

Morphological variability and temporal change in a Paleocene lucinid bivalve mollusk

SARA S. BRETSKY and ERLE G. KAUFFMAN



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Analysis of morphological variability, using six characters, in four stratigraphically successive populations of the lucinid bivalve mollusk *Myrtea (Gonimyrtea) uhleri* shows a unidirectional trend toward decreasing mean size. Differences in mean length for stratigraphically adjacent populations are significant at the 5% level of probability. Chronocline trends toward decreased magnitude of apical angle measurements and of increased magnitude of two form ratios associated with apical angularity can be explained by a tendency toward increase with growth in the quadrateness of the shell. Thus, populations of smaller mean size are also on average more trigonal. The observed decrease in mean size is associated with marine regression in the study area (Paleocene Brightseat and Aquia Formations of Maryland and Virginia, U.S.A.). Earlier representatives of the species are more common in an offshore facies, and later ones are more common in a nearer-shore but still subtidal one. Comparing specimens from nearshore and offshore facies without regard to stratigraphic position shows a statistically significant difference in size; the nearshore specimens are nearly 20% smaller, on average, than the offshore ones. Possible contributors to the size decrease may have been a slowdown of growth rate in the physically more rigorous nearshore facies; an increased probability of mortality at earlier ages in episodic sedimentation events, expected to occur more frequently nearer shore; or selection for accelerated maturation in more rigorous and unpredictable environments.

Sara S. Bretsky, Department of Earth and Space Sciences, State University of New York, Stony Brook, New York 11794, U.S.A. Erle G. Kauffman, Department of Paleobiology, U. S. National Museum, Washington, D. C. 20560, U.S.A. January 8th, 1977.

As part of a study of the systematics of lucinaclean bivalve mollusks of Paleocene age from the North American Coastal Plain, we have carried out a detailed morphological analysis on the longest-ranging and best-preserved species of these, one whose fossil record in the study area spans some 7 to 8 million years (Hazel 1969). We have observed an apparent 'chronocline', a decrease in mean size with consequent changes in some aspects of shape, which coincides with a shift in the habitat of the species, associated with an overall trend toward marine regression.

Geologic setting

Approximately 900 specimens of the small lucinid bivalve *Myrtea (Gonimyrtea) uhleri* (Clark 1895) were obtained from the Paleocene Brightseat and Aquia Formations in the Middle Atlantic Coast region. These specimens came from a total of 40 different, closely spaced stratigraphic levels at 11 geographic localities in the Potomac River Valley (figs 1 & 2). Fig. 2

provides a generalized stratigraphic section for the Brightseat and Aquia Formations in this region, indicating the portions of the section in which the species is most common. Descriptions of collecting localities and sampling horizons, and a breakdown by samples of the abundance of *M. (G.) uhleri*, are available on request, and will appear in a formal systematic treatment of the Potomac Valley lucinaceans (Kauffman & Bretsky, in preparation).

The Brightseat and Aquia Formations in the Potomac River Valley comprise a sequence of unconsolidated to partly lithified, dark greenish-gray quartz or quartz-glaucconite sands, with some admixtures of silt and clay (Kauffman & Beauchamp 1969; Kauffman & Bretsky, in preparation). Micropaleontological evidence (Berggren 1965; Hazel 1968, 1969) indicates that these strata represent about 7 to 8 million years, including an apparent gap of some 3 million years' duration between Brightseat and Aquia deposition. The lithology and macrofossils of the two formations, as opposed to the microfaunas, are, however, broadly quite similar (Beauchamp

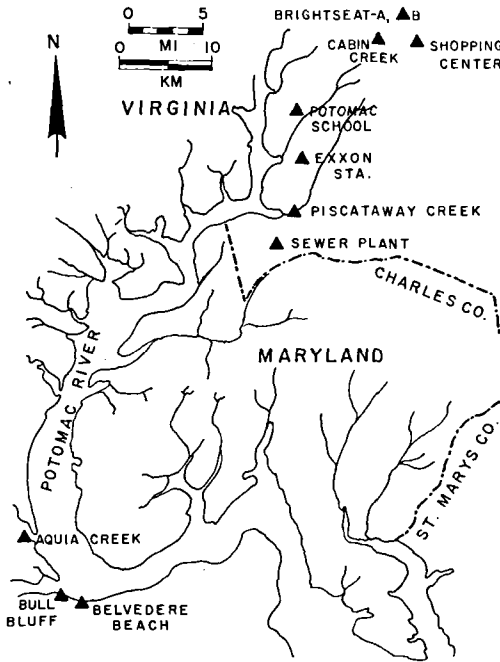


Fig. 1. Locality map indicating sites where specimens of *Myrtea* (*Gonimyrtea*) *uhleri* were obtained. Locality 'Brightseat A, B' corresponds to original type locality of Brightseat Formation ('Brightseat A'), now poorly exposed, and nearby reference section ('Brightseat B').

1969). In particular, the species with which we are here concerned, *Myrtea* (*Gonimyrtea*) *uhleri*, has been recorded from the lowest to the highest stratigraphic level of our collections from the combined Brightseat and Aquia Formations. Individual specimens from the two formations cannot be discriminated by any feature of dentition, sculpture, or musculature. Although the record of *M. (G.) uhleri* spans the full Brightseat-Aquia sequence of deposition, the species is distinctly more common in, though not exclusively confined to, certain portions of the lithofacies and paleoecological settings which make up these formations.

Biology of *Myrtea* (*Gonimyrtea*) *uhleri*

Lucinid adaptations

Myrtea (*Gonimyrtea*) *uhleri* is a member of the Family Lucinidae. In the context of the present study, the most salient points of the inferred

biology of *M. (G.) uhleri* are its infaunal habit (fig. 3), its communication with the water column via an anterior inhalant tube constructed of sediment grains, the control of its depth of burial by the maximum extensibility of the foot, and the probability that it, like living lucinids, was a very sluggish burrower (Allen 1958; Stanley 1970). These last two points suggest that either disinterment or burial beneath an influx of sediment exceeding some critical thickness would likely have had fatal results. The relevance of this supposition appears later with documentation of an apparent change of habitat preference of *M. (G.) uhleri* from a more offshore to a more nearshore environment. Another potential source of mortality, the attacks of shell-boring gastropods, appears to have remained constant at about 15% of the total sample of specimens from each sort of habitat.

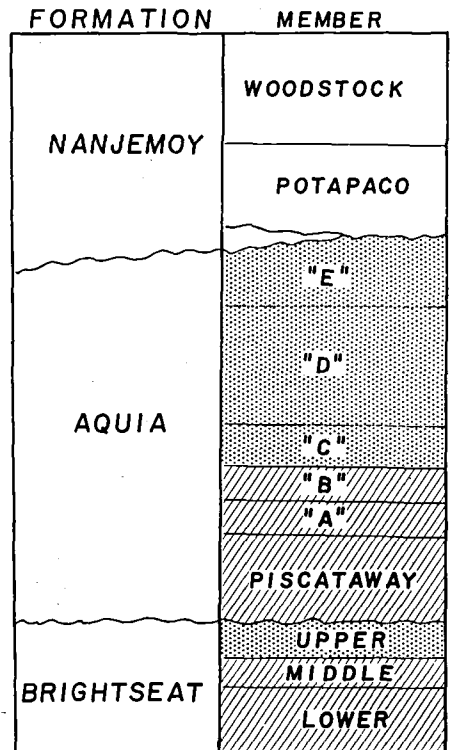


Fig. 2. Stratigraphy of Paleocene to Middle Eocene sediments in the Potomac River Valley. Nomenclature of members of the Brightseat and Aquia Formations follows an informal system pending a more formal proposal by Kauffman & Beauchamp (in preparation). Pattern of diagonal lines indicates Brightseat and Aquia units in which *M. (G.) uhleri* is common; dotted pattern indicates those in which it is present but rare. Total thickness of exposed Brightseat and Aquia in the region is about 100 feet.

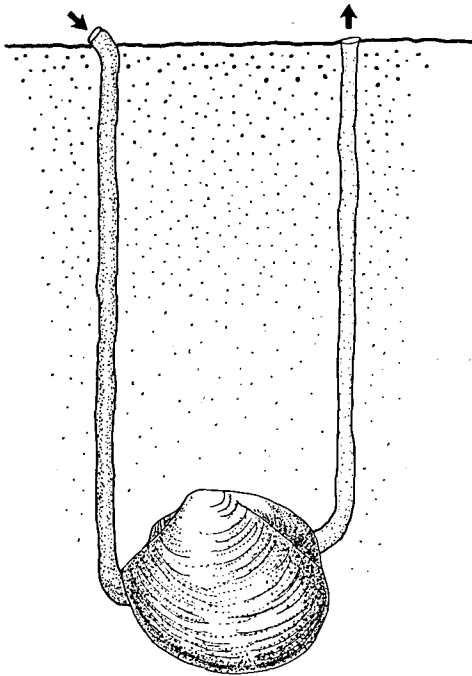


Fig. 3. Living position of a generalized lucinid (after Allen 1958). Arrows indicate location of anterior inhalant current, entering through feeding tube, and of posterior exhalant current, exiting through siphon. Not to exact scale; depth of burial of animal is typically 6 to 10 times height of shell.

Brightseat-Aquia paleoecology

One of us (EGK) has reconstructed the major features of Paleocene paleoecology in the study area on the basis of evidence from sediment type, macropaleontology, and physical and biogenic sedimentary structures (fig. 4). Our data on the occurrences of *Myrtea* (*Gonimyrtea*) *uhleri* within this paleoecological framework (Kauffman & Bretsky, in preparation) indicate that this species, like many other fossil lucinids (Bretsky 1976) but unlike the great majority of living lucinids which have been studied from an anatomical or ecological viewpoint (Allen 1958; Jackson 1973) preferentially inhabited a subtidal rather than an intertidal environment.

In a broad sense, Paleocene sedimentation in the Potomac River Valley records a regional regressive trend, but superimposed on this major trend are four shorter-term cycles of deepening and shallowing of the Paleocene sea. In each cycle of sedimentation the four onshore-to-

offshore facies diagrammed in fig. 4 appear to have been represented. We have found specimens of *M. (G.) uhleri* in sediments of all four facies, but only rarely in the most nearshore one.

In the Brightseat Formation and in the lower part of the Aquia, *M. (G.) uhleri* is common in an offshore assemblage made up mostly of species of rather small size (individuals generally less than 3 cm long). This assemblage is generally characteristic of Facies 3 (fig. 4), a silty quartz-glaucouite sand. In this part of the section *Myrtea* is also found in the most offshore, most clayey and least glauconitic facies (Facies 4, fig. 4), an environment characterized by low diversity and low abundance of shell-bearing organisms, but one in which the sediments are highly burrow-mottled. This setting may have been like those Recent occurrences which are unfavorable for most suspension-feeding organisms because of the presence of a zone of gill-clogging suspended organic detritus above the sediment-water interface (Rhoads 1974). It may, however, have been less inimical to *M. (G.) uhleri* if this species shared the common lucinid adaptations of tolerance of anaerobic conditions and ability to process large-sized detrital particles (Jackson 1973).

Another assemblage of which *M. (G.) uhleri* is a common member, more so in the upper part of the Aquia than in the Brightseat and lower Aquia (Facies 2, fig. 4), typically occurs in a fine-grained quartz-glaucouite sand representing nearshore, but still subtidal, deposition under conditions of intermittently high wave and current activity. Organisms in this assemblage generally belong to larger-sized species, and faunal diversity is higher, than in the assemblage characteristic of Facies 3.

Table 1 documents a shift through time in the occurrence of *M. (G.) uhleri* relative to sedimentary facies (fig. 4 portrays this change diagrammatically). In the Brightseat and the lower part of the Aquia, the species is most common in sediments of Facies 3, but is also relatively well represented in both Facies 2 and Facies 4. In the upper part of the Aquia it is most abundant in Facies 2, less so in Facies 3, and rare in Facies 4. In neither case, however, does it have more than occasional representation in the nearest-shore regime. The more nearshore Facies 2 itself becomes more commonly rep-

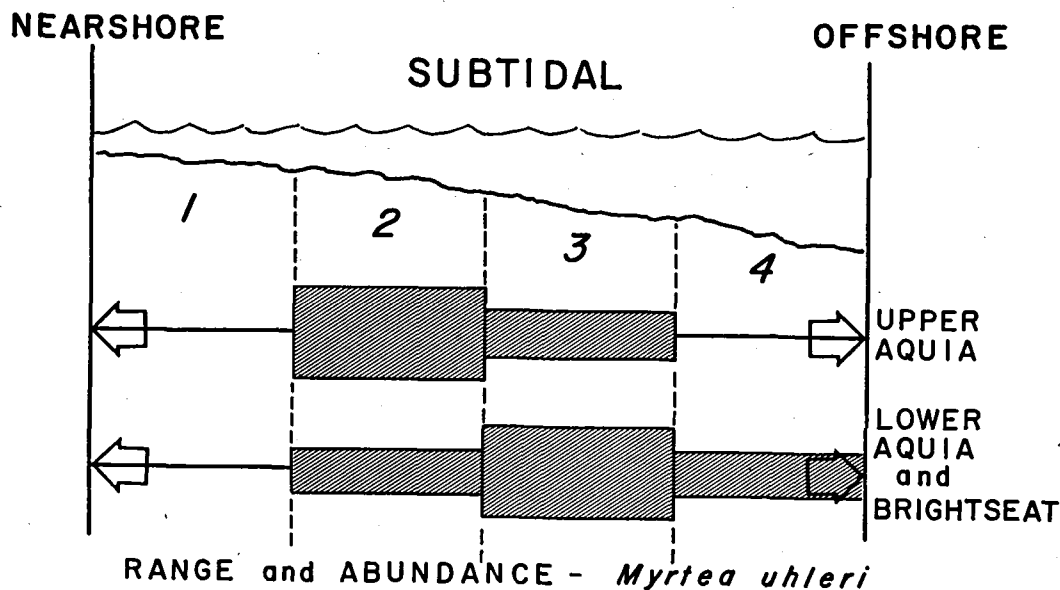


Fig. 4. Schematic reconstruction of Brightseat and Aquia paleoenvironments. Numerals correspond to four principal onshore-to-offshore facies, as follows: 1-indurated sandstone; glauconite about 40%; macrofossils abundant, heavy-shelled, usually more than 3 cm long, showing evidence of orientation by strong wave and current activity; species diversity low. 2-poorly indurated sands; glauconite about 40%; macrofossils abundant, usually more than 3 cm long often occurring in storm-laid shell beds; species diversity high; cross-bedding and *Callianassa* burrows common. 3-sands and sandy silts; glauconite about 30%; clay 10% or less; mac-

rofossils locally abundant and diverse, usually less than 3 cm long, not transported. 4-silty sands and sandy silts; clay 10-15%; glauconite 5% or less; macrofossils not abundant or diverse; highly burrow-mottled. Double-headed arrows indicate range of *M. (G.) uhleri*, with width of bar roughly proportional to abundance of the species in a particular facies (thin line indicates that the species is present but rare). Bulk samples totalling approximately one cubic meter of sediment per horizon were collected at each of some 60 horizons (40 of which yielded specimens of *M. (G.) uhleri*).

resented in the upper part of the section, as the general regression of the Paleocene sea proceeds.

Morphometric methods

Counts and measurements

On the basis of breaks in the abundant occurrence of *Myrtea* (*Gonimyrtea*) *uhleri* which cor-

respond to obvious lithological changes within the Brightseat and Aquia Formations, we have defined four stratigraphically-separated 'collections' of the species (fig. 2). All the Brightseat specimens are considered together, because 80% of the complete individuals from this formation come from a single 2-foot-thick interval at one locality (Shopping Center, fig. 1) where the boundaries of the middle Brightseat member are not well defined. We have three groups of specimens from the Aquia Formation. The lowest of these is from the Piscataway Member, which immediately overlies the Brightseat; the two others are from strata here informally designated as Member A and Member B (fig. 2).

These four groups of specimens, each of which includes enough well-preserved material to permit the carrying out of detailed morphometric analyses, are linked by the occurrence of occasional specimens (sometimes present only as fragments of valves) of *Myrtea* in what were presumably less favorable environ-

Table 1. Sedimentary facies and occurrences of specimens of *Myrtea* (*Gonimyrtea*) *uhleri*.

Stratigraphic unit	Specimens Counted	Percentage of specimens occurring in		
		Facies 4	Facies 3	Facies 2
Brightseat	520	7.1	82.5	10.4
Piscataway	209	0	46.4	53.6
Member A	82	0	100	0
Member B	68	0	0	100
Member C	1	100	0	0
Member D	11	0	0	100
Member E	6	0	0	100

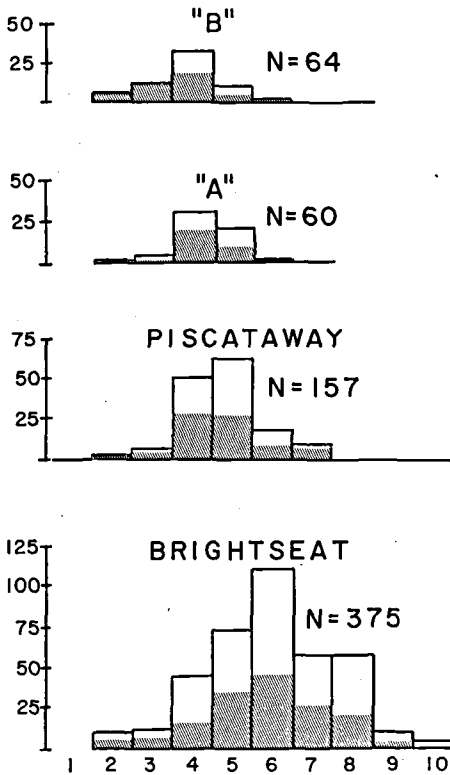


Fig. 5. Size-frequency distributions of *M. (G.) uhleri* from the Brightseat Formation and from the Piscataway Member and Members A and B of the Aquia Formation. Total height of bar indicates number of specimens for which either an exact measurement or an approximation of shell size was obtained; shaded portion of bar indicates number of complete specimens, subsequently used in principal components analysis and other biometric studies, of a particular size class. N=total number of specimens measured exactly or approximately.

ments for it. We have thus used natural breaks in the abundance of the species as criteria for defining 'statistical populations' of *M. (G.) uhleri*.

Many of the specimens which we identified as *M. (G.) uhleri* were broken; we believe this circumstance to be much less a reflection of immediate post-mortem reworking than a consequence of cracking and splitting after the valves had been collected, exposed to the atmosphere, washed free of sediment, and subjected to several cycles of identification and counting. We adopted the convention of recording as an individual specimen only a valve which retained the entire hinge line intact. A sample whose only occurrence of *M. (G.) uhleri* was as one or more

fragments of shell, with no portion of the hinge line present, was arbitrarily counted as having yielded one specimen. In all, 897 countable specimens were obtained from the 40 Brightseat and Aquia horizons where the species occurred. Of these, valves which preserved the entire anterior, posterior, or mid-ventral portion of the valve margin (670 specimens) were measured (using a binocular microscope and millimeter scale, since the specimens were too fragile for measurement with vernier calipers) for an approximation of shell size, employing the assumption that the valve is nearly circular and the umbo is centrally situated. As we shall show later, these assumptions are not entirely correct, but since the shell-size measurements made in this way were rounded to the nearest mm, the simplifying definitions of shell shape are accurate enough for a survey of size distribution in a large sample. Fig. 5 presents histograms summarizing the results of these measurements on 656 specimens from the four stratigraphically-defined 'collections'. Note that the modal size decreases progressively through time; sample sizes for each collection are given on the figure.

We then selected all those specimens (318 valves) for which the entire margin of the valve was complete, photographed these at a magnification of $\times 5$, and on each photograph made the six measurements defined in fig. 6. The use of photographs minimized handling of our small, fragile specimens; also, such characters as AL and Angle A (fig. 6) can be measured more easily on a photograph than on an actual specimen (cf. Andrews 1974). The measurements made on the magnified specimens were converted to natural-size values before statistical calculations were undertaken; the results of statistical analysis of the measurement data are reported below.

Although some of the computational programs which we used allow for missing data, we measured only complete valves in this phase of the study, believing our sample sizes to be large enough that including measurement data from incomplete specimens would not have provided sufficient additional information to justify the laborious photographic work involved in obtaining it. This decision also enhanced the confidence which could be placed in the results of our multivariate statistical analyses, as measures of correlation among the several pairs of characters

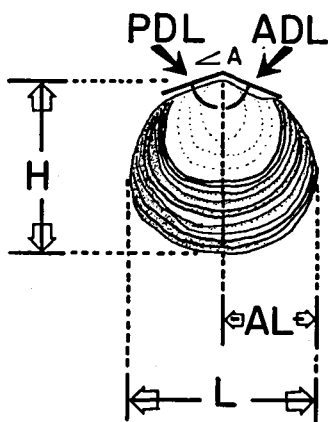


Fig. 6. Characters measured for multivariate analysis. *L*, shell length; *H*, shell height; *AL*, anterior length; *ADL*, anterior dorsal length; *PDL*, posterior dorsal length; *A*, apical angle. Note change in shell sculpture, from nearly smooth on juvenile to corrugated on adult portion of shell.

were based on the same number of comparisons in all cases. We found no evidence that differential breakage of specimens seriously affected the distribution of sizes in the sample of specimens used for statistical analysis. Specimens of *M. (G.) uhleri* seem to be about equally subject to breakage whether they are small or large. Size-frequency distributions based only the more accurately measured complete valves show virtually identical patterns to those based on a larger sample, including estimates of size of incomplete valves (fig. 5).

Criteria of maturity

In a study seeking to document evolutionary changes in size and form, it is important to establish that there is no serious discrepancy among the age structures of the populations of organisms being compared, so far as this is possible with fossil material. We assume that *M. (G.) uhleri*, like most bivalves, continued to grow throughout its life span, but that the rate of growth was notably faster for young than for older individuals (Wilbur & Owen 1964). Hall (1975) states that the annual rate of growth in young individuals of the Recent bivalve *Tivela stultorum* may be more than 20 times that in older ones. We are unable to state unequivocally that an increment in unit length on a Brightseat specimen necessarily represents the same lapse of time as a similar increment on an Aquia one.

We should like eventually, once the process of formal publication and selection of type material for our larger systematics study has been completed, to section some of our specimens from the various Brightseat-Aquia horizons and paleoenvironments for growth-increment analysis (Berry & Barker 1975; Clark 1975).

There is no clearly definable terminal adult stage in lucinid bivalves, but in studying other species of this group we have noticed that an apparent criterion of maturity is a tendency for the adductor muscle scars to be distinctly impressed, even appearing somewhat sunken into the valve interior. This probably comes about because the surface of the mantle within the pallial line, exclusive of the areas of muscle insertion, begins to deposit calcium carbonate more vigorously on the inner ostracum after growth at the valve margin has slowed down (Morton & Yonge 1964). In our material, only specimens less than about 3 mm long appeared by this criterion to be immature. Judging from the distribution of sizes in fig. 5, therefore, we regard all four of our major collections as being composed almost entirely of adult individuals. But, for the reasons stated above, we can neither confirm nor deny with certainty that the differences in modal size are strictly proportional to differences in age at death.

Another possible means of distinguishing juvenile from adult specimens of *M. (G.) uhleri* was suggested by the observation that with growth the nature of the shell sculpture changes (fig. 6). In early ontogeny the shell is nearly smooth, with only fine concentric lines of growth present. Subsequently the concentric costae on the valve become more elevated, with rather deep spaces between them producing a corrugated effect. As with the deep impression of the muscle scars, we interpret the change in sculpture as a consequence of decreasing growth rate with increasing age. Although the change in sculpture is a clearly marked phenomenon if one compares the earliest and the latest portions of a single large shell, on most valves the transition between smooth and corrugated sculpture is gradual rather than abrupt. In trying to quantify this character, we found it impossible to define consistently the exact onset of the corrugated sculpture, and thus we did not use the location of the transition as a character in our quantitative

study of morphological variation in *M. (G.) uhleri*.

We do, however, have results from a small-scale study of variation in the onset of sculptural change (data collected as part of a pilot study along conventional numerical taxonomic lines, before we had obtained any evidence on possible patterns of size variation). We used 40 randomly selected specimens representing the entire stratigraphic range and a broad spectrum of sizes (2.0–7.8 mm long) from the Brightseat and Aquia collections. In the specimens measured, the onset of the change in sculpture occurred at shell heights (fig. 6) of as little as 1.8 mm to as great as 5.6 mm. For the sample as a whole, the mean value for 35 valves, 2.6–7.8 mm long, was 3.2 mm; on 5 valves, ranging in length from 2.0 to 4.2 mm, the transition had not occurred. For each of the four collections, except perhaps that from Member A, the character shows considerable intrapopulation variability (CV 15.2 for Member A, 30.9–32.8 for the other samples); but individuals on which the change occurs at a shell height of 5 mm or more appear to be confined to the Brightseat. Analysis of variance indicates significant difference among the means for the four collections, but not at an outstanding level of significance ($0.05 > P > 0.02$). Considering the Brightseat versus the three combined Aquia samples, the mean value of the height at transition in sculpture is 4.2 mm for the former and 2.9 mm for the latter (corresponding approximately to the criterion of maturity based on strength of muscle-scar impression). Specimens on which the change occurs at a height as small as 2 mm, however, occur throughout the section. The possible significance of an apparent decrease in size at maturation will be discussed in more detail below.

Results of morphometric analysis

Size variation

The collections from the lower parts of the Brightseat-Aquia section are characterized by a greater proportion of large individuals of *M. (G.) uhleri* than are those from the upper ones. Modal size is 6 mm for the Brightseat collection, 5 mm for that from the Piscataway Member, and 4 mm for both the Member A and Member B ones.

Furthermore, although in the Brightseat a substantial proportion (20%) of the specimens are 7 mm in length or more, individuals of this size are quite rare in the other three collections (fig. 5). We doubt that the distribution of observed sizes has been seriously affected by bias due to the breakage of specimens.

We also consider preservational bias favoring small individuals in the stratigraphically higher samples (e. g., diagenetic effects, or differential size-sorting by syndepositional sedimentary processes) unlikely to account for the observed size differences. In all four collections, specimens of *Myrtea* occur with individuals of other bivalve species which may be up to 5 or 10 times larger than the lucinid. In the upper part of the Aquia, specimens of *Corbula* spp., common associates of *M. (G.) uhleri*, fall most frequently into a size range of 5–9 mm, closely corresponding to that portion of the total *Myrtea* size range which is apparently truncated in these upper horizons. Numerous juvenile individuals of a variety of characteristically large-sized (40–100+ mm in adult length) bivalve species, also falling into this approximate size range, are likewise found in our upper Aquia collections. We imply no necessary interaction among these species, but simply use these data to point out the unlikelihood that the relative rarity of large *Myrtea* specimens in the upper horizons results from a preservational bias operating only on lucinids.

Table 2 summarizes the basic univariate statistics for measurements of each of the characters defined in fig. 6 for the samples of complete specimens from the four horizons. To test for the statistical 'reality' of the apparent unidirectional decrease in shell size, we used an approximate *t*-test for samples whose variances are not assumed to be equal (Sokal & Rohlf 1969: 374–376) to compare mean lengths. By this test, the differences between means for stratigraphically adjacent Aquia samples are just on the borderline of statistical significance ($0.05 > P > 0.01$ for the Piscataway-Member A comparison, and $0.01 > P > 0.001$ for Member A vs. Member B). Differences between all other pairs of mean lengths are highly significant ($P \ll 0.001$). We turn to a consideration of a technique which assists us in determining the relationship between length, here regarded as an estimator of overall shell size, and the other characters. Data on the

Table 2. Means and standard deviations for L, H, AL, ADL, PDL, AND <A for each of the four collections of *Myrtea* (*Gonimyrtea*) *uhleri*.

	N	L (mm)		H(mm)		AL(mm)		ADL(mm)		PDL(mm)		<A(°)	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Brightseat	156	5.84	1.49	5.44	1.43	2.80	0.74	2.10	0.55	2.86	0.73	130.2	5.06
Piscataway	79	4.74	1.18	4.52	1.18	2.26	0.57	1.78	0.49	2.50	0.62	123.1	5.15
Member A	31	4.30	0.67	4.04	0.66	1.98	0.36	1.64	0.31	2.26	0.40	122.4	6.15
Member B	43	3.74	1.05	3.50	0.98	1.79	0.50	1.50	0.35	2.06	0.58	120.6	5.85

measurements of all these characters are summarized in table 2.

Principal components analysis

This multivariate statistical technique permits simultaneous consideration of variation in all the characters measured, and allows us to distinguish the effects of overall change in size with growth from those components of variability which are relatively independent of size (Blackith & Reyment 1971; Sneath & Sokal 1973). In our study we used the principal components analysis (PCA) program of the NTSYS (Numerical Taxonomy System) package of biometric and numerical taxonomic programs written by F. J. Rohlf, J. Kishpaugh, and D. Kirk of SUNY at Stony Brook.

We carried out PCA on the specimens from each of the four stratigraphically-defined collections of *M. (G.) uhleri* (N = 156, 79, 31, and 43, in ascending stratigraphic order), and on the total collection of complete specimens from the Brightseat and Aquia (N = 318). (The total collection included an additional 9 specimens, 5 from Member D and 4 from Member E of the Aquia; sample size was inadequate to justify performing separate statistical analyses on these two groups of specimens.) Results of the PCA on

the total sample are summarized in table 3; with a few minor exceptions to be mentioned subsequently, the patterns of variation in the five PCA's corresponded quite closely. The correlation matrix whose eigenvalues were extracted was calculated from the original measurements of the various characters, with angular values transformed to radians to bring the magnitude of these measurements into closer consonance with that of the dimensional ones. We also performed PCA's using logarithmically transformed data, but the only effect of this transformation was to increase modestly the percentage of variation explained by the first principal component axis.

For each of the five analyses, about 70–80% of the variation in the correlation matrices is explained by the first principal component, with which the five dimensional measures (L, H, AL, ADL, and PDL) are strongly associated (table 3). This principal component axis is readily interpreted as representing the influence of overall increase in size—a specimen 8 mm long will tend to be about twice as high as one which is 4 mm long, and the other dimensions will also be proportionately increased. The first axis explains 81% of the variability for the Brightseat sample, 78% for the Piscataway, 70% for Member A, and 84% for Member B.

Table 3. Results of principal components analysis of measurements on 318 Brightseat and Aquia specimens of *Myrtea* (*Gonimyrtea*) *uhleri*.

Matrix of correlations							Eigenvalues and Eigenvectors				
Character							Character	Axis and (Percent of variability explained)			
	L	H	AL	ADL	PDL	<A		1(83.2)	2(12.9)	3(1.9)	4(1.4)
L	1.000						L	0.993	0.032	0.060	-0.027
H	0.989	1.000					H	0.986	0.104	0.057	-0.051
AL	0.966	0.966	1.000				AL	0.974	0.031	-0.025	-0.206
ADL	0.922	0.926	0.909	1.000			ADL	0.944	0.146	-0.274	0.109
PDL	0.955	0.955	0.903	0.894	1.000		PDL	0.955	0.154	0.178	0.165
<A	0.499	0.435	0.485	0.384	0.382	1.000	<A	0.532	-0.846	-0.006	0.034

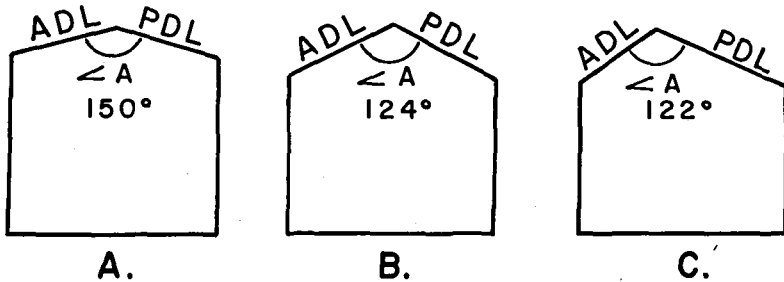


Fig. 7. Stylized representations of *M. (G.) uhleri* indicating manner in which magnitudes of measurements of dorsal length vary with change in apical angularity and with shift in position of the umbo (see text). Abbreviations as in fig. 6.

About 15% of the total variability in each of the collections is explained by the second principal component, which is associated predominantly with the apical angle measurement. In all cases the correlation between Angle A and the dimensional values is substantially lower than the correlations among these latter characters, although there is only one sample (Piscataway Member) in which the correlation of Angle A with length, etc., is not significantly different from zero. A good deal of the variability in the apical angle measurement is thus apparently independent of the size of the shell. To the second axis there is also generally a modest contribution, opposite in sign from that of Angle A, of ADL and/or PDL. These measurements, two legs of the triangle of which Angle A is the apex, are relatively longer on more trigonal (lower Angle A) than on more quadrate (higher Angle A) specimens of a given size. Since, when size is held constant and angularity varied, these two measurements will tend to decrease as Angle A increases, and vice versa, their association with angularity on Axis 2 is marked by an opposition between their sign and that of Angle A.

The third and fourth principal components together take up only 5% or less of the total variability (except in the sample from Member A, where they jointly account for 13%), but they illustrate some interesting minor features of variation. Axis 1 has presumably removed the effect of overall size and Axis 2 that of variation in angularity independent of size. If both size and angularity are held constant and only the location of the umbo is changed, ADL will be shorter and PDL longer on specimens where the umbo is

nearer the anterior end of the shell, and vice versa (figs. 7B, C). The negative association of these two characters on the third principal component axis presumably reflects this aspect of shape variability. The magnitude of a given measurement of ADL or PDL is thus influenced by three factors: the size of the shell (most importantly), the trigonality or quadreness of the shell, and the location of the beaks.

Axis 4, indicating a negative association between anterior length (AL) and the measures of dorsal length, may be affected by the presence of some specimens in which the valve is trigonal (high ADL and PDL) and the beaks are placed rather far forward (low AL). Such specimens occur in all four collections but are most abundant in that from Member A. In that sample the fourth axis represents 6% of total variability; in the others it accounts for 2% or less.

Variation in individual characters

Having determined that the broad patterns of relationship among morphological characters are constant throughout the history of *M. (G.) uhleri* in the Potomac Valley Paleocene, we turn to an examination of the pattern of change in individual characters. A linear trend toward decrease in mean size (table 1) is associated with a smaller mean size of the apical angle (a more trigonal shell) in the three Aquia samples than in the Brightseat sample. This association is, of course, predictable from the weak, but for the species as a whole still significant, correlation between angularity and size. In lucinacean bivalves, the ligament area (posterior to the beaks) is small and narrow in young individuals,

but tends to broaden as the shell grows, thus elevating the posterior dorsal termination of the valve nearer to the level of the umbo. In larger specimens of *M. (G.) uhleri*, also, the anterior dorsal termination of the valve develops a slight upward flare, apparently associated with the dorsal broadening of the anterior adductor impression. This similarly brings the anterodorsal margin upward. Both these effects tend to make large shells more quadrate. Since the stratigraphically higher collections have fewer large individuals, we expect them to be on average more trigonal.

The correlation between size and angularity is real, but imperfect. The original measurements of our six characters show that specimens 2 to 3 mm long (possibly still immature) never have an apical angle measurement greater than about 125°. Only the largest specimens (7 mm in length or more, occurring almost exclusively in the Brightseat) attain the maximum observed angular values of about 140°. But specimens ranging in size from 2 mm to 9 mm long may all have angularity values in the vicinity of 110°–125°. There is thus a certain asymmetry in the relationship of size to angularity, in that small specimens cannot be quadrate, only trigonal; but large ones may be either trigonal or quadrate. This relationship holds for all four collections. In that from the Piscataway Member, the correlation between size and angularity is nonsignificant because this sample lacks any highly quadrate large specimens to balance the several notably trigonal small ones.

We thus observe (table 2) a change from an early population spanning a broad range of sizes, with the smallest specimens being trigonal and the largest ones tending to be more quadrate, to later populations in which the size spread has been diminished by a virtual truncation of the large-size end of the range. Not only do the later populations have a smaller mean for Angle A, but the range of values for angularity shows a modest downward shift (116°–141° for the Brightseat; 112°–134° for the Piscataway; 108°–137° for Member A; and 108°–135° for Member B).

The relationships between angularity and the measures of dorsal length brought out by the principal component analysis (table 3; fig. 7) permit us to interpret the pattern of change in

ratios between pairs of dimensions, taking the largest dimension, length, as an estimator of overall size. Associated with the decrease in apical angularity are increases in the mean ratios of anterior dorsal length and posterior dorsal length to total length (table 4; fig. 8B). This pattern of change is predictable from the geometric relationship between angularity and dorsal lengths demonstrated earlier, such that more trigonal shells, which usually are also smaller shells, have relatively greater dorsal lengths. The other two size ratios, height/length and anterior length/length, show no discernible trends (table 4; fig. 8A), and, in fact, scarcely differ among the four collections, except that height/length has a slightly but significantly lower mean value for the Brightseat than for the three Aquia collections.

Interpretation of the observed pattern of change

The most evident feature of the Paleocene record of *Myrtea (Gonimyrea) uhleri*, as recorded by the characters chosen for this study, is the progressive diminution in modal and mean size (table 2; fig. 5). Associated with this change in size through time are changes in shape which, for anyone population, correspond to a small component of ontogenetic change in form. If it is conceded that we can largely eliminate substantial sampling bias as accounting for the differences in mean size, we suggest three possible environmental explanations for the observed correspondence between decreasing mean size and progressive shallowing of the Paleocene sea (fig. 4). On the basis of the available evidence, we are not able to determine which of these is most likely; and, indeed, more than one may have been operating. The postulated explanations are as follows:

(1) No difference in potential mean longevity of *M. (G.) uhleri* populations from the lower and the upper horizons, but a difference in rates of growth in more offshore and more nearshore environments, and thus in the average size of individuals of a particular age. Clark (1975: 103) has found that "individuals living in variable environments, such as shallow water, are subject to disturbances which can limit or preclude

Table 4. Means and standard deviations for the ratios H/L, AL/L, ADL/L, and PDL/L for each of the four collections of *Myrtea* (*Gonimyrtea*) *uhleri*.

	N	H/L		AL/L		ADL/L		PDL/L	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Brightseat	156	0.928	0.037	0.479	0.035	0.360	0.041	0.490	0.039
Piscataway	79	0.950	0.047	0.475	0.042	0.373	0.041	0.531	0.042
Member A	31	0.941	0.043	0.456	0.050	0.382	0.049	0.525	0.057
Member B	43	0.938	0.055	0.480	0.035	0.411	0.051	0.551	0.033

growth for periods of days or weeks, resulting in gaps in the growth [increment] record". He does not address the question of whether the interruptions in growth found to be more frequent in shallow-water environments substantially affect ultimate size in bivalves, but his findings do suggest a possible mechanism whereby growth rate might have been lessened in the higher-energy upper Aquia facies.

(2) Decrease in mean achieved longevity, resulting from an increasing incidence of (a) episodic sedimentation, with burial beneath thicknesses of sediment exceeding the maximum burrowing depth, or (b) disinterment by intermittently strong wave or current activity, with disinterred individuals, saddled with the inefficient burrowing mechanism which appears to characterize lucinids generally, being vulnerable to predation, desiccation, or starvation. The observed size decrease would then be a function of preservation of individuals which had died at progressively smaller sizes, as episodic mortality became more frequent during regression. This suggestion is not necessarily contrary to (1); in fact, both mechanisms may have acted in concert, with small-scale episodes of unfavorable environmental conditions causing temporary stoppage of growth, and large-scale ones proving fatal.

(3) Acceleration of the rate of maturation, with sexual maturity (and hence termination of the stage of rapid growth) occurring at progressively younger ages, as a result of more stringent selection for earlier maturation in environments more often subjected to intolerable conditions, as in (2). In such environments, those bivalves which could reproduce when relatively young and small would have a higher probability of living long enough to leave descendants than would those which had wait until later to reproduce.

We are not able to state for certain whether our data discussed earlier, suggesting a smaller size at transition from smooth to corrugated sculpture for the Aquia specimens than for those from the Brightseat, do reflect such a pedomorphic effect ('progenesis' of Gould 1976), or simply indicate an over-all slowdown in rate of growth.

In addition to our comparisons of mean size among stratigraphically successive samples, we have further compared mean lengths for those specimens occurring in the more nearshore Facies 2 and the more offshore Facies 3, without regard to stratigraphic position. (There are only 15 complete specimens from Facies 4; sample size is thus too small to merit including a Facies 4 comparison.) Observed mean length is 5.38 mm for Facies 3 specimens ($N = 199$), and 4.45 mm for those from Facies 2 ($N = 104$). By the approximate t-test appropriate when variances are not assumed to be equal, the difference between these means is highly significant ($P \ll 0.001$). Specimens from shallow subtidal environments thus average nearly 20% smaller than those from farther offshore. This evidence further strengthens our inference that size decrease (however achieved) was an adaptation to more rigorous environmental conditions recorded by the nearshore facies.

Many paleontological studies which have documented ecologically associated variation in form have sought some immediate selective advantage for the form changes themselves (e. g., increased burrowing efficiency in infaunal bivalves, greater mechanical stability in epifaunal bivalves and brachiopods). For *M. (G.) uhleri*, it is possible to postulate that smaller and hence more trigonal individuals may have been somewhat more efficient burrowers than larger and hence more quadrate ones, and thus have been more readily able to reorient themselves in

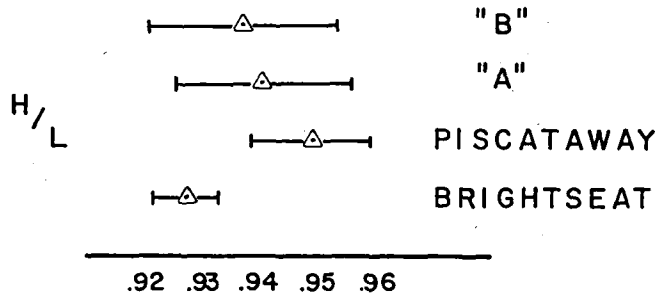
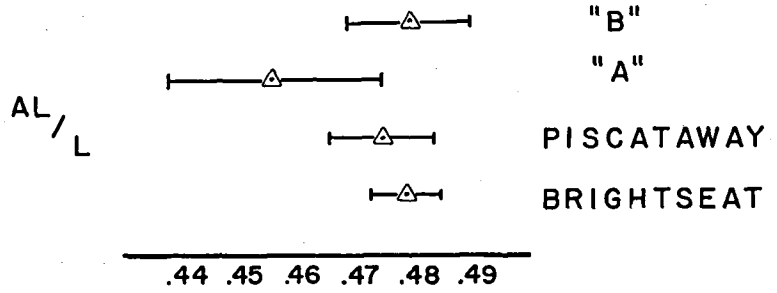


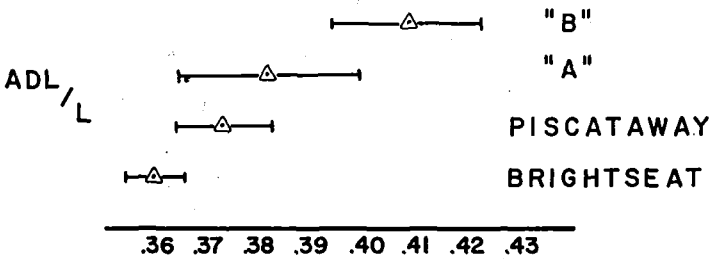
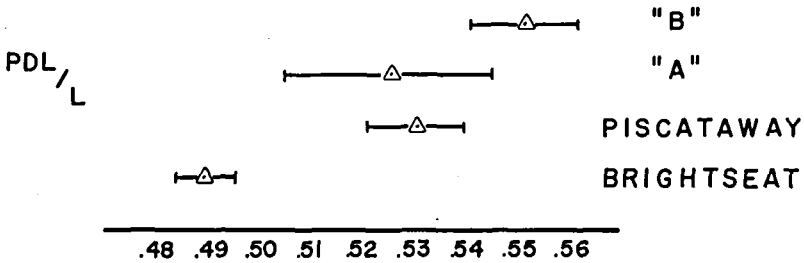
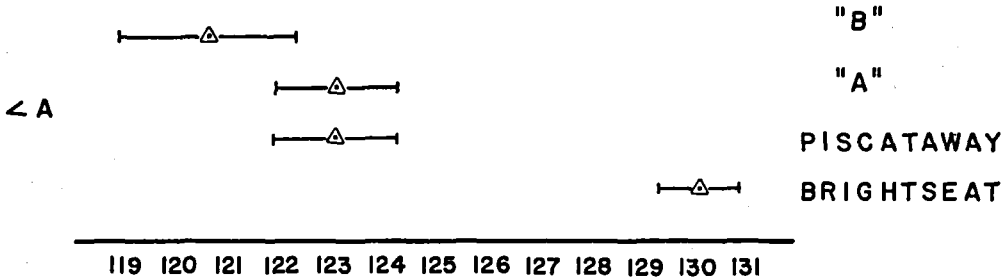
Fig. 8. Means (dots enclosed in triangles) and 95% confidence intervals (bars) plotted against stratigraphic position for four shape ratios and for apical angle (degrees). Abbreviations as in fig. 6. Fig. 8A: characters showing little or no change through time. Fig. 8B (p. 173): characters showing progressive change through time.

the sediment after the passage of storms. Such a macromorphological explanation, while plausible, appears not to be required here, for the very similar results of principal components analysis on the four individual collections indicate that the pattern of ontogenetic change in shape (essentially only change in apical angularity) did not change through time. Necessarily, therefore, samples composed on average of smaller individuals – whether the diminution in mean size resulted from slower growth rates, mortality at younger ages, selection for earlier maturation, or simply the inevitable vagaries of sampling error (which last proposition we believe can be largely discounted for our material) – also differ in the mean values of those characters describing angularity. We have no evidence of decreasing

apical angularity through time for individuals of constant size.

Conclusions

In earlier presentation of some of these results, one of us (Bretsky 1974) had interpreted the apparent unidirectional change in mean size of *M. (G.) uhleri* as a possible case of 'phyletic gradualism' (Eldredge & Gould 1972; Gould & Eldredge 1977). With a more refined understanding both of Brightseat-Aquia paleoenvironments and of the rigor of arguments necessary to document that morphological change is actually gradual, we now advocate a somewhat different interpretation of the data. The accuracy with



which individual beds at different localities in the Potomac River Valley Paleocene can be correlated is, unfortunately, not high enough to permit us to duplicate the fine subdivisions of evolving lineages presented by Kellogg (1975) and Gingerich (1976). Our study, like these two (as noted by Gould & Eldredge 1977) also lacks sufficiently broad geographic coverage, with adequate stratigraphic control, to permit a frame-by-frame reconstruction of evolutionary events throughout the entire distributional range of *M. (G.) uhleri*.

With, in effect, only four distinct stratigraphic levels of adequate sample size, we cannot per-

suasively argue for a constant unidirectional trend toward size decrease in *M. (G.) uhleri*. We believe, however, that the level of documentation does suffice to indicate an association between greater environmental rigor and smaller size. We hope that the presentation of these data will encourage other workers to look for similar relationships in relatively eurytopic species. If such findings can be duplicated elsewhere, perhaps observations can be made which might permit choice among the three possible population-level explanations for size decrease outlined above.

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Dansk sammendrag

Fire stratigrafisk adskilte populationer af den lucinide musling *Myrtea (Gonimyrea) uhleri* er analyseret med henblik på morfologisk variation. Analysen viser et tydeligt fald i gennemsnitlig størrelse op gennem lagserien. Da lagserien repræsenterer et regressivt forløb betyder det, at de kystnære former er mindre end dem fra dybere vand. Forskellen beløber sig til næsten 20%. Faldet i gennemsnitlig størrelse menes fremkommet ved en række miljømæssige påvirkninger, dog diskuteres også muligheden for, at der kunne være tale om en egentlig fyltetisk udvikling mod mindre gennemsnitlig størrelse.

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