

Learning from the Collector: A Survey of Azooxanthellate Corals Affixed by *Xenophora* (Gastropoda: Xenophoridae), with an Analysis and Discussion of Attachment Patterns

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ABSTRACT

All species of the gastropod family Xenophoridae affix foreign objects to the upper shell surface. Affixed objects may include bivalve shells, smaller gastropod shells, shell fragments, and coral skeletons, as well as a wide array of inorganic material. In deep water, *Xenophora* may serve as useful proxy collectors of benthic organisms. Since 1842, coral skeletons have been noted among the attached objects, but this association has never been studied in detail. This paper surveys 227 *Xenophora* shells, comprising 8 species from 69 stations, for affixed azooxanthellate corals. Five hundred and eighty-one coralla were found, representing 74 coral species, 2 of which remain undescribed. Twenty-four of the affixed coralla were alive at the time the *Xenophora* hosts were collected; *Xenophora* not only collect live corals, but corals can remain alive long after being affixed. Corals were found at 6 sites where they had previously been unknown, and the geographic ranges of 29 species of coral were expanded as a result of specimens found on *Xenophora*.

This paper has two sections. In the first, quantitative observations were made on the orientation of affixed corals; statistical analysis of these observations revealed non-random patterns of attachment, based on orientation of both the long axis of the coral and the coral calice. Qualitative observations suggest that species of *Xenophora* favor corals of particular shapes. In the second section, the speculations of previous authors regarding the ecological basis for attachment behavior are summarized and new theories are discussed. Four of these explanations suggest defensive adaptations, and the remaining 3 are functional support adaptations. Three of these hypotheses (armor, tactile camouflage, and snow-shoeing) are proposed for the first time in this paper.

Key words: Carrier shells, Mollusca, gastropods, ahermatypic corals.

INTRODUCTION

According to Ponder (1983), the monotypic gastropod family Xenophoridae contains 25 Recent species of *Xen-*

ophora, marine gastropods that inhabit the continental shelf and slope regions of tropical and temperate oceans. *Xenophora* have drawn the attention of naturalists and systematists since the early 1800s. This was caused primarily because of a peculiar behavioral pattern: all species affix objects to the upper surface of the shell throughout some or all of its growth (see Shank, 1969 for a detailed description of the affixing procedure in *X. conchyliophora* (Born, 1780)). Although objects are only affixed at the growing edge of the whorl, older attachments remain on the perimeter of earlier whorls as the shell increases in size. Older attachments often become secondarily affixed to the younger whorl that is formed beneath them. One of the traits used to distinguish species of *Xenophora* is the degree to which the shell surface is obscured by attachments (Ponder, 1983).

A great diversity of material has been found affixed to *Xenophora*: among the objects we observed in the course of this study were coral skeletons, bivalve and other mollusk shells, brachiopod shells, echinoderm spines and skeletal fragments, bryozoans, sponges, sharks' teeth, and a wide assortment of inorganic fragments.

Although corals typically comprise less than 10% of the affixed objects, their presence on *Xenophora* shells was first recorded a century and a half ago (Reeve, 1842). Pourtalès (1871) was the first to report a deep-sea (azooxanthellate) coral, *Caryophyllia cornuformis* Pourtalès, affixed to a *Xenophora* shell, collected from the Straits of Florida at 433-454 m. In this case, the coral remained alive after attachment. Morton (1958) listed living, solitary flabellid corals affixed to *X. corrugata* (Reeve, 1843) from New Zealand, and Kawase (1996) identified 4 species of azooxanthellate corals on *X. pallidula* (Reeve, 1842) from Japanese waters. Cairns (in press) reported 19 azooxanthellate species affixed to xenophorid shells collected from the slope region of

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Vanuatu (=New Hebrides) (Figure 6), prompting the research presented here. In summary, there have been several published observations of deep-water corals affixed to *Xenophora*, but no comprehensive review of the association.

Xenophora are not highly mobile (Berg, 1975). It is therefore possible for one to learn something about the benthic fauna of a particular region by examining the local *Xenophora*. Although some species are found only in shallow water, most *Xenophora* inhabit regions well below the penetration depth of photosynthetically active radiation, and specimens have been dredged from depths exceeding 1000 m (Ponder, 1983). Because relatively little is known about the deep-water benthos, deep-dwelling *Xenophora* are potentially useful as proxy collectors.

In the process of examining *Xenophora* shells for affixed corals, we noticed that there appeared to be some regularity in orientation of affixed objects with respect to the shell. These apparent trends, in the context of the previously documented observation that *Xenophora* attach lamellibranch valves with the concave side up (Ponder, 1983; Morton, 1958; Linsley and Yochelson, 1973; Shank, 1969), led us to look for statistical patterns in the manner and orientation of coral attachment. The results of that analysis are presented in this report.

MATERIAL AND METHODS

Two hundred and twenty-seven coral-bearing *Xenophora* shells were examined: 145 of these are from the collections of the National Museum of Natural History (USNM), Washington, DC; 42 from the Muséum national d'Histoire naturelle (MNHN), Paris; 38 from the Delaware Museum of Natural History (DMNH), Wilmington; and 2 from the Museum of Comparative Zoology (MCZ), Cambridge. Appendix 1 lists the stations at which coral-bearing *Xenophora* were collected, the station data, and the coral species collected at those stations. The study material includes shells collected throughout the Indo-West Pacific, Hawaiian Islands, and the Gulf of Guinea. Eight coral-bearing species of *Xenophora* were examined, a large majority of the specimens (166/227, including all shells borrowed from the MNHN and DMNH) belonging to the species *X. pallidula*. The other 7 species, in order of abundance were: *X. japonica* Kuroda and Habe, 1971, *X. peroniana kondoi* Ponder, 1983, *X. corrugata*, *X. cerea* (Reeve, 1845), *X. neozelandica* Suter, *X. crispa* (König, 1831), and *X. granulosa* Ponder, 1983. The 145 USNM specimens included all coral-bearing shells in the USNM collections, with the exception of those belonging to *X. conchyliophora*, which is typically found in shallow water (Ponder, 1983), and certain lots of *X. peroniana* and *X. japonica*, which preliminary examination showed to be redundant in terms of sites sampled and corals collected.

When possible, corals were identified to the species level; when only a coral fragment or badly eroded or damaged corallum was present, it was identified to the

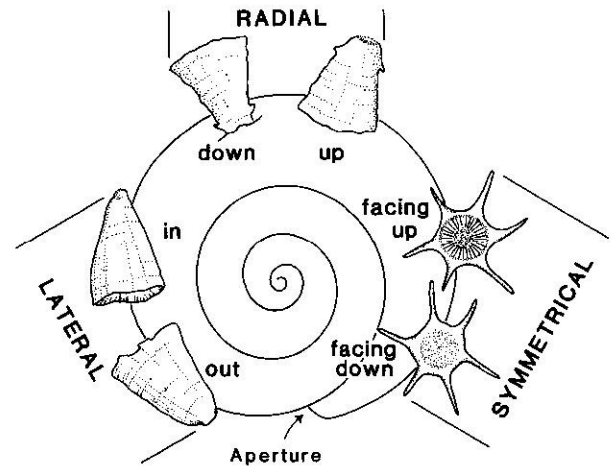


Figure 1. Diagram of the apical view of a *Xenophora* shell, illustrating the various types of orientations in which a solitary coral may be affixed: radial (up, down), lateral (out, in), and symmetrical (facing up, facing down). Note: Number of apical whorls underrepresented in figure.

lowest possible taxonomic level (typically genus). Undescribed species were designated by a letter. If a well-preserved but unidentifiable phenotype appeared repeatedly, it was given the designation n. sp. Any corallum that contained remnants of dried coral tissue or was exceptionally well preserved was considered to have been alive when the *Xenophora* was collected.

Every coral found was classified as a primary or secondary attachment. Primary attachments were those that were embedded in the shell and had clearly been affixed by the *Xenophora*; secondary attachments included those corals growing on a substrate which was subsequently affixed to the *Xenophora* and those that settled upon the surface through no action of the *Xenophora*. The length of the long axis (maximum dimension, regardless of the orientation of morphological features) of each coral skeleton was recorded. The orientation of the long axis was classified as radial, meaning roughly perpendicular to the arc of the whorl; lateral, meaning roughly parallel to the arc of the whorl; or symmetrical, meaning that all axes of the coral were equal. The orientation of the calice (Figure 1) was also noted as being: up or down (a subset of radial orientation), in or out (a subset of lateral orientation) or facing up or facing down (a subset of symmetrical orientation). We applied statistical hypothesis testing (chi-square test) to the orientation data, using as our null hypothesis the assumption that each type of orientation would have the same chance of occurring.

We measured each *Xenophora* shell across the shell base, and took the maximum diameter as a proxy for shell size. For selected *X. pallidula*, we measured the diameter of each whorl, both with and without attachments. Using a circular approximation for area, we calculated the ratio of shell basal area (radius measured, not including attachments) to expanded shell basal area

Table 1. Numerical distribution of azooxanthellate scleractinian genera, species, and individuals per families of coral-bearing *Xenophora*.

Family	Genera	Species	Individuals
Pocilloporidae	1	0	1
Fungiacyathidae	1	2	3
Micrabaciidae	1	1	3
Oculinidae	1	1	3
Anthemiphylliidae	1	3	9
Caryophylliidae	8	34	181
Turbinoliidae	5	5	6
Flabellidae	5	21	241
Gardineriidae	1	1	7
Guyniidae	2	2	4
Dendrophylliidae	3	4	56
Unidentifiable to genus	—	—	67
TOTALS:	29	74	581

(radius measured, including attachments) for each shell whorl. These ratios were analyzed for statistical trends; Pearson product-moment correlation coefficients and the respective tests of significance were computed with the aid of Statview SE statistical software. For selected *Xenophora solaris* (Linnaeus), we counted the number of spines per whorl and analyzed these data for any trends, again using Statview SE.

Lists of coral species previously reported were available for 2 series of stations (*Albatross Expedition*, Cairns and Zibrowius (1997); MUSORSTOM 8 Expedition (Cairns, in press)). We compared the list for each station with the corals that we found affixed to the *Xenophora* at that site, and noted any instances of affixed corals not previously known from that location, as well as which corals were potentially available for fixation but were not affixed.

RESULTS

A total of 581 azooxanthellate coralla were found affixed to *Xenophora* shells, 511 of which were identifiable to genus, and 411 to species. The affixed coral fauna represents a diverse taxonomic distribution, including species from all 5 suborders in 11 families, 29 genera, and 74 species. The only zooxanthellate coral species encountered was *Fungia (Cycloseris) vaughani*, found on *X. peroniana* from the Hawaiian Islands. Table 1 shows the numerical distribution of genera, species, and individuals among families of corals and the *Xenophora* species that affixed them. A taxonomic list of all azooxanthellate coral species is included in Appendix 2.

Sixty-seven of the 74 species were recognizable as described species of Scleractinia. Of the remaining 7, 5 (designated as sp. A or sp. B) are represented by single specimens and may be aberrant examples of described species. The remaining 2 are considered undescribed species. One of the undescribed species had previously been observed in dredged samples from the same re-

gion, and illustrated by Stolarski (1996) as "*Gardineriidae* gen. n." Seven well-preserved specimens of this taxon were found on 3 *X. pallidula* shells from MUSORSTOM stations 1008 (Figures 8–9), 1087, and 1088 off the coast of Vanuatu (= New Hebrides). The second undescribed species belongs to the genus *Placotrochides* and is represented by 4 specimens affixed to 2 *X. peroniana* shells from 2 stations in the Hawaiian Islands. The genus *Placotrochides* had not previously been collected near the Hawaiian Islands, and no other truncate flabellids (transversely dividing members of the family Flabellidae) are known from the area. Even though none of the specimens of *Placotrochides* n. sp. is particularly well preserved (Figure 10), they are clearly not members of other described *Placotrochides* species.

Large specimens of *Truncatoflabellum gardineri* Cairns and Keller proved to be new size records for that species. The previously listed maximum length for *T. gardineri* was 18.7 mm. We discovered 8 specimens larger than that, the largest (USNM M818232) measuring 27.5 mm from base to calice (Figure 7).

Xenophora frequently collected corals that were not previously known from their source station: in 74 instances, a coral species found affixed to *Xenophora* from a given site had not previously been found at that site. These discoveries expanded the known geographic ranges of 29 coral species. Coral-bearing *Xenophora* were also found at 6 sites (*Albatross* 5121, 5394, 5395, 5416, 5661; MUSORSTOM 8–1008) where dredging had not previously produced any corals at all.

There are definite patterns in the orientation of affixed corals. Seventy-two percent, 359 of 498 non-symmetric coralla, were positioned with the long axis radial rather than lateral (Figure 1); occurrence of such a high percentage of radially oriented coralla is extremely unlikely ($p \ll 0.01$) if *Xenophora* affix corals at random, without regard to orientation of the long axis. Calice orientation was also distinctly non-random. The down and out orientations were encountered significantly more times than it would have been if *Xenophora* ignored calice orientation ($p \ll 0.01$), whereas the up and in orientations were encountered significantly fewer times. Certain shape classes were attached in a specific manner: conical corals were typically oriented radially with the calice in the down position (Figures 1, 4), whereas flabellids were typically oriented laterally with the calice in the out position (Figures 1, 3, 5). Symmetrical flat corals were found (with only 1 exception among 92 flat corals) with the calice facing up (i.e., with the base cemented to the shell).

Early observations led us to hypothesize that *Xenophora* select objects preferentially based on shape. The shells from MNHN frequently collected *Bourneotrochus stellulatus* Cairns, a small, coin-shaped, spinose coral, but none of these morphological traits appeared in significant numbers at other regions or in other collections. By contrast, we noted a high frequency of attachment for both flabellate and comute coralla at widely distributed sites. It is difficult, however, to test these frequen-

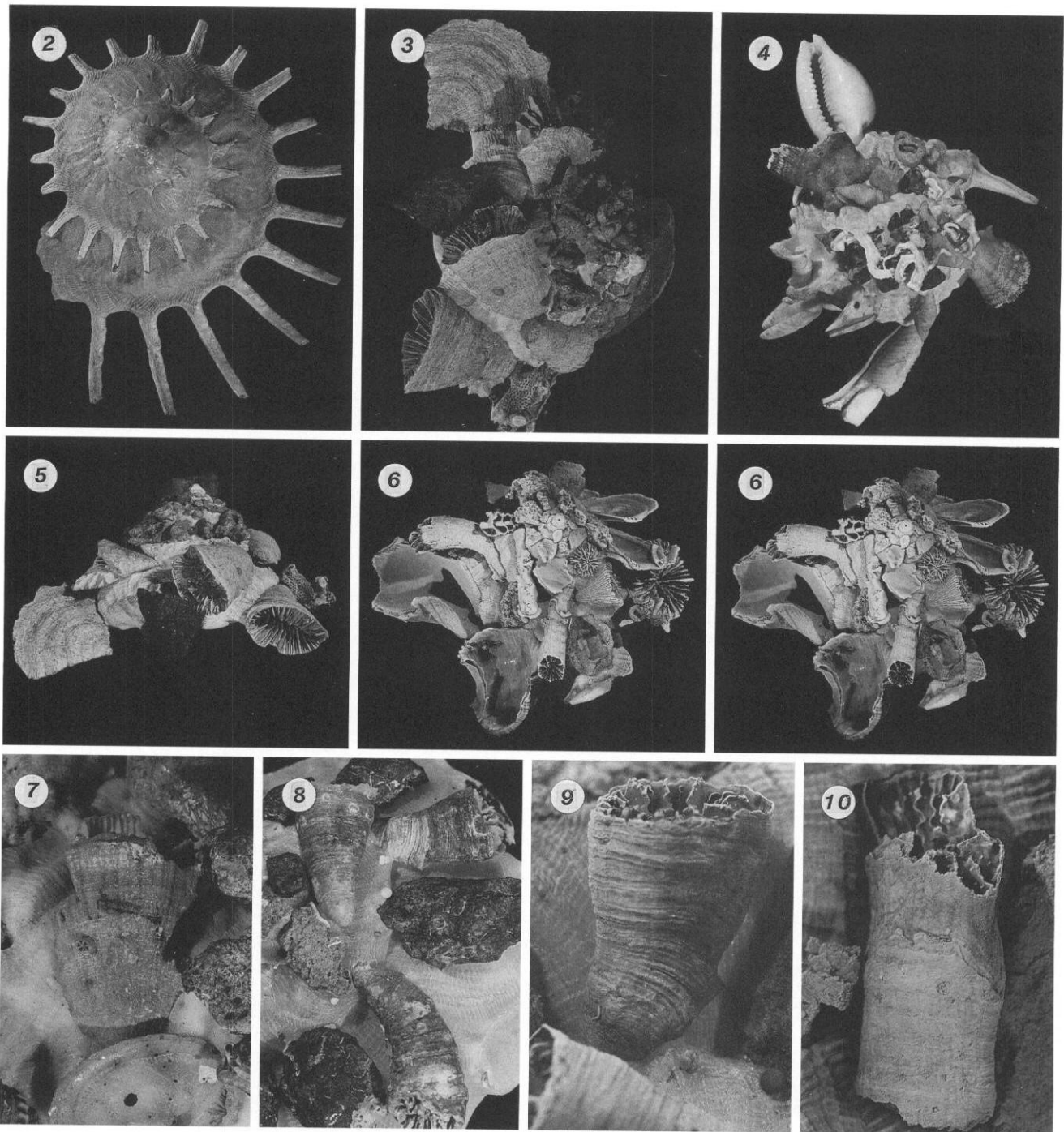


Figure 2. *Xenophora solaris* from Maqueda Bay, Philippines (DMNH 5173): apical view, $\times 0.82$. **Figures 3, 5.** *X. pallidula* from off Zululand (DMNH 20120): apical and lateral views showing live *Truncatoflabellum gardineri* affixed in the in and out lateral positions, $\times 0.75$, $\times 0.58$, respectively. **Figure 4.** *X. pallidula* from Sulu Sea (W498)(USNM M807763), showing two live coralla of *Trochocyathus cooperi* affixed in the radial (down) position. **Figure 6.** Stereo apical view of *X. pallidula* from MUSORSTOM 8-963 (MNHN), illustrating a heavily "encrusted" shell with 6 species of solitary coral. **Figure 7.** Largest known (length 27.5 mm) corallum of *Truncatoflabellum gardineri* affixed to *X. pallidula* from off Durban (W320) (USNM M818232), $\times 1.4$. **Figures 8-9.** Coralla of three live "Gardineriidae, n. gen. n. sp." affixed to *X. pallidula* from MUSORSTOM 8-1008 (MNHN), figure 9 showing rejuvenescence from presumed growth trauma scar following fixation, $\times 2.8$, $\times 6.5$, respectively. **Figure 10.** Corallum of *Placotrochides* n. sp. affixed to *X. peroniana* from David Starr Jordan TC32-2 (USNM M807659), $\times 7.1$.

cies for statistical significance, as each *Xenophora* has a different range of shapes available, and it would be necessary to know if the frequencies of attachment were significantly different from the frequencies at which the various shapes occur unattached. The latter figures are not available due to lack of data.

A small number of affixed corals (24 specimens, approximately 4%) were alive at the time their *Xenophora* hosts were collected. Only 3 of these were secondary attachments, allowing us to confirm that *Xenophora* actively affix living corals, if only at a low frequency. Living corals were often affixed to earlier whorls, and typically bore a visible growth-trauma scar on the theca (outer surface). The presence of live-at-collection corals on earlier whorls indicates that corals may survive after attachment, and a growth-trauma scar (Figure 9) suggests that they also continue to grow. Relative frequencies of "live" and "dead" corals on *Xenophora* shells cannot, unfortunately, be compared with relative frequencies of living corals and coral skeletons *in situ* because the latter figures are unknown. It is therefore impossible at this time to state whether *Xenophora* preferentially selects or avoids living corals, although the small number of living corals suggests that it is unlikely that live specimens are preferred.

DISCUSSION

DESCRIPTIVE DATA

The examination of 227 *Xenophora* shells brought to light 2 undescribed species of coral, increased the size range for one described species, and extended the geographic ranges for 29. Had the shells been examined immediately upon collection, the results would have been even more impressive: 215 of the 581 corals were found on *Xenophora* collected by the *Albatross* cruises before 1910, at which time 24 of the collected species (32%) were undescribed.

Admittedly, *Xenophora*-based sampling has limitations. There was not a single case in which we found every coral known to exist at a given site (i.e., at a station where coral was previously recorded) affixed to *Xenophora* shells. Altogether, 41 species of coral known to co-occur with *Xenophora* were not affixed by the gastropod. This may be an artifact of the small number of *Xenophora* typically known from each site, but, given the broad expanse of the benthic plain and the unknown population densities of *Xenophora*, samples are likely to remain small. Many of the non-collected coral species were only passed over 1 time (i.e., were only present at 1 *Xenophora* source station where they were not affixed). This single occurrence makes their omission statistically negligible, but others were conspicuously absent from *Xenophora* shells, suggesting that there are groups within azooxanthellate Scleractinia which *Xenophora* does not affix. The reasons behind this are often clear: for example, *Xenophora* is unlikely to affix any coral that settles and anchors firmly onto hard substrate. Similarly, colonial corals are typically too bulky and irregular to be

affixed. There is a strong possibility of a selection mechanism in *Xenophora* that causes them to choose certain more suitably shaped corals over others.

Still, it is difficult to dispute the usefulness of *Xenophora* as proxy-collectors. Examination of any *Xenophora* collected in a dredge sample may reveal attached species that were not otherwise collected in that sample. Because blind dredging is still the most common method for sampling the benthos, any method that complements or makes more complete use of the dredged sample should not be overlooked.

ATTACHMENT BEHAVIOR

Introduction: Arthur Adams (1848:248), the naturalist and assistant-surgeon on board the H.M.S. *Samarang*, observed *Xenophora* (species unknown) during an 1842 voyage from Singapore to Java. Adams remarked: "In order for them to escape from their enemies, nature has instructed them to cover their shells with the same material as those of the banks which they inhabit." Adams' rationale is understandable. Many people, both shell-collectors and scientists, have made the same assumption about *Xenophora*. In the modern era of deep-sea exploration, however, it is unreasonable to accept the visual camouflage hypothesis for those species of *Xenophora* that live below the depth of light penetration.

Although many of the frequently attaching species can be found in relatively shallow water, 2 of the most spectacularly encrusted species (*X. pallidula* and *X. japonica*) range deeper than their congeners (Ponder, 1983). Object attachment is an energetically expensive behavior (Shank, 1969). For *Xenophora* to attach an object to the growing edge of the shell it must first select and properly position the object (see Shank, 1969), and then affix it by secreting shell material around it, using more calcium carbonate than would be required to secrete an equivalent section of shell. Given that members of the family Xenophoridae are found in the fossil record as far back as the Cretaceous, it is unlikely that such an energetically expensive behavior would persist if it was purely non-adaptive.

A number of hypotheses have been suggested to explain attachment behavior. These fall into 2 broad, mechanistic categories: defense and functional support. Table 2 lists the various hypotheses and the authors that have supported them in the past. It is rare for any author to cite just one hypothesis, but no recent efforts have been made to collect and review all the hypotheses, although Linsley and Yochelson (1973) and St. Jean (1977, 1983) provided the most comprehensive review previous to this report.

Defense Theories: Most authors still regard camouflage as the most likely explanation for object fixation by *Xenophora*. Camouflage usually implies *visual concealment*, but in the case of deep-water *Xenophora*, it must be expanded to include *olfactory concealment* as well. Shank (1969: 5), one of the few people to maintain *Xen-*

Table 2. Outline of possible adaptive advantages of attachment behavior in *Xenophora*, and those authors who have discussed those views.

I. Defensive
A. Camouflage
1. Visual (Adams, 1848; Morton, 1958; Shank, 1969; Linsley and Yochelson, 1973; Berg, 1975; St. Jean, 1977, and 1983; Das, et al., 1981; Ponder, 1983)
2. Olfactory (Shank, 1969; Linsley and Yochelson, 1973; St. Jean, 1977, 1983; Ponder, 1983)
3. Tactile
B. Armor Hypothesis
II. Functional Support
A. Snowshoeing
B. Increased Shell Stability (Berg, 1975; St. Jean, 1983)
C. Feeding Cone Hypothesis (Shank, 1969; Linsley and Yochelson, 1973; Berg, 1975; St. Jean, 1977, 1983)

ophora alive in aquaria for any length of time, remarked that "everything [*Xenophora*] do points to a means of eluding detection." While observing captive specimens of *Xenophora conchyliophora*, a species typically found in shallower water, Shank witnessed the animals burying their feces, a behavioral trait generally associated with predator evasion (Shank, 1969; Linsley and Yochelson, 1973). Shank and others have also observed that the peculiar and discontinuous motion of *Xenophora* would be less likely to attract the attention of a predator, and might create less of a chemical trail than the "crawling" movement of many gastropods (Shank, 1969; Linsley and Yochelson, 1973; St. Jean, 1977, 1983).

These observations are of value for understanding the ecology of a shallow-water species of *Xenophora*, but may not be generalizable to all species in the family. Linsley and Yochelson (1973) observed (Linsley's observations) live *X. neozealanica* for several months and did not witness the feces-burying behavior recorded by Shank. Additionally, they noted that, despite the characteristically discontinuous motion of *X. neozealanica*, the animal's foot was in contact with the sediment frequently, implying that the discontinuous trail hypothesis is less likely for that species.

Tactile camouflage is also a possible advantage of affixing objects. If animals that find prey by touch encounter *Xenophora*, the peculiar assortment of attachments might confuse them. We consider this hypothesis unlikely due to the lack of complete shell-coverage in many species. Although *X. conchyliophora* and *X. japonica* are often completely covered, other species that frequently show attachments (e.g., *X. pallidula*, *X. peroniana*, and *X. crispa*) do not coat their entire shells with affixed objects. The attachment pattern of this latter group would probably only deter a cursory chemo-tactile search, and, in the case of shallow-water specimens, would be unlikely to deceive a visually orienting predator.

To our knowledge, the suggestion that objects are attached as a means of *armoring shells* against predators

has not previously been made. Ponder (1983), however, noted that the shells of some *Xenophora* species are quite thin. Considering the extent to which some species, such as *X. conchyliophora*, are encrusted, one may theorize that objects are affixed to enhance the protective value of the shell. There are a number of arguments that can be made against this hypothesis. Whereas it is not known what type of animal preys upon *Xenophora*, both Berg (1975) and Linsley and Yochelson (1973) attempted to elicit an escape response from *Xenophora* (*X. conchyliophora* and *X. neozealanica*, respectively) by confronting them with starfish and predatory gastropods. Linsley and Yochelson (1973: 5) reported that "the general reaction to these predators was one of apparent unconcern." Berg (1975) lists several species of fish as principle predators. Affixed objects may have made *Xenophora* immune to predation from drilling gastropods; however, armor of this type would provide little defense against predation by malacophagous fish, which routinely crush far more durable shells (Berg, 1975). As noted above, few *Xenophora* are as thoroughly covered as *X. conchyliophora*. The mechanism of attachment is arguably inefficient for producing armor: any object affixed in such a way that it projects out from the shell margin is largely useless as armor until the next whorl is formed under it. Finally, the species of *Xenophora* that do not frequently affix foreign objects produce either a projecting, unbroken flange, or a fringe of radial spines or digitations (Figure 2), which suggests a function analogous to that of the projecting fringe of attachments, but lack any armoring potential. It has been argued that other gastropods, such as the genus *Murex*, produce spines to expand their effective size and make themselves less vulnerable to predators (oral pers. comm., M. G. Harasewych). Berg (1975) has observed that the affixed objects quadruple the basal area of *X. conchyliophora*, so *Xenophora* may also be employing this mechanism.

Functional Support Theories: The gross morphological similarity between frequently attaching and spine/flange-producing species of *Xenophora* (Figure 2) is the source of several structural theories. That certain structural features appear to be present in all species argues powerfully for a common functional basis. Ponder (1983: 43) has noted this similarity remarking for *X. pallidula* that "this species habitually attaches large, often elongate shells in a radial fashion, so that they presumably function in the same way as digitations on some other species." We believe that the analogy can be expanded in some respects to all known species of *Xenophora*.

As mentioned above, the flange or spines produced by some *Xenophora* expand the effective radius of the shell in much the same way as the projecting fringe of attachments. One possible purpose for this projecting "skirt" is suggested by the material nature of the benthic plain: if *Xenophora* commonly inhabit soft (i.e., high water content) substrates, they run the risk of sinking and suffocation. Thayer (1975:185) has assembled a list of the various methods used by invertebrates to confront

this danger, among which is the so-called "snowshoe" effect: "The potential value of a broad, flat form to distribute the weight of an organism has long been recognized. In 1909, Hornell (p. 92) suggested that the windowpane oyster, *Placuna placenta*, was able to live on soft mud by employing 'the same principle as is embodied in the use of snowshoe'". Although snowshoeing has not been mentioned in the literature on *Xenophora*, both attachments and flanges seems to have the structural potential to serve that purpose.

More careful scrutiny reveals significant problems with this hypothesis. In order to snowshoe effectively, *Xenophora* would be expected to select for broad, lightweight objects that expand the contact profile as much as possible while minimizing the addition of weight. But *Xenophora* from certain regions manufacture an attachment fringe entirely from elongate gastropod shells, which would penetrate the surface of soft substrate with little resistance. Also, several species of *Xenophora* often bear more than their own weight in attachments (Shank, 1969; Linsley and Yochelson, 1973). Our own observations suggest that *Xenophora* attach objects with little regard to weight.

Because mass increases in proportion to volume, with the cube of length, we expected that the expanded basal area produced by the attachments would increase relative to the basal area of the shell as the animal grew to mature size. We found the opposite to be true for *X. pallidula*: the ratio of expanded shell basal area with attachments to shell basal area without attachments decreased significantly ($p < 0.01$) in the larger whorls. In other words, as *Xenophora pallidula* grow larger, their hypothetical snowshoe becomes relatively smaller. Though the same test could not be performed on the spines of *X. solaris* due to the large number of broken spines, we found that the number of spines per whorl increased statistically ($p < 0.01$). Thus, *X. solaris* is increasing the area of contact with the substrate by decreasing the angular interval between spine production (Figure 2). Although this itself is not convincing evidence of snowshoeing, it suggests that more thorough morphometric analysis of *X. solaris* is needed.

Multiple authors have noted that the expanded base provides added stability to the shell (Shank, 1969; Berg, 1975; St. Jean, 1983). Although Shank (1969) and Berg (1975) observed that *Xenophora* is capable of righting itself even if overturned in soft sediment, both also noted that the righting procedure is time-consuming. *Xenophora* may be in greater danger of predation when overturned, either due to lack of camouflage or to exposure of the apertural surface. If this is the case, reducing the amount of time spent overturned and in the righting process would give attaching and flange/spine-producing *Xenophora* an advantage over less derived forms. We consider this stability hypothesis to be relatively unimportant: although it is empirically true that *Xenophora* are more stable than they would be without the spines, flange, or attachments, without further ecological knowledge it is impossible to say whether this

provides a selective advantage. Some potential predators of *Xenophora*, such as fish, would certainly be capable of flipping the shell, even assuming that an upright shell would be less vulnerable than an overturned shell.

One significant structural feature is conserved among all species of *Xenophora*: the apertural surface of the shell is raised off the substrate, although different species may achieve that using different structures (e.g., spines, flange, attachments). This has been observed by Shank (1969), Linsley and Yochelson (1973), and St. Jean (1977, 1983). Linsley and Yochelson place particular emphasis on this trait, suggesting that the "stilt" effect provides a means of olfactory camouflage by allowing the *Xenophora*'s body to remain suspended above the substrate and thus leaving a discontinuous scent trail. We believe that the "stilts" may also aid in the feeding process by providing a broad-based feeding cone under which the animal is able to graze. This hypothesis is supported by its sedentary lifestyle. As Shank (1969:5) has commented, "when there is plenty of food it never reaches beyond its shell, but feeds entirely on the material beneath . . .". Whether or not this "feeding cone" provides *Xenophora* with some safety while feeding is subject to debate.

A number of more or less convincing theories have been presented as to the function and origin of the attachment behavior in *Xenophora*. Our observations of coral-bearing specimens have led us to conclude that there is some measure of truth in several of the various theories. We also suggest that different species of *Xenophora*, subject to different predation pressure and different environmental conditions, may have adapted the basic attachment behavior to serve different purposes. For example, it seems likely that shallow-dwelling, highly encrusted species, such as *X. conchyliophora*, camouflages itself against visually orienting predators, whereas the deep-water, spinose *X. solaris* may use the snowshoe effect to prevent suffocation. We conjecture that visual camouflage was the original function. The degree to which the other functions are derived presents an interesting evolutionary puzzle, but the attachment and flange/spine-producing behaviors can certainly be used to help clarify the phylogenetic relationships between the various species of *Xenophora*.

To achieve a more satisfactory understanding of the attachment behavior detailed morphometric analysis should be performed on the size, shape, spatial density, and orientation of attached objects. Ultimately, however, we need to know more about the life history of *Xenophora*. The differences and similarities in the biology, ecology, and behavior of the various species should provide important clues, and perhaps eventually answer the riddles posed by the remarkable carrier shells.

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Appendix 1. Names and localities of azooxanthellate coral species affixed to *Xenophora* shells.

MNHN

- MUSORSTOM 8-963 (20°20'S, 169°49'E, 400-440 m), on *X. pallidula*, MNHN: *F. variegatus* (1), *S. complicata* (1), *Caryophyllia* sp. A (1), *C. abrupta* (1), *T. brevispina* (1), *B. stellulatus* (2), *D. corrugatus* (1), *H. sulcatus* (2), *H. sp.* (1); *T. labidus* (1), *Flabellum* sp. (2), *F. aotearoa* (1), *T. kermadecensis* (1).
- MUSORSTOM 8-1008 (18°53'S, 168°53'E, 919-1000 m), on *X. pallidula*, MNHN: *Truncatoflabellum* sp. (1), gardineriid, n. gen. n. sp. (3).
- MUSORSTOM 8-1016 (17°53'S, 168°28'E, 291-300 m), on *X. pallidula*, MNHN: *C. abrupta* (1), *Conotrochus* sp. (1), *C. asymmetros* (1), *T. dens* (1).
- MUSORSTOM 8-1017 (17°53'S, 168°26'E, 294-295 m), on *X. pallidula*, MNHN: *Caryophyllia* sp. (1), *C. asymmetros* (1), *Conotrochus* sp. (1), *E. grayi* (1).
- MUSORSTOM 8-1018 (17°53'S, 168°25'E, 300-301 m), on *X. pallidula*, MNHN: *B. stellulatus* (1), *N. conicus* (1).
- MUSORSTOM 8-1023 (17°48'S, 168°49'E, 321 m), on *X. pallidula*, MNHN: *Caryophyllia* sp. (1), *Caryophyllia* sp. B (1), *B. stellulatus* (1), *Deltocyathus* sp. (1), *Conotrochus* sp. (2), *H. sulcatus* (1), *Truncatoflabellum* sp. (1), *Flabellum* sp. (1), *T. kermadecensis* (2).
- MUSORSTOM 8-1087 (15°10'S, 167°14'E, 394-421 m), on *X. pallidula*, MNHN: *Caryophyllia* sp. (1), *C. abrupta* (1), *C. decamera* (1), *Trochocyathus* sp. (1), *T. rhombocolumna* (1), *T. vasiformis* (1), *T. sp.* (1), *B. stellulatus* (2), gardineriid, n. gen. n. sp. (2).
- MUSORSTOM 8-1088 (15°09'S, 167°15'E, 425-455 m), on *X. pallidula*, MNHN: *C. abrupta* (2), *P. folliculus* (1), *T. discus* (2), *T. sp.* (1), *Truncatoflabellum* sp. (1), gardineriid, n. gen. n. sp. (2).
- MUSORSTOM 8-1091 (15°10'S, 167°13'E, 344-350 m), on *X. pallidula*, MNHN: *S. complicata* (1), *C. abrupta* (3), *C. lamellifera* (1), *Heterocyathus* sp. (1), *F. pavoninum* (1).
- MUSORSTOM 8-1092 (15°10'S, 167°12'E, 314-321 m), on *X. pallidula*, MNHN: *C. ambrosia* (1), *C. funiculumna* (3), *Truncatoflabellum* sp. (2).
- MUSORSTOM 8-1097 (15°05'S, 167°10'E, 281-288 m), on *X. pallidula*, MNHN: *S. complicata* (1), *B. stellulatus* (11), *Deltocyathus* sp. (1), *D. stella* (1), *H. sulcatus* (1), *C. asymmetros* (1), *C. brunneus* (1), *C. sp.* (1), *Flabellum* sp. (1), *T. pusillum* (1), *T. sp. A* (1), *G. annulata* (1).

MUSORSTOM 8-1106 (15°05'S, 167°11'E, 305-314 m), on *X. pallidula*, MNHN: *C. abrupta* (1), *B. stellulatus* (9), *D. heteroclitus* (2), *D. sp.* (1), *H. sulcatus* (1), *T. dens* (1), *T. pusillum* (3), *T. sp.* (2), dendrophylliid (2).

DMNH

Marinduque, Philippines, 124-126 m, on *X. pallidula*, DMNH 188571: *Caryophyllia* sp. A (2), *Flabellum* sp. (1), *Truncatoflabellum* sp. (1).

Marinduque, Philippines, depth not known, on *X. pallidula*, DMNH 189002 and 188943: *A. frustum* (1), *C. spinacarens* (4), *H. sulcatus* (1), *F. deludens* (1), *Truncatoflabellum* sp. (1), *B. cornu* (2).

Batangas, Philippines, 152-163 m, on *X. pallidula*, DMNH 189854: *T. formosum* (3).

Batangas, Philippines, depth unknown, on *X. pallidula*, DMNH 190007: *C. spinacarens* (1), *H. sulcatus* (1).

Philippines, depth unknown, on *X. pallidula*, DMNH 188572: *C. spinacarens* (7), *C. transversalis* (1).

Philippines, depth unknown, on *X. pallidula*, DMNH 188944: *C. spinacarens* (1), *T. pusillum* (1), *B. cornu* (1), *B. imperialis* (1).

Quezon, Philippines, 596 m, on *X. pallidula*, DMNH 189043: *Truncatoflabellum* sp. (1).

Off Zululand, 293 m, on *X. pallidula*, DMNH 11505-7, 11499, 17902: *Madracis* sp. (1), *Caryophyllia* sp. (2), *Flabellum* sp. (1), *F. pavoninum* (5), *Truncatoflabellum* sp. (6), *T. gardineri* (6), dendrophylliid (1).

Off Zululand, 220-293 m, on *X. pallidula*, DMNH 20120: *F. pavoninum* (4), *F. sp.* (1), *T. sp.* (1), *T. cf. formosum* (1), *T. gardineri* (10).

Off Natal, South Africa, 293-329 m, on *X. pallidula*, DMNH 186438: *Flabellum* sp. (1), *F. pavoninum* (1), *T. gardineri* (2).

off Japan, 110 m, on *X. pallidula*, DMNH 6180: *C. quadragenaria* (1), *P. dentiformis* (2), *F. pavoninum* (1), *Endopachys grayi* (1).

Sagami Bay, Japan, depth unknown, on *X. pallidula*, DMNH 55071: *F. paliferus* (1), *H. sulcatus* (1), *Truncatoflabellum* sp. (1).

off Kii, Japan, 183 m, on *X. pallidula*, DMNH 55070: *E. grayi* (1), *P. dentiformis* (2).

MCZ

Auckland, New Zealand, depth unknown, on *X. neozelandica*, MCZ 160266-67: *M. rubrum* (4).

USNM

Albatross 3810 (southeast of Oahu, Hawaiian Islands, 386-463 m), on *X. peroniana*, USNM M749844: *A. pacifica* (1), *E. grayi* (1).

Albatross 3838 (southeast coast of Molokai, Hawaiian Islands, 168-388 m), on *X. peroniana*, USNM M335067: *E. grayi* (5).

Albatross 4079 (Puniawa Point, Maui, Hawaiian Islands, 262-326 m), on *X. peroniana*, USNM M335063: *A. macrolobata* (3).

Albatross 5117 (13°52'22"N, 120°46'22"E, 216 m), on *X. pallidula*, USNM M243416: *C. spiniger* (1), *Flabellum* sp. (1).

Albatross 5131 (off Panabutan Point, Philippines, 49 m), on *X. pallidula*, USNM M243391: *C. secta* (1), *H. sulcatus* (1).

Albatross 5212 (12°04'15"N, 124°04'36"E, 198 m), on *X. pallidula*, USNM M277576: *F. lamellulosum* (2), *T. cf. gardineri* (1), *B. cornu* (3), *B. imperialis* (1).

Albatross 5213 (12°15'00"N, 123°57'30"E, 146 m), on *X. pallidula*, USNM M243398: *Truncatoflabellum* sp. (1).

Albatross 5265 (13°41'15"N, 120°00'50"E, 247 m), on *X. pallidula*, USNM M243347-9, -353, -356-357, -361-2, -366, -368, -370, -372, -373, -375, -376, -426, -881: *Anthemiphyllia* sp. (1), *C. spinacarens* (1), *C. secta* (2), *C. grayi* (1), *T. virgatus* (1), *H. sulcatus* (1), *D. philippinensis* (1), *C. pileus* (1), *Flabellum* sp. (3), *F. pavoninum* (1), *F. lamellulosum* (1), *T. formosum* (12), *T. dens* (1), *T. pusillum* (1), *T. sp.* (1), *B. cornu* (1), *B. imperialis* (2), *E. grayi* (1), *H. cochlea* (1).

Albatross 5273 (13°58'45"N, 120°21'35"E, 209 m), on *X. pallidula*, USNM M237519: *Balanophyllia* sp. (1).

Albatross 5278 (14°00'10"N, 120°17'15"E, 187 m), on *X. pallidula*, USNM M 243411: *C. octonaria* (1), *H. sulcatus* (3), *H. alternatus* (1), *A. rubescens* (1), *Tropidocyathus* sp. (1).

Albatross 5289 (13°41'50"N, 120°58'30"E, 315 m), on *X. pallidula*, USNM M237585: *T. formosum* (1), *T. incrustatum* (1).

Albatross 5312 (21°30'00"N, 116°32'00"E, 256 m), on *X. japonica*, USNM M243420: *T. cf. gardineri* (1).

Albatross 5391 (12°13'15"N, 124°05'03"E, 216 m), on *X. japonica*, USNM M238138: *H. sulcata* (1), *F. politum* (14), *T. candeanum* (1), *Balanophyllia* sp. (2).

Albatross 5392 (12°13'35"N, 124°02'48"E, 247 m), on *X. pallidula*, USNM M238192, 243394: *F. pavoninum* (2), *F. politum* (7), *F. sp.* (10), *B. cornu* (4).

Albatross 5392 (see above) on *X. japonica*, USNM M238192: *F. politum* (50), *F. pavoninum* (1), *F. sp.* (13), *B. cornu* (6), *B. sp.* (5).

Albatross 5394 (12°00'30"N, 124°05'36"E, 280 m), on *X. pallidula*, USNM M243415: *T. candeanum* (1).

Albatross 5395 (11°56'40"N, 124°14'E, 256 m), on *X. pallidula*, USNM M240513: *B. cornu* (1).

Albatross 5405 (10°49'20"N, 124°24'23"E, 479 m), on *X. pallidula*, USNM M238257: *Conotrochus* sp. (2).

Albatross 5408 (10°40'15"N, 124°15'00"E, 291 m), on *X. pallidula*, USNM M238277: *Fungiacyathus* sp. (1), *Madrepora oculata* (2), *H. sulcatus* (4).

Albatross 5416 (10°11'30"N, 123°53'30"E, 274 m), on *X. pallidula*, USNM M238372: *A. frustum* (2), *H. sulcatus* (5), *Flabellum* sp. (3), *T. angustum* (1).

Albatross 5417 (10°10'00"N, 123°53'15"E, 302 m), on *X. pallidula*, USNM M243381: *Deltocyathus* sp. (1), *Flabellum* sp. (2), *F. pavoninum* (2).

Albatross 5418 (10°08'50"N, 123°52'30"E, 291 m), on *X. pallidula*, USNM M243377: *M. oculata* (1), *D. andamanicus* (1), *Flabellum* sp. (1), *T. angustum* (1).

Albatross 5592 (4°12'44"N, 118°27'44"E, 558 m), on *X. pallidula*, USNM M229317: *H. alternatus* (1).

Albatross 5661 (5°49'40"S, 120°24'30"E, 329 m), on *X. pallidula*, USNM M239497: *Caryophyllia* sp. (1).

David Starr Jordan, stn TC32-2 (21°21'54"N, 158°12'24"W, 119-291 m), on *X. peroniana*, USNM M807659: *Anthemiphyllia* sp. (1), *E. grayi* (2), *Placotrochides* n. sp. (1).

David Starr Jordan, stn TC33-9 (21°00'06"N, 156°45'42"W, 227-234 m), on *X. peroniana*, USNM M807662: *A. pacifica* (1), *Flabellum* sp. (2), *F. pavoninum* (1), *Placotrochides* n. sp. (3).

- David Starr Jordan, stn TC40-8 (21°09'42"N, 157°24'42"W, 183 m), on *X. peroniana*, USNM M807631: *Balanophyllia* sp. (1), *E. grayi* (2).
- David Starr Jordan, stn TC52-99 (21°02'06"N, 156°47'15"W, 223 m), on *X. peroniana*, USNM M807652: *E. grayi* (3).
- Off Kisamaya, Somalia, depth unknown, on *X. pallidula*, USNM M819755: *F. pavoninum* (6).
- 16-32 km off southern Zululand, 293-329 m, on *X. pallidula*, USNM M635312-313: *H. sulcatus* (1), *F. pavoninum* (1), *T. gardineri* (1), *T. multispinosum* (2), *T. sp.* (2).
- W-320, off Natal, S. Africa, 37 m, on *X. pallidula*, USNM M818232: *H. sulcatus* (1), *Flabellum* sp. (1), *T. gardineri* (2).
- W-253, off Durban, S. Africa, 366 m, on *X. pallidula*, USNM M818231: *T. multispinosum* (1).
- Sagami Bay, Japan, depth unknown, on *X. pallidula*, USNM M346151: *C. dentata* (1), *P. dentiformis* (1), *T. candeanum* (1), *H. cochlea* (3).
- Kanabe, Kii, Japan, depth unknown, on *X. pallidula*, USNM M273680: *P. dentiformis* (9), *Heterocyathus* sp. (1), *Truncatoflabellum* sp. (1).
- Off Kii, Japan, depth unknown, on *X. pallidula*, USNM M605915: *P. dentiformis* (1), dendrophylliid (1).
- Minabe, Wakayama, Japan, 64 m, on *X. pallidula*, USNM M605785: *P. dentiformis* (1), *H. sulcatus* (1), dendrophylliid (1).
- Off Tosa, Japan, depth unknown, on *X. cerea*, USNM M346150: *C. jogashimaensis* (1), *Truncatoflabellum* sp. B (2).
- Off Japan (W-976), on *X. japonica*, USNM M348868: *Truncatoflabellum* sp. (2).
- Sulu Sea, Philippines (W-498), on *X. pallidula*, USNM M807763: *T. cooperi* (3), *H. sulcatus* (1), *P. laevis* (1), *H. cochlea* (2).
- Tayabas Bay, Philippines, 15-30 m, on *X. pallidula*, USNM M 876993: *H. sulcatus* (4).
- Stn CPL/8 (3°15'S, 128°08'E, 26-55 m), on *X. corrugata*, USNM M746695: *H. cochlea* (1).
- Stn KRVI (5°32'S, 132°41'E, 37 m), on *X. corrugata*, USNM M746948: *H. cochlea* (1).
- 22°19'S, 167°11'E, 290-310 m, on paratype of *X. granulosa*, USNM M842996: *D. heteroclitus* (1).
- LaRafalo*, stn 7 (5°18'N, 9°54'30"W, 200 m), on *X. crista*, USNM M762004: *C. smithii* (23).

Appendix 2. Taxonomic list of azooxanthellate Scleractinia affixed to *Xenophora* shells, and frequency of occurrence on those shells (in parentheses). See Appendix 1 for locality data of corals and shells.

Order Scleractinia

Suborder Astrocoeniina

Family Pocilloporidae

Madracis sp. (1)

Suborder Fungiina

Family Fungiacyathidae

Fungiacyathus paliferus (Alcock, 1902) (1)

F. variegatus Cairns, 1989 (1)

F. sp. (1)

Family Micrabaciidae

Stephanophyllia complicata Moseley, 1876 (3)

Suborder Faviina

Family Oculinidae

Madrepora oculata Linnaeus, 1758 (3)

Family Anthemiphylliidae

Anthemiphyllia frustum Cairns, 1994 (3)

A. pacifica Vaughan, 1907 (2)

A. macrolobata Cairns, in press (3)

A. sp. (1)

Suborder Caryophylliina

Family Caryophylliidae

Caryophyllia (C.) smithii Stokes and Broderip, 1828 (23)

C. (C.) abrupta Cairns, ms (9)

C. (C.) secta Cairns and Zibrowius, 1997 (3)

C. (C.) ambrosia Alcock, 1898 (1)

C. (C.) jogashimaensis Eguchi, 1968 (1)

C. (C.) lamellifera Moseley, 1881 (1)

C. (C.) octonaria Cairns and Zibrowius, 1997 (1)

C. (C.) quadragenaria Alcock, 1902 (1)

C. (C.) transversalis Moseley, 1881 (1)

C. (C.) sp. A (3)

C. (C.) sp. B (1)

C. (C.) sp. (7)

C. (A.) spinicarens (Moseley, 1881) (14)

C. (A.) decamera Cairns, in press (1)

C. (A.) dentata Moseley, 1876 (1)

C. (A.) grayi (Milne Edwards and Haime, 1848) (1)

C. (A.) spinigera Saville Kent, 1871 (1)

Premocyathus dentiformis (Alcock, 1902) (16)

Trochocyathus (T.) cooperi (Gardiner, 1905) (3)

T. (T.) discus Cairns and Zibrowius, 1997 (2)

T. (T.) rhombocolumna Alcock, 1902 (1)

T. (T.) vasiformis Bourne, 1903 (1)

T. (T.) sp. (2)

T. (A.) brevispina Cairns and Zibrowius, 1997 (1)

Tethocyathus virgatus (Alcock, 1902) (1)

Bourneotrochus stellulatus (Cairns, 1984) (25)

Deltocyathus heteroclitus Wells, 1984 (3)

D. andamanicus Alcock, 1898 (1)

D. corrugatus Cairns, in press (1)

D. philippinensis Cairns and Zibrowius, 1997 (1)

D. stella Cairns and Zibrowius, 1997 (1)

D. sp. (4)

Heterocyathus sulcatus (Verrill, 1866) (31)

H. alternatus Verrill, 1865 (2)

H. sp. (3)

Conotrochus asymmetros Cairns, in press (3)

C. funiculum (Alcock, 1902) (3)

C. brunneus (Moseley, 1881) (1)

C. sp. (6)

Family Turbinoliidae

Alatotrochus rubescens (Moseley, 1876) (1)

Tropidocyathus labidus Cairns and Zibrowius, 1997 (1)

T. sp. (1)

Cyathotrochus pileus (Alcock, 1902) (1)

Notocyathus conicus (Alcock, 1902) (1)

Peponocyathus folliculus (Pourtalès, 1868) (1)

Family Flabellidae

Flabellum (F.) politum Cairns, 1989 (71)

F. (F.) pavoninum Lesson, 1831 (26)

F. (F.) lamellulosum Alcock, 1902 (3)

F. (F.) sp. A (1)

F. (F.) sp. (43)

F. (U.) aotearoa Squires, 1964 (1)

F. (U.) deludens Marenzeller, 1904 (1)

Truncatoflabellum gardineri Cairns, 1993 (20)

T. sp. cf. T. gardineri (3)

T. formosum Cairns, 1989 (16)

T. sp. cf. T. formosum (1)

T. pusillum Cairns, 1989 (6)

T. angustum Cairns and Zibrowius, 1997 (2)

T. candeanum (Milne Edwards and Haime, 1848) (3)

T. dens (Alcock, 1902) (3)

T. incrustatum Cairns, 1989 (1)

T. multispinosum Cairns, 1993 (3)

T. sp. A (1)

T. sp. B (2)

T. sp. (25)

Placotrochides n. sp. (4)

Placotrochus laevis Milne Edwards and Haime, 1848 (1)

Monomyces rubrum (Quoy and Gaimard, 1833) (4)

Family Gardineriidae

Gardineriid n. gen. sensu Stolarski (1996) (7)

Family Guyniidae

Guynia annulata Duncan, 1872 (1)

Temnotrochus kermadecensis Cairns, 1995 (3)

Suborder Dendrophylliina

Family Dendrophylliidae

Dendrophylliid (5)

Balanophyllia cornu Moseley, 1881 (18)

B. imperialis Kent, 1871 (4)

B. sp. (9)

Endopachys grayi Milne Edwards and Haime, 1848 (17)

Heteropsammia cochlea (Spengler, 1781) (8)

Solitary corals unidentified to genus (67)