Crinoid Arms and Banana Plantations: An Economic Harvesting Analogy

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Abstract.—The pattern of arm branching and arm morphology in the camerate crinoid family Melocrinitidae became more complex during an evolutionary sequence which extended from Late Ordovician to Late Devonian. The fully evolved melocrinitid arm pattern bears an amazing resemblance to the theoretically ideal lay-out for harvesting roads on a banana plantation. This may not be coincidental since the problems faced by a banana plantation manager are much the same as those of a crinoid: the harvesting of an evenly distributed micro-particulate resource from an area and its delivery to a central point for processing. The analogy suggests a detailed explanation of the melocrinitid morphology and evolution. It also raises the question: why did the pattern not become dominant among crinoids if it was so efficient? It may have been unlikely to evolve; it may reflect an unusual food supply. I prefer an explanation in which the plantation pattern demands a rigidity of the crinoid crown which is characteristic of camerates but is uncommon among other crinoids: the latter have adopted a strategy of feeding which emphasizes flexibility in anatomy and behavior. The banana plantation pattern is equally rare among other organisms. Thus an “ideal” may not be common in a group of organisms for cost-benefit reasons. This does not mean that the adaptationist’s approach is improper, or that random, historical, or constructional constraints routinely overwhelm adaptation. Rather, it means that cost-benefit analysis should take a larger part in functional studies, as it does in natural selection, and that theoretical ideals should be viewed with caution.

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Introduction

There is a well-documented evolutionary lineage of camerate crinoids leading from the Ordovician Glyptocrinidae to the Melocrinitidae, a compact and well-defined family which flourished until Late Devonian times. Within this lineage there is a remarkably unidirectional trend toward the elaboration of unusual arm structures. Since crinoid arms are used for a gathering function (food, oxygen, sensory information) the arm elaboration of melocrinitids is probably related to changes in the style of harvesting from the environment. Yet the melocrinitid arm pattern is unusual among camerate crinoids and among crinoids and other filter-feeding organisms. This leads to two related questions—what was the particular advantage of the melocrinitid arm pattern that led to its selection through a long evolutionary lineage, and what was the particular disadvantage of the pattern, which is rare among crinoids as a whole?

Crinoids and Crinoid Arms

Crinoids form a class of echinoderms characterized functionally by the fact that the vis-
structures except in a very few genera, and once established, the plate structure of the cup is generally not subject to rapid adaptive change. Slow changes do take place, of course: individual plates may be added, subtracted, or fused with neighbors. But these changes are slow, can often be traced to provide a phylogeny at the family level or higher, and support rather than undermine confidence in the calical structures as valid taxonomic criteria. As a result, crinoid taxonomy remained relatively stable for several decades until the recent publication of the Treatise (see Lane 1978b).

Arms are not used for high-level classification. They are the sites of immediate interaction between organism and environment, and thus are more subject to smaller-scale adaptation to different food and current regimes than the calical plates. Quite varied arm structure can occur within a family or genus, allowing one to trace evolutionary sequences at this level. At higher levels, repeated homeomorphy makes arms difficult to use in evolutionary studies.

Crinoids normally have pentameral symmetry, and there is at least one primary arm in each of the five rays into which the calyx can be divided. Arms may branch, however, into two equal or unequal “daughter” arms, so that as adults most crinoids have multiple arms. Although branching may be radially symmetrical or asymmetrical, most crinoids have arms which look alike at any given radius from the calyx: in other words, there is usually little differentiation among the arms.

Many crinoids have added to the volume of the calyx by incorporating some of the proximal parts of the arms into the wall of the calyx. Thus at the top edge of the calyx, where the arms become free, there may have been enough branching events, incorporated during growth into the calyx, to have 10, 20, or even more branches attached as individual free arms. Free arms may branch further after they leave the calyx.

Further details on arm morphology are given by Breimer (1978a) and Ubaghs (1978a) in the Treatise. Feeding in Recent and fossil crinoids has been fully discussed in recent years (Breimer 1969; Rutman and Fishelson 1969; Meyer 1973, 1979; Lane and Breimer 1974; Macurda and Meyer 1974; Lane and Burke 1976; Meyer and Lane 1976; Breimer and Lane 1978; Ausich 1980).

Camerate Crinoids

Camerate crinoids were distinct from all other crinoid subclasses when they appeared in the Early Ordovician, and they ranged upwards into the Late Permian with a maximum representation in the Middle Paleozoic. Their thecal plates are tightly sutured and a roof-like tegmen is prominently developed, enclosing the viscera particularly securely within the calyx.

Camerate crinoids often have a great number of plates in the rigid calyx, and the proximal portions of the arms are routinely incorporated into the calyx. The free arms are often numerous, and a great variety of styles of arm branching is found within the subclass.

Camerate have pinnulate arms, a feature which is by no means universal among Paleozoic crinoids (see Lane and Breimer 1974). The pinnules are movable and probably operated in a typical crinoid feeding mode. But the microstructure of the stereom shows that the joints between the brachial plates of the arms, and the articulation between arms and calyx, bore ligaments rather than muscles (Lane 1978a, p. T297). Camerates must have operated a rather passive filtration fan, presumably in a rheophilic manner (Breimer and Lane 1978, p. T337), but probably they did not generally operate the multidirectional system of Meyer (1979), in which it is the individual arms which respond to currents, not the crown as a whole.

The Morphology and Evolution of the Melocrinitids

The Melocrinitidae is a family of monobathrid camerates, included within the suborder Glyptocrinina. The melocrinitid lineage undoubtedly evolved from the earliest known family of the suborder Glyptocrinina, the Glyptocrinidae: in fact, Brower (1976) included *Glyptocrinus* and *Pycnocrinus* among the Melocrinitidae. Although the evolutionary integrity of the melocrinitids has been recognized since the 19th century, it is chiefly Ubaghs (1953, 1958) and Brower (1973, 1976, 1978) who have pieced together the full story as we know it now. In this paper I follow the taxonomic arrangement of the Treatise (Ubaghs et al. 1978).
Among the ancestral glyptocrinids, *Pycnocrinus* (M.Ord.–U.Ord.) includes *P. ornatus* (Billings), which has ten unbranched free arms like other early camerates (Fig. 1). In *Glyptocrinus* (M.Ord.–U.Sil.), species such as *G. decadactylus* Hall have twenty free arms, resulting from one more dichotomous branching event in ontogeny.

*Alisocrinus* (U.Ord.–M.Sil.) is the earliest genus recognized as a member of the Melocrinidae in the Treatise. The family is distinguished from the Glyptocrinidae because it has one fewer basal plate in the calyx, and authorities agree that the two have ancestor/descendant relationship. *Alisocrinus* continued the arm condition of the advanced glyptocrinids, i.e., there are four arms in each ray, totalling twenty. The free arms are all equal in development, and are unbranched (Fig. 1).

*Promelocrinus* (M.Sil.–U.Sil.) had four equally developed arms in each ray in early ontogeny. The two outer arms in each ray grew without branching and carried pinnules in normal fashion. The two inner arms of each ray grew closely parallel, and branched, but only on their outer sides. Furthermore, they do not themselves bear pinnules, although the branches which they gave off are pinnulate. This morphological innovation in arm structure and branching is recognized by calling the non-pinnulate inner arms *arm trunks* and their pinnulate offshoots *ramules* or *ramuli*.

Because many ramules budded off from the inner arms (arm trunks), while the outer arms remained unbranched, each half-ray of the crinoid crown developed in a strongly asymmetrical pattern. The ramules budded from the inner arm lay parallel with the unbranched outer arm, and are morphologically identical with it. They carry different names because of their mode of formation, not because of their different structure or function. The two inner arms of *Promelocrinus*, modified into arm trunks, lie along the plane of symmetry of the ray (Fig. 1;
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Fig. 2A). Brower (1976) has given complete details of the structure and ontogeny of Promelocrinus. The basic arm pattern of melocrinitids is largely complete in Promelocrinus. The strong arm trunks were buttressed at the base: their constituent brachial plates became wider and heavier with growth, and small calical plates bound the proximal parts of the arms together (Brower 1976, fig. 2). This gave a rigidity to the proximal parts of the arm system which was maintained even when the arms were retracted into their most closed position (Brower 1976, pl. 100, fig. 1; pl. 102, fig. 1). Even the ramules were strengthened. As they grew, more and more of the brachial plates of the ramules fused together and to the arm trunk which bore them (Brower 1976, p. 669).

Further refinements are found in later melocrinitid genera. In Ctenocrinus (U.Sil.-L.Dev.) the adjacent arm trunks of the ray are sutured together. This usually occurs at the proximal ends but may extend distally to varying degrees (Fig. 1). The internal food grooves within the arm trunks are not coalesced, however. Ubaghs (1958) describes the morphology fully. The adoral surfaces of the arm trunks are covered proximally by tesselated small plates, rather than the normal paired ambulacral plates. They are an extension of the tegmen of the calyx onto the proximal area of the arm trunks (Ubaghs 1978a, p. T188) and serve to increase the relative rigidity of the proximal arms. More distal parts of the arm system were strengthened too. In Ctenocrinus the articulation between ossicles of the ramules was constructed to minimize flexion (Ubaghs 1978a, p. T173-T174). In C. gottlandicus there were even special spikes on the ossicles of the pinnules, presumably to hold adjacent pinnules together (Ubaghs 1978a, p. T154).

In Melocrinites (M.Dev.-U.Dev.) the outer arm of the ray, already reduced to the status of a ramule in earlier genera, did not develop in the adult stage. Technically, therefore, with the loss of the outer arm and the suturing of the inner arms, the number of free arms had been reduced to five in the later melocrinitids, unlike other camerates (Fig. 1).

In Trichotocrinus (U.Dev.) the ramules themselves are occasionally non-pinnulate and were modified into branches which in turn bore pinnulate ramules (Brower 1978, fig. 3). The genus is the last melocrinitid, and the family became extinct at the end of the Devonian.

The Function of Melocrinitid Arms

Brower (1973, 1974, 1976, 1978) has made a series of fine quantitative studies of the ontogeny and adult structure of melocrinitid arms, both of early forms without developed arm trunks and of later forms with the full melocrinitid arm structure. He has shown that in general, all crinoids grow to maximize food-gathering area in relation to size. However, crinoids with the fully-developed melocrinitid pattern of arms, ramules and pinnules show an astounding rate of development of food-gathering structures. According to Brower (1976, p. 675), the Silurian genus Promelocrinus shows isometry or positive allometry of the food-gathering system relative to tissue volume. In other
crinoids, this relationship is strikingly negative, as one would normally expect in a growing organism.

Brower also points out (1976, p. 676–678, fig. 6) that the melocrinid arm pattern, with its rows of parallel and pinnulate ramules, provided a better, more “complete” filtration net than that of a crinoid with simple unbranched arms, such as the ancestral *Pycnocrinus*. By “complete,” Brower probably means that the filtration net had no major gaps between pinnules when the arms were fully extended. Note that the filtration net of *Pycnocrinus* could only have been complete (without major gaps) if the arms were deployed in a partly flexed attitude. Thus a melocrinid arm system gave a larger collecting plan area than that of *Pycnocrinus*. In advanced camerates in the Mississippian there may be 8–10 free arms per ray (N. G. Lane, pers. comm.), but although the filter in such forms would have been complete (without major gaps) if the arms were deployed in a partly flexed attitude. Brower (1976, p. 678) regarded the parallel evolution of arm-trunk and ramule systems in five lineages of camerates as significant in producing “complete” (and efficient) filtration nets.

Banana Plantations

Fortunately a powerful analogy is available. Tanner (1967) studied plantation design, specifically seeking to benefit the banana industry of the (then) British West Indies. He tried to define the optimum lay-out for a road system to be used in banana harvesting by performing a cost-benefit analysis. Relevant factors included the cost of building the system (roads, vehicles), the cost of running it (labor, fuel, maintenance), and the benefit derived (price of bananas). Naturally there are many variables in the calculations, all subject to change. Nevertheless, the results of Tanner’s work are of broad general interest.

1. *Harvesting roads should be closely spaced.* In the cost framework that Tanner used, it is better to run a lot of roads through the plantation than to bear the continuing cost of human transport of bananas to distant roads.

2. *In any small area, harvesting roads should be parallel.* There is an optimum distance between harvesting roads: too far, and human transport costs are too high; too close, and there is redundancy and wasted area in road construction.

3. *There should be differentiation of road types.* As bananas are hauled to a single processing plant, roads will be more heavily used near the plant. It is better to spend more money for a paved road surface on a few heavily used arterial or trunk roads than to repair poor surfaces continuously; on the other hand, most harvesting roads on the plantation are lightly used and can be cheaply constructed.

4. *The processing plant should be central.* This is intuitively obvious, and saves transport costs.

5. *The main transport arteries should be radial.* This is to be expected, if the processing plant is central; but it is not obvious how many radial arteries there should be.
6. There is a very specific angle between the radial arteries and the harvesting roads. The harvesting roads are parallel to the bisector of the angle between the radial arteries (Fig. 2B). Too great or too small an angle between harvesting road and artery will result in wasted road surface.

Tanner made drawings of ideal road systems for circular flat plantations, with uniform crop density. Clearly, these are the simplest parameters to work with, and other, real, plantations would be more irregular. It is exciting to note, however, that Tanner's ideal designs for harvesting systems look almost identical in all respects to those evolved in melocrinitid crinoids (Fig. 2A, B). One case is a 2-dimensional, terrestrial, plantation road system; the other is a 3-dimensional water-filtering system. But both are harvesting systems designed to collect and transport material that is micro-particulate in size relative to the collecting system, evenly distributed over the harvesting area, predictable but not uniform in occurrence in time, and must be brought to a central processing plant in order to produce any benefit for the operator of the system. In both cases, indeed in all economic and biological systems, the expected yield over the lifetime of the system must repay not only the running costs but also the initial capital outlay.

There is a vast difference in scale between a banana plantation and a crinoid crown. The analogy drawn here is primarily related to the geometry of the systems, so that scale is immaterial. It is worth pointing out, however, that the relative size of a banana plantation and a bunch of bananas is about the same as that of a crinoid crown and a food particle (10^4 approximately).

In the cost structure used by Tanner (prices current in the mid-1960's), 3 or 4 radial trunk roads were appropriate; each trunk road collected produce from a “ray” of harvesting roads that were closely spaced and parallel with harvesting roads in their outer neighboring “half-ray.” Tanner calculated, however, that the specific number of trunks depended on the banana yield: and extremely heavy anticipated yield might make it economic to lay out 5 trunk roads on a circular plantation. In this case, the analogy with advanced melocrinitids would be more nearly complete. The pinnules are the pathways used by the plantation workers on foot, the ramules are the harvesting roads, and the arm trunks are the trunk roads.

The Analogy

For the analogy, it follows that in an ideal harvesting lay-out in a crinoid, ramules should be closely spaced and parallel, strongly differentiated from arm trunks in structure, and budded off at a specific angle to them. Arm trunks should be few in number and radially disposed. All these are true of melocrinitid arms, including the angles between arms and ramules.

Apart from the geometrical similarities between banana plantations and melocrinitid arms, there are analogies between their collection and/or transport modes, as listed below.

**Crinoids**

A. Food trapping by tube-feet  
B. Ciliary transport on pinnule  
C. Ciliary transport on ramule  
D. Ciliary transport on arm  
E. Delivery to digestive system in calyx

**Banana Plantation**

A. Cutting bananas by machete  
B. Hand-carrying in basket  
C. Truck transport on dirt road  
D. Truck transport on arterial road  
E. Delivery to processing plant.

At each stage, in both systems, there are quantum changes in style of transport or quantity of load handled, or speed of transport, or efficiency of transport, or costs of building and running the system. Each transport stage forms a hierarchical step decoupled from its predecessor by one or more of these factors. It is a matter of fact that this is so in the banana plantation, and it is a working hypothesis and reasonable inference that it is so in crinoids. The hypothesis is testable in principle through physiological work on living crinoids but would inevitably remain only an inference when applied to the extinct melocrinitid crinoids.

The analogy is not fortuitous, but has a functional basis. In any crinoid feeding in a particular microhabitat, there must be an optimum
length for a tube-foot operating a mucus-trapping system. The most efficient food collection by a filtration fan is made by sets of evenly-spaced tube-feet borne on pinnules (see Meyer 1979), each sub-set of pinnules being parallel and equally spaced. In plantation and in crinoid, a particulate harvest is gathered from a given area, and it is important that no items are lost by ineffective collection. (Both plantation and crinoid can increase their harvest at greater cost by growth at the perimeter, but that is a separate issue and does not affect the simple requirement for efficient collection within the perimeter.) Once the harvest is collected efficiently, by workers or by tube-feet, then it becomes important that it should be transported efficiently to the center. In both the crinoid and the plantation, the harvest is loaded very quickly into its eventual transporting devices (food-grooves and trucks), and a rational set of conduits delivers it to the center under the simple laws of geometry.

In the plantation, a hierarchical set of transport structures is necessary because of differential wear and tear on the various transport surfaces. This is not necessarily true in crinoids, but there are good functional reasons for the development of an analogous, hierarchical, set of differentiated transporting structures. In crinoids, the support for the arms and pinnules is not the solid earth, but each distal unit is supported by its proximal neighbor. If this were the only consideration, crinoids might be expected to have arms and pinnules that tapered uniformly from calyx to perimeter—and indeed some do. But in the special case of melocrinitid crinoids, I suggest the special geometry of the system dictates that there are quantum jumps in volume of material transported by pinnules, by ramules, and by arm trunks. This transport requirement dictates constraints on the minimum size of each of these components, and in turn specifies quantum jumps in mass and required support. Just as in banana plantation road systems, then, the morphology and hierarchical structure of the melocrinitid crown are functions of the transportation requirements of harvesting. Subtly different selective agents have caused a convergence on the same solution: to have more rigid transport surfaces in those units that carry more harvest.

Inferences on Melocrinitid Evolution

Analogies prove nothing, but they may suggest valuable inferences. In this case, I propose that the evolutionary sequence displayed in melocrinitid crinoids is an increasingly close approximation to an ideal harvesting system. All morphological features of the sequence can now receive functional explanation, given the initial morphology of Alisocrinus. The differentiation in branching between the inner and outer arms of the half-ray, accompanied by the budding of ramules rather than pinnules from the inner arm, set up the geometrically ideal collecting pattern, with a complete filtering net. The inner arm then received a great deal of food from its tributary ramules and was modified to act merely as a transport conduit, as in Promelocrinus. Further refinement of the system came with the partial suturing of the inner arm trunks, as in Ctenocrinus, which eliminated a final non-pinnulate gap in the filtering system, and strengthened the arterial transport system. The loss of the outer arm, as in Melocrinites, was merely a technical change in morphogenesis, for its place was taken by a ramule budded from the arm trunk early in ontogeny. In Trichotocrinus the addition of an even lower level of pinnulate structures may have added to the filtering area, but I am not sure of the functional significance of this final stage in the morphological sequence. Brower (pers. comm., 1980) believes that the morphology of Trichotocrinus has not been adequately described.

Throughout the sequence, structural modifications increased the strength and rigidity of the inner arms, particularly in their proximal parts, and other modifications strengthened the distal arms and ramules, even pinnules in some cases, to ensure their secure deployment in an effective filtering system. Although the diagrams used by Brower (1976), and Tanner's plantations, are 2-dimensional, there is no reason why the filtering surface of a melocrinitid should not have been 3-dimensional with a plan view like that shown in Fig. 2A.

The only significant morphological feature not explained by the analogy is the retention of two arm trunks in any ray, with only partial suturing between them: Tanner's model suggests that there should be one major radial ar-
tery. The retention of a "double" transport conduit may be related to the economics of ciliary transport, in which material is driven along a conduit by an array of cilia disposed along its surface. Amalgamation of two parallel conduits into one would have decreased the ratio of cilia to cross-sectional area, perhaps jeopardizing the smooth and effective flow of material towards the mouth. Many tunnels for human transportation are driven as twin parallel shafts, for analogous reasons.

Why Not the Best?

An immediate question arises. If indeed the melocrinitids were close to ideal in their arm deployment, why did this set of structures not become dominant, or even common, among crinoids? The melocrinitids themselves may have become involved in the shallow-water crisis which overtook many organisms at the end of the Devonian period: other groups with very impressive adaptations, such as the phacopid trilobites (Stockton and Cowen 1976) became extinct at this time. But what of the many crinoids which flourished before and after the late Devonian?

In fact, several different lines of camerate crinoids independently evolved crowns with arm trunks and ramules, disposed with a geometry rather similar to that of the melocrinitids (Ubaghs 1978b, p. T282, T285; Ubaghs et al. 1978, p. T409). Examples are:

Lampteterocrinus, M. Silurian, Tennessee (Treatise T430–T437)
Thamnocrinus, M. Devonian, New York (Treatise T447–T449)
Cytidocrinus, L. Mississippian, N. America (Treatise T458–T459)
Manillocrinus, L. Carboniferous, Australia (Treatise T458–T460)

These examples occur among all three major suborders of camerates, and on each side of the Devonian/Carboniferous boundary. They suggest that some features of camerate crinoids in particular were pre-adaptive to the repeated evolution of the plantation arm pattern. It is important to note, however, that only 8 camerate genera out of 209 have the melocrinitid pattern. This implies strongly that for all its apparent perfection, the pattern was appropriate only for very restricted conditions, and was in the end inferior to the more "normal" crinoid arm arrangement.

A few other camerates (Rhipidocrinus, M. Devonian, Europe, Treatise T430–T431; Steganocrinus, L. Mississippian, N. America, Treatise T445–T457; Trybliocrinus, L. Devonian, Spain, Treatise T503–T504; and Eucladocrinus, L. Mississippian, N. America, Treatise T515–T517) have a differentiated arm structure, with arm-trunks and ramules. Here there are 10 arm trunks, rather than five. I am not sure that this development can be convincingly linked with the plantation paradigm, but certainly this group of genera needs careful functional analysis. Even if a harvesting analogy can be sustained here, however, it does not remove the major problem of the lack of success of the "banana plantation" pattern.

Although the discussion so far has centered on camerate crinoids, there is no obvious reason why the harvesting analogy should not apply to any other crinoids, and so it is worth looking at other groups to see whether the plantation pattern evolved there. Indeed, differentiation of arms and development of ramules occurred sporadically in other Paleozoic groups, though much less frequently than among camerates.

Among the Disparida (inadequate crinoids with no pinnules), Daedalocrinus (M. Ord., Canada, Treatise T522–T523) has an almost perfect plantation pattern, even at this early stage in crinoid evolution. Among the early cladid inadequates, the Metabolocrinidae (Metabolocrinus, M. Ord., Estonia; Cyliocrinus, U. Sil., Sweden; and Pagecrinus, L. Dev., Indiana, Treatise T629–T630) all have rays dominated by arm trunks branching off ramules, though here too these crinoids lack pinnules. Among the Poteriocrinina several genera (cercocrinids, zeacrinitids) have arm branching patterns rather like melocrinitids, but here no arm loses its pinnules to become an arm trunk, and the differentiation of transport structures is not developed. I do not know of a plantation analog among fossil Flexibilia or Articulata, although Dr. C. R. C. Paul informs me (pers. comm., 1980) that a Jurassic pentacrinid he is studying may prove to be comparable.
Finally, it is exciting to note that living stalked crinoids, apparently with a plantation pattern of arms, have been discovered at depths of 2600–2700 meters during the CYAMEX Expedition to the East Pacific Rise (Fig. 3; Francheteau et al. 1979, cover picture of Nature; Roux 1980). Roux identifies this crinoid from photographs as a probable new genus of the Hyocrinidae, distinguished from other members of the family by having only a few robust pinnules (Fig. 3; crinoid D in Roux 1980, Pl. 1). No specimens are yet available, and the crinoid has been identified on photographs from only two locations. Clearly, it is worth attention as a living form which may allow testing of some of the paleobiological ideas proposed here.

Thus although the plantation pattern could have evolved, and did sporadically evolve, in several crinoid lineages, it never became anything more than an occasional curiosity. There are three possible reasons, all of which may have contributed to the rarity of the pattern.

Improbability of Evolving the Pattern

There may have been a phylogenetic constraint on the evolution of the plantation arm pattern: perhaps only a limited number of lineages could have adopted this morphology by any plausible sequence of events. Perhaps, for example, the pattern could only have evolved in crinoids which already were deploying only a few free arms in a geometrical, rheophilic, passive feeding crown. I suspect, however, that almost any crinoid lineage could have adopted the plantation pattern by neotenous modification of morphogenesis in the young stage. The history of melocrinids certainly suggests this, and Roux (1980) compares his "crinoid D" with the young stages of a related Atlantic form. Furthermore, even the inherent improbability of evolving the pattern does not explain why once established, the pattern did not become dominant.

Transportation Specialists

Dr. D. G. Stephenson (University of Keele, England) made this suggestion to me (pers. comm. 1980). Bananas may be an unusual crop. They are harvested in comparatively small batches, more or less continuously, instead of ripening all at once as most temperate fruits do. They must be harvested by hand and are very bulky. They come in awkwardly shaped bunches which are difficult to stack neatly. Altogether, this may mean that banana harvesting is controlled by transportation costs to an unusual extent.

Whether this is right or not, it suggests a hypothesis. Stephenson suggests that melocrinid crinoids were unusual among crinoids in having their feeding costs dominated by transportation rather than, for example, by costs of capture, costs of current resistance, or digestive costs. Thus the morphology of the arms would be dominated by adaptations to decrease transportation costs, perhaps at the expense of other functions. The inference is that melocrinid food may have differed from that of other crinoids.

Stephenson’s idea is innovative and imaginative. Furthermore, it is testable as soon as we have physiological information from living crinoids on the relative costs of arm deployment, food capture, transport, and digestion, and more information on the pinnule morphology of melocrinids, their sympatric suspension-feeding competitors, and their immediate paleoenvironments. It may apply to those few cases in
which the plantation pattern developed in non-camerate crinoids.

Rigidity and Flexibility

Stephenson’s idea is largely compatible with a third alternative I present here. Where Stephenson’s suggestion is largely paleophysiological, mine deals more with hard-part anatomy. To the extent that it is supported by currently available data, at the moment I find it the most satisfying of the three, especially as it relates to the camerate crinoids.

Modern crinoids (Articulata) and many fossil crinoids (Flexibilia and others) have arms with a great deal of flexibility. Modern crinoids are thus adapted to react to their environment, both solid and fluid, by continuous subtle or extreme variations in arm development and deployment, showing much physical and behavioral flexibility. Some unstalked crinoids can swim by flexing their arms. The structure of the arm ossicles of many fossil crinoids implies similar grades of physical flexibility (Lane and Burke 1976).

Modern rheophilic crinoids operate one of two feeding strategies (Breimer 1978, p. T322). They may live in rather turbulent and irregular environments, and filter from ambient currents by irregular and flexible positioning of individual arms, or they may seek out a gentle and unconfined current into which they extend their arms in a more or less holistic fan. The fan is variable in shape and is very versatile because any individual arm or arms can be twisted by muscular action into exactly the appropriate position and attitude (see Meyer 1979). The flexibility even extends to the formation of communal filtration fans by two or more crinoid individuals (Breimer 1978b).

Neither feeding style would have been available to camerate crinoids. Camerate crinoids had the most rigid calyx of any crinoid group, and their arm systems appear to have been only weakly mobile. Although camerates are pinnulate, there were apparently no muscular connections between brachia, or between arms and calyx (Lane and Burke 1976; Lane 1978a). Most camerate feeding systems must have been rheophilic, with the arms extended across a current to form a filtration fan. But anatomical or behavioral flexibility was not emphasized. Once disposed, the fan would have formed only a passive filter. There would have been a premium on accurate deployment, and the maintenance of the integrity of the fan in any fluctuations of the ambient current. The rigidity of the camerate calyx, and the inclusion of the proximal regions of the arms within it, are part of the appropriate adaptive complex for such a way of life. Rigidity would of course have been advantageous on the behavioral level too: there would have been no benefit from any response to micro-environmental current changes by individual arms. The filtering crown would have had to respond to any environmental change as one integrated unit. Such responses would have been triggered by the sensory elements in the nerve system in the arms, and would have been accomplished by some type of muscle-like action in the stem (see Haugh 1975).

In this model, melocrinitids evolved the rigidity of the camerate calyx and crown to an unusual degree. The support, strengthening, and secure deployment of the arms were apparently major factors in the evolution of the family. Any significant deviation from the standard lay-out of the evolved melocrinitid arm pattern would have seriously prejudiced the integrity of the filter as a whole. The plantation analogy suggests that the melocrinitid arm pattern is ideal for harvesting, but only in a situation where it is fixed as a unit. The pattern can be seen as an extreme extension of the camerate feeding style, and the rigid calyx of the camerates can be seen as pre-adaptive to the support of a heavy, fixed, arm system. In this view, the melocrinitids, and the four other camerate genera with the same arm pattern, are super-camerates in the same way that sauropods are super-dinosaurs, and Quetzalcoatlus is a super-pterosaur.

The camerates failed as a group, in this line of argument, because they lacked the flexibility of other rheophiles. Yet for much of the Paleozoic the rewards of relative rigidity were enough to foster great success for camerates. Perhaps in more restricted sets of environments, super-rigidity was also selected; in the case of the melocrinitids, it was selected over 100 million years, from Late Ordovician to Late Devonian. Melocrinitids occur in areas that were shallow tropical waters, but it is difficult to specify their preferred microhabitat. In the Wenlockian of England, melocrinitids occur with a diverse
shelly fauna including many other crinoids. In the Late Devonian of New York, however, *Melocrinites* often occurs in sedimentary facies which are devoid of other crinoids and of most other benthic invertebrates: for example, the dark shales of the Genesee, New Albany, and Ohio Formations. *Melocrinites* is associated in these occurrences with carbonized wood, leading to the inference that the crinoids may have been pseudoplanktonic (McIntosh 1978). Clearly, field studies of melocrinitids would be most valuable.

It is difficult to avoid the cliche that melocrinitids were "too specialized" for widespread success, but they were supremely adapted for some narrow range of environments. They would, on the other hand, have been less than ecologically ideal in most trophic settings. In economic terms, one would guess that the "capital" and "running" costs for a melocrinitid would have been so high as to prohibit profitable operations except in conditions assuring a high yield over a long term.

The final irony is that even the "ideal" banana plantation as devised by Tanner may never have been put into widespread operation. The West Indian islands for which it was devised became independent, and in most cases moved away from the colonialist plantation economy. In other words, the perceived cost-benefit ratios for banana plantations were changed, and the "ideal" changed with them.

**Unusual Sand Dollars**

Gould and Lewontin (1979) and Gould (1980) strongly advocate constructional morphology as an alternative to functional morphology. I would argue that where a constructional and a functional explanation are alternatives, the functional is to be preferred because it explains more about the organism. The case of the melocrinitids may be relevant here. In a beautiful example of the best that constructional morphology can offer, Seilacher (1979) has described and interpreted many of the skeletal features of sand dollars. In one section, Seilacher discusses the morphology of food grooves on the surfaces of a few unusual sand dollars in the context of constructional constraints, using a characteristically ingenious analogy with weaving patterns. However, these grooves are advective structures bearing food towards a central mouth. They are disposed on the skeleton in the same pattern as the advective structures of melocrinitid crinoids and banana plantations (Fig. 2C). They might receive similar functional interpretation after close analysis. Naturally, the development of a functional interpretation of these grooves would not necessarily alter anything of Seilacher's analysis, which by its nature is strictly morphogenetic; but it would add the *adaptive* basis for the constructional form.

As in the camerate crinoids, the development of banana plantation patterns is uncommon among sand dollars. Only the Echinarchniidae and the Arachnoididae show the pattern, and have evolved it independently (Seilacher 1979). Alone among graptolites, *Goniograptus* has banana plantation branching of the rhabdosome (Bulman 1970). In all these cases, then, the "ideal" pattern is the exception, not the rule.

**The Rarity of 'Ideal' Structures**

The melocrinitids show a structure that is close to a theoretical ideal, one which we would expect to find as the triumphant culmination of an adaptive lineage. Yet the structure was in the end unsuccessful, and is neither abundant nor frequent in the fossil record. Other, apparently less ideal arm patterns dominate past and present crinoid assemblages. Does this imply a failure of the adaptationist's way of looking at organisms? (Gould and Lewontin 1979; Gould 1980). No: it means that the adaptationist (and his critics) are not entitled to expect that the simplicity of an ideal structure should automatically be the most adaptive in a real world. It means that natural selection involves a cost-benefit analysis, and implies that such analysis should be routinely considered in the functional interpretation of organisms by paleobiologists. The apparently ideal structure may often not be worth building. We may wish to have a Mercedes, but settle for a Volkswagen.

In studying melocrinitid crinoids, one can marvel at their complexity and their beauty, understand their rarity, and at the same time admit with resignation that "the best" as judged by natural selection and cost-benefit analysis may not coincide with "the best" as judged by the functional analyst (and his critics) on the basis of theoretical models. Adaptive perfection
may be approached more closely by the normal than by the extravagant.

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