PLANORBOID SHELL IN SUBTERRANEAN GASTROPODS (CAENOGASTROPODA: TRUNCATELLOIDEA): SHELL ANCIENT GEOMETRY AS SELECTIVE FACTOR

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Abstract   Planispiral or nearly planispiral (extremely low spire) planorboid shells, common in the Palaeozoic, became extremely rare during the Mesozoic Revolution, eliminated by shell crushing predators. Among subterranean Caenogastropoda the planorboid shells are much more common than among the epigean ones. Hydrodynamics of the planorboid vs turbospiral shells is briefly discussed, as well as the consequences of the shell form determining the shape and size of the foot. The latter must be effective enough to prevent dislodgment by the water current. The costs of the shell formation of planorboid vs turbospiral shell is estimated as being higher for the planorboid one. No superiority in any respect of the planorboid shells has been found. Considering the fossil record, planorboid shell is considered as a plesiomorphy, gained in the Recent malacofauna several times by reversals, and not eliminated in subterranean habitats characterized by low predatory pressure. The planorboid shell, with wide umbilicus, is not adapted for the quasi-infaunal mode of life interstitially, being unable to move efficiently in narrow spaces, and its thin shell is prone to damage by predatory subterranean vertebrates, which prevents their passive transportation. This results in high endemism, with extremely narrow ranges of the species with planorboid shells, in comparison with the turbospiral ones.

Key words   Stygobiont, planispiral, turbospiral, predation, dispersal, plesiomorphy, endemism

INTRODUCTION

The gastropod shell could be treated as a logarithmic spiral, whose geometric parameters may be described in detail by mathematical formulae. There is a long history of fascination by this geometry (Moseley, 1838; Raup, 1961, 1966; Raup & Michelson, 1965; Cain, 1977, 1978a, b; Cameron, 1981; Cook & Jaffer, 1984; McNair *et al.*, 1981; Heath, 1985; Stanley, 1988; Schindel, 1990; Rice, 1998; Stone, 1999; McGhee, 2006; Okajima & Chiba, 2009, 2011, 2012; Noshita *et al.*, 2012). It must be noticed that within the morphospace theoretically available for such spirals, only a small part is exploited by the extant Gastropoda. It is also remarkable that much wider morphospace was filled by some extinct, mostly Palaeozoic forms. The typical coiled gastropod shell is turbospiral, with whorls growing down from the apex (or up in case of hyperstrophy) and forming a higher or lower spire. The shell may also be coiled in a single horizontal plane, with its diameter increasing away from the axis of coiling. Such shell is planispiral, typical of the swimming cephalopod *Nautilus pompilius* Linnaeus, 1758, and many extinct Ammonoidea. It is often believed that the ancestor of the Gastropoda had a planispiral shell, but there is no planispiral

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shell in any extant gastropod (see Falniowski, 1993 for details), although the term "planispiral" is often used for the shells with extremely low spires (Hershler & Ponder, 1998; Czaja *et al.*, 2019). Such gastropods present geometry and mechanical characteristics typical of planispiral shells. Perhaps "planorboid" is the best description of such shells. Such gastropods can be found in subterranean, also interstitial habitats, and we would try to explain why and how they inhabit subterranean waters.

PLANISPIRAL AND PLANORBOID GASTROPODS IN TIME AND SPACE

In the marine realm the predation intensity due to crushing enemies (like crabs or teleost fishes) drastically increased during the Mesozoic Revolution (Vermeij, 1977), decreasing the morphospace available for the shell of the Gastropoda. A good example may be the repaired injuries to the shells of fossil Pleurotomariidae that suggest predatory attack. These are found more often in turbiniform than planispiral species (Lindström & Peel, 2005). There has been a general reduction in the number of marine gastropod species with planorboid shells after the Permian (Cain, 1977). Only the smallest marine (like *Omalogyra*) or freshwater (*Valvata cristata* O. F. Müller, 1774)

Caenogastropoda (less than 10mm of the shell diameter) can have this geometry of the shell (McNair *et al*., 1981). The shells of freshwater snails simply correspond to geometric constraints (Okajima & Chiba, 2011). Almost all the North American members of the family Cochliopidae with "planispiral" shells are subterranean forms (Czaja *et al*., 2019). Planorboid Truncatelloidea in the Balkans occur either in subterranean habitats, or big old lakes (Radoman, 1983).

There are no planorboid shells on dry land. The spire index, defined as a shell's height divided by its diameter, shows a bimodal distribution in terrestrial gastropods: there are many high- and low-spired gastropods, but this low spire is still far from the planorboid condition, whereas middle-spired gastropods are rare (Cain, 1977, 1978a, b; Cameron, 1981; Cowie, 1995). In contrast, aquatic gastropods show a continuous distribution of spire indices (Cain, 1977). Terrestrial snails with tall shells are generally active on high-angled or vertical surfaces, and gastropods with flat shells are active on low-angled or horizontal surfaces (Cain & Cowie, 1978; Cameron, 1978; Cook & Jaffer, 1984). This bimodality must be related to the mechanics of shell balance during locomotion on different substrates (Cain & Cowie ,1978), a concept that was supported by theoretical analyses and empirical data (Okajima & Chiba, 2009, 2012). Noshita *et al*. (2012) demonstrated that land snails are more highly constrained than marine ones with regards to achieving a balance between postural stability and the available space for their soft body. In the freshwater pulmonates the bubble of air in their mantle cavity gives the shell buoyancy, which allows planorbiform shells to be common in the freshwater habitats. Without such buoyancy, the planorboid shell cannot survive in either marine or freshwater habitats. High-spired shells tend to be less stable than low-spired shells, given the range of substrate topographies encountered in natural environments. The snails with turriform shells with extremely high spires, tend rather to be the shell draggers; their shell may serve as an anchor in lotic habitats. On the other hand, low-spired forms support lower space availability for their soft bodies, and thus are likely to be disadvantaged in habitats where calcium carbonate is a limiting resource (Noshita *et al*., 2012). Whorl overlap decreases the amount of the shell material to be used, but also the space for the gastropod's body.

SUBTERRANEAN HABITATS

Caves and interstitial habitats are characterized by lack of light, low levels of oxygen and available organic matter as food (Poulson, 2012). They often have very restricted space and sometimes periodic strong water currents. On the other hand, there is lower competition, and lower predation. Some larger vertebrates, like olm – blind cave salamander *Proteus anguinus* Laurenti, 1768 – eat snails (personal observation), but not in the interstitial habitats that provide insufficient space for them. A turbospiral, relatively thick-walled shell may pass the gut of *Proteus* or a stygobiont fish untouched, with the snail still alive, thus passive transportation of subterranean vertebrates may expand the geographic ranges of some stygobiont snails. Epigean transportation of fresh- and brackish-water, as well as terrestrial snails by fishes and birds is well documented (e.g., Lyell, 1832; Darwin, 1859; Rees, 1965; Cadée, 1988; Wesselingh *et al*., 1999; Charalambidou & Santamaria, 2002; Figuerola & Green, 2002). The shortage of food results in minute and thin-walled shells, and the low predatory pressure results in the shells showing geometry rather unusual for the epigean gastropods: either with strikingly high spire (Figs 1M), sometimes even with some scalarity, or planorboid, nearly planispiral ones (Figs 1K); both forms of the shell are less resistant to crushing by predators, especially the planorboid or scalariform ones. Globular shells, typical of the epigean gastropods, are known to be an adaptation against crush-type predators (Seeley, 1986, DeWitt *et al*., 2000).

Flowing waters – caves and spring heads
Grego *et al*. (2017) stressed the importance of the high-water flow in the subterranean realm. They pointed to "the adhesive strength of gastropod musculature and slime important for attachment of the animal to the substrate". This needs some correction: perhaps somewhat contra-intuitively, the adhesive strength of the foot musculature, considering the minute surface of the foot sole, is nearly negligible. Shell morphology and foot size were not related to dislodgement speed in the flow tank experiment of Verhaegen *et al*. (2019). Rather, behavioural adaptations, like finding some crevices or temporary immobility, and especially mucous stickiness, prevent dislodgement. The classic studies on the intertidal limpets
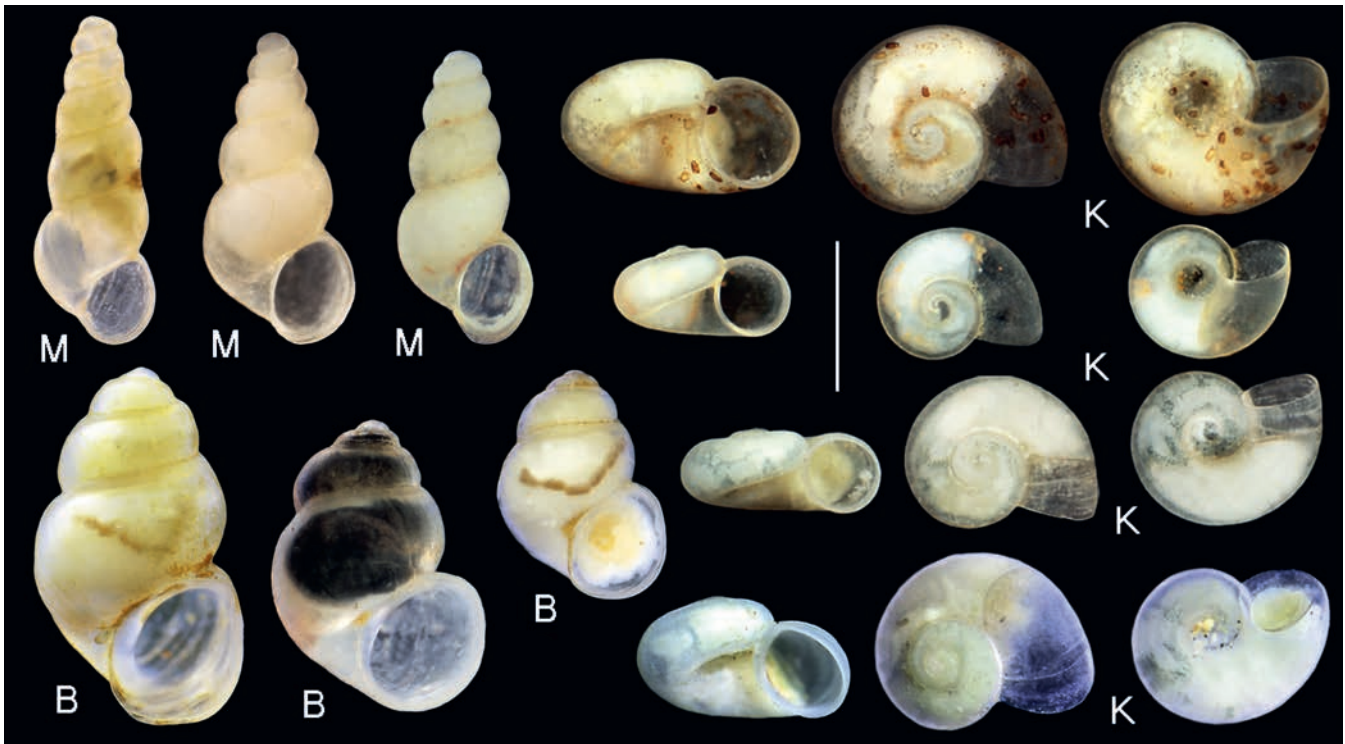
Figure 1 Shells of gastropod with different geometry: M – *Montenegrospeum bogici* (Pešić et Glöer, 2012), turbospiral, turreted; B – *Belgrandiella kusceri* (A. J. Wagner, 1914), turbospiral, conic; K – *Kerkia* spp., planorboid, with wide umbilicus; bar equals 1mm.

belonging to the Patellogastropoda (Branch & Marsh, 1978; Branch, 1985; Savies & Hawkins, 1998; Smith *et al.*, 1999; Smith & Morin, 2002; Smith, 2010) demonstrated that dehydration of mucous increased the stickiness of the foot sole which may result in unbelievingly high resistance to dislodgment (in kilograms per cm sq). According to Grego *et al.* (2017) the average flow velocity affects the shape of the shell, slenderer in more lotic places, with higher flow of water. Indeed, both drag and lift forces were stronger on globular compared to slender shells in the flow tank experiments of Verhaegen *et al.* (2019). It must be noted, however, that there are numerous observations showing that aquatic snails with globular shells with larger apertures, harbouring a larger foot, are usually typical of flowing, lotic waters (e.g., Lam & Calow, 1988; Wullschleger & Jokela, 2002; Kistner & Dybdahl, 2014; Verhaegen *et al.*, 2018). It is supposed that a larger foot, and thus larger sole, provides a larger attachment area, reducing the risk of dislodgement by the current. In fact, the size of the foot depends on the size of the animal, and thus the shell, but not the shell shape nor the size of the aperture (Verhaegen *et al.*, 2019). The globular shells are

more crush-resistant, thus possibly more resistant to damage caused by tumbling after dislodgement (Minton *et al.*, 2008). In general, gastropod shell phenotypic plasticity has been widely discussed (e.g., Gould, 1969; Wullschleger & Jokela, 2002; Hoverman *et al.*, 2005, 2007, 2014; Statzner, 2008; Dillon & Robinson, 2011; Dillon *et al.*, 2013; Whelan, 2021).

Czaja *et al.* (2019) in their paper on the stygobiont gastropods followed the ideas of Grego *et al.* (2017) and suggested that "flat shells with strongly inclined apertures could be attached flat to the surface and considerably reduce the frontal hydrodynamic resistance area and could be therefore favoured by selection (better resistance to stronger and turbulent water flow). The same applies also to the animal mobility within the (interstitial) sediment cavities, where a more inclined shell aperture position could be advantageous by creating lower resistance in the crevices during moving. The shape also indicates the habitat in larger interstitial cavities (with cavities several fold larger than the shell diameter) where the stronger water stream could appear at least periodically." They presented a few shells following the above characteristic. We must note,

however, that the survival of such planorboid forms in more lotic environment, if competition and especially predation are negligible, does not confirm that such forms are the fittest in such biotope. The shell kept flat on the bottom is an analogue of a flat roof, much less resistant for the dislodgment by the heavy wind than a steep one.

In fact, the shape and orientation of the gastropod shell aperture has been studied by several malacologists, since it is crucial in the context of handling the heavy shell filled with the viscera, still problematic even in aquatic habitats. Linsley (1977) for marine gastropods proposed "the law of tangential apertures", which states that the aperture plane is tangential to the body whorl, such that the aperture and ventral-most part of the body whorl lie together in one plane. Shells with such apertures may be clamped tightly to the substrate to reduce the risk of predation; this "law" was supported by detailed measurements of gastropods in diverse habitats (Noshita *et al.*, 2012). According to McNair *et al.*, (1981) snails that live on a hard substrate, like rocks or stones, have a planar aperture that provides an effective seal against the substrate and a foot that is accommodated under the margins of the aperture during clamping, and almost always have an apertural margin inclined adapically (prosocline) to the suture. Such an aperture requires more energy to build. The rock-clinging mode of life tends to result in a round aperture form. A high inclination of the axis of coiling permits the columellar muscle to insert directly above the foot, thus allowing an efficient and strong clamping force, enabling the shell to maintain its position during periods of turbulence (Linsley, 1978). The aperture cannot be elongated in rock clinging gastropods, because of geometrical restrictions. This results in less effective circulation within the mantle cavity.

Interstitial habitats

Besides caves, subterranean rivers, spring heads and other more spacious habitats there are also interstitial habitats, neither rare nor discontinuous, thus making possible migration between caves and other more spacious subterranean habitats (Lamoreaux, 2004; Culver *et al.*, 2009; Culver & Pipan, 2009, 2014; Dole-Olivier, 2011; Falniowski *et al.*, 2021). Williams (2008) stressed that in almost all caves the surrounding rock is fractured, forming small solution tubes that allow subsurface connections between caves; in karst areas, epikarst and associated formations, vertical percolation of water is more or less continuous. Some of the inhabitants of more spacious subterranean waters can also be found as meiofauna, thus the interstitial habitats may serve them as ways of dispersal. There are functional analogies between the freshwater gastropod meiofauna and much better studied marine infaunal gastropods. The majority (15 of 20 clades) of marine gastropods became infaunal as late as the Cenozoic and diversified in the Early Miocene (Vermeij, 2017). Many categories of shell form are not represented among marine infaunal species. These include shells that are loosely coiled, planispiral, widely umbilicate, broadly fusiform with an ovate aperture, turbinate, trochoid or limpet-like. Sand-burying cerithiids, mitrids and costellariids (but not conids) have on average more slender shells than their epifaunal counterparts (Vermeij, 2017). Turritelliform burrowing species should lack sculpture, possess columellar folds and a flat whorl profile, and have an orthocline or prosocline aperture (Signor, 1982). The umbilicus weakens the shell (Vermeij, 1977) and does not occur in sand-burying snails (Vermeij, 2017). Among the subterranean Balkan gastropods, the wide umbilicus characterises some genera, like *Horatia* Bourguignat, 1877 or *Kerkia* Radoman, 1978. Not one infaunal gastropod has the low-spired, flat, nearly planispiral shell (Vermeij, 1971, 1975, 1977, 2017a, b).

ESTIMATION OF SHELL FORMATION COSTS

As noted already above, low-spired forms support lower mechanical resistance as well as lower space availability for their soft body. One could suppose then that such shells may be superior since they need less material to be built. In karst habitats there is a lot of calcium, but the process of shell formation is energetically expensive (Palmer, 1983, 1992, Day *et al.*, 2000, Clark, 2020), which is especially important in subterranean habitats, usually poor in organic matter suitable as food. We could try to test such hypothesis, in a very simplified way. For the snails of the same soft parts' weight – thus the same soft part volume – we could provide rough estimates of their shell surface comparing the outer surface of the cone for "normal" conispiral shell and of the cylinder for the planorboid one. If half of the

breadth of the planorboid (approximately planispiral) shell is r_1, and the height of this shell is h_1, and, respectively, r_2 and h_2 for the turbospiral (conic) shell, the same volume would be given by the formula:

$$\pi r_1^2 h_1 = \pi r_2^2 h_2/3, \text{ thus } r_1^2 h_1 = r_2^2 h_2/3.$$

Assuming the same shell breadth ($r_1=r_2$): $h_1=h_2/3$; $3h_1=h_2$, which means that the turbospiral shell would be three times higher than the planorboid one with the same maximum breadth. The outer surface of the planispiral shell would equal: $2\pi r_1^2 + 2\pi r_1 h_1 = 2\pi r_1(r_1+h_1)$, and for the cone: $\pi r_2^2 + \pi r_2(r_2^2 + h_2^2)^{1/2}$; assuming again the same shell breadth ($r_1=r_2$) and, for the same volume $h_2=3h_1$, the cone surface would be: $\pi r_1^2 + \pi r_1(r_1^2+3h_1^2)^{1/2}$. The surface proportion would be then (turbospiral/planispiral):

$$[\pi r_1^2 + \pi r_1(r_1^2+3h_1^2)^{1/2}]/[2\pi r_1(r_1+h_1)], [r+(r^2+3h^2)^{1/2}]/[2(r+h)]$$

With real measurements for a planorboid, nearly planispiral stygobiont species of *Kerkia* (still unpublished description of this species), compared with an imaginary turbospiral shell of the same maximum breadth and volume, the proportion would be 1.33 This is a very rough estimate, but Okabe & Yoshimura (2017) considered the scaling exponent of the shell thickness as a morphological parameter, and demonstrated lower efficiency of use of shell forming materials for the planispiral shell. However, the amount of the material used for shell formation depends on the shell wall thickness. The assumption of isometric growth that shell wall thickness increases in proportion to shell size is usually not realistic; allometric growth results in the shell wall thickness increased not as quickly as the shell size, which saves energetic resources. Planorboid shells, whose geometry causes low resistance for crushing, are thus even less resistant because of their thin walls.

GEOGRAPHIC RANGES AND ENDEMISM

Wider geographic ranges of an organism may reflect its evolutionary success, higher selective value, wider range of possible adaptation, but also its historical and present possibilities of expansion. Stygobiont gastropods, like all the subterranean fauna, are usually thought to be, in general, narrow endemites (see Falniowski

et al., 2021). The estimation of the real levels of their endemism remains relatively unstudied so far, since most of them were described considering only the shell, whereas even anatomical characters are often insufficient in these snails to distinguish or simply determine a species (Falniowski, 2018; Osikowski *et al*., 2018). Thus only a few well documented cases may be considered. *Montenegrospeum bogici* (Pešić & Glöer, 2012) with high-spired, turriform shell (Figs 1M), was found within 236km range (Falniowski *et al*., 2021). *Belgrandiella kusceri* (A. J. Wagner, 1914), with similar shell (Figs 1B), was recorded within a distance 42km long (Falniowski *et al*., submitted). On the other hand, each of the ten molecularly distinct species of *Kerkia* Radoman, 1978, inhabiting the same part of the Balkans as *Montenegrospeum* and *Belgrandiella*, and having planorboid or very low-spired shell (Figs 1K), is restricted to an area of a couple of kilometres (Hofman *et al*., submitted).

CONCLUSION – WHY PLANORBOID AND WITH WHICH CONSEQUENCES?

Despite a rather extensive literature survey, I have not found any ideas concerning possible benefits for the gastropod with a planispiral or planorboid *versus* trochispiral shell with higher spire. Planispiral shells are inevitably supreme in swimming cephalopods (*Nautilus*, Ammonoidea) because of their hydrodynamic perfection, but in creeping gastropods this seems to be a bad solution. Only in freshwater pulmonates with a mantle cavity filled with air, resulting in shell buoyancy, may the diameter of the shell exceed ten millimetres (Planorbidae, but also some non-pulmonate ones, like *Marisa*, representing Architaenioglossa, which is also equipped with an air-filled kind of lung). Comparative anatomy suggests that the planispiral or nearly planispiral shell possibly characterised the hypothetical ancestor of the gastropods (see Falniowski, 1993 for review). The fossil record univocally presents numerous Palaeozoic gastropods with planispiral shells, which were later eliminated by predation and competition, during the Mesozoic Revolution. Thus, we can assume that a planispiral or nearly planispiral shell is a plesiomorphy within the Gastropoda, gained parallel by multiple reversals, and not eliminated later in some habitats characterized by weakened predation

and/or competition. Subterranean waters are such a habitat. Planorboid shells, even with wide umbilicus (characteristic of *Kerkia*), do not exclude these snails from subterranean habitats, but effectively decrease their active locomotion through interstitial habitats, as well as their passive transportation, due to their delicate, prone to damage shells. Finally, this results in strikingly narrow ranges of the stygobiont species with flat, planorboid shell.

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