VARIATIONS IN SHELL FORM IN THE GASTROPOD GENUS *DIODORA*

by

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INTRODUCTION

A spectrum of environments exists, and within any given physical environment there also exist a variety of possible ways for organisms to survive. The result of geographic variation in environment is geographic variation in intraspecific design.

Morphologic variation within modern species is commonplace and well documented. It is erroneous to regard all individuals of a species as replicas of the type. Minute taxonomic discrimination at a specific or lower level can be justified only if resulting groups have biological significance. Overemphasis on morphologic differences without evaluation of possible causes encourages unrealistic taxonomic splitting rather than recognition of environmentally influenced variation within species.

The purpose of this investigation is to evaluate variations in diodorid shell form and suggest possible controls on morphologic variation.

ECOLOGY OF THE LIMPET

Specimens used for this study belong to the gastropod genus <u>Diodora</u> (family <u>Fissurellidae</u>). This genus was selected for its broad geographic distribution and extensive fossil record.

Diodorids are univalved, shaped much like a low cone with an elliptical base. The very young generate a spiral shell with a marginal slit. With maturity shell material is added until the margin below the slit is fused. The spiral is resorbed and the foramen or key hole enlarges (Morris, 1973, Abbott, 1974). The low conical shape makes them well adapted to wave exposure and strong turbulence.

Because little has been published on the ecology of diodorids, I have relied predominantly on information on the families, <u>Patellidae</u> and <u>Acmaeidae</u> which are similar cap-shaped archeogastropods.

Limpets are found from the equator to arctic shores (Berry, 1973), from the intertidal zone to depths of 900 meters, and tolerate both fresh and hypersaline waters (Por, 1975). Feeding and defense responses are most effective on solid surfaces such as rock faces, large gravel, kelp, sea walls or other shells (Black, 1976). Within these habitats, microhabitats include both exposed and cryptic surfaces, such as crevices and under rocks and kelp leaves. Most species migrate to subtidal waters when temperatures fall below freezing or wave action increases significantly (Berry, 1973, and Seapy and Hoppe, 1973).

The apical hole in the diodorid shell allows the exhalent water current to escape from the mantle cavity. Because the shell is not an air-tight cover, the limpet's range in the intertidal habitat is near or below low water level where desiccation is minimized (Fretter and Graham, 1962). In Florida, all species of Diodora live in cryptic habitats (Vermeij, personal communication). Observations concerning diodorid habitat were not made in southeastern Florida.

INTERSPECIFIC DISTRIBUTION

Limpet species are often segregated by substrate preference, position on the substrate relative to sea level, and available food source (Fretter and Graham, 1962).

Branch's (1974) study of patellids distinguished two groups within a limpet community: 1.) specialists with narrow food requirements and restricted zonation, and 2.)

generalized species with broad feeding habits and an extended range. Species compete by interspecific confrontations and exploitation of food resources. Exploitation of various food resources results in wide distribution of the limpet population, thus exposing it to a greater range of environments. This makes survival and reproduction more difficult. The resulting higher mortality is compensated for by a higher replacement rate or a higher gonadial output and a faster growth to maturity. Both imply greater metabolic expenditures and short longevity.

Adults of non-migratory species of Patella settle and form 'home scars' or depressions in the rock, widely spaced on the substrate. They exhibit territorial behavior, protecting algae growing in the immediate vicinity of their scar. Reduction of intraspecific confrontations as a result of territoriality appears to be an evolutionary advantage. Territorial behavior reduces competition within species and allows individuals to remain in a stable environment, thus stablizing the population. Territorial species of Patella are characterized by slow growth, low gonadial output, and high longevity (Branch, 1976).

Hewatt (1940) and Collins (1977) did not observe such a hierarchy in their studies of the genus Acmaea. Sympatric species in the intertidal zone are distributed on the substrate relative to distribution of algae on which they feed. Hewatt (1940) recorded segregation with respect to distance up the shore from mean sea level, as well. Nicotri (1974) observed no apparent segregation of acmaeids. Distribution appeared to be random with respect to substrate, slope, algal or barnacle cover, or exposure to the sun. Breen (1973) found that acmaeids are distributed in the intertidal zone with respect to age. Young limpets settle low on the shore near mean sea level, and migrate up through successive years.

Fretter and Graham (1962) and Branch (1976) found an increase in barnacle cover associated with a decrease in limpet size and an increase in limpet density. This may result from mutual interference, where larger patellids ingest or dislodge barnacle larvae while grazing over the substrate, thus minimizing the barnacle population in that area. Likewise, where a dense barnacle population is established, larger patellids probably experience difficulty in both grazing and maintaining the close shell-substrate contact essential for defense.

Older individuals of patellids and acmaeids make a home scar by rasping into the substrate with the edge of the shell until a slight depression is created (Hewatt, 1940, Ward, 1966a, Branch, 1971,1975a,b,c,d, and Bowman, 1981).

After a feeding excursion, the limpet returns to its home scar and orients itself in precisely the same way each time (Wolcott, 1973). The shell margin of _A. scabra_ is very irregular and fits the animal's home scar perfectly, even if on an irregular surface (Fretter and Graham, 1962 and Breen, 1974). The animal will continue to revolve on the spot if there is not an approximate fit between shell and substrate. Survival depends on a good fit.

Patellids less than 25 mm in shell length usually settle on the shells of older, larger patellids and graze algae there. This protects smaller limpets from the bulldozing effect of larger individuals. Some communities accomodate three tiers in this manner (Fretter and Graham, 1962, Branch, 1976, and Bowman, 1981). _P. aspera_ commonly acquires a cap of _Mytilus_ and miscellaneous algae, effectively creating a microhabitat of shade and humidity (Bowman, 1981).

FEEDING

Non-migratory species of South African patellids feed by revolving on their home scar, cropping the surrounding algae, generally _Ralfsia_ and _Gelidium_. These 'gardens' are maintained by an optimum grazing pattern. Algae are cropped close to the substrate, but minute fragments sufficient to regenerate the plant are left (Branch, 1971).

Hughes' (1971) study of _Fissurella barbadensis_ and Wright and Hartnoll's (1981) study of patellids, report limpets grazing over rock surfaces, ingesting sand, rock particles, detritus, diatoms, forams, radiolaria, small crustaceans, bivalve spat, and algae, of which only the algae are digested.

Nicotri (1974) observed that acmaeids feed mainly on diatoms but are not selective grazers. Blue green algae, primarily _Lyngbya_, _Oscillatosia_, _Phormidium_, and _Anacystis_, are found most commonly in the gut of species of _Fissurella_. The most abundant green algae observed is _Chlorachytrium_, which is endophytic mainly in _Lyngbya_ (Ward, 1966a). Ward (1966a) concludes that most Fissurellids are herbivorous, some are detritivores, and _D. apertura_ feeds on sponges. _D. gibberula_, a species found in the Mediterranean Sea, is reported to be a filter feeder (George, 1979).

BEHAVIOR RELATED TO TERRITORIALITY

The California limpet, Lottia gigantea exhibits territorial behavior and when encountering a trespassor, retreats about 1 cm, lowers the anterior shell, and lurches forward delivering a quick shove. The opposing mollusc is dislodged and washes away with the next wave (Stimson, 1970). For carnivorous snails, it clamps its shell down on the foot of the gourmand, dislodging it, and causing it to be washed away.

Branch (1975c,d, 1976) observed similar behavior in non-migratory species of patellids. They are territorial of their gardens and home scar, which they defend against intruders. Intraspecific confrontations are rare.

REPRODUCTION

F. barbadensis lives about 18 months and spawns twice a year (Hughes, 1971). Spawning occurs from March to June and September to November in 1964 in Barbados (Ward, 1966b).

Species of Patella live up to 17 years (Wright and Hartnoll, 1981). The sexes spawn simultaneously in December in Britain. They spawn earlier in the northern extremities of their ranges (Bowman, 1981).

The female D. apertura sheds its eggs from the anterior end of the mantle cavity and uses the foot to spread the gelatinous mass over a suitable surface. Egg laying takes 2-3 hours and fertilization occurs after all eggs are laid. Spermatozoa are ejected through the apical hole of the male, then fertilize the eggs. Both trochophore and veliger stages are completed while still in the egg mass, and young emerge as miniature adults (Ward, 1966b).

Wolcott (1973) observed that acmaeids have a free spawning habitat and release pelagic eggs. These remain in suspension for two or three days, assuring mixing of gametes from individuals at all levels of the shore.

Spermatozoa of D. nubecula are shed in packets surrounded by testicular epithelium and enter the female gonad where the eggs are fertilized (Fretter and Graham, 1962, and Ward, 1966b).

The trochophore larva of F. barbadensis is free swimming and remains pelagic for 3 days in Barbados (Lewis, 1960). Larval patellids settle on the shore in wet cracks, pools, or among small Mytilus clumps 10-14 days after fertilization (Bowman, 1981).

About 12 percent of a given population of F. nubecula undergoes a sex reversal. A P. vulgata population experiences a 90 percent sex reversal (Orton, 1946) or is protandrous (Hewatt, 1940, Branch, 1976, and Wright and Hartnoll, 1981). Nearly all P. vulgata specimens below 10 mm in shell length are neuter. Ninety percent of the specimens between 16-25 mm in length are male. Numbers of the two sexes are equal at 40 mm, and 70 percent are female at 60 mm (Orton et al., 1956). No predominance of one sex at a certain size range was obvious in F.barbadensis (Ward, 1966b). Sex reversal is rare in P. aspera and P. depressa (Dodd, 1956). Hermaphrodites occur occassionally in P. vulgata, P. aspera, and P. depressa (Ward, 1966b, and Wright and Hartnoll, 1981).

Blackmore (1969) reports a change from male to female in patellids after a year. That may depend on the existing sex ratio. He offers no explanation as to what triggers the change.

Gonadial volume in acmaeids varies logarithmically with limpet size, thus larger individuals make a larger contribution to the reproductive effort than smaller ones (Nicotri,1974). On a yearly basis, the gonad:body weight ratio goes up as temperature goes down. This indicates that more larvae are released in colder weather (Markel,1974).

Patellid males in their third year commence gonad maturation in August through September. Testes develop to a maximum of 19 percent of the flesh weight. Older males and all females begin to mature earlier in July and gonads reach 40 percent of the flesh weight (Wright and Hartnoll, 1981).

Growth of the gonad occurs posteriorly and laterally in both sexes of F. barbadensis. At the end of the developing stage, a thick extension is formed at the dorsal posterior of the visceral mass (Ward, 1966b).

INTRINSIC CHARACTERISTICS

Other features may have an indirect influence on limpet behavior or shell design. Branch (1971) recorded symbionts and parasites in a significant portion of patellids in South African limpet populations. Behavioral or morphologic responses of the limpets to their inhabitants was not recorded.

Statocysts are located on the foot of some species of patellids. These induce a release response that cause the individual to drop when the substrate is inverted (Branch, 1971).

Wolcott (1973) observed negative phototaxis in acmaeids. This is probably a beneficial response to evade birds and the hot sun. Lindberg (1975) painted acmaeid shells and discovered that they receive light through certain parts of the shell.

Chemoreceptors located on the pallial margin of acmaeids are sensitive to water scented with predator starfish and signal the limpet to move up the substrate or out of bright light when threatened. Scented water flowing from above the limpets still cause them to move up the substrate. Water scented with starfish species that are not natural enemies of these limpets invoke no reaction (Phillips, 1975a,b, 1976).

A. mitra and D. aspersa do not attempt to escape predators. Against starfish, they extend their mantle to cover virtually the whole shell exterior, repelling the starfish or rendering the suction of the tube feet ineffective (Margolin,1964).

The Caribbean limpet A. pustulata exudes a sticky and persistent mucous that, among other functions, may be unpleasant or harmful to predators (Vermeij, 1978).

GROWTH

Food availability apparently governs growth cycles. Greatest growth in filter feeding limpets occurs in winter and subsides in summer (Nicotri,1974). This parallels Malouf's (1977) conclusion that growth fluctuations in filter feeding molluscs are related to changes in the quantity of particulate organic matter suspended in the water, which is often a function of season and temperature.

Wright and Hartnoll's (1981) study on energy budget in patellids indicates that when resources are scarce, gamete production has a higher priority than somatic growth.

Bowman (1981) observed that species of _Patella_ on patches of the alga _Lithothamnia_ grow slower than limpets living on open damp rock with a selection of algae.

Development of shell ribs is related to growth rate and desiccation. Patellids of all species reared permanently submerged in aquaria grow unusually quickly and develop smooth, thin, and faintly ribbed shells. No alteration in color pattern was observed (Bowman, 1981).

Ward (1967) recorded a thicker shell in _F_. _barbadensis_ in a partially exposed habitat as opposed to subtidal specimens. Bowman (1981) found that upper-shore pool and open rock patellids have prominent thickened ribs.

All patellid larvae are restricted to wet places. Juveniles of _P_. _vulgata_ and _P_. _depressa_ eventually move onto drier rock, while _D_. _aspera_, which has the weakest rib development, usually remains in pools until it is an adult (Bowman, 1981).

Weak rib development is also associated with late settlement and/or slow growth. Although individuals exhibiting poor rib development accrete normal shells when conditions improve, they remain severely retarded and abnormally slow growing (Bowman, 1981). This agrees with Stephens' (1932) conclusions regarding *Abra alba* and *Cardium edule*: shells with retarded initial growth continually grow more slowly than other specimens of their same generation.

Bowman (1981) observed a possible selective advantage displayed by *P. vulgata*. Because this species is more tolerant of desiccation than *P. aspera* or *P. depressa*, it is able to move out of the pools at an early age and exploit a more abundant food supply. Since stunted growth during the first few months following settlement can result in a retarded growth rate which persists even after conditions improve, it is advantageous to the young limpet to move to open rock as soon as possible, thus reducing competition, increasing growth rate, and maximizing potential gametic output.

SHELL MORPHOLOGY

Most research on limpets focusses upon their ability to survive aerial exposure for several days when emerged in the intertidal zone.

Hewatt (1940), Segal (1956), Ward (1967), Seapy and Hoppe (1973), Shotwell (1950) and Bannister (1975), agree that larger and higher-peaked shells of patellids and acmaeids occur higher in the intertidal zone, apparently because higher peaks offer a larger extra-visceral area to store water for respiration during emergence.

Branch (1974b) noted that Patella longicosta has a high peaked shell as a sedentary juvenile. As it grows and moves about, extending its mantle, the shell grows broader. Ebling (1962) transplanted a high peaked, high shore level limpet to a tidal pool where it remained in a relaxed state a greater portion of the time. The limpet began to accrete a rim around its shell as it started to grow to a relatively flatter posture.

Branch (1975a) speculates that a high domed shell allows development of huge adductor muscles used to clamp firmly to the substrate.

Intertidal limpets exposed to high wave action show a greater rate of increase in shell weight, volume under the shell, and extravisceral space with increasing wet weight of soft parts than those from a sheltered region. Rate of increase is also greater in shells found higher above mean sea level compared to those from a lower shore habitat (Ward, 1967).

Vermeij (1971) suggests an added advantage offered to larger limpets: having a relatively smaller surface contact to body volume ratio allows them to deviate from the substrate temperature, thereby experiencing less stress on hot, dry days.

Wolcott (1973), found no correlation between distribution and size in the intertidal zone. He attributes survival of exposed acmaeids to their ability to form a mucous sheet to seal the shell and affix it firmly to the substrate. All of his specimens demonstrated use of 'evaporative cooling' by lifting the shell in extreme heat. This might have been what Doran and McKenzie (1973) observed as 'aerial respiration at low tide.' Wolcott (1973) concludes that acmaeids high desiccation tolerance depends more on adaptation to high electrolyte concentrations at the cellular level. This is the result of respiration in a given amount of water over a length of time.

Based on these studies, it is apparent that limpets are well adapted to an environment in which predation and severe desiccation are common. In addition, some species exhibit an ability to alter their form to accomodate stress. How much variation in form is there within a species? Are observed variations predictably correlative to a given environment? If trends exist, can they be traced into the fossil record and used as an aid in determining paleoenvironments?

METHODS AND MATERIALS

NEONTOLOGICAL STUDY

The study of modern species of Diodora involved three hundred thirty specimens from the Biological Collection at the National Museum of Natural History of the Smithsonian Institution. Species included D. cayenensis, D. listeri, D. sayi, and D. tanneri. Collection sites range from the Florida Keys to the Chesapeake Bay, and from intertidal to 219 meters water depth in the Atlantic Ocean. Gulf of Mexico specimens were collected along the coast of Florida to a depth of 92 meters. A detailed list of collection localities is provided as Appendix B.

Four sets of data totalling 58 variables were recorded for each shell. The first set included orthogonal measurements. Parameters from each shell are listed and illustrated below. See Figure 1.

L=length

W=width

HW=height at widest point

HL=total height

FINC=angle of inclination of foramen to horizontal

PCURV=curvature of dorsal posterior

V=internal volume

M=dry mass

Linear measurements of specimens were made with a vernier caliper to the nearest .01 mm. Internal volume of each intact shell was measured by filling the shell with water from a titrating burrette. Values were recorded to the nearest .01 ml. The mass of each complete shell was obtained on a triple beam balance to the nearest .01 gram. Because ornamentation and curvature of the shell caused significant variability, shell thickness was not recorded. Shell volume, obtained by submersion and displacement, would have been an adequate alternative had more sensitive equipment been available.

The second set of variables included environmental factors: water depth in meters, latitude in degrees north, and marine province. Marine provinces delineated were the (1) Florida Keys, (2) Gulf Coast of Florida, (3) Atlantic Coast of Florida, (4) Coast from Georgia to Cape Hatteras,N.C., and (5) Coast from Cape Hatteras to the Chesapeake Bay. See Figure 2.

The third and fourth sets of variables, which include ornamentation and shell and foramen shape, were recorded

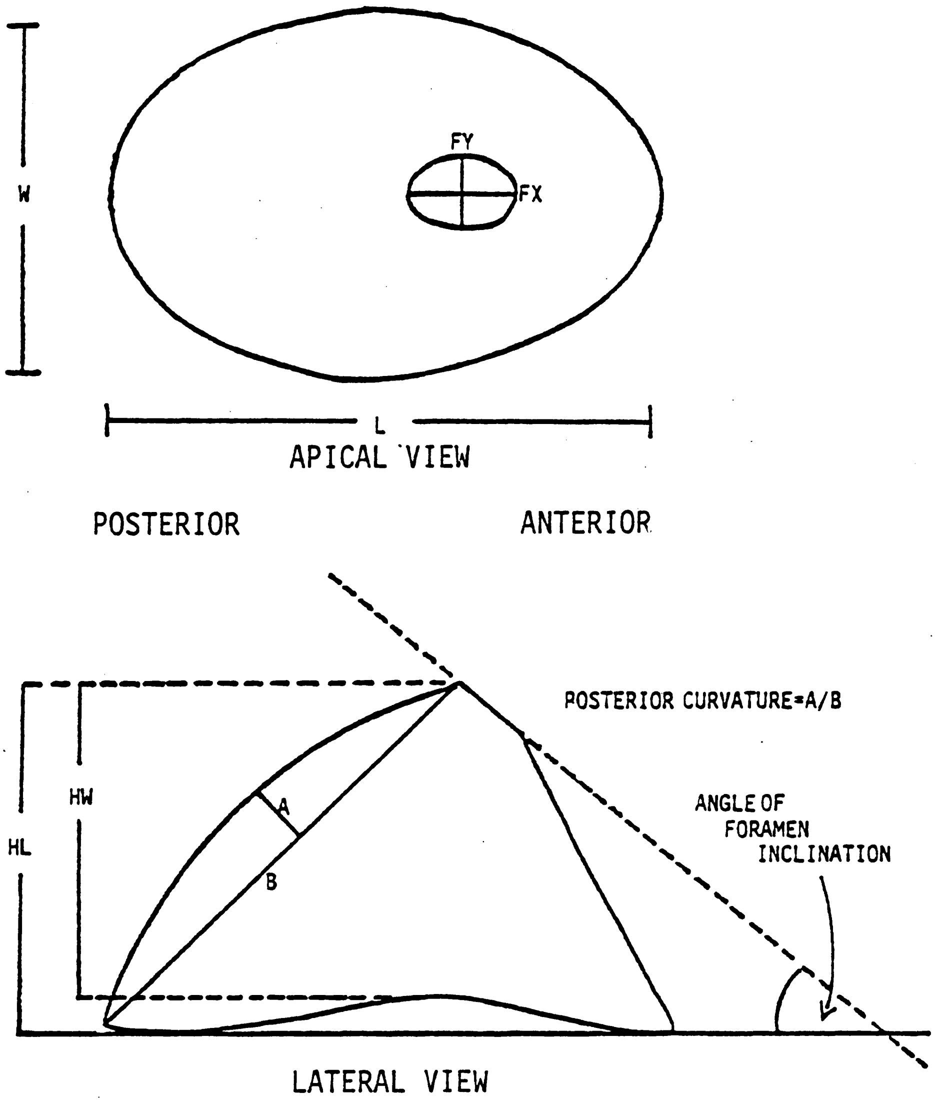


Figure 1: Parameters measured from shell

Figure 2: Marine provinces defined for this study. Numbers after each species listed refer to province collected in; 1.) Florida Keys, 2.) Florida Gulf Coast, 3.) Florida East Coast, 4.) Georgia to Cape Hatteras, N.C., and 5.) Cape Hatteras to Chesapeake Bay.

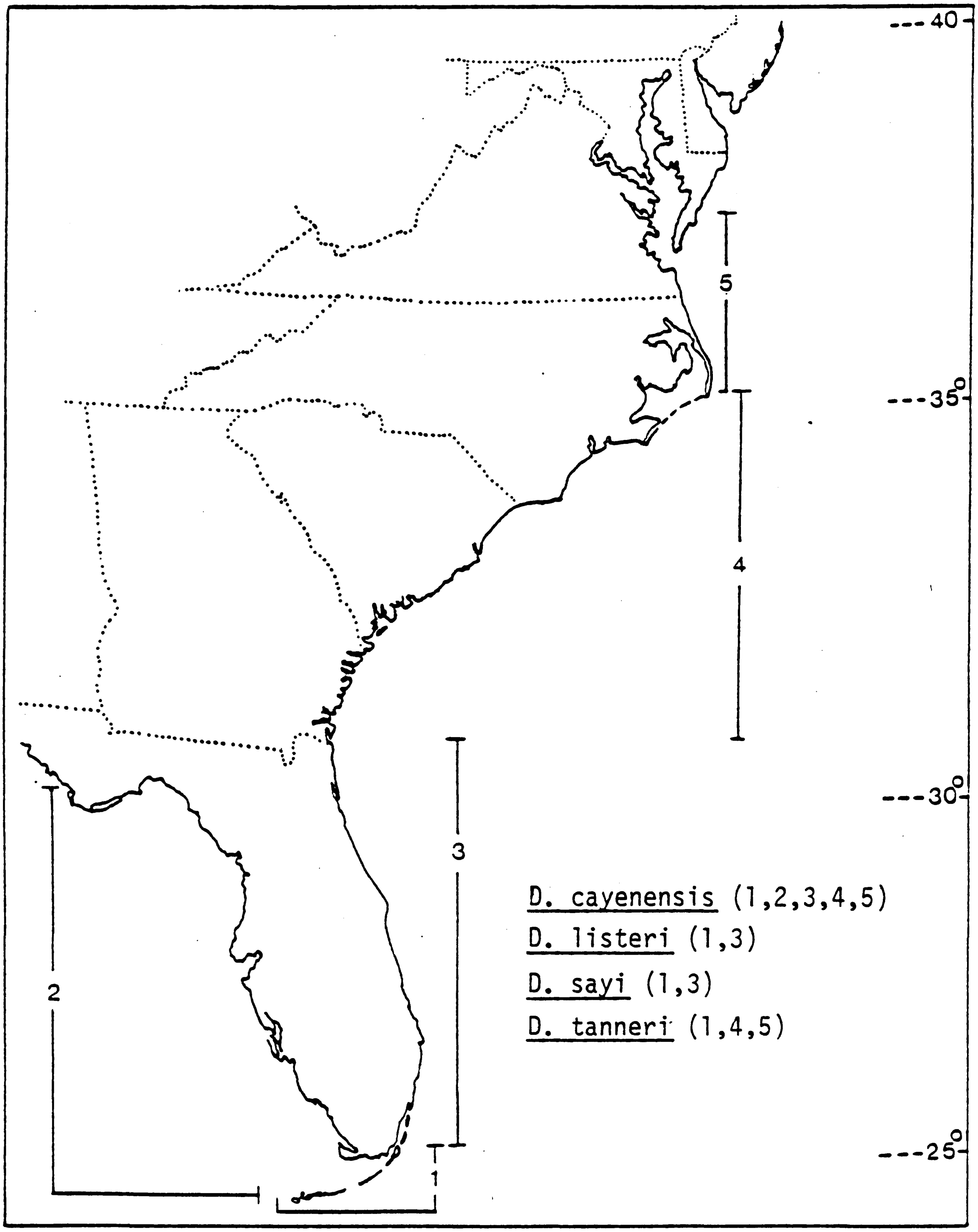


Figure 2: Oceanographic Provinces

only for 50 of the recent Diodorids. These specimens were selected at random from the original 330 and represent the four species over a range of water depths and marine provinces. Each of the 50 reference specimens was photographed from apical and lateral views. Specimens were dusted with ammonium chloride (NH_4Cl) immediately before photographing to enhance shell features. Photographs were taken with Technical Pan 2415 film using a Nikon F camera with a HOYA 52mm lens, and printed on Polycontrast Rapid II RC paper. An attempt was made to keep the same scale for each picture but change in focus caused slight size distortion. Third and fourth sets of data were acquired from examination of these photographs.

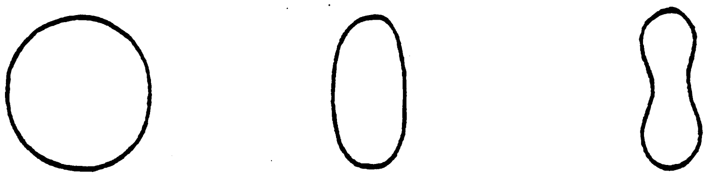
The third set of variables includes qualitatively assessed shell characteristics. The shape of the foramen was evaluated as 1.) near round, 2.) oval, or 3.) constricted and given a numerical value progressing from 1 to 3. See Figure 3.

Foramen profile was qualified as 1.) straight, 2.) peaked, or 3.) horned, and given a value. See Figure 3. A foramen with a shape value of (1) does not necessarily correspond with a foramen profile having a value of (1). Foramen length (FX) and foramen width (FY) were measured from the photographs to the nearest 0.1 mm. These dimensions were standardized to eliminate shell size factor, by expressing them as a ratio to one of the other shell parameters, Y90 or XA (discussed later in this section).

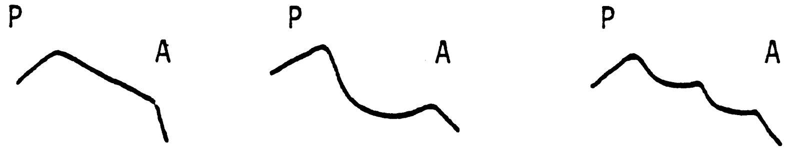
Robustness of ornamentation appears to be inversely related to the number of ribs on the shell: the finer the rib, the more ribs per unit surface area. Ribs were evaluated as large, medium, or small and counted in the right posterior quadrant of the shell.

The fourth set of varibles was derived from the outline of each reference specimen in apical and lateral views. Points around the rim and crest of each shell were selected and assigned x-y coordinates on a cardinal axis.

The method of selecting points to be digitized utilized a pattern of 19 rays spaced at 10 degree intervals encompassing 180 degrees. This pattern was superimposed on the photograph of each shell and centered so the shell 'rested' on the horizontal (0 and 180 degree rays) and the 90 degree ray passed through the point posterior of the foramen, which was usually but not always the highest point on the shell. The intersection of each ray and the shell outline determined a digitized point. For the lateral view, two additional rays were added to pass through the anterior- and posterior-most extremities, should they not fall on the abscissa. See Figure 4. The silouette of the shell is



(1) ELLIPTICAL (2) OVAL (3) CONSTRICTED



(1) STRAIGHT (2) PEAKED (3) HORNED

Figure 3: Foramen shape

expressed as an array of 42 cardinal coordinates, twenty one from each view. The advantage this method offers that orthogonal measurements do not, is its capacity to detect subtle surface inflections along the shell crest, as well as monitoring apex and foramen orientation.

The array of coordinates and foramenal dimensions were standardized to create a morphometric data set independent of shell size. This was accomplished by setting one of the digitized parameters equal to unity; all other coordinates measured from the photograph were expressed as a ratio to the unit length. Two opposing parameters (Y90 and XA) were used as units and two separate analyses were performed for each view. Only the correlations between variables that were statistically significant in both cases were considered.

Additional standardized data were calculated by deriving an hypotenuse or radius from the origin to each pair of coordinates. The length of this radius was used as a measure of relative inflation or constriction of the shell. Again, two opposing units were used in standardizing, and only correlation coefficients statistically significant in both analyses were considered. Comparison of relative magnitudes of these radii used a technique derived from Benson's (1967) Theta Rho Analysis.

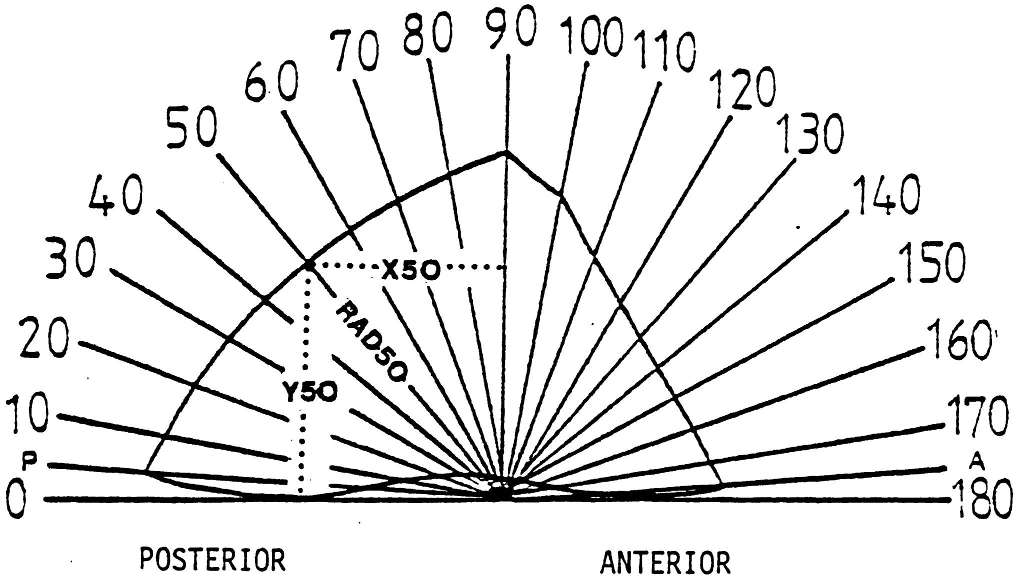


Figure 4: Digitized points around shell

The standardized values were used to create two additional variables.

SM= size/mass of the shell, derived by dividing the
area of a cone with elliptical base by its dry
mass in mg
= (3.142*R*(((R**2)+(HL**2))**(1/2))))/(M*1000)
when R=((L+W)/2)

FAREA=foramen area
= 3.142*((FORX*FORY)/4)
when FORX and FORY
represent the standardized values of foramen
length (FX) and width (FY) respectively

MORPHOLOGIC MODEL

Shell form varies somewhat independently of environmental factors examined in this study. Morphologic relationships among all measured shell parameters were correlated to generate a model for shell form variation. The base model was defined by variation in shell form of the most abundant and variable recent species in this study, *D. cayenensis*. Each other species was then compared to it and discussed in the species descriptions.

PALEONTOLOGICAL STUDY

A sample of 503 fossil Diodorids from the Smithsonian Institution Paleobiological Collection was compared to the neontological analysis of shell variation in *Diodora*. Species included *D. nucula*, *D. carolinensis*, *D. chipolana*, *D. cayenensis*, *D. carditella*, *D. griscomi*, *D. alticosta*, *D. caloosaensis*, *D. marylandica*, *D. redimicula*, and *D. catilliformis*. A morphotype labelled *D. griscomi* from New Jersey that differs from any other species also was included. This unique morphotype will be referred to as *Diodora sp.*. The fossil collection sites range from the Mid-Miocene Kirkwood Sand of New Jersey to the Pleistocene Fort Thompson of Florida. Specimens were measured and treated in a manner similar to that previously cited for recent specimens. Variables used were the same, except that water depth was eliminated and fossil age was added. Sixty one specimens of the original sample were selected at random to be reference specimens. This sample was photographed and digitized precisely as described for the sample of recent specimens.

Fossil specimens were first analyzed as a group (all species combined) then reanalyzed by 1.) species, 2.) latitude, 3.) geologic age, and 4.) groups of reanalyzed by

1.) species, 2.) latitude, 3.) geologic age, and 4.) groups of similar morphotypes.

Cluster Analysis was performed on the sets of recent and fossil reference morphotypes, eliminating size, latitude, and age as variables. The purpose of this mode of analysis was to examine the taxonomic control by associating similarities in shape.

ANALYTICAL METHODS

Principal Components Analysis

Principal Components Analysis transforms a set of observations into independent linear combinations of the original variables. The first component is that which accounts for the largest portion of total variation by having the greatest eigenvalue, the second component having the next greatest value, and so on. Relationships can then be viewed in a number of dimensions greatly reduced from the original number of variables.

Principal Components Analysis requires the calculation of eigenvalues and eigenvectors of A, an array of dimension (b*b) where b is the number of variables. The entire array can be envisioned as a cloud of points in multidimensional space, with b dimensions. The principal axis would be the 'line' with the greatest 'length' or amount of variation. The second axis is chosen orthogonal to the first, such that variability along this axis is next greatest, giving a maximum scatter in the plane formed by the two axes, and so on.

Eigenvectors include coefficients which define the principal component. The corresponding eigenvalues, the variances of the principal components, are a measure of the proportion of the total variation accounted for by each component. Coefficients comprising each component are then used to provide insight into the factors causing the interrelationships between original variates, factors that may not have been readily discernible from the original measurements.

The correlation matrix is consulted for coefficients giving degree of correlation between any two variables. In this study, correlations of .50 or better were considered in accordance with the table of critical values for correlation coefficients in Sokal and Rohlf (1973).

See Davis (1973) for a more complete description of Principal Components Analysis.

Principal Components Analysis was performed using the BMDP4M computer program.

Cluster Analysis

Cluster analysis is used to divide a large group of observations into smaller groups of greater similarity, making relationships between groups readiy apparent. Davis (1973) describes the analysis as performed on an (n*m) matrix of n observations, each with m variables. A measure of similarity is computed between every pair of objects in the matrix.

The (n*m) raw data matrix is standardized using a 'percent maximum coefficient' prior to computing similarities. This is performed by setting the highest value of each variable equal to unity and expressing all other variables as a percent of this maximum value. This gives equal weight to each variable and avoids giving the one with greatest magnitude heaviest weighting.

Euclidian distance is then computed between each pair of variables; a low distance indicates two objects are similar, and a large one dissimilarity.

The first step in clustering is to find the mutually highest correlations in the matrix to form the center of the clusters. Groups of similar pairs are then arranged in a heirarchy: groups or clusters are assigned to clusters according to their degree of similarity. The process is repeated until all observations have been assigned to a cluster. The similarity matrix is recomputed treating clustered elements as a single element, and the procedure continues.

Ultimately, the result is a set of relationships best illustrated with a dendrogram. The elements are connected by cross-branches, set at levels along a linear scale which express the degree of similarity of the elements. See the dendrogram refered to in 'Taxonomic Discrimination'.

Cluster Analysis was performed using a computer program written by Francis Plants, Arnie Miller, and Tom Rounds.

Theta Rho Analysis

Theta-rho analysis was designed to show quantitatively and objectively the extent of similarity existing between two placements of points on a surface. The process can be envisioned as putting an imaginary 'radar antenna' at the designated origin of the form to be analyzed. The radar beam begins to sweep around the specimen, in this case beginning at the posterior and continuing 180 degrees around the periphery, getting 'reflections' from the outer margin. Each point of contact is then assigned a bearing (theta) and a distance from the origin (rho). See the Theta Rho illustration in the description of Diodora sp.. These values are then transformed to x-y coordinates and analyzed with a number of different programs, including Principal Components Analysis and Cluster Analysis. For an explanation and example of this technique see Benson (1967).

Rho Group Illustration

Relationships exhibiting a significant correlation can be illustrated by the following configuration, called a Rho Group (Olson & Miller, 1958). The Rho Group model provides a mathematical basis for operations that involve biological theory and interpretation. In this analysis, correlation between any pair of variables is expressed as rho ( ). This provides a convenient form of abstract, quantitative representation of a species or group of specimens. The resulting numerical pattern is then unique to the morphology of a given species or sample.

Rho Groups are formed by selecting a rho value where a significant correlation exists. In this study, rho correlations are greater than .50 in accordance with Sokal and Rohlf (1973). Statistical significance of each correlation is greater than or equal to .95 in all cases. Variables are then bonded by correlation to construct the basic matrix. All pairs of variables with correlations greater than .50 are bonded. 'Basic pairs' have each variable more highly correlated to the other than to any other variable. Refer to the Rho Groups presented in the _D. cayenensis_ description and the General Conclusions. The number written over each bond is the correlation coefficient relating the two variables.

VARIABLES CREATED IN ANALYSIS

The following variables are some created for data analysis and will be encountered in Appendices D,E,F, and G.

SPNO= Reference specimen number
SP= Species
    1=D. cayenensis
    2=D. listeri
    4=D. sayi
    5=D. tanneri
    A=D. nucula
    B=D. chipolana
    C=D. carolinensis
    D=D. cayenensis (fossil)
    E=D. carditella
    F=Diodora sp.
    G=D. griscomi
    H=D. alticosta
    I=D. caloosaensis
    J=D. marylandica
    K and L=D. redimicula
    M=D. catilliformis
PROV= Oceanographic province
    1=Florida Keys
    2=Florida Gulf Coast
    3=Atlantic Coast of Florida
    4=Georgia to Cape Hatteras
    5=North of Cape Hatteras to Chesapeake Bay
LAT= Latitude
DEP= Water depth
AGE= Geologic age, mean value derived from Figure 10
L= Shell length
W= Shell width
M= Mass of shell
HW= Height of shell at widest point
HL= Total height of shell
HL/L= Ratio of total shell height to shell length
FX= Length of foramen measured from photograph
FY= Width of foramen measured from photograph
FTOP= Foramen shape from apical view
FSIDE= Foramen shape from lateal view
FINC= Foramen angle of inclination to horizontal
PCURV= Curvature of dorsal posterior surface of shell
LRIB= Number of relatively large ribs
MRIB= Number of relatively medium ribs
SRIB= Number of relatively small ribs
TOTRIB= Total number of ribs (LRIB+MRIB+SRIB)

OCEANOGRAPHIC PROVINCES

The oceanographic provinces for the recent specimens of this study are illustrated in Figure 2 and collection localities in Appendix B.

FLORIDA KEYS

Province (1), the Florida Keys, is biotically the richest region of the northern hemisphere Western Atlantic. The region has a high degree of endemism of about 55 percent (Van den Hoek, 1975). The Keys are a discontinuous barrier of Pleistocene limestone, 280 kilometers long, skirted by a line of coral reefs. These reefs are composed primarily of _Acropora_ and _Millepora_ that extend to a depth of about 25 meters. The back-reef lagoons are sheltered water with scattered communities of _Porites_, _Montastrea_, _Siderastrea_, and _Diploria_.

Annual water temperature ranges from 15 to 33 degrees Celsius. Salinity measurements, to a depth of 9 meters, are between .32 and .38 parts per thousand (ppt) (Bathhurst, 1976).

D. cayenensis, _D. listeri_, _D. sayi_, and _D.tanneri_ were collected from this province.

GULF COAST OF FLORIDA

Province (2), the Gulf Coast of Florida, has a humid, subtropical climate. Mean water temperature ranges from 32 degrees Celsius in July to 10 degrees Celsius in December (Dawes, 1974).

Evaporation generally exceeds precipitation during the summer in the Gulf (Capurro and Reid, 1972). Salinities offshore are comparable to those of normal seawater, .358-.360 ppt, but are influenced by local rainfall and runoff.

The outer coastline near Tampa Bay consists of elongate barrier islands of sand; limestone outcrops occur offshore. Wave action is generally moderate (Dawes, 1974).

Only D. cayenensis was collected from this province.

ATLANTIC COAST OF FLORIDA

Province (3), the Atlantic coast of Florida, appears to be a region transitional between Province (1), (the Florida Keys) and Province (4), (Georgia to Cape Hatteras, N.C.). Scattered reefs are present, surrounded by expanses of sandy substrate.

Salinities of the Gulf and ocean are comparable during the winter at equal latitudes, ranging from .358-.362 ppt in the Gulf to .355-.360 ppt along the Atlantic Coast of Florida (Worthington, 1976). There is a noticeable decrease in surface water temperature along the Atlantic Coast of Florida. Temperatures in the Gulf at depths less than 20 meters range from 10 to 32 degrees Celsius annually. Comparable ocean latitudes range from 7 to 17 degrees Celsius (Worthington, 1976).

D. cayenensis, *D. listeri*, and *D. sayi* were collected from this province.

GEORGIA TO CAPE HATTERAS

Province (4), Georgia to Cape Hatteras, North Carolina, has long shorelines of terrigenous sands with lagoon and estuarine systems that are inhospitable to most benthic algae (Chapman, 1971). A few widely scattered sublittoral reefs develop a more diversified flora (Schneider and Searles, 1973).

It is likely that the northern shores of the Gulf of Mexico resemble this region (Humm, 1969).

Only *D. cayenensis* was collected from this province.

CAPE HATTERAS, N.C. TO THE CHESAPEAKE BAY

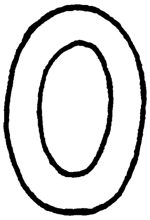
Province (5), Cape Hatteras, North Carolina, to the Chesapeake Bay, is situated north of the point where the Gulf Stream veers from the coast and flows northeast across the Atlantic Ocean. Lower water temperatures and lower salinities of this area result from the southward flowing Laborador Current (Gaskell, 1972). A slight increase in floral species diversity is recorded, compared to Province (4), south of the Cape (Van den Hoek, 1975).

D. cayenensis and *D. tanneri* were collected from this province.

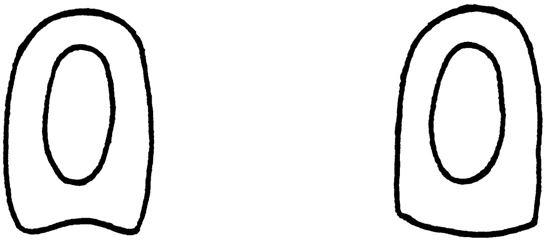
SPECIES DESCRIPTION

The shell of adult diodorids is a low cone shape with an elliptical base that is generally curved up off the substrate in the mid portion. The shell posterior is widest. Shell length is about 1.45 times the width; relative height is variable. The foramen is a small oval opening located in the anterior section and is always inclined forward. The apex of the shell is generally the point immediately posterior to the foramen. The foramen is surrounded on the interior by a deltoid callus that is truncated posteriorly. This feature distinguishes the shell of the genus Diodora from that of the genus Fissurella which has a callus that is not truncated posteriorly but is oval. See Figure 6. Ornamentation consists of radiating ribs, expressed around the basal margin as slight crenulations. The interior of the shell is smooth with little or no evidense of muscle scars.

The following pages are species descriptions for the recent and fossil diodorids included in this study. The letter or number preceding each species name is the code used in graphing. Species number (3) was omitted from analysis as it was collected outside the designated provinces.



Fissurella



D. griscomi

Diodora sp.

Diodora

Callus shapes of some Fissurellids

Figure 5

Included in the species descriptions is 1.) description of shell features, 2.) range as described in the literature, 3.) distribution of the collection localities of specimens used in this study, and 4.) analytical results, including; a.) geographic distribution of shell form variation, and b.) a morphologic model describing shell form variation independent of environmental factors.

Phylum: Mollusca
Class: Gastropoda
Subclass: Prosobranchia
Order: Archeogastropoda
Family: Fissurellidae
Subfamily: Diodorinae, Odhner, 1932
Genus: Diodora Gray, 1821
Type: D.graeca Linne, 1758, from Europe

RECENT SPECIES

(1) Diodora cayenensis (Lamarck) 1822

Fissurella cayenensis Lamarck, 1822, Animaux sans Vert. 6(2):12.

Fissurella alternata Say, 1822, Jour. Acad. Nat. Sci. Phila. 2:244.

Fissurediea alternata Dall, 1892, Trans. Wagner Free Inst. Sci. 3(2):428.

Diodora alternata alternata Johnsonia, 1934: 67.

Diodora cayenensis Farfante, 1943, Johnsonia 1(11):5.

DESCRIPTION: Specimens in this collection range to 5 cm in length. Shell form varies from a moderate to a high peak with slight to distinct curvature of the dorsal posterior profile. The mid-portion of the basal margin is raised to variable degrees.

The foramen is located just anterior of the shell center and inclined at angles ranging from a steep 40 degrees to nearly horizontal. It is oval to constricted in outline with a straight to horned profile.

The surface of the shell is sculptured, with 60 to 120 distinct, radiating ribs, usually every fourth rib accentuated. Ribs are reflected in fine crenulations around the basal shell margin.

The exterior of the shell is usually grey or grey and white striped. The interior is white.

RANGE: Maryland and south to Brazil; Gulf of Mexico, West Indies. Intertidal and subtidal.

_D._ _cayenensis_ shows greatest dispersion of recent _Diodora_ species included in this study. Specimens were collected from 42 localities from each of the provinces, including 10 localities in the Florida Gulf Coast, 8 localities in the Florida Keys, 8 localities along the Florida East Coast, 10 localities from Georgia to Cape Hatteras, and 6 localities from Cape Hatteras to the Chesapeake Bay. The specimens were collected from intertidal environments to a depth of 130 meters.

FOSSIL OCCURRENCE: Waccamaw and Caloosahatchee Formations (Dall, 1892).

For this study, fossils are from 6 localities, Early Pliocene Duplin Formation of North and South Carolina and Late Pliocene Caloosahatchee and Waccamaw Formations of Florida, and South Carolina, respectively.

ANALYTICAL RESULTS: The sample of D. cayenensis contained 202 specimens, 28 of which were selected for reference and digitized. Analysis of D. cayenensis shell form variation yielded the following conclusions:

1. Shells from Province (5), (north of Cape Hatteras to the Chesapeake Bay), have a greater total number of ribs than those from the other four provinces south of Cape Hatteras and may suggest a subspecies found north of Cape Hatteras. See Figure 7 and Appendix F.
2. Shells from greater than 2 meters of water, in all provinces, have a smaller mean size compared to larger specimens from intertidal environments. See length (L) and width (W) measurements in Table 1.
3. Shells from greater than 2 meters of water, in Provinces (1),(3), and (5) (Florida Keys, East Coast of Florida, and North of Cape Hatteras) have a lower mean relative shell height compared to the slightly taller intertidal specimens. Refer to the relative height ratio (HL/L) in Table 1.

4. The foramen of the three specimens from subtidal habitats is less constricted and has a straighter profile, with a lower angle of inclination, than those from an intertidal habitat. See Figure 8.
5. Shells from the Gulf Coast of Florida are taller and relatively heavier than D. cayenensis shells of the same length from other provinces. Refer to the HL/L ratio in Table 1.

The Rho Group diagram in Figure 9 illustrates the relationships between parameters measured from reference specimens of D. cayenensis and offers a better understanding for shell form variation.

MORPHOLOGIC MODEL: Larger shells of D. cayenensis displayed an increased total number of ribs as well as an increase in angle of inclination of the foramen to the horizontal. Compare specimen number 6 to specimen number 28 on Plate 1. Increase in foramen inclination was significantly correlated to increased relative height of the shell and to increased curvature of the dorsal posterior profile. See Figure 10.

Increase in posterior radii, 70 and 80, is correlated to a decrease in the vertical to anterior radii, 90 to 150 degrees. Additionally, posterior radii, P through 20, increase directly with anterior radii, 150 through 170. This

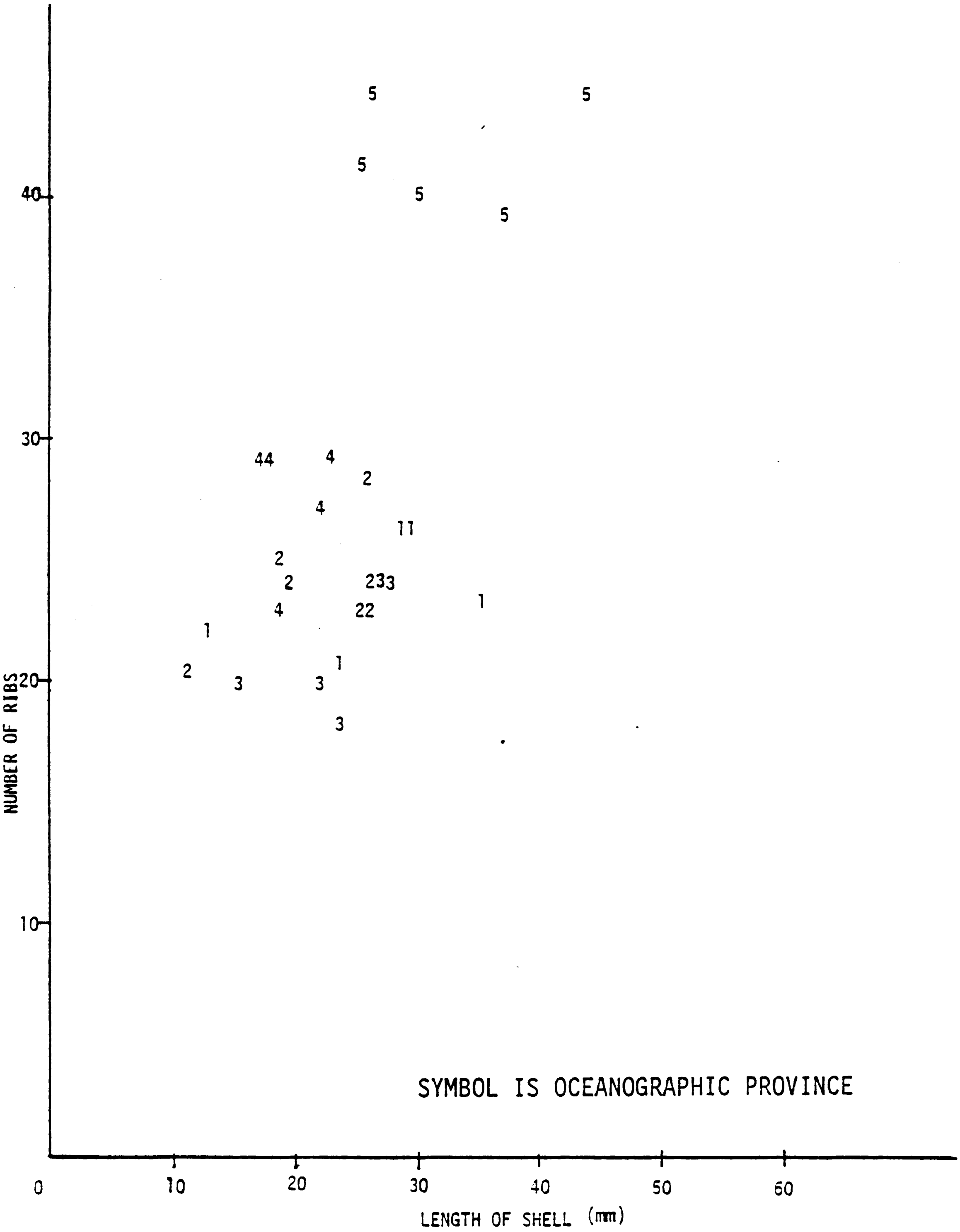


Figure 6: Rib number by shell length for D. cayenensis

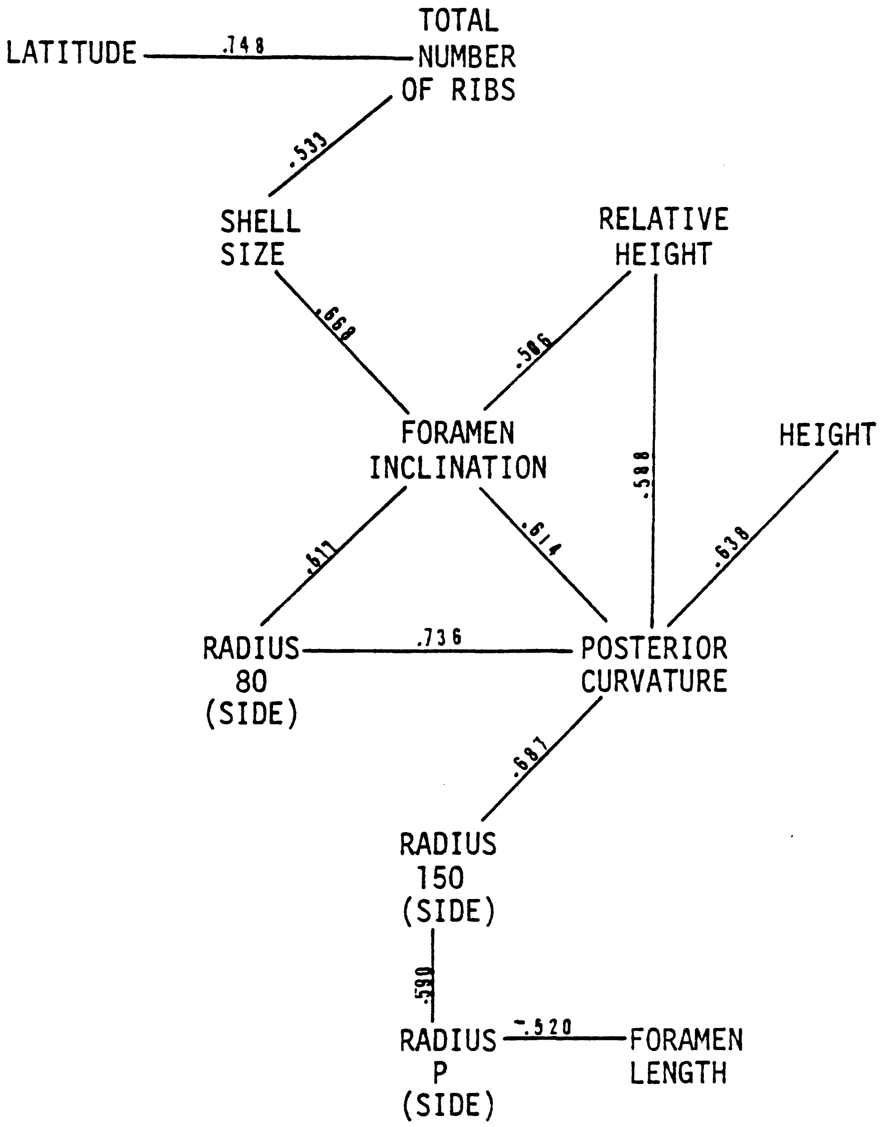
Table 1: Statistics for *D. cayenensis*

	FLORIDA GULF		FLORIDA KEYS		FLORIDA EAST COAST		GEORGIA-HATTERAS		NORTH OF HATTERAS	
	INTER-TIDAL	SUB-TIDAL	INTER-TIDAL	SUB-TIDAL	INTER-TIDAL	SUB-TIDAL	INTER-TIDAL	SUB-TIDAL	INTER-TIDAL	SUB-TIDAL
LATITUDINAL RANGE (degrees no.)	27.36-27.81	24.55-29.50	24.85-25.07	24.45-25.00	25.81-25.85	25.71-28.45	34.20-34.71	34.00-35.00	37.11-37.98	37.00-37.15
WATER DEPTH RANGE (m)	1.00	10.10-91.40	1.00	29.30-130.00	1.00	14.60-109.70	1.00-2.30	4.00-40.00	1.00	"off-shore"
SHELL LENGTH RANGE (mm)	19.15-26.45	11.91-23.40	23.85-35.25	5.85-17.25	6.10-28.45	4.20-23.25	15.15-23.85	5.00-34.00	25.40-44.05	19.80-30.15
MEAN L	23.64	18.50	29.33	9.06	21.07	12.40	20.25	13.50	32.36	24.98
STAND. DEV.	3.23	5.93	4.67	3.85	5.93	5.50	4.00	6.88	6.31	7.32
SHELL WIDTH RANGE (mm)	12.60-19.10	7.99-15.10	15.05-23.10	3.50-12.30	3.65-17.95	2.70-14.70	9.90-16.10	3.00-24.00	17.00-31.15	13.00-21.25
MEAN W	15.64	11.98	18.61	5.77	13.42	8.23	13.53	8.73	22.42	17.13
STAND. DEV.	2.39	3.63	3.38	2.85	3.82	4.69	2.83	4.59	4.82	5.83
SHELL HEIGHT RANGE (mm)	9.60-13.00	7.10-9.80	10.50-14.80	2.10-10.00	2.85-13.10	1.60-10.40	5.80-10.45	2.00-14.00	10.10-19.40	6.95-11.50
MEAN HL	11.11	8.80	12.53	3.76	9.01	4.66	8.85	5.96	13.42	9.23
STAND. DEV.	1.45	1.48	1.97	2.46	2.78	2.60	2.09	2.86	2.99	3.22
HEIGHT/LENGTH RANGE	.397-.567	.420-.596	.390-.470	.320-.580	.380-.470	.270-.490	.380-.490	0.33-0.56	.370-.470	.350-.380
MEAN HLL	.471	.495	.430	.399	.427	.368	.433	.436	.413	.365
STAND. DEV.	.061	.091	.034	.081	.032	.066	.048	.035	.035	.021
NUMBER OF SPECIMENS IN SAMPLE	7	3	4	9	14	15	4	37	9	2

FORAMEN SHAPE		HABITAT	
		Number of Intertidal Specimens	Number of Subtidal Specimens
	Near Round	—	1
	Oval	3	2
	Constricted	14	—

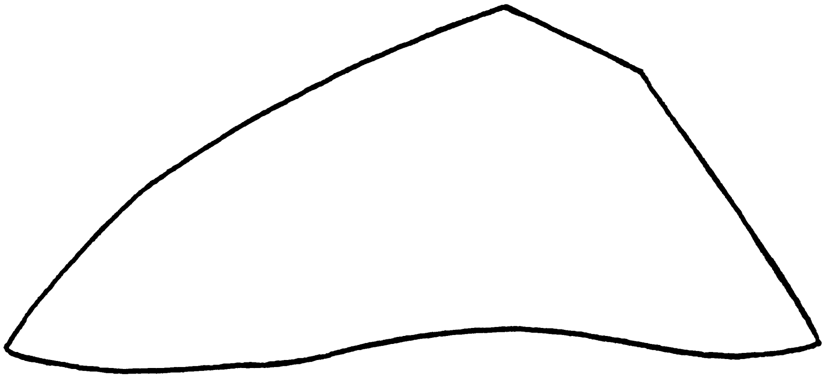
Foramen Shape of D. cayenensis by Water Depth

Figure 7

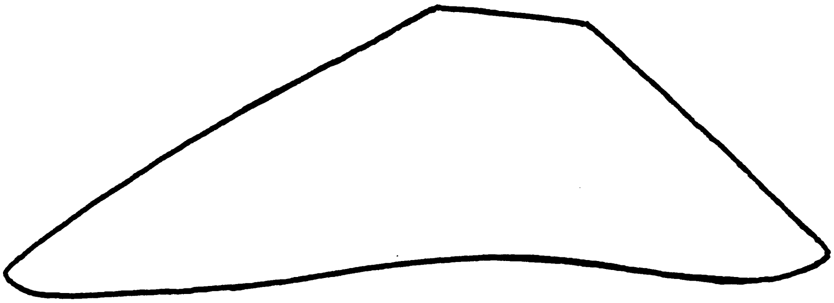


D. CAYENENSIS REFERENCE SPECIMENS

Figure 8



Specimen 6



Specimen 28

Factors affected:

1. relative height
2. posterior curvature
3. foramen inclination
4. abreviated anterior

Figure 9

growth pattern is related to increase in relative foramen length. For a review of radii location and orientation, see Figure 4.

These relationships are summarized to offer a general morphologic model for D. cayenensis that is compared to other species form variation in each species description. Larger shells display a greater number of ribs and a greater angle of inclination of the foramen to the horizontal. It is easy to envision the foramenal angle of inclination in a shell of greater relative height with an inflated posterior, and an abreviated anterior. General flattening of the shell is positively correlated to an increase in relative foramen length.

(2) Diodora listeri (Orbigny) 1842

DESCRIPTION: These shells range to 4 cm in length. Form variation is minimal. The shell is intermediate in elevation. Curvature of the dorsal posterior profile is conservative to non-existent. The mid-portion of the basal margin is raised slightly.

The foramen is located just anterior of the shell center and is gently to moderately inclined at 7 to 28 degrees. It is oval to constricted in shape with a straight to horned profile.

This species is recognized by its robust ornamentation, expressed as 36 to 40 radiating ribs, every other rib is quite large. The basal margin of the shell is coarsely scalloped due to the ribbing pattern.

The exterior of the shell is usually buff to grey and white striped. The interior is white.

RANGE: Bermuda, Florida to West Indies. Intertidal and subtidal.

For this study _D._ _listeri_ was collected predominantly from the intertidal zone, 7 localities in the Florida Keys and 3 localities along the southeast coast of Florida. One sample from 27 meters of water in the Keys contained specimens of _D._ _listeri_.

MORPHOLOGIC MODEL: Variation in shell form among the 11 reference specimens of _D._ _listeri_ reveals an increase in curvature of the dorsal posterior of the shell related to decrease in anterior radii, 170 and A. Compare specimens number 5 and 38 to specimen number 35 on Plate 2. Curvature of the posterior is also related to decrease in relative foramen length.

Specimens of _D._ _listeri_ with an increased length of the 50 through 70 degree radii have a straighter foramen profile. Examine Plate 2.

(4) Diodora Sayi (Dall) 1900

Diodora sayi Dall, 1900, Science ix:914.

DESCRIPTION: Specimens in this sample range to 2 cm in length. Shells are moderately flat with extreme curvature of the dorsal posterior profile. The basal margin is also curved.

The foramen is located in the anterior-most third of the shell and is slightly to moderately inclined from 9 to 24 degrees. It is uncommonly long with an oval to constricted outline and a straight to horned profile.

The surface of the shell is sculptured with 65 to 75 radiating ribs. In some specimens, every other rib is accentuated. Ribbing causes a delicate crenulation along the basal margin of the shell.

The shell is uniformly white or cream colored.

This species is recognized by the extreme anterior location of the foramen and noticeable curvature of the posterior surface.

RANGE: Southeast Florida to Brazil. Subtidal habitat. Specimens of D. sayi for this study were collected from 4 localities

2 off the Atlantic Coast of Florida and at 2 in the Florida Keys from. Collections were made between 36 and 164 meters of water.

ANALYTICAL RESULTS: The sample of _D_. _sayi_ contained 7 shells, 5 of which were selected as reference specimens and digitized.

In Province 3, (Atlantic Coast of Florida), an increase in water depth resulted in:

1. a decrease in rib size.
2. a decrease in relative mass, predominantly from the anterior portion of the shell.
3. a relatively shorter foramen.

Examine Plate 3.

MORPHOLOGIC MODEL: Shell form variation among the 5 reference specimens of _D_. _sayi_ reveals that larger shells, example specimen number 4, have a horned foramen compared to the straight or peaked profile of the smaller shells, specimens number 29 and 31 on Plate 3. Those shells with a greater curvature of the dorsal posterior surface are generally taller, with shorter 110 to 130 degree anterior radii. Increased posterior curvature is also related to a broader foramen and an increased curvature of the basal margin. Note the basal curvature of specimens number 4 and 32 compared to specimens number 29 and 31. A longer foramen, relative to shell size, generally exhibits a horned profile as well as an increase in length of anterior radii, 110 through A, and decreased posterior radii, 30 through 50. Examine Plate 3.

(5) Diodora tanneri (Verrill) 1882

Diodora tanneri Verrill, 1882, P.U.S. Nat. Mus. (Aug.-Sept.,1882):315-343.

DESCRIPTION: This is the largest modern species of Diodora, growing to 6 cm in length. Variation in shell form is minimal. The curvature of the dorsal posterior profile is slight to non-existent. The shell rests flat on a plane surface with insignificant curvature of the basal margin.

The foramen is located almost two thirds distance from the posterior of the shell and is moderately inclined from 10 to 28 degrees. It is round to elliptical in shape with a straight to peaked profile.

The shell appears thin and fragile and is ornamented with 190 to 220 delicate ribs of equal size. The basal margin is finely crenulated at the termination of each rib.

The shell is uniformly white in color.

This species is recognized by its large adult size, broad foramen, and delicate ornamentation.

RANGE: Delaware Bay to Florida. Deep subtidal habitat.

Specimens of D. tanneri in this study were collected from 4 deep water localities. Two samples were from the Florida Keys, 1 from Georgia to Cape Hatteras, and one sample from north of Cape Hatteras, though distribution of this species is probably continuous along the Atlantic Coast. Collections were taken between 104 and 219 meters of water.

ANALYTICAL RESULTS: Of the 8 specimens of D. tanneri, 6 were selected as reference specimens and digitized.

Specimens from the more northern province, north of Cape Hatteras collected from 104 meters of water, specimens number 11 and 12, were smaller with fewer ribs than those found in deeper water in the Florida Keys, specimens number 7 and 15. See the figure illustrating rib number by latitude for all recent reference specimens in 'General Conclusions'.

MORPHOLOGIC MODEL: Larger specimens of D. tanneri have more ribs than do smaller individuals. Compare specimens number 12 and 15 on Plate 4. Increase in foramen inclination is related to a decrease in anterior radii, 110 through A and a relative shortening of the foramen. The posterior profile of D. tanneri is generally straight, but those individuals which display posterior curvature, specimens number 11 and 12, are individuals with shorter anterior radii. Examine Plate 4.

FOSSIL SPECIES

(A) D.nucula(Dall) 1892

Fissuridea nucula Dall, 1892, Wagner Free Inst. Sci. Trans. 3(2):426.

Fissuridea nuclea Gardner and Aldrich, 1919, Acad. Nat. Sci. Phila. Proc. 71:18.

Diodora nucula Olsson and Harbison, 1957, Acad. Nat. Sci. Phila. mon. 8:359.

DESCRIPTION: This shell is very small, and does not exceed 1 cm in length. There is little variation in shell form. It is high peaked with prominent curvature of the dorsal posterior profile. Curvature of the basal margin is negligible.

The foramen is located just anterior of the center of the shell and only slightly inclined at 4 to 11 degrees. It is broadly elliptical with a straight profile.

The shell is ornamented with 43 to 63 radiating ribs of equal size.

This species is recognized by its small adult size, tall spire, and extreme curvature of the posterior surface.

FOSSIL OCCURRENCE: Caloosahatchee, Duplin, and Waccamaw Formations (Olsson and Harbison, 1953). For stratigraphic sequence of Coastal Plain formations see

Figure 11. For collection localities of fossil specimens refer to Appendix C.

For this study D. nucula was collected from 9 Pliocene localities from Florida to North Carolina. Formations from which specimens were collected include the Duplin, Waccamaw, and Calloosahatchee.

ANALYTICAL RESULTS: Of the 56 specimens measured in this sample, 3 were selected as reference specimens and digitized.

Latitude and geologic age are highly correlated throughout the distribution of D. nucula, so they will not be distinguished. Specimen number 61F, collected from Pliocene Duplin of South Carolina, has more ribs (63) and a less inflated shell than the specimen number 24F with 43F ribs from the southern-most end of the species' range (Pliocene Caloosahatchee of Florida). Examine Plate 5.

MORPHOLOGIC MODEL: Variation in form among the 3 reference specimens of D. nucula does not follow the D. cayenensis model closely. As a rule, this species has a very tiny shell. Larger specimens show no significant increase in ribs or foramen inclination, but do exhibit a relatively smaller foramen. Note specimens number 24F and 61F on Plate 5. An increase in foramen inclination is present in the flatter shell which shows a decrease in anterior radii, 170

EPOCH		TIME (my)	NEW JERSEY	MARYLAND	VIRGINIA	N.CAROLINA	S.CAROLINA	GEORGIA	FLORIDA
PLEISTOCENE	L	-1							Ft.Thompson
	E	-2				Croatan Formation	Waccamaw Formation		Caloosahatchee Formation
PLIOCENE	Late	-3			"Yadkin Beds"				
	Early	-4			Yorktown Formation (Upper Part)		Duplin Formation		Tamiami Fm. Pinecrest Member
		-5			(Lower Part)				
MIOCENE	Late	-6							
		-7							
		-8		Eastover Fm. / Cobham Bay Member					
		-9							
		-10		Claremont Manor Member					
		-11							
	Middle	-12		St. Mary's Formation					
		-13		"Cove Point"					
				Choptank Formation					
		-14	Kirkwood Formation	Calvert Formation		Pungo River Formation			
	Early (in part)	-15							
		-16							Chipola Formation
		-17							

From (Campbell et. al., 1975, and Ward and Blackwelder, 1980)

Figure 10

and A. Specimens with an increase in dorsal posterior curvature are generally taller shells. They are characterized by fewer ribs and an increase in length of the anterior portion of the shell. Compare specimen number 24F to specimen number 61F. The shorter 110 anterior radius is also characteristic of the shell with the smaller foramen. Examine Plate 5.

(B) D.chipolana (Dall) 1892

Fissuridea chipolana Dall, 1892, Wagner Free Inst. Sci. Trans. 3(2):426.

Diodora chipolana Mansfield, 1937, Fla. Dept. Cons. Geol. Bull. 15:186.

DESCRIPTION: This shell has been observed to grow to 4 cm in length. Morphology changes with age (Gardner, 1948). Smaller specimens have an elliptical base and grow to a pear shape that is transversely compressed in the anterior of larger specimens. The shell is only slightly elevated with moderate cuvature of the posterior.

The foramen is located anterior of the center of the shell and is inclined at 16 to 38 degrees. It is oval in shape and straight to peaked in profile.

The shell is ornamented with 45 to 55 ribs, every other one more prominent. Larger shells are more robustly ornamented with fewer ribs.

This species is recognized by its robust ornamentation and alternating rib size.

FOSSIL OCCURRENCE: Chipola (Dall, 1892, Mansfield, 1937, and Gardner, 1948), Yorktown (Gardner, 1948), Duplin (Dall, 1892 and Gardner, 1948), and Caloosahatchee Formations.

For this study _D. chipolana,_ was collected from two localities, Early Miocene Chipola Formation of northern Florida and Late Pliocene Caloosahatchee Formation of central Florida.

ANALYTICAL RESULTS: An insignificant number of specimens were available for analysis to draw intraspecific conclusions regarding shell form variation.

(C) _D. carolinenesis_ (Conrad) 1875

Fissurella carolinensis Conrad, 1875, N. Carolina Geol. Surv. Rept. A:22.

Fissuridea carolinensis Pilsbry and Johnson, 1892, Nautilus, 5:106.

Diodora carolinensis Gardner, 1948, U.S.G.S. Prof. Pap. 199B, p.183.

DESCRIPTION: The shell is relatively small; maximum size just over 1 cm. Variability within this species could not be evaluated as only one specimen was available for this study. It is a low shell with slight curvature of the posterior. The basal margin rises only slightly in the center.

The foramen is located anterior of the center of the shell and is moderately inclined at 16 degrees. It is constricted in shape with a peaked profile.

The shell is sculptured with 39 prominant, flat sided ribs, equal in size, causing a noticeably scalloped margin at the base.

This species is recognized by its 39 broad, equal sized ribs.

FOSSIL OCCURRENCE: Yorktown, Duplin, Waccamaw, Caloosahatchee (Gardner, 1948), and Pinecrest Formations. Only one specimen of D. carolinensis was available for study. This specimen was from the Early Pliocene Pinecrest Formation of Florida.

(D) D.cayenensis is described as a recent shell.

ANALYTICAL RESULTS: Of the 21 fossil specimens studied, 2 were selected for reference and digitized. When combined with the recent D. cayenensis specimens and analyzed, geologic age showed no correlation to morphologic variation.

(E) D.carditella(Dall) 1892

Fissuridea carditella Dall, 1892, Wagner Free Inst. Sci. Trans. 3(2):427.

Diodora carditella Olsson and Harbison, 1953, Acad. Nat. Sci. Phila. 8:358.

DESCRIPTION: This shell grows to 3 cm in length. Variability within the species is noticeable but slight. The shell is consistently low with varying degrees of posterior curvature The basal margin curves in proportion with the curvature of the dorsal posterior profile.

The foramen is near the center of the shell and only slightly inclined at 8 to 20 degrees. It is oval to constricted in shape with a horned profile. The horns on either side of the foramen are the highest points on the shell.

There are 55 to 75 radiating ribs crossed with concentric ridges, forming a pattern resembling small inverted hearts fitting into one another.

This species is recognized by its low shell profile, horned foramen, and distinctive ornamentation.

FOSSIL OCCURRENCE: Waccamaw and Caloosahatchee Formations (Dall, 1892 and DuBar, 1958).

Specimens in this study were collected from 8 Late Pliocene localities of the Caloosahatchee and Waccamaw Formations of Florida and South Carolina, respectively.

ANALYTICAL RESULTS: There were 53 shells in this sample, 10 of which were selected as reference specimens and digitized.

Specimens from higher latitudes (Waccamaw of South Carolina) display an increase in foramen width and area when compared to specimens collected further south (Caloosahatchee of Florida). Both formations are Pliocene in age. Compare specimens number 7F and 16F to specimens number 14F and 17F on Plate 7.

Similarity can be seen in variation in foramen shape correlated to latitude, when compared to the sample of recent diodorids.

MORPHOLOGIC MODEL: Among the 10 reference specimens of *D. carditella*, shells with a smaller foramen inclined at a greater angle display a shorter anterior section of the shell. Compare specimens number 16F and 17F to specimens number 7F and 14F on Plate 7.

(G) *D. griscomi* (Conrad) 1834

Fissurella griscomi Conrad, 1834, Jour. Acad. Nat. Sci. Phila. vii:143.

Fissuridea griscomi Dall, 1892, Trans. Wagner Free Inst. Sci. 3(2):425.

Diodora griscomi Vokes, 1957, Md. Dept. Geol. Mines and Water Res. Bull. 20.

DESCRIPTION: This species grows to 3 cm in length. Variability of shell form is minimal. They are medium to high peaked with a marked curvature of the dorsal posterior profile and an abbreviated anterior. The sides are laterally compressed giving the shell a narrow appearance.

The foramen is in the anterior portion of the shell and inclines at 25 to 30 degrees. It is oval to constricted in form and straight to horned in profile. The internal callus surrounding the foramen is deeply concave on the posterior end.

The shell is sculptured with 92 to 98 small, somewhat irregular ribs.

This species is recognized by its high spire, curved posterior, abreviated anterior, narrow appearance, slightly irregular ribbing, and the shape of the internal callus around the foramen.

FOSSIL OCCURRENCE: Kirkwood (Richards and Harbison, 1942), Calvert and Choptank Formations (Martin, 1904, Richards, 1942, Vokes, 1957, and Gilbert, 1962).

For this study _D. griscomi_ was collected from 3 localities of the Early Miocene Kirkwood Formation of New Jersey.

MORPHOLOGIC MODEL: The sample of _D. griscomi_ included 64 specimens, 5 of which were selected for reference and digitized. D. griscomi, has a tall, narrow shell with significant posterior curvature. Of the 5 reference specimens, those individuals that display a relatively longer anterior also have more ribs. Compare specimen number 8F to specimens number 52F,53F, and 54F on Plate 9. This slightly larger anterior is in turn related to a smaller, more narrow and horned foramen, and an extension of the posterior radii, 20 to 50 degrees.

(F) Diodora sp., labelled D.griscomi in Smithsonian collections.

DESCRIPTION: This shell grows to 3 cm in length. There is only slight variability of shell form within this species. It is somewhat high peaked with a gentle curvature of the dorsal posterior profile. This form is not as tall or as curved posteriorly as D.griscomi and has a more extended anterior.

The foramen is located anterior of the center of the shell and is medially inclined at 16 to 24 degrees. It is oval to constricted in shape with a straight to horned profile.

The ornamentation is expressed as 97 to 103 fine, equal sized ribs. There are slightly fewer ribs with less regularity in size on D.griscomi.

Another consistent difference between D.griscomi and this form is the shape of the callus that surrounds the foramen on the interior of the shell. In this form, it is not deeply concave at the posterior end as on D. griscomi, but instead gently convex. See Figure 6.

Figure 12 is a representation of the parameters calculated and used in the Theta Rho Analysis, comparing D.griscomi and Diodora sp.. The most outstanding feature depicted in this graph establishing the incongruity between these forms is the abreviation of the anterior portion of the shell and more anterior location of the foramen of D.griscomi.

FOSSIL OCCURRENCE: Diodora sp. was collected from 2 localities of the Early Miocene Kirkwood Formation of New Jersey.

MORPHOLOGIC MODEL: The sample of Diodora sp. included 35 specimens, 5 of which were selected as reference and digitized. There is no relationship between shell size, rib number or foramen orientation among the 5 reference specimens of Diodora sp.. However, those shells with greater foramen inclination do have a shorter 110 anterior radius. Curvature of the dorsal posterior surface is positively correlated to curvature of the basal margin. Compare specimens number 9F and 58F to specimens number 56F

Figure 11: Theta Rho comparison of *D. griscomi* and *Diodora sp*. morphologies. For a review of Theta Rho Analysis see Methods section. Radii orientation is illustrated in Figure &rad..

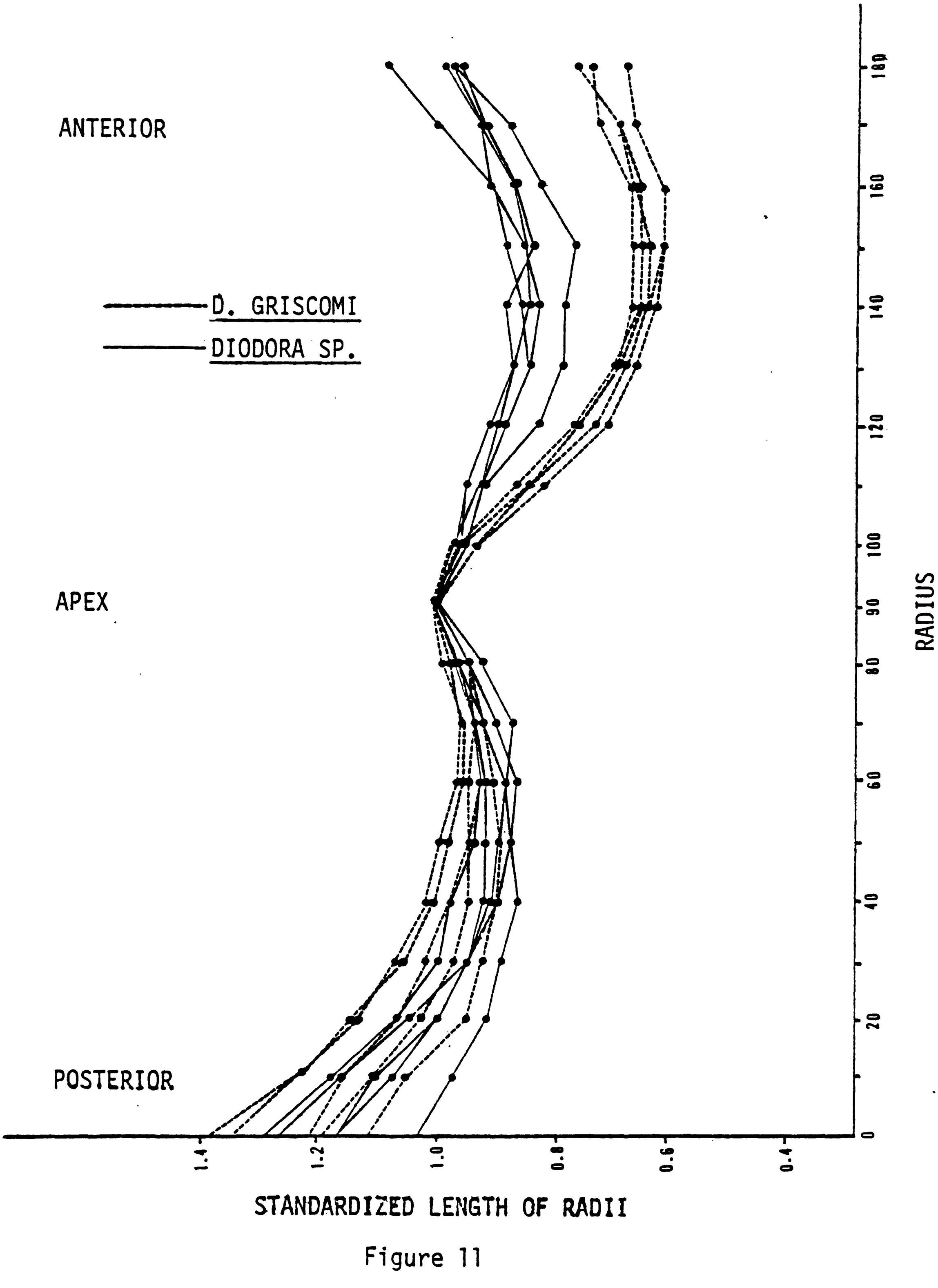

ANTERIOR
APEX
POSTERIOR
D. GRISCOMI
DIODORA SP.
RADIUS
0
20
40
60
80
90
100
120
140
160
180
1.4
1.2
1.0
0.8
0.6
0.4
STANDARDIZED LENGTH OF RADII

Figure 11

and 59F on Plate 8.

(H) D.alticosta (Conrad) 1834

Fissurella alticosta Conrad, 1834, Jour. Acad. Nat. Sci. Phila. 7:142.

Fissurella alticostata Meek, 1864, Miocene Creek List, Smith. Misc. Coll. (183): 14.

Fissuridea redimicula var. alticosta Dall, 1892, Trans. Wagner Free Inst. Sci. 3(2):425.

Diodora alticosta Martin, 1904, Md. Geol. Surv. Bull. Mio. p.266-267.

DESCRIPTION: These shells grow to 3.5 cm in length. Shell form varies significantly and grades to that of D.redimicula in relative height and foramen location. Dall (1892) records this form as a variety of D.redimicula. D. alticosta is generally higher peaked with a moderate curvature of the posterior surface.

The foramen is located near the center of the shell and is inclined intermediately to steeply at 16 to 39 degrees. It is broadly elliptical in shape with a straight to peaked profile.

The shell is sculptured with 118 to 159 fine radiating ribs. Often every fourth rib is slightly accented.

This species is recognized by the near center location of the foramen and the high spire.

FOSSIL OCCURRENCE: D. alticosta was collected from 5 localities of the Late Miocene Eastover Formation of Virginia.

MORPHOLOGIC MODEL: Larger of the 4 reference specimens of D. alticosta possess a greater number of ribs, a wider foramen relative to shell size and longer 30 through 50 degree posterior radii than the smaller specimens. Compare specimen number 4F to specimen number 44F on Plate 10. The shells with a greater inclination of the foramen also have an abreviated 110 degree radius. In this sample, length of the posterior radii is positively correlated to length of anterior radii and varies in proportion uniformly.

(I) D.caloosaensis(Dall) 1892

Fissuridea caloosaensis Dall, 1892, Trans. Wagner Free Inst. Sci. 3(2):427.

Diodora caloosaensis Olsson and Harbison, 1953, Acad. Nat. Sci. Phila. mon. 8:358.

DESCRIPTION: This shell extends to 5 cm in length. The shell is distinctively low with minimal curvature of the dorsal posterior.

The foramen is located in the anterior half of the shell where it is only slightly inclined at 8 to 17 degrees. It is oval to constricted in shape with a horned profile, the points of which represent the highest points on the shell.

The shell is usually extremely thick and sculptured with fine thread-like ribs that are bonded to form larger ribs with flat summits. This makes them difficult to distinguish and count but there appear to be 85 to 95 of these larger ribs.

This species is unique because of its ornamentation.

FOSSIL OCCURRENCE: D. caloosaensis was collected from 2 localities of the Florida Pliocene, in the Pinecrest (Dall, 1892, and DuBar, 1958) and Caloosahatchee Formations.

ANALYTICAL RESULTS: Of the 5 specimens measured for this sample, 4 were used as reference shells and digitized.

As latitude and geologic age closely correlate in the analysis, the two cannot be distinguished. The more northern Florida locality of older Pinecrest age (Lower Pliocene) contains the shell with a more extended anterior and less rounded apical silouette compared to specimens from the younger Caloosahatchee Formation (Upper Pliocene). Compare specimen number 2F to specimens number 10F, 11F, and 12F on Plate 11.

MORPHOLOGIC MODEL: Similar to form variation among recent _D. cayenensis_ sample, larger of the 4 reference specimens of _D. caloosaensis_ have an increased curvature of the dorsal posterior profile, an increased length of the posterior 30 through 70 degree radii, and an abreviated anterior from the 170 to A radii. Relatively heavier and wider shells have a larger anterior 120 to 160 degree radii and a slightly smaller anterior 170 to A, and posterior P radii. Wider shells also display an increase in length of the posterior radii, 30 through 70 degrees, a greater posterior curvature, and a slightly more pronounced curvature of the base. Compare specimen number 2F to specimens number 10F,11F, and 12F on Plate 11. Individuals with greater curvature of the posterior also have fewer ribs and greater curvature of the basal margin. Specimen number 2F on Plate 11 has more ribs, a greater anterior portion from the 130 to A radii, and a decreased posterior portion from 30 to 50 degrees than specimen numbers 10F,11F, and 12F.

(J) _D. marylandica_ (Conrad) 1841

Fissurella marylandica Conrad, 1841, Proc. Acad. Nat. Sci. Phila. 1:31.

Fissurella nassula Conrad, 1845, _Fossils of the Medial Tertiary_, 3:78.

Fissuridea catilliformis Dall, 1892, (not *F.catilliformis* Rogers), Trans. Wagner Free Inst. Sci. 3(2):425.

Diodora marylandica Vokes, 1957, Md. Dept. Geol. Mines and Water Res. Bull. 20.

DESCRIPTION: This shell grows to 5 cm in length. Variation in form within the species is minimal. The shells are of medium height with slight to intermediate curvature of the posterior surface.

The foramen is noticeably larger than any other species. It is located just anterior of the center of the shell and is inclined moderately at 17 to 29 degrees. It is elliptical in shape with a peaked profile.

Shell sculpture is expressed as 145 to 165 delicate radiating ribs, the fourth one of which is often but inconsistently accented.

This species is recognized by its unusually large foramen.

FOSSIL OCCURRENCE: Specimens of *D. marylandica* in this study were collected from Early to Middle Miocene deposits of Maryland, in the Calvert and Choptank Formations. (Pilsbry and Johnson, 1892, Martin, 1904, Conrad, 1941, Vokes, 1957, and Gilbert, 1962).

ANALYTICAL RESULTS: There were 72 shells in this sample, 7 of which were selected as reference specimens and digitized.

Shells from older, northern extremities of the species range (Middle Miocene Calvert Formation of Maryland), are smaller in size compared to those from the younger Upper Miocene Eastover Formation of Virginia. See Appendix E.

MORPHOLOGIC MODEL: Larger specimens of the 7 reference specimens of D. marylandica have an increased curvature of the posterior profile. Compare specimen number 60F to specimen number 48F on Plate 12. Individuals with an increased angle of inclination of the foramen have a shorter anterior section between the 110 and 130 degree radii.

(K) & (L) D. redimicula (Say) 1824

Fissurella redimicula Say, 1824, Jour. Acad. Nat. Sci. Phila. 4:132.

Fissuridea redimicula Dall, 1892, Trans. Wagner Free Inst. Sci. 3(2):425.

Diodora redimicula Gardner, 1948, U.S.G.S. Prof. Pap. 199B, p.182.

DESCRIPTION: This species grows to 5 cm in length. Variability within the species is great. Some specimens grade toward D. alticosta, D. catilliformis and D. marylandica.

The shell is low to moderately elevated with an intermediate degree of curvature of the posterior portion.

The foramen is located just anterior of the center of the shell and is inclined moderately to steeply at 18 to 34 degrees. It is a small to average ellipse with a straight to peaked profile. The size of the foramen is the primary distinguishing characteristic separating this morphology from that of *D. marylandica*.

The shell is sculptured with 118 to 167 fine radiating ribs. Those with the fourth rib accented are the variety, *D. redimicula virgilina* (Gardner).

This species is recognized by its ornamentation and foramen size and location.

FOSSIL OCCURRENCE: Specimens of *D. redimicula* for this study were collected from 24 localities from Virginia to Maryland in deposits ranging from Middle Miocene to Early Pliocene in age. Formations from which they were collected include the St. Mary's (Martin, 1904), Eastover, and Yorktown (Gardner, 1948).

ANALYTICAL RESULTS: *D. redimicula* displays a great deal of form variability within the species, illustrating little gradation between morphologic characters. Specimens can be segregated into two primary morphs; 1.) variety *D. redimicula virgilina* (Gardner) with every fourth rib accentuated and a more inflated lateral shell profile, and 2.) the remaining D. redimicula specimens which display a more pointed apex and more regular ornamentation. Analysis of these samples separately still did not yield patterns of shell variation.

(M) D.catilliformis (Rogers and Rogers) 1837

Fissurella catilliformis Rogers and Rogers, 1837, Amer. Philos. Soc. 5:332.

Diodora catilliformis Mansfield, 1930, Fla. Geol. Bull. 3:137.

DESCRIPTION: This species grows to be quite large, extending to 6.5 cm in length. Variability of form within this species is moderate with some specimens grading toward D.redimicula. They are distinguished mainly by their low shell profile, and ornamentation. There is a noticeable curvature of the posterior surface in the larger specimens.

The foramen is located just anterior of the center of the shell and is inclined slightly to moderately at 6 to 23 degrees. It is a broad ellipse in form with a straight to peaked profile.

The shell is ornamented with 133 to 195 equally sized ribs that range from delicate to intermediate in width.

This species is recognized by its low shell profile and uniform ornamentation.

FOSSIL OCCURRENCE: Specimens of D. catilliformis for this study were collected from 8 localities from North Carolina to Virginia, from the Late Miocene Eastover and the Early Pliocene Duplin Formations.

MORPHOLOGIC MODEL: The sample of D. catilliformis included 27 specimens, 6 of which were selected for reference and digitized. Larger of the 6 reference specimens of D. catilliformis express greater curvature of the basal margin. Note the gradation among specimens number 5F,28F,29F, and 30F on Plate 14. Shells that are relatively taller generally have more ribs and a shorter posterior P radius. Compare specimen number 28F to specimen number 30F on Plate 14. Increase in foramen inclination is related to increase in posterior curvature and a decrease in the anterior radius at 110 degrees. Compare specimens number 29F and 5F to specimen number 30F on Plate 14. Those shells with a longer anterior, radii 110 through A, have a relatively heavier shell for their size and a longer foramen.

GENERAL CONCLUSIONS REGARDING DIODORA

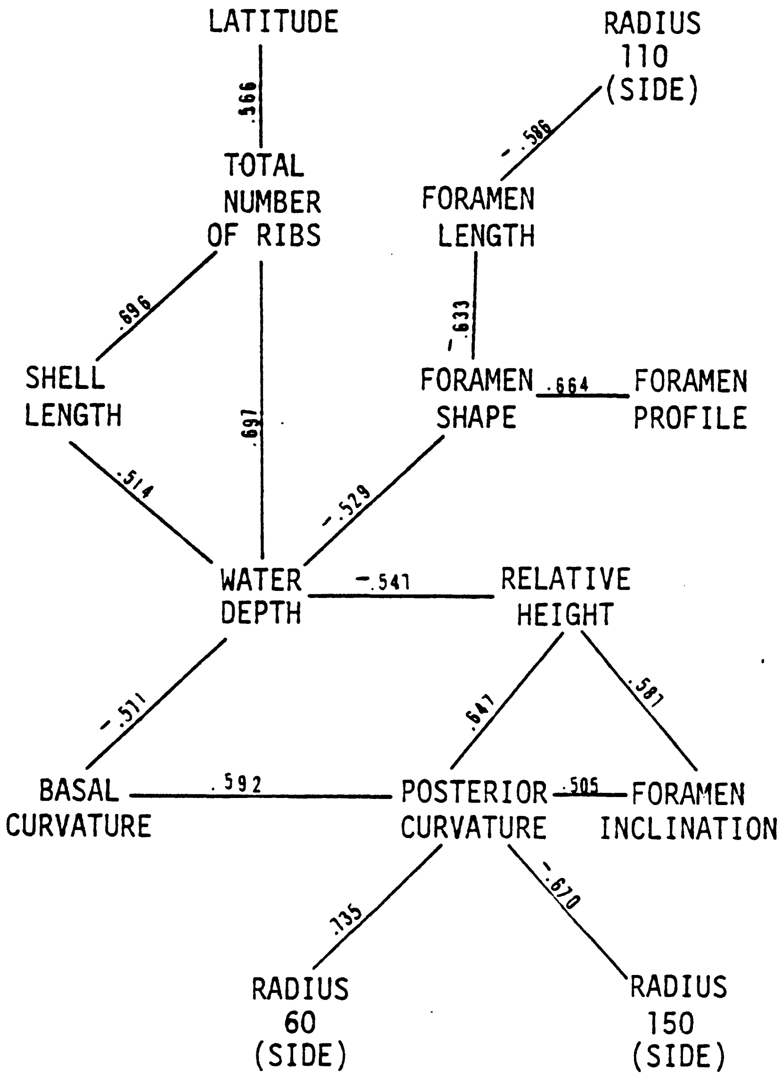
RECENT SPECIMENS

Results of Principal Components Analysis

Results of the Principal Components Analysis for the data set including all recent reference specimens reveals that the greatest amount of variation is in shell shape. The first Principal Component accounts for 29-43 per cent of the variance, depending on the standardizing unit used. The lateral view data analysis relates shell shape to foramen size. Specimens with a more curved posterior profile generally have a more curved basal margin. Those individuals that have a slight inflation of the anterior profile also have longer foramens. The second Principal Component of the lateral view data accounts for 21-24 per cent (50-67 per cent cumulative) of the variance and correlates shell height to foramen inclination. Relatively taller shells display a greater inclination of the foramen.

The first Principal Component of the apical view data (33-36 per cent of the variance) illustrates the gradation in basal shell form from elliptical to egg shaped. As the anterior dimensions become shorter, posterior dimensions lengthen. The second Principal Component of the apical view data accounts for 26-28 per cent (59-64 per cent cumulative) of the variance and relates latitude, shell size, and rib number. Specimens collected from more northern localities are generally larger and display more ribs. The third component accounts for 7-8 per cent (68-72 per cent cumulative) of the variance and relates water depth to foramen shape. Specimens from deeper water generally have a broader foramen than those collected from intertidal habitats.

Relationships between these parameters are best illustrated in the Rho Group diagram in Figure 14.



RECENT REFERENCE SPECIMENS

Figure 12

Specimens Grouped by Water Depth

The subtidal sample along the Atlantic Coast contained all four species, *D. cayenensis*, *D. listeri*, *D. sayi*, and *D. tanneri*. Collections were taken from 3 to 219 meters depth. Specimens from higher latitudes in Province (5) displayed:

1. an increase in total number of ribs on the shell. See Figure 15.
2. an increase in mean shell size. See Table 2.
3. a decrease in relative shell height. See Table 2.

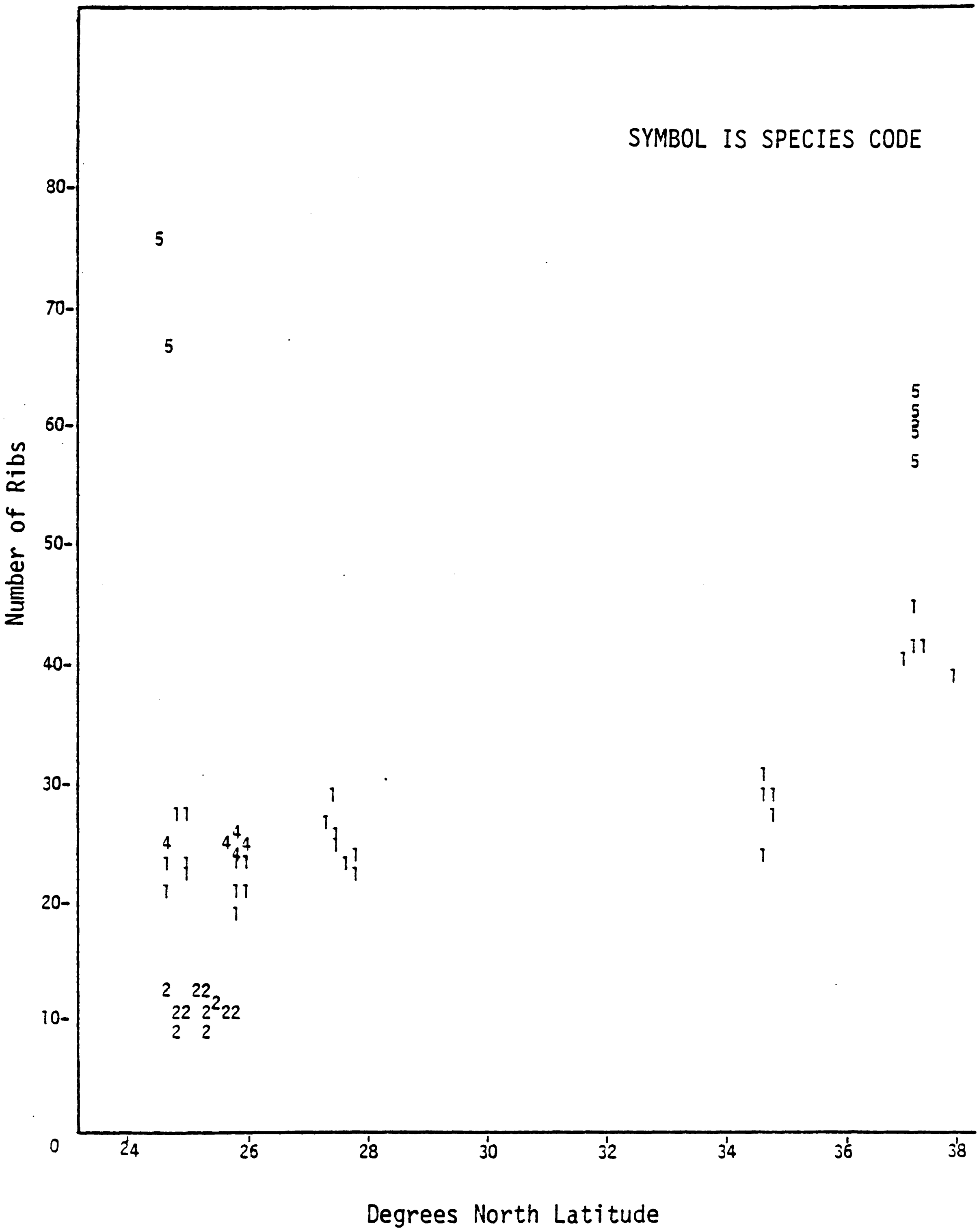

SYMBOL IS SPECIES CODE
Number of Ribs
0
10-
20-
30-
40-
50-
60-
70-
80-
24
26
28
30
32
34
36
38
Degrees North Latitude

Figure 13

Table 2: Statistics for Recent Diodorids

	FLORIDA GULF		FLORIDA KEYS		FLORIDA EAST COAST		GEORGIA-HATTERAS		NORTH OF HATTERAS	
	INTER-TIDAL	SUB-TIDAL	INTER-TIDAL	SUB-TIDAL	INTER-TIDAL	SUB-TIDAL	INTER-TIDAL	SUB-TIDAL	INTER-TIDAL	SUB-TIDAL
LATITUDINAL RANGE (degrees no.)	27.36-27.81	24.55-29.55	24.55-25.07	24.45-25.00	25.81-25.85	25.71-28.45	34.20-34.71	34.00-35.00	37.11-37.98	37.00
WATER DEPTH RANGE (m)	1.00	10.10-91.40	1.00	27.00-219.00	1.00-1.83	14.63-109.73	1.00-2.30	4.00-40.00	1.00	104.00
SHELL LENGTH RANGE (mm)	19.15-26.45	11.91-23.40	17.10-35.25	5.85-55.45	6.10-28.45	4.20-25.10	15.15-23.85	5.00-34.00	25.40-44.05	40.00-46.40
MEAN L	23.64	18.50	26.38	17.99	21.60	13.82	20.25	13.50	32.36	43.16
STAND. DEV.	3.23	5.93	4.77	14.91	5.67	5.70	4.00	6.88	6.31	3.01
SHELL WIDTH RANGE (mm)	12.60-19.10	7.99-15.10	11.00-23.20	3.50-37.00	3.65-18.20	2.70-20.40	9.90-16.10	3.00-24.00	17.00-31.15	26.65-29.25
MEAN W	15.64	11.98	17.44	11.60	13.84	9.04	13.53	8.73	22.42	28.20
STAND. DEV.	2.39	3.63	3.34	9.96	3.70	4.51	2.83	4.59	4.82	1.32
SHELL HEIGHT RANGE (mm)	9.60-13.00	7.10-9.80	5.95-15.25	2.10-17.70	2.85-13.10	1.60-10.40	5.80-10.45	2.00-14.00	10.10-19.40	12.25-14.45
MEAN HL	11.11	8.80	10.97	7.03	9.18	5.19	8.85	5.96	13.42	14.10
STAND. DEV.	1.45	1.48	2.51	5.41	2.60	2.51	2.09	2.86	2.99	1.26
HEIGHT/LENGTH RANGE	.397-.567	.420-.596	.332-.515	.319-.580	.376-.473	.268-.490	.380-.490	0.36-0.56	.370-.470	.310-.360
MEAN HLL	.474	.495	.413	.396	.425	.368	.433	.436	.413	.328
STAND. DEV.	.061	.091	.042	.066	.033	.057	.048	.035	.035	.024
NUMBER OF SPECIMENS IN SAMPLE	7	3	30	8-16	15-17	11-20	2-4	15-37	9	4

Specimens Grouped By Province

Recent specimens were grouped by oceanographic province from which they were collected and analyzed along a water-depth transect. Compared to intertidal specimens, subtidal individuals displayed:

1. a relatively smaller mean size. This relationship is exhibited in provinces (2) through (4), where *D. tanneri*, the largest and deepest water species was not collected (Florida Gulf Coast and the Atlantic Coast north to Cape Hatteras, N.C.) in specimens collected as deep as 164 meters. Species included are *D. cayenensis*, *D. listeri*, and *D. sayi*. See Table 2.
2. a longer posterior portion of the shell. This feature is exhibited only in Province (3), (Atlantic Coast of Florida) where *D. cayenensis* and *D. sayi* were collected to a depth of 82 meters. See Figure 16.
3. a lower mean relative shell height. This feature is exhibited in Provinces (1), (3), and (5), (Florida Keys, Atlantic Coast of Florida, and Cape Hatteras, N.C. to the Chesapeake Bay). *D. cayenensis*, *D. listeri*, *D. sayi*, and *D.tanneri* are included. These specimens were collected to a depth of 219 meters. See Table 2.

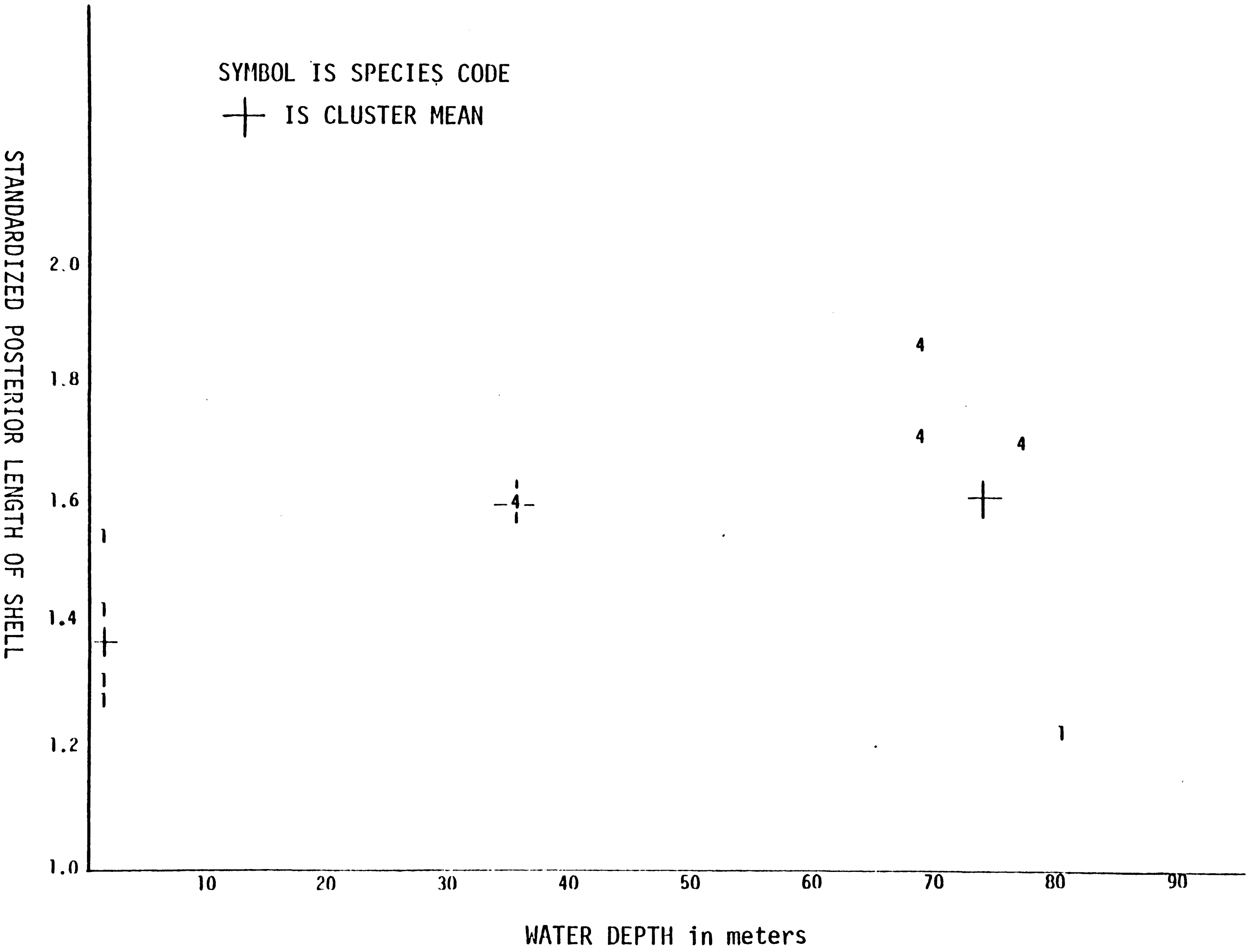

SYMBOL IS SPECIES CODE
+ IS CLUSTER MEAN
STANDARDIZED POSTERIOR LENGTH OF SHELL
2.0
1.8
1.6
1.4
1.2
1.0
10
20
30
40
50
60
70
80
90
WATER DEPTH in meters
1
1
1
1
4
4
4
4
1

Figure 14

FOSSIL SPECIMENS

Results of the Principal Components Analysis for the data set including all fossil reference specimens reveals that the greatest amount of variation within this sample occurs in shell shape correlated to latitude and total number of ribs. The first Principal Component accounts for 34-42 per cent of the variance, depending on the standardizing unit used. Specimens collected from higher latitudes are characterized by having a greater number of ribs. Relatively taller shells have a greater number of ribs, greater angle of inclination of the foramen and a slightly decreased size of the anterior portion of the shell. Lateral view data reveals an inflation of the posterior portion of the shell and a compression of the anterior portion in higher latitudes. The second component accounts for 24-27 per cent (58-69 per cent cumulative) of the variance and is composed of unstandardized parameters which represent the actual shell size factor.

Relationships between these parameters are illustrated in the Rho Group diagram in Figure 17. See also Figures 18 and 19.

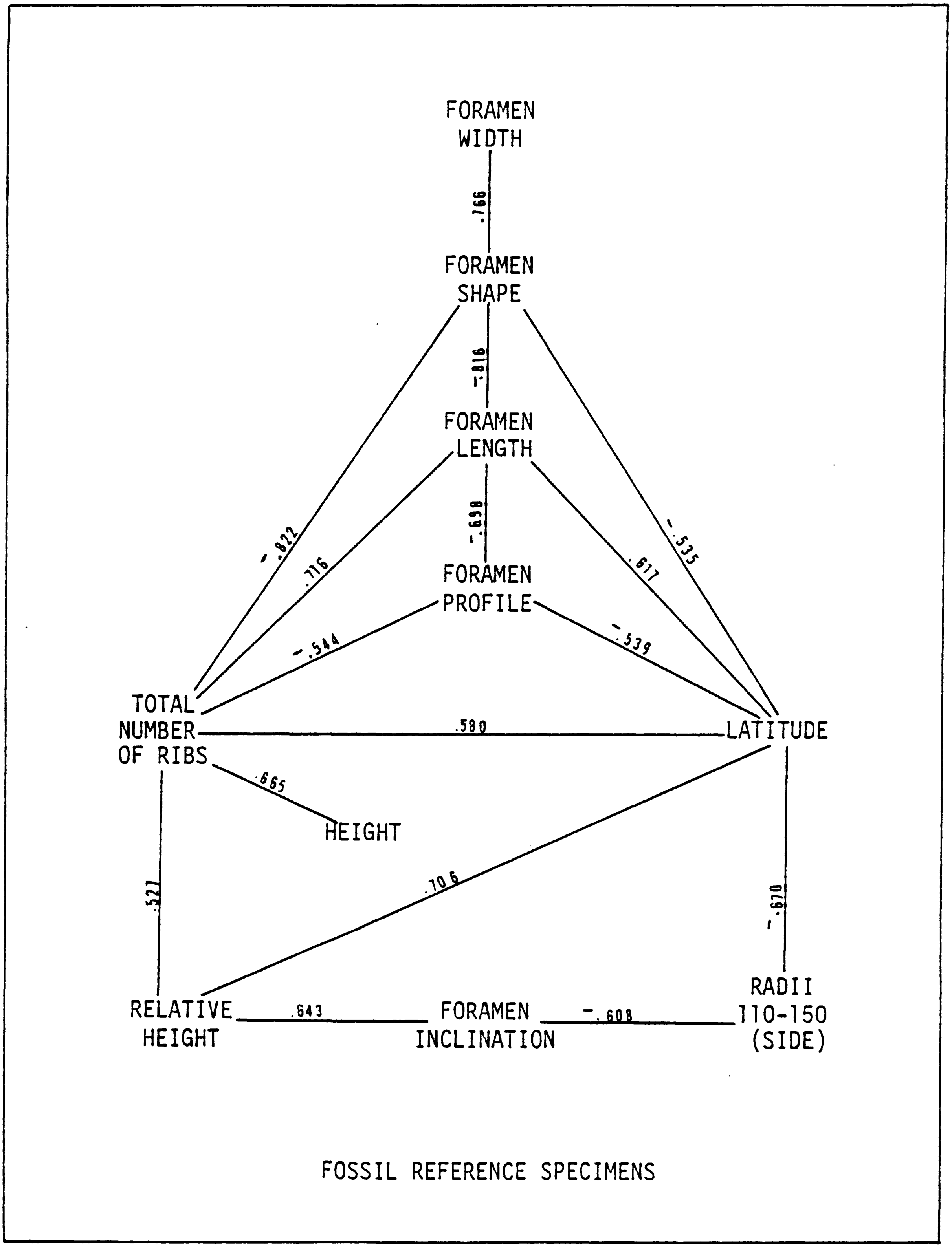

FORAMEN WIDTH
.166
FORAMEN SHAPE
-.816
FORAMEN LENGTH
-.698
FORAMEN PROFILE
-.822
.716
-.544
-.535
.617
-.539
TOTAL NUMBER OF RIBS
.580
LATITUDE
.665
HEIGHT
.527
.706
-.670
RELATIVE HEIGHT
.643
FORAMEN INCLINATION
-.608
RADII 110-150 (SIDE)
FOSSIL REFERENCE SPECIMENS

Figure 15

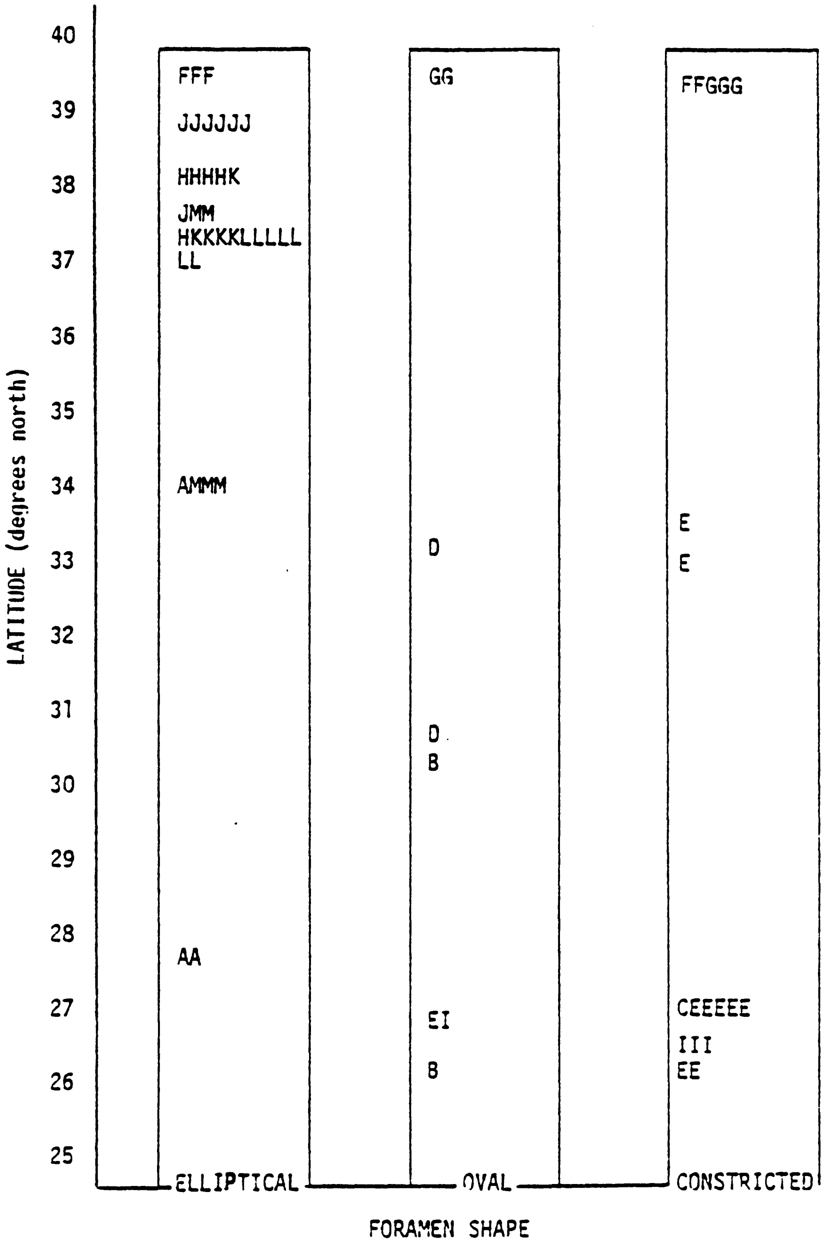

LATITUDE (degrees north)
40
39
38
37
36
35
34
33
32
31
30
29
28
27
26
25
FFF
JJJJJJ
HHHHK
JMM
HKKKKLLLLL
LL
AMMM
AA
GG
D
D
B
EI
B
FFGGG
E
E
CEEEEE
III
EE
ELLIPTICAL
OVAL
CONSTRICTED
FORAMEN SHAPE

Figure 16

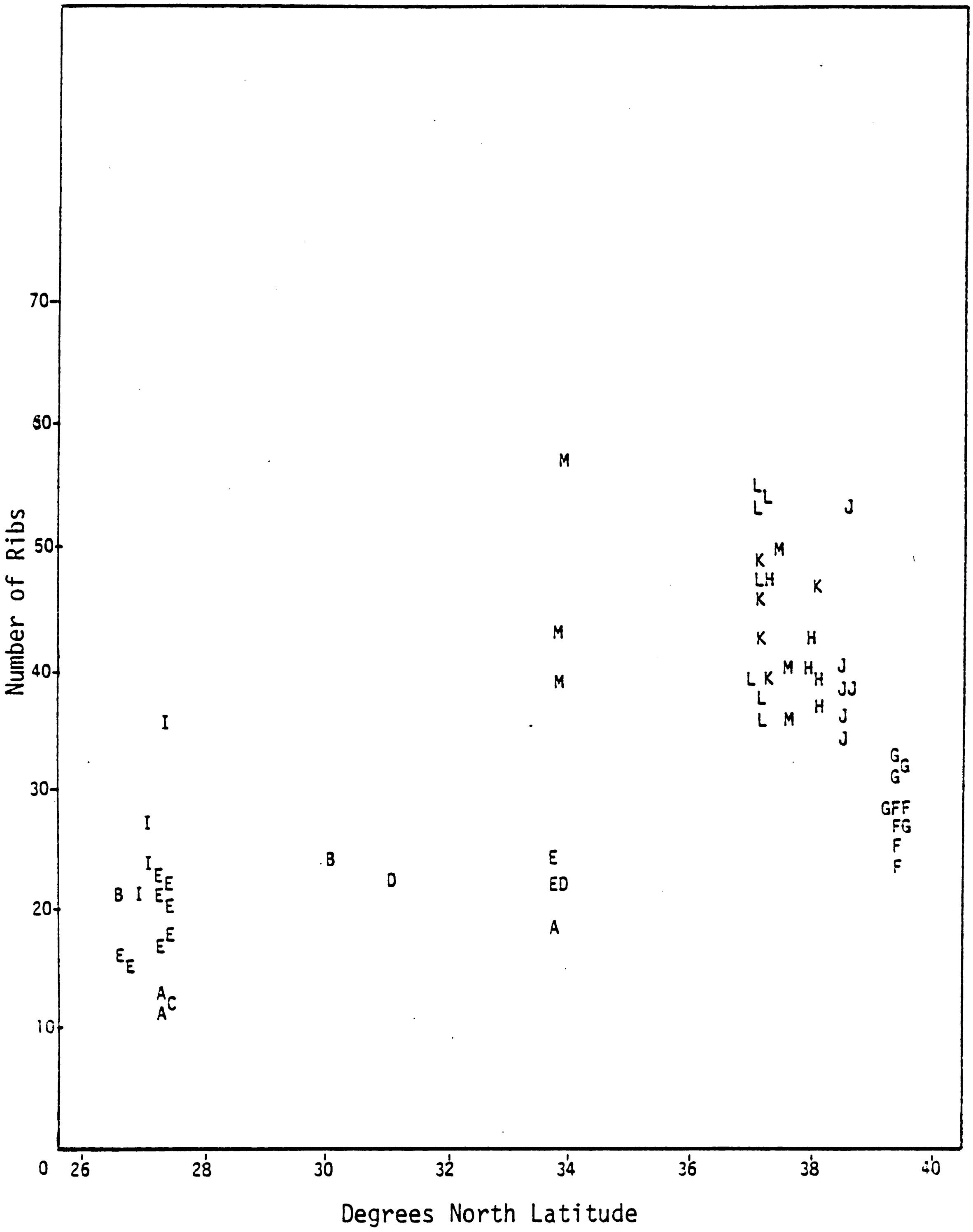

Number of Ribs
70
60
50
40
30
20
10
0
26
28
30
32
34
36
38
40
Degrees North Latitude
A B C D E F G H I J K L M

Figure 17

TAXONOMIC DISCRIMINATION

Species of *Diodora* are differentiated primarily by characteristics of the shell, as is common practice for most molluscs. The most obvious feature of the shell is ornamentation, expressed as many radiating ribs of varying sizes and numbers. Other distinctive features include 1.) location and shape of the foramen, 2.) general shell shape, and 3.) shell coloration.

Cluster Analysis of *Diodora* specimens, grouping recent reference specimens by 1.) rib size and number, 2.) foramen shape and location and 3.) curvature of the posterior, resulted in a clustering of specimens by species. See Figure 20. Specimens of *D. sayi* were included with the *D. cayenensis* cluster, attributed to the presence of ribs on the *D. sayi* specimens, similar in size to *D. cayenensis* ornamentation. The location of the foramen and degree of posterior curvature does, however, identify these specimens as *D. sayi*. *D. listeri* and *D. tanneri* were segregated in discrete groups, lending credence to the validity of the taxonomic criteria.

Foramen shape and general shell morphology remain consistent for all *D. cayenensis* specimens collected along the Atlantic Coast. Specimens of *D. cayenensis* from Province (5), North of Cape Hatteras, however, possess a

Figure 18: Dendrogram of cluster analysis of recent reference specimens. First column of numbers is order of data observations, second column is specimen number, third column is species code.

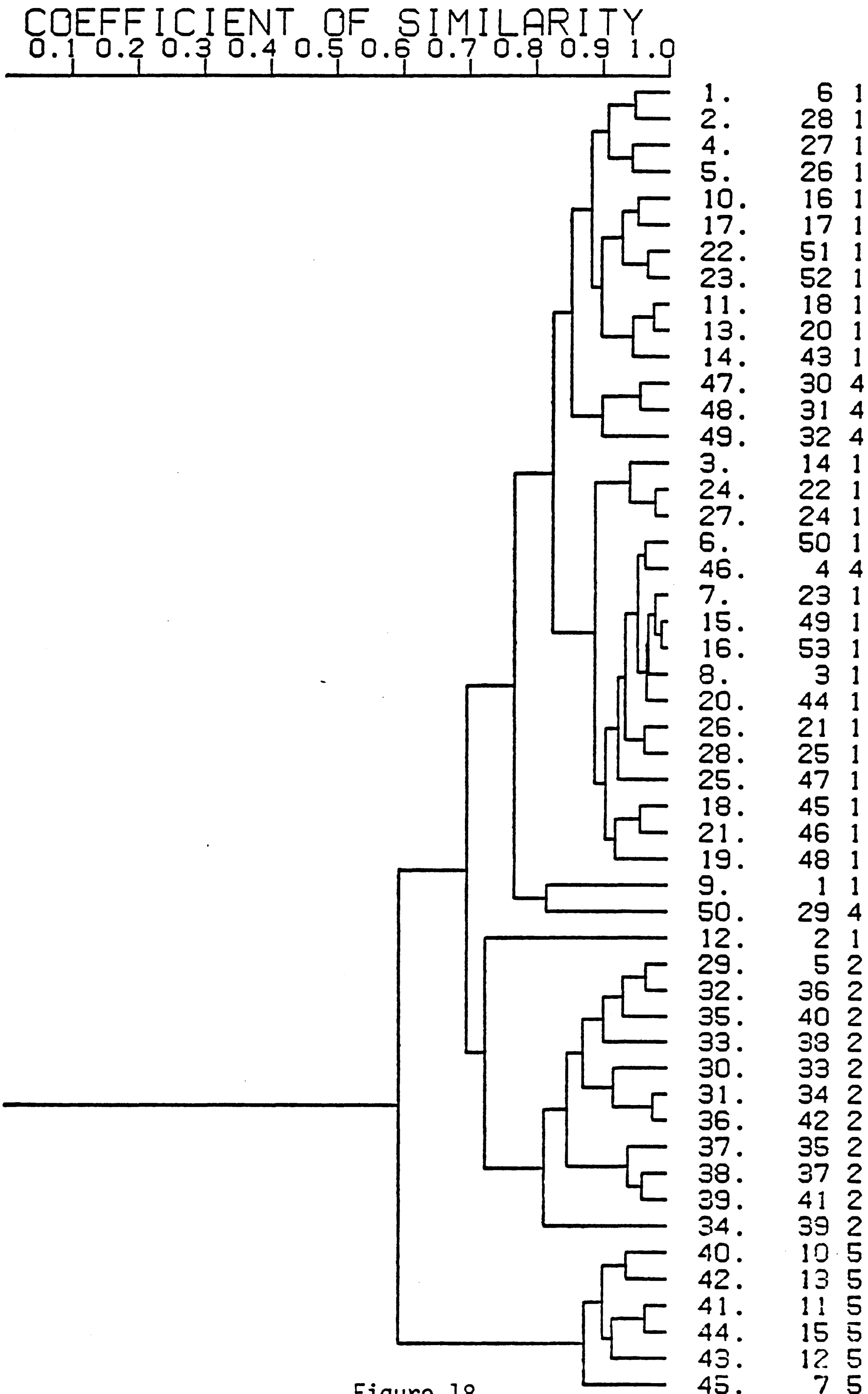

COEFFICIENT OF SIMILARITY
0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
1. 6 1
2. 28 1
4. 27 1
5. 26 1
10. 16 1
17. 17 1
22. 51 1
23. 52 1
11. 18 1
13. 20 1
14. 43 1
47. 30 4
48. 31 4
49. 32 4
3. 14 1
24. 22 1
27. 24 1
6. 50 1
46. 4 4
7. 23 1
15. 49 1
16. 53 1
8. 3 1
20. 44 1
26. 21 1
28. 25 1
25. 47 1
18. 45 1
21. 46 1
19. 48 1
9. 1 1
50. 29 4
12. 2 1
29. 5 2
32. 36 2
35. 40 2
33. 38 2
30. 33 2
31. 34 2
36. 42 2
37. 35 2
38. 37 2
39. 41 2
34. 39 2
40. 10 5
42. 13 5
41. 11 5
44. 15 5
43. 12 5
45. 7 5

Figure 18

significantly greater number of radial ribs than specimens of the same size collected south of the Cape. See Figure 7. This ornamentation dissimilarity may indicate a subspecies of D. cayenensis found north of Cape Hatteras, North Carolina.

Cluster Analysis of the fossil sample employing the same variables as the recent cluster analysis, did not yield discrete groups by species. The most heavily weighted criteria for segregation were 1.) rib size and number of ribs, and 2.) foramen shape and size. Since there is greater intraspecific variation in shell form among fossil species compared to recent species, form must be weighted more heavily to generate clusters by species. Because of this great variability in shell form, taxonomy is difficult and, as yet, imperfect concerning the fossil specimens.

Theta Rho Analysis reveals the significant incongruity of form between D. griscomi and Diodora sp.. See Figure 12. Additional differences support the separation of these two morphologies. D. griscomi has a slightly more narrow basal outline, fewer and irregular ribs, and an internal callus around the foramen that is strongly concave compared to that of Diodora sp. which is gently convex. See Figure 6.

DISCUSSION

Every organism exists in a habitat exposed to the pressures of its environment. For an organism to remain successfully in its habitat, it must be adapted to the environment. Adaptation requires that the individual efficiently apportion its available energy among such functions as feeding, growth, defense, and reproduction.

Resource availability varies in intensity over the surface of the earth, as along a latitudinal gradient or up a shore line. As physical environment along a gradient changes, so must the design of affected organisms. This can be reflected in behavior or architectural modifications that lend resilience against potentially harmful effects of the environment.

There exists another mode of adaptive pattern not related directly to physical pressures but to the surrounding biological community. Interactions include predation and competition for food and space.

In order to recognize and evaluate an adaptive pattern, one must be aware of a third influence: local conditions impose limitations on organism design that is expressed as a non-genetic response to the environment.

Demand for phenotypic plasticity would be particularly great in all species whose pelagic larvae are at the mercy of currents. Successive spawnings of the same local populations may be forced to colonize rather different areas with different environmental pressures. Gene flow would then be very free and result in highly panmictic conditions, counteracting local genetic differentiation and favoring developmental flexibility (Mayr, 1970).

Variations in limpet morphology are excellent illustrations of an organism's response to environmental limits and pressures to which living populations are exposed.

It is advantageous, at this point, to recall the environmental impacts associated with Diodorid morphologic variation. Specimens from higher latitudes generally display an increase in shell size, broadening of the foramen, and decrease in robustness of ornamentation. Increase in water depth is associated in some provinces with decrease in shell size, broadening of the foramen, decrease in robustness of ornamentation, and decrease in mean shell height.

The most important growth-stimulating factor is related to food availability. Malouf and Breese (1977) determined that growth fluctuations in the Pacific oyster Crassostrea gigas are independent of temperature and related to quantity of particulate organic matter suspended in the water. Malouf and Breese propose that animals have increased metabolic costs at higher temperatures near the equator. These costs are reflected in weight loss and possibly shell resorption when food is scarce. Secondly, food consumption relative to availability might be reduced in higher temperatures. Lastly, assimilation efficiency is inversely related to temperature, so that less energy is available for growth at higher temperatures (Malouf and Breese, 1977, p.11)

At the northern limits of its range, (southeast Florida and Bermuda), F. barbadensis reaches a larger size than in Barbados (Farfante, 1943, and Ward, 1967). Ward (1966b) proposes that the decrease in Fissurella barbadensis size in Barbados, compared to the size of specimens collected in Florida and Bermuda, is due to more extensive reproductive activity. This reasoning is inverse to Nicotri's (1974) observation that gonadial output is positively correlated to shell size.

Dehnel (1955) concludes from his study on mollusc embryos and larvae that rates of growth in northern populations are from two to nine times greater than for southern populations of the same species at a given comparable temperature. The possible extrinsic factor stimulating growth is better quality yoke in the eggs of northern specimens. This could possibly offer the organism an initial benefit with a lasting effect.

Similar studies concluding that northern specimens have a greater rate of growth were performed by Rao (1953, on the mussel Mytilus californianus), Moore (1934, on the barnacle Balanus balanoides), and Weymouth et al (1931, on the razor clam Siliqua patula).

Nutrient levels in most tropical waters are low and constant, whereas in areas of upwelling and along most temperate and polar shores, surface waters are rich in nutrients for part or all of the year. This is due to the greater productivity exhibited in polar waters (Vermeij,1978, and Branch 1971). Branch (1971) reports that species of Patella are larger on the colder west coast of the South African peninsula where shores are bathed in nutrient rich upwelling currents. It is important to remember that patellids and most diodorids are browsers and not filter feeders. Browsing limpet growth should be governed by algae growth related to light intensity and water temperature rather than nutrient supply in the water.

It is also possible that species of marine molluscs inhabiting colder waters of higher latitudes grow to a larger size because they experience a greater longevity than individuals of the same species from warmer waters (Ward, 1967).

The possibility that size relationships are a function of shell collecting methods and collector preferences cannot be disregarded.

These factors influencing growth in northern waters can be used to explain partially the decrease in size of subtidal specimens of Diodora in this study.

Sunlight penetrates water to varying depths, depending on: 1.) intensity and angle of radiation, 2.) amount of surface reflection, and 3.) transparency of the water. Seawater absorbs a great deal of incident light and, even in very clear water, only 35-38 percent of the sunlight reaches a depth of one meter. With increasing depth, light fades rapidly so that less than one percent remains below 50 meters. In coastal waters where sediment or plankton and turbid conditions produce low transparency, less than 1 percent of the sunlight filters past 10 meters. The photic zone is thus limited to the upper 30 meters or less along most turbid mainland coasts and to 150-175 meters in clearest open waters (Dawson, 1966).

Dawson (1966) continues to explain the increased photosynthetic efficiency when accessory pigments are activated in combination with chlorophyll a. The functional significance of these pigments is recognized in benthic algae. Thus the red pigments of Rhodophyta, a common patellid food source, are specially adapted for efficient absorption in deeper waters where green, blue, and violet light prevails.

The smaller size of subtidal diodorids may be a function of dwindling green and blue green algae supplies. Less food would be available to aportion energy toward growth of the shell. At 100 meters, where D. tanneri is encountered may mark the beginning of another diodorid trophic regime. No information is available in the literature concerning food preferences in D. tanneri, but a reasonable speculation might be red algae or sponges, both of which thrive in deeper waters. This could encourage this middle shelf limpet to attain its remarkable size.

Higher latitude and deeper water diodorids display a broader foramen. Generally, features of gastropod shell design are related more to predation than to physical factors. As environmental conditions become less limiting to life processes along a gradient, predation becomes a greater selective force (Vermeij, 1978). This line of reasoning may be used to support the theory that predation and shell destruction increases from high to low latitudes and nearshore to deeper water environments, thus reflecting greater shell sturdiness in intertidal tropical limpets.

Predators, such as asteroids, brachyuran and anomuran crabs, fishes, birds, octopods, and other gastropods, that enter the aperture or foramen of molluscs would be discouraged by a long narrow or constricted opening as opposed to a broad defenseless foramen (Vermeij, 1978).

Brachyuran crabs, stomatopods, lobsters, fishes and birds are known to break the shell to gain access to soft tissues within. This effort is discouraged by a thick shell with strong external sculpture. These features also inhibit muricid and naticid gastropods and octopods' attempts at drilling through the shell (Vermeij,1978).

Graus' (1974) study of shallow water marine gastropods along the Atlantic Coast of North America revealed the existence of a latitudinal trend in shell calcification. His measurements of shell density, shell thickness, and shell form indicate that organisms from higher latitudes, are more efficient, on the average, in their utilization of calcium carbonate. Supported by this fact, it is probable that gastropods respond directly to increased availability or decreased solubility of calcium carbonate in the external medium. This may explain variation in rib size of diodorids along the Atlantic Coast.

In the marine environment, calcium carbonate precipitates most readily when the solubility product of calcium carbonate is low or the concentration of calcium is high. Water temperature is probably the most important factor influencing precipitation (Graus,1974). An increase in temperature lowers the solubility product of calcium carbonate and the solubility of CO2, thereby increasing carbonate ion concentration (Revelle and Fairbridge,1957). The temperature increase toward the equator, then, facilitates the precipitation of calcium carbonate in the formation of organic skeletons.

Waters of the Gulf Stream flowing along the North American Coast, exhibit a temperature decrease with an increase in latitudinal. This gradient is interupted at Cape Hatteras, North Carolina, where the current veers from the coast and shelf to flow northeastward across the ocean. This point is the southernmost extension of eddies from the Laborador Current which bring chilling temperatures, low salinities, and nutrient rich waters southward (Gaskell, 1972).

Cape Hatteras also represents a morphologic boundary for diodorid shells. Shells collected from north of Cape Hatteras are not only larger in overall size but exhibit at least 40 percent more ribs on the external surface. The consequence of increased rib number is finer ribs, reflecting a more delicate ornamentation pattern.

Calcium carbonate availability decreases along a water depth gradient as well, still influenced by temperature. Nicol (1966 and 1967) observed that bivalve species living in cold waters of polar regions and the deep sea are almost always small, thin shelled, and devoid of color and external sculpture. Her specimens are from a significantly greater depth than my sample but the trend is illustrated by the delicate ornamentation expressed on the thin, white shell of _D_. _tanneri_ at 104-219 meters. Retention of large size in _D_. _tanneri_ could be explained by the comparably shallower depth, and probable increase in food availability.

Water depth and latitude are correlated to changes in shell morphology. Subtidal and more northern specimens have a mean relative height less than mean relative height in intertidal and southern samples.

Shotwell (1950), Segal (1956), Seapy and Hoppe (1973), and Bannister (1975) agree that larger and higher peaked shells of Patella and Acmaea are found further on shore within the intertidal zone. Their studies reveal that higher peaks offer larger extra-visceral area to store water for respiration during emergence. It is reasonable to conclude that individuals never aerially exposed would experience no selective pressure to develop a high peaked shell.

Branch (1974b) observed that Patella longicosta had a broader shell related to frequency of movement. Movement occurs by extending the mantle, thus extending the shell's secreting margin. This explanation can be modified to apply to limpets at depth. Numerous studies report intertidal limpets inhabiting a home 'scar' on the substrate and venturing only a few inches if at all to graze algae. Decrease in light at greater depths is related to decreasing food source of green and blue green algae, necessitating broader excursions to find food. Individuals then spend more time moving about with the mantle extended, thus secreting a broader shell.

Another explanation for taller shells was stated by Ebling (1962) who claims that limpets in the stressed environment of aerial exposure or increased turbulence spend a portion of each day tightly clamped to the substrate, maintaining the mantle edge in a constricted form. Shell secreted during this time would have a constricted base and a relatively high peak. Individuals that are never emerged would not experience regular spans of time with the mantle constricted; the shell would be allowed to grow to a broader, more relaxed morphology.

One can conclude that there is significant variability in diodorid shell form. Some morphologic characteristics correlate to environmental gradients, though it is not clear which patterns in form are genotypic and which are phenotypic.

FOSSIL FORM SIGNIFICANCE

Initially, questions were proposed concerning the existence of trends in diodorid morphology, their predictability along known gradients, and usefulness of these trends in reference to the fossil record. The study of specimens of *Diodora* supports the existence of morphologic variations along environmental gradients.

Utilizing the conclusions drawn and environmental interpretations regarding recent specimens of *Diodora*, it is now appropriate to extend their meaning to the fossil sample.

Fossil species observed in this study reflect a change in foramen shape and total number of ribs along a latitudinal range. This is similar to the sample of recent subtidal diodorid specimens. Northern individuals generally have a broader foramen with a straighter profile and a greater number of ribs, compared to those specimens collected further south. Refer to Figures 15, 18, and 19.

D. carditella, the one species collected over a geographic range, displays a morphologic change correlated to latitude. Specimens from the northern extremities of its range (Waccamaw Formation of South Carolina), exhibit broadening of the foramen and increase in foramen area, compared to those individuals collected further south (from the Caloosahatchee Formation of Florida). Both formations are Early Pleistocene age. Refer to Plate 7. This trend is coincident with recent subtidal specimens along a latitudinal range and supports the uniformitarian concept that environmental pressures are in existence today similar to those existing along the northwest Atlantic Margin in the Pleistocene, with possible regard to predatory pressures or calcium carbonate solubility.

The use of diodorid shell characteristics to determine paleoenvironments is an embryonic analytical technique. Perfect linear relationships between environmental gradients and morphologic characteristics do not exist. At best, there is moderate to good correlation between environmental factors and morphologic variation. For example, constricted foramens are most common in intertidal or lower latitude diodorids, but exist in deeper water and more northern specimens as well. Using only the conclusions from this study, diodorid shell form cannot be used as a sole determinant of paleoenvironments. I do believe that specimens displaying morphologic extremes can and should be used in conjunction with other factors to support a hypothesis or stimulate further investigation.

REFERENCES CITED

Abbott,R.T., 1974, American Seashells, Van Nostrand Reinhold Co., New York.

Bailey,R.H.,1973,Paleoenvironment, Paleoecology, and Stratigraphy of molluscan assemblages from the Yorktown Formation (Upper-Miocene to Lower Pliocene) of North Carolina, Ph.D.Dissert. U.N.C. Chapel Hill.

Bannister, J.V., 1975, Shell parameters in relation to zonation in Mediterranean limpets, Mar. Biol. 31(1):63-67.

Bathurst, R.G.C., 1976, *Carbonate Sediments and their Diagenesis*, Elsevier Scientific Publishing Co., New York, 658pp.

Benson,R.H.,1967, Muscle scar patterns of Pleistocene (Kansan) ostracodes, in *Essays in Paleontology*, R.C.Moore commemorative volume, edited by C.Teichert and E.Yochelson, Univ. Press of Kansas, Lawrence and London.

Berry, R.J. and P.J. Budge, 1973, Natural selection in Antarctic limpets, Br. Antarct. Surv. Bull., 35:73-81.

Black, R., 1976, Effect of grazing by *Acmaea insessa* on kelp in the intertidal zone, Ecology 57:265-277.

Blackmore, D.T., 1969, Growth, reproduction, and distribution in *Patella*, Jour. Exp. Mar. Biol. Ecol. 3:200-213.

Bowman, R.S., 1981, The morphology of *Patella spp.*jeuveniles in Britain and some phylogenetic inferences, Jour. Mar. Biol. Ass. U.K., 61:647-666.

Branch, G.M., 1971, Ecology of *Patella* from South Africa, Zoologica Afr. 6(1):1-38.

________, 1974(a), Ecology of *Patella linnaeus* from the Cape Penninsula, South Africa, Reproductive Cycles, Roy. Soc. S. Afr. Trans. 41:111-161.

________, 1974(b), Ecology of *Patella linnaeus* from the Cape Penninsula, South Africa, Growth Rates, Roy. Soc. S. Afr. Trans. 41:161-193.

________, 1975(a), Ecology of Patella species from Cape Penninsula, South Africa, Dessication, Mar. Biol. 32:179-188.

________, 1975(b), Ecology of <u>Patella</u> <u>concolor</u> and <u>Cellana</u> <u>Capensis</u> and effects of human consumption on limpet population, Zool. Afr. 10(1):75-85.

________, 1975(c), Intraspecific competition in <u>Patella</u> <u>cochlear</u>, Jour. Anim. Ecol. 44(1):263-280.

________, 1975(d), Mechanisms reducing intraspecific competition in <u>Patella</u> <u>spp</u>.: Migration, differentiation, and territorial behavior, Jour. Anim. Ecol. 44(2):575-600.

________, 1976, Interspecific competition experienced by South African <u>Patella</u> species, Jour. Anim. Ecol. 45(2):507-529.

Breen, P.A., 1973, Seasonal migration and population regulation in the limpet <u>Acmaea</u> <u>(Collisella)</u> <u>digitalis</u>, Veliger 15(2):133-141.

Campbell, L. et al., 1975, Plio-Pleistocene faunas of the Central Carolina Coastal Plain, Geologic Notes, 19(3), 123pp.

Chapman, R.L.,1971, The macroscopic marine algae of Sapelo Island and other sites on the Georgia coast, Bull. Georgia Acad. Sci. 29:77-89.

Collins, L.S., 1977, Abundance, substrate angle, and dessication resistance in two sympatric species of limpets, Veliger 19(2):199-203.

Conrad, T.A., 1841, New species of fossil shells from Tertiary of Maryland, Acad. Nat. Sci. Phila. Proc. 1:31.

Cupparo, L.R.A. and J.L. Reid, 1972, <u>Contributions</u> <u>to</u> <u>the</u> <u>Physical</u> <u>Oceanography</u> <u>of</u> <u>the</u> <u>Gulf</u> <u>of</u> <u>Mexico</u>, Gulf Pub. Co., Houston, Texas.

Dall, W.H., 1892, Tertiary mollusks of Florida, Part 1, Gastropoda, Wagner Free Inst. Sci. Trans. 3(2):427-30.

Dall,W.H.and J.Stanley-Brown,1892,Cenozoic geology along the Apalachicola River, G.S.A.Bull.5:147-170.

Davis, J.C.,1973, Statistics and Data Analysis in Geology, John Wiley &Sons, Inc.,New York.

Dawes, C.J.,1974, Marine Algae of the West Coast of Florida, Univ. of Miami Press, Coral Gables, Florida, 200 pp.

Dawson, E.Y., 1966, Marine Botany, Holt, Rinehart, and Winston, Inc., New York and Chicago.

Dawson, R.W., 1958, Ecologic and faunal analysis of the Miocene fossil invertebrate faunas at Grimesland and Magnolia, North Carolina, Masters Thesis, U.N.C., Chapel Hill, N.C.

Dehnel, P.A., 1955, Rates of growth of intertidal gastropods as a function of latitude, Physiol. Zool. 28:115-138.

Dodd, J.M., 1956, Studies on the biology of limpets, III, Hermaphrodism in the three British species of Patella, Jour. Mar. Biol. Ass. U.K., 35:327-340.

Doran, S.R. and D.S. McKenzie, 1973, Aerial and aquatic respiratory response to temperature variation in A.digitalis and A.fenestrata, Veliger 15(1):38-42.

DuBar, J.R., 1958, Stratigraphy and paleontology of the Late Neogene strata of the Caloosahatchee River area of Southern Florida, Fla. Geol. Surv. Bull. 40:206-207.

DuBar,J.R., H.S. Johnson, B.Thom, and W.O. Hatchell, 1974, Neogene stratigraphy and morphology, south flank of the Cape Fear Arch, N.C. and S.C. in "Post Miocene Stratigraphy, Central and Southern Atlantic Coastal Plain", Utah Univ. Press, edited by Oakes and DuBar.

Ebling, F.J., 1962, Ecology of Lough Ine, distribution and characteristics of Patellid species, Jour. Anim. Ecol. 31:457-467.

Farfante, I.P., 1943, The genera Fissurella, Lucapina, and Lucapinella in the western Atlantic, Johnsonia 1(10):1-20.

Fretter, V. and A. Graham, 1962, British Prosobranch Molluscs, Ray Society, London.

Gardner, J., 1948, Mollusca of the Miocene and Lower Pliocene of Virginia and North Carolina, U.S.G.S. Prof. Pap. 119b.

Gaskell, T.F., 1972, The Gulf Stream, Camelot Press, London.

George, J.D., 1979, Marine Life, Wiley Intersci. Pub., New York.

Gerant,R.E.,1970,Paleoecology of the Choptank Formation (Miocene), Md. and Va.,Md.Geol.Surv.Report of Invest. 12.

Gernant,R.E., T.G.Gibson,and F.C.Whitmore,1971,Environmental history of the Md. Miocene, Md.Geol.Guidebk. 3.

Glasser,J.D.,1968,Coastal Plain geology of Southern Md.,Md.Geol.Surv. Guidebk. 1.

Glibert, M., 1962, Les archeogastropoda fossiles du cenozoique etranger des collections de l' Institute royal des Sciences naturelles de Belgique, Inst. Roy. Sci. Naturelle du Belgique, Mem. 2(68):14.

Graus, R.R.,1974, Latitudinal trends in shell characteristics of marine gastropods, Lethaia 7:303-314.

Hack, J.T. and C.C. Nikiforoff, 1950, Coastal plain geology of southern Maryland, Johns Hopkins Univ. Studies in Geology, Guidebook 16(3) 56 pp.

Hazel, J.E., 1971, Ostracode biostratigraphy of the Yorktown Formation (Upper Miocene - Lower Pliocene) of Virginia and North Carolina, U.S.G.S. Prof. Pap. 704, 13pp.

Hewatt, W.G., 1940, Observations on the homing limpet, Acmaea scabra Gould, Amer. Midland Nat. 24:205-208.

Hughes, R.N., 1971, Ecological energetics of the key hole limpet, Fissurella barbadensis, Jour. Exp. Mar. Biol. Ecol. 6:167-178.

Humm, H.J., 1969, Distribution of marine algae along the Atlantic Coast of North America, Phycologia, 7:43-53.

Isphording,W.C.,1970,Petrology,stratigraphy,and redefinition of the Kirkwood Formation (Miocene) of New Jersey,J.Sed.Pet.40(3):986-997.

Lewis, J.B., 1960, The fauna of rocky shores of Barbados, West Indies, Can. Jour. Zool. 38:391-435.

Lindberg, D.R., 1975, Evidence of light reception through the shell of Notoacmaea persona, Veliger 17:383-386.

Malouf, R.E. and W.P. Breese, 1977, Seasonal changes in the effects of temperature and water flow on the growth of jeuvenile Pacific oysters, Crassostrea gigas (Thunberg), Aquaculture, 12(1):1-13.

Mansfield, W.C., 1937, Mollusks of the Tampa and Suwannee Limestone of Florida, Fla. Geol. Surv. Bull. 15:186.

Margolin, A.S., 1964, The mantle response to D.aspersa, Animal Behavior 12:187-194.

Markel, R.P., 1974, Aspects of the physiology of temperature acclimation on Acmaea limatula, Physiol. Zool. 47(2):99-108.

Martin, G.C., 1904, Maryland Geol. Surv., Miocene Text, Johns Hopkins Press, Baltimore.

Mayr, E., 1970, Populations, Species, and Evolution, Belknap Press of Harvard Univ. Press, Cambridge, Mass.

McLean, J.D., 1968, Foraminiferal zones and zone charts, an analysis and compilation, Manual of Micropaleont. Strat. 7, 42pp.

____________, 1970, A review of the paleoecology of the choptank Formation from data by Robert E. Gerant, In Ecological and Stratigraphic Studies of Foraminifera and Ostracoda, McLean Paleont. Lab. Rep. 10:6-57.

Moore,H.B.,1934,The biology of Balanus balanoides, Jour. Mar. Biol. Assoc., 19:851-868.

Morris, P.A., 1973, A Field Guide to Sea Shells, Houghton Mifflin Co., Boston. Nichol, D., 1967, Some characteristics of cold water marine Pelecypods, Jour. Paleo. 41(6):1330-1440.

Nicotri, M.E., 1974, Resource partioning, grazing activities and influence on microflora by intertidal limpets, Dissert. Abst. Int. B 35(8):3878.

Olsson, A.A., 1968, Notes on Siphocypraea, Bull. Amer. Paleont. 54(242):279-285.

Olsson, A.A., and A. Harbison, 1953, Pliocene mollusca of Southern Florida, Acad. Nat. Sci. Phila. Mon. 8:360.

Olson, E.C.21L.Miller, 1958, Morphological Integration, Univ. Chicago Press, Chicago.

Orton, J.H., 1946, Biology of Patella in Great Britain, Nature, Lond. 158:173-174.

Orton, J.H., A.J. Southward, and J.M. Dodd, 1956, Studies on the biology of limpets, II, The breeding of Patella vulgata L. in Britain, Jour. Mar. Biol. Ass. U.K. 35:149-176.

Phillips, D.W., 1975(a), Distance chemoreception triggered avoidance behavior of limpets to starfish,Jour. Exp. Zool. 191:199-210.

_______, 1975b, Localization and electrical activity of the distance chemoreceptors that mediate predator avoidance behavior in A.limatula and A.scutum, Jour. Exp. Biol. 63:403-412.

________, 1976, The effect of species-specific avoidance response to predatory starfish, Oecologia 23:83-94.

Pilsbry, H.A., and C.W.Johson, 1892, Catalogue of Fissurellidae of the United States, Natilus 5(9):106-107.

Por, F.D., and I. Dor, 1975, Ecology of the metahaline pool of Di Zahov, Gulf of Elat, Mar. Biol. Berlin 29:37-44.

Rao,K.P.,1953, Rate of water propulsion in Mytils californianus as a function of latitude, Biol. Bull. 104:171-181.

Revelle,R. and Fairbridge,R.,1957, Carbonate and carbon dioxide. In Treatise on Marine Ecology and Paleoecology, Vol.1,Ecology, Geo.Soc. of Amer.Memoir 67:239-295.

Rhodehamel,E.C.,1979,Geology of the Pine Barrens of New Jersey in Pine Barrens:Ecosystem and Landscape, edited by R.T.T.Forman,Academic Press, New York.

Richards, H.G., and A.Harbison, 19--, Miocene invertebrate fauna of New Jersey, Acad. Nat. Sci. Phila. Proc. 94:203.

Schneider, C.W. and R.B. Searles, 1973, North Carolina marine algae. II New records and observations of the benthic offshore flora, Phycologia, 12:201-211.

Seapy, R.R. and W.J. Hoppe, 1973, Morphological and behavioral adaptations to dessication in the intertidal limpet, Acmaea (Collisella) strigatella, Veliger 16(2):181-188.

Segal, E., 1956, Adaptive differences in water-holding capacity in an intertidal gastropod, Ecology 37(1):174-178.

Shotwell, J.A., 1950, Distribution and volume of and relative linear measurement changes in Acmaea, the limpet, Ecology 31:51-61.

Sokal, R.R., and F.J. Rohlf, 1973, Introduction to Biostatistics, W.H. Freeman & Co., San Francisco, 368 pp.

Stephens, A.C., 1932, Notes on the biology of certain Lamellibranch in the Clyde area, Jour. Mar. Biol. Ass. U.K. 18:51-68.

Stimson, J., 1970, Territorial behavior in the owl limpet, Lottia gigantea, Ecology 51:113-117.

Van den Hoek, C.,1975, Phytogeographic provinces along the coasts of the Northern Atlantic Ocean, Phycologia, 14(4):317-330.

Vermeij, G.J., 1971, Temperature relations of some tropical Pacific intertidal gastropods, Mar. Biol. 10:308-314.

________, 1978, Biogeography and Adaptations, Harvard Univ. Press, Cambridge, Mass.

Vokes, H.E., 1957, Miocene fossils of Maryland, Md. Dept. Geol. Mines and Res. Bull. 20, 83pp.

Ward, J., 1966a, Feeding, digestion, and hystology of the digestive tract of the keyhole limpet Fissurella barbadensis Gmelin, Bull. Mar. Sci. 16:668-684.

_________, 1966b, The breeding cycle of the keyhole limpet, Fissurella barbadensis Gmelin, Bull. Mar. Sci. 16:685-695.

_________, 1967, Distribution and growth of the keyhole limpet, Fissurella barbadensis Gmelin, Bull. Mar. Sci. 17:299-318.

Ward, L.W. and B.W. Blackwelder, 1980, Stratigraphic revision of Upper Miocene and Lower Pliocene beds of the Chesapeake Group, Middle Atlantic Coastal Plain, U.S.G.S. Bull. 1482 D, 65pp.

Weymouth, F.W., et al,1931, Latitude and relative growth in the razor clam, Siliqua patula, Jour. Exp. Biol. 8:228-249.

Willoughby, J.W., 1973, Field study on clustering and movement behavior in the limpet Acmaea digitalis, Veliger 15(3):223-230.

Wolcott, T.G., 1973, Physiological ecology and intertidal zonation in limpets (Acmaea): A critical look at limiting factors, Biol. Bull., Marine Biol. Lab., 145(2):389-422.

Woodas, N.A., 1965, Some lithologic and stratigraphic aspects of selected outcrops of Miocene and Pliocene formations in North Carolina, Masters Thesis, U.N.C., Chapel Hill, North Carolina.

Worthington, L.V., 1976, On the North Atlantic Circulation, Johns Hopkins Univ. Press, Baltimore and London.

Wright, J.R., and R.G. Hartnoll, 1981, The energy budget for a population of the limpet Patella vulgata, Jour. Mar. Biol. Ass. U.K. 61:627-646.

Appendix A

FOSSIL SPECIES AND THEIR ORIGIN

The following paragraphs are brief discussions of the paleoenvironments of the formations from which each specimen for this study was collected.

Kirkwood Formation (Middle Miocene)

Both *D. griscomi* and *Diodora sp.* were found in the Alloway Clay Member of the Kirkwood Formation. Specimens were collected west of Jerico, New Jersey. Fossils are uncommon in the Alloway Clay due to extensive leaching (Isphording, 1970). There is a highly fossiliferous portion of the Alloway Clay in the southern part of the state, known as the Shiloh Marl (Richards and Harbison, 1942). This marl consists of a drab colored clay. The fauna of this marl is at least roughly equivalent that of the Calvert Formation of Maryland.

Fauna of this unit represent types found in the inner to middle neritic zone on the continental shelf.

Minerals in the Kirkwood were derived largely from high ranked metamorphic and acid igneous rocks, most likely the crystalline rocks of the Piedmont (Isphording, 1970).

The numerous plant fossils are of types usually associated with a humid sub-tropical environment (Isphording, 1970).

Calvert Formation (Middle Miocene)

D. marylandica is found in the Calvert Formation of Maryland, which is believed to be equivalent to the Kirkwood Formation of New Jersey, but deposited further south in what is now the Chesapeake area. *D. marylandica* specimens were found in Zone 10, composed of diatomaceous earth and dark sandy clays with a tremendous accumulation of shells (Gardner, 1948, and Glasser, 1968).

Ostracode assemblages reveal a distinct shallowing trend from the lower units, yet some of the deep water species are present in modest abundance. Based on faunal evidence, it appears that Zone 10 was deposited in approximately 30-45 meters of water (Gerant et al.,1971).

Zone 10 is considered by Gerant (1971) to be "Allochthonous-Autochthonous" in origin, meaning the preserved organisms lived and died proximal but not at the cite of burial.

Articulated skeletons of porpoises are common throughout the Calvert Formation. Long-beaked porpoises are consistently present, indicating an environment of estuaries and rivers. Beginning in Zone 9 of the Calvert Formation, baleen whale skeletons are found disarticulated and scattered. Young whales are most common, suggesting the Chesapeake Bay area was a calving ground during the Miocene. Sea cows and gopher turtles indicate a climate that remained between freezing and 75 degrees Farenheit year round (Gerant et al., 1971).

Choptank Formation (Middle Miocene)

D. marylandica is also collected from the Choptank Formation, which was named for the Choptank River of the Eastern Shore of Maryland. This formation is exposed along a 20 mile wide band that runs parallel to the margin of the Calvert Formation.

The Choptank is composed of sand and sandy clay, with a comparatively greater fraction of sand than the Calvert Formation.

Zones 17 and 19 are quite fossiliferous with pelecypods, barnacles, and vertebrate remains. Gastropods are also present and in greater abundance than in the Calvert Formation (Gardner, 1948, and Hack, 1950). Ostracode data suggests that the Choptank Formation was deposited in between 10 to 30 meters of water in a restricted environment dissimilar to the Calvert or its superstratum, the St. Mary's Formation (McLean, 1970).

St. Mary's Formation (Middle Miocene)

D. redimicula was collected from the St. Mary's Formation, which lies unconformably on the Choptank Formation. The St. Mary's Formation in places is lithologically so similar to the Pleistocene beds of gravel, sand, silt, clay, and loam that it is difficult to discriminate between the two where fossils are not present. There are locations where the beds are a sandy clay with diverse fossil accumulation (Gardner, 1948, and Hack, 1950).

Ostracode data suggests a varying range of depths for the depositional environment of the St. Mary's Formation. McLean (1968) suggests a shoaling trend from Calvert time to St. Mary's, followed by the more stable and increasing depths of the Yorktown Formation.

Eastover Formation (Upper Miocene)

The Cobham Bay Member of the Eastover Formation is the source of *D. alticosta*, *D. redimicula* and *D. catilliformis* specimens. This unit consists of fine grained, well sorted, shelly sand. The fossil assemblage indicates a subtropical, open marine, shallow embayment. The abundant mollusc population indicates favorable substrates, abundant food supply, and warm temperate to subtropical conditions. Two main molluscan biofacies are present through the basin. One consists of a large number of small bivalves, *Spisula rappahannockensis* Gardner. This species thrived in northern sections of the basin and appears to have preferred quiet, slightly more silty substrates. The other biofacies is dominated by large species of *Chesapecten*, *Mercenaria*, and *Isognomon*. These taxa apparently preferred higher energy conditions and clean sandy substrates (Ward & Blackwelder, 1980).

Yorktown Formation (Lower Pliocene)

The Yorktown Formation has been divided into two zones (Gardner, 1948), three zones (Hazel, 1971), and five zones (Bailey, 1973) based on faunal composition.

D. redimicula is found in Bailey's (1973) Assemblage 3 of the Virginia Yorktown Formation. Specimens of *D. chipolana* and *D. carolinensis* have also been reported from this formation. This unit consists of fine to intermediate sands. High molluscan diversity suggests an intermediate to inner shelf environment, 40-100 meters deep, under conditions of normal salinity (Woodas, 1965).

Early Yorktown time was marked by a transgression southward. Increased molluscan diversity in Assemblage 3 may be related to the stabilization of level bottom communities after the initial rapid transgression and to generally warmer climates (13-22 degrees C) (Bailey, 1973).

Duplin Formation (Lower Pliocene)

D. nucula, *D. carolinensis*, and *D. catilliformis*, are from the Duplin Formation, the southern equivalent to the Yorktown. Generally, the Duplin is extremely fossiliferous, displaying excellent preservation. It is sandy with shallow marine and brackish water facies. West of the Mechanicsville Scarp there is a line of sand ridges speculated to be relict barrier islands. Seaward, erosional patches become more calcareous to nearly pure limestone and calcareous silty sands (Dawson, 1958, and Woodas, 1965).

Most of the fossil species lived in open marine environments in 6-20 meters of water. A few species suggested an enclosed brackish water environment. Salinity was probably normal (34-36 ppt). Water was well oxygenated, turbulent at times, and relatively clear with a temperature range similar to that found off the coast of South Carolina today (Dawson, 1958, and DuBar et al.,1974).

Waccamaw Formation (Pliocene)

D. nucula, *D. carolinensis*, *D. cayenensis*, and *D. carditella* were preserved in the Waccamaw Formation of the Carolinas. These deposits consist of poorly to moderately well sorted, semi-indurated, fine to coarse sands and argillaceous calcareous sands. Shell fragments make up 70% of the weight in some places. Carbonate content and sand grain size decrease inland whereas the silt-clay content increases (Woodas, 1965).

The most inland facies is commonly a dark gray to brown peaty clay. Sediment character, fossil content, and spatial relationships suggests a transition landward from a slightly calcareous shelf environment of 10-70 meters of water through a variety of restricted brackish environments, to bordering marshes and swamps.

Temperature range is speculated to be similar to that found off the coast of Florida today. Water turbulence did not greatly affect the bottom, however the water was well oxygenated (DuBar et al.,1974).

Chipola Formation (Lower-Middle Miocene)

D. chipolana is from the early Miocene Chipola Formation of northern Florida. This marl is a highly calcareous mixture of broken and complete shells, fine clay, and sand. It is replete with organic remains, often quite well preserved. Oddly, forams and echinoids are absent with only a few small solitary corals. The depositional environment is speculated to have been shallow, below wave base, under conditions of high nutrient supply. The formation is restricted in extent and exceeds 4 meters thick in only a few places (Dall, 1894).

Pinecrest Formation (Lower Pliocene)

The Pinecrest Formation is recorded as the Yorktown-Duplin equivalent. *D. caloosaensis* and *D.*

carolinenesis were collected from this formation. This unit contains shells and a trace of black phosphate in a clean, beach-like quartz matrix. A well preserved and diverse fauna is present containing specimens at some localities with high gloss and articulated valves and with both calcite and aragonite shells (Dall, 1894). According to Olsson (1968) the fauna of the Pinecrest consists of a mixture of tropical, sub-boreal, and boreal species.

Caloosahatchee Formation (Pliocene)

D. cayenensis, D. carolinensis, D. nucula, D. chipolana, D. carditella, and D. caloosaensis were collected from the Caloosahatchee Formation. It is composed of shelly, calcareous, fine sands, calcarenites, and limestones. Fossils are abundant, varied, and well preserved. In the type area, coral patch reefs occur. Echinoids, bryozoans and barnacles are common.

Caloosahatchee sediments are believed to have accumulated in a shallow marginal sea where water depth did not exceed 20 meters (DuBar et al., 1974).

The middle member, the Bee Branch, where most of the limpet specimens occur exhibits a shallow shelf environment with high salinity. It could be a bay feature between 25-35 meters in depth. The highest carbonate content is recorded here.

The upper-most member, Ayers Landing, where *D. nucula* occurs represents a brackish to high salinity bay, to fresh water environment during regression of the sea (DuBar et al.,1974).

Appendix B

RECENT SPECIMEN COLLECTION LOCALITIES

LOCALITY	LATITUDE
FLORIDA KEYS	
Sambo Reef	24.45
SW of Tortugas	24.45
Western Dry Rocks	24.48
SW of American Shoals	24.52
KEY WEST	24.54
Bush Key	24.60
Loggerhead Key	24.63
Smith Shoals, Key West	24.63
Dry Tortugas	24.65
Garden Key, Tortugas	24.65
Bahia Honda Key	24.66
Pirates Key	24.69
Long Reef	24.81
Lower Matecumbe Key	24.85
Indian Key	24.88
Florida Bay	¬25.00
Bottle Point Key	25.07
Key Largo	25.09
FLORIDA ATLANTIC COAST	
Sands Key	25.51
Ragged Key	25.53
Biscayne Bay	25.70
SE of Fowey Light	25.71
Fowey Light	25.78
Miami, Govt. Cut	25.81
NE of Fowey Light	25.85
Bird Key, Biscayne Bay	25.85
Jupiter Inlet	26.95
Cape Canaveral	28.45
St. Augustine	29.85
FLORIDA GULF COAST	
NW OF KEY WEST	24.55
Sanibel Island	26.45
Hemphill	26.60
Siesta Beach	27.28
Point of Rocks, Sarasota	27.34
Sarasota Bay	27.40
Long Boat Key	27.43
Long Boat Pass	27.44
Anna Maria Key	27.50

LOCALITY (continued)	LATITUDE
Tampa Bay	27.60
John's Pass	27.78
Madiera Beach	27.81
Seashore Key	29.09
Cedar Keys	29.13
Pepperfish Keys	29.50
Apalachicola	29.60
FLORIDA TO CAPE HATTERAS	
SW of Cape Fear	33.61
Myrtle Beach, S.C.	33.68
Off Little River Inlet, S.C.	33.86
SE of Cape Lookout, N.C.	34.38
17 mi SE of Cape Lookout	34.43
Beaufort Harbor	34.70
Morehead City, N.C.	34.71
Piners Island, N.C.	35.08
Cape Hatteras	35.23
NORTH OF CAPE HATTERAS	
MOUTH OF CHESAPEAKE BAY	37.00
Smith Island, Va.	37.11
Magothy Bay, Va.	37.15
Cobb Island, Va.	37.34
N. Paramore Island, Va.	37.57
Chincateague, Va.	37.98

Appendix C

FOSSIL COLLECTION LOCALITIES

LOCALITY	FORMATION	LATITUDE
FLORIDA		
W of Clewiston	Caloosahatchee	26.74
Clewiston	Caloosahatchee	26.74
La Belle	Caloosahatchee	26.74
SW of La Belle, Caloosahatchee R.	Caloosahatchee	26.74
Ortona Lock	Caloosahatchee	26.77
NW of Clewiston	Caloosahatchee	26.79
Moore Haven	Ft.Thompson	26.82
Shell Creek	Caloosahatchee	27.05
Warren Bros. Pit, East Sarosota	Pinecrest	27.32
Kissimee R., Seaboard R.R. bridge	Pinecrest	27.34
St. Petersburg	Caloosahatchee	27.76
Jackson Bluff	Pinecrest	30.39
Ten Mile Cr. on Chipola River	Chipola	30.50
GEORGIA		
Brunswick	Duplin	31.11
SOUTH CAROLINA		
Pee Dee R., rd.fr. Georgetn to Con	Waccamaw	33.64
NE of Myrtle Beach	Waccamaw	33.76
Tillys Lake	Waccamaw	33.83
SW of Little River on Rt. 17	Waccamaw	33.84
S of Mayesville	Duplin	33.86
NORTH CAROLINA		
Old Bells Br. on Tar River	Yktn. Z1	35.84
Roanoke R. below Palmyra	Waccamaw	36.05
NW of Halifax	Yktn. Z1	36.35
Watsons Mill near Murfreesboro	Yktn. Z1	36.44
N of Murfreesboro on Merrhin R.	Yktn. Z1	36.44
N of Murfreesboro	Yktn. Z1	36.47
VIRGINIA		
Nottoway R., Sycamore	Yktn. Z2	36.58
3 mi. W of Franklin	Yktn. Z2	36.68
NW of Suffolk	Yktn. Z2	36.73
N. of Chuckatuck	Yktn. Z2	36.87
Benns Church	Yktn. Z2	36.94
Smithfield	Yktn. Z2	36.98
Mogarts Beach on James R.	Yktn. Z2	37.03
Lieutenant Run, Petersburg	Yktn. Z2	37.06
Rushmere	Yktn. Z2	37.07
Rices Pit	Yktn. Z2	37.07
Camp Wallace on James R.	Yktn. Z2	37.13

LOCALITY (continued)	FORMATION	LATITUDE
Cobhams Warf on James R.	Eastover	37.14
below Yorktown	Yktn. Z2	37.16
SW of Petersburg	Yktn. Z2	37.16
Petersburg	Yktn. Z2	37.20
Moore House on York R.	Yktn. Z2	37.22
Yorktown	YKTN. Z2	37.23
Grove Warf on James R.	Yktn. Z2 or 1	37.23
Temple Place	Yktn. Z2	37.25
Glouster Pt.	Yktn. Z2	37.25
Walls Run, 2 mi. W of Garysville	Yktn. Z2	37.25
3 mi. above Yorktown	Yktn. Z2	37.26
Williiamsburg	Yktn. Z2 or 1	37.27
Bellfield, 5 mi. above Yktn	Yktn. Z2 or 1	37.28
Urbana	Eastover	37.64
Carters Grove on James R.	Eastover	38.10
MARYLAND		
Patuxent R. Cliffs	Choptank	38.39
Drum Cliffs	Choptank Z17	38.39
Calvert Cliffs	Choptank	38.39
Calvert Beach	Choptank	38.46
Long Beach	Choptank Z17	38.46
below Governors Run	Choptank	38.47
Parkers Cr. mouth	Choptank Z17	38.54
S. of Plum Point	Calvert Z10	38.57
		TO 38.60
Plum Point	Calvert Z10	38.61
5 mi.between Plum Pt. & Ches.Bch.	Calvert Z10	¬38.63
5 mi. SE of Easton on Choptank R.	Choptank	38.72
NEW JERSEY		
S of Greenwich	Kirkwood	39.39
W of Shilo	Kirkwood	39.45
S of Jericho	Kirkwood	39.46
Jericho	Kirkwood	39.56

Appendix D

PARAMETERS MEASURED FROM RECENT SPECIMENS

A value of zero indicates no reading was taken.

SPNO	SP	PROV	LAT	DEP	L	W	M	HW	HL	HL/L
0	1	1	24.45	130.00	17.25	12.30	0.00	9.10	10.00	0.58
2	1	1	24.55	0.00	11.85	8.15	0.00	6.35	6.80	0.57
0	1	1	24.65	29.26	5.90	3.50	0.00	0.00	2.10	0.36
0	1	1	24.65	29.26	6.45	3.70	0.00	0.00	2.50	0.39
1	1	1	24.65	29.26	13.00	7.80	0.20	3.95	4.25	0.33
0	1	1	24.69	0.00	13.65	8.05	0.15	5.45	5.75	0.42
0	1	1	24.69	0.00	15.10	9.35	0.23	6.65	7.25	0.48
0	1	1	24.69	0.00	17.70	11.20	0.00	8.00	8.40	0.47
0	1	1	24.85	0.00	15.70	10.50	0.20	5.75	6.20	0.39
0	1	1	24.85	0.00	22.10	14.95	0.85	9.05	9.90	0.45
3	1	1	24.85	0.00	23.85	15.05	0.95	8.90	10.50	0.44
0	1	1	25.00	69.49	8.05	5.35	0.00	0.00	3.20	0.40
0	1	1	25.00	69.49	8.25	5.50	0.00	3.20	3.85	0.47
0	1	1	25.00	69.49	10.25	6.30	0.00	0.00	3.30	0.32
51	1	1	25.07	1.00	28.80	17.45	1.18	11.65	13.50	0.47
52	1	1	25.07	1.00	29.40	18.85	1.05	10.70	11.35	0.39
53	1	1	25.07	1.00	35.25	23.10	1.85	13.10	14.80	0.42
0	1	1	25.09	0.00	22.60	14.85	0.68	10.50	11.80	0.52
0	1	2	26.45	0.00	11.45	6.75	0.15	4.50	4.75	0.41
0	1	2	26.45	0.00	11.75	7.65	0.15	5.10	5.10	0.43
0	1	2	26.45	0.00	12.00	7.40	0.15	5.70	5.95	0.50
0	1	2	26.45	0.00	13.00	8.45	0.15	5.50	6.95	0.53
0	1	2	26.45	0.00	13.15	8.00	0.20	5.20	5.45	0.41
0	1	2	26.45	0.00	14.85	9.65	0.25	6.00	7.15	0.48
0	1	2	26.45	0.00	16.05	11.00	0.35	7.15	7.05	0.44
0	1	2	27.34	0.00	18.90	12.00	0.45	8.55	8.75	0.46
0	1	2	27.34	0.00	19.60	12.05	0.25	6.95	7.45	0.38
44	1	2	27.36	1.00	19.15	12.60	0.65	8.35	9.60	0.50
46	1	2	27.36	1.00	22.65	15.60	1.37	11.75	12.85	0.57
45	1	2	27.36	1.00	26.25	19.10	1.85	11.45	13.00	0.50
47	1	2	27.36	1.00	26.45	17.15	1.20	9.30	10.50	0.40
0	1	2	27.44	10.06	20.20	12.85	0.58	8.25	9.50	0.47
0	1	2	27.50	0.00	14.35	8.85	0.13	5.40	5.80	0.40
0	1	2	27.60	0.00	10.25	6.45	0.10	4.30	4.60	0.45
0	1	2	27.60	0.00	10.85	7.05	0.10	4.60	5.10	0.47
0	1	2	27.60	0.00	18.15	11.90	0.33	6.00	6.00	0.33
0	1	2	27.60	0.00	20.40	8.20	0.00	8.60	9.15	0.45
48	1	2	27.81	1.00	19.45	12.60	0.62	9.00	9.70	0.50
50	1	2	27.81	1.00	25.30	15.50	0.60	9.25	10.10	0.40
49	1	2	27.81	1.00	26.20	16.90	1.10	10.40	12.00	0.46

Recent Specimens (continued)

SPNO	SP	PROV	LAT	DEP	L	W	M	HW	HL	HL/L
0	1	2	29.09	0.00	15.50	10.50	0.20	6.20	7.15	0.46
0	1	2	29.13	0.00	9.20	5.95	0.10	0.00	3.75	0.41
0	1	2	29.13	0.00	14.65	9.50	0.20	5.95	6.55	0.45
0	1	2	29.13	0.00	15.25	9.65	0.20	6.15	6.70	0.44
0	1	2	29.13	0.00	15.95	9.90	0.00	5.95	6.20	0.39
0	1	2	29.13	0.00	16.90	10.70	0.33	6.55	6.80	0.40
0	1	2	29.13	0.00	17.85	11.60	0.00	6.45	7.15	0.40
0	1	2	29.13	0.00	21.85	14.40	0.65	7.10	7.90	0.36
0	1	2	29.50	0.00	24.45	15.10	0.00	9.35	9.60	0.39
0	1	2	29.50	18.29	23.40	15.10	0.90	9.30	9.80	0.42
0	1	2	29.60	0.00	13.50	8.75	0.10	4.90	5.10	0.38
0	1	2	29.60	0.00	17.30	11.50	0.45	8.65	9.15	0.53
0	1	2	29.60	0.00	20.20	13.40	0.75	8.15	8.80	0.44
0	1	3	25.30	73.15	9.50	5.75	0.00	3.30	3.55	0.37
0	1	3	25.30	73.15	11.95	7.00	0.00	3.30	4.45	0.37
0	1	3	25.70	0.00	28.65	18.65	1.40	11.25	12.95	0.45
0	1	3	25.71	45.72	9.70	5.85	0.00	0.00	2.60	0.27
0	1	3	25.78	40.23	4.20	2.70	0.00	0.00	1.60	0.38
0	1	3	25.78	54.86	10.00	6.15	0.05	2.70	2.90	0.29
0	1	3	25.78	73.15	8.10	4.60	0.00	2.10	2.65	0.33
0	1	3	25.78	73.15	9.50	5.30	0.00	2.90	3.45	0.36
0	1	3	25.78	73.15	17.20	10.50	0.00	5.65	5.50	0.32
0	1	3	25.78	78.64	14.50	9.30	0.25	5.60	6.10	0.42
0	1	3	25.78	82.30	15.10	9.60	0.25	5.60	6.50	0.43
0	1	3	25.81	1.00	22.30	14.55	0.65	8.15	9.55	0.43
20	1	3	25.81	1.00	22.40	14.05	0.50	8.30	8.75	0.39
19	1	3	25.81	1.00	22.95	14.80	0.50	7.95	8.75	0.38
18	1	3	25.81	1.00	23.80	15.45	0.55	7.95	8.95	0.38
0	1	3	25.81	1.00	24.60	16.00	0.75	9.60	10.65	0.43
0	1	3	25.81	1.00	26.45	16.85	1.25	10.95	12.00	0.45
17	1	3	25.81	1.00	27.70	17.95	1.65	11.60	13.10	0.47
16	1	3	25.81	1.00	28.45	17.50	1.40	11.60	12.85	0.45
0	1	3	25.81	109.73	16.45	10.80	0.35	5.35	5.70	0.35
0	1	3	25.85	1.83	6.10	3.65	0.03	0.00	2.85	0.47
0	1	3	25.85	1.83	13.55	8.95	0.15	4.95	5.40	0.40
0	1	3	25.85	1.83	17.40	10.75	0.00	6.70	6.95	0.40
0	1	3	25.85	1.83	18.80	12.25	0.00	0.00	7.90	0.42
0	1	3	25.85	1.83	19.25	11.70	0.40	7.85	8.65	0.45
0	1	3	25.85	1.83	21.20	13.40	0.60	8.90	9.80	0.46
43	1	3	25.85	82.00	15.15	9.60	0.24	5.50	6.55	0.43
0	1	3	25.85	82.30	6.75	4.40	0.00	0.00	2.70	0.40
0	1	3	25.85	82.30	7.55	4.55	0.00	0.00	2.15	0.28
0	1	3	25.85	82.30	8.10	4.95	0.00	0.00	2.70	0.33
0	1	3	28.45	14.63	20.50	20.40	0.00	8.45	8.45	0.41
0	1	3	28.45	14.63	23.25	14.70	0.95	9.20	10.40	0.45
0	1	3	29.85	0.00	12.25	7.50	0.10	0.00	4.15	0.34
0	1	3	29.85	0.00	12.60	8.05	0.13	3.90	4.20	0.33
0	1	3	29.85	0.00	13.55	8.60	0.15	4.65	5.00	0.37

Recent Specimens (continued)

SPNO	SP	PROV	LAT	DEP	L	W	M	HW	HL	HL/L
0	1	3	29.85	0.00	13.70	8.50	0.15	4.75	5.15	0.38
0	1	3	29.85	0.00	14.65	9.35	0.15	4.40	4.85	0.33
0	1	3	29.85	0.00	15.95	10.45	0.20	5.50	6.00	0.38
0	1	3	29.85	0.00	19.95	12.90	0.60	7.80	8.75	0.44
0	1	3	29.85	0.00	23.00	14.95	0.75	9.00	9.70	0.42
0	1	3	29.85	0.00	25.45	16.65	1.30	10.15	11.40	0.45
0	1	4	33.61	16.46	17.95	12.05	0.00	0.00	7.30	0.41
0	1	4	33.61	25.60	5.30	3.25	0.03	0.00	2.25	0.42
0	1	4	33.61	25.60	9.85	6.35	0.10	4.15	4.50	0.46
0	1	4	33.61	25.60	14.90	9.50	0.25	5.60	6.45	0.43
0	1	4	33.61	25.60	15.35	9.90	0.25	5.30	6.20	0.40
0	1	4	33.61	25.60	17.05	10.40	0.00	7.20	7.85	0.46
0	1	4	33.61	25.60	18.75	11.40	0.55	8.65	9.30	0.50
0	1	4	33.68	0.00	26.00	16.85	1.00	9.80	10.95	0.42
0	1	4	33.86	0.00	9.95	6.00	0.00	3.55	3.75	0.38
0	1	4	33.86	0.00	12.85	9.00	0.10	4.90	5.30	0.41
0	1	4	33.86	0.00	16.60	10.80	0.15	6.00	6.45	0.39
0	1	4	33.86	13.72	5.15	3.35	0.00	0.00	2.30	0.45
0	1	4	33.86	13.72	5.90	3.70	0.00	0.00	2.75	0.47
0	1	4	33.86	13.72	6.15	4.15	0.00	0.00	0.00	0.00
0	1	4	33.86	13.72	6.75	4.55	0.00	0.00	3.00	0.44
0	1	4	33.86	13.72	7.60	5.00	0.00	3.00	3.45	0.45
0	1	4	33.86	13.72	9.80	6.40	0.00	0.00	0.00	0.00
0	1	4	33.86	13.72	10.50	6.80	0.00	3.90	4.40	0.42
0	1	4	33.86	13.72	12.75	8.55	0.00	5.95	7.10	0.56
0	1	4	33.86	13.72	13.00	8.35	0.00	5.05	5.45	0.42
0	1	4	33.86	13.72	13.10	8.45	0.13	5.40	6.00	0.46
0	1	4	33.86	13.72	14.65	9.65	0.00	5.50	6.30	0.43
0	1	4	33.86	13.72	14.90	9.35	0.00	5.30	6.05	0.41
0	1	4	33.86	13.72	15.60	9.75	0.20	6.30	6.95	0.45
0	1	4	33.86	13.72	18.00	11.40	0.35	6.90	7.85	0.44
0	1	4	33.86	13.72	20.15	13.00	0.00	6.95	7.80	0.39
0	1	4	33.86	13.72	23.20	15.40	0.75	8.85	9.90	0.43
0	1	4	33.86	13.72	34.00	23.50	2.90	12.45	14.00	0.41
0	1	4	34.20	2.29	19.00	12.70	0.00	8.90	9.30	0.49
0	1	4	34.20	2.29	23.85	16.10	0.00	9.30	9.85	0.41
0	1	4	34.38	0.00	4.45	2.95	0.00	0.00	2.00	0.45
0	1	4	34.38	0.00	8.10	4.85	0.00	3.00	3.25	0.40
0	1	4	34.43	40.23	5.80	3.60	0.00	0.00	2.45	0.42
0	1	4	34.43	40.23	5.85	4.00	0.00	0.00	2.40	0.41
0	1	4	34.43	40.23	9.70	6.00	0.05	3.85	4.15	0.43
0	1	4	34.70	0.00	9.00	6.90	0.00	0.00	3.05	0.34
0	1	4	34.70	0.00	11.95	8.05	0.00	3.65	4.00	0.33
0	1	4	34.70	0.00	12.15	7.95	0.00	5.00	5.30	0.44
0	1	4	34.70	0.00	12.35	7.85	0.00	4.45	4.80	0.39
0	1	4	34.70	0.00	12.50	8.00	0.00	4.70	5.35	0.43
0	1	4	34.70	0.00	12.80	8.60	0.10	5.20	5.60	0.44
0	1	4	34.70	0.00	13.95	8.85	0.13	5.25	5.65	0.41

Recent Specimens (continued)

SPNO	SP	PROV	LAT	DEP	L	W	M	HW	HL	HL/L
0	1	4	34.70	0.00	14.35	9.50	0.00	5.10	5.80	0.40
0	1	4	34.70	0.00	14.60	10.00	0.00	6.50	7.05	0.48
0	1	4	34.70	0.00	14.65	9.55	0.20	5.70	6.20	0.42
0	1	4	34.70	0.00	14.70	9.60	0.00	5.45	6.20	0.42
0	1	4	34.70	0.00	14.75	9.75	0.20	6.05	6.75	0.46
0	1	4	34.70	0.00	14.80	9.95	0.20	5.40	6.05	0.41
0	1	4	34.70	0.00	15.50	10.10	0.10	5.10	5.45	0.35
0	1	4	34.70	0.00	15.95	10.65	0.18	6.65	7.20	0.45
0	1	4	34.70	0.00	16.40	10.80	0.20	6.35	7.15	0.44
0	1	4	34.70	0.00	17.70	10.65	0.00	6.80	7.40	0.42
0	1	4	34.70	0.00	17.85	12.40	0.25	6.85	7.70	0.43
25	1	4	34.70	0.00	17.85	11.45	0.23	6.90	7.50	0.42
23	1	4	34.70	0.00	18.35	12.25	0.40	7.45	8.20	0.45
24	1	4	34.70	0.00	18.35	12.35	0.25	7.60	8.40	0.46
0	1	4	34.70	0.00	18.45	12.00	0.00	7.85	8.75	0.47
0	1	4	34.70	0.00	18.90	12.10	0.40	7.20	7.85	0.42
0	1	4	34.70	0.00	19.45	12.30	0.30	7.95	8.15	0.42
0	1	4	34.70	0.00	19.80	12.30	0.25	6.55	7.10	0.36
0	1	4	34.70	0.00	20.65	12.90	0.00	6.50	7.40	0.36
0	1	4	34.70	0.00	22.00	14.85	0.45	7.15	8.25	0.38
22	1	4	34.70	0.00	22.65	14.50	0.80	10.40	11.05	0.49
0	1	4	34.70	0.00	22.80	14.80	0.00	7.90	9.20	0.40
21	1	4	34.70	0.00	23.80	16.30	0.65	8.70	10.40	0.44
0	1	4	34.70	0.00	26.95	17.40	1.35	8.60	10.65	0.40
0	1	4	34.70	1.00	23.00	15.40	1.20	9.75	10.45	0.45
0	1	4	34.70	4.19	24.25	16.10	0.00	0.00	8.75	0.36
0	1	4	34.70	4.27	15.85	10.30	0.00	6.10	6.80	0.43
0	1	4	34.70	4.42	25.55	16.80	0.00	8.95	10.20	0.40
0	1	4	34.71	1.00	15.15	9.90	0.05	4.80	5.80	0.38
0	1	4	35.08	0.00	17.00	11.15	0.15	6.20	6.70	0.39
0	1	4	35.23	0.00	7.35	5.00	0.00	0.00	0.00	0.00
0	1	4	35.23	0.00	8.80	5.55	0.00	0.00	4.10	0.47
0	1	4	35.23	0.00	10.30	6.55	0.00	0.00	4.55	0.44
0	1	4	35.23	0.00	10.40	6.30	0.00	0.00	3.65	0.35
0	1	4	35.23	0.00	12.95	8.10	0.15	4.00	4.30	0.33
0	1	4	35.23	0.00	14.80	9.85	0.25	6.00	6.35	0.43
0	1	4	35.23	0.00	15.20	10.00	0.25	5.40	6.15	0.40
0	1	4	35.23	0.00	16.50	11.50	0.40	7.30	8.20	0.50
0	1	4	35.23	0.00	17.70	11.50	0.50	7.50	8.00	0.45
0	1	4	35.23	0.00	18.20	11.70	0.60	7.80	8.70	0.48
0	1	4	35.23	0.00	18.75	12.20	0.40	6.00	6.65	0.35
0	1	4	35.23	0.00	18.95	12.60	0.50	7.00	7.60	0.40
0	1	4	35.23	0.00	19.45	12.95	0.50	7.50	7.75	0.40
0	1	4	35.23	34.00	8.15	5.20	0.05	3.55	3.80	0.47
0	1	4	35.23	34.00	16.75	10.40	0.30	6.15	6.55	0.39
0	1	4	35.23	34.00	18.00	11.60	0.40	7.45	8.10	0.45
0	1	4	35.23	34.00	21.20	13.10	0.85	9.60	10.10	0.48
0	1	4	35.23	37.50	5.20	3.30	0.00	0.00	2.15	0.41

Recent Specimens (continued)

SPNO	SP	PROV	LAT	DEP	L	W	M	HW	HL	HL/L
0	1	4	35.23	37.50	6.00	3.85	0.00	0.00	2.70	0.45
0	1	4	35.23	37.50	7.00	4.40	0.00	0.00	3.20	0.46
28	1	5	37.00	0.00	30.15	21.25	1.75	9.85	11.50	0.38
0	1	5	37.11	0.00	25.40	17.00	1.55	11.00	12.00	0.47
27	1	5	37.11	0.00	26.85	18.35	0.85	9.45	10.40	0.39
26	1	5	37.11	0.00	27.00	17.50	0.84	9.20	10.10	0.37
0	1	5	37.11	0.00	35.05	25.30	4.20	13.60	14.50	0.41
0	1	5	37.15	0.00	19.80	13.00	0.25	6.10	6.95	0.35
14	1	5	37.34	0.00	44.05	31.15	5.40	16.15	19.40	0.44
0	1	5	37.57	0.00	30.15	21.25	1.80	9.85	11.10	0.37
0	1	5	37.98	0.00	28.35	20.00	1.40	11.35	12.80	0.45
0	1	5	37.98	0.00	36.90	24.30	3.25	13.00	14.85	0.40
6	1	5	37.98	0.00	37.45	26.95	3.80	13.35	15.60	0.42
0	2	1	24.55	0.00	14.90	9.40	0.30	6.00	6.55	0.44
0	2	1	24.55	0.00	19.75	12.80	0.65	6.70	7.25	0.37
0	2	1	24.55	0.00	20.15	13.25	0.73	7.75	8.60	0.43
0	2	1	24.55	0.00	20.70	14.10	0.80	7.80	8.50	0.41
0	2	1	24.55	0.00	21.15	14.00	0.85	6.90	7.60	0.36
0	2	1	24.55	0.00	21.65	14.55	0.75	7.60	8.55	0.39
0	2	1	24.55	0.00	22.45	14.80	0.85	8.00	9.00	0.40
0	2	1	24.55	0.00	22.75	14.50	1.00	7.65	8.65	0.38
0	2	1	24.55	0.00	22.80	15.20	0.98	9.00	9.80	0.43
0	2	1	24.55	0.00	22.90	16.20	1.05	8.70	9.55	0.42
0	2	1	24.55	0.00	23.00	15.75	1.20	8.00	8.20	0.36
0	2	1	24.55	0.00	23.10	14.85	1.10	8.95	10.10	0.44
0	2	1	24.55	0.00	23.35	16.05	1.00	7.60	8.90	0.38
0	2	1	24.55	0.00	23.55	15.70	1.10	8.20	9.20	0.39
0	2	1	24.55	0.00	24.50	15.85	1.35	10.20	11.10	0.45
0	2	1	24.55	0.00	25.00	16.70	1.50	9.30	10.15	0.41
0	2	1	24.55	0.00	25.10	17.20	1.30	8.95	9.85	0.39
0	2	1	24.55	0.00	25.40	17.20	1.55	10.55	11.40	0.45
0	2	1	24.55	0.00	25.50	17.45	1.40	8.90	10.00	0.39
0	2	1	24.55	0.00	25.95	16.85	1.50	9.50	10.50	0.40
0	2	1	24.55	0.00	25.95	17.45	1.60	10.10	11.05	0.43
0	2	1	24.55	0.00	26.25	17.15	1.50	9.35	10.40	0.40
0	2	1	24.55	0.00	26.25	18.10	1.45	10.55	11.70	0.45
0	2	1	24.55	0.00	26.40	18.45	2.70	12.95	14.70	0.56
0	2	1	24.55	0.00	27.00	18.20	1.90	11.70	12.90	0.48
0	2	1	24.55	0.00	27.20	19.60	1.95	11.20	13.20	0.49
0	2	1	24.55	0.00	27.35	17.90	1.80	11.00	12.00	0.44
0	2	1	24.55	0.00	28.15	19.00	1.80	11.40	12.65	0.45
0	2	1	24.55	0.00	29.45	20.80	1.90	10.10	11.55	0.39
0	2	1	24.55	0.00	30.20	19.40	1.95	10.10	11.20	0.37
0	2	1	24.55	0.00	30.90	20.35	2.40	11.80	12.70	0.41
0	2	1	24.55	0.00	34.70	23.10	2.65	14.50	15.45	0.45
0	2	1	24.55	1.00	17.10	11.00	0.38	5.90	5.95	0.35
0	2	1	24.55	1.00	19.25	12.85	0.75	7.15	7.85	0.41
0	2	1	24.55	1.00	19.55	12.50	0.60	6.95	7.75	0.40

Recent Specimens (continued)

SPNO	SP	PROV	LAT	DEP	L	W	M	HW	HL	HL/L
0	2	1	24.55	1.00	20.00	12.70	0.70	6.85	7.65	0.38
36	2	1	24.55	1.00	20.90	13.35	0.80	7.00	7.65	0.37
0	2	1	24.55	1.00	21.00	13.35	0.70	7.40	7.70	0.37
37	2	1	24.55	1.00	23.10	16.00	1.35	9.75	10.80	0.47
0	2	1	24.55	1.00	23.35	16.20	1.55	9.65	10.55	0.45
0	2	1	24.55	1.00	24.65	16.00	1.30	9.10	10.00	0.41
0	2	1	24.55	1.00	24.65	15.65	1.50	9.40	10.00	0.41
38	2	1	24.55	1.00	25.60	16.45	1.10	7.85	8.50	0.33
0	2	1	24.55	1.00	25.95	17.40	1.30	9.80	10.55	0.41
0	2	1	24.55	1.00	26.20	17.15	1.25	9.15	10.55	0.40
39	2	1	24.55	1.00	27.25	18.40	1.40	8.55	9.40	0.34
0	2	1	24.55	1.00	27.40	18.85	2.05	12.10	14.10	0.51
42	2	1	24.55	1.00	28.65	18.35	1.98	11.40	12.60	0.44
0	2	1	24.55	1.00	29.15	19.50	1.95	11.15	12.25	0.42
40	2	1	24.55	1.00	29.20	19.20	2.15	11.75	12.45	0.43
0	2	1	24.55	1.00	29.80	19.00	1.70	10.40	11.50	0.39
41	2	1	24.55	1.00	32.50	21.45	2.70	12.50	13.30	0.41
0	2	1	24.60	0.00	22.00	15.20	1.10	8.80	10.60	0.48
0	2	1	24.60	0.00	23.25	15.35	1.30	9.75	11.10	0.48
0	2	1	24.60	0.00	23.60	15.55	1.68	10.95	12.05	0.51
0	2	1	24.60	0.00	23.65	15.20	1.30	9.50	10.15	0.43
0	2	1	24.60	0.00	24.20	15.55	1.65	9.35	10.30	0.43
0	2	1	24.60	0.00	24.45	15.75	1.60	9.90	11.60	0.47
0	2	1	24.60	0.00	25.10	16.15	1.80	10.70	12.00	0.48
0	2	1	24.60	0.00	25.45	16.00	1.68	11.20	12.30	0.48
0	2	1	24.60	0.00	26.20	17.15	2.28	12.10	13.60	0.52
0	2	1	24.60	0.00	27.50	17.55	2.65	12.25	13.70	0.50
0	2	1	24.60	0.00	28.50	19.10	2.35	11.35	12.80	0.45
0	2	1	24.60	0.00	29.05	19.80	2.33	11.20	12.60	0.43
0	2	1	24.60	0.00	30.85	22.00	2.28	12.95	15.00	0.49
0	2	1	24.63	0.00	22.70	15.65	0.95	8.95	9.55	0.42
0	2	1	24.63	0.00	26.20	18.00	0.95	8.95	9.80	0.37
0	2	1	24.65	0.00	17.65	11.25	0.75	6.70	7.30	0.41
0	2	1	24.65	0.00	23.45	16.00	1.35	8.70	9.90	0.42
0	2	1	24.65	0.00	23.45	15.10	1.30	9.25	10.45	0.45
0	2	1	24.65	0.00	25.35	17.00	1.75	10.25	11.45	0.45
0	2	1	24.65	0.00	25.60	17.35	1.00	8.90	9.35	0.37
0	2	1	24.65	0.00	25.80	16.60	1.60	10.45	11.15	0.43
0	2	1	24.65	0.00	25.95	18.40	1.60	10.85	11.60	0.45
0	2	1	24.65	0.00	26.00	16.75	1.55	10.25	10.95	0.42
0	2	1	24.65	0.00	26.55	18.25	1.30	9.75	10.45	0.39
0	2	1	24.65	0.00	27.75	18.90	1.80	11.25	12.25	0.44
0	2	1	24.65	0.00	27.75	19.55	1.80	11.45	12.75	0.46
0	2	1	24.65	0.00	27.95	18.45	1.85	11.95	13.05	0.47
0	2	1	24.65	0.00	28.25	19.80	1.70	11.15	11.95	0.42
0	2	1	24.65	0.00	28.60	18.65	1.80	10.80	12.30	0.43
0	2	1	24.65	0.00	28.65	19.80	2.11	9.70	12.55	0.44
0	2	1	24.65	0.00	29.00	19.90	2.00	11.25	11.95	0.41

Recent Specimens (continued)

SPNO	SP	PROV	LAT	DEP	L	W	M	HW	HL	HL/L
0	2	1	24.65	0.00	29.40	20.10	2.05	12.00	12.65	0.43
0	2	1	24.65	0.00	29.50	20.80	3.20	13.00	15.00	0.51
0	2	1	24.65	0.00	29.60	19.95	2.05	10.90	12.80	0.43
0	2	1	24.65	0.00	29.80	19.75	2.05	10.75	11.85	0.40
0	2	1	24.65	0.00	30.50	19.95	2.35	12.75	13.90	0.46
0	2	1	24.65	0.00	30.55	21.05	2.10	10.75	12.10	0.40
0	2	1	24.65	0.00	30.70	19.95	1.81	10.05	11.10	0.36
0	2	1	24.65	0.00	30.80	21.20	2.70	12.10	15.20	0.49
0	2	1	24.65	0.00	30.90	20.05	2.68	13.85	15.10	0.49
0	2	1	24.65	0.00	33.70	22.85	3.75	13.25	15.30	0.45
0	2	1	24.65	0.00	33.80	22.50	3.30	13.75	14.95	0.44
0	2	1	24.65	0.00	33.90	22.20	0.00	16.50	18.00	0.53
0	2	1	24.65	0.00	34.25	22.85	2.70	14.50	15.85	0.46
0	2	1	24.65	0.00	35.85	24.95	3.80	14.40	16.00	0.45
33	2	1	24.65	27.00	14.15	9.15	0.23	5.20	5.75	0.41
34	2	1	24.65	27.43	19.00	12.60	0.75	7.10	8.00	0.42
35	2	1	24.65	27.43	31.70	21.50	2.95	12.85	14.85	0.47
0	2	1	24.66	1.00	24.80	16.65	1.25	9.05	9.90	0.40
0	2	1	24.66	1.00	32.00	21.70	2.60	11.25	12.55	0.39
0	2	1	24.88	0.00	34.00	23.50	3.45	14.00	15.80	0.46
0	2	1	24.88	1.00	20.70	13.90	0.85	8.80	9.30	0.45
0	2	1	24.88	1.00	28.70	19.45	2.15	11.10	12.45	0.43
0	2	1	24.88	1.00	29.65	21.05	2.60	12.40	14.55	0.49
5	2	1	24.88	1.00	33.25	23.20	3.00	13.65	14.30	0.43
0	2	1	24.88	1.00	33.70	22.45	4.05	14.35	15.25	0.45
0	2	3	25.81	1.00	19.60	12.85	0.65	7.80	8.20	0.42
0	2	3	25.81	1.00	24.80	16.40	1.40	10.35	11.20	0.45
0	2	3	25.81	1.00	27.90	18.20	1.25	9.05	10.50	0.38
0	2	3	25.85	0.00	23.40	14.85	0.95	8.05	9.55	0.41
0	2	3	26.95	0.00	27.40	18.65	1.40	9.30	9.95	0.36
0	4	1	24.52	164.59	14.95	8.60	0.10	5.00	5.95	0.40
30	4	1	24.55	64.01	23.95	14.60	0.75	7.55	8.80	0.37
0	4	3	25.78	68.49	18.00	11.10	0.15	5.40	6.45	0.36
32	4	3	25.78	68.50	14.20	8.65	0.22	5.25	5.00	0.35
31	4	3	25.78	69.00	17.95	11.10	0.23	5.45	6.45	0.36
29	4	3	25.78	76.81	15.00	9.80	0.25	5.00	5.95	0.40
4	4	3	25.81	36.58	25.10	16.75	1.30	8.20	9.00	0.36
7	5	1	24.45	219.00	55.45	37.00	4.70	17.60	17.70	0.32
15	5	1	24.48	164.00	47.10	30.25	4.00	17.40	17.60	0.37
0	5	4	35.23	0.00	46.55	32.90	5.38	18.85	19.80	0.43
0	5	5	37.00	0.00	23.75	16.20	0.30	7.45	7.25	0.31
13	5	5	37.00	104.00	40.00	26.65	1.90	12.15	12.25	0.31
12	5	5	37.00	104.00	41.30	27.55	2.70	15.00	15.05	0.36
11	5	5	37.00	104.00	44.95	29.35	2.90	15.10	14.65	0.33
10	5	5	37.00	104.00	46.40	29.25	3.70	14.35	14.45	0.31

Appendix E

PARAMETERS MEASURED FROM FOSSIL SPECIMENS

A value of zero indicates no reading was taken.

SPNO	SP	LAT	AGE	L	W	M	HW	HL	HL/L
0	A	26.74	2.05	3.60	2.25	0.00	0.00	1.60	0.44
0	A	26.74	2.05	3.65	2.40	0.00	0.00	2.40	0.66
0	A	26.74	2.05	4.30	2.80	0.00	0.00	2.40	0.56
0	A	26.74	2.05	4.75	3.00	0.00	0.00	2.35	0.49
0	A	26.74	2.05	6.20	4.20	0.00	0.00	3.25	0.52
0	A	26.77	2.05	3.75	2.60	0.00	0.00	2.25	0.60
0	A	26.77	2.05	3.95	2.65	0.00	0.00	2.35	0.59
0	A	26.77	2.05	4.40	3.00	0.00	0.00	2.75	0.63
0	A	26.77	2.05	4.45	3.25	0.00	0.00	2.10	0.47
0	A	26.82	0.12	3.45	2.20	0.00	0.00	1.90	0.55
0	A	26.82	0.13	4.75	3.15	0.00	0.00	2.50	0.53
25	A	27.26	2.05	5.95	4.20	0.00	0.00	3.65	0.61
24	A	27.26	2.05	6.80	4.85	0.00	4.15	4.25	0.62
0	A	30.39	4.00	4.50	3.25	0.00	0.00	2.55	0.57
0	A	30.50	16.10	3.25	2.25	0.00	0.00	1.20	0.37
0	A	30.50	16.10	5.65	3.95	0.00	0.00	3.05	0.54
0	A	33.76	2.05	3.00	2.00	0.00	0.00	1.50	0.50
0	A	33.76	2.05	3.70	2.45	0.00	0.00	1.80	0.49
0	A	33.76	2.05	3.75	2.40	0.00	0.00	2.60	0.69
0	A	33.76	2.05	4.00	2.65	0.00	0.00	1.90	0.47
0	A	33.76	2.05	4.30	2.90	0.00	0.00	2.35	0.55
0	A	33.76	2.05	4.50	3.30	0.00	0.00	2.35	0.52
0	A	33.76	2.05	4.70	3.35	0.00	0.00	2.70	0.57
0	A	33.83	2.05	3.40	2.30	0.00	0.00	2.10	0.62
0	A	33.83	2.05	3.65	2.35	0.00	0.00	1.95	0.53
0	A	33.86	4.00	3.90	2.70	0.00	0.00	2.15	0.55
0	A	33.86	4.00	4.00	2.85	0.00	0.00	2.15	0.54
0	A	33.86	4.00	4.00	2.65	0.00	0.00	2.15	0.54
0	A	33.86	4.00	4.10	2.65	0.00	0.00	2.15	0.52
0	A	33.86	4.00	4.10	2.60	0.00	0.00	2.00	0.49
0	A	33.86	4.00	4.15	2.75	0.00	0.00	2.10	0.51
0	A	33.86	4.00	4.20	2.90	0.00	0.00	2.20	0.52
0	A	33.86	4.00	4.30	2.95	0.00	0.00	2.15	0.50
0	A	33.86	4.00	4.30	3.00	0.00	0.00	2.10	0.49
0	A	33.86	4.00	4.35	2.90	0.00	0.00	2.45	0.56
0	A	33.86	4.00	4.45	3.15	0.00	0.00	2.40	0.54
0	A	33.86	4.00	4.45	2.90	0.00	0.00	1.95	0.44
0	A	33.86	4.00	4.50	3.00	0.00	0.00	3.00	0.67
0	A	33.86	4.00	4.55	3.20	0.00	0.00	2.50	0.55
0	A	33.86	4.00	4.65	3.20	0.00	0.00	2.90	0.62

Fossil Specimens (continued)

SPNO	SP	LAT	AGE	L	W	M	HW	HL	HL/L
0	A	33.86	4.00	4.70	3.10	0.00	0.00	2.75	0.59
0	A	33.86	4.00	4.70	3.15	0.00	0.00	2.20	0.47
0	A	33.86	4.00	4.80	3.25	0.00	0.00	2.55	0.53
0	A	33.86	4.00	4.80	3.35	0.00	0.00	2.45	0.51
0	A	33.86	4.00	4.85	3.60	0.00	0.00	2.90	0.60
0	A	33.86	4.00	4.90	3.20	0.00	0.00	2.75	0.56
0	A	33.86	4.00	4.95	3.40	0.00	0.00	2.35	0.47
0	A	33.86	4.00	5.05	3.35	0.00	0.00	2.45	0.49
0	A	33.86	4.00	5.05	3.30	0.00	0.00	2.40	0.48
0	A	33.86	4.00	5.10	3.45	0.00	0.00	2.95	0.58
0	A	33.86	4.00	5.45	3.85	0.00	0.00	2.90	0.53
0	A	33.86	4.00	5.60	3.90	0.00	3.10	3.10	0.55
0	A	33.86	4.00	5.65	0.00	0.00	0.00	2.90	0.51
61	A	33.86	4.00	5.95	4.20	0.00	3.35	3.40	0.57
0	A	33.86	4.00	6.00	4.00	0.00	3.35	3.40	0.57
0	A	33.86	4.00	6.05	4.00	0.00	3.40	3.45	0.57
15	D	26.74	2.05	31.10	19.70	1.31	9.95	11.85	0.38
13	B	26.74	2.05	43.05	30.05	5.00	15.95	16.00	0.37
0	B	26.74	2.05	46.30	0.00	5.80	17.10	18.30	0.40
1	B	30.50	16.10	7.35	4.75	0.00	0.00	3.20	0.44
0	C	26.74	2.05	13.95	7.40	0.00	3.90	4.25	0.30
3	C	27.34	4.00	11.25	7.15	0.00	0.00	1.15	0.10
0	D	26.74	2.05	6.25	3.90	0.00	2.80	3.10	0.50
0	D	26.74	2.05	9.35	5.45	0.00	3.30	3.50	0.37
23	D	31.11	4.00	22.85	14.90	0.65	8.15	9.00	0.39
0	D	33.64	2.05	8.55	5.40	0.00	3.15	3.35	0.39
0	D	33.76	2.05	8.70	5.30	0.00	2.90	3.10	0.36
0	D	33.76	2.05	23.95	16.35	0.80	8.65	10.00	0.42
0	D	33.83	2.05	4.55	2.85	0.00	0.00	1.55	0.34
0	D	33.83	2.05	4.70	3.10	0.00	0.00	1.80	0.38
0	D	33.83	2.05	4.90	3.10	0.00	0.00	2.40	0.49
0	D	33.83	2.05	5.15	3.15	0.00	0.00	1.85	0.36
0	D	33.83	2.05	5.50	3.90	0.00	0.00	2.15	0.39
0	D	33.83	2.05	5.55	3.35	0.00	2.25	2.40	0.43
0	D	33.83	2.05	5.85	0.00	0.00	0.00	2.35	0.40
0	D	33.83	2.05	5.95	3.90	0.00	0.00	2.30	0.39
0	D	33.83	2.05	6.00	3.95	0.00	0.00	2.15	0.36
0	D	33.83	2.05	6.25	4.20	0.00	3.00	3.25	0.52
0	D	33.83	2.05	7.55	5.00	0.00	2.90	3.10	0.41
0	D	33.83	2.05	11.35	7.60	0.00	4.00	4.30	0.38
0	D	33.83	2.05	13.35	8.95	0.00	5.30	5.95	0.45
6	D	33.83	2.05	14.45	9.40	0.00	4.85	5.25	0.36
0	D	33.86	4.00	7.20	4.45	0.00	0.00	2.95	0.41
0	E	26.74	2.05	5.80	3.65	0.00	0.00	2.20	0.38
0	E	26.74	2.05	17.30	9.45	0.25	5.25	5.60	0.32
0	E	26.74	2.05	22.95	18.10	0.60	6.70	7.70	0.34
14	E	26.74	2.05	33.00	21.00	1.54	9.75	9.85	0.30
0	E	26.77	2.05	3.80	2.30	0.00	0.00	1.20	0.32

Fossil Specimens (continued)

SPNO	SP	LAT	AGE	L	W	M	HW	HL	HL/L
0	E	26.77	2.05	3.85	2.50	0.00	0.00	1.60	0.42
0	E	26.79	2.05	39.10	0.00	0.00	0.00	11.20	0.29
22	E	27.26	2.05	15.45	9.50	0.36	4.65	5.25	0.34
21	E	27.26	2.05	19.05	10.70	0.41	5.40	6.25	0.33
20	E	27.26	2.05	21.00	15.35	0.87	7.45	8.35	0.40
19	E	27.26	2.05	21.00	12.75	0.45	5.40	6.20	0.30
18	E	27.26	2.05	23.75	14.30	0.69	6.45	7.70	0.32
17	E	27.26	2.05	26.00	15.15	0.87	7.15	8.15	0.31
0	E	27.32	4.00	9.70	6.30	0.00	3.50	3.80	0.39
0	E	27.32	4.00	11.25	7.50	0.00	4.15	4.55	0.40
0	E	27.32	4.00	13.95	9.05	1.50	6.15	6.90	0.49
0	E	27.32	4.00	17.70	11.70	0.00	6.25	7.10	0.40
0	E	27.32	4.00	19.75	13.25	0.00	8.05	8.90	0.45
0	E	27.32	4.00	20.70	13.30	0.00	7.10	8.05	0.39
0	E	27.32	4.00	21.15	15.90	0.00	8.75	10.15	0.48
0	E	27.32	4.00	21.70	14.00	0.45	6.40	7.15	0.33
0	E	27.32	4.00	22.00	14.25	0.70	8.85	9.80	0.45
0	E	27.32	4.00	23.25	15.65	0.80	8.40	10.35	0.45
0	E	27.32	4.00	24.15	15.80	0.60	9.10	10.95	0.45
0	E	27.32	4.00	24.70	14.90	0.80	6.75	8.20	0.33
0	E	27.32	4.00	31.00	20.40	2.00	11.45	12.75	0.41
0	E	27.32	4.00	31.45	22.40	2.30	11.70	13.00	0.41
0	E	27.32	4.00	32.40	22.05	3.10	12.80	15.30	0.47
0	E	27.32	4.00	33.00	22.65	2.80	11.95	14.50	0.44
0	E	27.32	4.00	35.20	24.30	2.95	13.40	15.15	0.43
0	E	27.32	4.00	35.75	24.20	3.10	12.50	14.90	0.42
0	E	27.32	4.00	37.60	26.45	4.60	15.40	18.55	0.49
0	E	27.32	4.00	41.00	26.75	6.20	15.30	17.30	0.42
0	E	27.32	4.00	41.65	27.45	3.75	12.20	14.10	0.34
0	E	27.32	4.00	43.20	29.30	0.00	16.15	17.95	0.42
0	E	30.50	16.10	4.15	2.60	0.00	0.00	1.45	0.35
0	E	30.50	16.10	5.25	3.20	0.00	0.00	1.95	0.37
0	E	30.50	16.10	6.05	3.85	0.00	0.00	2.80	0.46
0	E	30.50	16.10	6.95	3.65	0.00	0.00	2.30	0.33
0	E	30.50	16.10	7.00	4.10	0.00	0.00	2.60	0.37
0	E	30.50	16.10	7.20	4.70	0.00	0.00	2.80	0.39
0	E	30.50	16.10	7.50	4.95	0.00	0.00	2.65	0.35
0	E	30.50	16.10	8.00	5.05	0.00	0.00	2.75	0.34
0	E	30.50	16.10	8.15	5.25	0.00	0.00	3.75	0.46
0	E	30.50	16.10	9.15	5.85	0.00	0.00	4.30	0.47
0	E	30.50	16.10	9.20	6.10	0.00	0.00	4.00	0.43
0	E	30.50	16.10	11.00	6.95	0.00	0.00	4.35	0.40
0	E	33.76	2.05	20.00	12.15	0.50	6.00	6.85	0.34
0	E	33.76	2.05	20.25	11.80	0.35	5.15	6.00	0.30
0	E	33.76	2.05	22.90	14.35	0.85	7.15	8.50	0.37
7	E	33.76	2.05	25.80	16.20	0.70	6.20	6.55	0.25
16	E	33.84	2.05	30.10	17.65	0.94	7.45	8.20	0.27
0	F	39.46	14.30	5.45	3.50	0.00	0.00	1.70	0.31

Fossil Specimens (continued)

SPNO	SP	LAT	AGE	L	W	M	HW	HL	HL/L
0	F	39.46	14.30	7.70	4.95	0.00	0.00	2.65	0.34
0	F	39.46	14.30	8.45	5.45	0.00	0.00	3.20	0.38
0	F	39.46	14.30	9.10	5.80	0.00	0.00	3.05	0.34
0	F	39.46	14.30	11.25	7.35	0.00	0.00	3.90	0.35
0	F	39.46	14.30	12.40	8.10	0.30	4.00	4.30	0.35
0	F	39.46	14.30	13.15	8.60	0.00	4.30	4.65	0.35
0	F	39.46	14.30	13.25	8.70	0.30	4.60	4.70	0.35
0	F	39.46	14.30	13.40	8.90	0.00	5.05	5.40	0.40
0	F	39.46	14.30	14.80	11.35	0.00	4.80	5.05	0.34
0	F	39.46	14.30	15.85	10.25	0.35	4.75	5.05	0.32
0	F	39.46	14.30	17.25	0.00	0.00	0.00	6.65	0.39
0	F	39.46	14.30	17.45	11.40	0.45	6.45	6.80	0.39
0	F	39.46	14.30	17.45	11.40	0.00	6.45	6.70	0.38
0	F	39.46	14.30	17.85	11.60	0.00	6.40	6.90	0.39
0	F	39.46	14.30	17.85	0.00	0.00	6.35	6.85	0.38
0	F	39.46	14.30	18.70	13.00	0.45	6.90	7.65	0.41
0	F	39.46	14.30	20.30	13.35	0.00	6.95	7.55	0.37
0	F	39.46	14.30	20.35	13.40	0.55	7.15	7.55	0.37
0	F	39.46	14.30	20.60	14.05	0.55	7.75	8.05	0.39
0	F	39.46	14.30	20.70	13.55	0.65	8.30	8.85	0.43
0	F	39.46	14.30	21.10	14.45	0.75	9.00	9.70	0.46
0	F	39.46	14.30	21.30	13.95	0.65	9.10	9.55	0.45
59	F	39.46	14.30	22.00	14.80	0.80	9.10	9.60	0.44
0	F	39.46	14.30	22.60	15.95	0.65	0.00	8.65	0.38
9	F	39.46	14.30	25.70	16.40	1.05	11.00	11.25	0.44
0	F	39.46	14.30	25.90	17.55	0.00	11.55	12.15	0.47
0	F	39.46	14.30	26.05	16.95	1.05	10.10	10.50	0.40
0	F	39.46	14.30	26.20	16.85	0.00	10.25	10.55	0.40
58	F	39.46	14.30	26.40	18.00	0.84	10.95	11.70	0.44
57	F	39.46	14.30	28.60	18.35	0.44	12.60	13.60	0.48
56	F	39.46	14.30	29.15	19.80	1.37	13.00	14.45	0.50
0	F	39.56	14.30	14.25	9.05	0.00	6.05	6.65	0.47
0	F	39.56	14.30	15.40	10.45	0.30	5.35	5.55	0.36
0	F	39.56	14.30	23.20	15.30	0.00	0.00	0.00	0.00
0	G	39.39	14.30	26.00	16.25	1.85	13.35	14.70	0.57
0	G	39.46	14.30	5.95	3.70	0.00	0.00	2.85	0.48
0	G	39.46	14.30	6.75	4.30	0.00	0.00	2.90	0.43
0	G	39.46	14.30	6.80	4.50	0.00	0.00	2.95	0.43
0	G	39.46	14.30	9.35	5.90	0.00	0.00	3.70	0.40
0	G	39.46	14.30	11.65	7.30	0.25	4.35	4.80	0.41
0	G	39.46	14.30	12.50	7.60	0.25	0.00	4.85	0.39
0	G	39.46	14.30	12.60	8.25	0.00	5.00	5.50	0.44
0	G	39.46	14.30	13.00	8.60	0.00	5.45	5.90	0.45
0	G	39.46	14.30	13.05	8.50	0.40	6.70	7.20	0.55
0	G	39.46	14.30	13.10	8.65	0.35	5.45	5.85	0.45
0	G	39.46	14.30	13.55	8.25	0.35	5.80	6.30	0.46
0	G	39.46	14.30	13.75	8.60	0.40	6.35	6.70	0.49
0	G	39.46	14.30	13.80	8.80	0.30	5.25	5.75	0.42

Fossil Specimens (continued)

SPNO	SP	LAT	AGE	L	W	M	HW	HL	HL/L
0	G	39.46	14.30	14.20	9.10	0.40	6.15	6.55	0.46
0	G	39.46	14.30	14.30	9.00	0.35	5.55	5.85	0.41
0	G	39.46	14.30	14.65	9.15	0.35	5.80	6.40	0.44
0	G	39.46	14.30	15.15	9.60	0.35	6.30	6.75	0.45
0	G	39.46	14.30	15.35	9.60	0.35	6.75	7.25	0.47
0	G	39.46	14.30	15.60	10.25	0.40	7.30	7.70	0.49
0	G	39.46	14.30	15.60	10.30	0.00	6.90	7.95	0.51
0	G	39.46	14.30	15.80	9.85	0.40	6.65	7.00	0.44
0	G	39.46	14.30	15.90	9.50	0.40	6.45	6.75	0.42
0	G	39.46	14.30	15.95	10.30	0.40	6.35	6.95	0.44
0	G	39.46	14.30	16.00	10.25	0.00	6.30	7.00	0.44
0	G	39.46	14.30	16.05	0.00	0.00	7.55	8.10	0.50
0	G	39.46	14.30	16.40	10.75	0.40	6.45	6.90	0.42
0	G	39.46	14.30	16.75	11.00	0.00	7.20	7.85	0.47
0	G	39.46	14.30	17.60	10.95	0.50	7.30	7.70	0.44
0	G	39.46	14.30	17.65	11.40	0.58	8.10	8.50	0.48
0	G	39.46	14.30	17.75	10.35	0.50	7.90	8.20	0.46
0	G	39.46	14.30	17.90	11.30	0.50	7.45	8.20	0.46
0	G	39.46	14.30	17.95	11.60	0.45	6.65	7.50	0.42
0	G	39.46	14.30	18.35	11.15	0.60	8.15	8.75	0.48
0	G	39.46	14.30	18.60	12.50	0.65	8.40	9.10	0.49
0	G	39.46	14.30	18.70	12.55	0.40	7.10	8.40	0.45
0	G	39.46	14.30	18.80	11.75	0.55	8.10	8.75	0.47
0	G	39.46	14.30	18.95	12.00	0.65	8.30	8.80	0.46
0	G	39.46	14.30	18.95	11.85	0.55	7.30	7.65	0.40
0	G	39.46	14.30	19.20	12.30	0.60	7.40	8.20	0.43
0	G	39.46	14.30	19.35	12.35	0.40	7.25	7.60	0.39
0	G	39.46	14.30	19.55	12.40	0.70	8.75	9.45	0.48
0	G	39.46	14.30	20.50	13.25	0.55	8.20	8.95	0.44
55	G	39.46	14.30	20.95	13.70	0.95	10.70	11.45	0.55
0	G	39.46	14.30	21.20	13.95	0.00	9.05	9.60	0.45
0	G	39.46	14.30	21.30	13.85	0.00	9.00	9.55	0.45
0	G	39.46	14.30	21.35	17.45	1.40	10.75	11.85	0.56
0	G	39.46	14.30	21.95	13.95	1.00	9.65	10.75	0.49
0	G	39.46	14.30	22.30	14.60	0.75	7.65	8.55	0.38
0	G	39.46	14.30	22.60	14.70	0.95	9.80	10.50	0.46
54	G	39.46	14.30	22.95	15.45	1.00	10.50	11.00	0.48
0	G	39.46	14.30	23.25	14.55	1.00	10.00	10.40	0.45
0	G	39.46	14.30	23.50	14.65	0.00	12.10	13.00	0.55
0	G	39.46	14.30	24.20	0.00	0.00	0.00	11.25	0.46
53	G	39.46	14.30	25.10	16.30	1.14	11.95	13.00	0.52
52	G	39.46	14.30	25.55	16.55	1.10	11.15	12.05	0.47
8	G	39.46	14.30	26.65	17.85	1.25	12.30	13.15	0.49
0	G	39.56	14.30	12.35	8.00	0.00	5.40	5.95	0.48
0	G	39.56	14.30	12.80	8.25	0.00	0.00	5.50	0.43
0	G	39.56	14.30	16.60	10.30	0.00	6.25	6.80	0.41
0	G	39.56	14.30	16.85	10.85	0.45	6.65	7.45	0.44
0	G	39.56	14.30	17.45	11.20	0.45	7.55	8.20	0.47

Fossil Specimens (continued)

SPNO	SP	LAT	AGE	L	W	M	HW	HL	HL/L
0	G	39.56	14.30	18.80	11.65	0.50	8.05	8.95	0.48
0	G	39.56	14.30	25.75	16.00	0.00	11.90	12.95	0.50
0	H	37.13	7.73	34.80	26.75	0.00	17.10	19.55	0.56
0	H	37.13	7.73	35.65	27.60	0.00	18.35	21.60	0.61
40	H	37.20	4.00	31.95	24.35	1.50	12.40	14.00	0.44
0	H	37.23	4.00	32.00	24.85	2.50	15.40	17.60	0.55
0	H	37.23	4.00	36.30	29.10	4.00	19.45	20.45	0.56
0	H	37.23	4.00	36.85	27.00	0.00	19.90	22.15	0.60
0	H	37.25	4.00	26.85	20.70	0.00	10.25	12.50	0.47
44	H	38.10	7.73	22.45	17.65	0.60	10.80	12.40	0.55
42	H	38.10	7.73	25.20	20.55	1.10	13.95	15.95	0.63
43	H	38.10	7.73	26.45	20.80	0.90	10.30	13.05	0.49
4	H	38.10	7.73	26.90	21.50	0.86	13.40	15.60	0.58
12	I	27.05	2.05	39.60	30.00	3.51	12.70	13.60	0.34
11	I	27.05	2.05	45.85	36.70	7.57	16.25	18.30	0.40
10	I	27.05	2.05	46.60	38.20	7.84	15.80	17.65	0.38
0	I	27.32	4.00	36.05	29.30	2.50	10.85	12.55	0.35
2	I	27.32	4.00	36.65	27.75	2.80	11.00	10.40	0.28
0	J	27.34	4.00	20.40	14.85	0.00	0.00	7.60	0.37
0	J	27.34	4.00	37.50	27.00	0.00	0.00	16.00	0.43
0	J	37.14	7.73	36.45	23.75	0.00	13.75	15.15	0.42
0	J	38.39	13.40	10.50	7.45	0.00	0.00	3.50	0.33
0	J	38.39	13.40	33.10	22.85	0.00	10.15	11.15	0.34
0	J	38.46	13.00	15.75	0.00	0.00	0.00	4.40	0.28
0	J	38.46	13.00	23.10	15.60	0.50	6.25	7.00	0.30
0	J	38.47	13.00	21.50	14.50	3.50	7.00	7.35	0.34
0	J	38.47	13.00	25.35	16.40	0.00	8.40	9.00	0.36
0	J	38.54	13.00	22.55	14.05	0.40	7.95	8.35	0.37
0	J	38.54	13.00	39.10	26.60	3.05	16.90	17.55	0.45
0	J	38.57	14.00	33.90	24.00	1.60	14.30	15.40	0.45
0	J	38.57	14.00	37.20	26.15	2.15	15.00	16.20	0.44
0	J	38.58	14.00	23.60	16.60	0.35	9.15	9.40	0.40
0	J	38.58	14.00	26.70	19.00	0.55	9.00	9.65	0.36
51	J	38.58	14.00	30.85	21.70	1.40	14.30	14.90	0.48
0	J	38.58	14.00	30.85	21.70	1.30	12.20	12.75	0.41
49	J	38.58	14.00	33.30	23.35	1.35	12.65	14.45	0.43
50	J	38.58	14.00	33.35	23.35	1.30	13.50	14.80	0.44
48	J	38.58	14.00	34.80	25.95	0.00	14.20	15.80	0.45
0	J	38.58	14.00	34.90	23.85	0.00	12.20	13.00	0.37
60	J	38.58	14.00	38.50	27.60	2.80	16.90	17.55	0.46
0	J	38.58	14.00	39.25	27.00	2.40	16.10	18.25	0.46
0	J	38.58	14.00	39.30	28.25	0.00	14.15	15.00	0.38
47	J	38.58	14.00	39.40	27.90	2.55	17.65	19.35	0.49
0	J	38.58	14.00	44.95	30.95	3.45	16.50	18.50	0.41
0	J	38.59	14.00	22.45	15.90	0.00	7.90	8.10	0.36
0	J	38.59	14.00	27.40	20.70	0.90	0.00	11.75	0.43
0	J	38.59	14.00	49.70	33.20	4.25	18.65	21.50	0.43
0	J	38.60	14.00	6.75	4.40	0.00	0.00	2.50	0.37

Fossil Specimens (continued)

SPNO	SP	LAT	AGE	L	W	M	HW	HL	HL/L
0	J	38.60	14.00	9.65	6.60	0.00	0.00	3.70	0.38
0	J	38.60	14.00	9.90	6.65	0.00	0.00	3.40	0.34
0	J	38.60	14.00	11.40	7.60	0.00	0.00	4.65	0.41
0	J	38.60	14.00	12.45	8.25	0.05	4.65	5.00	0.40
0	J	38.60	14.00	15.00	10.85	0.10	5.40	6.25	0.42
0	J	38.60	14.00	16.80	11.70	0.10	6.00	6.20	0.37
0	J	38.60	14.00	20.50	14.45	0.00	7.35	7.40	0.36
0	J	38.60	14.00	20.75	14.35	0.35	8.60	8.95	0.43
0	J	38.60	14.00	26.70	18.35	0.00	9.95	10.20	0.38
0	J	38.60	14.00	26.95	19.70	0.00	10.45	10.45	0.39
0	J	38.60	14.00	27.40	20.70	0.00	12.20	13.25	0.48
0	J	38.60	14.00	29.50	21.00	0.00	12.65	13.45	0.46
0	J	38.60	14.00	30.45	21.20	1.35	14.05	14.60	0.48
0	J	38.60	14.00	31.65	21.45	1.35	11.65	11.50	0.36
0	J	38.60	14.00	32.90	24.15	1.45	12.95	14.00	0.43
0	J	38.60	14.00	34.40	24.95	1.20	12.80	12.80	0.37
0	J	38.60	14.00	37.65	26.80	2.50	14.90	15.15	0.40
0	J	38.60	14.00	38.60	26.00	4.10	18.70	0.00	0.00
0	J	38.63	14.00	21.90	14.55	0.00	9.10	9.65	0.44
0	J	38.63	14.00	27.50	20.65	0.00	10.30	0.00	0.00
0	J	38.63	14.00	28.30	19.20	1.20	13.10	13.45	0.48
0	J	38.63	14.00	29.70	20.95	1.15	12.30	12.80	0.43
0	J	38.63	14.00	29.75	20.15	0.00	11.60	12.35	0.42
0	J	38.63	14.00	34.25	21.90	1.70	11.80	12.80	0.37
0	J	38.63	14.00	37.60	25.25	2.85	18.00	18.95	0.50
0	J	38.63	14.00	37.60	25.00	2.25	15.70	16.70	0.44
0	J	38.72	13.00	20.65	13.40	0.25	5.70	5.95	0.29
0	J	38.72	13.00	23.80	0.00	0.00	6.95	7.55	0.32
0	J	38.72	13.00	26.20	17.10	0.55	6.40	7.00	0.27
0	K	36.05	4.70	33.10	23.95	0.00	16.00	17.50	0.53
0	K	36.05	4.70	50.60	36.10	0.00	21.70	22.25	0.44
0	K	36.44	4.70	33.95	23.85	2.25	16.30	16.75	0.49
0	K	36.58	4.00	27.80	22.60	1.45	0.00	15.30	0.55
0	K	36.73	4.00	33.85	25.55	0.00	12.65	13.50	0.40
0	K	36.87	4.00	11.60	8.70	0.00	4.65	4.85	0.42
0	K	36.87	4.00	29.30	22.15	1.50	12.15	12.50	0.43
0	K	36.87	4.00	37.00	27.45	3.30	16.45	17.55	0.47
0	K	36.94	4.00	30.00	22.85	0.00	15.15	15.90	0.53
0	K	36.98	4.00	21.95	16.75	0.00	9.80	10.20	0.46
0	K	36.98	4.00	24.85	18.90	0.00	9.30	9.40	0.38
0	K	37.06	4.00	31.40	24.20	2.05	13.50	14.75	0.47
0	K	37.06	4.00	32.25	24.25	0.00	16.00	16.45	0.51
0	K	37.06	4.00	38.25	29.50	3.55	16.10	17.40	0.45
0	K	37.07	4.00	34.95	26.15	0.00	16.70	17.95	0.51
0	K	37.07	4.00	40.65	31.15	5.95	17.05	18.45	0.45
31	K	37.07	4.00	50.10	37.80	0.00	22.45	24.00	0.48
0	K	37.07	4.00	52.70	37.60	0.00	21.40	0.00	0.00
0	K	37.13	7.73	28.75	23.40	0.00	12.20	13.10	0.46

Fossil Specimens (continued)

SPNO	SP	LAT	AGE	L	W	M	HW	HL	HL/L
0	K	37.13	7.73	35.80	27.70	0.00	0.00	18.85	0.53
0	K	37.13	7.73	43.30	32.30	0.00	19.40	21.70	0.50
0	K	37.13	4.00	48.30	34.00	0.00	20.10	21.60	0.45
0	K	37.14	7.73	32.25	23.65	2.50	15.95	18.00	0.56
0	K	37.14	7.73	35.00	26.20	0.00	15.10	17.40	0.50
0	K	37.16	4.00	38.60	28.60	2.90	15.55	16.40	0.42
0	K	37.20	4.00	12.10	8.85	0.00	0.00	0.00	0.00
0	K	37.20	4.00	15.65	11.50	0.10	5.95	6.20	0.40
0	K	37.20	4.00	21.65	16.30	0.00	0.00	0.00	0.00
0	K	37.20	4.00	29.40	22.80	0.00	0.00	0.00	0.00
0	K	37.20	4.00	33.20	23.05	2.50	15.90	16.65	0.50
0	K	37.20	4.00	33.40	25.20	2.00	12.85	13.50	0.40
0	K	37.20	4.00	34.30	25.15	0.00	0.00	0.00	0.00
39	K	37.20	4.00	34.85	26.35	2.95	16.70	18.85	0.54
38	K	37.20	4.00	38.35	28.70	3.67	19.10	20.40	0.53
37	K	37.20	4.00	38.95	30.70	2.85	17.65	18.55	0.48
0	K	37.22	4.00	31.30	22.15	1.80	12.95	13.30	0.42
0	K	37.22	4.00	41.40	30.90	3.90	18.55	20.40	0.49
0	K	37.23	4.00	34.70	25.30	2.95	14.85	15.35	0.44
0	K	37.23	7.73	35.85	26.15	0.00	15.65	16.95	0.47
0	K	37.23	4.00	39.25	28.40	0.00	17.30	17.50	0.45
0	K	37.23	4.00	39.40	28.15	0.00	17.65	18.65	0.47
0	K	37.23	4.00	45.25	34.85	5.05	20.60	22.90	0.51
0	K	37.63	4.00	4.30	2.95	0.00	0.00	1.90	0.44
0	K	37.63	4.00	34.70	25.95	3.00	17.90	19.50	0.56
0	K	38.10	7.73	19.55	15.20	0.40	8.50	9.00	0.46
0	K	38.10	7.73	29.55	21.95	1.50	15.30	16.90	0.57
41	K	38.10	7.73	37.95	28.30	2.71	16.60	19.10	0.50
0	K	38.61	14.00	37.30	27.30	2.00	14.65	15.85	0.42
0	L	35.84	4.70	16.10	12.10	0.30	7.70	7.95	0.49
0	L	35.84	4.70	20.25	15.15	0.00	9.30	10.30	0.51
0	L	35.84	4.70	21.75	16.20	0.95	11.20	11.50	0.53
0	L	35.84	4.70	22.80	17.60	0.60	10.50	11.85	0.52
0	L	35.84	4.70	25.45	19.55	1.10	12.85	14.00	0.55
0	L	36.35	4.70	32.45	25.10	0.00	14.25	14.80	0.46
0	L	36.44	4.70	28.35	22.00	1.15	11.65	11.75	0.41
0	L	36.47	4.70	27.15	21.30	1.15	13.00	13.75	0.51
0	L	36.58	4.00	5.95	4.15	0.00	0.00	2.50	0.42
0	L	36.58	4.00	25.00	18.45	0.65	0.00	9.95	0.40
0	L	36.58	4.00	26.70	20.00	1.35	12.45	13.55	0.51
0	L	36.58	4.00	34.70	24.85	0.00	17.95	19.30	0.56
0	L	36.87	4.00	7.60	5.35	0.00	0.00	2.55	0.34
0	L	37.07	4.00	22.70	16.00	0.00	9.70	10.30	0.45
46	L	37.07	4.00	26.70	20.70	1.15	12.25	13.10	0.49
0	L	37.07	4.00	33.10	0.00	0.00	13.55	14.80	0.45
0	L	37.07	4.00	33.90	25.20	3.25	16.40	17.50	0.52
0	L	37.07	4.00	34.00	24.50	3.65	18.85	19.50	0.57
45	L	37.07	4.00	41.00	30.50	5.60	17.60	18.20	0.44

Fossil Specimens (continued)

SPNO	SP	LAT	AGE	L	W	M	HW	HL	HL/L
0	L	37.13	7.73	14.70	11.10	0.20	5.40	5.75	0.39
36	L	37.13	7.73	21.00	16.15	0.45	7.45	8.00	0.38
35	L	37.13	7.73	22.65	17.70	0.85	10.15	12.00	0.53
0	L	37.13	7.73	27.95	20.75	1.15	12.65	13.25	0.47
34	L	37.13	7.73	30.80	23.25	1.14	12.55	13.50	0.44
0	L	37.13	7.73	31.35	23.65	1.35	16.45	16.95	0.54
33	L	37.13	7.73	35.25	26.95	2.55	15.75	16.95	0.48
32	L	37.13	7.73	40.35	29.85	3.59	18.60	19.95	0.49
0	L	37.23	4.00	33.40	25.00	2.60	17.90	19.40	0.58
0	L	37.23	4.00	34.00	23.55	2.65	17.60	18.95	0.56
0	L	37.25	4.00	30.45	24.00	1.30	13.65	15.20	0.50
0	L	37.26	4.00	11.40	8.35	0.00	0.00	4.30	0.38
0	L	37.28	4.00	16.35	11.75	0.00	0.00	0.00	0.00
0	L	37.28	4.00	20.35	15.25	0.00	8.75	9.40	0.46
0	L	37.28	4.00	33.25	25.00	0.00	15.85	16.50	0.50
0	L	38.10	4.00	36.15	24.15	0.00	0.00	0.00	0.00
0	M	30.39	4.00	40.50	28.90	2.65	15.05	16.20	0.40
0	M	33.86	4.00	11.30	8.10	0.00	3.85	3.95	0.35
0	M	33.86	4.00	12.55	9.15	0.00	4.55	4.95	0.39
30	M	33.86	4.00	15.75	11.70	0.15	5.40	5.45	0.35
29	M	33.86	4.00	31.20	22.75	1.75	11.45	11.70	0.38
28	M	33.86	4.00	45.45	34.65	5.05	19.00	20.75	0.46
0	M	35.57	4.70	36.90	27.35	2.80	13.55	14.00	0.38
0	M	36.68	4.00	5.45	3.90	0.00	0.00	2.00	0.37
0	M	36.68	4.00	14.15	10.10	0.00	5.20	5.55	0.39
0	M	36.68	4.00	14.30	10.15	0.00	4.85	4.95	0.35
0	M	36.68	4.00	15.00	10.75	0.00	5.35	5.70	0.38
0	M	36.68	4.00	17.75	12.60	0.00	6.15	6.40	0.36
0	M	36.68	4.00	20.55	15.35	0.00	7.45	7.95	0.39
0	M	36.68	4.00	23.80	17.40	0.70	7.75	7.95	0.33
0	M	36.68	4.00	25.40	19.30	1.05	9.00	9.65	0.38
0	M	37.07	4.00	14.60	10.50	0.00	5.55	5.80	0.40
0	M	37.07	4.00	22.75	16.70	0.85	8.50	8.85	0.39
0	M	37.07	4.00	26.20	19.00	0.00	9.55	10.00	0.38
0	M	37.07	4.00	28.80	22.00	1.55	10.80	11.50	0.40
0	M	37.07	4.00	30.45	22.60	1.50	11.85	12.15	0.40
0	M	37.23	4.00	23.25	17.50	0.50	7.35	8.10	0.35
0	M	37.23	4.00	28.85	0.00	0.00	11.65	12.00	0.42
0	M	37.27	4.00	29.05	22.90	1.50	10.70	11.60	0.40
0	M	37.64	7.73	31.05	20.00	0.00	10.25	10.30	0.33
27	M	37.64	7.73	40.25	29.65	2.60	13.95	14.65	0.36
26	M	37.64	7.73	50.00	34.10	6.00	19.40	22.75	0.45
5	M	37.64	7.73	64.50	45.95	7.50	19.95	22.90	0.36
0	N	26.74	2.05	52.00	41.15	0.00	0.00	17.75	0.34

Appendix F

DATA FOR RECENT REFERENCE SPECIMENS

SPNO	SP	FX	FY	FTOP	FSIDE	FINC	PCURV	LRIB	MRIB	SRIB	TOTRIB
20	1	3.9	2.0	3	3	22	0.057	0	10	10	20
50	1	5.0	2.1	3	3	22	0.070	0	23	0	23
1	1	5.8	3.9	2	1	1	0.068	0	11	11	22
21	1	4.0	2.0	3	3	29	0.071	0	29	0	29
51	1	5.4	2.9	3	3	25	0.096	0	13	13	26
2	1	4.8	3.1	2	3	30	0.108	15	5	0	20
22	1	4.7	2.8	3	3	29	0.118	0	27	0	27
52	1	6.1	3.0	3	3	24	0.084	0	13	13	26
3	1	8.5	4.0	4	3	33	0.078	0	21	0	21
23	1	3.8	1.8	3	3	24	0.083	0	23	0	23
43	1	2.8	1.8	3	3	17	0.056	0	10	10	20
53	1	7.0	4.0	3	3	27	0.102	0	23	0	23
14	1	8.1	3.1	3	3	37	0.118	0	41	0	41
24	1	4.1	2.0	3	3	32	0.127	0	29	0	29
44	1	4.0	1.0	3	3	19	0.088	0	25	0	25
25	1	3.1	1.7	3	3	28	0.065	0	29	0	29
45	1	5.0	2.2	3	2	33	0.106	0	24	0	24
6	1	10.2	4.1	3	3	35	0.117	0	20	19	39
16	1	5.0	2.8	3	3	40	0.141	0	12	12	24
26	1	5.0	3.0	3	3	25	0.085	0	11	33	44
46	1	4.1	2.1	3	2	27	0.131	0	25	0	25
17	1	5.0	3.0	3	3	33	0.116	0	12	12	24
27	1	5.6	2.5	3	3	30	0.081	0	0	41	41
47	1	5.0	2.1	3	2	22	0.067	0	28	0	28
18	1	4.8	2.0	3	3	17	0.066	0	9	9	18
28	1	6.1	2.3	3	3	23	0.057	0	20	20	40
48	1	3.1	2.0	3	2	36	0.077	0	24	0	24
49	1	4.9	2.1	3	3	35	0.103	0	23	0	23
40	2	4.8	2.4	3	2	19	0.074	5	5	0	10
41	2	5.0	2.8	3	2	12	0.103	6	6	0	12
42	2	5.0	2.8	2	1	28	0.111	5	5	0	10
33	2	2.0	1.1	3	1	10	0.071	5	5	0	10
34	2	2.8	2.0	2	1	7	0.105	5	5	0	10
5	2	9.0	4.6	3	3	17	0.053	5	5	0	10
35	2	5.0	2.5	2	2	28	0.143	6	6	0	12
36	2	3.0	1.8	3	3	16	0.065	5	5	0	10
37	2	3.5	2.1	3	2	22	0.133	6	6	0	12
38	2	3.1	2.0	3	2	14	0.076	5	5	0	10
39	2	4.0	2.1	3	3	7	0.000	5	5	0	10
30	4	5.5	2.2	3	3	24	0.113	0	0	24	24

Recent Reference Specimens (continued)

SPNO	SP	FX	FY	FTOP	FSIDE	FINC	PCURV	LRIB	MRIB	SRIB	TOTRIB
31	4	3.5	1.9	3	2	21	0.113	0	0	25	25
32	4	2.9	1.1	3	2	9	0.067	0	0	25	25
4	4	12.8	3.0	3	3	21	0.087	0	24	0	24
29	4	2.1	1.0	3	1	19	0.143	0	13	13	26
10	5	5.8	6.1	1	1	12	0.027	0	0	56	56
11	5	6.0	5.0	1	2	19	0.037	0	0	60	60
12	5	5.1	5.1	1	1	28	0.062	0	0	62	62
13	5	5.0	4.7	1	1	10	0.000	0	0	60	60
15	5	6.4	6.1	1	2	20	0.036	0	0	66	66
7	5	6.9	6.1	1	2	22	0.000	0	0	75	75

Appendix G

DATA FOR FOSSIL REFERENCE SPECIMENS

SPNO	SP	FX	FY	FTOP	FSIDE	FINC	PCURV	LRIB	MRIB	SRIB	TOTRIB
61	A	1.7	1.4	1	1	11	0.083	0	13	5	18
24	A	1.0	1.0	1	1	4	0.126	0	11	1	12
25	A	1.0	1.0	1	1	5	0.125	0	11	1	12
1	B	3.2	1.7	3	1	16	0.080	6	6	12	24
13	B	8.0	4.8	3	2	38	0.114	8	8	5	21
3	C	4.3	1.9	3	2	18	0.036	6	6	0	12
23	D	4.6	2.3	3	3	24	0.076	0	12	11	23
6	D	4.6	2.0	3	3	14	0.045	0	22	0	22
20	E	4.8	1.8	3	3	17	0.079	0	13	10	23
21	E	4.1	1.7	3	3	19	0.131	0	12	8	20
22	E	4.1	1.3	3	3	16	0.068	0	12	6	18
14	E	7.9	2.8	3	3	17	0.091	14	0	0	14
15	E	8.0	2.9	3	3	26	0.079	12	2	0	14
16	E	7.4	3.7	3	3	19	0.067	0	24	0	24
7	E	10.8	4.0	3	3	8	0.020	0	16	6	22
17	E	6.4	2.1	3	3	20	0.067	0	18	3	21
18	E	7.7	2.5	3	3	16	0.092	0	13	4	17
19	E	5.9	1.9	3	3	19	0.100	0	11	11	22
56	F	7.1	4.0	3	3	22	0.114	0	0	29	29
57	F	6.2	4.3	3	3	16	0.082	0	0	28	28
58	F	5.5	3.3	3	1	23	0.069	0	0	24	24
9	F	8.0	4.9	2	1	24	0.060	0	29	0	29
59	F	4.0	2.1	3	2	22	0.079	0	0	26	26
52	G	5.0	2.2	3	3	28	0.129	0	0	32	32
53	G	5.1	2.1	3	3	30	0.112	0	0	32	32
54	G	4.9	2.2	3	3	30	0.099	0	0	32	32
55	G	4.2	2.1	3	3	25	0.103	0	0	27	27
8	G	7.0	5.0	3	1	29	0.110	0	24	5	29
42	H	4.4	3.9	1	2	39	0.113	0	9	30	39
43	H	3.8	3.2	1	2	16	0.078	0	11	29	40
4	H	6.7	4.8	1	2	30	0.080	0	27	16	43
44	H	4.0	3.0	1	1	35	0.064	0	20	17	37
10	I	15.8	6.1	3	3	9	0.084	0	21	0	21
11	I	16.8	6.2	3	3	17	0.089	0	24	0	24
2	I	14.0	4.5	3	3	8	0.000	0	35	0	35
12	I	11.9	4.7	3	3	14	0.049	0	27	0	27
50	J	7.2	5.9	1	2	25	0.024	0	0	36	36
60	J	11.1	9.1	1	2	19	0.090	0	10	29	39
51	J	8.1	6.9	1	2	24	0.046	0	0	39	39
47	J	9.1	7.1	2	2	29	0.073	0	0	54	54

Fossil Reference Specimens (continued)

SPNO	SP	FX	FY	FTOP	FSIDE	FINC	PCURV	LRIB	MRIB	SRIB	TOTRIB
48	J	7.9	6.9	1	2	22	0.059	0	0	39	39
49	J	7.2	6.0	1	2	19	0.025	0	0	35	35
31	K	7.0	6.5	1	2	33	0.080	0	17	29	46
41	K	5.9	5.4	1	2	31	0.098	0	0	47	47
37	K	5.8	5.6	1	2	33	0.065	0	0	43	43
38	K	5.5	5.0	1	2	26	0.010	0	0	49	49
39	K	5.9	5.3	1	2	25	0.075	0	0	39	39
40	L	4.3	4.0	1	2	26	0.064	0	0	48	48
32	L	6.4	6.1	1	2	34	0.086	0	9	44	53
33	L	5.7	4.9	1	1	24	0.093	0	0	55	55
34	L	4.7	4.1	1	2	18	0.078	0	0	48	48
35	L	3.2	2.9	1	2	29	0.091	0	10	29	39
45	L	6.5	6.0	1	2	19	0.138	0	9	45	54
36	L	4.0	3.0	1	2	28	0.054	0	10	27	37
46	L	4.0	3.0	1	1	24	0.081	0	0	36	36
30	M	2.7	2.0	1	1	6	0.000	0	0	39	39
5	M	11.1	9.7	2	2	23	0.073	0	40	0	40
26	M	11.0	9.0	1	2	17	0.128	0	0	50	50
27	M	6.8	6.0	1	2	19	0.055	0	0	36	36
28	M	9.0	7.5	1	2	16	0.050	0	0	57	57
29	M	5.7	5.0	1	2	23	0.088	0	0	43	43

PLATE 1

D. cayenensis (Lamarck), a=apical view, b=lateral view

(Figure 1): Specimen number 2, Gulf side of Key West, Province 2, latitude= 24.55, water depth= 91.4 m.

(Figure 2): Specimen number 50, Madiera Beach, Fla., Province 2, latitude=27.81, water depth=intertidal.

(Figure 3): Specimen number 28, Chesapeake Bay, Province 5, latitude=37.0, no water depth recorded.

(Figure 4): Specimen number 6, Chincoteague Island, Va., Province 5, latitude=37.98, water depth=intertidal.

PLATE 1

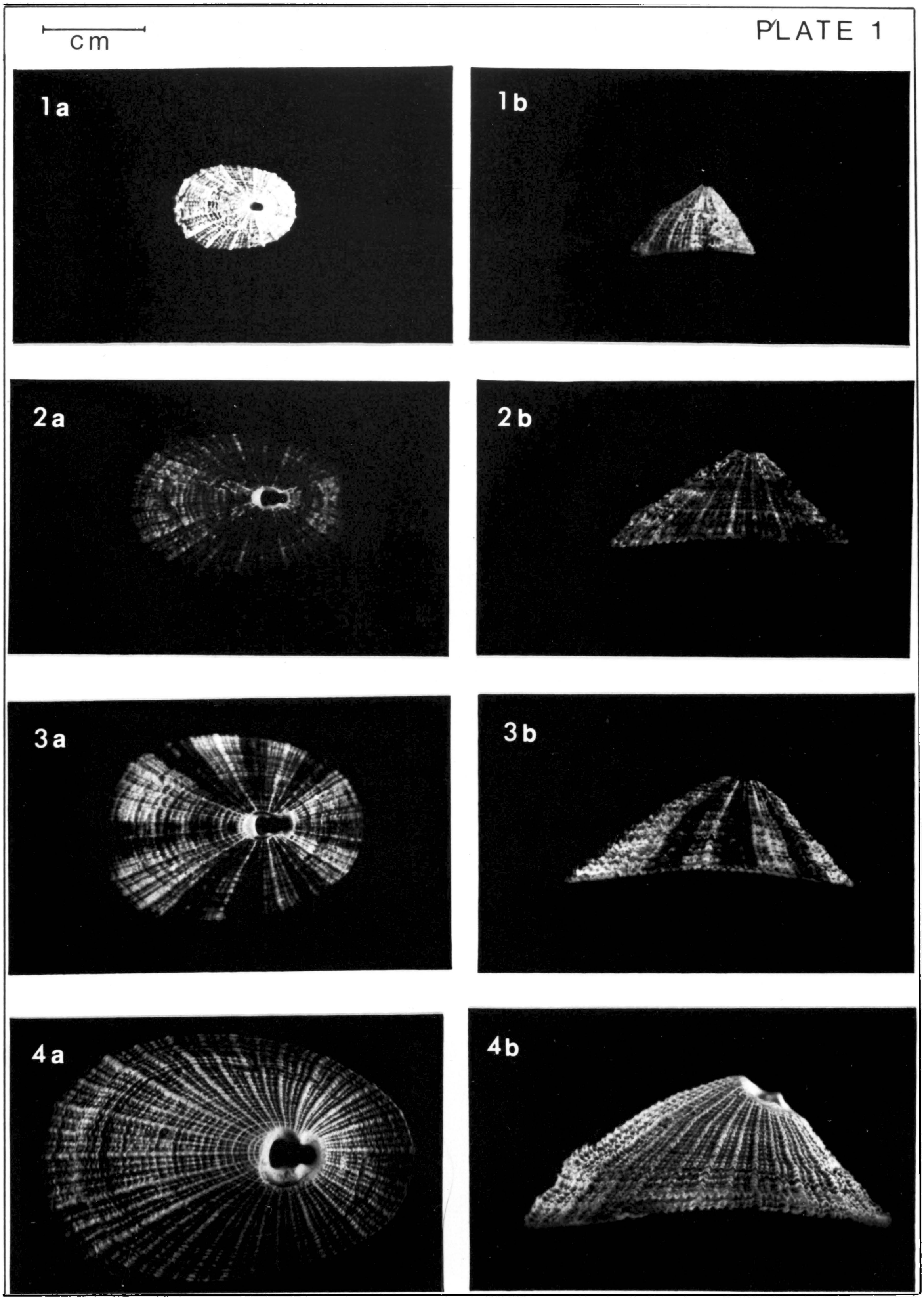


PLATE 2

D. listeri (Orbigny), a=apical view, b=lateral view

(Figure 1): Specimen number 36, Sand Key Reef, Fla., Province 1, latitude= 25.03, water depth= intertidal.

(Figure 2): Specimen number 38, Sand Key Reef, Fla., Province 1, latitude= 25.03, water depth= intertidal.

(Figure 3): Specimen number 35, Tortugas, Fla., Province 1, latitude= 24.65, water depth= 27 m.

(Figure 4): Specimen number 5, Indian Key, Fla., Province 1, latitude= 24.88, shore drift.

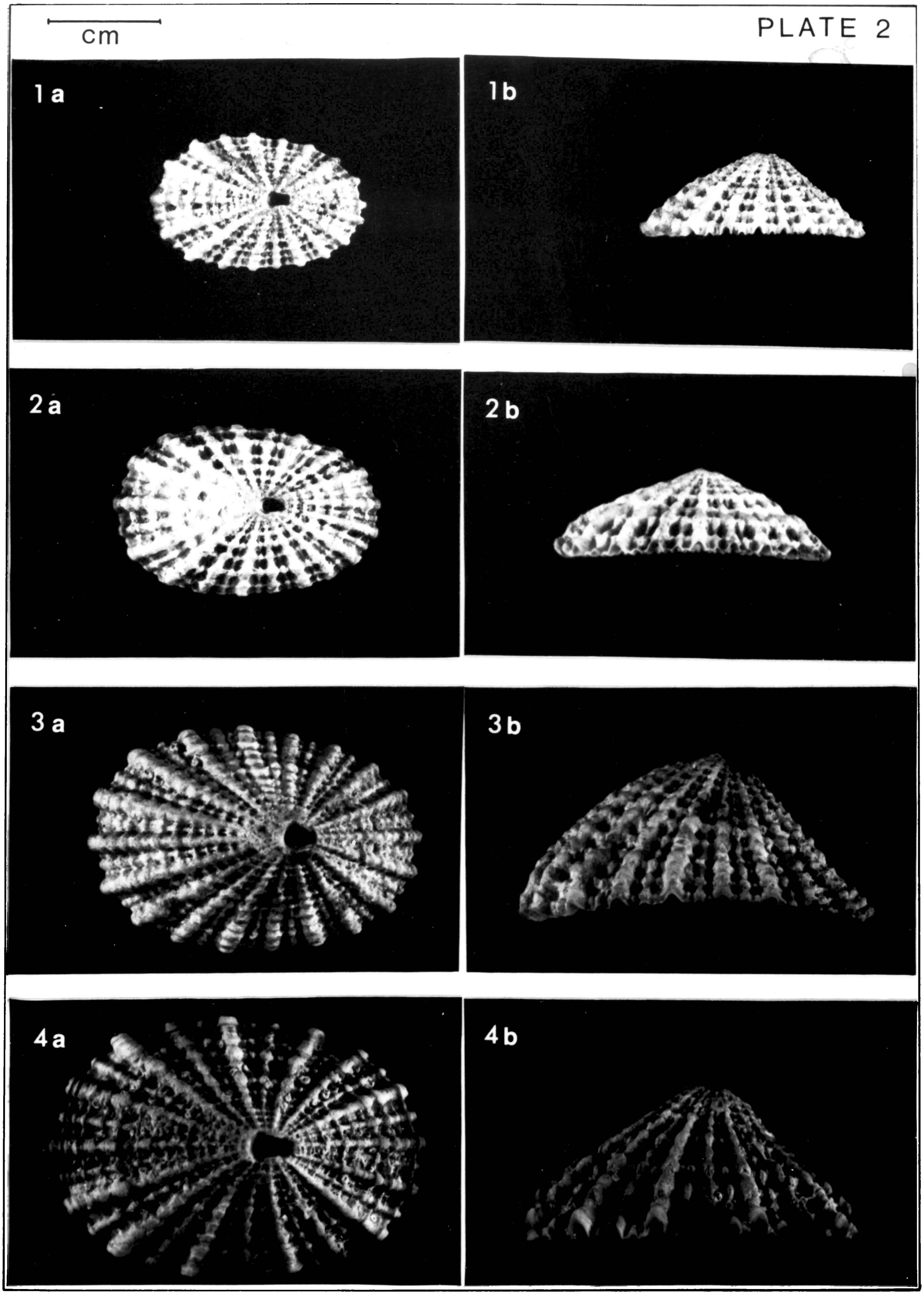


PLATE 2

PLATE 3

D.sayi (Dall), a=apical view, b=lateral view

(Figure 1): Specimen number 32, Fowey Light, Fla., Province 3, latitude= 25.78, water depth= 68.5 m.

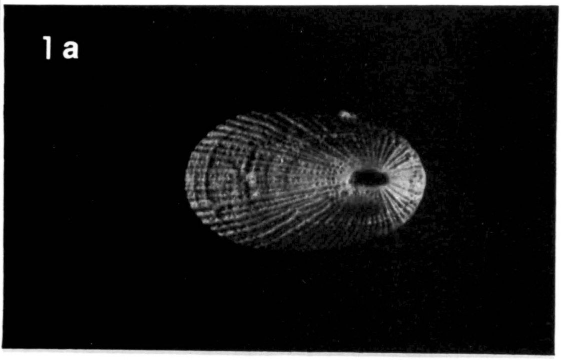
(Figure 2): Specimen number 29, Fowey Light, Fla., Province 3, latitude= 25.78, water depth= 76 m.

(figure 3): Specimen number 31, Fowey Light, Fla., Province 3, latitude= 25.78, water depth= 69 m.

(Figure 4): Specimen number 4, Miami, Fla., Province 3, latitude= 25.81, water depth= 36.6 m.

cm

PLATE 3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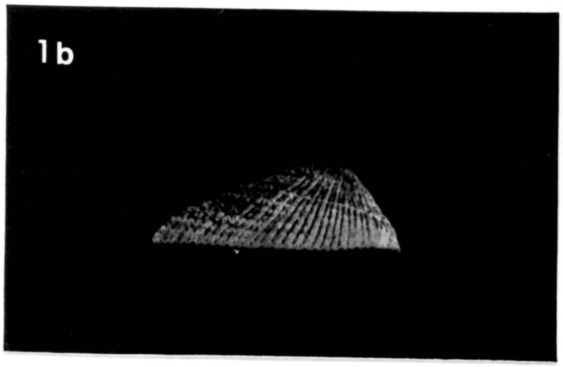
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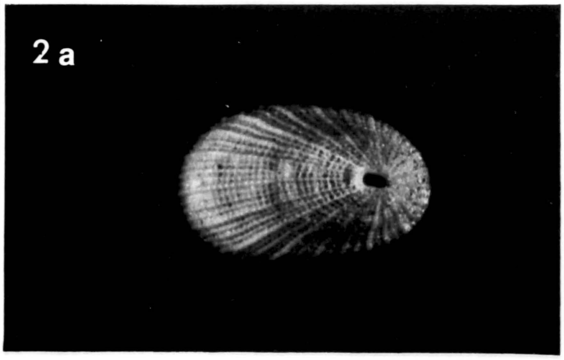
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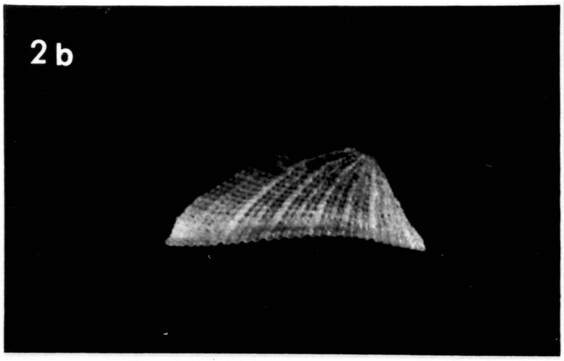
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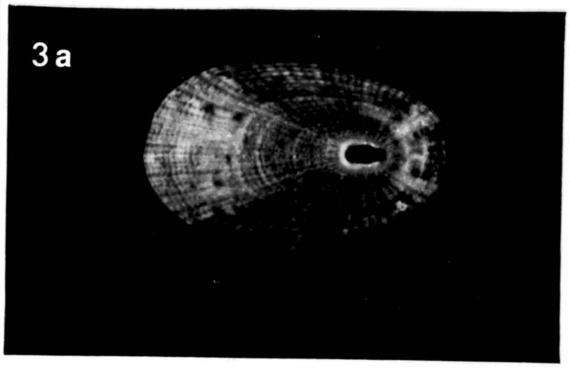
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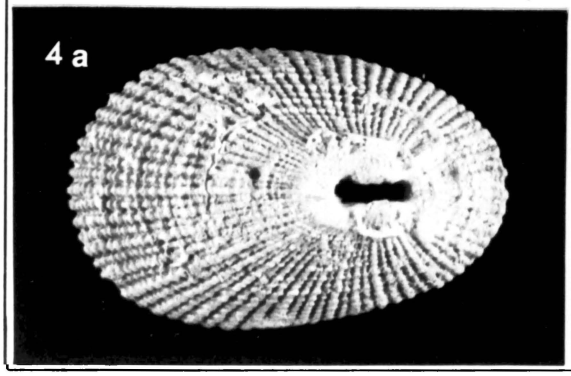
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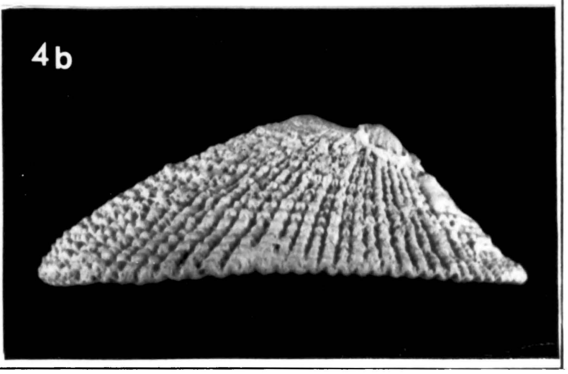

4b

PLATE 4

D. tanneri (Verrill), a=apical view, b=lateral view

(Figure 1): Specimen number 12, Chesapeake Bay, Province 5, latitude= 37.0, water depth= 104 m.

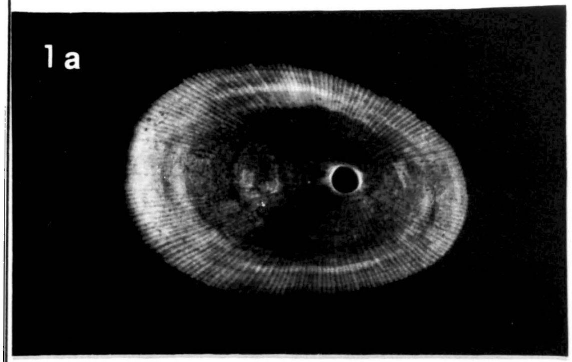
(Figure 2): Specimen number 11, Chesapeake Bay, Province 5, latitude= 37.0, water depth= 104 m.

(Figure 3): Specimen number 15, West Dry Rocks, Fla., Province 1, latitude= 24.48, water depth= 163 m.

(Figure 4): Specimen number 7, Sambo Reef, Fla., Province 1, latitude= 24.45, water depth= 219 m.

cm

PLATE 4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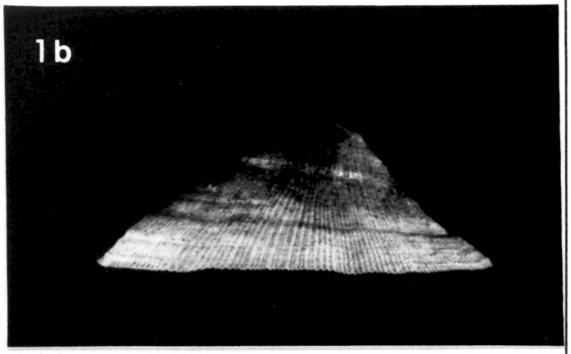
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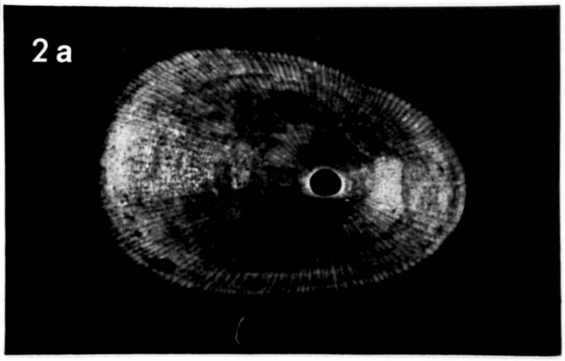
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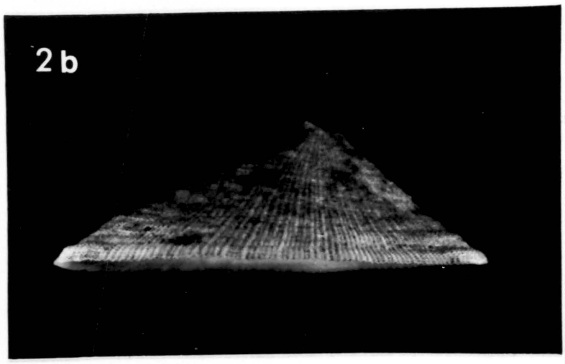
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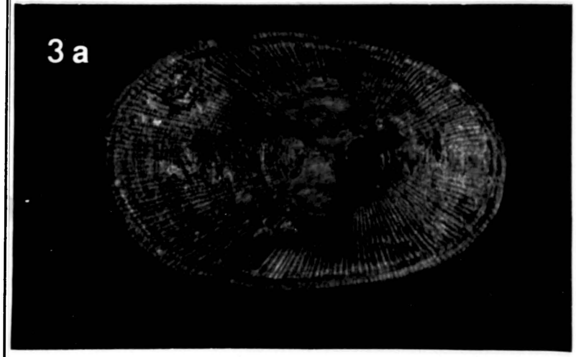
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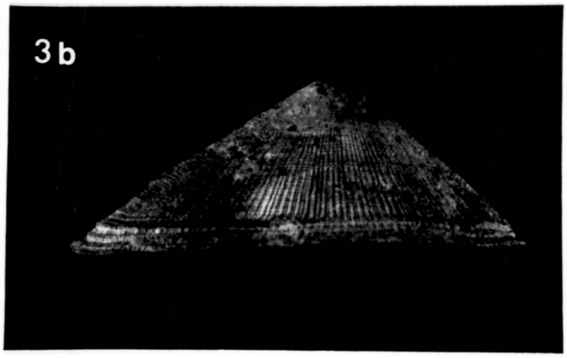
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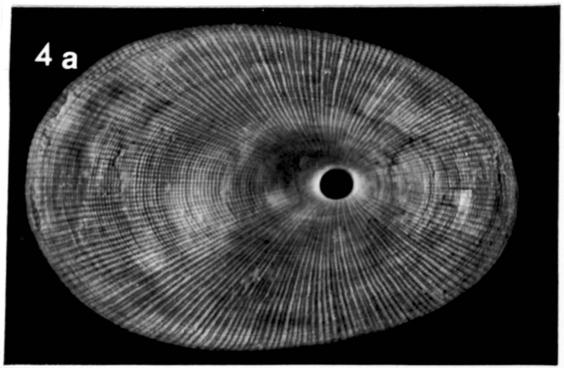
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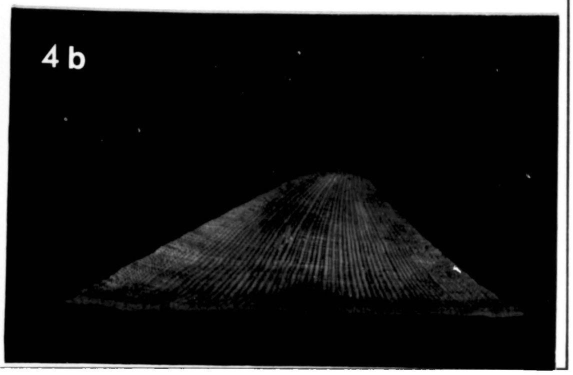

4b

PLATE 5

D. nucula (Dall), a=apical view, b=lateral view

(Figure 1): Specimen number 61F, Mayesville, S.C., latitude= 33.86, Early Pliocene Duplin.

(Figure 2): Specimen 24F, St. Petersburg, Fla., latitude= 27.76, Late Pliocene Caloosahatchee.

D. chipolana (Dall), a=apical view, b=lateral view

(Figure 3): Specimen 1F, Chipola R., Fla., latitude= 30.50, Early Miocene Chipola.

(Figure 4): Specimen number 13F, Caloosahatchee R., Fla., latitude= 26.74, Late Pliocene Caloosahatchee.

PLATE 5

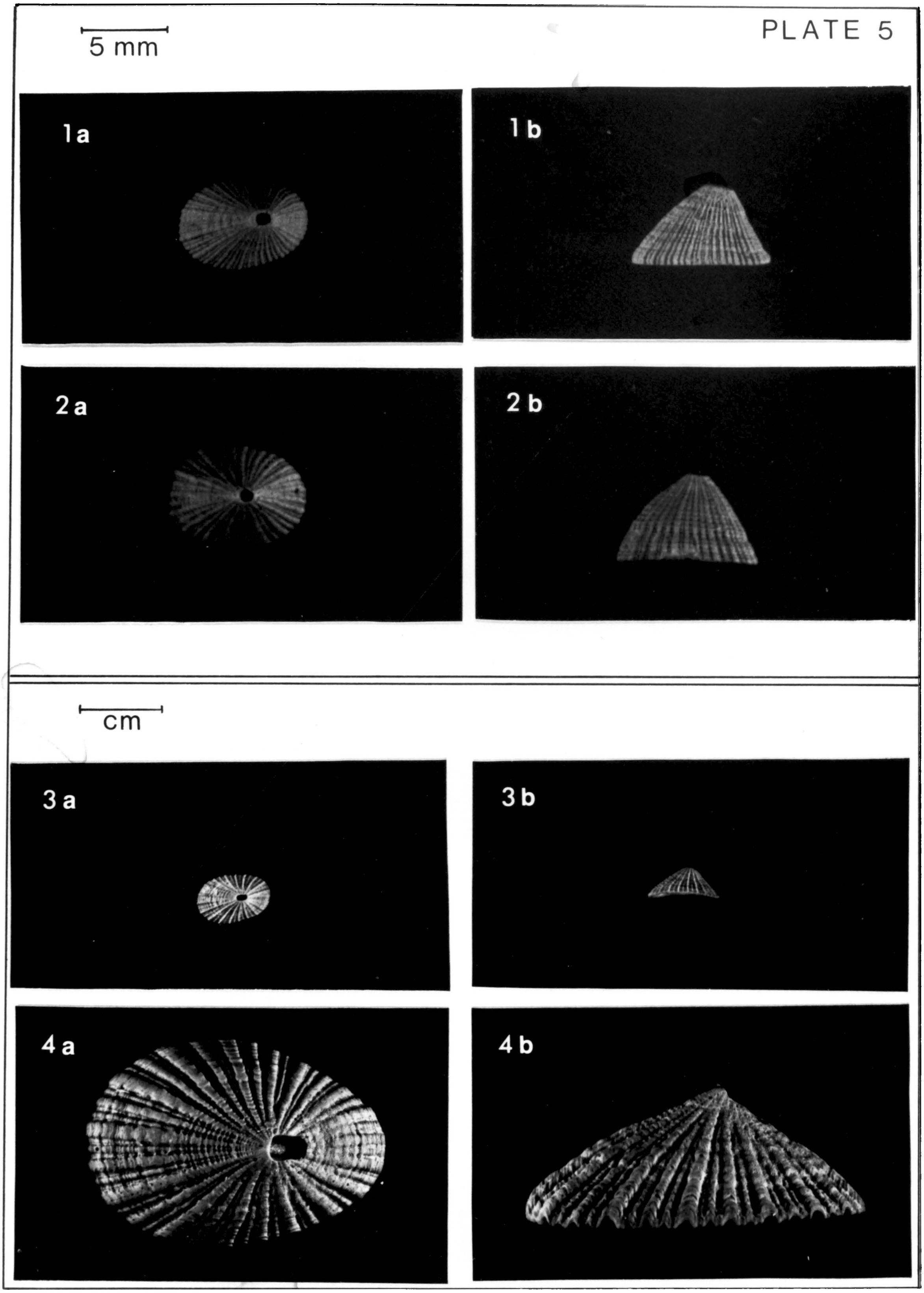


PLATE 6

D. carolinensis (Conrad), a=apical view, b=lateral view

(Figure 1): Specimen number 3F, Kissimee R., latitude= 27.34, Early Pliocene Pinecrest.

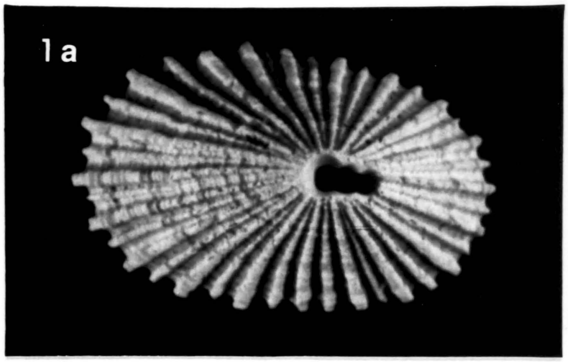
D. cayenensis (Lamarck), a=apical view, b=lateral view

(Figure 2): Specimen number 6F, Tilly's Lake, S.C., latitude= 33.83, Late Pliocene Waccamaw.

(Figure 3): Specimen number 23F, Brunswick, Ga., latitude= 31.11, Early Pliocene Duplin.

PLATE 6

5 mm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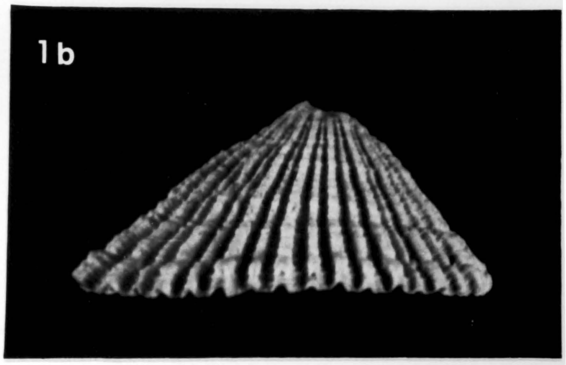
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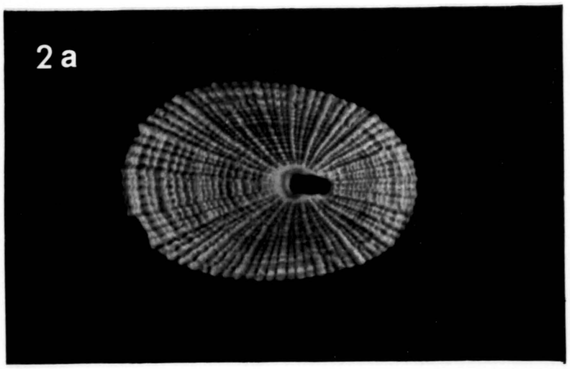
cm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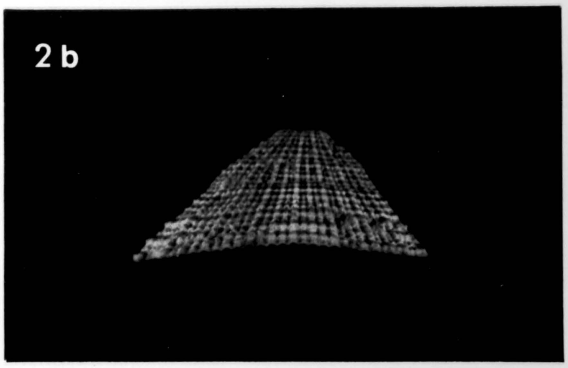
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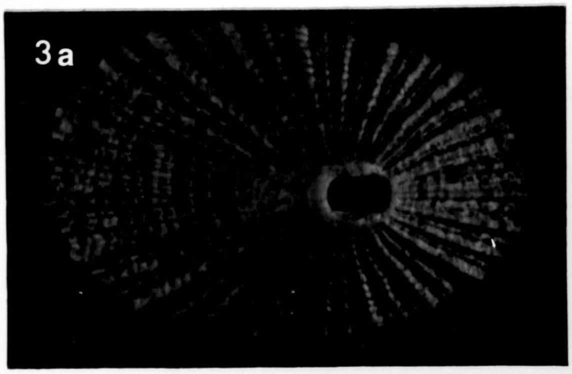
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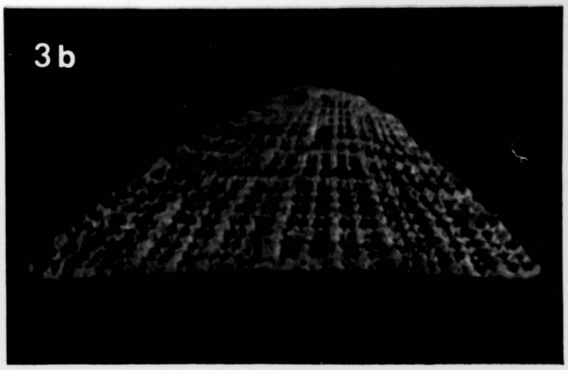

3b

PLATE 7

D. carditella (Dall), a=apical view, b=lateral view

(Figure 1): Specimen number 7F, Myrtle Beach, S.C., latitude= 33.76, Late Pliocene Waccamaw.

(Figure 2): Specimen number 17F, St. Petersburg, Fla., latitude= 27.76, Late Pliocene Caloosahatchee.

(Figure 3): Specimen number 16F, Little R., S.C., latitude= 33.84, Late Pliocene Waccamaw.

(Figure 4): Specimen number 14F, Caloosahatchee R., Fla., latitude= 26.74, Late Pliocene Caloosahatchee.

PLATE 7

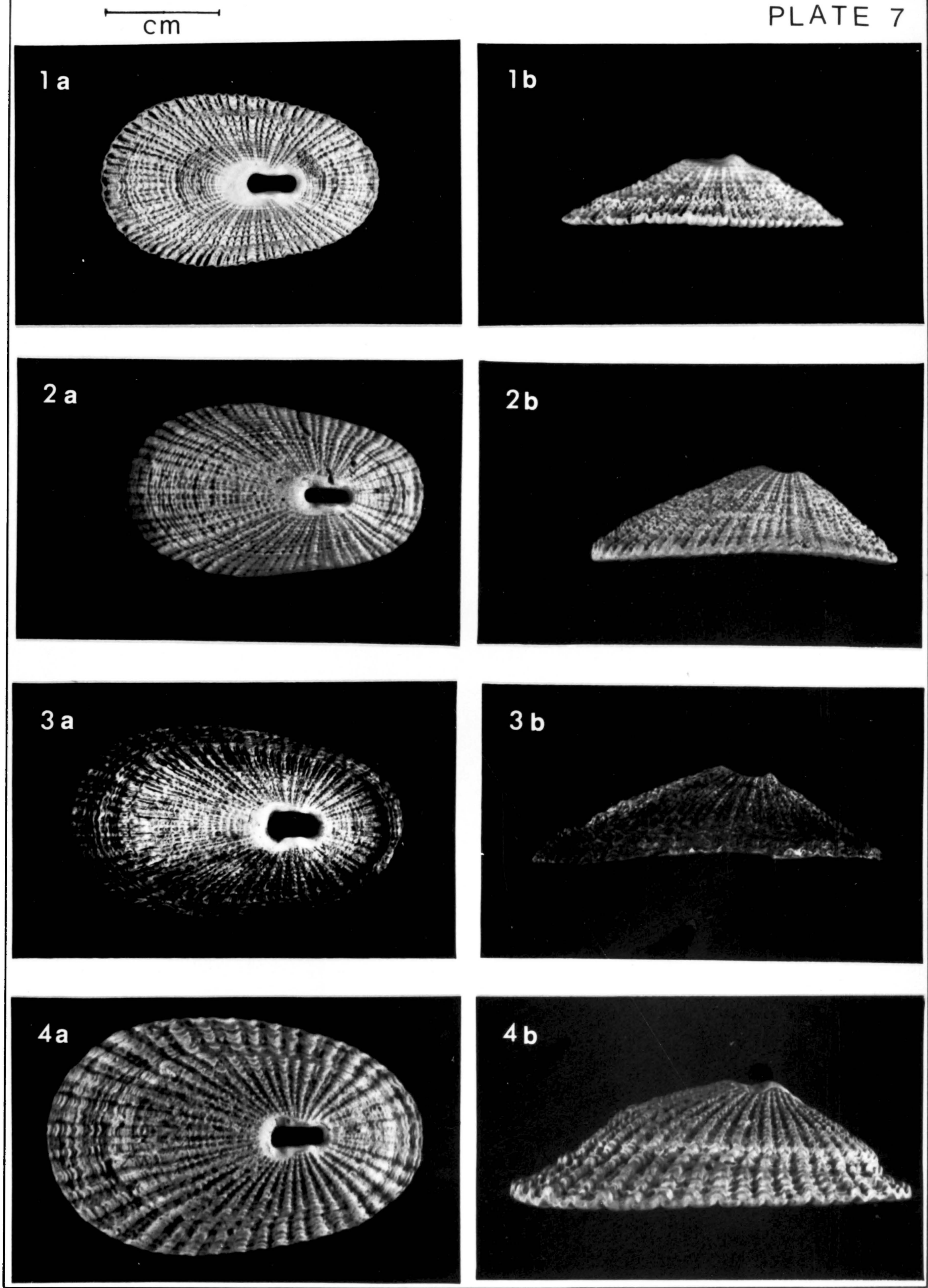


PLATE 8

Diodora sp., a=apical view, b=lateral view

All specimens are from Jerico, N.J., latitude= 39.46, Middle Miocene Kirkwood.

(Figure 1): Specimen number 59F

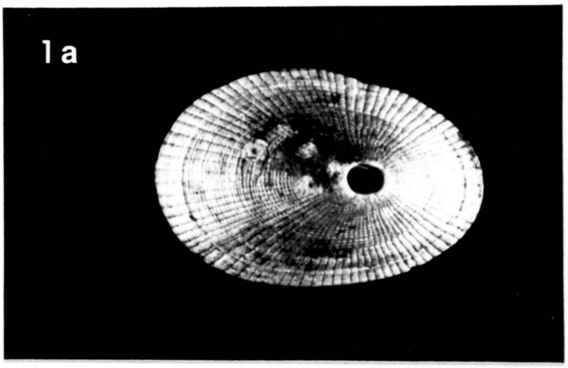
(Figure 2): Specimen number 58F

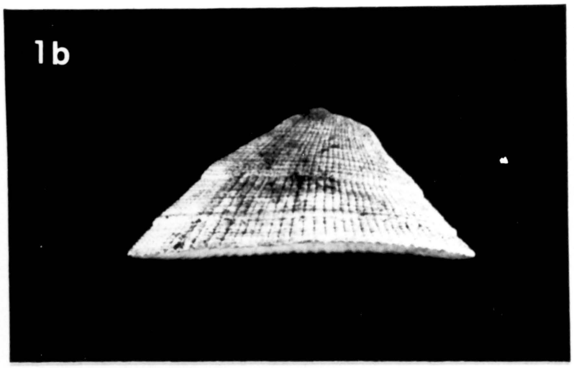
(Figure 3): Specimen number 56F

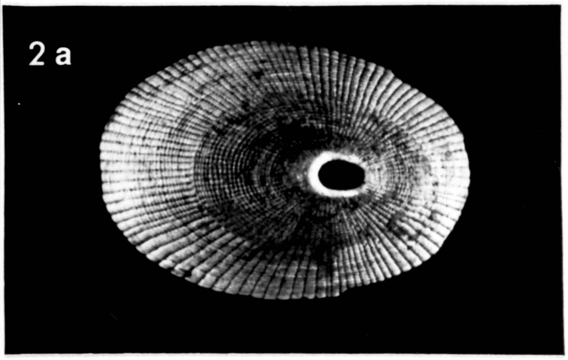
(Figure 4): Specimen number 9F

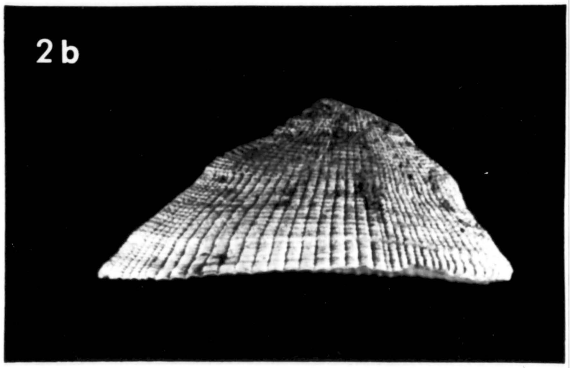
cm

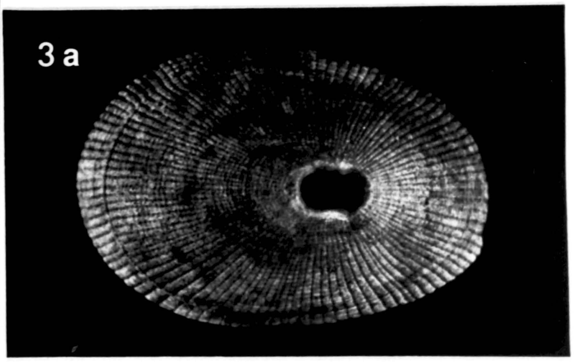
PLATE 8

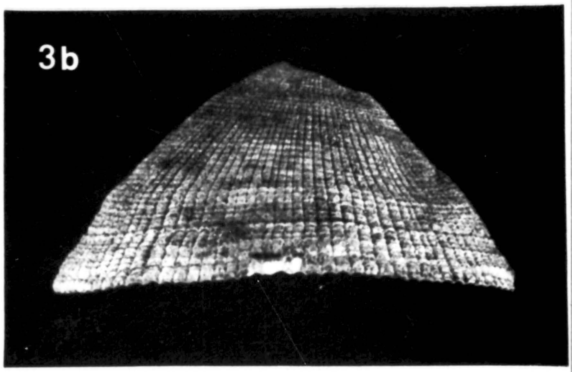


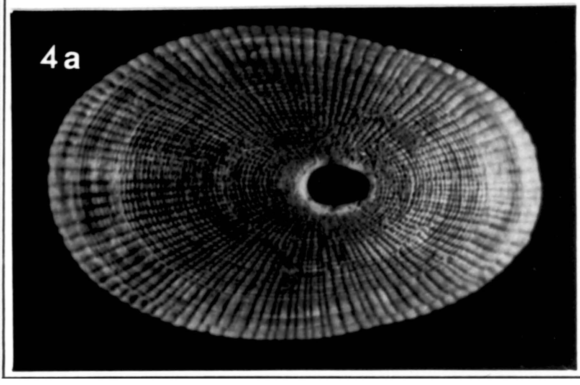












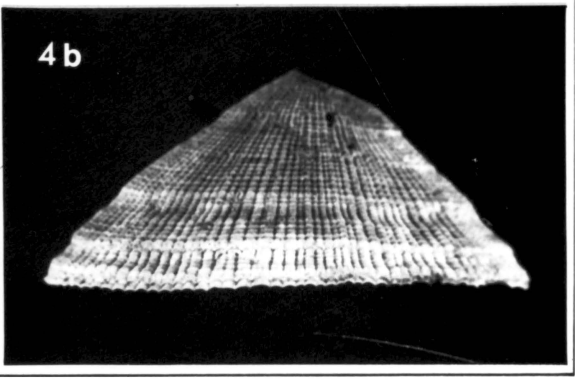


PLATE 9

D. griscomi (Conrad), a=apical view, b=lateral view

All specimens are from Jerico, N.J., latitude= 39.46, Middle Miocene Kirkwood.

(Figure 1): Specimen number 54F

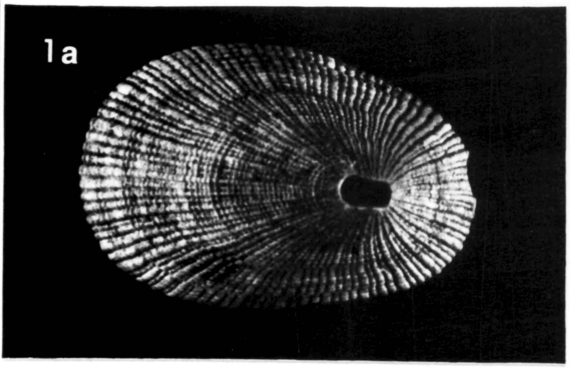
(Figure 2): Specimen number 53F

(Figure 3): Specimen number 52F

(Figure 4): Specimen number 8F

cm

PLATE 9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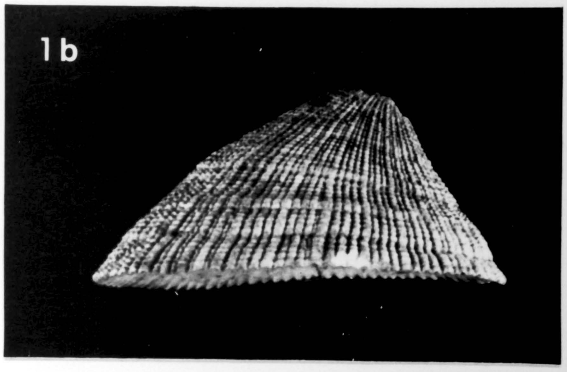
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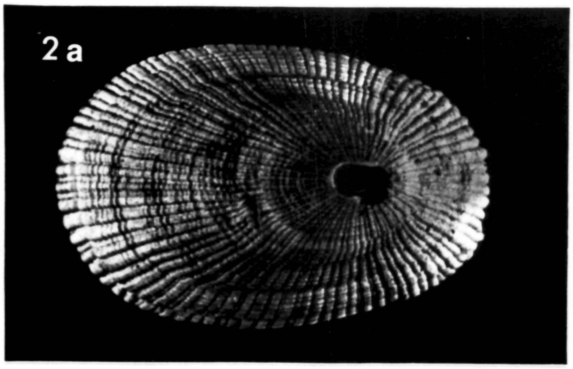
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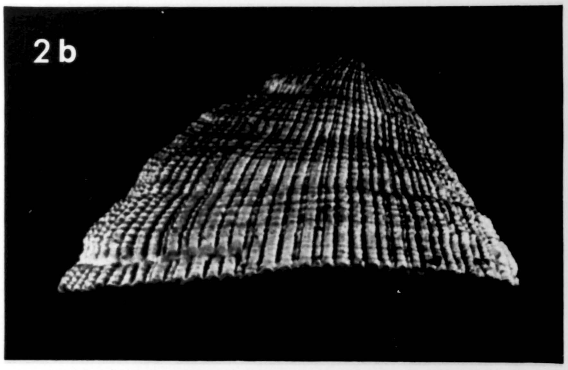
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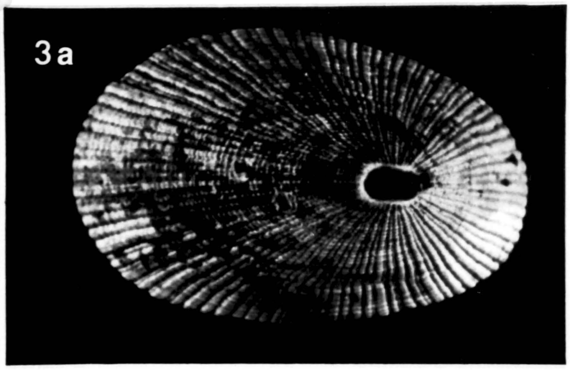
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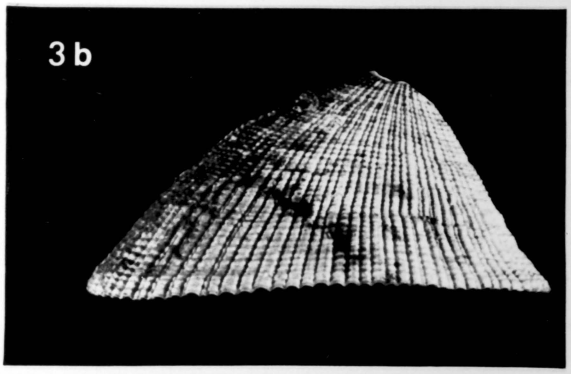
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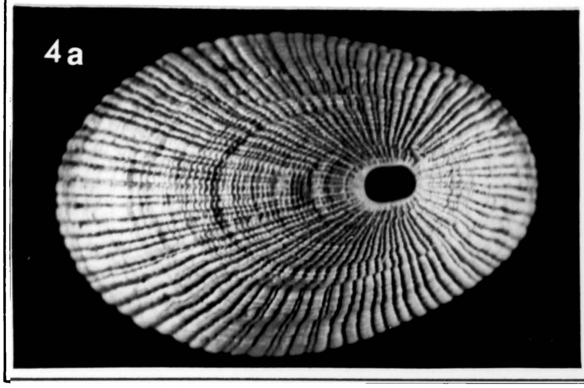
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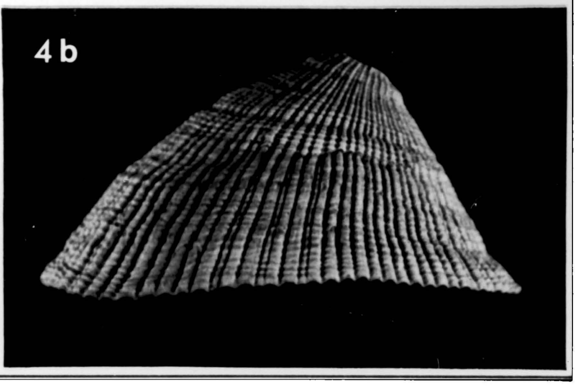

4b

PLATE 10

D. alticosta (Conrad), a=apical view, b=lateral view

All specimens are from Carter's Grove, Va., latitude= 38.10, Late Miocene Eastover.

(Figure 1): Specimen number 44F

(Figure 2): Specimen number 53F

(Figure 3): Specimen number 52F

(Figure 4): Specimen number 8F

PLATE 10

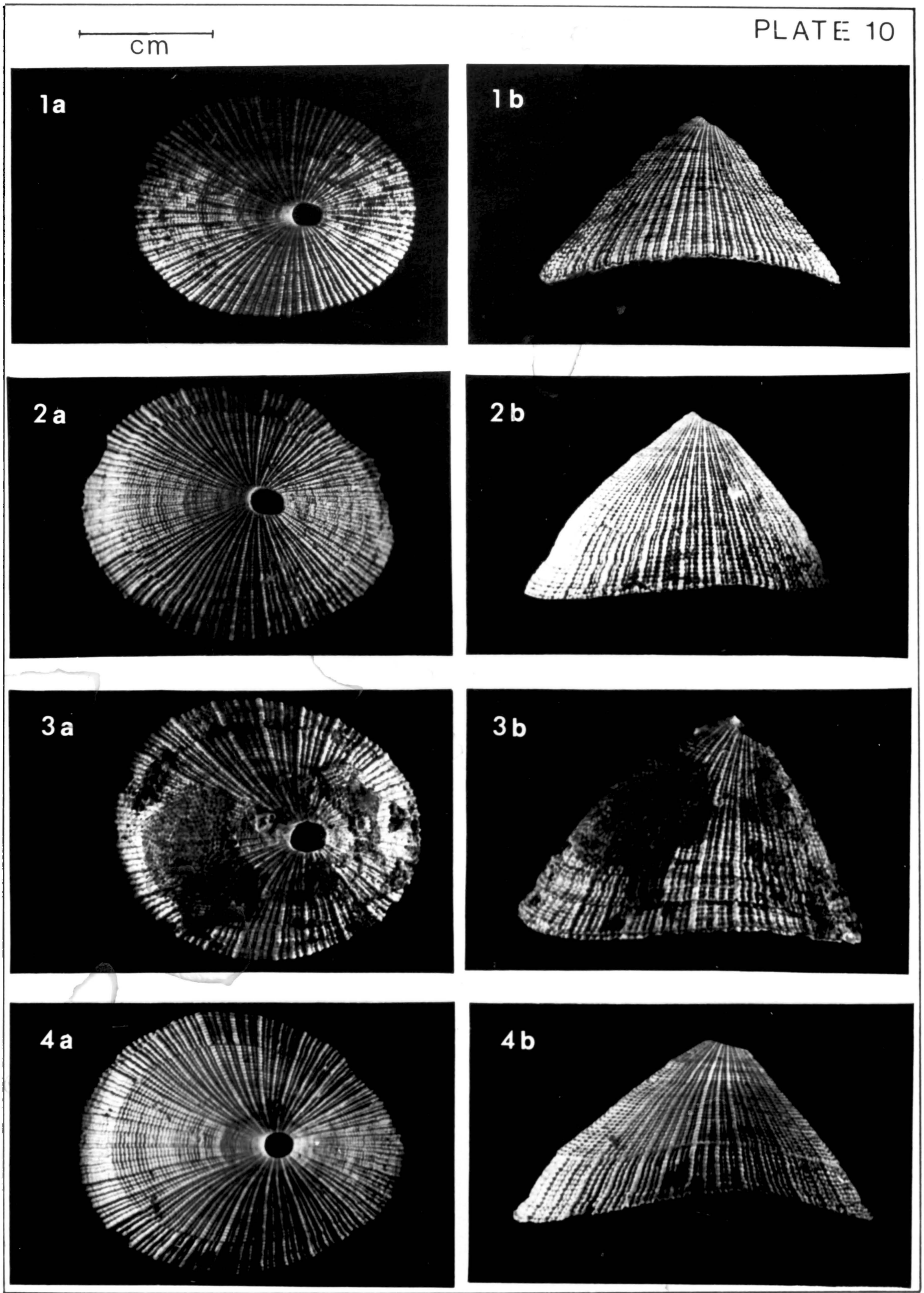


PLATE 11

D. caloosaensis (Dall), a=apical view, b=lateral view

(Figure 1): Specimen number 2F, Warren Bros. Pit, East Sarasota, Fla., latitude= 27.32, Early Pliocene Pinecrest.

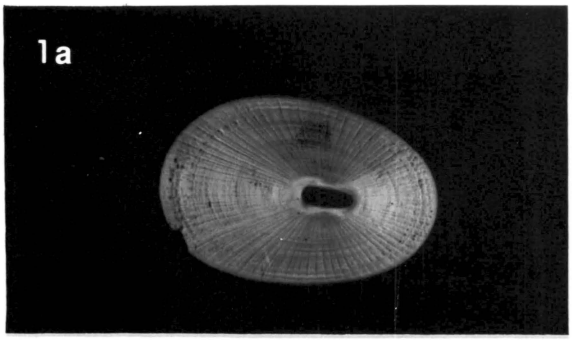
(Figure 2): Specimen number 12F, Shell Cr., Fla., latitude= 27.05, Late Pliocene Caloosahatchee.

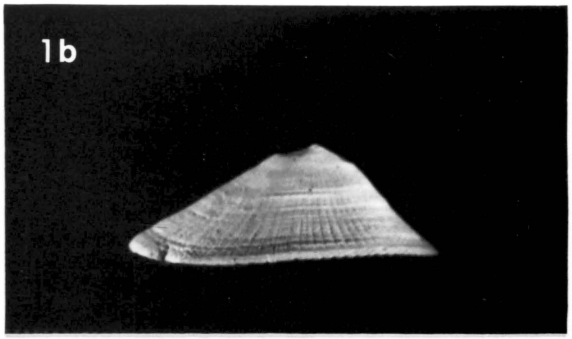
(Figure 3): Specimen number 11F, Shell Cr., Fla., latitude= 27.05, Late Pliocene Caloosahatchee.

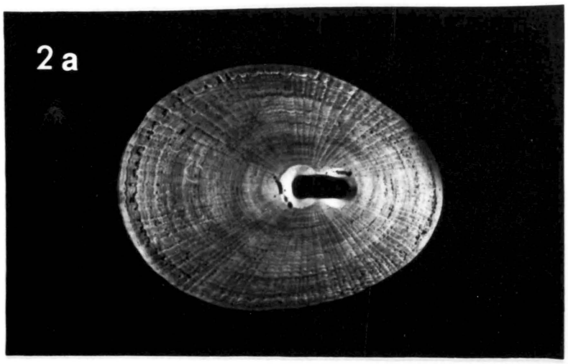
(Figure 4): Specimen number 10F, Shell Cr., Fla., latitude= 27.05, Late Pliocene Caloosahatchee.

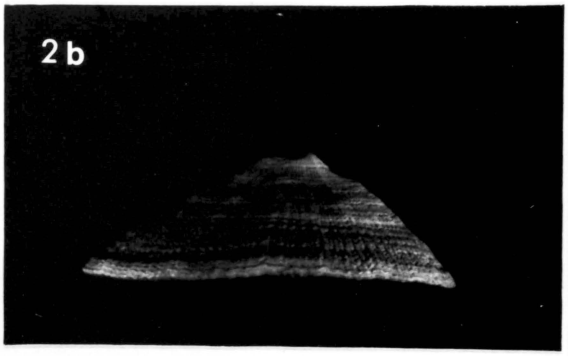
cm

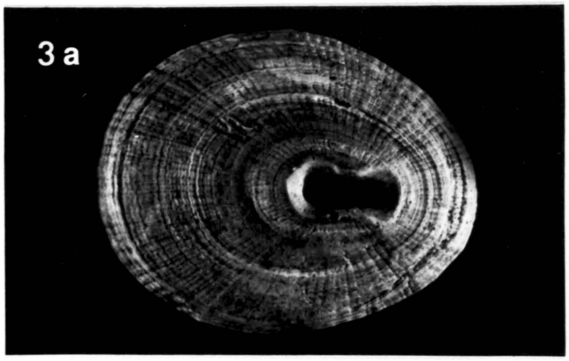
PLATE 11

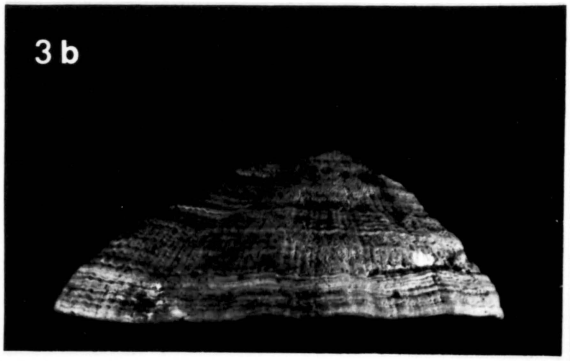


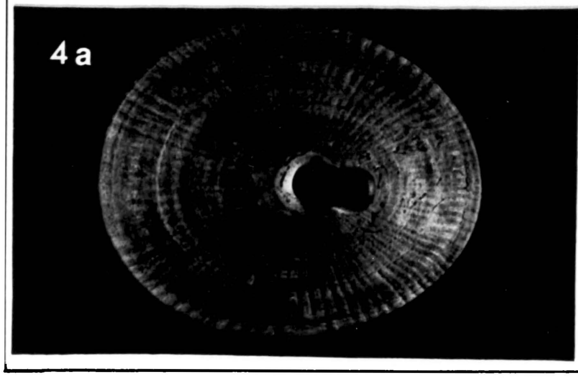












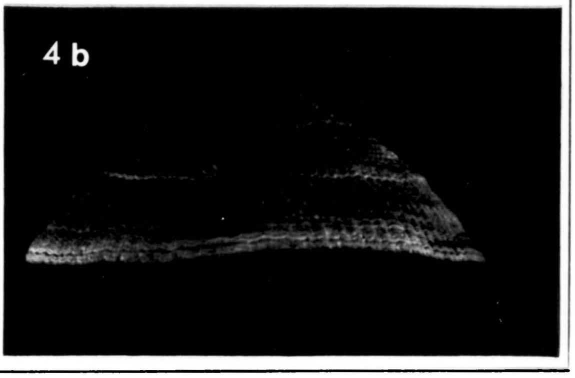


PLATE 12

D. marylandica (Conrad), a=apical view, b=lateral view

All specimens are from S. of Plum Point, Md., latitude= 38.58, Middle Miocene Calvert

(Figure 1): Specimen number 49F

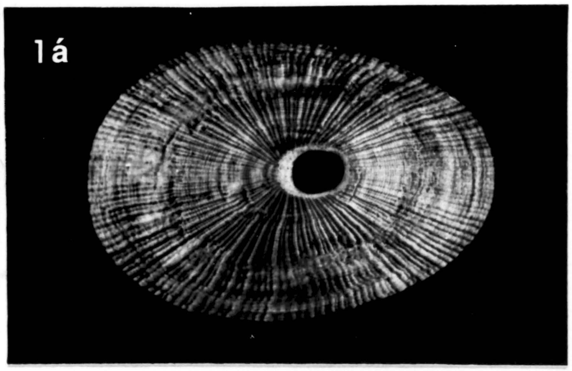
(Figure 2): Specimen number 50F

(Figure 3): Specimen number 48F

(Figure 4): Specimen number 60F

cm

PLATE 12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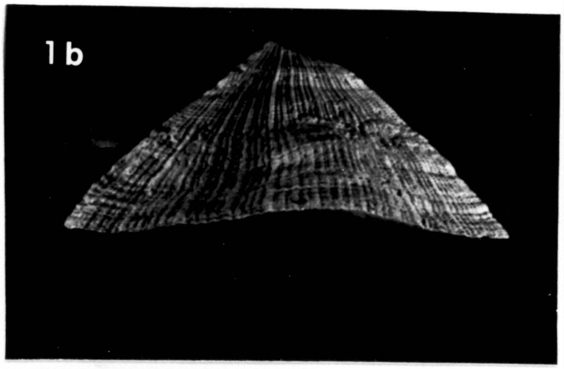
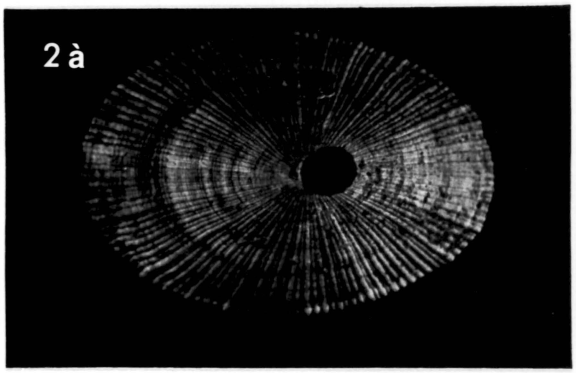

1b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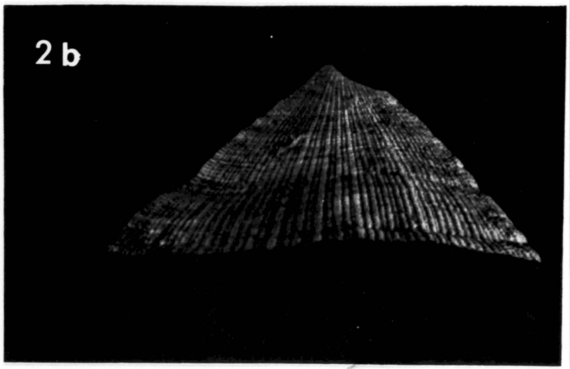
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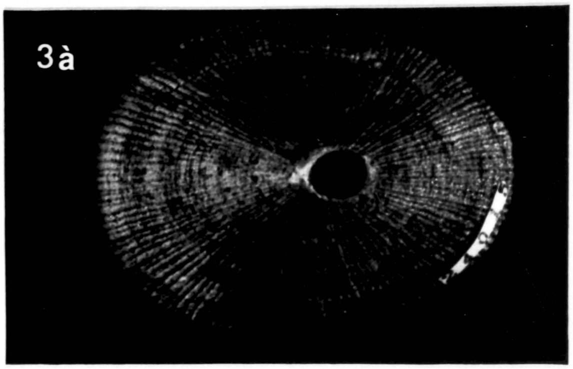
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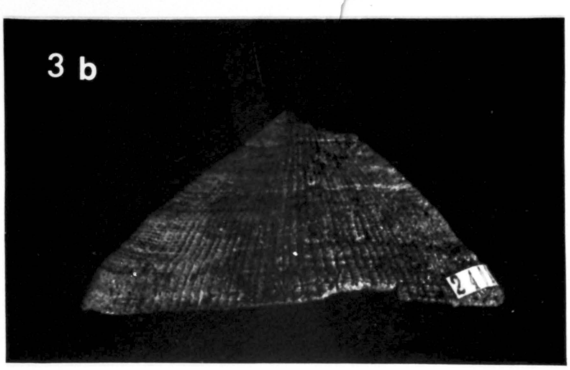
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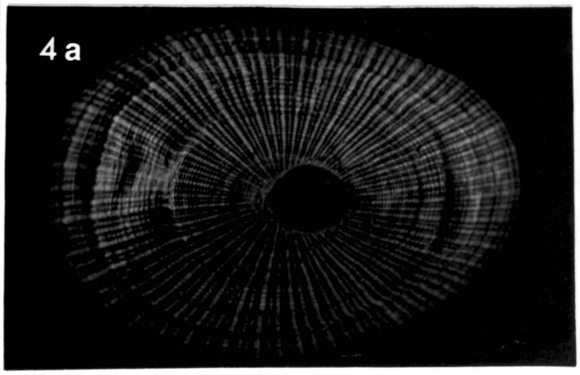
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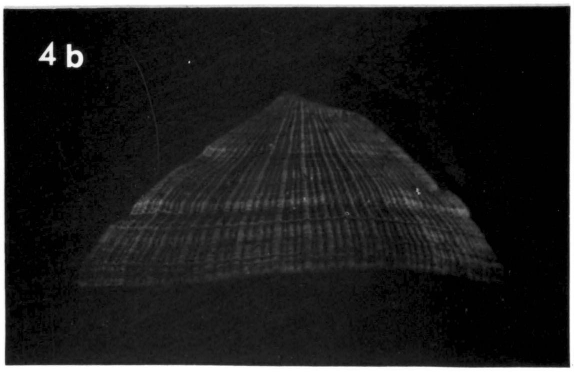

4b

PLATE 13

(Figure 1): Specimen number 36F, Ft. Boykins, Va., latitude= 37.13, Late Miocene Eastover.

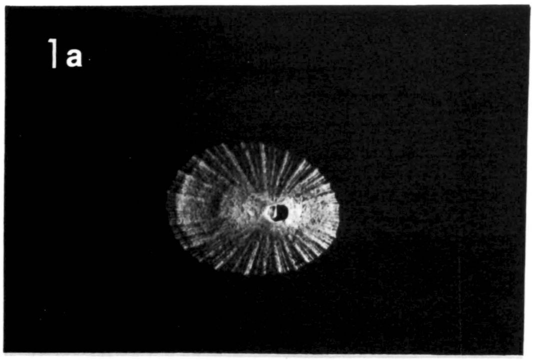
(Figure 2): Specimen number 35F, Ft. Boykins, Va., latitude= 37.13, Late Miocene Eastover.

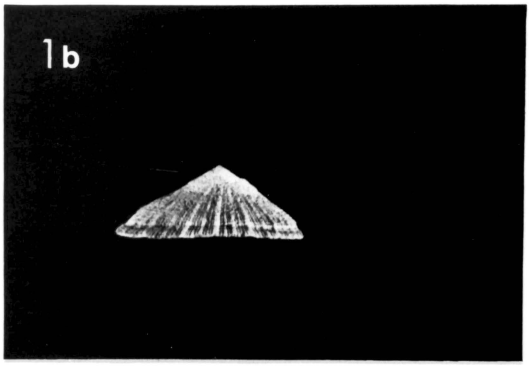
(Figure 3): Specimen number 33F, Ft. Boykins, Va., latitude= 37.13, Late Miocene Eastover.

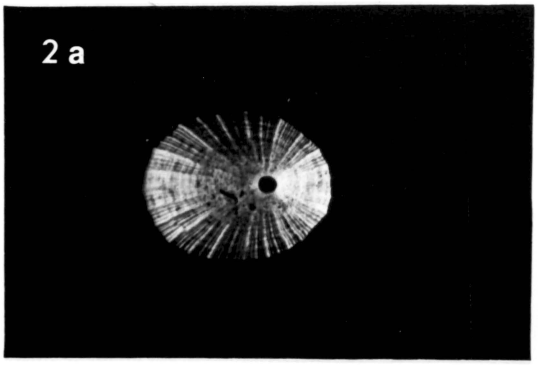
(Figure 4): Specimen number 45F, Rushmere, Va., latitude= 37.07, Early Pliocene Yorktown, Zone 2.

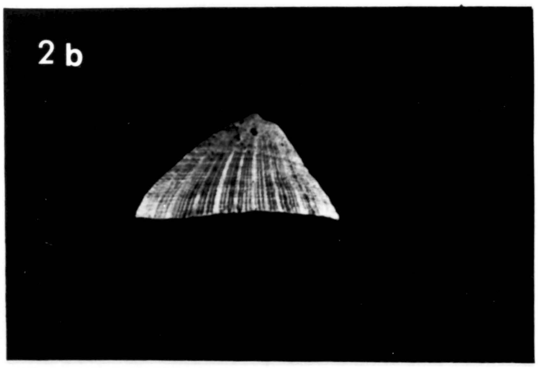
cm

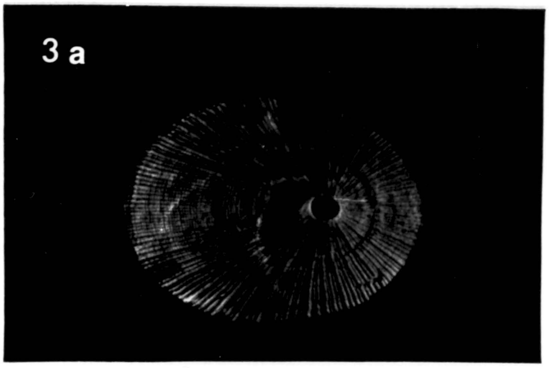
PLATE 13

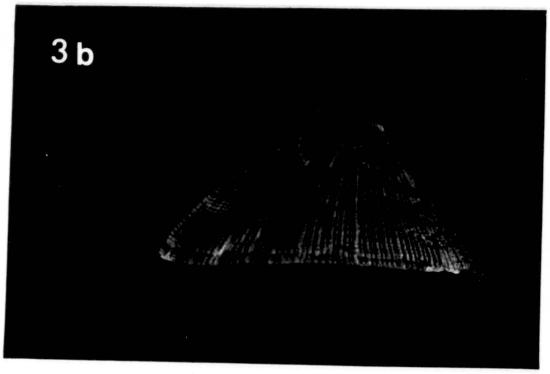


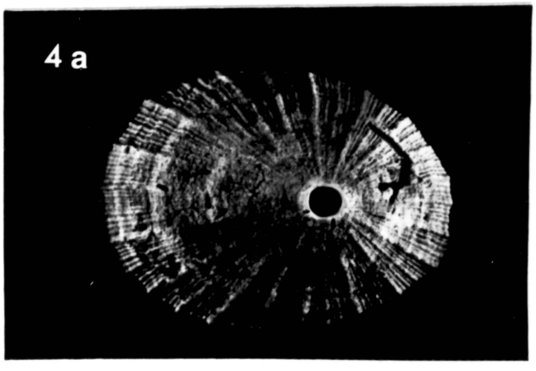












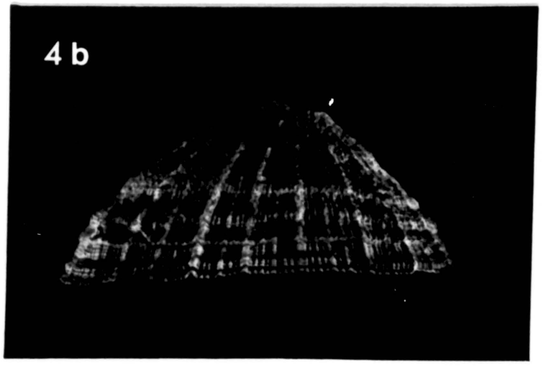


PLATE 14

D. catilliiformis (Rogers and Rogers), a=apical view, b=lateral view

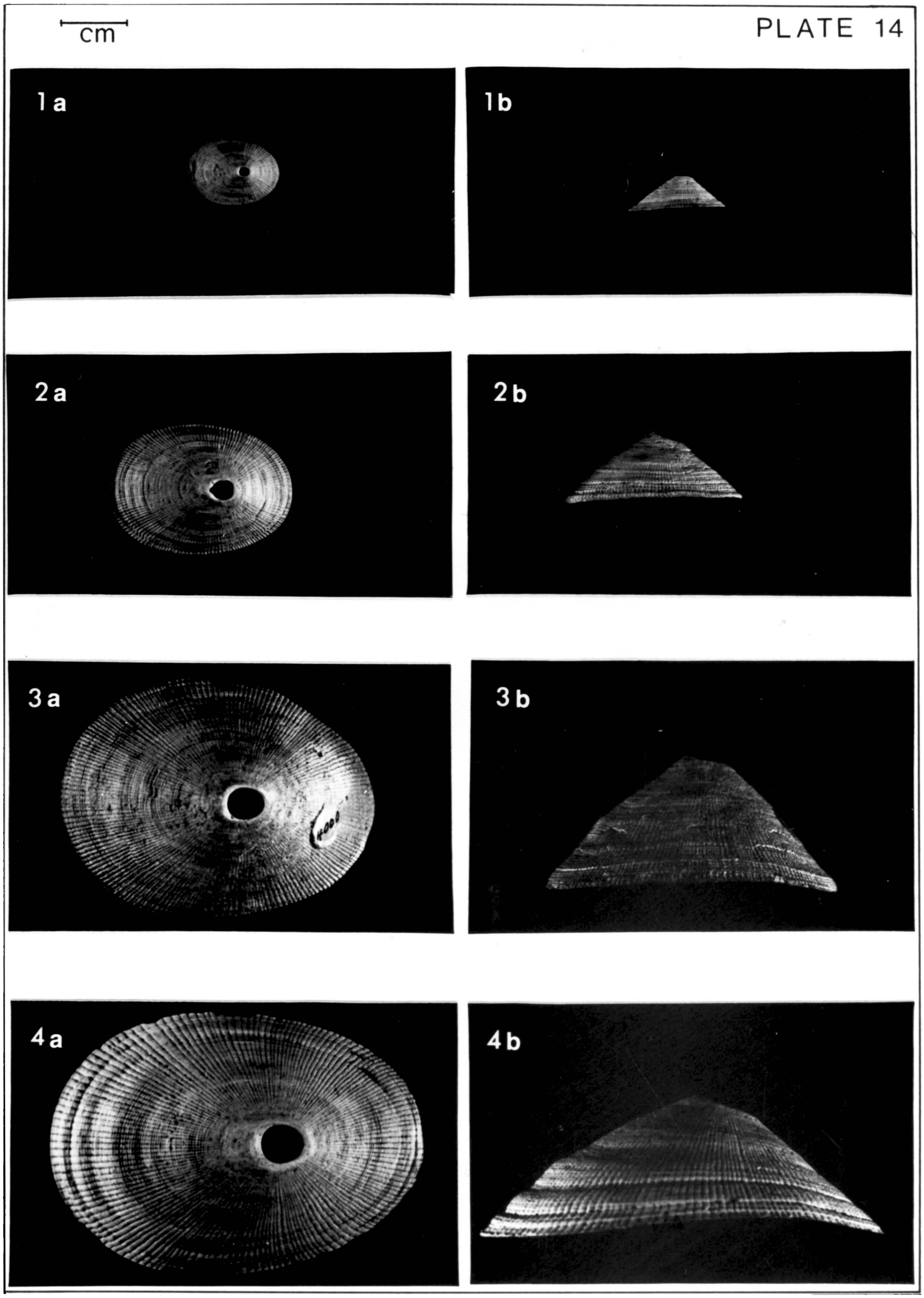
(Figure 1): Specimen number 30F, Mayesville, S.C., latitude= 33.86, Early Pliocene Duplin.

(Figure 2): Specimen number 29F, Mayesville, S.C., latitude= 33.86, Early Pliocene Duplin.

(Figure 3): Specimen number 28F, Mayesville, S.C., latitude= 33.86, Early Pliocene Duplin.

(Figure 4): Specimen number 5F, Bowler's Warf, Va., latitude= 37.64, Late Miocene Eastover.

PLATE 14



SHELL FORM ANALYSIS IN THE GASTROPOD GENUS *DIODORA*

by

Anne E. Maxson

(Abstract)

Recent specimens of the genus *Diodora* from the Smithsonian Institution Mollusc Collection were examined for the neontological portion of this study. Species included were *D. cayenensis*, *D. listeri*, *D. sayi*, and *D. tanneri*. Fifty eight measurements were made on each specimen and recorded with latitude and water depth at each collection site. Fifty specimens were selected as reference specimens, photographed, their perimeters digitized, and ornamentation and foramen shape evaluated qualitatively.

Principal Components Analysis shows that subtidal specimens are generally flatter, have a less constricted foramen and a greater number of ribs than intertidal specimens. Specimens from higher latitudes have a less constricted foramen and an increased number of ribs. In the subtidal sample, larger specimens characterize higher latitudes.

Analysis performed on all specimens of D. cayenensis, reveals 1.) a decrease in mean shell size and relative shell height in individuals collected from below the intertidal zone, 2.) shells from the province north of Cape Hatteras, N.C. have significantly more ribs than those of the same species from further south, and 3.) Gulf specimens are taller and relatively heavier for their size than those found elsewhere.

More than 500 fossil Diodorids from Smithsonian Institution collections were measured and analyzed as were the recent specimens. Shell morphology varies latitudinally like those of recent subtidal Diodorids: higher latitude specimens have more ribs and a less constricted foramen. Geologic age has little or no correlation to form.