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REDUCTIO AD ABSURDUM: TESTING THE EVOLUTIONARY RELATIONSHIPS OF EDIACARAN AND PALEOZOIC PROBLEMATIC FOSSILS USING MOLECULAR DIVERGENCE DATES

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ABSTRACT—Many of the late Neoproterozoic ‘‘Ediacaran fossils’’ have been referred to the Cnidaria, often on the basis of vague or poorly known features. However, representatives of the living Chondrophorina (=Porpitidae, Hydrozoa), Pennatulacea (Anthozoa), and Coronatae and/or Stauromedusae (Scyphozoa) have all been identified in Ediacaran biotas, based on specific morphological features preserved in a number of specimens. These three cnidarian groups have plausible Paleozoic representatives as well, but many of their Paleozoic fossils are also somewhat problematic. We test these systematic hypotheses by using them to calibrate divergence dates across the Cnidaria, based on an extensive molecular phylogeny of extant cnidarians. In this *reductio ad absurdum* approach, if a calibration based on one interpretation of a problematic fossil yields a glaringly inconsistent age for a better-known clade, that interpretation is likely to be mistaken. We find that assuming the existence of Pennatulacea and Scyphozoa in the ‘‘Ediacara biota’’ places the root of the Cnidaria between 800 and 1,000 Ma, a figure which is, at least, not out of line with other molecular clock estimates. However, assuming the existence of the Chondrophorina in the Neoproterozoic, or anywhere in the Paleozoic, pushes the root of the Cnidaria back to between 1,500 and 2,000 Ga, which is considerably older than the oldest previous estimates for the origin of the Cnidaria. We suggest that the likeliest explanation is that chondrophorines were not present in the late Precambrian or Paleozoic. The Ediacaran and Paleozoic fossils previously interpreted as chondrophorines probably represent other taxa.

INTRODUCTION

THE LATE Precambrian and earliest Cambrian soft-bodied fossils of the ‘‘Ediacara biota’’ are well-known paleontological enigmas. Consisting of a variety of structural types ranging from disc-shaped ‘‘medusoids’’ to leaflike ‘‘fronds,’’ they have been interpreted as everything from invertebrate animals in or near extant phyla (e.g., Glaessner, 1984; Fedonkin, 1990) to members of other kingdoms, such as protists or lichens (e.g., Zhuravlëv, 1993; Retallack, 1994) to members of independently multicellular taxa, not directly related to anything alive (e.g., Seilacher, 1992, 1994). Probably no single explanation will fit all the fossils. While some Ediacaran forms are quite unlike any known animal, others are still most plausibly interpreted as animals in or near extant phyla. These include representatives of the Porifera (Gehling and Rigby, 1996), Mollusca (Fedonkin and Waggoner, 1997), and possibly Arthropoda (Waggoner, 1999) and Annelida or Pogonophora (Sokolov, 1968).

Most Ediacaran fossils have historically been interpreted as cnidarians. The ‘‘medusoids,’’ which are the most abundant fossils at most Ediacaran sites, were generally described as jellyfish (e.g., Wade, 1972; Glaessner, 1984). A few ‘‘medusoids’’ show tetraradial symmetry, such as *Conomedusites* and *Stauridinium* (e.g., Fedonkin, 1990), which is typical for non-anthozoan cnidarians: the Medusozoa. However, many Ediacaran ‘‘medusoids,’’ if not all, are now thought to be benthic (e.g., Bruton, 1991; Gehling, 1991; Jenkins, 1992; Gehling et al., 2000). Some ‘‘medusoids’’ could be cnidarian polyps, and others are probably holdfasts for ‘‘frondlike’’ organisms that could be colonial cnidarians, but working out just what each specific type of ‘‘medusoid’’ was is difficult at this time. Other ‘‘medusoids,’’ such as *Tribrachidium* and *Albumares*, are triradially symmetrical fossils with relatively complex structure. These triradial fossils cannot easily be placed in any known metazoan group, although they may be of a cnidarian grade of complexity. However, most of the Ediacaran ‘‘medusoids’’ show no defined degree of symmetry. ‘‘Medusoid’’ taxonomy is currently highly problematic due to the extreme taphonomic variability and morphological simplicity of many of the fossils (Gehling et al., 2000).

However, there are three extant cnidarian groups which have been claimed, on well-defined anatomical grounds, to be represented in the Ediacara biotas. (Fig. 1) The first is the Chondrophorina or ‘‘sailors-by-the-wind,’’ a subclade of the Hydrozoa, whose extant genera *Porpita* and *Velella* are usually classified together in the family Porpitidae. Chondrophorines are disc-shaped pelagic colonial organisms that secrete a gas-filled float composed of multiple concentric chambers. The Ediacaran genera *Ovatoscutum*, *Chondroplon*, *Kaisalia*, *Kullingia*, and *Eoporpita* have been referred to the Chondrophorina (Gehling, 1991; Jenkins, 1992). Some of these are poorly known, taxonomically suspect, and/or interpreted as non-chondrophorines (e.g., Hoffman, 1988; Jenkins, 1992; Jensen et al., 2001). However, the Ediacaran genus *Ovatoscutum* looks very similar to the float of the living chondrophorine *Velella*. The genus *Eoporpita* shows extensive tentacles radiating from a central boss, which in some specimens appears chambered.

The second extant clade that may be represented in Ediacaran assemblages is the Pennatulacea or the ‘‘sea pens,’’ a clade of colonial anthozoans within the Octocorallia (Anthozoa). Pennatulaceans are composed of one large primary zooid which forms a central stalk or rachis, with multiple secondary feeding zooids branching from the primary zooid. In the most derived pennatulaceans, the secondary polyps are organized into leaflike structures branching from the rachis. Exemplified by living genera such as *Ptilosarcus*, *Pteroeides*, *Virgularia* and *Pennatula*, this arrangement produces the featherlike appearance that is ‘‘typical’’ of pennatulaceans; however, this shape actually is found in a minority of extant genera. In most pennatulaceans, the secondary polyps branch directly from the rachis, and the colony form may be club-shaped or fan-shaped (Williams, 1992, 1995). A number of frondlike Ediacaran fossils have been linked with the Pennatulacea, notably *Charnia*, *Charniodiscus*, *Rangea*, and *Glaessneria*; these have a leaflike shape with a stalk and round bulbous holdfast, and a few have structures interpreted as spicules, zooids, and polyp leaves (Ivantsov, 1996; Jenkins, 1985, 1996). These fossil taxa have been linked specifically with derived living pennatulaceans. Waggoner (1998) suggested a similarity between certain Ediacaran ‘‘fronds’’ and the extant pennatulacean *Renilla*, which has a broad frondlike expansion

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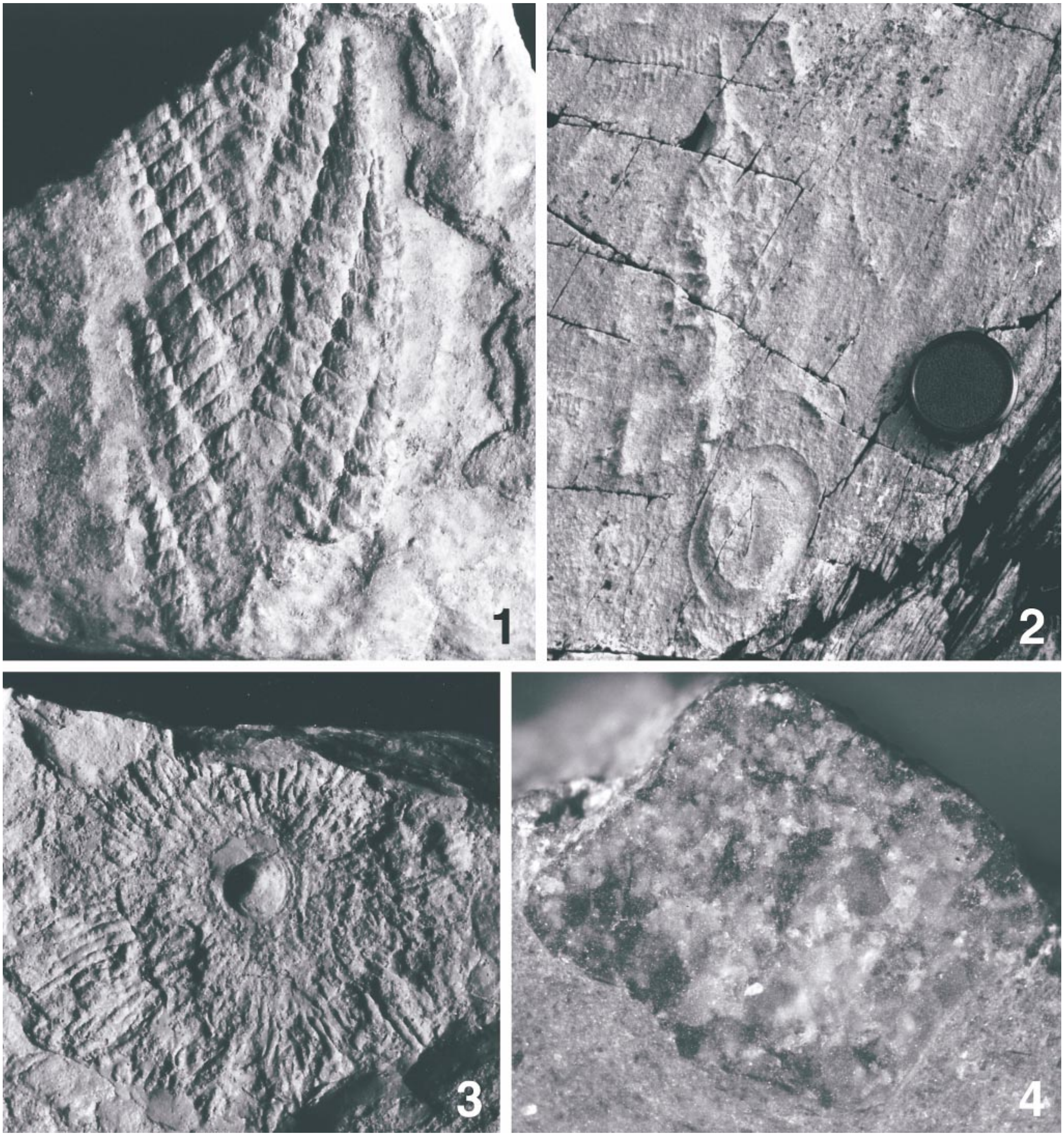

FIGURE *1*—Ediacaran taxa that may be members of the Cnidaria. *1,* a possible pennatulacean, *Charnia*, from the Winter Coast of the White Sea, north Russia (University of California Museum of Paleontology collection). *2,* field photograph of another possible pennatulacean referred tentatively to *Charniodiscus*, from Mistaken Point, Newfoundland. *3,* a possible chondrophorine, *Eoporpita*, from the Winter Coast of the White Sea, north Russia (University of California Museum of Paleontology collection). *4,* a possible coronate scyphozoan polyp tube, *Corumbella* (cross section), from the Mojave Desert of southern Nevada (Los Angeles County Museum of Natural History collection).

of the rachis with variable arrangements of the secondary polyps, but which lacks polyp leaves. The fossil *Ausia* from Namibia has been interpreted as similar to a more basal pennatulacean, resembling living pennatulaceans in the Veretillidae (Hahn and Pflug, 1985). Taken at face value, all these reports would suggest that the Pennatulacea was not only present in the Vendian, but had diversified into several extant subclades by the Vendian.

Finally, the third extant cnidarian group that may be represented in the Ediacara biota is the Scyphozoa (which may not be monophyletic; see below). As mentioned above, a few tetraradial ''medusoids'' could be scyphozoan jellyfish, but tetraradial symmetry is also typical of the Hydrozoa and Cubozoa. However, annulated tubes with definite tetraradial symmetry have been found in Ediacaran-age biotas in both South America and southwestern North America, and referred to the genus *Corumbella* (Hahn et al., 1982; Hagadorn and Waggoner, 2000). *Corumbella* is similar in many respects to the tubes secreted by the polyp stage of living coronate scyphozoans such as *Stephanoscyphus* (Leslie et al., 2001) and to the benthic cnidarians in the Stauromedusae (Collins et al., 2000). If the first hypothesis is true, *Corumbella* would be the earliest representative of Scyphozoa; if the second is true, *Corumbella* would belong to an outgroup of the extant Scyphozoa.

These hypotheses are difficult to test using Phanerozoic fossils. Pennatulaceans have a very sparse Phanerozoic record, although the Middle Cambrian fossil *Thaumaptilon* from the Burgess Shale is almost certainly a pennatulacean (Conway Morris, 1993). There is a sparse record of other octocorals in the early Paleozoic, including probable octocoral spicules from the early Cambrian of Australia (*Microcoryne*; see Bengtson et al., 1990); Cambrian polyps with eightfold symmetry and fringed tentacles, which are octocoral synapomorphies (*Xianguangia*; see Chen and Erdtmann, 1991 and Chen and Zhou, 1997); and a few plausible alcyonacean and gorgonian fossils from the Ordovician, Silurian, and Devonian (e.g., Glinski, 1956; Lindström, 1978; Bengtson, 1981). Paleozoic fossil scyphozoans are probably represented by the Conulariida, a fairly well-known Paleozoic taxon of ribbed, conical, tetraradial fossils referred to either the coronate scyphozoans (Werner, 1966; Van Iten, 1991) or the stauromedusae (Jerre, 1994; Collins et al., 2000). The oldest conulariids are from the Late Cambrian (Hughes et al., 2000). Other tetraradial forms such as the Middle Ordovician *Conchopeltis* are often grouped together with the Conulariida to form a subgroup of Scyphozoa called Conulata (Moore and Harrington, 1956; but see Oliver, 1984). Scyphozoans may also be represented by the Early Cambrian Chinese genus *Olivooides*, whose fossils show ontogenetic development from a spherical embryo into an annulated tube, although these animals appear to have pentameral symmetry (Zhao and Bengston, 1999).

Chondrophorines ostensibly have a fossil record throughout the Phanerozoic (Stanley, 1986), but many of the Paleozoic fossils attributed to chondrophorines are controversial at best. For example, *Plectodiscus* has been described as a well-preserved chondrophorine from the Lower Devonian-age Hunsrückschiefer of Germany, but Otto (2000) has argued that the known specimens of *Plectodiscus* are not chambered, lacked zooids, and are in fact large, thin-shelled brachiopods. A *Plectodiscus* specimen from the Hunsrückschiefer that supposedly preserves the zooids of a chondrophorine does not show the diagnostic float, and Otto (2000) states that it is a pyritized trace fossil. The Cambrian genus *Scenella*, known from the Burgess Shale and similar Lagerstatte, has been the subject of debate; at least some specimens assigned to *Scenella* are more likely to be cap-shaped shells (Landing and Narbonne, 1992). Other proposed Paleozoic ''chondrophorines'' have also been reinterpreted as mollusc or brachiopod shells, trace fossils, or rotational sweep marks (e.g., Horny, 1985; Kase, 1988; Jensen et al., 2001). Still others may belong to poorly known metazoan taxa that may or may not belong in any known phyla (e.g., Dzik, 1991; Conway Morris et al., 1991; Geyer, 1994), and others are probably too poorly preserved to be informative (e.g., Waggoner and Collins, 1995).

Only careful morphological study of well-preserved fossils will ultimately resolve these controversies. However, other sources of information can be brought to bear on the problem of interpreting these fossils. A recent molecular phylogenetic analysis of the Cnidaria (Fig. 2) allows us to use ''molecular clock'' approaches to examine the possibility of chondrophorines, coronate or stauromedusan scyphozoans, and pennatulaceans in the Ediacara biota and afterwards. There are two possible approaches to this problem:

- Calibrating the clock using well-established fossils, and using that calibration to derive the likely age of the basal nodes. This is the usual way of using the molecular clock, and it has been used extensively in estimating divergence dates for the Metazoa and for various animal phyla and superphyla (see Table 1). However, it is not the approach we have used in this study. The fossil record of extant cnidarians is not rich. Scleractinian corals are the only major exception, but in view of their sudden appearance in the Triassic, it has been considered very likely that they arose from a Paleozoic soft-bodied anthozoan clade with no clear fossil record. Using the Phanerozoic cnidarian fossil record to calibrate the molecular clock for the Cnidaria as a whole would introduce a great deal of bias, since most, if not all, of the first fossil occurrences are likely to be significantly younger than the actual origins of the clades. This is potentially a problem in all clock analyses, since the only way that a first fossil occurrence could not be younger than the origin of the clade is if the fossil is the ancestor of the clade itself. However, it is likely to be a particularly serious problem in the Cnidaria.
- Calibrating the clock using the controversial fossils, and checking whether that calibration yields dates of origin for other clades that are consistent with other lines of evidence. This could be called the *reductio ad absurdum* approach, after a well-known technique in mathematical logic, in which a proposition is disproved if the chain of consequences deduced from it leads to a contradiction. If a calibration based on one interpretation of a controversial fossil yields a highly improbable age for several better-known clades, that interpretation is likely to be incorrect. This is the approach that we use here. We have carried out multiple ''molecular clock'' estimates of branching dates within a hypothesized phylogeny of the Cnidaria, all of which can be compared with the fossil record and with molecular divergence estimates of other taxa. Each of these clock analyses has been calibrated based on different interpretations of the Ediacaran fossil record.

Other researchers have used a similar tactic of comparing the estimated ages of clades using different calibration points. In a study of primate molecular phylogeny, Nei and Glazko (2002) showed that two different calibrations derived from the fossil record generally gave mutually consistent results within the range of statistical error. The primate-artiodactyl divergence, estimated from the fossil record at 90 Ma, calibrated the human-orangutan divergence at 11.3–13.7 Ma depending on the method of analysis, overlapping with the fossil-based estimate of 13 Ma. The fossil date of 13 Ma for the human-orangutan divergence in turn yielded molecular clock dates of 85.6–143.7 Ma for the primate-artiodactyl divergence. Huchon et al. (2000) used eight different calibration points from the fossil record in their phylogenetic and molecular clock analysis of rodents. They noted that some pairs of calibration points gave mutually consistent results, while others gave mutually inconsistent results. They suggested the use of several ''cross-validated'' calibration points would reduce dating errors. However, this cross-validation tactic has to our knowledge not previously been used in estimating deep divergence dates within the Metazoa; nor has it been used previously to test proposals of the taxonomic affinity of problematic fossils.

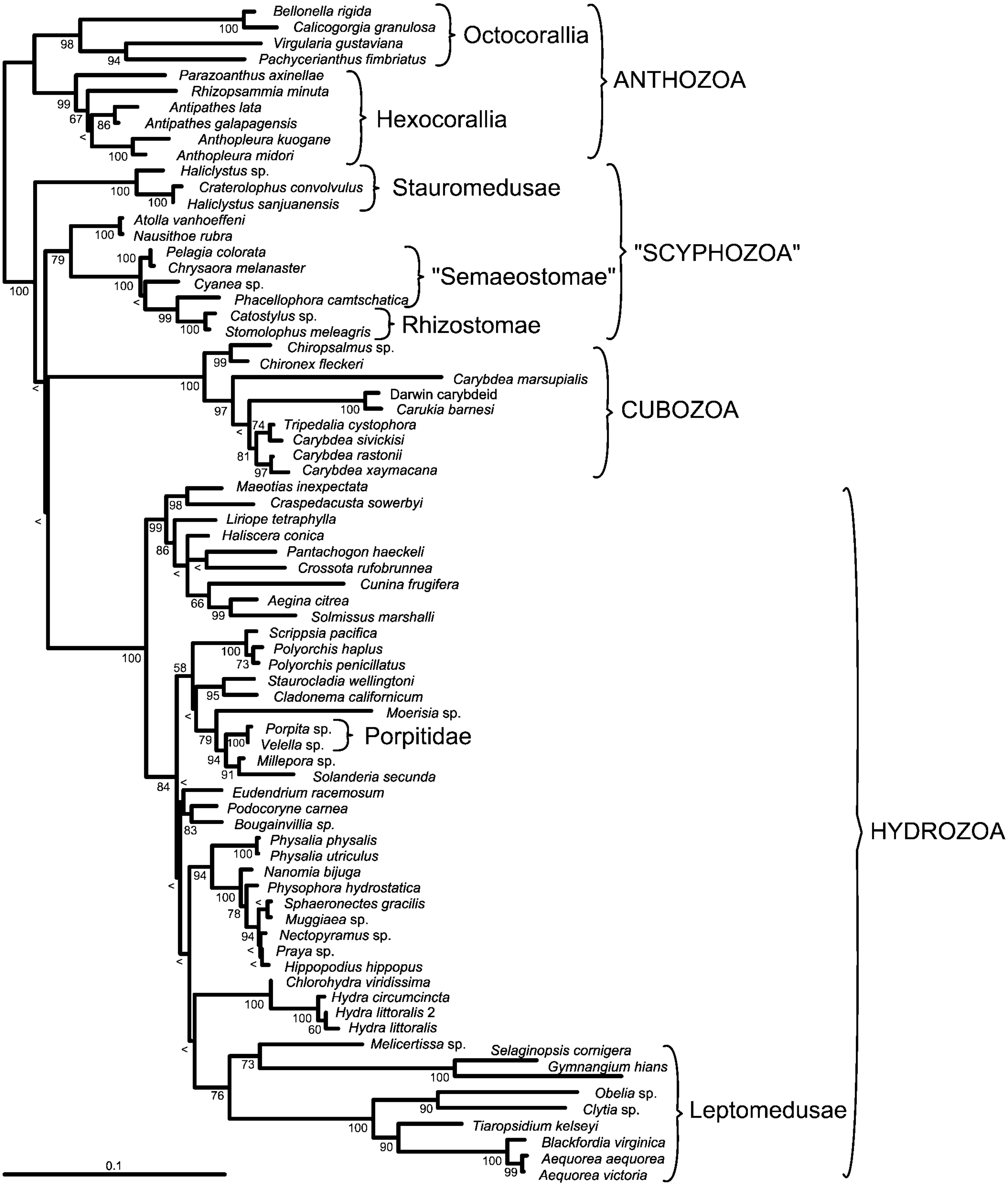

FIGURE 2—Maximum likelihood tree of 64 medusozoans plus 10 anthozoans as outgroups, assuming a general-time-reversible model of nucleotide evolution with rate heterogeneity. Score = −15,595.976. Scale bar denotes 0.1 nucleotide substitutions per site.

TABLE *1*—Molecular clock estimates from various sources giving upper or lower bounds or direct estimates of the divergence data for the basal Cnidaria. For clarity, confidence intervals are usually not shown, and many dates are approximations summarized from somewhat heterogeneous data. Dates in parentheses were not corrected for relative rates of change (see Feng et al., 1997).

Date	Divergence	Sequences used	Source
~670 Ma	protostome-deuterostome split	18 nuclear genes	Ayala et al., 1998
~750 Ma	protostome-deuterostome split	22 nuclear genes	Lee, 1999
730 Ma (850 Ma)	protostome-deuterostome split	64 amino acid sequences	Feng et al., 1997
750–1000 Ma	protostome-deuterostome split	complete mitochondrial genome	Bromham et al., 1998
~1200 Ma	protostome-deuterostome split	18S rRNA, 4 other mitochondrial genes, 4 nuclear genes	Wray et al., 1996
761 Ma	coelomate-pseudocoelomate split	57 amino acid sequences	Doolittle et al., 1996
815 Ma (1045 Ma)	coelomate-pseudocoelomate split	64 amino acid sequences	Feng et al., 1997
902 Ma	diploblast-triploblast split	10 mitochondrial genes	Lynch, 1999
~940 Ma	poriferan-eumetazoan split	aldolase, triose phosphate isomerase	Nikoh et al., 1997
965 Ma	animal-fungus split	57 enzyme amino acid sequences	Doolittle et al., 1996
~908–1188 Ma	animal-fungus split	22 nuclear genes	Lee, 1999
1130 Ma (1272 Ma)	animal-fungus split	64 amino acid sequences	Feng et al., 1997
~926–1211 Ma	animal-plant split	22 nuclear genes	Lee, 1999
1000 Ma	animal-plant split	57 enzyme amino acid sequences	Doolittle et al., 1996
~1070 Ma	animal-plant split	aldolase, triose phosphate isomerase	Nikoh et al., 1997
1200 Ma (1215 Ma)	animal-plant split	57 enzyme amino acid sequences	Feng et al., 1997

PROCEDURES

We used a molecular phylogeny for extant Cnidaria (Fig. 2) based on 18S rRNA sequences (1,768 nucleotides in length) for 74 taxa, aligned by hand. (See Table 2 for accession information; the full data set is publicly available at http://www.ucmp.berkeley.edu/archdata/Collins-Medusozoa/, as well as on request from the authors.) The optimal tree was found using 10 replicate searches using the ML (maximum likelihood) algorithm of the program PAUP* (Swofford, 2000). We used the program Modeltest (Posada and Crandall, 1998) to determine the model of nucleotide evolution that best fits the sequence data, using likelihood ratio tests. This gave us a general-time-reversible model with rate heterogeneity (assumed nucleotide frequencies: A = 0.2599; C = 0.1986; G = 0.2674; T = 0.2741; substitution types = 6, proportion of invariable sites = 0.5007, γ for variable sites = 0.5646, substitution rates equal to 1.000 except between A and G = 2.481 and C and T = 4.069). Further information on the phylogeny, along with a full discussion of its implications for cnidarian systematics and evolution, has been published in Collins (2002).

Ideally, all taxa would be simultaneously analyzed in a molecular clock analysis. However, a likelihood ratio test rejects the hypothesis that the 18S data has evolved in a clocklike manner, indicating that there is significant heterogeneity in rates across the 74 cnidarian taxa examined here. Deletion of the longest branches, using the relative rates test, did not yield clocklike evolution in the remaining sequences; repeated deletions ultimately led to the excision of entire clades of interest from the phylogeny. Therefore, we repeatedly selected quartets of taxa that span the origins of three major taxa: the Cnidaria itself, the Medusozoa (non-anthozoan Cnidaria), and the unnamed clade consisting of the Cubozoa plus the Hydrozoa. Each quartet consisted of two pairs of sister taxa, and each pair was assigned an estimated date of divergence based on the fossil record (Tables 3, 4). We used the program QDate 1.1.1 (Rambaut and Bromham, 1998; available at http://evolve.zoo.ox.ac.uk/) to estimate the date of divergence of the two pairs from each other, given divergence dates of each taxon pair (Fig. 3). QDate uses a maximum-likelihood approach to reconstruct the date of divergence of the pairs under the assumption that each pair evolves at its own substitution rate. Confidence intervals on the date are calculated using a log-likelihood approach. The program also runs a log-likelihood test for rate heterogeneity between the two pairs of taxa; quartets of taxa with heterogeneous substitution rates, in which all branches of the tree have their own substitution rates, can be identified and rejected. QDate allows dates to be reconstructed under a range of substitution models. We used the most flexible, the general time reversible model (GTR), in which each possible substitution is assigned its own probability, and the nucleotide frequencies and rate heterogeneity parameter (Γ, gamma) are specified. For each quartet, these parameters were estimated using maximum likelihood with PAUP* and subsequently provided to the QDate program.

Table 2 contains a number of relevant molecular clock estimates, including Lynch's 1999 estimate of abut 900 Ma for the origin of the diploblasts. Estimates of the date of the split between total-group Metazoa and total-group Fungi or Plantae place lower bounds on this branch point. Estimates of the date of the protostome-deuterostome divergence place rough upper bounds on the branch point, although these can only be tentative upper bounds because of the possibility that all extant cnidarian lineages diverged after the protostome-deuterostome split. Despite this potential problem, and despite the sizable margins for error of many of these estimates, it seems safe to say that a divergence date between 800 and 1,000 million years for the origin of the crown-group Cnidaria is, at the very least, not grossly contradicted by other analyses.

RESULTS

The ML tree derived from the general-time-reversible model of nucleotide evolution is generally well supported, and is very similar to trees derived from the same dataset using the maximum parsimony criterion (see Collins, 2002 for full discussion). Our results are summarized graphically in Figures 4 through 7; the raw numerical data is available at http://www.ucmp.berkeley.edu/archdata/Waggoner_Collins_2001/ or on request from the authors. There is a considerable range of estimates for the dates of origin for major cnidarian groups, depending on the quartet and the fossil calibration dates. For instance, the origin of Cnidaria is estimated to be 672 Ma if the Cubozoa had diverged by 300 Ma and the Scleractinia by 235 Ma. In contrast, the oldest inferred date for the origin of Cnidaria that does not violate the rate-homogeneity assumption is 1,811 Ma, based on the interpretation that both pennatulaceans and chondrophorines were present in the Late Neoproterozoic. Since these dates are not statistically independent of each other, it is not statistically meaningful to take their mean and standard deviation as a ''consensus'' estimate.

However, despite the scatter, the results do show general patterns. The distribution of estimates for the base of the Cnidaria is

TABLE 2—List of taxa used in this study. Accession numbers refer to the GenBank database.

Species	Major clade	Accession
Cladonema californicum	Capitata	AF358085
Millepora sp.	Capitata	AF358088
Moerisia sp.	Capitata	AF358083
Polyorchis haplus	Capitata	AF358089
Polyorchis penicillatus	Capitata	AF358090
Porpita sp.	Capitata	AF358086
Scrippsia pacifica	Capitata	AF358091
Solanderia secunda	Capitata	AJ133506
Staurocladia wellingtoni	Capitata	AF358084
Velella sp.	Capitata	AF358087
Atolla vanhoeffeni	Coronatae	AF100942
Nausithoe rubra	Coronatae	AF358095
Chironex fleckeri	Chirodropidae	AF358104
Chiropsalmus sp.	Chirodropidae	AF358103
Darwin carybdeid	Carybdeidae	AF358105
Carybdea sivickisi	Carybdeidae	AF358110
Carybdea marsupialis	Carybdeidae	AF358106
Tripedalia cystophora	Carybdeidae	L10829
Carybdea rastonii	Carybdeidae	AF358108
Carybdea xaymacana	Carybdeidae	AF358109
Carukia barnesi	Carybdeidae	AF358107
Bougainvillia sp.	Filifera	AF358093
Eudendrium racemosum	Filifera	AF358094
Podocoryne carnea	Filifera	AF358092
Anthopleura kuogane	Hexacorallia	Z21671
Anthopleura midori	Hexacorallia	Z86098
Antipathes galapagensis	Hexacorallia	AF100943
Antipathes lata	Hexacorallia	Z92907
Parazoanthus axinellae	Hexacorallia	U42453
Rhizopsammia minuta	Hexacorallia	Z92907
Chlorohydra viridissima	Hydridae	AF358081
Hydra circumcincta	Hydridae	AF358080
Hydra littoralis	Hydridae	U32392
Hydra littoralis 2	Hydridae	AF358082
Aequorea aequorea	Leptomedusae	AF358076
Aequorea victoria	Leptomedusae	AF358077
Blackfordia virginica	Leptomedusae	AF358078
Clytia sp.	Leptomedusae	AF358074
Gymnangium hians	Leptomedusae	Z86122
Melicertissa sp.	Leptomedusae	AF358075
Obelia sp.	Leptomedusae	Z86108
Selaginopsis cornigera	Leptomedusae	Z92899
Tiaropsidium kelseyi	Leptomedusae	AF358079
Craspedacusta sowerbyi	Limnomedusae	AF358057
Maeotias inexpectata	Limnomedusae	AF358056
Aegina citrea	Narcomedusae	AF358058
Cunina frugifera	Narcomedusae	AF358059
Solmissus marshalli	Narcomedusae	AF358060
Bellonella rigida	Octocorallia	Z49195
Calicogorgia granulosa	Octocorallia	Z92900
Pachycerianthus fimbriatus	Octocarallia	AF358111
Virgularia gustaviana	Octocorallia	Z86106
Catostylus sp.	Rhizostomae	AF358100
Stomolophus meleagris	Rhizostomae	AF358101
Chrysaora melanaster	Semaeostomae	AF358099
Cyanea sp.	Semaeostomae	AF358097
Pelagia colorata	Semaeostomae	AF358098
Phacellophora camtschatica	Semaeostomae	AF358096
Hippopodius hippopus	Siphonophora	AF358069
Muggiaea sp.	Siphonophora	AF358073
Nanomia bijuga	Siphonophora	AF358071
Nectopyramus sp.	Siphonophora	AF358068
Physalia physalis	Siphonophora	AF358065
Physalia utriculus	Siphonophora	AF358066
Physophora hydrostatica	Siphonophora	AF358072
Praya sp.	Siphonophora	AF358067
Sphaeronectes gracilis	Siphonophora	AF358070
Craterolophus convolvulus	Stauromedusae	AF099104
Haliclystus sanjuanensis	Stauromedusae	AF358102
Haliclystus sp.	Stauromedusae	AF099103
Crossota rufobrunnea	Trachymedusae	AF358063
Haliscera conica	Trachymedusae	AF358064
Liriope tetraphylla	Trachymedusae	AF358061
Pantachogon haeckeli	Trachymedusae	AF358062

almost bimodal (Figs. 4, 5). Estimates that do not use the Chondrophorina lie between 800 and 1,200 Ma. Those that do not include either the Cubozoa or Chondrophorina place the base of the Cnidaria between 750 and 1,000 Ma, with upper confidence limits up to 1,200 Ma and lower limits down to 700 Ma. This range of values is still very broad (the confidence limits span an interval the size of the Phanerozoic!), but is at least consistent with previous molecular estimates for the age of the Cnidaria (Table 1). On the other hand, almost all dates for the base of the Cnidaria that are based on the assumption that the Chondrophorina diverged in the Neoproterozoic or Paleozoic lie between 1,600 and 2,000 Ma, with low limits at about 1,400 Ma and high limits up to 2,400 Ma. Estimates for the Cnidaria that were calibrated using either Cubozoa at 300 Ma, or Chondrophorina at 220 Ma, fall in between these two ranges.

Dates for internal branches within the Cnidaria follow the same pattern as dates for the base of the Cnidaria: Dates based on Paleozoic and Proterozoic chondrophorines are always significantly older than dates based on any other taxa (Figs. 6, 7). For example, calibrations using chondrophorines at 555 Ma and cubozoans at 300 Ma yield an age of 1,978 Ma (+641/−457 Ma) for the Cubozoa-Hydrozoa split within the Cnidaria—which is older than most of our estimates for the age of the base of the Cnidaria. Some authors have suggested that not only were chondrophorines present in the Ediacara biota, but the two living lineages of chondrophorines, represented by the living genera *Porpita* and *Velella*, had diverged from each other by the late Neoproterozoic (e.g., Stanley, 1986). We attempted to use this as a calibration, but this violated the rate homogeneity test. However, this calibration did yield multiple estimates for the base of the Cnidaria that were consistently greater than 2,000 Ma. Our results do not support a *Porpita-Velella* divergence in the Neoproterozoic or Paleozoic.

The best-documented and least controversial fossil date in the analysis is the first fossil appearance of Scleractinia in the Middle Triassic. The statistically valid dates for the base of the Cnidaria that are based on a Triassic origin of the Scleractinia are unusually recent (649 and 527 Ma), except when both chondrophorines and Triassic scleractinians are used to calibrate the same analysis. Using both yields dates between 850 and 950 Ma for the base of the Cnidaria; apparently the effects of these two calibrations cancel each other out. Using the Triassic appearance of the Scleractinia as a calibration point yields unusually young dates for the base of the Cnidaria. However, the Scleractinia almost certainly evolved from soft-bodied sea anemones or anemone-like ancestors, and the Scleractinia-Actiniaria divergence probably happened millions of years before the first appearance of fossil scleractinian corals (Oliver, 1996). This probably explains why dates for the Cnidaria calibrated using the Middle Triassic appearance of Scleractinia are unusually young: the first appearance of scleractinian corals postdates the origin of the clade.

One way around this problem would have been to calibrate the clock using fossils of sea anemones. However, the fossil record of sea anemones is sparse and hard to interpret. We elected not to use purported soft-bodied anemone-like fossils, such as the Cambrian *Mackenzia* and the Ediacaran fossil *Inaria*, to calibrate our clock; their taxonomic position is unclear. However, a small group of Middle Ordovician corals, the Kilbuchophyllida, is thought to be a short-lived biomineralized offshoot of the lineage that gave rise to both Scleractinia and modern Actiniaria (Oliver, 1996). Assuming that kilbuchophyllids form an outgroup to both Actiniaria and Scleractinia, as implied by the phylogeny in Oliver (1996), this gives us an upper bound for the date of the Scleractinia-Actiniaria divergence. Using the Kilbuchophyllida to calibrate this divergence yields estimates for the base of the Cnidaria of 700–1,000 Ma, which are much more consistent with other

TABLE 3—Calibration points used in this study. Proterozoic and Cambrian dates from Benus (1988), Grotzinger et al. (1995) and Martin et al. (2000); others from Harland et al. (1990).

Taxon	Date	Locality	Source
Cubozoa	300 Ma	Mazon Creek, Illinois, USA: *Anthracomedusa*	Foster, 1979
Hydrozoa, Leptomedusae	510 Ma	Mt. Simon Fm, Wisconsin, USA: unnamed medusae	Gershwin et al., 2001; Hagadorn et al., 2002
Hydrozoa, Chondrophorina	220 Ma	Oldest Milleporina (sister taxon): *Heterastridium*	Stanley and Senowbari-Daryan, 1999
	400 Ma	Lower to Middle Devonian: *Plectodiscus*	Yochelson et al., 1983; Stanley, 1986
	520 Ma	Middle Cambrian: *Scenella, Gelenopteron*	Babcock and Robinson, 1988; Conway Morris, 1993
	530 Ma	Lower Cambrian: *Kullingia, Palaelophacmaea*	Stanley, 1986; Waggoner and Collins, 1995
	555 Ma	Winter Coast, White Sea, Russia: *Ovatoscutum*	Stanley, 1986; Fedonkin, 1992; Jenkins, 1992
Anthozoa, Scleractinia	235 Ma	Middle Triassic: oldest scleractinian corals	Oliver, 1996
	480 Ma	Middle Ordovician: Kilbuchophyllida	Oliver, 1996
Anthozoa, Zoantharia	520 Ma	Middle Cambrian: Cothoniida	Oliver, 1996
	530 Ma	Lower Cambrian: various Tabulaconida	Sorauf and Savarese, 1995; Oliver, 1996; Zhuravlev, 1999
Anthozoa, Pennatulacea	520 Ma	Burgess Shale, Canada: *Thaumaptilon*	Conway Morris, 1993
	565 Ma	Newfoundland: *Charnia, Charniodiscus*	Jenkins, 1985, 1992, 1996
Scyphozoa, Coronatae/Stauromedusae divergence	510 Ma	Upper Cambrian: oldest conulariids	van Iten, 1991; Hughes et al., 2000
	545 Ma	Mojave Desert, Nevada, USA: *Corumbella*	Hagadorn and Waggoner, 2000

estimates in this and other studies (Fig. 5). The Lower Cambrian corallike Tabulaconariida and Middle Cambrian Cothoniida are thought to be basal Hexacorallia (Oliver, 1996); using their ages to calibrate the clock also yields consistent dates of 700–1,000 Ma for the base of the Cnidaria.

DISCUSSION

Molecular clock analyses suffer from a number of well-known limitations that involve differential rates of molecular evolution across taxa and genomes, and in particular over time within lineages (Goodman et al., 1987; Ayala, 1997). Nevertheless, we draw two general conclusions from our results. First, choices of both fossil calibrations and taxa analyzed have a profound impact on divergence estimates based on molecular sequence data. These choices introduce inaccuracies into molecular clock analyses that are typically ignored when errors are calculated. The scatter in our results suggests that this source of error in other published studies may be substantial (see also Huchon et al., 2000, 2002). Second, our results are consistent with those of other molecular clock studies in suggesting that there is a sizable history of Metazoa that is absent from the recovered fossil record. Taphonomic hypotheses that could explain such a gap in the fossil record should be explored in greater detail.

There is certainly additional work that should be done to confirm and expand on our results. We suspect that the dates in this study are overestimates of the real branching dates; molecular clocks suffer from an inherent bias towards overestimation (Rodríguez-Trelles et al., 2002). Furthermore, in a molecular clock analysis of the divergence of the Metazoa, Bromham et al. (1998) found that dates based on 18S rRNA were considerably older, as well as being less well constrained, than dates based on mitochondrial genes. They suggested that the evolution of paired sites in rRNA was not adequately modeled by their dating method, and recommended that mitochondrial genes should be used in clock studies. Recent work by Peterson and Takacs (2002) has shown that using amino acid sequences of ''housekeeping'' genes yields clock dates that are not only younger than 18S rRNA dates, but that agree much more closely with the fossil record. We agree that other sequences may yield more accurate dates, and we hope to use other data sets in the near future to test our results. Also, relatively new methods of deriving divergence dates involving Bayesian inference (Huelsenbeck et al., 2000; Kishino et al., 2001) should be useful in future studies. These methods are in principle able to handle rate heterogeneity on all branches of a phylogeny.

TABLE 4—Taxon pairs used to calibrate the divergence dates of various higher taxa in this study.

Major taxon	Species pair
Anthozoa:	
Hexacorallia	*Parazoanthus axinellae, Rhizopsammia minuta*
Pennatulacea	*Virgularia gustaviana, Pachycerianthus fimbriatus*
Scleractinia	*Rhizopsammia minuta, Anthopleura kuogane*
Cubozoa:	*Chironex fleckeri, Tripedalia cystophora*
Hydrozoa:	
Chondrophorina	*Porpita* sp., *Millepora* sp.
Leptomedusae	*Hydra circumcincta, Melicertissa* sp.
Scyphozoa:	(1) *Haliclystus sanjuanensis, Atolla vanhoeffeni* (2) *Haliclystus sanjuanensis, Cyanea* sp.

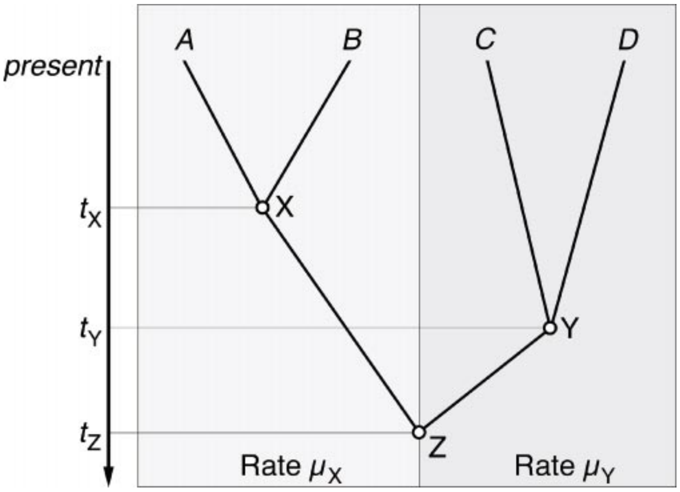

FIGURE 3—Model used by the program QDate (after Rambaut and Bromham, 1998). The divergence dates of each pair of taxa, t_x and t_y, are estimated from the fossil record. QDate then estimates t_z, the date for the basal node of the quartet, using a maximum-likelihood algorithm, under the assumption that each pair of taxa has its own mutation rate (μ_x and μ_y).

However, what is most important about our results is not so

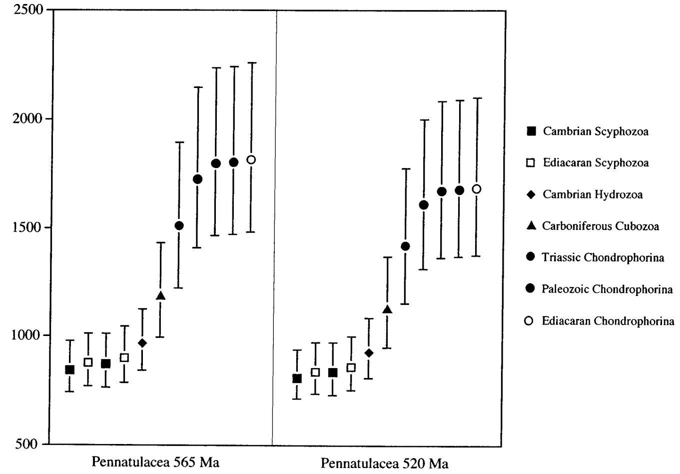

FIGURE 4—Molecular estimates for the age of the base of the Cnidaria, calibrated using Ediacaran and Cambrian ages for the Pennatulacea. One of the species pair dates for each quartet is indicated along the X-axis; the other is indicated with symbols as shown in the key. Estimates with no error bars failed the rate-heterogeneity test.

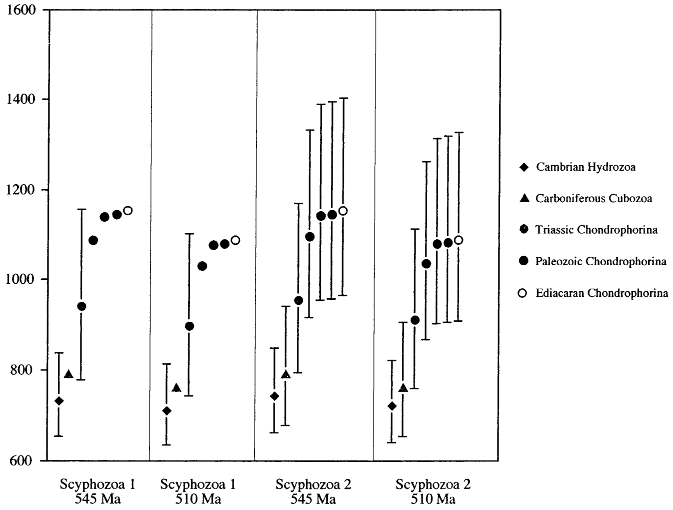

FIGURE 6—Estimates for the age of the base of the Medusozoa (i.e., Cnidaria minus Anthozoa). See Figure 4 caption for explanation of symbols.

much that they give the exact ages of basal cnidarian nodes. What is important is this: some hypotheses of what the Ediacaran fossils are lead to sets of deduced molecular dates that are both internally consistent with each other, and consistent with independent estimates based on other sequences, taxa, and calibrations. Other hypotheses of the affinity of certain Ediacaran fossils yield estimates that are neither internally nor externally consistent. We predict that molecular dates for the Cnidaria based on other sequences and algorithms will show the same pattern as our results from 18S rRNA: calibrations based on the assumption of chondrophorines in the Precambrian will be consistently older than others.

Our results do not contradict the hypotheses that pennatulaceans and scyphozoans were present in the ‘‘Ediacara biota’’ and/or in the Cambrian. In fact, pennatulaceans may not have been present as early as 565 Ma. The sea penlike forms from Mistaken Point, Newfoundland, show some striking differences, not just from pennatulaceans, but from metazoans in general (BW, personal observations, 2001). Furthermore, Dzik (2002) has argued that many of the frondlike Ediacaran forms should be considered stem-group ctenophores, not colonial cnidarians. However, moving the Pennatulacea calibration date forward from 565 million years, even well into the Cambrian, has little effect on the estimated date of divergence for the Cnidaria. On the other hand, the hypothesis of chondrophorines in the late Precambrian and Paleozoic is never supported. Calibrations using Ediacaran, Cambrian, and Devonian dates for the origin of the chondrophorines lead to age estimates for the base of the Cnidaria that are centered about 500 million years older than the most extreme previous proposal. When Cambrian and Ediacaran dates are used for the chondrophorines, the confidence limits on the basal Cnidaria date overlap with the age of the oldest known eukaryote body fossils (Han and Runnegar, 1992). In this context, it is worth noting that Fedonkin (1998) has suggested that several ovoid, strongly ribbed Ediacaran fossils, including the ‘‘chondrophorines’’ *Ovatoscutum* and *Chondroplon* as well as dickinsoniids and an undescribed taxon (informally named ‘‘*Andiva*’’), might be bilaterians with a relatively

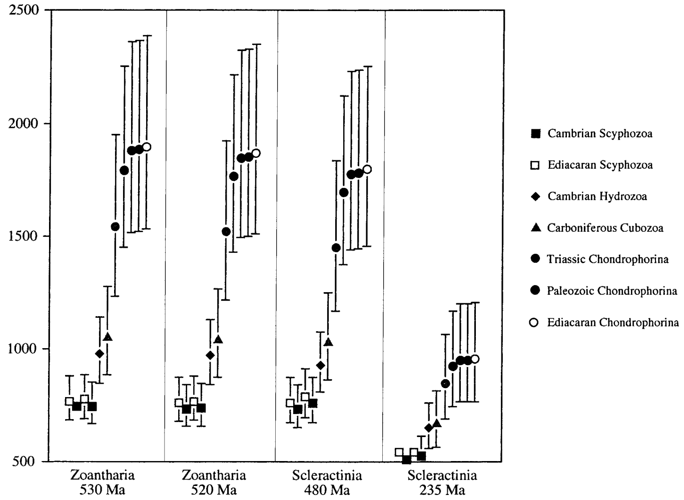

FIGURE 5—Estimates for the age of the base of the Cnidaria, calibrated using Cambrian ages for the Hexacorallia, and Devonian and Triassic ages for the Scleractinia. See Figure 4 caption for explanation of symbols.

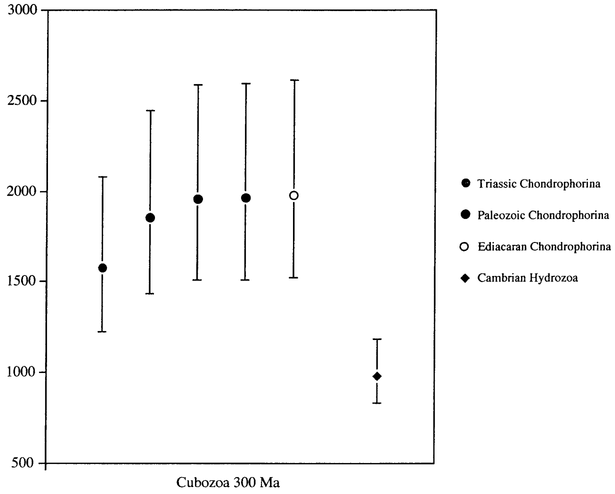

FIGURE 7—Estimates for the age of the Cubozoa-Hydrozoa split. See Figure 4 caption for explanation of symbols.

firm, segmented dorsal shield or carapace. *Eoporpita*, on the other hand, might be a benthic polyplike form. We suggest that alternative hypotheses such as these deserve closer attention.

We reiterate that molecular analyses of extant taxa, by themselves, cannot confirm or disprove hypotheses of the affinities of a problematic fossil. Only careful morphological and comparative analyses of the fossils themselves can do that. However, we believe that molecular phylogenetic dating, using the *reductio ad absurdum* approach, can provide useful information that can be brought to bear on testing the affinities of problematic fossils.

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