# *Compagicrinus fenestratus*, a new Lower Ordovician inadunate crinoid from North Greenland

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*Compagicrinus* n.gen., from the Nunatami Formation (Arenig) of Washington Land, North Greenland, is assigned to the Order Dendrocrinina. A unique arrangement of plates in the cup is intermediate between those of *Aethocrinus* (L. Arenig) and *Dendrocrinus* (M. Ordovician – M. Silurian). The plate arrangement of *Aethocrinus* is reinterpreted. *Compagicrinus* may have given rise to the Order Cyathocrinina via *Carabocrinus*. It is suggested that the usual radianal of dicyclic inadunates arose from the super-radianal of *Compagicrinus* and not the infer-radial of the C ray.

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During the summer season of 1976, J.S. Peel of Grønlands Geologiske Undersøgelse (GGU) collected a small slab from the Nunatami Formation (Ordovician; Arenig) at Nygaard Bugt, Washington Land, western North Greenland (fig. 1) on which were preserved two small crinoids. The Arenig age is, in itself, interesting as only three older or contemporary crinoid genera have been described to date. The specimens are fairly well preserved with parts of the arms and stems attached to the cups. The arms branch isotomously (i.e. into two equal parts) only twice, as far as we can tell, giving a total twenty ramules in life. They lack pinnules, but have a complex series of cover plates over the food grooves. The cup is dicyclic, and there is a large elongate anal sac.

The two specimens are preserved in different orientations so that different cup plates can be seen on each. We have thus been able to reconstruct the plate arrangement which is unique, although in some ways intermediate between those of *Aethocrinus* Ubaghs, from the Lower Arenig of southern France, and *Dendrocrinus* which ranges from the Middle Ordovician to Silurian.

We refer the two specimens to a new genus, *Compagicrinus,* which provides significant new information concerning the early evolution of the cup in dendrocrinine crinoids and suggests a connection with the cyathocrinine crinoids via *Carabocrinus*. Like *Aethocrinus, Compagicrinus* raises problems concerning the terminology of inadunate cup plates.

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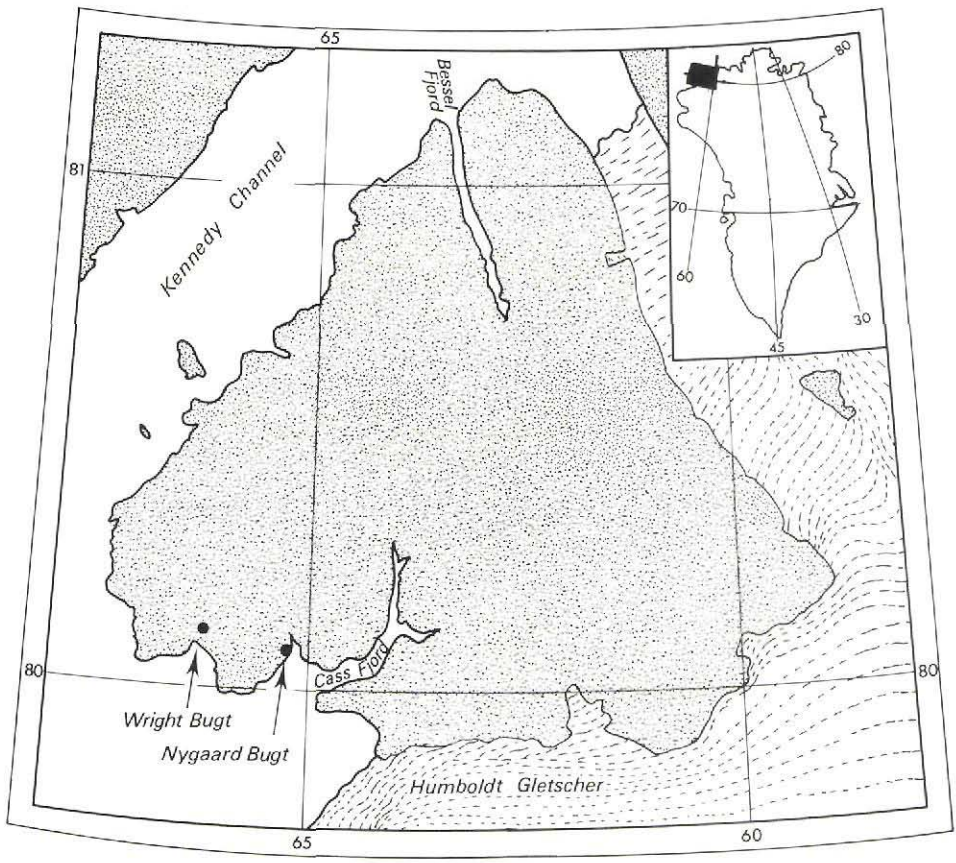


Fig. 1. Echinoderm localities in Washington Land. The specimens of *Compagicrinus* were collected at Nygaard Bugt; the locality at Wright Bugt produced the specimen of *Pleurocystites* described by Paul (this report).

Class Crinoidea Miller, 1821
Subclass Inadunata Wachsmuth & Springer, 1885
Order Cladida Moore & Laudon, 1943
Suborder Dendrocrinina Bather, 1899

Dendrocrinine crinoids are dicyclic, often with a large anal sac and have arms which branch isotomously or heterotomously. Ubaghs (1953, p. 751) included five families, Dendrocrinidae, Botryocrinidae, Ottawacrinidae, Thenarocrinidae and Cupulocrinidae, to which the family Aethocrinidae Ubaghs, 1969 may be added. Each of the last three of these includes a single genus in which the arrangement of cup plates differs from that of *Compagicrinus,* although there are some similarities, discussed below, with *Aethocrinus* and *Thenarocrinus*. *Compagicrinus* most closely resembles members of the Dendrocrinidae in the presence of a large anal sac, isotomously branched, non-pinnulate arms and in the general shape and ornament of the cup. Tentatively we assign it to the Dendrocrinidae.

## Family *Dendrocrinidae* Bather, 1890

*Diagnosis.* Dicyclic inadunates with a steeply conical cup with five infra-basals; radianal, anal x and sometimes other plates in the C-D inter-ray of the cup; radial facets narrow, horse-shoe shaped; prominent long anal sac; arms nonpinnulate, branching isotomously, but tending towards heterotomy.

This diagnosis is modified from Ramsbottom (1961, p. 14) and Moore (1962, p. 37) due to the inclusion of *Compagicrinus,* which has more plates within the cup than previously assigned genera.

### *Compagicrinus* n.gen.

*Type species. Compagicrinus fenestratus* n.gen. n.sp.

*Diagnosis.* A genus of Dendrocrinidae with infer- and super-radianals, C-D basal lying directly over an infra-basal and two anal plates incorporated into the cup.

*Remarks.* Typically, *Dendrocrinus* and other dendrocrinid genera have a radianal, an anal x and possibly one other anal plate incorporated into the cup (see Moore, 1962, fig. 9:5, p. 19). In *Compagicrinus* there is an extra plate in the basal circlet which we interpret as an infer-radianal (see discussion below). A super-radianal occurs below the radial of the C ray and two anal plates are incorporated into the cup. This plate arrangement is unique. *Thenarocrinus* has its solitary radianal directly overlying the C-D infra-basal, but has only one other anal plate (x) within the cup. In *Aethocrinus* there is a similar arrangement of plates in the anal region, but these have been subject to different interpretations (see Ubaghs, 1972). *Aethocrinus* also differs in having four plate circlets and inter-radials incorporated into the cup.

### *Compagicrinus fenestratus* n.gen. n.sp.

Fig. 2-6, 7B

*Types.* Both specimens are preserved on a single slab, from GGU sample 206322. The smaller specimen (MGUH 14253) has a more complete cup exposing the posterior side and is designated holotype (fig. 2A-C). The other (MGUH 14254), is designated paratype (fig. 2D-F).

*Occurrence.* GGU sample 206322 was collected from an isolated outcrop of the Nunatami Formation, probably somewhere near the top of the formation, on the western side of Nygaard Bugt, southern Washington Land, western North Greenland (fig. 1). W.B.N. Berry, quoted in Whittington (1968, p. 55), stated that pendant *Didymograptus* from the Nunatami Formation include forms which are "found in the highest *fruticosus* zone or slightly younger", which indicates an early Middle Arenig age. Fortey & Bruton (1973, p. 2238) state that the graptolite bearing beds occur near the base of the Nunatami Formation and that the youngest beds may possibly be of Whiterock age (= approximately the Arenig/Llanvirn boundary of the standard British succession). It is thus reasonably established that the crinoids are of Arenig age.

*Diagnosis.* As for the genus which is monotypic.

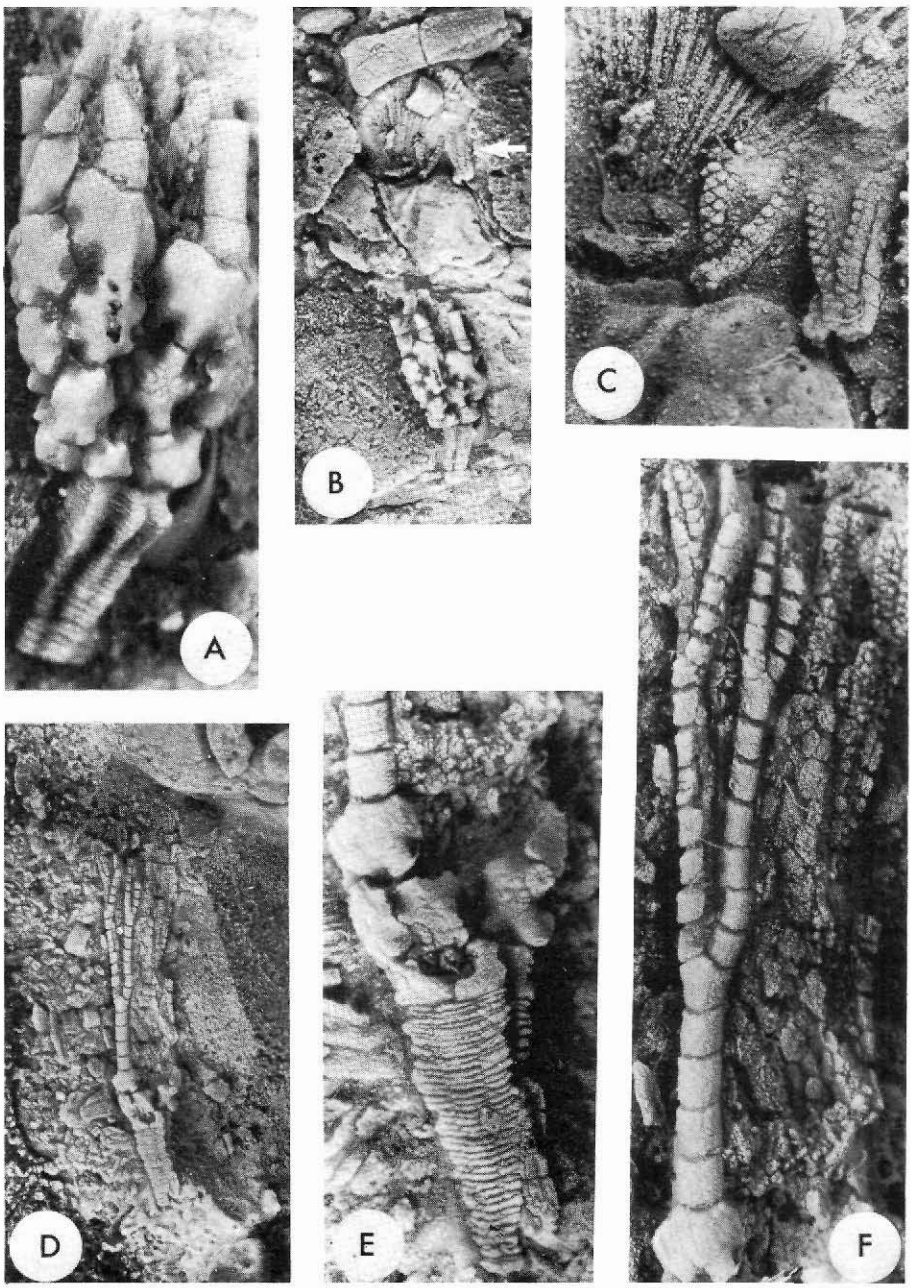


Fig. 2. *Compagicrinus fenestratus* n.gen. n.sp. A-C, holotype, MGUH 14253. A, detail of holotype to show lobate stem, ornament of cup plates and proximal parts of arms (cf. fig. 3A), × 10; B, general view to show cup and tips of distal ramules of arms (arrow), × 3; C, detail of distal ramules to show cover plates (cf. fig. 5A), × 10. D-F, paratype, MGUH 14254. D, general view, × 3; E, detail of stem and cup (cf. fig. 4), × 10; F, detail of arm and anal tube, × 10. Note isotomous branching of arm (cf. figs 4, 6). Both specimens on a single slab (GGU sample 206322); whitened with ammonium chloride sublimate.

*Description.* Stem (fig. 2A, C): Lobate (?pentalobate) in outline, tapering away from the cup. Each columnal is composed of several (?5) separate pieces, i.e. pentameres, which produce narrow zig-zag sutures more or less radially along the stem. Each piece itself has a lobate outline so that the sutures often lie in deep grooves in the stem. Crushing during preservation has accentuated this effect. In the holotype 31 sets of pentameres are preserved which taper from 1.56 mm across at the base of the cup to 0.95 mm in a length of 3.1 mm. In the paratype 39 sets of pentameres remain, tapering from 1.56 mm to 0.6 mm in 4.4 mm. The pentameres are very thin (approximately 0.1 mm) and not obviously arranged as nodals and inter-nodals as in the stems of *Aethocrinus* and some species of *Dendrocrinus*. The most distal preserved columnal in the paratype is thicker than the others. The stem of *Compagicrinus* is strongly reminiscent of that of *Dendrocrinus granditubus* Ramsbottom, from the Upper Ordovician of Scotland.

Cup (fig. 2A, B, E): Small, conical, higher on the posterior side. 2.8 mm high on the anterior face, by 3.0 mm wide at the level of the radial facets in the paratype; 4.0 mm high at the C ray radial by 3.25 mm wide in the holotype; 4.38 mm high to the top of the anal series incorporated within the cup. All plates are ornamented with ridges radiating from plate centres with the intervening areas deeply sunken (fig. 2A), appearing as if they were holes in the cup, hence the generic and trivial names (*Compages* Latin, a joining together, connection, hence frame, framework; *fenestra* Latin, a window).

Cup dicyclic (fig. 3) with (presumably) five unequal infra-basals; one of which lies approximately in the C-D inter-radius, is flat topped, not pointed, and is surmounted directly by the C-D basal. The basal circlet contains six plates, five basals and an extra plate which is here interpreted as an infer-radianal. The radial circlet contains eight plates. There are four simple radials of which those of the B and D rays are larger than those of the A and E rays. The C ray has two plates, interpreted as the radial of the C ray and super-radianal. Finally, two plates of the anal series lie one above the other in the C-D (posterior) inter-radius. The lower plate is interpreted as the anal x. Above the upper anal plate at least three more slender free anal plates are incorporated into the cup; these are much thinner than those within the cup and do not bear the characteristic ridged ornament of cup plates (fig. 2A, upper left). The facets of the radial plates are approximately half the width of the radials.

Arms (fig. 2C-D, F): Five uniserial arms reaching 8.75 mm long on the holotype and at least 9.5 mm, possibly as much as 11 mm originally, on the paratype (figs 2F, 4). There are two

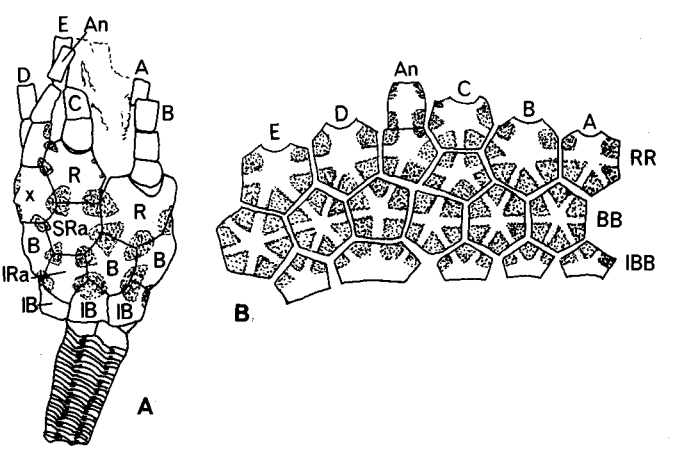


Fig. 3. Plate arrangement in *Compagicrinus fenestratus*. A, camera lucida drawing of the exposed plates in the holotype (MGUH 14253). B, reconstruction of plate arrangement. A-E, rays; An, anal plates; B, BB, basal plates; IB, IBB, infra-basal plates; IRa, infer-radianal; R, RR, radial plates; SRa, super-radianal; x, anal x plate.

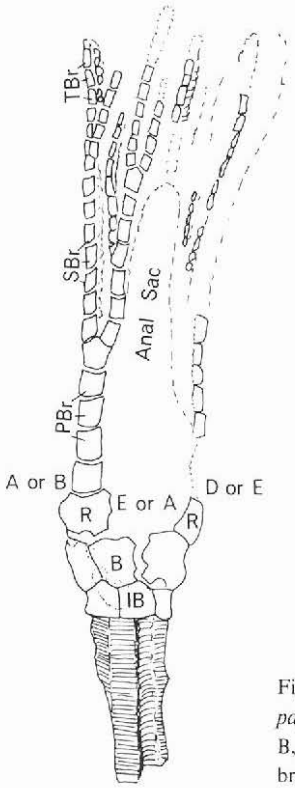


Fig. 4. Camera lucida drawing of the paratype (MGUH 14254) of *Compagicrinus fenestratus*, to show exposed cup plates and arm structure. A or B, E or A, D or E, rays; B, basal plate; IB, infra-basal plate; PBr, primibrachs; R, radial; SBr, secundibrachs; TBr, tertibrachs.

isotomous branches which apparently occurred in all arms. The most complete arm preserved (figs 2F, 4) has five primibrachs, the fifth an axil (i.e. a plate where the arm branches); then seven and eight secundibrachs in the first branches, the last being axils. The two pairs of distal ramules have seven and five, and seven and four, tertibrachs preserved. The arms are slender and non-pinnulate, the primibrachs being 0.5 mm wide proximally. The width of the brachials is reduced to about half at each branch of the arms. On the holotype only three or four primibrachs remain attached to the cup, but the presence of five arms can be confirmed. Further from the cup of the holotype, protected from weathering by an overhanging fossil fragment, the tips of four distal ramules are preserved exposing the cover plates to the food grooves and confirming the lack of

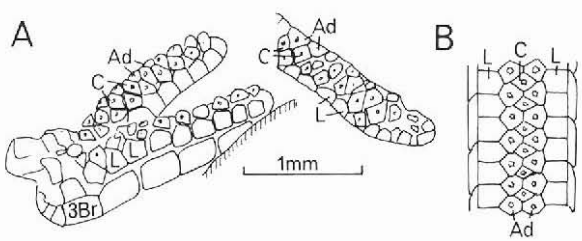


Fig. 5. Cover plates on the distal ramules of the holotype (MGUH 14253) of *Compagicrinus fenestratus*. A, camera lucida drawing of three ramules; B, diagrammatic reconstruction of the arrangement of cover plates in ventral view. Ad, adcentral cover plates; C, central cover plates; L, lateral cover plates; 3Br, tertibrachs.

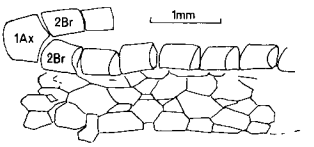


Fig. 6. Camera lucida drawing of the plates on the anal sac of *Compagicrinus fenestratus* (paratype, MGUH 14254). 1Ax, primaxil plate of arm; 2Br, secundibrachs.

pinnules (figs 2C, 5A). The cover plates form a ridge over the food grooves which is as high as the tertibrachs are deep. There is a complex series of plates apparently arranged in five rows. Those at the edge, (lateral cover plates) are smooth and apparently thin. There are approximately two lateral cover plates to every tertibrach. Central cover plates, between the peripherally located lateral plates, are each ornamented with a central raised tubercle and appear to be thicker than the laterals. Toward the tips of the ramules the arrangement of cover plates is not absolutely regular. There appears to be a central series of diamond shaped plates, separated by two rows of kite-shaped adcentrals on either side which meet at common sutures between the adjacent centrals (fig. 5B).

Remains of a long, poly-plated anal sac are preserved on the paratype (figs 2F, 6). Originally, it was probably as wide as the cup and almost as long as the arms a character typical of *Dendrocrinus,* but it is incomplete due to weathering.

## Relationship of *Compagicrinus*

The general similarity of *Compagicrinus* to *Dendrocrinus* is immediately apparent – even the plate ornament is very similar to, for example *D. rugocyathus* Ramsbottom. However, there are differences which require interpretation. To be absolutely certain of the precise plate arrangement it is necessary that a crinoid cup be preserved antire and free of matrix. An attempt to remove the cup of the holotype from the slab was unsuccessful and hence our interpretation of the plate arrangement in *Compagicrinus* is a composite based on visible plates in both specimens. Nevertheless, the critical posterior area is clearly exposed on the holotype. If our interpretation of the plates is wrong, even more plates must be present which would only serve to accentuate further the distinctiveness of *Compagicrinus.* However, our interpretation of the posterior part of the cup would remain unaffected.

Dicyclic inadunates have three plate circlets in their cups which are referred to, from the top of the stem upward, as infra-basal (abbreviated to IB, plural IBB), basal (B, BB) and radial (R, RR). Usually the IBB and, by definition, the RR are radial in position, i.e. in line with the arms; the BB are inter-radial. 5, 3, 2 or 1 of the radials may be represented by a pair of plates, one directly over the other. These are compound, or split, radials and the individual plates are known as infer- and super-radials (IR, IRR and SR, SRR). Moore (1962) assumed that the presence of compound radials was a primitive character, genera with five compound radials having given rise to those with three, two, etc. Where only one compound radial occurs, it is always in the C ray. Sometimes the lower plate is offset to the left, in which case it has long been known as the radianal (RA) plate. Moore assumed that the radianal was homologous with the C ray inferradial and that the radial of the C ray was originally a super-radial. We believe that this interpretation does not hold for dendrocrinine inadunates.

The C-D inter-radius is defined as posterior (alternatively the A ray is defined as anterior) and the cup may contain one or more anal plates in the C-D inter-radius, the lowest of which is called the anal x, or simply the x, plate. In all crinoids with anal plates incorporated into the cup, the anal x lies at, or above, the level of the radials.

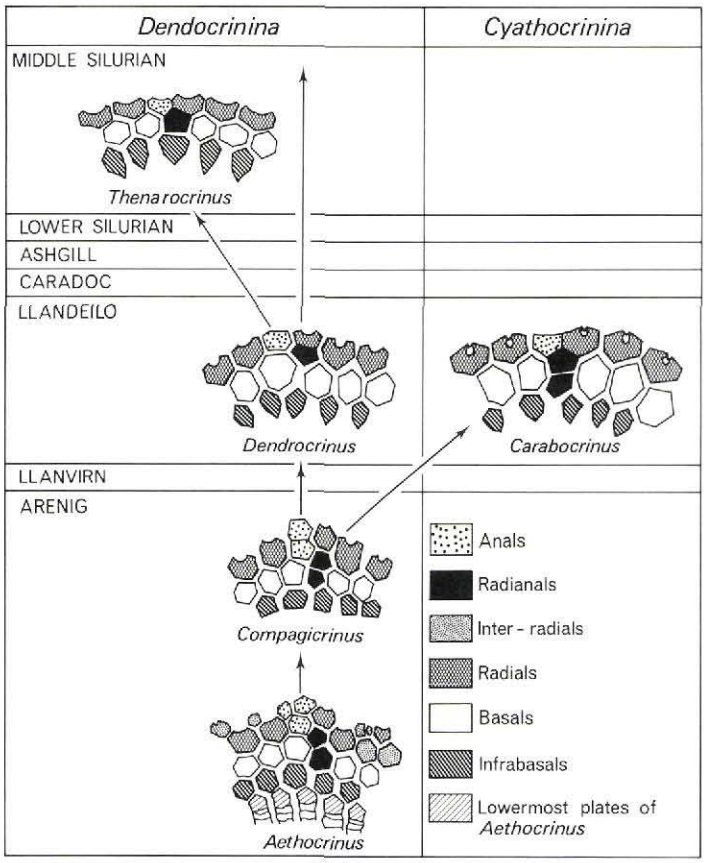


Fig. 7. Inferred evolutionary scheme for early Dendrocrinina and Cyathocrinina.

The interpretation of the plate arrangement of *Compagicrinus* depends to a certain extent on interpretations of similar genera, the most important of which are *Thenarocrinus* , *Carabocrinus, Aethocrinus* and *Dendrocrinus* (fig. 7). Of all dicyclic inadunates only *Thenarocrinus* has six plates in the basal circlet. The sixth plate is interpreted (Moore, 1962, fig. 9:3, p. 19) as a radianal and lies below and to the left of the C ray radial. *Thenarocrinus* has a single anal plate (x) and is confined to the Middle Silurian. *Compagicrinus* is thus the second known crinoid with six plates in the basal circlet, but the sixth cannot be a simple radianal as a perfectly good radianal occurs below the C ray radial (fig. 3B, 7).

*Carabocrinus* has, in effect, seven plates in the basal circlet. A pair, one above the other, occurs below and to the left of the C ray radial. Moore (1962, fig. 9:2, p. 19; and p. 24) interpreted these plates as a split radianal, *i.e.,* as infer- and super-radianals. On p. 24 he explicitly restricted these two terms to plates *within* the cup and stated that *Carabocrinus* was the only known genus with infer- and super-radianals. Previously the terms had been applied to free plates not incorporated into the cup, but occurring low in the C ray arm, as for example, in *Iocrinus*. Accepting Moore's restriction of these terms to plates within the cup, we interpret the

two plates below the C ray radial in *Compagicrinus* as infer- and super-radianal. In this interpretation, the plate above and to the left of the super-radianal is the anal x and one other anal plate is incorporated into the cup above the x (fig. 7). The plate arrangement in the cup of *Carabocrinus* differs only in having a single anal plate not two, although the oral surface is very different from that of dendrocrinine crinoids.

Although we argue that *Compagicrinus* has a unique plate arrangement, there are notable similarities to some aspects of the arrangement in the enigmatic Lower Arenig crinoid *Aethocrinus* Ubaghs. The cup of *Aethocrinus* is remarkable in having four circlets of plates, some interradials incorporated into the cup, and the lowest circlet of plates with their sutures in line with the sutures between the pentameres of the stem, not alternating with them. The dendrocrinine affinities of *Aethocrinus* are revealed by the moderate sized anal sac and by the five non-pinnulate arms. These branch isotomously only twice each and resemble closely those of *Compagicrinus* and some species of *Dendrocrinus*. In addition, the pentalobate stem, with alternating thick and thin pentameres, is strongly reminiscent of that in *D. rugocyathus* and not unlike the stem of *Compagicrinus*.

Interpretation of the cup plates in *Aethocrinus* is difficult and, not surprisingly, has lead to differing opinions. Ubaghs (1969) originally accepted the lowest circlet at the base of the cup as being composed of infra-basals and the succeeding two circlets as BB and RR. The plates from which the free arms arose were interpreted as fixed brachials (arm plates) incorporated into the cup. This interpretation raises some difficulties, the most obvious of which is the fact that the so-called radials (and infra-basals) do not lie in a radial position, but are more or less inter-radial. The asymmetry of the plate arrangement in *Aethocrinus* prevents most plates from being exactly radial or exactly inter-radial as defined by the positions of the arms.

Philip & Strimple (1971) took issue with Ubaghs' interpretation and, so to speak, started at the opposite end of the cup. They accepted the plates from which the arms arise as radials and the next two circlets down as BB and IBB. This restores the RR and IBB plates to an approximately radial position, as in all other crinoids, but leaves the lowest circlet of plates without homologues in any known crinoid. Philip & Strimple interpreted these plates as expanded pentameres from the topmost columnal of the stem.

Ubaghs (1972) re-evaluated these two interpretations and confirmed his original opinion. Among other points he argued that the plates of the lowest circlet of the cup were ornamented in exactly the same way as other cup plates, probably bore nerves of the aboral nervous system which hence lay within the cup at the level of these plates, and that new pentameres of the stem must have been introduced during growth *below* these plates. All these points argue that the plates belong to the cup and were hence infra-basals. Ubaghs also pointed out that under Philip & Strimple's interpretation there were six plates in the basal circlet, the sixth lying directly below the plate which Philip & Strimple tentatively interpreted as the anal x. Such a situation was unknown in any other crinoid, but it is exactly what occurs in *Compagicrinus*. Indeed, if one ignores the inter-radial plates and the plates of the lowest circlet (Ubaghs' IBB), then the plate arrangement of *Aethocrinus* is identical to that of *Compagicrinus* (see fig. 7). Furthermore, the sutures between the pentameres of the stem in *Compagicrinus* are apparently radial in position, as those of *Aethocrinus* become under Philip & Strimple's interpretation.

We attempt to resolve these difficulties by suggesting that the extra plate in the basal circlet under Philip & Strimple's interpretation does not lie below the anal x, but below the radianal. Thus *Aethocrinus* had infer- and super-radianals, as *Compagicrinus* and *Carabocrinus* have, and the plate below the anal x is the basal of the C-D inter-radius. We can then suggest the evolutio-

nary sequence depicted in fig. 7. *Aethocrinus* evolved into *Compagicrinus* by the loss of the plates at the top of the stem and the inter-radials, with the concomitant adjustment of the position of some of the basal plates. In turn, *Compagicrinus* gave rise to *Dendrocrinus* by the loss of the infer-radianal (or its fusion with the C-D basal which is larger than the other basals), and to the suborder Cyathocrinina, via its oldest member *Carabocrinus,* by the loss of the anal sac together with the second anal plate and the development of oral plates. This tentative phylogenetic scheme is the simplest one based on comparative morphology and it is also in accordance with the known ages of the constituent genera.

Finally, we must return to the homologies of the radianal plate. If the evolutionary scheme proposed here is correct, then the most primitive dicyclic inadunate crinoids had a split radianal and a normal radial in the C ray. Subsequently, the infer--radianal was lost, leaving only the super-radianal. The so-called "radianal" plate of later dendrocrinine crinoids (and presumably other dicyclic inadunates) is derived from a super-radianal not from the infer-radial of the C ray as Moore (1962) argued. The origin of compound radials is uncertain, but since all genera with compound radials are Middle Orodvician at the earliest, we believe that they cannot be the most primitive stock when older crinoids, like *Aethocrinus* and *Compagicrinus,* are known from the Lower Ordovician.

## Palaeoecology

Although now incomplete, the specimens of *Compagicrinus* were probably complete when buried and there is every reason to believe that they are *in situ.* Their present incompleteness is due to weathering, an interpretation born out by the presence of at least two grooves in the underlying limestone which connect the preserved tips of the distal ramules with the proximal portions of the arms still attached to the cup in the holotype. These grooves arose by pressure solution below the arms and indicate that the missing portions were originally buried. The two crinoids are preserved at right angles to each other indicating that they were not current orientated at, or soon after, death. They seem to have fallen over and been preserved before disarticulation. The slab on which they occur is a biosparudite, with possible algal laminated intraclasts, and may have an incipient hardground surface. Overlying this (way up is inferred from the weathered surface), is a sand grade biosparite skeletal grainstone which was originally shell sand. The crinoids may have been attached to the underlying hard- or firmground surface and were overwhelmed by this sand grade sediment, possibly as a storm deposit. Certainly they are preserved in association with the remains of the shell sand very close to the hardened surface.

The associated fauna includes gastropods, several trilobites, other echinoderm debris and brachiopods, a good shallow water, shelly association.

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