

SURFACE CRAWLING AND PEDAL SURFACE COLLECTING IN AQUATIC GASTROPODS: A CASE OF SCIENTIFIC AMNESIA

WINFRIED S. PETERS^{1,2}

¹ School of Biological Science, Washington State University, Pullman WA 99614, USA

² Department of Biology, Purdue University Fort Wayne, Fort Wayne IN 46835, USA
(e-mail: petersw@pfw.edu);  <https://orcid.org/0000-0002-5061-1497>

ABSTRACT: Aquatic gastropods, both freshwater and marine, often crawl along the water surface with the sole of the foot facing upward. Differential regulation of the activity of cilia on the sole turns the gliding mechanism into pedal surface collecting, by which food particles floating on the water are collected on the sole. Over the last 300 years, surface crawling and pedal surface collecting have been studied in numerous species, but the accumulated knowledge has fallen victim to scientific amnesia. Today, pedal surface collecting usually is considered a unique behaviour that evolved in the family Ampullariidae (Caenogastropoda), which includes the genus *Pomacea* with some of the globally worst invasive pests. Consequently it may appear feasible to tackle invasive *Pomacea* species specifically by delivering molluscicides via the water surface. Based on a review of our forgotten literature, I here argue that such an approach would have potentially devastating, unintended effects on native gastropod faunas.

KEY WORDS: Ampullariidae; invasive apple snail; pedal surface collecting; *Pomacea*; surface-crawling locomotion

INTRODUCTION: SCIENTIFIC AMNESIA

Aquatic gastropods like the great pond snail (*Lymnaea stagnalis* [L., 1758]; Lymnaeidae), a common holarctic omnivore, frequently move along the water surface (Fig. 1). Observing such common behaviour in the wild or in captivity is as easy as observing gastropods emerging from their shells, and hypotheses concerning the mechanism(s) of surface crawling have been developed and discussed since at least the 18th century. Modern malacologists addressing malacologist audiences therefore feel no need to explain what surface crawling is. When surface crawling is mentioned in the malacological primary literature where it is not the actual object of study, it is hardly ever described in detail (for instance, [PYRON & BROWN 2015](#): p. 388; for a recent example in this journal, see [LOMBARDO et al. 2021](#): table 1 on p. 124).

When students unfamiliar with a species' natural history notice a lack of explicit descriptions of its common activities in the recent literature, they

may conclude that the species' behaviour is poorly known. This seems likely to happen when a species becomes a 'model system' (as *L. stagnalis* did; [DAVISON & NEIMAN 2021](#)) for laboratory studies that are conducted by scholars who not necessarily are experts in the species' behavioural ecology. For example, [AONO et al. \(2008](#): p. 272) reported surface crawling in *L. stagnalis*, stating that "little is known about the mechanism of this upside-down gliding". Seemingly unaware of the older and some of the not-so-old literature, the authors apparently thought they had discovered "that upside-down gliding is an efficient active process involving the secretion of mucus ... to serve as a substrate upon which cilia beat to cause locomotion at the underside of the water surface" ([AONO et al. 2008](#): p. 272). Having passed peer review at *Biological Bulletin*, a well-respected international journal with a focus on neurobiology and behaviour, the paper has been cited eight times



according to the Clarivate Web-of-Science database (accessed through the library system of Washington State University on 26 June 2022). This figure is not insignificant; half of the 47 papers published in the same year that had the word ‘*Lymnaea*’ in their titles were cited less frequently. One has to conclude that readily accessible published knowledge has become terra incognita for parts of the community working in the field. In fact, locomotion was not mentioned in a recent review that explicitly claimed to “present the essential background information on the natural history of this freshwater snail” for scholars employing

L. stagnalis as a model in diverse disciplines (FODOR et al. 2020: p. 2). The scientific amnesia also covers pedal surface collecting, a type of surface-feeding behaviour that is closely related mechanistically to surface-crawling locomotion. Such unawareness of existing knowledge can foster misjudgments with potentially severe ecological consequences. Here I review classical work on surface-crawling locomotion and pedal surface collecting, hoping to clarify how our forgotten knowledge bears on current efforts to contain some of the globally most devastating invasive pests.

SURFACE CRAWLING LOCOMOTION, A BRIEF HISTORY

Attempting to identify the discoverer of a common natural phenomenon that everybody can easily observe would be naive. This certainly holds for the surface crawling of aquatic gastropods, and one must expect to find casual references to this behaviour in the older literature. For example, Martin Lister mentioned that “aquatiles vero cochleae, ope pedis, in summa aqua expansi quasi pendent, natantque” (aquatic snails use their foot to hang, as it were, suspended from the top of the water and swim; LISTER 1694: p. 8. All translations are my own). The earliest explicit statement concerning the mechanism of surface crawling that I am aware of is by Richard Bradley, who suggested that air serves the same mechanical role for surface-crawling snails as hard substrates do for animals creeping on the ground:

“The periwinkles or watersnails, whether in the sea or in the rivers, have the same mode of motion; we may observe them swimming on the surface of the waters, with their whole body and shell reversed in the water; so that they seem to take hold of the air, and to receive that resistance from it, which common snails do from the earth, or other solid bodies which they creep upon” (BRADLEY 1721: p. 56).

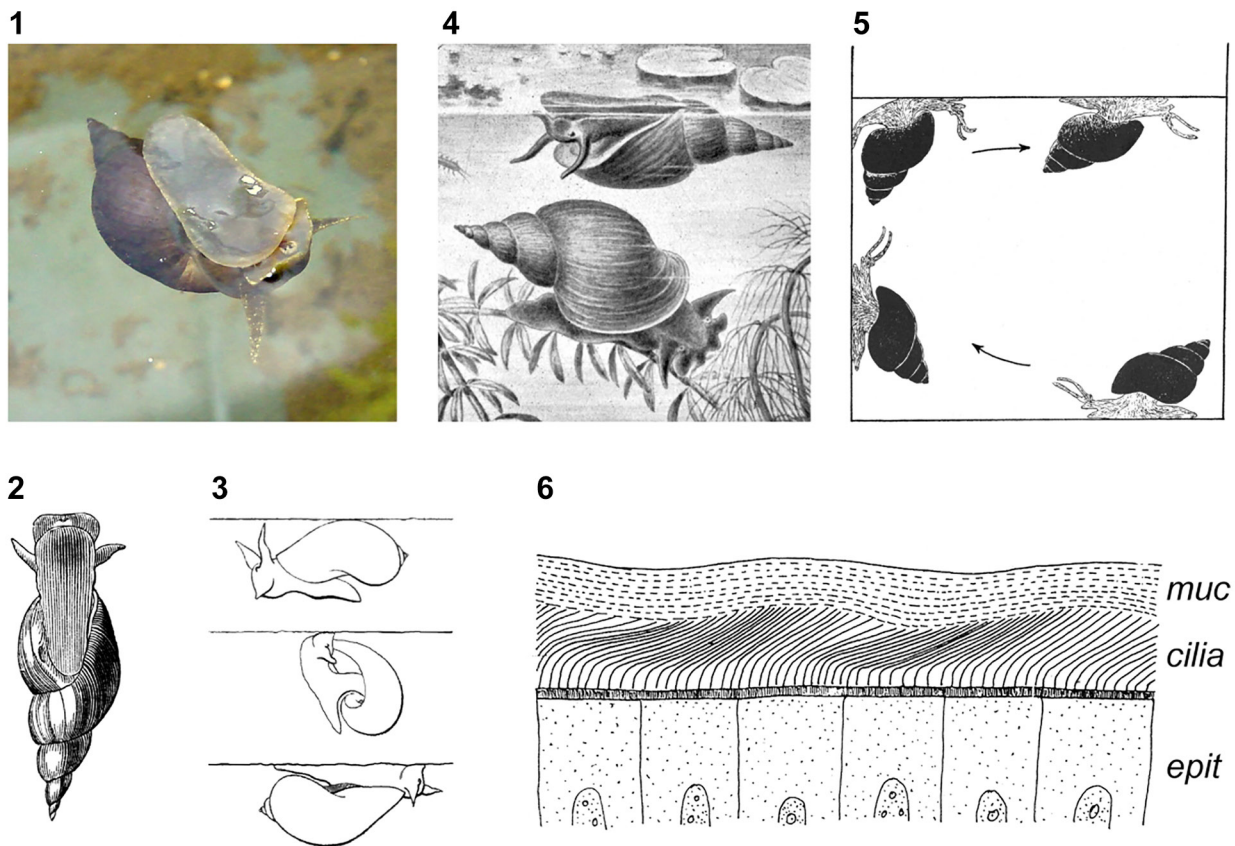
It is noteworthy that Bradley speaks of both freshwater snails (compare Figs 1–4) and marine species (compare Fig. 5). Evidently he was not considering an exotic phenomenon rarely seen in a few specific animals, but a commonly observed behaviour exhibited by various inhabitants of different habitats.

In the early 19th century, surface crawling in marine slugs was reported by ANTOINE RISSO (1826: *Duvaucelia manicata* [Deshayes, 1853]; *Philinopsis depicta* [Renier, 1807]) and discussed in some detail by ARMAND DE QUATREFAGES (1843: *Aeolidiella glauca* [Alder et Hancock, 1845]). The latter author noted that while it was known that “presque tous les Gastéropodes” (almost all gastropods) were able to crawl hanging down from the water surface, the mechanism of surface crawling had remained obscure. He rejected BRADLEY’S (1721) hypothesis cited above,

pointing to the much larger density of water compared to air: it seemed physically impossible that the sole of the gastropod’s foot acting on air could produce the force required to overcome the mechanical resistance of water. As an alternative, DE QUATREFAGES (1843: pp. 309–310) transferred the locomotory mechanism known to operate in planarians to molluscs. He had observed cilia on the entire body surface of *Aeolidiella*, and suggested that these cilia – not necessarily those on the sole – produced the force that drove the movement of surface-crawling gastropods.

To my knowledge, the first printed image of a snail moving along the water-air interface was GEORGE JOHNSTON’S (1850) *Lymnaea* in the characteristic surface-crawling posture seen from above (Fig. 2). The description accompanying this figure summarized common knowledge of the time and deserves to be quoted at length:

“All gasteropods are not confined, however, to crawl on the solid bottom: many of them can ascend to the surface, and make the water a liquid pavement, along which they creep in the same manner as they do on land, with the difference only of having their body and shell in a reversed position. The *Aplysiæ*, and many of our nudibranchial mollusca, may be seen crossing pools on our shore in this way; and there is reason to believe that all the marine naked mollusca possess the faculty [...] but it is the freshwater snails [...] which exhibit this not unremarkable mode of progression in the most perfect manner. On a summer’s day any one may see *Limnæi* [reference to the drawing reproduced here as Fig. 2] and *Planorbes* thus traversing the surface of ponds and ditches in an easy undulating line; or suspended there in luxurious repose [...] When thus suspended they will sometimes relax their hold and drop at once to the bottom, from which, in general, they emerge by crawling up some solid body; but occasionally I have seen them rise up direct through the water – a fact I can explain only by supposing that they have the power of compressing, in the first instance, the



Figs 1–6. Surface-crawling locomotion and its representation in the older literature: 1 – *Lymnaea stagnalis* crawling along the water surface (shell length 36 mm; animal from a pond in a forest near Frankfurt, west central Germany); 2 – The apparently first printed image of a surface-crawling gastropod by JOHNSTON (1850: fig. 21 on p. 129) presents a surface-crawling *Lymnaea* sp. seen from above; 3 – *Lymnaea ovata* floating under the water surface (top), turning over actively (center), and crawling along the surface (bottom; from WILLEM 1888: figs 2, 3, and 4 on the plate following p. 430); 4 – *Lymnaea stagnalis* crawling on submerged plants (bottom) and along the water surface (top; part of the plate following p. 192 in TASCHENBERG & SCHMIDT 1929); 5 – As an example of a surface-crawling marine species, *Peringia ulvae* is shown crawling up the wall of an aquarium to reach the water surface (NEWELL 1962: fig. 5 on p. 54; slightly modified); 6 – Cells of the epithelium (*epit*) of the sole of *Physella acuta*, showing the cilia acting on a mucus layer (*muc*; from KAISER 1960: fig. 2, labels added)

air in their pulmonary cavity, and of again allowing it to expand and dilate so as to render the body lighter than the medium in which they live” (JOHNSTON 1850: pp. 129–130).

JOHNSTON (1850: pp. 129–130) commented on the mechanism of surface crawling only in a footnote. He expressed doubts about the ciliary mechanism proposed by DE QUATREFAGES (1843), based on the observation that the movement of marine slugs along the water surface could stop while the cilia appeared to beat continuously. The possibility that this could be due to a switch from coordinated to non-coordinated ciliary beating seemed obvious to few researchers in the 19th century (e.g., BROCKMEIER 1887: p. 116).

A German translation of JOHNSTON’S (1850) above-quoted passage appeared in Brehms Thierleben, a popular encyclopedia of zoology that was widely distributed in central Europe in the late 19th century (SCHMIDT 1878: pp. 242–243; a later edition included

the image reproduced here as Fig. 4). While Oscar Schmidt emphasized the significance of cilia for movement, he followed Johnston regarding the role of air in the pulmonary cavity in producing buoyancy. This, however, seemed insufficient. SCHMIDT (1878: p. 243) noted that the sole of surface-crawling snails was slightly concave, and that snails sank immediately when they flattened the contour of their sole. He concluded that the somewhat boat-shaped foot actually worked like a boat, contributing to the buoyancy that kept surface-crawling animals afloat.

At the turn of the century, malacologists like HEINRICH BROCKMEIER (1887) maintained that ciliary action was too weak to propel macroscopic animals. If so, alternative mechanisms such as muscular waves had to be invoked. HEINRICH SIMROTH’S (1878, 1879) analyses of crawling land snails led him to conclude that a hydrostatic skeleton could not explain the locomotory process. He postulated that the muscular system of the gastropod foot consisted

not only of the usual contractile fibres but also of expansive one. While this hypothesis soon faced rejection (SOCHACZEWER 1881, CAR 1897, JORDAN 1901, CARLSON 1905), his observation of mucus tracks left by surface-crawling snails (including Lymnaeidae, Physidae, Planorbidae, and Viviparidae; SIMROTH 1882: pp. 28–30) had a lasting impact. SIMROTH (1882) realized that the animals did not glide along the water surface as such, but on a layer of non-wettable mucus that was less dense than water and did not mix with it. This ribbon of mucus was continuously expanded at the front part of the sole and driven backwards over the posterior margin of the foot into the water, providing the force that moved the snail forward.

Mucus tracks left on the water surface by freshwater snails were discovered independently by VICTOR WILLEM (1888), who reached similar conclusions concerning their role in surface crawling as SIMROTH (1882) had. ABIGAIL DIMON (1905: pp. 37–38) considered mucus essential for the surface crawling of two marine species (*Ecrobia truncata* [Vanatta, 1924], as *Rissoa minuta*; *Ilyanassa obsoleta* [Say, 1822], as *Nassa obsoleta*). But how did the snails push the mucus backwards across the posterior edge of the sole to generate forward thrust? JEAN DAWSON (1911: pp. 46–49) studied the production and movement of the mucus ribbon in some detail for *Physella* sp. and *L. stagnalis*. Movement of the animal and mucus flow both correlated with what appeared to be small-scale, irregular muscular contractions on the sole, but she refrained from claiming causal relationships. Less cautiously, HERBERT WALTER (1906: p. 31) concluded from his studies on the lymnaeid *Ladislavella elodes* (Say, 1821) (as *Lymnaeus elodes*) that “the mechanism of locomotion consists in a complex muscular foot clothed on the ventral surface with cilia which act on a mucus track”. At the time, problems with the routine detection of beating cilia prompted contradictory interpretations. For example, PARKER (1911: pp. 157–158) felt unable to explain the movements of *Ilyanassa obsoleta* as he found evidence neither for muscular waves nor for the presence of cilia on the sole of the foot. In contrast, MANTON COPELAND (1919) observed active cilia in the same species, performing experiments that established a correlation of speed of locomotion with the rate of ciliary activity. He also demonstrated cilium-mediated locomotion in *Neverita* species (Naticidae, Caenogastropoda), “the largest animals which have been reported as exhibiting ciliary locomotion” (COPELAND 1922: p. 132). While he observed surface crawling locomotion in this genus only once (COPELAND 1922: p. 133), the fact that the crawling on solid substrates of these large gastropods demonstrably was cilium-driven put BROCKMEIER’S (1887) argument concerning size limits for ciliary locomotion to rest.

In 1960, PETER KAISER set out to settle lingering doubts about the mechanism of surface crawling. He generally found the sole epithelium ciliated in species exhibiting this behaviour. However, distinguishing muscular waves from ciliary action was difficult as coordinated activity of the cilia often resulted in macroscopically visible waves propagating along the mucus that covered the sole (KAISER 1960). Moreover, muscular activities related to adjustments of the concave shape of the sole rather than to locomotion regularly occurred in surface-crawling snails (KAISER 1960). Therefore he selectively inhibited the cilia by localized application of various salts, and found that muscular action alone was insufficient to produce smooth gliding locomotion. Thus KAISER (1960) thought he had confirmed that surface-crawling snails moved forward because their sole cilia pushed mucus backwards (Fig. 6). Not everyone was convinced, though. In a relatively recent study, LEE et al. (2008) modeled the mechanism of surface crawling assuming that the snails’ movements were driven by muscular waves acting on the mucus layer. The authors justified this assumption by reference to macroscopically visible undulations on the sole (LEE et al. 2008: p. 2). Such observations, however, do not rule out a ciliary mechanism, as KAISER (1960) had shown. To clarify the issue, it would be desirable to examine the species LEE et al. (2008) had worked on. Unfortunately, “*Sorbeoconcha physidae*”, which the authors stated to have collected in the wild, is not a species but a combination of the names of a higher-level taxon (*Sorbeoconcha* Ponder et Lindberg, 1997) and a family (*Physidae* Fitzinger, 1833). Nonetheless, in commentaries in outlets from *Nature* (BALL 2008) to the *New York Times* (IMBLER 2021) and even in the primary literature (GOULD & VALDEZ 2021), “*Sorbeoconcha physidae*” became cited as if it were the archetypical surface-crawling snail.

COPELAND’S (1919) experiments had convinced him not only that ciliary action was necessary for locomotion in certain gastropods, but also that the activity of the ciliated epithelium of the sole was under neuronal control. The latter interpretation subsequently became firmly established (e.g., MCKENZIE et al. 1987, SYED & WINLOW 1989, LONGLEY & PETERMAN 2013). DELIAGINA & ORLOVSKY (1990a, b) investigated the ciliated epithelium on the sole of *Gyraulus acronicus* (J.B. Férussac, 1807) (as *Planorbis corneus*), and found it divided into six functional blocks, the left and right anterior, middle, and posterior zones. Ciliary activity in each of these zones is controlled by separate efferent locomotor neurons (see fig. 1 in DELIAGINA & ORLOVSKY 1990b). Thus the animals appear capable of switching their pedal cilia on and off, as it were, in each of the six zones independently. To fully reveal the significance of this fact, let me take a detour and introduce a devastating invasive pest.



PEDAL SURFACE COLLECTING AND INVASIVE PESTS

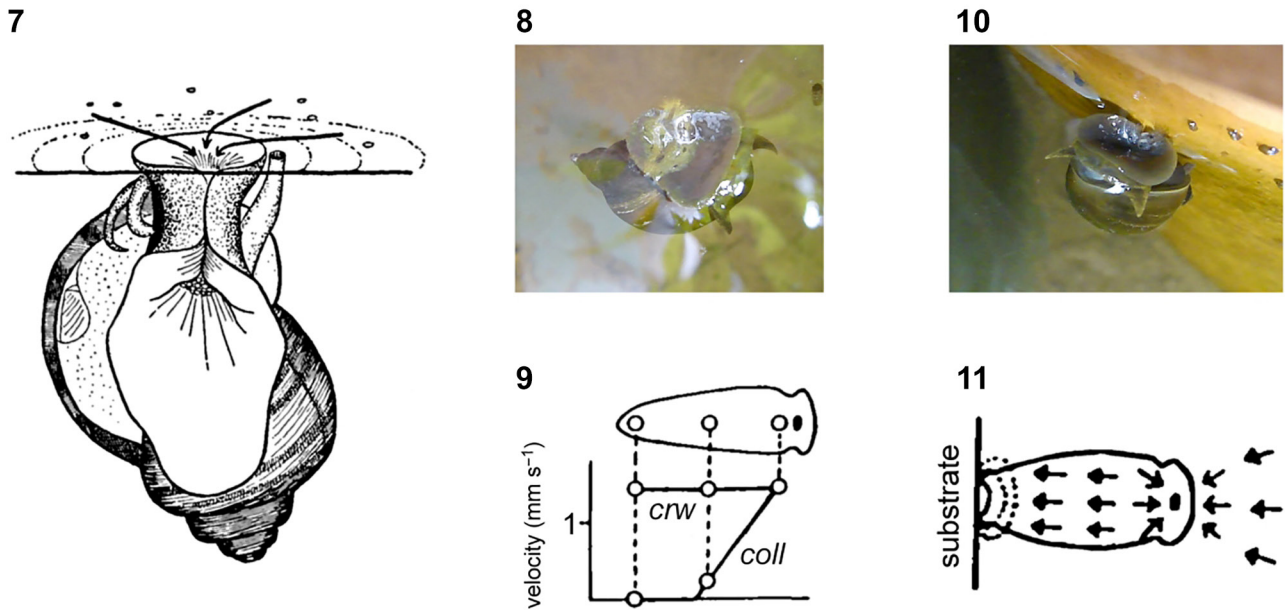
The pantropical apple snail family (Ampullariidae) includes some 150 freshwater species (HAYES et al. 2009). In the late 20th century, alien apple snails were introduced to various regions for food and as aquarium pets (RAWLINGS et al. 2007, HAYES et al. 2008, HORGAN et al. 2012). At least two of them, *Pomacea canaliculata* (Lamarck, 1822) and *P. maculata* Perry, 1810, became major invasive pests, especially in rice (HALWART 1994, HORGAN 2018); their expansion is continuing (BUDDIE et al. 2021). They also can have devastating effects on native ecosystems (CARLSSON et al. 2004, CATTANU et al. 2010, HAYES et al. 2015) and are listed among the most problematic invasive taxa (LOWE 2004, COWIE et al. 2009, NENTWIG et al. 2018). Various countermeasures are being applied with mixed success, and unintended effects on non-target taxa have been recorded for chemical (e.g., OLIVIER et al. 2016, HORGAN et al. 2018) as well as biological (e.g., WONG et al. 2009, CHEN et al. 2012) agents.

Invasive apple snails tend to eat more and faster than native gastropods, including non-invasive family members (KWONG et al. 2010, MORRISON & HAY 2011). Most Ampullariidae are omnivorous, and some may exploit food floating on the water surface (MARTÍN et al. 2019). As JOHNSON (1952) first described in *Pomacea paludosa* (Say, 1829), a snail sensing food on the surface will ascend on plants or other structures. Upon reaching the surface, the animal forms a funnel with the anterior part of its foot but remains attached to the vertical substrate by the posterior foot (Fig. 7). Then, cilia of the anterior sole “beat in such a rhythmical fashion so as to create a small current” into the funnel, leading to an accumulation at the funnel base of mucus carrying particles from the water surface (JOHNSON 1952: p. 4). The material collected on the posterior sole eventually is eaten. JOHNSON (1952) seemed to believe that he had reported a novel phenomenon. The only other case of a “ciliary feeding mechanism” he mentioned was the suspension-feeding *Viviparus viviparus* (L., 1758), which collects suspended particles in its mantle cavity rather than on the sole of its foot (COOK 1949, HÖCKELMANN & PUSCH 2000). Four years later, CHEESMAN (1956) published a less detailed description of the same behaviour in *P. canaliculata* without citing JOHNSON (1952) or any other malacological references. Taking the accumulating mucus for denatured protein, CHEESMAN (1956) asserted that protein films on the water surface were the only quantitatively relevant targets of the surface-feeding activity. This was not in line with a subsequent, more thorough experimental study. MCCLARY (1964: pp. 95–96) rather confirmed JOHNSON’S (1952) conclu-

sion that the unusual feeding behaviour was triggered by the presence of various kinds of food particles on the water surface, which the snails evidently could sense from below. JOHNSON’S (1952) report was extended by further research in *Pomacea* (CAZZANIGA & ESTEBENET 1984) and *Lanistes* (LOUDA & MCKAYE 1982). The peculiar behaviour, originally termed *ciliary feeding*, today is called *pedal surface collecting* (SAVEANU & MARTÍN 2013). In general terms, pedal surface collecting in gastropods is the collection of material from the water surface by means of currents that are actively generated by the sole of the foot.

The ability to switch between herbivory and surface feeding may explain why invasive apple snails persist after they have eradicated native macrophytes in the invaded ecosystems (CARLSSON et al. 2004, SAVEANU & MARTÍN 2015). This obviously suggests that the apparently unique surface collecting behavior of invasive apple snails might allow for specific ways of applying molluscicides for their control (SAVEANU & MARTÍN 2020). Unfortunately, the targeting of pedal-surface-collecting invaders by molluscicides administered through the surface layer would not be as specific as it may seem. After all, the first apple snail in which pedal surface collecting was described, *P. paludosa* (Fig. 7), is native to Florida, where its habitats are under threat by its invasive congeners (RAWLINGS et al. 2007, CONNER et al. 2008, POSCH et al. 2013). Analogous situations must be expected in other invaded regions since native Ampullariidae are found throughout the humid tropics and subtropics. In Thailand, for example, invasive *Pomacea* species appear to be replacing native ampullariids of the genus *Pila* (NG et al. 2020).

The problem is of a more general nature, though. VON LINDEN (1891) noted that snails applied surface crawling to reach potential food such as floating leaves of aquatic plants. Surface-crawling snails also took up small floating food items directly by mouth, and larger items that had become trapped on the sole were transferred to the mouth and eaten — the snails’ foot “combined the usefulness of a locomotory organ with that of a gripper tool” (VON LINDEN 1891: p. 766). But snail feet proved even more versatile. As discussed above, surface-crawling snails generate forward thrust by cilium-driven backward translocation of mucus on the sole (KAISER 1960). When ciliary action ceases on the posterior sole but continues on the sole’s front, the snail stops moving while mucus accumulates on the posterior sole together with particles that keep drifting onto the anterior sole from the water surface (Fig. 8). After some time, the head bends back ventrally to ingest the collected material. BROCKMEIER (1898) had first described



Figs 7–11. Pedal surface collecting in aquatic gastropods: 7 – Surface-feeding *Pomacea paludosa* seen through the glass wall of an aquarium to which it attaches with the flat posterior part of its foot (from JOHNSON 1952: fig. 1 on p. 4). The anterior foot forms a funnel the rim of which is kept at the level of the water surface. Active cilia on the sole of the anterior part of the foot drive a stream of mucus and particles from the water surface into the funnel. These materials accumulate at the narrow base of the funnel and eventually are eaten; 8 – *Lymnaea stagnalis* performing pedal surface collecting while floating upside-down at the water surface. Mucus with captured particles has accumulated on the posterior sole (shell length 37 mm); 9 – In surface-crawling *Gyraulus acronicus*, the velocity of particle transport is homogeneous on the entire sole (*crw*) but decreases in the posterior direction when animals sense food on the water surface and commence pedal surface collecting (*coll*; from DELIAGINA & ORLOVSKY 1990a: fig. 4d, modified); 10 – *L. stagnalis* attached to a solid vertical surface with the posterior part of its foot conducting pedal surface collecting with the funnel-shaped anterior foot (shell length 34 mm); 11 – Pedal surface feeding in *G. acronicus* with the posterior foot attached to a solid substrate (from DELIAGINA & ORLOVSKY 1990a: fig. 4c, modified). Arrows indicate particle transport. While larger particles are taken up directly by the snail's mouth, most particles and mucus accumulate on the posterior sole (dotted lines). Photographs of *L. stagnalis* (8, 10) show animals from a pond in a forest near Frankfurt, west central Germany

this “Planktonfischen” (plankton fishing) in the lymnaeid *Peregriana* (as *Limnaea*). His observations were confirmed in other Lymnaeidae (*Ladislavella*: WALTER 1906, as *Lymneus*; *Lymnaea*: DAWSON 1911) as well as in Physidae (*Physella*: DAWSON 1911, as *Physa*) and Planorbidae (*Gyraulus*: DELIAGINA & ORLOVSKY 1990a, as *Planorbis*; Fig. 9).

Evidently, caenogastropods such as *Pomacea* as well as heterobranchs like *Lymnaea* and *Gyraulus* conduct pedal surface collecting as defined above. In doing so, heterobranchs are mostly observed floating while *Pomacea* species commonly attach to solid substrates. This, however, merely reflects different frequencies of these behaviors. In *P. paludosa*, “the rear part of the foot usually adhered to the aquarium wall or some other solid surface, although on occasion a snail fed while suspended from the surface film” (MCCLARY 1964: p. 96). *Gyraulus* also performs floating as well as attached pedal surface collecting (DELIAGINA & ORLOVSKY 1990a; compare Figs 9, 11). *Lymnaea* may “attach themselves to aquatic plants with their tail end” (KAISER 1960: p. 374), or, as documented here (Fig. 10), hold on to solid structures while collecting

surface material. In this posture, *Lymnaea* resembles a surface-collecting *Pomacea* that adheres to an aquarium wall (compare Figs 7 and 10). For videos showing the described activities in *Lymnaea*, see PETERS (2022).

Hardly surprisingly, older malacologists concluded that the “surface layer plays a more or less significant role in the nutrition of most species” of freshwater gastropods (FRÖMMING 1956: p. 132). This knowledge has faded from the literature, as recently noted by PONDER et al. (2020: p. 176). In the most detailed investigation into the surface feeding of *Pomacea* available at the time, MCCLARY (1964: p. 100) still found it reasonable to hypothesize that the *Lymnaea*-style pedal surface collecting by floating animals “may anticipate” the pedal surface collecting by snails holding on to solid substrates. When reviewing suspension feeding in gastropods three decades later, DECLERCK (1995: pp. 552–553) stated that both Ampullariidae and Lymnaeidae performed “ciliary feeding” (while somewhat confusingly listing the former as using a “mucus net” to collect food) on the water surface. At the same time, however, pedal



surface collecting began to be portrayed as a peculiarity of the Ampullariidae in general treatments of freshwater gastropod ecology (HUTCHINSON 1993: p. 189, DILLON 2000: pp. 98–99) and in the primary literature (SAVEANU & MARTÍN 2013: p. 17, 2015: p. 75, 2020: p. 165, JOO et al. 2020: p. 1).

In surface-crawling *Lymnaea* and *Gyraulus*, the ciliated sole serves as a locomotory machine when all cilia work coordinately, but turns into a food collecting apparatus when the cilia on the posterior sole stop beating (Figs 8–11). Similarly, in *Pomacea* per-

forming pedal surface collecting, no ciliary activity is noticeable on the posterior sole, “indicating remarkable regional control and coordination of the pedal cilia” (JOHNSON 1952: p. 5). If the ciliated epithelium of the sole is functionally subdivided into six zones as it is in *Gyraulus* (DELIAGINA & ORLOVSKY 1990b), an inhibition of ciliary activity of the left and right posterior zones of the sole will be sufficient to turn the locomotor into a food collector. This functional switch could be controlled by two neurons only (DELIAGINA & ORLOVSKY 1990b).

CONCLUSIONS

The mechanisms of pedal surface collecting and surface crawling are closely related. In a sense, pedal surface collecting represents a malfunction of the locomotory machinery – a mechanistically minor but functionally consequential variation of the mechanism of surface crawling. This remarkable versatility of the foot’s structure-function relationship and its evolution deserve renewed attention.

Since surface crawling is common among marine and freshwater gastropods, it is hardly surprising that pedal surface collecting has been observed in numerous species. As a consequence, attempts to tackle invasive Ampullariidae specifically by delivering molluscicides via the water surface predictably will affect native gastropod faunas. In the history of our efforts to control pest molluscs, lacking familiarity

with the biology of non-target species has contributed to misjudgments with devastating consequences (CHRISTENSEN et al. 2021). This short review hopefully will help to avoid adding another failure to the list.

ACKNOWLEDGMENTS

I am indebted to TATIANA DELIAGINA (Karolinska Institutet, Stockholm) and JOHN HUTCHINSON (Senckenbergmuseum für Naturkunde, Görlitz) for critical comments on a draft version of the manuscript, three anonymous reviewers for constructive criticism, and to MONIKA GRAF for feeding my pond snails when I couldn’t.

REFERENCES

- AONO K., FUSADA A., FUSADA Y., SHII W., KANAYA Y., KOMURO M., MATSUI K., MEGURO S., MIYAMAE A., MIYAMAE Y., MURATA A., NARITA S., NOZAKA H., SAITO W., WATANABE A., NISHIKATA K., KANAZAWA A., FUJITO Y., YAMAGISHI M., ABE T., NAGAYAMA M., UCHIDA T., GOHARA K., LUKOWIAK K., ITO E. 2008. Upside-down gliding in *Lymnaea*. *Biological Bulletin* 215: 272–279. <https://doi.org/10.2307/25470711>
- BALL P. 2008. How to walk on water. <https://www.nature.com/articles/news.2008.915>, accessed 23 June 2022. <https://doi.org/10.1038/news.2008.915>
- BRADLEY R. 1721. A philosophical account of the works of nature. W. Mears, London, UK. <https://archive.org/details/aphilosophicala00bradgoog/mode/2up>
- BROCKMEIER H. 1887. Eine neue Erklärung für das Schwimmen mancher Schnecken an der Oberfläche des Wassers. *Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft* 19: 111–118. <https://www.biodiversitylibrary.org/item/98331#page/113/mode/1up>
- BROCKMEIER H. 1898. Süßwasserschnecken als Planktonfischer. *Forschungsberichte aus der Biologischen Station zu Plön* 6(II): 165. <https://www.biodiversitylibrary.org/item/47282#page/195/mode/1up>
- BUDDIE A. G., RWOMUSHANA I., OFFORD L. C., KIBET S., MAKALE F., DJEDDOUR D., CAFA G., VINCENT K. K., MUVEA A. M., CHACHA D., DAY R. K. 2021. First report of the invasive snail *Pomacea canaliculata* in Kenya. *CABI Agriculture and Bioscience* 2: 11. <https://doi.org/10.1186/s43170-021-00032-z>
- CAR L. 1897. Ueber den Mechanismus der Lokomotion der Pulmonaten. *Biologisches Centralblatt* 17: 426–438. <https://www.biodiversitylibrary.org/item/17868#page/438/mode/1up>
- CARLSON A. J. 1905. The physiology of locomotion in gasteropods. *Biological Bulletin* 8: 85–92. <https://doi.org/10.2307/1535857>
- CARLSSON N. O. L., BRÖNMARK C., HANSSON L.-A. 2004. Invading herbivory: the golden apple snail alters ecosystem functioning in Asian wetlands. *Ecology* 85: 1575–1580. <https://doi.org/10.1890/03-3146>



- CATTAU C. E., MARTIN J., KITCHENS W. M. 2010. Effects of an exotic prey species on a native specialist: example of the snail kite. *Biological Conservation* 143: 513–520. <https://doi.org/10.1016/j.biocon.2009.11.022>
- CAZZANIGA N. J., ESTEBENET A. L. 1984. Revisión y notas sobre los hábitos alimentarios de los Ampullariidae (Gastropoda). *Historia Natural* 4: 213–224.
- CHEESMAN D. F. 1956. The snail's foot as a Langmuir trough. *Nature* 176: 987–988. <https://doi.org/10.1038/178987b0>
- CHEN R.-S., WANG K.-L., WU C.-Y. 2012. Assessment of the camellia seed meal impact on loaches in paddy fields. *Paddy and Water Environment* 10: 291–300. <https://doi.org/10.1007/s10333-011-0280-4>
- CHRISTENSEN C. C., COWIE R. H., YEUNG N. W., HAYES K. A. 2021. Biological control of pest non-marine molluscs: a Pacific perspective on risks to non-target organisms. *Insects* 12: 583. <https://doi.org/10.3390/insects12070583>
- CONNER S. L., POMORY C. M., DARBY P. C. 2008. Density effects of native and exotic snails on growth in juvenile apple snails *Pomacea paludosa* (Gastropoda: Ampullariidae): a laboratory experiment. *Journal of Molluscan Studies* 74: 355–362. <https://doi.org/10.1093/mollus/eyn024>
- COOK P. M. 1949. A ciliary feeding mechanism in *Viviparus viviparus*. *Proceedings of the Malacological Society, London* 27: 265–271. <https://doi.org/10.1093/oxfordjournals.mollus.a064541>
- COPELAND M. 1919. Locomotion in two species of the gastropod genus *Alectrion* with observations on the behavior of pedal cilia. *Biological Bulletin* 37: 126–138. <https://doi.org/10.2307/1536353>
- COPELAND M. 1922. Ciliary and muscular locomotion in the gastropod genus *Polinices*. *Biological Bulletin* 42: 132–142. <https://doi.org/10.2307/1536576>
- COWIE R. H., DILLON R. T. JR., ROBINSON D. G., SMITH J. W. 2009. Alien non-marine snails and slugs of priority quarantine importance in the United States: a preliminary risk assessment. *American Malacological Bulletin* 27: 113–132. <https://doi.org/10.4003/006.027.0210>
- DAVISON A., NEIMAN M. 2021. Mobilizing molluscan models and genomes in biology. *Philosophical Transactions B* 376: 20200163. <https://doi.org/10.1098/rstb.2020.0163>
- DAWSON J. 1911. The biology of *Physa*. *Behavior Monographs* 1(4): 1–120 (with 10 separate figures). <https://www.biodiversitylibrary.org/item/31425#page/253/mode/1up>
- DECLERCK C. H. 1995. The evolution of suspension feeding in gastropods. *Biological Reviews* 70: 549–569. <https://doi.org/10.1111/j.1469-185X.1995.tb01651.x>
- DELIAGINA T. G., ORLOVSKY G. N. 1990a. Control of locomotion in the freshwater snail *Planorbis corneus*. I. Locomotory repertoire of the snail. *Journal of Experimental Biology* 152: 389–404. <https://doi.org/10.1242/jeb.152.1.389>
- DELIAGINA T. G., ORLOVSKY G. N. 1990b. Control of locomotion in the freshwater snail *Planorbis corneus*. II. Differential control of various zones of the ciliated epithelium. *Journal of Experimental Biology* 152: 405–423. <https://doi.org/10.1242/jeb.152.1.405>
- DE QUATREFAGES A. 1843. Mémoire sur l'Eolidine paradoxale (*Eolidina paradoxum* Nob.). *Annales des Sciences Naturelles (Seconde Série)* 19: 274–312. <https://www.biodiversitylibrary.org/item/47973#page/280/mode/1up>
- DILLON R. T. 2000. The ecology of freshwater molluscs. Cambridge University Press, Cambridge, UK.
- DIMON A. C. 1905. The mud snail: *Nassa obsoleta* (Cold Spring Harbor Monographs 5). Brooklyn Institute of Arts and Sciences, Brooklyn NY, USA.
- FODOR I., HUSSEIN A. A. A., BENJAMIN P. R., KOENE J. M., PIRGER Z. 2020. The natural history of model organisms. The unlimited potential of the great pond snail, *Lymnaea stagnalis*. *eLife* 9: e56962. <https://doi.org/10.7554/eLife.56962>
- FRÖMMING E. 1956. *Biologie der mitteleuropäischen Süßwasserschnecken*. Dunker & Humblot, Berlin.
- GOULD J., VALDEZ J. W. 2021. Locomotion with a twist: aquatic beetle walks upside down on the underside of the water's surface. *Ethology* 127: 669–673. <https://doi.org/10.1111/eth.13203>
- HALWART M. 1994. The golden apple snail *Pomacea canaliculata* in Asian rice farming systems: present impact and future threat. *International Journal of Pest Management* 40: 199–206. <https://doi.org/10.1080/09670879409371882>
- HAYES K. A., BURKS R. L., CASTRO-VAZQUEZ A., DARBY P. C., HERAS H., MARTÍN P. R., QIU J.-W., THIENGO S. C., VEGA I. A., WADA T., YUSA Y., BURELA S., CADIerno M. P., CUETO J. A., DELLAGNOLA F. A., DREON M. S., FRASSA M. V., GIRAUD-BILLOUD M., GODOY M. S., ITUARTE S., KOCH E., MATSUKURA K., PASQUEVICH M. Y., RODRIGUEZ C., SAVEANU L., SEUFFERT M. E., STRONG E. E., SUN J., TAMBURI N. E., TIECHER M. J., TURNER R. L., VALENTINE-DARBY P. L., COWIE R. H. 2015. Insights from an integrated view of the biology of apple snails (Caenogastropoda: Ampullariidae). *Malacologia* 58: 245–302. <https://doi.org/10.4002/040.058.0209>
- HAYES K. A., COWIE R. H., JØRGENSEN A., SCHULTHEISS R., ALBRECHT C., THIENGO S. C. 2009. Molluscan models in evolutionary biology: apple snails (Gastropoda: Ampullariidae) as a system for addressing fundamental questions. *American Malacological Bulletin* 27: 47–58. <https://doi.org/10.4003/006.027.0204>
- HAYES K. A., JOSHI R. C., THIENGO S. C., COWIE R. H. 2008. Out of South America: multiple origins of non-native apple snails in Asia. *Diversity and Distributions* 14: 701–712. <https://doi.org/10.1111/j.1472-4642.2008.00483.x>
- HÖCKELMANN C., PUSCH M. 2000. The respiration and filter-feeding rates of the snail *Viviparus viviparus* (Gastropoda) under simulated stream conditions. *Archiv für Hydrobiologie* 149: 553–568. <https://doi.org/10.1127/archiv-hydrobiol/149/2000/553>



- HORGAN F. G. 2018. The ecophysiology of apple snails in rice: implications for crop management and policy. *Annals of Applied Biology* 172: 245–267. <https://doi.org/10.1111/aab.12424>
- HORGAN F. G., BERNAL C. C., LETANA S., NAREDO A. I., RAMP D., ALMAZAN M. L. P. 2018. Reduced efficiency of tropical flies (Diptera) in the decomposition of snail cadavers following molluscicide poisoning. *Applied Soil Ecology* 129: 61–71. <https://doi.org/10.1016/j.apsoil.2018.05.003>
- HORGAN F. G., STUART A. M., KUDAVIDANAGE E. P. 2012. Impact of invasive apple snails on the functioning and services of natural and managed wetlands. *Acta Oecologica* 54: 90–100. <https://doi.org/10.1016/j.actao.2012.10.002>
- HUTCHINSON G. E. 1993. A treatise in limnology. Volume IV: The zoobenthos. John Wiley & Sons, New York, USA.
- IMBLER S. 2021. You won't believe how this beetle walks on water. *The New York Times* 26 July 2021. <https://www.nytimes.com/2021/07/26/science/upside-down-water-beetle.html>, accessed 23 June 2022.
- JOHNSON B. M. 1952. Ciliary feeding in *Pomacea paludosa* (Say). *Nautilus* 66: 3–5. <https://www.biodiversitylibrary.org/item/34884#page/15/mode/1up>
- JOHNSTON G. 1850. An introduction to conchology; or, elements of the natural history of molluscous animals. John van Voorst, London, UK. <https://www.biodiversitylibrary.org/bibliography/22266>
- JORDAN H. 1901. Die Physiologie der Locomotion bei *Aplysia limacina*. R. Oldenbourg, München, Germany. <https://www.biodiversitylibrary.org/bibliography/11244>
- JOO S., JUNG S., LEE S., COWIE R. H., TAKAGI D. 2020. Freshwater snail feeding: lubrication-based particle collection on the water surface. *Journal of the Royal Society Interface* 17: 20200139. <https://doi.org/10.1098/rsif.2020.0139>
- KAISER P. 1960. Die Leistungen des Flimmerepithels bei der Fortbewegung der Basommatophoren. *Zeitschrift für Wissenschaftliche Zoologie* 162: 368–393.
- KWONG K. L., DUDGEON D., WONG P. K., QIU J.-W. 2010. Secondary production and diet of an invasive snail in freshwater wetlands: implications for resource utilization and competition. *Biological Invasions* 12: 1153–1164. <https://doi.org/10.1007/s10530-009-9537-x>
- LEE S., BUSH J. W. M., HOSOI A. E., LAUGA E. 2008. Crawling beneath the free surface: water snail locomotion. *Physics of Fluids* 20: 082106. <https://doi.org/10.1063/1.2960720>
- LISTER M. 1694. *Exercitatio anatomica*. S. Smith & B. Walford, London, UK. <https://www.biodiversitylibrary.org/bibliography/39640>
- LOMBARDO P., MICCOLI F. P., CICHY A., STANICKA A., ŻBIKOWSKA E. 2021. No effects of waterproof marking on the behaviour and growth of *Physa acuta* Draparnaud, 1805 (Gastropoda: Hygrophila: Physidae) in the laboratory. *Folia Malacologica* 29: 121–131. <https://doi.org/10.12657/folmal.029.013>
- LONGLEY R. D., PETERMAN M. 2013. Neuronal control of pedal sole cilia in the pond snail *Lymnaea stagnalis appressa*. *Journal of Comparative Physiology A* 199: 71–86. <https://doi.org/10.1007/s00359-012-0770-x>
- LOUDA S. M., MCKAYE K. R. 1982. Diurnal movements of populations of the prosobranch *Lanistes nyassanus* at Cape Maclear, Lake Malawi, Africa. *Malacologia* 23: 13–21. <https://www.biodiversitylibrary.org/item/47256#page/27/mode/1up>
- LOWE S., BROWNE M., BOUDJELAS S., DE POORTER M. 2004. 100 of the World's Worst Invasive Alien Species: A selection from the Global Invasive Species Database. The Invasive Species Specialist Group (ISSG), a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN). http://www.iucn-gisd.org/gisd/100_worst.php, accessed 23 June 2022.
- MARTÍN P. R., BURELA S., SEUFFERT M. E., TAMBURI N. E., SAVEANU L. 2019. Invasive *Pomacea* snails: actual and potential environmental impacts and their underlying mechanisms. *CAB Reviews* 14: 042. <https://doi.org/10.1079/PAVSNNR201914042>
- MCCLARY A. 1964. Surface inspiration and ciliary feeding in *Pomacea paludosa* (Prosobranchia: Mesogastropoda: Ampullariidae). *Malacologia* 2: 87–104. <https://www.biodiversitylibrary.org/item/47249#page/105/mode/1up>
- MCKENZIE J. D., SYED N. I., TRIPP J., WINLOW W. 1987. Are pedal cilia in *Lymnaea* under neural control? In: BOER H. H., GERAERTS W. P. M., JOOSSE J. (eds). *Neurobiology. Molluscan models*. North Holland Publishing, Amsterdam, The Netherlands, pp. 26–30.
- MORRISON W. E., HAY M. E. 2011. Feeding and growth of native, invasive and non-invasive alien apple snails (Ampullariidae) in the United States: invasives eat more and grow more. *Biological Invasions* 13: 945–955. <https://doi.org/10.1007/s10530-010-9881-x>
- NENTWIG W., BACHER S., KUMSCHICK S., PYŠEK P., VILÀ M. 2018. More than “100 worst” alien species in Europe. *Biological Invasions* 20: 1611–1621. <https://doi.org/10.1007/s10530-017-1651-6>
- NEWELL R. 1962. Behavioural aspects of the ecology of *Peringia* (= *Hydrobia*) *ulvae* (Pennant) (Gastropoda, Prosobranchia). *Proceedings of the Zoological Society, London* 138: 49–75. <https://doi.org/10.1111/j.1469-7998.1962.tb05687.x>
- NG T., ANNATE S., JERATTHITIKUL E., SUTCHARIT C., LIMPANONT Y., PANHA S. 2020. Disappearing apple snails (Caenogastropoda: Ampullariidae) of Thailand: a comprehensive update of their taxonomic status and distribution. *Journal of Molluscan Studies* 86: 290–305. <https://doi.org/10.1093/mollus/eyaa015>
- OLIVIER H. M., JENKINS J. A., BERHOW M., CARTER J. 2016. A pilot study testing a natural and a synthetic molluscicide for controlling invasive apple snails (*Pomacea macu-*



- lata*). Bulletin of Environmental Contamination and Toxicology 96: 289–294.
<https://doi.org/10.1007/s00128-015-1709-z>
- PARKER G. H. 1911. The mechanism of locomotion in gastropods. Journal of Morphology 22: 155–170.
<https://doi.org/10.1002/jmor.1050220107>
- PETERS W. S. 2022. Four videos showing surface-crawling locomotion and pedal surface collection in *Lymnaea stagnalis* (Lymnaeidae, Gastropoda). Zenodo 6804938.
<https://doi.org/10.5281/zenodo.6804938>
- PONDER W. F., LINDBERG D. R., PONDER J. M. 2020. Biology and evolution of the Mollusca, Vol. 1. CRC Press, Boca Raton, USA.
- POSCH H., GARR A. L., REYNOLDS E. 2013. The presence of an exotic snail, *Pomacea maculata*, inhibits growth of juvenile Florida apple snails, *Pomacea paludosa*. Journal of Molluscan Studies 79: 383–385.
<https://doi.org/10.1093/mollus/eyt034>
- PYRON M., BROWN K.M. 2015. Introduction to Mollusca and the class Gastropoda. In: THORP J. H., ROGERS D. C. (eds). Ecology and general biology. Thorp and Covich's freshwater invertebrates, volume 1 (4th Ed.). Elsevier, Amsterdam, The Netherlands, pp. 383–421.
- RAWLINGS T. A., HAYES K. A., COWIE R. H., COLLINS T. M. 2007. The identity, distribution, and impacts of non-native apple snails in the continental United States. BMC Evolutionary Biology 7: 97.
<https://doi.org/10.1186/1471-2148-7-97>
- RISSE A. 1826. Histoire naturelle des principales productions de l'Europe méridionale et particulièrement de celles de environs de Nice et de Alpes Maritimes. F.-G. Levrault, Paris, France.
<https://www.biodiversitylibrary.org/bibliography/58984>
- SAVEANU L., MARTÍN P. R. 2013. Pedal surface collecting as an alternative feeding mechanism of the invasive apple snail *Pomacea canaliculata* (Caenogastropoda: Ampullariidae). Journal of Molluscan Studies 79: 11–18.
<https://doi.org/10.1093/mollus/eyt030>
- SAVEANU L., MARTÍN P. R. 2015. Neuston: a relevant trophic resource for apple snails? Limnologia 52: 75–82.
<https://doi.org/10.1016/j.limno.2015.03.005>
- SAVEANU L., MARTÍN P. R. 2020. An invader's peculiar trophic behaviour: diel fluctuations and environmental drivers. Biological Bulletin 239: 164–173.
<https://doi.org/10.1086/711489>
- SCHMIDT O. 1878. Die niederen Thiere (Brehms Thierleben. Große Ausgabe [2. Auflage], 4. Abtheilung, 2. Band). Verlag des Bibliographischen Instituts, Leipzig, Germany.
- SIMROTH H. 1878. Die Thätigkeit der willkürlichen Muskulatur unserer Landschnecken. Zeitschrift für Wissenschaftliche Zoologie 30 (Supplement): 166–224 (with Table VIII).
<https://www.biodiversitylibrary.org/item/161044#page/174/mode/1up>
- SIMROTH H. 1879. Die Bewegung unserer Landschnecken, hauptsächlich erörtert an der Sohle des *Limax cinereoniger* Wolf. Zeitschrift für Wissenschaftliche Zoologie 32: 284–322 (with Tables XVI and XVII).
<https://www.biodiversitylibrary.org/item/161292#page/306/mode/1up>
- SIMROTH H. 1882. Über die Bewegung und das Bewegungsorgan des *Cyclostoma elegans* und der einheimischen Schnecken überhaupt. Zeitschrift für Wissenschaftliche Zoologie 36: 1–67 (with Table I).
<https://www.biodiversitylibrary.org/item/161798#page/9/mode/1up>
- SOCHACZEWER D. 1881. Das Riechorgan der Landpulmonaten. Zeitschrift für Wissenschaftliche Zoologie 35: 30–46 (with Table III).
<https://www.biodiversitylibrary.org/item/161797#page/38/mode/1up>
- SYED N. I., WINLOW W. 1989. Morphology and electrophysiology of neurons innervating the ciliated locomotor epithelium in *Lymnaea stagnalis* (L.). Comparative Biochemistry and Physiology A 93: 633–644.
[https://doi.org/10.1016/0300-9629\(89\)90024-8](https://doi.org/10.1016/0300-9629(89)90024-8)
- TASCHENBERG E., SCHMIDT O. 1929. Niedere Tiere (Brehms Tierleben. Jubiläums-Ausgabe, 8. Band). Philipp Reclam jun., Leipzig, Germany.
- VON LINDEN M. 1891. Das Schwimmen der Schnecken am Wasserspiegel. Biologisches Centralblatt 11: 763–766.
<https://www.biodiversitylibrary.org/item/17522#page/773/mode/1up>
- WALTER H. E. 1906. The behavior of the pond snail *Lymnaeus elodes* Say. Cold Spring Harbor Monographs 6: 1–35.
- WILLEM V. 1888. Note sur le procédé employé par les Gastéropodes d'eau douce pour glisser à la surface du liquide. Bulletins de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique 58: 421–430.
<https://www.biodiversitylibrary.org/item/28484#page/435/mode/1up>
- WONG P. K., KWONG K. L., QIU J.-W. 2009. Complex interactions among fish, snails and macrophytes: implications for biological control of an invasive snail. Biological Invasions 11: 2223–2232.
<https://doi.org/10.1007/s10530-008-9378-z>

Received: July 7th, 2022

Revised: September 14th, 2022

Accepted: September 16th, 2022

Published on-line: October 21st, 2022

