Regulation of Spiral Coiling in the Terrestrial Gastropod Sphincterochila: An Experimental Test of the Road-Holding Model

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ABSTRACT
Hutchinson’s (‘89) road-holding model states that spiral ornaments of the snail shell (keels and low-curvature areas) dictate the growth path of the subsequent whorl, which in turn gives the signal for attachment of the next whorl. Experiments were performed with two species of the terrestrial snail Sphincterochila in order to test the role of the external keel in determining the correct coiling of successive turns. Experiments substituted a ridge made of silicone for the keel. This ridge ran either (1) abapical or (2) adapical of the original keel. In mode (1), subsequent growth continued by taking the false keel as the adapical limit of the whorl. In only very few instances of mode (2) did the whorls extend incipiently slightly adapical of the path of the original keel. Our results confirm that the keel is an important reference for the coiling strategy of the snail, although the keel itself probably does not constitute the reference, but rather the two flat ramps into which the keel divides the outer lip of the aperture. J. Morphol. 235:249–257, 1998.

With few exceptions, gastropod shells can be defined as monotonically expanding cones that coil helicospirally. Coiling is often so regular throughout growth that coiled shells have been the subject of theoretical morphology models aimed at obtaining computer simulations of actual morphologies (e.g., Raup and Michelson, ’65; Raup, ’66; Løvtrup and Løvtrup, ’88; Okamoto, ’88a; Ackerly, ’89). These models, whether they pertain to the categories of fixed or moving reference frames (see reviews in Savazzi, ’90; Okamoto, ’96; and Stone, ’96), treat the shell as the result of an expanding generating curve or aperture that follows a path dictated by mathematical expressions. A major advantage of these models is that they allow paleobiological inferences to be drawn from the portion of the theoretical morphospace (the range of all possible morphologies) occupied by actual morphologies. Additionally, computer simulations, by enabling accurate calculations of such biological parameters as centers of buoyancy (in floating forms) and gravity, reproduce natural orientations in fossil and recent forms. On this basis, the coiling strategy can sometimes be deciphered and reproduced (e.g., Okamoto, ’88b,c). As a limitation, the formulae that define the growth trajectory in these models are not homologous to the actual developmental process.

A different approach is to treat shell coiling as the result of a set of behavioral rules that give rise to trocho- or planispiral coiling. However, studies of this kind are rare. Besides the hypothesis by Okamoto (’88c) on uncoiled ammonites with meandering whorls, two other models fall into this category: the road-holding model (RHM) of Hutchinson (’89) and the dead-spiral model of Morita (’93). The latter (DSM) attributes translation of the gastropod shell along the coiling axis to the adhesive action of the retractor muscle to the columella. The RHM states that keels, flat surfaces or other types of longitudi-
nal relief of a given whorl of the snail shell serve as guides for the attachment of the subsequent whorl; in this way, while the aperture follows the "signal" deposited one whorl earlier, it secretes as well the rail for the subsequent whorl, so that if the aperture grows at a constant angular rate, a helicospiral is finally obtained. Contrary to the DSM, the RHM explains allometries (e.g., doming) successfully. Although he did not give conclusive evidence supporting his model, Hutchinson ('89, p. 441, '92, p. 434) realized that it could be tested experimentally. In this report, we provide this experimental evidence. Our working hypothesis states that if the keel of terrestrial snails determines the path for the subsequent whorl and if we substitute the natural keel with an artificial one with a different path, the subsequent whorl would deviate to the new path. Our main goal is to test the applicability of the RHM by comparing its predictions with our experimental results together with data provided by other specimens.

MATERIALS AND METHODS

Experiments were performed with the terrestrial snails Sphincterochila candidissima (Draparnaud, 1801) and S. baetica (Rossmaßler, 1854). These are medium (S. candidissima) to low (S. baetica) conispiral forms in which there is some degree of doming throughout ontogeny (Fig. 1). A keel divides the outer lip into a right and a left ramp from the earliest postembryonic stages; this keel attenuates and disappears in the last whorl (Fig. 2A). As in many terrestrial snails, adulthood in S. candidissima is marked by a slight deflection of the aperture toward the substratum in the last part of the last whorl. Specimens of S. candidissima are abundant in some karstic reliefs near the city of Granada (SE Spain), and our sample comes from nearby Sierra Elvira, whereas that of S. baetica comes from sandy coastal environments (vegetated dunes) near the village of Balera (province of Almería, SE Spain).

Specimens of Sphincterochila candidissima were manipulated following three different ways. In the first two, the original keel was replaced with an artificial ridge of silicone (made simply by stretching a drop of commercial silicone into a fine line over the shell). This artificial keel, always starting just in front of the aperture, runs either (1) abapically or (2) adapically of the original keel. In mode (2), the keel of the last whorl, in front of the aperture, was usually worn away to the extent that the shell was not broken through. In mode (3), a ramp made with a concave-out shell fragment, taken from the same or another specimen, was attached with silicone in front of the aperture in order to try to deviate the shell tube from its spiral path. Specimens of S. baetica were manipulated following only modes (1) and (2). In most specimens, the shell was also peeled back between one-half and three-quarters of a whorl in order to stimulate repair growth.

The animals were later transferred to cages, placed in the field, and allowed to grow for 5–10 months. For Sphincterochila candidissima, 103 specimens were allowed to grow in their native biotope during 1994–1995, 70 during 1995–1996, and 20 during 1996–1997 (see Table 1). Fifty-five specimens of S. baetica were also tested during 1994–1995 in the biotope found in the environments of the city of Granada. Forty-three individuals (22%) of S. candidissima and 23 (42%) of S. baetica were lost during the field experiment due to predation (mainly by beetles) and to the burrowing ability of the snails, which allowed some to escape. In 23 cases of S. candidissima and nine of S. baetica, the silicone ridge detached from the surface of the snail and the specimen became useless for our experiment. Many animals failed to grow appreciably after manipulation, mainly for two reasons. First, a severe drought occurred in SE Spain during 1994–1995, so that a portion of our experiments...
was affected by the lack of humidity, which limited activity of the animals. Thus it is not surprising that only six specimens (of 78 recovered) of *S. candidissima* and two (of 32) of *S. baetica* of the 1994–1995 experiment yielded results on the growth pattern. Better conditions were achieved during fall 1995–summer 1997, which allowed us to obtain results from a greater number of individuals of *S. candidissima* (48 out of 72 recovered). Second, food limitation affected the growth of *S. candidissima*; this species feeds on mosses, and it is possible that the surface area available within the cage...
(?0.5 m²) was insufficient to sustain natural growth rates. In the case of S. baetica, we had no means of breeding the animals in their native environment, this differing substantially from the experimental conditions used. Despite the apparently low number of valid specimens (Table 1), results were consistent enough to establish definite patterns.

Additional material of abnormally coiled specimens of these and other species added significant information, and this is used throughout the text.

All material cited and figured is housed at the Department of Stratigraphy and Paleontology of the University of Granada (labelled DPUG).

RESULTS

Best results with Sphincterochila candidissima were obtained from those individuals in which the artificial keel was displaced progressively abapically of the natural one (mode [1]). Most of these specimens (26 out of 27; Table 1) grew, always taking the artificial keel as the adapical limit of the labrum (Fig. 2B,C). The two specimens of S. baetica that grew after manipulation according to mode (1) showed the same results (Fig. 3A). In all cases, the false keel was covered to a lesser or greater extent by the parietal epibothelium, but in most specimens the top of the right ramp did follow the true keel of the preceding whorl. Generally, in these specimens, derallment makes the whole aperture slide adaxially along the basal lip of the previous whorl, thus invading the umbilicus. This is clearly seen in nonexperimental specimens (especially of S. baetica) in which, following traumatism (indicated by break scars on the shell), the spire very occasionally migrates adaxially (Fig. 4A). From a morphological point of view, both species of Sphincterochila offer the advantage over many other species of having an umbilicus (even though rather narrow), in which there is some room available to lodge the whorl when it becomes deviated adaxially during growth. For unknown reasons, one specimen of S. candidissima did not follow this pattern, and the false keel was engulfed by the labial edge of the aperture (Figs. 2D, 3B). The top of the right ramp remained just in front of, although slightly detached from, the original keel of the preceding whorl. The most abapical portion of the parietal lip between the false keel and the top of the right ramp also detached from the previous whorl.

Specimens of Sphincterochila candidissima with the silicone ridge displaced adapically of the original one (modality [2]) did not follow the false keel, except in three dubious instances (out of 17; Table 1) in which the silicone keel was very close to the position of the original one. In these three cases the top of the right ramp moved slightly adapically during growth with respect to the path of the original keel (Fig. 3C); the internal limit of the parietal edge did not move externally in an appreciable manner, judging by the scar left after the previous peeling-off of the aperture. Two additional specimens in which the keel was worn off, but which lost the silicone keel prior to repair growth, displayed incipiently repaired shells that extended noticeably adapically beyond the position of the original keel (Fig. 2E).

Finally, none of the specimens recovered (32 out of 39) with an attached ramp (mode [3]) (Table 1) grew beyond the “obstacle,” despite the fact that most of them repaired and extended the artificially damaged aperture (Fig. 2F).

DISCUSSION

In general, our results confirm that the keel is a key element for the regulation of shell shape in snails, since it sets the adapical limit of the top of the right ramp of the subsequent whorl. A close examination of

### Table 1. Number of experimental specimens/number of specimens recovered after field stage/number of specimens that added significant shell length during field stage/number of specimens which followed the false keel

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Sphincterochila candidissima</th>
<th>Sphincterochila baetica</th>
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<tbody>
<tr>
<td>Mode 1</td>
<td>42/31/3/2</td>
<td>45/37/24/24</td>
</tr>
<tr>
<td>Mode 2</td>
<td>22/15/3/17</td>
<td>25/18/14/27</td>
</tr>
<tr>
<td>Mode 3</td>
<td>39/32/0/-</td>
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1A false keel is placed abapical of the original one.
2A false keel is placed adapical of the original one.
3A concave-out shell fragment is placed in front of the aperture.
the only specimen in which the whorl did not follow the false keel (Figs. 2D, 3B) reveals that it followed this keel, but only to a point where the false keel became wavy and discontinuous (due to defective preparation of the specimen), after which the true keel was followed. Therefore, this specimen cannot be seen as an exception to the general rule.

Specimens with the false keel displaced apically of the original keel were not deceived. The reason might be the following. During preparation of many specimens, the keel was removed to the extent that the underlying shell did not disappear completely, but unavoidably, a smooth corner or high curvature zone remained. It is likely that this corner can still be “perceived” by the snail tracing a new whorl. In this sense Hutchinson (’92) stated that not only keels, but also flat surfaces bounded by curvature changes could be the path reference for the subsequent whorl. In providing evidence of this, he reported that in Trichia hispida (which is nonkeeled except in juvenile stages) the expansion rates of both the inner and outer margins of the aperture first increase and later decrease during growth, but the peak is one whorl later for the inner margin. He concluded that the expansion of the inner margin was constrained by that of the outer margin of the preceding whorl. In the case of Sphincterochila, it may be that the keel is not the signal in itself, but rather divides the otherwise round aperture into two ramps with lower curvature (Fig. 1). This idea is reinforced by examination of some abnormal scalariform specimens of S. candidissima found in the field (Figs. 2H, 4B). Scalariformity is the result of a sudden reduction in the relative area (expansion

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Fig. 3. Experimental (A–C) and nonexperimental (D) specimens of Sphincterochila baetica (A, D) and S. candidissima (B, C). A: Apertural view of a specimen (DPUG.SB.67) in which the false keel runs abapically with respect to the true one (mode [1]). ×6.1. B: Apertural view of mode (1) specimen (DPUG.SC.13) in which the whorl detaches between the false keel and the top of the right ramp (same specimen as in Fig. 2D). ×3.7. C: Apertural view of a specimen (DPUG.SC.45) in which the false keel runs adapically with respect to the original one (mode [2]). The top of the right ramp adheres to the false keel. ×3.9. D: Apertural view of a naturally peeled specimen (DPUG.SB.23) in which the new whorl secreted thereafter bulged adapically while attached to the keel of the preceding whorl, still formed by the old shell (same specimen as in Fig. 2G) ×4.9. In all cases, the top of the right ramp is indicated by an arrow.
rate) of the aperture. This "deflation" leads to a change in the shape of the aperture, which passes from being depressed to equidimensional; at the same time, the palatal edge of the aperture moves adaxially, so that the top of the right ramp no longer coincides with the keel of the preceding whorl. This is not the case with the columellar edge of the aperture, which remains more or less in place, so that the umbilicus retains its relative size. Therefore, in S. candidissima scalariforms, the aperture follows the edge of the umbilicus in preference to the keel during growth. This pattern might have some adaptive value, since a narrow umbilicus is an antipredatory trait (Vermeij, '87, and references therein).

Additional evidence that the keel also sets the adapical limit for the subsequent whorl comes from one specimen of Sphincterochila baetica in which the shell was peeled back by a predator for at least one-half whorl, leaving only a columellar-basal strip of shell in place (Figs. 2G, 3D). This strip consti-

Fig. 4. A: Axial section of a specimen of Sphincterochila baetica (DPUG.SB.7) in which, following a break scar, the whorl migrated adaxially and invaded the umbilicus. B: Axial section of a scalariform S. candidissima (DPUG.SC.15). A sudden reduction in the expansion rate of the aperture caused the top of the right ramp to migrate adaxially, whereas the most apical point of the columellar lip remained in its normal place.
tuted an obstacle that caused the new shell tube to be secreted more adapically. Nevertheless, the top of the right ramp remained attached to the keel of the previous whorl, which caused the whorl to swell at its palatal side.

The importance of the keel in shaping the shell is confirmed also by the fact that the relative height of the cone formed by the coiled shell is partly regulated by the relative position of the keel in the aperture. Using axial sections of specimens of Sphincterochila candidissima, we estimated the relative position of the keel as the length of the right ramp relative to the rest of the whorl perimeter (Fig. 5). As a measure of the relative height of the cone we chose the apical angle (α) of the cone; given the typical ontogenetic trend to doming, α is here defined as the angle formed by the coiling axis and the line subtended along the keel of the whorl being measured and the keel of the previous whorl (Fig. 5, top left). Measurements were made on 40 specimens, in each on a whorl cross section located at a consistent angular distance of 3.5 whorls from the end of the protoconch, in order to reduce an ontogenetic factor. A significant negative correlation (F-test, $P < 0.01$) exists between α and the relative length of the right ramp (Fig. 5, top right), which implies that higher-spired forms have relatively larger right ramps.

Fig. 5. Correlation of the apical angle ($\alpha$), the length of the right ramp ($R_r$) relative to the remainder of the perimeter ($P_2-R_r$) and the growth rate of the perimeter ($P_2/P_1$). The position of two extreme morphs is included for visual comparison. The apical angle correlates negatively with the relative length of the right ramp (upper right graph) and positively with the growth rate of the perimeter (lower right graph), which implies that in lower-spired forms the right ramp is relatively shorter and that whorls grow faster with the angle of revolution. A slight negative correlation exists between the growth rate of the perimeter and the relative length of the right ramp (lower right graph), i.e., faster-growing forms have relatively shorter right ramps.
It is apparent even to the naked eye that adult individuals with faster-growing apertures (and, hence, fewer whorls) are flatter than slower-growing forms. Accordingly, we estimated the growth rate of the whorl perimeter as the ratio of the perimeters of the reference whorl and the previous whorl. A significant ($P < 0.01$) positive correlation exists between $\alpha$ and the growth rate of the perimeter (Fig. 5, bottom left), i.e., fast-expanding shells are also flatter; this would follow as geometric constraint for shells if the degree of whorl overlap and the size of the umbilicus are maintained (Fig. 6). Finally, a negative, albeit slight ($P < 0.05$), correlation was observed between the relative length of the right ramp and the growth rate of the perimeter (Fig. 5, bottom right), implying an unexplained trend for fast-expanding whorls to be depressed in cross section in such a way that the palatal (right ramp) and columnar lips become reduced with respect to the parietal and basal lips of the aperture.

In conclusion, our experimental results are consistent with the main postulate of the road-holding model of Hutchinson (‘89): the snail uses the shape of the preceding whorl as a rail for the subsequent whorl during the construction of its spiral shell. Nevertheless, the issue of shell-shape control during growth in gastropods leaves many questions unanswered. For example, the role of potential shape-regulating shell features other than keels (e.g., spines, ribs, siphonal canals) also remains to be investigated. In still other cases, whorls do not touch each other, as in some Paleozoic sessile Euomphalidae, with evenly rounded whorls (unlike present-day uncoiled vermetids); in this case, the alignment of the soft body within the shell most probably provided the reference for correct coiling. This mechanism is discussed by Hutchinson (‘89).

There are groups of gastropods in which the apertures are evenly rounded, showing no keels, longitudinal ribs, or conspicuous curvature changes, and to which the road-holding model cannot be applied. In many groups of nonumbilicate gastropods with gently curved apertures (e.g., naticoideans, neritidoideans, helicids), the whorl might be prevented from being displaced adaxially by the shell tube grown one-half whorl previously. Representatives of the basommatophoran family Planorbidae secrete a non- to slightly ornamented discoidal shell that is carried vertical or inclined and with the aperture facing the substrate. In an experimental study (Checa and Jiménez-Jiménez, ‘98), we show that planorbids react to changes in the orientation of the shell by deflecting the direction of growth of the shell tube in order to reorient the aperture towards the substrate. Therefore, life attitude in planorbids regulates the correct alignment of whorls during growth. Given that planorbids evolved from fully terrestrial pulmonates (e.g.,
McMahon, '83), their coiling strategy is an apomorphy. Other unrelated groups of freshwater prosobranchs (Ampullariidae, Valvatidae) display shell morphologies and structures that make them appear to have a planorbid-like coiling strategy. Aquatic life may be a precondition for the development of this type of coiling, since it is based on flotability. In short, the road-holding model is but one of several possible ways to interpret shell coiling. From the standpoint of constructional morphology, coiling strategies are historical characteristics of medium (RHM of terrestrial pulmonates) to low rank (Planorbidae) and potentially useful in phylogeny. Given that we lack data on most groups (e.g., marine prosobranchs), placing the study of coiling patterns into a phylogenetic context will require a vast experimental research program aimed at mapping coiling strategies over gastropod phylogeny.

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LITERATURE CITED


