CUNCTOCRINUS, A NEW MIDDLE DEVONIAN CALCEOCRINID CRINOID FROM THE SILICA SHALE OF OHIO

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ABSTRACT—The only calceocrinid crinoid yet discovered in the much studied Silica Shale belongs to a new genus. It differs from the contemporary Halysiocrinus in having the A-ray radial fused with the B-ray inferradial on one side and the D-ray radial fused with the C-ray inferradial on the other side, so that the two resultant plates encircle the calyx. Our study shows that the same arrangement is present in Senariocrinus, a drastic new interpretation of calyx plates in that genus. From numerical cladistic procedures, a new evolutionary tree of the Calceocrinidae is proposed. Functional studies of morphology in Cunctocrinus and other calceocrinids support Jaekel's contention that the advanced genera lived with the column horizontal and elevated the upper part of the crown to a feeding position by a hinge between basals and radials.

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INTRODUCTION

IN THIS INVESTIGATION, a newly discovered Devonian crinoid proves to be exceptional in two ways. First, it is a new genus, extending our knowledge of the highly specialized calceocrinids. Second, its calyx structure has features previously undetected, which lead to the re-evaluation of morphology in other genera of the family.

The specimen was found by the junior author in the South Quarry of the Medusa Portland Cement Company near Silica, Ohio. At the Museum of Paleontology, The University of Michigan, it was carefully prepared by the senior author with fine needles and Airdent abrasion. Camera lucida sketches of the plates were prepared by Mr. Peter Burr Loomis, graduate research assistant. Typing was done by Mrs. Helen Mysyk and photographs were made by Mr. Karoly Kutasi. The manuscript was critically reviewed by Professor C. A. Arnold and Professor E. C. Stumm. We are also grateful to Mr. David L. Meyer for information about living crinoids.

Preliminary examination showed that the specimen belonged to a new genus, related to its contemporary Halysiocrinus. To place it in the evolutionary sequence, numerical methods were applied to the known characters of all calceocrinid genera.

The immediate result was the revelation that Senariocrinus, another Devonian genus known only from its type species, did not appear to have any ancestor closer than the ancestral Ordovician Cremacrinus. With long and extensive searches for these crinoids and the recent intensive study associated with preparation of the volume for The Treatise on Invertebrate Paleontology, it seemed to us odd that no lineage leading to this genus was known. Furthermore, as recently described, the morphology of Senariocrinus has been interpreted to combine very primitive features with unique advanced features; it also seemed to us odd that such a combination should appear suddenly.

Comparison of Senariocrinus with our new genus suggests that the current concept of calyx plates in Senariocrinus is incorrect. In our opinion, Senariocrinus can no longer be regarded as an aberrant form far removed from its Devonian contemporaries. On the contrary, we suggest that it is closely related to our new genus and descended directly from a crinoid like it in all essential character-states.

The evolutionary tree presented for the Calceocrinidae is based upon the numerical taxonomic procedures known as the Prim network and the Wagner groundplan-divergence method. The tree is not nearly as ramose as was previously believed.
The holotype and only known specimen of the new *Cunctocrinus* is catalogued and deposited in the Museum of Paleontology at The University of Michigan.

**SYSTEMATIC DESCRIPTION**

Family Calceocrinidae

Meek & Worthen 1869

**Diagnosis.**—Monocyclic inadunate crinoids with special hinge between BB and RR and with modifications of rays leading to bilateral symmetry through the E-ray.

**Remarks.**—Despite the excellent works by Jaekel (1918) and Springer (1926), the family has been misinterpreted even concerning the two chief characters. For example, Fenton & Fenton (1958, p. 130) presented a reconstruction of *Halysiocrinus* apparently devoid of hinge ment between BB and RR; and Easton (1960, p. 616) stated, "*Halysiocrinus* is also noteworthy because the whole calyx is grossly asymmetrical."

*Cunctocrinus* n. gen.

**Type species.**—Cunctocrinus fortunatus n. sp.

**Description.**—Calceocrinid with bilateral symmetry, E-ray developed with arm, A-ray and D-ray bearing lateral arms consisting of main axil and several branching axil-arms, B- and C-rays practically fused, and BB hinged with RR, as in most genera of the family. Two large plates encircling the dorsal cup, one formed from fusion of D-ray R and C-ray iR and the other formed from fusion of A-ray R and B-ray iR; these two fused plates separating iR and sR of the E-ray along the anterior edge at the plane of symmetry. B- and C-ray sRR fused to form a "subanal" plate, the lowermost plate of the anal series.

**Remarks.**—As described below, *Senarioocrinus* is the only other calceocrinid to have the A-ray R fused with B-ray iR and the D-ray R fused with C-ray iR. It differs from *Cunctocrinus* in that its BB are all fused and its main axils have degenerated until each consists of one thin axil-arm and one equally thin ramule; *Cunctocrinus* has three BB and several heteromously branched axil-arms on each main axil. The name is derived from the Latin *cunctus* ("fused together to form one") and refers to the fusion of RR and iRR elements in the dorsal cup.

*Cunctocrinus fortunatus* n. sp.

**Text-figs. 1-3, 13; pl. 1, figs. 1-4**

**Description.**—Dorsal cup subcylindrical, nearly elliptical in cross section, its base rounded and bearing columnar facet. Plates of cup consisting of three BB, one iR, two sRR, and two fused iR-R combinations. Strong specialized hinge between BB and RR.

All BB subtriangular. Two BB relatively large, equal, sharing the columnar facet (text-fig. 1). Columnar facet about ¼ the greatest diameter of the cup. Smaller B with its longest side forming the lower edge of the special BB-RR hinge, the upper edge being formed by the E-ray iR. Hinge thus horizontal (pl. 1, fig. 4), its outer margins excavated and bearing vertical close-set sharp-edged ridges, presumably for attachment of hinge elevator muscles.

Two calyx-encircling plates immediately above the triangular E-ray iR and the two larger, facet-bearing BB, one composed of A-ray R fused with B-ray iR and the other composed of D-ray R fused with C-ray iR; the two plates meeting along a long vertical suture anteriorly and attenuated to a very short vertical suture posteriorly. The B- and C-ray iRR being fused with the A- and D-ray RR, respectively, no actual B and C rays present in dorsal cup; in the so-called BC-interray, a posterior subquadrangular sR plate formed by fusion of the sRR of the C- and D-rays; posterior sR plate (the "subanal" plate of some authors) recessed into the large calyx-encircling plates, bearing anal X immediately above. Posterior groove, a vertical subcylindrical indentation, tapering upward on the BC-interray sR and X (perhaps extending onto X₂, but that plate not seen), apparently accommodating the column in the resting position (text-fig. 12). Along the posterior line of the plane of symmetry, therefore, from the columnar facet upward, (1) B-B suture, (2) suture between the fused iR-R plates, and (3) anal series of tapered uniramous plates (sR the lowermost and X next in line).

The two large fused plates of the cup at their anterior junction separating the iR and sR of the E-ray. As mentioned, iR triangular and hinged with BB. E-ray sR the lowermost plate of the median arm, subpentagonal, its broadly acuminate lower end inserted between upper ends of the two large fused plates (pl. 1, fig. 4).

Calyx plate arrangement bilaterally symmetrical through the E-ray and BC-interray, resulting in four arms or rays: E-ray producing the median arm, A- and D-rays producing lateral arms, and BC-interray producing the anal tube, a modified ray or combined arm and tube. Arms non-pinnulate. Median arm (E-ray) uniramous to PBr₅, the part above hidden by axil-arms of adjacent rays (pl. 1, fig. 4). PBr₂ shorter than PBr₅, strongly tapering from its
wide junction with sR. PBr₂ and PBr₃ quadratate, with subparallel sides.

Proximal plates of lateral arms non-axillary, strongly articulated with shoulder-like prominences on the large fused iR-R plates (pl. 1, figs. 2-4). In each lateral arm, the non-axillary, hinged plate followed by a series of articulating, laterally arranged plates bearing axil-arms along their upper border; the non-axillary and succeeding series composing the so-called main axil of each lateral arm. Each axil-arm gradually tapering. Axil-arms represented in specimen as far as sextaxil-arm; possibly another arm originally present, or possibly ω-ramule after sextaxil-arm. Axil-arms branching heterotomously, the ramules alternating from abanal (anterior) to adanal (posterior) sides. Primaxil-arm first axillary on αBr₄; secundaxil-arm and tertaxil-arm first on αBr₃; and quartaxil-arm and quintaxil-arm first on
Advanced features as fused primitive features as five RR and absence of main arm. Anal series nearly smooth. 

**Remarks.**—Only the type species is known, and it is represented by only the holotype. The lateral arms are not known in any axil-arm beyond the beginning of the ℓ-series; the median arm is not known beyond PBr₃, and the anal series is not exposed beyond X. The column is missing, but its proximal size is indicated by the diameter of the columnar facet.

In the reconstructions (text-figs. 2, 3, 13), we have presumed that the missing parts of *Cunctocrinus fortunatus* are similar to those of the closely related and contemporary *Halysiocrinus*. Despite its shortcomings, the holotype of the new species is about as well preserved as most calceocrinids, and additional specimens are not likely to be found in the near future.

**Occurrence.**—Middle Devonian Silica Formation. North Quarry of the Medusa Portland Cement Company at Silica, near Sylvania, Lucas County, Ohio. Specimen found in dump pile in southeastern extension of the quarry by junior author in 1967, presumed to have come from gradational contact zone between units 13 and 14 of Ehlers, Stumm, & Kesling (1951, p. 19) on the basis of lithology and associated fossils.

**Holotype.**—UMMP 57431.

**Notes on Senarioocrinus**

According to the recent revision and review of the Calceocrinidae by R. C. Moore (1962, p. 30–31, 33–37), *Senarioocrinus* combines such primitive features as five RR and absence of main axils on the lateral arms with such advanced features as fused iRR of the B- and C-rays, fused BB, contact of the lateral RR in the BC-interray, and strong separation of iR and sR of the E-ray by convergence of the adjacent RR. Its arms are extremely simple, each of the lateral arms (A- and D-rays) branching only once and the arm of the E-ray being uniramous. In Moore’s analysis (1962, fig. 5, no. 6), the fused iRR of B- and C-rays form a semicircular plate above the junction of the lateral RR, the sRR of these rays adjoin above with an oblique suture, and X is a thin plate atop the sR of the C-ray.

Several features seemed to us incompatible with the evolution of other calceocrinids. In all other descendants of the ancestral *Cremaocrinus*, the sRR of the B- and C-rays fused and the iRR remained distinct; yet in *Senarioocrinus* the reverse was proposed, the iRR fusing and the sRR remaining distinct. In all other calceocrinids the lateral RR failed to meet posteriorly; in *Senarioocrinus* it was stated that they met. In all other calceocrinids the sRR of the B- and C-rays (fused or unfused) reached to the BB; in *Senarioocrinus* they were said to be separated from the BB by both the fused iRR and the lateral RR. When these character-states were subjected to statistical comparison with those of other calceocrinids, *Senarioocrinus* appeared to be a unique descendant of the ancestral *Cremaocrinus*, with no close relatives among the Silurian or Devonian genera.

We compared *Senarioocrinus* closely with our new genus *Cunctocrinus*. In the latter, it is quite clear that the large lateral plates, together encircling the calyx, are on one side the fused A-ray R and B-ray iR and on the other side the fused D-ray R and C-ray iR. The same arrangement of two encircling plates is present in *Senarioocrinus*. The overlying posterior plate in *Cunctocrinus* is the fused sRR of B- and C-rays, in about the same position as the fused sRR of *Halysiocrinus*. The same arrangement of a single plate above the RR is present in *Senarioocrinus*. The diagonal junction reported of the next two (?) plates of *Senarioocrinus* needs further investigation; if it is indeed present, the lateral RR must be derived from an encircling basis.

**Explanation of Plate 1**

(All figures × 6; specimen lightly coated with sublimated ammonium chloride)

Figs. 1–4—*Cunctocrinus fortunatus* n. sp. Holotype UMMP 57431. Middle Devonian Silica Shale, Medusa South Quarry, Lucas County, Ohio. 1, posterior view (centered on BC-interray); fused sRR of B- and C-rays (so-called subanal plate) offset to left from normal position. 2, 3, lateral views of A- and D-rays, showing main axils and axil-arms. 4, anterior view (centered on E-ray) showing junction of A- and D-ray RR between iR and sR of E-ray.
Text-fig. 2—Cunctocrinus fortunatus n. sp. Restoration in lateral view.
Text-Fig. 3—Cunctocrinus fortunatus n. sp. Restoration in posterior view, showing axil-arms spread in presumed feeding position.
a junction it is unique among crinoids. We suspect that it is simply a crack through plate X.

We believe, therefore, that Seniocrinus does not possess five RR (counting sRR as RR) and that it does not have iRR of B- and C-rays fused together; instead, it has only four RR (like all other post-Ordovician genera) and its B- and C-ray iRR are fused respectively with the A- and D-ray RR (like those in its Devonian relative Cunctocrinus).

EVOLUTION OF CALCEOCHRINIDS

Previous Work

Jaekel (1918, p. 87–88) divided his suborder Calceocrinidae into two families, the Castocrinidae having four arms and the Calceocrinidae with three arms and the fourth suppressed. His Castocrinidae contained only Castocrinus Meek & Worthen (now Cremaacrinus Ulrich) and his Calceocrinidae included Euchi-rocrinus Meek & Worthen (now Calceocrinus Hall), Bicho-rocrinus n. gen. (no species assigned), Synchirocrinus n. gen., Dichirocrinus n. gen. (no species assigned), and Halysio-crinus Ulrich. Jaekel wrote (1918, p. 87, our translation):

Descended from heterocrinids, their A- and D-arms were symmetrically developed and finally branched like a hand, in such a way that from a short stem of each branch upward strong collateral branches became divided, which in older forms still bifurcated isomotically or heterotomously, and in younger forms (Synchirocrinus n. gen.) only divided off unilaterally paratomous ramiules. From the beginning on, their C-ray arm is unique among crinoids. We believe, therefore, that it is simply a crack through plate X.

In 1926, Springer studied evolution in some detail. He postulated the following modifications (1926, p. 95), which we translate into modern terminology:

1. Columnar facet from asymmetrical lateral to median position in plane of symmetry of the cup,
2. BB from four to three,
3. Lateral arms from three to two,
4. Segments of E-ray R from connected to disconnected,
5. Median arm from simple to many branched, and
6. Lateral arms from equal bifurcation to axil-arm system.

Springer discussed evolution by stages (1926, p. 90–93), which we summarize in Table 1. His work was both astute and sound. Subsequent changes and additions have come about mostly from drastic taxonomic revisions and from more recently discovered genera.

In his review of the Calceocrinidae, Moore (1962, p. 33–38) presented his concepts on

Table 1—Evolutionary Stages of Calceocrinidae from Springer’s (1926) Discussion.

<table>
<thead>
<tr>
<th>Character</th>
<th>Ancestor</th>
<th>Stage A</th>
<th>Stage B</th>
<th>Stage C</th>
<th>Stage D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Representative genus</td>
<td>Heterocrinus</td>
<td>Cremacrinus</td>
<td>Euchi-rocrinus</td>
<td>Calceocrinus</td>
<td>Halysio-crinus</td>
</tr>
<tr>
<td>Crown</td>
<td>Erect</td>
<td>Bent</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BB</td>
<td>5, equal</td>
<td>4, all touching stem; B of BC-interray eliminated</td>
<td>3, only two touching stem; BB of DE- and CD-interrays fused</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arms</td>
<td>5</td>
<td>4, C-ray arm eliminated</td>
<td>3, B-ray arm also eliminated</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stem</td>
<td>Centered in BB circle</td>
<td>Offset, touching all 4 BB; beside anal tube</td>
<td>Offset, touching all 4 BB; below anal tube</td>
<td>Offset, not touching fused BB of DE-CD-interray</td>
<td></td>
</tr>
<tr>
<td>Branching in lateral arms</td>
<td>Symmetrical, even</td>
<td>Slightly asymmetric</td>
<td>Strongly asymmetric</td>
<td>Axil-arms on successive axillaries aligned to form main axil</td>
<td></td>
</tr>
<tr>
<td>E-ray sR and iR</td>
<td>Long suture</td>
<td>Constricted, short suture</td>
<td>More constricted, very short suture</td>
<td>Separated by encroachment and junction of RR of A- and D-rays</td>
<td></td>
</tr>
<tr>
<td>C- and B-ray RR</td>
<td>iRR and sRR normally developed</td>
<td>iRR offset from sRR</td>
<td>iRR offset, sRR fused</td>
<td>iRR separated by sR</td>
<td>iRR joining below sR</td>
</tr>
</tbody>
</table>

1 Of Springer’s assigned species, all are now placed in Calceocrinus.
2 Of Springer’s assigned species, seven are now placed in Synchirocrinus and two in Delacrinus.
evolution of these crinoids, dealing with development of bilateral symmetry, features of the dorsal cup, anal tube, and structure of arms. He correctly called attention to several progressive evolutionary changes: (1) fusion of BB, reducing the number from four in Middle Ordovician genera to three in Silurian genera and Halysiocrinus and to one in Senariocrinus; (2) approach and fusion of the B- and C-ray sRR, separate in Ordovician calceocrinids but fused in all later genera to form the so-called "sub-anal" plate; and (3) shift of the anal tube from offset (above the C-ray) in Cremacrinus to in all later genera to form the so-called "sub-anal" plate; and (3) shift of the anal tube from offset (above the C-ray) in Cremacrinus to exactly in the plane of symmetry in all later genera.

Moore also postulated (1962, p. 35) that branching of the E-ray arm could be classified as primitive when unbranched, slightly advanced when branching isotomously near the distal end, more advanced when branching isotomously in the proximal part, and most specialized when branching many times heterotomously above the isotomous division; that this branching has no reflection in taxonomy is borne out by Moore's inclusion (1962, fig. 7) in Halysiocrinus of species with the E-arm unbranched (H. elephantinus), isotomously branched (H. bradleyi), and heterotomously branched (H. nodosus). As regards the main axils of the lateral arms, Moore (1962, p. 36) regarded poor development as primitive and strong development as advanced; he recognized, however, that this character did not evolve progressively or at constant rate within the family, especially in the case of Deltacrinus and Senariocrinus, which have very poorly defined main axils in sharp contrast to their contemporaries, Synchirocrinus and Halysiocrinus.

Moore also commented (1962, p. 36) on the number of axil-arms: two in Senariocrinus, two or three in Cremacrinus, two to four in Calceocrinus, three or four in Deltacrinus, and five to eight in Anulocrinus, Chirocrinus, Synchirocrinus, Chiropinna, and Halysiocrinus; he noted that the simple arm structure in the Devonian Senariocrinus "may denote regressive evolution." The multiple branching of the axil-arms in Chiropinna led him to call them "pinnulate," although (1962, p. 29) he qualified the statement, saying that pinnules were "relatively diminutive unbranched appendages of crinoid arms given off on opposite sides of the arm in alternation and borne by successive branchials."

Some of our reservations about Moore's suggested calceocrinid evolution stem from his interpretation of plates in the posterior region of the calyx in Senariocrinus. This has been discussed above. Furthermore, Moore was of the opinion (1936, p. 36) that Senariocrinus has no ramules and two axil-arms in each lateral ray; in our analysis, it has one ramule on one axil-arm.

According to Moore's suggested phylogeny (1926, p. 37–38), one line from the homocrinid ancestor led to Cremacrinus and thence to Senariocrinus through Anulocrinus; another line from the ancestor split, one branch to Chirocrinus and the other to Calceocrinus; from the latter, one line led to Deltacrinus and another line gave rise successively to Chirocrinus, Halysiocrinus, and Synchirocrinus.

Cladogram

From mathematical considerations, it is possible to determine mutual groupings of character-states between taxa and to arrange these character-complexes in a sequence in such a way that the network or tree has the fewest differences in character-states between adjacent taxa throughout its extent. This cladistic method connects taxa according to their ensembles of common features. The resulting tree explains how the taxa could have been derived from their common ancestor if trends persisted in evolution of the various characters. Such an objective procedure has greater likelihood of being the correct interpretation of evolution than any intuitive approach.

The method introduced by Camin & Sokal (1965) for construction of a cladogram, a form of tree, and later made into a computer program by Bartcher (1966), assumed:

1. Characters can be expressed in discrete states,
2. Character-states can be arranged in logical order,
3. Directions of evolutionary trends are known,
4. The ancestral state of any character arose only once in the history of the taxa at hand, and
5. Evolution is irreversible.

Somewhat simpler procedures are available which actually require only the first two assumptions, although data from the third greatly enhances their application and interpretation. Presumably, the primitive character-states comprise the majority in the ancestor. As for the irreversibility of evolution, it appears to hold true for the total array of characters, but well-known examples of terminal and near-terminal forms in evolutionary sequences seem to support the contention that one or another character may "revert" or "degenerate" to the ancestral state.
Prim Network

R. C. Prim of Bell System Laboratories considered the basic problem of interconnecting a given set of terminals with the shortest possible network of links (1957). Although the immediate application was planning of large-scale communication networks, the approach and method are well suited for a broad class of minimization problems, including connection of taxa into a logical evolutionary sequence or tree. Instead of minimizing mileages involved in linking terminals, we are concerned with minimizing total character differences in linking operational taxonomic units (OTU's).

Table 2 shows equivalent terms used in Prim's discussion, in graph theory, and in evolution. Translating Prim's concepts into appropriate terminology for evolution, he proposed two principles (1957, p. 1391): (1) any individual OTU can be connected to its most closely related OTU, and (2) any section of a cladogram can be connected to the most closely related OTU; to establish a complete cladogram, showing relationships most accurately according to the observations of character-states, he proposed that two conditions must be met (1957, p. 1392): (1) every OTU in the cladogram is connected to at least one most closely related OTU, and (2) every section of the cladogram is connected to at least one most closely related OTU.

As applied to evolution, the cladogram so produced minimizes phenetic differences involved in its construction; this is the same as saying it shows the maximum possible character similarities. Even though such an evolutionary tree is hypothetical, it best fits the data on character-states and has high probability of approaching the actual phylogenetic tree.

The procedure outlined by Prim has advantages over many other cladistic programs in that (1) it is not necessary to know which OTU is ancestral, since the same lines of relationship are produced regardless of which OTU is treated first, and (2) the mathematics need not involve a computer, since the operations are simple. It provides objective handling of basic observations to discover evolutionary lines of descent.

Data matrix.—The Prim network is developed along the general plan of all systems of numerical taxonomy (see Sneath, 1964, p. 43–45). The first step is the same as that used by Sokal & Sneath (1963), construction of a data matrix. For the Calceocrinidae, genera are the OTU's. They are accepted as currently defined and coded as:

| A | Cremacrinus Ulrich 1886 |
| B | Calceocrinus Hall 1852 |
| C | Deltacrinus Ulrich 1886 |
| D | Chirocrinus Angelin 1878 |
| E | Synchirocrinus Jaekel 1918 |
| F | Chirophinna Moore 1962 |
| G | Senariocrinus Schmidt 1935 |
| H | Halysiocrinus Ulrich 1886 |
| I | Cunctocrinus n. gen. |
| J | Anulocrinus Ramsbottom 1960 |
| K | Grypocrinus Strimple 1963 |

Characters and their states (from 0 to 4 in presumed evolutionary sequence) are coded as:

- **a** - number of RR and sRR
  - 0 - Five
  - 4 - Four
- **b** - number of BB
  - 0 - Four
  - 2 - Three
  - 4 - One
- **c** - development of “pinnulate” arm-axils
  - 0 - not “pinnulate”
  - 4 - “pinnulate”

Table 2—Equivalent Terms Used in Applying the Prim Network to Communications, Graph Theory, and Evolution.

<table>
<thead>
<tr>
<th>Communications</th>
<th>Graph Theory</th>
<th>Evolution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Terminal</td>
<td>Vertex</td>
<td>Operational taxonomic unit (OTU)</td>
</tr>
<tr>
<td>Nearest neighbor</td>
<td>Edge</td>
<td>Most closely related OTU (MCR)</td>
</tr>
<tr>
<td>Link</td>
<td>“Length” or “weight” of edge</td>
<td>Link (direct relationship)</td>
</tr>
<tr>
<td>Length of link</td>
<td>Phenetic difference (summation of differences in character-states)</td>
<td></td>
</tr>
<tr>
<td>Fragment</td>
<td>Section of cladogram</td>
<td></td>
</tr>
<tr>
<td>Distance table</td>
<td>Matrix of phenetic differences</td>
<td></td>
</tr>
<tr>
<td>Connection network</td>
<td>Spanning subtree (SSS)</td>
<td></td>
</tr>
<tr>
<td>Shortest connection network (SCN)</td>
<td>Tree</td>
<td></td>
</tr>
<tr>
<td>Shortest spanning subtree (SSS)</td>
<td>Cladogram (evolutionary tree)</td>
<td></td>
</tr>
</tbody>
</table>
d – E-ray iR and sR
0 – broad contact
1 – narrow contact
2 – very narrow contact or slightly separated
3 – slightly separated by RR of A- and D-rays
4 – strongly separated by RR

e – B- and C-ray iRR
0 – widely separated
1 – narrowly separated
2 – in contact or nearly in contact
3 – fused with RR of A- and D-rays

f – position of columnar facet
0 – four BB
1 – three BB
2 – two BB and tangent to third B
3 – two BB only
4 – one B (occurs after fusion of all BB)

g – development of main axils
0 – not developed
1 – poorly developed
2 – moderately developed
3 – highly developed

The data matrix for calceocrinid genera, according to our interpretations of character-states, is shown in table 3.

### Table 3—Data Matrix of Calceocrinidae.

<table>
<thead>
<tr>
<th>OTU</th>
<th>a</th>
<th>b</th>
<th>c</th>
<th>d</th>
<th>e</th>
<th>f</th>
<th>g</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>B</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>C</td>
<td>4</td>
<td>2</td>
<td>4</td>
<td>0</td>
<td>3</td>
<td>1</td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>4</td>
<td>2</td>
<td>4</td>
<td>0</td>
<td>3</td>
<td>1</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td>E</td>
<td>4</td>
<td>2</td>
<td>4</td>
<td>0</td>
<td>3</td>
<td>1</td>
<td>17</td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>4</td>
<td>2</td>
<td>4</td>
<td>0</td>
<td>2</td>
<td>4</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>4</td>
<td>2</td>
<td>4</td>
<td>0</td>
<td>4</td>
<td>4</td>
<td>20</td>
<td></td>
</tr>
<tr>
<td>H</td>
<td>4</td>
<td>2</td>
<td>4</td>
<td>0</td>
<td>4</td>
<td>4</td>
<td>20</td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>4</td>
<td>2</td>
<td>4</td>
<td>0</td>
<td>4</td>
<td>4</td>
<td>21</td>
<td></td>
</tr>
<tr>
<td>J</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>K</td>
<td>4</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>14</td>
<td></td>
</tr>
</tbody>
</table>

Phenetic differences.—Next a matrix is prepared of the summations of differences in character-states, termed phenetic differences (see Farris, 1967, p. 46–48). In table 3, OTU A differs from OTU B in character a by 4 and in character d by 1; \(4 + 1 = 5\), which is the phenetic difference of the pair A-B. Similarly, OTU C differs from OTU G in character b by 2, in character e by 4, in character f by 1, and in character g by 1; \(2 + 4 + 1 + 1 = 8\) for the phenetic difference of the pair C-G. Phenetic differences for all pairs are shown in table 4.

### Table 4—Matrix of Phenetic Differences.

<table>
<thead>
<tr>
<th>OTU</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
<th>F</th>
<th>G</th>
<th>H</th>
<th>I</th>
<th>J</th>
<th>K</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
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<td>1</td>
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<td></td>
</tr>
<tr>
<td>B</td>
<td>5</td>
<td>6</td>
<td>6</td>
<td>10</td>
<td>13</td>
<td>15</td>
<td>14</td>
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<tr>
<td>C</td>
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<td>5</td>
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<td>8</td>
<td>6</td>
<td>7</td>
<td>12</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>11</td>
<td>6</td>
<td>3</td>
<td>4</td>
<td>9</td>
<td>11</td>
<td>7</td>
<td>8</td>
<td>9</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>E</td>
<td>15</td>
<td>10</td>
<td>5</td>
<td>4</td>
<td>9</td>
<td>11</td>
<td>3</td>
<td>4</td>
<td>13</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>16</td>
<td>13</td>
<td>9</td>
<td>9</td>
<td>20</td>
<td>12</td>
<td>13</td>
<td>16</td>
<td>8</td>
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</tr>
<tr>
<td>G</td>
<td>20</td>
<td>15</td>
<td>11</td>
<td>11</td>
<td>20</td>
<td>8</td>
<td>7</td>
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<tr>
<td>H</td>
<td>18</td>
<td>13</td>
<td>6</td>
<td>7</td>
<td>3</td>
<td>12</td>
<td>8</td>
<td>1</td>
<td>16</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>I</td>
<td>19</td>
<td>14</td>
<td>7</td>
<td>8</td>
<td>4</td>
<td>13</td>
<td>7</td>
<td>1</td>
<td>17</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>J</td>
<td>2</td>
<td>5</td>
<td>12</td>
<td>9</td>
<td>13</td>
<td>16</td>
<td>16</td>
<td>17</td>
<td>10</td>
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<td></td>
</tr>
<tr>
<td>K</td>
<td>12</td>
<td>7</td>
<td>8</td>
<td>5</td>
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<td>14</td>
<td>6</td>
<td>7</td>
<td>10</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Preliminary tree.—Since OTU A (table 3) has the lowest total of character-states, it is considered to be the most primitive (see Wagner, 1961, p. 842–843, and Benson, 1962, p. 415, for criteria of primitive) and would be a logical choice to treat first. The procedure follows that used by Prim (1957, p. 1398–1400) in his discussion of “Computational Technique.” OTU A is entered on the tree and its vertical column is deleted from table 4. In the horizontal row for A, its MCR (most closely related OTU) is J (phenetic difference = 2). OTU J is entered on the tree, linked to A, and its phenetic difference (2) is noted (text-fig. 4). Now vertical column J is also deleted from table 4; the horizontal rows for A and J are inspected for the MCR closest to the section of cladogram A-J, which happens to be B. OTU B is added to the tree and linked to its MCR, which in this case can be A or J; both
have the same phenetic difference (5). Actually, the plotted connection can be either B-A or B-J, for after the weighting procedure outlined below, the revised tree will come to be the same whichever is chosen; let us arbitrarily link B to J. Upon elimination of vertical column B from table 4, the horizontal rows for A, B, and J are scanned for the MCR to section A-J-B; it is OTU D, and the enlarged section of the tree is shown in text-figure 5.

When all OTU’s of table 3 have been used, the evolutionary tree will look like text-figure 6. It is the only tree which connects the OTU’s with only 42 units of phenetic differences; any other would contain more units and show less accurate relationships.

Weighting.—Not all characters have entered equally in production of this tree. To determine their relative significance (how well they correlate) differences are determined character by character (text-fig. 7). Next the total path of difference distances is computed for each character used; for a, the total path is 4; for g it is 10; all distances are entered in table 5. Their lowest common denominator is 280. Now a weighting factor is computed for each character by placing each of the total path distances over the common denominator and inverting; hence, 280/4 = 70, 280/7 = 40, etc.

Using these values to weight the various character-states, a revised data matrix is produced (table 6), in which each character enters equally into the production of the tree. Of all characters used, g contributed least to the tree, inasmuch as it has the lowest weighting factor.

Revised tree.—It is now possible to make a revised matrix of phenetic differences (table 7) and construct a revised tree. This turns out to be like the first except in the values for phenetic differences (text-fig. 8). If we now total up the difference distances for each character throughout the tree, it is found to be a constant — 280. This demonstrates that all data have been considered in their proper contribution to the revised tree. The phenetic differences indicate greater similarity between OTU’s H and I than between H and E or between I and G. It is also clear that OTU B is not closely similar to its ancestor J or to its descendant D.

Wagner Groundplan-divergence Method

Procedures suggested by Wagner (1954, 1961) provide for further minimization of overall phenetic differences in the evolutionary tree by the insertion of hypothetical OTU’s. Such
OTU's would have existed whenever closely related known OTU's shared some character changes from their common ancestor; insofar as the tree is concerned, the introduction of a hypothetical OTU extends the common line of descent from the ancestor nearer to the descendants and thereby combines parts of two formerly divergent paths. Such OTU's may indeed have evolved, although as yet undiscovered and unknown in paleontology.

In Wagner's method, the state of each character can be predicted for any hypothetical OTU. Among three OTU's in proximity and linked in the cladogram, one of the following relationships must exist for each character they share:

1. The character-state is the same in all three OTU's, in which case the intermediate hypothetical OTU will be assigned that character-state.
2. The character-state is the same in two of the OTU's, in which case the hypothetical OTU will be assigned that character-state, or
3. The character-state is different in all three OTU's, in which case the hypothetical OTU will be assigned the intermediate character-state.

### Table 5—Character-state Differences in Text-figure 7.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Character</th>
</tr>
</thead>
<tbody>
<tr>
<td>a b c d e f g</td>
<td></td>
</tr>
<tr>
<td>Total path 4 4 4 7 5 8 10</td>
<td></td>
</tr>
<tr>
<td>Weighting factor 70 70 70 40 56 35 28</td>
<td></td>
</tr>
</tbody>
</table>

### Table 6—Weighted Data Matrix.

<table>
<thead>
<tr>
<th>OTU</th>
<th>a</th>
<th>b</th>
<th>c</th>
<th>d</th>
<th>e</th>
<th>f</th>
<th>g</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>40</td>
<td>0</td>
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<td>28</td>
</tr>
<tr>
<td>C</td>
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<td>140</td>
<td>0</td>
<td>160</td>
<td>0</td>
<td>105</td>
<td>28</td>
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<tr>
<td>D</td>
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<td>140</td>
<td>0</td>
<td>120</td>
<td>0</td>
<td>70</td>
<td>56</td>
</tr>
<tr>
<td>E</td>
<td>280</td>
<td>140</td>
<td>0</td>
<td>120</td>
<td>56</td>
<td>105</td>
<td>112</td>
</tr>
<tr>
<td>F</td>
<td>280</td>
<td>140</td>
<td>280</td>
<td>0</td>
<td>0</td>
<td>70</td>
<td>112</td>
</tr>
<tr>
<td>G</td>
<td>280</td>
<td>280</td>
<td>0</td>
<td>160</td>
<td>224</td>
<td>140</td>
<td>0</td>
</tr>
<tr>
<td>H</td>
<td>280</td>
<td>140</td>
<td>0</td>
<td>160</td>
<td>168</td>
<td>105</td>
<td>112</td>
</tr>
<tr>
<td>I</td>
<td>280</td>
<td>140</td>
<td>0</td>
<td>160</td>
<td>224</td>
<td>105</td>
<td>112</td>
</tr>
<tr>
<td>J</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>80</td>
<td>0</td>
<td>0</td>
<td>56</td>
</tr>
<tr>
<td>K</td>
<td>280</td>
<td>140</td>
<td>0</td>
<td>80</td>
<td>56</td>
<td>35</td>
<td>112</td>
</tr>
</tbody>
</table>

In Wagner's method, the state of each character can be predicted for any hypothetical OTU. Among three OTU's in proximity and linked in the cladogram, one of the following relationships must exist for each character they share:

1. The character-state is the same in all three OTU's, in which case the intermediate hypothetical OTU will be assigned that character-state,
2. The character-state is the same in two of the OTU's, in which case the hypothetical OTU will be assigned that character-state, or
3. The character-state is different in all three OTU's, in which case the hypothetical OTU will be assigned the intermediate character-state.
To determine the possibility of an intermediate hypothetical genus Q in the sequence H-I-G (text-fig. 8), consider first character a (table 6); it is the same in all OTU's and is assigned that value in Q. Character b is the same in OTU H and OTU I and is assigned the same value in Q. In successive characters (c through g) we find that the intermediate hypothetical genus Q would have all character-states identical with those of genus I—therefore, no such hypothetical genus need be proposed.

Nevertheless, by repeated tries, hypothetical genera can be found for the tree. Hypothetical genus W occurs between A and J and B; hypothetical genus X occurs between B and C and D; Y occurs between D and E and K; and Z occurs between Y and K and F. Their character-states are shown in table 8.

Entry of the hypothetical genera produces the tree in text-figure 9. It will be noted that

<table>
<thead>
<tr>
<th>OTU</th>
<th>a</th>
<th>b</th>
<th>c</th>
<th>d</th>
<th>e</th>
<th>f</th>
<th>g</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>W</td>
<td>0</td>
<td>0</td>
<td>80</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>108</td>
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<tr>
<td>X</td>
<td>280</td>
<td>140</td>
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<td>120</td>
<td>0</td>
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<td>0</td>
<td>638</td>
</tr>
<tr>
<td>Y</td>
<td>280</td>
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<td>120</td>
<td>56</td>
<td>70</td>
<td>0</td>
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<td>Z</td>
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<td>0</td>
<td>80</td>
<td>56</td>
<td>70</td>
<td>0</td>
<td>738</td>
</tr>
</tbody>
</table>

Text-fig. 8—Cladogram with weighted values of phenetic differences.

Text-fig. 9—Revised cladogram with hypothetical intermediate genera added.
the total path is now 1834 instead of the former 1960.

Interpretation

We can now proceed to enumerate the changes at each step of calceocrinid evolution which are consistent with the data used (text-fig. 10).

Fossil record.—Our postulated lines of descent in calceocrinids agree rather well with the fossil record; no genus appears to have descended from a much younger ancestor. In the final consideration, however, time must be a factor. In modern terms (see Kaesler, 1967, p. 63–64), our cladogram has a chronistic bias.

That the fossil record is seriously deficient is suggested by the evolutionary position of Senarioocrinus. This genus is known only from Europe, whereas its ancestors Cunctocrinus and Halysioocrinus are known only from North America. In addition, the oldest known Senarioocrinus is Early Devonian (Hunsrück Shale), whereas Cunctocrinus and Halysioocrinus have their first recorded appearance in Middle Devonian. It may be emphasized that only the type species at the type locality is known for Senarioocrinus and for Cunctocrinus. We infer that representatives of these genera, and undoubtedly of other calceocrinids, remain to be discovered in other places and in strata of other ages.

Branching and changes.—Unexpectedly the chronistic cladogram or probabilistic evolutionary tree for the eleven genera of Calceocrinidae has only three lateral branches (text-fig. 10). High values of phenetic differences (text-fig. 9) show where gaps exist in our knowledge of these crinoids.

From Cremacrinus through Cunctocrinus the main stem of the tree shows reduction of BB, development of lateral main axils, pinching off the contact between iR and sR of the E-ray by encroachment and meeting of the lateral RR, posterior shift of the columnar facet, and approach and final meeting of the B- and C-ray iRR. Although these evolutionary trends did not proceed at the same rate, all of them were progressive throughout calceocrinid history.

The tip of the evolutionary main branch, Senarioocrinus, is marked by the unexpected degeneration of the two main axils. Each has only one thin axil-arm, which bears one long uniramous ramule of about the same diameter, so that the two appear to comprise an isotomous bifurcation. The suggestion by Schmidt (1934, p. 17) that the genus may have become a swimmer deserves further consideration. Certainly, the sudden reversal of a trend that had continued uninterrupted from Ordovician to Devonian is a drastic change in morphology and probably indicates an equally drastic change in the crinoid’s mode of life.

The Ordovician offshoot, Anulocrinus, differs from the ancestor Cremacrinus in details of the E-ray and in minor advances in development of the main axils. The next offshoot, Deltaocrinus, shows two changes: (1) accelerated separation of E-ray iR and sR, to the state not reached in the main line until Devonian, and (2) further shift of the columnar facet away from the common junction of the three BB. The last offshoot is from the lineage leading from Chirocrinus to Synchirocrinus; it contains two genera. In this offshoot, the E-ray iR and sR revert to a very slight separation or even to a narrow contact, resembling the Ordovician Anulocrinus. In Grypocrinus, the columnar facet seems also to have reverted to a previous stage, having migrated back to lie on three BB. Chiropinna has been discussed in literature for its advanced branching of the axil-arms, described as “pinnulate”; nevertheless, more unexpected developments are the reversion of the B- and C-ray iRR to a wide separation and the reversion of the E-ray iR and sR back to a broad contact, rivaling that of the Ordovician Cremacrinus.

Characters of family.—Bilateral symmetry through the E-radius and a hinge between BB and RR perpendicular to the plane of symmetry were not included in the data matrix because they are features shared, at least to an appreciable degree, by all genera of the family. The Calceocrinidae is not polythetic (see Sokal & Sneath, 1963, p. 14), inasmuch as all its genera share characters (namely, the peculiar bilateral symmetry and the BB-RR hinge) which are absent in other crinoids.

Future revision.—We do not presume that the tree presented here is correct in all details; we claim only that it accords with our understanding of character-states in calceocrinids. Nor do we doubt that other and better suggestions will be forthcoming, for additional data should greatly improve our understanding and interpretation of evolution.

Coding of the character-states may become a matter of viewpoint on morphology. For example, character c used in constructing the tree concerned development of “pinnulate” arm-axils, which were coded only as $0 = \text{not \{pinnulate\}}$, and $4 = \text{pinnulate}$. If, however, we interpret the “pinnules” as being ramules given off by every axil-arm brachial and alternating from side-to-side, then the character might be
ROBERT V. KESLING and JAMES P. SIGLER

TEXT-FIG. 10—Cladogram with chronology made into postulated evolutionary tree, showing changes at each stage.
considered as maximum number of ramules on primaxil-arm, and coded as:

- 0 – one ramule (*Senarioocrinus*)
- 1 – three (*Anulocrinus, Deltacrinus*)
- 2 – four (*Synchirocrinus*)
- 3 – five to ten (*Cremacrinus, Chirocrinus, Halysiocrinus, Cunctocrinus*)
- 4 – over ten (*Chiropinna*)

One of the faults of using a maximum is that the coded character-state may not apply to immature specimens or to certain species of the genus. Similarly, one could consider the number of axil-arms per lateral ray as a character, which might be coded as:

- 0 – one (*Senarioocrinus*)
- 1 – two or three (*Cremacrinus*)
- 2 – two to four (*Calceocrinus*)
- 3 – three or four (*Deltacrinus*)
- 4 – five or more (*Chirocrinus, Synchirocrinus, Chiropinna, Halysiocrinus, Cunctocrinus*)

In this case, the overlapping ranges show that the character-states are not discrete; for practical intent, we are combining two characters, the minimum number of axil-arms per lateral ray and the maximum number of axil-arms per lateral ray. All species of *Calceocrinus*, for example, would not code the same if the maximum number was used as a character. This illustrates the unsurmountable problem that arises when attempting to use at the generic level a character which at the specific level of any one genus has more than one character-state.

Hence, any character used in future revisions of calceocrinids should have a discrete character-state in each genus assigned to the family. In turn, this focuses attention on the need for better-preserved specimens and for more reliable observations.

**PALEOECOLOGY**

*Previous work.*—For many years it was supposed that the calceocrinids lived with the column upright, as did other crinoids, and that the calyx hung down alongside it. Even the nature of the hinge between BB and RR was misunderstood.

The first functional morphological interpretation of these unusual crinoids that approached modern concepts was made by Jaekel (1918, p. 86–87). He characterized his suborder Calceocrinites, to which he assigned the known calceocrinids of his day, as (our translation):

Reef-dwellers with incumbent (prone) stem and sharply upright crown, which, bilateral on the E-ray, is crooked against the stem. A-ray and D-ray large with heterotomous or unilaterally paratomous arms, E-ray small, as a rule with a broad undivided arm, which in the folded state serves to cover the crown. The C-ray, and from Upper Silurian on also the B-ray, arm degenerate. Anal tube in the plane of symmetry as a vertical series.

These specialized forms have been up to now so interpreted that their stem normally would have been erect and their crown hung down. The sharp bend of stem and crown thereby remained immovable, like the peculiar development of their arms. Also, it was difficult to assume that their ciliary grooves should have jointed directed the foodstuff upward. Their organization and life habits are understood in all respects when we portray them as shown in fig. 83 [this is the widely copied figure of a calceocrinid]. They obtained their nourishment like all crinoids from above, while they were protected against changes of the ebb current by their onesidedness on the bottom after folding up. Their front broad arm (E-ray) also served especially in this regard, in the folded condition lying over the arms like a roof.

Through this peculiar mode of life the arm- and calyx-structure was strongly modified, so that an entirely new organizational kind of crinoid resulted.

Springer (1926, p. 99) endorsed Jaekel’s interpretation of calceocrinid morphology and ecology and added some thoughts of his own:

A more recent interpretation has been given by Jaekel . . . which better with the observed facts. He considers these crinoids . . . to be reef-dwellers, living exposed to tidal currents, the stem lying recumbent upon the bottom, where when at rest the crown was closed down at one side like a barnacle. When feeding, the arms opened out toward the current, for which but little movement of the crown as a whole upon the base was required. When the tide turned, the arms would readily close down, the larger ones serving as a protection for the more delicate parts against injury from the ebb-current. Thus, the crown habitually was in a horizontal position to start with, from which only a relatively small movement was needed beyond the ordinary opening of the arms to enable the organism to obtain food from above like other crinoids . . . This interpretation presupposes a sessile condition by means of a distal attachment of the stem to the reefs. Some evidence of this is seen in specimens from Dudley, England, in which the stem is sometimes found rather short with a foreign object attached . . . With the recumbent position as that of rest, in which the crinoid habitually reclined except when feeding, the diminution in size of the arms toward the posterior side, which became such a marked character of the post-Ordovician forms, is accounted for as the result of a cramped position, pressure, and loss of motion.

The latest contribution to calceocrinid paleoecology is by Brower (1966). He neatly characterized these crinoids under the old proposed mode of life, with stem upright and crown recumbent, as “droopers”; those under
the later proposed mode of life, with stem extended along the substrate, he termed "runners." He envisioned the calceocrinids as invaders into another ecological niche, competing with brachiopods, pelecypods, and other bottom-dwellers instead of other crinoids. As for the conditions under which they lived, Brower stated (1966, p. 615):

At first glance it might appear that the calceocrinids were adapting to a reef or some other agitated habitat. In this case with the hinge in the closed position the animal would have been recumbent along the sea floor, wholly or partially in the laminar flow zone and thus at least partially shielded from the zone of agitation. In the open position the calceocrinid crown was elevated, presumably for more efficient feeding. Another possibility is that the calceocrinids lived in small nooks and crannies in reefs which would have protected them from wave agitation. However, if this were the primary adaptation then all calceocrinids should occur in agitated habitats.

Brower goes on to point out that the two oldest calceocrinids (Black River in age) are Crema-crinus arctus from the Platteville Limestone, definitely deposited in quiet water, and Anulo-crinus sp. from the Bromide Limestone, deposited in alternating quiet and agitated conditions. He continued:

This curious dualism of quiet and rough water habitats can also be seen in the later geologic history.

Agitated environments in which calceocrinids are found, he pointed out, are represented by the Beech River Formation of Tennessee and the Burlington Limestone, and quiet water is represented by the Rochester Shale of New York and the Keokuk Shale of Indiana.

Our subsequent comments on paleoecology are based on these three very significant references; substantiating material and similar suggestions are found in the works of Sardeson (1928), Strimple (1963), and others.

Modern comatulids.—Calceocrinids lived near the bottom in relatively shallow water, like the living comatulid crinoids. For comparison, we direct attention to certain features of comatulid ecology.

Libbie Hyman has said (1955, p. 113), "Comatulids in general inhabit rough and rocky bottoms, most frequently coral reefs, and very few occur on sandy or muddy substrate." Nevertheless, she also reported that cirri of comatulids have become adapted for at least three modes of attachment: long strong cirri for finding purchase among rocks, short strong cirri for grasping small objects (such as seaweed), and long thin processes for anchorage in soft sediments.

Hyman (1955, p. 105) quoted H. L. Clark regarding the light sensitivity of certain shallow-water species: "If a rock bearing comatulids on its underside was turned over, the animals would promptly move, usually to the new under-surface of the same rock or, less often, into available crevices and shaded sites."

Magnus (1963) recorded observations on the comatulid Heterometra savignyi in the Red Sea. This animal feeds nocturnally, and turns so that the abambulacral sides of the arms face into the current.

Mr. David L. Meyer, formerly a student at The University of Michigan and now doing graduate studies at Yale University, is currently investigating living crinoids by scuba-diving in the Caribbean region. He reported (to the senior author) that certain species could scarcely be found during the daylight hours, but crept out to conspicuously exposed places at night and there spread their arms into the feeding posture. He also noted that whenever currents were active, comatulids twisted their arms to turn and to maintain the ambulacral grooves away from the current; thus, the arms of the feeding comatulid may spread more like a fan than like an upright funnel.

Excretion creates a problem in Antedon. Hyman wrote (1955, p. 107):

A weak ciliation at the base of the anal cone beating upward was noticed, but it is too feeble to carry feces away. The latter are formed into large yellow balls held together by mucus; these balls usually fall upon the disk, where they gradually slide off through the movements of the animal.

Living position of calceocrinids.—All evidence supports Jaekel's suggestion that calceocrinids lay with the column on the bottom and fed with the calyx upright (text-fig. 11). Advanced genera, such as Halysiocrinus, could not extend the crown to alignment with the column; at their limit of hinge movement, the arms would have been about perpendicular to the column. If the column was upright, this would be a very inefficient feeding position. The so-called "resting" position of the crinoid, with the crown folded back alongside the column (text-fig. 12), appears to have served no purpose if the column was vertical; other stemmed crinoids live with the crown erect at all times.

Development of the unique BB-RR hinge can only be explained as an adaptation for life with the column horizontal upon the substrate. If, as seems reasonable to assume, the calceocrinids descended from homocrinid ancestors, the first representatives had a poorly developed hinge, capable only of elevating the crown from the substrate. The oldest known calceo-
**TEXT-FIG. 11**—Calceocrinid in presumed feeding position, lateral view.

**TEXT-FIG. 12**—Calceocrinid in presumed resting position, lateral view.
crinid, *Cremacrinus*, from Middle Ordovician strata, already had a hinge which could bend the crown back alongside the column. *Cremacrinus* had one arm-bearing R on one side (D-ray) and two arm-bearing RR on the other (A- and B-rays); hence, the hinge was perfected before bilateral symmetry was fully established. The asymmetric position of the columnar facet, situated in the BC-interray and offset from the anal series, undoubtedly caused the hinge of *Cremacrinus* to be inefficient, since torque was generated by elevation of the crown. Later calceocrinids did not have this problem.

The pattern of evolution in the family was directed toward perfection of bilateral symmetry, which in turn increased the efficiency of the BB-RR hinge. The loss of the B-arm in post-Ordovician genera was a step toward balancing arm and plate structures on the E-radius plane. The fusion of plates appears to strengthen the modified calyx, so that it came to operate as two hinged units, (1) the BB on one side, attached to the column, and (2) the RR on the other side, bearing in the symmetry plane the E-arm and anal tube and at the sides the matched A- and D-ray arms.

The whole evolutionary sequence leaves no doubt that, from the first, these crinoids lived with the stem extended on the substrate. Only in that orientation could the hinge have served any purpose. The extension of the hinge perpendicular to the symmetry plane formed a basal projection outward on each side to help balance the erect crown.

**Posterior groove.**—Many calceocrinids have a vertical groove, but it has not been accorded taxonomic value and few authors have noted it. It is reasonable to endorse Springer's (1926, p. 110) remarks about *Cremacrinus punctatus* Ulrich, "The position of the stem to the right of the anal tube in the hollow of the right posterior interray is admirably shown . . . with the deep indentation resulting from contact when the crown was recumbent." Springer was convinced that this offset vertical indentation in *C. punctatus* was comparable with the groove in *Halysiocrinus carinatus*, shaped like a cylindrical gouge along the midline of the anal series, beginning immediately above the BB and tapering out above X.

Similar indentations are present in other species of *Halysiocrinus* and in *Cunctocrinus* (text-fig. 3), and perhaps also in other calceocrinids; but no indentation can be found in some species of *Halysiocrinus*, in which the lower plates of the anal series are rounded and inflated. We agree with Springer that this groove served to accommodate the column in the resting position, occurring in those species in which the column was sharply flexed near its attachment to the BB. This and other adaptations seem designed to make the resting crown as low and inconspicuous as possible on the bottom.

**Anchorage.**—Jaekel (1918, explanation of fig. 83) and Springer (1926, p. 99) mentioned evidence of a holdfast or anchor in calceocrinids. Brower (1966, p. 614) mentioned an undescribed specimen from the Bromide Formation of Oklahoma, apparently preserved intact, consisting of a crown 19 mm long and a stem only 6.5 mm long; adjacent to the distal tip of the stem was a holdfast. We suspect that all of these crinoids were attached, but for a different purpose than that previously proposed. Both Jaekel and Springer thought the calceocrinid fed when the current came from its posterior direction and folded down for protection when the ebb-current set in from its anterior direction. Both authors concluded that the crinoids lived in and around reefs, where reversed tidal currents were normal.

Field evidence from the site where *Cunctocrinus fortunatus* was found shows that the living zone of this calceocrinid lay well below the zone of turbulence. Currents were at most times gentle, or may have ceased for brief intervals. There is no reason to think that ebb-currents would extend to these depths. The current may have shifted from time to time, however, but such shifts were probably gradual.

We believe the purpose of the anchorage (text-fig. 13) in *Cunctocrinus* was to allow shifting with current change, so that the crown was always down-current from the attachment and therefore in position to feed by intercepting food particles from the current. We suppose that the crinoid could shift like a weather vane to maintain the best feeding orientation, always presenting its posterior edge to the current.

If indeed the crinoid was attached and shifted position, it must have been able to maintain the crown uppermost by adjustments in the column. Other stalked echinoderms have the ability to turn the crown somewhat, and calceocrinids may have been able to right the crown rather quickly.

As pointed out by Schmidt (1934) the reduced arms and feeble column of *Senarioocrinus* may have resulted from a change from the normal calceocrinid way of life.

**Feeding position.**—In those genera having well-developed main axes, each axis has a hinge with the R plate. This can be seen in *Cunctocrinus fortunatus* (pl. 1, figs. 2–4) and in specimens of *Halysiocrinus nodosus*. The latter has, in addition, hinges developed between
plates of the main axil, so that the whole structure was flexible and could unfold to the side.

From the so-called resting position (text-fig. 12) to the feeding position (text-figs. 3, 11) the axil-arms rose and spread, like feathers in the tail of a peacock. In the feeding position, the ambulacral grooves faced posteriorly, toward the current. This was undoubtedly very advantageous to a ciliary mucus feeder, which captured small organisms or seized on particles of detritus borne along by the current.

The orientation of the ramules seems to have been shaped by the folding and unfolding of the crown. In species of Halysiocrinus, for example, the folded axil-arms have the $\beta$, $\gamma$, and $\epsilon$-ramules exposed but the $\alpha$, $\gamma$, and $\epsilon$-ramules are turned inward and concealed in many specimens. In other words, each axil-arm has its anterior ramules turned inward, with their ambulacral grooves directed posteriorly, but its posterior ramules lie outside, with their ambulacral groove directed toward the median plane of symmetry. Brower (1966, p. 617-618) also noted the twisting in certain calceocrinids; he supposed that the main purpose of this configuration was protection in the resting position. He wrote (1966, p. 618): "In this case the smaller and more fragile ramules and main branches are themselves protected by larger and more massive portions of the axil arms." We suspect that the complex arm-folding developments may simultaneously have served an additional purpose.

When the main axils spread apart in feeding, each swinging away from the side of the cup on its hinge, all ambulacral grooves faced in the general posterior direction—toward the anchorage, the column, and the current. Yet when the arms were folded, the overlapping of alternate ramules by the adjacent arm produced the most compact crown possible.

"Resting" position.—So much of the calceocrinid evolution was devoted to the perfection of the BB-RR hinge, that we doubt the folding back of the crown alongside the column was strictly designed for resting. Other crinoids manage to rest without such an elaborate device and to achieve the feeding position without so much expenditure of energy.

Hyman has called attention to the problem attendant to defecation in the comatulids (see above). In the feeding position, the problem for calceocrinids was undoubtedly more acute; the anal tube emptied up-current from the network of ambulacra. It seems possible that the calceocrinid avoided fouling its own food-gathering tracts by defecating in the prone position; therewith, the arms were tightly folded with their ambulacral grooves concealed. If a current was flowing, the feces could have been swept away before the next feeding period; even if the current was weak, the feces would be left below the feeding level.

The hinge enabled the crinoid to flip its crown from erect to prone and back to erect with great efficiency. We suspect that the movement was cyclic, probably daily, and that the prone position served more for protection than for rest. Thus, the calceocrinid may have fed only at night, and spent the day inconspicuously upon the bottom with the arms tightly folded. In this position, it may have resembled dead crinoid remains and thereby escaped the notice of daytime predators.

Therefore, we presume that the calceocrinids show some remarkable resemblances to certain of the comatulids. Both kinds of crinoids were night feeders. Both sought to avoid enemies during daylight hours, the calceocrinid folding its arms alongside the column and assuming an inconspicuous outline on the sea floor, and the comatulid tightly enrolling its arms and retreating to a crevice or protected niche. Both took advantage of current direction in feeding, the calceocrinid by its up-current anchorage, movable main axils, and peculiar
orientation of ramules, and the comatulid by active movement and twisting of the arms. The two kinds of crinoids, however, differed in their relationship to the current, the calceocrinid striving to bring its ambulacra to face into the current and the comatulid striving to bring its ambulacra to face away from the current. By elaborate structures in the sessile calceocrinid and by motility in certain comatulids, they seem to have converged ecologically.

LITERATURE CITED


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