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MORPHOLOGICAL VARIATION OF THE FORAMINIFER AMMONIA BECCARII (LINNE) FROM THE ATLANTIC COAST OF THE UNITED STATES

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ABSTRACT

The foraminifer *Ammonia beccarii* (Linné) was studied from various Holocene environments of the Atlantic coast of the United States in order to define its morphological variation and to determine the possible causes of the variation.

At the beginning of the study, 45 morphological characters were measured from each of 221 specimens from two areas located in the northern and the southern portions of the coast. Comparison of characters indicated that many of the characters are intercorrelated, and each character has different significance in revealing the geographical variation of morphology. After elimination of the correlated characters and the nonsignificant characters, eight characters were considered sufficient to describe the morphology of the animal. Using these eight characters, the average sample size necessary for discrimination among samples from different environments was estimated to be about 30 specimens per sample.

Based on the guidelines given by the above study, 25 samples from the coast were used for studying geographical variation of the morphology. The sample sizes ranged from 6 to 56. Each specimen was measured for its eight selected characters. Statistical analysis showed that among the characters measured, proloculus size and umbilicus size have relatively large variation among samples and small variation within samples. Evidently these two characters are the most useful in discrimination among samples from different areas. Further consideration of sample location suggested that there are two geographical varieties of the animal: one variety with large proloculus and large umbilicus existing north of Cape Hatteras, and the other variety with small proloculus and small umbilicus existing south of Cape Hatteras.

The relationships of 14 environmental factors to morphological variation were studied. Two water masses separated by Cape Hatteras were shown to be the most important factors affecting the morphological variation. Five other important factors are runoff from land, sediment size, macrohabitat, tidal range, and winter climate as measured by annual snowfall. The macrohabitats considered include estuary, bay, tide pool, and open sea. Actually these five factors represent local conditions, which modify regional characteristics of the water mass and cause some variation of the morphology.

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INTRODUCTION

Ammonia beccarii (Linné) is a common foraminiferal species, which grows in almost every brackish or shallow marine environment from the tropic to the temperate regions of the world. It also occurs commonly in strata from the Cretaceous to the Holocene. Based on the distribution of the living species, the fossil forms of the species have been useful as an indicator of ancient nearshore depositional environments.

The morphology of this species has been known to be extremely variable both within localities and among localities (see the section Previous Work below for details), but the manner and the possible causes of the variation have not been understood. The purpose of the present study is twofold: 1) to define quantitatively the morphological variation of the animal in the present ocean, and 2) to determine the factors controlling this variation. Results from this study are expected to be applicable to fossil forms to aid in deciphering ancient depositional environments.

The Atlantic coast of the United States was selected as an ideal area for the present study for the following reasons:

1) The Atlantic coast of the United States covers broad subtropical and temperate climatic regions, in which *A. beccarii* exists.

2) There are a number of different environments, including continental shelf, lagoon, marsh, estuary, and tide pool.

3) Many marine stations are located on the coast where detailed environmental surveys have been conducted, so that good environmental data are available.

4) Numerous surface-sediment samples from the coast have been collected by these marine stations and are available for study.

The specimens studied have been deposited with The University of Kansas Museum of Invertebrate Paleontology (specimen numbers 2013813 to 2014563). The original measurements of the morphological characters of the specimens will not be shown in the present paper, but were tabulated in Chang's dissertation (1973).

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Some statistical tests and computer programs used in this study were prepared by Dr. F. James Rohlf and his associates in 1969 and were documented as parts of NT-SYS, numerical taxonomy system of multivariate statistical programs, in The University of Kansas Computation Center.

Most of the samples were originally collected by the staff of the Woods Hole Oceanographic Institution. Other samples were collected by the staff of the U.S. Army Coastal Engineering Research Center; Drs. Barry W. Holliday, John C. Ludwick, and Donald J. P. Swift of the Old Dominion University, Norfolk, Va.; Dr. Ruth Todd of the U.S. Geological Survey, Washington, D.C.; Dr. Barun K. Sen Gupta of The University of Georgia, Athens; and Messrs. H. Meade Cadot and Michael D. Brandos of The University of Kansas, Lawrence. The authors are grateful to these institutions and people for their contribution of material.

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PREVIOUS WORK

Ammonia beccarii (Linné) was originally designated *Nautilus beccarii* from the Mediterranean Sea and also has been referred to as *Rotalia beccarii* and *Streblus beccarii*. Cifelli (1962) re-

viewed the synonymy and established the validity of the genus *Ammonia*.

Because of the great morphological variation of the animal, various names of different taxonomic ranks have been proposed for different morphs of the species. Many paleontologists (Brooks, 1967; Buzas, 1965; Cushman, 1944; Lynts, 1962; Moore, 1957; Murray, 1968; Parker & Athearn, 1959; and Schnitker, 1971) have reported occurrences of *A. beccarii* from the Atlantic coast of the United States. In addition, Parker (1952) reported *A. beccarii* var. *tepida* and *A. beccarii* var. *sobrina* from the New England coast; Ellisor & Nichols (1970) reported *A. beccarii* var. *tepida* and *A. beccarii* var. A from an estuary of Virginia; Todd & Low (1961) reported *A. beccarii tepida* off Massachusetts; Wilcoxon (1963) reported *A. tepida* from the southern Atlantic continental shelf of the United States; and Grossman (1967) identified *A. limbatobeccarii, A. sobrina,* and *A. tepida* from a sound in North Carolina.

The similar nomenclatural variability is characteristic of the taxonomy of *A. beccarii* wherever it occurs. Thus, from the Atlantic coast of South America, Boltovskoy (1959) reported that *A. beccarii beccarii* occurs in the south and *A. beccarii ex gr. parkinsoniana* occurs in the north. He employed *A. beccarii ex gr. parkinsoniana* to include many forms which he believed had been incorrectly referred by other workers to *A. beccarii* var. *tepida, A. limnetes,* and others.

The confusion in taxonomy arises because there are no clearly defined criteria for identifying this extremely variable species. Most study of the morphological variation has been made without the benefit of statistical analysis. Consequently, a criterion used in one identification may not be applicable to other identifications. In the present study, morphological characters have been measured quantitatively from specimens selected at random. The morphological variability therefore can be expressed explicitly with reference to the population. More significantly, explicit conclusions from comparison of samples can be drawn from various statistical analyses.

DESCRIPTION OF AREA

The Atlantic coast of the United States extends about 3,000 km from latitude 25° north to 45° north. The coastline from Maine to Cape Cod, Massachusetts, is extremely irregular in shape because the rocky coast includes deep, fjordlike estuaries and offshore bars. To the south of Cape Cod, the coastline is less irregular in shape. Between Cape Cod and Cape Lookout, North Carolina, much of the coastline is bounded by a series of long narrow barrier islands which protect extensive lagoons, marshes, and estuaries. To the south of Cape Lookout, the coast is low, and frequently marshy islands predominate. On the Florida peninsula, extensive sand beaches with shallow lagoons are present on the coastline.

The continental shelf from Maine to Cape Cod is about 400 km wide, extending to a depth of 150 m. There are many broad basins, shallow banks, undulating swells, and irregularly crested ridges on the shelf. To the south of Cape Cod, the continental shelf is about 100 km wide, the shelf break occurring at a depth of 100 m or less. The topography is smooth with sand swells, channels, coral mounds, and terraces. The continental shelf off Florida becomes narrower, and the shelf break becomes shallower toward the south. In the area south of Cape Kennedy, the continental shelf is 10 to 50 km wide, and the break occurs at 60 m or less in depth (Uchupi, 1968).

Bottom sediment in estuaries, lagoons, and marshes immediately adjacent to rivers is usually quartzose sand and mud. The continental shelf north and east of New York Harbor is covered by glacial deposits, which comprise a mixture of gravel, sand, and mud. Quartzose sand also occurs throughout most of the shelf from New York Harbor to Cape Hatteras, North Carolina. Shelf sediment south of Cape Hatteras is characteristically highly calcareous. The sediment consists of quartzose sand, oolite, and fragments of molluscs, coralline algae, and barnacles (Milliman, 1972; Uchupi, 1963).

To the north of Cape Hatteras, the coastal water is formed by mixing of the slowly southward-drifting Labrador Current Extension (Gerlach, 1970), land runoff, and indrift of slope water. The Labrador Current Extension is cold water with low salinity. Its temperature is usu-

ally 15° C or less, and its salinity is usually less than 35 parts per thousand (Bigelow, 1924; Bumpus & Pierce, 1955; Ketchum & Corwin, 1964). To the south of Cape Hatteras, the coastal water is formed by Gulf Stream water and runoff from the land, but the contribution of land runoff is minimal. The water of the Gulf Stream is characterized by a temperature of 19° to 23° C and a salinity of about 36 parts per thousand (Bumpus & Pierce, 1955; Wennekins, 1959). It moves northward along the continental slope and broadly invades the continental shelf. Bumpus & Pierce (1955) called the water on the shelf north of Cape Hatteras Virginian Coastal water and the water south of Cape Hatteras Carolinian Coastal water.

Although periodical storms may cause the water north of Cape Hatteras to move southward around Cape Hatteras, at most times there is little direct communication between the two coastal water masses. Cape Hatteras and its offshore Diamond Shoals constitute an important physical barrier between the two water masses. This hydrographical barrier shows in molluscan distribution (Abbott, 1954; Johnson, 1934) and in foraminiferal distribution (Schnitker, 1971). For the purpose of convenience in the present study, the coastal water north of Cape Hatteras will be called the northern coastal water and that south of Cape Hatteras, the southern coastal water.

A clear summary of topography, water, life, and sediments of the Atlantic coast of the United States was given by Emery & Uchupi (1972). The known occurrences of *A. beccarii* from this coast are shown in Table 1. The survival range, from which the living animal has been observed, is from the surface to a depth of about 40 m.

TABLE 1. *Occurrence of Living* Ammonia beccarii *on Atlantic Coast of United States.*

LATITUDE (°N)	MACRO-HABITAT	REPORTED WATER DEPTH (m)	PRESENCE, +, OR ABSENCE, —, OF *A. beccarii*	REFERENCES
42.5-43	open sea	9-208	—	Parker, 1948; Phleger, 1952
42	bay	0-38	—	Phleger & Walton, 1950
41-41.5	bay, sound	0-32	+	Brooks, 1967; Buzas, 1965; Murray, 1968, 1969; Parker, 1952; Parker & Athearn, 1959; Todd & Low, 1961
40-41	open sea	16-680	—	Murray, 1969; Parker, 1948
38-39	open sea	22-610	—	Parker, 1948
37-38	estuary	0-20	+	Ellison & Nichols, 1970; Nichols & Norton, 1969
36	open sea	22-28	+	Schnitker, 1971
36	open sea	29-159	—	Schnitker, 1971
34-35.5	open sea	18-36	+	Murray, 1969
34-35.5	open sea	41-332	—	Murray, 1969; Wilcoxon, 1963
25	reef	0-42	—	Moore, 1957
25	bay	0-3	+	Lynts, 1962; Moore, 1957
24.5	reef	1-24	—	Howard, 1965

SAMPLE COLLECTION AND PREPARATION

All the samples used in the present study are grab samples of surface sediments from the present ocean (Fig. 1). Most of the samples were collected by the staff of the Woods Hole Ocean-

ographic Institution. The remaining samples were collected by the various people and institutions acknowledged previously.

One hundred thirty-five samples were prepared. Among them, 23 were used early in the study for the experimental design. They came from two traverses with closely spaced stations off Georgia and one traverse off Rhode Island. Water depth of each traverse ranged from 5 to 40 m. The other samples were selected in order to cover evenly the water from 0 to 40 m depth on the Atlantic coast of the United States.

Before preparation, each sample was about 75 cm^3 in volume. The procedures of preparation were as follows:

1) Samples were wet-sieved with a 74 micron (200 mesh) sieve and oven dried.

2) The dry residue was differentiated using tetrachloroethylene with a specific gravity of 1.6.

3) The floated portion of the residue was dried.

4) *A. beccarii* were picked from the floated portion of the residue. Because *A. beccarii* has a thin-walled calcareous test with hollow chambers, its tests were concentrated in the floated portion of the residue.

Only undamaged specimens were used in the study. Such specimens indicate little postmortem transportation, thereby improving the chance that they were collected from the place where the animals grew. Furthermore, there is no way to assess the loss of information due to the damage of tests.

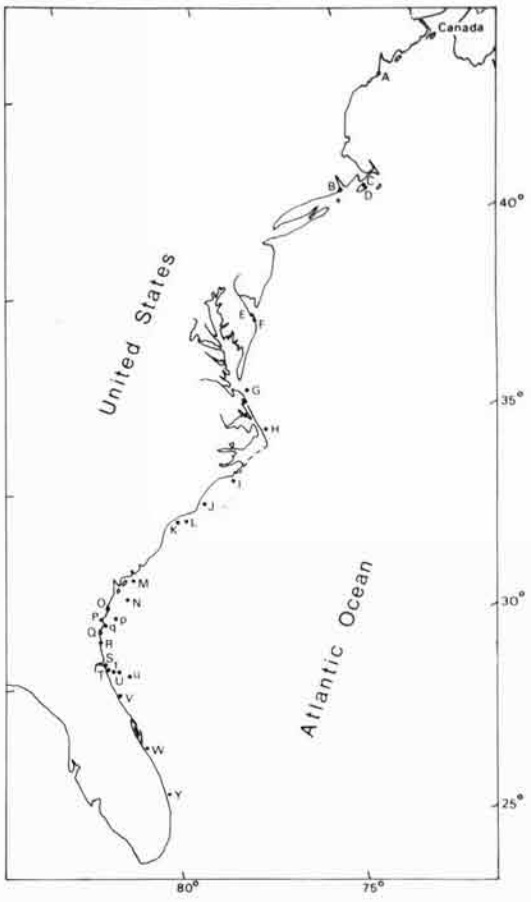

FIG. 1. Locality map of samples. As explained in Tables 2 and 7, each letter on the map represents a sample.

EXPERIMENTAL DESIGN

In order to plan an efficient study, an experimental design was carried out for selecting useful morphological characters and for estimating the necessary sample size. The test of *A. beccarii* (Fig. 2) can be described by combinations of any of several measurements made from a number of its morphological characters (Chang, Kaesler, & Merrill, in press). It is known that many characters of other organisms are controlled by the same growth mechanism. These characters react simultaneously to the environment and may be highly correlated. If two characters are highly correlated, it is possible to predict one character from the other. After studying the correlations among 25 characters of a species of fusulinid foraminifera, Koepnick & Kaesler (1974) demonstrated that three characters were sufficient to describe the morphology and that the other characters furnished little additional information about the morphology.

Because the samples used in the experimental design came from the northern and the southern parts of the Atlantic coast of the United States, study of them should result in some guidelines useful for the regional study of morphological variation.

Characters Measured.——From the 23 samples mentioned, 221 undamaged specimens of *A.*

beccarii were found in 12 samples (see Table 2 and Fig. 1). The morphology of these specimens was studied in detail. The distances between any two adjoining points on the broken lines, shown in Figure 2, were measured using a Filar micrometer. On the dorsal side of the test, the rectangular coordinate axes were laid down based on the following two points: 1) center of the first chamber, or proloculus, serving as the origin of the coordinate axes, and 2) fusing point of the apertural face of the eleventh chamber with the spiral curve of whorl serving as a point through which one coordinate axis will pass. If a shell had less than 11 chambers, the seventh chamber was used for referring the coordinate axis. This alternative was made because, from specimens with many chambers, it was usually found that the first, seventh, and eleventh chambers are located on a straight line. The angles each chamber and each apertural face possess with respect to the center of the first chamber were also measured.

Based on the measurements taken, 45 morphological characters were calculated for each specimen. These characters and the symbols that represent them are explained below. When it is possible, the explanation is referred to Figure 2, in which the measured points from the dorsal view of the test are indicated by capital letters and those from the ventral and the apertural views of the test, by lower case letters.

1) *AM, AN, AK,* and *AVAR:*

From a study of chamber sizes measured from the dorsal view of the test, it was found that the size of chambers generally increases in the fashion of a sigmoidal curve. This curve fits very well the equation:

$$Y=1+(A_m-1)[1-e^{-A_k(X-1)}]^{A_n},$$

where X=chamber number, Y=size of chamber X relative to the first chamber based on area on dorsal view, and A_m, A_n and A_k are three constants (for theoretical derivation of the equation, see Beverton & Holt, 1957, p. 32-35). For convenience of presentation, $ln(A_m)$, $ln(A_n)$ and A_k are symbolized by *AM, AN* and *AK*. *AVAR* =average of squared deviations from the sigmoidal curve$=[\Sigma(Y_{obs}-Y_{exp})^2]/(N_{ch}-1)$, where

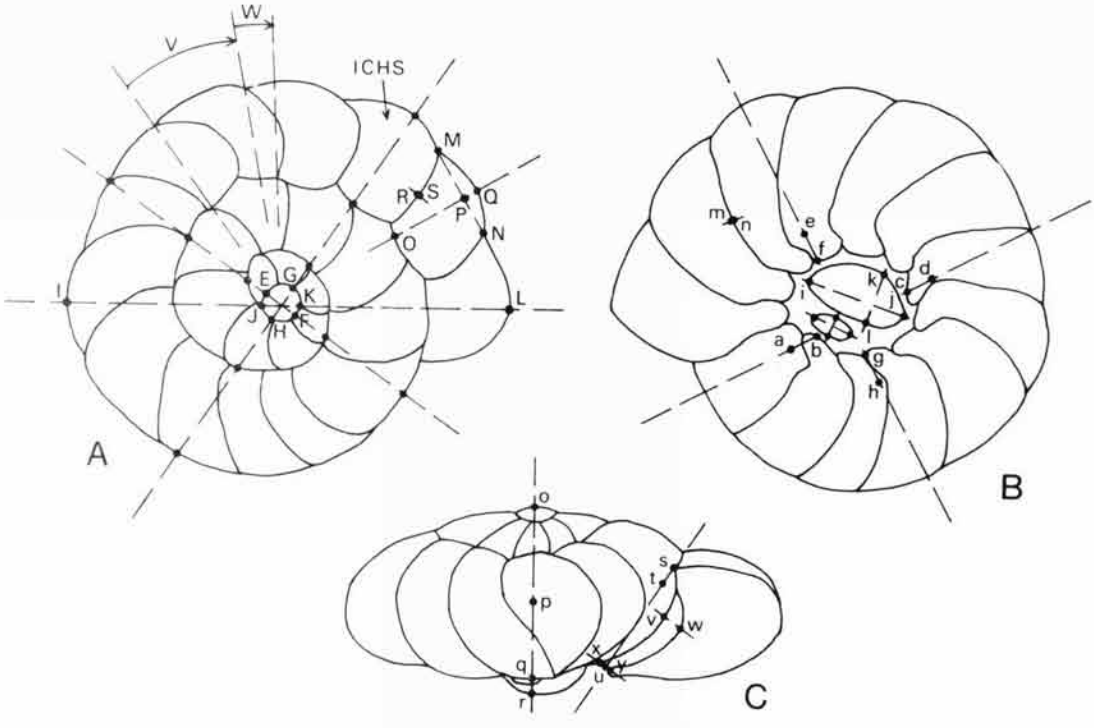

FIG. 2. Morphology of *Ammonia beccarii* in three different views. *A, B,* and *C,* respectively, show dorsal, ventral and apertural views. Each letter on the pictures indicates a point used in measurement of morphological characters.

TABLE 2. *Locality of Samples Used in Experimental Design.*

SAMPLE SYMBOL	SAMPLE NUMBER	LOCALITY		WATER DEPTH (m)	NUMBER OF SPECIMENS STUDIED
		LONGITUDE (°W)	LATITUDE (°N)		
q	WH2277	81.30	30.32	6	2
R	WH2286	81.48	30.72	7	29
P	WH2276	81.30	31.40	8	28
Q	WH2279	81.42	31.13	8	6
S	WH2285	81.38	30.37	8	25
O	GE0054	81.03	31.67	10	9
t	WH1505	81.22	31.17	15	4
T	WH1504	81.33	30.25	15	56
p	GE0052	80.85	31.60	19	1
U	WH1506	81.02	30.17	21	7
u	WH1686	80.77	30.00	36	1
B	WH1936	71.42	41.48	13	53

Y_{obs}=observed Y, Y_{exp}=expected Y from the sigmoidal curve, and N_{ch}=total number of chambers. The Appendix shows the method of calculating Y.

2) *AN*, see this symbol under *AM*.

3) *AK*, see this symbol under *AM*.

4) *APER1*=length of basal line of apertural face in microns=distance *(su)*.

5) *APER2*=length of aperture in microns=distance *(tu)*.

6) *APER3*=height of aperture in microns=distance *(vw)* when distance *(vw)* $\geq$ distance *(xy)*, or distance *(xy)* when distance *(vw)* $<$ distance *(xy)*.

7) *APER4*=length of apertural opening at umbo in microns=distance *(xy)*.

8) *APERT*=ratio of height to length of aperture=*APER3* divided by *APER2*.

9) *AVAP* and *SDAP:*

AVAP=average of all values of W, where W =offset angle of apertural face in radians. *SDAP* =standard deviation of W.

10) *AVAR*, see this symbol under *AM*.

11) *AVCO* and *SDCO:*

AVCO=average of all values of V, where V =coiling angle of chamber in radians. *SDCO*= standard deviation of V.

12) *B*, *C*, and *SDB:*

The coiling angle of a chamber, V, may change regularly with its chamber number, X. The first approximation of this relationship is a linear equation of $V=b_1X+c_1$, where b_1 and c_1 are constants. In the presentation, $B=100b_1$, $C=c_1$, and *SDB*=standard deviation of b_1, multiplied by 100.

13) *BAP*, *CAP*, and *SDBAP:*

The offset angle of an apertural face, W, may change regularly with its chamber number, X. The first approximation of this relationship is a linear equation $W=b_2X+c_2$, where b_2 and c_2 are constants. In the presentation, $BAP=100b_2$, $CAP=c_2$, and *SDBAP*=standard deviation of b_2, multiplied by 100.

14) *C*, see this symbol under *B*.

15) *CAP*, see this symbol under *BAP*.

16) *CURV1*=length of penultimate chamber in microns=distance *(MN)*.

17) *CURV2*=inflational height of penultimate chamber in microns=distance *(PQ)*.

18) *CURVE*=curvature of penultimate chamber=*CURV1* divided by *CURV2*.

19) *D* and *SDD:*

The growth of spiral curve of whorl can be expressed approximately by a linearly expanding

curve (see Appendix), $S_r=S_a\theta+S_b$, whereS_r= radius of the curve from center of the first chamber in microns=radius separating angle *W* from angle *V* in Figure 2,*A*, S_a=expanding rate of the curve in microns per radian, θ=rotational angle in radians, and S_b=radius of first chamber curve (see Appendix), $S_r=S_a\theta+S_b$, where S_r= in microns=half of *D1* (explained below). Since S_r, S_b, and θ are known for each chamber, S_a and its standard deviation can be calculated. Symbols *D* and *SDD* respectively stand for S_a and its standard deviation.

20) *D1*=diameter of first chamber in microns $=\sqrt{d_1d_2}$, where d_1=distance *(EF)* and d_2= distance *(GH)*. Assuming d_1 and d_2 are the major and the minor axes of an ellipse, the above calculation converts the ellipse to a circle without changing the total area and estimates the diameter of the circle as *D1*. This principle of calculation is also applied to obtain *DCHLT*, *DPLUG* and *DUMBO*.

21) *DCHLT*=length of chamberlet in microns $=(\sqrt{d_3d_4}-d_5)/2$, where d_3=distance *(ad)*, d_4 =distance *(eh)*, and d_5 is explained below under symbol *DUMBO*. The chamberlet is a nodular extension of a regular chamber near the umbilicus. There is no internal shell material to partition the chamberlet from the regular chamber, but the boundary between them is indicated by a contraction of the passage between them. Points *a*, *d*, *e*, and *h* of Figure 2,*B* are the intersections of the coordinate axes and the boundaries between chamberlets and regular chambers.

22) *DM*=largest diameter of shell in microns =distance *(IL)*.

23) *DPLUG*=diameter of an imaginary circle whose area equals the sum of all areas of the plugs on ventral view=$\sqrt{\Sigma d_6d_7}$, in which each pair of d_6 and d_7 represent two observations from a plug. Using the large plug in Figure 2,*B* as an example, d_6=distance *(ij)* and d_7=distance *(kl)*.

24) *DUMBO*=diameter of umbilicus in microns=$d_5=\sqrt{d_8d_9}$, where d_8=distance *(bc)* and d_9=distance *(fg)*.

25) *HTPC*=height of penultimate chamber in microns=distance *(OQ)*.

26) *IAPTP*=shape of aperture, 1 for *APER4* less than *APER3* and 2 for *APER4* greater than or equal to *APER3*.

27) *IBEAD*=beads beside ventral suture, 0 for absence and 1 for presence of beads.

28) *ICHS, TCSD,* and *TCSV:*

ICHS=number of a particular chamber. *TCSD*=septum thickness of chamber *ICHS* from dorsal view in microns=distance *(RS)*. *TCSV*= septum thickness of chamber *ICHS* from ventral view in microns=distance *(mn)*.

29) *ICOIL*=coiling direction of shell, 1 for sinistral coiling and −1 for dextral coiling.

30) *ISDEP*=outer appearance of ventral suture, 0 for smoothness and 1 for depression.

31) *NCH*=total number of chambers.

32) *NCHW1*=number of chambers in first whorl. If a specimen does not have a complete first whorl, zero is recorded.

33) *NCHW2*=number of chambers in second whorl. If a specimen does not have a complete second whorl, zero is recorded.

34) *NPLUG*=number of plugs.

35) *SDAP*, see this symbol under *AVAP*.

36) *SDB*, see this symbol under *B*.

37) *SDBAP*, see this symbol under *BAP*.

38) *SDCO*, see this symbol under *AVCO*.

39) *SDD*, see this symbol under *D*.

40) *TCSD*, see this symbol under *ICHS*.

41) *TCSV*, see this symbol under *ICHS*.

42) *THIC1*=thickness of dorsum in microns= distance *(op)*.

43) *THIC2*=thickness of venter in microns= distance *(pq)*.

44) *THIC3*=thickness of plug in microns= distance *(qr)*.

45) *THICK*=thickness of whole shell in microns=distance *(or)*.

Correlations among Characters.——Product-moment correlation coefficients were used to measure the relationships between all pairs of characters. Those characters whose correlation coefficients had absolute values greater than 0.7 were grouped together. The result of grouping is shown in Table 3.

Intuitively, some characters cannot be considered as morphologically meaningful. For example, *ICHS* is just the number of a chamber in the last whorl. From this chamber, *TCSD* and *TCSV* were measured. In fact, *ICHS*, which indicates a stage of growth, was intended to provide a basis for correcting growth differences in *TCSD* and *TCSV* in various growth stages. After correction, the new values of *TCSD* and *TCSV* would represent characters of specimens and could be used for comparison. Since the means of correction could not be determined, all the characters were

TABLE 3. *Result of Grouping Characters from Experimental Design and Reasons for Eliminating Characters from Regional Study.* [Symbols for characters are explained in the text.]

GROUP NUMBER	REPRESENTATIVE CHARACTER	OTHER CHARACTERS	REASONS FOR ELIMINATION FROM REGIONAL STUDY
1	APER4	APER3, APERT	
2	C	B	
3	CURV2	CURVE	
4	D1	D	
5	DM	APER1, APER2, CURV1, D, DCHLT, HTPC, THIC1, THIC2, THICK	
6	DUMBO	DPLUG	
7	ICOIL		
8	NCH	ICHS, NCHW2, SDB	
9	NCHW1		
10		AM	
11		AN	Growth, characteristic of chamber size, which can be expressed equally well by C.
12		AK	
13		AVAP	Hard to obtain, affects the shell morphology as a whole only slightly.
14		AVAR	Variation of growth from generalized trend, affects the shell morphology as a whole only slightly.
15		AVCO	Expressed better by C.
16		BAP, CAP	Hard to obtain, affects the shell morphology as a whole only slightly.
17		DPLUG, NPLUG	Directly related to DUMBO, usually NPLUG=1 when plugs present.
18		IAPTP	Related to APER3 and APER4, which have been found to be intercorrelated.
19		IBEAD	Usually zero.
20		ISDEP	Presence-absence record, character state difficult to define.
21		SDAP	Variations from generalized trends, affect the shell morphology as a whole only slightly.
22		SDB, SDBAP	
23		SDCO	
24		SDD	
25		TCSD	No correlation with ICHS found, too thin to be measured accurately with microscope.
26		TCSV	
27		THIC3	Usually zero.

treated equally for studying their correlations. It was hoped that this study would suggest valid methods for correction. For example, if a good correlation was found between *TCSD* and *ICHS*, it would indicate that a linear relationship exists between the two that could be expressed by the regression equation of *TCSD* on *ICHS*. Then, if *ICHS* was given, *TCSD* could be estimated from the equation to represent a general trend of *TCSD*. The difference between the observed *TCSD* and the estimated *TCSD* would indicate the deviation of an individual from the general trend and, thus, would be a meaningful parameter for comparison with other individuals.

Correlation of characters implies that one character from a group of characters can represent other characters. Thus, only one character from a group of characters need be measured in the second phase, the study of regional variation of morphology. To keep the future work efficient and useful, the following principles were used to help in selecting the representative characters: 1) Those selected are easy to observe and measure, and 2) they have been employed previously by paleontologists. After deleting some for reasons given in Table 3, the following were selected as representative: *APER4, C, CURV2, D1, DM, DUMBO, ICOIL, NCH* and *NCHW1*.

Requirements of Statistical Analyses.—For drawing inferences from samples of limited size to be applied to entire populations and to allow mathematical manipulation of data, parametric statistical techniques employed in this study require the following conditions: 1) random sampling, 2) independence of experimental errors, 3) normal distribution of characters, 4) homogeneous covariances, and 5) additivity of main effects.

When samples were collected in the field, *A. beccarii* could not be seen. In the laboratory preparation, specimens were picked at random so that the ultimate samples could be considered to be random. Independence of experimental errors has not been tested. However, all samples used in this study were prepared and measured by the same methods. If a bias occurred, it was consistent and constant in all the samples.

Histograms of frequency distributions were used for determining the normal distribution of the nine representative characters. Characters *C* and *NCHW1* were found to have normal distributions while the other characters had skewed distributions. In a very few cases, zero was initially recorded for *NCHW1* to indicate a specimen without a complete first whorl. Since this value is not realistic, it was replaced by seven, the average of all values of *NCHW1*, for the analysis.

Character *ICOIL* is an attribute, including 1 and −1 as two possible states of observation. No transformation could be applied to alter its frequency distribution.

In addition to having skewed distributions, values of *CURV2* are always greater than two, values of *DM* are always greater than 100, and values of *DUMBO* are either zero or greater than 3.5. Based on this information and judging from the histograms of frequency distributions, the following transformations were applied to obtain normal distributions of the characters. Let *APER4, CURV2, D1, DM, DUMBO* and *NCH* be represented by x_1, x_2, x_3, x_4, x_5, and x_6, respectively. Also, let symbols *TAPER4, TCURV2, TD1, TDM, TDUMBO* and *TNCH* represent the transformed y_1, y_2, y_3, y_4, y_5 and y_6, respectively. Then the transformations were:

$y_1 = log(x_1 + 100)$
$y_2 = log(x_2 - 2)$
$y_3 = log(x_3 + 75)$
$y_4 = log(x_4 - 100)$
$y_5 = log(x_5 + 15)$
$y_6 = log(x_6)$

The distribution of x_5 tends to be bimodal because x_5 is always greater than 3.5 if it is not zero. In order to obtain a unimodal distribution, the zero value was replaced by 3.5 before applying the transformation.

Each population from which samples were drawn can be represented by an ellipsoid in a multidimensional space. The condition of homogeneous covariances implies that all ellipsoids are the same in size and are oriented in the same direction. If the condition holds, the analysis is valid. If the condition is not met, the analysis is theoretically no longer valid. However, the analysis may be considered as an approximation, and the result of the analysis should be interpreted with caution. The statistical test of homogeneous covariances was given in each individual analysis.

The mathematical model used in the present statistical analyses includes only linear relationships among variables. This model implies that

the analyses apply only to additivity of the variables. In other words, no interaction among the variables can be determined.

Differences among Samples.—Discriminant analysis (see Anderson, 1958, p. 142-152) was applied to examine the differences among the samples using the nine representative characters. For simplicity, each sample was designated by a letter shown in Table 2. The results of the analysis are shown in Table 4.

Samples P, Q, R, and S came from seven to eight meters of water depth off the coast of Georgia. They were tested in order to determine possible differences of morphology within the same depth off Georgia. No significant difference was shown when pairs of the samples were tested. However, the simultaneous test indicated very significant differences among the four samples. Clearly, testing four samples simultaneously becomes a more sensitive test due to higher degrees of freedom associated with the F-value. Consequently, it is concluded that within a particular water depth, the morphology can be different. A further study (see Fig. 3) suggests that the main differences among the samples exist between sample Q and the other three samples.

Morphological differences among samples from the same depth but different locations suggested that there might be morphological differences among samples from different depths. Therefore, the four samples, P, Q, R, and S, were treated as one group and samples q and T, taken from a depth of 15 m off the Georgia shore, were used as another group. Since samples from the same depth are different, grouping samples by depth should result in even greater variation within a group. The discriminant analysis of these groups, thus, will give a conservative answer to the hypothesis being tested. Results of this analysis indicated that there are highly significant differences between groups from the two water depths.

In order to determine whether morphology varies from north to south along the Atlantic coast of the United States, the two groups from the Georgia shore and sample B from 13 m of water off Rhode Island were tested. Although the indicated heterogeneous covariance matrices violate

TABLE 4. *Result of Discriminant Analysis among Samples Used in Experimental Design.* [Symbols representing samples are shown in Table 2. Some tests for equality of covariance matrices are not applicable due to one sample having fewer specimens than characters. Tests with nonsignificant results ($P>0.05$) are indicated by n.s.; tests with highly significant results ($P<0.001$) by ***.]

SAMPLES USED	X^2-VALUE FOR TESTING EQUAL COVARIANCE MATRICES	DEGREES OF FREEDOM FOR X^2-VALUE	F-VALUE FOR TESTING EQUAL MEANS	DEGREES OF FREEDOM FOR F-VALUE
P,Q	(not applicable)		1.33 n.s.	9, 24
P,R	31.23 n.s.	45	1.04 n.s.	9, 47
P,S	23.57 n.s.	45	1.32 n.s.	9, 43
Q,R	(not applicable)		0.56 n.s.	9, 25
Q,S	(not applicable)		0.85 n.s.	9, 21
R,S	31.17 n.s.	45	0.85 n.s.	9, 44
P,Q,R,S,	65.48 n.s.	90	2.89***	27, 223
q,T	(not applicable)		0.89 n.s.	9, 50
(P+Q+R+S), (q+T)	59.67 n.s.	45	5.40***	9, 138
(P+Q+R+S),B	192.43***	45	38.16***	9, 131
(q+T),B	112.57***	45	20.77***	9, 103
(P+Q+R+S), (q+T),B	243.73***	90	34.78***	18, 380

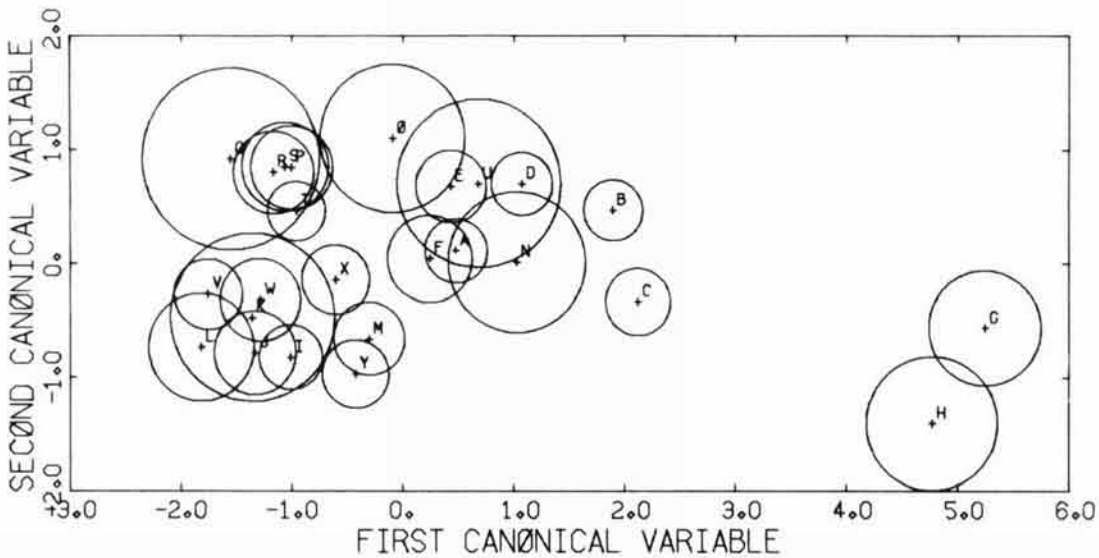

FIG 3. Morphological characters of 25 samples from Atlantic coast of United States, as summarized by first two canonical variables. Each letter on the picture represents a sample as indicated in Table 7. The crosses represent sample means, and the circles represent 95 percent confidence limits.

the requirement of the analysis, the resulting F-value was so high (Table 4) that it was still possible to suggest that differences among the three groups are real.

Discriminatory Significance of Characters.—Although the above study clearly demonstrated morphological differences among samples from different localities, the question of which characters contributed most importantly to the differences remained. The stepwise discriminant analysis (Dixon, 1970, p. 214a-t, BMD07M computer program) was useful for answering this question. This analysis performed the discriminant analysis in a stepwise manner. At each step, variables were computed for their entering F-values, each of which was a measure of the variation among samples relative to the variation within samples. In other words, an entering F-value represented the discriminatory power of a variable. The variable with the highest entering F-value was then selected to enter the discriminant analysis. As more steps were carried out, the variables with less discriminatory power were included in the discriminant analysis. The analysis stopped when all the variables had been used.

Table 5 shows the results of the analysis when two groups of samples off Georgia were studied. Table 6 shows the results of the analysis when two groups off Georgia and one sample off Rhode Island were studied. In both tables, the F-values at each step of the analysis showed highly significant differences, suggesting that the variables included in the discriminant analysis at any step were sufficient to reveal the differences among the samples.

The sequence of variables entering the analysis in the two tables was different. This might indicate that the important characters for discriminating populations from different depths and populations from different latitudes were not the same.

Because of its low discriminatory power (Tables 5 and 6), *APER4* was eliminated from the next phase of the study, regional variation of morphology. An additional reason for eliminating it was that it was difficult to hold the specimen in a proper position under the microscope for measuring the character. Thus, including it in the study greatly increased the time spent without adding very much new information.

Sample Size.—If two samples are drawn from two different populations, the minimum sample size necessary to reveal the difference between the two samples can be estimated (see Appendix). For discriminating two samples, one from seven to eight meters and the other from 15 m of water off Georgia, the required sample size was estimated to be 14 to 30, depending on

TABLE 5. *Results of Stepwise Discriminant Analysis between Two Groups of Samples off Georgia.* [Symbols for variables are explained in the text. The tests with highly significant results ($P<0.001$) are indicated by ***. Minimum sample sizes were estimated with 95 percent confidence, or with 0.05 significant level.]

STEP TO ENTER A VARIABLE	NAME OF ENTERING VARIABLE	F-VALUE WITH ENTERING VARIABLE	F-VALUE OF DISCRIMINATION AFTER VARIABLE ENTERED	DEGREES OF FREEDOM FOR F-VALUE OF DISCRIMINATION	ESTIMATED MINIMUM SAMPLE SIZE
1	TNCH	18.24	18.24***	1, 146	17
2	TD1	15.60	17.86***	2, 145	14
3	C	4.88	13.84***	3, 144	17
4	TCURV2	2.40	11.08***	4, 143	18
5	TDM	2.64	9.49***	5, 142	20
6	NCHW1	1.40	8.17***	6, 141	22
7	TDUMBO	0.34	7.02***	7, 140	26
8	TAPER4	0.11	6.11***	8, 139	28
9	ICOIL	0.00	5.40***	9, 138	30

TABLE 6. *Results of Stepwise Discriminant Analysis among Two Groups of Samples off Georgia and One Sample off Rhode Island.* [Symbols for variables are explained in the text. The tests with highly significant results ($P<0.001$) are indicated by ***.]

STEP TO ENTER A VARIABLE	NAME OF ENTERING VARIABLE	F-VALUE WITH ENTERING VARIABLE	F-VALUE OF DISCRIMINATION AFTER VARIABLE ENTERED	DEGREES OF FREEDOM FOR F-VALUE OF DISCRIMINATION
1	TDM	88.89	88.89***	2, 198
2	TD1	20.59	50.71***	4, 394
3	TNCH	23.45	44.84***	6, 392
4	TDUMBO	6.04	35.97***	8, 390
5	NCHW1	3.82	29.94***	10, 388
6	ICOIL	3.44	25.83***	12, 386
7	TAPER4	3.66	22.96***	14, 384
8	C	2.27	20.51***	16, 382
9	TCURV2	1.75	†18.49***	18, 380

† This value is different from the corresponding one in Table 4. Possibly due to low tolerance level in some steps of calculation, different programs result in different answers.

the characters used. The detailed estimates are shown in Table 5.

Character *TNCH* was the most powerful character for discriminating the samples, and the necessary sample size was 17. When *TD1* was added for the discrimination, the required sample size decreased to 14. Further additions of characters, however, caused the necessary sample size to increase to 30, for including them decreased the second degrees of freedom associated with the

F-value for discrimination and made the discrimination test less sensitive (E. B. Cobb, pers. commun.).

If the eight characters selected in the above study were used for discriminating samples, the necessary sample size was determined to be about 30. However, it was not necessary to have an equal sample size for all samples. From statistics, it is known that the variation of sample means is inversely proportional to the sample size. Thus, if two samples are used for comparison and one of the samples has a smaller sample size, the statistical test can be compensated to give the same result when the other sample has a larger sample size. Furthermore, it is known that the animal exists in a depth range broader than the range used in estimating the sample size. Based on the observed effects of depth on morphology, a broader depth range implies a greater morphological variation. Accordingly, the required sample size for studying samples from the entire depth range could be smaller than 30.

Conclusions.—From the above analyses, the following conclusions were drawn. They were used in planning an effective regional study of morphological variation.

1) *A. beccarii* showed different morphologies at different water depths and at different latitudes.

2) Many of the 45 characters studied showed high correlations and had different significances in revealing geographical variation. After elimination of the correlated characters and the non-significant characters, the following eight were sufficient for studying geographical variation: *C, CURV2, D1, DM, DUMBO, ICOIL, NCH* and *NCHW1.*

3) Using the above eight characters, sample sizes of about 30 should be sufficient to indicate morphological differences of animals from two environments close to each other.

REGIONAL STUDY OF MORPHOLOGICAL VARIATION

In order to implement the experimental design, 112 samples from the Atlantic coast of the United States were prepared and 17 were found to contain at least six undamaged specimens of *A. beccarii.* If a sample consisted of numerous specimens, about 40 specimens were selected at random. A total of 25 samples (Table 7 and Fig. 1), including eight that conformed to the experimental design, were used in the regional study of morphological variation. The sample size ranged from 6 to 56 and average size was 29.7. The eight representative characters were measured from the newly prepared 17 samples. *D1* was measured parallel to *DM,* equivalent to distance *(JK)* of Figure 2,*A. C* was estimated either from *NCHW1* and *NCHW2* or from the number of chambers in a half whorl if the specimen did not have many (see Appendix). These two methods were modified from those used in the experimental design in order to make measurements easier.

Discriminatory Significance of Characters.—After transforming the data by the methods used in the experimental design, a chi-square test was applied to 21 samples for examining equality of covariance matrices. Samples *WH1451, WH1506,* and *WH2279* had sample sizes smaller than the observed number of characters, and the character *NCHW1* was invariant in sample *WH1486.* These samples were excluded from the test, because it was not possible to perform the test when determinants of a covariance matrix were zero. The test result of $X^2=1713.60$ with 720 degrees of freedom indicated significant differences among the covariance matrices.

As explained previously, the heterogeneous covariance matrices violate the requirement of parametric statistics. Consequently, the parametric statistical analyses are not theoretically applicable. However, if the results of the analyses are interpreted with caution, the parametric statistics are useful methods for summarizing masses of data and for drawing inferences about the studied populations. For example, when stepwise discriminant analysis was applied to the samples with different covariance matrices, the sequence of including variables in the discriminant analysis could not be viewed strictly as they were shown by the analysis. But that sequence was the most likely arrangement if a variable selected to enter the analysis had an entering F-value much higher than those associated with the variable left out in the selection.

The results of stepwise discriminant analysis of the 25 samples are shown in Table 8. In the first step of the analysis, *TDI,* a measure of proloculus size, was shown to have an entering F-value much higher than those of other variables. Clearly this indicated that proloculus size

TABLE 7. *Environmental Factors and Morphological Characteristics of* Ammonia beccarii *in 25 Samples from Atlantic Coast of United States.* [Symbols representing columns are explained in the text, except the following: *CAX1*=sample mean in first canonical variable for morphology of *A. beccarii; CAX2*=sample mean in second canonical variable for morphology of *A. beccarii; CONF*=1.96 times of standard deviation of means for a sample, evaluated in canonical variables; *NAME*=sample number; *NSPM*=number of specimens studied; *SS*=sample symbol.]

SS	NAME	XLON	YLAT	DEEP	APPI	AROF	ASNF	IHBT	IMAS	ISED	SALS	SALW	TIDE	TMAX	TMIN	NSPM	CAX1	CAX2	CONF
A	MA0001	69.33	43.95	0.	1.02	0.58	1.62	3	1	1	32.	32.	3.20	20.00	−1.11	48	0.48	0.11	0.28
B	WH1935	71.42	41.48	13.	1.02	0.58	0.51	1	1	2	32.	32.	1.22	23.89	0.	53	1.90	0.47	0.27
C	MS5703	70.55	41.45	1.	1.02	0.56	0.51	2	1	1	32.	33.	1.07	23.33	0.	44	2.12	−0.34	0.30
D	MS5760	70.55	41.42	1.	1.02	0.56	0.51	2	1	3	32.	33.	1.07	23.33	0.	50	1.07	0.70	0.28
E	DL0002	75.10	38.80	2.	1.02	0.46	0.30	2	1	1	31.	32.	1.52	26.11	0.56	38	0.43	0.68	0.32
F	DL0001	75.70	38.70	3.	1.02	0.46	0.20	2	1	1	31.	32.	1.52	26.11	0.56	26	0.24	0.04	0.38
G	WH2057	75.75	36.82	22.	1.02	0.20	0.20	4	1	4	32.	32.	1.22	27.78	3.33	15	5.24	−0.56	0.51
H	WH2065	75.50	35.83	23.	1.22	0.20	0.20	4	1	3	33.	34.	1.22	28.33	6.67	11	4.77	−1.40	0.59
I	WH2314	76.63	34.62	16.	1.42	0.30	0.10	4	2	3	35.	35.	1.37	28.89	10.56	47	−1.01	−0.82	0.29
J	WH2308	77.73	34.23	13.	1.22	0.30	0.10	4	2	3	35.	35.	1.52	28.89	10.56	28	−1.33	−0.78	0.37
K	WH1451	75.25	34.17	25.	1.22	0.25	0.10	4	2	3	35.	34.	1.68	28.89	10.56	7	−1.36	−0.47	0.74
L	WH2250	78.45	33.78	13.	1.22	0.25	0.10	4	2	3	35.	34.	1.68	28.89	10.56	17	−1.82	−0.73	0.48
M	WH2298	80.08	32.55	9.	1.02	0.25	0.	4	2	3	35.	34.	2.13	28.89	10.56	37	−0.30	−0.66	0.32
N	WH1486	80.50	31.97	18.	1.22	0.25	0.	4	2	3	35.	35.	2.13	29.44	10.56	10	1.03	0.01	0.62
O	GE0054	81.03	31.67	10.	1.22	0.25	0.	4	2	3	35.	34.	2.44	29.44	10.56	9	−0.09	1.10	0.65
P	WH2276	81.30	31.40	8.	1.22	0.25	0.	1	2	1	35.	34.	2.44	29.44	10.56	28	−1.00	0.84	0.37
Q	WH2279	81.42	31.13	8.	1.22	0.25	0.	1	2	3	35.	34.	2.59	29.44	10.56	6	−1.55	0.92	0.80
R	WH2286	81.48	30.72	7.	1.22	0.25	0.	1	2	2	35.	34.	2.59	29.44	10.56	29	−1.17	0.80	0.36
S	WH2285	81.38	30.37	8.	1.22	0.25	0.	4	2	3	35.	34.	2.44	29.44	11.11	25	−1.06	0.85	0.39
T	WH1504	81.33	30.25	15.	1.22	0.25	0.	4	2	3	35.	35.	2.29	29.44	12.22	56	−0.96	0.46	0.26
U	WH1506	81.02	30.17	21.	1.22	0.25	0.	4	2	3	35.	36.	1.98	30.00	13.89	7	0.68	0.70	0.74
V	WH1518	81.03	29.35	18.	1.22	0.25	0.	4	2	1	35.	36.	1.83	30.00	13.89	40	−1.76	−0.27	0.31
W	WH1538	80.50	28.00	17.	1.22	0.25	0.	4	2	3	36.	36.	1.22	30.00	17.78	29	−1.29	−0.32	0.36
X	WH1547	80.13	27.50	20.	1.42	0.25	0.	4	2	3	36.	36.	0.91	30.00	20.00	41	−0.61	−0.14	0.31
Y	WH1551	80.05	27.03	20.	1.42	0.25	0.	4	2	3	36.	36.	0.91	30.00	20.00	42	−0.43	−0.97	0.30

TABLE 8. *Results of Stepwise Discriminant Analysis among 25 Samples from Atlantic Coast of United States.* [Symbols for variables are explained in the text. The tests with highly significant results ($P<0.001$) are indicated by ***.]

STEP TO ENTER A VARIABLE	NAME OF ENTERING VARIABLE	ENTERING F-VALUES								F-VALUE OF DISCRIMINATION AFTER VARIABLE ENTERED	DEGREES OF FREEDOM FOR F-VALUE OF DISCRIMINATION
		TD1	TDUMBO	NCHW1	TNCH	TDM	TCURV2	C	ICOIL		
1	TD1	41.12	27.49	14.10	5.24	27.10	5.38	4.43	1.49	41.12***	24, 718
2	TDUMBO	—	13.50	9.67	10.87	11.51	4.93	4.38	1.49	25.60***	48, 1434
3	NCHW1	—	—	9.29	8.11	7.71	4.66	4.54	1.49	19.52***	72, 2141
4	TNCH	—	—	—	8.16	7.89	3.72	2.73	1.50	16.41***	96, 2835
5	TDM	—	—	—	—	5.65	2.92	2.61	1.68	14.04***	120, 3514
6	TCURV2	—	—	—	—	—	2.69	2.61	1.76	11.91***	144, 4175
7	C	—	—	—	—	—	—	2.40	1.77	10.40***	168, 4815
8	ICOIL	—	—	—	—	—	—	—	1.67	9.19***	192, 5432

has relatively large variation among samples and small variation within samples, and that it is the most important character for discriminating samples. For the same reason, umbilicus size, which is represented by *TDUMBO*, was shown to be the next most important character for discrimination. *NCHW1*, *TNCH*, and *TDM* were selected in the next three steps of the analysis. Since the entering F-values associated with these three variables were similar, the order of the variables for entering the discriminant analysis was less precisely determined. The last three characters to enter the analysis were *TCURV2*, *C*, and *ICOIL*. Because of their low entering F-values, they were nonsignificant for discrimination.

Geographical Variation of Morphology.— From the original values of variables, canonical analysis computes the new values of uncorrelated variables with emphasis on differences among sample means. The new variables are called canonical variables and are arranged in order according to their ability to explain variability among sample means. In other words, the first canonical variable accounts for the maximum variability among sample means in the transformed space, the second canonical variable, whose axis is located at right angles to the axis of the first canonical variable, accounts for the next greatest variability among sample means, and so on (see Seal, 1964, p. 124-152). Usually, the first few canonical variables are able to account for most of the variability among sample means, so they are used to summarize the information of samples before studying the differences among samples (Buzas, 1966, 1972; Reyment & Brännström, 1962; Reyment & Ramdén, 1970).

The BMD07M computer program also performed these computations and was applied to analyze the 25 samples. The results showed that eight canonical variables accounted for 68.81, 12.21, 6.22, 5.12, 3.40, 2.85, 0.87 and 0.52 percent of the total variation among sample means, respectively.

Since the first two canonical variables explained a great amount of the variation among samples, their relations to the eight morphological characters are shown in Table 9. Assuming that y is a canonical variable, x_i is the ith original variable, $\bar{x}_i$ is the grand mean of x_i over all the samples, and u_i is a coefficient, the y-value of a specimen can be estimated by the equation $y=\Sigma u_i(x_i-\bar{x}_i)$ (see Dixon, 1970, p. 214k-t). In considering all samples, the term $x_i-\bar{x}_i$ can be represented by the standard deviation of the sample means. Thus, the absolute value resulting from the multiplication of the standard deviation of the sample means for a variable and the corresponding u_i is a measure of the average contribution of an original variable to the canonical variable. Based on these values (Table 9), it is obvious that the first canonical variable is strongly affected by proloculus size *(TD1)* and umbilicus size *(TDUMBO)*, and that the second canonical variable is strongly affected by proloculus size and number of chambers in the first whorl *(NCHW1)*. The above results further substantiated the previous conclusion that proloculus size and umbilicus size were powerful in discriminating samples.

The variance of a population evaluated in the canonical variables has been set to be unity, so the standard deviation of means for a sample is $1/\sqrt{N}$, where N is the observed sample size (see Seal, 1964, p. 129, 137). Let $\bar{y}$ be a sample mean, then 95 percent confidence limits of the mean will be $\bar{y} \pm (1.96/\sqrt{N})$. The values of sample means and confidence limits, evaluated in the first two canonical variables, are shown in Table 7 and Figure 3.

Samples represented by letters (Fig. 3) are shown in Table 7. Letters were arranged in ascending alphabetical order according to decreasing latitude of sample locations. Figure 3 shows that samples G and H were extremely different from the other samples studied. Although most of the samples were similar, their first canonical variables showed the following geographical significance: Eight samples from A to H were located on the positive side of the first canonical variable, and most of samples from I to Y were on the negative side of the variable. Among samples I to Y, two exceptions located on the positive side of the variable were samples N and U. The geographical feature dividing samples A to H from samples I to Y is Cape Hatteras, which is also a barrier separating northern coastal water from southern coastal water.

Possible Factors Controlling Morphology.—The following 14 environmental factors, each represented by a symbol, were available for the present study:

1) *APPT*=mean annual precipitation of nearest land in meters.

2) *AROF*=mean annual surface water runoff from nearest land in meters.

3) *ASNF*=mean annual snowfall of nearest land in meters.

4) *DEEP*=water depth in meters.

5) *IHBT*=macrohabitat, 1 for estuary, 2 for bay, 3 for tide pool, and 4 for open sea.

6) *IMAS*=water mass, 1 for northern coastal water and 2 for southern coastal water.

7) *ISED*=grain size of substrate sediment, 1 for clay, 2 for silt, 3 for sand, and 4 for gravel.

8) *SALS*=mean summer salinity of surface water in parts per thousand.

9) *SALW*=mean winter salinity of surface water in parts per thousand.

10) *TIDE*=tidal range of spring tide in meters.

11) *TMAX*=maximum summer temperature of surface water in degrees centigrade.

12) *TMIN*=minimum winter temperature of surface water in degrees centigrade.

13) *XLON*=longitude of sample location in degrees north.

TABLE 9. *Result of Canonical Analysis among 25 Samples from Atlantic Coast of United States.* [Symbols for variables are explained in the text. The average contribution of an original variable to a canonical variable was calculated by taking the absolute value of multiplying the standard deviation of 25 sample means by the coefficient attached to the original variable.]

NAME OF ORIGINAL VARIABLE	COEFFICIENTS ATTACHED TO ORIGINAL VARIABLE		STANDARD DEVIATION OF 25 SAMPLE MEANS	AVERAGE CONTRIBUTIONS OF ORIGINAL VARIABLE	
	FOR FIRST CANONICAL VARIABLE	FOR SECOND CANONICAL VARIABLE		TO FIRST CANONICAL VARIABLE	TO SECOND CANONICAL VARIABLE
C	0.67	1.12	0.07	0.05	0.08
ICOIL	0.07	–0.14	0.24	0.02	0.03
NCHW1	0.54	1.21	0.44	0.24	0.53
TCURV2	–0.24	–2.07	0.10	0.02	0.21
TD1	14.75	–14.27	0.07	1.03	1.00
TDM	1.44	1.27	0.23	0.33	0.29
TDUMBO	2.51	1.79	0.19	0.48	0.34
TNCH	1.69	–5.34	0.05	0.08	0.27

14) *YLAT*=latitude of sample location in degrees west.

The measurements of these factors from the localities of the 25 samples (Gerlach, 1970; Haythaway, 1966) were tabulated in Table 7.

Longitude and latitude of a sample location are pure artifacts, irrelevant to the animal's life. Other factors may not have direct effect on the animal. However, they were used in this study because they may relate to some environmental properties unavailable for measurement but which could affect the morphology of the animal. For example, snowfall of the nearest land seems an unimportant factor in the habitat of an animal living in the sea. However, snowfall on the sea possibly affects the habitat because it is a character of winter climate that causes changes of water temperature and salinity. Unfortunately, no measurement has been made of snowfall at sea. Since the environment of interest is a narrow band of water adjacent to land, the observed snowfall of the nearest land was selected as a reasonable estimator. Should this factor prove to be irrelevant to the morphology of the animal, this study is designed to reject it as nonsignificant.

It was shown in the above section on Geographical Variation of Morphology that the first two canonical variables accounted for 81.02 percent of the total variation among the sample means. Thus, these two variables were considered representative of morphological variation, and were used to relate the 14 environmental factors by means of stepwise regression analysis. This analysis (Dixon, 1970, p. 233-257d, BMD02R computer program) computes a sequence of multiple linear regression equations in a stepwise manner. At each step, the independent variable that shows the highest partial correlation coefficient with the dependent variable is added to the regression equation. The results of the analysis are shown in Table 10.

Based on multiple correlation coefficients

TABLE 10. *Results of Stepwise Regression Analysis of Morphological Characteristics of* Ammonia beccarii *from Atlantic Coast of United States on 12 Environmental Factors and Latitude and Longitude.* [Symbols representing environmental factors are explained in the text.]

	FIRST CANONICAL VARIABLE AS DEPENDENT VARIABLE		SECOND CANONICAL VARIABLE AS DEPENDENT VARIABLE	
STEP TO ENTER AN INDEPEND. VARIABLE	INDEPEND. VARIABLE ENTERED	MULTIPLE CORREL. COEFF. OF ENTERED INDEP. VARIABLES ON DEP. VARIABLE	INDEPEND. VARIABLE ENTERED	MULTIPLE CORREL. COEFF. OF ENTERED INDEP. VARIABLES ON DEP. VARIABLE
1	IMAS	0.74	IHBT	0.54
2	AROF	0.88	TIDE	0.71
3	ISED	0.90	ASNF	0.73
4	DEEP	0.91	AROF	0.80
5	TIDE	0.92	ISED	0.82
6	SALW	0.92	XLON	0.84
7	ASNF	0.93	IMAS	0.86
8	TMAX	0.94	YLAT	0.88
9	XLON	0.95	SALS	0.90
10	YLAT	0.95	TMAX	0.90
11	SALS	0.96	TMIN	0.90
12	APPT	0.96	APPT	0.90
13	IHBT	0.96	DEEP	0.90
14	TMIN	0.96	SALW	0.90

shown in various steps of the analysis (Table 10), the first canonical variable was mainly dependent on water mass *(IMAS)*, water runoff from land *(AROF)*, and sediment size *(ISED)*; and the second canonical variable was mainly dependent on macrohabitat *(IHBT)*, tidal range *(TIDE)*, winter climate as measured by snowfall of nearest land *(ASNF)*, and water runoff from land. Since the correlation coefficient between the first canonical variable and water mass is as high as 0.74, it is obvious that the characteristics of the two water masses separated by Cape Hatteras are possibly the most important properties affecting the morphology of *A. beccarii*. The other factors, including water runoff from land and sediment size, were local conditions which could modify the regional characteristics of water mass and cause some variation of morphology.

The second canonical variable related importantly to macrohabitat, which in this study includes four categories, namely estuary, bay, tide pool, and open sea. The influx of fresh water from land into these macrohabitats is different. In quantifying this environmental factor, four macrohabitats were ranked from 1 to 4 according to the decrease of fresh water influx into the habitat. Therefore, it might be concluded that the influences of land contributed somewhat to morphological variation.

It was shown in the experimental design that morphology varied with water depth. As revealed in the present stepwise regression analysis, water depth *(DEEP)* was not an important environmental factor. Between water depth and the first and the second canonical variables, however, the correlation coefficients are 0.12 and −0.49, respectively. Clearly water depth had some relationship with the second canonical variable. The first two highest correlation coefficients that water depth showed with other environmental factors were −0.69 with water runoff from land *(AROF)* and 0.63 with macrohabitat *(IHBT)*. Evidently, after macrohabitat and water runoff from land were included in the regression analysis, most of the relationship the second canonical variable had with water depth had been counted by the included variables. Thus, there was little variation of morphology remaining for which water depth could account.

Conclusions.—Following are the conclusions drawn from the regional study of morphological variation:

1) Among the eight characters measured, proloculus size and umbilicus size were shown to have relatively large variation among samples and small variation within samples. Thus, these two characters are powerful in discriminating samples from different areas.

2) The variation of the eight characters among 25 samples could be summarized parsimoniously by the first two canonical variables, which accounted, respectively, for 68.81 and 12.21 percent of the total variation among samples.

3) Eight samples from the coast north of Cape Hatteras were positive on the first canonical variable, and 15 out of 17 samples from the coast south of Cape Hatteras were negative on the first canonical variable. That the first canonical variable was computed with strong influence of proloculus size and umbilicus size suggests that north of Cape Hatteras *A. beccarii* generally has a large proloculus and a large umbilicus, and south of Cape Hatteras it generally has a small proloculus and a small umbilicus.

4) Among 14 environmental factors studied, difference in the water masses separated by the barrier off Cape Hatteras was shown to be the most important factor relating to the first canonical variable. Other factors relating to the first two canonical variables were water runoff from land, winter climate as measured by snowfall on land, macrohabitat, sediment size, and tidal range. Accordingly, it is suggested that water mass is the most important factor determining the morphological variation and that the other factors, which represent local conditions, could modify the regional characteristics of the water mass and cause some variation of the morphology.

ADDITIONAL CONSIDERATIONS

This study has demonstrated that the morphology of *A. beccarii* varies with environment and that, of the eight characters studied, proloculus size and umbilicus size were best for indicating the morphological variation. Many characters were not investigated in the regional study of morphological variation. However, based on the results of the experimental design (Table 3),

growth rate of whorl thickness *(D)* and plug size *(DPLUG)*, which were highly correlated with either proloculus size or umbilicus size, could also be expected to be useful characters in showing geographical variation. The high positive correlation between proloculus size and growth rate of whorl thickness suggested that specimens with larger prolocuti usually have thicker whorls. In other words, when specimens with a constant number of chambers per whorl were compared, the specimen with a larger proloculus was larger in size than the specimen with a small proloculus. The high positive correlation between umbilicus size and plug size indicated that plug size is generally proportional to umbilicus size. Consequently, it can be concluded that the regional variation of the animal has the following pattern: in comparison with the animal from the coast south of Cape Hatteras, the animal from the coast north of Cape Hatteras has a relatively larger proloculus, thicker whorl, larger umbilicus, and larger plug.

Although water mass was the most important environmental factor affecting the morphological variation, other environmental factors also played important roles in the morphological variation. Samples G and H were collected from an area directly north of Cape Hatteras. The morphology of *A. beccarii* from these samples was quite different from that of the samples collected from other areas (Fig. 3). The important environmental factors associated with samples G and H are the northern coastal water, a low runoff from land, and a substrate of coarse sediment (Table 9). The combination of these environmental factors may have caused the extremely different morphology of the two samples.

Because water mass is generally defined by the characteristics of water temperature and salinity, water mass is highly correlated with water temperature and salinity. In the case of the present observations (Table 7), the correlation coefficients of water mass *(IMAS)* with its maximum summer temperature *(TMAX)*, minimum winter temperature *(TMIN)*, mean summer salinity *(SALS)* and mean winter salinity *(SALW)* are 0.82, 0.87, 0.96 and 0.80, respectively. That water mass is the most important environmental factor affecting the morphology suggests that water temperature and water salinity can affect strongly the morphology. However, water mass entered the stepwise regression analysis earlier than water temperature and salinity (Table 10). In other words, the morphology has a higher correlation with water mass than with water temperature or water salinity. It is not known what physical characteristics of the water mass contribute to this higher correlation. One possible interpretation of this result is that due to geographical separation of the two water masses, *A. beccarii* has developed morphological differences.

This study deals only with morphological characters available from study with a microscope and with environmental factors available from the literature. Many other morphological characters, such as wall structure, and environmental factors, such as amount of nutrients in the sea, might be useful for studying geographical variation of the animal. However, using the available morphological characters and environmental factors, this study has resulted in a picture of the manner and the possible causes of the geographical variation of *A. beccarii*.

Because the study has demonstrated that the morphology of *A. beccarii* varies with the environment, this information can be applied to fossil forms of *A. beccarii* in geological records for reconstructing ancient depositional environments.

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APPENDIX. MATHEMATICAL DERIVATION OF SOME EQUATIONS

Calculation of Area Covered by Linearly Expanding Curve.—A linearly expanding curve in polar coodinates (Fig. 4,*A*) is represented by the following equation:

$$r=a\theta+b \quad (1)$$

where r=radius of the curve, θ=rotational angle, a=expanding rate of the curve, b=constant of r when $\theta=0$. Let W=area covered by a segment of the curve and lines connecting both ends of the segment with the origin. From calculus, it is known that

$$dW=\pi r^2 d\theta/(2\pi) \quad (2)$$

and that

$$d\theta=dr/a. \quad (3)$$

Substituting equation (3) into equation (2) and integrating the result, we obtain

$$W=(r_1^3-r_2^3)/(6a) \quad (4)$$

where r_1 and r_2 are radii attached to both ends of the segment of the curve.

Calculation of Area of a Chamber on Dorsal Side of Coiling Shell.—Figure 4,*B* shows a part of coiling shell and the representation of symbols. If distances b_1, b_2, c_1 and c_2 on the axes of the rectangular coordinates, angles θ for locating r_3 and r_4, and angles $\angle AOC$ and $\angle BOD$ are given, we have enough information to calculate the area of a chamber, which is indicated by area $(ABDC)$ and is symbolized by V.

Area V can be partitioned into the following components:

V=area (OCD) + area (OBD) − area (OAB) − area (OAC).

Using equation (4) and the equation to estimate area of a triangle, the above equation becomes

$$V=[(r_4^3-r_3^3)/(6a_2)]+[r_2r_4(\sin\angle BOD)/2]-[(r_2^3-r_1^3)/(6a_1)]-[r_1r_3(\sin\angle AOC)/2] \quad (5)$$

Since $a_1=2(c_1-b_1)/\pi$ and θ_1 equals the summation of $\angle AOC$ and angle θ for locating r_3, length r_1 can be estimated from $r_1=a_1\theta_1+b_1$. Similarly, a_2, r_2, r_3 and r_4 can be estimated from the given constants. Substituting a_1, a_2, r_1, r_2, r_3, r_4, $\angle BOD$ and $\angle AOC$ to equation (5), we will get V for the area of a chamber.

Estimation of Constants for Equation Showing Linear Relationship between Coiling Angles of Chamber and Chamber Numbers.—Referring to Figure 4,*C*, we let:

X=chamber number, Y=coiling angle of chamber X, p and q=two constants for the linear equation of $Y=pX+q$, and $T_{X+0.5}$= total coiling angle from chamber 2 to chamber X.

In real world, X is a discrete variable. For converting it to a continuous variable for integration, a correction term of 0.5 is added to X before calculation. Integrating Y with respect to X and knowing $T_{1.5}=0$, we obtain

$$T_{X+0.5}=(pX^2/2)+qX-[(9p+12q)/8]. \quad (6)$$

If two values of $T_{X+0.5}$, such as $T_{m+0.5}$ and $T_{n+0.5}$, are known, p and q can be solved from two simultaneous equations obtained by substituting $T_{m+0.5}$ and $T_{n+0.5}$ and their associated m and n to equation (6). The answers of p and q are as follows:

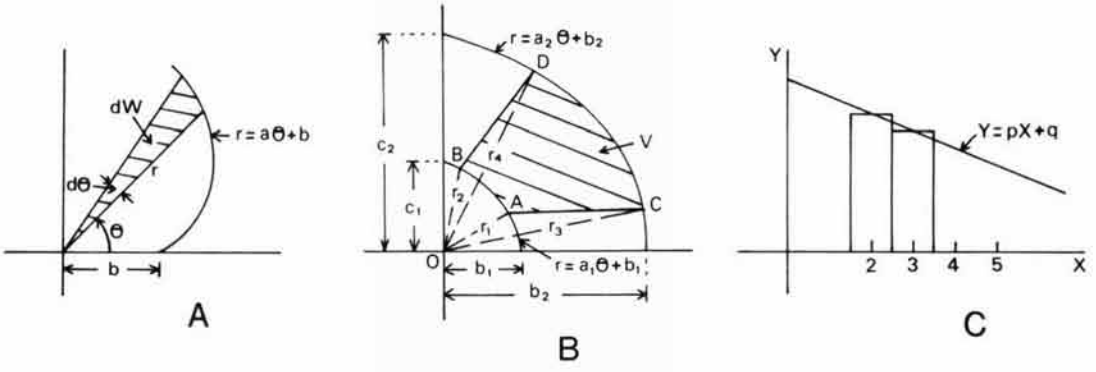

FIG. 4. Mathematical representation of coiling shell of *Ammonia beccarii*. *A* shows the growth curve of spiral whorl. *B* shows the area of a chamber on dorsal side. *C* shows the relation of coiling angles of chamber, *Y*, to their chamber numbers, *X*.

$$p=[(n-1.5)T_{m+0.5}-(m-1.5)T_{n+0.5}]/K \quad (7)$$

$$q=[(m^2-2.25)T_{n+0.5}-(n^2-2.25)T_{m+0.5}]/(2K). \quad (8)$$

where $K=[(m^2-2.25)(n-1.5)-(n^2-2.25)(m-1.5)]/2$.

Estimation of Minimum Sample Size.—The T^2-statistic, which is usually called Hotelling T^2 and is used to test whether two samples were drawn from the same population, has the following relationship with the F-statistic (see Anderson, 1958, p. 109):

$$[(n_1+n_2-2)p/(n_1+n_2-p-1)]F_{(p,n_1+n_2-p-1)}=T^2=[n_1n_2/(n_1+n_2)][\bar{X}_1-\bar{X}_2]'\Sigma^{-1}[\bar{X}_1-\bar{X}_2] \quad (9)$$

where n_1=size of first sample, n_2=size of second sample, p=number of variables, F=F-statistic, T^2=T^2-statistic, $\bar{X}_1$=mean vector of first sample, $\bar{X}_2$=mean vector of second sample, Σ="pooled sum of squares" from two samples, $=[n_1\Sigma_1+n_2\Sigma_2]/(n_1+n_2-2)$, where Σ_1= covariance matrix of first sample, and Σ_2=covariance matrix of second sample.

Let $K=[\bar{X}_1-\bar{X}_2]'\,\Sigma^{-1}[\bar{X}_1-\bar{X}_2]$ and F_{obs}= an estimate of F, then equation (9) is equivalent to

$$K=[(n_1+n_2)(n_1+n_2-2)pF_{obs}]/[n_1n_2(n_1+n_2-p-1)] \quad (10)$$

Assuming F_{obs} is a best estimate of parametric F from two different populations, we can use it to estimate the possible minimum sample size, from which an F-statistic will show the significant difference between the two populations. Let n=minimum sample size drawn from each population, and α=significant level for F-statistic, then equation (9) becomes

$$[2(n-1)p/(2n-p-1)]F_{\alpha(p,2n-p-1)}=(nK)/2.$$

Substituting K of equation (10) into the above equation and simplifying the relationship of the resulting equation, we obtain

$$F_{\alpha(p,2n-p-1)}=[n(2n-p-1)(n_1+n_2)(n_1+n_2-2)F_{obs}]/[4(n-1)n_1n_2(n_1+n_2-p-1)] \quad (11)$$

Since the unknown n is included in both sides of equation (11), only an iterative method can result in a solution for n.