Molecular and morphological supertree of stony corals (Anthozoa: Scleractinia) using matrix representation parsimony

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(Received 1 July 2004; revised 25 February 2005; accepted 11 March 2005)

ABSTRACT

The supertree algorithm matrix representation with parsimony was used to combine existing hypotheses of coral relationships and provide the most comprehensive species-level estimate of scleractinian phylogeny, comprised of 353 species (27% of extant species), 141 genera (63%) and 23 families (92%) from all seven suborders. The resulting supertree offers a guide for future studies in coral systematics by highlighting regions of concordance and conflict in existing source phylogenies. It should also prove useful in formal comparative studies of character evolution. Phylogenetic effort within Scleractinia has been taxonomically uneven, with a third of studies focussing on the Acroporidae or its most diverse genera. Sampling has also been geographically non-uniform, as tropical, reef-forming taxa have been considered twice as often as non-reef species. The supertree indicated that source trees concur on numerous aspects of coral relationships, such as the division between robust versus complex corals and the distant relationship between families in Archaeocoeniina. The supertree also supported the existence of a large, taxonomically diverse and monophyletic group of corals with many Atlantic representatives having exsert corallites. Another large, unanticipated clade consisted entirely of solitary deep-water species from three families. Important areas of ambiguity include the relationship of Astrocoeniidae to Pocilloporidae and the relative positions of several, mostly deep-water genera of Caryophylliidae. Conservative grafting of species at the base of congeneric groups with uncontroversial monophyletic status resulted in a more comprehensive, though less resolved tree of 1016 taxa.

Key words: Archaeocoeniina, Caryophylliina, coral reefs, divide and conquer, evolution, Faviina, Meandriina, systematics.

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I. INTRODUCTION

Scleractinian corals are a group of exclusively marine animals with over 1314 described extant species. Spurred mainly by concern for the conservation of reef-building species, there is mounting interest in their evolution and systematics. Corals are increasingly used as a model in phylogenetic studies of marine speciation (Knowlton et al., 1997; Hatta et al., 1999; Vollmer & Palumbi, 2002). As well, coral systematics, based primarily on macroscopic skeletal characters, has come under intense scrutiny with the discovery that many genera have come under intense scrutiny with the discovery that traditional, morphology-based taxonomy is at considerable variance with molecular phylogenetic studies (Romano et al., 1996; Veron, 1996; Fukami et al., 2004). There are now several dozen phylogenetic studies that have examined interspecific relationships in corals, but no summary of these analyses exists to illuminate areas of agreement and conflict. Numerous other longstanding issues in coral biology concerning the origin and diversification of morphological, reproductive, community ecological and biogeographical characteristics could also be uniquely informed by being considered in the context of a large and comprehensive phylogeny. Here, I combine existing phylogenies of corals into a supertree summary that can aid in directing future phylogenetic effort and provide a consensus for addressing studies of character evolution.

II. THE SUPERTREE APPROACH

Supertrees are large phylogenies generated from the topological information provided by smaller trees. This way of producing large phylogenies is in contrast to the ‘total evidence’ or ‘supermatrix’ approach (sensu Kluge, 1989) whereby overlapping sets of compatible character data (e.g., nucleotide sequences) are combined in a single large matrix before analysis. Instead, in a supertree procedure, trees with overlapping sets of taxa are combined directly, obviating the need for compatible character sets. Currently the most practicable and widely used supertree algorithm is matrix representation with parsimony (MRP), a method introduced independently by Ragan (1992), Doyle (1992) and Baum (1992). The method is based on a result by Poincaré (1901) showing that there exists a unique matrix encoding certain graphs, including those formed by a collection of directed tree graphs as used to represent phylogenetic history. First, a set of rooted trees is coded as a taxon × tree-node matrix. Each species is represented by a row of entries recording that species membership in source-tree clades that head each column. A matrix entry is scored ‘1’ if the jth node subtends the ith species, ‘0’ if not, and is scored as missing if the species does not occur in the tree with the jth node. An all-‘0’ outgroup is appended and the matrix is subjected to a maximum parsimony phylogenetic analysis. Source trees or individual nodes can also be weighted according to their trustworthiness, such that inferred from bootstrap proportions (Bininda-Emonds & Bryant, 1998).

The supertree approach has the advantage of being relatively easy to implement and is the quickest, most economical route to a complete and accurate phylogeny of groups the size of Scleractinia. Criticisms of the supertree method centre on the potential loss of information that could occur from not considering the primary character data (Gatesy et al., 2002) or the creation of novel clades unsupported by any source tree (Pisani & Wilkinson, 2002). However, spurious clades are ‘exceptionally’ rare in simulation studies (Bininda-Emonds, 2003) and do not occur in any large supertree to date (Bininda-Emonds, 2004d). Moreover, simulation studies show that MRP recovers relationships as well as total evidence, particularly when matrix elements are weighted by nodal support (Bininda-Emonds & Sanderson, 2001; Bininda-Emonds, 2003). Empirical studies (Kennedy & Page, 2002; Salamin, Hodkinson & Savolainen, 2002) also find high concordance between trees generated by total evidence and supertree methods.

The accuracy of supertrees and the ability of MRP to generate an objective working hypothesis of relationships for very large groups has made it attractive to systematists.
seeking a synthesis of existing phylogenetic information (e.g., Liu et al., 2001; Greynar & Purvis, 2003) and to comparative biologists desiring a base for testing macroevolutionary hypotheses (review in Gittleman, Jones & Price, 2004). Complete species-level phylogenies, including some of the largest phylogenies yet made, now exist for primates (Purvis, 1995), carnivores (Bininda-Emonds, Gittleman & Purvis, 1999), lagomorphs (Stoner, Bininda-Emonds & Caro, 2003), bats (Jones et al., 2002), procellariiform seabirds (Kennedy & Page, 2002) and pine trees (Schwikl & Ackerly, 2001). Of the 27 supertree studies published by 2004 and listed in Bininda-Emonds (2004a), ten include over 200 terminal taxa.

III. METHODS

(1) Data preparation

I searched for phylogenies from articles in the BIOSIS database, which extends to 1969, by using the wildcard search terms phylogen* and cladist* coupled with a variety of truncated colloquial or supraspecific taxonomic names, e.g., coral*, scleractinia* or favid*. Discovered papers were mined for other articles potentially containing phylogenies. I only collected relationships based on the formal phylogenetic construction algorithms neighbour-joining, maximum-parsimony, maximum-likelihood and Bayesian inference. When multiple trees estimated from a single dataset were presented in a study, I chose the authors’ favoured tree or, when no clear preference was given, the least resolved tree, assuming that these were the most conservative estimates of relationship. The final set of papers included all those published to 2004 inclusive and papers in press that were made available to me.

Some studies relied heavily on previously published datasets. For example, Le Goff-Vitry, Rogers & Baglow (2004) include many sequences from Romano & Cairns (2000), while the latter study is expanded from Romano & Palumbi (1996, 1997). Some authors (Purvis, 1995; Gatesy et al., 2002) suggest inclusion of such studies biases supertree analyses by implicitly giving greater weight to the data held in common. However, I consider all such analyses here because (1) most generally, all weighting schemes, including an implicitly equal weighting via use of non-duplicated character sets, are subjective without reference to a probability distribution specified by a model, (2) novel taxa added in a later analysis potentially affect support for previous relationships and hence, provide unique, independently derived information (Bininda-Emonds, 2004d), (3) later studies are not always more inclusive of previous ones and there is no non-arbitrary way of weighting the independent and non-independent portions of the data and trees, (4) different alignment and phylogenetic estimation procedures, even on the same dataset, contribute to the ‘independence’ of analyses (Bininda-Emonds, 2004d), and finally, (5) I wished to estimate a combined tree over all prior work, since it is each independent analysis that traditionally contributes to discussions of, and de facto assessments of confidence in, phylogenetic relationship.

While I do not differentially weight source trees per se based on data overlap, another form of weighting is used. Simulation studies (Bininda-Emonds & Sanderson, 2001) indicate that weighting of source-tree nodes according to their bootstrap support significantly improves accuracy of reconstruction. I follow this recommendation here. In effect, studies having low branch support, such as those based on few characters, will be down-weighted compared to those with highly supported, more probable clades. Nodes lacking support values were assigned a weight half that of the minimum reportable percentage (usually 50%). One study using Bayesian analysis (Le Goff-Vitry et al., 2004) gives branch support as posterior probabilities (Huelsenbeck & Ronquist, 2001). Using simulations, Hillis & Bull (1993) found that 70% bootstrap support corresponded to about a 95% chance that the subtended clade was true [but see qualifications in Sanderson & Wojciechowski (2000) and Erixon et al. (2005)]. Assuming that 0 and 100% bootstrap support corresponds to identical probabilities of a true clade, then this suggests an empirical relationship that I used to convert the partition probabilities in Le Goff-Vitry et al. (2004) to bootstrap values,

\[ B(C) = e^{4.6052P(C) - 9.4328}, \]

where \( B(C) \) and \( P(C) \) are, respectively, the calculated bootstrap proportion and the reported posterior probability of clade \( C \).

Another important factor affecting supertree accuracy is taxonomic coverage, the average number of source trees in which a taxon appears (Bininda-Emonds & Sanderson, 2001; Roshan et al., 2004). Low taxonomic overlap between source trees results in extended computation times and numerous equally most parsimonious solutions because of poorly constrained placements of the singleton sequences. To circumvent this problem, Bininda-Emonds & Sanderson (2001) suggest seeding a supertree analysis with a tree based on a taxonomic hierarchy that includes taxa from all source trees. This approach was not valid here, since numerous taxonomic groups within Scleractinia are certainly polyphyletic (Romano & Palumbi, 1996; Chen, Wallace & Wolstenholme, 2002; Fukami et al., 2004) and thus are a poor guide to potential relationships. Instead, and as Bininda-Emonds & Sanderson (2001) also suggest, I specified a constraint tree that retained as monophyletic well-accepted taxonomic groupings (e.g. Agariciidae, Dendrophylliidae, Acropora, Porites) uncontested by bootstrap proportions greater than 0.5 in any of the source trees estimated from molecular data.

Several analyses using morphological characters (Cairns, 1984, 1997, 2001; Hoeksema, 1989; Pandolfi, 1992; Wallace, 1999) did not provide bootstrap proportions. Hence, these analyses were redone using PAUP* 4b10 (Swofford, 2003) using the authors’ full character matrices. Daly, Fautin & Cappola (2003) provide a comprehensive combined molecular and morphological analysis lacking bootstrap values. This analysis could not be duplicated without information on which combination of species served as their genus-level exemplars. Consequently, I arbitrarily assigned bootstrap proportions of 0.5 to all nodes, while
recognising that this most likely down-weighted some well-supported nodes. In redoing the complete Acropora phylogeny in Wallace (1999), only the 29 species in common with the other source trees were used, so as to eliminate the effect that the remaining 84 singletons would have had on increasing computation time in the supertree analysis. But more importantly, this restriction had the effect of strengthening support within the morphological analysis, which was based on only 23 characters, for relationships among the reduced set of species. Unfortunately, the alternative, that of including the morphological source tree with all Acropora species (on very weak branches), resulted in a supertree for which the arrangement of the better supported molecular exemplars was identical to that in which the morphology-based Acropora tree was not included (results not shown). Finally, the genus Acropora is recognised as being composed of numerous syngameons and hybrid forms with species status (Hatta et al., 1999; van Oppen et al., 2001; Vollmer & Palumbi, 2002; Márquez et al., 2003). Therefore, I also thought it conservative to restrict exemplars from this genus to those that appeared to be ‘good’ species, as indicated by the molecular analyses. One species present in our supertree analysis, A. hemprichii, was not examined in Wallace (1999), but according to Wallace (1999), differs by only one unspecified character in her matrix from the putative sister species A. austera. Therefore, in the reanalysed matrix, I switched the latter species’ name for the former. Finally, I also estimated a phylogeny of Scleractinia based on data from Pires & Castro (1997), who provide a character matrix based on ctenid morphology for 52 scleractinian and three corallimorpharian species, which served as outgroups.

The taxonomy and spelling used in the source trees were changed to reflect Cairns, Hoeksema & van der Land (1999) for azooxanthellate species and Veron (2000) among zooxanthellate and apozooxanthellate forms, except when contradicted by Wallace (1999) for Acropora spp. When it was unclear how to resolve the apparent use of different synonyms of congeneric exemplars in studies by different authors (e.g. as with intransitive assignments to Meandrina spp.), all the exemplars were included in the supertree. Species only identified to a genus in the source trees were retained in the supertree, unless they could be deleted from a clade in the supertree comprised of all congeners.

(2) Analysis

For re-analyses in PAUP of fewer than 16 species, I used branch-and-bound searches. For larger datasets, I used two rounds of tree searching to minimise search times. In the first round, I identified the likely length of the best trees by performing a heuristic search with 1000 random-addition replicates having a limit of $10^6$ rearrangements per replicate and saving a maximum of only one minimal-length tree per replicate, collapsing zero-length branches, with tree-bisection-reconnection branch-swapping on multiple minimal-length trees. Finally, I sought to sample widely minimal-length tree islands by repeating the heuristic searches as before, but saving only trees of minimum length as inferred from the previous round (via the command NCHUCK = 1), while keeping a maximum of 500 minimal length trees per replicate. The 500 bootstrap resamplings were done as in the first round of searching described above, but with only 20 random-addition replicates per resampling and while saving all minimal-length trees per replicate. Fifty-percent majority-rule consensus trees with bootstrap values were converted to nested lists (i.e. PHYLIP- or Newick-formatted trees) and combined in a NEXUS-formatted matrix representation using scripts in MATHEMATICA 5.0 (Wolfram, 2003), which was analysed in PAUP* 4.0b10 (Swofford, 2003). Heuristic tree searches on this matrix were identical to those for the reanalyses of morphological data, but with a limit of $10^4$ rearrangements per replicate and the use of a constraint tree, as noted above, with the monophyly option in effect.

I assessed the degree to which the dataset supported each node in a 50% majority-rule consensus tree. For this, bootstrap proportions and decay values (Bremer, 1988) have been most often used (Bininda-Emonds et al., 1999, Liu et al., 2001, Greyner & Purvis, 2003), however, the meaning of these standard measures of nodal support in a supertree is neither straightforward nor well understood (Bininda-Emonds, 2003). Instead, I give nodal support using a method developed for supertrees, Bininda-Emond’s (2003) index of ‘qualitative support,’ or QS, by using PERL scripts provided by that author, as well as a ported DOS executable version by P. Shah and D. Pisani (Pennsylvania State University). Unlike Bremer decay or bootstrap proportions, the QS index summarises support for clades in a supertree by direct comparison to the source trees. Support for a clade in the supertree is quantified by assigning the clade a number between −1 and 1 based on its kind of conflict with a source tree, and then these numbers are summed over the source trees for that clade. Support for the entire supertree is derived by averaging over the support values of the individual clades. A value of −1 indicates that every source tree contradicts the supertree clade, while a value of 1 signifies entirely supportive source trees (see Bininda-Emonds, 2003 for a detailed explanation).

The constraint tree and all source trees with bootstrap values in Phylip/Newick/AltNexus format (with full Latin binomials divided by underscores), the Nexus files, the MATHEMATICA and PAUP code for the supertree analysis, and the reanalyses of the morphology-based trees are available from the author.

Post hoc grafting of species unsampled in any phylogenetic analysis to a tree can be desirable when independent evidence exists for a conservative placement of those species on the tree [e.g., Webb, 2000; Weihlen, Oyawa & Donoghue, 2000; Wilkinson et al., 2001]. This can increase the statistical power of comparative tests provided the procedure is insensitive to, or can account for, the increased uncertainty, such as by summing over the likelihoods of the increased number of resolutions of the tree (Weihlen et al., 2000) or considering only sister-clade size (Sanderson & Donoghue, 1994). This procedure increases the size of a tree, and thus the statistical power of subsequent character analyses. Hence, I grafted additional species onto the node subtending their least inclusive Linnaean taxon when the added-species’ membership in the taxon cum clade was...
uncontroversial. For example, the remaining *Porites* spp. not included in the supertree analysis were grafted to the base of the *Porites* clade. Similarly, *Favia*, while clearly polyphyletic, is nevertheless restricted in all phylogenetic analyses to a large faviine clade comprised primarily of faviids, mussids, pectinids and merulinids (Cuif et al., 2003; Fukami et al., 2004). Hence, the remaining species of *Favia* were placed at the base of this large clade. By contrast, some genera, such as those in Mussidae and Oculinidae, appear in widely separated positions in the supertree, so member species could not be confidently placed and are excluded.

IV. RESULTS AND DISCUSSION

(1) Descriptive statistics

I found 36 independent estimates of relationship for scleractinian coral species in 28 published studies (Table 1). The earliest formal phylogenetic hypothesis is from 1984 by Cairns (1984) on Fungiidae. Since then, there has been an exponential-like rise in the cumulative number of publications of coral phylogenies, with 55% of studies completed since 2000 (Fig. 1). Phylogenetic effort has been uneven.
across scleractinian taxa. Of the 36 phylogenies, 12 studies (or 33%) focussed on Acroporidae or its most speciose genera, Acropora and Montipora, largely to address issues of marine speciation and species boundaries in this most speciose and ecologically dominant group of reef corals (e.g. van Oppen et al., 2001; Vollmer & Palumbi, 2002). Much effort has also been directed at resolving higher-level scleractinian relationships, with 10 analyses (26%) with members drawn from four to all seven suborders, while one recent study (Fukami et al., 2004) broadly sampled species across two suborders in separate analyses of three gene regions. One hundred and twenty-one species or 35.3% of the taxa occurred only once in the source trees.

Four trees were ultimately not used in the supertree analysis because they either assigned outgroup status to an exemplar conspecific with an ingroup member (Diekmann et al., 2001) or because exemplars displayed rampant hybridisation/incomplete lineage sorting in which no monophyletic species could be discerned (McMillan et al., 1991; Hatta et al., 1999; Márquez et al., 2003). The final list of exemplars from the 32 usable studies consisted of 353 species (or about 27% of extant species) from 141 genera (63%), 23 families (92%) and all seven suborders. The matrix consisted of these species, an hypothetical outgroup and 2383 parsimony-informative pseudocharacters (sensu Bininda-Emonds & Bryant, 1998). There was a total of 40 000 distinct most parsimonious trees of length 3157 was recovered from 80 different tree ‘islands’ (with a limit of 500 trees per island). These trees were probably representative of optimal trees over the entire tree space, as ten other runs under identical search conditions, as well as a run recovering over 250 000 shortest trees before crashing, also found equal length shortest trees and produced strict consensus trees identical to the first run of 40 000 trees. The majority-rule consensus trees differed between these runs either not at all or in minor ways accounted for by multifurcations in the consensus of the first run shown in Fig. 2. In this tree, 171 nodes of a maximum possible 352, or 48.9%, were bifurcate; the consistency index (CI) and rescaled CI = 0.101, homoplasy index (HI) = 0.899 and the retention index (RI) = 0.300.

Qualitative support QS for the nodes impinging on the discussion is given in Fig. 2. These values and those at other nodes where negative, except for a few nodes subtending species generally found in only one or two source trees. Values between −1 and 0 most often indicated ‘soft conflicts’ or ‘soft mismatches’ between a supertree clade and source trees (Bininda-Emonds, 2003). A soft conflict occurs when a source tree clade is missing some of the species from the supertree clade and those species may only insert in the source tree so that they either contradict the supertree clade or are equivocal. This is expected when source trees are relatively small and overlap between source trees is low as in this study. Further, there were no source trees with clades that fully matched (‘hard match’) and only a few that fully contradicted (‘hard mismatch’) any supertree clade. In fact, under QS most source trees were considered to be ‘equivocal,’ neither supporting nor contradicting the supertree clades. Hence, it is interesting that the supertree, nevertheless, retained so much of the general structure seen in the Linnaean hierarchy and the molecular analyses of Scleractinia. For example, the supertree recovered Acroporidae as a clade, though most member species were missing from any given source tree. In cases like this, a lack of hard matches and thus lower QS support were attributable, at least in part, to having specified in the constraint tree that certain genera (e.g., Acropora) remain monophyletic.

Grafting species to the supertree resulted in a considerably larger, though less resolved tree (Fig. 3). I grafted another 649 species to an Adams consensus for a total of 1016 species (Table 2). This reduced the resolution of the tree, since some grafted species were added to bifurcate clades and the number of bifurcate nodes was reduced to 1016 species (Table 2). This reduced the resolution of the tree, since some grafted species were added to bifurcate clades and the number of bifurcate nodes was reduced to 164, or 46.5% of the nodes in the supertree.

(2) Clade structure

Below, I discuss in turn each of the mostly monophyletic groups labelled in Fig. 3 and summarised in Fig. 4. Particular attention is paid to the coverage and support provided by the source trees. The systematic aims in this study are (1) to summarise the last 20 years of phylogenetic effort, (2) to expose where phylogenetic effort has been in conflict and more study is desirable to resolve a clade’s topology and position within Scleractinia and (3) to identify areas in the scleractinian tree that appear confidently resolved and unlikely to change.

Fig. 1. Rise in publication of phylogenies of Scleractinia to the year 2004 inclusive.
Fig. 2. Supertree of Scleractinia. A 50% majority-rule consensus of 40,000 most-parsimonious trees of 353 species. Majority-rule consensus percentages given above branches and qualitative support values ($QS_{\text{clade}}$) below; a ‘C’ indicates that the clade was part of the constraint tree. The left and right basal subclades are, respectively, Complexa and Robusta.
Fig. 3. For legend see opposite page.
Table 2. Number of species grafted to supertree with monophyletic taxonomic groups. Dendrophylliidae from the genera Balanophyllia, Bathysamnia, Cladoopsamnia, Dendrophyllia, Egachisamnia, Enallopsamnia, Endopachys, Endopsamnia, Heropsamnia, Rhabdamnia, Trachpsamnia. Faviines from the genera Favia, Faviales, Goniastrea, Scolymia. Poritidae from the genera Poritopsis, Stylarnea.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species Grafted</th>
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<tr>
<td>Acanthastrea</td>
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<td>Acropora</td>
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<td>Cladocora</td>
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<td>Closomusosa</td>
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</table>

(a) General relationships

The supertree (Fig. 4) recovered the basal ‘robust’ and ‘complex’ clades of Romano and Palumbi (1996), which for brevity are labelled herein as ‘Robusta’ and ‘Complexa’, respectively. These two large clades constitute one of the best-supported and most unexpected findings in coral systematics since the application of molecular methods. Membership in Robusta and Complexa is fairly consistent across different genes via all subsequent ordinal-level phylogenies, excepting one analysis in Romano and Cairns (2000), which is derived from a short (222-base pair) fragment of 28S rDNA and which differs topologically largely in the position of its root. The basal partition between Robusta and Complexa highlights the rampant polyphyly of morphologically based suborders, families, and even genera that lie on both sides of the partition.

Within the Robusta, there are three large, derived clades: Plocoida (comprised of numerous species with exsert corallites – defined and discussed in Section IV.2a below) and its sister clade of Fungiidae plus siderastreids (in Siderastreididae 1 and Siderastreididae 2+Faviidae 1) (Fig. 4).

Sister to these groups is the third large robust clade, Faviina 1+Meandrina 1. Most molecular analyses examining higher-level scleractinian relationships include exemplars from only one or two of these three groups (Chen et al., 1995, 2002; Romano & Palumbi, 1996; Veron et al., 1996; Cuif et al., 2003; Fukami et al., 2004). Those studies with full representation either show the Fungiidae or Fungiidae + siderastreids as sister to the remaining groups (16S in Romano & Cairns, 2000), show Plocoida paraphyletic below Fungiidae (28S in Romano & Cairns, 2000), or recover the supertree relationship (Daly et al., 2003; Le Goff-Vitry et al., 2004). The latter three studies share a core set of 16S sequences from about 30 species. Hence, it is likely that this dataset is ultimately driving the relationship of the three large, derived clades in Robusta seen in the supertree. The relatively close relationship between these groups supports the placement of fungiids and siderastreids within the suborder Fungiina (Veron, 1986) and is consistent with microstructural similarities between fungiids and several families of favines (Morycowa & Roniewicz, 1993).

Within Complexa are four large clades (Figs 3 and 4): Dendrophylliidae, its sister group Poritidae 2, below that, a multi-family deep-water group Bathycola (comprised of Fungiacyathidae, Flabellidae and Turbinoliidae; defined below in Section IV.2a), and further below, a large diverse, but poorly resolved clade that includes Acroporidae and Agaricidae. Assuming for the moment the monophyly of these four large groups, only one study displays the supertree relationships between them (Le Goff-Vitry et al., 2004). The other studies with exemplars from all four groups (Romano & Palumbi, 1996; 28S in Romano & Cairns, 2000) show some lack of resolution, but generally place Dendrophylliidae sister to Poritidae 2, i.e. Poritidae minus Acropora. This sister relationship supports a similar inference regarding these two clades derived from the morphology of extant and fossil corals in Veron et al. (1996). However, unlike Robusta, virtually none of the other higher-level relationships within Complexa match relationships suspected from morphological data (Wells, 1956; Roniewicz & Morycowa, 1989; Roniewicz, 1996; Veron et al., 1996).

A taxonomically diverse paraphyletic group of small clades (Fig. 4) comprised of Astrocoeniidae 1, Gueniidae 1, Caryophyllidae 1, Pocilloporidae, Oculinidae 1 and Caryophyllidae 2, occurs at the base of Robusta, and Anthemiophyllidae and Caryophyllidae 4, both at the base of Complexa. With the exception of Pocilloporidae, members of these clades have been poorly sampled, often occurring in only one or two source trees. Hence, a comprehensive sampling of these groups in a single study may find, perhaps excepting Pocilloporidae, that this paraphyletic group is joined into fewer, larger clades. Alternatively, if the number of these clades is fairly accurate, then their small sizes reflect lack of sampling within these mostly lesser-known, often deep-water groups.
Astrocoeniidae 1

This clade consists solely of Madracis spp. Relationships within this genus are largely uninvestigated, but it appears to consist of several para- to polyphyletic species (Deikmann et al., 2001). Two species of Madracis have been sequenced for higher-level phylogenetic analyses and form part of only two studies. One of these studies suggests a close relationship between Madracis and Pocilloporidae, the family from which it was recently removed (Veron, 2000), finding it sister to the pocilloporids Stylophora + Seriatopora with high support (28S in Romano & Cairns, 2000). A second study recovered Madracis at the base of Complexa with low support (Cuif et al., 2003). A third study recovered Madracis at the base of Complexa with low support (Cuif et al., 2003). The supertree resolved the conflict by placing Madracis at the base of Robusta near the Pocilloporidae.

Guyniidae 1

This clade appeared in all of the optimal trees, but had equivocal Q5 support, i.e. a value near zero (Fig. 2). This appears due to the member species occurring in a single source tree (Cuif et al., 2003). In this source tree, as well as the supertree, the group is sister to the remaining robust corals. Guyniidae 1 consists solely of Stenocyathus, which, based on microstructural characters, has been hypothesised as being most closely related to either Flabellidae or Guynia by Stolarski (2000), and who on these criteria places it in the new family Stenocyathidae. Neither of the evolutionary scenarios suggested by Stolarski (2000) are supported by the source trees or supertree.

Pocilloporidae

Members of Pocilloporidae appear in most broad-scale phylogenetic studies of Scleractinia, but no study includes more than two of the three currently recognised genera (Veron, 2000). This sampling accounts for the lack of resolution between the pocilloporid genera in the supertree. Nearly all source trees position pocilloporid taxa near the base of Robusta. Surprisingly, however, Cuif et al. (2003) recover their exemplar well within the faviines. They note

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**Fig. 4.** Summary tree of higher-level relationships derived from Fig. 3 and discussed in the text.
the sensitivity of this position to nucleotide alignment parameters and attribute the unorthodox position to long-branch attraction. Indeed, re-analysing their data while excluding the difficult to align 3’ end of their 28S fragment recovered the pocilloporids near the base of Robusta regardless of most alignment parameter values (results not shown).

(e) Oculinidae 1 and Caryophylliidae 2

Oculinidae 1 consists solely of Madrepora oculata, while Caryophylliidae 2 includes three heterogeneric species. Together, all four species occurred as exemplars in only one source tree (Le Goff-Vitry et al., 2004). The deep divergence between, and the paraphyletic arrangement of, Oculinidae 1 and Caryophylliidae 2 in Le Goff-Vitry et al. (2004) was also recovered by the supertree.

(f) Siderastreidae 1 and Siderastreidae 2 + Faviidae 1

These two clades form part of a trifurcation that includes Fungiidae. Siderastreidae 1 consists of the genus Coscinaraea, while Siderastreidae 2 and Faviidae 1 form a clade of Psammocora and Leptastrea, respectively. Most studies did not include all three genera plus fungiids. In those that did, the arrangement of these genera with Fungiidae varies considerably, contributing to their lack of resolution in the supertree. In their 16S analysis, Romano & Cairns (2000) found an unresolved multifurcation of these groups. Using a dataset expanded from Romano & Cairns (2000), Le Goff-Vitry et al. (2004) found that Psammocora is polyphyetic, with Leptastrea and Coscinaraea sister to one another. However, in their analysis, branch support for these relationships was uniformly small. Nevertheless, both studies found that the three genera plus fungiids form a clade with high support. The close relationship between the siderastreids Psammocora and Coscinaraea and the faviid Leptastrea has been discussed by Romano & Cairns (2000), who remark that while Leptastrea’s relation to most other faviids has long been unclear, the genus shares no known morphological characters with the siderastreid genera or the fungiids with which molecular analyses find them closely aligned.

(g) Fungiidae

No worker has argued that fungiids do not form a natural, i.e. monophyletic group. Nevertheless, molecular studies have not confirmed the monophyly of Fungiidae in relation to closely allied siderastreids or have not included the potential sister groups. Le Goff-Vitry et al. (2004), though, found poor support for paraphyly of Fungiidae. The family appears monophyletic in the supertree only under a constraint imposed by the analysis, which was justified by the numerous presumed synapomorphies in reproductive, lifecycle and skeletal characters (Hoeksema, 1989). Relationships within the Fungiidae in the supertree are influenced largely by two comprehensive morphological analyses (Cairns, 1984; Hoeksema, 1989). These studies rooted their topologies with a Cretaceous solitary form that necessarily places colonial fungiids in a derived position. Supporting this result is the greater age of fossil solitary fungiids (at least Palaeocene) compared to that of colonial fungiids. The predominance of solitary forms within Fungiidae and colonial forms within several genera also accords with a derived and convergent condition for coloniality within the family (Veron, 2000).

(h) Plocoida

This clade consists of numerous members with exert to pronounced plocoid corallites. The clade is taxonomically diverse and comprised of members from Caryophylliidae, Faviidae, Meandrinidae, Oculinidae and Rhizangiidae. About half of the members appear to be from the western Tethys Ocean, what is now the Atlantic and Eastern Pacific Oceans (Table 3). The only other clade with a higher concentration of Atlantic species is one recently discovered by Fukami et al. (2004) within the Faviina and comprised entirely of Atlantic forms from the Faviidae and Mussiidae. In phylogenetic analyses that include members of Plocoida, the group appears as monophyletic and sister to Faviina (Cuif et al., 2003; Le Goff-Vitry et al., 2004), as a paraphyletic pair of clades below Fungiidae (28S in Romano & Cairns, 2000) or as part of an unresolved multifurcation that includes either Faviina (16S in Romano & Cairns, 2000) or Fungiidae (Daly et al., 2003). Fukami et al. (2004) find the meandrinid members of this group monophyletic with high support, but this arrangement seems outweighed by the contribution of other source trees weakly supporting the group as a grade or as polyphyletic. Hence, while Plocoida might be paraphyletic and meandrinids monophyletic, plocoidans appear to be, nevertheless, all closely related. The supertree resolution in favour of monophyly appears to be driven by the greater weight of higher bootstrap support for this arrangement.

Table 3. Putative taxonomic composition of Plocoida. Sampled species are those appearing in source trees, all of which are Atlantic (A) or eastern Pacific (EP) endemics

<table>
<thead>
<tr>
<th>Family</th>
<th>Genus</th>
<th>Species</th>
<th>Atlantic and EP spp.</th>
<th>N sampled</th>
</tr>
</thead>
<tbody>
<tr>
<td>Caryophylliidae</td>
<td>Paracyathus</td>
<td>19</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Polyca thyus</td>
<td>17</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Cladocora</td>
<td>4</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Phyllangia</td>
<td>7</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Rhizosmilia</td>
<td>6</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Faviidae</td>
<td>Solenastrea</td>
<td>2</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Meandrinidae</td>
<td>Dichocoena</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Dendrogrca</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Eusmilia</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Meandrina</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Oculinidae</td>
<td>Oculina</td>
<td>9</td>
<td>8</td>
<td>2</td>
</tr>
<tr>
<td>Rhizangiidae</td>
<td>Astrangia</td>
<td>15</td>
<td>13</td>
<td>1</td>
</tr>
<tr>
<td>Totals</td>
<td></td>
<td>84</td>
<td>46</td>
<td>15</td>
</tr>
<tr>
<td>% of Plocoida</td>
<td></td>
<td>100</td>
<td>54.8</td>
<td>17.9</td>
</tr>
<tr>
<td>% of A+EP spp.</td>
<td></td>
<td>100</td>
<td>100</td>
<td>32.6</td>
</tr>
</tbody>
</table>
A. M. Kerr

(i) Faviina 1 + Meandriina 1

This clade is also quite diverse at the family level, comprised mostly of species from the Faviidae. Scattered amongst the faviids are members from Meandrinidae, Merulinidae, Mussidae, Pectinidae and Trachypelidiidae (Fig. 2). The branching order in the supertree largely reflects the three independent and highly supported estimates from Fukami et al. (2004). Other source trees with less comprehensive representation from this group are also fairly congruent with the supertree. For example, the supertree recovered the clade of Fukami et al. (2004) consisting entirely of Atlantic species (from Scolymia cubensis to Diploria strigosa in Figure 2). However, in the supertree, this clade also bears the Indo-Pacific mussid Blastomussa merleti. This species occurs in only one source tree (Cuif et al., 2003), where it also occurs within a clade of the Atlantic endemics. One possibility then is that the clade identified by Fukami et al. (2004) as monophyletic for Atlantic endemism in fact contains one, and possibly more, faviine species from the Indo-Pacific. More likely, Cuif et al.’s (2003) recovery of B. merleti within the Atlantic group is due to alignment difficulties mentioned above regarding the same study’s placement of Pocilloporidae. These authors point out the sensitivity of B. merleti’s position to nucleotide alignment parameters. A preliminary reanalysis of their data that excludes the more quickly evolving 3′ end of the 28S fragment recovered B. merleti outside of the Atlantic clade and below Plocoidea (as defined here), regardless of alignment parameter values (results not shown).

(j) Caryophylliidae 4 and Anthemiphylliidae

These two groups of three and one species, respectively, form a clade in the supertree at the base of the Complexa. The four species appear together in three source trees, where the three species from Caryophylliidae 4 always form a single clade like that in the supertree. The position of Caryophylliidae 4 and Anthemiphylliidae with respect to one another, however, varies between source trees. The two form a clade that is sister to Complexa with high bootstrap support (Le Goff-Vitry et al., 2004) or is sister to Robusta with low support (28S from Romano & Cairns, 2000). Finally, in a third source tree (16S from Romano & Cairns, 2000), the two groups each contribute to a multifurcation at the base of Scleractinia.

(k) Siderastreidae 3 and Caryophylliidae 5

These two small groups are comprised of one and two species, respectively, and form part of a multifurcation in Complexa that includes Acroporidae and Agariciidae (Fig. 3). Siderastreidae 3 is comprised solely of Pseudosiderastrea tamayi, which appears in different positions in three source trees (Veron et al., 1996; Chen et al., 2000; 28S in Romano & Cairns, 2000). Caryophylliidae 5 consists of two Thalamophyllia spp. that between them appear in three source trees as either sister to Agariciidae (16S in Romano & Cairns, 2000; Daly, Fautin & Cappola, 2003; Le Goff-Vitry et al., 2004) or as sister to Pseudosiderastrea (28S in Romano & Cairns, 2000).

(l) Oculinidae 3 and Agariciidae

Oculinidae 3 is comprised of Galaxea spp. [which now includes Acrhelia; see Veron (2000)]. Among source trees with both groups, Galaxea appears sister to Agariciidae (Cuif et al., 2003), sister to Agariciidae plus Thalamophyllia (Le Goff-Vitry et al., 2004) or as part of a multifurcation (Romano & Palumbi, 1996; 16S in Romano & Cairns, 2000; Chen et al., 2002).

(m) Acroporidae 1 and 2 and Poritidae 1

The supertree recovered a clade consisting of acroporids and a poritid genus, Alveopora. The supertree arrangement occurs in three source trees (cytB in Fukami, Omori & Hatta, 2000; 16S in Romano & Cairns, 2000; Le Goff-Vitry et al., 2004). Romano & Cairns (2000) discuss the systematic implications of the branching order. These molecular studies are at variance with the weakly supported morphological phylogeny of Acroporidae of Wallace (1999). While consisting of the genera assigned to Acroporidae, the supertree group also includes Poritidae 1, an unidentified Alveopora sp. This species occurs in two source trees derived from an overlapping dataset (16S in Romano & Cairns, 2000; Le Goff-Vitry et al., 2004). Alveopora is morphologically distinct from the rest of Poritidae (Veron, 2000) and the finding from molecular data of its distant relationship to other poritids is discussed by Romano & Cairns (2000).

(n) Guyniidae 2 and Astrocoeniidae 2

These two groups consist of a species each from Guynia and Stephanocoenia, respectively. Together they form a clade that is sister to much of the derived Complexa (Fig. 2). QS and majority-rule support is relatively high because these species occur in only one source tree (Le Goff-Vitry et al., 2004), also as a clade, and so are not contradicted by any other tree.

(o) Bathycola

This clade is named in reference to the habitus of its members. It is a large group consisting entirely of small solitary corals in deep-water from three families with similar septal characters (Cairns, 1989): Fungiacyathidae, Flabellidae and Turbinoliidae. Two analyses used exemplars from all three families, 16S in Romano & Cairns (2000) and Le Goff-Vitry (2004). In the former study, the bathycolan species form part of a large multifurcation in Complexa. Hence, the monophyly of these families in the supertree appears to be driven by the high support for this group in the latter study and by the constraints that several genera in these families appear monophyletic. Another family of small, solitary deep-water corals, the Micraboraciidae, with skeletal characters most similar to that of fungiocyathids (Cairns, 1989) may also belong here, but has not yet been included in phylogenetic studies. The three families comprising Bathycola are discussed below in turn.

Within Fungiacyathidae, at most only two congeneric species occur in the source trees, which are constrained to be monophyletic in the supertree. Flabellidae is represented
in the supertree by three species from three genera that appear in four source trees, one of which (Le Goff-Vitry et al., 2004) finds the family monophyletic. Another source tree (28S in Romano & Cairns, 2000) roots Scleractinia within Flabellidae. If Flabellidae is indeed monophyletic (Cairns, 1989), then the paraphyly of this study appears due to an incorrect rooting, one not seen in any other source tree. The supertree recovers the family as monophyletic without a constraint and its sister as Turbinoliidae. Two molecular studies have included two heterogeneric species from Turbinoliidae: Romano & Cairns (2000), which recover them in a large complex multifurcation, and Le Goff-Vitry (2004), which finds them as sister groups. This family was constrained to be monophyletic in the supertree because of poor overlap between source trees. The branching order within the family is driven by a single morphological analysis by Cairns (1997).

(p) Siderastreidae 4 and Poritidae 2

Siderastreidae 4 is comprised solely of the genus Siderastrea, whose topology is due to a single source tree (Forsman, 2003). Siderastrea glynni was included in the source tree as a sister to S. siderea, though the former may be conspecific with the latter (Forsman, 2003). Siderastrea occurs in three source trees, either within dendrophylliid genera (28S in Romano & Cairns, 2000), in a trifurcation including Porites and a dendrophylliid clade (Cuif et al., 2003), or as monophyletic and sister to the dendrophyllids (Forsman, 2003). Poritidae 2 is comprised of Porites and Goniopora. In the six source trees with both genera, the sister relation is obtained in five (Romano & Palumbi, 1996; 16S and 28S in Romano & Cairns, 2000; Chen et al., 2000; Le Goff-Vitry et al., 2004). But in a combined morphological and molecular analysis, the genera are only distantly related (Daly et al., 2003).

(q) Dendrophylliidae

Several source trees included multiple exemplars from Dendrophylliidae. Most find the family monophyletic, with variable bootstrap support. Internal support for generic arrangements is invariably weak. In this study, the family was constrained to be monophyletic, as in the molecular studies able to resolve the group (28S in Romano & Cairns, 2000; Le Goff-Vitry et al., 2004), and based on the presumed synapomorphies of characters restricted to this group: synapticulothecae, confluence of tissue within and without the corallum, a variably present epitheca and elongated and fused higher-order septa (Cairns, 2001). The most comprehensive analysis of the group is a morphological phylogeny by Cairns (2001), which appears to drive the overall shape of the family in the supertree.

V. CONCLUSIONS

(1) Supertrees are currently the only formal method available for constructing complete phylogenies of very large groups of organisms and they constitute a rapidly developing branch of systematics (Bininda-Emonds, 2004b, c). They provide the only objective alternative to building large phylogenies by ‘cutting and pasting’ (Jones et al., 2002) smaller trees, offering an explicit and testable summary of the source trees. The primary goal of the supertree analysis of Scleractinia in this study was systematic, e.g. to summarise the state of the field as a single testable phylogenetic statement. But another aim was to provide a comprehensive phylogeny for use in comparative biology. Below, I conclude with a summary of the main implications of this study in light of these goals.

(2) In this study, the topology in many parts of the supertree appeared most congruent with the tree by Le Goff-Vitry et al. (2004). This is perhaps because MRP favours recovering relationships in large trees (Ronquist, 1996), since such trees contain more information (more species and nodes), though the tree of Le Goff-Vitry et al. (2004) was also among the best-supported source trees. As well, the latter study used many sequences also used in Romano & Palumbi (1996) and Romano & Cairns (2000). This had the effect of weighting areas of agreement between these three analyses. Areas of disagreement between this and other source trees occurred most often when smaller or less taxonomically broad-based studies (e.g. Forsman, 2003; Fukami et al., 2004) possessed high support for relationships in restricted parts of the tree. In general, the topology of molecular studies trumped that of morphology-based ones, as the latter were based on fewer characters and so had less branch support, which translated into less weight in the supertree analysis.

(3) Majority-rule consensus percentages for clades in some parts of the coral supertree were less than 100% (indicating zero Bremer support), showing that there is still disagreement among phylogenetic hypotheses in numerous areas of the tree. This disagreement is also summarised by Q5 support values, which tended to be negative. For example, the supertree could not confidently identify relationships within Acropora, Montipora and Porites. Part of the uncertainty in the supertree topology is caused by low taxonomic overlap between source trees. I minimised the influence of low overlap by constraining certain groups whose monophyly is uncontroversial to form clades in the supertree. Assuming the monophyly of even uncontroversial clades (e.g. Acropora or Madracis) renders the deeper partitions in the supertree contingent on these constraints, though the constraints are themselves testable propositions.

(4) There are two ways to increase taxonomic overlap between studies and thereby increase resolution of the supertree in future. The first is to include routinely in at least the more comprehensive character-based analyses, a set of widely available species. Currently, studies of corals involving different genetic markers often use different species or genera to represent particular higher-level taxonomic units (e.g. Pocilloporidae). This selection appears to be determined largely by ease of obtaining a sample. However, a trade-off can exist between choice of a regionally available sample and the study’s usefulness in building a complete supertree of corals. A second method to increase supertree resolution is to construct a study whose exemplars are specifically selected to maximise the contribution of
existing source trees to a supertree analysis. Graph theoretic-based methods of dataset decomposition can guide exemplar selection in such studies (Roshan et al., 2004). Another important, if obvious, source of uncertainty in the supertree was that even among relatively well-sampled groups, source-tree topologies were equally uncertain about a relationship. This resulted in a well-supported multifurcation appearing in the source trees and the supertree.

(5) The statistical power of formal comparative evolutionary analyses is greatly enhanced by using a large, comprehensive estimate of relationships (perhaps of several hundred species), which in many cases can only be provided by a supertree (Donoghue & Ackerly, 1996; Ree & Donoghue, 1999; Weiblen et al., 2000). However, most workers in coral biology deal exclusively with corals that are either reef-building (mostly shallow-water and colonial) or non-reef building (mostly deep-water, soft-bottom, often solitary). But in a comparative approach, understanding the evolution of either group will often require contrasting its characters against those from the other group in a phylogenetic setting. Currently, the literature and expertise in coral biology fracture along the divide between reef and non-reef taxa. Further, the more charismatic reef-forming species receive far more attention than the equally (probably more) diverse, soft-bottom-dwelling forms. Even among many reef species, however, we know surprisingly little about aspects of basic biology, such as reproduction and soft-tissue anatomy. Therefore, while a supertree will greatly inform fundamental and longstanding questions in coral biology via the first formal comparative analyses in the field [e.g. with phylogenetically-controlled independent contrasts (Felsenstein, 1985) and tests of diversification rates (Sanderson & Donoghue, 1994)], a supertree will also spur the growth and systematising of our knowledge of the natural history of corals that will form the basis of these comprehensive tests.

VI. ACKNOWLEDGEMENTS

I am indebted to numerous people for their help: O. Bininda-Emonds provided valuable criticism, Q5 analyses and access to a paper in press; S. Romano furnished key unpublished literature and advice on morphological studies; S. Cairns clarified taxonomy; while A. Baird, T. Hughes, M. Kosnik and J. Wolstenholme vetted an early draft. Financial support for this work came from a James Cook University (JCU) Merit Research Grant and an Australian Research Council (ARC) fellowship to the author, as well as an ARC Discovery Grant to T. Hughes. This is contribution number 135, Centre for Coral Reef Biodiversity, JCU and contribution number 570, University of Guam Marine Laboratory.

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