

Evolution of
Athleta petrosa stock
(Eocene, Gastropoda) of Texas

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EVOLUTION AND ONTOGENY OF *ATHLETA PETROSA* STOCK

Ontogenetic and evolutionary development of the *Athleta petrosa* stock is judged from changes of several morphologic features including (1) growth stages, (2) protoconch, (3) growth patterns, (4) size, based on height, width, and height of spire, (5) body whorl ornamentation, (6) columellar folds, (7) labral denticulation, (8) shape, (9) anterior siphonal canal and fasciole, (10) spines, and (11) parietal callus. Certain morphologic features of the stock can be stated easily in quantitative terms; others are less readily translated to quantitative terms and are considered qualitatively. Summaries of quantitative methods and data are included as Appendix A.

GROWTH STAGES

Four growth stages, based mostly on morphogeny of ornamentation, are recognized in specimens of the *A. petrosa* stock. Initially, there is a smooth protoconch, followed by a ribbed stage which has simple, slightly curved, longitudinal ribs. Later, ribs become divided along the posterior part of the whorl by a shoulder and spiral subsutural ridge, resulting in a cancellate sculpture. Nodes, which in later whorls increase in size to form spines, develop at the intersections of longitudinal ribs with the shoulder and subsutural ridge. Initial enlargement of nodes is followed by reduction to a broad low tubercle. This stage coincides with loss of subsutural ridge and is followed by development of adult spinose ornamentation. Reduced tubercles may result from resorption of shell material by the mantle. Growth stages are thus designated (1) protoconch stage, (2) ribbed stage, (3) cancellate-nodose stage, and (4) spinose stage (figs. 1, 2). A terminal, gerontic growth stage is represented by extensive callus deposition. This stage is partly coincident with the spinose stage and is especially characteristic of *A. tuomeyi* Conrad.

In *Volutocorbis*, the inferred ancestor of the *A. petrosa* stock, the protoconch, ribbed

stage, and cancellate-nodose stage comprise the entire shell; in the *A. petrosa* stock, the fourth or spinose stage is added and comprises up to three of the last whorls in all but earliest forms of the stock and certain juvenile forms. The four stages are present in all subspecies of *A. petrosa* (Conrad); post-protoconch stages appear progressively earlier among successive groups of the stock. An analysis of ornamentation pattern of different stages is given in the section on Ornamentation and Sculpture.

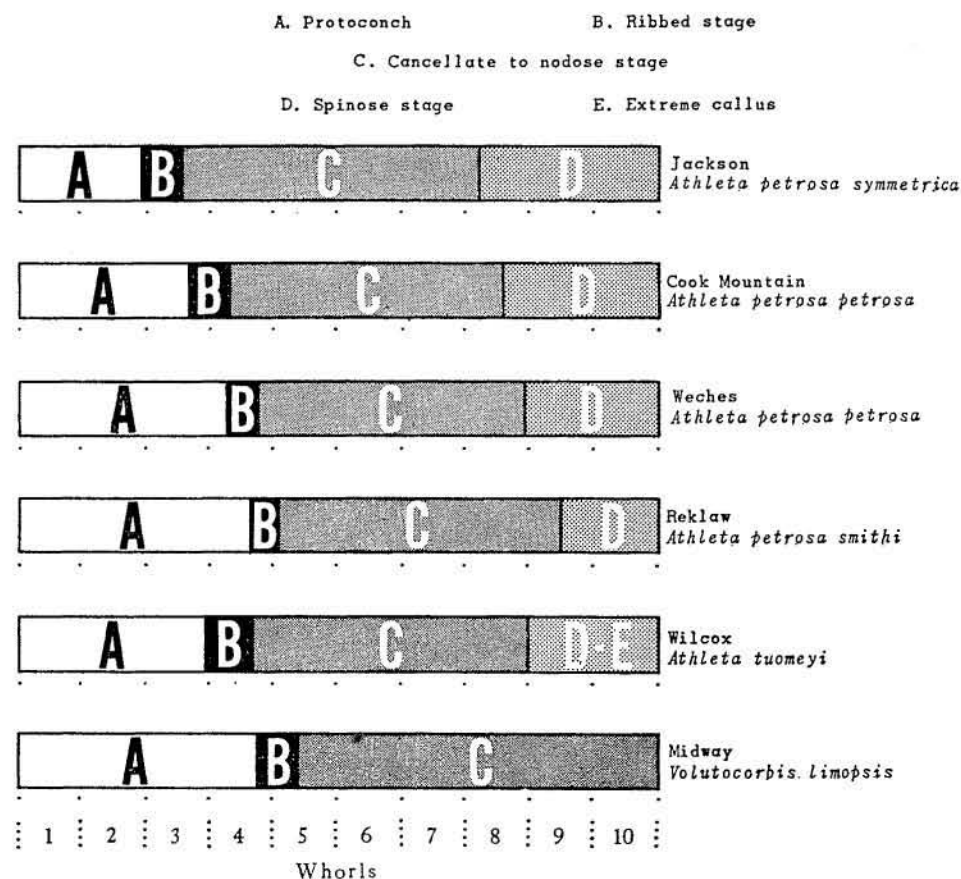
PROTOCONCH

Phyletic change in the protoconch of *A. petrosa* (Conrad) is indicated by a decrease in number of whorls, from the longer-whorled protoconch of *A. petrosa smithi* Fisher & Rodda to the shorter-whorled protoconch of *A. petrosa symmetrica* (Conrad) (figs. 3, 4). Mean lengths of protoconchs in number of whorls for successive groups within *A. petrosa* (Conrad) are as follows:

<i>A. petrosa symmetrica</i> (Conrad)	2.3
<i>A. petrosa petrosa</i> (Conrad) [Cook Mountain]	2.9
<i>A. petrosa petrosa</i> (Conrad) [Stone City]	3.2
<i>A. petrosa petrosa</i> (Conrad) [Weches]	3.1
<i>A. petrosa petrosa</i> (Conrad) [Total]	3.1
<i>A. petrosa smithi</i> Fisher & Rodda	3.5

A slight exception to successive shortening of the protoconch is shown among Stone City forms of *A. petrosa petrosa* (Conrad). Longer protoconchs of Stone City forms are associated with slightly anomalous ornamentation patterns; both features are discussed in the section on Ornamentation and Sculpture.

Total number of whorls in *A. petrosa* (Conrad) is generally 7 to 9; thus, decrease in number of protoconch whorls coincides with increase in number of

FIG. 2. Growth and ornamentation stages in *Athleta petrosa* stock.

whorls in the teleoconch. Addition of whorls in the teleoconch accounts for increase in size; an addition of one whorl to the teleoconch results in a size increase on the order of 40 percent. Although phyletic changes in the protoconch coincide with phyletic size increase, and possibly control phyletic size increase, the significance of protoconch change is difficult to evaluate. We have designated the protoconch as the smooth, apical part of the shell; in cross section the material of this part of the shell is homogenous and does not have the shell-wall differentiation that occurs in the teleoconch or ornamented part of the shell. Lebour (1937), Cox (1960, pp. 1112-1113), and Fretter and Graham (1962, pp. 62, 73, 471) have indicated that transition from the smooth part of the shell to the ornamented part of the shell does not ne-

cessarily indicate a transition from larval to a later stage; later whorls of the protoconchs of several gastropods are ornamented in various degrees. Assuming that what we have designated as the protoconch is the larval shell, there remains the problem of determining whether progressive shortening of the protoconch indicates progressive shortening of the larval stage and what evolutionary significance such shortening may imply. Larval development in certain Recent volutids occurs within the egg, and transition to the benthonic stage occurs without a free-swimming stage (Cox, 1960, p. 1113). The general shape and size of the protoconch on *A. petrosa* (Conrad), however, are similar to shells of free-swimming larvae (planktotrophic larvae of Thorson, 1950).

Fretter and Graham (1962, p. 472) in-

descriptions of large, well-documented, stratigraphically and geographically diverse collections and (2) statistical study of 1,600 specimens from 50 localities in Texas, Alabama, Louisiana, and Mississippi.

The *Athleta petrosa* stock in Texas consists of four species: *A. petrosa* (Conrad, 1833), *A. tuomeyi* Conrad, 1853, *A. lisbonensis* (Aldrich, 1897), and *A. dalli* (Harris, 1895). Most common and typical species of the stock in Texas, *A. petrosa* (Conrad), is divided into three successional subspecies: *A. petrosa smithi* Fisher & Rodda, n. subsp., from the Reklaw Formation; *A. petrosa petrosa* (Conrad, 1833) from the Weches, Stone City, and Cook Mountain Formations; and *A. petrosa symmetrica* (Conrad, 1854) from Jacksonian rocks. Other species of the stock are related closely to *A. petrosa* (Conrad), the main-line species of the stock, but show morphologic trends that define separate, diverging lines. These are *A. tuomeyi* Conrad, 1853, from the Wilcox Group; *A. lisbonensis* (Aldrich, 1897) from the Weches, Stone City, and Cook Mountain Formations; and *A. dalli* (Harris, 1895) from the Weches and Stone City Formations. The phylogeny and evolution of the *Athleta petrosa* stock, as interpreted by us, is shown diagrammatically in Plate II (pocket). Divisions are, in part, arbitrarily defined, as morphologic transitions occur throughout the stock. Nature and degree

of morphologic transition between stratigraphic and evolutionary divisions of the stock and nature of phylogenetic trends within the stock are demonstrated statistically.

Earliest descriptions of forms here included in the *Athleta petrosa* stock were by T. A. Conrad and Isaac Lea during the middle part of the last century (Selected Bibliography). Since that time, these forms have been discussed by several workers and new species have been established. The most thorough investigations of the evolution of *A. petrosa* and related species were undertaken by Burnett Smith (1906, 1907b). Smith illustrated general phylogenetic relationships of *A. petrosa* (Conrad) and related species as developed in the Eocene of Alabama and recognized 10 intraspecific taxa or morphotypes which he designated as races and named according to stratigraphic occurrence.

Moore (1962) has published a valuable catalog of Conrad's types at the Academy of Natural Sciences of Philadelphia.

Morphologic terms used in this report in descriptions of the *A. petrosa* stock are illustrated in figure 1. Classification of Paleogene rocks in Texas is given in table 1. Computer programs and descriptions of programs used in quantitative study, as well as summary of quantitative data and tabulated data of number of ornaments per whorl in growth series, are included as Appendix A.

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Bureau of Economic Geology were collected by Stenzel. H. G. Richards, Academy of Natural Sciences of Philadelphia, loaned certain of Conrad's type specimens. The Computation Center, The University of Texas, made available use of its CDC 1604 Computer. Burke Burkhart and R. A. Davis, now graduate students at Rice University and University of Illinois, respectively, ably assisted in various phases of the project. Finally, we express our thanks to all other individuals, especially various colleagues of the Bureau of Economic Geology

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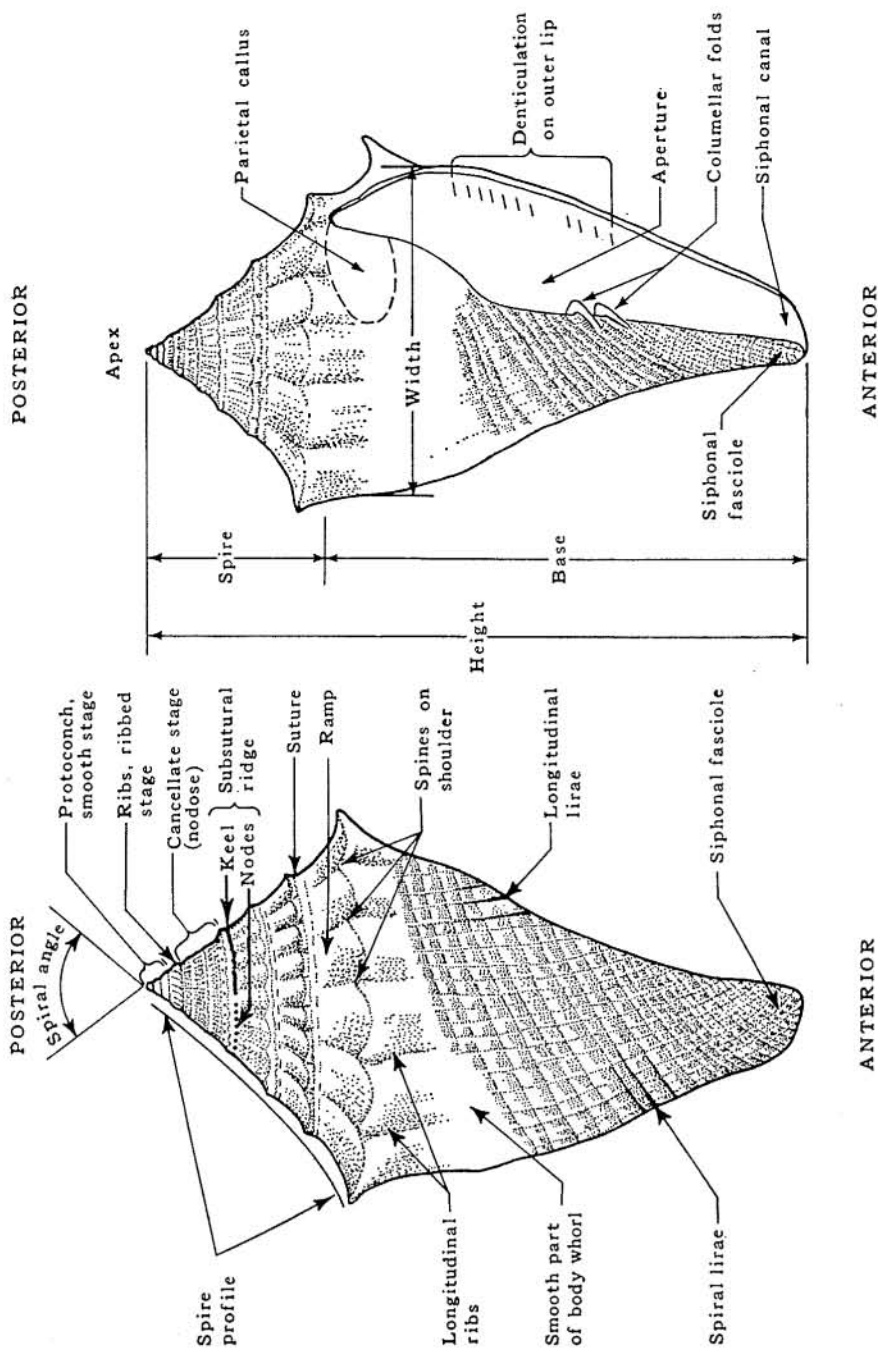


FIG. 1. Generalized *Athleta petrosa* (Conrad) showing terminology of various parts.

Evolution of *Athleta petrosa* Stock (Eocene, Gastropoda) of Texas

W. L. Fisher, Peter U. Rodda, and John W. Dietrich

ABSTRACT

Study of approximately 1,700 specimens of Eocene volutid gastropods of the *Athleta petrosa* stock from 85 localities in Texas permits the recognition of four evolutionary lines within the stock; these lines are characterized by *A. tuomeyi* Conrad, 1853, from the Wilcox Group, *A. petrosa* (Conrad, 1833) from Claibornian and Jacksonian rocks, and *A. lisbonensis* (Aldrich, 1897) and *A. dalli* (Harris, 1895) from the Claibornian. *A. petrosa* (Conrad) is the typical and characteristic species of the stock and is divided into successional, morphologically transitional subspecies: *A. petrosa smithi* Fisher & Rodda, n. subsp., from the Reklaw Formation; *A. petrosa petrosa* (Conrad, 1833) from the Weches, Stone City, and Cook Mountain Formations; and *A. petrosa symmetrica* (Conrad, 1854) from the Jacksonian.

Athleta petrosa (Conrad) shows the following phyletic trends: (1) decrease in number of whorls in smooth protoconch, (2) increase in size, (3) decrease in number and increase in size and prominence of peripheral ornamentation, including nodes and spines, (4) decrease in length and prominence of longitudinal ribs on body whorl, (5) increase in number and prominence of labral denticles, (6) enlargement and accentuation of anterior siphonal canal and fasciole, (7) increase in extent and amount of parietal callus, (8) accentuation of spiral lirae on anterior part of body whorl, (9) changes in gross shape from subfusiform to substrombiform to subfusi-

form, and (10) changes in shape of aperture corresponding to reduction of spines and reduction of peripheral angulation. Phyletic trends indicated in peripheral ornamentation, columellar folds, longitudinal ribs, lirae, and anterior siphonal canal and fasciole are related directly to and are a function of phyletic size increase, which in turn is apparently controlled by changes in length and size of the protoconch. Deposition of parietal callus appears to be partly a gerontic feature and is especially characteristic of the divergent species *A. tuomeyi* Conrad. Gross shape of shell and shape of aperture are controlled partly by size, but changes in these shapes also apparently reflect changes in the mantle not directly related to increasing shell size.

Statistical and quantitative study of approximately 1,600 specimens from 50 localities in Texas, Louisiana, Mississippi, and Alabama support testable qualitative conclusions. A program was prepared for the Control Data Corporation Model 1604 digital computer for the calculation of 20 combinations (sums and ratios) of the following parameters for each individual: height, maximum width, height of spire, number of columellar folds, and number of longitudinal ornaments (nodes, spines, and ribs) on body whorl; certain other parameters were analyzed quantitatively but without use of the digital computer. More than half of the programmed combinations were significant and showed distinct separation of taxa and trends among populations within the *Athleta petrosa* stock.

INTRODUCTION

Volutid gastropods of the *Athleta petrosa* stock are among the most abundant and best-preserved fossil mollusks in Eocene marine rocks of the Gulf Coastal Plain. The abundance, good preservation, and easily distinguished morphologic features of these fossils make them well suited for detailed study of evolution and phylogeny.

Purpose of restudying and redescribing *A. petrosa* (Conrad) and related species in the Eocene of Texas is (1) to define and illustrate ontogenetic and evolutionary features of the *A. petrosa* stock in both qualitative and quantitative terms, (2) to compare the evolutionary development of the

stock with general features of gastropod evolution, (3) to describe systematically taxa within the stock, and (4) to demonstrate stratigraphic utilization of successional divisions of the stock.

Approximately 1,700 specimens from 85 localities (Appendix B; Pl. I) and ten formations (table 1) were studied from Eocene rocks of Texas. Additional specimens, largely from the Sabinian and Jacksonian, were studied from 12 localities in Alabama, Louisiana, and Mississippi. The present interpretation of taxonomy, evolution, and phylogeny of the *Athleta petrosa* stock is based on (1) detailed morphologic

TABLE 1. Classification of Paleogene rocks (in outcrop) of the Texas Gulf Coastal Plain. Arrows denote occurrence of *Athleta petrosa* stock.

SYSTEM	SERIES	STAGE	FORMATION			
PALEOGENE	EOCENE	JACKSON	Whitsett			
			Manning			
			Wellborn			
			➔	Caddell		
			➔	Moody's Branch		
		CLAIBORNE	➔	Yegua		
			➔	Cook Mountain		
			➔	Stone City		
			Sparta			
			Therrill			
			➔	Weches		
			➔	Queen City		
			➔	Reklaw		
			Carrizo			
			SABINE	Wilcox Group	➔ Sabinetown	
					Rockdale	➔ Pendleton
		Simsboro				
		Hooper			Marthaville	
		Seguin				
	PALEOCENE	MIDWAY	Solomon Creek Porters Creek Kincaid			

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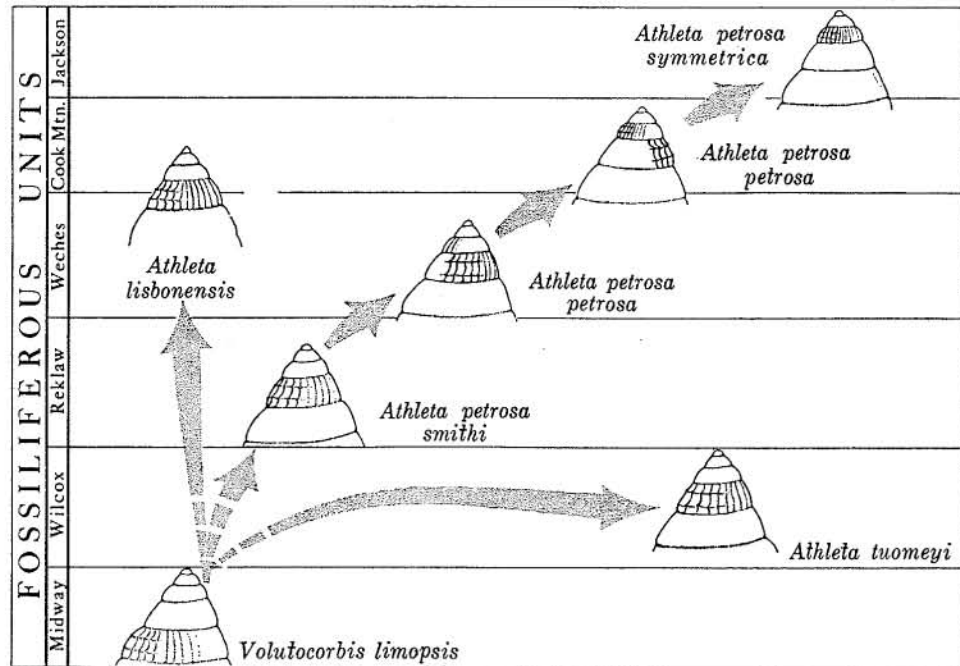
The benefits of education and of useful knowledge, generally diffused through a community, are essential to the preservation of a free government.

SAM HOUSTON

Cultivated mind is the guardian genius of Democracy, and while guided and controlled by virtue, the noblest attribute of man. It is the only dictator that freemen acknowledge, and the only security which freemen desire.

MIRABEAU B. LAMAR

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FIG. 3. Size and length of protoconch in *Athleta petrosa* stock.

indicated that a long protoconch is found on gastropods with a long pelagic stage, with shorter protoconchs characteristic of shorter pelagic stages; nonpelagic forms have small, nearly spherical protoconchs. Thus, a progressive shortening of the larval stage is indicated within *A. petrosa* (Conrad) assuming that transition from the smooth to ornamented part of the shell represents termination of the larval stage. Slight protoconch modification is observed among certain species that may be cladogenetic elements of the *A. petrosa* stock. Smith (1907b) reported a short, bulbous protoconch on *A. clayi* Smith from Louisiana (Cook Mountain Formation) and on *A. sayana* (Conrad) from Alabama (Gosport Formation); these species may represent forms of the stock without a pelagic stage. Smith concluded that protoconch modification within the *A. sayana* (Conrad) lineage was induced environmentally. A loosely coiled protoconch on some forms of *A. tuomeyi* Conrad may also represent an environmentally controlled modification. Certain specimens of the *A. petrosa*

main line from the Stone City Formation have, compared with contemporaneous forms of *A. petrosa* (Conrad), anomalously long protoconchs; these longer protoconchs show no modification in form and shape.

We judge larval evolution in the *A. petrosa* stock, primarily on the apparent relationship of phyletic change in size of protoconch and phyletic increase in size of the teleoconch, to be basic to the evolution of the stock as a whole. Lack of knowledge of the larval histories of Recent volutid gastropods, even of general ecological types, precludes a proper evaluation of the larval history of forms within the *A. petrosa* stock and its role in the evolution of the stock. According to Anderson (1960, p. 26), the life history of only one species of volute has been studied, the Australian Baler shell *Melo umbilicatus* Sowerby (Allan and Middleton, 1946; Allan, 1950, pp. 163-164). The shell of *Melo* is large, inflated, has a large bulbous protoconch, and bears little resemblance to *Athleta*.

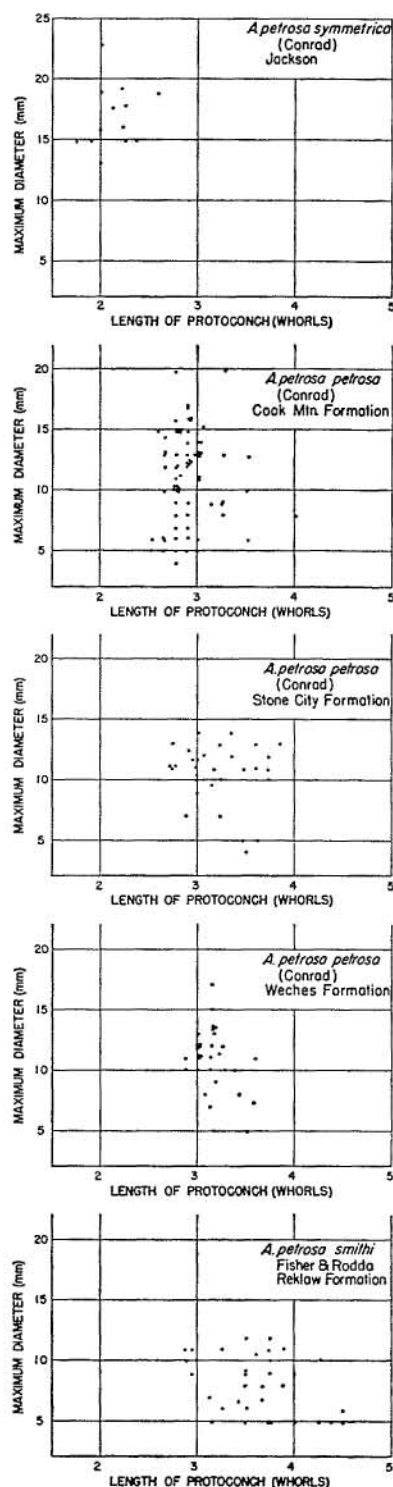


FIG. 4. Scatter diagrams of length of protoconch (number of whorls) versus width of body whorl (mm) in *Athleta petrosa* (Conrad).

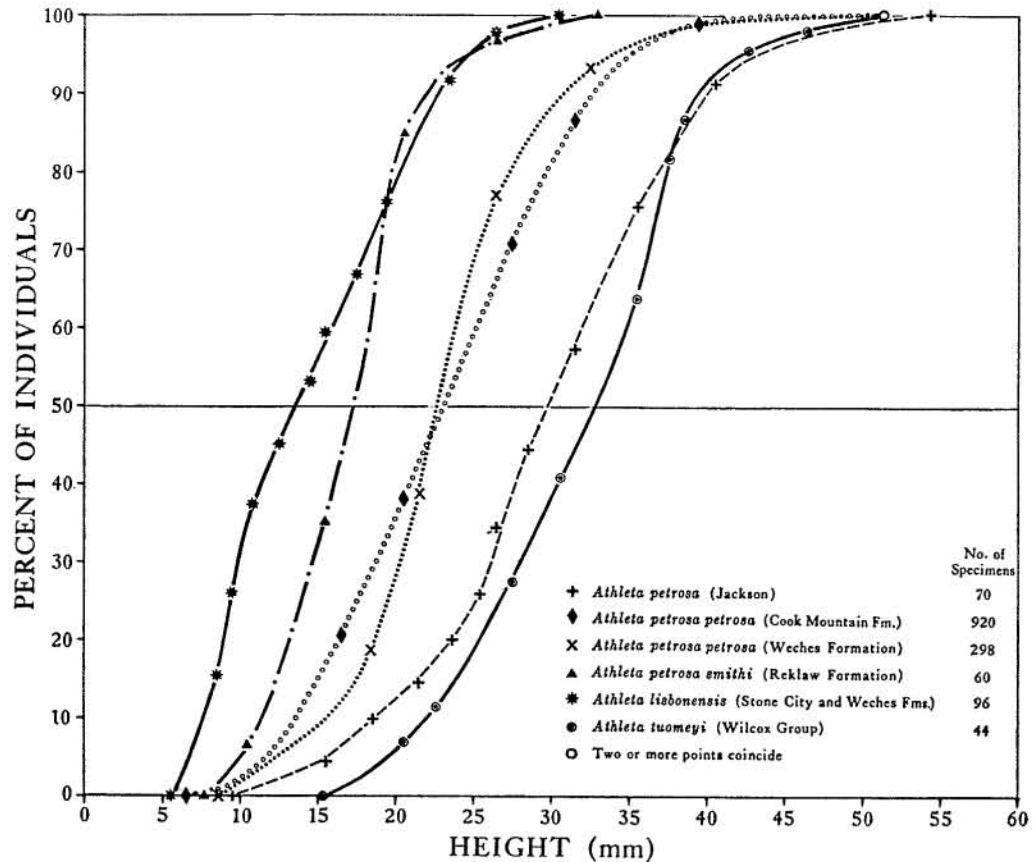
SIZE

Comparison of height, width, and spire height demonstrates certain phylogenetic trends in the *Athleta petrosa* stock. Our collections are probably biased slightly to large specimens, and confirmation of these trends must be made in a manner that eliminates inherent size bias (see section on General Limitations). Use of ratio of height to width reduces, but does not eliminate, this bias. Specimens from each locality are part of a growth series, and valid comparisons only can be made at the same growth stage or with individuals of the same size. Growth stage comparisons were made and are presented in the section on Ornamentation and Sculpture. Results of this study generally substantiate conclusions derived from size measurements alone.

Cumulative curves (fig. 5) and modified Dice-Leraas diagrams (fig. 6) of height distinguish three main groups in the *A. petrosa* stock. *A. petrosa smithi* Fisher & Rodda and *A. lisbonensis* (Aldrich) are the smallest forms, *A. petrosa petrosa* (Conrad) is the medium-size form, and *A. petrosa symmetrica* (Conrad) and *A. tuomeyi* Conrad are the largest forms of the stock. Ranges of height for 80 percent of the sample (excluding smallest and largest 10 percent) are:

<i>A. petrosa symmetrica</i> (Conrad)	18.5 to 40.0 mm
<i>A. petrosa petrosa</i> (Conrad) [Cook Mountain]	13.5 to 33.0 mm
<i>A. petrosa petrosa</i> (Conrad) [Weches]	15.5 to 30.5 mm
<i>A. petrosa smithi</i> Fisher & Rodda	11.5 to 22.0 mm

All taxa have about the same minimum height, the smallest forms of each representing various size juveniles. Maximum size is also similar for all taxa except *A. lisbonensis* (Aldrich) and *A. petrosa smithi* Fisher & Rodda. Small size reported for *A. lisbonensis* (Aldrich) is interpreted largely as the result of sample bias; large, complete specimens are rare, though fragments are common. Mean height and range of height are similar for *A. petrosa symmetrica* (Conrad) and *A. tuomeyi* Conrad. A progressive increase in mean height oc-

FIG. 5. Cumulative curves of height in *Athleta petrosa* stock.

curs among successive subspecies within *A. petrosa* (Conrad). The probability (P), determined by Student's *t*-tests (Simpson et al., 1960, pp. 176-178), that the observed difference in mean height could be equaled in samples drawn from identical populations is as follows:

<i>A. petrosa petrosa</i> (Conrad) [Cook Mountain] /	
<i>A. petrosa petrosa</i> (Conrad) [Weches] /	$P \ll 0.001$
<i>A. petrosa petrosa</i> (Conrad) [Cook Mountain] /	$P = 0.6 \text{ to } 0.7$
<i>A. petrosa smithi</i> Fisher & Rodda /	
<i>A. petrosa petrosa</i> (Conrad) [Weches]	$P \ll 0.001$

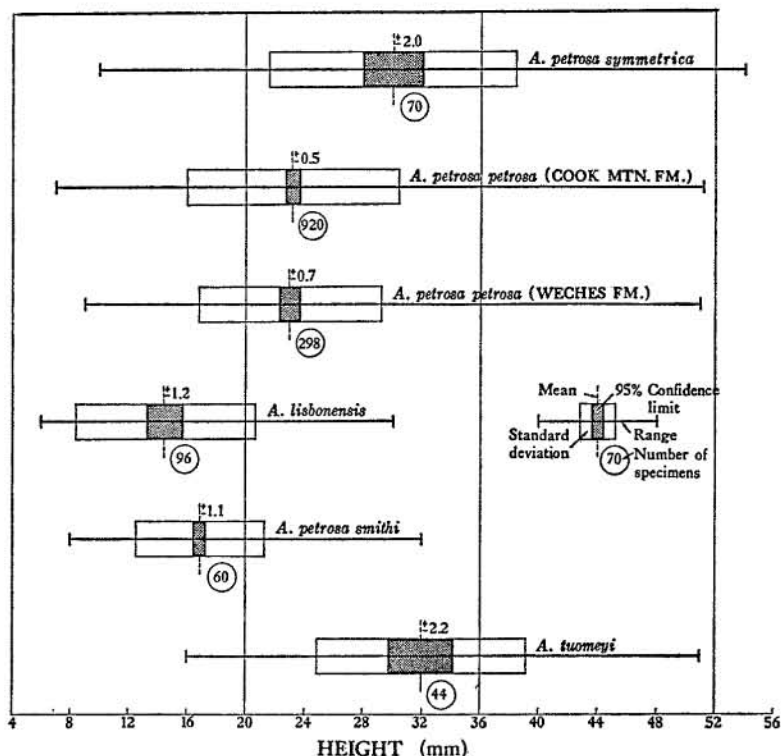
Cumulative curves (fig. 5) of Weches and Cook Mountain forms of *A. petrosa* (Conrad) intersect due to the greater proportion of small forms in the Cook Mountain

sample. This difference apparently is due to sample bias and has no discernible taxonomic or evolutionary significance.

Cumulative curves (fig. 7) and modified Dice-Leraas diagrams (fig. 8) of width show about the same relationships as height in the *A. petrosa* stock. The three main groups characterized by similar mean height have similar mean width. Ranges of width for 80 percent of the sample (excluding smallest and largest 10 percent) are:

<i>A. petrosa symmetrica</i> (Conrad)	10.5 to 19.5 mm
<i>A. petrosa petrosa</i> (Conrad) [Cook Mountain]	6.0 to 14.5 mm
<i>A. petrosa petrosa</i> (Conrad) [Weches]	7.5 to 13.5 mm
<i>A. petrosa smithi</i> Fisher & Rodda	5.0 to 10.5 mm

As in mean height, there is also a pro-

FIG. 6. Modified Dice-Leraas diagrams of height in *Athleta petrosa* stock.

gressive increase in mean width. *A. tuomeyi* Conrad has a range of width and mean width similar to terminal forms of *A. petrosa* (Conrad). Results of Student's *t*-tests of the significance of the difference of mean width in *A. petrosa* stock are:

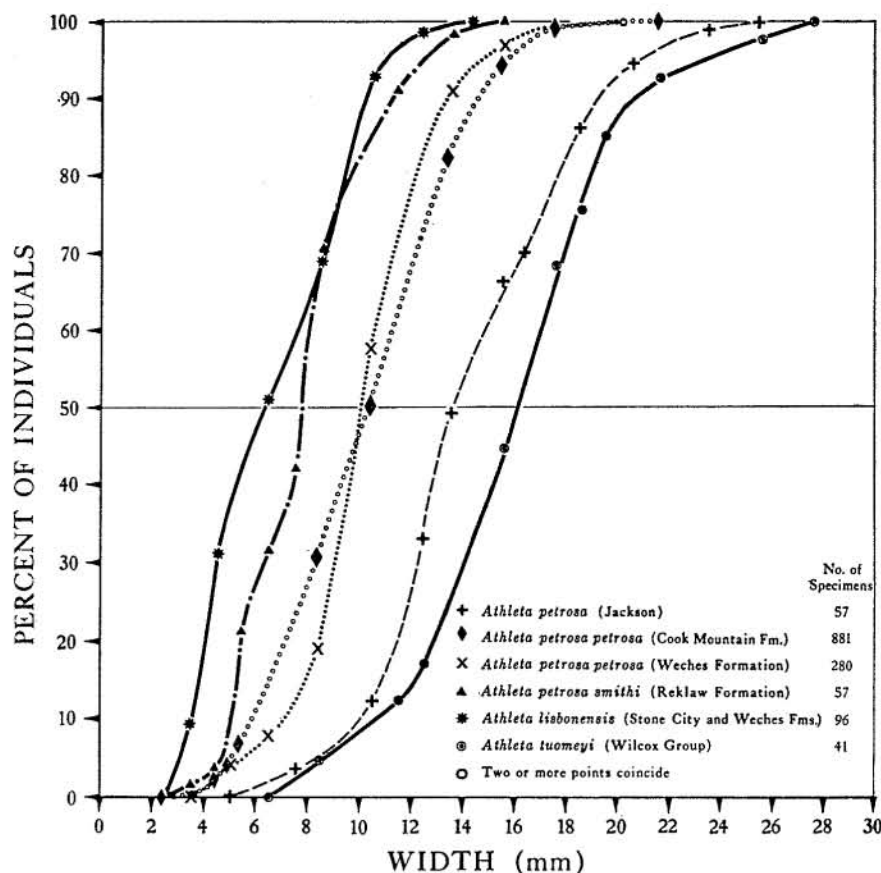
<i>A. petrosa petrosa</i> (Conrad) [Cook Mountain] / <i>A. petrosa symmetrica</i> (Conrad)	$P \ll 0.001$
<i>A. petrosa petrosa</i> (Conrad) [Weches] / <i>A. petrosa petrosa</i> (Conrad) [Cook Mountain]	$P = 0.6$ to 0.7
<i>A. petrosa smithi</i> Fisher & Rodda / <i>A. petrosa petrosa</i> (Conrad) [Weches]	$P \ll 0.001$

Groups within the *A. petrosa* stock based on differences in height and width are also characterized by differences in height of spire. Ranges of height of spire for 80 percent of the sample (excluding smallest and largest 10 percent) are:

<i>A. petrosa symmetrica</i> (Conrad)	7.3 to 15.2 mm
<i>A. petrosa petrosa</i> (Conrad) [Cook Mountain]	4.6 to 11.5 mm
<i>A. petrosa petrosa</i> (Conrad) [Weches]	5.5 to 11.0 mm
<i>A. petrosa smithi</i> Fisher & Rodda	4.1 to 9.8 mm

There is a general increase in maximum and mean spire height (figs. 9, 10) among successive subspecies of *A. petrosa* (Conrad). In contrast to this progressive increase, mean spire height is greater for Weches forms of *A. petrosa petrosa* (Conrad) than for Cook Mountain forms of that subspecies; Student's *t*-tests indicate small probability that the difference could be equaled in samples drawn from identical populations. Results of Student's *t*-tests of differences of mean spire height are:

<i>A. petrosa petrosa</i> (Conrad) [Cook Mountain] / <i>A. petrosa symmetrica</i> (Conrad)	$P \ll 0.001$
--	---------------

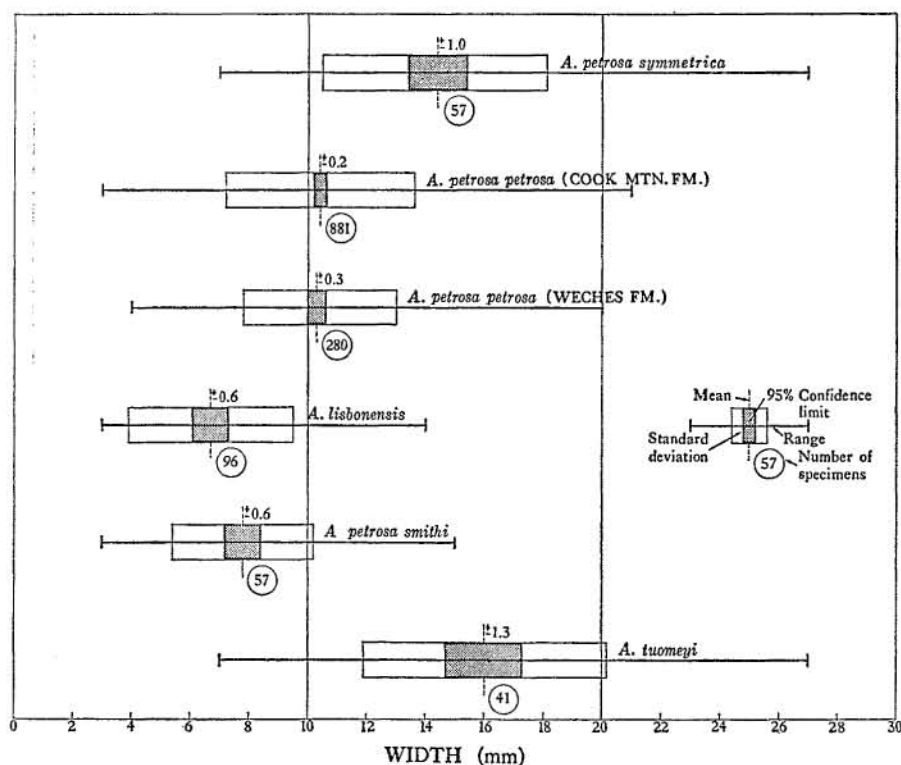
FIG. 7. Cumulative curves of width in *Athleta petrosa* stock.

A. petrosa petrosa
(Conrad) [Weches] /
A. petrosa petrosa (Conrad)
[Cook Mountain] $P = 0.01$ to 0.001
A. petrosa smithi
Fisher & Rodda /
A. petrosa petrosa
(Conrad) [Weches] $P \ll 0.001$

Cumulative curves (fig. 11) and modified Dice-Leraas diagrams (fig. 12) of ratios of height to width indicate two main groups within the *A. petrosa* stock. *A. tuomeyi* Conrad is relatively wider than the remainder of the stock, owing to extensive deposits of callus in the parietal area of the shell. Most forms of *A. petrosa smithi* Fisher & Rodda are relatively narrow and have high ratios of height to width. Trend lines drawn from contoured scatter points of height plotted against width (Pl. VI, pocket) are straight and similar for *A.*

lisbonensis (Aldrich) and subspecies of *A. petrosa* (Conrad), indicating a similar isometric growth pattern for these forms; projected trend lines pass through the origin (0/0). Due to extensive callus deposits on *A. tuomeyi* Conrad, the trend line for this species is distinct from those of the remainder of the stock, intersecting the others at points where height is 16 to 20 mm and width is 7 to 9 mm. When projected, the trend of *A. tuomeyi* Conrad does not pass through the origin, indicating a curved trend line and an early stage of allometric growth. Among larger forms of *A. tuomeyi* Conrad, the trend line is straight and growth pattern is isometric as in the remainder of the stock.

Increase in size corresponds to increase in number of teleoconch whorls (fig. 13). There is a slight decrease in total number

FIG. 8. Modified Dice-Leraas diagrams of width in *Athleta petrosa* stock.

of whorls from oldest to youngest forms of *Athleta petrosa* (Conrad), accompanying phyletic size increase, though decrease in total number of whorls is less than decrease in number of protoconch whorls (compare figs. 4 and 13).

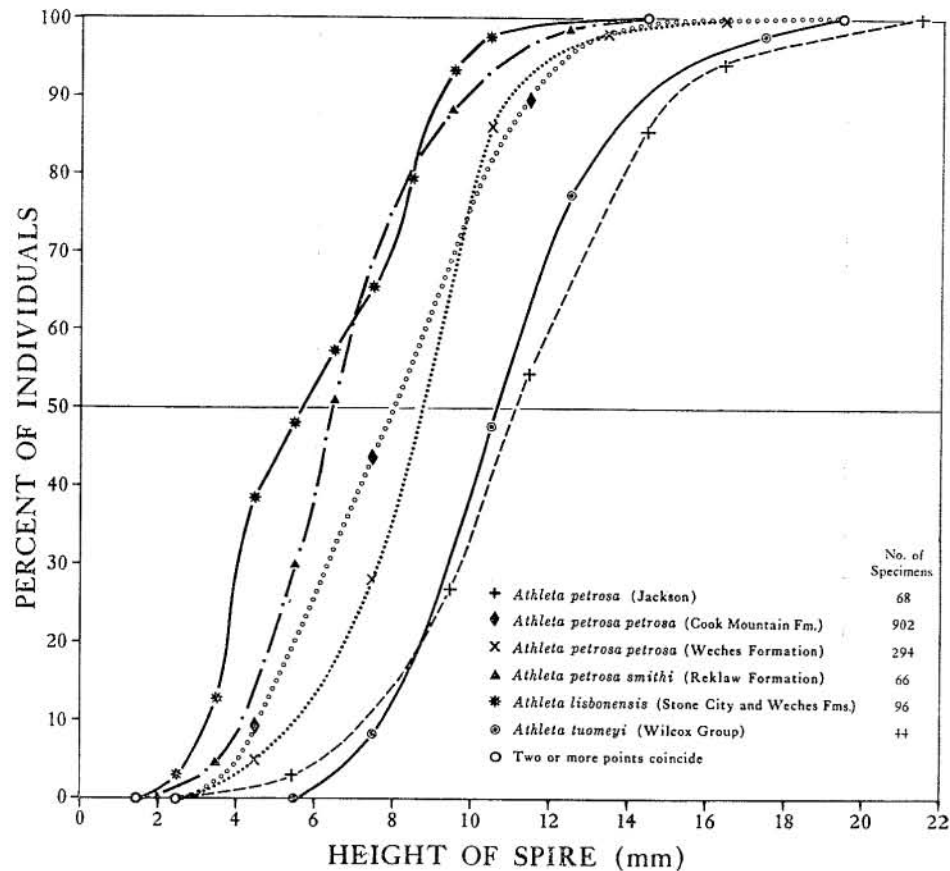
Size relationships within the *A. petrosa* stock are shown diagrammatically in figure 14.

Progressive increase in size of adults among several phyletic lines of animals has been demonstrated and documented by a number of paleontologists. Rensch (1960, p. 206) has designated this general trend among animals as Cope's Rule. Rensch (1960, pp. 206-218) gave a number of examples of phyletic size increase in animals, especially among terrestrial vertebrates, and Newell (1949) recorded several examples of phyletic size increase in invertebrates. The significance of phyletic size increase in specific features of evolution has been discussed by several paleontol-

ogists. Stenzel (1949, p. 48) noted the coincidence of shell size and shell-wall thickness among oysters of the *Ostrea sellaeformis* stock, and Newell (1949) discussed the coincidence of certain evolutionary changes and phyletic size increase. Excepting gross changes in shape and addition of certain gerontic features, observable phyletic changes in morphology in the *A. petrosa* stock coincide with changes in size and are either directly or indirectly controlled by phyletic size increase. These features of the stock are discussed subsequently.

ORNAMENTATION AND SCULPTURE

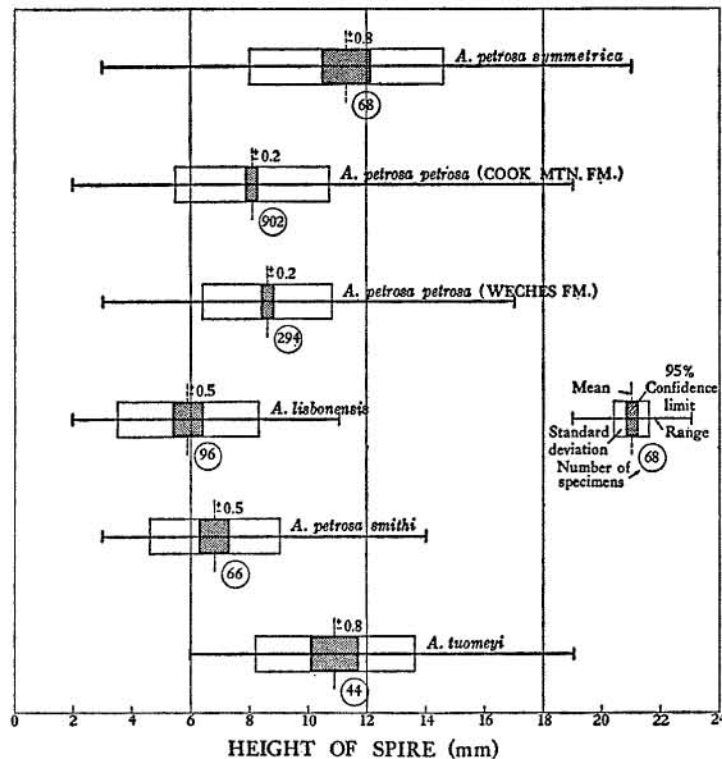
Ornamentation in *A. petrosa* (Conrad) develops from the generally cancellate ornamentation in early forms of *A. petrosa smithi* Fisher & Rodda, to the spinose and intervening smooth ornamentation of *A. petrosa petrosa* (Conrad) and *A. petrosa symmetrica* (Conrad) (figs. 14, 15). In the

FIG. 9. Cumulative curves of height of spire in *Athleta petrosa* stock.

development of *A. petrosa* (Conrad), spines progressively become larger and more widely spaced. Spines situated on the shoulder possibly marked the temporary position of a posterior siphon. Phyletic increase in size of the spines, or siphonal notches, corresponds to phyletic size increase within the stock. In terminal forms of *A. petrosa* (Conrad), spines become long and slender and tend to be recurved posteriorly, suggesting a special, though slight, adaptation. In *A. lisbonensis* (Aldrich) and *A. dalli* (Harris), initial enlargement of nodes is followed by gradual reduction; spines are not present. These forms have a relatively wider aperture than the spinose form of *A. petrosa* (Conrad), probably indicating a change in the arrangement of the mantle. Individual spines on *A. tuomeyi* Conrad, partly cov-

ered and resorbed by deposits of parietal callus, commonly tend to split and form two or more smaller spines. The irregularity of spines on *A. tuomeyi* Conrad agrees with the general irregularity of this species. A double row of spines also was observed on one specimen of *A. petrosa petrosa* (Conrad).

Changes in longitudinal ribs on the body whorl correspond to changes in spines. As spines become more widely spaced, longitudinal ribs are more widely spaced, but as spines become relatively larger, longitudinal ribs become relatively smaller and are absent in some of the terminal forms of the stock (fig. 15). The opposite of this trend is shown in *A. lisbonensis* (Aldrich) where, with the gradual reduction of nodes, longitudinal ribs become relatively larger and extend farther anteriorly on the body

FIG. 10. Modified Dice-Leraas diagrams of height of spire in *Athleta petrosa* stock.

whorl. In *A. dalli*, longitudinal ornaments become smaller and more closely spaced, with development of cancellate sculpture on body whorl.

Cumulative curves (fig. 16) and modified Dice-Leraas diagrams (fig. 17) of ornaments (number of spines or longitudinal ribs on the body whorl) show three main groups within the *A. petrosa* stock: *A. petrosa smithi* Fisher & Rodda has a relatively large number of ornaments; *A. lisbonensis* (Aldrich) has a moderate number of ornaments; and the remainder of the stock—*A. tuomeyi* Conrad, *A. petrosa petrosa* (Conrad), and *A. petrosa symmetrica* (Conrad)—have a relatively small number of ornaments. These relationships are shown by the ranges of number of ornaments on the body whorl of 80 percent of the sample (excluding lowest and highest 10 percent):

A. petrosa symmetrica
(Conrad) 12 to 8

A. petrosa petrosa
(Conrad) [Cook Mountain] 13 to 9
A. petrosa petrosa
(Conrad) [Weches] 14 to 9
A. petrosa smithi
Fisher & Rodda 30 to 10
A. lisbonensis
(Aldrich) 16 to 12
A. tuomeyi
Conrad 14 to 9

Within *A. petrosa* (Conrad) there is a progressive decrease in mean and maximum number of body whorl ornaments among successive subspecies (table 2). Minimum number of ornaments on body whorl in *A. petrosa* (Conrad) is similar for all subspecies. In *A. petrosa smithi* Fisher & Rodda, the earliest form of *A. petrosa* (Conrad), cancellate sculpture persists on the body whorl of most adult specimens. Mean number of ornaments on *A. petrosa smithi* Fisher & Rodda is not strictly comparable to mean number of ornaments on other subspecies of *A. petrosa* (Conrad)

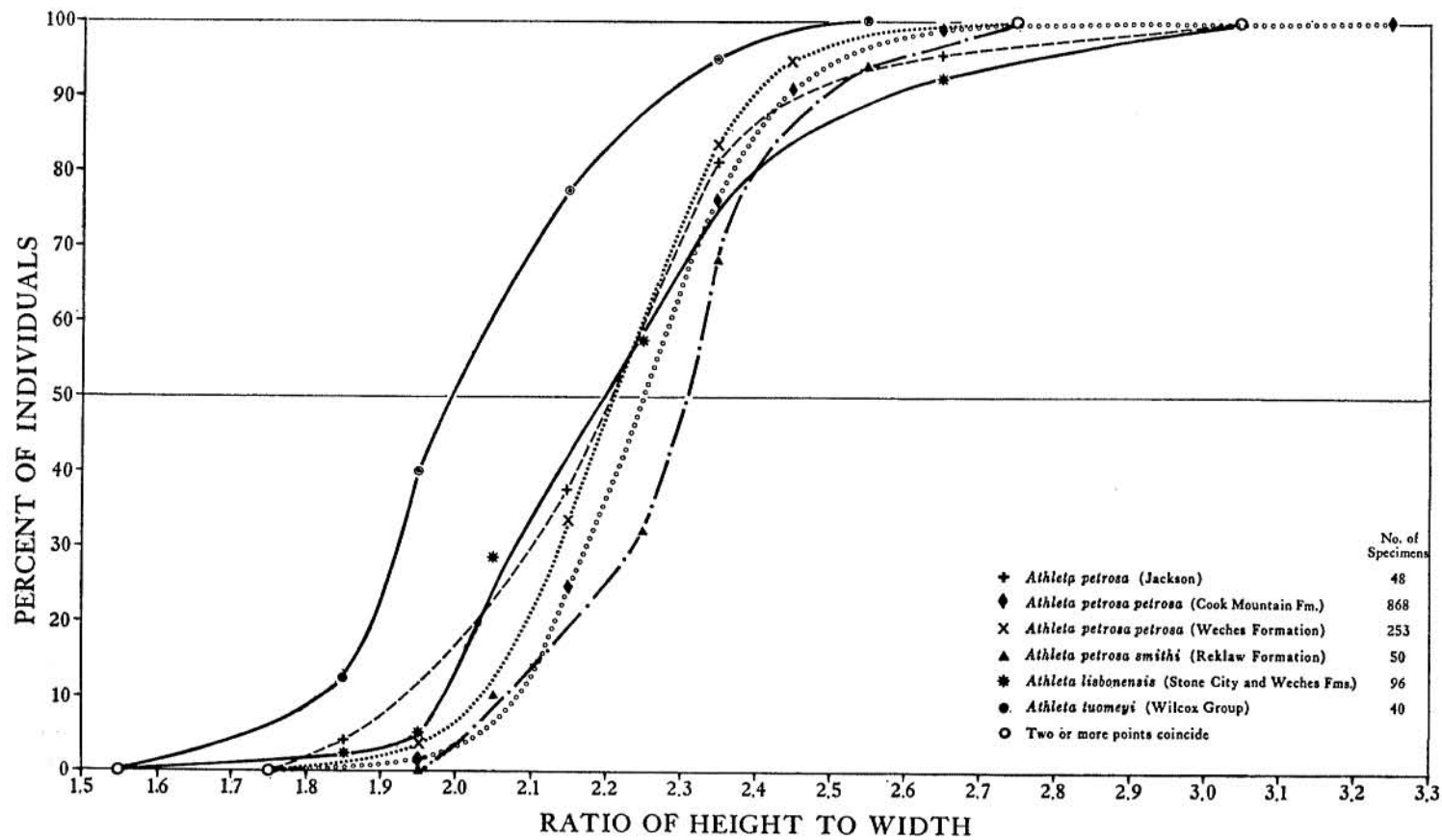


FIG. 11. Cumulative curves of ratio of height to width in *Athleta petrosa* stock.

TABLE 2. Number of longitudinal ornaments on body whorl.

Height (mm)		<i>Athleta tuomeyi</i>	<i>A. petrosa smithi</i>	<i>A. petrosa</i> [Queen City]	<i>A. petrosa</i> petrosa [Weches]	<i>A. petrosa</i> petrosa [Stone City]	<i>A. petrosa</i> petrosa [Cook Mtn.]	<i>A. petrosa</i> symmetrica	<i>A. lisbonensis</i>	<i>A. dalli</i>
4	Maximum	17
	Minimum	14
	Mean	15.3
5	Maximum
	Minimum
	Mean	26.0	18.0
6	Maximum	26	17	17
	Minimum	24	15	15
	Mean	25.0	15.4	15.8
7	Maximum	24	15	16
	Minimum	22	14	15
	Mean	23.0	14.3	14.0	15.5	17.0
8	Maximum	17	23
	Minimum	13	14
	Mean	25.0	14.8	15.7
9	Maximum	25	23	15	16	16
	Minimum	23	15	13	13	12
	Mean	24.2	18.0	14.0	14.0	14.7
10	Maximum	19	15	16	19
	Minimum	16	11	12	17
	Mean	27.0	22.0	17.5	15.0	13.1	13.0	14.0	18.0
11	Maximum	30	15	21
	Minimum	20	11	13
	Mean	25.0	14.0	12.4	15.3	19.0
12	Maximum	32	22	16	16
	Minimum	27	17	10	14
	Mean	29.3	19.5	13.0	15.0	12.1	14.7
13	Maximum	32	14	18	14
	Minimum	23	13	10	12
	Mean	27.0	21.0	13.5	12.8	15.0	13.0	21.0
14	Maximum	26	15	15	14
	Minimum	23	14	10	13
	Mean	18.0	24.5	14.5	16.0	12.7	13.3
15	Maximum	25	16	16	16	14	25
	Minimum	23	10	15	10	12	22
	Mean	23.7	13.8	15.5	12.2	13.0	23.5

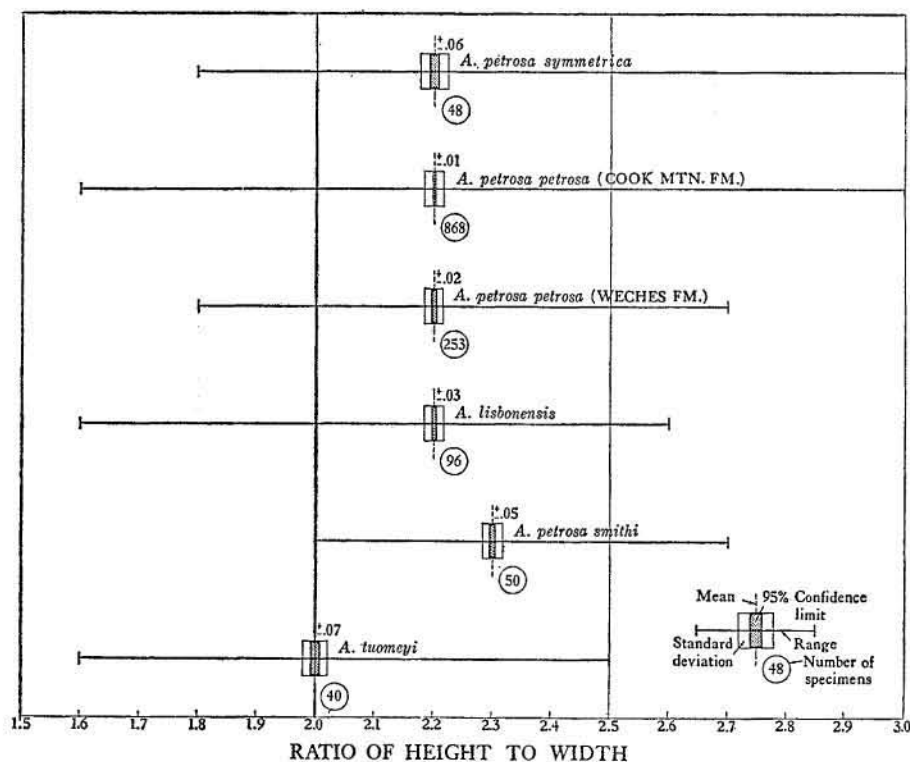
TABLE 2. (continued)

Height (mm)		<i>Athleta tuomeyi</i>	<i>A. petrosa smithi</i>	<i>A. petrosa</i> [Queen City]	<i>A. petrosa</i> petrosa [Weches]	<i>A. petrosa</i> petrosa [Stone City]	<i>A. petrosa</i> petrosa [Cook Mtn.]	<i>A. petrosa</i> symmetrica	<i>A. lisbonensis</i>	<i>A. dalli</i>
16	Maximum Minimum Mean 14.0	25 23 23.7 24.0 10.0 12.0	16 9 11.1	18 13 14.8
17	Maximum Minimum Mean 20.0	12 11 11.4	14 8 11.7 12.0	15 13 13.8
18	Maximum Minimum Mean	26 19 22.3	14 10 11.1	14 8 11.5	15 12 13.8
19	Maximum Minimum Mean	22 13 17.0	13 9 11.2 11.0	14 9 11.8 12.0	22 12 15.2
20	Maximum Minimum Mean	15 13 14.0	30 15 22.5	16 8 10.5 11.0	13 8 10.4 13.0	17 11 13.7 26.0
21	Maximum Minimum Mean 12.0	21 11 16.0	15 8 11.3	11 10 10.7	16 7 10.9 11.0	19 11 14.2
22	Maximum Minimum Mean	14 9 11.0	15 8 10.2	12 11 11.5	12 8 10.0 14.0	17 12 13.8
23	Maximum Minimum Mean	14 12 13.0	13 8 10.6	12 9 10.5	12 8 10.1 10.0	17 15 16.0
24	Maximum Minimum Mean 12.0	12 8 10.1	11 9 10.0	13 7 9.8	19 11 15.2
25	Maximum Minimum Mean	12 11 11.5	14 8 10.0	12 11 11.3	13 7 10.0	13 8 10.0 90.0
26	Maximum Minimum Mean 10.0	12 8 10.1	12 8 10.0	12 10 10.8 16.0
27	Maximum Minimum Mean	13 11 12.0 9.0	12 8 9.8	11 9 10.0	12 8 9.9	12 10 11.3

TABLE 2. (continued)

Height (mm)		<i>Athleta tuomeyi</i>	<i>A. petrosa smithi</i>	<i>A. petrosa</i> [Queen City]	<i>A. petrosa</i> petrosa [Weches]	<i>A. petrosa</i> petrosa [Stone City]	<i>A. petrosa</i> petrosa [Cook Mtn.]	<i>A. petrosa</i> symmetrica	<i>A. lisbonensis</i>	<i>A. dalli</i>
28	Maximum Minimum Mean 10.0	12 8 9.5	11 10 10.5	13 8 9.8	18 10 12.5
29	Maximum Minimum Mean	13 12 12.5	10 9 9.3	11 10 10.5	11 8 9.9 10.0
30	Maximum Minimum Mean	11 9 10.0 10.0	16 8 10.0	11 9 10.0 22.0 95.0
31	Maximum Minimum Mean 10.0	15 9 11.0	12 9 10.4 11.0 16.0
32	Maximum Minimum Mean	13 10 11.7 10.0	15 8 10.0 9.0	12 9 10.0	11 8 9.3
33	Maximum Minimum Mean	14 11 12.5	11 7 9.5	11 9 10.0
34	Maximum Minimum Mean	15 11 13.0	11 10 10.5	16 8 9.9	12 8 10.0
35	Maximum Minimum Mean 10.0	12 8 9.8	10 8 9.3
36	Maximum Minimum Mean	18 7 13.0	13 8 11.0	12 9 10.1 9.0 13.0
37	Maximum Minimum Mean	11 10 10.5	11 9 9.7	11 9 10.0
38	Maximum Minimum Mean	11 9 10.1
39	Maximum Minimum Mean	13 8 9.8	11 8 9.7

Height (mm)		<i>Athleta tuomeyi</i>	<i>A. petrosa smithi</i>	<i>A. petrosa</i> [Queen City]	<i>A. petrosa</i> <i>petrosa</i> [Weches]	<i>A. petrosa</i> <i>petrosa</i> [Stone City]	<i>A. petrosa</i> <i>petrosa</i> [Cook Mtn.]	<i>A. petrosa</i> <i>symmetrica</i>	<i>A. lisbonensis</i>	<i>A. dalli</i>
40	Maximum Minimum Mean	11 9 10.0 8.0	10 8 9.0 9.0
41	Maximum Minimum Mean 10.0 11.0
42	Maximum Minimum Mean 10.0 9.0 10.0
43	Maximum Minimum Mean
44	Maximum Minimum Mean 9.0 9.0
45	Maximum Minimum Mean	11 10 10.5 140.0
46	Maximum Minimum Mean 10.0 11.0 8.0
47	Maximum Minimum Mean 9.0
48	Maximum Minimum Mean 10.0
49	Maximum Minimum Mean
50	Maximum Minimum Mean
51	Maximum Minimum Mean 13.0 7.0
54	Maximum Minimum Mean 10.0

FIG. 12. Modified Dice-Leraas diagrams of ratio of height to width in *Athleta petrosa* stock.

due to differences in growth stages represented on adult forms; such comparisons do, however, indicate evolutionary change and show the decrease in number of ornaments from the cancellate to spinose growth stages. Nodes are reduced in *A. lisbonensis* (Aldrich), but longitudinal ribs are present which in other forms represent anterior extensions of spines. With reduction of nodes there is an increase in number of longitudinal ribs on *A. dalli* (Harris) (table 2).

Results of Student's *t*-tests of the significance of differences between mean number of body whorl ornaments are:

A. petrosa petrosa
(Conrad) [Cook Mountain] /
A. petrosa symmetrica (Conrad) $P \approx 0.01$

A. petrosa petrosa
(Conrad) [Weches] /
A. petrosa petrosa (Conrad)
[Cook Mountain] $P = 0.1$ to 0.2

A. petrosa smithi
Fisher & Rodda /
A. petrosa petrosa
(Conrad) [Weches] $P \ll 0.001$

Main groups characterized by number of body whorl ornaments within the *A. petrosa* stock are also shown in ratios of number of ornaments to height and to width (figs. 18, 19, 20). Maximum values are similar for all samples, reflecting similarity among juvenile forms of each species or subspecies. A progressive decrease in maximum and mean values occurs among successive subspecies of *A. petrosa* (Conrad). *A. lisbonensis* (Aldrich) has the greatest range of values of the stock. *A. tuomeyi* Conrad and *A. petrosa symmetrica* (Conrad) have nearly identical values for ratio of ornaments to width; *A. tuomeyi* Conrad has a greater number of ornaments but is also wider.

Ranges of ratio values of number of ornaments to height for 80 percent of the

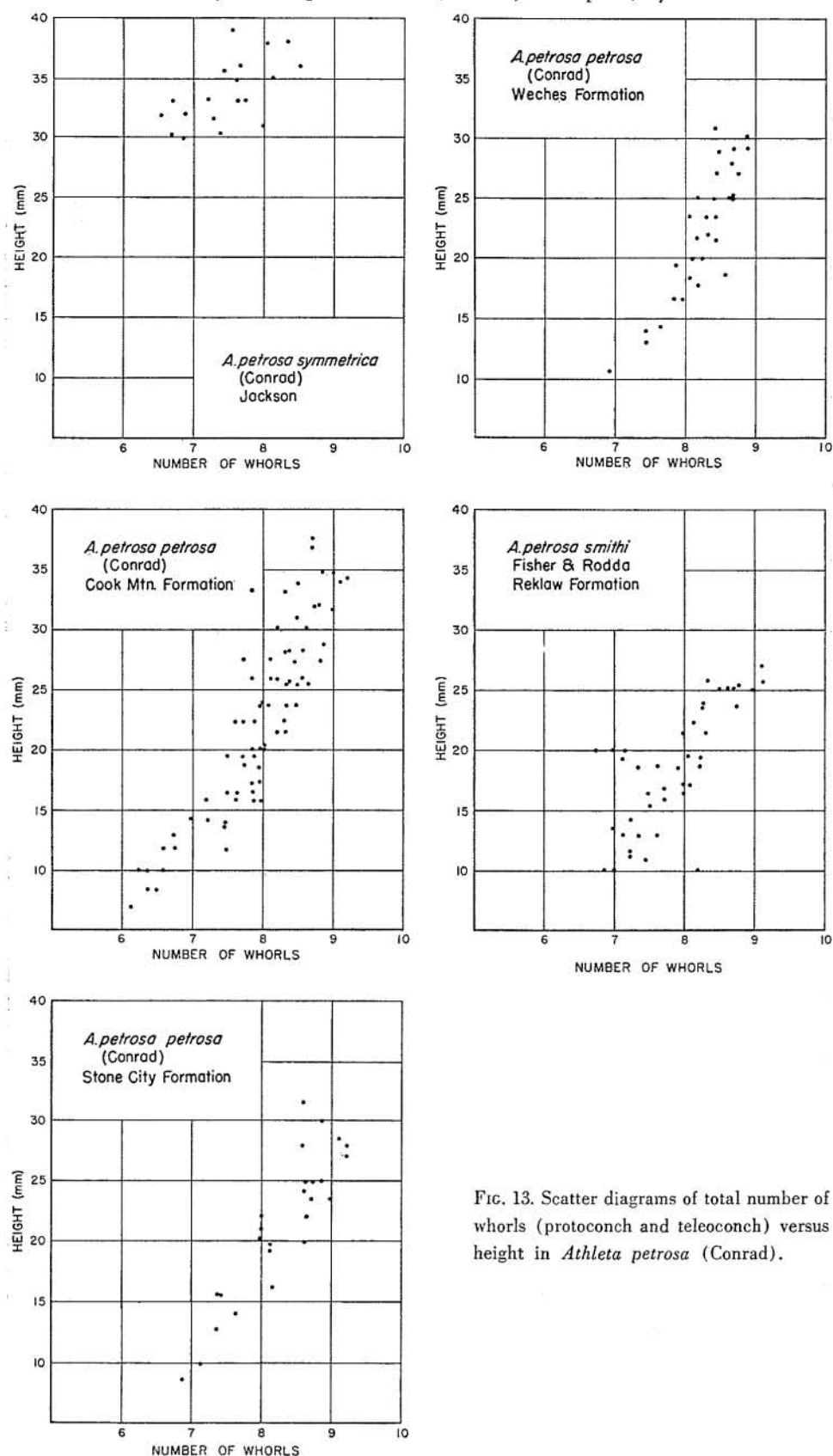


FIG. 13. Scatter diagrams of total number of whorls (protoconch and teleconch) versus height in *Athleta petrosa* (Conrad).

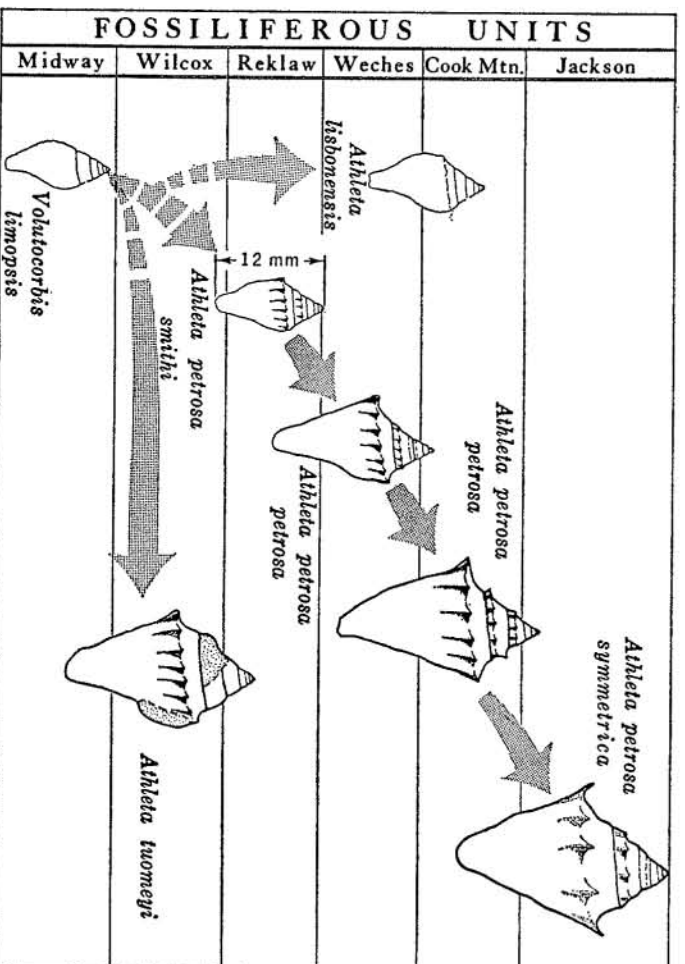


FIG. 14. Size, shape, and spinosity in *Athleta petrosa* stock. (Size indicated by scale is approximately mean value.)

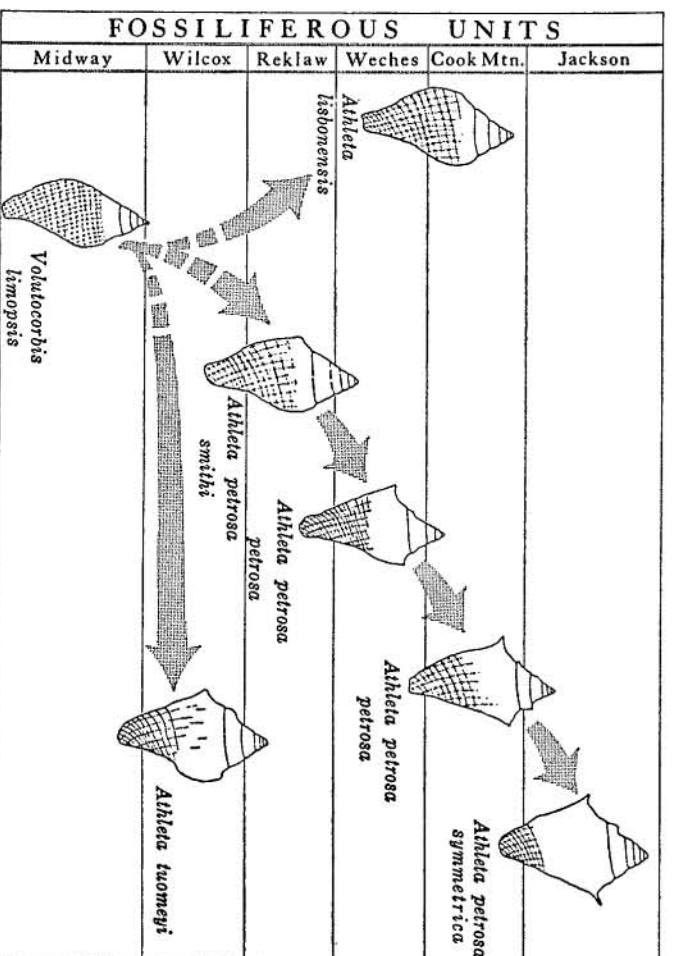


FIG. 15. Distribution of longitudinal and spiral lirae in *Athleta petrosa* stock.

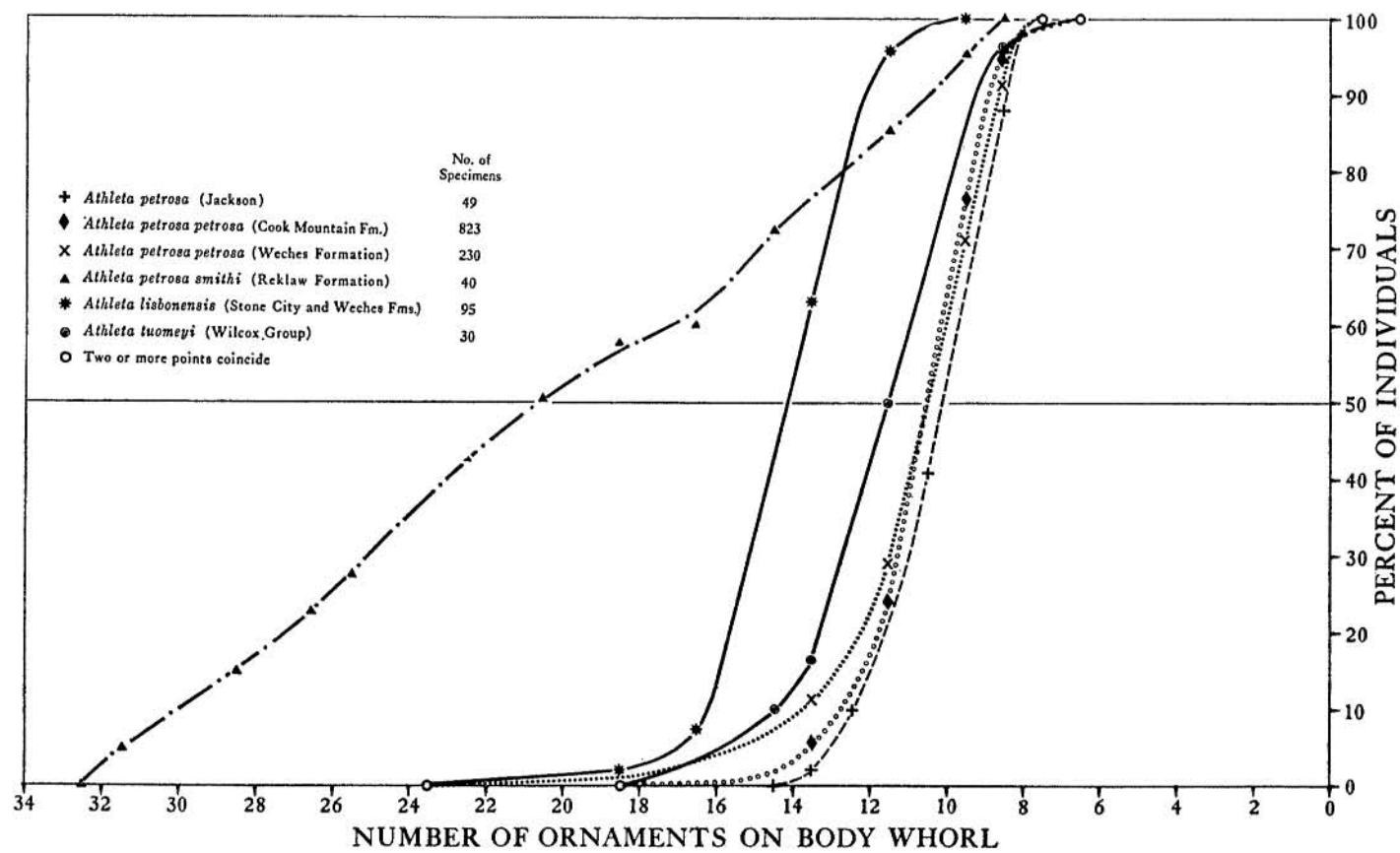


FIG. 16. Cumulative curves of ornaments on body whorl in *Athleta petrosa* stock.

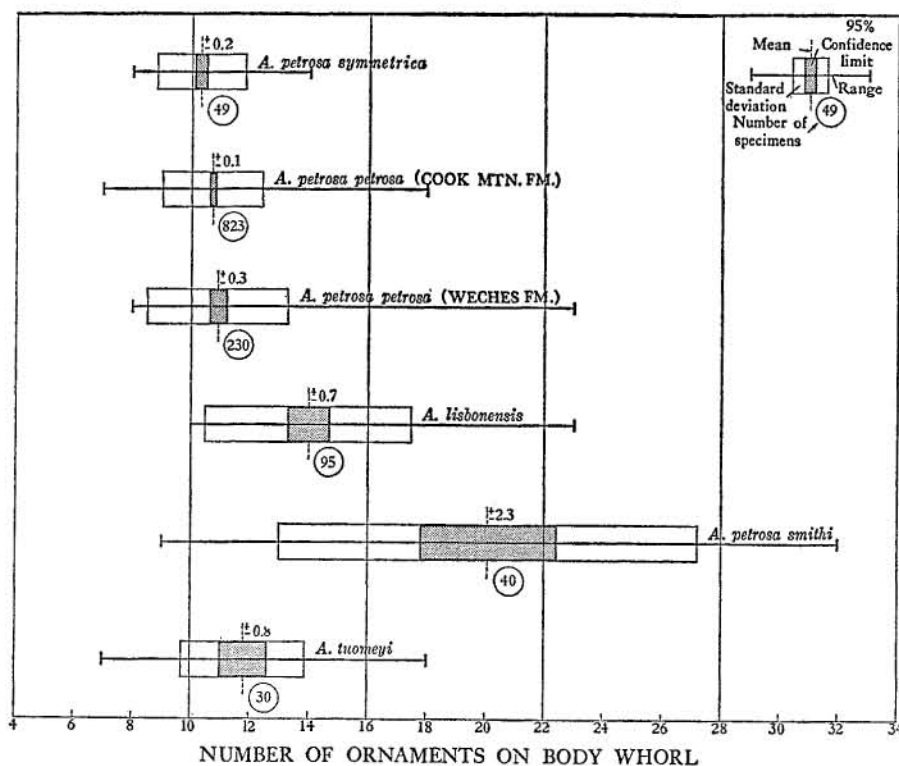


FIG. 17. Modified Dice-Leraas diagrams of number of ornaments on body whorl in *Athleta petrosa* stock.

sample (excluding highest and lowest 10 percent) are:

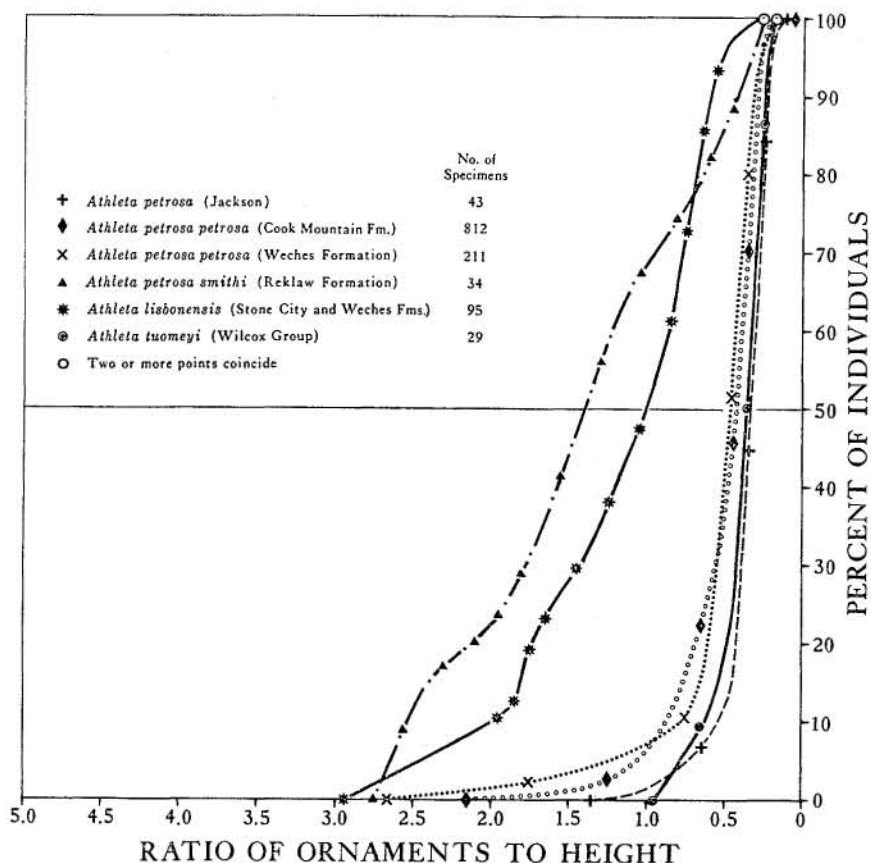
<i>A. petrosa symmetrica</i> (Conrad)	0.55 to 0.25
<i>A. petrosa petrosa</i> (Conrad) [Cook Mountain]	0.90 to 0.30
<i>A. petrosa petrosa</i> (Conrad) [Weches]	0.80 to 0.30
<i>A. petrosa smithi</i> Fisher & Rodda	2.55 to 0.40
<i>A. tuomeyi</i> Conrad	0.65 to 0.25
<i>A. lisbonensis</i> (Aldrich)	1.95 to 0.60

Results of Student's *t*-tests of the significance of the difference between means of the ratios of number of ornaments to height and number of ornaments to width are:

	Ornaments/height	Ornaments/width
<i>A. petrosa petrosa</i> (Conrad) [Cook Mountain] / <i>A. petrosa symmetrica</i> (Conrad)	$P < 0.001$	$P < 0.001$

<i>A. petrosa petrosa</i> (Conrad) [Weches] / <i>A. petrosa petrosa</i> (Conrad) [Cook Mountain]	$P \approx 0.35$	$P \approx 0.3$
<i>A. petrosa smithi</i> Fisher & Rodda / <i>A. petrosa petrosa</i> (Conrad) [Weches]	$P < 0.001$	$P < 0.001$

Trend lines drawn from contoured scatter points of width plotted against number of body whorl ornaments (Pl. VI, pocket) characterize three main groups within the *A. petrosa* stock. Groups differ in amount and rate of ornament reduction on body whorls. Trend lines for specimens of each subspecies or species having more than 15 ornaments on the body whorl show little curvature or change, reflecting uniformity of growth patterns among juveniles throughout the stock. Juvenile-type growth pattern for the stock persists into adult forms of *A. petrosa smithi* Fisher & Rodda, indicating the lower position of that subspecies within the phyletic species *A.*

FIG. 18. Cumulative curves of ratio of ornaments on body whorl to height in *Athleta petrosa* stock.

petrosa (Conrad). The trend line for Queen City forms of *A. petrosa* (Conrad) indicates a pattern transitional to *A. petrosa smithi* Fisher & Rodda and later forms of *A. petrosa* (Conrad). In *A. petrosa petrosa* (Conrad) and *A. petrosa symmetrica* (Conrad), there is a reduction in number of ornaments for a given size and also a progressive decrease in the rate of ornament reduction with increase in size. *A. petrosa symmetrica* (Conrad) has a trend line similar in shape to *A. petrosa petrosa* (Conrad), though a few forms are relatively thinner (contour scatter diagrams of height against width, Pl. VI, pocket) than *A. petrosa petrosa* (Conrad) and accordingly have a slightly greater density of ornaments; thin forms are from a single locality (La-28). The trend line of *A. tuomeyi* Conrad is similar in shape to *A.*

petrosa petrosa (Conrad) and *A. petrosa symmetrica* (Conrad), indicating similar patterns; *A. tuomeyi* Conrad has a higher density of ornaments. Trend line of *A. lisbonensis* (Aldrich) is similar in shape to *A. tuomeyi* Conrad and advanced forms of *A. petrosa* (Conrad) but differs in showing a pattern with a more rapid decrease in rate of ornament reduction. Change in number of ornaments on the body whorl with size is allometric and contrasts with the isometric pattern shown in diagrams of height against width (Pl. IV, pocket).

Variation in ornamentation patterns among individuals within a single population of *A. petrosa* (Conrad) is similar to change in ornamentation patterns of individuals of *A. petrosa* (Conrad) in evolutionary sequence. Ornamentation pattern is based on plots of number of longitudinal

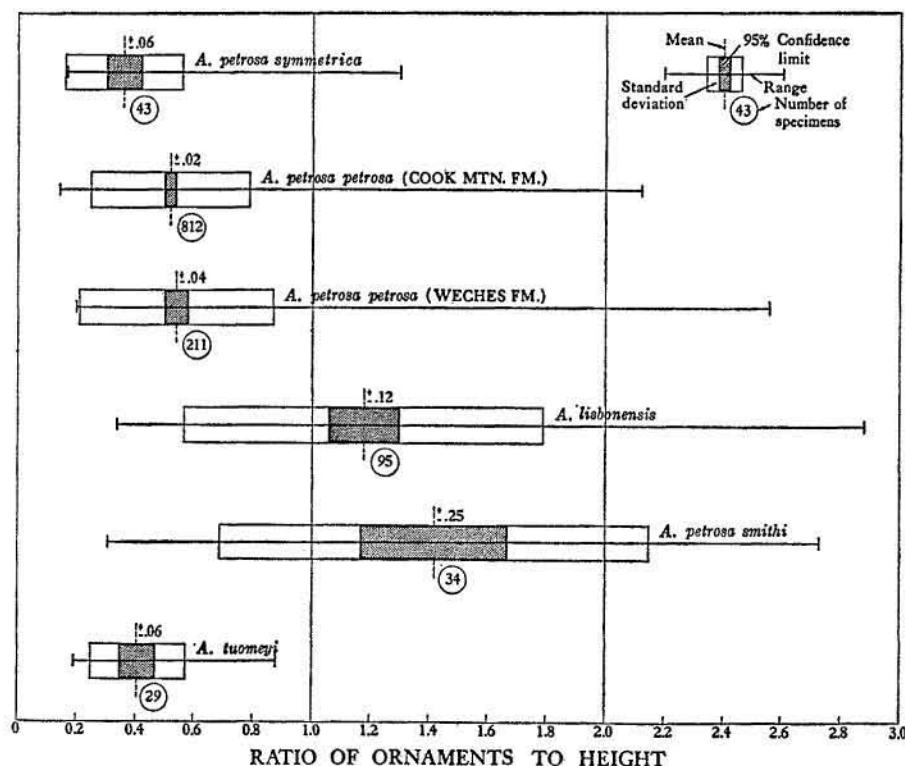
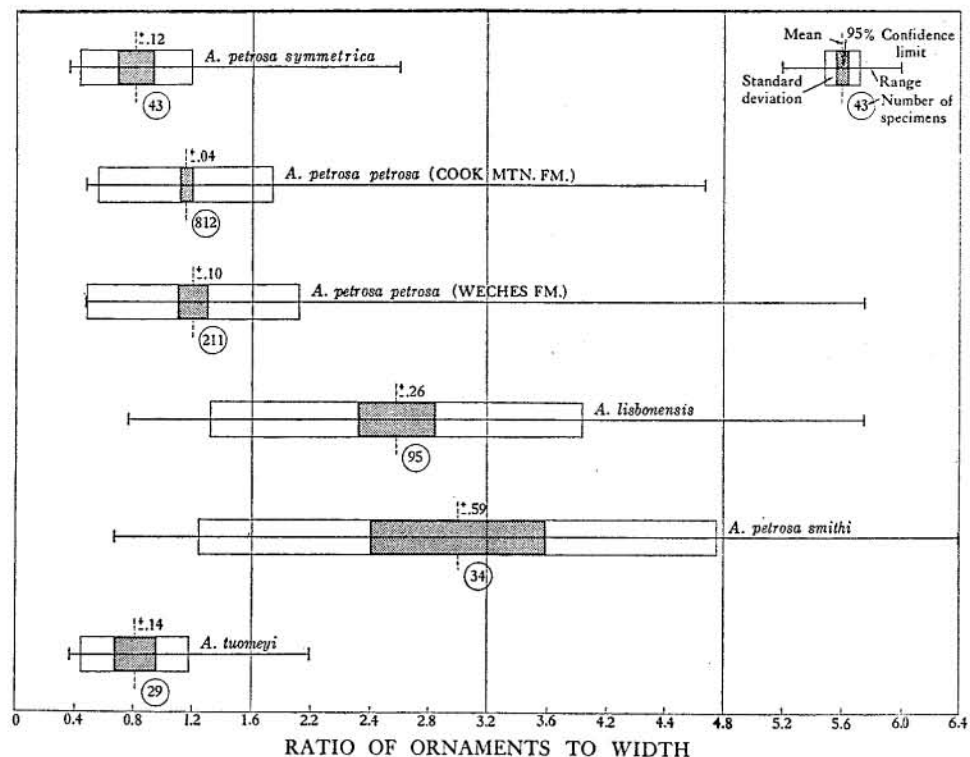


FIG. 19. Modified Dice-Leraas diagrams of ratio of ornaments to height in *Athleta petrosa* stock.

ornaments per whorl versus whorl number, numbering successive whorls from protoconch anteriorly. Longitudinal ornaments on the teleoconch, beginning with a small interval (about $\frac{1}{4}$ whorl) of simple, slightly arcuate ribs, gradually increase in number per whorl reaching a maximum, in most forms, near the middle part of the teleoconch; thereafter, number of ornaments per whorl decreases (fig. 21). Maximum number of ornaments in earliest forms of the stock reflects development of a distinct cancellate stage. Commonly, this stage persists among adults of *A. petrosa smithi* Fisher & Rodda, though a few specimens of this subspecies develop a spinose stage in final whorls with a decrease in number of ornaments. A similar pattern of ornamentation increase, followed by ornament reduction, is developed on later forms of *A. petrosa* (Conrad) but with maximum number of ornaments per whorl progressively less and appearing progressively

earlier in whorl development of successive later forms. Earlier appearance of maximum ornamentation is further accentuated by progressive shortening of the protoconch among later forms of the stock. Ornamentation patterns of the first teleoconch whorls are similar for all forms of *A. petrosa* (Conrad). That part of the teleoconch with maximum number of ornaments per whorl in later forms of *A. petrosa* (Conrad) is analogous to the cancellate stage of *A. petrosa smithi* Fisher & Rodda but forms a less distinct stage. Cumulative curves of number of ornaments per whorl (fig. 22) show progressive decrease in cumulative number of ornaments among successive forms of *A. petrosa* (Conrad). Curves are essentially straight lined, except that of *A. petrosa smithi* Fisher & Rodda. Distinction of the curve of that subspecies is due to high frequency of ornaments in the cancellate stage.

FIG. 20. Modified Dice-Leraas diagrams of ratio of ornaments to width in *Athleta petrosa* stock.

As mentioned previously, Stone City individuals of *A. petrosa petrosa* (Conrad) have a longer protoconch than immediately older forms of the stock (Weches forms of *A. petrosa petrosa*) and are an exception, at least in mean values, to the general trend of protoconch reduction. Stone City forms further show an anomalous ornamentation pattern. In plots of numbers of ornaments against whorl number (fig. 21), Stone City forms of *A. petrosa petrosa* (Conrad) show a pattern on the first $1\frac{1}{2}$ teleoconch whorls identical to that of *A. petrosa smithi* Fisher & Rodda. Subsequently, curves of the two forms diverge as Stone City forms attain maximum number of ornaments early in development and thereafter closely parallel other forms of *A. petrosa petrosa* (Conrad) in ornamentation pattern; body whorl of Stone City forms is similar to body whorl of other forms of *A. petrosa petrosa* (Conrad). Anomalous features of Stone City forms are not understood, though cer-

tain of the following factors may have bearing on the problem: (1) *A. lisbonensis* (Aldrich), a divergent species of the *A. petrosa* stock, rather than *A. petrosa petrosa* (Conrad) is the dominant representative of the stock within Stone City populations; (2) a slight dichotomy exists among Stone City forms of *A. petrosa petrosa* (Conrad) with certain specimens similar in protoconch length and initial ornamentation pattern to other forms of *A. petrosa petrosa* (Conrad) and others with protoconch and initial ornamentation pattern more like those of earlier forms of the stock, *A. petrosa smithi* Fisher & Rodda; (3) complete fauna of the Stone City Formation is less diverse and generally reflects a more restricted environment than do faunas of such Eocene units as the Weches, Wheelock, and Hurricane Lentil of the Landrum (Stenzel, Krause, and Twining, 1957); (4) Stone City Formation is a marine unit preceding main marine

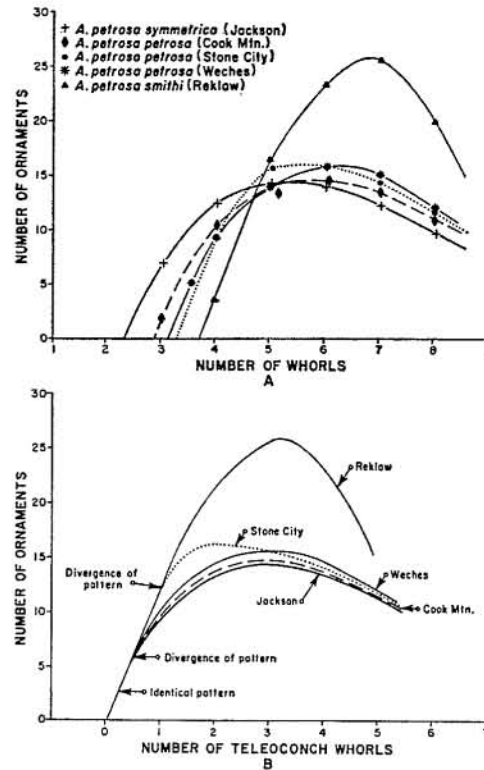


FIG. 21. Ornamentation pattern in *Athleta petrosa* (Conrad) expressed as number of longitudinal ornaments per whorl. Lines represent composite trends drawn from plots of average number of ornaments per whorl from specimens with identical length protoconchs.

transgression of the Cook Mountain; similar units generally precede all main Eocene marine transgression, though none have as well-developed marine fauna as the Stone City. Possibly certain forms of the main phyletic line of the *A. petrosa* stock, living in apparently restricted marine environments such as that represented by the Stone City Formation, evolved at a different rate than other forms of the stock and may be an example of slightly arrested evolution of one element within a generally phyletic species.

Quantitative summary of whorl analyses of *A. petrosa* (Conrad) is given in Appendix A.

Distribution of longitudinal and spiral lirae on earliest forms of *A. petrosa* (Conrad) and ancestral volutocorboid forms gen-

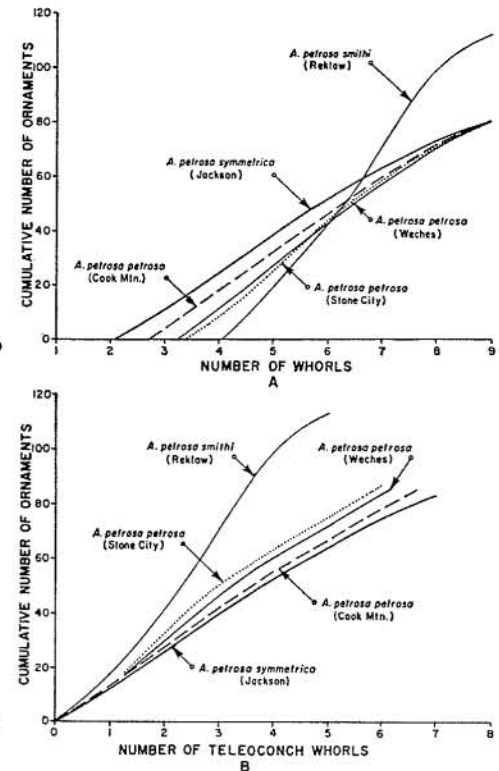
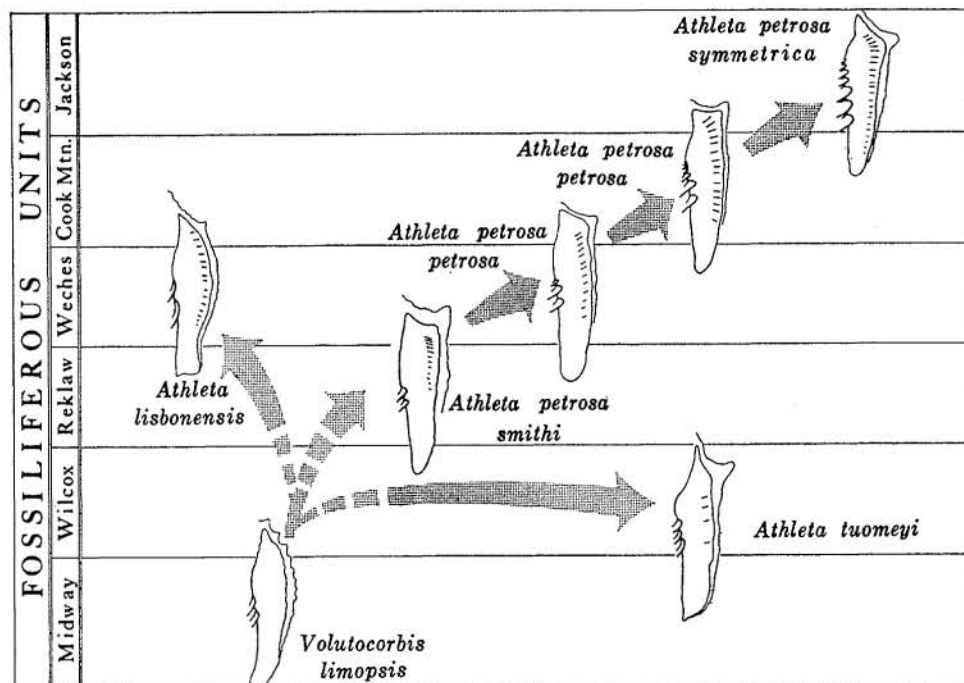


FIG. 22. Cumulative curves of number of longitudinal ornaments per whorl in *Athleta petrosa* (Conrad). Lines represent composite trends drawn from plots of average number of ornaments per whorl from specimens with identical length protoconchs.

erally is uniform, producing a cancellate sculpture. In subsequent development of the stock, lirae distribution is variable. In general, spiral lirae on the body whorl of *A. petrosa* (Conrad) tend to be accentuated anteriorly with the development of a slight siphonal canal and fasciole (fig. 15); however, at any one stage of development all variations exist from uniform distribution of lirae to complete lack of them on parts of the body whorl. In the divergent species *A. lisbonensis* (Aldrich) and *A. dalli* (Harris), lirae generally are uniform over the entire body whorl.

COLUMELLAR FOLDS

Earliest forms of *A. petrosa* (Conrad) have small columellar folds. These grad-

FIG. 23. Columellar folds and labral denticulation in *Athleta petrosa* stock.

ually increase in number and prominence in the development of the stock (fig. 23). Additional folds, appearing first as small secondary folds, are generally added posterior to the primary folds. Generally, increase in number and prominence of columellar folds corresponds to increase in shell size; however, more advanced forms always have relatively more prominent folds than older forms, even though the advanced forms may be smaller in size than certain of the older forms.

Columellar folds were counted for quantitative presentation, but due to inconsistencies in counting, the data could not be considered.

LABRAL DENTICULATION

Denticulation of the inner side of the outer lip is variable in occurrence in *A. petrosa* (Conrad) but generally is developed more extensively in later forms (fig. 23). Divergent species *A. lisbonensis* (Aldrich) and *A. dalli* (Harris) are characterized by prominent denticles but relatively small columellar folds.

Labral denticulation and columellar folds probably reflect folding of the mantle in order to accommodate to the size of the aperture of the shell (Fretter and Graham, 1962, pp. 56, 57, 62).

SHAPE

Early forms of the *A. petrosa* stock have a subfusiform shape, similar to that of their inferred *Volutocorbis* ancestor. With progressive increase in peripheral angulation and size of spines on the periphery, shape becomes substrombiform as shown in *A. petrosa petrosa* (Conrad). The youngest forms of the stock, *A. petrosa symmetrica* (Conrad), tend to have a subfusiform shape, comparable, in gross outline, to the shape of early forms of the stock (fig. 14). Divergent species of the *A. petrosa* stock, *A. lisbonensis* (Aldrich) and *A. dalli* (Harris), show a transition in shape from substrombiform to subfusiform. Fusiform or subfusiform shape in the *A. petrosa* stock is due to widening of the aperture, reduction of peripheral angulation, and loss or modification of spines.

Changes in shape are directly expressed in the shape of the aperture (table 3).

Modification of the mantle is indicated in *A. petrosa symmetrica* (Conrad) by more slender and recurved spines; this modification is accompanied by a widening of the aperture. Whether spines represent mantle folds or the position of an exhalant siphon is not known. Further modification in the arrangement of the mantle is suggested in *A. lisbonensis* (Aldrich) and *A. dalli* (Harris) by lack of spines, reduction of peripheral angulation, and by further widening of the aperture. *A. tuomeyi* Conrad has a substrombiform shape which is modified in varying degree by parietal callus.

PARIETAL CALLUS DEPOSITS

Within *A. petrosa* (Conrad) there is a tendency for the formation of a slight parietal callus; this tendency is greater in more advanced forms of *A. petrosa* (Conrad) (fig. 24) and probably corresponds to a larger mantle accompanying larger size. *A. tuomeyi* Conrad, morphologically similar to *A. petrosa* (Conrad) in most respects, differs in the gradual formation of extensive callus deposits in the parietal area of the shell. In more advanced forms of this species, the parietal callus is very thick, modifies the shape of the shell, and commonly covers and resorbs large parts of the shell. Extensive callus deposition in *A. tuomeyi* Conrad possibly represents a gerontic growth stage resulting from an acceleration and exaggeration of a physiological potential present in all members of the *A. petrosa* stock. Even slight deposits

of parietal callus are not common in *A. lisbonensis* (Aldrich) and *A. dalli* (Harris).

SUMMARY

The *Athleta petrosa* stock, as here interpreted and defined, consists of one main-line or phyletic species, *A. petrosa* (Conrad), divided into three successional subspecies: *A. petrosa smithi* Fisher & Rodda from the Reklaw Formation; *A. petrosa petrosa* (Conrad) from the Weches, Stone City, and Cook Mountain Formations; and *A. petrosa symmetrica* (Conrad) from Jacksonian rocks. *A. petrosa* (Conrad) represents progressive or phyletic evolution. Divergent or cladogenetic species of the stock include *A. tuomeyi* Conrad from the Wilcox Group; *A. lisbonensis* (Aldrich) from the Weches, Stone City, and Cook Mountain Formations; and *A. dalli* (Harris) from the Weches and Stone City Formations. We judge phyletic changes in *A. tuomeyi* Conrad and *A. lisbonensis* (Aldrich) do not warrant subspecific delineation.

A. petrosa (Conrad) is the typical species of the stock and is characterized by the following phylogenetic trends:

1. Increase in size.
2. Increase in amount of parietal callus.
3. Anterior accentuation and posterior loss of spiral lirae on body whorl.
4. Ornamentation from cancellate to nodose to spinose; spines increase in size and become slender and recurved in terminal forms.
5. Acceleration in appearance of growth stages.
6. Increase in prominence of denticulation on inside of outer lip.
7. Peripheral elements of ornamentation progressively reduced in number but progressively more prominent in expression.

TABLE 3. Average ratios of aperture length to aperture width, based on 20 specimens of each species or subspecies.

	Gross shape of shell	Aperture length/ aperture width
<i>A. petrosa symmetrica</i> (Conrad)	fusiform to strombiform	4.2
<i>A. petrosa petrosa</i> (Conrad)	strombiform	4.9
<i>A. petrosa smithi</i> Fisher & Rodda	fusiform to strombiform	4.3
<i>A. lisbonensis</i> (Aldrich)	fusiform	3.6
<i>A. dalli</i> (Harris)	fusiform	3.8
<i>A. tuomeyi</i> Conrad	fusiform to strombiform	4.3

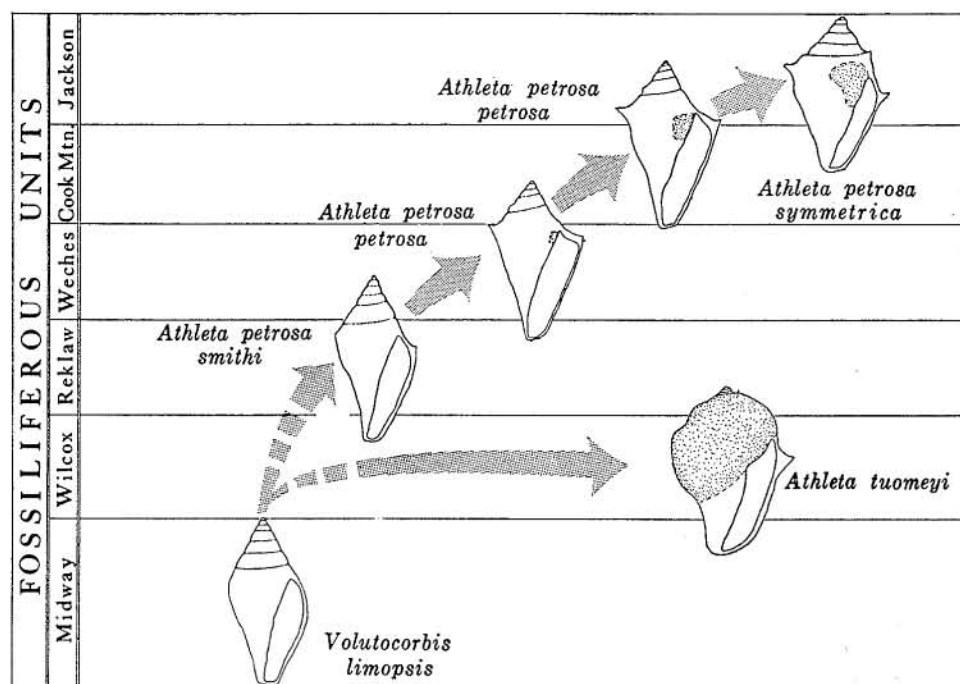


FIG. 24. Parietal callus deposits in *Athleta petrosa* stock. (Callus indicated by stippled pattern.)

8. Decrease in number of whorls and related size of protoconch.
9. Increase in number and relative prominence of columellar folds.
10. Development of shallow anterior canal and slight siphonal fasciole.
11. Development and increase in prominence of shoulder and ramp; subsutural ridge disappears.
12. Change from subfusiform to substrombiform shape; secondarily subfusiform in terminal forms.
13. Decrease in length of longitudinal ribs on body whorl.
14. Changes in shape of aperture corresponding to modification or reduction of spines and reduction of peripheral angulation.

A. tuomeyi Conrad represents an early divergence from the *A. petrosa* main line. Phylogenetic trends in *A. tuomeyi* Conrad are distinct but in many respects parallel those of *A. petrosa* (Conrad); they include:

1. Increase in size.
2. Increase in amount of parietal callus; becomes extensive on terminal forms.
3. Anterior accentuation and posterior loss of spiral lirae on body whorl.

4. Increase in size and decrease in number of prominent peripheral spines; prominent spines tend to split into smaller spines.
5. Development of denticulation on inside of outer lip.
6. Change from subfusiform to substrombiform shape; shape modified by addition of parietal callus.
7. Decrease in length of longitudinal ribs on body whorl.

The relationship of *A. lisbonensis* (Aldrich) to *A. petrosa* (Conrad) is not well known or documented, though morphologic features of *A. lisbonensis* (Aldrich) show progressive divergence from those of *A. petrosa* (Conrad). Early growth stages of the two are similar. Phylogenetic trends within *A. lisbonensis* (Aldrich) include:

1. Increase in size.
2. Changes from substrombiform to subfusiform shape.
3. Loss of shoulder and subsutural ridge with general reduction of peripheral angulation.
4. Reduction of nodes; spines do not develop.
5. Anterior extension and slight decrease in density of longitudinal ribs.
6. Development of prominent denticulation of inside of outer lip.
7. Decrease in prominence of columellar folds.

8. Anterior accentuation of spiral lirae on body whorl.
9. Widening of aperture.
10. Loss of parietal callus.

A. dalli (Harris) is a distinct form within the *A. petrosa* stock and possibly represents a divergence from *A. petrosa* (Conrad). It is characterized by the following trends:

1. Development of an adult cancellate sculpture.
2. Reduction of peripheral nodes.
3. Development of subfusiform to fusiform shape.
4. Reduction of peripheral angulation.
5. Widening of aperture.
6. Development of prominent denticulation on inside of outer lip.
7. Loss of parietal callus.
8. Decrease in prominence of columellar folds.

Morphologic changes are expressed in individual lineages in three main ways: (1) phyletic size increase accompanied by changes in peripheral ornamentation, columellar folds, longitudinal ribs, lirae, labral denticulation, and anterior siphonal canal and fasciole; phyletic size increase is, in turn, apparently controlled by phyletic changes in size of protoconch; (2) phyletic changes at least partly independent of phyletic size increase, mostly involving changes in gross shape, aperture shape, and position of spines; and (3) terminal addition of gerontic features, mainly deposition of parietal callus.

Similarity of growth and phyletic features in *A. petrosa* (Conrad) are judged by similarity of trends in growth series of single populations, whorl development of single specimens, and trends shown in comparing similar size individuals from successive stratigraphic levels. Relationships are well shown in comparison of ornamentation patterns of successional forms. All show similar development in ornamentation, with an initial ribbed stage, followed by a stage with maximum number of ornaments per whorl (represented by a distinct cancellate stage in earliest forms), and terminated by a spinose stage characterized by increase in size and reduction in number of ornaments. Among certain forms of *A. petrosa smithi* Fisher & Rodda, earliest subspecies of *A. petrosa* (Conrad),

a cancellate stage persists and forms adult ornamentation. The stage with maximum number of ornaments per whorl, considered analogous to a cancellate stage, decreases in number of ornaments per whorl, becomes less distinct, and appears progressively earlier in whorl development among successively later forms of *A. petrosa* (Conrad). Further, a subsutural keel developed on part of the whorls of earliest forms of *A. petrosa* (Conrad) is not present on later subspecies; the ribbed stage is indistinct on some terminal individuals of the species.

Length of protoconch and early teleoconch ornamentation of Stone City individuals of *A. petrosa* (Conrad) are not consistent with inferred general phyletic trends of that species; however, anterior whorl development, morphologic features on the body whorl, and size of these forms are intermediate to preceding and subsequent divisions of *A. petrosa petrosa* (Conrad). Possibly Stone City individuals represent ecologic selection or an arrested element within the phyletic or main-line species, *A. petrosa* (Conrad).

Main evolutionary features of the *A. petrosa* stock are summarized diagrammatically in Plate II (pocket).

GENERAL LIMITATIONS

In an attempt to document quantitatively an evolutionary sequence such as the *A. petrosa* stock, several limitations are apparent: bias of a geologic nature, bias resulting from sampling and utilization of existing collections, and limitations in determining biologic significance of certain statistical analyses.

Collection bias can be reduced by collecting all specimens of a given fossil in a large, standardized volume of rock. This was attempted for two localities, B.E.G. 113-T-9 (Cook Mountain Formation) and B.E.G. 173-T-17 (Weches Formation). Approximately 2 cubic feet of bulk sample were taken from main fossiliferous horizons at each locality; in all cases an insufficient number of specimens were recovered. From study of bulk samples and computa-

tions made from field data, an exceedingly large bulk sample (approximately 1 cubic yard of the most fossiliferous horizon) would be needed to yield a statistically valid sample. Another attempt was made to reduce sampling bias by collecting all visible specimens of *A. petrosa* (Conrad) on the outcrop of a fossiliferous unit. A fossiliferous, glauconitic marl at B.E.G. locality 113-T-9 (Stenzel, 1940, bed 1) was examined for about 100 yards along the outcrop, and 62 specimens of *A. petrosa* (Conrad) were collected. Specimens in this sample have about the same size range as specimens in existing collections from this locality, but the mean size of the existing sample (height, 25.1 mm) is larger than the mean size of the later sample (height, 21.5 mm), indicating a bias to large specimens in the existing collections. It is probable that this bias applies to most of our collections; information provided by size measurements alone must be considered largely as sample description and used only with discretion as a basis for phylogenetic interpretation.

In addition to collecting bias, there is an inherent geological bias, including such factors as selective fossilization, state of preservation, reworking, transport, sorting, and mixing, which affect the sample before it is collected. Most of these limitations can be overcome by careful examination of the preservation of the fossils, the orientation of the fossils in the rock, and associated fossils. Probably most specimens in our collections have been transported short distances, though preservation generally is not affected.

Assuming a living population could be sampled adequately, comparison of size frequency distributions of samples from different localities would not be entirely justified as a basis of phylogenetic interpretation. As each sample represents a part of a growth series, only specimens of the same size or the same growth stage throughout the growth series should be compared (Joysey, 1959). We have noted stages in the ontogenetic development of peripheral ornamentation and also have recorded size as a function of growth stage

for samples of *A. petrosa* (Conrad) from several localities (Appendix A, Whorl Analyses). Results of these studies generally substantiate conclusions of evolutionary trends based on size and peripheral ornamentation.

Nonfossiliferous or incomplete stratigraphic sections are additional geologic limitations. The Eocene sequence of the Gulf Coast Province largely consists of alternations of thin, marine, mostly glauconitic, fossiliferous units, and thick, mostly nonfossiliferous units. Nonfossiliferous units were deposited rapidly in contrast to relatively slow deposition of the fossiliferous units; accordingly, gaps in the fossil record are not great. Locally, fossiliferous lenses within generally nonfossiliferous sequences contain forms intermediate to those in main fossiliferous units above and below, e.g., Queen City forms of *A. petrosa* (Conrad) intermediate to *A. petrosa smithi* Fisher & Rodda and *A. petrosa petrosa* (Conrad).

Evaluation of evolutionary significance of variation due to paleoecology and paleogeography is difficult because of a paucity of data on depositional environments of Eocene rocks. Possibly *A. dalli* (Harris) and *A. lisbonensis* (Aldrich) can be interpreted as ecologic variants of *A. petrosa* (Conrad) rather than as divergent species. Paleoecologic evidence is lacking. There is some suggestion that part of the variation in *A. petrosa* (Conrad) is due to environment. Specimens of *A. petrosa* (Conrad) from the Stone City Formation, which represents a relatively restricted environment (Stenzel et al., 1957), have longer protoconchs (in number of whorls) and more peripheral ornaments than do either Weches or Cook Mountain specimens. There is also a suggestion that specimens of *A. petrosa* (Conrad) from sandstone beds, such as locality 21-T-6 at the mouth of the Little Brazos River, have consistently different ornamentation than specimens from clay beds. This ornamentation difference has not been confirmed as specimens in sandstone generally are poorly preserved.

Determining biologic significance of

certain statistical tests and analyses commonly is difficult; we have included and noted data we judge to be significant, as well as certain data of which significance is not apparent. Interpretations of certain, seemingly significant, features of shell morphology in terms of anatomical functions, life history, and life processes are limited by lack of information about related living forms. For example, larval history as reflected by successive changes in the protoconch of *A. petrosa* (Conrad) seems especially significant to over-all evo-

lution of the stock; yet little is known of the larval history of living volutid gastropods. According to Anderson (1960, p. 26), "only one species [of Volutidae] has been investigated as to its life history." This is the large Australian Baler shell *Melo umbilicatus* Sowerby, which bears little relationship to *Athleta*.

Certain morphologic features, such as gross form or shape of individual morphologic elements, are not amenable to quantitative treatment and must be stated almost entirely in qualitative terms.

SYSTEMATIC DESCRIPTIONS

Brief descriptions are included of genera to which Gulf Coastal Plain species of *Athleta petrosa* stock have been assigned. More detailed discussion is given of the genus *Athleta*, which we judge to be the correct generic assignment of this stock.

Phylum MOLLUSCA
Class GASTROPODA
Order NEOGASTROPODA
Family VOLUTIDAE

Genus *VOLUTA* Linnaeus, 1758

Author.—Linnaeus, C., 1758, *Systema Naturae per regna tria naturae, etc.*, ed. 10, tomus 1, p. 729.

Type species.—*Voluta musica* Linnaeus, 1758.

Type designation.—Subsequent by Montfort, D. de (1810) *Conchyliologie systématique et classification méthodique des coquilles*, Tome second, Coquilles univalves, non cloisonnées, p. 551.

First description of type species.—Linnaeus, C. (1758) *Systema naturae per regna tria naturae, etc.*, ed. 10, tomus 1, p. 733, no. 370.

Type locality and horizon of type species.—Living in the Caribbean area.

Illustration.—*Voluta musica* Linnaeus, 1758; B.E.G. No. 35274; Recent; Barbados, West Indies (Pl. VII, fig. 7).

Description.—Shells thick, commonly with low spire; periphery acutely angulate and nodose or spinose; siphonal canal wide, deep and recurved; columella with 5 or more prominent primary folds and several secondary folds posterior to primary folds; outer lip without denticles and with slight anterior taper; neck short, about one-fourth the height of the shell; smooth protoconch of 3 to 3½ whorls followed by adult ornamentation of 8 to 10 broad, rounded longitudinal ribs per whorl (fig. 25); few spiral lirae on body whorl, most prominent and most abundant on the anterior part of the body whorl. (Description of *Voluta musica* Linnaeus, 1758.)

Range of genus.—Eocene to Recent (Newton, 1906, p. 103).

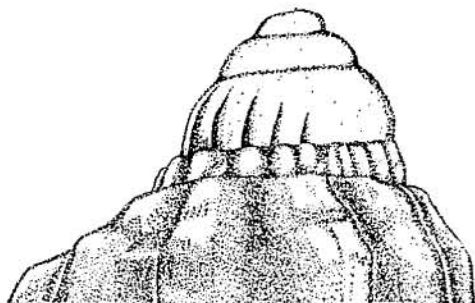


FIG. 25. Protoconch and posterior teleoconch whorls of *Voluta musica* Linnaeus, 1758, type species of *Voluta* Linnaeus, 1758.

Genus *PLEJONA* Röding, 1798

Author.—Röding, P. F., 1798, *Museum Boltenianum sive catalogus cimeliorum, etc.*, pt. 2, p. 59.

Type species.—*Voluta ebraea* Linnaeus, 1758.

Type designation.—Subsequent by Dall, W. H. (1889) Reports on the results of dredging, etc., XXIX—Report on the Mollusca, Pt. II—Gastropoda and Scaphopoda; Harvard Coll., Mus. Comp. Zool., Bull., vol. 18, p. 146. Stewart (1926, p. 408) first called attention to this previously overlooked designation. See also Winkworth (1945).

First description of type species.—Linnaeus, C. (1758) *Systema naturae per regna tria naturae, etc.*, ed. 10, tomus 1, p. 733, no. 372.

Type locality and horizon of type species.—Living "in tropical and subtropical parts of the Western Atlantic" (Dodge, 1955, p. 126).

Remarks.—*Plejona* Röding, 1798, is a subjective synonym of *Voluta* Linnaeus, 1758 (Stewart, 1926, p. 408; Dodge, 1955, p. 127).

Genus *VOLUTILITHES* Swainson, 1831

Author.—Swainson, W., 1831, *Zoological illustrations, etc.*, ser. 2, vol. 2, pl. 53.

Type species.—*Voluta muricina* Lamarck, 1803.

Type designation.—Subsequent by Dall, W. H. (1906) Notes on some names in the

Volutidae: Nautilus, vol. 19, no. 12, p. 143. (Also see Newton, 1906.)

First description of type species.—Lamarck, J. B. P. A. de (1803) Sur les fossiles des environs de Paris: Paris Mus. Nat. Hist., Ann., vol. 1, p. 477.

Type locality and horizon of type species.—Paris Basin, Lutetian (Eocene).

Illustration.—*Volutilithes muricina* (Lamarck, 1803); B.E.G. No. R18328; Lutetian; Boury, France (Pl. VII, fig. 10); B.E.G. No. R18058; Lutetian; Grignon, France (Pl. VII, fig. 11).

Description.—Shell thick, tall; spire about one-half the height of shell; obtusely angulated periphery bears spines at the apex of thick longitudinal ribs on body whorl; anterior canal wide, but shallower and less recurved than in *Voluta*; spiral sculpture consists of spiral lirae covering entire shell with a few coarse lirae near the siphonal fasciole; columella with one prominent fold and several minor folds posterior to the prominent one; outer lip with only slight anterior taper and without denticles; neck about one-fourth the height of the shell; smooth 2-whorled protoconch followed by adult ornamentation of 8 or 9 rounded longitudinal ribs per whorl (fig. 26).

Remarks.—*Volutilithes* Swainson, 1831, possibly is invalidated by Article 20 of the

International Code of Zoological Nomenclature which states that if *-ithes* is substituted for the original termination of the genus-group name, the modified name, if applied only to fossils, is not available unless there is clear intent to establish a distinct genus or subgenus. Swainson (1831, pl. 53) stated, "The fourth principal division of the Lamarckian Volutes has hitherto been found only in a fossil state, unless, indeed, the *Voluta Braziliensis* really belongs to this type."

Species definitely included in *Volutilithes* by Swainson were known only as fossils, but he did not exclude the possibility of a living species being assigned to this genus. The possible inclusion of a Recent species, and the statement that this is "The fourth principal division of the Lamarckian Volutes. . .," seem to indicate intent to establish a distinct genus not necessarily restricted to fossil shells. We conclude that *Volutilithes* Swainson, 1831, is available under Article 20.

Species assigned to *Volutilithes* by Swainson (1831) were *V. muricina* Lamarck and *V. pertusa* Swainson. Swainson gave as the type of his genus, "*Voluta musicalis* ?, Lam.," and further stated, "The pre-eminent type may probably be the *V. musicalis* of Lamarck. . . ." Swainson was familiar with *V. musicalis* Lamarck only by description and figure. The equivocal nature of this designation does not seem to conform to Articles 67(b), 67(c), and 68(a) of the Code of Zoological Nomenclature, and *V. musicalis* Lamarck probably cannot be the type species. An unequivocal designation of *V. muricina* as type of *Volutilithes* was made by Dall (1906, p. 143). If *V. musicalis* is considered the type of *Volutilithes*, then Swainson's genus is a subjective synonym of *Voluta* Linnaeus because *V. musicalis* Lamarck commonly is considered a synonym of *V. musica* Linnaeus, the type of *Voluta*. If not synonymous, the two species are at least similar and probably of not more than specific difference. If this taxonomic procedure is followed, the species now assigned to *Volutilithes* would take the name *Eosephaea* Fischer, 1883, the type species

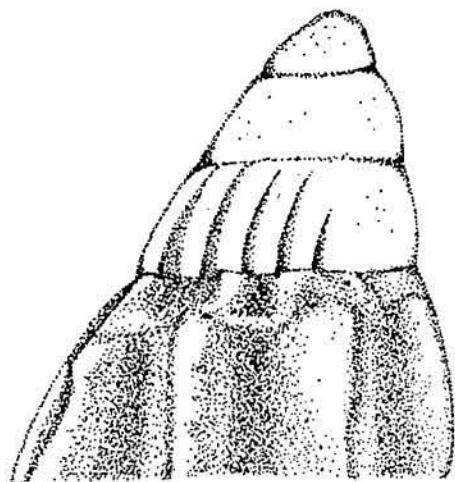


FIG. 26. Protoconch and posterior teleoconch whorls of *Voluta muricina* Lamarck, 1803, type species of *Volutilithes* Swainson, 1831.

of which is *V. muricina* Lamarck by original designation (Fischer, 1883, p. 607).

Range of genus.—Cretaceous (Turonian) to Eocene (Newton, 1906, p. 103).

Genus *VOLUTOCORBIS* Dall, 1890

Author.—Dall, W. H., 1890, Contributions to the Tertiary fauna of Florida, etc., Part 1: Wagner Free Inst. Sci., Trans., vol. 3, pt. 1, p. 75.

Type species.—*Volutilithes limopsis* Conrad, 1860.

Type designation.—Original.

First description of type species.—Conrad, T. A. (1860) Descriptions of new species of Cretaceous and Eocene fossils of Mississippi and Alabama: Acad. Nat. Sci. Philadelphia, Jour., 2d ser., vol. 4, p. 292, pl. 47, fig. 24.

Type locality and horizon of type species.—Probably from Matthews Landing on the Alabama River, Wilcox County, Alabama. Matthews Landing Marl Member, Porters Creek Formation (Paleocene).

Illustration.—*Volutocorbis limopsis* (Conrad, 1860); B.E.G. No. 35273; Naheola Formation; B.E.G. locality Ala-6 (Pl. VII, figs. 1, 2).

Description.—Shell less thick than *Voluta*, tall, fusiform to subfusiform; spire about one-third the height of shell; periphery rounded, nonangulate, with 10 or more longitudinal, fine to coarse ribs; numerous fine spiral lirae form nodes at intersection with longitudinal ribs; sculpture generally cancellate; anterior siphonal canal narrow, shallow, and slightly recurved, as in *Volutospina*; outer lip with gradual taper from shoulder anteriorly, and with no or few faint denticles; anterior end of columella pointed, thin; neck long, about one-third the height of the shell; columella with 2 subequal prominent folds, largest anteriorly, and commonly with several small secondary folds posteriorly; smooth protoconch of 4 to 5 whorls followed by a ribbed stage of about one-half whorl (fig. 27); cancellate sculpture of early whorls persists and characterizes the adult shell.

Range of genus.—(?) Late Cretaceous, Paleocene to (?) Recent.

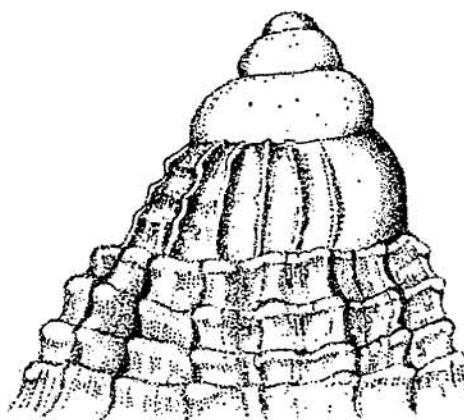


FIG. 27. Protoconch and posterior teleoconch whorls of *Volutocorbis limopsis* (Conrad, 1860), type species of *Volutocorbis* Dall, 1890.

Genus *VOLUTOSPINA* Newton, 1906

Author.—Newton, R. B., 1906, Note on Swainson's genus *Volutilithes*: Malac. Soc. London, Proc., vol. 7, p. 103 (= *Volutilithes* Swainson, 1840, not Swainson, 1831).

Type species.—*Conus spinosus* Linnaeus, 1758.

Type designation.—Original.

First description of type species.—Linnaeus, C. (1758) Systema naturae per regna tria naturae, etc., ed. 10, tomus 1, p. 715, no. 271.

Type locality and horizon of type species.—Probably from the Paris Basin. Lutetian (Eocene).

Illustration.—*Volutospina spinosa* (Linnaeus, 1758); B.E.G. No. 18492; Lutetian; Grignon, France (Pl. VII, figs. 8, 9).

Description.—Shell less thick than *Voluta*; substrombiform; spire about one-third the height of the shell; shoulder angulation near 90 degrees; about 12 spines per whorl occur on the shoulder situated at the apex of longitudinal ribs on the body whorl; numerous spiral lirae present, being prominent on the anterior half of the body whorl; anterior siphonal canal shallow, slightly recurved, narrower than in *Volutilithes*; outer lip commonly denticulate and with anterior taper; anterior end of columella narrow and pointed; neck very long, about one-third the height of the

shell; columella with 1 or 2 prominent folds well inside the aperture, and several secondary and minor folds posterior to the prominent folds; one minor fold may occur between 2 prominent folds; small smooth protoconch occupies 2 to 3 whorls followed by a ribbed stage of one-quarter to one-half whorl and a cancellate stage of 2 to 2½ whorls (fig. 28); adult ornamentation consists of spinose shoulder, ramp, and subsutural ridge which generally bears short spines opposite the larger shoulder spines.

Range of genus.—Cretaceous (Turonian) to Pliocene (Cossmann, 1899, pp. 136-137).

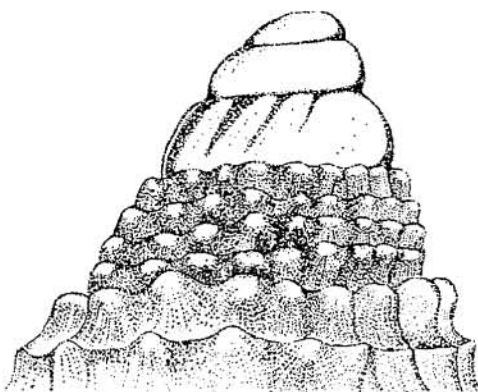


FIG. 28. Protoconch and posterior teleoconch whorls of *Volutospina spinosa* (Linnaeus, 1758), type species of *Volutospina* Newton, 1906.

Genus *ATHLETA* Conrad, 1853

- 1833 *Voluta*: Conrad, Fossil shells of the Tertiary formations of North America, vol. 1, no. 3, p. 29 (not *Voluta* Linnaeus, 1758).
- 1848 *Voluta* (in part): H. C. Lea, Catalogue of the Tertiary Testacea of the United States: Acad. Nat. Sci. Philadelphia, Proc., vol. 4, no. 4, p. 107 (not *Voluta* Linnaeus, 1758).
- 1850 *Voluta*, Linné, 1758 (in part): d'Orbigny, Prodrome de paleontologie stratigraphique universelle des animaux mollusques, etc., vol. 2, p. 352.
- 1853 *Athleta*: Conrad, Synopsis of the genera *Cassidula*, Humph., and of a proposed new genus *Athleta*: Acad. Nat. Sci. Philadelphia, Proc., vol. 6, p. 449.
- 1854 *Volutilithes*, Swains.: Conrad, Rectification of the generic names of Tertiary fossil shells: Acad. Nat. Sci. Philadelphia, Proc., vol. 7, no. 1, p. 31 (not *Volutilithes* Swainson, 1831).
- Volutilithes* Swains. (error for *Volutilithes*): Conrad, Fossil Testacea of the Tertiary green-sand marl-bed of Jackson, Miss., in Wailes, B.L.C., Report of the agriculture and geology of Mississippi, p. 289 (not *Volutilithes* Swainson, 1831).
- 1855 *Volutilithes* Swains. (error for *Volutilithes*): Conrad, Observations on the Eocene deposit of Jackson, Mississippi, etc.: Acad. Nat. Sci. Philadelphia, Proc., vol. 7, no. 7, p. 260 (not *Volutilithes* Swainson, 1831).
- 1857 *Volutilithes* Swainson (error for *Volutilithes*): Conrad, Description of Cretaceous and Tertiary fossils: U. S. and Mexican Boundary Survey, Rept., Pt. II, p. 162 (not *Volutilithes* Swainson, 1831).
- 1865 *Athleta* Conrad: Conrad, Catalogue of the Eocene and Oligocene Testacea of the United States: Amer. Jour. Conch., vol. 1, no. 1, p. 24 (as a subgenus of *Volutilithes* Swainson).
- Volutilithes*, Swainson: Conrad, Description of new Eocene shells of the United States: Amer. Jour. Conch., vol. 1, no. 2, p. 144 (not *Volutilithes* Swainson, 1831).
- 1868 *Athleta*: Conrad, Notes on Recent and fossil shells with descriptions of new genera, etc.: Amer. Jour. Conch., vol. 4, no. 4, p. 248.
- 1877 *Volutilithes*, Swainson, 1831 (in part): Gabb, Notes on American Cretaceous fossils with descriptions of some new species: Acad. Nat. Sci. Philadelphia, Proc. 1876, p. 290.
- Athleta* Con., 1953: Gabb, *ibid.*, p. 291.
- 1883 *Athleta*, Conrad: Tryon, Structural and systematic conchology, Vol. II, p. 166.
- 1890 *Volutilithes* Swainson, 1831 (error for 1840) (in part): Dall, Contributions to the Tertiary fauna of Florida, etc., Part 1: Wagner Free Inst. Sci., Trans., vol. 3, pt. 1, p. 74.
- Athleta* Conrad, 1853: Dall, *ibid.*, p. 75.
- 1895 *Volutilithes*: Harris, New and otherwise interesting Tertiary Mollusca from Texas: Acad. Nat. Sci. Philadelphia, Proc. 1895, Pt. 1, p. 67 (not *Volutilithes* Swainson, 1831).
- 1897 *Volutilithes*: Aldrich, Notes on Eocene Mollusca, with descriptions of some new species: Bull. Amer. Paleont., vol. 2, no. 8, p. 14 (not *Volutilithes* Swainson, 1831).
- 1899 *Volutilithes*, Swainson, 1840 (in part): Cossmann, Essais de paleoconchologie comparée, livr. 3, p. 135 (= *Volutospina* Newton, 1906).
- Athleta*, Conrad, 1853: Cossmann, *ibid.*, p. 140.
- 1901 *Volutilithes* Swainson: Clark and Martin, Systematic paleontology, Eocene, Mollusca: Maryland Geol. Survey, Eocene, p. 130 (not *Volutilithes* Swainson, 1831).

- 1902 *Volutilithes*: Casey, The Jackson outcrops on Red River: Science, n.s., vol. 15, p. 716 (not *Volutilithes* Swainson, 1831).
- 1905 *Volutilithes*: Burnett Smith, Senility among gastropods: Acad. Nat. Sci. Philadelphia, Proc., vol. 57, pp. 346, 347 (not *Volutilithes* Swainson, 1831).
- 1906 *Volutilithes* (in part): Burnett Smith, Phylogeny of the races of *Volutilithes petrosus*: Acad. Nat. Sci. Philadelphia, Proc., vol. 58, p. 52, et seq.
Plejona Bolten, 1798 (in part): Dall, Note on some names in the Volutidae: Nautilus, vol. 19, no. 12, p. 143.
Athleta Conrad: Cossmann, Phylogeny of the races of *Volutilithes petrosus* by Burnett Smith: Rev. Crit. de Paleozoologie, Dix. Ann., 1906, no. 4, p. 222.
- 1907 *Plejona* Bolten (in part): Dall, 1907, A review of the American Volutidae: Smithsonian Inst. Misc. Coll., vol. 48, no. 1663, p. 353.
Athleta: Burnett Smith, [Review of] "A review of the American Volutidae" by W. H. Dall: Nautilus, vol. 20, no. 11, p. 131.
Plejona (in part): Dall [Correspondence] Nautilus, vol. 20, no. 12, p. 143.
Athleta Conrad: Burnett Smith, A new species of *Athleta* and a note on the morphology of *Athleta petrosa*: Acad. Nat. Sci. Philadelphia, Proc., vol. 59, pp. 229-230.
- 1909 *Volutilithes* Swainson: Grabau and Shimer, North American index fossils, p. 790 (not *Volutilithes* Swainson, 1831).
Athleta: Cossmann, Essais de paleoconchologie comparée, livr. 8, pp. 209-210.
- 1937 *Athleta* Conrad, 1853: Palmer, The Claibornian Scaphopoda, Gastropoda, and dibranchiate Cephalopoda of the southern United States: Bull. Amer. Paleont., vol. 7, no. 32, p. 370.
- 1939 *Volutospina*: Stenzel, The geology of Leon County, Texas: Univ. Texas Pub. 3818, pp. 112, 156.
- 1943 *Athleta* Conrad, 1853: Wenz, Gastropoda, Handbuch der Paläozoologie, Band 6, Teil 6, pp. 1319-1320, 1321.
- 1944 *Volutocorbis* Dall 1890 (in part): Shimer and Shrock, Index fossils of North America, p. 508.
- 1945 *Volutocorbis* Dall (in part): Gardner, Mollusca of the Tertiary formations of north-eastern Mexico: Geol. Soc. Amer. Mem. 11, p. 222.
Volutospina Bullen-Newton (in part): Gardner, *ibid.*, p. 224.
Eoathleta Gardner, *ibid.*, p. 227.
- 1947 *Athleta* Conrad, 1853: Palmer, The Mollusca of the Jackson Eocene, etc. Second section, Univalves: Bull. Amer. Paleont., vol. 30, no. 117, p. 391.
- 1952 *Athleta* Conrad: Moore, Lalicker and Fischer, Invertebrate fossils, p. 318.
- 1953 *Athleta* Conrad, 1853: Palmer, Eocene mollusks from Citrus and Levy counties, Florida, Part 2, Gastropoda: Florida Geol. Survey Bull. 35, pp. 34-35.
- 1954 *Volutovetus*: Pilsbry and Olsson, Systems of the Volutidae: Bull. Amer. Paleont., vol. 35, no. 152, p. 22.
- Type species*.—*Voluta rarispina* Lamarck, 1811.
- Type designation*.—Subsequent by Dall, W. H. (1890) Contributions to the Tertiary fauna of Florida, etc., Part 1: Wagner Free Inst. Sci., Trans., vol. 3, pt. 1, p. 75.
- First description of type species*.—Lamarck, J. B. P. A. de (1811) Sur la détermination des espèces parmi les animaux sans vertèbres, et particulièrement parmi les mollusques testacés: Paris Mus. Nat. Hist., Ann., vol. 17, p. 79 [not seen].
- Type locality and horizon of type species*.—Aquitaine Basin, France. Burdigalian (Miocene).
- Illustration*.—*Athleta rarispina* (Lamarck, 1811); B.E.G. No. 35265; Burdigalian; Cabarines (Landes), southwestern France (Pl. VII, figs. 5, 6).
- Description*.—Shell moderately thick, like *Volutospina*, substrombiform to subfusiform; spire about one-fifth to one-third the height of the shell; shoulder angulate and commonly spinose, with spines at apex of longitudinal ribs; longitudinal ribs prominent to faint or absent; numerous spiral lirae anterior to the shoulder and tend to be accentuated anteriorly on the body whorl; spiral lirae rare or absent on ramp; siphonal canal and outer lip as in *Volutospina*; neck long, at least one-third the height of the shell; siphonal canal wide, shallow, slightly recurved; columella with 2 or 3 subequal prominent folds, largest anteriorly, and commonly with several secondary folds posterior to prominent folds. Smooth protoconch of $1\frac{1}{2}$ to $4\frac{1}{2}$ whorls is followed by ribbed stage of one-half to one-fourth whorl and cancellate stage of 1 to $1\frac{1}{2}$ whorls; most common adult ornamentation consists of nodose to spinose shoulder with ramp, and subsutural ridge without spines (fig. 29); spines may be absent and shoulder re-

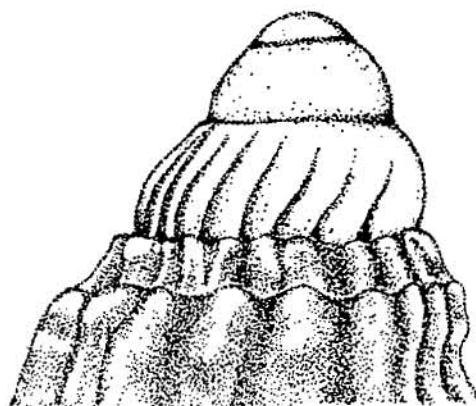


FIG. 29. Protoconch and posterior teleoconch whorls of *Athleta rarispina* (Lamarck, 1811), type species of *Athleta* Conrad, 1853.

duced. Certain forms of *Athleta* have extensive, thick callus deposits.

Remarks.—*Athleta* Conrad, 1853, is the oldest name for the group of Tertiary volutid gastropods that includes *Voluta petrosa* Conrad, 1833, and associated forms. The early whorls and the development of ornamentation of *A. rarispina* (Lamarck), the type species, are very similar to those of *A. petrosa* (Conrad) and *A. tuomeyi* Conrad. Also columellar folds are similar in size and number, and all three species tend to have parietal callus deposits. This is especially true of *A. rarispina* (Lamarck) and *A. tuomeyi* Conrad.

Volutospina Newton, 1906, resembles *Athleta*, but the early whorls are different; a cancellate stage is retained longer in *Volutospina*. Also in *Volutospina* the subsutural ridge generally bears a row of prominent nodes, in some cases spines, and the columellar folds are much less prominent than in *Athleta*.

We can make no statement regarding the generic phylogeny of this group, *Athleta*, *Volutospina*, etc. If future work should favor a more local application of genera, or perhaps subgenera, the name *Eoathleta* Gardner, 1945, is available for this group in the Atlantic and Gulf Coastal Plains. The type species of *Eoathleta* is *A. tuomeyi* Conrad, 1853, by original designation (Gardner, 1945, p. 227). Generic assignment of the species and subspecies treated

here to *Athleta* is on the basis of shell morphology; no close phyletic relation between these local species and subspecies to *Athleta rarispina* (Lamarck) is implied.

Range of genus.—(?) Paleocene, Eocene to Miocene.

ATHLETA PETROSA (Conrad, 1833)

Additional citations of *Athleta petrosa* (Conrad) are starred (*) in the Selected Bibliography.

- 1833 *Voluta petrosa*: Conrad, Fossil shells of the Tertiary formations of North America, vol. 1, no. 3, p. 29. (August 29, 1833, *vide* Wheeler, 1935, p. 104.)
Voluta parva: Isaac Lea, Contributions to geology, p. 173, pl. 6, fig. 181. (December 2, 1833, *vide* Wheeler, 1935, p. 105.)
Voluta vanuxemi: Isaac Lea, *ibid.*, p. 173, pl. 6, fig. 182. (December 2, 1833, *vide* Wheeler, 1935, p. 105.)
- 1834 *Voluta petrosa* Conrad: Conrad, Catalogue of the fossil shells of the Tertiary formations of the United States; appendix to Morton, S. G., Synopsis of the organic remains of the Cretaceous group of the United States, p. 5.
- 1835 *Voluta petrosa*: Conrad, Fossil shells of the Tertiary formations of North America, vol. 1, no. 3 (reprint), p. 41, pl. 16, fig. 2.
- 1846 *Voluta petrosa* Conrad: Conrad, Observations on the Eocene formation of the United States, etc.: Amer. Jour. Sci., 2d ser., vol. 1, p. 220.
- 1848 *Voluta parva* Lea: H. C. Lea, Catalogue of the Tertiary Testacea of the United States: Acad. Nat. Sci. Philadelphia, Proc., vol. 4, no. 4, p. 107.
Voluta petrosa Conrad: H. C. Lea, *idem*.
Voluta vanuxemi Lea: H. C. Lea, *idem*.
- 1850 *Voluta petrosa* Conrad, 1833: d'Orbigny, Prodrome de paleontologie stratigraphique universelle des animaux mollusques, etc., vol. 2, p. 353.
- 1854 *Volutalithes dumosa* Conrad: Conrad, Fossil Testacea of the Tertiary green-sand marl-bed of Jackson, Miss., in Wailes, B.L.C., Report on the agriculture and geology of Mississippi, p. 289, pl. 16, fig. 1.
Volutalithes symmetrica Con.: Conrad, *ibid.*, p. 289, pl. 15, fig. 6.
- 1865 *Volutalithes dumosa* Conrad: Conrad, Catalogue of the Eocene and Oligocene Testacea of the United States: Amer. Jour. Conch., vol. 1, no. 1, p. 23.
Volutalithes impressa Conrad: Conrad, *idem* (nomen nudum); Descriptions of new Eocene shells of the United States: Amer. Jour. Conch., vol. 1, no. 2, p. 144; Descriptions of new Eocene shells, and references with figures to published spe-

- cies: Amer. Jour. Conch., vol. 1, no. 3, p. 211, pl. 20, fig. 3.
Volutilithes indenta Conrad: Conrad, Amer. Jour. Conch., vol. 1, no. 1, p. 23 (*nomen nudum*); vol. 1, no. 2, p. 144; vol. 1, no. 3, p. 221, pl. 21, fig. 10.
Volutilithes petrosa Conrad: Conrad, Amer. Jour. Conch., vol. 1, no. 1, p. 23.
Volutilithes symmetrica Conrad: Conrad, Amer. Jour. Conch., vol. 1, no. 1, p. 24.
- 1866 *Volutilithes impressus*, Conrad: Conrad, Check list of the invertebrate fossils of North America, Eocene and Oligocene: Smithsonian Inst. Misc. Coll., vol. 7, no. 200, p. 16.
Volutilithes indentus, Conrad: Conrad, *idem*.
Volutilithes petrosus, Conrad: Conrad, *idem*.
- 1890 *Voluta petrosa* (Conrad) De Greg.: De Gregorio, Monographie de la faune Eocénique de l'Alabama, p. 63, pl. 4, figs. 50-51, 53, 59-60 (not pl. 4, figs. 52, 54-58, 61).
- 1891 *Volutilithes petrosa* Conrad: Heilprin, The Eocene Mollusca of the State of Texas: Acad. Nat. Sci. Philadelphia, Proc. 1890, p. 396.
- 1892 *Volutilithes dumosa* Conrad: Kennedy, A section from Terrell, Kaufman County, to Sabine Pass on the Gulf of Mexico: Texas Geol. Survey 3d Ann. Rept. (1891), p. 57.
- 1895 *Volutilithes petrosa* Conrad: Kennedy, The Eocene Tertiary of Texas east of the Brazos River: Acad. Nat. Sci. Philadelphia, Proc., vol. 47, pp. 100, 113, 114, 116, 117, 123, 126, 128.
Volutilithes petrosa var. *indenta* Conrad: Kennedy, *ibid.*, pp. 117, 118, 130.
Volutilithes petrosus Conrad: Vaughan, The stratigraphy of northwestern Louisiana: Amer. Geol., vol. 15, pp. 214, 219.
- 1896 *Volutilithes petrosus* Conrad: Vaughan, A brief contribution to the geology and paleontology of northwestern Louisiana: U. S. Geol. Survey Bull. 142, pp. 17, 20, 40, 50, 51.
- 1899 *Volutilithes petrosus* Conrad (in part): Harris, The Lignitic Stage, Part II, Scaphopoda, Gastropoda, Pteropoda, and Cephalopoda: Bull. Amer. Paleont., vol. 3, no. 11, pp. 33-34.
- 1902 *Volutilithes petrosus*: Harris, The geology of the Mississippi embayment with special reference to the State of Louisiana: Louisiana Geol. Survey, Rept., Pt. VI, Spec. Rept. 1, pp. 20, 22, 23, 24, 25.
- 1903 *Volutilithes petrosus* Conrad: Dumble, Geology of southwestern Texas: Amer. Inst. Min. Eng., Trans., vol. 33, pp. 943-944, 950-952.
Volutilithes petrosus var. *indenta* Con.: Dumble, *ibid.*, p. 943.
Volutilithes, sp.: Dumble, *ibid.*, p. 951.
- 1906 *Volutilithes petrosus* Conrad: Burnett Smith, Phylogeny of the races of *Volutilithes petrosus*: Acad. Nat. Sci. Philadelphia, Proc., vol. 58, pp. 58-59, 65-69, 72-76, text fig. 7, tables 1-3, pl. 2, figs. 4, 7; Veatch, Geology and underground water resources of northern Louisiana and southern Arkansas: U. S. Geol. Survey Prof. Paper 46, pl. 14, figs. 2, 2a.
Volutilithes petrosus: Veatch, *ibid.*, pp. 243, 244, 272.
- 1907 *Athleta petrosa*: Burnett Smith, A new species of *Athleta* and a note on the morphology of *Athleta petrosa*: Acad. Nat. Sci. Philadelphia, Proc., vol. 59, pp. 230, 232-234, 235-242, text figs. 3, 6, tables 1-3.
- 1914 *Plejona petrosa* (Conrad): Deussen, Geology and underground waters of the southeastern part of the Texas Coastal Plain: U. S. Geol. Survey Water-Supply Paper 335, pp. 58, 62, 64.
Plejona petrosa var. *indenta* (Con.): Deussen, *ibid.*, pp. 57, 64.
- 1915 *Volutilithes petrosus* Conrad: Dumble, Some events in the Eocene history of the present coastal area of the Gulf of Mexico in Texas and Mexico: Jour. Geol., vol. 23, no. 6, p. 491.
- 1920 *Volutilithes petrosa* Conrad: Dumble, The geology of east Texas: Univ. Texas Bull. 1869, pp. 88, 89, 91-92, 95, 97, 99, 100, 107.
Volutilithes petrosus: Dumble, *ibid.*, p. 171.
Volutilithes petrosus Conrad: Dumble, *ibid.*, pp. 108, 132, 137, 138.
Volutilithes petrosa var. *indenta* Conrad: Dumble, *ibid.*, pp. 89, 92, 97, 98, 107.
Volutilithes petrosus var. *indenta* Con.: Dumble, *ibid.*, p. 132.
Volutilithes petrosus var. *indenta* Har.: Dumble, *ibid.*, p. 108.
- 1923 *Plejona petrosa* (Conrad): Trowbridge, A geologic reconnaissance in the Gulf Coastal Plain of Texas, near the Rio Grande: U. S. Geol. Survey Prof. Paper 131-D, pp. 94, 95, 96.
Plejona sp.: Trowbridge, *ibid.*, pp. 95, 96.
- 1924 *Plejona petrosa* Conrad: Deussen, Geology of the Coastal Plain of Texas west of Brazos River: U. S. Geol. Survey Prof. Paper 126, pp. 22, 62.
Plejona petrosa (Conrad): Deussen, *ibid.*, pp. 67, 77.
Plejona petrosa (Conrad)? : Deussen, *ibid.*, p. 95.
(?) *Plejona* sp.: Deussen, *ibid.*, pp. 22, 79, 82.
- 1931 *Plejona petrosa* (Conrad): Renick and Stenzel, The lower Claiborne on the Brazos River, Texas: Univ. Texas Bull. 3101, p. 93.

- Plejona (Volutilithes) petrosa* (Conrad): Renick and Stenzel, *ibid.*, pp. 101, 106.
- 1933 *Volutocorbis petrosa* (Conrad): Plummer, Cenozoic systems in Texas: Univ. Texas Bull. 3232, pp. 625, 645, 646, 663; Trowbridge, Tertiary and Quaternary geology of the lower Rio Grande region, Texas: U. S. Geol. Survey Bull. 837, p. 85, pl. 42, figs. 1-3.
Volutocorbis petrosus (Conrad): Plummer, *ibid.*, p. 693.
Volutocorbis sp.: Plummer, *ibid.*, p. 694.
Volutocorbis petrosa: Trowbridge, Tertiary and Quaternary geology of the lower Rio Grande region, Texas: U. S. Geol. Survey Bull. 837, p. 120.
- 1935 *Plejona petrosa* Conrad: Lonsdale, Geology and ground-water resources of Atascosa and Frio counties, Texas: U. S. Geol. Survey Water-Supply Paper 676, p. 32.
- 1937 *Athleta petrosa* (Conrad) (in part): Palmer, The Claibornian Scaphopoda, Gastropoda, and dibranchiate Cephalopoda of the southern United States: Bull. Amer. Paleont., vol. 7, no. 32, pp. 372-375, pl. 58, figs. 1-4, 6, 8-10, 14; pl. 88, figs. 1, 7, 11.
Athleta petrosa indenta (Conrad): Palmer, *ibid.*, p. 375, pl. 58, figs. 5, 7.
- 1939 *Volutospina petrosa* (Conrad): Stenzel, The geology of Leon County, Texas: Univ. Texas Pub. 3818, p. 112.
- 1945 *Volutospina clayi* (Burnett Smith)? : Gardner, Mollusca of the Tertiary formations of northeastern Mexico: Geol. Soc. Amer. Mem. 11, pp. 224-225, table 3, pl. 22, fig. 14 (not *Athleta clayi* Smith, 1907).
Volutospina impressa (Conrad): Gardner, *ibid.*, p. 225, pl. 23, figs. 1, 3.
Volutospina indenta (Conrad): Gardner, *ibid.*, p. 225, pl. 23, figs. 8, 9.
Volutospina petrosa (Conrad): Gardner, *ibid.*, p. 224, pl. 16, fig. 18.
Volutospina symmetrica (Conrad): Gardner, *ibid.*, pp. 16, 37, 226, pl. 22, fig. 8; pl. 23, figs. 7, 10.
- 1947 *Athleta petrosa* (Conrad): Palmer, The Mollusca of the Jackson Eocene of the Mississippi embayment, etc. Second section, Univalves: Bull. Amer. Paleont., vol. 30, no. 117, pp. 391-393, pl. 53, figs. 1-4.
- 1953 *Athleta petrosa* (Conrad): Palmer, Eocene mollusks from Citrus and Levy counties, Florida, Part 2, Gastropoda: Florida Geol. Survey Bull. 35, p. 35.
Athleta petrosa indenta Conrad: Palmer, *ibid.*, p. 35.
Volutospina: Stenzel, The geology of Henrys Chapel quadrangle, northeastern Cherokee County, Texas: Univ. Texas Pub. 5305, p. 75.
- 1954 *Volutovetus petrosa* (Conrad): Pilsbry and Olsson, Systems of the Volutidae: Bull. Amer. Paleont., vol. 35, no. 152, p. 22, pl. 2, fig. 8.

Original description.—Shell subglabrous; body whorl marked with from eight to ten longitudinal folds, terminating on the shoulder in compressed subacute tubercles, which are also distinct on the spire; transversely striated at base; two folds on the columella. Length $1\frac{1}{2}$ inches. (Conrad, 1833, p. 29.)

Revised description.—Shell subfusiform and small in early forms, substrombiform and larger in advanced forms, secondarily subfusiform in terminal forms; spire elevated, conical; spire profile smooth in early forms, shouldered and stepped in advanced forms, spiral angle increases among advanced forms. Total number of teleoconch and protoconch whorls generally uniform; adult shells with 5 to 8 teleoconch whorls, increase in number of teleoconch whorls in advanced forms. Protoconch small, smooth, regularly coiled, consists of $3\frac{1}{2}$ to 4 whorls in earliest forms, 2 to $2\frac{1}{2}$ whorls in advanced forms (fig. 30); smooth stage of protoconch grades into ribbed stage with slightly curved, uniform, longitudinal ribs; ribbed stage occupies about one-fourth whorl, and grades into cancellate stage, marked by development of subsutural ridge and shoulder with intervening ramp; nodes initially present at intersection of longitudinal ribs and shoulder and subsutural

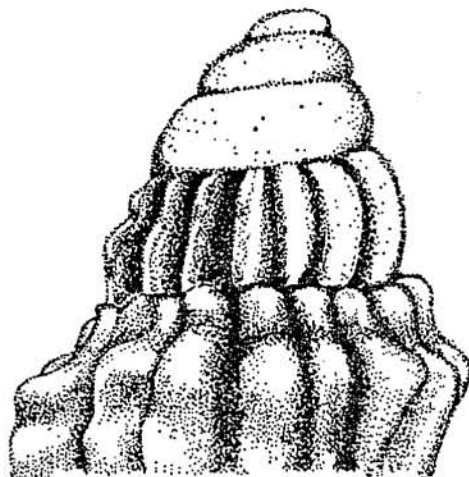


FIG. 30. Protoconch and posterior teleoconch whorls of *Athleta petrosa* (Conrad, 1833).

ridge; nodes on shoulder gradually increase in size and decrease in number per whorl; nodes grade into spines which are larger on larger forms; spines and larger nodes on shoulder situated at apex of anteriorly extending longitudinal ribs; ribs more prominent in later growth stages of individuals than in early growth stages; spiral angle increases and ramp is more prominent as spines become larger; nodes on subsutural ridge become larger but never as large as nodes and spines on shoulder; subsutural ridge disappears in later whorls of more advanced forms; nodes on subsutural ridge coalesce in certain forms to produce a slight keel; spiral and longitudinal lirae uniform in distribution and expression on all whorls of early forms but uniform only on juvenile whorls of advanced forms; lirae on body whorl generally variable but spiral lirae tend to become faint and are lost on the posterior part of the body whorl; spiral lirae tend to be accentuated on the anterior part of the body whorl in advanced forms in connection with development of a slight, siphonal fasciole. Aperture narrow, becoming slightly wider in terminal forms, corresponding to modification of spines and reduction of peripheral angulation. Columella with 2 small but distinct folds in early forms; number and prominence of folds tending to increase with development of secondary folds on some advanced forms; folds either equal or decrease in size posteriorly. Anterior siphonal canal slightly recurved in early forms but nearly straight in advanced forms; inside of outer lip smooth in early forms to denticulate in advanced forms.

Remarks.—In addition to forms of *Athleta petrosa* (Conrad) classed as *A. petrosa smithi* Fisher & Rodda, n. subsp., *A. petrosa petrosa* (Conrad), and *A. petrosa symmetrica* (Conrad), there are a few forms of *A. petrosa* (Conrad) from the Queen City Formation (B.E.G. locality 11-T-39) that are not subspecifically classified. Queen City forms are morphologically similar to both *A. petrosa smithi* Fisher & Rodda and *A. lisbonensis* (Aldrich). All specimens from the Queen City

Formation are small and probably represent juveniles.

Yegua forms, illustrated as *A. petrosa symmetrica* (Conrad) (Pl. X, fig. 1), are morphologically similar to *A. petrosa symmetrica* (Conrad) and *A. petrosa petrosa* (Conrad). This similarity, as well as their stratigraphic occurrence, suggests Yegua forms are intermediate to forms of *A. petrosa* (Conrad) from the Cook Mountain Formation (Claibornian) and Jacksonian rocks. Certain of the Yegua forms have posteriorly recurved spines on the body whorl, a morphologic feature characteristic of *A. petrosa symmetrica* (Conrad).

Type data.—Lectotype(?), Cat. No. 14411, Academy of Natural Sciences, Philadelphia, Pennsylvania. According to Moore (1962, p. 87), neither of the remaining specimens at the Academy agrees with the height given for the lectotype designated by Palmer (1937, p. 375).

Type locality.—Claiborne Bluff, Alabama River, Monroe County, Alabama.

Occurrence.—Claibornian and Jacksonian rocks of Gulf and Atlantic Coastal Plains. In Texas the species occurs in the marine facies of the Queen City Formation, Reklaw Formation, Weches Formation, Stone City Formation, Cook Mountain Formation, Yegua Formation, and Jacksonian rocks. Occurrences are cited under subspecies entries.

ATHLETA PETROSA SMITHI Fisher & Rodda, n. subsp.
(Pl. VIII, figs. 8, 9; Pl. XI, figs. 1-5)

1933 *Volutocorbis petrosa* (Conrad): Plummer, Cenozoic systems in Texas: Univ. Texas Bull. 3232, p. 625.

1953 *Volutospina*: Stenzel, The geology of Henrys Chapel quadrangle, northeastern Cherokee County, Texas: Univ. Texas Pub. 5305, p. 75.

(?) *Volutocorbis* sp. cf. *V. lisbonensis* Aldrich: Stephenson, Probable Reklaw age of a ferruginous conglomerate in eastern Texas: U. S. Geol. Survey Prof. Paper 243-C, pp. 35-37.

(?) *Volutocorbis* sp.: Stephenson, *ibid.*, pp. 35, 36, 37.

Description.—Includes earliest forms of *Athleta petrosa* (Conrad) in Texas and is characterized by small, cancellate, subfusi-

form shells. Number of whorls ranges from 8 in smaller forms to 10 in larger forms. Protoconch occupies $2\frac{7}{8}$ to $4\frac{1}{4}$ smooth whorls and is followed by a ribbed stage marked by slightly curving simple ribs that persist for one-fourth to one-half whorl; ribbed stage develops into a slight shoulder and subsutural ridge, both bearing nodes and separated at first by a poorly defined ramp. Nodes on the shoulder gradually increase in size and decrease in number per whorl; in largest forms, nodes become small spines situated at the termination of slight longitudinal folds on the body whorl; nodes on the subsutural ridge variable in density, subdued, and characteristically coalesce to form slightly crenulated keel. Ramp between subsutural ridge and shoulder more prominent in later whorls than in early whorls but is relatively slight as the spire profile remains low and is not stepped. Longitudinal and spiral lirae uniform and characteristically cover entire shell to give a cancellate appearance. Few larger forms show reduction of spiral lirae on posterior part of body whorl; spiral lirae persist on the ramp and are slightly accentuated on the anterior part of body whorl. Few larger forms with a slight parietal callus. One or 2 subequal folds on columella are slight on small forms and prominent on large forms. A slight siphonal fasciole, accompanied by an accentuation of spiral lirae on the anterior part of the shell, is developed on larger forms.

Dimensions.—Based on measurements of 69 specimens, dimensions are: height, 8 to 32 mm, mean 16.9 mm; width, 3 to 15 mm, mean 7.8 mm; height of spire, 3 to 14 mm, mean 6.8 mm.

Remarks.—*A. petrosa smithi* Fisher & Rodda is distinguished from other subspecies of *A. petrosa* (Conrad) by (1) smaller size, (2) nearly uniform cancellation on body whorl, (3) subfusiform shape, (4) large protoconch, (5) general lack of prominent spines and parietal callus, (6) fewer and smaller columellar folds, (7) slight or no denticles on outer lip.

At B.E.G. locality 28-T-9, a few specimens have the shoulder elevated, giving a more sharply stepped and higher spire

than in typical forms. In other respects, they are identical with typical forms of *A. petrosa smithi* Fisher & Rodda.

Type data.—Holotype (B.E.G. No. 35288) at the Bureau of Economic Geology, The University of Texas, Austin, Texas. Dimensions: height, 19 mm; width, 9 mm; height of spire, 6 mm.

Type locality.—Bluff on Ridge Creek, 6.2 miles west of Smithville, Bastrop County, Texas; B.E.G. locality 11-T-7.

Occurrence.—Reklaw Formation of Texas at the following B.E.G. localities: 11-T-7, 11-T-35, 11-T-36, 28-T-9, 165-T-13, and 200-T-1.

Source of name.—Named for Burnett Smith, in recognition of his pioneer studies of the phylogeny of *A. petrosa* (Conrad).

ATHLETA PETROSA PETROSA (Conrad, 1833)
(Pl. VIII, figs. 1-4; Pl. X, figs. 6-10;
Pl. XI, figs. 6-10)

- 1833 *Voluta petrosa*: Conrad, Fossil shells of the Tertiary formations of North America, vol. 1, no. 3, p. 29. (August 29, 1833, *fide* Wheeler, 1935, p. 104.)
Voluta parva: Isaac Lea, Contributions to geology, p. 173, pl. 6, fig. 181. (December 2, 1833, *fide* Wheeler, 1935, p. 105.)
Voluta vanuxemi: Isaac Lea, *ibid.*, p. 173, pl. 6, fig. 182. (December 2, 1833, *fide* Wheeler, 1935, p. 105.)
- 1834 *Voluta petrosa* Conrad: Conrad, Catalogue of the fossil shells of the Tertiary formations of the United States, appendix to Morton, S. G., Synopsis of the organic remains of the Cretaceous group of the United States, p. 5.
- 1835 *Voluta petrosa*: Conrad, Fossil shells of the Tertiary formations of North America, vol. 1, no. 3 (reprint), p. 41, pl. 16, fig. 2.
- 1846 *Voluta petrosa* Conrad: Conrad, Observations on the Eocene formation of the United States, etc.: Amer. Jour. Sci., 2d ser., vol. 1, p. 220.
- 1848 *Voluta parva* Lea: H. C. Lea, Catalogue of the Tertiary Testacea of the United States: Acad. Nat. Sci. Philadelphia, Proc., vol. 4, no. 4, p. 107.
Voluta petrosa Conrad: H. C. Lea, *idem*.
Voluta vanuxemi Lea: H. C. Lea, *idem*.
- 1850 *Voluta petrosa* Conrad, 1833: d'Orbigny, Prodrome de paleontologie stratigraphique universelle des animaux mollusques, etc., vol. 2, p. 353.
- 1865 *Volutilithes impressa* Conrad: Conrad, Catalogue of the Eocene and Oligocene Testacea of the United States: Amer. Jour. Conch., vol. 1, no. 1, p. 23 (*nomen nu-*

- dum); Descriptions of new Eocene shells of the United States: Amer. Jour. Conch., vol. 1, no. 2, p. 144; Descriptions of new Eocene shells, and references with figures to published species: Amer. Jour. Conch., vol. 1, no. 3, p. 211, pl. 20, fig. 3.
- Volutilithes indenta* Conrad: Conrad, Amer. Jour. Conch., vol. 1, no. 1, p. 23 (*nomen nudum*); vol. 1, no. 2, p. 144; vol. 1, no. 3, p. 221, pl. 21, fig. 10.
- Volutilithes petrosa* Conrad: Conrad, Amer. Jour. Conch., vol. 1, no. 1, p. 23.
- 1866 *Volutilithes petrosus*, Conrad: Conrad, Check list of the invertebrate fossils of North America, Eocene and Oligocene: Smithsonian Inst. Misc. Coll., vol. 7, no. 200, p. 16.
- 1892 *Volutilithes dumosa* Conrad: Kennedy, A section from Terrell, Kaufman County, to Sabine Pass on the Gulf of Mexico: Texas Geol. Survey 3d Ann. Rept. (1891), p. 57.
- 1895 *Volutilithes petrosa* Conrad: Kennedy, The Eocene Tertiary of Texas east of the Brazos River: Acad. Nat. Sci. Philadelphia, Proc., vol. 47, pp. 113, 114, 116, 117, 123, 126, 128.
- Volutilithes petrosa* var. *indenta* Conrad: Kennedy, *ibid.*, pp. 117, 118, 130.
- 1896 *Volutilithes petrosus* Conrad: Vaughan, A brief contribution to the geology and paleontology of northwestern Louisiana: U.S. Geol. Survey Bull. 142, pp. 17, 20, 40.
- 1899 *Volutilithes petrosus* Conrad (in part): Harris, The Lignitic Stage, Part II, Scaphopoda, Gastropoda, Pteropoda, and Cephalopoda: Bull. Amer. Paleont., vol. 3, no. 11, pp. 33-34.
- 1902 *Volutilithes petrosus*: Harris, The geology of the Mississippi embayment with special reference to the State of Louisiana: Louisiana Geol. Survey Rept., Pt. VI, Spec. Rept. 1, p. 20.
- 1903 *Volutilithes petrosus* Conrad: Dumble, Geology of southwestern Texas: Amer. Inst. Min. Eng., Trans., vol. 33, pp. 943-944, 950-952.
- Volutilithes petrosus* var. *indenta* Con.: Dumble, *ibid.*, p. 943.
- Volutilithes*, sp.: Dumble, *ibid.*, p. 951.
- 1907 *Athleta petrosa*: Burnett Smith, A new species of *Athleta* and a note on the morphology of *Athleta petrosa*: Acad. Nat. Sci. Philadelphia, Proc., vol. 59, table 1.
- 1914 *Plejona petrosa* (Conrad): Deussen, Geology and underground waters of the southeastern part of the Texas Coastal Plain: U. S. Geol. Survey Water-Supply Paper 335, pp. 58, 62, 64.
- 1920 *Volutilithes petrosa* Conrad: Dumble, The geology of east Texas: Univ. Texas Bull. 1869, pp. 88, 89, 91-92, 95, 97, 99, 100, 107.
- Volutilithes petrosus*: Dumble, *ibid.*, p. 171.
- Volutilithes petrosa* var. *indenta* Conrad: Dumble, *ibid.*, pp. 89, 92, 97, 98, 107.
- Volutilithes petrosus* var. *indenta* Con.: Dumble, *ibid.*, p. 132.
- Volutilithes petrosus* var. *indenta* Har.: Dumble, *ibid.*, p. 108.
- 1923 *Plejona petrosa* (Conrad): Trowbridge, A geologic reconnaissance in the Gulf Coastal Plain of Texas, near the Rio Grande: U. S. Geol. Survey Prof. Paper 131-D, pp. 94, 95, 96.
- (?) *Plejona* sp.: Trowbridge, *ibid.*, pp. 95-96.
- 1924 *Plejona petrosa* (Conrad): Deussen, Geology of the Coastal Plain of Texas west of Brazos River: U. S. Geol. Survey Prof. Paper 126, pp. 22, 62, 67, 77.
- 1931 *Plejona petrosa* (Conrad): Renick and Stenzel, The lower Claiborne on the Brazos River, Texas: Univ. Texas Bull. 3101, p. 93.
- Plejona* (*Volutilithes*) *petrosa* (Conrad): Renick and Stenzel, *ibid.*, pp. 101, 196.
- 1933 *Volutocorbis petrosa* (Conrad): Plummer, Cenozoic systems in Texas: Univ. Tex. Bull. 3232, pp. 645, 646, 663.
- Volutocorbis petrosa*: Trowbridge, Tertiary and Quaternary geology of the lower Rio Grande region, Texas: U. S. Geol. Survey Bull. 837, p. 120.
- 1935 *Plejona petrosa* Conrad: Lonsdale, Geology and ground-water resources of Atascosa and Frio counties, Texas: U. S. Geol. Survey Water-Supply Paper 676, p. 32.
- 1937 *Athleta petrosa* (Conrad) (in part): Palmer, The Claibornian Scaphopoda, Gastropoda, and dibranchiate Cephalopoda of the southern United States: Bull. Amer. Paleont., vol. 7, no. 32, pp. 372-375, pl. 58, figs. 2-8; pl. 88, figs. 1, 6, 7, 11.
- 1939 *Volutospina petrosa* (Conrad): Stenzel, The geology of Leon County, Texas: Univ. Texas Pub. 3818, p. 112.
- 1945 (?) *Volutospina clayi* (Burnett Smith)? : Gardner, Mollusca of the Tertiary formations of northeastern Mexico: Geol. Soc. Amer. Mem. 11, pp. 224-225, table 3, pl. 22, fig. 14 (not *Athleta clayi* Smith, 1907).
- Volutospina impressa* (Conrad): Gardner, *ibid.*, p. 225, pl. 23, figs. 1, 3.
- Volutospina indenta* (Conrad): Gardner, *ibid.*, p. 225, pl. 23, figs. 8, 9.
- 1953 *Athleta petrosa indenta* Conrad: Palmer, Eocene mollusks from Citrus and Levy counties, Florida, Part 2, Gastropoda: Florida Geol. Survey Bull. 35, p. 35.
- 1954 *Volutovetus petrosa* (Conrad): Pilsbry and Olsson, Systems of the Volutidae: Bull. Amer. Paleont., vol. 35, no. 152, p. 22, pl. 2, fig. 8.
- 1961 *Athleta petrosa*: Stuckey, Zingula, and Rainwater, Middle Eocene of Houston County, Texas: Soc. Econ. Paleo. and Min., Gulf Coast Section, Field Trip Guidebook, p. 35.

Athleta: Brock, Notes on selected fossil localities in eastern Texas, etc., Houston Geol. Soc., p. 47.

Original description.—Shell subglabrous; body whorl marked with from eight to ten longitudinal folds, terminating on the shoulder in compressed subacute tubercles, which are also distinct on the spire; transversely striated at base; two folds on the columella. Length $1\frac{1}{2}$ inches. (Conrad, 1833, p. 29.)

Revised description.—Subfusiform to mostly substrombiform; size moderate among early forms to relatively large among later forms; spines slight to prominent in expression. Protoconch occupies $2\frac{1}{2}$ to $4\frac{1}{2}$ whorls, teleoconch $6\frac{1}{2}$ to $7\frac{1}{2}$ whorls. Ribbed stage of slightly arcuate longitudinal ribs, one-fourth to one-half whorl in duration, follows smooth protoconch. Ribbed stage is gradually modified by slight subsutural ridge and slightly angulated shoulder; small nodes are developed at intersection of longitudinal ribs and subsutural ridge and shoulder. Subsutural ridge subsequently lost; nodes on shoulder become larger and grade into spines which among more advanced forms are large and tend to be slightly recurved posteriorly. Spines on adults are larger than spines on adults of *A. petrosa smithi* Fisher & Rodda. Shoulder becomes more sharply angulated as ramp angle becomes smaller, resulting in an angulated spiral profile. Spines situated at apex of longitudinal ribs which decrease in length and prominence as spines increase in size.

Longitudinal and spiral lirae uniform only on juveniles and earliest adults; lirae gradually lost on posterior part of body whorl, but spiral lirae accentuated anteriorly with development of slight siphonal fasciole. Few individuals have lirae both anterior and posterior to the periphery of body whorl.

Parietal callus deposits are moderate in advanced forms but less than those on *A. petrosa symmetrica* (Conrad). Columella with 2 to 3 prominent, subequal folds; 2 to 4 smaller, secondary folds posterior to prominent folds on more advanced forms; columellar folds are largest anteriorly. Denticulation on outer lip is progressively

more prominent with increasing size of shell.

Dimensions.—Based on measurements of 1,268 specimens, dimensions are: height, 7 to 51 mm, mean 23.1 mm; width, 3 to 21 mm, mean 10.4 mm; height of spire, 2 to 19 mm, mean 8.2 mm.

Remarks.—*Athleta petrosa petrosa* (Conrad) is by far the most abundant and widespread subspecies and, especially in populations from the Cook Mountain Formation, represents the acme of *A. petrosa* (Conrad) in Texas. This is partly an evolutionary expression but is emphasized by the more widespread occurrence of fossiliferous marine rocks in the Cook Mountain Formation than in Lower Eocene rocks. Certain morphologic distinctions can be made among adults of *A. petrosa petrosa* (Conrad) from the Weches and Cook Mountain Formations; these distinctions are the result of gradual evolutionary change but are, among most populations, too slight to warrant subspecific distinction. In order to define more precisely the evolutionary change in *A. petrosa* (Conrad), forms from the Weches and Cook Mountain Formation are illustrated and considered separately in the nonsystematic part of this report.

Type data.—Lectotype (?), Cat. No. 14411, Academy of Natural Sciences, Philadelphia, Pennsylvania. See type data for *A. petrosa* (Conrad) (p. 43).

Type locality.—Claiborne Bluff, Alabama River, Monroe County, Alabama (Gosport Formation).

Occurrence.—Widespread and common in marine Claibornian rocks and of the Gulf Coastal Plain. Present in Texas at the following B.E.G. localities: 11-T-2, 26-T-5, 26-T-6, 37-T-4, 113-T-37, 145-T-1, 145-T-32, 145-T-37, 145-T-38, 173-T-11, 173-T-17, 173-T-19, 173-T-24, and 201-T-2 (Weches Formation); 7-T-17, 11-T-75, 26-T-1, and 201-T-5 (Stone City Formation); 7-T-16, 11-T-29, 11-T-40, 11-T-71, 21-T-1, 26-T-2, 26-T-4, 75-T-3, 89-T-9, 89-T-10, 113-T-2, 113-T-9, 144-T-1, 144-T-2, 144-T-5, 144-T-7, 145-T-51, 145-T-52,

145-T-53, 145-T-54, 145-T-58, 145-T-59, 145-T-60, 145-T-62, 145-T-72, 145-T-80, 145-T-83, 197-T-2, 201-T-3, 201-T-22, 201-T-23, 239-T-3, 239-T-9, 239-T-12, and 252-T-5 (Cook Mountain Formation).

ATHLETA PETROSA SYMMETRICA (Conrad, 1854)
(Pl. VIII, figs. 7, 10, 11; Pl. X, figs. 1-5)

- 1854 *Volutilithes dumosa*: Conrad, Fossil Testacea of the Tertiary green-sand marl-bed of Jackson, Miss., in Wailes, B.L.C., Report on the agriculture and geology of Mississippi, p. 289, pl. 16, fig. 1.
Volutilithes symmetrica: Conrad, *ibid.*, p. 289, pl. 15, fig. 6.
- 1855 *Volutilithes symmetrica* Conrad: Conrad, Observations on the Eocene deposit of Jackson, Mississippi, etc.; Acad. Nat. Sci. Philadelphia, Proc., vol. 7, no. 7, p. 260.
- 1857 *Voluta dumosa*: Harper, Preliminary report on the geology and agriculture of the State of Mississippi, p. 145.
- 1860 *Voluta dumosa*: Hilgard, Report on the geology and agriculture of the State of Mississippi, pp. 108, 132.
- 1865 *Volutilithes dumosa* Conrad: Conrad, Catalogue of the Eocene and Oligocene Testacea of the United States: Amer. Jour. Conch., vol. 1, no. 1, p. 23.
Volutilithes symmetrica: Conrad, *ibid.*, p. 24.
- 1881 *Volutilithes dumosus*: Miller, North American Mesozoic and Cenozoic geology and paleontology, p. 174.
Volutilithes symmetricus: Miller, *ibid.*, p. 174.
- 1884 *Voluta dumosa*: Heilprin, The Tertiary geology of the eastern and southern United States: Acad. Nat. Sci. Philadelphia, Jour., 2d ser., vol. 9, p. 145.
- 1899 *Volutilithes symmetricus* Con.: Cossmann, Essais de paleoconchologie comparée, livr. 3, p. 137.
- 1936 *Volutilithes dumosus*: Chawner, Geology of Catahoula and Concordia Parishes: Louisiana Geol. Survey Bull. 9, p. 84.
Volutilithes dumosa Conrad: Chawner, *ibid.*, p. 89.
Volutilithes dumosus Conrad: Chawner, *ibid.*, p. 90.
Volutilithes symmetrica Conrad: Chawner, *ibid.*, p. 90.
- 1937 *Athleta petrosa* (Conrad): Palmer, The Claibornian Scaphopoda, Gastropoda, and dibranchiate Cephalopoda of the southern United States: Bull. Amer. Paleont., vol. 7, no. 32, p. 372, pl. 58, figs. 1, 9, 10, 14.
- 1938 *Volutilithes dumosa*: Fisk, Geology of Grant and LaSalle Parishes: Louisiana Geol. Survey Bull. 10, p. 98.
- 1939 *Volutilithes dumosa* Conrad: Huner, Geology of Caldwell and Winn Parishes: Louisiana Geol. Survey Bull. 15, p. 166.
Volutilithes symmetrica Conrad: Huner, *ibid.*, p. 166.
- 1945 *Volutospina symmetrica* (Conrad): Gardner, Mollusca of the Tertiary formations of northeastern Mexico: Geol. Soc. Amer. Mem. 11, pp. 16, 37, 226; pl. 22, fig. 8; pl. 23, figs. 7, 10.
- 1947 *Athleta petrosa* (Conrad): Palmer, The Mollusca of the Jackson Eocene of the Mississippi embayment, etc. Second section, Univalves: Bull. Amer. Paleont., vol. 30, no. 117, pp. 391-393, pl. 53, figs. 1-4.

Original description.—Listed and illustrated by Conrad (1854b, p. 289, pl. 16, fig. 1). Described by Conrad (1855, p. 260).

Description.—Shell substrombiform to roughly fusiform in advanced forms as the periphery becomes more broadly angulate and as posterior part of the body whorl becomes convex. Shape is approximately that of early forms of *A. petrosa* (Conrad), but shell is much larger and more inflated medially. Protoconch consists of $1\frac{3}{4}$ to $2\frac{3}{4}$ smooth whorls, followed by a ribbed stage that occupies one-fourth to one-half whorl. Ribbed stage grades into a shoulder and subsutural ridge stage with nodes arising at the intersection of longitudinal ribs and these ridges. Nodes on the shoulder increase in size rapidly, forming spines on later whorls. Spines are long, slender, and posteriorly recurved on the body whorl. The ramp, flattened where it first separates the subsutural ridge and shoulder, is more steeply sloped and smoother in profile in later whorls. Long, narrow spines are accentuated by sloping of the ramp, loss of longitudinal ribs, and general inflation of posterior part of the body whorl. Aperture is relatively wider than on older forms of *A. petrosa* (Conrad). Parietal callus is slight on most forms but, in general, is more extensive than on other forms of *A. petrosa* (Conrad). Columella generally has 3 prominent folds with up to 4 smaller secondary folds posterior to the primary or prominent folds; columellar folds are largest anteriorly. Outer lip denticulate; siphonal fasciole distinct; spiral lirae on

body whorl distinct to absent; longitudinal lirae indistinct.

Dimensions.—Based on measurements of 85 specimens, dimensions are: height, 10 to 54 mm, mean 30.1 mm; width, 7 to 27 mm, mean 14.4 mm; height of spire, 3 to 21 mm, mean 11.3 mm.

Remarks.—*A. petrosa symmetrica* (Conrad) is the terminal part of the *A. petrosa* stock. This subspecies is abundant in the Moodys Branch and Danville Landing Formations of the Jackson Group of the eastern and central Gulf Coastal Plain, but it is rare and generally poorly preserved in Jacksonian rocks of Texas.

A. petrosa symmetrica (Conrad) is distinguished from other forms of *A. petrosa* (Conrad) by (1) larger size, (2) tendency toward subfusiform shape, (3) longer and more slender, posteriorly recurved spines, (4) more numerous and prominent columellar folds, (5) shorter protoconch, and (6) relatively wider aperture.

Forms of *A. petrosa* (Conrad) collected from the upper part of the Yegua Formation at Robinson Ferry on the Sabine River (B.E.G. locality 201-T-14) are, in certain respects, morphologically intermediate to forms from the Cook Mountain and Moodys Branch Formations (Pl. X, fig. 1). This fauna has been variously assigned to the Claiborne and Jackson; however, Stenzel (1939b) has demonstrated that the stratigraphic units exposed at this locality are a marine lentil in the uppermost part of the Yegua Formation (Creola Member). Forms of *A. petrosa* (Conrad) are relatively small, and Gardner (Stenzel, 1939b, p. 872) stated they were juveniles. We assign forms of *A. petrosa* (Conrad) from this locality to *A. petrosa symmetrica* (Conrad) principally on basis of similarity of spines and shape.

In 1854, Conrad named and figured two species, *Volutilithes dumosa* and *V. symmetrica*, forms now placed in the genus *Athleta*. Subsequently, *V. symmetrica* was described (Conrad, 1855, p. 260), but no description of *V. dumosa* has been published. Judging from Conrad's (1854b) illustrations of the two species and his

description (1855), *V. symmetrica* apparently was distinguished from *V. dumosa* by (1) smaller size and (2) presence of distinct spiral lirae on the body whorl anterior to the periphery of the shell. Among populations of *A. petrosa* (Conrad) that we have studied from Jacksonian rocks we have been unable to demonstrate the presence of two distinct forms. Conrad's two species apparently represent morphologic end-points in gradational populations, and we consider Jacksonian forms of *A. petrosa* (Conrad) as a single subspecies, *A. petrosa symmetrica* (Conrad).

Priority of the trivial name *symmetrica* is established herein on the basis of the first reviser provision of Article 24 (International Code of Zoological Nomenclature). No previous citations conform to this article. Other citations of *dumosa* and *symmetrica* are in faunal lists without discussion of the two forms. Conrad (1855, p. 260) described *V. symmetrica* but did not mention *V. dumosa*. Conrad (1865a, pp. 23-24) listed *V. dumosa* and *V. symmetrica* in alphabetical order without any indication of synonymy. Cossmann (1899, p. 137) merely listed "*V. symmetricus*" in a list of Claibornian species of "*Volutilithes*"; *V. dumosa* was not mentioned. Palmer (1937, p. 372; 1947, pp. 391-393) included both *V. symmetrica* and *V. dumosa* as synonyms of *V. petrosa* Conrad. Palmer (1937) did not discuss these names. Palmer (1947, p. 392) noted that *V. symmetrica* and *V. dumosa* are extreme forms that can be found at the same localities and are connected by intermediate forms. However, neither name was chosen for this taxon; both were placed in synonymy with *V. petrosa*. Gardner (1945, p. 226) described specimens of *V. symmetrica* from northeastern Mexico, but she did not include *V. dumosa* in the synonymy of *V. symmetrica*, and *V. dumosa* is not mentioned in the text.

Choice of *symmetrica* probably will best ensure stability and universality of nomenclature.

Type data.—Holotype, Cat. No. 13207, Academy of Natural Sciences, Phila-

delphia, Pennsylvania (Moore, 1962, p. 100). Type of *V. dumosa* Conrad is missing (*ibid.*, p. 56).

Type locality.—Moodys Branch Formation, Riverside Park, Jackson, Hinds County, Mississippi.

Occurrence.—B.E.G. locality 227-T-9 (?Caddell Formation); B.E.G. localities 89-T-11 and 201-T-14 (Yegua Formation).

ATHLETA TUOMEYI Conrad, 1853
(Pl. VIII, figs. 5, 6; Pl. IX, figs. 5-9)

- 1848 *Voluta* n. sp.: Hale, Geology of south Alabama: Amer. Jour. Sci., 2d ser., vol. 6, p. 355.
- 1853 *Athleta tuomeyi*: Conrad, Synopsis of the genera *Cassidula*, Humph., and of a proposed new genus *Athleta*: Acad. Nat. Sci. Philadelphia, Proc., vol. 6, p. 449.
- 1858 *Voluta tuomeyi* Conrad: Tuomey, Lists of fossils from the Cretaceous and Tertiary formations in Alabama and Mississippi: Alabama State Geologist, 2d Bien. Rept., Appendix 3, pp. 268, 270.
- 1860 *Volutilithes (Athleta) tuomeyi*: Conrad, Descriptions of new species of Cretaceous and Eocene fossils of Mississippi and Alabama: Acad. Nat. Sci. Philadelphia, Jour., 2d ser., vol. 4, p. 298, pl. 47, fig. 35.
Voluta petrosa: Hilgard, Report on the geology and agriculture of the State of Mississippi, p. 108.
Voluta petrosa Conrad: Hilgard, *ibid.*, p. 121.
(?) *Voluta* (sp. undet.): Lesquereux, Botanical and palaeontological report on the Geological State Survey of Arkansas, in Owen, D. D., Second report of a geological reconnaissance of the middle and southern counties of Arkansas, etc., pl. 9, fig. 5.
- 1865 *Volutilithes Tuomeyi* Conrad [as "Subgenus *Athleta*, Conrad"]: Conrad, Catalogue of the Eocene and Oligocene Testacea of the United States: Amer. Jour. Conch., vol. 1, p. 24; Observations on the Eocene Lignite Formation of the United States: Acad. Nat. Sci. Philadelphia, Proc., vol. 17, p. 71; Observations on the Eocene Lignite Formation of the United States: Amer. Jour. Sci., 2d ser., vol. 40, p. 266.
- 1866 *Volutilithes (Athleta) Tuomeyi* Conrad: Conrad, Check list of the invertebrate fossils of North America, Eocene and Oligocene: Smithsonian Inst. Misc. Coll., vol. 7, no. 200, p. 16.
- 1868 *Voluta tuomeyi*: Conrad, Notes on Recent and fossil shells, etc., 5, Notes on the genera *Pyrifusus* and *Athleta*, etc.: Amer. Jour. Conch., vol. 4, no. 4, p. 248.
- 1877 *Athleta tuomeyi* Conrad: Gabb, Notes on American Cretaceous fossils with descriptions of some new species: Acad. Nat. Sci. Philadelphia, Proc. 1876, p. 291.
- 1880 *Voluta Tuomeyi* (Con.): Mell, The Claiborne Group and its remarkable fossils: Amer. Inst. Min. Eng., Trans., vol. 8, p. 313.
- 1881 *Voluta (Athleta) Tuomeyi* Conr.: Heilprin, On some new Lower Eocene Mollusca from Clarke Co., Alabama, etc.: Acad. Nat. Sci. Philadelphia, Proc. 1880, p. 365.
- 1883 *Athleta tuomeyi* Conrad: Tryon, Structural and systematic conchology, Vol. II, pp. 166, 405, pl. 54, fig. 30.
- 1885 *Athleta tuomeyi* Conrad: Aldrich, Observations upon the Tertiary of Alabama: Amer. Jour. Sci., 3d ser., vol. 30, p. 304.
- 1887 *Athleta tuomeyi* Conrad: Smith and Johnson, Tertiary and Cretaceous strata of the Tuscaloosa, Tombigbee, and Alabama Rivers: U. S. Geol. Survey Bull. 43, pp. 40, 41, 44.
- 1890 *Voluta (Athleta) Tuomey* Conr.: De Gregorio, Monographie de la faune Éocénique de l'Alabama, p. 70, pl. 5, fig. 22 (not fig. 23 as stated on p. 70).
- 1894 (?) *Volutilithes petrosa*: Harris, The Tertiary geology of southern Arkansas: Arkansas Geol. Survey, Ann. Rept. 1892, vol. 2, p. 45.
(?) *Volutilithes petrosa*?: Harris, *ibid.*, p. 31.
Volutilithes petrosa var. *tuomeyi*: Harris, On the geological position of the Eocene deposits of Maryland and Virginia: Amer. Jour. Sci., 3d ser., vol. 47, p. 303.
Athleta tuomeyi Conrad: Smith, Johnson, and Langdon, Report on the geology of the Coastal Plain of Alabama, pp. 150, 151, 156.
Voluta (Athleta) Tuomeyi, Conr.: Smith, Johnson, and Langdon, *ibid.*, pp. 235, 236, 237, 238.
Voluta petrosa? Con.: Smith, Johnson, and Langdon, *ibid.*, pp. 235, 236.
- 1896 *Volutilithes (Athleta) tuomeyi*: Clark, The Potomac River section of the middle Atlantic coast Eocene: Amer. Jour. Sci., 4th ser., vol. 1, pp. 370, 372.
Volutilithes (Athleta) tuomeyi Conrad: Clark, The Eocene deposits of the middle Atlantic slope in Delaware, Maryland, and Virginia: U. S. Geol. Survey Bull. 141, pp. 44, 57, 65, 104, pl. 10, figs. 1a, 1b.
Volutilithes petrosa Conrad: Clark, *ibid.*, p. 44.
- 1897 *Volutilithes petrosus* var. *tuomeyi*: Harris, The Lignitic Stage, Part 1, Stratigraphy and Pelecypoda: Bull. Amer. Paleont., vol. 2, no. 9, p. 10.
- 1899 *Athleta tuomeyi* Conrad: Cossmann, Essais de paleoconchologie comparée, livr. 3, pl. 5, fig. 5.

- Volutilithes petrosus* Conrad (in part): Harris, The Lignitic Stage, Part II, Scaphopoda, Gastropoda, Pteropoda, and Cephalopoda: Bull. Amer. Paleont., vol. 3, no. 11, pp. 33-34, pl. 4, fig. 1.
- Volutilithes petrosus* vars.: Harris, The Cretaceous and Lower Eocene faunas of Louisiana: Louisiana Geol. Survey Rept. for 1899, Spec. Rept. 6, p. 305.
- 1901 *Volutilithes petrosus* Conrad: Clark and Martin, The Eocene deposits of Maryland: Maryland Geol. Survey, Eocene, pp. 59, 74-75, 85, 86, 88, 130-131, pl. 21, figs. 4, 5, 5a.
- 1902 *Volutilithes petrosus*: Harris, Eocene outcrops in central Georgia: Bull. Amer. Paleont., vol. 4, no. 16, p. 7.
- 1903 *Volutilithes petrosus* Conrad: Dumble, Geology of southwestern Texas: Amer. Inst. Min. Eng., Trans., vol. 33, pp. 935, 942, 949, 950, 951.
- 1905 *Volutilithes petrosus*: Burnett Smith, Sensitivity among gastropods: Acad. Nat. Sci. Philadelphia, Proc., vol. 57, pp. 346, 347, 348 (in part), 349, 350, 351, 357(?).
- Volutilithes petrosus* Conrad: Burnett Smith, *ibid.*, p. 360, pl. 30, figs. 4-5.
- 1906 *Volutilithes petrosus* Conrad: Burnett Smith, Phylogeny of the races of *Volutilithes petrosus*: Acad. Nat. Sci. Philadelphia, Proc., vol. 58, pp. 58-59 (in part), 60-65, 72-74, text fig. 4, tables 1-3, pl. 2, figs. 3, 5, 6, 8-10.
- Volutilithes petrosus* var. *tuomeyi* Conrad: Veatch, Geology and underground water resources of northern Louisiana and southern Arkansas: U. S. Geol. Survey Prof. Paper No. 46, pl. 18, fig. 3.
- 1907 *Athleta tuomeyi* Conrad: Burnett Smith, [Review of] "A review of the American Volutidae" by W. H. Dall: Nautilus, vol. 20, no. 11, p. 131.
- Athleta tuomeyi*: Dall, [Correspondence] Nautilus, vol. 20, no. 12, p. 142.
- Volutilithes tuomeyi*: Dall, *idem*.
- Athleta petrosa tuomeyi*: Burnett Smith, A new species of *Athleta* and a note on the morphology of *Athleta petrosa*: Acad. Nat. Sci. Philadelphia, Proc., vol. 59, pp. 230-231.
- 1909 *Volutilithes petrosus* (Conrad) (in part): Grabau and Shimer, North American index fossils, p. 790, fig. 1156.
- 1914 *Plejona petrosa* (Con.) var.: Deussen, Geology and underground waters of the southeastern part of the Texas Coastal Plain: U. S. Geol. Survey Water-Supply Paper 335, p. 41.
- 1916 (?) *Volutilithes petrosa* (Conrad)? : Stephenson and Crider, Geology and ground waters of northeastern Arkansas: U. S. Geol. Survey Water-Supply Paper 399, p. 53.
- 1920 *Volutilithes petrosus*: Dumble, The geology of east Texas: Univ. Texas Bull. 1869, p. 44.
- 1924 *Plejona tuomeyi* (Conrad): Cooke, American and European Eocene and Oligocene mollusks: Bull. Geol. Soc. Amer., vol. 35, p. 852.
- Plejona petrosa* Conrad subsp. *tuomeyi* (Conrad): Deussen, Geology of the Coastal Plain of Texas west of Brazos River: U. S. Geol. Survey Prof. Paper 126, pl. 15, figs. 6, 6a.
- 1926 *Volutospina tuomeyi* (Conrad): Cooke, The Cenozoic formations, in Geology of Alabama: Alabama Geol. Survey Spec. Rept. 14, pl. 94, fig. 4.
- 1931 *Volutilithes petrosus* Conrad: Aldrich, Description of a few Alabama Eocene species and remarks on varieties: Alabama Geol. Survey, Alabama Mus. Nat. Hist., Mus. Paper 12, p. 6, pl. 6, fig. 3.
- 1933 *Plejona petrosa* var. *tuomeyi* Conrad: Lowe, Coastal Plain stratigraphy of Mississippi, Part first, Midway and Wilcox Groups: Mississippi State Geol. Survey Bull. 25, p. 103.
- Plejona petrosa* var. *tuomeyi* (Conrad): Lowe, *ibid.*, p. 104.
- Volutocorbis petrosa* subsp. *tuomeyi* (Conrad): Trowbridge, Tertiary and Quaternary geology of the lower Rio Grande region, Texas: U. S. Geol. Survey Bull. 837, pl. 38, figs. 1, 2.
- 1934 *Volutilithes petrosus* var. *tuomeyi*: Howe and Garrett, Louisiana Sabine Eocene Ostracoda: Louisiana Geol. Survey Bull. 4, p. 14.
- 1935 (?) *Volutilithes petrosa* (Conrad)? : Spooner, Oil and gas geology of the Gulf Coastal Plain in Arkansas: Arkansas Geol. Survey Bull. 2, p. 115.
- 1937 *Athleta petrosa* (Conrad) (in part): Palmer, The Claibornian Scaphopoda, Gastropoda, and dibranchiate Cephalopoda of the southern United States: Bull. Amer. Paleont., vol. 7, no. 32, pp. 372-375, pl. 58, figs. 11-13.
- 1940 *Athleta petrosa* (Conrad): Toulmin, The Salt Mountain Limestone of Alabama: Alabama Geol. Survey Bull. 46, pp. 29, 32, 35, 36.
- 1941 *Athleta petrosa* (Conrad) var.: Le Blanc and Barry, Fossiliferous localities of Midway Group in Louisiana: Bull. Amer. Assoc. Petrol. Geol., vol. 25, no. 4, p. 737.
- 1942 *Athleta petrosa*: Barry and Le Blanc, Lower Eocene faunal units of Louisiana: Louisiana Geol. Survey Bull. 23, p. 17.
- Athleta petrosa* (Conrad): Barry and Le Blanc, *ibid.*, pp. 16, 25, 27, 137-140, pl. 17, figs. 5-11, table 2.
- 1943 *Volutospina* sp. cf. *V. tuomeyi* Conrad: Cooke, Geology of the Coastal Plain of

- Georgia: U. S. Geol. Survey Bull. 941, p. 52.
- Athleta petrosa* (Conrad): Wasem and Wilbert, The Pendleton Formation, Louisiana and Texas: Jour. Paleont., vol. 17, no. 2, p. 193.
- 1944 *Volutocorbis petrosus* (Conrad) (in part): Shimer and Shrock, Index fossils of North America, p. 508, pl. 209, figs. 3-5.
- 1945 *Volutospina (Eoathleta) corvocada*: Gardner, Mollusca of the Tertiary formations of northeastern Mexico: Geol. Soc. Amer. Mem. 11, pp. 35, 227, pl. 12, figs. 2, 9; pl. 27, fig. 10.
- Volutospina (Eoathleta) tuomeyi*: Gardner, *ibid.*, p. 8.
- Volutospina (Eoathleta) tuomeyi* (Conrad): Gardner, *ibid.*, pp. 35, 228, pl. 12, figs. 10-12; (?) pl. 22, fig. 6.
- 1951 *Volutospina petrosa* (Conrad): Toulmin, LaMoreaux, and Lanphere, Geology and ground-water resources of Choctaw County, Alabama: Alabama Geol. Survey Spec. Rept. 21 and County Rept. 2, p. 56.
- Volutospina tuomeyi* (Conrad): Toulmin, LaMoreaux, and Lanphere, *ibid.*, p. 80.
- 1953 *Volutospina petrosa* (Conrad): LaMoreaux and Toulmin, The Midway and Wilcox Groups in central and western Alabama: Mississippi Geol. Soc., 10th Field Trip, Guidebook, pp. 21, 25.
- Volutospina tuomeyi* (Conrad): LaMoreaux and Toulmin, *ibid.*, p. 27.
- 1959 (?) *Volutocorbis petrosus* (Conrad): LaMoreaux and Toulmin, Geology and ground-water resources of Wilcox County, Alabama: Alabama Geol. Survey County Rept. 4, p. 129.
- Volutocorbis tuomeyi* (Conrad): LaMoreaux and Toulmin, *ibid.*, p. 144.

Original description.—Ovato-turbinate, with revolving lines distinct on the lower half and obsolete above the body whorl; shoulder with distant prominent acute spines; between the spines and suture the side is flattened, swelling a little near the suture, and has a few revolving raised unequal lines; penultimate whorl concealed by the callus, above which the whorls are finely tuberculated and somewhat turritid; columella with 2 prominent plaits and 3 obsolete ones. Length $1\frac{1}{4}$ inch. (Conrad, 1853, p. 449.)

Revised description.—Early whorls similar to early whorls of *A. petrosa* (Conrad); later whorls, except for parietal callus and modification resulting from callus deposition, similar to *A. petrosa* (Conrad). Protoconch consists of 3 smooth whorls, regularly, but in a few specimens loosely, coiled, grading into ribbed stage occupy-

ing one-fourth to one-half of the fourth whorl. Subsequently, the ribbed stage develops into a slight shoulder and subsutural ridge, separated by a ramp, and bearing nodes which, on the shoulder, develop into spines on the last whorls. Subsutural nodes slightly larger in later whorls, commonly coalescing to form a subdued, crenulated keel, which becomes fainter on later whorls and finally disappears. Callus commonly extreme, covering and spreading from parietal region to cover most of the spire. Longitudinal lirae persistent on body whorl; spiral lirae subdued posteriorly and accentuated anteriorly. Denticulation of outer lip and prominence of columellar folds approximately at same stage of development as in *A. petrosa* (Conrad).

Dimensions.—Based on measurements of 46 specimens, dimensions are: height, 16 to 51 mm, mean 32.0 mm; width, 7 to 27 mm, mean 16.0 mm; height of spire, 6 to 19 mm, mean 10.9 mm.

Remarks.—Conrad (1853) originally described *A. tuomeyi* as a distinct species within a new genus, *Athleta*. Dall (1890, p. 75) suggested, and Smith (1906) stated, that *A. tuomeyi* Conrad represented a variation of typical *A. petrosa* (Conrad). Smith, as well as most subsequent writers, considered *A. petrosa* (Conrad) and *A. tuomeyi* Conrad synonymous. Gardner (1945), however, recognized *A. tuomeyi* Conrad as a distinct species, making it the type of a new subgenus, *Eoathleta*.

At least 10 different elements have been recognized within forms constituting *A. tuomeyi* Conrad. These include 2 species from northeastern Mexico (Gardner, 1945), 4 races from Louisiana (Barry and Le Blanc, 1942), and 4 races from Alabama (Smith, 1906). Such distinctions were based on stages in degree of callosity and variations in stratigraphic and geographic occurrence.

Athleta tuomeyi Conrad differs morphologically from *A. petrosa* (Conrad) in having extensive deposits of callus on the parietal area of the shell. Previous considerations of the relationship of *A.*

tuomeyi Conrad and *A. petrosa* (Conrad) were based on this morphological feature. Those minimizing the significance of parietal callus deposits (e.g., Smith, Palmer, Barry and Le Blanc) have considered *A. tuomeyi* Conrad and *A. petrosa* (Conrad) synonymous. Others (e.g., Conrad, Gardner) considered the presence of parietal callus significant and recognized *A. tuomeyi* Conrad as a distinct species.

Our treatment of the two forms as distinct species is based primarily on phylogenetic grounds. Although *A. tuomeyi* Conrad represents the first appearance of the *A. petrosa* stock, it cannot be classed as a subspecies of the main line of the stock because it shows certain more advanced morphologic features than the earliest forms of the main line of the stock. For example, earliest known forms of *A. tuomeyi* Conrad have shorter protoconchs than earliest known forms of *A. petrosa* (Conrad). In other morphologic features common to both species, such as spinosity, size, columellar folds, *A. tuomeyi* Conrad is comparable to *A. petrosa petrosa* (Conrad) and more advanced than *A. petrosa smithi* Fisher & Rodda. Trends in such features as size, spinosity, columellar folds, and body whorl liration in *A. tuomeyi* Conrad closely parallel the same trends in *A. petrosa* (Conrad). These and other trends are more accelerated in *A. tuomeyi* Conrad than in *A. petrosa* (Conrad). For example, there is a tendency for the formation of callus on the parietal region of advanced and terminal forms of *A. petrosa* (Conrad); however, on no form is callus as extensive as that on *A. tuomeyi* Conrad. Our recognition of *A. tuomeyi* Conrad as a distinct species is interpreted on an evolutionary position of *A. tuomeyi* Conrad inconsistent with successional development of the main line of the stock, and the presence of separate morphologic trends in *A. tuomeyi* Conrad. That *A. tuomeyi* Conrad is a part of the *A. petrosa* stock is shown by the close similarity and parallel development of certain morphologic features of *A. tuomeyi* with certain forms of *A. petrosa* (Conrad). If judged only by the most obvious morphologic distinction, that of ex-

tensive parietal callus resulting from an exaggeration of a feature more or less common to the stock as a whole, and not in an evolutionary context, specific distinction of *A. tuomeyi* Conrad and *A. petrosa* (Conrad) would be unwarranted. Many writers have considered extensive development of parietal callus as environmentally induced; Harris (1899a, p. 34) referred to *A. tuomeyi* Conrad as a "diseased" form. There is a potential for callus deposition among all forms of the *A. petrosa* stock, and possibly some combination of environmental conditions might have induced exaggeration of this character in *A. tuomeyi* Conrad. A few Wilcox mollusks, such as *Venericardia planicosta* Lamarck, 1806 (s.l.) and *Pseudoliva vetusta* (Conrad, 1833), also show abnormal thickening of their shells, but the vast majority of Wilcox mollusks apparently are normal in this respect. Callus formation, comparable to that in *A. tuomeyi* Conrad, occurs in the type species of *Athleta*, *A. rarispina* (Lamarck, 1811), from the Burdigalian (Miocene) of France (Pl. VII, figs. 5, 6).

In addition to extreme callosity, other, apparently aberrant, features, such as loosely coiled protoconch and a double row of spines on the shoulder, occur on a few specimens of *A. tuomeyi* Conrad. Aldrich (1931, p. 6, pl. 6, fig. 3) has illustrated a specimen of *A. tuomeyi* Conrad with a double row of shoulder spines. One specimen of *A. petrosa petrosa* (Conrad) (B.E.G. locality 201-T-3) similarly has a double row of spines on the body whorl shoulder.

Type data.—Lectotype, Cat. No. 5883, Academy of Natural Sciences, Philadelphia, Pennsylvania.

Type locality.—Bashi Creek, Clarke County, Alabama (Bashi Member, Hatchetigbee Formation).

Occurrence.—*Athleta tuomeyi* Conrad is common in marine Wilcox rocks of eastern Texas (Pendleton and Sabinetown Formations). The species is common throughout the Atlantic and Gulf Coastal Plains, occurring in the Wilcox Group of northeastern Mexico; Wilcox Group (late Paleocene and early Eocene) of Louisiana; the

Nanafalia Formation, Gregg's Landing and Bells Landing Members of the Tuscahoma Formation and the Bashi Member of the Hatchetigbee Formation of Alabama; and the Aquia Formation of Virginia. B.E.G. localities in Texas are 201-T-1 and 201-T-13.

ATHLETA LISBONENSIS (Aldrich, 1897)
(Pl. IX, figs. 1, 2, 10-14)

- 1890 *Volutilithes precursor*: Dall, Contributions to the Tertiary fauna of Florida, etc., Part 1: Wagner Free Inst. Sci., Trans., vol. 3, p. 84, pl. 6, fig. 1 (not *Volutilithes praecursor* Bellardi, 1887).
- 1891 *Volutilithes precursor* Dall: Heilprin, The Eocene Mollusca of the State of Texas: Acad. Nat. Sci. Philadelphia, Proc. 1890, p. 397.
- 1895 *Volutilithes precursor* Dall: Kennedy, The Eocene Tertiary of Texas east of the Brazos River: Acad. Nat. Sci. Philadelphia, Proc., vol. 47, pp. 114, 123, 125, 126, 128.
(?) *Volutilithes praecursor* Dall var.: Kennedy, *ibid.*, p. 117.
- 1897 *Volutilithes lisbonensis*: Aldrich, Notes on Eocene Mollusca, with descriptions of some new species: Bull. Amer. Paleont., vol. 2, no. 8, p. 14, pl. 2, figs. 1, 1a.
- 1899 *Volutilithes lisbonensis*: Cossmann, Essais de paleoconchologie comparée, livr. 3, p. 137.
Volutilithes wheelockensis: Cossmann, *idem.* (= *V. precursor* Dall, not *V. praecursor* Bellardi, 1887).
- 1903 *Volutilithes precursor* Dall: Dumble, Geology of southwestern Texas: Amer. Inst. Min. Eng., Trans., vol. 33, p. 935.
- 1905 *Volutilithes precursor* Dall: Schuchert, Catalogue of the type specimens of fossil invertebrates in the Department of Geology, United States National Museum: U. S. Nat. Mus. Bull. 53, pt. 1, p. 697.
- 1914 *Plejona precursor* (Dall): Deussen, Geology and underground waters of the southeastern part of the Texas Coastal Plain: U. S. Geol. Survey Water-Supply Paper 335, p. 64.
- 1920 *Volutilithes precursor* Dall var.: Dumble, The geology of east Texas: Univ. Texas Bull. 1869, pp. 92(?), 95-96, 97, 99.
- 1923 *Plejona precursor* (Dall)?: Trowbridge, A geologic reconnaissance in the Gulf Coastal Plain of Texas, near the Rio Grande: U. S. Geol. Survey Prof. Paper 131-D, p. 95.
- 1931 (?) *Volutilithes* sp. near *lisbonensis* Aldrich: Renick and Stenzel, The lower Claiborne on the Brazos River, Texas: Univ. Texas Bull. 3101, p. 101.
- 1933 *Volutocorbis lisbonensis* (Aldrich) var. *crockettensis*: Plummer, Cenozoic systems in Texas: Univ. Texas Bull. 3232, pp. 813-814, pl. 9, fig. 19.
Volutocorbis lisbonensis (Aldrich) var. *wechesensis*: Plummer, *ibid.*, pp. 813-814, pl. 9, figs. 17-18.
Volutocorbis wheelockensis (Cossmann) var. *bastropensis*: Plummer, *ibid.*, pp. 813-814, pl. 9, fig. 16.
Volutocorbis wheelockensis (Cossmann) var. *sabinensis*: Plummer, *ibid.*, pp. 813-814, pl. 9, figs. 20-21.
(?) *Volutocorbis petrosa* (Conrad): Trowbridge, Tertiary and Quaternary geology of the lower Rio Grande region, Texas: U. S. Geol. Survey Bull. 837, pl. 42, fig. 3.
- 1937 *Athleta lisbonensis* (Aldrich): Palmer, The Claibornian Scaphopoda, Gastropoda, and dibranchiate Cephalopoda of the southern United States: Bull. Amer. Paleont., vol. 7, no. 32, p. 383, pl. 59, figs. 14, 15.
Athleta lisbonensis crockettensis (Plummer): Palmer, *ibid.*, pp. 383-384, pl. 59, fig. 11.
Athleta lisbonensis wechesensis (Plummer): Palmer, *ibid.*, p. 384, pl. 59, figs. 5, 9.
Athleta wheelockensis (Cossmann): Palmer, *ibid.*, pp. 380-381, pl. 59, figs. 6, 7, 12.
Athleta wheelockensis bastropensis (Plummer): Palmer, *ibid.*, p. 381, pl. 59, figs. 3, 4, 8.
Athleta wheelockensis sabinensis (Plummer): Palmer, *ibid.*, pp. 381-382, pl. 59, figs. 10, 13.
- 1945 *Volutocorbis wheelockensis* (Cossmann): Gardner, Mollusca of the Tertiary formations of northeastern Mexico: Geol. Soc. Amer. Mem. 11, p. 223.
(?) *Volutocorbis* ? sp. cf. *V. ? wheelockensis* (Cossmann): Gardner, *ibid.*, pp. 223-224, table 3, pl. 22, fig. 11.

Original description.—Shell as in figure; whorls 8, the first 3 forming the nucleus which is smooth, the periphery of remaining whorls ornamented with rather sharp spines, body whorl with 11 ribs, spaces between shining and smooth, though very fine lines of growth are present; shell shoulder above the spines and ornamented with 3 spiral lines, also slightly spinous, directly above the others; suture distinct; aperture nearly two-thirds the length of the shell; columella with 2 large plaits, with a small one between; outer lip lirate within; basal part of body whorl closely covered with fine spirals partly impressed and partly raised.

This species resembles in general outline *V. precursor* Dall, but that species has no shoulder spines and its ribs are flattened. This form is related to *V. petrosus* Con., but is much more

slender, smoother, has stronger ribs and more numerous whorls. (Aldrich, 1897, pp. 14-15.)

Revised description.—*A. lisbonensis* (Aldrich) is similar to *A. petrosa* (Conrad) in the first 5 or 6 whorls. Smooth protoconch occupies $3\frac{3}{4}$ to $4\frac{1}{2}$ whorls, grading into ribbed stage which persists for one-quarter to three-fourths of the succeeding whorl. As in *A. petrosa* (Conrad), the ribbed stage passes into a stage with a well-defined shoulder and subsutural ridge, both bearing a single row of nodes at their crests. On the next 1 to 2 whorls, the nodes increase slightly in size, increasing more on the shoulder than on the subsutural ridge. Subsequently, nodes are reduced in size but may become larger on terminal whorls of large specimens. Remaining whorls show the morphologic characters that define the species.

Intermediate forms.—These forms, typified by *Plejona lisbonensis wechesensis* Plummer, 1933, and *Plejona lisbonensis crockettensis* Plummer, 1933, are intermediate to *A. petrosa* (Conrad) and end members of *A. lisbonensis* (Aldrich); the subsutural ridge, and to some extent the shoulder, is subdued, and the whorls have a smooth, gently rounded profile marked by 4 slight, spiral ridges instead of the subsutural ridge and shoulder. The anterior spiral ridge, delineating the ramp and the remainder of the body whorl, retains small nodes. The shell tends toward a subfusiform shape. Two varieties recognized by Plummer (1933, p. 813) are morphologically transitional and differ only in size and spiral angle.

Advanced forms.—These forms, typified by *Volutilithes precursor* Dall, 1890, *Plejona wheelockensis sabinensis* Plummer, 1933, and *Plejona wheelockensis bastropensis* Plummer, 1933, show a continuation of the morphologic trends discussed above; nodes are very weak or absent, the posterior part of the body whorl is marked by 3 or 4 slight, spiral ridges, the shoulder is indistinct, the periphery is rounded, the shape of the shell is subfusiform, and the longitudinal ribs are narrow but extend anteriorly on most of the body

whorl. In our opinion, these intermediate and advanced forms of *A. lisbonensis* (Aldrich) do not warrant separate, formal designation.

Other features of *A. lisbonensis* (Aldrich) are similar to *A. petrosa* (Conrad). Longitudinal lirae persist throughout all whorls. Spiral lirae are distributed uniformly on the body whorl but on some specimens are accentuated anteriorly; a slight siphonal fasciole is present on advanced forms. Prominent denticulation on the inside of the outer lip is characteristic of more advanced forms. The columella has 2 small primary folds; secondary folds are uncommon.

Dimensions.—Based on measurements of 96 specimens, dimensions are: height, 6 to 30 mm, mean 14.5 mm; width, 3 to 14 mm, mean 6.7 mm; height of spire, 2 to 11 mm, mean 5.9 mm.

Remarks.—*Athleta lisbonensis* (Aldrich, 1897) shows a marked tendency toward reduction of nodes in the last whorls. Accompanying reduction of nodes is a tendency for steepening of the spiral profile or reduction of the spiral angle, the development of 3 to 4 slight spiral ridges on the ramp, and an anterior extension and narrowing of the longitudinal ribs on the body whorl.

Forms that are here, for convenience, designated as intermediate and advanced occur together, although the intermediate forms are more abundant in the Weches Formation and the advanced forms more abundant in the Stone City and Cook Mountain Formations. This, to an extent, suggests that *A. lisbonensis* (Aldrich) is a monophyletic offshoot from *A. petrosa* (Conrad), and that the morphologic gradations within *A. lisbonensis* (Aldrich) are an expression of evolutionary lineage. On the other hand, these forms may represent an environmentally induced population variant of *A. petrosa* (Conrad), occurring at different places and times, with different morphologic types from any one locality representing variants in a normal population of *A. petrosa* (Conrad). Advanced features of *A. lisbonensis* (Aldrich) gen-

erally occur on larger forms; however, there are a few exceptions to this generalization. In light of present knowledge, we judge *A. lisbonensis* (Aldrich) as an evolutionary lineage and consider it a distinct species, taking by priority the oldest valid name of forms within this group.

In summary, *A. lisbonensis* (Aldrich) is distinguished from contemporaneous forms of *A. petrosa* (Conrad) by (1) reduction of nodes, (2) reduction of peripheral angulation, (3) extension of longitudinal ribs to cover most of body whorl, (4) subfusiform shape, and (5) longer protoconch.

Type data.—Holotype, number 638996, at U. S. National Museum, Washington, D. C.

Type locality.—Claiborne Bluff, Alabama River, Monroe County, Alabama (Lisbon Formation).

Occurrence.—Lisbon Formation of Alabama; occurs in Texas at the following B.E.G. localities: 11-T-2, 26-T-5, and 201-T-2 (Weches Formation); 7-T-17, 26-T-1, 26-T-48, 113-T-36, 142-T-2, 144-T-1, 197-T-3, and 201-T-5 (Stone City Formation); 21-T-1, 21-T-6, 145-T-51, 145-T-53, and 201-T-33 (Wheelock Member, Cook Mountain Formation).

ATHLETA DALLI (Harris, 1895)
(Pl. IX, figs. 3, 4)

- 1891 *Caricella reticulata* Aldrich: Heilprin, The Eocene Mollusca of the State of Texas: Acad. Nat. Sci. Philadelphia, Proc. 1890, p. 394 (*vide* Harris, 1895, p. 67).
- 1895 *Volutilithes dalli*: Harris, New and otherwise interesting Tertiary Mollusca from Texas: Acad. Nat. Sci. Philadelphia, Proc. 1895, p. 67, pl. 6, fig. 8, 8a.
Volutilithes dalli Harris, n. sp.: Kennedy, The Eocene Tertiary of Texas east of the Brazos River: Acad. Nat. Sci. Philadelphia, Proc. 1895, Pt. 1, p. 123.
- 1899 *Volutilithes Dalli* Gilb. Harr.: Cossmann, Essais de paleoconchologie comparée, livr. 3, p. 137.
- 1907 *Volutilithes dalli* of Harris: Burnett Smith, A new species of *Athleta* and a note on the morphology of *Athleta petrosa*: Acad. Nat. Sci. Philadelphia, Proc., vol. 59, p. 230.
- 1920 *Volutilithes dalli* Harris, n. sp.: Dumble, The geology of east Texas: Univ. Texas Bull. 1869, p. 96.
- 1931 *Volutilithes dalli* Harris: Renick and Stenzel, The lower Claiborne on the Brazos

River, Texas: Univ. Texas Bull. 3101, p. 106, pl. 6, fig. 9.

- 1933 *Volutocorbis dalli* (Harris): Plummer, Cenozoic systems in Texas: Univ. Texas Bull. 3232, p. 645.
Volutocorbis dalli (Harris) var. *smithvillensis*: Plummer, *ibid.*, pp. 813-814, pl. 9, figs. 14, 15.
- 1937 *Athleta dalli* Harris: Palmer, The Claibornian Scaphopoda, Gastropoda, and dibranchiata Cephalopoda of the southern United States: Bull. Amer. Paleont., vol. 7, no. 32, p. 382, pl. 61, figs. 11-14.
Athleta dalli smithvillensis (Plummer): Palmer, *ibid.*, p. 383, pl. 61, figs. 9, 10.
- 1939 *Volutocorbis dalli* (Harris): Stenzel, The geology of Leon County, Texas: Univ. Tex. Pub. 3818, p. 112.

Original description.—Size and general form as indicated by the figures; whorls about 7; spiral whorls and shoulder of the body whorl generally coarsely cancellated with revolving lines and transverse costae; humeral angle of the body whorl often spinose; medial portion of the body whorl with finer but very distinct revolving striae and fine lines of growth; base of body whorl as in other members of this genus [*Volutilithes*]; labrum strongly lirated within; columella with two well-defined oblique plaits and sometimes one or more rudimentary ones.

The amount of reticulation or ornamentation possessed by different individuals of this species varies greatly. Some specimens are quite smooth on the medial portion of the body whorl, and show but slight irregularities on the shoulder. A form of this character is shown in fig. 8a. Such specimens have usually two well-marked folds on the columella and no trace of additional ones.

This species is evidently related to *V. haleanus* Whitf. but is less strongly sculptured, and wants the peculiar concave humeral zone of that species. Moreover, *haleanus* has three distinct and well-defined columellar plaits. This species is named in honor of W. H. Dall, the well-known authority on *Volutidae*. (Harris, 1895, pp. 67-68.)

Revised description.—Early whorls like contemporaneous forms of *A. petrosa* (Conrad) with protoconch of $3\frac{1}{2}$ to $4\frac{1}{8}$ smooth whorls followed by one-half whorl marked by simple axial ribs. Slight shoulder and subsutural ridge follow the ribbed stage but are subdued anteriorly as the posterior part of the whorl becomes rounded in profile and is marked by 4 slight spiral ridges instead of a subsutural ridge and shoulder. Most anterior ridge, situated on the periphery of the whorl, develops nodes which are lost anteriorly.

Spiral and longitudinal lirae cover en-

tire body whorl to give a cancellate sculpture. Shape is subfusiform; outer lip lirate and denticulate. Columella simple, straight to slightly curved, and marked by 2 primary folds. Anterior canal shallow but distinct.

Dimensions.—Based on measurement of 30 specimens, dimensions are: height, 4 to 30 mm, mean 11.9 mm; width, 2 to 18 mm, mean 6.3 mm; height of spire, 2 to 15 mm, mean 4.2 mm. The mean ratio of height to width is 2.2 mm.

Remarks.—We judge *A. dalli* (Harris), and specimens illustrated by Plummer (1933, p. 813, pl. 9, figs. 14, 15) as a variety of *A. dalli* (Harris), to be a part of the *A. petrosa* stock. Early whorls of *A. dalli* (Harris) are similar to early whorls of contemporaneous forms of *A. petrosa* (Conrad) but later whorls differ. The shoulder and subsutural ridge of *A. dalli* (Harris) are subdued and eventually replaced by 4 slight ridges; spines are not present. Nodes are developed only slightly and pass into the adult cancellate stage.

A. dalli (Harris) is distinguished from contemporaneous forms of the *A. petrosa* stock by its cancellate sculpture, subfusi-

form shape, lack of spines, and longer protoconch.

Type data.—Holotype (Harris, 1895, pl. 6, fig. 8) designated by Palmer (1937, p. 383, pl. 61, fig. 13) is at the Bureau of Economic Geology, The University of Texas, Austin, Texas; B.E.G. No. 35508. The specimen is poorly preserved; only one whorl of the spire is now present, and the columella is missing. Dimensions: height, 30 mm; width, 18 mm. The other specimen figured by Harris (1895, pl. 6, fig. 8a) is also at the Bureau of Economic Geology and has B.E.G. No. 35507. It appears to be in about the same condition as when it was drawn for Harris's publication. The specimen was once considerably larger; about one-half whorl has been broken off, and the tip of the spire is missing. Dimensions: height, 34 mm; width, 15 mm; height of spire, 9 mm.

Type locality.—Bluff on Colorado River at Smithville, Bastrop County, Texas; B.E.G. locality 11-T-2 (Weches Formation).

Occurrence.—B.E.G. localities 11-T-2, 145-T-32, 197-T-2, and 197-T-4 (Weches Formation); 89-T-12 and 197-T-3 (Stone City Formation).

TABLE 4. Chief distinguishing features of taxa within *Athleta petrosa* stock.

Taxon	Mean Size (mm) Height	Width	Gross Shape	Adult Whorl Ornamentation	Average Length of Protoconch	Parietal Callus	Labral Denticulation	Columellar Folds	Siphonal Fasciole	Peripheral Angulation	Stratigraphic Occurrence in Texas
<i>A. petrosa symmetrica</i> (Conrad, 1854)	30.1	14.4	Subfusiform to substrombiform	Long, slender, posteriorly recurved spines	2¼ whorls	Moderate	Moderate	Prominent 3 primary 2 or more secondary	Moderate	Moderate	Caddell(?) and Yegua Formations
<i>A. petrosa petrosa</i> (Conrad, 1853)	23.1	10.4	Strombiform	Moderate to prominent spines	3⅞ whorls	Moderate to slight	Moderate to slight	Moderate to prominent, 2 primary 1 or more secondary	Slight	Sharp	Cook Mountain, Stone City, and Weches Formations
<i>A. petrosa smithi</i> Fisher & Rodda, n. subsp.	16.9	7.8	Fusiform to substrombiform	Small spines to cancellate	3½ whorls	Slight to none	Slight to none	Slight, 2 primary	Slight	Moderate	Reklaw Formation
<i>A. lisbonensis</i> (Aldrich, 1897)	14.5	6.7	Fusiform	No spines, elongated longitudinal ribs	4⅞ whorls	Slight	Prominent	Slight, 2 primary	Slight	Broad to rounded	Cook Mountain, Stone City, and Weches Formations
<i>A. dalli</i> (Harris, 1895)	25	13	Fusiform	No spines, cancellate	3¾ whorls	Slight	Prominent	Moderate, 2 primary	Slight to moderate	Broad to rounded	Stone City and Weches Formations
<i>A. tuomeyi</i> Conrad, 1853	32	16	Substrombiform	Moderate spines, double row of spines on some specimens	3 whorls	Thick and extensive	Moderate to slight	Moderate, 2 primary 1 or more secondary	Slight to moderate	Moderate	Sabinetown and Pendleton Formations

EXPLANATION OF CLASSIFICATION EMPLOYED

The grouping and classifying of fossils, such as the *Athleta petrosa* stock, so that hierarchial rank reflects both morphology and evolution is a difficult task. We have used a classification that is essentially phylogenetic, based on morphology and superposition; taxa designate lineages within the stock and successive elements along one lineage. Classification here employed is as follows:

Genus—*Athleta* Conrad

(Stock)—informal, regional: *Athleta petrosa* stock

Species—

1. Phyletic or progressive species, main line of stock—*A. petrosa* (Conrad)
2. Contemporaneous, divergent or cladogenetic species—*A. lisbonensis* (Aldrich) and *A. dalli* (Harris)
3. Temporally isolated, divergent or cladogenetic species—*A. tuomeyi* Conrad

Subspecies—3 successive taxa designated arbitrarily but correspond to established stratigraphic divisions: *A. petrosa smithi* Fisher & Rodda, *A. petrosa petrosa* (Conrad), and *A. petrosa symmetrica* (Conrad).

In a phylogenetic sense, *A. petrosa* (Conrad) and contemporaneous, divergent species are more closely related than are any of these species and *A. tuomeyi* Conrad, an earlier, divergent species. A formal classification that would reflect these phylogenetic distinctions would be advantageous. This could be accomplished by inserting in the above classification an additional higher category, namely that of subgenus. *Eoathleta* Gardner, 1945, and *Volutovetus* Pilsbry & Olsson, 1954, proposed as subgenus and genus respectively, are available, and might be used in place of the informal term stock, or as a rank above that of species and below that of stock. In the case of the *A. petrosa* stock, we judge the disadvantages of such a classification to outweigh the advantages. Morphologic distinction within the stock is no more than specific; subgeneric rank is best reserved, in our opinion, for larger scale provincial divisions of the genus *Athleta* (e.g., Gulf Coast, Paris and London Basins).

ORIGIN OF *ATHLETA PETROSA* STOCK

The marked similarity of early whorls of *Athleta petrosa* (Conrad), *A. tuomeyi* Conrad, and certain species of *Volutocorbis*, suggests that some form of *Volutocorbis* was the ancestor of the *A. petrosa* stock. Both groups have a smooth protoconch followed by a short, simple, ribbed stage. In both, the ribbed stage passes anteriorly into a cancellate-nodose stage. In species of the *A. petrosa* stock, the cancellate-nodose stage is progressively shortened, generally occupying less than 2 whorls, and is a part of the juvenile ornamentation in all but earliest forms; in *Volutocorbis* the cancellate-nodose stage persists and is the adult ornamentation (fig. 2). Relationships are judged through close similarity of several aspects of ontogenetic development. Species of *Volutocorbis* are common in the Midway Group of Paleocene age and so occur in a logical stratigraphic position for an ancestor of the Eocene *A. petrosa* stock.

Volutocorbis limopsis (Conrad, 1860) (Pl. VII, figs. 1, 2) is the most generalized species of *Volutocorbis*, and either this species or some form morphologically similar to it is considered a probable ancestor of the *A. petrosa* stock.

Although the scarcity and poor preservation of forms that might be considered ancestral or transitional to *A. petrosa* (Conrad) and *A. tuomeyi* Conrad inhibit an adequate study of the origin of these species, certain features may be outlined. Specimens of *A. tuomeyi* Conrad from the lowermost part of the Wilcox Group (Paleocene) in Louisiana (Barry and Le Blanc, 1942, p. 140) and the lower part of the Wilcox Group (Eocene) in Alabama (Burnett Smith, 1906, p. 61) are morphologically similar to certain forms of *A. petrosa* (Conrad) and show little or no callus deposition; they are, however, transitional to more callous forms. Burnett

Smith (1906, pp. 61, 74) stated that these noncallous forms, which have a protoconch of 3 whorls, represent the earliest part of the *A. petrosa* stock in Alabama. Among early Claibornian forms in Texas (*A. petrosa smithi* Fisher & Rodda from the Reklaw Formation) are forms morphologically more primitive than the noncallous Wilcox forms in having a longer protoconch (mean length, 3.6 whorls) and a

longer cancellate stage. This suggests that *A. tuomeyi* Conrad is an early divergence from the main line of the stock as it does not fit logically with the subsequent development of the *A. petrosa* main line, though it is morphogenetically similar and is included in the *A. petrosa* stock. Burnett Smith (1906, p. 65) apparently had only a few, poorly preserved early Claibornian forms of *A. petrosa* (Conrad).

GENUS *ATHLETA* IN THE GULF COASTAL PLAIN

Three additional species in the Eocene of the Gulf Coastal Plain have been assigned to the genus *Athleta*. These include *A. haeleanus* (Whitfield), *A. sayana* (Conrad), and *A. clayi* Burnett Smith and are found in Jacksonian and Claibornian rocks of Mississippi and Alabama. General phylogenetic relationship of taxa within the genus *Athleta* in the Gulf Coastal Plain, based primarily on Burnett Smith's (1906, 1907b) studies in Alabama and our study in Texas, is outlined in figure 31.

Athleta haeleanus (Whitfield, 1865).—The first 7 whorls of forms included in this species are very similar to early whorls of forms within the *A. petrosa* stock. The last 2 whorls, however, differ significantly. Nodes on the subsutural ridge and shoulder never become spines. Nodes on the subsutural ridge characteristically coalesce to form a distinct, crenulate keel. Keel formation in *A. haeleanus* (Whitfield) is paralleled by keel formation on the Texas early Claibornian form of *A. petrosa* (Conrad), *A. petrosa smithi* Fisher & Rodda. Spiral lirae are distributed uniformly on the body whorl; longitudinal lirae are faint. Closely spaced, small, longitudinal ribs, occurring with spiral lirae, produce a cancellate sculpture on the body whorl. Shape is subfusiform. A Jacksonian form, *A. haeleanus jacksonia* Palmer, 1947, based on three poorly preserved specimens, was distinguished by Palmer (1947) on the basis of general coarsening and thickening of body whorl sculpture and ornamentation.

A. haeleanus (Whitfield) is common in the Lisbon Formation of Alabama; the

Jackson subspecies of Palmer occurs at Montgomery, Louisiana. The species has not been found in Texas.

Athleta clayi Smith, 1907, and *A. sayana* (Conrad, 1853) (Pl. VII, figs. 3, 4).—According to Burnett Smith (1907b, pp. 234–242), these two species are related as they show a similar modification of the protoconch; other features of the species, especially sculpture, are different. In both, the protoconch is relatively larger than that in *A. petrosa* (Conrad) but occupies only $1\frac{1}{2}$ to $1\frac{3}{4}$ whorls. *A. clayi* Smith is subfusiform and spinose, closely resembling *A. petrosa* (Conrad), and, according to Burnett Smith (1907b, pp. 234–242), is intermediate to *A. petrosa* (Conrad) and *A. sayana* (Conrad). Specimens of *Athleta* with short protoconchs (cf. *A. clayi*) and long protoconchs (cf. *A. petrosa*) occur together in the Cook Mountain Formation at St. Maurice, Louisiana (Smith, 1907, pp. 235–239) and in the Wautubbee Formation, 3 miles east of Newton, Newton County, Mississippi (B.E.G. locality Miss-1).

A. sayana (Conrad) is the common volutid gastropod in the upper part of the Claiborne Group (Gosport Formation) of Alabama and is characterized by variation in body whorl sculpture. One variant, typified by *Volutilithes ipnotica* De Gregorio (1890), is characterized by uniform distribution of spiral lirae on the body whorl; another variant, typified by *Volutilithes mica* De Gregorio (1890), shows a loss of spiral and longitudinal lirae on the posterior half of the body whorl. These variants are figured by Palmer (1937, pl. 60).

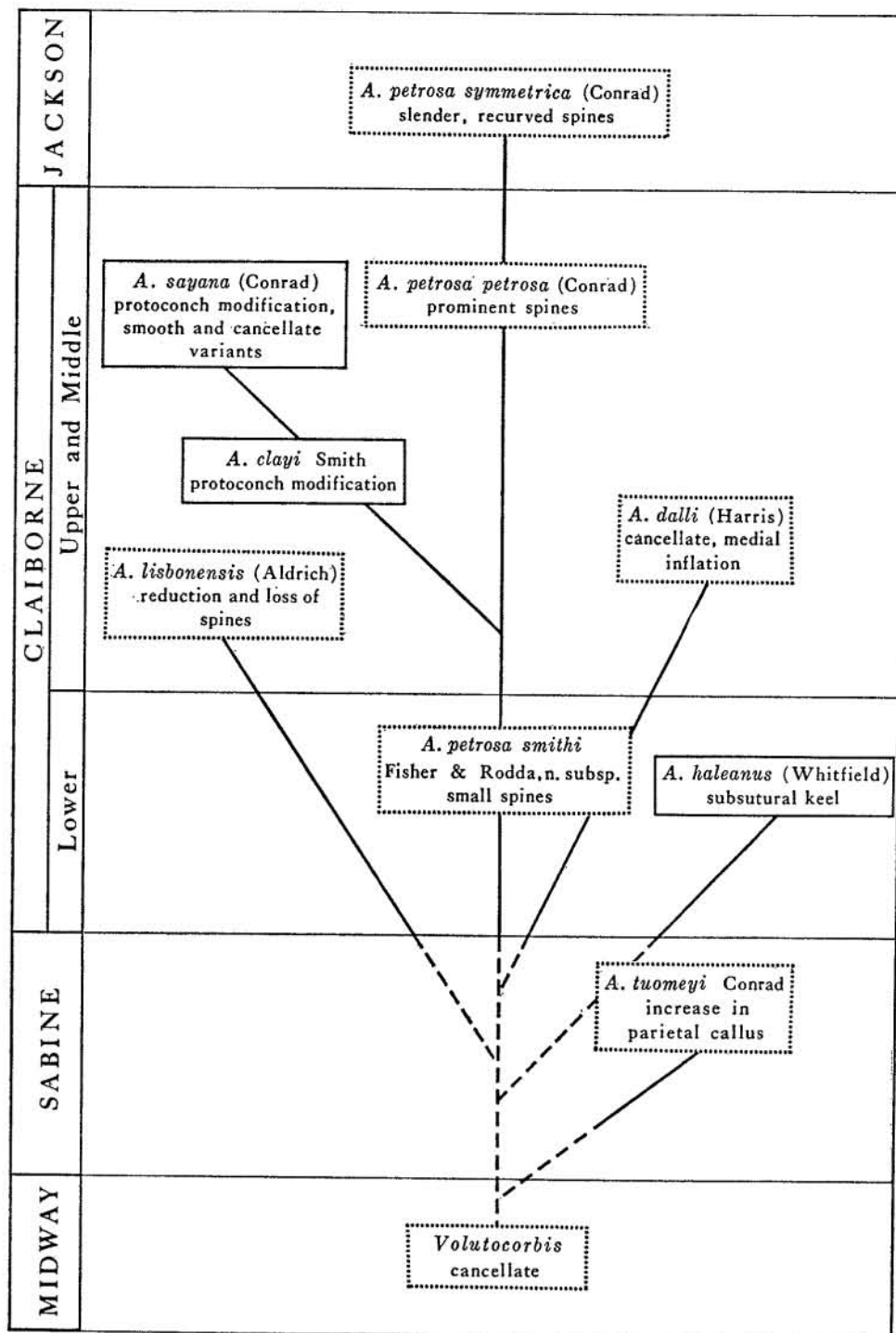


FIG. 31. Phylogenetic relationship of taxa within genus *Athleta* of Gulf Coastal Plain. Taxa enclosed by dotted lines occur in Texas.

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APPENDIX A

QUANTITATIVE STUDY OF *Athleta petrosa* STOCK

INTRODUCTION

Quantitative study and statistical analyses of the *Athleta petrosa* stock were designed to (1) evaluate and characterize specific samples, (2) test certain qualitative observations, and (3) present certain ontogenetic and evolutionary features of the stock in quantitative terms. Basic morphologic features, height, width, height of spire, number of columellar folds, and number of ornaments were measured or counted from approximately 1,600 specimens from 50 localities in Texas, Alabama, Louisiana, and Mississippi. Summary histograms of observed and computed data are given by locality in Plate III (pocket). A summary of quantitative data is included as a part of this appendix.

DATA PROCESSING

Two programs were prepared for the Control Data Corporation Model 1604 digital computer. Program I is designed to calculate 20 combinations of the five observed data for each individual represented in a data block and to provide a statistical summary of each item of observed and calculated data. Program II is designed to summarize three of the observed data by plotting cumulative curves of relative frequency and by plotting scatter diagrams illustrating the relationship between each pair of variables. Both programs are written in Fortran language and consist of intermixed conventional Fortran statements and symbolic machine instructions. Number of data blocks processed by either program during a single computer run is determined by a control factor loaded with data for the run.

Observed data for each specimen are entered in five number fields on an IBM punch card. All observed values are positive; the negative entry, -99.0, indicates that the morphologic feature could not be measured. Two number fields contain

identification numbers, a 3-digit number identifying the county in Texas (or state other than Texas) where the specimen was collected and a 6-digit number that is unique for cards of specimens from a single county (or state). These cards were the source of data processed by the computer; cards were machine-sorted to provide basic data for histograms of height, height of spire, width, and number of ornaments (Pl. III, pocket).

Program I.—Program I (Pl. IV, pocket) is a Fortran program designed to calculate 20 combinations of five observed data for each specimen in a data block and to provide a statistical summary of observed or calculated data. For the purpose of discussion, the program is divided into five sections: program requirements, preliminary operations, data input, specimen data calculations, and statistical summary.

Statements that reserve and identify blocks of magnetic-core cells, define symbol fields on data cards, and provide instructions for printing the results are grouped under the heading *program requirements*.

A group of *preliminary operations* must be performed before loading the first block of specimen data. Number of specimen-data blocks to be processed during the run and headings used in printing the results are read from 6 preliminary data cards (examples 1 and 2). Any number of data blocks may be processed during a computer run; the remainder of the program is repeated by the run-control loop until the specified number of blocks is processed.

Specimen data are transferred from data cards to the computer by the *data input* routine. Data cards are arranged in blocks of 1 to 400 specimen cards preceded by a lead card. During this study, each block included the data from specimens of a single locality. County name, locality number, and the number of specimen-data cards in the block are entered on the lead

data card (example 3). The 6-digit identification number and the 5 observed data are transferred to the computer from each specimen-data card (example 4).

Observed data for each specimen are processed separately in the section headed *specimen data calculations*. If all observed data are available, the following 20 combinations are calculated:

height/width
height/height of spire
width/height of spire
number of columellar folds/height
number of columellar folds/width
number of columellar folds/height of spire
number of columellar folds/number of ornaments
number of ornaments/height
number of ornaments/width
number of ornaments/height of spire
height/ratio of number of columellar folds to number of ornaments
width/ratio of number of columellar folds to number of ornaments
height of spire/ratio of number of columellar folds to number of ornaments
number of columellar folds/ratio of height to width
number of ornaments/ratio of height to width
sum = height + width + height of spire
height/sum
width/sum
height of spire/sum
ratio of height to height of spire/sum

One or more morphologic features could not be measured on incomplete specimens included in this study. Calculations are bypassed if the required data are not available. Observed and calculated data are printed in tabular form after all specimen data are processed.

In the final section of the program, *statistical summary*, each item of observed and calculated data is summarized by the following:

N	=	number of individuals in data block for which an observed value is available
ΣX	=	sum of data values
ΣX^2	=	sum of squares of data values
$\bar{X} = \frac{\Sigma X}{N}$	=	arithmetic mean, a measure of central tendency of data values

$$S = \sqrt{\frac{\Sigma X^2 - \frac{(\Sigma X)^2}{N}}{N - 1}} = \text{standard deviation, a measure of variability of the data values}$$

The summary table is printed after all summary values are calculated.

Program II.—Program II (Pl. V, pocket) is a Fortran program designed to compile nonfractional values of 3 variables for each specimen in a data block, print data points on a cumulative curve of relative frequency for each variable, and plot scatter diagrams showing the relationship of each pair of variables. For the purpose of discussion, this program is divided into six sections: program requirements, preliminary operations, data input, compilation, diagrams, and curves.

Statements grouped under the heading *program requirements* perform the same functions as in Program I. *Preliminary operations* include transfer of headings, symbols, and constants from 12 preliminary data cards (example 1), definition of constants, and generation of number groups used in the compilation of data and the printing of graphical output.

The *data input* routine controls transfer of specimen data from cards to computer and, indirectly, length of computer run. Data are arranged in blocks of 1 to 1,300 specimen cards preceded by a lead card (example 2). Four data fields on the lead card contain block identifications that are reproduced in headings on the output sheets, the number of specimen data cards in the block, and a compilation-control factor. Entries in 3 data fields are transferred to the computer from each specimen data card (example 4) if the indicated number of specimen cards is within the range 1–1,300. Only digits to the left of the decimal point are transferred; fractional data cannot be processed by this program. The computer run is terminated if the indicated number of specimen data cards is outside the range 1–1,300. A special lead card (example 3, blank in columns 65–70) is placed after the last data block to terminate the run.

Either of two processing routines is

selected by testing the compilation-control factor early in *compilation*. Data loaded as a block are processed as a unit and summarized in one set of curves and diagrams if the factor is zero (either a cipher or blank) or negative. Data loaded as a block are divided into two groups by entering the number of specimens in the first group as the compilation-control factor. Three sets of curves and diagrams are prepared—one set for the data block as a unit and another for each of the data groups.

The large magnetic-core capacity of the CDC 1604 computer permits concurrent compilation of data for 3 cumulative curves and 3 scatter diagrams. Data for a specimen are tested to determine whether observed values are available. Each observed value is counted in the compilation block for the appropriate cumulative curve and tested to determine whether it is within the range of the computer-plotted diagram. Data for points that fall outside the diagram are printed on the summary data sheet. The specimen is counted in appropriate cells of four compilation blocks for each scatter diagram if observed values for both variables are within the range of the computer-plotted diagram. The routine is repeated for each specimen to be represented on a set of curves and diagrams.

Conversion of compiled data to a set of diagrams is controlled by the section headed *diagrams*. Space requirements for each diagram are determined by scanning the compiled data. Number of specimens, number of observed values for each variable, number of computer-plotted points and printer sheet requirements for each scatter diagram, and observed data values for points outside the range of computer-plotted diagrams are printed on the summary data sheet.

Scatter diagram data are printed on a field of points representing intersections of lines on a grid of half-inch squares. The point field is formed by decimal points spaced at intervals of 5 characters on each third line printed by the IBM 407 line printer. The number of specimens plotted at a point is printed to the left of the dec-

imal point; the number of specimens plotted within a 9-point accumulation pattern (fig. 32a) centered at a point is printed below the point. Nonsignificant zeros are suppressed. A second copy of the diagram, containing only the 9-point accumulation values, is printed for use as a work-sheet. Contours representing concentrations of specimens and a trend line representing maximum concentration of specimens are drawn manually on the work-sheet. Contour diagrams in Plate VI (pocket) are drafted from contoured computer-output sheets.

Frequency distribution data compiled for each variable are converted to cumulative curves of relative frequency in the section headed *curves*. Cumulative curve data are printed on the IBM 407 line printer. Each class entry is a line consisting of cumulative percentage of specimens smaller than or equal to the upper class limit, upper class limit entered as scale value for curve, and a field of 101 symbols (either blank or decimal points) representing 0 through 100 percent on the curve. Cumulative percent values are calculated from compiled data and are used to control assembly of the 101 characters that make up the body of the curve. Points are entered at the 0 and 100 percent positions on each line to provide scale references. Cumulative percent values other than 0 or 100 are represented by two points bounding the 1-percent interval that includes the value.

Scatter diagrams.—Certain similarities and differences of taxonomic units are readily demonstrated by distribution of points on scatter diagrams. Numbers, symbols, and contours were considered as possible indicators of the concentration of data points; contours were chosen because their use permits publication at a smaller scale.

There are less than 100 specimens in 4 of the 6 taxonomic units for which diagrams were prepared. The irregular distribution of the small number of data points on a grid based on primary classes of observed data precluded effective contouring. Two methods of improving the

distribution of data points were considered. The number of grid points could be reduced by grouping data in secondary classes before plotting, or the total number of data points within a selected area around each grid point could be accumulated and entered at the point for contouring control. The accumulation method was used because grouping in secondary classes would have reduced the number of classes for 1 variable to 6 or less for each of the smaller groups of specimens.

A 9-point accumulation pattern (fig. 32a) was selected as the most practical pattern for the data to be presented. The total number of specimens plotted at points A through I is entered at the center of the square (point E). The accumulation process is repeated for each of the points within the area of the diagram. A sample area covering 48 grid points of the diagram, width versus height for *A. petrosa smithi* Fisher & Rodda (fig. 32b), is used to illustrate the results of the accumulation method. Within the sample area 29 specimens are plotted at 12 of the grid points. Mid-point values of the primary data classes are the coordinate values of the plotted points. The variables of a specimen plotted at a grid point (X_c, Y_c) have true values (X_t, Y_t) within the ranges

$$X_c - 0.50 \leq X_t < X_c + 0.50$$

$$Y_c - 0.50 \leq Y_t < Y_c + 0.50$$

Nine-point accumulation values that can be determined from data within the area of the sample are shown in figure 32c. The variables of a specimen counted at a grid point (X_c, Y_c) have true values (X_t, Y_t) within the ranges

$$X_c - 1.50 \leq X_t < X_c + 1.50$$

$$Y_c - 1.50 \leq Y_t < Y_c + 1.50$$

In effect, the observed data for each variable have been grouped in overlapping secondary classes that are three times as large as the primary classes and are centered at the mid-point of each primary class.

Contours shown in figure 32d are based on accumulation values and indicate the percentage of total specimens with observed

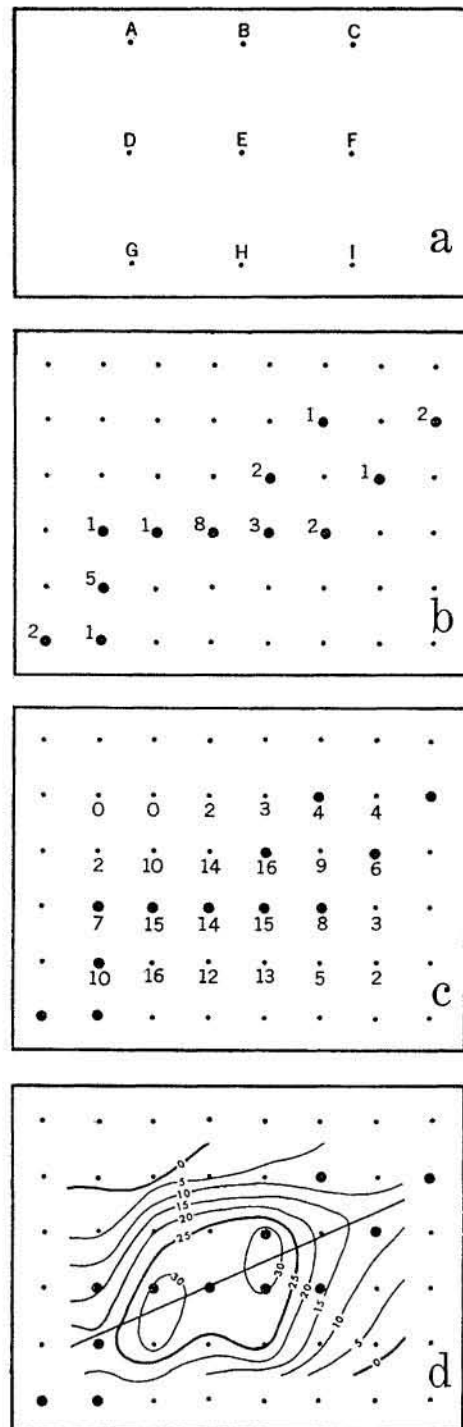


FIG. 32. Accumulation pattern used to prepare scatter diagrams for contouring.

values of the 2 variables within 1.5 mm of the grid point coordinate values. The trend line is fitted by observation through the maximum concentration of specimens indicated by the contours. It is entered primarily for use as a reference line in comparing distributions of data points on 2 or more contoured scatter diagrams.

Modified Dice-Leraas diagrams.—Modified Dice-Leraas diagrams, made for

graphic comparison of range, mean, standard deviation, and 95 percent confidence limits of morphologic features for different taxonomic units, were constructed following procedure of Simpson et al. (1960, pp. 351–354).

Student's t-tests.—Student's *t*-tests for the significance of the difference between means were calculated following Simpson et al. (1960, pp. 176–178).

1. The first part of the document is a list of the names of the members of the committee.

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SUMMARY OF QUANTITATIVE DATA

Locality	Number of measured specimens	Height		Mean (mm)	95% Confidence limit (mm)	Standard deviation (mm)
		Range (mm)				
		Minimum	Maximum			
<i>Athleta petrosa symmetrica</i> (Conrad)						
Miss-13	23	23	48	32.2	6.8	15.8
La-24	6	10	44	23.3	14.1	13.5
La-25	6	22	46	32.0	9.0	8.6
La-26	2	17	20	18.5	12.9	1.4
La-28	33	16	54	30.2	2.8	7.8
Total	70	10	54	30.1	2.0	8.4
<i>A. petrosa petrosa</i> (Conrad) [Cook Mountain]						
La-19	5	12	23	18.2	5.0	4.1
201-T-20	22	12	39	21.0	2.4	5.3
201-T-3	18	8	40	22.5	4.4	8.9
3-T-16	29	8	36	19.9	3.1	8.1
113-T-2	190	9	42	23.6	0.9	6.5
113-T-9	319	7	45	25.1	0.8	7.0
145-T-52	208	8	51	22.2	1.1	7.9
145-T-53	6	13	34	22.2	8.2	7.8
145-T-71	14	14	39	19.8	3.6	6.2
145-T-72	64	9	30	18.2	1.3	5.2
21-T-7	10	16	38	26.0	4.6	6.5
144-T-1	6	18	24	21.3	2.3	2.2
11-T-26	7	20	35	26.1	4.5	4.5
11-T-29	16	10	34	20.7	3.6	6.7
75-T-3	3	30	32	31.0	2.5	1.0
252-T-5	2	30	34	32.0	25.2	2.8
239-T-12	1	28.0
Total	920	7	51	23.2	0.5	7.2
<i>A. petrosa petrosa</i> (Conrad) [Weches]						
173-T-11	2	12	23	17.5	70.5	7.8
173-T-17	39	9	33	20.6	1.8	5.6
173-T-19	122	15	32	22.6	0.6	3.4
173-T-24	6	15	24	19.3	3.0	2.9
37-T-4	2	23	26	24.5	18.9	2.1
113-T-17	4	14	51	24.0	27.6	18.0
113-T-37	9	10	33	23.0	6.2	8.1
145-T-16	11	10	34	25.3	6.0	9.0
145-T-38	5	28	42	36.0	6.2	5.0
145 T-103	2	13	36	24.5	147.0	16.3
197-T-4	10	12	37	24.7	5.7	7.9
26-T-5	2	20	22	21.0	12.7	1.4
144-T-6	9	9	46	25.3	7.8	10.2
11-T-2	69	9	40	23.8	1.7	6.9
Total	292	9	51	23.0	0.7	6.2
<i>A. petrosa petrosa</i> (Conrad) TOTAL						
	1212	7	51	23.1	0.4	7.0

Height (continued)

Locality	Number of measured specimens	Range (mm)		Mean (mm)	95% Confidence limit (mm)	Standard deviation (mm)
		Minimum	Maximum			
<i>A. petrosa</i> (Conrad) [Queen City]						
11-T-39	30	5	16	8.5	1.1	2.9
<i>A. petrosa smithi</i> Fisher & Rodda, n. subsp.						
11-T-7	20	14	32	19.1	1.7	3.6
11-T-35	7	8	23	14.0	5.0	5.4
11-T-72	33	10	27	16.2	1.5	4.3
Total	60	8	32	16.9	1.1	4.4
<i>A. petrosa petrosa</i> (Conrad) TOTAL	1372	5	54	22.9	0.4	7.5
<i>A. tuomeyi</i> Conrad						
Ala-1	13	21	51	35.2	5.0	8.2
Ala-66	7	20	37	28.1	4.7	5.1
201-T-13	24	16	40	31.3	2.8	6.6
Total	44	16	51	32.0	2.2	7.1
<i>A. lisbonensis</i> (Aldrich) [Stone City]						
201-T-5	42	6	24	13.6	1.9	6.2
113-T-36	8	8	19	13.9	2.8	3.1
197-T-3	32	6	29	12.7	1.9	5.3
26-T-1	3	21	30	24.3	12.3	4.0
Total	85	6	30	13.7	1.3	5.9
<i>A. lisbonensis</i> (Aldrich) [Weches]						
26-T-5	4	17	22	19.8	3.5	1.8
11-T-2	7	17	26	21.9	3.0	3.0
Total	11	17	26	21.1	1.9	2.8
<i>A. lisbonensis</i> (Aldrich) TOTAL	96	6	30	14.5	1.2	6.1

		Width				
Locality	Number of measured specimens	Range (mm)		Mean (mm)	95% Confidence limit (mm)	Standard deviation (mm)
		Minimum	Maximum			
<i>Athleta petrosa symmetrica</i> (Conrad)						
Miss-13	16	12	19	15.4	0.6	1.2
La-24	2	5	23	14.0	80.9	9.0
La-25	4	11	25	17.2	18.0	11.3
La-26	2	8	10	9.0	9.0	1.0
La-28	33	7	27	13.9	1.2	3.5
Total	57	7	27	14.4	1.0	3.9
<i>A. petrosa petrosa</i> (Conrad) [Cook Mountain]						
La-19	5	6	13	10.0	2.7	2.7
201-T-20	22	6	18	10.0	1.2	2.6
201-T-3	17	4	17	9.9	2.0	3.9
3-T-16	29	4	19	9.7	1.5	4.5
113-T-2	187	3	18	10.6	0.4	3.0
113-T-9	313	3	21	11.2	0.3	3.1
145-T-52	188	4	18	9.8	0.5	3.4
145-T-53	5	6	12	8.6	3.0	2.4
145-T-71	13	6	11	8.5	1.0	1.6
145-T-72	59	4	14	8.3	0.7	2.6
21-T-7	8	7	14	10.8	2.0	2.4
144-T-1	4	8	10	9.0	1.3	0.8
11-T-26	6	9	16	12.5	2.7	2.6
11-T-29	18	4	15	9.5	1.6	3.3
75-T-3	3	14	15	14.3	1.4	0.6
252-T-5	2	14	16	15.0	12.7	1.4
239-T-12	2	13	15	14.0	12.7	1.4
Total	881	3	21	10.4	0.2	3.2
<i>A. petrosa petrosa</i> (Conrad) [Weches]						
173-T-11	1	10.0
173-T-17	36	4	16	9.2	1.0	3.0
173-T-19	119	7	16	10.4	0.3	1.7
173-T-24	7	8	11	9.0	0.9	1.0
37-T-4	3	10	11	10.7	1.4	0.6
113-T-17	4	6	9	7.2	2.0	1.3
113-T-37	8	5	13	10.5	2.2	2.7
145-T-16	11	5	20	12.3	3.1	4.7
145-T-38	2	12	17	14.5	31.4	3.5
145-T-103	2	6	15	10.5	57.3	6.4
197-T-4	10	7	19	12.2	2.7	3.8
26-T-5	1	9.0
144-T-6	6	5	13	9.0	2.7	2.6
11-T-2	66	4	19	10.5	0.8	3.1
Total	276	4	20	10.3	0.3	2.7
<i>A. petrosa petrosa</i> (Conrad) TOTAL						
	1157	3	21	10.4	0.2	3.1

Width (continued)

Locality	Number of measured specimens	Range (mm)		Mean (mm)	95% Confidence limit (mm)	Standard deviation (mm)
		Minimum	Maximum			
<i>A. petrosa</i> (Conrad) [Queen City]						
11-T-39	30	2	7	3.7	0.5	1.2
<i>A. petrosa smithi</i> Fisher & Rodda, n. subsp.						
11-T-7	21	7	15	8.8	0.8	1.8
11-T-35	6	3	10	6.2	2.8	2.6
11-T-72	30	5	12	7.4	0.9	2.5
Total	57	3	15	7.8	0.6	2.4
<i>A. petrosa</i> (Conrad) TOTAL	1301	2	27	10.3	0.2	3.4
<i>A. tuomeyi</i> Conrad						
Ala-1	12	9	27	17.3	3.2	5.0
Ala-66	7	10	23	15.4	3.7	4.0
201-T-13	22	7	20	15.5	1.6	3.6
Total	41	7	27	16.0	1.3	4.1
<i>A. lisbonensis</i> (Aldrich) [Stone City]						
201-T-5	42	3	11	6.3	0.8	2.7
113-T-36	8	4	9	6.9	1.1	1.5
197-T-3	32	3	13	5.8	0.9	2.4
26-T-1	3	9	14	11.0	6.6	2.2
Total	85	3	14	6.4	0.6	2.7
<i>A. lisbonensis</i> (Aldrich) [Weches]						
26-T-5	4	8	10	9.0	1.4	0.7
11-T-2	7	8	11	9.4	1.2	1.2
Total	11	8	11	9.3	0.7	1.1
<i>A. lisbonensis</i> (Aldrich) TOTAL	96	3	14	6.7	0.6	2.8

Spire Height						
Locality	Number of measured specimens	Range (mm)		Mean (mm)	95% Confidence limit (mm)	Standard deviation (mm)
		Minimum	Maximum			
<i>Athleta petrosa symmetrica</i> (Conrad)						
Miss-13	23	7	16	11.2	1.0	2.2
La-24	3	3	15	10.3	13.4	5.4
La-25	5	7	17	11.8	4.8	3.9
La-26	2	5	6	5.5	4.5	0.5
La-28	35	7	21	11.8	1.2	3.4
Total	68	3	21	11.3	0.8	3.3
<i>A. petrosa petrosa</i> (Conrad) [Cook Mountain]						
La-19	7	4	9	6.7	1.7	1.8
201-T-20	22	4	14	7.0	1.0	2.2
201-T-3	17	3	16	7.9	1.7	3.4
3-T-16	28	4	13	7.5	1.2	3.1
113-T-2	184	3	15	8.5	0.4	2.6
113-T-9	316	3	14	8.6	0.3	2.4
145-T-52	207	2	19	7.7	0.4	3.0
145-T-53	6	5	11	7.8	2.4	2.3
145-T-71	13	5	19	7.4	2.2	3.7
145-T-72	64	3	11	6.1	0.5	1.8
21-T-7	7	7	14	9.1	2.1	2.3
144-T-1	6	7	8	7.7	0.5	0.5
11-T-26	8	6	11	8.9	1.3	1.6
11-T-29	17	4	12	7.4	1.2	2.3
75-T-3	3	10	11	10.3	1.5	0.6
252-T-5	0	----	----	----	----	----
239-T-12	2	9	12	10.5	18.9	2.1
Total	902	2	19	8.1	0.2	2.6
<i>A. petrosa petrosa</i> (Conrad) [Weches]						
173-T-11	0	----	----	----	----	----
173-T-17	35	3	11	7.6	0.8	2.2
173-T-19	126	5	12	8.6	0.3	1.5
173-T-24	8	6	9	7.2	0.8	1.0
37-T-4	3	8	10	9.0	2.5	1.0
113-T-17	5	6	17	8.8	5.2	4.2
113-T-37	8	4	13	9.2	2.3	2.7
145-T-16	9	4	14	9.3	3.0	3.9
145-T-38	1	----	----	10.0	----	----
145-T-103	2	5	13	9.0	51.3	5.7
197-T-4	8	7	13	9.8	1.6	1.9
26-T-5	2	7	7	7.0	0.0	0.0
144-T-6	10	3	13	8.7	1.9	2.7
11-T-2	71	3	16	8.8	0.6	2.6
Total	287	3	17	8.6	0.2	2.2
<i>A. petrosa petrosa</i> (Conrad) TOTAL						
	1189	2	19	8.2	0.1	2.5

Spire Height (continued)

Locality	Number of measured specimens	Range (mm)		Mean (mm)	95% Confidence limit (mm)	Standard deviation (mm)
		Minimum	Maximum			
<i>A. petrosa</i> (Conrad) [Queen City]						
11-T-39	30	2	6	3.4	0.5	1.3
<i>A. petrosa smithi</i> Fisher & Rodda, n. subsp.						
11-T-7	25	5	14	7.7	0.8	2.0
11-T-35	7	3	9	5.6	1.8	2.1
11-T-72	34	3	11	6.4	0.8	2.2
Total	66	3	14	6.8	0.5	2.2
<i>A. petrosa</i> (Conrad) TOTAL	1353	2	21	8.2	0.1	2.7
<i>A. tuomeyi</i> Conrad						
Ala-1	12	7	19	11.5	2.4	3.6
Ala-66	7	8	12	10.0	1.3	1.4
201-T-13	25	6	16	10.9	1.0	2.5
Total	44	6	19	10.9	0.8	2.7
<i>A. lisbonensis</i> (Aldrich) [Stone City]						
201-T-5	42	2	10	5.5	0.8	2.6
113-T-36	8	3	8	6.1	1.2	1.4
197-T-3	32	2	11	5.1	0.8	2.1
26-T-1	3	8	11	9.3	3.8	1.2
Total	85	2	11	5.6	0.5	2.4
<i>A. lisbonensis</i> (Aldrich) [Weches]						
26-T-5	4	7	9	8.0	1.4	0.7
11-T-2	7	7	10	8.3	1.0	1.0
Total	11	7	10	8.2	0.6	0.9
<i>A. lisbonensis</i> (Aldrich) TOTAL	96	2	11	5.9	0.5	2.4

Ornaments on Body Whorl

Locality	Number of measured specimens	Range (mm)		Mean (mm)	95% Confidence limit (mm)	Standard deviation (mm)
		Minimum	Maximum			
<i>Athleta petrosa symmetrica</i> (Conrad)						
Miss-13	18	8	12	9.7	0.6	1.2
La-24	2	9	13	11.0	18.0	2.0
La-25	4	8	14	10.2	4.0	2.5
La-26	3	12	13	12.3	----	----
La-28	22	8	13	10.5	0.5	1.2
Total	49	8	14	10.3	0.2	1.5
<i>A. petrosa petrosa</i> (Conrad) [Cook Mountain]						
La-19	5	9	15	11.6	2.7	2.2
201-T-20	21	7	16	12.5	0.8	1.7
201-T-3	17	9	17	11.6	1.1	2.2
3-T-16	24	8	15	10.4	0.7	1.6
113-T-2	171	8	15	10.7	0.2	1.2
113-T-9	295	7	15	10.3	0.2	1.5
145-T-52	186	7	15	10.9	0.2	1.6
145-T-53	6	8	12	10.3	1.5	1.5
145-T-71	11	9	13	11.1	1.0	1.4
145-T-72	49	7	14	11.2	0.5	1.8
21-T-7	4	8	10	9.0	1.3	0.8
144-T-1	4	7	11	9.2	2.7	1.7
11-T-26	6	9	10	9.5	0.5	0.5
11-T-29	18	7	18	10.8	1.2	2.4
75-T-3	3	9	11	10.0	2.5	1.0
252-T-5	2	16	16	16.0	0.0	0.0
239-T-12	1	----	----	10.0	----	----
Total	823	7	18	10.7	0.1	1.7
<i>A. petrosa petrosa</i> (Conrad) [Weches]						
173-T-11	0	----	----	----	----	----
173-T-17	29	8	16	11.7	1.0	2.2
173-T-19	98	8	14	10.1	0.3	1.4
173-T-24	7	8	16	11.9	2.2	2.4
37-T-4	2	9	12	10.5	18.9	2.1
113-T-17	1	----	----	16.0	----	----
113-T-37	8	12	17	14.4	1.4	1.7
145-T-16	5	9	12	10.4	1.4	1.1
145-T-38	4	9	13	10.2	3.0	1.9
145-T-103	2	13	13	13.0	0.0	0.0
197-T-4	5	11	13	11.6	1.1	0.9
26-T-5	1	----	----	12.0	----	----
144-T-6	8	8	18	11.6	2.4	3.0
11-T-2	56	8	23	10.7	0.8	2.9
Total	226	8	23	10.9	0.3	2.4
<i>A. petrosa petrosa</i> (Conrad) TOTAL						
	1049	7	23	10.7	0.1	1.8

Ornaments on Body Whorl (continued)

Locality	Number of measured specimens	Range (mm)		Mean (mm)	95% Confidence limit (mm)	Standard deviation (mm)
		Minimum	Maximum			
<i>A. petrosa</i> (Conrad) [Queen City]						
11-T-39	18	17	26	23.5	1.1	2.2
<i>A. petrosa smithi</i> Fisher & Rodda, n. subsp.						
11-T-7	12	10	30	16.8	3.7	6.3
11-T-35	2	12	31	21.5	121.0	13.4
11-T-72	26	9	32	21.6	2.8	7.0
Total	40	9	32	20.1	2.3	7.1
<i>A. petrosa</i> (Conrad) TOTAL	1156	7	32	11.2	0.2	3.2
<i>A. tuomeyi</i> Conrad						
Ala-1	2	10	13	11.5	18.9	2.1
Ala-66	7	10	13	11.9	1.0	1.0
201-T-13	21	7	18	11.8	1.1	2.5
Total	30	7	18	11.8	0.8	2.1
<i>A. lisbonensis</i> (Aldrich) [Stone City]						
201-T-5	41	11	17	14.0	0.4	1.4
113-T-36	8	13	23	15.6	2.8	3.2
197-T-3	32	10	16	13.8	0.6	1.6
26-T-1	3	12	16	13.7	5.2	1.7
Total	84	10	23	13.7	0.8	3.5
<i>A. lisbonensis</i> (Aldrich) [Weches]						
26-T-5	4	13	17	14.0	3.2	1.7
11-T-2	7	14	22	16.9	2.3	2.3
Total	11	13	22	15.8	1.7	2.5
<i>A. lisbonensis</i> (Aldrich) TOTAL	95	10	23	14.0	0.7	3.5

Ratio of Height to Width

Locality	Number of measured specimens	Range (mm)		Mean (mm)	95% Confidence limit (mm)	Standard deviation (mm)
		Minimum	Maximum			
<i>Athleta petrosa symmetrica</i> (Conrad)						
Miss-13	15	1.90	2.40	2.15	0.08	0.14
La-24	2	1.91	2.00	1.96	0.36	0.04
La-25	4	1.84	2.16	2.04	0.25	0.16
La-26	2	2.00	2.13	2.06	0.54	0.06
La-28	25	1.90	3.00	2.32	0.10	0.23
Total	48	1.84	3.00	2.22	0.06	0.22
<i>A. petrosa petrosa</i> (Conrad) [Cook Mountain]						
La-19	3	2.00	2.11	2.04	0.15	0.06
201-T-20	22	1.67	2.33	2.08	0.07	0.16
201-T-3	15	2.00	2.60	2.26	0.09	0.16
3-T-16	28	1.64	2.43	2.13	0.07	0.19
113-T-2	187	1.91	3.00	2.25	0.02	0.14
113-T-9	312	1.92	2.82	2.26	0.02	0.17
145-T-52	186	1.83	2.75	2.30	0.02	0.16
145-T-53	5	2.17	2.50	2.30	0.16	0.13
145-T-71	13	2.00	2.43	2.18	0.07	0.12
145-T-72	58	1.83	2.50	2.20	0.04	0.14
21-T-7	8	2.14	2.33	2.22	0.06	0.07
144-T-1	4	2.33	2.50	2.42	0.11	0.07
11-T-26	5	2.14	2.27	2.20	0.05	0.04
11-T-29	16	1.89	2.50	2.20	0.07	0.14
75-T-3	3	2.00	2.29	2.17	0.38	0.15
252-T-5	2	2.12	2.14	2.13	0.93	0.01
239-T-12	1	----	----	2.15	----	----
Total	868	1.64	3.00	2.25	0.01	0.16
<i>A. petrosa petrosa</i> (Conrad) [Weches]						
173-T-11	1	----	----	2.30	----	----
173-T-17	31	1.93	2.60	2.21	0.06	0.15
173-T-19	112	1.83	2.67	2.19	0.02	0.13
173-T-24	5	2.00	2.38	2.20	0.16	0.13
37-T-4	2	2.09	2.36	2.23	1.71	0.19
113-T-17	3	2.14	2.33	2.25	0.25	0.10
113-T-37	7	1.80	2.54	2.19	0.23	0.25
145-T-16	11	1.85	2.25	2.08	0.08	0.12
145-T-38	2	2.18	2.33	2.25	0.99	0.11
145-T-103	2	2.17	2.40	2.28	1.44	0.16
197-T-4	8	1.85	2.44	2.20	0.18	0.22
26-T-5	1	----	----	2.22	----	----
144-T-6	5	1.80	2.50	2.23	0.32	0.26
11-T-2	60	1.92	2.55	2.23	0.04	0.14
Total	250	1.80	2.67	2.21	0.02	0.15
<i>A. petrosa petrosa</i> (Conrad) TOTAL						
	1118	1.64	3.00	2.24	0.01	0.16

Ratio of Height to Width (continued)

Locality	Number of measured specimens	Range (mm)		Mean (mm)	95% Confidence limit (mm)	Standard deviation (mm)
		Minimum	Maximum			
<i>A. petrosa</i> (Conrad) [Queen City]						
11-T-39	30	1.80	3.00	2.31	0.11	0.29
<i>A. petrosa smithi</i> Fisher & Rodda, n. subsp.						
11-T-7	17	2.00	2.50	2.24	0.08	0.15
11-T-35	6	2.00	2.67	2.29	0.22	0.21
11-T-72	27	2.00	2.67	2.30	0.06	0.16
Total	50	2.00	2.67	2.28	0.05	0.16
<i>A. petrosa</i> (Conrad) TOTAL	1246	1.64	3.00	2.24	0.01	0.17
<i>A. tuomeyi</i> Conrad						
Ala-1	12	1.89	2.53	2.12	0.13	0.20
Ala-66	7	1.61	2.07	1.86	0.24	0.26
201-T-13	21	1.85	2.50	2.02	0.08	0.18
Total	40	1.61	2.53	2.02	0.07	0.22
<i>A. lisbonensis</i> (Aldrich) [Stone City]						
201-T-5	42	1.60	2.57	2.17	0.06	0.18
113-T-36	8	2.00	2.11	2.01	0.04	0.04
197-T-3	32	1.89	2.50	2.20	0.06	0.16
26-T-1	3	2.14	2.33	2.23	0.24	0.08
Total	85	1.60	2.57	2.17	0.03	0.15
<i>A. lisbonensis</i> (Aldrich) [Weches]						
26-T-5	4	2.13	2.22	2.19	0.16	0.10
11-T-2	7	2.13	2.56	2.23	0.30	0.30
Total	11	2.13	2.56	2.27	0.08	0.12
<i>A. lisbonensis</i> (Aldrich) TOTAL	96	1.60	2.57	2.18	0.03	0.17

Ratio of Ornaments to Height

Locality	Number of measured specimens	Range (mm)		Mean (mm)	95% Confidence limit (mm)	Standard deviation (mm)
		Minimum	Maximum			
<i>Athleta petrosa symmetrica</i> (Conrad)						
Miss-13	16	0.21	0.44	0.30	0.08	0.15
La-14	2	0.20	1.30	0.75	4.94	0.55
La-25	4	0.17	0.64	0.33	0.29	0.18
La-26	2	0.65	0.71	0.68	0.27	0.03
La-28	19	0.18	0.46	0.34	0.03	0.08
Total	43	0.17	1.30	0.36	0.06	0.20
<i>A. petrosa petrosa</i> (Conrad) [Cook Mountain]						
La-19	3	0.58	1.25	0.81	0.95	0.38
201-T-20	21	0.33	1.33	0.64	0.22	0.48
201-T-3	15	0.26	2.12	0.70	0.26	0.47
3-T-16	23	0.28	1.88	0.64	0.16	0.37
113-T-2	171	0.21	1.36	0.48	0.03	0.18
113-T-9	294	0.21	2.00	0.45	0.03	0.24
145-T-52	185	0.14	1.56	0.57	0.04	0.29
145-T-53	6	0.24	0.92	0.54	0.27	0.26
145-T-71	11	0.41	0.93	0.62	0.10	0.15
145-T-72	48	0.28	1.56	0.66	0.08	0.28
21-T-7	4	0.33	0.41	0.36	0.06	0.04
144-T-1	4	0.29	0.55	0.43	0.18	0.11
11-T-26	5	0.29	0.50	0.37	0.10	0.08
11-T-29	16	0.29	1.38	0.62	0.18	0.34
75-T-3	3	0.28	0.35	0.32	0.10	0.04
252-T-5	2	0.47	0.53	0.50	0.40	0.04
239-T-12	1	----	----	0.36	----	----
Total	812	0.14	2.12	0.52	0.02	0.27
<i>A. petrosa petrosa</i> (Conrad) [Weches]						
173-T-11	0	----	----	----	----	----
173-T-17	25	0.32	1.67	0.67	0.14	0.34
173-T-19	93	0.29	0.78	0.46	0.02	0.11
173-T-24	5	0.40	0.80	0.58	0.18	0.15
37-T-4	1	----	----	0.39	----	----
113-T-17	1	----	----	1.07	----	----
113-T-37	7	0.42	1.70	0.70	0.42	0.45
145-T-16	5	0.29	0.61	0.40	0.16	0.13
145-T-38	4	0.24	0.36	0.29	0.10	0.06
145-T-103	2	0.36	1.00	0.68	4.06	0.45
197-T-4	5	0.30	1.08	0.52	0.41	0.33
26-T-5	1	----	----	0.60	----	----
144-T-6	6	0.25	2.00	0.68	0.68	0.65
11-T-2	53	0.20	2.56	0.57	0.13	0.48
Total	208	0.20	2.56	0.54	0.04	0.33
<i>A. petrosa petrosa</i> (Conrad) TOTAL						
	1020	0.14	2.56	0.52	0.01	0.28

Ratio of Ornaments to Height (continued)

Locality	Number of measured specimens	Range (mm)		Mean (mm)	95% Confidence limit (mm)	Standard deviation (mm)
		Minimum	Maximum			
<i>A. petrosa</i> (Conrad) [Queen City]						
11-T-39	18	1.42	5.20	2.71	0.52	1.05
<i>A. petrosa smithi</i> Fisher & Rodda, n. subsp.						
11-T-7	9	0.31	1.50	0.96	0.30	0.39
11-T-35	2	0.52	1.94	1.23	9.00	1.00
11-T-72	23	0.33	2.73	1.61	0.33	0.77
Total	34	0.31	2.73	1.42	0.25	0.73
<i>A. petrosa</i> (Conrad) TOTAL	1115	0.14	5.20	0.58	0.03	0.45
<i>A. tuomeyi</i> Conrad						
Ala-1	2	0.22	0.25	0.24	0.24	0.03
Ala-66	7	0.27	0.65	0.44	0.10	0.11
201-T-13	20	0.19	0.88	0.41	0.08	0.17
Total	29	0.19	0.88	0.41	0.06	0.16
<i>A. lisbonensis</i> (Aldrich) [Stone City]						
201-T-5	41	0.46	2.83	1.24	0.20	0.64
113-T-36	8	0.75	2.88	1.23	0.57	0.64
197-T-3	32	0.34	2.50	1.31	0.67	1.87
26-T-1	3	0.53	0.59	0.57	0.06	0.02
Total	84	0.34	2.88	1.24	0.15	0.62
<i>A. lisbonensis</i> (Aldrich) [Weches]						
26-T-5	4	0.65	0.77	0.71	0.14	0.07
11-T-2	7	0.62	1.16	0.79	0.17	0.17
Total	11	0.62	1.16	0.76	0.10	0.15
<i>A. lisbonensis</i> (Aldrich) TOTAL	95	0.34	2.88	1.18	0.12	0.61

Ratio of Ornaments to Width

Locality	Number of measured specimens	Range (mm)		Mean (mm)	95% Confidence limit (mm)	Standard deviation (mm)
		Minimum	Maximum			
<i>Athleta petrosa symmetrica</i> (Conrad)						
Miss-13	15	0.44	1.00	0.65	0.08	0.15
La-24	2	0.39	2.60	1.50	9.89	1.10
La-25	3	0.36	1.27	0.74	1.24	0.50
La-26	2	1.30	1.50	1.40	8.99	0.10
La-28	21	0.43	1.32	0.81	0.10	0.21
Total	43	0.36	2.60	0.81	0.12	0.38
<i>A. petrosa petrosa</i> (Conrad) [Cook Mountain]						
La-19	5	0.69	2.50	1.31	0.87	0.70
201-T-20	21	0.50	2.67	1.07	0.25	0.55
201-T-3	16	0.59	4.25	1.52	0.50	0.93
3-T-16	24	0.47	3.75	1.32	0.33	0.78
113-T-2	171	0.50	3.00	1.08	0.06	0.42
113-T-9	292	0.48	4.67	1.02	0.06	0.56
145-T-52	177	0.47	3.50	1.29	0.10	0.66
145-T-53	5	0.83	2.00	1.36	0.49	0.49
145-T-71	11	0.82	2.17	1.35	0.26	0.39
145-T-72	48	0.58	3.50	1.44	0.18	0.62
21-T-7	4	0.71	0.90	0.79	0.13	0.08
144-T-1	4	0.70	1.38	1.05	0.44	0.28
11-T-26	6	0.62	1.11	0.79	0.20	0.19
11-T-29	18	0.67	3.00	1.33	0.37	0.75
75-T-3	3	0.64	0.79	0.70	0.10	0.08
252-T-5	2	1.00	1.14	1.07	0.10	0.10
239-T-12	1	----	----	0.77	----	----
Total	808	0.47	4.67	1.15	0.04	0.59
<i>A. petrosa petrosa</i> (Conrad) [Weches]						
173-T-11	0	----	----	----	----	----
173-T-17	27	0.73	3.75	1.53	0.81	0.81
173-T-19	95	0.60	1.75	1.00	0.05	0.24
173-T-24	7	0.89	1.78	1.33	0.28	0.30
37-T-4	2	0.82	1.20	1.01	2.43	0.27
113-T-17	1	----	----	2.29	----	----
113-T-37	7	1.00	3.40	1.54	0.79	0.85
145-T-16	5	0.62	1.22	0.84	3.06	0.25
145-T-38	1	----	----	0.75	----	----
145-T-103	2	0.87	2.17	1.52	8.26	0.92
197-T-4	4	0.58	1.33	0.83	0.54	0.34
26-T-5	1	----	----	1.33	----	----
144-T-6	6	0.77	3.60	1.55	1.08	1.03
11-T-2	53	0.47	5.75	1.29	0.29	1.05
Total	211	0.47	5.75	1.20	0.10	0.72
<i>Athleta petrosa petrosa</i> (Conrad) TOTAL						
	1019	0.47	5.75	1.16	0.04	0.62

Ratio of Ornaments to Width (continued)

Locality	Number of measured specimens	Range (mm)		Mean (mm)	95% Confidence limit (mm)	Standard deviation (mm)
		Minimum	Maximum			
<i>A. petrosa</i> (Conrad) [Queen City]						
11-T-39	18	3.40	13.00	6.29	1.22	2.46
<i>A. petrosa smithi</i> Fisher & Rodda, n. subsp.						
11-T-7	10	0.67	3.75	2.00	0.70	0.98
11-T-35	2	1.20	4.43	2.81	13.80	2.28
11-T-72	25	0.75	6.40	3.41	0.78	1.89
Total	37	0.67	6.40	3.00	0.59	1.75
<i>A. petrosa</i> (Conrad) TOTAL						
1117		0.36	13.00	1.29	0.06	1.04
<i>A. tuomeyi</i> Conrad						
Ala-1	2	0.42	0.48	0.45	0.39	0.05
Ala-66	7	0.43	1.30	0.83	0.23	0.25
201-T-13	20	0.37	2.00	0.84	0.19	0.41
Total	29	0.37	2.00	0.81	0.14	0.37
<i>A. lisbonensis</i> (Aldrich) [Stone City]						
201-T-5	41	1.10	5.67	2.68	0.39	1.25
113-T-36	8	1.67	5.75	2.49	1.12	1.25
197-T-3	32	0.77	5.33	2.88	0.51	1.41
26-T-1	3	1.14	1.33	1.26	0.24	0.08
Total	84	0.77	5.75	2.69	0.28	1.29
<i>A. lisbonensis</i> (Aldrich) [Weches]						
26-T-5	4	1.44	1.70	1.55	0.20	0.11
11-T-2	7	1.45	2.75	1.83	0.31	0.31
Total	11	1.44	2.75	1.73	0.24	0.36
<i>A. lisbonensis</i> (Aldrich) TOTAL						
95		0.77	5.75	2.58	0.26	1.26

The following tabulation includes counts of longitudinal ornaments per whorl and number of protoconch and teleoconch whorls, in relation to size (height and width) of several specimens of *Athleta petrosa* (Conrad); specimens of various subspecies were selected from different localities and stratigraphic units. Only those specimens with perfectly preserved protoconchs were studied. Orientation of the conch for study and delineation of whorl number was as shown in figure 33. Data are arranged by subspecies and stratigraphic occurrence (oldest to youngest); specimens are arranged within each unit according to length of protoconch (longest to shortest). Interpretation of data here in-

cluded is given in the sections concerning evolution and ontogeny of the stock.

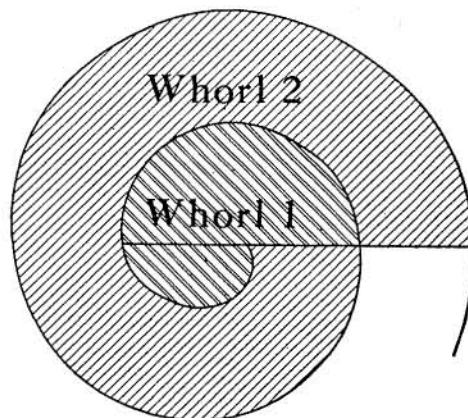


FIG. 33. Shell orientation in whorl analyses.

In mm		Whorl Number									
Height	Width	1	2	3	4	5	6	7	8	9	10
EXPLANATION											
<p>The diagram shows a cross-section of a nautilus whorl divided into segments. Arrows point from labels to specific segments: 'PROTOCONCH' points to the first segment (whorl 1), 'RIB STAGE WITH NUMBER OF RIBS' points to the fourth segment (whorl 4), 'TELEOCONCH' points to the sixth segment (whorl 6), 'NUMBER OF LONGITUDINAL ORNAMENTS' points to the eighth segment (whorl 8), and 'TERMINATION OF CONCH' points to the tenth segment (whorl 10). Numerical values are placed within the segments: '4' in whorl 4, '16' in whorl 6, and '14' in whorl 8.</p>											

A. PETROSA SMITHI Fisher and Rodda
Reklaw (11-T-7)

[illegible]

Whorl analyses, A. PETROSA stock

In mm		Whorl Number									
Height	Width	1	2	3	4	5	6	7	8	9	10
Weches (11-T-2)	19 8				5 8	16	15	15	14		
	28 13				5 10	16	14	14	11	7	
	17 7				4 9	17	17	15	14		
	24 12				3 11	14	16	16	11	3	
	26 12				5 13	14	15	14	11	7	
	22 10				3 10	15	15	16	16	6	
	25 12				5 9	14	15	16	12	3	
	24 11				4 11	13	16	15	10	2	
	22 10				4 14	14	15	14	4		
A. PETROSA PETROSA (Conrad) Weches (173-T-19)	23 12				3 4	17	16	16	10	1	
	10 5				4 3	13	14	14			
	19 8				5 5	14	17	16	15	6	
	21 10				4 6	17	17	15	12	4	
	22 10				4 14	14	17	16	12	6	
	26 13				4 12	15	17	17	14	10	1
	25 12				4 9	14	16	15	15	10	
	17 9				4 10	15	18	18	11	1	
	11 5				3 11	13	14	14	5		
	27 13				5 7	18	17	19	17	11	2
	17 8				3 11	17	17	16	15		
	17 8				4 7	13	16	16	15	3	
	25 12				5 8	15	16	16	14	8	
	21 10				4 11	18	18	16	12	4	
	23 11				4 7	15	16	15	16	7	
	22 11				4 9	15	15	15	14	7	
	22 10				4 7	15	19	18	16	7	
	— 17				3 7	15	19	16	18	12	3
	17 8				4 9	16	21	17	10		
	31 15				3 13	18	15	14	9	5	
	25 11				4 12	15	18	18	13	6	
	25 12				4 11	15	16	18	14	6	

A. PETROSA PETROSA (Conrad)
Stone City (11-T-75)
Weches (173-T-19)

[illegible]

Whorl analyses, A. PETROSA stock

A. PETROSA PETROSA (Conrad)
Stone City (26-T-1)

In mm		Whorl Number									
Height	Width	1	2	3	4	5	6	7	8	9	10
6	3					5	9	19	4		
28	13					5	16	18	14	14	11
7	3					6	18	16	6		
4	2					6	19	9			
7	3					5	18	15	8		
—	6					5	16	13	13	4	
21	10					6	17	15	15	14	8
25	11					4	18	15	15	14	10
27	12					7	18	17	16	16	12
29	13					4	21	18	17	17	10
6	3					7	19	17	5		
7	4					4	3	17	16	9	
—	6					5	1	19	18	17	12
20	9					7	2	18	18	15	8
22	10					6	2	20	18	17	13
25	12					5	2	21	16	16	14
25	11					10	1	15	19	17	14
24	11					5	2	19	20	17	15
—	5					5	5	18	13	12	
10	5					5	5	16	13	14	1
—	3					5	5	16	15		
6	3					6	6	20	15		
13	6					5	4	17	16	16	5
30	14					8	4	15	16	15	14
25	12					3	9	18	16	18	13
21	9					3	9	18	16	17	13
16	7					4	12	17	17	16	5
21	9					3	10	13	13	14	10
32	14					3	10	13	15	14	10
15	7					4	11	15	15	16	9
22	11					5	15	16	16	16	12
16	7					4	14	16	20	18	5

Whorl analyses, A. PETROSA stock

In mm		Whorl Number										
Height	Width	1	2	3	4	5	6	7	8	9	10	
Stone City (201-T-5)												
24	11				6	16	14	15	15	9		
17	8				8	19	16	15	15			
—	7				6	21	19	16	14			
11	5				6 ²	18	17	17	9			
10	5				6 ²	17	18	16	3			
9	4				4 ⁵	20	16	12				
27	13				4	10	17	15	13	9	1	
20	10				4	13	15	17	16	2		
28	13				4	14	13	14	14	12	6	
A. PETROSA PETROSA (Conrad)												
47	20				5	7	12	15	17	13	11	8
—	13				4	6	11	13	13	12	10	
32	15				4	7	13	14	16	12	8	
26	12				4	6	9	14	14	12	6	
—	11				5	6	10	13	14	14	6	
—	7				4	10	14	16	15	9		
33	14				4	12	14	13	13	10	3	
31	14				5	10	12	12	13	11	9	
23	10				4	11	15	14	12	8		
19	8				4	10	13	13	14	9		
—	4				4	11	13	14	5			
37	17				4	13	12	13	13	11	8	
38	17				3	15	12	12	12	10	8	
35	16				6	9	10	11	15	12	10	
27	12				4	12	16	15	13	8		
26	12				4	13	13	14	14	11	2	
—	12				6	7	11	13	14	13	6	
—	16				4	13	14	14	14	9	5	
—	7				3	18	14	15	12	3		
23	11				4	12	13	12	11	7		
—	8				5	13	15	14	12	4		
13	6				4	14	15	15	11			
—	4				7	15	15	16	2			

Whorl analyses, A. PETROSA stock

In mm		Whorl Number									
Height	Width	1	2	3	4	5	6	7	8	9	10
10	4			4	15	15	12	3			
30	15			5	13	13	12	12	9	3	
26	11			5	14	15	15	13	11	1	
—	9			4	14	13	14	12	8		
46	20			3	13	13	13	12	11	11	
—	7			6	12	16	14	13			
12	5			4	11	13	11	7			
14	6				6	18	16	15	8		
16	7			5	11	17	17	13	6		
—	8				4	12	14	14	12	9	
25	12				6	14	16	14	13	11	2
26	13				5	16	14	13	8		
22	10				4	21	17	14	13	5	
16	8			4	11	17	17	15	10		
16	7			4	10	18	17	15	12		
11	5			4	15	20	16	13	4		
16	7			5	7	10	13	15	13		
21	9			4	7	13	14	14	11		
—	13			5	9	14	13	16	12	4	
24	11			6	7	12	14	14	15	4	
34	15			4	9	10	12	14	13	12	1
28	13			4	10	15	14	16	12	4	
32	15			4	9	11	14	13	11	9	
23	11			5	9	11	13	14	12	5	
28	13			5	9	13	15	15	16	11	
29	14			4	8	12	12	14	14	11	1
29	15			4	10	13	14	14	12	9	
—	6			4	9	13	14	15	6		
14	6			4	10	15	13	13	6		
25	11			4	8	13	13	14	14	5	
21	9			4	9	13	13	15	11		

(21-T-1)

(21-T-21)

A. PETROSA PETROSA (Conrad)

(113-T-9)

Cook Mountain

Whorl analyses, A. PETROSA stock

A. PETROSA PETROSA
Cook Mountain (113-T-9)

In mm		Whorl Number										
Height	Width	1	2	3	4	5	6	7	8	9	10	
7	3				3	11	12	14	1			
19	8				4	9	13	13	16	12		
12	5				5	9	12	14	14			
27	13				4	8	11	13	12	11	4	
25	11				6	9	12	14	14	12	7	
27	12				5	10	10	13	15	11	7	
20	9				5	9	11	13	12	11		
10	4				5	11	14	14	6			
35	16				4	8	11	14	13	10	9	
—	9				5	13	14	15	14	10		
17	8				4	9	12	16	15	10		
18	8				4	11	11	12	13	12		
24	10				4	9	12	16	14	11	2	
23	11				5	10	10	13	12	11	3	
—	15				5	11	11	14	16	11	9	
18	8				6	8	11	16	15	11		
34	15				5	12	13	13	15	10	4	
21	10				5	10	13	15	17	14		
33	15				4	13	12	14	12	8		
20	9				3	14	12	13	10	7		
27	13				4	13	14	17	17	12	5	
16	7				4	12	13	12	15	3		
26	13				4	11	12	12	14	10	3	
—	14				5	16	16	15	13	10	5	
19	9				4	16	13	18	16	11		
10	4				4	15	17	15	10			
—	12				4	14	15	15	15	12	1	
23	10				4	14	13	15	14	11	1	
25	12				4	9	11	13	13	11	2	
22	10				4	9	10	14	14	12	3	
23	11				3	13	12	13	11	8		
23	10				4	12	12	15	14	12	2	
28	13				5	2	13	15	15	15	11	4

Whorl analyses, A. PETROSA stock

In mm		Whorl Number									
Height	Width	1	2	3	4	5	6	7	8	9	10
(113-T-9)	17	7			6/0	12	11	11	12	6	
	32	15			4/1	12	14	14	15	11	8
	26	11			3/3	15	13	13	12	9	
	20	9			4/4	13	14	12	10	4	
	15	7			4/3	12	14	14	14	3	
	15	6			4/4	13	14	13	11		
A. PETROSA PETROSA (Conrad) Cook Mountain (201-T-23)	—	8			6	13	17	20	17	5	
	—	15			5	11	14	15	14	12	8
	21	10			5	11	14	16	17	16	
	—	8			6	11	12	13	13	3	
	—	12			5	13	13	15	16	12	1
	—	9			4	15	15	16	15	11	
	10	5			5	13	14	15	9		
	12	5			4	12	12	12	9		
	9	5			4	15	14	16	8		
	9	4			6	14	14	17	6		
	21	10			5/2	14	14	18	16	11	
	17	8			5	7	13	15	16	9	
(201-T-20)	28	14			3	13	13	16	17	13	4
	—	9			5	12	14	18	18	9	
	22	10			6	11	15	17	17	14	
	24	11			5	11	13	15	14	11	
	—	16			4	14	14	16	18	14	13
	—	11			4	13	14	16	15	11	1
	25	12			4/2	12	14	16	17	14	4
	12	6			4/6	14	16	16	13		
(201-T-22)	25	12			4	10	13	14	15	10	4
	30	14			4/1	13	14	16	15	13	7
	28	13			4/1	11	12	14	14	14	7

A. PETROSA SYMMETRICA (Conrad)
Jackson

[illegible]

APPENDIX B

LOCALITY REGISTER

TEXAS LOCALITIES

Angelina County

- 3-T-16. Gully at intersection of U. S. Highway 59 and east-west county road, north of county road and west of highway culvert; 6.1 miles north on a direct line from center of Lufkin and 0.6 mile north of crossing of road to Redland. Coll.: H. B. Stenzel. Cook Mountain Formation.

Atascosa County

- 7-T-16. Fossiliferous boulders in field along county road 0.5 mile southeast of Jourdan-
ton. Coll.: W. L. Fisher & P. U. Rodda. Cook Mountain Formation.
- 7-T-17. Road cut at first eastward bend of U. S. Highway 281, 0.5 mile south of southern city limits of Pleasanton. Coll.: H. B. Stenzel; W. L. Fisher & P. U. Rodda. Stone City Formation.

Bastrop County

- 11-T-2. Bluff on right bank of Colorado River at Smithville, approximately 200 yards downstream from Colorado River bridge on State Highway 71. Coll.: F. B. Plummer; G. D. Harris. Viesca Member, Weches Formation.
- 11-T-7. Bluff along Ridge Creek, 1.0 mile above Missouri, Kansas, and Texas Railroad trestle and county road bridge, 6.2 miles west of Smithville, 0.8 mile east of Upton. Coll.: H. B. Stenzel. Marquez Member, Reklaw Formation. (Type locality of *Athleta petrosa smithi* Fisher & Rodda.)
- 11-T-26. Pinoak Creek at crossing of Smithville-Winchester road. Coll.: H. J. Plummer. Cook Mountain Formation.
- 11-T-29. Shipp's Ford, right bank of Colorado River just west of Bastrop-Fayette County line, at mouth of small tributary having several waterfalls over clay-ironstone ledges, 550 yards southeast of sharp bend in gravel road leading to Smithville-La Grange road (State Highway 71), approximately 4 miles east of Smithville. Coll.: H. B. Stenzel. Cook Mountain Formation.
- 11-T-35. Davids Bottom, banks of Colorado River, 0.5 mile south of junction of Alum Creek and Little Alum Creek, immediately south of dead-end, gravel road leading to State Highway 71. Coll.: F. B. Plummer. Reklaw Formation.

- 11-T-36. Devils Eye, island in Colorado River, 8.0 miles southeast of Bastrop, between B.E.G. locality 11-T-39 (Kennedy Bluff) and B.E.G. locality 11-T-35 (Davids Bottom). Coll.: H. J. Plummer. Marquez Member, Reklaw Formation.
- 11-T-39. Kennedy Bluff, left bank of Colorado River, below mouth of Alum Creek, south of State Highways 71 and 95, 3.6 miles by road from bridge over Colorado River at Smithville. Coll.: H. B. Stenzel. Queen City Formation.
- 11-T-70. Pinoak Creek, bluff on left bank, adjoining the north-south county road that forks from Farm Road 153 and leads to Center Union School, 600 yards north of ford at this road fork; road forks from Farm Road 153, 1.1 miles northwest of concrete bridge over Pinoak Creek. Coll.: F. B. Plummer. Cook Mountain Formation, probably Landrum Member.
- 11-T-71. Barton (or Borden) Creek, bluff on right side of creek, $\frac{1}{4}$ mile downstream from county road bridge of old Smithville-Flatonia road, at Bastrop-Fayette County line, $3\frac{1}{4}$ miles airline distance south-southwest of State Highway 71 crossing of Shipp's Lake. Coll.: H. B. Stenzel & V. E. Barnes. Cook Mountain Formation.
- 11-T-72. High bluff along right bank of Colorado River, 1 mile east of Upton and 0.4 mile east or downstream from the mouth of Ridge Creek, approximately 6.5 miles west of Smithville. Coll.: unknown. Reklaw Formation.
- 11-T-75. Pinoak Creek, bluff on left bank at end of narrow farm lane; 0.4 miles south of Pinoak Church, 6.7 miles northeast of Smithville, 3.5 miles upstream (north) of locality 11-T-70. Coll.: J. T. Twining & J. E. Elliott. Stone City Formation.

Brazos County

- 21-T-1. Little Brazos River, north side of bridge over Little Brazos River on Stone City-Bryan road (State Highway 21) west of Riverside, 9.5 miles west of Bryan. Coll.: H. B. Stenzel; W. L. Fisher, P. U. Rodda & A. J. Scott. Wheelock Member, Cook Mountain Formation.
- 21-T-6. Left side of Brazos River, 500 yards below mouth of Little Brazos River. Coll.: H. B. Stenzel; W. L. Fisher, P. U. Rodda & A. J. Scott. Wheelock Member, Cook Mountain Formation.

- 21-T-7. Small left branch of left tributary of Campbell Creek, 0.4 mile northeast of U. S. Highway 190 and State Highway 6 and 0.6 mile southeast of intersection of U. S. Highway 190 and Old San Antonio Road. Coll.: H. B. Stenzel. Landrum Member, Cook Mountain Formation.

Burleson County

- 26-T-1. Right bank of Brazos River, immediately upstream from bridges of State Highway 21 and Southern Pacific Railroad, opposite Stone City (Moseleys Ferry) on Bryan-Caldwell road, 11.4 miles west of courthouse in Bryan and 11.5 miles northeast of intersection of State Highways 21 and 36 at Caldwell. Coll.: H. B. Stenzel; P. U. Rodda. Stone City Formation.
- 26-T-2. Southeast corner of town of Caldwell. Coll.: Woodfin. Cook Mountain Formation.
- 26-T-4. Northeast corner of town of Caldwell. Coll.: unknown. Landrum Member, Cook Mountain Formation.
- 26-T-5. Brazos River, 1.5 miles south of north line of Burleson County, near old bridge. Coll.: unknown. Weches Formation.
- 26-T-6. Colliers Ferry (Burleson Bluff) on right bank of Brazos River, northeast part of county, at end of long reach, 5.0 miles airline distance from road junction at Fraimville and 13.6 miles airline distance northeast of Caldwell. Coll.: H. B. Stenzel. Weches Formation.
- 26-T-48. Banks along Dead Creek, a small stream entering right side of Brazos River, 4.0 miles upstream from bridge of State Highway 21 over Brazos River and B.E.G. locality 26-T-1. Coll.: unknown. Stone City Formation.

Caldwell County

- 28-T-9. Dump by old copper mine shaft, E. Pullen survey, east of Sandy Fork Creek, 4.8 miles by road northeast of Harwood, Gonzales County. Coll.: P. Applin & L. Reed; F. B. Plummer. Reklaw Formation.

Cherokee County

- 37-T-4. Grange Hall School at Linwood on State Highway 21, 0.9 mile south of school on small creek, at waterfall of about 10 feet, at crossing of county road. Coll.: H. B. Stenzel & F. E. Turner. Weches Formation.

Fayette County

- 75-T-3. Bluff on right side of Colorado River, 0.8 mile downstream from Bastrop-Fayette County line, and 1.6 miles airline distance northeast of community of Kirtley. Coll.: H. B. Stenzel. Cook Mountain Formation.

Gonzales County

- 89-T-9. Cost, $\frac{3}{4}$ mile from Cost School on U. S. Highway 97, on spur road to monument. Coll.: H. B. Stenzel. Cook Mountain Formation.
- 89-T-10. Road cut on Farm Road 2091, 0.5 mile north of junction with U.S. Highway 90A, 4.0 miles west of Gonzales. Coll.: W. L. Fisher, E. A. King, Jr. & P. U. Rodda. Cook Mountain Formation.
- 89-T-11. Fossiliferous boulders along side of old Nixon-Smiley road, 0.3 mile southeast of intersection with U. S. Highway 87 (present Nixon-Smiley road). Coll.: W. L. Fisher & P. U. Rodda. Yegua Formation.
- 89-T-12. Bluff along lower part of Nagel Creek, south of Guadalupe River; northeast-flowing creek paralleling county road from Monthalia to Oak Forest; 1.9 miles due south of Oak Forest. Coll.: Carl Chelf. Stone City Formation.

Houston County

- 113-T-2. Hurricane Bayou; bed of creek, 0.2 to 0.5 mile upstream from bridge on Crockett-Rusk county road (mail route 1), 3.5 miles northeast of Crockett. Coll.: H. B. Stenzel. Hurricane Lentil, Landrum Member, Cook Mountain Formation.
- 113-T-9. Alabama Ferry, east bank of Trinity River, 0.3 mile below abandoned ferry, 7.5 miles west-southwest of Porter Springs. Coll.: H. B. Stenzel; W. L. Fisher & P. U. Rodda. Hurricane Lentil, Landrum Member, Cook Mountain Formation.
- 113-T-14. In gully on west slope of Cooks Mountain, 3 miles northwest of Crockett, just north of Farm Road 229; Ralph Lundy tract; Wm. White survey. Coll.: H. B. Stenzel. Cook Mountain Formation (type locality).
- 113-T-17. Wheeler Springs School, waterfall on intermittent, left tributary of Little Elkhart Creek, at wagon road, 0.4 mile airline distance southwest of Wheeler Springs School. Coll.: H. B. Stenzel. Tyus and Viesca Members, Weches Formation.
- 113-T-36. Bluff on east bank of Trinity River at sharp bend, 0.9 mile airline distance north of Alabama Ferry (B.E.G. locality 113-T-9). Coll.: H. B. Stenzel. Stone City Formation.
- 113-T-37. Rock Flat west of Percilla, rock flat over which a left tributary to Murchison Creek flows southward, 0.1 mile north of Farm Road 228, and 0.7 mile airline distance west of Percilla Post Office. Coll.: H. B. Stenzel. Tyus Member, Weches Formation.

La Salle County

- 142-T-2. Road cut, east side of U. S. Highway 81, 4.5 miles south of Cotulla. Coll.: P. U. Rodda & W. L. Fisher. Stone City Formation.

Lee County

- 144-T-1. Prices Crossing of Elm Creek, bluff on right bank of Elm Creek at left turn of creek at the upstream end of a large S curve, 0.3 mile downstream from bridge on Giddings-Fedor road, 5.2 miles by road northwest of Giddings, 0.5 mile south of Farm Road 21. Coll.: H. J. Plummer. Cook Mountain Formation.
- 144-T-2. Evergreen Crossing of Elm Creek, on Farm Road 1624, 0.4 mile west of U. S. Highway 77, about 5 miles north of Giddings. Coll.: unknown. Cook Mountain Formation.
- 144-T-5. Orells Crossing of Elm Creek, bluff on right bank of Elm Creek at first large horseshoe bend, 200 yards upstream from bridge on Farm Road 2440, 1.7 miles southeast of Manheim and State Highway 21. Coll.: H. J. Plummer. Cook Mountain Formation.
- 144-T-6. Left bank of Big Creek, a left tributary of Middle Yegua Creek, 0.3 mile downstream from bridge on county road from Lexington to Fedor, 0.2 mile south of Lexington Cemetery. Coll.: H. B. Stenzel; H. J. Plummer. Viesca Member, Weches Formation.
- 144-T-7. Prices Crossing of Elm Creek, bank of Elm Creek, about 100 yards upstream from bridge on county road from Farm Road 2440 to State Highway 21, 0.3 mile southeast of State Highway 21. Coll.: H. J. Plummer. Cook Mountain Formation.

Leon County

(See geologic map of Leon County, Stenzel, 1939)

- 145-T-1. State Highway 7 (Concord-Centerville road), north ditch, 0.6 mile southeast of Robbins. Coll.: H. B. Stenzel. Tyus and Viesca Members, Weches Formation.
- 145-T-16. Spring Creek, field on hill slope 0.1 mile south of Spring Creek, 3.2 miles southeast of Cullinan Station. Coll.: H. B. Stenzel. Tyus Member, Weches Formation.
- 145-T-32. Old Iron Bridge, northwest-pointing hill of Weches cuesta, opposite abandoned iron bridge over Navasota River, 8.0 miles airline distance west of Normangee. Coll.: H. B. Stenzel. Tyus Member, Weches Formation.
- 145-T-37. State Highway 7 (Concord-Centerville road), south ditch, 5.2 miles west of Centerville, between left tributary of McDaniel Creek and road leading south along Beauchamp survey west line, 0.2 mile west of Redland Methodist Church. Coll.: H. B. Stenzel. Viesca Member, Weches Formation.
- 145-T-38. State Highway 7 (Concord-Centerville road), north ditch, 5.2 miles west of Centerville between left tributary of McDaniel Creek and Sparta nose, 0.3 mile west of Redland Methodist Church. Coll.: H. B. Stenzel. Viesca Member, Weches Formation.
- 145-T-51. Butler Branch, left bank 50 feet below bridge on Farm Road 977 (Leona-Two Mile School road), 4.6 miles southeast of Leona. Coll.: H. B. Stenzel. Upper part of Wheelock Member, Cook Mountain Formation.
- 145-T-52. Two Mile Creek, five bluffs at the steel bridge of Farm Road 977 (Leona-Two Mile School road) near Two Mile School, 5.3 miles southeast of Leona. Coll.: H. B. Stenzel. Lower part of Landrum Member, Cook Mountain Formation.
- 145-T-53. Middleton, west ditch of Middleton-Spillers Store county road (extension of Farm Road 1119), 0.2 mile northeast of steel bridge over Boggy Creek, 0.7 mile south of Middleton Post Office. Coll.: H. B. Stenzel. Upper part of Wheelock Member, Cook Mountain Formation.
- 145-T-54. Middleton sawmill, north ditch of Middleton-Guys Store county road (southwestern extension of Farm Road 811), southwest end of steel bridge over Keechi Creek, opposite sawmill, 1.7 miles from Middleton road fork. Coll.: H. B. Stenzel. Upper part of Wheelock Member, Cook Mountain Formation.
- 145-T-58. Flat Branch, bank along stream, 200 feet above confluence with Bear Branch, 0.4 mile from entrance gate on Middleton-Guys Store county road (southwestern extension of Farm Road 811). Coll.: H. B. Stenzel. Upper part of Wheelock Member, Cook Mountain Formation.
- 145-T-59. Bear Branch, banks about 300 feet above intersection with Flat Branch, 0.4 mile from entrance gate on Middleton-Guys Store county road (southwestern extension of Farm Road 811). Coll.: H. B. Stenzel. Upper part of Wheelock Member, Cook Mountain Formation.
- 145-T-60. Guys Store or Bear Branch School, dump at water well test hole in woods about 100 feet southeast of Middleton-Guys Store county road (southwestern extension of Farm Road 811) and 0.2 mile southwest of Bear Branch School. Coll.:

H. B. Stenzel. Upper part of Wheelock Member, Cook Mountain Formation.

145-T-62. Red Bank Creek, banks 100 feet below bridge of county road, 1.7 miles south of Wealthy, and 0.4 mile south of county line. Coll.: H. B. Stenzel. Upper part of Wheelock Member, Cook Mountain Formation.

145-T-72. Left bank of Two Mile Creek, between first and second fords upstream from Two Mile Church. Coll.: H. B. Stenzel. Lower part of Landrum Member, Cook Mountain Formation.

145-T-80. Right bank of a dry branch in woods about 200 feet below fence and tank, 0.5 mile north of Middleton-Sulphur Springs School county road, in south corner of F. C. Wilson tract, A. Richardson survey. Coll.: H. B. Stenzel. Mt. Tabor Member, Cook Mountain Formation.

145-T-83. In bed of Spring Branch of Two Mile Creek, west from bridge of U. S. Highway 75, about 2.0 miles northwest of Madison-Leon County line. Coll.: H. B. Stenzel. Landrum Member, Cook Mountain Formation.

145-T-103. Bed in Rocky Branch, eastern part of Sarah Wiley 100-acre tract, Joe Wiley Survey, 4.4 miles east-northeast of Davisville. Coll.: unknown. Weches Formation.

Milam County

165-T-13. Banks of Two Mile Creek, 0.6 mile upstream from junction with Brazos River, 0.2 mile downstream from county road crossing of Two Mile Creek, southeast on county road 1.2 miles from U. S. Highway 79, at a point 3.9 miles northeast from center of Gause. Coll.: H. B. Stenzel. Reklaw Formation.

Nacogdoches County

173-T-11. Road cuts along both sides of State Highway 21 on east slope of hill to Brown Cash Store, approximately 3.0 miles east of Melrose High School, 0.9 mile west of Sandhill Church and School. Coll.: C. L. Baker & J. Suman; H. B. Stenzel. Weches Formation.

173-T-17. Gully on north side of State Highway 21 on west slope of hill, 2.6 miles east of Melrose High School, 1.2 miles west of Sandhill Church and School. Coll.: H. B. Stenzel. Weches Formation.

173-T-19. South side of State Highway 21 on ascent westward from flood plain of Polysot Creek, between Sandhill School and Paul's Valley, 1.4 miles east of Sandhill School. Coll.: H. B. Stenzel. Weches Formation.

173-T-24. Road cut, State Highway 7 on steep ascent 2.3 miles west of Terrapin Creek crossing, 3.0 miles west of Martinsville, 1.2 miles east of Swift. Coll.: H. B. Stenzel. Weches Formation.

173-T-25. Road cut, north side of State Highway 21, between east and west junctions of State Loop 34 to Chireno. Coll.: P. U. Rodda, W. L. Fisher & J. W. Dietrich. Weches Formation.

Robertson County

197-T-2. Banks along Campbell Creek, on J. Dunn's ranch, 0.5 mile northwest of Old San Antonio Road at a point 5.0 miles northeast of intersection with U. S. Highway 190. Coll.: unknown. Weches Formation.

197-T-3. Cedar Creek, 200 yards north of Brazos-Robertson County line on Old San Antonio Road at a point 1.7 miles east of intersection with Farm Road 46. Coll.: unknown. Stone City Formation.

197-T-4. Cobb Branch, bluff on right bank near its head at ford south of old house, 0.6 mile northwest of Camp Creek School. Coll.: B. C. Renick & H. B. Stenzel. Weches Formation.

Rusk County

200-T-1. Borrow pit on north side of U. S. Highway 84 on east bank of Angelina River, 300 feet west of river, 2.6 miles east of Reklaw. Coll.: H. B. Stenzel & H. C. Fountain. Newby Member, Reklaw Formation.

Sabine County

201-T-1. Pendleton Bluff, right bank of Sabine River at Pendleton, approximately 0.3 mile upstream from bridge over Sabine River on Louisiana State Highway 6-Texas State Highway 21. Coll.: C. L. Baker & J. Suman; F. B. Plummer. Pendleton Formation.

201-T-2. Banks of Sabine River, 2.0 miles southeast of Sabinetown. Jessy Low survey. Coll.: unknown. Weches Formation.

201-T-3. West bank of Sabine River, 0.8 mile above old community of Columbus, Louisiana. Coll.: C. L. Baker & J. Suman. Cook Mountain Formation.

201-T-5. Right bank of Sabine River at center of Harpers Bend, opposite section 36, T. 5 N., R. 13 W., Sabine Parish, Louisiana, 0.5 mile northeast of Crane Pond, 1.0 mile air-line distance northwest from U. S. Geol. Survey Benchmark 164 at old community of Columbus, Louisiana. Coll.: C. L. Baker. Stone City Formation.

201-T-13. Upper end of bluff on Sabine River, one-fourth mile below old ferry landing at

Sabinetown. Coll.: unknown. Sabinetown Formation.

201-T-14. Three thousand feet downstream from Texas landing of Robinson Ferry, in bluff below road, 0.7 mile east and opposite third house east of Blue Springs School, 2.3 miles east of intersection with Farm Road 944, 2.4 miles north of Fairdale. Coll.: H. B. Stenzel. Marine lentil in uppermost part of Yegua Formation (Creola Member).

201-T-20. Right bank of Sabine River on east-west reach opposite section 35, T. 5 N., R. 13 W., Sabine Parish, Louisiana, 0.4 mile northwest of Crane Pond. Coll.: unknown. Cook Mountain Formation.

201-T-22. In bed of right branch of Lows (Coma) Creek downstream from bridge 0.2 mile south of logging road from road intersection, 0.8 mile east of Harpers Chapel. Coll.: H. B. Stenzel. Cook Mountain Formation.

201-T-23. Right branch of Lows (Coma) Creek, upstream from bridge 0.2 mile south on logging road from road intersection, 0.8 mile east of Harpers Chapel. Coll.: H. B. Stenzel. Wheelock Member, Cook Mountain Formation.

San Augustine County

202-T-27. Road cut on east side of Farm Road 2213 (San Augustine-Chinquapin road), just south of bridge over Caney Creek, on slope below Roberts School and Church, 2.5 miles south of courthouse in San Augustine. Coll.: H. B. Stenzel. Weches Formation.

Trinity County

227-T-9. White Rock Creek about 50 yards below the end of a dirt road leading west from secondary road (east of State Highway 45) at old abandoned church, 8.0 miles north of Trinity. Coll.: W. L. Fisher, E. A. King, Jr. & P. U. Rodda. ?Caddell Formation (Jacksonian).

Webb County

239-T-3. Chacon Creek, 200 feet south of bridge over creek on State Highway 359 east of Laredo. Coll.: P. Applin & L. Reed. Cook Mountain Formation.

239-T-9. Chacon Creek, about 0.5 mile upstream from bridge over creek on State Highway 359 east of Laredo. Coll.: P. Applin & L. Reed. Cook Mountain Formation.

239-T-12. Bluff along Rio Grande, 2.0 miles north of Dolores ranch, opposite upper end of small island. Coll.: unknown. Cook Mountain Formation.

Wilson County

246-T-3. Isolated hill in field, 1.0 mile west of U. S. Highway 181 and 1.6 miles northwest of intersection of State Highway 541 and U. S. Highway 181, at Poth. Coll.: F. B. Plummer. Cook Mountain Formation.

Zapata County

252-T-5. Vicinity of Arroyo Molletes, near U. S. Highway 83, 12.0 miles southeast of Ygnacio, 4.0 miles northwest of Zapata. Coll.: unknown. Cook Mountain Formation.

OTHER LOCALITIES

Alabama

Ala-1. Bluff on left side of Alabama River immediately below abandoned Bells Landing, Monroe County, Alabama. Coll.: H. B. Stenzel. Bells Landing Member, Tuscaloosa Formation, Wilcox Group.

Ala-6. One mile west of Oak Hill, Wilcox County, Alabama. Coll.: unknown. Midway Group [*Volutocorbis limopsis* (Conrad)].

Ala-66. Road cut east side of Alabama Highway 69, just south of Bashi Creek crossing, near type locality of Bashi Member, Clarke County, Alabama. Coll.: W. L. Fisher, J. D. Powell, P. U. Rodda & A. J. Scott. Bashi Member, Hachetigbee Formation.

Ala-67. Claiborne Bluff and Landing at east end of bridge over Alabama River, U. S. Highway 84 and Alabama Highway 11, T. 7 N., R. 5 E., Monroe County, Alabama. Coll.: P. U. Rodda, A. J. Scott & W. L. Fisher. Lisbon & Gosport Formations.

Louisiana

La-18. Cut at back and south side of hospital in Natchitoches, Louisiana, approximately $\frac{3}{4}$ mile north of concrete bridge over Cane River, in town, Natchitoches Parish, Louisiana. Coll.: H. B. Stenzel. Cane River (Weches) Formation.

La-19. Negreet-Columbus road, Sabine Parish, Louisiana, cut on east side of road on steep, wooded blackland hill, 7.2 miles from school at Negreet, center of N $\frac{1}{4}$, section 32, R. 12 W., T. 5 N. Coll.: H. B. Stenzel. Cook Mountain Formation.

La-24. Grandview Bluff, bluff on right bank of Ouachita River, about 2 miles east-southeast of Copenhagen, and 7.5 miles southeast of Columbia, Caldwell Parish, Louisiana. Coll.: H. B. Stenzel & E. Hurlbut, Jr. Moodys Branch Formation, Jackson Group.

- La-25. Bunker Hill Bluff, Ouachita River, 2.5 miles east-southeast of Copenhagen, Caldwell Parish, Louisiana. Coll.: H. B. Stenzel & E. Hurlbut, Jr. Moodys Branch Formation.
- La-26. Heison Landing west side of Ouachita River, 1.8 miles east of Copenhagen, about 7 miles southeast of Columbia, Caldwell Parish, Louisiana. Coll.: H. B. Stenzel and E. M. Hurlbut, Jr.; W. L. Fisher, P. U. Rodda, and J. W. Dietrich. Moodys Branch Formation.
- La-28. Bluff on left bank of Bayou Toro, 0.8 mile airline distance southeast of Toro, Louisiana, 0.4 mile due south of the north line of Vernon Parish, SE $\frac{1}{4}$, NW $\frac{1}{4}$, section 6, R. 11 W., T. 3 N., Vernon Parish, Louisiana. Coll.: H. B. Stenzel; P. U. Rodda, W. L. Fisher & J. W. Dietrich. Danville Landing Formation, Jackson Group.
- Mississippi**
- Miss-1. Cut of Alabama and Vicksburg Railroad, Indian Mound, 3 miles east of Newton, Newton County, Mississippi. Coll.: H. B. Stenzel. Wautubbee Formation.
- Miss-13. Town Creek, in Jackson, Hinds County, Mississippi; exposure along Town Creek, NE $\frac{1}{4}$, SW $\frac{1}{4}$, section 10, T. 5 N., R. 1 E., in south part of Jackson. Coll.: H. B. Stenzel & A. L. Lyth. Moodys Branch Formation.

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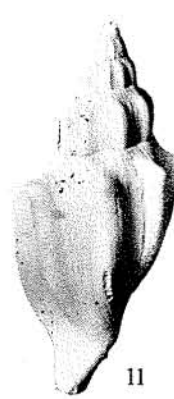
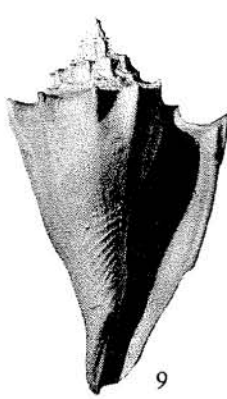
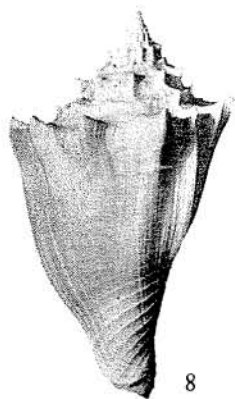
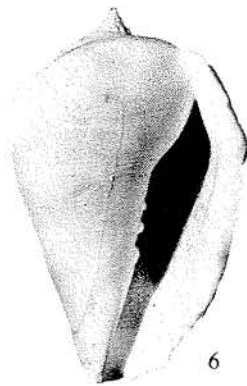
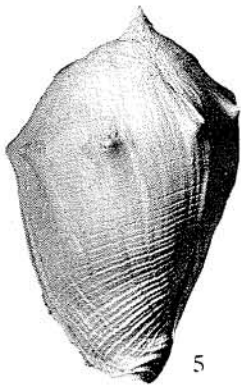
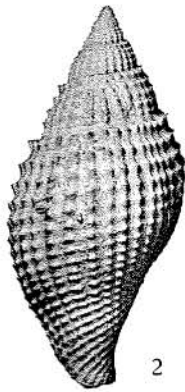
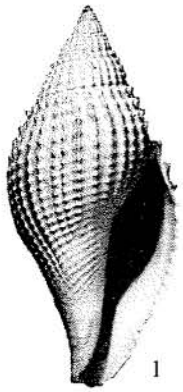


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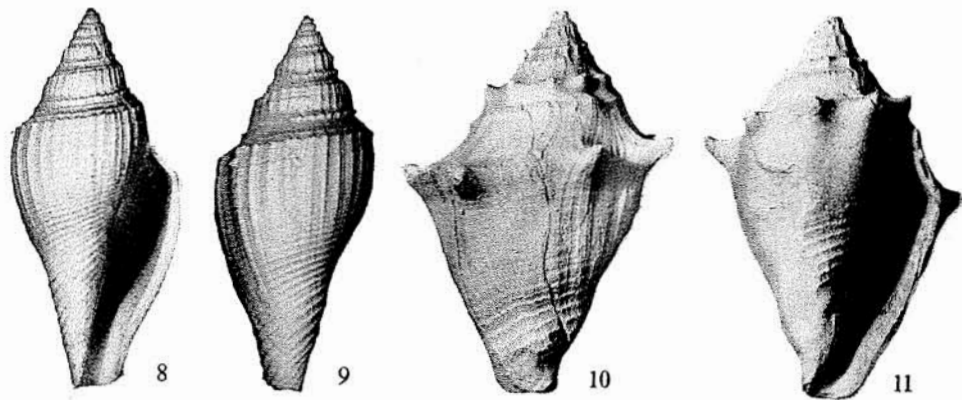
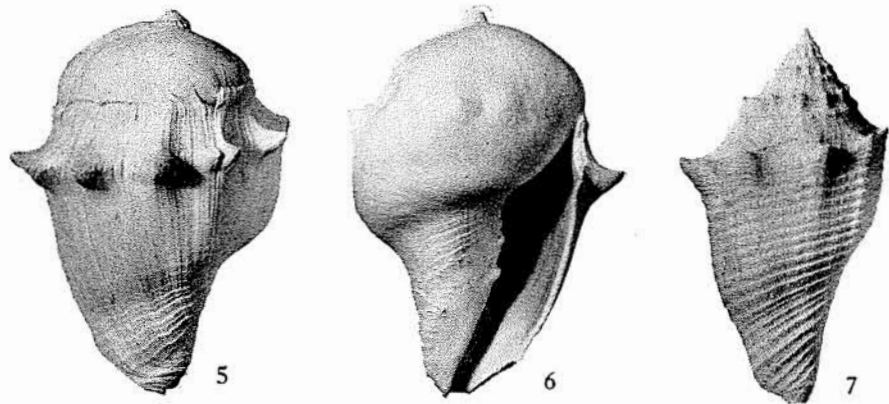
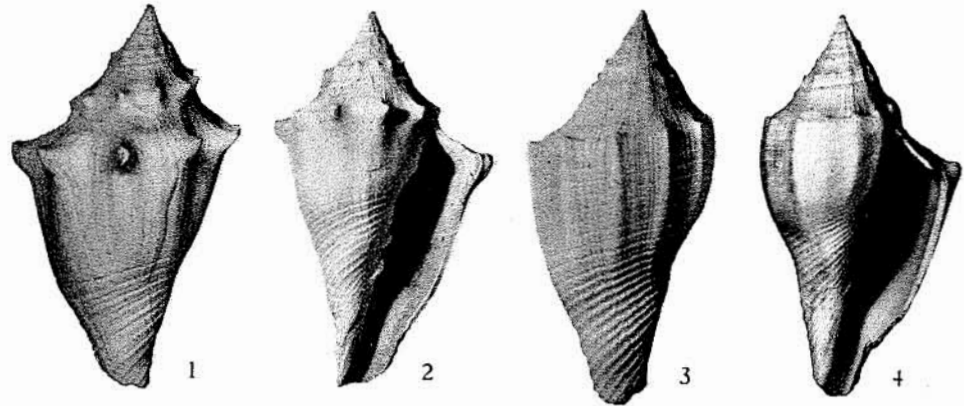


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Evolution of *Athleta petrosa* Stock

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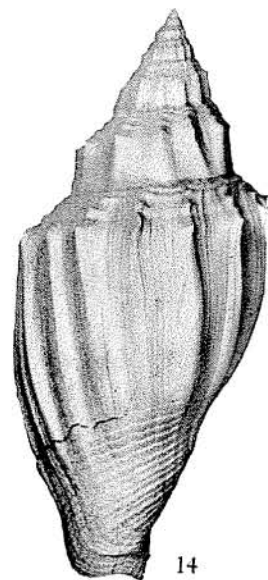
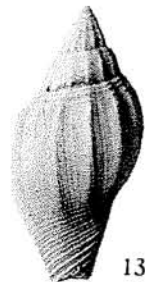
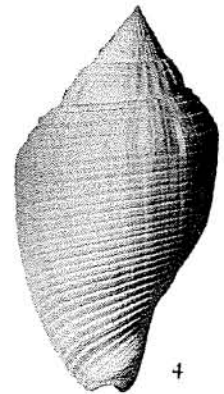
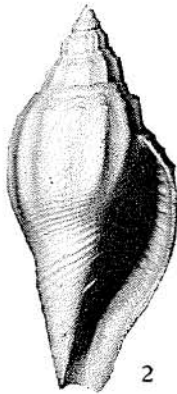
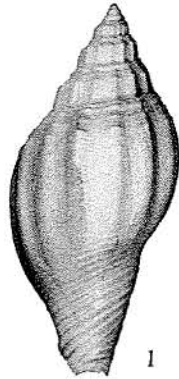


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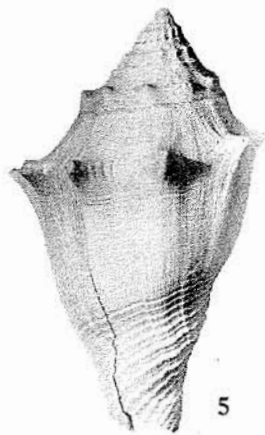
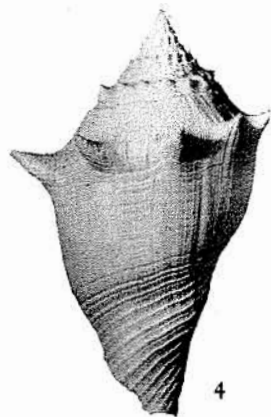
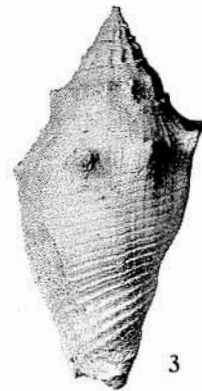
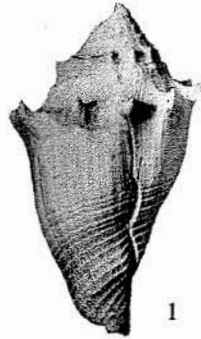


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| 3. B.E.G. No. 35272; Reklaw Formation; B.E.G. Loc. No. 28-T-9, x1.7. | |
| 4. B.E.G. No. 35287; Reklaw Formation; B.E.G. Loc. No. 11-T-7, x 1.5. | |
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Evolution of *Athleta petrosa* Stock

Plate XI



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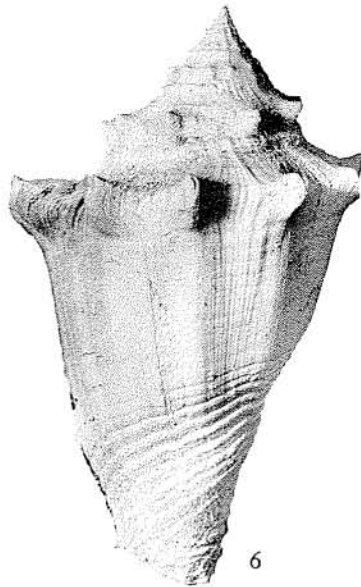
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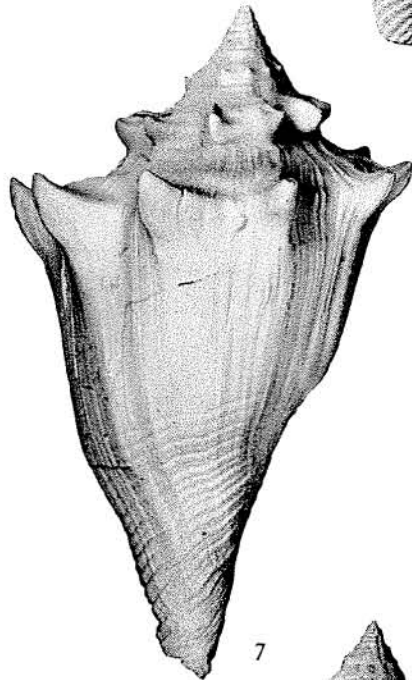
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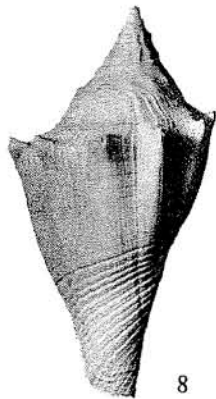
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