Annales Societatis Geologorum Poloniae (1991), vol. 61: 221 – 230
PL ISSN 0208-9068

DEPTH-RELATED SHAPE VARIATION IN *AMMOBACULITES AGGLUTINANS* (D'ORBIGNY)

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Kaminski M. A. & Kuhnt W. 1991. Depth-related shape variation in *Ammobaculites agglutinans* (D'Orbigny). *Ann. Soc. Geol. Polon.*, 61: 221 – 230.

Abstract: Specimens of *Ammobaculites agglutinans* from ALBATROSS stations in the North Atlantic can be separated into two populations relative to water depth. Specimens from abyssal calcareous oozes are larger in size and commonly possess more uniserial chambers than specimens from shallower depths on the continental margin. In addition, the amount of dimorphism between megalosphaeric and microsphaeric individuals increases with depth. These size and shape variations may allow abyssal populations to be distinguished from bathyal and neritic populations.

Manuscript received 16 May 1991, accepted 5 September 1991

INTRODUCTION

Ammobaculites agglutinans (d'Orbigny), originally described from the Miocene of the Vienna Basin, is one of the most widely recognized species of agglutinated foraminifera. It is the type species of *Ammobaculites* Cushman, 1910. This species is found today in a wide range of environments, and has been reported from sediments ranging in age from Permian to Recent (Brady, 1884). Since agglutinated foraminifera have been the focus of an increasing number of paleoenvironmental studies in recent years, it is important to document trends in test morphology relative to known environmental parameters. By applying iniformitarian principles, information gained by studying morphological patterns among modern forms can then be directly applied to the fossil record.

During a recent visit to the Department of Paleobiology at the US Natural History Museum of the Smithsonian Institution, we had the opportunity to study specimens of *Ammobaculites agglutinans* housed in the Cushman Collection. Routine examination of slides revealed that Cushman's ALBATROSS specimens display considerable variation in size and shape. When we removed the slides from their trays and resorted them according to water

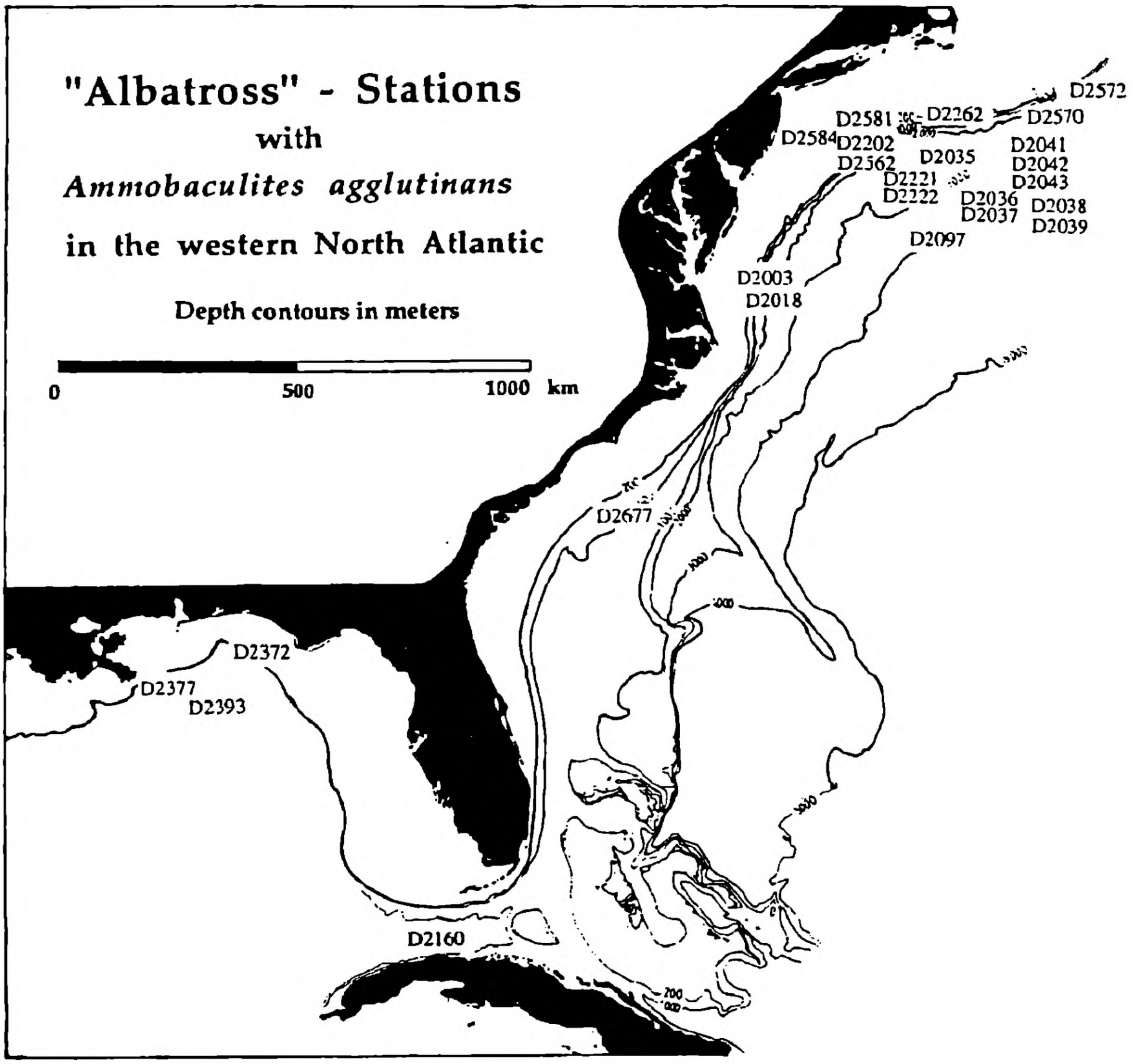

Fig. 1 Location of ALBATROSS stations with *Ammobaculites agglutinans* preserved in the Cushman Collection.

depth, trends in test morphology became readily apparent. A more rigorous morphometric study of this species is presented there in order to accurately define its observed variability.

CUSHMAN'S ALBATROSS MATERIAL

In 1906, while still a 25-year-old graduate student at Harvard, Joseph Cushman received a contract from the US Natural History Museum to study the dredge samples recovered during surveys by the US Fish Commission Ship ALBATROSS. Under the terms of his agreement, Cushman was to prepare a report of his findings for the museum and mount a set of slides containing any new or previously reported species. In return , the museum agreed to

Table 1

Sample localities of *Ammobaculites agglutinans* in the North Atlantic.
Water depth is listed in fathoms (as recorded by Cushman) with the metric equivalents.

ALBATROSS Station:	Location (lat. - long.)		Water Depth fathoms	meters	No. of specimens	Reported Lithology
D2003	37°,16'30"N	74°,20'36"W	641	1172	2	–
D2018	37°,12'22"N	74°,20'04"W	788	1441	2	blue mud
D2035	39°,26'16"N	70°,02'37"W	1362	2491	4	*Globigerina* ooze
D2036	38°,52'40"N	69°,24'40"W	1735	3173	6	*Globigerina* ooze
D2037	38°,53'00"N	69°,23'30"W	1731	3166	7	*Globigerina* ooze
D2038	38°,30'30"N	69°,08'25"W	2033	3718	13	*Globigerina* ooze
D2039	38°,19'26"N	68°,20'20"W	2369	4332	18	*Globigerina* ooze
D2041	39°,22'50"N	68°,25'00"W	1608	2941	8	*Globigerina* ooze
D2042	39°,33'00"N	68°,26'45"W	1555	2844	8	*Globigerina* ooze
D2043	39°,49'00"N	68°,28'30"W	1467	2683	1	*Globigerina* ooze
D2097	37°,56'20"N	70°,57'30"W	1917	3506	7	*Globigerina* ooze
D2160	23°,10'31"N	82°,20'37"W	167	305	2	coral
D2202	39°,38'00"N	71°,39'45"W	515	942	6	green mud
D2221	39°,05'30"N	70°,44'30"W	1525	2789	4	gray ooze
D2222	39°,03'15"N	70°,50'45"W	1537	2811	4	gray ooze
D2262	39°,54'45"N	69°,29'45"W	250	457	4	green mud & sand
D2372	29°,15'30"N	85°,29'30"W	27	49	4	gravel
D2377	29°,07'30"N	88°,08'00"W	210	384	1	gray mud
D2393	28°,43'00"N	87°,14'30"W	525	702	1	light gray mud
D2562	39°,15'30"N	71°,25'00"W	1434	2623	4	gray ooze
D2570	39°,54'00"N	67°,05'30"W	1813	3315	5	*Globigerina* ooze
D2572	40°,29'00"N	66°,04'00"W	1769	3236	1	gray ooze
D2581	39°,43'00"N	71°,34'00"W	394	721	4	green mud
D2584	39°,05'30"N	72°,23'20"W	541	989	1	gray mud
D2677	32°,39'00"N	76°,50'30"W	478	874	1	gren mud

publish Cushman's findings and allow him to keep a duplicate set of slides. Ina later stage of the project, Cushman received remuneration for his efforts amounting to $0.15 per slide (Todd, 1985). Cushman's study of agglutinated foraminifera from the ALBATROSS samples resulted in three monumental works published in several parts, covering the foraminifera of the North Pacific (Cushman, 1910, 1911), Atlantic (Cushman, 1918, 1920) and Philippines (Cushman, 1921).

The slides housing *Ammobaculites agglutinans* are of an old type, constructed of wood with a black enamel specimen chamber, covered by a mica plate held in place with brass clips. They occupy four trays in the "secondary types" collection of this species at the USNM. Specimens from the North Atlantic ALBATROSS stations comprise the majority of this collection. Cushman (1920) recorded this species from 30 ALBATROSS stations in the North Atlantic region. Twenty-six of these stations are from the continental shelf and slope off New Jersey, with the four remaining stations from the western Gulf of Mexico. Cushman also provided a table that lists the location, depth, sediment type, and number of specimens collected at each station. Slides from 25 of the 30 Atlantic stations listed by Cushman are preserved in the collection. The location of each station is plotted in Figure 1, and the substrate characteristics and number of specimens preserved in Cushman's slides are given in Table 1.

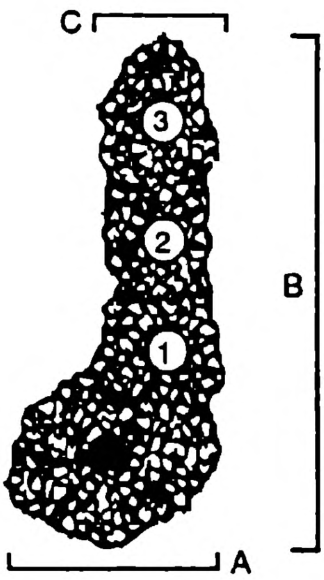

Fig. 2 Measured parameters in *Ammobaculites agglutinans* from the ALBATROSS Collection. *A′* – maximum width across the initial spire, *B* – length of the test, *C* – maximum width of the uniserial portion, and the number of chambers in the uniserial part

METHODS

A total of 122 specimens, housed in 28 slides, are preserved in Cushman's North Atlantic sample set. Five parameters were measured on each specimen using an optical micrometer: length of the specimen, width across the initial spire, width across the uniserial portion, number of uniserial chambers, and the presence or absence of a depressed umbilicus in the initial portion of the test (Fig. 2). In all cases, we recorded the width of the specimen at its widest point. Specimens were also recorded as microsphaeric or megalosphaeric forms based on the dimensions of the initial spire. Camera lucida drawings were made of representative specimens.

SYSTEMATICS

Ammobaculites agglutinans (d'Orbigny)

Fig. 3

Spirolina agglutinans D'ORBIGNY, 1846, p. 137. pl. 7, figs. 10-12
Haplophragmium agglutinans (d'Orbigny). - Brady, 1884, p. 301, pl. 32, figs. 19, 20, 24-26.
Ammobaculites agglutinans (d'Orbigny). - Cushman, 1910, p. 115, fig. 176.

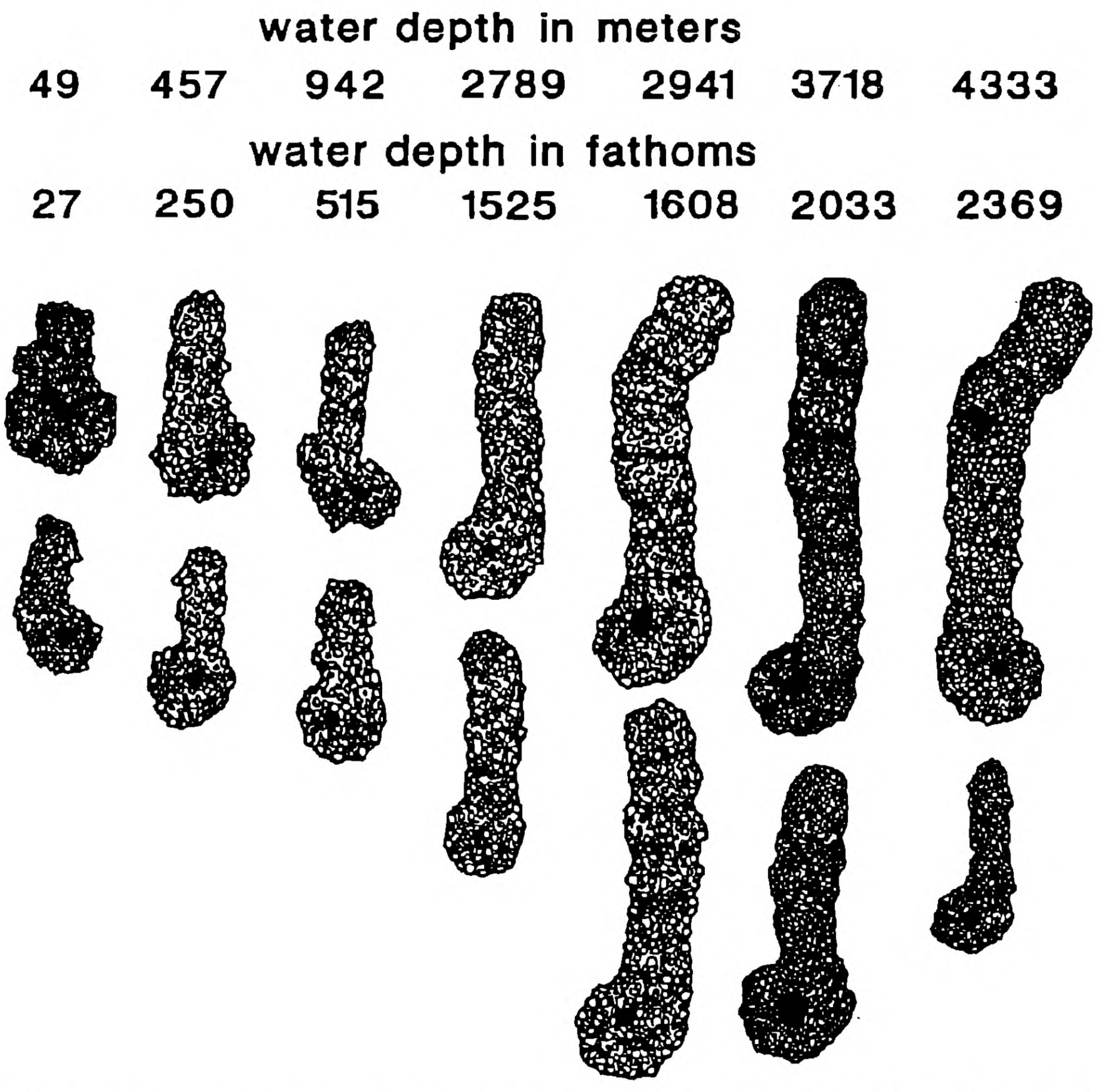

Fig. 3 Representative specimens of *A. agglutinans* from Cushman's ALBATROSS samples, showing the range of size and shapes present in the collection. The depth of station in fathoms and meters is also given. All specimens drawn to the same scale

Diagnostic features. Test robust, initially planispiral, later uniserial. Planispiral portion is involute, with slightly depressed umbilicus and four or five chambers in the final whorl. Uniserial portion is rectilinear and round in cross section, extending tangentially from the initial portion, with as many as nine chambers. Chambers in the uniserial portion are broader than high, and round in cross section. Sutures are usually indistinct in the planispiral part, straight and depressed in the uniserial part. Aperture terminal, a single oval to round opening without a lip. Wall of medium to coarse, poorly sorted grains that are mainly of quartz, but may include some calcareous material.

Remarks. *Ammobaculites agglutinans* was originally described by d'Orbigny (1846) from the upper Miocene of the Vienna Basin, and has subsequently been reported by numerous authors from sediments ranging in age from Permian to Recent. Brady (1884) was the first to apply the term *Haplophragmium agglutinans* to the modern deep-water inhabitant, and he noted the large variation in both its size and bathymetric range. The modern bathyal to abyssal forms compare well with d'Orbigny's types, but they commonly display more variability in the size of the agglutinated grains, and may possess more chambers in the uniserial portion of the test. In the modern ocean, *A. agglutinans* occurs from neritic to abyssal depths. Brady listed it from nine CHALLENGER stations in the North Atlantic ranging in depth from 530 to 2750 fathoms; from two stations in the South Atlantic (2200 and 2900 fathoms); and from 12 stations in the Pacific from 2 to 3125 fathoms (2.6 to 5715 m). Balkwell and Wright (1885) reported *A. agglutinans* from 17 fathoms (31 m) off Skerries, Ireland and from 50 fathoms (91 m) in the Lambay Deep, northeast of Dublin, Ireland. Goes (1894) illustrated a specimen from 1,704 m depth in the North Atlantic.

However, J.A. Cushman gathered what is probably the largest collection of modern specimens of *A. agglutinans*. Cushman (1920) reported it from 30 ALBATROSS stations in the North Atlantic, ranging in depth from 27 to 2369 fathoms (49 to 4333 m). Representative specimens from these stations are illustrated in figure 3.

Cushman noted that *A. agglutinans* was common at many stations, but that „it is best developed in fairly deep, cold water". Cushman also provided a detailed description of the modern deep-water form:

„Test elongate, early portion closely coiled, planispiral, of one or usually more coils, each with five to seven chambers, later portion uncoiled, sub-cylindrical, made of a linear series of chambers, in adult specimens making up the larger portion of the test; wall rather coarsely arenaceous, somewhat variable in its surface, usually roughened but occasionally fairly smooth. Aperture in the early portion slit-like, at the base of the apertural face; in the uncoiled portion the aperture is is the middle of the terminal face and is rounded. Color variable, usually gray."

RESULTS

The 122 specimens preserved in the Cushman collection do not constitute a rigorous statistical assemblage because we have no way of determining whether there was any bias in the collecting procedure. However, since both large and small specimens are present in the slides, we must assume that Cushman did not pre-select his specimens according to their size. The measured size parameters of these specimens are presented in figure 4.

Our observations of the preserved material reveal that two depth-related trends in morphology are present, allowing us to separate neritic to bathyal forms from abyssal forms. First, there is a general increase in the length of megalospheric individuals with increasing depth (Fig. 4a). The mean and standard deviation of length measurements of specimens from neritic to bathyal stations (above 2,000 m depth) is 1.13 ± 0.19 mm, whereas among the abyssal specimens, these values are. 1.44 ± 0.51 mm. The largest abyssal individuals may be over 2.7 mm long. A Student's t-test reveals that these

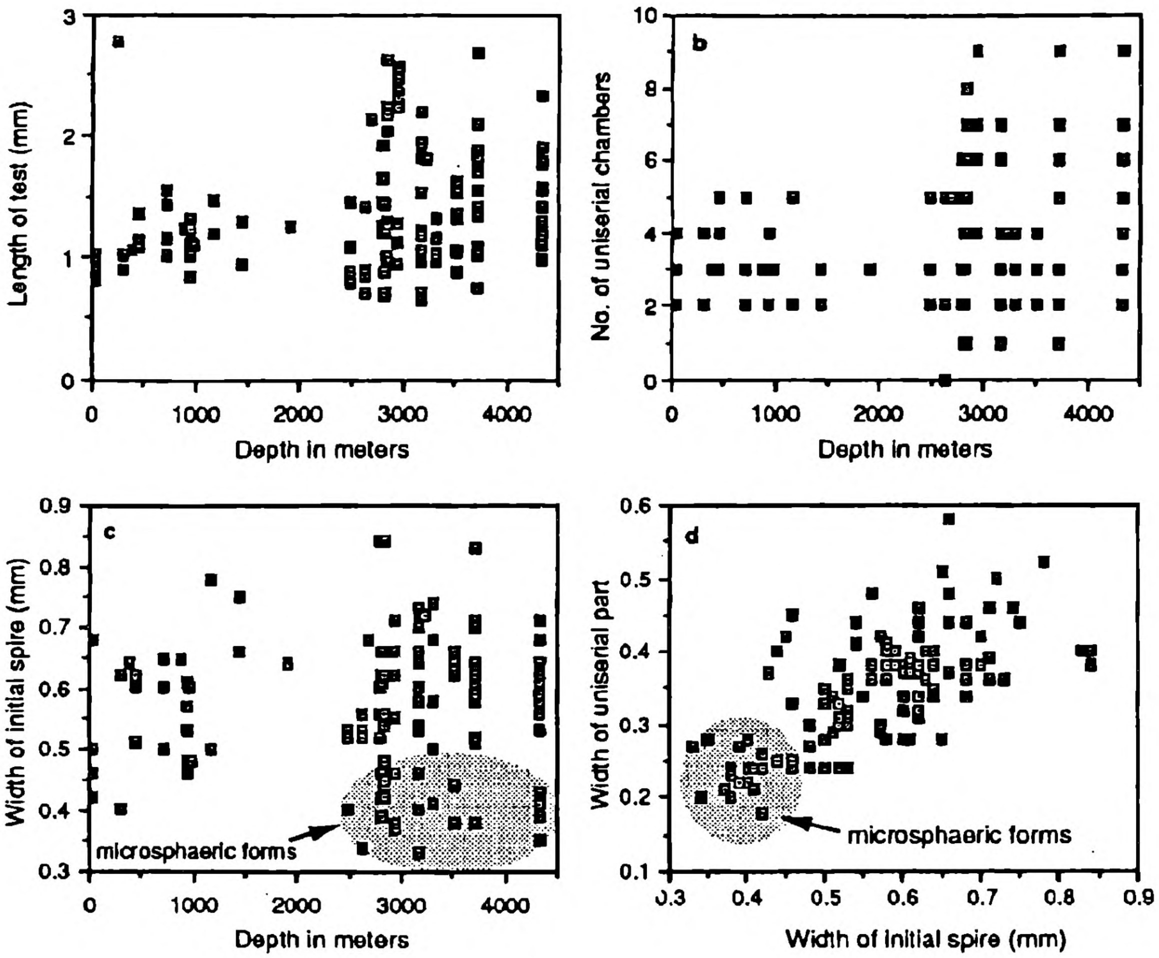

Fig. 4 Measured parameters of ALBATROSS specimens from the North Atlantic preserved in the Cushman Collection, arranged according to depth

differences in length are significant ($t_s = 3.28$; $P < 0.001$). The differences in length are attributed to differences in the number of chambers in the uniserial portion of the test (Fig. 4b). Specimens with an equal number of uniserial chambers did not differ significantly in mean length between bathyal and abyssal populations. Specimens from neritic and bathyal stations rarely possess more than four uniserial chambers, whereas the specimens from abyssal stations may possess as many as nine uniserial chambers.

The second morphologic trait that appears to vary between bathyal and abyssal populations is the diameter of the initial spire. The size differences between megalosphaeric and microsphaeric individuals are more pronounced in the abyssal morphotype. The coefficient of variation in the width is the initial spire is 16.1 for neritic to bathyal stations, but 20.5 for abyssal stations. For the three deepest stations, the distribution of the width of the initial spire is distinctly bimodal, allowing for the easy recognition of the microspheric generation (Fig, 4c, d). In general, the maximum width of the uniserial part increases in proportion to the diameter of the initial spire. The nature of agglutinated grains incorporated in the test wall also changes with depth. The neritic to bathyal morphotype may incorporate calcareous particles into its wall, whereas the abyssal form uses only fine quartz grains bound by a brownish organic cement.

We also tested what effect substrate alone might have on the mean length of the test. Cushman classified his samples according to sediment type (Table 1). By coincidence, all samples collecdted from stations deeper than 2,000 m were reported as either "*Globigerina* ooze" or "gray ooze". However, when we compared the subset of 77 specimens from the "*Globigerina* ooze" alone with the subset of 45 specimens from all other substrates (including the samples listed as "gray ooze"), the Student's t-test revealed a greater level of significance ($t_s = 4.22$; $P < 0.0001$) than that observed between our arbitrarily defined bathyal and abyssal populations. The mean length of specimens from "Globigerina ooze" is 1.50 ± 0.51 mm, compared with 11.15 ± 0.28 mm from all other sediment types.

DISCUSSION

The clear morphological distinction between modern neritic to bathyal populations and abyssal populations of *Ammobaculites agglutinans* in the western North Atlantic suggests that the shape of this species may be useful for estimating the paleobathymetry of ancient sediments. However, it is unlikely that these size variations can be attributed to water depth alone - they are more likely due to some other factor (or combination of factors) correlated with water depth, such as the composition of the substrate or the availability of some limiting trophic resource. Our analysis of Cushman's specimens suggest that individuals collected from "Globigerina ooze" constitute a morphologic end-member, but we must point out that all these samples were collected from abyssal depths.

In any case, the observation that specidmens collected from abyssal calcareous oozes are larger and possess more chambers than those collected from shallower stations suggests a difference in the life history of *Ammobaculites agglutinans*. In theory, organisms inhabiting the abyssal regions of the ocean should display slower growth rates than those living at neritic depths, presumably due to the rapid decline in the amount of available food with increasing water depth (Sanders and Hessler, 1969). In general, abyssal populations depend upon a seasonal supply of nutrients ultimately derived from the spring phytoplankton bloom. As a result, reproduction among abyssal benthic foraminifera may take place on a yearly basis in much of the deep ocean. If this is the case, slow, but continued growth during the year among abyssal foraminifera may result in the addition of more uniserial chambers before the individual reproduces. The continental rise of eastern North America, however, may not be representative of the deep ocean as a whole. The continental slope and rise of New Jersey, where the majority of Cushman's samples were collected, is an area of high abyssal kinetic energy. The region is influenced by both thermohaline boundary currents, and benthic storms that produce locally high turbidity (Hollister & McCave, 1984). As a result, organisms inhabiting the lower continental slope and rise in regions affected by boundary currents may benefit from the lateral advection of food particles, and therefore may locally grow to larger didmensions than at other localities. For example, Schafer *et al.* (1983) noted an assemblage consisting of large agglutinated forms beneath the core of the Western Boundary Undercurrent off Newfoundland. This raises the possibility that Cushman's "*Globigerina* ooze" samples may have been more winnowed by deep-sea currents than the "gray ooze" samples. Whether the presence of two different morphotypes of *A. agglutinans* in a given basin is actually related to bathymetry, substrate, or local hydrography remains to be tested by additional observations in other basins.

CONCLUSIONS

Our observations of specimens of *Ammobaculites agglutinans* preserved in the collections of the US Natural History Museum reveal the existence of two bathymetrically-related populations in the western North Atlantic. Unlike many other modern species of benthic foraminifera, in *Ammobaculites agglutinans* there is a general increase in the size of megalospheric individuals with depth. The bathyal morphotype is stout with fewer than four chambers in the uniserial part. The abyssal morphotype possesses as many as nine uniserial chambers, and displays greater variability in the width of the initial spire, which can be attributed to a greater amount of dimorphism between the megalospheric and microspheric generations. We speculate the morphological variability reflects differences in the life history between bathyal and abyssal populations in the western North Atlantic.

ACKNOWLEDGMENT

We are grateful to Martin Buzas and Brian Huber for the hospitality afforded us during our visit to the Smithsonian in February 1990. Thoman Gibson, Brian Huber, and R. Spencer reviewed this manuscript. This is contribution no. 33 of the Deep-Water Agglutinated Foraminifera Project.

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Streszczenie

ZMIENNOŚĆ KSZTAŁTU ZALEŻNA OD GŁĘBOKOŚCI W *AMMOBACULITES AGGLUTINANS* (D'ORBIGNY)

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Wśród okazów gatunku *Ammobaculites agglutinans* znajdujących się w kolekcji Cushmana z rejsu statku ALBATROSS (Fig. 1), przechowywanej w Muzeum Historii Naturalnej w Instytucie Smithsona w Waszyngtonie, można wyróżnić dwie populacje różniące się głębokością występowania. Okazy z głębinowych mułów wapiennych są większe i mają więcej komór niż okazy z mniejszych głębokości na krawędzi kontynentalnej (Fig. 2 – 4). Ponadto, stopień dymorfizmu między formami megalosferycznymi a mikrosferycznymi wzrasta z głębokością. Stwierdzone zróżnicowanie kształtu pozwala na odróżnianie populacji abysalnych od populacji batialnych i nerytycznych.