

REASSESSMENT OF THE PHYLOGENETIC POSITION OF CONULARIIDS (?EDIACARAN–TRIASSIC) WITHIN THE SUBPHYLUM MEDUSOZOA (PHYLUM CNIDARIA)

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SYNOPSIS Fossil taxa of uncertain phylogenetic affinities can play a crucial role in the analysis of character evolution within major extant groups. Marques & Collins (2004) concluded that conulariids (?Ediacaran–Triassic) are an extinct group of medusozoan cnidarians most closely related to Stauromedusae. However, only six of the 87 characters used by these authors can be observed in conulariid fossils. Rescoring the character states of conulariids in a conservative manner yields a new hypothesis for the phylogenetic position of conulariids, namely that they are the sister group of the scyphozoan order Coronatae rather than Stauromedusae, which is revealed as the earliest diverging lineage of Medusozoa. This new hypothesis also implies several different sequences of character evolution within Cnidaria. Specifically, the presence of a periderm completely covering the polyp in conulariids and coronates appears to be derived within Scyphozoa. Strobilation appears to be a synapomorphy uniting conulariids, Coronatae, Rhizostomeae and Semaestomeae. This result supports the controversial interpretation of one exceptionally preserved conulariid that potentially shows that these animals produced ephyrae by strobilation. Finally, the pelagic adult medusa stage and the giant fibre nerve net appear to be features that are derived within Medusozoa.

KEY WORDS phylogeny, systematics, cladistics, affinities, Phanerozoic, morphology, Cnidaria, Medusozoa, conulariids

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INTRODUCTION

Problematical fossil taxa, or problematica, pose some of the most challenging problems of interpretation currently facing systematic biologists and paleontologists. Problematica have been defined as '[fossil] organisms whose body plans are so unusual that they cannot be placed in extant phyla (Freeman & Herron 1998: 453).' This long-standing emphasis on the morphological differences between problematica and extant taxa has led in some cases (e.g. conulariids; Babcock 1991; Babcock & Feldmann 1986*a,b*) to the erection of new, extinct phyla. The advent of phylogenetic systematics (Hennig 1979), with its recognition of the cardinal importance of shared derived similarities (synapomorphies) and monophyletic groups, has helped to foster a new understanding of the potential role of problematica in elucidating more general problems in systematics and evolutionary biology. Arguing within a cladistic framework, some students of problematical fossil groups (e.g. Fisher & Nitecki 1982; Schram 1991) have sought to identify and test putative synapomorphies, at various levels in the taxonomical hierarchy, using both traditional criteria of homology and cladistic parsimony. In addition to helping to break the conceptual log jams associated with non-cladistic concepts of classification, this approach has the potential to illuminate sequences of character evolution within the major clades to which problematica most probably belong. In view of recent advances in cladistic methodology and molecular biology, reassessing alternative hypotheses of the phylogenetic affinities of problematica promises to give us a more holistic understanding of the history of life.

Conulariids comprise a distinctive group of marine metazoans with a fossil record that extends from perhaps the Ediacaran (= Vendian; Ivantsov & Fedonkin 2002; Van Iten *et al.* 2005) and at least from the Late Cambrian (Hughes *et al.* 2000), to the Late Triassic (Waterhouse 1979). The phylogenetic affinities of conulariids have been debated for over 170 years, with arguments being marshaled in favour of their alliance with a number of widely divergent extant taxa (for a review of previous opinions on this question see, e.g. Babcock & Feldmann 1986*a*). Most genera currently referred to the conulariids, including *Conularia* Miller in Sowerby 1821, are characterised by a steeply pyramidal, four-sided, finely lamellar apatitic skeleton bearing transverse ridges or transverse rows or longitudinal files of small nodes. Circonulariids (Silurian–Devonian), which differ from conulariids in having a conical skeleton (Bischoff 1978), and conulariid-like small shelly fossils from the Lower Cambrian (e.g. Conway Morris & Chen 1992), have also been classified as conulariids. However, the problem of whether these taxa and conulariids constitute a single, monophyletic group that excludes all other taxa has not been investigated using cladistic methods. Resolving this question hinges, at least in part, on determining the higher-level phylogenetic affinities of these fossils.

Based on comparisons of the anatomy, morphogenesis and palaeoautecology of conulariids and extant taxa, many investigators (e.g. Kiderlen 1937; Moore & Harrington 1956; Werner 1973*a*; Bischoff 1978; von Salvini-Plawen 1978; Bouillon 1981; Van Iten 1991*a*, 1992*a,b*; Jerre 1994; Wade 1994; Bergström 1995; McKinney *et al.* 1995; Van Iten *et al.* 1996, 2000; Hughes *et al.* 2000; Nielsen 2001; Collins 2002) have concluded that conulariids were scypho-

zoan cnidarians or close relatives of this group. Although the hypothesis of a scyphozoan affinity for conulariids has not been universally accepted, opponents of this hypothesis (e.g. Kozłowski 1968; Steul 1984; Babcock 1991; Babcock & Feldmann 1986*a*; Brood 1995) have yet to offer alternative phylogenetic hypotheses based on demonstrably homologous similarities uniquely shared by conulariids and groups outside of Cnidaria. Steul (1984), for instance, proposed that *Conularia* from the Hunsrück Slate (Lower Devonian, Germany) contain pyritised soft parts homologous to the internal organs of vertebrates, but these interpretations have since been shown to have been based on orthoconic nautiloid specimens misidentified as conulariids or on 'wispy pyritic masses . . . [showing] no discrete, identifiable, soft part structures (Hughes *et al.* 2000: 829).' Other authors (e.g. Babcock 1991; Babcock & Feldmann 1986*a*; Brood 1995), citing the fact that conulariids differ from cnidarians in certain characters, for example the mineral composition of the skeleton, have asserted on this basis that conulariids cannot have been cnidarians. However, the mere fact that conulariids differ from known cnidarians (and other taxa) has no bearing on the problem of their phylogenetic affinities, which can potentially be resolved only through analysis of patterns of shared similarities (Bergström 1995; Van Iten *et al.* 1996). In addition to documenting the rather general similarities between conulariids and Scyphozoa – a taxon traditionally interpreted (e.g. Hyman 1940) as consisting of five extant orders (Stauromedusae, Coronatae, Cubomedusae, Rhizostomeae and Semaestomeae) – advocates of a scyphozoan affinity for conulariids have also discovered uniquely shared, complex similarities between certain conulariids and stauromedusans (e.g. Kiderlen 1937; Van Iten 1991*a*, 1992*a*; Jerre 1994; Wade 1994; Marques & Collins 2004) and between conulariids and coronates (e.g. Werner 1966, 1967, 1973*b*; Van Iten 1991*a,c*, 1992*a,b*; Van Iten *et al.* 1996, 2000). These potential synapomorphies raise the possibility that conulariids were more closely related to one of these two groups than they were to other scyphozoans. However, these similarities do not rule out the possibility that conulariids form the sister group of Medusozoa, a diverse taxon that includes cubozoans and hydrozoans as well as scyphozoans (Werner 1973*a*; von Salvini-Plawen 1978; Bouillon 1981; Nielsen 2001).

Alternative interpretations of the phylogenetic relationships between conulariids and extant cnidarians had not been explicitly tested until Marques & Collins (2004) conducted a cladistic analysis of 87 morphological and life history characters of medusozoan cnidarians. The extant members of Medusozoa share several putative synapomorphies including the possession of linear mitochondrial DNA (Bridge *et al.* 1992) and a medusoid life stage. Additional evidence of the monophyly of Medusozoa is provided by molecular sequence data (Medina *et al.* 2001; Collins 2002). A noteworthy aspect of Marques & Collins' (2004) study is that it dealt not only with extant medusozoans, but also with the extinct order Conulatae, a taxon consisting of conulariids and the Ordovician genus *Conchopeltis* Walcott (Wade 1994). Their analysis suggested that Conulatae is more closely related to Stauromedusae than it is to Coronatae or any other medusozoan order. These authors went on to redefine the class Scyphozoa as including only Coronatae, Semaestomeae and Rhizostomeae and they erected the class Staurozoa for the clade consisting of Conulatae and Stauromedusae. Cubomedusae

had already been given its own class status as Cubozoa on the basis of life history characteristics (Werner 1973*b*, 1975; Calder & Peters 1975).

Marques & Collins (2004) relied chiefly on soft part anatomy and life history characters in order to investigate the phylogenetic relationships within Medusozoa. Thus, conulariids posed a particular challenge for their analysis because the states of these types of characters cannot easily be determined from evidence intrinsic to the vast majority of currently available conulariid specimens. With very few possible exceptions, conulariid fossils consist exclusively of the finely lamellar apatitic skeleton (or moulds or casts), regarded by advocates of a scyphozoan affinity for conulariids as a mineralised ectodermal periderm. Also, Marques & Collins' analysis excluded certain aspects of the complex morphology of conulariid skeletons as well as independent evidence (Steul 1984; Babcock & Feldmann 1986*a,b*; Van Iten 1989, 1991*a*; Hughes *et al.* 2000) that may bear on the anatomy of conulariid soft parts.

The purpose of the present study is to reinvestigate the systematic position of conulariids in Medusozoa and to assess the impact of alternative character scoring decisions for conulariids on the inferred evolution of these characters in Medusozoa. In agreement with Marques & Collins (2004) and other investigators cited above, we interpret conulariids as extinct close allies of extant medusozoan cnidarians. We also assume that conulariids having a finely lamellar pyramidal skeleton form a monophyletic taxon. The hypothesis that conulariids were closely related to *Conchopeltis* is weakly supported, being based on the shared presence of a more or less rectangular transverse cross-section and a pyramidal form (Oliver 1984). For this reason, we do not treat *Conchopeltis* here. As will be shown below, application of Marques & Collins' (2004) cladistic analytical procedures to our revised medusozoan data set indicates that conulariids are best interpreted as the sister group of Coronatae rather than of Stauromedusae and that Stauromedusae is the earliest diverging clade of Medusozoa.

REASSESSMENT OF CHARACTER CODING FOR CONULATAE

The 87 characters defined by Marques & Collins (2004) are presented here in Appendix 1. For the taxon Conulatae (= conulariids + *Conchopeltis*), Marques & Collins (2004: appendix 2) scored 72 of these characters as a question mark (meaning that the states of these characters are unknown or were deemed non-comparable). The states of the remaining 15 characters (i.e. characters 17, 18, 23, 26, 27, 36, 37, 39, 43, 44, 48, 62, 63, 71 and 72) are specified. While six of Marques & Collins' choices of character states have some basis in evidence intrinsic to conulariid fossils, the states of the remaining nine characters (characters 17, 23, 26, 27, 37, 44, 62, 71 and 72) cannot be inferred from currently available fossil material.

More specifically, characters 26 and 27 involve soft-part structures (the nectosome (26) and the pneumatophore (27)) that are present only in certain siphonophore hydrozoans. Character 17 (life habit of the adult stage) is scored as 'adults benthic;' however, there is no documented intrinsic evidence that conulariid fossils, which in life probably were benthic (e.g. Finks 1955; Harland & Pickerill 1987; Van

Iten 1991*a,b,c*; Van Iten *et al.* 1996; Simões *et al.* 2000; Rodrigues *et al.* 2003), represent individuals that were capable of sexual reproduction. Therefore, there is no prior reason to conclude that conulariid fossils represent adults. In a clear typographical error in coding, character 23 (oocyte development) is scored as 'oocytes develop with accessory cells,' a determination that cannot be made using currently available fossils. Character 37 (polymorphic polyps) is scored as 'absent,' a choice based on the absence of anatomical features in conulariids that can be interpreted as reflecting polymorphism. Character 44 (hydrotheca/gonotheca) is also scored as 'absent,' again on the basis of the absence of unambiguous evidence of conulariid colonies exhibiting differentiation of the component polyps. Character 62 (septa in the gastrovascular cavity), which in Marques & Collins' (2004) table of characters (their appendix 1) is listed under 'characters of the medusae,' is scored as 'present.' This character illustrates the difficulties one faces when trying to score features of different life stages across Cnidaria. Thus, some groups are referred to as medusae despite their benthic nature (e.g. Stauromedusae), while others are referred to as polyps even though their homology to other cnidarians is uncertain or in doubt (e.g. Narcomedusae). Kiderlen's (1937) hypothesis that conulariid specimens bearing an apical wall (schott) were free-living medusae is probably false (Van Iten 1991*c*) and, with the exception of a few specimens containing possible relic ephyrae (Van Iten 1989, 1991*a*), no conulariid fossils have yet been documented that indicate the existence of a pelagic or free-swimming life stage in this group. For this reason, characters 71 (adult medusoid shape) and 72 (shape of the horizontal cross-section (of the medusa)), previously scored as 'pyramidal' and 'quadrate,' respectively, might best be scored as 'unknown.' Alternatively, character 72 could be scored as 'circular,' based on the 'circular feature' documented by Van Iten (1991*a*) in the holotype of *Eoconularia amoena* Sinclair and interpreted by that author as a relic circular ephyra.

Specified scores of the remaining six characters have at least some basis in evidence intrinsic to conulariid fossils. Character 18 (symmetry) is scored as 'radial tetramerous,' an inference that can reasonably be drawn from comparisons of conulariid skeletons with the soft parts and periderm of extant scyphozoans and stauromedusans (Kiderlen 1937; Werner 1966, 1967; Van Iten 1991*a*, 1992*a*; Jerre 1994; Bergström 1995; Van Iten *et al.* 1996). Character 36 (polypoid phase) is scored as 'present,' an interpretation based on occurrences of conulariids preserved *in situ*, in life orientations similar to those of erect scyphopolyps (e.g. Finks 1955; Van Iten 1991*a,c*; Van Iten *et al.* 1996; Simões *et al.* 2000; Rodrigues *et al.* 2003) and on comparisons of conulariid skeletons with the periderm of coronate polyps. Character 39 (periderm) is scored as 'present and covering most of the polyp.' Again, this interpretation is based on comparisons of conulariid fossils and the coronate periderm. Character 43 (septa in polyp) also is scored as 'present,' a decision that is based on uniquely shared similarities between the Y-shaped midline carinae of *Eoconularia loculata* (Wiman) and the Y-shaped gastric septa of stauromedusans (Kiderlen 1937; Van Iten 1991*a*, 1992*a*; Jerre 1994). Character 48 (gastrodermal musculature) is scored as '[present and] organized in bunches of ectodermal origin.' While features interpretable as relic muscles have not been documented in conulariid fossils, several authors have argued that such features were present at

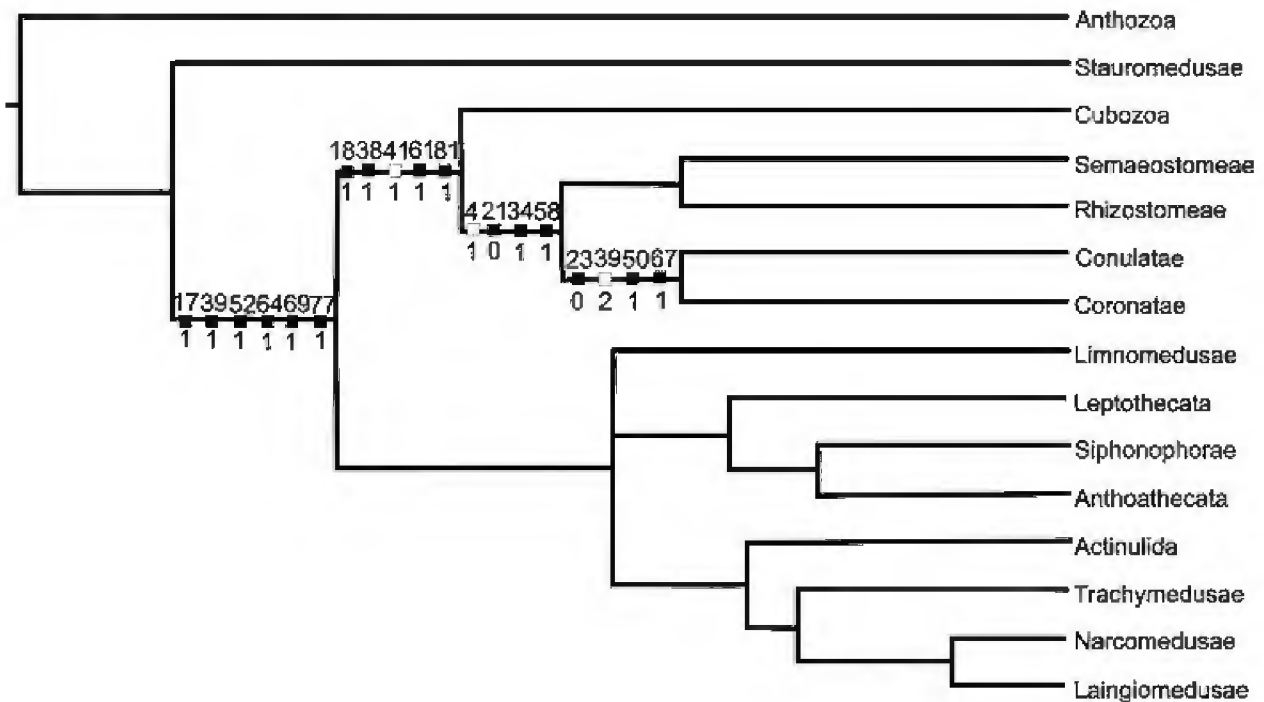


Figure 1 Cladistic hypothesis of medusozoan relationships based on 87 characters after rescaling those for conulariids (characters weighted through successive approximation by maximum values of rescaled consistency indices; strict consensus of three most parsimonious trees; length = 77.57, consistency index = 0.92, rescaled consistency index = 0.86). Relevant characters have been mapped at the appropriate nodes.

the conulariid midlines, on the basis of internal skeletal structures located at these sites (Bischoff 1978; Van Iten 1992a) and on the basis of specimens exhibiting lappet-like infoldings of their apertural region (Moore & Harrington 1956; see also Reed 1933 and Kowalski 1935). Finally, character 63 (septal shape (in the medusa)) is scored as 'Y-shaped.' Although this character is listed in the section for characters of medusae, the presence of Y-shaped midline carinae in *E. loculata* can be interpreted as indicating that this conulariid, at least, originally possessed four endodermal septa that were more or less Y-shaped (and supported by mineralised ectodermal hard parts).

If one recodes the foregoing characters, especially those pertaining to the polyp or medusa stages, in a way that more accurately reflects current knowledge of conulariid anatomy and life history, then one is left with six characters, 18 (type of symmetry), 36 (polypoid phase), 39 (periderm), 43 (septa in polyp), 48 (gastrodermal musculature) and 63 (septal shape), whose states in at least some conulariids can be inferred on the basis of evidence intrinsic to conulariid fossils. Character 48 (gastrodermal musculature), while not directly inferable from conulariid fossils, can reasonably be coded as 'present.' In contrast, characters 17 (life habit (of adults)), 23 (oocyte development), 62 (septa (in the gastrovascular cavity of the medusa)), 71 (adult medusoid shape) and 72 (shape of horizontal cross-section (of the medusa)), probably are best coded as unknown. Although based on negative evidence, we see no reason to rescore characters 26 (nectosome), 27 (pneumatophore), 37 (polymorphic polyps) and 44 (hydrotheca/gonotheca), all scored by Marques & Collins (2004) as 'absent.' The remaining 72 characters may be left as unknown or, alternatively, characters 21 and 22 may be

changed from unknown to 'strobilation' and 'polydisc,' respectively.

Following the recoding of conulariid character states explained above, we constructed two new character matrices that differ from each other only in how characters 21 and 22 are scored for conulariids (Appendix 2). We left Marques & Collins' (2004) codings of the states for extant cnidarians unchanged. We also followed these authors' cladistic analytical procedures, using the branch-and-bound algorithm of PAUP* 4.0 (Swofford 2001). Our initial step was to search for most parsimonious trees (cladograms) with all characters weighted equally. From the trees obtained in these primary analyses we calculated strict and semi-strict consensus trees. In the final step, we employed successive approximation weighting (Farris 1969; see also Carpenter 1988, 1994) using maximum values of rescaled consistency indices (RC).

IMPACT OF RESCORING CHARACTERS FOR CONULATAE

The analysis of our two revised data sets with characters weighted equally resulted in 10 trees (not shown; length (L) = 124, consistency index (CI) = 0.74, resolution index (RI) = 0.73), while the successive weighting analysis resulted in three trees (Fig. 1; L = 77.57, CI = 0.92, RI = 0.86). The strict consensus topologies resulting from the weighted and unweighted analyses differ only in the arrangements among the hydrozoan taxa. The hypothesis of Marques & Collins (2004), which was obtained by an identical successive weighting analysis of characters, differing only in

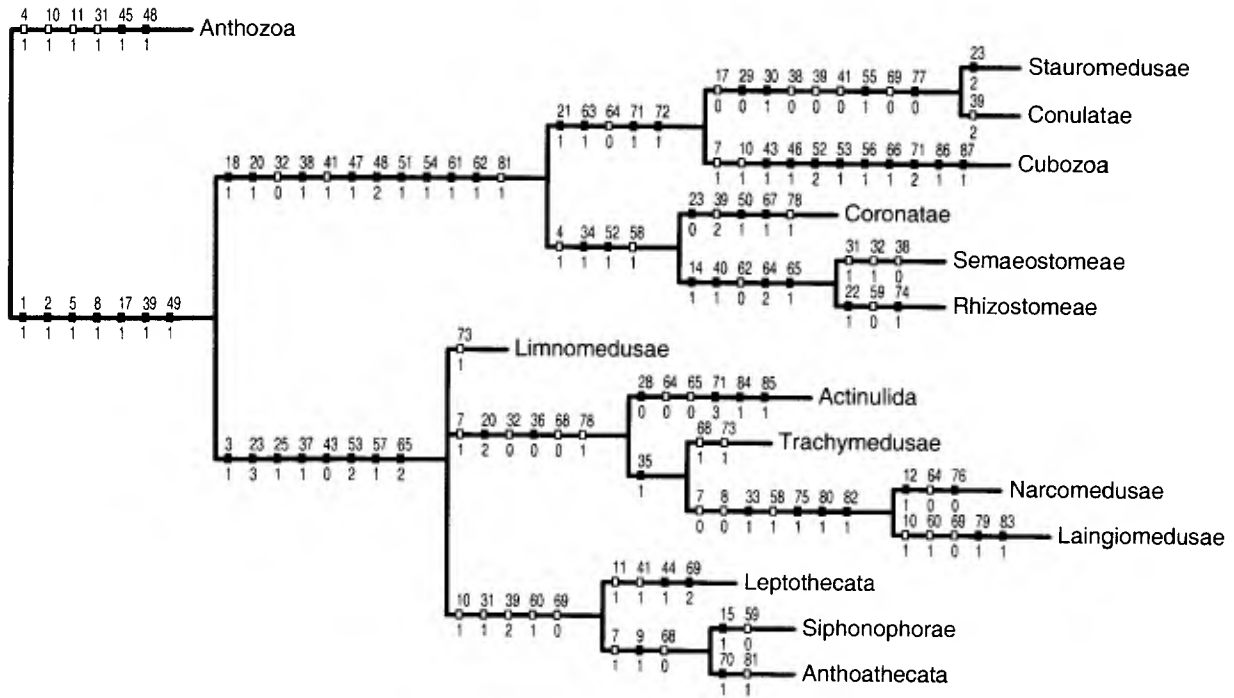


Figure 2 Cladistic hypothesis of Marques & Collins (2004) based on 87 characters (characters weighted through successive approximation by maximum values of rescaled consistency indices; strict consensus of three most parsimonious trees; length = 76.65, consistency index = 0.93, rescaled consistency index = 0.93).

the scoring for conulariids, is shown in Fig. 2. Rather than conulariids being the sister group of Stauromedusae (Fig. 2), the alternative scoring choices here advocated suggest that conulariids are the sister group of Coronatae (Fig. 1). These two groups form a clade with Rhizostomeae and Semaestomeae that is the sister group to Cubozoa. Stauromedusae now branches at the base of Medusozoa. The rest of the topology involving hydrozoan taxa is the same as that derived by Marques & Collins (2004) and will not be discussed further here.

We also used PAUP* to implement two tests to determine if the topology favoured by the analysis of Marques & Collins (2004) is significantly less optimal than that obtained here. Both a parametric test (Kishino & Hasegawa 1989) and a non-parametric test (Templeton 1983) yielded *p*-values (0.15/0.08 and 0.22/0.11 for the two data sets and two tests, respectively) that indicated that the data presented here do not strongly contradict the phylogenetic arrangement of Marques & Collins (2004). Nevertheless, Fig. 1 represents a more parsimonious phylogenetic explanation of our data than does Fig. 2. Moreover, rescoring of conulariids has resulted in a hypothesis of medusozoan relationships that is better corroborated by independent evidence. Specifically, except for the hypothesised relationships between some of the hydrozoan taxa, our results for the extant taxa are entirely consistent with hypotheses based on recent analyses of ribosomal gene sequence data (Fig. 3; see also Collins *et al.* 2006).

The results of the present study also have a number of important implications for character evolution within Cnidaria. In the analysis of Marques & Collins (2004; see Fig. 2), all four non-homoplastic synapomorphies shown at the node

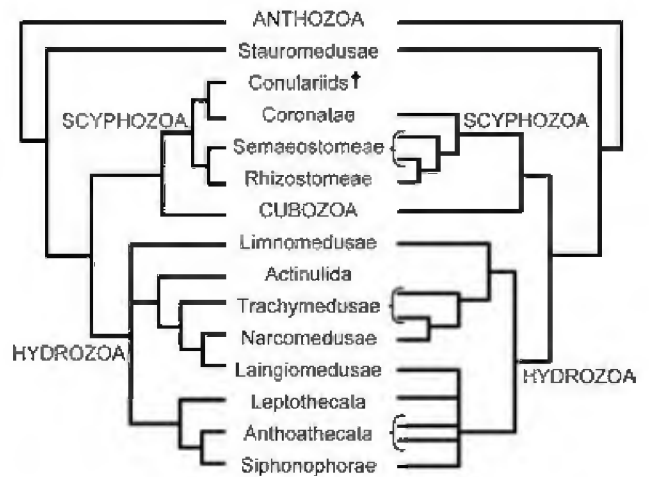


Figure 3 Correspondence between the phylogenetic hypothesis presented here (left), based on morphology and life history characteristics and the medusozoan relationships (right) inferred from a combined analysis of small and large subunit nuclear ribosomal gene data (Collins *et al.* 2006).

uniting Conulatae and Stauromedusae involve soft part characters whose states in conulariids are unknown. These synapomorphies are: planula ciliation absent (character 29), planula with 16 endodermal cells (character 30), coronal muscle marginal and tiny (character 55) and giant fibre nerve net absent (character 77). These four putative synapomorphies are artifacts of the ACCTRAN optimisation

employed by Marques & Collins. The remaining five putative synapomorphies (characters 17, 38, 39, 41 and 69) supporting the node are homoplastic with other cnidarians and no evidence exists to support the assertion that any of these characters are synapomorphies shared by conulariids and Stauromedusae. As noted earlier in this paper, it is not currently known whether conulariid fossils represent adults (character 17). Characters 38 (desmocytes), 41 (hollow tentacles) and 69 (statocysts) also are artifacts of ACCTRAN optimisation. Finally, character 39 (periderm) is an optimisation resulting from general parsimony; no periderm has been reported for stauromedusans.

In the present analysis, ACCTRAN optimisation also resulted in artifactual synapomorphies for the node uniting Conulatae and Coronatae. Specifically, all three of the non-homoplastic putative synapomorphies inferred for this node involve soft part characters (23, oocyte development; 50, pedalia of coronate type; and 67, coronal furrow) that have not been observed in conulariid fossils. However, one other putative synapomorphy, the presence of a periderm that fully covers the polyp, is supported by comparisons of conulariid fossils with directly comparable and arguably homologous structures of polypoid coronates. Although the presence of a periderm appears to be homoplastic, having also evolved within Hydrozoa, previous authors (e.g. Werner 1966, 1967, 1973*b*; Van Iten 1992*a, b*; Van Iten *et al.* 1996) have documented detailed and uniquely shared similarities between conulariid skeletons and the periderm of coronates. These same authors have interpreted these similarities as evidence of homology (i.e. that conulariids and coronates inherited their periderm from a common cnidarian ancestor) and the present analysis, which does not include these characters, supports this conclusion.

Looking more deeply within the tree, the analysis of Marques & Collins (2004) (Fig. 2) suggested that Stauromedusae and Conulatae formed a clade with Cubozoa. For this node, the states of three out of the four non-homoplastic, soft-part synapomorphies, including the type of apical medusa formation (character 21), are unknown for conulariids. Only one of these putative synapomorphies, the shared presence of Y-shaped gastric septa (character 63), is based on evidence intrinsic to conulariid fossils (Kiderlen 1937; Van Iten 1991*a*, 1992*a*; Jerre 1994). However, this evidence consists of features of the mineralised conulariid (*E. loculata*) skeleton, a hard-part structure, that are strongly suggestive of the former presence of four gastric septa, which in extant scyphozoans are soft-part structures (see also Babcock & Feldmann 1986*a*). The remaining three synapomorphies (characters 21, 71 and 72) all involve aspects of the soft-part anatomy of the medusoid life stage and, again, there is no intrinsic fossil evidence that indicates unequivocally that conulariids possessed such a stage. Character 64 (radial canals) is listed as a homoplastic synapomorphy; again, however, this is an artifact of optimisation.

In the present analysis, conulariids are part of a clade with the scyphozoan taxa Coronatae, Rhizostomeae and Semaestomeae. For this clade, the characters strobilation (21) and ephyra (34) are putative synapomorphies regardless of whether these two characters are coded as 'present' in conulariids. In extant medusozoans, medusa formation through strobilation is typical of Coronatae, Semaestomeae and Rhizostomeae. Although the evidence for strobilation in conulariids (Van Iten 1989, 1991*a*) is open to alternat-

ive interpretations (see in particular the discussion of conulariid soft part anatomy in Hughes *et al.* 2000), Van Iten's (1989, 1991*a*) suggested interpretations are somewhat buttressed by the present analysis since coding these characters as unknown still results in the inference that conulariids are at least descended from ancestors with strobilation and ephyrae. Two other putative synapomorphies for this clade, cellular mesoglea (4) and a lobed umbrellar margin (58), are not observable in conulariid fossils.

The conulariid–scyphozoan clade, characterised by the production of ephyrae by strobilation, is the sister group to Cubozoa (Fig. 1). This clade is putatively united by five synapomorphies, four of which are not known from conulariid fossils. Symmetry for these groups, however, generally is radial tetramerous in their pre-adult polyp stages. There are some hints of bilaterality in the extant members of these groups, which often develop two initial polyp tentacles. The tetradial symmetry exhibited by scyphozoans is also shared by Stauromedusae, so it is possible that this character is ancestral for Medusozoa and has subsequently been lost in the ancestry of extant hydrozoans.

Finally, our analysis suggests that Stauromedusae is the earliest diverging lineage of Medusozoa, buttressing a hypothesis that has recently been obtained on the basis of mitochondrial 16S data (Collins & Daly 2005) and nuclear ribosomal gene data (Collins *et al.* 2006). Because both anthozoans and stauromedusans are benthic animals, one can infer that the evolutionary origin of a pelagic medusa is a derived feature within Medusozoa. The clade consisting of non-stauromedusans is united by six putative synapomorphies, including planktonic adults (17), periderm limited to the lower portion of the polyp (39), development of primary polyp tentacles into sensory structures (52), presence of radial canals (64), statocysts present (69) and the origin of the giant fibre nerve net (77).

CONCLUDING REMARKS

It is tempting to claim that the phylogenetic affinities of conulariids should no longer be considered problematical. After all, conulariids and extant stauromedusans and coronate scyphozoans share relatively complex anatomical similarities that are unique to members of these groups. No uniquely shared similarities of comparable complexity have been shown to exist between conulariids and any other taxon. Therefore, we think it reasonable to infer that the similarities between conulariids and scyphozoans are homologous and that a cladistic analysis including conulariids among cnidarian groups is justified.

We have found that the most likely candidates for the extant nearest relatives of conulariids are the coronate scyphozoans, a group whose polyp stage is encased in a morphologically complex periderm that exhibits detailed and uniquely shared similarities to skeletons of conulariids. Although there are grounds for inferring the (former) presence of Y-shaped gastric septa in *Eoconularia loculata*, our analysis suggests that the shared presence of these soft-part structures in this conulariid and stauromedusans is either primitive or homoplastic. Our analysis also suggests that conulariids had a free-living, sexual medusa stage produced by strobilation.

Finally, merely by refining the character scoring of the fossil conulariids, we have derived a cladistic hypothesis of

relationships between extant medusozoans that is remarkably similar to that recently derived from molecular data. This hypothesis implies that Scyphozoa as traditionally conceived is paraphyletic (as do the results of Marques & Collins), but that, together with conulariids, all other extant taxa (Cubozoa, Coronatae, Rhizostomeae and Semaestomeae) originally placed in Scyphozoa constitute a clade within Medusozoa. To be sure, the lack of prior knowledge of much of the life history and soft-part anatomy of conulariids makes resolving their position within Medusozoa particularly challenging. Indeed, there are few characters of any kind whose states in conulariids are known or can be inferred with a high degree of confidence. Moreover, most of these characters (e.g. symmetry, life habit, presence or absence of a periderm) are fairly general. In view of what is presently known about conulariid anatomy, then, alternative interpretations of the systematic position of conulariids within Medusozoa must be regarded as provisional, with no single hypothesis enjoying a substantially higher likelihood of being true than any other.

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APPENDIX 1: LIST OF CHARACTERS AND STATES AND DATA MATRIX

Cellular and microstructural characters

1. Cnidocil (0, mobile; 1, immobile).
2. Mitochondrial DNA (0, circular; 1, linear).
3. Gap junction plaques (0, absent; 1, present).
4. Mesoglea (0, non-cellular; 1, cellular).
5. Collagen structure (0, homotrimerous; 1, heterotrimerous).

Cnidome characters

6. Cnidae (0, absent; 1, present).
7. Stenoteles (0, absent; 1, present).
8. Euryteles (0, absent; 1, present).
9. Desmonemes (0, absent; 1, present).
10. Mastigophores (0, absent; 1, present).
11. Basitrichous isorhizas (0, absent; 1, present).
12. Apotrichous isorhizas (0, absent; 1, present).
13. Isorhizas (holotrichous or atrichous) (0, absent; 1, present).
14. Heterotrichous anisorhizas (0, absent; 1, present).
15. Birhopaloids (0, absent; 1, present).
16. Rhopalonemes (0, absent; 1, present).

Life habit and symmetry characters

17. Life habit (0, benthic adults; 1, planktonic adults).
18. Symmetry (0, radial; 1, radial tetramerous; 2, biradial).

Characters of reproduction

19. Sexual condition (0, hermaphroditic; 1, gonochoric).
20. Location of medusa formation (0, lateral, budding from an entocodon; 1, apical/oral; 2, direct development without polyp stage).
21. Type of apical medusa formation (0, strobilation; 1, metamorphosis without transverse fission).
22. Strobilation type (0, polydisk; 1, monodisk).
23. Oocyte development (0, oocytes develop without accessory cells; 1, oocytes develop with accessory cells; 2, oocytes develop within follicles; 3, oocytes develop from uptake of somatic or other germ line cells).
24. Spermaphore (0, absent; 1, present).
25. Location of gonads (0, gastrodermis; 1, epidermis).

Characters of body organisation

- 26. Nectosome (0, absent; 1, present).
- 27. Pneumatophore (0, absent; 1, present).

Characters of the planula

- 28. Planula larva in the life cycle (0, present; 1, absent).
- 29. Planula ciliation (0, ciliated; 1, non-ciliated).
- 30. Number of endodermal cells of the planula (0, varied number; 1, constant, $n = 16$).
- 31. Glandular cells in the planula (0, absent; 1, present).
- 32. Nervous cells in the planula (0, absent; 1, present).
- 33. Relationship between axes of planula and adult (0, oral–aboral axis in the adult derived from the longitudinal axis of the planula; 1, oral–aboral axis in the adult derived from the transverse axis of the planula).

Post planula characters

- 34. Ephyrae (0, absent; 1, present).
- 35. Actinula (0, absent; 1, present).
- 36. Polypoid phase (0, absent; 1, present).
- 37. Polymorphic polyps (0, absent; 1, present).
- 38. Desmocytes (0, present; 1, absent).
- 39. Periderm (0, absent; 1, limited to the basal area of body or to podocysts; 2, present).
- 40. Podocysts (0, absent; 1, present).
- 41. Structure of polyp tentacles (0, hollow; 1, solid).
- 42. Number of tentacular whorls (0, one; 1, two or more).
- 43. Septa in polyp (0, absent; 1, gastrodermic folds present; 2, present).
- 44. Hydrotheca/gonotheca (0, absent; 1, present).
- 45. Stomodeum (0, absent; 1, present).
- 46. Organisation of the nervous system (0, in one or two nets; 1, with nerve rings).
- 47. Canal system (0, absent; 1, present).
- 48. Gastrodermic musculature (0, not organised in bunches; 1, organised in bunches of gastrodermic origin; 2, organised in bunches of ectodermic origin).

Medusoid characters

These characters apply to an adult life phase that typically follows an intermediate polyp stage. While homology between cnidarian medusoid phases has long been debated, the strong similarity in morphology of different medusae leads us to score these characters across the medusozoan groups. Anthozoa has no comparable life history phase and is scored accordingly throughout.

- 49. Medusoid phase (0, absent; 1, present).
- 50. Pedalium of coronate type (0, absent; 1, present).
- 51. Rhopalia/rhopalioids (0, absent; 1, present).
- 52. Complexity of rhopalium/rhopalioids (0, simple hollow structures; 2, rhopalia; 3, rhopalia with complex eyes).
- 53. Nerve ring(s) (0, absent; 1, one; 2, two).
- 54. Gastric filaments (0, absent; 1, present).
- 55. Coronal muscle (0, well developed; 1, marginal and tiny).
- 56. Pedalium of the cubozoan type (0, absent; 1, present).
- 57. Velum (0, absent; 1, present).
- 58. Umbrellar margin (0, smooth and continuous; 1, lobed).
- 59. Tentacles (0, absent; 1, present).
- 60. Tentacular bulbs (0, absent; 1, present).
- 61. Statolith composition (0, MgCaPO₄; 1, CaSO₄).
- 62. Septa (0, absent; 1, present).
- 63. Septal shape (0, straight; 1, Y-shaped).
- 64. Radial canals (0, absent; 1, present; 2, present in the form of complex structures).
- 65. Circular canal (0, absent; 1, partially present; 2, fully present).
- 66. Velarium (0, absent; 1, present).
- 67. Coronal furrow (0, absent; 1, present).
- 68. Gonadal location (0, manubrium; 1, radial canals).
- 69. Statocysts (0, absent; 1, endodermic; 2, ectodermic).
- 70. Perradial ‘mesenteries’ (0, absent, 1, present).
- 71. Adult medusoid shape (0, bell; 1, pyramidal; 2, cubic; 3, actinuloid).
- 72. Shape of horizontal cross-section (0, circular; 1, quadrate, i.e., with four-part symmetry).
- 73. Urticant rings (0, absent; 1, present).
- 74. Oral arms with suctorial mouths (0, absent; 1, present).
- 75. Tentacular insertion (0, umbrellar margin; 1, away from the umbrellar margin).
- 76. Manubrium (0, absent; 1, present).
- 77. Nervous system organisation (0, GFNN absent; 1, GFNN present).
- 78. Structure of medusa tentacles (0, hollow; 1, solid).
- 79. Tentacular morphology (0, straight tentacles in their whole extension; 1, tentacles with an angular inflection).
- 80. Peronia (0, absent; 1, present).
- 81. Ocelli (0, absent; 1, present).
- 82. Peripheral system (0, absent; 1, present).
- 83. Umbrellar furrow (0, absent; 1, present).
- 84. Development of the umbrella (0, fully developed; 1, aboral cone).
- 85. Number of tentacular whorls (0, 1 whorl; 1, two whorls).
- 86. Velar canals (0, absent; 1, present).
- 87. Frenulae (0, absent; 1, present).

APPENDIX 2: RE-CODED DATA MATRIX OF CHARACTERS

?, unknown state; N, non-comparable; x/y, polymorphic.

TAXA	1	2	3	4	5	6	7	8	9	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	
	0	1	2	3	4	5	6	7	8	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9
Anthozoa	0	0	0	1	0	1	0	0	0	1	1	0	1	0	0	0	0	2	1	N	N	N	1	0	0	0	0	1	1
Stauromedusae	?	1	0	0	?	1	0	1	0	0	0	0	1	0	0	0	0	1/2	1	1	1	N	2	0	0	0	0	1	0
Conulatae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	?	?	?	?	1	?	?	0	0	?	?
Conulariids	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	0	0	?	?
reassessed																													
Cubozoa	1	1	0	0	?	1	1	1	0	1	0	0	1	0	0	0	1	1/2	1	1	1	N	?	0/1	0	0	0	1	1
Coronatae	?	?	0	1	?	1	0	1	0	0	0	1	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	1	1
Semaeostomeae	1	1	0	1	1	1	0	1	0	0	0	1	1	0	0	1	1/2	1	1	1	0	0	1	0	0	0	0	1	1
Rhizostomeae	?	1	0	1	?	1	0	1	0	0	0	0	1	1	0	0	1	1/2	1	1	0	1	1	0	0	0	0	1	1
Limnomedusae	1	1	?	0	?	1	0	1	0	0/1	0	0	1	0	0	0	1	0/2	1	0	N	N	3	0	1	0	0	1	1
Actinulida	?	?	?	0	?	1	1	0/1	?	0	0	0	1	0	0	0	1	N	1	2	N	N	?	0	1	0	0	0	N
Trachymedusae	?	1	1	0	?	1	1	1	0	0	0	1	0	0	0	1	N	1	2	N	N	3	0	1	0	0	1	1	
Narcomedusae	?	?	?	0	?	1	0	0	0	0	0	1	1	0	0	0	1	N	1	2	N	N	3	0	1	0	0	1	1
Laingiomedusae	?	?	?	0	?	1	0	0	0	1	0	0	1	0	0	0	1	N	?	?	N	N	?	0	1	0	0	?	?
Leptothecata	1	1	?	0	?	1	0	0/1	0	1	0	1	0	0	0	1	0/2	1	0	N	N	?	0	1	0	0	0	1	1
Siphonophorae	1	1	1	0	?	1	1	1	1	1	0	0	1	0/1	1	0/1	1	0/2	0/1	0	N	N	?	0	1	0/1	0/1	1	1
Anthoathecata	1	1	1	0	?	1	0/1	1	1	1	0/1	0	1	0/1	0	0	1	0/2	1	0	N	N	3	0	1	0	0	1	1

TAXA	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5	5	5	5
	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	8
Anthozoa	0	1	1	0	0	0	1	0/1	0	0	0	0	0	2	0	1	0	0	1	0	N	N	N	N	N	N	N	N	N	
Stauromedusae	1	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	1	2	1	0	1	0	0	1	1	0	0	0	0	
Conulatae	?	?	?	?	?	?	1	0	?	2	?	?	?	2	0	?	?	?	2	?	?	?	?	?	?	?	?	?	?	
Conulariids	?	?	?	?	?	?	1	0	?	2	?	?	?	2	0	?	?	?	2	?	?	?	?	?	?	?	?	?	?	
reassessed																														
Cubozoa	0	?	?	0	0	0	1	0	1	1	?	1	0	1	0	0	1	1	2	1	0	1	2	1	1	0	1	0	0	
Coronatae	0	?	?	0	1	0	1	0	1	2	0	1	0	2	0	0	0	1	2	1	1	1	1	0	1	0	0	0	1	
Semaeostomeae	0	1	1	0	1	0	1	0	0	1	1	1	0	2	0	0	0	1	2	1	0	1	1	0	1	0	0	0	1	
Rhizostomeae	0	0	0	0	1	0	1	0	1	1	1	1	0	2	0	0	0	1	2	1	0	1	1	0	1	0	0	0	1	
Limnomedusae	0	0	1	0	0	0	1	0/1	0	1	0	0	0	0	0	0	0	0	1	0	0	N	2	0	0	0	0	1	0	
Actinulida	N	N	N	N	0	0	N	N	N	N	N	N	N	N	N	N	N	N	N	1	0	0	N	?	0	?	0	N	0	
Trachymedusae	0	0	0	0	0	1	0	N	N	N	N	N	N	N	N	N	N	N	N	1	0	0	N	2	0	0	0	1	0	
Narcomedusae	0	0	0	1	0	1	0	N	N	N	N	N	N	N	N	N	N	N	N	1	0	0	N	?	0	0	0	1	1	
Laingiomedusae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	N	?	0	?	0	1	1	
Leptothecata	0	1	1	0	0	0	1	1	0	2	0	1	0	0	1	0	0	0	0	1	0	0	N	2	0	0	0	1	0	
Siphonophorae	0	1	1	0	0	0	1	1	0	0/2	0	0	?	0	0	0	?	0	0	1	0	0	N	2	0	0	0	1	0	
Anthoathecata	0	1	1	0	0	0	1	1	0	2	0	0/1	0/1	0	0	0	0	0	0	1	0	0	N	2	0	0	0	1	0	

TAXA	5	6	6	6	6	6	6	6	6	6	7	7	7	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	8
	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	7
Anthozoa	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	0	0
Stauromedusae	1	?	N	1	1	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0/1	0	0	0	0	0	0	0
Conulatae	?	?	?	1	1	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Conulariids	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
reassessed																														
Cubozoa	1	0	1	1	1	0/1	0	1	0	1	1	0	2	1	0	0	0	1	1	0	0	0	1	0	0	0	0	1	1	1
Coronatae	1	0	1	1	0	1	0	0	1	1	1	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0
Semaeostomeae	1	0	1	0	N	2	1	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0
Rhizostomeae	0	N	1	0	N	2	1	0	0	1	1	0	0	0	0	1	N	1	1	N	N	0	1	0	0	0	N	0	0	
Limnomedusae	1	0	?	0	N	1	2	0	0	1	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0/1	0	0
Actinulida	1	0	?	0	N	0	0	0	0	0	1	0	3	0	0	0	0	1	?	1	0	0	0	0	0	0	1	1	0	0
Trachymedusae	1	0	0	0	N	1	2	0	0	1	1	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
Narcomedusae	1	0	?	0	N	0	2	0	0	0	1	0	0	0	0	0	0	1	0	?	1	0	1	0	1	0	0	0	0	0
Laingiomedusae	1	1	N	0	N	1	2	0	0	0	0	0	0	0	0	0	1	1	?	1	1	1	0	1	1	0	0	0	0	0
Leptothecata	1	1	0	0	N	1	2	0	0	1	2	0	0	0	0	0	0	1	1	0	0	0	0/1	0	0	0	0	0	0	0
Siphonophorae	0	1	N	0	N	1	2	0	0	0	0	0	0	0	0	0	0	1	1	N	N	0	0	0	0	0	0	N	0	0
Anthoathecata	1	1	N	0	N	1	2	0	0	0	0	1	0	0	0	0	0	1	1	0/1	0	0	1	0	0	0	0	0	0	0