

THE ORIGIN OF ARTICULATE CRINOIDS

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ABSTRACT. Cladistic analysis of various Palaeozoic and post-Palaeozoic crinoids indicates that the latter constitute a monophyletic clade, the Articulata, whose origins lie among the late Palaeozoic Ampelocrinidae of the inadunate order Cladida. The Cladida, raised to subclass alongside the Disparida and Camerata, is extended to include the Flexibilia and Articulata. Early articulates differ from some Palaeozoic cladids only in the absence of an anal plate in the adult cup, but a suite of characters can be used to identify progressively more derived members of the articulate stem group. Re-evaluation of two stem-group articulate families, the Ampelocrinidae and Cymbiocrinidae, indicates that there is little to justify retaining them as distinct families and that fewer than half of the constituent genera should be retained there. The remainder have been either wrongly assigned (*Allosocrinus*, *Halogetocrinus* and *Paracymbiocrinus*) or are based on material inadequate for establishing phylogenetic position (*Armenoocrinus*, *Arroyocrinus*, *Moundocrinus*, *Oklahomacrinus*, *Polusocrinus*, *Spheniscocrinus*, *Aenignocrinus* and *Lecobasicrinus*). Furthermore, several genera (including *Nowracrinus* and *Tibrachyrcrinus*) currently excluded show clear affinities with the Ampelocrinidae.

In his seminal work of 1821, J. S. Miller erected the 'Division' Articulata for a number of Mesozoic and extant taxa. Since that time there has been a general consensus amongst crinoid workers that most, if not all, post-Palaeozoic crinoids can be assigned to the Articulata (since afforded the status of subclass) while all Palaeozoic crinoids are excluded. Although Miller included only a selection of Mesozoic and extant taxa in his Articulata, nowhere did he state that Palaeozoic taxa were excluded from this group. In fact, Miller's original description (see below) is sufficiently imprecise that it encompasses a range of late Palaeozoic forms.

Since Miller's work, the articulates have remained a rather poorly-defined group, almost invariably regarded as synonymous with post-Palaeozoic crinoids. Previous diagnoses have utilized characters which, although ubiquitous among post-Palaeozoic taxa, are by no means unique to them. Partly as a consequence of this, the relationship of articulates to late Palaeozoic taxa has never been investigated adequately and they have, at various times, been considered to have affinities with a wide variety of Palaeozoic taxa. Much of this confusion has arisen as a result of the inadequate documentation of many Palaeozoic crinoid taxa, thereby hindering the compilation of a comprehensive database by which to compare articulates with their putative ancestors. This is further compounded by the huge diversity of crinoids in the Carboniferous and Permian so that at present it is impossible to produce an overall phylogeny of, for instance, families within the paraphyletic subclass Inadunata.

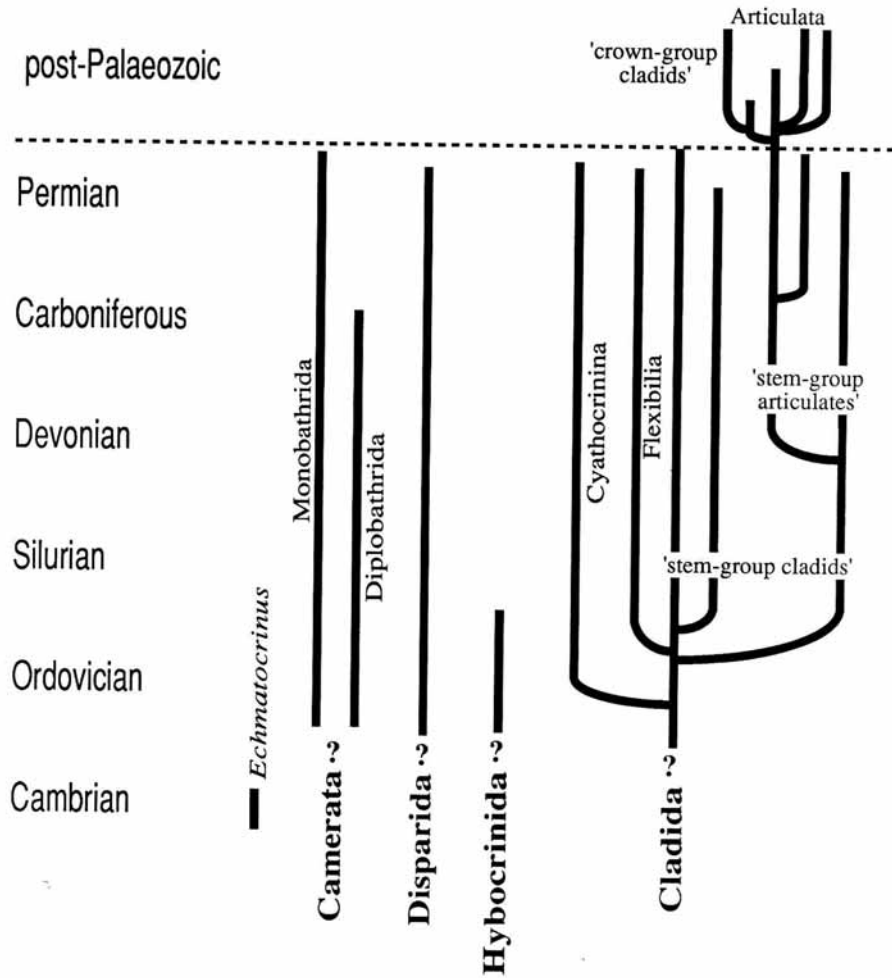
Despite these obstacles, we have attempted, by cladistic analysis, to reinterpret the relationship of post-Palaeozoic crinoids to the various Palaeozoic crinoid taxa with which affinities have been suggested in the past. This is based upon a re-examination of the morphology and relationships of Triassic crinoids and of various Palaeozoic taxa whose taxonomic position is critical to our understanding of the phylogeny of stem articulates.

DEFINITION OF THE SUBCLASS ARTICULATA

The currently accepted crinoid classification, as used in the *Treatise on Invertebrate Paleontology* (Moore and Teichert 1978), recognizes four main taxonomic groupings, each accorded subclass rank. The Articulata are exclusively post-Palaeozoic whilst the Camerata, Inadunata and Flexibilia are confined to the Palaeozoic. The camerates comprise two orders, the Monobathrida and

Diplobathrida. The inadunates contain three orders, the Disparida, Cladida and Hybocrinida, with the Cladida further subdivided into the suborders Cyathocrinina, Dendrocrinina and Poterocrinina. The Coronata have been transferred from the Inadunata to the Blastozoa (Brett *et al.* 1983). Increasingly it has been recognized that not all of these divisions can justifiably be retained as natural taxa. The broad relationships of the various taxa are summarized in Text-figure 1.

The Articulata, the earliest of the four major crinoid taxa to be established, is also the one to have experienced the least revision. In his original description Miller (1821, p. 17) stated: 'The joints resting on the first or superior columnar joint, and forming the cup containing the viscera, articulate by liplike and transverse processes, having a minute perforation.' The 'liplike and transverse



TEXT-FIG. 1. Stratigraphical distribution and inferred relationships of the major crinoid clades recognized herein.

processes' we interpret to refer to the fulcral ridge and the muscular and ligament fossae on the radial plates, while the 'minute perforation' presumably refers to the axial canal, which pierces this articulation. Although his description implies that only a single canal is present, his inclusion within the Articulata of *Encrinurus*, which has paired axial canals, suggests that he considered the presence, rather than the number, of axial canals to be the critical character. However, he described another division (Miller 1821, p. 66), the Crinoidea Semiarticulata, in very similar terms: 'The plate-like joints resting on the superior columnar joint, and forming the cup containing the viscera, articulate by transverse processes having a minute central perforation.' From this it is clear that the primary character which Miller used to define the Articulata was the presence of well-developed muscular and ligament fossae on the radial-brachial articula rather than the presence of an axial canal in the radials. Significantly, he did not mention in either description whether the cup is perfectly symmetrical or instead has the pentaradiate symmetry interrupted by the addition of one or more anal plates. It is the lack of an anal plate in the cup of adult post-Palaeozoic crinoids that is considered now to be one of the primary diagnostic characters of the Articulata (Simms 1988).

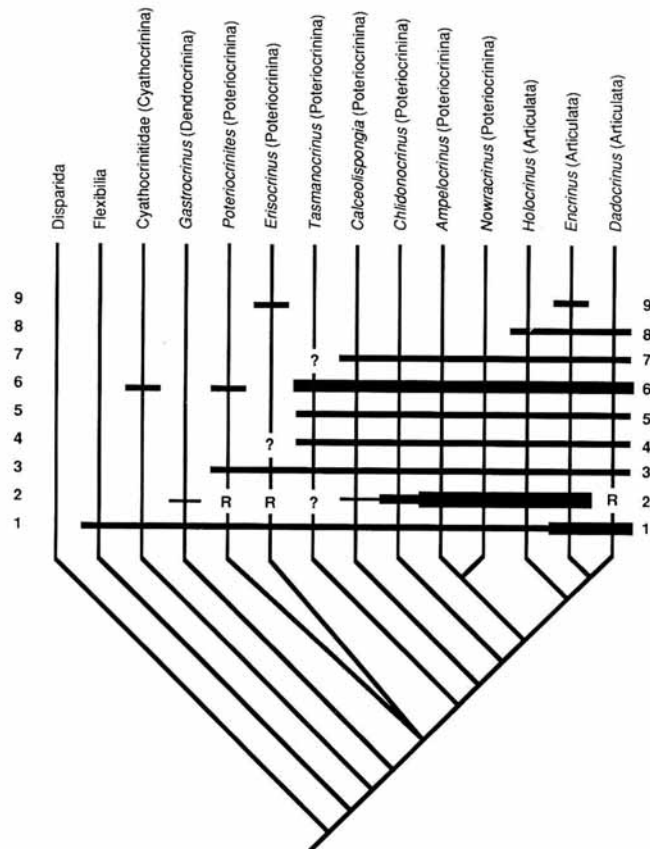
It is clear from the characters listed by Miller (1821), and from reference to our cladogram (Text-fig. 2), that the Articulata, as defined by Miller, must encompass a significant number of Palaeozoic taxa in addition to the post-Palaeozoic forms, which without exception can be assigned to his original concept. However, it would appear that all subsequent attempts to define the Subclass Articulata have, in fact, been based upon the morphology of post-Palaeozoic crinoids without direct reference to Miller's original description. Attempts to produce a concise and unambiguous definition of the articulates (in the sense of workers since Miller and hence synonymous with post-Palaeozoic crinoids) repeatedly have proven problematic, and it has been necessary to refer to a variety of characters additional to those listed by Miller. The definition given by Rasmussen (*in* Moore and Teichert 1978, p. 816) incorporates most of the diagnostic characters of post-Palaeozoic crinoids, but it lacks conciseness and cites so many exceptions found in highly derived taxa that its usefulness is obscured. At present no single character can be considered diagnostic of post-Palaeozoic crinoids, since examples of Palaeozoic taxa can be found which also possess such characters, either through convergence or through shared common ancestry. Nonetheless, articulate crinoids possess an apparently unique combination of characters and it is this character suite which establishes their monophyly. Each of these characters defines an increasingly inclusive clade, the crown group of which is characterized by the absence of an anal plate in the adult cup and corresponds to the articulates (post-Palaeozoic crinoids) as interpreted by later authors.

MORPHOLOGICAL CHARACTERS OF ARTICULATES

The characters which we have found useful in defining the crown group and various plesions within the stem group of post-Palaeozoic crinoids, and which are incorporated in the cladogram of Text-figure 2, are discussed below.

Cup dicyclic or cryptodicyclic. Crinoid cups can be grouped into two main types on the basis of the number of circlets, primitively each of five plates, of which they are constructed; those in which the cup comprises two circlets of plates are termed monocyclic, while those in which a third circlet is present are termed dicyclic. In some dicyclic taxa it can be proven that the lowermost circlet (termed infrabasals) are vestigial or secondarily lost; in such cases the cup is termed cryptodicyclic or pseudomonocyclic. All post-Palaeozoic crinoids, and their stem group, have a cup which is either dicyclic or cryptodicyclic, as do other cladids, flexibles and diplobathrid camerates.

The primitive condition among post-Palaeozoic crinoids, found also in the Palaeozoic taxa mentioned above, is for the cup to be dicyclic with the infrabasals clearly exposed, as in the early Triassic *Holocrinus*. In virtually all other articulates the infrabasals are greatly reduced in size and lie concealed between the overlying circlet (termed basals) and the top of the stem (Clark 1908; Simms 1989, pl. 10, fig. 34); hence they are cryptodicyclic. Although derivation of articulates from monocyclic ancestors has been suggested on more than one occasion (Wachsmuth and Springer 1886, 1889; see below), the presence of infrabasals in the former group does not



TEXT-FIG. 2. A cladogram for some early articulate crinoids and various Palaeozoic taxa which have been proposed as ancestral to the articulates or whose morphology suggests close affinities with them. Character states as listed below (R = character reversal).

- | Primitive | Derived |
|--------------------------------------|--|
| 1. Cup monocyclic | Cup dicyclic (thin line)
Cup cryptodicyclic (thick line) |
| 2. No cirri on stem | Cirri with multiradiate articular throughout (thin line)
Cirri with multiradiate articular distally and
transverse ridge articular proximally (medium line)
Cirri with transverse ridge articular throughout (thick line) |
| 3. Arms non-pinnulate | Arms pinnulate |
| 4. Brachial articular without fossae | Brachial articular with ligamentary and clearly
defined muscular fossae |
| 5. First arm division variable | First arm division on IBr2 |
| 6. Entoneural system open | Entoneural system enclosed in single canal (thin line)
Entoneural canal enclosed in paired canal (thick line) |
| 7. No syzygial articular in arms | Syzygial brachial pairs in arms |
| 8. Anal plate(s) in/above adult cup | Anal plates absent from adult cup |
| 9. Uniserial arms | Biserial arms |

support this. Such a scenario would require the convergent evolution of a third cirlet of plates in Palaeozoic and in post-Palaeozoic crinoids, for which there is no supporting evidence.

Cirri. Although true cirri are absent from many post-Palaeozoic crinoid taxa, they are present in *Holocrinus* and are considered to represent the primitive condition for articulate crinoids (Schubert *et al.* 1992). Brett (1981) suggested that cirri evolved independently in several groups. Certainly, it seems probable that the cirri of camerates were derived independently of those in inadunates. In both groups the presence of cirri is a derived trait and they are lacking in early taxa. Within the inadunates, which is a demonstrably paraphyletic group (see discussion below), it is highly probable that cirri evolved more than once. Cirri are found in the disparid genus *Pisocrinus* and in the Myelodactylidae, though considering the aberrant morphology of the latter group it is quite possible that cirri evolved independently in these two groups. Since there is little evidence for a close phylogenetic relationship between disparids and cladids (Donovan 1988), it is probable also that the cirri in these disparid taxa were derived independently of the cirri found in the cladid orders Dendrocrinina and Poteriocrinina. However, since the present distinction between dendrocrinine and poteriocrinine cladids is largely artificial, with the Poteriocrinina best regarded as a 'grade group' comprising a variety of the more derived cladids, it is more parsimonious to suggest that cirri evolved only once in the dendrocrinine-poteriocrinine clade.

This cannot be assumed unequivocally since documentation of the morphology of cirri is lacking for most taxa. Furthermore, initial observations suggest a striking morphological distinction between the cirri of most articulates and those of most cirri-bearing cladids. This has been interpreted as evidence for an independent origin for cirri in the two groups (Simms 1988). In the slender cirri of articulates, such as those of isocrinids and comatulids, the articula bear a prominent transverse ridge which articulates with a corresponding groove on the proximal face of the next cirral ossicle (Pl. 1, figs 2-3). This type of cirral articulation is found in *Holocrinus*, the earliest articulate (Schubert *et al.* 1992) and in some encrinids (Hagdorn 1982), but occurs also in several late Palaeozoic genera such as *Ampelocrinus*, *Cymbiocrinus* and *Nowracrinus*. However, in many other poteriocrinine cladids the cirral articulations are essentially the same as those of the columnals, typically taking the form of a multiradiate symplectial articulum (Pl. 1, fig. 9). Even in *Calceolispongia*, which in several other respects appears to lie close to the common ancestry of articulate crinoids (Text-fig. 2), the cirral articula are symplectial (Webster 1990). Nonetheless, the synapomorphies which *Calceolispongia* shares with *Ampelocrinus* and its allies suggest that transverse-ridge cirri may have been derived from the symplectial-type cirri rather than having an independent origin. *Calceolispongia* is of importance, therefore, in lying close to the common ancestry of all crinoids with transverse ridge cirri. Critical evidence that the transverse-ridge-type cirri were derived from the multiradiate symplectial-type cirri comes from a series of specimens from the Pennsylvanian (upper Bashkirian-lower Moscovian) Marble Falls Formation of Texas, described by Strimple and Watkins (1969) as *Chlidonocrinus echinatus*. In this species the nodal columnals each bear five cirral scars with prominent transverse-ridge-type articula (Pl. 1, fig. 1). The first four cirral ossicles have similar depressed elliptical articula, with the same groove-and-ridge style of articulation clearly visible in lateral view (Pl. 1, figs 1, 10). The fifth cirral ossicle is unique in having on its proximal face a depressed elliptical articulum with transverse ridge, tapering distally to a circular articulum with a multiradiate symplectial type of articulation (Pl. 1, fig. 10). From the sixth cirral ossicle distally the ossicles are cylindrical with multiradiate articula, although in more distal parts of the cirri (which may comprise more than 40 ossicles) the crenulae may be very weakly developed or absent. Multiradiate cirral articula also occur in several Triassic isocrinid taxa, but it remains to be ascertained whether this character arose through convergence in these taxa or represents a heterochronic trait related to the ancestral character state. Cirri are absent from the stem of many articulates, including a number of Triassic taxa such as *Dadocrinus* (Text-fig. 2), but it can be demonstrated that this represents a secondary loss and is no indication of a close phylogenetic relationship with any Palaeozoic taxa which lack cirri.

Pinnulate arms. Traditionally, branches which arise from opposite sides of alternate brachials, and which do not branch themselves, are termed pinnules, whereas side branches which show further branching, and typically are more widely spaced, are termed ramules. The relative size of these side branches also is of importance; pinnules are significantly smaller than the arms from which they arise, whereas ramules typically are of comparable diameter to that of the arm. More recent attempts to define these types of side branching have judged the most significant difference to be the presence of a muscular articulation at the base of each pinnule, where it articulates with the arm, whereas ramules lack such muscular articula (Lane and Breimer 1974; Broadhead 1988). However, neither definition is entirely satisfactory, since the former would exclude the branched pinnules of *Nowracrinus* (Willink 1979), while in the case of the latter it is difficult to establish the

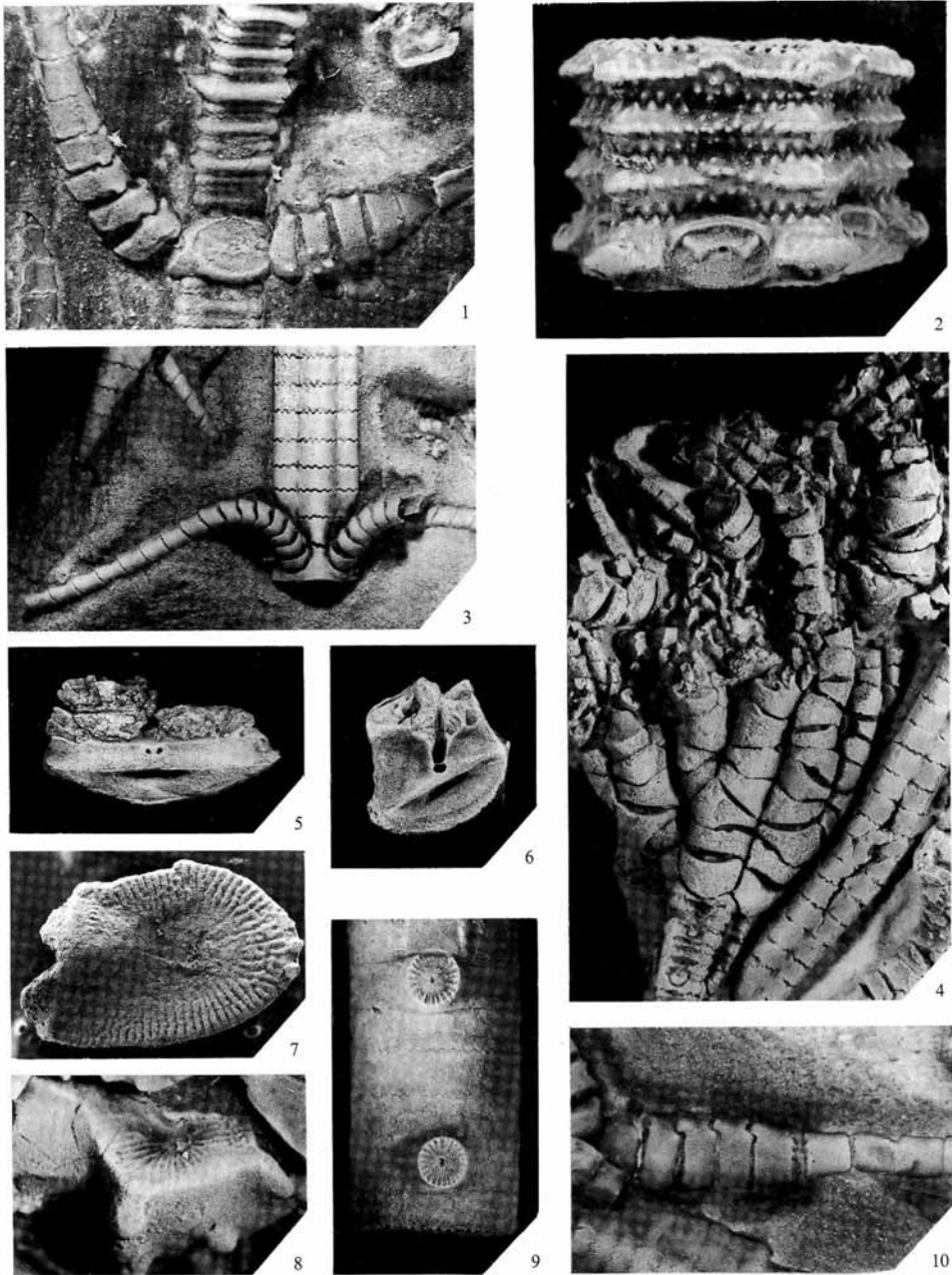
nature of such articula, whether muscular or ligamentary, in most fossil material (see discussion below). Furthermore, since pinnules are a derived trait in both camerates and cladids they evidently are not homologous structures. Consequently, the precise definitions cited above are unwarranted unless separate terms are coined for the 'pinnules' of camerates and cladids. We consider that the term 'pinnule' should be applied more informally to small side branches which arise from a majority of the brachials in a crinoid arm. No sense of homology is implied in this definition, and each case should be treated on its own merits in any phylogenetic study.

Pinnules are absent from the Hybocrinida, Flexibilia, Cyathocrinina and most Disparida and Dendrocrinina. The pinnules of Poteriocrinina and advanced Dendrocrinina, although probably homologous with each other and with those of articulates, almost certainly are convergent with those of camerates, since they are found only in the more derived cladids which appeared long after they had diverged from the camerates. Without exception the arms of adult post-Palaeozoic crinoids bear pinnules at regular intervals (Text-fig. 3). In all cases a single pinnule arises from alternate sides of successive brachials, though they are not developed on axillary brachials or on proximal brachials of pairs united by ligamentary articulations (hypozygal brachials). No examples of hyperpinnulation (more than one pinnule per brachial) or branching pinnules (ramules) are known among post-Palaeozoic crinoids. Pinnules in the majority of the more derived Poteriocrinina though lie close to the articulate stem group do not differ significantly from those of articulates themselves, though the Permian *Nowracrinus* represents a notable exception since the pinnules dichotomize several times (Willink 1979), and hence equally may be termed ramules.

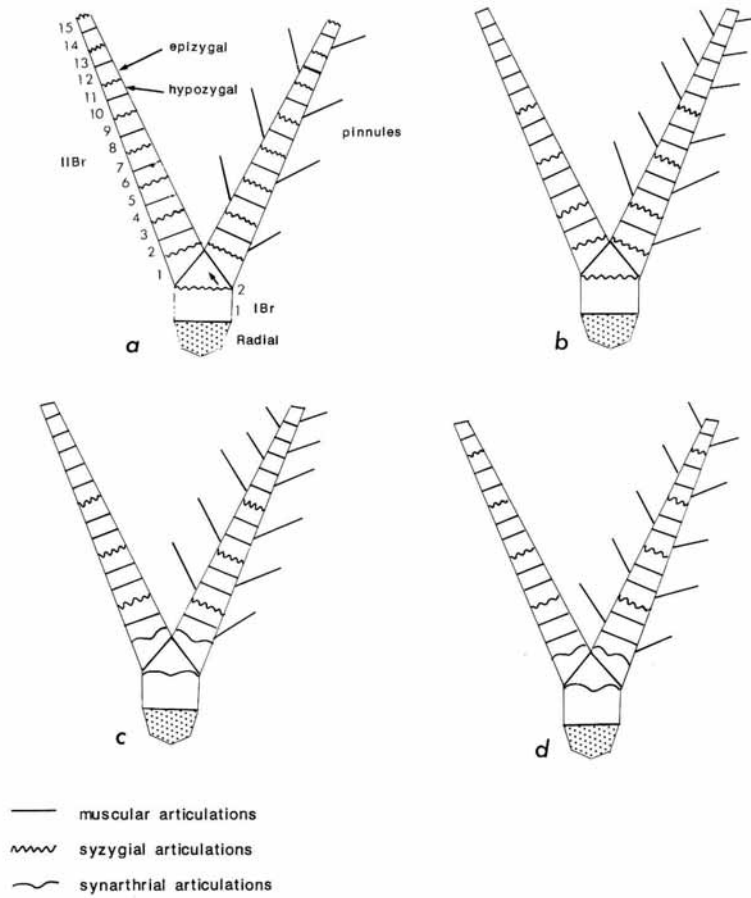
Muscular articula in arms. Muscular brachial articula of the type characteristic of articulates, with a transverse ridge bounded by muscular and ligament fossae, are well developed in most post-Palaeozoic crinoids. The presence of these features was the primary criterion in Miller's (1821) original description. Among Palaeozoic taxa, muscular brachial articula appear confined to certain Poteriocrinina though their presence, or absence, is difficult to prove conclusively (Lane and Macurda 1975) and is rarely stated in descriptions of Palaeozoic taxa. Ausich (1977) suggested, on the basis of variations in stereom type on the articula of the radial-brachial articulation, that muscles may have been present between the radials and arms

EXPLANATION OF PLATE I

- Figs 1, 8, 10. *Chlidonocrinus echinatus* Strimple and Watkins, 1969 ('Cladida'; stem-group Articulata). Pennsylvanian, Lemons Bluff Member, Marble Falls Formation (upper Bashkirian/lower Moscovian); San Saba County, Texas, USA. 1, USNM S5136; part of stem and cirri of paratype showing the transverse ridge by which the cirri articulate on the cirrinodal and the ridge-and-groove arrangement by which the proximal ossicles of the cirri articulate with each other, $\times 7.5$. 8, USNM S5136; syzygial articulum on secundibrach, $\times 12$. 10, USNM S5174; proximal region of cirrus showing the ridge-and-groove style of articulation between the first five ossicles and the development of a multiradiate symplectial type of articulation between the fifth and sixth ossicles and further distally, $\times 6.5$.
- Figs 2, 6. *Isocrinus robustus* (Wright, 1858) (Articulata). Jurassic, Carixian; Humber side, England. 2, BM E70492; pluricolumnal showing the transverse ridge on the cirral scar characteristic of articulates and more advanced representatives of the articulate stem group, $\times 6$. 6, BM E70485; distal articulum of proximal secundibrach showing development of distinct ligament and muscular fossae and a single axial canal, $\times 4$.
- Figs 3-4. *Balanocrinus gracilis* (Charlesworth, 1847) (Articulata). 3, BM E70331; part of stem and cirri showing the ridge-and-groove style of articulation between cirral ossicles; Jurassic, Domesian; Dorset, England, $\times 3$. 4, BM E70344; proximal stem and crown showing the concealment of the infrabasals, arm branching on the second primibrachial (IBr2) and the presence of both muscular and syzygial/synarthrial articulations in the arms; the two arms on the left-hand side terminate at the syzygies on the distal articula of IBr3; Jurassic, Domesian; Gloucester, England, $\times 2.5$.
- Fig. 5. *Encrinus liliiformis* Lamarck, 1801 (Articulata), BM E49926; distal articulum of radial plate pierced by paired axial canals; Triassic, Ladinian, Germany, $\times 3.5$.
- Fig. 7. BM E70631; syzygial articulum on brachial of indeterminate isocrinid (Articulata). Jurassic, Carixian, Gloucestershire, $\times 15$.
- Fig. 9. BM E14306; pluricolumnal of indeterminate ? cladid crinoid showing the multiradiate symplectial type of cirral articulation characteristic of most Palaeozoic crinoid taxa; Dinantian, Ironstone Beds; Ridsdale, Northumberland, England, $\times 4$.



SIMMS and SEVASTOPULO, *Chlidonocrinus*, *Isocrinus*, *Balanocrinus*, *Encrinus*



TEXT-FIG. 3. Distribution of pinnules and syzygial articulations in the arms of an ampelocrinid (Cladida; stem-group Articulata) and representative articulate taxa. *a*, *Nowracrinus* (Ampelocrinidae). *b*, *Holocrinus* (Articulata: early Triassic). *c*, Isocrinida (Articulata: late Triassic to Recent). *d*, Millericrinida (Articulata: ?mid-Triassic to Recent).

in the disparid *Pisocrinus*. This may have been true of other disparids (Ubachs in Moore and Teichert 1978, p. 164) and has been suggested also for the camerate *Planacrocrinus* (Ubachs in Moore and Teichert 1978). However, although in extant crinoids there is some correlation between stereom type and tissue type, there still exists considerable variation between species in the morphology of the stereom associated with muscle attachment (Ausich 1977). Furthermore, Smith (1980) has shown that, in echinoids, muscular tissue is found associated with five out of the seven main stereom types. Considering the phylogenetic distance between articulate crinoids and certain of the Palaeozoic groups, such as camerates or disparids, it is perhaps to be expected that considerable differences might exist between the stereom types associated with muscular tissue in the various major Palaeozoic clades. This is even more likely if it is considered that muscular arms may have evolved more than once in the Crinoidea, and so it is perhaps unrealistic to expect to find the same stereom

type associated with muscular tissue throughout the history of the group. On purely functional grounds, we find it difficult to visualize how most Palaeozoic crinoids could have operated in the absence of muscular articulations in the arms, since ligamentary tissue, even of the catch-connective type (Wilkie and Emson 1988), cannot move parts of the skeleton actively but can only hold them in a particular position. The currently accepted notion, that most Palaeozoic crinoids lacked any musculature in the arms, seems incompatible with their remarkable success in late Palaeozoic times even if catch-connective tissue did play a more important role early in the history of echinoderms (Wilkie and Emson 1988). We believe that muscular arms were far more prevalent in Palaeozoic crinoids than generally has been accepted, but that details of this musculature, and the associated stereom, may have differed significantly from that of articulates and hence may prove difficult to identify in fossil material.

Arms branching on the first primibrach (IBr2). With the exception of a few highly derived taxa, the arms branch on IBr2 in all post-Palaeozoic crinoids (Pl. 1, fig. 4), this being the primitive state for Triassic and later taxa. This character appears much more strongly fixed than in any Palaeozoic taxon other than the camerates, which also have arms branching almost invariably at IBr2. Only in a small minority of articulate taxa do the arms remain unbranched or divide at any other position, but in all instances it can be demonstrated that such taxa are comparatively derived. Few examples are known prior to the Cretaceous and, with the exception of one morphotype (?species) of *Dadocrinus*, in which the arms remain unbranched, arm branching at IBr2 is ubiquitous among Triassic crinoids.

Among late Palaeozoic cladids considerable variation exists in the position of the first arm division, although it occurs most frequently at IBr1. The Erisocrinidae are one such example with the first axillary at IBr1 and this, together with other characters, suggests their biserial arms and bowl-shaped cup to be convergent with the morphology of the Triassic family Encrinidae rather than indicating any close phylogenetic relationship between these taxa (see below). A significant proportion of the remaining cladid genera have arms which branch at IBr2, although in many cases this is more probably due to convergence and they otherwise share few, if any, synapomorphies with articulates. However, in those taxa which share several 'articulate' characters the arms usually branch at IBr2. These include the Permian *Nowracrinus* (Willink 1979) as well as a number of other genera (see Table 1).

Perforate brachials and thecal plates. All post-Palaeozoic crinoids have enclosed entoneural canals piercing the brachial and thecal plates. The presence of these entoneural canals, enclosed and clearly differentiated from the ventral groove, was one of the main characters which Miller (1821) used in his definition of the Articulata and Semiarticulata. All early Triassic and the great majority of Middle Triassic crinoid taxa have paired axial canals (Pl. 1, fig. 5), or in some cases fused pairs, but by late Ladinian and early Carnian times, a significant proportion of taxa had unpaired canals (Pl. 1, fig. 6), the dominant condition in post-Carnian crinoids. Pairing of axial canals in the brachial and thecal plates evidently is the primitive condition among articulates. Single entoneural canals have been documented for the brachials of a variety of Palaeozoic taxa, including the cyathocrinitids, and a few camerates and flexibles. However, in only a relatively small number of late Palaeozoic taxa have paired entoneural canals been observed. A triple entoneural canal system has also been documented in the brachials of an unidentified cladid from the Brigantian (Lower Carboniferous) of Scotland (Sevastopulo and Keegan 1980), though the relationship of this material to articulates, or their stem group, remains unclear. In flexibles, camerates, disparids, hybocrinids and most cladids the entoneural system was not enclosed in the thecal plates (Ubahgs in Moore and Teichert 1978, p. 193), though in many taxa a very short entoneural canal was developed through the distal part of the radial and the most proximal brachial or, in some taxa, extended farther along the arms. However, although it is known that the entoneural system was not enclosed in the thecal plates of most Palaeozoic crinoids, data on the presence or absence of this character is lacking for many of the more derived cladids and so it is impossible to ascertain when this character first appeared.

Teichert (1949) documented a series of canals located just beneath the inner surface within the thecal plates of the Permian *Calceolispongia*. The largest of these canals, which he termed primary canals, appear to correspond fairly closely to the expected position of the entoneural system in extant crinoids. Certainly, the canals in *Calceolispongia* show a remarkable similarity to those of *Marsupites* (see Sieverts 1927), the most obvious difference being that the primary canals are paired in *Calceolispongia* and single in *Marsupites* (see Moore and Teichert 1978, p. 193, fig. 163).

It is possible that the presence of entoneural canals penetrating the thecal plates will prove to be a critical character in tracing the phylogeny of the articulates and their stem group, though at present this character is too poorly documented for its value to be realized fully. However, enclosure of the entoneural system within

TABLE 1. Data on character distribution for genera included within the Ampelocrinidae and Cymbiocrinidae by Moore and Teichert (1978) and for other taxa considered here to have close affinities with *Holocrinus* and stem-group articulate. Taxa marked with an asterisk are those which we consider can be justifiably included within the emended Ampelocrinidae.

	Cup	Cirri	Pinnules	Muscular arms	Arm branching	Axial canal	Syzygial pairs	Anal plates	Arm type
Ampelocrinidae									
* <i>Ampelocrinus</i>	dicyclic	transverse	alternate	yes	I Br2	paired	common	1	uniserial
<i>Armenocrinus</i>	dicyclic	?	?	?	I Br2/4	?	?	1	uniserial
<i>Arroyocrinus</i>	dicyclic	?	alternate	?	I Br1	?	absent	3	uniserial
* <i>Chlidonocrinus</i>	dicyclic	transverse	alternate	yes	I Br2	?	some	1	uniserial
<i>Halogetocrinus</i>	dicyclic	present	present	?	I Br3/4	?	some	1	uniserial
<i>Moundocrinus</i>	dicyclic	?	alternate	yes	I Br2	?	?	1	uniserial
<i>Polusocrinus</i>	dicyclic	?	alternate	?	I Br2	?	?	3	uniserial
<i>Spheniscoerinus</i>	dicyclic	?	alternate	yes	I Br2	?	absent	1	uniserial
Cymbiocrinidae									
* <i>Cymbiocrinus</i>	dicyclic	present	alternate	yes	I Br2	?	common	1	uniserial
<i>Aenigmocrinus</i>	dicyclic	?	alternate	yes	I Br2	?	?	2	uniserial
* <i>Aesiocrinus</i>	dicyclic	present	alternate	yes	I Br2	paired	?	1	uniserial
<i>Allosocrinus</i>	dicyclic	absent	alternate	yes	no	?	common	1	uniserial
<i>Lecobasicrinus</i>	dicyclic	?	alternate	?	I Br2	?	?	1	uniserial
<i>Oklahomacrinus</i>	dicyclic	present	alternate	yes	I Br2	?	?present	1	uniserial
<i>Paracymbiocrinus</i>	dicyclic	?	hyper.	yes	I Br2	?	?	1	uniserial
* <i>Proallosocrinus</i>	dicyclic	?	alternate	yes	I Br2	paired	some	1	uniserial
Miscellaneous									
* <i>Tribrachyrcinus</i>	dicyclic	present	alternate	yes	I Br2	paired	common	3/4	uniserial
<i>Calceolispongia</i>	dicyclic	multiradiate	alternate	yes	no	paired	common	1	uniserial
<i>Jimbacrinus</i>	dicyclic	absent	alternate	yes	no	paired	some	1	uniserial
<i>Meganotocrinus</i>	dicyclic	multiradiate	alternate	yes	I Br3/4	?	some	1	uniserial
<i>Araeocrinus</i>	dicyclic	?	alternate	yes	I Br4/5	?	common	3	uniserial
<i>Chariantocrinus</i>	dicyclic	in pairs	alternate	?	I Br17+	?	?present	3	uniserial
* <i>Nowracrinus</i>	dicyclic	transverse	branching	yes	I Br2	paired	common	1	uniserial
<i>Tasmanocrinus</i>	dicyclic	?	alternate	yes	I Br2	paired	?	1	uniserial
<i>Corythocrinus</i>	dicyclic	absent	alternate	yes	I Br3	?	common	1	uniserial
<i>Holocrinus</i>	dicyclic	transverse	alternate	yes	I Br2	paired	common	0	uniserial

the brachials appears more prone to convergence, having occurred independently on a number of occasions, though the presence of paired entoneural canals appears to have been restricted to the articulates and their immediate stem group. Although this character too has been largely overlooked in most descriptive work, enough is known of its taxonomic distribution for it to be of considerable importance in elucidating the phylogeny of articulate crinoids.

Syzygial pairs of brachials in arms. All post-Palaeozoic crinoids have a muscular articulation between the radial and first brachial (Pl. 1, fig. 5) (although this may be greatly modified, by enlargement of the aboral ligament fossa, in certain highly derived taxa, e.g. *Seirocrinus* and *Apiocrinites*), followed by a ligamentary articulation between the first and second brachial (I Br1-2). In the primitive state among articulates this articulation is syzygial (Pl. 1, fig. 7) and followed by further syzygial articulations at I I Br1-2, I I Br3-4, I I Br5-6, etc., alternating with muscular articulations at I Br2-I I Br1, I I Br2-3, I I Br4-5, etc. (Text-fig. 3). In every instance pinnules arise only from the distal brachial (epizygial) of a syzygial pair, and the proximal brachial (hypozygal) lacks a pinnule. In virtually all post-Palaeozoic taxa this regular alternation of syzygial and muscular articulations is present only in the proximal part of the arms and is lost as syzygies become more widely spaced in the distal parts of the arms. In most articulates syzygial articulations typically are developed at I I Br3-4 and

IIBr6-7 as well as more irregularly distal to this, although in the Millericrinida they are found instead at IIBr4-5 and IIBr7-8 (Taylor 1983; Text-fig. 3D). Furthermore, the most proximal syzygies (at IBr1-2 and IIBr1-2) are often modified into a synostosomal or synarthrial articulation in more derived members of the Articulata (Pl. 1, fig. 4).

Among Palaeozoic crinoids this pattern of alternating muscular and syzygial articulations, with pinnules restricted to the epizygals, is uncommon and confined to a subset of those Poteriocrinina which have typical 'articulate-type' muscular articulations in the arms (Pl. 1, fig. 8). Furthermore, in descriptions of Palaeozoic taxa, syzygies often have been identified only by the arrangement of pinnules on the arms rather than by direct observation of the brachial articula, so in some instances their presence must remain equivocal. The taxonomic treatment, within Moore and Teichert (1978), of genera considered to possess syzygial pairs of brachials is symptomatic of the chaos which currently surrounds the taxonomy of Palaeozoic crinoids. It includes representatives of the Ampelocrinidae, placed within the Superfamily Agassizocrinacea; the Cymbiocrinidae in the Texacrinacea; the Corythocrinidae in the Scytalocrinacea; and *Araeocrinus*, placed in the Rhenocrinidae of the Superfamily Rhenocrinacea. Cladistic analysis of certain of these from both the Ampelocrinidae and Cymbiocrinidae demonstrates them to constitute the stem members of a monophyletic clade incorporating the post-Palaeozoic crinoids as crown group (Text-fig. 2). The present separation into disparate superfamilies is, therefore, quite unjustified. Furthermore, a reappraisal of the morphology of constituent genera currently placed within the Ampelocrinidae and Cymbiocrinidae reveals that for at least half of them there is, at best, insufficient data to establish their phylogenetic position or, at worst, clear evidence that they bear no close phylogenetic relationship with either family (Table 1).

Anal plate in adult cup. The dorsal cup in adult articulates characteristically exhibits an unbroken pentamerous symmetry, comprising two, or sometimes three, circlelets of five plates each. In contrast, this symmetry is interrupted in most cladid crinoids by the presence of one or more additional plates, termed anal plates, in the posterior, or CD, interray of the cup. Ubaghs (*in* Moore and Teichert 1978) questioned whether anal plates are homologous throughout the Class Crinoidea although their homology within the Cladida seems probable. However, it is clear that their reduction and loss from the cup has occurred independently on several occasions (Simms 1990a). Among the Poteriocrinina the anal series usually includes two major elements, the radianal and the anal X. Although absent in adult articulates an anal plate does occur in the cystidean and pentacrinoid stages of some comatulids, and presumably other post-Palaeozoic crinoids. Ubaghs (*in* Moore and Teichert 1978) discussed the origin and development of the radianal and anal plates and concluded that the single anal plate in juvenile articulates is homologous with the radianal, rather than with the anal X.

It is only the absence of an anal plate in the adult cup which distinguishes the post-Palaeozoic crown group (articulates) from their stem group representatives among Palaeozoic taxa. However, the absence of an anal plate is not, in itself, sufficient to establish that a given crinoid can be referred to the crown group, since this character shows convergence in a number of Palaeozoic taxa. Taxa lacking an anal plate in the cup are known among camerates and flexibles, and there are numerous other examples among the inadunates. Among late Palaeozoic Poteriocrinina several groups exhibit a reduction in the number of anal plates in the cup. Many genera retain only a single plate, the anal X, whilst some lose it. A large proportion of the latter taxa are aberrant, highly neotenous forms which can be shown, from other aspects of their morphology, to have no close phylogenetic relationship to post-Palaeozoic crinoids. Certain of the Erisocrinacea represent a notable exception to this. In *Erisocrinus* and *Sinocrinus* the anal plate is vestigial or absent and this, together with the biserial arms and bowl-shaped cup, renders both genera superficially similar to the Triassic Encrinidae. However, in all of those taxa which lie close to the stem group of post-Palaeozoic crinoids the cup retains at least one anal plate, the anal X (Text-fig. 2; Table 1); thus it is the eventual loss of this plate which has been taken as the critical diagnostic character for the crown group articulates and identifies the monophyletic clade which encompasses all post-Palaeozoic crinoids.

Although the final loss of the anal X appears to have occurred very late in the Palaeozoic, no post-Palaeozoic crinoids are known in which an anal X is present in the adult cup, and even in the juvenile stages it is rare for both the radianal and anal X to be present (Clark 1915). Only two fossil specimens, both from the Anisian Stage of the Middle Triassic, are known to us in which the pentamerous symmetry of the cup is interrupted by the presence of an additional plate. The more striking of these is a crown of *Encrinus carnalli* (BM E14868) in which a roughly quadrangle occupies a position between the upper edge of two of the basals and the lower edge of the overlying radials. The second example occurs in a specimen of *Dadocrinus kumishi* (BM E6072), in which one of the basals has a square outline above which an irregular pentagonal plate occupies a position between adjacent basals and the overlying radials. In both instances these plates apparently are homologous with the radianal in juvenile articulates rather than the anal X in Poteriocrinina. Hence these two

Triassic examples represent merely the aberrant retention of a juvenile character into the adult state, and cannot be considered as evidence for any direct link between these taxa and the stem group of post-Palaeozoic crinoids.

Biserial arms. Among post-Palaeozoic crinoids truly biserial arms have developed only once, in certain of the Triassic Encrinidae, and in all other taxa the arms are uniserial. Cladistic analysis of Triassic crinoids, undertaken by one of us (M.J.S.) in collaboration with Hans Hagdorn, shows the encrinids to be a highly derived clade within the articulates rather than sister group to all other post-Palaeozoic crinoids (Simms 1988). The development of biserial arms in encrinids has a purely functional explanation; increasing the number of pinnules on the arms improves the effectiveness of the filtration fan (Simms 1990b). Similarities to Palaeozoic taxa with biserial arms, such as the Erisocrinacea, appear due to convergence and do not indicate any close phylogenetic relationship.

THE RELATIONSHIP OF PALAEOZOIC CRINOIDS TO POST-PALAEOZOIC TAXA

The most recent classification of the Class Crinoidea (Moore and Teichert 1978) divides them into four subclasses: the Camerata, Inadunata, Flexibilia and Articulata. Sprinkle and Moore (*in* Moore and Teichert 1978) created a fifth subclass, the Echinocrinea, for the Middle Cambrian *Echinocrinus brachiatus*, though the taxonomic position of this species remains enigmatic and its status as a distinct subclass is questionable. The broad relationships of the major crinoid groups, and their stratigraphical distribution, are depicted in Text-figure 1.

Our analysis of post-Palaeozoic crinoids confirms their monophyletic status and suggests close affinities with the inadunate order Cladida as currently understood (Text-fig. 2). Similarly, the Flexibilia represents another monophyletic clade also derived, via *Archaeotaxocrinus*, from the Cladida (Lewis 1981). Thus the Cladida, Flexibilia and Articulata together constitute a monophyletic clade (Sevastopulo and Lane 1988), with the cladids as an obviously paraphyletic group within this clade.

Two other orders, the Disparida and Hybocrinida, have been included within the Inadunata, while the Coronata, considered by Moore (*in* Moore and Teichert 1978) to be a distinct inadunate order, are now regarded as blastozoans (Brett *et al.* 1983). The relationship of both disparids and hybocrinids to the clade comprising cladids, flexibles and articulates remains unclear. The disparids almost certainly are not closely related to the cladids and may lie even farther from them than from the camerates (Kelly 1986; Donovan 1988). In hybocrinids the presence of a supposed radial plate in the cup may perhaps indicate affinities with the Cladida (Sevastopulo and Lane 1988), though there is little other evidence to support this.

Our current understanding of the Camerata suggests that they are a monophyletic clade which was already quite distinct from other crinoids at its first appearance early in the Ordovician. The orders Monobathrida and Diplobathrida may be monophyletic too, but it is doubtful that many of the sub-ordinal taxa currently recognized within these clades will, upon closer inspection, prove to be natural taxa. Camerates possess several autapomorphies, in particular the possession of a rigid theca incorporating fixed brachials and interbrachials together with a usually rigid tegmen forming a vaulted ceiling over the thecal cavity. The camerates are excluded from the cladogram (Text-fig. 2) since it is evident from even the most preliminary comparison that no close relationship exists between camerates and articulates. Although many camerates resemble articulates in the possession of pinnulate arms branching on the second primibrach, it is clear that this is a convergent trait. Since both the earliest camerates and the earliest cladids are non-pinnulate, pinnules must have evolved independently in the two groups. Similarly, a few camerates have enclosed axial canals piercing the radials and brachials, but this too must be an isolated character which has arisen through convergence.

It is obvious that the presently accepted higher-level classification of crinoids is unsatisfactory. Although the present interpretation of the Articulata clearly differs from Miller's original concept, it is desirable to retain this taxon in its currently understood form since it represents one of the few major monophyletic clades whose limits within the Crinoidea are clearly defined. Of greater concern

is the growing awareness among crinoid workers that the Inadunata is an unnatural paraphyletic, or even polyphyletic, grouping. Within the Inadunata, the Cladida includes the stem representatives of the articulates, flexibles and possibly hyocrinids, and hence is itself paraphyletic, while the Disparida can no longer justifiably be considered to have a close phylogenetic relationship with the cladids. Even within the Cladida the Dendrocrinina and the Poteriocrinina are largely artificial 'grade groups' and their true phylogeny is obscured. Only the cladid suborder Cyathocrinina can perhaps be considered a monophyletic clade, though its relationship to other cladids remains unclear.

PREVIOUS SUGGESTIONS FOR THE ORIGIN OF POST-PALAEOZOIC CRINOIDS

The considerable morphological diversity of post-Palaeozoic crinoids has led to many suggestions concerning their relationship to Palaeozoic taxa. Both monophyletic and polyphyletic origins from any of the major Palaeozoic groups have been invoked at different times, with more recent accounts (Taylor 1983) favouring an origin among the derived cladids ('suborder Poteriocrinina'). We have included most of these proposed articulate stem groups in our cladogram (Text-fig. 2) and discuss each below.

Disparida. Wachsmuth and Springer (1886) considered the Anisian (Middle Triassic) *Holocrinus beyrichi* to be related to the disparid family Belemnocrinidae, which at that time was monotypic. Subsequently the extant *Holopus*, *Hyocrinus* and *Bathycrinus* were referred to the Disparida (Wachsmuth and Springer 1889; Jaekel 1918). This appears to have been based only on superficial similarities between otherwise disparate taxa. In particular, the dicyclic or cryptodicyclic cup and pinnules of post-Palaeozoic taxa contrast markedly with the monocyclic cup and non-pinnulate arms of disparids, indicating a close relationship to be unlikely. As already discussed, it is quite possible that the disparids are even less closely related to *Holocrinus* than are the camerates. Furthermore, it is by no means certain that *Belemnocrinus* has been assigned to the Disparida correctly. It may well be a cryptodicyclic cladid.

Flexibilia. Various post-Palaeozoic crinoid taxa have, at different times, been referred to the Subclass Flexibilia. Wanner (1916) compared the extant *Holopus* to the Permian *Palaeoholopus* and *Brachypus*, in the family Lecanocrinidae. The late Cretaceous *Marsupites* and *Uintacrinus* have also been referred to the Flexibilia on a number of occasions (Schlüter 1878; Neumayr 1889; Zittel 1895). More recently Klikushin (1983) assigned the Triassic encrinid *Traumatocrinus* to the Sagenocrinidae, although he himself later cast doubt on this (Klikushin 1987). Again, any similarities between particular articulates and representatives of the Flexibilia are based on convergent or plesiomorphic characters, notably the presence of interbrachial plates in the latter three genera. Representatives of the Flexibilia lack nearly all of the critical articulate synapomorphies, notably the pinnulate arms with syzygial pairs of brachials.

Cyathocrinitidae (Cladida, Suborder Cyathocrinina). Jaekel (1892) suggested that the extant *Hyocrinus* and the Jurassic *Plicatocrinus* and *Saccocoma* were derived from the Cyathocrinitidae. Although the Cyathocrinitidae possess a dicyclic cup and have the entoneural system enclosed in the brachials (though apparently not in the thecal plates), they otherwise lack the characters used to diagnose articulates and possess a number of distinct autapomorphies, notably the presence (primitively) of goniospires, or traces of them, in the cup. Any close phylogenetic relationship between cyathocrinitids and articulates is, therefore, highly improbable.

Botryocrinidae (Cladida, Suborder Dendrocrinina). Rasmussen (in Moore and Teichert 1978) suggested that the Triassic Holocrinidae might have evolved from, amongst others, the dendrocrinine family Botryocrinidae. *Gastrocrinus* is similar to holocrinids in the possession of a dicyclic cup and cirriferous stem but lacks other synapomorphies of the articulate stem group, such

as the pinnulate arms with syzygial pairs of brachials. Hence a close phylogenetic relationship between these taxa is unlikely.

Poteriocrinites. Hildebrand (1926) considered the structure of the cup in Triassic Dadocrinidae and Holocrinidae to be more similar to the late Palaeozoic *Poteriocrinites* than to the Triassic Encrinidae. However, the cup in *Poteriocrinites* retains several anal plates and, although the radial articularia have enclosed entoneural canals in both articulates and *Poteriocrinites* (Miller 1821), the latter has only a single canal, unlike the paired canals of the Triassic taxa. Furthermore, *Poteriocrinites* lacks the syzygial pairs of brachials characteristic of post-Palaeozoic crinoids, lacks well-developed muscular fossae of the articulate type on other brachial articularia (Miller 1821), has arms which divide at positions as high as IBr14, and lacks cirri. The enclosed entoneural system of *Poteriocrinites* may be homologous with that in articulates, perhaps representing an earlier evolutionary stage prior to the development of paired canals, but equally it may represent a convergent trait. This hypothesis is difficult to test since, although *Poteriocrinites* clearly is a member of the articulate stem group, the absence of certain characters (Text-fig. 2) indicates that the genus lies away from the main line of descent.

Erisocrinidae. The Triassic Encrinidae have often been compared with the late Palaeozoic cladid Erisocrinidae on account of the biserial arms found in both groups. A close phylogenetic relationship between these taxa, though not necessarily with other articulates, has been suggested on several occasions (Jaekel 1892; Hildebrand 1926; Piserá and Dzik 1979; Simms 1988). The Encrinidae were even placed in the superfamily Erisocrinacea by Moore *et al.* (in Moore and Teichert 1978). Koenen (1895) also considered the Triassic *Dadocrinus* to be related to *Erisocrinus* despite the obviously uniserial arms of the former. However, although erisocrinids have a bowl-shaped cup and biserial arms superficially similar to those of encrinids, these clearly are convergent traits and they otherwise lack many other encrinid synapomorphies, such as the entoneural system enclosed in the thecal plates, arm branching at IBr2 and syzygial articularia in the arms.

Ampelocrinidae. Strimple (in Moore and Teichert 1978, p. 301) suggested that the late Carboniferous ampelocrinids, particularly *Chlidonocrinus*, might lie close to the stem group of post-Palaeozoic crinoids on account of the arms branching at IBr2, the presence of syzygial pairs of brachials and the pentaradiate stem with cirrinodals. As can be seen from the cladogram (Text-fig. 2) and Table 1, it is clear that *Ampelocrinus*, along with several other closely allied genera, possess several other critical characters in addition to those listed by Strimple, notably the transverse-ridge type of cirri and the paired entoneural canals in the brachials. Indeed, it can hardly be doubted that a close phylogenetic relationship exists between certain late Palaeozoic Ampelocrinidae and the early Triassic *Holocrinus*.

Nowracrinus and *Tasmanocrinus*. In his description of these two monotypic Permian genera, Willink (1979) noted their highly derived morphology and similarities to post-Palaeozoic crinoids. However, he was reluctant to assign them to any established crinoid family or comment on their relationship to articulates, other than to conclude that they belonged to the cladid suborder Poteriocrinina. It is clear from our analysis (Text-fig. 2) that both lie much closer to the ancestry of post-Palaeozoic crinoids than do members of the Erisocrinacea, despite earlier assertions to the contrary (Simms 1988); it is equally evident that they do not lie on the direct line of ancestry, since both possess distinctive autapomorphies. In *Nowracrinus* the branching of the pinnules is a trait apparently unique to this genus, while the unusual structure of the cup in *Tasmanocrinus* (see Willink 1979 for a fuller description) is unlike that of any post-Palaeozoic crinoid.

Polyphyletic origin. A polyphyletic origin for the articulates has been suggested on several occasions. Rasmussen (in Moore and Teichert 1978) considered it unproven whether the articulates were

monophyletic or polyphyletic, while Ubachs (*in* Moore and Teichert 1978) advocated a 'moderate polyphyletism' of the articulates from more than one poteriocrinine ancestor. The strongest statement proposing articulate polyphyly was given by Moore (*in* Rhodes 1967, p. 63) in which it was suggested that the articulates comprised 'a hodge-podge of derivatives from all three Palaeozoic crinoid subclasses, though typical representatives of each and all have disappeared'. However, in all instances the similarities between post-Palaeozoic groups and the Palaeozoic taxa which he cites are clearly attributable to convergence, and there is no justification for advocating a polyphyletic origin for the articulates.

A REVISED HIGHER-LEVEL CLASSIFICATION OF CRINOIDS

Our analysis has been concerned primarily with post-Palaeozoic crinoids and those Palaeozoic taxa which lie close to the stem group of the articulates. Hence we confine ourselves to only brief comments concerning the recognition of major monophyletic clades among Palaeozoic crinoids. Nonetheless, our research has highlighted some of the inadequacies of the generally accepted classification (Moore and Teichert 1978), and has identified some of the problems which would appear to be inherent in any attempt to undertake a phylogenetic analysis of Palaeozoic crinoids.

Problems with the current classification are evident at all taxonomic levels from at least generic level upwards. In Moore and Teichert (1978) representatives of the articulate stem group are distributed primarily in two cladid families, the Ampelocrinidae Kirk, 1942 and the Cymbiocrinidae Strimple and Watkins, 1969, which are further separated into distinct superfamilies. However, the only character, of those listed, which differs between these two families is that the radial facets are directed outwards in the ampelocrinids and inwards in the cymbiocrinids. On the basis of other characters (see Table 1) we consider that *Ampelocrinus* does not differ sufficiently from *Cymbiocrinus* to warrant their separation into different families, or superfamilies, and we regard the Cymbiocrinidae as a junior synonym of the Ampelocrinidae. However, from Table 1 it is also evident that only five (*Ampelocrinus*, *Chlidonocrinus*, *Cymbiocrinus*, *Aesiocrinus* and *Proallosocrinus*) out of the sixteen genera currently included within these two families can, with any confidence, be retained in the emended family Ampelocrinidae (the monotypic *Proampelocrinus* Gupta and Webster, 1974, has been excluded from this analysis) although other taxa currently excluded (*Nowracrinus* and *Tribrachyocrinus*) could justifiably also be included in the Ampelocrinidae. For most of the remainder there is insufficient data available for them to be assigned to a particular family, whilst in some cases (*Allosocrinus*, *Halogetocrinus* and *Paracymbiocrinus*) it is almost certain that genera have been assigned to this family incorrectly. Reference to original descriptions of taxa rarely provides any significant information additional to that contained in the *Treatise*. Furthermore, re-examination of much type material preserved in museums in the UK and the USA has revealed that in a majority of cases critical detail of character states is obscured by poor preservation and/or over-zealous mechanical preparation of specimens. Such factors will pose a considerable problem in any future attempts to revise the low-level taxonomy of Palaeozoic crinoids.

At higher taxonomic levels we recognize several major clades. We assign traditional categorial rank to these clades but appreciate that the choice of rank is entirely arbitrary. Future work may produce a more phylogenetically consistent classification of the Crinoidea.

Class Crinoidea. Like most previous authors, we accept that the Crinoidea constitutes a monophyletic clade whose common ancestry probably can be traced back to the Cambrian. However, the Middle Cambrian *Echmatocrinus brachiatus*, supposedly the oldest known crinoid, remains of uncertain phylogenetic position pending further investigation. Of the four subclasses currently recognized within the Crinoidea we retain only one, the Camerata, at subclass level. We recommend the abandonment of the Inadunata, a paraphyletic taxon, but retain the Flexibilia and Articulata as taxa of lower rank.

Subclass Camerata. The camerates, with their distinctive thecal morphology, almost certainly represent a monophyletic clade. Two orders, the Monobathrida and the Diplobathrida, are recognized. Both are morphologically distinct from their earliest appearance and hence, on current understanding, constitute monophyletic clades pending further evidence concerning their relationship to each other.

Subclass Disparida. Although the disparids have been grouped with the cladids, as an order within the Inadunata, there is no evidence for a close phylogenetic relationship between cladids and disparids and already it is recognized that they may be farther removed from cladids than from the camerates (Kelly 1986; Donovan 1988). They are regarded here as a monophyletic clade, for convenience classified at subclass level.

Subclass Cladida. As discussed earlier, the order Cladida, in the sense of Moore and Teichert (1978), is an obviously paraphyletic taxon incorporating stem-group representatives of several monophyletic clades, including the Articulata, Flexibilia and Cyathocrinina of earlier classification schemes. To remedy this unsatisfactory situation we recommend elevation of the Cladida to the level of subclass, and to include within this subclass all representatives of the Articulata and Flexibilia of earlier classification schemes, now reduced to the level of Infraclass, and the Cyathocrinina, elevated to Infraclass. The remaining taxa comprise stem-group representatives of these three major clades as well as almost certainly containing additional monophyletic clades. Formerly these were divided among the suborders Dendrocrinina and Poteriocrinina, two obviously paraphyletic groups, but we recommend the abandonment of these formal terms and instead group them together informally as 'stem-group cladids' pending further work on relationships within this group.

Incertae Sedis (Subclass) Hybocrinida. Sevastopulo and Lane (1988) considered the hybocrinids to be a monophyletic group, but were unable to resolve their phylogenetic position. This situation has not changed, and we tentatively accord them the rank of subclass pending further investigation.

Class CRINOIDEA Miller, 1821

Subclass CAMERATA Wachsmuth and Springer, 1885

Order MONOBATHRIDA Moore and Laudon, 1943

Order DIPLOBATHRIDA Moore and Laudon, 1943

Subclass DISPARIDA Moore and Laudon, 1943

Subclass CLADIDA Moore and Laudon, 1943

'stem-group cladids'

Infraclass CYATHOCRININA Bather, 1899

Infraclass FLEXIBILIA Zittel, 1895

Infraclass ARTICULATA Miller, 1821

Incertae Sedis ('Subclass') HYBOCRINIDA Jaekel, 1918

THE ARTICULATE PROBLEM

As already demonstrated, currently understood definitions of articulate crinoids have relied more on our understanding of post-Palaeozoic crinoid morphology than upon Miller's (1821) original description of the group. Our reassessment of Miller's diagnosis indicates that a number of late Palaeozoic taxa could justifiably be included within the Articulata. A case might be made, therefore, for extending the taxonomic range of the Articulata to incorporate these Palaeozoic forms and thereby conform to Miller's original description. However, in view of the clear monophyly of post-Palaeozoic crinoids it is perhaps more desirable that recognition is given to articulate crinoids in the sense of later authors. Consequently, we recommend that the Articulata, reduced to the level of

Infraclass, be retained in its presently understood sense of post-Palaeozoic crinoids. Miller's original diagnosis of the group was not based on any phylogenetic methodology, and the characters which he considered important are often difficult to identify in fossil material. Consequently, we redefine the Articulata on the basis of characters which are confined to post-Palaeozoic crinoids, i.e. a dicyclic or cryptodicyclic cup lacking any anal plates in the adult and with the entoneural system enclosed within the thecal plates. Those Palaeozoic taxa, such as *Nowracrinus*, *Ampelocrinus*, *Cymbiocrinus* and *Aesiocrinus*, which appear to lie close to the common ancestry of the Articulata are perhaps best referred to informally as 'stem-group articulates', while the monophyletic clade which encompasses all post-Palaeozoic taxa constitutes the 'crown-group articulates'.

CONCLUSIONS

Reassessment of Miller's (1821) original definition of the Articulata suggests that this group has been widely misinterpreted by subsequent authors, and that a variety of Palaeozoic cladid taxa might justifiably be assigned to the Articulata alongside the post-Palaeozoic articulates of later authors. However, cladistic analysis has demonstrated that all post-Palaeozoic crinoids belong to a monophyletic clade derived from a common ancestor of probable late Permian or early Triassic age, and hence we recommend that the Articulata, reduced to the level of infraclass, be retained in the currently understood sense of post-Palaeozoic crinoids only. This clade is characterized by the absence of an anal plate from the adult cup and an entoneural system enclosed within the thecal plates, together with a suite of characters found in progressively more crownward members of the stem-group of this clade. Miller's definition incorporates a number of Palaeozoic taxa which lie close to the common ancestry of articulates and are best referred to informally as 'stem-group articulates'.

Our analysis of the articulates and their Palaeozoic sister taxa highlights, once again, the inadequacy both of the current classification scheme and of the documentation of many Palaeozoic crinoid taxa. Without a radical revision of many Palaeozoic taxa at generic level, which would necessitate re-examination of much of the original material, it is impossible for us to attempt any more than the most preliminary revision of crinoid classification. Nonetheless, we recommend the abandonment of the Inadunata as an obviously paraphyletic group, and the raising of the Disparida and Cladida to subclass level alongside the Camerata. We take the Cladida to include the Articulata and Flexibilia, both reduced to infraclass level; the Cyathocrinina, raised to infraclass level; and an unresolved group which we refer to informally as 'stem-group cladids'. The Hybocrinida are nominally assigned subclass status pending further investigation of their phylogenetic position.

Although such a classification is clearly still far removed from the ideal of phylogenetic systematics (see Craske and Jefferies 1989), with the retention of four groups at subclass level implying a common origin, it is the best that can be achieved in the present state of knowledge of early crinoid morphology. We simply do not know how the major groups of Palaeozoic crinoids are related. It is to be hoped that future discoveries, and reassessment of existing material, may help to resolve these problems, and that the classification scheme which we have proposed here will be superseded by one which more closely reflects the phylogeny of crinoids.

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