

ECOLOGICAL OBSERVATIONS ON THE RECENT
ARTICULATE BRACHIOPOD *ARGYROTHECA*
BERMUDANA DALL FROM THE
BERMUDA PLATFORM

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ABSTRACT

The occurrence and life habits of the diminutive articulate brachiopod *Argyrotheca bermudana* have been investigated along a general NW-SE traverse across the Bermuda Platform, incorporating all seven biotopes recognized by Upchurch (1970). Sediment samples indicate that brachiopod tests comprise a consistent though minor (<1%) fraction in reefal shoal sediments, but are totally absent from lagoonal sediments.

Preliminary transects reveal that in the reef-front terrace, north reef and central and south reef biotopes, *A. bermudana* is cryptic in habit, occurring on the undersides of the foliaceous hermatypic corals *Montastrea cavernosa* (L.), *M. annularis* (Ellis and Solander), and *Agaricia fragilis* Dana. The main host coral for brachiopods on the south shore reefs and associated reef-front terrace is *M. cavernosa*, on the north reef-front terrace, north and central reefs it is *M. annularis*, while *A. fragilis* is more important on the lagoonal and near-shore reefs.

Brachiopod densities generally decrease shorewards from the edge of the Platform. The distribution and density of brachiopods appears to be controlled primarily by the relative abundance of the host corals and their growth form, although other limiting factors may be at work. Clumped distributions are common, probably the result of brooded larvae and intense competition for living space. Inter-island areas such as Castle Harbor and Harrington Sound are virtually devoid of brachiopods, although a relict population exists marginally in an unusual sub-boulder habitat in land-locked Walsingham Pond.

Following early work by Rudwick (1962), there has been a recent resurgence of interest in the ecology of modern articulate brachiopods, mainly cool and cold-water forms. Thus examples of laboratory and/or field-oriented studies include those by Rickwood (1968), Foster (1969), Neall (1970), McCammon (1971, 1973), and Logan and Noble (1971). Some of the studies mentioned above have combined ecological observations with growth and behavioral studies and have greatly advanced our knowledge of this once-prolific phylum.

Studies on warm-water extant brachiopods, especially those forms existing on shallow-water coral reefs, have been somewhat neglected by comparison, presumably because brachiopods have traditionally been regarded as rare in such environments (Elliott, 1950; Rudwick, 1965). The advent of SCUBA, however, has allowed close obser-

vation of coral reefs, particularly their cryptic habitats, and articulate brachiopods, such as megathyrids and thecidiods, have been shown by Jackson, Goreau and Hartman (1971) to be important members of a cryptic brachiopod-coraline sponge community in the Caribbean (Jamaica, Curaçao), Red Sea (Ros Muhammad), and Pacific (Guam, Saipan) areas. These workers have noted high densities of brachiopods in intimate association with coraline sponges in two cryptic habitats in the coral reefs: on the undersides of foliaceous corals or overhangs, and in the interiors of crevices and caves. Grant (1971 and *personal communication*, 1973) has observed species of *Frenulina* and *Thecidellina* in similar habitats on the reefs of Eniwetok Atoll, Marshall Islands, Pacific.

The present study records observations on the life habits of the diminutive megathyrid *Argyrotheca bermudana* from the Bermuda Platform. Data on the contribution of

this species to the sediments of the area are also included. Such documentation of an additional reef brachiopod may hopefully stimulate further search for brachiopods in cryptic reef habitats elsewhere and help dispel the impression that modern coral reefs are almost devoid of brachiopods.

For discussion on the role of brachiopods in fossil coral reefs, particularly those of the post-Paleozoic, the reader is referred to Elliot (1950), while Grant (1971) has stressed the importance of brachiopods in the essentially non-coral-bearing Permian "reefs" of west Texas.

GENERAL REMARKS ON ARGYROTHECA

The genus *Argyrotheca* Dall, which belongs to the family Megathyrididae, extends as far back as the Late Cretaceous and is widely distributed in modern seas, being represented by several species, most of which are continental shelf dwellers (Elliot, 1951). In the Caribbean faunal province, at least six species of *Argyrotheca* occur, according to Dall (1920) and Cooper (1934, 1954). Of these Caribbean species, only *A. bermudana* occurs in Bermudian waters but is not confined to the region.

Argyrotheca bermudana was first formally described by Dall in 1911, presumably from seven specimens collected by Haycock from Harrington Sound and now in the U.S. National Museum (Dall, 1920). Verrill (1903) had previously illustrated this form and identified it, on the advice of C. E. Beecher, as a variety of the European *Cistella cistellula* (Searles Wood). Verrill (op. cit., p. 592) provided the first and only published reference to the life habits of this species when he remarked: "By examining carefully the underside of unbleached specimens of the delicate foliaceous coral, *Mycidium fragile*¹, I found a number of small specimens, mostly immature, of a reddish species of *Cistella*. A few were also found on the underside of *Isophyllia dipsacea* and on the base of *Oculina*. Most of these, if not all, were taken in

Harrington Sound, just below low-tide mark."

Gautier (1965, unpublished report, Bermuda Biological Station; *personal communication*, 1972) recorded *A. bermudana* from sediment samples across the Bermuda Platform but was able to collect live specimens only from Walsingham Pond, where they occurred in shallow water beneath rocks on a talus slope. Lowenstam (1961; *personal communication*, 1972) has obtained this species live from the undersides of the coral *Agaricia fragilis* within undercuts in Harrington Sound in 1 m of water and also on undercuts in the vicinity of North Rock at depths of 12 m.

Prior to the present study, however, no systematic search has successfully been made for living populations of this species from Bermuda, in spite of the fact that it forms a consistent though minor element in most sediment samples from reefal shoal areas across the Platform.

Various aspects of the embryology and development of *Argyrotheca* and related megathyrids have been described by Shipley (1883), Schulgin (1884), Plenk (1913) and Atkins (1960). Studies by Senn (1934) and earlier workers have shown that the species *A. cordata* and *A. cuneata* are hermaphroditic and possess paired brood pouches in which free-swimming larvae are retained until a relatively late stage of development. In addition, Atkins (1960) has described the escape of such larvae from brood pouches in *A. cordata*. Brood pouches containing larvae in various developmental stages are clearly seen in *A. bermudana*; possession of such pouches appears to be characteristic of most members of the genus.

PHYSIOGRAPHY AND OCEANOGRAPHY OF THE BERMUDA PLATFORM

The physiography, oceanography and meteorology of the Bermuda Platform is relatively well known and recent detailed accounts are available by Stanley and Swift (1968), Upchurch (1970) and Garrett et al. (1971). Suffice to say here that, because

¹ Now *Agaricia fragilis* Dana

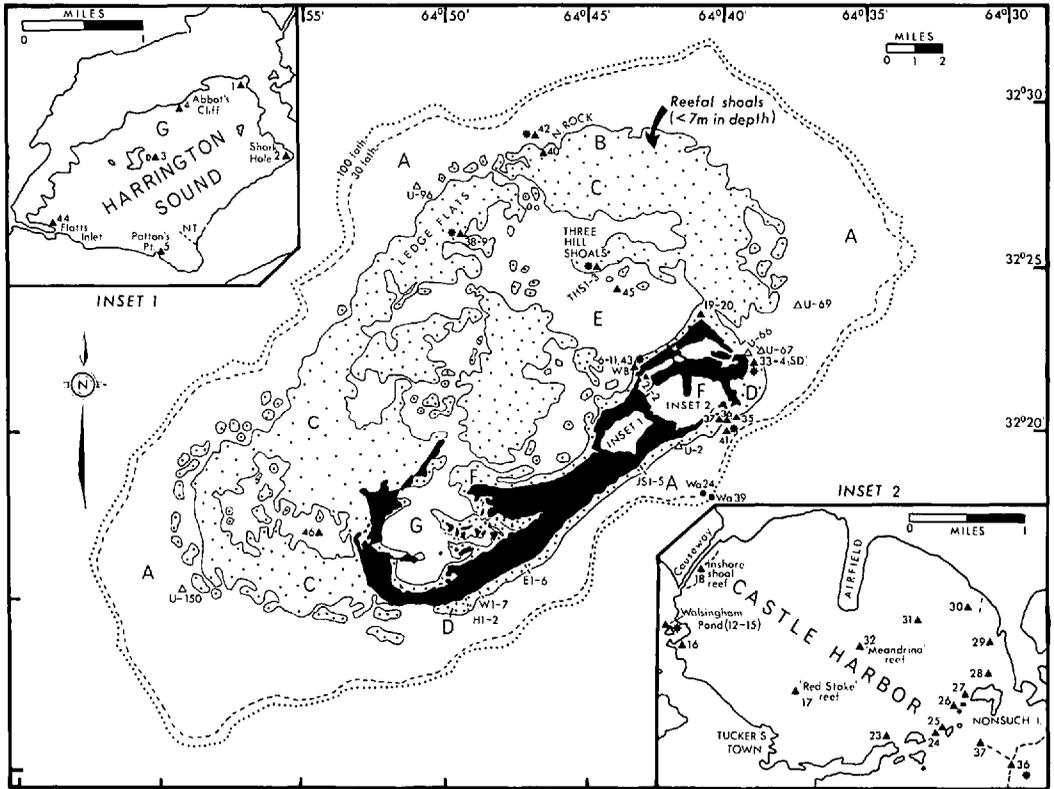


Figure 1. Map of Bermuda Platform, showing collecting and sediment sample localities. (★ = localities yielding living brachiopod populations, ▲ = author's sediment sample localities, △ = Upchurch's (1970) sediment samples bearing brachiopods in > 2 mm fraction, ● = Waller's (1973) brachiopod-bearing sediment samples. A-G = Upchurch's biotopes, NT = Neumann's transect, WB = Whalebone Bay, SD = St. David's Head. For key to south shore transects, see Table 3).

of its northerly latitude of 32°N , the Platform, composed mainly of calcareous aeolianites capping an irregular volcanic cone of Tertiary age, supports a much-reduced Caribbean marine fauna and flora. The islands themselves lie along the southeastern margin of the Platform, rising to a maximum elevation of about 250 feet (76 m). Living coral-algal or, more rarely, algal-gastropod reefs lie close to shore on Bermuda's south and south-east coast; elsewhere they form a discontinuous, elongate arc of reefal shoals surrounding a shallow, central lagoon rarely exceeding 20 m in depth (Fig. 1). Physiographically, the Platform resembles an atoll, from which it differs in that coral-algal

growth here does not take place at the edge of the Platform, so that significant growth rarely occurs below about 20 m. Also, coral-algal growth, with a few exceptions (see Ginsburg and Schroeder, 1973) is largely superficial, forming only a thin veneer on aeolianite ridges whose relict topography appears to control the orientation and distribution of reefal shoals. Thus throughout this paper the term "reef" is used *sensu* Stanley and Swift (1968), that is, for a wave resistant mass composed of both organic and inorganic material.

Conditions of near normal salinity are present over the Platform with all-year round values ranging little ($< 1\text{‰}$) around a mean of 36.5‰ , while winter water temperatures

range from about 19-27°C in the open ocean around the islands to 16-29°C within North Lagoon (Schroeder and Stommel, 1969; Beers and Herman, 1969). Tidal range is small, with low tidal current velocities except in localized areas such as Flatt's Inlet, Harrington Sound (Moore, 1946). Winds are generally from the south and south-west during the summer months and produce heavy swells on the south shore (Macky, 1956). The lagoon and north reef areas are partially protected by the islands from the effects of these winds in the summer. However, in winter the dominant wind direction is from the north and north-west and gale force winds bring heavy seas to the relatively unprotected northern areas of the Platform.

METHODS OF STUDY

Upchurch (1970) recognized seven major biotopes on the Bermuda Platform: the reef-front terrace, north reef, central and south reef, boiler, basin center, nearshore-sandy substrate, and nearshore-muddy substrate biotopes. In this study, localities were sampled along a general NW-SE traverse across the Platform, encompassing all of these biotopes. At each locality preliminary line transects revealed the type and relative abundance of the coral colonies present. From collections obtained from these preliminary transects, those species of corals supporting brachiopods were delimited (Table 1). Detailed collecting of colonies of these corals in larger quantities then followed, from which significant numbers of living brachiopods were obtained (Table 2). Coral colonies, in whole or in part, were brought to the surface by divers, and examined and measured later in the laboratory. The distribution and abundance of brachiopods on the host coral were then noted, following which they were removed, measured and preserved. The associated fauna and flora were also recorded.

At each locality, attempts were made to search all internal cavities in the reef as diligently as possible for brachiopods. None were found, which is somewhat surprising

in view of their comparative abundance in similar habitats in the Caribbean and elsewhere (Jackson et al., 1971). Dr. P. Garrett and Dr. T. P. Scoffin, engaged in independent studies on internal cavities and structures in Bermudian patch reefs, likewise report an absence of brachiopods from the interior of excavated reef blocks examined by them at the surface (*personal communications*, 1972).

Numerous sediment samples were collected from all biotopes across the Bermuda Platform (Fig. 1). In addition, transects were run at four south shore beach localities, sediment samples being taken from the back-shore, foreshore, nearshore, inner shoal and outer shoal areas. The 2 mm, 1 mm, and 0.5 mm fractions of all sediment samples were examined for brachiopods. Because of their very coarse punctation, brachiopods were easily distinguished and identification of even small fragments was regarded as completely accurate. Standard 300-grain or 400-grain counts were not performed, mainly because the accuracy of this method is questionable for constituent grains rare in the overall sample (Pettijohn, 1955); thus brachiopod were calculated on a weight percentage basis after appropriate factors were applied. It was found that almost all sediment samples adjacent to reefal shoals contained less than 1 percent of brachiopod tests, irrespective of biotope.

OCCURRENCE AND DISTRIBUTION OF *A. BERMUDANA* OVER THE PLATFORM

Individuals of *Argyrotheca bermudana* rarely exceed 2 mm in width and therefore may be regarded as meiobenthos for most of their existence. The shell is generally free of epizoans and is cream in color, with irregular, non-divaricate, pink-red bands which are particularly prominent near the anterior margin (Fig. 2). The only ornament, apart from color bands, consists of concentric growth lines which become progressively more crowded around the anterior margin as growth slows down in older individuals.

The usual life habit of *A. bermudana* is

Table 1. Numbers of reef coral colonies (or parts thereof) obtained, and approximate coral surface areas examined, in square meters (parentheses), in preliminary traverses at various localities along a general NW-SE transect across the Bermuda Platform. [P] and [A] denote presence or absence, respectively, of the brachiopod *A. bermudana* on these coral colonies.

Sampling locality: description and approximate position (see fig. 1 and Admiralty Charts 334 and 868)	Unchurch (1970) Biotope	Depth (metres)	Substrate	Turbulence	<i>Diploria</i> ssp.	<i>Montastrea</i> ssp.	<i>Porites</i> ssp.
Upper reef-front terrace, N. of North Rock (32°29'2"N, 64°46'18"W)	A	18-19	Coralgal veneer on aeolianite; sand channels	Medium	19 (0.9) [A]	25 (0.6) [P]	13 (0.4) [A]
North Ledge Flats, south of Hog Breaker (32°27'18"N, 64°49'24"W)	B	9-12	Coralgal veneer on aeolianite; sand channels	Medium- high	21 (2.3) [A]	27 (1.0) [P]	25 (0.8) [A]
Three Hill Shoals, patch reef (32°25'6"N, 64°44'0"W)	C	5-7	Coralgal veneer on aeolianite; sand channels	Low- medium	20 (2.2) [A]	25 (0.8) [P]	27 (0.9) [A]
Reefs outside entrance to Whalebone Bay (32°21'53"N, 64°42'55"W)	F	5-8	Poorly-devel- oped coralgal reef	Usually low	11 (0.5) [A]	11 (0.3) [P]	3 (0.1) [A]
Shark Hole, Harrington Sound (32°20'10"N, 64°42'11"W)	F	1-5	Aeolianite cliff; sands and sparse corals at base	low	—	—	—
Abbot's Cliff, Harrington Sound (32°20'23"N, 64°43'21"W)	F	1-4	Cliff; sands, blocks and sparse corals at base	low	—	—	—
Patton's Point, Harrington Sound (32°19'21"N, 64°43'10"W)	F	2-4	Cliff; sands, blocks and sparse corals at base	low	—	—	—
N. side Flatts Inlet, Harrington Sound (32°19'22"N, 64°44'7"W)	F	2-4	Aeolianite cliff; sands and sparse corals at base	low- medium	—	—	—
N. side, Walsingham Pond (32°20'49"N, 64°42'30"W)	G	1-3	Steeply-dipping aeolianite talus slope above mud	low	—	—	—
"Red Stake" pinnacle reef, Castle Harbor (32°20'35"N, 64°41'20"W)	F	1-5	Coralgal pin- nacle reef	usually low	11 (0.3) [A]	—	17 (0.6) [A]
"Meandrina" pinnacle reef, Castle Harbor (32°20'47"N, 64°40'52"W)	F	2-6	Coralgal pin- nacle reef	usually low	8 (0.2) [A]	2 (.05) [A]	21 (0.7) [A]
Inshore shoal reef, Causeway, Castle Harbor (32°21'16"N, 64°42'20"W)	F	1-3	Poorly-devel- oped coralgal inshore shoal reef	usually low	2 (.05) [A]	—	3 (0.1) [A]
South reefs, SE of Nonsuch Island (32°20'24"N, 64°39'23"W)	D	3-12	Coralgal veneer on aeolianite	medium- high	22 (1.1) [A]	18 (0.5) [P]	11 (0.4) [A]
Upper reef-front terrace, ENE of St. David's Head (32°22'12"N, 64°38'43"W)	A	9-18	Coralgal veneer on aeolianite	medium- high	1E (0.8) [A]	21 (0.6) [P]	14 (0.5) [A]
Upper reef-front terrace, SE of Gurnet Rock (32°20'5"N, 64°39'32"W)	A	18-22	Coral veneer on aeolianite; sand channels	medium	16 (0.8) [A]	22 (0.7) [P]	8 (0.3) [A]

Table 1. (Continued)

Sampling locality: description and approximate position (see fig. 1 and Admiralty Charts 334 and 868)	<i>Millepora</i> <i>albicornis</i>	<i>Agaricia</i> ssp.	<i>Isophyllia</i> ssp.	<i>Oculina</i> ssp.	<i>Siderastrea</i> ssp.	Other herma- typic coral species	Boulder Substrate
Upper reef-front terrace, N. of North Rock (32°29'2"N, 64°46'18"W)	—	3 (.06) ^A	3 (.05) ^A	—	—	—	—
North Ledge Flats, south of Hog Breaker (32°27'18"N, 64°49'24"W)	20 (0.1) ^A	11 (0.2) ^P	4 (.07) ^A	4 (—) ^A	8 (.05) ^A	5 (.04) ^A	—
Three Hill Shoals, patch reef (32°25'6"N, 64°44'0"W)	16 (0.1) ^A	11 (0.2) ^P	6 (0.1) ^A	11 (—) ^A	8 (.05) ^A	10 (.07) ^A	—
Reefs outside entrance to Whalebone Bay (32°21'53"N, 64°42'55"W)	3 (.02) ^A	8 (0.2) ^P	2 (.03) ^A	4 (—) ^A	3 (.02) ^A	—	—
Shark Hole, Harrington Sound (32°20'10"N, 64°42'11"W)	1 (.01) ^A	41 (0.8) ^A	46 (0.8) ^A	10 (—) ^A	21 (0.1) ^A	—	—
Abbot's Cliff, Harrington Sound (32°20'23"N, 64°43'21"W)	—	36 (0.7) ^A	22 (0.4) ^A	21 (—) ^A	18 (0.1) ^A	—	—
Patton's Point, Harrington Sound (32°19'21"N, 64°43'10"W)	—	39 (0.8) ^A	30 (0.5) ^A	18 (—) ^A	22 (0.1) ^A	—	—
N. side Flatts Inlet, Harrington Sound (32°19'22"N, 64°44'7"W)	—	52 (1.0) ^A	12 (0.2) ^A	5 (—) ^A	6 (.04) ^A	—	—
N. side, Walsingham Pond (32°20'49"N, 64°42'30"W)	—	—	—	—	—	—	(9.0) ^P
"Red Stake" pinnacle reef, Castle Harbor (32°20'35"N, 64°41'20"W)	12 (.06) ^A	22 (0.4) ^A	30 (0.5) ^A	18 (—) ^A	7 (.05) ^A	16 (0.1) ^A	—
"Meandrina" pinnacle reef, Castle Harbor (32°20'47"N, 64°40'52"W)	18 (0.1) ^A	95 (0.5) ^A	44 (0.7) ^A	14 (—) ^A	11 (.07) ^A	20 (0.1) ^A	—
Inshore shoal reef, Causeway, Castle Harbor (32°21'16"N, 64°42'20"W)	2 (.01) ^A	5 (0.1) ^A	1 (.02) ^A	—	—	—	—
South reefs, SE of Nonsuch Island (32°20'24"N, 64°39'23"W)	3 (.01) ^A	14 (0.3) ^P	5 (0.1) ^A	—	6 (.07) ^A	1 (.01) ^A	—
Upper reef-front terrace, ENE of St. David's Head (32°22'12"N, 64°38'43"W)	2 (.01) ^A	17 (.03) ^P	8 (0.1) ^A	—	3 (.02) ^A	2 (.01) ^A	—
Upper reef-front terrace, SE of Gurnet Rock (32°20'5"N, 64°39'32"W)	—	5 (0.1) ^A	2 (.02) ^A	—	—	—	—

Table 2. Distributional data on brachiopod *A. bernudana* obtained from undersides of colonies of those hermatypic coral species found to yield brachiopods in preliminary traverses (Table 1). Surface area sampled for each coral species is additional to that sampled in preliminary traverses, but still an approximate measure of its abundance relative to the other two species sampled at that locality. (N.S. = Not significant, in view of small yield of brachiopods).

Sampling Locality (for position, see Table 1 and Fig. 1)	Biotope (Upchurch 1970)	Host coral species	Surface area sampled (m ²)	No. of brachiopods collected	% of colonies yielding brachiopods	Mean brachiopod density per m ²	Overall brachiopod density per m ²	Max. brachiopod density/m ² on single colony	Variance (S ²)/Mean (λ) Ratio for brachiopods per 100 cm ² standard sample area
Upper reef-front terrace, N. of North Rock	A	<i>A. fragilis</i>	0.05	0	—	—	—	—	—
		<i>M. annularis</i>	0.40	69	44.0	172.5	75.9	1244	S ² = 31.56; λ = 1.73
		<i>M. cavernosa</i>	0.15	11	33.0	73.3	25.4	800	S ² = 19.98; λ = 0.73
North Ledge Flats, south of Hog Breaker	B	<i>A. fragilis</i>	0.25	2	1.4	N.S.	N.S.	N.S.	—
		<i>M. annularis</i>	1.35	119	24.0	88	21.1	722	S ² = 8.40; λ = 0.89
		<i>M. cavernosa</i>	0.30	22	14.0	73.3	10.3	227	S ² = 0.40; λ = 0.73
Three Hill Shoals, patch reef	C	<i>A. fragilis</i>	1.89	113	15.0	60.0	9.0	2875	S ² = 7.75; λ = 0.60
		<i>M. annularis</i> <i>M. cavernosa</i>	2.00 0.06	1 0	1.0 —	N.S. —	N.S. —	— —	— —
Reefs outside entrance to Whalebone Bay	F	<i>A. fragilis</i>	0.55	24	13.0	43.6	5.7	674	S ² = 1.37; λ = 0.44
		<i>M. annularis</i>	1.00	3	7.0	N.S.	N.S.	N.S.	—
		<i>M. cavernosa</i>	0.01	0	—	—	—	—	—
South reefs, south-east of Nonsuch Island	D	<i>A. fragilis</i>	0.64	4	5.0	N.S.	N.S.	N.S.	—
		<i>M. annularis</i> <i>M. cavernosa</i>	0.20 0.63	11 60	37.5 25.0	55.0 95.2	20.6 23.8	85 3125	S ² = 0.24; λ = 0.55 S ² = 1.23; λ = 0.95
Upper reef-front terrace, ENE of St. David's Head	A	<i>A. fragilis</i>	0.57	14	22.0	24.6	5.4	555	S ² = 2.86; λ = 0.25
		<i>M. annularis</i>	0.14	15	20.0	107.1	21.4	150	S ² = 5.42; λ = 1.07
		<i>M. cavernosa</i>	0.42	118	49.0	281.0	137.7	3210	S ² = 62.75; λ = 2.81
Upper reef-front terrace, SE of Gurnet Rock	A	<i>A. fragilis</i>	0.02	0	—	—	—	—	—
		<i>M. annularis</i>	0.05	0	—	—	—	—	—
		<i>M. cavernosa</i>	0.40	60	25.0	150.0	37.5	3595	S ² = 36.06; λ = 1.50

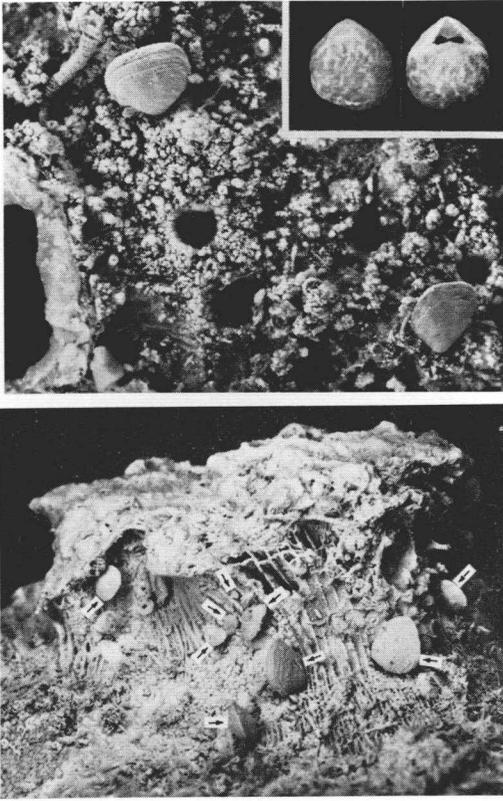


Figure 2 (top). *Argyrotheca bermudana* on underside of *Agaricia fragilis*, south reefs south-east of Nonsuch Island, 12 m depth, $\times 6$. Inset, pedicle and brachial valve, showing coarse punctation and color banding, specimen from sediments within sand channel, Three Hill Shoals patch reef, 5 m depth, $\times 6$; (bottom) Group of *A. bermudana* (arrowed) around base of pedestal of *Agaricia fragilis*, reefs outside Whalebone Bay, 5 m depth, $\times 4$.

one of attachment by the pedicle to the underside of foliaceous or encrusting corals in coral-dominated macrohabitats; occasional attachment to the underside of boulders in bedrock-dominated macrohabitats is also known. The shell is normally orientated in an almost vertical position (Fig. 2), with the anterior margin thrust well clear of all associated encrusting organisms, such as algae, sponges, bryozoans, and foraminifera.

At all localities sampled, the distribution of individuals upon the host corals appeared

to be patchy and rarely did more than 50 percent of the corals collected yield brachiopods. Nevertheless, to test whether distribution was random or truly aggregated the variance/mean ratio of brachiopod abundance for a standard sample area (100cm^2) for each biotope was calculated, following the method outline by Pielou (1969). In all cases involving sizeable numbers of brachiopods the ratio exceeds unity significantly (Table 2), suggesting a large measure of aggregation, such gregariousness probably resulting from late release of brooded larvae, rapid settlement, and post-settlement competition with other organisms.

The following biotopes recognized by Upchurch (1970) were sampled across the Platform:

Reef-front Terrace Biotope

The reef-front terrace biotope was defined by Upchurch (op. cit.) as extending from the edge of the Platform at 10-15 fathoms (18-27 m) inward to the reef tract. Its physiographic equivalent has been described by Bigelow (1905), Stanley and Swift (1967, 1968) and Stanley (1970). Skeletal fragments from samples from this biotope have been examined by Upchurch (1970) and Waller (1973), both of whom recorded *Argyrotheca bermudana* tests from their samples, Waller (op. cit., p. 40) suggesting that the tests were derived from "living sites among and beneath small corals".

Southern Development.—The reef-front terrace biotope on Bermuda's south shore was examined by the author at a locality about 150 meters south-east of Gurnet Rock, (the reef edge) at a depth of 22 meters. The effects of the strong surge are felt at this depth and energy conditions may be described as medium. Long ridges and mounds of coral-encrusted aeolianite, many orientated almost at right angles to the trend of the coastline, are separated by 9-12 m channels of coarse, rippled sand. These winnowed sands contain mostly *Homotrema rubrum* and shell fragments, including tests

of *A. bermudana*. It is believed that these tests are mainly derived from local spurs of aeolianite reef rock encrusted with large heads of *Diploria* ssp. and *Montastrea* ssp., mainly *M. cavernosa* (L.). *H. rubrum* occurs in great abundance beneath both these corals but is associated with brachiopods only beneath *M. cavernosa* and, to a lesser extent, beneath *M. annularis* (Ellis and Solander). The latter species is less common than *M. cavernosa* here and, in contrast to the heavy sheet-like overhangs produced by *M. cavernosa* (Fig. 3), usually forms pockets of small, shingle- or plate-like colonies with little overhang for possible attachment sites (Fig. 3, bottom). Brachiopod yields from this species are correspondingly low (Table 2).

A second locality about 100 m off the reef front at St. David's Head was also examined and yielded a sizeable brachiopod population, again mostly from *M. cavernosa*. Hydrographic conditions are similar here to those encountered at the previous locality.

Of the brachiopods obtained from the two localities in the south shore reef-front terrace biotope, most came from *M. cavernosa*. Distribution is nevertheless patchy (Table 2) and some colonies are totally barren, mainly because of heavy organic growth on the underside of the host corals. The coral *Agaricia fragilis* is rare at both localities; where present it occurs in sheltered areas and is "molded" to the aeolianite rock (Fig. 3, top), supporting little or no cryptofauna on its undersurface. The brachiopod tests encountered by Waller (1973) from sediment samples taken at depths of 34 m and 51 m south of Tucker's Town (Fig. 1) may be, in part at least, locally derived from coral-algal encrusted patches which Waller states are present at that depth, but most are probably derived from the reef and upper reef-front terrace by downward movement of sediment along the sand channels which transect this zone.

Northern Development.—The topography of the reef-front terrace in the northern part of

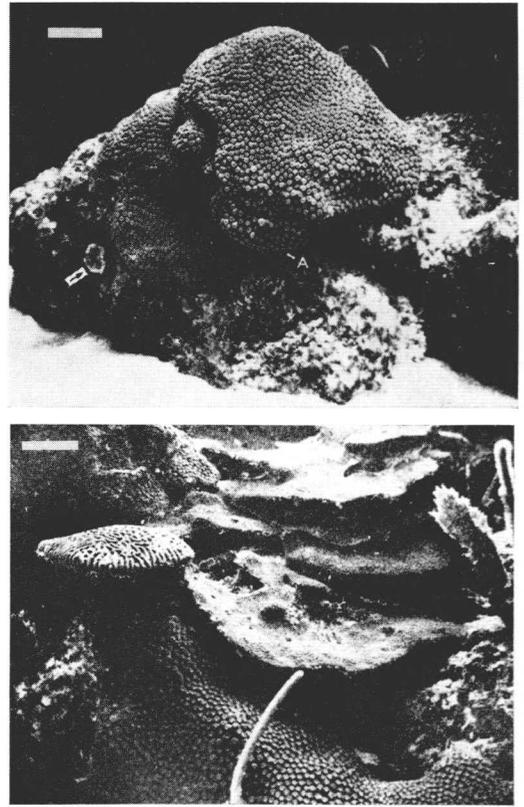


Figure 3 (top). *Montastrea cavernosa* on aeolianite, upper reef-front terrace, south-east of Gurnet Rock, 20 m depth. Arrow indicates flattened colony of *A. fragilis*, A shows typical overhang favored by brachiopods. Width of white bar represents 10 cm; (bottom) Platelike growth of *M. annularis* between massive *M. cavernosa* on aeolianite, same locality as above, 17 m depth. Width of white bar represents 10 cm.

the Platform is similar to that in the south. From the outer reef edge coral-encrusted ridges, separated by valleys of rippled sand, grade seawards into sand wedges. The most important bio-constructional agents are *Diploria* ssp., *Montastrea annularis* and *Porites astreoides*, with *M. cavernosa* here reduced to a minor role. Medium energy conditions again prevail and *M. annularis* produces mushroom-like heads, ideal for brachiopod attachment (Fig. 4), whereas *M. cavernosa* has a mamillated or bulbous growth form

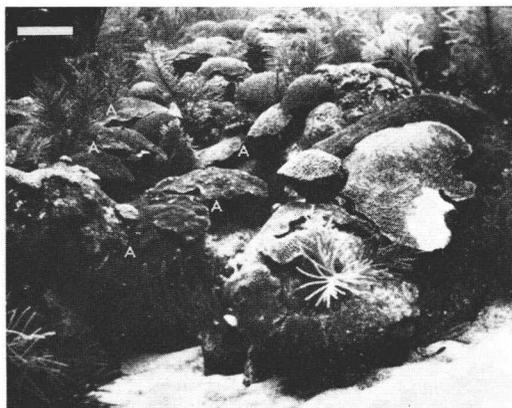


Figure 4. Mushroom-like heads of *M. annularis* (A) and *Diploria* ssp., upper reef-front terrace, north of North Rock, 18 m depth. Width of white bar represents approximately 30 cm.

enclosing little or no cryptic habitat. At a locality 1.2 km north of North Rock, most brachiopods were obtained from the former species. *H. rubrum* is again an important faunal associate. *Agaricia fragilis* colonies are rare and support few cryptic organisms. Upchurch (1970) has recorded brachiopod tests from greater than 2 mm fractions from his sediment sample 96 located on the reef-front terrace about 0.5 mile west of Hog Breaker at the outer edge of the north reefs (water depth estimated at 22 m). Local reefal mounds may contribute some tests here, the others presumably being derived from the main reef tract.

In summary, the medium energy reef-front terrace biotope, with its prolific growth of large coral heads, provides a favorable environment for attachment of *Argyrotheca bermudana*, which is a common constituent of the cryptofauna on the underside of sheet-like overhangs of species of *Montastrea*.

North Reef Biotope

Upchurch (1970) restricts this biotope to the northern part of the reef tract. It shares the rich coral growth of the reef-front terrace biotope but because framework organisms grow upwards to the intertidal zone, higher energy conditions are often encountered, es-

pecially at the seaward edge of the reefs (e.g. North Rock) and large, flat coral encrustations, poor in brachiopods, prevail. Lagoonwards, away from the surf zone, energy conditions for coral growth are similar to those on the reef-front terrace and very large, sheet-like or mushroom-like encrustations of *Montastrea* ssp. occur, together with large heads of *Diploria* ssp.

The north reef biotope was sampled on North Ledge Flats about 1.3 km almost due south of Hog Breaker, in waters of up to 12 m in depth. Most brachiopods were taken from the underside of *M. annularis*, the commonest of the framework-building corals at this locality. The growth form of this species is similar to that seen on the northern reef-front terrace, where medium energy conditions also prevail. Common associates of the brachiopods include *H. rubrum* in great abundance, together with ectoproct bryozoans and coralline algae.

Central and South Reef Biotope

Much of the reef tract on the eastern, western and southwestern margins of the Platform is included within this biotope by Upchurch (1970). Here energy conditions are lower than in the previous two biotopes, particularly in the east-west trending tract of patch reefs known at Three Hill Shoals, which lie approximately midway between North Rock and the northern shore of the eastern part of the Islands.

An unnamed patch reef in Three Hill Shoals was sampled in shallow water not exceeding 7 m in depth. The main reef-building corals present are *Millepora alcicornis*, *Porites astreoides*, *Montastrea annularis* and species of *Diploria*. Preliminary investigations revealed that brachiopods were rare at this locality and this was confirmed after detailed collecting, *A. bermudana* being recorded mainly from the undersides of colonies of *Agaricia fragilis* in deep, shaded clefts in the reef (Fig. 5). *M. cavernosa* is less common than *M. annularis* here, the latter usually exhibiting a shingle-like, overlapping growth form (see Garrett *et al.*,

1971, Fig. 5) which might be expected to provide a suitable niche for brachiopods. However, the undersides of colonies of this species are profusely overgrown with purple and green algal encrustations which cover almost the entire available surface; other notable epibionts include red and black sponges, *Halimeda* and encrusting cheilostomatous bryozoans. Such profusion of growth on *Montastrea* has rarely been seen elsewhere on the Platform. *Homotrema rubrum* is much reduced in numbers and confined to the inner areas of the host colonies. The larvae of both this species and *A. bermudana*, with which it is often associated, may have great difficulty in finding a suitably firm substrate for settlement, in the face of this prolific growth. Isolated high densities of brachiopods have been recorded (Table 2) but such occurrences are extremely rare and the overall yield per colony is low. Many of the brachiopods collected in July 1972 were very small and obviously immature, suggesting a recent spatfall.

Although brachiopod tests are consistently present in sediment samples from sand pockets, sand channels and reef flanks in the Three Hill Shoals patch reef, they are absent from the nearby lagoonal sediments, confirming the observation of Jordan (1973) that movement of reef-derived sediments lagoonwards from patch reefs through reef face channels in Bermuda is in the order of only tens of feet.

Boiler Biotope

Upchurch (op. cit.) restricts this biotope to the innermost reefs along the southeastern shore of the Islands and to a few outer reefs along the northern part of the reef tract east of North Rock. The boilers themselves are small, cupshaped, algal-vermetid gastropod reefs and their main characteristics have been described by Iams (1970) and Ginsburg, Schroeder, and Shinn (1971). The fauna and cements of the internal cavities within south shore cup reefs have been investigated by Ginsburg, Marszalek, and Schneidermann (1971) and Ginsburg and Schroeder (1973),



Figure 5. Typical *Agaricia fragilis* colony in shaded cleft, Three Hill Shoals patch reef, 6 m.

none of whom note the presence of brachiopods. However, Schroeder (*personal communication*, 1972) remarks that specimens possibly belonging to *A. bermudana* have been noticed by him within internal sediments in some Bermudian cup reefs.

Boilers were encountered along transects run transverse to the shoreline at Horseshoe Bay, Warwick Long Bay, Elbow Bay, and John Smith's Bay (Fig. 1). Brachiopods were found in several sediment samples, including one taken at the base of a boiler at Warwick Long Bay, but they may have been derived from the outer reefs in this case.

Seaward of the boiler zone on the south shore are isolated coral developments similar to those seen in the north reef and central and south reef biotopes and it is possible that both biotopes are represented in a discontinuous and attenuated form along the south shore. Most of the common reef-building corals, again occurring on aeolianites under medium energy conditions, were sampled at a locality south-east of Nonsuch Island (see inset 2 of Fig. 1). Significant numbers of brachiopods were obtained only from the undersides of large encrustations of *Montastrea cavernosa*, which is the dominant coral at this locality.

Basin Center Biotope

This biotope occurs in the deeper parts of the lagoon, is largely devoid of foliaceous

reef-building corals and therefore does not support any brachiopod populations. In addition sediment samples obtained from North and West Lagoon contained no brachiopod tests.

Nearshore-Sandy Substrate Biotope

Three localities, representing different aspects of this biotope, were sampled:

Whalebone Bay.—Whalebone Bay is exposed to the open ocean and intensive wave action; nevertheless it is representative of the more open-water part of this biotope, and therefore the poorly-developed coralgal reefs off the mouth of this bay were sampled for brachiopods. A preliminary traverse revealed that most of the common reef-building corals were present here, though much reduced in areal coverage. Small numbers of brachiopods were obtained mainly from *Agaricia fragilis*. As at Three Hill Shoals, *M. annularis* colonies, although often shingle-like in growth form, were heavily encrusted with algae, bryozoans, and sponges on the underside and brachiopods were consequently rare.

Castle Harbor.—Castle Harbor is a shallow, semi-enclosed basin (inset 2, Fig. 1) with east-west connections to the open ocean and an essentially sandy substrate. The reefs of Castle Harbor have been described by Frazier (1970) and the composition and distribution of sediments by Robelen (1970).

Three areas were sampled in Castle Harbor; an inshore shoal reef near the Causeway, and two pinnacle reefs (named "Red Stake" and "Meandrina" reefs by the author) in the central part of the Harbor. Species of *Montastrea* are rare in Castle Harbor, while colonies of *Agaricia fragilis*, though relatively common, have only a thin algal-sediment slime on their undersides; consequently no living brachiopods were obtained from any of these reefs. Sediment samples from the eastern and western ends of the Harbor yielded a small number of brachiopod tests, but they are believed to have been derived from reefal areas outside the Har-

bor. Brachiopods were not recorded from either reefs or sediments within the Harbor by Frazier (1970), Robelen (1970) or myself, lending support to the premise by Mackenzie et al. (1965) that little sand-sized sediment is transported into Castle Harbor from open-water areas.

It is conceivable that brachiopods inhabited Castle Harbor reefs before dredging operations for Kindley Field Air Base (1941-45) began and two cores taken near the pinnacle reefs revealed isolated and worn brachiopod tests at depths about 4 cm beneath the present surface of the sediment. However, no systematic faunal surveys were ever carried out by any investigators prior to the dredging—in addition, evidence from Bigelow (1905) suggests that the waters of the Harbor have always been silty. A cause and effect relationship would therefore be difficult to prove.

Harrington Sound.—Harrington Sound represents a shallow restricted basin (inset 1, Fig. 1) with access to North Lagoon through only a narrow tidal inlet at Flatt's Village. The hydrography, ecological zonation and sedimentology of Harrington Sound have been described by Neumann (1965). Many of the corals abundant on the reefal shoals of the Platform, such as *M. annularis* and *M. cavernosa*, are absent here; on the other hand *Agaricia fragilis* is the most abundant coral, especially in the Rocky Zone (Neumann, 1965). Nevertheless, I did not find living brachiopods at any of the five localities sampled (Table 2), although Lowenstam (*personal communication*, 1972) reported finding *A. bermudana* behind colonies of *Agaricia fragilis* in shallow water near Flatt's Inlet. Traces of rather worn brachiopod tests occurred at five station in the Sandy Zone, along Neumann's transect east of Devil's Hole, at depths between 3-4 m, and 5.5-7 m approximately, but it is not thought that significant living populations of *A. bermudana* now exist in Harrington Sound. Their absence is problematical, for suitable substrates are present, while Beers and Herman (1969) have shown

that Harrington Sound has above-average levels of nutrients and phytoplankton following the breakdown of the seasonal thermocline in late summer. Bretsky (1967) has attributed the scarcity of the arcid bivalve *Barbatia domingensis*, a common associate of *A. bermudana*, partly to the absence of large corals for attachment and partly to the sheltered and almost enclosed situation of the Sound which restricts larval intake from open waters and limits wave and current activity necessary for their distribution within the Sound.

Nearshore-Muddy Substrate Biotope

Typically this biotope is characterised by mangrove roots and a mud substrate, with hard corals invariably absent. Such a biotope would thus not normally be expected to support brachiopods unless some other kind of firm substrate was present.

Walsingham Pond is a shallow, land-locked, marine pond east of Harrington Sound with vertical rock walls, mangroves and a muddy substrate. Because of tidal exchange with Castle Harbor through caves and fissures, salinity values in the Pond are almost normal. The pond has been studied by many investigators, notably Gould (1968), Walton (1969) and Waller (1973). On the northeastern side of the pond a rock fall has produced a talus slope which extends from above the surface of the water to about 4.5 m in depth. Brachiopods were first recorded from this locality, living on the undersides of boulders on the talus slope, by Gautier (1965, unpublished report, Bermuda Biological Station). I have found them in the same situation; distribution is patchy with only about 40 percent of boulders from 0-3 m in depth yielding brachiopods. Up to 34 individuals on a single boulder have been found for a maximum density of 365/m². Such bouldery substrates are unusual in Bermuda but it should be remembered that the sub-boulder habitat is commonly colonized by cool-water brachiopods living at shallow depths elsewhere (Logan and Noble, 1971).

The occurrence of brachiopods in Wal-

singham Pond is even more unexpected when one considers their absence from most of Castle Harbor, with which the Pond is connected. It is likely that a relict population survives here, protected from the silty waters of Castle Harbor.

POSSIBLE LIMITING FACTORS AFFECTING BRACHIOPOD DISTRIBUTION ACROSS THE BERMUDA PLATFORM

From the preliminary traverses (Table 1) it is clear that *A. bermudana* occurs almost exclusively on the undersides of the foliaceous hermatypic corals *Montastrea cavernosa*, *M. annularis* and *Agaricia fragilis*. Table 2 indicates that, notwithstanding the clumped distributions, mean brachiopod densities per square meter generally decrease shorewards from the edge of the Platform, with brachiopods virtually absent from most of Castle Harbor and Harrington Sound, surviving marginally only in land-locked Walsingham Pond in an unusual sub-boulder, talus slope environment. This general distribution of *A. bermudana* parallels quite closely that of its common associates, the encrusting foraminifer *Homotrema rubrum* (Rooney, 1970) and the small arcid bivalve *Barbatia domingensis* (Bretsky, 1967) and suggests that similar limiting factors might be operating to control the distribution of these and other associated filter-feeding species. Some possible limiting factors are here reviewed:

Salinity

Recent experimental data obtained by Thayer (1974) on salinity tolerances of four Recent cool-water species of articulate brachiopods show a remarkable tolerance of salinity extremes by these species. It therefore does not seem reasonable to assume that the slight seasonal variation in salinity encountered on the Platform could affect distribution of the argyrothecid brachiopod populations.

Temperature

Under natural conditions, the amount of tolerance of *A. bermudana* to wide ranges in

temperature is not known. Nevertheless the lagoonal temperature range of 12.7 C in Bermuda is more than that normally encountered for other articulate brachiopods (McCammon, 1973) and may be a subsidiary limiting factor responsible for the comparative scarcity of brachiopods in lagoonal and near-shore regions. The low winter water temperatures across the Platform have been invoked to account for a faunal and floral diversity considerably lower than that of the Caribbean (Upchurch, 1970). This may also, in part at least, account for the lower brachiopod diversity in Bermuda and the complete absence of sclerosponges, common associates of brachiopods in the Caribbean and elsewhere (Jackson et al., 1971).

Depth and light

Brachiopods have been recorded by the author from low water mark to 28 m in Bermuda, which should be regarded as the limit of observations rather than the lower limit of the depth range of brachiopods. Because coral growth is sparse at the lower limit of this range, it has not been possible to ascertain whether brachiopod densities increase with depth off the reef front in Bermuda. However Jackson et al., (1971) note that *Argyrotheca johnsoni* from Jamaican fore-reef slopes increases in density with depth and suggest that density can be correlated with low light intensity. Similarly, Grant (*personal communication*, 1973) reports finding *Frenulina* sp. from 17-130 feet on Eniwetok reefs but notes an increase in density with increasing depth.

If light intensity is a factor in brachiopod distribution, then it probably operates in the larval periods of the species in question. Mano (1960) has shown that the articulate brachiopod *Frenulina sanguinolenta* (Gmelin) is initially photopositive but becomes photonegative in its latest larval stage, seeking out shaded areas of low light intensity immediately prior to settlement.

Food Supply

Assuming that articulate brachiopods, especially those inhabiting shallow waters, take

in a mixture of phytoplankton and dissolved nutrients as food supply (McCammon, 1969; Suchanek and Levinton, 1974), then the distribution of brachiopods (and other filter feeders) in Bermuda may be in part controlled by the availability of seasonal phytoplankton supplies supported by nutrients brought in by convergence of major water masses.

Boden (1952) has shown that plankton are conserved and concentrated in the area of a convergence of water masses in summer; thus the water flowing lagoonwards over the reefs is rich in both plankton and nutrients from the convergence and supports a rich and diverse flora and fauna in these areas. Both nutrients and plankton are gradually depleted as the water passes into the lagoon.

Biotic Associations

A. bermudana is commonly associated with sponges, tunicates, Foraminifera, bryozoans, bivalves and calcareous algae. Important and distinctive forms include the red foraminifer *Homotrema rubrum* and the bivalves *Barbatia domingensis*, *Lima hians*, *Spondylus americanus*, and *Lithophaga nigra*, as well as chamid species. Areal coverage of the undersides of corals by encrusting cheilostomatous bryozoans, sponges, and algae, in particular, is often high and brachiopods are consequently rare at these localities, perhaps arriving at a relatively late stage in the succession of such communities. Cuffey (1973) has shown that encrusting cheilostomatous bryozoans are most abundant in lagoonal reefs, such as Three Hill Shoals, and it is at such localities that the undersides of colonies of *Montastrea annularis*, for instance, are most profusely overgrown, to the detriment of brachiopod and *Homotrema* populations.

Thus, although *A. bermudana* has no known predator, competition for living space may be an important limiting factor in its overall distribution across the Platform.

Substrate

The presence or absence of a suitably firm substrate for attachment is regarded as the

main limiting factor in the distribution and density of brachiopods on the Platform. The commonest occurrence is one of attachment by the pedicle to the undersides of species of the hermatypic coral genera *Montastrea* and *Agaricia*. This somewhat restricted microhabitat is usually utilized by brachiopods wherever these corals occur in coral-dominated macrohabitats (i.e. reefal shoals). The distribution of these host corals across the Platform has been outlined by Griggs and Atchinson (1967, unpublished report, Bermuda Biological Station) and further information was obtained by the writer during the preliminary traverses. Basically, the two species of *Montastrea* are common on the outer ledge flats and patch reefs within the lagoon, but decrease to insignificance within restricted interisland waters such as Castle Harbor, Ferry Reach and Harrington Sound. Further, the dominant species of *Montastrea* on the south shore reefs is *M. cavernosa*, while *M. annularis* is the dominant form on the north reefs. *Agaricia fragilis*, on the other hand, occurs most commonly in near-shore protected waters and is of major importance in Harrington Sound. However, I have not found brachiopods on this coral in either Harrington Sound or Castle Harbor, so I assume that factors additional to substrate are at work in controlling brachiopod distribution.

The factors contributing to the growth form of corals are probably not yet entirely understood; certainly ambient light intensity is important (Goreau, 1959, 1963) but considerable overlapping of growth forms of *M. annularis*, for instance, has been recorded by Lewis (1960) and Barnes (1973), suggesting that other factors (as yet undetermined) are involved.

In Bermuda, shingle-like growth forms of *M. annularis* are common on all parts of patch reefs in North Lagoon (Garrett et al., 1971, Fig. 5), while lobate or club-shaped growth forms of *M. cavernosa* occur on the marginal ridge and reef face of such patch reefs (Garrett et al., 1971, Fig. 9). In both cases light intensity is high and depths are

shallow. It is likely that energy conditions and substrate are also important in determining growth form. Where energy conditions are high, encrusting sheets of *M. annularis* and *M. cavernosa* generally occur (Fig. 3); in medium and low energy environments, *M. annularis* gradually becomes more shingle-like, while *M. cavernosa* assumes a bulbous growth form. *A. fragilis* is flattened against the substrate in high and medium energy conditions (Fig. 3, top) and offers poor attachment sites for brachiopods, yet adopts a more emergent growth form in lower energy environments. In areas where coral growth forms a relatively thin veneer on an aeolianite substrate (e.g. north and south reefs), the growth form of the coral is normally encrusting, with the overall form of the colony closely conforming to the contours of the aeolianite base (Fig. 3, top). The lee sides of overhangs produced by peripheral growth from encrusting or massive growth forms of *Montastrea* ssp. near the sediment floor in medium energy environments offer the most promising sites for brachiopod attachment on the Bermuda Platform.

The marked preference of argyrothecid brachiopods in Bermuda for three particular host corals species is peculiar. Jackson et al., (1971) point out that *A. johnsoni* from Jamaica shows no preference for any one coral species as substrate, although noting that species of the foliaceous corals *Montastrea* and *Agaricia* provide most of the favorable undersurfaces for brachiopods. Nevertheless, it is surprising that other coral species of mound or plate-like growth form in Bermuda, such as *Porites astreoides*, *Isophyllia* ssp., and *Diploria* ssp. do not support brachiopods, especially as *Homotrema rubrum* and *Barbatia domingensis* are common beneath these corals. This anomaly is, as yet, unexplained.

POPULATION STRUCTURE

Width-frequency histograms of living specimens of *A. bermudana* collected from five localities across the Platform during July

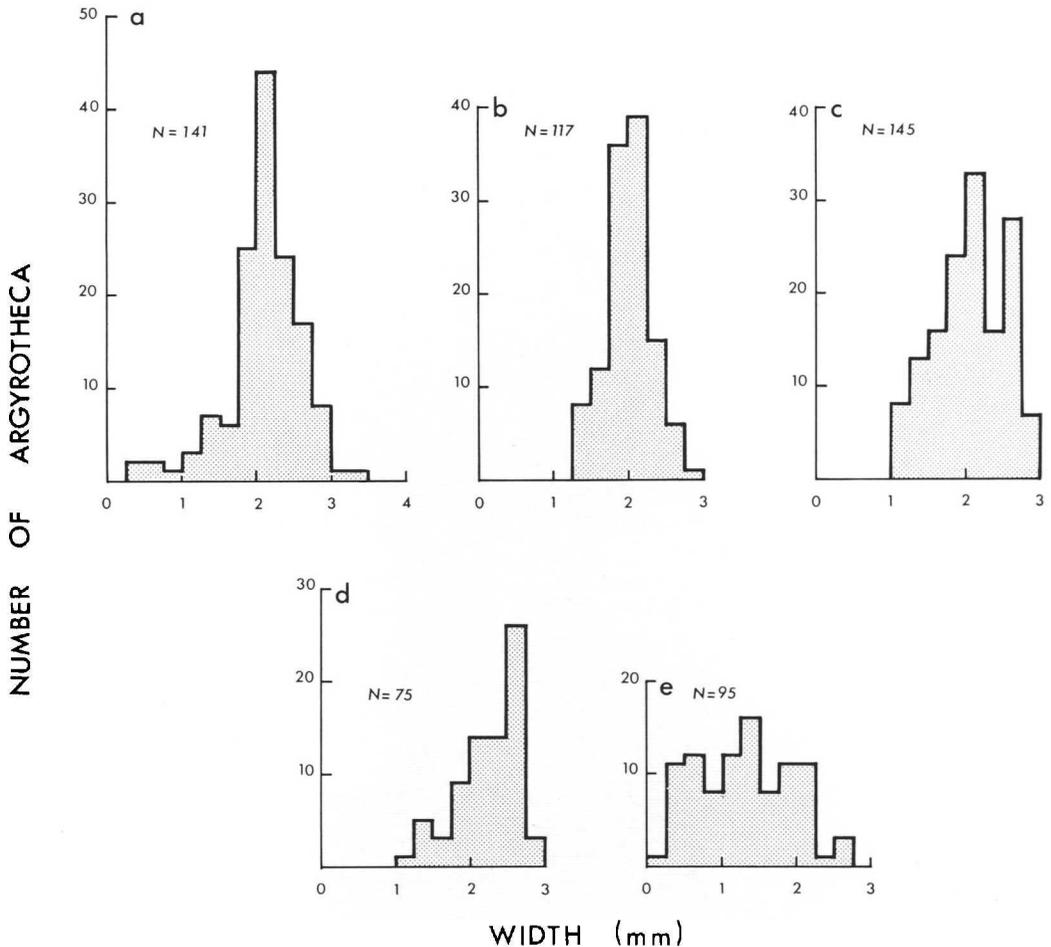


Figure 6. Width-frequency histograms of *A. bermudana*. a. North Ledge Flats, south of Hog Breaker, collected July 26th., 1972. b. North side of Walsingham Pond, collected July 6th., 1972. c. upper reef-front Terrace, ENE of St. David's Head, collected July 24th., 1972. d. south reefs, south-east of Non-such Island, collected July 24th., 1972. e. Three Hill Shoals patch reef, collected July 12th., 1972.

1972 were constructed (Fig. 6). With one exception, all showed normal or near normal distributions; only the sample from Three Hill Shoals (Fig. 6e) showed a relatively high proportion of juveniles. Similar distributions for living brachiopods from other areas have been obtained by Rudwick (1962), Paine (1969), and Neall (1970), although Percival (1944) and Logan and Noble (1971) obtained positively-skewed curves for their brachiopod populations.

Any conclusions based on only summer

observations for 1 year must necessarily be tentative, especially as growth rate data are lacking. However, the dominance of large individuals at four out of five localities sampled on the Bermuda Platform suggests the following possibilities:

(a) A high juvenile mortality caused by selective destruction of small shells by predators. Paine (1969) has suggested this explanation for *Terebratalia transversa* populations from the west coast of North America, based on the high rate of incidence of damage

caused by predators, probably crabs, on most individuals in his samples. While *A. bermudana* has no known predators, this explanation must remain a possibility until proven otherwise.

(b) The population represents the growth to maturity of a single spatfall, which, having survived the earliest settlement stages, competes successfully against later spatfalls in that area until its death. This explanation has been advanced by Neall (1970) to explain the relative absence of young individuals in populations of *Neothyris lenticularis* from New Zealand. Neall notes that young individuals of this species rarely settle on the adults or in the adult colony, whereas the population structure of the species *Magasella sanguinea* from the same area is much different, showing an intermixture of young and adult individuals to form a stable age pyramid. Brookfield (1973) has invoked a similar explanation to account for an adult-dominated distribution in the Jurassic brachiopod *Torquirhynchia inconstans* from England.

(c) Thayer (in press) has recently suggested that unimodal size-frequency distributions in brachiopods may indicate patchy larval dispersion and local recruitment failure rather than exclusion of juveniles by adults.

(d) The peaks may represent accumulations of brachiopods of many ages due to near-cessation of growth at about 2½-3 mm width.

The correct interpretation of the available data cannot be resolved until growth rates are known and localities are sampled on an all-year round basis.

ACKNOWLEDGMENTS

I am indebted to Dr. A. C. Neumann of the University of North Carolina for splits of sediment samples collected by him from a traverse near Devil's Hole, Harrington Sound, and to Dr. C. D. Gebelein of the Bermuda Biological Station for sediment samples from North and West Lagoon. I also acknowledge the assistance of Stephen Dryer and the cooperation of the staff of the Bermuda Biological Station. The work was supported by National Research Council of Canada operating grant A-4331. This contribution is No. 594 of the Bermuda Biological Station.

ADDENDUM

Since the manuscript was prepared the author has examined coral reefs on the west coast of Barbados, W. I., where two small species of *Argyrotheca* co-exist on the undersides of reef-building corals of platy growth form, such as *Agaricia fragilis*, *A. agaricites*, *Montastrea annularis*, and *Mycetophyllia lamarckiana*. A transect run due east of the Bellairs Research Institute at St. James indicated that the brachiopods *Argyrotheca bermudana* (Dall) and *A. cf. schrammi* (Crosse and Fischer) range from the Reef Crest Zone of the fringing reefs (Lewis, 1960) at 20 feet (6m) depth to the effective limit of prolific hermatypic coral growth at a depth of about 150 feet (46m), within Lewis's "mixed coral community." While *A. bermudana* commonly outnumbered *A. cf. schrammi* by about five to one, overall densities of both species at shallow depths are extremely low (<1/m²). Numbers increase gradually in deeper water, *A. bermudana*, for instance, averaging 180/m² at 150 feet (46m), with occasional maximum densities reaching 360/m² at that depth. Patchy distributions and low juvenile counts (Aug. 1974) are typical of both species and the overall life habits of reef-dwelling argyrothecids from Barbados appear to be closely similar to those from Bermuda.

I thank the Bellairs Research Institute of McGill University for use of facilities and Dr. G. A. Cooper of the U. S. National Museum for help in identifying brachiopods.

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