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SYMPOSIUM

Rethinking the Phylogeny of Scleractinian Corals: A Review of Morphological and Molecular Data

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Synopsis Scleractinian corals, which include the architects of coral reefs, are found throughout the world's oceans and have left a rich fossil record over their 240 million year history. Their classification has been marked by confusion but recently developed molecular and morphological tools are now leading to a better understanding of the evolutionary history of this important group. Although morphological characters have been the basis of traditional classification in the group, they are relatively few in number. In addition, our current understanding of skeletal growth and homology is limited, and homoplasy is rampant, limiting the usefulness of morphological phylogenetics. Molecular phylogenetic hypotheses for the order, which have been primarily focused on reef-building corals, differ significantly from traditional classification. They suggest that the group is represented by two major lineages and do not support the monophyly of traditional suborders and most traditional families. It appears that once a substantial number of azooxanthellate taxa are included in molecular phylogenetic analyses, basal relationships within the group will be clearly defined. Understanding of relationships at lower taxonomic levels will be best clarified by combined analyses of morphological and molecular characters. Molecular phylogenies are being used to inform our understanding of the evolution of morphological characters in the Scleractinia. Better understanding of the evolution of these characters will help to integrate the systematics of fossil and extant taxa. We demonstrate how the combined use of morphological and molecular tools holds great promise for ending confusion in scleractinian systematics.

Introduction

Scleractinian corals are found throughout the world's oceans, including temperate and polar regions, from the intertidal to the deepest trenches. Members of the phylum Cnidaria, they are polyps with a calcareous skeleton that have left a well-preserved and rich fossil record that starts in the mid-Triassic. There are approximately 1300 described extant species (Cairns 1999) comprised of two main groups. About half the species are reef-building corals, largely colonial, and zooxanthellate and occurring in the clear, shallow waters of the tropics. The other half of the order is largely solitary and azooxanthellate, occurring in all regions of the oceans, including the greatest depths.

Confusion has been a hallmark of scleractinian classification since stony corals were recognized as a related group of organisms in the 16th century and originally classified as plants (Vaughan and Wells 1943). The name Zoophyta (Gr. *zoon*: animal; *phyton*: plant) was applied to them through the 1800s (Hyman 1940). While confusion about their classification diminished as they were studied in greater detail, it reemerged in the late 20th century when molecular techniques began to be applied to scleractinian systematics. In fact, molecular phylogenetic analyses have revolutionized our understanding of scleractinian evolution.

Here, we review the use of morphological and molecular characters in the study of scleractinian

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relationships. We briefly review traditional classification of the order and provide an overview of morphological characters. We discuss contributions to understanding of scleractinian evolution from separate phylogenetic analyses of morphological and molecular data. While molecular data have provided new hypotheses for scleractinian relationships, development of new morphological characters has also improved our understanding of scleractinian evolution. We provide examples of how morphological and molecular data used together can advance our understanding of evolution in the order. The use of molecular phylogenetics in combination with more sophisticated morphological studies holds promise for enhancing resolution of scleractinian relationships.

Traditional classification

Traditional classification of the Scleractinia has been based largely on skeletal characters. Workers in the 19th and early 20th century studied the scleractinian skeleton in detail, with the work of Milne Edwards and Haime (1857) being the most influential. Stolarski and Roniewicz (2001) presented a thorough review of the history of scleractinian classifications. Classifications in the 19th and early 20th centuries were based on easily measured macromorphological characters derived from both paleontological and recent samples. Some characteristics of the living animal were also included (e.g., Duerden 1902; Matthai 1914). These classifications, based only on the extensive knowledge of the authors (e.g., Milne Edwards and Haime 1857; Duncan 1885), were considered a hypothesis for evolutionary relationships within the order.

In the mid to late 20th century, scleractinian classifications continued to be based on macromorphological characters with the addition of knowledge of microstructural characters. The ''traditional'' scleractinian classification system that is most widely used by coral biologists was developed by Vaughan and Wells (1943) and Wells (1956). Their work consisted of a complete revision of the order, including both paleontological and recent samples and was based on skeletal morphology observed by way of an optical microscope. Wells' system recognizes five suborders (all extant) and 33 families (20 extant) with an evolutionary tree as a hypothesis for relationships among families within the order (Fig. 1). The five suborders derived from two lineages that first appear in the late Triassic. No relationship was hypothesized between the suborder Astrocoeniina and the other four suborders. Even relationships between the four suborders derived from the same lineage were depicted as tenuous.

The advent of SCUBA in the mid 20th century reenergized the study of scleractinian taxonomy by enabling scientists to study corals *in situ*. Many studies, starting in the 1960s, demonstrated the extent of intraspecific variability in scleractinian skeletal characters (recently reviewed by Todd [2008]) and the value of characteristics of the living animal in differentiating species (Lang 1984). In Australia during the 1970s, Veron and colleagues did extensive field studies of the scleractinians of the Great Barrier Reef (Veron and Pichon 1976, 1980, 1982; Veron et al. 1977; Veron and Wallace 1984; Veron 1985, 1986), providing the first detailed studies that included information about the living animal. This work formed the basis for Veron's analysis of reef-building Scleractinia world wide. Veron (1995, 2000) refined the Wells (1956) evolutionary tree, adding two new extant suborders (13 in all) and four new extant families (59 families total; Fig. 2). However, his evolutionary tree has even less resolution among families and suborders than did the scheme of Wells (1956).

General overview of morphological characters

Skeletal architecture

Traditional taxonomic approaches to scleractinians depend almost exclusively on the coral skeleton. Like other anthozoans, the basic morphological unit is the polyp, which is supported by a skeletal cup or ''calice'' on the upper exoskeleton or ''corallum'' surface (Fig. 3). The cylindrical extension of an individual calice below the corallum surface is known as a ''corallite''. Many of the most important morphological features used in traditional taxonomy are related to the architecture of corallites. They involve the morphogenesis of the skeleton, including the budding and integration of corallites within colonial corals (Wells 1956, p. F350–2), development of ''septa'' (radially arranged vertical partitions within corallites), ''costae'' (extensions of the septa beyond the wall), the ''columella'' (vertical central axial structure), the corallite ''wall'' (vertical structure enclosing a corallite), and the ''coenosteum'' or ''peritheca'' (skeleton between corallites). Also important is the development of ''synapticulae'' (horizontal rods that extend between septa), ''dissepiments'' (horizontal or diagonal platforms within and outside of the corallite wall, termed ''endotheca'' and ''exotheca'', respectively), and ''epitheca'' (external sheath surrounding an individual corallite or corallum). Further definitions of these terms and terms for many additional skeletal features

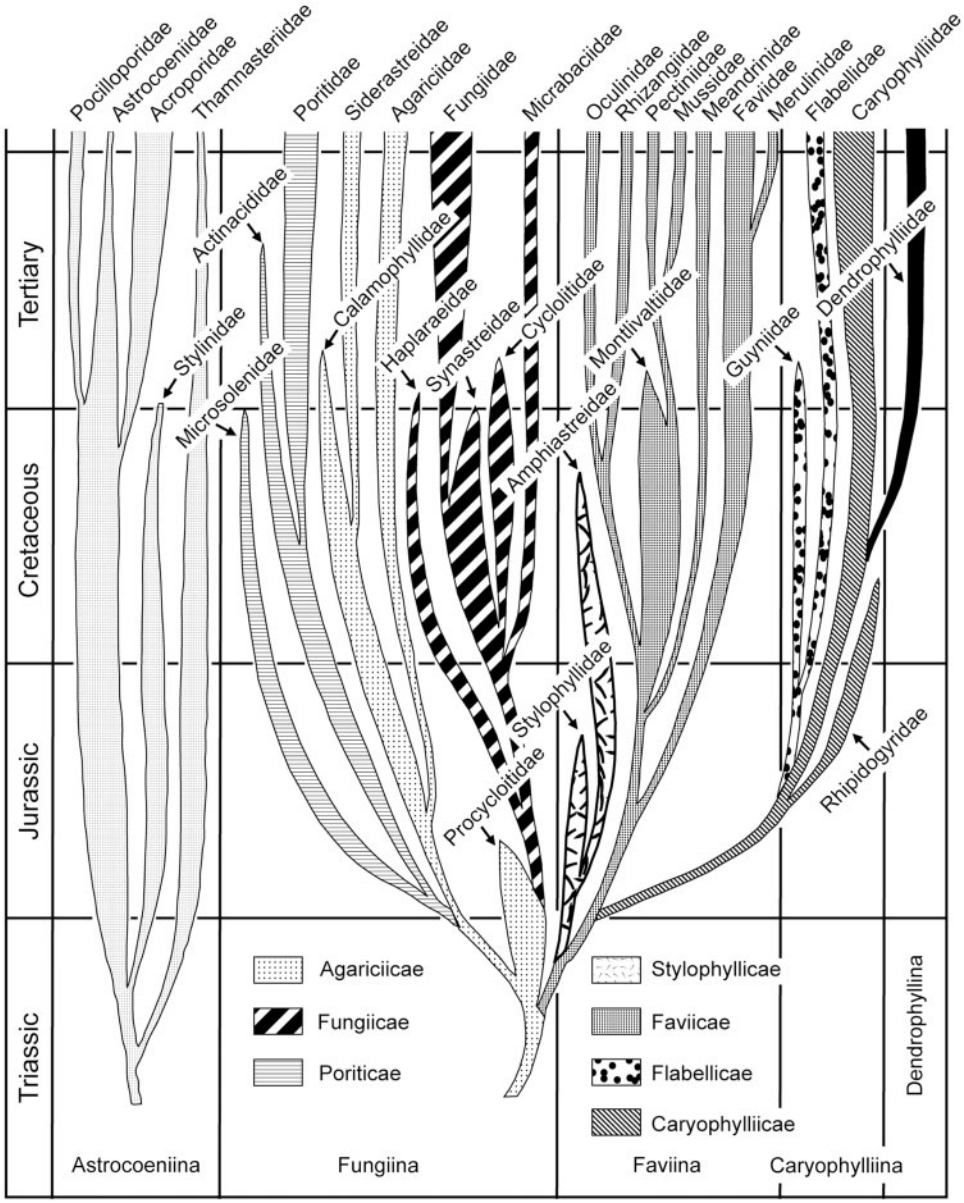

Fig. 1 Phylogeny of scleractinian corals proposed by Wells (1956, p. 363). Branches represent families, patterns represent superfamilies, and columns represent suborders. From *Treatise on Invertebrate Paleontology*, courtesy of and © 1956, The Geological Society of America and The University of Kansas.

are given by Vaughan and Wells (1943), Wells (1956), Alloiteau (1957), and Chevalier and Beauvais (1987).

Skeletal morphological features can be broadly grouped into three categories (Budd and Stolarski 2009): (1) *Macromorphology*: the size and shape of many features related to corallite architecture and the integration of corallites within colonies (3D observations made using an optical microscope); (2) *Micromorphology*: the shapes of teeth and granules along the margins and faces of septa (3D observations made using regular light or scanning electron microscopy of calical surfaces); (3) *Microstructure*: the arrangements of centers and fibers within septa and the corallite wall (2D observations made using transverse thin sections and scanning electron microscopy of polished and etched transverse sections). Of these three categories, macromorphological characters are important in traditional taxonomy at the generic and specific levels, whereas micromorphological characters are also important at the familial level and above (Wells 1956, p. F368). With the exception of Alloiteau (1957) and Chevalier and Beauvais (1987), microstructural characters are less commonly used in traditional taxonomy. For example, Alloiteau (1957) raised three families (Stylinidae, Meandrinidae, Amphiastreidae) to subordinal rank based on number of vertical rods or

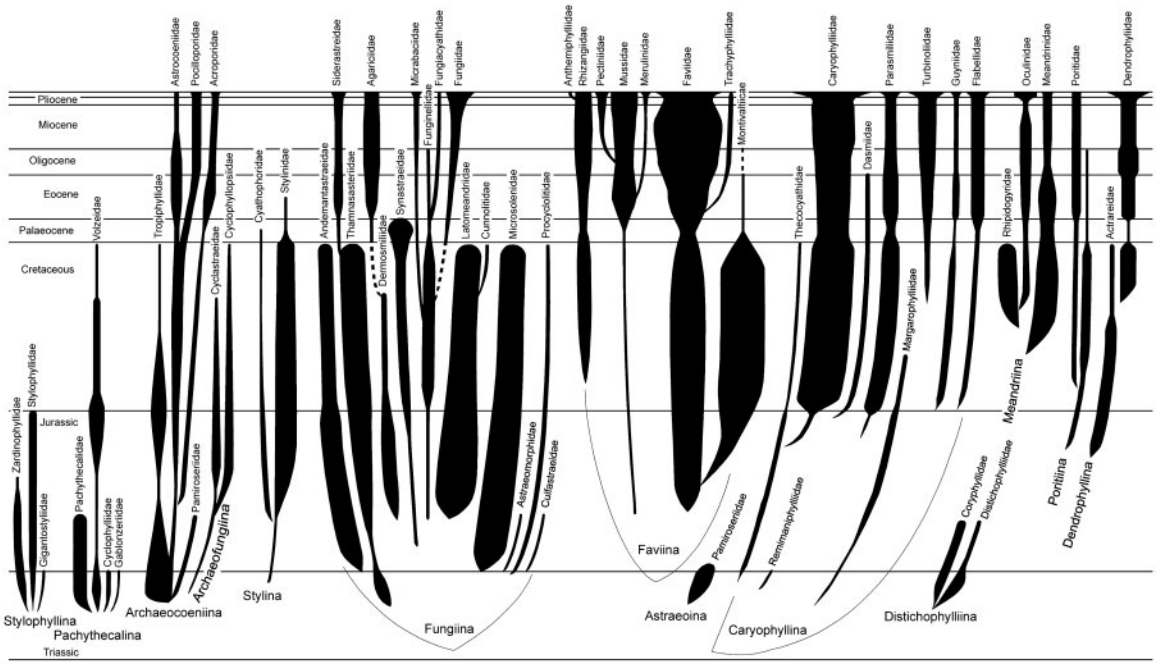

Fig. 2 Phylogeny of scleractnian corals proposed by Veron (1995, p. 110). Branches represent families (thickness is in proportion to number of genera); suborders are indicated by horizontal labels. Modified from *Corals of the World* (Veron 2000, vol. 1, p. 36) by J. E. N. Veron and used with Veron's permission.

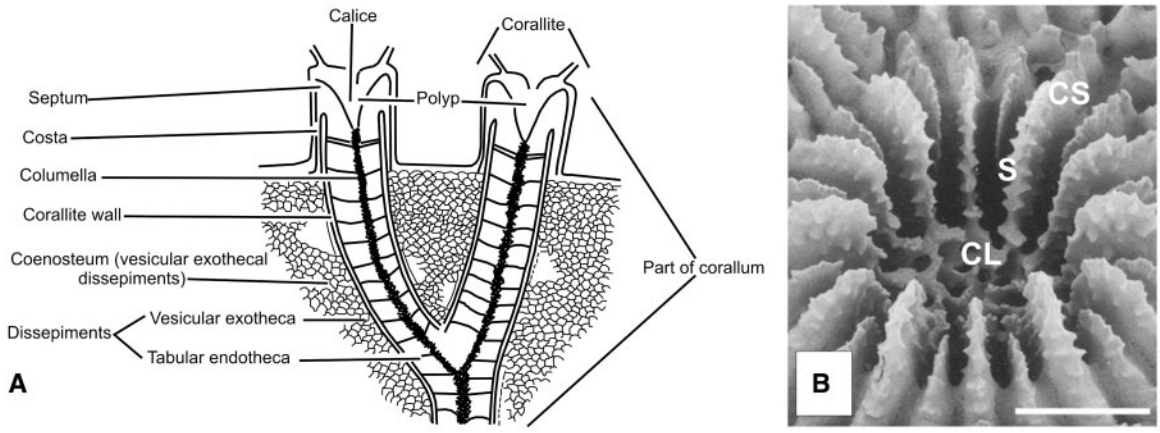

Fig. 3 Traditional morphological features used in scleractinian classification. (**A**) Drawing by Wells (1956, p. F336), illustrating several primary skeletal architectural features (corallite, septum, costa, columella, wall, coenosteum, dissepiments). From *Treatise on Invertebrate Paleontology*, courtesy of and © 1956, The Geological Society of America and The University of Kansas. (**B**) Scanning electron microscope (SEM) photograph showing septum (S), costa (CS), columella (CL).

"trabeculae" per septum, wall structure, and development of septal ornamentation. Chevalier and Beauvais (1987) added three more suborders to those distinguished by Alloiteau (1957), using features such as the presence of a medioseptal plane and structure of the trabeculae and thickening deposits.

Traditional model of septal growth

Several micromorphological features, which are related to the construction of the septa, are diagnostic of traditional families and higher categories (Fig. 4). These features were originally observed using regular light microscopy and are based on the traditional model of septal growth and the concept of "trabeculae" (Ogilvie 1897; Bryan and Hill 1941; Vaughan and Wells 1943; Wells 1956). In this model, septa are formed by discrete vertical rods termed trabeculae, which form dentations or "teeth" along outer septal margins. The teeth may be formed by single trabeculae (Fig. 4A) or by a trabecular fan (Fig. 4B).

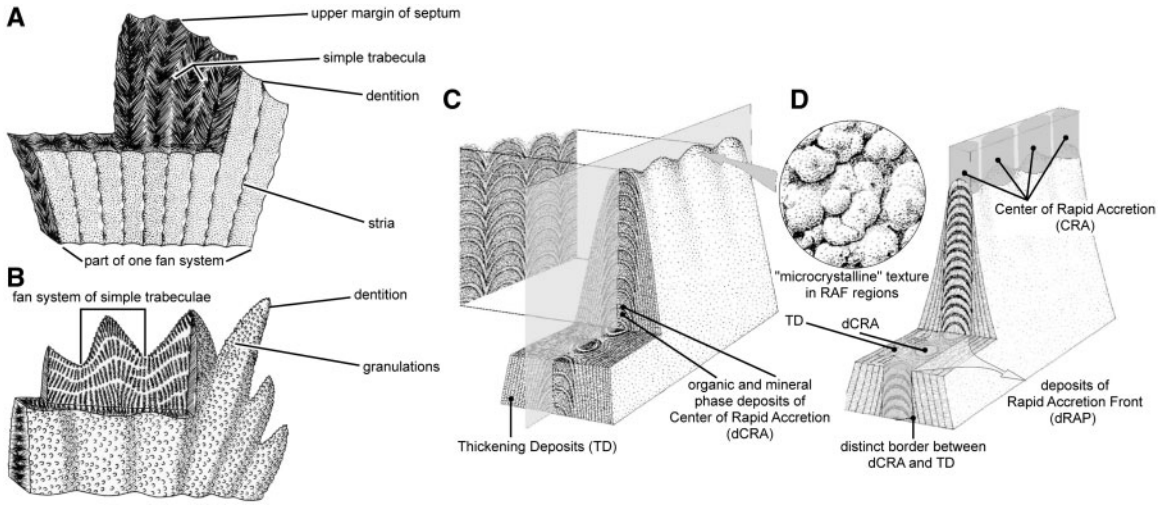

Fig. 4 Comparison between traditional model of septal growth based on regular light microscopy (**A, B**) and a more up-to-date model of septal growth based on electron microscopy (**C, D**). (A and B) In the traditional model (after Wells 1956, p. F338), septa are formed by discrete rods called trabeculae or by trabecular fans. From *Treatise on Invertebrate Paleontology*, courtesy of and © 1956, The Geological Society of America and The University of Kansas. (C and D) In the up-to-date model (Stolarski 2003, p. 519), the trabeculae consist of centers of rapid accretion, which are surrounded to varying degrees by thickening deposits, and are not discrete. With permission from *Acta Palaeontologica Polonica*, Institute of Paleobiology PAS.

In transverse thin section, the trabeculae appear as centers of calcification surrounded by fibers. The trabeculae themselves may be ''simple'' (formed by a single line of centers and fibers, termed a ''sclerodermite'') or ''compound'' (formed by complex arrangements of centers and fibers, or ''bundles of sclerodermites'').

The five suborders of Vaughan and Wells (1943) and Wells (1956) are based on this traditional model of septal growth. Five of the most important diagnostic characters include: (1) porosity of the septa; (2) relative number of trabeculae per septum; (3) number of trabecular fan systems per tooth; (4) simple versus compound trabeculae; and (5) the presence or absence of synapticulae. The five suborders are characterized as follows:

Astrocoeniina: ''laminar'' (nonporous) or spinose septa, formed by few simple or compound trabeculae.

Fungiina: ''fenestrate'' (porous) septa, formed by numerous simple or compound trabeculae, united by synapticulae.

Faviina: laminar (nonporous) or spinose septa, formed by one or more fan systems of numerous simple or compound trabeculae.

Caryophylliina: laminar septa, formed by one fan system of numerous simple trabeculae.

Dendrophylliina: laminar or irregularly perforated septa, formed by one fan system of numerous simple trabeculae, united by synapticulae.

In addition to macromorphological features such as structure of the wall, presence or absence of dissepiments, intracalicular versus extracalicular budding of corallites within colonies, micromorphological characters are also important for distinguishing traditional families. For example, within the suborder Faviina, the traditional family Faviidae is distinguished by regular septal teeth (''simple trabeculae'') and one trabecular fan system per septum. The traditional family Mussidae is distinguished by large septal teeth (''simple trabeculae''), each of which is formed by a trabecular fan system. The traditional family Merulinidae is distinguished by irregular septal teeth (''compound trabeculae'') and one trabecular fan system per septum.

New perspectives on morphological characters

Our understanding of coral biomineralization and skeletal growth has improved considerably over the past three decades, primarily due to modern technological advances (e.g., electron microscopy). Most important has been the discovery of an intra-fibrous organic meshwork that controls aragonite crystallization, and the recognition of a two-step process in the formation and growth of septa and related skeletal features (Cuif et al. 1997, 1999, 2003; Cuif and Sorauf 2001; Stolarski 2003; Cuif and Dauphin 2005a, 2005b). The first step produces a 3D skeletal framework (constructed by centers of calcification, which form axes of calcification), and the second step follows and is independent of the first. It

involves incremental growth of thickening deposits (fibers) around the framework, with the increments corresponding to the successive positions of the secretory ectodermal layer. Stolarski (2003) has pointed out that the two steps actually occur simultaneously and that a layered model may better describe the process whereby deposits of the "Rapid Accretion Front" consist of both "Centers of Rapid Accretion" and "Thickening Deposits". Taxa differ in the size, shape, and positions of centers, and in the amount and arrangement of different types of thickening deposits, including the thickness and regularity of growth increments. They also differ in the degree of differentiation between the centers of rapid accretion and thickening deposits (Fig. 4C and D). Mineral/organic phase alterations in thickening deposits are less distinct and less regular in azooxanthellate corals in comparison to zooxanthellate corals, and the differences appear to be ecological (Stolarski 2003).

Due to continuous upward growth of the septa, the 3D skeletal framework is manifest on the uppermost surfaces of the septa in micromorphological features (e.g., septal teeth and granulations) that are best observed using low-magnification scanning electron microscopy (Fig. 5). Microstructural features involving the structure and growth of thickening deposits can be observed in transverse sections (petrographic thin sections) (Fig. 6) or by scanning electron microscopy of polished and etched skeletal surfaces. Definition of micromorphological and microstructural morphological characters that can be effectively used in systematics is still in its infancy, but preliminary results are promising and many different authors have commented on their potential taxonomic utility (e.g., Cuif et al. 2003). For example, with regard to micromorphology, in Atlantic members of the traditional family Mussidae, septal teeth are spine-like in shape, teeth in different septal cycles have the same shape, the area between teeth is banded (horizontal bands), and septal granulations consist of scattered spikes. In contrast, in Pacific members of the family, teeth are triangular in shape; they may differ in shape in different septal cycles, the area between teeth is smooth or palisade-like in structure, and septal granulations consist of diffuse knobs (Fig. 5). Closer examination reveals that, in both Atlantic and Pacific mussids, teeth are formed by calcification axes in multiple directions, the primary axis in both groups being along the septal plane. Secondary axes are better developed in the teeth of Atlantic mussids; whereas

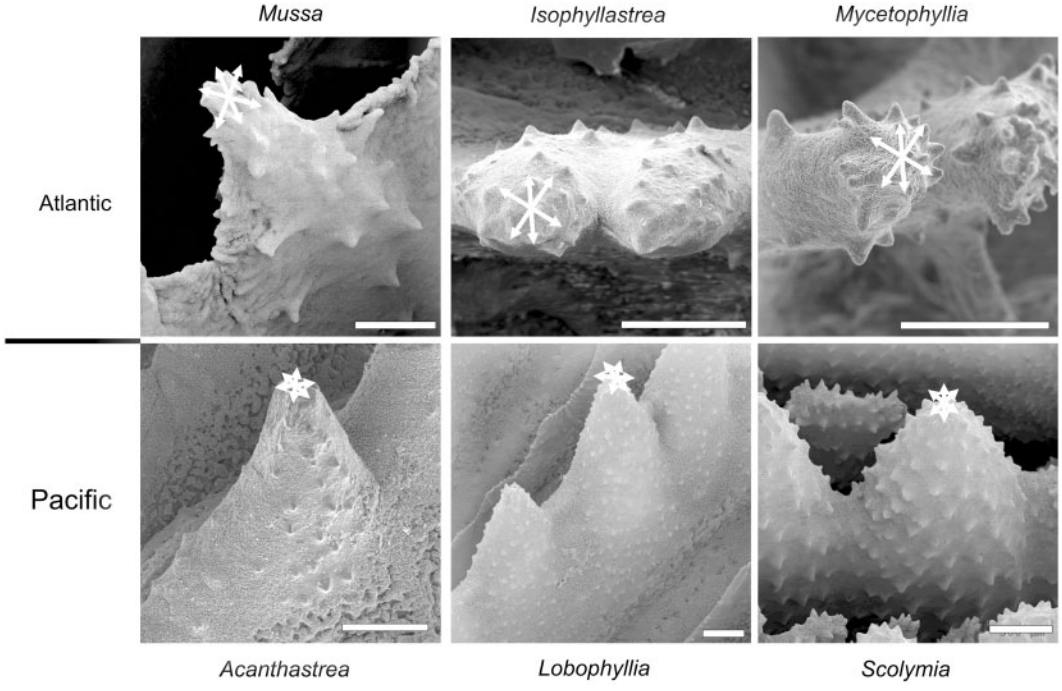

Fig. 5 Micromorphology involves the study of the shapes of teeth along the upper margins of septa (and other architectural features), and of granulations on septal faces. Observations are made on the skeletal surface using a SEM. In Atlantic members of the family Mussidae, septal teeth are spine-like in shape, and septal granulations consist of scattered spikes. In Pacific members of the family, teeth are triangular in shape, and septal granulations consist of diffuse knobs. Closer examination reveals that secondary calcification axes (white arrows) are better developed in the teeth of Atlantic mussids, whereas thickening deposits are more extensive in Pacific mussids. Scale bars are 500 μm. After Budd and Stolarski (2009).

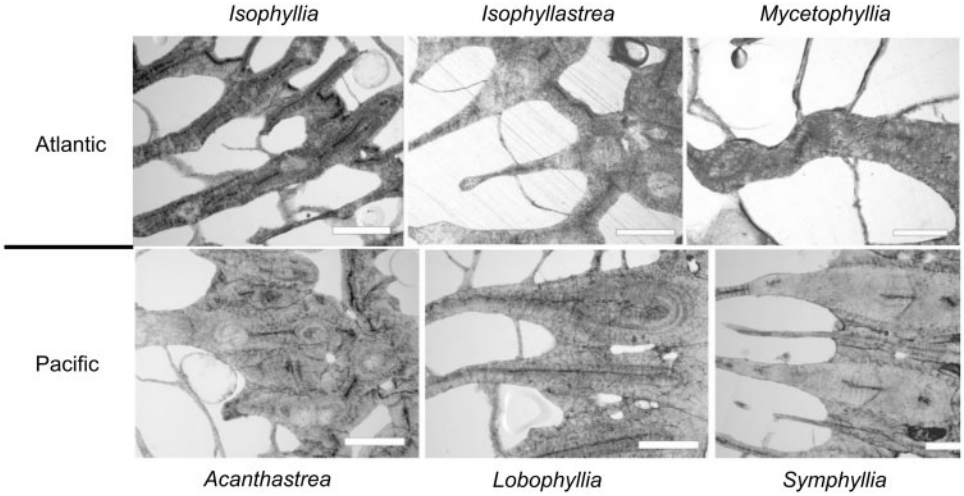

Fig. 6 Microstructure involves the study of the internal structure within septa (the horizontal features above), specifically the arrangement of calcification centers and fibers. Observations are made on transverse petrographic thin sections, and on polished and etched cuts using SEM. In Atlantic mussids, corallite walls are usually thin, and septa are formed by discrete clusters of calcification centers connected by medial lines. In Pacific mussids, corallite walls are thickened extensively by layered deposits, and septa are composed of faint, irregular clusters of calcification centers. Scale bars are 1 mm. After Budd and Stolarski (2009).

thickening deposits are more extensive in Pacific mussids, resulting in triangular teeth. As a result of the longer secondary axes and less extensive thickening deposits, granulation is more spike-like in Atlantic mussids (Budd and Stolarski 2009). With regard to microstructure, in Atlantic mussids, corallite walls are usually thin, and the septa are formed by discrete clusters of calcification centers connected by medial lines. In Pacific mussids, corallite walls are thickened extensively by stereome (layered deposits), whereas the septa are composed of faint, irregular clusters of calcification centers (Fig. 6). These observations agree with molecular results in placing Atlantic and Pacific mussids in separate family-level clades, and indicating the family Mussidae to be polyphyletic (Fukami et al. 2004, 2008).

Morphological phylogenetics of the order

Morphological phylogenetic analyses have not contributed significantly to our understanding of scleractinian evolution to date, primarily due to low numbers of morphological characters, high homoplasy, and limitations in current understanding of skeletal growth and homology. With the exception of the phenetic analyses of Powers and Rohlf (1972), published work (Table 1) has focused on relationships among species or genera within individual families, and not on differences between suborders or between ''Robust'' versus ''Complex'' corals (see below). In general, the resulting trees are low in resolution [e.g., 5976 and 1547 MPTs, respectively, in the papers by Cairns (1997, 2001)], and many analyses involve >25 taxa and low numbers of characters relative to numbers of taxa. More effective designs for sampling taxa need to be explored. The phenetic analyses of Powers and Rohlf (1972) are noteworthy, because although the results do not unequivocally distinguish ''Robust'' versus ''Complex'' corals, members of the genera *Fungia* and *Psammocora* are distinct from complex corals and have relationships more closely resembling the molecular trees constructed by Fukami et al. (2008). Their analyses also show the family Faviidae to be clearly polyphyletic. Nevertheless, because the analyses of Powers and Rohlf (1972) are phenetic, the characters responsible for the resulting clusters cannot be readily assessed.

Most of the characters used in morphological phylogenetic analyses are traditional skeletal macromorphological characters. For example, in Cairns' initial pioneering analysis of the Fungiidae (Cairns 1984), he used six macromorphological features (coloniality, size of the corallum, shape of the upper corallum, equality of costae in different cycles, and form of the colony) and four coarsely defined micromorphological features (porosity of thecae, shape and density of costal spines, size of septal teeth). He listed ornamentation of costal spines (a micromorphological feature) but did not include it in the analysis. In subsequent work on the Turbinoliidae (Cairns 1997) and Dendrophylliidae (Cairns 2001), Cairns used one or two micromorphological features in his analysis (i.e., costal spines and ornamentation in the Turbinoliidae; structure of the synapticulae

Table 1 Published morphological phylogenetic analyses

Publication	Taxonomic group	Number of taxa	Number of characters	Character types	Analytical methods	Results
Powers and Rohlf (1972)	15 scleractinian families (five suborders)	54 species	60 binary characters	35 macro, 10 micro, 15 nonskeletal	UPGMA using coefficients of correlation and distance	Generally consistent with the suborders of Vaugan and Wells (1943)
Cairns (1984)	Fungiidae	18 genera and subgenera	10 characters, 25 states	10 macro	Maximum parsimony (Wagner-78)	34 steps (16 parallelisms, nine reversals)
Hoeksema (1989, 1991)	Fungiidae	40 species	55 binary characters	31 macro, 24 micro	Manual	155 steps
Pandolfi 1992	Mussidae	12 genera	39 binary characters	36 macro, 3 micro	Maximum parsimony (Hennig-86)	Two MPTs, length = 290, CI = 0.45, RI = 0.58
Pandolfi (1992)	*Symphyllia*	5 species	54 binary characters + 1 dummy variable	All macro	Maximum parsimony (Hennig-86)	Six MPTs, length = 315, CI = 0.60, RI = 0.70
Pandolfi (1992)	Siderastreidae	6 genera	17 binary characters	16 macro, 1 micro	Maximum parsimony (Hennig-86)	One MPT, length = 86, CI = 0.69, RI = 0.60
Pandolfi (1992)	*Coscinaraea*	7 species	62 binary characters + 1 dummy variable	All macro	Maximum parsimony (Hennig-86)	Three MPTs, length = 392, CI = 0.56, RI = 0.70
Hoeksema (1993)	Fungiidae	6 species	16 characters (33 states)	10 macro, 5 micro, 1 nonskeletal	Maximum parsimony (Hennig-86)	19 steps, CI = 0.89, RI = 0.81
Cairns (1997)	Turbinoliidae	28 genera	16 characters (49 states)	14 macro, two micro	Maximum parsimony (PAUP)	Equal weighting = 5876 MPTs; successive weighting = 82 MPTs, 99 steps, CI = 0.657, rCI = 0.442
Johnson (1998)	Faviidae	40 species	23 characters (64 states)	All macro	Maximum parsimony (PAUP 3.1.1)	78 MPTs, length = 175, rCI = 0.14, RI = 0.78
Wallace (1999)	Acroporidae	7 genera	11 characters (26 states)	10 macro, 1 nonskeletal	Maximum parsimony (Hennig-86)	Two MPT
Wallace (1999)	*Acropora*	102 species	23 characters (94 states)	22 macro, 1 micro	Maximum parsimony (Hennig-86; PAUP 3.1.1)	325 steps, CI = 0.212, RI = 0.722
Cairns (2001)	Dendrophylliidae	30 genera	10 characters (41 states)	8 macro, 1 micro, 1 nonskeletal	Maximum parsimony (PAUP)	Equal weighting = 1547 MPTs; successive weighting = 27 MPTs, 64 steps, CI = 0.531
Budd and Smith (2005)	Atlantic Faviidae and Mussidae	25 species	25 characters (86 states)	21 macro, 4 micro	Maximum parsimony (PAUP 4.0)	132 MPTs, length = 132, CI = 0.424, RI = 0.730
Huang et al. (2009)	Pacific Faviidae	67 taxa (32 species)	21 characters (63 states)	17 macro, two micro, 2 nonskeletal	Maximum parsimony (TNT 1.1)	15 MPTs

CI, consistency index; RI, retention index.

in the Dendrophylliidae). Limited use of micromorphological characters is similarly true of most of the other analyses listed in Table 1. One exception is the phylogenetic analysis by Hoeksema (1989), who not only used micromorphological features such as septal perforations, but also the arrangement of granules on septal faces and on the corallite wall, and the shape and number of septal teeth and costal spines. In Hoeksema's (1989) analysis, he recognized only one synapomorphy for the family Fungiidae, compound synapticulae or ''fulturae'', which is micromorphological, and five synapomorphies for clades within the family, four of which are micromorphological. These results underscore the importance of micromorphological and microstructural characters in interpreting scleractinian evolution, and they point to the need for including such characters in future morphological phylogenetic analyses.

Molecular phylogenetics

Over the past 20 years, molecular phylogenetic analyses have revolutionized our understanding of scleractinian evolution at all levels. Robust phylogenies based on molecular data have made it possible to test a wide variety of hypotheses derived from morphological studies, from the issue of monophyly of the order to the role of hybridization in scleractinian evolution. Although the focus of this review is how the integrated use of morphological and molecular data are informing our understanding of scleractinian evolution, here we also provide a short summary of how molecular phylogenetic analyses are addressing other questions in scleractinian evolution.

One of the important areas to which molecular phylogenetic analyses have contributed is the debate on the monophyly of the Scleractinia. Paleontologists have long debated the origins of the order Scleractinia, which is defined by its calcium carbonate skeleton (Oliver 1980; Stanley 2003). This debate generated the ''naked coral'' hypothesis, based on fossil and morphological data, which proposes that coral lineages (polypoid cnidarians with a skeleton) can lose their skeleton during stressful periods in evolutionary history (Stanley and Fautin 2001; Stanley 2003). Some molecular phylogenetic analyses based on limited molecular markers and/or taxa lend support to this hypothesis (Chen et al. 1995; Berntson et al. 1999; Romano and Cairns 2000; Daly et al. 2003; Medina et al. 2006), but more recent analyses, including more sequence data and a wider range of taxon sampling, clearly reject this hypothesis (Barbeitos 2007; Brugler and France 2007; Fukami et al. 2008).

Molecular data have also provided insight into scleractinian evolution at lower taxonomic levels. Fukami (2008) provided a short review of how molecular analyses are changing our understanding of the evolution of scleractinians at the familial level and below. At the species level and below, molecular phylogenetic analyses are contributing to our understanding of the role hybridization may have played in the Scleractinia in the past and how it might affect their survival in the future (Willis et al. 2006; Richards et al. 2008).

Molecular phylogenetic analyses have, arguably perhaps, had the greatest impact on our understanding of the higher level systematics of the Scleractinia. They have provided new hypotheses for relationships among genera and families that are unlike those proposed on the basis of traditional classification. They suggest that the order includes two distinct lineages that originate very early in the evolutionary history of the group, termed ''Complex'' and ''Robust'' by Romano and Palumbi (1996). These two lineages have evolved separately from each other since the origin of the order, and do not conform to the five suborders of Wells (1956) or the suborders of other authors. In molecular phylogenetic analyses, traditional suborders, and families are not recovered as monophyletic clades.

The first molecular phylogenetic studies of Scleractinia based on mitochondrial 16S and nuclear 28S ribosomal DNA sequences show no concordance between traditional and molecular suborders (Romano and Palumbi 1996; Veron et al. 1996; Romano and Palumbi 1997; Romano and Cairns 2000). For the most part, traditional families form monophyletic clades but traditional suborders are polyphyletic. Relationships within each of the two major lineages are not well resolved by these analyses. The only suborder that appears to be monophyletic is the azooxanthellate family Dendrophylliidae.

Although the initial molecular hypotheses for the Scleractinia are in stark contrast to hypotheses based on morphological characters, subsequent work has supported this very different view of scleractinian evolution. Molecular phylogenetic analyses, including additional mitochondrial and nuclear molecular markers (Fukami 2008; Huang et al. 2009) as well as a wider sampling of taxa, have generated hypotheses that are largely congruent with those from the initial studies (Chen et al. 2002; Cuif et al. 2003; Daly et al. 2003; Fukami et al. 2004; Le Goff-Vitry et al. 2004; Medina et al. 2006; Fukami et al. 2008; Nunes et al. 2008; Huang et al. 2009) supporting the existence of two major lineages within the Scleractinia and the polyphyly of traditional

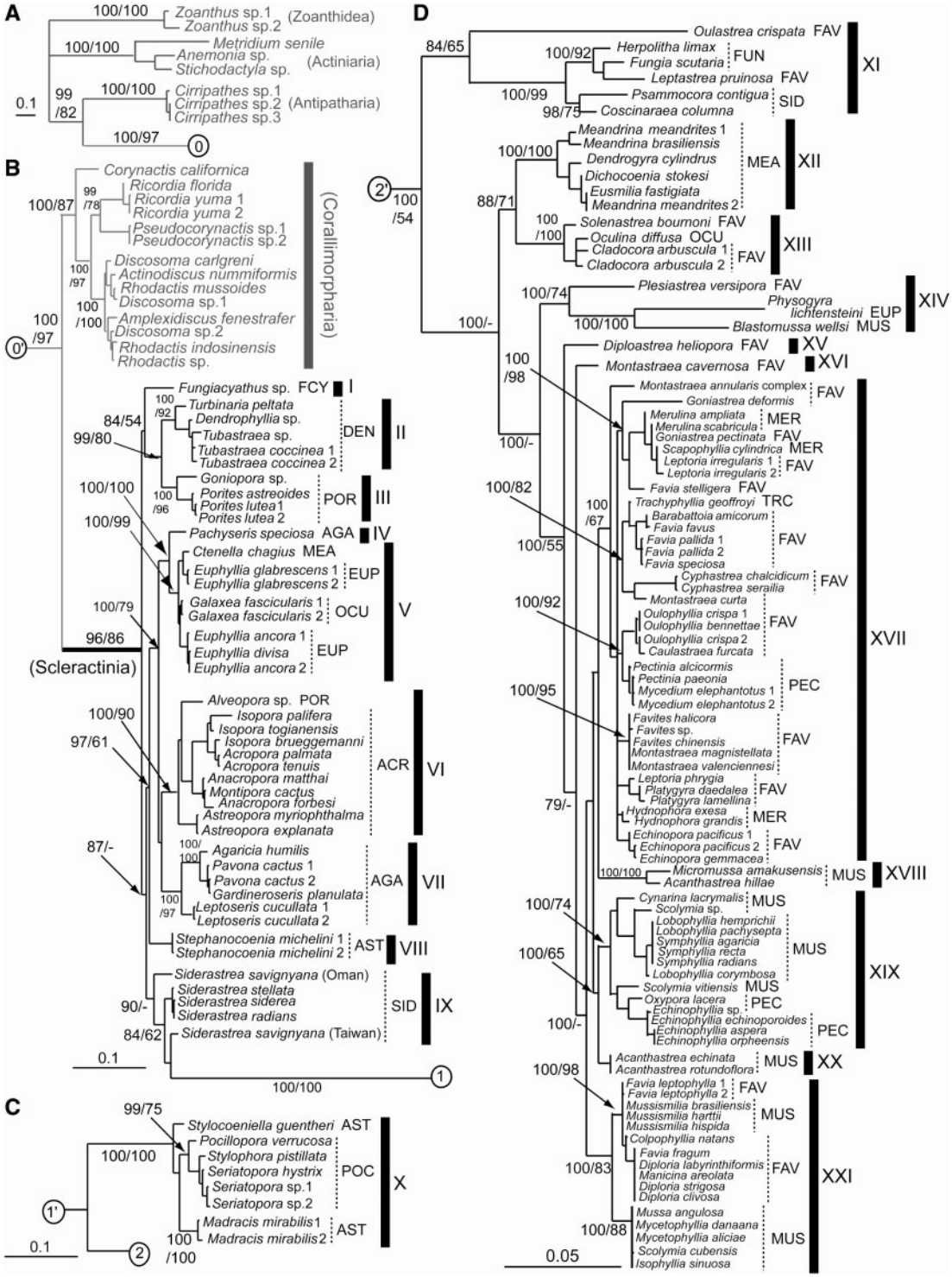

Fig. 7 Phylogenetic relationships among scleractinian corals. Topology was inferred by Bayesian analysis, based on combined mitochondrial *cox1* and *cob* DNA sequences. Numbers on main branches show percentages of Bayesian probability (>70%) and bootstrap values (>50%) in ML analysis. Numbers in circles show the connection of trees from A to D. Three letter codes correspond with traditional families; numbers in roman numerals indicate clades interpreted from the tree. After Fukami et al. (2008, p.3).

suborders. The work by Fukami et al. (2008), including the largest numbers of taxa, the greatest number of molecular characters from a variety of mitochondrial and nuclear markers, and more sophisticated analyses, suggests the greatest differences from hypotheses based on morphological characters (Fig. 7). Each lineage has representatives of a number of suborders and families. So far, 14 of the 24 extant

families have been determined not to be monophyletic (Romano and Cairns 2000; Cuif et al. 2003; Barbeitos 2007; Fukami et al. 2008). Eight of these families have representatives in both the ''Robust'' and ''Complex'' clades. Even families that are monophyletic appear to include representatives that have traditionally been placed in other families. Work by Fukami et al. (2008) and others also demonstrates that some genera are not monophyletic (Benzoni et al. 2007; Huang et al. 2009).

Molecular phylogenetic hypotheses for the Scleractinia provide a more complex perspective on interrelationships of scleractinian families and genera than morphological hypotheses, yet still uncertainties remain at all levels. Although all molecular analyses thus far support the existence of the ''Complex'' and ''Robust'' lineages, there are basal taxa whose position is uncertain and so they may even represent a third lineage (Romano and Cairns 2000; Barbeitos 2007; Fukami et al. 2008). Many relationships within the ''Complex'' and ''Robust'' clades remain unresolved. In addition, reef-building corals have been the focus of molecular phylogenetic analyses thus far. The inclusion of azooxanthellate taxa, which represent approximately half the species in the order (Cairns 1999), may heavily influence relationships within the ''Complex'' and ''Robust'' clades. The azooxanthellate, deep-water family Caryophylliidae has been found to be polyphyletic with representatives distributed throughout both the ''Complex'' and ''Robust'' clades (Romano and Cairns 2000; Barbeitos 2007). Analyses by Barbeitos (2007) include several well-supported clades in which reef-building species are paraphyletic with respect to azooxanthellate species. Work in progress (M. Kitahara, personal communication) to add azooxanthellate taxa to the large dataset of reef-building corals should help to clarify relationships within the two main scleractinian lineages.

Phylogenetic studies based on molecular techniques have provided a new set of characters for the study of scleractinian evolution that circumvent some of the difficulties inherent in morphological characters. Unlike previous evolutionary hypotheses for the Scleractinia, molecular phylogenetic analyses provide robust hypotheses for relationships among taxa. The strengths of molecular characters are their independence from morphological variability, the ability to independently assess confidence in the homology of these characters, and the greater number of characters available allowing for robust phylogenetic trees. While the determination of homology in molecular characters has its own difficulties, the greater number of characters available provides the potential for generating more robust hypotheses of evolutionary relationships, and the opportunity for reciprocal illumination between datasets.

While molecular phylogenetic analyses have provided new perspectives on scleractinian evolution they can also be problematic. Reef-building corals have been the focus of the majority of scleractinian molecular phylogenetic studies. The symbiotic relationship of corals with zooxanthellae means that caution must be used in collecting sequence data from whole tissue. Mitochondrial DNA markers that have been useful for phylogenetic studies in most other organisms have low rates of molecular evolution in anthozoan mitochondrial DNA (Shearer et al. 2002; Hellberg 2006; Shearer and Coffroth 2008; Huang et al. 2009). As a result, resolution of higher level relationships has been difficult. As the majority of reef-building corals are broadcast spawners (Baird et al. 2009), the possibility of interspecific hybridization has made relationships at the generic level and below difficult to unravel. Another weakness of molecular techniques is the inability to collect molecular data from fossil samples.

A 21st century perspective on scleractinian evolution

At the beginning of the 21st century we now have a greatly improved toolbox for studying scleractinian evolution. Scientists using both morphological and molecular tools have formed the Scleractinia Working Group (SWG) in an effort to use a combination of morphological and molecular tools for furthering studies of scleractinian evolution (Budd 2009). The working group is an outgrowth of a Synthesis Meeting sponsored by the Encylopedia of Life and the Treatise on Invertebrate Paleontology in June 2009. The consensus of the SWG is ''that existing classification systems for scleractinians are inadequate, and a revised system that better reflects new molecular results needs to be adopted as soon as possible'' (Budd 2009). The SWG agrees that composition of scleractinian families is best reflected in the numbered clades observed in the tree prepared by Fukami et al. (2008). This system of classification is being adopted by Corallosphere (http://www.corallosphere.org), ''a web application developed with the aim of exploring new approaches to compiling taxonomic information on extant and extinct scleractinian corals'' (Cairns et al. 2008), which is also being used in the current revision of the Treatise of Invertebrate Paleontology. This system of classification is also now starting to be used at a

practical level as evidenced by its adoption as the taxonomic framework for a guide to the Scleractinia fauna of Taiwan (Dai and Horng 2009a, 2009b).

Integrating diverse types of data is critical for understanding the physical and biological events that have shaped scleractinian evolution. Kerr (2005) used a supertree analysis, combining all existing phylogenetic hypotheses for scleractinian relationships, based on both morphological and molecular data. The resulting supertree included both the Robust and Complex clades as well as other similarities to molecular phylogenetic hypotheses. This kind of an approach reveals areas of congruence and disagreement that can then be used to guide more fine-scale studies. It provides an example of how integration of diverse types of data can inform our understanding of the evolutionary history of the Scleractinia.

Another example of the value of integrating diverse data types is provided in a comparison of molecular and morphologic phylogenetic analyses of Atlantic members of the families Faviidae and Mussidae. Figure 8 shows that the two datasets are generally congruent. Furthermore, the relative positions of taxa that are incongruent (e.g., *Mussa angulosa*, *Colpophyllia natans*) are not among the most well-supported nodes by either dataset. Branch support in the molecular tree is generally higher in basal nodes; whereas branch support in the morphologic tree is generally higher near the tips of branches. The most parsimonious trees from the combined dataset are therefore well-resolved relative to the results of the molecular or morphological analyses individually. Indeed, recent studies of diverse taxa including butterflies, skippers, mammals, mollusks, and ferns suggest that congruence between morphological and molecular estimates of phylogeny may be better than previously expected (Wahlberg et al. 2005; Jablonski and Finarelli 2009; Lee and Camens, 2009; Schneider et al. 2009). Perhaps the strongest argument for synthesizing molecular and morphological datasets of scleractinian corals is the increased insight that can be provided by the diverse scleractinian fossil record. Our understanding of macroevolutionary patterns in scleractinians, including times of divergence of major clades, evolution of complex traits, patterns of diversification through time, and biogeographic relationships, hinges in part on accurately placing scleractinian fossils in a robust phylogenetic framework. The reciprocal illumination provided by both molecular and morphological datasets can also yield new insight into homology and patterns of evolution of characters that were not

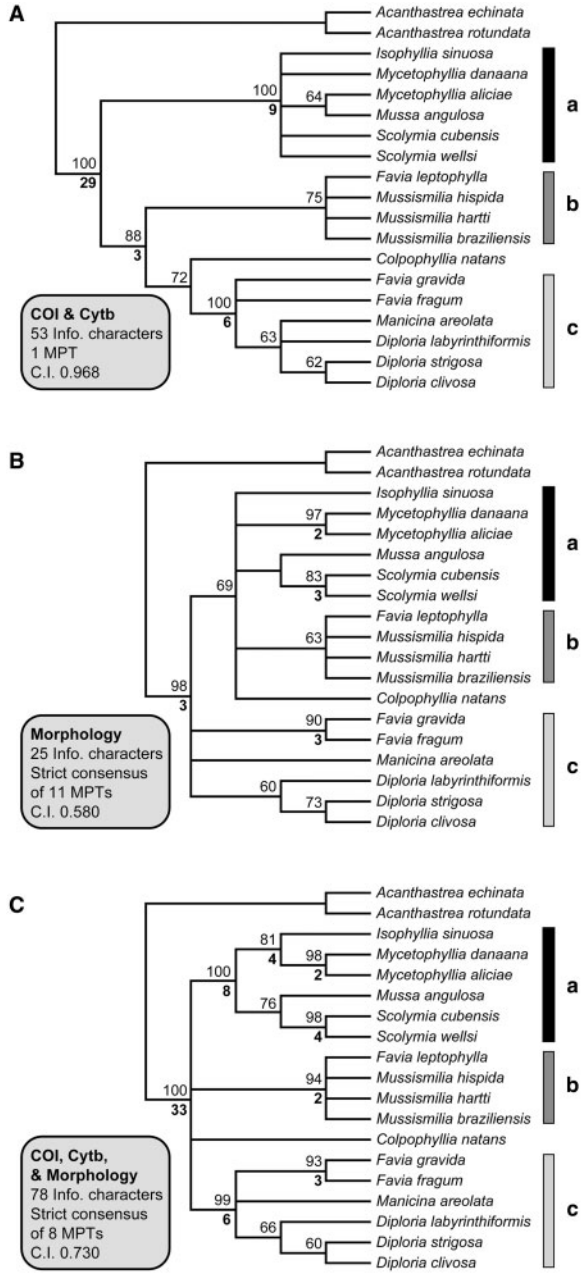

Fig. 8 Phylogenetic analyses of Clade XXI (Fukami et al. 2008) consisting of Atlantic members of the traditional scleractinian families Faviidae and Mussidae. All analyses were performed using maximum parsimony based on a heuristic search (TBR, 1000 random addition sequence replicates) in PAUP* (Swofford 2002); two species of the Pacific genus *Acanthastrea* served as outgroups. Numbers above and below nodes are, respectively, bootstrap values and Bremer support values. Subclades within Clade XXI are indicated by the letters a, b, and c. (**A**) Analysis based on COI and cytB genes, (**B**) analysis performed using 25 morphological characters (nine macromorphological, five microstructural, 11 micromorphological), and (**C**) combined analysis including both molecular and morphological datasets.

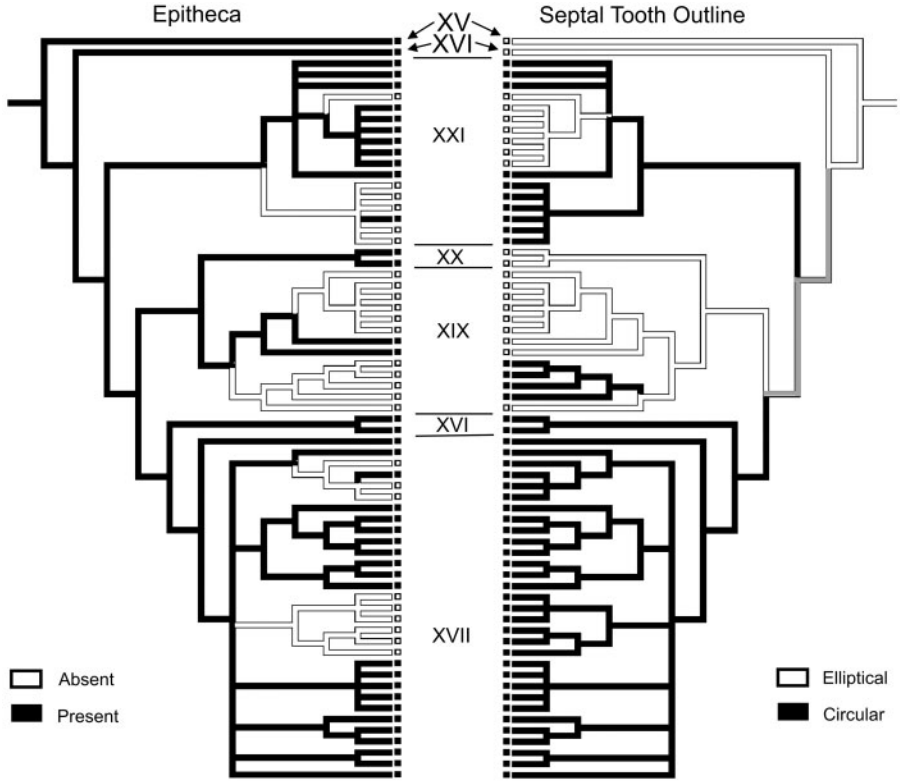

Fig. 9 Phylogenetic character mapping of two morphological characters on a subset (Clades XV–XXI) of the molecular tree of Fukami et al. (2008). Ancestral states have been reconstructed using parsimony and calculated using Mesquite v.2.72 (Maddison and Maddison 2009); equivocal branches are indicated in grey. Epitheca has a consistency index (CI) of 0.125 and a retention index (RI) of 0.720, whereas tooth outline has a CI of 0.250 and a RI of 0.842.

possible before. Novel relationships present in molecular phylogenies, in and of themselves, suggest the presence of new morphological characters that may diagnose the same clades (Fukami et al. 2008). This "reverse taxonomy" may prove useful in discovering novel morphological characters. Additionally, utilizing comparative methods to map morphological traits onto molecular "scaffold" trees (*sensu* Murphy et al. 2001) can aid in refining morphological hypotheses of homology, and the tempo and mode of the evolution of traits. An example is given in Fig. 9. Reconstructions of the macromorphological character epitheca, show that epitheca may have been lost at least twice in each of clades XXI, XIX, and XVII, with a possible reversal in clade XVII. The presence of epitheca is nevertheless clearly plesiomorphic. Reconstructions of the micromorphological character, septal tooth outline, show transformations from elliptical to circular in clades XXI, XIX, XVI + XVII, with a reversal in clade XXI. Homoplasy is present in both characters, but the transformation from elliptical to circular occurs at a more basal level within the tree than observed in epitheca. Thus, although the absence/presence of epitheca changes more across the tree, the shape of septal tooth outline may have been more evolutionary labile earlier in the clade's history.

In addition, epitheca appears to have been lost six times, and only gained at most twice (Fig. 9), suggesting the possibility of an asymmetry in rates of character state transitions (Mooers and Schluter 1999). As a brief example, we explicitly tested this hypothesis using the "Markov k-state 1" (Lewis 2001) and "Asymmetrical Markov k-state 2" parameter models as implemented in Mesquite (Maddison and Maddison 2009). We performed these tests with a subset (clades XV to XXI) of the phylogenetic topology and branch lengths from Fukami et al. (2008; see also Fig. 9), and with the subset topology from Fukami et al. (2008) with all branches set equal to one. Utilizing the conventional cutoff of a difference in log likelihood exceeding 2.0 for significance (Edwards 1972), support for a two-rate model was not significant for either analysis (difference in log likelihood with branch lengths: 0.943; difference in log likelihood with all branch lengths equal to one: 0.002). Additionally, we simulated 500 character histories on the Fukami et al. (2008) subset topology

with branch lengths, utilizing the ''Markov k-state 1'' model, and the maximum likelihood estimate of the rate parameter (60.7664) from the above analysis. We then created a null distribution of log likelihood differences between the one-rate and two-rate models by calculating these values across all 500 simulated character histories in Mesquite (Maddison and Maddison 2009). Our original log likelihood difference of 0.943 was not significantly different from this distribution ($P = 0.308$), again suggesting that despite the apparent discrepancy between gains and losses implied by the parsimony reconstructions, there is no support for asymmetrical rates of gain and loss of epitheca in this sample of scleractinian corals. Although these examples are rather simple, they illustrate the increased capacity for hypothesis testing when diverse types of data on scleractinian morphology and phylogeny are available. More rigorous comparative methods to test for possible rate asymmetries have recently been developed (Maddison 2006; Maddison et al. 2007; Goldman and Igić 2008), and their application to scleractinian case studies should prove fruitful.

Other examples of how ''reverse taxonomy'' can be useful in understanding scleractinian evolution include investigations of the genera *Psammocora* and *Coscinaraea*, and their relationship to members of the Fungiidae and Siderastreidae, in which morphological characters were also mapped onto molecular trees (Benzoni et al. 2007; Stefani et al. 2008). In addition, Baird et al. (2009) used the molecular phylogeny for Scleractinia to test hypotheses concerning the evolution of sexuality and mode of larval development. Their analysis examined extensive information on reproductive characters, and provided strong support for the hypotheses that gonochoric sexuality is the ancestral state in Scleractinia and that mode of larval development is relatively labile. Ultimately, adding a temporal dimension to scleractinian phylogenetic trees by incorporating fossils in analyses and using their geologic ages to estimate divergence times will provide more rigorous hypotheses of rates of change of characters. Major questions that remain to be addressed include: (1) Are certain classes of morphological characters (e.g., macromorphological, micromorphological, and microstructural) significantly more (or less) congruent with relationships inferred from molecular data? (2) Do different morphological characters exhibit significantly different rates of change? (3) Do some morphological characters exhibit strong asymmetries in direction of change of character states? (4) Are some morphological characters associated with shifts in diversification rates?

The combined use of molecular and morphological tools holds great promise for ending confusion in scleractinian systematics. Further molecular analyses, including a wider range of azooxanthellate taxa, should lead to a better understanding of relationships along the main branches of the scleractinian tree. Finer-scale analyses of clades towards the tips of the trees, using both morphological and molecular data, should lead to a better understanding both of relationships among genera as well as of the evolution of morphological characters within the order. Better understanding of the evolution of characters will help to integrate the systematics of fossil and extant taxa. Given the rich scleractinian fossil record, integration of diverse types of data from fossil and extant taxa will provide a means for reconstructing the complex evolutionary history of the group.

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