EOL Synthesis Meeting Report:

Systematics and evolution of scleractinian corals



National Museum of Natural History Smithsonian Institution Washington, DC

June 15-19, 2009

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Introduction

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 of the Smithsonian Institution in Washington DC. The workshop was sponsored and funded by the Encyclopedia of Life (EOL), with additional support from the Treatise on Invertebrate Paleontology (TIP). It was led by A. Budd, S. Cairns, and N. Knowlton. Workshop participants consisted of: M. Barbeitos (postdoc), R. Baron-Szabo, F. Benzoni (postdoc), C.A. Chen, J. Darrell, H. Fukami, A. Gittenberger, B. Hoeksema, K. Johnson, J. Klaus, B. Lathuilière, C. Morrison, M. Pichon, S. Romano, E. Roniewicz, B. Rosen, G. Stanley, F. Stefani (postdoc), T. Stemann, J. Stolarski, and C. Wallace. Five graduate students attended: D. Huang, J. Jung, M. Kitahara, F. Nunes, and K. Rhodes. Workshop participants were based in ten countries: Australia, France, Italy, Jamaica, Japan, Netherlands, Poland, Taiwan, U.K., U.S.A.

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. One goal of the SWG is to develop a classification system and phylogeny for the Scleractinia; a new taxonomic synthesis, which would integrate morphologic and molecular data and replace various pre-molecular age classifications (e.g. Wells 1956, TIP). To this end, the workshop brought together a diverse group of paleontologists and marine biologists, including both taxonomic experts and those skilled in modern systematics techniques, to develop a strategy. The SWG is currently working on three community projects involving taxonomic data:

(1) <u>Corallosphere</u> (www.corallosphere.org), a web-based project led by Ken Johnson – Corallosphere not only serves as a central community database but provides a dynamic system for collecting, updating, and disseminating data and images. It involves fossil and modern coral genera. It facilitates rapid publication, and is readily available to the public. All data are funneled through Corallosphere before they are shared with TIP, EOL, and other databases.

(2) <u>the Scleractinian volumes of the Treatise on Invertebrate Paleontology, TIP</u> (paleo.ku.edu/treatise), led by Jarek Stolarski – part of a printed series of volumes published by the Paleontological Institute, University of Kansas. This series synthesizes taxonomic information about all known invertebrate fossil genera.

(3) <u>the Encyclopedia of Life, EOL</u> (www.eol.org) – a web-based species-level database covering all living organisms (~1.8 million known species) on Earth.

Specific goals of the workshop for Corallosphere were:

- Develop a plan for the glossary of morphologic terms
- Develop a consistent approach to morphologic diagnoses
- Finalize protocols involving spatial and temporal distributions
- Provide individual instruction to authors who are entering data for genera

Specific goals of the workshop for <u>TIP</u> were:

- Get commitments from authors and determine timetable (both volumes)
- Review progress with regard to data entry in volume 2 (~1636 genera, ~100 families)
- Discuss transfer of data from Corallosphere to TIP
- Discuss illustrations, bibliography, and other production matters with Jill Hardesty (TIP)

The main goal of the workshop for <u>EOL</u> was to develop a plan for sharing between EOL and Corallosphere.

Goals for molecular workers included:

- Determine high priority taxa for genetic analyses (including all type species of the type genus of each scleractinian family; more azooxanthellates)
- Develop a system for retaining specimens used in molecular analyses, so that they can be used in morphologic analyses

In the initial discussion of workshop goals, the group reiterated the importance of establishing a new classification system in the very near future, so that this information would be available to ecologists and conservation biologists.

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, Dendrophyllidae) 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). Gardineriidae and Micrabaciidae fall outside of the Scleractinia; Flabellidae, Turbinoliidae, Fungiacyathidae, Guyniidae belong to the complex clade, while Anthemiphyllidae, Caryophylliidae, Stenocyathidae, Rhizangiidae belong to the robust clade. As many as five families contain both zooxathellate and azooxathellate corals. Caryophylliidae is polyphyletic, but many other azooxanthellate families are not (e.g., Gardineriidae, Micrabaciidae, Flabellidae, Fungiacyathidae).

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. These macromorphological characters should be given less weight (or discarded) when performing morphological phylogenetic analyses. 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 (?two major suborders)

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. Discussion of observations based on these photos can be summarized as follows:

Table 1. Co	mparisons	between	complex	and	robust c	orals

F 1				Features common to
Family	Taxa being compared	Complex	Robust	both taxa
	Siderastrea (complex, IX) –vs-			
Siderastreiidae	<i>Psammocora/Coscinaraea</i> (robust, XI)	compact wall	perforated wall	synapticulae
Siderastrenidae				no
		compact septa	perforated septa	peritheca/coneosteum
		extracalicular budding	intracalicular budding	trabecular columella
		spinulose septal ornament	"septal paddles"	
		fulturae absent	fulturae present	
		regular septal fusion	irregular septal fusion	
	Stankan a sain (secondar			
	<i>Stephanocoenia</i> (complex, VIII) –vs-			
A	Madracis/Stylocoeniella	and the second second		1.6. 1.6
Astrocoeniidae	(robust, X)	smooth peritheca	spinulose peritheca	styliform columella
		vesicular peritheca	partially vesicular to solid peritheca	smooth septal margin
		septothecal (?) wall	perithecal (?) wall (marginotheca)	no synapticulae
		costae	no costae	
		pali	no pali	
		strong, zigzag median line; well- developed granules	small calc centers and extensive thickening deposits; median line not well-defined	
	<i>Galaxea</i> (complex, V) –vs- <i>Oculina/Cladocora</i> (robust,			
Oculinidae	XIII)	smooth septal margin	dentate septal margin	strong median line
		rudimentary axial structure	well-developed axial structure	no synapticulae
		no pali	pali	
		para-septothecal	septothecal	
		blistered coenosteum (dissepimental)	solid coenosteum (heavily calcified)	
		smooth peritheca	spinulose peritheca	

Euphylliidae	<i>Euphyllia</i> (complex, V) –vs- <i>Physogyra</i> (robust, XIV)	trabeculothecal wall	parathecal wall	strong median line
		less extensive thickening deposits	more extensive thickening deposits	smooth septal margin
				no peritheca
				no synapticulae
				columella absent
Meandrinidae	<i>Ctenella</i> (complex, V) –vs- other meandrinids (robust, XII)	parathecal wall	trabeculothecal/septothecal wall	strong median line
		lamellar columella	trabecular columella	smooth septal margin
		vesicular coenosteum	dense coenosteum	no synapticulae
		smooth peritheca	spinulose peritheca	

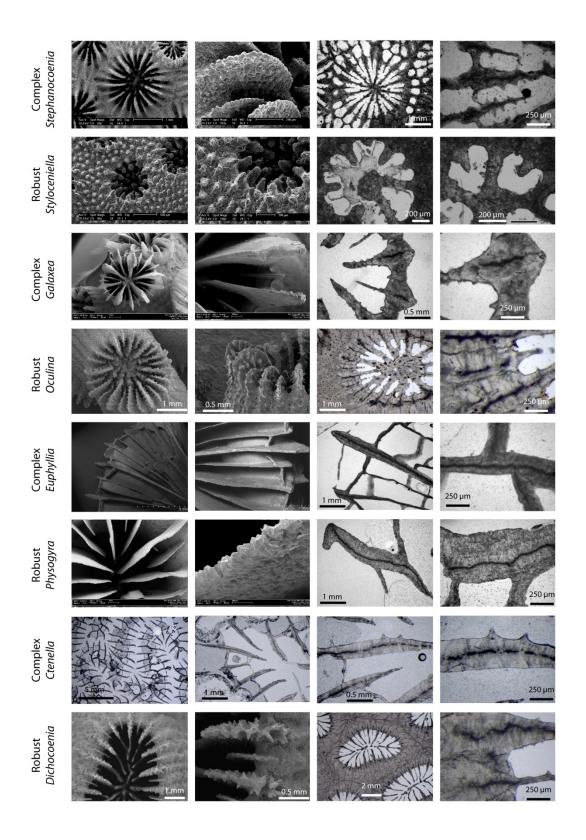


Figure 1. SEM and thin section images showing features given in Table 1.

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.

<u>Acroporidae</u>: Extracalicular budding; synapticulothecate; spiniform septa; absent or weak columella; extensive reticulate coenosteum, generally spinose or striate on surface.

<u>Poritidae</u>: 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.

In sum, no single character or character combination appears 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.

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, especially in light of the fact that the phylogeny constructed by Roniewicz and Morycowa using simple microstructural characters is inconsistent with regard to complex and robust corals.

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 breakout groups, with 5-8 members per group: Complex corals (moderator= Pichon, recorders= Wallace & Romano; Fukami clades I-IX) Robust I (moderator= Stolarski, recorder= Klaus; Fukami clade X) Robust II (moderator= Hoeksema, recorder= Gittenberger; Fukami clades XI-XIV) Robust III (moderator= Budd & Fukami, recorder= Johnson; Fukami clades XV-XXI)

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 final list of characters and character matrix are included as Appendices A & B. The characters consisted of:

<u>Colony-level macromorphology [11 characters]</u>: 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 (?=peritheca) and epitheca; costae continuous over the coenosteum (=confluent septa) [Notes: colony shape was not included because it is not a homologous character as traditionally defined; plocoid was not included because it is the same as presence of coenosteum; peritheca surface and other coenosteal characters were not included]

<u>Corallite-level macromorphology [10 characters]</u>: septal fusion of higher cycles; compactness of radial elements; presence/absence of costae, endotheca, fulturae, paliform lobes, pali, synapticulae; columella development and structure [<u>Notes</u>: numbers of septal cycles, septal insertion, septal cycle symmetry, and septal lobes were not included]

<u>Micromorphology [9 characters]</u>: 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 [Notes: the states for shapes of different types of "ornamentation" were not coded using a consistent set of well-defined terms and need to be re-evaluated across all micromorphological characters simultaneously; simple vs compound trabeculae may be redundant with the shape of costoseptal margins].

<u>Microstructure [4 characters]</u>: parathecal, septothecal, synapticulothecal, trabeculothecal walls (coded as separate characters) [<u>Notes</u>: centers of calcification, fibers, thickening deposits, median lines, etc were not included].

Inapplicable and unknown character states were not always coded in the same way, with many "inapplicable" data entries being coded as "unknown". Similarly many characters with "absent" states were coded as "unknown". These inconsistencies make it difficult to assess the extent of missing data in the matrix. Perusal of the matrix (Appendix B), however, indicates that many micromorphologic and microstructural characters were coded as "unknown" in many taxa, due to the lack of necessary SEM and thin section images.

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

<u>Alternative 1</u>: Treatise on Invertebrate Paleontology (TIP) breakout session (Cairns)

On June 18, a subset of the EOL-sponsored workshop on coral evolution and classification met for a morning session. The following people were present: Baron-Szabo, Budd, Cairns (moderator), Darrell, Gittenberger, Hardesty (representing TIP), Hoeksema, Johnson, Klaus, Lathuilière, Pichon, Rhodes, Roniewicz, Rosen, Stanley, Stemann, Stolarski, and Wallace.

First on the agenda, Jarek Stolarski reported on the progress of volume 1, which concerns the morphology, biology, and classification part of the Treatise. Now that certain morphological issues have been resolved, he feels confident that authors of that volume will be able to formulate their contributions. Concerned about the homogeneity of illustrations for this volume, Jarek asked Jill Hardesty if funds would be available for an illustrator to make critical drawing for this volume. Jill indicated that this was a good possibility, as long as a budgeted proposal was submitted to the Treatise office explaining the need for this service. The bibliography was also discussed at this time, which currently is empty. Again Jill Hardesty said that if we individually send to her files of citations from Endnote or Procite, she would employ a Kansas University student starting in Fall 2009 to create a single bibliography. Bernard Lathuilière also mentioned the Mesozoic bibliography, which might be a starting point for our bibliography. Jill Hardesty also reminded us that color pages cost about \$500 per page, but less if arranged in signatures. Stolarski suggested that the text of volume 1 might be ready by the end of 2010.

We then discussed volume 2, the taxonomic volume, starting with a progress report from the five team leaders concerning the number of generic names their teams have entered into Corallosphere and the composition of their teams (Appendix E). Thus far, all 1636 names have been assigned to an editor, and about 750 names (or 45%) have been entered into Corallosphere, although very few have associated images. Ultimately, it was suggested that we might need an illustration editor to arrange the various images into discrete figures, a service until recently accomplished by Treatise editors. It was noted that the 100 families also need to be assigned and added to Corallosphere. Cairns volunteered to construct the data points necessary for a family account. Ken Johnson also explained the review procedure that each genus will be subjected to before it is considered worthy of being submitted to the TIP office. It was also suggested that Corallosphere entry guideline be loaded onto Corallosphere, to help first time users. Essentially such a guide was circulated by Cairns last year, which can be modified and put in the system.

After a short break, TIP editor Jill Hardesty reviewed the four other volumes now in progress, concluding that ours was one of the more advanced in that we are using a web-based entry format for the generic accounts, i.e. Corallosphere. Rosemarie Baron-Szabo asked Jill if money was available for travel to museums to examine types, and Jill responded in the affirmative, asking that individual proposals be routed through the four co-coordinating editors of the group.

A set of deadlines was proposed by Cairns for the next three phases of volume 2: drafts of all genera by December 2009, images of all genera by June 2010, and all genera reviewed by the end of 2010, coincident with the anticipated completion of volume 1. However, it was pointed out by Hardesty, that volume 2 could be published independent of volume 1, and even prior to volume 1. These deadlines may be optimistic, but little discussion ensued, except to suggest that another joint meeting be held soon in order to code taxa.

After lunch, George Stanley presented the options for the reporting of geographic and stratigraphic ranges for the genera, discussing the standard narrative protocol characteristic of the TIP; a slightly more codified protocol based on drop down menus for age and coarse localities, which would be more appropriate for Corallosphere; and a third more highly detailed mapping of all occurrences, which would correlate to plate boundaries over time and thus be more geologically meaningful. No decisions were made about which system(s) to use.

<u>Alternative 2</u>: Discussion of unresolved issues in molecular analyses (Chen & Knowlton)

SUMMARY OF MOLECULAR BREAK-OUT SESSION

PRESENT: Nancy Knowlton, Allen Chen, Hiro Fukami, Sandra Romano, Marcelo Kitahara, Danwei Huang, Flavia Nunes, Fabrizio Stefani, Arjan Gittenberger, Cheryl Morrison, Marcos Barbeitos

General needs which were identified:

1) A formal working group in response to TARA Ocean expedition (Francesca chief contact) (list of Red Sea/ Indian Ocean taxa, collection permits, other issues)

2) CoralGene--- a listserv for coral molecular geneticists, information sharing (such as molecular markers) (Allen is working on this)

3) Database of "type species" photos (*Corallosphere* – Ken Johnson)

4) Mt genome sequencing of *Gardineria* (basal taxa to both complex and robust clades) to construct the mt genome tree

5) Mitochondrial genomes - better understanding of mt slow-down, role of secondary and tertiary structure, more taxa needed – choose on basis of Hiro/Marcelo trees.

6) Confirm species identities of vouchers that were only identified to genus in molecular trees.

7) Fossil record – any Paleozoic analogues? Use new mt gene/genome trees and fossils to date nodes.

8) Need more markers, especially nuclear. May be helped by 454 sequencing of *Lophelia*. Tree of Life is using 16S, COI, 12S?, 28S, 18S

9) Generate other trees from same data – e.g. ML alternatives

10) Correct erroneous GenBank sequences

11) Storage protocols - -80 C freezers vs other preservation methods.

Individual clades/taxa to be examined:

1) Clade 14----Blastomussa (also vs Parasimplastrea), Pleurogyra, Physogyra, Pleisastrea (Francesca's lab), add Pleiastrea devientieri (Gulf of Aden). Morphology- especially Physogyra/Pleurogyra vs Euphyllia. COI, rDNA, b-tubulin intron, 28S – does clade hold together?

2) Other Euphylliidae---Catalaphyllia, Nemenzophyllia (Allen's lab)

3) *Leptastrea* vis a vis relationship with fungiids Microstructure examination— compare with fungiids More species and nuclear markers (ITS?) needed.

4) *Pachyseris*--- (Francesca) Morphological examination and look at genetics of other species – are they all euphylliids??

5) Paulastrea (Astrocoenciina/ Pocillporidae) - check relationship to Madracis

6) Azooxanthellata taxa- check more *Trochocyathus* species using different gene loci (b-tubulin intron, etc.), particularly the paraphyletic status with *Pleisastrea* in Marcelo's COI tree (Marcelo working on this)

7) Large Pacific clade ("Bigmessidae") of Pacific faviids, Atlantic Montastraea, problem genera such as "Pacifavia" and others – needs better resolution (Danwei working on this for thesis, at least in part)

8) Atlantic sequences of Scolymia - there may be two very different ones.

<u>Afternoon demos</u>

On the afternoon of the fourth day, demos were provided of the following web-based projects:

- (1) EOL, Encyclopedia of Life, http://www.eol.org [Cyndy Parr, parrc@si.edu]
- (2) BHL, Biodiversity Heritage Library, http://www.biodiversitylibrary.org [Tom Garnett, garnettt@si.edu]

Ten major natural history museum libraries, botanical libraries, and research institutions have joined to form the Biodiversity Heritage Library Project. The group is developing a strategy and operational plan to digitize the published literature of biodiversity (pre-1923) held in their respective collections. This literature will be available through a global "biodiversity commons."

(3) Corallosphere, http://www.corallosphere.org [Ken Johnson]

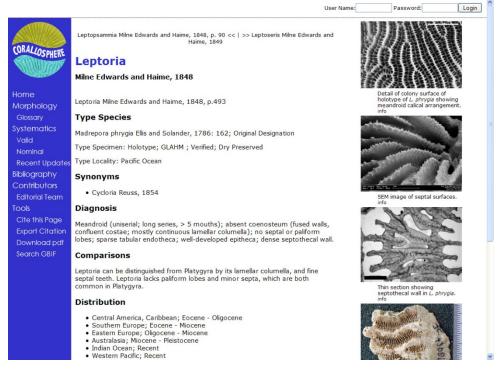


Figure 2. Example of a genus page in Corallosphere.

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.

Continuing work on the morphologic character matrix and phylogenetic analysis

Phylogenetic analyses were performed using the computer programs TNT v.1.1 (maximum parsimony analysis) and MrBayes v.3.1 (Bayesian inference) on the morphologic character matrix. In the first set of analyses, no taxa were assigned as outgroups. Maximum parsimony analysis resulted in five equally parsimonious trees; Bayesian analyses yielded >1000 trees. Because of numerous inadequacies in the matrix, the resulting consensus trees had very little resolution. The maximum parsimony analyses were later rerun using *Montlivaltia caryophyllata* as an outgroup, resulting in four equally parsimonious trees; the results are given in Appendix C. The inadequacies with the morphologic character matrix were discussed and are summarized as follows:

(1) many of the characters are not homologous (e.g., columella development) and characters at all levels (macromorphology, micromorphology, microstructure) need to be more rigorously evaluated to make sure that they are homologous;

(2) micromorphologic and microstructural characters are relatively new to scleractinian systematics, and their states need to be more methodically differentiated and consistently applied; different breakout groups used different terms for the same state;

(3) many micromorphologic and microstructural characters were overlooked by the breakout groups (as noted above), and need to be added to the matrix in order to provide a more complete representation of morphology;

(4) there were a lot of missing data in the matrix (especially micromorphology, microstructure) due to the lack of readily available SEM and thin section work;

(5) more taxa (especially Mesozoic fossils) needed to be added to the matrix to serve as outgroups;

(6) various character weighting schemes need to be considered in future analyses, possibly based on character maps using molecular trees. Many characters seem to provide more noise than phylogenetic signal.

Probably the biggest take-home message of the workshop was the plethora of available morphologic terms. Not only do different scleractinian workers use different morphologic terms for the same feature, but they also use the same term differently. A carefully written glossary of morphologic terms, such as the one in progress for Corallosphere, is essential for future morphologic work.

As part of the discussion of future work on the morphologic character matrix, a revised list of taxa was created increasing the total number of taxa from 42 to 62 (Appendix D). The additional taxa were included to better represent all of the clades represented in the molecular trees. A few more taxa still need to be added to serve as outgroups. Various participants in the workshop volunteered to contribute images of SEMs, transverse thin-sections, and longitudinal cuts. It was decided that these images would be shared using Flickr (ww.flickr.com), in part because EOL shares images and data with Flickr. After the SWG Flickr site is created and populated with images, participants in the workshop will be asked to study the images in preparation for a smaller follow-up meeting, which will focus on refining micromorphological and microstructural characters in the morphologic character matrix. The purpose of the follow-up meeting will be to finalize the character matrix and identify synapomorphies for families and higher taxa. The images and data in Flickr will be shared with Corallosphere (most importantly, the morphologic glossary in Corallosphere) and with EOL.

Sharing data with EOL

Workshop participants 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 will be implemented in Corallosphere over the next few months, and editors will be asked to assign genera to families. Ken Johnson will work with Cyndy Parr (EOL) to ensure transfer of the resulting classification system.

Dissemination of workshop results

It was agreed that a report of the workshop would be sent to various newsletters and listservs, such as ISRS (Reef Encounter), Fossil Cnidaria, Coral List etc. A publication based on the workshop will be considered after the morphologic character matrix and phylogenetic analysis are complete.

Conclusion

Workshop participants agreed that existing classification systems for scleractinians are inadequate, and a new revised system needs to be adopted as soon as possible. This revised system should better reflect the results of new molecular analyses, such as Fukami et al (2008). The revised system should provide the basic framework for three ongoing community projects involving taxonomic data: Corallosphere, TIP, and EOL. Before morphologic and molecular data can be integrated and fossils added to the revised classification system, work still needs to be done defining morphologic characters and their states. Existing morphologic characters are not formulated with enough rigor or consistency or using a comprehensive approach; therefore, they cannot be used effectively to identify synapomorphies or perform morphological phylogenetic analyses. Micromorphological and microstructural characters based on new microscopic

technology have promise, but are unstudied in many taxa. The much-needed morphologic work will be pursued by a smaller subset of morphologic experts who agree on common procedures.

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Appendix A: Final List of morphologic characters

Numbers in parenthesis refer to the number of the corresponding character in the pre-meeting list of characters based on the morphologic glossary in Corallosphere

1. Corallum type (1):

- 0. solitary
- 1. occasionally colonial
- 2. colonial

2. Attachment (3):

- 0. attached
- 1. detached

3. Extracalicular budding (5):

- 0. absent
- 1. present

4. Intracalicular budding (5):

- 0. absent
- 1. present

5. Cerioid (6):

- 0. absent
- 1. present

6. Circumoral budding (6):

- 0. absent
- 1. present

7. Meandroid (6):

- 0. absent
- 1. present

8. Phaceloid (6):

- 0. absent
- 1. present

9. Parathecal wall (7):

- 0. absent
- 1. present

10. Septothecal wall (7):

- 0. absent
- 1. present

11. Synapticulothecal wall (7):

- 0. absent
- 1. present

12. Trabeculothecal wall (7):

- 0. absent
- 1. present

13. Epitheca (9):

- 0. absent
- 1. present

14. Synapticulae (10):

- 0. absent
- 1. present

15. Compactness of radial elements (13):

- 0. compact
- 1. perforate
- 2. spines

16. Costae (16):

- 0. absent
- 1. present

17. Costae continuous over coenosteum (16):

- 0. absent
- 1. present

18. Costal distal ornamentation (18):

- 0. beaded
- 1. dentate
- 2. granular

19. Septal distal margins ornamentation orientation:

- 0. parallel
- 1. perpendicular

20. Septal distal margins ornamentation shape (24):

- 0. acute
- 1. fan
- 2. multidirectional axes
- 3. rounded
- 4. smooth
- 5. triangular

21. Septal axial margins ornamentation orientation:

- 0. parallel
- 1. perpendicular

22. Septal axial margins ornamentation shape (35):

- 0. acute
- 1. fan
- 2. multidirectional axes
- 3. rounded
- 4. granulose
- 5. triangular

23. Septal axial margins ornamentation size:

- 0. small
- 1. medium
- 2. large

24. Septal lateral faces ornamentation arrangement (26):

- 0. absent=smooth
- 1. aligned
- 2. carinae
- 3. scattered

25. Septal lateral faces ornamentation shape (25):

- 0. acute
- 1. rounded
- 2. acute & rounded
- 3. granular
- 4. pennulae

26. Fusion of higher septal cycles (22):

- 0. absent
- 1. present

27. Columella development (27):

- 0. absent
- 1. weak
- 2. strong

28. Columella structure (29):

- 0. lamellar
- 1. papillose
- 2. spongiose
- 3. styliform

29. Paliform lobes (30):

- 0. absent
- 1. present

30. Pali (31):

- 0. absent
- 1. present

31. Fulturae (10):

- 0. absent
- 1. present

32. Endotheca (36):

- 0. absent
- 1. present

33. Coenosteum = peritheca (39):

- 0. absent
- 1. present

34. Trabecula structure (44):

- 0. simple
- 1. compound

Appendix B: Morphologic character matrix

Acropora 2 0 1 0 0 0 0 0 0 0 1 0 1 1 2 0 - - - - - - 0 - 0 0 - 0 0 0 0 1 0 Agaricia 2 0 1 1 1 1 0 0 0 0 1 1 0 1 0 1 1 2 1 0 - - - 0 0 0 2 0 0 0 1 0 1 0 1 0 Aqathiphyllia explanata 2 0 1 0 0 0 0 0 0 1 1 ? 1 1 0 1 0 0 ? 3 ? 3 ? ? ? 0 2 2 1 0 0 1 1 1 Alveopora 2 0 1 0 1 0 0 0 0 0 1 0 1 1 2 0 - - - - - - 0 - 0 1 - 0 0 0 0 0 0 Anacropora 2 0 1 0 0 0 0 0 0 0 1 0 ? 1 2 0 - - - - - - 0 - 0 0 - 0 0 0 0 0 0 Anthemiphyllia 0 1 0 0 0 0 0 0 0 1 0 0 0 0 1 0 2 1 3 ? 4 2 1 2 0 0 1 0 0 0 0 0 0 0 Astreopora 2 0 1 0 0 0 0 0 0 0 1 0 1 1 2 0 - - - - - - 0 - 0 0 - 0 0 0 0 1 0 Blastomussa merleti 2 0 1 0 0 0 0 1 0 1 0 0 1 0 0 1 - 2 1 4 1 0 ? ? 0 0 2 1 0 0 0 1 0 1 Caryophyllia 0 0 0 0 0 0 0 0 1 0 0 0 0 1 - 2 ? ? ? ? ? 1 3 0 2 1 0 1 0 0 0 0 Conophyllia 1 0 0 1 0 0 0 0 0 0 0 0 1 0 0 1 - ? 1 3 0 3 2 ? 4 0 2 3 0 0 0 1 0 0 Conotrochus 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 1 - 2 - ? ? - - 1 1 0 2 2 0 0 0 0 0 ? Deltocyathus 0 1 0 0 0 0 0 0 1 0 0 0 0 0 1 - 2 ? ? ? 4 0 1 2 ? - 1 1 1 0 0 0 0 Dendracis 2 0 1 1 0 0 0 0 0 0 1 0 ? 1 2 0 - - - - - - 0 - 0 - ? 0 0 0 ? 1 0 Euphyllia 2 0 0 1 0 0 1 1 0 1 0 1 1 0 0 1 - ? - - - - ? 1 0 0 - 0 0 0 1 0 0 Favia fraqum 2 0 1 1 1 0 0 0 0 1 0 0 1 0 0 1 0 1 1 1 1 1 1 1 1 0 0 2 2 1 0 0 1 1 1 Flabellum 0 1 0 0 0 0 0 0 0 1 0 0 1 0 0 0 - - 0 3 0 3 0 0 2 0 - - 0 0 0 0 0 0 Fungia fungites 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 - 1 1 2 0 0 ? ? 0 1 1 1 1 0 1 0 0 1 Fungiacyathus 0 1 0 0 0 0 0 0 0 1 0 0 0 1 0 1 - 1 0 ? 0 0 2 0 1 1 1 1 0 0 0 0 0 0 Lobophyllia corymbosa 2 0 0 1 0 0 0 1 1 0 0 0 0 0 0 1 - 1 0 5 0 5 2 3 1 0 2 2 0 0 0 1 0 0 Madrepora 2 0 1 0 0 0 0 0 0 0 1 0 0 0 1 1 2 0 4 0 - 0 1 1 0 1 2 0 0 0 0 1 0 Merulina ampliata 2 0 0 1 1 0 1 0 0 0 0 1 0 0 0 1 - - 0 2 0 2 1 3 0 0 2 2 0 0 0 0 0 1 Montipora 2 0 1 0 0 0 0 0 0 0 1 0 1 1 2 0 - - - - - - 0 - 0 0 - 0 0 0 0 1 0 Montlivaltia caryophyllata 1 1 0 0 0 0 0 1 0 0 1 0 0 1 - 1 1 2 1 0 ? 2 0 0 0 - 0 0 0 1 0 1 Oulastrea crispata 2 0 0 1 0 0 0 0 ? ? ? ? 0 ? 0 1 1 1 ? 2 ? ? ? ? 0 1 - 1 1 1 0 ? 1 ? Pocillopora 2 0 1 0 1 0 0 0 0 1 0 0 0 0 2 0 - - 0 3 ? - 0 0 - 0 0 3 0 0 0 1 1 0 Porites 2 0 0 0 1 0 0 0 0 0 1 0 0 1 1 0 - - 0 2 0 2 2 ? 3 1 1 3 1 ? 0 0 0 0 Psammocora contigua 2 0 0 1 1 0 0 0 0 0 1 0 0 1 1 0 - - 1 ? 1 0 ? ? ? 1 2 3 0 0 0 0 0 1 Siderastrea 2 0 1 0 1 0 0 0 0 0 1 0 0 1 0 0 - ? 0 0 0 0 0 3 0 1 2 3 0 0 0 0 0 0 Stenocyathus 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 - 2 ? ? ? ? ? 1 1 0 2 3 0 1 0 0 0 ? Stephanocoenia 2 0 1 0 1 0 0 0 1 0 0 1 1 0 0 0 - - 0 3 ? ? ? ? ? 0 2 3 1 0 0 1 0 0 The cocvathus 0 1 0 0 0 0 0 0 0 0 0 1 0 0 0 - - ? ? ? ? ? ? 1 0 2 1 0 1 0 0 0 ? Turbinolia 0 1 0 0 0 0 0 0 1 0 0 0 0 1 - 2 0 3 0 3 0 0 1 0 2 3 0 0 0 0 0 0 0

- unknown, ? inapplicable

Other formats of this matrix are available from A. Budd.

Appendix C: Preliminary phylogenetic analysis

Maximum parsimony, T. N. T., Tree Analysis Using New Technology, v. 1.1

Goloboff, P., J. S. Farris, and K. Nixon, 2003. T. N. T., Tree Analysis Using New Technology, program and documentation available at http://www.zmuc.dk/public/phylogeny/

```
Matrix (34x42, 16 states)
Outgroup is taxon 28 - Montlivaltia caryophyllata
Repl. Algor.
                     Tree
                                    Score
                                                   Best Score
                                                                   Time
                                                                                 Rearrangs.
                 149 of 150
                                                                  0:00:00
                                                                                8,137,561
150 TBR
                                   ____
                                                  193
Completed 150 random addition sequences.
Total rearrangements examined: 8,137,561.
Best score hit 4 times out of 150 (some replications overflowed).
Best score (TBR): 193. 4 trees retained.
   Majority rule tree (from 4 trees, cut 50)
      Montlivaltia_caryophyllata
           Stephanocoenia
           Pocillopora
           Mussa angulosa
          — Madrepora
           Lobophyllia_corymbosa
           Euphvllia
          - Dendrophyllia
           Cyphastrea
           Conophyllia
          - Blastomussa_merleti
           Agaricia
          - Acanthastrea hillae
        100-Plesiastrea_crispata
Oulastrea_crispata
                - Plesiastrea_versipora
              - Montastraea cavernosa
        75-
              — Favia_fragum
               Diploastrea_heliopora
   100
        75
             - Agathiphyllia_explanata
-- Siderastrea
        100
             100-Psammocora_contigua
Porites
                    - Pectinia_alcicornis
            100 Peccinic____
Oxypora_lacera
                   - Merulina_ampliata
            L75-
                 — Hydnophora
                Alveopora
                   - Montipora
                    Dendracis
                   Astreopora
                  - Anacropora
                   Acropora
                 Conotrochus
                 75-Caryophyllia
        100
                                Deltocyathus
                       r100-
                             — Anthemiphyllia
— Turbinolia
                  100-

    Thecocyathus

                                 - Flabellum
                            100-
                       L<sub>100</sub>.
                                    - Fungiacyathus
                                 FungiaCyathas
Fungia_fungites
                            L<sub>100</sub>-
```

Tree 1, worse fit (diff.=0.24286)

Characters with better fit on tree 1, fit difference

		+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
ſ	0					0.13				0.10	
	10						0.15	0.15			
ĺ	20			0.04		0.04				0.07	0.07
	30		0.17		0.07						

Characters with worse fit on tree 1, fit difference

		+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
	0	0.15 0.10	0.03	0.07				0.25	0.10		0.05
1	20							0.02			
3	30			0.13							

Tree 2, worse fit (diff.=0.02381)

Characters with better fit on tree 2, fit difference

		+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
	0					0.07					
	10	0.15			0.10					0.04	0.02
	20	0.15		0.04		0.04					0.07
ĺ	30		0.27		0.17						
1											

Characters with worse fit on tree 2, fit difference

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0 10	0.15	 0.03			 0.10		0.25		0.13	
20 30			0.17				0.02			

Tree 3, worse fit (diff.=0.35703)

Characters with better fit on tree 3, fit difference

	+0	+1	+2	+3	+4	+5	+6	+7	+8	+9
0					0.07					
10 20			0.04	0.05						0.02
30		0.10		0.07						0.07

	+0	+1	+2	+3	+4	+5	+6	+7	+8	
0	0.15		0.07				0.25			(
10						0.10				
20										ĺ
30			0.17)
1						1	1		1	1

Characters with worse fit on tree 3, fit difference

+9

Taxon	SEM	Transverse thin- section	Longitudinal break
Acanthastrea echinata	Budd	Budd	Budd
Acanthastrea hillae	Budd	Budd	Budd
Acropora	Stolarski	Stolarski	Stolarski
Actinacis	NHM	USNM	NHM
Agaricia	Stemann	Stemann	Stemann
Agathiphyllia explanata	Budd	Budd	Budd
Alveopora	Stolarski, Wallace	Wallace	Wallace
Anacropora	Wallace	Wallace	Wallace
Anthemiphyllia	Stolarski	Stolarski	Stolarski
Astrangia	Stolarski	Stolarski	Stolarski
Astreopora	Wallace	Wallace	Wallace
Astrocoenia	Klaus	Klaus	Klaus
Balanophyllia	Stolarski	Stolarski	Stolarski
Blastomussa merleti	Stolarski, Budd	Budd	Budd
Caryophyllia	Stolarski	Stolarski	Stolarski
Catalaphyllia	Stolarski	Stolarski	Stolarski
Cladocora	Stolarski, Budd	Stolarski	Stolarski
Conophyllia	Roniewicz	Roniewicz	Roniewicz
Conotrochus	Stolarski	Stolarski	Stolarski
Cycloseris sinensis	Stolarski	Stolarski	Stolarski
Cyphastrea	Budd	Budd	Budd
Deltocyathus	?Stolarski	Stolarski	?USNM
Dendracis	Wallace	Wallace	Wallace
Dendrophyllia	Cairns	USNM	USNM
Dichocoenia	Budd	Budd	Budd
Diploastrea heliopora	Budd	Budd	Budd
Euphyllia	Budd	Budd	Budd
Favia fragrum	Budd	Budd	Budd
Favia pallida	Budd	Budd	Budd
Flabellum	Stolarski	Stolarski	Stolarski
Fungia fungites	Hoeksema, Stolarski	Stolarski	Hoeksema
Fungiacyathus	Stolarski	USNM	USNM
Galaxea	Stolarski	Stolarski	Stolarski
Hydnophora	Budd	Budd	Budd
Javania	?Stolarski	Stolarski	Stolarski

Appendix D: Proposed list of taxa and image contributors

Leptoseris	Stolarski	Stolarski	Stolarski
Lobophyllia corymbosa	Budd	Budd	Budd
Madracis	Klaus	Klaus	Klaus
Madrepora	Stolarski	Stolarski	Stolarski
Meandrina	Budd	Budd	Budd
Merulina ampliata	Budd	Budd	Budd
Montastraea cavernosa	Budd	Budd	Budd
Montipora	Wallace	Wallace	Wallace
Montlivaltia caryophyllata	Lathuilière, NHM	Lathuilière, NHM	Lathuilière, NHM
Mussa angulosa	Budd	Budd	Budd
Oculina	Stolarski, Budd	Stolarski	Stolarski
Oulastrea crispata	Benzoni	Budd	Budd
Oxypora lacera	Budd	Budd	Budd
Pectinia alcicornis	Budd	Budd	Budd
Physogyra lichtensteini	Budd	Budd	Budd
Plesiastrea versipora	Bensoni	Budd	Budd
Pocillopora	Stolarski, Klaus	Stolarski, Klaus	Stolarski, Klaus
Porites	Stolarski, Budd	Budd	Budd
Psammocora contigua	Stolarski	Stolarski	Stolarski
Siderastrea	Benzoni	Budd	Budd
Stenocyathus	Stolarski	Stolarski	Stolarski
Stephanocoenia	Stolarski, Budd	Budd	Budd
Stephanophyllia	Cairns	USNM	USNM
Thecocyathus	Stolarski	Stolarski?	Stolarski?
Trachyphyllia	Budd	Budd	Budd
Turbinolia	Stolarski, Cairns	USNM	USNM
Zardinophyllum	Stolarski	Stolarski	Stolarski

Appendix E: Treatise on Invertebrate Paleontology, Summary: June 2009

The 1956 Treatise covered 33 families, and 1022 generic and subgeneric names: 478 valid, 491 junior synonyms or homonyms, 21 of uncertain position, 14 unrecognizable, and 18 invalid. We will be including 100 families and about 1636 names.

	Names assigned	Text done	Figures done
Cenozoic and Reco	ent Azooxanthellates	(Team leader: Cairns), 291 names
Cairns	184	184	~40
Stolarski	61	0	
Szabo	18	?	
Budd	18	0	
Roniewicz	2	0	

Cenozoic and Recent Zooxanthellates (Team leader: Budd), 415 names

Budd	~149	0
Benzoni	56	1
Hoeksema	35	?
Wallace	24	?
Stemann	51	?
Cairns	2	2
Klaus	12	?
Pichon	18+	?
Lathuilière	1	?
Morsch	4	?
Baron-Szabo	49	?
Unassigned	16	0

Cretaceous (Team leader: Szabo), 442 names

Szabo	423	?423	0
Cairns	16	16	
Stolarski	3	0	

Jurassic (Team leader: Lathuilière), 353 names

Lathuilière	225	25	0
Martin Garin	1	0	
Morsch	5	0	
Olivier	1	0	

Panday	15	12
Roniewicz	76	"some"
Stolarski	9	0
Szabo	21	?

Triassic (Team leader: Roniewicz), 135 names

Roniewicz Turnsek	135 ?	92	~2
Morycowa Stanley	? ?		
TOTALS:	1636	~754	~42

Proposed Deadlines

Now
Finish first drafts of all 1636 genera
Finish adding images; start review process, if not before
Submit final to TIP