

Stylobates: A Shell-Forming Sea Anemone (Coelenterata, Anthozoa, Actiniidae)¹

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ABSTRACT: Anatomy and cnidae distinguish two species of deep-sea actinians that produce coiled, chitinous shells inhabited by hermit crabs of the genus *Parapagurus*. The actinian type species, *Stylobates aeneus*, first assigned to the Mollusca, occurs around Hawaii and Guam with *P. doffeini*. *Stylobates cancrisocia*, originally described as *Isadamsia cancrisocia*, occurs off east Africa with *P. trispinosus*.

MANY MEMBERS OF THE ORDER Actiniaria attach obligately or facultatively to gastropod shells inhabited by hermit crabs. Some of these partnerships seem to be strictly phoretic, the normally sedentary sea anemone being transported by the motile hermit crab (Ross 1971, 1974b). The relationships between other species pairs are mutualistic, the anemone gaining motility while protecting its associate from predation (Balasch and Mengual 1974; Hand 1975; McLean and Mariscal 1973; Ross 1971, 1974b; Ross and von Boletsky 1979). As the crustacean grows, it must move to increasingly larger shells. Some species of hermits detach their sea anemones from the smaller shells and place them on the larger, whereas in other associations, the anemones transfer themselves from shell to shell (Ross 1974a). The crustacean *Pagurus prideauxi* Leach need never change shells when in association with the cloak anemone, *Adamsia palliata* Bohadsch (family Hormathiidae), which wraps around the hermit's abdomen and grows as the crab does. In the process, the

pedal disk secretes a chitinous cuticle over the small mollusk shell which the pagurid had initially occupied and to which the small actinian had first attached, often extending the cuticular material beyond the lip of the shell (Bals 1924, Faurot 1910, Gosse 1858). This arrangement affords the crab mainly mechanical protection (Ross 1971).

Carlgren (1928a) described as a new genus and species *Isadamsia cancrisocia* (family Actiniidae), an actinian attached to a shell occupied by a hermit crab, from four specimens collected by the Deutschen Tiefsee-Expedition (1898–1899) at 818 m in the Pemba Channel off east Africa. The generic name recognizes two points of superficial similarity with *Adamsia*: (1) the sea anemone is oriented on the shell so that its mouth is beneath that of the crustacean; (2) the coiled shell, called by Carlgren (1928a, 1928b) a *carcinocium*, is almost entirely produced by the actinian. Carlgren (1928a, 1928b) did not note that a shell-making actinian had been reported previously. Dall (1903: 61) described what he thought was a new genus and species of trochid gastropod, *Stylobates aeneus*, based on shells "of a flexible, horny consistency. . ." "occupied by hermit crabs and completely covered by the extended basal membrane of a large *Actinia*" that had been collected at 220–436 fm (402–797 m) by the U.S. Fish Commission steamer *Albatross* in waters of the Hawaiian Islands. Sixteen years later, having seen a collection of similar but irregularly shaped shells, Dall (1919:

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80) published a note identifying them and *S. aeneus* as "secretions from the bases of the Actinias." Neave (1940) lists *Stylobates* as a mollusk, although the catalog of Dall's names (Boss, Rosewater, and Ruhoff 1968) correctly includes it among the coelenterates.

MATERIALS AND METHODS

We have examined numerous carcinoecia formed by *Stylobates* from Hawaii and Guam, most containing hermit crabs and covered by actinians. Material from Guam is in the collection of the Department of Invertebrate Zoology, California Academy of Sciences, catalog 011027-011030; Hawaiian specimens are in the Division of Invertebrate Zoology, Bernice P. Bishop Museum, accession 1971.197 and 1979.529, the latter received from the National Marine Fisheries Service (Southwest Center), Honolulu. We have examined the holotype of *Stylobates aeneus*, U.S. National Museum molluscan lot 795117, which is represented only by the shell although it was collected with actinian and crustacean (Dall 1903). We were able to locate only one of the four specimens of *Isadamsia cancrisocia* from Deutschen Tiefsee-Expedition station 246. There is no indication in the catalog nor on the label that this specimen (Museum für Naturkunde, Berlin, GDR, catalog 6957) is the holotype. A piece has been removed from the margin, apparently for histological study; the apex has been cracked; and it is illustrated in the original description (Carlgren 1928a: plate 2, fig. 9), so it certainly was studied by Carlgren.

Histological sections (8 μ m thick) of specimens from Hawaii and Guam were stained with hematoxylin and eosin. One of us (DFD) measured cnidae of seven Pacific specimens as well as of the specimen of *Isadamsia cancrisocia* from smash preparations. Not all tissues of every non-type specimen were examined.

RESULTS

All the actinians belong to a single actiniid genus. Carlgren (1949) called it *Isadamsia*,

and accurately characterized it as having smooth column, circumscribed endodermal sphincter muscle, short tentacles, several cycles of perfect mesenteries of which the first three orders are sterile, and weak, diffuse mesenterial retractor muscles. The name *Stylobates*, however, has priority over *Isadamsia*. The type species, by monotypy, is *S. aeneus* Dall 1903 (Boss, Rosewater, and Ruhoff 1968), described from *Albatross* station 3893, in the Kaiwi Channel between Molokai and Oahu, Hawaiian Islands, based on the shell. Although the name was based on "the work of an animal," since it was published prior to 1931, it is available for the actinian [Article 16 (a) (viii), International Code of Zoological Nomenclature].

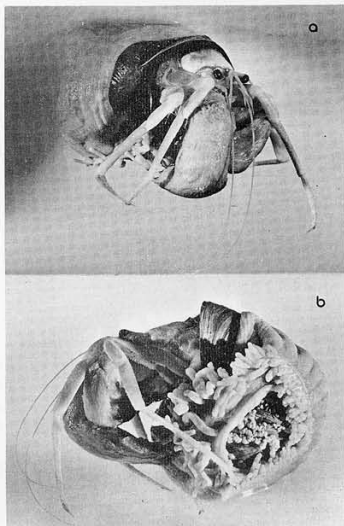


FIGURE 1. Two views of *Stylobates aeneus* and *Parapagurus dofleini* (specimen 011029, California Academy of Sciences). Shell aperture 35 mm greatest diameter. *a*, apex of shell at upper left; *b*, mesenterial filaments visible through gaping mouth, typical of preserved specimens; longitudinal ridges due to mesenterial insertions pulling on thin column wall. (Photograph by Lloyd E. Ullberg.)

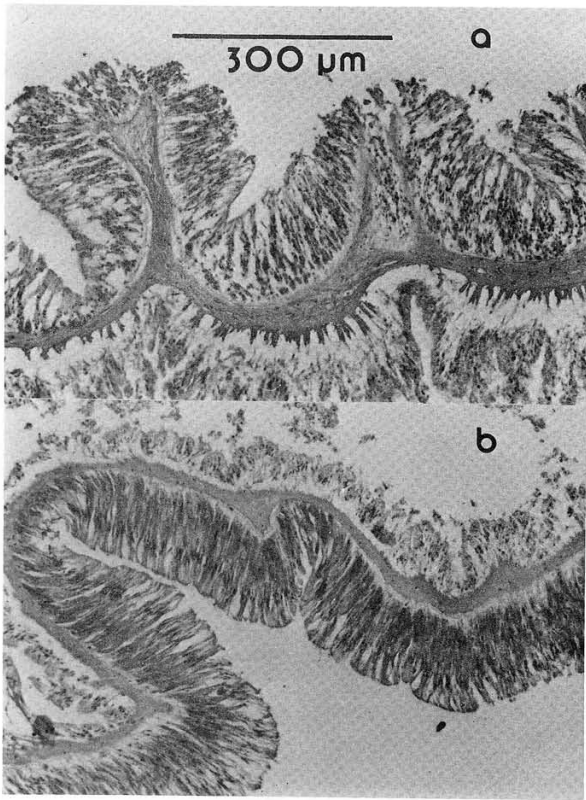


FIGURE 2. Photomicrograph of column (a) and pedal disk (b) ectoderm of *Stylobates aeneus* (specimen 011030, California Academy of Sciences).

The word *stylobates*, which may be translated roughly as “a walker on stilts,” is perhaps even more appropriate for the actinian than it was for Dall’s presumed mollusk. [And in naming the species *aeneus* (Latin, meaning “made of copper or bronze”), could Dall also have had in mind Aeneas, who carried his father on his back out of fallen

Troy? The old master was not above this sort of thing.]

The actinian is oriented with its oral disk behind and below the aperture of the carinoecium, beside the umbilicus (Figure 1). The pedal disk completely covers the shell in life, although in preserved specimens it is drawn back from the lip (Figure 1). Typical

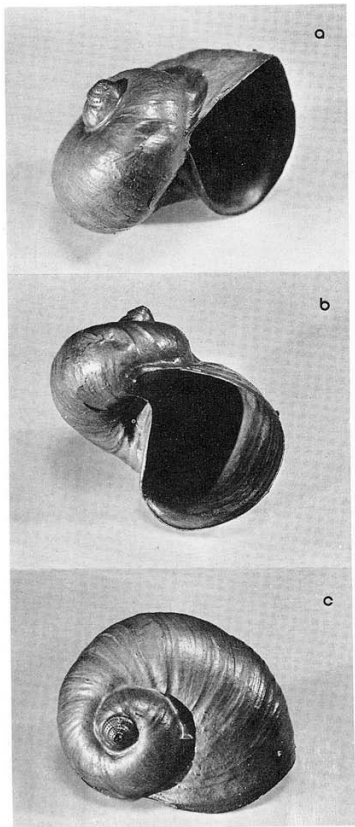


FIGURE 3. Three views of anemone shell (carcinocodium) made by *Stylobates aeneus* (ex Bishop Museum lot 1979.529). Note growth rings, papillose "protoconch" at angle to carcinocodium, umbilicus. Shell aperture 30×38 mm; greatest width of shell 60 mm. (Photograph by Lloyd E. Ullberg.)

actinians are cylindrical in shape, with oral and pedal disks perpendicular to the column wall. However, the column of an average-

sized *Stylobates* is about 50 mm long on one side (at right in Figure 1b), extending almost completely around the shell, but only about 6 mm long on the opposite side (at left in Figure 1b). Thus, pedal disk and column wall are parallel over the shell, which they invest like a membrane. The animal is bilaterally symmetrical, with its directive axis perpendicular to the median oral-aboral plane passing through the shortest and longest spans of the column (the directive axis is nearly vertical in Figure 1b). The column of the anemone is pale pinkish-tan to colorless, but the pedal disk is typically either deep brown or lighter in hue than the column. This gross difference is apparently attributable to histological differences between column and pedal disk ectoderm (Figure 2). Cells of the former are loose and vacuolated; those of the latter are tightly packed, high columnar, and glandular. We infer, as did Dall (1919) and Carlgren (1928a, 1928b), that the pedal disk secretes the carcinocodium, and this histology supports that conclusion.

The *Stylobates* shell was well described by Dall (1903); all that we examined are trochoid with dextral coiling, three to four whorls, a broadly ovate aperture, and a deep umbilicus (Figure 3; Carlgren 1928b: figs. 8-10). They are brassy in color, opaque, of a papery texture, and readily dented or torn. Growth rings (Figures 1b, 3) concentric with the lip [also noted by Dall (1903) and Carlgren (1928b)] are typically the only sculpture, but the apical surface of one is papillose (Figure 3).

The anemones from Hawaii and Guam belong to a single species, judging from sphincter form and cnidae. Their shells being of similar size and nature to Dall's holotype, we refer them to *Stylobates aeneus*. The single east African specimen that we examined, illustrated in Carlgren's (1928a: plate 2, fig. 9) original description of *Isadamsia cancrisocia*, represents a distinct species, the second of the genus, *S. cancrisocia*. Cnidae of most categories are smaller in the latter than in the former species (Table 1), the difference being greatest in column basitrichs. It is unlikely that this is related to the only slightly smaller size of the east

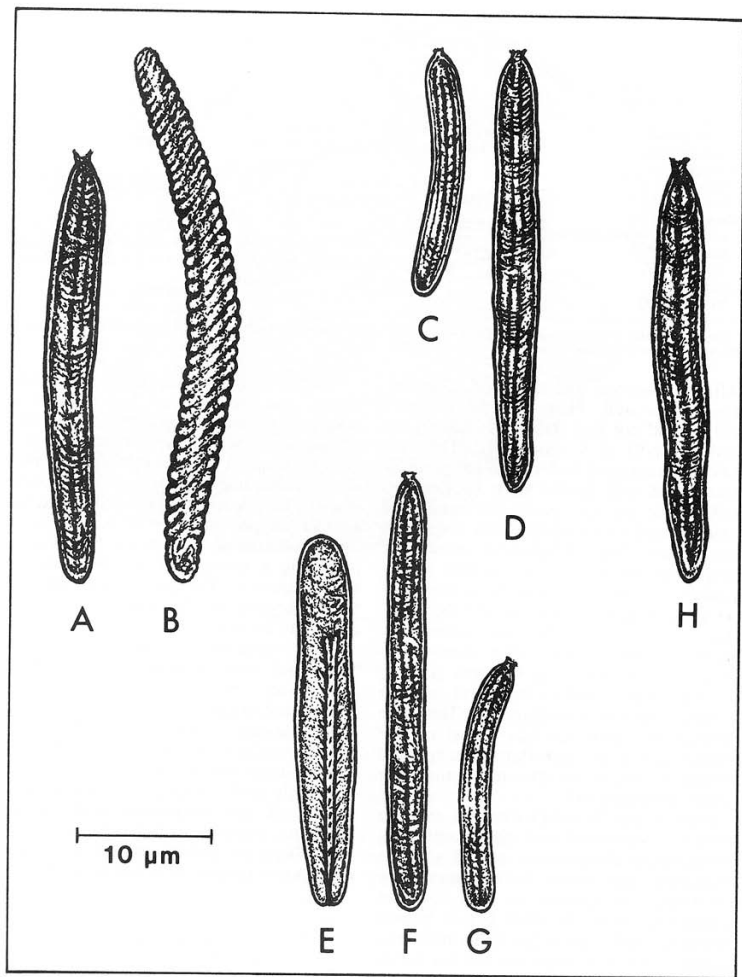
FIGURE 4. Cnidocytes of *Stylobates aeneus*. (Drawings by Steven Sechovec.)

TABLE 1
CNIDAE OF *Stylobates aeneus* AND *S. cancrisocia*

<i>S. aeneus</i>	<i>S. cancrisocia</i>
Tentacle	
basitrichs (A)	27.9–36.1 × 3.1–3.9, N = 43
spirocysts (B)	(25.4) 28.7–44.3 × 2.9–4.1 (4.9), N = 40
Actinopharynx	
basitrichs (C)	17.2–21.3 × 2.5–3.1, N = 9
basitrichs (D)	(26.2) 29.5–37.7 × 2.9–4.1, N = 38
Mesenterial filaments	
microbasal <i>p</i> -mastigophores (E)	21.3–29.5 × 3.9–5.7, N = 27
basitrichs (F)	29.5–36.1 × 2.5–3.9, N = 21
basitrichs (G)	15.6–23.0 × 2.1–3.3, N = 58
Column	
basitrichs (H)	29.5–36.1 × 2.9–3.5, N = 24
	27.1–30.3 × 2.5–3.3, N = 11
	23.8–39.4 × 2.7–3.3, N = 10
	Not seen
	27.1–31.2 × 2.5–3.3, N = 10
	18.9–23.0 × 4.1–5.7, N = 11
	(25.4) 27.9–32.8 × 4.1–5.5, N = 14
	14.8–18.0 (20.5) × 2.1–2.5, N = 8
	23.0–28.7 × 2.7–3.3, N = 12

NOTE: N = number of cnidae measured; measurements in parentheses are for single cnidae falling well outside the usual range. Measurements are in micrometers. Letters refer to illustrations of cnidae from *S. aeneus* in Figure 4.

African specimen, and there are other differences as well. First, like us, Carlgren (1928a) did not find small basitrichs in the actinopharynx of *S. cancrisocia*. [The sizes of cnidae measured by DFD do not precisely correspond with figures given by Carlgren (1928a); he did not specify the number of animals and cnidae upon which his figures were based.] Second, sphincter muscles of several specimens of *S. aeneus* that we examined are similar (Figure 5) in that they have a stronger mesogleal axis, and the secondary mesogleal lamellae are consistently more pinnately arrayed than those of *S. cancrisocia* illustrated by Carlgren (1928a), in which the secondary mesogleal lamellae radiate from a short primary axis. Third, the shell of *S. cancrisocia* has a keel on the penultimate whorl just above the aperture (Figure 6, arrow), but that may be only an individual peculiarity.

Among the Hawaiian material are two very small trochoid snail shells containing specimens of *Parapagurus*, one of which is ovigerous, that could not be specifically identified. The actinian on each does not completely cover the shell but is located beside the umbilicus on the shell's underside, oriented as is *Stylobates*, and the few nematocysts we measured correspond in size to those of *S. aeneus*. In both, a thin, narrow sheet of brittle, translucent, yellow-brown chitinous material is attached to the lip of the shell and extends over the paguroid.

Four of 21 *Stylobates aeneus* shells from Hawaii that we dissected had remains of calcareous material in the apical region: two of these were gastropods, and two were portions of serpulid worm tubes. In all cases, the carcinoecium is of typical trochoid shape. The gastropod shell underlying the apex of the one specimen of *S. cancrisocia* that we examined is relatively high spired, producing a sharp apex on the anemone shell (Figure 6; Carlgren 1928a: plate 2, fig. 9). Beyond this "protoconch," the carcinoecium is trochoid.

Large numbers of carcinoecia from *Stylobates*, most containing hermit crabs and covered by actinians, are taken in Hawaii and Guam by dredging and in fish traps. The depth range of 93 trapped specimens from Guam was 250–500 m; the substratum in the area of capture was primarily or entirely sand (except for one site with 57 percent silt and 43 percent sand) (L. G. Eldredge, personal communication, May 1980). Depth and substratum correspond well with what is known of the habitat in Hawaii.

DISCUSSION

The evidence at hand suggests that *Stylobates* settles on a shell either before or after a hermit crab has occupied it. The pedal disk of the actinian secretes a chitinous membrane that gradually coats the shell.

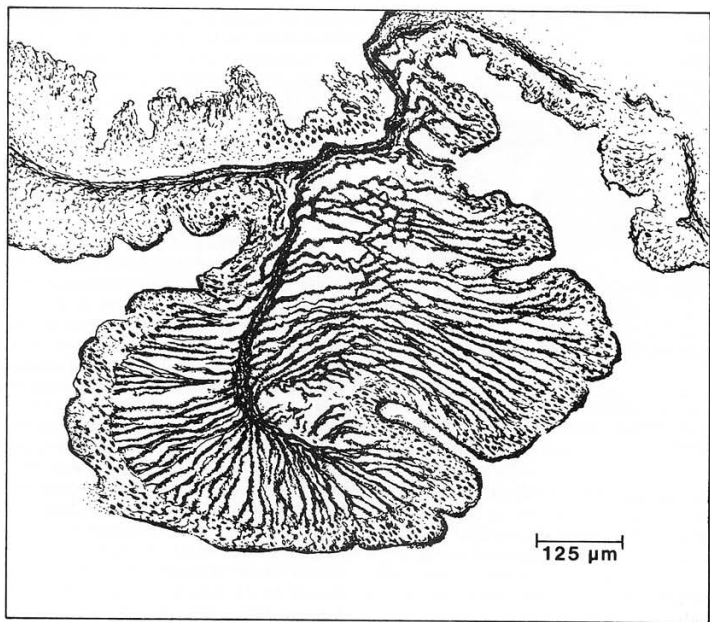


FIGURE 5. Cross section of circumscribed endodermal sphincter muscle of *Stylobates aeneus* (specimen 011030, California Academy of Sciences). (Drawing by Steven Sechovec.)

Sculpture on the original shell may be embossed into the apex of the anemone shell (Figure 3). We agree with Carlgren's (1928a) assumption that in cases where a large carinoecium lacks a calcareous shell beneath the apex, the shell has dissolved. The solubility of calcium carbonate increases with ocean depth (Correns 1955: 377). Species of the sea anemone *Paracalliactis* living at depths of several thousand meters completely cover the gastropod shells to which they are attached (Doumenc 1975), unlike shallow-water actinians which usually cover only a portion of the shell's surface. We favor a functional interpretation of this correlation, viz. that coverage of a shell impedes its dissolution at depth and thus is advantageous for both symbionts.

Our observations indicate that the shape of the original hermit shell exerts little if any effect on the ultimate shape of the trochoid carinoecium. The anatomy of the actinian, especially the curvature of its pedal disk and the difference in column length from one side to the other, may dictate the basic shell form. The fact that the axis of the sculptured "protoconch" of the shell illustrated in Figure 3 is set at an angle to the axis of the anemone shell supports this hypothesis. It is also possible that the hermit crab, in one way or another, mediates shell form. The hermit crab's larger cheliped, which closes the aperture of the shell much like a gastropod operculum, may serve as a template for the configuration of the growing apertural edge. Furthermore, all *Stylobates* shells

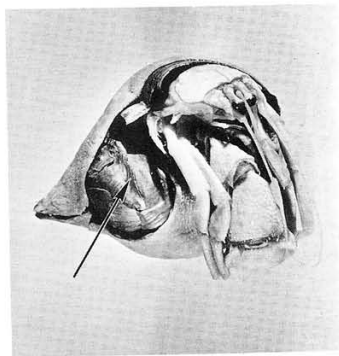


FIGURE 6. *Stylobates canerisocia* and *Parapagurus trispinosus* (specimen 6957, Museum für Naturkunde). Arrow indicates keel. (Photograph by Lloyd E. Ullberg.)

that we have seen are dextrally coiled. We know of nothing intrinsic to the anemone's anatomy to require preferential coiling in one direction, but the symbiotic hermit crabs are asymmetric and coiled to the right. Perhaps the paguroid's abdomen is the guide, as it evidently is in *Adamsia*, where the edges of the ovoid pedal disk wrap around the crustacean, its symmetrically elongate edges meeting along the dorsal midline, following the curve of the crab's abdomen (Faurot 1910).

In terms of Raup's (1966) geometric analysis of shell coiling, the *Stylobates* shell falls within the gastropod field, having low whorl expansion rate (w), moderate translation rate (t), and little distance between generating curve and axis (d). This correspondence is doubly intriguing because *Stylobates* lays down its shell from an external position, whereas mollusks secrete their shells while ensconced within. The *Stylobates umbilicus* is apparently produced by a portion of the anemone's pedal disk protruding inside it.

Perhaps the irregular shells that convinced Dall (1919) that he was not dealing with a gastropod might be products of anemones that could not produce an appropriate generating curve from positions on nontrochoid

shells. It is also possible that the shapes of some shells might totally prevent extension by *Stylobates* [e.g., that illustrated by Carlgren (1928a:plate 2, fig. 6; 1928b:fig. 1a)]. They may also be products of more than one actinian per shell, a situation that has been reported (Dall 1919, Miyake 1978) but that we have not seen. It seems highly improbable that two or three sea anemones could coordinate efforts to produce a single shell of such precise geometry.

The pedal disks of some actinians other than *Adamsia* and *Stylobates* also produce chitinous secretions. The hormathiid *Paracalliactis* is defined in part by its ability to form a cuticle that extends the shell to which the actinian attaches, and members of the monogeneric pelagic family Minyadidae form a basal, chitinous, porous mass that acts as a float (Carlgren 1949).

Another unanswered question is whether a single individual paguroid lives with a single actinian throughout the latter's life, or whether a succession of individual paguroids of the same or different species occupy one shell. Unless it were displaced by a more aggressive individual, as occurs in typical hermit crabs (Hazlett 1966, 1970), there should be no reason for the crustacean to leave a shell it had not outgrown; this assumes that the actinian can extend the carcinoecium fast enough to keep pace with the growth of the paguroid. Moreover, the delicacy of the shells, which might be torn during exit and entry, suggests that transfers are rare or absent. A definitive answer will require observation of living animals through time.

Shells of *Stylobates aeneus* that we examined are inhabited by *Parapagurus dofleini* Balss (identified by M. Takeda). The crab in the shell of *S. canerisocia* is the smaller *P. trispinosus* Balss. [Balss (1912) listed three female specimens of *Parapagurus arcuatus* var. *trispinosa* (but no actinians) from station 246. Saint Laurent (1972) recognized this variety as a distinct species, *P. trispinosus*. Carlgren (1928a) said that two of the four actinians from station 246 lacked crustaceans; he called them *P. armatus* var. *trispinosus*, clearly a *lapsus*.] This suggests species specificity between paguroids and ac-

tinians. It is possible that a single shell might be sequentially occupied by specimens of *P. trispinosus* and *P. dofleini*, which are broadly sympatric (although *P. trispinosus* is absent in Hawaii; Saint Laurent 1972). However, anatomy and physiology of these anemones are so specialized for a shell-making way of life that growth rate may well be adjusted to that of a specific crustacean associate.

Other published records allude to additional symbioses of this sort. Japanese specimens of *Parapagurus dofleini* reportedly live in shells "usually encrusted with one or two sea anemones" (Miyake 1978:76), but the nature of the shells is not given, and therefore they may be gastropod shells. Japanese *P. diogenes* are said to "inhabit in thin-shelled snails which are usually encrusted with one or two sea anemones. They were occasionally found in a large thin cuticular snail and a small true snail was embedded in the apex" (Miyake 1978:74). If this were a third species of *Stylobates*, the hypothesis of specificity between species of *Parapagurus* and species of *Stylobates* would be strengthened. An actinian identified as *Isadamsia cancrisocia* was reported from about 3500 m in the North Atlantic (Doumenc 1975). It is most unlikely that this identification is correct, but it probably means that a shell-forming actinian occurs there.

Small specimens of these symbiotic species of *Parapagurus* inhabit gastropod and other calcareous shells, and larger ones are also known to live in them (Miyake 1978). Presumably, the relationship with actinians is facultative for the crustacean. We also believe that the carcinoecium must be occupied continually by a hermit crab for the actinian to survive. In the absence of its symbiont, the sea anemone would probably lack for food, and the light shell might tumble about and thereby abrade the anemone. Thus, it is likely that the relationship is obligate for the actinian.

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