

A twist of nature: a left-handed *Bythinella schmidtii* (Küster, 1852) (Caenogastropoda: Bythinellidae)

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Abstract. As most extant snails, *Bythinella schmidtii* is characterised by dextral (right-handed) coiling of the shell. Nevertheless, a small sinistral (left-handed) individual from the spring on a mountain pasture was sampled, together with its larger dextral conspecifics. In our report on this first case of sinistrality within the superfamily Truncatelloidea, we discuss its shell abnormalities and provide a review on chirality in snails.

Key words: *Bythinella*, sinistrality, shell abnormalities, spring, Slovenia

Izvleček. Zasuk narave: levosučna *Bythinella schmidtii* (Küster, 1852) (Caenogastropoda: Bythinellidae) – Kot za večino obstoječih vrst je tudi za vrsto *Bythinella schmidtii* značilna desnosučnost, torej zavrtost hišice v smeri urinega kazalca. A v izviru na planinskem pašniku smo med večjimi desnosučnimi sovrstniki našli tudi majhnega levosučneža te vrste. V poročilu o prvem primeru levosučnosti znotraj naddružine Truncatelloidea obravnavamo opažene nepravilnosti v zgradbi hišice in podajamo pregled objav o sučnosti polžev.

Gljučne besede: *Bythinella*, levosučnost, nepravilnosti hišice, izvir, Slovenija

Introduction

Handedness is the phenomenon relating to the ability to classify chiral objects into right- and left-handed. Most snail species in nature show either uniform right- or left-handedness. Sinistral species are rare, especially in the marine realm, where such taxa have independently originated only 19 times among Cenozoic gastropod clades (Vermeij 2002). Some 90–99% of snail species exhibit dextral shell coiling (Asami 1993, van Batenburg & Gittenberger 1996); i.e., when oriented with the shell apex pointing upwards and the shell's aperture opening facing the viewer, the opening is on the right-hand side. However, a few cases of the consistent mirror-image shell coiling within the same snail species exist as well. The earliest discovery of a single-gene mutation that can cause a complete left-to-right and right-to-left inversion of the body axis was made on pond snails *Lymnaea stagnalis* (Linnaeus, 1758) and

Radix peregra (O. F. Müller, 1774), which is nowadays synonymized with *R. baltica* (Linnaeus, 1758). Moreover, this was the first maternal effect gene mutation discovered (Freeman & Lundelius 1982, Gurdon 2005). Both snails have been used to study asymmetry for more than 120 years (references listed in Liu et al. 2013) and the sinistral individuals are reported to represent up to 2% of their populations (Wandelt & Nagy 2004; while one author of this notice (AF) did not find a single sinistral individual among about 3,000 examined *R. peregra* from Poland). On the other hand, in the south-east-Asian tree snail *Amphidromus* (*Amphidromus*) *inversus* O. F. Müller, 1774, and some 30 other species from this subgenus, dextrals and sinistrals appear at about even rates (Craze et al. 2006, Sutcharit et al. 2007, Schilthuizen & Haase 2010). Their balanced chiral dimorphism is one of the extremely rare cases of genetic antisymmetry. In most other snail species, such reversals of asymmetry are rather exceptional. Among thousands of right-handed shells there may be one or the other unique sinistral specimen, which are informally referred to as snail kings. These »*conchylia sinistralia*« can be found as special addition to different shell collections from the Renaissance era onwards. Such findings have been reported already from the Cambrian (Parkhaev 2007) to the Cenozoic (Pierce 1996).

Within the uniformly dextral superfamily Truncatelloidea, the genus *Bythinella* Moquin-Tandon, 1856 comprises tiny (2–4 mm shell height) dioecious freshwater snails belonging to the family Bythinellidae. It has been demonstrated that it is impossible to identify and separate out *Bythinella* species without molecular data (Falniowski & Szarowska 2011), although the morphology must be considered in identification as well (Bichain et al. 2007, Haase et al. 2007). More than 120 recognised species and subspecies occur in springs, caves and groundwater (Giusti & Pezzoli 1977, Falniowski 1987, Yildirim et al. 2006) from northern Africa and NE Spain across central Europe to W Turkey, with at least two richness centres in France and the Balkans (Glöer & Pešić 2014). Many taxa are liable to become endangered due to their limited range and vulnerable habitat.

While checking for the presence of *Belgrandiella* A.J. Wagner, 1927 in the Karavanke Mountains (Slovenia), several specimens of *Bythinella* were found in a spring. It was only when the individuals were examined in the laboratory under the stereo microscope that it turned out that among dextral *Bythinella* cf. *schmidti* (Küster, 1852) much smaller snail king of the species was present as well. Here, we present this first case of sinistrality within the superfamily Truncatelloidea.

Materials and methods

Several live miniature snails were collected from the stones in a small spring bubbling up just beside a marked trail to Kofce mountain chalet (N Slovenia) by the first author of this article (SP). Forceps were used to remove individuals from the stones and put into the plastic vial filled with spring water. The spring is located on a pasture grazed by livestock some 50 m above the Matizovec farm, north-east of Podljubelj village (N of the town Tržič, 1100 m a.s.l., coordinates; 46°24'55.56"N 14°18'30.0"E) (Fig. 1).

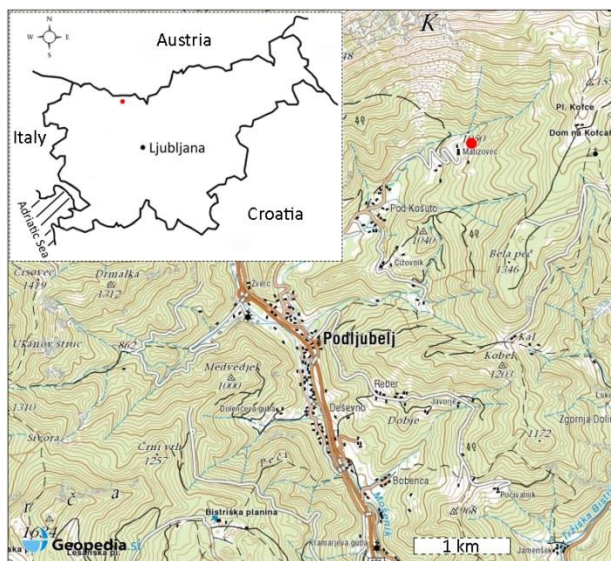


Figure 1. Map showing locality inhabited by left-handed individual of *Bythinella cf. schmidtii*. The base map was taken from the portal geopedia.si.

Slika 1. Lokacija izvira, kjer je bil najden levosučni osebek vrste *Bythinella cf. schmidtii*. Osnovna karta je bila vzeta s portala geopedia.si.

Results and discussion

The sinistral specimen (Figs. 2A–B) is not a mirror image of its dextral conspecifics (Figs. 2C–E): there are fewer whorls present, the suture is deeper (Fig. 2A), the shell shows scalarity (tendency to open coiling) (Fig. 2B) and the umbilicus is abnormally broad (Fig. 2B). In addition, it is about twice smaller than the dextral ones. Despite its smallness, the specimen seems to be adult or nearly adult since the shell aperture is surrounded by abnormally broad and prominent lip (Fig. 2A).

Coiling direction in snails, studied mainly in pulmonates, is known as determined by a single Mendelian locus. Either the »dextral« or »sinistral« allele is dominant (Schilthuizen & Davison 2005, Schilthuizen & Haase 2010), even though Utsuno & Asami (2010) discovered also a chirality randomizing gene in *Bradybaena*. The long history of various, not necessarily correct theories about the genetic background of the chirality (the so-called maternal inheritance) (e.g. Boycott & Diver 1923, Sturtevant 1923, Diver et al., Boycott & Garstang 1925) was caused by the fact, that phenotypical expression of this maternal effect gene is delayed by a generation. Since the opposite direction of the shell coiling results in the mirror organization of the ventral sac and pallial organs, such conspecifics can't orient their bodies for copulation, which leads to interchiral reproductive isolation.



Figure 2. Shells of *Bythinella* cf. *schmidti* from the spring above the Matizovec farm (Podljubelj): A–B - sinistral specimen, C–E - "normal", dextral specimens; a bar equals 0.5 mm (photo: A. Falniowski).

Slika 2. Polžki vrste *Bythinella* cf. *schmidti* iz izvira nad kmetijo Matizovec (Podljubelj): A–B – levosučni ošebek, C–E – "normalni" desnouščni ošebki; merilce meri 0.5 mm (foto: A. Falniowski).

Nevertheless, the latter is usually due to behavioral rather than purely physical constraints, thus possibly promoting saltational, single-gene and sympatric speciation (Asami et al. 1998, Gittenberger 1988, Schilthuizen & Davison 2005, Davison et al. 2009). This and other hypotheses about evolution and persistence of sinistral lineages have been tested using computer simulations (e.g. Johnson et al. 1990, Orr 1991, van Batenburg & Gittenberger 1996, Stone & Björklund 2002) and through study of populations (e.g. Asami 1993, Asami et al. 1998, Ueshima & Asami 2003, Davison et al. 2005, Schilthuizen et al. 2005, Schilthuizen et al. 2007, Sutcharit et al. 2007). Importantly, Davison et al. (2005, p. 1569) noted that, precisely due to the maternal effect gene, the reproductive isolation is unstable. While some researchers suggested the possibility of one-gene saltational sympatric speciation (e.g. Ueshima & Asami 2003), some other remained unconvinced (e.g. Davison et al. 2005, Schilthuizen & Davison 2005) due to individual cases that show almost balanced intra-population coil dimorphism (i.e. previously mentioned species in the subgenus *Amphidromus*). Such dimorphism is probably maintained by sexual selection favouring mates of the opposite chirality (Sutcharit et al. 2007, Schilthuizen et al. 2007, Schilthuizen & Looijestijn 2009). However, in hermaphroditic pulmonates, a population of new sinistral species could also be established through self-fertilization of the sole sinistral individual, despite their effective behavioural restrictions against interchiral copulation. In dioecious caenogastropods, like *Bythinella*, this is not possible. Vermeij (2002) has demonstrated that among living dioecious sinistral neogastropods, all have a nonpelagic (intracapsular) development. This confirms that a new (sub)population of sinistral snails within such population of dextrals may evolve only if the offspring of a parent is not scattered across larger area.

Shell abnormalities are not a typical feature of snail kings, although anomalies associated with sinistrality have been reported in *Lymnaea stagnalis* (Asami 2007), *Achatinella* (Asami 2001), *Conus adversarius* (Hendricks 2009) and *Bradybaena* (Utsuno & Asami 2007). Also, Shibasaki et al. (2004) have demonstrated that the oppositely coiling embryos of *L. stagnalis* are not the perfect mirror images of one another. The observed shell abnormality of our *Bythinella*, i.e. its slight scalarity, deeper suture, broader umbilicus and smallness, can be due to pleiotropic effects resulting from incompatibility of the reversed chirality and the rest of the genomic and developmental environment, causing a reduction of fitness. Similar irregularities have been reported in *Cerion* (Gould et al. 1985) and *Partula suturalis*, in which the sinistral shells are somewhat lower and squatter (Gould et al. 1985, Johnson 1987, Johnson et al. 1993, Davison et al. 2009). Our snail king's pronounced dwarfism is most likely not reflecting possible damage inflicted in an early stage of life, but rather another generation, whose development took place in harsh conditions (e.g., during winter). This is not a rare phenomenon among hydrobioid members (Wilke & Falniowski 2001, Falniowski et al. 2012).

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