

Systematics of the Hexacorallia (Cnidaria: Anthozoa)

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Received January 2003; accepted for publication June 2003

The composition of and relationships among higher-level groups within the anthozoan subclass Hexacorallia (= Zoantharia) has been controversial because independent analyses of anatomy, life history, ultrastructure, and molecular sequences have failed to provide a consistent framework for drawing taxonomic boundaries or understanding phylogenetic relationships. The relationship among stony corals (order Scleractinia), sea anemones (order Actiniaria), and corallimorpharians (order Corallimorpharia) has been particularly problematic. We synthesize existing studies and provide new anatomical and molecular evidence that bear on the question of ordinal circumscription and relationships. We find that orders Actiniaria, Antipatharia, Ceriantharia, Corallimorpharia, Scleractinia, and Zoanthidea are monophyletic; Corallimorpharia is most closely related to Scleractinia. We infer that many traditional diagnostic characters are shared primitive features and thus poor indicators of phylogenetic relationships. Although the major nodes of the hexacorallian tree are well supported by multiple types of data, questions about skeletal evolution and subordinal taxonomy remain unanswered pending denser taxonomic and character sampling. © 2003 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2003, **139**, 419–437.

ADDITIONAL KEYWORDS: Actiniaria – Anthozoa – Cnidaria – combined data – evolution – Scleractinia – systematics.

INTRODUCTION

Subclass Hexacorallia (= Zoantharia) of cnidarian class Anthozoa currently contains six orders: Actiniaria (sea anemones), Antipatharia (black corals), Ceriantharia (tube anemones), Scleractinia (stony corals), Corallimorpharia (corallimorpharians), and Zoanthidea (zoanthids). A mosaic of traits not exclusive to any one group diagnoses each order (Table 1). The composition of these groups, the ranks assigned to them, and the hypothesized phylogenetic relationships among them have changed dramatically over time (McMurrich, 1891; Stephenson, 1921; Hyman, 1940; Carlgren, 1944, 1949; Berntson, France & Mullineaux, 1999). The monophyly of the two largest orders, Actiniaria and Scleractinia, has been challenged (e.g. Stephenson, 1921; Schmidt, 1974; Chen *et al.*, 1995); Corallimorpharia may also be polyphyletic (e.g. Duerden, 1900; Chen *et al.*, 1995; Pires & Castro, 1997). Ceriantharia is considered monophyl-

etic, but its relationship to other orders is obscure (Hyman, 1940; Wells & Hill, 1956; Berntson *et al.*, 1999). Recent attention to the problem of circumscription, taxonomy, and phylogeny within the Hexacorallia using molecular sequences and ultrastructural information has only increased confusion about the boundaries and histories of the various hexacorallian orders. Hypotheses and information from various sources have not been synthesized or reconciled, making it impossible to assess the state of knowledge, evaluate proposed taxonomic schemes for the Hexacorallia, or explore the evolution of major features like the scleractinian skeleton, the arrangement of mesenteries, or coloniality.

We conduct simultaneous analyses using data from anatomy, biology, ultrastructure of sperm, cnidae, life history, and molecular sequences to provide a comprehensive assessment of phylogenetic relationships among hexacorallians. The assembled matrix provides a way to explore phylogenetic relationships and character evolution, and serves as an assessment of the state of knowledge of the various hexacorallian orders. A comprehensive study of all of the relevant evidence should result in well-defined, monophyletic groups

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Table 1. Summary of the traditional diagnostic morphological features for each hexacorallian order. The characterization of scleractinians (and corallimorpharians) as lacking a marginal sphincter muscle is questionable; the manifestation of this feature is actually unknown for most species in these groups

Order	Exoskeleton	Habit	Mesenterial filament	Siphonoglyph	Marginal sphincter muscle	Mesentery arrangement
Actiniaria	Absent	Solitary or clonal	Unilobed or trilobed	None to two or more	Endodermal, mesogloal, or none	Monomorphic or dimorphic coupled pairs
Antipatharia	Proteinaceous	Colonial	Unilobed	Two	None	Monomorphic coupled pairs
Ceriantharia	Absent	Solitary	Trilobed	One	None	Monomorphic couples
Corallimorpharia	Absent	Solitary or clonal	Unilobed	None	None??	Monomorphic coupled pairs
Scleractinia	Calcareous	Solitary or colonial	Unilobed	None	None??	Monomorphic coupled pairs
Zoanthidea	Absent	Solitary or colonial	Trilobed	One	Endodermal, mesogloal, or none	Dimorphic coupled pairs

(Kluge, 1989; Nixon & Carpenter, 1996). Because taxonomy is increasingly expected to represent or accommodate historical relationships between taxa (e.g. de Queiroz & Gauthier, 1992), phylogenetic and taxonomic issues are explored simultaneously. We find that although the trees resulting from independent analyses of each type of data set differ, the phylogenetic signals of the morphological, 16S, 18S, and 28S sequence data are congruent. We infer from the combined molecular and morphological data that Corallimorpharia and Scleractinia form a clade to the exclusion of Actiniaria. Many subordinal groups, especially within the Scleractinia, are para- or polyphyletic, confounding comparisons between our results and hypotheses that use higher level taxonomic groups as terminal taxa.

HEXACORALLIAN MORPHOLOGY AND TAXONOMY

Despite the basic structural simplicity imposed by the absence of organs or organ systems, the anatomy of hexacorallian polyps can be quite complex (e.g. Fautin & Mariscal, 1991). The cylindrical polyp is closed on the distal end by the oral disc; the proximal end may be an adhesive pedal disc, a rounded physa, or a thin sheet of tissue that lines the skeletal cup. The oral disc is perforated by a central mouth that leads to a tubular actinopharynx; the actinopharynx varies in length but never extends the length of the column. The internal cavity, or coelenteron, is divided by mesenteries, sheets of tissue that extend from the column wall. The term 'septa', which is sometimes used instead of 'mesenteries', should be reserved for

the calcareous, radial projections that flank the mesenteries of scleractinians (Vaughan & Wells, 1943; Bayer, Grasshoff & Verseveldt, 1983). Mesenteries that extend from column wall to actinopharynx are termed perfect (or complete); imperfect (incomplete) mesenteries do not extend all the way to the actinopharynx (Fig. 1). In some orders, mesenteries are added simultaneously in series called cycles; mesenteries of different cycles may differ in morphology. The free edge of the mesentery is elaborated into a unilobed or trilobed mesenterial filament that bears gland cells and cnidae.

Cnidae are the defining characteristic of phylum Cnidaria, and are especially important in anthozoan taxonomy (Doumenc & Van Praët, 1987; Fautin, 1988; Fautin & Mariscal, 1991). The diversity of nematocysts is greatest within Hydrozoa, but Anthozoa is characterized by the greatest degree of cnidae diversity, as its members have two types of cnidae in addition to nematocysts (Watson & Wood, 1988; Fautin & Mariscal, 1991). Spirocysts have a tubule with thread-like mini-tubules that entwine prey or other objects; these cnidae have been described as restricted to Hexacorallia (e.g. Mariscal, 1974). Ptychocysts have an unarmed tubule that is pleated rather than helically folded; these cnidae are found only in ceriantharians, and are used in the construction of their felt-like tube (Mariscal, Conklin & Bigger, 1977). The morphology, size, and distribution of nematocysts are used to define groups, particularly within Actiniaria and Corallimorpharia, in which attributes of cnidae characterize families, genera, or species (e.g. Carlgren, 1940, 1945; Allcock, Watts & Thorpe, 1998).

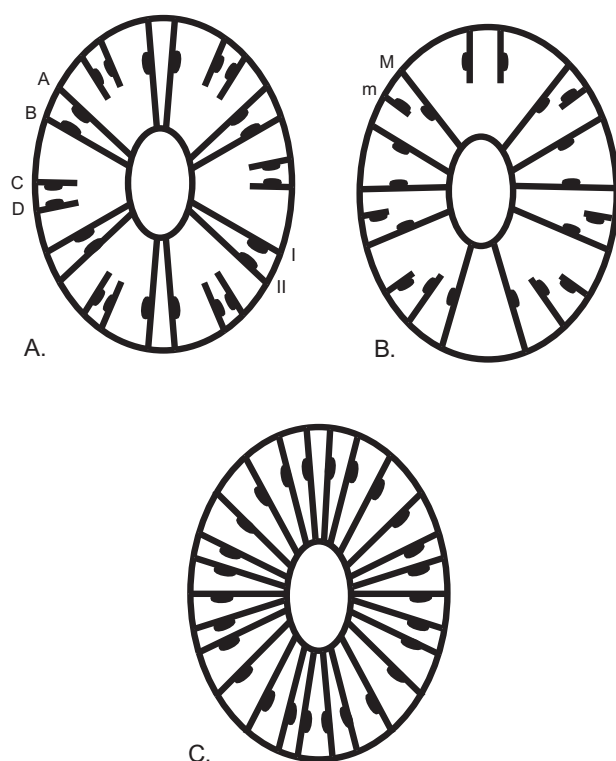


Figure 1. Schematic cross-section through hexacorallians at the level of the actinopharynx, showing arrangement of mesenteries. The radial lines represent mesenteries, the central oval represents the actinopharynx. The filled oval on each mesentery represents the retractor muscle. A, hexamerously arranged, paired, coupled mesenteries typical of Actiniaria, Scleractinia, and Corallimorpharia. Mesenteries labelled A, B, I, and II are perfect; C and D are imperfect. A and B, C and D, and I and II are paired; I and II are coupled with A and B. B, hexamerously arranged, paired, coupled mesentery arrangement typical of Zoanthidea. Mesenteries labelled M and m are part of a dimorphic pair; the macrocneme (M) is larger than microcneme (m). C, unpaired, coupled arrangement typical of Ceriantharia. In ceriantharians, the longitudinal muscle of the mesentery is not hypertrophied into a separate retractor muscle; the filled ovals indicate the surface of the mesentery on which the longitudinal muscle fibres run.

Despite the apparent simplicity of these features, their diversity has not been adequately described. Cappola & Fautin (2000) found that Ptychodactiaria belongs within Actiniaria, and concluded that the separation of order Ptychodactiaria was based on misconceptions about the anatomy and histology of ptychodactiarians. Internal anatomy and histology are virtually unknown for most scleractinians and antipatharians (e.g. Moseley, 1881; Duerden, 1902b; Grigg & Opresko, 1977; Lang, 1984). Anatomy and life history can be difficult to interpret as both can be

influenced by environmental and ecological factors (Carlgren, 1942; Veron, 1995; Chen, Willis & Miller, 1996; Miller & Babcock, 1997). Species descriptions of actiniarians, ceriantharians, corallimorpharians, and zoanthideans generally include an inventory of the types of cnidae (= cnidom); although the cnidom is unknown for most species of scleractinians, it has been detailed in a few systematic works (e.g. Carlgren, 1940, 1945; Schmidt, 1972, 1974; den Hartog, 1980; Hidaka, 1992; Pires, 1997; Pires & Castro, 1997).

Most of the traditional diagnostic features of each order are inapplicable to members of other hexacorallian groups, complicating the assessment of shared history among hexacorallians (Lang, 1984). The calcareous exoskeleton defines Scleractinia, and its variation is the basis of intra-ordinal taxonomy (e.g. Wells, 1956); it has no homologue in the other orders. Among the soft-bodied forms, taxonomy focuses on exclusive features such as the mesenterial arrangement of zoanthideans or cnidae and cnidae-bearing structures of Ceriantharia (e.g. Herberts, 1987; Tiffon, 1987).

Comparison across hexacorallian orders is further complicated by terminology. Terms describing modes of asexual reproduction are not standardized (Fautin, 2002). Budding is used as a general term for scleractinian asexual reproduction and to describe several specialized modes of asexual reproduction in particular scleractinians (e.g. Kramarsky-Winter & Loya, 1996), corallimorpharians (e.g. Chadwick-Furman & Spiegel, 2000), and zoanthideans (e.g. Ryland, 1997a). Although given different names, the process of longitudinal fission in actiniarians and corallimorpharians closely parallels the process of extratentacular budding in scleractinians (Cairns, 1988).

The nomenclature of cnidae is similarly problematic; terms referring to a type of nematocyst with an abrupt transition between the basal and distal tubule include 'penicillus' (e.g. Stephenson, 1929; den Hartog, 1980), 'p-mastigophore' (e.g. Weill, 1934; Carlgren, 1940; Cutress, 1955; Mariscal, 1974), and 'p-rhabdoid' (e.g. Schmidt, 1969, 1974; Pires & Castro, 1997).

Hexacorallian phylogeny is unresolved not simply because of character incompatibility or terminological imprecision, but because basic anatomical features do not circumscribe the same exclusive groups (Table 1). For example, mesenterial filament histology links zoanthideans and actiniarians; mesentery arrangement groups actiniarians with scleractinians and corallimorpharians. The boundaries and ranks of higher-level hexacorallian groups have shifted with focus on different subsets of these characters. The seemingly mosaic distribution of some biological traits may reflect ecological plasticity or some other external influence, or may indicate that certain groups as currently constituted are heterogeneous.

ACTINIARIA, CORALLIMORPHARIA, AND SCLERACTINIA

Much of the confusion about ordinal relationships centres on the two largest orders, Actiniaria and Scleractinia, and their relationship to Corallimorpharia. Members of Corallimorpharia have attributes of both Actiniaria and Scleractinia. Corallimorpharia has been considered the sister-group to Scleractinia (e.g. Duerden, 1898), a subgroup within Actiniaria (e.g. Stephenson, 1921), and a separate group, equal in rank to Actiniaria and Scleractinia (e.g. Carlgren, 1942, 1949).

A corallimorpharian polyp resembles an actinarian in lacking an external or internal skeleton. The tentacle arrangement of a corallimorpharian is similar to that of an anemone in the family Stichodactylidae, in that multiple tentacles arise from the space between members of a mesenterial pair (Duerden, 1898; den Hartog, 1980; Dunn, 1981); more typically in hexacorallians, a single tentacle arises from each intermesenterial space (Stephenson, 1921, 1928). Duerden (1898, 1900) considered corallimorpharians closely related to stichodactylid anemones; within his Stichodactylinae, he recognized similarities in tentacle arrangement and morphology between corallimorpharian genera such as *Ricordea* and actinarian genera such as *Stoichactis* (now termed *Stichodactyla*) not shared with other corallimorpharians like *Corynactis* or *Rhodactis*. Stephenson (1921) noted that internal anatomy of *Corynactis*, *Rhodactis*, and *Ricordea*, although within the range of variation seen among actinarians, was unlike that of *Stoichactis* and other stichodactylid anemones, and suggested that they be considered Madreporaria (= Scleractinia) of unknown affinity. Carlgren (1942) used differences in histology to justify removing *Corynactis*, *Rhodactis*, *Ricordea*, and other corallimorpharians from Stichodactylidae, creating the order Corallimorpharia.

With respect to internal anatomy and histology, a corallimorpharian polyp resembles a scleractinian polyp in having a unilobed mesenterial filament, lacking basilar muscles, and, in most species, lacking a marginal sphincter muscle (den Hartog, 1980; Dunn, 1982). Additionally, the cnidom of corallimorpharians is more like that of scleractinians: both scleractinians and corallimorpharians bear holotrichous nematocysts in the tentacles (Duerden, 1898; Stephenson, 1921; den Hartog, 1980; Pires & Castro, 1997); these holotrichs are of a size and morphology not generally found in Actiniaria and entirely absent in Stichodactylidae (Dunn, 1981).

Corallimorpharia and Scleractinia have been separated primarily because a corallimorpharian does not secrete a skeleton (Hertwig, 1882a,b; Duerden, 1898; Stephenson, 1921). The calcareous exoskeleton has been regarded as a necessary and sufficient criterion

for membership in Scleractinia; all extant hexacorallian species with a calcareous exoskeleton belong to Scleractinia. However, the skeleton may have arisen multiple times, and may not be homologous between major clades of corals (Fautin & Lowenstein, 1994; Romano & Palumbi, 1996; Romano & Cairns, 2000; Stanley & Fautin, 2001). The phylogenetic value of the calcareous skeleton has been re-evaluated in other cnidarian groups: all hydrozoans with a calcareous exoskeleton were initially grouped together in Hydrocorallina, but its constituent groups Milleporina and Stylasterina are now considered more closely related to skeletonless taxa than to one another, indicating that calcareous skeletons have been lost or have evolved independently (Petersen, 1979). Similarly, Foraminifera, previously thought to include only shelled amoebae, includes naked species (Pawlowski *et al.*, 1999).

STRATEGIES AND SOLUTIONS

Higher-level systematics within the morphologically simple Hexacorallia has been re-invigorated by the advent of technologies that provide additional characters for phylogenetics and taxonomy. Molecular sequence and protein data have been used to assess phylogenetic relationships among hexacorallian subclasses (France *et al.*, 1996; Berntson *et al.*, 1999; Won, Rho & Song, 2001), orders (Fautin & Lowenstein, 1994; Chen *et al.*, 1995; Song & Won, 1997; Daly, Lipscomb & Allard, 2002), and families (Romano & Palumbi, 1996; Chen *et al.*, 1996; Romano & Cairns, 2000; Chen, Wallace & Wolstenholme, 2002). Ultrastructure and cnidae have been explored in the context of intra- and interordinal relationships (Schmidt, 1972, 1974; Schmidt & Zissler, 1979; den Hartog, 1980; Steiner, 1993; Pires, 1997; Pires & Castro, 1997; Harrison & Jamieson, 1999). Because gene sequences, protein similarity, and ultrastructural features of sperm and nematocysts are potentially available for all hexacorallians, these kinds of data circumvent the problem of incompatibility that plague traditional diagnostic features.

Despite the promise of these new technologies, molecular and ultrastructural data have proven no better than anatomy or life history at resolving phylogenetic or taxonomic problems within Anthozoa. For example, Ceriantharia was recognized as a third anthozoan subclass (either alone or combined with Antipatharia into subclass Ceriantipatharia) because its members are morphologically and developmentally unlike other hexacorallians (Hyman, 1940; Wells & Hill, 1956). Evidence from gene sequences (Berntson *et al.*, 1999) and from ultrastructure (Schmidt, 1974; Mariscal *et al.*, 1977; Schmidt & Zissler, 1979) confirms the distinctiveness of ceriantharians but offers

few clues to their kinship. Sequences of nuclear large subunit ribosomal genes (28S) were interpreted by Chen *et al.* (1995) as supporting corallimorpharian polyphyly. Sequences from other nuclear (18S) and mitochondrial (16S) ribosomal genes have been construed as supporting Corallimorpharia as a grade most closely related to a monophyletic Scleractinia (Berntson *et al.*, 1999; Romano & Cairns, 2000), or as supporting a monophyletic Corallimorpharia within a polyphyletic Scleractinia (Daly *et al.*, 2002). There is no way to arbitrate among these conflicting results because no character or character system performs significantly better than any other, and no character is free from concern about homoplasy. Although molecular data are not as obviously influenced by ecological or environmental factors as some morphological characters, gene evolution is not free from constraint (e.g. Brown *et al.*, 1982; Swofford *et al.*, 1996). Furthermore, the independence of each ultrastructural detail or of each position within a particular region of a gene is poorly understood. Sperm morphology may be correlated with reproductive mode rather than phylogeny; in general, the sperm of brooding species of Scleractinia differs in structure and morphology from that of broadcast spawning species (Harrison & Jamieson, 1999). Finally, ultrastructural and sequence data alone are inappropriate for redefining taxonomic boundaries because these features are not readily evaluated, are unknown for many species, and are not accessible to many of the people who use taxonomy.

MATERIAL AND METHODS

MORPHOLOGICAL CHARACTERS

All the anatomical and biological attributes in our morphological data set have been used to diagnose or differentiate higher taxa within the Hexacorallia. Coloniality and possession of algal symbionts are commonly used taxonomic characters within Scleractinia (Wells, 1956; Veron, 1995, 2000a); clonality is potentially important in Actiniaria (Fautin & Smith, 1997; Pearse & Francis, 2000; Geller & Walton, 2001). Although life history is typically constant within species (but see Glynn *et al.*, 1996), life history characteristics like sexuality, mode of gamete release, and methods of asexual reproduction may vary within genera or families (e.g. Dunn, 1982; Veron, 1995; Pearse, 2002).

The shape of a colony, method of colony formation, and attributes of the individual calices are the basis of scleractinian taxonomy (e.g. Wells, 1956; Veron, 1995, 2000a; Wallace, 1999). Because skeletal characteristics have no homologue in the other hexacorallian orders, these features may seem ill-suited to analyses

of relationships between scleractinians and soft-bodied hexacorallians. However, because skeletal features figure prominently in hypotheses of coral evolution (Wells, 1956; Scrutton & Clarkson, 1991; Veron, 1995), and in scenarios relating scleractinians to actiniarians and corallimorpharians (Hand, 1966; Fautin & Lowenstein, 1994; Stanley & Fautin, 2001), we include them in our analyses.

TAXA

We gathered morphological data for hexacorallians for which two of the three most commonly sequenced genes (16S, 18S, and 28S) are available in GenBank (Table 2). To minimize the effect of this restriction on our taxonomic sample, we concatenated sequences for different genes from two members of a genus into a single row of data when sequences were not available for the same species. We sequenced 16S, 18S, and 28S genes for a few species whose phylogenetic positions have been uncertain (Table 2). All putative hexacorallian orders are represented by two or more exemplars.

Although hexacorallian monophyly is well established (Schmidt, 1974; France *et al.*, 1996; Berntson *et al.*, 1999), basal relationships within the subclass are unclear. We used *Alcyonium* and *Virgularia*, members of Alcyonaria, the sister-subclass of Hexacorallia, as outgroups. Alcyonarians and hexacorallians differ sufficiently in morphology that the correspondence of structures is difficult to assess.

MATRIX AND ANALYSIS

The combined matrix includes 782 characters that are parsimony-informative for these 48 hexacorallians (Table 3): 436 sites in mitochondrial 16S rDNA, 222 sites in 18S rDNA, 62 sites in nuclear 28S rDNA, and 55 morphological features. The anatomical, biological, and ultrastructural data were taken primarily from species descriptions. We made and examined histological sections of many species included in this analysis to supplement or confirm published information. The incompleteness of the morphological matrix (Table 3) reflects our understanding of hexacorallian anatomy and biology; this list will be amended, refined, and broadened as data accumulate on character systems common to all hexacorallians.

Our 16S rDNA alignment builds on that of Romano & Cairns (2000); our 18S rDNA alignment builds on that of Daly *et al.* (2002). The 28S rDNA sequences were aligned using the program DAPSA (Harley, 1996), which was also used to adjust the 16S and 18S alignments to accommodate additional taxa.

The combined matrix was analysed using the 'island-hopping' algorithms (Nixon, 1999a) in NONA (Goloboff, 1995). These algorithms allow many

Table 2. Taxa included in the study, with GenBank accession numbers for sequences used. Genera marked with an asterisk are represented by multiple species. Higher taxonomic categories are from Wells (1956) Dunn (1982), and Cappola & Fautin (2000). Carlgren (1949) used 'tribe' to refer to groups of families within Actiniaria; actiniarian tribes are thus equivalent to suborders or superfamilies

Order	Suborder or Tribe	Family	Genus	16S	18S	28S
Actiniaria	Acontiaria	Aiptasiidae	<i>Aiptasia</i>	AY345875	AY046885	U69684
Actiniaria	Endomyaria	Actiniidae	<i>Anemonia</i> *	–	X53498	U69685
Actiniaria	Endomyaria	Actiniidae	<i>Anthopleura</i>	AF375815	Z21671	–
Actiniaria	Endomyaria	Actiniidae	<i>Bunodosoma</i> *	AF375814	U52974	–
Actiniaria	Ptychodacteae	Preactiidae	<i>Dactylanthus</i>	AY345877	AF052896	AY345873
Actiniaria	Athenaria	Edwardsiidae	<i>Edwardsia</i>	–	AF254376	AY345870
Actiniaria	Acontiaria	Metridiidae	<i>Metridium</i>	AF000023	U19550	–
Actiniaria	Athenaria	Edwardsiidae	<i>Nematostella</i>	–	AF254382	AY345871
Actiniaria	Endomyaria	Stichodactylidae	<i>Stichodactyla</i> *	AY345874	U52977	U69687
Actiniaria	Endomyaria	Actiniidae	<i>Urticina</i>	U91750	–	AY345872
Antipatharia	–	Antipathidae	<i>Antipathes</i>	–	AF100943	AY026365
Antipatharia	–	Antipathidae	<i>Stichopathes</i>	U40286	AF052899	–
Ceriantharia	–	Cerianthidae	<i>Ceriantheopsis</i>	U40289	AF052898	–
Ceriantharia	–	Cerianthidae	<i>Cerianthus</i>	U40288	AF052897	–
Corallimorpharia	–	Actinodiscidae	<i>Amplexidiscus</i>	AY345878	–	U69692
Corallimorpharia	–	Corallimorphidae	<i>Corynactis</i> *	U40293	AF052895	U69689
Scleractinia	Faviina	Anthemiphylliidae	<i>Anthemiphyllia</i>	AF265596	–	AF265652
Scleractinia	Dendrophylliinae	Dendrophylliidae	<i>Balanophyllia</i> *	AF265587	U52973	AF265626
Scleractinia	Caryophylliina	Caryophylliidae	<i>Caryophyllia</i>	AF265599	–	AF265642
Scleractinia	Caryophylliina	Caryophylliidae	<i>Catalaphyllia</i>	L76000	–	AF265637
Scleractinia	Faviina	Faviidae	<i>Cladocora</i>	AF265612	–	AF265633
Scleractinia	Caryophylliina	Caryophylliidae	<i>Crispatotrochus</i>	AF265600	–	AF265640
Scleractinia	Faviina	Meandrinidae	<i>Dichocoenia</i>	AF265607	–	AF265635
Scleractinia	Dendrophylliinae	Dendrophylliidae	<i>Enalllopsammia</i>	U40294	–	AF052885
Scleractinia	Caryophylliina	Flabellidae	<i>Flabellum</i>	AF265582	–	AF265649
Scleractinia	Fungiina	Fungiidae	<i>Fungia</i>	L76005	AF052884	AF265631
Scleractinia	Fungiina	Poritidae	<i>Goniopora</i> *	L76008	–	U65515
Scleractinia	Faviina	Merulinidae	<i>Hydnophora</i>	L76009	–	U65526
Scleractinia	Dendrophylliinae	Dendrophylliidae	<i>Leptopsammia</i>	AF265579	–	AF265628
Scleractinia	Faviina	Mussidae	<i>Lobophyllia</i>	L76013	–	AF265624
Scleractinia	Caryophylliina	Flabellidae	<i>Monomyces</i>	AF265583	–	AF265651
Scleractinia	Faviina	Oculinidae	<i>Oculina</i>	AF265601	–	AF265636
Scleractinia	Caryophylliina	Caryophylliidae	<i>Paracyathus</i>	AF265603	–	AF265644
Scleractinia	Fungiina	Agaraciidae	<i>Pavona</i>	L76016	AF052883	AF263350
Scleractinia	Faviina	Rhizangiidae	<i>Phyllangia</i>	AF265605	AF052887	AF265641
Scleractinia	Caryophylliina	Flabellidae	<i>Placotrochus</i>	AF265589	–	AF265650
Scleractinia	Faviina	Faviidae	<i>Platygyra</i>	AF265611	–	AF263361
Scleractinia	Caryophylliina	Caryophylliidae	<i>Polycyathus</i>	AF265606	–	AF265643
Scleractinia	Fungiina	Poritidae	<i>Porites</i>	L76020	–	AF265630
Scleractinia	Dendrophylliinae	Dendrophylliidae	<i>Rhizopsammia</i>	–	Z92907	AF265629
Scleractinia	Astrocoeniina	Astrocoeniidae	<i>Stephanocoenia</i> *	AF265582	–	AF265623
Scleractinia	Caryophylliina	Caryophylliidae	<i>Thalamophyllia</i>	AF265590	–	AF265638
Scleractinia	Dendrophylliinae	Dendrophylliidae	<i>Tubastraea</i>	L76022	Z92906	AF265625
Scleractinia	Dendrophylliinae	Dendrophylliidae	<i>Turbinaria</i>	AF265609	–	U65513
Scleractinia	Caryophylliina	Caryophylliidae	<i>Vaughanella</i>	AF265595	–	AF265646
Scleractinia	Fungiina	Fungiidae	<i>Zoopilus</i>	L76024	–	AF265632
Zoanthidea	Brachycnemina	Sphenopidae	<i>Palythoa</i> *	AF282932	AF052892	–
Zoanthidea	Macrocnemina	Parazoanthidae	<i>Parazoanthus</i>	AF398921	U42453	–

Table 3. Morphological characters used in this study. Characters are given for genera listed in Table 2; a dash indicates that the state assignment for a particular character is unknown or inapplicable for a given taxon. Genera are grouped by order; within each order, genera are listed alphabetically

	1-10	11-20	21-30	31-40	41-50	51-56
Actiniaria						
<i>Aiptasia</i>	2--1110100	0-0001-110	10011--011	11-100----	--01100001	100011
<i>Anemonia</i>	00-0110100	-001010110	1000111101	111100----	--11100001	-----
<i>Anthopleura</i>	2000110100	0001111110	1000111101	111100----	--11110001	010010
<i>Bunodosoma</i>	2000110100	0001011110	1000111101	111100----	--11110001	010010
<i>Dactylanthus</i>	0--00-0-01	-000011110	1010011100	01--00----	--10000001	-----
<i>Edwardsia</i>	0000000100	1000001111	000011-001	022100----	--01100001	000001
<i>Metridium</i>	2000010110	0100010110	1001101011	111100----	--01100--1	010011
<i>Nematostella</i>	0001000100	1000001111	000011-001	022100----	--01100001	000001
<i>Stichodactyla</i>	2--0110111	-000111110	1000111101	111-00----	--01100001	-----
<i>Urticina</i>	01-0000100	-000110110	1000101100	111100----	--01-10--1	010010
Antipatharia						
<i>Antipathes</i>	1010--0000	-00001-1-0	00000--00-	000-020---	--1---0--1	110001
<i>Stichopathes</i>	1010--0000	-00001-1-0	00000--00-	000-020---	--1---0--1	110001
Ceriantharia						
<i>Ceriantheopsis</i>	0-1--010-0	-00000010-	010011-002	0--000----	--10101001	010011
<i>Cerianthus</i>	0-1--010-0	-00000010-	010011-002	0--000----	--10101001	010011
Corallimorpharia						
<i>Amplexidiscus</i>	0-00100011	000002-110	10000--001	000000----	--11100001	-----
<i>Corynactis</i>	2000-10110	101002-110	10000--102	000000----	--11100111	011111
Scleractinia						
<i>Anthemiphyllia</i>	0--0000100	--1002-110	10000--00-	000-01110-	42----0--1	-----
<i>Balanophyllia</i>	0100000100	--1002-110	10000--00-	000-01110-	5211100111	0111-1
<i>Caryophyllia</i>	000-000100	--1002-111	10000-----	000-01110-	0011100--1	-----
<i>Catalaphyllia</i>	1--01-0100	-01002-110	10000--00-	000-010000	32----0--1	-----
<i>Cladocora</i>	1---1-010-	--1002-110	10000-----	01--011104	-2111-0--1	01111-
<i>Crispatotrochus</i>	0---0-010-	--1002-110	10000-----	01--01110-	52----0--1	-----
<i>Dichocoenia</i>	1---120110	--1002-110	10000-----	01--011003	21----0--1	-----
<i>Enallopsammia</i>	1--0-10-00	--1002-110	10000--00-	000-010101	3----0--1	-----
<i>Flabellum</i>	0---0-0100	--1002-111	10000-----	00--01100-	4011100--1	-----
<i>Fungia</i>	0-00--0101	2-1002-110	10000--00-	000-01110-	4211100111	001111
<i>Goniopora</i>	110-110100	--1002-110	10000-----	00--011-03	00111-0--1	0-----
<i>Hydnophora</i>	1-1-12010-	--1002-110	10000-----	00--011-01	22----0--1	-----
<i>Leptopsammia</i>	0---0-010-	--1002-110	10000-----	00--01110-	52111-0--1	-----
<i>Lobophyllia</i>	101-12010-	--1002-111	10000-----	00--011-0-	22----0--1	-----
<i>Monomyces</i>	0---0-010-	--1002-110	10000-----	00--011-0-	5----0--1	-----
<i>Oculina</i>	1--0110100	--1002-110	10000--00-	000-011101	12----0--1	-----
<i>Paracyathus</i>	0---0-010-	--1002-110	10000-----	00--011104	12----0--1	-----
<i>Pavona</i>	10-0120100	--1002-110	10000--00-	000-01--02	0--1100--1	011111
<i>Phyllangia</i>	1--0010100	--1002-110	10000--00-	000--11100	1211100--1	-----
<i>Placotrochus</i>	----0-010-	--1002-110	10000-----	00--01--0-	-----0--1	-----
<i>Platygyra</i>	1-101-0100	--1002-110	10000--00-	000-011100	22----0--1	011111
<i>Polycyathus</i>	1---01010-	--1002-110	10000-----	00--011104	12----0--1	-----
<i>Porites</i>	1-00110100	--1002-110	00000--00-	000-01--01	0111100101	111101
<i>Rhizopsammia</i>	1--0010100	--1002-110	10000--00-	000-011000	1211100--1	-----
<i>Tubastraea</i>	1-10010100	--1002-110	10000--00-	000-011100	121---0101	-----
<i>Turbinaria</i>	100-1-0110	--1002-110	10000-----	00--011-02	1----0--1	011111
<i>Thalamophyllia</i>	0---0-010-	--1002-110	10000-----	00--01010-	5----0--1	-----
<i>Vaughanella</i>	0---0-010-	---002-110	10000-----	00--01110-	52----0--1	-----
<i>Zoopilus</i>	1---12010-	--1002-110	10000-----	00--01-103	02111-0--1	-----
Zoanthidea						
<i>Palythoa</i>	1-10130100	-00000-111	12001--011	001110----	--11100001	010001
<i>Parazoanthus</i>	1-00130100	-00000-111	12001--101	001110----	--1--00001	100001

topologies to be sampled, and thus approximate an exhaustive search (Nixon, 1999b). We ran four replications of 1000 iterations, using a random seed tree and sampling 78 characters (10% of the matrix). Two trees were held at each step. Character evolution was explored using Winclada (Nixon, 1999a). Combined evidence trees were compared to trees supported by each single data set. To examine whether any subset contains a phylogenetic signal that differs significantly from that of the combined matrix, we used tests of incongruence-length differences (Farris *et al.*, 1994; 100 replicates, maximum trees held 100 000).

RESULTS

All 12 primary trees ($L = 3501$; $CI = 0.62$; $RI = 0.64$) agree on the monophyly of each hexacorallian order as currently defined (Figs 2, 3). We found no significant difference in phylogenetic signal between the combined data set and the morphological, 16S, 18S, or 28S subsets.

The subclass Hexacorallia and each of its constituent orders is monophyletic. Monophyly of the subclass Hexacorallia is supported by 22 18S substitutions and two morphological characters: trilobed mesenterial filaments and solitariness. The most basal group within Hexacorallia is the Ceriantharia; members of this order share non-retractile tentacles arranged in labial and marginal cycles, ptychocysts, and 25 18S substitutions. The monophyly of the sister-group to Ceriantharia, a clade containing all other hexacorallian orders, is supported by nine 18S substitutions, microbasic *p*-mastigophores, and paired mesenteries. Actiniaria is the only order characterized solely by molecular data; the putative order Ptychodactaria lies within Actiniaria. Zoanthidea is characterized by dimorphic mesentery pairs, mesogloal canals, mesenteries added only in the ventrolateral exocoels, and 54 molecular substitutions. Antipatharia is characterized by a proteinaceous skeleton, non-retractile polyps, spherically headed sperm, and eight molecular substitutions. Corallimorpharia is characterized by having multiple tentacles per endocoel and 16 molecular substitutions. Scleractinia is characterized by a calcareous exoskeleton with a columella, macrobasic *p*-mastigophores in the filaments, and 20 molecular substitutions. Additionally, the scleractinians included in this study share a sequence inversion (not coded separately from the rest of the alignment) at position 148 in the 28S alignment; this three-base segment, read as 'CCT' in scleractinians and as 'TCC' in all other hexacorallians, is flanked by conserved sequences.

Based on these data, Hexacorallia is divisible into at least two major clades, Actiniaria and Zoanthidea–Antipatharia–Corallimorpharia–Scleractinia. Although no

morphological features characterize the large clade, it is supported by substitutions in both the 16S and the 18S genes. Monophyly of the clade containing Antipatharia, Scleractinia, and Corallimorpharia is supported by 14 molecular substitutions, unilobed mesenterial filaments, and weak parietal muscles. Scleractinia and Corallimorpharia group to the exclusion of Antipatharia based on 42 molecular substitutions, a paired secondary cycle of mesenteries, and sperm in which the centriolar complex has parallel proximal and distal centrioles linked by a centriolar ligament.

Scleractinia contains two groups that have been called the 'complex' and 'robust' clades (e.g. Romano & Palumbi, 1996; Romano & Cairns, 2000; Chen *et al.*, 2002; Fig. 3). Although the names refer to skeletal attributes, only molecular substitutions unambiguously support these clades in our analysis: the robust clade is characterized by three 16S and two 28S substitutions; the complex clade is united by 11 16S and three 28S substitutions.

Actiniaria contains three clades, roughly corresponding to the groups Carlgren (1949) referred to as the Endomyaria (*Actinia*, *Anemonia*, *Anthopleura*, *Bunodosoma*, *Stichodactyla*, *Urticina*, and the ptychodactarian *Dactylanthus*), Acontiaria (*Metridium* and *Aiptasia*), and Edwardsiidae (*Edwardsia* and *Nematostella*) (Figs 2, 3). The endomyarian clade includes actinarians that have an endodermal marginal sphincter muscle (or no sphincter); this clade is further characterized by asymmetrical sperm and one 18S substitution. Most endomyarians included in this analysis are members of the largest family of actinarians, Actiniidae; Actiniidae is polyphyletic with respect to the ptychodactarian *Dactylanthus* and the stichodactyline *Stichodactyla*. The possession of acontia – nematocyst-packed threads borne on the edge of some mesenteries – is unique to the members of the acontiarian clade. Members of the acontiarian clade also share a mesogloal marginal sphincter muscle, and eight 18S substitutions. The members of Edwardsiidae share relatively longer tentacles in the outermost cycle, fertile directive mesenteries, restricted retractor and parietal muscles, sperm without a nuclear depression, and five 18S substitutions.

DISCUSSION

PHYLOGENETIC RELATIONSHIPS

The proposed sister-group relationship for Zoanthidea–Antipatharia–Scleractinia–Corallimorpharia contradicts much of the historical literature that groups Actiniaria, Corallimorpharia, and Scleractinia. Antipatharians are poorly known, and have been presumed to be primitive hexacorallians,

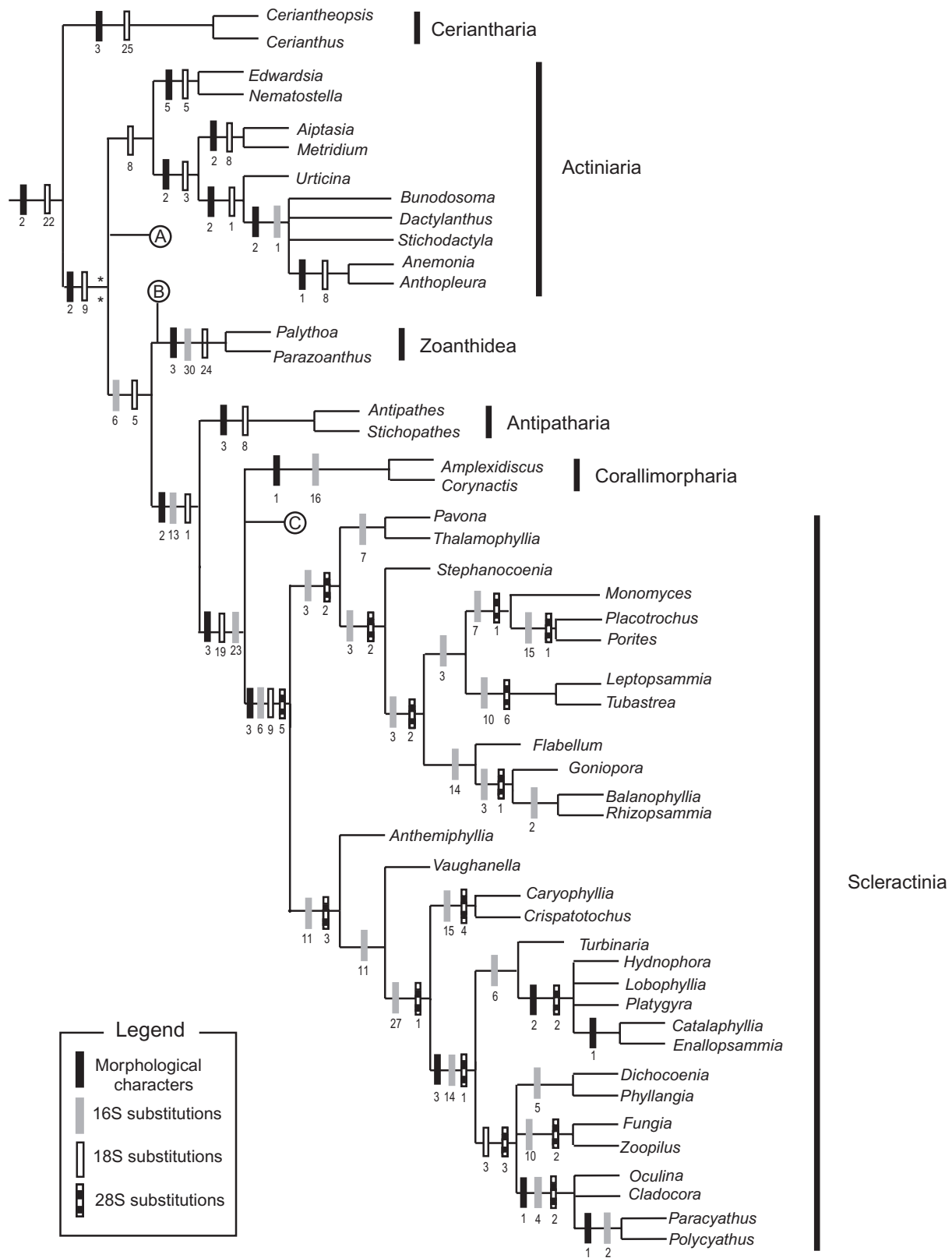


Figure 2. Strict consensus of 12 equally parsimonious trees ($L = 3510$; $CI = 0.62$; $RI = 0.64$), with number and types of characters unambiguously supporting each node indicated. Asterisks and lettering of branches relate to discussion of skeletal evolution in the text. Ordinal groups are labelled; more detailed taxonomic information is given in Table 2.

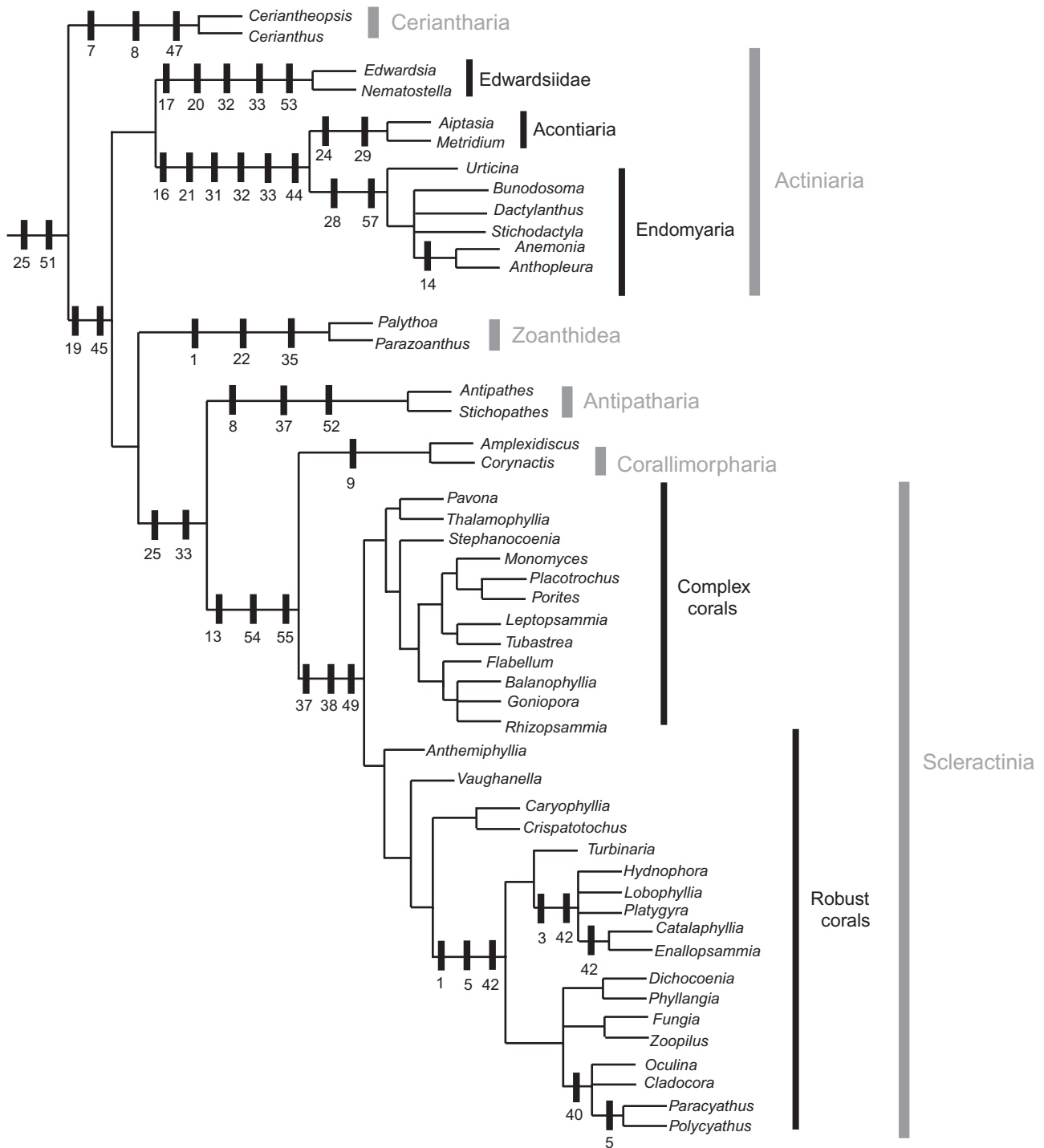


Figure 3. Tree from Fig. 2, with intra-ordinal clades labelled and morphological synapomorphies optimized. Numbers refer to Table 3. Double asterisk indicates alternative optimization of calcareous skeleton; branches along which skeleton would have to have been lost are labelled A, B, and C; see text for further explanation.

possibly allied to ceriantharians (Hyman, 1940; Wells & Hill, 1956). However, the Antipatharia–Corallimorpharia–Scleractinia clade has been found in modern phylogenetic analyses of 18S sequences

(Berntson *et al.*, 1999; Won *et al.*, 2001) and morphology (Won *et al.*, 2001).

In finding that Corallimorpharia and Scleractinia are sister taxa, we concur with, for example, Duerden

(1898), Schmidt (1974), Schmidt & Zissler (1979), den Hartog (1980), Pires & Castro (1997), Romano & Cairns (2000), Won *et al.* (2001), and Daly *et al.* (2002). The Scleractinia–Corallimorpharia clade is corroborated by substitutions in two genes, two sperm ultra-structural features, cnidae distribution, and gross anatomy. The similarities between corallimorpharians and stichodactylid actinians are parallelisms.

Our results indicate that the morphologically defined scleractinian suborders Caryophylliina, Dendrophylliina, and Faviina (Wells, 1956) are polyphyletic. In our tree, members of the Dendrophylliina and Caryophylliina are not closely related (in contrast to Wells, 1956). The close relationship between Poritidae and Dendrophylliidae suggested by Veron *et al.* (1996) is supported by the sister-group relationship between *Goniopora* and a clade containing the dendrophylliids *Balanophyllia* and *Enallopsammia*, but refuted by the close relationship between *Porites* and the flabellids *Monomyces* and *Placotrochus*. The para- and polyphyly of most higher level scleractinian groups may explain the discrepancies between our interpretation of scleractinian phylogeny and those that consider only morphological characters.

Because the members of the Actiniaria are anatomically diverse and because the order lacks a unique morphological diagnostic character, it has been seen as a possibly heterogeneous assemblage of species that cannot be accommodated in Scleractinia, Corallimorpharia, or Zoanthidea (Stephenson, 1921; Schmidt, 1974). Our combined analysis, like many independent analyses of single gene data sets (e.g. France *et al.*, 1996; Song & Won, 1997; Berntson *et al.*, 1999; Won *et al.*, 2001; Daly *et al.*, 2002) and like an earlier non-specific immunoassay (Fautin & Lowenstein, 1994), found a monophyletic Actiniaria. Because Actiniaria is as old and diverse as its sister-group, the diversity of Actiniaria can be explained by its phylogenetic position, relative to the other hexacorallian orders, rather than by polyphyly.

CHARACTER EVOLUTION

Some of the morphological characters used in this analysis are reconstructed as part of a nested series of transformations that characterize increasingly less inclusive groups. This contradicts historical conceptualizations of these features as exclusive alternative states. For example, the arrangement of mesenteries in members of Hexacorallia has been presented as a single character with three alternative states (Fig. 1): unpaired couples; paired, monomorphic couples; and paired, dimorphic couples. These character states are inadequate to describe the diversity and variability of mesenterial arrangements in hexacorallians, and obscure the shared similarities between states. The

transformation series compatible with our phylogenetic tree suggests that couples and pairs are two separate characters, and that couples, which are primitive for Hexacorallia, evolved before paired mesenteries. Pairs are primitively monomorphic, with dimorphism evolving independently within Actiniaria (in Edwardsiidae) and in Zoanthidea. The shared similarity of paired, monomorphic couples, which has been offered as evidence of an Actiniaria–Corallimorpharia–Scleractinia grouping (Hyman, 1940), is a shared primitive feature, and thus not evidence of an exclusive relationship. This interpretation suggests that hexacorallians have a primitively biradial symmetry, in contrast to the radial symmetry characteristic of many other cnidarians.

Marginal sphincter muscles have similarly been characterized as having three alternative states: absent, endodermal, or mesogloeal. Although these three states accurately describe the variation in marginal musculature, this way of thinking about the sphincter muscle does not accord with its inferred evolutionary history. The evolutionary history of sphincter muscles across Hexacorallia is complex: hypertrophy of the columnar circular muscles at the margin occurred independently in Zoanthidea and Actiniaria, and was reversed at least once, in the ptychodactylid *Dactylanthus*. However, the two clades in Actiniaria characterized as having marginal sphincter muscles are sister taxa, suggesting a single origin for the hypertrophy into a sphincter. In Actiniaria, the presence of a marginal sphincter muscle is a synapomorphy, with subsequent differentiation (i.e. whether ectodermal or mesogloeal) characterizing less inclusive groups.

According to our results, there have been several transitions from solitariness to coloniality or clonality. Clonality is not an intermediate state between solitariness and coloniality; both clonality and coloniality are best interpreted as derived from solitariness. Clonality is common among actinians; within Actiniaria, shifts between solitary and clonal mode of life have happened several times (see Geller & Walton, 2001, for a discussion of this phenomenon in *Anthopleura*). In Scleractinia, a transition from solitary to colonial characterizes the crown robust clade; within this clade, there are two subsequent shifts back to solitariness (*Fungia* and *Paracyathus*). The inferred ancestral condition of the complex Scleractinia clade is solitariness, but further optimization is ambiguous: delayed optimization favours several independent adoptions of coloniality, whereas accelerated optimization interprets at least one clade (*Balanophyllia*–*Goniopora*–*Rhizopsammia*) as being characterized by coloniality, with *Balanophyllia* re-adopting solitariness. The evolution of coloniality within scleractinians is congruent with Wells' (1956) hypothesis of morpho-

genetic trends within Scleractinia, and his conclusion that solitary corals are ancestral to colonial forms.

Reproductive and sexual features do not unambiguously characterize any group because of the number of taxa missing entries for these features. However, we infer from their distribution on the tree that these characters may be phylogenetically important. Gonochorism is the ancestral condition of hexacorallians, including scleractinians. All brooding scleractinians are part of the crown clade within the complex corals, signifying that reproduction may be related to evolutionary history as well as to ecology.

In his surveys of anthozoan cnidae, Carlgren (1940, 1945) found that holotrichous and atrichous nematocysts were the types most widely distributed; in 1940, he speculated that other types of nematocysts were derived from either holotrichs or atrichs. Electron microscopy demonstrated that atrichs are holotrichs with extremely small spines (Westfall, 1965), thus simplifying Carlgren's (1940) scheme: holotrichs are the most primitive nematocysts. Our analysis agrees with one of the predictions of Carlgren's hypothesis: holotrichs are primitively present in the Hexacorallia. However, according to our interpretation of nematocyst distribution, microbasic *b*-mastigophores are also part of the ancestral hexacorallian cnidom. Diversification of nematocysts must have preceded the diversification of modern hexacorallian groups.

Homology of the scleractinian skeleton has been questioned on three grounds: in light of the fossil record (e.g. Wells, 1956; Veron, 1995; Oliver, 1996; Veron *et al.*, 1996; Stanley & Fautin, 2001), in light of ecological evidence for its ephemerality (Buddemeier & Fautin, 1996), and in light of scleractinian and corallimorpharian relationships (e.g. Romano & Cairns, 2000; Daly *et al.*, 2002). Our results can address only the phylogenetic argument. We find that Scleractinia is not polyphyletic with respect to Corallimorpharia or Actiniaria; Scleractinia is monophyletic and thus the skeleton potentially has a single origin (Fig. 3).

COMBINED ANALYSIS

Our examination of morphology and multiple gene sequences includes more taxa and more detail about relationships within hexacorallian orders than any previous study of a single type of data (cf. Schmidt, 1974; Schmidt & Zissler, 1979; Romano & Palumbi, 1996; Pires & Castro, 1997; Song & Won, 1997; Berntson *et al.*, 1999; Romano & Cairns, 2000; Won *et al.*, 2001; Daly *et al.*, 2002). The controversial relationships Chen *et al.* (1995) found with 28S sequences alone, like a polyphyletic Actiniaria or a particularly close relationship between *Edwardsia* and *Aiptasia*, are not evident in this combined analysis. Both 16S

and 28S characters support many of the terminal nodes in the Scleractinia.

Although the combined data are congruent with both the 16S and 18S subsets, the results of our combined analysis differ in a few respects from analyses considering only one of them. In analysis of only 18S sequences, *Metridium* is more closely related to *Edwardsia* and *Nematostella* than to the endomyarians (Daly *et al.*, 2002), and *Stichodactyla* is more closely related to *Anemonia* or *Anthopleura* than to *Dactylanthus* (Berntson *et al.*, 1999; Daly *et al.*, 2002). Our findings disagree with earlier 16S analyses with respect to some relationships within Scleractinia (Fig. 2): in our trees, *Turbinaria* is in the robust rather than the complex clade (cf. Romano & Palumbi, 1996; Romano & Cairns, 2000); Romano & Cairns (2000) found that *Porites* and *Goniopora* are sister taxa, whereas we interpret *Porites* as more closely related to *Placotrochus* than to *Goniopora*; using only 16S sequences, Romano & Cairns (2000) were unable to resolve the phylogenetic position of *Placotrochus*.

Our results can also be contrasted with previous morphological studies. Based on his examination of nematocyst ultrastructure, Schmidt (1974) interpreted Actiniaria as paraphyletic with respect to Zoanthidea and Antipatharia. Schmidt & Zissler (1979) similarly interpreted sperm ultrastructure as supporting a paraphyletic Actiniaria. By contrast, we find strong support for actiniarian monophyly. Similarities in cnidae morphology and distribution led Schmidt (1974) to consider the Edwardsiidae as part of the Endomyaria; we infer that edwardsiids are distantly related to endomyarian anemones. Pires & Castro (1997) questioned the monophyly of major scleractinian families and subfamilies based on nematocyst distribution; although many taxa included in their analysis are missing from ours, we concur that Caryophylliidae and Faviina are polyphyletic.

Despite concern that morphological characters are inadequate or insufficient for recognizing groups within Hexacorallia, many of the traditional diagnostic features are recovered as synapomorphies. However, given the past emphasis on exclusive features (e.g. Lang, 1984), the more critical test of the value of morphological characters is their ability to characterize groups consisting of several orders. Two anatomical features (mesenterial filament morphology and paired mesenteries) and two types of nematocyst (microbasic and macrobasic *p*-mastigophores) characterize large groups within Hexacorallia. Coloniality is likewise a phylogenetically significant character, although it has a complex evolutionary history. Most of the morphological features characterize ordinal or subordinal groups, confirming that the problem with morphology is one of emphasis and focus, rather than of quality. The RI of the morphological characters is

slightly lower than the RI of the whole data set (0.59 vs. 0.63), indicating that the morphological data are slightly less phylogenetically informative than the molecular data.

UNRESOLVED QUESTIONS AND FUTURE DIRECTIONS

We interpret several classical taxonomic features as having little or no value for reconstructing relationships among hexacorallians. Trilobed mesenterial filaments in actinarians and zoanthideans are either a sympleisiomorphy or are derived independently in actinarians and zoanthideans. Paired mesenteries of equal size are likewise interpreted as a shared primitive feature. The seemingly unpaired mesenteries of antipatharians may have resulted from reduction of musculature. In zoanthideans, however, the ancestral arrangement of paired, equally sized mesenteries would have to undergo much more significant modification, including a modification of the placement and pattern of insertion for new mesenteries.

The most parsimonious interpretation, given our tree, is that paired mesenteries arose in the common ancestor of zoanthideans, actinarians, corallimorpharians, and scleractinians, and that a skeleton arose only in Scleractinia, a septum being secreted between the members of each mesenterial pair. An alternative explanation is that the ancestor to the Hexacorallia (occupying the position indicated by two asterisks in Fig. 2) had an exoskeleton, which was lost in some lineages. The loss of a skeleton could have happened many times, but the only non-skeletalized lineages of which we have knowledge are those with extant descendants. Several lineages of skeletalized hexacorallians represented in the fossil record have no known modern representatives (Scrutton & Clarkson, 1991). Based on our tree, such a loss would have had to occur minimally three times (at the branches marked A, B, and C in Fig. 2).

Hand (1966) was the first to suggest Scleractinia is ancestral to Actinaria and Corallimorpharia (and perhaps Zoanthidea), recognizing that paired mesenteries have no obvious function in non-skeletalized hexacorallians, and are not required by size alone, as ceriantharians can grow to considerable size without them. He reasoned that having a mesentery on each side of a septum equalizes the force of contraction on the two sides of the septum, preventing tearing of the mesenteries. Paired mesenteries might also serve to flush the interseptal spaces in animals in which the basal end is inflexibly attached to the rigid skeleton.

The absence of a fossil record for non-skeletalized hexacorallians makes it difficult to establish directionality in the relationship between skeletalized and non-skeletalized taxa. Fautin & Lowenstein (1994) attempted to introduce the time dimension by using a

radioimmunoassay of proteins from whole animals and calibrating the tree at the known divergence point for two scleractinian genera. They interpreted their data to support Scleractinia as ancestral to Actinaria and Corallimorpharia. Additional sequences for Corallimorpharia, and for scleractinians such as *Lep-topenus* or *Fungiacyathus*, which may be closely related to them (see Fautin & Lowenstein, 1994; Pires & Castro, 1997), are necessary to make further progress towards addressing this problem.

Increased taxonomic sampling is clearly essential to addressing other taxonomic and evolutionary questions within Hexacorallia. The importance of a broad taxonomic sample for phylogenetic reconstruction is well documented (e.g. Hillis, 1996; Graybeal, 1998; Halanych, 1998). Because of the variability of morphology and biology within orders, taxonomic sample plays an especially important role in interpreting the evolution of morphological features within Hexacorallia. The Ceriantharia and Zoanthidea are each represented by just two taxa, making discussion of intra-ordinal relationships impossible for these groups at this time. The taxonomic sample of actinarians in the combined analysis is both smaller and narrower than that of some analyses that consider only 18S sequences (e.g. Song & Won, 1997; Berntson *et al.*, 1999; Daly *et al.*, 2002). Consequently, the current interpretation of the evolution of some attributes differs from that of earlier studies. For example, basilar muscles are a synapomorphy for the clade containing Acontiaria and Endomyaria in this combined analysis, but are interpreted as a parallelism when more actinarian taxa and fewer types of data are considered (Daly *et al.*, 2002). Mesogloal marginal sphincter muscles are a synapomorphy for the Acontiaria in this analysis, but may actually characterize a clade consisting of Acontiaria and Mesomyaria, a group of actinarians whose members lack acontia but have mesogloal marginal sphincters. Particularly critical to assessing the phylogenetic significance of acontia would be the inclusion of acontiate abasiliarians. Furthermore, the selection of taxa included in this analysis is ecologically biased: because of their accessibility, intertidal and shallow subtidal species predominate. This bias may affect the interpretation of clonality, which is related to habitat (Francis, 1988).

Although our results (Fig. 2) support the monophyly of each hexacorallian order as currently defined, the limited taxon sample also affects the severity of tests of ordinal monophyly. Members of Sideractiidae, a family of corallimorpharians, are essential for testing corallimorpharian and scleractinian monophyly, as members of this group have one tentacle per endocoelic and exocoelic space, like many scleractinians and most actinarians, rather than multiple tentacles, like most other corallimorpharians. Although

most scleractinians are inferred to have a single tentacle per endocoelic space (e.g. Hyman, 1940; Schmidt, 1974; Chevalier, 1987), the tentacle arrangement is unknown for most corals, and may be variable (e.g. Duerden, 1904). Actiniaria contains three suborders: Protantheae, Endocoelantheae, and Nynanthae. Only the largest, Nynanthae, is represented. Protantheae has been linked to Scleractinia (Schmidt, 1974); the inclusion of members of this group would strongly test monophyly of Actiniaria and Scleractinia. In members of Endocoelantheae, the second cycle of mesenteries are inserted in the lateral endocoels. This pattern is unlike that of other actinarians, and thus illustrates variation in phylogenetically informative features that we have not sampled. Carlgren (1914) suggested that similar variation might occur in other hexacorallians, particularly in Scleractinia, a group in which soft-tissue anatomy has received little emphasis.

The absence of information on scleractinian soft-tissue morphology has three important consequences. Although molecular data resolve groups within Scleractinia, at least some of these groups are supported by only a few substitutions. Morphological data may further support (or contravene) these clades. Without information on scleractinians, we cannot estimate the degree and type of variation within each order for gross morphological features, determine the number of states, or evaluate proposed character transformation series for characters that occur in all hexacorallians. The absence of information about most scleractinians compromises the value of soft tissue characters across Hexacorallia: because scleractinians are interpreted as potentially having any character state for many of these features, soft tissue characters cannot be optimized unambiguously even for taxa for which we have concrete information.

The current equivalency in rank between the hexacorallian orders does not accurately reflect history or relationship. Ceriantharia is the most basal group in Hexacorallia, and is the sister-group to the remaining orders; Actiniaria is the sister-group to a clade containing Antipatharia, Corallimorpharia, Scleractinia, and Zoanthidea. Subdividing Actiniaria into smaller, monophyletic groups is not yet possible, as intra-ordinal relationships are ambiguous. The Athenaria, an intra-ordinal grouping of burrowing anemones proposed by Carlgren (1949) that includes *Edwardsia* and *Nematostella*, is polyphyletic (e.g. Berntson *et al.*, 1999; Daly *et al.*, 2002), effectively rendering Endomyaria, Mesomyaria, and Acontaria polyphyletic. There is no morphological character by which to recognize Actiniaria; although this is a problem regardless of rank, a formal reclassification would entail diagnosis, which is impossible at this stage. Reclassification of Actiniaria should follow more detailed, densely sampled analyses aimed at identifying new

morphological characters and incorporating sequences for taxa from Sideractiidae, Protantheae, and Exocoelantheae; such studies will make it possible to address remaining questions about taxonomy and phylogeny of Hexacorallia.

ACKNOWLEDGEMENTS

This work was supported by NSF grants DEB 99-78106, DEB 95-21819 (in the programme Partnerships to Enhance Expertise in Taxonomy) to D.G.F. and OCE 00-03970 (in the National Oceanic Partnership program) to D.G.F. and R. W. Buddemeier. S. D. Cairns and J. E. N. Veron kindly answered questions about scleractinian taxonomy; any errors and omissions are ours. D. R. Smith, T. R. White, and C. W. Cunningham assisted with collection of sequence data. Comments and suggestions from S. D. Cairns, C. Hand, and two anonymous reviewers significantly improved this manuscript.

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CHARACTER LIST

BIOLOGY

1. Polyp organization: (0) solitary; (1) colonial; (2) clonal.
2. Spawning type: (0) broadcasting; (1) brooding.
3. Sexuality: (0) gonochoric; (1) hermaphroditic.
4. Transverse fission: (0) absent; (1) present.
5. Zooxanthellae: (0) absent; (1) present.
6. Budding and longitudinal fission: (0) none; (1) longitudinal fission (extratentacular budding); (2) intratentacular budding; (3) stolon budding.

ANATOMY

7. Tentacles: (0) marginal only; (1) marginal and labial.
8. Tentacles retractile: (0) no; (1) yes.
9. Tentacle/coelenteron relationship: (0) 1 tentacle per endocoel and per exocoel; (1) 1 tentacle per exocoel, multiple per endocoel.
10. Tentacle length: (0) greater than or approximately equal to oral disc radius; (1) less than oral disc radius.
11. Relative tentacle lengths: (0) inner tentacles longer than outer tentacles; (1) inner tentacles shorter than outer tentacles; (2) inner tentacles equal to outer tentacles.
12. Catch tentacles: (0) absent; (1) present.
13. Acrospheres: (0) absent; (1) present.
14. Marginal spherules: (0) absent; (1) holotrichous.
15. Adhesive columnar protrusions: (0) absent; (1) present.
16. Siphonoglyph: (0) one; (1) two or more; (2) absent.
17. Directives: (0) sterile; (1) fertile.
18. Coupled mesenteries: (0) absent; (1) present.
19. Paired mesenteries: (0) absent; (1) present.
20. Pair morphology: (0) members same size; (1) members differ in size.
21. Paired secondary cycle: (0) absent; (1) present.
22. Mesenterial addition pattern: (0) mesenteries added around circumference; (1) added ventrally; (2) added in ventrolateral exocoelic spaces only.
23. Mesenterial fusion: (0) absent; (1) present.
24. Acontia: (0) absent; (1) present.
25. Trilobed ciliated filaments: (0) absent; (1) present.
26. Gonads on mesenteries of 1st cycle: (0) absent; (1) present.

27. Gonads on mesenteries of 2nd and subsequent cycles: (0) absent; (1) present.
28. Endodermal sphincter: (0) absent; (1) present.
29. Mesogloal sphincter: (0) absent; (1) present.
30. Ectodermal longitudinal muscle: (0) absent; (1) tentacles and oral disc only; (2) whole body.
31. Basilar musculature: (0) absent; (1) present.
32. Retractor muscle: (0) weak – not forming distinct muscle; (1) diffuse (comb-like); (2) restricted (kidney shaped).
33. Parietal muscle: (0) absent; (1) diffuse (tall, narrow); (2) restricted (squat, wide).
34. Mesogloal cell inclusions: (0) absent/rare; (1) present.
35. Mesogloal lacunae: (0) absent; (1) present.

SKELETAL MORPHOLOGY

36. Skeleton: (0) absent; (1) mineralic; (2) proteinaceous.
37. Columella: (0) absent; (1) present.
38. Costae: (0) absent/weak; (1) present.
39. Colony shape: (0) encrusting; (1) erect; (2) plate-like; (3) massive (boulder); (4) reptoid.
40. Skeletogenic tissue: (0) ectoderm; (1) mesogloea.
41. Corallum morphology: (0) cerioid; (1) plocoid; (2) meandroid; (3) flabello-meandroid; (4) discoidal or cupolate; (5) trochoid or turbinate.
42. Columella: (0) styloid; (1) laminar; (2) spongy (trabecular).

CNIDAE

43. Holotrichs: (0) absent; (1) present.
44. Microbasic *p*-mastigophores: (0) absent; (1) present.
45. Microbasic *b*-mastigophores: (0) absent; (1) present.
46. Long, thin, basitrichs: (0) absent; (1) present.
47. Ptychocysts: (0) absent; (1) present.

48. Macrobasic *p*-mastigophores in filaments: (0) absent; (1) present.
49. Macrobasic *p*-mastigophores in tentacles: (0) absent; (1) present.
50. Spirocysts: (0) absent; (1) present.

SPERM ULTRASTRUCTURE

51. Sperm head shape: (0) conical; (1) spherical.
52. Sperm nuclear depression: (0) absent; (1) present.
53. Sperm centriolar orientation: (0) perpendicular; (1) parallel.
54. Centriolar ligament: (0) absent; (1) present.
55. Cytoplasmic collar at sperm midpiece: (0) absent; (1) present.
56. Sperm symmetry: (0) asymmetrical; (1) symmetrical.

Sources: Babcock *et al.* (1986); Cairns (1982, 1984, 1989, 2000); Cappola & Fautin (2000); Carlgren (1912, 1921); Chadwick-Furman & Spiegel (2000); Chadwick-Furman, Spiegel & Nir (2000); Dewel & Clark (1972); Duerden (1898, 1900, 1902a,b); Dunn (1975); Fadlallah (1983); Fadlallah, Karlson & Sebens (1984); Gerodette (1981); Glynn *et al.* (1991, 1994, 1996); Goffredo, Teló & Scanabissi (2000); Haddon (1898); Haddon & Shackelton (1891a,b); Hand (1955a,b, 1956); Hand & Uhlinger (1992); Harriot (1983); Harrison (1985, 1990); Harrison & Jamieson (1999); Harrison & Wallace (1990); den Hartog (1980); Heltzel & Babcock (2002); Hinsch & Moore (1992); Holts & Beauchamp (1993); Krupp (1983); Manuel (1981); Parker, Mladenov & Grange (1997); Pax (1940); Pires & Castro (1997); Rinkevich & Loya (1979); Ryland (1997b, 2000); Schmidt (1972, 1974); Schmidt & Zissler (1979); Shick (1991); Steiner (1991, 1993); Steiner & Cortes (1996); Stephenson (1920, 1921, 1922, 1928, 1935); Stoddart & Black (1985); Tranter, Nicholson & Kinchington (1982); Veron (2000a,b,c); Wells (1956).