Palaeontographica Americana 54
1984

Dec. 28, 1984

AN APPLICATION OF PHYLOGENETIC ANALYSIS TO THE SCLERACTINIA: FAMILY FUNGIIDAE

STEPHEN D. CAIRNS
U.S. National Museum of Natural History, Washington, DC, U.S.A.

ABSTRACT

The terminology and principles of phylogenetic analysis (cladism) are briefly discussed. Three myths commonly ascribed to cladism are discussed and dispelled. They are: 1) that cladism is completely objective, 2) that complete reliance is placed on evolutionary parsimony, and 3) that fossil evidence is not relevant. A step-by-step procedure is outlined for the phylogenetic analysis of the genera and subgenera of the Fungiidae. The procedure includes: 1) construction of a character table, 2) selection of an out-group, 3) polarizing and ordering the character states by out-group comparison, 4) coding the character states, and 5) interpretation of the computer-generated cladogram. The advantages of the cladogram over the previous phylogeny of the Fungiidae (Wells, 1966) are: 1) a more reasonable interpretation of the evolution of the subgenera of *Fungia*, 2) a significantly more parsimonious tree including less homoplasy, 3) an understandable methodology subject to verification and modification, and 4) a better basis for the interpretation of characters. This is the first application of phylogenetic analysis to the Scleractinia and its fourth usage in the Coelenterata.

INTRODUCTION

Phylogenetic Systematics, frequently called cladism, is not often used to establish the phylogeny of a group of lower invertebrates. This report represents only its fourth usage within the Coelenterata (Schmidt, 1972 and 1974; Gerhart, 1983; Cairns, in press) and its first application to the Scleractinia. The infrequent use of cladism probably stems from the paucity of characters found in lower invertebrates and the difficulty of character analysis. It is the purpose of this paper to apply the cladistic method to an analysis of the fungiid genera in order to serve as a guide and example for other such studies. All procedural steps are explained and the resultant cladogram is interpreted and compared to the traditional phylogeny of the Fungiidae proposed by Wells (1966). The Fungiidae was chosen for this analysis because there is a good data set available for the characteristics of the genera and a proposed evolutionary scheme for the family to serve as a comparison, both provided by Wells (1966). Only those characters described by Wells (1966) are used in the cladistic analysis in order to allow for a valid comparison. Other characters, such as corallum microstructure, histology of soft parts, and characters observed in the field, can and should be used in any subsequent, more thorough analysis of the group. The methodology of cladism is particularly amenable to deletions, additions, and changes within the data set.

Before I proceed with the analysis, I would like to dispel three myths commonly ascribed to cladism. Firstly, the idea that cladism is an entirely objective method. There are elements of subjectivity at several points of the analysis, *e.g.*, choice of out-group, ordering of multistate characters, and choice of alternative, equally parsimonious cladogram branches. Secondly, the claim that evolution proceeds in the most parsimonious manner. This also is not true. Cladism will arrange taxa such that their character states change with the least amount of convergence and reversal, *i.e.*, most parsimoniously; however, the decision to invoke parsimony is simply a philosophical choice employed to minimize our acceptance of assumptions, not necessarily the method of determining truth (Cracraft, 1983). The third myth is that fossils should not be used in a cladistic analysis. Fossils *can* be used both as taxa in a cladistic analysis and as an out-group for cladistic analysis. Their statigraphic ranges can serve to falsify or substantiate a cladistic model, and fossil taxa can also be integrated into a classification with minimal disruption (Wiley, 1981, pp. 214–225).

A cladistic analysis is best performed by an expert on the group being analyzed and preferably on a group recently revised. I acknowledge that I am not an expert on the Fungiidae, but I have relied on the excellent work of Wells (1966), updated by Veron and Pichon (1980) and Pillai and Scheer (1976), and I have examined 31 of the approximately 62 species of fungiids, including specimens of the type-species of every genus and subgenus and a representative of *Acrosmilia*.

TERMINOLOGY AND PRINCIPLES OF CLADISM

The three basic methods of determining relationships among organisms are phenetics, evolutionary taxonomy, and phylogenetic analysis or cladism. Phenetics is a numerical approach that groups by overall similarity and does not weight characters. This method does not necessarily reflect the evolutionary history of

the group being analyzed. Traditional evolutionary taxonomists attempt to reflect evolutionary history, by giving more weight to some characters, using the fossil record to identify missing links, and intuitively constructing evolutionary trees based on experience. Cladism also attempts to portray the evolutionary history of a group by determining shared derived characters among the taxa. In the simplest example, among three taxa the two considered most closely related are those that share a unique character. This shared derived character is called a *synapomorphy* and its expression in the two taxa is considered homologous. In Text-figure 1, the acquisition of character 1 is a synapomorphy for taxa A–D and unites them in a *monophyletic* assemblage (a *clade*). Character 2 is a synapomorphy for the monophyletic group A–C. Character 4 is unique to taxon A and therefore is derived but not shared. It is therefore not a synapomorphy but instead is termed an *autapomorphy*.

Cladism is highly dependent on accurate character analysis, *i.e.*, the determination of which character states are ancestral (*plesiomorphic*) and which are derived (*apomorphic*). Character states are *polarized* by a method called *out-group comparison*. For example: assume that in Text-figure 1, A–C is considered to represent all fungiid genera and D represents the most closely related genus to the fungiids, *Acrosmilia*, the out-group. If the theca of *Acrosmilia* and fungiid genus C are imperforate and that of taxa A–B perforate, then the imperforate character state is considered plesiomorphic and the perforate state is considered derived, the change occurring where number 3 → p is drawn on the diagram. This also implies there was a common ancestor, X, to both *Acrosmilia* and the fungiids that had an imperforate theca, a character state that remained in *Acrosmilia* and fungiid genus C. The character state of perforate is also considered a synapomorphy for taxa A–B. If C is considered to represent *Cycloseris*, *Diaseris*, and *Heliofungia*, and A–B represents the remaining fungiid genera, then the previously described example reflects the representation of character 5 (thecal porosity) on the cladogram of Text-figure 3. Out-group comparison provides the most reliable basis for polarizing character states. Therefore, choosing the correct sister group (that out-group most closely related to the group being studied) is of great importance.

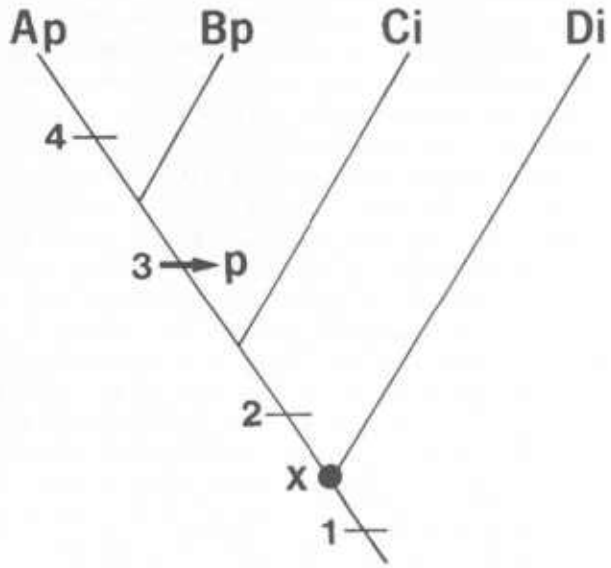
General references on cladism that explain methodology and terminology are: Eldredge and Cracraft (1980), Wiley (1981), and Funk and Humphries (in press). There are several computer algorithms available for cladistic analyses; I used the Wagner 78 program, developed by J. S. Farris (State University of New York, Stony Brook, New York).

PROCEDURE FOR OBTAINING THE CLADOGRAM

The first step of the analysis was to produce a character table or tabular key for the fungiid genera and subgenera (Appendix 1). The information for this table was taken from Wells (1966) and Veron and Pichon (1980) and verified by personal observation. Only generic level characters used by Wells (1966) were included in the analysis; however, additional information, such as number of species and stratigraphic range, can be included at this point for informational purposes (but not to be considered as characters).

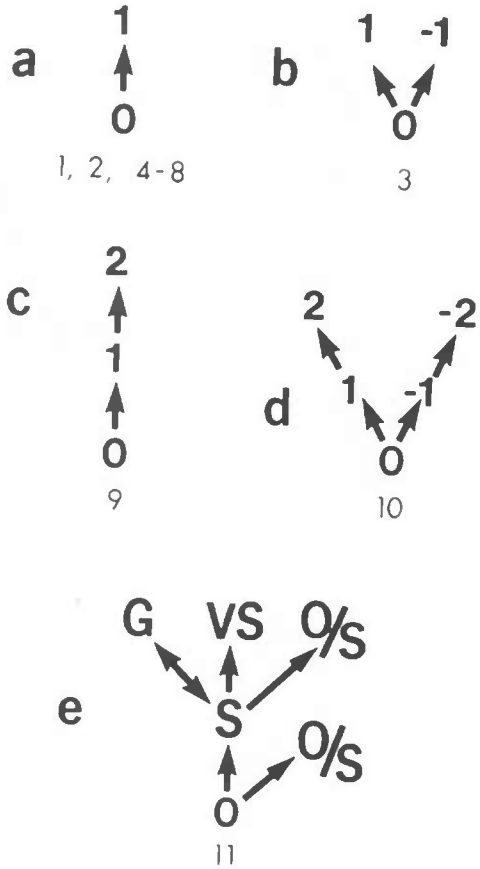
Next, the Cretaceous synastreid *Acrosmilia* was chosen as the out-group. This was based on hypotheses of the higher classification of the Scleractinia proposed by Vaughan and Wells (1943, pp. 91, 95), Wells (1956, pp. 363, 366), and Wells (1966, pp. 226–227, 230). It was also chosen to be consistent with Wells' premise in his fungiid revision. If subsequent study reveals a group of corals that is more closely related to the fungiids than *Acrosmilia* then this closer relative should be used as the out-group and as the basis for character polarization.

The third step was to polarize and order the character states used in Appendix 1 based on out-group comparison. Seven of eleven of the characters were easily polarized from the out-group because they are two-state characters for which the out-group state is known



Text-figure 1.—Cladogram illustrating the hypothetical interrelationships among four taxa, A–D. Numbers 1–3 represent character state changes or synapomorphies for the taxa they define. Synapomorphy 3 represents the change from an imperforate theca (i) to a perforate theca (p). Character 4 is an autapomorphy. X is a hypothetical ancestor.

(Text-fig. 2a). Thus, because *Acrosmilia* is solitary, this state is considered ancestral, and colonial is considered derived (character 1). Likewise, because *Acrosmilia* has fine costae, this state is considered ancestral and coarse costae is considered derived (character 6), and so forth. The remaining four characters, however, are multistate characters, each having three to five character states. Thus, for character 3 (shape of upper corallum), discoidal was chosen as the ancestral state because of its occurrence in *Acrosmilia*, but out-group comparison does not provide a basis to order the other two states. Therefore, parsimoniously these two states were both provisionally assumed to originate from the discoidal state (Text-fig. 2b). For character 9 (septal dentition), the small state was chosen as ancestral because of its occurrence in *Acrosmilia*, and a trend was hypothesized leading from small septal teeth to large to very large (Text-fig. 2c). Character 10 (budding pattern) is more complicated, with five character states. The lack of budding was considered ancestral and it was intuitively hypothesized that the circumoral/marginal state



Text-figure 2.—Proposed character state transformation series for the characters used in the analysis. The numbers and letters correspond to the coding found in Appendix 1. The numbers in lightface indicate the characters in Appendix 1 that follow that pattern.

proceeded through an exclusively circumoral state, and that the intramural/circumoral state proceeded through an exclusively intramural state. This progression is supported by the ontogenetic development of the corals. These two lines were kept separate, resulting in Text-figure 2d. (Because ordering of these multistate characters includes varying degrees of subjectivity and intuition they are subject to reevaluation once the cladogram has been constructed.) Character 11 (costal ornamentation) could not be polarized from the out-group and no intuitive scheme could be suggested for its transformation, therefore it was not included in the analysis.

The fourth step of the analysis was to code the data for the computer. Usually a binary code is used, customarily with zero representing the plesiomorphic state and the number one representing the derived state. For multistate characters higher numbers may be used; for series of branching character states, negative numbers and even multiple columns may be used to code one character. The coding of the ten characters used in the analysis is given in the explanation to Appendix 1 and the coded data matrix is provided in Appendix 2. Two taxa, *Cycloseris* and *Danafungia*, were subdivided because they possess two character states for the same character. For example, some species of *Cycloseris* have equal costae, whereas others have unequal costae; thus, *Cycloseris* A was coded for those species having equal costae and *Cycloseris* B coded for those with unequal costae.

In the final step the computer algorithm linked the taxa together, one at a time, ultimately producing a tree "rooted" at the out-group (Wiley, 1981, pp. 178–192). Theoretically, the tree produced is the shortest one possible, *i.e.*, the one with the least number of steps or character state changes (*i.e.*, the most parsimonious). For small data sets, as in this example, it is not always necessary to run a computer program; a tree can be produced manually by trial and error. The resultant cladogram from the Wagner 78 program is illustrated in Text-figure 3. Autapomorphies and characters such as costal ornamentation, which were not used in the analysis, can be added at this stage for informational value; they will not change the branching sequence.

DISCUSSION

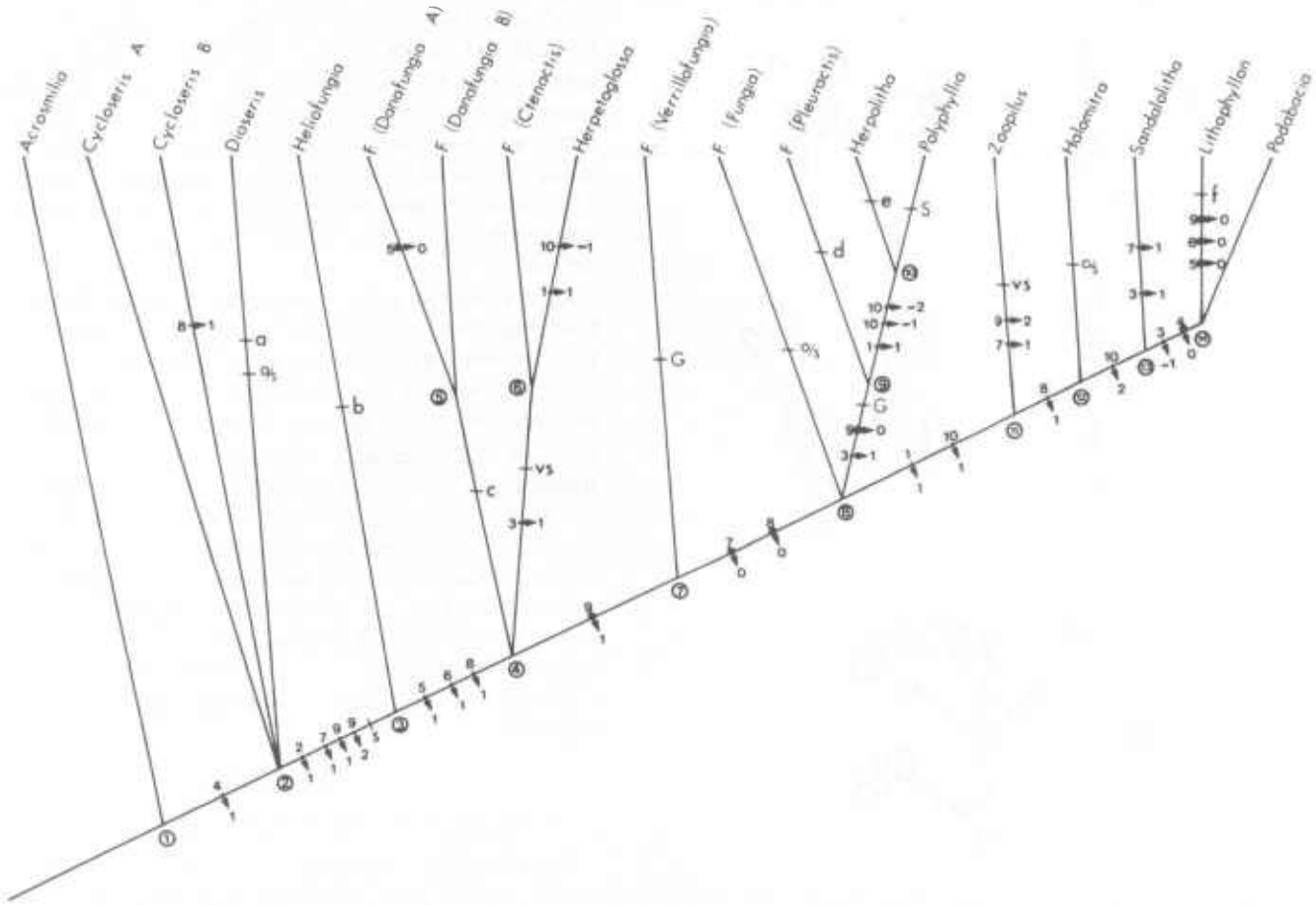
Comparison to the Phylogeny of Wells (1966)

To facilitate a comparison of the cladogram and Wells' (1966) tree, the latter was redrawn with the following modifications: 1) straight lines were used, 2) *Diaseris* was added as a derivative of *Cycloseris*, 3) *Cycloseris* and *Danafungia* were subdivided as they

were for the coding in the cladogram, 4) *Parahalomitra* was changed to *Sandalolitha* (see Pillai and Scheer, 1976), and 5) *Heliofungia* was considered as a separate genus (see Veron and Pichon, 1980). None of these changes was thought to affect the intent of Wells' phylogeny. Finally, the character state changes used in the phylogenetic analysis, which were also those used by Wells, were placed on his diagram in such a way as to produce the least number of steps. Autapomorphies and characteristics of costal ornamentation were also added. This resulted in Text-figure 4.

The two trees are similar in that they both place *Cycloseris, Diaseris,* and *Heliofungia* near the ancestor, and they both maintain the clade composed of *Pleuractis, Herpolitha,* and *Polyphyllia*; however, they differ in most other points. Wells' diagram arranges the remaining taxa in four groups, labelled I–IV on Text-figure 4, each originating in the Miocene as a separate subgenus of *Fungia*. Each subgenus persists to the Recent and each produces a small adaptive radiation of colonial genera starting in the late Miocene and extending to the Recent. Each group of genera is distinguished by a distinctive combination of septo-costal characteristics described by Wells (1966, p. 235, fig. 4) and represented in my character table as characters 6–9 and 11.

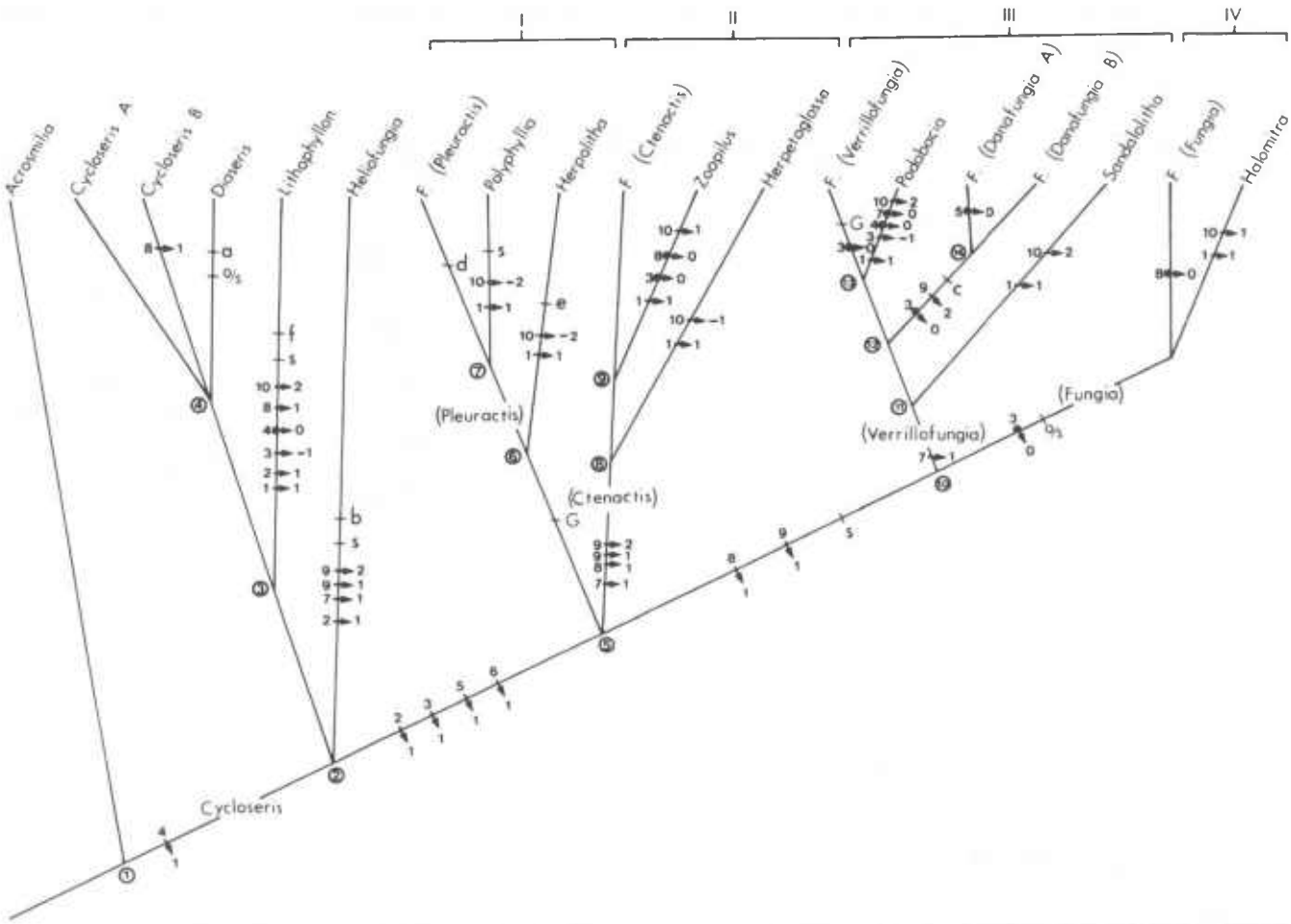
Whereas the Wells phylogeny is strongly influenced by the weighting of septo-costal structures, the cladogram is strongly influenced by the synapomorphy of coloniality (characters 1 and 10). Directly after *Heliofungia,* the cladogram branches off the remaining solitary taxa, the subgenera of *Fungia,* almost in sequential order. Then coloniality is evolved twice: at internodes 9–10 and 8–11. The rudimentary coloniality of *Herpetoglossa* is different from that of the other colonial genera and apparently evolved quite recently (Veron and Pichon, 1980). The last three genera on the cladogram are further differentiated by a synapomorphy of increasing complexity of coloniality.



Text-figure 3.—Cladogram of the fungiids. Encircled numbers are arbitrarily numbered nodes. Numbers at the origin of arrows denote characters; numbers at the arrow tips denote character states of those characters (Appendix 1: columns 1–10). Lowercase letters indicate autapomorphies (Appendix 1: column 12); uppercase letters indicate characteristics of costal spine ornamentation (Appendix 1: column 11). Character state reversals are indicated by a square on the arrow.

My main objection to the phylogeny of Wells is that, although it evolves most of the subgenera of *Fungia* in a relatively tight clade in the Miocene, the subgenera are subsequently scattered throughout the Recent genera. For instance, according to the Wells diagram *F.* (*Fungia*) is more closely related to *Halomitra* and *Sandalolitha* than it is to any of its other sister subgenera. Cladistically this is unacceptable because the subgenera of *Fungia* do not form a monophyletic group (clade) in the Recent. The cladogram does not group the subgenera of *Fungia* as a monophyletic genus either; however, the subgenera are at least sequentially derived, thus all occur in the same area of the cladogram. A strict interpretation of the cladogram would require each subgenus of *Fungia* to be a separate genus unless a synapomorphy could subsequently be found to unite them. Currently, *Fungia* is defined on plesiomorphic characters and characters that are also shared with other genera; it has no uniquely derived characters of its own.

In addition to a more meaningful arrangement of the fungiid subgenera, the cladogram offers several other advantages over the traditional phylogeny: 1) The Wells phylogeny required 48 character state changes, including 35 cases of convergence or parallelism and nine reversals, to fit the character states to each taxon, whereas the cladogram required only 34 steps, including 16 cases of convergence or parallelism and nine reversals. The cladogram is therefore considerably more parsimonious. This is also reflected in the character consistency indices (CI) listed in Appendix 1. The CI is defined as the range of a character state transition series divided by the number of times this character changed on the cladogram (Farris, 1969). For example, character 1 has a range of one and it changed from state 0 to state 1 three times on the cladogram, producing a CI of ⅓ or 0.33. A CI of 1.0 implies a perfectly congruent character for a cladogram. The average CI for the cladogram is 0.48; that for the Wells phylogeny, 0.38. 2) The cladogram is more repeatable in meth-

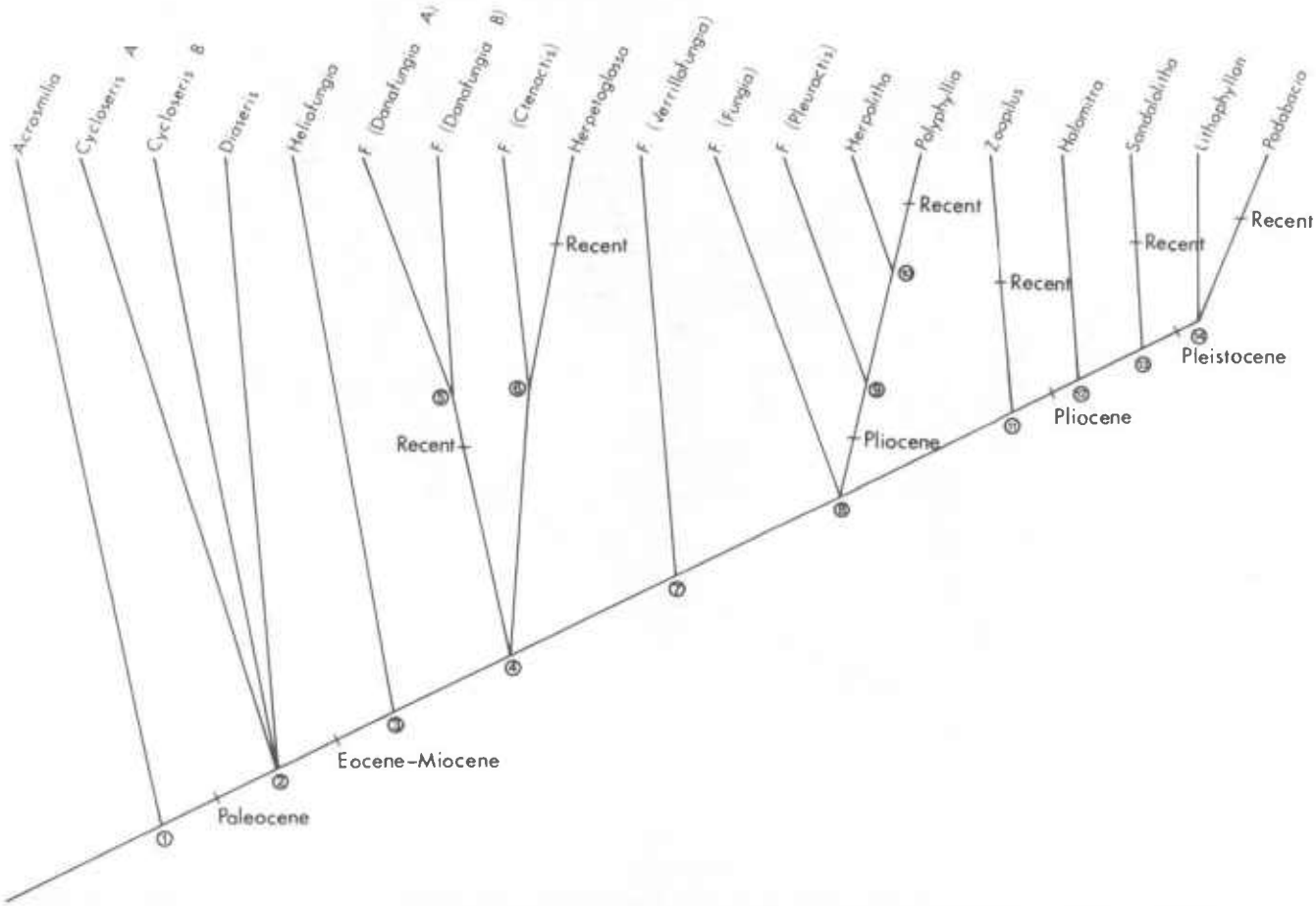


Text-figure 4.—Modified phylogeny of Wells (1966, fig. 3). Labelling conventions are the same as for Text-figure 3. Roman numerals I–IV indicate the four groups of genera implied by Wells.

odology and easily allows for additions or changes of data in the matrix. Each stem is justified by at least one character state change. The reasoning supporting the Wells phylogeny is not explained and five of the stems are not supported by character state changes (internodes 2–3, 6–7, 8–9, 11–12, and 12–13 of Text-fig. 4). 3) The cladogram allows a better interpretation of the characters. Character 11 (costal ornamentation) was not used in the analysis because its states could not be ordered; however, the cladogram suggests a reasonable hypothesis, which is illustrated in Text-figure 2e.

Proposed Scenario

If the earliest fossil record of each taxon is placed on the cladogram as a character, using the transformation series of Paleocene to Recent (Text-fig. 5), then the following scenario may be suggested. *Cycloseris* evolved from *Acrosmilia,* or a common ancestor of the two (node 1), in the Paleocene, differing from it primarily by its free corallum. But it was not until the Miocene that the adaptive radiation of the fungiids began. The hypothetical ancestor of the remaining fungiids (node 3) became larger and acquired arborescent costal spines. *Heliofungia* evolved from this ancestor. Then two significant changes occurred: the hypothetical ancestor represented at node 4 developed a perforate theca and coarse costal spines, which paved the way for the evolution of the closely related subgenera of *Fungia,* each differing from the others by various combinations of septo-costal characteristics. The earliest record of *F.* (*Danafungia*) is the Recent, but one would infer from the cladogram an older fossil record. *Herpetoglossa* evolved from *F.* (*Ctenactis*) in the Recent by acquiring a rudimentary coloniality. *F.* (*Pleuractis*) evolved from the common ancestor to *F.* (*Fungia*), node 8, in the Pliocene. The ancestor of *F.* (*Pleuractis*), node 9, gave rise to two colonial genera, *Herpolitha* and *Polyphyllia,* the latter in the Recent. Still in the Miocene, the hypothetical ancestor to the remaining genera, node 8, evolved circumoral budding, which produced *Halomitra* in the Pliocene and the stem that produced *Zoopilus* in the Recent. The ancestor represented at node 12 acquired marginal



Text-figure 5.—Cladogram with earliest known fossil records of taxa superimposed on the branching pattern.

budding in addition to circumoral budding and gave rise to the stem that produced *Sandalolitha* in the Recent and the Pleistocene stem that resulted in *Lithophyllon* and *Podabacia*. The implication of the analyses of both Wells (1966) and Veron and Pichon (1980, p. 195) is that *Lithophyllon* belongs at the opposite end of the cladogram as a polystomadeal derivative of *Cycloseris*. On the cladogram, the stem supporting *Lithophyllon* includes three reversals, which suggests that this is a questionable placement; in fact, the most poorly supported stem of the cladogram. However, the stem supporting *Lithophyllon* in the Wells phylogeny includes seven character state changes, including one reversal, which is the longest stem on the tree and also an indication of a questionable placement. The position of *Lithophyllon* in either phylogeny is unsatisfactory; analysis of additional characters might resolve the problem.

Because they are highly speculative, scenarios extrapolated from cladograms and stratigraphic ranges should be accepted only as working hypotheses.

CONCLUSIONS

Phylogenetic analysis is a logical method of producing a phylogeny which, in many ways, does not differ from that used for many years by evolutionary taxonomists. Cladism simply forces one to justify and explain every step of the analysis and thus to scrutinize organisms and characters more closely. It allows for verification by others and easy modification of the data set as new information is discovered. For some, the cladogram is the final product, but for others it is just the beginning, laying the foundation for additional character analyses, zoogeographical considerations, coevolutionary studies, and paleontological predictions.

APPENDIX 1

Character table for the genera and subgenera of the Fungiidae.

	Ten characters used in cladistic analysis												Presumed septo-costal homologues	Number of species	Stratigraphic range
	1	2	3	4	5	6	7	8	9	10	11	12			
Acrosmilia	S	S	D	A	I	F	S	E	S	O	?		*Cycloseris*	?	Jur.–Cret.
Cycloseris	S	S	D	F	I	F	S	E/U	S	O	O			14+	Paleo.–Rec.
Diaseris	S	S	D	F	I	F	S	E	S	O	O/S	a	*Cycloseris*	4+	? ?
Heliofungia	S	L	D	F	I	F	A	E	VL	O	S	b		1	Mio.–Rec.
F. (Danafungia)	S	L	D	F	I/P	C	A	U	VL	O	S	c		11–12	Recent
F. (Ctenactis)	S	L	E	F	P	C	A	U	VL	O	VS			1	Mio.–Rec.
Herpetoglossa	C	L	E	F	P	C	A	U	VL	1	VS		(*Ctenactis*)	1	Recent
F. (Verrillofungia)	S	L	D	F	P	C	A	U	L	O	G			5–6	Mio.–Rec.
F. (Fungia)	S	L	D	F	P	C	S	E	L	O	O/S			1	Mio.–Rec.
F. (Pleuractis)	S	L	E	F	P	C	S	E	S	O	G	d		3	Plio.–Rec.
Herpolitha	C	L	E	F	P	C	S	E	S	I/C	G	e	(*Pleuractis*)	2	Plio.–Rec.
Polyphyllia	C	L	E	F	P	C	S	E	S	I/C	S		(*Pleuractis*)	1	Recent
Zoopilus	C	L	D	F	P	C	A	E	VL	C	VS		(*Ctenactis*)	1	Recent
Halomitra	C	L	D	F	P	C	S	U	L	C	O/S		(*Fungia*)	1	Mio.–Rec.
Sandalolitha	C	L	E	F	P	C	A	U	L	C/M	S		(*Verrillofungia*)	2	Mio.–Rec.
Lithophyllon	C	L	F	A	I	F	S	U	S	C/M	S	f		1–2	Mio.–Rec.
Podabacia	C	L	F	A	P	C	S	U	L	C/M	S		(*Verrillofungia*)	1	Mio.–Rec.

Key to character states listed above, their computer coding and character consistency indices for both Wells' tree and cladogram

Characters	Computer code	Consistency indices	
		Wells	Cladogram
1. Coloniality:		0.12	0.33
S = Solitary (monostomous)	0		
C = Colonial (polystomous)	1		
2. Corallum size:		0.33	1.0
S = Small (usually less than 5 cm diameter)	0		
L = Large (adult usually more than 5 cm)	1		
3. Shape of upper corallum:		0.28	0.50
D = Discoidal (round to slightly elliptical)	0		
E = Strongly elliptical to elongate rectangular	1		
F = Foliaceous (irregular in shape)	−1		
4. Corallum attachment as an adult:		0.33	0.50
A = Attached	0		
F = Free	1		
5. Porosity of theca:		0.50	0.33
I = Imperforate	0		
P = Perforate	1		
6. Density of costal spines:		1.0	0.50
F = Fine (3–7 per mm)	0		
C = Coarse (0.5–2.0 per mm)	1		
7. Shape of costal spines:		0.25	0.25
S = Simple	0		
A = Simple and arborescent	1		
8. Width of adjacent costae:		0.17	0.25
E = Equal	0		
U = Unequal	1		
9. Size of septal dentition:		0.33	0.33
S = Small (3–6 teeth per mm)	0		
L = Large (1–2 teeth per mm)	1		
VL = Very large (less than 1 tooth per mm)	2		
10. Budding pattern:		0.50	0.80
O = No budding (solitary)	0		
C = Circumoral budding	1		
C/M = Circumoral plus marginal budding	2		
I = Intramural budding	−1		
I/C = Intramural plus circumoral budding	−2		
11. Ornamentation of costal spines:		Not coded or used in analysis	
O = No ornamentation (smooth)			
O/S = Smooth sides and spinose tips			
S = Spinose			
VS = Very spinose			
G = Granular			
12. Autapomorphies:		Not coded or used in analysis	
a = Corallum reproduces by fracturing			
b = Tentacles and polyps very large			
c = Higher cycle costae not spinose			
d = Supernumerary calices sometimes present			
e = Circumoral calices are small and few in number			
f = Encrusting growth form			

APPENDIX 2

Coded data matrix used in the phylogenetic analysis.

	1	2	3	4	5	6	7	8	9	10
Acrosmilia	0	0	0	0	0	0	0	0	0	0
Cycloseris A	0	0	0	1	0	0	0	0	0	0
Cycloseris B	0	0	0	1	0	0	0	1	0	0
Diaseris	0	0	0	1	0	0	0	0	0	0
Heliofungia	0	1	0	1	0	0	1	0	2	0
F. (*Danafungia* A)	0	1	0	1	0	1	1	1	2	0
F. (*Danafungia* B)	0	1	0	1	1	1	1	1	2	0
F. (*Ctenactis*)	0	1	1	1	1	1	1	1	2	0
Herpetoglossa	1	1	1	1	1	1	1	1	2	−1
F. (*Verrillofungia*)	0	1	0	1	1	1	1	1	1	0
F. (*Fungia*)	0	1	0	1	1	1	0	0	1	0
F. (*Pleuractis*)	0	1	1	1	1	1	0	0	0	0
Herpolitha	1	1	1	1	1	1	0	0	0	−2
Polyphyllia	1	1	1	1	1	1	0	0	0	−2
Zoopilus	1	1	0	1	1	1	1	0	2	1
Halomitra	1	1	0	1	1	1	0	1	1	1
Sandalolitha	1	1	1	1	1	1	1	1	1	2
Lithophyllon	1	1	−1	0	0	0	0	1	0	2
Podabacia	1	1	−1	0	1	1	0	1	1	2

REFERENCES CITED

Cairns, S. D.

[in press] *A generic revision of the Stylasteridae (Coelenterata: Hydrozoa). Part 2. Phylogenetic analysis.* Bulletin of Marine Science, vol. 34, No. 2.

Cracraft, J.

1983. *Cladistic analysis and vicariance biogeography.* American Scientist, vol. 71, pp. 273–281.

Eldredge, N., and Cracraft, J.

1980. *Phylogenetic patterns and the evolutionary process.* Columbia University Press, New York. 349 pp.

Farris, J. S.

1969. *A successive approximations approach to character weighting.* Systematic Zoology, vol. 18, No. 4, pp. 374–385.

Funk, V. A., and Humphries, C. J.

[in press] *Cladistics: a beginner's guide.* Columbia University Press, New York.

Gerhart, D. J.

1983. *The chemical systematics of colonial marine animals: an estimated phylogeny of the order Gorgonacea based on terpenoid characters.* Biological Bulletin, vol. 164, pp. 71–81.

Pillai, C. G. S., and Scheer, G.

1976. *Report on the stony corals from the Maldive Archipelago.* Zoologica, vol. 43, No. 126, 83 pp., 32 pls.

Schmidt, H.

1972. *Die Nesselkapseln der Anthozoa und ihre Bedeutung für die phylogenetische Systematik.* Helgoländer wissenschaftliche Meersuntersuchungen, vol. 23, pp. 422–458.

1974. *On the evolution of the Anthozoa.* Proceedings of the Second International Coral Reef Symposium, vol. 1, pp. 533–560, 16 figs.

Vaughan, T. W., and Wells, J. W.

1943. *Revision of the suborders, families, and genera of the Scleractinia.* Geological Society of America Special Papers, No. 44, 363 pp., 51 pls., 39 text-figs.

Veron, J. E. N., and Pichon, M.

1980. *Scleractinia of Eastern Australia. Part 3.* Australian Institute of Marine Sciences Monograph Series, vol. 4, 459 pp., 857 figs.

Wells, J. W.

1956. *Scleractinia,* pp. F328–F444, text-figs. 222–339, *in* Moore, R. C. (ed.), *Treatise on invertebrate paleontology.* University of Kansas Press, Lawrence.

1966. *Evolutionary development in the scleractinian family Fungiidae.* Symposia of the Zoological Society of London, No. 16, pp. 223–246, 4 figs.

Wiley, E. O.

1981. *Phylogenetics: the theory and practice of phylogenetic systematics.* Wiley-Interscience, New York. 439 pp.