Larval Settlement Behavior and Shell Morphology of *Malleus candeanus* (d'Orbigny) (Mollusca: Bivalvia)

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ABSTRACT

Data on larval settlement behavior and shell morphology of the little known bivalve, *Malleus (Malvufundus) candeanus* (d'Orbigny, 1842), were obtained from an experiment designed for obtaining data on the distribution of boring microorganisms. Plastic (PVC) tubes with screened ends enclosing crushed coral fragments were set out on a transect line crossing the reef at Carrie Bow Cay, Belize. Epifaunal bivalves, half of which proved to be members of this species, attached to the containers during the 10-month sampling period. The distribution of specimens of *M. candeanus* among opaque versus transparent tubes and the positions of attachment sites on the walls of containers suggest that their planktonic larvae are both photonegative and geonegative at time of settlement. In nature the larvae probably swim to a dark area beneath an overhang and then move laterally to the intersection of two surfaces, such as the bottom of a crevice, where they attach with a byssus and then metamorphose.

Malleus candeanus trapped in the tubular containers approached full adult size in less than 10 months. Unlike naturally occurring specimens they have a more regular shell outline and better developed posterior auricles and lack a central constriction and distal flare in the posteroventral prismatic extension of the shell. Therefore, the lack of a posterior auricle and presence of an irregular shell outline are probably phenotypic characteristics that cannot be relied on in taxonomic studies.

Introduction

Malleus (Malvufundus) candeanus has received little attention in the literature on western Atlantic Mollusca since its original description by d'Orbigny (1842) as *Avicula candeana* (type-locality, Santiago de Cuba, in a large sponge). Johnson (1918) reported the presence of the species in Bermuda and briefly discussed its taxonomy. The only other detailed treatment is that of Boss and Moore (1967), who established that the species is broadly distributed, though "rarely encountered," in Bermuda, the tropical western Atlantic, and the tropical eastern Pacific. More recently, however, Waller (1973 and unpublished data) and Abbott (1974) found that the species is common among corals in Bermuda, the east coast of Florida, and in Belize, and Rosewater (1975 and unpublished data) found it to be common among rocks at Ascension Island in the South Atlantic. Specimens are seldom encountered not because they are rare, but because their cryptic living habit and irregular, fragile shell make them difficult to find and collect.

The present study is concerned with specimens of this species found byssally attached in cylindrical plastic containers with screened ends that were placed on a transect line crossing the reef at

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Carrie Bow Cay, Belize. The distribution of these specimens among opaque and transparent containers and their preferred living positions yield information on the settling behavior of larvae; the size of the shells gives an estimate of minimum growth rate; and the shapes of the post-larval shells provide insight into the relationship between shell form and living habit. Comparison of specimens from the containers with those from natural habitats in the same area suggests that some features previously considered important in the taxonomy of *Malleus* are phenotypic responses to living conditions.

MORPHOLOGY AND SYSTEMATICS.—Like other members of the Order Pterioida (emend. Waller, 1978), *Malleus* (*Malvufundus*) *candeanus* has a shell composed of an inner layer of nacreous aragonite and an outer layer of simple prismatic calcite (Taylor et al., 1969). As in the closely related species *Malleus* (*Malvufundus*) *regulus* (Forskål), the anatomy and habits of which have been described by Yonge (1968), nacreous aragonite is limited to the dorsal one-fourth of the shell and prismatic calcite forms a long extension of the shell margin in a posteroventral direction. The visceral-pedal mass occupies the nacreous dorsal region, whereas only the mantle and ctenidia lie in the prismatic extension.

Several subgeneric names based primarily on the presence or absence of anterior and posterior extensions of the hinge have been introduced for groups within the genus *Malleus*. Boss and Moore (1967) questioned the taxonomic reliability of hinge extensions except in two groups: one having both anterior and posterior hinge extensions [*Malleus* (*Malleus*) Lamarck, the "hammer oyster"]; the other having "hardly any lateral extension of hinge line" and designated *Malleus* (*Parimalleus*) Iredale. Hertlein and Cox (1969) and Keen (1971) used the prior subgeneric name *Malvufundus* De Gregorio for the second group, thereby suggesting that minor differences in poorly developed hinge extensions originally used to separate *Parimalleus* and *Malvufundus* are insignificant for the distinction of subgenera. Variations in the development of a posterior auricle in

M. candeanus are well documented: d'Orbigny (1842) showed a distinct posterior auricle; Johnson (1918) showed only a slight irregular posterior extension of the dorsal region; and Boss and Moore (1967) showed none.

Many species names have been introduced for populations of the subgenus *Malvufundus* that occur in the tropical and warm-temperate regions of the world oceans. All exhibit a highly irregular shell form and tend to settle on hard substrates in crevices or beneath overhanging ledges. A taxonomic review of these nominal taxa has not yet appeared, and there is no agreement on the number of valid species. Boss and Moore (1967:87) have summed up the problem of relationships concisely: "The major problem with *Malvufundus* is whether or not there is only a single extremely variable species in the Mediterranean-Indo-Pacific region [*Malleus regulus*], and if so, whether that species can be truly differentiated from *M. candeanus*."

In distinguishing the New World *Malleus candeanus* from the Mediterranean-Indo-Pacific species complex, Boss and Moore (1967) considered three regions of the shell: (1) a dorsal part frilled on the exterior by broad, overlapping sheets of prismatic calcite, some of which may fuse to form large, enclosed voids; (2) a central, narrow region—the "shank"—which is not strongly frilled on the exterior and is buttressed by a single rib on the inner shell surface; and (3) a flared, "fan-shaped" ventral area. They suggested that this tripartite division of the shell is more distinct in *M. candeanus* than in other species of the subgenus *Malvufundus*.

ECOLOGY.—In the vicinity of Carrie Bow Cay, Belize, specimens of *Malleus candeanus* are common from a depth of 5 m in the high-relief spur and groove zone seaward to the deepest area explored by SCUBA diving, 46 m on the steeply inclined fore-reef slope (Figure 211). Specimens are less common in shallower water. In the wave-washed *Millepora complanata* Lamarck of the reef-crest zone and in the lagoon landward of Carrie Bow Cay, *Malleus* is uncommon and is replaced by *Isognomon radiatus* (Anton), which is very similar morpholog-
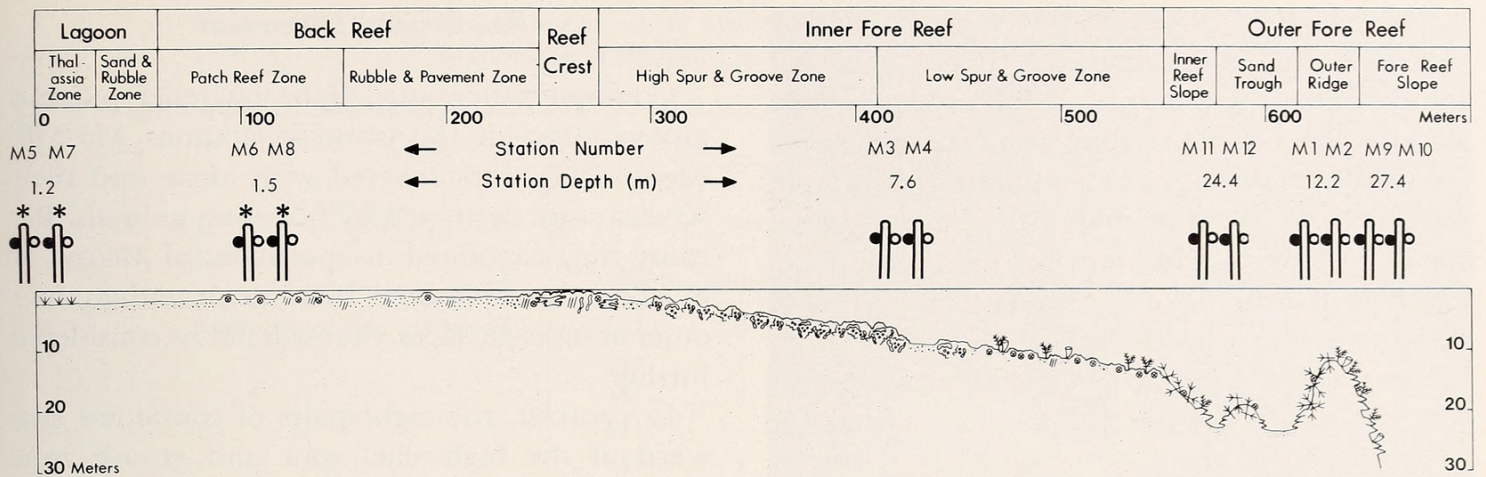
Lagoon		Back Reef		Reef Crest	Inner Fore Reef		Outer Fore Reef			
Thalassia Zone	Sand & Rubble Zone	Patch Reef Zone	Rubble & Pavement Zone		High Spur & Groove Zone	Low Spur & Groove Zone	Inner Reef Slope	Sand Trough	Outer Ridge	Fore Reef Slope

FIGURE 211.—Profile of reef at Carrie Bow Cay, Belize, showing location of stations, each station consisting of two containers, one opaque and the other transparent (asterisks indicate algal-covered and damaged containers that yielded no specimens).

ically and ecologically, living in holes and crevices and beneath overhanging ledges. Although morphologically similar species of *Isognomon* and *Malleus* (*Malvufundus*) may co-occur in abundance in some regions of the Pacific Ocean (Yonge, 1968), this is not the case in Belize.

Individuals of *Malleus candeanus* commonly live on the downward facing surfaces of overhanging ledges. The shells are attached by a strong byssus, with the dorsal or right anterodorsal region of the shell against the attachment surface and the posteroventral extension hanging downward. Specimens were common at the inner limits of overhangs, less common on vertical walls. In only one case were young specimens found on an upward facing surface; one individual was hanging downward inside a dead, articulated, nearly closed shell of *Spondylus*. As noted by Boss and Moore (1967), Waller (1973), and in the present study, specimens do not ordinarily live in sponges, the type description notwithstanding. Quantitative data on population density are lacking, but our observations during diving suggest that *Malleus candeanus* is not unusually abundant in the area of the reef transect.

Materials and Methods

Twelve pairs of sediment containers holding crushed coral fragments were placed at intervals along a transect line crossing the reef at Carrie Bow Cay, Belize, by Macintyre for the purpose of gathering information on distribution of boring microorganisms (unpublished). Each container was a cylinder of either opaque gray or transparent colorless plastic PVC (polyvinyl chloride) pipe 65 mm in length and 50 mm in diameter and each had gray, plastic-coated fiberglass screening (mesh size about 1 mm) fastened with epoxy resin over each end. The containers were positioned in pairs, one opaque and one transparent, at each station in the manner shown in Figure 212. Distance from the containers to the bottom was approximately 50 cm. Distribution of stations along the transect line is shown in a profile (Figure 211), and the location of the transect is shown by Rützler and Macintyre (herein, Figure 4). The containers were set out between 7 June and 13 June 1972 and were collected between 5 April and 11 April 1973, approximately 10 months later.
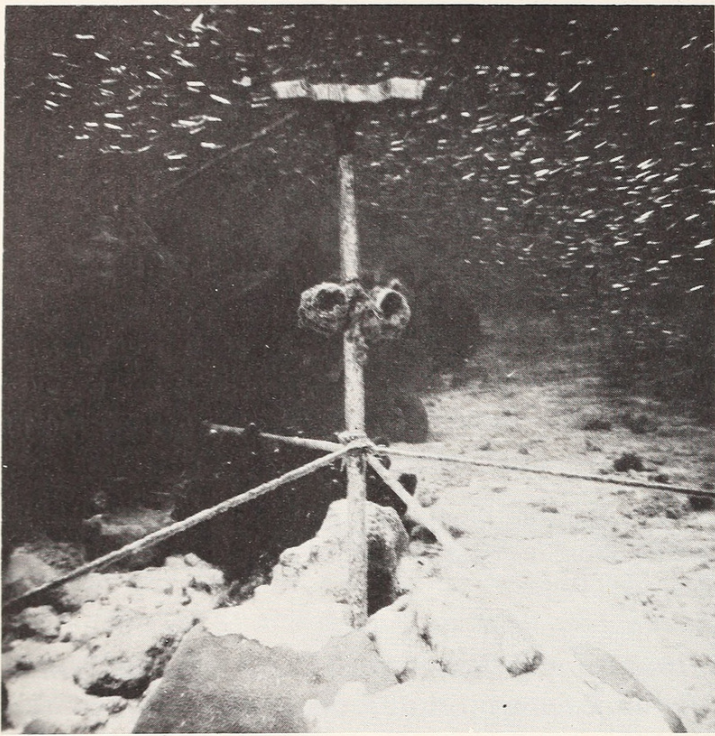
FIGURE 212.—Substrate station M6 in the patch reef zone. Browsing fish have destroyed the screened ends of the cylindrical sediment containers.

The containers were placed in neutral buffered formalin at the time of collection. Because it was not apparent until they were emptied at a later time that they contained *Malleus*, no on-site data on the final orientation of the cylinders or of the exact living positions of bivalves in them were taken. The top and bottom of the containers, however, could be inferred later from the distribution of encrusting organisms, the top surface generally being covered with algae and the bottom having sparsely distributed worm tubes. The attachment sites of *Malleus* on the interiors of several of the cylinders could be determined by examination with a binocular microscope, because the byssus was left attached to the wall of the container when specimens were removed.

The dorsal region of the shell of one small specimen from station M11 (USNM 782900, Figure 213) was washed in neutral distilled water, sputter coated with carbon and then gold palladium to a thickness not exceeding 7.5 nm, and examined in a Coates and Welter 106B scanning electron microscope.

Results and Discussion

Containers shoreward of the low-relief spur and groove zone on the transect (stations M5–M8, Figure 211) were covered with algae and their screens were destroyed by browsing animals. Because they contained no specimens of *Malleus* or of any other epifaunal bivalves on either their outer or inner surfaces, they will not be considered further.

In contrast, the eight pairs of containers seaward of the high-relief spur and groove zone remained intact (with the exception noted below) and contained an assemblage of five species of living epifaunal bivalves at the time of collection. The distribution of these specimens with respect to the inside and outside of opaque and transparent containers at each station is given in Table 42. Thirteen of the 27 individuals tabulated are *Malleus candeanus*, a surprising result in view of the fact that there does not seem to be an unusually dense population of the species in this area.

A striking difference in settlement behavior among the five species of bivalves can be seen in Table 42. Of the 13 specimens of *Malleus candeanus*, nine attached to the inner walls of the cylinders. Only one individual of the 14 specimens of other species was found inside a cylinder; all of the other specimens were on outer walls or on outer sides of screens. Furthermore, all of the specimens of *M. candeanus* found on inner walls were in opaque containers. In contrast, individuals of all species attached to outer walls were about evenly divided between opaque and transparent containers.

The veliger larvae of *Pinctada*, *Spondylus*, and *Chama* are known to be planktonic (Martinez-Escarbassiere, 1970; Kennedy et al., 1970; La-Barbera and Chanley, 1971; Rosewater, 1975; Waller, unpublished data), lifting themselves off the bottom by the action of a ciliated velum. Larvae of *Lopha*, after an initial brooded stage (Stenzel, 1971), are also planktonic. Although living larvae of *Malleus candeanus* have never been observed, their small prodissoconch-I stage (now known to represent the initial phase of larval

TABLE 42.—Epifaunal bivalves in or on cylindrical containers at Carrie Bow Cay, Belize (stations listed landward to seaward for each species)

| Species | Station | Number of specimens | | | | Maximum dimension of measured specimen(s) (mm) |
| | | Opaque containers | | Transparent containers | | |
		Inside	Outside	Inside	Outside	
Malleus candeanus (d'Orbigny)	M3	0	0	0	1	12
	M4	1	2	0	0	37
	M11	3	1	0	0	24
	M12	1	0	0	0	41
	M1	1	0	0	0	(broken)
	M2	2	0	0	0	40
	M10	1	0	0	0	(broken)
Pinctada imbricata Röding	M3	0	0	0	2	14
Spondylus sp.	M9	0	1	0	0	5.5
Lopha frons (Linnaeus)	M3	0	2	0	1	16
	M4	1	0	0	0	13
	M12	0	2	0	0	5.6
	M10	0	0	0	2	28
Chama sp.	M11	0	0	0	1	5
	M9	0	0	0	2	5

growth before the valves of the larval shell can enclose the body) and relatively large pro-dissoconch-II stage (Figure 213) indicate a planktonic, planktotrophic mode of life (Ockelmann, 1965; Waller, 1981). A planktonic mode of life is also indicated by the fact that the larvae entered containers 50 cm off the bottom.

The fact that all of the specimens of *M. candeanus* occurring on inner walls were in opaque containers cannot readily be explained except in terms of larval behavior during the swimming and crawling stage just prior to and at the time of settlement. The sizes of prodissoconchs (larval shells) of all species found on and in containers (Table 43) are well below the 1 mm mesh size of the screens. Despite the reduction in size of mesh openings caused by algal encrustations, these openings were still adequate to allow penetration of bivalve larvae. It thus appears that larvae of *M. candeanus* are distinctly photonegative at the time of settlement and that they have a greater ability to select and enter dark, obstructed spaces than other larvae present during the sampling period.

Additional information on the settling behavior of *Malleus candeanus* can be obtained from the attachment sites on container walls. Three byssal attachments found on the inside walls were at or near the top adjacent to a plug of epoxy resin, which was holding the rope that fixed the container to the pole (Figure 212). Attachment sites on the outside walls were either at the bottom, between the tube wall and the folded-back edge of the screen, or (in one case) in a downward opening crevice formed between an attached oyster and the wall of the container. The larvae of *M. candeanus* thus appear to be geonegative as well as photonegative at the time of settlement. They probably swim upward until they contact a suitable overhang and then move laterally until they perceive a crevice or an intersection of two surfaces.

The sizes of the shells of trapped specimens of *Malleus candeanus* give a rough indication of growth rate. With the exception of one individual (station M1), all specimens in the cylinders were living and presumably actively growing at the time of collection. The only dead specimen, which
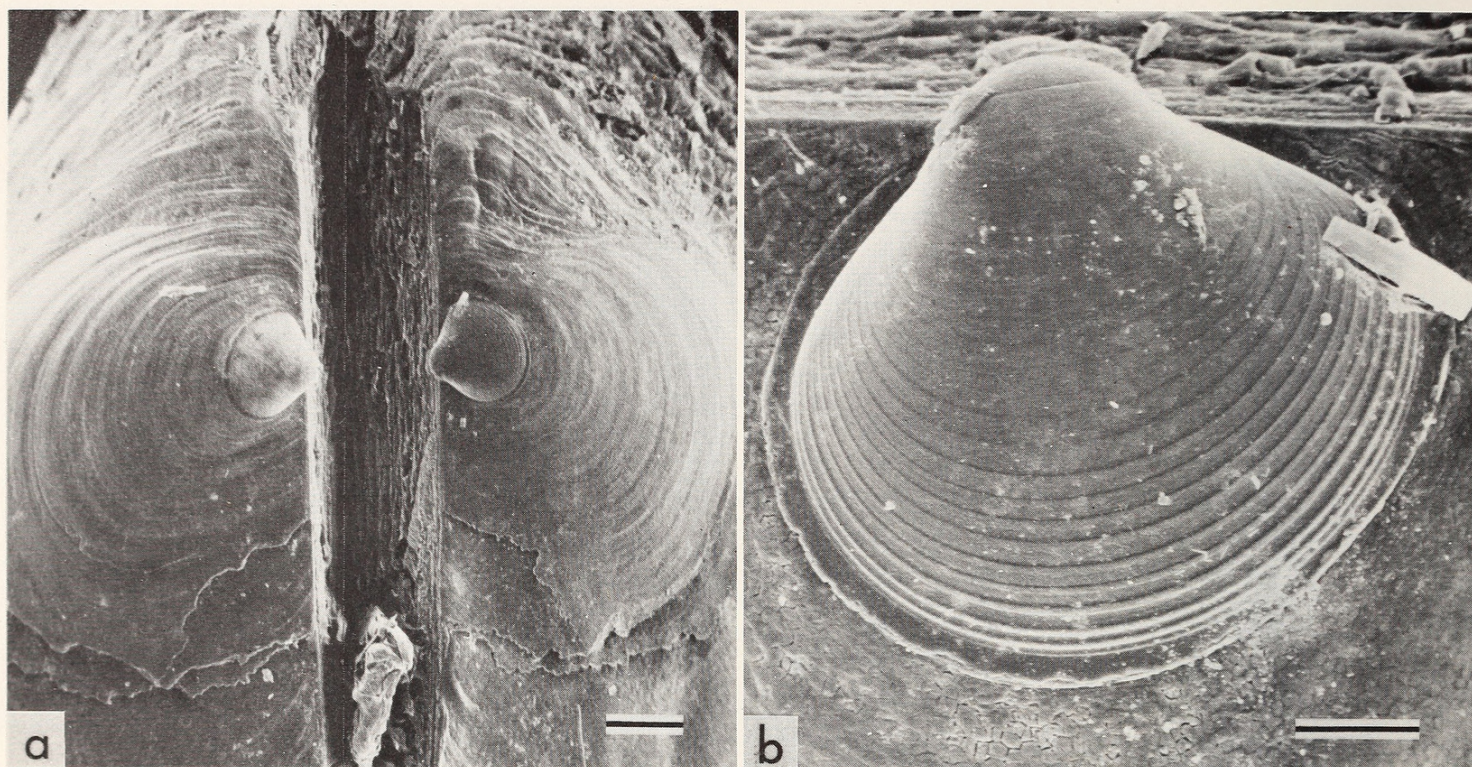
FIGURE 213.—Prodissoconch of *Malleus (Malvufundus) candeanus* from station M11, USNM 782900: *a*, dorsal view of dorsal region, anterior toward top, × 43, scale bar = 200 μm; *b*, detail of right valve of prodissoconch showing small prodissoconch-I stage (top) and relatively large, commarginally ridged prodissoconch-II stage, × 280, scale bar = 50 μm.

TABLE 43.—Prodissoconch size of specimens on or in containers at Carrie Bow Cay, Belize

Species	Number of specimens measured	Length of prodissoconch (μm)		
		Min.	Max.	Mean
Malleus candeanus (d'Orbigny)	13	265	326	288
Pinctada imbricata Röding	1	–	–	306
Spondylus sp.	1	–	–	194
Lopha frons (Linnaeus)	4	398	428	416
Chama sp.	1	–	–	184

had a circular hole with beveled edge on its left valve, was killed by a predatory gastropod that entered the container through a large hole in one of the screens. Measuring from beak to the margin of the posteroventral prismatic extension of the shell, we observed a maximum size of 56 mm in shells of this species in the Division of Mollusks, National Museum of Natural History (USNM 457011, Southwest Channel, Tortugas, Florida, depth 18 m). The largest trapped individual (40 mm, station M12) had attained 73 percent of the size of the largest museum specimen and must have been approaching maturity. If it be assumed that the larva of the 40 mm specimen entered the container at the beginning of the 10-month sampling period, its growth rate would be 4 mm per month. This represents a minimum estimate; if the larva entered later, the calculated growth rate would be higher.

The shells of specimens removed from the containers differ from those of specimens living under natural conditions in that they have a posterior auricle and lack a central "shank" and distal flare (Figure 214). Both differences appear to result from the unusual environment in which larvae settled. Compared to natural settlement surfaces, the walls of the plastic tubes were relatively free of epifauna and presented a smooth surface for attachment. Subsequent growth away from the
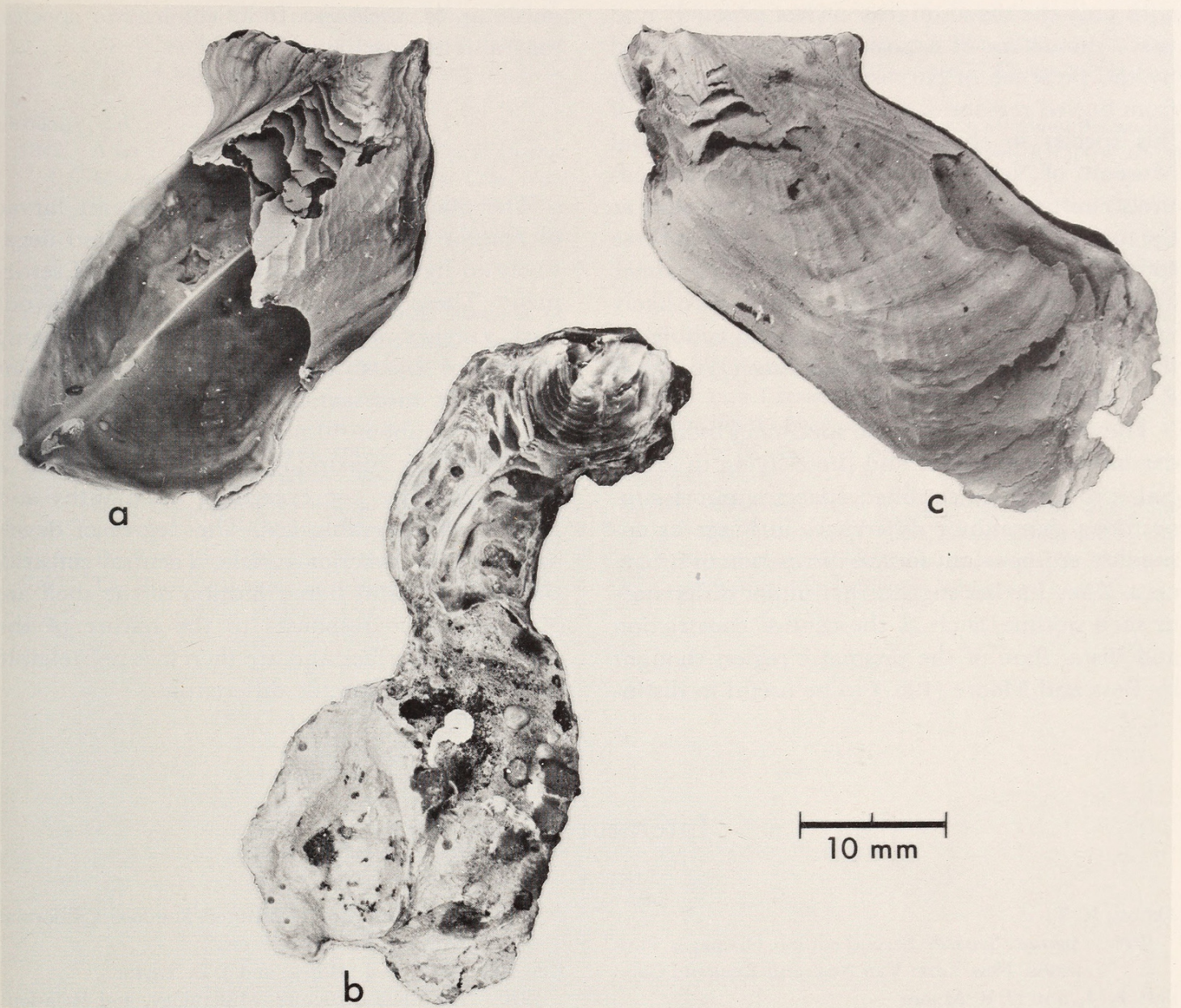
FIGURE 214.—*Malleus* (*Malvufundus*) *candeanus*: *a*, right side of specimen from inside container at Station M4, USNM 782901; *b*, right side of specimen from natural habitat on Carrie Bow Cay reef at depth of 9 m, USNM 782902; *c*, left side of specimen from inside container at Station M12, USNM 782903; all × 2, lightly coated with ammonium chloride.

surface was into a protected and, in view of the small maximum size of this species, unconfined space.

The development of a posterior auricle is apparently hindered in naturally occurring specimens because dorsal shell expansion is confined to a narrow or irregular space. Among museum specimens, a posterior auricle is absent from specimens of *Malleus candeanus* and closely related or conspecific Pacific taxa collected from reefs, where they presumably lived in holes and crevices. In contrast, a posterior auricle is present in many specimens of *M.* (*Malvufundus*) *regulus*, which appears to occur on bare rock surfaces more commonly than in holes and crevices (Yonge, 1968). Extreme development of a posterior auricle and an anterior auricle-like extension of the dorsal margin occurs in *M.* (*Malleus*), the "hammer oyster." Yonge (1968:387), in referring to *M. malleus*, said that the shell "is always buried

with only the distal quarter or less exposed" and that "the extent of exposure is usually revealed by the presence of encrusting organisms absent from buried regions of the shell." In specimens of this species in the collections of the National Museum of Natural History both valves are entirely encrusted with organisms that were alive at the time of collection, and thus we infer that these specimens cannot have been buried in the manner assumed by Yonge to be typical. They more likely were attached to rocky surfaces or to rubble on the bottom, as reported by Chuang (1961) and R. T. Abbott (pers. comm.).

These differences between specimens living under natural conditions and those living in artificial, protected, unconfined spaces support suppositions that minor differences in hinge extension are unimportant for the distinction of subgenera. They further suggest that minor differences in shell outline, such as the central constriction and distal flare of the prismatic region thought by Boss and Moore (1967) to be useful in distin-guishing *M. candeanus* from congeneric species, may also be unreliable.

Conclusions

The planktonic planktotrophic veliger larvae of *Malleus* (*Malvufundus*) *candeanus* respond negatively to light and gravity at the time of settlement. These responses allow them to seek out dark crevices and holes beneath overhanging ledges for byssal attachment and subsequent growth. *M. candeanus* can attain a maximum dimension of about 40 mm, which is about three-fourths of its maximum known size, within a period of time not exceeding 10 months and possibly considerably less. The degree of development of a posterior auricle, a central constriction, and a distal flared portion of the shell are all phenotypic responses to the nature of the attachment surface and are therefore not reliable subgeneric and specific differentia.

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