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SOME ASPECTS OF THE FUNCTIONAL MORPHOLOGY OF THE SHELL
OF INFAUNAL BIVALVES (MOLLUSCA)

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ABSTRACT

Measures of streamlining, gapage, umbo position, and pallial sinus depth were taken from 632 species of Bivalvia in 13 families. Two types of gapage were measured: exchangeable gapage due to the rocking motion of the shells along a dynamic dorso-ventral axis, and permanent gapage, that portion of the gapage that could not be closed by the rocking movement. Models were given to predict changes in shell shape as an adaptation to infaunal life. Three stages occur in the sequence of shell shapes from shallow to deep infaunal dwellers for the families studied. The first stage is represented by unstreamlined, often sculptured shells with complete valve closure. The second, or intermediate stage, consists of an increase in streamlining, a loss of sculpture, central placement of the umbo, and temporary gapes in the shell for pedal and siphonal outlets. These gapes may be opened and closed by rocking the shells along a dorso-ventral axis (exchangeable gapage). Two paths are evident out of the intermediate stage into the third. The myid path results in unstreamlined shells with central umbos. The solenid path results in streamlined shells with a variable umbo position. Some families, such as the Mactridae, have members along both paths.

The entry into this sequence requires a particular set of pre-existing morphological conditions. The lack of these conditions in most species studied has resulted in a bottleneck, with few species in the deep infaunal zone. The constraints of bivalve shell geometry have limited the success of that group in otherwise favorable habitats.

Key words: Bivalvia, morphospace, functional morphology, ecology, phylogeny.

INTRODUCTION

The class Bivalvia of the phylum Mollusca is the most diverse group of organisms extant that principally have radiated into the deep infaunal zone. Nevertheless, the fossil record shows that this colonization required nearly 200 million years to become widespread, although the earliest known representatives of this class may have been shallow infaunal burrowers (Pojeta et al., 1973; Jell, 1980; but see Yochelson, 1981).

The deep infaunal habitat has several potentially positive adaptive features. Predation is reduced because of the general lack of burrowing molluscivores. The sediment acts as a buffer, ameliorating thermal, salinity, pH, and other environmental extremes. Desiccation is minimized. For these reasons, this habitat is advantageous to an organism associated with this niche.

Therefore why did so few members of the Bivalvia colonize the deep infaunal zone? It is probable that the changes required in evolving into the deep infaunal zone involve such considerable morphological modifications that members of few lineages have survived

or ever began the transition. Burrowing in the substrate to greater depths must have occurred by degrees, where each modification was either adaptively or neutrally selective. Such intermediate morphological steps would have had their own immediate selective advantage.

The acquisition of shell structures and behaviors associated with deep burrowing has occurred in relatively few members of the bivalve families. This implies that characteristics that made for survival in this habitat served another function in another habitat, and that these particular characteristics were selected upon by natural factors or processes that resulted in deep burial. Members of lineages lacking these prerequisite characteristics could not attain a deep infaunal existence. These characteristics include the anatomy of the living individual, behavior, and the shape of the shell. This study is limited to a consideration of the shell.

Shell Shape

It is here hypothesized that bivalves associated with the deep infaunal habitat should

have a similar shell shape if there exists a suite of characteristics necessary to achieve this type of existence. The presence of homeoplasmy (similar shell shapes by convergence, parallelism, or iteration) by individuals of deep infaunal species across suprageneric taxonomic levels would support this hypothesis. This study proposes to obtain measures of shell shape describing differences that may arise in a transition from a shallow to a deep infaunal existence. These measures are:

(1) degree of streamlining. This is a measure of the amount of surface area of the shell that is oriented perpendicular to the long axis of shell.

(2) relative position of the umbo. The placement of the umbo on the shell, standardized to remove size effects.

(3) relative depth of the pallial sinus. The depth of the pallial sinus, standardized to remove size effects.

(4) amount of permanent gape. Some bivalve shells do not close completely, leaving gapes anteriorly and posteriorly. These shells may open and close along a dorso-ventral axis to close much of the gape, but some portion may remain open. These are permanent gapes. The amount of permanent gape is the sum of the anterior and posterior gapes in the commissure of the shell that cannot be closed by rocking the shells along a dorso-ventral axis (Fig. 1: $g_1 + g_2$).

(5) amount of exchangeable gape. The amount of gape created by rocking the shells along a dorso-ventral axis minus the amount of permanent gape (Fig. 1: $pg + sg - g_1 - g_2$).

These parameters are discussed in detail under "Methods."

Shell shapes form a predictable sequence among individuals that inhabit the shallow to deep infaunal habitats because a necessary suite of shell characteristics is needed to succeed in a deep infaunal habitat. This sequence is defined by the distribution of each measurement specified for representatives of the species in this study. The existence of a sequence could explain the rarity of deep infaunal bivalves and the degree of homeoplasmy present in burrowing bivalves in general. It may be that few Recent representatives of bivalve lineages are deep infaunal burrowers because ancestral members of the lineage lacked the shell characteristics necessary to enter the sequence.

The sequence may be divided into three phases. The shallow infaunal phase contains

bivalves that do not have exchangeable gape. The deep infaunal phase contains forms with permanent gape. These individuals often are deep burrowing or sedentary forms. The intermediate phase connects these two phases and contains forms having exchangeable gape. Homeoplasmy would be the expected result if only a few sequences of shell shape morphologies existed among those individuals that occur in these phases.

It has long been known that there is convergence in shell characteristics in bivalves. Seed (1980b: 32) stated that "perhaps one of the most striking features concerning the evolution of such a diverse group as the bivalves has been the repeated appearance of a comparatively restricted number of very successful shell morphologies." Linnaeus, Cuvier, Bruguière, and Lamarck placed bivalves in only a few genera. They based their criteria for classification primarily upon shell form and a consideration of hinge dentition, but little internal anatomy. This is in contrast to a recent classification (Vaught, 1989) that lists nearly 1,000 genera. Taxa not known to be related may possess similar shells when internal anatomy, dentition, and larval types are also examined. This has been a major obstacle to the study of fossil forms.

Two hypotheses may be formed to explain this convergence, and they are not mutually exclusive. The first states that similar shells have arisen in response to similar environmental pressures. Convergence has occurred because of natural selection "favoring" a specific shell shape. However, evolution may only act upon available morphological material. Pre-existing structures may be co-opted for a different use or an improved original function if the genetic program can be modified in such a fashion. This is the basis behind the second hypothesis of convergence in shell shapes: bivalve shells may be similar because there is only a limited range of values for shell geometric parameters that occur in nature. Convergence may be expected because of this restriction if there are few viable alternative shell shapes.

The results of this study suggest that the cause of convergence in bivalve shell shape may be explained as the consequence of a sequence of morphologies. This sequence represents a compromise between natural selection and morphological constraints. Evolution is conditional and the changes at any step in a phylogeny depend upon the characteristics of the previous step. Such "trends"

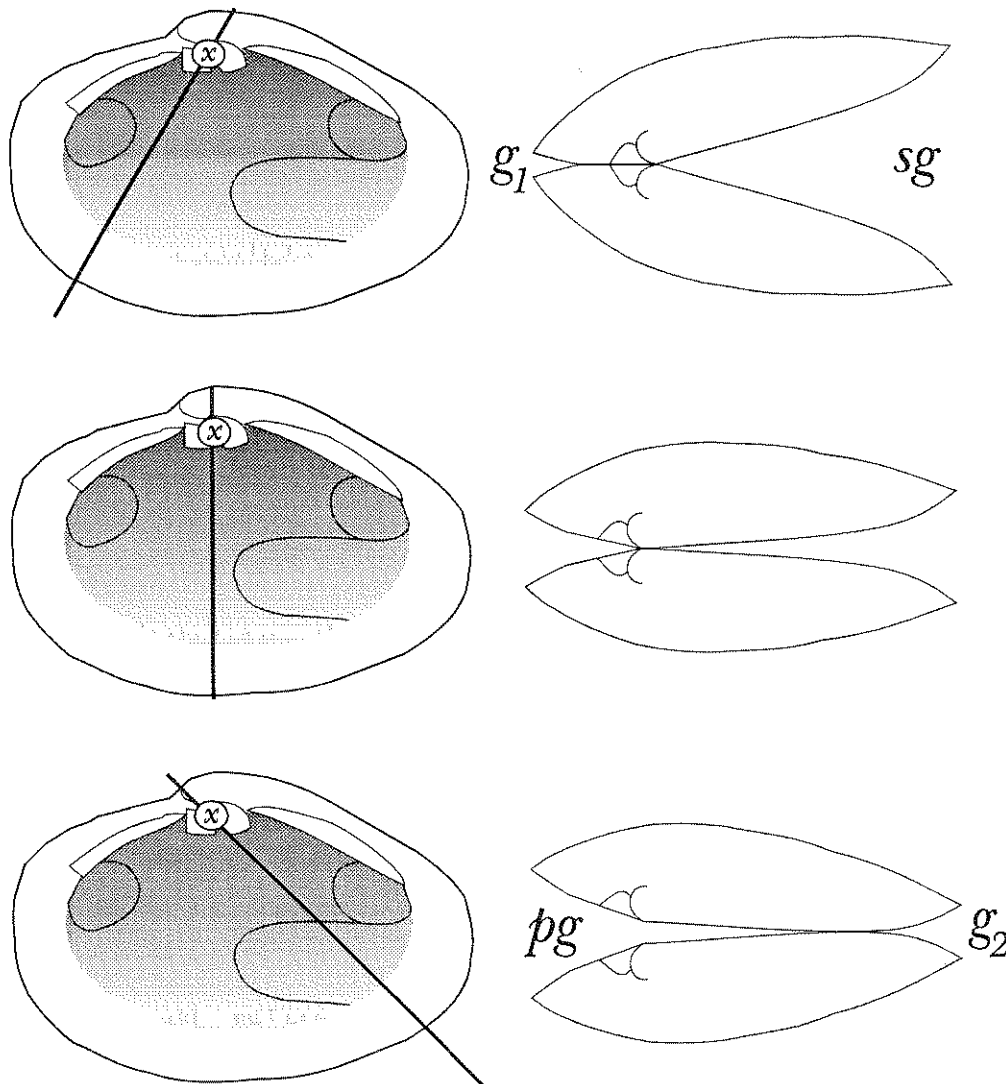


FIG. 1. Rocking of shells along a dorso-ventral axis. Heavy line: Axis. x : Fixed pivot at cardinal teeth. Top: Shells rocked forwards to open siphonal gape (sg). Middle: Shells at neutral position. Bottom: Shells rocked backwards to open pedal gape (pg). g_1 : Non-closable permanent anterior gape. g_2 : Non-closable permanent posterior gape.

have been modeled satisfactorily by a Markov process or random walk (Bookstein, 1987). As an example, Cope's Law of Phyletic Size Increase has been shown to be stochastic (Stanley, 1973). The convergence of bivalve shell shapes may be such a stochastic process.

The molluscan shell has long been recognized as a geometric form, at least in the ar-

tistic sense. Examples of this geometry, as a by-product or necessity of biological design, were not popularized until Thompson (1942) published *On Growth and Form*. The further study of shell geometry did not progress past this recognition stage for many years. The computations were time consuming and the results difficult to visualize as three-dimensional shapes. Recently, geometric studies of

this type have been facilitated by computers. Raup (1961, 1962, 1963, 1966, 1967) identified the basic parameters of spiral coiling and generated simulations of molluscan shells by computer emulation. He demonstrated that a simple gastropod or cephalopod shell design could be modeled with few variables. Savazzi (1987) produced an even more realistic computer generated model, and the recent work of Fowler et al. (in press) has produced amazing simulations. The science of "theoretical morphology" (Raup & Michelson, 1965) and, more specifically, "conchylometry" (coined by Naumann, 1840), became a discipline belonging as much, if not more, to computer programmers and mathematicians as to biologists. The course of these studies culminated in Bayer's (1978) and Illert's (1992) purely mathematical analyses of shell shape using morphogenetic programs. The emphasis of these studies had shifted from the biological aspects of shell geometry to a consideration of the biometrics as the sole purpose of the investigation.

In 1970, Stanley published a study on marine bivalves that marked a turning point in molluscan morphometrics. He presented a synthesis of shell geometry, systematics, ecology, and field observation. For the first time, on a comprehensive scale, explanations were advanced for why shells were shaped like they were, rather than how they were shaped. Following the studies of Trueman et al. (1966a) and Nair & Ansell (1968) on the dynamics of bivalve burrowing, Stanley's work showed that members of such diverse groups as the solecurtines, the solenids, the cardiids, and the mactrids had highly convergent shells because of similar habitats. From his results, I have inferred the possibility of analogous, predictable shell shapes in equivalent niches despite phylogenetic position.

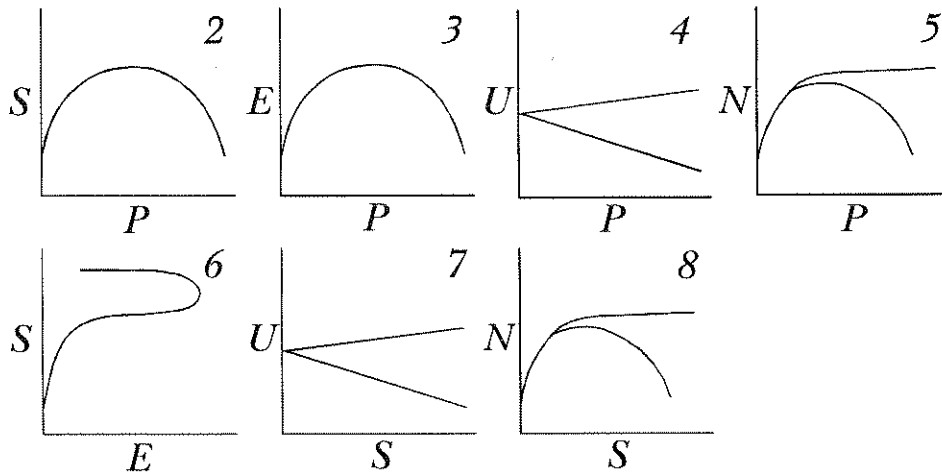
Stanley (1969, 1970, 1972, 1975, 1977b, 1981) documented the probable function of many types of marine bivalve sculpture. I believe that the single most important conclusion of these works was the concept of "composite sculpture," the exaptation (*sensu* Gould & Vrba, 1982) of pre-existing sculpture for vicarious multiple tasks. Gould and Vrba coined this term for previous adaptations or nonadaptations that have been co-opted for a new function. For example, radial ribs may have originated as sculpture strengthening the shell in individuals of the Cardiidae (Stanley, 1981). That sculpture has been exapted to function as a burrowing device in many

members of the trachycardiine cockles. As aspects of the function of shell sculpture have been discussed elsewhere, they generally will not be addressed in this study.

Of central importance to this analysis is the concept of the theoretical morphospace: the array of potential shapes that an organism may possess. This space usually is limited to a few parameters, such as size, coiling rate, or color, for experimental studies and represents the possible range of values of that parameter. The theoretical morphospace may be contrasted with the actual morphospace. The actual morphospace is the observed values of that parameter, or in a broader sense, the form in which the organism is found in nature. The actual morphospace is always a subset of the theoretical morphospace. In its simplest form, this methodology addresses the question: why are things shaped the way they are? Or conversely, why aren't they shaped like something else? It is the latter question that may be the most insightful, for it implies a limitation of form and a constraint on possible morphologies. The cause of this constraint may be fundamental to understanding the organism in question. The idea of the theoretical morphospace has been applied to the morphological features of several groups, most notably coiling in cephalopods (Raup, 1967).

Convergence is most apparent in a morphospace scenario. Phylogenetically unrelated groups that consistently occupy the same morphospace have converged toward the same values of the morphospace parameters. In this study, the sum of overlapping regions is shown to lie along a sequence of shell shapes.

Rudwick (1965) is usually given credit for advancing the use of the paradigm approach in biology, although this method of analysis may have been in use for many years. The term is from the Greek *paradeigma*, meaning "example" or "model." The methodology allows the worker to form hypotheses concerning the potential characteristics of an organism possessing a certain life style or behavior, given information on the necessities of the organism's life and its general morphology. For example, given the morphological characteristics of a small dinosaur, what changes are necessary to metamorphose it into a bird? The result is a model having parameters describing the organism in that life style as dictated by the logic of the investigator and the presumed efficiency of those characteristics.



FIGS. 2-8. Models of shell shape. 2. Model for interaction between permanent gapage (P) and streamlining (S). 3. Model for interaction between permanent gapage (P) and exchangeable gapage (E). 4. Model for interaction between permanent gapage (P) and position of umbo (U). 5. Model for interaction between permanent gapage (P) and depth of sinus (N). 6. Model for interaction between exchangeable gapage (E) and streamlining (S). 7. Model for interaction between streamlining (S) and position of umbo (U). Fig. 8. Model for interaction between streamlining (S) and depth of sinus (N).

The value of the model is in its degree of resemblance to the actual organism. What are the discrepancies, if any, and how are they significant?

The paradigm model is similar to the theoretical morphospace. Both analyses compare actual and hypothetical characteristics of an organism. The model represents a region of the theoretical morphospace that has a high probability of being the actual morphospace, based on outside inferences. Both form a consistent pattern against which to compare the results of analyses.

Models of Shell Shape

It is possible to predict sequences in the values of shell shape parameters using the paradigm methodology. These parameters may be taken as a whole to describe the overall shell shape. The models are understood most easily as pairwise comparisons of the parameters.

Permanent Gapage and Streamlining: Streamlining would be expected first to increase into the intermediate phase with increasing depth of burrowing, and then decrease as permanent gapage becomes pronounced (Fig. 2). Increased streamlining occurs as bivalves become more suited to burrowing in the shallow infaunal zone. At a

critical depth, which varies from sediment to sediment and depends upon the size of the bivalve, the weight of the substrate limits the depth of burial. Deeper burrowing can occur in a lineage only by the formation of exchangeable gapage. This is the beginning of the intermediate phase. The increasing degree of exchangeable gapage should begin to diminish the amount of streamlining. As exchangeable gapage is modified into permanent gapage, streamlining should decrease continuously as the life style shifts from efficiently moving in the shallow substrate to a deeply buried sedentary existence.

Permanent Gapage and Exchangeable Gapage: As with streamlining, levels of exchangeable gapage should rise and then fall with increasing permanent gapage and deeper infaunal existence (Fig. 3). The peak of exchangeable gapage lies within the intermediate phase. Streamlining is modified into exchangeable gapage, which in turn is modified into permanent gapage.

Permanent Gapage and Relative Position of Umbo. The model suggests that the umbo, as a relative measure of the position of the cardinal teeth, should become centralized to allow maximum exchangeable gapage as a lineage enters the intermediate phase (Fig. 4). The position of the umbo in individuals

past the intermediate phase may depend upon the type of life style. The location of the umbo may be unimportant in sedentary forms that lack both a functional foot and rocking of the shell along a dorso-ventral axis. The umbo may become placed anteriorly in tube-dwelling forms, which have large muscular feet, because of its associated pedal muscle insertions. Thus two paths are expected out of the intermediate phase.

Permanent Gapage and Relative Depth of Sinus. As burrowing depth increases, so must the length of the siphons in non-tube dwelling forms. This entails an increase in sinus depth to accommodate them. The depth of the sinus will be high within the intermediate phase (Fig. 5). Two paths are predicted as the lineage passes into permanent gapage. Siphons in tube-dwelling species do not increase if they remain permanently exterior to the shell, as in members of the solenaceans. Siphons may remain retractile in other forms, requiring a deep pallial sinus.

Exchangeable Gapage and Streamlining. Streamlining is expected to increase into the intermediate phase until exchangeable gapage becomes more evident (Fig. 6). As exchangeable gapage is modified into permanent gapage, both exchangeable gapage and streamlining should decrease. Thus, there should be both a path out and in along the exchangeable gapage axis.

Streamlining and Relative Position of Umbo. The relative position of the umbo should become centralized for maximum exchangeable gapage as streamlining passes into the intermediate phase (Fig. 7). As previously mentioned, the fate of the position of the umbo depends upon factors not accounted for in this model, and two paths are expected out of the intermediate phase.

Streamlining and Relative Depth of Sinus. With increasing streamlining, the relative depth of the sinus should increase into the intermediate phase (Fig. 8). Past this point the sinus depth may remain constant or decrease.

METHODS AND MATERIALS

Taxa Used in the Study

Representatives of 632 Recent species and subspecies of bivalves were used in this

study. Specimens were acquired from the following repositories and collections: Museum of Comparative Zoology, Cambridge, Massachusetts; National Museum of Natural History, Washington, D. C.; Ohio State University Museum of Zoology, Columbus, Ohio; and the author's private collection. The identification of museum specimens was taken from collection records, with the following exceptions at Ohio State University. Individuals of southeastern United States in the genus *Eliptio*, and a few members of other genera from that region, were identified by the author, as were all marine species from that collection. These identifications may not reflect the views of systematists at that institution. The higher systematic levels are taken from Vaught (1989).

Members of 15 families were selected for study, representing most of the living infaunal bivalve groups. These families, and the number of species or subspecies used in this study for each in parentheses, are: Mactridae (41), Cardiidae (56), Myidae (6), Psammobiidae (25), Solenidae (8), Cultellidae (9), Tellinidae (42), Semelidae (7), Donacidae (18), Veneridae (103), Petricolidae (1), Unionidae (276), Hyriidae (16), Mycetopodidae (13), and Mutelidae (11). Many families were chosen because they displayed a wide range of shell forms: streamlined vs. rotund, sculptured vs. unsculptured, etc. Others, such as the Solenacea, were chosen because their unique forms offered insight into this study. Some families subsequently were divided into subfamilies, and others grouped into orders better to indicate functionally alike groups. The Unionaceans, which have been omitted from most studies of this sort, were represented by the most taxa. They were included because no other group of Recent bivalves encompasses such a wide range of shell shapes. Other infaunal bivalve groups were not included, for the following reasons. Individuals of the anomalodesmaceans generally are too rare to obtain a reasonable sample. The Arcidae, Mytilidae, and Pinnidae have infaunal members, but most are sessile and byssate, and thus different from the free living infaunal groups chosen for study (Newell, 1969; Rosewater, 1961; Soot-Ryen, 1955, 1969). Members of other groups, such as the Astartidae, are too homogeneous to warrant repetitive measurements. Individuals of the Lucinidae are infaunal and have a wide range of shell shapes, and members of many species are common. However, the mode of circulating

water of the lucinids is quite different from the groups included here (Allen, 1958). The differences are sufficient to eliminate it from this study of infaunal groups. Because this study deals only with Recent species, otherwise interesting groups such as the largely extinct Trigoniacea were excluded.

Measurements and Derived Values

The following measurements, all in mm, were taken on individuals for each of the 632 species.

Length—the greatest length along an anterior-posterior line (Fig. 9a). This line usually was parallel to the hinge axis.

Height—the greatest dorsal-ventral height, perpendicular to the line for length (Fig. 9d). This line often extended through the umbo.

Width—the greatest lateral width, with both valves closed (Fig. 9c).

Position of umbo—the distance from the anterior margin to the umbo, along the length line (Fig. 9b).

Depth of pallial sinus—maximum depth of the sinus measured out to a curve that follows the pallial line (Fig. 9e).

Anterior permanent gape—the maximum width of any anterior space between the valves when the valves are closed and rocked forward, if possible (Fig. 9f). All measurements of gape were made on dry shells with separated ligaments and no commissural periostracum. The values obtained therefore may be overestimated uniformly to some degree.

Posterior permanent gape—the maximum width of any posterior space between the valves when the valves are closed and rocked backwards, if possible (Fig. 9h).

Anterior exchangeable gape—the total anterior gape is the maximum width of any space created anteriorly between the valves when the valves are rocked backwards (Fig. 9g). The anterior exchangeable gape is the total minus the permanent anterior gape.

Posterior exchangeable gape—the total posterior gape is the maximum width of any space created posteriorly between the valves when the valves are rocked forwards (Fig. 9i). The posterior exchangeable gape is the total minus the permanent posterior gape.

The following derived values were calculated from the above measurements.

Streamlining (S)—a univariate estimate of the relative amount of surface area exposed perpendicular to the direction of maximum length. The algorithm was devised for this

study to permit the simple quantification of a parameter that has been expressed historically as a multivariate construction. The metric is dimensionless, independent of size, and has a finite range of values. Its derivation, characteristics, and application will be treated in detail.

Workers in bivalve morphometrics have realized that some shells are more elongate than others and should offer less resistance to the substrate in burrowing activities. Stanley (1970) and subsequent authors (notably Morton, 1976) have attempted to illustrate this shape by graphing ratios of shell measurements against one another and delineating a region of the theoretical morphospace as "streamlined." The difficulty with this approach is that it requires two dimensions to describe elongation. If one wishes to investigate the relationships between elongation and any other parameter, one must use multivariate correlations (at least three variables). This has not been attempted, except in the study of Thomas (1975) on glycymerid bivalves.

Streamlining in a different sense has been mathematically defined and quantified by engineers working with fluid and aerodynamics, and several attempts have been made to treat organisms in the same manner as ships and planes. These studies generally focus on optimum shapes for maximum speed, or the reverse, maximum speeds given a certain shape. One study calculated swimming speeds of extinct marine reptiles (Massare, 1988). She calculated the total drag on reptiles using an estimate of surface area, water velocity, density of the medium, and the Reynolds number (a function of body shape in lamellar or turbulent flow). Such an analysis is not applicable to bivalves burrowing through a mixed substrate.

It must be emphasized that the use of the term "streamlined" by malacologists working with bivalves is not that of Massare. That expression is used here as a descriptive variable, crudely measuring only the relative amount of surface area normal to the long axis of the shell, generally coinciding with the direction of burrowing. It carries no connotation of, or resemblance to, fluid dynamic theory. Neither is it a dynamic value dependent on burrowing speed, current velocity, or substrate type. Although univariate, the quantification of streamlining put forth in this study is identical with the sense of that term used in describing bivalve shell shape by Trueman et

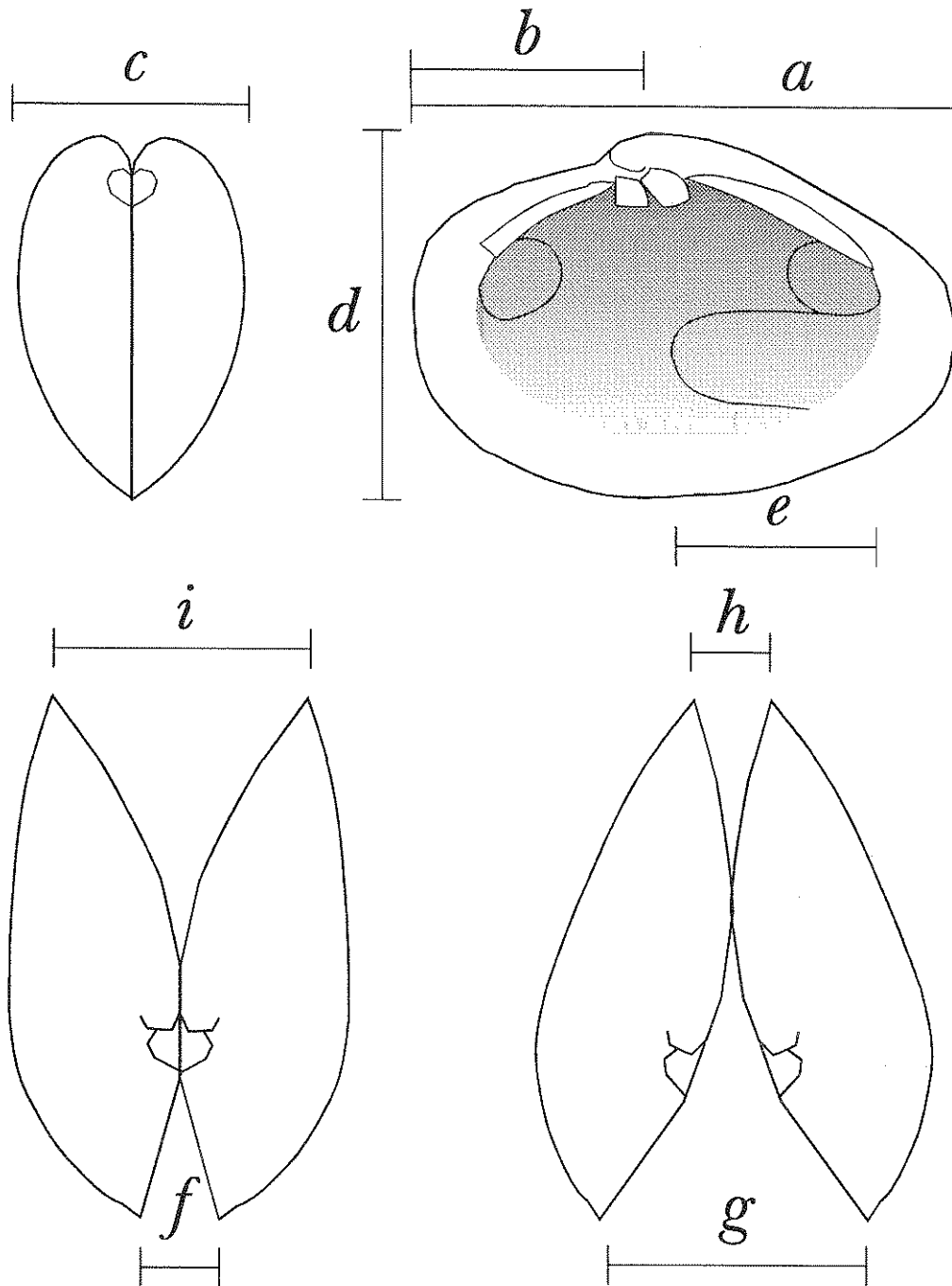


FIG. 9. Measurements used in study. a: Length. b: Distance of umbo from anterior margin. c: Width. d: Height. e: Depth of pallial sinus. f: Permanent anterior gape. g: Total anterior gape. h: Permanent posterior gape. i: Total posterior gape.

al. (1966b), Stanley (1970), Alexander (1974), Eagar (1974, 1978), Thomas (1975), Morton (1976), and Seed (1980a, b).

The calculation of streamlining (S) in this study estimates the shell shape as a rectangular solid of dimensions Length \times Width \times Height. The value of S lies between two hypothetical limits, interpreted as the minimum and maximum amount of streamlining for the rectangular model. At the theoretical minimum, Height and Width equal a unit measure (Height and Width = 1), and Length = 0. Movement is in the direction of Length, perpendicular to Height and Width. The model resembles a sheet of paper moving perpendicular to the face of the page. This is the minimum amount of streamlining. The theoretical maximum is achieved when Length = 1 and Height and Width both = 0. This model resembles a line of no thickness moving parallel to itself. Bivalves lie between the two extremes. The calculation is dependent on the relationship between Length and the remaining descriptors. This has the effect of standardizing data by size by removing any influence of Length. The equation can be written as:

$$S = \frac{(\text{Width}/\text{Length})(\text{Height}/\text{Length})}{(\text{Length}/\text{Length})} \quad (1)$$

When Height and/or Width is very small relative to Length, S approaches 0. Conversely, when Length is very small relative to Height and/or Width, S approaches infinity (∞). It is possible to limit these theoretical boundaries by raising the natural logarithm (e) to the exponent S and taking the inverse. Removing the cancelled expression (Length/Length), and raising e to the remaining parameters yields the equation:

$$S = \frac{e((\text{Height}/\text{Length})}{(\text{Width}/\text{Length}))} \quad (2)$$

Now as Length/Height or Length/Width \rightarrow 0, $S \rightarrow \infty$, and as Height/Length or Width/Length \rightarrow 0, $S \rightarrow 1$. Taking the inverse of the function has the following effect. As Length/Height or Length/Width \rightarrow 0, $S \rightarrow 0$; as Height/Length or Width/Length \rightarrow 0, $S \rightarrow 1$. The equation has the final form:

$$S = \frac{1/(e((\text{Height} \times \text{Width})/(\text{Length})^2))}{(\text{Length})^2)} \quad (3)$$

The resulting parameter is independent of original size, unitless, and ranges from a

value of 0 for no streamlining to a value of 1 for maximum streamlining. Although the values resemble percentages, they are not. As S is univariate, it may be compared with other morphometric parameters without the necessity of multivariate analysis. The function is nearly rectilinear within the biological range of its values. In this study, a maximum S of 0.99 was encountered in several members of the solenid genus *Ensis*; a minimum of 0.01 was found in individuals of the epifaunal cardiid *Corculum cardissa* (Linnaeus, 1758).

The choice of length as the direction of motion was necessitated by the lack of knowledge of the actual life positions of most bivalves used in this study (Stanley, 1970). The use of this metric is considered a normalizing method. Arguments may be raised against its use based upon the well-known fact that maximum length does not always correspond to burrowing direction. This particularly is true of such groups as the lucinids not treated here (Allen, 1958). This discrepancy between length and direction of movement exists primarily in individuals of very shallow infaunal species, having a low S and no gapage. It can be shown that as S increases, the angle of offset diminishes, for the few species for which data are available (Fig. 10). Most of the species discussed here have an S value $>$ 0.8. Thus, for most the forms covered, the incongruity between length and direction of movement is small. Even at large offset angles the discrepancy is overestimated. The species at this level of S are generally circular in outline, or nearly so. The line of greatest length is a secant through the shell outline, as would be the direction of movement. Both approximately would be equal in length. Height would differ little between the two lines, and Width not at all. The calculation of S may therefore be accurate even at low levels of S.

Relative position of umbo (U)—the measurement of the position of the umbo was divided by total length to standardize this variable. The metric is a percentage of the total length.

Relative depth of pallial sinus (N)—calculated as for U, using depth of pallial sinus.

Relative permanent gape (P)—standardized with the formula:

$$\frac{(\text{anterior permanent gape} + \text{posterior permanent gape})/(2 \times \text{width})}{\text{width}} \quad (4)$$

Relative exchangeable gape (E)—standardized with the formula:

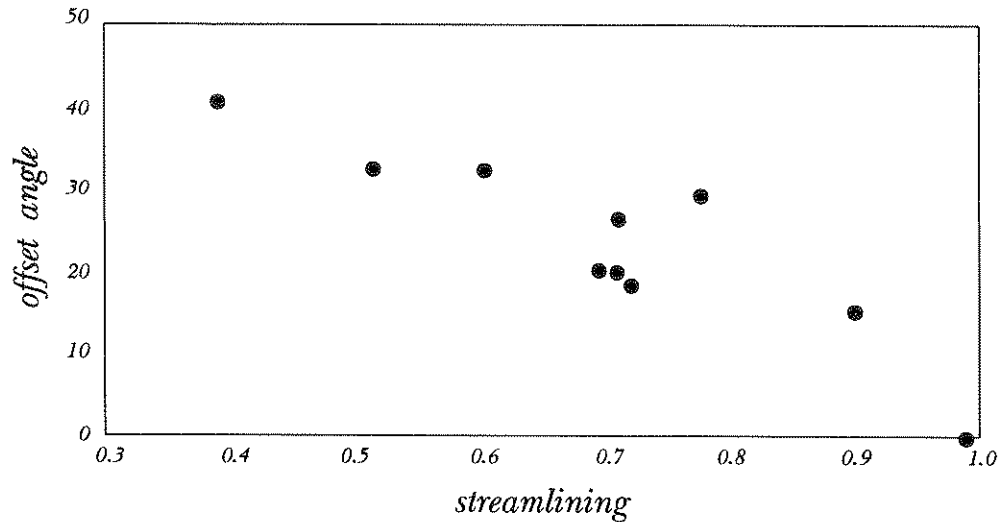


FIG. 10. Offset angle (burrowing angle relative to greatest length) vs. streamlining.

(anterior exchangeable gape + posterior exchangeable gape)/(2 × width) (5)

RESULTS

Comparison of Shell Shapes With Models

Permanent Gape and Streamlining: A comparison with the results reveals that although streamlining initially does increase as permanent gape increases, past the intermediate phase the degree of streamlining becomes constant rather than decreases in many individuals (Fig. 11). There are two paths out of the intermediate phase, although the numbers of individuals in that region are so few that it is difficult to make such a claim with certainty. Individuals of the Tellinidae and Myidae conform to the predicted model given above. Deep burrowing forms have lost streamlining and may be sedentary as adults. Members of the solenaceans and some solecurtine psammobiids have maintained high levels of streamlining despite pronounced permanent gape. This is due in large part to the ability of many of these forms to construct tubes in which they move (Drew, 1907, 1908). The highest degree of streamlining is found in the tube-dwelling members of *Solen*. Levels of permanent gape and streamlining are both high in these forms because these bivalves no longer burrow through the sub-

strate, but rather move within water filled tubes.

Permanent Gape and Exchangeable Gape: The results support the model, but two paths are suggested (Fig. 12). Members of the solenaceans and some solecurtines occupy one path, but the individuals of the Myidae and other members of the Solecurtinae occur on the other path. The first path contains forms having high levels of exchangeable gape and permanent gape as the result of their tube-dwelling behavior. It is important to note that members of the Solecurtinae have participated in both paths, and that forms of the mastrids also are diverging. This suggests that members of a single family may not follow a single morphological path. This result occurs in several families.

Permanent Gape and Relative Position of Umbo: Two paths are evident out of the intermediate phase (Fig. 13). The model predicts 0.5 for maximum exchangeable gape, but most bivalves have the umbos placed slightly anterior to act as a source of attachment and a buttress for pedal muscles. The intermediate phase average relative position of the umbo is approximately 0.4. From that point (and perhaps before), the umbo may be placed either anteriorly or slightly posteriorly. The forms with anteriorly positioned umbos are those that use the foot either as an anchor

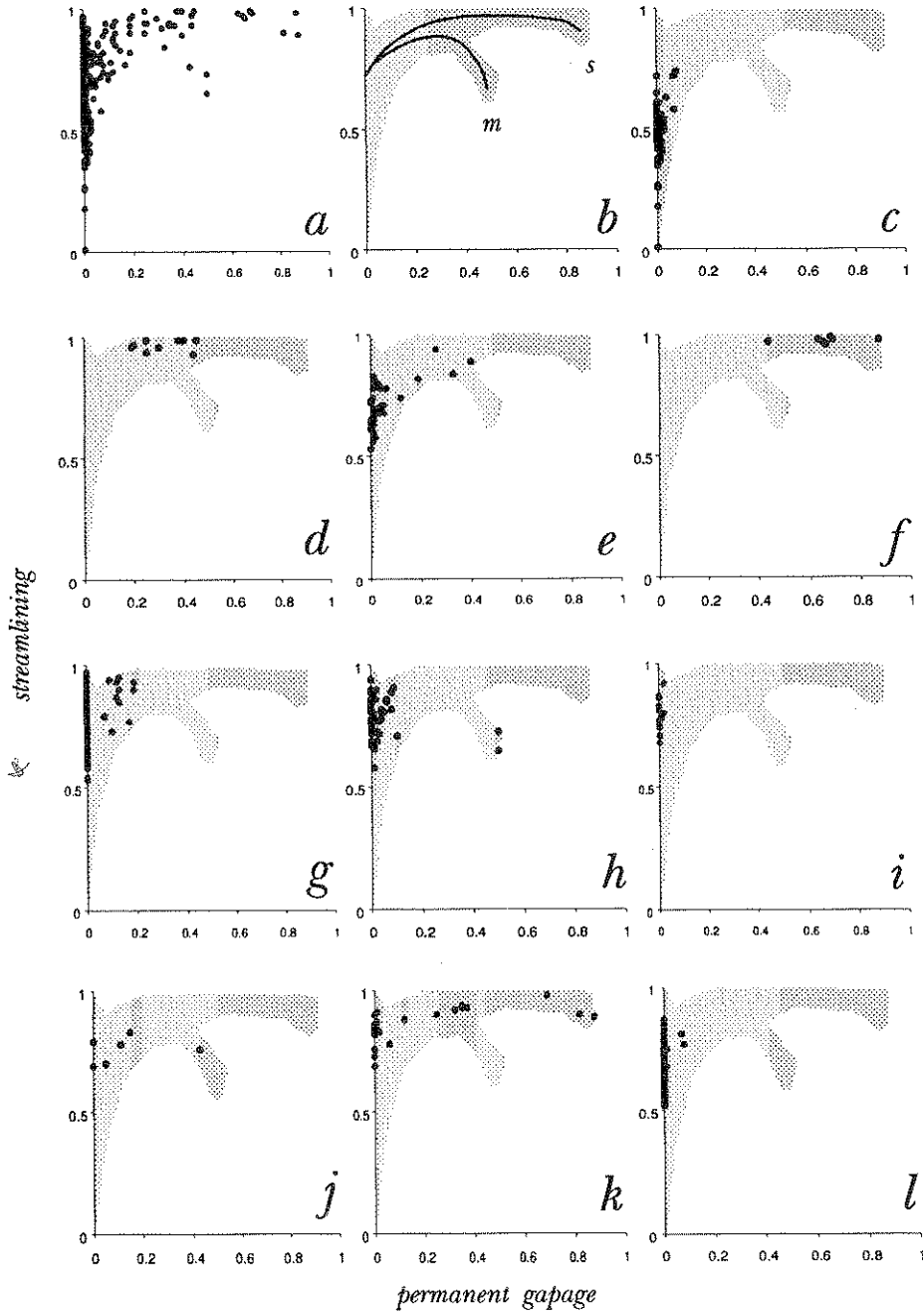


FIG. 11. Permanent gapage vs. streamlining. a: All data. b: Hypothesized paths. c: Cardiidae. d: Donacidae. e: Mactridae. f: Solenidae. g: Unionoida. h: Tellinidae, Semelidae. i: Cultellidae. j: Myidae. k: Psammobiidae. l: Veneridae, Petricolidae. Shaded area: Actual morphospace. m: Myid path. s: Solenid path.

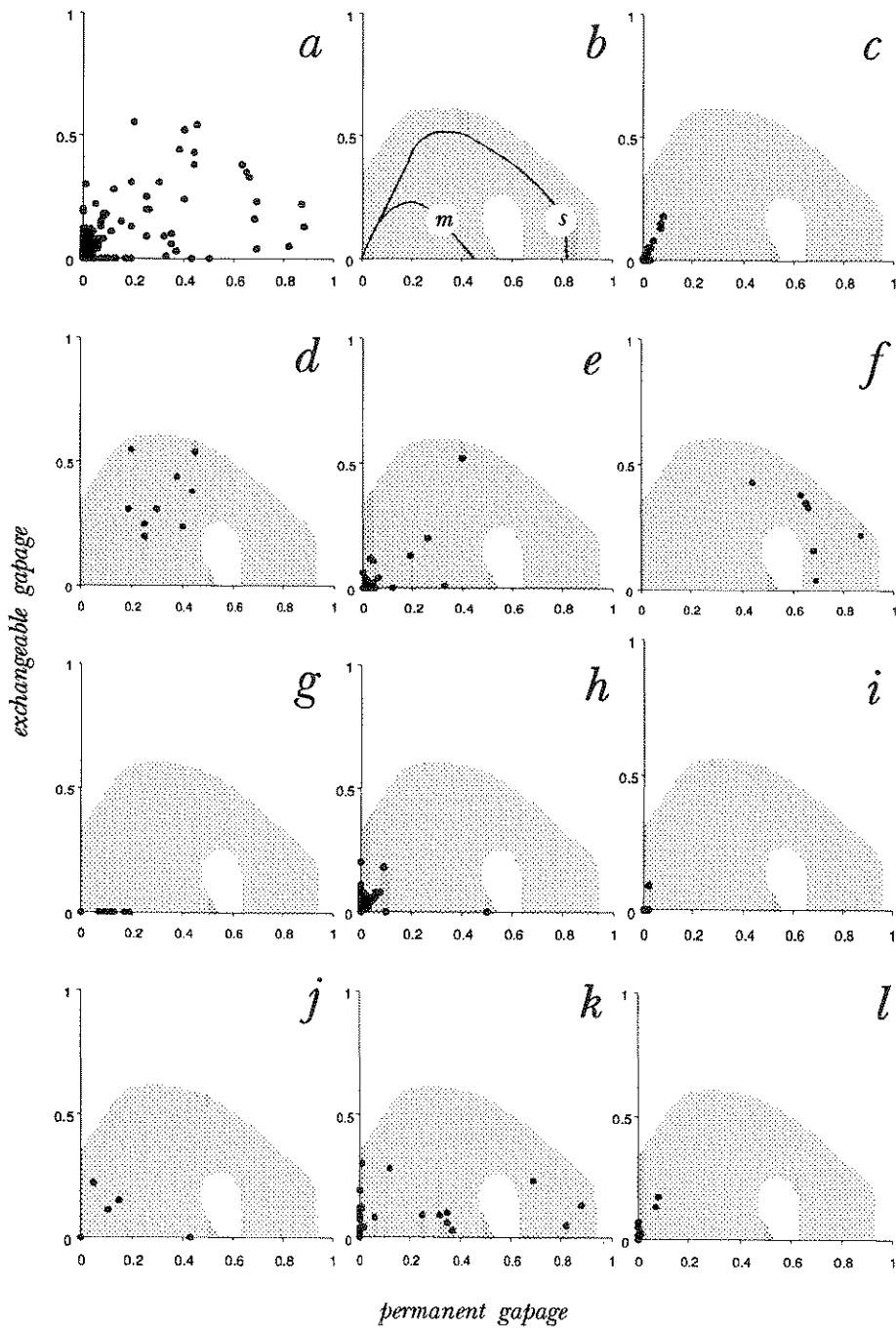


FIG. 12. Permanent gapage vs. exchangeable gapage. See Fig. 11 for details.

(Unionoida) or a wedge within a burrow (solonaceans, cultellids), not as a device for active burrowing. The second path tends toward

the theoretical value of 0.5, indicating the emphasis on active burrowing and exchangeable gapage in most of its members (Tellinidae,

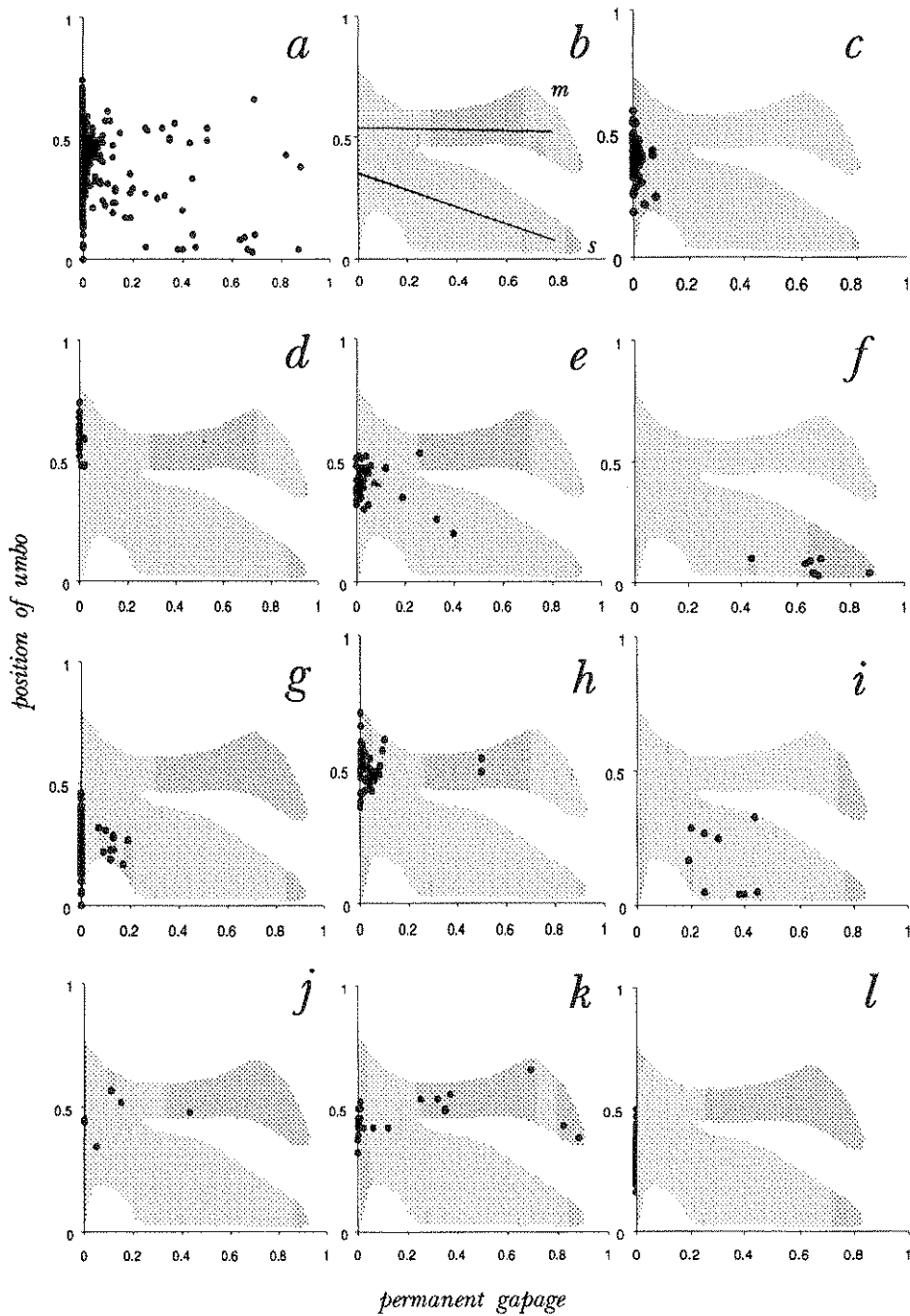


FIG. 13. Permanent gapage vs. position of umbo. See Fig. 11 for details.

Solecurtinae, and others). The families Cardiididae and Mactridae have morphologies tending toward both directions.

Permanent Gapage and Relative Depth of Sinus: The results seem to suggest two ill-defined routes away from the intermediate

phase. One toward slightly increased sinus depth and the other toward greatly reduced depth (Fig. 14). Within members of a family, both paths may be found (Solecurtinae, Tellinidae, and Mactridae). Members of the solenaceans have reduced the sinus to a minimum despite their deep infaunal habitat. This is due to a reduction in siphon length. Individuals of solenaceans live in water-filled tubes and may dwell at the surface, only retreating to the bottom of the burrow to escape.

Exchangeable Gapage and Streamlining: Streamlining is expected to increase into the intermediate phase as exchangeable gapage becomes more evident. The results support this prediction (Fig. 15). Members of all families lie upon a fairly narrow region of the theoretical morphospace. This is unexpected in view of the original prediction: as exchangeable gapage is exapted into permanent gapage, both exchangeable gapage and streamlining should decrease. Thus, there should be a path out and in. However, the parameters used could not differentiate these paths.

Streamlining and Relative Position of Umbo: Two paths are apparent out of the intermediate phase (Fig. 16). The first is toward a slightly more posterior position and contains members of the Tellinidae, Donacidae, Solecurtinae, and Myidae. The second, toward a more anterior placement, contains forms of the solenaceans and the Unionoida. The Mactridae and Veneridae have members in both paths.

Streamlining And Relative Depth Of Sinus: The relative depth of the sinus is predicted to increase into the intermediate phase. Two paths are possible beyond the intermediate phase and this pattern is supported by the results (Fig. 17), along with an unexpected result. Members of the order Unionoida do not participate in this path but reach a high level of streamlining with no appreciable sinus (or siphons). The presence of individuals of the Myidae so far back on the path suggests that the sequence is reversible along its path.

DISCUSSION

Family Accounts

Cardiidae. The cockles are a large family of shallow infaunal dwellers with heavy compos-

ite sculpture. Anti-scouring, anchoring, and burrowing sculptures may exist in the same species (Stanley, 1981). These sculptural devices are suited particularly to a shallow infaunal existence. Few members have colonized the deeper infaunal zone.

However, three of the five subfamilies have members that have entered the intermediate phase. None have evolved beyond it. In the Protocardiinae, containing the most primitive living cockles, members of the genus *Lophocardium* are in the intermediate phase. This is a rarely encountered group of perhaps three species. The Laevicardiinae contains the intermediate phase members in the genus *Fulvia*. This genus also is composed of very few species. The Trachycardiinae includes the genus *Papyridea*, containing seven or eight species.

The premier example of a group in the intermediate phase is members of the cardiid genus *Papyridea*. One must know something about their ancestral stock to appreciate their remarkable modifications. *Papyridea* is a genus of the trachycardiinine cockles, which is a widespread group of tropical and sub-temperate species. The members of the subfamily are characterized by: (1) strongly, radially ribbed shells, ornamented with complex composite sculptures used for burrowing and anti-scouring (Stanley, 1981); (2) short siphons, limiting them to a shallow infaunal existence; (3) central, or nearly so, umbos; and (4) a short hinge plate with simple interlocking lateral teeth and centrally located cardinals. The pronounced ribs apparently act as strengthening devices and on the shell margin tend to interdigitate to form a "ventral hinge" (Carter, 1968).

Members of *Papyridea* have these shell characteristics modified into features predicted for exchangeable gapage. The dorso-ventral axis of shell rocking employs the following changes: (1) the central umbo and cardinal teeth become the static dorsal pivot; (2) the interdigitation of the ribs on the ventral margin becomes a dynamic pivot as the sculpture functions like the teeth on two intermeshed gears; and (3) the lateral teeth disengage in the resting position, but alternately mesh as the shells are rocked along the dorso-ventral axis forward or backward. The shell has become more streamlined ($S = 0.74$) than most other cockle shells. The ribbed sculpture is minimized on the disc of the shell, although the composite sculpture is retained. The ligament is shortened and po-

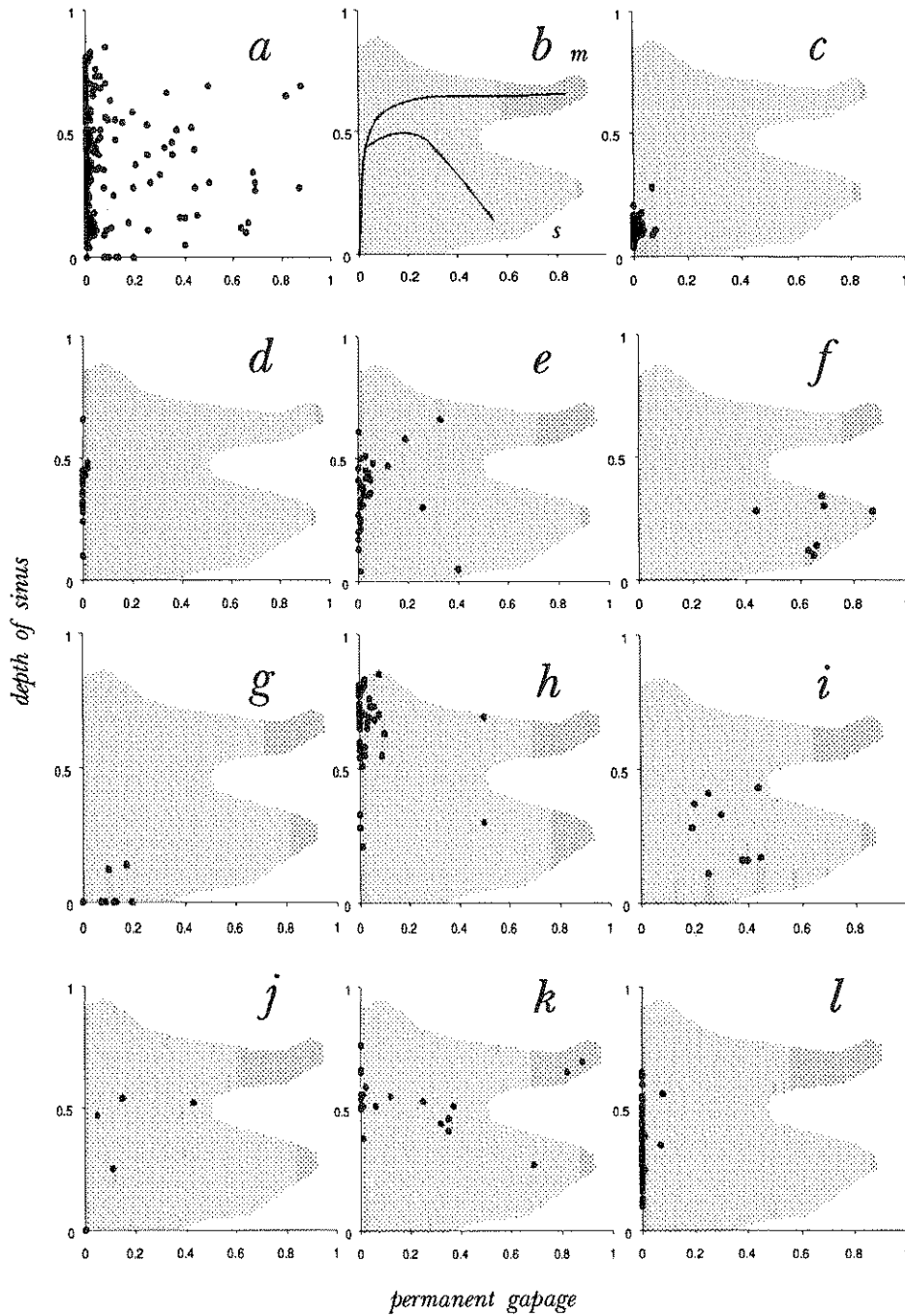


FIG. 14. Permanent gapage vs. depth of sinus. See Fig. 11 for details.

sitioned near the umbo where it does not interfere with the rocking movements. The short siphons have become more elongate (Stan-

ley, 1970). Unlike the shallow infaunal habitat of other members of the Trachycardiinae, members of *Papyridea* are known to burrow

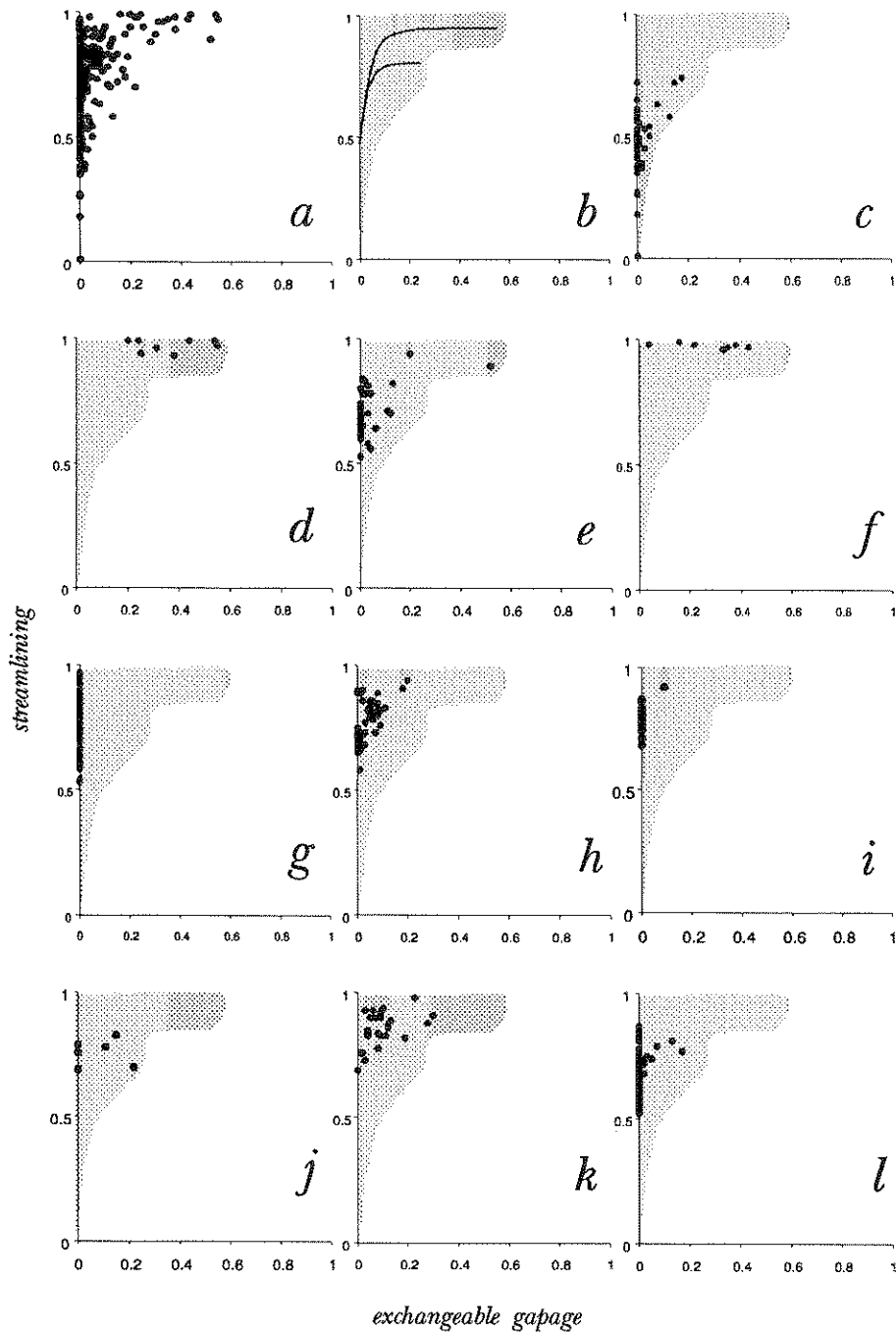


FIG. 15. Exchangeable gapage vs. streamlining. See Fig. 11 for details.

to approximately one half their length and are moderately rapid burrowers. Stanley (1970: 158) stated that an individual of *P. soleni-*

formis (Bruguière, 1789) "has longer siphons and lives at a greater depth than other cardids studied."

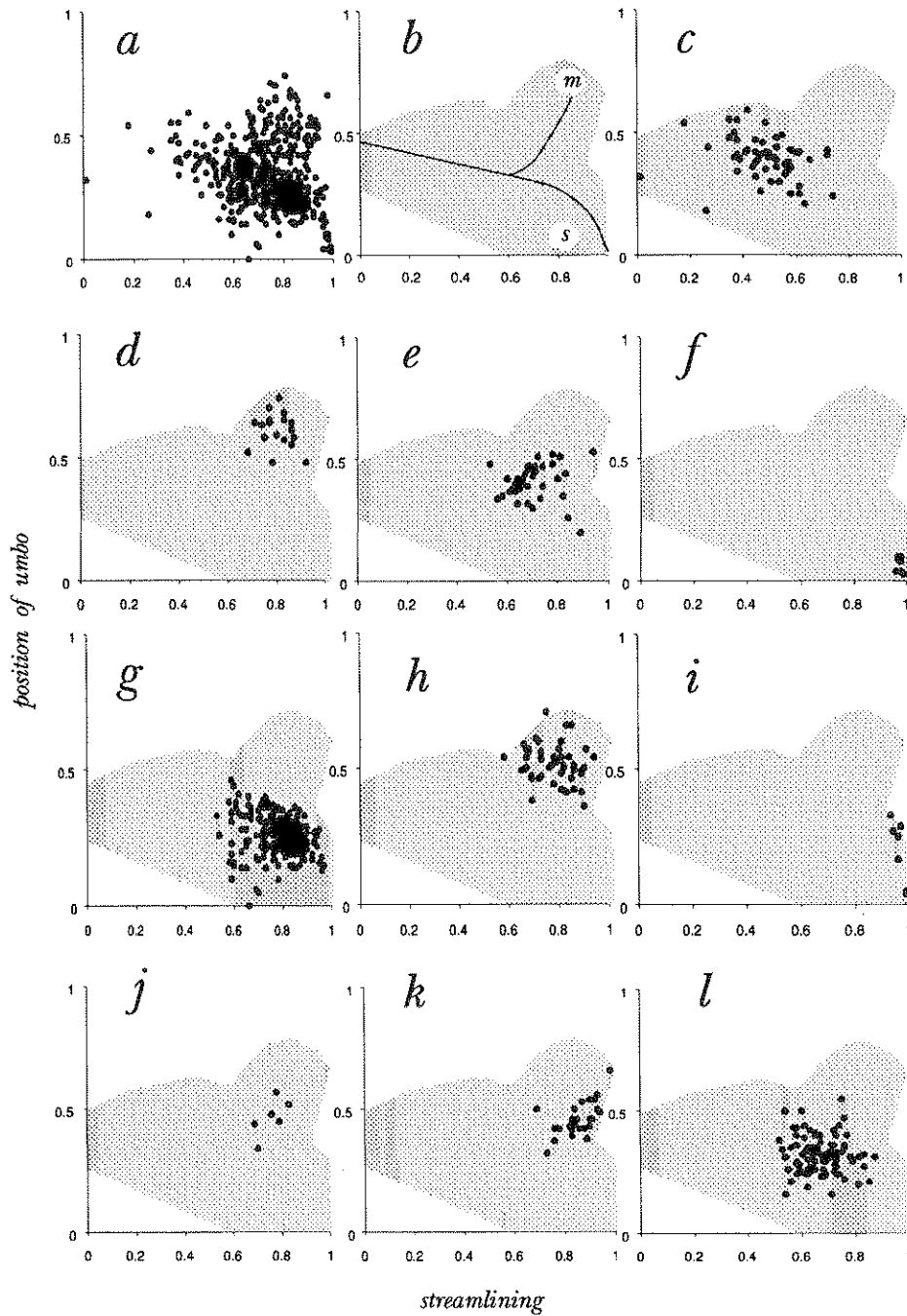


FIG. 16. Streamlining vs. position of umbo. See Fig. 11 for details.

Members of the *Papyridea* lineage are in the process of colonizing the deeper infaunal habitat. It is one of the few modern groups in

the intermediate phase. Most bivalves are either bottlenecked behind this position (including most of the members of the Cardidae), or

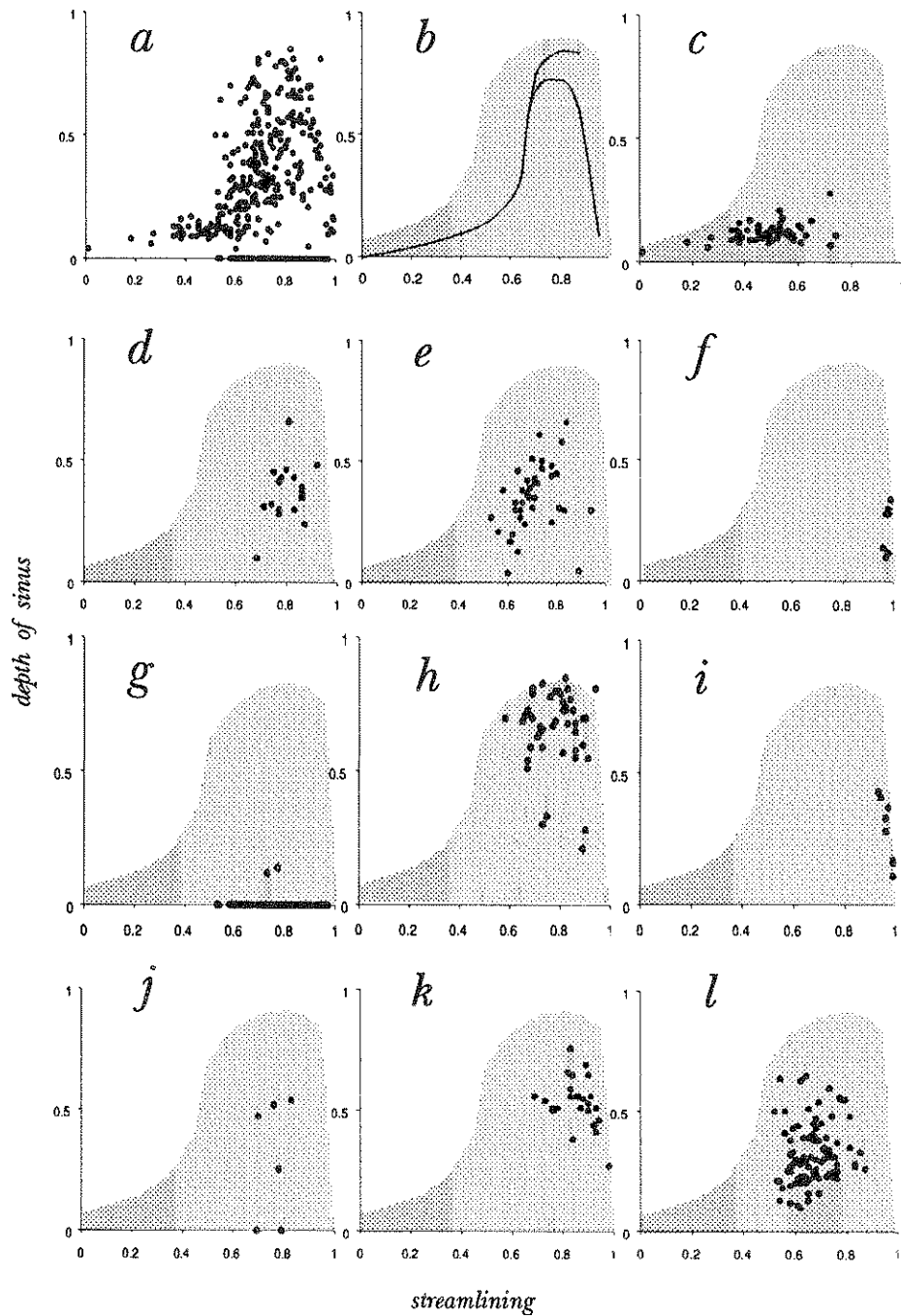


FIG. 17. Streamlining vs. depth of sinus. See Fig. 11 for details.

have advanced into the permanent gapage phase (members of the solenids, cultellids, and solecurtines).

Members of *Papyridea* stand out from the few groups in the same level of transition because of their high degree of modification of

pre-existing shell characteristics. The central position of the umbo, the short central ligament, and the simple lateral teeth all are prerequisite to enter the intermediate phase. It must be emphasized that entry into this phase depends upon the chance alignment of several shell characteristics, therefore the great number of shallow infaunal species bottlenecked behind this morphological barrier.

Veneracea (Veneridae and Petricolidae). The true, or venus, clams comprise the largest single family of living bivalves. Ansell (1961) categorized individuals of this family as soft substrate-dwelling with few burrowing modifications. They successfully have exploited the shallow infaunal zone with little invasion of the deeper infaunal zone. None have achieved a streamlining coefficient greater than 0.9 or a permanent gavage of greater than 0.15. None have entered the intermediate phase. This is because venerids have not achieved the suite of characteristics necessary to enter that part of the sequence. Ansell (1961: 514) remarked that "[in members of the genus *Petricola*], well developed hinge teeth and the long ligament make rocking movements of the shell valves . . . impossible." Yet the members of the group have already begun to diverge along the streamlining/relative position of the umbo paths (Fig. 16). Members of the Meretricinae are tending toward a more central umbonal position. Individuals of the Tapetinae and some elements of the Pitarinae (forms in *Macrocallista*) and the Chioninae (members of *Protothaca*) are on the path toward an anteriorly positioned umbo.

Macridae. The surf clams encompass more morphological forms than any other family in this study. The group contains venerid-like shallow infaunal forms as well as deep infaunal dwelling individuals reminiscent of some members of the solenaceans. Stanley (1972, 1977a) has pointed out the convergence in morphology of macrids with that of individuals of such other families as the Myidae, Veneridae, and Tellinidae.

A singular shell design is prevalent in this family and has been modified for the intermediate phase. The ligament has been partially internalized and positioned beneath the umbo in a resilifer, where it serves as a fulcrum during rocking as well as providing the opening moment of the valves (Yonge, 1982). The result is a central ligament independent of streamlining (Seilacher, 1984) and offering little resistance to exchangeable gavage.

Two paths may be taken out of the inter-

mediate phase. Members of four genera have entered the intermediate phase and/or exceeded it into the area of permanent gavage. As in the Cardiidae, the species within each genus are very few. These groups are members of the lutrariine genera *Lutraria* and *Psammophila*, both of European seas, and the Indo-Pacific zenatiine genera *Zenatia* and *Resania* [Beu (1966) places the latter in its own subfamily, the Resaniinae]. Members of *Resania* tend toward the path to a centrally located umbo. Members of the other three all lie on a path toward an anterior umbo (Fig. 13). For the relative depth of the sinus, members of *Lutraria* and *Psammophila* are tending toward a deep sinus, whereas those of *Resania* and *Zenatia* are approaching a very shallow sinus reminiscent of that found in members of the solenaceans. For exchangeable gavage, individuals of *Psammophila* are on the path of the myids, whereas the members of the remaining three genera are on the solenacean path.

Individuals of *Lutraria* and *Tresus* have a reduced foot as adults (Yonge & Allen, 1985), indicative of diminished burrowing ability. Members of *Tresus* may live at substrate depths of 50 cm, where they are sedentary as adults (Yonge, 1982). Cotton (1961: 297) gave this account of an individual of *Lutraria rhynchaena* Jonas, 1844, a species in intermediate phase (note the modifications for exchangeable gavage):

[It] burrows deeply in sandy mud . . . siphons reaching upwards to the surface. . . . The short ligament allows considerable movement at the ends without opening the shell throughout. With the valves in their ordinary positions the shell gapes equally at each end, but the arrangement of teeth and ligament is such that the front of the shell may be entirely closed.

That members of *Lutraria* lie on the solenacean path is not surprising. Beu (1966) described their life habits as tube dwelling in the manner of individuals of *Solen*.

Beu (1966) also noted the exchangeable gavage of members of *Resania* and *Zenatia*. He believed the former to be an active burrower in sand in the wave zone, and the latter to be a sedentary burrower offshore.

Lineages of the macrids are evolving (in the sense of the variables studied here) in diverse directions, more so than any other family covered in this study. The family has members in all possible paths and in all three morphological phases.

Tellinacea (Tellinidae and Semelidae). The tellins and semelids are large groups of active, streamlined, shallow to moderate depth burrowing bivalves. Most are unsculptured, and the few groups that are (some members of *Scutarcopagia* and *Strigilla*, for example) have composite burrowing sculptures. They are within the intermediate phase and are on the path of the myids. They have extensive siphons and a pronounced sinus, also a central umbo, and the shell of many forms has some degree of exchangeable gapage. Members of a few species can burrow to moderate depths (Hughes, 1969).

Yonge (1949) believed that forms of the Tellinidae, Solecurtinae, and Donacidae were derived independently from members of the Psammobiinae resembling individuals of *Gari*. Pohlo (1982) offered a different phylogeny, making members of the Tellinidae the end of the sequence Donacidae → Solecurtinae → Psammobiinae → Tellinidae. The present study does not support this contention, and suggests a phylogeny more similar to that of Yonge. Members of the donacids may be an offshoot of the tellins specialized to the high-energy environment of the sandy intertidal zone.

Most, if not all, tellins, also some forms of the psammobiids, have a unique "X"-shaped muscle, the cruciform muscle, connecting the ventral margins of the shells. Yonge (1949) noted that this muscle occurs at the ventral base of the siphonal attachment and believed that it functioned to anchor the siphons at this margin during protraction and retraction. This muscle group also could serve as a ventral connection during a rocking motion, limiting the ventral pivot to a specific point. This differs from the dynamic ventral pivot of most other groups in the intermediate phase.

Psammobiinae and Sanguinolariinae (Psammobiidae). Members of these subfamilies are the morphological precursors of the solecurtine psammobiids, and occupy the intermediate phase for this family. They are morphologically the analog of the tellins. But unlike them, members of the Psammobiidae have a permanent gapage group, the Solecurtinae. Members of the family lie upon the myid path.

Solecurtinae (Psammobiidae). Individuals of this subfamily are a fairly small group that resemble the razor clams in many shell characteristics. Members of the Solecurtinae, except forms of *Tagelus*, do not construct tube-like burrows, and have extensive siphons

(and deep sinuses). The members of *Tagelus* are similar ecologically and behaviorally to those of the solenaceans (Stanley, 1970). They occupy many of the same paths as that group. The major difference is the position of the umbos, which are central in members of *Tagelus* and anterior in solenaceans. Other groups of solecurtines are on different morphological paths.

Solenaceans. The razor clams have diverged from most infaunal bivalves in behavior and habitat. They construct tube burrows in which they move horizontally. This habit has produced a distinct alternative path out of the intermediate phase. Siphons and sinus may be greatly reduced because the animal may dwell at the surface, becoming deep infaunal in the sense of this study only to avoid danger. Because they can retreat into the deep substrate, permanent gapage is available. As tube dwellers, the highly streamlined shape is retained at maximum permanent gapage. This combination of characteristics has led to two paths out of the post-intermediate phase morphologies. Yonge (1951c: 429) recognized the important principle that shell and anatomy are separate entities: "There is the fundamental, though largely unrecognized, fact that throughout the Mollusca the growth of the body and the growth of the shell must be considered separately."

Myidae. The myids are few in species number but quite variable in morphology and ecology. Members of the genus *Cryptomya* live at depths of up to 50 cm, have only short siphons, and "tap" into the water filled cavities of burrowing crustaceans and echinoderms (Yonge, 1951a). Members of *Platydora* bore into soft stone (Yonge, 1951b). These specializations aside, the members of the genus *Mya* illustrate the expected result of the modeled path. All exchangeable gapage has been modified into permanent gapage, streamlining is reduced, teeth are non-functional, and the sinus is shallow as the siphons become increasingly non-retractable. Like forms in the Mactridae, the myids have a central, internalized ligament carried within a resilifer (Yonge, 1982). Analogs in the Hiatellidae (not included in this study), are individuals of *Panopea*, the geoduck clams.

Order Unionoida. Members of the four families of the freshwater unionoids participate in few of the paths discussed here. This seems attributable to their lack of fused mantle tissue, necessary to form siphons. Without siphons, deep burrowing is not obtainable un-

less tubes are constructed, as in the solenaceans, a behavior unknown in members of the Unionoida. Although the members of the unionoids achieve a high level of streamlining, this type of shell form appears to function in quick reburial rather than in efficient movement while buried (Watters, in prep). Individuals of the unionoids lie upon the solenacean path rather than upon the path of the other groups studied for streamlining and the relative position of the umbo. This is not to imply that unionoids are following the solenaceans in morphology. Individuals of unionoids have no true siphons (with the possible exception of members of *Leila*), usually cannot burrow far below the substrate/water level, and do not construct burrows.

Pholadacea. Although not used in this study, the shipworms and relatives briefly are discussed here because of their novel use of exchangeable gape. The antero-posterior rocking motion of the shells is used not only to protrude foot and siphons, but as a mechanical rasping device to excavate burrows in wood, shell, and stone. The shell and musculature have been reorganized to maximize this movement. These innovations have been discussed by Röder (1977) and Hoagland & Turner (1981). A recent study (Fuller & Castagna, 1989) also documents the complicated ontogeny of individuals of one species of this group.

Underlying Assumptions and Paradigms

The fundamental assumption of this study is that there is a definite selective advantage to becoming deep infaunal. The underlying question, then, is why aren't there more deep infaunal bivalves? The reason is related to the possible ways that a bivalve shell can be modified for this habitat. These modifications require a particular suite of characteristics, and only bivalves having this prerequisite suite can colonize the deep infaunal region. If the morphology of the lineage cannot be modified, that group cannot succeed in that habitat. Entry into this sequence would be rare if there was little or no adaptive significance to the lineage possessing the suite, or if another suite had high selective value. In the former case, the acquisition of the suite would depend on random fluctuations in the characteristics of the morphology. In the latter, there may be no impetus to move from one adaptive peak to another. A paucity of deep-

dwelling forms would be the expected result if either of these factors occurred in the evolution of the bivalves. Convergence also would be the expected result if only a few viable sequences of morphologies were available.

These constraints are due in part to the interactions between sediment and shell with increasing depth of burial. For simplicity, I will consider the substrate to be homogeneous. The addition of heterogeneous and stratified sediment variables, while a much more realistic scenario, cannot adequately be accounted for in this model. It is suggested that the simpler model may be extrapolated to the more complex.

The mechanics of burrowing in shallow infaunal bivalves have been documented by Trueman (1966), Trueman et al. (1966a), and Stanley (1970, 1975). However, the members of all groups studied, such as *Mercenaria mercenaria* (Linnaeus, 1758) in Stanley (1975), have low S values, no exchangeable gape, and no permanent gape. The steps in burrowing in such forms may be given briefly:

- (1) The foot probes the substrate.
- (2) The siphons are closed.
- (3) Adductor muscles close the valves, raising pressure in the haemocoel, which is transferred to the foot, forming an anchor.
- (4) Simultaneously, water is ejected from the mantle cavity, which momentarily loosens the immediately surrounding substrate.
- (5) The anterior pedal retractor contracts, pulling the animal forward against the anchored foot.
- (6) The posterior pedal retractor contracts, returning the shell to the original burrowing position.
- (7) The adductor muscles relax, diminishing haemocoel pressure and redirecting fluid out of the anchored foot. The siphons are opened.

This process continues until the animal is buried. Other factors also may be involved. Sculpture may assist burrowing, as may the presence of a prosogyre shape and a lunule (Stanley, 1969, 1975, 1981). But the focus of this study is deep-dwelling bivalves. The burrowing model given above may work for only a few of the groups in this study. The rocking motion around a dorso-ventral axis becomes impossible to accomplish as shells become more elongate (S increasing; Stanley, 1970). The foot must protrude from the anterior gape and is often as large in cross-section as the shell in streamlined forms. It appears, by its larger size, to be much stronger than the foot

of shallow infaunal burrowers of the same shell size. Eagar (1978) reported that the force of the pedal retractors may be equal to 100 times the weight of the shell in water in individuals of deep dwelling *Ensis*, but equal to only one-quarter the weight in members of shallow infaunal *Mercenaria*. These factors may be necessary in these groups to offset the lack of burrowing assistance that is found in shallow-dwelling forms afforded by the burrowing movement, shell sculpture, and lunule. Expulsion of water to loosen sediment appears still to be important. Many deep-dwelling forms have ventrally fused mantle tissue that presumably directs water forward during a burrowing cycle.

The ability to enter efficiently the substrate is a function of shell shape. Nair & Ansell (1968) found that elongate shells offer the least resistance to burrowing. In this study, the design most suited to burrowing is found in the entity having the highest S value, all other factors being equal. This often takes the form of a laterally compressed, antero-posterior elongated blade-like shape. Sculpture typically is lost, and Stanley (1970) has shown that coarse-sculptured species are slow burrowers. In members of a species that have both infaunal and epifaunal individuals, the infaunal morphs are more elongate (Seed, 1980a). Within the same genus, deep-burrowing members are more streamlined than are shallow-burrowing ones (Alexander, 1974; Eagar, 1974), although Agrell (1949) made a correlation between shell morphology and the trophic level of the water body.

The sediment load pressure increases with increasing depth of burial (Nair & Ansell, 1968). The animal must exert a force to open and maintain open the shells (Stanley, 1970). In bivalves this is accomplished typically by the ligament and/or haemocoel pressure. The shells must be opened to allow protrusion of the foot and siphons. Trueman et al. (1966a, b) have shown that the sediment pressure may exceed the opening moment of the ligament at critical depths, effectively limiting burial depth. One solution to this problem is the incorporation of permanent shell gapes into the morphology. The foot and siphons may be protruded through these openings or permanently left exposed. But the primary function of the shell is defense, and therefore the vast majority of epifaunal or shallow infaunal forms have complete closure of the valves. But a selective advantage is to be gained by penetrating the substrate further,

including a concomitant decrease in predation and an increase in habitat stability.

A solution to this problem requires having the shells retain their function as protective devices, while allowing the foot and siphons to protrude in a manner independent of the ligamental opening moment. Such a suite of characteristics does exist, and apparently represents the only compromise found in living bivalves. I have termed this unique morphology the intermediate phase, between the shallow and deep infaunal existence phases. It has a suite of predictable and testable characteristics that may be compared with actual forms.

The key innovation is exchangeable gavage (Fig. 1). The shells rotate along a dynamic dorso-ventral axis rather than along the dorsal hinge axis. Movement is effected by the adductor muscles rather than by the weaker ligament or haemocoel pressure. Contraction of the anterior adductor muscle closes the anterior (pedal) gape and opens the posterior (siphonal) gape. Contraction of the posterior adductor muscle has the opposite effect. Several important morphological requirements must be met for this mechanism to work.

First, the umbo must be approximately central. This orientation allows the maximum amount of exchangeable gavage at both ends. Second, the ligament also must be central and reduced. A long opisthodontic ligament would not allow rocking along a dorso-ventral axis. Third, cardinal teeth must be retained to act as the dorsal pivot of the axis. Lateral teeth may or may not be present, but if present, they must be able to disengage smoothly as the rocking movement takes place. Fourth, the valve commissure must be open anteriorly and posteriorly, creating a gape when the shells are rocked.

This morphology may have an adverse side effect. The simultaneous contraction of the adductor muscles may split the valves at the umbo along a line of structural weakness if the shell is sufficiently thin. This is known to happen in all members of the anomalodesmacean genus *Laternula* and some *Periploma* (Morton, 1976). Individuals of other species, all within or past the intermediate phase, may have an internal rib or buttress at this position to counteract the stress: *Nuculites* (Nuculidae); *Capistrocardia* (Saxicavidae); *Cleidophorus* (Ledidae); *Siliqua*, *Cultellus*, and *Phaxus* (Solenacea); *Sanguinolaria*, *Nuttallia*, *Solecurtus*, and *Tagelus* (Psammobiidae); among others (Gill & Darragh, 1964, and this study). In other

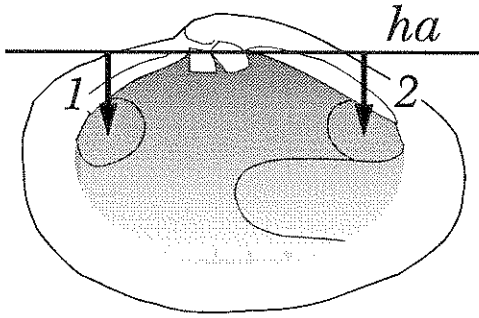


FIG. 18. Opening moment of movement around hinge axis (ha). 1: Anterior torque arm. 2: Posterior torque arm. Magnitudes of torque arms do not change during movement.

species, additional buttresses may be present.

The presence and the position of these buttresses are not simply the result of adductor muscles contracting within a shell with anterior and posterior gapes during normal closure (around the hinge axis). Factors influencing the disposition of internal buttresses are tied to the mechanics of exchangeable gavage. In most shells, the valves rotate along an axis determined by the hinge line, particularly the line through the ligament. The insertions of the adductor muscles on the valves remain the same distance from that axis throughout contraction and the adductor muscles work in concert (Fig. 18). The situation is different during the process of exchangeable gavage. The dorsal pivot of the axis is anchored, usually by the cardinal teeth. But the ventral pivot moves along the ventral margin of the shell, sweeping out an angle defined by the anterior and posterior-most positions of the axis (Fig. 19). The distance from the adductor muscles to this dynamic axis changes in a linear fashion during this rocking motion. The adductor muscles are antagonistic during this motion.

Thomas (1975) estimated the amount of force generated during valve closure, the adductor moment, by:

$$\begin{aligned} & \text{(cross-sectional area of adductor)} \\ & \times \text{(distance to axis)} \end{aligned} \quad (6)$$

The cross-sectional area is an estimate of force. The distance to the axis represents the torque arm. In his calculations, which involved no exchangeable gavage, the adductor moments are constant during closure. The mo-

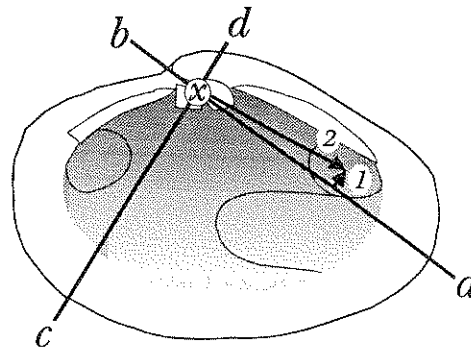


FIG. 19. Opening moment of movement around dynamic dorso-ventral axis. x: Fixed pivot at cardinal teeth. 1: Posterior torque arm at minimum posterior closure with axis along ab. 2: Posterior torque arm at maximum posterior closure with axis along cd. Magnitude of torque arm changes during movement. Anterior torque arm would behave in the opposite manner.

ments during exchangeable gavage are not (Fig. 20). The lines of adductor moments may or may not cross, depending on the location of the adductor muscles and the shape of the shell. If the shell is thin, a buttress generally will occur near the angle at which the moments are equal. This angle represents the point during an exchangeable gavage rocking motion that the anterior and posterior adductor forces are equal, thereby placing maximum strain on the shell between them if they are contracted simultaneously (Fig. 21). The buttress reinforces this region. Buttresses also may occur at the beginning and end of the exchangeable gavage angle. These may counteract the forces generated by the adductor muscles attempting to contract beyond the limit of the allowable angle. The central buttress may be placed at the bisection of the angle, but other evidence suggests that it is dependent on the point of equal moments. For the individual in Figure 22, the lines do not cross and the central buttress is absent, although the two flanking ones limiting the angle are prominent. Figure 23 illustrates the moment lines for a form in which the lines cross only at the end of the angle. The formation of internal buttresses is a modification for forces generated on the shell by the adductor muscles during exchangeable gavage.

Past the intermediate phase, the deeply buried bivalve may take on equally predictable characteristics. Movement within the sub-

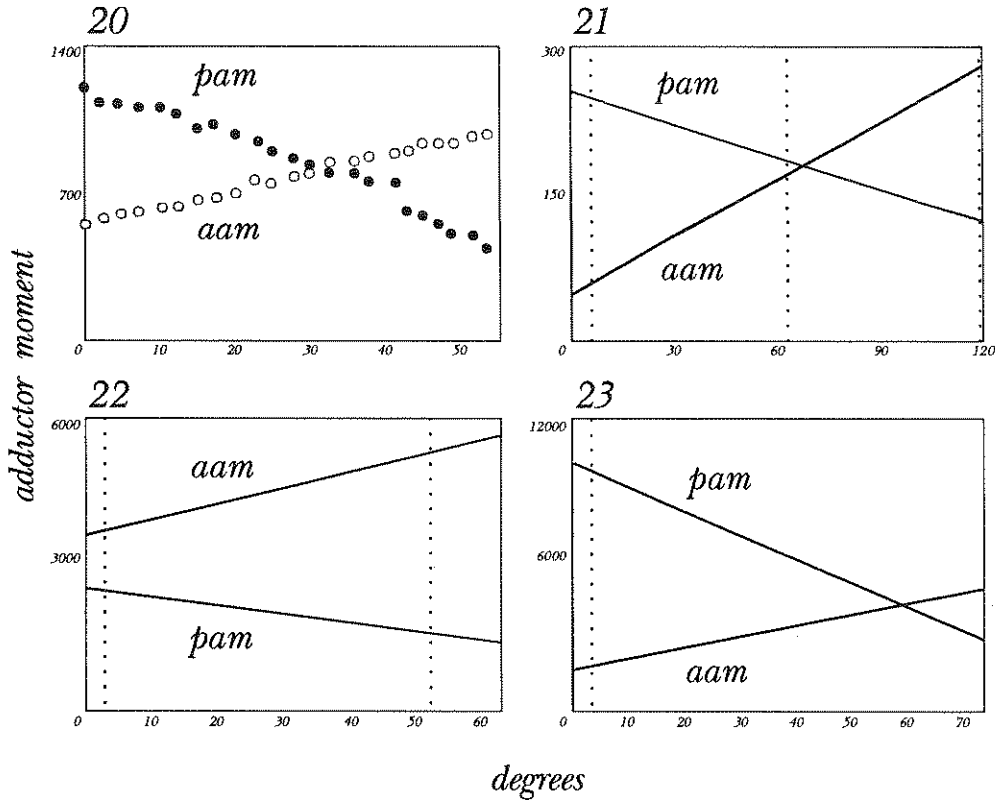


FIG. 20. Anterior (aam) and posterior (pam) adductor moments for *Tresus nuttali* (Conrad, 1837) through entire angle of exchangeable gape.
 FIG. 21. Anterior (aam) and posterior (pam) adductor moments for *Tagelus divisus* (Spengler, 1794), through entire angle of exchangeable gape. Dotted lines indicate angles at which buttresses are positioned.
 FIG. 22. Anterior (aam) and posterior (pam) adductor moments for *Resania lanceolata* Gray, 1862, through entire angle of exchangeable gape. Dotted lines indicate angles at which buttresses are positioned.
 FIG. 23. Anterior (aam) and posterior (pam) adductor moments for *Siliqua patula* (Dixon, 1789), through entire angle of exchangeable gape. Dotted lines indicate angles at which buttresses are positioned.

strate is minimized as exchangeable gape is modified into less streamlined permanent gape. Shell shape may return to a non-streamlined form reminiscent of the shallow infaunal stage. Sculpture, lost in the transition, remains absent as the substrate becomes the primary protective device (Stanley, 1970). Shell thickness, also originally protective, may be minimized (Stanley, 1970; Morton, 1976). The teeth, reduced or weakly meshed in the intermediate phase, may become rudimentary as all shell/shell movement is lost (both along the horizontal hinge line and along the dynamic hinge of exchangeable gape). The siphons may become partially or wholly non-retractable, resulting in a decrease of the sinus depth. Members of some species have been

shown to possess an atrophied foot as an adult, suggesting a sedentary habit. Individuals of *Panopea abrupta* (Conrad, 1855), a hiattellid, may live immotile in burrows 90 cm deep (Yonge, 1949).

Evolutionary Considerations

Most forms studied are uniform for the calculated parameters. The position of the umbo is distributed about a mode of 0.3. The depth of the sinus is generally less than 0.1 (reflecting the large numbers of members of the Unionoida in the study). Streamlining is quite high, with a mode of 0.9, indicating that most bivalves, even shallow infaunal ones, are somewhat streamlined. But high levels of ex-

changeable gavage and permanent gavage are rare. This suggests that most forms are still in the streamlining phase of the sequence. Few have made the transition to the intermediate phase. Why is this the case?

To enter the intermediate phase requires a specific set of shell characteristics. The umbo and cardinal teeth must be central, the laterals must be able to disengage, and the ligament must be short and central. Presumably, this suite of morphological characteristics is not met in most bivalves. This has resulted in a bottleneck at the intermediate phase. Species occurring before this stage are numerous. It is hypothesized here that the acquisition of the necessary combination of characteristics needed to continue in the sequence may be determined by chance. Like billiard balls thrown at random on the table, one may drop in the pocket, but most continue rolling.

Once in the intermediate phase, morphological change may be rapid. The change from intermediate phase to exchangeable gavage phase may be brief on a geological time scale. Radiation usually is rapid after a morphological or ecological innovation (Hoagland & Turner, 1981). Of the several hundred species of Mactridae, members of fewer than a dozen are in the intermediate phase, and the percentage is less for forms in the Cardidae. Although members of the Mactridae have been in existence since at least the late Cretaceous, the groups now in the intermediate phase are no older than the Miocene. But within that small group, speciation may be high. Beu (1966) has recognized three distinct lineages within the members of the genus *Zenatia*.

Geary (1987) found that slow rates of change in the lineage of species of *Pleurocardia* are punctuated with quick major changes. Stanley (1977a) and Stanley & Yang (1987) also found low levels of phyletic change in members of the Veneridae and Tellinidae, two families with members still predominantly in the streamlining phase. The bottlenecking of morphologies has created a steady, but low rate of evolution in these taxa. Even so, as stated by Stanley (1979: 118), "there is no evidence that a limit [to diversity] is being approached even after more than 400 My of radiation." But the acquisition of the intermediate phase must be seen as a major morphological step opening a new area of the morphospace.

Within and after the intermediate phase, members of lineages would be expected to

radiate to fill the new morphospace. As an example, the Anomalodesmata is a large, diverse group, with many of its members tending toward deep-dwelling, sedentary habits (Morton, 1977). The Solenacea also is a large group of species, the members of most in the permanent gavage phase. They are recognizable as solenaceans as far back as the Cretaceous, suggesting that they had passed through the intermediate phase prior to that time. Most of the basic adaptive radiation of the Bivalvia had occurred by the Cretaceous (Nicol, 1986), though 96% of the species, and 52% of the families became extinct during the Permo-Triassic extinction (Raup, 1979). This suggests that the sequence of morphologies discussed here is an ongoing process, taking place asynchronously in different lineages as the necessary morphological prerequisites are obtained.

No clades have been defined in this study of Recent species. The phylogeny of most bivalves is too insufficiently known to allow the concepts developed here to be tested by the fossil record. If the sequences of shell shape change are reversible, then the precursors of modern groups may have assumed a wide variety of forms. While some obvious trends within clades exist, such as those culminating in *Papyridea*, others are too ambiguous. The trends in shell shape described here are trends between clades acting simultaneously on unrelated taxa.

Is the evolution of these groups predictable? To a certain extent the answer may be yes. If continued studies show that other groups of bivalves lie along these paths, then we may assume that bivalve lineages entering a path may evolve toward the shell shapes of individuals already on the path. The great degree of convergence in bivalves supports this hypothesis. Several groups, such as the mactrids and venerids, have members in both the myid and solenacean paths. Members of *Resania* look remarkably like those in its solenacean counterpart, *Phaxus*. They occupy the same place in the path. Will there eventually be a mactrid counterpart to *Solen*? Members of *Lutraria* already have adopted the tube dwelling habit of that genus.

SUMMARY

A hypothesis is advanced to explain: (1) the changes in shell shape in individuals of spe-

cies as a continuously deeper infaunal habitat is colonized; and (2) the degree of convergence in shell shapes among infaunal bivalves. A maximum depth of burrowing for streamlined morphologies will be reached as sediment weight becomes significant. Up to this point, forms will adopt streamlined shapes for more efficient penetration of and movement in the substrate.

To achieve a deeper infaunal existence requires that the shell possess gapes through which the foot and siphons may extend. This would make the animal susceptible to predation and other immediate environmental dangers because the shell functions as the main defensive mechanism. Only one morphological "solution" has been adopted by the bivalves. This entails the antero-posterior rocking of the shell such that a pedal or siphonal gape alternately may be opened and closed. Because this action is caused by the adductor muscles, rather than by the much weaker ligamental or haemocoel opening mechanisms, the problem of sediment weight has been bypassed at this depth. The acquisition of exchangeable gapage requires several pre-existing morphological conditions. These conditions must be modified to new functions in this stage of development, termed here the intermediate phase.

The cardinal hinge teeth must still function as a dorsal pivot, but on a dorso-ventral axis. These teeth must be located centrally to maximize exchangeable gapage. The laterals must be able to disengage (or no movement along that axis could take place). The hinge must be centralized to avoid interference with the rocking motion of the shells. This may be accomplished by a shortening of the ligament or the internalizing of it in a resilifer ventral to the umbo.

Movement into a deeper infaunal position may be possible once the intermediate phase is reached. This entails a further decline in predation and environmental extremes. At this point, exchangeable gapage may be modified into permanent gapage. The animal may be sedentary, with a reduced foot and externalized siphons. Shell thickness may decrease as the result of the reduced dependency on the shell for defense.

Comparisons between these models and the actual shell shapes of the individuals of the species studied show a general agreement. The morphologies are found in the predicted morphospace. The hypothetical suite of specialized characteristics does occur

in real species in the intermediate phase. Members of lineages follow a specific path, a sequence of body shapes, as they increasingly become infaunal. This results in unrelated species sharing the same general morphological pattern because they are at the same point on this path. The constraints of this sequence are such that some paths may move in both directions, whereas in others a separate course may exist for each direction.

Two paths occur out of the intermediate phase, termed here the solenacean and the myid paths after the typical member of each route. The solenacean path differs because of the behavior of its members, which construct tube burrows, allowing the shell to retain its streamlining along with exchangeable gapage. The unionoids appear to lie on this path but the convergence is superficial. The members of that group lack the fused mantle tissue necessary to form true siphons.

That so few forms exist in the intermediate phase or in the exchangeable gapage phase supports the idea that the specific suite of shell characteristics necessary to enter the intermediate phase has not been attained by most groups. Shallow infaunal species, though high in diversity, are bottlenecked at this point. The entry into the intermediate phase may allow a new morphological radiation. This passage may be quick in geological time and be largely the product of chance.

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