

PALAEOECOLOGY AND HISTORY OF THE CALCEOCCRINIDAE (PALAEOZOIC CRINOIDEA)

by WILLIAM I. AUSICH

ABSTRACT. The morphologically divergent and long-ranging Calceocrinidae (inadunate crinoids, middle Ordovician to early Permian) are reinterpreted to have been leeward, passive, suspension feeders. Calceocrinid success is measured relatively by species diversity and by the relationship of calceocrinid species diversity to total crinoid generic diversity. The major change in calceocrinid importance occurred immediately after the Silurian, and this decline is judged to have been the consequence of biotic interactions. Both increased predation pressure and competition from fenestrate bryozoans are offered as potential causes for the decline; of the two, competition for living sites and exclusion by habitat modification by fenestrates is favoured. Accordingly the Devonian calceocrinid decline is argued to be the result of partial ecologic replacement of calceocrinids by fenestrate bryozoans. This study provides an example illustrating the impact that ecologic processes may have in evolutionary time.

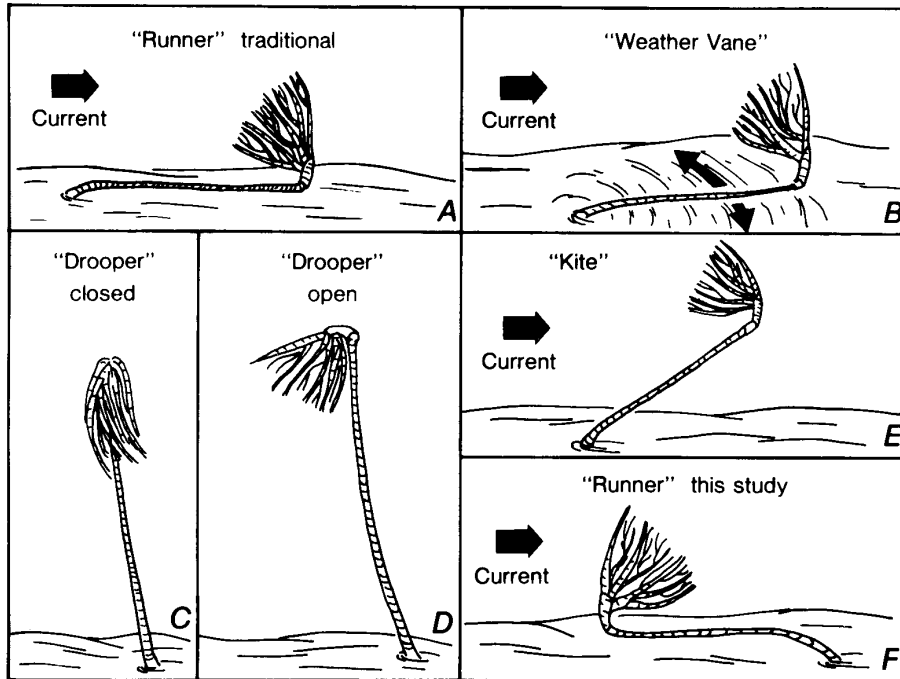
THE Calceocrinidae are among the most morphologically divergent groups of crinoids. Rather than having aboral cup plates in circlets above the column arranged radially about the oral-aboral axis, members of this crinoid family have their two circlets of cup plates articulated with one another along a hinge. The radial plates and arms lay over the basal plates and column. In addition the five-arm body plan, characteristic of most crinoids, was altered to either a four or three-arm arrangement. The total morphological change was toward a bilaterally symmetrical crown with highly modified cup and arms. This body plan proved successful for approximately 230 million years. The first calceocrinids appeared in the middle Ordovician (Blackriverian, Llanvirn), and they are last recorded from the early Permian (Leonardian, Artinskian). Their absolute success varied during this time: they were relatively quite abundant and diverse from the middle Ordovician through to the Silurian, but their role in echinoderm communities declined in the Devonian, and they met apparent near extinction in the early Mississippian. Calceocrinids have not been reported from middle Mississippian to early Permian rocks. It is my purpose here to examine the palaeoecology of calceocrinids and to offer explanations for their evolutionary history.

CALCEOCCRINID AUTECOLOGY

Scientists tend to spend more time studying and debating various aspects of morphologically unusual taxa than 'normal' taxa. This has been true for crinoids, as illustrated by the calceocrinids. Four main autecological modes have been suggested for calceocrinids: 'drooper', 'runner', 'weather-vane', and 'kite' modes.

The drooper mode is the paradigm of a typical stalked crinoid with an erect column (text-fig. 1C, D). In this posture the closed calceocrinid crown would have hung vertically down along the column, and an open crown would have been orientated horizontally (Ringueberg 1889).

An alternative to the drooper mode was proposed by Jaekel (1918). This reconstruction, the runner mode (text-fig. 1A), has received wide support (Springer 1926; Ramsbottom 1952; Moore 1962; Brower 1966, 1977; and others). According to the runner theory the highly modified crown was an adaptation for life with the column prostrate along the sea floor. In a closed posture the arms would have been folded over the column along the substratum; in the open posture the arms would have been positioned vertically in the water column. Calceocrinids have been reconstructed with the arms orientated such that currents impinged on the oral side of the arms (Jaekel 1918).



TEXT-FIG. 1. Various reconstructions of modes of life for calceocrinids. A, traditional runner mode with currents striking the oral surface of arms (Jaekel 1918; followed by most subsequent workers). B, weather-vane mode, a variation of the runner mode (Kesling and Sigler 1969). C, D, drooper mode, an interpretation consistent with the upright posture of most stalked crinoids (Ringueberg 1889). E, kite mode, a variation of the runner mode (Breimer and Webster 1975). F, runner mode, with currents striking the aboral arm surface, proposed herein.

The weather-vane mode (Kesling and Sigler 1969) and kite mode (Breimer and Webster 1975) are variations of the runner mode. Both are based on the assumption that currents struck the oral side of the arms. Kesling and Sigler (1969) proposed that open calceocrinid arms caught the current and shifted, like a weather-vane, depending upon the prevailing current direction (text-fig. 1B). Breimer and Webster (1975) included calceocrinids in their discussion of current-derived lift for crinoids. They considered that calceocrinids would have lain on the substratum in slack currents, and that in higher current conditions the open crown would have gained lift and been elevated above the sediment (text-fig. 1E).

In addition to these general reconstructions, Schmidt (1934) proposed that the five-armed Devonian calceocrinid, *Senariocrinus*, was a free-swimming pelagic crinoid.

Preferred model

Living crinoids orientate their filtration fans perpendicular to unidirectional currents. According to the drooper model the open arms of a calceocrinid would have been orientated horizontally, or nearly so, unlike living crinoids. It seems unlikely that the calceocrinid stock would have developed such a divergent morphology to lead the same erect, suspension-feeding life style as that of other crinoids. This suggestion against the drooper theory is supported by morphological criteria. Brower (1966, 1977) has reported two specimens of *Calceocrinus longifrons* Brower with the arm length

greater than the stem length. Although the stem in most calceocrinids is relatively much longer, these specimens must have been recumbent along the sea floor. Ausich (1984a) described an *in situ* holdfast of *Trypheroocrinus brassfieldensis* Ausich that must have conformed to the runner theory. In this specimen the distal column projected vertically from the sediment, but the column orientation was changed to horizontal by a series of wedge-shaped columnals. This stem arrangement resulted in an obligate recumbent posture. Similarly, Eckert (1984) and Brett (1985) reported calceocrinid holdfasts with the column facet orientated vertically, thereby dictating a recumbent stem posture.

Although inconclusive alone, taphonomic evidence further supports the suggestion that calceocrinids lived along the bottom. In collections made by the author from the lower Silurian Brassfield Formation, Ohio (Ausich 1984a), and the lower Mississippian Edwardsville Formation, Indiana (Ausich *et al.* 1979), calceocrinids were among taxa most commonly well preserved. The typical preservation of a nearly complete crown, commonly with stem attached, may be the result of the fact that calceocrinids lived on the bottom—where they would have been buried alive and preserved whole more easily than if they stood erect.

The weather-vane and kite modes (modifications of the runner mode) both seem unlikely. No known calceocrinid holdfasts possess an articulation that would have afforded the rotational movement implied by the weather-vane model. As argued by Eckert (1984), rather than having a horizontal holdfast-column articulation that would have allowed maximum rotation, many calceocrinid holdfast-column articulations are at a steep angle. Brower (1977) concluded that the kite mode may have been possible for some calceocrinids, some of the time, while Brett (1981) considered that the kite mode could only have been effective in high energy environments. Even in such settings it seems unlikely that the large calceocrinid crowns could have acquired sufficient lift from the currents. In addition, the kite mode implies that the column acted as a flexible tether rather than a rigid support structure. The latter seems much more plausible and is consistent with the functional morphology of living crinoids.

Both the weather-vane and kite modes require that calceocrinids were orientated with the oral side of their arms facing the current—the classic interpretation of calceocrinid orientation to currents. It stands in contrast, however, to what is known about both crinoid feeding and passive suspension feeding among other marine invertebrates. It is argued below that calceocrinids were probably orientated like modern crinoids, with ambulacral grooves on the down-current side. This interpretation further denies the weather-vane and kite modes.

In summary, from ideas on suspension feeding and morphological constraints, it appears that calceocrinid morphology was the result of a series of adaptations for life on the bottom with the stem prostrate along the sea floor, as first suggested by Jaekel (1918).

Orientation to current

From the time of Jaekel's (1918) original calceocrinid work to the present, calceocrinids have been reconstructed such that feeding currents impinged upon the oral (ambulacral) side of the arms. This interpretation has persisted despite the fact that living crinoids are now known to be leeward passive suspension feeders (feeding currents strike the aboral side of the arms) (Magnus 1963, 1964, 1967; Macurda and Meyer 1974; Warner 1977; Meyer 1982). It is appropriate to re-examine this aspect of calceocrinid autecology.

Living crinoids located in unidirectional current conditions typically form either planar or parabolic filtration fans (Meyer 1982), and food is captured by tube feet in the ambulacral grooves on the down-current side of the fan (Macurda and Meyer 1974; Meyer 1973, 1982; Byrne and Fontaine 1981). Comatulid crinoids with multi-layered fans rotate certain arms so that all ambulacral grooves are in this leeward position. In tidal dominated settings with bidirectional currents, comatulid crinoids rotate their pinnular ambulacra to keep them in a leeward position (Meyer 1982). This preference for leeward food capture is common among many suspension feeders. Warner (1977) argued from experimental evidence that passive suspension feeders must utilize leeward food capture for maximum suspension-feeding efficiency and cited examples of leeward passive suspension feeding among hydroids, bryozoans, and crinoids.

Although *absolute* adherence to modern analogues is not a wise philosophy, there is no compelling morphological reason to suggest that calceocrinids abandoned the leeward passive suspension feeding mode. The construction of arm plates and ambulacral grooves appears to be similar to other Palaeozoic crinoids. Arm modifications are only modifications in arm branching style, which is an extremely common evolutionary trend among crinoids. Consequently, modification of the arms and aboral cup is more readily explained as an adaptation for life on the substratum rather than as a deviation from leeward suspension feeding. It is perhaps counter-intuitive to interpret calceocrinids as leeward suspension feeders, but the orientation of living crinoids was misinterpreted by intuitive judgement until *in vivo* observation demonstrated their leeward orientation.

The runner mode with a leeward ambulacral orientation is preferred (text-fig. 1F) because it is consistent with behaviour of both living crinoids and most other passive suspension feeding organisms. In a leeward orientation, juvenile calceocrinids would have grown into the current (which is reasonable for a rheophilic organism), and the action of unusually high currents would have pushed the arms into a closed, protected resting posture on the stem. Known occurrences of calceocrinids are in settings that were well below normal wave base; such settings would generally have experienced predominantly unidirectional currents during normal conditions. Calceocrinids could have orientated themselves during growth to the prevailing currents.

Niche position of calceocrinids

Epifaunal suspension-feeding communities commonly have a well-developed vertical niche structure termed 'tiering'. The characteristic history of tiering development through the Phanerozoic has been summarized by Ausich and Bottjer (1982). During the Palaeozoic all tiers contained adult stalked echinoderms. However, stalked echinoderms (especially crinoids) were responsible for establishing the higher tier levels throughout the Palaeozoic and part of the Mesozoic. Calceocrinids, recumbent on the sea floor, deviated from this typical crinoid ecological trend to stand above the bottom. Calceocrinids and a few other stalked echinoderm groups (Frest and Strimple 1978; Ausich and Bottjer 1985a) occupied lower tiers of Palaeozoic communities. Calceocrinids would have been situated in the 0 to +5 and +5 to +10, 15 or 20 cm tiers of Ausich and Bottjer (1982), or in the low-level crinoid tier of Ausich (1980).

The ecologic position of calceocrinids in the lower level of diverse, multi-level stalked echinoderm communities afforded these crinoids an adaptive advantage. Because food resources generally move horizontally across the sea floor, calceocrinids in low tiers would not have directly competed for food with most adult crinoids in higher tiers (Lane 1963; Ausich 1980). Competition with other crinoids would have been reduced for a crinoid in the low tier (Brett 1981). This ecologically advantageous position may explain in part the temporal success of this family.

DATA FOR DISTRIBUTION TRENDS

Data for this study have been gathered for diversity trends within the Calceocrinidae, generic diversity of Palaeozoic crinoids, generic diversity of crinoids of the suborder Disparida, and diversity of the fenestrate bryozoans. These are evaluated at face value, recognizing that some aspects of the data may reflect the incompleteness of the fossil record.

Species diversity is used to display temporal trends within the Calceocrinidae. All valid calceocrinid species are included. Species diversity is used for a number of reasons. Twenty-one calceocrinid genera are recognized, a relatively small number compared with the one hundred and seven valid species and species-level taxa. The significance of generic diversity trends, as opposed to species trends, is questioned due to their relatively low value. Additionally, species taxonomy of calceocrinids has been relatively stable, whereas generic taxonomy and generic assignment of species have been in a state of flux (Brower 1966, 1977, 1982; Brett 1981; Ausich 1984a). Geographic and temporal distributions would be less reliable for genera than for species.

Generic diversity of all Palaeozoic crinoids and of disparids is taken uncritically from the *Treatise* (Moore and Teichert 1978), with one exception. Until very recently few early Silurian crinoids of

any kind were known. Descriptions of three new early Silurian crinoid faunas by Witzke and Strimple (1981), Eckert (1984), and Ausich (1984*a, b*, in prep.) have added many new crinoid genera and new calceocrinid species. Calceocrinid species from these studies are included in species distribution trends, so it was considered appropriate to add new early Silurian genera to the *Treatise* counts. Few new calceocrinid species have been described from times other than the early Silurian since the publication of the *Treatise*. Despite inherent problems with *Treatise* data sets of this kind, it is the most comprehensive and current information available.

In the absence of information about fenestrate abundance through time, fenestrate numeric diversity is used. The term 'fenestrates' is used to refer to the reteporiform bryozoans of the Order Fenestrata (*sensu* Boardman *et al.* 1983). Three basic data sets are considered: 1, species nomenclatorial diversity of *Fenestella*; 2, generic diversity of fenestrates (Bassler 1953); and 3, generic diversity of fenestrates from Cuffey and McKinney (1979), Ross (1979, 1981, 1982), and Ross and Ross (1982). The species nomenclatorial diversity data are from A. S. Horowitz (unpublished listing). These data include all species names assigned to *Fenestella* up to 1974. Many of these species are presently reassigned or synonymized within the Fenestrata. Most early bryozoan taxonomic studies were completed before 1974. Accordingly, this information is used as a relative index of fenestrate diversity. The Pennsylvanian diversity low is judged to be more an effect of monographic bias than biotic diversity.

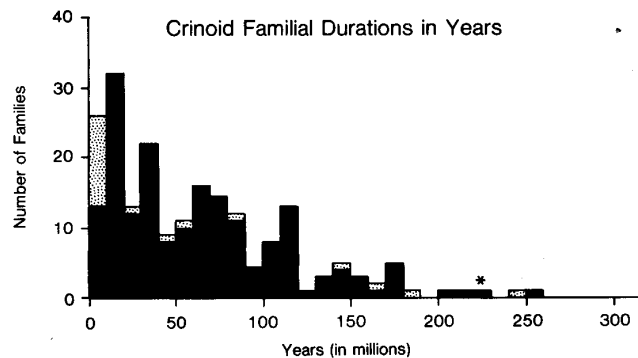
Generic diversity from the *Treatise* (Bassler 1953) is also used. Included are the Fenestellidae, Acanthocladiidae, and Phylloporinida, *sensu* Bassler (1953). Although outdated, Bassler's compilation remains the last comprehensive summary of fenestrate generic distributions. Subsequent to Bassler, Cuffey and McKinney (1979) have qualitatively discussed the Devonian history of fenestrates, and Ross (1979, 1981, 1982) and Ross and Ross (1981) have treated Mississippian, Pennsylvanian, and Permian fenestrates.

All three sets of fenestrate information agree that diversity increased rapidly during the Devonian and was relatively high during the remainder of the Palaeozoic.

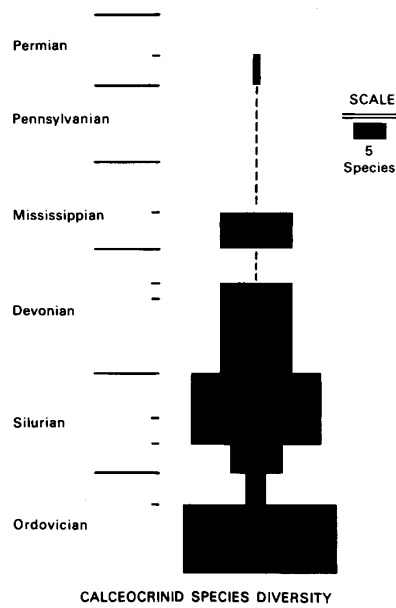
CALCEOCRINID DISTRIBUTION

Temporal distribution

The family Calceocrinidae is the third most long-ranging crinoid family known (text-fig. 2), existing for approximately 230 million years from the middle Ordovician (Blackriverian, Llanvirn) into the



TEXT-FIG. 2. Histogram of temporal duration in years of crinoid families, as determined from Moore and Teichert (1978) and Harland *et al.* (1982). Stippled areas record families with living representatives; asterisk denotes Calceocrinidae.



TEXT-FIG. 3. Spindle diagram of calceocrinid species diversity; only valid taxa are included.

early Permian (Leonardian, Artinskian). Absolute success of the members of this family varied tremendously during this time. Text-fig. 3 displays the number of calceocrinid species through time; the wide diversity fluctuations could call the data into question. No calceocrinids are known from the late Devonian or from the late Mississippian to the Pennsylvanian, yet numerous and diverse crinoid communities are known throughout these intervals. The absence of calceocrinids during certain intervals is considered to be noteworthy rather than totally a consequence of incomplete data.

The five diversity declines shown on text-fig. 3 consist of: 1, end of the middle Ordovician, with a diversity increase in the Silurian; 2, end of the Silurian, with subsequent diversity levels never as high; 3, end of the middle Devonian, with no late Devonian forms but recurrence in the early Mississippian; 4, end of the early Mississippian, with no later Carboniferous occurrences reported; and 5, in the early Permian, after which no calceocrinids are known.

Geographic distribution

The first record of the calceocrinids is in the middle Ordovician from North America. By the late Ordovician calceocrinids were present in both Europe and North America, with genera shared between continents. Calceocrinids were on both continents with shared taxa through the Silurian, but they were strictly endemic after the Silurian. The last recorded occurrence of a calceocrinid in North America is in the early Mississippian; calceocrinids disappeared in Europe after the middle Devonian, with the exception of *Epihalysiocrinus* Arendt in the early Permian of the USSR.

Environmental distribution

During the Ordovician and Silurian, calceocrinids were apparently best adapted to shallow-water carbonate platform settings commonly associated with clastic input. Calceocrinids typically occur in sequences composed of alternating limestone and shale, such as the middle Ordovician Bromide Formation (Sprinkle 1982) and late Silurian Brownsport Formation (Amsden 1949). They also occur in units dominated by carbonates, such as the early Silurian Brassfield Formation, or in units

dominated by shale, such as the middle Silurian Rochester Shale (Brett, in press). Ordovician and Silurian calceocrinids probably lived in a range of conditions, as evidenced by variable amounts of fine clastics, but in general a shallow carbonate setting was typical.

Calceocrinids were present from the Devonian in a wider array of habitats. In addition to carbonate platform settings, Devonian calceocrinids were more common in clastic settings, such as the Moscow Shale of New York and the Oriskany Sandstone of Maryland. Mississippian calceocrinids are present on the Burlington Limestone carbonate ramp in Iowa and in deltaic sediments. On the Borden delta in Indiana and Kentucky, calceocrinids were present on carbonate banks and in mudstone and shale facies (Ausich *et al.* 1979; Kammer *et al.* 1983).

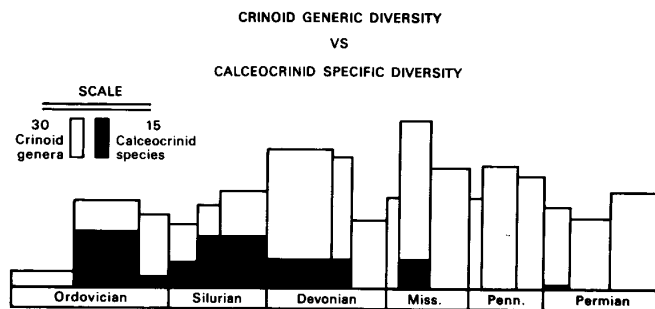
Lane (1971) recorded an environmental shift in the occurrence of crinoids from the Silurian to the Devonian. During the middle Silurian camerate crinoids were dominant in both terrigenous and carbonate settings, whereas by the middle Devonian inadunates dominated in terrigenous areas. Although calceocrinids remained in Devonian carbonate environments, they paralleled the general trend of inadunates by their presence in a more diverse array of clastic settings. Calceocrinids are conspicuously absent after the early Mississippian. Facies populated by pre-early Mississippian calceocrinids are repeated commonly after this time, and diverse stalked echinoderms are also common, yet nevertheless, calceocrinids are not reported again until the early Permian.

CALCEOCRINID DIVERSITY DECLINES

The search for causes of specific events in evolutionary history is, at best, speculative. Nevertheless it is an essential step to a fuller understanding of the earth's biotic history. The *a priori* assumption that causes cannot be isolated due to the stochastic nature of evolution or the multiplicity of possible causes is an unacceptable substitute for a thorough analysis of the palaeoecology and history of a group under study. Admittedly, a multitude of potential factors may have influenced the group's evolutionary history. It is the interaction of these numerous factors which have yielded overall stochastic evolutionary patterns (e.g. Raup *et al.* 1973; Raup and Gould 1974). Yet specific evolutionary events had specific causes, and these causes should be isolated where possible. Potential specific causes must be consistent with community ecologic structure, the autecology of the group studied, the physical environmental setting, and the ecology and history of associated organisms. The calceocrinid declines could have resulted either from biotic interactions, such as competition or predation pressure, or from physical environmental changes.

Diversity decreases are considered here in two ways: first, as numeric diversity changes (text-fig. 3); and second, by a comparison of numeric calceocrinid species diversity with total numeric generic diversity of all crinoids for series throughout the Palaeozoic (text-figs. 4 and 5). This second measure is a representation of the contribution or relative importance of calceocrinids to all crinoids during given times. No trend exists among all points plotted in text-fig. 5A ($r^2 = 0.04$). However, two clusters of points are present, each with a high value of r^2 . The points in the cluster with the lower slope are Ordovician to Silurian data, with one exception, and the points in the cluster with the higher slope are post-Silurian. The one exception is the Late Ordovician which falls in the cluster of post-Silurian points. Text-figs. 4 and 5 show that calceocrinids played a consistent role during the Ordovician and Silurian (with the exception of the late Ordovician) but were a much less important aspect of crinoid faunas after the Silurian. I argue that this shift in the apparent importance of calceocrinids is the most significant calceocrinid diversity change; potential reasons for this shift will be the primary topic of discussion below.

In addition to the decline after the Silurian, text-figs. 4 and 5 record other fluctuations in calceocrinid diversity. The first, from middle to Late Ordovician, was both a decline in absolute diversity and a decline in the relationship between calceocrinids and all crinoids. This decline accompanied a faunal turnover of all pelmatozoan classes. During the middle Ordovician, pelmatozoan faunas were characterized by diverse blastozoans and crinozoans. The composition of Late Ordovician faunas was very different; many blastozoan classes had become extinct, starting a general decline of blastozoans, and different crinoid groups dominated. These facts notwithstanding,



TEXT-FIG. 4. Superimposed histograms of crinoid generic diversity (as determined from Moore and Teichert 1978) and calceocrinid specific diversity by series. The comparison of these two data sets is judged to indicate the relative importance of calceocrinids to crinoid communities through time.

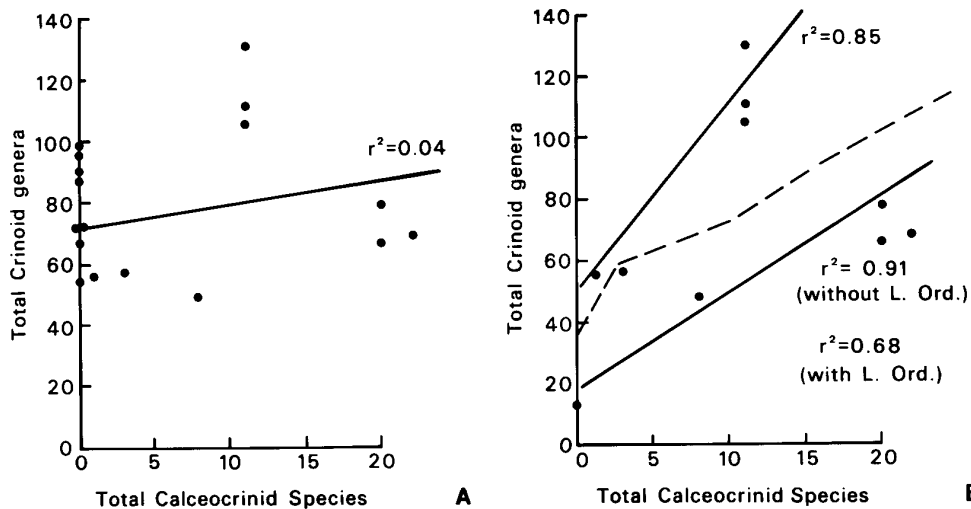
late Ordovician stalked echinoderms are known from relatively few areas. Assuming that this indicated Ordovician decline reflects reality, its effect was short lived. By the early Silurian, calceocrinid species diversity had increased so that its relationship to all crinoids was similar to that of the Middle Ordovician. This relationship continued throughout the remainder of the Silurian.

Calceocrinids declined again from the late Silurian to the early Devonian, both in numeric diversity and in relation to all crinoids (text-fig. 4). They never recovered from this decline, and hypotheses for it will be discussed below. From this position of lesser importance, calceocrinids experienced three additional declines: 1, they disappeared from the record after the middle Devonian; 2, after reappearing during the early Mississippian they disappeared from the record again; and 3, they presumably became extinct after a single showing in the early Permian. Although the absence of late Devonian calceocrinids is in part an artifact of an incomplete record, the decline did occur: six calceocrinid genera are recognized in the early Devonian, two are known in the middle Devonian, while the single Mississippian genus, *Halysiocrinus*, was also present during the Devonian. Calceocrinids were endemic from the Devonian to the Permian. By the end of the Devonian all known European calceocrinids had disappeared, and in North America only *Halysiocrinus* survived. The Mississippian calceocrinid increase records speciation in North America within *Halysiocrinus*.

The most intriguing aspect of post-Silurian calceocrinids may not be their occurrences. Rather, where were they during their absence from the fossil record? From a lessened role, perhaps calceocrinids shifted after the middle Devonian into facies where their preservational potential was low. They did expand into a variety of habitats during the early Mississippian, but were excluded again after the middle Mississippian (after the Osagian-Meramecian crinoid extinction). Their one Permian record may have been a slight re-expansion into a facies that preserved echinoderms. No causal hypotheses can be reasonably advanced for the Devonian or Mississippian declines unless they were the result of the same ecological pressures discussed below for the Silurian-Devonian decline, but this suggestion cannot be effectively tested. Whether the calceocrinids became extinct during the early Permian or later with the general Permian extinction of crinoids is not known, and no testable hypotheses can be offered for the calceocrinid extinction.

Silurian to Devonian decline

I offer two primary hypotheses as potential causes for the Silurian-Devonian decline of the calceocrinids, arguing more strongly for one; both enlist biotic interaction as the primary factor influencing the calceocrinid decline. The data perspective employed here seems to rule out physical environmental causes. No apparent significant environmental change occurred in epicontinental



TEXT-FIG. 5. Scatter diagrams of crinoid generic diversity versus calceocrinid species diversity, by series. Same data as presented in text-fig. 4. A, all data; regression line with $r^2 = 0.04$. B, points below dashed line from Ordovician and Silurian, points above dashed line post-Silurian; regression line r^2 values for Ordovician and Silurian series are $r^2 = 0.68$ (with lower Ordovician) or $r^2 = 0.91$ (without lower Ordovician), and for Devonian to Permian series $r^2 = 0.85$; series with no reported calceocrinids are omitted.

seas from the Silurian to the Devonian and, where present, calceocrinids appear to have been adapted to a wider array of environmental settings after the Silurian-Devonian decline than before.

Among biotic interactions that may have affected calceocrinids, pressure from increased predation and increased competition are suggested. The role of fishes and other durophagous predators expanded considerably during the Devonian (Signor and Brett 1983, 1984). Laudon (1957) suggested that sharks were important crinoid predators, and Meyer and Ausich (1981, 1983) and Signor and Brett (1983, 1984) argued that predation pressure has been an important factor in shaping crinoid evolution. Despite the possible effect of increased predation pressure, it seems unlikely that this alone could have been primarily responsible for the post-Silurian calceocrinid decline, because of aspects of calceocrinid autecology and the timing of the durophagous increase.

Kesling and Sigler (1969) suggested that the calceocrinid morphology, close to the substratum, was an anti-predator adaptation; a closed calceocrinid crown on the sea floor would have been a less susceptible target for predation. However, when the calceocrinids first appeared in the middle Ordovician, predation pressures were probably relatively quite low (Brett 1981; Signor and Brett 1984). If calceocrinid design offered anti-predation advantages during the Devonian, it was pre-adapted for this purpose.

Taxonomic and morphologic changes inferred from increased predation occurred during the Devonian (Signor and Brett 1984). The abundance of durophagous predators reached a diversity maximum in the early Mississippian, and inferred responses by their prey are most apparent in the late Devonian and early Mississippian. The primary decline of calceocrinids took place at or near the Silurian-Devonian boundary, before the potential effects of increased durophagous pressure were generally realized, but the decline in calceocrinid numeric diversity by the close of the middle Devonian is within the time range during which Signor and Brett (1984) concluded that many groups were adjusting to increased predation pressure. If predation pressure did adversely affect the fortunes of the calceocrinids, it must have done so in conjunction with other factors.

The low-level suspension-feeding tier of the calceocrinids was occupied by a variety of invertebrates, including brachiopods, corals, bryozoans, and other crinoids. Although the essence of a stalked echinoderm is that of an erect organism feeding above the substratum, numerous forms at many times secondarily assumed a suspension-feeding habit directly adjacent to the substratum (bottom dwelling) (Frest and Strimple 1978; Ausich and Bottjer 1985a). Ausich and Bottjer (1985a) surveyed all stalked echinoderms interpreted to have been bottom dwellers; they were relatively common during the Ordovician, Silurian, Mississippian, and Permian. The only Devonian bottom-dwelling echinoderms are calceocrinids, the Edriocrinidae (typically confined to high energy facies), a few diploporite cystoids, and the blastoid *Eleutherocrinus*. It appears that competition decreased for calceocrinids from other stalked echinoderms during the Devonian.

The decline of the calceocrinids is independent of a more general, later decline of the inadunate order Disparida (which includes the Calceocrinidae). When the calceocrinid post-Silurian diversity decline began, total generic diversity of disparids was increasing towards a middle Devonian high. Disparid diversity declined after the middle Devonian.

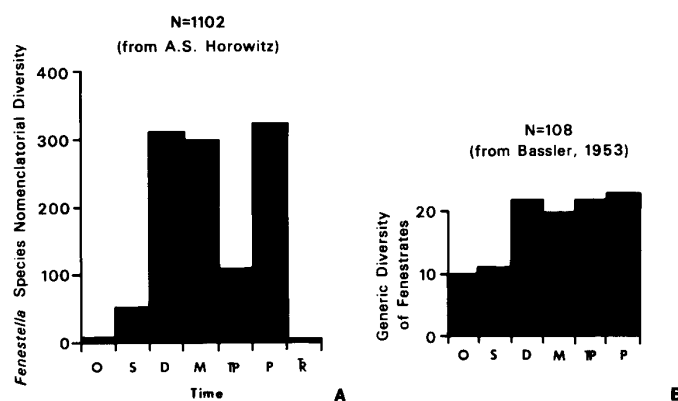
Other low-level, suspension-feeding invertebrates could have been potential competitors. Changes among brachiopods and molluscs should have had no effect because they probably fed from a level immediately below calceocrinids, and they most likely ingested a smaller modal food size. Corals should not have offered a severe competitive threat because, unlike crinoids, they presumably fed only on live animal tissue in suspension. The increase of diversity and abundance in fenestrate bryozoans which began in the early Devonian may have had an impact on calceocrinids. Fenestrate bryozoans were erect suspension feeders, elevated commonly up to 20 cm above the substratum. Fenestrates and calceocrinids occupied the same ecological space, fed from the same parcels of water, and were thereby potentially in competition. This second hypothesis appears to be a likely cause for the post-Silurian calceocrinid decline.

BRYOZOAN REPLACEMENT MODEL

Discussions with other palaeontologists have confirmed my impression from field studies that the abundance of fenestrate (reteporiform) bryozoans increased substantially during the Devonian, but data to document this increase in fenestrate abundance are not available. A less precise but nevertheless meaningful alternative to abundance data is fenestrate diversity data; the three data sets discussed above all agree. A significant increase in fenestrate diversity occurred from the Silurian to the Devonian. Diversity increased rapidly during the early part of the Devonian and remained relatively high, with fluctuations, throughout the remainder of the Palaeozoic (text-fig. 6).

By the Mississippian, if not earlier, fenestrates had erect zoaria that were at least 20 cm above the substratum. From the Devonian, fenestrates occurred typically in densely populated aggregations (Stratton and Horowitz 1977; Lees 1964; Waters 1977). Fenestrates and calceocrinids must have occupied the same tier within the ecological structure of epifaunal communities, where they co-occurred, but they probably fed on different sized particulate food. Assumptions about ingested food size are based upon size restrictions imposed by the skeleton in areas where food is captured or ingested and are consistent with aerosol filtration theory (Rubenstein and Koehl 1977; Ausich 1980). Winston (1981) demonstrated that a high correlation exists between mean orifice width and mouth diameter in living cyclostome and cheilostome bryozoans. She suggested that mean orifice width could be used to predict mouth diameter in fossil cyclostomes and cheilostomes. Mouth diameter places an upper limit on the food size of ingested particles (Winston 1981, p. 5). Mean mouth diameter is approximately 0.23 as large as mean orifice width in cyclostomes and approximately 0.34 as large in cheilostomes. The width of the ambulacral groove controls the size of ingested food particles among living crinoids. The minimum food particle dimension can be no larger than the ambulacral groove width (Rutman and Fishelson 1969).

The relationships of skeletal dimensions of Palaeozoic crinoid adoral groove widths to ambulacral groove widths, and of fenestrate bryozoan apertures to mouth size are not known, but the dimensions of the skeletons can be measured to give potential relationships for relative food size



TEXT-FIG. 6. Fenestrate bryozoan diversity. A, specific nomenclatorial diversity of *Fenestella*; most taxa are reassigned to other fenestrate genera (data compiled by A. S. Horowitz and include species named up to 1974). B, generic diversity of fenestrate bryozoans (Fenestellidae, Acanthocladiidae, and Phylloporinidae; data from Bassler (1953).

TABLE 1. Statistics for early Carboniferous fenestrate bryozoan apertures. The maximum aperture diameter is given, thereby providing the largest measure possible. All measurements are from specimens at a single locality from a limited stratigraphic interval. The calceocrinid *Halysiocrinus tunicatus* (Hall) is present in this fauna. Lower Carboniferous (lower Mississippian), Edwardsville Formation, Indiana University locality number 15109 (see Ausich 1983). X, mean; SD, standard deviation; N, number of measurements; measurements in mm.

Taxon	Maximum aperture diameter		
	X	SD	N
<i>Fenestella</i> spp.	0.12	0.02	48
<i>Penniretepora</i> spp.	0.11	0.04	100
<i>Polypora</i> spp.	0.10	0.02	30
<i>Thamniscus</i> spp.	0.16	0.04	63

differences. Comparisons are made from an early Carboniferous example where fenestrates and a calceocrinid do co-occur (Table 1). Measurements are from specimens from a single locality (Indiana University locality 15109) in the Edwardsville Formation of Indiana (Ausich 1983). Four genera of fenestrates and one species of calceocrinid, *Halysiocrinus tunicatus* (Hall) are considered. The mean maximum aperture diameter of fenestrates varies from 0.10 to 0.16 mm (to be conservative the largest dimension was measured rather than aperture width). A single specimen of *H. tunicatus* is preserved such that the adoral groove width of food gathering branches can be measured as 0.65 mm (Ausich 1980). Acknowledging all the potential problems of soft part dimensions and adherence to modern analogues, the measured skeletal dimensions that were probably related to controls on food size were different in early Carboniferous fenestrates and calceocrinids: adoral groove widths in calceocrinids ranged from 4.1 to 6.5 times larger than the maximum aperture widths of fenestrate bryozoans. It follows that fenestrates may have been restricted to food particles smaller than those available to calceocrinids. Therefore, even though they occupied the same ecologic space, they may not have directly competed for the same food resources.

Despite this potential lack of direct competition for food, fenestrates and calceocrinids probably did compete. Dense aggregations of fenestrates would have precluded the establishment of a calceocrinid with its column extended along the bottom; the current baffling ability of a dense fenestrate aggregation could have created a very low current setting at the substratum; and the relatively larger food size captured by calceocrinids (Ausich 1980) would probably have been carried by stronger currents than may have been present within dense fenestrate aggregations. This habitat modification could have adversely affected calceocrinid survival. Also, in 'head-to-head' competition for substratum space and for space within lower tiers, calceocrinids would most probably have lost by virtue of the generally slower growth rate of solitary as opposed to colonial organisms (Jackson 1977).

DISCUSSION

The considerable temporal success of the Calceocrinidae was blemished by sharply diminished diversity and abundance after the Silurian. Two biotic changes, concurrent with the calceocrinid decline, are isolated as potential causes: an increase in predation pressure and an increase in competition by fenestrate bryozoans. Both causes are reasonable with what is generally understood about the palaeoecology of Palaeozoic crinoids. Nevertheless, it is judged that effects from competition with fenestrate bryozoans have a more significant impact on calceocrinids. The mere correlation of the calceocrinid decline with the rise in fenestrates does not prove a causal link, but it is consistent with the palaeoecology of calceocrinids that fenestrates could have severely restricted calceocrinid success. The decline of the calceocrinids in the early Devonian is considered to represent an example of *partial ecologic replacement* of calceocrinids by fenestrate bryozoans. A test of the fenestrate hypothesis would be a comprehensive palaeoecologic analysis of post-Silurian communities with and without calceocrinids. Such an analysis is beyond the scope of the present study, but an initial survey suggests that, with rare exception, post-Silurian calceocrinids were most successful in settings with low fenestrate abundance.

An important implication of this study is that ecologic processes probably had a strong impact on the evolutionary history of the Calceocrinidae. This counters ideas that ecologic processes cannot have an important impact in evolutionary time. Ausich and Bottjer (1985a) argued that there is no *a priori* reason to discount the additive evolutionary potential of such processes; Meyer and Ausich (1983) and Ausich and Bottjer (1985a) also argued for a strong ecologic impact on the evolution of the Crinoidea.

This study may also support the component concept of community palaeoecology (Ausich 1983). Ausich argued that communities could be subdivided into trophic/taxonomic groups termed 'components'. Each component responded to different physical environmental pressures, thereby having independent distributions. Evolution should be sensitive to components, and readjustments of taxa through time should take place within components. The diversification of fenestrates resulted in a readjustment within the component of organisms limited by conditions at the sediment-water interface (*sensu* Ausich 1983).

Acknowledgements. A. S. Horowitz and R. J. Cuffey provided information on fenestrate bryozoan diversity. Discussions with D. B. Blake, A. S. Horowitz, and R. J. Cuffey were very useful. N. G. Lane, A. S. Horowitz, and two anonymous reviewers improved earlier drafts of this study. Helen Jones typed the manuscript. Acknowledgement is made to the Donors of the Petroleum Research Fund, administered by the American Chemical Society, for partial support of this research.

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Typescript received 3 January 1985
Revised typescript received 15 April 1985

WILLIAM I. AUSICH
Department of Geology and Mineralogy
125 South Oval Mall
The Ohio State University
Columbus, Ohio 43210-1398
USA