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

BY

ROBERT V. KESLING and JAMES P. SIGLER

The University of Michigan and Bowling Green University

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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.

CONTENTS

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 hingement 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, *Senariocrinus* 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 heterotomously 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 ⅓ 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 X_2, 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 PBr_3, the part above hidden by axil-arms of adjacent rays (pl. 1, fig. 4). PBr_1 shorter than PBr_2, strongly tapering from its
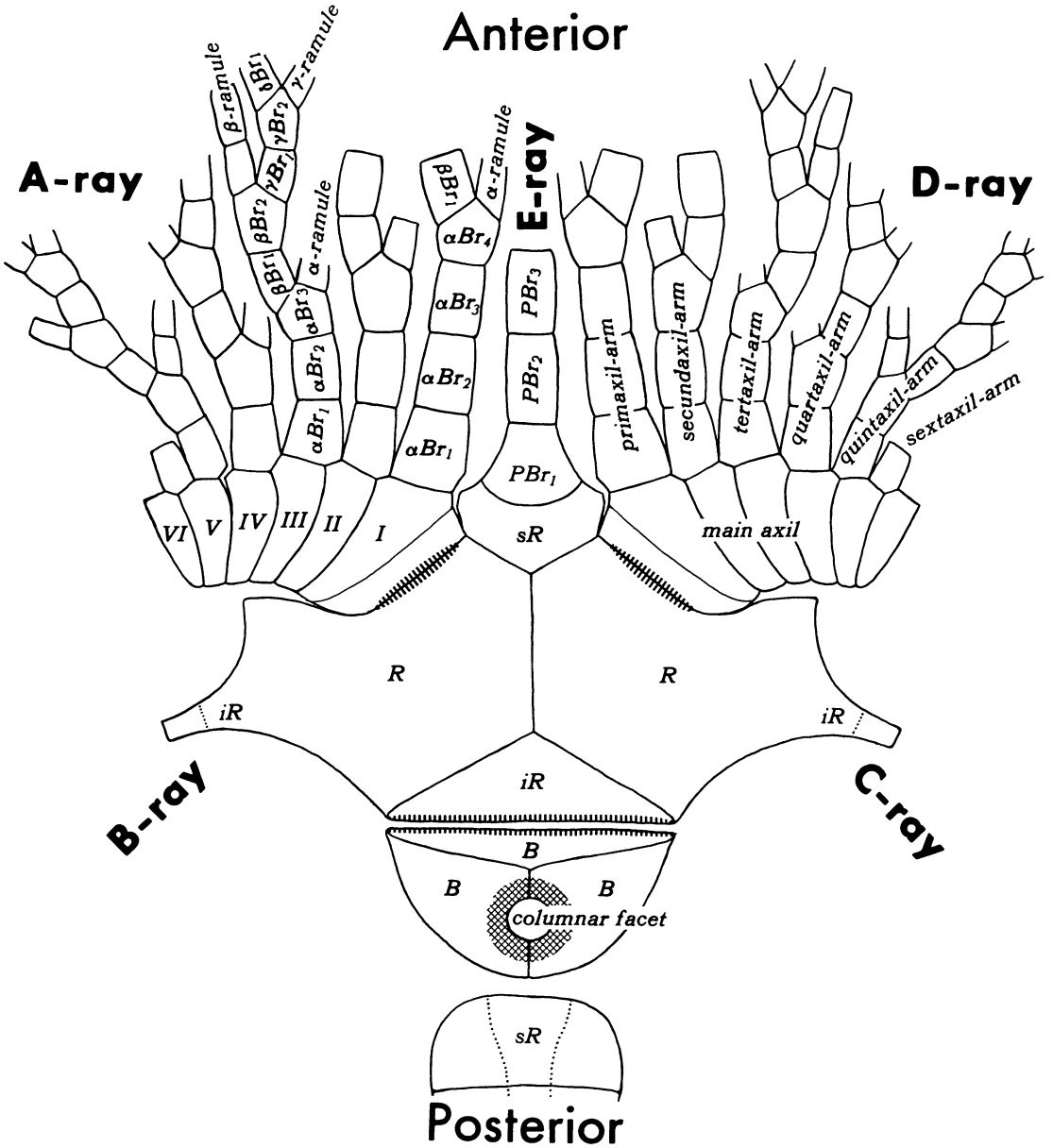
TEXT-FIG. 1—*Cunctocrinus fortunatus* n sp. Plate diagram with maximum extent of preserved lateral arms filled in for both A- and D-rays. Fine dotted line represents crest outlining posterior groove. Hatching represents hinges.

wide junction with sR. PBr$_2$ and PBr$_3$ quadrate, 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 αBr$_4$; secundaxil-arm and tertaxil-arm first on αBr$_3$; and quartaxil-arm and quintaxil-arm first on
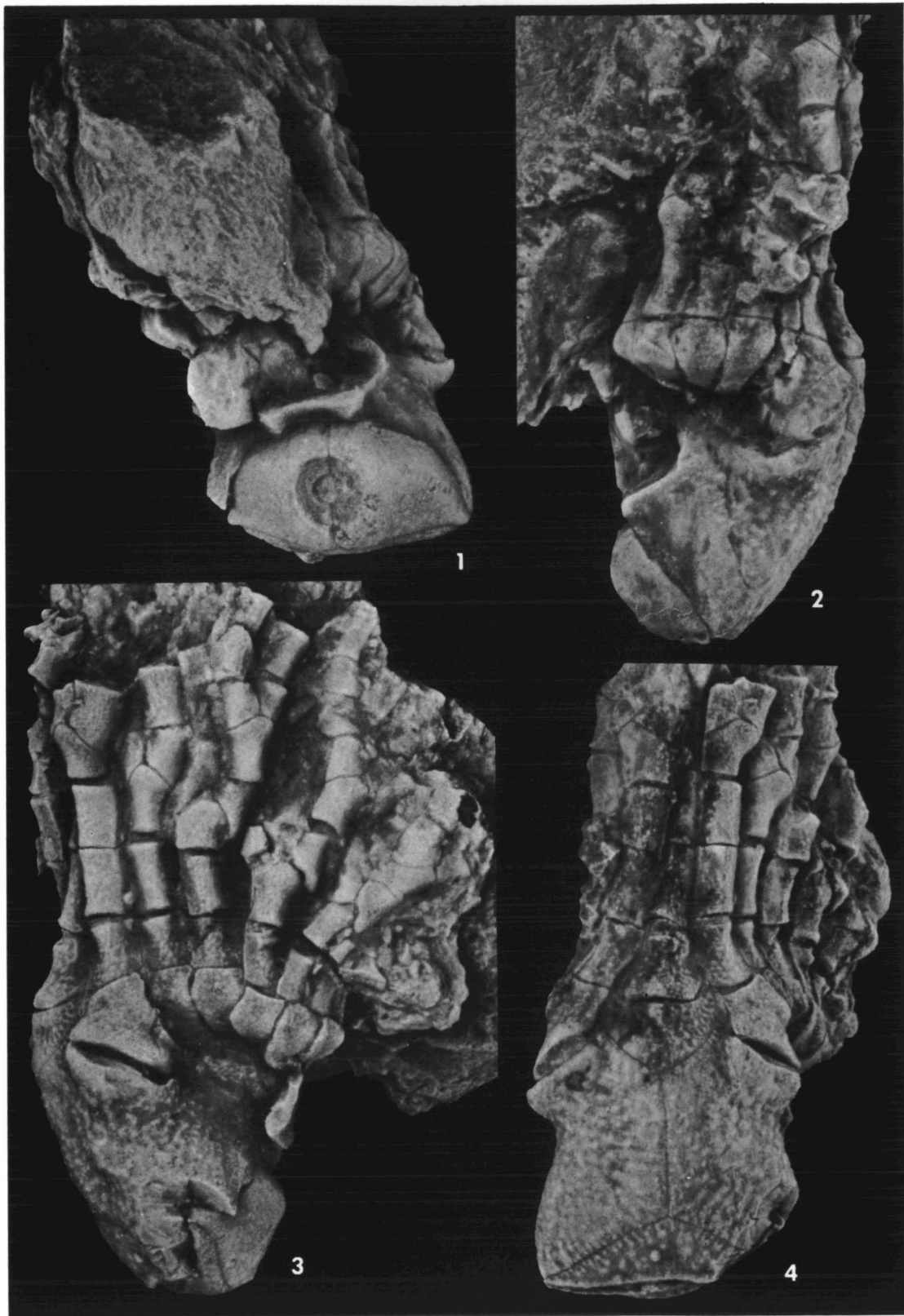
PLATE 1

αBr_2. Tertaxil-arm (pl. 1, fig. 3) next axillary on βBr_2 and then axillary on γBr_2. Distal ends of arms missing. Ramules slightly narrower than main branch at each bifurcation.

Anal series represented only by sR of BC-interray and X; succeeding plates not seen. Ornamentation consisting of small irregular nodes or tubercles, especially prominent on the large fused iR-R plates, producing an overall roughened appearance. 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 δ-series; the median arm is not known beyond PBr_3; 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 *SENARIOCRINUS*

According to the recent revision and review of the Calceocrinidae by R. C. Moore (1962, p. 30–31, 33–37), *Senariocrinus* 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 *Cremacrinus*, the sRR of the B- and C-rays fused and the iRR remained distinct; yet in *Senariocrinus* the reverse was proposed, the iRR fusing and the sRR remaining distinct. In all other calceocrinids the lateral RR failed to meet posteriorly; in *Senariocrinus* 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 *Senariocrinus* 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, *Senariocrinus* appeared to be a unique descendant of the ancestral *Cremacrinus*, with no close relatives among the Silurian or Devonian genera.

We compared *Senariocrinus* 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 *Senariocrinus*. 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 *Senariocrinus*. The diagonal junction reported of the next two (?) plates of *Senariocrinus* needs further investigation; if it is indeed

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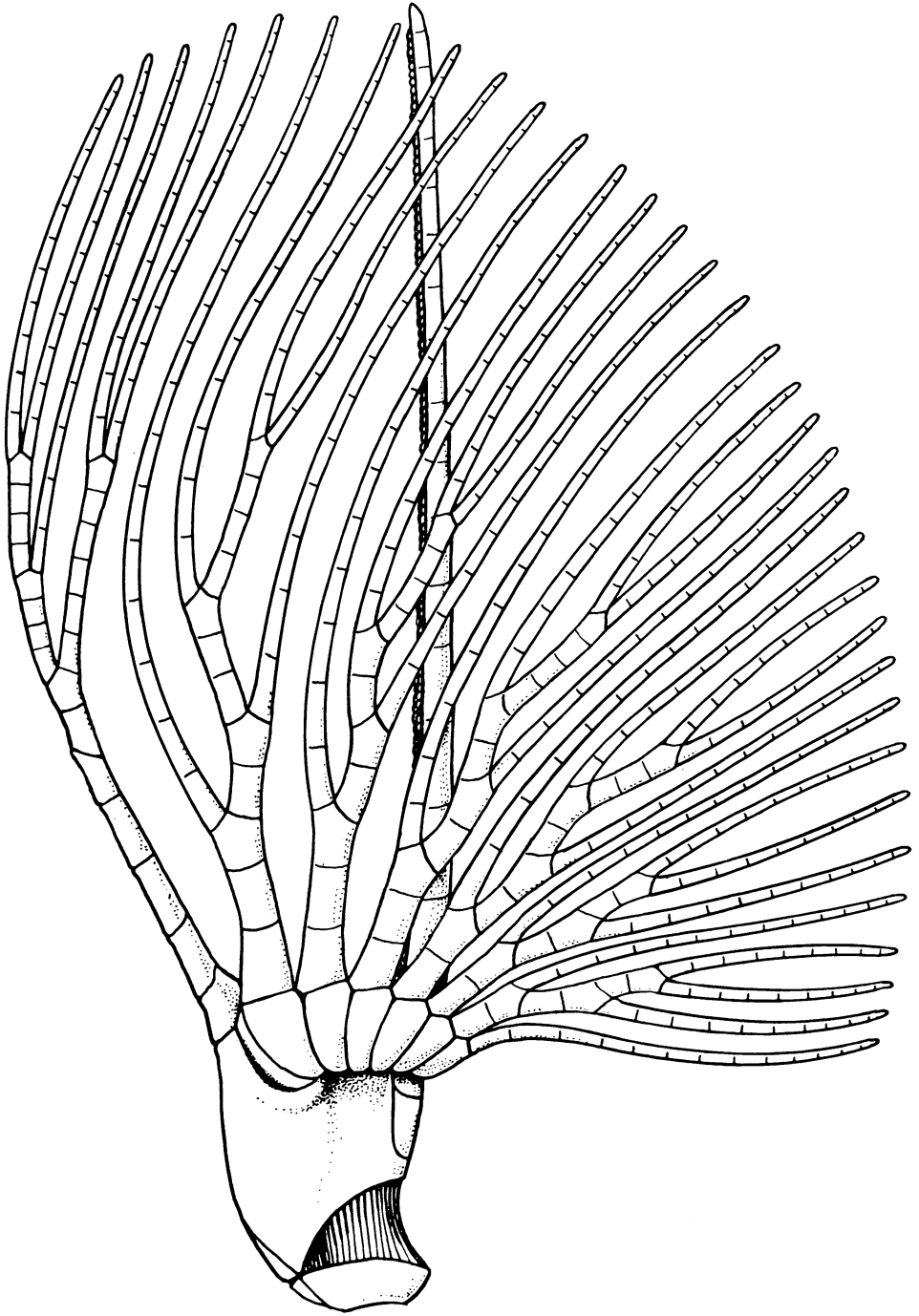
TEXT-FIG. 2—*Cunctocrinus fortunatus* n. sp. Restoration in lateral view.
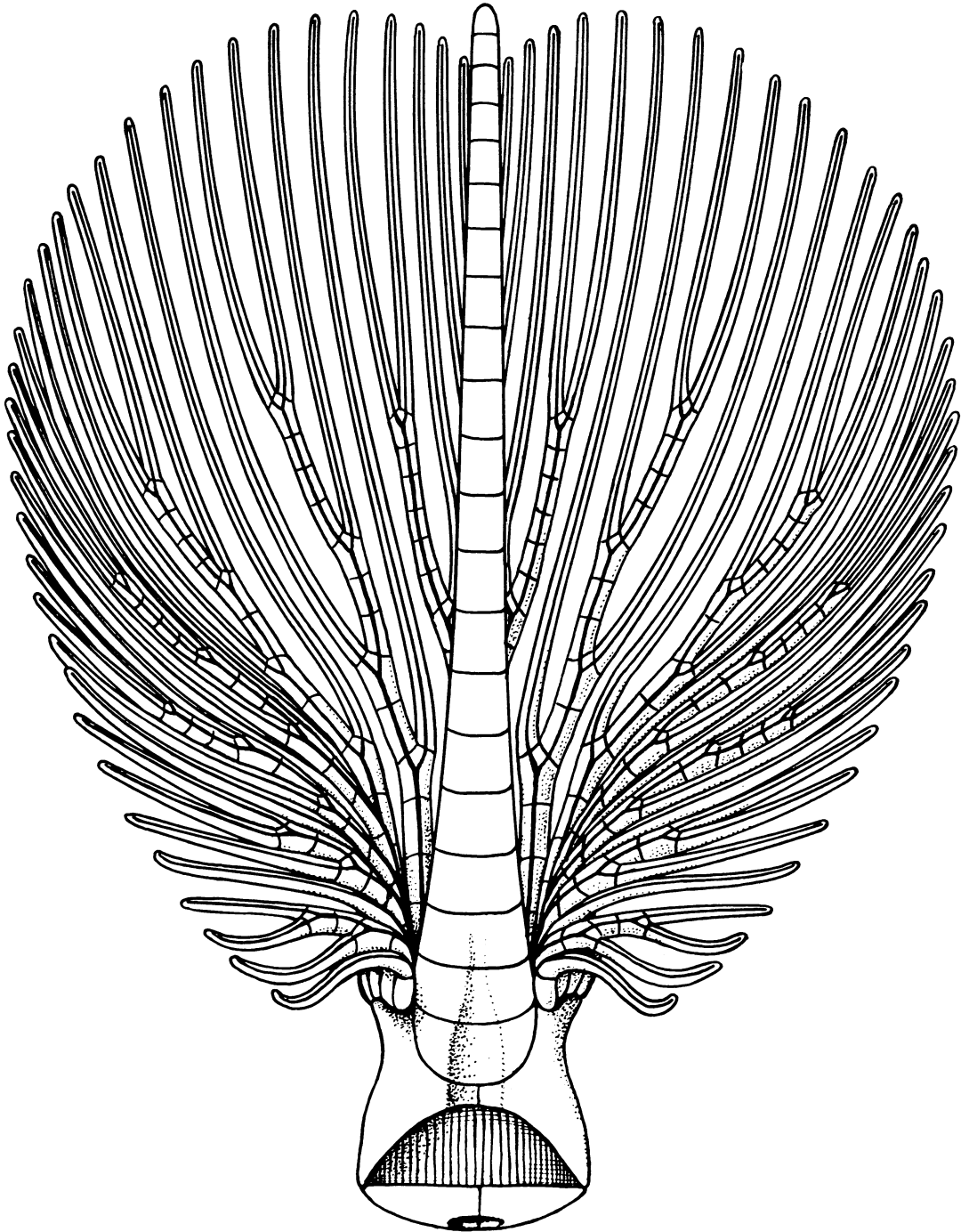
TEXT-FIG. 3—*Cunctocrinus fortunatus* n. sp. Restoration in posterior view, showing axil-arms spread in presumed feeding position.

a junction it is unique among crinoids. We suspect that it is simply a crack through plate X.

We believe, therefore, that *Senariocrinus* 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 CALCEOCRINIDS
Previous Work

Jaekel (1918, p. 87–88) divided his suborder Calceocrinites 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 *Cremacrinus* Ulrich) and his Calceocrinidae included *Euchirocrinus* Meek & Worthen (now *Calceocrinus* Hall), *Bichirocrinus* n. gen. (no species assigned). *Synchirocrinus* n. gen., *Dichirocrinus* n. gen. (no species assigned), and *Halysiocrinus* 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 isotomously or heterotomously, and in younger forms (*Synchirocrinus* n. gen.) only divided off unilaterally paratomous ramules. From the beginning on, their C-ray arm had disappeared, then also the B-arm was stunted, while the E-arm became adapted as a protective

organ and lost its original nutritional character. Corresponding to the development of the A- and D-arms, their calyx shows large A- and D-ray RR, which finally met below the E-ray sR and thereby squeezed out the E-ray iR; the C-ray R and thereafter the B-ray R became stunted, although the B-ray iR maintained itself as a little plate. Between the front abanal BB and the three overlying plates a joint developed, which is covered with little platelets. The anal tube is mostly covered by the side arms, so that it often appears shorter, as perhaps it is. The strange type developed early (Middle Lower Silurian) [now Middle Ordovician] and persisted to the Carboniferous.

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.

Character	Ancestor	Stage A	Stage B	Stage C	Stage D
Age	Ord.	Ord-Sil.	Sil.	Sil.	Dev.-Miss.
Representative genus	*Heterocrinus*	*Cremacrinus*	*Eucheirocrinus*[1]	*Calceocrinus*[2]	*Halysiocrinus*
Crown	Erect	Bent	Strongly bent		
BB	5, equal	4, all touching stem; B of BC-interray eliminated		3, only two touching stem; BB of DE- and CD-interrays fused	
Arms	5	4, C-ray arm eliminated	3, B-ray arm also eliminated		
Stem	Centered in BB circlet	Offset, touching all 4 BB; beside anal tube	Offset, touching all 4 BB; below anal tube	Offset, not touching fused BB of DE-CD-interray	
Branching in lateral arms	Symmetrical, even	Slightly asymmetric	Strongly asymmetric	Axil-arms on successive axillaries aligned to form main axil	
E-ray sR and iR	Long suture	Constricted, short suture	More constricted, very short suture	Separated by encroachment and junction of RR of A- and D-rays	
C- and B-ray RR	iRR and sRR normally developed	iRR offset from sRR	iRR offset, sRR fused	iRR separated by sR	iRR joining below sR

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 *Deltacrinus*.

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 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 un-branched (*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 brachials."

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 *Chiropinna* 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 – *Chiropinna* 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.

Communications	Graph Theory	Evolution
Terminal	Vertex	Operational taxonomic unit (OTU)
Nearest neighbor		Most closely related OTU (MCR)
Link	Edge	Link (direct relationship)
Length of link	"Length" or "weight" of edge	Phenetic difference (summation of differences in character-states)
Fragment		Section of cladogram
Distance table		Matrix of phenetic differences
Connection network	Spanning subtree	Tree
Shortest connection network (SCN)	Shortest spanning subtree (SSS)	Cladogram (evolutionary tree)

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
    3 – in contact or nearly in contact
    4 – 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
    4 – 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.

OTU	a	b	c	d	e	f	g	Total
A	0	0	0	1	0	0	1	2
B	4	0	0	2	0	0	1	7
C	4	2	0	4	0	3	1	14
D	4	2	0	3	0	2	2	13
E	4	2	0	3	1	3	4	17
F	4	2	4	0	0	2	4	16
G	4	4	0	4	4	4	0	20
H	4	2	0	4	3	3	4	20
I	4	2	0	4	4	3	4	21
J	0	0	0	2	0	0	2	4
K	4	2	0	2	1	1	4	14

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.

OTU	A	B	C	D	E	F	G	H	I	J	K
A	==	5	12	11	15	16	20	18	19	2	12
B	5	==	7	6	10	13	15	13	14	5	7
C	12	7	==	3	5	12	8	6	7	12	8
D	11	6	3	==	4	9	11	7	8	9	5
E	15	10	5	4	==	9	11	3	4	13	3
F	16	13	12	9	9	==	20	12	13	16	8
G	20	15	8	11	11	20	==	8	7	20	14
H	18	13	6	7	3	12	8	==	1	16	6
I	19	14	7	8	4	13	7	1	==	17	7
J	2	5	12	9	13	16	20	16	17	==	10
K	12	7	8	5	3	8	14	6	7	10	==

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

J
0002002
|2
A
0001001
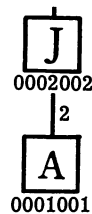
TEXT-FIG. 4—Section of cladogram.

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
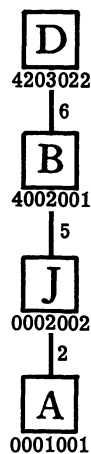
TEXT-FIG. *5*—Section of cladogram.
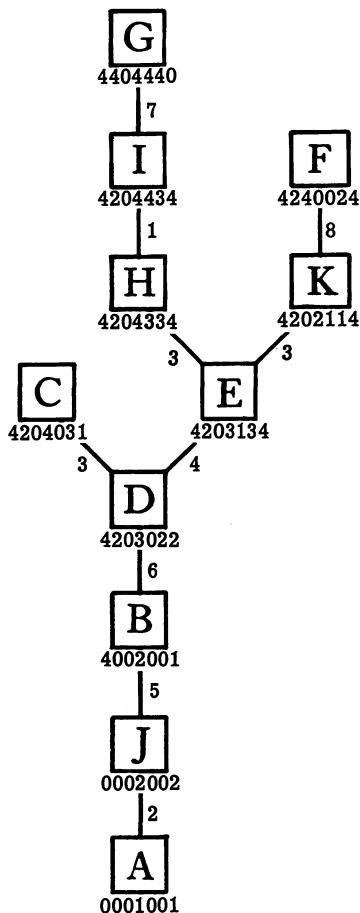
TEXT-FIG. *6*—Cladogram with character-states for each OTU and phenetic difference between neighboring OTU's.
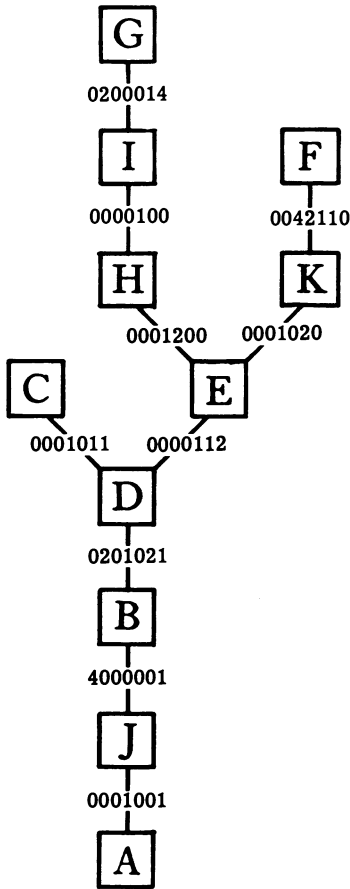
TEXT-FIG. 7—Cladogram with character-state differences between neighboring OTU's.

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.

TABLE 5—CHARACTER-STATE DIFFERENCES IN TEXT-FIGURE 7.

Measurement	Character						
	a	b	c	d	e	f	g
Total path	4	4	4	7	5	8	10
Weighting factor	70	70	70	40	56	35	28

TABLE 6—WEIGHTED DATA MATRIX.

OTU	a	b	c	d	e	f	g
A	0	0	0	40	0	0	28
B	280	0	0	80	0	0	28
C	280	140	0	160	0	105	28
D	280	140	0	120	0	70	56
E	280	140	0	120	56	105	112
F	280	140	280	0	0	70	112
G	280	280	0	160	224	140	0
H	280	140	0	160	168	105	112
I	280	140	0	160	224	105	112
J	0	0	0	80	0	0	56
K	280	140	0	80	56	35	112

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 7—MATRIX OF WEIGHTED PHENETIC DIFFERENCES.

OTU	A	B	C	D	E	F	G	H	I	J	K
A	==	320	645	598	745	894	1072	897	953	68	635
B	320	==	325	278	425	654	752	577	633	308	315
C	645	325	==	103	180	559	427	252	308	633	290
D	598	278	103	==	147	456	530	299	355	530	187
E	745	425	180	147	==	491	495	152	208	677	110
F	894	654	559	456	491	==	986	643	699	906	451
G	1072	752	427	530	495	986	==	343	287	1060	605
H	897	577	252	299	152	643	343	==	56	829	262
I	953	633	308	355	208	699	287	56	==	885	318
J	68	308	633	530	677	906	1060	829	885	==	567
K	635	315	290	187	110	451	605	262	318	567	==

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

TABLE 8—DATA MATRIX OF HYPOTHETICAL GENERA.

OTU	a	b	c	d	e	f	g	Total
W	0	0	0	80	0	0	28	108
X	280	140	0	120	0	70	28	638
Y	280	140	0	120	56	70	112	778
Z	280	140	0	80	56	70	112	738
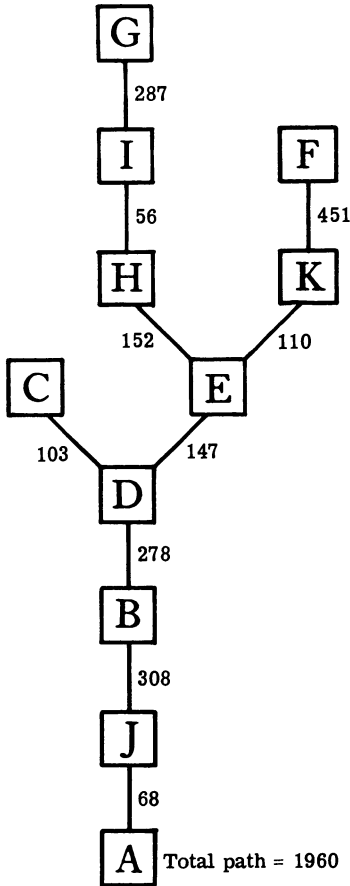
TEXT-FIG. 8—Cladogram with weighted values of phenetic differences.

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
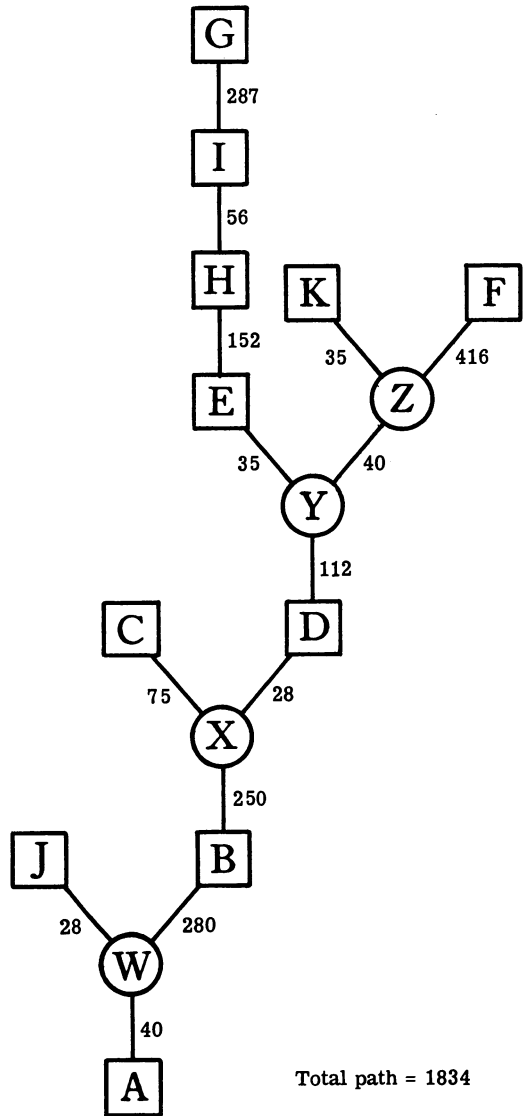
TEXT-FIG. 9—Revised cladogram with hypothetical intermediate genera added.

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 *Senariocrinus*. This genus is known only from Europe, whereas its ancestors *Cunctocrinus* and *Halysiocrinus* are known only from North America. In addition, the oldest known *Senariocrinus* is Early Devonian (Hunsrück Shale), whereas *Cunctocrinus* and *Halysiocrinus* have their first recorded appearance in Middle Devonian. It may be emphasized that only the type species at the type locality is known for *Senariocrinus* 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, *Senariocrinus*, 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. Cer-tainly, 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, *Deltacrinus*, 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 = not "pinnulate," and 4 = "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

| SENARIOCRINUS |

BB fused together
Main axils degenerate

| CUNCTOCRINUS |

B- and C-ray iRR fused with
        lateral RR

| HALYSIOCRINUS |

E-ray iR and sR strongly separated
B- and C-ray iRR in contact

Devonian
=========================
Silurian

| CHIROPINNA |

| GRYPOCRINUS |

Facet revert-
    ing to 3 BB

Arm-axils "pinnulate"
E-ray iR and sR further re-
    verting to broad contact
B- and C-ray iRR reverting
    to wide separation

| SYNCHIROCRINUS |

Facet on only two BB, not
    tangent to third B

(Z)

E-ray iR and sR reverting to very nar-
    row contact or slight separation

(Y)

B- and C-ray iRR only narrowly separated
Main axils highly developed

| CHIROCRINUS | | DELTACRINUS |

Main axil from poorly to
    moderately developed

Strong separation of E-ray iR and sR
Facet on two BB, not tangent to third B

(X)

BB reduced from 4 to 3
E-ray iR and sR slightly separated
Silurian   Facet shifted to 2 BB, tangent to third
=========================
Ordovic | CALCEOCRINUS |

| ANULOCRINUS |

Reduction from 5 to 4 RR

Main axil from poorly to
    moderately developed
(BB tending to fuse)

(W)

E-ray iR and sR from narrow
    to very narrow contact

| CREMACRINUS |

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 *(Senariocrinus)*
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 *(Senariocrinus)*
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 jointlʸ 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 seems to accord 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 *Cremacrinus arctus* from the Platteville Limestone, definitely deposited in quiet water, and *Anulocrinus* 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 have been 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-
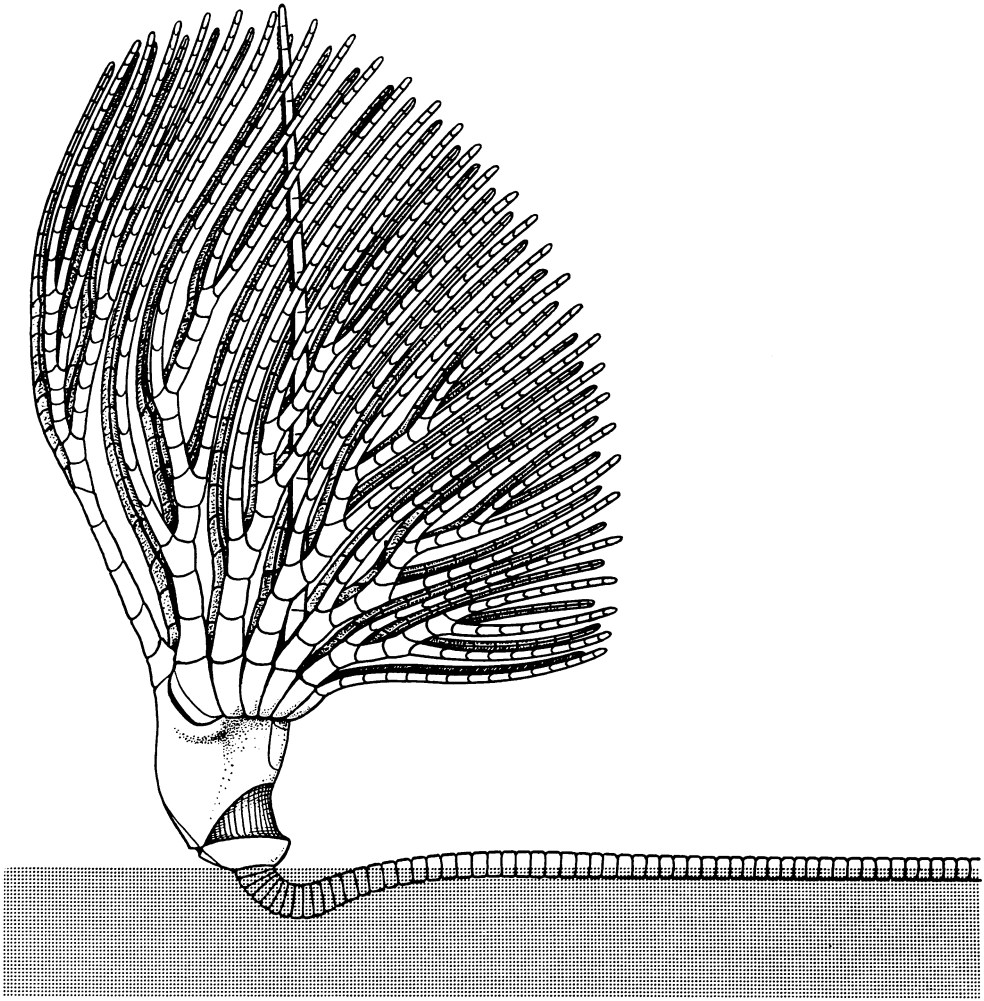
TEXT-FIG. *11*—Calceocrinid in presumed feeding position, lateral view.
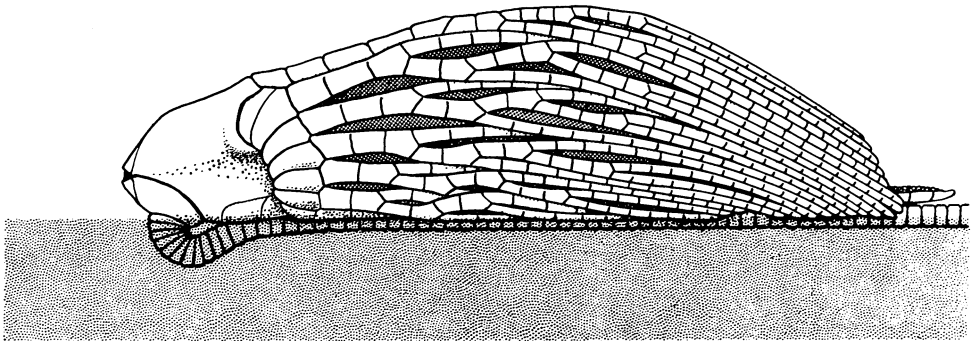
TEXT-FIG. *12*—Calceocrinid in presumed resting position, lateral view.

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 *Senariocrinus* may have resulted from a change from the normal calceocrinid way of life.

Feeding position.—In those genera having well-developed main axils, each axil 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
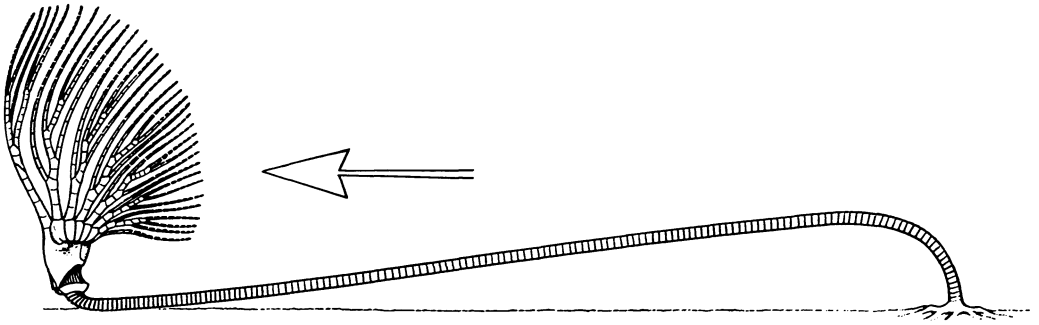
Text-fig. 13—*Cunctocrinus fortunatus* n. sp. in presumed feeding position.

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 β-, δ-, and ζ-ramules exposed but the α-, γ-, and ε-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 all 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

BARTCHER, R. L., 1966, Fortran IV program for estimation of cladistic relationships using the IBM 7040: Kansas State Geol. Survey, Computer Contrib. 6, 54 p.

BENSON, LYMAN, 1962, Plant taxonomy, methods and principles: ix + 494 p., illus., Ronald Press, New York.

BROWER, J. C., 1966, Functional morphology of Calceocrinidae with description of some new species: Jour. Paleontology, v. 40, no. 3, p. 613–634, pl. 75, 2 text-figs.

CAMIN, J. H., & SOKAL, R. R., 1965, A method for deducing branching sequences in phylogeny: Evolution, v. 19, no. 3, p. 311–326.

EASTON, W. H., 1960, Invertebrate paleontology: 701 p., illus., Harper & Bros., New York.

EHLERS, G.M., STUMM, E. C., & KESLING, R. V., 1951, Devonian Rocks of Southeastern Michigan and Northwestern Ohio. Prepared for the Stratigraphic Field Trip of the Geological Society of America, Detroit Meeting, November 1951: iv + 40 p., 3 figs., 5 pls., Ann Arbor: Edwards Bros., Inc.

FARRIS, J. S., 1967, The meaning of relationship and taxonomic procedure: Syst. Zoology, v. 16, no. 1, p. 44–51.

FENTON, C. L., & FENTON, M. A., 1958, The fossil book: 482 p., illus., Doubleday & Co., Garden City, N. Y.

HYMAN, L. H., 1955, Echinodermata, the coelomate Bilateria: The invertebrates, v. 4, vii + 763 p., 280 figs., McGraw-Hill Book Co., Inc., New York.

JAEKEL, OTTO, 1918, Phylogenie und System der Pelmatozoen: Paläontol. Zeitschr., v. 3, no. 1, p. 1–128, 114 text-figs.

KAESLER, ROGER, 1967, Numerical taxonomy in invertebrate paleontology: Univ. Kansas Dept. Geology Spec. Publ. 2 (Essays in Paleontology & Stratigraphy, Raymond C. Moore Commemorative Volume), p. 63–81.

LAUDON, L. R., 1936, Notes on the Devonian crinoid fauna of the Cedar Valley Formation of Iowa: Jour. Paleontology, v. 10, no. 1, p. 60–66, 15 figs.

MAGNUS, D. B. E., 1963, Der Federstern *Heterometra savignyi* im Roten Meer: Natur und Museum, v. 93, p. 355–368.

MOORE, R. C., 1962, Revision of Calceocrinidae: Univ. Kansas Paleontol. Contrib., Echinodermata, Art. 4, 40 p., 3 pls., 21 text-figs.

PRIM, R. C., 1957, Shortest connection networks and some generalizations: Bell System Tech. Jour., v. 36, no. 6, p. 1389–1401, 11 figs.

SARDESON, F. W., 1928, Derivation of the Calceocrinidae: Pan-American Geologist, v. 49, no. 1, p. 35–46, pl. 1.

SCHMIDT, W. E., 1934, Die Crinoideen des rheinischen Devons, Teil 1, Die Crinoideen des Hunsrückschiefers: Preuss. geol. Landesanst., Abh., N. F., v. 163, p. 1–149, pls. 1–34.

SNEATH, P. H. A., 1964, Introduction *in* HEYWOOD, V. H., & McNEILL, J., Phenetic and phylogenetic classification, II. Numerical taxonomy: Systematics Assoc., Publ. no. 6, p. 43–45.

SOKAL, R. R., & SNEATH, P. H. A., 1963, Principles of numerical taxonomy: xvi + 359 p., W. H. Freeman & Co., San Francisco.

SPRINGER, FRANK, 1926, American Silurian crinoids: Smithsonian Instit., Publ. 2871, iv + 239 p., 33 pls.

STRIMPLE, H. L., 1963, Crinoids of the Hunton Group (Devonian-Silurian) of Oklahoma: Okla. Geol. Survey Bull. 100, 169 p., 12 pls., 30 text-figs.

WAGNER, W. H., JR., 1954, The fern genus *Diellia*: Univ. Calif. Publ. Botany, v. 26, p. 1–167, pls. 1–21, 30 figs.

——— 1961, Problems in the classification of ferns: Recent Advances in Botany (IX Internat. Bot. Congress, Montreal, 1959), v. 1, sec. 9, p. 841–844.