The New Systematics of Scleractinia: Integrating Molecular and Morphological Evidence

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Abstract

The taxonomy of scleractinian corals has traditionally been established based on morphology at the "macro" scale since the time of Carl Linnaeus. Taxa described using macromorphology are useful for classifying the myriad of growth forms, yet new molecular and small-scale morphological data have challenged the natural historicity of many familiar groups, motivating multiple revisions at every taxonomic level. In this synthesis of scleractinian phylogenetics and systematics, we present the most current state of affairs in the field covering both zooxanthellate and azooxanthellate taxa, focusing on the progress of our phylogenetic understanding of this ecologically-significant clade, which today is supported by rich sets of molecular and morphological data. It is worth noting that when DNA sequence data was first used to investigate coral evolution in the 1990s, there was no concerted effort to use phylogenetic information to delineate problematic taxa. In the last decade, however, the incompatibility of coral taxonomy with their evolutionary history has become much clearer, as molecular analyses for corals have been improved upon technically and expanded to all major scleractinian clades, shallow and deep. We describe these methodological developments and summarise new taxonomic revisions based on robust inferences of the coral tree of life. Despite these efforts, there are still unresolved sections of the scleractinian phylogeny, resulting in uncertain taxonomy for several taxa. We highlight these and propose a way forward for the taxonomy of corals.

Keywords

Azooxanthellate • Cnidaria • Coral • Integrative taxonomy • Phylogenetics • Reef • Species boundaries • Zooxanthellae

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4.1 Introduction

Stony corals belonging to the order Scleractinia (Anthozoa: Hexacorallia) are a clade of cnidarians that build a calcium carbonate skeleton in the form of aragonite, and are sister group to the non-stony corallimorpharians (Daly et al. 2003; Fukami et al. 2008; Kitahara et al. 2014; Lin et al. 2014). At present, Scleractinia contains 31 families, about 240 genera, and over 1,500 species (Cairns 1999, 2009; Appeltans et al. 2012; Huang and Roy 2015), including both zooxanthellate—hosting the symbiotic dinoflagallate *Symbiodinium*—and azooxanthellate corals. Zooxanthellate species typically inhabit shallow waters surrounding warm-subtropical and tropical seas and comprise the main coral reef framework builders with about 800 valid species. Azooxanthellate species are widely distributed in the world's oceans from shallow to deep waters and consist of about 700 valid species. Neither zooxanthellate and azooxanthellate nor shallow and deep species are distinguished phylogenetically and only partially separated at the family level taxonomically. Due to the ecological and economic importance of tropical coral reefs—e.g., high species diversity and mass fisheries production—zooxanthellate taxa have been the subject of a greater volume of research relative to azooxanthellate species. However, both groups have comparable richness, having diversified successfully over hundreds of millions of years. Therefore in this chapter on coral systematics, they deserve equal attention, limited only by the amount of published data available.

The coral skeleton has been and continues to be the main source of morphological characters used in scleractinian classification. Most coral species are colonial, but solitary corals have evolved in at least six lineages independently (Barbeitos et al. 2010). Among colonial species, each corallite (skeletal unit formed by an individual polyp) within a colony or species may have varying characteristics depending on growth rate, position in the colony and other environmentally-influenced traits. Consequently, morphological boundaries between species are generally obscure, and the task of identifying corals falling within and outside the limited pool of systematists has remained challenging at every taxonomic level since Linnaeus (1758) established *Madrepora*.

Fortunately, molecular phylogenetic analyses in the last two decades have undoubtedly advanced coral taxonomy by making large amounts of data available and inspiring the next generation of systematists. Understandably, the numerous name changes across the entire coral phylogeny that have ensued can cause considerable confusion for coral researchers outside the limited circle of systematists. To address this apparent disarray, we track the history of molecular data used for phylogenetic reconstruction, summarise the most recent phylogenetic understanding of corals, and describe recent taxonomic research at family, genus and species levels. Finally we conclude by highlighting taxonomic issues that remain unresolved in the hope that research efforts will be refocused to stabilise all of the problematic taxa.

4.2 The Rise of Molecular Phylogenetic Methods

Genetic data have been collected from scleractinian corals since the early 1980s, but these were first based on allozyme allelic frequencies obtained using gel electrophoresis (Ridgway 2005). Stoddart (1983, 1984) examined the genetic diversity of *Pocillopora damicornis* using up to ten enzymes, and found that populations from Western Australia and Hawaii were maintained predominantly via asexual reproduction. Willis and Ayre (1985) analysed eight enzyme loci from Great Barrier Reef *Pavona cactus* to show that genetically similar colonies tended to show the same growth form, and overall the species comprised highly clonal populations (Ayre and Willis 1988). Allozyme electrophoresis was also employed to clarify genetic boundaries of closely-related morphotypes, such as between *Montipora* species (Heyward and Stoddart 1985), *M. digitata* populations (Stobart and Benzie 1994), within the *Orbicella* (previously "*Montastraea*") *annularis* species complex (Knowlton et al. 1992; van Veghel and Bak 1993), and among *Platygyra* morphospecies (Miller and Benzie 1997).

Another early genotyping method was restriction fragment length polymorphism (RFLP), which hybridised digested DNA fragments to probes for determining their lengths, or to genomic DNA of known species to establish identity. McMillan and Miller (1988) used RFLP to distinguish the morphologically confusing corals, *Acropora formosa* (= *A. muricata*) and *A. "nobilis"* (= *A. intermedia*; see Veron and Wallace 1984).

The first set of scleractinian DNA sequence data to be published comprised highly repetitive sequences of 118 bp each, otherwise known as minisatellites, cloned from *Acropora muricata* and *A. latistella* (McMillan and Miller 1989). Five more species were sequenced for these repeats in a follow-up study, in which a maximum parsimony analysis did not support most of the morphological subgroups (McMillan et al. 1991).

The use of polymerase chain reaction (PCR), an essential technique of today, began for corals with the amplification of nuclear 28S ribosomal DNA (rDNA) that was then sequenced for reconstructing the phylogeny of Anthozoa (Chen et al. 1995). This analysis included nine species of scleractinian corals, and two families tested with more than one species each were recovered as clades. In a subsequent analysis that focused on Scleractinia, Veron et al. (1996) added six species with improved representation from Fungiidae and Poritidae, which were found to be monophyletic.

At about the same time, the mitochondrial 16S rDNA was sequenced from 34 species to reconstruct a larger scleractinian phylogeny (Romano and Palumbi 1996, 1997). This analysis showed that all five genera and nine of ten families for which more than one taxon were tested formed monophyletic groups. However, of the seven suborders examined, only three—Meandriina, Poritiina and Dendrophylliina—were recovered unambiguously as clades, although only Dendrophylliina remains the only monophyletic suborder to emerge from recent studies (e.g., Fukami et al. 2008; Arrigoni et al. 2014a).

Other PCR-based methods were adopted earlier on but these contributed little to phylogenetic reconstruction and have largely been discontinued owing to the fall in DNA sequencing costs in recent years. For instance, random amplified polymorphic DNA (RAPD) detected by four 10-mer primers showed that *Favia fragum* and *Porites astreoides* underwent high levels of self-fertilisation (Brazeau et al. 1998). Five RAPD primers were also used to assess differentiation among populations of *Acropora surculosa* (= *A. hyacinthus*) in Guam (Romano and Richmond 2000). The four populations studied were not significantly distinct from one another, but the eastern and western coasts of Guam were found to be genetically distinct when the respective populations were pooled. Amplified fragment length polymorphism (AFLP) is another PCR-based tool related to the RFLP technique that amplifies the restriction fragments which are subsequently separated by gel electrophoresis. This method aided in the discrimination of *Orbicella faveolata* from the other two species of the *O. annularis* complex (Lopez and Knowlton 1997; Lopez et al. 1999). Interestingly, AFLP was able to detect a much greater proportion of distinct *Pavona cactus* genotypes at Eclipse Island compared to allozyme genotypes (Smith et al. 1997), which indicated highly clonal populations instead (Ayre and Willis 1988).

Microsatellites, short tandem sequence repeats of between two and five bp, are typically used in population genetic studies and in tests of species boundaries among closely-related species. The first coral microsatellite to be utilised was detected in *Orbicella franksi* and used to distinguish among members of the *O. annularis* complex (Lopez et al. 1999). Many taxon-specific sets of microsatellite markers were published at the turn of the century (Maier et al. 2001; Le Goff and Rogers 2002; Magalon et al. 2004; Miller and Howard 2004; Severance et al. 2004a; Shearer and Coffroth 2004), and continue to be developed in recent years (Davies et al. 2013; Torda et al. 2013c; Boulay et al. 2014; Serrano et al. 2014; Zilberberg et al. 2014; Addamo et al. 2015; Tay et al. 2015). Unfortunately, the extreme polymorphism exhibited by these markers even among sibling species diminishes their utility for inferring phylogenies, but they continue to be the main workhorse for population genetic studies.

The first multi-species evolutionary trees of Scleractinia were reconstructed on the basis of the mitochondrial 16S rDNA (Romano and Palumbi 1996) and nuclear 28S rDNA (Veron et al. 1996). Shortly after, the nuclear internal transcribed spacers 1 and 2 (ITS), which include the 5.8S rDNA between them (White et al. 1990), were amplified and sequenced from the *Orbicella annularis* complex (Lopez and Knowlton 1997), as well as species from *Acropora* (Odorico and Miller 1997) and *Porites* (Hunter et al. 1997). Lopez and Knowlton (1997) also obtained sequence data from the β-tubulin coding and intron regions, but found that ITS and these loci showed no diagnosable variability among the three *Orbicella* species. The *Acropora* species exhibited varying degrees of molecular separation, with only *A. longicyathus* clearly distinguished from the other four studied species (Odorico and Miller 1997). However, ITS from five species of *Porites* analysed under maximum parsimony appeared to resolve evolutionary relationships among them (Hunter et al. 1997).

These taxon-specific patterns of genetic resolution prompted researchers to expand on the repertoire of loci from both the nuclear and mitochondrial genomes for phylogenetic purposes (Severance et al. 2004b; Concepcion et al. 2006, 2010; Flot et al. 2008; Chen et al. 2009). These markers, along with the primers used to amplify them, are often clade specific. Among the nuclear loci that are still in use today, some of the earliest to be developed include the intron region of the mini-collagen gene (Wang et al. 1995), used almost exclusively to investigate the evolutionary history of *Acropora* (Hatta et al. 1999; Vollmer and Palumbi 2002; Fukami et al. 2003; Palumbi et al. 2012; Suzuki and Fukami 2012). The Pax-C 46/47 intron, introduced by van Oppen et al. (2000, 2001), continues to be used for *Acropora* phylogenetics (Richards et al. 2008, 2013) and taxonomically broader reconstructions (Fig. 4.1). The divergence of Pax-C intron is low among sibling species (van Oppen et al. 2000) but is much higher for more inclusive clades (van Oppen et al. 2001).

The awareness that gene duplication (Lopez and Knowlton 1997; Odorico and Miller 1997) and heterozygosity (van Oppen et al. 2000) are common in nuclear loci led many to clone their PCR products and sequence multiple clones in hopes of capturing intragenomic variability. These include amplifications of the Pax-C intron (van Oppen et al. 2001, 2004; Márquez et al. 2002; Richards et al. 2008, 2013), β-tubulin (Fukami et al. 2004b; Stefani et al. 2008a), ITS (Medina et al. 1999; van Oppen et al. 2000, 2002; Diekmann et al. 2001; Rodriguez-Lanetty and Hoegh-Guldberg 2002; Márquez et al. 2003; Chen et al. 2004; Vollmer and Palumbi 2004; Forsman et al. 2005, 2006, 2009, 2010, 2015; Wei

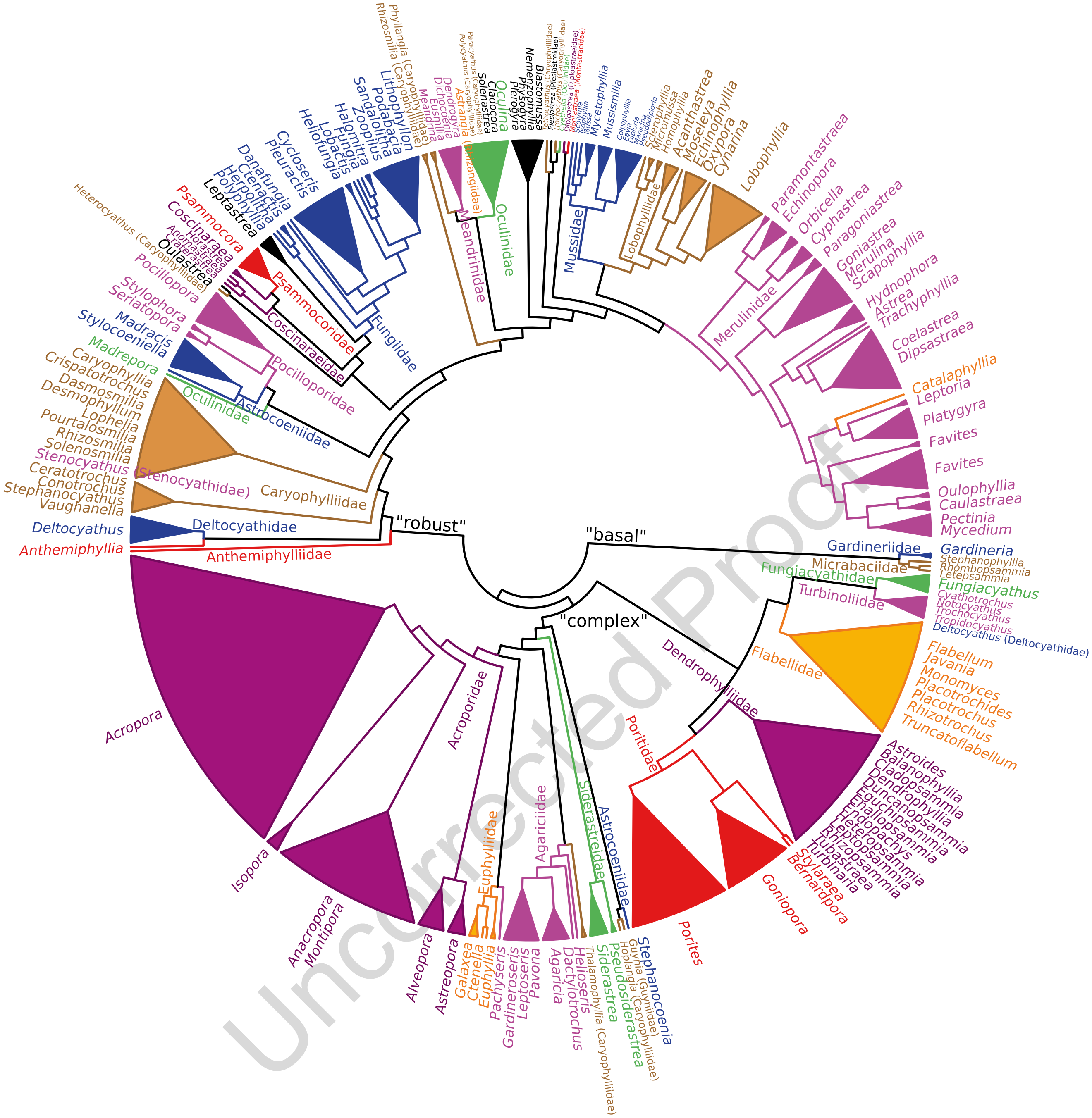

Fig. 4.1 Maximum likelihood genus-level phylogeny (576 species) of Scleractinia based on 12 DNA markers: mitochondrial 12S rDNA, 16S rDNA, ATP synthase subunit 6, cytochrome c oxidase subunit I, control region, cytochrome b and NADH dehydrogenase subunit 5; nuclear 18S rDNA, 28S rDNA, histone H3, internal transcribed spacers and Pax-C 46/47 intron. Data unavailable for Schizocyathidae, the only valid extant family not represented here. Branch supports not assessed in detail. *Colours* differentiate adjacent families and are not unique for any taxa, except for genera assigned *incertae sedis* that are shown in *black*

et al. 2006; Stefani et al. 2011; Kitano et al. 2013, 2014), and 28S rDNA (Chen et al. 2000; Cuif et al. 2003; Wolstenholme et al. 2003). For regions that have not diverged considerably between paralogues, such as the ITS, mixed PCR products can be split into two dominant sequences based on phase reconstruction of forward and reverse chromatograms of distinct lengths (Flot and Tillier 2006; Flot et al. 2006). The software Champuru was developed (Flot 2007) and used for processing direct sequencing data from *Pocillopora* (Flot et al. 2008, 2010; Schmidt-Roach et al. 2013; Adjeroud et al. 2014) and *Stylophora* (Flot et al. 2011). Variable amplicons with no intra-individual length variation can also be resolved statistically using SeqPHASE (Flot 2010). Furthermore, direct sequencing of ITS has been carried out following PCR with primers demonstrating high fidelity for a single copy (Takabayashi et al. 1998a, b, 2003; Lam and Morton 2003; Benzoni et al. 2007, 2010, 2011, 2012a, b, 2014; Mangubhai et al. 2007; Stefani et al. 2008b; Knittweis et al. 2009; Huang et al. 2011; Benzoni and Stefani 2012). Nevertheless, since the intra-individual variability of these nuclear markers is not fully understood (Chen et al. 2004; Vollmer and Palumbi 2004), caution should be exercised even when using these primer sets.

Mitochondrial loci have also been popular markers in phylogenetic analyses. These are haploid, and thus unambiguous sequences can be obtained generally without cloning. While mitochondrial genes typically evolve faster than nuclear genes in metazoans, anthozoans show an opposite pattern (van Oppen et al. 1999; Shearer et al. 2002; Fukami and Knowlton 2005; Tseng et al. 2005; Hellberg 2006; Huang et al. 2008; Chen et al. 2009). Therefore, these genes are more informative for reconstructing deep coral phylogenies. Other than the 16S rDNA that established widespread subordinal non-monophyly (Romano and Palumbi 1996, 1997; Le Goff-Vitry et al. 2004), 12S rDNA, cytochrome b and cytochrome c oxidase subunit I (COI) were purposed for corals relatively early (Medina et al. 1999; van Oppen et al. 1999; Chen and Yu 2000; Fukami et al. 2000) and have been used for inferring large scleractinian trees effectively (Chen et al. 2002; Fukami et al. 2004b, 2008; Barbeitos et al. 2010; Kitahara et al. 2010b, 2013; Stolarski et al. 2011; Arrigoni et al. 2012, 2014c; Huang 2012; Huang and Roy 2013, 2015; Marcelino et al. 2013; Curnick et al. 2015; Fig. 4.1). The gene encoding ATP synthase subunit 6 is also commonly used, but primarily for Acroporidae (Fukami et al. 2000; Forsman et al. 2010).

Different taxa contain various intergenic regions within their mitochondrial genomes, but these may not be orthologous across species or are not amenable for alignment across distant clades. The noncoding intergenic region identified by Fukami et al. (2004a), for instance, was too variable to be aligned across all of Merulinidae (Huang et al. 2011) and is not orthologous with the intergenic region (or the putative control region) in *Acropora* (van Oppen et al. 2001; Wolstenholme 2004; Richards et al. 2008, 2013), *Montipora* (van Oppen et al. 2004; Forsman et al. 2010), *Porites* (Forsman et al. 2009) or Agariciidae (Luck et al. 2013; Pochon et al. 2015). These fast-evolving mitochondrial markers remain useful for phylogenetic studies among closely-related species.

Whole mitochondrial genomes have also been extremely important sources of data for large coral phylogenies (Medina et al. 2006; Emblem et al. 2011; Kayal et al. 2013; Lin et al. 2011, 2014). Nevertheless, we note that major clades appear to exhibit distinct patterns of mtDNA sequence evolution that could be responsible for various topological inconsistencies, such as the paraphyly of Scleractinia with respect to Corallimorpharia (Kitahara et al. 2014), i.e., the “naked coral” hypothesis (Medina et al. 2006).

On the one hand, single-gene analyses were the rule among the earliest studies because of the high cost of DNA sequencing and the paucity of suitable markers, primers and publicly available data. On the other hand, there were studies drawing phylogenetic inference based on more than one loci, including Lopez and Knowlton’s (1997) analyses of two nuclear genes and AFLP. Early researchers also acknowledged that nuclear and mitochondrial genes evolve at different rates and thus both should be examined, albeit as separate datasets (Medina et al. 1999; Romano and Cairns 2000; van Oppen et al. 2001). Sequence data were combined beginning with the seminal study by Fukami et al. (2004b), which concatenated the cytochrome b and COI genes after passing the incongruence length difference test (Farris et al. 1995). The use of more than one marker for inferring species relationships has become the norm in more recent studies, aided by a variety of nucleotide substitution models (Posada and Crandall 2001) and the ability to use mixed models in a multilocus partitioned-by-gene analysis (Ronquist and Huelsenbeck 2003; Stamatakis 2006).

Authors remain split between concatenating markers to obtain hidden support (Huang et al. 2011; Addamo et al. 2012; Arrigoni et al. 2012, 2014a, b, c; Benzoni et al. 2012b) and making separate estimations of gene trees (Benzoni et al. 2011, 2012a, 2014; Gittenberger et al. 2011; Bongaerts et al. 2013; Kitano et al. 2013, 2014; Huang et al. 2014a; Arrigoni et al. 2015). With more markers available for inferring phylogenies, combined analyses of multilocus data may be the way forward. Recent large-scale studies (>450 species) have sought to concatenate data from seven or more loci (Huang 2012; Huang and Roy 2013, 2015; Curnick et al. 2015; Fig. 4.1). However, different genes cannot be assumed to share the same evolutionary history, and the phylogeny reconstructed for every gene may differ from the actual species history (Maddison and Knowles 2006). Thus, for species classifications, methods that use coalescent theory to jointly estimate gene trees and the species tree would be more appropriate (Liu and Pearl 2007; Liu 2008; Liu et al. 2008; Heled and Drummond 2010). A recent study of *Porites* corals based on the multilocus coalescence showed that the three branching forms found in the Caribbean are probably not distinct species (Prada et al. 2014).

These species tree methods have become especially relevant with the development of high-throughput sequencing technologies because it is now possible to generate orthologous sequence data in great abundance (McCormack et al. 2013). Such data can be obtained through the sequencing of expressed sequence tags (Philippe and Telford 2006), restriction site associated DNA (Rubin et al. 2012), and probe-based target enrichment of nuclear ultraconserved elements

(Faircloth et al. 2012; Lemmon et al. 2012), among several others. The assembly of the complete *Acropora digitifera* genome (Shinzato et al. 2011) has provided a much-needed reference to identify and utilise orthologous regions for phylogenetic analyses. Indeed, we expect these new methods to be applied on scleractinians extensively in the next decade, sustaining the "molecular revolution" (Stolarski and Roniewicz 2001: 1101) of coral systematics.

4.3 The Phylogeny of Scleractinia: Integrating Molecular and Morphological Evidence

The origin of modern Scleractinia is not well understood. Fossils appeared abruptly in the Middle Triassic (ca. 240 Ma ago) already represented by a wide variety of solitary and colonial forms (Roniewicz and Morycowa 1993; Veron 1995; Stanley Jr 2003). From colony integration, e.g., phaceloid, meandroid and thamnasteroid (Wells 1956; Stanley Jr 2003), to the structural organisation within individual corallites, e.g., septal ornamentation and axial structures (Roniewicz 1989; Roniewicz and Stanley Jr 1998; Roniewicz and Stolarski 1999, 2001), the range of morphological diversity observed among Triassic fossils is comparable to that in modern scleractinians. Moreover, the recent proposal that *Kilbuchophyllia* (Ordovician, ca. 450 Ma ago; Scrutton and Clarkson 1991; Scrutton 1993), *Numidiaphyllum* and *Houchangocyathus* (Permian, ca. 265–255 Ma ago; Ezaki 1997, 2000) were true scleractinian corals, in addition to molecular clock estimates (Stolarski et al. 2011), suggest an extensive Palaeozoic evolutionary history for Scleractinia.

The foundational studies of evolutionary relationships in the late nineteenth and early twentieth centuries relied exclusively on macromorphological skeletal characteristics of extant and extinct scleractinians. As they are sessile or have restricted capacity for movement (e.g., free-living and/or solitary), corals are subjected to the environmental conditions at their place of settlement. Consequently, they exhibit considerable morphological plasticity, driven in part by various ecological factors (Foster 1979a, b, 1980; Best et al. 1984; Hoeksema 1991; Budd 1993; Todd 2008). According to Lowenstein (1985), taxonomic research based exclusively on morphology is plagued by two major limitations. The first arises from convergence, in which unrelated taxa resemble one another as a result of having adapted to living in similar environments, so morphological similarities are not indicative of close evolutionary relationships. The second limitation concerns traits that may evolve at distinct rates in different lineages. Not surprisingly, the small number of "reliable" macromorphological characters, as indicated by Cairns (2001), and the uncertain impact of environmental variables on skeletal morphology have severely hampered attempts to infer relationships among scleractinian suborders and families (Romano and Cairns 2000; Stolarski and Roniewicz 2001; Le Goff-Vitry et al. 2004; Fukami et al. 2008). As such, evolutionary hypotheses based on morphological characters have resulted in several different taxonomic schemes (e.g., Vaughan and Wells 1943; Alloiteau 1952; Wells 1956; Chevalier and Beauvais 1987; Veron 1995; for a review of the first four schemes, see Stolarski and Roniewicz 2001). Despite the long history of the subject (e.g., Linnaeus 1758; Pallas 1766; Forskål 1775; Esper 1795; Lamarck 1801), taxonomic and evolutionary relationships within this important habitat-forming anthozoan order remain largely uncertain to date.

In their first comprehensive and consistent scheme that was heavily influenced by the skeletal macromorphological research of Milne Edwards and Haime (e.g., 1848a, b, c, d, e, 1850, 1851a, b, 1857), Vaughan and Wells (1943) hierarchically ordered several characters and devised keys to genera centered around an evolutionary hypothesis of Scleractinia. Although more recent analyses have included additional and more detailed subcorallite morphology, the revised version of this scheme published in the *Treatise on Invertebrate Paleontology* (Wells 1956) is still widely applied (Wood 1983; Veron 1986, 2000). The essence of Wells' (1956) scheme is that five scleractinian suborders can be distinguished based on characteristics of septal trabeculae and septal structure, with 33 families differentiated by wall type, occurrence of endotheca and type of budding.

The incorporation of subcorallite data into scleractinian classification was pioneered by Alloiteau (1952, 1957), who recognised a total of 65 families (30 with extant representatives) belonging to eight suborders. These groupings were later revised with greater emphasis on microstructural characters by Chevalier and Beauvais (1987), who proposed 11 suborders embracing 55 families. However, according to Stolarski and Roniewicz (2001: 1095), the microstructural criteria applied "to distinguish suborders containing only extinct taxa (i.e., Pachythecaliina, Distichophylliina, Archaeofungiina) are unclear or have not been supported by further research".

The most recent Scleractinia-wide classification divided the order into 13 suborders (7 with extant representatives) and 61 families (24 extant) (Veron 1995). However, as explicitly stated by the author, it had many points of uncertainty at subordinal and family levels. According to Budd et al. (2010), this evolutionary scheme had even lower resolution among families and suborders than the classification of Wells (1956), and by that time cladistic analyses had yet to contribute significantly to our understanding of scleractinian evolution. Indeed, the use of morphological characters to establish phylogenetic relationships within coral families have proved challenging and, as a consequence, applied to only a small number of extant families—Fungiidae (Cairns

1984; Hoeksema 1989, 1991, 1993), Mussidae and Siderastreidae (Pandolfi 1992), Turbinoliidae (Cairns 1997), Faviidae (Johnson 1998), Acroporidae (Wallace 1999), Dendrophylliidae (Cairns 2001), Atlantic Faviidae and Mussidae (Budd and Smith 2005), and Pacific Faviidae (Huang et al. 2009).

The recent recognition that the scleractinian skeleton is biologically controlled and not easily perturbed by environmental factors at the microstructural level (Janiszewska et al. 2011, 2013) has led to more detailed subcorallite observations (Cuif et al. 2003; Budd et al. 2012; Kitahara et al. 2012, 2013; Arrigoni et al. 2014a; Huang et al. 2014b; Janiszewska et al. 2015). Indeed, greater attention has been given to previously overlooked micromorphological and microstructural characters. Specifically, micromorphology considers the shapes of teeth along the wall, septa, columella, and septal face granulations, while microstructure is concerned with the cross-sectional wall structure, arrangements of rapid accretion centres and thickening deposits within the wall, septa, and columella (Cuif and Perrin 1999; Budd and Stolarski 2009, 2011). Together with improvements in our understanding of skeletal ontogeny, new studies of subcorallite morphology are shedding light on evolutionary relationships within the order. Indeed, the finding that intra-fibrous organic matrices containing complex macromolecular assemblages actually control nucleation, spatial delineation and organisation of basic microstructural skeletal units (Lowenstam and Weiner 1989) has provided support for several molecular clades (e.g., Cuif et al. 2003; Benzoni et al. 2007; Budd and Stolarski 2009, 2011; Janiszewska et al. 2011, 2015; Kitahara et al. 2012, 2013).

DNA sequences provide large numbers of phylogenetically informative characters that are independent of the high morphological variability of the coral skeleton. Various degrees of incongruence between morphological and molecular phylogenies are seen at all taxonomic levels, but the most striking is found at the subordinal level. While five suborders are recognised in the most widely-accepted morphological scheme (Wells 1956), only three main clades at the deepest nodes—"basal", "complex" and "robust"—have been recovered based on molecular analyses (Romano and Palumbi 1996; Kitahara et al. 2010b; Stolarski et al. 2011; Huang 2012). Nearly every genetic locus tested to date supports these latter groupings. The 28S rDNA (Chen et al. 1995; Cuif et al. 2003), 16S rDNA (Romano and Palumbi 1996, 1997; Le Goff-Vitry et al. 2004; Kitahara et al. 2010a), 12S rDNA (Chen et al. 2002), combined 16S rDNA and 28S rDNA (Romano and Cairns 2000), combined cytochrome b and COI, as well as β-tubulin (Fukami et al. 2008) all support the split between the "complex" and "robust" clades. The sister relationship between the "basal" clade and the rest of Scleractinia has been recovered by 12S rDNA, COI, 28S rDNA (Kitahara et al. 2010b; Stolarski et al. 2011), and most other mitochondrial loci (Huang 2012; Huang and Roy 2013, 2015; Kitahara et al. 2014; Lin et al. 2014). To date, no morphological characters associated with the hard skeleton have been found to correlate directly with the molecular splits. Interestingly, an examination of four "complex" and seven "robust" corals revealed that the two clades differ in embryonic developmental morphology ("prawn chip" in "complex" corals), with the notable exception of the "complex" *Pavona decussata*, which is more similar to "robust" clade representatives in this respect (Okubo et al. 2013). Expectedly, without any trace of soft tissue preserved, it would be even more challenging to position the extinct suborders on the coral phylogeny.

At the family level, the picture is not very different. Most families composed exclusively of zooxanthellate species have been shown by molecular data to be polyphyletic (Fukami et al. 2004b, 2008; Arrigoni et al. 2012). Among these, the most poorly understood families were Faviidae, Merulinidae, Pectiniidae and Trachyphylliidae (sensu Veron 2000). The Indo-Pacific representatives of these taxa had been called the "Bigmessidae" for their extremely chaotic and unnatural classification (Budd 2009; Huang et al. 2011). In contrast, the molecular evolutionary hypothesis posits that most families composed exclusively or predominantly of azooxanthellate corals are monophyletic. Therefore, apart from Caryophylliidae and Oculinidae, molecular groupings of azooxanthellate taxa are broadly consistent with classical taxonomy (Kitahara et al. 2010b; Stolarski et al. 2011).

According to our present understanding, the order Scleractinia comprises at least 30 clades that correspond to family-level groups. Among them, Gardineriidae and Micrabaciidae belong to the "basal" clade; Acroporidae, Agariciidae, Astrocoeniidae, Dendrophylliidae, Euphylliidae, Flabellidae, Fungiacyathidae, Guyniidae, Poritidae, Siderastreidae and Turbinoliidae from the "complex" clade; and Anthemiphylliidae, Caryophylliidae, Coscinaraeidae, Deltocyathiidae, Diploastraeidae, Fungiidae, Lobophylliidae, Meandrinidae, Merulinidae, Montastraeidae, Mussidae, Oculinidae, Plesiastreidae, Pocilloporidae and Psammocoridae represent the "robust" clade (Fig. 4.1). Genetic sampling for three families is limited or nonexistent. Rhizangiidae is represented only by the mitochondrial genome of an *Astrangia* species (Medina et al. 2006), which is closely related to *Oculina* (Huang 2012; Huang and Roy 2013, 2015). Stenocyathidae consists of three monotypic genera, of which only *Stenocyathus* has been sequenced and found nested within Caryophylliidae (Cuif et al. 2003; Kitahara et al. 2010b; Stolarski et al. 2011). Schizocyathidae contains three monotypic genera that have never been sampled for genetic data. Among the "robust" corals, *Madrepora* and *Heterocyathus* + *Oulastrea* appear to be two phylogenetically distinct lineages that cannot be placed in any of the above families.

4.4 New Taxonomic Revisions of Families and Genera

The abundance of taxonomic revisionary studies is increasing in recent years, but the resolution of all scleractinian families and genera is far from complete. A large amount of data and comprehensive taxonomic coverage are necessary to justify formal name changes following the International Code of Zoological Nomenclature, which have taken considerable time and effort by numerous coral taxonomists. Consequently, the first revision to jointly consider DNA sequence data and traditional forms of evidence such as morphology and reproduction in a phylogenetic context only emerged more than a decade after the first scleractinian molecular phylogenies by Romano and Palumbi (1996) and Veron et al. (1996).

The pioneering study by Wallace et al. (2007) used one mitochondrial (cytochome b) and one nuclear (histone 2a and 2b) gene to show that subgenus *Isopora*, previously placed within *Acropora*, was sufficiently distinct to be elevated to genus within family Acroporidae. *Isopora* tends to form more than one axial corallite per branch, while *Acropora* contains only a single axial corallite (Wallace et al. 2012). Reproductively, *Isopora* broods planula larvae and its oocytes are attached via a stalk to the mesenteries, in contrast to *Acropora* spp. which are broadcast spawners and have unstalked gonads.

Acroporidae expanded further when, following the comprehensive reconstruction of Fukami et al. (2008), Dai and Horng (2009a) transferred *Alveopora* from Poritidae to Acroporidae (see also Licuanan 2009). Like its new confamilials, *Alveopora* possesses synapticulothecal walls (Wallace 2012). Its exact phylogenetic placement is unstable to date, although evidence has pointed to a close relationship with *Astreopora* (Fukami et al. 2008; Kitahara et al. 2010b, 2014; Huang and Roy 2015; Kitano et al. 2014; Fig. 4.1).

Another group that underwent taxonomic changes relatively early was Siderastreidae. Fukami et al. (2008) first showed that the family was polyphyletic, with *Siderastrea* placed in the "complex" clade while the rest of the family was deep within the "robust" clade. Furthermore, Benzoni et al. (2007, 2010) found strong support to distinguish *Psammocora* from other "robust" siderastreids and resurrected Psammocoridae to accommodate the genus. The most recent analyses indicated that *Coscinaraea*, *Craterastrea*, *Horastrea* and *Anomastraea* constituted a monophyletic group that is sister to Psammocoridae, so the family Coscinaraeidae was proposed to contain these genera (Benzoni et al. 2012b; see also Huang 2012; Huang and Roy 2013, 2015).

These revisions implicated the closely-related Fungiidae as two former polystomatous and attached siderastreids, *Coscinaraea wellsi* and *Psammocora explanulata*, were genetically nested within the predominantly monostomatous and free-living Fungiidae and possessed the fungiid synapomorphy of compound synapticulae or fulturae, continuous buttress-like structures connecting the septa (Benzoni et al. 2007). The two rogue species were eventually transferred into *Cycloseris* (Benzoni et al. 2012a). Siderastreidae has thus been split into Siderastreidae, Psammocoridae and Coscinaraeidae, with two species transferred into Fungiidae. The latter also underwent a major reclassification based primarily on COI and ITS data, which supported the elevation of several subgenera previously in *Fungia* to genus, including *Cycloseris*, *Danafungia*, *Lobactis* and *Pleuractis* (Gittenberger et al. 2011). Several movements between genera were also proposed, such as the transfer of members of *Fungia (Verrillofungia)* into *Lithophyllon*, *Lithophyllon mokai* into *Cycloseris*, *Fungia (Danafungia) fralinae* into *Heliofungia*, and *Fungia (Wellsofungia) granulosa* into *Pleuractis*. Transformations of life history traits onto the molecular phylogeny further showed that the ability to be free living was lost four times and the evolution of multiple mouths occurred ten times, all independently throughout the evolutionary history of Fungiidae (Gittenberger et al. 2011).

The extreme polyphyly of the "robust" families Faviidae, Merulinidae, Mussidae and Pectiniidae revealed by Fukami et al. (2004b, 2008), coupled with the large number of species and genera in these taxa, posed severe challenges for taxonomic definitions of these corals. There was widespread acknowledgement that reclassification was necessary (Fukami 2008; Budd 2009; Budd et al. 2010), but the convergence of most macromorphological characters conventionally used to define genera and families hindered revisionary work. Many molecular (Huang et al. 2009, 2011; Benzoni et al. 2011; Arrigoni et al. 2012; Schwartz et al. 2012) and morphological (Budd and Smith 2005; Budd and Stolarski 2009, 2011) studies identified problematic taxa and highlighted phylogenetically informative characters—including molecular markers, macromorphology, micromorphology and microstructure—before the first taxonomic monograph was published.

In a massive undertaking, Budd et al. (2012) expanded Merulinidae to include all members of the "Bigmessidae" clade (XVII sensu Fukami et al. 2008), made up of mostly Indo-Pacific species from Faviidae, Merulinidae, Pectiniidae and Trachyphylliidae as defined by Veron (2000). They also relegated Faviidae to subfamily Faviinae as a group restricted to the Atlantic, and synonymised Pectiniidae and Trachyphylliidae as Merulinidae. Mussidae was redefined to include Mussinae (Atlantic mussids) and Faviinae. Finally, Pacific "mussids", the three remaining pectiniid genera, *Echinomorpha*, *Echinophyllia* and *Oxypora*, as well as

Moseleya were placed in the new family Lobophylliidae (Dai and Horng 2009b).

Budd et al. (2012) also proposed several modifications at the genus level. The highly polyphyletic *Favia* and *Montastraea* were trimmed of their Indo-Pacific and "Bigmessidae" members, which were accommodated by *Dipsastraea* and *Phymastrea* respectively, so that *Favia* now contains *F. fragum* and *F. gravida*, while *Montastraea* only includes *M. cavernosa. Montastraea* and *Diploastrea* were also placed in their own respective families Montastraeidae and Diploastraeidae as appropriate for their distinctiveness. *Scolymia* became an Atlantic genus, so its Indo-Pacific constituents became *Homophyllia australis* and *Parascolymia vitiensis*.

More recently, Huang et al. (2014a, b) examined Merulinidae more closely and found that more revisions at the genus level were necessary. In particular, *Astrea* was resurrected and a new genus *Paramontastraea* established to contain some species from *Phymastrea*, which was synonymised as *Favites. Coelastrea* was revived and a new genus *Paragoniastrea* described to accommodate distinct species previously classed in *Goniastrea*. *Barabattoia* and *Paraclavarina* were neither genetically nor morphologically separated from *Dipsastraea* and *Merulina* respectively, and were thus synonymised.

Major changes to the recently-established Lobophylliidae are ongoing, as Arrigoni et al. (2014b) considered *Australomussa* as a junior synonym of *Parascolymia*, and also resurrected *Sclerophyllia* to accommodate *S. margariticola* and its sister species *S.* (previously *Acanthastrea*) *maxima* that are endemic to waters surrounding the Arabian peninsula (Arrigoni et al. 2015).

Several taxa thought to be closely affiliated with Pacific "faviids" and "mussids"—Merulinidae and Lobophylliidae respectively—are now in distant "robust" taxa. Dai and Horng (2009b) transferred *Plesiastrea* into Plesiastreidae (clade XIV sensu Fukami et al. 2008), although only the move of the type species *P. versipora* has been validated since *P. devantieri* is in *Astrea*, Merulinidae (Huang et al. 2014b). *Blastomussa* was also transferred into Plesiastreidae (Dai and Horng 2009b), but it has been considered *incertae sedis* more recently (Budd et al. 2012; Benzoni et al. 2014) as *Plesiastrea* is more closely related to the azooxanthellate species *Cyathelia axillaris*, *Trochocyathus efateensis* and *Tethocyathus virgatus* (Kitahara et al. 2010b; Benzoni et al. 2011; Huang 2012; Huang and Roy 2013, 2015). Furthermore, the closest relatives of *Blastomussa* are *Physogyra*, *Plerogyra* and *Nemenzophyllia*, all previously in the "complex" Euphylliidae and now *incertae sedis* (Fukami et al. 2008; Kitahara et al. 2010b; Benzoni et al. 2014). *Oulastrea* is part of a deep-branching clade sister to Fungiidae, Psammocoridae and Coscinaraeidae (Huang 2012; Huang and Roy 2013, 2015), and may revert to the family Oulastreidae (Veron 2013). Perhaps the most enigmatic and still unresolved case of a former Pacific "faviid" is that of *Leptastrea*, which has been consistently shown as closely related to Fungiidae based on different markers (Romano and Palumbi 1996; Romano and Cairns 2000; Fukami et al. 2008; Kitahara et al. 2010b) despite striking differences in morphology between this genus and any of the known mushroom coral genera.

While the first integrative taxonomic revision was performed for Acroporidae in the "complex" clade, progress on other "complex" groups has been limited compared to the "robust" corals. Only recently was the first comprehensive revision of Poritidae published. Kitano et al. (2014) analysed samples from all five poritid genera using COI and ITS to show that *Porites* was monophyletic, but *Machadoporites* and *Poritipora* cannot be distinguished from *Goniopora* and were thus synonymised. The authors also found that *Goniopora stutchburyi* was genetically isolated from its congenerics but was the only sister species of *Stylaraea*, and thus moved it into a new genus, *Bernardpora*.

The azooxanthellate corals have lagged far behind in terms of revisionary work, due to much fewer taxonomists working on the numerous scleractinian lineages that contain them. Nevertheless, problematic taxa have been identified through broad-scale phylogenetic analyses (Kitahara et al. 2010b; Stolarski et al. 2011), and revisions have commenced. For instance, *Dactylotrochus cervicornis* was genetically nested among Agariciidae species, so Kitahara et al. (2012) moved it from Caryophylliidae into Agariciidae, making it the first extant agariciid that is solitary and azooxanthellate. An azooxanthellate shallow-water agariciid, *Leptoseris troglodyta*, was described shortly after (Hoeksema 2012). Finally, a new family Deltocyathiidae that included nearly all the species of *Deltocyathus* was established for an early-diverging clade traditionally placed in Caryophylliidae (Kitahara et al. 2013).

4.5 Detection of Species Boundaries

Identification of coral species has always been problematic. The overlap of morphological variation between and within colonies (i.e., between corallites) obscures species boundaries. Although species delimitation among scleractinian corals has been studied for many corals, data are still limited. The most studied coral in this respect is the *Orbicella annularis* complex. This group of three species, *O. annularis*, *O. franksi* and *O. faveolata*, is amongst the dominant corals of many Caribbean reefs. Historically, they have been considered as one species, *O. annularis*, with several morphs distributed along various environmental gradients, including different depths and reef zones (Graus and Macintyre 1976, 1989). However, a tremendous number of studies on morphology, reproduction, ecology, growth rates and genetics have been carried out (Knowlton et al. 1992, 1997; van Veghel and Bak 1993, 1994; van Veghel 1994; van Veghel and Kahmann 1994; Weil and Knowlton 1994; van Veghel and Bosscher 1995; van Veghel et al. 1996; Lopez and Knowlton 1997; Szmant et al. 1997; Lopez et al. 1999; Medina et al. 1999; Manica and Carter 2000; Knowlton and Budd 2001; Fukami et al. 2004a; Levitan et al. 2004, 2011), nearly all of which showing that the complex is not a single species with high morphological variation but comprises three separate species.

The research effort devoted to resolving the *Orbicella annularis* complex was unprecedented for corals, and remains unmatched for other taxa that are seemingly as complex. Nevertheless, there have been several cases whereby species complexes showed varied levels of separation and no taxonomic action was taken. We describe some of these examples as follows.

In order to investigate species boundaries, crossing experiments and spawning observations are the most precise approaches to test for reproductive isolation between species (Lang 1984). However, data from such studies are limited in terms of taxonomic and geographic coverage. Crosses have been tested for a variety of *Acropora* species and interspecific fertilisation observed in several combinations (Willis et al. 1997; Hatta et al. 1999; van Oppen et al. 2002; Fukami et al. 2003; Isomura et al. 2013). Nevertheless, interspecific fertilisation rates tend to be lower than intraspecific ones (Wei et al. 2012), allowing species boundaries to be defined (Willis et al. 2006). *Acropora* colonies with intermediate morphologies between species are generally not used for such experiments and remain challenging subjects for taxonomic research. Species boundaries of such difficult morphologies have been explored in two instances. First, five species and seven morphs from the *A. humilis* species group were examined by Wolstenholme (2004) for their reproductive patterns and molecular phylogeny. The data indicated that the five species were valid and the morphs at different stages of divergence from the valid species. Second, Suzuki and Fukami (2012) analysed the fertilisation rates and molecular phylogenetic relationships of three morphs of *A. solitaryensis* and found that two morphs were actual variants of the species while the last one was an undescribed species.

The merulinid genus *Platygyra* has also been used in multiple experimental crosses due to its abundance in the Indo-Pacific and problematic species identities. Miller and Babcock (1997) performed crossing experiments and recorded spawning times to show that reproductive isolation was severely limited among seven species in the Great Barrier Reef. Moreover, Miller and Benzie (1997) found that three species, *P. daedalea*, *P. sinensis* and *P. pini* contained no fixed differences in allozyme frequencies. However, contrary to these results, molecular phylogenetic analysis using ITS sequences revealed clear genetic differences between *P. sinensis* and *P. pini* in Hong Kong (Lam and Morton 2003). To date, species boundaries among *Platygyra* species remain unresolved, although results have so far suggested that geographic variation in the degree of species separation is apparent.

Cryptic diversity within species exists in several other corals. For example, comparisons of *Mycedium elephantotus* colonies between different localities in Taiwan revealed the existence of at least two reproductive groups based on timings of gametogenesis and spawning, supported by allozyme electrophoretic data (Dai et al. 2000). In fact, intraspecific differentiation was detected between co-occurring populations of *Cycloseris costulata* in Indonesia (Gittenberger and Hoeksema 2006), *P. daedalea* in Kenya (Mangubhai et al. 2007), and *Favites valenciennesi* in Japan (Fukami and Nomura 2009). Larger geographic contrasts such as between Red Sea and Pacific Ocean populations of *Dipsastraea* and *Stylophora* have also revealed molecular separation between regions (Stefani et al. 2011; Arrigoni et al. 2012; Keshavmurthy et al. 2013). However, to reach a stage where taxonomic revisions can be attempted, broad geographic sampling across the Indo-Pacific and detailed studies of closely-related species are necessary, such as in the case of species in *Astreopora* (Suzuki and Nomura 2013), *Pocillopora* (Pinzón and LaJeunesse 2010; Pinzón et al. 2012, 2013; Torda et al. 2013a, b; Marti-Puig et al. 2014; Schmidt-Roach et al. 2013, 2014) and *Psammocora* (Benzoni et al. 2010; Stefani et al. 2008a). In particular, boundaries among *Psammocora* species were clarified through a series of rigorous molecular and morphological analyses (Stefani et al. 2008a, b; Benzoni et al. 2007, 2010), which saw 24 nominal species reorganised as seven valid species—*P. albopicta*, *P. contigua*, *P. digitata*, *P. haimiana*, *P. nierstraszi*, *P. profundacella* and *P. stellata*.

Crossing experiments are usually performed for broadcast-spawning corals because it is relatively easy to collect eggs and sperm, but are difficult to apply on species that brood, are gonochoric or release daughter colonies asexually. Temporal reproductive isolation has been examined in some fungiids (Loya et al. 2009), but for other taxa, detailed morphological analyses with type material combined with molecular methods have been used to define species boundaries, such as in *Pocillopora damicornis* (Schmidt-Roach et al. 2014) and *Goniopora stokesi* (Kitano et al. 2013). Considering that coral spawning usually occurs once a year, it may be prudent to use these approaches on top of crossing experiments. Unfortunately, the latter may be the only way to tell species apart as some closely-related corals may be indistinguishable with morphological and molecular methods (e.g., Forsman et al. 2009).

An important goal of species delimitation is to characterise intraspecific morphological variation, but cryptic species that are still undergoing introgression may occur without fixed morphological differences throughout their distribution, such as in *Acropora cytherea* and *A. hyacinthus* (Ladner and Palumbi 2012). We expect more corals to possess such a signature, but an unambiguous procedure to deal with them taxonomically remains to be established.

4.6 Unresolved Taxa and the Future of Coral Systematics

Much of biology depends critically on a reliable taxonomic framework (Wheeler 2004). In modern times, such a framework has been built with molecular data on top of traditional and updated morphological evidence that has been the mainstay of taxonomy. Often, developmental, reproductive, and other ecological data are also gleaned for such research. Within the last two decades, coral biologists have developed a systematic phylogenetic approach that integrates these lines of evidence. Indeed, molecular data have been the major driving force in modern coral taxonomy, and together with the application of new techniques to explore subcorallite morphology, new light is still being shed on scleractinian phylogeny.

Although morphological evidence to support the three deep molecular clades is still scarce, microstructural characters such as the structure and arrangement of rapid accretion deposits and thickening deposits have proven to be phylogenetically informative at the family level (Budd and Stolarski 2011; Kitahara et al. 2013; Arrigoni et al. 2014a). Micromorphological traits such as shape of septal teeth, the development of secondary calcification axes and corresponding granulation on septal teeth and faces, the shape of the area between teeth, fulturae (Gill 1980), and others, are also useful for the differentiation of some genera within zooxanthellate coral families and genera (Benzoni et al. 2007; Budd and Stolarski 2009). In the same way, the delineation of primarily azooxanthellate coral families has largely been resolved, with few notable exceptions including Caryophylliidae (Kitahara et al. 2010b, 2012, 2013; Stolarski et al. 2011) and Oculinidae (Kitahara et al. 2010b; Huang and Roy 2015).

While rapid improvements have been achieved in scleractinian systematics, there are still unresolved taxa. In reality, the evolutionary positions of some families and genera, especially those still based solely on macromorphological characters (e.g., Wells 1956), remain tentative. Furthermore, only about one-third of all scleractinian species have been examined phylogenetically (Fig. 4.1; Huang and Roy 2015), and for most of these species, few genetic markers have been used. Families that are still showing considerable uncertainties in their evolutionary positions include Anthemiphylliidae, Astrocoeniidae, Caryophylliidae, Oculinidae and Siderastreidae (Benzoni et al. 2007; Fukami et al. 2008; Kitahara et al. 2010b, 2012; Huang 2012; Huang and Roy 2013, 2015). In the case of genera, the emerging picture is even more concerning, as we are still unable to place many of them precisely on the phylogeny. They include *Anthemiphyllia*, *Astrangia*, *Catalaphyllia*, *Cladocora*, *Culicia, Gyrosmilia, Indophyllia*, *Leptastrea*, *Montigyra*, *Paracyathus*, *Polycyathus*, *Simplastrea*, *Solenastrea* and *Stephanocyathus*. Representatives of some of these genera are rare or restricted to remote localities and sampling them for molecular analyses poses a practical challenge. Nevertheless, some genera with sufficient numbers of representatives tested have been shown to be para- or polyphyletic. Among them, some of the most problematic genera are within the families Agariciidae (*Leptoseris* and *Pavona*), Dendrophylliidae (*Balanophyllia*, *Cladopsammia*, *Dendrophyllia* and *Rhizopsammia*), Caryophylliidae (*Phyllangia* and *Rhizosmilia*), Euphylliidae (*Euphyllia* and *Galaxea*), Flabellidae (*Flabellum* and *Truncatoflabellum*) and Oculinidae (*Oculina*). Unfortunately, only a few genetic markers have been sequenced from these genera, and most are only informative at higher taxonomic levels.

Endeavouring to improve our understanding of scleractinian evolution as a lineage and as a system, we recognise and consider some important future research directions. Amongst these, the most obvious is “the species problem in corals” as foreshadowed by Hoffmeister (1926: 151) and nowadays made increasingly clear by the application of molecular techniques; establishing a clear and unambiguous phylogenetic framework must be one of the first challenges to be addressed. Since reliable taxonomic information is essential for the interpretation of molecular phylogenies, institutional and financial investments should be made toward building strong specimen collections and spurring rigorous taxonomic research. In particular, the inclusion of more material with broader taxon coverage and multiple sampling localities in future phylogenetic studies should be supported consistently by in situ images, collection of voucher specimens and fixed tissue samples for deposition in accessible repositories. This will allow re-examination of evidence as new molecular and morphological techniques become available. Moreover, importance should also be accorded to existing historical reference collections, including type material of extant and extinct coral taxa for which only a morphological approach can be used.

Although coral molecular phylogenetic studies generally focus heavily on few mitochondrial or ribosomal markers, and whilst these have greatly improved our understanding of scleractinian phylogenetic relationships, it is now clear that to achieve higher resolution and to be able to investigate all taxonomic levels, multiple genetic markers are essential (e.g., Dunn et al. 2008; Philippe et al. 2009; Regier et al. 2010). In the case of corals, a stumbling block to applying such multilocus phylogenetics is the paucity of single copy nuclear markers that have been tested. To cross this hurdle, we must turn to high-throughput sequencing technologies for obtaining genomic or transcriptomic data for a range of corals. These methods could be used to collect near-exhaustive molecular data possibly containing phylogenetic signal at all levels. However, notwithstanding the progress expected with phylogenomics, we stress that improvement of techniques and better understanding of the taxonomic signals and environment-induced variability of morphological characters are essential for advancing the field.

As we go forth in this new age of coral systematics, the gap between the state-of-the-art classification and practical needs of the broader scientific community appears to be widening. Indeed, while taxonomic changes resulting from integrative analyses are increasingly being published, the outdated but understandably more widely-accepted scheme is still being applied in some recent work on corals and their associates (e.g., Ho and Dai 2014; Tsang et al. 2014; Work and Aeby 2014). A lag is to be expected before the new framework is embraced outside the restricted circle better informed of the ongoing revisions. To bridge this gap more rapidly, we urge more active collaborations between taxonomists and ecologists, as well as more user-friendly literature such as field illustrations of corals under the revised classification (e.g., Dai and Horng 2009a, b; Licuanan 2009).

Thus, apart from encouraging a new generation of taxonomists, molecular biologists, and paleontologists, the foment of multi- and interdisciplinary studies including taxonomy, ecology, morphology, molecular biology, palaeontology and oceanography, will shape future studies positively to help improve our understanding of scleractinian evolution. This is indeed a welcome development in a time of major scientific interest and intense public concern due to the uncertain fate of coral reefs in the face of anthropogenic challenges.

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