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A GENERIC REVISION OF THE STYLASTERIDAE (COELENTERATA: HYDROZOA). PART 3. KEYS TO THE GENERA

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ABSTRACT

Dichotomous and tabular keys to the 23 genera, 2 subgenera, and 5 species groups of the Stylasteridae are presented. The keys stress easily recognized external skeletal characters, most of which can be seen using a dissecting microscope, such as: coordination of dactylopores and gastropores, presence or absence of gastro- and dactylostyles, cyclosystem orientation, dactylopore spine shape, ampullar position, gastropore tube shape, dactylopore tube length, and coenosteal texture. Each of these characters is briefly discussed in the context of its discriminating power and its phylogenetic value. Two new terms are introduced to characterize dactylopore tubes: axial and peripheral. Numbers of valid species for each genus and their geographic and bathymetric ranges are listed. Two hundred twenty-four stylasterid species are considered to be valid, including 24 exclusively fossil species. Stylasterids are cosmopolitan, but insular, in distribution, ranging from 0–2,789 m.

This is the third of an originally conceived two part series, the first part being the description of the stylasterid genera (Cairns, 1983b), the second part a phylogenetic analysis of those genera (Cairns, 1984). However, faced with the need to identify a large collection of stylasterids following a 2-year hiatus from their study, I found it useful to construct and herein publish both dichotomous and tabular keys to the genera of the family. Such a tabular key could have been extracted from the coded data matrix published in part 2 (Cairns, 1984: 52–53, appendix 2); however, those data were not presented in a fashion that allowed easy interpretation or ready use as a key.

The aim of these keys is to provide an efficient and accurate method to identify and compare stylasterid genera using the most easily recognized characters. The characters used are therefore not necessarily the most important phylogenetically (Cairns, 1984; 1987), but those that group or distinguish genera or groups of genera based on obvious, easily recognized characters. The keys are therefore artificial keys, but reflect in their organization many of the phylogenetic divisions suggested by Cairns (1984; 1987). The order of the genera in both keys is therefore roughly phylogenetic, in descending order of degree of derivation.

Discussion of Characters Used in the Tabular Key

The order of the characters used in the tabular key was determined both by their ability to discriminate taxa and their ease in recognition: the more conservative and easily recognized characters are listed from left to right. Characters 1–5 and 10 are all based on external skeletal characters; characters 6–8 require observations of a cross or longitudinal section of a branch; and character 9 is best viewed with the aid of scanning electron microscopy. Each character will be briefly discussed; illustrations and definitions of all structures can be found in Cairns (1983a; 1983b; 1986a; 1986b; Table 1).

The increase in coordination of gastropores and dactylopores is considered to be a major evolutionary trend within the Stylasteridae (Cairns, 1987): a lack of coordination is considered to be the least derived state and the cyclosystem arrangement the most derived. The arrangement of dactylopores and gastropores

in pore rows (a row of gastropores closely flanked by two rows of dactylopores) probably occurred twice in stylasterid evolution (Cairns, 1984), once leading to *Distichopora,* and again leading to *Gyropora,* but neither falling on the main line of evolution leading to the more advanced cyclosystemate genera. In *Gyropora* the pore rows meander over the branch surface, whereas in *Distichopora* the pore row is usually restricted to branch edges. However, in one species (i.e., *D. irregularis*) the pore row meanders, and in several species (e.g., *D. anomala*) only one dactylopore row is developed. Pore rows are often discontinuous. Among those genera in which there is no coordination between pore types, there may still be a linear arrangement of gastropores and dactylopores. For instance, both gastro- and dactylopores are aligned in *Phalangopora,* and the dactylopores are aligned in several species of *Lepidopora,* but in both cases, there is no coordination between the different pore types.

The presence or absence of a gastrostyle is an easily observed character that is consistent at the generic level and is very useful in distinguishing both cyclosystemate and noncyclosystemate groups of genera. Characteristics of the gastrostyle length (height : width ratio) and shape (e.g., ridged or not) add more useful information to the key. The ancestral stylasterid was assumed to have had a gastrostyle and it was hypothesized to have been lost on two occasions (Cairns, 1984): once leading to the lesser derived group of genera *Phalangopora, Pliobothrus,* and *Adelopora,* and a second time, in concert with several other changes, leading to the most derived double-chambered gastropore group of cyclosystemate genera: *Crypthelia, Astya,* and *Conopora. Pseudocrypthelia,* despite its rudimentary gastrostyle, is most similar to the latter nongastrostyle cyclosystemate group; the style in this case representing a partial reacquisition of the structure.

The presence or absence of a dactylostyle, although much smaller than the gastrostyle, is still easily seen at high magnification (×50) with a dissecting microscope, and helps to distinguish certain noncyclosystemate genera. The ancestral stylasterid is presumed to have lacked dactylostyles and they are hypothesized to have evolved at least three times: once in the evolutionary stem leading to *Inferiolabiata* and *Lepidotheca,* once in *Paraerrina,* and once in the evolutionary stem leading to *Errinopora* and the cyclosystemate genera (Cairns, 1984). It is further hypothesized that dactylostyles were lost, along with the gastrostyle and gastrozooid tentacles, on the stem leading to the cyclosystemate genera having a double-chambered gastropore tube.

The orientation of cyclosystems on a branch may be random, sympodial, or unifacial, which is assumed to be the general evolutionary sequence in the family (Cairns, 1987). The sympodial arrangement, characteristic of many species of *Stylaster,* consists of cyclosystems alternately arranged on opposite (lateral) branch edges. Many species, especially those with polychaete symbionts, have an anterolateral sympodial arrangement of cyclosystems, which appears to be a transitional step to the unifacial arrangement.

The shape of the dactylopore spines of the noncyclosystemate genera is of great diagnostic value. Dactylopore spines may be absent (flush), conical, or U-shaped (in cross section). In U-shaped spines, if the opening (slit) of the U is directed toward the distal branch tip, it is termed abcauline; if it opens toward the proximal end of the branch, adcauline. Abcauline spines are usually thin walled; adcauline, thick walled. The thick walled adcauline spines, characteristic of *Errina* and *Errinopora,* seem to have been the precursor of the dactylopore spines of the cyclosystemate genera (Cairns, 1987). Some genera are dimorphic regarding dactylopore spines, their species simultaneously having two types of spines.

All stylasterid species thus far examined, with the single exception of *Stylaster*

Table 1. Tabular key to the genera, subgenera, and species groups of the Stylasteridae

	Coordination (and position) of gastro- and dactylopores	Gastrostyle	Dactylostyle	Cyclosystem orientation	Dactylopore shape and orientation	Prominence of ampullae
Pseudocrypthelia	Cyclosystem	Present[7]	Absent	Unifacial		Superficial[8]
Crypthelia	Cyclosystem	Absent	Absent	Unifacial[9]		Superficial
Astya	Cyclosystem	Absent	Absent	Unifacial		Superficial
Conopora A[3]	Cyclosystem	Absent	Absent	Sympodial		Superficial
Conopora B[3]	Cyclosystem	Absent	Absent	Random		Superficial
Stenohelia	Cyclosystem	Present	Present	Unifacial		Superficial
Stylantheca	Cyclosystem	Present[11]	Present[12]	Random		Internal
Stylaster A[4]	Cyclosystem	Present	Present[12]	Random		Superficial
Stylaster B[5]	Cyclosystem	Present	Present	Sympodial[13]		Superficial
Stylaster C[6]	Cyclosystem	Present	Present[14]	Sympodial		Superficial
Calyptopora	Cyclosystem	Present	Present[12]	Unifacial		Superficial
Errinopora	Variable[15]	Present	Present[12]		Variable[15,16]	Superficial
Inferiolabiata	None	Present[17]	Present[14]		Abcauline	Superficial
Paraerrina	None	Present[17]	Present		Dimorphic: flush, abcauline	Superficial
Gyropora	Pore rows[18]	Present[17]	Absent		"Gyroporine"[18,19]	Superficial
Distichopora (*Distichopora*)	Pore rows[20]	Present[21]	Absent		"Distichoporine"[22]	Superficial[23]
Distichopora (*Haplomerismos*)	Pore rows	Present[21]	Absent		"Distichoporine"[22]	Internal
Cheiloporidion	None[25]	Present	Absent		Conical, formed of platelets	Superficial
Errinopsis	None	Present	Absent		Dimorphic: conical, adcauline	Superficial
Stellapora	None	Present	Absent		Dimorphic: conical, abcauline	Superficial
Sporadopora	None	Present[21]	Absent		Round, flush	Internal

Table 1. Continued

Shape of gastropore tube	Dactylopore tube length	Coenosteal texture[1]	Other diagnostic characters	Number of valid species (Fossil + Recent): geographic and bathymetric range of Recent species[2]
Double-chambered	Peripheral	L-I	Gastropores partially covered by fixed lids	1: Indonesia.—1,089 m
Double-chambered	Peripheral	L-I	Gastropores partially covered by fixed lids	26: Cosmopolitan.—140–2,789 m
Double-chambered	Peripheral	L-I	Prong projects into gastropore ring constriction	2: Philippines.—914 m
Double-chambered	Peripheral	L-I		4: Indo-West Pacific, Subantarctic, Antarctic.—110–2,355 m
Double-chambered	Peripheral	R-G		2: Providence Island, Indian Ocean.—228 m
Cylindrical, ring palisade[10]	Peripheral	L-I		11: W. Pacific, Antipodes, Galápagos, N. Atlantic.—91–2,021 m
Cylindrical, ring palisade	Peripheral	R-G and papillose	Corallum encrusting, purple or pink	3: Northeast Pacific.—0–18 m
Cylindrical, ring palisade	Peripheral	R-G		24: Central and N. Pacific, Atlantic, Subantarctic.—5–1,400 m
Cylindrical, ring palisade	Peripheral	R-G, L-I, R-I		19: Pacific, Atlantic, Antarctic.—0.5–1,440 m
Cylindrical, ring palisade	Peripheral	R-G, L-I, R-I		37: Cosmopolitan.—1–1,244 m
Cylindrical, ring palisade	Peripheral	R-G	Gastropores with rudimentary fixed lids	1: New Zealand Region.—349–2,010 m
Cylindrical	Peripheral	R-G		1: Mauritius, Indian Ocean.—238–274 m
Cylindrical, ring palisade	Peripheral	R-I		2: Subantarctic and Antarctic.—87–2,100 m
Cylindrical	Peripheral	R-G		1: Mauritius, Indian Ocean.—238–274 m
Cylindrical	Peripheral	R-G	Red-purple coenosteum	1: South Africa.—22 m
Cylindrical, ring palisade[24]	Axial	R-G		21: Indo-West Pacific, Galápagos, W. Atlantic.—1–717 m
Cylindrical, ring palisade[24]	Axial	Granular	Corallum bilobate	1: Laysan, Hawaiian Islands.—658–736 m
Cylindrical	Peripheral	R-Smooth	Corallum loosely fenestrate	1: Off Southeast S. America.—642–1,137 m
Cylindrical	Peripheral	R-G, L-I	Corallum regularly fenestrate	2: Off Southern S. America.—250–771 m
Cylindrical[24]	Peripheral	R-G	Gastropores stellate	1: Off Southeast S. America.—205–1,647 m
Cylindrical[24]	Axial	R-Porous	Branches robust, blunt tipped	4: New Zealand, Subantarctic.—122–1,498 m

Table 1. Continued

	Coordination (and position) of gastro- and dactylopores	Gastrostyle	Dactylostyle	Cyclosystem orientation	Dactylopore shape and orientation	Prominence of ampullae
Lepidopora	None, but dactylopores aligned	Present[17]	Absent		Conical	Superficial[23]
Errina	None	Present	Absent		Dimorphic: adcauline, flush	Superficial[23]
Lepidotheca	None	Present	Absent[27]		Abcauline	Superficial
Phalangopora	None[28]	Absent	Absent		Abcauline	Superficial[29]
Pliobothrus	None	Absent	Absent		Conical	Internal
Adelopora	None[30]	Absent	Absent		Conical	Superficial

Footnotes:
[1] R-G = Reticulate-Granular; L-I = Linear-Imbricate; R-I = Reticulate-Imbricate; L-G = Linear-Granular.
[2] Three species listed *Incertae Sedis* by Cairns (1983b) not tabulated in the Table.
[3] Species Group sensu Cairns (1983b).
[4] Species Group sensu Cairns (1983b), previously known as *Allopora*.
[5] Species Group sensu Cairns (1983b), *Stylaster* s.s. (annectant group).
[6] Species Group sensu Cairns (1983b).
[7] Gastrostyle rudimentary.
[8] Female ampullae unknown.
[9] One species, *C. trophostega*, bifacial.
[10] Gastropore tubes usually curved sharply 90°, such that gastrostyle tip not seen from outside.
[11] One to 12 gastrostyles per cyclosystem.
[12] Dactylostyles very robust.
[13] Cyclosystems primarily sympodially arranged, but with additional cyclosystems on anterior and posterior faces.
[14] Lateral dactylostyles (Cairns, 1986a) sometimes present.
[15] Coordination variable among species; some species with no coordination; some with gastropores in vertical or horizontal rows flanked by rows of dactylopores; some with pseudocyclosystem.

roseus, have separate sexes. Female colonies are inferred by the presence of large (e.g., 1 mm in diameter) hemispherical ampullae, that, when ripe, release a planula through a single lateral efferent pore about 0.15–0.20 mm in diameter. Males are inferred by the presence of smaller (60–70% size of female) ampullae with much smaller (e.g., 10–20 μm in diameter), often multiple, apical efferent pores. Since the ampullae of most genera are superficial, this character is of limited value in the key, but several of the lesser derived noncyclosystemate genera and *Stylantheca* have internal ampullae, which communicate their gametes or planulae to the branch surface via efferent tubes.

Another trend noted (Cairns, 1987) in stylasterid evolution is the tendency for the gastropore tube to be constricted about halfway down its length. This is achieved by a simple narrowing of the gastropore tube, the construction of a ring palisade (Cairns, 1984), or a gastropore ring constriction (Cairns, 1986b). The gastropore ring constriction, characteristic of the most derived cyclosystemate genera, produces a double-chambered gastropore tube. Characteristics of gastropore tube shape can only be seen in a branch cross section.

Dactylopore tubes, which can only be seen in cross or longitudinal sections, may be either long: extending for millimeters parallel to the branch axis, or short: 1–2 mm long and roughly perpendicular to the branch axis. The short dactylopore tubes, characteristic of most stylasterid genera, are herein termed *peripheral*; the longer dactylopore tubes are termed *axial*, and appear to be characteristic of the lesser derived noncyclosystemate genera (Cairns, 1987).

Table 1. Continued

Shape of gastropore tube	Dactylopore tube length	Coenosteal texture[1]	Other diagnostic characters	Number of valid species (Fossil + Recent): geographic and bathymetric range of Recent species[2]
Cylindrical, ring palisade[23]	Axial	L-I, R-G, L-G		12: S. Pacific, S. Africa, Atlantic (including Scotia Ridge).—60–1,874 m
Cylindrical, ring palisade	Peripheral	R-G[26]		18: New Zealand, Galápagos, N. Atlantic, Antarctic.—6–1,772 m
Cylindrical, ring palisade	Peripheral	L-I		10: Indo-West Pacific, Galápagos, Caribbean, Subantarctic.—85–2,010 m
Cylindrical, ring palisade	Peripheral	L-I		1: Off Mauritius.—238–274 m
Globular	Axial	L-I	Large coenosteal pores common	6: N. Atlantic, Indonesia.—80–1,600 m
Cylindrical	Axial	L-I	Gastropores covered by hinged opercula	1: Subantarctic seamounts.—298–915 m

[16] Dactylopore spine U-shaped, like those of *Errina*, but with variable orientation on branch.
[17] Gastrostyle with low height : width ratio (i.e., less than 10).
[18] Gastro- and dactylopores arranged in meandering pore rows and pseudocyclosystems.
[19] Dactylopore spines U-shaped, like those of *Errina*, but laterally fused, their dactylotomes (slits) directed toward gastropore row; pseudocyclosystems sometimes present.
[20] See text for exceptions to this arrangement.
[21] Gastrostyles with high height : width ratio (i.e., over 10) and ridged.
[22] Greater axis of elliptical to oval dactylopores oriented perpendicular to gastropore row.
[23] Most species have superficial ampullae; but several species with internal ampullae (see Cairns, 1983b).
[24] Gastropore tubes long (axial).
[25] No coordination between pore types, but gastropores concentrated on branch edges.
[26] Three of the 18 species have L-I coenosteal texture.
[27] *Lepidotheca tenuistylus* has an aberrant dactylostyle.
[28] No coordination between pore types, but gastropores aligned on branch faces, dactylopores aligned on branch edges.
[29] Male colonies unknown.
[30] No coordination between pore types, but gastropores only occur at branch axils.

Coenosteal texture, which I originally thought might provide a valuable key to the distinction and evolution of the stylasterids, appears to be a widely convergent character and sometimes not even consistent within a genus. Nonetheless, the coenosteal textures listed in the tabular key serve as a guide in distinguishing several genera. Coenosteal texture is abbreviated in the key: the first letter indicating the shape of the coenosteal strip (i.e., Reticulate or Linear) and the second letter indicating the ornamentation on the strip (i.e., Granular or Imbricate). Texture is best viewed with the aid of a scanning electron microscope at a magnification of 50–250, but also usually can be detected with a dissecting microscope at a magnification of 50, especially if a small section is temporarily dyed with a colored felt-tipped marker.

Some genera are readily diagnosed by one or more easily recognized skeletal characters, which are listed in column 10 of the tabular key and used throughout the dichotomous key. Such characters include: fixed gastropore lids, hinged gastropore opercula, unusual growth form, coenosteal color, and gastropore shape.

Although not considered to be a character, the number of species in each genus and their geographic and bathymetric ranges are presented in the eleventh column of the tabular key. These data summarize and supplement the tabulation presented in part 1 (Cairns, 1983b) of this series and may serve to reinforce or question a particular identification arrived at by using the keys. In my earlier papers, 184–185 valid species were listed, including 24 exclusively fossil species. Currently, I consider there to be 224 valid species, including 24 exclusively fossil species, and

therefore 200 valid Recent species. Four of the 23 genera constitute 65% of the species: *Stylaster* (including "*Allopora*"), 80 species; *Crypthelia,* 26 species; *Distichopora,* 22 species; and *Errina,* 18 species. Eight genera are monotypic. Geographically, stylasterids are cosmopolitan, ranging from the Arctic Circle to off continental Antarctica. They appear to be highly endemic and characteristic of insular environments. Bathymetrically, they occur from 0–2,789 m, although they are most commonly collected between 200–500 m. Only five genera contain species that occur in water shallow enough to be collected by SCUBA or snorkeling: *Stylantheca, Stylaster, Distichopora, Errina,* and *Gyropora.* Only one of the 42 species known from the western Atlantic, *Stylaster roseus,* occurs in shallow water (Cairns, 1986a).

Dichotomous Key to the Genera, Subgenera, and Species Groups of the Stylasteridae

1a. Distinct cyclosystems present 2
1b. Distinct cyclosystems absent: coordination of gastro- and dactylopores random or arranged in rows but never in cyclosystems 12
2a. Gastrostyles absent 3
2b. Gastrostyles present 6
3a. Cyclosystems unifacial 4
3b. Cyclosystems not unifacial: arranged randomly or sympodially ..... 5 (*Conopora*)
4a. Fixed lid partially covers gastropore ..... *Crypthelia*
4b. Lid absent, but small prong projects into gastropore ring constriction ..... *Astya*
5a. Cyclosystems randomly arranged on branch ..... *Conopora* A
5b. Cyclosystems sympodially arranged on branch ..... *Conopora* B
6a. Gastrostyles rudimentary; gastropore tube double-chambered; dactylostyles absent ..... *Pseudocrypthelia*
6b. Gastrostyles well-developed; gastropore tube single-chambered (cylindrical, constricted, or bent); dactylostyles present 7
7a. Corallum encrusting, purple or pink; often more than 1 gastrostyle per cyclosystem ..... *Stylantheca*
7b. Corallum branching, variable in color but most often white; 1 gastrostyle per cyclosystem 8
8a. Cyclosystems unifacial 9
8b. Cyclosystems not unifacial: occur randomly or primarily sympodially ..... 10 (*Stylaster* s.l.)
9a. Rudimentary fixed lids cover part of cyclosystem; coenosteum reticulate granular ..... *Calyptopora*
9b. Cyclosystems without lids; coenosteum linear-imbricate ..... *Stenohelia*
10a. Cyclosystems uniformly spaced on all sides of branches; number of dactylopores per cyclosystem low, e.g., 7–9; colonies massive, branches usually blunt tipped; dactylostyles robust ..... *Stylaster* A (="*Allopora*")
10b. Cyclosystems primarily sympodially arranged; number of dactylopores per cyclosystem relatively high, e.g., 10–15; colonies delicate, branches usually slender; dactylostyles rudimentary 11
11a. Cyclosystems exclusively sympodially arranged ..... *Stylaster* C
11b. Cyclosystems primarily sympodially arranged but with additional cyclosystems on anterior and posterior faces ..... *Stylaster* B
12a. Gastrostyles present 13
12b. Gastrostyles absent 25
13a. Dactylostyles present 14
13b. Dactylostyles absent 16
14a. Dactylostyles robust; dactylopore spines oriented randomly, linear, or as pseudocyclosystems ..... *Errinopora*
14b. Dactylostyles rudimentary; dactylopore spines abcauline 15
15a. One to four dactylostyles per dactylopore; coenosteum reticulate-imbricate; dactylpore spines tall ..... *Inferiolabiata*
15b. One very rudimentary dactylostyle per dactylopore; coenosteum reticulate granular; dactylopore spines absent or very short ..... *Paraerrina*
16a. Gastro- and dactylopores linearly arranged in pore rows: the gastropores aligned in a sunken

sulcus flanked on both sides by U-shaped dactylopore spines, their openings (slits) directed toward the gastropores 17
16b. Gastro- and dactylopores not arranged in pore rows: pores usually randomly arranged, but if dactylopores are linear, they are conical in shape (*Leipidopora*) or abcauline (*Phalangopora*) and not intimately associated with a gastropore row 19
17a. Gastro- and dactylopores and gastrostyles extremely long (height : width ratio of gastrostyle often over 10), often stabilized by transverse tabulae; pore rows usually restricted to branch edges; spines on gastrostyle pointed ..... 18 (*Distichopora*)
17b. Gastro- and dactylopores and gastrostyles short (height : width of gastrostyle 1.5–4.0); pore rows meander over branch faces; spines on gastrostyle blunt, clavate ..... *Gyropora*
18a. Corallum branching (flabellate or bushy) ..... *Distichopora (Distichopora)*
18b. Corallum flabellate, bilobate ..... *Distichopora (Haplomerismos)*
19a. Corallum fenestrate 20
19b. Corallum freely branching with little or no anastomosis 21
20a. Gastropores aligned; coenosteum smooth; dactylopore spines conical; gastrostyles squat (H: W = 1.5), with a pointed tip ..... *Cheiloporidion*
20b. Gastropores randomly arranged; coenosteum granular or imbricate; dactylopore spines conical and adcauline; gastrostyles lanceolate (H:W = 3–4) ..... *Errinopsis*
21a. Gastropore stellate in shape ..... *Stellapora*
21b. Gastropores round to elliptical 22
22a. Dactylopores flush with coenosteal surface, not raised as spines; ampullae internal ..... *Sporadopora*
22b. Dactylopores flanked by dactylopore spines (abcauline, adcauline, or conical); ampullae superficial 23
23a. Dactylopore spines conical; dactylopore tubes axial ..... *Lepidopora*
23b. Dactylopore spines U-shaped (abcauline or adcauline); dactylopore tubes peripheral 24
24a. Dactylopore spines adcauline, with thick walls ..... *Errina*
24b. Dactylopore spines abcauline, with thin walls ..... *Lepidotheca*
25a. Dactylopore spines conical; gastro- and dactylopores randomly arranged; dactylopore tubes axial 26
25b. Dactylopore spines U-shaped; gastro- and dactylopores linearly arranged; dactylopore tubes peripheral ..... *Phalangopora*
26a. Hinged operculum covers gastropore; coenosteal pores small; ampullae superficial ..... *Adelopora*
26b. Opercula absent; large, elongate coenosteal pores common between coenosteal strips; ampullae superficial ..... *Pliobothrus*

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