MOLECULAR PHYLOGENETIC HYPOTHESES FOR THE EVOLUTION OF SCLERACTINIAN CORALS

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ABSTRACT

The evolutionary history of scleractinian corals is based on knowledge of skeletal characters and their 250 million yr fossil record. However, homologies of skeletal characters are not well-understood and fossil documentation of these characters is incomplete. As a result, relationships among families and suborders are poorly understood. We have analyzed a 225 bp segment of the nuclear 28S ribosomal RNA gene from 45 species of corals and a 566 bp segment of the mitochondrial 16S ribosomal RNA gene from 68 species. Unlike previous analyses of smaller numbers of taxa, the dataset presented here includes both reef-building and non-reef-building taxa from 20 of 24 families and all seven suborders. Nuclear sequences analyzed under maximum parsimony and minimum evolution criteria did not resolve relationships among families and suborders. Similar analyses of mitochondrial sequences resulted in a robust phylogenetic hypothesis. The mitochondrial hypothesis, like previous analyses of a subset of these data, did not agree with morphological hypotheses about relationships among families and suborders, and supports a polyphyletic origin of the scleractinian skeleton. Instead of seven major monophyletic groups as hypothesized from morphological data, mitochondrial data suggest that the Scleractinia is represented by two major clades. Relationships within these major clades are not clearly differentiated but each clade is comprised of families from different morphological suborders as defined by Veron (1995). The mitochondrial topology gives no support for the morphological suborders Archaeocoeniina, Fungiina, Caryophylliina, or Meandriina as monophyletic groups but is consistent with a monophyletic Faviina, Poritiina, and Dendrophylliina. Monophyletic morphological families are supported with the exception of the Faviidae, Caryophylliidae, Poritidae, and Oculinidae. The mitochondrial topology also supports the most recent taxonomic treatments of *Psammocora* and *Fungiacyathus,* genera that have been the subject of taxonomic debate.

A biological classification that reflects hypotheses about evolutionary relationships is the foundation for understanding the patterns and processes of diversification of any group of organisms (Wiley, 1981). However, evolutionary hypotheses are only as reliable as the characters and analyses used to establish the classification from which they are derived. Revolutions in technology in recent years have made it possible to construct robust phylogenetic hypotheses from quantitative analyses of genotypic characters in the form of nucleotide sequences. These methods now make it possible to test phenotypically based hypotheses with genotypic characters, creating new possibilities for understanding evolutionary patterns and processes.

Scleractinian corals are relatively simple metazoans with a continuous fossil record that begins in the mid-Triassic. They are polyp animals with an aragonitic calcium carbonate skeleton, the distinguishing characteristic of the order which is comprised of approximately 1300 species in 220 extant genera (Cairns, 1999) represented by 24 families and seven suborders (Veron, 1995). The best known examples of scleractinians are the reef-building corals that form the framework for tropical coral reefs, the world's most diverse marine communities. An equally large number of scleractinians are found throughout the world's oceans, from the intertidal zone to over 6000 m in depth. Extreme mor-

phological variability and paleontologic evidence have made the task of determining rela-
tionships within the order difficult. Consequently, the evolutionary history of the group is
poorly understood.

Phylogenetic hypotheses for the Scleractinia have been based largely on phenotypic
characters and come from detailed studies of skeletal characters of both Recent and fossil
corals. Variability of the macromorphological characters commonly used in scleractinian
taxonomy, such as septal, corallite, and corallum structure, is inherent in corals (see
Wijsman-Best, 1974; Veron and Pichon, 1976; Brakel, 1977; Foster, 1977; Lang, 1984;
Foster, 1985; Willis, 1985). Variation can be intracolonial, intrapopulational,
interpopulational and regional (Veron and Pichon, 1976; Foster, 1980; Best et al., 1984;
Veron, 1995). Thus homology assessment of skeletal characters is often unreliable and
has led to considerable taxonomic confusion (Randall, 1976; Potts, 1984). In addition,
fossil documentation is incomplete and macromorphological characters essential for
scleractinian taxonomy (e.g., septal ornamentation and wall construction) are difficult to
interpret in many fossils (Foster, 1979; Best et al., 1984; Lathuilière, 1996a; Veron, 1995).
While microstructural analysis of fossil taxa is proving highly useful, such studies have
not been carried out on a wide range of extant taxa. Variability of microstructural charac-
ters has been studied in only a limited number of fossil taxa and even fewer extant taxa
(Lathuilière, 1996a,b). Other problems with skeletal characters also make cladistic analy-
sis difficult: at least some characters may be interdependent and they are limited in num-
ber (Romano, 1995; Lathuilière, 1996b).

Underwater observations of scleractinian corals have greatly increased our understand-
ing of morphological variation and relationships among closely related species but rela-
tionships among genera and families have remained very poorly understood (Veron, 1995).
In the last 30 yrs other phenotypic characters such as reproduction, polyp morphology,
behavior, ecology, and physiology [reviewed in Lang, (1984)] have been used for
scleractinian taxonomy, primarily in distinguishing species, but none of these data have
provided an evolutionary perspective of the entire order. A phenetic analysis (Powers and
Rohlf, 1972) based on 60 skeletal, polyp, ecological and biochemical characters of 30
genera of Scleractinia from the Indo-Pacific and the Caribbean gives some support to
phylogenetic hypotheses suggested by Vaughan and Wells (Vaughan and Wells, 1943;
Wells, 1956). However, the limited number of taxa and the phenetic methods used in this
analysis do not provide a thorough test of traditional morphological hypotheses. Until
very recently, no genotypic data have been available from scleractinian corals for testing
hypotheses derived from problematic phenotypic characters.

DNA sequences are independent of the morphological variation of skeletal characters
and of the scleractinian fossil record that is often difficult to interpret (Romano, 1995;
Romano and Palumbi, 1996). Developments in molecular techniques have made it fea-
sible to use molecular tools to collect genotypic characters for analyses of relationships
among coral species (McMillan and Miller, 1990; Miller et al., 1990; McMillan et al.,
1991; Medina et al., 1996; Hunter et al., 1997; Lopez and Knowlton, 1997; Hatta et al.,
1999; van Oppen et al., 1999), genera (Best and Thomas, 1993; Beauchamp and Powers,
1996; Snell, 1997), and families (Chen et al., 1995; Romano, 1995; Romano, 1996; Romano
and Palumbi, 1996; Veron et al., 1996; Romano and Palumbi, 1997; Fukami et al., 2000).
Previous molecular analyses of higher level relationships within the order have used ei-
ther mitochondrial ribosomal sequences (Romano, 1995; Romano, 1996; Romano and
Palumbi, 1996) or nuclear ribosomal sequences (Veron et al., 1996) from a small number

of reef-building taxa. These studies demonstrate the utility of molecular characters for assessing evolutionary relationships among a limited number of genera and families of scleractinians. They suggest an evolutionary history for the group that is in contrast to hypotheses based on morphological data (Alloiteau, 1952; Wells, 1956; Chevalier and Beauvais, 1987; Roniewicz and Morycowa, 1993; Veron, 1995). Previous molecular data suggest that the Scleractinia as currently defined is polyphyletic, implying that many of the evolutionary trends observed in the order are the result of convergent evolution.

Unlike previous molecular analyses of higher order relationships within the Scleractinia, the data presented herein include sequences from both nuclear and mitochondrial genes from taxa representative of the majority of scleractinian families, including both reef-building and non-reef-building taxa. Our analyses of mitochondrial DNA sequences include representatives of the entire order Scleractinia, including 56 of the 220 extant genera (~25%) in 20 of 24 extant families and all seven hypothesized extant suborders (Veron 1995). The nuclear sequences analyzed here are representative of 33 genera in 15 families and all seven suborders. We demonstrate that, unlike in previous analyses (Veron et al., 1996), the small segment of the nuclear 28S ribosomal gene from corals is not informative and so is not useful for testing hypotheses based on mitochondrial or morphological data. However the nuclear sequences do suggest some support for hypotheses based on mitochondrial data. The phylogenetic hypotheses derived from mitochondrial sequences representative of the entire order are consistent with previous molecular analyses of a limited number of scleractinian taxa (Romano and Palumbi, 1996; Veron et al., 1996). Unlike previous analyses, the taxa in the analyses presented here are representative of the entire order and so this dataset is useful for comparing molecular and morphological hypotheses. These data provide hypotheses for relationships within the Scleractinia. They do not support traditional hypotheses, based on morphological data, about relationships among families and suggest widescale taxonomic revisions for the order.

MATERIALS AND METHODS

SAMPLE COLLECTION AND DNA EXTRACTION.—In this analysis, 88 species of corals (Table 1) were sampled from 71 genera in 20 of 24 families and all seven suborders described by Veron (1995). Sequences from some of these corals (Table 1) were previously published: 36 mitochondrial 16S sequences (France et al., 1996; Romano, 1996) and 18 nuclear 28S sequences (Chen et al., 1995; Veron et al., 1996). New taxa included in this study are 32 sequences from the 16S ribosomal mtDNA region and 27 from the nuclear 28S ribosomal RNA region. These samples do not include representatives of all scleractinians as our sampling was opportunistic due to time and financial constraints. We attempted to sample as many different genera and families as possible but we were not able to sample type genera and species. We did sample larger numbers of genera from larger families as well as those considered to contain taxa that might not be closely related (e.g., Faviidae). Azooxanthellate samples were particularly difficult to obtain. The azooxanthellate corals sampled are from collections belonging to or on loan to the USNM (where a small portion of the collections have been preserved in alcohol), from collections by H. Zibrowius, or from samples that were obtained by dredging and then stored frozen at Harbor Branch Oceanographic Institute. Zooxanthellate Pacific samples were identified using scleractinian taxonomic works (Alloiteau, 1952; Wells, 1956; Veron and Pichon, 1976; Maragos, 1977; Veron et al., 1977; Veron and Pichon, 1980; Veron and Pichon, 1982; Veron and Wallace, 1984; Veron, 1986; Chevalier and Beauvais, 1987) and with the help of taxonomic experts (J. Maragos, C.C. Wallace). All Atlantic and azooxanthellate samples were identified by S. Cairns or H. Zibrowius.

Table 1. Species sampled, including taxonomic classification, where the sample was collected, which genes were sampled, how much sequence was obtained for each gene and Genbank accession number for each sequence. Source includes museum catalogue number where appropriate (HBOI = Harbor Branch Oceanographic Institute; WA = Waikiki Aquarium; USNM = United States National Museum, NTM = Northern Territories Museum). Gene lengths in parentheses indicate previously published sequences. N/A = no Genbank Accession No. available.

SUBORDER Family (# genera in family)	Source	Genes	Length Seq'd	Genbank Acc. No.
ARCHAEOCOENIINA				
Astrocoeniidae (2)				
Stephanocoenia michelini	Bahamas/HB 2-VII-87-2-022	16S	565	AF265581
Pocilloporidae (4)				
Pocillopora damicornis	Hawaii	16S	(425)	L76019
Pocillopora meandrina	Hawaii	16S	(425)	L76018
Seriatopora hystrix	Veron et al. 1996	28S	(222)	U65520
Stylophora pistillata	Veron et al. 1996	28S	(222)	U65519
Madracis pharensis	Bahamas	28S	222	AF265622
Acroporidae (4)				
Montipora capitata	Hawaii	16S	(536)	L76015
Montipora digitata	Palau/WA	16S	(534)	L75993
Anacropora sp.	Palau/WA	16S	(536)	L75992
Acropora (Acropora) cytherea	Guam	16S	(536)	L75995
Acropora (Acropora) humilis	Guam	16S	(536)	L75996
Acropora (Isopora) palifera	Madang, PNG	16S	536	AF265593
Astreopora sp.	Madang, PNG	16S	546	AF265591
FUNGIINA				
Siderastreidae (6)				
Psammocora stellata	Hawaii	16S	(412)	L76021
Coscinaraea sp.	Solomon Islands	16S	(412)	L76001
Siderastrea siderea	Bahamas/HB 29-VI-87-4-008	28S	304	AF265634
Pseudosiderastrea tayami	Veron et al. 1996	28S	(222)	U65518
Agariciidae (7)				
Pavona varians	Hawaii	16S	(536)	L76016
Leptoseris incrustans	Hawaii	16S	(536)	L76012
Fungiidae (11)				
Fungia (Lobactis) scutaria	Hawaii	16S	(412)	L76005
		28S	222	AF265631
Fungia (Cycloseris) fragilis	Hawaii	16S	(412)	L75998
Fungia (Cycloseris) vaughani	Hawaii	16S	(412)	L75999
Fungia (Fungia) fungites	Veron et al. 1996	28S	(222)	U65523
Zoopilus echinatus	Fiji/WA	16S	(410)	L76024
		28S	222	AF265632
Sandalolitha robusta	Veron et al. 1996	28S	(222)	U65522
Fungiacyathidae (1)				
Fungiacyathus marenzelleri	N. Pacific/ USNM 93941	16S	(563)	L76004

Table 1. Continued.

SUBORDER	Source	Genes	Length Seq'd	Genbank Acc. No.
Family (# genera in family)				
FAVIINA				
Pectinidae (5)				
Pectinia alcicornis	Palau/WA	16S	(409)	L76017
Mycedium sp.	Madang, PNG	16S	410	AF265608
Mycedium elephantotus	Veron et al. 1996	28S	(222)	U65527
Mussidae (13)				
Lobophyllia hemprichii	Palau/WA	16S	(410)	L76013
		28S	304	AF265624
Lobophyllia pachysepta	Veron et al. 1996	28S	(222)	N/A
Cynarina sp.	Madang, PNG	16S	408	AF265613
Acanthastrea echinata	Veron et al. 1996	28S	(222)	U65524
Merulinidae (5)				
Hydnophora rigida	Palau/WA	16S	(409)	L76009
Hydnophora sp.	Veron et al. 1996	28S	(222)	U65526
Merulina scabricula	Fiji/WA	16S	(409)	L76014
Anthemiphyllidae (1)				
Anthemiphyllia spinifera	Wallis &	16S	457	AF265596
	Futuna/	28S	304	AF265652
	USNM 98573			
Faviidae (24)				
Caulastrea furcata	Fiji/WA	16S	(409)	L75997
Cyphastrea ocellina	Hawaii	16S	(408)	L76132
Echinopora lamellosa	Fiji/WA	16S	(409)	L76003
		16SB	(563)	AF265586
Leptastrea bottae	Hawaii	16S	(412)	L76010
Leptoria phrygia	Guam	16S	(409)	L76011
Montastrea sp.	Madang, PNG	16S	409	AF265610
Montastrea valenciennesi	Veron et al. 1996	28S	(222)	U65525
Platygyra sp.	Madang, PNG	16S	409	AF265611
Cladocora caespitosa	Mediterranean	16S	409	AF265612
		28S	304	AF265633
Favia fragum	France et al. 1996	16S	(410)	U40295
CARYOPHYLLIINA				
Caryophylliidae (51)				
Catalaphyllia jardinei	Indo-Pac/WA	16S	(409)	L76000
		28S	306	AF265637
Euphyllia ancora	Palau/WA	16S	(409)	L76002
		16SB	(537)	AF265598
Rhizosmilia maculata	Bimini	16S	418	AF265602
Thalamophyllia riisei	Bimini	28S	307	AF265639
Thalamophyllia gasti	Mediterranean/	16S	535	AF265590
	USNM 98473	28S	307	AF265638
Caryophyllia inornata	Mediterranean/	16S	420	AF265599
	USNM 98480	28S	304	AF265642

Table 1. Continued.

SUBORDER Family (# genera in family)	Source	Genes	Length Seq'd	Genbank Acc. No.
Phyllangia mouchezii	Mediterranean/	16S	409	AF265605
	USNM 98486	28S	304	AF265641
Polycyathus muellerae	Mediterranean/	16S	409	AF265606
	USNM 98489	28S	304	AF265643
Paracyathus pulchellus	Mediterranean/	16S	408	AF265603
	USNM 98481			
Crispatotrochus rugosus	Vanuatu/	16S	420	AF265600
	USNM 98588	28S	303	AF265640
Odontocyathus weberianus	New Caledonia/	16S	465	AF265594
	Bathus 4-915	28S	304	AF265647
Vaughanella sp.	Vanuatu	16S	466	AF265595
		28S	304	AF265646
Ceratotrochus magnaghii	Mediterranean/	16S	471	AF265597
	USNM 98482	28S	304	AF265645
Flabellidae (10)				
Flabellum impensum	Antarctica/	16S	563	AF265582
	USNM 89307	28S	304	AF265649
Monomyces pygmaea	Mediterranean/	16S	562	AF265583
	USNM 98471	28S	304	AF265651
Placotrochus laevis	Beagle Gulf/	16S	566	AF265589
	NTM 08052	16SB	407	AF265604
		28S	304	AF265650
Turbinoliidae (22)				
Tropidocyathus labidus	Wallis & Futuna/	16S	562	AF265585
	USNM 98759			
Notocyathus sp.	New Caledonia/	16S	563	AF265584
	Balthus 4-915			
Guyniidae (7)				
Guynia annulata	Mediterranean	16S	542	AF265580
MEANDRIINA				
Oculinidae (10)				
Galaxea fascicularis	Guam	16S	(537)	L76006
Acrhelia horrescens	Fiji/WA	16S	(517)	L75994
Oculina patagonica	Mediterranean/	16S	409	AF265601
	USNM 98485	28S	306	AF265636
Meandrinidae (4)				
Meandrina meandrites	Veron et al. 1996	28S	(222)	U65521
Dichocoenia stokesi	Bahamas/HB	16S	409	AF265607
	1-VII-VII-87-1-007	28S	304	AF265635
PORITIINA				
Poritidae (4)				
Porites compressa	Hawaii	16S	(562)	L76020
		28S	304	AF265630

Table 1. Continued.

SUBORDER	Source	Genes	Length Seq'd	Genbank Acc. No.
Family (# genera in family)				
Porites australiensis	Veron et al. 1996	28S	(222)	U65516
Porites cylindrica	Veron et al. 1996	28S	(222)	N/A
Porites lutea	Veron et al. 1996	28S	(222)	U65517
Gonipora stokesii	Palau/WA	16S	(546)	L76008
Goniopora sp.	Palau/WA	16S	(546)	L76007
Goniopora minor	Veron et al. 1996	28S	(222)	U65515
Alveopora sp.	Madang, PNG	16S	546	AF265592
DENDROPHYLLIINA				
Dendrophylliidae(19)				
Turbinaria peltata	Indo-Pac/WA	16S	(562)	L76023
		16SB	(409)	AF265609
Turbinaria mesenterina	Veron et al. 1996	28S	(222)	N/A
Tubastraea coccinea	Hawaii	16S	(562)	L76022
		28S	222	AF265625
Tubastraea micrantha	Veron et al. 1996	28S	(221)	U65514
Rhizopsammia sp.	Madang, PNG	28S	304	AF265629
Dendrophyllia gracilis	Bahamas/	16S	562	AF265588
	HB 20-XI-86-2-010	28S	304	AF265627
Balanophyllia regia	Mediterranean/	16S	563	AF265587
	USNM 98479	28S	304	AF265626
	Veron et al. 1996	28S	(222)	N/A
Leptopsammia pruvoti	Mediterranean/	16S	563	AF265579
	USNM 98472	28S	304	AF265628
Enallopsammia rostrata	France et al. 1996	16S	545	U40294

Genomic DNA extractions of new samples were carried out as described in Romano and Palumbi (1997) using either a modified chloroform phenol protocol or a modified protocol for the ProMega Wizard Minipreps system. All newly collected sequences have been deposited in GenBank and their accession numbers are indicated in Table 1.

DNA AMPLIFICATION.—All DNA amplifications were carried out in a Perkin-Elmer Cetus Model 9600 thermocycler. Polymerase chain reaction (PCR) amplification of the16S ribosomal gene region was as described in Romano and Palumbi (1997). Amplification of the 28S ribosomal gene region was carried out using published anthozoan primers (Chen et al., 1995) and one reverse primer designed specifically for scleractinians (5'AACTTTCCCTCACGGTACTTGT3') which anneals to positions 360–380 in the mouse sequence (Qu et al., 1988).

PCR products were purified in one of two ways. Some PCR products were precipitated by incubation at 37°C for 15 min with an equal volume of 20% PEG 8000/2.5M NaCl. After centrifugation the pellet was washed two times with 80% ethanol, dried and then suspended in 25 µL dH$_2$O. Other products were run on a 0.8% low-melting point agarose gel. Desired bands were cut out, weighed, and soaked in 1ml of distilled water for 5–15 min twice. The slices were then equilibrated with 0.1 volume of 10X β-Agarase buffer (New England BioLabs, Inc., Beverly, Massachusetts) and digested according to the manufacturers' recommendations. DNA concentration was determined using a spectrophotometer. This template was subsequently used directly in cycle sequencing reactions.

DNA SEQUENCING.—Cycle sequencing reactions were carried out in a Perkin-Elmer Cetus Model 9600 thermocycler using the ABI PRISM Ready Reaction DyeDeoxy™ Terminator Cycle Sequenc-

ing Kit with AmpliTaq, DNA Polymerase or the Dye Terminator Cycle Sequencing Ready Reaction Kit with AmpliTaq, DNA Polymerase, FS following the ABI protocol using 50–100 ng of template. In some cases, DMSO was added to a concentration of 1% in cycle sequencing reactions. Sequences were electrophoresed on a 6% acrylamide gel run on a Perkin-Elmer/Applied Biosystems Inc. (Foster, California) DNA Sequencing System (Model 373A or 377) following the protocol supplied by the manufacturer. All samples were sequenced in both directions.

SEQUENCE ANALYSIS.—Sequences were verified and manipulated with Sequencher ver. 3.0 (Gene Codes Corporation). They were aligned to previously published alignments (Romano, 1996; Chen et al., 1995) with SeqPup (Gilbert, 1996) and by eye. The alignments are available through the EMBL database. The accession numbers are DS42960 for the 28S sequences and DS42961 for the 16S sequences. Any positions with insertions or deletions were not included in analyses. Three outgroups were used in analyses of the 28S sequences: an actiniarian *Aiptasia pulchella*, and two corallimorpharians, *Corynactis viridis* and *Rhodactis howesii* (see Chen et al., 1995). Different outgroup taxa were used in analyses of 16S sequences: the hydrozoan *Hydra vulgaris* (see Cunningham and Buss, 1993), the octocorallian *Renilla muelleri* (see Bridge et al., 1995), and the corallimorpharian *Corynactis californica* (see France et al., 1996). Phylogenies were constructed using PAUP* 4.0d65 (Swofford, 1999).

Previously published 28S sequences (Chen et al., 1995; Veron et al., 1996) were shorter and from different taxa than those obtained for this study. For this reason, three different combinations of 28S sequences were analyzed to utilize all available data: (1) 222 bp from 45 taxa (46 parsimony informative characters), (2) 222 bp from 22 taxa and 304 bp from 24 taxa, and (3) 304 bp from 24 taxa. The data were analyzed under both minimum evolution and maximum parsimony criteria. For minimum evolution analyses, the software program Modeltest (Posada and Crandall, 1998) was used to determine which model of evolution best fit the data by comparing nested models of DNA substitution in a hierarchical hypothesis-testing framework (Huelsenbeck and Crandall, 1997). Maximum parsimony analyses were performed including successive weighting with the rescaled consistency index (Farris, 1969; Carpenter, 1994) and transversion parsimony. Heuristic searches were carried out with 10 random addition sequences. One thousand bootstrap replicates, using the 'fast' stepwise addition option, were used to determine the support for groupings found in all analyses.

Sequences from the mitochondrial ribosomal 16S gene region were analyzed as described above for 28S analyses. In addition, two different tests were used to compare morphological and molecular topologies given molecular data. The T-PTP test (Faith, 1991) as implemented in PAUP* was used to compare the strength of the tree topology derived from molecular data relative to that derived from morphological data by testing for non-monophyly. This test generates a distribution of length differences between the shortest tree consistent with molecular data (non-monophyletic suborders) and the shortest tree consistent with morphological hypotheses (monophyletic suborders) in 100 randomized datasets. Recent studies have demonstrated that using the T-PTP test with the null hypothesis of non-monophyly does not produce the biased results obtained with the null hypothesis of monophyly (Faith and Trueman, 1996; Swofford et al., 1996b). The Kishino-Hasegawa test (Kishino and Hasegawa, 1989) as implemented in PAUP* was used to determine if the difference in the lengths of the two trees, based on molecular data, is significantly different from zero (Swofford et al., 1996a).

RESULTS

28S RIBOSOMAL SEQUENCES.—Sequences collected for this study from the 28S nuclear ribosomal gene region of 27 coral species ranged in size from 222 to 225 bp as compared to 225 bp for previously published sequences from scleractinians (Chen et al., 1995; Veron et al., 1996). An additional 82 bp of sequence were collected from 24 species sequenced for this study. Sequences collected from three additional taxa (*Montipora verrucosa, Acropora humilis, Acropora cytherea*) aligned poorly with sequences from other corals

and were not included in any analyses. Although *C. viridis* is considered to be an outgroup (from the anthozoan order Corallimorpharia), in some of our analyses it grouped among the Scleractinia. Therefore, although we included it in all analyses it was not designated as an outgroup.

The twenty-seven nuclear ribosomal sequences collected for this study were analyzed along with 18 published sequences (Chen et al., 1995; Veron et al., 1996), for a total of 45 sequences representing 41 genera in 14 families and all seven extant suborders of Scleractinia. The g_I statistic for 10,000 randomly generated trees from these data ($g_I = -0.366$) indicated that the data were significantly more structured than random (Hillis and Huelsenbeck, 1992). The greatest (Tamura-Nei) distance among species pairs was 24.1%.

The Tamura and Nei (1993) model of evolution was found to be the best fit for analyses of 222 bp from all 45 taxa for minimum evolution analyses. Distances were calculated with maximum likelihood estimates of the proportion of invariable sites (0.4174) and of the gamma shape parameter (0.4476). The neighbor-joining topology generated from these distances failed to resolve relationships among those taxa (Fig. 1). Analyses with only taxa from which 304 bp of sequence were available or with all sequence available from all taxa (some taxa with only 222 bp, some with 304 bp) also did not resolve relationships among taxa (results not shown). Very few of the groupings are supported by bootstrap values greater than 70%. Unweighted maximum parsimony analyses of 46 parsimony informative characters produced 898 trees of 190 steps. The topology generated using successive weighting or transversion parsimony did not differ from the unweighted maximum parsimony topology (data not shown). Neither of the analyses supported a monophyletic grouping of the Scleractinia. The clades supported [BP(bootstrap proportions) >70%)] in both analyses consisted of genera within the same family, although only three of these groupings (Fungiidae, Meandrinidae and Poritidae) included all of the genera sampled from a family.

16S Ribosomal Sequences.—The 32 sequences collected for this study from the 16S mitochondrial ribosomal gene region ranged in size from 407 to 566 bp. These sequences were analyzed in combination with 36 previously published sequences [(France et al., 1996; Romano and Palumbi, 1996); Table 1]. These 68 sequences represent 61 genera in 20 (of 24 total) extant families and all seven extant suborders of Scleractinia. The g_I statistic for 10,000 randomly generated trees ($g_I = -0.25$) from these data indicates that the data are significantly more structured than random (Hillis and Huelsenbeck, 1992). The greatest (HKY+Γ) difference observed between any pair of corals is 69%. However, within each major clade differences range from 0–13.3% ('complex' corals) and 0–19% ('robust' corals). All of the sequences are easily alignable to previously published sequences due to highly conserved blocks between variable regions (Romano and Palumbi, 1997). Comparison of nucleotide composition, transition and transversion substitutions, rates of divergence, and secondary structure of previously published 16S sequences demonstrates that scleractinian mitochondrial 16S sequences are evolving under similar evolutionary constraints (Romano and Palumbi, 1997).

In previous analyses of 16S sequences, multiple amplification products were obtained from three different species (Romano and Palumbi, 1997). This same phenomenon was observed in one additional species among the new taxa sampled for this study, *Placotrochus laevis*. The longer amplification product was used in analyses as it is very similar to sequences from other genera in the Flabellidae. The shorter amplification product, which

Figure 1. Neighbor-joining phylogram generated from 222 bp of the nuclear 28S rRNA gene from 45 species of scleractinians. Distances were calculated using the Tamura and Nei (1993) model with maximum likelihood estimates of the proportion of invariant sites (0.4174) and the gamma distribution parameter (0.4476). Bootstrap proportions from 1000 replicates are shown- neighbor-joining above branches, maximum parsimony below branches. Branches without numbers are supported by bootstrap proportions of less than 70. Symbols represent morphological suborders: □=Archaeocoeniina, △=Fungiina, ■=Faviina, ◇=Caryophylliina, ●=Meandrina, and ▲=Dendrophylliina. Left: topology with unsupported branches shown. Right: topology with unsupported branches not shown.

was not used in analyses, is designated as a β sequence as in Romano and Palumbi (1997). The nature of these β sequences remains unclear.

For the mitochondrial sequences, the Hasegawa et al. (1985) model with rate variation (referred to as HKY+Γ) was determined to be the best fit for minimum evolution analyses. Distances were calculated with a maximum likelihood estimate of the gamma shape parameter (0.7824) and no invariable sites. A heuristic search, based on maximum parsimony with 189 informative characters, yielded 612 shortest length trees of 677 steps. The deepest branches of all 612 trees are identical, the only differences among the trees being in the placement of terminal taxa. *Corynactis* always grouped within the Scleractinia, to the exclusion of the other two outgroups (another anthozoan and a hydrozoan). Minimum evolution and maximum parsimony analyses yielded similar topologies (Fig. 2) with two exceptions. The Poritidae clade in the 'complex' corals has some support (BP = 71) from maximum parsimony analysis but no support (BP < 50) in minimum evolution analyses. Among the 'robust corals', the clade consisting mostly of members of Faviina with some caryophylliids has some support (BP = 72) from maximum parsimony anlyses but little support (BP = 51) from minimum evolution analyses.

The basal topology from the 16S sequences (Fig. 2) is highly robust. Maximum parsimony analyses with transversions weighted two or ten times more than transitions resulted in the same deep structure of 'complex' and 'robust' corals with major clades within each of these groupings (data not shown). Analyses including only one representative of taxa whose sequences were very similar also resulted in the same deep structure (data not shown). Likewise, analyses with successive weighting resulted in the same deep structure (data not shown). The basal groups of the topology appear in all analyses.

None of the well-supported branches of the 16S topology are equivalent to morphological groupings above the family level. The shortest topologies (158 total) that include monophyletic suborders as hypothesized by morphology (Veron, 1995) are 936 steps long. None are compatible with the topology generated from the molecular data (Fig. 2). These trees were found using a heuristic search based on maximum parsimony where the only trees kept were compatible to a constraint tree representing monophyletic suborders as hypothesized by morphology (Veron, 1995). However, even the tree length of the shortest trees consistent with morphological suborders is much shorter than the shortest tree length (1937 steps) observed among 1,000,000 randomly generated trees. The observed difference in length between the molecular topology and the morphological topology based on the molecular dataset is greater than 99% of differences generated from randomized datasets. This indicates that the difference in lengths could not be achieved by chance alone. The T-PTP test indicated support (P ≤ 0.01) for non-monophyly of scleractinian suborders as observed in the molecular topology. The Kishino-Hasegawa test was significant at the 0.0001 level indicating that the two trees are significantly different from each other.

10% divergence
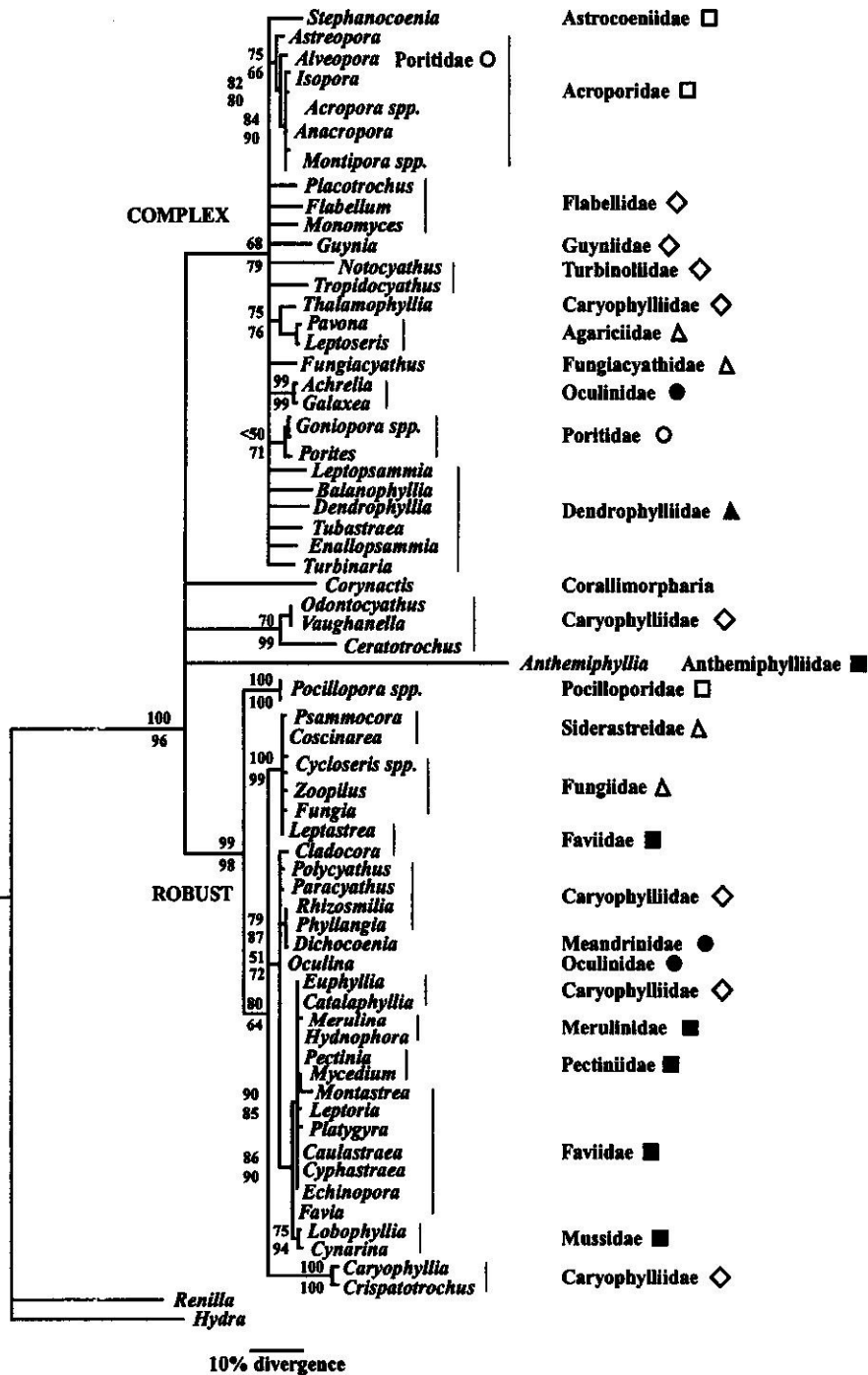
DISCUSSION

28S RIBOSOMAL SEQUENCES

The short sequences from the nuclear ribosomal gene region obtained in this study do not provide enough resolution to provide any hypotheses about relationships among scleractinian families. In addition, comparisons of results from 28S and 16S sequences are not readily made because sequences from the exact same taxa are not available from both genes. If unsupported branches are considered, analyses of 28S sequences results in a topology that is consistent with the topology generated from 16S sequences, including groupings of representatives of 'complex' and 'robust' corals (Fig. 1, left). While the overall structure of the 28S topology is quite similar to the 16S topology, very few of the groupings are supported by bootstrap analyses (Fig. 1, right). Strongly supported groupings are of species within a genus and genera within a family (Fig. 1, right) as was observed in a previous analysis of 28S sequences from a smaller sample of scleractinian taxa (Veron et al., 1996).

One similarity between the 28S and 16S analyses is the lack of a close relationship between the Acroporidae and Pocilloporidae in the suborder Archaeocoeniina. The 28S sequences collected from representatives of the Acroporidae (*M. verrucosa, A. humilis,* and *A. cytherea*) that aligned poorly with sequences from other corals were clearly 28S sequences. Approximately the first 100 bp of these sequences aligned well with other coral 28S sequences while the rest of the segment was not alignable. The sequences were alignable among each other. They do not appear to be an amplification or sequencing artifact. These acroporid sequences are quite distinct from pocilloporid sequences (they don't align well with each other) and as in analyses based on 16S sequences, these two families do not appear to be closely related.

Hypotheses based on morphology suggest that the Acroporidae and Pocilloporidae are closely related due to three characters that they share: (1) very small polyps, (2) corallites that rarely have more than 12 septa and (3) septa that are composed of relatively few trabeculae (Wells, 1956). These are among the characters that distinguish the Archaeocoeniina from all other suborders and consequently the Archaeocoeniina are considered to have evolved separately from other scleractinians during the entire evolutionary history of the group (Alloiteau, 1952; Wells, 1956; Chevalier and Beauvais, 1987; Roniewicz and Morycowa, 1993). Analyses of 28S sequences do not support these morphological hypotheses. Other molecular evidence from internal transcribed spacer (ITS) regions of the nuclear ribosomal RNA of *Acropora* spp. supports the hypothesis that acroporids are distinct from other scleractinians. These ITS sequences are shorter than sequences from other genera in the Acroporidae. The Acroporidae ITS sequences are the
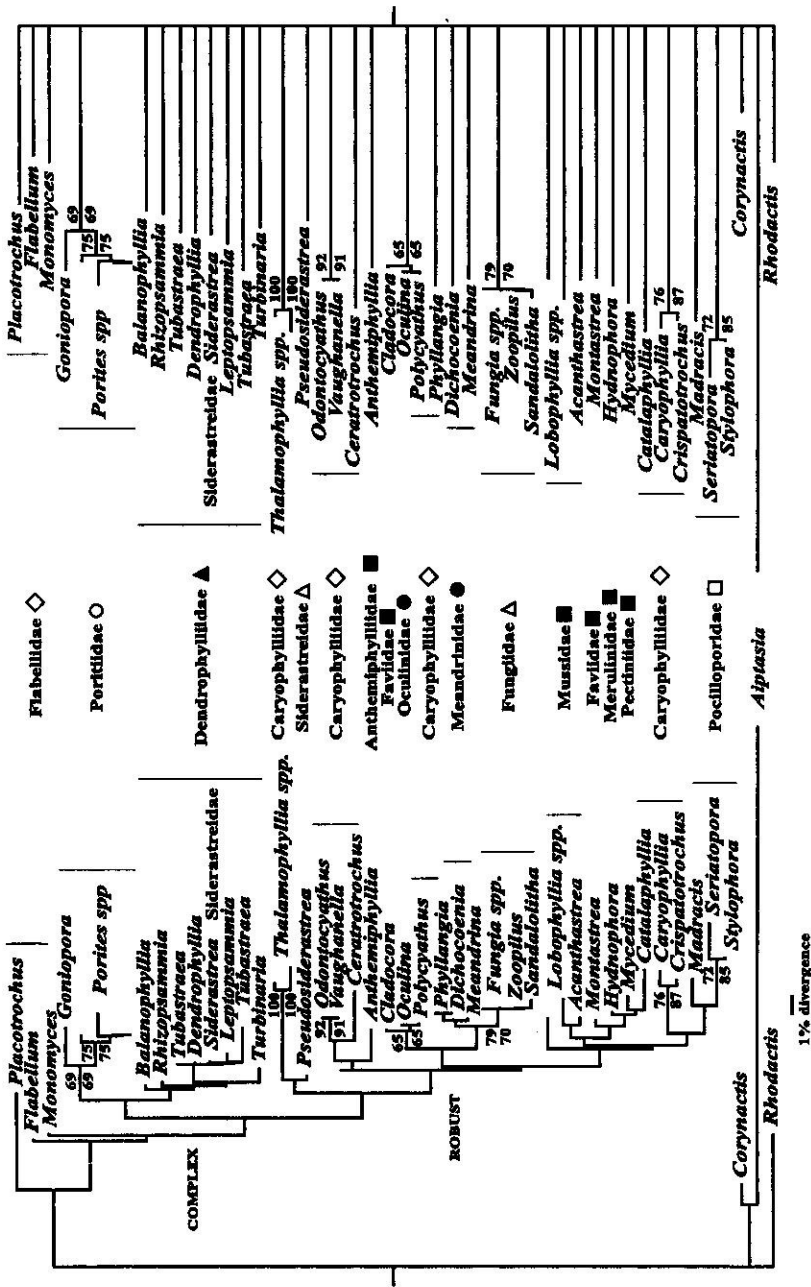
Figure 2. *(opposite page)* Neighbor joining phylogram generated from 566 bp of the mitochondrial 16S rRNA gene from 68 species of scleractinians. Distances were calculated using the HKY+Γ model, with a maximum likelihood estimate of the gamma shape parameter (0.7824) and no invariant sites. Bootstrap proportions from 1000 replicates using the neighbor-joining method are shown above branches; numbers below branches are from 10,000 replicates with the fast stepwise addition option of the maximum parsimony algorithm. Only branches supported by bootstrap proportions of greater than 70 (in one of the analyses) are shown. Symbols represent morphological suborders: □=Archaeocoeniina, △=Fungiina, ■=Faviina, ◊=Caryophylliina, ●=Meandriina, ○=Poritiina, and ▲=Dendrophylliina.

shortest characterized to date in the Metazoa, and appear to be atypical of the Anthozoa (Chen et al., 1996; Odorico and Miller, 1997).

If the unsupported branches of the 28S topology are considered (Fig. 1, left), there are striking similarities to the 16S phylogenetic tree (Fig. 2). Representatives of 'complex' and 'robust' corals group together. One well-supported grouping in the 16S analysis of genera from different families representing different suborders is also found in the 28S analysis. *Phyllangia*, a caryophylliid, forms a clade with *Dichocoenia* and *Meandrina*, two meandrinids (Fig. 1). In the 16S analysis *Phyllangia* also forms a clade with *Dichocoenia* (and this clade also includes another caryophylliid, *Rhizosmilia*; Fig. 2). While a close relationship between these two genera is not supported by previous morphological hypotheses that place them in different families largely because of differences in budding, their septal structure is similar (septa composed of one fan system with simple trabeculae) (Wells, 1956; Chevalier and Beauvais, 1987). In addition, *Odontocyathus, Vaughanella, Ceratotrochus,* and *Anthemiphyllia,* which don't group in either of the major clades and are basal in the 16S analysis, form a clade in the 28S analysis (Fig. 1). In the 28S analysis *Cataphyllia*, a caryophyllid, forms a clade with representatives of the Pectiniidae, Merulinidae, Faviidae, and Mussidae. These taxa all group together in the 16S analysis.

The similarities of the nuclear and mitochondrial analyses described above are tantalizing but more molecular data will be necessary to determine if data from these independent gene regions support the same hypotheses about scleractinian phylogeny. Lack of resolution from the 28S sequences appears to be due to the few number of variable characters (46) in relation to the 45 taxa in the analysis. Perhaps more sequence data from the 28S rRNA gene spanning at least another variable domaine will provide enough additional characters to differentiate relationships within the Scleractinia and determine whether nuclear and mitochondrial phylogenies are concordant. Other less conserved nuclear genes may also be useful for these same purposes.

16S RIBOSOMAL SEQUENCES

As in previous published analyses (Romano and Palumbi, 1996; Romano and Palumbi, 1997), the scleractinian 16S sequences grouped into two distinct clades (i.e., 'robust' and 'complex' corals) which are estimated to have diverged from each other at least 300 ma (Romano and Palumbi, 1996). This divergence time implies that the ancestral lineages that separated from each other were polyp animals without skeletons because the scleractinian skeleton does not appear in the fossil record until 240 ma. However, unlike previous analyses, in the analysis presented here four taxa did not group within either of the two distinct clades but contributed to a basal polytomy of five branches. Two of these branches lead to the distinct clades of 'robust' and 'complex' corals discussed above. The third branch represents another order of anthozoan, the corallimorpharian *Corynactis*. Three taxa (*Odontocyathus, Vaughanella,* and *Ceratotrochus* in the family Caryophylliidae) grouped together forming a fourth basal branch. The fifth branch of the polytomy is *Anthemiphyllia,* representative of the monotypic family Anthemiphylliidae in the Faviina. These basal branches appear to represent very distinct scleractinians. Despite the taxa that do not group into either of the two major clades, support for these two clades is very strong as evidenced by the relatively high bootstrap values under different analyses (minimum evolution and maximum parsimony). However, as evidenced by this five branch polytomy and the lack of resolution for the most part within each of these clades, the

mitochondrial 16S gene region is not capable of completely resolving relationships among the basal clades or among families within each of the two major clades.

The mitochondrial 16S gene region appears to be evolving very slowly when genetic distances between taxa are compared to divergence times for these taxa calculated from the fossil record (Romano and Palumbi, 1997). This has also been observed for other scleractinian mitochondrial gene regions (Best and Thomas, 1993; Snell, 1997; van Oppen et al., 1999). However, these data do not differentiate relationships among the basal lineages in the phylogeny presented. There are two hypotheses to explain this result. It is possible that these basal lineages diverged from each other in a very short time period making it difficult to resolve relationships among the clades with this slowly evolving gene. While the family lineages in each of the two major clades appear at different times since the Triassic, estimation of the rate of evolution within these lineages demonstrates that they diverged at least 300 Ma before the appearance of any of these families in the fossil record [(Romano and Palumbi, 1996) see discussion below]. It is therefore possible that the ancestral soft-bodied lineages diverged from each other over a very short time period and so a more rapidly evolving gene region would be necessary to delineate relationships among the basal lineages.

Alternatively, it is possible that the divergence of the basal lineages occurred so long ago that the signal has been lost from even this relatively slowly evolving gene. Although the ratio of transitions to transversions for all taxa is 1.6, it approaches 1 in comparisons at the family level and above (Romano and Palumbi, 1996), an indication that these data are approaching saturation for comparisons of higher level relationships. In this case, a more slowly evolving nuclear gene might provide the necessary resolution for more clearly delineating relationships among the basal clades in the 16S topology and among scleractinian families.

COMPARISON OF MOLECULAR AND MORPHOLOGICAL HYPOTHESES

The phylogenetic hypothesis presented here based on mitochondrial DNA sequences does not agree with phylogenetic hypotheses generated from morphological data above the family level (Alloiteau, 1952; Wells, 1956; Chevalier and Beauvais, 1987; Veron, 1995). While in most cases genera group into morphological families, genera from different families (e.g., *Dichocoenia, Rhizosmilia,* and *Phyllangia*) and families from different suborders (e.g. Caryophylliidae and Agariciidae) group together. Any tree consistent with morphological hypotheses is considerably longer than the shortest molecular phylogeny. The T-PTP test indicates strong support of non-monophyly of morphological suborders ($P \leq 0.01$). Likewise the Kishino-Hasegawa test demonstrates that the molecular and morphological hypotheses are significantly different from each other. Thus, the morphological hypothesis appears to be a poor explanation for the molecular data relative to the molecular hypothesis.

It is possible that a combined analysis of morphological and molecular characters would provide the most complete perspective on scleractinian evolution. However, these analyses are not feasible given our current level of understanding of skeletal homologies. Lack of understanding of skeletal homologies makes identification of informative morphological characters very difficult. To date, a cladistic analysis of the entire order using morphological characters has not been carried out. A cladistic analysis of 48 skeletal characters, ascertained from the literature, from a limited number of reef-building corals had a relatively low consistency index of 0.61 indicating high levels of homoplasy within

the dataset (Romano, 1995). In this analysis, the majority of morphological characters have at least one character state that is found in more than one suborder and one character state that varies in at least one family. The limited number of currently available morphological characters relative to molecular characters (235 informative nuclear and mitochondrial characters) means that morphological characters would have relatively little influence in any combined analysis.

While the segment of the mitochondrial 16S ribosomal gene used in this study is not able to resolve relationships among families of Scleractinia, it does provide some insight into the evolutionary history of the order. Romano and Palumbi (1996) concluded that the differentiation of the two principal scleractinian clades ('robust' and 'complex') occurred at least 300 Ma, before the appearance of the scleractinian skeleton in the fossil record 240 Ma. This implies that the scleractinian skeleton has evolved more than once from a soft-bodied, anemone-like ancestor. The more comprehensive analysis of the order presented here is consistent with Romano and Palumbi's (1996) conclusions that the Scleractinia, with the defining characteristic of an aragonitic calcium carbonate skeleton and cyclic insertion of septa, is not monophyletic. These new data suggest the possibility that the scleractinian skeleton could have evolved as many as four times.

The origin of the scleractinian skeleton has been a subject of some debate (Vaughan and Wells, 1943; Roniewicz and Morycowa, 1993; Veron, 1995; Oliver, 1996; Ezaki, 1997; Ezaki, 1998) and there is abundant evidence in the fossil record for the hypothesis that the scleractinian skeleton evolved more than once (see Wendt, 1990; Scrutton and Clarkson, 1991; Oliver, 1996; Scrutton, 1997). Two other orders of skeletonless hexacoralians, the Actiniaria and the Corallimorpharia, are considered very closely related to scleractinians because all three groups have nearly identical mesenterial arrangements (Wells and Hill, 1956), which means that the basic architecture of the polyps is the same. In fact, the Corallimorpharia are often described as scleractinians without skeletons although corallimorpharians also have a different tentacular arrangement, a greater diversity of nematocysts, and possess cells in the mesoglea. The scleractinian skeleton first appeared as two distinct lineages in the Mid-Triassic (Vaughan and Wells, 1943; Veron, 1985; Roniewicz and Morycowa, 1993) but there is disagreement as to which of the two lineages gave rise to modern corals. All of this evidence clearly demonstrates that soft-bodied hexacoralians have acquired skeletons multiple times. The scleractinian skeleton is characterized by enormous variability such that homologies of skeletal characters have proven difficult to understand (Cuif, 1980; Roniewicz and Morycowa, 1993; Veron, 1995) and so it is difficult to clearly demonstrate that the scleractinian skeleton is monophyletic. Therefore it seems possible that the skeletal structures of all scleractinians are not homologous and this lack of homology is due to separate evolutionary histories over hundreds of millions of years. While the molecular data provide support for the hypothesis of multiple origins of the scleractinian skeleton, a greater understanding of skeletal homologies along with molecular data from another gene region will be necessary before this hypothesis can be thoroughly tested.

IMPLICATIONS FOR SCLERACTINIAN TAXONOMY

Suborders.—The mitochondrial data presented here support previous suggestions (Chevalier and Beauvais, 1987; Roniewicz and Morycowa, 1993; Veron, 1995) that morphological phylogenetic hypotheses for relationships among scleractinian families and suborders, and in some cases genera, need to be reevaluated. Molecular data alone cannot

be used for taxonomic classification and recent work by palaeontologists has demonstrated the phylogenetic utility of in-depth study of skeletal characters (Budd et al., 1994; Lathuilière, 1996; Stolarski, 1996). However, in conjunction with knowledge of scleractinian biology, molecular data can be useful for generating new hypotheses to be tested as well as for differentiating among competing hypotheses that have been proposed based on morphology.

Molecular data do not support the hypothesis that suborders erected based on morphology are monophyletic [the five suborder classification of Wells (1956), the seven suborder classification of Veron (1995) or the classification based on microstructural characters proposed by Roniewicz (1993)]. However, they do support some of the relationships within these schemes such as those hypothesized within the suborder Faviina, between the families Poritidae and Dendrophylliidae, and for genera within families. Similarities between morphological and molecular hypotheses are described in more detail in the discussion below. Based on these results, scleractinian suborders as currently defined need to be reexamined. The molecular data presented here suggest at least two major subgroupings within the Scleractinia ('complex' and 'robust' corals). However, further work will be necessary to differentiate relationships within each of these major subgroupings and to determine the status of the remaining four taxa that branch outside of the two major clades.

The Archaeocoeniina consists of three families considered to have evolved separately from other corals since the Triassic, throughout the evolutionary history of the order. This suborder is distinguished from others by both skeletal and polyp characters (Wells, 1956). The distinguishing skeletal character of the suborder is that septa are composed of few trabeculae not arranged in a fan system (Wells, 1956; Chevalier and Beauvais, 1987). The polyps of families in the Archaeocoeniina are distinguished from all other scleractinians by rarely having more than two cycles of tentacles and lacking stomodaeal ridges (Wells, 1956). Molecular data do not support a monophyletic origin of these families or a close relationship between them. The Pocilloporidae and the Acroporidae group apart from one another, each in one of the major clades of the molecular topology. The close relationship between these two families has been questioned by Kinzie (1996) based on an analysis of speciation and reproductive characters.

Fungiina consists of five extant families originating in the Triassic. These families are grouped together morphologically based on the generally perforate architecture of their septa which also have beaded or dentate margins and are joined together by synapticulae (Alloiteau, 1952; Wells, 1956; Chevalier and Beauvais, 1987). There is no molecular support for monophyly of this suborder as proposed by Veron et al. (1996). Morycowa and Roniewicz (1995) have pointed out that patterns of septal and synapticular structure do no support the monophyly of this suborder. Although the Siderastreidae and the Fungiidae group together in the mitochondrial analysis (in the 'robust' clade), the other two families sampled from this suborder (Agariciidae and Fungiacyathidae; Table 1) are found in the second major clade (the 'complex' corals). The distinctness of the Fungiidae from other families in the Fungiina has also been suggested based on phenetic analysis and microstructural characters (Powers, 1970; Gill, 1980; Roniewicz and Morycowa, 1993; Morycowa and Roniewicz, 1995; Lathuilière, 1996). Morycowa and Roniewicz (1995) note the shape and arrangement of trabeculae of *Fungia* resembles those of faviids, pectiniids, and mussids, families that form a well-supported clade in the 'robust' corals where the Fungiidae also group.

The Faviina consists of seven living families with Jurassic origins. The distinguishing character of this suborder is septa that are strongly dentate (Alloiteau, 1952; Wells, 1956; Chevalier and Beauvais, 1987). The mitochondrial data support a monophyletic origin of families within the suborder but do not differentiate relationships among these families. All families sampled in the Faviina except the monotypic family Anthemiphylliidae form a distinct clade within the major clade of 'robust' corals. Two genera in the Faviidae, *Leptastrea* and *Cladocora*, do not group with other members of this family suggesting that the placement of these two genera needs to be reexamined. The Anthemiphylliidae appears quite distinct from all other species in the molecular topology. There is little paleontological history for this family (Gerth, 1921; Wells, 1977) which has been placed within the Faviina based on its strongly dentate septa (Wells, 1956) but it appears that its affinities need to be reexamined.

Caryophylliina consists of five living families that originate in the Jurassic. This suborder does not have a distinguishing character but is defined by a combination of skeletal characters which include lamellar septa with a smooth margin that are composed of one fan system of compound, small trabeculae (Alloiteau, 1952; Wells, 1956; Chevalier and Beauvais, 1987; Roniewicz and Morycowa, 1993). Although most of the minor families of the suborder Caryophylliina group within the 'complex' corals, representatives of the Caryophylliidae are found throughout the molecular topology. This is the only large family in which all genera are not monophyletic. Caryophylliidae is the largest family of azooxanthellate corals and considered the most successful of all scleractinian groups in adaptation to extremes of environment (Wells, 1956). These molecular data suggest that this suborder is not monophyletic and the combination of shared ancestral characters that have been used to define it may not be sufficient for differentiating these taxa from other scleractinians.

Veron (1995) erected the suborder Meandriina by removing the Oculinidae and the Meandrinidae from their traditional placement in the Faviina. Both of these families have Cretaceous origins. However, our molecular data do not support the placement of these two families in their own suborder. They are found in the same major clade as the Faviina (although see further discussion of the Oculinidae below) but do not appear to be closely related to other families in the suborder. In fact both families appear to be more closely related to representatives of the Caryophylliina.

The Poritiina and Dendrophylliina are each represented by one living family with origins in the Jurassic. Molecular data are consistent with Veron's (1995) hypothesis that they are more closely related to each other than to any other families. They both group within the 'complex' corals, separately from representatives of the Fungiina, the suborder in which the Poritidae has traditionally been placed. Veron et al. (1996) hypothesized a close relationship between the Poritidae and Dendrophylliidae due to their parathecate wall structure and fused septal configurations. However, it is not yet clear from the molecular data whether the Poritidae should be elevated to suborder status as proposed by Veron et al. (1996).

Families.—While in general genera within families grouped together, genera from the Caryophylliidae are found throughout the mitochondrial topology. Three other families have one or two genera that group separately from other members of the family: the very large zooxanthellate family Faviidae, the Poritidae and the Oculinidae. All representatives of the Faviidae are found within the 'robust' corals but two genera (*Leptastrea* and *Cladocora*) fall outside the other genera in the family. Likewise, all members of the

Poritidae are found within the 'complex' corals however one genus (*Alveopora*) grouped with the family Acroporidae instead of other poritids. Genera from different sub-families in the Oculinidae grouped in different major clades.

The Caryophylliidae has the largest number of genera of any scleractinian family. It is defined by a combination of shared ancestral skeletal characters, not by one distinguishing, derived character. The six sub-families within the Caryophylliidae are not clearly morphologically distinct one from the other but differ quantitatively, grading into each other (Wells, 1956) and these groupings have been ignored by most taxonomists over the last 20 yrs. However, the subfamilies are somewhat apparent in the mitochondrial phylogenetic tree, with only samples in the subfamily Caryophylliinae not all grouping together. Cairns (1997) elevated the subfamily Turbinoliinae to family level because his phylogenetic analysis of morphological characters demonstrated that the taxa in this subfamily are united by a shared derived character, a completely invested corallum. The two representatives of the Turbinoliidae do group in the same major clade of the molecular analysis, among the 'complex' corals.

Most representatives of the Caryophylliidae group in the clade of 'robust' corals. *Thalamophyllia* grouped with representatives of the Agariciidae among the 'complex' corals. *Thalamophyllia* has the combination of characters that defines other caryophyllids in the 'robust' clade but it is the only representative of the subfamily Desmophyllinae in our analysis. Desmophyllinae is differentiated from other subfamilies of Caryophylliidae by a combination of characters including the presence of a weakly developed endotheca (Cairns, 1997). In addition, *Thalamophyllia* has a wall structure described as trabeculothecate (J. Stolarski, pers. comm.) instead of the septothecate wall characteristic of the Caryophylliina. The other caryophyllids that group outside the 'robust' clade are *Odontocyathus, Vaughanella* and *Ceratotrochus*, which group together but basally to both of the major clades. These genera belong to the subfamily Caryophyllinae which is differentiated from other subfamilies of caryophyllids by a combination of characters. *Odontocyathus* and *Vaughanella* are so similar that they could be considered subgenera and are found in very deep waters.

Although eight caryophyllids group within the 'robust' corals, they do not all group together within that clade. *Euphyllia* and *Catalaphyllia* group with representatives of the Faviina as part of a well-supported clade that is exclusive of the other caryophyllids in the 'robust' clade. These two genera are in the subfamily Eusmiliinae, the only caryophyllid subfamily with zooxanthellate, reef-building taxa. The grouping of these two genera with other zooxanthellate, reef-building taxa is therefore perhaps not surprising. Pires and Castro (1997) found that the cnidom of another genus in the Eusmiliinae, *Physogyra*, is distinct from other caryophyllids that were studied. The placement of *Polycyathus* and *Paracyathus* (subfamily Caryophylliinae) in the Caryophylliidae has long been debated and most recently Verheij and Best (1987) suggested that these genera should be placed in the family Rhizangiidae. We did not sample any members of the Rhizangiidae, but *Polycyathus* and *Paracyathus* did group together (but this grouping was not supported by a high bootstrap proportion). *Rhizosmilia* and *Phyllangia*, both in the subfamily Parasmilinae, group together with *Dichocoenia*, a meandrinid. These three genera do share some characters: septa constructed by one fan system of simple trabeculae, a septothecate corallite, coloniality, and attachment to the substratum (Wells, 1956; Cairns, 1994). The septa of *Dichocoenia* are minutely dentate, similar to the nearly smooth septal margins characteristic of caryophyllids. *Caryophyllia* and *Crispatotrochus*, both in the

subfamily Caryophylliinae, form a well-supported clade. These molecular data somewhat support subfamily groupings within the Caryophylliidae but suggest that the lack of distinguishing characters for the subfamilies and the use of a combination of morphological characters to define the family and subfamilies is not sufficient for determining the relationships of these taxa to each other or to other scleractinians.

The Faviidae has the largest number of genera of any zooxanthellate family (Veron 1995). While the genera in this family are well defined, the relationships among genera have been considered unclear. It is perhaps not so surprising that (in the 16S analysis) two genera did not group with other members of the family. *Cladocora,* along with some caryophyllids, grouped in the clade of 'robust' corals along with all of the other faviids but not in the faviid clade itself. The affiliation of *Cladocora* to the Faviidae has been considered dubious and this genus has most recently been placed in the Caryophylliidae by Cairns (in press). *Leptastrea* also grouped in the 'robust' corals with all of the other faviids but not in the faviid clade itself. Instead, *Leptastrea* grouped with representatives of the Fungiidae and Siderastreidae. There is no morphological or taxonomic precedence for this grouping. These molecular data suggest that the morphological characters of this genus need to be reexamined.

The Poritidae is distinguished from other scleractinian families by its unique septal and wall architecture. Three of the four genera in the family were sampled. While representatives of *Porites* and *Goniopora* grouped together, *Alveopora,* which does not have the characteristic poritid pattern of septal fusion, grouped with members of the Acroporidae. Veron (1995) states that *Alveopora* is taxonomically isolated within the family and has unclear affinities. It has a highly porous skeleton. The morphological basis for its placement in the Poritidae does not appear strong and it does have morphological similarities to the Acroporidae, such as the lack of well-defined septa.

The family Oculinidae has a poor fossil record (Veron, 1995) and is sometimes divided into two subfamilies. The Oculininae consists of primarily non-reef-building genera that are dendroid with a dense coenosteum (Wells, 1956). The genus sampled in this study representative of Oculininae, *Oculina,* comprises both azooxanthellate and zooxanthellate species (Veron, 1986). The second subfamily, Galaxeinae, represented here by *Acrhelia* and *Galaxea,* consists of reef-building, zooxanthellate genera that are ramose or plocoid with a vesicular coenosteum and highly exsert septa (Wells, 1956). The representatives of these two sub-families are very different from each other at the molecular level, each grouping in a different major clade. The two subfamilies are morphologically distinct and so it is perhaps not surprising that they don't group together in the molecular analysis although it is difficult to explain why they might be as different at the molecular level as they are.

Genera.—In general none of our molecular data provide resolution of relationships among genera. However, two of the genera sampled have been the subject of taxonomic debate. Molecular data from these samples do provide support for different hypotheses that have been proposed for these taxa.

The genus *Psammocora* was included in the family Thamnasteriidae, suborder Astrocoeniina (= Archaeocoeniina), by Wells (1956) due to septa composed of a small number of trabeculae and to the similarity of tentacles to some genera in the Pocilloporidae (another family in the Astrocoeniina). Veron (1986) placed this genus in the Siderastreidae (suborder Fungiina) because of the greater number of skeletal characters, such as the presence of synapticulae, confluent septa and the presence of collines, that it shares with

Coscinarea (Wells, 1956; Chevalier and Beauvais, 1987). These skeletal characteristics are typical of genera in the Agariciidae and Siderastreidae (Veron and Pichon, 1976). The two genera only differ in that *Psammocora* has a slightly different synapticulothecal wall, only compound trabeculae and smaller corallites than *Coscinaraea* (Wells, 1956; Chevalier and Beauvais, 1987). The mitochondrial data clearly support this hypothesis. *Psammocora* appears to be closely related to *Coscinaraea* in the Siderastreidae. Both genera are more closely related to the Faviidae than to the Pocilloporidae.

The genus *Fungiacyathus* has traditionally been placed in the Fungiidae. Chevalier and Beauvais (1987) elevated this genus to family status because of its unique wall stucture among the Fungiina. Pires and Castro (1997) noted that the cnidom of *Fungiacyathus* is distinct from the Fungiidae. Family status separate from the Fungiidae is supported by these molecular data as *Fungiacyathus* does not group with genera in the Fungiidae. In fact, in the 16S analysis *Fungiacyathus* groups with members of the Poritidae and the Dendrophylliidae in the major lineage that does not include the Fungiidae. Pires and Castro (1997) found that the tentacle cnidom of *Fungiacyathus* is composed of the same elements as that of the Poritidae, a family also found among the robust corals.

SUMMARY

Although these molecular data provide a new set of characters for understanding scleractinian evolution, much work remains to determine exactly how they may change phylogenetic hypotheses for the Scleractinia. Further work is necessary to determine whether the mitochondrial topology is the result of unusual characteristics of scleractinian mtDNA or the reflection of the actual phylogenetic history of the suborder. Additional molecular data from a nuclear gene would (1) provide a molecular test of scleractinian polyphyly, (2) provide a more refined estimate of the date of divergence of the major groups within the mitochondrial topology and (3) provide greater resolution of relationships among taxa in the major clades of the mitochondrial topology. Although many questions about these molecular data remain to be addressed, they do provide new, testable hypotheses for the evolution of the Scleractinia. While the sequence data from the nuclear 28S ribosomal gene gathered to date holds little information, sequence data from the mitochondrial 16S ribosomal gene has provided a phylogenetic hypothesis for higher order relationships within the Scleractinia that is quite different from hypotheses based on morphology and the fossil record. Clearly, a revision of relationships among families and certain genera within the Scleractinia is called for.

Lack of congruence between molecular data and morphological hypotheses above the family level can be explained by either problems with molecular data or problems with morphological data. As discussed above, additional molecular data would allow for a better understanding of possible problems in molecular characters. A more complete, detailed understanding of microstructural and macromorphological skeletal characters would aid in evaluating problems in morphological characters. Analyses of microstructural skeletal characters have advanced greatly in recent years although fossil taxa have been the focus of these studies. Detailed study of microstructural characters in a wider variety of extant taxa will be of great assistance in more thoroughly evaluating morphological hypotheses called into question by molecular data. Likewise, more detailed studies of homologies and variation among macromorphological characters is necessary. Com-

bined analyses of morphological and molecular characters may provide the most complete perspective on scleractinian evolution. However, these analyses are not feasible given our current level of understanding of skeletal homologies (Romano, 1995). Better understanding of both molecular and morphological problems will be necessary before a complete evaluation of competing morphological and molecular hypotheses can be carried out.

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