Phylogenetic Implications of Calcium Carbonate Mineralogy in the Stylasteridae (Cnidaria: Hydrozoa)

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The carbonate mineralogy of the calcified hydrozoan family Stylasteridae is controlled largely by phylogenetic rather than environmental factors. In a comprehensive study—the first of its kind—of the mineralogy of almost an entire family of calcareous organisms, this finding is well documented. X-ray diffraction analyses of 24 of 25 genera indicate that the skeletons of most species analyzed (54 species in 20 genera) were aragonite; only 7 species in 4 genera were calcite. In addition, several species contained coexisting carbonate polymorphs: 7 calcitic species with traces of aragonite; 1 aragonitic species with traces of calcite; and two species with variable percentages of both polymorphs, which is dependent on the distance from the growing tip. In the last two species, staining and progressive X-ray diffraction analyses showed that the ontogenetically earlier polymorph was calcite, the later aragonite. Mole % magnesium carbonate in calcite ranged from 6.5–10.0,

but had no correlation to any known variable.

Likewise, no correlation was found between polymorph type and any morphological or environmental variable, except for a generalized temperature effect, wherein genera with calcitic coralla are restricted to waters colder than 13° C; aragonitic coralla occur at temperatures from −1.5° to 30° C. However, there is a close correlation of polymorph type to the generic phylogeny of the family: the calcite polymorph clustered in the center of the cladogram, aragonite occurring on both ends, including the out-groups. Because the correlation of polymorph types to the cladogram was not perfect, it prompted a re-examination of the placement of some of the stylasterid species and genera. Based on its mineralogy, a Tertiary calcitic stylasterid would probably belong to the Errinopsis-Errina-Errinopora species complex and have occurred in water less than 13° C; on the other hand, Tertiary aragonitic stylasterids were broadly distributed. The adaptive value of calcium carbonate polymorphs in Stylasteridae is still poorly understood.

INTRODUCTION

The first determination of calcium carbonate polymorphs in stylasterid corals was that of Meigen (1901), who found that species of two stylasterid genera, *Distichopora* and *Stylaster*, have aragonitic skeletons. Meigen's methodology was to use a chemical stain dependent on an aragonitic reaction with cobalt nitrate (see Friedman, 1959). The specimens he ana-

lyzed are assumed to have been of shallow, warm-water species. Meigen also determined that the skeleton of another calcified hydrozoan, *Millepora*, was aragonitic.

Using Meigen's reaction, Broch (1914) determined that four deep-sea (cold water) northeast Atlantic stylasterid species belonging to the genera *Pliobothrus* and *Stylaster* (Table 1) were also aragonite.

Also using the "Meigen reaction," Clarke and Wheeler (1922) obtained aragonitic determinations from three species of *Distichopora* (Table 1), as well as three species of *Millepora*. Without additional analyses, Bøggild (1930) assumed that all stylasterids and milleporids, then collectively called the Hydrocorallinae, were exclusively aragonitic. He also suggested, based primarily on his work with mollusks, that temperature did not have an effect on the presence of calcium carbonate polymorphs, a view generally accepted (e.g., Odum, 1951) until 1954.

The aragonitic nature of all hydrocoral skeletons was also generally accepted without challenge through 1954 (e.g., Lowenstam, 1954c, p. 310); however, in 1955 Thompson and Chow analyzed the Sr/Ca ratio of nine stylasterids, and, finding an unusually low ratio in *Errinopora zarhyncha*, inferred that its skeleton was calcitic. The other eight species were stated to be aragonitic (Table 1).

Lowenstam was the first to use non-chemical techniques (i.e., X-ray diffraction) to determine calcium carbonate polymorphs in stylasterids. In advance of his more detailed papers in 1964, he (Lowenstam, 1963, p. 145) made the statement that aragonite and calcite coexisted in the skeletons of certain calcified hydrozoans.

Using X-ray diffraction, Lowenstam (1964a) determined that three species of shallow-water stylasterids and one milleporid were aragonitic (Table 1). In a more detailed paper, also using X-ray diffraction, Lowenstam (1964b) analyzed eight stylasterid species belonging to two genera, *Allopora* (=*Stylaster*) and *Errinopora*, including *E. zarhyncha*. He found that four of the species were calcitic, three were aragonitic, and one
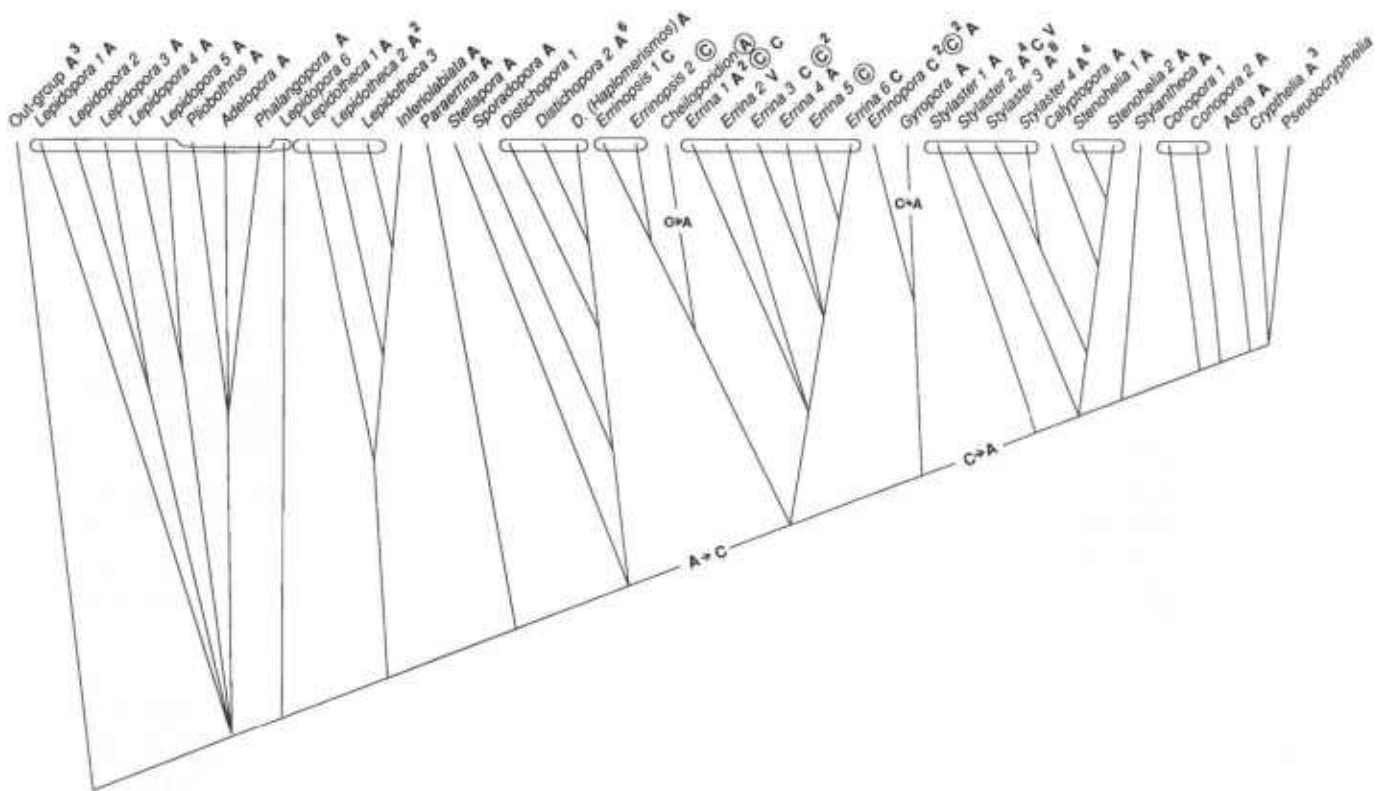
FIGURE 1—Cladogram of stylasterid genera (based on Cairns, 1984), illustrating distribution of calcium carbonate polymorphs: A, 100% aragonite; C, 100% calcite; Ⓐ, primarily aragonite with some calcite; Ⓒ, primarily calcite with some aragonite; V, coexisting polymorphs of variable percentage. Superscripts following these letters indicate how many species were analyzed in that genus; a lack of superscript implies only one species. The cladogram also indicates the major stems on which transitions between polymorphs are hypothesized to have occurred. *Stephanohelia* and *Systemapora* are not included.

(*Allopora boreopacifica*) had coexisting polymorphs, as well as confirming Thompson and Chow's (1955) diagnosis of calcite in *E. zarhyncha*. Lowenstam also suggested that the polymorph present in stylasterids was, in a general way, dependent on temperature, i.e., calcite and coexisting polymorphs were found in waters less than 3° C, and aragonitic skeletons were found in waters above 3° C. This hypothesis was consistent with previous experimental results in which it was shown that calcium carbonate polymorphs of some species of bivalves, gastropods, bryozoa, and tube-dwelling polychaetes were dependent on environmental temperature (Lowenstam, 1954a, b; Dodd, 1963).

In a generalized paper on coelenterate microstructure, Sorauf (1974) determined the mineralogy of another three stylasterid species by X-ray diffraction, all being aragonite (Table 1), but made the incorrect assumption that all stylasterids were aragonitic, apparently unaware of Lowenstam's paper ten years earlier. In the same issue as the Sorauf paper, Fenninger and Flajs (1974) analyzed the mineralogy of 12 stylasterid species in five genera, presumably by X-ray diffraction (Table 1), finding all but one (*Distichopora violacea*) to be aragonitic, stating that it had a "considerable portion" of 12 mole % magnesium carbonate. The finding of calcite in *D. violacea* contradicts our findings for that species as well as those of Thompson and Chow (1955) and Lowenstam (1964a). Furthermore, the finding of calcite in *Distichopora* is inconsistent with all other species in the genus (Table 1) as well as the general position of the genus on the cladogram (Fig. 1). Finally, the mole % magnesium carbonate re-

ported by Fenninger and Flajs is considerably higher than that of any other calcitic stylasterid. This evidence suggests that a calcitic contaminant (e.g., a bryozoan or alga) may have been present on the sample analyzed by Fenninger and Flajs.

No additional analyses appear to have been published since 1974. All of the determinations of polymorph types cited above are consistent with our results (Table 1), with the exception of *D. violacea* reported by Fenninger and Flajs and discussed above.

The purpose of this paper is to provide an overview of the distribution of the aragonite and calcite calcium carbonate polymorphs of the genera of the Stylasteridae and to determine whether the polymorphs are environmentally dependent (i.e., temperature dependent as suggested by Lowenstam [1964b]), or related to the phylogeny of the family.

TABLE 1—Data and results for all specimens analyzed for CaCO3 polymorph type.

Sample number[1]	Species name[2]	USNM number	Station number[3]	Locality
1	*Millepora alcicornis*	84652	SOFLA 1023	26°03′ N, 82°08′ W
D	*Millepora tenera*			Pelau
2	*Janaria mirabilis*	68460	Alb-2794	7°37′ N, 78°46′ W
3	*Axopora solanderi*	I80889		Anvers, France
4	*Lepidopora 1 granulosa* (P)	52698	Elt-740	56°06′ S, 66°19′ W
5	*Lepidopora 3 dendrostylus* (P)	60251	NZOI A910	43°04′ S, 178°39′ W
6	*Lepidopora 4 cryptocymas* (P)	85087	NZOI E846	34°08′ S, 171°58′ E
7	*Lepidopora 5 glabra*	7167	Alb-2152	off Havana
A	*Pliobothrus symmetricus*		Ingolf 55, 57	66°33′ N, 15°02′ W
8	*Pliobothrus symmetricus*	72113	Gerda-598	24°47′ N, 80°25′ W
9	*Adelopora pseudothyron* (P)	60128	Elt-254	59°49′ S, 68°52′ W
10	*Adelopora pseudothyron* (P)	60131	Elt-1343	54°50′ S, 129°51′ W
11	*Phalangopora regularis* (H)			Mauritius
12	*Lepidotheca 1 macropora*	84698	JSL-1914	1°17′ S, 90°17.4′ W
13	*Lepidotheca 2 fascicularis* (P)	60112	Elt-1423	56°21′ S, 158°28′ E
14	*Lepidotheca 2 robusta* (H)	85106	NZOI I96	32°11′ S, 167°21′ E
15	*Stephanohelia praecipua* (P)	85108	NZOI E861	32°25′ S, 167°35′ E
16	*Inferiolabiata labiata*	59951	Elt-2092	76°00′ S, 168°49′ W
17	*Paraerrina decipiens*	76368	AB-420A	2°42′ S, 40°53′ E
18	*Stellapora echinata*	59945	Elt-1593	54°43′ S, 56°37′ W
19	*Sporadopora dichotoma*	66098	Elt-1593	54°43′ S, 56°37′ W
20	*Sporadopora dichotoma*	60099	Hero 715-895	55°00′ S, 64°50′ W
B	*Distichopora 2 coccinea*			South Sea Islands
G	*Distichopora 2 coccinea*			Pacific
G	*Distichopora 2 granulosa*			?
B	*Distichopora 2 nitida*			Micronesia
G	*Distichopora 2 nitida*			?
21	*Distichopora 2 rosalindae* (P)	71773	Alb-4932	16°06′ N, 81°10′ W
B	*Distichopora 2 sulcata*			off Havana
F	*Distichopora 2 sulcata*	10861	Alb-2319	23°10′ N, 82°20′ W
22	*Distichopora 2 sulcata*	10861	Alb-2319	23°10′ N, 82°20′ W
C	*Distichopora 2 violacea*			Marshall Is.
D	*Distichopora 2 violacea*			Pelau
G	*Distichopora 2 violacea*			?
23	*Distichopora 2 violacea*	76340		Gekeit Atoll
24	*Distichopora 2 violacea*	75171		Aldabra
25	*Distichopora (H.) anceps* (P)	56339	SANGO-8	24°55′ N, 171°55′ W
26	*Systemapora ornata* (P)	85117	NZOI P46	28°42′ S, 167°57′ E
27	*Errinopsis 1 reticulum*		WH 19-176	54°49′ S, 57°52′ W
28	*Errinopsis 2 fenestrata*	83591	Elt-601	53°20′ S, 42°42′ W
29	*Cheiloporidion pulvinatum*	83590	Elt-601	53°20′ S, 42°42′ W
F	*Errina 1 antarctica*	52652	Elt-222	56°15′ S, 66°51′ W
G	*Errina 1 antarctica*			?
30	*Errina 1 antarctica*	59845	Hero 715-856	54°34′ S, 64°10′ W
31	*Errina 1 aspera*	75603		Straits of Messina
32	*Errina 1 hicksoni* (P)	76516	NZOI A748	47°41′ S, 179°03′ E
33	*Errina 1 reticulata* (P)	60248	NZOI D17	52°31′ S, 160°31′ E
34	*Errina 2 kerguelensis* a) distal b) middle c) proximal	59903	Elt-1952	66°40′ S, 162°48′ E
35	*Errina 3 bicolor* (P) white	60249	NZOI D172	51°00′ S, 166°03′ E
36	*Errina 3 bicolor* (P) orange	60249	NZOI D172	51°00′ S, 166°03′ E

TABLE 1—Continued.

Sample number[1]	Depth (m)	Temperature (°C)[4]	Method of analysis	% Arag.	% Calcite (mole % MgCO$_3$)
				Results	
1	17	23	X	100	0
D	shallow	?	X	100	0
2	113	*15.3	X	100	0
3	Eocene		X	100	0
4	384–494	3.7	X	100	0
5	549	8.0	X	100	0
6	343–417	11.0	X	100	0
7	708	*9.4	X	100	0
A	594–658	*4.0	M	100	0
8	183	21.0	X	100	0
9	512–622	2.6	X	100	0
10	567–604	4.5	X	100	0
11	238–274	18.0	X	100	0
12	166–172	*14.3	X	100	0
13	1574–1693	2.0	X	100	0
14	356	13.0	X	100	0
15	308–383	13.0	X	100	0
16	526	−1.1	X	100	0
17	140	20.0	X	100	0
18	339–357	4.5	X	100	0
19	339–357	4.5	X	100	0
20	438–548	4.5	X	100	0
B	?	?	M	100	0
G	?	?	X?	100	0
G	?	?	X?	100	0
B	?	?	M	100	0
G	?	?	X?	100	0
21	165	*24.1	X	100	0
B	143–179	19.0	M	100	0
F	262	17.0	X	100	0
22	262	17.0	X	100	0
C	?	?	S	100	0
D	shallow	?	X	100	0
G	?	?	X?	?	? (12.0)[6]
23	0–3	30.0	X	100	0
24	12	27.5	X	100	0
25	658–736	6.0	X	100	0
26	450–475	11.0	X	100	0
27	230–250	3.5	X	0	100 (7.5)
28	417–514	1.8	X	4	96 (7.5)
29	417–514	1.8	X	97	3 (8.5)
F	80	4.0	X	100	0
G	?	?	X?	100	0
30	73	4.5	X	100	0
31	100	15.0	X	100	0
32	62	7.5	X	9	91 (8.5)
33	124	12.0	X	0	100 (8.0)
34	153	−0.5	X		
				61	39 (8.5)
				74	26
				95	5
35	179	8.5	X	4	96 (8.5)
36	179	8.5	X	7	93 (9.0)

MATERIALS AND METHODS

Table 1 presents the data of the 113 known calcium carbonate polymorph determinations of stylasterid corals, consisting of the 41 previously published analyses and 72 new determinations. Data are now available for 71 of the 261 (27%) stylasterid species and 24 of the 25 genera (see Cairns, 1983b, 1991a, b), only *Pseudocrypthelia* being unavailable for analysis. Specimens of *Millepora, Janaria* and *Axopora,* three other calcified hydrozoan taxa, were also analyzed, the latter considered to be the sister group of the Stylasteridae (Cairns, 1984). Table 1 is arranged phylogenetically according to the cladogram of Cairns (1984) and includes two recently described genera, *Stephanohelia* Cairns (1991b) and *Systemapora* Cairns (1991b), which have not yet been integrated into the working cladogram; the former is thought to have affinities to *Lepidotheca* and *Inferiolabiata,* the latter to *Distichopora.* In some cases, for instance in the genera *Errina* and *Stylaster,* genera were divided into as many as six components in order to facilitate coding of character states for phylogenetic analysis (see Cairns, 1984). Between one and 19 species were analyzed for each genus; however, usually only one specimen per species was tested.

Incorporated within the phylogenetic selection of specimens was also a range of other environmental and biological variables, including: temperature, geographic and bathymetric distribution, corallum color, corallum density, coenosteal texture (e.g., linear-imbricate vs. reticulate-granular), presence of symbiotic relationships, and sex of colony.

Parent lots of specimens used in our analyses are deposited at the National Museum of Natural History, as are those of Clarke and Wheeler (1922), Thompson and Chow (1955), Lowenstam (1964b), and Sorauf (1974). Environmental temperatures were directly available from station logs of only 17 of the 113 samples analyzed (Table 1). Therefore, other references were used to estimate the temperatures used in Table 1 and

TABLE 1—Continued.

Sample number[1]	Species name[2]	USNM number	Station number[3]	Locality
37	*Errina 3 cheilopora*	85134	NZOI E830	40°57′ S, 166°09′ E
38	*Errina 3 novaezelandiae*	85122	NZOI Q748	George Sound, NZ
39	*Errina 4 macrogastra*	84708	JSL-1916	1°18′ S, 89°49′ W
40	*Errina 5 fissurata*	59883	Elt-1997	72°00′ S, 172°28′ E
41	*Errina 6 laterorifa*	59898	Elt-2026	75°06′ S, 176°37′ W
42	*Errinopora cestoporina* (P)	60141	Elt-1593	54°43′ S, 56°37′ W
43	*Errinopora nanneca*	52248	Alb-3599	42°05′ N, 177°40′ W
E	*Errinopora pourtalesi*	52253	Alb-3159	37°47′ N, 123°10′ W
44	*Errinopora pourtalesi*	52253	Alb-3159	37°47′ N, 123°10′ W
E	*Errinopora stylifera*	42873	Alb-5016	46°44′ N, 143°43′ W
45	*Errinopora stylifera*	52250	Alb-5017	46°43′ N, 143°45′ W
C	*Errinopora zarhyncha*	52247	Alb-3480	52°06′ N, 171°45′ W
E	*Errinopora zarhyncha*	52247	Alb-3480	52°06′ N, 171°45′ W
46	*Errinopora zarhyncha*	52247	Alb-3480	52°06′ N, 171°45′ W
47	*Gyropora africana*			Cape of Good Hope
A	*Stylaster 1 norvegicus*		Ingolf	63–66° N, 13–25° W
G	*Stylaster 1 norvegicus*			?
48	*Stylaster 1 norvegicus*	75620		Rockall Bank
E	*Stylaster 2 boreopacificus*	76530	Alb-5017	46°43′ N, 143°45′ W
49	*Stylaster 2 boreopacificus* a) distal b) middle c) proximal	76530	Alb-5017	46°43′ N, 143°45′ W
50	*Stylaster 2 boreopacificus* a) distal b) middle c) proximal	42872	Alb-5016	46°44′ N, 143°45′ W
C	*Stylaster 2 californicus*			California
E	*Stylaster 2 californicus*			Pt. Buchanan, CA
E	*Stylaster 2 californicus*	81035		Santa Catalina, CA
51	*Stylaster 2 californicus*	81035		Santa Catalina, CA
52	*Stylaster 2 eguchii*	60096	Elt-1411	51°01′ S, 162°01′ E
E	*Stylaster 2 norvegicus pacificus* (=*S. verrillii*)	76536	Alb-5016	46°44′ N, 143°45′ W
53	*Stylaster 2 norvegicus pacificus* (=*S. verrillii*)	76536	Alb-5016	46°44′ N, 143°45′ W
54	*Stylaster 2 robustus* (P)	52637	Elt-993	61°25′ S, 56°30′ W
C	*Stylaster 2 venustus*			California
E	*Stylaster 3 campylecus*	?		Sitka, Alaska
C	*Stylaster 3 campylecus parageus*	?		Gulf of Alaska
E	*Stylaster 3 campylecus trachystomus*	76811	Alb-4784	52°55′ N, 173°30′ E
55	*Stylaster 3 campylecus trachystomus*	76811	Alb-4784	52°55′ N, 173°30′ E
A	*Stylaster 3 erubescens*		Ingolf	63–66° N, 13–26° W
56	*Stylaster 3 erubescens*	72192	Gerda 132	24°23′ N, 80°48′ W
A	*Stylaster 3 gemmascens*		Ingolf	66°18′ N, 25°59′ W
G	*Stylaster 3 gemmascens*			?
57	*Stylaster 3 polyorchis*	76540	Alb-3480	52°06′ N, 171°45′ W
58	*Stylaster 3 roseus*	72255		Buenaventura, Panama
59	*Stylaster 3 roseus*	74997		Carrie Bow Cay, Belize
C	*Stylaster 3 sanguineus*			Marshall Is.
C	*Stylaster 3 elegans* (=*sanguineus*)			?Hawaii
D	*Stylaster sanguineus*			Pelau
F	*Stylaster sanguineus*	45156		Bikini

TABLE 1—Continued.

Sample number[1]	Depth (m)	Temperature (°C)[4]	Method of analysis	% Arag.	% Calcite (mole % $MgCO_3$)
37	514–534	7.5	X	0	100 (7.5)
38	20–25	13.0	X	9	91 (9.0)
39	545–562	*7.3	X	100	0
40	530–549	0.0	X	9	91 (7.0)
41	796–808	0.5	X	0	100 (6.5)
42	339–357	4.5	X	100	0
43	101	4.5	X	0	100 (9.0)
E	49	9.0	X	0	100
44	49	9.0	X	7	93 (10.0)
E	117	*−1.5	X	0	100
45	117	*−1.5	X	0	100 (7.0)
C	518	3.3	S	0	100
E	518	3.3	X	0	100 (8.5)
46	518	3.3	X	9	91 (9.0)
47	20	18	X	100	0
A		0–7	M	100	0
G	?	?	X?	100	0
48	165	8.0	X	100	0
E	117	*−1.5	X	83	17
49	117	*−1.5	X		
				68	32 (6.5)
				83	17
				89	11
50	117	*−1.5	X		
				78	22 (6.5)
				80	20
				92	8
C	?	?	S	100	0
E	9	12.0	X	100	0
E	33	*13.5	X	100	0
51	33	*13.5	X	100	0
52	333–371	8.0	X	100	0
E	117	*−1.5	X	0	100 (6.5)
53	117	*−1.5	X	0	100 (6.5)
54	300	−0.5	X	100	0
C	?	?	S	100	0
E	15–25	5–6	X	100	0
C	?	?	S	100	0
E	247	3.5	X	100	0
55	247	3.5	X	100	0
A		0–8	M	100	0
56	275–302	15.0	X	100	0
A	620	−0.8	M	100	0
G	?	?	X?	100	0
57	518	3.5	X	100	0
58	1–3	28.0	X	100	0
59	5–6	28.5	X	100	0
C	?	?	S	100	0
C	?	?	S	100	0
D	shallow	?	X	100	0
F	22–30	29.0	X	100	0

Figures 1–3: Ridgway (1968) and Garner (1969), New Zealand region; Townsend (1901), North Atlantic and North Pacific *Albatross* stations; Discovery Committee (1929), South Atlantic and Subantarctic; and Gorshkov (1976, 1977), Pacific and Atlantic, in general. Finally, because polymorph determination of calcium carbonate based on chemical reaction is sometimes unreliable (see Lowenstam, 1964b; Carter, 1980b), the method of analysis is always indicated in Table 1: 97 were made by X-ray diffraction, 7 by the Meigen reaction, and 9 by a combination of inference of the Sr/Ca ratio and "chemical methods" (Thompson and Chow, 1955).

The skeleton analyzed was generally taken from uncontaminated branch tips; however, for *Stylaster boreopacificus* and *Errina kerguelensis,* in which coexisting polymorphs or variable percentages were found, analyses were made on distal, intermediate, and proximal branches and thin sections from these three regions were stained with Feigl's solution (Friedman, 1959) in order to localize the different polymorph components as they relate to ontogeny.

The carbonate mineralogies were determined by standard powder X-ray diffraction techniques with CuK α radiation (Chave, 1954; Milliman, 1974). The mole % magnesium carbonate in the calcites was calibrated from α (211) spacings in relation to quantitative curves constructed by Goldsmith and Graf (1958). In samples containing both aragonite and calcite, the amount of the polymorphs present was determined by peak-area analysis in reference to a standard curve for aragonite concentrations (Boardman, 1976).

Although only clean skeletal material, free from all encrusting organisms, was carefully selected for mineralogical analyses, there was some concern that stylasterids with coexisting polymorphs could contain microborings filled with secondary carbonate. For instance, Houck, Buddemeier, and Chave (1975) were led to the erroneous conclusion that the

TABLE 1—Continued.

Sample number[1]	Species name[2]	USNM number	Station number[3]	Locality
G	*Stylaster 3 sanguineus*			Samoa
60	*Stylaster 4 brunneus* (white)	86943	NZOI I85	29°08′ S, 168°15′ E
61	*Stylaster 4 brunneus* (brown)	86944	NZOI P18	29°34′ S, 168°03′ E
62	*Stylaster 4 densicaulis*	60016	Elt-1593	54°43′ S, 56°37′ W
63	*Stylaster 4 duchassaingi*	52250	Alb-2333	23°10′ N, 82°19′ W
64	*Stylaster 4* sp.	60027	Elt-1343	54°50′ S, 129°51′ W
65	*Calyptopora reticulata*	60008	Elt-1851	49°40′ S, 178°53′ E
66	*Calyptopora reticulata*	60010	Elt-1991	54°39′ S, 170°22′ E
67	*Stenohelia 1 pauciseptata* (P)	71797	Alb-2753	13°34′ N, 61°03′ W
G	*Stenohelia 2 profunda*			?
68	*Stenohelia 2 profunda*	52244	Alb-2753	13°34′ N, 61°03′ W
C	*Stylantheca porphyra*			California
69	*Stylantheca porphyra* (S)	43276		Carmel Bay, CA
70	*Conopora 2 verrucosa*	87539	NZOI D39	50°58′ S, 165°45′ E
71	*Astya aspidopora* (P)	87559	NZOI U599	30°43′ S, 173°17′ E
C	*Crypthelia trophostega*			Bering Sea
G	*Crypthelia floridana*			Florida
72	*Crypthelia cymas* (P)	72017	Alb-2818	0°29′ S, 89°54′ W

[1] Numbers refer to samples analyzed for this paper. Letters pertain to previously published results: A (Broch, 1914), B (Clarke and Wheeler, 1922), C (Thompson and Chow, 1955), D (Lowenstam, 1964a), E (Lowenstam, 1964b), F (Sorauf, 1974), and G (Fenninger and Flajs, 1974).

[2] Numbers between genus and species names refer to group designation on cladogram (see Cairns, 1984). Letters in parentheses following name refer to type status: H (holotype), P (paratype), S (syntype).

[3] Station or vessel abbreviations: AB (*Anton Bruun*), Alb (*Albatross*), Elt (*Eltanin*), JSL (*Johnson-Sea-Link*), NZOI (New Zealand Oceanographic Institute), WH (*Walther Herwig*).

[4] *In situ* benthic temperatures at time of capture prefaced with an asterisk.

[5] Methods of analysis: M (Meigen's reaction), S (Sr/Ca ratio), X (X-ray diffraction).

[6] Data suspect (see text).

scleractinian *Porites lobata* formed skeletons with as much as 46% primary skeletal calcite, not realizing that the calcite was contributed by secondary infillings of microborings (Macintyre and Towe, 1976). To avoid similar error, longitudinal and transverse thin sections of coralla containing coexisting polymorphs were stained with Feigl's solution, which revealed that both calcite and aragonite are forming original skeletal material.

RESULTS

Among the 71 stylasterid species analyzed (Table 1), coralla of 54 species are entirely aragonitic and in another species predominantly so. Pure calcite occurs in seven species and is predominant in another seven. Coexisting polymorphs of variable percentage occur in *Stylaster boreopacificus* and *Errina kerguelensis*. The mineralogy of the three nonstylasterid calcified hydrozoans (samples 1–3 of Table 1) is exclusively aragonitic. These data are graphically illustrated on a cladogram (Fig. 1), which shows that the species having pure calcite, predominantly calcitic, or partially calcitic coralla are grouped in the center of the cladogram. No relationship between mineralogy and corallum color, density, sex, or geographic or bathymetric distribution was found; however, it was noted that all calcitic species have reticulate-granular coenosteal texture and lack polychaete symbionts.

The relationship of calcium car-

bonate polymorphs to temperature is explored in Figures 2–4. Aragonitic coralla are found throughout the entire range of oceanic temperatures (−1.5° to 30° C), whereas calcitic coralla are restricted to water temperatures below 13° C (Fig. 2). However, there appears to be little correlation between water temperature and type of polymorph; sometimes two species collected from the same station have different polymorphs. Figures 3 and 4 show a similar lack of correlation for species of the genera *Errina* and *Stylaster*. In the case of *Stylaster*, it appears that calcitic species are rare and occur only in cold water, but aragonitic species of *Stylaster* are also known from polar waters.

Calcitic mole % magnesium carbonate ranged from 6.5–10.0, but no

TABLE 1—Continued.

Sample number[1]	Depth (m)	Temperature (°C)[4]	Method of analysis	% Arag.	% Calcite (mole % MgCO₃)
				Results	
G	?	?	X?	100	0
60	290	14.0	X	100	0
61	86–90	17.0	X	100	0
62	339–357	4.5	X	100	0
63	309	16.0	X	100	0
64	567–604	4.5	X	100	0
65	476–540	5.5	X	100	0
66	1862–2103	2.2	X	100	0
67	514	*8.9	X	100	0
G	?	?	X?	100	0
68	514	*8.9	X	100	0
C	?	?	S	100	0
69	0–1	15.0	X	100	0
70	465–549	6.0	X	100	0
71	590–640	9.0	X	100	0
C	?	?	S	100	0
G	?	?	X?	100	0
72	717	*6.6	X	100	0

and at the base of gastropore tubes in the gastrostyle region (Fig. 5d).

DISCUSSION

Temperature Effects

Lowenstam's (1964b: fig. 1) suggestion that calcium carbonate polymorphs of stylasterid species were, in a general way, dependent on temperature was based on a relatively small number of samples (i.e., 5) in one genus, *Allopora* (=*Stylaster*). Based on additional determinations it can now be shown that stylasterid polymorphs are not strongly related to environmental temperature when analyzed as a group (Fig. 2) or by genus (Figs. 3, 4). There is a very general temperature effect, as Lowenstam (1964b) suggested, in that calcitic coralla are confined to waters colder than 13° C. This kind of temperature sensitivity was termed "transitional" by Lowenstam (1954b), which included taxa having aragonite-secreting species in warm waters and calcite-secreting species at lower temperatures. Regardless, this kind of temperature response is herein in-

correlation was found between its values and any other variable: phylogenetic, environmental, or morphological.

Staining for aragonite with Feigl's solution of distal, intermediate, and proximal branches of *Stylaster boreopacificus* and *Errina kerguelensis* revealed that calcite was concentrated in the growing tips and consequently the inner branch cores of larger branches, the outer layers being aragonitic (Fig. 5a–c). These results are consistent with the overall percentage aragonite determined from the same branch areas (Table 1), the branch tips having 61–78% aragonite, which increases to 89–95% toward the corallum base. Thin sections of *Errina fissurata* and *E. hicksoni*, two species having predominantly (91%) calcitic coralla, were also stained with Feigl's solution, in an effort to localize the aragonitic (9%) component. In these species aragonite appears to concentrate near the branch core, beneath ampullae,
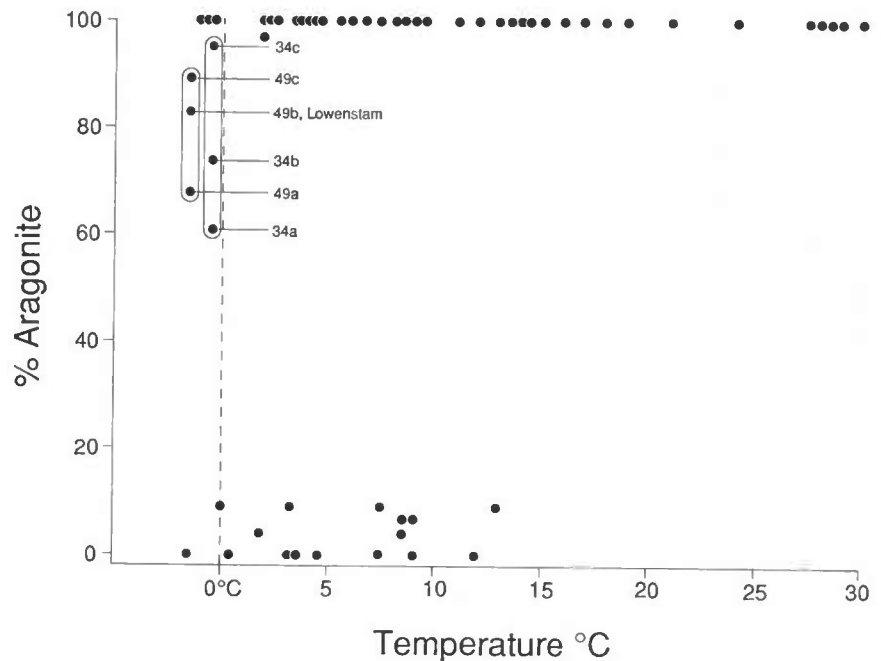

FIGURE 2—Graph of percent aragonite vs. temperature (°C) for all stylasterids listed in Table 1. Two species having coexisting polymorphs (34, 49) are plotted for their distal (a), middle (b), and proximal (c) branch segments.
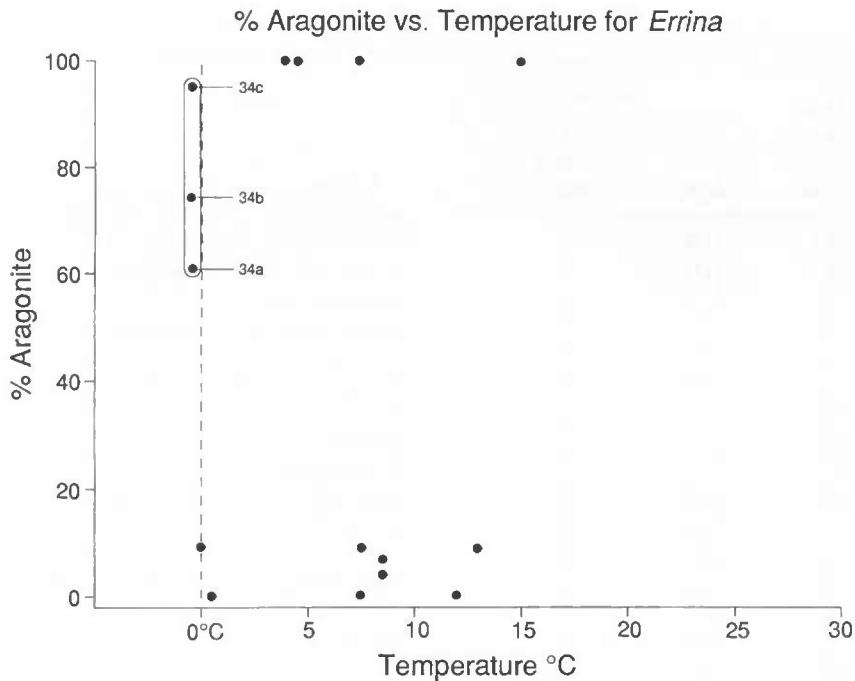
% Aragonite vs. Temperature for *Errina*

FIGURE 3—Graph of percent aragonite vs. temperature (°C) for all species of *Errina* listed in Table 1. *Errina kerguelensis,* a species with coexisting polymorphs (34), is plotted for its distal (a), middle (b), and proximal (c) branch segment.
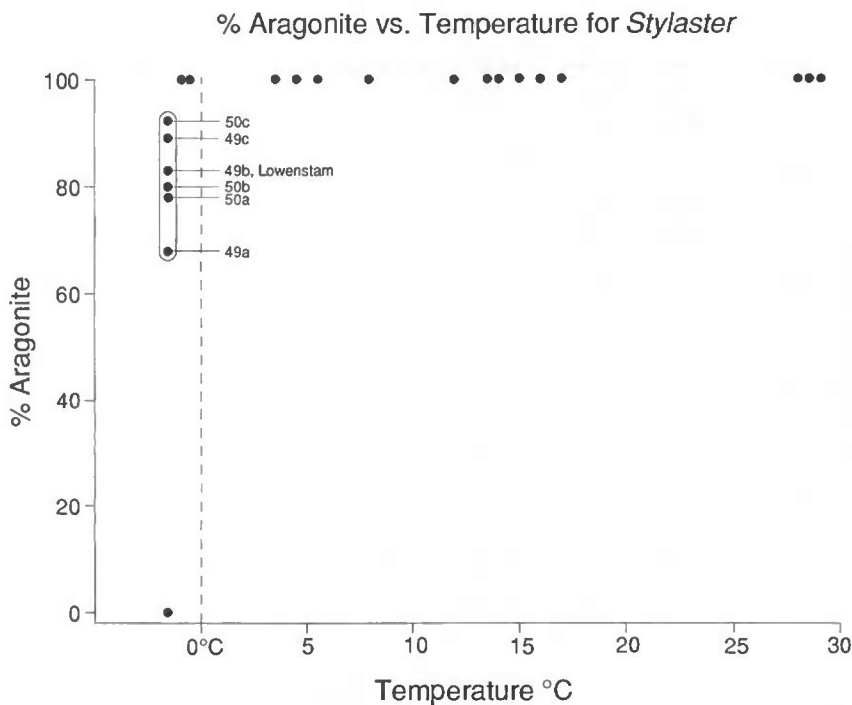
% Aragonite vs. Temperature for *Stylaster*

FIGURE 4—Graph of percent aragonite vs. temperature (°C) for all species of *Stylaster* listed in Table 1. *Stylaster boreopacificus,* a species with coexisting polymorphs (49, 50), is plotted for its distal (a), middle (b), and proximal (c) branch segment.

terpreted as phylogenetic, not a direct response to environmental temperature. In referring to the calcite and aragonite found in mineralized skeletons, Lowenstam and Weiner (1989, p. 210) recently stated that, although there are many exceptions, "In general, . . . there is no consistent distribution pattern and, for the most part, the polymorph formed is determined completely by the organism, irrespective of the environment in which it lives." We believe this to be the case for stylasterids, in that the phylogeny of the family, not the environment, is the causative factor for the distribution of the polymorphs.

Phylogenetic Implications

Because the distribution of calcium carbonate polymorphs on the cladogram (Fig. 1) is considered to have been produced by non-environmental causes (i.e., evolution), skeletal mineralogy can now be used as an independent character to evaluate the previously published cladogram (Cairns, 1984) that was based entirely on morphological characters. The probability that all nine calcitic polymorphs would concentrate in any particular region of the cladogram spanning 13 taxa (e.g., as in Fig. 1) as a result of random distribution is quite low: 0.0000006675 or 1 in approximately 1.5 million. (This is based on the probability statement: $n - (x + y) \cdot x! \cdot y! \cdot [(n - (x + y))! - (n - x - 2y - 1)!]/n!$, where $n = 37$ (coded taxa in the cladogram), $x = 9$ (calcitic taxa), and $y = 2$ (taxa with both calcite and aragonite).) Nonetheless, the character state distribution of calcite vs. aragonite is not perfectly congruent with the cladogram and thus requires some explanation.

It is logical to assume that the Stylasteridae began its evolution as aragonitic because all three calcified non-stylasterid hydrozoans (out-groups to varying degrees to the Stylasteridae) are completely aragonitic, as are the ten most plesiomorphic stylasterid genera. The most conservative explanation of the distribution of calcium carbonate polymorphs on the cladogram would be to suggest a change from aragonite to calcite at
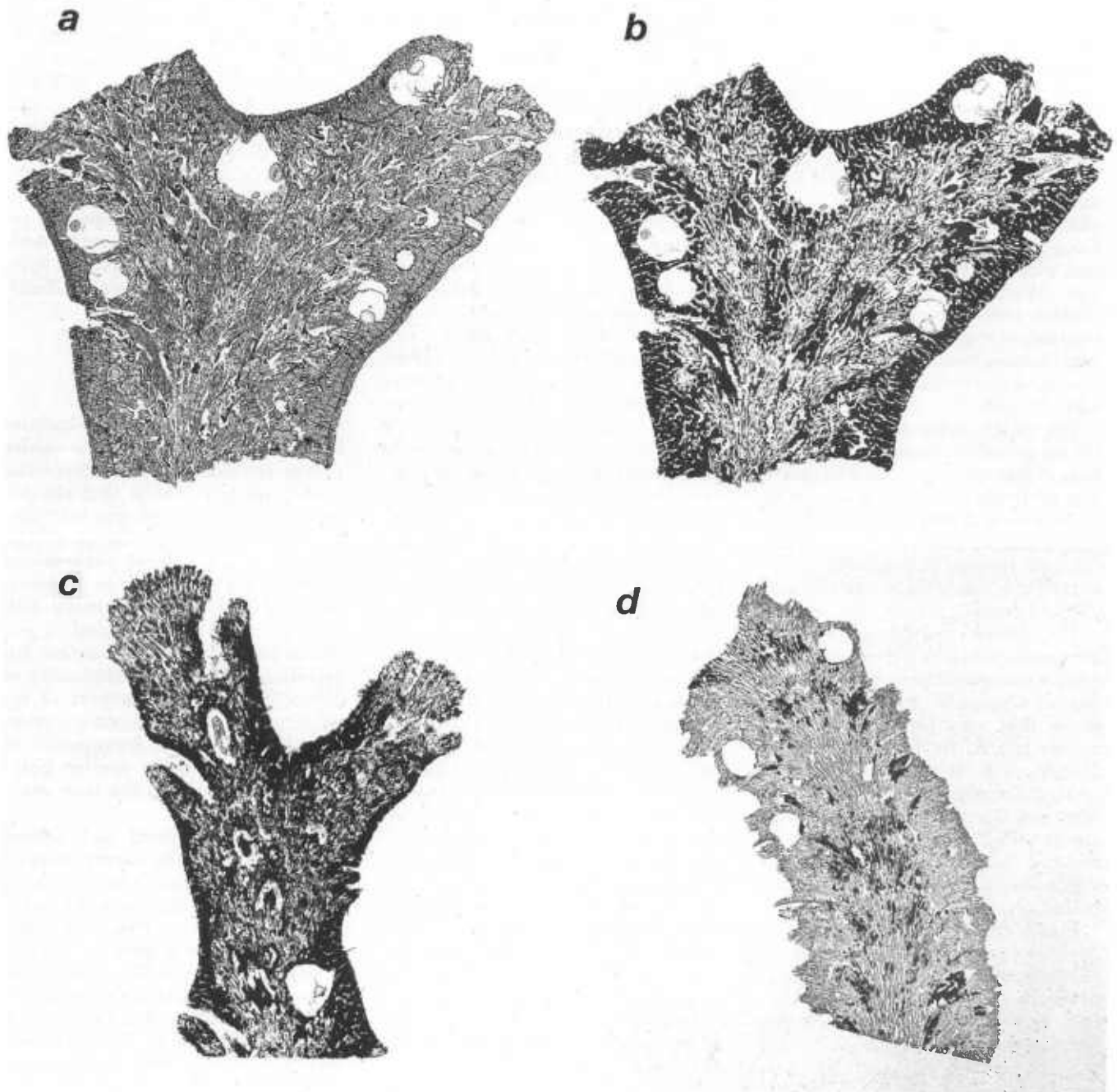
FIGURE 5—Photomicrographs of longitudinal thin sections of stylasterids stained with Feigl's solution. **a)** and **b)** *Stylaster boreopacificus* before and after staining, respectively. Black stain indicates that the aragonite concentrates in the outer layers of the colony; **c)** *Stylaster boreopacificus*, light areas in this stained and dominantly aragonitic branch (70% aragonite by X-ray diffraction) further demonstrates that calcite occurs in the central axis and growing tips; **d)** *Errina fissurata*, dark patches in this stained section show that aragonite is limited to patchy infillings in porous areas of the central axis, gastropore, and base of ampullar cavities (9% aragonite by X-ray diffraction).

the stem between *Distichopora* and *Errinopsis* and a reversal back to aragonite on the stem after *Gyropora,* as well as an independent acquisition of a calcitic skeleton in some species of *Stylaster* (2) and a second reversal to aragonite in some species of *Errina* and *Gyropora* (Fig. 1). The stem between *Distichopora* and *Errinopsis* represents a major evolutionary change within the Stylasteridae from species having thin-walled, abcauline

dactylopore spines to those with thick-walled, adcauline dactylopore spines—the precursor of the cyclosystem. The reversal back to aragonite is suggested to have occurred at the stem between *Gyropora* and *Stylaster,* when the cyclosystem was actually attained.

Some other phylogenetic implications of the mineralogy of the genera follow. The aragonitic corallum of *Errinopora cestoporina* is inconsistent with all other species in the genus. When originally described (Cairns, 1983a), it was stated to have pseudocyclosystems, which, upon re-examination, could be interpreted as true cyclosystems and thus place it with *Stylaster* 2.

The six divisions of *Errina* are artificial groupings made only to facilitate character coding. An alternative way to divide the genus would be to use calcite and aragonite as defining characters, which would then require only one reversal to aragonite to distribute this character among the species of *Errina.*

The finding of aragonite in *Gyropora* and calcite in *Errinopora* suggests a re-examination of the affinities of *Gyropora,* a poorly known genus that may prove to be more closely related to *Stylaster* or even *Distichopora.* If the synapomorphy uniting *Errinopora* and *Gyropora* is removed, *Gyropora* would naturally group with *Stylaster,* and the basal reversal from calcite to aragonite might then occur between *Errinopora* and *Gyropora.*

Finally, the finding of aragonite in *Stylaster norvegicus* and calcite in *Stylaster norvegicus pacificus* reaffirms the distinction of *S. pacificus* (=*S. verrillii*) as a separate species (see Cairns, 1983b).

Adaptive Advantages and
Paleontological Implications of
Calcium Carbonate Polymorphs

The question of the adaptive advantages of calcite or aragonite in stylasterid coralla was discussed by Broch (1914, p. 2) and Clarke and Wheeler (1922, p. 58) but without conclusion or even hypotheses. More recently, Lowenstam and Weiner (1989, p. 237) concluded that in most organisms it is unknown why one polymorph is preferred to another or even if one polymorph is adaptively superior to another. However, Carter (1980a) noted that calcite is 7.5% less dense than aragonite, slightly less hard on Moh's scale, has perfect cleavage (aragonite has imperfect cleavage), and is the more stable polymorph of calcium carbonate. Based on these characteristics, Carter suggested several adaptive advantages of calcite in certain bivalve shells, including: 1) having a lower density shell, which would be advantageous in certain swimming species and "floating" in soft ooze; more rapidly secreting large shells; and being more economical in shell secretion, 2) enhancing fracture localization rather than propagating fracture energy throughout the colony, and 3) reducing shell dissolution, calcite being less soluble than aragonite. It is difficult to adopt any of these hypotheses as adaptively significant to the stylasterids with the exception of hypothesis 2: enhanced fracture localization. Branches of stylasterid colonies are sometimes fractured from the colony, each detached branch having the capacity to asexually form a new colony. Therefore, fracture localization might be advantageous in increasing asexual reproduction in calcitic species; however, coralla of calcitic species are not noticeably more brittle than those composed of aragonite, nor are they often found regenerated from basal fragments. Perhaps, as Lowenstam and Weiner (1989) hypothesized, the polymorph type is of little or no adaptive value, being simply a pleiotropic side effect of another adaptive change, such as dactylopore shape and orientation.

Some cautious attempts have been made to use calcium carbonate polymorphs as paleoenvironmental indicators (Lowenstam, 1954b, 1963; Dodd and Stanton, 1981); however, lack of knowledge of the paleoenvironment as well as of the distribution of polymorphs in Recent and fossil species of stylasterids make this premature. But we can say that, whereas an aragonitic Tertiary stylasterid corallum may not have environmental or taxonomic implications, by analogy to Recent species, a calcitic Tertiary stylasterid skeleton probably lived in waters less than 13°C and was probably related to the *Errinopsis-Errina-Errinopora* genus complex. A temperature of less than 13°C, however, could have been encountered in the deep-water tropics or a shallower, but more temperate region, and thus only the warm, shallow-water tropics are excluded from consideration for the calcitic Tertiary specimen.

CONCLUSIONS

We believe that the close correlation of the distribution of the calcite polymorph to a distinct region on the cladogram is evidence that the occurrence of polymorph type is strongly related to the phylogeny of the family. A secondary, generalized temperature effect is also acknowledged (Fig. 2), wherein genera with calcitic coralla are restricted to waters colder than 13° C. Another interesting result is the confirmation of Lowenstam's (1964b) report of coexisting polymorphs in one stylasterid species, *Stylaster boreopacificus*: the ontogenetically earlier polymorph being calcite, the later polymorph aragonite.

According to Dodd and Schopf (1972), much of the survey work in biogeochemical analyses relies on specimens that happen to be available at the time but that do not necessarily provide a base to analyze phylogenetic effects. This was the case in previous analyses of the Stylasteridae (e.g., Meigen, 1901; Broch, 1914; Clarke and Wheeler, 1922; Thompson and Chow, 1955; Lowenstam, 1964b). Our specimens, however, were carefully selected from the largest and most comprehensive stylasterid collection in the world in order to test both phylogenetic and environmental effects. Our analysis is also unique in that it compares mineralogical results to a detailed, fine-scale phylogenetic cladogram in order to test the effect of evolution on the distribution of polymorphs.

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