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A GENERIC REVISION OF THE STYLASTERIDAE (COELENTERATA: HYDROZOA)

PART 2: PHYLOGENETIC ANALYSIS

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ABSTRACT

A phylogenetic analysis was performed on the 23 genera of stylasterid corals. *Hydractinia*, a genus of athecate hydroid, was chosen as the out-group based primarily on morphological homology and secondarily on ontogeny, fossil record and advocacy. The evolutionary polarities of the 19 characters used in the analysis were established by out-group comparison and transformation series of multistate characters were ordered by apparent structural complexity and the process of reciprocal illumination. Several equally parsimonious cladograms are discussed and the justifications for choosing one in preference to the others are given. The interrelationships of the genera are discussed: *Lepidopora* is considered to be the most plesiomorphic genus, *Pseudocrypthelia* the most apomorphic. The final cladogram is compared to the evolutionary tree proposed by Moseley (1881). Within the context of the final cladogram, the relative value of the characters and degree of homoplasy are discussed. The stylasterids are considered as a family of athecate hydroids and the subfamilial designations are recommended to be abolished.

Stylasterid corals are fragile, usually small, uniplanar to slightly arborescent colonial hydrozoans of the phylum Coelenterata. Their calcium carbonate skeletons are often brightly pigmented orange, red, blue or violet. The approximately 185 known species (Cairns, 1983b) occur in all ocean basins from continental Antarctica to the Arctic Circle at depths between 0–2,800 m. They are most diverse and abundant at depths of 200–500 m. They are known from the Paleocene to the Recent. Opinion is divided as to whether they should be considered a separate order in the Hydrozoa or simply a family of calcified hydroids in the Hydroida. This analysis is based on the redescription of the 23 stylasterid genera as revised by Cairns (1983b).

Ideally, a phylogenetic analysis should be based on out-group comparison, supplemented by evidence derived from ontogeny (Stevens, 1980). Unfortunately, the ontogeny of stylasterids is virtually unknown and the out-group chosen for this analysis is a genus of uncalcified athecate hydroids. All characters used in the classification of stylasterids at all taxonomic levels are based on the calcium carbonate skeleton, which makes comparison to an uncalcified out-group difficult. Nonetheless, certain characters can be polarized from the out-group, and those that could not were ordered into transformation series by their apparent structural complexity and by the process of reciprocal illumination, a method of testing hypotheses of character state series against one another (discussed later). The 43 taxa analyzed represent 23 presumably monophyletic genera (Cairns, 1983b). Some generalized references on phylogenetic analysis, particularly on how to determine polarity and order multistate characters are: Eldredge and Cracraft (1980), Watrous and Wheeler (1981) and Mickevich (1983).

This is the second application of phylogenetic systematic methods to a coelenterate group. The first was by Schmidt (1972; 1974), concerning the ordinal classification of the class Anthozoa.

Methods

Choice of Out-Group.—Hydroids of the genus *Hydractinia* were chosen as the out-group for this analysis as they are hypothesized to be the sister group of the stylasterids. This decision was based primarily on morphological homology, supported by ontogeny and advocacy, and was not contradicted by the fossil record.

Homology. A decalcified stylasterid coral is indistinguishable from an athecate hydroid, a fact that no one has disputed since Moseley (1876) showed that stylasterids were not scleractinian corals but, in fact, belonged to the Hydrozoa. Within the subclass Athecata *sensu* Petersen, 1979, stylasterids are most closely allied to the order Filifera, because they both have filiform, noncapitate, gastrozooid tentacles. Within the Filifera, stylasterids are most similar to the Pandeida Petersen, 1979, one of three suborders in the Filifera. The Pandeida and stylasterids are characterized by having spindle-shaped gastrozooids with tentacles arranged in one whorl around a conical hypostome. Within the Pandeida, stylasterids are most similar to the Hydractinoidea Bouillon, 1978, one of three superfamilies in the Pandeida. The most important character in common at this level is the high degree of polyp polymorphism of the two taxa. Of the three or four families in the Hydractinoidea, stylasterids are most similar to the Hydractiniidae Agassiz, 1862. Hydractiniids have developed the potential for calcification, as evidenced by *Janaria, Hydrocorella* and *Polyhydra*, which are the only hydroid genera to do so. For this reason, Stechow (1921) suggested that one of these genera may have been the evolutionary link between hydroids and stylasterids. Another character in common between the hydractiniids and stylasterids is their simple, noncapitate dactylozooids. Within the hydractiniids it is tempting to think, as did Stechow (1921), that one of the three calcified genera is most closely related to the stylasterids; however, detailed examination indicates otherwise. The coenosteal texture of the calcified hydroids is quite different from the reticulate-granular or linear-imbricate coenosteum of stylasterids. Furthermore, vesicles of unknown function are found in great abundance in *Janaria* and *Hydrocorella*. Stechow (1921; 1962) identified these vesicles as gonophores but histological examination reveals that they are not gonophores, gastrozooids or dactylozooids; there is no counterpart of this structure in any other hydroid or in the stylasterids. The stylasterids are, in fact, more similar to species of *Hydractinia*, particularly because they both have spines and they both lack the medusoid stage. Stechow (1962: 418) suggested that the surface spines of *Hydractinia* were the predecessors, and thus homologs, of the stylasterid gastrostyle, achieved by deposition of calcium carbonate around the hydractiniid spine. Certain hydractiniid spines are very similar to stylasterid gastrostyles (Fig. 1) and thus fulfill one of the most important criteria for homology: similarity of positional hierarchy (Rieger and Tyler, 1979). Furthermore, these two structures contradict most of Rieger and Tyler's (1979) criteria for analogy, i.e., (1) they are not under the influence of a common selective pressure, (2) they are composed of different materials (chitin vs. calcium carbonate), (3) they are not the only possible means to accomplish a particular function (the double-chambered gastropore chamber without a gastrostyle retains the gastrozooid as well as a gastropore without a style), 4) they both develop from ectoderm (Fritchman, 1974) and 5) they are not under selective pressure to evolve mimicry. Therefore, I agree with Stechow (1962) that the *Hydractinia* spine is homologous to the stylasterid gastrostyle. To summarize, the differences between stylasterids and *Hydractinia* are minor, mostly involving a constellation of changes associated with the deposition of a calcium carbonate skeleton, i.e., gonophores encapsulated as ampullae, gastro- and dactylozooids encased in calcified tubes and the transformation of the protective spines into a supportive gastrostyle.

Ontogeny. Very little is known about the ontogeny of stylasterid corals. In one of the few studies on stylasterid development, Fritchman (1974) noted a similarity of the gland cells of the planulae of the stylasterid *Allopora petrograpta* and the hydractiniid *Hydractinia echinata* and stated that the method of skeleton formation of stylasterids and *Hydractinia* was so similar that it was undoubtedly an homologous structure, even though one is chitinous and the other is calcareous.

Fossil Record. Very few hydroids are known from the fossil record but *Hydractinia* is one of the exceptions, known from the Eocene to Recent and questionably as far back as the Cretaceous (Hill and Wells, 1956). The earliest known stylasterids are from the Paleocene. This is certainly not proof of an evolutionary connection, but the hypothesis is not contradicted by the fossil evidence.

Advocacy. Stylasterid corals customarily have been placed in a separate order (Boschma, 1956), the Stylasterina; however, as early as 1914, Broch considered them as a family of hydroids, closely allied to either *Clathrozoon* or *Hydractinia*. Stechow (1921; 1922; 1923; 1925; 1962) agreed with Broch that the stylasterids represented a family of hydroids closely related to the Hydractiniidae, especially the calcified hydractiniids. The stylasterids were considered as one of four families in Bouillon's (1978) superfamily Hydractinoidea, one of the other families being the Hydractiniidae. Finally, Petersen (1979: 112), in his reorganization of the higher taxa of the Athecata, placed the Stylasteridae and Hydractiniidae as sister groups. I concur with these authors in considering the stylasterids to be a family of calcified hydroids within the superfamily Hydractinoidea.

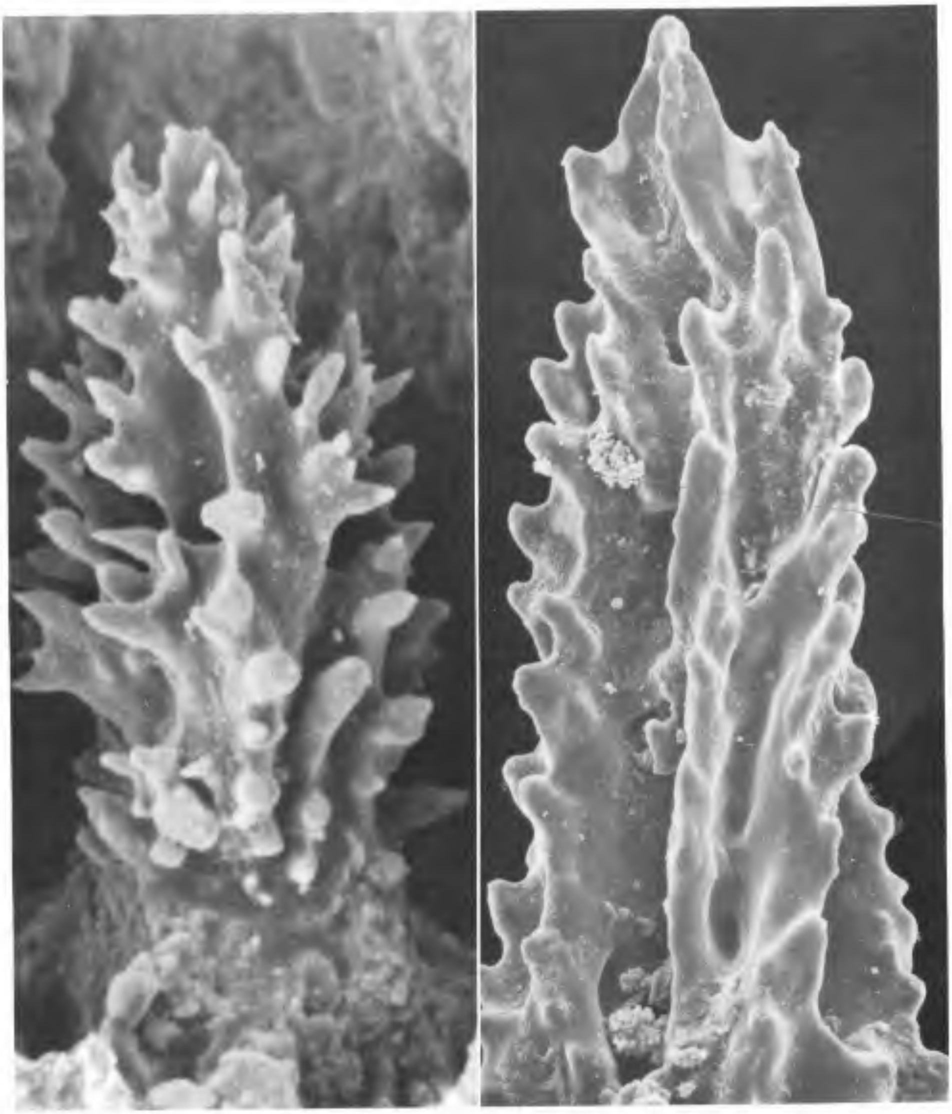

Figure 1. Scanning electron micrographs of the calcareous gastrostyle of *Errina aspera* (left, 250×) and the chitinous spine of *Hydractinia echinata* (right, 125×).

Coding of Character States and Computer-Generated Cladograms.—Nineteen characters were used in the phylogenetic analysis of the stylasterid genera. Most of these characters have more than two character states and one has as many as 10 character states. Because the multistate characters are not always interpreted as being linear in their evolution and because these data must be coded for the computer, often more than one data column was required to code each character state (Appendices 1 and 2). Ultimately, 44 columns were used to code the 19 characters.

The characters used in the analysis were, for the most part, conservative at the generic level; however, sometimes species or groups of species within genera differed in one or more character states. For instance, most species of *Stenohelia* have randomly arranged ampullae (Appendix 1: character 3: state A), but *S. profunda* has its ampullae concentrated around its gastropores (character 3: state B). To allow for an accurate coding of this genus, it was divided into two components: *Stenohelia* 1 and

Stenohelia 2, the former coded as having randomly arranged ampullae, the latter as having concentrated ampullae. In theory, these two component taxa should reunite in the final cladogram as a monophyletic unit, as they did in this case. It should be stated that autapomorphies for genera that were subdivided were still considered as autapomorphies, not synapomorphies of the subdivided genera. It was necessary to use this technique for 8 of the 23 genera, some of which were divided into as many as six component taxa. A total of 20 additional taxa were added in this manner (Appendix 2). Not all of the component taxa regrouped into monophyletic units in the final cladogram, indicating that, based on these data, these genera are evidently not monophyletic. The implications will be discussed later. With a total of 23 genera, 20 additional subdivided "genera," and the out-group, a total of 44 taxa were considered, producing a 44 × 44 data matrix (Appendix 2).

In two cases, both concerning dactylopore spine shape, all of the species of a genus had two character states for the same character. For instance, *Errinopsis* always has both conical (coded: 010000) and abcauline (coded: 000010) dactylopore spines (character 19). It was therefore coded as 010010.

The cladograms discussed in the remainder of the paper were produced by the Wagner 78 algorithm, which is discussed by Farris (1970) and Wiley (1981: 178–192). The program was installed on the Smithsonian's Honeywell computer by James S. Farris in 1979. The advantages of a Wagner analysis—tree stability, allowance for reversals, usage of all data and adherence to parsimony—are discussed by Mickevich (1978) and Farris (in press).

The first cladogram generated (not illustrated) was based on only those 11 of the 19 characters (Appendix 1: characters 1–10, 19) that could be polarized from out-group comparisons. As a simple example, the random arrangement of ampullae (character 3: state A) is considered plesiomorphous because *Hydractinia* has randomly arranged gonophores; ampullae concentrated around gastropores is thus considered to be a derived state (character 3: state B). As a more complex example, the random coordination of gastro- and dactylopores (character 9: state A) is considered plesiomorphous because this is the condition found in *Hydractinia*. However, there are another eight character states to which out-group comparison cannot be applied. In these cases, the character states were either coded in a very noncommittal manner, in which they were all independently derived from the plesiomorphous state, or estimates were made as to their transformation series based on increasing morphological complexity. In this particular case, six of the nine states were provisionally linked to the ancestral state but the *Gyropora*-type and cyclosystem arrangements (states I and J) were hypothesized to have derived from the *Errinopora*-type condition (state H). This was based on the observation that some species of *Errinopora* have pseudocyclosystems very similar to those of the Stylasterinae and some species have linearly arranged adjacent dactylopore spines very similar to those of *Gyropora*. Thus, the gastro-dactylopore coordination of *Errinopora* was interpreted as a transition between those genera with randomly arranged dactylopores and those in which the dactylopores are coordinated into a cyclosystem. As another example, the dactylopore arrangement of *Distichopora* 1 (state F) was hypothesized to be a less derived predecessor of the more highly coordinated pore row of *Distichopora* 2. Therefore, the character diagram illustrated in Appendix 1 (Fig. 4, drawing 9) was used for this character. These hypotheses of character state order were considered provisional and subject to change if contradicted by a more parsimonious cladogram resulting from two or more other more reliable characters. This process of testing one hypothesis against other hypotheses of character state transformation series has been called reciprocal illumination (Hennig, 1966; Wiley, 1981) and will be discussed again later.

The preliminary cladogram, based on these 11 polarized characters, was highly resolved in the upper levels but poorly resolved in the lower levels of the Wagner tree, with 20 of the 43 taxa originating directly or indirectly from one basal polychotomy. Therefore, the remaining eight characters were polarized and ordered based on the same principles described above, only this time the out-group was considered to be the 20 taxa in the basal polychotomy. A second, much more highly resolved cladogram resulted (not illustrated), which was not very different from the finally proposed cladogram.

At this point in the analysis, the character state changes for each character were reanalyzed in relation to the branching pattern of the second cladogram in the process of reciprocal illumination. For instance, for character 17 (shape of gastropore chamber) both the *Pliobothrus*-type (state C) and the cylindrical gastropore (state B) were previously hypothesized to have originated from the ancestral condition (state A); however, cladogram 2 implied that it would be more parsimonious to derive the *Pliobothrus*-type from the cylindrical. Seven minor changes of this type were made in the character coding. A series of computer runs was then made, each run differing in the order of taxa in the data matrix ("shuffling the deck"). After eight runs a consistently most parsimonious tree was used for cladogram 3 (Fig. 2).

The changes made between cladogram 3 and the final cladogram 4, resulted from: 1) a reevaluation of character 19: dactylopore shape, 2) two equally parsimonious alternatives for minor branches of the cladogram, 3) the addition of characteristics of coenosteal texture and 4) the addition of autapomorphous characters.

Dactylopore shape was coded in a very generalized manner for cladogram 3 (Appendix 1: character

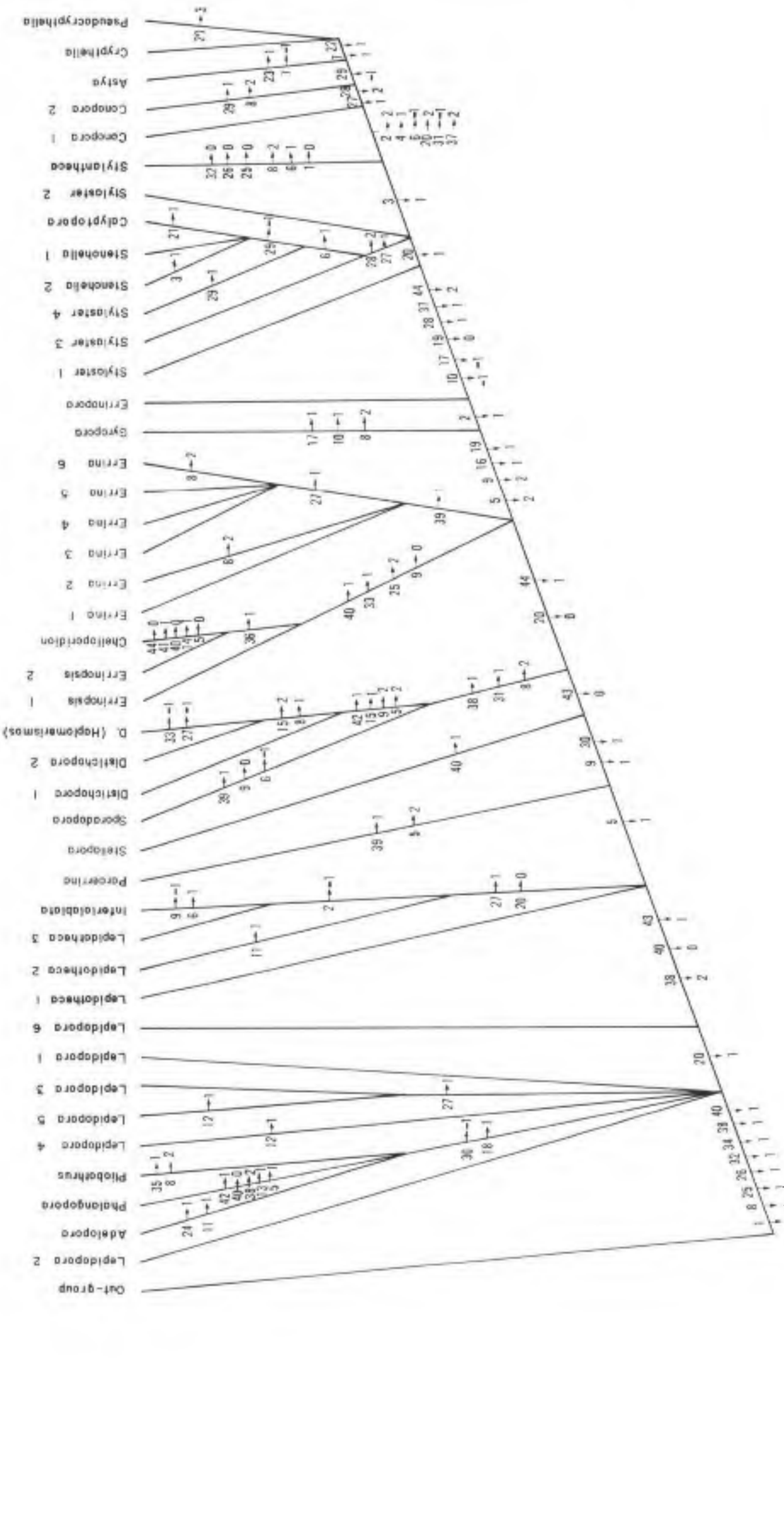

Figure 2. Cladogram 3: Unmodified computer-generated cladogram, showing all character state changes. Numbers to the left and above arrows are the data column numbers; those to the right and beneath the arrows are the character states of those columns. These numbers are coded in Appendix 1.

19); 18 steps, including 7 convergences and 5 reversals, were required to fit the character states to the taxa. If, however, the conical dactylopore is assumed to be a generalized structure that gave rise to the flush, elliptical, abcauline, and cone of platelets dactylopore spines (Appendix 1: character 19′), then only 16 steps are required, including 7 convergences and only 2 reversals. Making this change produces a stem for the *Lepidotheca-Inferiolabiata* branch and collapses *Stellapora* into the polychotomy with *Sporadopora* and *Distichopora*.

A minor change, resulting in an equally parsimonious tree, was made by uniting *Lepidopora* 5 and *Lepidopora* 4 with the synapomorphy of character 9 (state C: gastropores restricted to anterior face). This change created another convergence for character 13 (state C: pointed branch tips), but this was considered justified based on the high variability of the latter character and the stability of the former. Another equally parsimonious change united *Gyropora* and *Errinopora* by the synapomorphy of multitipped gastrostyle spines (character 10: state C). This created a convergence for the presence of dactylostyles (character 2: state B), occurring once for *Errinopora* and again for the next segment of the cladogram. This change was felt to be justified because the dactylostyles of *Errinopora* are much more robust than any of the other stylasterid dactylostyles and suggests a reinterpretation as a different kind of style.

Coenosteal texture was recently introduced (Cairns, 1983a) as an easily distinguishable (with scanning electron microscopy) character that is usually conservative at the generic level. Initially, I thought that it might serve as an important character in the phylogenetic analysis. Unfortunately, the character states of coenosteal texture are very unstable, occurring in parallel and reversing with great frequency, defying attempts to polarize or order the character states. Therefore, coenosteal texture (Appendix 1: character 20) was not used to produce the computer-generated cladograms, but was added to the final cladogram in an unpolarized fashion to increase resolution. The five minor changes it made in the final cladogram were: 1) to unite *Lepidopora* 2 and *Lepidopora* 3, 2) to help produce a monophyletic group of *Errinopsis* 1 and 2, 3) to unite *Errina* 5 and *Errina* 6, 4) to unite *Stylaster* 3 and *Stylaster* 4 and 5) to produce a monophyletic group of *Stenohelia* 1 and 2.

Finally, the addition of autapomorphous characters helped to unite *Errinopsis* 1 and 2. Ordinarily the addition of autapomorphous characters does not change the branching of a cladogram, but because eight of the genera were subdivided, there was a potential for their reunion using autapomorphous characters.

Results and Discussion

Discussion of the Cladogram.—The results of the phylogenetic analysis are summarized in cladogram 4 (Fig. 3). The genus with the least number of derived characters is *Lepidopora*, specifically the *Lepidopora* 1, 2 and 4 components. Although three other genera are linked to a common polychotomy, all of the *Lepidopora* components are at least two character state changes less derived, even *Lepidopora* 6. *Lepidopora*, unfortunately, does not resolve as a monophyletic unit, which is an indication that, pending further study, it should be divided into more than one genus or that more characters should be used in the analysis. Moseley (1881), without explanation, designated *Sporadopora* as the "ancestral" stylasterid genus. Broch (1914) suggested that *Pliobothrus* was the most "primitive" genus based on its lack of coordination of gastro- and dactylopores, simple dactylozooids and lack of gastrostyles; however, in 1942 (Broch, 1942: 7, 33) he vacillated between *Sporadopora* and *Pliobothrus* as the most primitive. The phylogenetic analysis places *Pliobothrus* near the root of the cladogram but, because the absence of gastrostyles is considered as a derived state, *Lepidopora* results in having the least number of derived characters.

Three genera, *Pliobothrus*, *Adelopora* and *Phalangopora*, are grouped by their lack of gastrostyles, and their stem is placed in the polychotomy with *Lepidopora*. Such lack of resolution in the lower levels of a cladogram is apparently not uncommon (pers. comm., V. Funk, 1982). It is interesting to note that *Adelopora*, having perhaps the most sophisticated adaptation of all the stylasterids—the hinged operculum—is otherwise quite underived.

Lepidopora 6 is distinguished from the first polychotomy by a relatively minor and variable character: sharply pointed gastrostyle spines.

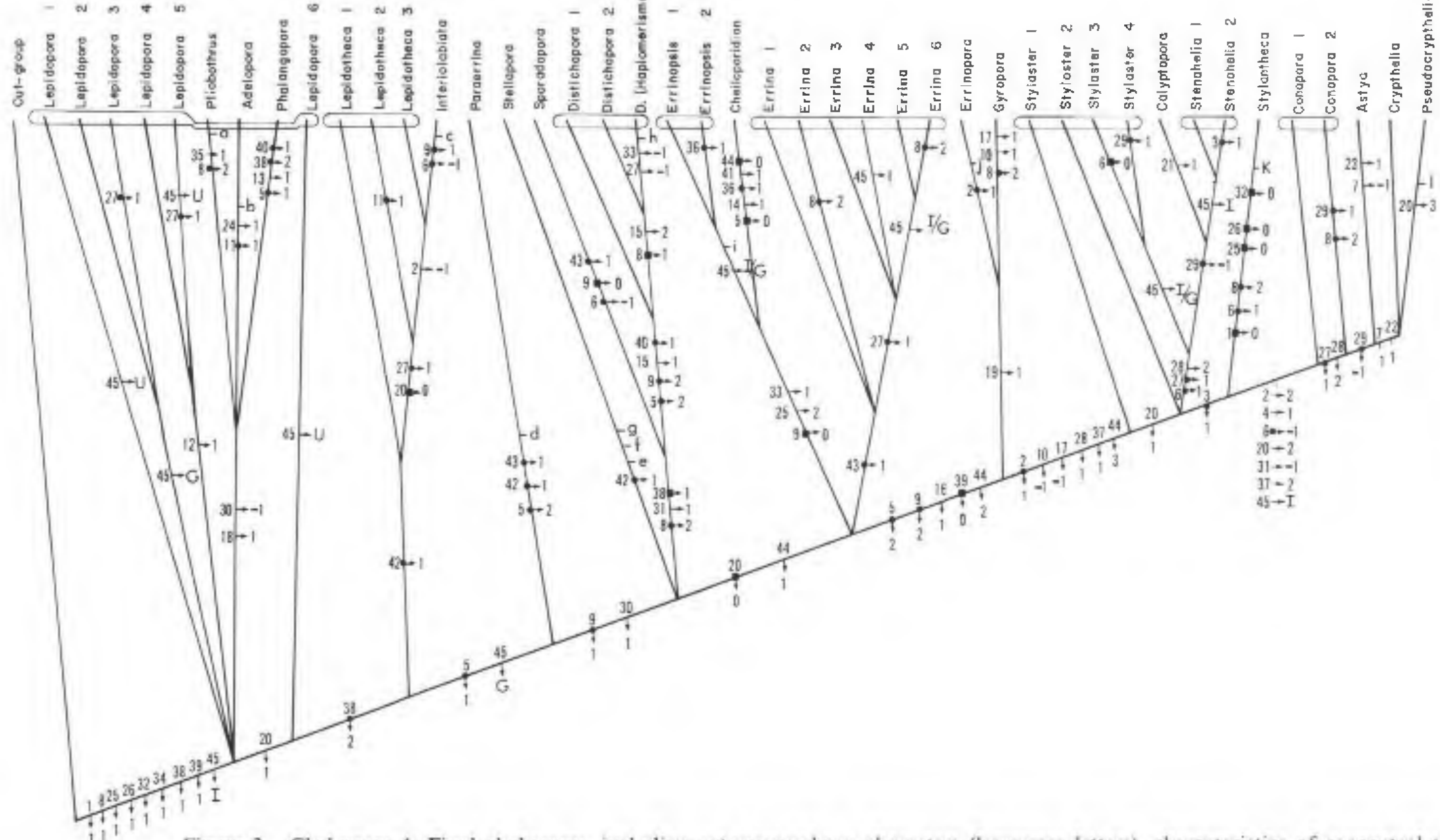

Figure 3. Cladogram 4: Final cladogram, including autapomorphous characters (lowercase letters), characteristics of coenosteal texture (character 20, data column 45), reevaluation of equally parsimonious alternatives (see text), and reevaluation of dactylopore shape (Fig. 4: character 19′, alternate). Components of divided genera united by circles at top of cladogram. Character reversals are indicated by solid squares; characters evolved in parallel by solid circles. Autapomorphies: a) rudimentary tabulae present in gastropore, b) unique gastrozooid shape, c) dactylopore spines ridged, d) gastrostyle unique, e) conical dactylopore retained, f) dactylopore spines composite, g) gastropores often stellate, h) coenosteum ridged, i) colony attached to substrate at numerous points, j) ampullae may be conical, k) usually more than one gastrozooid per cyclosystem and l) upper gastropore linear-imbricate.

The next branch of the cladogram, *Lepidotheca* and *Inferiolabiata*, is characterized by the transformation of the conical dactylopore to the abcauline dactylopore spine. The three components of *Lepidotheca* are adjacent (paraphyletic) but are not monophyletic on the cladogram.

Paraerrina is distinguished by having both abcauline and flush dactylopores, both presumably derived from the conical dactylopore. The abcauline spines of *Paraerrina* are much smaller than those of *Lepidotheca* and found only on branch tips, therefore suggesting a reinterpretation as a different kind of dactylopore spine instead of a convergence with those of *Lepidotheca.*

Ridged gastrostyles are found in the remainder of the genera that have gastrostyles. *Stellapora* has moderately ridged gastrostyles and very tall, clustered, composite, abcauline dactylopore spines, again presumably derived from the conical dactylopore; however, because these dactylopore spines are so different from those of *Lepidotheca* or *Paraerrina*, they might also be reinterpreted as a different kind, not necessarily a parallelism with the other abcauline dactylopore spines.

Sporadopora and *Distichopora* seem to form a natural unit, united by the synapomorphies of very long, deeply ridged gastrostyles; internal ampullae (a case of convergence); and long dactylopore tubes (a reversal). *Distichopora*, which resolves as a monophyletic unit, is distinguished from *Sporadopora* by its more highly coordinated gastro- and dactylopores and its elliptical dactylopores. *Distichopora* 1 (=*D. providentiae*) forms an intermediate between *Sporadopora* and *Distichopora* 2, evidenced by its intermediate level of gastro- and dactylopore coordination; *D.* (*Haplomerismos*) appears to be a highly derived offshoot from *Distichopora* 2.

The remaining genera are characterized by thick, adcauline or adcauline-like dactylopore spines. The cladogram branch containing *Errinopsis* and *Cheiloporidion* has individualized adcauline dactylopore spines, and shares the synapomorphy of branches that are rectangular in cross section and fenestrate in arrangement. The two *Errinopsis* resolve as a monophyletic group distinct from *Cheiloporidion*. The latter genus is distinguished by an unusual modification of the conical dactylopore.

The six component taxa of *Errina* resolve as a monophyletic unit, united by the presence of both adcauline and flush dactylopores. The further resolution within *Errina* is based on characters subsequently interpreted as being highly variable.

The remaining genera all have exclusively adnate dactylozooids, no conical dactylopore, and a higher degree of gastro-dactylopore coordination, ranging from lines of adjacent dactylopores to cyclosystems. *Errinopora* and *Gyropora* are united by the synapomorphy of multiheaded gastrostyle spines. *Gyropora* is slightly more derived, having internal ampullae (a convergence) and common walls between adjacent dactylopore spines. The dactylopore spine walls of *Errinopora* are adjacent but discrete; *Errinopora* also has very well developed dactylostyles.

The remaining genera, traditionally called the subfamily Stylasterinae, all have true cyclosystems. The four taxa immediately following *Gyropora*—the nonmonophyletic assemblage of *Stylaster*—have dactylostyles and constricted gastropore chambers, each with a ring palisade. *Stylaster* 1 and 2, previously known as *Allopora*, are differentiated from each other only on the basis of having sharp or blunt gastrostyle spines, a highly variable character. *Stylaster* 3 and 4 are differentiated from "*Allopora*" by having pointed branch tips, cyclosystems restricted in distribution, and a mixture of imbricate and granular coenosteal texture. *Stylaster* 4 is distinguished by having coenosteal papillae and cyclosystems arranged exclusively on the branch edges.

The clade consisting of *Calyptopora* and *Stenohelia* is distinguished from *Stylaster* by the synapomorphy of unifacial cyclosystem orientation. *Calyptopora* is distinguished by its enlarged pseudosepta, which approximate lids, and the two *Stenohelia* are united by the synapomorphy of imbricate coenosteal texture.

The remaining genera have their ampullae concentrated around their gastropores. The next branch, *Stylantheca*, is distinguished by a series of reversals, all related presumably to its reversion to the ancestral state of an encrusting habit. It also has the autapomorphy of more than one gastrozooid per cyclosystem.

The group consisting of the four remaining genera has the largest number of derived characters and is strongly differentiated by the loss of gastro- and dactylostyles; the gain of large, round nematopores containing large nematocysts; the transition to a double-chambered gastropore chamber; and a reversion to imbricate coenosteal texture. This represents a change equivalent in magnitude to that which occurred with the advent of cyclosystems. The two *Conopora* resolve as a paraphyletic (not monophyletic) group. *Conopora* 2 is distinguished from *Conopora* 1 by having cyclosystems arranged only on the edges of slender, pointed branches and by having internal ampullae.

The last three genera all have unifacially oriented cyclosystems. *Astya* has the autapomorphy of nematopores concentrated exclusively on the edges of the pseudosepta, and a prong jutting into the gastropore tube. *Crypthelia* and *Pseudocrypthelia* share the synapomorphy of having both randomly arranged and concentrated nematopores and a lid over each cyclosystem. *Pseudocrypthelia* is considered the most highly derived genus with its unusual gastrostyle and textured upper gastropore chamber.

Moseley (1881: 98–101) is the only person to have proposed a phylogeny of the stylasterid genera; at that time there were only 12. He stated that the descent of the genera "from a parent form seems to be traceable with especial clearness." His tree included several hypothetical ancestors and the evolution of genera from other Recent genera. His approach was intuitive. Only that part of his tree dealing with the most advanced genera, those with cyclosystems, corresponds to my cladogram; the remainder is at variance with my results.

The cladogram of Figure 3 does not allow for the monophyletic separation of the four traditionally recognized subfamilies of stylasterids and I therefore suggest the abolishment of the subfamily level in the stylasterids.

Discussion of the Characters.—One hundred fourteen character state changes were required to distribute the 19 characters within the tree in the most parsimonious manner. Of these 114 changes, 14 are reversals and 49 are parallelisms or convergences. This relatively high rate of homoplasy, including 55% of the character state changes, is apparently not uncommon (pers. comm., V. Funk, 1982), and suggests two related explanations: (1) stylasterids were quite convergent in their evolution, developing similar structures many times and even reversing the trend of evolution on occasion, or (2) the characters chosen to produce the cladogram are not conservative at the generic level; more characters should be analyzed and/or the polarity of the original characters reevaluated. Both of these explanations are probably responsible, to varying degrees, for the high rate of homoplasy. However, once the 19 characters were chosen and polarized, none was dropped from the data matrix, regardless of its apparent homoplasy. This was done to avoid prejudicing the results by using only "good characters" subjectively chosen to support an a priori hypothesis. In theory, a well-corroborated cladogram would not be influenced by several highly homoplastic characters but would, in fact, serve to illustrate where these homoplasies occurred. With regard to the final

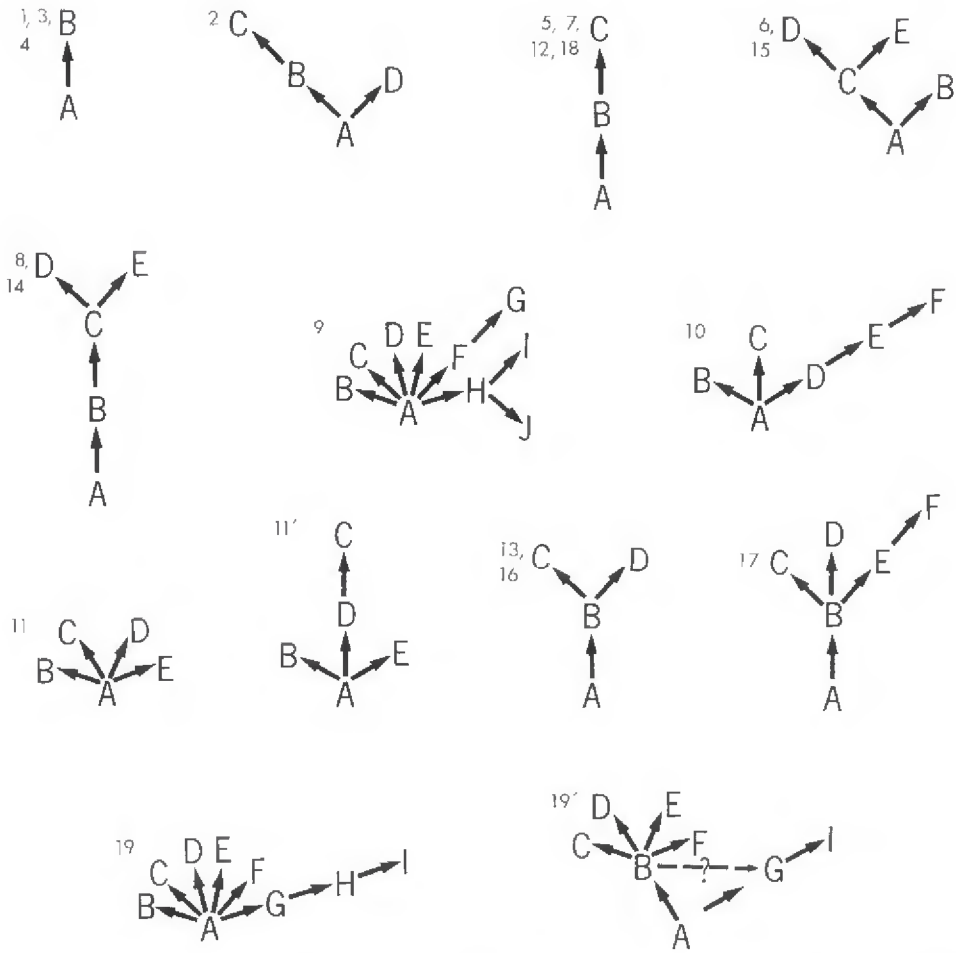

Figure 4. Character state transformation series for the 19 characters used to construct cladograms 3 and 4. Numbers and letters correspond to the characters and character states, respectively, as listed in Appendix 1. Drawing 11′ is an equally parsimonious interpretation derived from cladogram 4. Drawing 19 was used for cladogram 3; 19′ for cladogram 4.

cladogram, two characters were particularly homoplastic: prominence of ampullae (character 7: 7 convergences, 1 reversal; CI = 0.22) and condition of the branch tips (character 13: 6 convergences, 1 reversal; CI = 0.37). [Consistency indices of characters, CI, are defined by Farris (1969).] Not surprisingly, these are the two characters most often used to divide genera into smaller units to facilitate coding, which is an indication that they are probably not conservative at the generic level. On the other hand, character 9 (coordination of gastro- and dactylopores) has a high consistency index of 0.9 and thus yielded much information for its construction and interpretation. Other highly consistent characters were: 2, dactylostyle type (CI = 0.75); 4, presence of gastrozooid tentacles (CI = 1.0); 8, position of dactylopore spines (CI = 0.5); 12, branch anastomosis (CI = 0.67); 15, presence of gastrostyle ridges (CI = 1.0) and 17, gastropore chamber shape (CI = 0.83). Characters 8, 9 and 19 had some degree of overlap.

It is interesting to note that an alternative way of coding character 11 (Appendix 1, Fig. 4: 11′), implying the evolution of the fixed cyclosystem lid from the prong of *Astya*, produces the same cladogram in an equally parsimonious manner. Moseley (1881: 101) vacillated on the interpretation of this interrelationship but eventually drew his tree to reflect this alternative.

Other Observations.—The fossil record of stylasterids is not well known despite the fact that 28 of the 231 nominal species are known exclusively as fossils; most of these are from the Paleocene of Denmark (Nielsen, 1919) and the Eocene of Eua, Tonga (Wells, 1977). Also, most of the fossils are not well preserved and are of dubious generic identity (Cairns, 1983b). One fossil genus, *Congregopora*, containing only one known species from the Paleocene, is not included in this analysis because of the lack of diagnosable characters. Speculations concerning the evolutionary position of this genus and *Axopora* will be made at a later time. When the poorly known geological ranges are superimposed on the generic cladogram, only a very generalized picture emerges. One of the most derived genera, *Crypthelia*, was present in the Eocene, and the least derived genus, *Lepidopora*, was only questionably present in the Paleocene (Cairns, 1983b). The implication is that many, if not all, of the genera evolved in a rapid radiation in the late Paleocene or early Eocene, shortly after diverging from the hydractiniid hydroids.

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APPENDIX 1: CODING OF CHARACTER STATES

	DATA COLUMN
Character 1: Shape of Colony	1
A Encrusting	0
B Branching	1
Character 2: Dactylostyles	2
A Absent	0
B Type 1 (one row of slender elements per dactylopore)	1
C Loss of Type 1	2
D Type 2 (several rows of thick elements per dactylopore)	−1
Character 3: Location of Ampullae	3
A Randomly arranged on branch	0
B Concentrated around gastropore	1
Character 4: Gastrozooid Tentacles	4
A Present	0
B Absent	1

Appendix 1: Continued

Character 5: Dactylozooid Tentacles	5
A Simple	0
B Simple and adnate	1
C Exclusively adnate	2

Character 6: Nematopores	6	7
A None	0	0
B Papillae	1	0
C Round pores, randomly arranged	−1	0
D Round pores, randomly arranged and concentrated around gastropore	−1	1
E Round pores, concentrated around gastropores	−1	−1

Character 7: Prominence of Ampullae	8
A No skeletal evidence	0
B Superficial	1
C Internal	2

Character 8: Position of Dactylopore Spines	9	10
A Lacking or widely spaced	0	0
B Clustered	1	0
C Adjacent, arranged in rows; separate walls	2	0
D Adjacent, arranged in rows; common walls	2	1
E Adjacent, arranged in cyclosystems	2	−1

Character 9: Coordination of Gastro- and Dactylopores	11	12	13	14	15	16	17
A Random	0	0	0	0	0	0	0
B Gastropores at branch axils	1	0	0	0	0	0	0
C Gastropores restricted to anterior face	0	1	0	0	0	0	0
D Gastropores on both faces	0	0	1	0	0	0	0
E Gastropores restricted to branch edges	0	0	0	1	0	0	0
F Rudimentary pore rows	0	0	0	0	1	0	0
G Pore rows	0	0	0	0	2	0	0
H Dactylopores arranged in discontinuous lines adjacent to gastropores; pseudocyclosystems present	0	0	0	0	0	1	0
I Dactylopores arranged in lines; dactylopores have common walls; pseudocyclosystems present	0	0	0	0	0	1	1
J Cyclosystem arrangement	0	0	0	0	0	1	−1

Character 10: Spination of Gastrostyles	18	19	20
A Blunt	0	0	0
B Loss of blunt	1	0	0
C Multiheaded	0	1	0
D Sharp	0	0	1
E Loss of sharp	0	0	2
F Rudimentary (*Pseudocrypthelia*)	0	0	3

Character 11: Covering of Gastropore	21	22	23	24
A None	0	0	0	0
B Enlarged pseudosepta	1	0	0	0
C Fixed lid	0	1	0	0
D Prong	0	0	1	0
E Hinged operculum	0	0	0	1

Character 12: Branch Anastomosis	25
A Encrusting, no branches	0
B Branches free or slightly anastomotic	1
C Branches regularly fenestrate	2

Character 13: Branch Tips	26	27
A Encrusting, no branches	0	0
B Blunt	1	0
C Pointed, slender	1	1
D Lobate	1	−1

APPENDIX 1: CONTINUED

Character 14: Orientation of Cyclosystems	28	29
A No cyclosystems	0	0
B Random	1	0
C Primarily on branch edges but some on faces	2	0
D Exclusively on branch edges	2	1
E Unifacial	2	−1

Character 15: Ridges of Gastrostyle	30	31
A No ridges on style	0	0
B Loss of nonridged style	−1	0
C Moderately ridged	1	0
D Deeply ridged	1	1
E Loss of ridged style	1	−1

Character 16: Branch Cross Section	32	33
A Encrusting, no branches	0	0
B Round to slightly elliptical	1	0
C Rectangular	1	1
D Lamellar	1	−1

Character 17: Shape of Gastropore Chamber	34	35	36	37
A No chamber	0	0	0	0
B Cylindrical	1	0	0	0
C Unique (*Pliobothrus*)	1	1	0	0
D Constricted	1	0	1	0
E Constricted, with ring palisade	1	0	0	1
F Double chamber	1	0	0	2

Character 18: Length of Dactylopore Tubes	38
A None	0
B Long, extending down branch axis	1
C Short, terminating within 2 mm	2

Character 19: Shape of Dactylopore	39	40	41	42	43	44
A None	0	0	0	0	0	0
B Flush	1	0	0	0	0	0
C Conical	0	1	0	0	0	0
D Cone of platelets	0	0	1	0	0	0
E Elliptical	0	0	0	1	0	0
F Abcauline	0	0	0	0	1	0
G Adcauline	0	0	0	0	0	1
H Adcauline-type, linearly arranged	0	0	0	0	0	2
I Adcauline-type, arranged in cyclosystems	0	0	0	0	0	3

Character 19′: Shape of Dactylopore (alternate)	39	40	41	42	43	44
A None	0	0	0	0	0	0
B Conical	1	0	0	0	0	0
C Elliptical	1	1	0	0	0	0
D Cone of platelets	1	0	1	0	0	0
E Abcauline	1	0	0	1	0	0
F Flush	1	0	0	0	1	0
G Adcauline	0	0	0	0	0	1
H Adcauline-like, linearly arranged	0	0	0	0	0	2
I Adcauline-like, arranged in cyclosystems	0	0	0	0	0	3

Character 20: Coenosteal Texture	45
Linear-imbricate	I
Reticulate-granular	G
Both linear-imbricate and reticulate-granular	I/G
Unique, each case being a different texture	U

APPENDIX 2: DATA MATRIX FOR CLADOGRAMS 3 AND 4 (Figures 2 and 3)

Characters	1	2	3	4	5	6		7	8		9							10			11				12	13		14		15		16		17				18	19						20
Taxa / Data Columns	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
Out-Group	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	U
Lepidopora 1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	U
Lepidopora 2	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	G
Lepidopora 3	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	G
Lepidopora 4	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	I
Lepidopora 5	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	U
Pliobothrus	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	-1	0	1	0	1	1	0	0	1	0	1	0	0	0	0	I
Adelopora	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	-1	0	1	0	1	0	0	0	1	0	1	0	0	0	0	I
Phalangopora	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	-1	0	1	0	1	0	0	0	2	0	0	0	1	0	0	I
Lepidopora 6	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	U
Lepidotheca 1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	2	0	0	0	0	1	0	I
Lepidotheca 2	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	0	2	0	0	0	0	1	0	I
Lepidotheca 3	1	-1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	0	2	0	0	0	0	1	0	I
Inferiolabiata	1	-1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	0	2	0	0	0	0	1	0	I
Paraerrina	1	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	2	1	0	0	0	1	0	G
Stellapora	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	1	0	1	0	0	0	2	0	1	0	0	1	0	G
Sporadopora	1	0	0	0	1	-1	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	1	1	0	1	0	0	0	1	1	0	0	0	0	0	G
Distichopora 1	1	0	0	0	2	0	0	2	2	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	1	1	0	1	0	0	0	1	0	0	0	1	0	0	G
Distichopora 2	1	0	0	0	2	0	0	1	2	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	1	1	0	1	0	0	0	1	0	0	0	1	0	0	G
D. (Haplomerismos)	1	0	0	0	2	0	0	1	2	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	1	1	-1	0	0	1	1	1	-1	1	0	0	0	1	0	0	0	1	0	0	G
Errinopsis 1	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	1	0	1	1	1	0	0	0	2	0	1	0	0	0	1	I/G
Errinopsis 2	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	1	0	1	1	1	0	1	0	2	0	1	0	0	0	1	I/G
Cheiloporidion	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	1	0	1	1	1	0	1	0	2	0	0	1	0	0	0	G
Errina 1	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	1	0	0	0	2	1	0	0	0	0	1	G
Errina 2	1	0	0	0	1	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	1	0	0	0	2	1	0	0	0	0	1	G
Errina 3	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1	0	1	0	0	0	2	1	0	0	0	0	1	G
Errina 4	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1	0	1	0	0	0	2	1	0	0	0	0	1	I
Errina 5	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1	0	1	0	0	0	2	1	0	0	0	0	1	I/G
Errina 6	1	0	0	0	1	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1	0	1	0	0	0	2	1	0	0	0	0	1	I/G
Errinopora	1	1	0	0	2	0	0	1	2	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	0	0	1	0	1	0	1	0	0	0	2	0	0	0	0	0	2	G
Gyropora	1	0	0	0	2	0	0	2	2	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	1	0	0	0	1	0	1	0	1	0	0	0	2	0	0	0	0	0	2	G
Stylaster 1	1	1	0	0	2	0	0	1	2	-1	0	0	0	0	0	1	-1	0	0	0	0	0	0	0	1	1	0	1	0	1	0	1	0	1	0	0	1	2	0	0	0	0	0	3	G
Stylaster 2	1	1	0	0	2	0	0	1	2	-1	0	0	0	0	0	1	-1	0	0	1	0	0	0	0	1	1	0	1	0	1	0	1	0	1	0	0	1	2	0	0	0	0	0	3	G
Stylaster 3	1	1	0	0	2	0	0	1	2	-1	0	0	0	0	0	1	-1	0	0	1	0	0	0	0	1	1	1	2	0	1	0	1	0	1	0	0	1	2	0	0	0	0	0	3	I/G
Stylaster 4	1	1	0	0	2	1	0	1	2	-1	0	0	0	0	0	1	-1	0	0	1	0	0	0	0	1	1	1	2	1	1	0	1	0	1	0	0	1	2	0	0	0	0	0	3	I/G
Calyptopora	1	1	0	0	2	1	0	1	2	-1	0	0	0	0	0	1	-1	0	0	1	1	0	0	0	1	1	1	2	-1	1	0	1	0	1	0	0	1	2	0	0	0	0	0	3	G
Stenohelia 1	1	1	0	0	2	1	0	1	2	-1	0	0	0	0	0	1	-1	0	0	1	0	0	0	0	1	1	1	2	-1	1	0	1	0	1	0	0	1	2	0	0	0	0	0	3	I
Stenohelia 2	1	1	1	0	2	1	0	1	2	-1	0	0	0	0	0	1	-1	0	0	1	0	0	0	0	1	1	1	2	-1	1	0	1	0	1	0	0	1	2	0	0	0	0	0	3	I
Stylantheca	0	1	1	0	2	1	0	2	2	-1	0	0	0	0	0	1	-1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	2	0	0	0	0	0	3	G
Conopora 1	1	2	1	1	2	-1	0	1	2	-1	0	0	0	0	0	1	-1	0	0	2	0	0	0	0	1	1	0	1	0	1	-1	1	0	1	0	0	2	2	0	0	0	0	0	3	I
Conopora 2	1	2	1	1	2	-1	0	2	2	-1	0	0	0	0	0	1	-1	0	0	2	0	0	0	0	1	1	1	2	1	1	-1	1	0	1	0	0	2	2	0	0	0	0	0	3	I
Astya	1	2	1	1	2	-1	-1	1	2	-1	0	0	0	0	0	1	-1	0	0	2	0	0	1	0	1	1	1	2	-1	1	-1	1	0	1	0	0	2	2	0	0	0	0	0	3	I
Crypthelia	1	2	1	1	2	-1	1	1	2	-1	0	0	0	0	0	1	-1	0	0	2	0	1	0	0	1	1	1	2	-1	1	-1	1	0	1	0	0	2	2	0	0	0	0	0	3	I
Pseudocrypthelia	1	2	1	1	2	-1	1	1	2	-1	0	0	0	0	0	1	-1	0	0	3	0	1	0	0	1	1	1	2	-1	1	-1	1	0	1	0	0	2	2	0	0	0	0	0	3	I

Appendix 2: Continued

The character states of character 20 (coenosteal texture) were not ordered and therefore were not used to produce the computer-generated cladograms. See Appendix 1 for a key to the characters and how they were coded. Eight genera were subdivided as follows:

Lepidopora 1: Species with randomly arranged dactylopores, blunt branch tips, and linear-granular coenosteal texture: *L. diffusa, L. granulosa.*

Lepidopora 2: One species with randomly arranged dactylopores, blunt branch tips, and reticulate-granular coenosteal texture: *L. decipiens.*

Lepidopora 3: Species with randomly arranged dactylopores, slender branch tips, and reticulate-granular coenosteal texture: *L. carinata, L. sarmentosa.*

Lepidopora 4: One species with dactylopores restricted to lateral edges of branch, blunt branch tips, and linear-imbricate coenosteal texture: *L. eburnea* (Calvet, 1903) (=*L. hicksoni* Boschma, 1963).

Lepidopora 5: One species with dactylopores restricted to lateral edges of branches, slender branch tips, and a unique coenosteal texture: *L. glabra.*

Lepidopora 6: One species with randomly arranged dactylopores, slender branch tips, and a unique coenosteal texture: *L. acrolophos.*

Lepidotheca 1: Species with blunt branch tips, sharp gastrostyle spines, and without dactylostyles: *L. cervicornis, L. hachijoensis, L. japonica.*

Lepidotheca 2: Species with slender branch tips, blunt gastrostyle spines, and without dactylostyles: *L. ramosa, L. fascicularis, L. horrida.*

Lepidotheca 3: One species with slender branch tips, blunt gastrostyle spines, and dactylostyles: *L. tenuistylus.*

Distichopora 1: One species with rudimentary pore rows: *D. providentiae.*

Distichopora 2: All other species of *Distichopora*, all having well-developed pore rows.

Errinopsis 1: One species with a cylindrical gastropore chamber: *E. reticulum.*

Errinopsis 2: One species with a constricted gastropore chamber: *E. fenestrata.*

Errina 1: Species with reticulate-granular coenosteal texture, superficial ampullae, and blunt branch tips: *E. antarctica, E. cruenta, E. aspera, E. capensis.*

Errina 2: One species with reticulate-granular coenosteal texture, internal ampullae, and blunt branch tips: *E. kerguelensis.*

Errina 3: Species with reticulate-granular coenosteal texture, superficial ampullae, and slender branch tips: *E. gracilis, E. cheilopora, E. novaezealandiae, E. rubra, E. dabneyi, E. atlantica, E. cochleata.*

Errina 4: One species with linear-imbricate coenosteal texture, superficial ampullae, and slender branch tips: *E. macrogastra.*

Errina 5: Species with both reticulate-granular and imbricate coenosteal texture (the latter only on the dactylopore spines), superficial ampullae, and slender branch tips: *E. fissurata, E. boschmai.*

Errina 6: One species with both reticulate-granular and imbricate coenosteal texture (the latter only on the dactylopore spines), internal ampullae, and slender branch tips: *E. laterorifa.*

Stylaster 1: One species in *Stylaster* (Group A) *sensu* Cairns, 1983b, with blunt gastrostyle spines: *S. norvegicus.*

Stylaster 2: The remaining species in *Stylaster* (Group A): about 21 species.

Stylaster 3: *Stylaster* (Group B) *sensu* Cairns, 1983b: 16 species.

Stylaster 4: *Stylaster* (Group C) *sensu* Cairns, 1983b: 27 species.

Stenohelia 1: Species with randomly distributed ampullae: all species except for *S. profunda.*

Stenohelia 2: One species having ampullae clustered around gastropores: *S. profunda.*

Conopora 1: *Conopora* (Group B) *sensu* Cairns, 1983b: two species.

Conopora 2: *Conopora* (Group A) *sensu* Cairns, 1983b: three species.