PHYLOGENY AND PALAEOBIOLOGY OF
MARSUPITES AND *UINTACRINUS*

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ABSTRACT. The Upper Cretaceous *Marsupites* and *Uintacrinus* are among the morphologically most unusual of all fossil crinoids. Both have a large theca, ten extremely long arms, and lack any anchoring structure in both adult and juvenile stages; this morphology appears so unlike that of other articulate crinoid groups that earlier attempts to identify possible sister groups have been inconclusive. Cladistic analysis indicates that both genera are closely related to the Comasteridae, with *Uintacrinus* being less derived than *Marsupites*. Both genera have a virtually world-wide distribution through a limited stratigraphical interval within the Santonian Stage. Their widespread distribution, combined with the absence of a mode of attachment, has led to the conclusion that they were pelagic. However re-examination of their morphology indicates that *Marsupites* and *Uintacrinus* were benthic. The global distribution of these taxa probably reflects a long-lived planktotrophic larval stage in the life cycle.

IN 1821, J. S. Miller published his 'Natural History of the Crinoids, or Lily-shaped Animals' in which he outlined a scheme which still forms the basis of their classification. Among the many fossil crinoids which he described was a bizarre form from the Chalk of southern England. It possessed a large cup composed of three circlets of plates and a single centrodorsal plate at the base. There was no trace of a stem or cirri arising from the centrodorsal as in the other stemless group of which Miller was aware, the comatulids. He named it *Marsupites ornatus* on account of its similarity to a purse, or marsupium, and the ornamented nature of the plates. It had earlier been described by Parkinson (1808), as the 'Tortoise Encrinite', and by Schlotheim (1820) as *Fungites testudinarius*, although Miller was the first to appreciate its stemless nature.

Marsupites was originally a manuscript name used by Gideon Mantell and published in the following year (Mantell 1822). In 1876, a large crinoid from the Niobrara Chalk of Kansas was described under the name *Uintacrinus socialis* by Grinnel, who noted its similarity to the English *Marsupites*. Two years later, the stemless nature of *Uintacrinus* was confirmed by additional material from the Upper Chalk of Westphalia, described as a distinct species *Uintacrinus westfalicus* (Schlueter, 1878). Subsequent discovery of several large groups of *Uintacrinus socialis*, the largest covering ninety five square metres and including more than 1200 individuals, led to a series of publications culminating in Springer's monumental work on the structure and relations of *Uintacrinus* (Clark 1893; Williston and Hill 1894; Bather 1896; Springer 1899, 1900). However, despite these exhaustive descriptions and a number of subsequent publications (Clark 1911; Sieverts 1927; Rasmussen 1961), a great deal of uncertainty has continued to surround their phylogenetic position and possible mode of life. The purpose of the present contribution is to assess the phylogeny and palaeobiology of *Marsupites* and *Uintacrinus*.

Terminology of the crinoid endoskeleton used herein follows Ubaghs (1978).

GENERAL MORPHOLOGY

Exhaustive accounts of the morphology of *Marsupites* were given by Sieverts (1927) and Rasmussen (1961, 1978). The morphology of *Uintacrinus* has been described by Bather (1896), Springer (1901) and Rasmussen (1961, 1978).

In *Marsupites*, the calyx is large. Mature specimens are commonly 65 mm high and 60 mm in diameter. It is sub-globose to oval in shape and composed of sixteen polygonal plates which are united by straight sutures (Text-fig. 1A). In general, the plates from stratigraphically older specimens
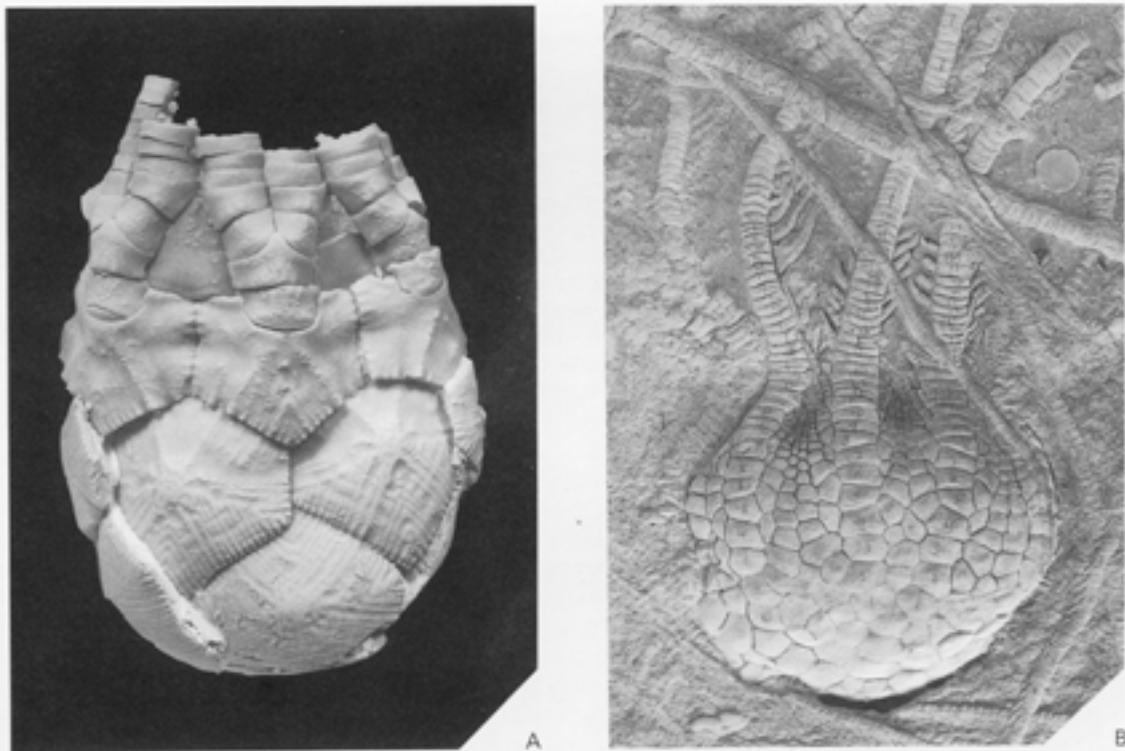
TEXT-FIG. 1. Calyces of *Marsupites* and *Uintacrinus*; from the collections of the Natural History Museum, London. A, *Marsupites testudinarius*; E14261; *M. testudinarius* Zone, Upper Chalk; Brighton, Sussex, England; calyx with interbrachial plates; ×1·4. B, *Uintacrinus socialis*; E6328; Smokey Hill Formation, Santonian; Elkader, Kansas, USA; calyx and arms; ×0·85.

are smooth, whilst in younger specimens they become more ornate and are sculpted with a series of narrow straight ridges or rows of granules. Structurally, the plates are formed of two calcitic layers. An outer regular network of calcite covers a less dense internal layer. Thecal plates are arranged in three circlets around a dorsal centrale. The plate circlets have been interpreted as radials, basals and infrabasals. A tegmen is unknown.

The length of arms is unknown for *Marsupites*. They are sharply demarcated from the theca, and are believed to bifurcate only once on the second primibrach. Small, thin, interbrachial plates which cover the area between the radials and the brachials are present up to approximately $IIBr_3$. The articulations at IBr_{1-2}, $IIBr_{1-2}$ and $IIBr_{3-4}$ were described by Rasmussen (1961) as syzygial. However, due to the paucity of culmina on the facets, he commented that they resemble a synarthrial articulation. These articulations were described more accurately by Clarke (1909) as pseudosyzygies. Muscular articulations, which are consistently straight, occur at $RR–IBr_1$, $IBr_2–IIBr_1$, $IIBr_{2-3}$ and $IIBr_{4-5}$. Distally, they become more common. Syzygial articulations in which the culmina are finer and more numerous are generally found within the intervals $IIBr_{4-8}$ and $IIBr_{8-13}$. Pinnule sockets are found from $IIBr_2$ onwards in the distal ends of the brachials with muscular articulations.

Uintacrinus has a large, globose theca. Mature specimens are normally 62·5–75·0 mm in diameter. The theca is composed of a variable number of smooth, slightly arched, polygonal plates. There are five radials, five basals, occasionally five infrabasals and a centrale (Text-fig. 1B). In addition, there are three types of supplementary plates (Bather 1896): interbrachials, interdistichials and interpinnulars. These are positioned above the radials between the fixed brachials. The ventral surface is covered by a tegmen which is preserved as a carbonized membrane studded with small irregular calcareous grains.

The length of arm branches in *Uintacrinus* is extremely difficult to measure. Despite the frequency with which articulated arm sections are preserved, arms are invariably tangled and interlaced. Based on the rate of arm tapering in a single arm, Bather (1896) concluded that the minimum arm length was 0·9 m. Using a similar technique, Springer (1901) concluded that the arm length was 1·25 m. The arms branch only once, at IBr_2. They are not clearly demarcated from the theca, with a varying number of brachials, up to $IIBr_8$, being fixed in the thecal structure. Muscular articulations are found at $RR–Br_1$, $IBr_2–IIBr_1$, $IIBr_{2-3}$ and further distally. IBr_{1-2} are syzygial. Syzygies also occur further distally at frequent intervals interspersed with muscular articulations. The first fixed pinnule is given off from $IIBr_2$ on the outer side of the ray. Thereafter, pinnules are connected to $IIBr_4$, $IIBr_5$, $IIBr_7$, $IIBr_9$ on alternate sides of the brachial. From $IIBr_{10}$, pinnules occur on every brachial, except where the distal articulation is syzygial. All pinnular sockets are muscular.

PHYLOGENETIC ANALYSIS OF *MARSUPITES* AND *UINTACRINUS*

The cladistic approach stresses the similarities between taxa as a means of identifying homologies. This is an essential step in any attempt to reconstruct the phylogeny of a particular group upon which a more natural classification can then be based. Crinoids, with their complex, multi-element skeletons, are ideal subjects for this approach. *Marsupites* and *Uintacrinus* inherently lack any of the suite of characters present in the column of most other crinoids, but the available characters nonetheless enable comparisons to be made with various groups with which affinities have been suggested in the past.

The cladogram in Text-figure 2 incorporates representatives of all articulate crinoids which have been considered as possible sister taxa to *Uintacrinus* and *Marsupites*. Palaeozoic taxa have been excluded since it has been shown by Simms and Sevastopulo (1993) that the articulates are a monophyletic taxon derived from a single Late Palaeozoic group of cladids. No close relationship exists between any disparid or camerate taxon and any post-Palaeozoic crinoid. The data were analysed using the PAUP program on an Apple Macintosh IIsi. Five hundred bootstrap replications were undertaken, with the relatively small number of taxa (fifteen) and characters (nineteen) allowing a branch-and-bound search. *Holocrinus*, the oldest and the most stemward articulate crinoid known, was selected as outgroup and the characters were initially unweighted. The data matrix is reproduced along with the cladogram in Text-figure 2.

A total of twenty-eight possible trees were obtained from the original data. The Consistency Index (CI) was 0·600; the Retention Index (RI) was 0·788. Throughout, *Uintacrinus* and *Marsupites* were grouped together as sister taxa and maintained a constant position as derived sister group to the comasterids. The one area of inconsistency lay among the five comasterid taxa. In a strict consensus of twenty-eight trees, the relationship of these five taxa was entirely unresolved. However, characters were reweighted by the maximum value of the rescaled consistency index, and a further branch-and-bound search undertaken. This was undertaken three times consecutively to enhance resolution. Seven trees were obtained. *Comanthina* was consistently placed as the least derived taxon but the relationship of the four remaining taxa was resolved only at the fifty per cent Majority-rule consensus of the seven trees. This is the cladogram reproduced in Text-figure 2.

This analysis confirms the close phylogenetic relationship of *Marsupites* and *Uintacrinus* with the extant Family Comasteridae, a conclusion first reached in part by Springer (1901). However, a rather surprising result of the analysis is the consistent position of the millericrinids, *Apiocrinus* and *Ailsacrinus*, rather than the isocrinids, *Isocrinus* and *Isselicrinus*, as a sister group to the comatulids.
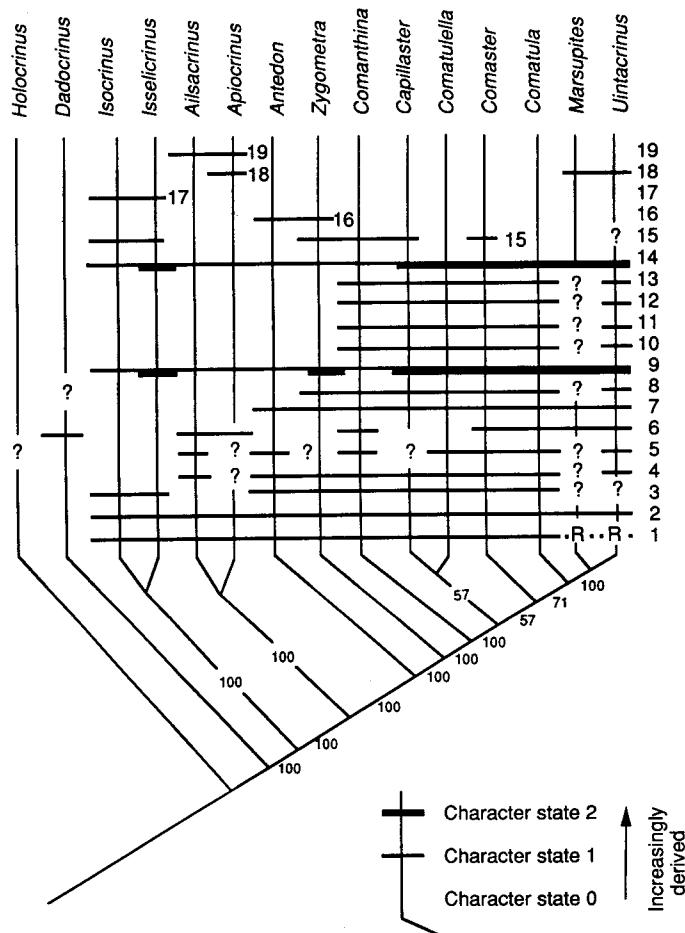
TEXT-FIG. 2. Data matrix and fifty per cent Majority-rule consensus of seven trees for *Marsupites*, *Uintacrinus* and other selected articulate crinoids. Figures shown give percentage support for each node in the cladogram. Characters are listed below. R = character reversal.

1, Infrabasals exposed (0) / cryptic (1). 2, Axial canal in brachials paired (0) / single (1). 3, Larval stem articula synostosial (0) / synarthrial (1). 4, Tegmen tessellate (0) / of scattered plates (1). 5, Grooveless arms or pinnules absent (0) / present (1). 6, Cirri present in adult (0) / absent (1). 7, Stem present in adult (0) / absent (1). 8, Ambulacral grooves with cover plates (0) / without (1). 9, IBr_{1-2} syzygial (0) / synarthrial (1) / pseudosyzygial (2). 10, Mouth central (0) / marginal (1). 11, Anal cone central (0) / marginal (1). 12, Ambulacra endocyclic (0) / exocyclic (1). 13, Proximal pinnules straight (0) / with combs (1). 14, $IIBr_{1-2}$ syzygial (0) / synarthrial (1) / pseudosyzygial (2). 15, Arms divide once (0) / more than once (1). 16, Basals discrete (0) / fused to rosette (1). 17, Stem without cryptosymplexies (0) / with them (1). 18, Interbrachial plates absent (0) / present (1). 19, Syzygy at $IIBr_{3-4}$ (0) / at $IIBr_{4-5}$ (1).

This may be, in part, a consequence of the small size of the database analysed, but it also stresses the need to investigate the phylogenetic position of the millericrinids, a rather poorly understood group, in greater depth.

PREVIOUS IDEAS ON THE PHYLOGENETIC POSITION OF *MARSUPITES* AND *UINTACRINUS*

There has been no clear consensus on the origin and affinities of *Marsupites* and *Uintacrinus*. This is reflected in their current taxonomic status, in which the two genera are assigned to separate families within a distinct order, the Uintacrinida, comprising only three species in total. This has arisen through a tendency to stress the differences between taxa rather than the similarities (Paul and Smith 1988). It is comparable with the situation amongst many early Palaeozoic echinoderms, in which numerous small, short-lived groups were elevated to the rank of Class (Sprinkle 1973). Many taxa have, at some time or other, been associated with *Uintacrinus* and *Marsupites*. These are discussed below.

Palaeozoic crinoids

Marsupites and *Uintacrinus* have been assigned to various Palaeozoic crinoid taxa, including cladids, flexibles and camerates. *Uintacrinus* bears a superficial similarity to some flexible crinoids (e.g. *Forbesiocrinus*) in the development of interbrachial plates. The theca of *Marsupites*, with its large infrabasals and ornate thecal plates, is reminiscent of many camerates and some cladids, such as *Rhodocrinites* and *Sphaerocrinus*. However, both *Marsupites* and *Uintacrinus* share numerous synapomorphies with the exclusively post-Palaeozoic subclass Articulata, notably the pinnulate arms branching at IBr_2, muscular articulations on most brachials, a single axial canal piercing each brachial, ligamentary articulations at IBr_{1-2}, $IIBr_{1-2}$, $IIBr_{3-4}$ and at intervals beyond, and the absence of an anal plate in the dicyclic or cryptodicyclic cup. These characters are largely absent from any suggested Palaeozoic ancestors (Simms and Sevastopulo 1993).

Dadocrinus

Bather (1896) first suggested that the Middle Triassic genus *Dadocrinus* represented the closest known relative to *Uintacrinus*, a hypothesis supported by Kirk (1911). At that time, *Dadocrinus* was considered intermediate between the Articulata and the Palaeozoic Erisocrinidae. *Dadocrinus* is now recognized as a uniserial member of the exclusively Triassic family Encrinidae, other representatives of which bear a superficial similarity to the Palaeozoic Erisocrinidae. Among the characters of *Dadocrinus* which Bather (1896) considered as evidence for a link with *Uintacrinus* are the cryptodicyclic cup, the pinnulate arms branching only once on the second primibrach, and the axial canal in the thecal and brachial plates. However, these are characteristic of most, if not all, articulates. The primibrachs of *Dadocrinus* and *Uintacrinus* are also united by interbrachials but this is not unique to these taxa. A similar arrangement is also found in the Pentacrinitidae, Apiocrinitidae and many Palaeozoic taxa, suggesting widespread homoplasy in this character. Bather (1896) also considered the arrangement of syzygies in the arms of *Dadocrinus* to indicate a close relationship with *Uintacrinus*, but this too is a plesiomorphic character shared also by the Palaeozoic stem group of the articulates (Simms and Sevastopulo 1993). However, although the non-muscular articulations in the arms of most early Triassic taxa were syzygial throughout, in most later taxa the more proximal articula, those at IBr_{1-2} and $IIBr_{1-2}$, were modified into synarthrial articula. *Marsupites* and *Uintacrinus* are comparatively unusual in that they represent post-Triassic taxa in which these particular articulations would appear to have retained the primitive, syzygial, condition. However, these syzygial articula have fewer and coarser crenulae than those further distally in the arms, and were described by Rasmussen (1961) as 'somewhat resembling a synarthrial articulation'. It would appear that rather than representing true syzygies, they in fact represent a modification of synarthrial articula, as demonstrated by Clarke (1909). The apparent similarities of articulation style in the arms of *Dadocrinus* and *Uintacrinus* are due, in part, to convergence.

Millericrinida

A close phylogenetic relationship between *Marsupites*, *Uintacrinus* and the millericrinid Apio-crinitidae was suggested by Pisera and Dzik (1979), based largely on the development of the interbrachial plates in the two groups, a character already suggested as prone to homoplasy. They admitted that there was otherwise a considerable morphological distance between them. Furthermore, *Apiocrinus* has the characteristic millericrinid synapomorphy of a syzygial articulation at $IIBr_{4-5}$ rather than at $IIBr_{3-4}$ as in *Marsupites*, *Uintacrinus* and most other articulates (Taylor 1983). Also, the stem is thick and well developed in *Apiocrinus* itself, although a related millericrinid genus, *Ailsacrinus* (Taylor 1983), has a greatly reduced stem.

Comatulida

Marsupites and *Uintacrinus* have been grouped with the comatulids on a number of occasions, although sharing few obvious homologies with them. Typical comatulid taxa, such as *Antedon*, resemble *Marsupites* and *Uintacrinus* only in the absence of a stem in the adult and in the weak plating of the tegmen. Otherwise their morphology is essentially plesiomorphic, retaining characters of their sister group the Pentacrinitidae.

Marsupites and *Uintacrinus* have articula at IBr_{1-2} and $IIBr_{1-2}$ which resemble syzygies, though they appear to represent secondarily modified synarthrial articula. Clark (1909) coined the term 'pseudosyzygy' for this type of articulation, although Moore and Teichert (1978) incorrectly regarded pseudosyzygy as a synonym of cryptosyzygy, the latter term generally being applied to poorly defined syzygial articula found in many isocrinids. Pseudosyzygies are found at IBr_{1-2} and $IIBr_{1-2}$ in several genera of the comasterids and in the isselicrinids (Simms 1988). In *Comaster*, the pseudosyzygial articula found in the adults develop from cryptosynarthries in the juveniles. *Marsupites* and *Uintacrinus* are united with the Comasteridae by a suite of distinctive synapomorphies. These synapomorphies led Springer (1901) to consider a close relationship between *Uintacrinus* and the Comasteridae, although he still maintained that *Marsupites* was sufficiently distinct as to be referred to the subclass Inadunata. Among the characters which Springer felt united *Uintacrinus* and *Comatula* (= *Actinometra* of his account) was the structure of the oral surface. In the great majority of articulates where it is known, the mouth is central and the anal tube marginal. Among comasterids, this condition is encountered only in some small or juvenile individuals; the remainder have a central anal tube and a marginal or subcentral mouth. The preservation of many of the specimens of *Uintacrinus* is sufficient to reveal that the configuration of the oral surface in this genus is identical to that in comasterids. Because of this arrangement of mouth and anus, the ambulacral grooves on the tegmen of both *Uintacrinus* and the Comasteridae are modified into a horseshoe-shaped, or exocyclic, configuration around the anal tube. Further similarities are also seen in the ambulacral system. In both taxa, cover-plates and side-plates are entirely absent from both arms and pinnules.

These characters (the development of pseudosyzygies and the unique structure of the tegmen and ambulacral system) suggest a close phylogenetic relationship between *Uintacrinus* and the Comasteridae, in particular with the extant genera *Comaster* and *Comatula*. Other similarities also exist which, although less distinctive than those just discussed, lend further support to suggestions of a sister group relationship. The centrodorsal in all three comasterid genera cited is small and low, with only a few small cirri at most. In adult specimens, it is often reduced still further, to a small pentagonal or stellate plate lying flush with the radial circlet and lacking cirral sockets altogether; this invites comparison with the centrale of *Uintacrinus*.

The Zygometridae appear to be a plesiomorphic sister taxon to the Comasteridae and Marsupitidae (*Marsupites* and *Uintacrinus*). They retain cirri on the centrodorsal, have a central anus and marginal mouth, and arms which divide several times. They also have spines on the distal ossicles of the cirri, a synapomorphy which they share with the Comasteridae, while the ambulacral

skeleton is poorly developed by comparison with many comatulids. Furthermore, although the articulation at $IIBr_{1-2}$ retains the plesiomorphic synarthrial arrangement, that at IBr_{1-2} is the more derived pseudosyzygial type characteristic of comasterids and maruspitids.

These comparisons indicate that *Uintacrinus* has a close phylogenetic relationship with the extant comatulid family Comasteridae. However, much of the data on which this is based is due to the fortuitous preservation of the arms and oral surface in many specimens of *Uintacrinus*. Similar data for *Marsupites* are lacking; although many intact thecae are known, some with the proximal parts of the arms preserved, details of the ambulacral system and the oral surface remain unknown. Thus, the evidence for *Marsupites* having close phylogenetic links with the Comasteridae is less convincing than for *Uintacrinus*, although comparison of *Marsupites* with *Uintacrinus* suggests that they are sister taxa.

SIMILARITIES BETWEEN *MARSUPITES* AND *UINTACRINUS*

Despite their overall morphological similarity and almost coincident stratigraphical distribution, *Marsupites* and *Uintacrinus* have frequently been considered as only distantly related, and have even been grouped in different subclasses. This has arisen largely through the tendency of earlier workers to compare differences between the two genera rather than similarities. The most striking difference, albeit superficial, lies in the construction of the cup. In *Marsupites*, the thecal plates are large, approximately equal in size and arranged in three circlets. These have been interpreted as the radials, basals and infrabasals, with a centrale at the base, and typically ornamented with radiating ridges. In contrast, *Uintacrinus* has much smaller thecal plates which are a little larger than the brachials. Both two-circlet and three-circlet forms of *Uintacrinus* are known; both forms have a small centrale at the base of the cup.

The arms in *Marsupites* and *Uintacrinus* are very similar, at least as far as can be judged from the limited data available for the former. Both have arms which divide only once on IBr_2 and have pseudosyzygial articulations at IBr_{1-2} and $IIBr_{1-2}$. Interbrachial plates are a distinctive feature of *Uintacrinus* and are almost as well developed, although rarely preserved, in *Marsupites*. The overall shape of the brachials differs very little between the two genera, with configuration of the distal articulum being strikingly similar. In both taxa, this latter articulum, which is straight muscular, is considerably narrower than the total width of the radial itself and is deeply excavated. The final and perhaps most obvious synapomorphy of these two genera is the absence of a stem at all known growth stages.

EVOLUTION OF *MARSUPITES* AND *UINTACRINUS*

The sudden, apparently inexplicable, appearance of *Marsupites* and *Uintacrinus* in the Late Cretaceous has remained one of the enigmas of post-Palaeozoic crinoid evolution. Their morphology appears so unlike other articulate crinoids that attempts to identify possible sister groups have been largely inconclusive. No obvious candidate has been found among other Cretaceous taxa but cladistic analysis suggests that they share a common ancestor with the Comasteridae among the comatulids. However, as with many other comatulids, comasterids have a poor fossil record and it is only the existence of *Marsupites* and *Uintacrinus* that establishes the presence of the Comasteridae as far back as the Late Cretaceous. Assuming, therefore, that the marsupitids arose from *Comatulella*-like comasterids during the Santonian (Late Cretaceous), it remains to be explained how and why their aberrant morphology developed.

Of the two, *Uintacrinus* has a less derived morphology than that of *Marsupites*. With one exception, this is based on degree of development rather than simple presence or absence of characters. In *Uintacrinus socialis*, the earliest of three marsupitid species, the thecal plates are smooth and the radials are comparable in size to the brachials in other comatulids. Infrabasals, or

plates at the base of the cup interpreted as such, are present in only about half of the individuals (Springer 1901), and in all cases are very much smaller than the other thecal plates. In contrast, the thecal plates of *Marsupites* are all very much larger than the brachials, often have their surfaces heavily ornamented with radiating ridges, and plates interpreted as infrabasals are always well developed. Although the presence of infrabasals is actually apomorphic for articulates as a whole, their reappearance in *Marsupites* and *Uintacrinus* is a derived condition by comparison with other comatulids.

The aberrant morphology of these two genera is the reason why they have so often been classified erroneously. It also raises the question of how such an apparently bizarre morphology could evolve from 'normal' comatulids. The key to this, perhaps, lies in the ontogeny of certain comasterids. Immature examples of genera such as *Comatula* and *Comaster* have well-developed cirri on the centrodorsal but, in mature and gerontic individuals, the cirri are lost and the centrodorsal reduced to a small smooth plate. Adult comatulids also lack basals and infrabasals, but these are present early in the ontogeny of comatulids. The three-circlet arrangement of thecal plates in these taxa would, therefore, appear to be a juvenile trait, whereas the form of the centrodorsal, its lack of cirri, and also the shape of the brachials would, by comparison with comasterids and other articulates, appear to be extreme gerontic traits.

In conclusion, *Marsupites* and *Uintacrinus* appear to show, to differing degrees, a combination of heterochronic traits. On the one hand, there are features which recall the early ontogeny of comasterids, while, on the other, there is a series of extreme peramorphic traits which have carried the morphology of the two taxa well beyond the morphology of the adult comasterid.

GEOGRAPHICAL, STRATIGRAPHICAL AND FACIES DISTRIBUTIONS

The geographical distribution of *Marsupites* has been reviewed by Sieverts (1927) and Rasmussen (1961), and of *Uintacrinus* by Rasmussen (1961). Both genera have a cosmopolitan distribution, occurring on the continents of North America, Europe, Asia (including India), Africa and Australia. *U. socialis* and *M. testudinarius* are only known with certainty from the Upper Santonian.

Most of these crinoids are found in chalks, which are extensively developed in the Upper Santonian, although there are also records from marls and sandstones. Many of the older records give little detail of lithology. It is possible to show in Northern Ireland that the species occur only in chalks and are absent in co-eval glauconitic sandstones and other facies (Wilson and Manning 1978). Similarly, in Picardie in northern France, *Marsupites* is absent from lenses of granular phosphorite, but present in laterally equivalent chalks (Jarvis 1980). Pechersky *et al.* (1983) summarized records of *Marsupites* in calcareous facies (mainly chalks) of the Crimea, Caucasus and Kopet Dag, and contrasted these occurrences with the absence of the genus in clays and glauconitic sandstones to the north, on the Russian Platform. *Marsupites*, however, is present in sandstones at Plymouth Bluff in Mississippi, where it occurs rarely in a single 50 mm bed. It can be concluded that the distribution of *Marsupites* and *Uintacrinus* is controlled by the nature of the substrate, with a strong predilection for chalks, from which it may be inferred that they were benthic.

M. testudinarius (above) and *U. socialis* (below) occur in the Upper Santonian, with or without a short overlap of range. *U. anglicus* occurs only in England and succeeds *Marsupites*; it is best considered to be of earliest Campanian age. Besairie (1936) claimed that the *Marsupites* occurrence in Madagascar is of Campanian age. This appears to be improbable in view of its Santonian age elsewhere.

TAPHONOMY

Springer (1901) gave a detailed account of the occurrence and mode of preservation of the large groups of intact *Uintacrinus socialis* in the Niobrara Chalk of Kansas. Uintacrinids occur in the upper part of the chalk in lenticular deposits, only 25 mm thick in the centre. They generally cover

a few square metres, although the largest outcrop recorded covered an area of more than ninety square metres (Springer 1901). In all circumstances, it is the lower surface of the slabs which displays the articulated crinoid remains, whereas the upper surface is covered with disarticulated ossicles. The junction between the crinoidal layer, and the much softer underlying and overlying chalk is very sharp, whilst the sediment component in the crinoidal layer is negligible. The differential preservation between the upper and lower surfaces, and the lack of the interstitial sediments, is very similar to that seen in the pseudoplanktonic pentacrinitids (Simms 1986). After the death of a colony, current action winnows and sorts the exposed material, whilst the lower surface is protected.

Grinell (1876) observed that in the Kansas material uintacrinid calyces lie flattened-out, usually on their sides. Specimens with the basal plates visible are not uncommon, but the upper portions of the uintacrinid calyx are never shown. Springer (1901) also noted that the most common calyx orientation was lying on its side. However, he stated that many were embedded base downwards, leaving the basal plates exposed on the lower slab surface; calyces preserved with the ventral surface orientated downwards were rare. Similar orientations are observed for *Marsupites* from the Santonian Chalk of Bridlington, Yorkshire. This indicates that the *Marsupites* and *Uintacrinus* were orientated with the oral surface facing upwards.

FUNCTIONAL MORPHOLOGY

Three mechanisms might be envisaged by which *Marsupites* and *Uintacrinus* could achieve a pelagic mode of life; passively through reduction in weight of the skeletal plates and generation of buoyancy by means of oil or gas; actively by swimming continually to maintain lift; or by attaching themselves to some independently floating material and becoming pseudoplanktic.

Structure of the ossicles

The absence of any means of attachment, such as a stem, indicates that *Marsupites* and *Uintacrinus* were free living. According to Bather (1896), Springer (1901) and Rasmussen (1961), the plates of both genera are extremely thin and fragile. However, the ossicles of specimens from the Upper Santonian of Britain are extremely robust and heavily calcified. These differences in mechanical properties of the plates may arise from differences in diagenetic alteration. Ossicles from the Niobrara Chalk, Kansas, have been subjected to diagenetic dissolution and subsequent micritization (Neugebauer 1978).

The thecal plates and robust, heavily calcified brachials of *Marsupites* and *Uintacrinus* do not show evidence of skeletal lightening. By contrast, the brachials of pelagic roveacrinids are often hollow and reduced to the minimum weight.

Nektonic potential

The endoskeleton of *Marsupites* and *Uintacrinus* is composed of high magnesium calcite, the density of which is significantly greater than that of sea water. The soft tissue component would also have been denser than sea water. Therefore, if *Marsupites* and *Uintacrinus* were pelagic, they must have either been continuously active in order to generate lift, or they must have possessed a special buoyancy mechanism. Effective swimming motion in crinoids is generated from the basal half of the arm (Shaw and Fontaine 1990). The critical articulation occurs between the radial facet and IBr_1, where the muscles that flex during the recovery stroke and the ligaments that contract during the power stroke are concentrated. Thus, the articular facet of the comatulids and nektonic roveacrinids dominates the radial plates. Reconstructions using fossil material have shown that the nektonic roveacrinids were capable of sweeping their arms through extensive arcs. *Hyalocrinus* from the Lower Cretaceous Gault of Folkestone, Kent, was capable of moving its arms through 105° (Griffiths 1989).

Mobility in *Marsupites* and *Uintacrinus* is severely restricted, due to the incorporation of proximal brachials into the thecal structure. In *Marsupites*, where the radial plates may form the ventral margin of the calyx, the curved nature of the facet would restrict movement. In addition, the musculature on such facets was poorly developed. The fulcral ridge terminates abruptly before it reaches the facet margin, and the muscle and ligament fossae are relatively small.

Planktonic potential

Bather (1896) proposed that the calyces of *Marsupites* and *Uintacrinus* have been expanded to accommodate a buoyancy mechanism. If a low density material was present in the calyx, the crinoid would only be stable if the calyx were orientated with the ventral surface facing downwards. Gislén (cited in Peck 1955) stated that it would be difficult for a crinoid to catch sinking particles of food if it were orientated with the mouth down.

Orientation

Bather (1896) suggested that *Marsupites* and *Uintacrinus* were orientated with the mouth directed upwards and were stabilized by strongly recurved arms that acted as a counterweight. In such an orientation, it might be anticipated that the thecal plates would be thickened dorsally. This would lower the centre of gravity and thus increase stability. However, the thecal plates are all of equal thickness.

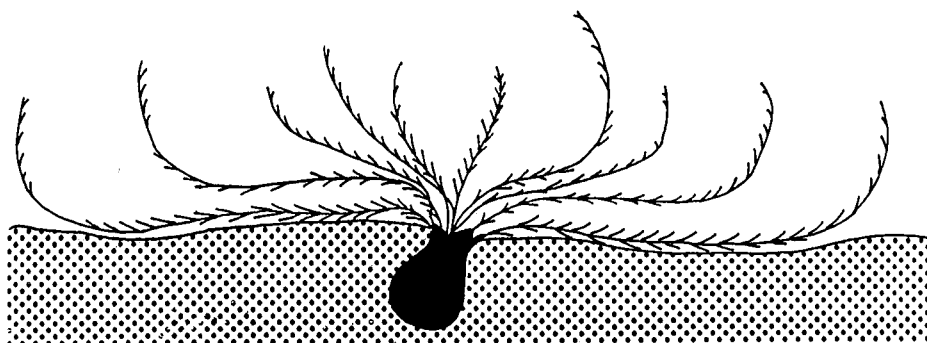## MODE OF LIFE

Previous work

A planktonic mode of life for *Marsupites* and *Uintacrinus* was first proposed by Bather (1896). He based his conclusions on the presence of a light flexible calyx, long movable arms, and the absence of any means of attachment. Jaekel (quoted in Bather 1896) had suggested that *Saccocoma* may have been lightened by a slight development of gas within the theca. Bather implied that such a buoyancy aid may have also existed in *Marsupites* and *Uintacrinus*. He concluded that *Uintacrinus socialis*, which dominates in the Niobrara Chalk of Kansas, was pelagic and lived in swarms. However, as the European species *U. westphalis* occurs as isolated specimens, Bather (1896) designated it pelagic, but not gregarious.

Springer (1901) also concluded that *Uintacrinus socialis* was pelagic. He envisaged the crinoids swimming together in schools aided by their long and powerful arms. He suggested that specimens may have become entangled when there was no suitable site of attachment available, as occurs in antedons (Carpenter 1866). Springer thus indirectly suggested that these schools were usually pseudopelagic, presumably attached to a float by their arms. A pseudopelagic mode of life was also proposed by Schuchert (1904). He suggested that *Uintacrinus socialis* may have held itself to foreign objects by its long slender arms.

Proposed mode of life

The heavily calcified endoskeleton of *Marsupites* and *Uintacrinus* is not indicative of a pelagic mode of life. The presence of a buoyancy mechanism is discounted because the thecal volume has not been expanded and is proportional to arm length. Also, if such a mechanism were present, the crinoid would only be stable if it was orientated with the oral surface facing downwards. This contradicts the taphonomic and morphological evidence which indicates that *Marsupites* and *Uintacrinus* were orientated with the oral surface upwards. Limited flexibility in the proximal arm section, and the weakly developed musculature of the brachials, indicates that they were unable to swim and were not therefore nektonic. Finally, there is no direct evidence, in the form of associated driftwood or similar substrate, for a pseudoplanktonic mode of life.

We propose that *Marsupites* and *Uintacrinus* lay on the sea floor with the calyx embedded in the sediment (Text-fig. 3). The proximal sections of the arms lay on the sediment surface, stabilizing the

TEXT-FIG. 3. Proposed mode of life for *Uintacrinus* and *Marsupites*; stipple represents sea bed sediments.

crinoid, whilst the distal ends curved upwards to form a feeding bowl. The distal section of the arms was flexible so that when a slight current was present, the arms could be orientated with the aboral surface facing down-current to increase the feeding efficiency, as observed by Meyer (1973) in the comatulids. However, such rheophobic feeding is extremely rare in extant crinoids. Meyer (1973) states that deep sea species of comatulids may be rheophobic, but the collecting bowl is only a temporary feeding method employed when currents are slack.

The crinoids may have been mobile. It is possible that they were able to move across the substrate by repeated extension and contraction of the pinnules in the distal parts of their long arms. Shaw and Fontaine (1990) demonstrated that crawling in comatulids involves the distal arm section and loss of only twenty per cent of the arm limits crawling activity. When extended, the pinnules would produce a larger surface area to 'push off' from, and as the arm lifted away from the substrate, flattening the pinnules against the main arm axis, drag would have been minimized. However, the heavily calcified endoskeleton and weakly developed musculature would have limited such activity.

The world-wide distribution of *Marsupites* and *Uintacrinus* probably reflects a plankotrophic larval stage. Such larvae are able to subsist on planktic food, which allows a long larval duration (Jablonski and Lutz 1983) and hence high dispersal capability. Thorson (1950) estimated that seventy per cent of all benthic marine species undergo planktotrophic development. In temperate-water species, this planktic stage generally lasts from two to six weeks (Thorson 1961), allowing for a dispersion of 150–550 km in a current of only 0·5 km/hr (Scheltema 1977). However, tropical benthos may remain as plankton for up to six months and thus may be carried great distances by ocean currents.

CONCLUSIONS

Phylogenetic analysis reveals that *Marsupites* and *Uintacrinus* are united in a single clade, the Marsupitidae, whose sister taxon is the Comasteridae. Functional analysis of their morphology indicates that *Marsupites* and *Uintacrinus* were benthic. We propose that they lay on the sea floor with the calyx embedded in the sediment. The proximal section of the arms provided support, whilst the distal arm sections formed a feeding bowl. The world-wide distribution of *Marsupites* and *Uintacrinus* probably reflects a long larval stage.

advice on the phylogenetic analyses, and Hazel E. Clark (Liverpool John Moores University) drafted the diagrams.

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