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ENVIRONMENTAL FACTORS INFLUENCING THE
DISTRIBUTION OF *BARBATIA DOMINGENSIS*
(MOLLUSCA, BIVALVIA) ON THE BERMUDA PLATFORM

SARA S. BRETSKY
DEPARTMENT OF GEOLOGY, YALE UNIVERSITY

ABSTRACT

Eight localities, representing four generalized environments, were sampled to determine the environmental relations of the small, byssally attached arcid bivalve *Barbatia (Acar) domingensis* on the Bermuda Platform. The species was most abundant in turbulent environments and least abundant in the protected bays and sounds. It usually attaches to the underside of corals; occasionally it is found attached to rocks. The principal limiting factor on the distribution of the species appears to be the availability of suitable coral substrata for attachment.

INTRODUCTION

Except for a few commercially important groups such as the pearl oysters, scallops, shipworms, and edible oysters, almost nothing is known of the factors which control the distribution patterns of marine bivalve molluscs. This is particularly true for the abundant and diverse Superfamily Arcacea, a widely distributed group which is most common in tropical and warm temperate seas. As a contribution toward understanding the environmental relations of this important superfamily, the small arcid bivalve *Barbatia (Acar) domingensis* (Lamarck) — often erroneously called *Barbatia reticulata* (Gmelin) — was intensively studied on the Bermuda Platform for three weeks in August, 1965. This species is found in the West Indies, Bermuda, and along the east coast of the United States as far north as Cape Hatteras. It is one of seven species of arcids, representing the genera *Arca*, *Anadara*, *Barbatia*, and *Arcopsis*, known from Bermuda (Dall, 1889; Warmke and Abbott, 1961; Neumann, 1965). *B. domingensis*, like most other arcids, has been little studied except for reports of distribution based mostly on empty shells from dredge samples.

Preliminary observations showed that *B. domingensis* normally lives attached to the underside of corals and rocks in shallow water. To further analyze the occurrences, corals were collected by shallow diving at eight localities (Fig. 1) and examined in the laboratory, where the attached *Barbatia* were counted and their attachment sites noted. In collecting the corals, no effort was made to determine the presence or absence of *Barbatia*; instead, at each locality a sample of corals was obtained which represented the overall coral diversity and abundance at that place. Other hard bottom materials, such as rock fragments and bivalve shells, were also examined to discover whether they might serve as attachment sites for *Barbatia*. This sampling produced 221 *Barbatia* specimens: 215 from 95 corals and the other 6 removed directly from rocks. Some individuals were kept alive in the laboratory for several days and their behavior noted. Sediment samples were taken at some *Barbatia* collecting localities in order to determine the relative abundance of *Barbatia* valves in the sediment.

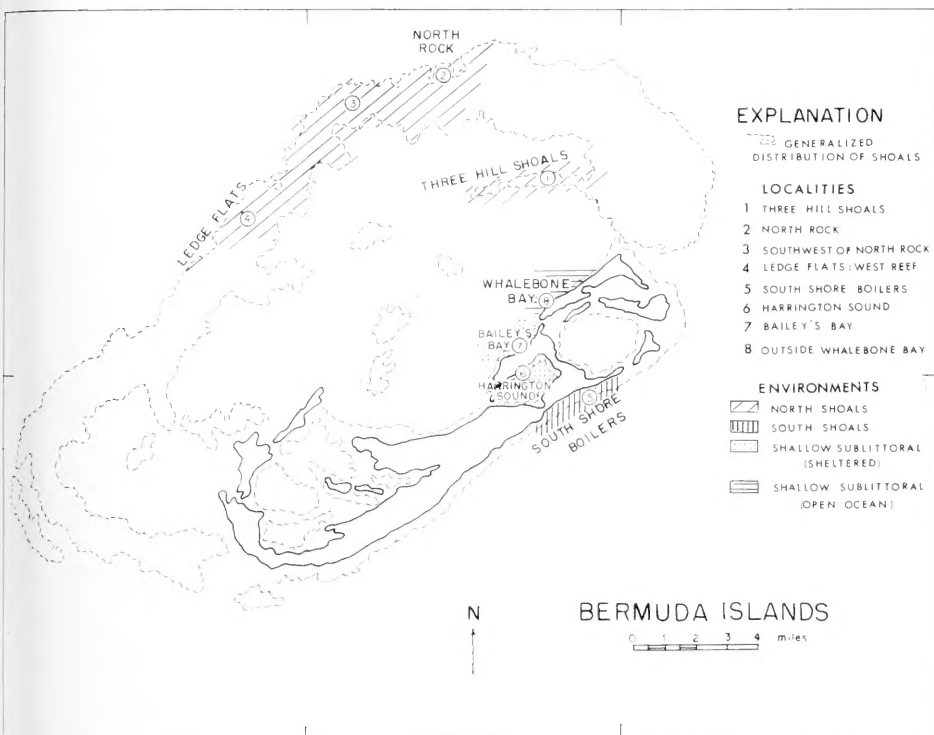


FIGURE 1. Map of Bermuda Islands showing sampling localities and generalized environments.

ANATOMY AND BEHAVIOR

The anatomy of *Barbatia domingensis* has been studied in detail by Heath (1941). No additional anatomical studies were made, but observations of general behavior patterns were made to supplement Heath's descriptions of preserved specimens.

The average shell length is about 10 mm, with an observed range between 3 and 25 mm. The ligament is long and opisthodontic. The byssus is strong. If the clam is dislodged from its attachment site, the remnants of the old byssus are expelled from the foot and a new byssus is produced. The process requires about 30 minutes in the smaller, more active, and presumably younger

animals. In the larger *Barbatia*, byssus re-formation may require 6 to 24 hours and sometimes does not occur at all. Lacking the accustomed coral substratum, the animals may attach to the sides of the aquarium or to one another's shells.

In nature, *Barbatia domingensis* is found attached by its byssus to the undersurfaces of corals and, less commonly, of rocks (Fig. 2). The species has no adaptive specialization for boring into hard materials, but shows a definite preference for nestling in crevices in corals and in the burrows formed by other organisms, such as the sponge *Cliona* and the mytilid bivalve *Lithophaga*. Many specimens, especially the larger ones, are excellently camouflaged by encrustations of serpulid worm tubes and the pink foraminifer *Homotrema rubrum* (Lamarck).

The inhalant current appears to enter ventrally and somewhat anteriorly, and the exhalant current is posterior and dorsal (Fig. 2).

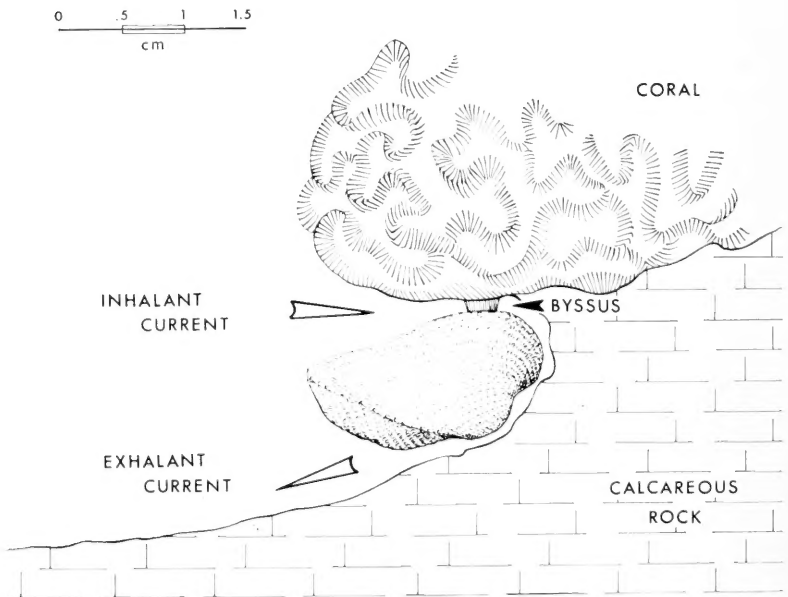


FIGURE 2. Vertical section showing living position of *Barbatia domingensis*, mode of attachment, and direction of inhalant and exhalant currents.

ECOLOGY OF SAMPLING LOCALITIES

The sampling localities (Fig. 1) represent four major environments: the North Shoals (localities 1, 2, 3, 4); the South Shoals (locality 5); the sheltered shallow sublittoral (localities 6 and 7); and the open-ocean shallow sublittoral (locality 8). Table 1 summarizes the major features of these environments.

SHOALS

The coral communities of the North and South Shoals show probably the greatest faunal diversity of any environment on the Bermuda Platform. The epifauna of the shoals is dominated by scleractinian, alcyonarian, and hydrozoan corals (Table 1). A number of small epifaunal animals, including sponges, foraminifers, tunicates, bryozoans, and bivalves, are attached to the bases of these corals. *Barbatia domingensis* was the most common bivalve found on coral bottoms; it was sometimes associated with the pectinid *Lima lima* (Linné).

The North Shoals and South Shoals are faunally quite similar. The main difference between them is that, though both may be characterized by notable turbulence in appropriate weather, wave action is particularly spectacular at the South Shore Boilers (locality 5).

Table 2 indicates the considerable variation in abundance of *Barbatia* among the four localities of the most extensively collected environment, the North Shoals. A total of 62 *Barbatia* were collected from 68 corals, the number of *Barbatia* on a single coral ranging from 0 to 7. *Barbatia* was actually living on only 34% of the corals examined.

Barbatia was strikingly more common at locality 5 on the South Shoals than anywhere on the North Shoals, with 15 corals harboring an average of 2.4 *Barbatia* each and *Barbatia* living on 80% of the corals collected (Table 2). Up to 10 bivalves were found on one coral.

No preference for any coral species or kind of coral was apparent. The corals collected from the shoals ranged in diameter from 2 to 27 cm; the largest corals usually had the most bivalves, but many large corals had none.

SHALLOW SUBLITTORAL

The shallow sublittoral collecting localities (6, 7, and 8) have carbonate-sand bottoms littered with rock debris from the shoreline cliffs. Harrington Sound (locality 6) has only a narrow connection to the open ocean; hence wave activity is subdued. Corals are sparse and usually small, and some of the abundant shoal corals are lacking or rare (Table 1). Large bivalves (10-15 cm long) are quite common and form a major element of the epifauna. My observations and the little comparative information available (Nielsen, n. d.) indicate that the diversity of both epifaunal and infaunal bivalves is much greater in Harrington Sound than on the shoals. The epifaunal bivalves listed in Table 1, except for *Barbatia*, were also identified by Neumann (1965), in his comprehensive study of carbonate sedimentation in Harrington Sound. Most of these bivalves are byssally attached to shells, corals, or rocks in shallow water, thus occupying about the same ecological niche as *Barbatia*.

Six corals were collected from Harrington Sound, near Abbott's Cliff on the northwest side of the Sound. Three *Barbatia* individuals were found on one of these. A number of rocks and bivalve shells were also examined, but *Barbatia* was not found on any.

Bailey's Bay (locality 7) is partly cut off from the open ocean by a chain of small islands, and thus is nearly as sheltered as Harrington Sound. These two localities are therefore grouped as the sheltered shallow sublittoral environment. Small corals occur sparingly here; those examined contained no *Barbatia*. Twenty-four arcids were collected from under rocks. Only six of these, however, were *Barbatia domingensis*; the other 18 were the closely related *Arcopsis adamsi* (E. A. Smith), a slightly smaller arcid with a triangular ligament between the umbones.

The shallow sublittoral area just outside Whalebone Bay (locality 8) was grouped with the two previous localities in Table 1 because of the similarities in water depth and type of bottom, but in some respects it is more similar to the shoal localities. It is exposed to the open ocean and thus to intensive wave action. In size and diversity of corals (Table 1), it is intermediate between the shoals and the sheltered environment. The only bivalves found here were *Barbatia* and *Spondylus*. All the speci-

mens of *B. domingensis* collected here, a total of 112, were found on a single large (39 cm diameter) coral of the genus *Diploria*. Such a coral is unusually large for the shallow sublittoral environment of Bermuda, though its size would not be unusual for a shoal coral. It was collected near the beginning of my study, and it was expected at first that similar densities of concentration of *Barbatia* would occur on the larger corals at other localities. Comparable aggregations were found, however, on only two corals, both from the South Shoals; these, with diameters of 14 and 15 cm (area therefore about 1/9 that of the Whalebone Bay coral) had, respectively, 9 and 10 *Barbatia*. All other corals in the study on which *Barbatia* was found were considerably less densely populated with *Barbatia*. Possible ecological explanations for the presence of dense aggregations of bivalves will be discussed in the section "Factors Affecting Distribution."

COMPARISON OF *BARBATIA* AND *ARCOPSIS* DISTRIBUTION

The apparent contrast in distribution between *Barbatia domingensis* and another small arcid bivalve, *Arcopsis adamsi*, which was found with *B. domingensis* at locality 7 (Bailey's Bay), strongly indicates that, while the two species are not mutually exclusive, *B. domingensis* is specialized for life on corals and *A. adamsi* for rocks. *Arcopsis* was never found living on corals. Though both were only minor contributors to the sediment samples examined, *Barbatia* always made up 1-2% of the coarse fraction (>4 mm), whereas only three or four disarticulated *Arcopsis* valves were found in shoal sediments. Possibly the preference of *Barbatia* for nestling in burrows of other organisms precludes its living on talus fragments, which may be less likely than corals to be burrowed. Another suggestive observation is that the byssus of *Arcopsis* is smaller and less strong than that of *Barbatia*. Possibly both nestling and the stronger byssus are adaptations of *Barbatia* to a more turbulent environment; *Arcopsis* may require sheltered areas like Bailey's Bay. Aquarium observations, however, indicated that *Arcopsis* is more mobile than *Barbatia*, and the byssus of *Arcopsis* is usually re-formed in an hour or less—faster than in all but the smallest *Barbatia*. Perhaps *Barbatia* requires an anchored attachment site, whereas *Arcopsis* may be able to live on a less stable sandy substratum because it can move

TABLE 1. SUMMARY OF ENVIRONMENTS

| ECOLOGICAL PARAMETER | SHALLOW SUBLITTORAL | |
|--------------------------------|--|--|
| | SHOALS | SHELTERED OPEN OCEAN |
| | No. Shoals So. Shoals (Loc. 1-4) (Loc. 5) | Harrington Sound Bailey's Bay (Loc. 6) (Loc. 7) Whalebone Bay (Loc. 8) |
| Water depth | Mean low tide mark to 7 m | Mean low tide mark to 2 m |
| Sediment, type of bottom | Submerged Pleistocene eoli- anites veneered by corals; carbonate sediment ac- cumulating in topographic lows | Carbonate sand bottom with talus fragments |
| Turbulence | Fairly high, Consistently high dependent on weather con- ditions | Very low Low |
| Corals | Scleractinians <i>Diploria</i> (dominant) <i>Porites</i> <i>Siderastrea</i> <i>Montastrea</i> | Scleractinians <i>Isophyllia</i> <i>Siderastrea</i> <i>Porites</i> <i>Agaricia</i> <i>Diploria</i> (rare) |
| | | Fairly high, dependent on weather con- ditions |
| | | Scleractinians <i>Diploria</i> <i>Porites</i> <i>Siderastrea</i> <i>Montastrea</i> |

TABLE 1 (continued)

| | Loc. 1-5 | Loc. 6 | Loc. 7 | Loc. 8 |
|--|--|--|------------------------------------|-------------------------------------|
| | Hydrozoan <i>Millepora</i> Alcyonarians <i>Gorgia</i> <i>Plexaura</i> <i>Pseudoplexaura</i> | Hydrozoan <i>Millepora</i> | Hydrozoan <i>Millepora</i> | Hydrozoan <i>Millepora</i> |
| Epifaunal bivalves | <i>Barbatia</i> <i>Lima</i> | <i>Barbatia</i> <i>Arca</i> Mytilids Pectinids <i>Chama</i> <i>Spondylus</i> <i>Ostrea</i> <i>Pinctada</i> <i>Anomia</i> | <i>Barbatia</i> <i>Arcopsis</i> | <i>Barbatia</i> <i>Spondylus</i> |
| Size range of collected corals (max. diam. of base) | Scleractinians: 2-27 cm Alcyonarians: 3-15 cm | <5-25 cm | <5-10 cm | <5-40 cm |

TABLE 2. ABUNDANCE OF *BARBATIA* IN BERMUDA ENVIRONMENTS

| | NORTH SHOALS | | | SOUTH SHOALS | | | SHALLOW SUBLITTORAL | |
|---|--------------|--------|--------|--------------|--------|--------|---------------------|--------|
| | Loc. 1 | Loc. 2 | Loc. 3 | Loc. 4 | Loc. 5 | Loc. 6 | Loc. 7 | Loc. 8 |
| No. corals | 10 | 19 | 7 | 32 | 15 | 6 | 5 | 1 |
| No. <i>Barbatia</i> | 7 | 21 | 14 | 20 | 36 | 3 | 6* | 112 |
| <i>Barbatia</i> /coral (avg.) | 0.7 | 1.1 | 2.0 | 0.6 | 2.4 | 0.5 | ** | (112) |
| % of corals with <i>Barbatia</i> | 20 | 47 | 57 | 25 | 80 | 17 | 0 | (100) |

*Plus 18 *Arcopsis adamsi*

**All from rocks

about and reattach itself if necessary. The adaptive significance of the different types of ligaments—long and straight in *Barbatia*, short and triangular in *Arcopsis*—is not obvious, but a larger and perhaps stronger ligament may also be of more value to a bivalve living in turbulent waters. The most important control on the distribution of the two species, however, appears to be the distribution of the preferred attachment sites.

FACTORS AFFECTING DISTRIBUTION

Some of the important factors to be considered in accounting for the distributional pattern of any marine bivalve are salinity, temperature, depth, nutrients, competitors, larval ecology, and substratum.

All the localities in this study were in areas of normal marine salinity, about 36‰ (Neumann, 1965). Since the study encompassed only the last three weeks in August, and was limited to a small geographic area and a narrow depth range, temperature effects could not be assessed. Within the accessible range, no depth control on the distribution of *Barbatia* was evident.

No precise information on nutrient distribution was available. Wave turbulence and current activity may be important both in the distribution of nutrients and in larval ecology. In this connection it may be noted that the area of greatest turbulence, the South Shoals locality, apparently exhibits the most consistent concentration of *Barbatia*; and the occurrence of 112 bivalves on one coral at Whalebone Bay was also in an area of considerable wave activity.

To determine whether size of coral (maximum diameter of base as an indication of surface area available for attachment) influences the number of *Barbatia* living there, data from the North Shoals, South Shoals, and Harrington Sound were combined. The corals collected at these localities ranged in size from 2 to 27 cm. *Barbatia* was never found on corals smaller than 9 cm. The Pearson product-moment correlation coefficient between size of coral and number of *Barbatia* per coral was 0.307 ($N=89$), which is a significant correlation at the 0.1% level but far from a perfect linear relationship.

In the shoal environment, both inter- and intraspecific competition must be important in the densely populated "coral-

bottom community." The intensity of competition for living space and food may to some extent explain why the larger corals tend to support more bivalves. But in many cases *Barbatia* is absent from corals of large diameter. Here predation may have been particularly intense. In some large corals, burrows and crevices were lacking, so that surface area for attachment may actually have been relatively small. In Harrington Sound, competition from other epifaunal bivalves may have combined with the reduction in number of corals to diminish the numerical importance of *Barbatia*. Direct competition with *Barbatia* appears more likely in the case of *Arcopsis* than in the larger bivalves, and the different substratum preferences of the two small arcids may have evolved as a means of reducing competition between them.

The patchy distribution may also be a function of the larval ecology of *Barbatia*. Unfortunately, there is no specific information on the larval development of *Barbatia*, and little is known about that of other West Indian arcids. Nothing is known, for example, about the length of the pelagic life of *Barbatia*. Marine pelagic larvae may spend from a few hours to several months in the water mass before settling (Johnson, 1964). Thorson (1957) noted that 85-90% of all tropical marine species have a long (3 weeks or more) pelagic larval life. On the other hand, Purchon (n. d.) estimated the pelagic lifetime of the Malayan arcid *Anadara granosa* as one to two weeks. Loosanoff and Davis (1963) found that spat of *Anadara transversa*, a species from the Atlantic coast of the United States, set in the laboratory 27 to 37 days after fertilization. Arctic species of arcids, however, may have a very brief or nonexistent pelagic stage (Ockelmann, 1958). A short pelagic larval life might result in a patchy distribution with high concentrations near the areas where spawning took place; a long larval life would permit more thorough coverage of the accessible environments but might be cancelled by increased exposure to predation, distribution patterns of currents, and other factors.

It has been established (Thorson, 1957) that larvae of many marine invertebrates are able to select suitable substrata and to postpone metamorphosis until they find a substratum fitted to the requirements of the adults. Korringa (1940) described the preference of oyster larvae for the lower surfaces of objects; such selectivity may account for the occurrence of *Barbatia* on the bottom of corals and rocks.

In the latter stages of this study, I observed a young form of either *Barbatia* or *Arcopsis* from sediment from Bailey's Bay which displayed the prominent, extensible foot and a structure resembling the valvular membrane described by Carriker (1961) for the plantigrade (latest larval) stage of *Mercenaria mercenaria*. This individual, about a millimeter long, was extremely active for several hours, eventually attaching itself to the side of the aquarium near the air-water interface. It appears likely, therefore, that the young of these arcids are able to choose where they will settle, and may be mobile after settling.

In some bivalves, particularly sessile epifaunal forms, the larvae are apparently attracted to concentrations of adults of their own species (Thorson, 1957; Verwey, 1952). Possibly gregariousness, whether or not it operates in conjunction with brief larval life, may partly account for localized concentrations of *Barbatia* such as that on the Whalebone Bay *Diploria* and to a lesser extent on some of the shoal corals.

The rarity of *Barbatia* in Harrington Sound is likely to be explained partly by the lack of many large corals for attachment, and partly by the sheltered and nearly enclosed situation of the Sound. Either *Barbatia* larvae are only rarely brought into Harrington Sound, or wave and current activity there is so limited that the young *Barbatia* are not widely distributed throughout the Sound and are therefore unable to chance upon the attachment sites that do exist.

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This paper is Contribution Number 410 from the Bermuda Biological Station. Specimens of *Barbatia domingensis* and *Arcopsis adamsi* collected in the study are permanently deposited in the collections of the Peabody Museum, Yale University.

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