

HANDEDNESS IN THE BRITISH PLANORBIIDAE

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ABSTRACT

Most descriptions of planorbid species, the aquatic ram's-horn snails, assume that the shell is sinistral in its coiling. Observations of the structure of the shell and the behaviour of the live animals suggest that these species are dextral. In particular, the handedness of *Segmentina nitida* Shining Ram's-horn is confirmed as dextral.

DESCRIPTIONS OF THE PLANORBIIDAE IN THE LITERATURE

Identification, especially of unfamiliar or rare species, depends on accurate descriptions in the literature. Whether a ram's-horn shell is left- (sinistral) or right-handed (dextral) is therefore important in this respect.

Depending on the direction of the coiling of the shells, gastropods are either dextral (the shell coils in a clockwise direction when viewed from the spire surface and the aperture is on the right) or sinistral (the shell coils in an anti-clockwise direction with the aperture on the left). Problems arise in determining which surface contains the spire, especially in flattened shells such as the ram's-horns. As can be seen in the extracts below, there is still much argument in deciding whether ram's-horns are dextral or sinistral (or even a mixture of dextral and sinistral species) and this uncertainty has implications in interpreting descriptions of the various species.

Brown (1845) describes the genus *Planorbis* Müller in the following terms:

'Shell discoidal, umbilicate; spire depressed; apex always distinct; volutions heterostrophe, or revolving from right to left, convolving always on the same plane, and apparent on both sides ... outer lip [of aperture] thickened, expanded, and its under part always extended forward ...'

This description of the aperture seems to imply a sinistral shell but the coiling is described from right to left, in other words, dextral. His illustration of the aperture view shows *Planorbarius corneus* with a sinistral shell. However, he pictures *Planorbis carinatus* and *Planorbis marginatus* [sic] as dextral in aperture view.

In the reprint of Woodward's fourth edition (1880), *Planorbis* Müller, referring to *Planorbarius corneus*, is described in the following terms:

'Shell discoidal, dextral, many-whorled; aperture crescentic peristome thin, incomplete, upper margin projecting.'

This describes a dextral shell. However, later he says:

‘Some species of *Planorbis* have the sutures and spire deeply sunk and the umbilicus flattened.’

This seems to imply a mistaken identification of spire and umbilicus, suggesting left-handedness. Reeve (1863) states:

‘Sometimes the shell of *Planorbis* is coiled to the right, sometimes to the left, but in a shell of discoid growth it is not easy to detect the difference. The best mode of observing it, is to notice the obliquity of the aperture. The upper disk of the shell is the side on which the margin of the aperture is the most advanced in growth.’

That last sentence of Reeve’s gets to the heart of the problem and it is therefore strange that later writers ignore this observation.

Step (1901) writes:

‘Here it will be seen ... that instead of an elevated spire with the whorls one above the other they are all in the same plane, and that the mouth of the shell is to the left instead of the right as in *Lymnaea*. The spiral is therefore described as dextral, the shell discoidal.’

He appears to be describing a sinistral shell and calling it dextral! This paradoxical description is perpetuated in later editions of the book.

Ellis (1926) seems definite that the planorbids are sinistral:

‘The *Planorbiidae*, represented in Britain by *Planorbis* and *Segmentina*, are sinistral, with a flattened disk-like shell coiled in one plane.’

He goes on to say:

‘The shell is carried by the animal upside down, and is usually figured in that position, but as it is sinistrally coiled, the true upper side is that which is uppermost when the shell is held with the aperture on the left facing the observer.’

Janus (1965) describes the *Planorbiidae* as:

‘Common freshwater snails, having a sinistral (left-wound) shell coiled in one plane. The animal normally carries the shell upside-down ... The spire is commonly intorted or sunken, in some species to such a degree that the umbilicus is convex and one might believe the shell to be dextral.’

One wonders why the thought that perhaps the shell *is* dextral did not register more forcefully! Beedham (1972) describes just eight species and, although not actually stating that each is sinistral, draws all of them as sinistral shells, with the aperture shown on the left.

Macan (1977) notes that:

‘There is disagreement among authorities as to whether the shells of *Planorbis* and *Segmentina* are dextral or sinistral; it seems to be most convenient to refer to the side which is uppermost when the animals is crawling along as the upper side.’

Using this argument he refers to *Bathyomphalus (Planorbis) contortus* as dextral but in others avoids the problem by drawing aperture views in a vertical plane or not at all!

However, Fitter and Manuel (1986) state:

‘For the purposes of the terminology used here, planorbid shells are assumed to be dextral.’

Glöer *et al.* (1992) describe the European planorbids (including all the British species) as left-handed, with the apertures shown on the left.

Pfleger (1999) takes the argument a stage further by reference to morphology:

‘The main feature of the European species of this family [*Planorbiidae*] is their flat discoid shell. Although it appears to be dextral (from its position during crawling and the organisation

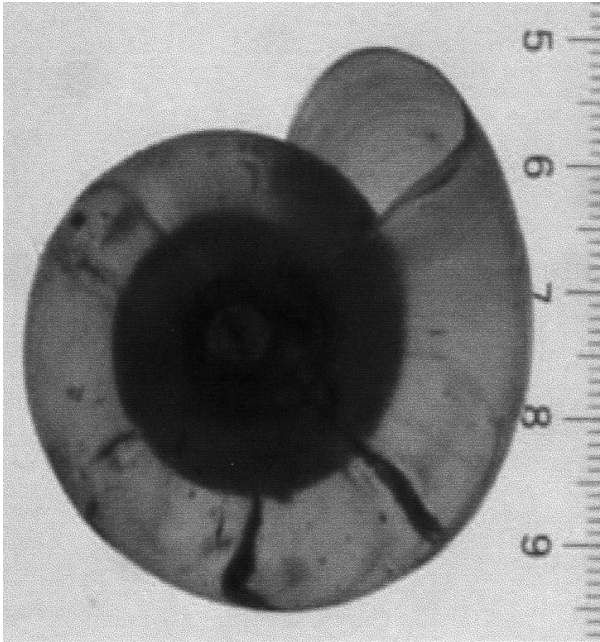


Fig. 1 Ventral view of the transparent shell of *Segmentina nitida*. Note the upper part of the aperture opening overlapping the lower, assuming a dextral shell; photo Graham Rix.

of the aperture and the two sides), the morphology of the animal itself corresponds to that of sinistral gastropods (the respiratory and the genital orifice are on the left side).'

TOPOGRAPHY OF THE SHELL OF PLANORBIDS

All the ram's-horn shells have an asymmetrical aperture with the lip projecting further forward on one side than the other (Fig. 1). We must remember that in emerging from its shell, the animal has to obtain purchase on the substrate for forward locomotion.

The coils of the shell adhere more closely at the shoulders, with the upper edge of the aperture merging with the body wall at a definite position. In contrast, the coils around the umbilicus are more tumid with greater separation and the lower lip merges with the body whorl over a longer length.

Further intimations are obtained from examining a shell under the microscope when tiny ridges can be seen where the striae end in the shoulders of the whorls around the spire (Fig. 2). Such sculptures are characteristically seen on the shoulders of the shell whorls in gastropods with elongated spires, not around the umbilicus, or, if more general sculpturing is present, it is less obtrusive near the umbilicus.

Examination of the spire and umbilicus themselves also has relevance here. The spire in all species is always visible as a domed structure, it is easy to imagine it being drawn out into the typical structure of other gastropods such as the Lymnaeidae. The umbilicus, on the other hand, with its smoother, more tumid coils, descends deeply and no domed structure is seen. It is difficult to imagine it could accommodate a protoconch!

Differences in the topography of the shell of ram's-horn snails are most striking when viewed from the aperture aspect and these provide the easiest means of identification of species, where not only the relative size and shape of the aperture in relation to the rest of the shell is easily seen, but also the presence and position of a keel is more readily determined. Even very

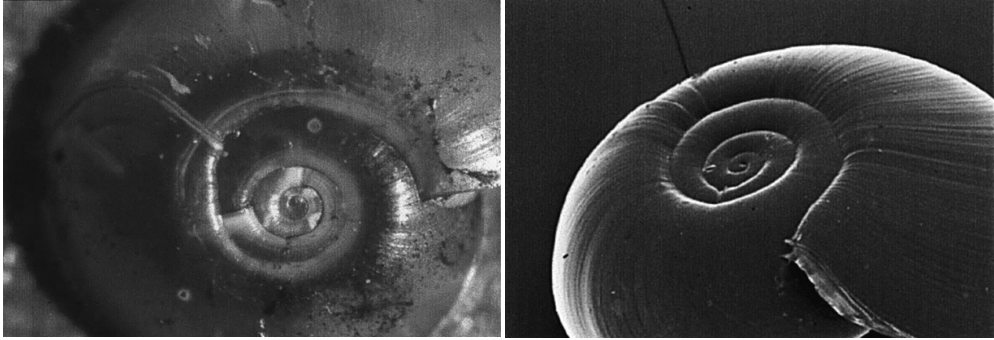


Fig. 2 Details of sculpturing on *S. nitida*. Left, photograph of spire region; photo Graham Rix. Right, scanning electron micrograph of spire region; photo Michael Proctor

young ram's-horn snails can be identified in the field with the use of a x10 hand lens; the overall shape changes little with age although the numbers of whorls may increase.

BEHAVIOUR OF THE LIVING SNAIL

In spite of all these differences of opinion on handedness, when taking into account both the architecture of the aperture lip and the behaviour of the live animal, there can be little doubt that the shell is dextral. If we follow this line, then the animal will emerge with the further-projecting part of the aperture above its head, making it quicker and easier to obtain a purchase on the substrate over the shorter lower lip, the upper extended lip of the aperture acting as a 'porch' to the aperture. Experiments with *Segmentina nitida* have shown that if the animal is placed in this position in a dish (Fig. 3), it immediately emerges and moves forward. If placed upside down with the 'porch' nearest the substrate, it manoeuvres itself to turn the shell over before crawling (Hill-Cottingham 2004). This points up the importance of observation of the living animal. Other species which do this quite obviously are *Anisus vortex*, *Gyraulus crista* and *Hippeutis complanatus*; they also crawl flat on the surface and right themselves on emerging. Other species, such as *Planorbarius corneus*, usually hold their shell at an angle to the substrate but the upper surface forms the greater angle to the vertical.

Some species such as *Planorbis planorbis*, whilst adhering to the substrate at an angle, may also be seen hanging from the water surface. Another example of the latter is *Bathyomphalus contortus* and, in this species, the degree of overhang of the upper side of the aperture is less marked.

IS THE STRUCTURE OF THE SHELL THE BEST GUIDE TO HANDEDNESS?

We are left with a paradox. Either we adhere to the shell topography in determining handedness or we assume that handedness of the shell is linked to the positioning of the respiratory and genital ducts and the arrangement of internal organs. It seems to me more likely that the Planorbiidae are a more distinct evolutionary family than has been hitherto accepted and that further studies, perhaps in DNA analysis, may well reveal other differences separating them more clearly from other freshwater gastropods. A possible example is the presence of haemoglobin as the respiratory pigment in the ram's-horn snails. In view of the behaviour of the animals themselves as well as the details of shell structure, one can only conclude that the Planorbiidae are dextral.

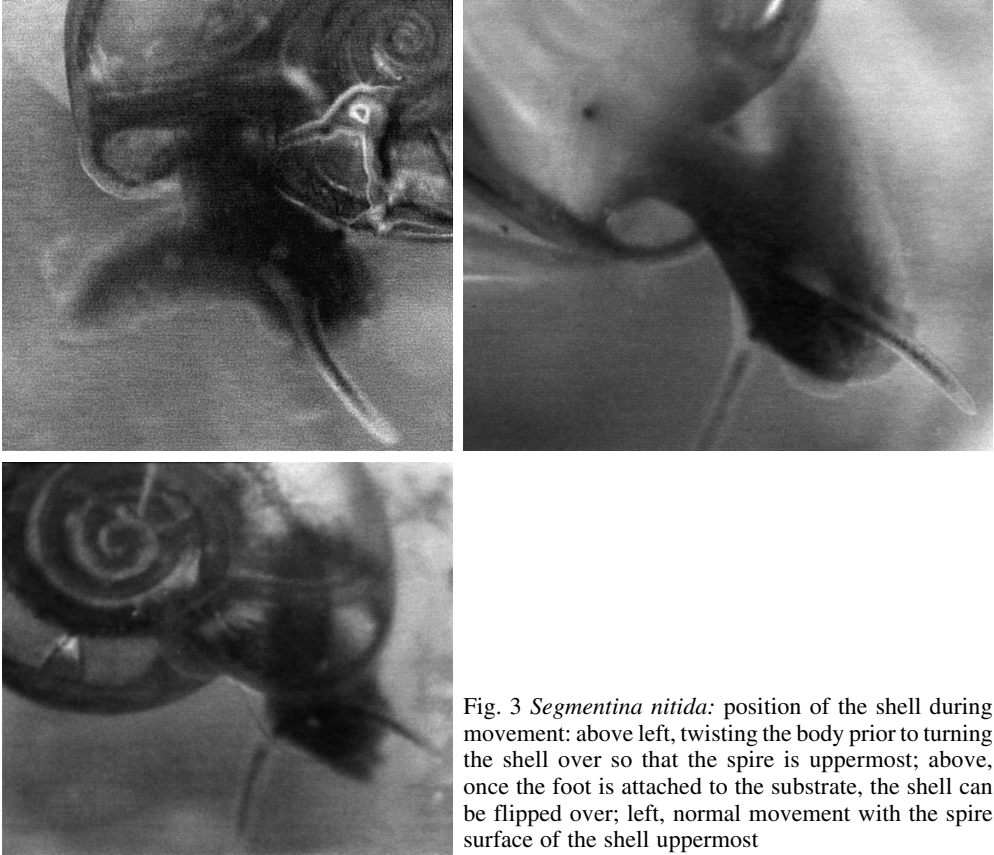


Fig. 3 *Segmentina nitida*: position of the shell during movement: above left, twisting the body prior to turning the shell over so that the spire is uppermost; above, once the foot is attached to the substrate, the shell can be flipped over; left, normal movement with the spire surface of the shell uppermost

The best solution therefore, is to adopt Reeve's definition that '*the upper disk of the shell is the side on which the margin of the aperture is the most advanced in growth.*'

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Pat Hill-Cottingham is a former teacher and environmental consultant, who has recently gained her PhD on one of the Planorbisid snails – *Segmentina nitida*, and who specialises in the invertebrate fauna of ditches.

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