

# The functional significance of aperture form in gastropods

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Aperture form of marine prosobranch gastropods has evolved under the influence of a number of different selective forces, including: generation of shell form; protection from predation; accommodation of the foot during clamping behavior; and accommodation of water currents in and out of the mantle cavity. Aperture form correlates positively with foot shape in most gastropods and foot shape, in turn, correlates moderately well with substrate preference. Almost all gastropods that have non-round apertures elongate the aperture parallel to the foot so that water currents tend to flow anteriorly to posteriorly. Fresh-water pulmonates have responded to somewhat different stresses. They exhibit clamping behavior and thus show correspondence between foot shape and aperture shape. They show less apertural strengthening as crab (or crayfish) predation is less of a factor and presumably because calcium carbonate is less available. They also lack anterior–posterior apertural elongation due to the absence of water currents through their mantle cavity. Due to the absence of mantle cavity water currents and clamping behavior, terrestrial gastropods do not show the apertural modifications associated with these two factors. In addition, few adaptations of apertural form are present to resist predation. Instead, many of the apertural modifications of terrestrial pulmonates seem to be concerned with the problems of water loss during estivation.

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No other feature of the gastropod shell is involved in as many functions of the organism as is its aperture. It is through this opening that a snail must conduct all of its business with the outside world; it is into this hole that it must retreat for protection from predators or the vicissitudes of the environment; it is by the margins of this hole that it must generate the entire form of its growing shell. It is no wonder that the form of the aperture and lip have been selected as the most important criteria for taxonomy of fossil gastropods.

We have found in our studies, however, that the classical concept of the aperture is inappropriate for an understanding of the significance of many aspects of apertural form. Few of the existing illustrations of gastropods taken from the literature were of any use to us in our study. Most illustrations are made so that the viewer is looking at the shell parallel to or perpendicular to the axis of coiling. However, the plane of the aperture is rarely in a plane parallel to the coiling axis (Linsley 1977), rather the plane of the aperture is at some angle (Angle *E* of Vermeij 1971) to the axis of coiling. As a result, almost all

existing illustrations of gastropods give a somewhat distorted view of the shape of the true aperture.

We have found that since the aperture and its lip serve a variety of functions, it can best be considered in a variety of ways, with a separate definition for each function. The primary functions of the aperture are: (1) to receive the organism during withdrawal; (2) to accommodate the head–foot mass during clamping; and (3) to accommodate water currents through the mantle cavity. In addition the lip of the aperture: (1) serves as the generating curve of the growing shell; and (2) provides protection from predation and dessication after withdrawal. Furthermore, the aperture of some gastropods has been modified for very specific functions like accommodating copulation or opening up bivalves or even serving as a hydrofoil during free fall after dislodgement (Palmer 1977). We are primarily concerned in this paper with more general adaptations.

In much of the paleontological literature, the generation of shell form is the classical concept of the aperture. In most computer simulations of

shell form (Raup 1966) the generating curve is presumed to be a cross section of the whorl taken through a plane that intersects the axis of coiling. Yet as has been pointed out, the true generating curve (the aperture) is a projection of the axial cross section onto a plane inclined at Vermeij's angle  $E$  (Eckelmann & Linsley 1978). The great majority of gastropods exhibit whorl overlap, hence the generating curve or actual surface of accretion of all three shell layers in the growing animal is not a closed geometric figure. While some gastropods have an entire apertural margin, the accreting surface of the majority of them is constituted by the outer lip, sometimes augmented by a siphonal canal. The area of the parietal lip is formed by the previous whorl, although it is commonly overlain by a parietal inductura.

The second function of the aperture, that of receiving the organism during retraction, has not to date been considered in any detail, but is presently being investigated by Louis F. Gainey, University of Southern Maine (personal communication). Closely related to this is the third function, that of providing protection after withdrawal, which has recently been treated by Vermeij (1976, 1977).

All three of these functions view the aperture in the rather classical fashion. However, in order to understand the significance of apertural form in relation to clamping and accommodation of water currents, we have found it advantageous to redefine the aperture for each function.

### Clamping, aperture shape and foot shape

'Clamping' is a behavioral trait of all marine and fresh water shelled gastropods. During most active phases of behavior, including locomotion or grazing, the aperture is held above the substrate with the plane of the aperture parallel to the surface. In this position the tentacles usually protrude beyond the shell margin. If the animal is disturbed, it withdraws the tentacles and clamps the shell down tight against the substrate. This clamping behavior occurs in all aquatic snails whether they live on a hard substrate or a soft substrate.

Snails that live on a hard substrate, such as the rock clingers of the intertidal zone, have a planar aperture that provides an effective seal against the substrate and a foot that is accommodated

under the margin of the aperture during clamping. In contrast, gastropods that live on a soft substrate frequently have a foot which extends beyond the apertural margin so that clamping behavior only provides protection for the head. In these forms, the foot is generally extended into the substrate and covered by sediment, so it is not necessary for clamping to provide protection for the foot. Because the apertural margin can be pulled into the substrate, it is not necessary for the aperture to have the perfect planar form that is found in gastropods that live on a hard substrate. Snails that live on a hard substrate almost always have an apertural margin that is inclined adapically (prosocline) relative to the suture, while those that live on a soft substrate can get by with a prosocyrat margin. The latter aperture is still a tangential aperture since the outer portion of the lip is inclined adapically, but the margin curves back as it approaches the upper suture and thus is orthocline at the suture. This aperture presumably requires less energy to build since it uses less calcareous material than does a prosocline aperture.

There seem to be at least two alternative adaptive strategies for apertural modifications for epifaunal gastropods. The outer lip is flared in many strombids and muricids, and even extended into spines. These organisms have generally adopted the strategy of remaining perched on top of the sediment and their foot does not penetrate deeply into the sediment during locomotion. Those epifaunal snails whose foot penetrates below the sediment during locomotion (i.e. *Busycon* or *Fasciolaria*) most frequently have a sharp apertural margin that penetrates the sediment during clamping and sometimes serves as a plow to push the sediment aside during locomotion.

The portion of the aperture that is effective during clamping behavior constitutes our definition of the 'clamping aperture'. In this definition we include the inner margin of the outer lip and exclude spines or projections. We also include all inductural deposits on the parietal wall but exclude all siphonal or anal extensions (Fig. 1). The boundary between the siphonal canal area and the clamping aperture is well marked by an internal angulation on all shells studied. This allowed the clamping aperture to be objectively determined in all cases.

It should be no surprise that with an aperture defined in this manner, there is a positive correlation between foot shape and aperture shape in

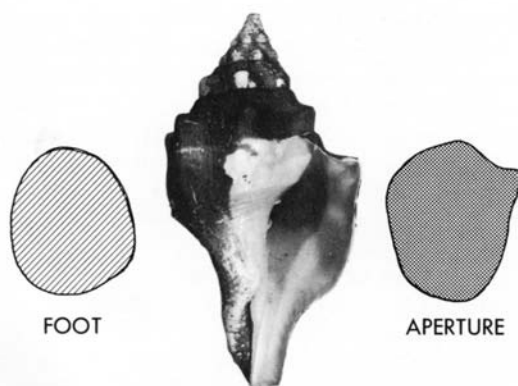


Fig. 1. Diagram showing definition of clamping aperture. The parietal indutural deposits were used as an indication of the medial edge of the aperture. The siphonal extensions, whose border with the aperture was indicated by an internal angulation, were excluded.

gastropods that live on hard substrates. We were surprised that foot shape could also be correlated with aperture shape for gastropods that live on soft substrates, even though the clamped aperture does not envelop and thus restrict the form of the foot. Since Miller (1974a) has already demonstrated that foot shape can be an indication of substrate preference, this now allows us to infer foot shape and thus substrate in some fossil gastropods.

Approximately sixty species of marine gastropods from the Caribbean and South Pacific were examined for the comparison of foot shape and aperture shape. Each snail was photographed from a ventral vantage point in a glass aquarium. Care was taken to photograph the snail only when it was actively moving in a straight line. Under these circumstances, it was found that foot size and shape were quite constant for a given individual. From these photographs the outline of the foot was traced onto a blank piece of paper and cut out so that we could subjectively analyze foot shape without the distractions and possible bias provided by other information. The shell aperture was then photographed so that the plane of the aperture was placed as it would have been in the photographs taken of the foot of the live animal. In all cases the plane of the aperture was perpendicular to a sight line from the camera, since the plane of the aperture is parallel to the substrate during locomotion. The outline of the clamping aperture was then drawn on the photograph, traced, and

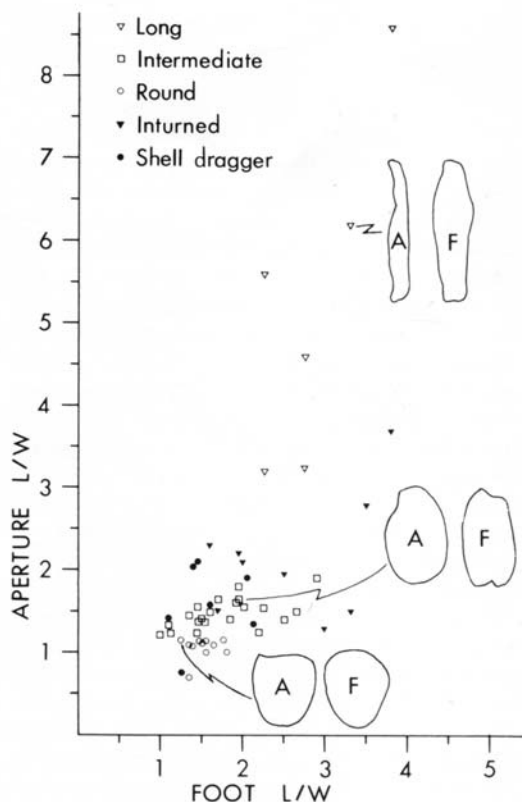


Fig. 2. Relationship between foot length to width ratios and aperture length to width ratios.

cut out of a blank piece of paper as had been done for the foot. Length/width ratios were recorded for each specimen's foot and aperture, and these values were plotted (Fig. 2). 'Length' was measured along the longest anterior-posterior axis with the orientation of the shell determined by its position during life. 'Width' was measured perpendicular to length.

The great majority of gastropods fall into a 'main sequence' or elongated cluster of points on the graph and show a direct correspondence between aperture shape and foot shape. The gastropods of the main sequence have been arbitrarily divided into three groups: Group I (round apertures), with an aperture length/width ratio ranging from 0.7 up to 1.25; Group II (intermediate apertures) with a ratio of 1.26 to 2.5; and Group III (long apertures) with an aperture length/width ratio exceeding 2.5. Fig. 2 includes an illustration of the shape of the aperture (A) and foot (F) of one example from each of these three groups.

Gastropods of Group I (round apertures) have a more or less rounded foot whose length/width ratio varies from 1.1 to 1.8, typically being slightly narrower than the clamping aperture, but still quite rounded in its general form. A foot with a rounded shape is apparently well adapted for adhesion, for without exception the members of this group can be described as 'rock-clingers'. Included in this first group are the genera *Nerita*, *Littorina*, *Turbo*, *Tectarius*, *Cittarium*, and *Trochus*. All are common inhabitants of the rocky intertidal zone and are well adapted to clinging to rocks, at home on vertical surfaces or even hanging upside down on the undersides of boulders or rock overhangs. All are dependent on clamping as a defense mechanism against dislodgement by predators or waves and as a protection from desiccation. We feel confident that these traits can be extrapolated into the paleontological record for all gastropods with similar apertures.

Group III gastropods of the main sequence (long sequence) form another compact, decipherable group. They include members of the Conidae, Olividae, and Mitridae, all with a long, narrow aperture and a long, narrow foot. The majority of the species in this group inhabit soft substrates. The mitrids and olivids are effective burrowers. While many species of conids live in rocky areas, their foot seems poorly adapted to adhering to the rocks with the same effectiveness as members of Group I. For the most part, their activity consists of crawling over the rocks, but they are not particularly adept at hanging below or on the vertical surfaces of rocks. All members of this group are active carnivores, but it would be with trepidation that we would extend this character to all comparable forms in the paleontological record. However, we do expect the substrate restrictions to hold for all gastropods with elongate apertures, because we suspect that the elongate foot is not as well adapted to holding the substrate as firmly as a round foot.

In contrast to categories I and III, category II with intermediate apertures does not form a homogeneous group. They include genera such as *Fasciolaria*, *Astraea*, *Thais*, *Melongena*, and *Murex*. It is obvious that a great range of adaptations is present in this group and little extrapolation to the past could be made for gastropods with this shape of clamping aperture at this time. However, within this group are aperture shapes which could generally be described as 'oval',

'rectangular', 'triangular', and so forth, which cannot be treated with our relatively crude ratio of length/width. It is hoped that a more sophisticated treatment using Fourier analysis will allow us to objectively treat aperture shape of Group II in a more elegant fashion, which in turn may allow the discovery of correlations with substrate preference which are not now discernible.

In addition to the main sequence gastropods, there are three galaxies of snails that could be considered as renegades in that they do not follow the patterns that characterize the great majority of snails. However, each group can be recognized on the basis of shell characters and thus does not effect the utility of aperture shape in interpreting the fossil record.

The first of these renegade categories are the short-aperture shell draggers. All members of this group are characterized by a low length/width ratio for both aperture and foot. The foot of a snail in this group is invariably short and stubby, ranging in shape from squarish to slightly elongate. Apertural shape is generally round or slightly ovate. They can be easily distinguished from other round-aperture shells by their high-spire, so that their total 'shell length' (measured along the axis of coiling) is more than twice as great as their aperture length. Substrate preference in this group is not predictable. Some are infaunal, some are epifaunal. Some prefer soft substrates, some prefer hard substrates. About all that can be said for certain is that they are not rock-clingers in high energy zones, the habitat for other round apertured forms.

A second group of renegades are those snails whose shells have inturned outer lips. In all of these gastropods the shell departs inward from the projected logarithmic spiral to form the adult lip. This group includes *Cypraea*, *Trivia*, *Cyphoma*, *Nitidella*, *Columbella*, and *Mitrella*. In most cases we found that the foot of these animals was narrower than would be predicted from aperture shape. The explanation for this may lie in the fact that we had to alter our definition of the clamping aperture for many members of this group and perhaps we defined it inappropriately. Since members of the Superfamily Cypraeacea have a complete inductura, we obviously could not use the inductura to mark the outline of the aperture. Instead, we chose to describe the aperture of this group as including the entire flattened, oval ventral portion of the shell. The substrate pre-

ference for this group is varied, including both hard and soft substrates. But again, these forms seem to spend most of their time clambering over rocks rather than clinging on them as seen in the round-aperture forms.

The final renegade groups are the stompers or leapers, including the Strombidae, Xenophoridae, Lambidae. Since these gastropods do not clamp their shell, we have not defined a clamping aperture for them and did not try to plot them in Fig. 2. Again, this group could be recognized in the fossil record (Linsley, Yochelson & Rohr, 1978) and so do not detract from the general utility of the clamping aperture. For the most part, foot shape is variable in this group, ranging from very long and narrow in the strombids and lambids to a short, stubby hour-glass shape in the xenophorids (Linsley & Yochelson 1973). Substrate preference in this group is also variable although they prefer a firm (not necessarily impenetrable) substrate for the foot to press against during locomotion.

In summary, there is a positive correlation between the shape of the clamping aperture of marine prosobranch gastropods and the shape of their foot. There is a fair correlation between aperture shape and substrate preference, but at present we would have to admit that this is more in terms of promise for the future than actuality for the present.

### The aperture shape relative to water currents

Linsley (1977) suggested as his Fifth Law that the long axis of the aperture is subparallel to the long axis of the foot, but at the time of that publication had no quantitative data to support that claim. The data presented in this paper allow us to refine and elaborate on the original statement.

For this portion of the study, the aperture is defined in a similar manner as the clamping aperture was defined except that inhalant and exhalant extensions are included. The animal was photographed through the bottom of an aquarium while it was moving forward in a straight line. A photograph of the empty shell was taken with the plane of the aperture held perpendicular to the line of sight from the camera. The outline of the water current aperture was then drawn on a print of the picture and a line was constructed through the longest axis that could be drawn through this

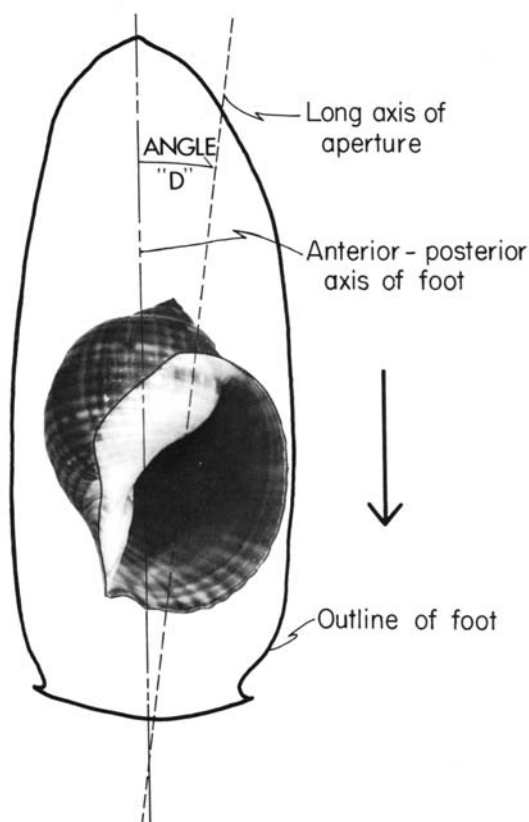


Fig. 3. Diagram showing method of measurement of angle of deviation of long axis of foot from anterior-posterior axis of foot. Arrow indicates direction of movement.

outline. A tracing was made of the foot and this was then transferred onto the photograph of the shell with the foot properly aligned to the shell. The anterior-posterior axis of the foot was then drawn in and the angle between the axis of the foot and the axis of the shell was measured (Fig. 3). The angular deviation of these two axes was plotted (Fig. 4).

This study indicates that if a gastropod has an elongated aperture (length/width ratio  $> 1.2$ ), the elongation is subparallel to the long axis of the foot. As Fig. 4 indicates, only one genus was found in the more than sixty studied with a deviation of more than  $10^\circ$  between the long axis of the aperture and the foot axis: this was the genus *Littorina*, where the deviation approaches  $30^\circ$ . Unfortunately, we have found no way to exclude this genus from the general group on the basis of shell characters and thus



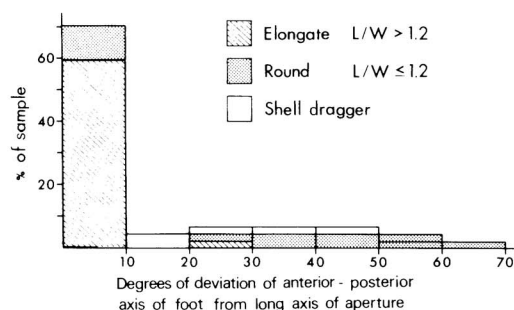


Fig. 4. Relationship between percent of sample and degrees of deviation of anterior-posterior axis of foot from long axis of aperture for elongate apertures, round apertures, and shell dragging gastropods.

could not recognize this variant in the fossil record. We can only speculate that since this genus typically lives so high up in the intertidal zone, anterior-posterior water currents are not as important in determining aperture shape.

Three other groups of gastropods fail to show a correlation between aperture elongation and foot elongation: they are the shell draggers, shells with radial apertures (neither group holds the shell in a specific orientation relative to the foot) and gastropods with a round aperture (length/width ratio  $< 1.2$ ).

An aperture may be round for several reasons. If a snail possesses two gills, for example the pleurotomarians, two inhalant streams would be present and any elongation of the aperture would hinder this flow. In addition, the rock clinging mode of existence tends to result in a round aperture form. With high inclination of the axis of coiling, the columellar muscle can insert directly above the foot and thus allow an efficient and strong clamping force in addition to ease in holding the shell in turbulence (Linsley 1978). If inclination is high and selected for, as it is in rock clinging forms, then there are geometrical restrictions placed on aperture shape and the aperture cannot be elongated in an anterior-posterior direction.

There are a number of advantages associated with an elongate aperture in a gastropod with a single gill and hence a single water current through the mantle cavity. If the aperture is elongate, the inhalant stream is placed anteriorly and a more efficient and directional means of sensing the water in front of the snail is allowed. The elongation of the aperture also allows the exhalant stream to be concentrated at the pos-

terior end of the mantle cavity, an obvious advantage for the removal of waste products. Because of the close association between apertural form and the water movements through the mantle cavity, the aperture tends to be elongated with its long axis nearly parallel to the long axis of the foot which is, in turn, an indication of the direction of movement. The elongation is close to parallel in the majority of the specimens that we analyzed.

## Aperture form in pulmonates

It is beyond the scope of this paper to offer an exhaustive analysis of pulmonate gastropods, but a preliminary investigation suggests significant differences between marine prosobranchs and fresh water pulmonates. In addition, there are great differences between aquatic gastropods and terrestrial forms and it is on these obvious differences that we would like to comment.

Both aquatic and terrestrial pulmonates balance their shell during locomotion as do prosobranchs (Linsley 1977) but the differences are significant in each group. Fresh-water pulmonates keep a bubble of air in the mantle cavity which results in a buoyant factor causing the shell to be positioned very differently than is the case for prosobranchs. In fact, it allows shell forms such as planorbiform to be dominant shell forms with pulmonates while only the smallest marine prosobranchs (less than 10 mm) can have this geometry. All aquatic pulmonates that we have investigated also hold the aperture of the shell parallel to the substrate and perform the clamping behavior when bothered by predators, such as fish nibbling at the protruded tentacles. As a result, there is a high correspondence between foot shape and the shape of the clamping aperture. But since they have no inhalant or exhalant currents, the rules of aperture elongation do not apply. Thus, with the absence of strictures imposed by water currents through the mantle cavity and reduced levels of shell breaking predation in fresh-water systems (Vermeij & Covich 1978) the apertures are free to approach a more circular form and increase the living space per unit of deposited shell (Graus 1977).

In contrast to aquatic gastropods, the terrestrial gastropods do not exhibit clamping behavior and do not carry the shell with the aperture parallel to the substrate. There is apparently no tormentor for terrestrial gastropods that

is the equivalent of the fish in the aquatic realm. It is probably for this reason that the eyes of land snails are most commonly situated at the tips of the tentacles (stylomatophoran), while those of aquatic and all clamping prosobranchs have their eyes located at the base of their tentacles (basomatophoran). It is frequently the case that aquatic gastropods have the tips of their tentacles nipped off by fish while the tentacles of terrestrial forms are normally intact (personal observation by Linsley).

Since retreating quickly under the apertural margins is not a necessary adaptation for terrestrial gastropods, the entire shape of the foot and relation of the cephalopedal mass to the shell is very different from aquatic forms. The foot of terrestrial gastropods is typically far longer than broad (typical foot length/width values ranging from 30 to 50), while the apertures do not exhibit a corresponding elongation (apertural length/width values ranging from 1.0 to 1.7). Hence the head of the organism generally protrudes far beyond the confines of the aperture and clamping is clearly impossible. On the basis of the very little data available, there also seems to be a correlation between foot length and speed, with the long foot correlating with rapid locomotion. In addition, the number of direct monotaxic waves that move over the sole of the foot during locomotion may frequently be as many as ten, whereas in marine prosobranchs, there are rarely more than two or three waves on the foot at once (Miller 1974).

In spite of the fact that clamping does not occur in terrestrial gastropods, almost all possess a tangential aperture, and a large number of low-spined forms exhibit a downward deflection of the body whorl so that the plane of the aperture is rotated from roughly  $30^\circ$  relative to the axis of coiling in juveniles to  $60^\circ$  in adults (Fig. 5). The functional significance of the tangential aperture in terrestrial gastropods does not accrue from clamping but from estivation. Thus when a juvenile, low-spined, heliciform snail estivates, the plane of the aperture is parallel to the substrate and mucus is secreted to bond the shell to that surface, preventing water loss. In juvenile forms, the result is that the shell is positioned precariously since the longest diameter is the shell width (which is subperpendicular to the apertural plane) and is inclined at a high angle to the substrate. Consequently, dislodgement is relatively easy. In contrast, deflection of the body whorl in the adult rotates the apertural

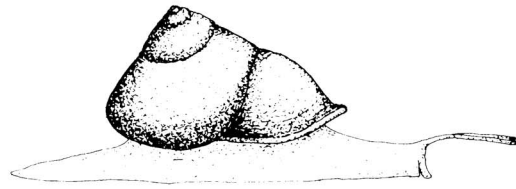


Fig. 5. Illustration of a terrestrial pulmonate showing the deflection of the final whorl and the reflexed lip, features which are advantageous during estivation. Also note that the aperture is not held parallel to the substrate, nor can it be clamped to protect the head.

plane subparallel to the long axis of the shell which lowers the center of gravity of the shell during estivation and reduces the ease with which the shell may be dislodged. In addition, the reflexed adult apertural margin found in so many terrestrial gastropods increases the surface area of adherence during the estivating process.

In summary, the apertural margin of land snails functions differently than it does in marine or fresh-water snails. Its form is not adapted to providing protection from predation so much as it is a deterrent to water loss during estivation by aiding the attainment of a good seal by the epiphram and the substrate.

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