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Phylogenetic analysis of cyrtocrinid crinoids and its influence on traditional classifications

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ABSTRACT - The cyrtocrinids are a group of mostly Mesozoic articulated crinoids, with rare Cenozoic forms and only two extant taxa. A careful analysis of previous studies indicates that the systematic arrangement of cyrtocrinids is very weak and unsatisfactory for several reasons. In particular, most of the original descriptions and diagnosis date from the past century and are logically influenced by a classical typological philosophy. Not being based on phylogeny, the currently accepted groups for cyrtocrinids must be putatively regarded as "artificial". In addition, an inappropriate use of characters has been used, typically considered as diagnostic in other groups of crinoids but only marginally applicable to cyrtocrinids (the latter differently characterized for several highly distinctive and autapomorphic characters). In order to mitigate these problems and to arrive at the definition of characters and clades based on unambiguous synapomorphies, we present in this paper a preliminary and exploratory phylogenetic analysis based on parsimony of cyrtocrinids. The obtained topology showed how the traditionally recognized groups prove to be highly paraphyletic and polyphyletic, indicating the need for a complete revision of cyrtocrinids taxonomy, based on phylogeny. The gap-weighting method used for codifying morphometric continuous character, has proved to be a powerful tool to obtain well-resolved and consistent cladograms, even with a limited number of characters.

Keywords: Mesozoic crinoids; Articulata; Cyrtocrinida; Cladistics analysis; Gap-weightingt.

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1. INTRODUCTION AND STATE OF ART

Quantitative phylogenetic analysis of a group of selected Mesozoic crinoids with the addition of some extant species, practically the whole stem group Cyrtocrinida (*sensu* Hess, 2011; see also Dadocrinida *sensu* Nicosia, 1991), was performed on the basis of morphological characters. Phylogenetic analysis is required to clarify the evolutionary history and the systematics of the group.

At present, computer assisted, cladistic analysis of crinoids is highly under investigated, consisting in few principal studies (Cohen et al., 2004; Rause et al., 2013; Ausich et al., 2015); moreover only the former of them examinees the major taxa of Articulata. Rause et al. (2013) analysed the DNA of 59 extant crinoid species (37 feather-stars, 10 isocrinids, 6 bourgueticrinids, 3 cyrtocrinids and 3 hyocrinids). In particular they analysed three mitocondrial gene fragments (COI, 16 S and Cyth) and two nuclear gene fragments (18S and 28S). Unfortunately such genetic analysis is not useful for our purposes, since, morphological characters are not considered in the study. The paper by Ausich et al. (2015) concerned only Palaeozoic forms, with 150 used characters that are very difficult (if not impossible) to apply to cyrtocrinids.

Cohen et al. (2004) analyzed, based on both molecular and morphological characters, a group of living taxa including a bourgueticrinid (*Bathycrinus*), two comatulids (*Dorometra* and *Florometra*), three isocrinids (*Endoxocrinus,* two species of *Metacrinus*); other taxa of uncertain position, such as *Guillecrinus* [Roux (1985) placed it among Inadunata; on the contrary in the Treatise (Hess, 2011) *Guillecrinus* is placed in the Guillecrinina (Comatulida)] and *Caledonicrinus* [Mironov (2000) placed it among Bourguetticrinina whereas after a molecular analysis Cohen et al. (2004) placed it among cyrtocrinids] along with morphological data from *Proisocrinus* and three living forms (*Gymnocrinus, Cyathidium* and *Holopus*) are ascribed by those authors to cyrtocrinids. Only the last three were taken into consideration in our work; even if the position of the living specimens ascribed to *Gymnocrinus (Gymnocrinus sensu* Bourseau et al., 1987 = *Neogymnocrinus* Hess, 2006), referred by the authors to cyrtocrinids, is still uncertain being based just on the similar morphology of the brachial plates (probably not homologous).

Among the 30 morphological characters used by Cohen et al. (2004), one subdivides approximately stemless and stemmed forms; four characters describe the composition of the cup, five some features of the arms. Other characters concern overall shape and organization of columnals. Only five of the characters defined in that paper were used herein after being redefined and recoded, whereas all the others were considered useless for the present analysis, because most of these features can only be observed and codified using complete and articulated specimens.

The present study constitutes a first, preliminary attempt to define homologous phylogenetic characters and character states for a group with a very peculiar evolution. Indeed cyrtocrinids are a group of Articulata crinoids that, as presently defined (Hess, 2011), includes 46 genera and many tens of species (almost all Mesozoic and very few Cenozoic and living forms).

The principal characters of this group can be summarized as follows: 1) small dimensions; 2) usually the cup is made by rigidly sutured radial plates, frequently fused; 3) basal plates are rare, even if still present in some genera; 4) relatively short arms with a single axillary (usually IBr2Ax); 5) short stemmed or stemless forms are widespread as well as bent forms. These characters were ascribed to a strong adaptation to peculiar environments, occupied by these crinoids during the early stages of their evolution (Manni and Nicosia, 1996) and then characterized these forms for their whole occurrence. In fact cyrtocrinids, typical Tethysian forms, most probably appeared during the first phases of the Tethys Ocean rifting (Fabbi and Santantonio, 2012) from which originated some isolated, relatively shallow water, mud-dominated, small areas. In such areas cyrtocrinids were able to survive, dwell and specialize, taking further advantages by a special ability in shell-debris settling on muddy bottoms and niche partitioning. The almost synchronous extinction of many forms fits well with the hypothesis, that extinction resulted from geodynamically controlled disappearance of their small habitats (Manni and Nicosia, 1996).

The systematics of cyrtocrinids is quite unsatisfactory and strongly needs a complete revision. This originates from different causes, and it is closely related to the peculiar characters of this group, definitely different from other crinoid clades (Hess, 2011). Unfortunately the cyrtocrinid systematics has been deeply affected by the influence of characters used in the classification of other crinoid groups, such as stem and arm organization, kind of pinnulae and type of articular surfaces between ossicles (syzigial, synostosial a.s.o.); all characters mostly useless for cyrtocrinids (generally these crinoids are preserved disarticulated). On the contrary, the characters that are fundamental for this group have been commonly ignored or under considered. Furthermore, the lack of unambiguous definition of plesiomorphic and apomorphic character states and of the homoplasic ones, has led to excessive taxonomic lumping or to splitting, according to the different authors philosophies. Some taxa or groups of taxa were ascribed to this clade just because a better solution was lacking or simply on the basis of an established tradition. Such an approach partially transformed the group in a sort of taxonomic 'garbage-basket'.

The aim of the present work is to consolidate the character analysis in order to solve some of these major problems by means of phylogenetic analysis and to amend some undesirable mistakes and shortcomings.

2. MATERIAL AND METHODS

2.1. Taxa selection

In the present study more than 50 taxa, genera, groups and species, formerly ascribed to cyrtocrinids in different traditional classifications and most of the 46 genera included into the order Cyrtocrinida in the Treatise (Hess, 2011) were carefully analyzed, in the attempt of include only well-defined forms referable to the same monophyletic group (Tabs. 1, 2). Notice that Hess (2011) presented the hypothesis of a polyphyletic group, whereas monophyly is suggested by Cohen et al. (2004).

The result of this preliminary work are quite complex due to the non-uniform rationales and philosophies of classification adopted by previous authors and, consistently, to the variable descriptions and systematic arrangements. In addition this work is complicated by the dramatic plasticity of the crinoid phenotype as a whole and of this group in particular (Manni et al., 1996). Moreover cyrtocrinids have morphological variations so consistent (see for example the different specimens of *Eugeniacrinites cariophilites* in Manni et al., 1996) that we preferred to base the present analysis on just a few forms, or on single specimens as representatives of genera (see "the matrix" below).

It is important to stress that most of recognized evolutionary features and the related cladogenetic events concerning this group seem to be frequently linked to heterochrony phenomena: an aspect that implies further major problems in distinguishing different taxa from diverse development stages. In the few cases in which different ontogenetic stages are well known (Manni and Nicosia, 1987, 2004; Hess, 2014), we preferred to exclude forms that could be just juveniles of taxa already considered. Such an approach also applies to Early Jurassic forms, generally those of very small absolute size (and in which it is practically impossible to distinguish juvenile and mature specimens) and to groups with juveniles almost identical to each other, that differentiated only subsequently during later phases of ontogenesis (e.g. phyllocrinids; under preparation, UN Pers. Obs.).

After this selection, we included only forms that could be referred quite confidently to the Order Cyrtocrinida Sieverts Doreck 1952 (*sensu* Rasmussen 1978). A few taxa, subsequently established (*Nerocrinus* Manni and Nicosia 1999; *Ticinocrinus* Hess 2006) were included,

Apsidocrinus Jaekel, 1907; Late Jurassic-Early Cretaceous.
Bilecicrinus Manni and Nicosia, 1990; Early Jurassic.
Brachiomonocrinus Arendt, 1974; Early Cretaceous.
Cotylederma Quenstedt, 1852; Early Jurassic; Late Jurassic?
Crataegocrinus Manni and Nicosia, 1985; Middle Jurassic.
Cyathidium Steenstrup, 1847; Late Jurassic-Holocene.
Cyrtocrinus Jaekel, 1891; Middle Jurassic-Early Cretaceous.
Dadocrinus von Meyer, 1847; Middle Triassic.
Dinardocrinus Manni and Nicosia, 1990; Early Jurassic.
Eudesicrinus de Loriol, 1882; Early Jurassic-Late Jurassic.
Eugeniacrinites Miller, 1821, early Late Jurassic, here includes only the type species *E. cariophilites* (Schlotheim, 1813); codified in the matrix as Eucaryophylla.
"E. alpinus" informal name including all the Tethyan cups (in need of a new genus name) originally ascribed to *Eugeniacrinites* and to *Lonchocrinus,* probably more close to *Psalidocrinus*, and strongly different from *E. cariophilites*; codified in the matrix as Eugeniaalpinus.
Fischericrinus Castellana, Manni, and Nicosia, 1989; Middle Jurassic-Late Jurassic.
Gammarocrinites Quenstedt, 1858; Late Jurassic.
Hemibrachiocrinus Arendt, 1968; Early Cretaceous.
Hemicrinus d'Orbigny, 1850; Late Jurassic-Early Cretaceous.
Holopus d'Orbigny, 1837; Paleogene-Holocene. .
Hoyacrinus Delogu and Nicosia, 1986; Late Jurassic.
Neodadocrinus Manni and Nicosia, 1990; Early Jurassic.
Nerocrinus Manni and Nicosia, 1999; *Early Jurassic.*
Paracotylederma Manni and Nicosia, 1990b; *Early Jurassic.*
Paragammarocrinites Jäger, 1982; Late Cretaceous.
Phyllocrinus d'Orbigny, 1850; Middle Jurassic-Early Cretaceous.
Plicatocrinus Münster, 1839; Early Jurassic-Late Jurassic.
Proholopus Jaekel, 1907; Late Jurassic-Early Cretaceous.
Psalidocrinus Remeš, 1913; Late Jurassic-Early Cretaceous.
Quenstedticrinus Klikushin, 1987; Early Jurassic.
Remisovicrinus Arendt, 1974; Middle Jurassic-Late Jurassic.
Sacariacrinus Nicosia, 1991; Early Jurassic.
Strambergocrinus Žitt, 1979; Early Cretaceous.
Tetracrinus Münster, 1839; Middle Jurassic-Early Cretaceous.
Ticinocrinus Hess, 2006; Early Jurassic.
Torynocrinus Seeley, 1866; Early Cretaceous.

Tab. 1 – List of the taxa selected and enclosed in the analysis.

as well as the genus *Neodadocrinus* Manni and Nicosia 1990 (although recently ascribed to Millericrinida Sieverts Doreck 1952 by Hess, 2006, 2011). In respect to the systematic arrangement adopted in the Treatise (Hess, 2011), some forms were excluded either being of doubtful affinity (e.g. *Capsicocrinus* Delogu and Nicosia 1987; *Ninocrinus* Castellana et al. 1990; *Neogymnocrinus* Hess 2006), being based only on referred brachials and columnals (e.g. *Castaneacrinus selliformis* Hess 2006); being based on the shape of brachials (e.g. *Lonchocrinus* Jaekel, 1907).

The resulting list of taxa available for the analysis includes 33 taxa; most of them had a Jurassic-Early Cretaceous occurrence and only two extended into Cenozoic. A well known Triassic genus (*Dadocrinus*) was included as the outgroup for character polarization.

In Table 1, the taxa selected for the analysis are listed with information summarizing their institution and some nomenclatural problems, along with their respective occurrences. In Table 2 reasons for the exclusion of other taxa are made explicit.

2.2. Character analysis

In the analysis were mainly considered characters of the cups and of RR-IBrBr articulations, whereas less importance was given to characters of the stem and arm

Arzocrinus Hess, 2006; Early Jurassic, excluded because based only on radial plates and unarticulated columnals.
Ascidicrinus Hess et al., 2011, Late Jurassic, excluded because the type species probably is a very small juvenile.
Capsicocrinus Delogu and Nicosia, 1987; Early Jurassic, excluded for its uncertain systematics position.
Dibrachiocrinus Arendt, 1968; Early Cretaceous, originally described as a distinct genus but presently included into *Hemibrachiocrinus* Arendt, 1968 by Zitt (1979).
Dolichocrinus de Loriol, 1891; Middle Jurassic-Late Jurassic, form based on insufficient material.
Gymnocrinus Loriol 1879; genus originally based only on AxAx, name subsequently used for including a living form (see *Neogymnocrinus* Hess, 2006).
Lonchocrinus Jaekel, 1907; Middle Jurassic-Early Cretaceous, genus originally based only on BrBr.
Neogymnocrinus Hess, 2006; living, probably ascribed to cyrtocrinids only on the basis of the morphology of AxAx (similar to the IBr2 ascribed to *Gymnocrinus*).
Ninocrinus Castellana, Manni, and Nicosia, 1991; Middle Jurassic, form based on insufficient material.
Pilocrinus Jaekel, 1907; Late Jurassic, excluded for its doubtful composition, sometimes considered related to *Gymnocrinus* Loriol 1879 for the type of presumptively assigned 1BrB2.
Praetetracrinus Jäger, 1995; Early Jurassic-Middle Jurassic, probably synonym of *Sacariacrinus*.
Proeudesicrinus Améziane-Cominardi and Bourseau, 1990; living, form based on insufficient material.
Pustulocrinus Hess, 2006; Early Jurassic, perhaps a millericrinid, probably junior synonym of *Shroshaecrinus* Klikushin, 1987.
Sclerocrinus Jaekel, 1891; Upper Jurassic-Early Cretaceous, probably extreme morphological variations of *Gammarocrinites*.
Scutellacrinus Hess, 2012, Middle Jurassic, form based on insufficient material.

Tab. 2 - Taxa excluded from the analysis.

distal portions due to the repetitiveness of these characters in different taxa (but also taking into consideration the almost total lack of articulated specimens for many cyrtocrinids). Characters were excluded from the analysis if a high percentage of missing entries existed (when a character could be codified in fewer than the 25% of taxa it was excluded on the basis of the confidence limits reported by Wiens, 2001, 2003a, b).

Qualitative characters were subdivided conservatively in to few large character states, in order to reduce the influence of the huge variability. Whenever possible, qualitative characters were converted into quantitative ones through dimension ratios among anatomical lengths (in this way the absolute size has no influence for the analysis). The values of quantitative characters (expressed as ratios) were subsequently used to apply the Gap weighting method (Thiele, 1993; Romano and Nicosia, 2015).

In principle, low significance were ascribed to the type of articulation among the plates and the stem elements, characters sometime concealed and extremely subject to weathering, decay and diagenetical changes, and, perhaps, depending also on growth stage (but see Simms, 1988; Klikushin, 1987; Hess, 2014; Cohen et al., 2004; for contrasting hypotheses).

The characters used and the character state rationale is given as Appendix 1.

2.3. The matrix

The analyzed matrix (Appendix 2) was made by 35 taxa (see Fig. 1; subsequently reduced to 33 by the exclusion of *Sclerocrinus* and *Pilocrinus*) (see Figs 2, 3); this condition

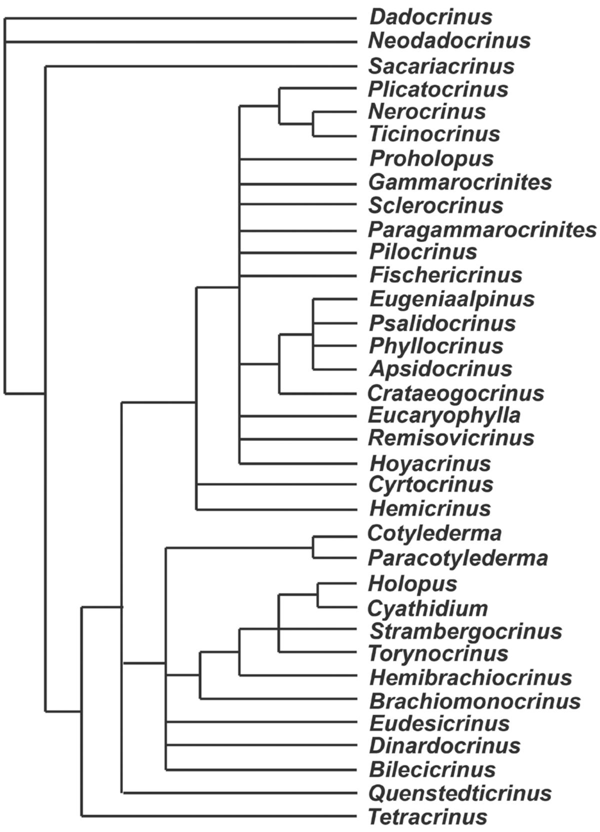

Fig.1. The strict consensus of 495 equally parsimonious trees obtained with the first analysis.

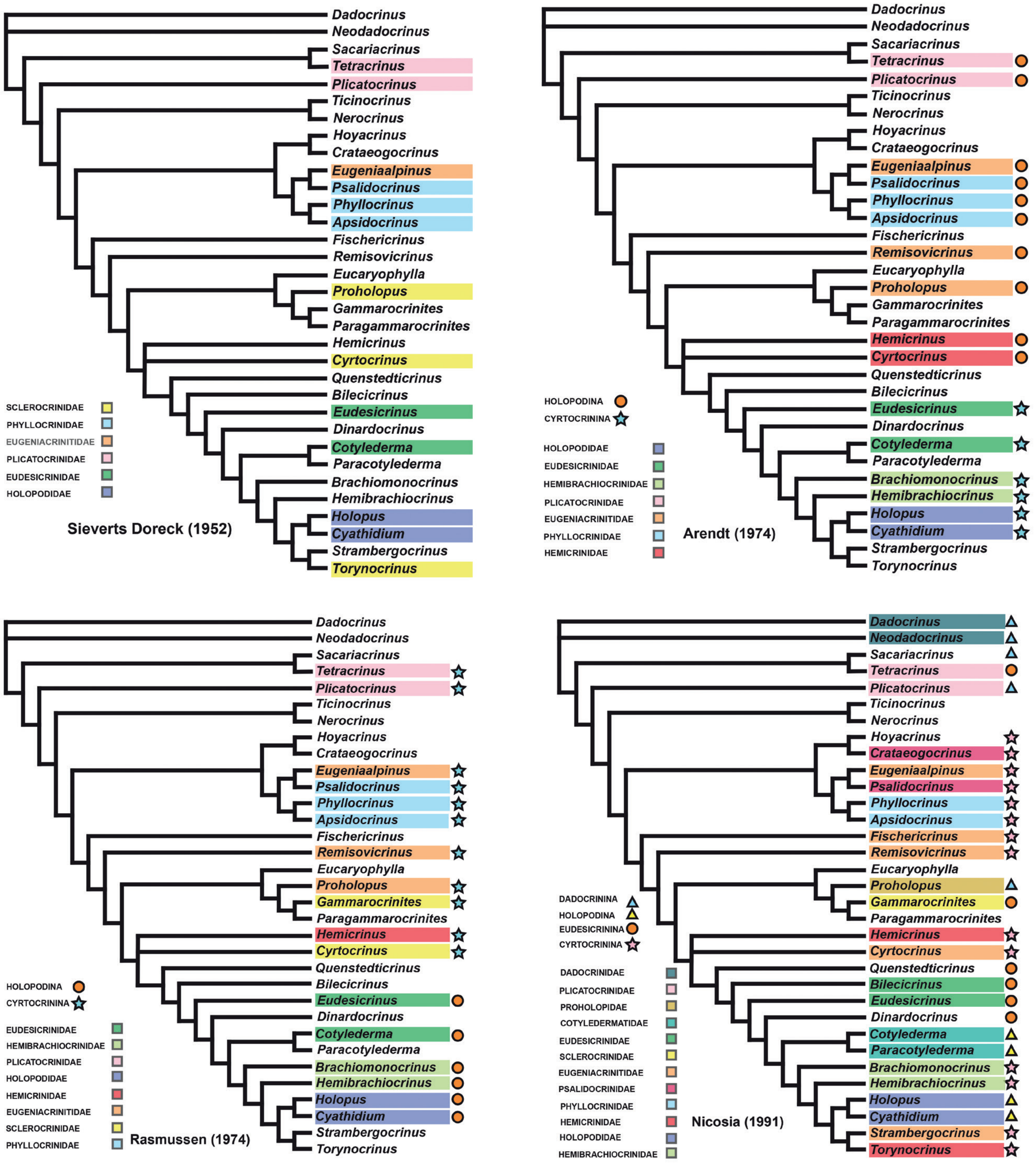

Fig. 2 - Comparison between the reference topology (obtained with the gap-weighting method) and the classification by Sieverts Doreck (1952), Arendt (1974), Rasmussen (1974) and Nicosia (1991).

changed in the matrix prepared for the gap-weighting method (higher number of character states, see below).

In general, we based character definition, on the holotype of the type species of the genus, or on the basis of a single better preserved specimen (85% of cases) in order to prevent ambiguities or possible chimaeras; in few cases characters are based on co-specific specimens.

3. PHYLOGENETIC ANALYSIS

The matrix was subjected to the test of character congruence based on parsimony in the software PAUP* 4.0b10 for Windows (Swofford, 2002). For the analysis, the heuristic search algorithm was used with 1000 addition sequence replicates, to avoid the searches from

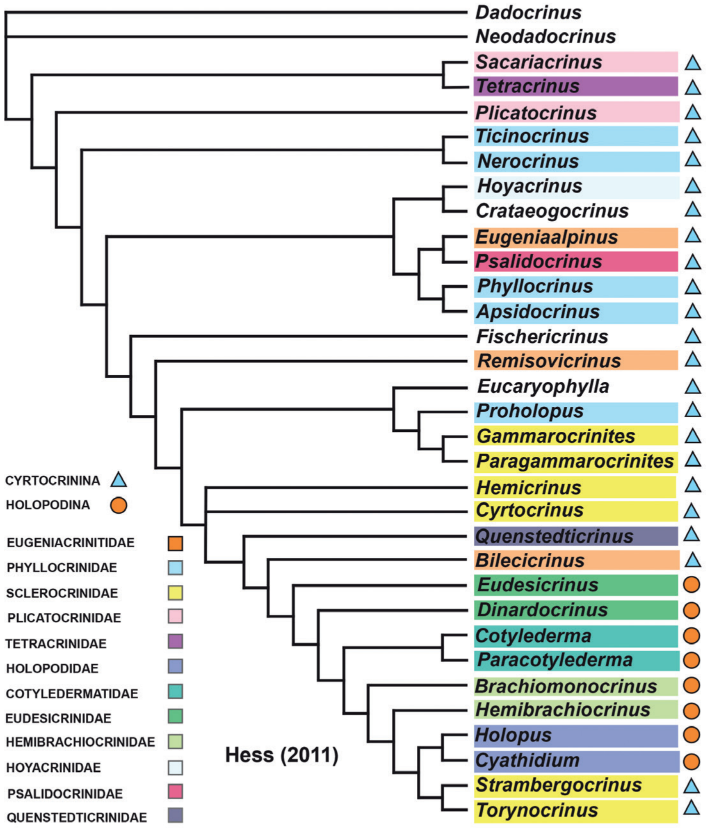

Fig. 3 - Comparison between the reference topology (obtained with the gap-weighting method) and the classification proposed by Hess (2011).

becoming trapped in a local tree-length minimum (Maddison, 1991). The accelerated transformation (ACCTRAN in PAUP* 4.0b10) was selected for the evolutionary optimization of characters.

The analysis found 495 equally parsimonious trees with a length of 149 steps, consistency index (CI) of 0.403, homoplasy index (HI) of 0.597 and retention index (RI) of 0.709. The strict consensus tree (Figure 1) presents several unresolved portions represented by extensive uninformative polytomies.

In order to get a more resolved cladogram, an encoding of the continuous characters (i.e. based on the morphometric ratios) was attempted by using the gap weighting method by Thiele (1993). The use of characters as dimensional ratios that vary continuously has always represented a topic of heated debate in cladistics, with several works that question the consistency of these characters for reconstructing the correct phylogeny in the group under study (e.g. Crisp and Weston, 1987; Pimentel and Riggins, 1987; Cranston and Humphries, 1988; Cox and Urbatsch, 1990). However, recent phylogenetic analyses of the Caseidae (Synapsida, Caseasauria) (Romano and Nicosia, 2015) has shown how this method allows inclusion of very fragmented specimens or represented by very incomplete material, leading to plausible and well resolved topology.

Over time, different methods have been proposed to codify discretely continuous characters which include among others the "gap coding" (Mickevich and Johnson, 1976), "segment coding" (Colless, 1980; Thorpe, 1984; Chappill, 1989) and "generalized gap coding" (Archie, 1985). For the present work the "gap weighting" proposed by Thiele (1993) is chosen and preferred. This is a method able to take into account (and to weigh proportionally) the relative magnitude of the gap between considered values. Furthermore, the method resulted as the best performing in the comparative analysis by Garcia-Cruz and Sosa (2006), leading to the largest number of well-supported clades, with matrices comprised of a higher number of informative characters.

In accordance with the gap-weighting method, the seven morphometric characters (6, 10, 11, 12, 13, 17, 24) were discretized using the formula proposed by Thiele (1993), considering 32 states of character (limit for a 32-bit machine in PAUP* 4.0b10). The states of the selected character, as can be found in the obtained matrix (Appendix 2), are specifically: 0, 1, 2, 3, 4, 5, 6, 7, 8, 9, A, B, C, D, E, F, G, H, I, L, M, N, X, P, Q, R, S, T, U, V, Z, W (the letter "X" was used instead of the letter "O" to avoid possible confusion with the number state "0").

The new matrix, with the morphometric characters codified with 32 states, was subjected again to the tests of congruence of parsimony in PAUP. Still in accordance with the Thiele method (1993), a weight of 32 was attributed to qualitative classical characters, to make them equivalent to the number of states used in the continuous ones. The latter were included in the program as ordered. For the analysis it was used again the heuristic search algorithm with 1000 addition sequence replicates and the accelerated transformation (ACCTRAN).

The analysis, with 12056489 rearrangements tried, resulted in three equally parsimonious trees with a length of 32 578 steps, consistency index (CI) of 0.520, homoplasy index (HI) of 0.480 and retention index (RI) of 0.572. As can be seen (Fig. 2), the strict consensus tree is completely resolved apart from the position of *Cyrtocrinus* in relationship of polytomy with *Hemicrinus*. It is probable that the taxon can be considered a synonym of *Hemicrinus*, with strings of characters that are mostly superimposed, except for minor differences. Thus, once pruning this taxon from the tree, the obtained topology can be considered as completely resolved.

3.1. Consideration on the obtained topology

Looking at the obtained topology it is possible to appreciate the organization of some groups, for example the grouping as sister taxa for *Nerocrinus+Ticinocrinus*, *Eugeniaalpinus+Psalidocrinus, Phyllocrinus+Apsidocrinus, Holopus+Cyathidium*, *Gammarocrinites+Paragammarocrinites* and *Cotylederma+Paracotylederma*. Also the sequence of *Quenstedticrinus*, *Bilecicrinus*, *Eudesicrinus*, *Dinardocrinus* can be shared. Fully appreciable is the position of the group *Nerocrinus+Ticinocrinus* at the base of the phyllocrinids (s.s.) and the arrangement (*Crataegocrinus+Hoyacrinus)* (*Eugeniaalpinus+Psalidocrinus*) (*Phyllocrinus+Apsidocrinus*). More unexpected is the position of strongly modified forms like *Strambergocrinus* and *Torynocrinus*, possibly due to convergent evolution: the relationship among these taxa and between these genera with other problematic forms (for example see Zitt, 1979 on the relationships between *Strambergocrinus* and the hemibrachiocrinids) needs careful reexamination.

In order to compare the results with respect to the classification, the strict consensus tree, obtained with the new coding of morphometric characters, was compared with traditional (non cladistic) present and past classifications reported as in the literature.

Before discussing these analysis, a problem must be highlighted. The problem of *Eugeniacrinites cariophilites* and its historical use. Indeed for a long time the name was a 'cumulative name' that included many forms strongly different from each other and subsequently split in different genera (see Tab. 3). Due to its long history, *Eugeniacrinites*, instead of being considered a specific form with peculiar derived features and a small geographical and chronological distribution, assumed the role of eponymous representative of this group of crinoids and appeared in all the classifications as a family (or higher taxa) name-bearing genus. Indeed, it is present in different levels, such as in all the more recent systematic arrangements [e.g. Eugeniacrinidées Loriol, (1982-84); Eugeniacrinitacea Arendt (1968); Eugeniacrinidae Zittel (1876-1880); Eugeniacrinitidae *sensu* Sieverts-Doreck (1953) and Eugeniacrinitidae *sensu* Rasmussen (1978)]. It should also be noted that the family Eugeniacrinitidae included different genera in each arrangement. This fact contributed to uncertainty when analyzing the previous classifications in respect to the obtained topology.

In Figure 2 the classification by Sieverts-Doreck (1952, in Rasmussen, 1978) is plotted on the reference topology. Even considering that the number of genera known at the time was quite low, the only family that is strictly monophyletic is the Holopodidae, with *Holopus* and *Cyathidium* properly arranged in sister group relation. In contrast, the families Sclerocrinidae and Eudesicrinidae are polyphyletic, whereas the Phyllocrinidae would be paraphyletic due to the sister group relation of *Psalidocrinus* with *Eugeniacrinites*, the latter referred to Eugeniacrinitidae according to Sieverts-Doreck (1952) (but see the preceding caveat on *Eugeniacrinites*).

In the classification proposed by Arendt (1974) (Fig. 2), the two suborders Holopodina and Cyrtocrinina are fairly consistent with the topology presented here (not considering the numerous genera present in the cladogram and not included in the classification because not yet established at that time). However, the Holopodina *sensu* Arendt (1974) can be considered monophyletic starting from taxa more derived than *Bilecicrinus*, whereas the

E. aberrans de Loriol, 1882 = type of *Dolichocrinus* de Loriol, 1891

E. compressus Goldfuss, 1829 = type of *Gammarocrinites* Quenstedt, 1858;

E. deslongchampsi de Loriol, 1882 subsequently and alternatively assigned either to *Amaltheocrinus* by Jäger (1985) or to *Quenstedticrinus* by Klikushin (1987) or to *Sacariacrinus* by Nicosia (1991).

E. dumortieri de Loriol, 1882 = type species of *Lonchocrinus* Jaekel, 1907;

E. holopiformis Remeš, 1902 = type species of *Proholopus* Jaekel, 1907;

E. moniliformis Münster, in Goldfuss, 1829 = type species of *Tetracrinus* Münster, 1839;

E. moussoni Desor, 1845 = *type species of Pilocrinus* Jaekel, 1907;

E. nutans Goldfuss, 1829 = type species of *Cyrtocrinus* Jaekel, 1891;

E. strambergensis Remeš, 1912 = *Psalidocrinus strambergensis* (Remeš, 1912);

Tab. 3 – Main historical name changes for Eugeniacrinites

Cyrtocrinina are necessarily paraphyletic, not including all the descendants of a common ancestor. Again in Figure 2 the subdivision into families by Arendt (1974) is presented. As can be seen, the only phylogenetic valid family based on the new topology is the Holopodidae with sister group *Holopus* + *Cyathidium*.

In the classification proposed by Rasmussen (1978) (Fig. 2), as already observed in the one by Arendt (1974), the two suborders Holopodina and Cyrtocrinina are fairly congruent with the topology. However, once again the Cyrtocrinina is strictly paraphyletic and the Holopodina are monophyletic starting from taxa more derived than *Bilecicrinus*. Again the subdivision into families, has the Holopodidae as the only valid monophyletic family.

In Figure 2 the classification by Nicosia (1991) is plotted on the reference topology. Although the taxa in sub-orders are positioned very closely in the cladogram, the tree structure makes all such groupings paraphyletic and in many cases also polyphyletic. Among the reported families, only the Dadocrinidae, Cotyledermatidae and Holopodidae result strictly monophyletic clades on the basis of the obtained topology.

In Figure 3 the most recent and complete classification for the Cyrtocrinida proposed by Hess (2011) in the Treatise on Invertebrate Paleontology is plotted on the reference topology. As can be seen, the Suborder Holopodina is strongly paraphyletic, because it does not include the common ancestor and all its descendants; in fact the sister group *Strambergocrinus* + *Torynocrinus* referred by Hess (2011) to the Cyrtocrinina are positioned within the Holopodina, in a sister group relation with *Holopus* + *Cyathidium*. The condition for Cyrtocrinina is even more critical, because on the basis of the topology, the taxon is polyphyletic. In fact, the two taxa *Strambergocrinus* + *Torynocrinus* are in a derived position, not sharing a direct common ancestor with the Cyrtocrinina placed at the base of the cladogram.

In Figure 3 the subdivision in Families provided by Hess (2011) is plotted on the reference cladogram. Even in this case, some major problems are detected among "artificial" and "natural" taxa, the latter based on the putative phylogeny of the group. Among the considered Families, only the Cotyledermatidae and Holopodidae result phylogenetically valid, because strictly monophyletic. The other families are polyphyletic on a cladistic level, with taxa placed in different parts of the topology suggesting an independent evolution from different ancestors. Even in cases such as the Hembrachiocrinidae where the two taxa *Brachiomonocrinus* and *Hemibrachiocrinus* are positioned close to each other, their pectinate arrangement and the more derived group formed by *Holopus*, *Cyathidium*, *Strambergocrinus* and *Torynocrinus* make the family paraphyletic.

4. DISCUSSION AND CONCLUSIONS

As briefly highlighted in the study, the systematic arrangement of cyrtocrinid crinoids is unsatisfactory for a series of interconnected major reasons. First, most of the original descriptions and diagnoses date from the past century and are logically influenced by a classical typological philosophy, which had not yet metabolized the monumental Phylogenetic Systematic by Hennig (1966), milestone for the cladistic and phylogenetic approach to systematic.

Second place, there is an inappropriate use of characters typically considered as diagnostic in other groups of crinoids but only marginally applicable to cyrtocrinids for their highly distinctive and autapomorphic characters. In the same way, the typical autapomorphic characters for this group were unfortunately widely ignored or left without proper emphasis. Moreover, the absence of non-ambiguous definition of plesiomorphic and autapomorphic characters has inevitably led to phenomena of excessive lumping or splitting, according to the different philosophies embraced over time by various authors.

Another very common problem in the systematics for quite complex groups (sometimes only superficially compact) is the classic "garbage-basket" effect: i.e. taxa difficult to classify have been simply included into cyrtocrinid without a solid foundation of characters or character states.

To try to overcome these crucial problems and arrive at the definition of characters and clades based on unambiguous synapomorphies (and more objectively communicable), the first cladistic phylogenetic analysis based on parsimony was conducted, and reported in the present work. The new reference topology, indicates the traditional classifications do not faithfully reflect the phylogeny of the group. The new phylogenetic tree, although representing just a first and explorative attempt (it can be improved by additional taxa, and recoding or addition of new characters) strongly highlight the need for cladistic analysis in order to base the classification on 'natural taxa' (i.e. based on the phylogeny of the taxa in the studied group). In fact, the cladistic method is a very powerful tool that allows not only identification of different natural groups but also to provide for each node or clade the detailed list of unambiguous synapomorphies supporting the taxon (which are directly inherited from a common ancestor). The list of such synapomorphies, as returned by the software and discussed by the authors, can be unambiguously communicated, emphasizing the characters and states of character on which taxa are based.

The use of the gap-weighting method led to a completely resolved and entirely satisfactory topology, solving the polytomies caused by coarse coding (very few character states) of the continuous characters. Also, the use of a large number of character states (32) probably was able to intercept, in a more refined way, the putative phylogenetic signal contained in the considered dimensional ratios. Whereas for other groups, such as vertebrates, a large number of characters are usually available (e.g. in recent cladistic analysis of Caseidae by Romano and Nicosia, 2015, up to 477 morphological characters were identified), for many invertebrate groups the number of recognizable characters is remarkably reduced. This necessarily leads very frequently to a low number of characters for a quite high number of taxa included in the analysis, making it difficult to obtain fully resolved topologies. Thus, through the inclusion of several dimensionless ratios, the gap-weighting method could be a useful tool for reconstructing the phylogeny in other groups of complex invertebrates such as gastropods, bivalves, ammonites and belemnites.

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APPENDIX

Appendix 1

Characters and character states rationale

Ch 1 - number of RR 5 (0) ≠ 5 (1) fuse (2)

The number of RR is considered primitive (plesiomorphic) when the pentaradiated symmetry is preserved whereas fusion and reduction in RR number is considered the outcome of a phylogenetic meaningful process (e.g. *Tetracrinus, Bilecicrinus*) and thus derived (apomorphic). In some cases RR are variable from 4 to 6 (e.g. *Plicatocrinus*); in these cases the character could be codified as polymorph but, in this first attempt we took a conservative method codifying the state of character of a single specimen. In a second step it would be possible to increase the number of character states, but this could lead to very misleading results considering that epigenetic phenomena are very likely as well as ecomorphotypic and teratologic variations.

Ch 2 - RR difference in dimensions absent (0) apparent (1)

Even if a certain amount of variability is always present, in some cases one R (or two) is constantly more developed in respect to the others (probably as a reaction to prevailing unidirectional currents).

Ch 3 - iBiB present (0) absent (1)

Character that is present only in the outgroup *Dadocrinus*; it is codified for character polarization.

Ch 4 - BB conditions 5 (0) less than 5 (basal circlet) (1) absent (2) (reverse) (3)

BB are present in very few cases; it is clear that, in each case, it seems a primitive condition, the only exception could be *Paragammarocrinites*. According to Jäger (1982) BB in *Paragammarocrinites* could be interpreted as a reversal; that however is based only on the age of the specimens and not on a phylogenetic level. This is also the only autapomorphy of the genus, thus the character state, coded as 3, has to be cautiously considered.

Ch 5 - BB visibility apparent (0) concealed (1) absent (2)

Ch 6 - Cup height composition Htot/HRR > 1 (0) = 1 (1)

Ch 7 - Cup shape (lateral view) tulip (0) conical (1) artichoke (2) irregular (3)

Feature subject to a large variability due to the strong intraspecific polymorphy (ontogenetic, ecomorphotypic and functional) and consistently a high degree of convergence is expected). In the future this variability could be codified as a polymorph character.

Ch 8 - Cup regularity yes (0) no (1)

Character describing the regular repetition, continuous or not of all the elements in a cycle.

Ch 9 - Cup shape (aboral view) rounded (0) polygonal (1) lobed (2) irregular (3)

Ch 10 - MaxL iR / MaxL R ≤ 1.2 (0) ≥ 1.21 (1)

Ch 11 - R-iR diameter / MaxW art. facet ≤ 2.9 (0) ≥ 3 (1)

Ch 12 - Slenderness Hmax / (Wart. fac/W stem articular facet) ≤ 30 (0) 31-59 (1) ≥ 60 (2)

The height is measured from the plane of articular facet with the stem, to the articular facets plane.

Ch 13 - Cup height H max / max W alto ≥ 3 (0) ≤ 2.9 (1)

Ch 14 - Bending (degree) absent (0) faint (1) strong (2)

The character considers the folding of structural cup. It measures the inclination of the plane of facets relative to the horizontal (0-10°; 11-45°, ≥46°). Character present more or less in all the minor clades , perhaps due to convergence (a high level of homoplasy expected).

Ch 15 - Bending (origin) stem or absent or BE or DE (0) RR different development. (1)

Split of the character 14; it should eliminate some of homoplasy.

Ch 16 - Cup proximal portion open (0) closed (1)

Character defined only by the RR, related to the disappearance of the BB.

Ch 17 - Cup capacity Cavity diameter/Max W ≥ 0.7 (0) 0.69-0.31 (1) ≤ 0.3 (2)

Takes into account the trend for a strengthening of RR and to the transfer of the soft parts in a cavity formed only by the BrBr.

Ch 18 - Cup cavity shape Flat (0) conical (1) sub-spherical (2)

Ch 19 - iR projections absent (0) short (1) long (2) (vault) (3)

It characterizes the clade of Eugeniacrinitina . The encoding can be either 0-1-2, including the vault shaped projections into the long ones, or 0-1-2-3 or, less likely as 0-1-(2-3) considering it as polymorphic.

Ch 20 - iR profile iR absent (0) rounded (1) triangular (2) needle (3)

Ch 21 - N° articular facets /n° RR 1 (0) ≠ 1 (1)

Character in general corresponding to the number of RR. For the group of hemibrachiocrinids the reduction is considered the character of an anagenetic process. In the case the RR result fused, the character is codified as (1).

Ch 22 - Articular facet type plenary (0) angustary (1)

Ch 23 - Type of ridge implenary (0) explenary (1)

Ch 24 - Muscular fossae area/ligamentary area ratio ≥ 3 (0) ≤2.9 (1)

Ch 25 - Stem present (0) absent (1)

Stem is considered as present when it shows two or more columnal elements.

Ch 26 - cup attachment stem (0) eB (1) eD (2) columnal (3)

In stemmed crinoids the proximal element is considered Basal when it derives from the BB fusion; in other case it is considered Dorsal element.

Ch 27 - Stem facet/adoral cup side ratio total (0) partial (1) absent (2)

This ratio distinguishes stalked crinoids taking advantage of a current lift from reophobic stemmed forms.

Ch 28 - Stem articular facet circular (0) polygonal (1) absent/irregular (2)

Character that describes the shape of the articular facet for the stem (and the shape of the proximal stem element).

Ch 29 - Axillary IBr2 (0) IBr1 (1)

Ch 30 - Cup ornamentation absent (0) present (1)

Ch 31 - Sutures among RR apparent (0) absent (1)

Ch 32 - Type of attachment apparatus roots (0) disk (1) attachment apparatus (2)

Ch 33 - (septum) absent (0) present (1)

Ch 34 - Ligamentary facet sub rectangular (0) sub triangolar (1) semilunate (2)

The character describes the radial facet shape but also the shape of the proximal part of the IBr1.

Ch 35 - iR projection ornamentation (grains/spines) absent (0) present (1)..

Ch 36 - RR facet nervous canal two (0) one (1)

Character distinguishing *Dadocrinus* from *Neodadocrinus*. In reality is the far reflex of an important set of characters regarding the reduction of nervous system canals penetrating the cup plates.

Ch 37 - iR outward projecting absent (0) intermediate (1) strong (2)

Ch 38 - Interradial projections absent (0) present (1)

Ch 39 - Type of articular facet for arms cotyledermatid (0) eudesicrinid (1) cyrtocrinid (2)

Character distinguishing the forms with linear articular facet (cotyledermatid) from the ones with a large ligamentary lip (eudesicrinids and eugeniacrinitids) and, between the latter, it differentiates forms with different muscular facet.

Obviously the code for characters 6, 10, 11, 12, 13, 17, 24, changed when we applied the gap weighting method. (see text).

Appendix 2

Data Matrix I

CHARACTER:	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
TAXA										
Dadocrinus	0	0	0	0	0	0	1	0	0	0
Neodadocrinus	0	0	0	0	0	0	1	0	0	0
Sacariacrinus	1	0	1	1	0	0	1	0	0	0
Plicatocrinus	1	0	1	1	0	0	1	0	0	?
Proholopus	0	0	1	2	2	1	1	0	1	0
Cotylederma	0	0	1	2	2	1	?	0	1	0
Paracotylederma	0	0	1	0	0	0	1	0	1	0
Holopus	2	1	1	2	2	1	3	1	3	?
Cyathidium	2	0	1	2	2	1	1	0	1	0
Quenstedticrinus	0	1	1	0	1	1	3	0	1	0
Tetracrinus	1	0	1	1	0	0	?	0	1	0
Eudesicrinus	0	1	1	2	2	1	3	0	1	0
Dinardocrinus	0	1	1	2	2	1	?	0	1	0
Bilecicrinus	1	1	1	2	2	1	?	?	1	0
Gammarocrinites	0	0	1	2	2	1	0	0	1	0
Paragammarocrinites	0	0	1	3	1	1	0	0	1	0
Cyrtocrinus	0	1	1	2	2	1	3	0	2	0
Nerocrinus	0	0	1	1	0	0	2	0	2	0
Ticinocrinus	0	0	1	0	0	0	2	0	2	1
Fischericrinus	0	0	1	2	2	1	2	0	2	0
Eugeniaalpinus	0	0	1	2	2	1	2	0	0	0
Eucaryophylla	0	0	1	2	2	1	1	0	1	?
Remisovicrinus	0	0	1	2	2	1	3	0	1	?
Strambergocrinus	2	1	1	2	2	1	3	1	3	?
Crataegocrinus	0	0	1	2	2	1	2	0	1	0
Psalidocrinus	0	0	1	2	2	1	2	0	?	?
Phyllocrinus	0	0	1	2	2	1	?	0	?	0
Apsidocrinus	0	0	1	2	2	1	2	0	0	0
Hoyacrinus	0	0	1	2	2	1	2	0	2	1
Hemicrinus	0	1	1	2	2	1	3	1	3	?
Torynocrinus	2	1	1	2	2	1	3	1	3	?
Hemibrachiocrinus	2	1	1	2	2	1	3	1	3	?
Brachiomonocrinus	2	1	1	2	2	1	3	1	3	?

CHARACTER:	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
TAXA										
Dadocrinus	0	0	1	0	0	0	1	0	0	0
Neodadocrinus	0	?	1	0	0	0	1	0	0	0
Sacariacrinus	0	0	1	0	0	0	1	0	0	0
Plicatocrinus	1	0	1	0	0	0	?	0	1	?
Proholopus	0	?	1	1	1	1	0	0	1	1
Cotylederma	0	0	1	1	0	0	0	1	0	0
Paracotylederma	0	0	1	1	1	0	0	1	0	0
Holopus	?	?	?	2	1	0	?	0	1	1
Cyathidium	0	?	1	2	1	1	0	0	1	1
Quenstedticrinus	0	?	1	2	1	0	1	0	0	0
Tetracrinus	0	?	1	1	1	0	1	0	0	0
Eudesicrinus	0	0	1	1	1	1	1	1	0	0
Dinardocrinus	0	2	0	2	1	1	1	1	0	0
Bilecicrinus	0	0	1	2	1	1	1	1	0	0
Gammarocrinites	0	0	1	1	1	1	1	0	1	?
Paragammarocrinites	0	0	1	1	1	0	2	0	1	?
Cyrtocrinus	0	0	1	2	1	1	0	0	0	0
Nerocrinus	1	0	1	0	0	0	0	0	1	3
Ticinocrinus	1	0	1	0	0	0	?	0	1	1
Fischericrinus	0	0	1	0	0	1	1	0	1	1
Eugeniaalpinus	0	0	1	0	0	1	0	1	2	3
Eucaryophylla	?	?	1	2	1	1	?	0	1	?
Remisovicrinus	0	0	1	0	0	1	?	?	1	?
Strambergocrinus	0	0	1	2	1	1	?	0	0	0
Crataegocrinus	0	0	1	0	0	1	?	1	1	1
Psalidocrinus	?	0	1	0	0	1	?	1	3	3
Phyllocrinus	1	0	?	0	0	1	?	1	2	2
Apsidocrinus	1	0	?	0	0	1	2	1	2	3
Hoyacrinus	1	0	1	0	0	1	1	1	1	1
Hemicrinus	?	?	?	2	1	1	?	0	0	0
Torynocrinus	?	2	0	2	1	1	1	0	0	0
Hemibrachiocrinus	?	0	1	1	1	1	?	0	0	0
Brachiomonocrinus	?	?	?	?	1	0	?	1	0	0

CHARACTER:	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**
TAXA										
Dadocrinus	0	0	0	1	0	0	0	1	0	0
Neodadocrinus	0	0	0	1	0	0	?	?	0	0
Sacariacrinus	0	0	1	1	0	1	0	0	?	0
Plicatocrinus	0	1	0	1	0	1	0	0	1	0
Proholopus	1	0	0	1	0	3	1	0	0	0
Cotylederma	0	0	0	1	1	2	2	2	0	0
Paracotylederma	0	0	1	0	1	2	2	2	0	1
Holopus	1	0	1	?	1	2	2	2	1	1
Cyathidium	1	0	0	1	1	2	2	2	1	1
Quenstedticrinus	0	0	0	1	0	0	1	0	0	1
Tetracrinus	0	0	0	0	0	0	0	0	1	1
Eudesicrinus	0	0	0	1	1	2	2	2	0	1
Dinardocrinus	0	0	0	0	1	2	2	2	?	0
Bilecicrinus	1	0	0	1	1	2	2	2	0	1
Gammarocrinites	0	0	0	1	0	3	1	0	?	1
Paragammarocrinites	0	0	0	1	0	0	1	0	?	1
Cyrtocrinus	0	1	0	?	0	3	0	0	?	0
Nerocrinus	0	1	0	1	0	0	0	0	?	0
Ticinocrinus	0	1	0	?	0	0	1	0	?	0
Fischericrinus	0	1	0	1	0	0	1	0	0	0
Eugeniaalpinus	0	1	0	1	0	0	0	0	0	0
Eucaryophylla	0	1	0	?	0	0	0	?	0	1
Remisovicrinus	0	?	0	1	0	0	1	0	0	0
Strambergocrinus	1	0	1	1	1	2	2	2	?	0
Crataegocrinus	0	1	0	1	0	0	0	0	?	0
Psalidocrinus	0	1	0	?	0	0	0	0	0	?
Phyllocrinus	0	1	0	?	0	0	0	?	0	0
Apsidocrinus	0	1	0	1	0	0	0	0	0	0
Hoyacrinus	0	1	0	0	0	0	0	0	?	0
Hemicrinus	0	1	0	?	0	0	?	?	1	1
Torynocrinus	1	0	0	1	1	2	2	2	1	0
Hemibrachiocrinus	1	0	0	0	1	2	2	2	1	0
Brachiomonocrinus	0	0	0	0	1	2	2	2	1	0

CHARACTER:	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**
TAXA									
Dadocrinus	0	1	0	2	0	0	0	0	0
Neodadocrinus	0	1	0	2	0	1	0	0	0
Sacariacrinus	0	?	0	2	0	1	0	0	1
Plicatocrinus	0	0	0	2	0	1	0	1	0
Proholopus	0	?	0	2	0	1	0	1	0
Cotylederma	0	2	0	0	0	1	0	0	0
Paracotylederma	0	2	0	2	0	1	0	0	0
Holopus	1	2	0	2	0	1	0	1	0
Cyathidium	1	2	0	0	0	1	0	1	0
Quenstedticrinus	0	?	0	2	0	1	0	0	1
Tetracrinus	0	?	0	2	0	1	0	0	1
Eudesicrinus	0	2	0	2	0	1	0	0	1
Dinardocrinus	0	2	0	2	0	1	0	0	1
Bilecicrinus	0	2	0	2	0	1	0	0	1
Gammarocrinites	0	?	0	2	1	1	0	1	1
Paragammarocrinites	0	?	0	2	1	1	0	1	1
Cyrtocrinus	0	?	0	2	0	1	0	0	2
Nerocrinus	0	1	0	2	0	1	0	1	2
Ticinocrinus	0	?	0	1	0	1	0	1	2
Fischericrinus	0	?	0	1	0	1	0	1	2
Eugeniaalpinus	0	1	0	2	0	1	1	1	2
Eucaryophylla	0	1	0	2	0	1	1	1	2
Remisovicrinus	0	?	0	2	0	1	?	1	?
Strambergocrinus	1	?	0	2	0	1	0	0	2
Crataegocrinus	0	?	0	2	0	1	0	1	2
Psalidocrinus	0	1	0	2	?	1	?	1	2
Phyllocrinus	0	?	1	2	0	1	?	1	2
Apsidocrinus	0	?	1	2	0	1	?	1	2
Hoyacrinus	0	?	1	?	0	1	0	1	2
Hemicrinus	0	0	0	2	0	1	0	0	2
Torynocrinus	1	?	0	2	0	1	0	0	2
Hemibrachiocrinus	1	2	0	2	0	1	0	0	?
Brachiomonocrinus	1	2	0	2	0	1	0	0	?

Data Matrix II (gap-weighting method)

CHARACTER:	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
TAXA										
Dadocrinus	0	0	0	0	0	?	1	0	0	7
Neodadocrinus	0	0	0	0	0	4	1	0	0	9
Sacariacrinus	1	0	1	1	0	3	1	0	0	7
Plicatocrinus	1	0	1	1	0	0	1	0	0	?
Proholopus	0	0	1	2	2	0	1	0	1	9
Cotylederma	0	0	1	2	2	0	?	0	1	D
Paracotylederma	0	0	1	0	0	6	1	0	1	D
Holopus	2	1	1	2	2	?	3	1	3	?
Cyathidium	2	0	1	2	2	0	1	0	1	B
Quenstedticrinus	0	1	1	0	1	0	3	0	1	4
Tetracrinus	1	0	1	1	0	5	?	0	1	C
Eudesicrinus	0	1	1	2	2	0	3	0	1	6
Dinardocrinus	0	1	1	2	2	W	?	0	1	6
Bilecicrinus	1	1	1	2	2	0	?	?	1	2
Gammarocrinites	0	0	1	2	2	0	0	0	1	5
*Paragammarocrinite*0	0	1	3	1	?	0	0	1	7	
Cyrtocrinus	0	1	1	2	2	?	3	0	2	1
Nerocrinus	0	0	1	1	0	2	2	0	2	3
Ticinocrinus	0	0	1	0	0	1	2	0	2	Q
Fischericrinus	0	0	1	2	2	0	2	0	2	0
Eugeniaalpinus	0	0	1	2	2	0	2	0	0	8
Eucaryophylla	0	0	1	2	2	?	1	0	1	?
Remisovicrinus	0	0	1	2	2	0	3	0	1	?
Strambergocrinus	2	1	1	2	2	0	3	1	3	?
Crataegocrinus	0	0	1	2	2	0	2	0	1	C
Psalidocrinus	0	0	1	2	2	0	2	0	?	N
Phyllocrinus	0	0	1	2	2	0	?	0	?	9
Apsidocrinus	0	0	1	2	2	0	2	0	0	7
Hoyacrinus	0	0	1	2	2	0	2	0	2	W
Hemicrinus	0	1	1	2	2	?	3	1	3	?
Torynocrinus	2	1	1	2	2	?	3	1	3	?
Hemibrachiocrinus	2	1	1	2	2	?	3	1	3	?
Brachiomonocrinus	2	1	1	2	2	?	3	1	3	?

CHARACTER:	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
TAXA										
Dadocrinus	5	2	2	0	0	0	1	0	0	0
Neodadocrinus	2	?	4	0	0	0	3	0	0	0
Sacariacrinus	4	6	3	0	0	0	3	0	0	0
Plicatocrinus	T	2	1	0	0	0	?	0	1	?
Proholopus	2	?	3	1	1	1	3	0	1	1
Cotylederma	2	6	1	1	0	0	1	1	0	0
Paracotylederma	2	0	1	1	1	0	1	1	0	0
Holopus	?	?	?	2	1	0	?	0	1	1
Cyathidium	5	?	0	2	1	1	0	0	1	1
Quenstedticrinus	1	?	2	2	1	0	3	0	0	0
Tetracrinus	1	?	2	1	1	0	1	0	0	0
Eudesicrinus	0	5	2	1	1	1	2	1	0	0
Dinardocrinus	0	U	W	2	1	1	W	1	0	0
Bilecicrinus	0	2	3	2	1	1	3	1	0	0
Gammarocrinites	3	6	1	1	1	1	2	0	1	?
Paragammarocrinites	4	2	1	1	1	0	1	0	1	?
Cyrtocrinus	5	A	5	2	1	1	6	0	0	0
Nerocrinus	I	8	3	0	0	0	4	0	1	3
Ticinocrinus	I	5	2	0	0	0	1	0	1	1
Fischericrinus	7	1	3	0	0	1	4	0	1	1
Eugeniaalpinus	6	1	3	0	0	1	3	1	2	3
Eucaryophylla	?	?	?	2	1	1	?	0	1	?
Remisovicrinus	3	5	3	0	0	1	?	?	1	?
Strambergocrinus	6	1	3	2	1	1	?	0	0	0
Crataegocrinus	6	3	1	0	0	1	1	1	1	1
Psalidocrinus	D	3	5	0	0	1	3	1	3	3
Phyllocrinus	W	1	3	0	0	1	3	1	2	2
Apsidocrinus	T	4	5	0	0	1	5	1	2	3
Hoyacrinus	F	4	2	0	0	1	1	1	1	1
Hemicrinus	?	?	?	2	1	1	?	0	0	0
Torynocrinus	?	W	G	2	1	1	?	0	0	0
Hemibrachiocrinus	?	5	1	1	1	1	?	0	0	0
Brachiomonocrinus	?	?	?	?	1	0	?	1	0	0

CHARACTER:	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**
TAXA										
Dadocrinus	0	0	0	4	0	0	0	1	0	0
Neodadocrinus	0	0	0	4	0	0	?	?	0	0
Sacariacrinus	0	0	1	B	0	1	0	0	?	0
Plicatocrinus	0	1	0	3	0	1	0	0	1	0
Proholopus	1	0	0	1	0	3	1	0	0	0
Cotylederma	0	0	0	4	1	2	2	2	0	0
Paracotylederma	0	0	1	H	1	2	2	2	0	1
Holopus	1	0	1	?	1	2	2	2	1	1
Cyathidium	1	0	0	3	1	2	2	2	1	1
Quenstedticrinus	0	0	0	3	0	0	1	0	0	1
Tetracrinus	0	0	0	H	0	0	0	0	1	1
Eudesicrinus	0	0	0	7	1	2	2	2	0	1
Dinardocrinus	0	0	0	D	1	2	2	2	?	0
Bilecicrinus	1	0	0	2	1	2	2	2	0	1
Gammarocrinites	0	0	0	1	0	3	1	0	?	1
Paragammarocrinites	0	0	0	5	0	0	1	0	?	1
Cyrtocrinus	0	1	0	?	0	3	0	0	?	0
Nerocrinus	0	1	0	7	0	0	0	0	?	0
Ticinocrinus	0	1	0	?	0	0	1	0	?	0
Fischericrinus	0	1	0	6	0	0	1	0	0	0
Eugeniaalpinus	0	1	0	5	0	0	0	0	0	0
Eucaryophylla	0	1	0	?	0	0	0	?	0	1
Remisovicrinus	0	?	0	7	0	0	1	0	0	0
Strambergocrinus	1	0	1	8	1	2	2	2	?	0
Crataegocrinus	0	1	0	4	0	0	0	0	?	0
Psalidocrinus	0	1	0	5	0	0	0	0	0	?
Phyllocrinus	0	1	0	9	0	0	0	?	0	0
Apsidocrinus	0	1	0	8	0	0	0	0	0	0
Hoyacrinus	0	1	0	W	0	0	0	0	?	0
Hemicrinus	0	1	0	?	0	0	?	?	1	1
Torynocrinus	1	0	0	0	1	2	2	2	1	0
Hemibrachiocrinus	1	0	0	C	1	2	2	2	1	0
Brachiomonocrinus	0	0	0	U	1	2	2	2	1	0

CHARACTER:	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**
TAXA									
Dadocrinus	0	1	0	2	0	0	0	0	0
Neodadocrinus	0	1	0	2	0	1	0	0	0
Sacariacrinus	0	?	0	2	0	1	0	0	1
Plicatocrinus	0	0	0	2	0	1	0	1	0
Proholopus	0	?	0	2	0	1	0	1	0
Cotylederma	0	2	0	0	0	1	0	0	0
Paracotylederma	0	2	0	2	0	1	0	0	0
Holopus	1	2	0	2	0	1	0	1	0
Cyathidium	1	2	0	0	0	1	0	1	0
Quenstedticrinus	0	?	0	2	0	1	0	0	1
Tetracrinus	0	?	0	2	0	1	0	0	1
Eudesicrinus	0	2	0	2	0	1	0	0	1
Dinardocrinus	0	2	0	2	0	1	0	0	1
Bilecicrinus	0	2	0	2	0	1	0	0	1
Gammarocrinites	0	?	0	2	1	1	0	1	1
Paragammarocrinites	0	?	0	2	1	1	0	1	1
Cyrtocrinus	0	?	0	2	0	1	0	0	2
Nerocrinus	0	1	0	2	0	1	0	1	2
Ticinocrinus	0	?	0	1	0	1	0	1	2
Fischericrinus	0	?	0	1	0	1	0	1	2
Eugeniaalpinus	0	1	0	2	0	1	1	1	2
Eucaryophylla	0	1	0	2	0	1	1	1	2
Remisovicrinus	0	?	0	2	0	1	?	1	?
Strambergocrinus	1	?	0	2	0	1	0	0	2
Crataegocrinus	0	?	0	2	0	1	0	1	2
Psalidocrinus	0	1	0	2	?	1	?	1	2
Phyllocrinus	0	?	1	2	0	1	?	1	2
Apsidocrinus	0	?	1	2	0	1	?	1	2
Hoyacrinus	0	?	1	?	0	1	0	1	2
Hemicrinus	0	0	0	2	0	1	0	0	2
Torynocrinus	1	?	0	2	0	1	0	0	2
Hemibrachiocrinus	1	2	0	2	0	1	0	0	?
Brachiomonocrinus	1	2	0	2	0	1	0	0	?