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UPPER ORDOVICIAN XENOCRINIDS (CRINOIDEA,
CAMERATA) FROM SCOTLAND

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ABSTRACT

Two species of *Xenocrinus*, *X. multiramus* Ramsbottom and *X. breviformis* Brower, n. sp., are known from the Upper Ordovician of Scotland. The ontogeny of *X. multiramus* was studied statistically. Xenocrinids are found to be characterized by slow growth vectors for dimensions of the interbrachial plates relative to overall size of the calyx. Throughout ontogeny, the rays and interrays expand continuously, and this in conjunction with slow developmental vectors for the interbrachial plate dimensions requires the intercalation of new interbrachials between older ones. Consequently, adult xenocrinids have interbrachial areas consisting of numerous small irregular plates, and the areas occupied by them resemble the flexible plate-studded integuments of some living crinoids.

In other camerate crinoids with many fixed-brachials (e.g., glyptocrinids), the growth rates for dimensions of the interbrachials are large relative to size. All new glyptocrinid interbrachials developed at distal borders of the interbrachial areas, where fixed-brachials were incorporated into the calyx; new interbrachials were not intercalated between older plates. The resulting adult interbrachial areas are composed of a small number of large, regular, and rigidly joined plates. Several multivariate statistical techniques yield information about phylogeny. Xenocrinids were probably derived from *Proxenorcrinus*, a Lower Ordovician genus with relatively large and regular interprimibrachs. The numerous small and irregular interbrachials of xenocrinids are believed to comprise an advanced evolutionary character rather than a primitive feature as judged by some crinoid specialists.

INTRODUCTION

GENERAL STATEMENT

Xenocrinids are monocyclic camerate crinoids of Ordovician age. Their most striking characteristic is the small size, large number and irregularity in shape and arrangement of interbrachials. Other monocyclic camerates have large, less numerous, and more regular interbrachials.

Knowledge of Scottish xenocrinids dates back

to 1961 when Ramsbottom described *Xenocrinus multiramus* and an unidentified species which he thought referable to *Xenocrinus*. The latter crinoid cannot now be assigned to any genus. *X. multiramus* is represented by a growth sequence consisting of seven specimens which range from 5.0 to 19 mm in calyx height. This developmental sequence is the most complete known for any xenocrinid. A growth study is presented

here and development is compared with that of a glyptocrinid camerate.

Moore & Laudon (1943) in their important work on evolution of Paleozoic crinoids considered xenocrinids to be primitive forms based on two main characters. Firstly, they (*ibid.*, p. 76-101) followed previous workers, such as Wachsmuth & Springer (1897, p. 182), in interpreting *Xenocrinus* as having interbrachials (interprimibrachs) located between the radials in all interrays except *CD*. Examination of numerous American and Scottish specimens shows this to be incorrect. The radials of xenocrinids are generally in contact in the lateral interrays (includes all interrays except *CD*) as in tanaocrinids and periechocrinids. The second character consists of the numerous small and irregular interbrachials. The ontogeny of *X. multiramus* suggests that this is a specialized and advanced feature. Reevaluation of xenocrinid phylogeny indicates that these crinoids probably descended from *Proexenocrinus*, an Early Ordovician crinoid with a smaller number of larger and more regular interbrachials.

ACKNOWLEDGMENTS

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Most of my work on xenocrinids was completed while I was on academic leave from Syracuse University and provided with study facilities at the Royal Scottish Museum during 1969-70. I was graciously helped by Dr. Waterston and the staff of the Geology Department of the Museum.

The figures and photographs were prepared by John Fonda and John Merriam, both of Syracuse University.

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D. F. Merriam, of Syracuse University, and Dr. R. C. Moore of the Paleontological Institute at the University of Kansas critically read the manuscript and made suggestions for improvement. Special thanks are due to Dr. Reyment for much helpful discussion on the sampling properties of principal components extracted from correlation matrices.

Computer time was supplied by the Syracuse University Computing Center.

TERMINOLOGY AND MEASUREMENTS

Generally, the terminology follows that of Moore (1952, text-fig. 18-2). Most of the basic plate symbols and terminology are shown in Figure 1. The proximal plate of the camerate *CD* (posterior) interray is designated primanal, following Jaekel (1918, p. 28). Brachials rigidly incorporated into the dorsal cup are termed fixed-brachials.

The ray orientation system is that of Carpenter (1884, text-fig. 2). The *A* and *C* rays of Carpenter correspond, respectively, to the anterior and right-posterior rays of most authors. The interray areas are designated by the flanking rays; for example, the posterior interray which lies between the *C* and *D* rays is the *CD* interray. In this paper, the other interrays are not differentiated but are merely referred to as lateral interrays; the interrays included in this category are *AB*, *BC*, *AE*, and *DE*.

The camerate crinoids examined here have two to four free arms in each ray. Two-armed species show two half-rays; the area between these and the equivalent position in four-armed crinoids is termed an interhalf-ray, the calyx plates of which are intersecundibrachs. In four-armed taxa, two half-rays are present, each consisting of two free arms called quarter-rays. The space between two quarter-rays is designated the interquarter-ray and its plates are intertertibrachs. All plates located between the rays are interprimibrachs. These include interray plates occurring between the radials, primibrachs, secundi-brachs, etc. The collective term for undifferentiated interprimibrachs, intersecundibrachs, intertertibrachs, etc., is interbrachs.

The camerate plate sequence directly over-

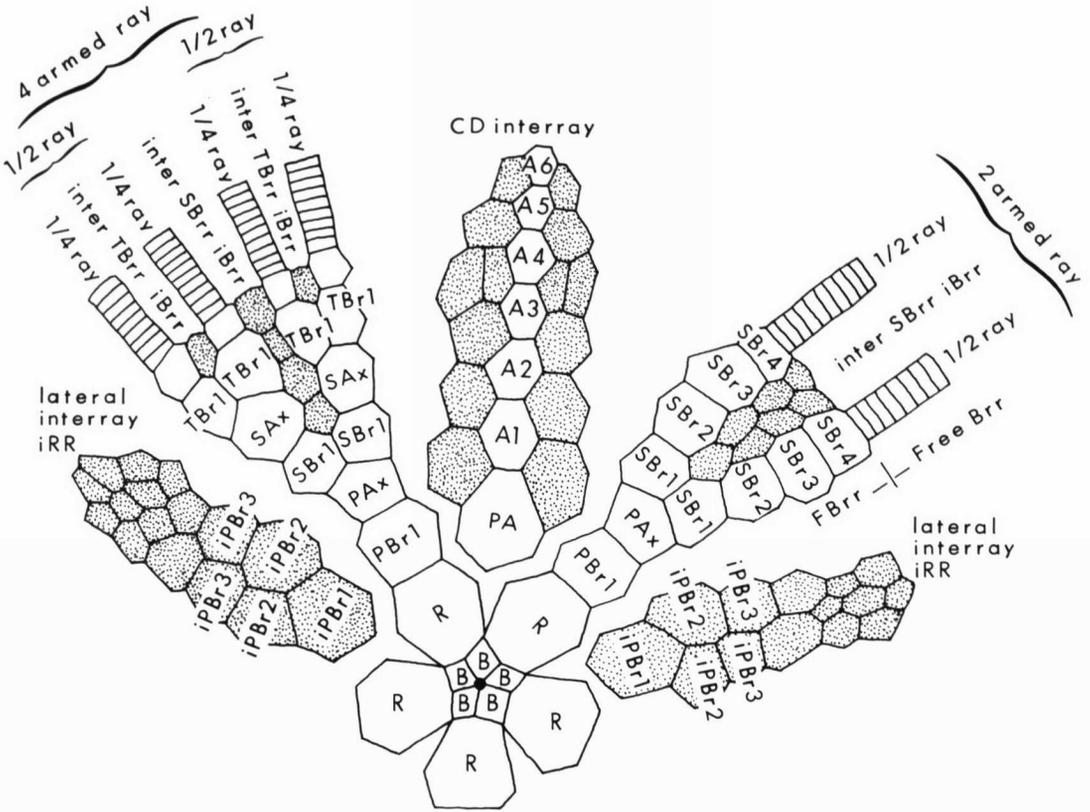


FIG. 1. Schematic sketch of glyptocrinid camerate crinoid showing the basic plate symbols.

Plate names and symbols for one and several plates are listed as follows: Basal, *B* (pl., *BB*); radial, *R* (pl., *RR*); first primibrach, *PBr1* (pl., *PBr1*); primaxil, *PAx* (pl., *PAxx*); secundibrach, *SBr* (pl., *SBr*), numbered 1 through *n* from proximal to distal; secundaxil, *SAX* (pl. *SAXx*); tertibrach, *TBr* (pl., *TBr*); primanal, *PA*; anal series plates, *A* (pl., *AA*), numbered from 1 through *n* from proximal to distal; interprimibrach, *iPBr* (pl.,

iPBr), numbered 1, 2 etc., from proximal to distal, all plates within single range receive the same number designation; intersecundibrach, *iSBr iBr*, (pl., *iSBr iBr*), numbering follows that of *iPBr*; intertertibrach, *iTBr iBr* (pl., *iTBr iBr*), numbering follows that of *iPBr*. Half-rays denoted by $\frac{1}{2}$ ray; quarter-rays by $\frac{1}{4}$ ray. All interbrachials are stippled. See text for discussion of terminology.

lying the primanal is the anal series (anitaxis), the elements of which are anal-series plates. From proximal to distal, the anal series plates are designated secundanals, tertanals, quartanals, etc. The anal series is generally separated from the *C* and *D* rays by *CD* interprimibrachs.

One of the major problems in relative-growth studies is determination of a standard relative-age parameter. For camerate crinoids, the most satisfactory measure is "size" which consists of height from the calyx base to the distal primaxil margin (full discussion in Brower, 1973). Throughout this paper, "size" refers to this

measurement whereas size, lacking quotation marks, denotes size in a general sense. It must be noted that the growth rate of "size" is not constant with respect to time. Living and fossil crinoids are characterized by slow-fast-slow time-size growth rates, *i.e.*, "size" growth with respect to time is slow in young and adult individuals, but juvenile animals show comparatively rapid developmental rates (Brower, 1973). Consequently, "size" measures only relative age, not absolute chronological age.

Heights of ray plates were measured along or parallel to the ray axis and the interray plates

were determined parallel to the interray axis. Width was taken at right angles to height and maximum values were used. For computation of regression lines, the fixed-brachials were coded in terms of the following numerical scale (Fig. 1): First secundibrach, proximal portion, 8.0, distal portion, 9.0; secundaxil, proximal part, 10.0, distal part, 11.0; first tertibrach proximal and distal portions, 12.0 and 13.0, etc. The standard calyx width (hereafter termed calyx width) includes one ray plus one lateral interray, measured at the primaxil midlevel of the adjacent rays. Calyx height ranges from the base of the calyx to the distal margin of a lateral interray area.

STATISTICAL METHODS

The basic growth data are derived from correlation and reduced major-axis regression. The reduced major axis (Imbrie, 1956; Hayami & Matsukuma, 1970) was selected because it is a descriptive equation where the slope estimate is not biased by choice of the independent and dependent variables. The analysis of variance in conjunction with regression indicates that the variables are linearly distributed with respect to one another and that logarithmic transformations are not required. The slopes yield the growth rates of the dependent variable *Y*, relative to unit increments of the independent variable *X*. The initial intercept is considered as a location parameter which reflects the early size of *Y* compared to *X*. In subsequent discussion, observed values of *X* in smallest and largest crinoids are treated along with the corresponding equation values of *Y*. Hopefully, this depicts the ontogeny of the average or normal crinoid. The utilized correlation coefficients are the Pearson product-moment (Sokal & Rohlf, 1969, chap. 15).

Principal components extracted from a correlation matrix serve to ascertain the relationships among the variables. Excellent general discussions of principal components are available in Morrison (1967, chap. 7) and Davis (1973, p. 152-168, 473-500). Inspection of the principal component coefficient matrix discloses the relations between the variables. Standardized principal component scores were calculated from *Z* scores for the original data times the principal component coefficients. The *Z* scores standardize each variable so that the mean equals zero and

the standard deviation is unity. Thus, given identical principal component coefficients, each variable will contribute equally to the principal component scores. These scores were back-checked with the original data to show the relations among the individuals within the ontogenetic sequence. This aids greatly in interpretation of the principal components. For examples of use of principal components in ontogeny studies, Jolicoeur & Mosimann (1960) and Jolicoeur (1963a, 1963b; also Morrison, 1967, chap. 7) should be consulted. The linear discriminant function clarifies the contrasts in growth patterns between xenocrinids and glyptocrinids (see Van de Geer, 1971, chap. 18; Morrison, 1967, chap. 4).

The relationships between xenocrinids and allied crinoids were determined by several numerical taxonomic methods (the calculations are discussed by Sokal & Sneath, 1963, appendix). The data matrix of numerical taxonomy treats the operational taxonomic units (OTU's) as variables and the characters as observations. In this situation all OTU's are species. Data are standardized by characters so that each contributes equally to the similarity coefficients. Two types of similarity coefficients (between species) were calculated: Pearson product-moment correlation coefficients and squared-distance coefficients. The related groups were extracted from the distance and correlation matrices by the average linkage cluster method. Principal components also were derived from the correlation matrix between the species. These conclusions were followed up using principal coordinate analysis, a technique which is annotated in detail by Gower (1966) and Blackith & Reyment (1971, p. 163-185). The similarity coefficients between the species are of the type proposed by Gower. The principal coordinates comprise the normalized eigenvectors or characteristic vectors extracted from the transformed similarity matrix (the reader should consult Davis, 1973, p. 152-163 or Morrison, 1967, p. 61-64, 221-258 for basic discussions of eigenvectors and the corresponding eigenvalues). The similarity matrix transformation is required to maximize the information conveyed in the first few eigenvectors. Plots of the eigenvector coefficients display the relationships between the species.

The character interrelationships during the evolutionary sequence were ascertained by direct

inspection of a correlation matrix between the variables. Principal components and cluster analysis were not attempted because many of the correlations are not significant and because the number of variables exceeds the number of observations (species). The latter effect leaves the correlation matrix incompletely defined because its maximum possible rank is less than the number of variables.

The following computer programs were used

(the program names are given in capital letters). Correlation and regression, a program written by me in the APL language; correlation matrix and principal components, BMDO1M and BMDO2D (Dixon, 1970, p. 49-59, 150-158); squared-distance coefficients and cluster analysis, HGROUP (Veldman, 1967, p. 308-319); discriminant analysis, BMDO7M (Dixon, 1970, p. 214a-t); principal coordinates, PCOORD (Blackith & Reyment, 1971, p. 171-185).

SYSTEMATIC DESCRIPTIONS

Subclass CAMERATA Wachsmuth & Springer, 1885

Order MONOBATHRIDA Moore & Laudon, 1943

[*nom. correct.* Ubaghs, 1953 (*pro* Monobathra Moore & Laudon, 1943)]

Suborder TANAOCRININA Moore, 1952

Superfamily XENOCRINACEA Ubaghs, 1953

[*nom. correct.* Ubaghs, 1973 (*pro* Xenocrinace Ubaghs, 1953)]

Family XENOCRINIDAE S. A. Miller, 1889a

Genus XENOCRINUS S. A. Miller, 1881a, p. 71

Type Species.—*X. penicillus* S. A. Miller, 1881a, p. 72, pl. 1, fig. 3a-c.

Diagnosis.—A primitive monocyclic camerate with primanal in the radial circlet; stem quadrangular, with pentagonal axial canal; basals four with sutures in *B*, *E*, *C*, and *D* rays; radials usually adjoining each other in all interrays except posterior; sutures between some adjacent radials covered by small supplementary plates; interbrachials composed of numerous small irregular plates in areas strongly depressed below adjacent rays and the anal series; rays with two, three, or four arms, branched half-rays usually having axillary fixed secundibrach 2; brachials uniserial or immature biserial with proximal and distal faces converging on each other and joining near pinnule facets (*i.e.*, brachials roughly cuneiform and interlocking).

Remarks.—Most recent diagnoses of *Xenocrinus* follow Wachsmuth & Springer (1897, p. 183) in stating that the radials are separated by

interprimibrachs in the lateral interrays (the term lateral interrays includes all interrays except *CD*). For example, Moore & Laudon (1943, p. 76-101) judged that this character has great taxonomic and evolutionary significance. Examination of numerous xenocrinid specimens at the United States National Museum shows that the radials usually join each other in the lateral interrays, instead of being separated by proximal interprimibrachs. In *X. penicillus* S. A. Miller, about 130 lateral interrays observed in roughly 50 crinoids studied show radials in contact except between the *C* and *D* rays. In many specimens, the radial margins bear small spines or nodes which Wachsmuth & Springer probably mistook for small spinose or nodose interprimibrachs. A few crinoids exhibit *AB*, *BC*, *AE*, and *DE* interrays where the sutures between the radials are covered by small spinose supplementary plates; however, these are external features which do not intervene between the radials. A similar condition is observed in *X. baeri* (Meek). Forty lateral interrays were tabulated, of which 39 had the radials in contact, whereas only one specimen had several small interprimibrachs separating the adjacent radials. The small spinose supplementary plates also are known in this species. Wachsmuth & Springer (1897, p. 183) noticed this to some extent because they stated:

"*Xenocrinus* is the only monocyclic genus in which interradians [interprimibrachs] come in contact with the basals at all sides, but we doubt if its interradians [interprimibrachs] separated the rays as completely as in the case of the Rhodocrinidae [Rhodocrinitidae]. In a specimen of *X. Baeri* from the collection of Mr. I. H. Harris (Plate IX, Fig. 5c), in which portions of the inner floor are exposed, it is plainly seen that the lower ends of adjoining radials touch

each other, and after a careful study of the structure we are inclined to believe that the small accessory pieces, which seem to separate the radials, rest upon the lower outer margins of the plates, and not between the plates."

Variation in the Scottish forms is discussed later.

Xenocrinids are most closely related to *Proxenoocrinus* Strimple & McGinnis (1972, p. 73), *Tanaocrinus* Wachsmuth & Springer (1897, p. 185), and *Compsocrinus* S. A. Miller (1883, p. 223). *Proxenoocrinus* occurs in the Lower Ordovician, and the other genera are Late Ordovician in age. All taxa are confined to North America except *Xenocrinus*, which also is known from the Upper Ordovician of Scotland. *Xenocrinus* may be separated from the other taxa cited by the following differences. 1) Quadrangular stems are found in xenocrinids and compsocrinids, but the other crinoids mentioned have round stems. 2) In *Xenocrinus*, the radials are usually in contact in the lateral interrays, although a few individuals show interprimibrachs between these plates. Small supplementary plates rest on top of the radial sutures in some specimens. The radials of compsocrinids and tanaocrinids are in contact except at the *CD* interray. Supplementary plates are not known. *Proxenoocrinus* is characterized by large first interprimibrachs intervening between the radials. 3) The interbrachial areas of *Xenocrinus* consist of numerous small plates which are depressed below the adjacent rays. Those of *Proxenoocrinus*, *Tanaocrinus*, and *Compsocrinus* are fewer in number, larger, more regular, and less depressed than in the other crinoids. 4) In *Tanaocrinus*, each half-ray branches two or three times. The first branch is located on secundibrachs 6 or 7, whereas the second branch, if present, is near tertibrach 20. *Proxenoocrinus* has only two unbranched arms in each ray. Xenocrinids and compsocrinids may have two, three, or four arms to a ray; secundibrach 2 generally comprises the axillary plate in branched half-rays. 5) The brachials of *Proxenoocrinus* are uniserial. Those of the related crinoids are either uniserial or immature biserial.

Occurrence.—Upper Ordovician, North America and Scotland.

XENOCRINUS MULTIRAMUS Ramsbottom

Plate 1; Plate 2, figures 2,3; Plate 3, figure 1; Figure 2,A-F

Xenocrinus multiramus Ramsbottom, 1961, p. 21, pl. 6, fig. 1-4.

Diagnosis.—A species of *Xenocrinus* characterized by four arms in each ray; calyx slender relative to its height; column weakly quadrangular.

Description of Adult.—Young specimens are described in the ontogeny section. Calyx conical; height/width ratio about 1.1; rays strongly convex and upraised; ray plates with slightly incised sutures; interrays depressed below adjacent rays; interbrachials nodose, with depressed sutures.

Basals 4; *CD* and *EB* basals are large and 6-sided; height/width ratio 1.1; small basals pentagonal. Radials also pentagonal, in contact in lateral interrays, interprimibrachs 1 separate the radials in one specimen; in *CD* interray, primanal separating the *C* and *D* radials; primibrachs 1 roughly equal to radials in size, with height/width ratio of 1.2. Primibrach 1 roughly rectangular with convex sides, height/width ratio 1.4. Primaxil pentagonal, distally supporting secundibrachs 2, height/width ratio 1.2. Half-rays typically composed of secundibrachs 1 and axillary 2. Secundibrach 1 roughly rectangular, height/width ratio 1.6. Secundibrach 2 pentagonal, height/width ratio 1.4. Tertibrachs 1 to 4 fixed into calyx; all nonpinnulate except for tertibrachs 4; width of all plates roughly constant but heights decreasing distally; tertibrach 1 height/width ratio 1.7; tertibrach 4 height/width ratio about 1.2.

Lateral interray interbrachial areas depressed compared to adjacent rays. All interbrachials small and irregular, much smaller than adjacent ray plates; average height/width ratio approximately 1.2. Total number of plates in one interray about 115; 40 to 55 plates are located below the secundibrach 1 level and the primaxil level ranges comprise roughly 7 plates. Interprimibrachs terminate at tertibrach 4 level.

Intersecundibrachial areas like those of the interprimibrachs; about 70 plates are present. Intertertibrachial areas contain approximately 35 plates. These interbrachial areas end at the tertibrach 4 level.

CD interray begins with primanal located between the *C* and *D* radials, resting on the *CD* interray basal; primanal followed by 3 plates of which the central one is an anal-series plate and the two flanking ones are *CD* interprimibrachs.

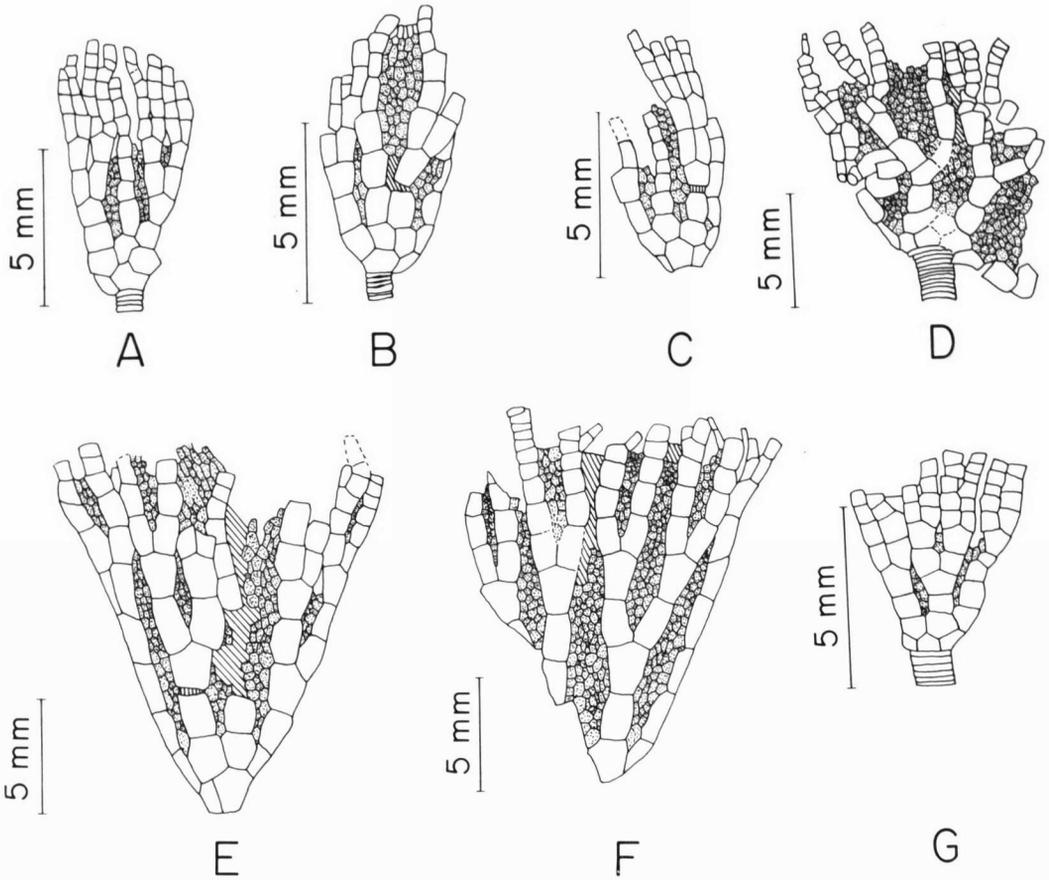


FIG. 2. *Xenocrinus* from Scotland. Interbrachials stippled; gapping sutures vertically ruled; outlines of damaged portions of crinoids oblique-ruled.

- A. *X. multiramus* Ramsbottom, figured specimen, (RSM 1970.40), "size" 3.2 mm, *CD* interray.
- B,C. *X. multiramus* Ramsbottom, paratype (BM E47329 a,b, counterparts), "size" 3.3 mm, *A* ray (a) and *CD* interray (b), respectively.
- D. *X. multiramus* Ramsbottom, paratype (BM E47320 b), "size" 3.8 mm, lat. view, note 3-armed ray in

- center and interprimibrachs separating the radials.
- E,F. *X. multiramus* Ramsbottom, holotype (BM E47328 a,b, counterparts), "size" ranges from 7.5 to 7.8 mm in different rays, *CD* interray (a) and *A* ray (b), respectively.
- G. *X. brevisformis* Brower, n. sp., holotype (HM E3526), "size" 2.3 mm, lat. view.

Anal series plates arranged in vertical unbranched sequence; these plates large, convex, usually higher than wide. *CD* interradiial areas depressed below the anal series; *CD* interbrachs similar to those in the lateral interrays, small, irregular and numerous; total number of plates and distal *CD* interbrachials unknown.

Tegmen partially known in one young specimen (BM E47329b), consisting of numerous small undifferentiated plates which are similar to the interbrachials.

Arms normally 4 in each ray, rarely 3, incompletely preserved, best known in BM E47320b, long and slender relative to calyx size. Mature brachials uniserial with strongly converging proximal and distal faces, average height/width ratio roughly 0.45; pinnule facets protuberant, moderately large. Proximal brachials become higher, more angular and less mature; proximal pinnule located on tertibrachs 2, 3, or 4, height/width ratio about 0.9; tertibrachs 1 nonpinnulate, height/width ratio 1.6. Pinnules slender, composed of 4 to 6 elongate pinnulars.

Stem quadrangular, with rounded edges and flat sides, best known in BM E47320b. Columnals wide, disc-shaped. Distal preserved portion of stem consists of 3 columnal orders; 1st order nodose with heights ranging from 0.28 to 0.23 mm; 2nd order also nodose with average height about 0.18 mm; 3rd order not invariably fully developed, slightly nodose, with heights ranging from 0.07 to 0.05 mm. Proxistele has only 2 orders; 1st order with heights ranging from 0.13 to 0.20 mm and 2nd with height averaging about 0.07 mm. Orders 1 and 2 columnals originated below the calyx, and subsequent calcite deposition increased the thickness of these plates; 3rd order formed by intercalation between the older plates. Distal part of dististele and holdfast not preserved.

Variation.—The number of arms can be determined in 8 rays, located on 7 specimens. Seven rays bear 4 arms and 1 ray has only 3. The mean comprises 3.9 arms with a 9.1 percentage standard deviation.

Examination of 14 rays distributed among the 7 specimens shows that all are characterized by the presence of two primibrachs. As in most crinoids, the ray structure becomes more variable distally. The number of secundibrachs was tabulated in 19 branched half-rays, which have an axillary secundibrach lacking in unbranched half-rays. Branched half-rays thus have two arms whereas unbranched ones only possess one arm. Of the 19 half-rays examined, 17 exhibit axillary secundibrachs 2, and the remaining 2 half-rays bifurcate on secundibrachs 1 or 3. The average half-ray has 2 plates with a 16.7 percentage standard deviation.

In describing *Xenocrinus multiramus*, Ramsbottom (1961, p. 22) noted that adjacent radials usually touch each other in the lateral interrays, whereas the radials of American species generally

are separated by the proximal interprimibrach. Ramsbottom suggested that xenocrinids were variable in this respect and that the taxonomic importance of this character had been exaggerated by Moore & Laudon (1943, p. 76-101). Twelve *X. multiramus* lateral interrays were examined and the radials in all but 3 of them were found to be in contact. The 3 interrays where the radials are separated by the proximal interprimibrach belong to the same specimen (BM E47320b). To express this variation on a more continuous scale, the radial mutual contact percentage [*i.e.*, (height of radial in contact with an adjacent radial) \times 100 \div (total radial height along its outer margin)] was calculated. If the proximal interprimibrach separates the adjacent radials, these are not in contact and the contact percent is nil. A high percentage denotes radials that are nearly in full contact. The *X. multiramus* radial contact percentages range from zero to 94% with a 60% mean. The percentage standard deviation consists of 63% which clearly indicates wide variation in this character.

Comparison.—*Xenocrinus multiramus* Ramsbottom is characterized by 4 arms in each ray. This separates the Scottish form from the American species, both of which have only 2 arms to a ray; these comprise: *X. baeri* (Meek, see 1873, p. 37, pl. 2, fig. 1a,b) (S. A. Miller, 1880, p. 234, pl. 7, fig. 4; Wachsmuth & Springer, 1897, p. 185, pl. 9, fig. 5a-d) and *X. penicillus* S. A. Miller (1881a, p. 72, pl. 1, fig. 3, 3a-c; 1889, p. 287, fig. 444; Wachsmuth & Springer, 1897, p. 183, pl. 9, fig. 6a,b). In addition, *X. baeri* shows a relatively wider calyx and a more strongly quadrangular stem. The *X. multiramus* stem is less angular than that of *X. penicillus*.

Proxenoocrinus Strimple & McGinnis (1972, p. 72) has only 2 arms in each ray rather than 4

EXPLANATION OF PLATE 1

Xenocrinus multiramus Ramsbottom

All figures are of rubber casts which were whitened with ammonium chloride.

FIGURE

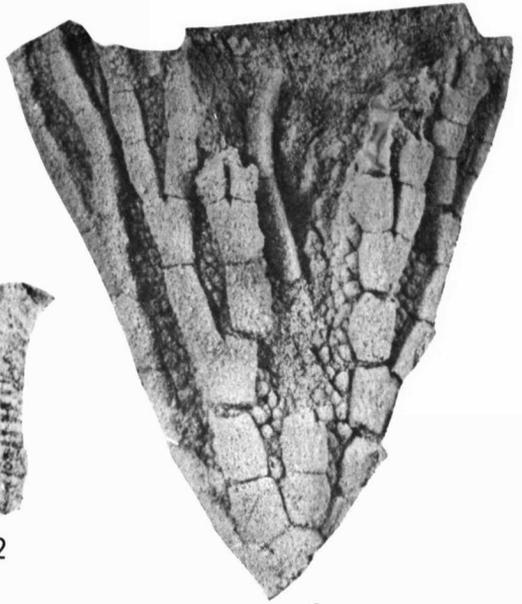
- 1-3. Holotype (BM E47328a,b, counterparts), largest specimen, "size" ranging from 7.5 to 7.8 mm.—1. A-ray view of BM E47328b, $\times 4.7$.—2. Stem segment (BM E47328a), $\times 5$.—3. CD-interray view of BM E47328a, $\times 4.7$.
4. Paratype, lat. view of crown (BM E47320b), "size" 3.8 mm, note 3-armed ray and interprimibrachs separating the radials, $\times 3.3$.
5. Paratype, lat. view of crushed young specimen (BM E47321b), "size" 3.0 mm, $\times 6.7$.



1



2



3



4



5

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Paper 67, Plate 2

Brower—Upper Ordovician Xenocrinids



3



2



1

as in *X. multiramus*. The proexenocrinid interbrachials are larger, more regular, and fewer in number. Seemingly, *Proexenocrinus* exhibits a round column, in contrast to the 4-sided stem of xenocrinids.

Material.—Holotype, BM E47328a,b (counterparts). Paratypes, BM E47329a,b, E47320a,b, E47321a,b. Figured specimen, RSM 1970.40.

Occurrence.—Upper Ordovician, Ashgill; Upper Drummuck Group; Thraive Glen, about 5 miles northeast of Girvan, Ayrshire, Scotland.

XENOCRINUS BREVIFORMIS Brower, new species

Plate 2, figure 1; Figure 2,G

Diagnosis.—A species of *Xenocrinus* with 4 arms in each ray; calyx relatively wide and small compared to total crown size; column facet wide; column facet and stem strongly quadrangular.

Description.—Known only from the holotype, "size" 2.3 mm. Calyx slightly higher than wide with broad base; height/width ratio 1.2; rays strongly convex and upraised, wider than interrays; ray plates with smooth or slightly impressed sutures; all interbrachial areas narrow and depressed below adjacent rays; all interbrachials small, nodose, with impressed sutures.

Basals presumably 4; only small ones known, pentagonal, height/width ratio about 0.9. Radials basically pentagonal, all observed ones in lateral contact with the others, radials and primaxils largest ray plates, height/width ratio of radials 0.9. Primibrachs 1 approximately rectangular, smaller than radials and primaxils, height/width ratio approximately 0.7. Primaxils pentagonal with height/width ratio of 0.7, primaxils bearing 2 secundibrachs. Secundibrachs 1 large, nonpinnulate, rough 6-sided, equidimensional. Secundibrachs 2 large, pentagonal, nearly equidimensional, forming highest fixed-brachial.

Lateral interrachial areas narrow, constricted and depressed below adjacent ray plates. All in-

terprimibrachs much smaller than adjacent ray plates, with irregular shapes. Total number of interprimibrachs uncertain although about 9 plates occur below the level of secundibrachs 2; primaxil level range consists of 2 or 3 plates; interprimibrachs terminating at the secundibrach 2 level.

Intersecundibrachial areas narrow and depressed, composed of small irregular plates. A total of 3 plates in a single area is known, ending at the secundibrach 2 level.

CD interray and tegmen unknown.

Arms 4 in each ray, not completely preserved, long and heavy relative to calyx size. Mature brachials uniserial with gently converging proximal and distal faces, average height/width ratio about 0.3; pinnule facets small, protuberant. Proximal brachials become higher, more angular, and less mature; tertibrach 2 is most proximal pinnulate brachial, height/width ratio around 0.8; secundibrach 1 nonpinnulate, generally equidimensional. Pinnules slender, incompletely preserved.

Stem quadrangular, with prominent thickened edges, areas between the edges are slightly concave. Columnals wider than high. Dististele bearing 3 columnal orders; 1st order nodose with heights ranging from 0.23 to 0.27 mm; 2nd order also nodose, with height about 0.17 mm; 3rd order not nodose; with height of 0.07 to 0.10 mm; all three orders completely developed in dististele. Proxistele only shows 1 or 2 columnal types which correspond to the 1st and 2nd orders of the dististele; order 3 is absent. The 3rd order columnals must have originated by intercalation between older plates; 1st order formed immediately below the calyx; 2nd order may have developed in either or both ways. Distalmost part of stem and holdfast unknown.

Remarks.—This species is based on one small crown, "size," 2.3 mm, with part of the column

EXPLANATION OF PLATE 2

Xenocrinus

All figures are of rubber casts which were whitened with ammonium chloride.

FIGURE

1. *Xenocrinus breviformis* Brower, n. sp., holotype (HM E3526), "size" 2.3 mm, lat. view, $\times 4.4$.
- 2,3. *Xenocrinus multiramus* Ramsbottom, paratype (BM

E47329a,b, counterparts), "size" 3.3 mm, young specimen, $\times 9.8$.—2. A-ray view of BM E47329b.
—3. CD-interray view of BM E47329a.

preserved. *Xenocrinus breviformis* Brower, n. sp., is most similar to *X. multiramus* Ramsbottom which also has 4 arms to a ray. The new species is easily separated from young *X. multiramus* of about the same "size" by several characters. First, *X. breviformis* has a more quadrangular column. Secondly, the calyx is much wider compared to its height or "size." This is mainly due to the relatively wide radials, primibrachs, and primaxils. The shapes of the interbrachials are similar in both taxa.

Xenocrinus breviformis differs from the American species *X. penicillus* S. A. Miller and *X. baeri* (Meek) in having 4 rather than 2 arms in each ray. In addition, *X. breviformis* has a wider calyx than *X. penicillus* and the ornamentation of the interbrachials contrasts greatly.

The specific name *breviformis* alludes to the relatively short and wide dorsal cup.

Measurements.—"Size," 2.3 mm; calyx height, 3.2 mm; width of one ray and interray at primaxil level, 1.2 mm.

Holotype.—HM E3526.

Occurrence.—Upper Ordovician, Ashgill; Upper Drummuck Group; Thraive Glen, about 5 miles northeast of Girvan, Ayrshire, Scotland.

UNCLASSIFIED CAMERATE CRINOID

Plate 3, figures 2, 3

Xenocrinus sp. Ramsbottom, 1961, p. 22.

Remarks.—In 1961, Ramsbottom mentioned a poorly preserved crinoid which he believed to be a xenocrinid with 2 arms to the ray. I examined this specimen (BM E47312a,b, counterparts) and one other conspecific crinoid (HM E3580a,b). The calyx plate structure cannot be determined, but the pattern of median-ray ridges suggests a dicyclic rather than a monocyclic base. Otherwise, since the calyx structure is unknown, no generic assignment can be made based on the available material.

Occurrence.—Upper Ordovician, Ashgill; Upper Drummuck Group; Thraive Glen, about 5 miles northeast of Girvan, Ayrshire, Scotland.

ONTOGENY OF XENOCRINUS MULTIRAMUS

The geometry of a xenocrinid calyx is basically similar to the glyptocrinid type except for the various interbrachial areas. In glyptocrinids, the interbrachials are generally large and regular. When the animal was alive, these plates probably were joined together rigidly. The xenocrinid interbrachials are small and irregular, and their areas closely resemble the tegmens of some flexible and modern crinoids. Such tegmens consist of perisome studded with numerous tiny plates. Presumably, the structures were somewhat flexible during life of the animal. The morphology of the xenocrinid interbrachials strongly suggests flexible, plate-studded integuments rather than rigidly joined walls of plates.

The only known xenocrinid growth sequence is *Xenocrinus multiramus* which is based on 5 specimens ranging from 3.0 to 7.8 mm in "size" (Pl. 1; Pl. 2, fig. 2,3; Pl. 3, fig. 1; Fig. 2,A-F). Seven data sets are available because 2 specimens yielded measurements from both part and counterpart. For comparative purposes, a growth sequence of *Glyptocrinus dyeri* Meek, consisting of 8 individuals varying from 2.3 to 10.2 mm in "size", was studied; these crinoids were figured

by Wachsmuth & Springer (1897, pl. 20, fig. 1a, b; pl. 21, fig. 3a-f, 6; Fig. 3 of this paper). Graphs are presented in Figure 4, and equation data are listed in Tables 1 and 2.

Young specimens of both taxa have the first or second secundibrachs fixed into the calyx. New fixed-brachials formed throughout ontogeny at rapid incorporation rates (see equation 3 in Tables 1, 2). Fixation of these plates was most rapid in *Glyptocrinus dyeri*, 2.9 numerical scale fixed-brachials per 1 mm "size" increment versus a 1.8 fixed-brachial rate in the xenocrinid (Fig. 4,A,B). Prior to their incorporation in the calyx, the brachials were typical free-arm plates. During fixation, the potential fixed-brachials developed angular lateral margins by accelerating their growth vectors for mid-level width. Once joined to the calyx, their growth became integrated and coordinated with that of the neighboring plates. After incorporation, the plate was bounded on all sides by other calyx plates, and the number of its sides remained constant throughout subsequent growth. Fixed pinnulars originated in the same fashion as fixed-brachials. Some fixed pinnules retained their identity (*e.g.*,

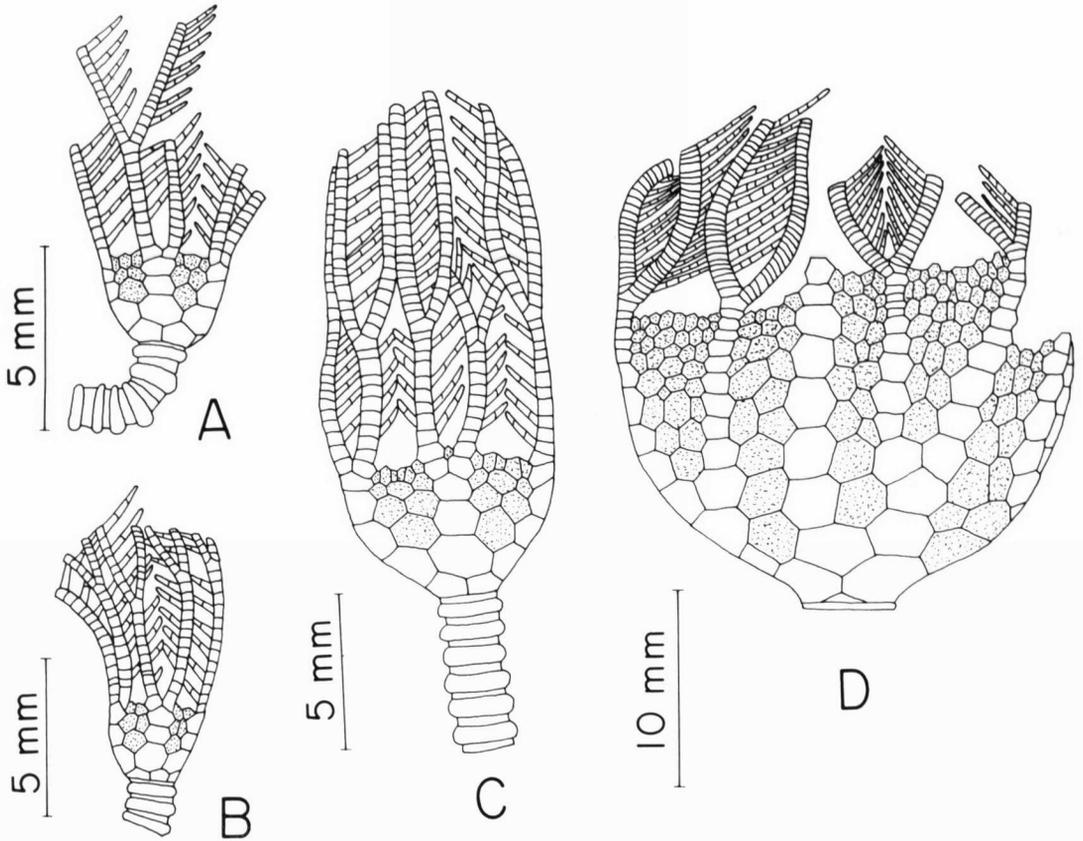


FIG. 3. Growth sequence in *Glyptocrinus dyeri* Meek, Upper Ordovician, Richmond, Cincinnati, Ohio, North America.

Various names have been applied to this species including *Glyptocrinus dyeri* Meek, *G. shafferi* S. A. Miller, and *G. shafferi* var. *germanus* S. A. Miller. Statistical study confirms the conclusions of Wachsmuth & Springer (1897, p. 271-273, pl. 20, fig. 1a-c; pl. 21, fig. 3a-f, 6) that these crinoids are simply growth variants of a single species. The name *G. dyeri* has nomenclatural priority. Other possible synonyms of *G. dyeri* are *G. subglobosus* Meek, *G. richardsoni* Wetherby, and *G. dyeri* var. *sublaevis* S. A. Miller but these have not been investigated statistically. [Interbrachials stippled.]

the large pinnule on secundibrach 2 of *G. dyeri*), but others lost their identity and became submerged in interbrachials. The origin of the fixing interbrachials was not studied because the tegmens are unknown in these species. One possibility is that the plates represent old tegmental interambulacra. Alternatively, the fixing interbrachials might constitute new plates that were intercalated between the tegmen periphery

- A. Type specimen of *G. shafferi* S. A. Miller, "size" 2.4 mm, lat. view.
- B. Type specimen of *G. shafferi* var. *germanus* S. A. Miller, (USNM 40767), "size" 2.45 mm, lat. view.
- C. Specimen of *G. dyeri*? illustrated by Wachsmuth & Springer (1897, pl. 21, fig. 3f), (USNM S60), "size" 3.95 mm, lat. view.
- D. Specimen of *G. dyeri* figured by Wachsmuth & Springer (1897, pl. 20, fig. 1b), (USNM S167), "size" 9.4 mm, CD interray view.

and the most distal interbrachials. At any rate, mature glyptocrinids have secundibrach 15 as the most distal fixed-brachial whereas xenocrinids are characterized by the presence of tertibrachs 4 (secundibrachs 2 being axillary).

The ontogeny of calyx width contrasts greatly between the two crinoids discussed (Tables 1, 2, equation 1). The different calyx shapes of the two crinoids is only a species-level character

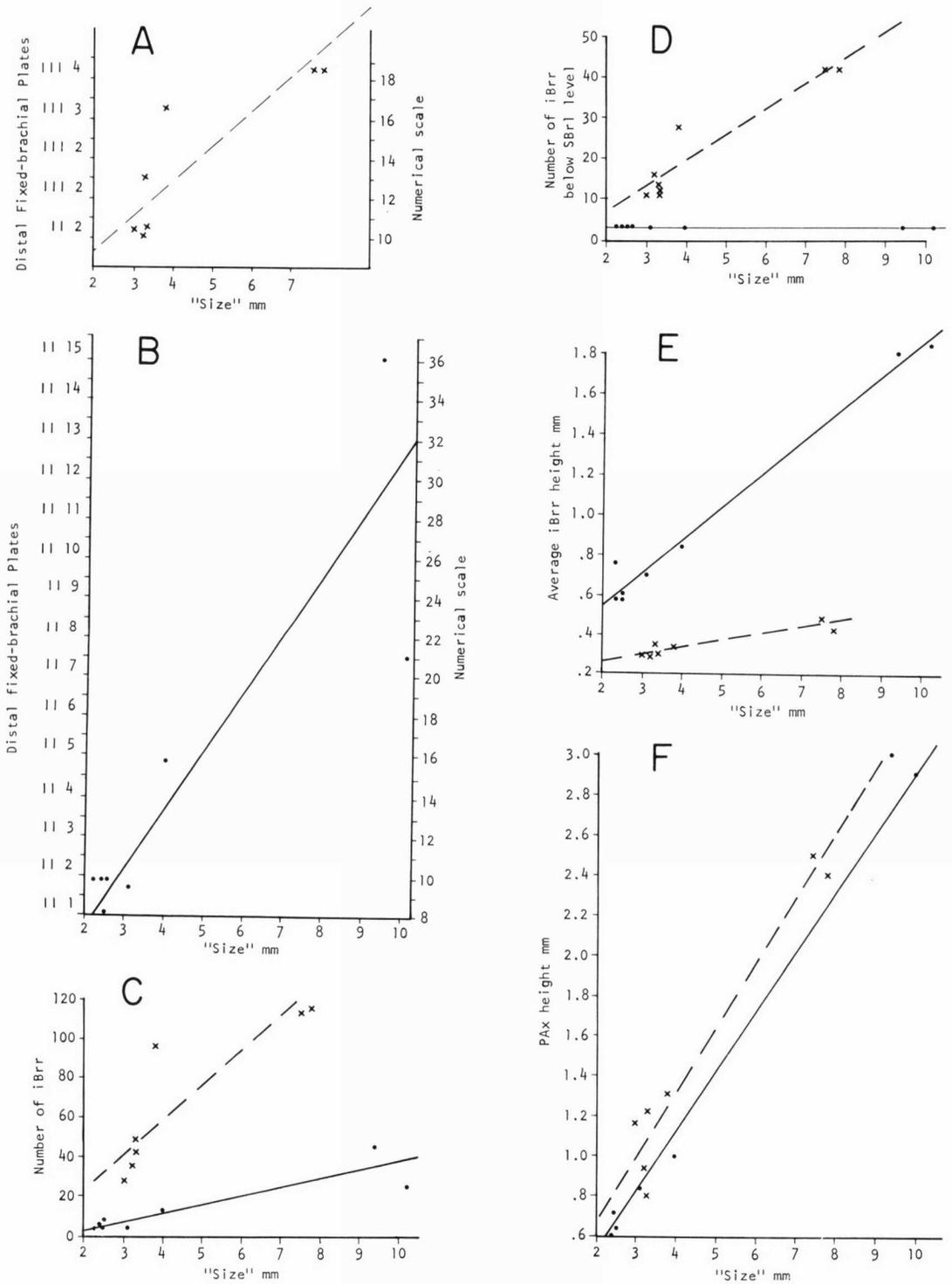


FIG. 4. Graphs showing growth of *Xenocrinus multiramus* Ramsbottom and *Glyptocrinus dyeri* Meek. Xenocrinid regression lines dashed, those of glyptocrinids solid. Xenocrinid data points are x's; those for glyptocrinids are solid dots.

TABLE 1. Equation data for *Xenocrinus multiramus* Ramsbottom.

Equation number	Independent variable X	Dependent variable Y	Initial			Y eqn.		Y eqn.
			Slope	intercept	X min.	min.	X max.	max.
1	"Size"	Calyx width	0.39	0.75	3.00	1.90	7.80	3.80
2	"Size"	Calyx height	2.97	-4.20	3.00	4.70	7.80	19.00
3	"Size"	Fixed-brachials	1.80	5.70	3.00	11.10	7.80	19.80
4	"Size"	Number of iPBrr across at PAX level	0.95	0.48	3.00	3.30	7.80	7.90
5	"Size"	Number of iPBrr below SBr2	6.54	-6.40	3.00	13.20	7.80	44.60
6	"Size"	Total number of iPBrr	17.90	-13.80	3.00	39.80	7.80	126.00
7	"Size"	Height of average iBrr	0.04	0.19	3.00	0.30	7.80	0.50
8	"Size"	Width of average iBrr	0.03	0.21	3.00	0.29	7.80	0.40
9	"Size"	Height of iPBrI	0.15	-0.10	3.00	0.37	7.80	1.10
10	"Size"	Width of iPBrI	0.11	0.01	3.00	0.33	7.80	0.85
11	"Size"	Height of PAX	0.32	0.00	3.00	0.97	7.80	2.50
12	"Size"	Width of PAX	0.26	0.02	3.00	0.81	7.80	2.10
13	"Size"	Height of PBrI	0.27	0.10	3.00	0.91	7.80	2.20
14	"Size"	Width of PBrI	0.19	0.09	3.00	0.67	7.80	1.60
15	"Size"	Height of R	0.29	-0.10	3.00	0.78	7.80	2.20
16	"Size"	Width of R	0.22	0.26	3.00	0.93	7.80	2.00
17	"Size"	Height of B	0.29	-0.19	3.00	0.67	7.80	2.00
18	"Size"	Width of B	0.21	0.39	3.00	1.00	7.80	2.10
19	Height of average iBrr	Width of average iBrr	0.70	0.08	0.28	0.27	0.49	0.42
20	Height of iPBrI	Width of iPBrI	0.69	0.08	0.33	0.31	1.30	0.96
21	Height of PAX	Width of PAX	0.81	0.02	0.80	0.67	2.50	2.00
22	Height of PBrI	Width of PBrI	0.72	0.02	0.85	0.63	2.20	1.60
23	Height of R	Width of R	0.76	0.34	0.82	0.96	2.20	2.00
24	Height of B	Width of B	0.75	0.53	0.67	1.00	2.00	2.00

See Fig. 1 for morphological term abbreviations.

which is not basic to the taxonomy of camerate crinoids with many fixed-brachials. Young individuals of both forms possess grossly similar outlines, although the glyptocrinids tend to be wider relative to "size" or calyx height. Further divergence occurred throughout subsequent development because the glyptocrinid exhibited a relatively high growth vector (slope) for calyx width of 0.99 mm per 1 mm "size" increment but that of *X. multiramus* was only 0.39 mm. Consequently, adult specimens of *G. dyeri* are globose, whereas mature xenocrinids are comparatively slender and graceful.

The differential ontogenetic patterns of calyx width were produced by development of the component plates. Again, the plates of young crinoids show similar shapes, although the glyptocrinids have somewhat wider plates. The differential plate shapes were maintained during subsequent development because the growth vectors for width relative to 1 mm "size" and 1 mm plate-height increments in *G. dyeri* were larger than those of the xenocrinid (see data for the basals, radials, primibrachs, primaxils, and first interprimibrachs in equations 10, 12, 14, 16, 18, 20-24, Tables 1,2). The contrasts in growth rates

are smallest for the width of basals. Compared to "size," juvenile crinoids exhibit large and wide basal circlets. However, mature glyptocrinids formed a relatively narrow, constricted base in comparison to xenocrinids which retained a wide, firm base with respect to "size."

The height of the calyx grew rapidly and the height developmental vectors (slopes) comprised 2.3 and 3.0 mm per 1 mm "size" increment in the glyptocrinid and xenocrinid, respectively (Tables 1, 2, equation 2). These vectors represent the fixed-brachial fixation rates, their shapes when incorporated in the calyx, and the subsequent height ontogeny of all plates joined to the calyx. *X. multiramus* shows relatively slow fixed-brachial fixation rates involving high and angular plates. Conversely, the glyptocrinid fixed-brachials are comparatively short but numerous brachials were incorporated in the calyx during ontogeny. The result was a slightly slower development vector of calyx height in *G. dyeri*.

Ontogeny of the heights of the basals, radials, primibrachs, and primaxils relative to "size" follows the same general pattern in both crinoids. This pattern also characterizes most camerate crinoids with many fixed-brachials. In the small-

TABLE 2. Equation data for *Glyptocrinus dyeri* Meek.

Equation number	Independent variable X	Dependent variable Y	Initial			Y eqn.		Y eqn. max.
			Slope	intercept	X min.	min.	X max.	
1	"Size"	Calyx width	0.99	-0.81	2.30	1.50	10.2	9.3
2	"Size"	Calyx height	2.30	-2.98	2.30	2.30	10.2	20.5
3	"Size"	Fixed-brachials	2.92	1.86	2.30	8.60	10.2	31.7
4	"Size"	Number of iPBr across at PAx level	0.00	2.00	2.30	2.00	10.2	2.0
5	"Size"	Number of iPBr below SBrI level	0.00	3.00	2.30	3.00	10.2	3.0
6	"Size"	Total number of iPBr	4.32	-5.59	2.30	4.40	10.2	38.5
7	"Size"	Height of average iBr	0.16	0.22	2.30	0.60	10.2	1.9
8	"Size"	Width of average iBr	0.15	0.07	2.30	0.41	10.2	1.6
9	"Size"	Height of iPBrI	0.34	-0.05	2.30	0.72	10.2	3.4
10	"Size"	Width of iPBrI	0.40	-0.32	2.30	0.62	10.2	3.8
11	"Size"	Height of PAx	0.32	-0.14	2.30	0.59	10.2	3.1
12	"Size"	Width of PAx	0.32	0.17	2.30	0.91	10.2	3.5
13	"Size"	Height of PBrI	0.31	-0.18	2.30	0.52	10.2	3.0
14	"Size"	Width of PBrI	0.35	0.17	2.30	0.97	10.2	3.7
15	"Size"	Height of R	0.36	0.03	2.30	0.86	10.2	3.7
16	"Size"	Width of R	0.36	0.29	2.30	1.20	10.2	4.0
17	"Size"	Height of B	0.09	0.35	2.30	0.55	10.2	1.2
18	"Size"	Width of B	0.18	0.51	2.30	0.92	10.2	2.3
19	Height of average iBr	Width of average iBr	0.92	-0.14	0.58	0.40	1.8	1.6
20	Height of iPBrI	Width of iPBrI	1.20	-0.25	0.78	0.69	3.4	3.8
21	Height of PAx	Width of PAx	1.00	0.31	0.59	0.91	3.0	3.4
22	Height of PBrI	Width of PBrI	1.10	0.37	0.48	0.92	2.8	3.6
23	Height of R	Width of R	1.00	0.26	0.83	1.10	3.6	3.9
24	Height of B	Width of B	2.00	-0.18	0.38	0.58	1.2	2.2

See Fig. 1 for morphological term abbreviations.

est glyptocrinids, radials are the largest ray plates; the percentage height contributions to "size" equal: Radials, 37%; primibrachs, 23%; primaxils, 26%. The youngest xenocrinid plates exhibit roughly equal percentage heights with respect to "size": Radials, 26%; primibrachs, 30%; primaxils, 32%. Adults of the two forms tended to retain the same ray plate geometry seen in the youngsters; for example, the *X. multiramus* figures consist of: Radials, 28%; primibrachs, 28%; primaxils, 32%. This was clearly dictated by the ontogeny of the component plates relative to "size" (Tables 1,2, equations 11, 13, 15). All plates have comparable growth rates relative to "size" and the smallest observed plate heights. The growth rates for plate height per 1 mm of

additional "size" range from 0.27 to 0.32 mm in the xenocrinid and 0.31 to 0.36 mm in the glyptocrinid. The height of the glyptocrinid basals became progressively smaller relative to "size" but the *X. multiramus* basals retained nearly the same proportions throughout development. This reflects the low glyptocrinid growth rate for basal height of 0.088 mm per 1 mm "size" increment compared with the higher rate of 0.29 mm for xenocrinids.

The most important growth contrasts between the two species are observed in the interbrachials. New plates of this category were formed throughout ontogeny of both taxa but the interbrachial "formation" rates of the xenocrinid were much higher than those of *G. dyeri*. For example, the

EXPLANATION OF PLATE 3

Xenocrinus and unclassified camerate

All figures are of rubber casts which were whitened with ammonium chloride.

FIGURE

1. *Xenocrinus multiramus* Ramsbottom, figured specimen (RSM 1970.40), "size" 3.2 mm, CD-interray view of poorly preserved young individual, $\times 9.4$.
- 2,3. Unclassified camerate crinoid.—2. Specimen cited

- by Ramsbottom (1961, p. 22) as *Xenocrinus* sp. (BM E47312a), "size" 6.3 mm, lat. view, $\times 2.9$ —
3. Figured specimen (HM E3580b), "size" 6.2 mm, CD-interray view, $\times 4.1$.



interprimibrach "formation" rates are 18 new plates per 1 mm increment of "size" versus 4.3 new plates (Tables 1, 2, equation 6; Fig. 4,C). In glyptocrinids, the number of interbrachials was stabilized at any given level after these joined the fixed brachials in the calyx. For example, the number of interprimibrachs in one lateral interray range at the primaxil level equals two plates, and the number of interprimibrachs below the secundibrach 1 level is three regardless of "size" and age (Table 2, equations 4, 5; Fig. 4,D). This denotes that once formed, "new" interbrachials were not intercalated between older plates.

Conversely, xenocrinids intercalated new interbrachials between the older ones during development. The youngest animals have about 3 interprimibrachs in a range at the primaxil level, whereas adult crinoids show about 7 plates (Table 1, equation 4). The smallest xenocrinids possess 12 to 16 interprimibrachs and the largest one has 42 such plates below the secundibrach 1 level of a single lateral interray. The other interbrachial areas show the same pattern. Within the observed growth sequence, about 75% of the new plates must have been added by intercalation between previously developed plates (Table 1, equation 3; Fig. 4,D).

The contrasts in interbrachial ontogeny are reflected by morphology of the adult crinoids. *Glyptocrinus dyeri* bears relatively uniform-sized interbrachials at any given calyx level (Fig. 3,D). For example, in a 10.2 mm-"sized" crinoid, the average percentage standard deviation for interprimibrach height and width is only 25% at the level of secundibrach 4. More interprimibrach size and shape variability is observed in xenocrinids. The distribution of interbrachial sizes at any one level is usually bimodal, smaller plates being intercalated more or less late in ontogeny, whereas larger ones are previously formed plates. This is reflected by the *X. multiramus* 40% average percentage standard deviation for interprimibrach height and width at the secundibrach 2 level of the largest crinoid.

The presence of interbrachial intercalation in xenocrinids and lack of it in glyptocrinids seems clearly to reflect differences in the developmental rates of interbrachial height and width relative to "size" and in comparison to these rates in the nearby ray plates and basals. The interrays of both forms expanded in height and width

throughout ontogeny. In *Glyptocrinus dyeri*, the average growth rates for interprimibrachs consisted of 0.16 mm (height) and 0.15 mm (width) per 1 mm "size" increment (Table 2, equations 7,8; Fig. 4,E). The growth vector for the interprimibrach height relative to "size" equals about 50% of that for the primaxil among the adjacent ray plates (Table 2, equation 11; Fig. 4,F). Due to the comparatively large growth rates of interbrachial size, intercalation of new ones was unnecessary.

The xenocrinid developmental vectors for interprimibrach size are only 0.036 mm of height and 0.025 mm of width per 1 mm "size" increment (Table 1, equations 7,8; Fig. 4,E). The growth rate for the interprimibrach height relative to "size" is only about 11% of that for the adjacent primibrachs (Table 1, equation 11; Fig. 2,F). These slow developmental rates required the intercalation of new plates, for otherwise gaps would have been left between the interbrachials as interrays expanded during ontogeny.

The linear discriminant function which best separates the two discussed species was calculated along with discriminant function scores for all crinoids. Determination of correlation coefficients between the original variables and the discriminant function scores shows that the number of fixed brachials and all interbrachial measurements, height, width, and number of plates at various levels, best differentiate the two taxa. The fixed-brachial contrast is probably only a species character, but the interbrachial measurements reflect fundamentally different developmental patterns of the two calyx types.

When the basals, radials, and orals first develop in a young Recent crinoid, they are isolated from one another. The plates of a single circlet are commonly somewhat irregularly arranged, and individual plates show wide variation in size and shape (see basals and orals in *Antedon bifida* illustrated by A. H. Clark, 1921, fig. 1181, 1189). This suggests that the growth of a given plate is poorly coordinated and integrated with other plates in the same or adjacent circlets during this stage.

Calcite accretion eventually brings all of the adjacent, subjacent, and superjacent plates together. For example, in *Comactina meridionalis*, the major calyx plates are mostly joined together when the proximal secundibrachs appear (Spring-

er, 1920, pl. B,C). Presumably, camerates developed in the same general fashion. These earliest growth stages are not preserved, and the youngest known camerates have all calyx plates and brachials in lateral contact. Once the plate lateral margins joined, plate growth became better coordinated and integrated.

At this time, the camerate calyx was composed of a series of adjacent plates which enclosed the viscera; "holes" were located at strategic points where food grooves entered the tegmen, where axial nerve cords penetrated the stem, and where the anus opened. Growth of individual plates must have been adjusted so that this configuration was maintained; otherwise, gaps would have developed between adjacent plates and the skeleton would no longer have supported soft tissues. Thus in the absence of resorption, if one plate increased in size, its neighbors must have done the same. Growth gradients were complex and probably changed in time. Nevertheless, the geometric requirements necessary to prevent the occurrence of gaps between adjacent plates provide an approach to studies of growth. A correlation matrix provides information on the degree of integration and coordination between adjacent, subjacent and superjacent plates necessary to have retained the surfaces of the plates in apposition to each other (Macurda, 1968).

The ranges of correlation coefficients involving the fixed-brachials, first interprimibrachs, average interbrachials, and all other parameters such as "size," calyx height, radial height, etc., are indicated in Table 3. The correlations are typically high, and most coefficients exceed the 0.05 probability-level values. This denotes a generally high level of integration and coordination of calyx development in both taxa. The correlation coefficient ranges also illustrate the different interbrachial development patterns of the two crinoids. In *Glyptocrinus dyeri*, all interbrachial correlations are close to the same as for other parameters. This denotes a uniform amount of developmental correlation for all calyx plates, including ray plates, basals, fixed-brachials, and interbrachials. In turn, this can be related to the lack of interbrachial intercalation and the large growth vectors for interbrachial dimensions with respect to "size." The *Xenocrinus multiramus* relationships are very different. The interbrachial correlation coefficients range distinctly lower than

TABLE 3. Correlation coefficient ranges for *Xenocrinus multiramus* Ramsbottom and *Glyptocrinus dyeri* Meek.

	<i>Xenocrinus multiramus</i>	<i>Glyptocrinus dyeri</i>
Correlations involving fixed-brachials	0.98 - 0.82	0.994 - 0.81
Correlations involving number of interbrachials	0.99 - 0.68	0.994 - 0.81
Correlations involving first interprimibrach	0.97 - 0.38	0.999 - 0.83
Correlations involving average interbrachial plates	0.93 - 0.38	0.994 - 0.88
Correlations involving all other parameters	0.998- 0.85	0.999 - 0.88
Correlation coefficient at 0.05 level of significance	0.754 based on 7 specimens	0.707 based on 8 specimens

those of other characters, disclosing a lower degree of growth integration and coordination of these plates relative to the remainder of the calyx. This clearly reflects the intercalatory origin of many interbrachials which was dictated by the comparatively slow growth rates of interbrachial dimensions with respect to the other calyx plates and calyx-size parameters.

Principal components were extracted in this study from correlation matrices of the two species based on the following variables: "size," height of radials, calyx height, total number of interprimibrachs, and average height and width of the interbrachials (Table 4). Only some of the variables were treated in these analyses in order to obtain defined correlation matrices where the number of specimens (7 or 8) exceeds the number of variables, 6 for both taxa. In a defined correlation matrix, the matrix can be of full rank although such is not invariably so. The sampling properties of principal components taken from defined correlation and variance-covariance matrices are partly known and these are subject to some measures of statistical inference. Such is not true for undefined matrices where the number of variables exceeds the number of specimens.

Plots of the principal component scores indicate that the first principal components of both species represent overall size change in all variables during ontogeny; large specimens are characterized by high scores whereas small individuals have low scores. Principal component I accounts

for 91% and 97% of the correlation matrix variance in *Xenocrinus multiramus* and *Glyptocrinus dyeri*, respectively. The important point is that more of the correlation matrix variance is associated with overall size increase in the glyptocrinid than in the xenocrinid. The coefficients for principal component I in *G. dyeri* are nearly identical for all variables (Table 4). This is caused by a monotonous correlation matrix where most of the correlation coefficients are high and relatively uniform. In *Xenocrinus multiramus*, the principal component I coefficients for the interbrachials average slightly less than those of the other characters (Table 4). This is because the correlation coefficients involving the interbrachials are lower than those of the other variables.

Principal component II of the glyptocrinid is associated with 3% of the variance. The only significant coefficient is -0.86 for the total number of interprimibrachs (Table 4). The principal component scores are not correlated with size of the crinoids and this principal component is considered as growth independent variation in the number of interprimibrachs of the larger specimens.

Principal components II-IV of the xenocrinid are grouped with 9% of the correlation matrix variance. Although the interpretation of these principal components is somewhat uncertain, the

largest coefficients are mostly for the various interbrachial parameters (Table 4). Plots of the principal component scores disclose that size independent variation of the interbrachials is involved, although its exact nature is unknown.

To summarize, only 3% of the correlation matrix variance in *Glyptocrinus dyeri* reflects growth independent variation of the interbrachials whereas 97% of the variance is related to overall size increase in all dimensions. This is due to the nature of the correlation matrix where most of the coefficients are roughly the same. A high and uniform amount of developmental integration and coordination was present throughout ontogeny of all variables, including the interbrachial parameters. Much more of the correlation matrix variance (9%) in *Xenocrinus multiramus* is accounted for by growth independent variation in the interbrachials, but only 91% of the variance is attributed to overall size increase. Here, the correlation coefficients involving the interbrachials range lower than those of the other variables. This discloses that the interbrachials were less well integrated and coordinated with overall size increase than the other calyx parameters. The contrasts in the principal components between the two taxa are mainly caused by the previously mentioned differences in interbrachial developmental patterns.

EVOLUTION OF XENOCRINIDS

The following species were examined in conjunction with this study:

1. *Proxenoocrinus inyoensis* Strimple & McGinnis (1972, p. 73, text-fig. 1a,b), Lower Ordovician, Arenig, California, North America. Measurements from photographs of holotype and paratype.
2. *Xenocrinus penicillus* S. A. Miller (best illustrations in Wachsmuth & Springer, 1897, p. 183, pl. 9, fig. 6a,b), Upper Ordovician, Richmond, Ohio, North America. Measurements made on approximately 50 USNM and Springer Collection specimens including all primary and secondary types.
3. *X. baeri* (Meek) (see Wachsmuth & Springer, 1897, p. 185, pl. 9, fig. 5a-d), Upper Ordovician, Richmond, Ohio and Indiana, North America. Data compiled from about 40 USNM and Springer Collection crinoids including crowns figured by Wachsmuth & Springer.
4. *X. multiramus* Ramsbottom, Upper Ordovician, Ashgill, Scotland. [*X. brevisformis* Brower, n. sp.

was omitted because this form is known from only one small specimen and inclusion of it would lead to misleading interbrachial similarities. As mentioned earlier, *X. brevisformis* is similar to young *X. multiramus* and these two taxa are believed to be closely related.]

5. *Compsocrinus harrisi* (S. A. Miller) (1881, p. 74, pl. 1, fig. 4, 4a; see Wachsmuth & Springer, 1897, p. 517, pl. 21, fig. 8a,b), Upper Ordovician, Richmond, Ohio, North America. Six USNM and Springer Collection specimens including all types.
6. *C. miamiensis* (S. A. Miller) (1882, p. 34, pl. 1, fig. 1; see Wachsmuth & Springer, 1897, p. 518, pl. 21, fig. 7a,b), Upper Ordovician, Richmond, Ohio, North America. Six USNM and Springer Collection specimens including all types.
7. *Tanaocrinus typus* Wachsmuth & Springer (1897, p. 186, pl. 9, fig. 7a,b), Upper Ordovician, Richmond, Ohio, North America. USNM S716, holotype and paratype, the only known specimens. [The diagnosis of Wachsmuth & Springer stresses

TABLE 4. Principal components for *Xenocrinus multiramus* Ramsbottom and *Glyptocrinus dyeri* Meek.

Variables	Principal component coefficients					
	<i>Glyptocrinus dyeri</i>		<i>Xenocrinus multiramus</i>			
	I	II	I	II	III	IV
"Size"	0.41	0.33	0.42	0.34	0.044	0.22
Height of the radials	0.41	0.28	0.42	0.40	-0.16	0.19
Height of the calyx	0.41	0.0058	0.42	0.29	0.12	0.20
Total number of interprimibrachs	0.39	-0.86	0.40	0.39	0.79	-0.15
Average height of interbrachials	0.41	0.25	0.41	-0.0068	-0.34	-0.84
Average width of interbrachials	0.41	-0.050	0.38	-0.70	-0.46	0.39
Percent of correlation matrix variance associated with listed principal component	97.1%	2.9%	90.9%	5.2%	2.2%	1.7%

the supposedly small and irregular interbrachials. These plates only seem small and irregular because of the way they were scraped when the specimen was prepared. In reality, they are large and moderately regular, although the interbrachial areas are greatly depressed. The figures of Wachsmuth & Springer show about 3 times as many interbrachials as actually exist.]

Table 5 presents the original data matrix. Each species is coded by its mean value for 17 characters. Data sets for individual specimens were not used because of difficulty in obtaining complete suites of measurements from single specimens. Also the sample sizes differ greatly for the various species.

Table 6 lists the first three principal coordinates, and Figure 5 shows a plot of the first two principal coordinates. The distance between the taxa on the plot is inversely proportional to their morphological similarity, *i.e.*, small distances denote very similar species and vice versa for large distances. The analysis only indicates species most similar to one another with respect to the included characters. It neither weights the characters nor does it denote similarities produced by convergent evolution. Any phylogenetic interpretation is subjective. However, in this situation, close morphological similarity is believed to indicate evolutionary relationship because there is no evidence to the contrary. Although only the principal coordinates are tabulated here, it is noteworthy that all numerical taxonomic techniques and the principal coordinates lead to the same phylogenetic interpretation. This consistency may or may not be biologically meaningful. At any rate, all techniques extract the same basic structure and relationships from the data.

Proxenoocrinus inyoensis, from the Lower Or-

dovician, is the oldest known xenocrinid and probably constitutes the ancestral stock of Upper Ordovician tanaocrinids, xenocrinids, and compsocrinids. The principal coordinates disclose that *Tanaocrinus* and *Proxenoocrinus* are somewhat similar and presumably tanaocrinids were lineal descendents of *P. inyoensis*. The unique arm-branching pattern of *Tanaocrinus* shows that it is not close to any of the Ordovician camerates examined here.

The 10-armed *Xenocrinus penicillus* and *X. baeri* are closely allied, for these species are almost identical except for minor differences in fixed-brachials and shape of the calyx and brachials. *Compsocrinus miamiensis* and *C. harrisi* also belong close together, as indicated by similarities of their interbrachials and arm branching. The main contrasts between the two compsocrinids appear in their fixed-brachials and arm number. *C. harrisi* bears 4 arms in each ray with secundibrachs 2 forming the axillary; a total of 20 arms is present. In *C. miamiensis*, some half-rays branch on secundibrachs 2 or 3, but other half-rays are unbranched. The average number of arms is about 13.

The *Xenocrinus* species with 4 arms in each ray, *X. multiramus* and presumably *X. breviformis*, join the *Compsocrinus* group rather than 10-armed xenocrinids. Here arm branching similarities outweigh the interbrachial differences. Offhand, this might suggest that *X. multiramus* and *X. breviformis* should be placed in *Compsocrinus* instead of *Xenocrinus*. However, this is not done here because calyx characters including interbrachials are weighted more heavily in camerate taxonomy and phylogeny than arm features (*e.g.*, Moore & Laudon, 1943, p. 76-101;

TABLE 5. Original data matrix for numerical taxonomy of *Xenocrinus* and allied forms.

Species	Number of columnal sides 100=round	Number of basals	Number of lateral interrays where the radials are separated by the first interprimibrach	Sutures between the adjacent radials covered by supplementary plates or not (1=no, 2=yes)	Size of interbrachials (1=small, 2=large)	Interbrachials depressed (1=no, 2=yes)	Number of interprimibrachs below secundibrach 7 level	Number of interprimibrachs in range at primaxil level	Total number of interprimibrachs in one interray	Distal fixed-brachial (plate scale)	Distal fixed-brachial (numerical scale)	Total number of arms	Type of brachial arrangement (1=uniserial, 2=immature biserial)	Number of secundibrachs in first half-ray (100=unbranched)	Number of secundibrachs in second half-ray (100=unbranched)	Number of tertibrachs in first half-ray (100=unbranched)	Number of tertibrachs in second half-ray (100=unbranched)	Number of quaribrachs in all half-rays (100=unbranched)
<i>Proexenocrinus</i>																		
<i>inoensis</i>	100	5	4.0	1	2	2	6.0	2.3	8.7	IIBr2	10.5	10.0	1.0	100.0	100.0	0	0	0
<i>Xenocrinus</i>																		
<i>baeri</i>	4	4	0.3	2	1	2	25.0	6.0	55.0	IIBr5	16.5	10.0	1.4	100.0	100.0	0	0	0
<i>penicillus</i>	4	4	0.0	2	1	2	23.0	5.5	90.0	IIBr10	26.5	10.0	1.8	100.0	100.0	0	0	0
<i>multiramus</i> ..	4	4	1.0	1	1	2	42.0	7.3	113.0	IIIBr4	18.5	19.5	1.0	2.0	2.0	100	100	0
<i>breviformis</i> ..	4	4	0.0	1	1	2	5.0	2.0	8.0	IIBr2	10.5	20.0	1.0	2.0	2.0	100	100	0
<i>Tanaocrinus</i>																		
<i>typus</i>	100	5	0.0	1	2	2	6.0	2.0	41.0	IIBr5	16.5	35.0	1.0	6.0	6.0	24	24	100
<i>Compsocrinus</i>																		
<i>miamiensis</i> ..	4	4	0.0	1	2	2	7.3	2.3	31.0	IIIBr4	18.5	13.1	1.1	2.3	100.0	100	0	0
<i>harrisi</i>	4	4	0.0	1	2	1	5.8	2.4	47.0	IIIBr8	26.5	20.0	1.0	2.0	2.0	100	100	0

Ubahgs, 1953, p. 734-743). The rationale for this is clearly seen in camerate evolution. Generally, the first step is differentiation of a new calyx type, which comprises an evolutionary breakthrough later exploited by arm evolution.

In *Proexenocrinus*, the proximal interprimibrachs separate the radials in the lateral interrays so that the radial cirlet contains 10 plates (5 radials, 4 proximal interprimibrachs, and the primanal). All Upper Ordovician *Xenocrinus*, *Compsocrinus*, and *Tanaocrinus* have the radials joined together in all interrays except CD where the primanal is located between the adjacent radials. The first interprimibrachs were displaced above the radial cirlet so that they occur between the first primibrachs. The exact mechanism of this change is unknown, but presumably it acted through "mutations" (most general sense, including gene changes, chromosome inversions, and additions, etc.) which affected the ontogeny of young crinoids by causing subsequent growth divergences. Several functional benefits may be attributed to this change. The number of plates in the radial cirlet is reduced, probably augmenting its mechanical strength and reducing problems of growth integration and

coordination by simplification of plate structure. Each major camerate calyx plate bears an aboral nerve cord knot on the plate interior (Brower, 1973). Displacing the first interprimibrach upward would have shortened and simplified the aboral nerve cord system, at least at the critical radial-cirlet level. This was immediately above the chambered organ or central nerve plexus of the crinoid.

The interprimibrachs of *Proexenocrinus* consist of a few large and regular plates. The Upper Ordovician *Tanaocrinus* and *Compsocrinus* retained this ancestral type of interbrachial structure. Doubtless, these plates were joined together rigidly when the crinoids were alive. Presumably, a nonintercalatory mode of development characterized these interbrachials (see previous discussion of growth). One would expect that minimum problems of ontogenetic integration and coordination were associated with this interbrachial type.

The interbrachials of *Xenocrinus* diverged greatly from the ancestral proexenocrinid type by developing smaller and less regular plates along with small growth rates of interbrachial size and a complex intercalatory type of ontogeny. This

TABLE 6. Principal coordinates for *Xenocrinus* and allied forms.

	Principal coordinate		
	I	II	III
<i>Proexenocrinus inyoensis</i> ..	-0.095	0.58	-0.084
<i>Xenocrinus baeri</i>	0.53	0.058	0.049
<i>X. penicillus</i>	0.59	-0.00094	0.0081
<i>X. multiramus</i>	-0.042	-0.52	0.26
<i>Tanaocrinus tytus</i>	-0.48	0.27	0.33
<i>Compsocrinus miamiensis</i> ..	-0.14	-0.030	-0.32
<i>C. harrisi</i>	-0.36	-0.35	-0.23
Percentage of similarity matrix trace associated with listed principal coordinate	37.6%	30.0%	12.7%

developmental complexity introduces considerable problems of growth integration and coordination. As mentioned earlier, the interbrachial areas of xenocrinids resemble the flexible plate-studded integuments observed in the tegmens of some flexible and Recent crinoids. The nature of burial of xenocrinids and reteocrinids, both of which have similar interbrachials, demonstrates that these areas were flexible. Commonly specimens are found preserved with the interbrachial areas folded but not fractured. Presumably, the xenocrinid interbrachial areas were flexible during life of the animal, which suggests that they may be related to respiration. Exchanges of gases during respiration of living crinoids is a surface-area process involving the water vascular system, epidermis, and surfical mesenchyme where the epidermis is lacking. Gases possibly could diffuse through the tissue between the plates more rapidly than through the organic matrix bearing porous plates. Kesling & Paul (1968) and Paul (1968, 1972) have advocated vaguely similar respiratory functions for cystoid pore-rhombs and diplopores and for crinoid goniospires. Perhaps flexible interbrachial areas could have pulsed in and out so as to agitate the surrounding water, thus ensuring a continual supply of oxygenated water. At any rate, the xenocrinid type of interbrachials is considered an advanced and specialized character. This contrasts with the interpretation of Moore & Laudon (1943, p. 76-101) who thought that these small and irregular interbrachials were a primitive feature. The stratigraphic positions of the crinoids show that the Moore & Laudon hypothesis is incorrect. However, most crinoids with large and regular interbrachials usually re-

duced the number of these plates with progressive evolution as demonstrated by Moore & Laudon (1943, p. 76-101). Dicyclic camerate crinoids exhibited similar evolution where late Middle Ordovician and Late Ordovician reteocrinids with small, numerous and irregular interbrachials were probably descended from Early Ordovician and early Middle Ordovician archaeocrinids which have large and regular interbrachials.

Study of the correlation matrix shows relations between parameters. The size of the interbrachials is inversely correlated with the number of these plates at any and all levels, such correlation coefficients ranging from -0.81 to -0.97. The total number of interprimibrachs and number at any one level are also correlated with the

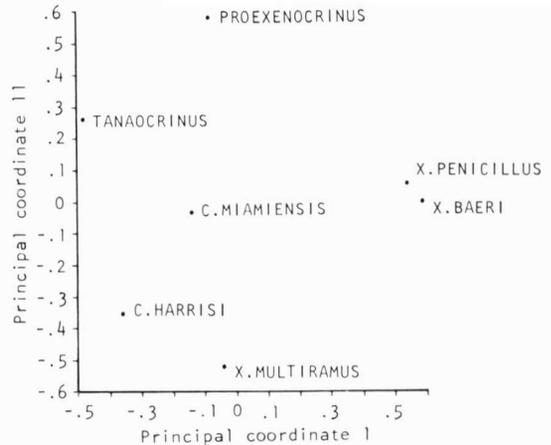


Fig. 5. Graph showing principal coordinates for xenocrinids and allied species (see Table 6 for data).

coefficients distributed over the 0.86 to 0.98 interval. This clearly illustrates the differences in interbrachials between xenocrinids and all the other crinoids. Within either the xenocrinids or crinoids with large and regular interbrachials, the number of these plates and number of fixed-brachials tend to increase together.

The proexenocrinid ancestor has two arms in each ray and a total of 10 arms. Each arm bears a prominent proximal pinnule located on the interray side of secundibrach 2 or 3. This arm configuration was retained by *Xenocrinus penicillus* and *X. baeri*, although the proximal pinnule is less prominent or absent. The other xenocrinids and *Compsocrinus* tended to develop 4

arms to a ray with an axillary secundibrach 2 or rarely 3. *Compsocrinus miamiensis* is intermediate because some half-rays branch on the secundibrachs like *Xenocrinus multiramus*, *X. breviformis*, and *C. harrisi*; other *C. miamiensis* half-rays do not branch, as in the 10-armed crinoids. The geometry suggests that the proximal pinnule on secundibrach 2 of 10-armed types is homologous with the outer-half-ray arm of 20-armed species. If so, the change affected the ontogeny of young crinoids by converting the proximal pinnule into a pinnulate arm. This involved transforming the nonpinnulate pinnulars into pinnulate brachials and increasing the plate addition rate in the proximal pinnular. Such arm evolution is common in camerate crinoids and can be documented in the

glyptocrinid-melocrinitid lineage among others.

Tanaocrinus evolved arms with several widely spaced branches which give 6 to 8 arms in a ray. These arms are strikingly dissimilar to those of related Upper Ordovician crinoids, and tanaocrinids are believed to represent independent offshoots from *Proexenocrinus*. The common trend in all crinoids was to increase complexity of the arms. Presumably this augmented the area of water covered by the food-gathering system.

Xenocrinids comprised an evolutionary blind alley and these crinoids seem to have died out at the end of Ordovician time. Tanaocrinids or compsocrinids or both were an important ancestral stock which gave rise to Silurian periechocrinids and allied forms.

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