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Further twists in gastropod shell evolution

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The manner in which a gastropod shell coils has long intrigued laypersons and scientists alike. In evolutionary biology, gastropod shells are among the best-studied palaeontological and neontological objects. A gastropod shell generally exhibits logarithmic spiral growth, right-handedness and coils tightly around a single axis. Atypical shell-coiling patterns (e.g. sinistroid growth, uncoiled whorls and multiple coiling axes), however, continue to be uncovered in nature. Here, we report another coiling strategy that is not only puzzling from an evolutionary perspective, but also hitherto unknown among shelled gastropods. The terrestrial gastropod *Opisthostoma vermiculum* sp. nov. generates a shell with: (i) four discernable coiling axes, (ii) body whorls that thrice detach and twice reattach to preceding whorls without any reference support, and (iii) detached whorls that coil around three secondary axes in addition to their primary teleoconch axis. As the coiling strategies of individuals were found to be generally consistent throughout, this species appears to possess an unorthodox but rigorously defined set of developmental instructions. Although the evolutionary origins of *O. vermiculum* and its shell's functional significance can be elucidated only once fossil intermediates and live individuals are found, its bewildering morphology suggests that we still lack an understanding of relationships between form and function in certain taxonomic groups.

Keywords: conchology; snail; karst; Malaysia; Mollusca; morphology

1. INTRODUCTION

Over the past 150 years, evolutionary biology has benefited from the many qualities of the gastropod shell (Schilthuisen 2002). It is essentially a complex three-dimensional structure that acts as the snail's interface with the biotic and abiotic environments. Consequently, it is of great importance for survival and the target of multifarious natural (and possibly sexual; Schilthuisen 2003) selection pressures. Yet, it answers to a very limited set of growth parameters, which makes its evolution reducible to few character-state changes

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(Thompson 1942). The gastropod evolutionary history reveals a dominance of shells resembling helicospiral cones that monotonically expand according to a logarithmic function (Thompson 1942 and references therein). In addition, most shells are right handed and possess overlapping whorls that coil around a single axis (figure 1a). Spiral coiling also appears to be dictated by a set of 'behavioural' rules involving shell sculpture. For example, Hutchinson's (1989) road-holding model (RHM) postulates that shell ornamentation (e.g. keels and low curvature areas) is the vital reference spot for the attachment of subsequent whorls.

Several groups of gastropods, however, possess shell-coiling patterns that depart from the above-mentioned conventions. For instance, shells of marine vermetids generally deviate from logarithmic spiral growth late in their ontogeny. In the terrestrial genus *Opisthostoma*, shells are not right handed, but 'sinistroid' (figure 1c) due to a reversal in coiling direction in the last half-whorl (Gittenberger 1995). Furthermore, *Opisthostoma* shells can possess two (e.g. *Opisthostoma concinnum*; figure 1b) or three different coiling axes (e.g. *Opisthostoma castor*). In another terrestrial genus, *Ditropopsis*, the body whorls can detach to produce an 'uncoiled' shell (figure 1d). Interestingly, detached whorls of uncoiled gastropods do not adhere to the sculptural features of previous whorls; they remain either coiled around the primary teleoconch axis (figure 1d) or coil in an irregular manner (e.g. marine vermetids).

Taking these exceptions into account, we can refine our earlier generalizations of gastropod shells: (i) they possess an upper limit of three coiling axes, (ii) detached body whorls do not reattach to the preceding whorls, and (iii) whorls once detached either coil around a primary teleoconch axis or deviate haphazardly. In this paper, we describe a new species of terrestrial gastropod with a shell that pushes these evolutionary boundaries even further. In addition, we discuss its evolutionary origins, functional significance and coiling strategy.

2. MATERIAL AND METHODS

The specimens upon which the species description was based were deposited in the Zoological Reference Collection (ZRC), Mollusc Section (MOL), Raffles Museum of Biodiversity Research (RMBR) and National University of Singapore. Using visual inspection and flotation techniques to extract shells, 38 individuals (including fresh dead specimens) were obtained from a total of six different 8 m² plots at the type locality. Descriptions are based on the shell characters and nomenclature follows van Benthem-Jutting (1952) and Vermeulen (1994). Measurements of shells were based on images obtained from a scanning electron microscope and are in millimetre. Height refers to the longest dimension of the shell, while width refers to its perpendicular dimension.

3. SYSTEMATICS

Higher taxon names: Mesogastropoda Thiele 1925; Diplommatinidae Pfeiffer 1856; and Genus *Opisthostoma* Blanford & Blanford 1860.

(a) *Type species*

Opisthostoma nilgiricum Blanford & Blanford 1860.

(b) *Description*

(i) *Opisthostoma vermiculum* Clements & Vermeulen, n. sp.

Height: holotype 1.5, paratype 1.5. Width: holotype 0.9, paratype 1.0. Shell thin, cream or white, not transparent

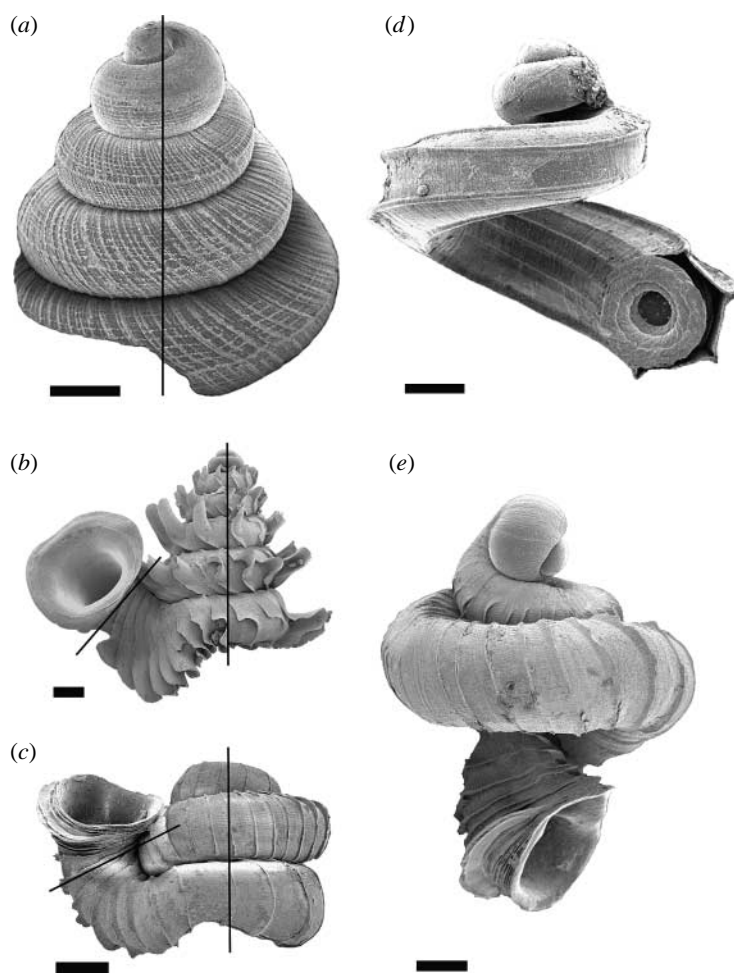


Figure 1. Different gastropod shell-coiling patterns. (a) *Queridomus conulus* exhibiting logarithmic helicospiral growth with tightly coiled whorls around a single axis (black line), (b) *O. concinnum* and (c) *Opisthostoma hailei* exhibiting 'sinistroid' growth with two different coiling axes (black lines), (d) *Ditropopsis* sp. demonstrating uncoiling with detached whorls that never reattach and (e) a mutant individual of *O. hailei*. Scale bars, 200 μm .

and slightly shiny. First whorl smooth; subsequent whorls sculptured with fine, white, regularly spaced radial ribs, becoming widely spaced and flared nearing aperture before being compressed; spiral striae absent. Whorls 4.5–5, convex, increasing in radius, uncoiling at the end of second whorl; detached third whorl returns to reattach to the base of second whorl, followed by a phase of detachment, reattachment and detachment; whorls deviate from primary teleoconch axis to coil around three additional axes. Suture deep. No umbilicus. Aperture round, vertical, without teeth. Peristome duplex, continuous, circular to rounded triangular.

(c) *Remarks*

An internal constriction, which qualifies placement under the genus *Opisthostoma* (see Vermeulen 1994), was detected in this species. All 38 specimens demonstrated four changes in the coiling direction and underwent similar detachment–reattachment phases, but displayed slight variations in the angles of each coiling axis (see electronic supplementary material). Intraspecific variation ($n=6$) among shell dimensions appeared to be low, with a mean (\pm s.d.) height and width of 1.5 ± 0.1 and 0.9 ± 0.1 , respectively.

(d) *Types, locality and distribution*

Holotype: ZRC.MOL.002824, Gunung Rapat ($4^{\circ} 33' \text{N}$, $101^{\circ} 7' \text{E}$), Perak, Peninsular Malaysia, held in RMBR. Two paratypes: ZRC.MOL.002825 and ZRC.MOL.002826, same data as holotype. Known only from the type locality.

(e) *Etymology*

'*vermiculum*' meaning wormy, as the shell resembles a worm-like organism. Clements and Vermeulen are assigned as authors for *O. vermiculum* sp. nov.

4. DISCUSSION

Evolutionary responses of shell traits to environmental pressures are among the best-documented microevolutionary processes (Endler 1986). For example, uncoiling in freshwater gastropods appeared to correspond with periods of high chemical stress during the Miocene epoch (Nutzell & Bandel 1993). The impact of environmentally induced mutations (figure 1e) on the phenotype of *O. vermiculum*, however, cannot be ascertained without fossil records and historical environmental data. Novel shell characters can also result from hybridization (Woodruff & Gould 1987), during which the developmental factors or the gene

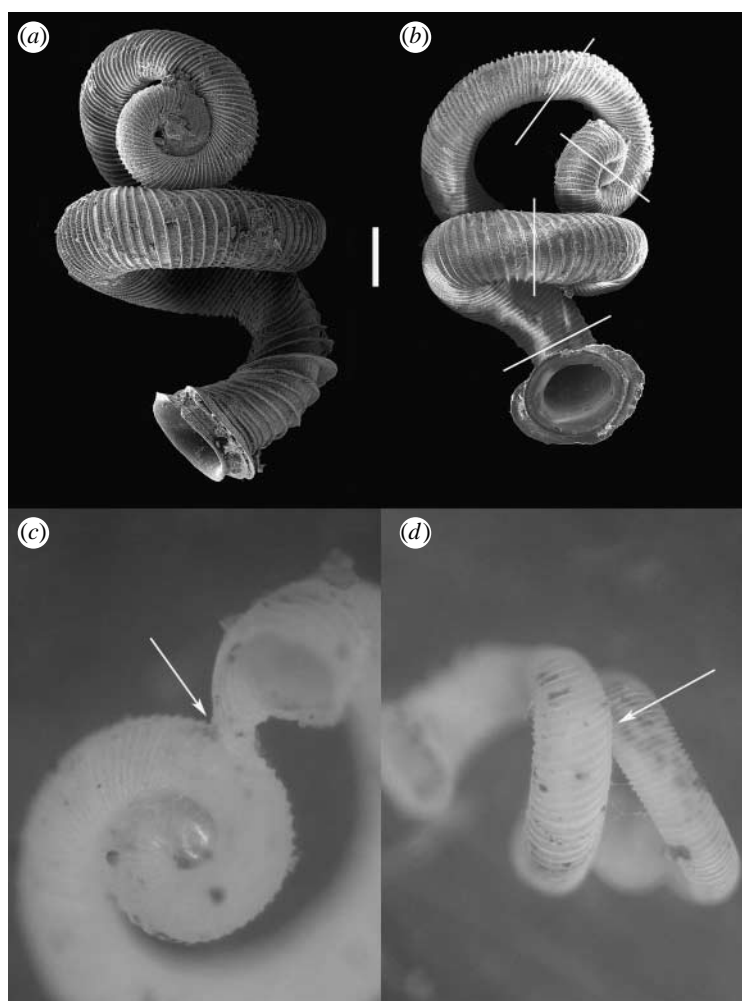


Figure 2. *Opisthostoma vermiculum* sp. nov. (a) Ventral view, (b) side view indicating four coiling axes (white lines), (c) first and (d) second reattachment points of detached whorls (white arrows). Scale bar, 100 μm .

interactions related to morphologies of different species produce new features (Chiba 2005). However, the distinctive and invariant coiling patterns of *O. vermiculum* specimens examined in our study suggest that its conchology is under fairly strict developmental-genetic control and is unlikely to be a product of hybridization between two other congeners that occur sympatrically on the same karst—*Opisthostoma megalomphalum* and *Opisthostoma paulucciae*; obvious differences in their shell sculpture (e.g. rib spacing and presence of apertural flares) further reduce the likelihood that *O. vermiculum* is an intermediate species.

The gastropod shell sculpture could have evolved to cope with predation (Palmer 1977), feeding (Illert 1981) or movement (Cain & Cowie 1978). In some species of *Opisthostoma*, the evolution of intricate shell ornamentation may be driven by sexual selection (Schilthuizen 2003), although empirical evidence thus far suggests only the role of ‘Red Queen’ coevolutionary interactions with the snails’ predators (Schilthuizen *et al.* 2006). The functional significance of uncoiling (especially in *O. vermiculum*), however, remains unclear (Morton 1965; Nutzel & Bandel 1993). Uncoiled shells may facilitate predator evasion in some species (i.e. whorl detachment makes snails effectively larger; Rex & Boss 1976), but appear energetically disadvantageous to construct (i.e. uncoiling weakens shells and consumes additional shell

material; Rex & Boss 1976) and may even hinder movement (Clarke 1973). Uncoiling has also been associated with sessility (e.g. in marine gastropods; Gould 1968) and gerontic conditions (Yochelson 1971), but the former is precluded in terrestrial snails and the latter is unlikely because whorl detachment in *O. vermiculum* begins early in its ontogeny.

The coiling axis of a gastropod shell is not easily discernable (Okamoto 1988; Savazzi 1990), but numerous ‘fixed axes’ mathematical models have been used to explain shell geometries (Raup 1961; Raup & Michelson 1965; Løvtrup & Løvtrup 1988; Illert 1989; Savazzi 1990). The presence of four coiling axes in *O. vermiculum* (figure 2b), which is the highest number known for a shelled gastropod, poses a challenge to the development of a model that accounts for such a morphologically bizarre shell. Reorientation of shell-coiling axes has been attributed to a simple rotation of the snail body inside the shell (Ackerly 1989). A more remarkable and unique aspect, however, is the departure of the second whorl from the primary teleoconch axis to revolve around a secondary (almost perpendicular) axis before latching back onto the preceding whorl (figure 2c), after which it proceeds to a detachment–reattachment (figure 2d)—detachment phase. The importance of shell ornamentation (e.g. keels and ribs) for spiral coiling has been corroborated by experimental

tests on the RHM (e.g. *Checa et al.* 1998), but the detached whorls in *O. vermiculum* consistently reattach to preceding whorls without any apparent need for reference support.

Ultimately, the functional significance and coiling regulatory mechanism of the shell in *O. vermiculum* cannot be investigated without studying live individuals, but the novelty of its shell-coiling pattern is indisputable. It is also interesting to note that such phenotypic peculiarities often occur among microgastropods (less than 5 mm) such as *Opisthostoma*. Unfortunately, *Opisthostoma* snails are particularly vulnerable to extinction (IUCN 2004) as most species are restricted to limestone karsts (Vermeulen 1994), which have become increasingly threatened by quarrying activities (Clements *et al.* 2006). We hope the finding of this species will not only encourage further research into the relationship between form and function in gastropods, but also promote more inventories of limestone karsts due to their potential for yielding important taxonomic and evolutionary discoveries (e.g. Morwood *et al.* 2004).

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