Meeting Report – Towards a new phylogeny and classification system for scleractinian corals

Scleractinian coral systematics is in the midst of a revolution resulting from advances in molecular systematics and in the microscopic technology used for extracting morphologic information. New research (e.g., Fukami et al. 2008) has shown that the majority of taxa at the suborder and family level are polyphyletic. From June 15-19, 2009, the Scleractinia Working Group (SWG) convened a 5-day workshop entitled "Systematics and evolution of scleractinian corals" at the National Museum of Natural History Museum of the Smithsonian Institution in Washington DC. The main goal of the workshop was to develop a strategy for revising the traditional phylogeny and classification system for Scleractinia and creating a new taxonomic synthesis, which integrates morphologic and molecular data. The synthesis will replace out-dated systems currently used in marine ecology, conservation biology, and paleontology. The workshop was sponsored by the Encyclopedia of Life (EOL), with additional support from the Treatise on Invertebrate Paleontology (TIP), and led by Ann Budd, Stephen Cairns, and Nancy Knowlton. The twenty-six participants (18 professionals, 3 postdocs, 5 graduate students) consisted of marine biologists and paleontologists based in ten countries (Australia, France, Italy, Jamaica, Japan, Netherlands, Poland, Taiwan, U.K., U.S.A.), and included both taxonomic experts and those skilled in modern systematics techniques.

SWG is currently engaged in three community database projects:

(1) Corallosphere (www.corallosphere.org), led by Ken Johnson. Corallosphere is a publically-accessible taxonomic database containing >1600 fossil and modern genera. It provides a dynamic central system for collecting, editing, and disseminating data and images. All data and images are first entered into Corallosphere before they are shared with other databases.

(2) Scleractinian volumes of the Treatise on Invertebrate Paleontology (paleo.ku.edu/treatise), led by Jarek Stolarski. These volumes will be part of a printed series of volumes published by the Paleontological Institute, University of Kansas; recent volumes are available online as downloadable chapters and a searchable database. The series synthesizes taxonomic information about all known invertebrate fossil genera.

(3) Encyclopedia of Life (www.eol.org). EOL is a web-based species-level database covering all living organisms (~1.8 million known species) on Earth. The classification system adopted in Corallosphere is being shared with EOL.

Figure 1: Workshop participants

Day 1: Introductions and primers

The first day of the workshop was devoted to reviewing new advances in molecular systematics and in the microscopic technology used for extracting morphologic information. Nancy Knowlton set the stage by reviewing the molecular phylogeny provided in Fukami et al. (2008), which shows that 11 of 16 families of modern reef-building scleractinian families (Acroporidae, Astrocoeniidae, Pocilloporidae, Euphylliidae, Oculinidae, Meandrinidae, Siderastreidae, Agariciidae, Fungiidae, Pectiniidae, Merulinidae, Mussidae, Faviidae, Trachyphylliidae, Poritidae, Dendrophylliidae) are polyphyletic. Allen Chen reviewed molecular analyses examining the monophyly of the Scleractinia, and concluded that the Order Scleractinia is monophyletic. The discrepancies in the results of different research teams concerning scleractinian monophyly appear to be the result of taxon sampling. One result that is repeated in all analyses is the existence of two distinct clades, termed "complex" and "robust" by Romano and Palumbi (1996), which do not conform with the five suborders of Wells (1956) or the suborders of other authors. George Stanley reviewed the "naked coral" hypothesis (i.e., the ephemeral nature of the skeleton and the close evolutionary relationships between corallimorpharians and scleractinians) from a paleontological perspective, and showed that this hypothesis does not conflict with scleractinian monophyly.

Other new unpublished molecular phylogenies were presented by Marcelo Kitahara and Marcos Barbeitos. Kitahara's trees included representatives of 10 primarily azooxanthellate families (Gardineriidae, Micrabaciidae, Flabellidae, Turbinoliidae, Fungiacyathidae, Guyniidae,

Anthemiphyllidae, Caryophyllidae, Stenocyathidae, Rhizangiidae) in addition to the 16 families treated in Fukami et al. (2008).

The disagreement found between the molecular results and traditional scleractinian classification indicates that many traditional morphologic characters are not effective at diagnosing groups above the genus level (subfamilies, families, suborders, etc) and that new diagnostic morphologic characters need to be discovered based on models of skeletal growth and assessed for homology. Several new micromorphological and microstructural characters were proposed in presentations by Jarek Stolarski (at scales >1000x), and by Nancy Budd (at scales of 50-500x). The effectiveness of these characters can be evaluated by mapping their states onto molecular trees. The shapes of teeth and granules along the margins and faces of septa conform better with molecular trees than do traditional macromorphologic characters, such as colony shape and form (cerioid, plocoid, meandroid, phaceloid etc), corallite diameter, and number of septal cycles. Preliminary attempts at morphological phylogenetics indicate that molecular data are more effective at diagnosing nodes at the base of the tree, whereas morphological data are more effective at branch tips. Ken Johnson described problems in usage of morphologic terms and ongoing efforts to create a glossary of morphologic terms as part of Corallosphere. The first-day session spilled over into the second day with Ewa Roniewicz' description of her previous attempt to construct a phylogeny for the Scleractinia using microstructural data and the fossil record (Roniewicz and Morycowa, 1993). Although diverse in growth forms and architectures, the early Mesozoic record contains many taxa that do not readily fit into the complex and robust clades found in Recent corals.

Day 2: Robust –vs- complex corals

The second day of the workshop was devoted to examining morphologic characters that distinguish complex and robust corals. The session began with a presentation by Sandra Romano, who reviewed her earlier work (Romano and Palumbi, 1996, 1997; Romano and Cairns, 2000), which noted the following morphologic differences between robust and complex corals:

- Robust: "relatively solid, heavily calcified skeletons that result from solid (septothecal or parathecal) construction of corallite walls"

- Complex: "less heavily calcified, perhaps as a result of the relatively porous (synapticulothecal) construction of corallite walls. In addition, in all but one of the taxa in this clade, the septal walls are built from simple trabeculae that form a porous and loose network of skeletal elements, resulting in a relatively light, complex architecture"

The session continued with discussion of the morphology of five traditional families whose members belong to both complex and robust clades in the Fukami et al. (2008) tree:
    -Siderastreids [Benzoni]: *Siderastrea* (complex, clade IX) –vs- *Psammocora/Coscinaraea* (robust, clade XI)
    -Astrocoeniids [Klaus]: *Stephanocoenia* (complex, clade VIII) –vs- *Madracis/Stylocoeniella* (robust, clade X)

-Oculinids [Kitahara]: *Galaxea* (complex, clade V) –vs- *Oculina/Cladocora* (robust, clade XIII)
-Euphylliids [Hoeksema]: *Euphyllia* (complex, clade V) –vs- *Physogyra* (robust, clade XIV)
-Meandrinids [Budd]: *Ctenella* (complex, clade V) –vs- other meandrinids (robust, clade XII)

These comparisons involved a review of the taxonomy of each family, followed by a series of photos illustrating various macromorphological, micromorphological, and microstructural features. In general, no single character or character combination appeared to separate complex from robust corals; there are no apparent synapomorphies. Synapticulae and porous walls/septa are common in complex corals, but there are many exceptions, e.g., as indicated in the table above, complex siderastreids have compact walls, and complex astrocoeniids, complex euphylliids, complex oculinids, and complex meandrinids do not have synapticulae. Parathecal walls (e.g., complex meandrinids, robust euphylliids) and septothecal/trabeculothecal walls (e.g., complex astrocoeniids, complex euphylliids, robust oculinids, robust meandrinids) occur in both complex and robust groups. Pali occur in complex astrocoeniids but not in robust astrocoeniids; pali occur in robust oculinids but not in complex oculinids. The best possible distinguishing characteristic appears to be related to thickening deposits; in general, robust corals tend to be more heavily calcified than complex corals. This feature warrants further microstructural investigation, as does the size and complexity of septal dentition and other micromorphological features.

Other problematic taxa that were discussed include:
Blastomussa (Benzoni, Stefani), clade XIV: *Blastomussa* is similar to *Physogyra* (also in clade XIV) in that it has strong median lines, smooth septal margins, septal lobes, and well-developed thickening deposits. However, it differs by having a septothecal wall, and trabecular columella. One of the two species is similar to *Parasimplastrea*.

The afternoon began with discussion of the morphology of three families that more clearly fit into either the complex or robust clade. For the complex corals, Carden Wallace described the morphology of acroporids and Michel Pichon the morphology of the poritids.
Acroporidae: Extracalicular budding; synapticulothecate; spiniform septa; absent or weak columella; extensive reticulate coenosteum, generally spinose or striate on surface.
Poritidae: Extracalicular budding; synapticulothecate; lacking coenosteum; perforate septa formed by loosely connected vertical trabeculae; innermost trabeculae sometimes differentiated as 'pali'; columella formed by a single trabecula.
Alveopora has many traits that are more similar to the acroporids (e.g., spiniform septa, absent columella) but it lacks the extensive reticulate coenosteum.
For the robust corals, Bert Hoeksema summarized the fungiids: Mono- or polystomatous; laminar septa connected laterally by bar-like elements called "compound synapticulae" or "fulturae" (a synapomorphy for the family); teeth on the margins of septocostae vary in shape from simple to complex, and are usually species-specific. *Leptastrea* and *Oulastrea* do not fit because they lack fulturae.
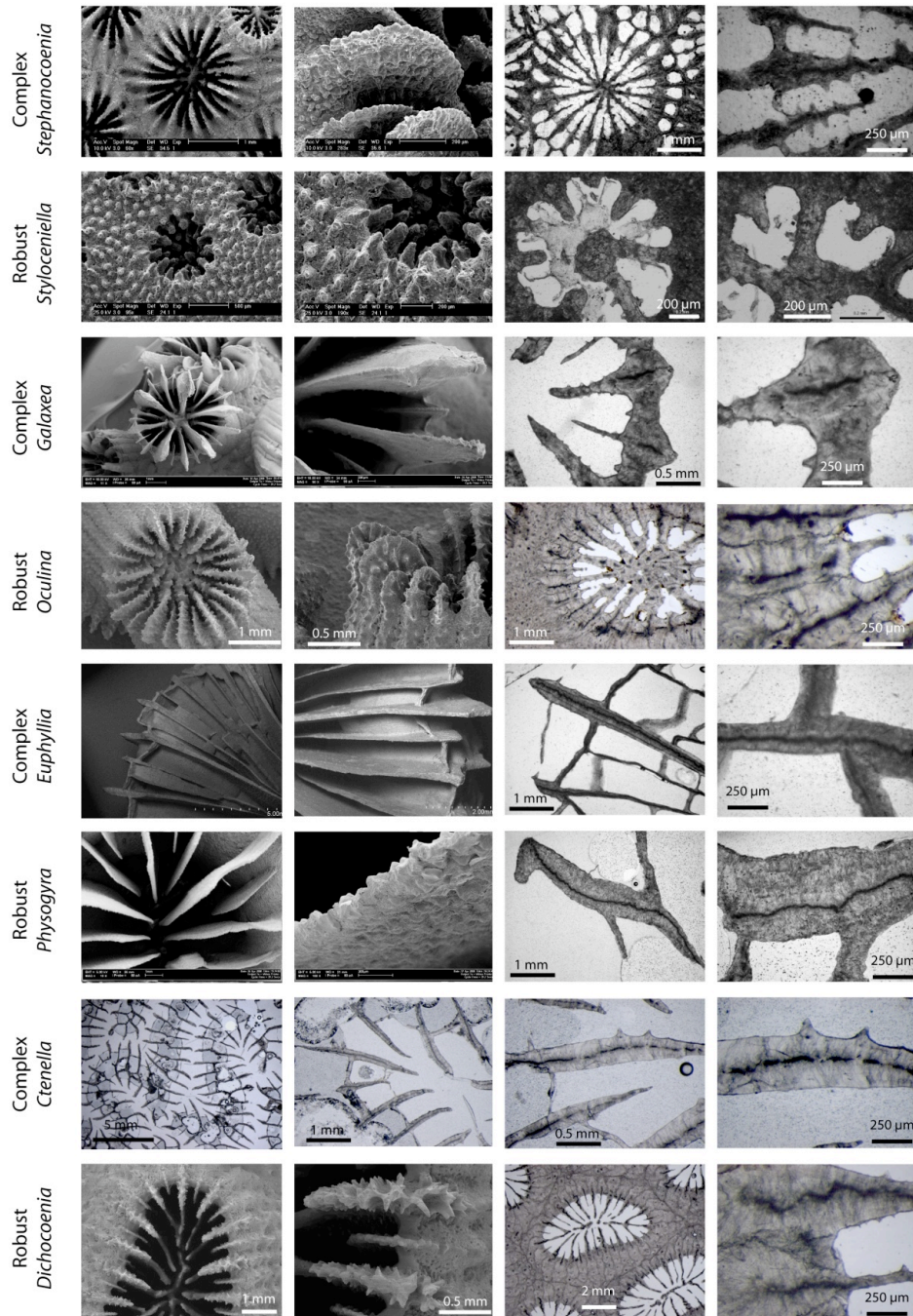
Figure 2: Comparisons between robust and complex corals within families that contain members of both molecular groups.

The discussion of complex vs robust corals then turned to the fossil record. Ken Johnson presented an overview of the Late Cenozoic fossil record in which he compared evolutionary patterns in the Caribbean and SE Asia. Extinction events occurred at the Oligo-Miocene and Plio-Pleistocene in the Caribbean, but not in SE Asia. Robust corals are more diverse in both regions, and were more susceptible to Plio-Pleistocene extinction in the Caribbean. Tom

Stemann provided a review of modern families that extend back to the Eocene as well as extinct early Cenozoic families. Bernard Lathuilière then summarized many of the problems involved in determining whether robust and complex corals extend back into the Mesozoic. Among the problems, in addition to there being no diagnostic characters of robust and complex corals, (1) no clear diagnostic characters of the suborder Scleractinia (and how it is distinguished from other similar Mesozoic anthozoan groups, which have skeletons), (2) many Triassic families appear to be evolutionary experiments (a "lawn" rather than a tree) and bear no relationship to modern robust vs complex corals, (3) many Jurassic families have presumed diagnostic characters similar in nature to modern families, but no comprehensive or rigorous comparisons have been performed as yet. Lathuilière emphasized the need for further detailed study of microstructure.

Day 3: Morphologic character matrix of scleractinian families (taxonomically-defined breakout groups)

On the third day of the workshop, the SWG made an initial attempt to construct a morphologic character matrix for selected members of ~100 valid scleractinian families. This matrix will serve two purposes: (1) to provide the basis for a morphologic phylogenetic analysis, which includes fossils, and (2) to construct morphologic diagnoses of families for Corallosphere and TIP. Prior to workshop, a list of ~100 scleractinian families was constructed by the editors of Corallosphere and TIP (Roniewicz for Triassic, Lathuilière for Jurassic, Baron-Szabo for Cretaceous, Budd for Cenozoic zooxanthellates, Cairns for Cenozoic azooxanthellates). The editors then either composed morphologic diagnoses for these families themselves or recruited experts to compose diagnoses. The diagnoses were used to construct a list of 49 morphologic characters (185 states) based on the morphologic glossary in Corallosphere (written for the most part by Brian Rosen and Jill Darrell, and organized by Ken Johnson). The list of families and the list of characters were provided to workshop participants to serve as a guide in selection of taxa and characters for the workshop character matrix.

The workshop then split up into four taxonomically-defined breakout groups. Each group first decided on 5-10 taxa, which it would code, and suggested 5-10 characters, which are especially important for coding these taxa. The suggested characters were used to construct a list of characters and character states for all four breakout groups to use in coding. Altogether the four breakout groups selected 42 taxa and 34 characters with a total of 90 states. The characters consisted of:

Colony-level macromorphology [11 characters]: corallum type (solitary vs colonial); attachment; intracalicular and extracalicular (coded as separate characters); types of calical arrangement such as cerioid, meandroid, phaceloid, circumoral (coded as separate characters); presence/absence of coenosteum and epitheca; costae continuous over the coenosteum (=confluent septa)
Corallite-level macromorphology [10 characters]: septal fusion of higher cycles; compactness of radial elements; presence/absence of costae, endotheca, fulturae, paliform lobes, pali, synapticulae; columella development and structure
Micromorphology [9 characters]: costal distal ornamentation shape; septal axial margins ornamentation (orientation, shape, size); septal distal margins ornamentation (tooth orientation, shape); septal lateral faces ornamentation (arrangement, shape); simple vs compound trabeculae

Microstructure [4 characters]: parathecal, septothecal, synapticulothecal, trabeculothecal walls (coded as separate characters).

Day 4: TIP and molecular breakout sessions; Corallosphere, EOL, BHL

During the morning of the fourth day, the group split up into two subgroups to discuss logistics and future directions associated with ongoing community projects. These included: (1) Treatise on Invertebrate Paleontology (TIP) breakout session (led by Steve Cairns), and (2) Discussion of unresolved issues in molecular analyses (led by Allen Chen & Nancy Knowlton).

During the afternoon, demos were provided of:
(1) EOL, Encyclopedia of Life, http://www.eol.org [Cyndy Parr]
(2) BHL, Biodiversity Heritage Library, http://www.biodiversitylibrary.org [Tom Garnett]
(3) Corallosphere, http://www.corallosphere.org [Ken Johnson]
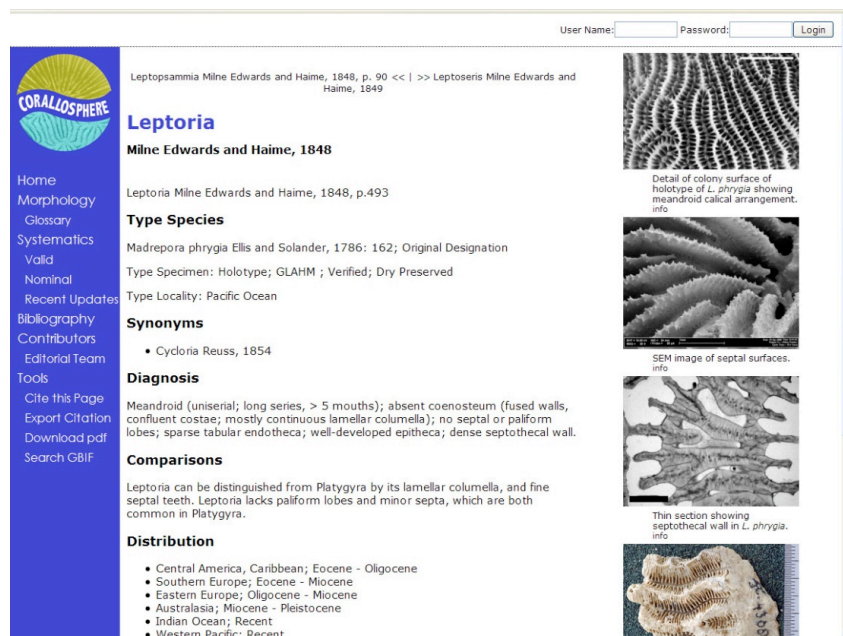

Figure 3. Example of a genus page in Corallosphere.

Day 5: Museum tours and final wrap-up

The morning of the fifth day was devoted to museum tours and the afternoon to a wrap-up session. Bert Hoeksema began the afternoon session with a review of ongoing work on coral biodiversity and biogeography, and the importance of individual species ranges and species richness patterns in understanding biogeographic shifts. He suggested that the study of coral symbionts may provide further insight into phylogenetic patterns of the coral hosts and coral reef biodiversity.

A preliminary phylogenic analysis using the character matrix constructed on the third day was performed, and inadequacies with morphologic characters were discussed. Problems identified included: (a) the plethora of existing terms, (b) the lack of homology in character definition, (c) the relative newness of micromorphologic and microstructural characters and lack of usage and rigorous definition, and (d) the need for character weighting. In addition, several unresolved issues in the molecular analyses were discussed. A follow-up meeting was planned to finalize the character matrix and identify synapomorphies for families and higher taxa.

In conclusion, SWG agreed that existing classification systems for scleractinians are inadequate, and a revised system that better reflects new molecular results needs to be adopted as soon as possible. It was agreed that the classification system used in Corallosphere would be shared with EOL, and wherever possible, family compositions (i.e., included taxa) would be based on the Fukami et al. (2008) tree. In order to share the classification system in Corallosphere with EOL, family pages are being implemented in Corallosphere.

A detailed report is available for downloading from the Corallosphere website.

References

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