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HOUSES SPEAK VOLUMES ABOUT THEIR INHABITANTS

The small shells of juvenile snails are highly important for paleontological research.

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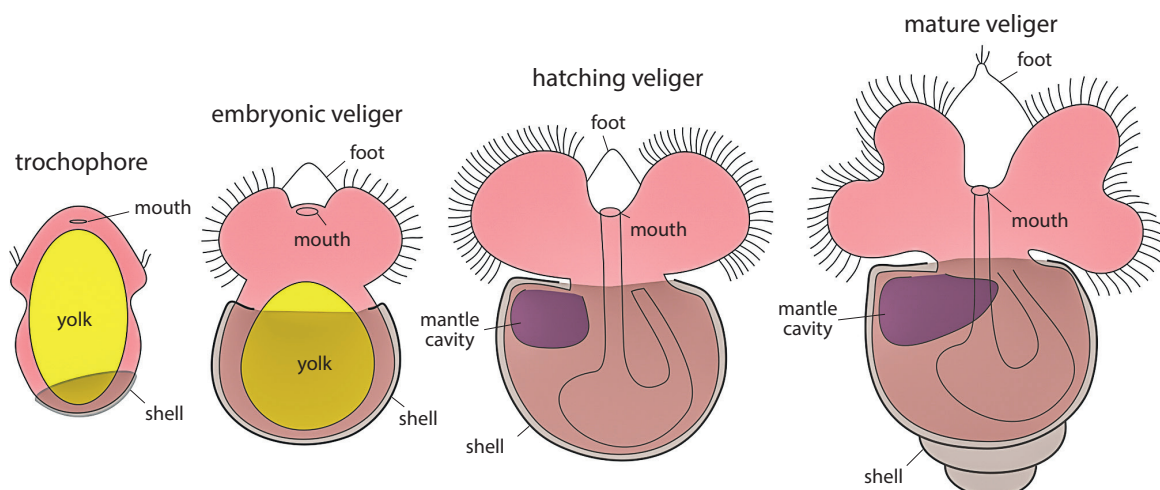
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is estimated that of the nearly 200,000 mollusk species that have been described, some 75% are snails. It is also estimated that perhaps only one-quarter of snail species have been described so far, or even fewer for sea snails. This great taxonomic diversity goes hand-in-hand with diverse morphologies and lifestyles, ranging from herbivorous and filter-feeding to scavenging, parasitic, and predatory strategies. While modern snail systematics relies on molecular studies, fossil forms must be identified almost exclusively based on shell morphology.

Such research faces a major issue in the form of numerous morphological convergences, i.e. when species from different higher-order groups (families, orders) exhibit very similar shells. However, paleontologists do have certain ways to try to cope with this. Larval and juvenile shells, which show significant morphological conservatism, often allow for the identification of higher-order units in species with similar adult shells. The development of precision imaging technologies, particularly scanning electron microscopy (SEM), has been invaluable here, given that taxonomically significant shell parts often do not

Snails are the largest and most diverse group of mollusks, and more broadly of invertebrates – second only to insects. Their great adaptability has led them to be found in almost every environment on Earth: marine, freshwater, and terrestrial. They have not taken to the air, although there are known instances of them traveling with birds, as “stowaways.” The full species diversity of snails is unknown, but it

Schematic development of a larval snail from the group Neogastropoda (Adapted from: Croll 2009)





From sampling, to sieving (in the field), to selected specimens. Coon Creek, Tennessee, USA, August 2022

exceed 2 mm in size. The advent of such microscopes in the 1970s and their increasing availability since the 1980s therefore touched off a renaissance in the study of fossil snails.

Different developmental paths

Sea snails exhibit two main types of larval development. In the most primitive groups, such as the orders Patellogastropoda (e.g. true limpets) and Vetigastropoda (e.g. turban snails, popular in Asian cuisine), the egg hatches into a trochophore larva, which then transforms into a veliger stage, relying on yolk reserves without feeding from the water column and without building additional larval shell. Consequently, the larval shell part is usually limited to a small embryonic shell not exceeding 0.3 mm in diameter. For other sea snails, such as neritimorphs (including Poland's freshwater river nerite), caenogastropods (e.g. the common Mediterranean turret snails), and many opisthobranch snails, the trochophore stage is shortened and the larva immediately enters the veliger stage. During this stage, snails undergo *torsion*, a process involving a 180° rotation of the visceral mass relative to the head-foot. As a result, the internal organs cross over, and some organs on one side of the body are reduced. This gives snails their characteristic bilaterally asymmetrical body morphology.

Most of these more advanced snails (if marine) have a two-part larval shell, consisting of an embryonic shell (also called “protoconch 1”) and a larval shell proper (called “protoconch 2”). Depending on the size of the egg and richness of the yolk, snail larvae may consume only the yolk’s resources during their larval stage (lecithotrophic larvae) or, if those resources are scarce, they may be forced to feed independently while in the water column (planktotrophic larvae). There are also snails that hatch directly from the egg as miniature adults (most freshwater and terrestrial snails). In lecithotrophic development, the embryonic shells are usually large, and the larva produces few (up to two) whorls of the larval shell, usually staying near the sea bottom. In planktotrophic development, the embryonic shell is small, and the larva (called a “veliger”) produces many whorls (sometimes more than five) and typically floats in the water column for several weeks, often traveling many kilometers using ocean currents. Some have even been known to cross the Atlantic Ocean in this manner.

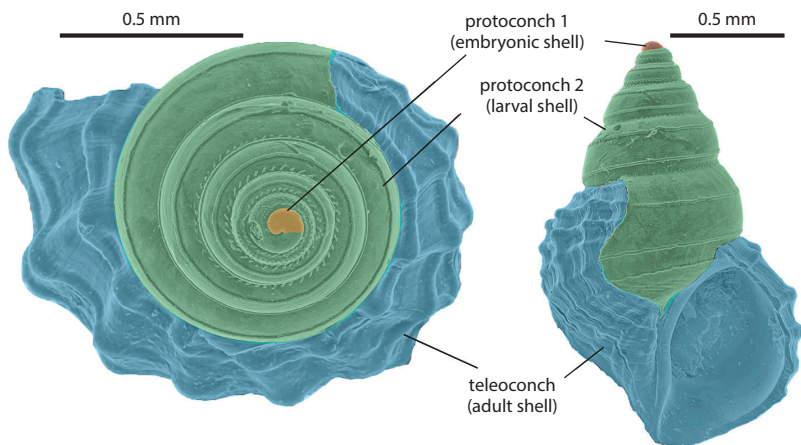
Maturing

Eventually, the larva settles on the bottom and undergoes metamorphosis, starting to produce its adult shell (known as the “teleoconch”). This traumatic experience is usually well visible in the shell morphology,



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The embryonic shell, larval shell, and teleoconch of a Jurassic snail from the genus *Maturifusus*

marked by a distinct suture and a change in ornamentation pattern. In opisthobranch snails, after metamorphosis, the direction of the shell's coiling changes (e.g., from left-handed to right-handed). The protoconch is often positioned at a 180° angle with respect to the adult shell (this is known as "hyperstrophy"), but sometimes it is positioned at a different angle (known as "heterostrophy" – e.g. 90°). The shells of these groups are easily recognizable even under a simple binocular microscope.

Carboniferous larval snail shells:
 A – with an open-coiled first whorl (from Frýda 2004),
 B – vetigastropod shell – an exclusively embryonic shell,
 C – caenogastropod shells, with a larval shell forming in the same direction as the adult snail shell,
 D – mathildid shell with a heterostrophic protoconch (positioned at a 90° angle to the adult shell)

Larval shells, especially those with planktotrophic larvae, can have beautiful ornamentation, visible only under high magnification. Often, larval shells in higher-order systematic groups have characteristic shapes and ornaments that allow for quick identification. However, larval shells are often damaged in adults, mostly due to apex corrosion (especially in large snails), sometimes intentionally discarded by the snail itself, as in the worm snails (Vermetidae) or deep-water sea snails Provannidae, and sometimes the larval shell is covered by the shell material of subse-

quent adult shell whorls, as in Stromboidea sea snails (highly prized by collectors) and Cypraeidae (cowries), making it inaccessible for observation. Neritimorphs, on the other hand, are known for dissolving their internal larval shell whorls. In such cases, ontogenetic sequences, consisting of shells at various consecutive growth stages, have to be pieced together in order to link the larval shells to the adult snail.

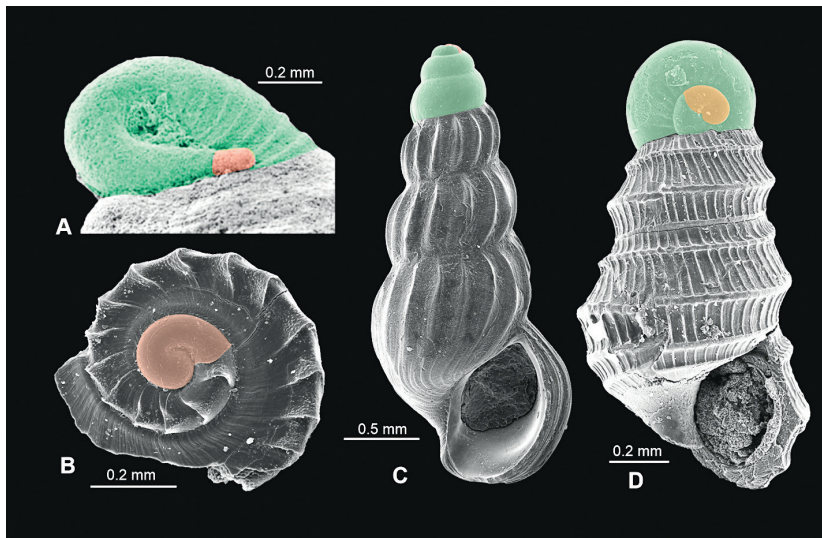
The oldest representatives

In the fossil record, larval mollusk shells are known from as early as the Cambrian period. However, interpreting these as snail shells is difficult due to their state of preservation and the presence of numerous extinct basal mollusk groups. The situation improves significantly starting from the Ordovician period, where sediment layers are dominated by larval shells with an open-coiled first whorl. This feature was gradually replaced during the Paleozoic by tightly coiled shells, similar to those of modern snails, and eventually disappeared.

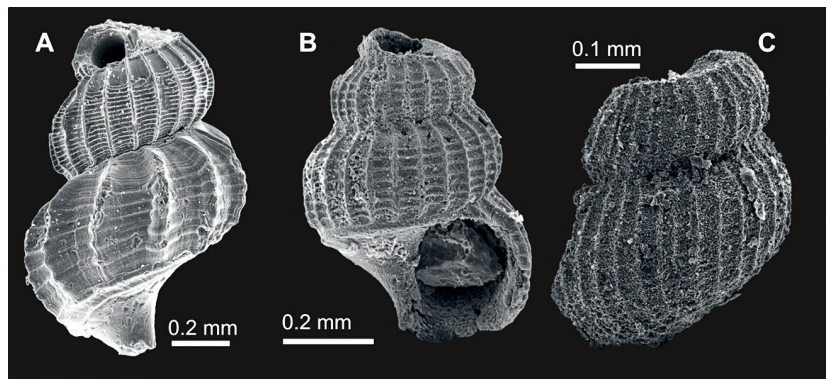
Larval shells are composed of a less durable crystallographic variant of calcium carbonate, specifically aragonite. Consequently, they often do not preserve their original mineralogy in the fossil record but are instead replaced by other minerals such as apatite, silica, or pyrite. The apatite preservation is prevalent in Paleozoic sediments, which were particularly conducive to phosphatization, making them relatively common in the fossil record, forming so-called taphonomic windows. Larval shells can also be preserved with all their details through the replacement of aragonite with silica. Such well-preserved shells come from fossil hydrocarbon seep deposits, where silicification is an early diagenetic process occurring shortly after the seep's activity ceases, resulting in very precise aragonite replacement. There are also rare cases of precise shell replacement by pyrite in massive sulfide deposits from ancient hydrothermal vents.

The first well-documented occurrence of aragonitic shells is known from Carboniferous sediments in the United States (the famous Buckhorn Asphalt deposit). Starting from the Late Triassic, occurrences of aragonitic snail shells become more frequent, particularly in clay sediments where the shells were additionally impregnated from circulating solutions by the presence of hydrocarbons. In Poland, such shells are known from the iron-bearing clays around Częstochowa and the Łuków glacial drift (both from the Middle Jurassic) and from the Early Cretaceous near Tomaszów Mazowiecki. Starting from the beginning of the Cenozoic, such shells become common.

Larval snail shells are very useful in studying the phylogenetic relationships between contemporary and extinct groups, as well as in searching for ancestors of

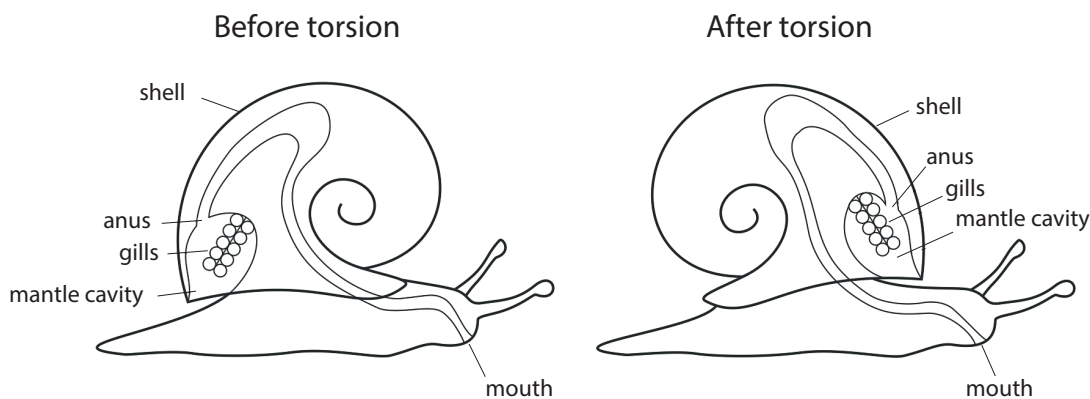


modern groups. In our current research, we are trying to identify the ancestors of predatory snails from the Neogastropoda group, which is currently one of the most diverse groups of snails (encompassing nearly 25% of all snail species). They began to diversify rapidly from an unspecified basal group. To this end, we have examined the larval shells of three families of extinct snails suspected of being ancestors of neogastropods (Pseudotrioniidae, Maturifusidae, and Purpurinidae). Based on the morphology of the protoconch (as well as the structure of the shell aperture), we concluded that the latter are likely to be the direct ancestors of the Neogastropoda group, while the other two are extinct sister groups. Interestingly, the larval shells of contemporary neogastropods are characterized by exceptionally large size. Such large dimensions already appear in the Jurassic representatives of these groups, whereas earlier they were still similar in size to those of more primitive caenogastropods.



The oldest known occurrence of a snail very similar to modern neogastropods comes from Poland – documented from Valanginian (Lower Cretaceous) clays from the now abandoned and re-cultivated Wąwał clay pit near the town of Tomaszów Mazowiecki. ■

Various styles of larval shell preservation in the fossil state:
 A – pristine aragonite from clay,
 B – silicified from hydrocarbon seeps,
 C – pyritized from hydrothermal vents.
 Cretaceous specimens from: Poland (A), Japan (B), Cyprus (C)



Early mollusk before torsion and snail after torsion (from: Page 2006)

Triassic **Jurassic** **Cretaceous** **Today**

Purpurinidae Purpurinidae Muricoidea Muricoidea

Pseudotrioniidae Maturifusidae Volutoidea

0.5 mm

Evolution of protoconch size in neogastropod ancestors. Research funded by NCN grant 2018/31/B/ST10/03415

Further reading:
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