A Detailed Taxonomy of Upper Cretaceous and Lower Tertiary Crassatellidae in the Eastern United States—An Example of the Nature of Extinction at the Boundary

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A Detailed Taxonomy of Upper Cretaceous and Lower Tertiary Crassatellidae in the Eastern United States— An Example of the Nature of Extinction at the Boundary

By G. LYNN WINGARD

U.S. GEOLOGICAL SURVEY PROFESSIONAL PAPER 1535

A detailed qualitative and quantitative taxonomic analysis of the Crassatellidae (Mollusca, Bivalvia) at the Cretaceous-Tertiary boundary demonstrates the inaccuracy of the published fossil record

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For readers who wish to convert measurements from the metric system of units to the inch-pound system, the conversion factors are listed below.

Multiply	By	To obtain
	Length	
millimeter (mm)	0.039	inch
centimeter (cm)	0.394	inch
meter (m)	3.281	foot
kilometers (km)	0.621	mile

A DETAILED TAXONOMY OF UPPER CRETACEOUS AND LOWER TERTIARY CRASSATELLIDAE IN THE EASTERN UNITED STATES—AN EXAMPLE OF THE NATURE OF EXTINCTION AT THE BOUNDARY

By G. Lynn Wingard

ABSTRACT

Current theories on the causes of extinction at the Cretaceous-Tertiary boundary have been based on previously published data; however, few workers have stopped to ask the question, "How good is the basic data set?" To test the accuracy of the published record, a quantitative and qualitative analysis of the Crassatellidae (Mollusca, Bivalvia) of the Gulf and Mid-Atlantic Coastal Plains of the United States for the Upper Cretaceous and lower Tertiary was conducted. Thirty-eight species names and four generic names are used in publications for the Crassatellidae within the geographic and stratigraphic constraints of this analysis. Fourteen of the 38 species names are represented by statistically valid numbers of specimens and were tested by using canonical discriminant analysis. All 38 names, with the exception of 1 invalid name and 4 names for which no representative specimen could be located, were evaluated qualitatively. The results show that the published fossil record is highly inaccurate. Only 8 valid, recognizable species exist in the Crassatellidae within the limits of this study, 14 names are synonymized, and 11 names are represented by indeterminate molds or poorly preserved specimens. Three of the four genera are well founded; the fourth is based on the juvenile of another genus and therefore synonymized. This detailed taxonomic analysis of the Crassatellidae illustrates that the published fossil record is not reliable. Calculations of evolutionary and paleobiologic significance based on poorly defined, overly split fossil groups, such as the Crassatellidae, are biased in the following ways:

- Rates of evolution and extinction are higher,
- Faunal turnover at mass extinctions appears more catastrophic,
- Species diversity is high,
- Average species durations are shortened, and
- Geographic ranges are restricted.

The data on the taxonomically standardized Crassatellidae show evolutionary rates one-quarter to one-half that of the published fossil record; faunal change at the Cretaceous-Tertiary boundary that was not catastrophic; a constant number of species on each side of the Cretaceous-Tertiary boundary; a decrease in abundance in the Tertiary; and lower species diversity, longer average species durations, and expanded geographic ranges. Similar detailed taxonomic studies need to be conducted on other groups of organisms to test the patterns illustrated for the Crassatellidae and to determine the extent and direction of the bias in the published fossil record. Answers to our questions about evolutionary change cannot be found in the literature but rather with the fossils themselves. Evolution and extinction occur within small populations of species groups, and it is only through detailed analysis of these groups that we can achieve an understanding of the causes and effects of evolution and extinction.

INTRODUCTION

Evolutionary rates of organisms have received a great deal of attention in the last decade, particularly in discussions of the causes of mass extinction at the Cretaceous-Tertiary boundary. Two major factions have formed: (1) those who support a catastrophic extraterrestrial cause for the extinctions (for example, Alvarez and others, 1980; Emiliani, 1980; Davis and others, 1984; Alvarez and Muller, 1984; and Hut and others, 1987) and (2) those who look to terrestrial causes, whether catastrophic or gradual, to explain the extinctions (for example, Officer and Drake, 1983; Hallam, 1984; Lutz, 1987; and Crocket and others, 1988). Proponents of each side of this debate have relied on calculations of evolutionary rates that are based on plots of compiled faunal lists of species, genera, or families through time (for example, Raup and Sepkoski, 1982; Kitchell and Penna, 1984), yet very few authors have asked, "How reliable are these data?"

Perhaps the most notable use of compiled faunal lists is in Raup and Sepkoski (1982; 1984; 1986; for a complete list of the sources for the compiled data see Sepkoski, 1982a). Raup and Sepkoski (1982) concluded from their plots of families through the Phanerozoic that two types of extinction rates were operating: (1) normal background extinction and (2) mass extinctions. They also concluded that the total rate of background extinction has declined since the Early Cambrian. Subsequently, on the basis of the same set of compiled data, Raup and Sepkoski (1984; 1986) determined that a periodicity existed in the rate of mass extinctions.

Raup and Sepkoski are aware of the constraints of their data set. Sepkoski (1982b, p. 285) stated,

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> Several major problems are encountered when using global taxonomic data to identify and delimit mass extinctions. It is generally impossible to determine how abrupt an event was because of the long and unequal durations of the stratigraphic intervals used to tabulate the data. This problem is further aggravated by inherent sampling errors which push the apparent ends of stratigraphic ranges backward in time, blurring the effects of mass extinctions . . . . Distortion is also introduced by the use of genera and higher taxonomic units in global data. Adequate data on global species' ranges have never been compiled, partly because of inconsistencies in defining fossil species from country to country and from generation to generation and partly because of the sheer magnitude of such a task . . . .

Raup made several references to the problems of the data set; he discussed the need for "complete data" that has "as tight a time resolution as possible" (Raup, 1984, p. 12) and described the data as "noisy and uncertain" (Raup, 1987, p. 3). Raup and Boyajian (1988, p. 112), in a paper on the patterns of extinction, devoted a section to the "variable quality of taxonomy" in which they stated,

> The products of taxonomic research contain many problems and uncertainties familiar to all systematic biologists and paleobiologists. Some groups are over- or under-split, and concepts of the genus and family vary greatly. A genus in one group may be equivalent to a family in another group.

The limitations of the data were enunciated most clearly by Sepkoski (1982b, p. 288), who stated,

> And even with the best available data sets, questions remain about the temporal duration, taxonomic universality, and geographic distribution of the various events. Clearly, these questions must be answered, at least in part, before any comprehensive theory of the general causes of mass extinction can be formulated.

The revelation of possible periodicity of extinction caused a surge of reports by astronomers, astrophysicists, and geologists contemplating probable theories to explain the periodicity, including oscillations in the galactic plane (Swartz and James, 1984), a companion star (Davis and others, 1984), and comet showers (Hut and others, 1987). These authors paid little attention to the reservations expressed by Raup and Sepkoski. Hallam (1984, p. 686) advocated caution when he stated, "In assessing the value of these speculative papers it is clearly necessary first to scrutinize the Raup and Sepkoski analysis on which they are based," and in closing he commented that "Before astronomers indulge in further speculations about the cause of mass extinctions they would do well to learn something about the rich stratigraphical record of their own planet" (Hallam, 1984, p. 687). Other authors (Quinn, 1987, p. 475; Stanley, 1984, p. 69, for example) expressed criticism of the conclusions of Raup and Sepkoski (1984; 1986) and of the basic data set (Signor and Lipps, 1982; Newell, 1982, p. 260), but the debate about the causes of mass extinctions rages on with little regard for these concerns. Few steps are being taken, other than by Raup and Sepkoski themselves (see comment by Raup and Boyajian, 1988, p. 110–111), to rectify the inherent problems of the compiled faunal lists.

Rates of evolution based on compilations of data have been applied to other paleontological problems in addition to discussions of mass extinction. They have been used to describe the Phanerozoic marine diversity in general (Fischer and Arthur, 1977; Sepkoski, 1981) and bivalve diversity in particular (Miller and Sepkoski, 1988). Survivorship of Bivalvia was analyzed by Gilinsky (1988). Phanerozoic background extinction (Boyajian, 1986) and rates of origination and extinction in higher taxa (Gilinsky and Bambach, 1987) also were studied using previously published faunal lists.

With all of this attention paid to counts of taxa through time, it is surprising that so few researchers have investigated the question raised by Raup and Sepkoski and their critics, "How accurate are previously published faunal lists?" Koch (1978) compared the published fossil record to the actual fossil record for the molluscan fauna of the Upper Cretaceous of the Western Interior; he found that the published record underestimated species diversity by a factor of approximately three to four. In addition, he noted that there is "no readily available 'correction factor'" to compensate for the "deficiencies in the published record" (Koch, 1978, p. 371). An extensive comparison of compiled taxonomic data from the literature and taxonomically standardized museum collections of living benthic Foraminifera led Culver, Buzas, and Collins (1987, p. 169) to conclude that

> Evolutionary generalizations based on data generated from the literature only are often unreliable and may be directly in opposition to reality. Extensive attempts at taxonomic standardization should be the norm in paleobiological investigations.

Wingard and Sohl (1990) attempted taxonomic standardization of the Upper Cretaceous genus *Nucula* and concluded that the genus had been split on the basis of assumptions of geographic and stratigraphic separation of species; this splitting led to an overestimate of species diversity for the *Nucula* and an underestimate of species duration. Presumably, paleontologists and stratigraphers working within a limited time frame and a restricted geographic region are aware of each other's taxonomic contributions. The degree of splitting recorded for *Nucula* within these narrowly defined stratigraphic and geographic limits, however, suggests that this is not the case. In fact, the degree of splitting seen for the *Nucula* would suggest that when a major system boundary, such as the Cretaceous-Tertiary, is crossed, the problem of splitting will be intensified. In the past, paleontologists and stratigraphers often worked exclusively in the Cretaceous or in the Tertiary and were not concerned with constructing unified taxonomies through both periods. Yin (1985, p. 590) addressed this issue for the bivalves at the Permian-Triassic boundary and found that the two groups were not as dissimilar as previously described, nor were the differences concentrated at the boundary; he stated,

> To these evidences of gradual changes and replacements should be added the consideration that the disparity between Permian and Triassic bivalves may have been artificially accentuated for supposed biostratigraphic convenience by authors specializing below or above the erathem boundary. Furthermore some genera may be synonymous . . . or even certain species . . . . In short, the replacement of pectinaceans from the Paleozoic to the Mesozoic occurs step by step over a period of at least 10 million years. The erathem boundary can hardly be selected on pectinacean or bivalve evidence alone.

In recent years more authors have begun to examine fossils across the Cretaceous-Tertiary boundary in an attempt to gain a better understanding of the nature of extinction at the boundary (Heinberg, 1979; Hansen and others, 1987; Jones and others, 1987; Hansen, 1988). Still, we lack detailed taxonomic analyses of individual groups of organisms, particularly the macrofossils. Hansen (1982, p. 231) pointed out that

> The literature is top-heavy, however, in that a great deal more speculation has been published concerning the time than actual detailed stratigraphic studies of the interval. Nowhere is this lack more evident than with studies of latest Cretaceous and earliest Tertiary macrofauna. In this regard, macropaleontology lags far behind micropaleontology. Numerous studies exist documenting the detailed stratigraphic ranges of microfossil taxa up to and across the K/T [Cretaceous-Tertiary] boundary, but it is surprisingly difficult to find a similar treatment of the macrofossils.

The purpose of this investigation is to develop a standardized taxonomy for one family of molluscs, the Crassatellidae, across the Cretaceous-Tertiary boundary to examine the issues raised above. First, how reliable is the basic data set? Second, are calculations of evolutionary rates based on previously published faunal lists accurate? If not, then by how much do these calculated rates differ from the picture obtained from the fossil record? Examining the evolution, extinction, and migration that have occurred within one family across the Cretaceous-Tertiary boundary should shed some light on the nature of extinction at the boundary. The analysis of this one family serves as an example of the type of studies that could be done with other groups of organisms to evaluate theories concerning evolution and extinction.

The primary taxonomic unit under investigation in the Crassatellidae is the species. As Raup and Boyajian (1988, p. 112) state, "The ultimate objective of any study of extinction should probably be to assess mortality at the level of species." Newell (1982, p. 260) pointed out, "Evolutionary biologists are agreed that the species is the only taxon with objective reality and it is at this level that both evolution and extinction take place." Both of these papers go on to state that the species unfortunately cannot be used because of problems in the species record. But if species are the basic units of evolution, then paleontologists should clarify and quantify the problems in the species record so that it can be put to use in evolutionary studies; that is the intent of this analysis of the Crassatellidae.

Species and genera of the family Crassatellidae are here examined from the lower Campanian through the Wilcox Stages in the eastern Gulf Coastal Plain and the Mid-Atlantic Coastal Plain of the United States (figs. 1, 2). This geographic area was selected because of the author's knowledge of the stratigraphy of that region and because the detailed attention this area has received in the literature provides tight time-stratigraphic control. In addition, many of the Crassatellidae described in North America for this time period occur in this geographic region. The northern part of the Mid-Atlantic region was included particularly to observe any possible migrations due to changing climatic regimes.

The Crassatellidae were selected because they occur on both sides of the Cretaceous-Tertiary boundary, are fairly well preserved (often in their original aragonitic state), and exhibit an interesting evolutionary history according to the published literature. Figure 3 illustrates the subfamilies and genera for the Crassatellidae as recorded in the *Treatise of Invertebrate Paleontology* (Chavan, 1969, p. N573–N578). A rapid radiation of the Crassatellidae appears to have occurred in the Cretaceous, but of the seven genera found prior to the Cretaceous-Tertiary boundary, only three survived into the Cenozoic. The recorded pattern of evolution and extinction of the Crassatellidae make this family an interesting test case for the evaluation of previously published taxonomic data.

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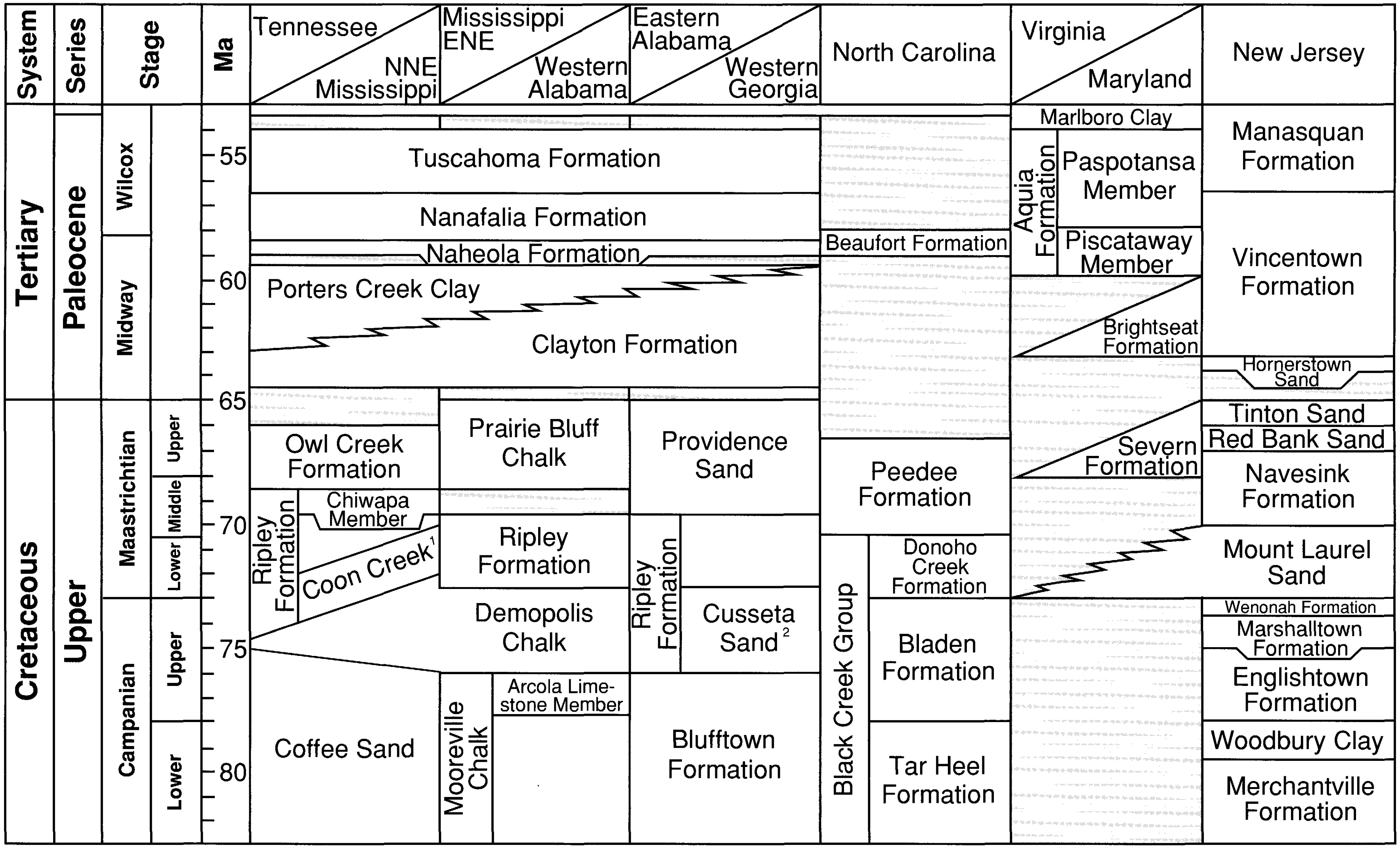
The contributions of Carl Koch, Old Dominion University, as a reviewer and in our many discussions on statistical analyses, are greatly appreciated. John



[1] Coon Creek Tongue of Ripley Formation in Mississippi; Coon Creek Formation in Tennessee.

[2] Cusseta Sand in western Georgia; Cusseta Sand Member of Ripley Formation in Alabama.

FIGURE 1.—Stratigraphic units within the Gulf and Mid-Atlantic Coastal Plains for the time frame of this study. (Data were compiled from the following sources: Frederiksen and others, 1982; Gibson and others, 1982; Harland and others, 1982; Owens and others, 1970; Sohl and Owens, 1991; and L.M. Bybell, T.G. Gibson, N.F. Sohl, U.S. Geological Survey, oral commun., 1989.)

Pojeta, U.S. Geological Survey, Anthony G. Coates and Philip W. Wirtz, George Washington University, and Martin A. Buzas, U.S. National Museum of Natural History, provided advice and suggestions at different phases of the research. Ralph Chapman, U.S. National Museum of Natural History, wrote the digitizing program used in this analysis and provided instruction and resources to aid in its application. Linda Gosnell, Robert Wingard, and Robin Espenschade provided technical assistance. L. Gosnell drafted the canonical variable plots; without her assistance, these plots would not be interpretable. Linda Jacobsen's (U.S. Geological Survey) contributions as editor have been invaluable and deserve special thanks.

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SUMMARY OF PREVIOUS WORK ON THE CRASSATELLIDAE

Crassatella Lamarck, 1799 was first recognized in the United States in 1824 (Say, 1824, p. 49) in the middle Tertiary deposits of Maryland. Starting in 1830 and continuing for the next 45 years, Conrad named and described 12 species of crassatellids in the Upper Cretaceous and lower Tertiary beds of the Gulf and Mid-Atlantic Coastal Plains (table 1; fig. 4). Only 4 of these 12 species are represented by well-preserved specimens and are present in significant numbers in the sediments of this region. Three of the five crassatellid names contributed by Gabb (table 1) also were named from poorly preserved specimens. Other workers who named crassatellids in the 1800's include Morton (1834), Rogers and Rogers (1839), d'Orbigny (1850), Safford (1864), Whitfield (1865; 1885), and Heilprin (1880).

Whitfield's (1885) monograph on the Cretaceous and Tertiary paleontology of New Jersey marked a turning point in the taxonomic literature on the crassatellids in North America. Unlike the cursory information provided by his predecessors, Whitfield's discussions on 11 crassatellid species (2 of them new) contained detailed descriptions and comparisons to other species. Dall (1903), in an account of the Tertiary fauna of Florida, extensively discussed the Crassatellidae and particularly emphasized the evolutionary significance of the hinge and resilifer.

Continuing the trend of providing detailed species descriptions into the 20th century, Gardner (1916) reported on the crassatellids of the Upper Cretaceous deposits of Maryland. Stephenson (1914) included many occurrence charts of species at various localities in the eastern Gulf region, including crassatellids. It was not until 1923, however, that Stephenson began his detailed taxonomic descriptions of the crassatellids. During the remainder of his career, Stephenson named two subspecies, five species, and one genus of Crassatellidae within the eastern Gulf and Mid-Atlantic Coastal Plains alone (table 1; fig. 4).

Stewart's (1930) comprehensive analysis of the genera of Crassatellidae clarified many taxonomic questions. He named and described the genus *Bathytormus* and identified *Crassatella protexta* Conrad as the type species (see pl. 21, figs. 11 and 13 for an example); *C. alaeformis* Conrad was recognized as a member of this genus. *Bathytormus* Stewart is distinguished from *Crassatella* Lamarck by a ligamental cavity that extends to the ventral border of the hinge plate in all ontogenetic stages (Stewart, 1930, p. 137). Stewart (1930, p. 138) noted that the diagnostic character of the hinge is often not developed and therefore not apparent on juveniles of the family. He stated, "The restricted ligamental cavity [of *Crassatella*] is not always shown on small specimens, particularly on those less than 15 mm in length. In fact, one might easily place the immature form in *Bathytormus* while the adult would be a typical *Crassatella*."

In 1965, Palmer and Brann prepared a *Catalogue of the Paleocene and Eocene Mollusca of the Southern and Eastern United States*. Four species of *Bathytormus*, 23 species of *Crassatella*, and 12 *Crassatella* sp. remain at the conclusion of their synonymizations of the Crassatellidae; 12 of these 39 species fall within the geographic and stratigraphic limits of this study.

Chavan (1939; 1952; 1969) and Vokes (1946; 1973; 1988) conducted the most extensive research on the Crassatellidae in recent years. In 1952, Chavan erected two subfamilies within the Crassatellidae, Crassatellinae and Scambulinae. Crassatellinae contains 11 genera and 8 subgenera (Chavan, 1969, p. N573–N577), and Scambulinae contains 4 genera and 2 subgenera (Chavan, 1969, p. N577–N578) (fig. 3). As did Dall (1903) and Stewart (1930), Chavan considered the characters of the hinge to be of primary importance in distinguishing genera.

Table 1 is a summary of all the published generic and specific names used for the Crassatellidae within the Upper Cretaceous and lower Tertiary of the Gulf and Mid-Atlantic Coastal Plains from 1830 to the present. Stratigraphic ranges are illustrated on figure 4. A glance

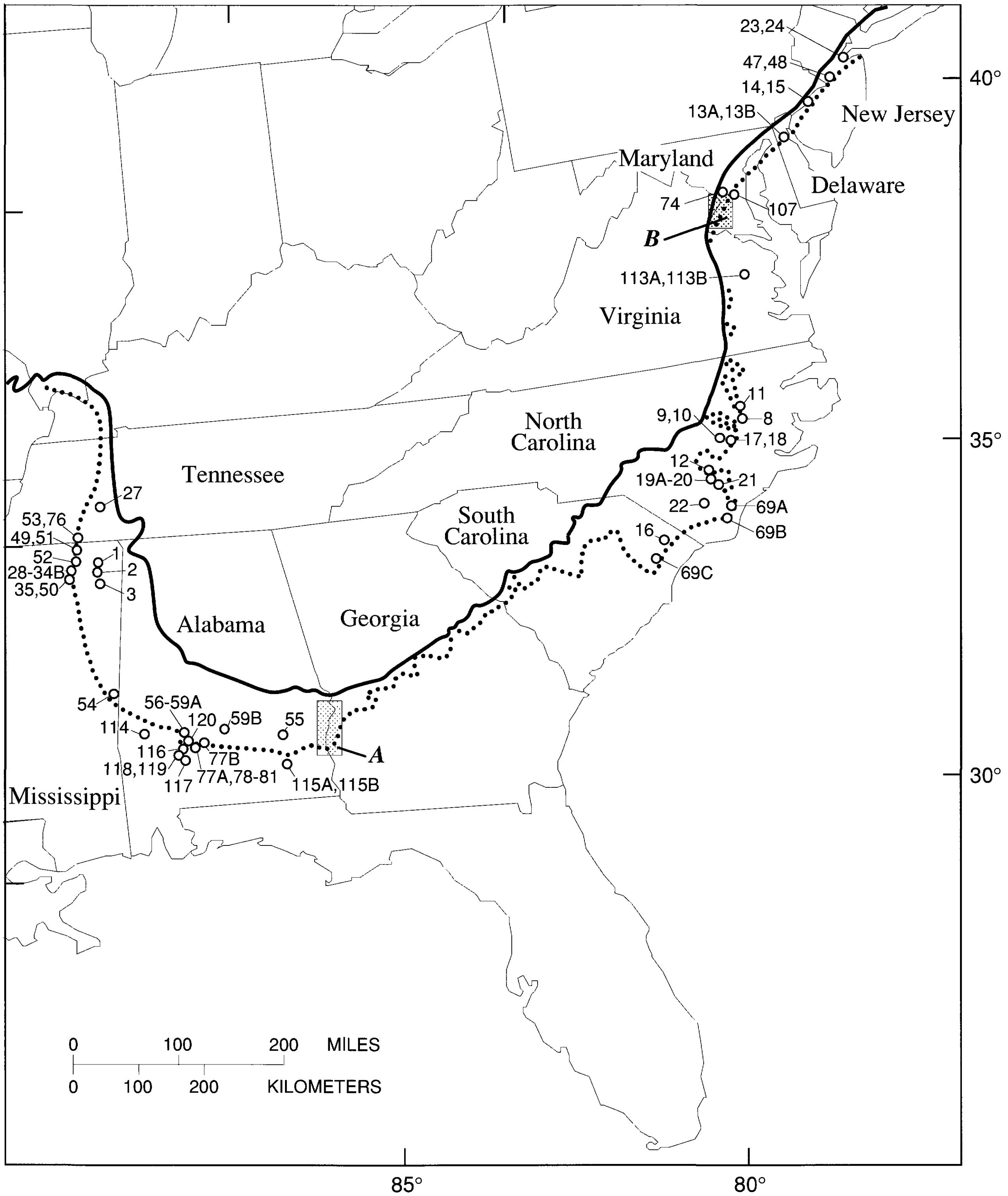

FIGURE 2.— Outcrop pattern of the Cretaceous-Tertiary contact (dotted line), limits of the sedimentary cover of the Coastal Plain (bold solid line), and localities (numbered open circles) (see app. 9 for locality descriptions). *A*, enlargement of Chattahoochee River region, Alabama and Georgia. Solid squares are place names. *B*, enlargement of Washington, D.C., and Potomac River region, Fairfax, Arlington, Prince William, Stafford, and King George Counties in Virginia, and Montgomery, Prince George's, Charles, and St. Mary's Counties in Maryland.

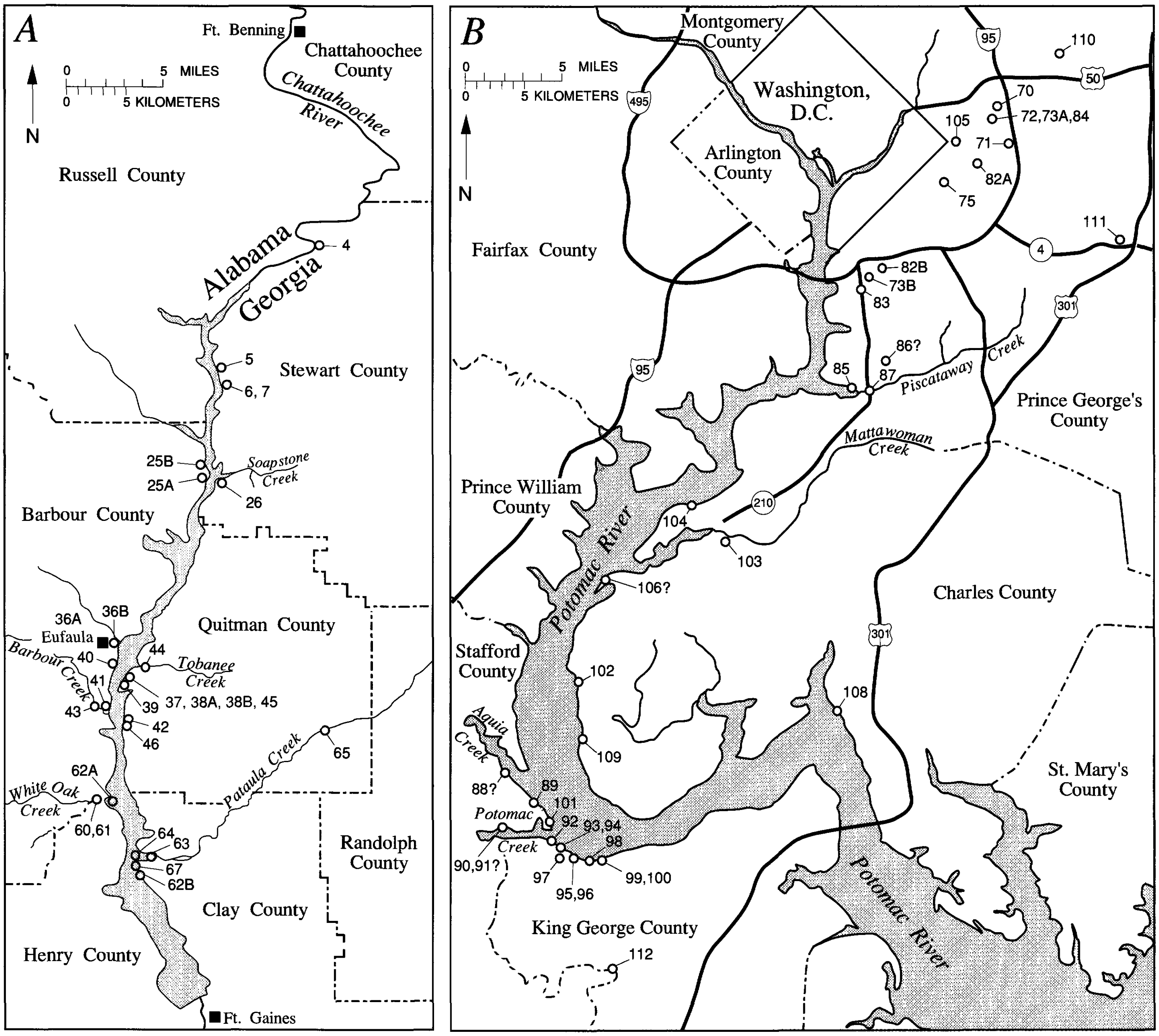

FIGURE 2.—Continued.

at table 1 gives some indication of the proliferation of names in the Crassatellidae, even within the narrow geographic and stratigraphic limits of this study. Several problems are evident throughout the published record of the Crassatellidae. First is the prevalence of names assigned to poorly preserved material; it is impossible to statistically or morphologically evaluate these specific names. Second, and less apparent, is the failure to recognize different stages in the ontogenetic sequence of a single species. Finally, the early workers often had limited sample sizes and did not have the benefit of comparing large suites of specimens. Consequently, intraspecific variation often was not recognized, and end members of a single species were split into separate taxa. Statistical evaluation can help resolve these latter problems.

To answer the question "How good is the basic data set?" all species names represented by well-preserved material were statistically analyzed. Diagnostic characters used by the original authors or subsequent workers were combined to form the basis for the discriminating variables selected for the statistical analysis. These diagnostic characters include features of the shell's general outline, such as the shape of the posterior extremity, posterior-dorsal margin, anterior margin, and ventral margin; the convexity; and the height and orientation of

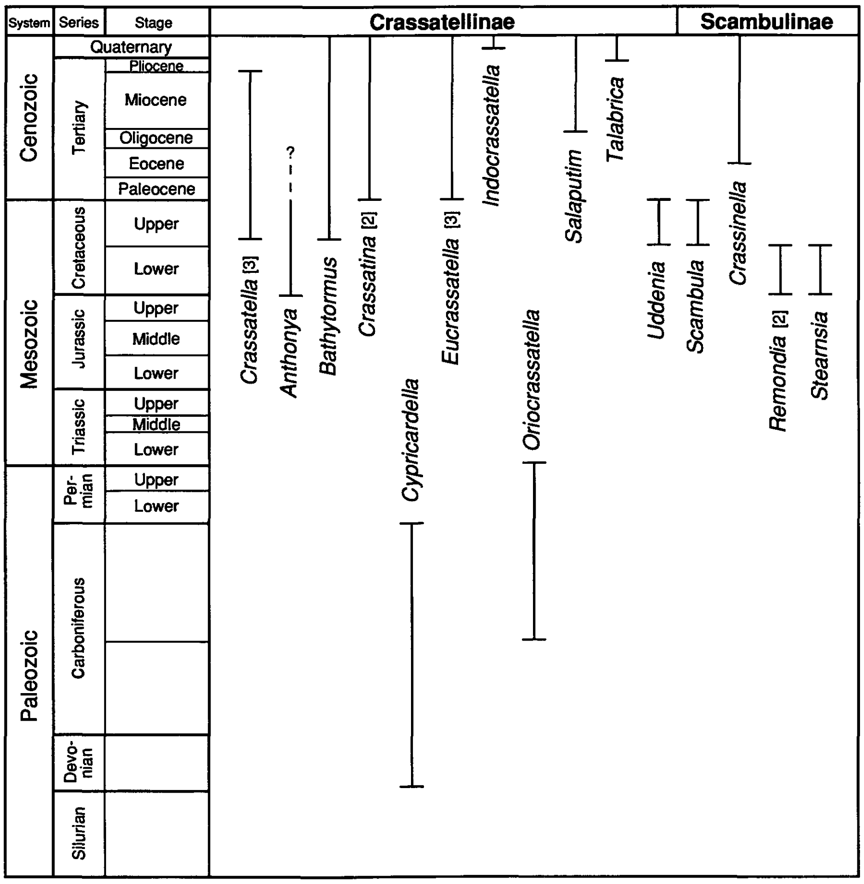

FIGURE 3.—Ranges of the genera of the two subfamilies of Crassatellidae, Crassatellinae and Scambulinae, as recorded in the *Treatise of Invertebrate Paleontology* (Chavan, 1969, p. N573–N578). Number of subgenera indicated in brackets.

the beaks. Other authors used length, height, and thickness of the shell to distinguish taxa. The superficial characters of the ornament and the posterior ridge were significant identifiers to still other workers. Internally, the musculature, hinge characters, and presence or absence of marginal crenulations were deemed diagnostic. At the generic level, the characters of the hinge were the primary diagnostic features; orientation of the beaks also was important at this level. I used the characters selected by the original authors to test the validity of the specific and generic names they erected.

STATISTICAL METHODS

The statistical analysis of the Crassatellidae was divided into four phases:

1. Compiling historical data,
2. Collecting specimens from the field and assembling specimens from established collections for analysis,
3. Creating a morphometric data base through a digitization process, and
4. Statistically testing four subsets of the data. Each of the four subsets were put through two canonical discriminant analyses: the first tested only adult whole abundant named specimens; the second tested all the specimens. The four subsets are
   - Subspecies of *Crassatella vadosa,*
   - Species of *Crassatella,*
   - Species of *Bathytormus,* and
   - Genera of Crassatellidae.

In the first phase, references to the genera and species of Crassatellidae were compiled, and their geographic and stratigraphic positions were identified. The bulk of these data came from the U.S. Geological Survey Mesozoic invertebrate species card file, the U.S. Geological Survey Tertiary invertebrate species card file, Sherborn (1902; 1922–1933), Ruhoff (1980), the Zoological Record of the Zoological Society of London (1869–1983), Palmer and Brann (1965), Sohl and Koch (1983; 1984), Boyle (1893), and from numerous individual articles. Although taxonomic analyses are usually based only on information from other taxonomic papers, for the Crassatellidae, biostratigraphic papers listing species occurrences offer

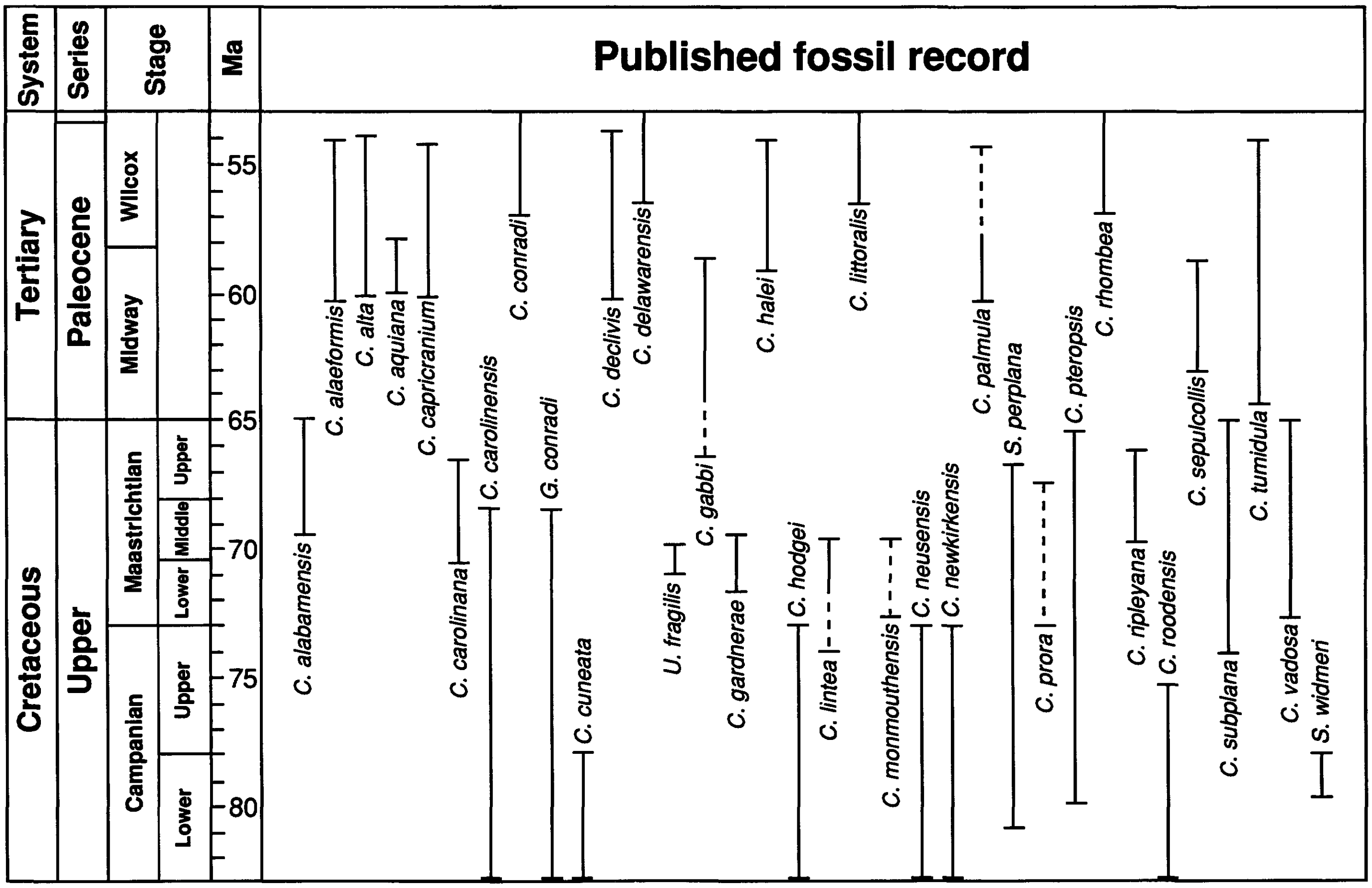

FIGURE 4.—Ranges of the published Crassatellidae names of the Upper Cretaceous and lower Tertiary of the Gulf and Mid-Atlantic Coastal Plains. Generic abbreviations: *C.*, *Crassatella* (incorporates *Crassatellites*, junior synonym of *Crassatella*); *G.*, *Gouldia*; *U.*, *Uddenia*; *S.*, *Scambula*. Species are arranged in alphabetical order. Four species names were omitted due to lack of stratigraphic information. See table 1 for complete listing of species.

valuable information on distribution; thus, data from such papers are included in the compilation. The data files were assembled using SAS (SAS Institute, 1982) on the George Washington University (GWU) IBM-4341 mainframe computer.

In the second phase of the analysis, type specimens and suites of crassatellids were assembled from the U.S. Geological Survey Mesozoic (USGS) and Cenozoic collections (USGS-CENO), the U.S. National Museum of Natural History (USNM) Mesozoic and Cenozoic collections, the Paleontological Research Institution (PRI), and the Academy of Natural Sciences of Philadelphia (ANSP). An attempt was made to obtain material from all stratigraphic and geographic occurrences indicated by the literature search in phase one.

In phase three of the analysis, the morphometric data base was created by using a series of 14 points digitized from selected specimens assembled in phase two. Since the purpose of this study is to test the accuracy of previous specific and generic classifications of the Crassatellidae, I selected the diagnostic characters as close as possible to those identified by the authors of the original species descriptions as discussed in the preceding chapter. The digitization process was based on six homologous characters (fig. 5, points 1–6), following the recommendations of Bookstein and others (1985). These characters are closely tied to the biology of the animal and can be readily identified; thus, the results obtained in digitizing are reproducible. Pelecypods, however, lack any fixed points along the anterior, posterior, and ventral margins of their shells, yet general outline was the character most often cited as diagnostic by previous authors. In order to include marginal points and still keep the results reproducible, I constructed eight lines formed by the intersection of two homologous character points. Where these lines crossed the margin of the shell, a projected point was digitized (fig. 5, points 7–14).

Any specimens missing one or more of the six homologous points (with the exception of internal molds, as discussed below, p. 13) were eliminated from consideration. In collections containing more than 30 individuals, 30 specimens were selected randomly for digitization. In

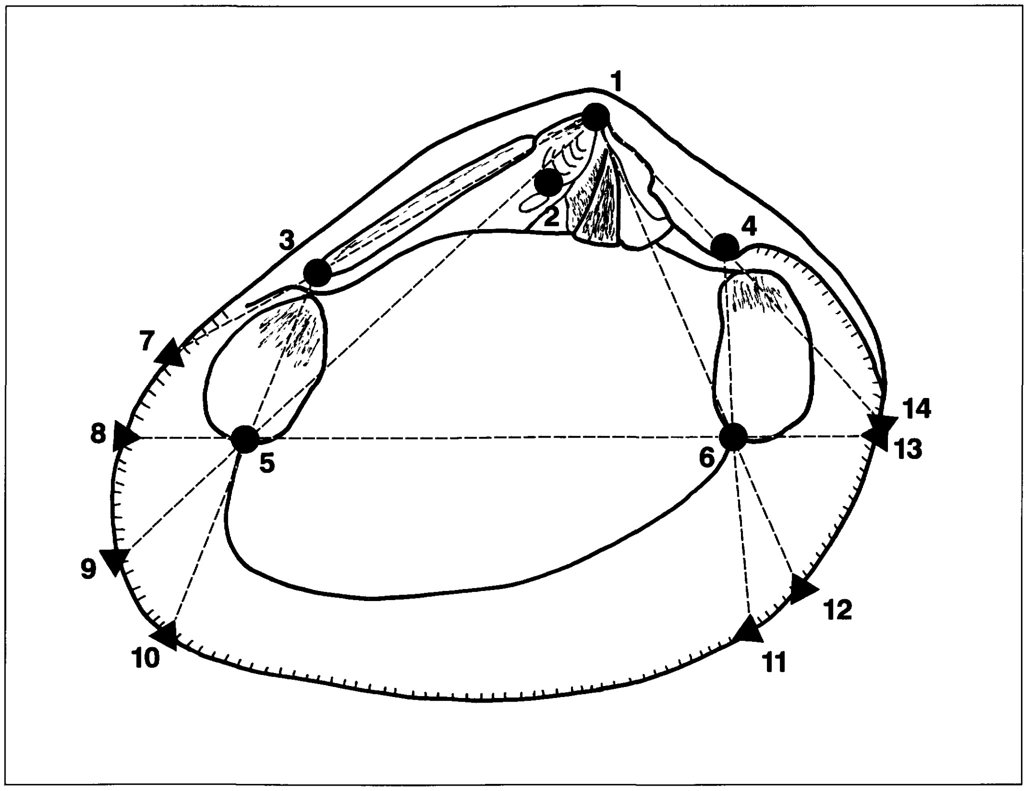

FIGURE 5.—Digitized points on a typical crassatellid shell; these points were used to construct the character variables defined in table 2. Points 1 to 6 represent homologous characters on the individual specimens: 1, the beak; 2, the base of the resilifer; 3, the ventral end of the posterior lateral ridge; 4, the ventral end of the anterior lateral ridge; 5, the point on the base of the posterior adductor where it intersects the pallial line; and 6, the point on the base of the anterior adductor where it intersects the pallial line. Points 7 to 14 represent the projected points on the perimeter of the shell, formed by constructing a line through two homologous characters (modified from Wingard, 1991).

collections of 30 or fewer individuals, all specimens were retained for digitization if all six of their homologous points were present. Digitization was done from photographs or photocopies of the selected specimens. Shells less than 1 cm in length, internal molds, and type specimens were photographed; all others were photocopied.

Each fossil was assigned eight labels: (1) genus, (2) species, (3) locality number, (4) specimen number, (5) left versus right valve, (6) preservation, (7) juvenile versus adult, and (8) measure of width in millimeters. The purpose of the statistical analyses was to test the accuracy of previously defined taxonomic categories; to make the statistical analysis as unbiased as possible, I refrained from critically examining the specimens and imposing my own concepts of genera and species (labels 1 and 2). Instead, I identified the generic and specific categories from a cursory examination of the diagnostic characters mentioned by the previous authors and the locality and the stratigraphic unit in which the specimen was found. For distinguishing between the genera *Bathytormus* and *Crassatella,* I followed Stewart's (1930, p. 137) diagnosis, and for *Scambula* I used Conrad's (1872, p. 51) description. Categorizing *Uddenia* proved to be difficult (discussed in detail in the "Systematic Paleontology" section). To statistically test the validity of the genus, however, specimens labeled as *Uddenia* were classified as such if they came from localities where, according to the published literature, *Uddenia* occurred. In the process of selecting the *Uddenia,* I recognized a fifth unnamed group (genus and species unknown) that was also included in the analysis. *Scambula, Uddenia,* and the unnamed group were included only in the generic level tests because, within the confines of this study, these are monotypic taxa in my opinion. Specimens were assigned a specific name only if their characters matched the original species description and only if they came either from the type locality and stratigraphic unit of the species or from a locality and stratigraphic unit where there was a published account of the species occurrence. If a specimen did not meet both of these criteria then it was classified as an unnamed species (*C.* sp., for example) within a given genus.[1] If a specimen's generic identity could not be determined, it was classified as genus and species unknown.

Specimens were assigned to one of three categories of preservation (label 6): (1) the shell has all homologous and projected points and intact margins, (2) the shell has all six homologous points but, due to a broken shell margin, one or two projected points may be extrapolated, or (3) the specimen is an internal mold so the resilifer point and the measurement of width are missing entirely and the other points are compromised. Internal molds were retained in the digitized collection for localities if original shell material was absent or extremely rare or if the molds were the original types.

The decision to designate any fossil shell as a juvenile or as an adult specimen (label 7) is arbitrary because by definition this transition is marked by the development of gametes, and this event is not ordinarily recorded in the hard parts of the fossil. For *Bathytormus* and *Crassatella*, arbitrary limits were established at lengths of 15 and 30 mm; specimens less than 15 mm in length were identified as juveniles[2]; specimens greater than 30 mm in length were identified as adults. Specimens having lengths between 15 and 30 mm were analyzed according to their characters: (1) a well-developed hinge, a change in surface ornamentation, or a change in posterior shape were considered adult characters or (2) the absence of these characters caused a specimen to be identified as a juvenile.

The measure of the width of the specimen (label 8) is a measure of the convexity of the shell.[3] This third dimension of the specimens (not reflected in the digitized measurements) is included because some of the original authors discussed this aspect of shell shape in their diagnoses. A device designed specifically for this study measures what, on a perfectly equivalved specimen, would be one-half of the width, to the nearest 100th millimeter (±0.05 mm) (fig. 6).

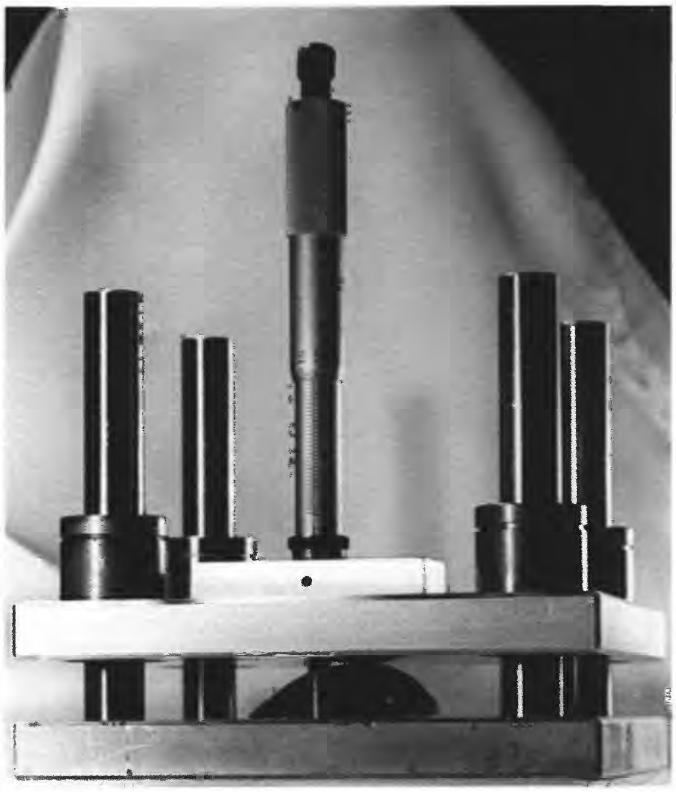

FIGURE 6.—Device used to measure valve width. The fossil rests on its plane of commissure, and any protruding parts of the hinge drop into a depression on the lower platform; the upper platform is lowered, and the micrometer indicates the width of one valve to the nearest 100th millimeter (± 0.05 mm). (Device patent pending; designed by R. Wingard.)

The specimens were digitized on a Summagraphics digitizing pad linked to a personal computer, using "Measure," a digitization program (written in Turbo Basic by Ralph Chapman, U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C., 1987). The six homologous points and eight projected points (fig. 5) were digitized for all specimens (excluding internal molds, which do not retain the resilifer character), and the eight labels were entered from the keyboard. The coordinate file created by these procedures serves as the main data base. From a variable template file, actual measurements were calculated as the distance or angle between two or three of the coordinate points (table 2). Simple distance measurements were used as much as possible because they are the most independent type of data. However, the angular data contribute valuable discriminating information[4] and are the best linear expression of hinge, posterior, and anterior shapes, all characters mentioned as diagnostic by original authors of crassatellid species. The final data file contains close to 1,000 digitized specimens from 28 species categories and 5 generic categories, with 7 categorical variables and 34 continuous variables recorded for each specimen.

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[1] A few exceptions were made to this rule in the case of the subspecies of *Crassatella vadosa*. At two outcrops in the type are (locs. 51, 52) for *C. vadosa ripleyana*, the collections contain a mixture of specimens that fit the descriptions of *C. vadosa vadosa* and *C. vadosa ripleyana*. Although *C. vadosa vadosa* is the only species present at these two localities according to the published accounts, the specimens were categorized into either subspecies according to their morphologic features.

[2] The lower limit was based on a statement by Stewart (1930, p. 138) in a discussion of the differences in hinges between *Bathytormus* and *Crassatella* in which he commented that, for specimens less than 15 mm, the hinges do not serve well as a diagnostic character.

[3] Width for pelecypods is defined as the distance between two planes parallel to the commissural plane that are tangent to the outermost parts of the two valves (Pojeta, 1987, p. 411).

[4] Wingard and Sohl (1990) found the angles to be of primary importance in discriminating between species of Nucula.

TABLE 2.—*Thirty-four morphological variables constructed for the statistical analysis*

[D, distance measurement. A, angle. Variable points, digitized points on figure 5 used to construct each variable; *, convex values not digitized. Discriminant analysis columns 1–4 indicate which variables were used (X) in the analysis of the four subsets of the data: (1) subspecies of *Crassatella vadosa*, (2) species of *Crassatella*, (3) species of *Bathytormus*, and (4) genera of Crassatellidae. N, nonnormal variable, deleted from the data set for all four analyses. Totals at bottom reflect runs in which no internal molds were used]

Description of variable	Variable abbreviation	Variable		Discriminant analysis			
		Type	Points	1	2	3	4
One-half the measure of shell width	CONVEX	D	*	X	X	–	–
Length	LENGTH	D	8–13	–	X	X	X
Distance from the beak to the posterior	POSTHT	D	1–9	–	X	–	X
Distance from the beak to the anterior	ANTHT	D	1–12	X	X	–	X
Hinge angle	HINGE	A	3–1–4	N	–	–	–
Posterior angle	POST	A	7–9–10	N	–	–	–
Height of the posterior region	POSTWID	D	7–10	X	–	–	–
Anterior angle	ANTER	A	11–12–14	X	X	–	X
Height of the anterior region	ANTWID	D	11–14	X	–	X	–
Length of the ventral margin	VENTRAL	D	10–11	X	X	–	–
First increment of posterior height	POSTWID1	D	7–8	–	X	–	X
Second increment of posterior height	POSTWID2	D	8–9	–	X	–	X
Third increment of posterior height	POSTWID3	D	9–10	N	–	–	–
First increment of anterior height	ANTWID1	D	13–14	–	X	X	X
Second increment of anterior height	ANTWID2	D	12–13	X	X	–	–
Third increment of anterior height	ANTWID3	D	11–12	N	–	–	–
Length of the posterior dorsal margin	POSTDOR	D	1–8	X	X	X	–
Length of the anterior dorsal margin	ANTDOR	D	1–13	X	X	X	X
Height of the anterior margin	ANTVERHT	D	4–11	–	X	–	X
Height of the posterior margin	POSVERHT	D	3–10	X	–	X	X
Length of the resilifer	RESILIF	D	1–2	N	–	–	–
Length of the posterior lateral ridge	POSTLAT	D	1–3	X	X	X	X
Length of the anterior lateral ridge	ANTLAT	D	1–4	–	X	X	X
Width of the hinge plate	HINGEPL	D	3–4	X	X	X	X
Angle from anterior lateral to resilifer	RESILANG	A	1–4–2	X	X	X	X
Distance from posterior lateral to margin	POSTLAT2	D	3–8	–	X	–	–
Distance from anterior lateral to margin	ANTLAT2	D	4–13	X	X	X	X
Height of the posterior adductor	POSTADHT	D	3–5	–	X	–	X
Height of the anterior adductor	ANTADHT	D	4–6	X	–	–	–
Width of the mantle cavity	MANTCAV	D	5–6	–	–	X	X
Internal posterior angle	INTPOST	D	1–5–6	–	X	X	X
Internal anterior angle	INTANT	D	1–6–5	X	X	–	X
Distance from posterior adductor to ventral	POSADDST	D	5–10	X	X	X	X
Distance from anterior adductor to ventral	ANTADDST	D	6–11	X	X	X	X
Total number of variables included				18	24	15	21

In phase four, the morphometric data base assembled in phase three was used to quantitatively evaluate the discrete species and generic categories. The first step in the statistical analysis phase was to "clean" and reduce the original morphometric data base (created in phase three). To clean the data, outliers, miscodes, and nonnormal variables were identified and removed. Outliers and miscodes were detected by running the entire data set through the discriminant analysis procedure. Once these were removed, univariate tests uncovered five nonnormal variables, which were also eliminated from the data set (see table 2, discriminant analysis column 1). Next, the clean data set was separated into four subsets representing the four taxonomic categories of Crassatellidae being studied: (1) the subspecies of *Crassatella*, (2) the species of *Crassatella*, (3) the species of *Bathytormus*, and (4) the genera of Crassatellidae. Four separate stepwise discriminant analyses were done on the subsets of the data to further reduce the data set by identifying those variables that contributed significantly (to a level of 0.1) to the differences among the categories; the remainder of the variables were eliminated for each subset (see table 2 for a list of variables included in each analysis).

The second and last step in phase four was to test the four refined subsets of data using canonical discriminant analysis and classificatory discriminant analysis to quantitatively evaluate the primary question being asked, "How accurate is the published fossil record?" Are the genera and species cited in the literature statistically distinct and well defined, or is there a significant degree of overlap between the categories? Discriminant analysis is an excellent statistical procedure for testing a priori groups because it forces maximum separation among the groups and minimum separation within groups; any overlap seen between categories is therefore significant because the statistical bias is towards separation. Two separate canonical discriminant analyses were executed on each of the four subsets of the data. The first excluded the unnamed species categories, the broken specimens, the internal molds, and the juveniles. The second analysis for each subset included all of the data. Classificatory discriminant analyses were done to test the model developed by each canonical discriminant analysis and to test the unknown species categories. All of the statistical computer analyses in phase four were done using SAS on the GWU IBM mainframe. The results of the multivariate statistical analyses of the refined data set are discussed in the following section.

STATISTICAL ANALYSIS

Several aspects of canonical discriminant variable analysis and classificatory discriminant analysis must be understood before the results of the subspecies and subsequent analyses are considered. First, the maximum possible separation between the defined classes is found along each canonical variable; consequently, any overlap between groups is significant. Second, narrowly defined groups (for example, small local populations) by their very nature show higher classification results than broadly defined groups. Finally, in the classificatory discriminant analysis, classification results are always high when the calibration data set itself is classified because these are the data upon which the model is based.

SUBSPECIES OF *CRASSATELLA VADOSA*

Before proceeding with an evaluation of the species of Crassatellidae, two questions need to be answered: (1) are the proposed subspecies valid and (2), if valid, are any subspecies worthy of being raised to specific rank. *Crassatella vadosa* Morton, 1834 has been split into three subspecies: (1) *Crassatella vadosa ripleyana* Conrad, 1858, originally described as a species from the Owl Creek Formation in Tippah County, Miss. (loc. 52), (2) *Crassatella vadosa wadei* Stephenson, 1941, described from the Coon Creek Formation, at Coon Creek, Tenn. (loc. 27), and (3) *Crassatella vadosa vadosa* represented by replaced specimens and internal molds from the Prairie Bluff Chalk, Prairie Bluff, Ala. (loc. 56). In addition, numerous other localities of *C. vadosa* have been reported (see apps. 1, 2), but none of these specimens have been assigned to a subspecies.

To test whether *Crassatella vadosa ripleyana* and *C. vadosa wadei* should be raised to specific rank, the initial assumption is that the two described subspecies, *C. vadosa ripleyana* and *C. vadosa wadei*, do represent valid species categories for the statistical analysis. The category *Crassatella vadosa* includes the type Prairie Bluff specimens (*C. vadosa vadosa*) as well as all other reported *C. vadosa* specimens. The null hypothesis[5] is that no statistically significant differences exist between "*C. ripleyana*," "*C. wadei*," and *C. vadosa*. If the null hypothesis cannot be rejected, this would indicate that "*C. wadei*," "*C. ripleyana*," and *C. vadosa* are members of the same species, as previous authors have indicated. The alternative hypothesis is that distinctive differences exist between "*C. ripleyana*," "*C. wadei*," and *C. vadosa*; therefore, the subspecies should be raised to specific rank. If the degree of overlap seen between the categories is substantial, this would indicate that even the validity of the subspecies categories should be questioned.

Analysis.—First, 145 well-preserved adult specimens[6] were divided into 3 categories and treated as distinct taxonomic units or "species": (1) *Crassatella vadosa* (21 specimens), (2) "*C. ripleyana*" (33 specimens), and (3) "*C. wadei*" (91 specimens). The specimens are from seven localities in the Upper Cretaceous units of the Gulf Coast and Mid-Atlantic regions (app. 1). Eighteen morphologic measurements (table 2) were used to discriminate the three "species" categories.

An examination of the univariate statistics for the analysis (table 3, first analysis) shows that the mean values of the distance measurements are fairly close together for each of the three categories. The group means on each variable for "*Crassatella wadei*," however, are generally larger than the grand means for all three classes combined, whereas the group means for *C. vadosa* and "*C. ripleyana*" are closer together and smaller than the grand means. An examination of the standard deviations (table 4, first analysis) reveals that

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[5] This is the general hypothesis comprising different hypotheses that are tested at different stages of each discriminant analysis. The F test of the Mahalanobis' distances tests the null hypothesis that the group means of each class are equal. If this null hypothesis cannot be rejected, then the means of the two groups will be close together on the canonical discriminant variables. During the canonical discriminant procedure, the null hypothesis being tested is that the canonical correlation for each canonical variable and all correlations that follow equal 0. If this null hypothesis cannot be rejected, then the canonical variables do not correlate to the original data, and the whole procedure is invalid. For more detailed information, refer to Davis (1973, p. 442–456) and *SAS User's Guide: Statistics* (SAS Institute, 1982, p. 369–380).

[6] The criteria for classifying specimens into ontogenetic and preservational categories are discussed in the section on "Statistical Methods," page 13.

TABLE 3.—*Class means and grand means for subspecies of* Crassatella vadosa *on each variable used in both canonical discriminant analyses*

[For the purpose of the analysis, each subspecies was treated as a "species" category. See table 2 for an explanation of the morphological variables. 1, the means from the first canonical discriminant analysis, including adult whole specimens only; 2, the means from the second canonical discriminant analysis of all specimens, including juveniles, broken specimens, and internal molds; *, in the second analysis, CONVEX and RESILANG were removed because these values are not available for internal molds]

Morphological variable	Class mean						Grand mean	
	C. vadosa		"*C. ripleyana*"		"*C. wadei*"			
	1	2	1	2	1	2	1	2
CONVEX	10.62	*	12.17	*	13.02	*	12.48	*
ANTHT	25.15	25.88	26.18	26.19	32.05	31.87	29.71	28.40
POSTWID	12.78	14.60	12.09	12.09	18.78	18.68	16.39	15.83
ANTER	147.70	144.27	145.89	145.73	145.39	145.35	145.84	144.97
ANTWID	13.56	14.81	13.68	13.86	19.51	19.42	17.32	16.54
VENTRAL	25.23	28.62	25.61	25.60	34.94	34.73	31.41	30.60
ANTWID2	8.83	8.24	9.90	9.97	11.71	11.64	10.88	9.95
POSTDOR	28.22	29.68	28.75	28.84	35.51	35.29	32.92	31.84
ANTDOR	19.90	21.11	20.33	20.34	25.56	25.42	23.55	22.74
POSVERHT	18.10	18.83	18.50	18.50	23.81	23.68	21.77	20.76
POSTLAT	16.50	17.97	16.91	16.93	20.88	20.78	19.34	18.94
HINGEPL	20.41	23.10	20.15	20.22	27.15	27.00	24.58	24.19
RESILANG	21.06	*	22.43	*	22.30	*	22.15	*
ANTLAT2	9.82	10.43	10.09	10.10	13.46	13.39	12.16	11.59
ANTADHT	7.97	8.89	8.15	8.18	10.52	10.46	9.61	9.41
INTANT	72.19	68.39	74.43	74.22	68.32	68.33	70.27	69.40
POSADDST	9.73	9.67	10.03	10.06	12.93	12.85	11.81	11.05
ANTADDST	10.42	10.02	10.83	10.87	14.34	14.26	12.97	11.91

TABLE 4.—*Standard deviations, the value for F, and the probability of F for the canonical discriminant analyses of the subspecies of* Crassatella vadosa *on each variable used in the analyses*

[For the purpose of the analysis, each subspecies was treated as a "species" category. See table 2 for an explanation of the morphological variables. Total, total sample standard deviations of the data from all "species" categories combined. Within class, pooled within-class standard deviations for the "species" categories. Between class , between-class standard deviations for the "species" categories. 1, data from the first canonical discriminant analysis, including adult whole specimens only; 2, data from the second canonical discriminant analysis of all specimens, including juveniles, broken specimens, and internal molds; *, in the second analysis, CONVEX and RESILANG were removed because these values are not available for internal molds]

Morphological variable	Standard deviation						F		Probability F	
	Total		Within class		Between class					
	1	2	1	2	1	2	1	2	1	2
CONVEX	2.16	*	2.00	*	1.03	*	12.81	*	0.0001	*
ANTHT	4.64	5.13	3.51	4.24	3.73	3.55	54.53	54.13	.0001	0.0001
POSTWID	3.90	3.71	2.36	2.71	3.81	3.11	126.31	101.64	.0001	.0001
ANTER	6.36	9.28	6.35	9.31	.97	.73	1.13	.48	.3277	.6202
ANTWID	3.93	4.20	2.72	3.44	3.48	2.98	79.26	57.68	.0001	.0001
VENTRAL	6.79	6.89	5.04	5.89	5.61	4.42	60.05	43.45	.0001	.0001
ANTWID2	2.21	2.80	1.91	2.35	1.38	1.89	25.01	49.87	.0001	.0001
POSTDOR	5.41	6.10	4.25	5.39	4.13	3.56	45.66	33.56	.0001	.0001
ANTDOR	3.76	3.99	2.71	3.31	3.20	2.76	67.41	53.41	.0001	.0001
POSVERHT	3.59	3.76	2.44	2.87	3.24	2.99	85.16	83.31	.0001	.0001
POSTLAT	3.26	3.65	2.59	3.30	2.45	1.93	43.37	26.41	.0001	.0001
HINGEPL	4.37	4.52	2.83	3.74	4.09	3.13	101.07	53.88	.0001	.0001
RESILANG	3.14	*	3.13	*	.55	*	1.51	*	.2247	*
ANTLAT2	2.34	2.37	1.62	1.84	2.06	1.85	77.69	77.92	.0001	.0001
ANTADHT	1.67	1.79	1.19	1.55	1.44	1.12	70.86	40.13	.0001	.0001
INTANT	4.26	5.91	3.37	5.50	3.21	2.74	43.71	19.18	.0001	.0001
POSADDST	2.16	2.40	1.60	1.87	1.79	1.86	60.57	76.04	.0001	.0001
ANTADDST	2.65	3.12	1.98	2.41	2.18	2.43	58.44	77.70	.0001	.0001

TABLE 5.—*Mahalanobis' distances between classes for the first canonical discriminant analysis of the adult whole specimens of the subspecies of* Crassatella vadosa

[For the purpose of the analysis, each subspecies was treated as a "species" category]

"Species"	Mahalanobis' distance[1] between classes		
	C. vadosa	"*C. ripleyana*"	"*C. wadei*"
C. vadosa	—	—	—
"*C. ripleyana*"	2.1486	—	—
"*C. wadei*"	4.7413	5.7794	—

[1] Mahalanobis' distances are a measure of the separation of the multivariate means of two classes (Davis, 1973, p. 450–451).

all but two of the variables, anterior angle and resilifer angle (ANTER, RESILANG, see table 2 for an explanation of all variables), show statistically significant differences among the three "species," but just over half of the variables have higher between-class standard deviations as compared to within-class standard deviations. On the basis of the univariate statistics, the following predictions can be made: (1) "*C. ripleyana*" will fall closer to the group mean for *C. vadosa* along the canonical variables than "*C. wadei*," (2) the variables with the higher between-class standard deviations may be the primary discriminating variables, and (3) anterior angle and resilifer angle will contribute the least to the discrimination of the three classes.

The Mahalanobis' distances computed between classes (table 5) support the initial conclusions drawn from the univariate statistics; the distance between *Crassatella vadosa* and "*C. ripleyana*" is less than the distance between *C. vadosa* and "*C. wadei.*" An F test on the Mahalanobis' distances shows all values to be greater than the critical value for F at the 5 percent level of significance, so the null hypothesis of equal class means is rejected.

The plot of canonical variables 1 and 2 (fig. 7) illustrates the predicted separation of "*Crassatella wadei*" from *C. vadosa* and "*C. ripleyana*," and the overlap of *C. vadosa* and "*C. ripleyana*," to the point that the group mean for "*C. ripleyana*" falls within the zone of overlap of the two classes. "*C. wadei*" is isolated primarily along canonical variable 1, which accounts for 95.83 percent of the variance between the classes and has a canonical correlation value of 0.93. The standardized canonical coefficients (table 6) reveal which variables are contributing significantly to the discrimination of the classes; the most significant discriminator (highest absolute value of standardized canonical coefficients) along canonical variable 1 is the height of the posterior margin (POSVERHT). Along canonical variable 2, which accounts for 4.17 percent of the variance and has a canonical correlation value of 0.48, "*C. wadei*" falls between *C. vadosa* and "*C. ripleyana.*" The most significant discriminator along canonical variable 2 is the distance from the beak to the anterior margin (ANTHT) (table 6). The length of the anterior dorsal margin (ANTDOR) and the width of the hinge plate (HINGEPL) are important discriminators on both canonical variables 1 and 2.

TABLE 6.—*Standardized canonical coefficients for the first canonical discriminant analysis of the adult whole specimens of the subspecies of* Crassatella vadosa

[See table 2 for an explanation of the morphological variables. Canonical variables 1 and 2 are plotted on figure 7]

Morphological variable	Standardized canonical coefficient	
	Canonical variable 1	Canonical variable 2
CONVEX	−0.7050	−0.9580
ANTHT	.3260	11.6356
POSTWID	.6271	−0.8973
ANTER	.4720	1.2720
ANTWID	1.0136	1.7628
VENTRAL	.3015	−1.6285
ANTWID2	−0.4572	−3.0255
POSTDOR	−0.9133	3.1803
ANTDOR	−1.9750	−9.8455
POSVERHT	2.1341	−1.7142
POSTLAT	.3319	−6.0909
HINGEPL	1.3759	6.2692
RESILANG	.2966	−0.0772
ANTLAT2	.8279	2.6150
ANTADHT	.1379	−1.1625
INTANT	−0.6542	.4028
POSADDST	−1.3466	.9122
ANTADDST	.4989	−2.4066

TABLE 7.—*Results of the classificatory discriminant analysis of the adult whole specimens of the subspecies of* Crassatella vadosa; *calibration data set tested against itself*

[For the purpose of the analysis, each subspecies was treated as a "species" category. Of the total number of specimens (145), 93.8 percent classify into the predicted "species" categories]

Original "species" category[1]	Total no. of specimens	Number of specimens (percentage of specimens) within the "species" category determined by analysis		
		C. vadosa	"*C. ripleyana*"	"*C. wadei*"
C. vadosa	21	15 (71.43)	6 (28.57)	0 (0)
"*C. ripleyana*"	33	3 (9.09)	30 (90.91)	0 (0)
"*C. wadei*"	91	0 (0)	0 (0)	91 (100.0)
Total	145	18	36	91

[1] "Species" category assigned prior to analysis.

A discriminant analysis was conducted to obtain classification results for the adult whole specimens of *Crassatella vadosa*, "*C. ripleyana*," and "*C. wadei*" (table 7). The variables that measure shell width and resilifer angle (WIDTH, RESILIF) were deleted from this subset of the data so that internal molds, which lack measurements on these two variables, could be tested against the data set consisting of the adult whole specimens. An intermingling of *C. vadosa*, which covers a wide

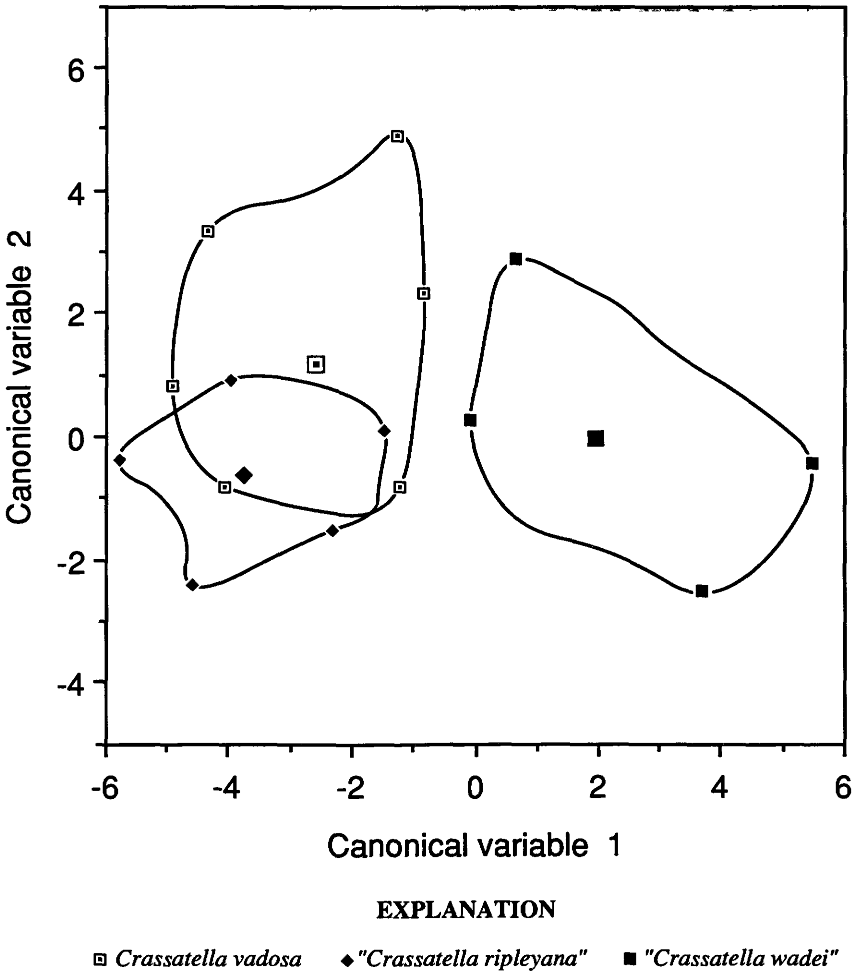

FIGURE 7.—Canonical variables 1 and 2 for the first canonical variate analysis of the subspecies of *Crassatella vadosa*. For the purpose of the analysis, each subspecies was treated as a "species" category. Data for the analysis include adult whole specimens only. Large symbols for the "species" categories represent the midpoints of those categories. Canonical variable 1 accounts for 95.83 percent of the variance between "species" categories and has a canonical correlation of 0.93. Canonical variable 2 accounts for 4.17 percent of the variance between "species" categories and has a canonical correlation of 0.48. See table 6 for standardized canonical coefficients.

geographic range, with the isolated population of "*C. ripleyana*" (71.43 percent of *C. vadosa* classify correctly[7] is seen in the classification results (table 7), but "*C. ripleyana*" was fairly discrete (90.91 percent classify correctly). *C. vadosa* occurs over a broad geographic range, whereas "*C. ripleyana*" and "*C. wadei*" are from discrete populations, so it is expected, due to the nature of discriminant analysis, that the category for *C. vadosa* would have lower classification results than either "*C. ripleyana*" or "*C. wadei.*" "*C. wadei*" classify correctly 100 percent of the time. Next, only the juveniles, broken specimens, and internal molds were tested against the model established by the discrimination of the adult whole specimens (table 8). Only 34.9 percent of all the specimens classify correctly. In this analysis of the juveniles, broken specimens, and internal molds, 50 percent of the specimens representing *C. vadosa* classify as "*C. wadei,*" whereas none of the adult whole specimens of *C. vadosa* had classified as "*C. wadei,*" and 25 percent of "*C. wadei*" specimens classify into *C. vadosa.*

In the final step in the examination of the subspecies of *Crassatella vadosa* all the adult whole specimens,

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[7] Classify correctly, in the discussion of discriminant analysis results, refers to classification in the statistical sense only and does not refer to taxonomic classification.

TABLE 8.—*Results of the classificatory discriminant analysis of the juveniles, broken specimens, and internal molds of the subspecies of* Crassatella vadosa, *tested against the calibration data set of the adult whole specimens*

[For the purpose of the analysis, each subspecies was treated as a "species" category. Of the total number of specimens (86), 34.9 percent classify into the predicted "species" categories]

Original "species" category[1]	Total no. of specimens	Number of specimens (percentage of specimens) within the "species" category determined by analysis		
		C. vadosa	*"C. ripleyana"*	*"C. wadei"*
C. vadosa.......	74	22 (29.73)	15 (20.27)	37 (50.00)
"C. ripleyana"..	8	3 (37.50)	5 (62.50)	0 (0)
"C. wadei"......	4	1 (25.00)	0 (0)	3 (75.00)
Total.........	86	26	20	40

[1] "Species" category assigned prior to analysis.

TABLE 9.—*Mahalanobis' distances between classes for the second canonical discriminant analysis of all the specimens of the subspecies of* Crassatella vadosa, *including juveniles, broken specimens, and internal molds, measured for this analysis*

[For the purpose of the analysis, each subspecies was treated as a "species" category]

"Species"	Mahalanobis' distance[1] between classes		
	C. vadosa	*"C. ripleyana"*	*"C. wadei"*
C. vadosa..............	—	—	—
"C. ripleyana".........	2.2226	—	—
"C. wadei"............	2.8438	3.6007	—

[1] Mahalanobis' distances are a measure of the separation of the multivariate means of two classes (Davis, 1973, p. 450–451).

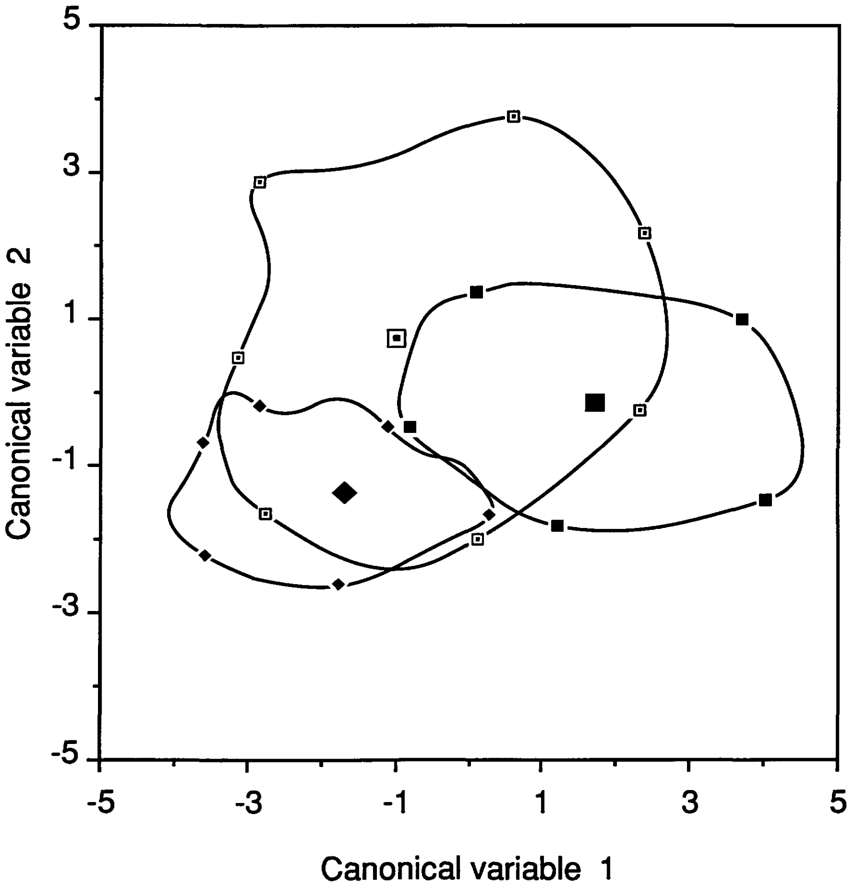
juveniles, broken specimens, and internal molds were included in the same analysis. The data set consists of 231 specimens from 13 localities (app. 2) distributed among the three classes as follows: (1) *C. vadosa* (95 specimens) spread over the reported geographic range of the species, including *C. vadosa vadosa*, (2) *"C. ripleyana"* (41 specimens), and (3) *"C. wadei"* (95 specimens). The classes were analyzed by using 16 of the morphologic variables (table 2); width and resilifer angle were deleted from the data set in order to include internal molds.

The univariate analysis of the class means (table 3, second analysis) on each variable shows very little change for *"Crassatella ripleyana"* and *"C. wadei"* from the first analysis of the adult whole specimens, as would be expected since very few specimens have been added to these classes for this analysis. The inclusion of internal molds is significant to the class of *C. vadosa*, however, because the topotype specimens of *C. vadosa* Morton are internal molds from Prairie Bluff, Ala., and these specimens represent *C. vadosa vadosa*. In addition, the size of this class more than quadrupled with the addition of the juveniles, broken specimens, and internal molds. The individual class means on each variable for *C. vadosa* moved closer to the grand mean on most variables (table 3) as a result of these additions to the category. A comparison of standard deviations (table 4, second analysis), shows the height of the posterior region (POSTWID) to be the only variable having significant differences in between-class versus within-class standard deviation. Anterior angle (ANTER) fails the F test at the 5 percent level of significance. The univariate statistics therefore indicate that there is more overlap between *C. vadosa* and *"C. wadei"* than in the previous analysis, and that the height of the posterior region (POSTWID) contributes significantly to the discrimination of the classes.

The Mahalanobis' distances again support the initial conclusions drawn from an examination of the univariate data. The distances between *"Crassatella wadei"* and *"C. ripleyana"* and *"C. wadei"* and *C. vadosa* decrease when the full data set is examined (table 9). All Mahalanobis' distances pass the F test at the 5 percent level of significance, so the null hypothesis of equal means among the classes is rejected.

The plot of canonical variables 1 and 2 (fig. 8) illustrates overlap between all three classes when all of the specimens are included in the data set. The class means for *"Crassatella ripleyana"* and *"C. wadei"* fall within the region of overlap with *C. vadosa*. Canonical variable 1, which contributes more to the separation of *"C. wadei"* from *C. vadosa* and *"C. ripleyana,"* accounts for 78.70 percent of the variance seen between the classes and has a canonical correlation value of 0.83. Characters of the dorsal margin (POSTDOR, POSTLAT, ANTLAT2, HINGEPL) and the anterior adductor (ANTADHT, ANTADDST) seem to contribute the most to the discrimination of the classes along canonical variable 1, although none of the standardized canonical coefficient values are particularly large (table 10). Canonical variable 2, which accounts for 21.30 percent of the variance seen between the classes and has a canonical correlation value of 0.60, causes the separation of *C. vadosa* from the other two classes. The standardized canonical coefficients (table 10) indicate that most of the separation along canonical variable 2 can be attributed to characters on the anterior portion of the shell (ANTDOR, ANTHT).

Discussion.—The analysis of the adult whole specimens of *"Crassatella ripleyana," "C. wadei,"* and *C. vadosa* reveals that measurable differences do exist between the three groups of specimens. Evidence of the separation is seen in the results of the F tests on the univariate class means, the results of the F test on the Mahalanobis' distances, the separation visible on the plot of the canonical variables (fig. 7), and the classification results (table 7). These differences are evident on the figured specimens as well, particularly when *C. vadosa vadosa* and *C. vadosa ripleyana* are compared to *C. vadosa wadei* (compare pl. 1, figs. 2–4, 16 to pl. 7, fig. 15). The null hypothesis being examined in this portion of



EXPLANATION

⊡ *Crassatella vadosa* ◆ *"Crassatella ripleyana"* ■ *"Crassatella wadei"*

FIGURE 8.—Canonical variables 1 and 2 for the second canonical variate analysis of the subspecies of *Crassatella vadosa*. For the purpose of the analysis, each subspecies was treated as a "species" category. Data for the analysis include all adults, juveniles, broken specimens, and internal molds. Large symbols for the "species" categories represent the midpoints of those categories. Canonical variable 1 accounts for 78.70 percent of the variance between "species" categories and has a canonical correlation of 0.83. Canonical variable 2 accounts for 21.30 percent of the variance between "species" categories and has a canonical correlation of 0.60. See table 10 for standardized canonical coefficients.

the analysis therefore can be rejected; statistically significant differences do exist between "*C. ripleyana*," "*C. wadei*," and *C. vadosa*. The degree of overlap seen on the plot of the entire data set (fig. 8), however, indicates that these differences are not of specific rank. The question remains, however, are the subspecies divisions valid?

The answer to this question does not lie in statistics and may be impossible to ascertain given the present state of disagreement among taxonomists on the concept of subspecies. According to Blackwelder (1967, p. 172), a valid subspecies occupies a distinct geographical area and has "structural features partially setting" it apart as a subspecies. He further states that "species can be distinguished because of gaps in the variation of their features. Subspecies as usually defined cannot be so distinguished, except in some percentage of cases, a figure often placed at 75 percent" (Blackwelder, 1967, p. 172–173).

Blackwelder's criteria for a valid subspecies initially seem to be met for the adult whole specimens of *Crassatella vadosa wadei* included in this analysis. All of the

TABLE 10.—*Standardized canonical coefficients for the second canonical discriminant analysis of all the specimens of the subspecies of* Crassatella vadosa, *including juveniles, broken specimens, and internal molds measured for this analysis*

[See table 2 for an explanation of the morphological variables. Canonical variables 1 and 2 are plotted on figure 8]

Morphological variable	Standardized canonical coefficient	
	Canonical variable 1	Canonical variable 2
ANTHT	−0.6401	2.1524
POSTWID	.5945	−0.1776
ANTER	.2725	.1222
ANTWID	−0.0030	.3559
VENTRAL	.2622	−1.3210
ANTWID2	−0.0356	−1.4529
POSTDOR	−1.0591	1.2989
ANTDOR	−0.6537	−3.5760
POSVERHT	.7326	1.9542
POSTLAT	−0.7357	.7061
HINGEPL	1.5190	.6126
ANTLAT2	1.8134	.0839
ANTADHT	−0.7790	.2839
INTANT	.1063	−1.3712
POSADDST	−0.4112	−1.3354
ANTADDST	1.1318	−0.1538

specimens of *C. vadosa wadei* come from a single locality (app. 1) and presumably a single population.[8] The complete separation of "*C. wadei*" along canonical variable 1 (fig. 7) and the classification results of 100 percent correctly classified (table 7) certainly meet the requirements of partially setting "*C. wadei*" apart from *C. vadosa*; however, such high classification values are to be expected when the calibration data set itself is classified. The separation of "*C. wadei*" also can be explained partially by its stratigraphic isolation from "*C. ripleyana*" and *C. vadosa*. As the groups are defined for this analysis, "*C. wadei*" occurs in the Coon Creek Formation in Tennessee (loc. 27), upper Campanian to lower Maastrichtian, whereas the specimens of *C. vadosa* and of "*C. ripleyana*" occur in the middle and upper stratigraphic units of the Maastrichtian. Nevertheless, there are some real morphologic differences between "*C. wadei*," "*C. ripleyana*," and *C. vadosa*.

In contrast, the adult whole specimens of *Crassatella vadosa ripleyana* do not clearly meet Blackwelder's criteria for subspecies. For example, "*C. ripleyana*" and *C. vadosa* occur in the middle and upper Maastrichtian, and the type locality for *C. vadosa ripleyana* is Owl Creek, in Tippah County, Miss. (loc. 52), but *C. vadosa ripleyana* also has been reported from Owl Creek beds at Providence School, in Tippah County, Miss. (loc. 51). An examination of both collections from the Providence School and Owl Creek localities reveals a combination of typical *C. vadosa* and *C. vadosa ripleyana* forms, yet surprisingly Providence School is predominantly *C. vadosa ripleyana* and Owl Creek is predominantly *C. vadosa*. The classification results (table 7) also illustrate a blending of "*C. ripleyana*" and *C. vadosa* forms; the relatively poor (71.43 percent) classification results for *C. vadosa* can be explained, at least in part, by the wide geographic spread of the group.

The true nature of the relationship between *Crassatella vadosa ripleyana*, *C. vadosa wadei*, and *C. vadosa* is revealed in the analysis that includes the internal molds (all of which are *C. vadosa vadosa*), broken specimens, and juveniles. Although the juveniles are not discussed by the authors of the original descriptions, they are members of the population and must be considered. The general overlap seen on the canonical variable plots for *C. vadosa*, "*C. ripleyana*," and "*C. wadei*," and the occurrence of the group means of "*C. ripleyana*" and "*C. wadei*" in the region of overlap, is significant because canonical discriminant analysis tends to maximize separation. Notably, the Prairie Bluff topotype specimens of *C. vadosa vadosa* occur in the entire area of the plot for *C. vadosa*, except in the region of overlap with "*C. ripleyana*." This area of the plot is occupied by the Tippah County, Miss., specimens of *C. vadosa*. Also, the juveniles of all three categories occur clustered around the group mean for *C. vadosa*. The classification results from the discriminant analysis of the juveniles, broken specimens, and internal molds (table 8) also reveal this intermingling; only 34.9 percent of all of the specimens classify correctly (all less than or equal to the 75 percent limit of Blackwelder, 1967, p. 173). Specimens of *C. vadosa* classify as *C. vadosa*, "*C. ripleyana*," or "*C. wadei*." The misclassified specimens of "*C. ripleyana*" are three broken specimens from the type locality (loc. 52), so their misclassification may simply be a result of the damage to the specimens. The misclassified specimen of "*C. wadei*" is a juvenile.

The results of the analysis that includes broken and juvenile specimens indicate from the following evidence that *Crassatella vadosa ripleyana* and *C. vadosa wadei* are two end members of the *C. vadosa* species: (1) the close proximity of the univariate means, (2) the deficiency of variables having higher between-class standard deviations than within-class standard deviations, (3) the overlap of groups on the plot of canonical variables 1 and 2, and (4) the classification results less than or equal to 75 percent. Whether or not *C. vadosa ripleyana* and *C. vadosa wadei* are valid subspecies of *C. vadosa* depends on how a subspecies is defined. If the term subspecies is simply a convenient way to acknowledge morphologic

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[8] In the case of fossils, the concept of population is not equivalent to a biologic population representing a single point in time. Even if all the specimens come from one locality and one stratigraphic unit, they still represent a span of time. The population therefore consists of generations of descendants.

variation within a species, then *C. vadosa ripleyana* and *C. vadosa wadei* are valid terms because they do possess distinctive differences in overall shape among the adult specimens. If, however, subspecies must be completely isolated geographically from one another to be valid then *C. vadosa ripleyana* and *C. vadosa wadei* are not valid subspecies. Although *C. vadosa wadei* and *C. vadosa ripleyana* have never been reported outside the area of their type localities, a close examination of the collections from the Gulf Coast and Mid-Atlantic regions reveals *C. vadosa ripleyana*-like specimens (pl. 9, fig. 3, and pl. 11, fig. 3) and *C. vadosa wadei*-like specimens (pl. 11, figs. 8–10) do occur in other areas. In the Gulf Coast and Maryland the forms appear intermixed with specimens of the typical *C. vadosa vadosa*-like form. The North Carolina and New Jersey forms tend to be similar to *C. vadosa wadei*. The close proximity of the juveniles of all three categories to the group mean for *C. vadosa* on the plot (fig. 8) raises the possibility that environmental influences acted on the individuals of the populations as they matured and caused the variations seen; the specimens of *C. vadosa* and *C. vadosa ripleyana* from the Owl Creek Formation in Tippah County, Miss., may indicate an area undergoing environmental fluctuation. Another possibility is that the variations in form are the result of sexual dimorphism, but the patterns of distribution illustrated in this analysis do not support this interpretation.

Blackwelder (1967, p. 174) summarized the difficulties in dealing with subspecies:

> The problems involved here are (1) whether there is in nature enough diversity within some species to be usefully studied; (2) if so, whether this diversity can be treated in the taxonomic system; and (3) if so, whether the segregates can or should be named in the formal system of nomenclature. The first question is generally answered in the affirmative. The second question has scarcely ever been faced; it is the crux of the present problem and is here believed to be likely to be eventually answered in the negative. The third question has clouded the second and is answered either negatively or affirmatively according to the experience of the speakers. The Rules of Nomenclature have for a half-century permitted such naming.

In the case of the subspecies of *Crassatella vadosa*, there is indeed enough diversity to be examined and discussed, but I do not believe the differences are significant enough to warrant isolation into formal subspecies categories. This issue is discussed further in the "Systematic Paleontology" section. The most important question is whether or not either of the subspecies under discussion should be raised to species rank; that question has definitely been answered in the negative.

SPECIES OF *CRASSATELLA*

The purpose of this analysis is to test the validity of the many species names that have been proposed for the genus *Crassatella* within the stratigraphic and geographic limits of this study (table 1). The null hypothesis[5] is that no statistically significant differences exist between the species categories of *Crassatella*. If the null hypothesis cannot be rejected for any pair of species categories, this would indicate the existence of synonyms. The alternative hypothesis is that the species names are all valid. A comparison of the species of *Crassatella* across the Cretaceous-Tertiary boundary is of particular importance to this study because the bulk of the species names (32 of 38, table 1) examined herein occur within this genus.

Analysis.—In the first part of the analysis, 239 adult whole specimens were tested from the following species categories[9] (see app. 3 for geographic and stratigraphic distribution):

Species[9]	No. of specimens
Crassatella vadosa Morton, 1834....................	145
C. gardnerae Harbison, 1945........................	53
"*C. hodgei* (Stephenson), 1923" (and *C. carolinensis* Conrad, 1875).	8
C. lintea Conrad, 1860.............................	13
C. tumidula Whitfield, 1865	14
"*C. halei* Harris, 1897a" (= *C. tumidula*)...........	6

Species categories having five or fewer specimens measured for the group were excluded from this first analysis; all unnamed specimens also were excluded. The specimens are distributed among 18 localities in the Upper Cretaceous and lower Tertiary units of the Gulf and Mid-Atlantic Coastal Plains (app. 3). The species of *Crassatella* were discriminated on the basis of 24 morphologic measurements (table 2).

An examination of the univariate class means (table 11, first analysis) on each distance measurement reveals that, in general, "*Crassatella hodgei*" (and *C. carolinensis*), "*C. halei*" (= *C. tumidula*), and *C. lintea* have values lower than the grand mean of all species categories combined. *C. vadosa*, *C. gardnerae*, and *C. tumidula* tend to have univariate class mean values larger than the

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[9] The criteria for assigning specimens to species categories are discussed in the "Statistical Methods" section (p. 12–13). Critical evaluation of specimens was deliberately avoided for the statistical analysis. Consequently, when the specimens were later evaluated, the following incorrect assignments were detected: (1) all specimens initially assigned to *Crassatella halei* are actually *C. tumidula*, (2) 1 specimen assigned to *C. tumidula* is a *C. halei*, (3) 2 specimens assigned to *C.* sp. C belong to a species different from the other 123 specimens of the total measured, (4) 3 of the specimens assigned to *C.* sp. A belong to a species different from the other 211 specimens of the total measured, and (5) the category *C. hodgei* actually contains 2 species, *C. hodgei* (9 specimens total measured) and *C. carolinensis* (4 specimens total measured). Items 1 and 5 above are significant in that they lead to a misrepresentation in the statistical analysis.

on each variable (table 12, first analysis) show that only the variable that measures the internal posterior angle (INTPOST, see table 2 for an explanation of all variables) has a higher standard deviation between classes than that within classes. The lack of clear patterns emerging from the univariate statistics, and the lack of variables having high standard deviations between classes, leads to the prediction that a plot of the canonical variables will grand mean on most variables. The standard deviations show a great deal of overlap among species categories. In addition, classification results are not expected to be high.

The Mahalanobis' distances computed between classes (table 13) reveal patterns that are more distinctive than those of the univariate statistics, particularly if their ranked order is examined. The seven largest distances are between Cretaceous and Tertiary species of *Crassatella*. The smallest distances are between *C. vadosa*, *C. gardnerae*, and *C. lintea*. From these patterns, it is expected that Cretaceous and Tertiary species will be separated on the plot of the canonical variables and that at least three of the four Cretaceous species will occur in proximity to each other. All of the values for the Mahalanobis' distances are greater than the critical value for F at the 5 percent level of significance, so the null hypothesis of equal means is rejected.

The plot of canonical variables 1 and 2 (fig. 9) illustrates the separation of *Crassatella tumidula* (both divisions), the Tertiary species, from *C. vadosa*, *C. gardnerae*, and *C. lintea*, three of the Cretaceous species, along canonical variable 1. "*C. hodgei*" (and *C. carolinensis*), a Cretaceous form, falls closer to the plot of the Tertiary species than to other Cretaceous species categories. Canonical variable 1 accounts for 61.61 percent of the variance between the groups and has a canonical correlation of 0.90. The standardized canonical coefficients (table 14) reveal that the variables pertaining to the dorsal region of the shell and the hinge characters (POSTDOR, ANTDOR, ANTLAT, ANTLAT2) contribute the most to the discrimination of the classes along canonical variable 1. Along canonical variable 2, which accounts for 14.70 percent of the variance between the groups and has a canonical correlation of 0.71, only "*C. hodgei*" (and *C. carolinensis*) is clearly separated. The discriminating variables (POSTDOR, ANTDOR, ANTLAT, ANTLAT2) remain the same for canonical variable 2 as for canonical variable 1. The plot of canonical variables 2 and 3 (fig. 10) shows overlap of all species areas; "*C. hodgei*" (and *C. carolinensis*) is the most isolated, and *C. vadosa*, the least isolated, falls in the central region of the plot. Canonical variable 3 accounts for 12.20 percent of the variance between the categories and has a canonical correlation of 0.68; the primary discriminating variables are characters of the dorsal region (POSTDOR, POSTLAT)

A discriminant analysis was executed to obtain classification results (table 15) on the adult whole named specimens of *Crassatella* having more than five specimens measured per species category. The variables that measure shell width and resilifer angle (CONVEX, RESILIF) were eliminated from this subset of the data so that internal molds could be tested against the calibration set of adult whole specimens. *C. vadosa*, *C. gardnerae*, and *C. lintea* show a tendency to intermix in the classification process, as would be expected from the results of the canonical discriminant analysis; significantly, none of these specimens classify as Tertiary forms. One Cretaceous *Crassatella* specimen, a "*C. hodgei*" (and *C. carolinensis*), does classify as a Tertiary form, and likewise the two Tertiary species categories, *C. tumidula* and "*C. halei*" (= *C. tumidula*), show a tendency to combine with "*C. hodgei*" (and *C. carolinensis*) in the classification process.

A second canonical discriminant analysis was conducted, including the adult whole specimens tested in the first analysis, unnamed specimens (*Crassatella* sp.), juveniles, broken specimens, internal molds, and species having five or fewer specimens measured. The unnamed specimens are those *Crassatella* from localities that do not have a published citation of an occurrence of a particular species of *Crassatella*. The additional species of *Crassatella* tested in this portion of the analysis are the Cretaceous species (1) *C. prora*, (2) *C. monmouthensis*, (3) *C. transversa*, (4) *C. subplana*, and (5) *C. carolinana* and the Tertiary species (6) *C. gabbi* and (7) *C. sepulcollis*. These specimens were excluded from the initial analysis because they do not include statistically significant numbers and because some occur only as internal molds. They are included here, however, to reveal any relationship to the well-represented categories. For this portion of the analysis, 710 specimens were included from 16 species categories (including 3 separate categories of *Crassatella* sp. groups). The specimens come from 51 localities of Upper Cretaceous and lower Tertiary units of the Gulf Coast and Mid-Atlantic regions (app. 4).

In comparison to the analysis of the abundant whole adult specimens, the univariate statistics for the analysis of all of the specimens of the *Crassatella* species show more variables having greater values for between-class standard deviation than for within-class standard deviation (table 12, second analysis). The individual class means (table 11, second analysis) for each category on each variable show change primarily in the means of *Crassatella tumidula*, compared to the earlier results. *C. carolinana* has the largest average size of all of the species categories being tested, followed by

TABLE 11.—*Class means and grand means for species of* Crassatella *on each variable used in both canonical discriminant analyses*

[See table 2 for an explanation of the morphological variables. 1, the means from the first canonical discriminant analysis, including adult whole named specimens only (excluding species categories with ≤5 specimens); 2, the means from the second canonical discriminant analysis of all specimens, including juveniles, broken specimens, internal molds, unnamed specimens, and species categories with ≤5 specimens; —, species excluded from the first analysis; *, in the second analysis, CONVEX and RESILANG were removed because these values are not available for internal molds]

Morphological variable	Class mean									
	C. vadosa		*C. gardnerae*		*C. hodgei* (and *C. carolinensis*)		*C. prora*		*C. monmouthensis*	
	1	2	1	2	1	2	1	2	1	2
CONVEX	12.48	*	13.15	*	7.19	*	—	*	—	*
LENGTH	42.67	41.00	44.45	44.08	31.96	31.98	—	24.14	—	26.73
POSTHT	37.42	35.94	38.25	37.88	27.57	26.83	—	19.42	—	22.12
ANTHT	29.71	28.40	29.19	29.03	22.20	21.69	—	14.37	—	16.57
ANTER	145.84	144.97	147.25	147.00	142.13	140.64	—	139.29	—	149.65
VENTRAL	31.41	30.60	34.96	34.61	24.86	25.19	—	21.79	—	24.18
POSTWID1	6.56	6.57	4.98	4.95	4.35	4.45	—	4.25	—	4.85
POSTWID2	6.46	5.92	6.28	6.22	5.49	4.91	—	2.52	—	3.49
ANTWID1	2.34	2.85	3.17	3.13	5.25	4.74	—	3.48	—	3.21
ANTWID2	10.88	9.95	9.35	9.33	5.78	5.62	—	1.86	—	2.73
POSTDOR	32.92	31.84	34.03	33.71	23.64	23.50	—	18.32	—	19.68
ANTDOR	23.55	22.74	24.12	23.95	19.12	18.67	—	13.19	—	15.15
ANTVERHT	22.58	21.31	21.79	21.68	16.47	15.66	—	6.86	—	10.29
POSTLAT	19.34	18.94	19.63	19.41	14.41	14.32	—	9.66	—	12.04
ANTLAT	11.43	11.24	11.81	11.69	9.46	9.31	—	9.21	—	7.93
HINGEPL	24.58	24.19	25.49	25.21	19.95	19.88	—	16.25	—	17.12
RESILANG	22.15	*	22.63	*	14.69	*	—	*	—	*
POSTLAT2	13.82	13.20	14.53	14.43	9.38	9.36	—	8.95	—	7.97
ANTLAT2	12.17	11.59	12.40	12.34	10.01	9.64	—	4.45	—	7.44
POSTADHT	9.98	9.73	10.20	10.13	6.98	7.03	—	7.13	—	6.39
INTPOST	41.00	40.95	40.10	40.27	45.46	43.76	—	40.15	—	41.57
INTANT	70.27	69.40	66.83	66.73	60.54	60.12	—	53.78	—	56.17
POSADDST	11.81	11.05	11.37	11.31	8.66	7.81	—	4.16	—	6.67
ANTADDST	12.97	11.91	11.73	11.68	7.78	7.40	—	2.38	—	3.66

Morphological variable	Class mean									
	C. transversa		*C.* sp. A		*C. tumidula*		*C. halei* (=*C. tumidula*)[1]		*C. gabbi*	
	1	2	1	2	1	2	1	2	1	2
CONVEX	—	*	—	*	12.81	*	10.78	*	—	*
LENGTH	—	47.74	—	37.33	44.29	35.60	35.06	35.06	—	42.90
POSTHT	—	38.45	—	32.61	36.01	29.15	30.98	30.98	—	36.57
ANTHT	—	28.13	—	25.35	34.51	27.88	27.25	27.25	—	26.72
ANTER	—	147.25	—	145.78	140.80	136.90	137.92	137.92	—	139.67
VENTRAL	—	43.52	—	28.29	30.75	24.53	22.59	22.59	—	33.45
POSTWID1	—	.59	—	5.61	5.60	4.40	6.33	6.33	—	7.79
POSTWID2	—	5.04	—	5.65	7.23	5.91	6.34	6.34	—	6.75
ANTWID1	—	7.65	—	3.11	5.90	5.31	7.07	7.07	—	6.23
ANTWID2	—	5.31	—	8.29	9.10	7.32	7.74	7.74	—	5.77
POSTDOR	—	35.34	—	28.69	32.90	26.47	27.50	27.50	—	31.95
ANTDOR	—	25.23	—	20.67	29.91	24.15	23.54	23.54	—	22.98
ANTVERHT	—	19.35	—	19.24	24.76	19.98	20.53	20.53	—	18.59
POSTLAT	—	18.39	—	17.03	20.08	16.21	16.56	16.56	—	21.04
ANTLAT	—	12.54	—	10.26	13.26	11.05	10.86	10.86	—	10.73
HINGEPL	—	26.44	—	22.19	25.94	21.28	22.16	22.16	—	27.47
RESILANG	—	*	—	*	24.42	*	21.02	*	—	*
POSTLAT2	—	16.96	—	11.83	13.03	10.44	11.29	11.29	—	11.27
ANTLAT2	—	13.30	—	10.51	16.92	13.39	13.22	13.22	—	12.45
POSTADHT	—	11.85	—	8.56	10.03	8.18	9.08	9.08	—	7.45
INTPOST	—	37.36	—	41.44	52.72	51.92	51.19	51.19	—	40.24
INTANT	—	55.80	—	67.64	61.89	62.62	65.73	65.73	—	58.63
POSADDST	—	9.41	—	10.24	9.51	7.63	8.26	8.26	—	12.52
ANTADDST	—	8.01	—	10.54	10.64	8.70	8.83	8.83	—	8.60

TABLE 11.—*Class means and grand means for species of* Crassatella *on each variable used in both canonical discriminant analyses*—Continued

Morphological variable	Class mean							
	C. sepulcollis		*C.* sp. C		*C. subplana*		*C. carolinana*	
	1	2	1	2	1	2	1	2
CONVEX	—	*	—	*	—	*	—	*
LENGTH........	—	25.39	—	17.61	—	43.42	—	63.60
POSTHT	—	21.39	—	15.11	—	34.33	—	49.91
ANTHT	—	17.40	—	12.01	—	34.57	—	46.50
ANTER	—	139.51	—	143.50	—	137.46	—	140.37
VENTRAL......	—	17.70	—	11.72	—	31.62	—	47.97
POSTWID1......	—	4.95	—	2.73	—	5.74	—	8.56
POSTWID2......	—	3.78	—	2.79	—	5.37	—	8.14
ANTWID1.......	—	3.25	—	2.54	—	3.37	—	6.94
ANTWID2.......	—	4.73	—	3.16	—	11.51	—	15.01
POSTDOR.......	—	19.11	—	13.41	—	30.85	—	44.58
ANTDOR........	—	15.18	—	10.32	—	27.33	—	39.74
ANTVERHT....	—	12.39	—	8.59	—	25.98	—	34.52
POSTLAT.......	—	12.31	—	9.38	—	21.31	—	23.95
ANTLAT........	—	7.02	—	5.67	—	13.92	—	18.35
HINGEPL.......	—	16.39	—	12.46	—	28.89	—	34.97
RESILANG.....	—	*	—	*	—	*	—	*
POSTLAT2......	—	7.14	—	4.28	—	10.25	—	21.08
ANTLAT2.......	—	8.39	—	4.80	—	13.47	—	21.67
POSTADHT.....	—	5.98	—	3.61	—	9.38	—	16.72
INTPOST	—	45.52	—	45.00	—	45.56	—	46.58
INTANT	—	64.23	—	63.45	—	62.55	—	62.76
POSADDST	—	6.84	—	5.31	—	10.14	—	13.46
ANTADDST.....	—	5.20	—	4.26	—	15.30	—	17.52

Morphological variable	Class mean				Grand mean	
	C. lintea		*C.* sp. B			
	1	2	1	2	1	2
CONVEX	6.20	*	—	*	12.09	*
LENGTH........	28.35	25.23	—	39.99	41.83	35.09
POSTHT	24.36	21.51	—	32.59	36.32	30.43
ANTHT	19.69	17.69	—	27.49	29.02	24.12
ANTER	140.30	141.46	—	139.68	145.23	144.53
VENTRAL......	17.06	15.77	—	27.43	30.94	26.08
POSTWID1......	6.14	5.38	—	7.03	6.05	5.29
POSTWID2......	4.96	4.27	—	6.21	6.34	5.23
ANTWID1.......	2.85	2.79	—	5.38	2.98	3.11
ANTWID2.......	7.22	6.15	—	9.52	9.99	7.82
POSTDOR.......	21.33	18.89	—	29.01	32.08	26.94
ANTDOR........	15.87	14.45	—	23.10	23.48	19.77
ANTVERHT....	15.94	13.95	—	20.93	21.91	18.03
POSTLAT.......	12.61	11.39	—	15.89	18.85	16.23
ANTLAT........	7.96	7.33	—	10.97	11.35	9.84
HINGEPL.......	17.13	15.63	—	22.44	24.24	21.13
RESILANG.....	17.94	*	—	*	21.88	*
POSTLAT2......	9.07	7.86	—	13.31	13.46	10.95
ANTLAT2.......	7.98	7.21	—	12.27	12.22	10.05
POSTADHT.....	6.76	6.05	—	9.53	9.73	8.10
INTPOST	43.26	44.03	—	45.07	42.01	42.45
INTANT	69.46	67.30	—	64.00	68.53	66.84
POSADDST	8.91	8.04	—	8.88	11.22	9.46
ANTADDST.....	9.48	8.10	—	11.10	12.09	9.71

[1] Data set for analyses 1 and 2 is identical.

TABLE 12.—*Standard deviations, the value for F, and the probability of F for the canonical discriminant analyses of the species of* Crassatella *on each variable used in the analyses*

[See table 2 for an explanation of the morphological variables. Total, total sample standard deviations of the data from all species categories combined. Within class, pooled within-class standard deviations for the species categories. Between class, between-class standard deviations for the species categories. 1, data from the first canonical discriminant analysis, including adult whole named specimens only (excluding species categories with ≤5 specimens); 2, data from the second canonical discriminant analysis of all specimens, including juveniles, broken specimens, internal molds, unnamed specimens, and species categories with ≤5 specimens; *, in the second analysis, CONVEX and RESILANG were removed because these values are not available for internal molds]

Morphological variable	Standard deviation						F		Probability F	
	Total		Within class		Between class					
	1	2	1	2	1	2	1	2	1	2
CONVEX	2.94	*	2.37	*	1.93	*	26.35	*	0.0001	*
LENGTH	9.12	12.22	8.24	8.35	4.46	9.30	11.69	55.04	.0001	0.0
POSTHT	7.67	10.67	6.86	7.25	3.89	8.15	12.82	56.06	.0001	.0
ANTHT	6.41	8.58	5.77	5.93	3.18	6.45	12.09	52.51	.0001	.0
ANTER	7.21	8.50	6.91	8.29	2.52	2.29	5.28	3.38	.0001	.0001
VENTRAL	8.35	10.36	7.32	7.20	4.54	7.77	15.33	51.70	.0001	.0
POSTWID1	2.61	2.52	2.54	2.13	.79	1.43	3.87	19.84	.0022	.0001
POSTWID2	1.44	1.96	1.39	1.56	.47	1.25	4.51	28.65	.0006	.0001
ANTWID1	1.97	1.91	1.61	1.76	1.27	.80	24.99	9.15	.0001	.0001
ANTWID2	2.62	3.43	2.28	2.38	1.45	2.58	16.10	52.37	.0001	.0
POSTDOR	6.95	9.49	6.21	6.48	3.55	7.22	13.01	55.02	.0001	.0
ANTDOR	5.37	6.91	4.80	4.91	2.75	5.06	13.09	47.16	.0001	.0
ANTVERHT	4.76	6.59	4.40	4.52	2.11	5.00	9.19	54.35	.0001	.0
POSTLAT	4.13	5.28	3.75	3.91	1.98	3.72	11.16	40.13	.0001	.0
ANTLAT	2.47	3.21	2.28	2.40	1.10	2.23	9.32	38.57	.0001	.0
HINGEPL	5.03	6.54	4.66	4.81	2.21	4.63	8.96	41.14	.0001	.0
RESILANG	3.84	*	3.44	*	1.94	*	12.66	*	.0001	*
POSTLAT2	3.09	4.44	2.76	2.87	1.58	3.53	12.97	67.08	.0001	.0
ANTLAT2	3.28	3.93	2.91	2.84	1.72	2.84	13.93	44.53	.0001	.0
POSTADHT	2.11	3.07	1.92	2.04	1.00	2.39	10.82	61.04	.0001	.0
INTPOST	4.49	4.14	3.10	3.23	3.59	2.72	53.64	31.59	.0001	.0001
INTANT	4.73	5.30	3.90	4.58	2.99	2.84	23.40	17.05	.0001	.0001
POSADDST	2.47	3.16	2.25	2.31	1.16	2.25	10.51	41.96	.0001	.0
ANTADDST	2.89	3.92	2.57	2.70	1.50	2.97	13.60	53.52	.0001	.0

TABLE 13.—*Mahalanobis' distances between classes for the first canonical discriminant analysis of the adult whole named specimens of the species of* Crassatella, *excluding species categories with five or fewer specimens*

Species	Mahalanobis' distance[1] between classes					
	C. vadosa	*C. gardnerae*	*"C. hodgei"* (and *C. carolinensis*)	*C. tumidula*	*"C. halei"* (=*C. tumidula*)	*C. lintea*
C. vadosa	—	—	—	—	—	—
C. gardnerae	2.2441	—	—	—	—	—
"*C. hodgei*" (and *C. carolinensis*)	6.2539	5.9276	—	—	—	—
C. tumidula	7.6723	7.2716	6.9087	—	—	—
"*C. halei*" (=*C. tumidula*)	7.5436	7.3763	5.3784	5.6798	—	—
C. lintea	3.4546	4.0800	5.5032	7.4944	7.8419	—

[1] Mahalanobis' distances are a measure of the separation of the multivariate means of two classes (Davis, 1973, p. 450–451).

C. transversa and then by the group composed of *C. vadosa*, *C. gardnerae*, and *C. subplana*. *C.* sp. C has the smallest mean size for the majority of the linear distance measurements.

The Mahalanobis' distances (table 16) between classes show very low values for the group of Cretaceous *Crassatella*, *C. vadosa*, *C. gardnerae*, and *C. lintea* and *C.* sp. A as well (similar results were obtained in the analysis of the adult whole specimens, table 13). Note that the category for *C. sepulcollis*, consisting of a single specimen being tested, fails the F test of the Mahalanobis' distances at the 5 percent level of significance when paired with "*C. hodgei*" (and *C. carolinensis*), *C. monmouthensis*, *C. lintea*, and *C.* sp. C. The null hypothesis of equal means between these pairs cannot be rejected, but, because the category *C. sepulcollis* is represented by only two specimens, failure of the F test is not surprising.

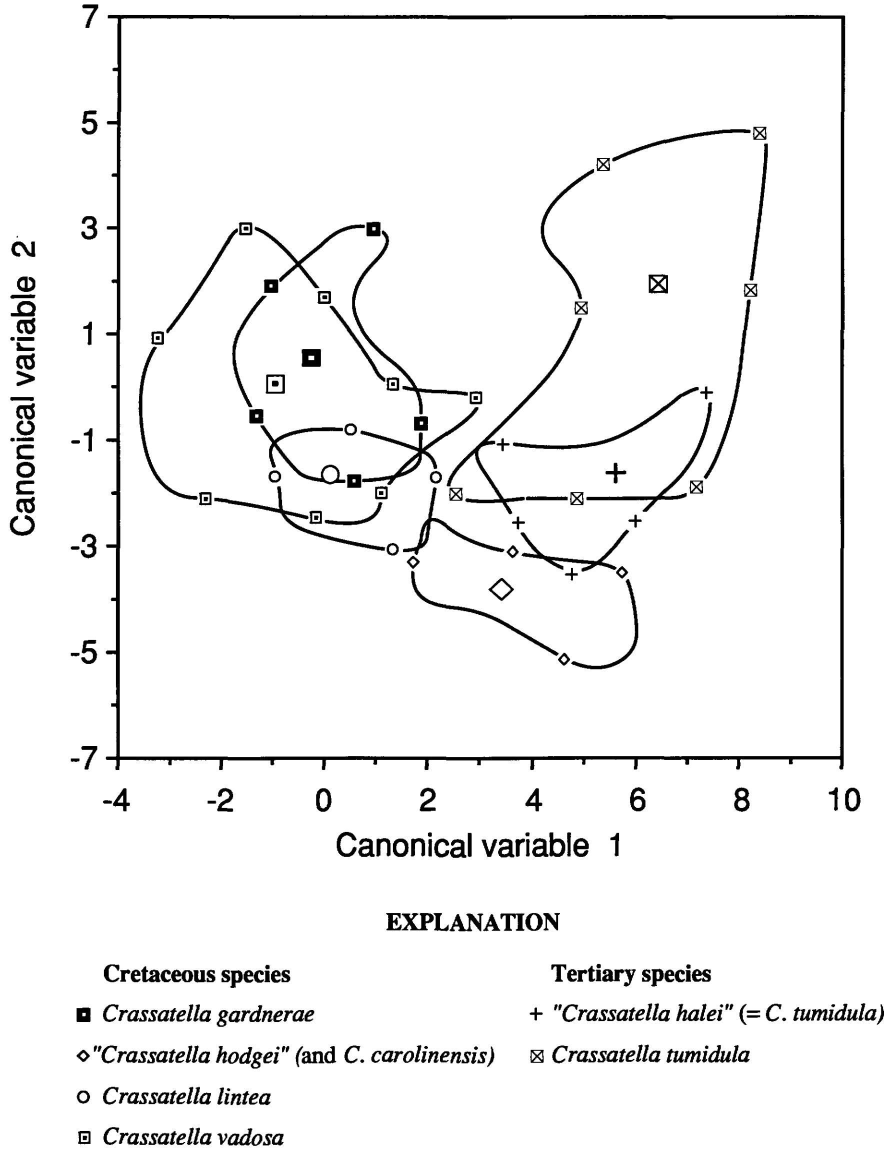


FIGURE 9.—Canonical variables 1 and 2 for the first canonical variate analysis of the species of *Crassatella*. Data for the analysis include adult whole specimens from named species categories only (excluding species categories with five or fewer specimens). Large symbols for the species categories represent the midpoints of those categories. Canonical variable 1 accounts for 61.61 percent of the variance between species categories and has a canonical correlation of 0.90. Canonical variable 2 accounts for 14.70 percent of the variance between species categories and has a canonical correlation of 0.71. See table 14 for standardized canonical coefficients.

The plot of canonical variables 1 and 2 (fig. 11) illustrates the nearly complete overlap of the Cretaceous species *Crassatella vadosa*, *C. gardnerae*, *C. lintea*, and *C.* sp. A; even the group means of the four categories fall within the region of overlap. The Tertiary forms, *C. tumidula* and "*C. halei*" (= *C. tumidula*), are partially separated from the Cretaceous cluster of the *C. vadosa* group; "*C. halei*" (= *C. tumidula*) falls almost completely within the area of *C. tumidula* on the plot, and the group means fall close together. "*C. hodgei*" (and *C. carolinensis*) and *C.* sp. C fall between and partially overlap the Cretaceous and the Tertiary groups on the plot. The remaining points are the individuals from the categories represented by five or fewer specimens. Both canonical

TABLE 14.—*Standardized canonical coefficients for the first canonical discriminant analysis of the adult whole named specimens of the species of* Crassatella, *excluding species categories with five or fewer specimens*

[See table 2 for an explanation of the morphological variables. Canonical variables 1, 2, and 3 are plotted on figures 9 and 10]

Morphological variable	Standardized canonical coefficient		
	Canonical variable 1	Canonical variable 2	Canonical variable 3
CONVEX	−0.4800	1.7845	−0.4576
LENGTH	−0.3832	4.3320	6.2305
POSTHT	−8.4422	−9.0325	−4.5286
ANTHT	−5.2809	1.3375	.7294
ANTER	−0.3508	−0.0216	−0.2975
VENTRAL	.1531	.9370	1.5889
POSTWID1	.3921	−0.0093	.7650
POSTWID2	1.5642	1.3739	.8153
ANTWID1	−0.2364	.1103	−0.1385
ANTWID2	1.6373	−0.6230	.0488
POSTDOR	20.2462	−12.2669	−14.6049
ANTDOR	−33.1656	23.8356	−5.1876
ANTVERHT	1.1318	1.0139	−1.7285
POSTLAT	−3.4113	8.3909	10.9802
ANTLAT	17.8982	−11.0322	2.6541
HINGEPL	−4.0296	.6731	−4.0325
RESILANG	−0.0123	.5736	−0.2303
POSTLAT2	−5.8452	7.2593	5.3419
ANTLAT2	22.3020	−16.4472	2.8537
POSTADHT	.1264	−1.0203	−0.5526
INTPOST	.1582	.1763	1.0047
INTANT	−1.2863	.6965	1.2254
POSADDST	−0.8206	−0.4561	−0.3214
ANTADDST	−0.5879	−0.6163	1.4400

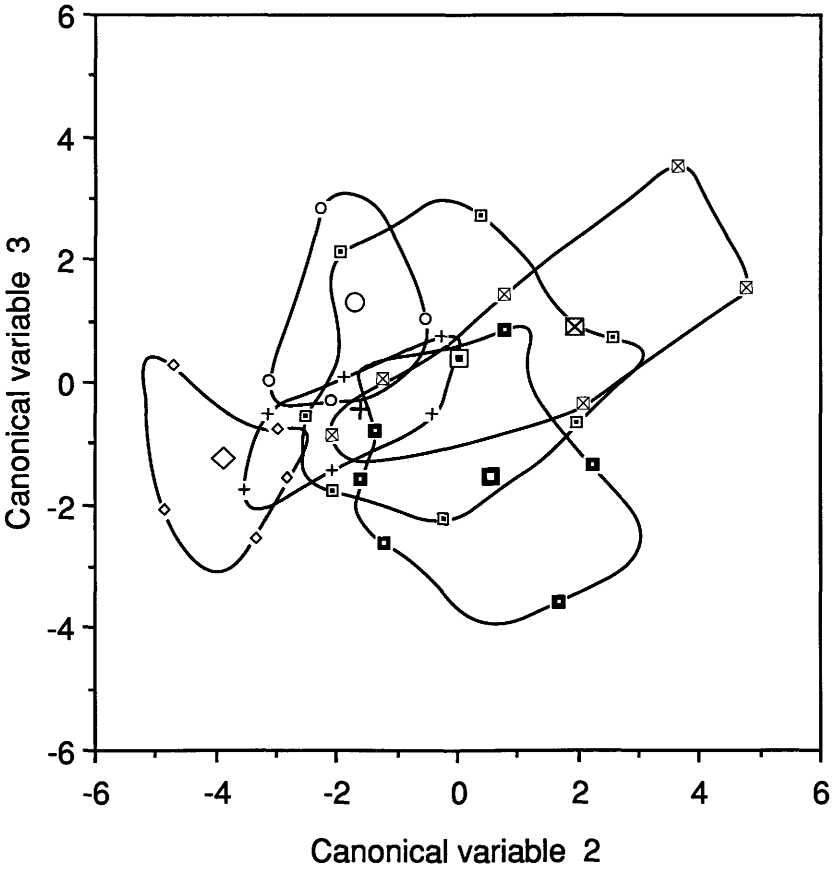
TABLE 15.—*Results of the classificatory discriminant analysis of the abundant adult whole named specimens of the species of* Crassatella; *calibration data set tested against itself*

[Of the total number of specimens (239), 84.9 percent classify into the predicted species categories]

Original species category[1]	Total no. of specimens	Number of specimens (percentage of specimens) within the species category determined by analysis					
		C. vadosa	*C. gardnerae*	"*C. hodgei*" (and *C. carolinensis*)	*C. tumidula*	"*C. halei*" (=*C. tumidula*)	*C. lintea*
C. vadosa	145	134 (92.41)	9 (6.21)	1 (0.69)	0 (0)	0 (0)	1 (0.69)
C. gardnerae	53	13 (24.53)	38 (71.70)	1 (1.89)	0 (0)	0 (0)	1 (1.89)
"*C. hodgei*" (and *C. carolinensis*)	8	0 (0)	1 (12.50)	6 (75.00)	0 (0)	1 (12.50)	0 (0)
C. tumidula	14	0 (0)	0 (0)	1 (7.14)	12 (85.71)	1 (7.14)	0 (0)
"*C. halei*" (=*C. tumidula*)	6	0 (0)	0 (0)	2 (33.33)	0 (0)	4 (66.67)	0 (0)
C. lintea	13	2 (15.38)	2 (15.38)	0 (0)	0 (0)	0 (0)	9 (69.23)
Total	239	149	50	11	12	6	11

[1] Species category assigned prior to analysis.

variables 1 and 2 seem to contribute to the partial separation of the Cretaceous and Tertiary clusters. Canonical variable 1 accounts for 48.05 percent of the variance and has a canonical correlation of 0.84; canonical variable 2 accounts for 22.59 percent of the variance and has a canonical correlation value of 0.72. The primary discriminating variables on canonical variable 1 are characters of the hinge and dorsal regions (POSTDOR, ANTDOR, POSTHT) (table 17). The plot of canonical variables 2 and 3 (fig. 12) shows only two distinctive differences from the plot of canonical variables 1 and 2; *C. transversa* is isolated on the plot, and *C. carolinana* falls within the region of the plot defined by *C. tumidula*. Canonical variable 3 accounts for 9.91 percent of the variance between the groups and has a canonical correlation of 0.57; the variables that measure attributes of the dorsal margin (POSTDOR, ANTDOR, POSTLAT, ANTLAT2) (table 17) again contribute to



EXPLANATION

Cretaceous species

◘ *Crassatella gardnerae*

◇ *"Crassatella hodgei"* (and *C. carolinensis)*

○ *Crassatella lintea*

⊡ *Crassatella vadosa*

Tertiary species

\+ *"Crassatella halei"* (= *C. tumidula)*

⊠ *Crassatella tumidula*

FIGURE 10.—Canonical variables 2 and 3 for the first canonical variate analysis of the species of *Crassatella*. Data for the analysis include adult whole specimens from named species categories only (excluding species categories with five or fewer specimens). Large symbols for the species categories represent the midpoints of those categories. Canonical variable 2 accounts for 14.70 percent of the variance between species categories and has a canonical correlation of 0.71. Canonical variable 3 accounts for 12.20 percent of the variance between species categories and has a canonical correlation of 0.68. See table 14 for standardized canonical coefficients.

the discrimination of the groups, as they do on canonical variables 1 and 2.

The last step of the analysis was to classify the juveniles, broken specimens, internal molds, and unnamed specimens. The juveniles, broken specimens, and internal molds of all the species categories were tested against the calibration data set of the adult whole specimens (excluding the variables for shell width and resilifer angle; table 2). An intermingling of Cretaceous and Tertiary specimens can be seen on table 18, but all of the Cretaceous forms that classify as Tertiary are either internal molds or damaged specimens. In contrast, many of the Tertiary forms classify as Cretaceous, and the majority of these are juveniles. A strong bias is introduced in this classification process by forcing *Crassatella prora*, *C. monmouthensis*, *C. transversa*, *C. subplana*,

TABLE 16.—*Mahalanobis' distances between classes for the second canonical discriminant analysis of all the specimens of the species of* Crassatella, *including juveniles, broken specimens, internal molds, unnamed specimens, and species categories with five or fewer specimens, measured for this analysis*

Species	Mahalanobis' distance[1] between classes							
	C. vadosa	*C. gardnerae*	"*C. hodgei*" (and *C. carolinensis*)	*C. prora*	*C. monmouthensis*	*C. transversa*	*C.* sp. A	*C. tumidula*
C. vadosa	—	—	—	—	—	—	—	—
C. gardnerae	1.9305	—	—	—	—	—	—	—
"*C. hodgei*" (and *C. carolinensis*).	3.4722	3.2328	—	—	—	—	—	—
C. prora	7.9647	7.8076	6.4822	—	—	—	—	—
C. monmouthensis	4.4165	4.1834	2.8867	5.4848	—	—	—	—
C. transversa	8.0443	6.8900	7.0203	8.0550	7.1475	—	—	—
C. sp. A	1.4569	1.4620	2.8307	7.8722	3.9693	7.6407	—	—
C. tumidula	5.9406	5.9602	4.6777	8.6545	6.3767	9.5181	5.7276	—
"*C. halei*" (=*C. tumidula*)	5.8055	6.2065	4.7792	8.2005	6.5100	9.6258	5.7786	4.0999
C. gabbi	6.8753	6.5786	6.1239	10.0480	6.6685	8.6420	6.4906	8.7731
C. sepulcollis	3.6551	3.8835	3.0798	7.2060	3.7238	8.0120	3.4231	4.9323
C. sp. C	3.8867	4.0081	2.9857	7.2103	3.5324	8.2454	3.3918	5.2485
C. subplana	7.3230	7.9185	7.7201	11.0466	8.7533	11.3130	7.6424	7.9509
C. carolinana	7.4486	7.4730	8.0443	10.7847	9.0966	9.4030	7.7568	8.4179
C. lintea	2.5513	3.1172	3.5768	7.9953	4.4351	8.4654	2.3080	5.5580
C. sp. B	4.6523	4.4632	3.9604	8.1558	5.7214	8.5268	4.4404	5.0930

Species	"*C. halei*" (=*C. tumidula*)	*C. gabbi*	*C. sepulcollis*	*C.* sp. C	*C. subplana*	*C. carolinana*	*C. lintea*	*C.* sp. B
C. gabbi	9.1522	—	—	—	—	—	—	—
C. sepulcollis	4.9632	6.9743	—	—	—	—	—	—
C. sp. C	5.6142	7.1824	2.3241	—	—	—	—	—
C. subplana	9.1523	10.0712	8.1448	7.8491	—	—	—	—
C. carolinana	8.7397	10.8616	8.4403	9.4071	8.4184	—	—	—
C. lintea	5.7025	7.2253	3.0444	2.7290	7.5618	7.9922	—	—
C. sp. B	5.3963	7.4589	5.2331	5.4708	8.6646	6.7387	4.6710	—

[1] Mahalanobis' distances are a measure of the separation of the multivariate means of two classes (Davis, 1973, p. 450–451).

and *C. carolinana* (the poorly preserved or rare species categories), and *C.* sp. A (the unnamed species category) to classify as one of the species categories from the original calibration data set (the abundant adult whole named specimens).

The final discriminant analysis tested all specimens (except internal molds) against a calibration data set based on all specimens except unnamed forms and internal molds (table 19); the purpose was to establish how the unnamed specimens would classify into the existing categories. Categories containing only one specimen were not considered valid for the calibration data set by the requirements of the discriminant analysis program. The results show that the two unnamed categories of Cretaceous *Crassatella*, *C.* sp. A, and *C.* sp. B fall almost exclusively into the group composed of *C. vadosa*, *C. gardnerae*, and *C. lintea*; 1.46 percent are categorized as "*C. hodgei*" (and *C. carolinensis*). *C.* sp. C, in contrast, has at least some members that classify as almost every other species category; 56 percent, the largest percent, classify as *C. lintea*.

Discussion.—The results of the analysis of *Crassatella* species in the Upper Cretaceous and lower Tertiary reveal several interesting points. First, taxonomic splitting occurs within the Cretaceous and Tertiary individually but not across the boundary. Second, there is some separation between the Cretaceous and the Tertiary species groups that have good representation. These two points imply that a faunal change actually occurred at the boundary. Third, this data set may provide some clues to the nature of evolution and extinction among the *Crassatella*.

Statistically, there is no doubt that *Crassatella vadosa*, *C. gardnerae*, *C. lintea*, *C.* sp. A, and *C.* sp. B are all members of the same species. Prior to the statistical analysis, a cursory examination of the specimens indicated that this was indeed the case (compare pl. 1, figs. 3, 4, 10, 12; pl. 8, figs. 4, 6; pl. 9, figs. 1, 9). *C. lintea* is in fact the juvenile of *C. vadosa* (discussed in detail in the "Systematic Paleontology" section). Many lines of statistical evidence support this synonymy: (1) the proximity of the univariate means, even if the

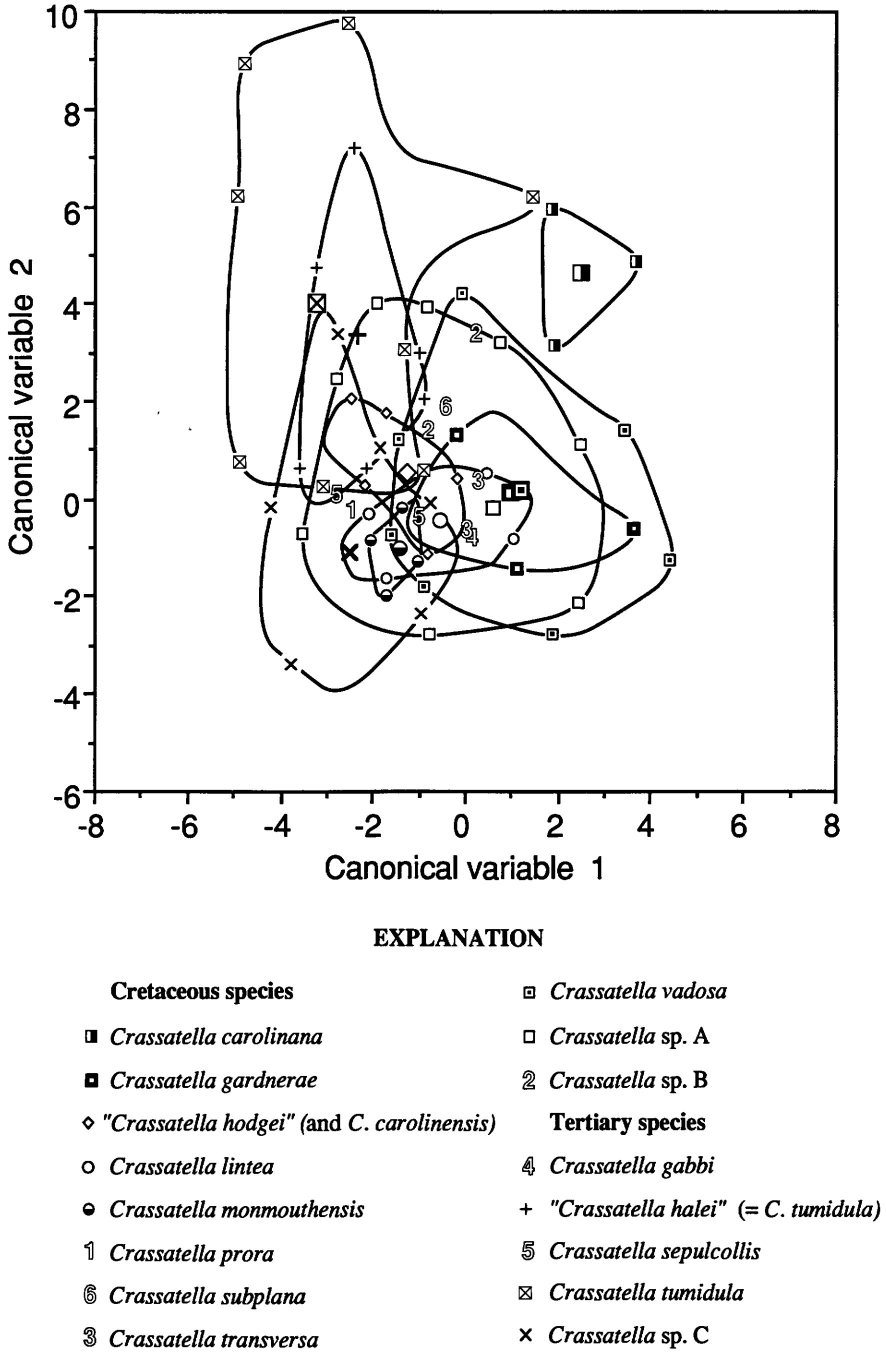


FIGURE 11.—Canonical variables 1 and 2 for the second canonical variate analysis of the species of *Crassatella*. Data for the analysis include all adults, juveniles, broken specimens, internal molds, unnamed specimens, and species categories with five or fewer specimens. Large symbols for the species categories represent the midpoints of those categories. Species categories represented on the plots by a single digit number contain only one or two specimens. Canonical variable 1 accounts for 48.05 percent of the variance between species categories and has a canonical correlation of 0.84. Canonical variable 2 accounts for 22.59 percent of the variance between species categories and has a canonical correlation of 0.72. See table 17 for standardized canonical coefficients.

TABLE 17.—*Standardized canonical coefficients for the second canonical discriminant analysis of all the specimens of the species of* Crassatella, *including juveniles, broken specimens, internal molds, unnamed specimens, and species categories with five or fewer specimens, measured for this analysis*

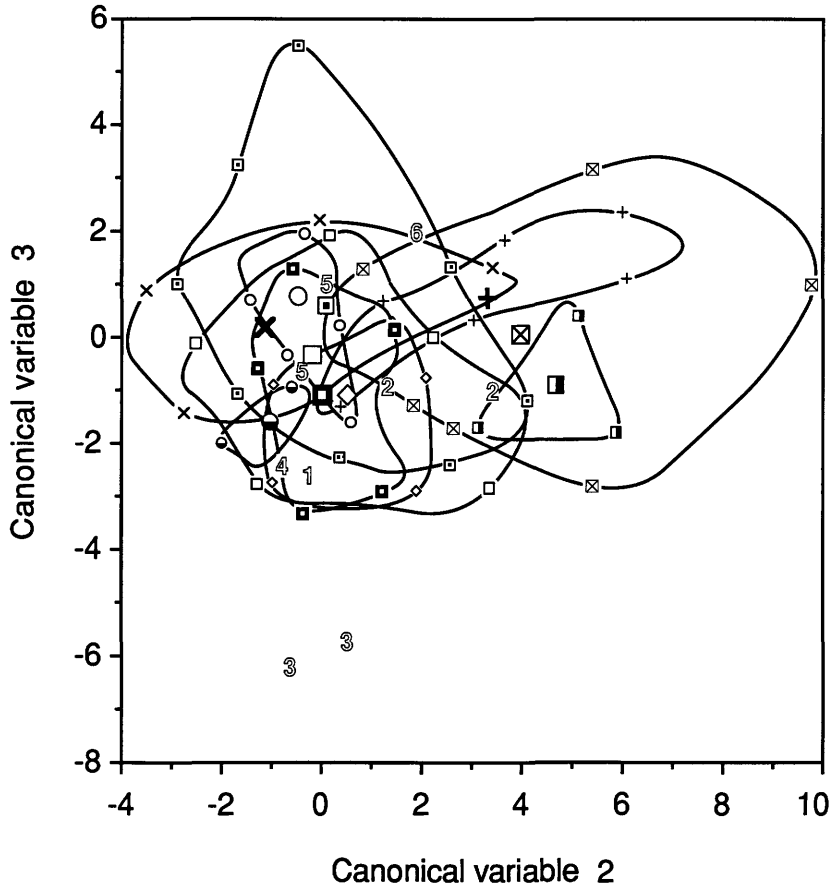
[See table 2 for an explanation of the morphological variables. Canonical variables 1, 2, and 3 are plotted on figures 11 and 12]

Morphological variable	Standardized canonical coefficient		
	Canonical variable 1	Canonical variable 2	Canonical variable 3
LENGTH	1.7503	−2.6327	−4.4273
POSTHT	10.2151	−12.5081	−5.3438
ANTHT	3.0475	−3.0141	−7.6214
ANTER	.1173	−0.1927	−0.2621
VENTRAL	.3287	2.6223	2.0052
POSTWID1	.1658	.4616	.4428
POSTWID2	−1.7893	2.2949	.6471
ANTWID1	.2125	.0257	−0.1808
ANTWID2	−0.8272	1.6498	2.8317
POSTDOR	−20.8921	7.4673	−14.5584
ANTDOR	11.0329	−11.4191	−12.0118
ANTVERHT	.0388	−0.2743	−2.2727
POSTLAT	3.5808	2.0018	16.4662
ANTLAT	−5.9259	7.7648	9.2925
HINGEPL	1.2267	−1.3658	−5.9064
POSTLAT2	6.5912	1.9237	6.9561
ANTLAT2	−7.6462	9.3645	10.4175
POSTADHT	−0.8584	−1.5754	1.9501
INTPOST	−0.1648	.1802	.2937
INTANT	.8757	.1320	−0.2924
POSADDST	.7728	−1.2541	.8585
ANTADDST	−0.2562	.7090	2.6425

TABLE 18.—*Results of the classificatory discriminant analysis of the juveniles, broken specimens, and internal molds of the species of* Crassatella, *tested against the calibration data set of the adult whole named specimens*

Original species category[1]	Total no. of specimens	Number of specimens (percentage of specimens) within the species category determined by analysis					
		C. vadosa	*C. gardnerae*	"*C. hodgei*" (and *C. carolinensis*)	*C. tumidula*	"*C. halei*" (=*C. tumidula*)	*C. lintea*
C. vadosa	86	39 (45.35)	24 (27.91)	11 (12.79)	1 (1.16)	3 (3.49)	8 (9.30)
C. gardnerae	3	1 (33.33)	1 (33.33)	0 (0)	0 (0)	0 (0)	1 (33.33)
"*C. hodgei*" (and *C. carolinensis*)	4	0 (0)	2 (50.00)	2 (50.00)	0 (0)	0 (0)	0 (0)
C. prora	1	0 (0)	0 (0)	1 (100.00)	0 (0)	0 (0)	0 (0)
C. monmouthensis	5	0 (0)	0 (0)	5 (100.00)	0 (0)	0 (0)	0 (0)
C. transversa	2	0 (0)	0 (0)	2 (100.00)	0 (0)	0 (0)	0 (0)
C. sp. A	33	11 (33.33)	6 (18.18)	7 (21.21)	1 (3.03)	1 (3.03)	7 (21.21)
C. tumidula	13	0 (0)	0 (0)	4 (30.77)	6 (46.15)	1 (7.69)	2 (15.38)
C. sp. C	58	0 (0)	0 (0)	27 (46.55)	0 (0)	2 (3.45)	29 (50.00)
C. subplana	1	1 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
C. carolinana	1	1 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
C. hodgei	1	0 (0)	1 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)
C. lintea	7	0 (0)	0 (0)	3 (42.86)	0 (0)	0 (0)	4 (57.14)
Total	215	53	34	62	8	7	51

[1] Species category assigned prior to analysis.



EXPLANATION

Cretaceous species

◨ *Crassatella carolinana*
▣ *Crassatella gardnerae*
◇ *"Crassatella hodgei"* (and *C. carolinensis*)
○ *Crassatella lintea*
◒ *Crassatella monmouthensis*
1 *Crassatella prora*
6 *Crassatella subplana*
3 *Crassatella transversa*
⊡ *Crassatella vadosa*
□ *Crassatella* sp. A
2 *Crassatella* sp. B

Tertiary species

4 *Crassatella gabbi*
\+ *"Crassatella halei"* (= *C. tumidula*)
5 *Crassatella sepulcollis*
⊠ *Crassatella tumidula*
× *Crassatella* sp. C

FIGURE 12.—Canonical variables 2 and 3 for the second canonical variate analysis of the species of *Crassatella*. Data for the analysis include all adults, juveniles, broken specimens, internal molds, unnamed specimens, and species categories with five or fewer specimens. Large symbols for the species categories represent the midpoints of those categories. Species categories represented on the plots by a single digit number contain only one or two specimens. Canonical variable 2 accounts for 22.59 percent of the variance between species categories and has a canonical correlation of 0.72. Canonical variable 3 accounts for 9.91 percent of the variance between species categories and has a canonical correlation of 0.57. See table 17 for standardized canonical coefficients.

TABLE 19.—*Results of the classificatory discriminant analysis of all the specimens of the species of* Crassatella, *except internal molds, measured for this analysis, tested against the calibration data set of all specimens of* Crassatella *measured for the analysis, except unnamed specimens and internal molds*

Original species category[1]	Total no. of specimens	Number of specimens (percentage of specimens) within the species category determined by analysis								
		C. vadosa	*C. gardnerae*	"*C. hodgei*" (and *C. carolinensis*)	*C. tumidula*	"*C. halei*" (=*C. tumidula*)	*C. sepulcollis*	*C. carolinana*	*C. hodgei*	*C. lintea*
C. vadosa	188	176 (93.62)	10 (5.32)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (1.06)
C. gardnerae	56	19 (33.93)	35 (62.50)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (3.57)
"*C. hodgei*" (and *C. carolinensis*).	12	0 (0)	0 (0)	12 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
C. sp. A	206	137 (66.50)	50 (24.27)	3 (1.46)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	16 (7.77)
C. tumidula	27	0 (0)	0 (0)	1 (3.70)	23 (85.19)	2 (7.41)	0 (0)	1 (3.70)	0 (0)	0 (0)
"*C. halei*" (and *C. tumidula*).	6	0 (0)	0 (0)	1 (16.67)	1 (16.67)	4 (66.67)	0 (0)	0 (0)	0 (0)	0 (0)
C. gabbi	1	0 (0)	1 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
C. sepulcollis	2	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (50.00)	0 (0)	0 (0)	1 (50.00)
C. sp. C	125	6 (4.80)	4 (3.20)	14 (11.20)	9 (7.20)	4 (3.20)	15 (12.00)	0 (0)	3 (2.40)	70 (56.00)
C. subplana	1	1 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
C. carolinana	2	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (100.00)	0 (0)	0 (0)
C. hodgei	2	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (100.00)	0 (0)
C. lintea	20	2 (10.00)	0 (0)	1 (5.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	17 (85.00)
C. sp. B	2	1 (50.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (50.00)
Total	650	342	100	32	33	10	16	3	5	109

[1] Species category assigned prior to analysis.

juveniles, broken specimens, and internal molds are included (table 11), indicates similarity along each variable, (2) the low values for the Mahalanobis' distances between the classes (tables 13, 16) show the lack of multivariate separation between the species categories, (3) the nearly complete overlap of the areas for each species category on the plots of canonical variables 1 and 2 (figs. 9, 11) is indicative of a single species, especially since canonical discriminant analysis tends to maximize differences between groups, (4) the occurrence of the group means in the area of overlap (especially on fig. 11) illustrates the similarity of the populations as a whole, and (5) the classification results (tables 15, 18, 19) generally are low for *C. gardnerae, C. lintea*, and *C.* sp. A but show that the majority of the misclassified species fall within one of the species categories of this group. The low classification values for *C. gardnerae* are especially surprising considering that all specimens come from a single locality, which usually causes higher classification values than expected; this is further evidence that *C. gardnerae* is a junior synonym of *C. vadosa.*

The results from the other Cretaceous *Crassatella* species categories are more difficult to interpret, primarily because of the small numbers of individuals included in these categories. "*C. hodgei*" (and *C. carolinensis*) is of particular interest because it occupies a position on the plots (figs. 9–12) midway between the other Cretaceous species and the Tertiary species. In addition, *C. tumidula* and "*C. hodgei*" intermix in the classification results (tables 15, 18, 19). These patterns indicate a morphologic similarity of "*C. hodgei*" (and *C. carolinensis*) to the Tertiary species categories and may imply an evolutionary link that cannot be explained readily. The misassigned specimens[9] probably did not contribute to this unexpected pattern because superficially the *C. hodgei* measured appear to be very similar to the *C. carolinensis* measured (compare pl. 4, fig. 13 and pl. 5, fig. 12 to pl. 5, figs. 13, 15–20). The diagnostic characters of the two species are discussed in the "Systematic Paleontology" section.

Twelve of the 14 individuals from both species categorized as "*C. hodgei*" come from a single locality, Blufftown, Ga. (loc. 4). Their identification as *C. hodgei* was based on Stephenson's (1923, p. 273) and Cooke's (1943, p. 22) citations of the species at that locality, and in addition, the specimens seem consistent with the type description for *C. hodgei.* The other two specimens of *C. hodgei* are from Stephenson's (1923, p. 272) type locality at Snow Hill, N.C. (loc. 8). Given the low stratigraphic position of the Blufftown specimens, it is not surprising that they are isolated partially from the *C. vadosa* group on the plots (figs. 9, 10). The remainder of the Cretaceous species are not present in statistically significant numbers to draw any conclusions about their relationships to the well-defined species categories.

The statistical analysis of the Tertiary forms indicates that *Crassatella tumidula* and "*C. halei*" are synonymous, which is the expected result considering that all the specimens in the category "*C. halei*" are in fact *C. tumidula.*[9] The individuals assigned to *C.* sp. C demonstrate a fair degree of overlap with the Cretaceous forms on figures 11 and 12. This overlap can be attributed to the smaller than average size of *C.* sp. C (table 11); 45 percent of the specimens assigned to this category are juveniles. Qualitative evaluation proved that the majority of the specimens (117 of 125) assigned to this category belong to the species *C. sepulcollis* (herein = *C. aquiana* Clark). The juveniles of this species have a general outline similar to the juveniles of *C. vadosa* and the measured specimens of *C. hodgei* and *C. carolinensis* (compare pl. 3, figs. 2, 5 to pl. 5, figs. 6–10); this similarity probably causes the overlap seen on the plots. The categories of *C. gabbi* and *C. sepulcollis* are not represented by statistically significant numbers of individuals.

A separation of the Tertiary and Cretaceous forms does exist, as an examination of the ranked Mahalanobis' distances (table 13) shows and as the partial separation along canonical variables 1 and 2 on the plots illustrates (figs. 9, 11). The classification results exhibit a curious pattern; in general, Cretaceous forms classify as other Cretaceous categories when they do not classify correctly. The Tertiary species categories, however, classify as either Cretaceous or Tertiary forms. Specimens of *Crassatella tumidula* and specimens of "*C. halei*" (and *C. tumidula*), each come from a small geographic area (app. 4) and thus would be expected to have high classification results (≥90 percent) and occupy limited areas on the plots. The plots of the individuals on the canonical variables, however, reveal a wide scatter. For comparison, examine the areas of the plot covered by *C. vadosa* versus *C. tumidula* (fig. 11); the area for *C. vadosa* is the result of plotting 231 individual specimens from 13 localities, whereas the area for *C. tumidula* is a plot of only 27 specimens from 4 localities. Apparently, a large degree of intragroup diversity exists in the Tertiary forms, especially in *C. tumidula*; this diversity may explain the low classification results (<90 percent).

Finally, in a simple examination of the statistical results presented here, several ideas emerge concerning the nature of evolution and extinction at the Cretaceous-Tertiary boundary for the genus *Crassatella*. The members of the genus were fairly abundant but had low diversity just below the Cretaceous-Tertiary boundary in the upper Maastrichtian beds. In the lower Tertiary, abundance was very low, but intragroup diversity appears to have been high. These Tertiary individuals seem to bear more resemblance to their Campanian ancestors than to the adult Maastrichtian *Crassatella*, but they do show a degree of morphological overlap with the juveniles of the Maastrichtian group. Perhaps this is a case of different environmental influences acting upon the adults of the Cretaceous and Tertiary groups, or perhaps the Tertiary forms are exhibiting neoteny (see Raup and Stanley, 1978, p. 353 for explanation).

SPECIES OF *BATHYTORMUS*

Only two species of *Bathytormus* Stewart, 1930 have been identified within the geographic and stratigraphic constraints of this study: (1) *B. pteropsis* (Conrad), 1860, a Cretaceous species, and (2) *B. alaeformis* (Conrad), 1830, a Tertiary species. The purpose of this analysis is to determine if the Upper Cretaceous form is continuous across the Cretaceous-Tertiary boundary and to determine if numerous specimens from localities that have no published record of *Bathytormus* occurrence are synonymous with the established species. The null hypothesis[5] is that no statistically significant differences exist between the two species categories and the two categories of unnamed specimens (*Bathytormus* sp.). Failure to reject the null hypothesis for any pair of species categories would indicate the existence of synonyms. The alternative hypothesis is that the species names are valid and that the unnamed specimens represent new species.

Analysis.—The first segment of the analysis tested 111 adult whole specimens divided between the two named species: (1) *Bathytormus pteropsis* (13 specimens) and (2) *B. alaeformis* (98 specimens). The individuals of *B. pteropsis* included in this analysis come from the Gulf Coast region exclusively, whereas the *B. alaeformis* specimens are limited to the Mid-Atlantic region; a total of 28 localities were examined (app. 5). The *Bathytormus* species were discriminated on the basis of 15 morphologic measurements (table 2).

An examination of the univariate class means (table 20, first analysis) reveals some differences in shape between *Bathytormus pteropsis* and *B. alaeformis*. The variables measuring the height and shape of the anterior margin (ANTWID, ANTWID1, ANTLAT, ANTADDST, see table 2 for an explanation of all variables) show very similar class means between the two groups, so similar in fact that they fail the F test for equality of variance (tables 20, 21, first analysis). The variables measuring length and the shape of the posterior margin, however, are considerably different. No significance should be placed on the proximity of the univariate means of *B. alaeformis* to the grand mean of both classes combined; the similarity is the result of a disproportionate number of *B. alaeformis* included in the analysis. Despite the differences seen in the univariate class means, all of the variables show greater within-class variation than between-class variation as measured by standard deviation (table 21, first analysis). Nevertheless, the univariate statistics show that some separation of the two classes is indicated for the multivariate analysis.

TABLE 20.—*Class means and grand means for species of* Bathytormus *on each variable used in both canonical discriminant analyses*

[See table 2 for an explanation of the morphological variables. 1, the means from the first canonical discriminant analysis, including adult whole named specimens only; 2, the means from the second canonical discriminant analysis of all specimens, including juveniles, broken specimens, and unnamed specimens; —, species excluded from the first analysis]

Morphological variable	Class mean								Grand mean	
	B. pteropsis		*B.* sp. A		*B. alaeformis*		*B.* sp. B			
	1	2	1	2	1	2	1	2	1	2
LENGTH	28.37	27.23	—	25.58	37.41	37.59	—	37.01	36.35	35.30
ANTWID	12.07	11.66	—	10.12	12.77	12.83	—	12.76	12.69	12.40
ANTWID1	4.42	4.18	—	3.73	4.97	5.18	—	5.14	4.91	4.92
POSTDOR	20.54	19.75	—	18.27	27.65	27.61	—	27.27	26.81	25.86
ANTDOR	14.51	13.92	—	13.03	17.44	17.76	—	17.73	17.10	16.90
POSVERHT	10.65	10.38	—	10.16	13.08	12.96	—	12.73	12.79	12.40
POSTLAT	10.36	9.94	—	9.35	16.79	16.98	—	17.48	16.04	15.60
ANTLAT	8.55	8.19	—	7.31	9.71	9.92	—	9.90	9.57	9.47
HINGEPL	16.08	15.37	—	14.21	23.41	23.81	—	24.19	22.56	22.07
RESILANG	19.65	19.39	—	21.73	21.32	21.11	—	20.58	21.12	21.00
ANTLAT2	6.34	6.08	—	5.95	8.16	8.31	—	8.29	7.95	7.86
MANTCAV	18.43	17.52	—	16.70	25.84	26.22	—	26.14	24.97	24.42
INTPOST	39.40	39.64	—	39.97	33.69	33.94	—	34.27	34.36	35.13
POSADDST	4.62	4.55	—	4.87	7.03	6.92	—	6.96	6.75	6.50
ANTADDST	6.86	6.70	—	5.85	6.86	6.79	—	6.86	6.86	6.67

TABLE 21.—*Standard deviations, the value for F, and the probability of F for the canonical discriminant analyses of the species of* Bathytormus *on each variable used in the analyses*

[See table 2 for an explanation of the morphological variables. Total, total sample standard deviations of the data from all species categories combined. Within class, pooled within-class standard deviations for the species categories. Between class, between-class standard deviations for the species categories. 1, data from the first canonical discriminant analysis, including adult whole named specimens only; 2, data from the second canonical discriminant analysis of all specimens, including juveniles, broken specimens, and unnamed specimens]

Morphological variable	Standard deviation						F		Probability F	
	Total		Within class		Between class					
	1	2	1	2	1	2	1	2	1	2
LENGTH	8.51	9.58	8.03	8.51	4.11	5.20	14.53	20.17	0.0002	0.0001
ANTWID	3.20	3.49	3.20	3.39	.32	1.05	.56	5.20	.4568	.0017
ANTWID1	1.54	1.76	1.53	1.69	.25	.60	1.50	6.70	.2235	.0002
POSTDOR	6.12	6.93	5.70	6.02	3.23	4.02	17.83	24.09	.0001	.0001
ANTDOR	4.49	4.93	4.40	4.64	1.33	2.02	5.09	10.27	.0261	.0001
POSVERHT	3.03	3.06	2.94	2.88	1.10	1.23	7.78	9.85	.0062	.0001
POSTLAT	4.11	4.77	3.56	3.75	2.93	3.43	37.42	45.33	.0001	.0001
ANTLAT	2.37	2.70	2.35	2.56	.52	1.07	2.74	9.40	.1005	.0001
HINGEPL	5.43	6.40	4.91	5.28	3.33	4.24	25.58	34.81	.0001	.0001
RESILANG	3.09	3.48	3.06	3.47	.76	.61	3.40	1.65	.0679	.1786
ANTLAT2	2.39	2.52	2.32	2.36	.83	1.06	7.10	10.81	.0089	.0001
MANTCAV	6.19	7.10	5.73	6.13	3.37	4.22	19.16	25.61	.0001	.0001
INTPOST	3.20	3.64	2.62	2.82	2.59	2.68	54.24	49.04	.0001	.0001
POSADDST	1.83	1.85	1.66	1.65	1.10	1.00	24.21	19.73	.0001	.0001
ANTADDST	1.88	1.97	1.89	1.96	.00	.36	.00	1.82	.9960	.1448

The division of the data into just two species classes requires that only one Mahalanobis' distance and only one canonical variable be calculated. The value of 5.23 for the Mahalanobis' distance passes the F test at the 5 percent level of significance, so the null hypothesis of equal means is rejected. The histogram (fig. 13) shows the frequency distribution of each category along canonical variable 1, which accounts for 100 percent of the variance and has a canonical correlation of 0.86. The means of the two species categories are clearly separated on the histogram, and the only overlap is from a single specimen of *Bathytormus pteropsis*. An examination of the specimen does not reveal an explanation for the overlap. The standardized canonical coefficients (table 22) reflect the role of elongation of *B. alaeformis* in separating the two species categories. All of the variables that contribute significantly to the discrimination of the two classes are measurements of length: (1) the

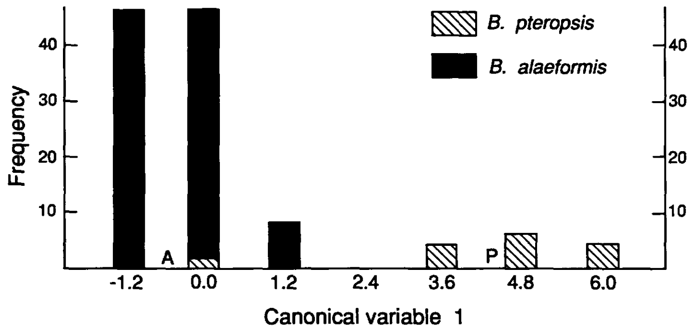


FIGURE 13.—Canonical variable 1 for the first canonical variate analysis of the species of *Bathytormus*. The number of individual specimens occurring along the canonical variable is recorded on the *y* axis. Data for the analysis include adult whole specimens from the two named species categories only: *Bathytormus pteropsis* and *Bathytormus alaeformis*. The P marks the midpoint for the *Bathytormus pteropsis* category, and the A marks the midpoint for the *Bathytormus alaeformis* category. Canonical variable 1 accounts for 100 percent of the variance between species categories and has a canonical correlation of 0.86. See table 22 for standardized canonical coefficients.

TABLE 22.—*Standardized canonical coefficients for the first canonical discriminant analysis of the adult whole named specimens of the species of* Bathytormus

[See table 2 for an explanation of the morphological variables. Canonical variable 1 is plotted on figure 13]

Morphological variable	Standardized canonical coefficient
	Canonical variable 1
LENGTH	15.1993
ANTWID	−0.2318
ANTWID1	−0.1643
POSTDOR	−10.2462
ANTDOR	−33.3512
POSVERHT	.4992
POSTLAT	12.5984
ANTLAT	17.7743
HINGEPL	−18.7929
RESILANG	.0150
ANTLAT2	13.1903
MANTCAV	3.8122
INTPOST	2.1238
POSADDST	−1.3739
ANTADDST	1.6371

length of the anterior and posterior dorsal margins (ANTDOR, POSTDOR), (2) the width of the hinge plate (HINGEPL), (3) the length of the anterior and posterior lateral ridges (ANTLAT, POSTLAT), (4) the length of the shell (LENGTH), and (5) the distance between the end of the anterior lateral ridges and the anterior margin (ANTLAT2).

A discriminant analysis of the adult whole specimens of *Bathytormus* produced the classification results seen in table 23. A total of 99 percent of all the specimens classify correctly[7]; again the only incorrectly classified specimen was a single *B. pteropsis*.

TABLE 23.—*Results of the classificatory discriminant analysis of the adult whole named specimens of the species of* Bathytormus; *calibration data set tested against itself*

[Of the total number of specimens (111), 99.1 percent classify into the predicted species categories]

Original species category[1]	Total no. of specimens	Number of specimens (percentage of specimens) within the species category determined by analysis	
		B. pteropsis	*B. alaeformis*
B. pteropsis	13	12 (92.31)	1 (7.69)
B. alaeformis	98	0 (0)	98 (100.00)
Total	111	12	99

[1] Species category assigned prior to analysis.

TABLE 24.—*Mahalanobis' distances between classes for the second canonical discriminant analysis of all the specimens of the species of* Bathytormus, *including juveniles, broken specimens, and unnamed specimens measured for this analysis*

Species	Mahalanobis' distance[1] between classes			
	B. pteropsis	*B.* sp. A	*B. alaeformis*	*B.* sp. B
B. pteropsis	—	—	—	—
B. sp. A	1.6712	—	—	—
B. alaeformis	4.6454	4.7555	—	—
B. sp. B	4.9681	4.9921	0.9161	—

[1] Mahalanobis' distances are a measure of the separation of the multivariate means of two classes (Davis, 1973, p. 450–451).

A second canonical discriminant analysis was conducted to include the unnamed specimens (*Bathytormus* sp.), the juveniles, and the broken specimens, in addition to the adult whole specimens. For this portion of the analysis, 216 specimens from 4 species categories were tested: (1) *B. pteropsis* (15 specimens), (2) *B.* sp. A (27 specimens), (3) *B. alaeformis* (148 specimens); and (4) *B.* sp. B (26 specimens). These specimens were distributed over 42 localities (app. 6), and the inclusion of *B.* sp. A brings a few Mid-Atlantic specimens from the Cretaceous into the analysis.

An examination of the univariate class means indicates a similarity of *Bathytormus pteropsis* and *B.* sp. A on most variables (table 20, second analysis); *B. alaeformis* and *B.* sp. B have nearly identical class means on all variables. The standard deviations again show higher values for within-class variation than for between-class variation (table 21, second analysis). The results of the univariate analyses indicate that *B. pteropsis* and *B.* sp. A will overlap at least partially on the plots and that *B. alaeformis* and *B.* sp. B will have class means in proximity to each other but that there will be at least some separation between the Tertiary and Cretaceous forms.

An examination of the Mahalanobis' distances (table 24) supports the univariate conclusions. The F test of the Mahalanobis' distances between *Bathytormus alaeformis* and *B.* sp. B, and between *B. pteropsis* and *B.* sp. A, fails at the 5 percent level of significance, so the null

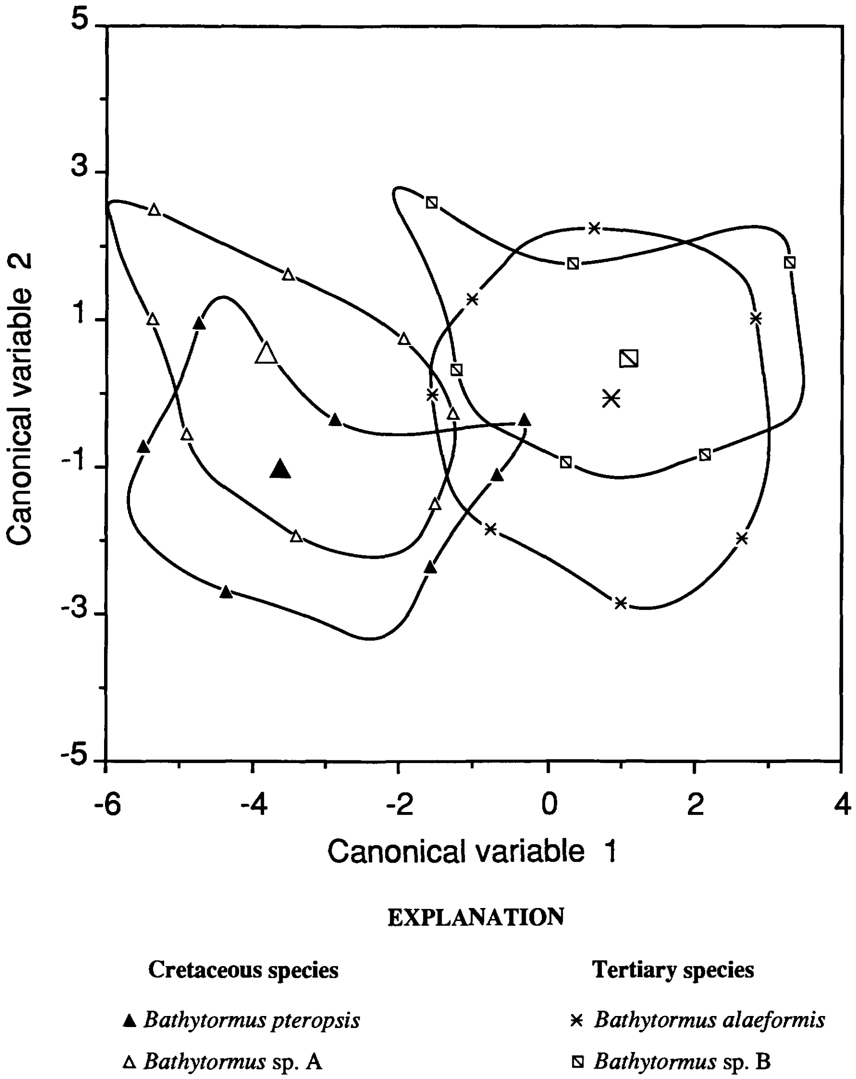


FIGURE 14.—Canonical variables 1 and 2 for the second canonical variate analysis of the species of *Bathytormus*. Data for the analysis include all adults, juveniles, broken specimens, and unnamed specimens. Large symbols for the species categories represent the midpoints of those categories. Canonical variable 1 accounts for 94.39 percent of the variance between species categories and has a canonical correlation of 0.88. Canonical variable 2 accounts for 3.81 percent of the variance between species categories and has a canonical correlation of 0.35. See table 25 for standardized canonical coefficients.

hypothesis of equal means between the two pairs of species categories cannot be rejected. The species are maintained as discrete categories for the remainder of the analysis, however, to test their relationship further.

The plot of canonical variables 1 and 2 (fig. 14) reinforces the initial conclusions. *Bathytormus alaeformis* and *B.* sp. B overlap, as do *B. pteropsis* and *B.* sp. A, and the group means of the two pairs fall within the region of overlap for the pairs. The overlap on the plots (fig. 14) between the Cretaceous and Tertiary groups of *Bathytormus* is the result of three specimens; one *B. alaeformis* is broken, one *B. pteropsis* is the same specimen responsible for the overlap seen on figure 13, and one specimen is an unremarkable *B.* sp. A. The separation of the Cretaceous from the Tertiary forms occurs along canonical variable 1, which accounts for 94.39 percent of the variance between groups and has a canonical correlation of 0.88; the discriminating variables along canonical variable 1 (table 25) are length, anterior dorsal, anterior lateral, and hinge plate (LENGTH,

TABLE 25.—*Standardized canonical coefficients for the second canonical discriminant analysis of all the specimens of the species of* Bathytormus, *including juveniles, broken specimens, and unnamed specimens, measured for the analysis*

[See table 2 for an explanation of the morphological variables. Canonical variables 1 and 2 are plotted on figure 14]

Morphological variable	Standardized canonical coefficient	
	Canonical variable 1	Canonical variable 2
LENGTH	−10.9961	9.2503
ANTWID	.6148	−3.7702
ANTWID1	−0.2231	1.5982
POSTDOR	7.0707	−11.0292
ANTDOR	20.6716	.5176
POSVERHT	.1440	3.2492
POSTLAT	−7.1878	5.1676
ANTLAT	−11.5272	−3.7458
HINGEPL	13.2149	.5377
RESILANG	−0.3030	.4489
ANTLAT2	−7.3407	−3.2960
MANTCAV	−3.2927	.6239
INTPOST	−1.6815	1.3196
POSADDST	.6263	−1.0838
ANTADDST	−1.5308	2.1979

TABLE 26.—*Results of the classificatory discriminant analysis of the juveniles, broken specimens, and unnamed specimens of the species of* Bathytormus, *tested against the calibration data set of the adult whole named specimens*

Original species category[1]	Total no. of specimens	Number of specimens (percentage of specimens) within the species category determined by analysis	
		B. pteropsis	*B. alaeformis*
B. pteropsis	2	2 (100.00)	0 (0)
B. sp. A	11	10 (90.91)	1 (9.09)
B. alaeformis	50	1 (2.00)	49 (98.00)
B. sp. B	13	1 (7.69)	12 (93.31)
Total	76	14	62

[1] Species category assigned prior to analysis.

ANTDOR, ANTLAT, HINGEPL), all measurements of length as in the first analysis. Canonical variable 2 accounts for only 3.81 percent of the variance between groups and has a canonical correlation of 0.35. Along this axis, the length of the valve (LENGTH), and the length of the posterior dorsal regions (POSTDOR) contribute to the discrimination of the specimens.

A discriminant analysis of the juvenile, broken, and unnamed specimens was done using the calibration data set of the adult whole specimens (table 26). Ninety-six percent of the specimens classify as expected; the majority of *Bathytormus* sp. A classify as *B. pteropsis*, and the majority of *B.* sp. B classify as *B. alaeformis*. Of the three specimens that do not classify as expected, two are broken and one is a juvenile. A final discriminant analysis tested all specimens of *Bathytormus* against a calibration data set based on all specimens of *B. pteropsis* and *B. alaeformis* to determine how the unnamed specimens would classify (table 27). Only three specimens of *B.* sp. A classify as the Tertiary *B. alaeformis*; two of these specimens are broken, and the third is one of the three specimens responsible for the overlap seen on figure 14. The single specimen of *B.* sp. B, which classifies as the Cretaceous *B. pteropsis*, is a juvenile.

TABLE 27.—*Results of the classificatory discriminant analysis of all the specimens of the species of* Bathytormus, *including juveniles, broken specimens, and unnamed specimens, measured for this analysis, tested against the calibration data set of all the named specimens of* Bathytormus *measured for the analysis, including juveniles and broken specimens*

Original species category[1]	Total no. of specimens	Number of specimens (percentage of specimens) within the species category determined by analysis	
		B. pteropsis	*B. alaeformis*
B. pteropsis	15	14 (93.33)	1 (6.67)
B. sp. A	27	24 (88.89)	3 (11.11)
B. alaeformis	148	1 (0.68)	147 (99.32)
B. sp. B	26	1 (3.85)	25 (96.15)
Total	216	40	176

[1] Species category assigned prior to analysis.

Discussion.—The results of the analysis of the species of *Bathytormus* illustrate that two species existed within the stratigraphic and geographic ranges of this study, the Upper Cretaceous *B. pteropsis* and the lower Tertiary *B. alaeformis*. The geographic and stratigraphic ranges of *B. pteropsis* and *B. alaeformis* are expanded by the inclusion of the unnamed specimens into the established species categories. The patterns seen in the genus *Bathytormus* differ substantially from those exhibited by *Crassatella*. The taxonomic splitting demonstrated in the analysis of *Crassatella* has not occurred with *Bathytormus*. In addition, the statistical separation between the Cretaceous and Tertiary *Bathytormus* species is more clear-cut than that illustrated by the *Crassatella* species.

An examination of the specimens assigned to *Bathytormus* sp. A, prior to the analysis, indicated that they were members of *B. pteropsis* (compare pl. 17, figs. 3–4 to pl. 17, figs. 12, 17, juvenile portion of shell); and, likewise, that specimens assigned to *B.* sp. B were members of *B. alaeformis*; these observations were confirmed by the statistical tests. Several lines of statistical evidence point to the synonymy of *Bathytormus* sp. A with *B. pteropsis*, and of *B.* sp. B with *B. alaeformis*: (1) the similarity of the univariate means for each pair of species (table 20), (2) the failure of the Mahalanobis' distances for the two pairs to pass the F test, (3) the conterminous boundaries of the two pairs on the plot of canonical variables 1 and 2 (fig. 14), (4) the proximity of the class means of the two pairs on the plot, and (5) the percentage of *B.* sp. A classified as *B. pteropsis*, and of *B.* sp. B classified as *B. alaeformis*, in the discriminant analysis (table 27).

The Cretaceous and Tertiary species of *Bathytormus* are fairly discrete (compare pl. 2, fig. 3 to pl. 3, fig. 14). Only a few specimens overlap on the plots (figs. 13, 14), and the classification results are in the 90-percent range for most of the species categories (tables 23, 26, 27). An examination of the standardized canonical coefficients (tables 22, 25) indicates that changes in the length and in the posterior region separate the Tertiary from the Cretaceous forms. Intraspecific diversity appears to have been about the same on either side of the Cretaceous-Tertiary boundary, but abundance appears to have increased dramatically. This pattern differs from that seen in the *Crassatella*, in which intraspecific diversity increased in the Tertiary and abundance decreased.

GENERA OF CRASSATELLIDAE

The purpose of this portion of the statistical analysis is to determine the validity of the generic names used for the family Crassatellidae within the geographic and stratigraphic limits of this study. A few specimens from the Astartidae family are included for comparison. The null hypothesis is that no statistically significant differences exist between the generic categories being tested. If the null hypothesis cannot be rejected for any pair of generic categories, this would indicate the existence of synonyms. The alternative hypothesis is that all the generic names are valid. In addition, the distribution of species categories within the genera are examined for *Bathytormus* and *Crassatella*, and the validity of the generic assignments for all the species of Crassatellidae included in this analysis are tested.

Analysis.—In the first part of the analysis, 700 adult whole specimens from 6 generic categories were tested: (1) *Crassatella* Lamarck, 1799 (495 specimens), (2) *Bathytormus* Stewart, 1930 (140 specimens), (3) *Scambula* Conrad, 1869a (32 specimens), (4) *Uddenia* Stephenson, 1941[10] (19 specimens), (5) the unnamed group (genus and species unknown; 7 specimens), and (6) astartids (7 specimens). Appendix 7 lists the 72 localities for the specimens included in this analysis from the Upper Cretaceous and lower Tertiary units of the Gulf Coast and Mid-Atlantic regions. The genera were discriminated on the basis of 21 morphologic measurements[11] (table 2).

The univariate class means (table 28, first analysis) are fairly distinct for each variable in the six generic categories. The means for *Uddenia* and the astartids show the greatest correspondence, in part due to their similar overall size. Most of the variables have higher values for between-class standard deviation than those for within-class standard deviation (table 29, first analysis). The univariate results indicate that the genera will occupy fairly discrete areas on the plots of the canonical variables, but that some overlap between *Uddenia* and the astartids is likely. Apparently, at least some of the separation of the generic categories can be attributed to the average size of the individuals assigned to each genus.

All of the Mahalanobis' distances (table 30) computed between the generic categories are greater than the critical value for F at the 5 percent level of significance, so the null hypothesis of equal group means is rejected. An examination of the ranked order of the Mahalanobis' distances reveals the multivariate relationship of the generic categories. The smallest distance measurement is between *Scambula* and the astartids. The next three closest values are pairs that include *Uddenia*: the astartids and *Uddenia*, *Crassatella* and *Uddenia*, *Scambula* and *Uddenia*. The three pairs of generic categories that have the greatest Mahalanobis' distances are pairs that include the unnamed group: *Uddenia* and the unnamed group, *Crassatella* and the unnamed group, *Bathytormus* and the unnamed group.

The plot of canonical variables 1 and 2 (fig. 15) illustrates the isolation of *Bathytormus* along canonical variable 1, which accounts for 66.16 percent of the variance between all the groups and has a canonical correlation of 0.94. The remaining generic categories all overlap along canonical variable 1. Canonical variable 2, which accounts for 27.80 percent of the variance between groups and has a canonical correlation of 0.87, separates *Scambula* from *Crassatella* and *Bathytormus*. The remaining three categories, *Uddenia*, the unnamed group, and the astartids, all overlap on both canonical variables 1 and 2. *Uddenia* and the astartids were expected to show a fair amount of overlap on the basis of their ranked Mahalanobis' distances, but the unnamed group was expected to be more discrete. Close examination of the plots, however, reveals that only one individual of *Scambula* falls within the area of the unnamed group on the plot. The standardized canonical coefficients (table 31) show that overall length and the characters

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[10] The method for identifying specimens as *Uddenia* is discussed in the section "Statistical Methods" on page 12. Unlike the other categories, *Uddenia* specimens were not categorized on the basis of morphologic characters.

[11] The stepwise discriminant analysis (see "Statistical Methods," p. 14, for a complete explanation) determined that 22 morphologic measurements were important discriminators for the generic analysis. No measurements of shell width were taken on *Uddenia* specimens, however, due to their diminutive size, so this variable was deleted. Only the classification results for *Scambula* were affected by the exclusion of the variable for shell width.

TABLE 28.—*Class means and grand means for the genera of Crassatellidae (and related groups) on each variable used in both canonical discriminant analyses*

[See table 2 for an explanation of the morphological variables. 1, the means from the first canonical discriminant analysis, including adult whole specimens only; 2, the means from the second canonical discriminant analysis of all specimens, including juveniles, broken specimens, and internal molds; —, generic category excluded from the first analysis; all specimens in category are internal molds]

Morphological variable	Class mean							
	Crassatella		*Bathytormus*		*Scambula*		*Uddenia*	
	1	2	1	2	1	2	1	2
LENGTH	37.99	35.09	35.80	35.30	8.04	8.34	4.88	5.06
POSTHT	33.02	30.43	28.30	27.70	6.40	6.66	4.18	4.29
ANTHT	26.09	24.12	19.01	18.88	5.42	5.63	3.39	3.52
ANTER	145.24	144.53	133.89	134.51	144.76	144.62	150.42	150.16
POSTWID1	5.59	5.29	1.82	1.94	.84	.83	.69	.68
POSTWID2	5.77	5.23	4.43	4.18	1.73	1.79	.73	.76
ANTWID1	3.06	3.11	4.92	4.92	1.29	1.23	.73	.73
ANTDOR	21.29	19.77	16.96	16.90	4.69	4.87	2.79	2.91
ANTVERHT	19.64	18.03	13.70	13.51	3.40	3.51	2.36	2.48
POSVERHT	19.02	17.55	12.64	12.40	3.50	3.62	2.89	2.93
POSTLAT	17.40	16.23	15.67	15.60	4.04	4.19	2.56	2.64
ANTLAT	10.47	9.84	9.51	9.47	3.58	3.68	1.70	1.77
HINGEPL	22.55	21.13	22.15	22.07	5.53	5.71	3.43	3.57
RESILANG	20.50	18.45	21.35	21.00	19.45	19.39	15.46	15.52
ANTLAT2	10.92	10.05	7.88	7.86	1.13	1.21	1.10	1.15
POSTADHT	8.67	8.10	5.96	5.91	.99	1.03	1.04	1.05
MANTCAV	24.99	23.33	24.51	24.42	4.91	5.12	3.46	3.58
INTPOST	42.12	42.45	34.88	35.13	51.32	51.28	43.45	43.62
INTANT	67.47	66.84	58.28	58.08	59.22	59.16	62.55	62.04
POSADDST	10.35	9.46	6.70	6.50	2.51	2.60	1.85	1.88
ANTADDST	10.71	9.71	6.86	6.67	2.47	2.52	1.38	1.46

Morphological variable	Class mean						Grand mean	
	Unnamed group[1]		Indeterminant crassatellid molds		Astartids[1]			
	1	2	1	2	1	2	1	2
LENGTH	2.05	2.05	—	41.35	4.31	4.31	34.59	33.14
POSTHT	1.65	1.65	—	33.38	3.73	3.73	29.47	28.08
ANTHT	1.64	1.64	—	25.21	3.28	3.28	22.64	21.61
ANTER	132.71	132.71	—	138.57	140.82	140.82	142.92	142.36
POSTWID1	2.55	2.55	—	4.29	.48	.48	4.40	4.26
POSTWID2	.32	.32	—	4.36	.73	.73	5.08	4.72
ANTWID1	4.04	4.04	—	6.22	.27	.27	3.27	3.38
ANTDOR	1.44	1.44	—	22.37	2.75	2.75	18.78	18.03
ANTVERHT	1.29	1.29	—	17.72	2.05	2.05	16.88	15.99
POSVERHT	1.35	1.35	—	19.12	2.43	2.43	16.25	15.43
POSTLAT	1.22	1.22	—	16.63	2.68	2.68	15.73	15.19
ANTLAT	1.16	1.16	—	10.62	2.03	2.03	9.55	9.26
HINGEPL	1.78	1.78	—	23.48	3.50	3.50	20.77	20.17
RESILANG	6.65	6.65	—	3.21	18.76	18.76	20.33	18.84
ANTLAT2	.30	.30	—	12.07	.73	.73	9.39	8.95
POSTADHT	.34	.34	—	10.37	.75	.75	7.41	7.13
MANTCAV	1.44	1.44	—	31.10	2.95	2.95	22.93	22.24
INTPOST	53.93	53.93	—	38.06	50.20	50.20	41.33	41.32
INTANT	58.27	58.27	—	57.02	63.47	63.47	64.98	64.46
POSADDST	1.01	1.01	—	8.76	1.69	1.69	8.85	8.30
ANTADDST	.96	.96	—	7.62	1.35	1.35	9.12	8.50

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[1] Data set for analyses 1 and 2 is identical.

TABLE 29.—*Standard deviations, the value for F, and the probability of F for the canonical discriminant analyses of the genera of Crassatellidae (and related groups) on each variable used in the analyses*

[See table 2 for an explanation of the morphological variables. Total, total sample standard deviations of the data from all generic categories combined. Within class, pooled within-class standard deviations for the generic categories. Between class, between-class standard deviations for the generic categories. 1, data from the first canonical discriminant analysis, including adult whole specimens only; 2, data from the second canonical discriminant analysis of all specimens, including juveniles, broken specimens, and internal molds]

Morphological variable	Standard deviation						F		Probability F	
	Total		Within class		Between class					
	1	2	1	2	1	2	1	2	1	2
LENGTH	13.03	13.45	9.27	11.27	10.06	7.98	137.44	71.60	0.0	0.0001
POSTHT	11.27	11.58	7.89	9.67	8.85	6.92	146.72	73.09	.0	.0001
ANTHT	9.07	9.26	6.30	7.67	7.17	5.62	151.05	76.67	.0	.0001
ANTER	8.93	9.65	7.57	8.64	5.24	4.69	55.99	42.02	.0001	.0001
POSTWID1	2.80	2.81	2.09	2.28	2.04	1.78	110.91	87.41	.0	.0
POSTWID2	1.99	2.06	1.46	1.77	1.50	1.14	123.32	60.00	.0	.0001
ANTWID1	2.04	2.15	1.78	1.91	1.11	1.06	45.44	44.13	.0001	.0001
ANTDOR	7.26	7.50	5.12	6.28	5.66	4.44	142.52	71.41	.0	.0001
ANTVERHT	7.02	7.11	4.83	5.85	5.59	4.38	156.08	80.05	.0	.0
POSVERHT	6.54	6.54	4.29	5.19	5.41	4.31	186.06	98.49	.0	.0
POSTLAT	5.72	5.97	4.00	5.00	4.48	3.55	146.41	72.22	.0	.0001
ANTLAT	3.27	3.51	2.35	3.00	2.49	1.98	130.85	62.03	.0	.0001
HINGEPL	7.24	7.63	4.95	6.29	5.80	4.70	159.85	79.60	.0	.0
RESILANG	4.16	6.08	3.82	5.83	1.83	1.91	26.87	15.36	.0001	.0001
ANTLAT2	4.20	4.23	3.00	3.53	3.23	2.54	134.80	73.81	.0	.0001
POSTADHT	3.23	3.32	2.23	2.71	2.56	2.08	154.90	84.12	.0	.0
MANTCAV	8.73	9.17	6.26	7.68	6.68	5.44	132.92	71.46	.0	.0001
INTPOST	5.56	5.55	3.90	4.06	4.36	4.11	145.51	146.32	.0	.0
INTANT	5.73	6.21	4.18	4.92	4.31	4.10	124.48	98.91	.0	.0
POSADDST	3.51	3.50	2.35	2.82	2.86	2.25	172.63	90.86	.0	.0
ANTADDST	4.04	4.08	2.94	3.45	3.05	2.37	125.18	67.39	.0	.0001

TABLE 30.—*Mahalanobis' distances between classes for the first canonical discriminant analysis of the adult whole specimens of the genera of Crassatellidae (and related groups)*

Generic category	Mahalanobis' distance[1] between classes					
	Crassatella	*Bathytormus*	*Scambula*	*Uddenia*	Unnamed group	Astartids
Crassatella	—	—	—	—	—	—
Bathytormus	6.8839	—	—	—	—	—
Scambula	6.9111	8.4885	—	—	—	—
Uddenia	4.9761	7.5138	5.3996	—	—	—
Unnamed group	10.1253	12.2380	6.3019	8.7428	—	—
Astartids	6.2193	8.7321	3.0862	4.2505	7.0025	—

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[1] Mahalanobis' distances are a measure of the separation of the multivariate means of two classes (Davis, 1973, p. 450–451).

of the anterior dorsal region are the primary discriminating variables along canonical variable 1 (LENGTH, ANTDOR, ANTLAT, ANTLAT2, see table 2 for an explanation of all the variables). The separation seen along canonical variable 2 is due primarily to the variables that measure the height of the posterior region (POSTVERHT, POSTADHT, POSADDST).

A discriminant analysis of the adult whole specimens of Crassatellidae produced the classification results seen in table 32. The variable for resilifer angle was deleted from the analysis so that the internal molds, which lack this measurement, could be tested against the calibration data set of the adult whole specimens. *Crassatella*, *Bathytormus*, and the unnamed group show very high classification results (>99 percent) and little or no overlap with the other generic categories. *Scambula*, *Uddenia*, and the astartids, however, show a tendency to intermingle in the classification process, as expected from the results of the canonical discriminant analysis plot. Notably, *Scambula* produced much higher classification results (90.63 percent) when the variables measuring shell width and resilifer angle were included, but the inclusion of shell width excludes the unnamed group from the analysis.

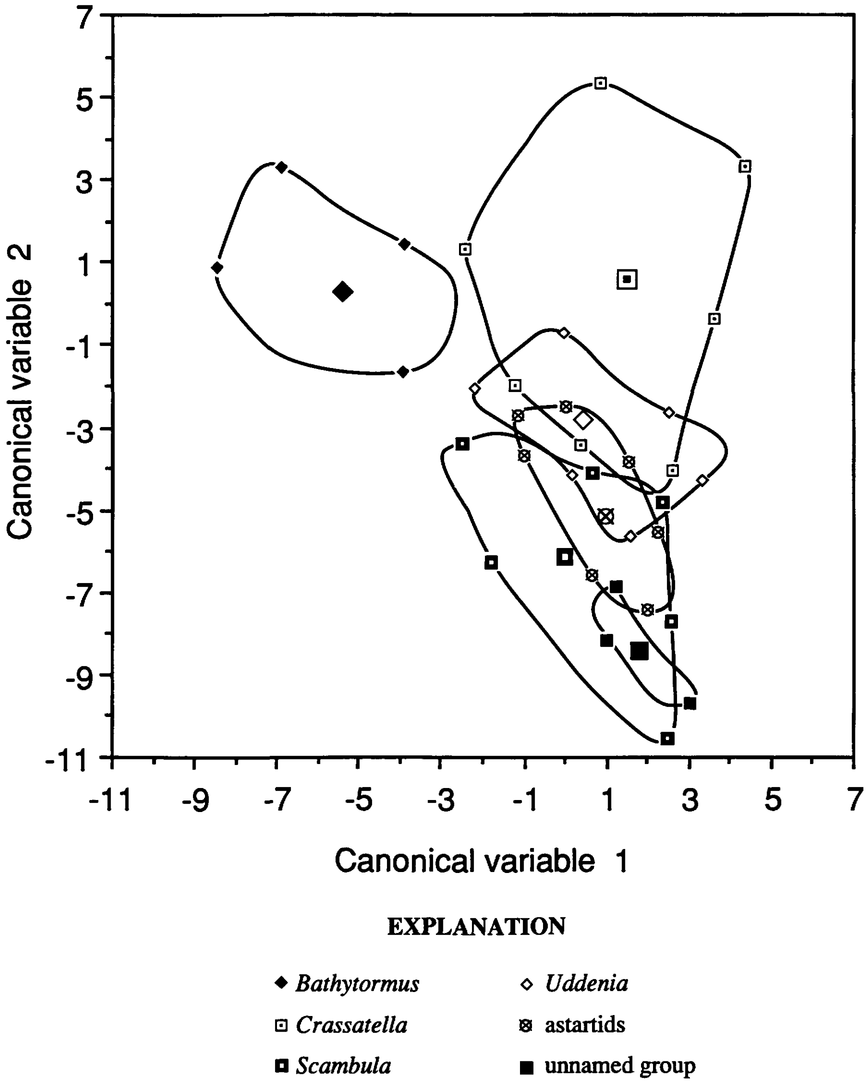

FIGURE 15.—Canonical variables 1 and 2 for the first canonical variate analysis of the genera of Crassatellidae (and related groups). Data for the analysis include adult whole specimens only. Large symbols for the generic categories represent the midpoints of those categories. Canonical variable 1 accounts for 66.16 percent of the variance between generic categories and has a canonical correlation of 0.94. Canonical variable 2 accounts for 27.80 percent of the variance between generic categories and has a canonical correlation of 0.87. See table 31 for standardized canonical coefficients.

Juvenile specimens, broken specimens, and internal molds were added to the data set for a second canonical discriminant analysis. A total of 999 specimens from 7 generic categories was tested: (1) *Crassatella* (710 specimens), (2) *Bathytormus* (216 specimens), (3) *Scambula* (35 specimens), (4) *Uddenia* (21 specimens), (5) the unnamed group (7 specimens), (6) the astartids (7 specimens), and (7) internal molds of unknown generic identity (3 specimens). Twenty-one morphologic variables were used to test the generic categories[11] (table 2). Resilifer angle was not excluded here, as it was during previous analyses that included internal molds, because the position of the resilifer is a diagnostic character in distinguishing the genera of Crassatellidae.[12] The data were distributed among 91 localities in the Upper Cretaceous and lower Tertiary of the Gulf Coast and Mid-Atlantic regions (app. 8).

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[12] On all internal molds, the digitized point for the resilifer was identical to the point for the beak. Any variable that incorporates the resilifer point on internal molds is therefore not a real measurement. The number of internal molds in this analysis, however, is so small (6 percent) that the benefits of including the variable for resilifer angle outweigh the disadvantages.

TABLE 31.—*Standardized canonical coefficients for the first canonical discriminant analysis of the adult whole specimens of the genera of Crassatellidae (and related groups)*

[See table 2 for an explanation of the morphological variables. Canonical variables 1 and 2 are plotted on figure 15]

Morphological variable	Standardized canonical coefficient	
	Canonical variable 1	Canonical variable 2
LENGTH.............	−8.4739	−2.3855
POSTHT	−0.7869	−4.4664
ANTHT	.8653	3.2726
ANTER	.3753	.0621
POSTWID1............	−0.0925	−0.2824
POSTWID2............	−0.3063	.7440
ANTWID1.............	.0690	−0.1317
ANTDOR..............	18.1394	−0.4294
ANTVERHT..........	−1.0260	3.8146
POSVERHT...........	−0.4580	−83.1007
POSTLAT.............	.1109	−2.5836
ANTLAT..............	−9.5596	1.1067
HINGEPL.............	2.3137	4.9093
RESILANG...........	−0.3443	.0512
ANTLAT2.............	−9.3746	.2454
POSTADHT...........	1.9207	42.0158
MANTCAV............	3.7714	−1.6972
INTPOST	1.1069	−2.1768
INTANT	.5773	.7930
POSADDST...........	2.2493	46.2336
ANTADDST...........	1.3019	−4.3411

The inclusion of the additional specimens caused only slight changes in the values of the univariate class means, most notably on *Crassatella* (table 28). A very different pattern is seen, however, for the standard deviation values. In the first analysis of the adult whole specimens, the majority of the variables have higher values for between-class standard deviation than those for within-class standard deviation (table 29); in contrast, all but one of the variables have higher values for within-class standard deviation than those for between-class standard deviation in the second analysis. The Mahalanobis' distances (table 33) calculated between the generic categories all pass the F test at the 5 percent level of significance, so the null hypothesis of equal means is rejected. Patterns similar to those seen in the analysis of the adult whole specimens emerge when the ranked Mahalanobis' distances are examined. *Scambula* and the astartids show the shortest distance value, and the four greatest distance values are categories paired with the unnamed group.

The configuration of the plot of canonical variables 1 and 2 (fig. 16) resembles the plot for the adult whole specimens (fig. 15), but the presence of the juveniles in this analysis can be seen in the central portion of the plot

TABLE 32.—*Results of the classificatory discriminant analysis of the adult whole specimens of the genera of Crassatellidae (and related groups); calibration data set tested against itself*

[Of the total number of specimens (700), 97.6 percent classify into the predicted generic categories]

Original generic category[1]	Total no. of specimens	Number of specimens (percentage of specimens) within the generic category determined by analysis					
		Crassatella	*Bathytormus*	*Scambula*	*Uddenia*	Unnamed group	Astartids
Crassatella	495	493 (99.60)	1 (0.20)	1 (0.20)	0 (0)	0 (0)	0 (0)
Bathytormus	140	0 (0)	140 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)
Scambula..........................	32	0 (0)	0 (0)	24 (75.00)	3 (9.38)	4 (12.50)	1 (3.13)
Uddenia	19	0 (0)	0 (0)	1 (5.26)	15 (78.95)	0 (0)	3 (15.79)
Unnamed group	7	0 (0)	0 (0)	0 (0)	0 (0)	7 (100.00)	0 (0)
Astartids	7	0 (0)	0 (0)	2 (28.57)	1 (14.29)	0 (0)	4 (57.14)
Total	700	493	141	28	19	11	8

[1] Generic category assigned prior to analysis.

TABLE 33.—*Mahalanobis' distances between classes for the second canonical discriminant analysis of all the specimens of the genera of Crassatellidae (and related groups), including juveniles, broken specimens, and internal molds measured for this analysis*

Generic category	Mahalanobis' distance[1] between classes						
	Crassatella	*Bathytormus*	*Scambula*	*Uddenia*	Unnamed group	Indeterminant crassatellid molds	Astartids
Crassatella	—	—	—	—	—	—	—
Bathytormus	5.6403	—	—	—	—	—	—
Scambula..................................	5.3830	7.1883	—	—	—	—	—
Uddenia	3.6027	5.9556	4.6916	—	—	—	—
Unnamed group	8.0383	10.1542	4.7753	7.4593	—	—	—
Indeterminant crassatellid molds	4.4980	6.3256	7.3949	5.7263	8.5243	—	—
Astartids	4.5563	7.2805	2.8095	3.7752	5.6473	6.6917	—

[1] Mahalanobis' distances are a measure of the separation of the multivariate means of two classes (Davis, 1973, p. 450–451).

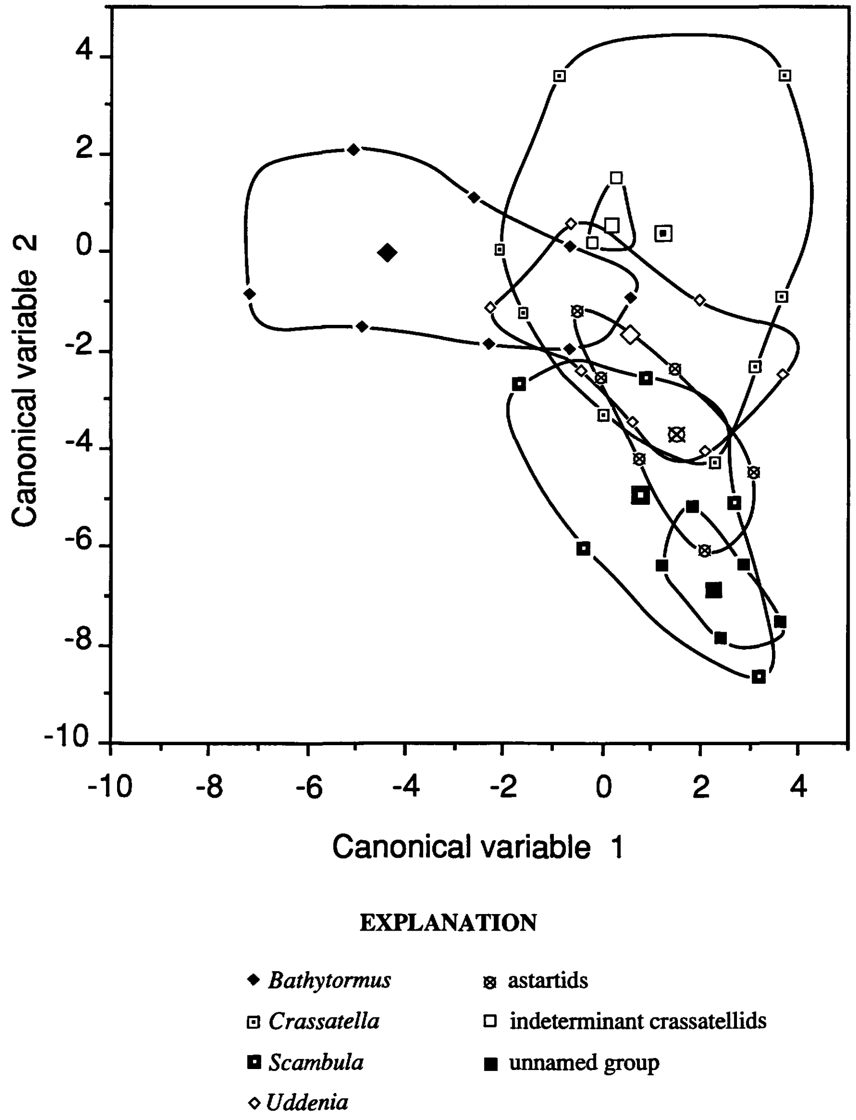

FIGURE 16.—Canonical variables 1 and 2 for the second canonical variate analysis of the genera of Crassatellidae. Data for the analysis include all adult and juvenile specimens measured for the statistical analysis, including broken specimens and internal molds. Large symbols for the generic categories represent the midpoints of those categories. Canonical variable 1 accounts for 74.83 percent of the variance between generic categories and has a canonical correlation of 0.92. Canonical variable 2 accounts for 19.95 percent of the variance between generic categories and has a canonical correlation of 0.77. See table 34 for standardized canonical coefficients.

where most of the areas impinge upon one another. Canonical variable 1, which accounts for 74.83 percent of the variance between the generic categories and has a canonical correlation of 0.92, is again primarily responsible for separating *Bathytormus* from the other generic categories. *Crassatella* and *Bathytormus* overlap, but they are separated at least partially from the other generic categories along canonical variable 2, which accounts for 19.95 percent of the variance between categories and has a canonical correlation of 0.77. The primary discriminating variables along canonical variable 1 are the length of the anterior dorsal margin (ANTDOR) and the variables that measure the height of the posterior region of the shell (POSVERHT, POSTADHT, POSADDST) (table 34). The primary discriminating variables along canonical variable 2 are the same three variables that measure the height of the posterior region of the shell.

A discriminant analysis, using the adult whole specimens as a calibration data set, classified the juveniles, broken specimens, and internal molds of the Crassatellidae genera (table 35). Excluding the three indeterminant internal molds, the majority (83.5 percent) of the individuals classify correctly.[7] Although only 2 specimens of *Uddenia* are included in this analysis, 27 specimens classify as *Uddenia*, including at least 1 specimen from the other 3 described generic categories, *Crassatella*, *Bathytormus*, and *Scambula*. All of the specimens of *Crassatella* and *Bathytormus* that classify as *Uddenia* are juveniles; the one specimen of *Scambula* that classifies as *Uddenia* is a broken specimen. The internal molds of uncertain generic identity classify as *Crassatella*.

TABLE 34.—*Standardized canonical coefficients for the second canonical discriminant analysis of all the specimens of the genera of Crassatellidae (and related groups), including juveniles, broken specimens, and internal molds, measured for this analysis*

[See table 2 for an explanation of the morphological variables. Canonical variables 1 and 2 are plotted on figure 16]

Morphological variable	Standardized canonical coefficient	
	Canonical variable 1	Canonical variable 2
LENGTH	−5.6640	−3.0648
POSTHT	−1.6533	−3.6660
ANTHT	.6003	3.9756
ANTER	.2798	.0375
POSTWID1	−0.0373	−0.3753
POSTWID2	−0.1286	.7292
ANTWID1	.0405	−0.2489
ANTDOR	12.1673	4.5711
ANTVERHT	−1.4645	3.4238
POSVERHT	24.4325	−28.5845
POSTLAT	.4775	−4.1009
ANTLAT	−7.2886	−2.1722
HINGEPL	1.2537	6.3376
RESILANG	−0.3119	.0091
ANTLAT2	−6.2436	−2.4344
POSTADHT	−10.9092	15.1830
MANTCAV	3.7634	−1.1582
INTPOST	1.2940	−1.9351
INTANT	.6483	1.0135
POSADDST	−11.3798	16.5807
ANTADDST	1.4818	−4.0842

The purpose of the final portion of the analysis was to determine if correct generic assignments had been made for each species in this study. A discriminant analysis was conducted using as a calibration data set all 999 specimens digitized. The same 999 specimens were classified into the calibration data set using their specific assignments. The results (table 36) show that the majority, 94.98 percent, of the specimens in each species category classify into the correct generic category. Species categories having fewer than 10 specimens tend to have few individuals that classify correctly, but these results are not statistically significant. The low classification results for the species of *Scambula* may appear to be problematic, but, when the variables for shell width and resilifer angle are included in the data set, 91.1 percent of the specimens classify correctly. Specimens of *Uddenia* classify as *Bathytormus*, *Scambula*, and the astartids, as an examination of the canonical variable plots (figs. 15, 16) indicates.

Finally, to determine the pattern of species distribution within the genera for *Crassatella* and *Bathytormus*, the data points for the individual species were plotted within the area of the genus on the plot of canonical variable 1 and canonical variable 2 for the adult whole specimens (fig. 17). For *Bathytormus*, the Cretaceous species *B. pteropsis* and *B.* sp. A, and the Tertiary species *B. alaeformis* and *B.* sp. B, occupy distinct regions of the generic area plot, with some overlap occurring in the central region around the group mean for the genus. The picture is quite different, however, for the *Crassatella*; all the species categories, Tertiary and Cretaceous, are centered around the group mean for this genus.

Discussion.—The results of the generic analysis reveal that as a whole the genera of Crassatellidae are well defined and that the species categories are properly assigned to them. Although overall size appears to be responsible for at least some of the separation of the generic categories, this is a valid attribute of a genus and

TABLE 35.—*Results of the classificatory discriminant analysis of the juveniles, broken specimens, and internal molds of the genera of Crassatellidae (and related groups), tested against the calibration data set of the adult whole specimens*

[Excluding the indeterminant molds, 83.5 percent of the specimens classify into the predicted generic categories]

Original generic category[1]	Total no. of specimens	Number of specimens (percentage of specimens) within the generic category determined by analysis					
		Crassatella	*Bathytormus*	*Scambula*	*Uddenia*	Unnamed group	Astartids
Crassatella	215	175 (81.40)	3 (1.40)	7 (3.26)	21 (9.77)	0 (0)	9 (4.19)
Bathytormus	76	3 (3.95)	69 (90.79)	0 (0)	4 (5.26)	0 (0)	0 (0)
Scambula	3	0 (0)	0 (0)	2 (66.67)	1 (33.33)	0 (0)	0 (0)
Uddenia	2	0 (0)	0 (0)	1 (50.00)	1 (50.00)	0 (0)	0 (0)
Indeterminant crassatellid molds	3	3 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Total	299	181	72	10	27	0	9

[1] Generic category assigned prior to analysis.

TABLE 36.—*Results of the classificatory discriminant analysis of all the specimens of the species of Crassatellidae measured for this analysis, tested against the calibration data set consisting of the same specimens, but classified into the genera of Crassatellidae*

[Excluding the two categories of indeterminant crassatellids, 94.98 percent of the specimens classify into the predicted generic categories]

Original species category[1]	Total no. of specimens	Number of specimens (percentage of specimens) within the generic category determined by analysis						
		Crassatella	*Bathytormus*	*Scambula*	*Uddenia*	Unnamed group	Indeterminant crassatellid molds	Astartids
Crassatella carolinana	3	3 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
C. gabbi	1	1 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
C. gardnerae	56	56 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
"*C. halei*" (=*C. tumidula*)	6	6 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
C. hodgei	2	2 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
"*C. hodgei*" (and *C. carolinensis*)	12	12 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
C. lintea	20	20 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
C. monmouthensis	5	5 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
C. prora	1	0 (0)	1 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
C. sepulcollis	2	2 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
C. subplana	1	1 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
C. transversa	2	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (100.00)	0 (0)
C. tumidula	27	27 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
C. vadosa	95	92 (96.84)	1 (1.05)	0 (0)	0 (0)	0 (0)	2 (2.11)	0 (0)
C. vadosa ripleyana	41	41 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
C. vadosa wadei	95	95 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
C. sp. A	214	205 (95.79)	0 (0)	0 (0)	4 (1.87)	0 (0)	2 (0.93)	3 (1.40)
C. sp. B	2	2 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
C. sp. C	125	117 (93.60)	0 (0)	3 (2.40)	4 (3.20)	0 (0)	0 (0)	1 (0.80)
Bathytormus alaeformis	148	0 (0)	147 (99.32)	0 (0)	1 (0.68)	0 (0)	0 (0)	0 (0)
B. pteropsis	10	0 (0)	10 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
B. sp. A	32	4 (12.50)	27 (84.38)	0 (0)	1 (3.13)	0 (0)	0 (0)	0 (0)
B. sp. B	26	2 (7.69)	24 (92.31)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Scambula perplana	15	0 (0)	0 (0)	11 (73.33)	2 (13.33)	1 (6.67)	0 (0)	1 (6.67)
S. sp.	20	0 (0)	0 (0)	15 (75.00)	2 (10.00)	3 (15.00)	0 (0)	0 (0)
Uddenia sp. A	16	0 (0)	1 (6.25)	1 (6.25)	12 (75.00)	0 (0)	0 (0)	2 (12.50)
U. sp. B	5	0 (0)	0 (0)	1 (20.00)	4 (80.00)	0 (0)	0 (0)	0 (0)
Unnamed group	7	0 (0)	0 (0)	1 (14.29)	0 (0)	6 (85.71)	0 (0)	0 (0)
Cretaceous indeterminant crassatellid molds.	2	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (100.00)	0 (0)
Tertiary indeterminant crassatellid molds.	1	1 (100.00)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Astartids	7	1 (14.29)	0 (0)	2 (28.57)	1 (14.29)	0 (0)	0 (0)	3 (42.86)
Total	999	695	211	34	35	4	8	10

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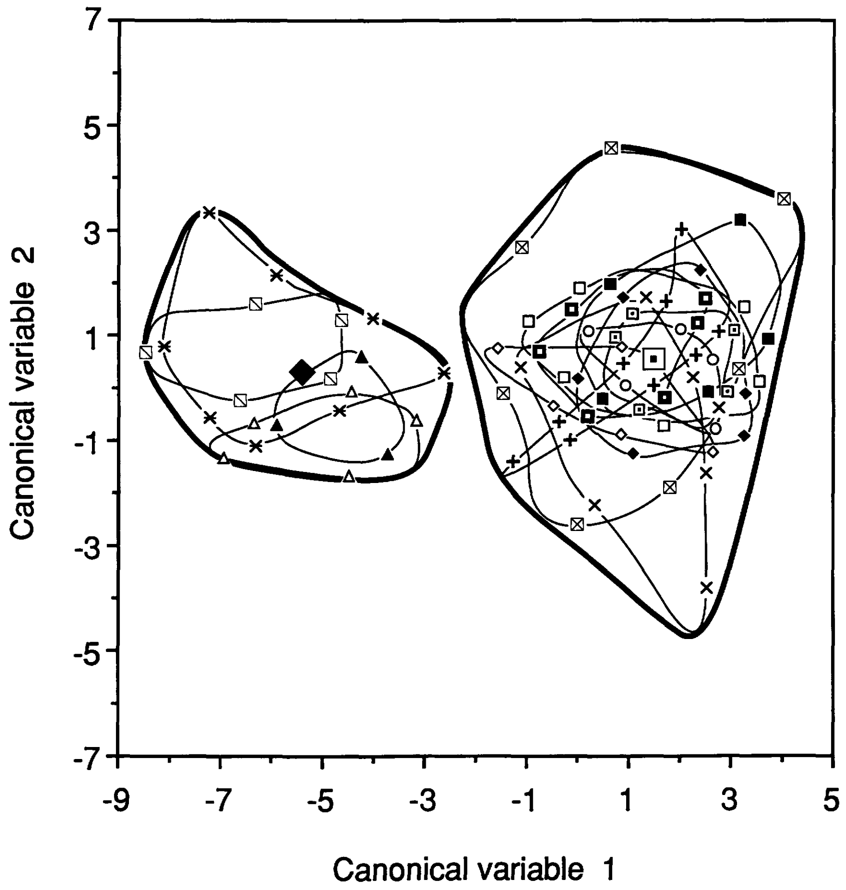
[1] Species category assigned prior to analysis.

should not cause concern about the legitimacy of the results. Characters of the hinge are most often cited as diagnostic features of the genera of Crassatellidae, but these characters do not prove to be primary discriminating variables within the confines of this statistical analysis. Rather, the characters of the posterior region of the shell prove to be the primary discriminators between generic categories.

All of the evidence presented, the univariate class means, the plots of the canonical variables, and the classification results, illustrate statistically that *Crassatella* and *Bathytormus* are valid, well-defined genera. This is not surprising considering the vast amount of attention they, particularly *Crassatella*, have received in the scientific literature. This extensive coverage, however, has contributed to the problem of taxonomic splitting illustrated earlier in the analysis of the species of *Crassatella*. A comparison of the species distribution within the areas defined for *Crassatella* and *Bathytormus* (fig. 17) is revealing. The species categories within *Crassatella* overlap one another as rings of various diameters centered around the group mean for the genus. This pattern (1) may be indicative of the oversplitting which has occurred within the *Crassatella*, (2) may illustrate a pattern of gradual evolution within the genus, or (3) may simply be an artifact of the analytical techniques, particularly the variables selected for inclusion at this stage of the analysis. The species that



EXPLANATION

Cretaceous species

▲ *Bathytormus pteropsis*
△ *Bathytormus* sp. A
◘ *Crassatella gardnerae*
◇"*Crassatella hodgei*" (and *C. carolinensis*)
○ *Crassatella lintea*
⊡ *Crassatella vadosa*
◆ *Crassatella vadosa ripleyana*
■ *Crassatella vadosa wadei*
□ *Crassatella* sp. A

Tertiary species

✱ *Bathytormus alaeformis*
⧅ *Bathytormus* sp. B
+ "*Crassatella halei*" (= *C. tumidula*)
⊠ *Crassatella tumidula*
× *Crassatella* sp. C

FIGURE 17.—Pattern of species distribution within the genera for *Crassatella* and *Bathytormus*. Plot of canonical variables 1 and 2 is a magnification of the figure 15 plot. The heavy lines define the areas for the genera *Crassatella* and *Bathytormus* as they appear on figure 15. Large symbols for the generic categories represent midpoints of the genera. The distribution of the species categories within the plots for the genera are illustrated. Species categories with only one or two specimens have been left off the plot, although they were included in the analysis.

compose a genus define the characters of the genus, but it is reasonable to expect each species to contribute a unique attribute to that genus. Unique contribution of species to the genus is not the picture seen in *Crassatella* but is illustrated by *Bathytormus*. The two species[13] of *Bathytormus* occupy distinct morphological areas of the genus but overlap in the central portion where their common generic characters link them. The internal molds of indeterminant generic origin prove to be members of the genus *Crassatella* as well; the position of these unknown specimens on the canonical variable plots and the classification results are evidence of the generic affinity.

The results for *Scambula*, *Uddenia*, and the unnamed group require close scrutiny to determine whether or not they are legitimate generic categories. *Scambula* appears distinct from all other genera of Crassatellidae (compare pl. 21, figs. 1–5, 7, 9 to pl. 21, figs. 6, 8, 10–17), and this distinction is corroborated by the univariate class means. The multivariate analyses, however, do not substantiate the initial conclusions. The lowest Mahalanobis' distances both with and without the juveniles and broken specimens are between *Scambula* and the astartids. On the canonical variable plots (figs. 15, 16), *Scambula* is overlapped by the unnamed group, *Uddenia*, and the astartids; in the classification results, only 71 percent of the specimens classify correctly on an average. If the *Uddenia*, the astartids, and the unnamed group are ignored, however, *Scambula* occupies a discrete area on the plot. The percent of *Scambula* that classify correctly rises to the 90 percent range when the variables for shell width and resilifer angle remain in the classification analysis. These variables are obviously important in discriminating the genus *Scambula*, and their inclusion illustrates that *Scambula* is statistically distinct, just as initial observations suggest.

The statistical results for *Uddenia* indicate it is a poorly defined generic category. In the process of conducting this study, I discovered that the name *Uddenia* is a junior synonym of *Crassatella*; the type specimen is a juvenile *C. vadosa* (see the "Systematic Paleontology" section for a complete explanation). The ambiguity surrounding *Uddenia* explains the overlap of *Uddenia* with *Crassatella*, *Bathytormus*, and *Scambula*, particularly on figure 16, which includes the juveniles. The intermingling of *Uddenia* and the juveniles of other genera in the classification results further illustrates the invalid nature of the generic category *Uddenia*.

The unnamed group forms a distinct category composed of individuals that superficially appear to match Stephenson's (1941, p. 181) original description for *Uddenia texana*. The distinctive univariate class means, the high values for Mahalanobis' distances, and the high classification results, as well as the distinctive appearance indicate that the unnamed group is a separate taxonomic category. The overlap with *Scambula* seen on the plots is the result of a single specimen of *Scambula* falling in the area for the unnamed group. Further examination reveals that this group is not a member of the Crassatellidae; thus, statistical separation is expected (see "Systematic Paleontology," p. 57–58 for full explanation).

The astartids were included in this analysis for several reasons. First, many specimens of the astartids were found in museum collections labeled as *Uddenia*. Second, I wanted to examine the possibility that the genus *Scambula* may actually be a member of the family Astartidae. A strong similarity between *Scambula* and the Astartidae is indicated, and the juvenile specimens of all the genera of Crassatellidae analyzed here bear a resemblance to the specimens of Astartidae included in this study. Finally, the Astartidae and the Crassatellidae are thought to share a common ancestor. The small number of Astartidae included here are not enough to reach any conclusions, but the results warrant further study.

SUMMARY OF STATISTICAL ANALYSES

The purpose of the statistical analysis was to test the previously defined species and genera of the family Crassatellidae for the Gulf and Mid-Atlantic Coastal Plains (table 1), in order to quantitatively evaluate the validity of the taxa. The following issues have been resolved. The subspecies of *Crassatella vadosa* represent end members of the species when the full spectrum of individuals assigned to *C. vadosa* is evaluated. *C. gardnerae* and *C. lintea* are synonyms of *C. vadosa*. The lower Campanian forms, *C. hodgei* and *C. carolinensis* are quantitatively different from the younger species of *Crassatella*, and likewise the Tertiary species *C. tumidula* is statistically distinct from the older species of *Crassatella*. Two well-defined species of *Bathytormus* exist, *B. pteropsis* and *B. alaeformis*. At the generic level, *Crassatella*, *Bathytormus*, *Scambula*, and the unnamed group (genus and species unknown), are quantitatively recognizable genera, whereas *Uddenia* appears to be poorly defined statistically. Consequently, questions about 10 of the 38 species names, the 2 subspecies names and all of the generic names listed in table 1 have been quantitatively resolved.

The statistical analysis has failed, however, to resolve the validity of the majority of the names applied to Crassatellidae within the geographic and stratigraphic

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[13] The analysis of the *Bathytormus* species illustrates that *B.* sp. A is synonymous with *B. pteropsis* and that *B.* sp. B is synonymous with *B. alaeformis*.

limits of this study. This failure can be primarily attributed to the lack of specimens representing many of the names presented in table 1. In some cases only single type specimens exist, and often the types are in such a poor state of preservation that their morphologic characters cannot be digitized. These names can only be evaluated qualitatively, not quantitatively, and their validity is discussed in the following section on "Systematic Paleontology."

Additionally, the statistical methods I employed for evaluating the taxonomic categories limited the effectiveness of this analysis in answering the initial question, "How accurate is the published fossil record for the Crassatellidae?" First, there is the problem of reducing a three dimensional form to two dimensions. I attempted to overcome this limitation by including the measurement of shell width, but this variable only provides a value for the distance to the widest point on the shell's surface. It does not impart any information about where the widest point lies, if it is a single point or a broad area of the shell, and if there are any fluctuations in width on the shell's surface; these characters proved to be important diagnostic features in the qualitative analysis of the taxa that follows. Other characters that proved to be important in diagnosing taxa but were excluded from consideration in the statistical analysis were characters of the ornament, the posterior ridge, and the height and curvature of the beak.

Many avenues for future quantitative analysis of this data set need to be explored, for example elimination or addition of variables and the effects on the results, but for now the purpose has been served. The majority of the taxa are evaluated in the following section by the qualitative examination of large suites of Crassatellidae.

SYSTEMATIC PALEONTOLOGY

The following diagnoses and descriptions are restricted to the genera and species of Crassatellidae that are found in the Upper Cretaceous and lower Tertiary deposits of the Mid-Atlantic and Gulf Coastal Plains of the United States. The synonymies include references that contain pertinent discussions, descriptions, or illustrations; they are by no means complete. Papers using a generic or specific name in faunal lists only are excluded below, unless the paper contains the first documented use of that name. The following abbreviations indicate depositories:

AMNH	American Museum of Natural History, New York, N.Y.
ANSP	Academy of Natural Sciences of Philadelphia, Philadelphia, Pa.
CNHM	Chicago Field Museum of Natural History, Chicago, Ill.
PRI	Paleontological Research Institution, Ithaca, N.Y.
USGS	U.S. Geological Survey, Reston, Va. Mesozoic locality numbers, the majority of these samples are housed at the U.S. Geological Survey in Reston, Va. Cenozoic locality numbers, the majority of these samples are housed at the U.S. National Museum of Natural History in Washington, D.C.
USNM	U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C.

The dental formulas given in the descriptions follow the system outlined by Boyd and Newell (1968, p. 7–10; 1969, p. N908–N910); a "1" indicates an elevated portion of the hinge (either a tooth or a ridge); a "0" indicates a recessed area (either a socket or a simple depression); parentheses enclose indicators of ambiguous teeth and their corresponding depressions; horizontal lines separate the cardinal and lateral series; an "R" indicates the position of the resilifer.

Phylum MOLLUSCA

Class BIVALVIA
Subclass HETERODONTA Neumayr, 1884
Order VENEROIDA H. Adams & A. Adams, 1856
Superfamily CRASSATELLACEA Ferussac, 1822
Family CRASSATELLIDAE Ferussac, 1822

The origin of the concept of the family Crassatellidae can be traced to Lamarck (1799); he differentiated the crassatellids from the mactrids on the basis of differences in the hinge structure and whether or not the valves closed. Deshayes (1824, p. 32–33) further outlined these differences, stating that crassatellids can be distinguished from mactrids by having (1) margins that close completely [that is, no shell gape], (2) the absence of lateral teeth [lateral ridges, however, are present], and (3) the absence of a pallial sinus. Deshayes described the latter as being "without contradiction the best of all characters for separating the two genera, and probably to distance this genus [*Crassatella*] from the family of the mactras" (translated from French, Deshayes, 1824, p. 33).

The astartids and the crassatellids were formally united in the family Crassatellidae by Ferussac (1822). D'Orbigny (1844, 1845, 1853) agreed that, on the basis of similarities in their "organic functions," a closer relationship existed between the astartids and the crassatellids than between the mactrids and the crassatellids. He considered the absence of a pallial sinus and the absence of shell gape, both features characteristic of the astartids and the crassatellids, to represent a similarity in "organic functions," whereas the similarity of the ligament seen in both the mactrids and the crassatellids is a "mechanical function." Gray (1847), however, limited the family Crassatellidae to the single genus *Crassatella*. Deshayes

(1860, p. 734) agreed with Gray and discussed his "repugnance" at placing a genus with an external ligament (the astartids) in the same family as a genus with an internal ligament (the crassatellids). Stoliczka (1871, p. 292) further pointed out distinctive differences in the soft anatomy of the rectum between astartids and crassatellids. Since 1847, the majority of workers have maintained two separate families, the Crassatellidae and the Astartidae, currently united under the superfamily Crassatellacea (Chavan, 1969).[14]

Chavan (1952) divided the Crassatellidae into two subfamilies, the Crassatellinae and the Scambulinae. The Scambulinae are distinguished by the following characters (Chavan 1952, p. 120; 1969, p. N577): (1) "stretched" teeth, (2) long lamellar teeth, extending down from near the beak, (3) a narrow resilifer, and (4) strongly opisthogyrous or orthogyrous beaks. In contrast, the Crassatellinae illustrate these characters (Chavan, 1969, p. N473): (1) lamellar teeth that do not extend the length of the dorsal margin and that begin below the cardinals, (2) a well-developed resilifer, and (3) prosogyrous or orthogyrous beaks.

Numerous detailed discussions of the morphology and anatomy of the crassatellids have been completed since Lamarck's (1799, p. 85) definition of the genus *Crassatella*. The most comprehensive were written by d'Orbigny (1844, p. 72–74),[15] Deshayes (1860, p. 735–737), Fischer (1887, p. 1020–1022),[16] and Lamy (1916, p. 197–205). The three genera and eight species of Crassatellidae examined within the geographic and stratigraphic limits of this study are united by the morphologic characteristics of the family. All are equivalved and do not have gaping valves. The shells are inequilateral with varying degrees of posterior elongation. Exteriorly, a lunule and escutcheon and posterior ridge are apparent; the ornament is comarginal. The musculature consists of anterior and posterior adductors and anterior and posterior pedal retractors. The pallial line is entire. The hinge structure is composed of an internal resilifer that originates at the beak and is posterior to the cardinals; one true cardinal is present in the right valve, and two are in the left valve; the laterals are not true teeth but are simple raised ridges.

The statistical analysis supports the conclusion that three valid, well-defined genera exist in the family Crassatellidae within the constraints of this study: *Crassatella* Lamarck, 1799, *Bathytormus* Stewart, 1930, and *Scambula* Conrad, 1869a. These genera are statistically discriminated by characters measuring length, the anterior dorsal region, and the height of the posterior region. A high degree of intrageneric diversity is quantitatively illustrated for the Crassatellidae.

Subfamily CRASSATELLINAE Ferussac, 1822

Genus *Crassatella* Lamarck, 1799

Crassatella LAMARCK, 1799, p. 85. LAMARCK, 1801, p. 119. LAMARCK, 1805, p. 407–408. DESHAYES, 1824, p. 32–33. CONRAD, 1838, p. 20–21. REEVE, 1842, p. 42. NYST, 1843, p. 83. D'ORBIGNY, 1844, p. 72–74. D'ORBIGNY, 1845, p. 577–578 [modified copy d'Orbigny, 1844]. CONRAD, 1846, p. 395. D'ORBIGNY, 1853, p. 287–288 [modified copy d'Orbigny, 1844]. DESHAYES, 1860, p. 735–737. STOLICZKA, 1871, p. 293–294. MARTENS, 1880, p. 22. TRYON, 1884, p. 224 [partim]. WHITFIELD, 1885, p. 115 [partim; not = *Etea* Conrad]. FISCHER, 1887, p. 1020–1022 [partim]. LAMY, 1916, p. 197 [partim]. STEWART, 1930, p. 134–137. CHAVAN, 1939, p. 27. STEPHENSON, 1941, p. 176–177. CHAVAN, 1952, p. 119. DARTEVELLE and FRENEIX, 1957, p. 136. CHAVAN, 1969, p. N573–N574. FRENEIX, 1972, p. 135–149. VOKES, 1973, p. 48–52.

Crassatellites KRUEGER, 1823, p. 465–466. DALL, 1903, p. 1468–1469 [partim]. GARDNER, 1916, p. 648–649. IREDALE, 1921, p. 207–208. SHIMER and SHROCK, 1944, p. 419. GARDNER, 1945, p. 90.

Pachythaerus CONRAD, 1869a, p. 47. VOKES, 1946, p. 177.

Crassatella (Pachythaerus) CONRAD, 1872, p. 50. STEWART, 1930, p. 137. CHAVAN, 1939, p. 27. CHAVAN, 1952, p. 119. CHAVAN, 1969, p. N574. FRENEIX, 1972, p. 146.

Crassatellites (Crassatellites) Krueger. WOODRING, 1925, p. 93–94.

Uddenia STEPHENSON, 1941, p. 180. CHAVAN, 1952, p. 119, 120. CHAVAN, 1969, p. N577.

Crassatella (Landinia) CHAVAN, 1952, p. 119. CHAVAN, 1969, p. N574.

[non] *Crassatella (Scambula)* TRYON, 1884, p. 224. FISCHER, 1887, p. 1022. DALL, 1903, p. 1467.

[non] *Crassatella (Crassinella)* DALL, 1903, p. 1468. LAMY, 1916, p. 244–251. COSSMANN, 1921, p. 135–136.

Additional subgenera proposed but not considered herein:

Crassatella (Rochella) FRENEIX, 1972, p. 135–136 [Upper Cretaceous; Morocco].

Crassatella (Sublandinia) FRENEIX, 1972, p. 142 [Lower Cretaceous; Morocco].

Crassatella (Riosatella) VOKES, 1973, p. 48–59 [Holocene; offshore, Rio Grande, Southern Brazil].

Type species.—*Crassatella tumida* Lamarck, 1805 = *Crassatella gibba* Lamarck, 1801 = *Venus ponderosa* Gmelin, 1791 [non *Mactra cygnea* Chemnitz, 1782].

Characters of Coastal Plain Crassatella.—The species of *Crassatella* included in this analysis are all equivalved, inequilateral, and prosogyrous and have no shell gape;

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[14] Boyd and Newell (1968), in a paper on Paleozoic Crassatellacea, indicate that the resemblance of the Astartidae and the Crassatellidae is due to convergence. Consequently, Bernard (1983) proposed erecting a superfamily Astartellacea to further separate the Astartidae and the Crassatellidae. For the present, I follow Chavan's (1969) usage until these larger questions can be resolved.

[15] D'Orbigny's (1844; 1845; 1853) discussion indicates he has inverted the left and right valves on the crassatellids. For the right valve, he mentions two divergent teeth and three fossettes of which the anteriormost fossette is the largest; d'Orbigny says that the ligament is situated in this anterior fossette. He is clearly speaking of the left valve because the widest and posteriormost section of the hinge platform contains the resilifer in the Crassatellidae.

[16] The illustration in Fischer (1887, fig. 768) is incorrectly labeled as a right valve; it is a left valve. His discussion and the labels on the diagram indicate that this was simply a typographical error.

outlines vary from ovate, to trigonal, to quadrilateral; anterior margins are always rounded; posterior margins are highly variable; a lunule and an escutcheon are present, but the lunule is usually better defined on the left valve, and the escutcheon is usually better defined on the right valve; a posterior ridge is always present, but has varying degrees of strength. The shell ornament is comarginal and highly variable, even within species, but juveniles within a given species show fairly consistent patterns of ornamentation; an underlying radial element may be visible on worn shells. The typical pattern for the dentition of this genus, moving from posterior lateral ridges across the hinge plate to the anterior lateral ridges, is as follows (see fig. 18):

Right Valve 0 1 0—R(1) 0 1 0 (1)–1 0 1
Left Valve 1 0 1—R(0) 1 0 1 (0)–0 1 0

The right valve dentition consists of one posterior lateral ridge[17] separated from the resilifer (R) by an edentulous space. The resilifer originates at the beak on a platform formed by the rear wall of the trigonal socket, below and slightly anterior to the resilifer. The rear wall of this socket may form a small narrow raised ridge, which has been identified as a cardinal tooth by some authors[18] but which I consider, at best, a pseudocardinal even when maximally developed. One large cardinal tooth lies anterior to the beak and is preceded anteriorly by a socket. The anterior edge of the hinge plate may be raised in a thin narrow ridge; this anterior-most ridge has been identified also as a cardinal (Fischer, 1887, p. 1021; Dall, 1903, p. 1465) but it also is a pseudocardinal at best. Two anterior lateral ridges are present[17] (Fischer, 1887, p. 1021, mentions only one), separated by a groove. The left valve dentition consists of two posterior lateral ridges[17] (Fischer, 1887, p. 1021, mentions only one), separated by a groove. The resilifer originates at the beak on an edentulous space posterior to the beak. A small receptor pit occurs at the flared base of the posterior cardinal; two well-defined cardinals are separated by a socket. Forward of the anterior-most cardinal is a narrow groove that functions as a receptor for the anterior-most raised ridge of the opposite valve. One anterior lateral ridge[17] is present. The ligament of *Crassatella* is internal, originates at the beak, and extends part way across the hinge plate. Interiorly, two well-developed, deeply incised adductors can be found (fig. 18); although the existence of quick and catch muscles among the Crassatellidae has been reported (Boss, 1982, p. 1136), there is no evidence of such division among the species of *Crassatella* herein studied. In addition, a small discrete anterior pedal retractor is located above the anterior adductor and near the end of the anterior lateral ridge (fig. 18; pl. 4, fig. 14; pl. 7, fig. 14; and pl. 14, fig. 17). A posterior pedal retractor occurs as a small notch continuous with the dorsal-most corner of the posterior adductor scar (fig. 18; pl. 7, fig. 14; and pl. 14, fig. 17). The pallial line is distinct and entire (pl. 7, fig. 14), and the ventral margin is at least partially crenate on all well-preserved adults. These characters are all consistent with Lamarck's (1799, p. 85) original definition.

Discussion of Type Designation.—Lamarck first recognized the genus *Crassatella in* 1799 from specimens collected in the Eocene of the Paris basin. He described it simply as an inequilateral shell, subtransverse, having closing valves, sunken lunule and escutcheon, and having the resilifer located under the beak and above the hinge teeth (Lamarck, 1799, p. 85). The type species was designated as *Mactra cygnea* Chemnitz, 1782; this designation has led to questions concerning Lamarck's intentions, identification of subsequent types (see table 37 for a partial listing), and the correct name for the genus.

Fischer (1887) was the first author to raise the issue of the correct assignment for *Mactra cygnea* Chemnitz. He believed that the shell for which Lamarck proposed the genus *Crassatella* probably belonged to the genus *Mactra* (Fischer, 1887, p. 1021). *Crassatella plumbea* (Chemnitz), 1783 is the species Fischer cites as the type for the genus (table 37). He indicated that *Crassatella plumbea* (Chemnitz), 1783 was the next specific name used by Lamarck in 1801; in actuality, Lamarck (1801, p. 119) had used the name *Crassatella gibba*, but he referred to Chemnitz (1783, Conchylien Cabinet, plate 69, figs. A–D) illustration of *C. plumbea*. Fischer seems to have correctly recognized *C. gibba* as a junior synonym of *C. plumbea.*

Dall (1903, p. 1468) concurred that Lamarck's original type was a *Mactra*, so he accepted *Crassatellites* Krueger, 1823, as the next valid name. Krueger's (1823, p. 466) description of *Crassatellites* lacked any significant details, but his reference to Lamarck's original description of the genus indicates he was not erecting a new generic name. Instead, Krueger added the suffix -ites to indicate a fossil species, following a common practice of his time (fide Iredale, 1921, p. 207–208). *Crassatellites sinuatus* Krueger is listed as the type for the genus (Krueger, 1823, p. 466).

Stewart (1930, p. 134–137) and Vokes (1973, p. 48–52) provided the most thorough examinations of the problem of the type designation for *Crassatella*. They both concluded that *Mactra cygnea* Chemnitz was indeed a *Mactra* but that it clearly was not the specimen that

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[17] Dall (1903, p. 1465) stated that "there are nowhere any developed laterals at all." He believed the "bevelled" dorsal margins are obsolete laterals. Deshayes (1824, p. 33) referred to the lateral teeth as "absent."

[18] Fischer (1887, p. 1021) termed the ridge a rudimentary posterior cardinal. Dall (1903, p. 1465) stated that three cardinals exist in the right valve but that the posteriormost is "more or less smothered and obliterated by the descending resilium." The Lamy (1916, p. 199–200) description is consistent with that of Dall.

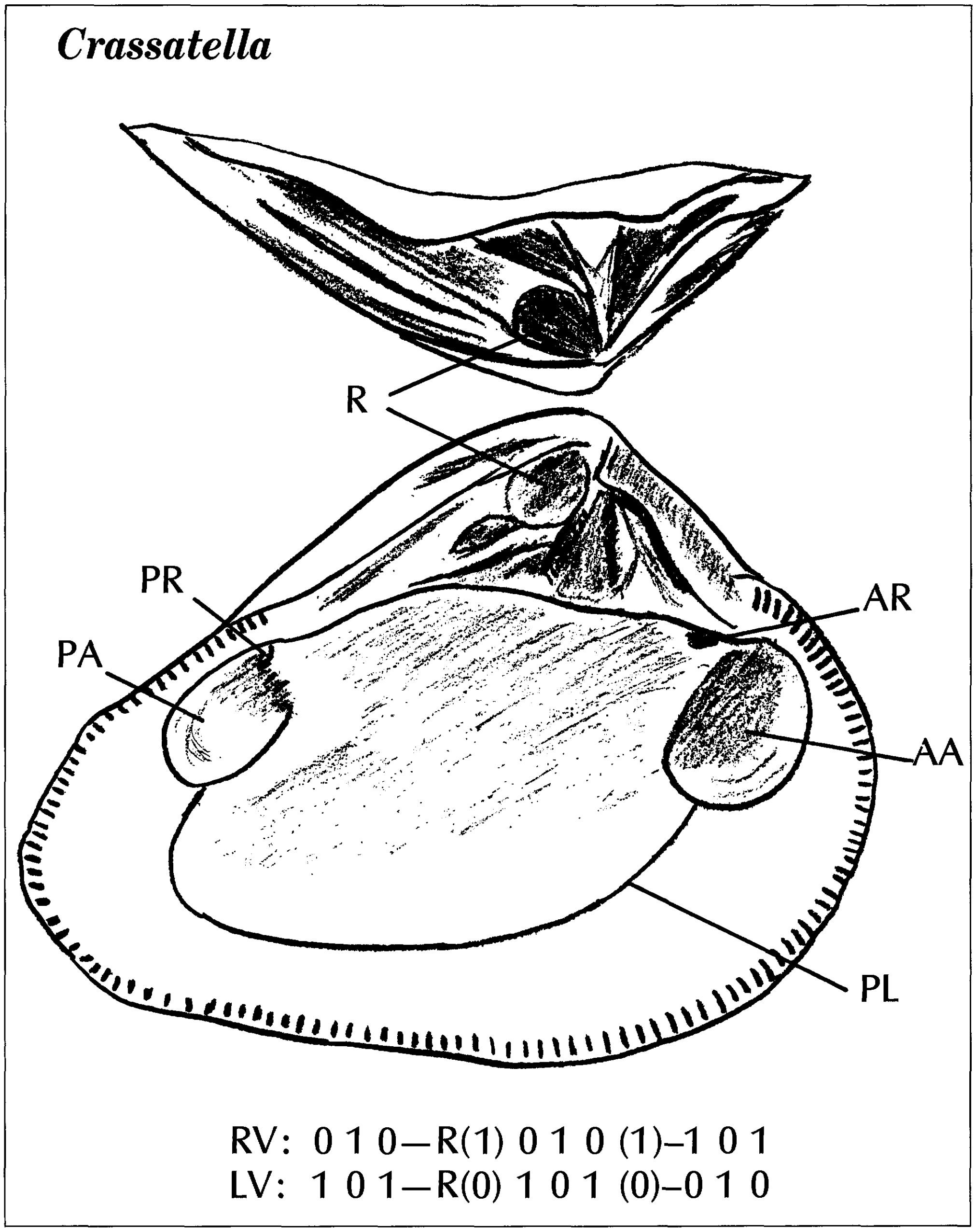

FIGURE 18.—Hinge characters and musculature of *Crassatella*. Dental formulas read from the posterior lateral ridges to the anterior lateral ridges. RV, right valve; LV, left valve. AA, anterior adductor; AR, anterior pedal retractor; PA, posterior adductor; PL, pallial line; PR, posterior pedal retractor; R, resilifer.

Lamarck described. Vokes (1973, p. 49) described Chemnitz's figure (Chemnitz, 1782, pl. 21, fig. 207) as "a rather poorly executed oblique view of paired valves of a shell marked by apparently well-defined and depressed lunule and escutcheon. No illustration is given of the hinge structure and the description of the species (p. 217) [presumably Chemnitz, 1782] mentions it only in generalized and non-definitive terms." "Obviously Lamarck was basing his description of the genus upon some source other than the Chemnitz figure and had mistakenly identified the form there shown with the material before him" (Vokes, 1973, p. 49). Stewart (1930) and Vokes (1973) concluded that the name *Crassatella* Lamarck is valid (although both state that the International

TABLE 37.—*Specific names relevant to Lamarck's original designation of* Crassatella *that have been used as type species for the genus*

[*, objective synonyms based on the author's references to the same set of figures. These names are discussed on p. 52–55, this paper. For a complete discussion of subsequent type designations see Stewart (1930, p. 134–136)]

Species	Author	Date	Reference	Comment
Unknown.............	Chemnitz	?	"Naturf. 19, t. 8, f. a–d".	This reference is cited by Chemnitz (1783) and Gmelin (1791), but the publication referred to and species illustrated are unknown.
Mactra cygnea.........	Chemnitz	1782	Conchylien Cabinet, v. 6, pl. 21, fig. 207.	
*Venus plumbea**.......	Chemnitz	1783	Conchylien Cabinet, v. 7, p. 5, pl. 69, figs. A, B.	Refers to Chemnitz, "Naturf. 19, t. 8, f. a–d."
*Venus ponderosa**	Gmelin	1791	Systema Naturae, v. 1, pt. 6, p. 3280.	Refers to Chemnitz, "Naturf. 19, t. 8, f. a–d et Conch. 7, t. 69, f. A–D."
Mactra cygnea.........	Lamarck	1799	Memoire Societe d'Histoire Naturelle, v. 1, p. 85.	Lamarck lists species as type for new genus. Refers to "Chemn. 6, t. 21, f. 207," which subsequent authors attribute to Chemnitz (1782), but description does not match Chemnitz figure (fide Vokes, 1973).
*Crassatella gibba**.....	Lamarck	1801	Systema Animaux Sans Vertebres, p. 119.	Lamarck refers to Chemnitz, "Conch. 7, Supp. t. 7, Supp. 69, litt. A, B, C, D. *Mactra*. Encycl. pl. 259, f. 3, a. b." The first part of this reference corresponds to Chemnitz (1783); the second is unknown.
*Crassatella tumida**...	Lamarck	1805	Annales du Muséum d'Histoire Naturelle, v. 6, p. 408–409.	Lamarck refers to Chemnitz, "Conch, vol. 7, tab. 69, litt. A, B. *Mactra*. Encyclop. pl. 259, f. 3, a, b. *An mactra Cygnus*. [sic] Gmel. syst. nat. 5, p. 3060?" First part of reference corresponds to Chemnitz (1783).

Commission on Zoological Nomenclature should rule on the generic name and its type species) on the basis that (1) Lamarck was naming and describing a distinct group and (2) Lamarck (1805, p. 408–409) stated that he "established" *Crassatella tumida* as characteristic of the genus. Vokes (1973, p. 52) further pointed out that "the name *Crassatellites* is not available under the provisions of articles 20 and 56(b) of the International Code." Article 56(c) of the most recent code (International Commission on Zoological Nomenclature, 1985, p. 105) states, "A genus-group name formed for use in palaeontology by substituting -ites, -ytes, or -ithes for the original termination of a generic name, and applied only to fossils, enters into homonymy."

The confusion about Lamarck's original designation has led to the use of numerous specific names as types for the genus *Crassatella*; the names relevant to Lamarck's original designation are listed in table 37. As stated above, when Lamarck (1799, p. 85) identified *Mactra cygnea* Chemnitz as the type species for *Crassatella*, he was examining a *Crassatella*. A comparison of the generic descriptions for *Mactra* (Lamarck, 1799, p. 85) and *Crassatella* (Lamarck, 1799, p. 85) resolves any doubts; *Crassatella* is described as having closed valves, whereas *Mactra* has gaping valves. Two species of *Crassatella* were listed by Lamarck in 1801. *Crassatella gibba* (Lamarck, 1801, p. 119) refers to a specimen illustrated by Chemnitz "Chemn. Conch. 7, Supp. t. 69, litt. A, B, C, D; [Conchylien Cabinet, 1783] *Mactra.* Encycl. pl. 259, f. 3, a. b.[19]). Subsequently, Lamarck (1805, p. 408–409) named and described *Crassatella tumida* (figured by Lamarck, 1807, pl. 20, figs. 7a, 7b); it is this species that he identified as being characteristic of the genus. Lamarck gave the same citation for *Crassatella tumida* in 1805, as he had given for *C. gibba* in 1801: Chemnitz, "Conch. vol. 7, tab. 69, litt. A, B. *Mactra*. Encyclop. pl. 259, f. 3, a, b.," adding "An *mactra Cygnus*. [sic] Gmel. syst. nat. 5, p. 3060?" *Crassatella tumida* is therefore a synonym of *C. gibba*. Complicating matters further, Gmelin (1791, p. 3280) cited the same Chemnitz illustrations "Naturf. 19, t. 8. f. a–d et Conch. 7. t. 69. f. A–D" under the name *Venus ponderosa*. Finally, Chemnitz (1783, p. 5) referred to his own illustration (Conch. Cab., Supp. v. 7, pl. 69, figs. A–D) as *Venus plumbea*.

All of these names—"*Mactra cygnea* Chemnitz" Lamarck, 1799 [non *M. cygnea* Chemnitz, 1782], *Crassatella gibba* Lamarck, *Crassatella tumida* Lamarck, *Venus ponderosa* Gmelin, and *Venus plumbea* Chemnitz—have been considered synonymous by some authors and therefore used as types for the genus *Crassatella* (table 37). Vokes (1973, p. 50) pointed out that *V. plumbea*, however, is not available because the International Commission on Zoological Nomenclature ruled that new specific names published in Neues Systematiches Conchylien Cabinet by Martini and Chemnitz

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[19] I have been unable to identify what text Lamarck is referring to when he cites "Encycl." Vokes (1973) and Stewart (1930) do not discuss this.

are rejected because the rules of binomial nomenclature were inconsistently applied.

Chavan (1969, p. N573) and Vokes (1973, p. 50) retain *Mactra cygnea* Lamarck, 1799 [non *M. cygnea* Chemnitz, 1782],[20] along with *Crassatella tumida*, *Crassatella gibba*, and *Venus ponderosa*, as synonyms and the type species for *Crassatella*. I prefer Stewart's (1930, p. 135) type designation, which omits *M. cygnea*; I agree with Vokes[20] that *M. cygnea* Lamarck does not exist, but I also believe it is too presumptuous to assume the specimen Lamarck saw in 1799 was the same species he cites in 1801 and again in 1805. *Crassatella tumida* Lamarck, 1805 is clearly identified as characteristic of the genus by Lamarck, so this species, and any which are synonymous with it, should be considered the type species of *Crassatella*. I therefore follow Stewart; the type species for *Crassatella* Lamarck should be cited as *Crassatella tumida* Lamarck, 1805 = *Crassatella gibba* Lamarck, 1801 = *Venus ponderosa* Gmelin, 1791 [non *Mactra cygnea* Chemnitz, 1782].

Subdivision of Crassatella.—The name *Crassatella* historically has been applied to many diverse species no longer considered part of the genus. Since Lamarck's original description of the genus in 1799, numerous subdivisions have been proposed. Conrad (1869a, p. 47) was the first to attempt such subdivision, believing he detected a generic level difference in the hinge structure of the Cretaceous through Eocene *Crassatella*, versus the Miocene and younger *Crassatella*. He erected a new genus *Pachythaerus* for the older species and designated *Crassatella Vindiemensis* d'Orbigny [sic, Conrad; = *C. Vindinnensis* d'Orbigny, 1844] as the type species. The following key points in general were noted correctly by Conrad[21]: (1) the triangular receptor pit behind the cardinal tooth, and below the resilifer on the right valve, is wider in species older than Miocene, (2) a small pit at the base of the posterior cardinal, below the resilifer, on the left valve is present in species older than Miocene but is absent in many younger species, (3) the interior ventral margins of the older species are always crenulated [in well-preserved adult specimens], whereas the Miocene or younger species may or may not be crenulated, and (4) the resilifer of the Cretaceous species is much smaller than that of Miocene and younger species, but the difference in early Tertiary species is not as distinctive (compare pl. 21, fig. 15 to pl. 21, figs. 8, 10, and pl. 21, fig. 17). Despite these correct observations, Conrad should have retained the name *Crassatella* for the older group because the type for the genus *Crassatella tumida* [= *C. gibba* = *Venus ponderosa*] (Eocene, Paris basin) falls in this category.

In 1872, Conrad (1872, p. 50) reduced *Pachythaerus* to subgeneric rank; he included three unrelated species in the subgenus: *Crassatella Pteropsis* [sic] Conrad [herein = *Bathytormus pteropsis* (Conrad)]; *C. Ripleyana* [sic] Conrad [herein = *C. vadosa* Morton]; and *C. ligeriensis* d'Orbigny, 1844. The inclusion of *B. pteropsis* in the subgenus *Pachythaerus* blurs Conrad's (1869a, p. 47) original distinction of the group because the hinge of *Bathytormus* does not fit the character of the hinge of *Pachythaerus* as described by Conrad (1869a, p. 47). In fact, the hinge of *Bathytormus* bears a striking resemblance to many of the Miocene and younger forms, and *Bathytormus* may very well have been the ancestor to the more recent forms of crassatellids as discussed in the section "Patterns and Trends Among the Crassatellidae," page 92 (compare pl. 21, figs. 13 to 15). Since 1869, *Pachythaerus* has been alternately synonymized with *Crassatella* (Tryon, 1884, p. 224; Whitfield, 1885, p. 115; Fischer, 1887, p. 1022; Dall, 1903, p. 1467, 1468), maintained as a distinct subgenus (Stewart, 1930, p. 137; Chavan, 1952, p. 119; Chavan, 1969, p. N574), and maintained as a distinct genus (Vokes, 1946, p. 177).

Scambula Conrad, 1869a, has been included in *Crassatella* as a subgenus or section by several authors (Tryon, 1884, p. 224; Fischer, 1887, p. 1022; Dall, 1903, p. 1467), but it is clearly a distinct genus (compare pl. 21, figs. 5 to 8), as the statistical analysis in this paper verifies, and is discussed under its own heading (p. 88).

The subgenus *Landinia* was described by Chavan (1952, p. 119; 1969, p. N574) as a "Narrow form, elongated in back, with persistent lamellous cords; hinge with two more oblique, anterior lamellars longer than *Crassatella*; strong furrow and ridge, fPII, PIII, elongated" (translated from French, Chavan, 1952, p. 119, footnote 3). *Crassatella landinensis* Nyst, 1843 is the type species. Chavan included *Crassatella vadosa* Morton, among other species, in *Landinia*.

The genus *Crassatella* was clarified and refined by Stewart (1930, p. 137–140); he evaluated the crassatellids and identified one new genus, *Bathytormus*, and discussed in detail *Eucrassatella* Iredale, 1924. Species having unrestricted resilifers extending to the border of the hinge plate were separated into the genus *Bathytormus*. Gardner (1916, p. 649) was the first to note distinctive differences between individuals herein assigned to *Bathytormus* and typical *Crassatella*. It was, however, the differences in shape of the posterior margin between *C. vadosa* Morton and *C. pteropsis* Conrad [herein = *Bathytormus pteropsis*] that she recognized,

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[20] Vokes (1973, p. 50) uses the form "*Mactra cygnea* Chemnitz' Lamarck, 1799 [non *M. cygnea* Chemnitz, 1782]" and correctly states, "It is to be noted that Lamarck did not describe any species in 1799 and technically there is no such species as '*Mactra cygnaea* [sic] Lamarck.' " The latter is the form used by Chavan (1969, p. N573).

[21] There are exceptions to any generalization. Crassatellids fitting Conrad's description of the Late Cretaceous and early Tertiary group have been found in recent oceans (Vokes, 1973), but the majority of prevalent species reflect the characters noted in Conrad's observations.

not the generic level differences seen in the hinge (compare pl. 21, fig. 8, to figs. 10, 17). Following the publication of Stewart's revision, Stephenson (1941, p. 176) recognized two subgroups within the Cretaceous species of *Crassatella* on the basis of the same differences in the hinge noted by Stewart, but he did not recognized or discuss *Bathytormus*. Although the position and extent of the resilifer is the key diagnostic character of *Bathytormus*, this genus proved to be distinct from *Crassatella* during the statistical analysis portion of this study, even when variables related to the resilifer were not included.

The genus *Eucrassatella*, as defined by Iredale (1924, p. 202) and recognized by Stewart (1930, p. 139–141), contains Neogene species having a large ligamental cavity and smooth internal margin (pl. 21, figs. 15, 16, for example). The characters cited as distinctive of *Eucrassatella* parallel those differences discussed by Conrad when he separated the Cretaceous and lower Tertiary species into *Pachythaerus* (Conrad, 1869a, p. 47). Despite Stewart's recognition and discussion of the characters originally used by Conrad in the separation of *Pachythaerus* from *Crassatella*, he did not synonymize *Pachythaerus* with *Crassatella*. Stewart allowed the subgenus to stand for the Upper Cretaceous species on the basis of the presence of higher beaks and steeper umbonal slopes, characters not originally mentioned by Conrad.

The genus *Crassatella*, as herein defined, encompasses those species having a restricted ligamental cavity and crenulated margin in their adult stages. Any further subdivision of the genus obfuscates the natural variability seen within the species, populations, and individuals of *Crassatella* and imposes a false order. Using the characters that Chavan (1969, p. N573–N574) considered diagnostic of the three subgenera, *Landinia*, *Pachythaerus*, and *Crassatella* s.s., it is impossible to assign the individual species herein studied to a subgenus. The characters cited, such as "obliquely truncate posteriorly; compressed" (Chavan, 1969, p. N574) for *Landinia*, or "prominent dorsal slope" (Chavan, 1969, p. N574) for *Pachythaerus*, vary within single individuals during their ontogeny. Furthermore, Chavan (1952, p. 119) assigns *C. vadosa* Morton to the subgenus *Landinia*, whereas *C. ripleyana* Conrad was assigned by Conrad (1872, p. 50) to the subgenus *Pachythaerus*; these two species are herein demonstrated to be synonymous. Finally, such species as *C. tumidula* (pl. 15, figs. 1–17) do not fit in any subgeneric category as currently defined, so either revision of the subgenera or the erection of a new subgenus would be necessary to accommodate them. I believe the subgeneric divisions *Landinia* and *Pachythaerus* should be suppressed. The genus *Crassatella* should be allowed to stand by itself, including its full range of variation; false subdivisions lacking diagnostic characters should not be imposed.

In addition to the subgenera relevant to this study and discussed above, the following subgenera have been proposed for *Crassatella*: *Crassatella* (*Rochella*) Freneix (1972, p. 135–136); *Crassatella* (*Sublandinia*) Freneix (1972, p. 142); and *Crassatella* (*Riosatella*) Vokes (1973, p. 48–59). I have not examined the validity of these names, but if they are based on continuously variable characters, as are the subgenera examined above, instead of clearly diagnostic characters, then these names should also be suppressed.

Distribution and validity of species.—One of the early discoveries of *Crassatella* (as herein defined) in North America was by Conrad (described by Morton, 1834, p. 66) in the Prairie Bluff Chalk in Alabama (pl. 1, figs. 2, 3). Conrad (1838, p. 20; 1846, p. 395) also recognized the genus in Tertiary deposits of New Jersey, Maryland, Virginia, North Carolina, and Alabama and in Cretaceous deposits of New Jersey (figs. 2, 19). Numerous species names have been proposed over the years since Conrad's first recognition of the genus in 1834 (table 1). Dall (1903, p. 1469) correctly pointed out that many of the names that exist in the literature for North American crassatellids are "nominal." However, many of the 12 species, such as *C. sepulcollis* [herein = *C. aquiana* Clark], that Dall (1903, p. 1469) stated were nominal and "ill-defined or doubtful Eocene forms described from fragments or internal casts," are species that are abundant and represented by extremely well preserved material. Furthermore, *C. carolinensis* Conrad, 1875, a Cretaceous form, is included in Dall's (1903, p. 1469) list of Eocene crassatellids.

Three valid species in the Cretaceous, and two valid species in the lower Tertiary, are herein recognized for the eastern Gulf Coast and Mid-Atlantic regions of the United States (fig. 19). The statistical analysis herein demonstrates that, within this group of *Crassatella*, there is a large degree of intraspecific variation that contributes to the difficulty of isolating species characters. The five Crassatella species described below can be distinguished visually by the characters of the juvenile, the details of the ornament, the position and height of the beak, and the characters of the posterior margin. The best statistical discriminators of the species are the characters of the dorsal margin and the height of the posterior margin.

One problem prevalent in the taxonomic literature of the Crassatellidae is the failure to recognize juvenile members of the fauna. Immature specimens often are identified as separate species, or even separate genera, which contributes to the proliferation of taxonomic names. This problem was first acknowledged for the crassatellids by Smith (1881, p. 489–491). Specific names

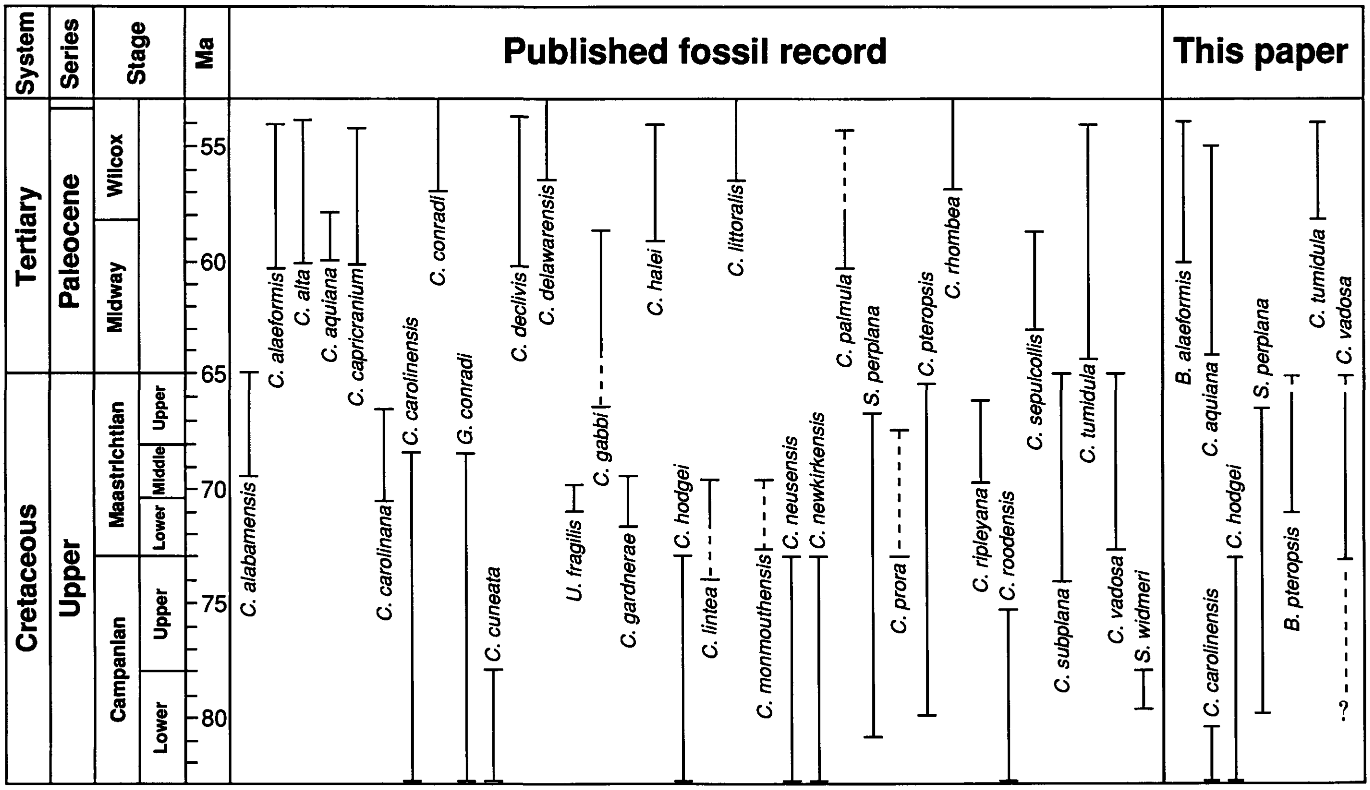

FIGURE 19.—Comparison of the ranges of the published Crassatellidae species (see fig. 4) with ranges determined in this study. Generic abbreviations: *C.*, *Crassatella* (incorporates *Crassatellites*, junior synonym of *Crassatella*); *G.*, *Gouldia*; *U.*, *Uddenia*; *S.*, *Scambula*; *B.*, *Bathytormus*. Species are arranged in alphabetical order. Four species names were omitted due to lack of stratigraphic information. See table 1 for complete listing of species.

based on juveniles are synonymized herein and are discussed under the heading of their new assignments.

Uddenia Stephenson is the one genus, within the Crassatellidae studied herein, that was founded on a juvenile specimen. Stephenson (1941, p. 180) designated *Gouldia conradi* Whitfield [non *Crassatella conradi* Whitfield] as the type species for his new genus; the description of *Uddenia* is as follows:

> This tiny member of the Crassatellidae has heretofore been referred by different authors to *Crassatellites*, *Gouldia*, and *Eriphyla* (of the Astartidae), though it obviously forms a group different from any of these genera. It is apparently nearest to *Crassatella*, from which it differs in its diminutive size, its shorter and higher outline, its straight, long steeply descending dorsal margins, its relatively long, narrow lateral teeth and sockets, and the high position of its adductor scars.

With the exception of the steeply sloping dorsal margins, these characters are compatible with the description of a juvenile *Crassatella*, and I believe this inconsistency can be attributed to the incomplete preservation of the type specimens of *G. conradi* Whitfield (ANSP 18735; pl. 22, figs. 1–4). Stewart (1930, p. 147) indicated *Gouldia* was a juvenile *Crassatella*, and an examination of the type specimens of *G. conradi* Whitfield confirms this. The genus *Uddenia* is therefore considered a junior synonym of *Crassatella*.

Many additional small specimens have been assigned to *Uddenia* since its inception. Where possible, these are synonymized below, but the poor preservational state of many of the shells (pl. 22, figs. 5, 6, for example) makes reassignment impossible in all cases. The hinge of *U. texana* Stephenson (1941, p. 181) is not visible on the type material, but the exterior characters resemble a small triangulate form (pl. 13, figs. 1–5) found with *Crassatella vadosa* Morton in the Gulf Coast and Mid-Atlantic deposits. *U. texana* and the unnamed group (genus and species unknown) have the general appearance of a *Crassinella*, but an examination of the hinge of the unnamed group reveals that it is not a member of the Crassatellidae (compare pl. 13, figs. 1–3 to pl. 12, figs. 2, 4 and pl. 6, fig. 2). Unlike Crassatellidae, the resilifer of the triangulate form is located centrally below the beak and between the cardinals. The lack of any knowledge about the internal characters of *U. texana* makes it impossible to determine whether it is a juvenile crassatellid, like *Gouldia conradi*, or whether it belongs in a different family. The statistical analysis of the genera of Crassatellidae supports the conclusions drawn here;

Uddenia was statistically a poorly defined genus that intermingled with other Crassatellidae on the plots and classification results. The unnamed group was statistically distinct from the other genera.

Many names exist in the literature that cannot be resolved (table 1; fig. 19). The following are species assigned to *Crassatella* within the geographic and stratigraphic ranges of this study but are based on specifically indeterminable internal molds or poorly preserved specimens:

1. *Crassatella alta* CONRAD, 1835, p. 335–336 [mentioned in a discussion of the stratigraphy; contains no description or illustration of species].
   Crassatellites alta CLARK and MARTIN, 1901, p. 182–183, pl. 42, fig. 3. PALMER and BRANN, 1965, p. 98 (= *C.* sp., p. 107).
   [non] *Crassatella alta* CONRAD, 1832, p. 21, pl. 7.

   Conrad originally named and described *Crassatella alta* in 1832 from the bluffs at Claiborne, Ala. (Conrad, 1832, p. 21); thus, the reported range of *C. alta* in general falls outside the stratigraphic limits of this study. The synonymy given above is incomplete and, besides the original citation, only includes the specimens that fall within the stratigraphic and geographic ranges herein considered. Clark and Martin (1901, p. 182) found an imperfect specimen, having exterior characters preserved, in beds of the Aquia Formation at Hardesty, Prince George's County, Md.[22] They based their specific determination on a notation made by Conrad (1835, p. 335) stating that he had found a cast of *C. alta* in a stream bed in Upper Marlboro, Prince George's County, Md., an area where the Aquia Formation is known to crop out. The lack of complete preservation of Clark and Martin's specimen, the fact that Conrad's specimen was only a cast, and the fact that no such specimens have since been found in the well studied Aquia make this specific determination tenuous at best.

2. *Crassatella palmula* CONRAD, 1846, p. 396, pl. IV, fig. 1. CLARK, 1896, p. 93.
   [non] *Bathytormus alaeformis* (Conrad) PALMER and BRANN, 1965, p. 49.

   Crassatella palmula was named and described by Conrad (1846, p. 396) from deposits near Upper Marlboro, Prince George's County, Md. After giving a complete description of the species, Conrad (1846, p. 396) states, "A single imperfect valve is all I have found of this species." This specimen (ANSP 30580; pl. 3, figs. 11, 13) appears to be a crassatellid, but it is in such a poor state of preservation that few diagnostic characters can be derived from it. Clark (1896, p. 93) arrived at the same conclusion; he states the name should be "debarred from the list of Eocene fossils of the Middle Atlantic slope." Although the name cannot be "debarred," it should be restricted to the type specimen. Palmer and Brann (1965, p. 49) have synonymized *C. palmula* with *Bathytormus pteropsis* (Conrad), a species that occurs in the type area of *C. palmula*, but I believe synonymization of such a poorly preserved specimen is impossible.

3. *Crassatella monmouthensis* GABB, 1860a, p. 302, pl. 48, fig. 19 [text lists as fig. 20]. WHITFIELD, 1885, p. 119, pl. 17, figs. 21, 22.
   Etea monmouthensis (Gabb). CONRAD, 1877, p. 275.
   Crassatellites monmouthensis (Gabb). JOHNSON, 1905, p. 14.
   Etea trapezoidea (Conrad). WELLER, 1907, p. 543–546, pl. 58, figs. 20, 21, pl. 59, fig. 7 (*C. monmouthensis* Gabb junior synonym of *Venilia* [sic] *trapezoidea* Conrad, 1860, p. 282, pl. 47, fig. 7).
   Veniella (*Etea*) *trapezoidea* Conrad. RICHARDS, 1958, p. 175, pl. 28, figs. 8, 9, pl. 29, figs. 7, 15.

The type collection contains four internal molds from Monmouth County, N.J. (ANSP 18738; pl. 22, figs. 7–9), the smallest of which is labeled "type." I agree with Weller's (1907, p. 545) comments that the smallest specimen appears different from the other three and that the smaller specimen is probably not the one that Gabb (1860a, pl. 48, fig. 19) illustrated; the quality of the original illustration, however, makes an absolute determination impossible. On the basis of the strong angulation of the posterior ridge and the low profile of the adductors on the internal molds, I believe the three larger molds are specimens of *Etea* (Arcticidae). The state of preservation of the smallest specimen makes a familial as well as generic determination difficult. Since Gabb's description and illustration correspond more closely to *Etea* than to *Crassatella*, the name *Crassatella monmouthensis* is not discussed further in this study of the Crassatellidae.

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[22] Presumably the Hardesty referred to by Clark and Martin (1901) is located in Prince George's County, 0.8 km west of the Patuxent River, off Queen Anne Bridge Road, below Route 214, and 11.25 km northeast of Upper Marlboro; this location can be found on the 1913 map of Prince George's County (Maryland Geological Survey, 1911). In addition to the Hardesty in Prince George's County, present-day maps show a Hardesty in Anne Arundel County on Route 2 between the intersections of Route 2 with Route 214 and Route 424, south of Edgewater, approximately 9.5 km east-northeast of the Hardesty in Prince George's County; this locality cannot be found on the 1907 Maryland Geological Survey Atlas map of Anne Arundel County (Maryland Geological Survey, 1917).

4. *Crassatella delawarensis* GABB, 1860a, p. 303, pl. 48, fig. 20 [text lists as fig. 21].

   Etea delawarensis (Gabb). CONRAD, 1877, p. 275.

   Crassatellites delawarensis (Gabb). JOHNSON, 1905, p. 14.

   Additional descriptions of specimens that have been synonymized with *Crassatella delawarensis* Gabb:

   Crassatella delawarensis Gabb. WHITFIELD, 1885, p. 119, p. 210, pl. 27, figs. 14, 15. PALMER and BRANN, 1965, p. 106 (*C. delawarensis* Whitfield non Gabb = *C.* sp.).

   Etea delawarensis (Gabb). WELLER, 1907, p. 546, pl. 59, figs. 8, 9. RICHARDS, 1958, p. 177, pl. 28, fig. 4, pl. 29, fig. 11, pl. 31, fig. 1.

   Named from a single internal mold having a portion of replaced shell material adhering to the mold, this specimen (ANSP 18733; pl. 22, figs. 10–12) is of dubious locality and stratigraphic position. A label in Gabb's handwriting found with the specimen lists the locality as Crosswicks, N.J., but the text states the type locality is a "deep cut, Delaware and Chesapeake Canal" (Gabb, 1860a, p. 303). The age of the specimen is therefore questionable; the Delaware and Chesapeake Canal locality is Cretaceous, and the present-day Crosswicks Creek locality is Cretaceous, but since Crosswicks Creek drains both Cretaceous and Tertiary strata, a specimen from Crosswicks Creek could be from either period. Whitfield (1885, p. 210) and, later, Weller (1907, p. 546) believed that they found individuals of this species in the Manasquan Formation (late Paleocene and early Eocene). Richards (1958) figures three specimens of *Etea delawarensis*; the first (Richards, 1958, pl 31, fig. 1) is the type specimen; the second (Richards, 1958, pl. 29, fig. 11) is similar in form to the type and, like the type, appears extremely worn; the third (Richards, 1958, pl. 28, fig. 4) appears similar to *Crassatella transversa* Gabb. The type specimen resembles a *Bathytormus* because of its elongate posterior, oblique posterior adductor, and strong posterior ridge. The questionable locality information and the poor preservational state of the specimen, however, make it necessary to restrict the name *C. delawarensis* Gabb to the type specimen.

5. *Crassatella cuneata* GABB, 1861a, p. 168–169 [new assignment for *Crassatella pteropsis* GABB, 1860b, p. 395, pl. 68, fig. 28, non Conrad, 1860].

   Crassatella gabbi SAFFORD, 1864, p. 368 [new assignment for *Crassatella pteropsis* GABB, 1860b, p. 395, pl. 68, fig. 28, non Conrad, 1860].

   The following citations have been synonymized with *Crassatella pteropsis* Gabb non Conrad, but a direct relationship to the type cannot be confirmed:

   Crassatella cuneata Gabb. WHITFIELD, 1885, p. 118, pl. 17, figs. 18–20.

   Crassatella gabbi Safford. HARRIS, 1896, p. 63, pl. 5, figs. 7–11 [Palmer and Brann, 1965 say, "in part, pl. 5, figs. 7, 7a type, 8, 9, not figs. 10, 11"]. PALMER and BRANN, 1965, p. 100–101. TOULMIN, 1977, p. 147–148, pl. 2, figs. 1, 2.

   Crassatellites cuneatus (Gabb). WELLER, 1907, p. 556, pl. 61, figs. 11, 12. RICHARDS, 1958, p. 185, pl. 31, fig. 2.

   Crassatellites gabbi (Safford). GARDNER, 1933, p. 151–152.

   Gabb's original description of *Crassatella pteropsis* [non Conrad] in 1860 gives the following locality information: "Ripley Group, Hardeman Co., Tenn., Prof. Safford; and from the same formation at Eufaula, Ala. Collection of the Smithsonian Institution, No. 553" (Gabb, 1860b, p. 395). USNM specimen 553 is extremely damaged, but no notation with the specimen indicates that this damage occurred since it was designated as Gabb's type, nor is there any indication of provenance. The figure presented by Gabb (1860b, pl. 68, fig. 28) and the measurements given in the text (Gabb, 1860b, p. 395) do not seem to correspond to USNM 553, although the damage to the specimen leaves room for doubt. The type locality for *C. pteropsis* Gabb [non Conrad] remains questionable, although subsequent authors have presumed (probably correctly) that it was Hardeman County, Tenn.

   The age and formation of the species also have been questioned by various authors. Gabb placed the species in the Cretaceous Ripley "Group," but the Ripley, as previously defined in Tennessee, has included lower Tertiary beds. In addition, an examination of the other species Gabb included in the Cretaceous Ripley "Group" contains some distinctly Tertiary fauna such as the *Turritella* species (Gabb, 1860b, p. 392, pl. 68, fig. 13). Confounding the problem of stratigraphic position, both Cretaceous and Tertiary beds crop out in Hardeman County, Tenn.

   In 1861, Gabb (1861a) recognized his name *Crassatella pteropsis* as a junior homonym of Conrad's species and renamed it *C. cuneata*. Subsequently, Safford (1864, p. 368), apparently oblivious to Gabb's reassignment, himself reassigned *Crassatella pteropsis* to *C. gabbi* Safford. From this point on, not a single author acknowledged that *Crassatella cuneata* Gabb and *C. gabbi* Safford were based on the same original species description and type, *C. pteropsis* Gabb non Conrad, and are therefore synonyms. Gardner (1933, p. 151) states, "The Cretaceous species was later renamed *C. cuneata* by Gabb (1861a), the Midway species, *C. gabbi* by Safford," but there is no indication that either Safford or Gabb intended a division of the species by age; both authors cite the occurrence of the species as the Cretaceous, Ripley Group. The name *Crassatella cuneata* [=*Crassatellites cuneatus* (Gabb)] has been applied to several Cretaceous internal molds and casts from New Jersey (Whitfield, 1885; Weller, 1907; Richards, 1958). These subsequent designations cannot be confidently synonymized with Gabb's type because they are far removed from the type locality and are poorly preserved. In the Gulf Coast, *Crassatella gabbi* [=*Crassatellites gabbi* (Safford)] has been applied to Tertiary specimens of varying description (Harris, 1896; Gardner, 1933; Toulmin, 1977). Although the Gulf Coast specimens are closer geographically to Gabb's presumed type, the state of preservation of the type specimen and the brief description do not permit confident synonymization here either. Harris (1896, p. 63, pl. 5, figs. 7, 7a) examined and figured Safford's "type," which can no longer be located (fide Palmer and Brann, 1965), but Safford never published a description or illustration of *C. gabbi*.

The name *Crassatella cuneata* Gabb is the senior synonym of *C. gabbi* Safford, and this name resides with the USNM specimen 553 by Gabb's (1860b, p. 392) original designation; in my opinion, the name should be restricted to this specimen. The poor condition of the type makes it impossible to determine the validity of the assignments made by subsequent authors. The specimens that have been synonymized with *C. cuneata* Gabb and its junior synonym *C. gabbi* Safford need to be reevaluated. The New Jersey specimens assigned to *C. cuneata* are specifically indeterminable molds and casts. The Gulf Coast specimens assigned to *C. gabbi* may prove to be synonymous with other species, or an examination of the material may illustrate the need to erect a new species.

6. *Crassatella transversa* GABB, 1861b, p. 364–365. WHITFIELD, 1885, p. 122, pl. 17, figs. 16, 17.
   Etea transversa (Gabb). CONRAD, 1877, p. 275.
   Crassatellites transversus (Gabb). JOHNSON, 1905, p. 14. RICHARDS, 1958, pl. 61, fig. 5 [figure of type but description taken from Weller, 1907].

Additional descriptions of specimens that have been synonymized with *Crassatella transversa* Gabb but that cannot be directly related to the type:

Crassatellites transversus (Gabb). WELLER, 1907, p. 555, p. 61, fig. 5. RICHARDS, 1958, p. 185 [description only; figure is of the type specimen].

The species description was based upon a single phosphatic internal mold in the collection of the Burlington County Lyceum of Natural History (now ANSP 18744; pl. 22, figs. 13–15); the locality and formation are listed simply as "Cretaceous, New Jersey." Many stratigraphic units later described as Tertiary were included originally in the Upper Cretaceous, so it is possible that this was not even a Cretaceous specimen. The specimen illustrated and described by Weller (1907, p. 555, pl. 61, fig. 5) and the description repeated by Richards (1958, p. 185) cannot be related to the type *Crassatella transversa* by locality or stratigraphic position since no details of provenance were given with the type. Weller's (1907, pl. 61, fig. 5) specimen is also an internal mold, as is the type, but the poor state of preservation of this specimen makes a specific determination impossible. The shape of the posterior margin, the oblique position of the posterior adductor, the ratio of height to length, and the strong posterior ridge of the type *C. transversa*, all bear a striking resemblance to the Tertiary *Bathytormus alaeformis* (Conrad), a fact noted by Whitfield when he stated "in form it presents many features in common with *C. protexta* Conrad" [= *Bathytormus alaeformis* (Conrad)] (Whitfield, 1885, p. 122). Without more specific locality information and additional specimens, however, it is impossible to relate the type *C. transversa* Gabb to other species; the name should therefore be restricted to the type specimen.

7. *Crassatella planata* CONRAD, 1866, p. 104, pl. 8, fig. 4. CONRAD, 1867, p. 270.

Conrad based this name on an incomplete internal mold; no locality or stratigraphic position were designated in the original description. In 1867, he stated that he found the species in "the Cretaceous marl near Barnsboro," N.J. The type specimen is apparently missing (it does not appear in Johnson's (1905, p. 14) catalogue of ANSP Cretaceous types), but doubtless if it was available it would provide no further clues as to its specific identity.

8. *Crassatella peralta* CONRAD, 1866, p. 104, pl. 8, fig. 1 [plate citation as given in text, but pl. 8, fig. 1 caption reads *Crassatella alta* Conrad]. CONRAD, 1867, p. 270.

Conrad (1866, p. 104) originally described this species from an internal mold found at Goshen, Cape May County, N.J., which is a Tertiary locality. He also mentions finding "A very perfect ferruginous cast of this species from a new locality," but where the new locality is, and whether the figured specimen is from the "new locality" or from Goshen, remains in doubt. I believe the specimen Conrad figured on plate 8, figure 1 is the specimen he intended to call *Crassatella peralta* (despite the caption reading *C. alta*) because his description of *C. peralta* matches this figure. In 1867, Conrad (1867, p. 270) stated that he found this species in "the Cretaceous marl near Barnsboro. They are not found in the Miocene, as I supposed from the locality named on the specimens in the collection of the Academy." It is unclear whether Conrad believed the original locality label to be wrong or whether he believes he was mistaken in designating the Cape May County locality as Tertiary. This confusion over stratigraphic and geographic position of the species, the poor preservation of the originally figured specimen, and the fact that the type appears to be missing (Moore, 1962, p. 84; not in Johnson's (1905, p. 14) catalogue) makes it impossible to determine the validity of this species.

9. *Crassatella prora* CONRAD, 1869b, p. 43, pl. 1, fig. 8. WHITFIELD, 1885, p. 120, pl. 18, figs. 10, 11.
   Etea prora (Conrad). CONRAD, 1877, p. 275.
   Crassatellites prorus (Conrad). JOHNSON, 1905, p. 14. WELLER, 1907, p. 558, pl. 61, figs. 6, 7. RICHARDS, 1958, p. 186, pl. 29, fig. 6, pl. 30, figs. 13, 14 [pl. 29, fig. 6 is a photograph of Conrad's type from ANSP; pl. 30, figs. 13, 14, is a reproduction of Whitfield's drawing of the same ANSP type].

Conrad's type specimen of *Crassatella prora* is an internal mold (ANSP 18739; pl. 22, figs. 16, 17). Another internal mold (pl. 22, figs. 18, 19) is present in the same box as the type specimen figured by Conrad (1869b), Whitfield (1885), Weller (1907), and Richards (1958). As far as I can determine, this second specimen has never been figured nor are there any notations on the labels to indicate where it came from, but it definitely belongs in the genus *Etea* (Arcticidae). Whitfield (1885, p. 121) indicated that a second smaller specimen "of the same form" was found with Conrad's type, but since the second specimen now residing with the type is larger than the type specimen, it would seem this is not the specimen to which Whitfield referred. No additional specimens from the type locality of Crosswicks, N.J., have been illustrated, although Richards (1958) indicates he found specimens of this species in the Merchantville Formation at Matawan, Monmouth County, N.J. The worn condition of Conrad's type specimen (pl. 22, figs. 16, 17) makes specific and even generic determination difficult, but it does appear to be a crassatellid. In the absence of determinant characters, the name *Crassatella prora* Conrad [= *Crassatellites prorus* (Conrad)] should be restricted to the type specimen illustrated by Conrad (1869b, pl. 1, fig. 8).

10. *Crassatellites newkirkensis* STEPHENSON, 1923, p. 268, pl. 67, figs. 17–19.

The holotype of *Crassatellites newkirkensis* is a compressed articulated calcite-replaced specimen (USNM 31744), and the paratype is an internal mold (USNM 31745). Three (herein = locs. 12, 19A, 20) of the six localities listed by Stephenson (1923, p. 269) for *Crassatellites newkirkensis* are also localities for *Crassatellites hodgei* Stephenson (1923, p. 272–273) [herein = *Crassatella hodgei* (Stephenson)]. The compressed nature of the holotype makes any detailed comparisons of shape between *Crassatellites newkirkensis* and other species impossible, but the preserved characters of the ornamentation are consistent with those of *Crassatella hodgei*. The relationship of the internal mold to the holotype is difficult to establish. Further, Stephenson's study collection from North Carolina was examined, and the majority of specimens he had labeled as *Crassatellites newkirkensis* were internal molds, most of which could easily have been assigned to either *Crassatella carolinensis* Conrad or *Crassatella hodgei*. In fact, Stephenson had originally labeled some of these specimens *Crassatellites carolinensis* [herein = *Crassatella carolinensis* Conrad] then later crossed this out and wrote *Crassatellites newkirkensis*. It is therefore recommended that the name *Crassatellites newkirkensis* reside only with the holotype specimen.

11. *Crassatellites neusensis* STEPHENSON, 1923, p. 270, pl. 67, figs. 1–3.

The holotype of *Crassatellites neusensis* (USNM 31735) has been destroyed,[23] and the two remaining

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[23] Several specimens of North Carolina types are lost or destroyed, probably due to an accident in the 1950's when a drawer of North Carolina types was dropped at the Smithsonian Institution (N.F. Sohl, U.S. Geological Survey, oral commun., 1987).

paratypes (USNM 31736 and USNM 31737, pl. 2, figs. 4, 5) are both worn left valves, with original shell material preserved, but encased in matrix so that the internal features are not visible. For *Crassatellites neusensis*, Stephenson (1923, p. 271) lists three localities, two of which are also localities for *Crassatellites hodgei* Stephenson [herein = *Crassatella hodgei* (Stephenson)]. *Crassatellites neusensis* could easily be a juvenile of *Crassatella hodgei* (compare pl. 2, figs. 4, 5 to pl. 2, figs. 8, 11 and pl. 5, fig. 9); the characters of general shape and the ornamentation remaining on the specimens are consistent with such a designation, and the largest specimen observed among the types and Stephenson's study collection was approximately 2.5 cm in length. The poor condition of the paratypes and the specimens in the study collection, however, prevents examination of such key characters as the hinge structure, the orientation of the muscle scars, and the details of the juvenile ornamentation, which would allow confident synonymization with *Crassatella hodgei*. Therefore, it is recommended that the name *Crassatellites neusensis* be restricted to the paratype specimens.

The following species names exist in the literature, but their validity cannot be confirmed due to the lack (or unavailability) of a type specimen and the lack of any specimen (topotype or otherwise) in existing collections that fits the original description:

1. *Crassatella alabamensis* D'ORBIGNY, 1850, p. 239.

   The type locality is Prairie Bluff, Ala., but d'Orbigny stated that the specimen had a different form from *Crassatella vadosa* Morton. Yet, he compared *Crassatella alabamensis* to *C. marrotiana* d'Orbigny, 1844, which bears a strong resemblance to *C. vadosa* Morton. The type Prairie Bluff Chalk has been studied extensively for the last 140 years, and no additional reports of *Crassatella alabamensis* have emerged.

2. *Crassatella littoralis* CONRAD [nomen nudum], 1868, p. 731. CONRAD, 1869b, p. 41, pl. 1, fig. 3. WHITFIELD, 1885, p. 212, pl. 28, figs. 6, 7. PALMER and BRANN, 1965, p. 102.
   Crassatellites littoralis (Conrad). WELLER, 1907, p. 559, pl. 61, figs. 9, 10.

   Conrad (1868, p. 731) included *Crassatella littoralis* in a list of fossils from the "blue marl layer" of the Shark River Formation of New Jersey; this places *Crassatella littoralis* in the Eocene, Claibornian Stage, and therefore out of the range of this study. Weller (1907, p. 559), however, extended the range of *Crassatellites littoralis* (Conrad) [= *Crassatella littoralis* Conrad] down into the Manasquan Formation, Wilcox Stage of the Paleocene, which is included in this study. The type specimen, an internal mold from Shark River, N.J., has apparently been lost from the collections of ANSP (Moore, 1962, p. 72), and the figure and description provided by Conrad do not distinguish this species from many similar forms of *Crassatella*. The question of the validity of this species must therefore remain unresolved.

3. *Crassatella rhombea* WHITFIELD, 1885, p. 213–214, pl. 27, figs. 16–19. PALMER and BRANN, 1965, p. 103.
   Crassatellites rhombea (Whitfield). WELLER, 1907, p. 561, pl. 61, fig. 8.

   Whitfield (1885, pl. 27, figs. 18–19) figured two specimens with his original description, one an internal mold from Squankum, N.J., and the other "preserving the shell" from near New Egypt, N.J. (Whitfield, 1885, pl. 27, figs. 16–17). Judging from Weller's (1907, pl. 61, fig. 8) photograph, the New Egypt specimen is little more than an internal mold that has some shell material adhering to the matrix. Whitfield (1885, p. 214) states that "The shell differs in its general form and outline from any American species hitherto described . . . . The internal cast differs from all American species in its transverse form and broad posterior end." Yet the illustrations for *Crassatella rhombea* display a striking resemblance to Whitfield's (1885, pl. 18, figs. 4–16) figures of *Crassatella subplana* Conrad in the same volume. Since Whitfield's designation of *Crassatella rhombea* as a Tertiary species is in agreement with current New Jersey stratigraphy, it is possible that *C. rhombea* is related to the Cretaceous form *Crassatella vadosa* Morton [herein = *C. subplana* Conrad]. On the other hand, *Crassatella rhombea* may be the internal mold of a common Tertiary form seen in the Gulf Coast, or it may be a separate species, but without better preservation and additional material none of these possibilities can be confirmed.

4. *Crassatella conradi* WHITFIELD, 1885, p. 209, pl. 28, figs. 1–5 [plate caption says *Crassatella curta* ?]. WELLER, 1907, pl. 61, figs. 9, 10 [figures illustrate Whitfield's type specimens; text synonymizes with *Crassatellites littoralis* (Conrad)]. PALMER and BRANN, 1965, p. 99–100.

   Crassatella conradi was named by Whitfield (1885, p. 209) from internal molds from Squankum and New Egypt, N.J. Three specimens are figured with the caption "*Crassatella curta* Conrad ?"; Whitfield discussed these individual specimens under *C.*

conradi, however, and mentioned that he "at first thought these casts might be the same specifically as that described by Conrad as *C. curta*" (Whitfield, 1885, p. 210). I believe the plate caption is in error and perhaps was prepared prior to the text. One specimen illustrated by Whitfield (1885, pl. 28, fig. 3) (AMNH 9015/1) is not a crassatellid (it may be a *Cucullea*). The other two specimens may be crassatellids, but since they are lost (fide Palmer and Brann, 1965, p. 100) no assignment, including Weller's (1907, p. 559) synonymization of *Crassatella conradi* under *Crassatellites littoralis*, can be validated.

The following species name is invalid:

Crassatella eufalensis [sic] Gabb. BOYLE, 1893, p. 101.

Boyle (1893, p. 101) lists Gabb (1860b, p. 394, pl. 68, fig. 26) as the author of the species, but this citation refers to *Corbula eufalensis* [sic] Gabb. The confusion may have resulted because Gabb cited *Corbula eufalensis* as *C. eufalensis* under the heading *Corbula*, but the facing page (Gabb, 1860b, p. 395) contains the *Crassatella* descriptions. Subsequent authors have included *Crassatella eufaulensis* [the modern spelling of Eufaula, Ala.] in faunal lists, but no description or illustration of *Crassatella eufalensis* [= *Crassatella eufaulensis*] exists in the literature. The name *Crassatella eufalensis* [= *Crassatella eufaulensis*] is not based on a specimen and is therefore unfounded.

The specific names presented below (p. 63–92) are herein considered valid species of Crassatellidae in the Upper Cretaceous and lower Tertiary strata of the Gulf Coast and Mid-Atlantic regions of the United States.

Crassatella vadosa **Morton, 1834**

Plate 1, figures 1–17; plate 5, figures 1, 3, 4, 6;
plate 7, figures 1–15; plate 8, figures 1–16;
plate 9, figures 1–13; plate 10, figures 1–17;
plate 11, figures 1–13; plate 12, figures 1–5;
plate 21, figures 6, 8

Crassatella vadosa MORTON, 1834, p. 66, pl. 13, fig. 12. GABB, 1877, p. 310–311. WHITFIELD, 1885, p. 116–117, pl. 17, figs. 12–15. HARBISON, 1945, p. 80, pl. 1, fig. 2.

Crassatella subplana CONRAD, 1853, p. 274, pl. 24, fig. 9. WHITFIELD, 1885, p. 121, pl. 18, figs. 14–16 [incorrectly cites Conrad, 1853, as p. 247].

Crassatella ripleyana CONRAD, 1858, p. 327, pl. 35, fig. 3.

Crassatella (Pachythaerus) ripleyana CONRAD, 1872, p. 50, pl. 1, fig. 7.

Crassatella lintea CONRAD, 1860, p. 279, pl. 46, fig. 5.

Crassatellites linteus (Conrad). JOHNSON, 1905, p. 14. GARDNER, 1916, p. 653, pl. 39, figs. 6, 7. WADE, 1926, p. 80. RICHARDS, 1958, p. 190, pl. 30, figs. 1, 2.

Crassatellites vadosus (Morton). JOHNSON, 1905, p. 14. GARDNER, 1916, p. 649, pl. 39, figs. 1–4. WADE, 1926, p. 79, pl. 25, figs. 6–8. SHIMER and SHROCK, 1944, p. 419, pl. 167, figs. 1–3. RICHARDS, 1958, p. 189, pl. 29, fig. 10.

Crassatellites subplanus JOHNSON, 1905, p. 14. WELLER, 1907, p. 553, pl. 61, figs. 1–4. GARDNER, 1916, p. 651 [quotes Conrad (1853, p. 274) and Weller (1907, p. 553–554)]. RICHARDS 1958, p. 187, pl. 29, figs. 9, 12, 13 [quotes Weller (1907, p. 553–554; figs. 12, 13 previously figured as Whitfield's (1885) pl. 18, figs. 14, 15].

Crassatellites ripleyanus JOHNSON, 1905, p. 14.

Crassatellites sp. STEPHENSON, 1923, p. 277, pl. 68, figs. 5–7.

Crassatellites carolinana STEPHENSON, 1927, p. 17, pl. 7, figs. 1, 1a, 2, pl. 8, figs. 1–3.

Crassatella vadosa ripleyana (Conrad). STEPHENSON, 1941, p. 177. STEPHENSON, 1955, p. 117, pl. 19, figs. 11–16.

Crassatella vadosa wadei STEPHENSON, 1941, p. 177.

Uddenia conradi (Whitfield). STEPHENSON, 1941, p. 180. RICHARDS, 1958, p. 191 [partim; description is copy of Whitfield (1885, p. 125); pl. 29, fig. 2 = *Crassatella* ? sp.]

Crassatella gardnerae HARBISON, 1945, p. 79, pl. 1, figs. 3, 4.

Uddenia fragilis HARBISON, 1945, p. 80, pl. 2, figs. 8, 9.

Crassatella (Landinia) vadosa Morton. CHAVAN, 1952, p. 119.

[?] *Gouldia conradi* WHITFIELD, 1885, p. 125, pl. 18, figs. 1–3.

[?] *Eriphyla conradi* (Whitfield). JOHNSON, 1905, p. 14. WELLER, 1907, p. 550, pl. 60, figs. 6–8 [partim; figs. 6–8 reproduction of Whitfield's (1885, pl. 18, figs. 1–3) types; non pl. 60, figs. 4, 5 = familial assignment unknown].

[non] *Crassatellites* (?) *conradi* (Whitfield). STEPHENSON, 1923, p. 274, pl. 67, figs. 10–16 [name preoccupied by *Crassatella conradi* Whitfield, 1885, p. 209, not = *Gouldia conradi* Whitfield, 1885, p. 125].

Diagnosis.—Ornamentation shifts gradually from sharp, fine regular comarginal lineations of juvenile to coarser more irregular comarginal lineations of adult. Subdued posterior ridge. Beak usually positioned at anterior one-third of shell length on adults. Resilifer restricted on right valve by broad triangular socket at edge of hinge plate, on left valve by flared posterior cardinal and by well-defined pit at base of cardinal. Height and length of valve nearly equal on early stages of juvenile.

Description.—Shell equivalve, inflation shallow to ventricose; maximum convexity one-third to one-half of height from beak; shell smoothly convex to slightly flattened across umbo when viewed from dorsal or ventral margin parallel to plane of commissure; exterior outline of adult varies from triangular to trigonally suboval to nearly subquadrate; nepionic outline quadrate, height and length nearly equal; juvenile gradually shifts from more quadrate to more trigonal form during ontogeny. Inequilateral; beak position of adults at anterior one-third of shell length, juveniles at anterior two-fifths; prosogyrous, beak strongly curved and pointed on juveniles, becoming less so on adults. Anterior dorsal margin straight to slightly concave; point of incurving varies from position just anterior to beak, to position opposite maximum width of lunule; slope of margin fairly steep; lunule well developed on left valve of adults with sharp ridge defining area, less well defined on right valve with no distinct ridge; anterior margin smoothly rounded. Posterior dorsal margin typically straight to slightly concave at end of escutcheon on adults, juveniles convex at point where escutcheon forming; slope of margin varies from nearly flat on juveniles to steep on adults with trigonal outline; escutcheon elongate, well defined on right valve with area defined by ridge, less well defined on left valve with ridge absent; shape of posterior margin delineated by presence of subdued posterior ridge; posterior area arcuately truncate. Ventral margin smoothly rounded anteriorly, varies posteriorly from slightly convex to flattened to slightly concave below adductor. Nepionic shell ornamented by distinct high comarginal ridges, comarginal threads may be visible in interspaces; approximately first third of adult shell has regular raised scaler or sharp comarginal ridges; spacing of comarginal threads remains constant throughout ontogeny and is continuous across interspaces and ridges; interspaces exhibit variation in topography; comarginal ridges gradually become more and more pronounced, rounded, and less regular over second third of adult shell, forming ribs; undulations may appear on final third of adult shell, comarginal threads and ribs intact; ribs and undulations rarely cross posterior ridge into posterior area; ornament of posterior area primarily ridges and comarginal threads; radial element underlies exterior shell surface and may be exposed when surface worn. Hinge angle variable, average 104.91 degrees on adults; juvenile hinge more obtuse, average 109.91; moving from posterior lateral ridges across hinge plate to anterior lateral ridges, dentition may be noted as follows:

Right Valve 0 1 0—R 0 1 0 –1 0 1

Left Valve 1 0 1—R(0) 1 0 1 0 (1)–0 1 0

Right valve dentition consists of one posterior lateral ridge, separated by edentulous space from resilifer (R); resilifer originates at beak on platform formed by rear wall of trigonal socket below and slightly anterior to resilifer; opening of resilial platform to umbonal cavity is obstructed by position of small trigonal socket; trigonal socket may have vertical grooves on rear wall; one large cardinal tooth with transverse grooves on sides lies anterior to beak; anterior socket may exhibit transverse grooves on anterior wall; two anterior lateral ridges present, separated by groove. Left valve dentition consists of two posterior lateral ridges, separated by groove; resilifer originates at beak; opening of resilial area to umbonal cavity is impeded by flared base of posterior cardinal and well-defined pit at base of posterior slope of cardinal; two well-defined cardinals with transverse grooves on sides separated by socket; forward of anterior-most cardinal is narrow groove followed by short ridge; one anterior lateral ridge present. Resilifer subcircular to suboval. Dentition of juveniles evident, resilifer may be discernible. Isomyarian adductor muscle scars; anterior immediately below ventral edge of anterior lateral ridge, on anterior margin, reniform, deep on adults; posterior immediately below ventral edge of posterior lateral ridge, on posterior margin, subcircular to suboval, may be less deep than anterior. Crescent-shaped anterior pedal retractor present underneath ventral end of anterior lateral and above anterior adductor; posterior pedal retractor occurs as notch in dorsal most corner of posterior adductor. Pallial line distinct, entire. Crenulations present from end of anterior lateral ridge ventrally to posterior lateral ridge on adults; development begins anteriorly so juveniles may display various stages of marginal crenulation. Prodissoconch subcircular and free of ornamentation.

Discussion.—*Crassatella vadosa* was first named and described by Morton (1834, p. 66) for a single specimen found by Conrad at the type locality of the Prairie Bluff Chalk (uppermost Maastrichtian) in Alabama. The preservation in the Prairie Bluff is either as molds or as calcite replaced shells; the type specimen (ANSP 19593; pl. 1, figs. 2, 3) is replaced by calcite, which preserves the fine details of ornament and internal characters. Morton acknowledged that this species was also found in New Jersey, thus establishing it as a wide-ranging form. Yet, over the next 150 years *C. vadosa* Morton, as herein defined, was assigned to six different species and two subspecies within the geographic and stratigraphic limits of this study. The authors of the junior synonyms of *C. vadosa* did not recognize the various stages in the ontogenetic sequence, nor did they recognize the degree of intraspecific variation of the species.

Crassatella subplana, a broad, flat subquadrate form, as the name implies (ANSP 18743; pl. 1, fig. 14; pl. 11, fig. 13), was described by Conrad (1853, p. 274) from imperfectly preserved material from Arneytown, N.J. Gabb (1861a, p. 169, list only) extended the range of *Crassatella subplana* to the Alabama Cretaceous "chalk formation." Whitfield (1885, p. 121) described and figured Conrad's specimens and cited the "elevated form" of the species as its distinguishing feature. Despite the overlap in ranges with *Crassatella vadosa*, no one attempted to directly compare the two species until Weller (1907, p. 554–555):

> These common casts of the Navesink marl were apparently identified as *C. vadosa* by Whitfield, at least in part, but after a study of the types of that species as well as numerous other examples from the South, it has not seemed possible to identify any of the New Jersey specimens with that species. *C. subplana* differs from *C. vadosa* in its much more depressed-convex valves, those of *C. vadosa* being quite ventricose, especially towards the umbo, although in their general outline and surface markings the two species are much alike.

Gardner (1916) expanded the range of *Crassatellites subplanus* [= *Crassatella subplana*] into Maryland. She (Gardner, 1916, p. 652–653) quoted Weller's (1907, p. 553–554) description of *Crassatellites subplanus* exactly, yet she reassigned all of his figures to either *Crassatellites vadosus* [= *Crassatella vadosa*] or *Crassatellites linteus* [= *Crassatella lintea*]; she disagreed with Weller's inclusion of *Crassatellites linteus* in the synonymy of *Crassatellites subplanus* but agreed with his distinction between *Crassatellites subplanus* and *Crassatellites vadosus.*

Crassatella ripleyana was diagnosed by Conrad (1858) from beds of the Owl Creek Formation[24] in Tippah County, Miss. The species, as Conrad described it, is "Triangular, very inequilateral, thick, . . .; umbonal slope angulated, subcarinated; . . ." (Conrad, 1858, p. 327) and also ventricose (ANSP 18741; pl. 1, figs. 1, 4, 9, 11, 16). In 1872, Conrad (1872, p. 50) included *C. ripleyana* in the subgenus *Pachythaerus*. For the next 68 years, authors of taxonomies disagreed with Conrad's contention that *C. ripleyana* was "very distinct from all others of this country" (Conrad, 1858, p. 327). Gabb (1877, p. 310) listed *C. ripleyana* as a junior synonym of *C. vadosa*; Whitfield (1885), Gardner (1916), and Wade (1926) concurred. Gardner (1916, p. 651) compared the typical representatives of *Crassatellites vadosus* and *C. ripleyana:*

> Conrad's *C. ripleyana* is doubtless a synonym [of *C. vadosa*], which includes the larger and heavier individuals. The young are quite uniform in outline and sculpture, but after the form has passed the typical *C. vadosus* stage there is a strong tendency for it to become produced posteriorly and to develop a rather heavy carina with the concomitant medial depression stage represented by the *C. ripleyana.*

The name *C. ripleyana* did not appear again until 1940, when it was included in faunal lists for the Owl Creek Formation (Stephenson and Monroe, 1940, p. 230, 247) as a subspecies of *C. vadosa*. Stephenson (1941, p. 176–177) discussed the "varietal forms" of *C. vadosa,* including *C. vadosa ripleyana,* and justified the division of the species into numerous subspecies by stating that "the fairly consistent differences" are "recognizable in collections from different horizons and localities" (Stephenson, 1941, p. 176).

Conrad (1860, p. 279) assigned the name *Crassatella lintea* to a moderately sized, flat subquadrate form with concentric ridges and fine striations (ANSP 19594; pl. 1, figs. 5–8, 10) from Eufaula Bluffs, Barbour County, Ala. In his discussion of *Crassatella lintea,* Conrad (1860) states "Accompanies *C. vadosa,* and nearly related to it, but numerous specimens of each compared showed a specific difference. It is thinner, less cuneiform posteriorly, and differs in the fine raised concentric lines. . . ." *Crassatellites linteus* [= *Crassatella lintea*] was identified as a juvenile of *C. vadosa* by Gabb (1877, p. 310–311) and Johnson (1905, p. 14); Whitfield remarks that *C. lintea* "appears to be the same species" as *C. vadosa* (Whitfield, 1885, p. 117). Weller (1907, p. 553), apparently noting the similarity in form, lists *Crassatella lintea* [= *Crassatellites linteus*] as a junior synonym of *C. subplana.* The species range was extended to Maryland in 1916 by Gardner (1916, p. 653–655). Gardner (1916, p. 654) expressed her disagreement with Johnson's and Weller's synonymies:

> *C. linteus* Conrad has been considered, without justification, as the young of some of the clearly allied and larger forms, such as *C. vadosus* and *C. subplanus.* Aside from the fact that it shows no evidence of immaturity, the shell is thinner and more compressed and much less strongly carinated posteriorly than *C. vadosus* of the same size. The resemblance to *C. subplanus* is more striking, but the concentric sculpture is finer and more sharply impressed in the former, and as a rule, the umbones are set farther forward and are more strongly prosogyrate.

She concluded by stating that *Crassatella vadosa* and *C. lintea* have a similar distribution in Maryland but that *C. lintea* is not as abundant. Wade (1926, p. 80–81) repeats Gardner's synonymy and description and extends the distribution of *Crassatella lintea* into Tennessee, where it also occurs with *C. vadosa.* The problems of identifying juvenile members of species within the Crassatellidae was addressed by Stewart (1930, p. 138). He discussed the slow development of the characters of the ligamental cavity and concluded that these characters fail as diagnostic features in very young Crassatellidae. *Crassatella lintea* is cited as an example of an immature specimen that has been improperly assigned due to the poor development of hinge characters (Stewart, 1930, p. 138). Shimer and Shrock (1944, p. 419) indicate *Crassatella lintea* is "probably" the juvenile of *C. vadosa,* but Richards (1958, p. 190) maintained *Crassatella lintea* as a separate species and expanded the range to New Jersey.

Gouldia conradi Whitfield (1885, p. 125) is a juvenile specimen of *Crassatella* that has alternately been placed in *Gouldia* (Astartidae), *Eriphyla* (Astartidae), and *Uddenia*[25] (Crassatellidae). Although the type specimens are imperfectly preserved (ANSP 18735; pl. 22, figs. 1–4), a comparison of Whitfield's shells with juvenile *Crassatella vadosa* (pl. 12, figs. 1–4) and juvenile *Crassatella hodgei* (pl. 5, fig. 9) reveals affinities to both species. However, the type *Gouldia conradi* more

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[24] See Sohl (1960, p. 5–6) for a discussion of the stratigraphic position of Conrad's collections.

[25] The problems of *Uddenia* are discussed in the section "Distribution and validity of species" on pages 57–58.

closely resembles *Crassatella vadosa*; therefore, they have been questionably synonymized. The other specimens assigned to *Gouldia conradi* cannot be synonymized with any crassatellid species due to their poor preservational state. Stephenson's (1923, p. 274) specimens, which he initially identified as *Crassatellites* ? *conradi* (Whitfield),[26] came from Snow Hill, N.C., in lower Campanian units. This locality is below the known stratigraphic range for *Crassatella vadosa* but falls within the range of *Crassatella carolinensis* Conrad and *Crasatella hodgei* (Stephenson) (fig. 19). Only two (USNM 31932; pl. 22, figs. 5, 6; USNM 31902, broken) of the six specimens that Stephenson (1941, pl. 67, figs. 10–16) figured are still present in the collections of the USNM; the rest have been lost or destroyed. Even these two specimens are so damaged that it is impossible to make a specific assignment. *Uddenia fragilis* Harbison (1945, p. 80) (ANSP 16216) is a juvenile *Crassatella vadosa*.

Internal molds of *Crassatellites carolinana* were originally described by Stephenson (1923, p. 277, pl. 68, figs. 5–7) as *Crassatellites* sp.; when additional specimens preserving characters of the exterior were located, Stephenson (1927, p. 17) named the specimens. *Crassatellites carolinana* has a large flattened subquadrate form with a broad hinge angle (USNM 73438, 73439; pl. 1, figs. 15, 17; pl. 10, fig. 16; pl. 11, figs. 11, 12). Stephenson recognized the similarities between *Crassatellites subplanus* and *Crassatellites carolinana* (compare pl. 1, fig. 14 to fig. 15), but stated that *Crassatellites subplanus* was "relatively shorter" (Stephenson, 1927, p. 18). He believed *Crassatellites vadosus* differed from *Crassatellites carolinana* by being "more convex and more sharply pointed posteriorly" and by having "a more sharply defined umbonal [posterior] ridge" and in the detailed characters of the hinge (Stephenson, 1927, p. 18–19).

Stephenson (1941, p. 177) separated the specimens originally identified by Wade (1926, p. 79) as *Crassatellites vadosus* from Coon Creek, McNairy County, Tenn., into the new subspecies *C. vadosus wadei*. The subspecies is distinguished from the typical form of the species in being "higher and flatter" and having "the beak more distantly removed from the anterior extremity" (Stephenson, 1941, p. 177) (USNM 32784; see pl. 9, figs. 7, 8, 11 for topotype examples).

The last name to be introduced for the group of specimens herein identified as junior synonyms of *Crassatella vadosa* was *C. gardnerae* (holotype, ANSP 16200; paratype, USNM 103753, see pl. 1, figs. 12, 13), named by Harbison (1945, p. 79) from deposits at Pleasant Ridge Lake, Union County, Miss. She distinguished this species from typical forms of *C. vadosa* on the basis of "a more prominent umbo; the umbonal [posterior] ridge is heavier, and especially the shell is more elongated" (Harbison, 1945, p. 80). *C. gardnerae* varies from the "Owl Creek form," presumably *C. vadosa ripleyana* (Harbison does not specify) in having more shallow muscle scars, a less triangular cardinal, and a longer, flatter valve, and less "prominent umbo" (Harbison, 1945, p. 80). In addition, she lists the occurrence of *C. vadosa* at Pleasant Ridge Lake in Union County, Miss., in the text (Harbison, 1945, p. 80) but does not include *C. vadosa* in the table entitled "Distribution and range of species found at Pleasant Ridge Lake, Mississippi" (Harbison, 1945, table I, p. 90). The specimen illustrated as *C. vadosa* (Harbison, 1945, pl. 1, fig. 2) is from the type locality of the Owl Creek Formation, Tippah County, Miss., as noted by Stephenson (1955, p. 117).

The species names *Crassatella subplana*, *C. ripleyana*, *C. lintea*, *C. gardnerae*, and *Crassatellites carolinana* and the subspecies names *Crassatella vadosa ripleyana* and *C. vadosa wadei* are junior synonyms of *Crassatella vadosa* Morton. The statistical analysis supports this conclusion; although the data for *Crassatella subplana* and *Crassatellites carolinana* are inconclusive, the results were not incompatible with synonymy. In the course of this study, I measured 520 individuals within this group and visually and microscopically examined hundreds more. Characters such as convexity, general outline, shape of the posterior margin, accentuation of the posterior ridge, and height and length, used by the original authors to justify separation into species and subspecies, do not persist as diagnostic characters when entire suites of specimens are examined. The range of variation of the species covers the complete spectrum encompassed by all the junior synonyms of *Crassatella vadosa*; it is impossible to maintain the individual species concepts represented by the junior synonyms. These separate species concepts can be united under *Crassatella vadosa* by the characters of the juveniles, the pattern and sequence of ornamentation, and the detailed characters of the hinge. Although some of the authors discussed herein claim to distinguish differences in even these features, I find the characters to be consistent within their normal range of variation and diagnostic on all well-preserved individuals.

Two morphotypes exist among the adult *Crassatella vadosa*. One is represented by the original concepts of *Crassatella subplana*, *C. vadosa wadei*, and *Crassatellites carolinana*. These individuals retain the juvenile characters of a subquadrate outline, broad hinge angle, reduced convexity, and subdued posterior ridge into adulthood (pl. 1, figs. 14, 15; pl. 7, figs. 1–15; pl. 8, fig. 15; pl. 9, fig. 8; pl. 10, figs. 14, 16). The other morphotype is

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[26] This assignment is in error because the name was already occupied by *Crassatella conradi* Whitfield (1885, p. 209). Stephenson was not synonymizing *Gouldia conradi* Whitfield (1885, p. 125) with *Crassatella conradi* Whitfield.

TABLE 38.—*Minimum, maximum, and mean values for characters of* Crassatella vadosa

[See table 2 for an explanation of the morphological variables. Data source: digitized data set; excludes broken specimens and internal molds]

Morphological variable	Adults (382 specimens)			Juveniles (31 specimens)			Combined (413 specimens)
	Minimum	Maximum	Mean	Minimum	Maximum	Mean	Mean
CONVEX	6.45	18.82	12.33	1.04	7.73	4.37	11.73
LENGTH	23.20	67.45	41.18	4.84	29.73	19.34	39.55
HINGE	78.35	125.13	105.08	100.09	125.65	110.16	105.46
POST	99.23	174.09	130.84	112.84	162.74	130.16	130.79
ANTER	129.10	168.66	145.97	127.76	168.77	144.09	145.83
ANTVERHT	13.31	36.96	21.29	2.18	17.72	10.65	20.49
POSVERHT	12.09	34.34	20.72	2.75	16.98	11.01	19.99

illustrated by the type concepts of *Crassatella vadosa* and *C. ripleyana*. A triangular outline, reduced hinge angle, inflated valve, and sharp posterior ridge defining a steeply sloped posterior area are characteristic of this second group of *Crassatella vadosa* (pl. 1, figs. 1–4, 16; pl. 8, figs. 11, 14; pl. 9, fig. 3; pl. 11, figs. 3, 4, 6). I do not believe, however, that these two morphotypes can be isolated into discrete species, or even subspecies, because a full range of variation exists between the two types (for example, pl. 5, fig. 1; pl. 8, fig. 7; pl. 9, fig. 9). Furthermore, both morphotypes can be found distributed throughout the range of *Crassatella vadosa*. The triangulate form can be found in Mississippi (pl. 1, figs. 1, 4, 16), Alabama (pl. 1, fig. 3), Georgia (pl. 9, fig. 3), and Maryland (pl. 11, fig. 3). The quadrate flattened form is also found in Mississippi (p. 10, fig. 14), Alabama (pl. 11, fig. 10), and Maryland, in addition to Tennessee (pl. 7, fig. 15), New Jersey, (pl. 1, fig. 14; pl. 10, fig. 17), and North Carolina (pl. 11, figs. 11, 12). Elongate shells (represented by the type concept of *Crassatella gardnerae*) are intermediate between the other two forms and occur with them in deposits in Tennessee, Mississippi, Alabama, and Georgia (pl. 8, figs. 4, 7; pl. 9, figs. 6, 12, 13; pl. 10, fig. 11; pl. 11, fig. 7). A large degree of variation can be seen even within a single population (pl. 8, figs. 6, 12, 15; pl. 9, figs. 7, 8, 10; pl. 11, fig. 7). At one point, I considered that these morphotypes illustrate sexual dimorphism, but their distribution, and the presence of intermediate forms, does not support this hypothesis. The variation seen within *Crassatella vadosa* is probably a reflection of environmental pressures on the individuals during growth.

Crassatella vadosa is a morphologically variable species that encompasses the two subgroups discussed above and the intermediate forms. The average values for the genus are presented in table 38. The most obvious variation is seen in the shape of the posterior margin and the resulting effects on the overall outline of the individual. The contribution of the posterior margin to the intraspecific variation was demonstrated during the statistical analysis of the described subspecies categories of *Crassatella vadosa*; height of the posterior region was the most significant discriminating variable (table 6). The extremes of variation in posterior elongation can be seen by comparing plate 9, figure 13, a trigonally suboval posteriorly elongate form in which length is much greater than height, to plate 8, figure 15, a subquadrate specimen in which height and length are more nearly equal. Intermediate to these forms is the typical form of *C. vadosa* (pl. 8, fig. 3), a triangular shell having a pointed posterior margin. The characters of the hinge angle and the slope of the posterior dorsal margin are linked to the shape of the posterior margin; posteriorly elongate and subquadrate forms (pl. 9, figs. 5, 12) have broad hinge angles and gently sloping posterior dorsal margins; triangular forms (pl. 11, figs. 2, 6) have narrower hinge angles and more steeply sloping posterior dorsal margins. Convexity of the adults of the species can vary from gently curved (pl. 8, figs. 6, 8, 12, 13) to ventricose (pl. 11, figs. 4, 5). Individuals with ventricose valves have well-defined posterior ridges and steeply inclined posterior areas (pl. 11, fig. 4), whereas specimens with reduced convexity tend to have subdued posterior ridges and flattened posterior areas (pl. 11, fig. 10). The position of the beak is fairly constant for the adults of the species at the anterior one-third of shell length (pl. 8, figs. 4, 9, 14), but a few adults retain the juvenile position at the anterior two-fifths of shell length (pl. 8, fig. 15; pl. 9, fig. 8). The posterior portion of the ventral margin varies from convex (pl. 9, fig. 8) to flat (pl. 9, fig. 7) to concave (pl. 9, fig. 13). The sequence of development of the ornamentation is consistent for the species, although some individuals may never develop the undulations seen on the lower third of other shells (compare pl. 8, fig. 9 to fig. 11). Interspaces between ridges may exhibit some variation in topography; a flat interspace having only the comarginal growth threads may be present, or small raised areas in between the dominant ridges may be seen. Some ridges are sharp and pointed (pl. 10, fig. 4), others scaled (pl. 10, figs. 9, 12; pl. 12, fig. 3), and still others slightly rounded (pl. 8, fig. 3), but these differences can be attributed to wear on the shell surface.

The ontogeny of *Crassatella vadosa* shows consistency in the sequence of events but variation in the size at which the adult characters are fully developed (compare pl. 10, fig. 5 to fig. 6). The prodissoconch of *C. vadosa* is rarely preserved, but when visible it is clearly distinguished from the nepionic portion of the shell (pl. 12, fig. 5). The nepionic portion of the shell is quadratic, with height and length being nearly equal (pl. 7, fig. 4; pl. 8, fig. 10); this shape results in a very broad hinge angle (pl. 7, fig. 8; pl. 10, figs. 6, 8). The juvenile portion of the shell is more strongly prosogyrous than the adult; the concave anterior dorsal margin at the point where the lunule is developing contributes to the prosogyrous appearance. At this stage, the primary pattern of ornamentation is already visible, with comarginal threads occurring in interspaces between the more pronounced comarginal ridges (pl. 12, figs. 1, 3). The posterior ridge is discernible, both internally and externally, but is subdued. The hinge platform displays the most obvious juvenile characters; here, the resilifer is not developed, and the resilial platform not yet defined; the cardinals and their corresponding sockets are small and narrow; only the lateral ridges are as well defined as they are on adult individuals (compare pl. 7, fig. 2 to fig. 14). The adductor muscle scars are shallow, as is the pedal retractor. An examination of plate 7, figures 1 to 15 illustrates a growth series for *C. vadosa.* As the shell matures, the shape gradually shifts from quadrate to more mature subquadrate to subtrigonal, along with concomitant changes in hinge angle, slope of the posterior dorsal margin, and development of the posterior ridge. The ornamentation gradually shifts from the very fine, well-defined ridges on the juvenile portion (which give *C. lintea* its name) to the more rounded ribs on the adult (compare ornament of umbo to ventral portion of shell on pl. 7, figs. 5, 7 and pl. 8, figs. 10, 14, 16); eventually, as the shell approaches old age, undulations may appear on the lower third of the shell causing the ventral margin to curve inward (pl. 11, fig. 4). Internally, the hinge characters gradually mature, as the resilifer becomes well defined and as the resilial platform becomes isolated from the edge of the hinge plate (compare pl. 7, fig. 2 to fig. 14). The muscle scars become more distinctive as the shell material thickens.

The shift from the more juvenile characters to the more adult characters most commonly occurs at one-third the size of the adult, but tremendous variation in size can be seen at the phase where the shift occurs. Some individuals acquire fully adult characters at a very small size and presumably young stage (pl. 8, figs. 1, 2; pl. 10, figs. 1, 5), whereas others retain the juvenile characters at a relatively large size and presumably older stage (pl. 10, figs. 13, 14). I believe some ecologic or environmental constraints are acting on the individuals that retain the juvenile characters at later stages; this subgroup is represented by the original concepts of *Crassatella vadosa wadei*, *C. subplana*, and *Crassatellites carolinana.*

Comparisons of *Crassatella vadosa* with the other members of the genus are made under the discussions of each of those species.

Occurrence.—See table 39 for *C. vadosa* localities, stratigraphic units, and collections studied. Refer to figure 2 and appendix 9 for locality positions and descriptions.

Stratigraphic range.—Lower(?) Campanian; upper Campanian through upper Maastrichtian (fig. 19).

Type material examined.—ANSP 19593; holotype *Crassatella vadosa* Morton. ANSP 19594; holotype *Crassatella lintea* Conrad. ANSP 18741; syntypes *Crassatella ripleyana* Conrad. ANSP 18743; syntypes *Crassatella subplana* Conrad. ANSP 18735; holotype *Gouldia conradi* Whitfield. USNM 73438; holotype *Crassatellites carolinana* Stephenson. USNM 73439; paratype *Crassatellites carolinana* Stephenson. USNM 103753; paratype *Crassatella gardnerae* Harbison.

***Crassatella tumidula* Whitfield, 1865**

Plate 15, figures 1–17; plate 16, figures 4, 6.

Crassatella tumidula WHITFIELD, 1865, p. 267, pl. 27, fig. 16. DE GREGORIO, 1890, p. 198–199, pl. 26, fig. 11. HARRIS, 1897, p. 56, pl. 11, figs. 3, 4. PALMER and BRANN, 1965, p. 105 [partim]. TOULMIN, 1977, p. 186, pl. 13, figs. 7–9.

Crassatellites tumidulus GARDNER, 1945, p. 91, pl. 6, figs. 4, 6 [discussed under *C. antestriatus*; figure reproduction of holotype].

[?] *Crassatella alta* Conrad. TUOMEY, 1858, p. 271 [list only].

[?] *Crassatella tumidula* Whitfield. ALDRICH, 1894, p. 242 [list only; assigned to *C. gabbi* Safford by Palmer and Brann (1965)].

Diagnosis.—Valves ovate trigonal in outline; unevenly convex, anterior ventricose, posterior attenuated; valve flat to slightly concave anterior to posterior ridge; posterior area narrow; posterior margin pointed; lunule well developed on both valves; escutcheon poorly developed on both valves. Ornamentation begins at beak as strong comarginal ridges, fading rapidly in ventral direction; comarginal growth threads continuous over entire surface. Elongate narrow resilifer descends half way across resilial platform; resilial platform open to umbonal cavity; anterior lateral ridges short.

Description.—Shell equivalve; inflation ventricose anteriorly, attenuated posteriorly; shell smoothly convex over anterior two-thirds, flattening or becoming slightly concave on posterior third as viewed from dorsal or ventral margin parallel to plane of commissure; adults ovate trigonal in outline, height nearly equals length; nepionic outline subcircular, posteriorly truncate; juveniles rapidly assume ovate trigonal outline; height-to-length ratio increases during ontogeny. Inequilateral, to

TABLE 39.—Crassatella vadosa—*Occurrence and collections studied*

[Fm, Formation. Collection number: USNM (U.S. National Museum) collection or specimen numbers, unless otherwise noted; ANSP, Academy of Natural Sciences of Philadelphia]

Locality number	State	County	Stratigraphic unit	Collection number
27....	Tennessee	McNairy	Coon Creek Fm	32784, 450436–450442, 450449–450451, 450455–450457, 450465, 450475, 450481, 451056, 451057, 451062, 451096, 453896.
28....	Mississippi	Union	Ripley Fm, Coon Creek Tongue	103753, 103754, 450447, 450448, 450460, 451060, 451061, 451067, 453873.
29....	....do........	....do........	....do........	453881.
30A..	....do........	Tippah	....do........	450453, 450454, 450478, 451063.
30B..	....do........	....do........	....do........	20820.
31....	....do........	Union	....do........	451058, 451064, 451065, 453870.
32....	....do........	....do........	....do........	450461, 450462, 451066.
34B..	....do........	....do........	Ripley Fm	453872.
35....	....do........	....do........	....do........	453868.
36A..	Alabama	Barbour	....do........	21125.
36B..	....do........	....do........	....do........	503, 505, 12670, 453878, 453882, 453886. ANSP: CONRAD (unnumbered collection), 19594.
37....	Georgia	Quitman	....do........	451081.
38A..	....do........	....do........	....do........	451093.
38B..	....do........	....do........	....do........	451079.
40....	Alabama	Barbour	....do........	450417, 450464, 450477, 450551.
41....	....do........	....do........	....do........	451103.
42....	Georgia	Quitman	....do........	451077.
43....	Alabama	Barbour	....do........	450459, 450466–450469, 451086, 451088, 451089, 451092.
44....	Georgia	Quitman	....do........	450807, 451084, 451090, 453876, 453885.
45....	....do........	....do........	....do........	450452, 450458, 451091.
47....	New Jersey	Burlington	Mount Laurel Sand and (or) Navesink Fm	ANSP 18743.
48....	....do........	Monmouth	....do........	450472, 453890, 453891.
49....	Mississippi	Tippah	Owl Creek Fm	20804.
51....	....do........	....do........	....do........	451068.
52....	....do........	....do........	....do........	20608, 128139, 450418, 450443–450446, 450474, 450509, 450510, 450851, 451052, 451054, 451069, 453867. ANSP 18741.
53....	Tennessee	Hardeman	....do........	453875.
54....	Mississippi	Kemper	Prairie Bluff Chalk	459095.
56....	Alabama	Wilcox	....do........	450471, 450500, 450853. ANSP 19593.
57....	....do........	....do........	....do........	450502.
58....	....do........	....do........	....do........	450820.
59A..	....do........	....do........	....do........	451071, 451080.
59B..	....do........	Lowndes	....do........	453887.
63....	Georgia	Clay	Providence Sand	451075.
64....	....do........	....do........	....do........	450554.
69A..	North Carolina	Pender	Peedee Fm	73438, 73439, 453871.
69B..	....do........	New Hanover	....do........	450511.
69C..	South Carolina	Georgetown	....do........	453892.
70....	Maryland	Prince George's	Severn Fm	450463, 450473, 451099, 451100.
71....	....do........	....do........	....do........	451095.
72....	....do........	....do........	....do........	450476, 451055.
73A..	....do........	....do........	....do........	131763, 131764, 131766, 450416, 450470, 450479, 450480, 450520, 451098, 453893.
73B..	....do........	....do........	....do........	453874.
75....	....do........	....do........	....do........	32291.
Questionable *C. vadosa* collections				
14....	New Jersey	Camden	Woodbury Clay	ANSP 18735.
63....	Georgia	Clay	Providence Sand	450816.
74....	Maryland	Anne Arundel	Severn Fm	451104.

nearly equilateral; beak position varies from anterior one-third length on juveniles to just anterior of one-half length on large adults; prosogyrous, beak strongly curved and pointed on juveniles, becomes less so on adults. Anterior dorsal margin generally straight, with slight indentation at maximum width of lunule; slope of margin steep; lunule broad, well developed on both valves of adults with sharp ridge defining area; anterior margin smoothly rounded. Posterior dorsal margin straight to slightly concave; slope of margin varies from moderate on juveniles to steep on adults; escutcheon narrow, poorly developed on both valves; posterior ridge subdued, preceded anteriorly by shallow depression or flattened area; posterior area very narrow on adults, broader on early stages of juvenile; posterior margin pointed. Ventral margin smoothly rounded anteriorly, ascending posteriorly to intersect dorsal margin. Ornamentation of nepionic portion of shell and of early juvenile stages distinct high comarginal ridges, descending into V-shaped interspaces, covered with comarginal growth threads; only first few comarginal ridges are continuous across shell surface from anterior to posterior, remainder fade anterior to posterior ridge; comarginal ridges rapidly disappear in ventral direction as well; remainder of shell surface covered with comarginal growth threads, and occasional undulations in shell surface. Hinge angle averages 102 degrees on adults, 118 degrees on juveniles; moving from posterior lateral ridges across hinge plate to anterior lateral ridges, dentition noted as follows:

Right Valve 0 1 0—R 0 1 0 –1 0 1
Left Valve 1 0 1—R(0) 1 0 1 0 (1)–0 1 0

Right valve dentition consists of one posterior lateral ridge, separated by edentulous space from resilifer (R); resilifer originates at beak and descends about half way across resilial platform; resilial platform open to umbonal cavity; narrow elongate trigonal socket lies anterior to resilial platform and just below beak; one large cardinal tooth, with transverse grooves on sides, lies anterior to beak; two short anterior lateral ridges present, separated by groove. Left valve dentition consists of two posterior lateral ridges, separated by groove; resilifer originates at beak and descends about half way down resilial area, leaving broad flat edentulous space below; resilial area open to umbonal cavity; small pit at base of posterior slope of cardinal; two well-defined cardinals with transverse grooves on sides separated by socket; forward of anterior-most cardinal is narrow groove followed by short ridge; one short anterior lateral ridge present. Resilifer elongate, narrow. Dentition defined at early stages of juvenile, resilifer may be discernible. Isomyarian adductor muscle scars, shallow on juveniles, deeper on adults; anterior reniform, posterior subcircular. Crescent shaped anterior pedal retractor present below anterior lateral ridge and hinge platform. Pallial line distinct, entire. Crenulations present from end of anterior lateral ridge ventrally to posterior lateral ridge on well-preserved adults; development begins anteriorly so juveniles may display various stages of marginal crenulation. Prodissoconch not seen.

Discussion.—Whitfield (1865, p. 267) first named and described *Crassatella tumidula* from a locality "six miles above, Claiborne, Ala., west side of the [Alabama] river." Harris (1897, p. 56) repeated Whitfield's original description and stated that the type locality was "doubtless Greggs Landing." In addition, Harris found the species at two other localities on the Alabama River: Bell's Landing and Yellow Bluff. For the next 80 years, *C. tumidula* appeared in faunal lists and discussions of the genus, but no other authors contributed to the understanding of the species. Palmer and Brann (1965, p. 101) synonymized *C. tumidula* Whitfield, Aldrich (1894, p. 242) with *C. gabbi* Safford. Since Aldrich's publication is only a list, there is no way to determine which species he was examining, but *C. tumidula* are known from the locality he cited ("the vicinity of Prairie Creek and Mr. McConnico's plantation," Aldrich, 1894, p. 242); therefore, it is reasonable to assume that Aldrich was correct. Based on locality, Palmer and Brann (1965, p. 105) synonymized *C. alta* Conrad, Tuomey (1858, p. 271) with *C. tumidula*. Again, this is only a list, so there is no way to determine what species Tuomey actually had, but *C. tumidula* is known to occur at Bell's Landing, whereas *C. alta* has never been reported from that locality since 1858. The possibility exists that Tuomey's specimen was a *Crassatella tumidula*. Toulmin (1977, p. 186) found the species at seven additional localities, all confined to the outcropping Tertiary sediments of southern Alabama. It appears that *C. tumidula* may have a fairly limited geographical distribution since examinations of museum, survey, and field collections have not revealed any localities outside Alabama.

The low degree of intraspecific variation displayed by *Crassatella tumidula*, when evaluated qualitatively, may be attributable in part to the limited extent of the species' geographic range. The consistency of characters seen is contrary to the results of the statistical analysis, which illustrate a high degree of intraspecific variation and a wide scatter on the plots. This statistical scatter can be explained in part by the ontogenetic changes as discussed below. Particularly unusual for this genus is the consistency of the exterior outline; although ontogenetic changes occur, adults at similar stages in their life history, generally look the same (compare pl. 15, fig. 14 to fig. 12 and to fig. 15). As with other species of *Crassatella*, the largest degree of variation in *C. tumidula* is seen in the degree of posterior elongation (compare

TABLE 40.—*Minimum, maximum, and mean values for characters of* Crassatella tumidula

[See table 2 for an explanation of the morphological variables. Data source: digitized data set; excludes broken specimens and internal molds]

Morphological variable	Adults (17 specimens)			Juveniles (15 specimens)			Combined (32 specimens)
	Minimum	Maximum	Mean	Minimum	Maximum	Mean	Mean
CONVEX	5.52	18.65	12.12	2.11	7.27	4.30	8.46
LENGTH	18.92	66.53	40.08	8.61	19.11	14.62	28.15
HINGE	82.02	121.22	103.34	110.34	126.40	116.86	109.68
POST	91.33	163.32	126.84	91.32	147.15	114.54	121.08
ANTER	126.84	156.90	139.73	116.61	163.89	134.16	137.12
ANTVERHT	9.87	40.66	23.36	4.03	10.50	7.32	15.84
POSVERHT	7.93	29.74	18.14	3.94	8.53	6.48	12.68

pl. 15, fig. 6 to fig. 7). The area anterior to the posterior ridge varies from deeply compressed to flattened (compare pl. 15, fig. 12 to fig. 15). Many of the differences seen between individuals can be ascribed to wear. For example, the presence or absence of crenulations is one of the primary criteria cited by the original authors for distinguishing *C. tumidula* from other species of Tertiary *Crassatella*, but a little abrasion can remove this diagnostic character (examine the intact anterior ventral portion versus the worn posterior portion of the specimen illustrated on pl. 15, fig. 17). Ornamentation may also be affected by erosion; the comarginal ridges usually seen across the umbo (pl. 15, figs. 3, 5, 6, 9) may be reduced, or the usually relatively smooth lower portions of the valve may appear to be more strongly ribbed and (or) have radial sculpture when the outer layer of shell material is removed (pl. 15, fig. 16). The summary of statistical measures for the species is found in table 40.

The nepionic stage of *Crassatella tumidula* begins as a subcircular form with prominent comarginal ridges (pl. 16, figs. 4, 6). Next, the juvenile passes through a suboval stage (pl. 15, figs. 9, 11); the posterior ridge is evident, and the depression anterior to the ridge may be formed, although the shell is still relatively flat; the posterior area at this phase is much broader than on the adults; the ornament is already past the stage of forming strong comarginal ridges, so only comarginal growth threads are present near the ventral margin (pl. 15, fig. 3) and the beak is strongly prosogyrous. The muscle scars and general character of the dentition are visible at these early stages, but the resilifer has not yet formed (pl. 15, figs. 2, 11). As *C. tumidula* matures, the shell becomes more inflated anteriorly, while the posterior remains flat, the posterior area becomes increasingly narrow, and the posterior margin more pointed (pl. 15, figs. 3, 6). The height-to-length ratio increases during ontogeny, causing the relative position of the beak to move closer to the midline of the shell and causing the hinge angle to become more acute. Faint crenulations begin to appear at about the same time the resilifer becomes discernable (pl. 15, fig. 7). An examination of plate 15, figures 1 to 17, reveals the various stages in the development of *C. tumidula.*

The species *Crassatella tumidula* has several unique features among the members of the genus herein considered. Unfortunately, these features are difficult to discern in previously published illustrations of the species and has led, I believe, to confusion of the species, primarily with the adult form of *C. halei* Harris [herein = *C. aquiana* Harris]. The ornamentation of *C. tumidula* and *C. halei* is similar (compare pl. 3, fig. 6 to pl. 15, fig. 1), and in addition the internal features of large adult *C. tumidula* are nearly identical to those of *C. halei* (compare pl. 3, fig. 9 to pl. 15, fig. 10). The similarity of internal features led to problems in the discrimination of these two species from the digitized specimens in the analysis portion of this study. No other species of Crassatellidae considered in this study exhibits the characteristic inflated anterior and attenuated posterior of *C. tumidula;* this feature, very obvious when viewed from the dorsal margin (pl. 15, figs. 5, 8), is difficult to detect on a conventionally illustrated specimen. In addition, the characters of the lunule and escutcheon are unique within the context of this study. All other members of the genus included here have a well-developed lunule on the left valve and a well-developed escutcheon on the right valve; the lunule on the right valve and the escutcheon on the left valve are less well defined (see pl. 8, fig. 13 for one example). *C. tumidula*, however, have a well-developed lunule on both valves and a poorly developed escutcheon on both valves; the left valve escutcheon is less well developed than the right (pl. 15, figs. 5, 8). This lack of development of the escutcheon is probably due to (or the cause of) the morphological constraints of an attenuated posterior. Finally, the posterior area of the adult *C. tumidula* is narrower than other members of the genus. Identification of these external features of *C. tumidula* distinguishes this species from all other members of the genus.

Occurrence.—See table 41 for *C. tumidula* localities, stratigraphic units, and collections studied. Refer to figure 2 and appendix 9 for locality positions and descriptions.

TABLE 41.—Crassatella tumidula—*Occurrence and collections studied*

[Fm, Formation; Mbr, Member. Collection number, USNM (U.S. National Museum) collection or specimen numbers]

Locality number	State	County	Stratigraphic unit	Collection number
114	Alabama	Marengo	Nanafalia Fm	129898, 450516, 450553, 450555, 450556, 450560, 450846, 450861.
115A.......	....do........	Pike	....do........	450522, 450847.
115B.......	....do........	Dale	Nanafalia(?) Fm	450848.
116	....do........	Wilcox	Tuscahoma Fm	450813, 450842.
117	....do........	Monroe	Tuscahoma Fm, Bells Landing Mbr	90968, 137064, 155060, 450517–450519, 450521, 450558, 450561, 450817, 450843.
118	....do........	....do........	Tuscahoma Fm, Greggs Landing Mbr	450559, 450812, 450814.
119	....do........	Wilcox	Tuscahoma Fm	453918, 459096.
120	....do........	Monroe	Tuscahoma Fm, Bells Landing Mbr	453917.

Stratigraphic range.—Wilcox (fig. 19).

Type specimen.—CNHM UC–24476; holotype *Crassatella tumidula* Whitfield.

Crassatella carolinensis **Conrad, 1875**

Plate 2, figure 9; plate 5, figures 5, 8, 11, 13, 15–20.

Crassatella carolinensis CONRAD, 1875, p. 6, pl. 2, fig 24. GROOT, ORGANIST, and RICHARDS, 1954, p. 46 [list only].

Crassatellites carolinensis STEPHENSON, 1923, p. 269, pl. 66, figs. 16, 17. RICHARDS, 1958, p. 184, pl. 30, fig. 12.

Diagnosis.—Evenly spaced comarginal ridges cover entire shell surface; no line of demarcation from juvenile to adult ornamentation. Fairly unobstructed area between resilifer and edge of hinge platform; right valve reduced triangular socket below resilifer; left valve reduced pit at base of posterior slope of cardinal. Exterior evenly convex as viewed from any margin parallel to plane of commissure. Posterior ventral edge of juvenile slightly rounded.

Description.—Shell equivalve, inflation somewhat reduced for genus; evenly convex as viewed from any margin parallel to plane of commissure; varying from subquadrate juveniles to trigonally suboval adults in outline; inequilateral, posteriorly elongate, with beak lying at approximately anterior two-fifths; prosogyrous, beak most strongly curved on juvenile portion, less obvious at later stages. Anterior dorsal margin moderately sloping, slightly concave at maximum width of lunule; lunule well developed on left valve of adults with sharp ridge defining area, less well defined on right valve with no distinct ridge; anterior margin smoothly rounded. Posterior dorsal margin generally straight, with occasional indentation corresponding to middle of escutcheon; escutcheon well developed on right valve of adults with ridge defining area, less well defined on left valve with no distinct ridge; slope of posterior dorsal margin increases with shell growth; posterior delineated by presence of posterior ridge, forming slightly curved truncate margin. Ventral margin smoothly curved anteriorly, flattening posteriorly below posterior adductor. Ornamentation consists of fairly evenly spaced, narrow, sharp, comarginal ridges covering entire shell surface, with faint comarginal threads occurring in interspaces; lower portion of adult shell may show undulations. Hinge angle variable, average 116 degrees; hinge platform normal for genus; moving from posterior lateral ridges across hinge plate to anterior lateral ridges, dentition noted as follows:

Right Valve 0 1 0—R 0 1 0 –1 0 1
Left Valve 1 0 1—R(0) 1 0 1 0 (1)–0 1 0

Right valve dentition consists of one posterior lateral ridge, separated by edentulous space from resilifer (R); resilifer originates at beak on platform formed by rear wall of small socket below and slightly anterior to resilifer; opening of resilial platform to umbonal cavity is partially obstructed by position of small socket; one large cardinal tooth lies anterior to beak; two anterior lateral ridges present, separated by groove. Left valve dentition consists of two posterior lateral ridges, separated by groove; resilifer originates at beak; opening of resilial area to umbonal cavity only slightly impeded by small depression at base of posterior slope of cardinal; two well-defined cardinals separated by socket; forward of anterior-most cardinal is narrow groove followed by short ridge; one anterior lateral ridge present. Resilifer spoon shaped. Juveniles display only partially developed hinge characters; resilifer poorly defined. Isomyarian adductor scars; anterior reniform; posterior subcircular. Anterior pedal retractor present. Pallial line distinct, entire. Crenulations present from end of anterior lateral ridge ventrally to posterior lateral ridge on adults; development begins anteriorly so juveniles exhibit various stages of marginal crenulation. Prodissoconch not seen.

Discussion.—Conrad's (1875, appendix, p. 6) original description of *Crassatella carolinensis* was based on two specimens, one from New Jersey and one from Snow Hill, N.C. The small shell figured by Conrad (1875, pl. 2, fig. 24) is probably the New Jersey specimen (fide Stephenson, 1923, p. 269) and represents a juvenile of the species as herein defined. Stephenson (1914) included *Crassatellites carolinensis* (Conrad) in faunal lists from various localities in Mississippi, Alabama, and Georgia, including the type locality of the Blufftown Formation on the Chattahoochee River, but these specimens were never illustrated or described. Labels on Stephenson's study collections indicate that many of the specimens he initially believed were *C. carolinensis*, he later reassigned to other species of *Crassatella*. Subsequently, Stephenson (1923, p. 269) discussed and figured Conrad's North Carolina specimen (USNM 31929; pl. 2, fig. 9). Groot, Organist, and Richards (1954, p. 46) did not describe or illustrate *Crassatella carolinensis* but included it in a list of fossils found in the Merchantville Formation at the Chesapeake and Delaware Canal, Del. Richards (1958, p. 184) simply repeated Conrad's original description and figure. Consequently, until now only two specimens of *C. carolinensis* have ever been figured, and a suite of specimens has never been examined.

Crassatella carolinensis displays less intraspecific variation than most species of *Crassatella* examined, but only one population of *C. carolinensis* was found.[27] Homogeneity is common for this genus within a single population; no doubt, if populations from additional localities had been observed, more variation in characters could be reported. Nevertheless, the Blufftown specimens do exhibit some dissimilarities, primarily in attributes of shape. The inflation of the shell ranges from relatively flat to fairly convex for the genus (compare pl. 5, figs. 11, 13 to fig. 17). The range of overall shape variation can be seen by comparing plate 5, figure 13 to figure 17; plate 5, figure 13 represents a posteriorly elongate, suboval individual in which the height-to-length ratio is two to three; the height-to-length ratio of figure 17 is four to five, forming a trigonal outline. The posterior ventral margin may be flattened below the posterior adductor (pl. 5, fig. 16) or slightly sulcate (pl. 5, fig. 18). The hinge characters and other internal features are generally consistent.

The ontogenetic sequence of *Crassatella carolinensis* is notable for this genus in its lack of clearly delineated stages. Adult characters are expressed fairly early in the ontogeny of the species; before the specimens have reached 10 percent of their adult size, the subcircular outline (illustrated on pl. 2, fig. 9; pl. 5, fig. 8) has given way to the more suboval form. On these earliest stages, the comarginal ridges are present, but the comarginal threads are not yet visible, and the posterior dorsal margin slopes away from the beak at a very low angle. The adult ornamentation is present by the time the specimens reach 20 percent of their adult size; the slope of the posterior dorsal margin increases gradually as the shell matures. The hinge characters are distinguishable by the time the specimens attain 25 percent of their adult size and are well developed by the time they reach 50 percent of their adult size.

Crassatella carolinensis Conrad differs from all other species of *Crassatella* examined for this paper in the regularity and continuity of its ornamentation across various growth stages (pl. 5, figs. 8, 13, 15, 17–20). Although juvenile *C. vadosa* display regular growth lines, they differ from *C. carolinensis* in several key features. Unlike *C. carolinensis*, *C. vadosa* undergo changes in their patterns of ornamentation as they mature (compare pl. 8, figs. 10, 11, 16 to pl. 5, figs. 17, 18). Another character applicable to all but the very young specimens is the shape of the anterior dorsal margin; when *C. carolinensis* are reaching full maturity, *C. vadosa* are usually still in their juvenile stages; at this point *C. vadosa* have noticeably concave anterior dorsal margins, whereas *C. carolinensis* have fairly straight to only slightly concave anterior dorsal margins (compare pl. 7, fig. 5 to pl. 5, fig. 19). *C. vadosa* retains the subcircular shape of the prodissoconch during the early stages of growth, but *C. carolinensis* passes almost immediately into a suboval outline. Finally, the minute details of the ornamentation can be used to distinguish juvenile *C. vadosa* from *C. carolinensis*. The comarginal growth threads of *C. carolinensis* are barely visible at the earliest stages of development, but quickly become distinctive and remain so throughout the growth stages of the shell; only two orders of ornamentation can be seen, the comarginal ridges and the comarginal threads. In contrast, the comarginal growth threads of juvenile *C. vadosa* are more readily apparent in the early stages (pl. 7, figs. 4, 10) and become less distinctive later on; a third order of ornamentation, more prominent than the threads, but less prominent than the ridges, develops approximately half way through the juvenile stage in the interspaces between the ridges. Adult *C. vadosa* are easily distinguished from *C. carolinensis* by their ontogenetic changes in ornamentation. *C. hodgei* (Stephenson), which coexists with *C. carolinensis* in the Blufftown Formation along the Chattahoochee River, is the other species most likely to be confused with *C. carolinensis*; these species are contrasted in the discussion of *C. hodgei*.

Occurrence.—See table 42 for *C. carolinensis* localities, stratigraphic units, and collections studied. Refer

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[27] Minimum, maximum, and mean values were not calculated for *Crassatella carolinensis* characters because of the limited number of specimens available.

TABLE 42.—Crassatella carolinensis—*Occurrence and collections studied*

[Fm, Formation. Collection number, USNM (U.S. National Museum) collection or specimen numbers]

Locality number	State	County	Stratigraphic unit	Collection number
4	Georgia	Stewart	Blufftown Fm	450423–450430, 450805, 450815, 453880.
8	North Carolina	Greene	Tar Heel Fm	31929.

to figure 2 and appendix 9 for locality positions and descriptions.

Stratigraphic Range.—Lower Campanian (fig. 19).

Type material examined.—USNM 31929; hypotype *Crassatellites carolinensis* (Conrad) Stephenson.

***Crassatella aquiana* Clark, 1895**

Plate 3, figures 1–10; plate 14, figures 1–18; plate 16, figures 1–3, 5.

Crassatella aquiana CLARK, 1895, p. 5. CLARK, 1896, p. 82, pl. 26, figs. 2a–2c.

Crassatella sepulcollis HARRIS, 1896, p. 64, pl. 6, figs. 1, 1a. PALMER and BRANN, 1965, p. 104. TOULMIN, 1977, p. 148, pl. 2, figs. 3, 4.

Crassatella halei HARRIS, 1897, p. 57, pl. 11, fig. 5. SHIMER and SHROCK, 1944, p. 419, pl. 167, fig. 12 [reproduction of Harris' figure]. PALMER and BRANN, 1965, p. 101 [partim].

Crassatellites aquianus (Clark). CLARK and MARTIN, 1901, p. 181–182, pl. 42, figs. 1, 2a, 2b.

[non] *Crassatella mississippiensis* Conrad. TUOMEY, 1858, p. 269, 271 [included in Palmer and Brann's (1965, p. 101) synonymy of *C. halei*].

[non] *Crassatella* sp. ALDRICH, 1886, p. 57 [questionably included in Palmer and Brann's (1965, p. 101) synonymy of *C. halei*].

Diagnosis.—Valves trigonally subquadrate; beaks high; significantly and evenly convex, with slight flattening anterior to posterior ridge on large adults. Ornament begins at beak as sharp high comarginal ridges, fading rapidly posteriorly and ventrally to comarginal growth threads alone.

Description.—Shell equivalve; adults and juveniles significantly convex, with maximum width close to beaks at approximately one-quarter of shell height; generally evenly convex as viewed from any side, although adults may show slight flattening anterior to posterior ridge; adults trigonally subquadrate in outline; juveniles suboval to subquadrate. Inequilateral; beaks high, position ranges from anterior one-quarter length on juveniles to anterior two-fifths length on adults; prosogyrous, beak strongly curved and pointed on juveniles, becoming less so on adults. Anterior dorsal margin straight to slightly concave at maximum width of lunule; slope of margin steep; lunule broad, well developed on left valve with ridge defining area, less well defined on right valve; anterior margin smoothly rounded on adults, elliptical on juveniles. Posterior dorsal margin straight, steeply inclined; escutcheon narrow, well developed on right valve with sharp ridge defining area, less well defined on left valve; posterior ridge subdued, preceded anteriorly on adults by slightly flattened area; posterior area broad; posterior margin truncate. Ventral margin rounded anteriorly to below beak; posteriorly margin varies from rounded to slightly concave below posterior adductor. Ornamentation of nepionic and early juvenile stages of shell consists of sharp high comarginal ridges with deep V-shaped interspaces; only first few comarginal ridges are continuous across shell surface from anterior to posterior, remainder fade anterior to posterior ridge, then rapidly disappear in ventral direction as well; comarginal growth threads are continuous across entire shell surface; later stages of adult shells may show undulations on surface. Hinge angle averages 110 degrees for adults; 109 degrees for juveniles; moving from posterior lateral ridges across hinge plate to anterior lateral ridges, dentition noted as follows:

Right Valve 0 1 0—R 0 1 0 –1 0 1
Left Valve 1 0 1—R(0) 1 0 1 0 (1)–0 1 0

Right valve dentition consists of one long posterior lateral ridge, separated by edentulous space from resilifer (R); resilifer originates at beak on platform formed by rear wall of socket below and slightly anterior to resilifer; socket relatively large obtuse triangular shape on juveniles, small acute triangular shape on adults; opening of resilial platform to umbonal cavity is partially obstructed by position of small socket; one large cardinal tooth lies anterior to beak; two short anterior lateral ridges present, separated by groove. Left valve dentition consists of two long posterior lateral ridges, separated by groove; resilifer originates at beak; small depression present on basal side of posterior slope of cardinal; two well-defined cardinals separated by socket; forward of anterior-most cardinal is narrow groove followed by short ridge; one short anterior lateral ridge present. Resilifer elongate, triangular, extends to near edge of hinge platform on large adults. Dentition defined at early stages of juvenile, resilifer may be visible. Isomyarian adductor muscle scars, anterior reniform, posterior subcircular. Crescent-shaped anterior pedal retractor present above anterior adductor and below anterior lateral ridge, tangent to edge of hinge platform. Pallial line distinct on adults, entire. Crenulations present on mature individuals, from anterior lateral ridge ventrally to below posterior adductor; very faint crenulations may

TABLE 43.—*Minimum, maximum, and mean values for characters of* Crassatella aquiana

[See table 2 for an explanation of the morphological variables. Data source: digitized data set; excludes broken specimens and internal molds]

Morphological variable	Adults (72 specimens)			Juveniles (47 specimens)			Combined (119 specimens)
	Minimum	Maximum	Mean	Minimum	Maximum	Mean	Mean
CONVEX	4.70	20.04	6.87	2.49	7.50	4.12	5.78
LENGTH	16.31	73.90	22.28	8.70	22.02	12.98	18.60
HINGE	93.48	120.44	109.84	94.66	121.05	107.92	109.08
POST	99.03	152.06	123.34	105.33	150.12	126.44	124.56
ANTER	128.28	163.49	144.33	123.39	172.13	143.00	143.80
ANTVERHT	6.78	37.81	10.81	3.93	11.66	6.43	9.08
POSVERHT	7.16	32.78	11.09	4.66	10.83	6.89	9.43

be present on late stages of juveniles. Prodissoconch not seen.

Discussion.—Clark (1895, p. 5) named *Crassatella aquiana* from a single articulated specimen found in the Aquia Formation, at Aquia Creek, Va. The original description was brief and limited to the exterior features of the shell: "Shell moderately large, attenuated posteriorly; surface with a few broad, shallow, concentric lines, often obscure; lunules broad, deeply depressed" (Clark, 1895, p. 5). In comparing *C. aquiana* to *C. alaeformis* [= *Bathytormus alaeformis*], an abundant fossil in the Aquia Formation, Clark (1895, p. 5) also mentioned the high umbones of *C. aquiana*. Clark (1896, pl. 26, figs. 2a–2c) figured the holotype the following year (USNM 207155; pl. 3, figs. 3, 8, 10), and in 1901 Clark and Martin (1901, p. 182) listed additional localities of *Crassatellites aquianus* [= *Crassatella aquiana*] in the Piscataway Member of the Aquia Formation from the Potomac River region.

Crassatella sepulcollis was named and described by Harris (1896, p. 64) from deposits in Wilcox County, Ala. (holotype, PRI 64, see pl. 3, figs. 1, 2, 5; paratype, PRI 65, see pl. 3, figs. 4, 7). Harris (1896, p. 65) stated, "Its high, anteriorly located and curving beaks, its broad post-umbonal slope, its hinge characters, and size and general outline distinguish it from any other known form." In 1897, Harris (1897, p. 57) named and described *C. halei* from deposits at Greggs Landing on the Alabama River, Monroe County, Ala. (PRI 140; pl. 3, figs. 6, 9).

A comparison of the descriptions for *Crassatella halei* and *C. sepulcollis* reveals only two significant differences: (1) *C. halei* is described as having a "faint longitudinal medial depression" on the "post-umbonal slope" (Harris, 1897, p. 57) and (2) *C. halei* has an oblique cardinal tooth in the right valve (Harris, 1897, p. 57). These differences can be attributed to ontogenetic change; *C. halei*, therefore, is the adult form of *C. sepulcollis*. Although Clark's description of *C. aquiana* is meager, nothing in the description is incompatible with Harris' description of *C. sepulcollis*. Furthermore, a comparison of the type specimen of *C. aquiana* (pl. 3, figs. 3, 8, 10) and additional specimens in the collection of the USNM (pl. 14, figs. 3, 8, 10) to the type specimens of *C. sepulcollis* (pl. 3, figs. 1, 2, 4, 5, 7) reveals that *C. aquiana* and *C. sepulcollis* are synonyms. Although no internal features are preserved on the Mid-Atlantic forms, both *C. aquiana* and *C. sepulcollis* possess the diagnostic high beaks, trigonally subquadrate outlines, and strong ornament near the beaks that fades ventrally and posteriorly (pl. 3, figs. 2, 3, 5; pl. 14, figs. 2, 5, 9–11). *C. aquiana* is therefore accepted as the senior synonym. The species is rare and poorly preserved in the type area, but abundant and better preserved in the Gulf Coast region, where *C. sepulcollis* and *C. halei* were originally described. Consequently, the description and diagnosis herein included are based primarily on the Gulf Coast forms. *C. aquiana* is probably an element of a warm water fauna, which occasionally migrated northward along the Atlantic coast during the Paleocene.

The species has received little consideration in the literature since the early 1900's. Palmer and Brann (1965, p. 101) included two names, *Crassatella mississippiensis* Conrad, Tuomey, 1858 (non Conrad, 1848) and ? *C.* sp. Aldrich, 1886, in their synonymy of *C. halei*. Both of these names originally appeared in list form only, so there was no means by which Palmer and Brann could establish what species the original authors were examining. Based on the localities cited for these two names, they should more likely be synonymized with *C. tumidula*. Since *C. tumidula* and *C. aquiana* overlap in occurrence in the Gulf Coast region, however, there is no way to verify assignments made in list form without examining the specimens.

The largest degree of intraspecific variation within *Crassatella aquiana* occurs between the various growth stages. There is, however, a range in variation of shape and posterior elongation, affected by the differences in height-to-length ratio. An examination of plate 14, figures 4, 6, 11, and 15 shows this range of differences; as height increases relative to length, the individual has a steeper posterior dorsal slope and shortened posterior compared to individuals having lower height-to-length ratios (see table 43 for the average measurements for the species). The posterior margin can range from rounded (pl. 3, fig. 8) to squarely truncate (pl. 14, fig. 7). Variation can also be seen in the extent of the "faint depression" anterior to the posterior ridge; the more depressed this area is, the more concave the posterior ventral margin is (see pl. 14, figs. 12, 15, 18). Abrasion of some individuals may remove or reduce the characteristically high comarginal ridges near the beak, as seen on two of the type specimens (pl. 3, figs. 6, 7).

The nepionic stage of *Crassatella aquiana* begins as a subcircular valve having coarse, high, comarginal ridges covering the surface (pl. 16, fig. 5). The early juvenile stage maintains this distinctive ornament, but the external outline becomes quadrate and has a broad flat posterior margin delineated by a distinct posterior ridge (pl. 16, figs. 1, 2). In these early stages, the beak is strongly prosogyrous, and the valves show a high degree of convexity for such small individuals. Internally the dentition is already defined (pl. 16, fig. 2), and the resilifer usually is visible; the adductor muscle scars are distinct but shallow (pl. 14, fig. 1); the anterior pedal retractor may not be apparent. Gradually, as the shell matures, the height-to-length ratio increases, and the beak migrates closer to the midline of the shell, giving the external outline a more triangular appearance and causing a decrease in the hinge angle and an increase in the slope of the posterior dorsal margin. These external changes are reflected internally in changes in the character of the dentition. In the younger stages, the right valve cardinal is nearly vertical and fairly broad for the size of the hinge plate, and the triangular receptor pit below the resilifer covers half of the posterior area of the hinge plate (pl. 14, fig. 4). As the hinge angle becomes more acute, the right valve cardinal no longer increases in breadth but becomes obliquely angled anteriorly (as noted by Harris (1897, p. 57) in his description of *C. halei*, and the triangular receptor pit below the resilifer becomes increasingly narrow, opening up the resilifer platform to the umbonal cavity (pl. 3, fig. 9). Concomitant changes can be noted in the left valve, although they are not as obvious as in the right valve. The later stages of the juvenile shell and the adult shell are covered only with comarginal growth threads; in the late stages of a mature adult, undulations may appear on the surface of the shell. Faint crenulations do not appear until very late in the juvenile stage (usually when length equals 20–25 mm) and gradually become more pronounced with maturity (pl. 14, fig. 14).

Crassatella aquiana occur with *C. tumidula* at many outcrops in Alabama, but the evenly convex nature of the valves of *C. aquiana*, as opposed to the attenuated posterior of *C. tumidula*, should serve to distinguish these two species (compare pl. 14, fig. 13 to pl. 15, fig. 5). The lack of any ornamental pattern other than comarginal growth threads on the adult *C. aquiana*, will set this species apart from all Cretaceous members of the genus. The absence of any character for ornament in the statistical analysis explains the quantitative overlap of *C. aquiana* juveniles with *C. vadosa*. Finally, the extremely large adult specimens of *C. aquiana*, which have relatively open resilial platforms, may resemble large adult members of *Bathytormus*, particularly *B. alaeformis*, which is found in abundance at the type locality of *C. aquiana*. The lack of extreme posterior elongation and an examination of the juvenile portions of the shell should differentiate *C. aquiana* from *Bathytormus* (compare pl. 14, figs. 17, 18 to pl. 18, fig. 22 and pl. 19, fig. 11).

Occurrence.—See table 44 for *C. aquiana* localities, stratigraphic units, and collections studied. Refer to figure 2 and appendix 9 for locality positions and descriptions.

Stratigraphic Range.—Midway and Wilcox (fig. 19).

Type material examined.—USNM 207155; holotype *Crassatella aquiana* Clark. PRI 64; holotype *Crassatella sepulcollis* Harris. PRI 65; paratype *Crassatella sepulcollis* Harris. PRI 140; *Crassatella halei* Harris.

Crassatella hodgei (Stephenson), 1923

Plate 2, figures 7, 8, 10, 11; plate 4, figures 1–19;
plate 5, figures 2, 7, 9, 10, 12, 14; plate 6, figures 1–6.

Crassatellites hodgei STEPHENSON, 1923, p. 271, pl. 67, figs. 4–9. RICHARDS, 1958, p. 187, pl. 31, figs. 3–4 [incorrect citation of type locality and of type specimen as USNM 31847].

Crassatellites roodensis STEPHENSON, 1923, p. 273, pl. 68, figs. 1–4. STEPHENSON, 1926, p. 246, pl. 90, fig. 5.

Crassatella hodgei (Stephenson). RICHARDS, 1954, p. 2, text figs. 1, 2.

[?] *Crassatella pteropsis* ? CONRAD, 1875, appendix, p. 6, pl. 1, fig. 25.

[?] *Crassatellites pteropsis* (Conrad). RICHARDS, 1950, p. 74, figs. 61b, 61c.

Diagnosis.—Indentation of posterior ventral margin and (or) sharply pointed posterior margin when present; prominent posterior ridge when present. Sharp, high, widely spaced comarginal ridges on early portions of shell; sharp angulation of posterior ventral edge of juvenile; early expression of adult form during ontogeny, including posterior ridge, indentation of posterior ventral margin, and crenulations. Flattening of umbo region as viewed from dorsal or ventral margins parallel to plane of commissure.

Description.—Shell equivalve, inflation shallow to fairly convex; maximum convexity at midpoint of height; shell flattens across umbo region as viewed from ventral or dorsal margins parallel to plane of commissure; adults vary from trigonally suboval to obtusely trigonal in outline; nepionic outline subcircular; juveniles rapidly

TABLE 44.—Crassatella aquiana—*Occurrence and collections studied*

[Fm, Formation; Mbr, Member. Collection number: USNM, (U.S. National Museum) collection or specimen numbers, unless otherwise noted; PRI, Paleontological Research Institution]

Locality number	State	County	Stratigraphic unit	Collection number
77A.............	Alabama	Wilcox	Clayton Fm, Pine Barren Mbr	129744.
78	....do........	....do........	Porters Creek Clay	154914, 450552, PRI 64.
79	....do........	....do........	Naheola Fm	PRI 65.
80	....do........	....do........	Porters Creek Clay	129745, 129749, 129750, 129754, 129756, 450543–450550, 450562–450565.
81	....do........	....do........	....do........	129753, 129755.
86	Maryland	Prince George's	Aquia Fm	450839.
87	....do........	....do........	....do........	450850.
88	Virginia	Stafford	....do........	207155.
91	....do........	....do........	....do........	450830, 450832.
92	....do........	King George	....do........	450833.
102	Maryland	Charles	....do........	450512, 450864.
104	....do........	....do........	....do........	136177, 450513, 450863.
105	....do........	Prince George's	....do........	450841, 450845.
106	....do........	Prince George's/ Charles	....do........	450514, 450862.
118	Alabama	Monroe	Tuscahoma Fm, Greggs Landing Mbr	450515. PRI 140.
119	....do........	Wilcox	Tuscahoma Fm	450818.
Questionable *C. aquiana* collections				
77A.............	Alabama	Wilcox	Clayton Fm, Pine Barren Mbr	129748.
80	....do........	....do........	Porters Creek Clay	129747.
82A.............	Maryland	Prince George's	Aquia Fm	450858.

assume adult shape; inequilateral; beak position highly variable, ranging from anterior one-quarter to near midlength of shell; early stages of shell prosogyrous; adult appears weakly prosogyrate to nearly orthogyrate as viewed perpendicular to plane of commissure. Anterior dorsal margin slightly concave to slightly convex at maximum width of lunule; margin slopes steeply away from beak; lunule well developed on left valve of adults with sharp ridge defining area, less well defined on right valve with no distinct ridge; anterior margin smoothly rounded. Posterior dorsal margin straight to slightly concave near end of escutcheon; slope of margin varies from steep to gentle depending on posterior elongation; escutcheon elongate, well defined on right valve with area defined by ridge, less well defined on left valve with ridge absent; posterior ridge varies from sharp raised carinate forms preceded by depression in shell surface to forms with simple ridge marked by bend in growth lines; posterior margin varies from pointed to quadrilaterally truncate on adults. Ventral margin gently curved anteriorly, flattened to rounded below beak, strongly incurved to flattened below posterior adductor. Ornamentation begins at beak as evenly spaced coarse raised ribs with broad interspaces reduced to raised sharp lines in posterior area, gradually shifts to closely spaced finer ribs at later stages, and in some cases fades entirely; comarginal threads begin near beak and continue across entire shell surface, including ribs, interspaces, and posterior area; lower portions of shell may show deep broad undulations of surface; stage at which shift in ornamentation occurs is highly variable. Hinge angle variable, average 113 degrees; moving from posterior lateral ridges across hinge plate to anterior lateral ridges, dentition noted as follows:

Right Valve 0 1 0—R 0 1 0 -1 0 1
Left Valve 1 0 1—R(0) 1 0 1 0 (1)–0 1 0

Right valve dentition consists of one posterior lateral ridge, separated by edentulous space from resilifer (R); resilifer originates at beak on platform formed by rear wall of a trigonal socket below and slightly anterior to resilifer; opening of resilial platform to umbonal cavity is incompletely obstructed by position of trigonal socket; trigonal socket may have vertical grooves on rear wall of socket; one large cardinal tooth lies anterior to beak, some with transverse grooves on sides of tooth; two anterior lateral ridges present, separated by groove. Left valve dentition consists of two posterior lateral ridges, separated by groove; resilifer originates at beak; opening of resilial area to umbonal cavity restricted by depression at base of posterior slope of cardinal; two well defined cardinals separated by socket, some with transverse grooves on sides of cardinals; forward of anteriormost cardinal is narrow groove followed by short ridge;

one anterior lateral ridge present. Resilifer shaped like elongate teardrop. Juveniles display well-developed hinge characters at early stages. Isomyarian adductor muscle scars; anterior reniform; posterior subcircular to suboval. Anterior pedal retractor present. Pallial line distinct, entire. Crenulations present from end of anterior lateral ridge ventrally to posterior lateral ridge on adults; development begins anteriorly early in ontogeny so young specimens may have complete marginal crenulations. Prodissoconch not known.

Discussion.—The concepts of *Crassatellites hodgei* Stephenson [= *Crassatella hodgei*] and *Crassatellites roodensis* Stephenson have been intertwined since their original description (Stephenson, 1923, p. 271–274). An examination of the type specimens selected by Stephenson illustrates the problem. The holotype of *Crassatella hodgei* (USNM 31930; pl. 2, figs. 7, 8) shows a prominent posterior ridge and an accompanying indentation of the posterior ventral margin, but the paratype (USNM 31931; pl. 2, figs. 10, 11) has only a smoothly rounded posterior ridge and a nearly flat posterior ventral margin. The holotype of *Crassatellites roodensis* is lost,[23] but two paratypes (USNM 31748 and 31749; pl. 4, figs. 10, 18) exhibit the same range of variation seen in the types of *Crassatella hodgei.* Plate 4, figure 10 illustrates a smoothly rounded posterior ridge and a flat posterior ventral margin; the specimen on plate 4, figure 18 shows a prominent posterior ridge and indented posterior ventral margin. The confusion is compounded by the state of preservation of the specimens; the exteriors of many of the shells have deteriorated (see pl. 4, figs. 9, 10, 17–19 for examples), and the internal characters of most of the specimens are not visible. It seems that Stephenson's (1923, p. 272) primary criterion for splitting the two species was one of size; he stated,

> The species [*Crassatellites hodgei*] is also closely allied to *C. roodensis*, from which it differs chiefly in size, being on the average about half as large. The many small individuals of the species found at several localities in North Carolina seem to justify separating it from *C. roodensis*, the many individuals of which are all large. Future studies may show the necessity for combining the two forms.

Crassatellites roodensis Stephenson is herein considered to be a junior synonym of *Crassatella hodgei* (Stephenson). The name *Crassatella hodgei* is retained as the senior synonym because it has page priority; in addition, the holotype of *C. hodgei* still exists, and Stephenson's original description of *C. hodgei* is thorough, incorporating the attributes he ascribed to *Crassatellites roodensis*. Other than Stephenson's original description of *Crassatella hodgei* and *Crassatellites roodensis* from North Carolina, South Carolina, and the Chattahoochee River region of Georgia and Alabama, no subsequent evaluation of the species has been made. Faunal lists have expanded the provenance of the species to New Jersey (Richards, 1954, p. 2)[28] and Mississippi (Sohl, 1964, p. 353; "affinities to *roodensis*").

TABLE 45.—*Minimum, maximum, and mean values for characters of* Crassatella hodgei

[See table 2 for an explanation of the morphological variables. Data source: digitized data set supplemented by data from specimens not included in discriminant analysis]

Morphological variable	Adults (13 specimens)		
	Minimum	Maximum	Mean
CONVEX	5.91	14.42	9.44
LENGTH	28.12	55.00	38.88
HINGE	91.71	116.50	110.54
POST	96.00	145.88	117.55
ANTER	131.00	147.92	140.68
ANTVERHT	14.87	26.50	19.02
POSVERHT	13.56	28.00	18.58

Crassatella hodgei, as originally defined by Stephenson (1923) and as herein expanded, is a highly variable species. My attempts to separate morphotypes into distinct species groups met with failure; the range of variation is continuous and gradational. Specimens that could be grouped one way on the basis of the characters of the posterior ridge and posterior ventral margin had to be regrouped when characters of the hinge or of the juvenile were considered. The largest and most obvious variation is seen in the characters of the posterior region of the shell. A comparison of plate 2, figure 11; plate 4, figures 11, 15, 16; and plate 5, figures 2, 12, 14 illustrates the extremes in overall form; plate 5, figure 12 is a trigonal form having a quadrilaterally truncate posterior, a moderately developed posterior ridge, and a slight indentation of the posterior ventral margin; plate 2, figure 11, the paratype, illustrates the obtusely trigonal, posteriorly elongate form, which has a diminished posterior ridge and flattened posterior ventral margin; plate 4, figures 11 and 16 illustrate the extent of development of the posterior ridge and the accompanying indentation of the posterior ventral margin. The hinge angle varies from obtuse (pl. 4, fig. 15) to a nearly right angle (pl. 5, fig. 2) depending on the degree of posterior elongation (see table 45 for the range of values); the slope of the posterior dorsal margin is fairly gentle on the obtuse forms and fairly steep on the forms approaching a right

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[28] Richards (1954, p. 2; 1958, p. 187) seems to have confused *Crassatella hodgei* and *Crassatellites roodensis* as defined by Stephenson (1923, p. 271–274), yet he did not synonomize the two species or even acknowledge that *C. roodensis* existed. He listed the known localities of *Crassatella hodgei* as being South Carolina, Georgia, and Alabama (Richards, 1954, p. 2); these were the localities Stephenson identified for *Crassatellites roodensis*. The type locality listed in the 1958 publication (Richards, 1958, p. 187) for *Crassatella hodgei*, Roods Bend, Chattahoochee River, Ala., is the type locality for *Crassatellites roodensis*. The USNM specimen number 31847 does not correspond to either *Crassatella hodgei* (USNM 31930) as Richards (1958, p. 187) indicated or to *Crassatellites roodensis* (USNM 31747).

angle. A comparison of figures 5, 10, 14, and 15 on plate 4 illustrates the variation in the ventral margin from rounded below the beak and posteriorly indented (pl. 4, figs. 14, 15) to rounded below the beak and flattened posteriorly (pl. 4, figs. 5, 10). The position of the beak can vary from the anterior one-third of shell length (pl. 4, figs. 5, 10) to near the midpoint of the shell (pl. 4, fig. 4; pl. 5, fig. 2). Convexity ranges from inflated (pl. 4, fig. 16) to depressed (pl. 5, fig. 12) (table 45). A considerable amount of variation is seen in the size of the shell at the point where the ornamentation shifts from the juvenile to the adult expression. The widely spaced prominent ridges of the early stages of the shell are clearly visible on plate 6, figures 1, 3, and 5 and plate 4, figures 3, 4, and 13. Plate 4, figure 13 shows the shift from the juvenile ornament to the broad closely spaced ridges of the adult form. Eventually, on some individuals (plate 4, fig. 16), the ridges begin to fade, and comarginal growth threads remain as the only form of ornament in the final stages of shell growth.

The ontogenetic sequence of *Crassatella hodgei* shows rapid development of many adult characters. The subcircular prosogyrous outline of the earliest stages of the shell (pl. 6, figs. 1, 3) rapidly gives way to the adult shape (pl. 5, figs. 7, 9; pl. 6, fig. 5). Internally, the muscle scars, pallial sinus, hinge characters, and marginal crenulations are well developed at very early stages for this genus (pl. 6, fig. 4). Changes in ornamentation occur at various stages as discussed above.

The species *Crassatella hodgei* is distinctive from all other members of the genus, and family, by the sum of its diagnostic characters. The extreme range of intraspecific variation, however, may cause confusion and result in some individuals being assigned to other species. Some specimens that lack a prominent posterior ridge may be confused with *C. vadosa* (compare pl. 5, fig. 1 to fig. 12), but the ornamentation of the juvenile portion of the shells quickly distinguishes the two species. The ornamentation of juvenile *C. vadosa* consists of fine ridges and comarginal lines that become coarser in later stages; the inverse is true for *C. hodgei*, which begins with coarse ornamentation that becomes finer as the shell matures (compare pl. 5, fig. 4 to fig. 9; pl. 4, fig. 11 to pl. 8, figs. 11, 16). In addition, the juvenile shells of *C. hodgei* rapidly assume the more trigonal form of the adults, whereas *C. vadosa* retains a subquadrate outline into advanced stages of the ontogenetic sequence (compare pl. 5, figs. 4, 6 to figs. 7, 10; pl. 6, fig. 4 to pl. 12, fig. 4).

Crassatella hodgei and *Crassatellites carolinensis* (Conrad) Stephenson [= *Crassatella carolinensis* Conrad] coexist in the Blufftown Formation along the Chattahoochee River; their similarity in general form at these localities may cause the two species to be confused. Differences in ornamentation clearly distinguish the two species (compare pl. 5, fig. 10 to fig. 17; fig. 12 to fig. 18); *Crassatella hodgei* displays shifts in ornamentation during maturation, whereas *C. carolinensis* does not. Although the adult specimens show similar outlines, the juveniles of the two species are distinctive. In the early stages, *Crassatella hodgei* have already developed a posterior ridge and an adult trigonal shape, with a sharply angled posterior region (pl. 5, fig. 9). *Crassatella carolinensis* juveniles are subquadrate with a rounded posterior and a nearly flat posterior dorsal slope (pl. 5, fig. 8). The convexity of the valves as viewed from the dorsal or ventral margins perpendicular to the plane of commissure is flattened across the umbo region for *Crassatella hodgei* and gently rounded for *C. carolinensis* (pl. 5, fig. 11). In addition, although some members of *Crassatella hodgei* share similar hinge characters with *C. carolinensis*, the average form for *C. hodgei* is distinctly different, primarily in the more complete obstruction of the resilial platform. The differences between the resilial platforms of *Crassatella carolinensis* and *C. hodgei* can be seen by comparing plate 5, figure 5 to figure 14; plate 4, figure 15 to plate 5, figure 16.

In the past, specimens of *Crassatella hodgei* have been assigned to *Crassatella pteropsis* [= *Bathytormus pteropsis* as herein defined] (Conrad, 1875; Richards, 1950). These specimens are discussed in detail under the *Bathytormus pteropsis* section, and they are considered synonyms of *C. hodgei.*

Occurrence.—See table 46 for *C. hodgei* localities, stratigraphic units, and collections studied. Refer to figure 2 and appendix 9 for locality positions and descriptions.

Stratigraphic range.—Lower through upper? Campanian (fig. 19).

Type material examined.—USNM 31930; holotype *Crassatella hodgei* (Stephenson). USNM 31931; paratype *Crassatella hodgei* (Stephenson). USNM 31748, 31749; paratype *Crassatellites roodensis* Stephenson.

Genus *Bathytormus* Stewart, 1930

Bathytormus STEWART, 1930, p. 137–138. CHAVAN, 1939, p. 27–30. CHAVAN, 1952, p. 120. CHAVAN, 1969, p. N574.

Crenocrassatella HABE, 1951, p. 105.

Crassatella (Bathytormus) Stewart, GLIBERT and VAN DE POEL, 1970, p. 92.

Type Species.—*Crassatella protexta* Conrad, 1832.

Characters of Coastal Plain Bathytormus.—The two species of *Bathytormus* included in this analysis are equivalved, inequilateral, and posteriorly elongate and have no shell gape; species may be orthogyrous or weakly prosogyrous; shell outlines are subelliptical or transversely trigonal; posterior margins are narrow;

TABLE 46.—Crassatella hodgei—*Occurrence and collections studied*

[Fm, Formation; Mbr, Member. Collection number, USNM (U.S. National Museum) collection or specimen numbers]

Locality number	State	County	Stratigraphic unit	Collection number
1..........	Mississippi	Prentiss	Coffee Sand	450408, 451059.
2..........	....do........	....do........	....do........	450419, 451053.
3..........	....do........	Lee	....do........	450409–450411, 453894.
4..........	Georgia	Stewart	Blufftown Fm	450402–450406, 450421, 450422, 450431–450435, 450501, 450815, 453880.
5..........	....do........	....do........	....do........	453862.
6..........	....do........	....do........	....do........	450407, 451094, 453879.
8..........	North Carolina	Greene	Tar Heel Fm	31930, 31931, 451097.
9..........	....do........	Wayne	....do........	453864.
10..........	....do........	Lenoir	....do........	451101.
11..........	....do........	Pitt	....do........	459093.
13A........	Delaware	New Castle	Merchantville Fm	450420.
13B........	....do........	....do........	....do........	450412.
16..........	South Carolina	Marion	Bladen Fm	31748, 31749, 453861.
17..........	North Carolina	Lenoir	....do........	450852.
18..........	....do........	....do........	....do........	451102.
19A........	....do........	Sampson	....do........	451106.
19C........	....do........	....do........	....do........	453856.
19D........	....do........	....do........	....do........	453857.
20..........	....do........	....do........	....do........	453858.
21..........	....do........	....do........	....do........	453859.
22..........	....do........	Bladen	....do........	453860.
25A........	Alabama	Barbour	Ripley Fm, Cusseta Sand Mbr	453863.
25B........	....do........	....do........	....do........	453866.
26..........	Georgia	Stewart	Cusseta Sand	450413–450415, 453865, 453884.
Questionable *C. hodgei* collection				
19B........	North Carolina	Sampson	Bladen Fm	453855.

anterior margins rounded. Anterior dorsal margins are moderately steep; a lunule is present but is usually narrow and poorly defined. Posterior dorsal margins are straight to slightly concave; the escutcheon is elongate, narrow, and fairly well defined on both valves, but the right valve is slightly broader. The posterior area is narrow and is delineated by a posterior ridge. The ventral margin is rounded from the anterior margin to below the posterior adductor; it may be straight to slightly concave just anterior to the posterior ridge. The characteristic ornament for the genus consists of distinct, raised evenly spaced comarginal ridges on the umbo region and comarginal growth threads continuous across the entire shell surface. The typical pattern for the dentition of this genus, moving from the posterior lateral ridges across the hinge plate to the anterior lateral ridges, is as follows (see fig. 20):

Right Valve 0 1 0— R(1) 0 1 0 (1) –1 0 1
Left Valve 1 0 1— R(0) 1 0 1 (0) –0 1 0

The right valve dentition consists of one sharp posterior lateral ridge. An elongate triangular resilifer originates at the beak and extends to the edge of the hinge platform. Anteriorly a narrow trigonal socket is separated from the resilifer by a low, sharp narrow ridge; the ridge is almost a bifurcation of the posterior dorsal edge of the cardinal. One cardinal tooth lies anterior to the beak and is preceded anteriorly by a narrow socket. The anterior edge of the hinge plate may form a thin narrow ridge. Two anterior lateral ridges are present and are separated by a groove. The left valve dentition consists of two posterior lateral ridges, separated by a groove. The triangular resilifer originates at the beak and extends to the edge of the hinge platform. Two narrow cardinals are separated by a socket; the posterior-most cardinal is broader and may have a small pit at the posterior base of the tooth on large adults; a narrow groove forward of the anterior-most cardinal functions as a receptor for the anterior-most raised ridge of the opposite valve. One anterior lateral ridge is present. The ligament of *Bathytormus* is internal, originates at the beak, and extends all the way across the hinge plate. The musculature of *Bathytormus* consists of two subequal adductor muscle scars; the anterior is reniform, and the

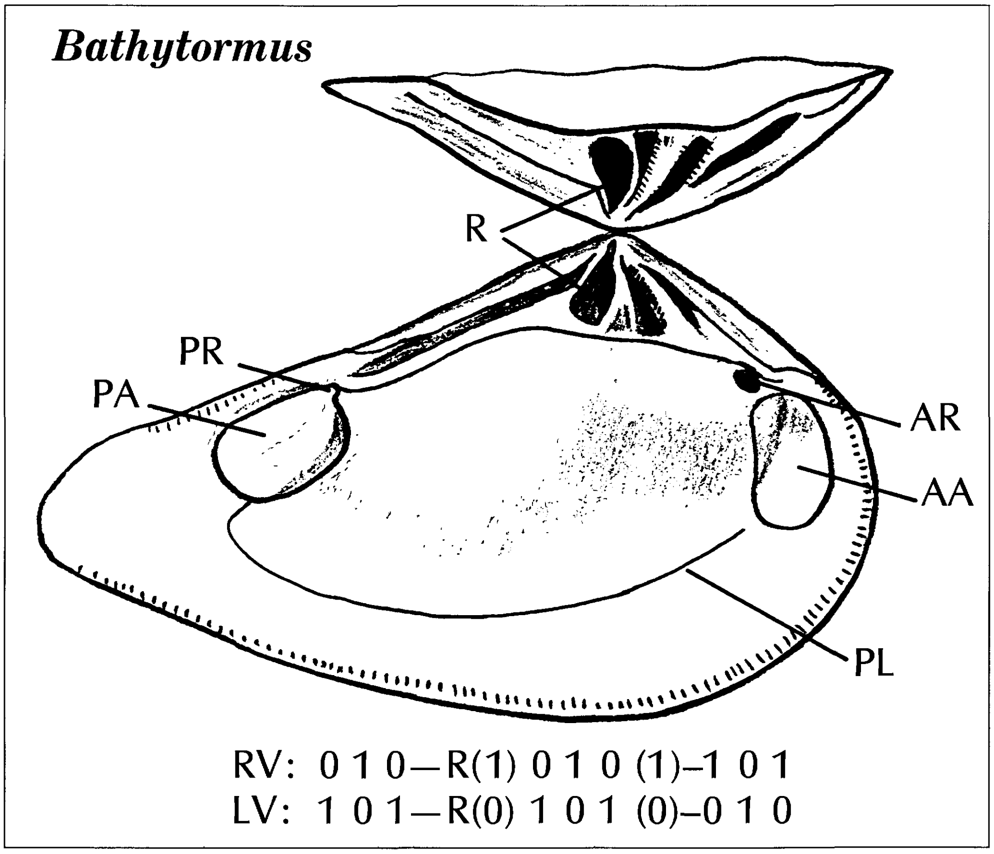

FIGURE 20.—Hinge characters and musculature of *Bathytormus*. Dental formulas read from the posterior lateral ridges to the anterior lateral ridges. RV, right valve; LV, left valve. AA, anterior adductor; AR, anterior pedal retractor; PA, posterior adductor; PL, pallial line; PR, posterior pedal retractor; R, resilifer.

posterior is parabolic. In addition, two pedal retractors are present; the anterior pedal retractor is crescent-shaped and distinct and is located above the anterior adductor and below the edge of the hinge plate; the posterior pedal retractor is continuous with the posterior adductor and forms a notch in the anterior-dorsal corner of the scar. The pallial line is distinct and entire, and the ventral border may be faintly crenulated on well-preserved, mature adults. These characters are consistent with Stewart's original designation and with the characters of the type species *Crassatella protexta* Conrad.

Discussion.—Stewart (1930, p. 137) erected *Bathytormus* and removed to this new genus the species originally classified as *Crassatella* that possess a "ligamental cavity extending to the ventral border of the hinge." The failure, however, of the ligamental cavity as a diagnostic character for juvenile *Bathytormus* versus juvenile *Crassatella* was discussed by Stewart (1930, p. 138). A comparison of plate 7, figures 1, 2, 6, and 8 to plate 17, figures 14, 16, 18, and 21 illustrates the problem; *Crassatella* do not develop their characteristic restricted resilifers until fairly late in ontogeny, thus juvenile *Crassatella* appear to possess a typical *Bathytormus* hinge. The failure of the resilifer as a diagnostic character for all ontogenetic stages, in addition to the doubtful assignment of some species to *Bathytormus*, led Glibert and Van de Poel (1970, p. 92–93) to reduce *Bathytormus* to subgeneric rank.

Chavan (1939, 1952, 1969) maintained *Bathytormus* as a valid genus. In a discussion of the genus *Crassatina*, Chavan notes similarities between *Bathytormus* and *Crassatina* and states that they are "two related genera probably issuing from a common origin" (Chavan, 1939, p. 29; translated from French). Both *Bathytormus* and *Crassatina* can be divided into two groups (Chavan, 1939, p. 28): the first having inflated orthogyrous beaks, elongate rostrated posterior, convex shell, and ornamentation of concentrically rounded cords and the second having small prosogyrous beaks, enlarged dilated (but not rostrate) posterior, flat shell, and ornamentation of lamellose spaced cords. Chavan (1939, p. 28) assigned

Crassatella protexta, the type species of the genus to the first group (pl. 21, figs. 11, 13) and *Bathytormus alaeformis* (pl. 21, figs. 14, 17), discussed below, to the second group (Chavan, 1939, p. 29) on the basis of its ornament. *Crenocrassatella* Habe (type species *Crassatella foveolata* Sowerby, 1870) was recognized as a junior synonym of *Bathytormus* by Chavan (1952, p. 120).

Bathytormus Stewart is herein recognized as a valid genus. In the Upper Cretaceous deposits of the Gulf Coast and Mid-Atlantic regions, *Bathytormus* is a rare but distinctive component of the fauna. The distribution of *Bathytormus* in the lower Tertiary deposits is restricted to the Mid-Atlantic region, but there it is relatively common. *Bathytormus* can be distinguished from adult *Crassatella* by the resilifer, which extends from the beak to the ventral edge of the hinge plate, and from all growth stages of *Crassatella* by the extreme posterior elongation and the narrow lunule. The shape of the posterior and characters of the dorsal margin were the primary discriminators between *Crassatella* and *Bathytormus* during the statistical analysis. Despite the statistical separation of the two species, *B. alaeformis* and *B. pteropsis* show a large degree of intraspecific variation.

***Bathytormus alaeformis* (Conrad), 1830**

Plate 3, figures 12, 14–19; plate 18, figures 1–22;
plate 19, figures 1–13; plate 20, figures 5, 7;
plate 21, figures 14, 17.

Crassatella alaeformis CONRAD, 1830, p. 228, pl. 10, fig. 1. CONRAD, 1846, p. 396, pl. 3, fig. 2 [not fig. 3 (= ? *Crassatella protexta*) as indicated in text and plate caption]. CLARK, 1895, p. 5. CLARK, 1896, p. 81–82, pl. 27, fig. 1a–1k. VOKES, 1961, p. 50, pl. 10, figs. 5, 6.

Crassatella capri-cranium ROGERS and ROGERS, 1839, p. 375–376, pl. 30, fig. 2 (two illustrations) [= ROGERS, 1884, p. 672, pl. 5, fig. 2 (reprint)].

Crassatella declivis HEILPRIN, 1880, p. 151–152, plate on p. 150, fig. 9. ALDRICH, 1897, p. 170, pl. 3, figs. 1, 1a.

Crassatella protexta Conrad. DE GREGORIO, 1890, pl. 25, fig. 12 [reproduction of Conrad, 1846, pl. 3, fig. 2 = *C. alaeformis* Conrad].

Crassatellites alaeformis (Conrad). CLARK and MARTIN, 1901, p. 180–181, pl. 41, figs. 1–8 [partim; not *C. palmula* Conrad]. WARD, 1985, pl. 2, fig. 7.

Bathytormus alaeformis (Conrad). STEWART, 1930, p. 137. CHAVAN, 1939, p. 29. PALMER and BRANN, 1965, p. 48–49 [partim; not = *C. palmula* Conrad].

Crassatella (Bathytormus) alaeformis Conrad. GLIBERT and VAN DE POEL, 1970, p. 92–93.

Crassatellites capricranium (Rogers and Rogers). WARD, 1985, pl. 1, fig. 9.

[non] *Crassatella palmula* CONRAD, 1846, p. 396, pl. 4, fig. 1.

Diagnosis.—Subelliptical; extreme posterior elongation; weakly prosogyrous adults; subdued posterior ridge; posterior area flattened to gently sloping. Ornament across umbone sharp, high comarginal ridges, gradually becomes rounded and less prominent ventrally and posteriorly; ventral portion of large adults lacks distinctive ornament in contrast to umbone. Resilifer extends to edge of hinge platform; posterior cardinal in right valve situated vertically. Crenulations faint, form late in ontogeny.

Description.—Shell equivalve, inflation shallow to moderately convex, anterior wider than posterior; adults subelliptical in outline, juveniles shift from quadrate to suboval during ontogeny. Inequilateral; extreme posterior elongation, beak position ranges from anterior one-quarter to two-fifths of shell length, average three-tenths; adults weakly prosogyrous, juveniles strongly prosogyrous; beak sharply pointed on juveniles, less so on adults. Anterior dorsal margin straight to slightly concave, moderately sloping; lunule very narrow, faint ridge defines area on left valve of juveniles and young adults, broader, more well defined on large, mature specimens; anterior margin evenly rounded. Posterior dorsal margin straight to slightly concave on adults; juveniles slightly concave at maximum width of escutcheon; margin gently sloping; escutcheon elongate, narrow, fairly well defined on both valves, right valve slightly broader; posterior margin elongate, narrow, truncates in gentle arc; posterior area narrow, gently sloping, delineated by subdued posterior ridge. Ventral margin rounded from anterior margin to below posterior adductor; straight to slightly concave just anterior to posterior ridge. Predominant ornamentation of juvenile portion of shell sharp, high evenly spaced comarginal ridges, with deep V-shaped interspaces; relief of ornament decreases ventrally and posteriorly; spacing becomes increasingly irregular, and ornament shifts to more rounded, broader comarginal ribs, then fades entirely leaving only comarginal growth threads, which are continuous across entire shell surface; ornament of posterior area subdued; faint radial lines may be seen under high magnification on young individuals or on ventral portion of large adults. Hinge angle variable, average 123 degrees for adults, 121 degrees for juveniles; moving from posterior lateral ridges across hinge plate to anterior lateral ridges, dentition noted as follows:

Right Valve 0 1 0—R(1) 0 1 0 (1)–1 0 1
Left Valve 1 0 1—R(0) 1 0 1 (0)–0 1 0

Right valve dentition consists of one sharp posterior lateral ridge; elongate triangular resilifer originates at beak, extends to edge of hinge platform; anteriorly very narrow trigonal socket separated from resilifer by low, sharp, narrow ridge; ridge almost bifurcation of posterior dorsal edge of cardinal; one cardinal tooth anterior to beak, preceded anteriorly by narrow socket; anterior edge of hinge plate may form thin narrow ridge; two anterior lateral ridges separated by groove. Left valve dentition consists of two posterior lateral ridges separated by groove; triangular resilifer originates at beak, extends to edge of hinge platform; two narrow cardinals separated by socket; posterior-most cardinal broader, vertical, may have small pit at posterior base of large adults; anterior-most cardinal angled forward; narrow groove forward of anterior-most cardinal functions as receptor for anterior-most raised ridge of opposite valve; one anterior lateral ridge is present. Dentition forms early in ontogeny, resilifer somewhat later. Two subequal adductor muscle scars, anterior reniform, posterior parabolic. Anterior pedal retractor crescent shaped, distinct, located above anterior adductor, below edge of hinge plate; posterior pedal retractor continuous with posterior adductor, forms notch in anterior-dorsal corner of scar. Pallial line distinct, entire. Crenulations appear very late in ontogeny, faint, extending from anterior lateral ridges around to below posterior adductor. Prodissoconch circular, free of ornament.

Discussion.—*Crassatella alaeformis* was named by Conrad (1830, p. 228) from a single specimen found in the lower Tertiary deposits at Piscataway Creek, Prince George's County, Md. (holotype, ANSP 30498, see pl. 3, figs. 14, 17). In his original description of the species Conrad inverted the anterior and posterior portions of the valve; he described the anterior portion as "rostrate" and the posterior portion as "short and rounded" (Conrad, 1830, p. 228). Subsequently, Conrad (1846, p. 396) corrected this error, noting that the posterior side of *C. alaeformis* was "produced, cuneiform, obliquely truncated at the extremity."

Since Conrad's original description, *Bathytormus alaeformis* (Conrad) has been recognized by many workers in the well-studied Aquia Formation (late Paleocene) of the Mid-Atlantic (Clark, 1895, p. 5; 1896, p. 81; Clark and Martin, 1901, p. 180; Vokes, 1961, p. 50; Ward, 1985). Clark (1895, p. 5) was the first author to recognize that *Crassatella capri-cranium* Rogers and Rogers and *C. declivis* Heilprin (USNM 2490; pl. 3, figs. 16, 18, 19) were junior synonyms of *C. alaeformis.* Some authors (Clark and Martin, 1901, p. 180; Palmer and Brann, 1965, p. 49) have questionably synonymized *C. palmula* Conrad with *C. alaeformis.* I believe the extremely poor preservation of the type specimen of *C. palmula* (ANSP 30580; pl. 3, figs. 11, 13) prevents even questionable synonymization.[29] Stewart (1930, p. 137) assigned *C. alaeformis* Conrad to his new genus *Bathytormus* on the basis of the hinge characters.

The large degree of intraspecific variation seen in *Bathytormus alaeformis* was first discussed and illustrated by Clark and Martin (1901, p. 180–181, pl. 41). While most of these differences can be attributed to ontogenetic change, variations in the degree of posterior elongation, height-to-length ratio, prominence of the beak, and inflation can be noted in individuals at the same stage in their life cycle (see table 47 for range of values). An examination of plate 18 illustrates different configurations of the posterior region; plate 18, figures 17 and 18 represent extremely elongate individuals, whereas plate 18, figure 20 shows a comparatively short specimen. The mixed distribution of posteriorly elongate forms with the shorter higher forms indicates the possibility that these variances in shape may be due to sexual dimorphism, but a conclusive determination has not been reached. Greater height-to-length ratios than average for the species can give specimens an oval appearance (pl. 19, figs. 3, 4). Degree of inflation can vary for similarly sized individuals (compare pl. 19, figs. 7, 8), but this is more commonly a function of ontogenetic stage. Variations also are noted in the degree of concavity of the posterior dorsal margin (compare pl. 18, fig. 14 to fig. 18), and in the posterior ventral margin (compare pl. 18, figs. 15, 17 to figs. 18, 20). The prominence of the beak varies somewhat (compare pl. 18, fig. 14 to fig. 22), but care must be taken to determine that this is not a function of wear; a few specimens illustrated by Clark and Martin (1901, pl. 41, fig. 2, for example) appear to be worn. In fact, abrasion can account for many differences seen in the ornament, the marginal crenulations, the prominence of the beak, and the shape of the posterior extremity.

TABLE 47.—*Minimum, maximum, and mean values for characters of* Bathytormus alaeformis

[See table 2 for an explanation of the morphological variables. Data source: digitized data set; excludes broken specimens and internal molds]

Morphological variable	Adults (112 specimens)		
	Minimum	Maximum	Mean
CONVEX	1.15	21.32	7.07
LENGTH	9.83	59.99	37.47
HINGE	110.40	135.30	122.59
POST	82.42	172.72	115.85
ANTER	118.16	161.15	134.64
ANTVERHT	3.82	23.98	13.94
POSVERHT	4.72	23.40	13.03

Ontogenetic changes account for the largest degree of intraspecific variation. The nepionic stage of *Bathytormus alaeformis* is subquadrate (pl. 20, figs. 5, 7), but the juvenile rapidly passes through a suboval form and assumes a truncated subelliptical outline (pl. 18, figs. 1, 2). At these early stages, the beak is highly pointed and strongly prosogyrous, and the ornament consists of high, sharp evenly spaced ridges with deep V-shaped interspaces; the interspaces are covered with sharp comarginal growth threads, and faint radial lines may be visible on specimens at high magnifications (pl. 20, fig. 5). The

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[29] For a complete discussion of *Crassatella palmula* Conrad see section "Distribution and validity of species" on page 58.

dentition, pallial line, and muscle scars are fully developed on young juveniles of *B. alaeformis*, although the resilifer may not be well defined (pl. 18, figs. 2, 5). The valves are shallow, and the posterior ventral margin is gently curved at this stage. As an individual matures, the resilifer becomes distinct, the inflation of the valve increases, and the posterior ventral margin becomes straight, then concave (pl. 18, fig. 13); the ornament gradually begins to shift to more rounded ribs, and, as the juvenile passes into the adult stage, faint marginal crenulations appear on the anterior ventral border (pl. 18, figs. 7, 12). Plate 18, figures 12 and 15, show the transition between juvenile and adult stages.

The continued maturation of the adult *Bathytormus alaeformis* is marked by an apparent increase in height relative to length (although this is difficult to confirm because very few large adult specimens have intact posterior margins) and increased convexity (examine the sequence of pl. 18, figs. 19, 21, 22). The increase in convexity is accompanied by the development of a broader, more well-defined lunule (pl. 19, figs. 6, 9), a less prominent configuration of the beaks, and a steeper posterior area. Ornamentation of the ventral portion of these large, mature adults consists of comarginal growth threads alone, in marked contrast to the distinctive ridges seen on the umbo. Plate 18, figures 21 and 22, illustrates the characteristics of a mature adult *B. alaeformis*. Finally, in the very largest individuals, the hinge assumes some characteristics seen on *Crassatella* throughout their life cycle: (1) a small pit appears at the base of the posterior cardinal of the left valve (pl. 19, fig. 13) and (2) the resilifer may no longer extend completely to the edge of the hinge plate, particularly in the right valve.

The comparison of a juvenile *Bathytormus alaeformis* (pl. 18, fig. 3, 8, or 11) to a large, mature adult member of the species (pl. 18, fig. 21 or fig. 22), without considering the intervening forms, may suggest that two species are present. *Crassatella capri-cranium* Rogers and Rogers, for example, represents the very mature members of *B. alaeformis*, which have well-developed lunules. The type specimen of *B. alaeformis* (pl. 3, fig. 14) is itself a fairly large adult, but it has not yet developed the broad, well-defined lunules. *C. declivis* Heilprin (USNM 2490; pl. 3, figs. 18, 19) illustrates the characteristic ornament of a young adult specimen of *B. alaeformis*. Careful examination of the sequence illustrated on plate 18, however, reveals that all these individuals are members of the same species, *B. alaeformis* (Conrad).

Bathytormus alaeformis can be distinguished from all *Crassatella* species by the generic differences in the hinge characters and by its extreme posterior elongation. Even on the largest members of *B. alaeformis*, the hinge can still be separated from the typical form of *Crassatella*. The pit on the back side of the posterior cardinal of the left valve of *B. alaeformis* is shallow, small, and occurs on the side of the tooth, whereas the typical pit of *Crassatella* is deeper, larger, and occurs at the base of the tooth and spreads onto the hinge platform itself (compare pl. 21, fig. 17 to fig. 8). Although the resilifer of the large, mature *B. alaeformis* does not extend to the very edge of the hinge platform, it is still more open and elongate than the resilifer of *Crassatella*. When internal features cannot be seen, the large specimens of *B. alaeformis* may be confused with *C. aquiana* where they co-occur in Maryland and Virginia. The posterior elongation, the gentle slope of the posterior dorsal margins, and the low, weakly prosogyrous beaks of *B. alaeformis* should be distinguishable from the posteriorly truncate, steeply sloping dorsal margins and high strongly prosogyrous beaks of *C. aquiana* (compare pl. 14, figs. 3, 8, 10 to pl. 19, figs. 6, 11 and pl. 18, fig. 21). The specific differences between *B. alaeformis* and *B. pteropsis* are discussed in the section on *B. pteropsis*.

Occurrence.—See table 48 for *B. alaeformis* localities, stratigraphic units, and collections studied. Refer to figure 2 and appendix 9 for locality positions and descriptions.

Stratigraphic Range.—Upper Midway through Wilcox (fig. 19).

Type material examined.—ANSP 30498; holotype and paratype *Crassatella alaeformis* Conrad. USNM 2490; holotype and paratype *Crassatella declivis* Heilprin.

***Bathytormus pteropsis* (Conrad), 1860**

Plate 2, figures 1–3; plate 17, figures 1–21;
plate 20, figures 1, 3, 4, 6; plate 21, figures 10, 12.

Crassatella pteropsis CONRAD, 1860, p. 279, pl. 46, fig. 9. GABB, 1877, p. 310. STEPHENSON and MONROE, 1940, pl. 9, figs. 4, 5.

Crassatella (*Pachythaerus*) *pteropsis* CONRAD, 1872, p. 50 [non pl. 1, fig. 1 = ? *Crassatella* sp.].

Crassatellites pteropsis (Conrad). GARDNER, 1916, p. 655, pl. 39, fig. 5 [partim; includes *C. pteropsis* Gabb in synonymy; incorrectly cites type locality as Owl Creek, Tippah Co., Miss.]. SHIMER and SHROCK, 1944, p. 419, pl. 167, fig. 4.

[?] *Crassatella pteropsis* Conrad. GABB, 1877, p. 310.

[non] *Crassatella pteropsis* GABB, 1860b, p. 395, pl. 68, fig. 28. CONRAD, 1869a, p. 47–48.

[non] *Crassatella pteropsis* ? CONRAD, 1875, appendix, p. 6, pl. 1, fig. 25 [= ? *Crassatella hodgei* (Stephenson)].

[non] *Crassatellites pteropsis* (Conrad). RICHARDS, 1950, p. 74, figs. 61b, 61c [= ? *Crassatella hodgei* (Stephenson)].

Diagnosis.—Transversely trigonal, rostrate adults; orthogyrous adults; uppermost portion of beak sharply pointed; narrow, poorly defined lunule; prominent posterior ridge, steeply sloping posterior area in adults. Comarginal ornament continuous across shell surface, gradually becomes rounded and less prominent, but

TABLE 48.—Bathytormus alaeformis—*Occurrence and collections studied*

[Fm, Formation; Mbr, Member. Collection number: USNM (U.S. National Museum) collection or specimen numbers, unless otherwise noted; ANSP, Academy of Natural Sciences of Philadelphia]

Locality number	State	County	Stratigraphic unit	Collection number
82A	Maryland	Prince George's	Aquia Fm	450823.
82B	do	do	do	450860.
83	do	do	do	450536.
84	do	do	do	450856.
85	do	do	do	115796, 450523, 450531–450533, 450572, 450808. ANSP 30498.
86	do	do	do	450839.
87	do	do	do	207153, 450857, 450859, 450865.
88	Virginia	Stafford	do	2490, 155549, 450526–450530, 450809, 450822, 450824, 450834.
89	do	do	do	136215, 450573.
90	do	do	do	450810.
91	do	do	do	450524, 450525, 450537, 450806, 450826, 450828, 450830, 450832.
92	do	King George	do	450534, 450833.
93	do	do	Aquia Fm, Paspotansa Mbr	453904.
94	do	do	do	366485, 450838, 450840, 453913–453915.
95	do	do	do	453910.
96	do	do	Aquia Fm	450811.
97	do	do	do	450539, 450829, 450837.
98	do	do	do	450540, 453906, 453909, 453911, 453912.
99	do	do	do	450825.
100	do	do	do	450827.
101	do	Stafford	do	450821.
102	Maryland	Charles	do	450538, 450831.
103	do	do	do	450535, 450835.
104	do	do	do	136177, 450569, 450570, 450571, 453922.
105	do	Prince George's	do	450841.
107	do	Anne Arundel	do	450819.
108	do	Charles	do	450836.
112	Virginia	King George	do	453908.
113A	do	Hanover	do	366477, 453905, 453907, 453919, 453920.
113B	do	do	do	453921.

remains distinctive, in later stages of shell growth. Resilifer elongate, narrow, extends to edge of hinge platform; cardinals in right valve angled anteriorly.

Description.—Shell equivalve, inflation moderate to fairly convex; exterior outline of adults transversely trigonal, rostrate; juvenile outline shifts from subcircular, to quadrate, to subtrigonal during ontogeny. Inequilateral; beak position of adults at approximately anterior one-third of shell length, early stages of juveniles approximately anterior two-fifths shell length; uppermost portion of beak sharply pointed; adults orthogyrous, juveniles slightly prosogyrous. Anterior dorsal margin varies from convex to straight to slightly concave; slope of margin fairly steep on adults; lunule very narrow and poorly defined on both valves, left valve slightly longer with faint ridge defining area; anterior margin smoothly rounded. Posterior dorsal margin slightly concave near end of escutcheon; slope of margin moderately steep on adults, gentle on juveniles; escutcheon elongate, narrow, slightly broader and better defined on right valve with sharp ridge delineating area; posterior margin rostrate on adults, trapezoidal on juveniles; posterior area delineated by presence of posterior ridge; ridge straight or arcuate, subdued on juveniles, becomes more prominent on adults; posterior area broad, flattened on juveniles, narrow, steeply sloping on adults. Ventral margin smoothly rounded anteriorly, flat to slightly concave posterior to beak. Ornamentation of juvenile stages sharp, high, evenly spaced, comarginal ridges, becomes more rounded and less distinctive in adult stages; ridges continue on posterior area only on earliest portions of shell, ornament subdued in posterior area in later stages; comarginal growth threads present over entire shell surface; later stages of adults may show undulations and faint radial lines on ventral margin. Hinge angle variable, average 117 degrees for adults, 114 for juveniles; moving from posterior lateral ridges across hinge plate to anterior lateral ridges, dentition noted as follows:

Right Valve 0 1 0—R(1) 0 1 0 (1)–1 0 1
Left Valve 1 0 1—R 1 0 1 (0)–0 1 0

Right valve dentition consists of one sharp posterior lateral ridge; elongate triangular resilifer originates at beak, extends to edge of hinge platform; anteriorly very narrow trigonal socket separated from resilifer by low narrow ridge; ridge almost bifurcation of posterior dorsal edge of cardinal; one narrow cardinal tooth anterior to beak, angled forward, preceded anteriorly by narrow socket; anterior edge of hinge plate may form thin narrow ridge; two anterior lateral ridges, separated by groove. Left valve dentition consists of two posterior lateral ridges, separated by deep groove; elongate triangular resilifer originates at beak, extends to edge of hinge platform; two narrow anteriorly angled cardinals separated by socket, posterior-most cardinal broader; narrow groove forward of anterior-most cardinal functions as receptor for anterior-most raised ridge of opposite valve; one anterior lateral ridge is present. Cardinal teeth transversely striated on sides, except posterior side of rear cardinal in left valve smooth. Dentition and resilifer fully developed at fairly young stages. Two subequal adductor muscle scars; anterior reniform; posterior parabolic, more deeply incised than anterior. Crescent-shaped anterior pedal retractor distinct, located above anterior adductor and below anterior lateral ridge, posterior pedal retractor indistinct, anterior-dorsal notch of posterior adductor. Pallial line distinct, entire. Crenulations distinct, fine, extend from anterior lateral ridge, ventrally to posterior lateral ridge, posterior portion may be faint; formation begins fairly late in ontogenetic sequence. Prodissoconch oval, free of ornament.

Discussion.—Conrad (1860, p. 279) named *Crassatella pteropsis* from elongate, posteriorly rostrate, specimens found in Union or Tippah County, Miss., probably from the Ripley Formation (see Sohl, 1960, p. 6, for a discussion of Conrad's localities). The absence of *C. pteropsis* Conrad from Johnson's (1905, p. 14) list of ANSP Cretaceous types indicates that it was probably among the specimens sent to Alabama and lost during the Civil War (N.F. Sohl, U.S. Geological Survey, oral commun., 1989). Fundamental topotype material is illustrated on plate 17, figure 5, 10, and 18, and hypotypes are shown on plate 2, figures 1, 2, and 3. Conrad noted the similarity in form between *C. pteropsis* and *C. alaeformis* Conrad, 1830 but concluded that differences in ornamentation could be used to distinguish the two species.

Gabb (1860b, p. 395) applied the name *Crassatella pteropsis* to a different species in the same year and in the same publication as Conrad's original description of *C. pteropsis*; *C. pteropsis* Gabb[30] is a junior homonym of *C. pteropsis* Conrad by page priority. Subsequently, Conrad (1869a, p. 47–48) believed *C. pteropsis* Gabb was a juvenile of *C. pteropsis* Conrad, but an examination of the type specimen of *C. pteropsis* Gabb (USNM 553) does not support this hypothesis. In 1872, Conrad (1872, p. 50) included *C. pteropsis* in the subgenus *Pachythaerus*; the problems with this assignment are discussed in the section "Subdivision of *Crasatella*" (p. 55).

Only a few individuals have recognized *Crassatella pteropsis* Conrad in the Cretaceous Coastal Plain sediments since Conrad's work. Gardner (1916, p. 649) separated *C. pteropsis* from typical *Crassatella* on the basis of the outline and posterior keel and provided the first detailed description of the species (Gardner, 1916, p. 655–656) (pl. 2, fig. 1 is Gardner's hypotype, USNM 32291). She does, however, include *C. pteropsis* Gabb in her synonymy of *C. pteropsis* Conrad, and she incorrectly lists Owl Creek, Tippah County, Miss., as the type locality for the species. Stephenson (1941, p. 176) recognized a subgroup of *Crassatella* within the Navarro Group of Texas, where "the resilifer descends in each valve to the inner hinge margin, and opens freely to the interior of the shell." This group was represented in Texas by *C. quinlanensis* Stephenson, 1941 and in the eastern Gulf by *C. pteropsis*. Although *C. quinlanensis* is outside the geographic limits of this study, future investigations will probably demonstrate it to be a synonym of *C. pteropsis* Conrad. Stephenson's subgroup comprises the Cretaceous members of *Bathytormus*, but this generic name has never been formally applied to any Cretaceous species. Chavan (1969, p. N574) lists the range of *Bathytormus* as Upper Cretaceous to Holocene (fig. 3), but the basis for his extension of the genus into the Cretaceous is not documented. Sohl and Koch (1983, 1984) were the first to recognize *B. pteropsis* in the Cretaceous, and applied the generic name in faunal lists of the Upper Cretaceous, Maastrichtian, *Haustator bilira* Assemblage Zone.

Bathytormus pteropsis is like most other crassatellids in that it exhibits the largest degree of intraspecific variation in characters of the posterior margin and in the ratio of height to length. The summary statistics for the species are given in table 49. The extremes of posterior elongation can be seen by comparing plate 17, figures 12 and 14, a highly elongate form, to plate 17, figures 20 and

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[30] For a discussion of *Crassatella pteropsis* Gabb see the section "Distribution and validity of species" on pages 59–60.

TABLE 49.—*Minimum, maximum, and mean values for characters of* Bathytormus pteropsis

[See table 2 for an explanation of the morphological variables. Data source: digitized data set; excludes broken specimens and internal molds]

Morphological variable	Adults (29 specimens)			Juveniles (8 specimens)			Combined (37 specimens)
	Minimum	Maximum	Mean	Minimum	Maximum	Mean	Mean
CONVEX	3.52	7.90	5.63	1.71	4.42	3.21	5.11
LENGTH	22.59	33.29	28.96	10.43	20.41	17.24	26.43
HINGE	109.00	131.37	116.51	108.29	126.48	114.84	116.15
POST	88.99	179.28	139.25	82.87	131.08	105.98	132.06
ANTER	113.77	145.69	131.61	122.86	139.53	127.99	130.82
ANTVERHT	7.69	15.30	12.56	5.48	9.56	7.87	11.54
POSVERHT	6.71	13.55	10.93	6.21	8.81	7.82	10.26

21, an abbreviated form; plate 17, figure 9 illustrates an unusually high form for the species. The degree of posterior elongation causes concomitant changes in the slope of the posterior-dorsal margin. The posterior ridge of *B. pteropsis* is fairly prominent in mature adults (pl. 17, figs. 12, 15, 19), but the degree of prominence varies (compare pl. 17, figs. 12, 17). Variations in the posterior ridge cause slight differences in the posterior-ventral margin; some specimens have slight indentations anterior to the posterior ridge (pl. 17, fig. 12), and others have a straight posterior-ventral margin (pl. 17, fig. 20). The anterior dorsal margin varies from slightly convex (pl. 2, figs. 1, 3; pl. 17, figs. 12, 15) to straight (pl. 17, figs. 10, 21) immediately anterior to the beak. Inflation of the valves can range from flattened (pl. 2, fig. 2) to fairly convex (pl. 17, fig. 13).

The majority of the intraspecific variation in *Bathytormus pteropsis* is seen between individuals at various stages in their ontogeny. The nepionic stage of the shell is subcircular (pl. 20, fig. 6) but rapidly passes into suboval then to trapezoidal stages (pl. 20, fig. 1; pl. 17, figs. 1–4). The beak is sharply pointed, as in the adults, but is slightly prosogyrous and located closer to the midline of the shell than on adults. The posterior ridge becomes visible in very early stages (pl. 17, figs. 3, 4) but is not prominent. The broad and flattened posterior area on the juveniles gives the shell its trapezoidal appearance and forms a gently sloping posterior-dorsal margin. Hinge characters develop at very young stages (pl. 20, figs. 3, 4); the pallial line, muscle scars, and marginal crenulations do not appear until later (pl. 17, fig. 1). Ornamentation on the juveniles consists of very strong, evenly spaced ribs and faint, barely visible comarginal threads (pl. 20, fig. 6; pl. 17, figs. 3, 4). As *B. pteropsis* mature, the convexity of the valves increases, the slope of the posterior-dorsal margin increases, the posterior ridge becomes more prominent, the slope of the posterior area increases, the shell becomes orthogyrous, and the beak position shifts anteriorly (pl. 17, figs. 5, 7, 8). The sharpness of the ornamental ridges on the shell surface decreases with maturity, and in later stages the shell surface may show undulations (pl. 17, fig. 15). The ontogenetic changes of *B. pteropsis* are primarily gradual, and variations can be seen in the size at which the changes occur.

Bathytormus pteropsis can be distinguished from the early Tertiary *B. alaeformis* on the basis of detailed characters of dentition and ornament and of overall shape. Statistically, the characters of length and shape of the posterior margin were the primary discriminating variables between the two species. The cardinal tooth in the right valve of *B. pteropsis* is angled anteriorly, whereas the corresponding tooth in *B. alaeformis* is nearly vertical (compare pl. 17, figs. 9, 16 to pl. 18, fig. 12 and pl. 19, fig. 2). Although not diagnostic on young individuals, the ornament of large adult *B. alaeformis* fades ventrally in contrast to the umbonal ornament. The ornament of adult specimens of *B. pteropsis* is less prominent than that of the juvenile stages but is still distinctive. Adult *B. alaeformis* appear more prosogyrous, whereas adult *B. pteropsis* appear orthogyrous (compare pl. 17, fig. 13 to pl. 19, figs. 6–9). The posterior regions of the two species are distinctive: *B. alaeformis* has an extremely elongate, arcuate truncate posterior, with a subdued posterior ridge and flattened posterior area (pl. 21, figs. 14, 17); *B. pteropsis* is proportionately less elongate with a pointed posterior margin, prominent posterior ridge, and steeply sloping posterior area (pl. 21, figs. 10, 12). The juveniles of the two species can be distinguished by their outline: *B. pteropsis* juveniles are trapezoidal and *B. alaeformis* juveniles are subelliptical (compare pl. 20, figs. 1, 7).

Bathytormus pteropsis can be distinguished from all *Crassatella* by the generic differences in hinge structure (compare pl. 21, figs. 8 to fig. 10). *C. vadosa* occurs with *B. pteropsis* in the Upper Cretaceous sediments of the Gulf and Mid-Atlantic Coastal Plains. In addition to the differences in hinge structure, *C. vadosa* and *B. pteropsis* can be distinguished by the extent of posterior elongation compared to height, the pointed posterior, the convex posterior-dorsal margin, and the pointed beak of *B. pteropsis*. The hinge characters fail as diagnostic characters on the juveniles, but immature *B. pteropsis* are posteriorly elongate trapezoidal and have highly pointed slightly prosogyrous beaks, whereas immature *C. vadosa* are quadrate and have strongly prosogyrous beaks (compare pl. 20, fig. 1 to pl. 12, figs. 1–4). The hinge of *C. carolinensis* is more like that of a *Bathytormus* than any other *Crassatella*, but the fine ornament of *C. carolinensis* distinguishes it from *B. pteropsis*.

Historically, *Bathytormus pteropsis* has been confused most often with the highly variable *Crassatella hodgei*. Triangulate, posteriorly elongate forms of *Crassatella hodgei* lacking a produced posterior ridge can bear a striking resemblance to *B. pteropsis* (compare pl. 2, figs. 1, 3 to figs. 8, 11). I believe Conrad (1875, p. 6) may have found a *Crassatella hodgei* at Snow Hill, N.C. He questionably identified it as a juvenile *Crassatella pteropsis*, but he did not discuss the specimen, and the figure is so poor that it does not provide any further information. During the extensive search of USGS and USNM collections for this study, no specimens of *B. pteropsis* were found from beds equivalent to the lower Campanian deposits found at Snow Hill; *Crassatella hodgei*, however, is relatively abundant in the lower Campanian. Gabb (1877, p. 310) also may have confused the two species when, in referring to *Crassatella pteropsis*, he stated, "A rare shell at Pataula Creek, Georgia, though very common in North Carolina." No *B. pteropsis* have been identified in North Carolina, although they are a rare component of the sediments at Pataula Creek; *Crassatella hodgei*, however, are abundant in North Carolina. Finally, Richards (1950, figs. 61b, 61c) illustrates two specimens identified as *Crassatellites pteropsis* from Snow Hill, N.C., that appear to be *Crassatella hodgei*. As with other members of their genera, *Crassatella hodgei* and *B. pteropsis* can be distinguished on the basis of their hinge characteristics (compare pl. 4, figs. 14, 15 to pl. 17, figs. 16, 18). If details of the hinge cannot be seen on a specimen, however, *B. pteropsis* may be distinguished from *Crassatella hodgei* by its narrower posterior area, more concave posterior-dorsal margin, and more pointed beak.

Occurrence.—See table 50 for *B. pteropsis* localities, stratigraphic units, and collections studied. Refer to figure 2 and appendix 9 for locality positions and descriptions.

Stratigraphic Range.—Maastrichtian (fig. 19).

Type material examined.—USNM 20845; hypotype *Crassatella pteropsis* Conrad, Stephenson and Monroe. USNM 32291; hypotype *Crassatella pteropsis* Conrad, Gardner.

Subfamily SCAMBULINAE Chavan, 1952

Genus *Scambula* Conrad, 1869

Scambula CONRAD, 1869a, p. 48. CONRAD, 1872, p. 51. WHITFIELD, 1885, p. 123. WELLER, 1907, p. 562–563. WOODRING, 1925, p. 94 [in discussion of *Crassatellites*]. CHAVAN, 1939, p. 31–33. STEPHENSON, 1941, p. 182. SHIMER and SHROCK, 1944, p. 419. CHAVAN, 1952, p.120. CHAVAN, 1969, p. N577.

[non] Anthonya GABB, 1877, p. 311.

[non] *Anthonya* (*Scambula*) STEWART, 1930, p. 147–148 [discussed under Gouldiidae].

[non] *Crassatella* TRYON, 1884, p. 224. FISCHER, 1887, p. 1020–1022 [incorrectly lists *C. perplexa* Conrad as type species].

[non] *Crassatellites* (*Scambula*) DALL, 1903, p. 1468.

[non] *Crassatella* (*Scambula*) LAMY, 1916, p. 202–203.

Type Species.—*Scambula perplana* Conrad, 1869[a].

Conrad (1869a, p. 48) first identified the genus *Scambula* from a single, rather poorly preserved specimen from the Upper Cretaceous deposits in Haddonfield, N.J. His initial description gives little indication of the unique characters of the genus and simply states, "Hinge with two approximate teeth in the right valve, the posterior one direct and ending at the apex; a long anterior double tooth parallel with the straight cardinal line; anterior muscular impression small, rounded" (Conrad, 1869a, p. 48). A subsequent discussion of the genus and species (Conrad, 1872, p. 51) provides more detail, including the compressed character of the valve and the unique nature of the hinge.

Considering the rare occurrence of *Scambula*, it has received considerable attention in the literature. *Scambula* has alternately been recognized as a distinct genus, as a synonym of other genera, or as a subgenus. Gabb (1877) considered *Scambula* a junior synonym of *Anthonya* Gabb; he stated that the hinges agree perfectly and that the only significant difference is that *Scambula* occurs in one plane, while *Anthonya* is twisted. Stewart (1930, p. 147) agreed with Gabb, and he included *Scambula* as a subgenus of *Anthonya* in the family Gouldiidae. *Scambula* was listed as a synonym of *Crassatella* by Tryon (1884, p. 224) and Fischer (1887, p. 1022). Dall (1903, p. 1464–1465) believed Conrad's species represented a juvenile of *Crassatellites*. He discusses *Scambula* as a section of *Crassatellites*, describing it as "Valves with the nepionic shell flattened, the adult usually elongated, the third right cardinal obsolete or absent, the resilium large; the inner margins of the valves rarely crenate but usually smooth" (Dall, 1903, p. 1467). Many of the species included in Dall's *Crassatellites* (*Scambula*) have later been reassigned to *Bathytormus* or *Eucrassatella*; these species do not possess the generic characters identified by Conrad (1869a; 1872) in his original description of *Scambula*. Lamy (1916, p. 202) agreed with Dall, whereas Woodring (1925, p. 94) points out the errors in Dall's assignment.

Whitfield (1885), Weller (1907), and Stephenson (1941) were among the authors who maintained *Scambula* as a distinct genus. Stephenson (1941, p. 182) stated, "although this genus [*Scambula*] differs considerably in form and proportions from *Crassatella*, it appears to be more closely allied to that genus than to the Gouldiidae in

TABLE 50.—Bathytormus pteropsis—*Occurrence and collections studied*

[Fm, Formation. Collection number: USNM (U.S. National Museum) collection or specimen numbers, unless otherwise noted; USGS, U.S. Geological Survey]

Locality number	State	County	Stratigraphic unit	Collection number
30A	Mississippi	Tippah	Ripley Fm, Coon Creek Tongue	450493, 451063.
31	do	Union	do	451064, 451065.
32	do	do	do	451066.
33	do	do	Ripley Fm	450492, 451070.
34A	do	do	do	20845, 450566–450568.
37	Georgia	Quitman	do	451081.
39	Alabama	Barbour	do	450487, 450488, 451082.
43	do	do	do	450496, 450498, 451086–451089, 451092.
44	Georgia	Quitman	do	450495, 451073, 451084, 451090.
45	do	do	do	450494, 451091.
46	do	do	do	USGS 25998.
60	Alabama	Barbour	Providence Sand	451085, 459094.
61	do	Barbour/Henry	do	451074.
62A	do	do	do	450489, 453877.
63	Georgia	Clay	do	450490, 450491, 450499, 450816, 451072, 451075.
64	do	do	do	451076.
65	do	Quitman	do	451078.
67	do	Clay	do	451083.
70	Maryland	Prince George's	Severn Fm	451099.
71	do	do	do	451095.
75	do	do	do	32291, 450497.

which Stewart places it." Chavan not only maintained *Scambula* as a distinct genus (Chavan, 1939), but also used the genus as the type for the subfamily of Crassatellidae, Scambulinae (Chavan, 1952, 1969). The relationship between *Bathytormus* and *Scambula* is discussed by Chavan (1939, p. 32); he believes *Scambula* "represents an evolved condition which is less advanced."

Within the Upper Cretaceous of North America only one species of *Scambula* is known (fig. 19). Only two other species names have been proposed for the genus since the definition of *Scambula* and *S. perplana* by Conrad (1869a, p. 48). *S. widmeri* was proposed by Richards (1962, p. 204) but is herein synonymized with *S. perplana*. *S. gilleti* was proposed by Chavan (1939, p. 32–33) for a specimen discussed and figured by Gillet (1921, p. 13–14, pl. 1, figs. 13–14) as *Astarte sinuata* from the Barremian (Lower Cretaceous) of Wassy, France. An examination of Gillet's figures indicates that Chavan is correct in assigning these specimens to the genus *Scambula*; however, Chavan's schematic drawing of *S. gilleti* is an inaccurate reproduction of Gillet's original figures. Her specimens bear a resemblance to *S. perplana*, but the posterior margins are broken; Chavan illustrated whole specimens having a quadrate posterior. Additionally, it seems likely that *Scambula* existed in the Cenomanian (lowermost Upper Cretaceous) of North Africa. Newton (1916, p. 572, pl. I, figs. 15, 16) illustrated and described a specimen identified as *Anthonya* cf. *baudeti* Coquand from Angola, which I believe is actually a *Scambula*. I have not examined any specimens of *Scambula* from the Cretaceous deposits of Europe or Africa, but it is unlikely that the range of *S. perplana* would extend down into the Lower Cretaceous. The genus *Scambula*, therefore, seems to have at least two or three species worldwide, restricted to the Cretaceous.

Scambula is recognized herein as a unique, rare genus of Crassatellidae within the geographic and stratigraphic ranges of this study.

Scambula perplana Conrad, 1869

Plate 2, figure 6; plate 20, figure 2;
plate 21, figures 1–5, 7, 9.

Scambula perplana CONRAD, 1869a, p. 47, pl. 9, figs. 7, 8. CONRAD, 1872, p. 51, pl. 1, fig. 2. WHITFIELD, 1885, p. 123–124, pl. 18, figs. 8–10. WELLER, 1907, p. 562–563, pl. figs. 13, 14. WADE, 1926, p. 82, pl. 25, figs. 11, 12, 15, 16. CHAVAN, 1939, p. 32 [in discussion of *Crassinella* and related genera]. STEPHENSON, 1941, p. 183, pl. 26, figs. 11, 12. SHIMER and SHROCK, 1944, p. 419, pl. 167, figs. 6, 7. STEPHENSON, 1955, p. 118, pl. 18, figs. 3–5. RICHARDS, 1958, p. 192, pl. 32, fig. 9.

Crassatella perplana (Conrad). STOLICZKA, 1871, p. 294, 295.

Crassatellites (Scambula) perplanus (Conrad). JOHNSON, 1905, p. 14.

Anthonya (Scambula) perplana (Conrad). STEWART, 1930, p. 147, 148.

Scambula widmeri RICHARDS, 1962, pt. 2, p. 204, pl. 93, figs. 19, 20.

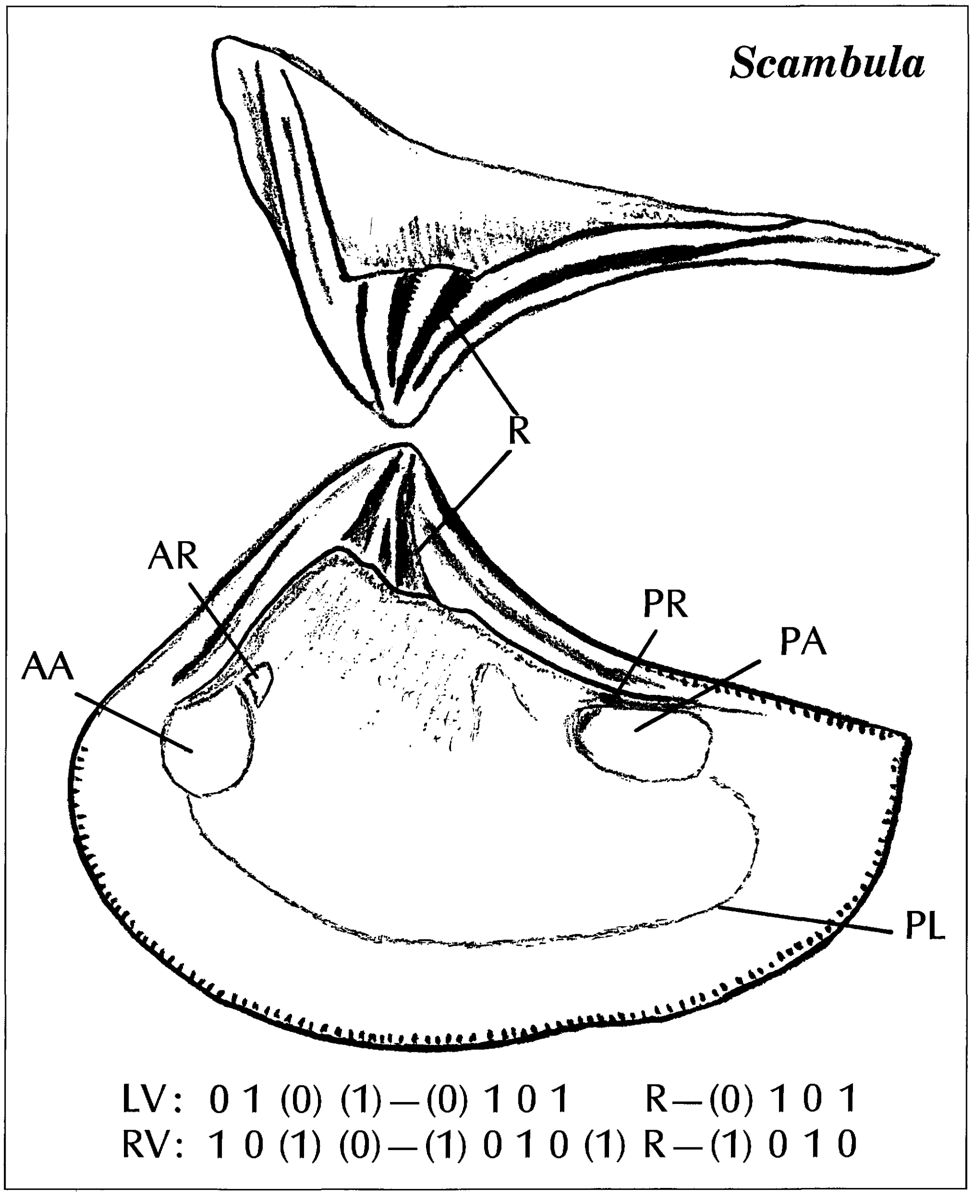

FIGURE 21.—Hinge characters and musculature of *Scambula*. Dental formulas are the reverse of the text and figures 18 and 20 and are read from the anterior lateral ridges to the posterior lateral ridges. LV, left valve; RV, right valve. AA, anterior adductor; AR, anterior pedal retractor; PA, posterior adductor; PL, pallial line; PR, posterior pedal retractor; R, resilifer.

Diagnosis.—Shell flat, triangular, opisthogyrous, with high pointed beaks. Raised posterior ridge absent. Anterior dorsal margin steeply sloping; anterior margin turns abruptly to ventral margin. Posterior dorsal margin concave. Ornament fine comarginal growth threads overlying broad rounded ribs, separated by incised fine lines. Cardinal teeth and resilifer narrow and posteriorly curved. Two independent pedal retractors present above the adductors and underneath the ventral edge of the lateral ridges (see fig. 21 for position of muscle scars).

Description.—Shell equivalve, flat; outline of shell triangular, adults posteriorly elongate, juveniles approaching equilateral. Inequilateral; beak position of adults at approximately anterior two-fifths shell length, juveniles closer to midlength of shell; beak high, pointed, opisthogyrous. Anterior dorsal margin straight to slightly convex, slopes steeply down to ventral margin; lunule extremely narrow, elongate; anterior margin turns abruptly to ventral margin. Posterior dorsal margin concave, slopes steeply away from beak, levels out above anterior termination of posterior adductor; escutcheon elongate, narrow, flattened; raised posterior ridge absent, posterior area demarcated by bend in ornament alone; posterior margin truncate. Ventral margin broadly rounded, shell material thickened at edge. Ornament consistent across shell surface; fine ornament of comarginal growth threads overlies dominant ornament of rounded raised ribs, separated by incised fine lines; lamellae of ribs may extend past dorsal margins giving rugose appearance. Hinge angle approaches right angle; moving from posterior lateral ridges across hinge plate to anterior lateral ridges, dentition noted as follows:

Right Valve 0 1 0 (1)—R(1) 0 1 0 (1)-(0) (1) 0 1
Left Valve 1 0 1 (0)—R 1 0 1 (0)-(1) (0) 1 0

Right valve dentition consists of one sharp raised posterior lateral ridge extending from beak to above posterior adductor, separated by shallow furrow from second faint posterior lateral ridge that fades into resilial area; elongate, narrow, triangular resilifer originates at beak, extends to edge of hinge platform, curves posteriorly; anteriorly very narrow trigonal socket separated from resilifer by low, sharp, narrow ridge; ridge almost bifurcation of posterior edge of cardinal; one strong medial cardinal tooth anterior to beak, curves posteriorly, vertical striations present on sides of tooth; deep, narrow, elongate socket separates strong medial cardinal from faint, narrow, low anterior ridge, which blends ventrally into hinge platform; one short anterior lateral ridge, separated by groove from long anterior lateral ridge, extends length of anterior dorsal margin to above anterior adductor. Left valve dentition consists of two sharp posterior lateral ridges, separated by deep groove; both posterior lateral ridges extend from above posterior adductor to beak but interior-most ridge fades slightly near beak; elongate, narrow, triangular resilifer originates at beak, extends to edge of hinge platform; two narrow cardinals separated by deep narrow socket, all curve posteriorly; anterior-most cardinal slightly broader; anterior-side of posterior cardinal and both sides of anterior cardinal covered with vertical striations; faint anterior lateral ridges continuous with edge of hinge platform, separated by groove from sharp anterior lateral ridge extending from beak along anterior dorsal margin to above anterior adductor. Edge of hinge platform continuous with umbonal cavity; cavity beneath hinge platform absent. Two subequal shallow adductor muscle scars, anterior oval, posterior subelliptical. Anterior and posterior pedal retractor scars independent, small, subcircular, located above adductor scars. Pallial line faint, entire. Fine, sharp marginal crenulations present from anterior lateral ridges ventrally to posterior lateral ridges. Prodissoconch not seen.

Discussion.—Conrad (1869a, p. 47) named *Scambula perplana* from a single specimen recovered from Cretaceous units in Haddonfield, N.J. Richards (1958, p. 192) identified ANSP 18740 (see pl. 2, fig. 6) as Conrad's type specimen, but this specimen is a left valve and is imbedded in matrix so that the exterior is not visible. Conrad, however, figures the exterior as well as the interior of a right valve of *S. perplana* (Conrad, 1869a, pl. 9, figs. 7, 8), so ANSP 18740 is clearly not the holotype specimen. Stephenson (1941, p. 183) mentions the existence of three left valves and two right valves at ANSP; presumably, if these specimens still exist, one of the right valves is the holotype.

Conrad (1872, p. 51) points out, "The hinge of this shell [*Scambula perplana*] is very distinct from that of *Crassatella*." On the basis of these fundamental differences in hinge structure, in addition to other distinctive characteristics of the species, most subsequent authors have maintained *S. perplana* in a separate genus. The exceptions are Stoliczka (1871, p. 295) and Johnson (1905, p. 14). Stoliczka believes *S. perplana* is similar to the Recent species *Crassatella radiata* and therefore should remain in the genus *Crassatella*. Weller (1907, p. 562, 563) is the first worker to find the species outside of the type locality; his collections are from the Woodbury Clay, Lorillard, N.J., and the Wenonah Formation, near Marlboro, N.J. The first recognition of *S. perplana* in the Gulf Coast Cretaceous deposits came in faunal lists of Stephenson (1914, p. 24, tables 2, 8), and the first illustration of *S. perplana* from the South was in Wade (1926, p. 82). Stephenson later expanded the range of *S. perplana* to Texas (Stephenson, 1941, p. 183) and Missouri (Stephenson, 1955, p. 118). In 1962, Richards identified a new species of *Scambula*, *S. widmeri*, from the Woodbury Clay of New Jersey and distinguished it from *S. perplana* on the basis of its small size and coarser sculpture. From the Richards (1962, p. 204, pl. 93, figs. 19, 20) illustration and description of the ornament and shape of *S. widmeri*, I believe it to be a juvenile of *S. perplana*, although the type specimen (ANSP 30750) has not yet been examined.

Variations in the shape of the posterior margin account for the largest degree of intraspecific diversity seen in *Scambula perplana* (see table 51 for the summary statistics for the species). The degree of posterior elongation is primarily a result of ontogeny, but differences can be seen among similarly sized individuals (compare pl. 21, fig. 1 to fig. 5). The typical posterior margin for *S. perplana* is truncate and flattened, as seen in plate 21, figure 5, but occasionally the posterior is almost pointed (pl. 21, fig. 1) or rounded. The more elongate the specimen, the flatter the ventral margin becomes

TABLE 51.—*Minimum, maximum, and mean values for characters of* Scambula perplana

[See table 2 for an explanation of the morphological variables. Data source: digitized data set; excludes broken specimens and internal molds]

Morphological variable	Adults (32 specimens)		
	Minimum	Maximum	Mean
CONVEX	0.34	1.00	0.62
LENGTH	3.28	16.37	8.04
HINGE	83.29	103.73	92.38
POST	119.25	163.05	145.23
ANTER	118.00	173.65	144.76
ANTVERHT	1.44	5.90	3.40
POSVERHT	1.37	5.69	3.50

compare pl. 21, figs. 3, 5), but the ventral margins of specimens of the same length can vary from flattened to rounded. Variations in the anterior dorsal margin range from straight (pl. 21, fig. 5) to slightly convex (pl. 21, fig. 7). Internally, the configuration of the hinge and the adductor muscle scars is fairly constant within the species (fig. 21) (pl. 21, figs. 3, 5). The pedal retractors, however, can be obvious and well defined or absent.

It is rare to find unabraded specimens of *Scambula perplana*, so few individuals preserve the fine details of the ornament (compare pl. 20, fig. 2 and pl. 21, fig. 7 to pl. 21, figs. 1, 2, 4). The ornament seen on well-preserved specimens, however, is consistent with the remnants seen on abraded shells, with the exception of the laminae, which extend past the dorsal margins of the shell (pl. 21, figs. 1, 4) giving a rugose appearance to those edges. The laminae have not been observed on well-preserved individuals, leaving some doubt as to whether this is a preservational or ontogenetic character or if it truly is a specific difference. All of the specimens found to preserve the details of ornament in this study were juveniles, and I believe it was this preservational bias that led Richards (1962, p. 204) to assign the name *S. widmeri* to small specimens of *S. perplana* with the ornament intact. Abrasion of shells can also affect the appearance of the beak (pl. 21, fig. 1) and the marginal crenulations.

The nepionic portion of *Scambula perplana* begins as a nearly equilateral triangular specimen, having virtually no posterior area and a steeply sloping, straight posterior dorsal margin (pl. 20, fig. 2). As the shell matures, the posterior becomes more and more elongate. Elongation causes the beak to shift anteriorly, so the shell becomes increasingly inequilateral. At these intermediate juvenile stages, the ventral margin is usually rounded, the hinge structure fully developed, and the posterior dorsal margin is concave; the muscle scars, pallial line, and marginal crenulations are faint or absent. Continued growth in the posterior direction produces an inequilateral adult, typically having a slightly flattened ventral margin, truncate posterior margin, strongly concave posterior dorsal margin, and fully developed muscle scars, pallial line, and marginal crenulations.

Scambula perplana can be distinguished from all other crassatellids considered in this study by the following generic characteristics. The opisthogyrous beaks and strongly concave posterior dorsal margin are unique and immediately apparent upon examination (compare pl. 21, figs. 4, 5 to figs. 6, 8 and to figs. 10, 12). The extremely flat shell also distinguishes *Scambula*; even juveniles of the other crassatellids studied have a higher degree of convexity. This distinction proved to be the key discriminating variable in the statistical analysis. Finally, the primary distinguishing characteristic is the hinge. The hinge structure of *Bathytormus* bears the most resemblance to that of *Scambula*, as Chavan (1939, p. 32) pointed out; both genera have a resilifer that extends from the beak to the edge of the hinge plate (compare figs. 20, 21; compare pl. 21, figs. 5, 10). The hinge platform of *Scambula*, however, is very narrow, as are the teeth and the resilifer, and the ventral margin of the hinge platform slopes posteriorly. The right valve of *Scambula* exhibits two posterior lateral ridges, and the left valve, two anterior lateral ridges; all other crassatellids studied have one ridge. The right valve of *Scambula* has a low ridge, anterior to the cardinal tooth, that fades into the hinge platform; on *Bathytormus* this anterior ridge is the dorsal edge of the hinge. The teeth and sockets of *Scambula* are curved posteriorly, and the sides of the teeth are covered with distinctive vertical ridges, as opposed to the transverse ridges seen on some *Crassatella* and *Bathytormus*.

Occurrence.—See table 52 for *S. perplana* localities, stratigraphic units, and collections studied. Refer to figure 2 and appendix 9 for locality positions and descriptions.

Stratigraphic Range.—Lower Campanian through Maastrichtian.

Type material examined.—ANSP 18740; supposed holotype *Scambula perplana* Conrad.

PATTERNS AND TRENDS AMONG THE CRASSATELLIDAE

The quantitative and qualitative analysis of the Crassatellidae resolves the initial question of the validity of the generic and specific names presented in table 1. More questions are raised than answered, however, about the evolutionary history and biogeographic patterns of the Crassatellidae.

The crassatellids of the Gulf and Mid-Atlantic Coastal Plains appear in the lowermost Campanian in the form of two species, *Crassatella hodgei*, an extremely variable species, and *C. carolinensis*, an extremely conservative

TABLE 52.—Scambula perplana—*Occurrence and collections studied*

[Fm, Formation. Collection number: USNM (U.S. National Museum) collection or specimen numbers, unless otherwise noted; ANSP, Academy of Natural Sciences of Philadelphia]

Locality number	State	County	Stratigraphic unit	Collection number
4............	Georgia	Stewart	Blufftown	453880.
14............	New Jersey	Camden	Woodbury Clay	ANSP 18740.
15............	....do........	....do........	....do........	450505, 453889.
27............	Tennessee	McNairy	Coon Creek Fm	450508, 451062, 451096.
31............	Mississippi	Union	Ripley Fm, Coon Creek Tongue	451064.
33............	....do........	....do........	Ripley Fm	450503, 451070.
37............	Georgia	Quitman	....do........	450504, 451081.
38A...........	....do........	....do........	....do........	451093.
41............	Alabama	Barbour	....do........	451103.
42............	Georgia	Quitman	....do........	451077.
43............	Alabama	Barbour	....do........	450506, 450507, 451086, 451092, 454609.
44............	Georgia	Quitman	....do........	451090.
45............	....do........	....do........	....do........	451091.
50............	Mississippi	Union	Owl Creek Fm	453869.
55............	Alabama	Montgomery	Prairie Bluff Chalk	453883.
63............	Georgia	Clay	Providence Sand	453897.

species (fig. 19). Both of these forms are rare, and which, if either of them, was the ancestor to the upper Campanian and Maastrichtian crassatellids is uncertain. The more open resilifer of *C. carolinensis* indicates that *C. carolinensis* may have given rise to *Bathytormus pteropsis*, but the juvenile *C. carolinensis* resembles the juvenile of *C. vadosa*. On the other hand, the more restricted resilifer of *C. hodgei* implies that *C. hodgei* is the ancestral *C. vadosa*, yet, in its posteriorly elongate form, it resembles *B. pteropsis* exteriorly. Consequently, either species could have been the precursor to *B. pteropsis* or to *C. vadosa*. Alternately, the *C. hodgei* and *C. carolinensis* lineages may have died out, but an ancestral *Crassatella* may have survived and spawned the younger forms. The concurrent ranges of *C. vadosa* and *C. hodgei* are based on the identification of a single specimen, the type *Gouldia conradi* Whitfield, as a juvenile *C. vadosa*. The condition of this specimen makes the determination questionable as discussed in the "Systematic Paleontology" section (p. 65–66). Whether the range of *C. vadosa* extends from the Maastrichtian into the lower Campanian or not, the pattern of stratigraphic occurrence of *C. hodgei* and *C. vadosa* suggests gradual evolutionary change from *C. hodgei* to *C. vadosa*.

In the Maastrichtian, three species representing three genera occur throughout the geographic range of this study: *Crassatella vadosa*, *Bathytormus pteropsis*, and *Scambula perplana*. *C. vadosa* is an abundant and morphologically varied species; *B. pteropsis* and *S. perplana* are rare species having low intraspecific variation. As stated above, the origin of *C. vadosa* and *B. pteropsis* is uncertain, but they seem to have arisen during the Campanian. *Scambula* probably arose during the Early Cretaceous (see discussion, p. 89), but it does not cross the Cretaceous-Tertiary boundary.

Paleocene sediments in the study area contain two species of *Crassatella*, *C. aquiana* and *C. tumidula*, and one species of *Bathytormus*, *B. alaeformis*. *C. vadosa* may be the predecessor of *C. aquiana* and *C. tumidula*, or *C. aquiana* and *C. tumidula* may be descended from a species outside the region of study. Certainly there is a strong resemblance between *C. aquiana* and *C. vadosa*. *B. pteropsis*, the only known Cretaceous member of that genus identified to date, is logically the ancestor of *B. alaeformis*.

No ancestral-descendent relationships can be proven for this group of crassatellids, but a phylogenetic analysis incorporating fauna from other regions and stratigraphic levels should be conducted. At present, the pattern appears to be one of gradual evolutionary change. All of the fauna studied herein can be united through the characters of their juveniles, and it may be the juveniles that provide the best clues to the patterns of evolution among the Crassatellidae. Dall (1903, p. 1464) implied that the crassatellid resilifer has progressively descended across the hinge plate through time. The pattern is not quite that simple; the lower Campanian forms of *Crassatella hodgei* and *C. carolinensis* possess less restricted resilifers than do the younger *C. vadosa*. One explanation for the open resilifers characteristic of *Bathytormus* and *Eucrassatella* may be the neotenous retention of juvenile hinge characters. Juvenile *Crassatella* have resilifers that open to the edge of the hinge platform; these juveniles may be confused with adult

Bathytormus. Possibly, the retention of the open resilifer later and later into adulthood produced a progressive phylogenetic trend from *Crassatella* to *Bathytormus* and from *Bathytormus* to *Eucrassatella* (compare pl. 21, figs. 8, 10, 15, 17). One piece of evidence supports this theory; on very large *B. alaeformis* the resilifer no longer extends entirely to the hinge plate (pl. 21, fig. 17, for example), indicating that a retracted resilifer, the adult condition for *Crassatella*, is a geriatric character for *Bathytormus*. *Scambula*, however, may play an important role in the development of the resilifer that is not yet understood. Perhaps *Scambula*, which first appears in the Lower Cretaceous, is the precursor to *Bathytormus*, and *Crassatella* represents the evolved condition.

Another question, which requires more data to be answered, is whether iterative evolution occurs within the Crassatellidae. There is some evidence in this data set to suggest that certain morphologic shapes are repeated at different intervals in time. Compare, for example, *Crassatella hodgei* (pl. 5, fig. 12), *C. vadosa* (pl. 10, fig. 10), and *C. aquiana* (pl. 14, fig. 15). Whether this similarity in form is the result of response to the environment, limitations of the basic bauplan, or a little of both is unknown at present.

The biogeographic distribution of *Bathytormus* and *Crassatella* before and after the Cretaceous-Tertiary boundary reveals an interesting pattern. *Bathytormus* is rare in the Upper Cretaceous, but it is found from Maryland to the Gulf Coast. *Crassatella* is an abundant member of the Upper Cretaceous fauna, and its distribution pattern is similar to that of *Bathytormus*. On the Tertiary side of the boundary, a very different pattern is seen. *Bathytormus*, restricted to the Mid-Atlantic region, is the abundant crassatellid, whereas *Crassatella* is a sparse component of the fauna. A few individuals of *C. aquiana* occur in the Mid-Atlantic Coastal Plain Paleocene deposits, but it is far more abundant in the Gulf Coast sediments. The implication is that *Bathytormus* is a cool water form, and *Crassatella*, a warm water form, but many other factors could explain this distribution.

The evolutionary and biogeographic patterns illustrated through a quantitative and qualitative analysis of the Crassatellidae provide some insight into the natural history of this family of molluscs and present many avenues for future research. Through such detailed analyses of other individual families, we can better understand the patterns of faunal change through time.

CONCLUSIONS

Through quantitative and qualitative analyses, this study demonstrates the high degree of inaccuracy of the published faunal record for one family of molluscs, the Crassatellidae, within the limited geographic and stratigraphic region of the Upper Cretaceous and lower Tertiary deposits of the Gulf and Mid-Atlantic Coastal Plains of the United States. Previous authors applied 38 specific names and 4 generic names to crassatellids within the limits of this study (table 1). Of the 38 original specific names, only 8 are valid recognizable species (fig. 19). Of the remaining 30 specific names, 14 were synonymized with the valid species, 11 are assigned to indeterminant internal molds or poorly preserved specimens, 1 was invalid, and no representative specimen could be located for 4 of the names. Three of the four genera were well founded; the fourth was based on the juvenile of another genus and therefore synonymized.

Crassatellidae at the Cretaceous-Tertiary boundary.— In addition to demonstrating the inaccuracy of the published fossil record, this analysis illustrates the following points for the Crassatellidae within the geographic and stratigraphic limits of this study:

- Rates of evolution and extinction based on previously published data are biased toward higher rates (fig. 22),
- Faunal change did occur at the boundary, but it was not catastrophic (compare published data to data from this paper, fig. 19),
- The number of species remained constant on each side of the boundary (fig. 23),
- A decrease in faunal abundance occurred in the early Tertiary, and
- The published data is biased toward higher species diversity, shorter average species durations, and restricted geographic ranges.

Rates of evolution and extinction calculated by using the published faunal record are two to four times too high (fig. 22). Averaging the 38 published specific names (table 1) over the 30-million-year time span covered by this study, the published record gives a rate of evolution of 1 new species every 790,000 years. On the basis of the eight valid species presented in this paper, this rate decreases to one species every 3.75 million years (fig. 22). Even if the 11 indeterminant species are added into this equation, the rate is only 1 species every 1.57 million years.

If the data are evaluated separately for each side of the Cretaceous-Tertiary boundary, the published faunal record for the Crassatellidae gives the appearance of dramatic turnover. Twenty-five of these 38 published species names are cited for the Upper Cretaceous, and 13 are cited for the Tertiary; a tremendous number of crassatellids seem to have gone extinct at the Cretaceous-Tertiary boundary and apparently were replaced during a period of rapid rebounding evolution in

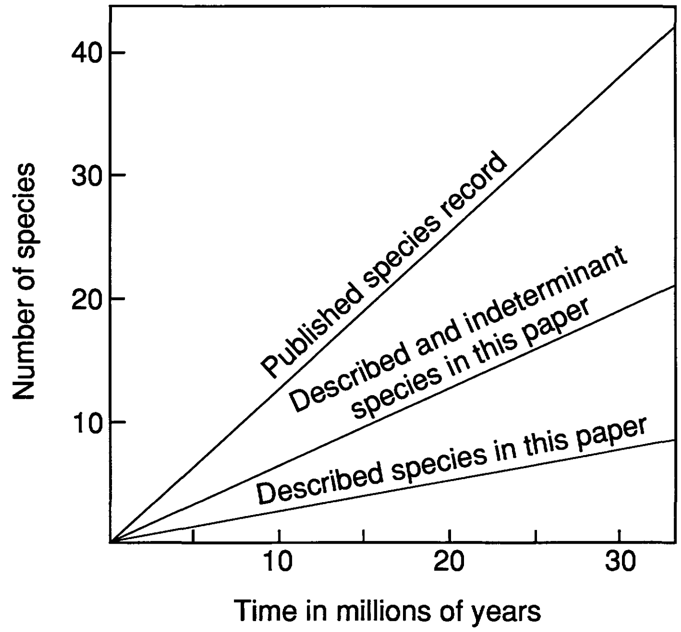

FIGURE 22.—Evolutionary rates based on the published fossil record compared to data obtained in this study. The published fossil record lists 38 species for the 30 million years covered by this study; the rate for the published record is illustrated on the upper line. Only eight of these species proved to be valid and are described in this paper; the rate for the described species is shown on the lower line. Even if the 11 indeterminate internal molds and poorly preserved specimens are included, the rate is still one-half that of the published record; the rate for the combined data set of described and indeterminant species is shown on the middle line. Rates illustrated are taxonomic frequency rates, which measure the number of species per million years. This diagram is a simplistic illustration of the contrast in rates between the published fossil record and the data contained here; it is not intended as an example of the way rates should be calculated.

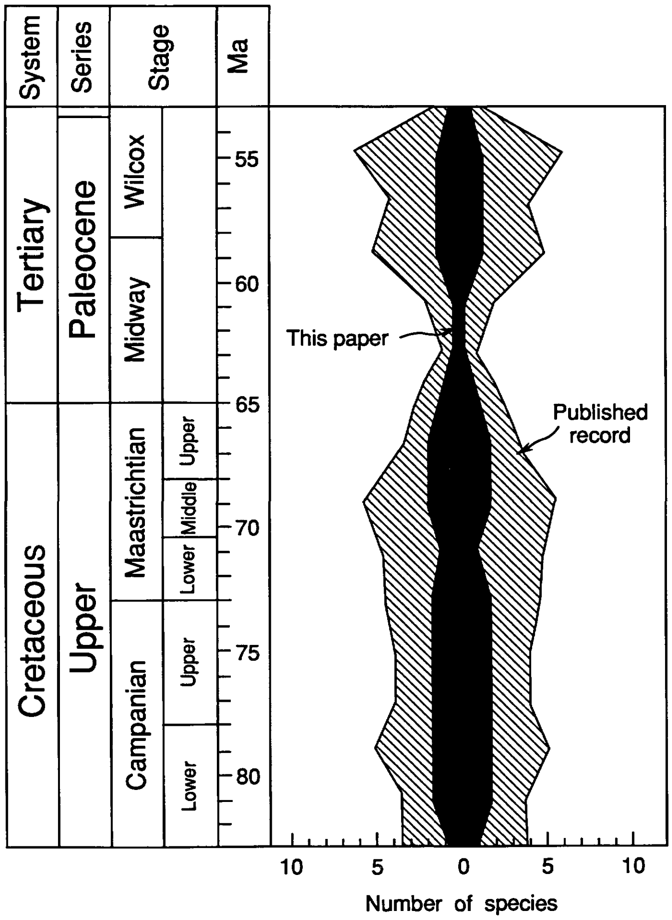

FIGURE 23.—Diversity patterns from the published record of Crassatellidae compared to the diversity patterns illustrated in this study. Information is restricted to the Campanian through Wilcox Stages of the eastern Gulf and Mid-Atlantic Coastal Plains.

the Paleocene. If rates of extinction are averaged over the 18-million-year span of the Upper Cretaceous, the published record indicates that one species went extinct every 720,000 years; the data presented here indicate that only one species went extinct every 3.6 million years on an average. For the Paleocene, the rate of evolution based on the published record would appear to be one new species every 920,000 years; however, the data in this analysis show a rate of only one new species every 4 million years.

In contrast to the catastrophic turnover illustrated in the published fossil record, this analysis illustrates an even faunal exchange, in terms of the number of species, for the Crassatellidae at the Cretaceous-Tertiary boundary. Five well-founded species went extinct during the Upper Cretaceous, three of these just below the boundary, and three well founded species appear in the Paleocene (figs. 19, 23). The genera of Crassatellidae show a decrease in diversity from three in the Upper Cretaceous to two in the Paleocene; the genus *Scambula* became extinct at the end of the Mesozoic.

Although diversity did not change much across the boundary, abundance of individuals seems to decrease dramatically in the Tertiary; 642 specimens of Cretaceous crassatellids were located for the quantitative analysis, but only 342 Tertiary crassatellids were located. This disparity in numbers may be the result of sampling bias, but I believe it is probably a reflection of a true decrease in numbers during the Tertiary. Every collection studied contains a larger number of Cretaceous individuals, and in addition the literature contains references to crassatellid occurrences in approximately the same proportions. I therefore conclude that Crassatellidae abundance truly did decrease in the Paleocene.

The net result of the splitting of the Crassatellidae demonstrated in this analysis, or of any group of organisms, is that basic paleobiologic information is compromised. Figures 19 and 23 illustrate the extent to which splitting can inflate measurements of species diversity. Intuitively, species durations are expected to be shortened by splitting, but averaging reduces any dramatic differences. The average species duration for the published fossil record of the Crassatellidae is 6.9 Ma; for the data presented here it is 8.4 Ma. When evaluating individual species durations, however, the stratigraphic ranges may increase, decrease, or remain the same following taxonomic standardization. *Crassatella vadosa* and *C. aquiana* display the expected increase in species duration (fig. 19) following synonymization, but the range of *C. hodgei* remains the same (or is shorter if you discount the questionable portion of the range). Species that were not synonymized (*C. tumidula* and *C. carolinensis* for example, fig. 19), tend to have shorter ranges after evaluation, due to revised stratigraphic information. Splitting also affects the geographic ranges of species. The published fossil record for the Crassatellidae contains many geographic isolates, for example *C. carolinana*, that have been synonymized with other species, thus broadening the geographic range.

Significance to evolutionary studies.—The high degree of inaccuracy of the published fossil record demonstrated for the Crassatellidae in this analysis raises questions about the use of published fossil data. If other groups of molluscs, and other organisms in general, exhibit the same degree of splitting illustrated here for the Crassatellidae, then studies based on the published fossil record are biased in the following ways:

- Rates of evolution and extinction are higher,
- Faunal turnover at mass extinctions appears more catastrophic,
- Species diversity is high,
- Average species durations are shortened, and
- Geographic ranges are restricted.

It may be that the Crassatellidae are the exception, not the rule; perhaps lumping of species is more common in the published fossil record, in which case the opposite bias would be seen. However, preliminary examination indicates that the problems illustrated here for the Crassatellidae are representative of the problems seen in the published literature for other groups of molluscs. Either way, it is important to do similar detailed taxonomic studies on other families of molluscs and other organisms in general in order to test the patterns illustrated for the Crassatellidae. The fossils themselves should be the source of data, not the literature, when we examine questions of paleobiologic significance. Evolution and extinction occur within small populations of species groups, and it is only through detailed analysis of those groups that we will achieve an understanding of the causes and effects of evolution and extinction.

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INDEX TO TAXONOMIC NAMES

[Italic numbers indicate primary discussion]

APPENDIXES 1–9

Appendixes 1 to 8 summarize the data provided for each discriminant analysis described in the chapter "Statistical Analysis." These data indicate how samples were classified for the statistical analysis only. In some cases, published species were incorrectly identified, as discussed in the text; therefore, these tables should not be used as indicators of species occurrence. Species occurrence tables are in the section "Systematic Paleontology."

Appendix 9 is the locality register.

APPENDIX 1

Data on specimens included in the analysis of subspecies of Crassatella vadosa, *comprising adult whole specimens only*

[For the purpose of the analysis, each subspecies was treated as a "species" category. Collections listed according to sequence of statistical analysis. Fm, Formation. Locality number corresponds to numbers on figure 2 and in appendix 9. Collection number: USNM (U.S. National Museum) collection or specimen numbers, unless otherwise noted; ANSP, Academy of Natural Sciences of Philadelphia]

"Species"[1]	Number of specimens[2]	Stratigraphic unit	State	County	Locality number[3]	Collection number
Crassatella vadosa	10	Owl Creek Fm	Mississippi	Tippah	52	451069
	1	Providence Sand	Georgia	Clay	63	451075
	1	Severn Fm	Maryland	Prince George's	72	451055
	4	....do........	....do........	....do........	73A	450520
	5	....do........	....do........	....do........	75	32291
Total	21					
Crassatella "ripleyana"........	3	Owl Creek Fm	Mississippi	Tippah	52	ANSP 18741
	2	....do........	....do........	....do........	52	128139
	14	....do........	....do........	....do........	52	450851
	1	....do........	....do........	....do........	52	451052
	4	....do........	....do........	....do........	52	450510
	2	....do........	....do........	....do........	52	451054
	7	....do........	....do........	....do........	51	451068
Total	33					
Crassatella "wadei"............	30	Coon Creek Fm	Tennessee	McNairy	27	451056
	31	....do........	....do........	....do........	27	451057
	29	....do........	....do........	....do........	27	451062
	1	....do........	....do........	....do........	27	32784
Total	91					

[1] Total "species": 3.
[2] Total specimens: 145.
[3] Total localities: 7.

APPENDIX 2

Data on specimens included in the analysis of subspecies of Crassatella vadosa, *comprising adults, juveniles, broken specimens, and internal molds*

[For the purpose of the analysis, each subspecies was treated as a "species" category. Collections listed according to sequence of statistical analysis. Fm, Formation. Locality number corresponds to numbers on figure 2 and in appendix 9. Collection number: USNM (U.S. National Museum) collection or specimen numbers, unless otherwise noted; ANSP, Academy of Natural Sciences of Philadelphia. —, no specimen for column]

"Species"[1]	Number of specimens[2]	Stratigraphic unit	State	County	Locality number[3]	Collection number	Number of broken specimens and internal molds	Number of juveniles
Crassatella vadosa	12	Owl Creek Fm	Mississippi	Tippah	52	451069	2	—
	2	Prairie Bluff Chalk	Alabama	Wilcox	57	450502	2	—
	4	....do........	....do........	....do........	58	450820	4	—
	12	....do........	....do........	....do........	56	450500	12	—
	4	....do........	....do........	....do........	56	450853	4	—
	1	....do........	....do........	....do........	56	ANSP 19593	1	—
	10	....do........	....do........	....do........	59A	451071	10	—
	16	....do........	....do........	....do........	59A	451080	16	—
	1	Providence Sand	Georgia	Clay	63	451075	—	—
	5	Severn Fm	Maryland	Prince George's	70	451099	5	—
	3	....do........	....do........	....do........	70	451099	3	—
	2	....do........	....do........	....do........	72	451055	1	—
	1	....do........	....do........	....do........	73A	131763	1	—
	1	....do........	....do........	....do........	73A	131764	1	—
	9	....do........	....do........	....do........	73A	450520	5	—
	10	....do........	....do........	....do........	75	32291	4	2
	2	....do........	....do........	Anne Arundel	74	451104	1	—
Total	95							
Crassatella "ripleyana"...	3	Owl Creek Fm	Mississippi	Tippah	52	ANSP 18741	—	—
	2	....do........	....do........	....do........	52	128139	—	—
	18	....do........	....do........	....do........	52	450851	4	—
	2	....do........	....do........	....do........	52	451052	1	—
	5	....do........	....do........	....do........	52	450510	1	—
	4	....do........	....do........	....do........	52	451054	1	1
	7	....do........	....do........	....do........	51	451068	—	—
Total	41							
Crassatella "wadei".......	31	Coon Creek Fm	Tennessee	McNairy	27	451056	1	—
	31	....do........	....do........	....do........	27	451057	—	—
	32	....do........	....do........	....do........	27	451062	1	2
	1	....do........	....do........	....do........	27	32784	—	—
Total	95							

[1] Total "species": 3.

[2] Total specimens: 231.

[3] Total localities: 13.

APPENDIX 3

Data on specimens included in the analysis of species of Crassatella, *comprising adult whole named abundant specimens only*

[Collections listed according to sequence of statistical analysis. Fm, Formation; Mbr, Member. Locality number corresponds to numbers on figure 2 and in appendix 9. Collection number: USNM (U.S. National Museum) collection or specimen numbers, unless otherwise noted; ANSP, Academy of Natural Sciences of Philadelphia; PRI, Paleontological Research Institution]

Species[1]	Number of specimens[2]	Stratigraphic unit	State	County	Locality number[3]	Collection number
C. vadosa	3	Owl Creek Fm	Mississippi	Tippah	52	ANSP 18741
	2	....do........	....do........	....do........	52	128139
	30	Coon Creek Fm	Tennessee	McNairy	27	451056
	31	....do........	....do........	....do........	27	451057
	29	....do........	....do........	....do........	27	451062
	14	Owl Creek Fm	Mississippi	Tippah	52	450851
	1	....do........	....do........	....do........	52	451052
	4	....do........	....do........	....do........	52	450510
	2	....do........	....do........	....do........	52	451054
	7	....do........	....do........	....do........	51	451068
	10	....do........	....do........	....do........	52	451069
	1	Coon Creek Fm	Tennessee	McNairy	27	32784
	1	Providence Sand	Georgia	Clay	63	451075
	1	Severn Fm	Maryland	Prince George's	72	451055
	4	....do........	....do........	....do........	73A	450520
	5	....do........	....do........	....do........	75	32291
Total	145					
C. gardnerae	5	Ripley Fm, Coon Creek Tongue	Mississippi	Union	28	103753
	4	....do........	....do........	....do........	28	451061
	7	....do........	....do........	....do........	28	451060
	37	....do........	....do........	....do........	28	451067
Total	53					
"*C. hodgei*"	2	Blufftown Fm	Georgia	Stewart	4	450805
(and *C. carolinensis*).	6	....do........	....do........	....do........	4	450815
Total	8					
C. tumidula	2	Tuscahoma Fm, Bells Landing Mbr	Alabama	Monroe	117	453916
	3	Tuscahoma Fm	....do........	Wilcox	116	450813
	1	Tuscahoma Fm, Bells Landing Mbr	....do........	Monroe	117	90968
	1	Tuscahoma Fm	....do........	Wilcox	116	450842
	4	Tuscahoma Fm, Bells Landing Mbr	....do........	Monroe	117	155060
	2	....do........	....do........	....do........	117	450843
	1	Tuscahoma Fm, Greggs Landing Mbr	....do........	....do........	118	450515
Total	14					
"*C. halei*"	1	Tuscahoma Fm, Greggs Landing Mbr	Alabama	Monroe	118	PRI 140
(= *C. tumidula*).	4	Nanafalia Fm	....do........	Marengo	114	129898
	1	....do........	....do........	....do........	114	450846
Total	6					
C. lintea	1	Ripley Fm	Alabama	Barbour	36B	ANSP 19594
	1	Severn Fm	Maryland	Prince George's	73A	131766
	1	Ripley Fm	Alabama	Barbour	43	451089
	3	....do........	Georgia	Quitman	45	451091
	1	....do........	....do........	....do........	38A	451093
	5	Severn Fm	Maryland	Prince George's	73A	451098
	1	....do........	....do........	....do........	70	451100
Total	13					

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[1] Total species: 6.

[2] Total specimens: 239.

[3] Total localities: 18.

APPENDIX 4

Data on specimens included in the analysis of species of Crassatella, *comprising adults, juveniles, broken specimens, internal molds, unnamed specimens, and rare species (fewer than five specimens)*

[Collections listed according to sequence of statistical analysis. Fm, Formation; Mbr, Member. Locality number corresponds to numbers on figure 2 and in appendix 9. Collection number: USNM (U.S. National Museum) collection or specimen numbers, unless otherwise noted; ANSP, Academy of Natural Sciences of Philadelphia; PRI, Paleontological Research Institution; USGS-CENO, U.S. Geological Survey, Cenozoic. —, no specimen for column]

Species[1]	Number of specimens[2]	Stratigraphic unit	State	County	Locality number[3]	Collection number	Number of broken specimens and internal molds	Number of juveniles
C. vadosa	3	Owl Creek Fm	Mississippi	Tippah	52	ANSP 18741	—	—
	1	Prairie Bluff Chalk	Alabama	Wilcox	56	ANSP 19593	1	—
	2	Severn Fm	Maryland	Anne Arundel	74	451104	2	—
	2	Owl Creek Fm	Mississippi	Tippah	52	128139	—	—
	1	Severn Fm	Maryland	Prince George's	73A	131763	1	—
	1	....do........	....do........	....do........	73A	131764	1	—
	31	Coon Creek Fm	Tennessee	McNairy	27	451056	1	—
	31	....do........	....do........	....do........	27	451057	—	—
	32	....do........	....do........	....do........	27	451062	1	2
	18	Owl Creek Fm	Mississippi	Tippah	52	450851	4	—
	2	....do........	....do........	....do........	52	451052	1	—
	5	....do........	....do........	....do........	52	450510	1	—
	4	....do........	....do........	....do........	52	451054	1	1
	7	....do........	....do........	....do........	51	451068	—	—
	12	....do........	....do........	....do........	52	451069	2	—
	2	Prairie Bluff Chalk	Alabama	Wilcox	57	450502	2	—
	4	....do........	....do........	....do........	58	450820	4	—
	12	....do........	....do........	....do........	56	450500	12	—
	4	....do........	....do........	....do........	56	450853	4	—
	10	....do........	....do........	....do........	59A	451071	10	—
	16	....do........	....do........	....do........	59A	451080	16	—
	1	Coon Creek Fm	Tennessee	McNairy	27	32784	—	—
	1	Providence Sand	Georgia	Clay	63	451075	—	—
	5	Severn Fm	Maryland	Prince George's	70	451099	5	—
	3	....do........	....do........	....do........	70	451099	3	—
	2	....do........	....do........	....do........	72	451055	1	—
	9	....do........	....do........	....do........	73A	450520	5	—
	10	....do........	....do........	....do........	75	32291	4	2
Total	231							
C. gardnerae	5	Ripley Fm, Coon Creek Tongue	Mississippi	Union	28	103753	—	—
	6	....do........	....do........	....do........	28	451061	2	1
	7	....do........	....do........	....do........	28	451060	—	—
	38	....do........	....do........	....do........	28	451067	1	—
Total	56							
"C. hodgei" (and *C. carolinensis).*	3	Blufftown Fm	Georgia	Stewart	4	450805	1	—
	9	....do........	....do........	....do........	4	450815	3	—
	1	Tar Heel Fm	North Carolina	Greene	8	31930	1	—
	1	....do........	....do........	....do........	8	31931	—	—
Total	14							
C. prora................	1	Mount Laurel Sand	New Jersey	Monmouth	48	ANSP 18739	1	—
Total	1							
C. monmouthensis	5	Unknown	New Jersey	Monmouth	Unknown	ANSP 18738	5	—
Total	5							
C.transversa	2	Unknown	New Jersey	Unknown	Unknown	ANSP 18744	2	—
Total	2							

APPENDIX 4—CONTINUED

Species[1]	Number of specimens[2]	Stratigraphic unit	State	County	Locality number[3]	Collection number	Number of broken specimens and internal molds	Number of juveniles
C. sp. A	2	Ripley Fm	Alabama	Barbour	36B	ANSP CONRAD	2	—
	1	....do........	....do........	....do........	36B	12670	—	—
	2	....do........	Mississippi	Union	30B	20820	—	—
	1	....do........	Alabama	Barbour	36A	21125	—	—
	5	....do........	....do........	....do........	36B	505	1	1
	2	Peedee Fm	North Carolina	New Hanover	69B	450511	2	—
	2	Coffee Sand	Mississippi	Prentiss	2	451053	1	—
	1	....do........	....do........	....do........	1	451059	1	—
	2	Prairie Bluff Chalk	....do........	Kemper	54	459095	2	—
	10	Ripley Fm	Georgia	Quitman	38B	451079	—	—
	15	....do........	Alabama	Barbour	43	451086	—	—
	16	....do........	....do........	....do........	43	451089	—	—
	19	....do........	....do........	....do........	40	450551	2	—
	10	....do........	....do........	....do........	41	451103	2	1
	17	....do........	....do........	....do........	36A	21125	—	—
	11	....do........	Georgia	Quitman	37	451081	—	1
	12	....do........	....do........	....do........	42	451077	5	—
	14	....do........	....do........	....do........	38A	451093	—	3
	1	....do........	....do........	....do........	44	450807	1	—
	32	Ripley Fm, Coon Creek Tongue	Mississippi	Tippah	30A	451063	—	1
	4	....do........	....do........	Union	31	451058	2	—
	30	....do........	....do........	....do........	31	451065	—	—
	5	Severn Fm	Maryland	Prince George's	70	451100	—	5
Total	214							
C. tumidula	2	Tuscahoma Fm, Bells Landing Mbr	Alabama	Monroe	117	453916	—	—
	1	....do........	....do........	....do........	120	453917	1	—
	2	Tuscahoma Fm, Greggs Landing Mbr	....do........	....do........	118	450812	—	2
	4	Tuscahoma Fm	....do........	Wilcox	116	450813	—	1
	2	Tuscahoma Fm, Greggs Landing Mbr	....do........	Monroe	118	450814	—	2
	1	Tuscahoma Fm, Bells Landing Mbr	....do........	....do........	117	90968	—	—
	4	Tuscahoma Fm	....do........	Wilcox	116	450842	3	1
	6	Tuscahoma Fm, Bells Landing Mbr	....do........	Monroe	117	155060	—	2
	4	....do........	....do........	....do........	117	450843	1	1
	1	Tuscahoma Fm, Greggs Landing Mbr	....do........	....do........	118	450515	—	—
Total	27							
"*C. halei*" (= *C. tumidula*).	1	Tuscahoma Fm, Greggs Landing Mbr	Alabama	Monroe	118	PRI 140	—	—
	4	Nanafalia Fm	....do........	Marengo	114	129898	—	—
	1	....do........	....do........	....do........	114	450846	—	—
Total	6							
C. gabbi	1	Clayton Fm (basal)	Tennessee	Hardeman	76	450854	—	—
Total	1							
C. sepulcollis	1	Porters Creek Clay	Alabama	Wilcox	78	PRI 64	—	—
	1	....do........	....do........	....do........	79	PRI 65	—	—
Total	2							

APPENDIX 4—CONTINUED

Species[1]	Number of specimens[2]	Stratigraphic unit	State	County	Locality number[3]	Collection number	Number of broken specimens and internal molds	Number of juveniles
C. sp. C	1	Tuscahoma Fm	Alabama	Wilcox	119	459096	—	—
	2	....do........	....do........	....do........	119	450818	—	2
	1	Nanafalia Fm	....do........	Dale	115B	450848	—	1
	58	Porters Creek Clay	....do........	Wilcox	80	USGS-CENO 264	1	22
	4	....do........	....do........	....do........	81	USGS-CENO 283	—	3
	39	Clayton Fm, Pine Barren Mbr	....do........	....do........	77A	129744	—	22
	6	Nanafalia Fm	....do........	Pike	115A	450847	—	6
	14	Porters Creek Clay	....do........	Wilcox	78	154914	1	—
Total	125							
C. subplana	1	Mount Laurel Sand	New Jersey	Monmouth/ Burlington	47	ANSP 18743	1	—
Total	1							
C. carolinana	1	Peedee Fm	North Carolina	Pender	69A	73438	—	—
	2	....do........	....do........	....do........	69A	73439	1	—
Total	3							
C. lintea..............	1	Ripley Fm	Alabama	Barbour	36B	ANSP 19594	—	—
	1	Severn Fm	Maryland	Prince George's	73A	131766	—	—
	3	Ripley Fm	Alabama	Barbour	43	451089	—	2
	6	....do........	Georgia	Quitman	45	451091	—	3
	1	....do........	....do........	....do........	38A	451093	—	—
	5	Severn Fm	Maryland	Prince George's	73A	451098	—	—
	3	....do........	....do........	....do........	70	451100	2	—
Total	20							
C. sp. B	2	Providence Sand	Georgia	Clay	63	450816	—	—
Total	2							

[1] Total species: 16.

[2] Total specimens: 710.

[3] Total localities: 51.

APPENDIX 5

Data on specimens included in the analysis of species of Bathytormus, *comprising adult whole named specimens only*

[Collections listed according to sequence of statistical analysis. Fm, Formation; Mbr, Member. Locality number corresponds to numbers on figure 2 and in appendix 9. Collection number: USNM (U.S. National Museum) collection or specimen numbers, unless otherwise noted; ANSP, Academy of Natural Sciences of Philadelphia]

Species[1]	Number of specimens[2]	Stratigraphic unit	State	County	Locality number[3]	Collection number
B. pteropsis..............	1	Providence Sand	Alabama	Barbour	60	451085
	2	....do........	....do........	Barbour/Henry	61	451074
	1	....do........	Georgia	Clay	67	451083
	1	....do........	....do........	....do........	64	451076
	1	....do........	....do........	....do........	63	451072
	2	....do........	....do........	....do........	63	451075
	1	....do........	....do........	....do........	63	450490
	1	....do........	....do........	Quitman	65	451078
	3	Ripley Fm	Mississippi	Union	34A	20845
Total	13					
B. alaeformis............	1	Aquia Fm	Maryland	Prince George's	85	ANSP 30498
	4	Aquia Fm, Paspotansa Mbr	Virginia	King George	93	453904
	5	Aquia Fm	....do........	....do........	98	453906
	1	....do........	....do........	....do........	98	453909
	3	Aquia Fm, Paspotansa Mbr	....do........	....do........	95	453910
	4	Aquia Fm	....do........	....do........	98	453911
	1	....do........	....do........	Stafford	88	450809
	2	....do........	....do........	King George	98	453912
	1	Aquia Fm, Paspotansa Mbr	....do........	....do........	94	453914
	13	....do........	....do........	....do........	94	453915
	2	....do........	....do........	....do........	94	453913
	1	....do........	....do........	Stafford	90	450810
	3	Aquia Fm	....do........	King George	96	450811
	3	....do........	Maryland	Anne Arundel	107	450819
	1	....do........	Virginia	Stafford	91	450537
	1	....do........	....do........	....do........	101	450821
	1	....do........	....do........	....do........	88	450822
	1	....do........	Maryland	Prince George's	82A	450823
	1	....do........	Virginia	Stafford	88	450824
	3	....do........	....do........	King George	99	450825
	1	....do........	....do........	Stafford	91	450826
	4	....do........	....do........	King George	100	450827
	1	....do........	....do........	....do........	97	450829
	2	....do........	....do........	Stafford	91	450830
	1	....do........	Maryland	Charles	102	450831
	1	....do........	Virginia	Stafford	91	450832
	3	....do........	....do........	....do........	88	450834
	3	....do........	Maryland	Charles	103	450835
	2	....do........	Virginia	King George	97	450837
	6	Aquia Fm, Paspotansa Mbr	....do........	....do........	94	450838
	2	Aquia Fm	Maryland	Prince George's	86	450839
	2	....do........	....do........	....do........	85	450808
	1	....do........	Virginia	Stafford	88	2490
	1	Aquia Fm, Paspotansa Mbr	....do........	King George	94	366485
	2	Aquia Fm	Maryland	Charles	104	136177
	4	....do........	....do........	Prince George's	85	115796
	5	....do........	....do........	Prince George's	87	450859
	1	....do........	Virginia	Stafford	88	450526
	4	....do........	....do........	....do........	89	450573
Total	98					

[1] Total species: 2.

[2] Total specimens: 111.

[3] Total localities: 28.

APPENDIX 6

Data on specimens included in the analysis of species of Bathytormus, *comprising adults, juveniles, broken specimens, and unnamed specimens*

[Collections listed according to sequence of statistical analysis. Fm, Formation; Mbr, Member. Locality number corresponds to numbers on figure 2 and in appendix 9. Collection number: USNM (U.S. National Museum) collection or specimen numbers, unless otherwise noted; ANSP, Academy of Natural Sciences of Philadelphia; USGS-CENO, U.S. Geological Survey, Cenozoic. —, no specimen for column]

Species[1]	Number of specimens[2]	Stratigraphic unit	State	County	Locality number[3]	Collection number	Number of broken specimens and internal molds	Number of juveniles
B. pteropsis	1	Providence Sand	Alabama	Barbour	60	451085	—	—
	2	....do........	....do........	Barbour/Henry	61	451074	—	—
	1	....do........	Georgia	Clay	67	451083	—	—
	1	....do........	....do........	....do........	64	451076	—	—
	1	....do........	....do........	....do........	63	451072	—	—
	2	....do........	....do........	....do........	63	451075	—	—
	1	....do........	....do........	....do........	63	450490	—	—
	1	....do........	....do........	Quitman	65	451078	—	—
	5	Ripley Fm	Mississippi	Union	34A	20845	—	2
Total	15							
B. sp. A...........	2	Ripley Fm	Alabama	Barbour	43	451086	—	—
	3	....do........	....do........	....do........	43	451087	1	—
	1	....do........	....do........	....do........	43	451088	—	—
	1	....do........	....do........	....do........	43	451089	—	—
	1	....do........	....do........	....do........	43	451092	—	—
	1	....do........	....do........	....do........	39	451082	—	1
	1	....do........	Georgia	Quitman	45	451091	—	—
	1	....do........	....do........	....do........	44	451073	—	—
	6	....do........	....do........	....do........	44	451084	2	2
	2	....do........	Mississippi	Union	33	451070	—	—
	1	Ripley Fm, Coon Creek Tongue	....do........	Tippah	30A	451063	—	1
	5	....do........	....do........	Union	31	451065	1	1
	2	Severn Fm	Maryland	Prince George's	70	451100	1	2
Total	27							
B. alaeformis	2	Aquia Fm	Maryland	Prince George's	85	ANSP 30498	1	—
	7	Aquia Fm, Paspotansa Mbr	Virginia	King George	93	453904	3	—
	7	Aquia Fm	....do........	....do........	98	453906	1	1
	1	....do........	....do........	....do........	112	453908	1	1
	2	....do........	....do........	....do........	98	453909	—	1
	3	Aquia Fm, Paspotansa Mbr	....do........	....do........	95	453910	—	—
	6	Aquia Fm	....do........	....do........	98	453911	—	2
	1	....do........	....do........	Stafford	88	450809	—	—
	3	....do........	....do........	King George	98	453912	—	—
	2	Aquia Fm, Paspotansa Mbr	....do........	....do........	94	453913	2	—
	1	....do........	....do........	....do........	94	453914	—	—
	24	....do........	....do........	....do........	94	453915	11	—
	2	....do........	....do........	....do........	94	453913	—	—
	1	Aquia Fm	Virginia	Stafford	90	450810	—	—
	3	....do........	....do........	King George	96	450811	—	—
	3	....do........	Maryland	Anne Arundel	107	450819	—	—
	1	....do........	Virginia	Stafford	91	450537	—	—
	2	....do........	....do........	....do........	101	450821	1	—
	1	....do........	....do........	....do........	88	450822	—	—
	1	....do........	Maryland	Prince George's	82A	450823	—	—
	2	....do........	Virginia	Stafford	88	450824	1	—
	3	....do........	....do........	King George	99	450825	—	—
	4	....do........	....do........	Stafford	91	450826	3	—
	5	....do........	....do........	King George	100	450827	1	—
	2	....do........	....do........	Stafford	91	450828	2	—
	2	....do........	....do........	King George	97	450829	1	—

APPENDIX 6—CONTINUED

Species[1]	Number of specimens[2]	Stratigraphic unit	State	County	Locality number[3]	Collection number	Number of broken specimens and internal molds	Number of juveniles
B. alaeformis—Continued.	3	Aquia Fm	Virginia	Stafford	91	450830	1	—
	1	....do........	Maryland	Charles	102	450831	—	—
	1	....do........	Virginia	Stafford	91	450832	—	—
	3	....do........	....do........	....do........	88	450834	—	—
	3	....do........	Maryland	Charles	103	450835	—	—
	2	....do........	Virginia	King George	97	450837	—	—
	9	Aquia Fm, Paspotansa Mbr	....do........	....do........	94	450838	3	—
	2	Aquia Fm	Maryland	Prince George's	86	450839	—	—
	2	....do........	....do........	....do........	85	450808	—	—
	3	....do........	Virginia	Stafford	89	136215	—	—
	1	....do........	....do........	....do........	88	2490	—	—
	1	Aquia Fm, Paspotansa Mbr	....do........	King George	94	366485	—	—
	7	Aquia Fm	Maryland	Charles	104	136177	5	—
	6	....do........	....do........	Prince George's	85	115796	2	—
	10	....do........	....do........	....do........	87	450859	5	—
	1	....do........	Virginia	Stafford	88	450526	—	—
	2	....do........	....do........	....do........	89	450573	1	—
Total	148							
B. sp. B..........	1	Aquia Fm	Maryland	Prince George's	105	450841	—	—
	10	....do........	Virginia	King George	92	450833	—	—
	2	....do........	Maryland	Charles	108	450836	1	—
	3	....do........	....do........	Prince George's	84	450856	2	1
	5	....do........	....do........	....do........	87	450857	4	—
	1	....do........	Virginia	Hanover	113A	366477	1	—
	4	....do........	....do........	....do........	113A	USGS-CENO 26337	4	—
Total	26							

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[1] Total species: 4.

[2] Total specimens: 216.

[3] Total localities: 42.

APPENDIX 7

Data on specimens included in the analysis of the genera of Crassatellidae, comprising adult whole specimens only

[Collections listed according to sequence of statistical analysis. Fm, Formation; Mbr, Member. Locality number corresponds to numbers on figure 2 and in appendix 9. Collection number: USNM (U.S. National Museum) collection or specimen numbers, unless otherwise noted; ANSP, Academy of Natural Sciences of Philadelphia; PRI, Paleontological Research Institution; USGS-CENO, U.S. Geological Survey, Cenozoic]

Genera[1]	Number of specimens[2]	Stratigraphic unit	State	County	Locality number[3]	Collection number
Crassatella ...	3	Owl Creek Fm	Mississippi	Tippah	52	ANSP 18741
	2	....do........	....do........	....do........	52	128139
	30	Coon Creek Fm	Tennessee	McNairy	27	451056
	31	....do........	....do........	....do........	27	451057
	29	....do........	....do........	....do........	27	451062
	14	Owl Creek Fm	Mississippi	Tippah	52	450851
	1	....do........	....do........	....do........	52	451052
	4	....do........	....do........	....do........	52	450510
	2	....do........	....do........	....do........	52	451054
	7	....do........	....do........	....do........	51	451068
	10	....do........	....do........	....do........	52	451069
	1	Coon Creek Fm	Tennessee	McNairy	27	32784
	1	Providence Sand	Georgia	Clay	63	451075
	1	Severn Fm	Maryland	Prince George's	72	451055
	4	....do........	....do........	....do........	73A	450520
	5	....do........	....do........	....do........	75	32291
	5	Ripley Fm, Coon Creek Tongue	Mississippi	Union	28	103753
	4	....do........	....do........	....do........	28	451061
	7	....do........	....do........	....do........	28	451060
	37	....do........	....do........	....do........	28	451067
	1	Ripley Fm	Alabama	Barbour	36B	12670
	2	Ripley Fm, Coon Creek Tongue	Mississippi	Union	30B	20820
	1	Ripley Fm	Alabama	Barbour	36A	21125
	3	....do........	....do........	....do........	36B	505
	1	Coffee Sand	Mississippi	Prentiss	2	451053
	10	Ripley Fm	Georgia	Quitman	38B	451079
	15	....do........	Alabama	Barbour	43	451086
	16	....do........	....do........	....do........	43	451089
	17	....do........	....do........	....do........	40	450551
	7	....do........	....do........	....do........	41	451103
	17	....do........	....do........	....do........	36A	21125
	10	....do........	Georgia	Quitman	37	451081
	7	....do........	....do........	....do........	42	451077
	11	....do........	....do........	....do........	38A	451093
	31	Ripley Fm, Coon Creek Tongue	Mississippi	Tippah	30A	451063
	2	....do........	....do........	Union	31	451058
	30	....do........	....do........	....do........	31	451065
	2	Tuscahoma Fm, Bells Landing Mbr	Alabama	Monroe	117	453916
	3	Tuscahoma Fm	....do........	Wilcox	116	450813
	1	Tuscahoma Fm, Bells Landing Mbr	....do........	Monroe	117	90968
	1	Tuscahoma Fm	....do........	Wilcox	116	450842
	4	Tuscahoma Fm, Bells Landing Mbr	....do........	Monroe	117	155060
	2	....do........	....do........	....do........	117	450843
	1	Tuscahoma Fm, Greggs Landing Mbr	....do........	....do........	118	450515
	1	....do........	....do........	....do........	118	PRI 140
	4	Nanafalia Fm	....do........	Marengo	114	129898
	1	....do........	....do........	....do........	114	450846
	1	Clayton Fm (basal)	Tennessee	Hardeman	76	450854
	1	Porters Creek Clay	Alabama	Wilcox	78	PRI 64
	1	....do........	....do........	....do........	79	PRI 65
	1	Tuscahoma Fm	....do........	....do........	119	459096
	35	Porters Creek Clay	....do........	....do........	80	USGS-CENO 264
	1	....do........	....do........	....do........	81	USGS-CENO 283
	17	Clayton Fm, Pine Barren Mbr	....do........	....do........	77A	129744
	13	Porters Creek Clay	....do........	....do........	78	154914

APPENDIX 8—CONTINUED

Genera[1]	Number of specimens[2]	Stratigraphic unit	State	County	Locality number[3]	Collection number	Number of broken specimens and internal molds	Number of juveniles
Unnamed group.	1	Woodbury Clay	New Jersey	Camden	14	451105	—	—
	3	Providence Sand	Georgia	Clay	62B	450091	—	—
	2	....do........	....do........	Quitman	65	451078	—	—
	1	Severn Fm	Maryland	Prince George's	71	451095	—	—
Total	7							
Indeterminant crassatellids.	1	Clayton Fm (basal)	Alabama	Lowndes	77B	459092	1	—
	2	Aquia Fm	Maryland	Prince George's	82A	450858	2	—
Total	3							
Astartids.......	7	Ripley Fm	Georgia	Quitman	44	451090	—	—
Total	7							

[1] Total genera: 7.
[2] Total specimens: 999.
[3] Total localities: 91.

APPENDIX 9

DESCRIPTION OF COLLECTION LOCALITIES

All of the specimens used in this study came from collections of the U.S. Geological Survey (USGS), the U.S. National Museum of Natural History, Smithsonian Institution (USNM), the Academy of Natural Sciences of Philadelphia (ANSP), and the Paleontological Research Institution (PRI). The following locality descriptions contain all of the information available for each collection; in some cases this information is vague; in other cases, precise. Author comments and ancillary information are in square brackets.

UPPER CRETACEOUS

CAMPANIAN

Coffee Sand

1 USGS Mesozoic locality 17783. USNM 450408, 451059. Roadcut on the northeast-facing slope of Young's Creek Valley, Prentiss County, Miss. (sec. 9, T. 6 S., R. 8 E.). Collection comes from 2.4 to 3.1 m (8 to 10 feet) above the contact of the Coffee Sand with the underlying Eutaw Fm.

2 USGS Mesozoic locality 6909. USNM 450419, 451053. 10 km (6 miles) east of Booneville on road to Hare's old mill site on Big Brown Creek, Prentiss County, Miss.

3 USNM 450409–450411, 453894. Roadcut of north-facing slope of Mantachie Creek Valley, just north of county school, and 3.2 km (2 miles) due west of Ratliff, Lee County, Miss. (S½ sec. 9, T. 8 S., R. 7 E.).

Blufftown Formation

4 USGS Mesozoic localities 844, 5392, 6405, 26033. USNM 450402–450406, 450421–450435, 450501, 450805, 450815, 453880. Bluffs on the left bank of the Chattahoochee River at Blufftown, 49.8 km (31 miles) below Columbus, Stewart County, Ga. (32°11′ N., 84°57′45″ W.). This is the type locality for the Blufftown Formation.

5 USGS Mesozoic locality 5395. USNM 453862. Chattahoochee River, 66 km (41 miles) below Columbus, near Florence, Stewart County, Ga.

6, 7 USGS Mesozoic localities 25563, 26023. USNM 450407, 451094, 453879. Bluffs at Florence, on the Chattahoochee River, 28.2 km (17.5 miles) above Eufaula Landing, Stewart County, Ga. (32°05′ N., 85°03′ W.).

Tar Heel Formation

8 USGS Mesozoic locality 5348. USNM 31929–31932, 451097. Small exposure in ravine near a schoolhouse in scarp bordering swamp west of town of Snow Hill, Greene County, N.C.

9 USGS Mesozoic locality 5418. USNM 453864. Right bank of the Neuse River, 127.9 km (79.5 miles) above New Bern, Wayne County, N.C.

10 USGS Mesozoic locality 5353. USNM 451101. Left bank of the Neuse River, at Auger Hole Landing, 116.8 km (73 miles) above New Bern, Lenoir County, N.C.

11 USGS Mesozoic locality 5347. USNM 459093. Right bank of the Tar River, at Blue Banks Landing, 11.3 km (7 miles) above Greenville and downstream from Tyson Creek, Pitt County, N.C.

12 USGS Mesozoic locality 5357. Black River, Mossy Log Landing, 115 km (71.5 miles) above Wilmington, Sampson County, N.C. The Tar Heel Formation is overlain by the Bladen Formation at this outcrop. [Specimens identified as *Crassatella newkirkensis* by Stephenson (1923) were examined from this locality. The poor preservational state of the specimens makes it impossible to determine if they should be reassigned to *C. hodgei* Stephenson (1923). For discussion, see Wingard, this paper, p. 61.]

Merchantville Formation

13A USNM 450420. Deep cut on the south side of the Chesapeake and Delaware Canal, just east of the Summit Bridge (Route 301), New Castle County, Del.

13B USGS Mesozoic locality 17698. USNM 450412. Old dump on road to Kirkwood, 0.8 km (0.5 mile) east of Summit Bridge over the Chesapeake and Delaware Canal, New Castle County, Del.

Woodbury Clay

14 USNM 451105. ANSP 18740, 18735. Haddonfield, Camden County, N.J.

15 USGS Mesozoic localities 16293, 31091. USNM 450505, 453889. Small east-flowing branch of Cooper Creek, south of Maple Avenue, small exposures 107 to 183 m (350–600 feet) east of

intersection of Maple Avenue with Grove Street, 1.6 km (1 mile) north of Haddonfield, Camden County, N.J.

Bladen Formation

16 USGS Mesozoic locality 5372. USNM 31748, 31749, 453861. Hodge's old mill site, 5.6 km (3.5 miles) southeast of Mullins, Marion County, S.C.

17 USGS Mesozoic locality 4135. USNM 450852. Small exposure on the left bank of the Neuse River, 20.1 km (12.5 miles) above Kinston and 100.6 km (62.5 miles) above New Bern, Lenoir County, N.C.

18 USGS Mesozoic locality 5354. USNM 31736, 31737, 451102. Right bank of the Neuse River at Whiteley Creek Landing, just above milepost 60 (96.5 km above New Bern), Lenoir County, N.C.

19A USGS Mesozoic locality 5358. USNM 451106. Right bank of the Black River, at Bryant Newkirks Marl Hole, 106.2 km (66 miles) above Wilmington, Sampson County, N.C.

19B USGS Mesozoic locality 5359. USNM 453855. Left bank of the Black River, 102.9 km (64 miles) above Wilmington, Sampson County, N.C.

19C USGS Mesozoic locality 5360. USNM 453856. Left bank of the Black River at Corbit's Landing, 101.8 km (63.25 miles) above Wilmington, Sampson County, N.C.

19D USGS Mesozoic locality 5361. USNM 453857. Right bank of the Black River, 100.5 km (62.5 miles) above Wilmington, Sampson County, N.C.

20 USGS Mesozoic locality 5362. USNM 453858. Left bank of the Black River, at Kerrs Cove, 100.1 km (62.25 miles) above Wilmington, Sampson County, N.C.

21 USGS Mesozoic locality 5365. USNM 453859. Left bank of the Black River at Hatchers Reaches, 87.7 km (54.5 miles) above Wilmington, Sampson County, N.C.

22 USGS Mesozoic locality 5368. USNM 453860. Right bank of the Cape Fear River at Walker's Bluff, just below 60-mile marker (96.5 km) and 20.9 km (13 miles) below Elizabethtown, Bladen County, N.C.

Wenonah Formation

23 USGS Mesozoic locality 31101. South bank of Big Brook, just west of Hillsdale Road and approximately 3.2 km (2 miles) east of Marlboro, Monmouth County, N.J. [Two casts of *Crassatella* sp. aff. *hodgei* were examined from this locality. These could not be confidently assigned to a species.]

24 USGS Mesozoic locality 16289. North-facing bluff on Big Brook, 121.9 m (400 feet) east of north-south road and 1.9 km (1.2 miles) east of Marlboro, Monmouth County, N.J. [Faint external impressions and poorly preserved internal molds of *Crassatella* sp.? were examined from this locality; no confident assignment can be made due to the poor preservation.]

UPPER CAMPANIAN AND LOWER MAASTRICHTIAN

Ripley Formation (Cusseta Sand Member)

25A USGS Mesozoic locality 5396. USNM 453863. Roanoke Bluff, just below Woolridge Landing, right bank of the Chattahoochee River, Barbour County, Ala.

25B USGS Mesozoic locality 6402. USNM 453866. Woolridge Landing, Upper Rood's Bend, right bank of the Chattahoochee River, 21.7 km (13.5 miles) above Eufaula Landing, Barbour County, Ala.

Cusseta Sand

26 USGS Mesozoic localities 6401, 27544. USNM 450413–450415, 453865, 453884. Lower Rood's Bend, left bank of the Chattahoochee River, just below the mouth of Soapstone Creek, 20.4 km (12.7 miles) above Eufaula Landing, Stewart County, Ga.

Coon Creek Formation

27 USGS Mesozoic localities 10198, 16951, 25406, 30762. USNM 32784, 450436–450442, 450449–450451, 450455–450457, 450465, 450475, 450481, 450508, 451056, 451057, 451062, 451096, 453896. Bluffs and bed of Coon Creek on the former Dave Week's place, 5.6 km (3.5 miles) south of Enville, 12 km (7.5 miles) north of Adamsville, and 198 m (0.125 mile) east of the main Henderson-Adamsville road in the northeastern part of McNairy County, Tenn. Type locality of the Coon Creek Formation. [The Coon Creek Science Center of the Memphis Museum System now exists at the site.]

Ripley Formation (Coon Creek Tongue)

28 USGS Mesozoic localities 18078, 18616, 18629, 25411. USNM 103753, 103754, 450447, 450448, 450460, 451060, 451061, 451067, 453873. Scraped area along the north side of the dam at Union County Lake, 1.8 km (1.1 miles) northeast of Pleasant Ridge, Union County, Miss. (NW¼ NE¼NE¼ sec. 11, T. 6 S., R. 4 E.).

29 USGS Mesozoic locality 26340. USNM 453881. Roadcut on secondary road about 4.2 km (2.6 miles, airline) south of Pleasant Ridge intersection, Union County, Miss. (NW¼SW¼NW¼ sec. 26, T. 6 S., R. 4 E.).

30A USGS Mesozoic locality 25407. USNM 450453, 450454, 450478, 450493, 451063. Roadcut on northeast-facing slope of Hall Creek, a tributary of the Tallahatchie River, 4.6 km (2.9 miles) due southwest of Dumas, Tippah County, Miss. (center S½NW¼ sec. 34, T. 5 S., R. 4 E.).

30B USNM 20820. 4 km (2.5 miles) south of Dumas, Tippah County, Miss.

31 USGS Mesozoic localities 6873, 17277, 25408, 25409. USNM 451058, 451064, 451065, 453870. Lee's old mill site, roadcut on northeast-facing slope of Tallahatchie River valley, 3.2 km (2 miles) north-northeast of Keownville on the road to Molino, Union County, Miss. (NW¼NE¼ sec. 17, T. 6 S., R. 4 E.).

32 USGS Mesozoic locality 25410. USNM 450461, 450462, 451066. Roadcut in east-facing slope of Hall Branch, 1.45 km (0.9 mile) west of Molino, Union County, Miss. (SW¼NE¼ sec. 8, T. 6 S., R. 4 E.).

Ripley Formation

33 USGS Mesozoic locality 25485. USNM 450492, 450503, 451070. Roadcuts on Mississippi Route 30 on the north-facing slope of Wilhite Creek valley from 1.1 to 2.7 km (0.7 to 1.7 miles) south of Keownville, Union County, Miss. (SE¼ sec. 30, T. 6 S., R. 4 E.).

34A USGS Mesozoic locality 711. USNM 20845, 450566–450568. Bed of Hall Branch of Tallahatchie River on the old C.R. Hall's farm near Molino, Union County, Miss. (sec. 5, T. 6 S., R. 4 E.).

34B USGS Mesozoic locality 13122. USNM 453872. 12.9 km (8 miles) northeast of New Albany near top of four-way divide, Union County, Miss. (SE¼? sec. 23, T. 6 S., R. 4 E.).

35 USGS Mesozoic locality 6468. USNM 453868. New Albany-Pontotoc Road, 4.8 km (3 miles) south of New Albany, south side of Kings Creek in Union County, Miss.

36A USGS Mesozoic locality 279. USNM 21125. Various localities within a 24.1- to 32.2-km (15–20 mile) radius of Eufaula, Barbour County, Ala.

36B USGS Mesozoic localities 26013, 27518, 28433. USNM 503, 505, 12670, 453878, 453882, 453886. ANSP 19594 and an unnumbered specimen from Conrad's collections. Bluffs at Eufaula, below Eufaula Landing, right bank of the Chattahoochee River, Barbour County, Ala. [Note: The label on collection 503 says simply "Eufaula, Alabama." Presumably this collection by F.B. Meek was made from the Bluffs at Eufaula.]

37, 45 USGS Mesozoic localities 27542, 28431. USNM 450452, 450458, 450494, 450504, 451081, 451091. Bluffs on the left bank of the Chattahoochee River, about 3.2 km (2 miles) below the Central of Georgia railroad crossing, Quitman County, Ga. [Locality 45 determined to be equivalent to locality 37.]

38A USGS Mesozoic locality 28438. USNM 451093. Left bank of the Chattahoochee River, 4.2 to 4.3 km (2.6–2.7 miles) south of Eufaula Landing, Quitman County, Ga.

38B USGS Mesozoic locality 26014. USNM 451079. Bluff on left bank of the Chattahoochee River, 4.5 km (2.8 miles) below Eufaula Landing, Quitman County, Ga.

39 USGS Mesozoic locality 27552. USNM 450487, 450488, 451082. Right bank of the Chattahoochee River, 7.9 km (4.9 miles) below Eufaula Landing and 0.24 km (0.15 mile) above mouth of Cool Branch, Barbour County, Ala. (NE¼ sec. 18, T. 10 N., R. 29 E.).

40 USGS Mesozoic locality 857. USNM 450417, 450464, 450477, 450551. Chattahoochee River, between Eufaula and Barbour Creek, 3.2 km (2 miles) below Eufaula Landing, Barbour County, Ala.

41 USGS Mesozoic locality 33305. USNM 451103. Bluffs on right bank of the Chattahoochee River, just above mouth of Barbour Creek, Barbour County, Ala. (S½SW¼ sec. 9, T. 10 N., R. 29 E.).

42 USGS Mesozoic locality 25991. USNM 451077. Bluffs of Chattahoochee River, left side about 396 m (0.25 mile) above the mouth of Barbour Creek and 6.4 km (4 miles) south of Eufaula in Quitman County, Ga.

43 USGS Mesozoic localities 27919, 27923, 27924, 28409, 28434. USNM 450459, 450466–450469, 450496, 450498, 450506, 450507, 451086–451089, 451092, 454609. Bluffs along right and left sides of Barbour Creek, between the first bend above and the first bend below the U.S. Route 431 bridge, Barbour County, Ala. (SE¼, sec. 7, T. 10 N., R. 29 E.).

44 USGS Mesozoic localities 5417, 25557, 25923, 27878, 27894, 28417. USNM 450495, 450807, 451073, 451084, 451090, 453876, 453885. Mercers Mill, between the old Central Georgia railroad bridge and the dam, 1.2 km (0.75 mile) due south

of Georgetown Courthouse, Tobanee Creek, Quitman County, Ga.

45 Locality 45 determined to be equivalent to locality 37.

46 USGS Mesozoic locality 25998. Left bank of the Chattahoochee River, 1.9 km (1.2 miles) below the mouth of Barbour Creek and 0.8 km (0.5 mile) above the mouth of Cheyneyhatchee Creek, just below mouth of Cool Branch and 8.7 km (5.4 miles) below Eufaula Landing, Quitman County, Ga.

MIDDLE AND UPPER MAASTRICHTIAN

Mount Laurel(?) Sand and (or) Navesink(?) Formation

47 ANSP 18743. Arneytown, Monmouth-Burlington County line, New Jersey.

48 USGS Mesozoic localities 31111, 31112. USNM 450472, 453890, 453891. ANSP 18739. East-northeast flowing tributary of Crosswicks Creek, 3.5 km (2.2 miles) west-northwest of Hornerstown and 1.9 km (1.2 miles) northeast of Arneytown, Monmouth County, N.J. [Note: ANSP 18739 is labeled simply "Crosswicks, New Jersey," but N.F. Sohl (USGS, oral commun., 1989) believes this is most likely the same locality as USGS Mesozoic localities 31111 and 31112.]

Owl Creek Formation

49 USGS Mesozoic locality 713. USNM 20804. Exposures in Walnut Creek bed, Braddock's farm on south-facing slope of Walnut Creek valley, 6 km (3.75 miles) east-southeast of Falkner and 11.3 km (7 miles) northeast of Ripley, Tippah County, Miss. (NE¼SE¼SE¼ sec. 16, R. 3 S., T. 4 E.).

50 USGS Mesozoic locality 6872. USNM 453869. Roadcut on route from New Albany to Ecru Road, about 3.2 km (2 miles) east of the main New Albany-Ecru road and 4.8 km (3 miles) south of New Albany on north-facing slope of King's Creek valley, Union County, Miss.

51 USGS Mesozoic locality 25422. USNM 451068. Roadcut on north-facing slope of a tributary to Fourth Creek, 1.4 km (0.9 mile) north of Providence School, Tippah County, Miss. (NE¼NW¼ sec. 27, T. 2 S., R. 4 E.).

52 USGS Mesozoic localities 707, 6464, 6876, 8309, 25423. USNM 20608, 128139, 450418, 450443–450446, 450474, 450485, 450486, 450509, 450510, 450851, 451052, 451054, 451069, 453867. ANSP 18741. Bluffs on south side of Owl Creek, 4 km (2.5 miles) northeast of Ripley, Tippah County, Miss. (N½SE¼ sec. 7, T. 4 S., R. 3 E.). This is the type locality for the Owl Creek Formation.

53 USGS Mesozoic locality 25420. USNM 453875. Roadcut on Tennessee State Route 57 on west-facing slope of Muddy Creek valley near old Trimm's mill, 5.3 km (3.3 miles) east of the junction that is 2.4 km (1.5 miles) south of Middleton, Hardeman County, Tenn. The Owl Creek Formation (loc. 53) is overlain by the Clayton Formation (loc. 76) at this locality.

Prairie Bluff Chalk

54 USGS Mesozoic locality 6480. USNM 459095. Roadcut on old U.S. Highway 45 at top of north-facing slope of Wahalak Creek valley, 9.7 km (6 miles) north of Scooba, Kemper County, Miss. (sec. 9, T. 12 N., R. 18 E.).

55 USGS Mesozoic locality 27530. USNM 453883. Roadcut on U.S. Highway 231, about 1.9 km (1.2 miles) north of road intersection in Orion and 182.9 m (200 yards) north of junction with Alabama State Route 94, Montgomery County, Ala. (NW¼ sec. 36, T. 12 N., R. 20 E.).

56 USGS Mesozoic localities 270, 6793. USNM 450471, 450500, 450853. ANSP 19593. Prairie Bluff, Alabama River, Wilcox County, Ala. This is the type locality for the Prairie Bluff Chalk.

57 USGS Mesozoic locality 310. USNM 450502. Dawson Bluff, just above mouth of Tear Up Creek, Alabama River, Wilcox County, Ala.

58 USGS Mesozoic locality 6439. USNM 450820. Old Canton Landing, about 22.5 km (14 miles) below mouth of Pine Barren Creek, Alabama River, Wilcox County, Ala.

59A USGS Mesozoic localities 25498, 26989. USNM 451071, 451080. Shell Bluff on Shell Creek, Wilcox County, Ala. (sec. 36, T. 14 N., R. 6 E.).

59B USGS Mesozoic locality 30660. USNM 453887. Roadcuts on Alabama State Highway 263, about 6.8 km (4.2 miles) southeast of intersection with county Route 7 and State Route 21, southeast of Braggs, Lowndes County, Ala. (sec. 22, T. 12 N., R. 13 E.).

Providence Sand

60 USGS Mesozoic localities 27906, 32935. USNM 451085, 459094. Left bank of White Oak Creek on bend about half way between county Route 47 bridge and powerline crossing, Barbour County, Ala. (SW¼SW¼ sec. 9, T. 9 N., R. 29 E.).

61 USGS Mesozoic locality 25921. USNM 451074. Bluffs of White Oak Creek at bridge of Barbour County Route 47 and Alabama State Route 95,

old Alexanders Mill site, at Barbour-Henry County line, Ala. (SE¼SW¼ sec. 8, T. 9 N., R. 29 E.).

62A USGS Mesozoic locality 25993. USNM 450489, 453877. White Oak Creek, 960 m (0.6 mile) above mouth and 160 m (0.1 mile) below powerline crossing over creek, Barbour-Henry County line, Ala. (NE¼ sec. 16, T. 9 N., R. 29 E.).

62B USGS Mesozoic locality 32250. USNM 450484, 459091. Fort Gaines Northeast No. 1 Well, depth 108 ft, Sandy Branch Public Use Area, eastern bank of the Walter F. George Reservoir, along the left bank of the Chattahoochee River valley, about 7.6 km (4.7 miles) northwest of Fort Gaines and 3.7 km (2.3 miles) south of Pataula Creek, Clay County, Ga.

63 USGS Mesozoic localities 6412, 25556, 25935, 28442. USNM 450490, 450491, 450499, 450816, 451072, 451075, 453897. 1.4 km (0.9 mile) above the mouth of Pataula Creek at the Narrows, right bank below the waterfalls, Clay County, Ga.

64 USGS Mesozoic localities 855, 25988. USNM 450554, 451076. Chattahoochee River at mouth of Pataula Creek, 20.8 km (12.9 miles) below Eufaula, Clay County, Ga.

65 USGS Mesozoic locality 25992. USNM 450482, 450483, 451078. Roadcut and drainage ditch of the north-northwest-facing slope of Pataula Creek valley, just southeast of bridge of U.S. Route 82 over Pataula Creek, 4.0 km (2.5 miles, airline) northwest of Morris, and 3.2 km (2 miles) northwest of junction with Georgia Route 29, Quitman County, Ga.

66 No locality assigned.

67 USGS Mesozoic locality 27560. USNM 451083. Left side of Chattahoochee River, about 91.4 m (100 yards) below mouth of Pataula Creek and 20.3 km (12.9 miles) south of Eufaula, Clay County, Ga.

68 No locality assigned.

Peedee Formation

69A USGS Mesozoic localities 12262, 13585. USNM 73438, 73439, 453871. New Rocky Point Quarry, Pender County, N.C.

69B USGS Mesozoic locality 780. USNM 450511. Castle Hayne Quarry, New Hanover County, N.C.

69C USGS Mesozoic locality 32344. USNM 453892. Allisons Landing, right bank of the Pee Dee River, 104.4 km (64.9 miles) above Georgetown, Georgetown County, S.C.

Severn Formation

70 USGS Mesozoic localities 32774, 32775. USNM 450463, 450473, 451099, 451100. Excavations for Landover Mall shopping center near intersection of Maryland Route 202, Interstate 95, and Brightseat Road, Prince George's County, Md. [USGS 32774 is from the concretion zone; USGS 32775 is from the loose sands associated with the concretion layer.]

71 USGS Mesozoic locality 28858. USNM 451095. Excavations immediately west of bridge of Interstate 95 and just north of Central Avenue (Route 214), within cloverleaf approach and exit 15 of capital beltway, Interstate 495/95 Prince George's County, Md.

72 USGS Mesozoic locality 9592. USNM 450476, 451055. Near head of small ravine about 1.4 km (0.9 mile) southwest of Brightseat, Prince George's County, Md. [Probably the same as locality 73A.]

73A USGS Mesozoic localities 851, 32772, 32773. USNM 131763, 131764, 131766, 450416, 450470, 450479, 450480, 450520, 451098, 453893. Exposures in small drainage ditch on the Wilson Dairy Farm south of Sheriff Road, Prince George's County, Md. Gardner's (1916) Brightseat locality.

73B USGS Mesozoic locality 21067. USNM 453874. Excavations for Oxon Hill High School, east of Indian Head Highway, Prince George's County, Md.

74 USNM 451104. Millersville, Anne Arundel County, Md.

75 USGS Mesozoic locality 852. USNM 32291, 450497. Near Oakland, about 11.3 km (7 miles) from Washington, D.C., Prince George's County, Md. [Oakland is west of District Heights in the triangle formed by Marlboro Pike, Walker Mill Road, and Silver Hill Road. This is 7 miles from the heart of Washington, D.C. (the Capitol building) but only 1.5 miles from the District line.]

PALEOCENE

Clayton Formation

76 USGS Cenozoic locality 18396. USNM 450854. See locality 53 for a complete description. [This collection is from the base of the Clayton and probably contains reworked Owl Creek Formation fossils.]

77A USGS Cenozoic locality 284. USNM 129744, 129748. Prairie Creek, Wilcox County, Ala. Pine Barren Member.

77B USNM 459092. Creek bottom in SE¼ sec. 28, T. 12 N., R. 14 E., Lowndes County, Ala. [This collection is from the basal Clayton and probably contains reworked Prairie Bluff fossils.]

Porters Creek Clay and (or) Naheola Formation

78 USGS Cenozoic locality 3102. USNM 154914, 450552. PRI 64. Graveyard Hill, west of Oak Hill, Wilcox County, Ala.

79 PRI 65. 1.6 km (1 mile) north of Allenton, Wilcox County, Ala.

80 USGS Cenozoic locality 264. USNM 129745, 129747, 129749, 129750, 129754, 129756, 137256, 137257, 450543–450550, 450562–450565. Prairie Creek, east of Rosebud, Wilcox County, Ala.

81 USGS Cenozoic locality 283. USNM 129753, 129755. Block Creek Branch of Prairie Creek, Wilcox County, Ala.

Aquia Formation

82A USGS Cenozoic locality 17126. USNM 450823, 450858. The former Brook's Estate; tributary of Cabin Branch stream at end of cul-de-sac of Cappy Avenue off Central Avenue, 1.2 km (0.75 mile) southeast of Central Avenue and Addison Road intersection, Prince George's County, Md.

82B USGS Cenozoic locality 17124. USNM 450860. 0.8 km (0.5 mile) east of Phelps Corner, in branch of Henson Creek, crossing Ernshaw Road, Prince George's County, Md. [Phelps Corner is just south of the capital beltway (I–95) interchange 37A, at the intersection of Oxon Hill Road, Brinkley Road, and St. Barnabus Road. Ernshaw Road was renamed Brinkley Road, probably in the 1950's.]

83 USNM 450536. Indian Head Highway, 12.9 km (8 miles) south of Washington, D.C., Prince George's County, Md. [Distance south of Washington probably refers to distance south of the heart of the city.]

84 USNM 450856. Vicinity of Brightseat, Prince George's County, Md.

85 USGS Cenozoic locality 2489. USNM 115796, 450523, 450531–450533, 450572, 450808. ANSP 30498. Piscataway Creek, Prince George's County, Md.

86 USNM 450839. 1.6 km (1 mile) northeast of Piscataway Creek, Prince George's County, Md.

87 USGS Cenozoic localities 17100, 17104. USNM 207153, 450850, 450857, 450859, 450865. North side of Piscataway Creek at Indian Head Highway crossing, Prince George's County, Md.

88 USGS Cenozoic locality 2508. USNM 2490, 155549, 207155, 450526–450530, 450809, 450822, 450824, 450834. Aquia Creek, Stafford County, Va.

89 USGS Cenozoic locality 2030. USNM 136215, 450573. Mouth of Aquia Creek, Potomac River, Stafford County, Va.

90 USNM 450810. North bank of Potomac Creek, 4 km (2.5 miles) above the mouth, Stafford County, Va.

91 USNM 450524, 450525, 450537, 450806, 450826, 450828, 450830, 450832. Potomac Creek, Stafford County, Va.

92 USNM 450534, 450833. Potomac River, 800 m (0.5 mile) below Potomac Creek, King George County, Va.

93 USNM 453904. Potomac River, above Belvedere Beach, King George County, Va. Paspotansa Member.

94 USGS 26359. USNM 366485, 450838, 450840, 453913–453915. Potomac River, 0.5 km (0.3 mile) above Belvedere Beach, King George County, Va. Paspotansa Member.

95 USNM 453910. Potomac River, below Belvedere Beach, King George County, Va. Paspotansa Member.

96 USNM 450811. Potomac River, 800 m (0.5 mile) below Belvedere Beach, King George County, Va.

97 USNM 450539, 450829, 450837. Paspotansa Creek, King George County, Va.

98 USNM 450540, 453906, 453909, 453911, 453912. Potomac River below Paspotansa Creek, King George County, Va.

99 USNM 450825. Potomac River, 3.2 km (2 miles) below Potomac Creek, King George County, Va.

100 USNM 450827. Potomac River, Fairview Beach, King George County, Va.

101 USNM 450821. South bank of Potomac River near Marlboro Point, above mouth of Potomac Creek, Stafford County, Va.

102 USNM 450512, 450538, 450831, 450864. Liverpool Point, Potomac River, Charles County, Md. [This is probably the collection site described by Dryden and Overbeck (1948, p. 78, loc. 5) as "Shore of Potomac River, 2150 feet south of wharf at Liverpool Point, about 17 miles W.S.W. of La Plata," although the note with the collection reads simply "Liverpool Point."]

103 USNM 450535, 450835. Mill, 1.6 km (1 mile) southeast of Mason Springs, Charles County, Md.

104 USGS Cenozoic locality 2243. USNM 136177, 450513, 450569–450571, 450863, 453922.

Glymont, Potomac River, Charles County, Md. [This is probably the collection site described by Dryden and Overbeck (1948, p. 78, loc. 2) as "Bluff about 1500 feet above (northeast of) Glymont wharf, Potomac River. Locality about 10½ miles N.W. of La Plata," although the note with the collection reads simply "Glymont, Potomac River."]

105 USNM 450841, 450845. Reedy Run, south branch of Chickawupen Creek near Posey's, Seat Pleasant, Prince George's County, Md.

106 USNM 450514, 450862. Near mouth of Mattawoman Creek, Prince George's-Charles County line, Md.

107 USNM 450819. South River Bridge, Anne Arundel County, Md.

108 USNM 450836. 4 km (2.5 miles) above Pope's Creek, Charles County, Md.

109 USGS Cenozoic locality 2349. USNM 148893. Clifton Beach, Charles County, Md. [Dryden and Overbeck (1948, p. 79, loc. 6) mention outcrops occurring "6880 to 1180 feet above Clifton Beach wharf." I examined specimens of *Bathytormus alaeformis* from this locality, but these specimens could not be located at the USNM when formal identification and numbering of specimens were conducted.]

110 Between Buena Vista and Collington, Prince George's County, Md. [I examined specimens of *Bathytormus alaeformis* from this locality, but these specimens could not be located at the USNM when formal identification and numbering of specimens were conducted. Because *B. alaeformis* and *Crassatella aquiana* co-occur in the Aquia deposits, this collection may have contained one, or the other, or a mixture of these two species.]

111 ANSP 30580. Upper Marlboro, Prince George's County, Md.

112 USNM 453908. Rappahanock River, north of Hop Yard, King George County, Va. [Hop Yard Landing is located 4 miles west of the intersection of U.S. Route 301 and State Route 3 at Office Hall, King George County, Va. (Port Royal, Va. 7.5-min quadrangle).]

113A USGS Cenozoic locality 26337. USNM 366477, 453907, 453919, 453920, 453905. 0.8 km (0.5 mile) east of Wickham Crossing, right bank of the Pamunkey River, Hanover County, Va. Piscataway Member.

113B USGS Cenozoic locality 26362. Right bank of the Pamunkey River, 1.5 km (0.95 mile) above the Route 301 bridge (airline miles), Hanover County, Va.

Nanafalia Formation

114 USGS Cenozoic localities 271, 5641. USNM 129898, 450516, 450553, 450555, 450556, 450560, 450846, 450849, 450861. Nanafalia Bluff, Tombigbee River, Marengo County, Ala.

115A USGS Cenozoic locality 10765. USNM 450522, 450847. 400 m (0.25 mile) northeast of Henderson on Natch Road, Pike County, Ala.

115B USGS Cenozoic locality 10769. USNM 450848. Becks Mill, 16.1 km (10 miles) from Brundridge, on the Pea River, Dale County, Ala. [Questionably assigned to Nanafalia Formation.]

Tuscahoma Formation

116 USGS Cenozoic locality 10782. USNM 450813, 450842. Yellow Bluff, Alabama River, Wilcox County, Ala.

117 USGS Cenozoic localities 2669, 3098, 5594. USNM 90968, 137064, 155060, 450517–450519, 450521, 450558, 450561, 450817, 450843, 453916. Bells Landing, Alabama River, Monroe County, Ala. Bells Landing Member.

118 USGS Cenozoic locality 9498. USNM 450515, 450559, 450812, 450814. PRI 140. Greggs Landing, Alabama River, Monroe County, Ala. Greggs Landing Member.

119 USGS Cenozoic localities 5601, 10779. USNM 450818, 450844, 453918, 459096. Lower Peach Tree, Alabama River, Wilcox County, Ala. [USNM 453918 was taken from a roadcut along the access to the ferry and is from the Bells Landing Member.]

120 USNM 453917. Cliffs below Blacks Bluff, Alabama River, Wilcox County, Ala. Bells Landing Member.

PLATES 1–22

Contact photographs of the plates in this report are available, at cost,
from the U.S. Geological Survey Photographic Library, Federal Center, Denver, CO 80225

PLATE 1

Type specimens of *Crassatella vadosa* Morton, 1834

FIGURES 1–17. *Crassatella vadosa* Morton, 1834.

- 1, 4, 9, 11, 16. Syntypes of *Crassatella ripleyana* Conrad, 1858 from the Owl Creek Formation at locality 52, Mississippi. ANSP 18741.
  - 1, 9. Exterior and interior right valve (×1).
  - 4. Exterior left valve (×1).
  - 11. Interior right valve of broken specimen (×1).
  - 16. Exterior right valve (×1).
- 2, 3. Interior and exterior left valve (×1) holotype *Crassatella vadosa* Morton, 1834 from the Prairie Bluff Chalk at locality 56, Alabama. ANSP 19593.
- 5–8, 10. Syntypes of *Crassatella lintea* Conrad, 1860 from the Ripley Formation at locality 36B, Eufaula, Alabama. ANSP 19594.
  - 5, 8. Exterior and interior right valve (×1.5).
  - 6, 7. Exterior and interior right valve (×1.5).
  - 10. Exterior left valve of articulated specimen (×1.5).
- 12, 13. Exterior and interior right valve (×1) paratype *Crassatella gardnerae* Harbison, 1945 from the Coon Creek Tongue of the Ripley Formation at locality 28, Mississippi. USNM 103753 (USGS 18629).
- 14. Partially preserved exterior right valve (×1) syntype *Crassatella subplana* Conrad, 1853 from the Mount Laurel Sand and (or) Navesink Formation at locality 47, New Jersey. ANSP 18743.
- 15, 17. Exterior and interior right valve (×1) paratype *Crassatellites carolinana* Stephenson, 1927 from the Peedee Formation at locality 69A, North Carolina. USNM 73439.

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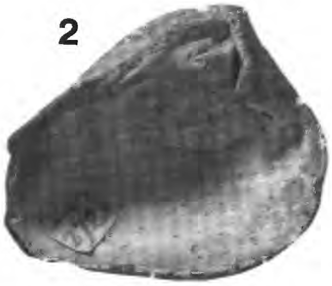

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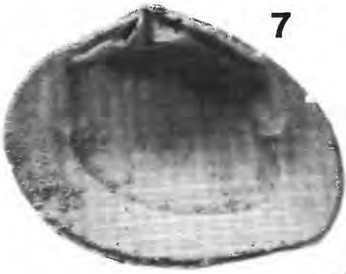

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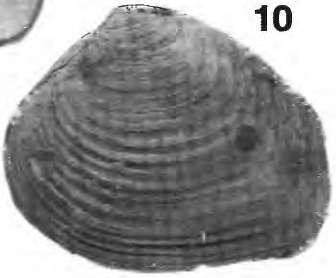

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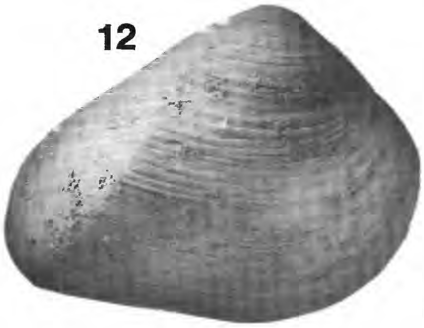

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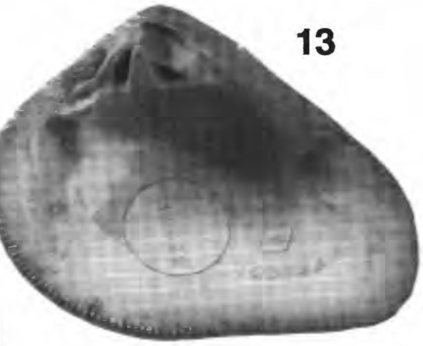

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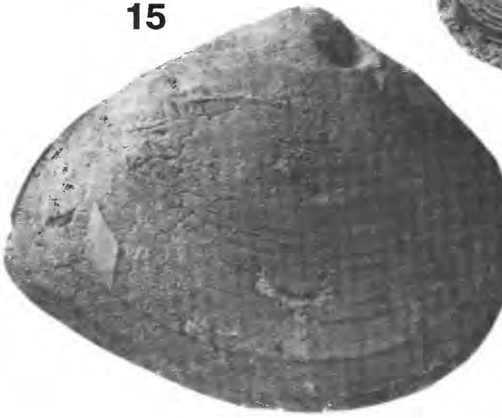

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CRASSATELLA

PLATE 2

Type specimens of Cretaceous Crassatellidae

FIGURES 1–3. *Bathytormus pteropsis* (Conrad), 1860.

1. Exterior right valve in matrix (×1.5), hypotype (Gardner, 1916, pl. 39, fig. 5), from the Severn Formation at locality 75, Maryland. USNM 32291.

2, 3. Articulated specimen, hypotype (Stephenson and Monroe, 1940, pl. 9, figs. 4, 5) from the Ripley Formation at locality 34A, Mississippi. USNM 20845.
   2. Dorsal view (×1.5).
   3. Exterior left valve (×1.5).

FIGURES 4, 5. *Crassatellites neusensis* Stephenson, 1923. Paratypes from the Bladen Formation at locality 18, North Carolina.

4. Exterior left valve (×1.5). USNM 31737.
5. Exterior left valve (×1.5). USNM 31736.

FIGURE 6. *Scambula perplana* Conrad, 1869. Interior left valve in matrix (×5), supposed holotype (according to Richards, 1958, p. 192; see discussion p. 90), from the Conrad collection from the Woodbury Clay at locality 14, New Jersey. ANSP 18740.

FIGURES 7, 8, 10, 11. *Crassatellites hodgei* Stephenson, 1923. Holotype and paratype from the Tar Heel Formation at locality 8, North Carolina.

7, 8. Interior and exterior left valve (×1.5) holotype. USNM 31930.

10, 11. Interior and exterior left valve (×1.5) paratype. USNM 31931.

FIGURE 9. *Crassatella carolinensis* Conrad, 1875. Exterior left valve in matrix (×2), hypotype (Stephenson, 1923, pl. 66, fig. 17), from the Tar Heel Formation at locality 8, North Carolina. USNM 31929.

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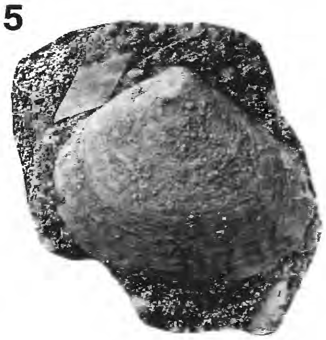

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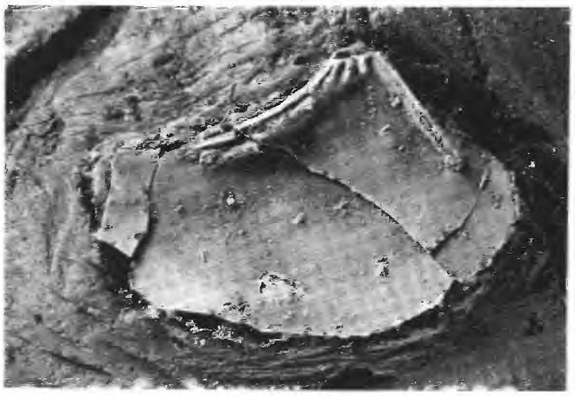

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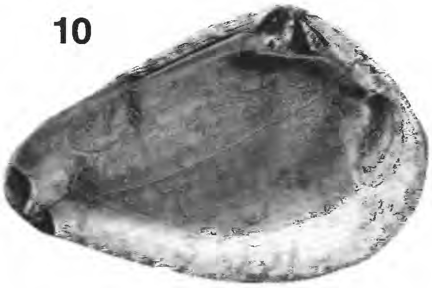

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BATHYTORMUS, CRASSATELLA, AND *SCAMBULA*

PLATE 3

Type specimens of Tertiary Crassatellidae

FIGURES 1–10. *Crassatella aquiana* Clark, 1895.

- 1, 2, 5. Left valve holotype *Crassatella sepulcollis* Harris, 1896 from the Porters Creek(?) Clay at locality 78, Alabama. PRI 64.
  - 1. Interior (×1.5).
  - 2. Specimen tilted to reveal characters of the umbo (×1.5).
  - 5. Exterior (×1.5).
- 3, 8, 10. Articulated specimen, holotype *Crassatella aquiana* Clark, 1895 from the Aquia Formation at locality 88, Virginia. USNM 207155.
  - 3. Dorsal view (×1).
  - 8. Exterior right valve (×1).
  - 10. Exterior left valve (×1).
- 4, 7. Interior and exterior right valve (×1.5) paratype *Crassatella sepulcollis* Harris, 1896 from the Naheola(?) Formation at locality 79, Alabama. PRI 65.
- 6, 9. Exterior and interior right valve (×1) holotype *Crassatella halei* Harris, 1897 from the Greggs Landing Member of the Tuscahoma Formation at locality 118, Alabama. PRI 140.

FIGURES 11, 13. *Crassatella palmula* Conrad, 1846. Interior (hinge visible) and exterior left valve (×1) holotype from the Aquia Formation at locality 111, Maryland. ANSP 30580.

FIGURES 12, 14–19. *Bathytormus alaeformis* (Conrad), 1830.

- 12, 14, 15, 17. Holotype and paratype *Crassatella alaeformis* Conrad, 1830 from the Aquia Formation at locality 85, Maryland. ANSP 30498.
  - 12, 15. Left valve paratype.
    - 12. Interior (×1).
    - 15. Specimen tilted to reveal ornament of umbo (×1).
  - 14, 17. Exterior and interior right valve (×1) holotype.
- 16, 18, 19. Holotype and paratype of *Crassatella declivis* Heilprin, 1880 from the Aquia Formation at locality 88, Virginia. USNM 2490.
  - 16, 19. Exterior and interior left valve (×1.5) paratype.
  - 18. Exterior right valve (×1.5) holotype.

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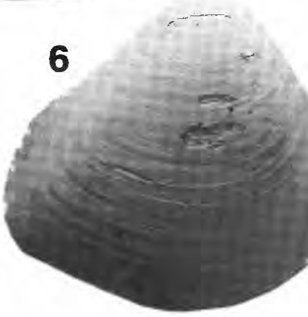

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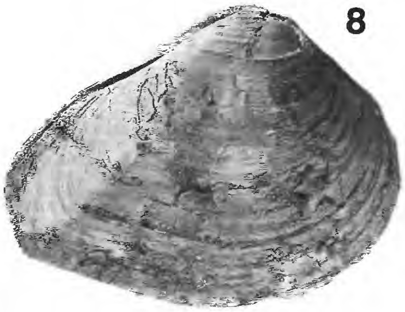

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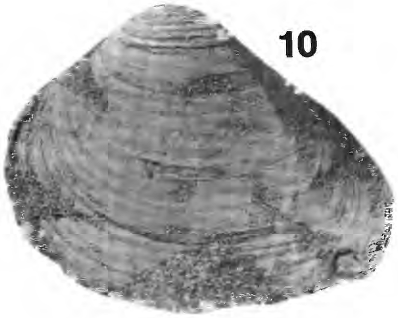

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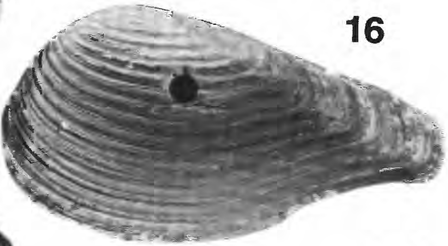

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CRASSATELLA AND *BATHYTORMUS*

PLATE 4

Morphologic variation within *Crassatella hodgei* (Stephenson), 1923

FIGURES 1–19. *Crassatella hodgei* (Stephenson), 1923.

- 1, 3, 5, 12, 13. Specimens from the Blufftown Formation at locality 4, Georgia.
  - 1. Exterior left valve (×2). USNM 450402 (USGS 6405).
  - 3. Exterior left valve (×1.5). USNM 450403 (USGS 844).
  - 5. Exterior left valve (×1). USNM 450404 (USGS 844).
  - 12. Interior left valve (×1.5). USNM 450405 (USGS 6405).
  - 13. Exterior left valve (×1.5). USNM 450406 (USGS 6405).
- 2. Exterior right valve (×1) of specimen from the Blufftown Formation at locality 6, Georgia. USNM 450407 (USGS 25563).
- 4. Exterior left valve (×1) of specimen from the Coffee Sand at locality 1, Mississippi. USNM 450408 (USGS 17783).
- 6, 7, 11, 14–16. Specimens from the Coffee Sand at locality 3, Mississippi.
  - 6, 7. Exterior and interior right valve (×1). USNM 450409.
  - 11, 14. Exterior and interior right valve (×1). AA, anterior adductor; AR, anterior pedal retractor; PA, posterior adductor; PR, posterior pedal retractor. USNM 450410.
  - 15, 16. Exterior and interior left valve (×1). USNM 450411.
- 8. Latex cast of exterior left valve (×1.5) of specimen from the Merchantville Formation at locality 13B, Delaware. USNM 450412 (USGS 17698).
- 9, 17, 19. Poorly preserved specimens from the Cusseta Sand at locality 26, Georgia (the type locality for *Crassatellites roodensis* Stephenson, 1923).
  - 9. Exterior left valve (×1). USNM 450413 (USGS 6401).
  - 17. Exterior left valve (×1). USNM 450414 (USGS 27544).
  - 19. Exterior right valve (×1). USNM 450415 (USGS 6401).
- 10, 18. Poorly preserved paratypes of *Crassatellites roodensis* Stephenson, 1923 from the Bladen Formation at locality 16, South Carolina. USGS 5372.
  - 10. Exterior right valve in matrix (×1). USNM 31748.
  - 18. Exterior left valve in matrix (×1). USNM 31749.

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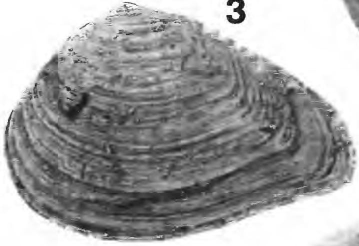

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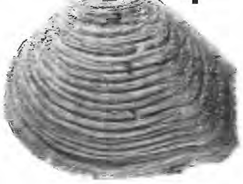

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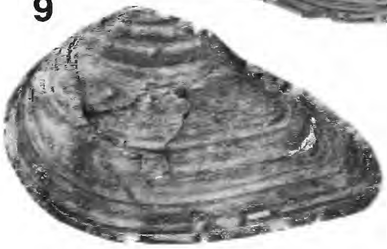

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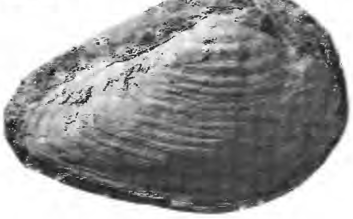

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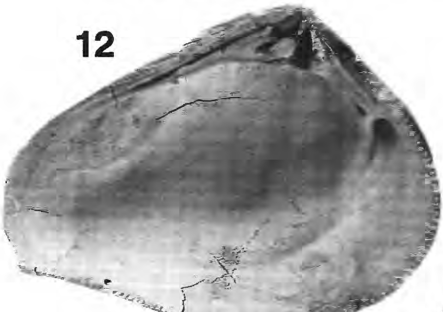

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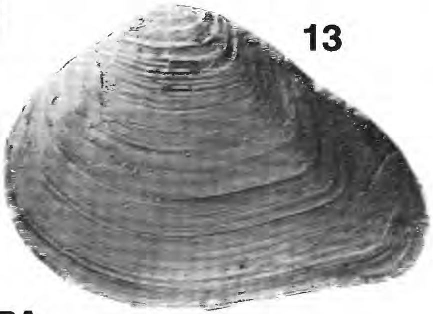

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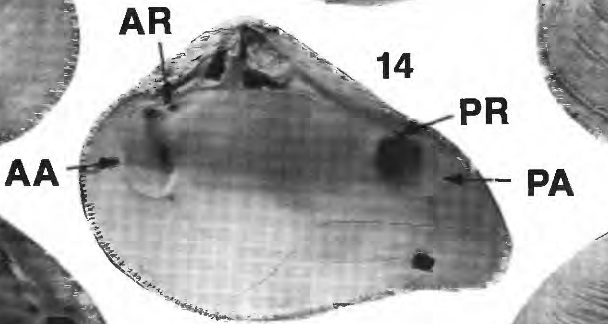

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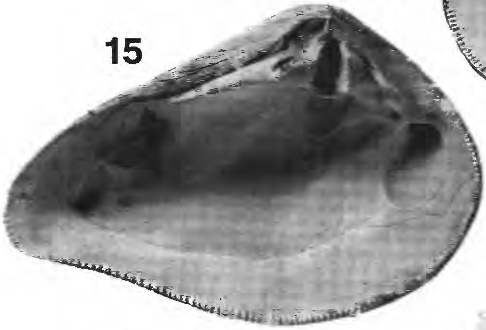

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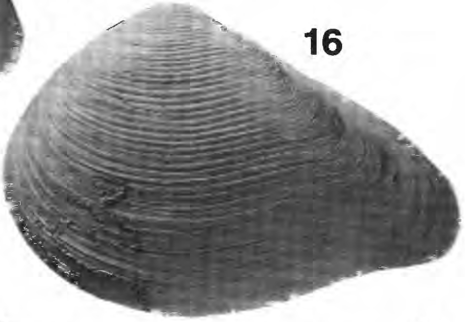

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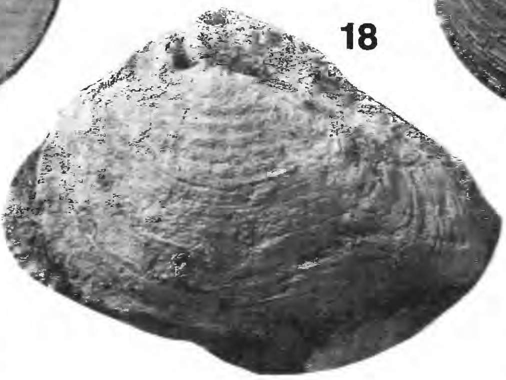

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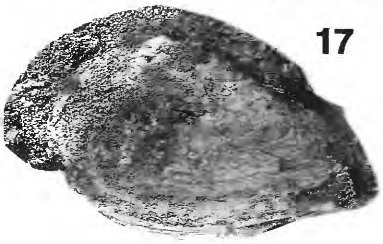

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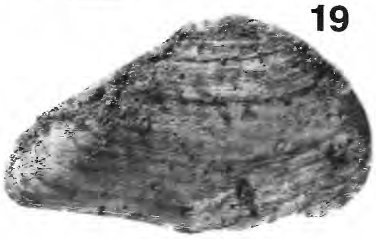

CRASSATELLA

PLATE 5

Morphologic variation within *Crassatella carolinensis* Conrad, 1875 and comparison to other Cretaceous *Crassatella*

FIGURES 1, 3, 4, 6. *Crassatella vadosa* Morton, 1834.

1, 3. Exterior and interior right valve (×1.5) of specimen from the Severn Formation at locality 73A, Maryland. USNM 450416 (USGS 32772).

4. Exterior left valve (×1.5) of specimen from the Ripley Formation at locality 40, Alabama. USNM 450417 (USGS 857).

6. Exterior left valve (×1.5) of specimen from the Owl Creek Formation at locality 52, Mississippi. USNM 450418 (USGS 6464).

FIGURES 2, 7, 9, 10, 12, 14. *Crassatella hodgei* (Stephenson), 1923.

2, 10. Interior and exterior right valve (×1) of specimen from the Coffee Sand at locality 2, Mississippi. USNM 450419 (USGS 6909).

7. Latex cast of exterior left valve (×2) of specimen from the Merchantville Formation at locality 13A, Delaware. USNM 450420.

9, 12, 14. Specimens from the Blufftown Formation at locality 4, Georgia. USGS 6405.

9. Exterior left valve (×3). USNM 450421.

12, 14. Exterior and interior right valve (×1.5). USNM 450422.

FIGURES 5, 8, 11, 13, 15–20. *Crassatella carolinensis* Conrad, 1875. Specimens from the Blufftown Formation at locality 4, Georgia.

5. Enlargement of right valve hinge (×1.5). USNM 450423 (USGS 6405).

8. Exterior left valve (×3). USNM 450424 (USGS 5392).

11, 13, 16. Left valve. USNM 450425 (USGS 6405).

11. Dorsal view (×1.5).

13, 16. Exterior and interior (×1.5). AA, anterior adductor; PA, posterior adductor; R, resilifer.

15. Exterior right valve (×1.5). USNM 450426 (USGS 5392).

17. Exterior left valve (×1.5). USNM 450427 (USGS 5392).

18. Exterior left valve (×1.5). USNM 450428 (USGS 5392).

19. Exterior right valve (×1.5). USNM 450429 (USGS 5392).

20. Exterior right valves in matrix (×1.5). USNM 450430 (USGS 26033).

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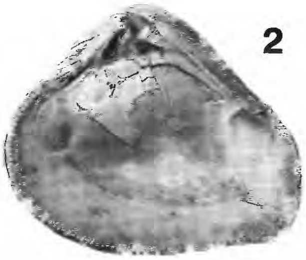

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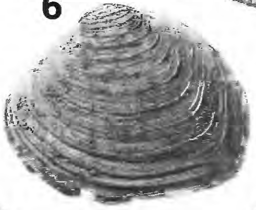

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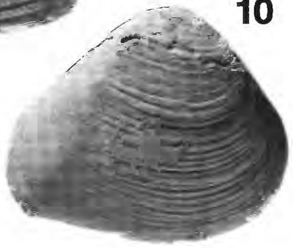

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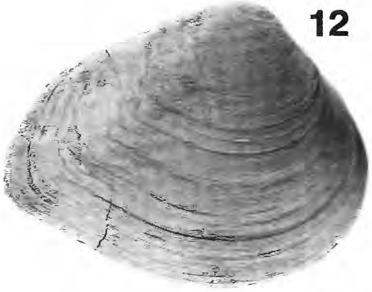

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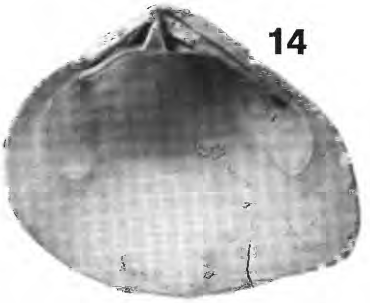

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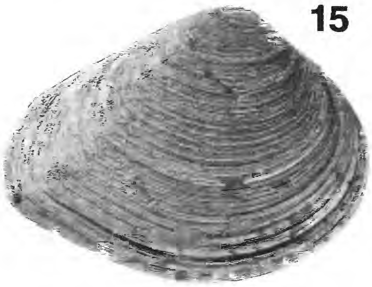

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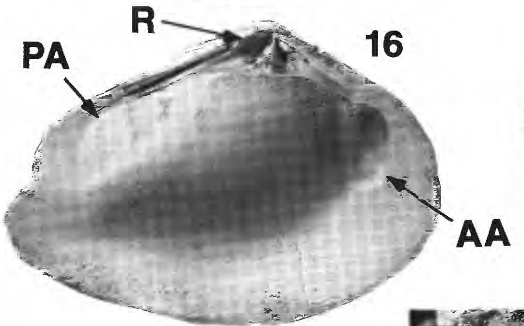

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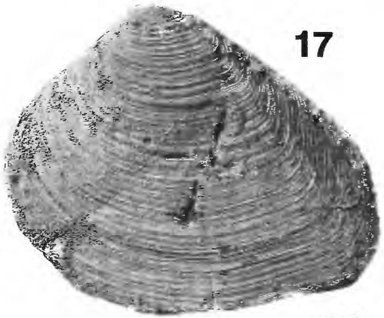

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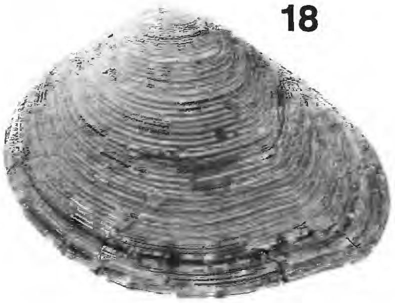

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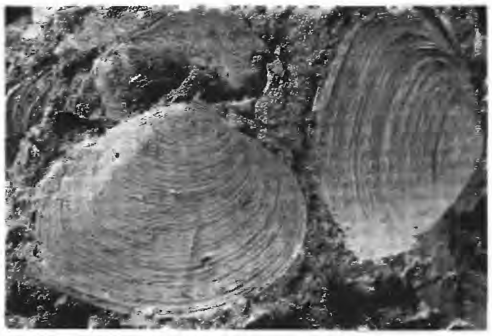


CRASSATELLA

PLATE 6

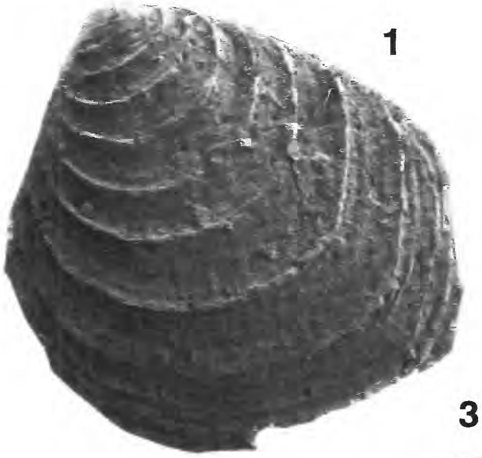
Juvenile *Crassatella hodgei* (Stephenson), 1923

FIGURES 1–6. *Crassatella hodgei* (Stephenson), 1923. Specimens from the Blufftown Formation at locality 4, Georgia. USGS 26033.

1. Exterior left valve (SEM ×25.8). USNM 450431.

2, 6. Right valve. USNM 450432.
   - 2. Interior (SEM ×31.7).
   - 6. Partially preserved prodissoconch and nepionic portions of shell (SEM ×122).

3. Exterior right valve (SEM ×41.7). USNM 450433.
4. Interior right valve (SEM ×9.11). USNM 450434.
5. Exterior right valve (SEM ×16.9). USNM 450435.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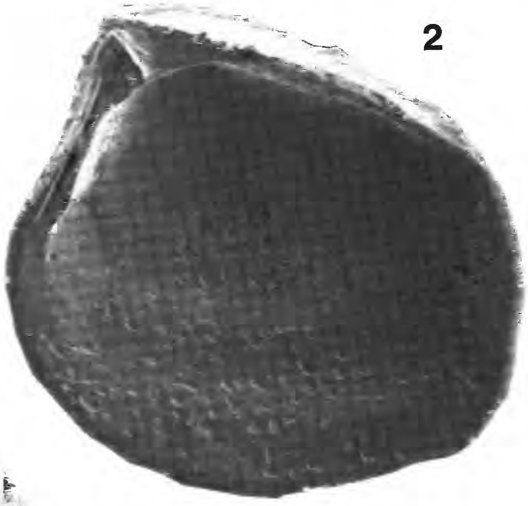
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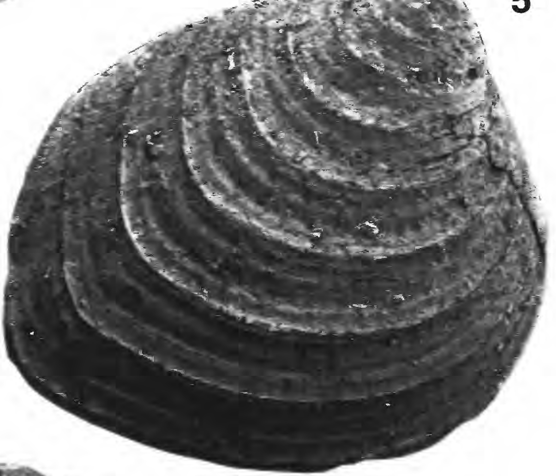
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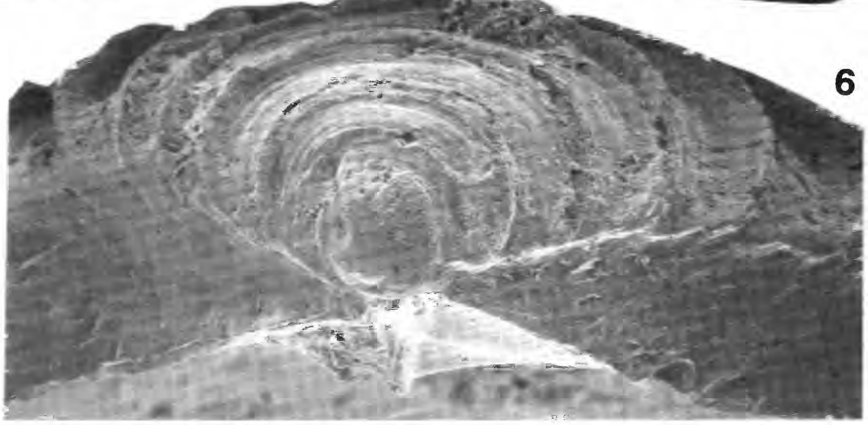
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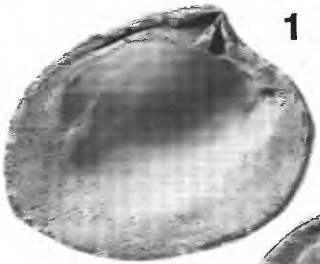
CRASSATELLA

PLATE 7

Growth series for *Crassatella vadosa* Morton, 1834

FIGURES 1–15. *Crassatella vadosa* Morton, 1834. Specimens from the Coon Creek Formation at locality 27, Tennessee. USGS 16951.

1, 5. Interior and exterior left valve (×1.5). USNM 450436.
2, 3, 4. Left valve. USNM 450437.
  2. Enlargement of hinge (×4).
  3, 4. Interior and exterior (×1.5).
6, 7. Interior and exterior left valve (×1.5). USNM 450438.
8, 10. Interior and exterior left valve (×1.5). USNM 450439.
9, 11. Interior and exterior left valve (×1.5). USNM 450440.
12, 13. Interior and exterior left valve (×1.5). USNM 450441.
14, 15. Interior and exterior left valve (×1.5). USNM 450442. AA, anterior adductor; AR, anterior pedal retractor; PA, posterior adductor; PL, pallial line; PR, posterior pedal retractor; R, resilifer.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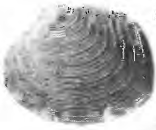
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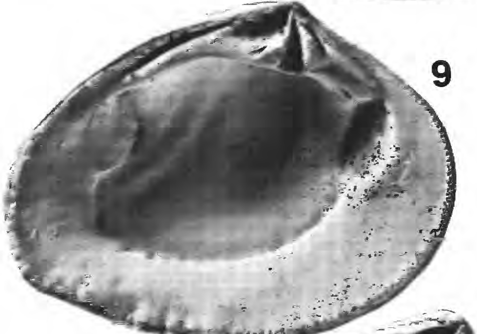
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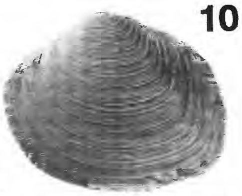
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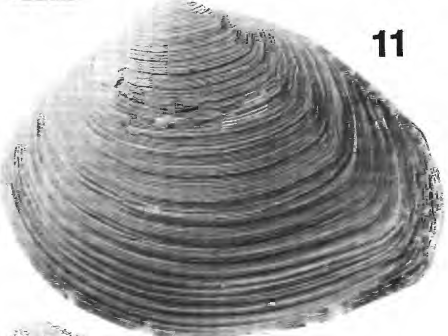
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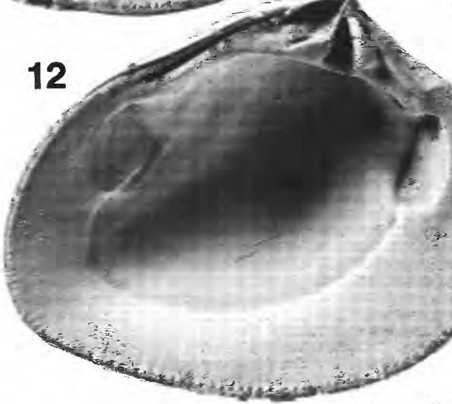
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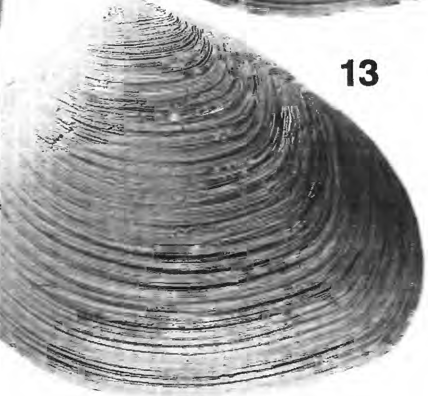
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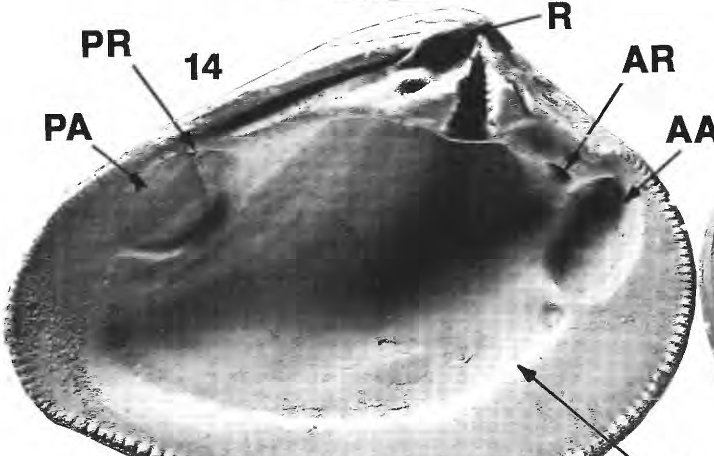
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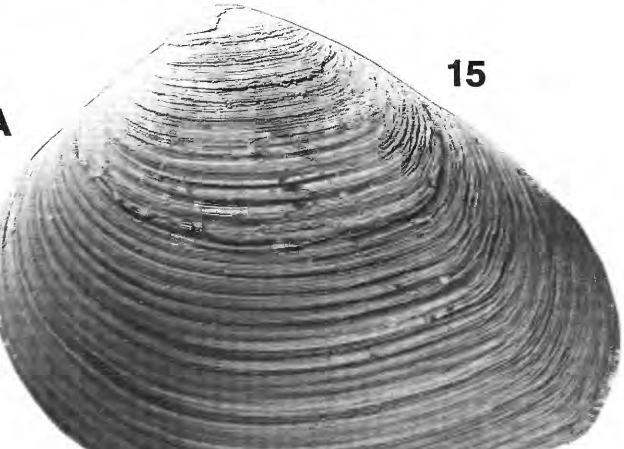
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CRASSATELLA

PLATE 8

Morphologic variation within *Crassatella vadosa* Morton, 1834

FIGURES 1–16. *Crassatella vadosa* Morton, 1834.

- 1–3, 11, 14, 16. Specimens, classified as "*Crassatella ripleyana*" (Conrad), 1858 for the canonical discriminant analysis of subspecies, from the Owl Creek Formation at locality 52, Mississippi. USGS 6464.
  - 1, 2. Interior and exterior left valve (×1.5). USNM 450443.
  - 3. Exterior left valve (×1). USNM 450444.
  - 11. Exterior left valve (×1.5). USNM 450445.
  - 14, 16. Left valve. USNM 450446.
    - 14. Exterior (×1).
    - 16. Specimen tilted and enlarged (×1.5) to reveal details of juvenile stage.
- 4, 5, 9. Specimens, classified as *Crassatella gardnerae* Harbison, 1945 for the canonical discriminant analyses of *Crassatella* species, from the Coon Creek Tongue of the Ripley Formation at locality 28, Mississippi. USGS 25411.
  - 4, 5. Interior and exterior right valve (×1). USNM 450447.
  - 9. Exterior right valve (×1). USNM 450448.
- 6, 8, 12, 13, 15. Specimens, classified as "*Crassatella wadei*" Stephenson, 1941 for the canonical discriminant analysis of subspecies, from the Coon Creek Formation at locality 27, Tennessee.
  - 6, 8. Articulated specimen. USNM 450449 (USGS 30762).
    - 6. Exterior right valve (×1).
    - 8. Dorsal view (×1.5). (Note character of nepionic portion of shell.)
  - 12, 13. Articulated specimen. USNM 450450 (USGS 30762).
    - 12. Exterior right valve (×1).
    - 13. Dorsal view (×1.5). E, escutcheon; L, lunule.
  - 15. Exterior left valve (×1). USNM 450451 (USGS 16951).
- 7, 10. Specimens from the Ripley Formation at locality 45, Georgia. USGS 28431.
  - 7. Exterior right valve (×1). USNM 450452.
  - 10. Dorsal view left valve (×1.5). USNM 450458.

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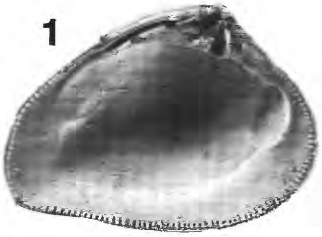

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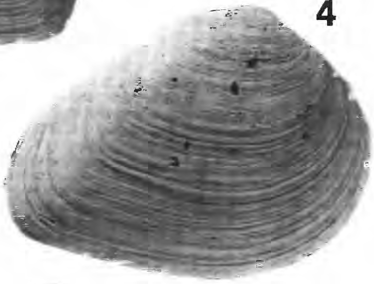

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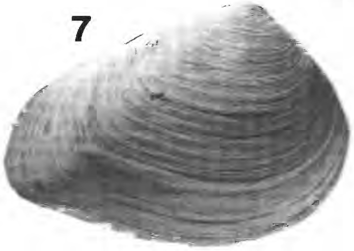

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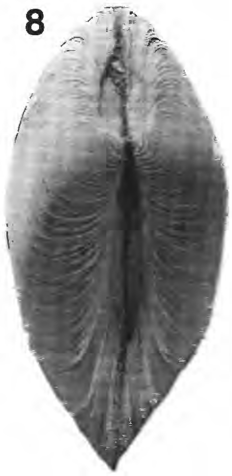

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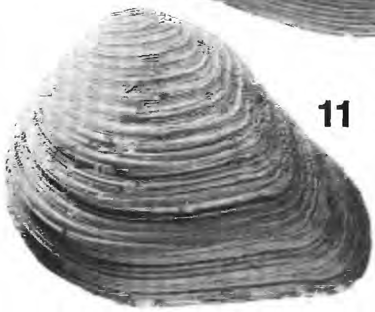

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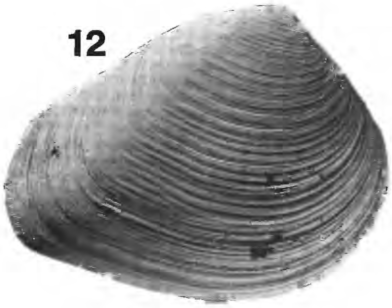

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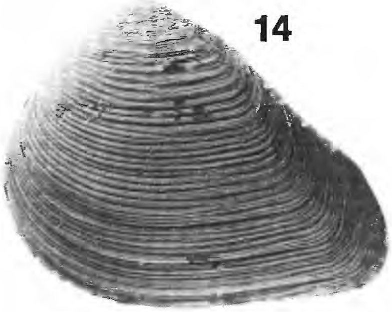

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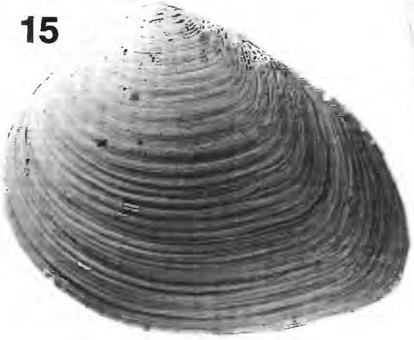

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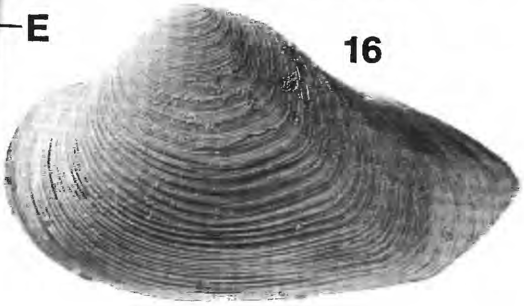


CRASSATELLA

PLATE 9

Morphologic variation within *Crassatella vadosa* Morton, 1834

FIGURES 1–13. *Crassatella vadosa* Morton, 1834.

1, 9. Specimens, classified as *Crassatella* sp. A for the statistical analysis, from the Coon Creek Tongue of the Ripley Formation at locality 30A, Mississippi. USGS 25407.

- 1. Exterior right valve (×1). USNM 450453.
- 9. Exterior left valve (×1). USNM 450454.

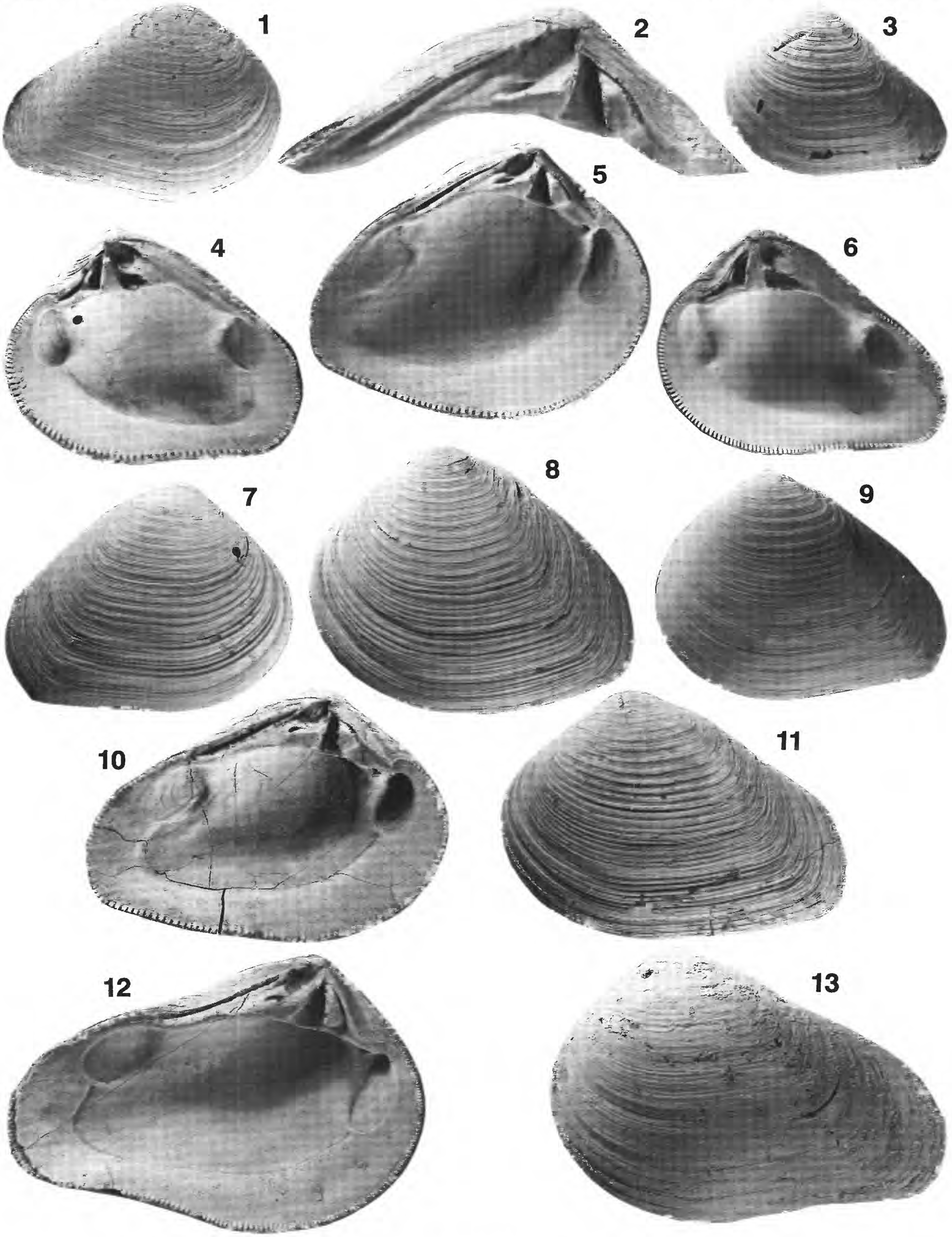
2, 4, 5, 7, 8, 10, 11. Specimens from the Coon Creek Formation at locality 27, Tennessee (type locality for *Crassatella vadosa wadei* Stephenson, 1941).

- 2, 5, 8. Left valve. USNM 450455 (USGS 25406).
  - 2. Enlargement of hinge (×2).
  - 5, 8. Interior and exterior (×1).
- 4, 7. Interior and exterior right valve (×1). USNM 450456 (USGS 16951).
- 10, 11. Interior and exterior left valve (×1). USNM 450457 (USGS 16951).

3. Exterior left valve (×1) of specimen from the Ripley Formation at locality 45, Georgia. USNM 450458 (USGS 28431).

6. Interior right valve (×1) of specimen from the Ripley Formation at locality 43, Alabama. USNM 450459 (USGS 28409).

12, 13. Interior and exterior left valve (×1) of specimen from the Coon Creek Tongue of the Ripley Formation at locality 28, Mississippi (type locality of *Crassatella gardnerae* Harbison, 1945). USNM 450460 (USGS 25411).



CRASSATELLA

PLATE 10

Juvenile characters and internal molds of *Crassatella vadosa* Morton, 1834

FIGURES 1–17. *Crassatella vadosa* Morton, 1834.

1, 5, 13, 14. Specimens from the Coon Creek Tongue of the Ripley Formation at locality 32, Mississippi. USGS 25410.
  1, 5. Exterior and interior right valve (×1.5). USNM 450461.
  13, 14. Interior and exterior left valve (×1.5). USNM 450462.

2. Dorsal portion of exterior left valve (×1) in shelly matrix from the Severn Formation at locality 70, Maryland. USNM 450463 (USGS 32774).

3, 12. Articulated specimen from the Ripley Formation at locality 40, Alabama. USNM 450464 (USGS 857).
  3. Dorsal view (×1.5).
  12. Exterior left valve (×1.5).

4. Exterior left valve (×3) of specimen from the Coon Creek Formation at locality 27, Tennessee. USNM 450,465 (USGS 16951).

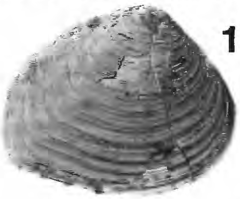
6–8, 10, 11. Specimens from the Ripley Formation at locality 43, Alabama. USGS 27919.
  6, 7. Interior and exterior right valve (×1.5). USNM 450466.
  8. Interior left valve (×1.5). USNM 450467.
  10. Exterior right valve (×1.5). USNM 450468.
  11. Exterior left valve (×1.5). USNM 450469.

9. Exterior right valve (×1.5) of specimen from the Severn Formation at locality 73A, Maryland. USNM 450470 (USGS 32772).

15. Left side of internal mold (×1) topotype from the Prairie Bluff Chalk at locality 56, Alabama. USNM 450471 (USGS 270).

16. Right side of internal mold (×1) paratype *Crassatellites carolinana* Stephenson, 1927 from the Peedee Formation at locality 69A, North Carolina. USNM 73439 (USGS 12262).

17. Left side of internal mold (×1) from the Mount Laurel Sand and (or) Navesink Formation at locality 48, New Jersey. USNM 450472 (USGS 31111).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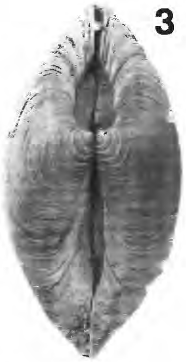
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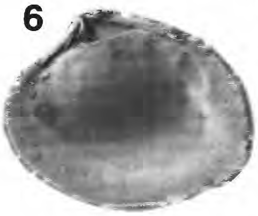
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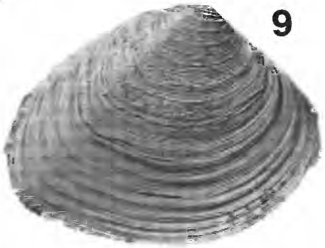
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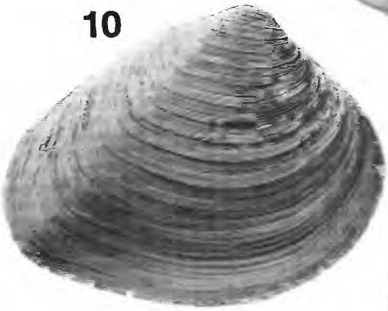
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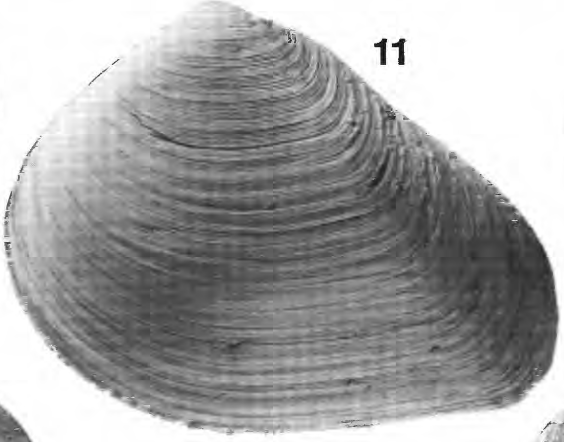
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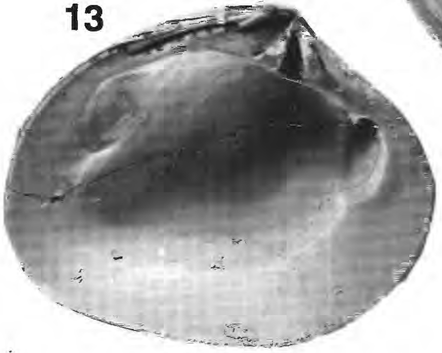
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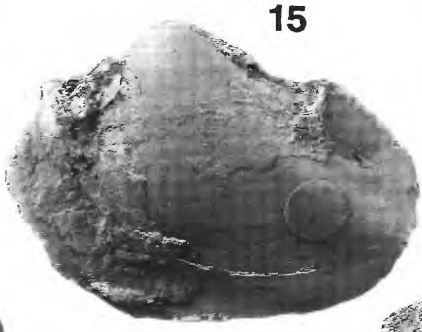
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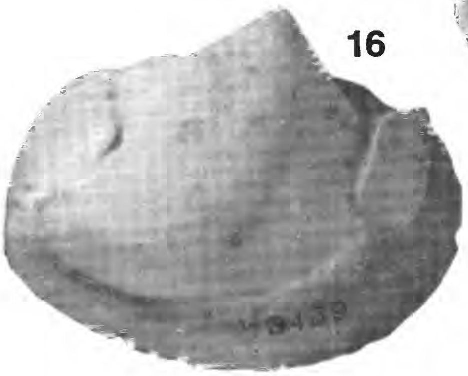
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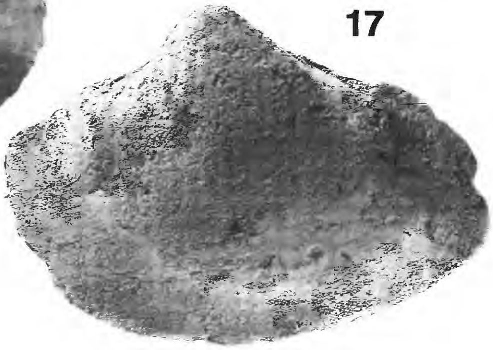
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CRASSATELLA

PLATE 11

Geographic variation of *Crassatella vadosa* Morton, 1834

FIGURES 1–13. *Crassatella vadosa* Morton, 1834.

1. Exterior left valve in matrix (×1), specimen from the Severn Formation at locality 70, Maryland. USNM 450473 (USGS 32774).

2, 3. Specimens from the Severn Formation at locality 73A, Maryland. USNM 131764.
  2. Interior right valve (×1).
  3. Exterior left valve (×1).

4–6. Right valve of specimen from the Owl Creek Formation at locality 52, Mississippi. USNM 450474 (USGS 25423).
  4, 6. Exterior and interior (×1).
  5. Dorsal view (×1).

7. Exterior right valve (×1) of specimen from the Coon Creek Formation at locality 27, Tennessee (type locality of *Crassatella vadosa wadei* Stephenson, 1941). USNM 450475 (USGS 16951).

8, 9. Exterior and interior right valve (×1.5) of specimen from the Severn Formation at locality 72, Maryland. USNM 450476.

10. Exterior left valve (×1.5) of specimen from the Ripley Formation at locality 40, Alabama. USNM 450477 (USGS 857).

11, 12. Interior and exterior left valve (×1) holotype *Crassatellites carolinana* Stephenson, 1927 from the Peedee Formation at locality 69A, North Carolina. USNM 73438 (USGS 12262).

13. Exterior left valve (×1) syntype *Crassatella subplana* Conrad, 1853 from the Mount Laurel Sand and (or) Navesink Formation at locality 47, New Jersey. ANSP 18743.


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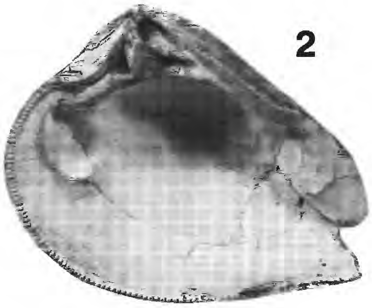
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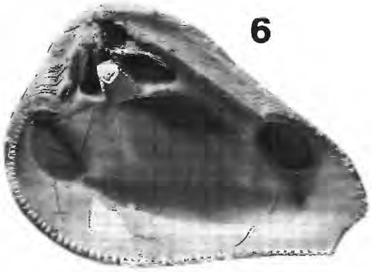
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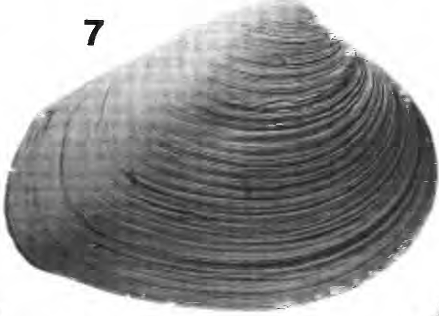
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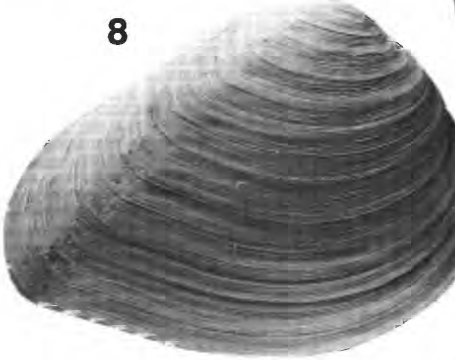
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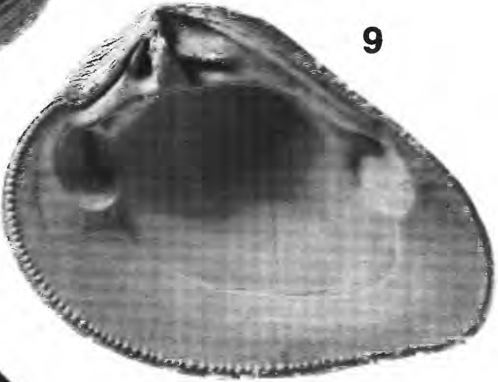
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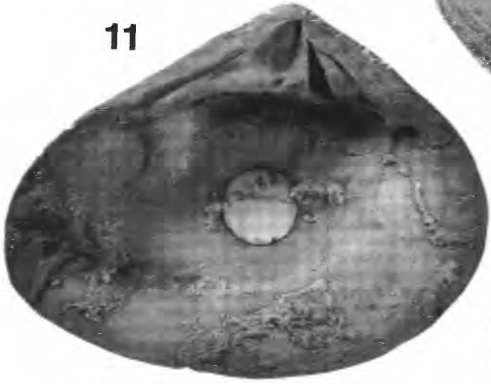
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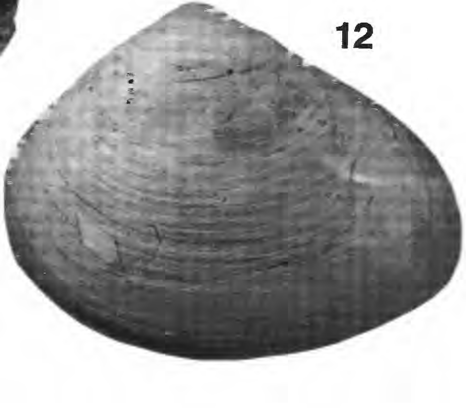
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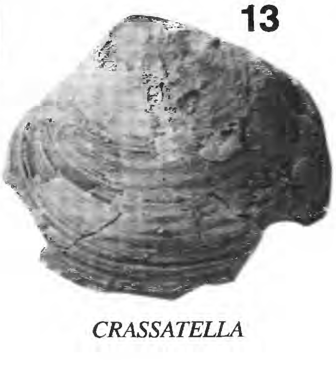
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CRASSATELLA

PLATE 13

Genus and species unknown

FIGURES 1–5. Specimens originally thought to be *Uddenia texana* Stephenson, 1941; however, hinge characters as illustrated here show that this unnamed group is not a member of the Crassatellidae (see discussion on p. 57–58 of text).

- 1, 3. Specimens from the Providence Sand at locality 65, Georgia. USGS 25992.
  - 1. Interior right valve (SEM ×25). USNM 450482.
  - 3. Interior left valve (SEM ×40.5). USNM 450483.
- 2. Interior left valve (SEM ×60) of specimen from the Providence Sand at locality 62B, Georgia. USNM 450484 (USGS 32250).
- 4, 5. Specimens from the Owl Creek Formation at locality 52, Mississippi. USGS 25423.
  - 4. Exterior right valve (SEM ×54). USNM 450485.
  - 5. Enlargement of beak of articulated specimen (SEM ×200). USNM 450486.

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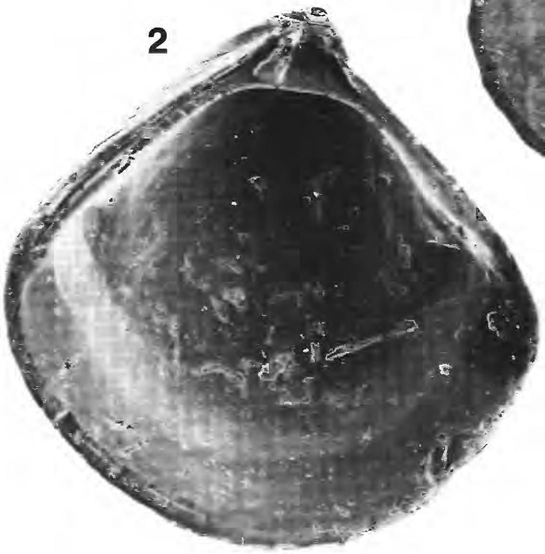

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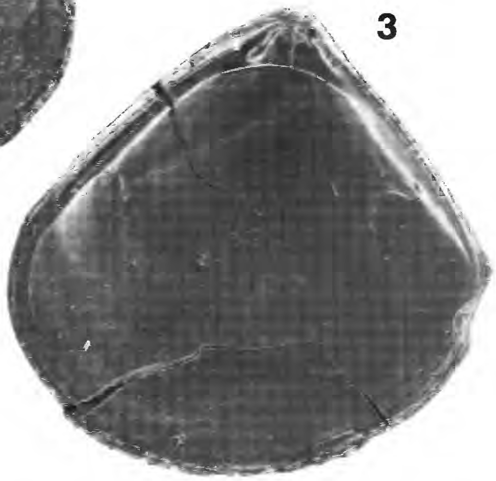

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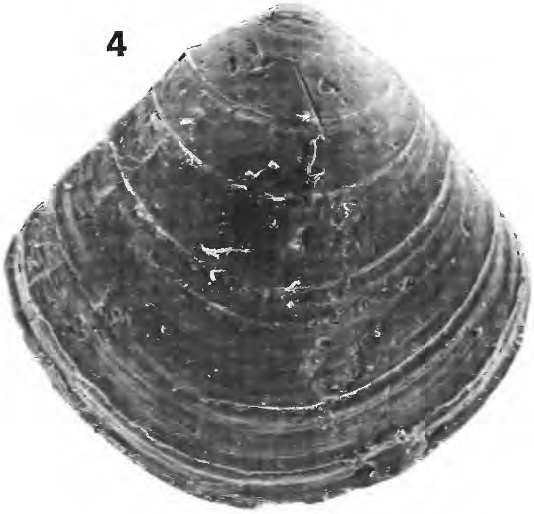

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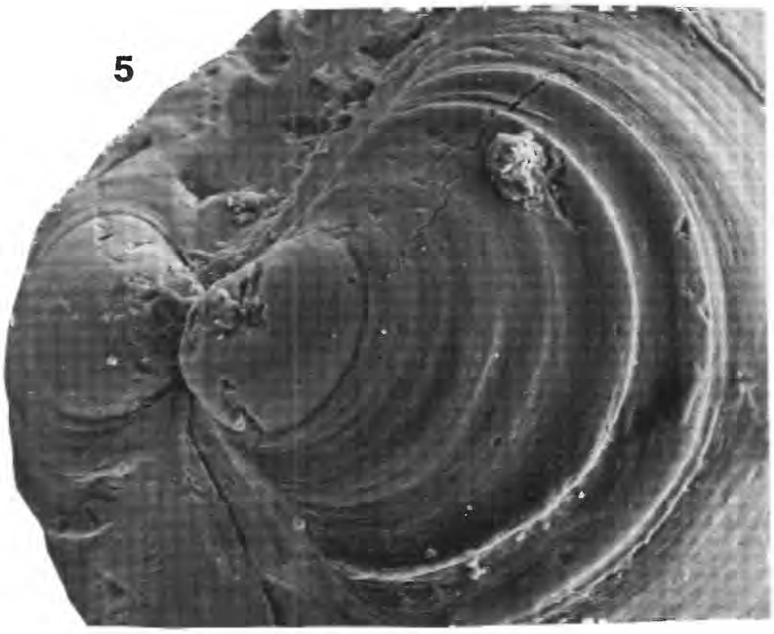
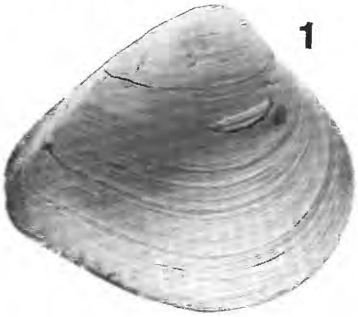


PLATE 15

Morphologic variation and ontogenetic sequence within *Crassatella tumidula* Whitfield, 1865

FIGURES 1–17. *Crassatella tumidula* Whitfield, 1865.
1, 4–8, 10, 16. Specimens from the Nanafalia Formation at locality 114, Alabama.
1, 4, 8, 10, 16. Two valves (probably from the same individual). USGS-CENO 271.
1, 10. Exterior and interior right valve (×1). USNM 450553. AA, anterior adductor; PA, posterior adductor; R, resilifer.
4, 16. Interior and exterior left valve (×1). USNM 450560.
8. Dorsal view of paired valves (×1.5). USNM 450553, 450560. L, lunule.
5. Dorsal view (×1.5) of articulated specimen. USNM 450555.
6. Exterior right valve (×2). USNM 450556.
7. Interior right valve (×2). USNM 450516 (USGS-CENO 5641).
2, 3, 9, 12–15, 17. Specimens from the Bells Landing Member of the Tuscahoma Formation at locality 117, Alabama.
2. Interior left valve (×2). USNM 450517.
3. Exterior left valve (×2). USNM 450558.
9, 13. Exterior (×2) and interior (×3) left valve. USNM 450519 (USGS-CENO 5594).
12. Exterior left valve (×1). USNM 450561.
14. Interior right valve (×1). USNM 450518.
15, 17. Exterior and interior left valve (×1). USNM 450521 (USGS-CENO 5594).
11. Interior left valve (×2) of specimen from the Greggs Landing Member of the Tuscahoma Formation at locality 118, Alabama. USNM 450559.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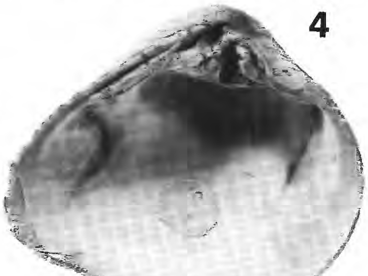
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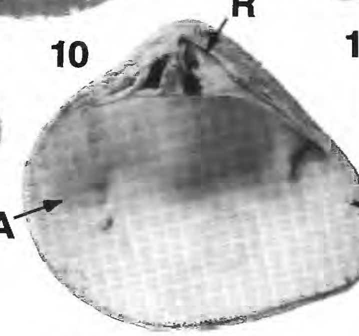
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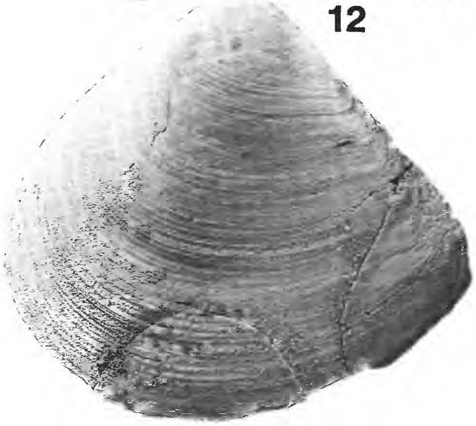
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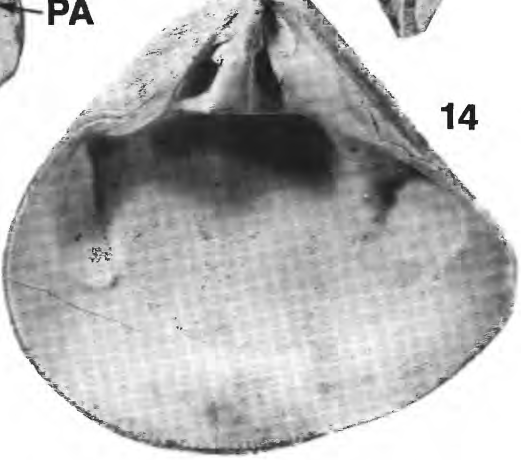
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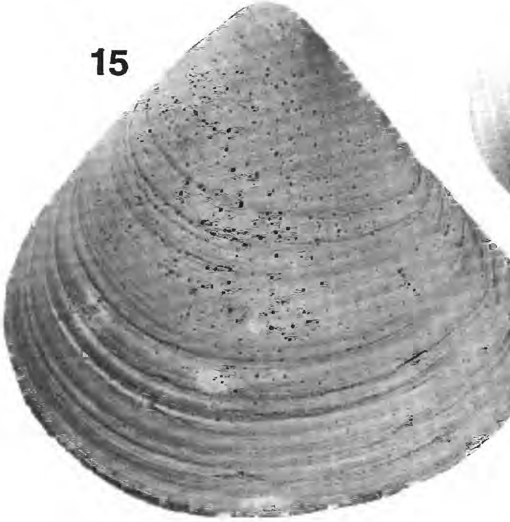
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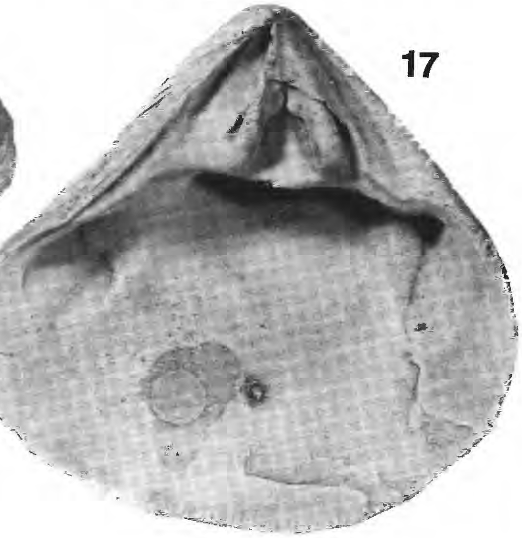
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CRASSATELLA

PLATE 16

Tertiary juvenile *Crassatella*

FIGURES 1–3, 5. *Crassatella aquiana* Clark, 1895. Specimens from the Porters Creek(?) Clay at locality 80, Alabama. USGS-CENO 264.

1. Exterior left valve (SEM ×11.9). USNM 450562.
2. Interior left valve (SEM ×14.6). USNM 450563.
3. Exterior left valve (SEM ×21.6). USNM 450564.
5. Partially preserved prodissoconch and nepionic portions of shell (SEM ×122). USNM 450565.

FIGURES 4, 6. *Crassatella tumidula* Whitfield, 1865. Right valve of specimen from the Nanafalia Formation at locality 115A, Alabama. USNM 450522 (USGS-CENO 10765).

4. Exterior (SEM ×9.31).
6. Enlargement of nepionic portion of shell (SEM ×21).

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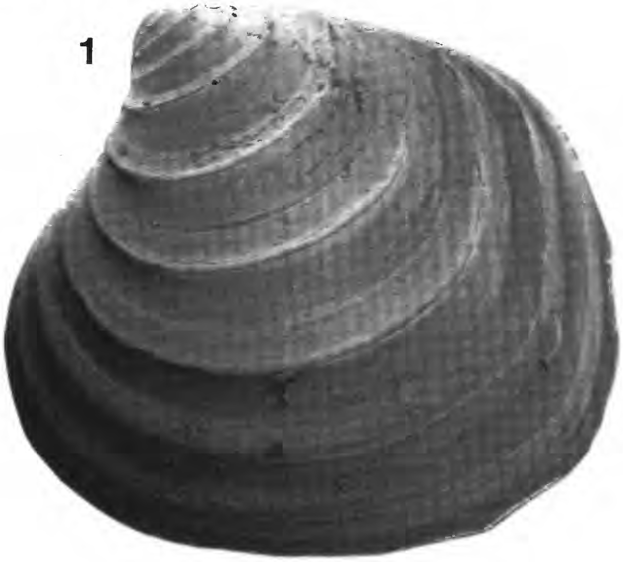

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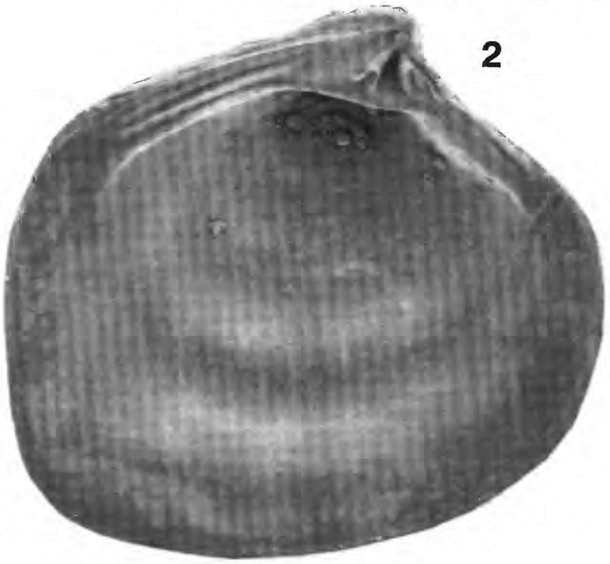

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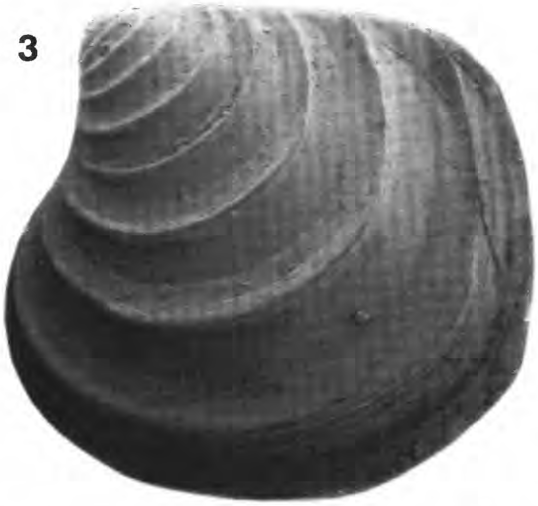

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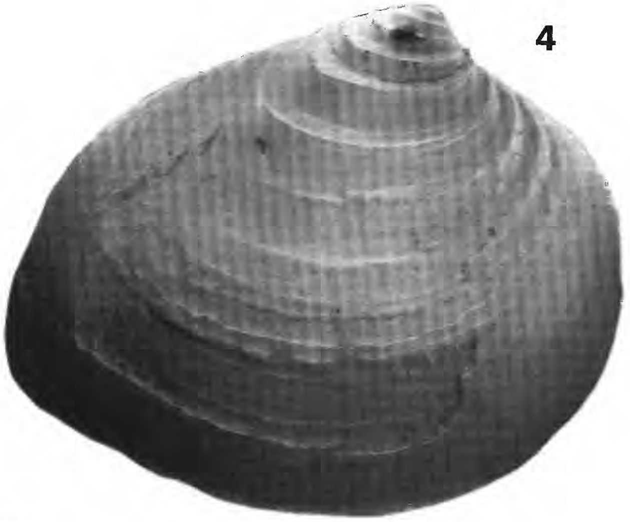

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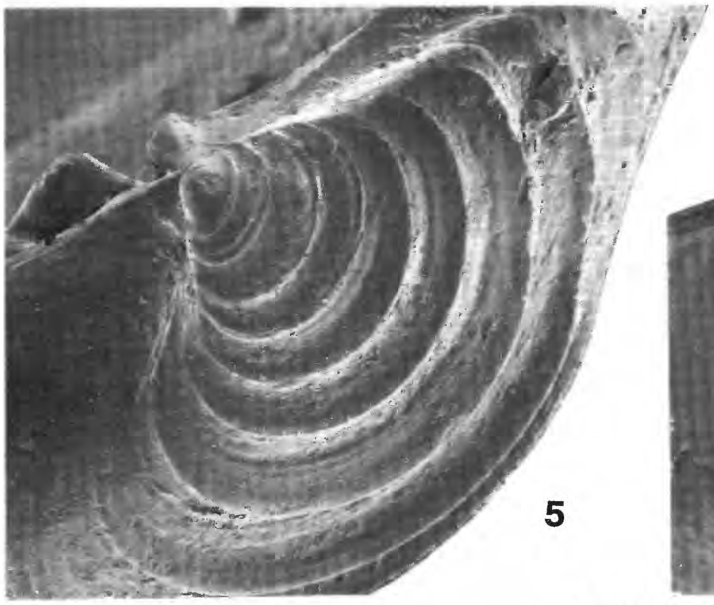

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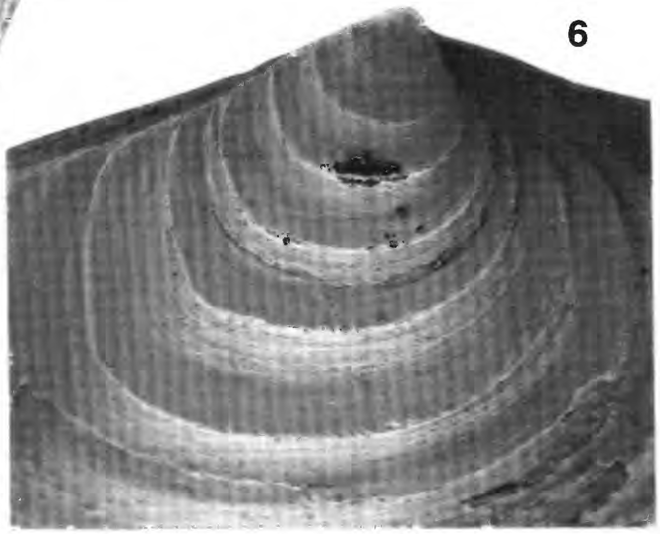


CRASSATELLA

PLATE 17

Morphologic variation and ontogenetic sequence within *Bathytormus pteropsis* (Conrad), 1860

FIGURES 1–21. *Bathytormus pteropsis* (Conrad), 1860.

1–4. Specimens, classified as *Bathytormus* sp. A for the statistical analysis, from the Ripley Formation at locality 39, Alabama. USGS 27552.
- 1, 4. Interior and exterior left valve (×3). USNM 450487.
- 2, 3. Interior and exterior left valve (×3). USNM 450488.

5, 10, 18. Specimens from the Ripley Formation at locality 34A, Mississippi. USGS 711.
- 5. Exterior left valve (×2). USNM 450566.
- 10. Exterior right valve (×1.5). USNM 450567.
- 18. Interior left valve (×1.5). USNM 450568.

6, 7. Interior and exterior left valve (×2.5) of specimen from the Providence Sand at locality 62A, Alabama. USNM 450489 (USGS 25993).

8, 12, 14. Specimens from the Providence Sand at locality 63, Georgia.
- 8. Exterior right valve (×2). USNM 450490 (USGS 28442).
- 12, 14. Exterior and interior left valve (×1.5). USNM 450491 (USGS 25935).

9. Interior right valve (×1.5) of specimen from the Ripley Formation at locality 33, Mississippi. USNM 450492 (USGS 25485). AA, anterior adductor; AR, anterior pedal retractor; PA, posterior adductor; PR, posterior pedal retractor; R, resilifer.

11. Interior right valve (×2) of specimen from the Coon Creek Tongue of the Ripley Formation at locality 30A, Mississippi. USNM 450493 (USGS 25407).

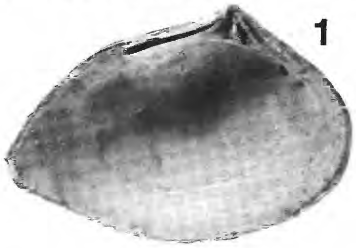
13, 19. Articulated specimen from the Ripley Formation at locality 45, Georgia. USNM 450494 (USGS 28431).
- 13. Dorsal view (×2). E, escutcheon; L, lunule.
- 19. Exterior right valve (×2).

15. Exterior right valve (×2) of specimen from the Ripley Formation at locality 44, Georgia. USNM 450495 (USGS 27878).

16. Interior right valve (×1.5) of specimen from the Ripley Formation at locality 43, Alabama. USNM 450496 (USGS 27919).

17. Exterior right valve (×1.5) of specimen from the Severn Formation at locality 75, Maryland. USNM 450497 (USGS 852).

20, 21. Exterior and interior right valve (×1.5) of specimen from the Ripley Formation at locality 43, Alabama. USNM 450498 (USGS 27924).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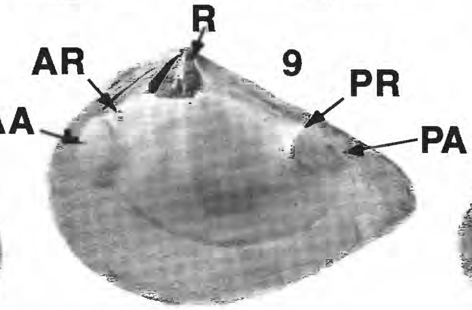
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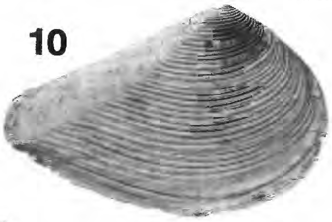
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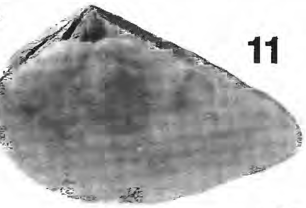
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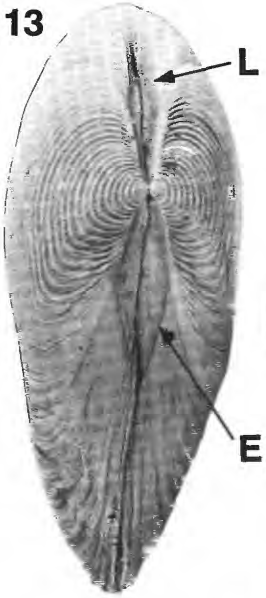
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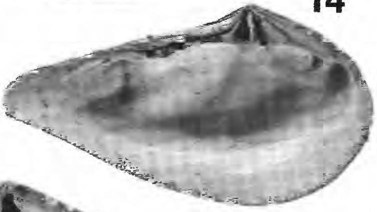
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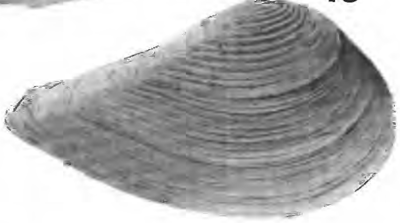
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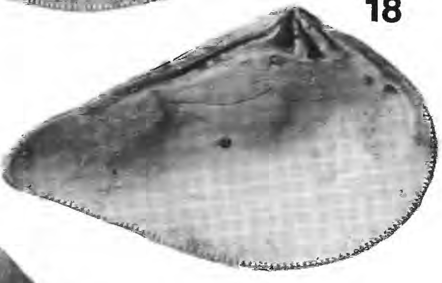
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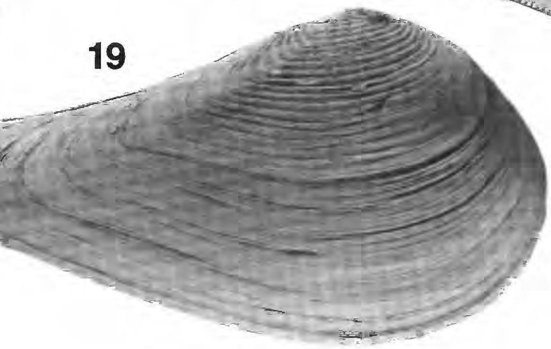
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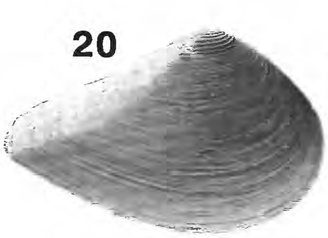
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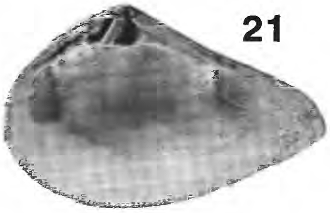
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BATHYTORMUS

PLATE 18

Morphologic variation and ontogenetic sequence within *Bathytormus alaeformis* (Conrad), 1830

FIGURES 1–22. *Bathytormus alaeformis* (Conrad), 1830.

- 1, 2. Exterior and interior right valve (×2) of specimen from the Aquia Formation at locality 85, Maryland. USNM 450523.
- 3, 5, 18. Specimens from the Aquia Formation at locality 91, Virginia.
  - 3, 5. Exterior and interior left valve (×1.5). USNM 450524.
  - 18. Exterior left valve (×1). USNM 450525.
- 4, 6, 7, 14, 20–22. Specimens from the Aquia Formation at locality 88, Virginia.
  - 4, 6, 7. Right valve. USNM 450526 (USGS-CENO 2508).
    - 4. Valve tilted to reveal characters of juvenile portion on umbo (×1).
    - 6, 7. Exterior and interior (×1).
  - 14. Exterior right valve (×1.5). USNM 450527.
  - 20. Exterior right valve (×1). USNM 450528.
  - 21. Exterior left valve (×1). USNM 450529.
  - 22. Exterior right valve (×1). USNM 450530.
- 8–10. Specimens from the Aquia Formation at locality 85, Maryland. USGS-CENO 2489.
  - 8. Exterior right valve (×1.5). USNM 450531.
  - 9. Exterior right valve (×1.5). USNM 450532.
  - 10. Exterior right valve (×1.5). USNM 450533.
- 11, 13, 16, 19. Specimens from the Aquia Formation at locality 104, Maryland. USGS-CENO 2243.
  - 11, 13. Exterior and interior left valve (×1). USNM 450569.
  - 16. Exterior right valve (×1). USNM 450570.
  - 19. Exterior left valve (×1). USNM 450571.
- 12, 15. Interior and exterior right valve (×1) of specimen from the Aquia Formation at locality 92, Virginia. USNM 450534.
- 17. Exterior left valve (×1) hypotype (Clark and Martin, 1901, pl. 41, fig. 7a) from the Aquia Formation at locality 87, Maryland. USNM 207153.

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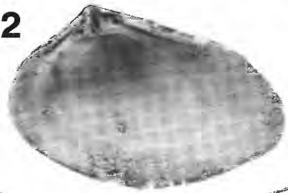

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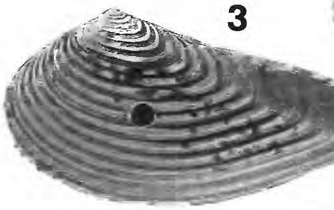

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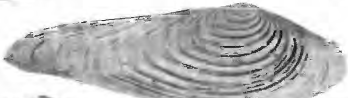

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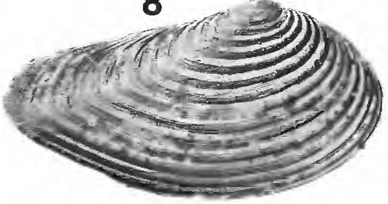

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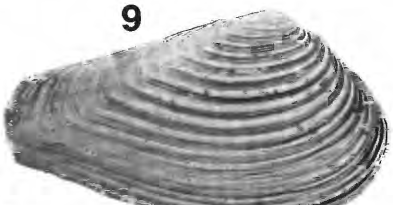

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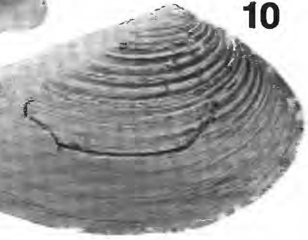

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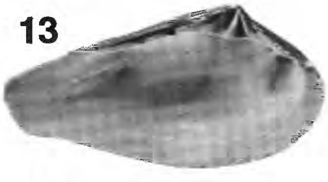

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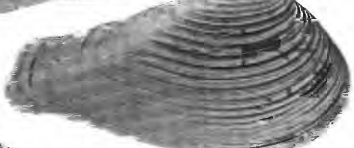

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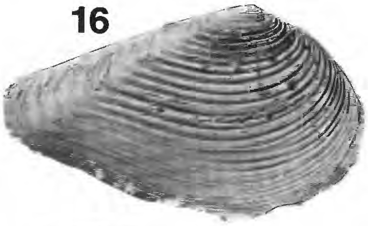

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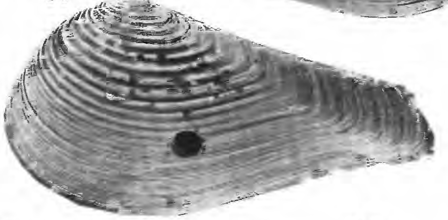

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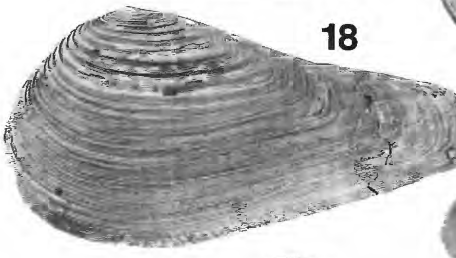

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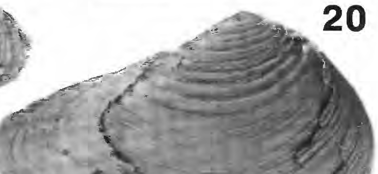

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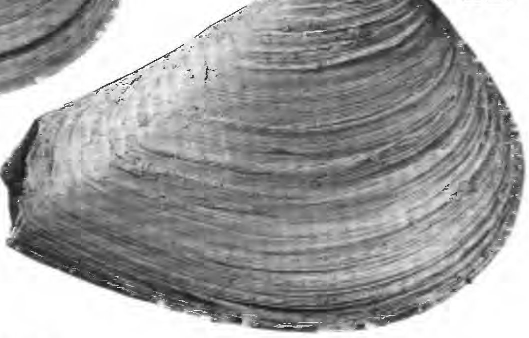

BATHYTORMUS

PLATE 19

Morphologic variation within *Bathytormus alaeformis* (Conrad), 1830

FIGURES 1–13. *Bathytormus alaeformis* (Conrad), 1830.

- 1–5, 8. Paired valves of specimen from the Aquia Formation at locality 103, Maryland. USNM 450535.
  - 1, 3. Interior and exterior left valve (×1.5).
  - 2, 4. Interior and exterior right valve (×1.5).
  - 5. Interior view through the ventral shell gape of the muscle scars and dentition of paired valves (×1.5). AA, anterior adductor; AR, anterior pedal retractor; PA, posterior adductor; R, resilifer.
  - 8. Dorsal view of paired valves (×1.5).
- 6. Dorsal view (×1.5) of articulated specimen from the Aquia Formation at locality 83, Maryland. USNM 450536.
- 7. Dorsal view (×1.5) of articulated specimen from the Aquia Formation at locality 91, Virginia. USNM 450537.
- 9, 10. Articulated specimen from the Aquia Formation at locality 102, Maryland. USNM 450538.
  - 9. Dorsal view (×1).
  - 10. Exterior right valve (×1).
- 11, 13. Exterior and interior left valve (×1.5) of specimen from the Aquia Formation at locality 97, Virginia. USNM 450539. AA, anterior adductor; AR, anterior pedal retractor; PA, posterior adductor; PR, posterior pedal retractor.
- 12. Exterior right valve (×1.5) of specimen from the Aquia Formation at locality 85, Maryland. USNM 450572 (USGS-CENO 2489).

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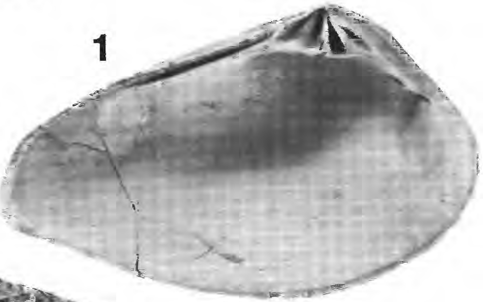

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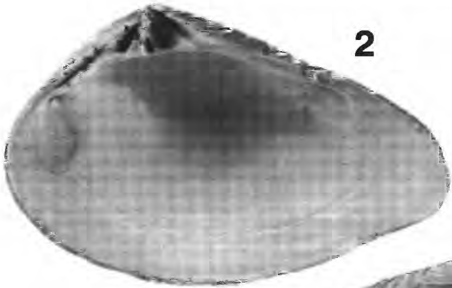

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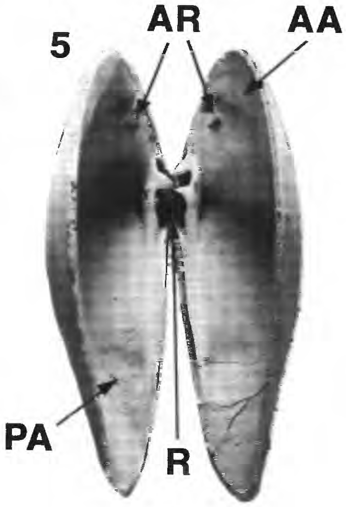

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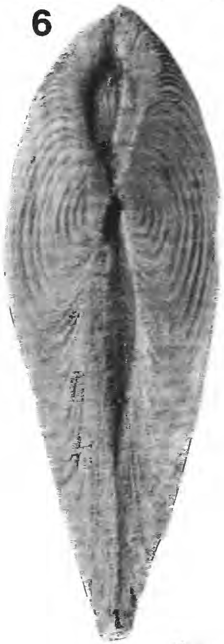

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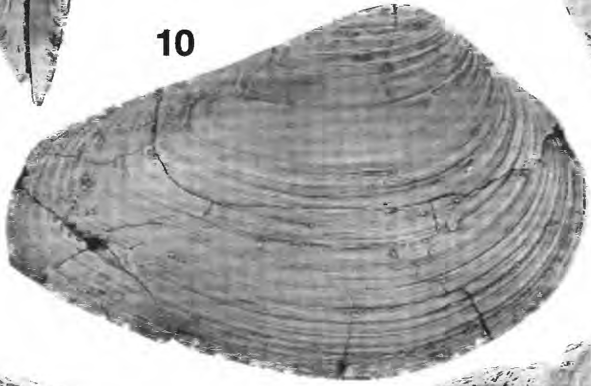

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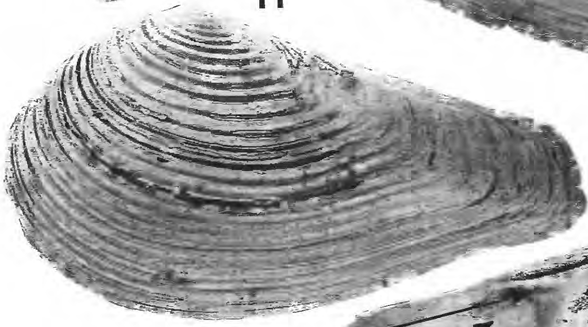

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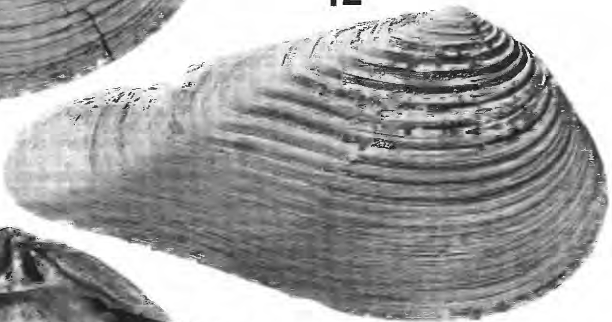

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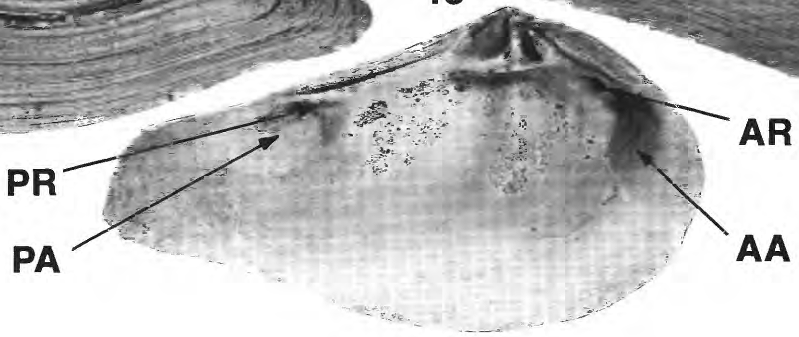

BATHYTORMUS

PLATE 20

Comparison of juvenile *Bathytormus* and *Scambula*

FIGURES 1, 3, 4, 6. *Bathytormus pteropsis* (Conrad), 1860. Right valve of specimen from the Providence Sand at locality 63, Georgia. USNM 450499 (USGS 25935).

1. Exterior (SEM ×14.9).
3. Enlargement of hinge platform (SEM ×34.3).
4. Interior (SEM ×15.9).
6. Detail of nepionic portion of shell (SEM ×48.7).

FIGURE 2. *Scambula perplana* Conrad, 1869. Exterior right valve (SEM ×21.2) of specimen from the Ripley Formation at locality 33, Mississippi. USNM 450503 (USGS 25485).

FIGURES 5, 7. *Bathytormus alaeformis* (Conrad), 1830. Left valve of specimen from the Aquia Formation at locality 98, Virginia. USNM 450540.

5. Detail of nepionic portion of shell (SEM ×26).
7. Exterior (SEM ×8.9).

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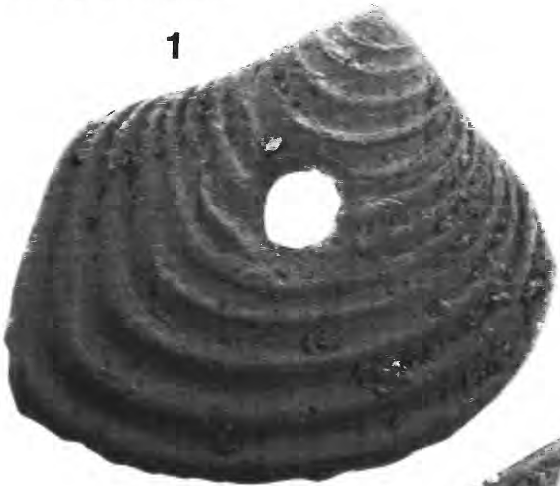

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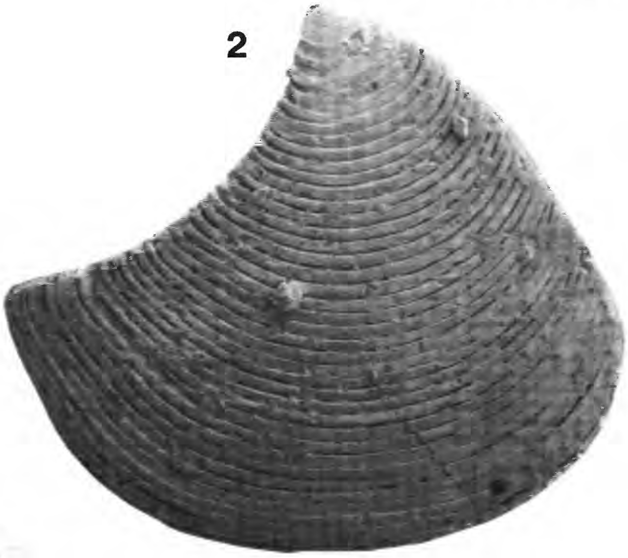

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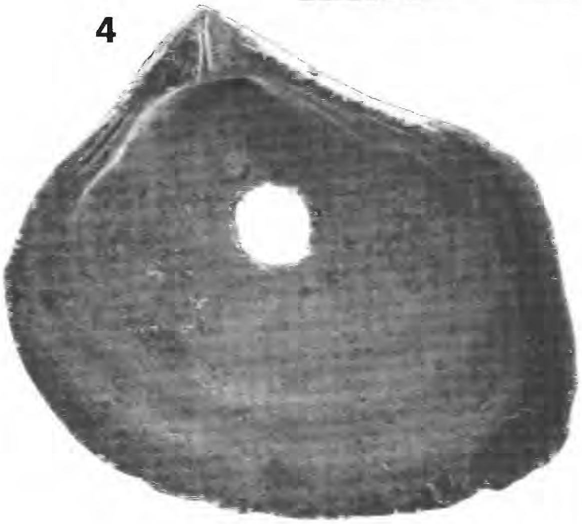

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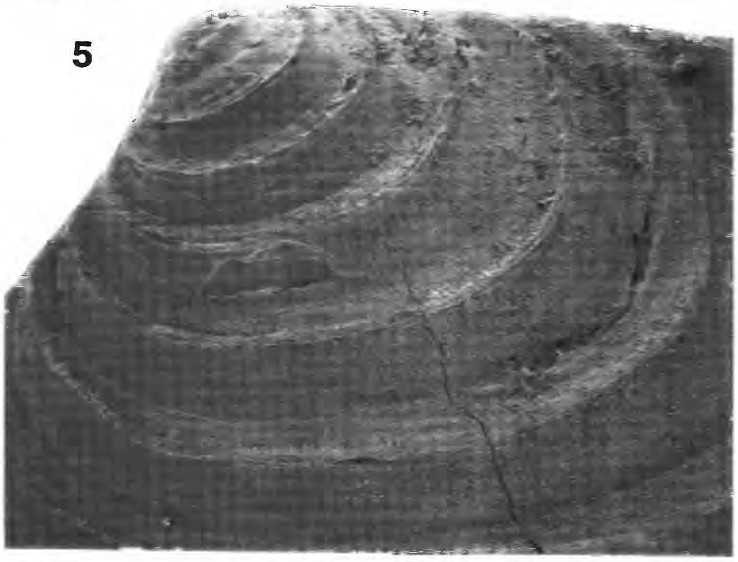

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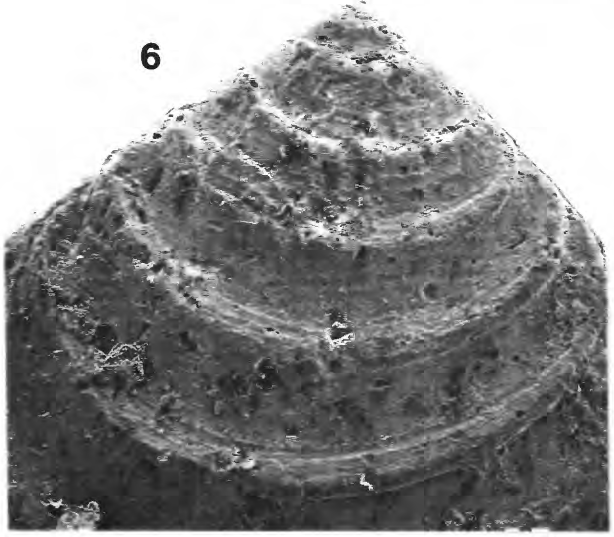

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BATHYTORMUS AND *SCAMBULA*

PLATE 21

Variation of hinge form, sculpture, and morphology in the Crassatellidae

Figures 1–5, 7, 9. *Scambula perplana* Conrad, 1869.

1. Exterior left valve (×4) of specimen from the Ripley Formation at locality 37, Georgia. USNM 450504 (USGS 27542).

2. Exterior right valve (×3) of specimen from the Woodbury Clay at locality 15, New Jersey. USNM 450505 (USGS 16293).

3–5. Specimens from the Ripley Formation at locality 43, Alabama. USGS 27919.

  3. Interior left valve (×4). USNM 450506.

  4, 5. Exterior and interior right valve (×4). USNM 450507. AA, anterior adductor.

7. Exterior left valve (×6) of specimen from the Ripley Formation at locality 43, Alabama. USNM 454609 (USGS 28434).

9. Enlargement of right valve hinge (×3) of specimen from the Coon Creek Formation at locality 27, Tennessee. USNM 450508 (USGS 25406). R, resilifer.

Figures 6, 8. *Crassatella vadosa* Morton, 1834. Exterior and interior left valve (×1) of specimen from the Owl Creek Formation at locality 52, Mississippi. USNM 450509 (USGS 25423). R, resilifer.

Figures 10, 12. *Bathytormus pteropsis* (Conrad), 1860.

10. Interior right valve (×1.5) of specimen from the Ripley Formation at locality 44, Georgia. USNM 450495 (USGS 27878).

12. Exterior right valve (×1.5) of specimen from the Ripley Formation at locality 43, Alabama. USNM 450496 (USGS 27919).

Figures 11, 13. *Bathytormus protextus* (Conrad), 1832. Exterior and interior right valve (×1) of specimen from the Eocene at Bells Landing, Alabama. USNM 450541 (USGS-CENO 1416).

Figures 14, 17. *Bathytormus alaeformis* (Conrad), 1830. Exterior and interior left valve (×1) of specimen from the Aquia Formation at locality 89, Virginia. USNM 450573 (USGS-CENO 2030). AR, anterior pedal retractor; PR, posterior pedal retractor; R, resilifer.

Figures 15, 16. *Eucrassatella undulata* (Say), 1824. Interior and exterior right valve (×1) of specimen from the Miocene at the West Branch of the Nansemond River, 7 miles below Suffolk, Virginia. USNM 450542 (USGS-CENO 2836). AR, anterior pedal retractor; PA, posterior adductor; R, resilifer. (Note the wide resilifer that projects down into the umbonal cavity.)

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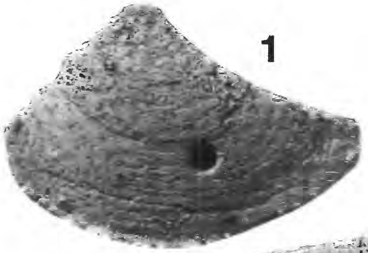

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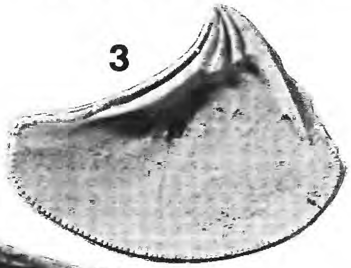

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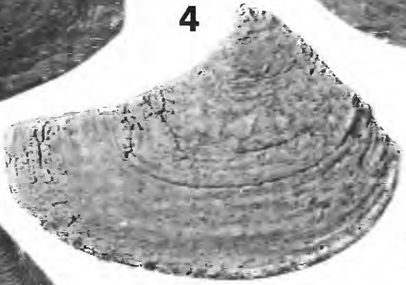

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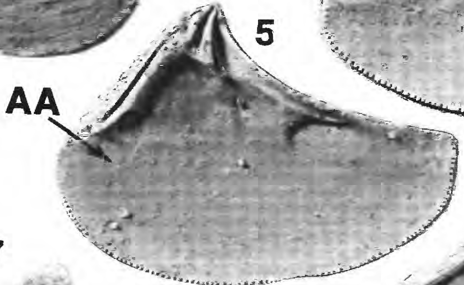

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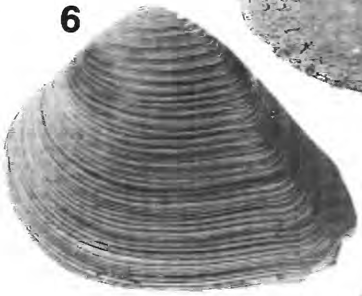

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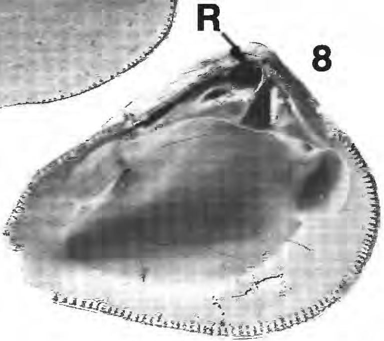

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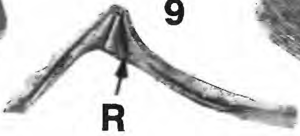

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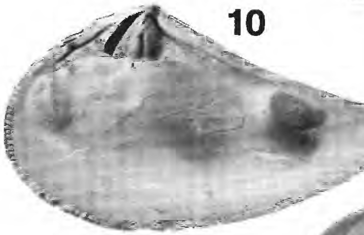

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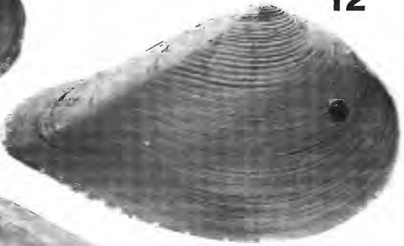

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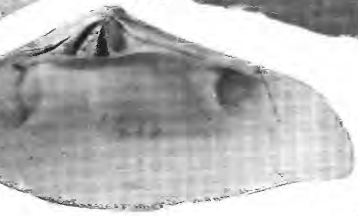

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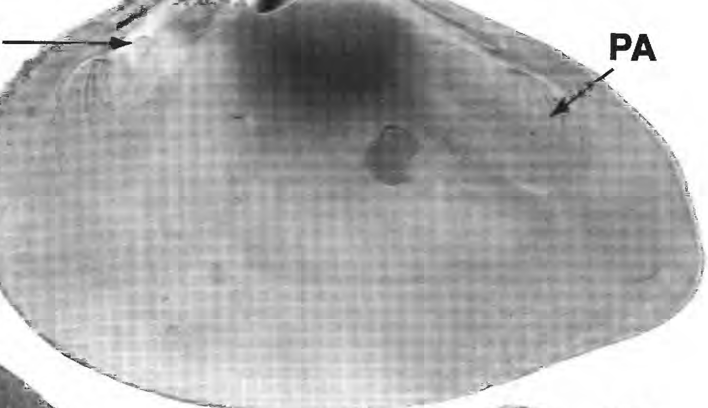

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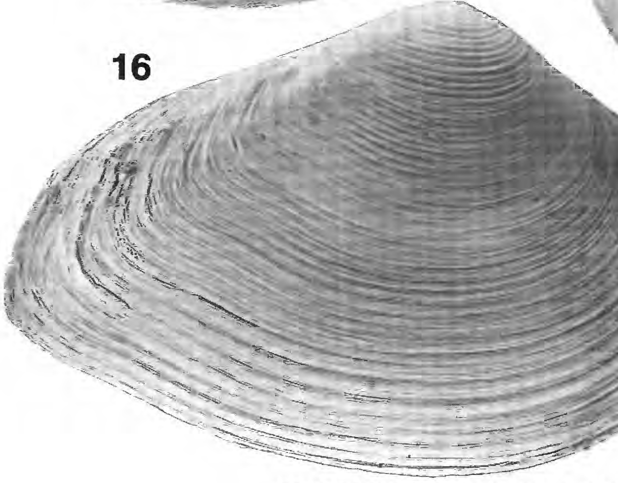

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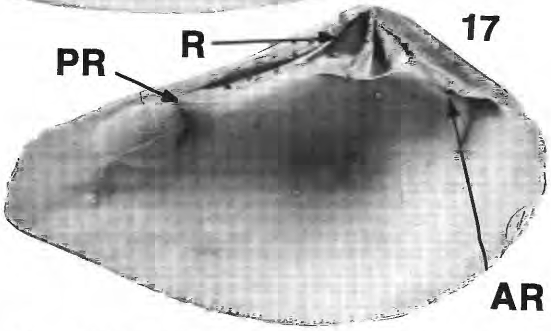

SCAMBULA, CRASSATELLA, BATHYTORMUS, AND *EUCRASSATELLA*

PLATE 22

Type specimens of questionable generic or familial assignment

FIGURES 1–4. *Gouldia conradi* Whitfield, 1885 [herein = *Crassatella vadosa* ? Morton, 1834]. Syntypes from the Woodbury Clay at locality 14, New Jersey. ANSP 18735.
- 1, 2. Exterior and interior right valve (×6).
- 3. Exterior right valve (×5).
- 4. Exterior right valve (×5).

FIGURES 5, 6. *Uddenia conradi* (Whitfield) Stephenson, 1923 (pl. 67, fig. 16). Exterior and interior right valve (×5) hypotype from the Tar Heel Formation at locality 8, North Carolina. USNM 31932.

FIGURES 7–9. *Crassatella monmouthensis* Gabb, 1860. Holotype and paratype from Monmouth County, New Jersey. ANSP 18738.
- 7, 8. Holotype, internal mold with adhering shell material.
  - 7. Right side of mold (×2.5).
  - 8. Dorsal view of mold (×2.5).
- 9. Paratype, right side of internal mold (×1.5), probable *Etea* (Arcticidae).

FIGURES 10–12. *Crassatella delawarensis* Gabb, 1860. Holotype, internal mold with adhering shell material from Monmouth County, New Jersey. ANSP 18733.
- 10. Right side (×1.5).
- 11. Left side (×1.5).
- 12. Dorsal view (×1.5).

FIGURES 13–15. *Crassatella transversa* Gabb, 1861. Holotype, internal mold from an unknown stratigraphic position and locality (listed simply as "Cretaceous, New Jersey"). ANSP 18744.
- 13. Dorsal view (×1).
- 14. Right side (×1).
- 15. Left side (×1).

FIGURES 16–19. *Crassatella prora* Conrad, 1869. Holotype and paratypes from the Mount Laurel Sand and (or) Navesink Formation at locality 48, New Jersey. ANSP 18739.
- 16, 17. Holotype, left side and dorsal view of partial internal mold (×2).
- 18, 19. Paratype(?), dorsal view and left side of internal mold (×2), probable *Etea* (Arcticidae).

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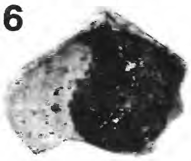

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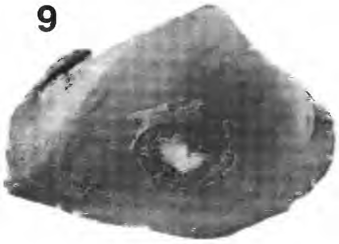

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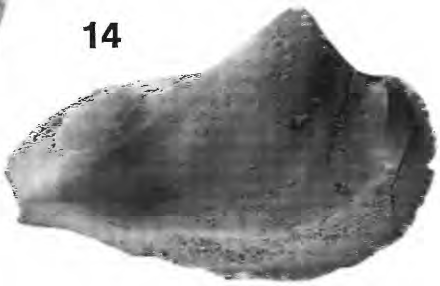

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Professional Papers are mainly comprehensive scientific reports of wide and lasting interest and importance to professional scientists and engineers. Included are reports on the results of resource studies and of topographic, hydrologic, and geologic investigations. They also include collections of related papers addressing different aspects of a single scientific topic.

Bulletins contain significant data and interpretations that are of lasting scientific interest but are generally more limited in scope or geographic coverage than Professional Papers. They include the results of resource studies and of geologic and topographic investigations, as well as collections of short papers related to a specific topic.

Water-Supply Papers are comprehensive reports that present significant interpretive results of hydrologic investigations of wide interest to professional geologists, hydrologists, and engineers. The series covers investigations in all phases of hydrology, including hydrogeology, availability of water, quality of water, and use of water.

Circulars present administrative information or important scientific information of wide popular interest in a format designed for distribution at no cost to the public. Information is usually of short-term interest.

Water-Resources Investigations Reports are papers of an interpretive nature made available to the public outside the formal USGS publications series. Copies are reproduced on request unlike formal USGS publications, and they are also available for public inspection at depositories indicated in USGS catalogs.

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Maps

Geologic Quadrangle Maps are multicolor geologic maps on topographic bases in 7.5- or 15-minute quadrangle formats (scales mainly 1:24,000 or 1:62,500) showing bedrock, surficial, or engineering geology. Maps generally include brief texts; some maps include structure and columnar sections only.

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Miscellaneous Investigations Series Maps are on planimetric or topographic bases of regular and irregular areas at various scales; they present a wide variety of format and subject matter. The series also includes 7.5-minute quadrangle photogeologic maps on planimetric bases that show geology as interpreted from aerial photographs. Series also includes maps of Mars and the Moon.

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Hydrologic Investigations Atlases are multicolored or black-and-white maps on topographic or planimetric bases presenting a wide range of geohydrologic data of both regular and irregular areas; principal scale is 1:24,000, and regional studies are at 1:250,000 scale or smaller.

Catalogs

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