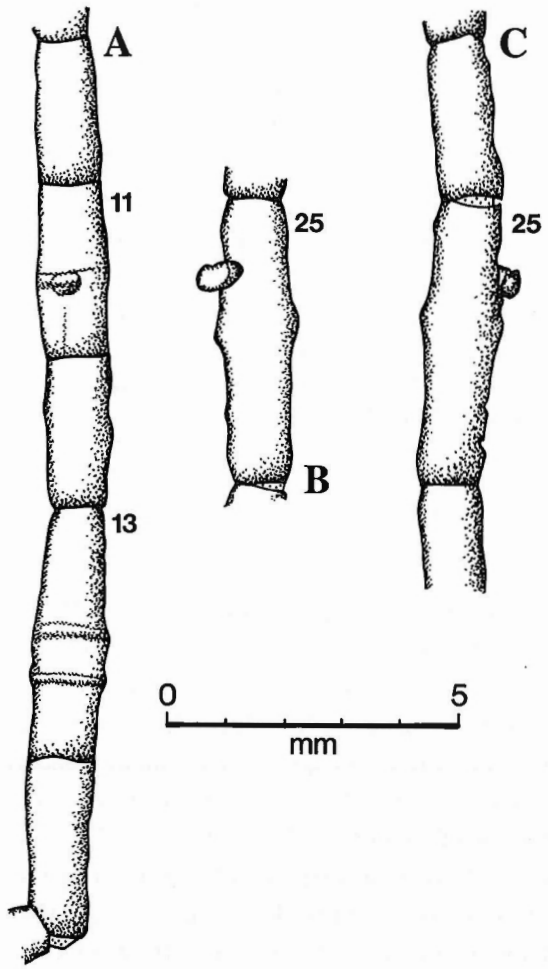


Fig. 3. *Democrinus brevis* (A. H. Clark, 1909). A, USNM E41938, detail of two unusually high columnals (11 and 13). B, C, USNM E41937, two views of the high columnal 25 bearing a nodose growth. Numbers next to some columnals indicate their positions in the stem. All figures camera lucida drawings of the stem.

ever, as a general observation of *D. chuni* and *D. brevis*, several of the specimens examined showed some sort of growth deformity in one or more columnals. An unusual specimen (Fig. 2G) is a headless' pluricolumnal, retaining part of the distal stem, that shows a distinct, proximal taper.

In juvenile specimens (Pl. 9, figs. 1-7) the column is long and slender. The base of the conical dorsal cup is narrow, but as wide as the proximal column (Pl. 9, figs. 3, 4). Columnals are low proximally, increasing in height away from the cup (Pl. 9, fig. 4) and becoming particularly elongate more distally (Pl. 9, figs. 1, 2, 5, 6). In lateral view these juvenile columnals show a well-developed arrangement of galleried stereom, with prominent trabeculae arranged parallel to the long axis of the column (Pl. 9, figs. 4-6). In the middle region of the column, the very tall columnals are distinctive in having a central, raised girdle in which area longitudinal trabeculae are seen to branch or coalesce (Pl. 9, figs. 5, 6). The longitudinal trabeculae of adjacent proximal columnals appear to interlock in at least some sutures (such as more distal articulations in Pl. 9, fig. 4), perhaps suggesting a syzygy-like articulation (syzygies *sensu stricto* do not occur in the crinoid stem; Moore *et al.*, 1978, p. T242). The section of a columnal in the distal part of the column shows it to be only 2-3 trabeculae in diameter (Pl. 9, fig. 7).

One mature specimen has an unusual proximal column that decreases in diameter away from the dorsal cup (Pl. 9, figs. 8, 9). The change from this 'hourglass-shaped' region, consisting of the most proximal 7-8 columnals, to the more normal column is abrupt (Pl. 9, fig. 9). Otherwise the column appears to be normal, although the most distal preserved columnal (about number 13) is only just developing synarthrial articulations (Pl. 10, fig. 5). It is considered pertinent to note that the arms of this specimen are missing above $1Br_1$ (Pl. 9, fig. 8).

Attachment structure: The morphology of the attachment structure is similar to that of *D. chuni*. Where the attachment has radicles arrayed essentially perpendicular to the column, these diverge at close to 90° between adjacent columnals (Fig. 2A). Some attachments are terminal, with little or no development of radice nodes or facets on the adjacent column (Pl. 10, fig. 1; Fig. 2I). Note also the reduction in the height of the columnals as the attachment is approached (Fig. 2I), also seen in some specimens of *D. chuni*. Radicles in some specimens reach over 15 mm in length (USNM E18604). Although robust proximally (Pl. 10, figs. 1, 2), radicles are composed of radicular ossicles that taper and may become branched more distally (Pl. 10, figs. 3, 7). Radicular ossicles are elongate, with unsculptured latera and synostosial articulations (Pl. 10, fig. 4).

Radice nodes are usually developed in a pattern similar to those of *D. chuni* (Pl. 8, fig. 3), occurring

first on the latus at either end of the fulcral ridge at the proximal end of the columnal. More distally, nodes become elongate with a distal articular facet for the articulation of radicles (Pl. 8, figs. 2, 5, 6). Multiple radicular facets are developed close to this original position more distally, sometimes showing evidence of branching within a single facet (Pl. 10, fig. 6).

One pluricolumnal (USNM E25944) is over 85 mm long and consists of 25 robust columnals. This fragment has radice nodes and/or facets developed on the most distal 23 columnals. The most distal columnal of this specimen is not terminal.

Discussion

Gross morphology: In both *D. chuni* and *D. brevis*, the column may be very slender and never exceeds a maximum diameter that equals the diameter of the base of the dorsal cup. The very slender columnals are interpreted as being juveniles (such as Pl. 9, figs. 1-7). This suggests that the growth of the column in *Democrinus* initially involves the rapid production of elongate columnals (Pl. 9, figs. 5, 6) which produce a column that elevates the crown above the sea floor early in development. Once the crown has attained, or while it is attaining, some maximum height, the growth of the columnals changes to increasing in diameter, thus making the column more robust. During growth the most proximal columnal (columnal 1, the proximale) articulates with the dorsal cup at a synostosis, but this is modified to an even more rigid articulation once maturity is reached, that is, once the (presumed; see, for example, Wulff and Ausich, 1989) generation of new columnals at the base of the cup has ceased. The presence of this modified synostosial articulation between the proximale and dorsal cup is considered herein to be a good indicator of maturity (although such syzygy-like articulations may possibly be present more distally in juvenile columns; Pl. 9, fig. 4). Similar articulations are developed in the more robust bourgueticrinine *Phrynocrinus nudus* (compare Pl. 1, fig. 4 herein with Donovan and Pawson, 1994, fig. 3.2).

Column: The geometry of the lumen of the *Democrinus* species discussed herein shows a stability that parallels that seen in isocrinids (Donovan, 1984). For most of the length of the column the lumen has an elliptical outline. At the base of the dorsal cup the lumen is rounded pentagonal in outline, becoming rounded in the proximale and elliptical at least by the columnal in which the synarthrial fulcra is developed, if not more proximally. Distally, in the attachment structure the lumen reverts to a circular outline when the articulation changes from synarthrial to synostosial. This stability of lumen geometry for most of the stem is an important factor when classifying Palaeozoic column and columnals within morphotaxa (Donovan, 1986).

The variation in diameter of the column in *D. chuni* and *D. brevis* possibly implies that their growth occurs in two distinct stages. Juvenile columns are slender and thread-like, with the same diameter as the base of the dorsal cup and composed of relatively few, very long columnals with a central girdle that presumably represents the initial zone away from which growth occurred (Pl. 9, figs. 1-6). (This girdle is sometimes retained in more mature columns; Fig. 3A.) Slender, thread-like columns, that are much narrower than the base of the dorsal cup, presumably represent immature individuals that have still to reach their full adult column diameter. This suggests that, once a column has reached its full juvenile length, growth may be concentrated in the crown. Such columns still appear to articulate synostosially with the base of the cup. Those columns that are as wide as the base of the dorsal cup are considered to be mature, also having developed a syzygy-like articulation between the base of the cup and columnal 1. Thus, during the early stages of growth, the column is deduced to increase rapidly in length, so that the crown attains its maximum elevation relatively early in development. The column only attains its full adult width later. Such a pattern of growth is surmised to be an adaptation to enable an individual to attain its optimum feeding height as early as possible. This is somewhat different from the pattern of growth shown by isocrinids, that continuously add columnals proximally (Oji, 1989) while being able to autotomize the distal column, and in which columnals attain both their maximum height

and diameter close to the base of the cup (Donovan, 1984). Rather, it is more reminiscent of the growth of the stem in the larval stages of comatulids and isocrinids (Breimer, 1978), from which bourgueticrinines are considered to have evolved by neoteny (Simms, 1989).

Pelmatozoan columns which articulate synarthrially are assumed to have been particularly flexible (Donovan, 1988), although, as with the all other crinoids (Donovan, 1989), flexing of the column would have been under the control of mutable collagenous tissues (Wilkie *et al.*, 1993) as no contractile tissues are present (Grimmer *et al.*, 1984). (This may not include the proxistele of glyptocystitid cystoids of the Palaeozoic, whose unique morphology is such that muscles or other contractile tissues are inferred to have been present; Paul, 1967, 1968.) While this inference is reasonable on the basis of functional morphology, direct evidence for this flexibility can be obtained by examination of encrusting epibionts, which presumably would be unable to encrust adjacent columnals by growing a single, rigid structure (but see comments on platycrinitids, below). This approach has already been applied to the cirri of comatulids by Donovan (1993). In *D. chuni* a similar association with epibionts, possibly collapsed, dehydrated ctenostome bryozoans (?), is noted herein (Pl. 4, fig. 6). In this example, colonial organisms on two adjacent columnals seem to form separate colonies that are separated by the suture between the ossicles. This suggests that continuous growth across the suture between the columnals was not possible, presumably due to frequent movements.

The unusual column illustrated in Fig. 2G is presumably some form of regenerated structure. However, it is more reminiscent of the Ordovician column figured by Ausich and Baumiller (1993) than other 'regenerations' of decapitated *Democrinus* documented by Donovan and Pawson (1997). Proximal regenerations in presumed decapitated individuals of both species of *Democrinus* documented herein tend to be more globular overgrowths, often with radicle-like extensions (Donovan and Pawson, 1996). In contrast, an attachment structure plus associated distal column, *Lichenocrinus dubius* S. A. Miller, 1880, from the Ordovician of Ohio shows a distinct proximal transition over an interval of 2-3 columnals to a much more slender column (Ausich and Baumiller, 1993). Although pentameric, this column is not dissimilar to USNM E17917 (Fig. 2G). However, although the *D. brevis* specimen may represent a second pattern of post-decapitation regeneration in this species, it could also conceivably be derived from a crowned specimen that showed less rapid expansion in diameter of the column more proximally (compare with Fig. 2F).

One specimen (Pl. 9, figs. 8, 9) is of particular interest as comparison with isocrinids suggests that this specimen may have been regenerating the crown by resorbing calcite from the proxistele. Amemiya and Oji (1992) documented the regeneration of the autotomized crown in the isocrinid *Metacrinus rotundus*. The described specimens either autotomized the entire crown above the basals or had it dissected out, but small, functional arms were regenerated within one year. This regeneration was at the expense of the proxistele, which showed a reduction in diameter over the same period from 5.0 to 3.3 mm. The illustrated specimen of *D. brevis* shows an at least analogous, although not identical, morphology (compare Pl. 9, fig. 9 herein with Amemiya and Oji, 1992, fig. 1f). The proxistele of an isocrinid is composed of numerous, low columnals, some of which have been resorbed more than others, giving the column a serrated profile. The proxistele of *D. brevis* is formed from fewer, more robust columnals. The thinnest part of the resorbed region of the column starts a little way down the column and not immediately beneath the cup. This position is presumably constrained by the necessity for the crinoid to retain a functional articulation between the crown and proximale. In bathycrinids the plates of the cup form a robust, well-sutured structure, so it may be impossible to autotomize the radials, as do isocrinids. However, numerous specimens have lost the arms above $1Br_1$, presumably mainly during collection. The illustrated example is obviously lacking the distal arms, which were being regrown, but which were autotomized again during collection. However, direct observational evidence is highly desirable to determine if the suite of processes postulated in this scenario actually occurs in bathy-

crinids.

Attachment structure: A distinctive feature of the articulation of the radicular branches of *Democrinus* spp. with the column is that they are often attached to a raised support, derived from a radice node, rather than directly to the column at a radice scar as in many other crinoids (see, for example, Ubaghs, 1978a, fig. 61). This structure is presumably a legacy of the structure of the radice nodes rather than providing any particular functional advantage to a structure that presumably was essentially rigid and lacked any contractile tissues (Donovan, 1989, 1993). Similar structures are not found in other groups with synostosially articulated radicles, such as the Palaeozoic myelodactylids (Donovan and Sevastopulo, 1989), which articulate directly to scars on nodal columnals. Further, the radicles of myelodactylids do not branch, unlike *Democrinus* spp., although this undoubtedly is due to the very different functional requirements of the two groups.

The position of radice nodes in set positions, that is, on the latus at each end of the fulcral ridge and at the anterior end of the columnal only, is presumably a functional adaptation for efficient attachment. By having radicles at the proximal end of the columnals only, roots from adjacent columnals don't interfere with each other during growth. This adaptation must be particularly important in areas where the column retains its flexibility above the actual attachment.

Comparison with platycrinitids

The platycrinitids (Fig. 4) are a large group of Upper Palaeozoic crinoids that range from the Famennian (Lane *et al.*, in review) to the Upper Permian (Broadhead and Strimple, 1977, p. 1168). Moore and Jeffords (1968, p. 40; see also Ubaghs, 1978b, p. T515; Donovan and Westhead, 1987, p. 211) diagnosed the platycrinitid stem as follows: "Stem may be circular in transverse section next below theca but most columnals are more or less compressed elliptical in outline, with well-developed fulcral ridges on their facets, those of opposite facets of each columnal being slightly to abruptly and strongly divergent in orientation so that the stem has a twisted form; columnals bearing [radicles] or lacking them". This is a rare example where the morphology of the stem is considered to be sufficiently distinct to be of diagnostic importance in a family of crinoids. The platycrinitids are the most diverse Palaeozoic crinoid group with bourgueticrinid-like stems (their close morphological similarity led Moore *in* Rhodes, 1967, p. 63, to erroneously suggest a close genetic relationship), although synarthrial articulations are also known from certain other ancient pelmatozoans (briefly reviewed in Donovan, 1985, fig. 2). The platycrinitid column mainly articulated synarthrially, apart from in the most proximal region of most species, where the columnals were circular and a symplexy was developed (Donovan and Westhead, 1987, fig. 1C; Fig. 4B herein); articulation through much of the column was by synarthry, with articular facets within each columnal often or usually showing divergent fulcral directions (Fig. 4A); and attachment was by a distal radicular structure. However, some features of the platycrinitid stem were obviously different from those of *Democrinus* spp. The platycrinitid stem is usually more robust than in bourgueticrinids, with some exceptions, such as *Phrynocrinus nudus* A. H. Clark; columnals are usually relatively lower than those of both *Democrinus* spp. and many other bourgueticrinids (compare Fig. 4A with, for example, Pl. 4, figs. 2, 3); the features of the articular facet may be different, although showing some parallel developments; and the pattern of radicular insertion shows differences in detail. Having examined the functional morphology of the stem in both *Phrynocrinus nudus* (Donovan and Pawson, 1994) and two species of *Democrinus* (see above), it is considered timely to use the insights thus obtained to make a direct comparison with the functional morphology of the platycrinitids. Studies of the morphology and function of the stem of platycrinitids that are of particular relevance to the present study include Moore (1939), Moore and Jeffords (1968), Sevastopulo and Keegan (1980), Głuchowski (1983) and Riddle (1989).

The disarticulated platycrinitid columnals figured herein (BMNH EE 5231-EE 5236; Pl. 11) were all collected from Salthill Quarry, Clitheroe, Lancashire, northwestern England (grid reference SD 755425). All

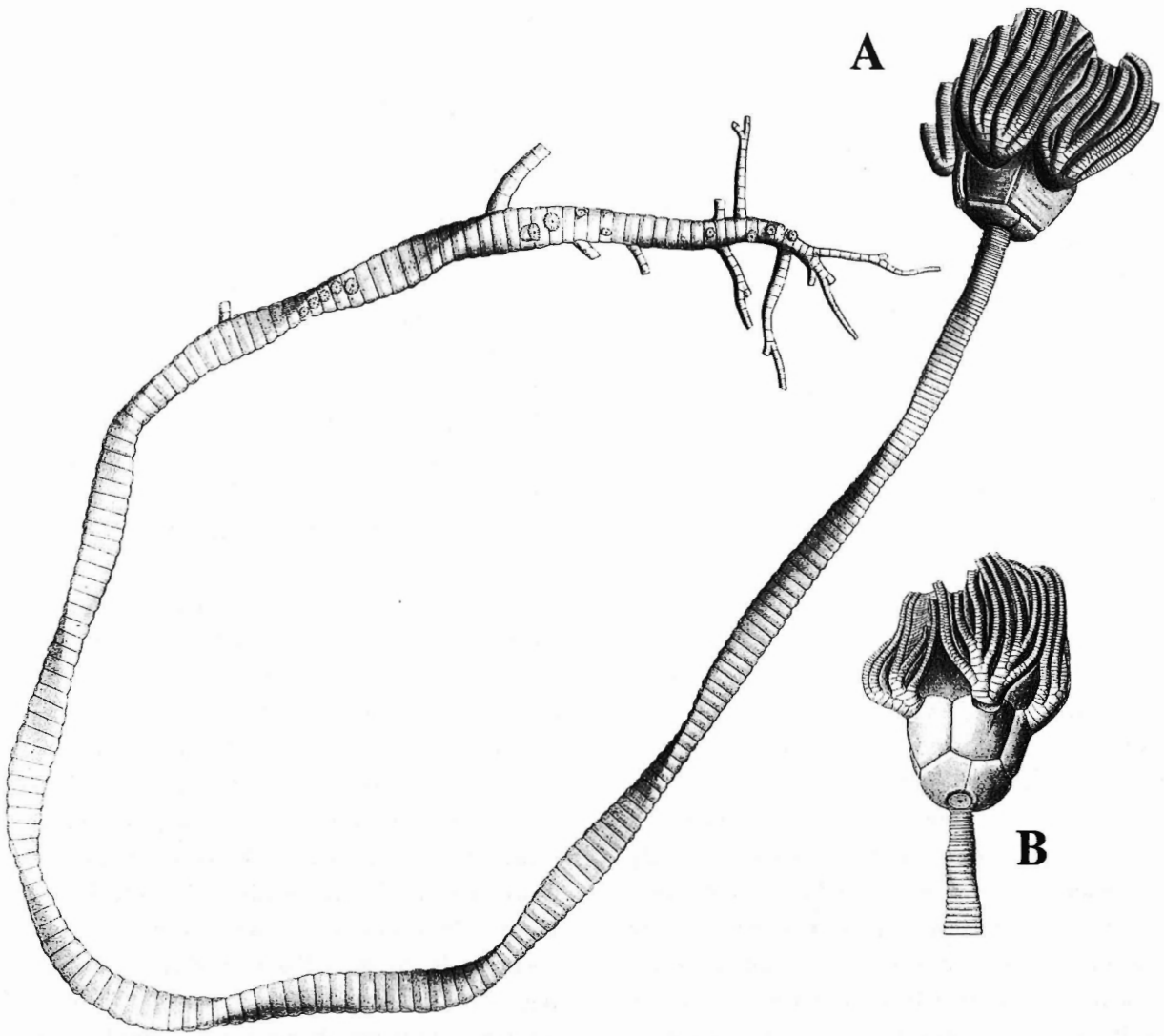


Fig. 4. A. *Platycrinites regalis* (Hall, 1861) (after Wachsmuth and Springer, 1897, pl. 72, fig. 1). Complete specimen showing circular proxistele of low columnals, 'twisted' nature of much of the column and radicular attachment. B. *Pleurocrinus halli* (Shumard, 1868) (after Wacksmuth and Springer, 1897, pl. 72, fig. 6a; see also Brower, 1969, p. 531). Crown and proximal column, showing the circular, symplectial facet at the base of the dorsal cup. Scales not given on original plate.

specimens are from Locality 3 of Grayson (1981), from the Salthill Cap Beds (Miller and Grayson, 1972), Dinantian Series (early Carboniferous), Chadian Stage (Riley *in* Donovan and Sevastopulo, 1985). All specimens were collected loose from the crinoid 'gravel' on the scraped surface. 10 nominal species of platycrinitid have been recorded from this quarry (Donovan, 1992). Additionally, articulated platycrinitids in the Springer Collection of the USNM have been examined in detail; locality details for particularly important specimens are listed in Appendix 3.

As a typical example of the platycrinitids, the following description is based mainly on the stem of *Platycrinites hemisphericus* (Meek and Worthen 1865), USNM S1410 (larger specimen of two). The column is *circa* 170 mm in length and consists of about 87 columnals. As in bourgueticrinines, the growth point is considered to have been at the base of the crown. A proxistele of rounded, symplectially articulating columnals is not definitely present, although it may be comprised of the most proximal

six columnals that form an obvious heteromorphic (N1) unit of higher and lower columnals; distal to this region the column is homeomorphic. Columnals of the mesistele have an elliptical facetal outline with synarthrial articulations. The latera of these columnals are strongly convex proximally, becoming less so more distally. Columnals of the mesistele have a distinctive tuberculated sculpture which first appears on columnal 24, although it may occur as proximally as columnals 10–11 (although this may be an artifact of cleaning). A strong geniculation of about 110° occurs in the column about columnals 22–24; more proximally the column is straight, while more distally it is gently curved. Columnals 33 and 80 are encrusted by bryozoans that do not extend onto adjacent columnals. In contrast, a bryozoan on columnal 77 extends onto columnals 78 and possibly 76, while encrusting bryozoans cross sutures in several places on the column of one specimen of USNM 380852, including a large colony that wraps around the column and encloses at least six columnals. Because of the excellent preservation of these complete crinoids, such encrustation is considered to have occurred during life. In this region an 180° twist of the column,

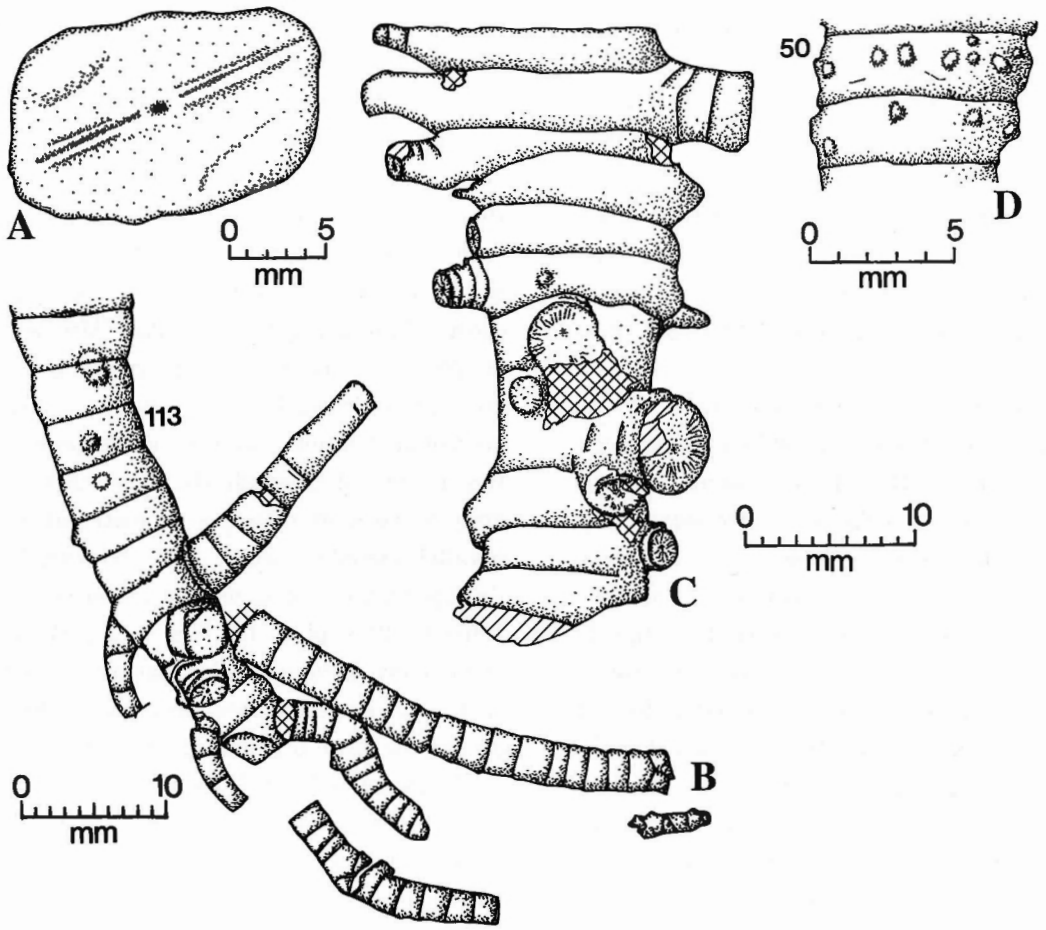


Fig. 5. *Platycrinites* spp. A. *Platycrinites* sp., USNM S3809 (figured Wachsmuth and Springer, 1897, pl. 2, fig. 9, in lateral view). Articular facet of pluricolumnal composed of unusually irregular columnals (compare with Pl. 11, figs. 3, 4, 6) ; note synarthrial ridge low and diagonal on tetragonal facet. B. *Platycrinites hemisphericus* (Meek and Worthen, 1865), USNM 380852. Distal column and attachment structure. C. *Platycrinites* sp., USNM unnumbered. Lateral view of a pluricolumnal from a distal part of the column, showing development of radices at either end of proximal fulcrum. D. *Platycrinites hemisphericus* (Meek and Worthen, 1865), USNM S1410. Detail of mesistele, showing tuberculation of latus. Numbers next to some columnals indicate their position in the stem. All figures camera lucida drawings of the stem.

produced by the offsets of articular facets in successive columnals, occurs over an interval of about 13–14 columnals (=about 13–14° offset per columnal), in contrast to the very abrupt twists of the column in *Democrinus* spp. (see above). Columnals become progressively taller, with less convex latera, along the length of the column. By about columnal 50 (Fig. 5D), tubercles are common on the latus. These occur at the mid-height of the columnal and all around the circumference. Distally columnals are high, with widely divergent facets (*circa* 60°), and radice nodes and scars developed on the latera, but only on the ends of fulcra, of the most distal seven or so columnals. The stem terminates in a dendritic radice (similar to Fig. 5B). Radice nodes first appear at about columnals 79–80 and are much larger, but occur less densely, than tubercles higher on the column; USNM S1410, including about 99 columnals before the distal dendritic radice, first shows radice nodes at about columnal 92. These occur at the ends of fulcra of the proximal facet. Radices articulate symplectially, at least proximally. One radice is encrusted by a bryozoan that crosses several joints. A symplexy is developed between columnals 116 and 117 of USNM 380852 (Fig. 5B).

Although broadly similar, the geometries of the articular facets of platycrinitids and bourgueticrinids are different in detail. Both have a small, central, circular lumen, a fulcral ridge on either side of the lumen that corresponds to the long axis of the facet and which is flanked by two depressed, arcuate ligamental areas (compare, for example, Pl. 2, figs. 1, 6 with Pl. 11, figs. 1–6, 8). Where the two groups differ is in their methods by which articulating fulcral ridges are stabilized. Presumably the principal problem of synarthrial articulation is that of having two ridges articulating against each other. This is an inherently unstable system and the ridges are likely to twist or slide apart laterally. In some structures, such as the cirri of isocrinids and comatulids (Donovan, 1985, fig. 1C), stability is produced by having only one fulcral ridge, which sits in a groove on an adjacent columnal. In systems where two ridges are present, stability is provided by giving the fulcra a finite breadth and often by providing an array of stabilizing crenulae which prevent lateral movement when adjacent columnals 'rock' against each other. In the bathycrinids discussed herein, crenulae are conspicuous as flanking elements along the length of each side of the synarthrial fulcra, at least distal to the proximal part of the column (Pl. 2, figs. 1, 2, 6, Pl. 3, figs. 1, 3, Pl. 5, fig. 8, Pl. 8, figs. 4, 6, 7), while in other bourgueticrinids such stabilizing structures are absent (see, for example, Rasmussen, 1961, pl. 24, figs. 4a, 6a, 7a; Donovan and Pawson, 1994, fig. 41.–4.4). In at least some platycrinitids (Pl. 11, figs. 1–6, 8), crenulae also have been developed to provide stability to the column (see also Sevastopulo and Keegan, 1980). However, platycrinitids show a greater range of facet architectures than bourgueticrinids. While peg-like crenulae may be developed perpendicular to and on either side of the ridge as in *Democrinus* spp. (Moore and Jeffords, 1968, pl. 4, figs. 5b, 6a), it is more common for crenulae to be concentrated as radiating arrays at the circumference of the articular facet at each end of the fulcrum (Pl. 11, figs. 1–6, 8 ; Sevastopulo and Keegan, 1980, p. 752, pl. 94, figs. 2, 4). Less commonly these arrays of crenulae are associated with a marginal crenularium of peg-like crenulae (Moore and Jeffords, 1968, pl. 3, figs. 8–10); sometimes only the marginal crenularium is developed in association with a slightly geniculate fulcrum (Moore and Jeffords, 1968, pl. 5, figs. 1a, 2a). Most peculiarly, some 'fulcra' are moderately broad with a surface geometry of longitudinal, parallel crenulae, which may be radially splayed through an arc approaching 90° at one end (Moore and Jeffords, 1968, pl. 4, figs. 2a, b, 3). While crenulae presumably serve a similar function in both groups, each of these geometries represents a different solution to the same problem of function.

The pattern of radicle insertion shown by the distal stem of *Democrinus* spp. is similar to that of the Upper Palaeozoic platycrinitids. The tuberculation of the platycrinitid stem in the mesistele (Fig. 5D) is apparently unrelated to the formation of radicles. The formation of radice nodes and scars at either end of the fulcrum adjacent to the proximal facet in both bathycrinids (Pl. 2, fig. 2, Pl. 8, fig. 7) and platycrinitids (Fig. 5B) is a convergence that surely indicates functional utility. Because of the rotation of

facets, radice nodes are arranged about the longitudinal axis of the column (Fig. 5C). Radices are sometimes asymmetrically developed in both groups (see, for example, Pl. 10, fig. 2), suggesting development in response to an external stimulus, presumably tactile and produced by the column resting on the sediment surface. By producing a pair of radice nodes in a set position on each columnals in a twisted column, it is ensured that at least some will come into contact with the sediment, and thus grow radices, whatever the topography of the substrate.

Paralleling the similar arrangement of bathycrinids, the articulation of the platycrinitid stem reverts to a symplexy in the region of the attachment (seen, for example, in lateral view between columnals 116 and 117 in Fig. 5B). The attachment structure is rigid, that is, it does not require the degree of flexibility found in most of the column. Symplexies (platycrinitids) and, particularly, synostoses (bathycrinids) (Donovan, 1990) are both less flexible than synarthries, and are thus better suited for intercolumnal articulations in the region of the attachment. It is significant to note that within each group the proximal and distal articulations are the same.

The columnals of both platycrinitids and bourgueticrinids show a range of morphologies from low and broad (Pl. 11, fig. 7, Figs. 4, 5 herein and Donovan and Pawson, 1994, fig. 4.5-4.7, respectively) to tall and slender (Pl. 11, figs. 1, 2, 4, 9 and Pl. 2, fig. 5, Pl. 4, figs. 2, 3, respectively). The former tend to occur in larger and more robust specimens, while the latter are found in small, gracile individuals. The only other noticeable pattern related to these differences in size is that the relative degree of fulcral rotation within a columnal may be less in larger individuals (contrast rotation of column in Fig. 4A with Pl. 4, fig. 3), although this is not invariably the case (note high divergences for robust *Phrynocrinus nudus* measured by Donovan and Pawson, 1994, p. 1337). The precise reason for this size-related variation is unknown, although is presumably related to the differing requirements of flexibility between smaller and larger individuals. Presumably the strongly twisted columns of bathycrinids are only poor adapted, at best, to exploit the deflected feeding currents produced by the column in more helically-coiled columns (Riddle, 1989).

Donovan (1993, p. 167, fig. 2C) used the position of an epizoan on a single cirral ossicle (that is, it had not extended onto adjacent ossicles) to infer the extreme flexibility and frequent flexure of the comatulid cirrus during life. Similar, tentative deductions were made for the column of *D. chuni* based on one specimen (Pl. 4, fig. 6). In contrast, bryozoans encrusting the column of *P. hemisphericus* were observed to extend over up to six adjacent columnals. These infestations occur on complete specimens in which the arms retain the pinnules, suggesting that burial was the cause of death (Blyth Cain, 1968; Donovan, 1991). Encrustation of the column must therefore have occurred during life. This in turn implies either that the column in these encrusted regions had only limited flexibility in life or, perhaps more probably, although potentially highly flexible, the encrusted regions spent most or all of their adult life in the same position, permitting infestation by bryozoans. Further observations on comparable material are necessary before either of these hypotheses can be confirmed.

As a final comment on the stem of platycrinitids, Moore and Jeffords (1968) illustrated a range of interesting columnal morphologies that have not, as yet, been related to complete specimens. It is at least possible that these different forms have a genetic basis, each occurring within a particular clade. Considering the large number of nominal species within *Platycrinites*, it is desirable that subdivision of this genus be made, although such attempts have been hampered by the lack of adequate morphological detail. However, the data that reside in the stem have not been touched. Thus, although the erection of new platycrinitid taxa based on columnals and pluricolumnals without crowns should be frowned upon (Broadhead and Strimple, 1977), it is recommended that descriptions of platycrinitids should, if possible, include detailed documentation of the features of the stem.

Conclusions

[1] Recent bourgueticrinine crinoids are good models for interpreting the function of the stem

in ancient groups such as the Upper Palaeozoic platycrinitids. In the two species of bathycrinid examined herein, *Democrinus chuni* and *Democrinus brevis*, the column is slender and gracile, with a proximal articulation with the dorsal cup that varies between synostosial (juvenile) to syzygy-like (mature); a short proxistele of low columnals that articulate synostosially; a long mesistele of high columnals that articulate synarthrially and show highly divergent fulcral angles between the facets within each columnal; and a distal, radicular attachment structure, either a runner, a rhizoidal holdfast or a dendritic radice, originating from columnals with synarthrial to synostosial articulations. Radicular ossicles articulate synostosially. The lumen is elliptical throughout most of the stem, but is rounded most proximally and most distally.

[2] Radices grow from paired radice nodes that occur on the latus, one at each end of the fulcrum at the proximal end of the columnals of the distal stem. Growth of radices from these structures is deduced to have been in response to tactile stimuli, leading to a diversity of radicular attachment morphologies. Attachment is facilitated by the rotations shown within columnals by the elliptical articular facets. Similar patterns of insertion occur in *Democrinus* spp. and platycrinitids.

[3] Regeneration of the arms in bathycrinids following autotomy or predation involves the resorption of calcite from the proximal column, as has been noted in isocrinids (Amemiya and Oji, 1992). The crown cannot be regenerated if it is completely lost, although different patterns of post-decapitation, proximal growth of the column are possible (Donovan and Pawson, 1996).

[4] Encrusting epibionts, such as bryozoans, that are limited to single columnals may be indicative of frequent flexure in that part of the column. Encrusters that infested two or more sequential columnals presumably immobilized the joints that were overgrown, suggesting that such regions of the column were essentially immobile. Such interpretations are best made on complete crinoids, which presumably represent catastrophic entombment of living specimens, and not on fragments that may have been infested post-mortem.

[5] The platycrinitids are the most diverse Palaeozoic crinoid group with stems that articulate synarthrially. The platycrinitid column mainly articulated synarthrially with elliptical columnals, apart from proximally, where the columnals were circular and a symplexy was developed. Articular facets within each elliptical columnal usually showing divergent fulcral directions. Attachment was by a distal radicular structure. Unlike bourgueticrinines, the platycrinitid stem is usually robust, columnals are usually relatively lower, the features of the articular facet may be different and the pattern of radicular insertion shows differences in detail.

[6] Stabilization of the synarthrial ridges between adjacent columnals shows a wider range of morphologies in platycrinitids than in bourgueticrinines. Fulcra of bourgueticrinines are either unstabilized or have crenulae flanking either side of each ridge. The latter is found in platycrinitids, which may alternately show development of crenulae marginally or at the circumference adjacent to the ends of the ridge, or the unusual formation of broad 'fulcra' with longitudinal crenulae.

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Appendix 1

Directory of specimens of Recent *Democrinus* spp. examined as part of this study.

Democrinus chuni (Döderlein, 1907)

Material and localities.—The specimens of *D. chuni* discussed herein were all collected by the R/V *Anton Bruun* and were identified by A. M. Clark.

USNM E11601. 1 specimen. Indian Ocean, Madagascar, Mozambique Channel, Juan de Nova Island. 17° 41′ S, 42° 31′ E; 2,125 m depth. 13th October, 1964.

USNM E11616. 11+ specimens. South Atlantic Ocean, South Africa, Durban. 30° 10′ S, 32° 9′ E; 700 m depth. 6th September, 1964.

USNM E11705. 39 specimens. Indian Ocean, South Africa, Natal, Durban. 30° 9′ S, 31° 37′ E; 930 m depth. 6th September, 1964.

USNM E11708. 4+ specimens. Indian Ocean, Mozambique, Inhambane. 24° 5′S, 36° 15′ E; 1,628 m depth. 28th September, 1994.

Democrinus brevis (A. H. Clark, 1909)

Material and localities.—The specimens of *D. brevis*, all from the north Atlantic Ocean, were collected and identified by the following : —

(1) Collected by R/V Gyre and identified by C. G. Messing.

USNM E41937. 9 specimens. Gulf of Mexico, southwest of Panama City, Florida. 28° 6′ 0″ N, 86° 35′ 18″ W; 1,170 m. 18th April, 1984.

USNM E41938. 7 specimens. Gulf of Mexico, southwest of Grand Island, Louisiana. 27° 48′ 0″ N, 90° 3′ 18″ W; 850 m. 27th November, 1983.

USNM E41940. 1 specimen. Gulf of Mexico, south of Louisiana Point, Louisiana. 27° 24′ 30″ N, 93° 18′ 54″ W; 576-732 m. 7th April, 1984.

(2) Collected by R/V *Citation* and identified by C. G. Messing.

USNM E41939. 1 specimen. Gulf of Mexico, southwest of Grand Island, Louisiana. 27° 29′ 35″ N, 89° 47′ 53″ W; 1,392 m. 15th November, 1984.

(3) Collected by R/V *Pillsbury* and identified by D. B. Macurda, Jr.

USNM E17747. 5 specimens. Straits of Florida, Miami, Florida. 25° 44′30″ N, 79° 50′ 00″ W; 302-366 m. 4th December, 1970.

USNM E17917. 12 specimens. Caribbean Sea, Zamuro Point, Venezuela. 11° 36′ 54″ N, 68° 42′ 00″ W; 684-1, 574 m. 26th July, 1968.

USNM E17929. 3 specimens. Caribbean Sea, Aguide, Venezuela. 11° 18′ 48″ N, 68° 22′ 0″ W; 384-607 m. 26th July, 1968.

USNM E17930. 1 specimen. Caribbean Sea, Tobago. 11° 37′ 48″ N, 60° 37′24″ W; 659-1,126 m. 2nd July, 1969.

USNM E17945. 2 specimens. Straits of Florida, Miami, Florida. 25° 44′30″ N, 79° 50′ 00″ W; 311 m. 5th December, 1970.

USNM E17992. 2 specimens. Caribbean Sea, Santa Marta, Colombia. 11° 16′54″ N, 74° 17′ 00″ W; 165-176 m. 31st July, 1968.

USNM E18604. 27 specimens. Caribbean Sea, Los Testigos Island, Venezuela. 11° 34′ 24″ N, 62° 10′ 42″ W; 597-598 m. 2nd August, 1966.

USNM E25944. 7 specimens. Caribbean Sea, Riohacha, Colombia. 11° 30′ 00″ N, 73° 26′ 30″ W; 531-567 m. 30th July, 1968.

(4) Collected by R/V *Gerda* and identified by D. B. Macurda, Jr.

USNM E17499. 4 specimens. Straits of Florida, Key Largo, Florida Keys. 25° 15′ 0″ N, 80° 10′ 0″ W; 79-86 m. 10th July, 1967.

USNM E17500. 5 specimens. Gulf of Mexico, Straits of Florida, Florida Keys. 24° 3′ 0″ N, 81° 49′ 0″ W; 742–805 m. 20th June, 1963.

USNM E17501. 1 specimen. Straits of Florida, Key West, Florida Keys. 24° 8′ 0″ N, 81° 36′ 0″ W; 514–558 m. 29th August, 1967.

USNM E17502. 6 specimens. Straits of Florida, Key Biscayne, Florida. 25° 37′ 00″ N, 80° 2′ 00″ W; 30 m. 7th July, 1967.

USNM E17972. 5 specimens. Straits of Florida, Key Largo, Florida Keys. 24° 36′ 00″ N, 80° 1′ 00″ W; 296–318 m. 12th July 1967.

USNM E26223. 1 specimen. Little Bahama Bank, Bahamas. 27° 25′ 00″ N, 79° 10′ 00″ W; 375–384 m. 30th September, 1967.

USNM E26224. 4 specimen. Straits of Florida, Key Biscayne, Florida. 25° 37′ 00″ N, 80° 2′ 00 W; 333–340 m. 7th July, 1967.

USNM E26226. 1 specimen. Straits of Florida, Miami, Florida. 25° 39′ 0″ N, 79° 58′ 0″ W; 332–338 m. 29th March, 1964.

(5) Collected by R/V *Gerda* and identified by D. L. Meyer.

USNM E25870. 16+ specimens. Gulf of Mexico, Straits of Florida, Florida Keys. 24° 14′ 00″ N, 82° 56′ 00″ W; 641–686 m. 18th June, 1963.

USNM E25929. 24 specimens. Straits of Florida, Key Biscayne, Florida. 25° 31′ 00″ N, 79° 57′ 00″ W; 351 m. 26th September, 1962.

(6) Collected by R/V *Oregon* and identified by D. B. Macurda, Jr.

USNM E17498. 52 specimens. Maranhao, Sao Luis, Brazil. 18° 00′ N, 44° 17′ W; 274 m. 3rd September, 1963.

Appendix 2

Specimens of *Democrinus* spp. mounted for scanning electron microscopy as part of this study.

Box I: *D. chuni* (Döderlein)

1. USNM E11616 - crownless stalk.
2. USNM E11616 - slender column.
3. USNM E11616 - dorsal cup, columnal 1 (box I, stubs 3–12 and box II, stubs 1–8 represent one, disarticulated specimen).
4. - columnals 2, 3.
5. - columnals 4, 5.
6. - columnals 6, 7.
7. - columnals 8, 9.
8. - columnals 10, 11.
9. - columnals 12, 13.
10. - columnals 14, 15.
11. - columnals 16, 17.
12. - columnals 18, 19.

Box II: *D. chuni* (Döderlein)

1. USNM E11616 - columnals 20, 21.
2. - columnals 22, 23.
3. - columnals 24, 25.
4. - columnals 26, 27.
5. - columnals 28, 29.
6. - columnals 30, 31.

7. - columnals 32, 33.
8. - ossicles of attachment structure.
9. USNM E11705 - distal, 'bone-shaped' columnals.
10. USNM E11705- two specimens, showing (i) column with epibionts(?) and (ii) a strange cup morphology.
11. USNM E11705- assorted attachment structures.
12. USNM E11705- assorted attachment structures.

Box III: *D. chuni* (Döderlein)
1. USNM E11705 - deformed cup and 5 columnals of proxistele.
2. USNM E11705 - columnals 34, 35 (box III, stubs 2-7, represent one, disarticulated specimen).
3. - columnals 36, 37.
4. - columnals 38, 39.
5. - columnals 40, 41.
6. - columnals 42, 43.
7. - columnals 44, 45.
[8-12. Not used.]

Box IV: *D. brevis* (A. H. Clark)
1. USNM E26224 - attachment structure.
2. USNM E26224 - attachment structure.
3. USNM E41940 - regenerating apical structure.
4. USNM E41939 - juvenile, whole specimen.
5. USNM E41938 - two attachment structures.
6. USNM E17747 - gall on columnal 23.
7. USNM E17917 - disarticulated ossicles of attachment structure.
8. USNM E41937 - cup with aberrant proxistele.
[9-12. Not used.]

Box V: *D. brevis* (A. H. Clark)
[1-2. Not used.]
3. USNM E17992 - cup, columnal 1 (box V, stubs 3-12 and box VI, stubs 1-12 represent one, disarticulated specimen).
4. - columnals 2, 3, 4.
5. - columnals 5, 6.
6. - columnals 7, 8.
7. - columnals 9, 10.
8. - columnals 11, 12.
9. - columnals 13, 14.
10. - columnals 15, 16.
11. - columnals 17, 18.
12. - columnals 19, 20.

Box VI: *D. brevis* (A.H. Clark)
1. - columnals 21, 22.
2. - columnals 23, 24.
3. - columnals 25, 26.

4. - columnals 27, 28.
5. - columnals 29, 30.
6. - columnals 31, 32.
7. - columnals 33, 34.
8. - columnals 35, 36.
9. - columnals 37, 38.
10. - columnals 39, 40.
11. - columnals 41, 42.
12. - columnals 43, 44.

Appendix 3

Directory of platycrinitid specimens in the Springer Collection, Department of Paleobiology, USNM, that were examined as part of this study. Data from some specimens labels has been revised, in part, by reference to Ausich and Kammer (1990).

USNM S1309 (3 specimens). *Platycrinites symmetricus* (Wachsmuth and Springer, 1889) (figured Wachsmuth and Springer, 1897, pl. 69, figs. 1a-c). Mississippian, Kinderhookian, Kinderhook Group. Le Grand, Marshall County, Iowa.

USNM S1374 (2 specimens). *Platycrinites brevinodus* (Hall, 1861) (figured Wachsmuth and Springer, 1897, pl. 70, figs. 2, 5). Mississippian, Osagean, Upper Burlington Limestone. Burlington, Iowa.

USNM S1376 (3 specimens). *Platycrinites cavus* (Hall, 1858). Mississippian, Osagean, Upper Burlington Limestone. Burlington and Pleasant Grove, Iowa.

USNM S1410 (Two separate lots, of 2 and 3 specimens, respectively).
Platycrinites hemisphericus (Meek and Worthen, 1865). Mississippian, Osagean, Keokuk Limestone. Crawfordsville, Indiana.

USNM S3809 (6 specimens). *Platycrinites* stem fragments (figured Wachsmuth and Springer, 1897, pl. 2, figs. 5, 8, 9, 11, 12). Mississippian, Osagean, Burlington Limestone. Burlington, Iowa.

USNM 380852 (Two lots, 1 specimen in each). *Platycrinites hemisphericus* (Meek and Worthen, 1865). Mississippian, Osagean, Borden Group. Crawfordsville, Montgomery Co., Indiana.

USNM (unnumbered) (4 specimens). *Platycrinites*. Mississippian, Osagean, Upper Burlington Limestone. Burlington, Iowa.

Plate 1

Figs. 1-6. *Democrinus chuni* (Döderlein, 1907), Recent.

Fig. 1. USNM E11616/box I/stub 3. Base of dorsal cup, showing central, pentagonal lumen and five sutures (each centered on a side of the lumen) between basal plates. × 130.

Figs. 2, 3, 5. USNM E11616/box I/stub 4. Columnal 2. 2, lateral view. x 115. 3, proximal articular facet showing synostosial articulation and elliptical lumen. × 110. 5, slightly oblique view of distal articular facet of columnal 2 (mounted in same relative orientation to 3 to show rotation of elliptical lumen); *mark positions of weakly-formed synarthrial fulcra. × 115.

Fig. 4. USNM E11616/box I/stub 3. Oblique lateral view of columnal 1, showing the proximal facet with syzygy-like articulation; note raised, radial ridges of stereom trabeculae that articulated with the sutures between basals at the base of the cup (cf. Pl. 1, fig. 1), Although not apparent in this view, the lumen is more rounded than that at the base of the cup. × 145.

Fig. 6. USNM E11616/box I/stub 2. Lateral view of base of dorsal cup (left) and proximal column of an individual with a slender (=immature) column. × 120.

All scanning electron micrographs of specimens coated with 60% gold-palladium. Specimens in Pl. 1, figs. 1-5, Pl. 2 and Pl. 3, figs. 1-3, 5, 6 are derived from the same crinoid.

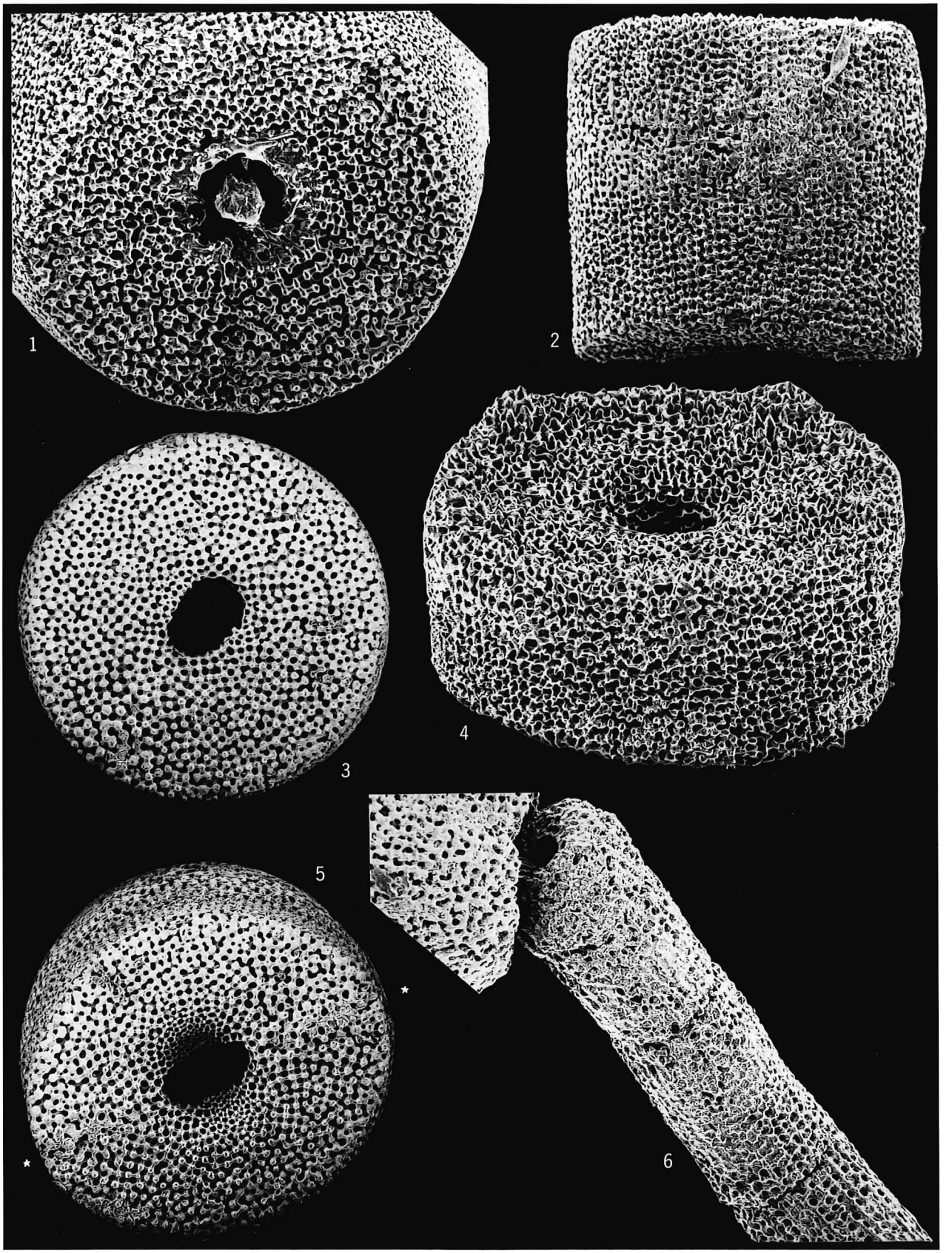

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Plate 2

Figs. 1-7. *Democrinus chuni* (Döderlein, 1907), Recent.

Fig. 1. USNM E11616/box II/stub 1. Articular facet of columnal 21. × 135.

Fig. 2. USNM E11616/box II/stub 7. Slightly oblique view of proximal articular facet of columnal 33, showing latus and radicular facets adjacent to fulcra. × 90.

Fig. 3. USNM E11616/box II/stub 6. Prominent, node-like radicular facet of columnal 31. × 500.

Fig. 4. USNM E11616/box II/stub 6. Incipient node adjacent to proximal facet of columnal 30. × 185.

Figs. 5, 6. USNM E11616/box II/stub 2. 5, lateral view of columnal 22 ; note relative differences in orientation of articular facets. × 60. 6, articular facet. × 100.

Fig. 7. USNM E11616/box II/stub 7. Anterior(?) end of columnal 32, showing node developed on one side only. × 115.

All scanning electron micrographs of specimens coated with 60% gold-palladium. Specimens in Pl. 1, figs. 1-5, Pl. 2 and Pl. 3, figs. 1-3, 5, 6 are derived from the same crinoid.

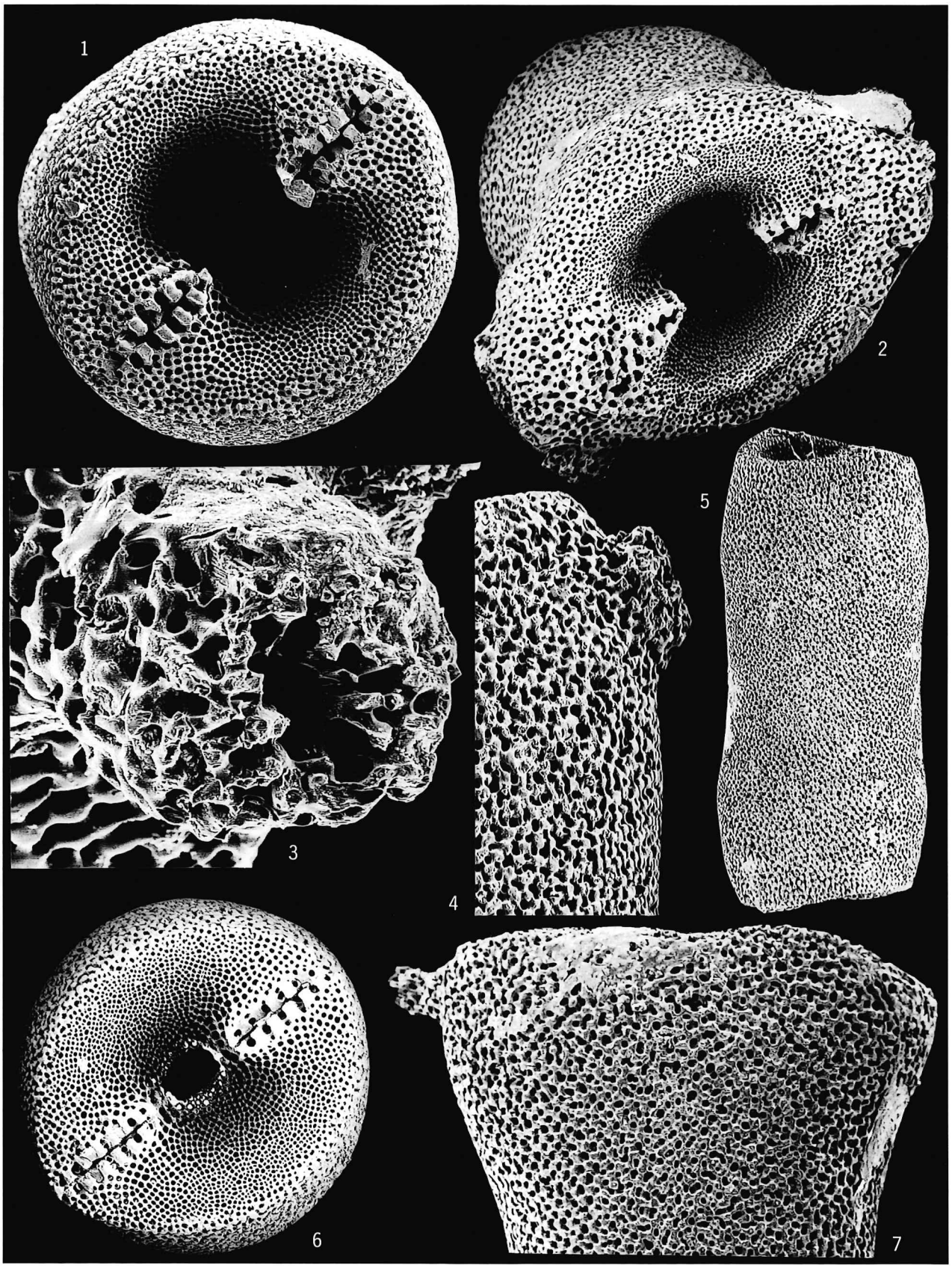

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Plate 3

Figs. 1-6. *Democrinus chuni* (Döderlein, 1907), Recent.

Figs. 1, 3. USNM E11616/box II/stub 8. Proximal (1) and distal (3) facets of columnal 34(?). 1. × 105. 3. × 85.

Fig. 2. USNM E11616/box II/stub 8. Probably terminal columnal (35?) with associated radicular ossicles. × 50.

Fig. 4. USNM E11705/box II/stub 12. Attachment structure. × 19.

Figs. 5, 6. USNM E11616/box II/stub 8. Articular facets of radicular ossicles. 5. × 190. 6. × 290.

All scanning electron micrographs of specimens coated with 60% gold-palladium. Specimens in Pl. 1, figs. 1-5, Pl. 2 and Pl. 3, figs. 1-3, 5, 6 are derived from the same crinoid.

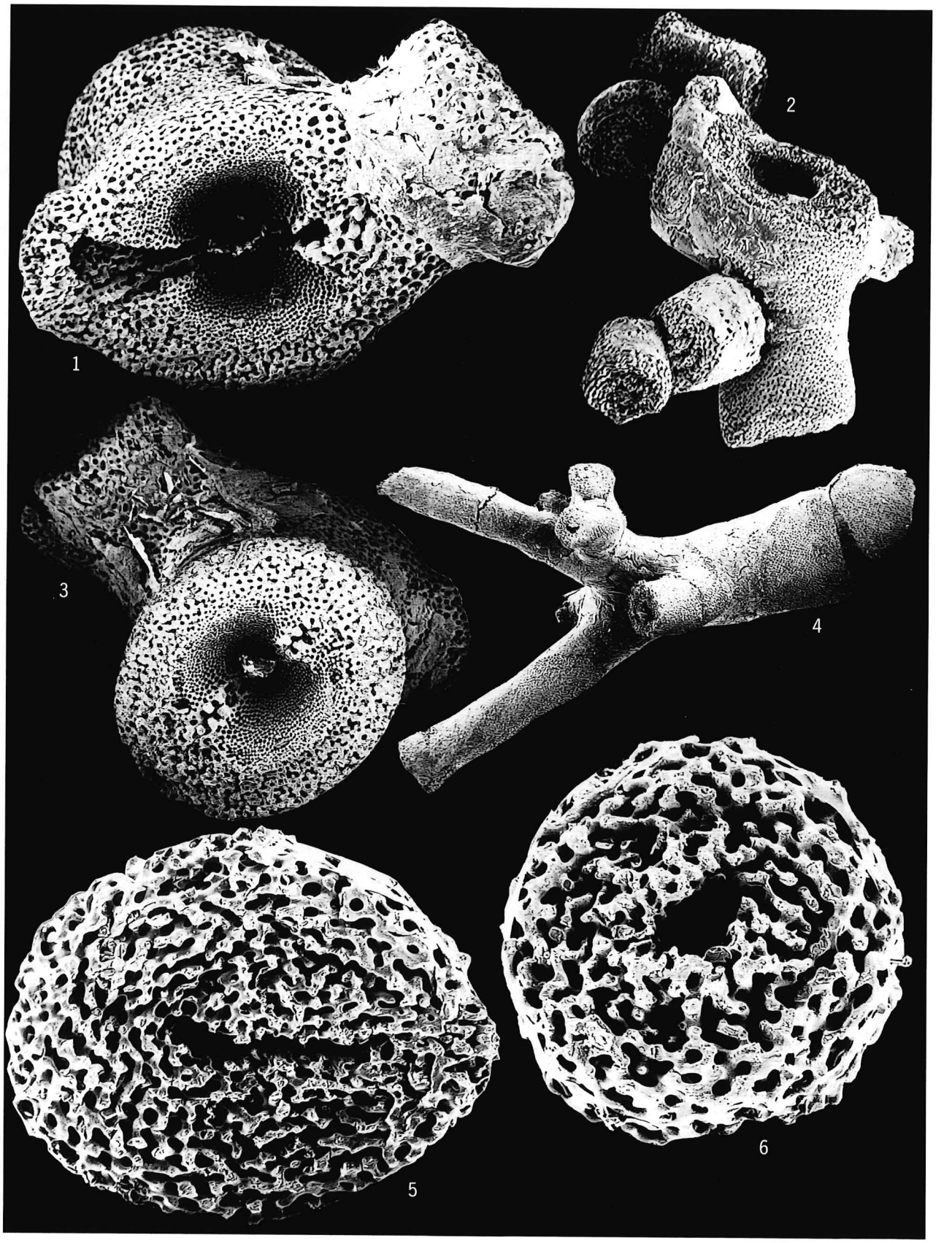

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Plate 4

Figs. 1-6. *Democrinus chuni* (Döderlein, 1907), Recent.

Figs. 1-5. USNM E11705/box 2/stub 9. Lateral views of stem (1-4) and complete specimen (5). 1. Proximal column immediately below cup (contrast with Pl. 1, fig. 6), showing columnals 1 to 4. × 46. 2. Pair of elongate columnals of mesistele. × 53. 3. More distal columnals with relatively broader facets. × 40. 4. Distal column and attachment structure. × 42. 5. Complete crinoid; arms autotomized above $1Br_1$. Strong curvature of column due to it having been stored in a jar. × 8.

Fig. 6. USNM E11705/box II/stub 10. Two columnals of proximal mesistele encrusted by epibionts, possibly collapsed, dehydrated ctenostome bryozoans (P. D. Taylor, written communication) (compare with Donovan, 1993, fig. 2C). × 53.

All scanning electron micrographs of specimens coated with 60% gold-palladium.

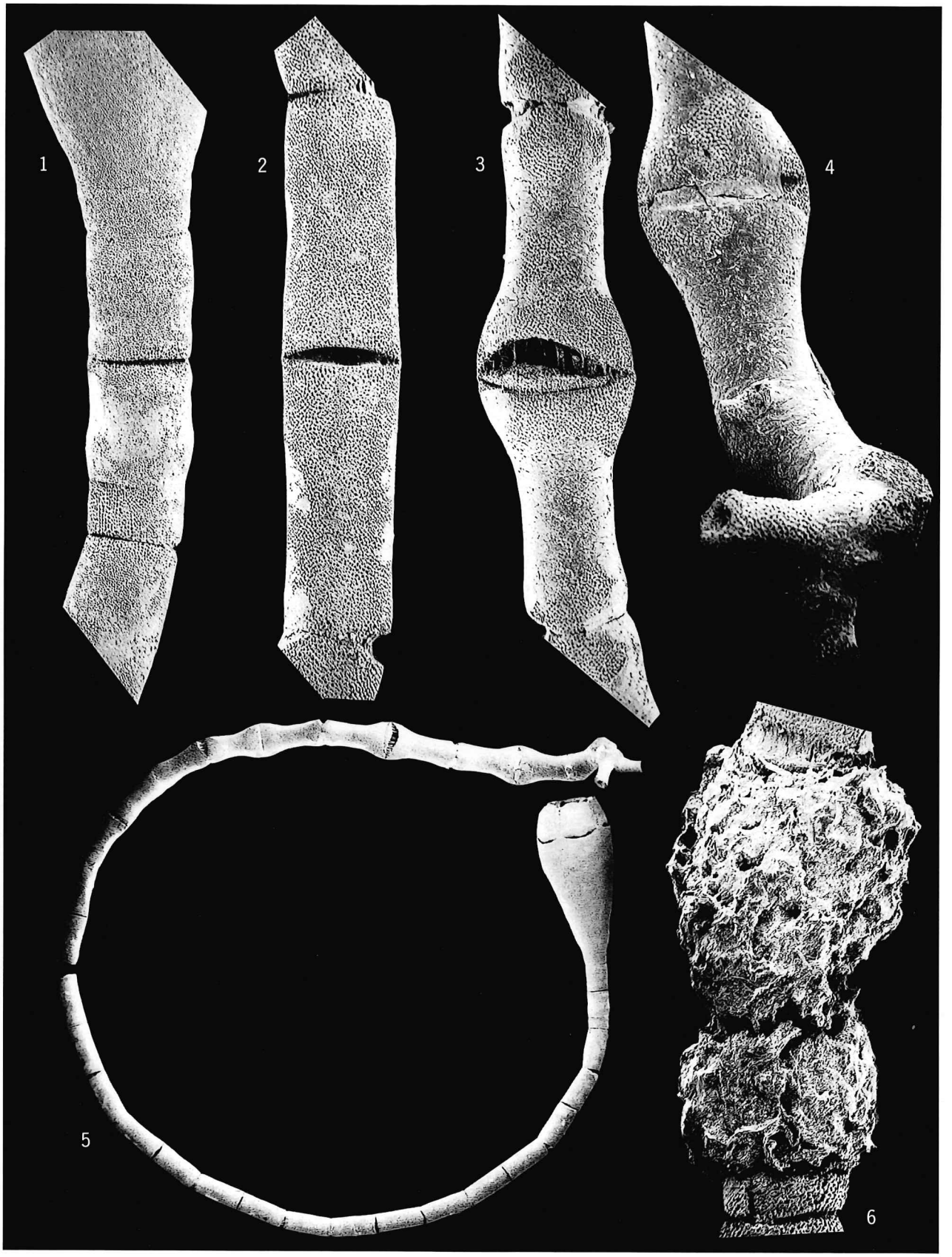

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Plate 5

Figs. 1-8. *Democrinus chuni* (Döderlein, 1907), Recent.

Fig. 1. USNM E11705/box III/stub 4. Lateral view of columnal 38. × 43.

Figs. 2, 3. USNM E11705/box III/stub 1. Proximal synostosis (2) and distal synarthry (3) of articular facets of columnal 5 (compare with Pl. 1, figs. 3, 5), 2. × 68. 3. × 64.

Fig. 4. USNM E11705/box III/stub 3. Lateral view of proximal latus of columnal 37. × 50.

Fig. 5. USNM E11705/box III/stub 4. Lateral view of proximal latus of columnal 39; note paired radicular facets. × 54.

Fig. 6. USNM E11705/box III/stub 5. Lateral view of columnal 41. × 62.

Fig. 7. USNM E11705/box III/stub 6. Lateral view of columnal 42. × 70.

Fig. 8. USNM E11705/box III/stub 2. Oblique view of articular facet and latus of columnal 35. × 64.

All scanning electron micrographs of specimens coated with 60% gold-palladium. Specimens in Pl. 5, figs. 1, 4-8 and Pl. 6, figs. 2, 4 are derived from the same crinoid.

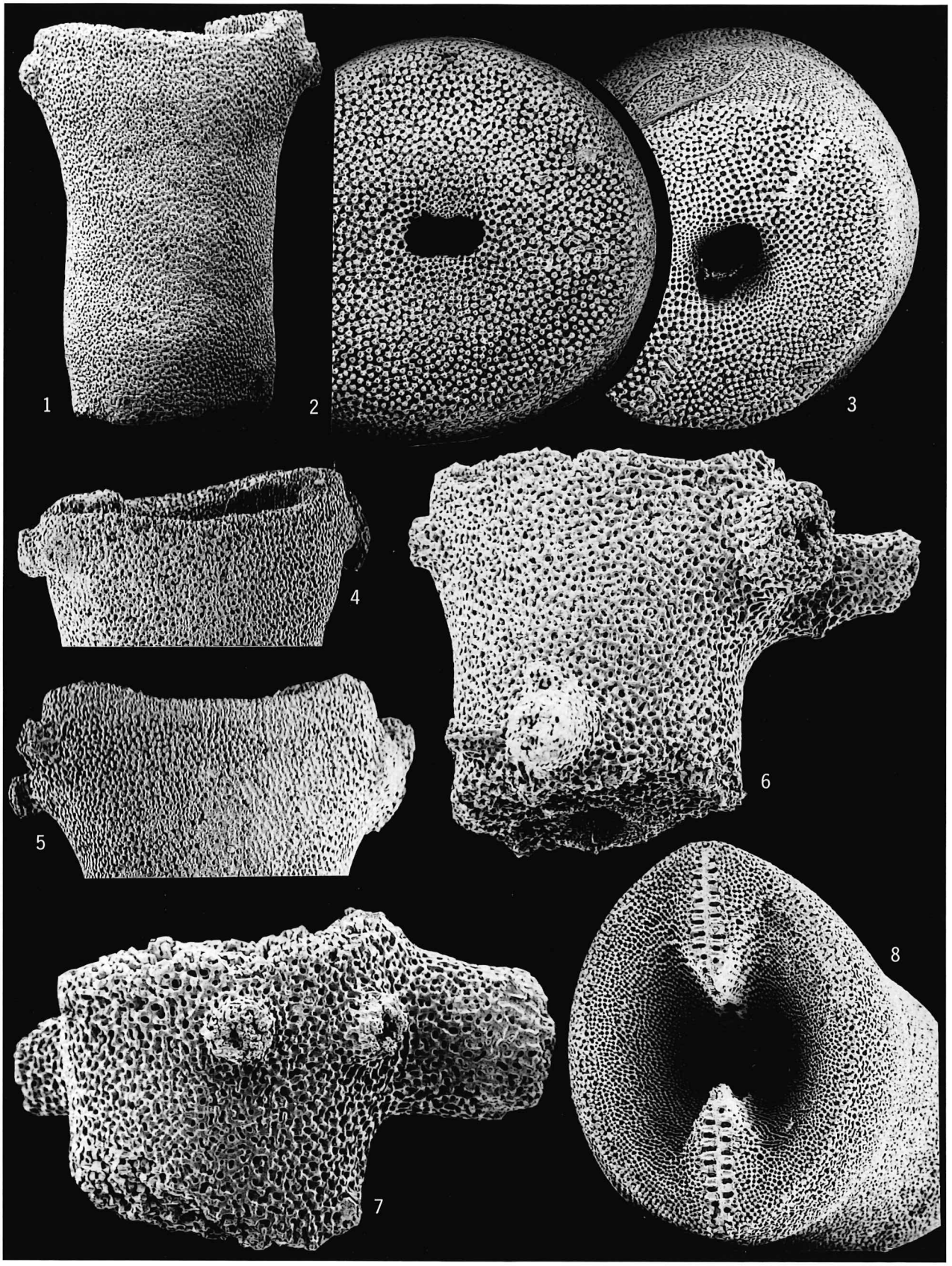

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Plate 6

Figs. 1-5. *Democrinus chuni* (Döderlein, 1907), Recent.

Figs. 1, 3, 5. USNM E11705/box II/stub 11. Three morphologies of attachment structure from three separate individuals. 1. × 29. 3. × 30. 5. × 21.

Figs. 2, 4. USNM E11705/box III/stub 6. Distal (2) and proximal (4) articular facets of a distal columnal with numerous node-like to elongate radicular structures. 2. × 70. 4. × 75.

Fig. 6. *Democrinus brevis* (A. H. Clark, 1909), Recent. USNM E17992/box V/stub 3, low columnal '0' attached to the base of the dorsal cup. × 93.

All scanning electron micrographs of specimens coated with 60% gold-palladium. Specimens in Pl. 5, figs. 1, 4-8 and Pl. 6, figs. 2, 4 are derived from the same crinoid; specimens in Pl. 6, fig. 6 and Pls. 7-8 are derived from the same crinoid.

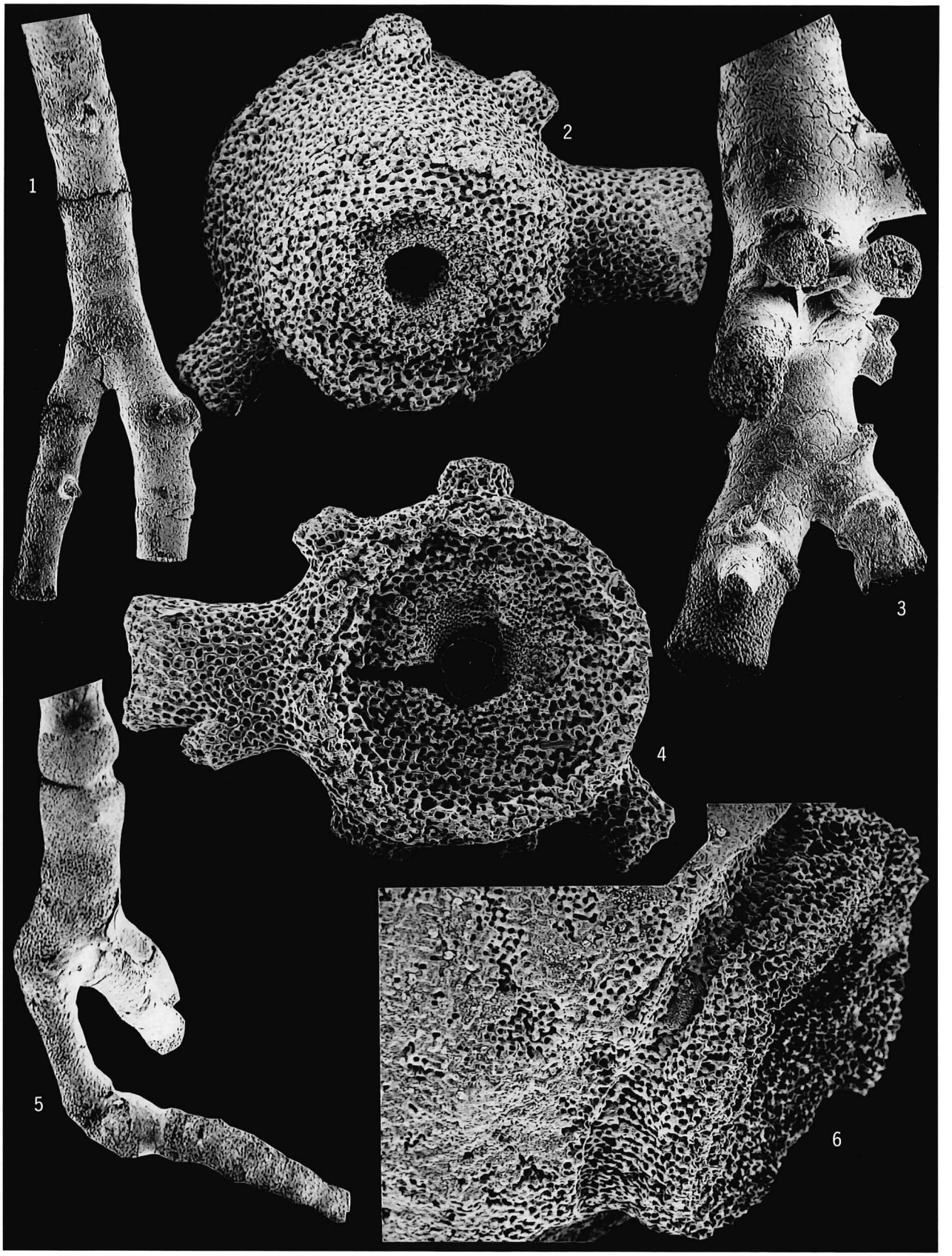

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Plate 7

Figs. 1-6. *Democrinus brevis* (A. H. Clark, 1909), Recent.

Fig. 1. USNM E17992/box V/stub 4. Oblique view of columnal 2. × 70.

Fig. 2. USNM E17992/box V/stub 4. Oblique view of columnal 3. × 70.

Figs. 3, 4. USNM E17992/box V/stub 5. Proximal(?) (3) and distal(?) (4) articular facets of columnal 6; * mark positions of weakly-formed synarthrial fulcra. Facets mounted in same relative orientations to show rotation of elliptical lumen within columnal. 3. × 70. 4. × 65.

Figs. 5, 6. USNM E17992/box V/stub 8. Articular facets of columnal 11. Facets mounted in same relative orientations to show rotation of fulcrum within columnal. 5. × 75. 6. × 68.

All scanning electron micrographs of specimens coated with 60% gold-palladium. Specimens in Pl. 6, fig. 6 and Pls. 7-8 are derived from the same crinoid.


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Plate 8

Figs. 1-7. *Democrinus brevis* (A. H. Clark, 1909), Recent.

Fig. 1. USNM E17992/box 6/stub 12. Oblique view of proximal articular facet and radicular extensions of columnal 44. × 33.

Fig. 2. USNM E17992/box 6/stub 12. Elongate radicular support of columnal 43. × 83.

Fig. 3. USNM E17992/box 6/stub 7. Node (=incipient site of radicular development) adjacent to fulcrum on proximal articular facet of columnal 34. × 72.

Fig. 4. USNM E17992/box 6/stub 10. Oblique view of the latus and articular facet of columnal 39. × 45.

Figs. 5, 6. USNM E17992/box 6/stub 11. Lateral view of well-developed radicular node (5) and proximal articular facet (6) of columnal 42. 5. × 95. 6. × 43.

Fig. 7. USNM E17992/box 6/stub 11. Proximal articular facet of columnal 41. × 48.

All scanning electron micrographs of specimens coated with 60% gold-palladium. Specimens in Pl. 6, fig. 6 and Pls. 7-8 are derived from the same crinoid.

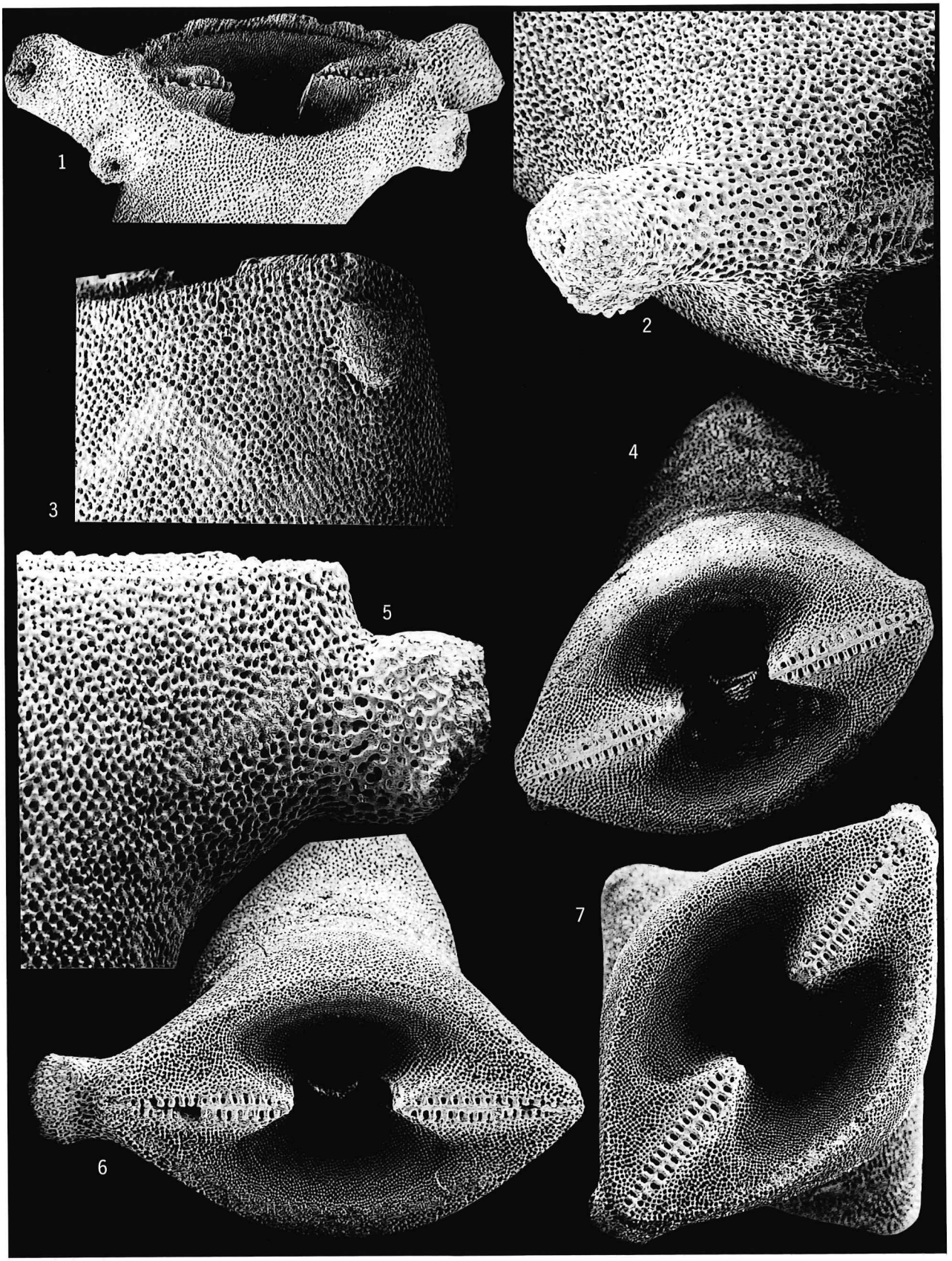

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Plate 9

Figs. 1-9. *Democrinus brevis* (A. H. Clark, 1909), Recent.

Figs. 1-7. USNM E41939/box IV/stub 4. Presumed juvenile specimen. 1, 2. Complete specimen; column broken in center, attachment structure not preserved. × 14. 3. Crown (note flange-like 1Br2) and proximal column. × 60. 4. Detail of proximal column. × 150. 5. High, slender columnal with central girdle from near center of column. × 125. 6. Lateral view of a more distal columnal. × 120. 7. Broken section (probably not the articular facet) of most distal preserved columnal showing trabeculae. × 500.

Figs. 8, 9. USNM E41937/box IV/stub 8 (see also Pl. 10, fig. 5). Regenerating(?) crown showing resorption of part of proxistele. 8. Whole specimen (only crown and proximal column preserved). × 11. 9. Detail showing column tapering away from base of cup. × 30.

All scanning electron micrographs of specimens coated with 60% gold-palladium.

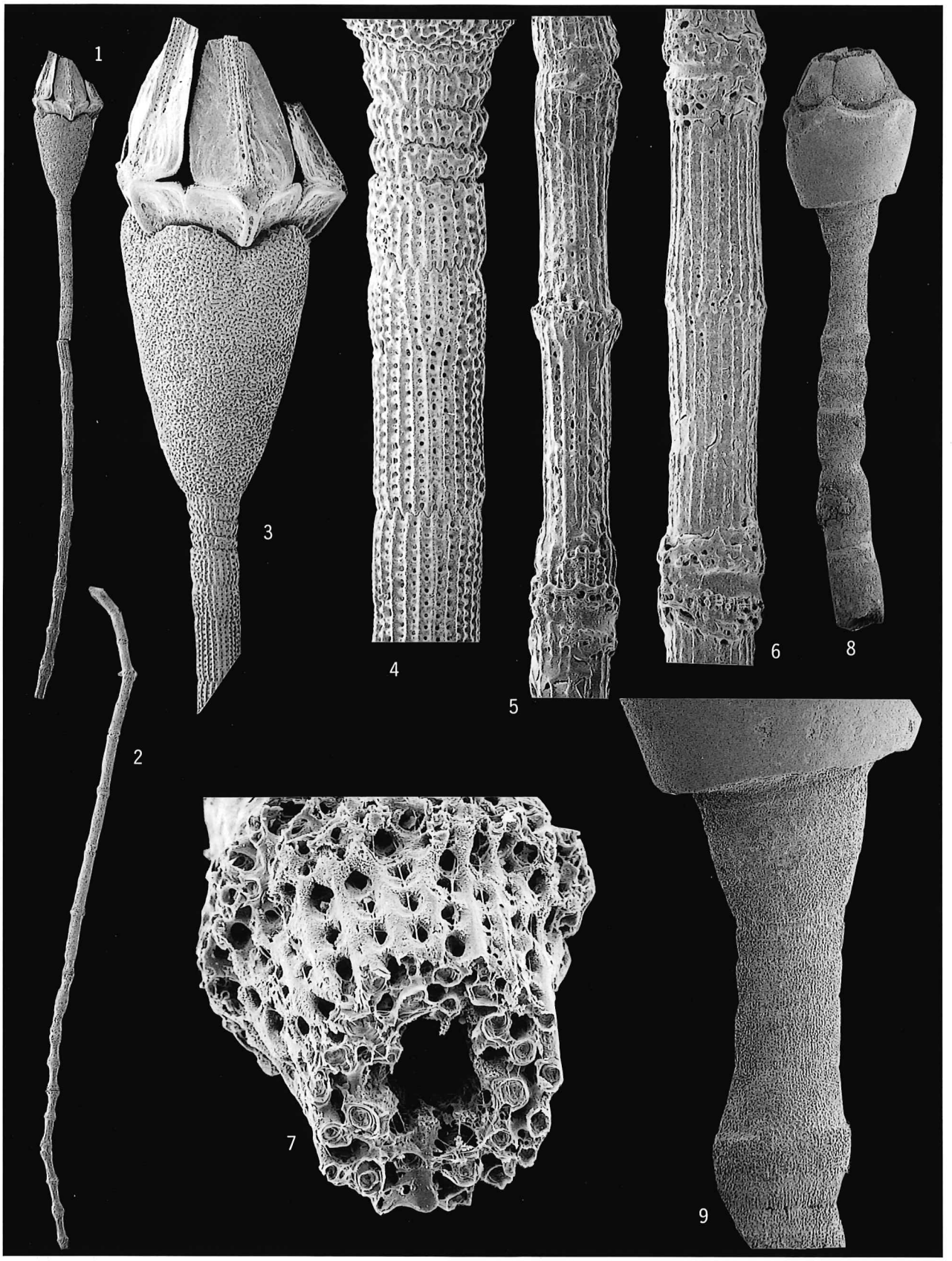

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Plate 10

Figs. 1-7. *Democrinus brevis* (A. H. Clark, 1909), Recent.

Figs. 1, 2. USNM E41938/box IV/stub 5. Attachment structures from two individuals. 1. Terminal attachment. × 12. 2. Runner-type attachment. × 10.

Fig. 3. USNM E26224/box IV/stub 2. Part of radicular attachment, showing branches of radicles. × 15.

Figs. 4, 6. USNM E17917/box IV/stub 7. 4. Radicular ossicle. × 65. 6. Paired axial canals on a radicular facet of a distal columnal. × 90.

Fig. 5. USNM E41937/box IV/stub 8 (see also Pl. 9, figs. 8, 9). Slightly damaged, synostosial facet of most distal columnal preserved with triangular synarthrial ridge developing (lower part of figure, left of centre; compare with Pl. 7, fig. 4), × 80.

Fig. 7. USNM E26224/box IV/stub 1. Attachment structure. × 14.

All scanning electron micrographs of specimens coated with 60% gold-palladium.

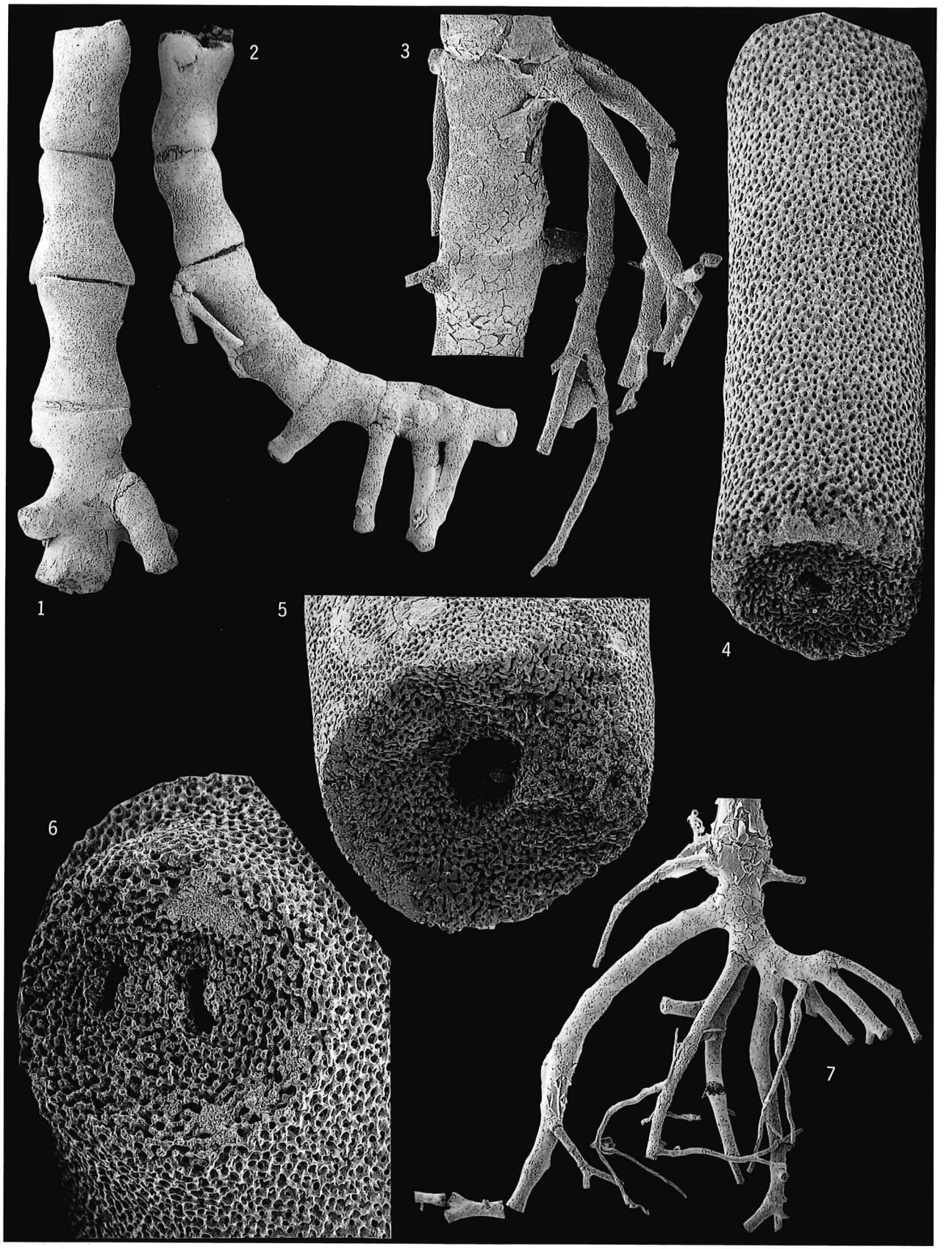

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Plate 11

Figs. 1-9. Indeterminate platycrinitid columnals, Lower Carboniferous.

Figs. 1, 2. BMNH EE 5234[1]. 5234[2], respectively. Oblique lateral views of high, tuberculated columnals. Note clustered crenulae on articular facet, particularly on EE 5234[2], × 40 and × 50, respectively.

Fig. 3. BMNH EE 5233[1]. Oblique view of facet and part of latus; note fulcrum, crenulae at either end and central, circular lumen. × 35.

Fig. 4. BMNH EE 5233[2]. Oblique view of high columnal, showing crenulae. × 35.

Fig. 5. BMNH EE 5231[1]. Articular facet and tubercle. × 35.

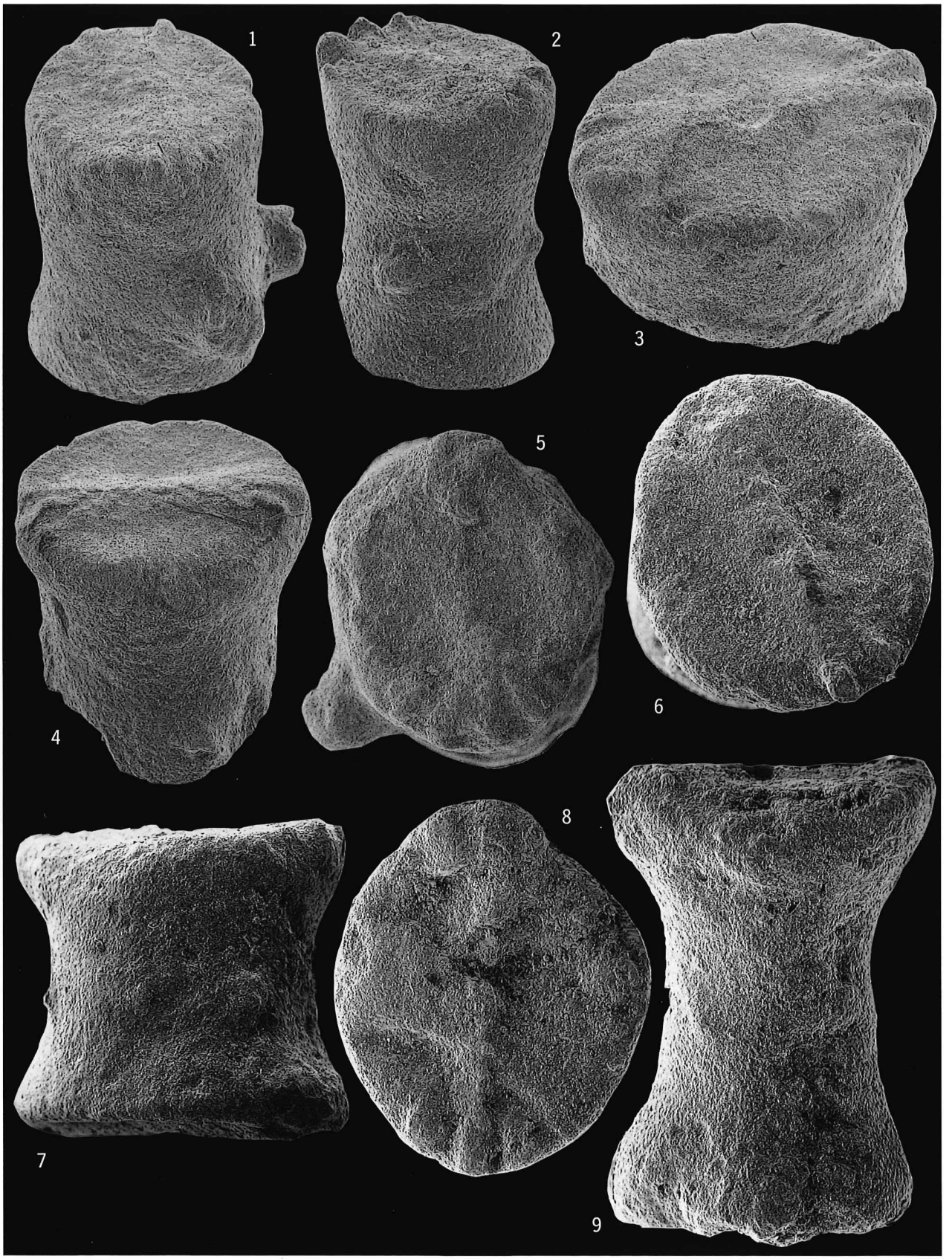
Fig. 6. BMNH EE 5236[1]. Articular facet, showing peg-like crenulae. × 50.

Fig. 7. BMNH EE 5235[1]. Lateral view of low columnal. × 36.

Fig. 8. BMNH EE 5236[2]. Articular facet preserving fulcrum and crenulae. × 40.

Fig. 9. BMNH EE 5235[2]. Lateral view of high columnal. × 40.

All scanning electron micrographs of specimens coated with 60% gold-palladium.


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