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Gastropoda

Behavioural and anatomical observations of the amphibious snail *Pirenella conica* (Gastropoda: Potamididae)

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Abstract

The coastal snail *Pirenella conica* (Gastropoda: Potamididae) was observed and photographed in its mud flat habitat (Alaçati Bay, Karaburun Peninsula, Türkiye) and in the laboratory. The snails were amphibious; they moved about in damp sediment when the sea had receded and readily left the water in the laboratory to move on dry surfaces. The siphon, normally used for the intake of oxygenated water in submerged snails, remained open when snails were out of water, suggesting that they can also breathe air. Videos of snails taken from below explained the mechanics of their stop-and-go locomotion. Close-up photographs also revealed the presence of a pallial eye at the top of the siphonal canal. When a snail was partially buried in soft sediment, its pallial eye remained above the sediment. The pallial eye may orient the snail and help it detect potential dangers when its tentacular eyes are obstructed.

Introduction

The snail *Pirenella conica* (Blainville, 1829), family Potamididae, usually lives in shallow muddy sand and tolerates a wide range of salinities from as low as 5 ppt up to ~100 ppt (Taraschewski & Paperna 1981, Reid & Ozawa 2016). Its distribution range covers the entire Mediterranean and the Red Sea, extends south along the east coast of Africa and east around the Arabian Peninsula all the way to the southern tip of India (Reid & Ozawa 2016). *Pirenella conica* is quite variable in its shell characteristics and although comparisons of DNA sequences indicated the conspecificity of individuals from different populations, additional work is necessary to better understand intraspecific variation (Reid and Ozawa 2016). A recent guide to the marine mollusks of Europe opined that *P. conica* may be a species complex (Alf et al. 2020). Anatomy, ecology, and shell characteristics of the species have been studied (Demian et al. 1966, Taraschewski and Paperna 1981, Sacchi et al. 1987), but published accounts of its behaviour, locomotion and ecological interpretations of its anatomy are sparse or nonexistent.

While exploring the north coast of Alaçati Bay, on the south coast of the Karaburun Peninsula, Türkiye (38.2605 N, 26.3830 E) during the early summer of 2011, I discovered a populous colony of *P. conica*. This initiated a series of observations of the snails both in the field and in the laboratory that were documented with photographs and videos. Subsequent examinations of the data revealed information about the snail's locomotion and anatomy. I am reporting my findings here in hopes of filling in gaps in the information available about the biology of this species. Behavioural and anatomical observations such as those reported here may also contribute to the resolution of the taxonomy of this species.

Methods

I carried out the observations reported here between June and early July sporadically over several years starting in 2011 and ending in 2022. Live snails were photographed and filmed under natural conditions in their habitat and in a makeshift laboratory set up in a summer house. Removal of snails to a laboratory was necessary to obtain better close-up photographs and videos. In the laboratory snails were allowed to move either in sea water in a plastic dish or outside of water on glass plates. Snails moving outside of water on glass plates were filmed from the front or the side. Snails moving in sea water in a plastic dish with a clear bottom were filmed from above and below. Salinities were measured with a hand-held salinity refractometer. Sixty-four dry shells and eight alcohol specimens have been deposited in the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A. (CM 182584). Anatomical terms are according to Houbrick (1984).

Identification and characteristics of the snails

Shells collected at the study area matched the photographs and descriptions of *P. conica* (Figure 1) (Reid & Ozawa 2016, Alf et al. 2020). Among the 216 shells examined, the tallest shell (missing its apical whorls) was 23.0 mm long, whereas the tallest shell with an intact protoconch was 16.7 mm long. All shells taller than 16.7 mm and many shorter ones lacked their protoconchs and sometimes additional apical whorls. Loss of apical whorls was not a postmortem process, because even live snails lacked them (Figures 4, 5). The protoconch (embryonic or larval shell) is brown, with about 1.5 whorls (Figure 1), smooth surface, which at high magnifications shows the presence of fine ridges and depressions. These characteristics of the protoconch agree with the description and photographs in Kowalke (2001). Faint spirals were visible on the initial whorls of the adult shell or teleoconch (Figure 1).

Snails in their habitat

The snails were found in an intertidal mudflat about 800 m wide along the coastline at the north shore of Alaçati Bay. On several occasions, especially during periods of strong northerly winds, the sea receded towards the south exposing large areas of mudflats. On those occasions I observed thousands of *P. conica* stranded in mud, sand and in shallow pools of water cut off from the receded sea (Figure 2). On 11 July 2012 the salinity of a water sample from a shallow pool containing many active snails was 51 ppt. In comparison, salinity near the rocky coast about 2 km south of the study area was 40 ppt in agreement with the normal salinity of coastal waters of the eastern Aegean Sea (Eronat and Sayin 2014). In areas where the sediment was wet, snails remained active and moved through the sediment leaving tracks behind. Snails that were stranded closer to the shore where the sand dried out in the sun withdrew into their shells and became inactive. On one occasion I collected 186 shells from dry sand and placed them in seawater in the laboratory. About 12 hours later 124 snails were active.

Locomotion of *P. conica*

In the laboratory snails displayed a tendency to crawl out of the water (Figure 3). Snails moving in or outside of water on a smooth surface exhibited a jerky progression. Videos of snails taken from below revealed the following three stages in their locomotion (Figure 4):

1. Foot moves forward, then stops.
2. Sole widens while foot remains stationary.
3. Shell is pulled forward while foot remains stationary.

These three stages constituted one unit of movement, which, when repeated successively, resulted in the stop-and-go locomotion of *P. conica*. The widening of the sole in stage 2 was especially noticeable in its anterior half. While a snail was moving its snout almost constantly moved from side to side with its tip often in contact with the surface. I observed this behaviour in the laboratory when snails were moving in sea water on a smooth surface and when they were partially buried in sediment. Snails moving on a glass plate outside of water displayed the same behaviour. Although it looked as if the snail was using its snout as a support when it was pulling its shell, in one video taken from the side of a snail on a glass plate there were instances when the snout was raised from the surface while the shell was being pulled. Snails exhibited the same jerky progression when they were moving in sediment in their natural habitat. Their movements seemed laborious in soft sediment.

Figure 1: A *P. conica* shell (height, 22.4 mm; protoconch missing) and the protoconch of a smaller shell from the top and the side. **sc**, siphonal canal.

Figure 2: Habitat of *P. conica* on 12 June 2016. Sea had receded exposing thousands of snails on the muddy sediment. Tracks of snails moving about are visible in the foreground.

Figure 3: Captive snails climbing out of the water.

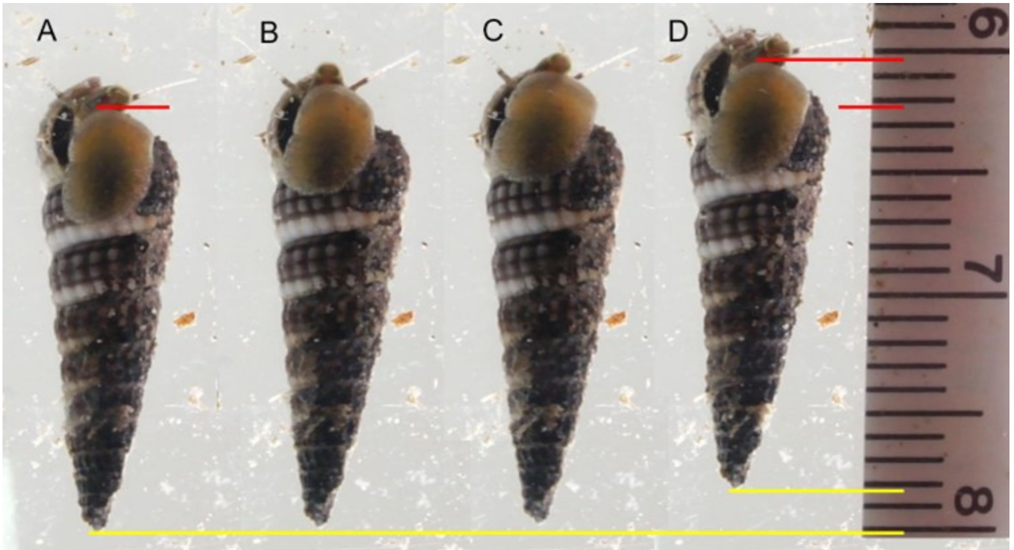

Figure 4: Frames from a video of a *P. conica* filmed from below. The snail was moving horizontally in sea water alongside a millimetric ruler on the bottom of a plastic container. **A.** Beginning of stage 1 during which the foot moves forward. **B.** Beginning of stage 2 when the foot becomes stationary, anterior foot starts to widen. **C.** End of stage 2 when the anterior foot is widest, the shell begins to move forward. **D.** End of stage 3 when the shell stops moving. Red and yellow lines mark the starting and ending positions of the anterior foot and the shell apex, respectively. The three stages constituted one unit of movement that took about 4 s, during which both the foot and the shell moved forward about 2 mm. Apical whorls of the shell were missing.

Eyes of *P. conica*

The snails have a pair of narrow cephalic tentacles. The slightly wider proximal stalk of each tentacle extended about a fourth of the total length of the tentacle and carried a small eye on its dorsal surface (Figure 5). When a snail was fully immersed in sea water without any obstructing sediment, its tentacles usually stretched out at an angle between 105 and 125°, with the eyes pointing upwards (Figure 5). Snails outside of water could not hold their tentacles erect, becoming limpid and stuck to the snout or the foot (Figure 6).

The notch present at the anterior columellar border of the aperture, the siphonal canal (Figure 1), was lined by the edge of the mantle forming the siphon into the mantle cavity. While examining close-up photographs of snails taken outside of water in the laboratory, I noticed the presence of a dark pallial eye at the edge of the mantle bordering the top of the siphonal canal (Figure 6). When a snail was fully withdrawn into its shell with its operculum closing the aperture, the pallial eye remained visible at the edge of the siphonal canal (Figure 7). During crawling the pallial eye occupied a more central and higher vantage point than the tentacular eyes. When a snail was moving in soft sediment, its snout and tentacles were usually buried in the sediment, but the pallial eye often remained above the sediment (Figure 8). Close-up photographs also showed a diffuse green patch on each side of mouth at the tip of the snout of some snails (Figure 6).

Discussion

Shell dimensions of *P. conica* given in the literature are variable. For example, the maximum shell lengths of *P. conica* from different localities in Egypt ranged from 13.5 mm to 32 mm (Demian et al. 1966). The mean shell lengths of snails from several localities along the coast of Sardinia ranged from 13 mm to 25 mm (Sacchi et al. 1987).

Figure 5: A *P. conica* in sea water. Apical whorls of the shell were missing. **sn**, snout; **te**, eyes on cephalic tentacles.

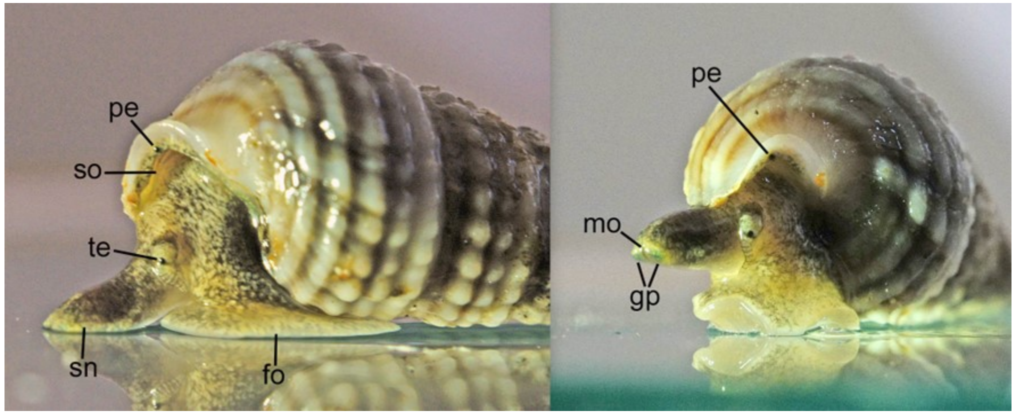

Figure 6: A captive *P. conica* outside of water on a glass plate. Cephalic tentacles were stuck to the snout, or the foot and the siphon was open. **fo**, foot; **gp**, green patches; **mo**, mouth; **pe**, pallial eye; **sn**, snout; **so**, siphonal opening; **te**, eyes on cephalic tentacles.

The maximum shell length of 23.0 mm measured in the present study falls within literature ranges. Besides genetic and environmental factors that probably control shell dimensions, the difficulty of determining whether a given snail is an adult and the somewhat random reduction in shell heights resulting from loss of apical whorls should be considered when comparing shell dimensions of spatially or temporally separated samples.

The locomotion of *P. conica* falls under the category “Type 1 discontinuous” of Miller’s (1974) classification of locomotion of marine gastropods. However, I have treated the widening of the sole as a separate stage rather than combining it with the pulling of the shell forward as Miller did. Widening of the sole of *P. conica* during stage 2 of a unit of movement presumably helps the sole form a stronger attachment to the surface and prevents the snail from sliding backward when pulling its shell forward. I have based this tentative conclusion on observations of snails moving on smooth glass or plastic surfaces; it is not clear whether the sole can also act as an anchor when a snail is moving in soft sediment, its natural habitat. Perhaps, when it is moving in sediment the snail indeed uses its snout to anchor itself during stage 3.

The green patches observed on the snout tip of the snails have not been reported in the literature before (Figure 6). I do not know the significance of this observation at present.

The presence of a pallial eye in *P. conica* was first reported by Demian et al. (1966). To my knowledge, this fact has not been mentioned again in the literature, including in recent taxonomic treatments (Reid & Ozawa 2016, Alf et al. 2020). These omissions may have been due to the difficulty of noticing the pallial eye in live snails unless one is examining the snails under magnification. Several other species in the family Potamididae have pallial eyes (Houbrick 1984, Reid & Ozawa 2016). Possible functions of this curious anatomical feature have

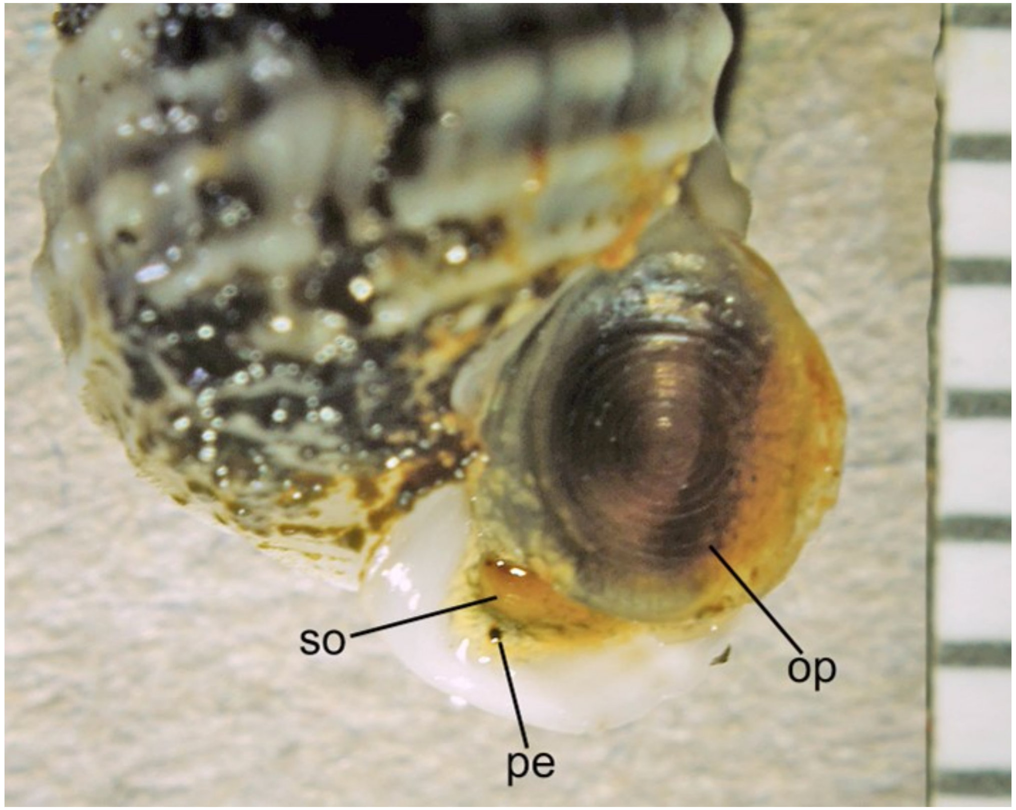

Figure 7: Shell aperture of a live *P. conica* withdrawn into its shell. Ruler is millimetric. **op**, operculum; **pe**, pallial eye; **so**, siphonal opening.

Figure 8: Video frame of two snails moving in soft sediment in a shallow pool in the field. Both snails had their snouts and tentacles buried in sediment. The pallial eye of the snail in the front (arrow) remained above the sediment and was presumably providing visual clues to the snail.

rarely been discussed in the literature. Speculations about the functions of the eyes, tentacular or pallial, of these snails assume that they can "see" to some extent, although what they can see is not known. The pallial eyes of *Cerithideopsis* species have a lens (Houbrick 1984) and some sort of image formation would, therefore, be expected. The pallial eye in *Cerithideopsis* species also remains at the edge of the aperture next to the operculum when a snail is withdrawn into its shell. Houbrick (1984) speculated that the pallial eye may allow snails to scan their surroundings (presumably for predators) prior to extending their bodies out of their shells. Demian et al. (1966) did not mention whether a lens was present in the pallial eye of *P. conica* but noted that there was a nerve exiting the eye.

The pallial eye of *P. conica* occupied a more medial and higher vantage point than the tentacular eyes (Figure 6). When a snail was in soft sediment, its snout and tentacles were often buried, but the pallial eye remained above the sediment (Figure 8). Thus, the pallial eye may enable the snail to orient itself and to detect obstacles and potential predators when its tentacular eyes are obstructed. When *P. conica* was outside of water its tentacles became limpid and stuck to the snout or the foot (Figure 6). It is not known how this condition interferes with the sensory functioning of the tentacles and the eyes on them. In contrast, the consistency of the mantle border that carries the pallial eye did not appear to be affected by exposure to air. It is likely that the functioning and the visual field of the pallial eye remain unchanged in air.

Although *P. conica* is a marine species, it has evolved semi-terrestrial adaptations that enable it not only to survive, but also to carry out some of its basic activities outside of water usually in microhabitats of high humidity. My observations show that the snails do not hesitate to leave water and can remain active outside of water–not only at the seashore, but also under rather unnatural conditions in the laboratory. I was able to revive by placing in sea water a considerable fraction of snails collected in dry sand. However, it is not known how long the snails can remain alive without access to sea water. In marine gastropods the siphon serves for the entry of oxygenated water into the mantle cavity and to the gill therein. When out of water *P. conica* keeps its siphon open (Figures 6, 7). This indicates snails can breathe air. On the other hand, in fully terrestrial snails (for example, pulmonates) the tentacles are always erect when a snail's head is outside its shell. The inability of *P. conica* to keep its tentacles erect when it is outside of water (Figure 6) is an indication of the evolutionarily intermediate position it occupies between fully marine and fully terrestrial snails.

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