

A NEW DEVONIAN CRINOID FROM AUSTRALIA

by DENIS E. B. BATES

ABSTRACT. *Pernerocrinus discus* sp. nov., a Devonian crinoid from the Lilydale Limestone, Victoria, is described. Additional information on the morphology of the genus is presented, supplementing that of Bouska.

THE specimens described in this paper were collected over a period of years by various geologists, and were deposited in the National Museum of Victoria. They were brought to the writer's attention by Professor A. Wood, who had examined the collection in 1955, with Mr. E. D. Gill of the Museum. I am grateful to both Mr. Gill and Professor Wood for their help, for critically reading the manuscript, and willingness to place their notes at my disposal. I would also like to thank Dr. I. Strachan of Birmingham University, who kindly lent specimens of *Crotalocrinites*, for comparative purposes.

The material comes from the lower Devonian Lilydale Limestone (Gill 1965, p. 119), probably upper Siegenian or lower Emsian in age. The limestone is a biostrome, of limited extent, containing principally corals and stromatoporoids. A near-shore environment is indicated by the presence of land plants in the underlying Ruddock Siltstone, and probably also by the succeeding brachiopod-bearing Cave Hill Conglomerate.

Crinoid crowns are rare in the limestone, but a large number of fragmentary specimens of *Pernerocrinus* has been collected over a considerable period of time. None of the specimens is complete, and serial sectioning of one specimen which was partially surrounded by matrix suggests that crowns have been rolled by current action before becoming incorporated in the sediment. Other specimens are overgrown by bryozoans, but again appear to have been rolled and abraded beforehand. It seems likely, therefore, that the reef waters were turbulent, at least intermittently.

Subclass INADUNATA Wachsmuth and Springer 1885
Order CLADOIDEA Moore and Laudon 1943
Suborder CYATHOCRINOIDEA Bather 1899
Family CROTALOCRINITIDAE Bassler 1938
Genus PERNEROCRINUS Bouska 1947

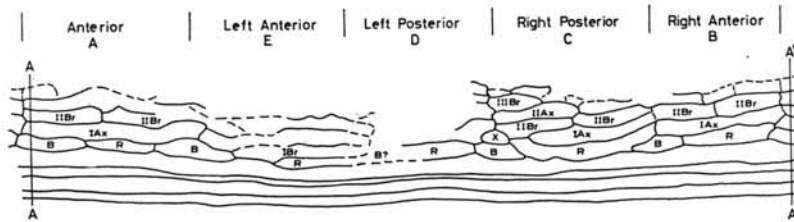
Diagnosis. Endoskeleton of tube-like column with very wide lumen, surmounted by a ring-like calyx formed of irregular plates; arms fused into a solid subhorizontal disc pierced by large axial canals and bearing on its upper surface ambulacral grooves; tegmen of irregular plates rigidly fused together and to the proximal arm plates; ambulacral grooves lead beneath tegmen; no anal tube.

Type species. *Pernerocrinus paradoxus* Bouska 1947

Discussion. The Australian specimens amply confirm the suggestions of Bouska (1950, p. 22) as to the relations between *Pernerocrinus* and the other Crotalocrinitidae. Both *P. paradoxus* and *P. discus* are lower to middle Devonian, much later than the Wenlock to Ludlow Crotalocrinitidae, yet they form a logical, if extreme, modification of the

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evolutionary trends shown by *Crotalocrinites* and *Syndetocrinus*. Instead of a regular sequence of infrabasals, basals, radials and anals, an irregular pattern with a vague pentamer symmetry is apparent. The basals and radials may have been united in one circlet, as in the holotype of *P. discus* (P26696, Pl. 57, fig. 9, text-fig. 1) and sixteen plates were identified in the first circlet in the larger specimen that was serially sectioned. Infra basals have not been recognized in the holotype, and if present could not be identified in the sectioned specimen. Comparison between these two specimens suggests that the holotype is immature, and that additional plates were added, with a decrease in regularity, during growth. Bouska (1950, p. 19) could not recognize any plates within the calyx, and suggested that they may have been partly or completely atrophied.



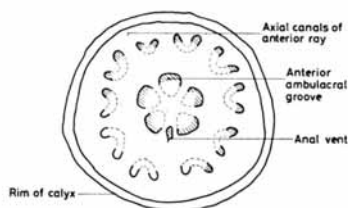
TEXT-FIG. 1. Sketch of upper columnals, basals, radials and proximal brachials, drawn from photographs of the holotype, P26696. A-A and A'-A' correspond.

The cup, which is globose and composed of large striated plates in *Crotalocrinites rugosus* (Wachsmuth and Springer 1888, pl. 20), varies in other species of *Crotalocrinites* and *Syndetocrinus* to a flared cup (Angelin 1878, Pl. 8, figs. 1-3), which is close to that of *Pernerocrinus*. Angelin's plate 8 has a mixture of forms, all ascribed to *C. pulcher*. Some have a large calyx with the sides convex in outline (figs. 8, 9), but another specimen (figs. 1-3) is shown as having a calyx concave in outline, and with irregular proximal brachials. This specimen closely approximates to the structure and appearance of both *Syndetocrinus* and *Pernerocrinus*. The calyx of *Syndetocrinus* (Kirk 1933, figs. 1-8, Bouska 1950, Pl. 2) is composed of low, regularly arranged but rather irregularly shaped infrabasals, basals and radials, in conventional circlets. Above them the brachials up to the fourth order are rigidly incorporated in the cup, and are somewhat irregular in disposition and shape. The brachials of the third and fourth orders are greatly deepened, extending inwards and upwards to form a solid platform, with the ambulacral grooves traversing its upper surface.

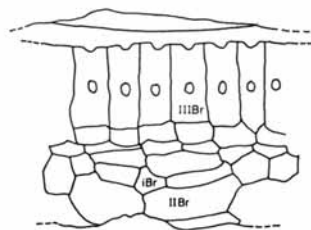
The free arms are not known, but the last brachials preserved have their outer and distal surfaces formed into facets, bearing prominent axial canals and ambulacral grooves.

The structure of *Pernerocrinus* is remarkably similar to that of *Syndetocrinus*, and can readily be interpreted as a variation of the latter genus, and to have evolved from it. In *Pernerocrinus* the irregularity of the fixed brachials apparent in *Syndetocrinus* has permeated to the base of the cup, though some order can still be seen, especially in the smaller specimens. The sides of the cup flare very gently until above the base of the

arms, but then curve round to the horizontal at least. The brachials at this level appear on the dorsal surface as rectangular plates, but in cross-section and in broken specimens are seen to be long and curved (Pl. 58, fig. 3). Very similar plates are shown by Wachsmuth and Springer (1888, pl. 19, fig. 2c) at a similar position in the cup of *Crotalocrinites rugosus*. Higher orders of brachials are incorporated in the rigid disc of *Pernerocrinus* than in *Syndetocrinus*, and it appears, from the preservation of articulating facets for covering plates on the ambulacral grooves, that the tegmen did not extend over the whole disc. It is not known whether the disc was bordered by movable arms.



TEXT-FIG. 2. Internal view of tegmen and calyx, drawn from P26701.



TEXT-FIG. 3. Sketch of plate arrangement on part of the cup, drawn from P26693. The proximal brachials are very irregular, and small irregular interbrachials are also present.

Although the movable arms are not preserved in *Syndetocrinus*, they may have been similar to those of *Crotalocrinites*. In *Crotalocrinites* the brachials are cross-shaped, with the cross pieces in adjacent arms connected to unite all the arms into a flexible net, pierced by apertures and capable of folding above the tegmen. The arms have prominent cover plates and axial canals, and in cross-section have the same proportions as those of the disc of *Pernerocrinus*. By changing the shape of the brachials (as seen in ventral view), and joining them rigidly both laterally and radially, one can form the rigid disc. There is no trace of the interbrachials described in *C. rugosus* by Wachsmuth and Springer (1888, pl. 19, fig. 1), which appear on the ventral surface. Interbrachials are apparently developed in *Pernerocrinus*, but occur between the lower brachials, at a lower level than the curved brachials (text-fig. 3).

Pernerocrinus discus sp. nov.

Plate 57, Plate 58, figs. 1, 3, 5-9

Holotype. Proximal stem, calyx, and partial disc (P26696). Diameter of base of calyx 21.0 mm.

Paratypes. Inner disc and cup apparently above the level of the radials (P26693). Diameter of specimen 22 mm. (approx). Partial cup and disc (P26695). Partial cup and disc (P26691). Partial disc (P26699). Inner disc and cup above the level of the radials (P26701).

Other figured material. Part of root system (P26714). Disc and partial cup (P26707). Partial disc and cup above the radials (P28037).

Type horizon and locality. Lilydale Limestone, Cave Hill Quarry, Victoria, Australia, Gill's locality 6 (1940, p. 258).

Description. Column circular, lumen about two-thirds the outside diameter or more, height to width ratio of columnals about one in ten. Irregular root system with branches each bearing a central canal with a kidney-bean shaped cross section.

BB (?) and RR (?) combined into one circle of plates resting on the top columnal, both approximately equal in height to the top columnal. RR twice as wide as BB and slightly overlapping them ventrally. Additional IRR and iBr in larger specimens, giving 15–17 plates in presumed B/R circlet and in succeeding circlets. Arms apparently start with IAx in each ray, wider than RR and in contact with each other in some rays, equal in height to RR. Branching isotomous. IIBr equal in height to IAx, two in number. IIBr forming flange and part of roof of tegmen, equal in height to preceding plates in external view, but curving upwards and inwards, each have the shape of a curved rod with a rectangular cross-section. Subsequent plates shorter and straighter, united with successive and lateral plates to form a rigid disc, with axial canal egg-shaped in cross-section, tapering upwards, in width half that of the plate. Axial canal with three vertical canals between each successive pair of plates, connecting the axial canal with the ventral surface: a wider central canal becoming narrower towards the ventral surface and flattened between adjoining plates, lateral canals narrower and opening in the sides of the ambulacral grooves. Ambulacral grooves just less than half the width of the intervening ridges, U-shaped in cross-section, dividing isotomously with the arms. Sides of grooves marked by openings of lateral canals at the plate junctions, and between them, 2–4 pits, probably for articulation of cover plates.

Tegmen composed of mosaic of small irregular plates, covering roof of body cavity and extending a variable distance out over the disc to cover the ambulacral grooves. Beneath the tegmen ambulacral grooves open as an upper series of pores with the axial canals forming a lower series. Ambulacral groove apertures usually ten in number, grouped in pairs corresponding to the five arms, normally branching once beneath tegmen to emerge on the ventral surface as 20 grooves. Axial canals appear on the inner surface as 20 in number, elongate radially and grouped in pairs corresponding to the ambulacral grooves. Position of anal vent (?) indicated internally in some specimens by a radially elongate slit positioned slightly excentric to the entrances to the ambulacral grooves, in an interradial position. Aperture on ventral surface not observed.

Pernerocrinus sp.

Plate 58, figs. 2, 4

Figured material. Partial disc, cup and root system (P26722).

Description. Calyx plates not observed. Root system irregular, attached directly to cup and disc, without intervening stem, formed of irregular plates each with a kidney-bean shaped cross-section. Internal diameter of cup about 90 mm., with an estimated 90 axial canals opening into it. Axial canals and central canals between BrBr very prominent, lateral canals apparently not developed.

DISCUSSION

The material available for study is extremely variable in size and shape, and two species are thought to be present. In general, the larger specimens are more irregular than the smaller.

Column diameter, measured by the diameter of the base of the calyx, varies from 18 to 40 mm, and wall thickness from 1.7 to 3.8 mm. There does appear to be a rough correlation between the two measurements, but there were insufficient specimens to determine the significance of this. Two specimens (P26740-1) of isolated lengths of column suggest that the lumen tapers markedly away from the calyx, with an increase in wall thickness towards the root system. Numerous radial pores are present between the columnals in these specimens, but have not been detected in the proximal parts of the column attached to some of the cup specimens. At the root system, the column splits into an irregular mass of roots, each composed of plates perforated by an axial canal with a distinctive 'kidney-bean' shaped cross-section. The concave wall of the canal bears a sharp cusp projecting inwards (P26714, Pl. 57, fig. 7). In *Pernerocrinus* sp. this root system is attached directly to the base of calyx, without any intervening column. The roots have spread out under the flange of the disc of arms.

Pernerocrinus paradoxus (Bouska 1950, p. 20, fig. 6, Pl. 3, fig. 1) has a much wider stem than *P. discus*, and appears to be similar in size and general proportions to *Pernerocrinus* sp. of this paper.

The irregular calyx plates can be roughly grouped into five divisions in only one specimen, the holotype of *P. discus* (P26696, Pl. 57, fig. 9; text-fig. 1), though part of the circle is not clear. Four small plates in interradial positions are interpreted as basals (it is not clear whether a fifth is present). They are separated by larger plates, which lie partly between them and partly overlap them. As these are succeeded vertically by a succession of plates, they are interpreted as radials. One other plate appears in this specimen, vertically above one basal, in an interradial position, and in a position corresponding to an internal slit which could be an anal vent. This plate could be interpreted as a single anal, similar to that in *Crotalocrinites*. The larger specimen that was serially sectioned shows a more complicated arrangement of presumed calyx plates, which cannot be satisfactorily identified. In neither specimen can any infrabasals be identified, and they are presumed to have atrophied.

Typical brachials are developed on the disc formed from the fusion of the arms, but the proximal ones are modified to form the upper part of the cup and above this the flange of the disc. The first brachial appears always to be a primaxial, and is followed by two secundibrachs at most before another division. The first four or five brachials in each ray are similar in appearance and height to the radials and basals: they serve to build the tub-like calyx upwards, with a slight outwards flare. They are not pierced by axial canals, nor do they bear ambulacral grooves: both of these structures enter the domed roof of the calyx at a higher level.

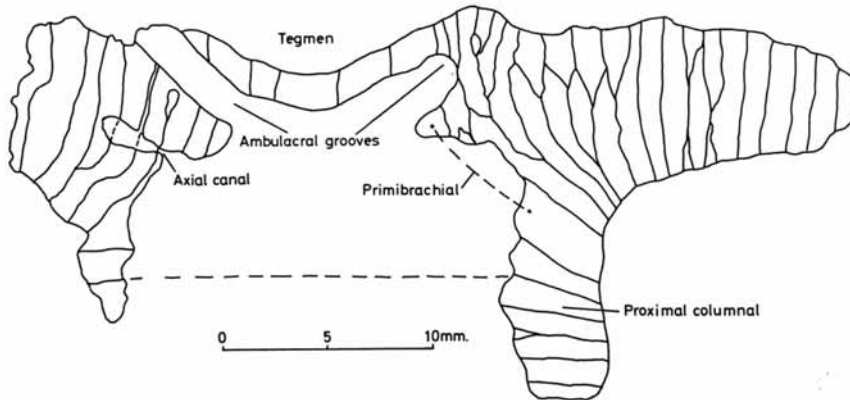
The succeeding brachials are greatly lengthened and modified. They are inclined inwards and upwards, and are bent at their mid-length upwards to the vertical (Pl. 58, fig. 3). At the bend each plate is pierced by an axial canal, and the upper end bears an

EXPLANATION OF PLATE 57

Figs. 1-9. *Pernerocrinus discus* gen. et sp. nov.

1-3. P26707. Ventral, dorsal, and lateral views. $\times 1.3$, $\times 1.3$, $\times 1.7$. 4. P26707. Enlargement of brachials showing axial canals, central and lateral canals, and syzygial sutures. $\times 7.0$. 5, 6, 8. P26693, paratype. Ventral, dorsal, and lateral views of cup lacking the disc. $\times 2.1$, $\times 2.1$, $\times 1.5$. 7. P26714, Portion of stem system. $\times 2.4$. 9. P26696, holotype. Posterior view of cup. $\times 1.9$.

ambulacral groove, and supports part of the tegmen. These brachials, together with the central part of the tegmen, form the domed roof of the calyx. In some specimens (e.g. text-fig. 4) the first of these long brachials is the first primibrachial, but in others (e.g. the holotype, P26696 and P26693) it is preceded by three or four circles of brachials. In text-fig. 4 the first primibrachial is shown as being present as two distinct pieces, though the calcite in both appears to have the same crystallographic orientation. The significance of this is not clear, but it may be interpreted as being due to changes during growth. As the crinoid increases in size, so the body cavity increases in volume, and partial resorption of the plate may result in separation of the two parts.



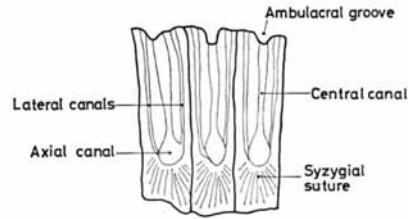
TEXT-FIG. 4. Approximately median section through calyx and proximal disc, drawn from an acetate peel of a serially sectioned specimen.

The roof of the tegmen is pierced by two circles of openings: a lower ring of axial canals and an upper one formed by the ambulacral grooves. These are best seen in specimen P26701, to which the following account refers. The axial canals form a ring of twenty openings, grouped into pairs by their proximity and by a groove linking them (text-fig. 2). The ambulacral grooves, emerging in a higher and smaller circle, are marked by five petal-shaped concavities in the roof. Between two of these is a radially directed slit-like opening into the roof of the calyx, which is interpreted as marking the internal entrance to the anal tube. However, this could not be recognised externally, either on this specimen or on others which showed a complete tegmen. The specimen that was serially sectioned showed a structure in this position, but no external aperture could be recognised.

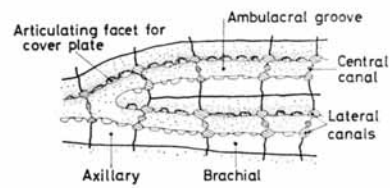
Succeeding brachial plates, all with ambulacral grooves and axial canals, become successively more upright. These typical plates are box-shaped, slightly wider than high, but deeper from the dorsal to the ventral surface of the disc. The dorsal surface of each plate is slightly domed. On the ventral surface the deep U-shaped ambulacral groove is half the width of the plate. The sides of the grooves are lined with 2-4 depressions, probably articulating facets for now vanished cover plates. Between successive plates

three canals link the groove with the axial canal (text-fig. 5). A central canal is more prominent internally, and is formed by an upward tapering of the axial canal. It is, however, less prominent externally (on the floor of the groove) than the two lateral canals, which open in large pores (on the sides of the grooves) which lie in sequence with the depressions interpreted as facets for the cover plates. Internally these lateral canals join the axial canal at its horizontal midline, i.e. halfway down the side of the axial canal.

The ambulacral grooves in *P. discus* are relatively much narrower than in *P. paradoxus*, and carried cover plates which were probably very similar to those of *Crotalocrinites*



TEXT-FIG. 5. Sketch of three adjacent brachials, showing their distal surfaces, based on P26707.



TEXT-FIG. 6. Portion of ventral surface of the disc, based on P26695.

(cf. Bouska 1950, pl. 1, fig. 9). The cover plates in *P. paradoxus* (Bouska 1950, pl. 3, figs. 4a, 4b) cover the complete width of each arm branch, so that in ventral view the plates interlock between branches as well as centrally within them.

Successive brachials interlock by a series of ridges, forming a syzygial suture. These ridges are particularly prominent on the upper and lower faces of the brachials (those faces pierced by the axial canal) where they tend to radiate dorsally from the canal. The faces between adjacent arms bear ridges which run parallel to the surface of the disc. Axillary brachials bear a bifurcating ambulacral groove, and have an internal bifurcation of the axial canal.

The tegmen is supported on the proximal brachials of the disc, and forms a roof over the ambulacral grooves, so that the mouth is subtegminal. It is composed of a mosaic of small plates, irregular and thick. In no specimen has an anal series of plates, or an anal vent, been observed. The original lateral extent of the tegmen—the extent to which it covered the ventral surface of the disc—is unknown. One specimen (P28037, Pl. 58, fig. 5) has a small portion of what appears to be tegmen plates lying appreciably

EXPLANATION OF PLATE 58

Figs. 1, 3, 5–9. *Pernerocrinus discus* gen. et sp. nov.

- 1, 6. P26695, paratype. Ventral view of partial cup; enlargement to show ambulacral grooves. $\times 1.3$, $\times 5.5$. 3. P26691, paratype. Lateral view of partial cup, with curved brachials, $\times 2.2$. 5. P28037. Ventral view of cup with abnormally irregular tegmen. $\times 1.1$. 8, 7. P26701, paratype. Dorsal view of cup with prominent anal vent, oblique dorsal view with prominent brachials. $\times 1.5$, $\times 3.8$. 9. P26699, paratype. Ventral view of badly weathered specimen. $\times 1.4$.

Figs. 2, 4. *Pernerocrinus* sp.

- 2, P26722. Oblique ventral view, interior of calyx to left; 4, further oblique ventral view, with part of attachment system at lower left-hand corner. Both $\times 1.5$.

further from the centre than the rest of the tegmen, and it also appears that in most specimens which show the tegmen that its outer limits are abraded. The cover plate facets are an indication, however, that the tegmen could not have been present where they occur, and this line of evidence seems to limit the original extent of the tegmen to its observed extent on most specimens.

Interradial and interbrachial plates are apparently of sporadic occurrence, and are found principally in the larger specimens. There appear to be none in the holotype, but in a paratype (P26693, Pl. 57, fig. 5; text-fig. 3) small irregular interbrachials are present associated with the proximal brachials. The larger serially sectioned specimen has a larger number of such plates, forming a number of circlets of brick-shaped plates on top of the column: the circlets must include infrabasal (?), basal, radial and brachial plates as well but it was not possible to identify each type of plate below the level at which brachials, with axial canals, were present.

Although the normal shape of *Pernerocrinus* is of a horizontal disc on a vertical column, there are variations on this (text-fig. 7). The disc can be either convex or concave on its upper surface. P26707 shows an umbrella-like disc, irregularly sloping away from the central tegmen, which is domed. Conversely, P26695 has a shallow bowl-shaped disc, with the tegmen in the centre of the depression.

P26722, and another specimen in the collection, P26730, appear to be more radically different, and are here ascribed to another species. The holdfast system is directly attached to the proximal part of the disc, without any columnals forming a normal stem. Secondly the internal diameter of the cup is very large, about 90 mm. The axial canals, where they emerge into the cup interior, are at least 90 in number. A further difference is that the axial canals are relatively larger, and the central canals connecting them with the ambulacral grooves are very prominent, and the lateral canals are apparently not developed. Some of these differences could be due to the much larger size of these specimens, but the absence of a stem may be more significant.

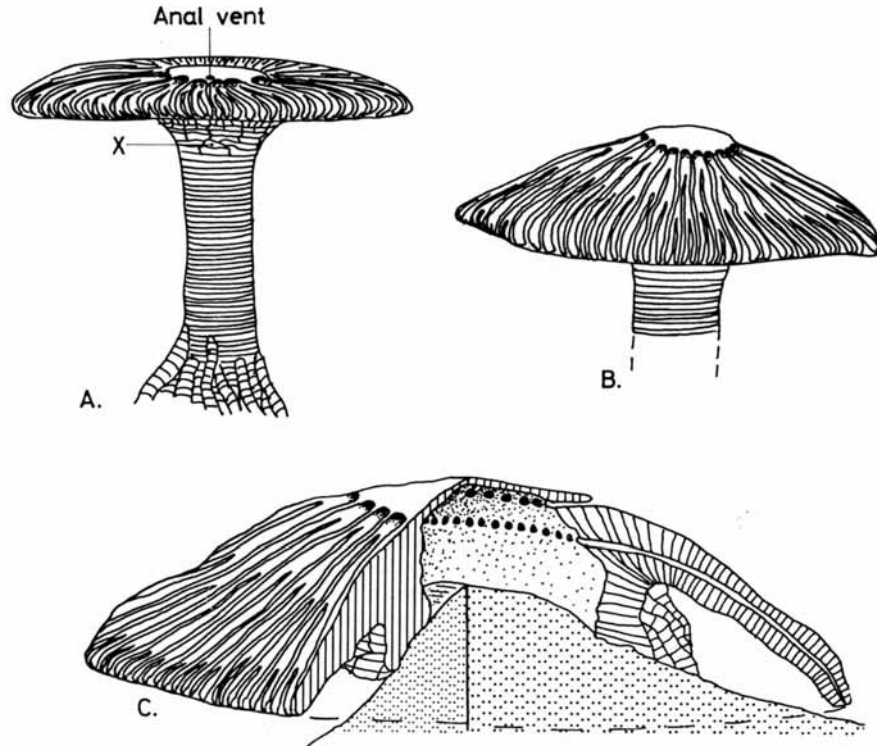
Parapernerocrinus sibiricus Yakovlev (1949) is another allied species. Yakovlev erected the genus *Parapernerocrinus* for species in which the limit between the stem and cup is distinct, the stem is not short, and does not have longitudinal seams in its segments.

However, these distinctions appear to be very slight, to judge from the illustrations, and secondly there may possibly be gradations between the two types of stem: the writer prefers to retain *Pernerocrinus* for all three species. Specifically *P. sibiricus* is distinct from *P. discus*; it appears, from Yakovlev's figure (pl. 1, fig. 6) to have lower brachial and cup plates which have sinuous outlines, and which have grown outwards and downwards over the top columnals. A further difference is that in *P. discus* the adjacent brachials do not always alternate with each other (text-fig. 6, Pl. 57, fig. 2, Pl. 58, figs. 1, 6, 9), though this is not invariably so. Yakovlev (1949, p. 16) describes the brachials of *P. sibiricus* as being hexagonal in shape, and to alternate with each other to give greater strength.

Mode of Life

The large surface area of the fused arms, together with the articulating facets for the cover plates, suggests that food gathering was carried out by the fused arms, and there may have been no separate flexible arms beyond the fixed disc. Bouska, however,

describes a rolled-up portion of arms in *P. paradoxus* which he interprets as being attached round the complete diameter of the disc (1950, fig. 6). No similar material has been recognized from Lilydale, and some Australian specimens suggest that the disc tapers in thickness to a rounded border. This is shown in the reconstructions (text-fig. 7).



TEXT-FIG. 7. A. Reconstruction of typical specimen of *Pereroocrinus discus*, based on the holotype, P26696: posterior view. B. Reconstruction based on P26707. C. Reconstruction of *Pereroocrinus* sp., based on P26722. The specimen is partially cut away to show the internal openings of the axial canals and the ambulacral grooves. The regularly stippled portion of the figure is the substratum.

Hence food gathering was entirely dependent on the rain of particles falling on the disc: there was no possibility of moving the arms to set up water currents to increase the food supply. If a water current was set up, it would have to be by action of the podia (unless there were pinnules attached to the disc). A further consideration is that there must have been some method of discharging waste from the (presumed) anal vent, and also ridding the disc of inorganic material falling on it. The surface of the disc between the food grooves may have carried cilia, as observed in modern crinoids, which would carry debris to the edge of the disc (cf. Gislén 1924, p. 272).

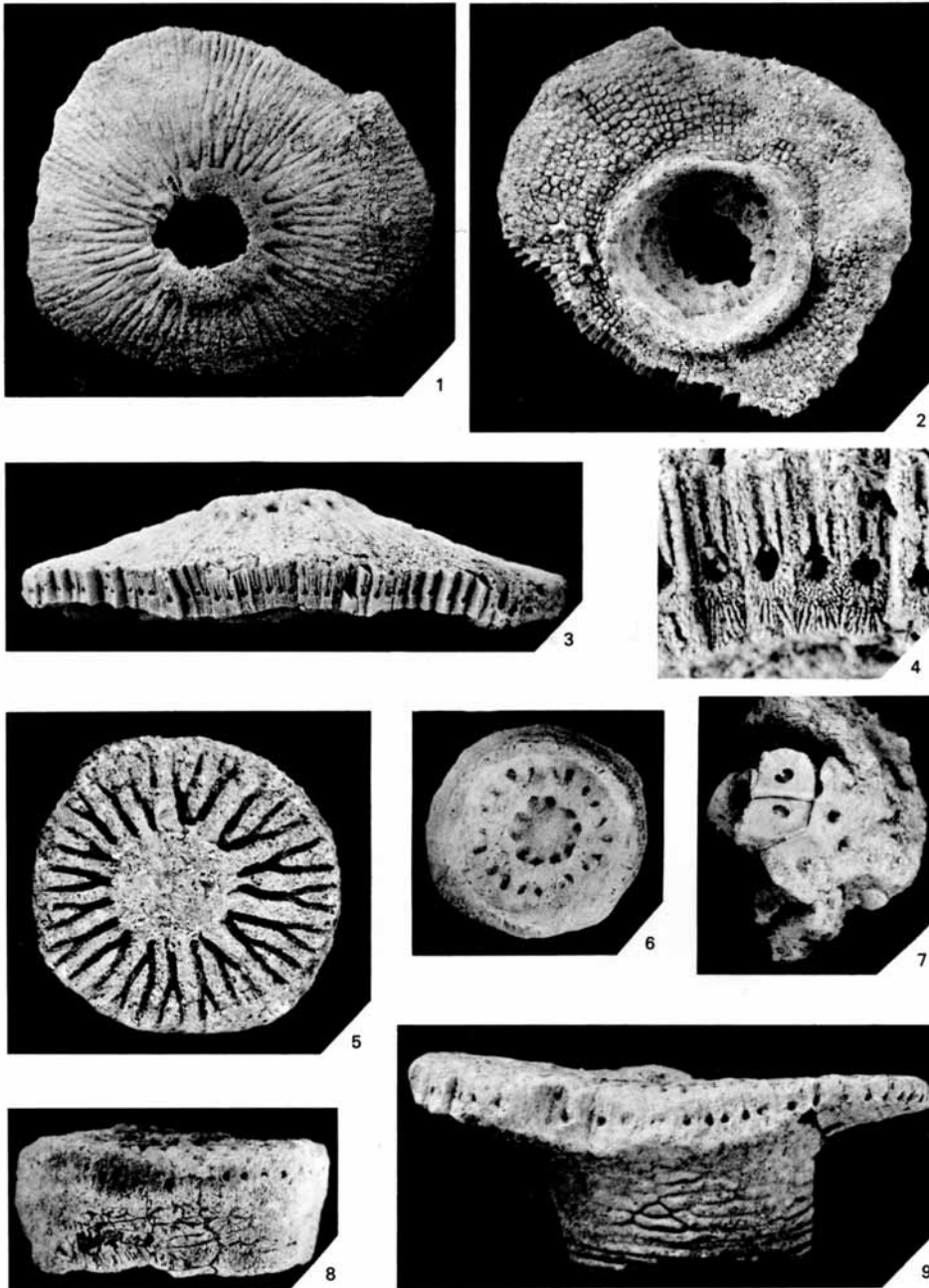
The axial canal system is very similar to that of *Crotalocrinites*, and is probably inherited from it, though the vertical canals could not be detected, by the writer, in specimens of *Crotalocrinites* available to him. In modern articulate crinoids the axial canals house the brachial nerves of the aboral system (Hyman 1955, p. 62), these nerves being responsible for arm movement, in contrast to the oral and deeper oral systems, whose function relates to the feeding system. Thus the large axial canals of *Crotalocrinites* can be explained in terms of the flexibility of the network of its arms. However, their prominent development in *Pernerocrinus* is puzzling, since the muscles for arm movement are presumably no longer needed. Either they are vestigial, or the nerves have been adapted to another use, or conceivably there may have been pinnules attached to the disc. In the last case, the lateral canals would have carried the branches of the brachial nerve to the pinnules. It is noticeable (text-fig. 6) that the lateral canals disrupt the sequence of facets on the sides of the ambulacral grooves. This suggests that there may have been either pinnules attached here, or a cluster of podia.

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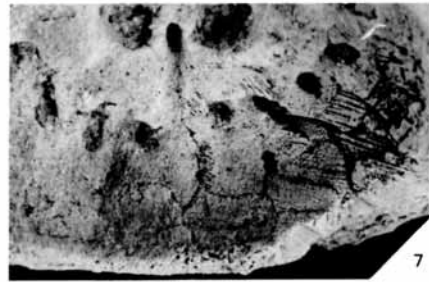
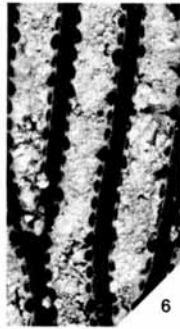
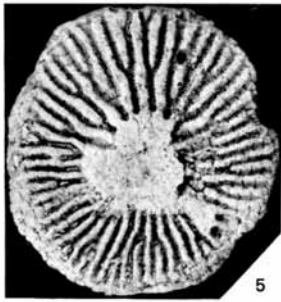
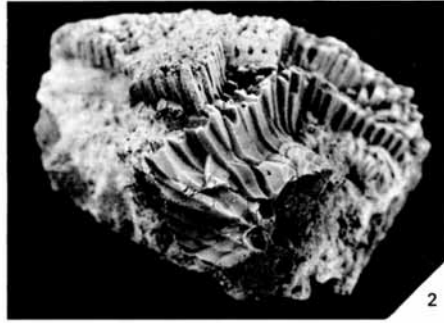
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