

Modern Trends in the Systematics, Ecology, and Evolution of
Hydroids and Hydromedusae

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23. Evolutionary trends in the Stylasteridae
(Cnidaria, Hydrozoa)

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ABSTRACT

A five-step procedure is discussed for the phylogenetic analysis of the genera of the Stylasteridae, including: (1) construction of character table, (2) selection of out-groups, (3) polarization and ordering of character states, (4) coding character states, and (5) running computer algorithm. *Axopora* and *Hydractinia* were chosen as the primary and secondary out-groups, respectively. Both Wagner and character compatibility analyses were performed and the resultant cladograms discussed. Significant character-state changes and trends were discussed based on the chosen cladogram. An evolutionary scenario incorporating the axoporids, janariids, and stylasterids is suggested based on an interpretation of the cladogram.

Introduction

Stylasterid hydrocorals occur in all ocean basins from the Arctic Circle to continental Antarctica, at depths of 0–2800 m; however, most species occur at depths of 200–700 m off the coasts of islands. There are about 219 valid species of stylasterids (Cairns 1983a, 1985b, 1986) arranged in 24 genera, but Cairns (1985a) estimated that this represents only about half of the living species. Stylasterids are first known from the Palaeocene (Danian) of Denmark, and 24 of the 219 known species are exclusively fossil.

Stylasterids customarily have been placed in a separate order (Boschma 1956), the Stylasterina. However, as early as 1914, Broch (1914) considered them as a family of hydroids, closely related to either *Clathrozoön* or *Hydractinia*. Stechow (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 the four families in Bouillon's (1978) superfamily Hydractinioidea, and Petersen (1979) placed the Stylasteridae and Hydractiniidae as sister families. I concur with these authors (Cairns 1984a, p. 39) and suggest that the Stylasteridae represent a highly successful adaptive radiation that followed the advent of a calcified

skeleton, in conjunction with several other subsequent skeletal modifications. The evolutionary trends within this adaptive radiation are the focus of this paper.

Statement of problem

This paper is intended as a culmination and synthesis of previous studies of the evolution of stylasterid corals at the generic level. Following a generic revision (Cairns 1983a) and a subsequent preliminary phylogenetic analysis of the genera (Cairns 1984a), I investigated two other groups of calcified hydroids, *Janaria* (see Cairns and Barnard 1984) and *Axopora* (see Cairns 1983b), as potential out-groups for a more refined phylogenetic analysis. The aim of this paper is to construct another cladogram of the genera of stylasterids and to use it as an explanation of the evolutionary trends within the group. This new cladogram is based on greater knowledge of the non-stylasterid calcified hydroids (i.e. *Janaria*, *Kerunia*, *Hydrocorella*, and *Polyhydra*), both Wagner and character compatibility analyses, and a better understanding of stylasterid characters.

Methods

Space does not permit a discussion of the underlying principles, terminology, advantages, and disadvantages of phylogenetic analysis (cladism). The reader is referred to Eldredge and Cracraft (1980), Wiley (1981), and Funk and Humphries (in prep.) for an understandable account of the philosophy of cladism. Voss and Voss (1982) have published an elegant example of the use of phylogenetic analysis regarding the genera of a family of Cephalopoda, and I (Cairns 1984b) have previously published a phylogenetic analysis of a group of coelenterates: the genera of the Fungiidae.

Every group of organisms and their corresponding character states are different and usually present unique or new problems that require special solutions. The 'procedure' of phylogenetic analysis is by no means codified, but I would like to suggest a five-step process that will result in a cladogram.

Step 1: construction of character table

The first step of the analysis is to construct a character table or tabular key of the taxa and out-groups to be analysed, a process that most systematists have done many times. Appendix 1 is a coded tabular key to the stylasterid genera and three potential out-groups. The character states are arbitrarily numbered, and a key to the numbering system is

provided in Appendix 1. Numbers are used instead of written character states simply to reduce the size of the table. Another set of numbers, the computer code, which will be discussed in step 4, is also listed in this appendix. Not all of the stylasterid genera were included in the analysis (see Cairns 1984a for a comprehensive analysis) because the purpose of the present paper is to show large-scale evolutionary trends; some of the less speciose genera were omitted. Also, characters found to have low-consistency indices in the previous analysis (Cairns 1984a) were not used in this analysis.

Step 2: choice of out-groups

Choosing the most appropriate out-group for the analysis is the most critical step because the polarization of character states (step 3) is primarily based on this decision. For my previous analysis (Cairns 1984a p. 39) I chose *Hydractinia* as the primary out-group based on morphological homology of the polyps and protective spines and on what was known of the ontogeny of both groups. I still believe that this was a valid, if somewhat conservative, choice. Since then, however, I have investigated *Axopora* and found it to be remarkably similar to the primitive stylasterids (Cairns 1983b), especially *Lepidopora*. It is more advanced than *Hydractinia* in having a calcified skeleton, gastropore tubes, *Lepidopora*-like gastrostyle spination, and a stylasterid-like coenosteal texture. *Axopora* is therefore considered to be the sister group to the stylasterids and the primary out-group; *Hydractinia* is considered as the secondary out-group.

The calcified hydroids—called the janariids herein (including *Janaria*, *Hydrocorella*, *Polyhydra*, and *Kerunia*)—were also considered as out-groups for the stylasterids. The janariids are very similar to typical hydractiniids and were classified as such (family Hydractiniidae) by Bouillon (1978). However, two features of the janariids, their unique coenosteal texture and the presence of coenosteal vesicles, suggest that they represent an evolutionary line that evolved independently from the ancestral hydractiniids. Their calcified skeleton is thus considered a parallel development, and they are not considered to be on the main line of evolution leading from the hydractiniids to *Axopora* and to the stylasterids. None the less, they are included in the phylogenetic analysis in order to show their possible relations to the other taxa studied.

Step 3: polarization and ordering of character states

Useful references to polarization and ordering of character states are Stevens (1980), Michevich (1983), Stuessey and Crisci (1984), Watrous and Wheeler (1981), and Maddison, *et al.* (1984). When possible, direct out-group comparison was used to polarize character states. For example, in characters 10 and 12, the lack of dactylostyles and

gastropore lids are considered to be ancestral (plesiomorphic) because this is the condition in the primary out-group, *Axopora*; dactylostyles and gastropore lids are thus considered to be derived (apomorphic) states. However, regarding character 13 (gastrozoid tentacles), since it is impossible to tell if *Axopora* had gastrozoid tentacles, the character state of *Hydractinia* (the secondary out-group) is considered in order to suggest that the presence of gastrozoid tentacles is the ancestral state.

Unfortunately, not all characters are so easily polarized and ordered, especially multistate characters. In several cases—for example, character 2 (shape of gastropore chamber) having five states—a process called functional out-group comparison (FOG) was employed (Watrous and Wheeler 1981). Using this method a preliminary cladogram was constructed using only those characters that could be polarized with certainty, and then the least-derived genus or genus complex of the taxa being analysed (in this case, *Sporadopora*, *Distichopora*, and *Lepidopora*) was considered as the functional out-group for the remaining taxa: the character states of the successive functional out-groups are then used to order the remaining character states. For instance, for character 2, states 0 and 1 were determined by out-group comparison (*Hydractinia* and *Axopora*, respectively), and states 2–4 were ordered by functional out-group comparison. The same process was applied to character 4.

Sometimes it was impossible to use out-group comparisons to order the entire transition series, in which case an independent derivation of all states was hypothesized from the plesiomorphous state (e.g. characters 6, 7, 9, 14), which introduces the least number of assumptions in the model. One can also estimate transition series based on increasing morphological complexity, which theoretically is related to ontogeny, but each step removed from out-group comparison increases the subjectivity of the hypothesized transition series.

The results of the polarized and ordered character states for each character are given in Fig. 23.1. The key to the coded numbers is found in Appendix 1.

Step 4: coding of character states

If the data set is large enough to warrant the use of a computer algorithm, then the character states tabulated in Appendix 1 must be (1) converted to binary notation and (2) expressed in a way that maintains the ordering of the character states as displayed in Fig. 23.1. This technical process, called additive binary coding, is explained by Brooks, Cairns, Platt, and Pritchard (1984). The binary code for each character state is given in the key to character states of Appendix 1, and the full conversion of Appendix 1 to the binary-coded data matrix is presented in Appendix 2. All multistate characters require more than one column to represent them.

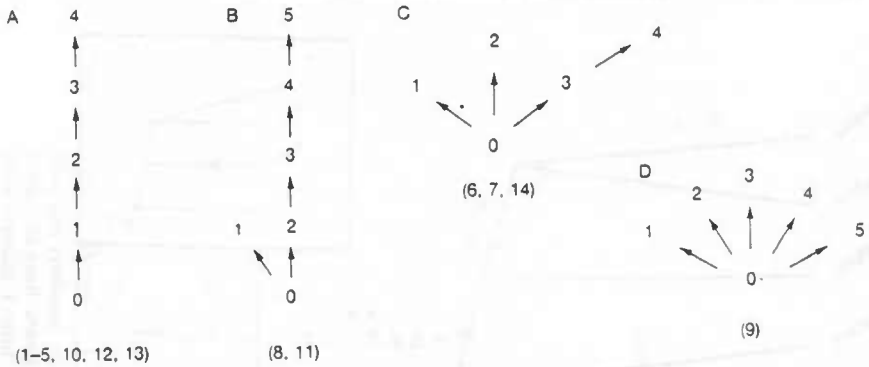


Fig. 23.1. Proposed character-state transformation series of the characters used in cladistic analyses. The numbers refer to the character states as coded in Appendix 1. The numbers in parentheses refer to the characters in Appendix 1 that follow that pattern. A–C may have more character states than occur in the character, but none the less will reflect the proper transformation series of the character states involved.

Step 5: computer algorithm

Two cladistic-based computer algorithms were applied to the data set: a Wagner-78 analysis and a character compatibility analysis (PHYLIP 2.1). The Wagner analysis produces a cladogram that groups taxa based on shared derived character states (synapomorphies) in the most parsimonious manner (see Wiley 1981, pp. 178–92). It uses all data available and indicates the most logical placement of parallelisms and reversals of the character states. Character compatibility analysis, sometimes called clique analysis, produces a cladogram resulting from the largest number of mutually compatible character states (LeQuesne 1982). It uses only those characters that are unique (no parallelisms) and unreversed. The resultant cladogram is similar to the Wagner cladogram in that taxa are united by shared derived character states but the cladogram is usually less resolved because fewer characters are being used. None the less, the more conservative, less informative estimate of a clique cladogram is a truer estimate of the phylogeny of the group and can often help to better analyse portions of the Wagner cladogram.

Results

Three runs of the Wagner program, each with a different order of the taxa entered, produced identical cladograms (Fig. 23.2). The cladogram has 47 steps (tree consistency index = 0.79) including five parallelisms, four reversals, and one character state (number 23) that could be equally

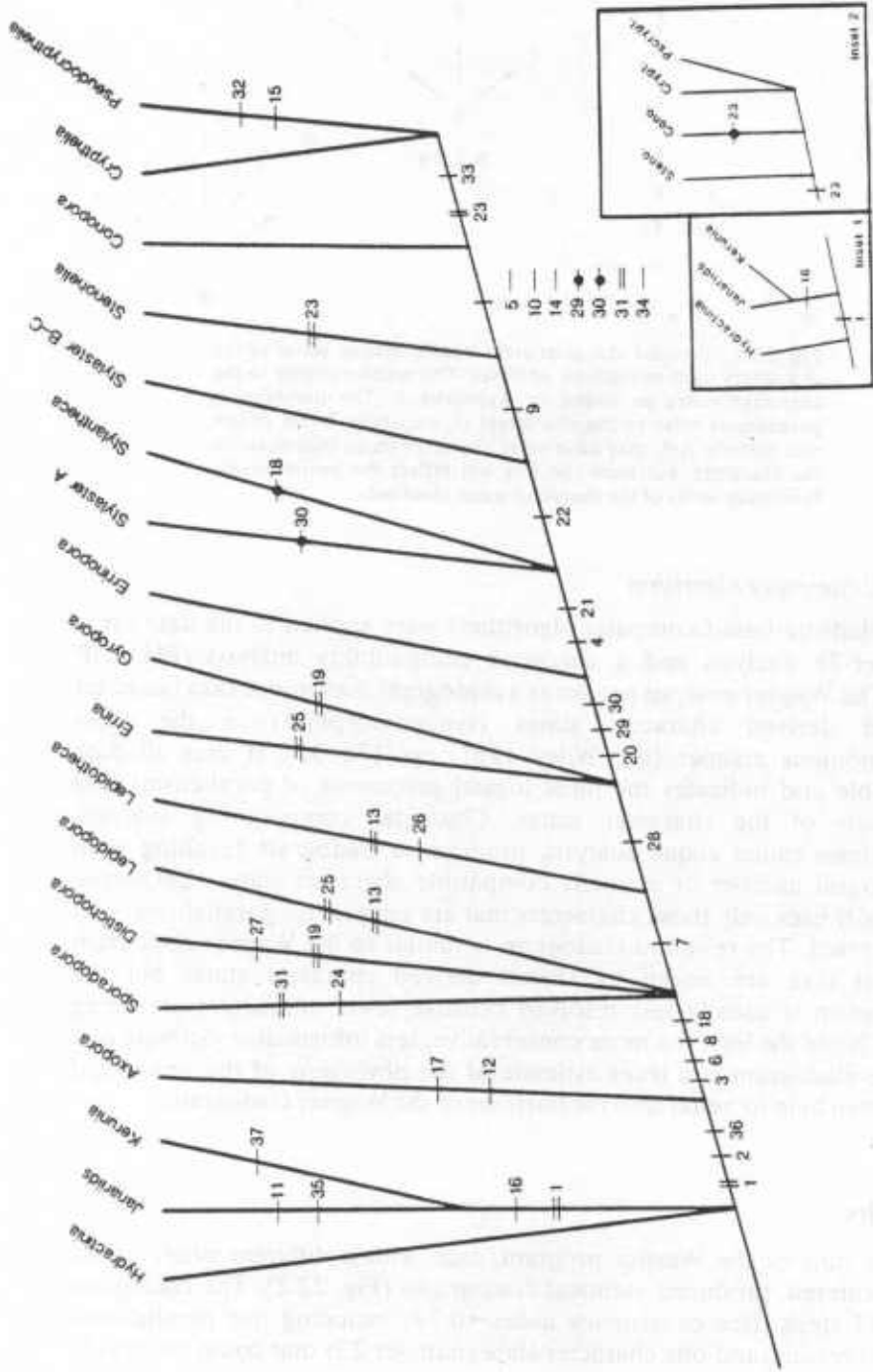


Fig. 23.2. Cladogram supported by Wagner analysis and clique 1 of character compatibility analysis. Numbers represent a change to the apomorphic state (1) of respective computer-coded characters (Appendix 1). Double lines indicate a parsimonious topology of the tree, but one that was deliberately ignored (see text). Inset 1 shows an alternative, equally parsimonious interpretation of character state 23.

parsimoniously interpreted as a parallelism or as a reversal (Fig. 23.2, inset 2). The stem supporting the janariids and *Kerunia* was deliberately changed to originate in a polychotomy with *Hydractinia* instead of coming from the basal line (Fig. 23.2, inset 1), which requires a parallelism for calcification of the colony, as previously discussed in step 2 of the methods.

Character compatibility analysis produced four equally large cliques, all with 28 compatible character states:

Clique 1: 2-12, 14-17, 20-22, 24, 26-28, 32-37.

Clique 2: 2-6, 8-17, 19-22, 24, 26-27, 32-37.

Clique 3: 2-6, 8-17, 20-22, 24, 26-28, 32-37.

Clique 4: 2-6, 8-12, 14-17, 19-22, 24-27, 32-37.

Therefore, each clique had nine incompatible character states, six of which were consistent for all four cliques (1, 18, 23, 28, 30, 31). Cliques 2 and 4 produced cladograms that were one step longer than cliques 1 and 3 (48 vs. 47 steps) and were therefore not considered. In addition to the six consistently incompatible character states, clique 1 was incompatible for character states 13, 19, and 25; clique 3 for character states 7, 19, and 25. Therefore, the only difference between the two most parsimonious cliques concerns character states 7 and 13, both of which affect the branching sequence of *Lepidopora* and *Lepidotheca*. This critical part of the cladogram is illustrated for both cliques in Fig. 23.3. There are two interpretations for each clique, depending on whether the incompatible character state is interpreted as a parallelism or as a reversal. All four topologies are equally probable according to the algorithm and, in fact, Fig. 23.3(A) is the same interpretation produced by the Wagner analysis. I chose the topology of Fig. 23.3(A) for the final cladogram for the following reasons. Between character state 7 (short dactylopore tube) and 13 (unridged gastrostyle) I feel that the characteristic of the dactylopore tube length is both easier to determine and more conservative in its evolution than the structure of the gastrostyle, which is sometimes equivocal or variable within a genus. This favours including character state 7 in the clique at the exclusion of character state 13. Between topologies represented by Fig. 23.3(A) and (B), I favour (A) because it seems more likely that the change from ridged to unridged gastrostyle spines (character state 13) occurred twice on two terminal taxa (i.e. *Lepidopora* and *Lepidotheca*) rather than a change occurring on the main line of evolution from ridged to unridged and then back to the ridged condition. Therefore, the final cladogram produced by clique analysis is the same as that produced by Wagner analysis. The advantage of using this technique (clique analysis) was that it provided several more equally parsimonious solutions for consideration that may or may not have been generated by the Wagner program.

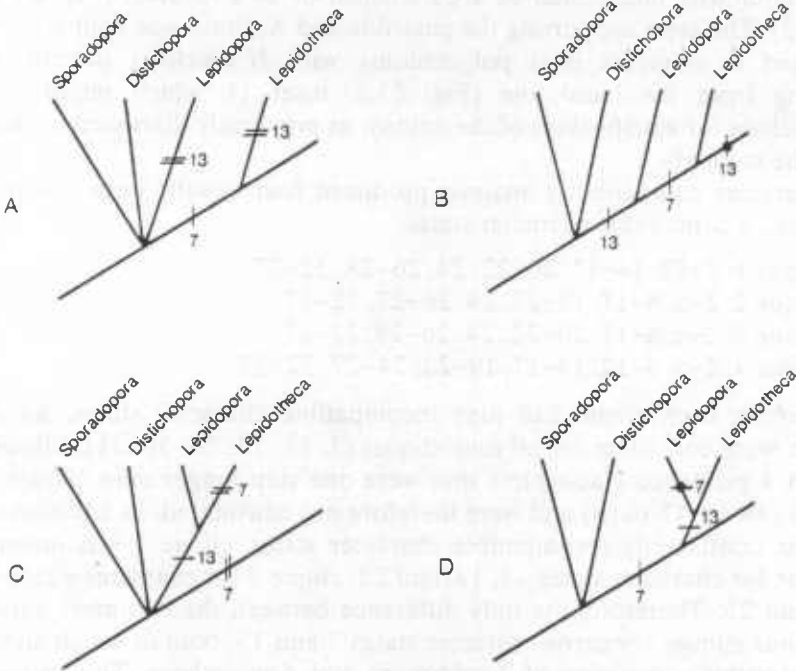


Fig. 23.3. Equally parsimonious tree topologies resulting from cliques 1 (A and B) and 3 (C and D), showing the options available for the interpretation of computer-coded character state 7 (short dactylopore tube) and 13 (unridged gastrostyle). Double lines indicate parallelisms; circles indicate reversals. Both cliques present two alternatives, depending on whether a reversal or a parallelism is hypothesized for the critical character.

Discussion

Evolutionary trends

Many of the significant character-state changes occurring in the Stylasteridae pertain to the structure and orientation of the dactylopore/dactylopore spine. A natural progression can be traced from simple, randomly-placed dactylopores to U-shaped spines united in a circle around a gastropore: the cyclosystem. Because the dactylozooid is the primary defensive and food-gathering structure, changes in its morphology are hypothesized to have increased the coral's ability to protect itself and improve its feeding efficiency.

The first significant change in stylasterid evolution was the calcification of the skeleton (Fig. 24.4, stems 1 and 2), hypothesized on the cladogram to have occurred twice and several other times within the

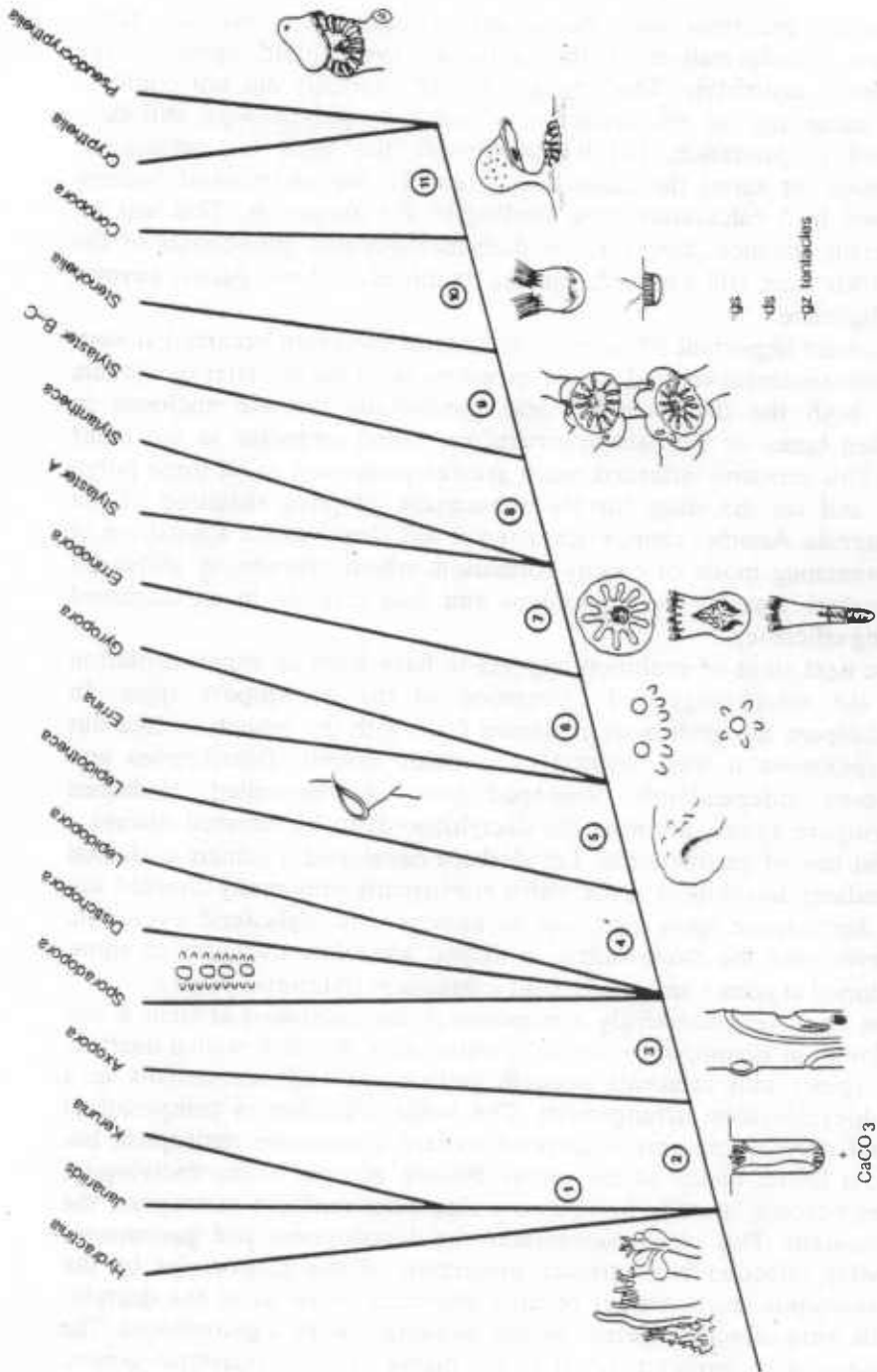


Fig. 23.4. Illustrated cladogram showing major trends in stylasterid evolution. Encircled numbers designate arbitrarily numbered stems. Abbreviations: 'gs, -ds, and -gz tentacles' represent the loss of gastrozooids, dactylostyles, and gastrozooid tentacles, respectively; CaCO₃ represents the acquisition of a calcified skeleton.

Cnidaria. Concurrent with the advent of calcification was the hypothesized transformation of the chitinous hydractiniid spine to the calcareous gastrostyle. This change in itself probably did not confer a great advantage on the hydractiniids, since its polyps were still fully exposed to predation, but it did provide the basis for subsequent evolution. At about the same time (stem 2), the gastrozoid became enclosed in a calcareous tube, leading to the axoporids. This was an important advance; however, the dactylozooids and gonozooids of the axoporids were still exposed, and the axoporids did not persist beyond the Oligocene.

The most important advances in stylasterid evolution occurred at stem 3, which separates the stylasterid ancestors from the stylasterids. At this point both the dactylozooids and gonozooids became enclosed in calcified tubes or specialized structures, called ampullae in the latter case. This probably afforded much greater protection to all three polyp types and set the stage for the subsequent adaptive radiation of the stylasterids. Another change occurring at this stem was the acquisition of the branching mode of colony formation, which presumably increased the surface area for feeding polyps and thus resulted in an increased feeding efficiency.

The next stage of evolution appears to have been an experimentation with the morphology and orientation of the dactylopore spine. In *Sporadopora* the gastropore remained flush with the branch surface but in *Lepidopora* it was elevated on a small mound. *Distichopora* and *Gyropora* independently developed rows of thin-walled, U-shaped dactylopore spines, allowing the dactylozooids to be directed toward a central row of gastrozooids. *Lepidotheca* developed a similar U-shaped (abcauline) dactylopore spine with a consistently proximally directed slit. The dactylopore spine that was to persevere in stylasterid evolution, however, was the thick-walled, U-shaped adcauline dactylopore spine, developed at stem 5 and found in all subsequent stylasterid genera.

The next step—seemingly a transitional one portrayed at stem 6 and still found in *Errinopora*—was an orientation of the thick-walled dactylopore spines into crescents beneath gastropores and occasionally in a pseudocyclosystem arrangement. The latter condition is composed of several dactylopore spines directed toward a common gastropore but without lateral fusion of the spines. Finally, at stem 7, the dactylopore spines become laterally fused into a ring surrounding a gastropore: the cyclosystem. This close coordination of dactylopores and gastropores probably afforded both greater protection of the gastrozoid by the dactylozooids and a greater feeding efficiency, since all of the dactylozooids were directly adjacent to and pointing toward a gastrozoid. The cyclosystem is characteristic of all the highly derived stylasterid genera. Also at this stage there is a tendency toward a constriction of the

gastropore tube about half-way down its length, either by a simple narrowing of the tube or by a ring palisade. This may have provided a slight barrier to predators, below which the gastrozoid could retract.

At stage 9 there is a further advance in the centralization of the polyps, with the gonozooids (ampullae) tending to concentrate near cyclo-systems.

Stem 10 represents a complex of changes that clearly separates the last three genera from the other stylasterids. The trend (of gastropore constriction) begun at stem 7 is now continued to produce a double-chambered gastropore tube with a narrow gastropore ring constriction separating the two chambers. The gastrostyles and dactylostyles are lost and the gastrozoid, which has now lost its tentacles, sits in the lower gastropore chamber. Also, nematophores containing batteries of large nematocysts are scattered over the coenosteum, and female efferent pores open into the relative safety of the cyclo-system instead of on the less-protected branch surface. Perhaps the protection previously afforded by the gastrostyle and dactylostyle and gastrozoid tentacles is no longer needed because of the strategically placed dactylozoids and the added presence of nematophores.

At step 11 the defensive structure of a fixed gastropore lid is introduced. The lid is usually heavily invested with nematophores and often contains the ampullae, either male or female. Also, the number of dactylozoids per cyclo-system is markedly increased.

Finally, the terminal taxon, *Pseudocrypthelia*, completes the centralization of structures by having strategically arranged nematophores, one on the outer edge of each pseudoseptum.

To recapitulate, the stylasterids have progressively and gradually evolved from an ancestral state of an uncalcified colony with randomly arranged, naked polyps (i.e. *Hydractinia*) to a highly structured, well-coordinated 'functional unit': the lidded cyclo-system, with contiguous ampullae and systematically arranged nematophores, epitomized by *Pseudocrypthelia*. Concomitant with this increase in organization is a hypothesized increase in feeding efficiency and a greater ability to protect the gastrozoids and gonozooids.

Evolutionary scenario

The calcified hydractiniids (referred to as the 'janariids' and *Kerunia*) are known from the Cretaceous to the Recent but are not considered to be on the main line of evolution leading to the stylasterids, as previously discussed. Instead, *Axopora* (Eocene to Oligocene) or an axopod-like ancestor is considered to have led to the stylasterids (Cairns 1983b). However, the earliest known stylasterids occur before the earliest known axopods: the Palaeocene (Danian of Denmark) and Eocene, respectively. This contradiction may have been resolved by the discovery of an older

axopoid, *Subaxopora*, from the Late Jurassic of Xizang Plateau, China (Deng 1982). Specimens of *Subaxopora* have not been examined by the author.

The fossil record of stylasterids is poor: most of the fossil species are known from the Palaeocene of Denmark (Nielsen 1919), the Eocene of Tonga (Wells 1977), and scattered localities from the Oligocene to the Pleiocene of Europe and Australia. The earliest stylasterids are from the Palaeocene, and one of the most advanced genera, *Crypthelia*, is known from the Eocene. It is therefore suggested that the stylasterids evolved from axopoid-like ancestors in the early Palaeocene—just after the great Cretaceous faunal extinction—and evolved most of their generic ground plans rapidly in the Palaeocene, perhaps taking advantage of the niches available following the faunal extinction.

The Danian stylasterids are found together with moderate-depth ahermatypic Scleractinia (50–80+ m, according to Floris 1972), suggesting that the lower-shelf to upper-slope habitat may have been the depth of origin of the stylasterids. Among the 195 Recent species, only about a dozen occur in shallow water (0–40 m); the remaining 94 per cent occur in the lower-shelf and upper-slope environments, especially between 200–700 m depth.

Conclusion

Based on a phylogenetic analysis of the genera of the Stylasteridae, it is hypothesized that the stylasterids evolved from an axopoid-like ancestor in the early Palaeocene, just after the great Cretaceous faunal extinction. A major trend in the evolution of the stylasterids was the structural modification and orientation of the dactylopore spine. Another important trend was the progressive co-ordination of all three polyp types and nematophores from a randomly arranged configuration to a well co-ordinated functional unit, i.e. the cyclo-system, with contiguous ampullae having internal female efferent pores and strategically placed nematophores. A third major trend, occurring in only the most derived genera, was the development of a double-chambered, lidded gastropore tube, with a concomitant loss of gastrostyles and dactylostyles and gastrozoid tentacles. All three trends—especially the first two concerning the dactylopore spines—are hypothesized to have increased the feeding efficiency of the colony and to have improved the hydrocoral's ability to protect its gastrozooids and gonozooids.

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Appendix 1. Coded tabular key to stylasterid genera

Genera	Characters													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Hydractinia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Janariids ¹	1	0	0	0 ⁵	1	0	1 ¹⁰	0	0	0	0	0	0 ¹⁹	1
<i>Kerunia</i>	1 ⁴	0	0	0 ⁵	0	0	1	0	0	0	0 ¹⁸	0	0 ¹⁹	3
<i>Axopora</i>	1	1	0	0 ⁵	0	1	2 ¹¹	0	0	0	0	0	0	2
<i>Sporadopora</i>	1	2	1	1	0	0	3	0	1	0	2	0	0	2
<i>Distichopora</i>	1	2	1	1	0	0	3	1 ¹²	4	0	0	0	0	2
<i>Lepidopora</i>	1	2	1	1	0	2	3	0 ¹³	2	0	0	0	0	2
<i>Lepidotheca</i>	1	2	2	1	0	2 ⁹	3	0	3	0 ¹⁷	0	0	0	2
<i>Errina</i>	1	2	2	1	0	0	3	0	2/5 ¹⁶	0	0	0	0	2
<i>Gyropora</i>	1	2	2	1	0	0	3	1	5	0	0	0	0	2
<i>Errinopora</i>	1	2	2	1	0	0	3	2	5	1	1	0	0	2
<i>Stylaster A</i> ²	1	3	2	1 ⁶	0	0	3	3	5	1	0	0	0	2
<i>Syrantheca</i>	1	3	2	1	0	0	0	3	5	1	1	0	0	2
<i>Stylaster B+C</i> ³	1	3	2	1	0	0	3	4	5	1	1	0	0	2
<i>Sienohelia</i>	1	3	2	2 ⁷	0	0	3	5	5	1	1	0	0	2
<i>Conopora</i>	1	4	2	3	0	3	3	4 ¹⁴	5	0	2 ²¹	0	1	2
<i>Crypthelia</i>	1	4	2	3	0	3	3	5 ¹⁵	5	0	2 ²¹	1	1	2
<i>Pseudocrypthelia</i>	1	4	2	3 ⁸	0	4	3	5	5	0	3	1	1 ²⁰	2

¹ Janariids = *Janaria*, *Polyhydra*, *Hydrocorella*, calcified *Hydractinia*, and ? *Cyclactinia*.

² *Stylaster A* sens. Cairns, 1983a, includes about 21 species. Previously known as *Allopora*.

³ *Stylaster B+C* sens. Cairns (1983a) includes about 43 species. Previously known as *Stylaster* sens. strict.

⁴ *Kerunia* is generally assumed to be calcified (Nopcsa 1905; Thomas 1937), but Stechow (1962, p. 427) suggested that it might have been chitinous.

⁵ Gonophores of Recent janariids are stalked as in *Hydractinia*. Gonophores of fossil janariids, *Kerunia*, and *Axopora*, are presumed to have been stalked also.

⁶ According to Ostarello (1973, p. 553), *S. californicus* has efferent pores opening into cyclostyles.

⁷ One species, *S. profunda*, has its ampullae clustered around the cyclostylem (see Cairns 1984a, p. 53).

⁸ Female colonies not known.

⁹ *Lepidotheca cervicornis* has slightly ridged gastrostyles.

¹⁰ Some janariids (e.g. *Polyhydra* and *Hydractinia pliocena*) are exclusively encrusting, without radial branches.

¹¹ Two species, *A. arborea* and *A. cleithridium*, are branching.

¹² One species, *D. providentiae*, has very rudimentary pore rows.

¹³ Four species of *Lepidopora* (*Lepidopora* 4 and 5 sens. Cairns 1984a) have linearly arranged dactylopores and/or gastrospores.

¹⁴ Two species (*Conopora* Group B sens. Cairns 1983a) have randomly arranged cyclostyles.

¹⁵ One species, *C. trophostega*, has bifacial cyclostyles.

¹⁶ Two character states are expressed simultaneously in all species of *Errina*.

¹⁷ *Lepidotheca tenuisyla* has an aberrant dactylostyle.

¹⁸ *Kerunia* is presumed not to have had specialized nematocyst structures.

¹⁹ *Kerunia* and the janariids are presumed to have had gastrozoid tentacles, as have most other hydroids.

²⁰ *Pseudocrypthelia* is presumed not to have gastrozoid tentacles; however, no preserved specimens were available for study.

²¹ Some species of *Crypthelia* have co-ordinated nematophores, but this character state is not exclusive to the genus.

Key to character states, and computer code to those states (number above line represents data in column in Appendix 2)

	Computer code			
<i>Character 1: calcification of skeleton</i>	<u>1</u>			
0 Not calcified	0			
1 Calcified	1			
<i>Character 2: shape of gastropore chamber</i>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>
0 Absent or a shallow pit	0	0	0	0
1 Cylindrical, narrow	1	0	0	0
2 Cylindrical, capacious	1	1	0	0
3 Cylindrical, capacious, constricted	1	1	1	0
4 Double chambered	1	1	1	1
<i>Character 3: length of dactylo pore tube</i>	<u>6</u>	<u>7</u>		
0 Absent	0	0		
1 Long, extending down branch axis in clusters	1	0		
2 Short, terminating within 2-3 mm	1	1		
<i>Character 4: position of gonophores (ampullae)</i>	<u>8</u>	<u>9</u>	<u>10</u>	
0 Stalked, random	0	0	0	
1 Ampullate, random, efferent pores apical	1	0	0	
2 Ampullate, near cyclo system, efferent pores apical	1	1	0	
3 Ampullate, near cyclo system, efferent pores open within cyclo systems	1	1	1	
<i>Character 5: presence of vesicles</i>	<u>11</u>			
0 Absent	0			
1 Present	1			
<i>Character 6: gastrostyle morphology</i>	<u>12</u>	<u>13</u>	<u>14</u>	<u>15</u>
0 Present, ridged	0	0	0	0
1 Present, aligned spines	1	0	0	0
2 Present, not ridged, spines random	0	1	0	0
3 Absent	0	0	1	0
4 Rudimentary (Cairns 1983c)	0	0	1	1
<i>Character 7: shape of colony</i>	<u>16</u>	<u>17</u>	<u>18</u>	
0 Encrusting	0	0	0	
1 Encrusting plus radial branches	1	0	0	
2 Lobate or massive	0	1	0	
3 Exclusively branching	0	0	1	

<i>Character 8: co-ordination of gastropores and dactylopores</i>	<u>19</u>	<u>20</u>	<u>21</u>	<u>22</u>	<u>23</u>
0 None	0	0	0	0	0
1 Linearly arranged	1	0	0	0	0
2 Dactylopores in crescents and pseudocyclosystems	0	1	0	0	0
3 Randomly arranged cyclosystems	0	1	1	0	0
4 Sympodially arranged cyclosystems	0	1	1	1	0
5 Unifacially arranged cyclosystems	0	1	1	1	1
<i>Character 9: shape of dactylopore spine</i>	<u>24</u>	<u>25</u>	<u>26</u>	<u>27</u>	<u>28</u>
0 Dactylopores absent	0	0	0	0	0
1 Flush with coenosteum	1	0	0	0	0
2 Conical (mound)	0	1	0	0	0
3 Abcauline	0	0	1	0	0
4 Elliptical	0	0	0	1	0
5 Adcauline	0	0	0	0	1
<i>Character 10: dactylostyle</i>	<u>29</u>				
0 Absent	0				
1 Present	1				
<i>Character 11: specialized nematocyst structures</i>	<u>30</u>	<u>31</u>	<u>32</u>		
0 Absent	0	0	0		
1 Papillae	1	0	0		
2 Randomly arranged nematophores	0	1	0		
3 Exclusively co-ordinated nematophores	0	1	1		
<i>Character 12: gastropore lid</i>	<u>33</u>				
0 Absent	0				
1 Present	1				
<i>Character 13: gastrozoid tentacles</i>	<u>34</u>				
0 Present	0				
1 Absent	1				
<i>Character 14: coenosteal texture</i>	<u>35</u>	<u>36</u>	<u>37</u>		
0 Absent (not calcified)	0	0	0		
1 Ornate granules	1	0	0		
2 'Stylasterid' (e.g. reticulate-granular, linear- imbricate)	0	1	0		
3 Unknown	0	0	1		

Appendix 2. Data matrix

Genera	Characters* (data column)†																																								
	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				
<i>Hydractinia</i>																																									
<i>Janariids</i>																																									
<i>Kerentia</i>																																									
<i>Axopora</i>																																									
<i>Sporadopora</i>																																									
<i>Distichopora</i>																																									
<i>Lepidopora</i>																																									
<i>Lepidatheca</i>																																									
<i>Erina</i>																																									
<i>Gyropora</i>																																									
<i>Erriopora</i>																																									
<i>Stylaster A</i>																																									
<i>Stylantheca</i>																																									
<i>Stylaster B+C</i>																																									
<i>Stenohelia</i>																																									
<i>Conopora</i>																																									
<i>Crypthelia</i>																																									
<i>Psylodocrypthelia</i>																																									

Blank spaces indicate the plesiomorphic state.

*Top row.

†Bottom row.

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