Malacopedia

São Paulo, SP, Brazil
Volume 8(2): 7-12

ISSN 2595-9913
12/Apr/2025

Limpetization revisited: the beak shells and the re-coiling process

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Abstract

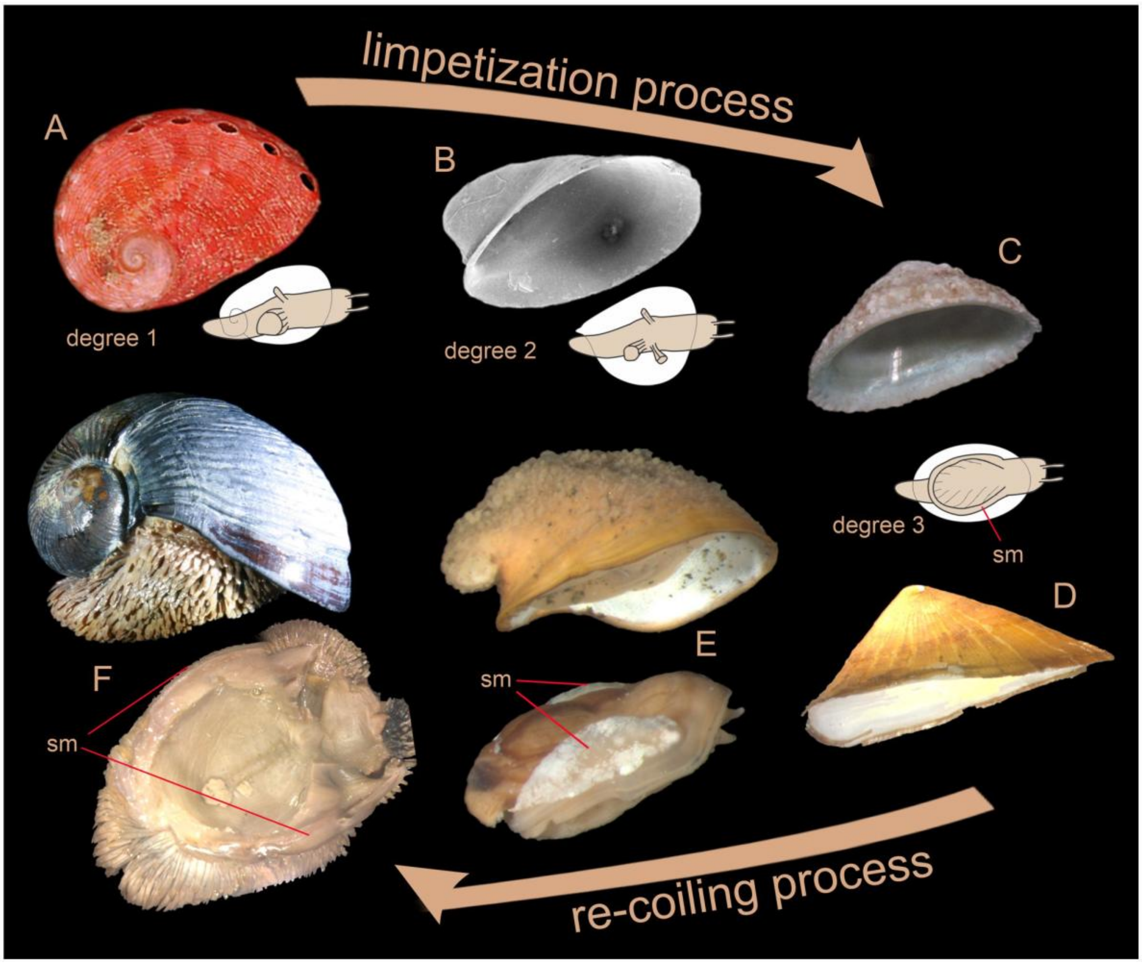
Limpetization, previously discussed in an earlier study, refers to the evolutionary process by which a coiled-shelled snail transforms into a limpet-like form. One of the key morphological changes involved in this process is the uncoiling of the shell. Interestingly, a reverse trend has been observed in some heterobranch, caenogastropod, and vetigastropod taxa, where limpet-like forms have evolved into beaked shells (featuring a coiled apex), and even into fully coiled 'limpets,' such as *Chrysomallon*. Despite the presence of a coiled shell, the internal anatomical structure in these cases remains limpet-like, characterized by features such as a horseshoe-shaped shell muscle serving as the retractor muscle for the head-foot complex.

Keywords: limpet, gastropod evolution, morphological modifications.

Introduction

Limpetization is the commonly used term for the evolutionary process that leads to the development of limpets—that is, snails (gastropod mollusks) characterized by a flattened, broadly conical, cap-shaped shell. This process was previously discussed in an earlier issue of Malacopedia (Simone, 2018). In that study, limpetization was categorized into three degrees:

- Degree 1 – Represented by ear-shells such as haliotids, where the shell retains some coiling and the main muscles attach to the shell at isolated points (Fig. 1A);
- Degree 2 – Represented by “almost-limpets,” such as former ancylids, which typically have tall, limpet-like shells, with the main muscles still attached at distinct, isolated points (Fig. 1B);
- Degree 3 – Represented by “true limpets,” which usually have low, conical shells, and a horseshoe-shaped muscle attachment pattern (Figs. 1C, D).



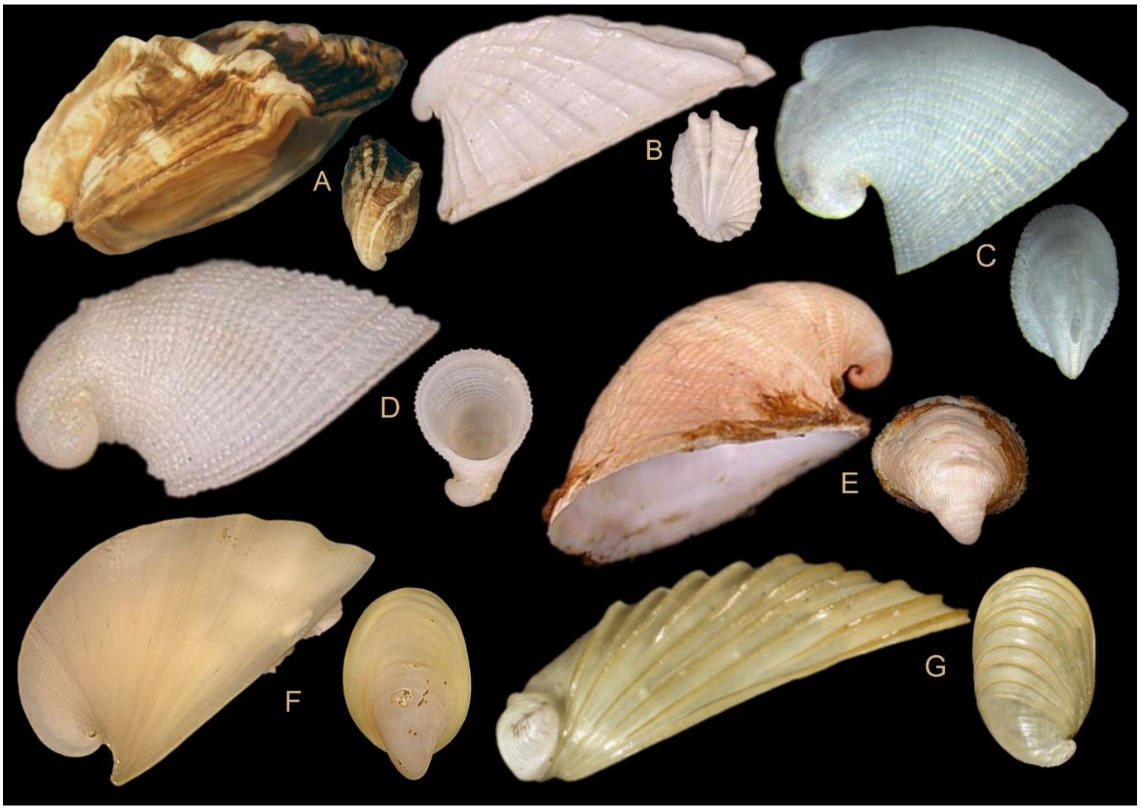
1. Examples of evolutionary steps towards limpetization and the steps back for re-coiling. **A**, *Haliotis aurantium* (L 26 mm), shell and a scheme of head-foot muscles attached to shell; **B**, same for *Gundlachia ticaga* (L 2 mm), **C**, same for *Fissurella mesoatlantica* (L 20 mm); **D**, *Neomphalus fretterae* (L 22 mm), shell in limpet form; **E**, *Lepetodrilus fucensis* (6 mm), beak shell weakly coiled, with specimen in right view; **F**, *Chrysomallon squamiferum* (L 32 mm), a coiled "limpet", whole specimen and a head-foot with haemocoel structures removed, dorsal view. All MZSP material. Lettering: sm: horseshoe-shaped shell muscle.

This paper explores a further stage in the evolution of true limpet taxa—namely, the development of beaked shells and the additional process of re-coiling. This evolutionary reversal was identified through anatomical studies, which revealed that some coiled forms retain a horseshoe-shaped retractor muscle rather than the typical columellar muscle found in coiled gastropods. A notable example is the scaly-foot gastropod *Chrysomallon squamiferum* (Chen et al., 2015) (Fig. 1F).

The case of the coiled *Chrysomallon squamiferum* represents the most advanced stage of a reverse limpetization process—a reversion toward a coiled shell form. Despite this external change, the species largely retains an internal organization characteristic of limpets. This evolutionary reversal appears to proceed through an intermediate and more commonly observed form known as "beak shells" (Fig. 1E).

Beak shells

Beak shells are, in fact, limpets, but with a taller profile or an elongated apex (Fig. 2). The apex is typically positioned away from the center of the base, most often located posteriorly and sometimes deflected to the right. In some cases, the apex may even show a slight degree of coiling.



2. Examples of taxa possessing beak shells. **A**, *Cyclothyca pacei* FMNH 301979 Florida (L 13 mm) (from Simone & Bieler, submit.); **B**, *Amathina tricarinata* (Femorale) Japan (27 mm) (both Heterobranchia); **C**, *Cranopsis alaris* MNHN 25305, Brazil (3 mm) (from Simone & Cunha, 2014) (Vetigastropoda); **D**, *Hipponix incurvus* (Femorale) Brazil (6 mm); **E**, *Capulus ungaricus* (Femorale) Greece (28 mm) (both Caenogastropoda); **F**, *Lepetodrilus marianae* NSMT-Mo 79483 (8 mm) (from SOSA et al., 2024) (Lepetellida); **G**, *Peltospira delicata* MNHN 31388, W Pacific (5 mm) (Neomphalida).

Although there is no distinct boundary between beak shells and true limpets, typical beak shells are characterized by a beak-like hump at the apex, which shelters part of the visceral mass (Fig. 1E). When the shell apex is coiled, the visceral portion housed within it also forms corresponding coils.

Beak shells are found across various gastropod lineages that have undergone limpetization (Simone, 2018). Among heterobranchs, amathinids clearly exhibit beak shells (Figs. 2A, B). This shell form is also present in caenogastropods, such as hipponicids (Fig. 2D) and capulids (Fig. 2E). In the true vetigastropod family Fissurellidae, beak-shaped shells also occur (Fig. 2C). Additionally, they are commonly found in the deep-sea taxa of the controversial vetigastropod clades Neomphalida (Fig. 2G) and Lepetellida (Fig. 2F).

All these almost- or semi-coiled taxa share a key anatomical feature: a head-foot retractor muscle arranged in a horseshoe-shaped pattern, similar to that of true limpets. This evolutionary trend extends further in some cases, leading to the emergence of what can be described as a "coiled limpet," which is discussed below.

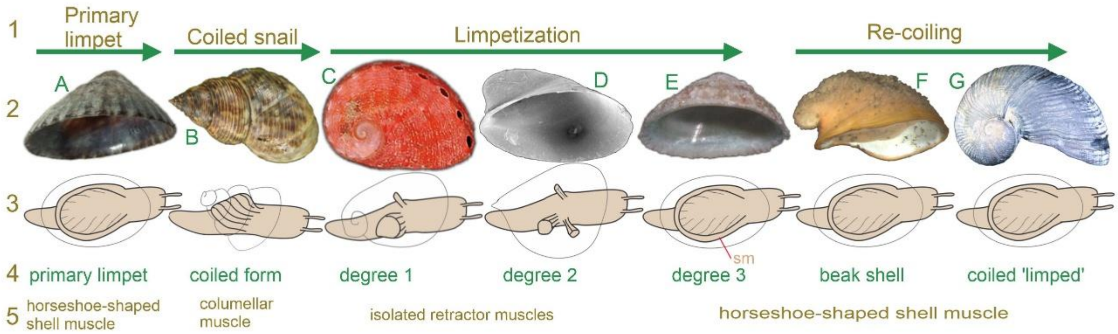
Coiled “limpet”

3. A typical coiled “limpet:” shell of *Chrysomallon squamiferum* (Neomphalida, Peltospiridae) (L 35 mm), from SW Indian Ocean (MZSP 168467), dorsal and apertural views. There is no columellar muscle, but so a horseshoe-shaped shell muscle (see Fig 1F: sm).

The re-spiralization process can progress to the point where the shell fully coils, resulting in a form that externally resembles a typical snail. A prime example of this is *Chrysomallon squamiferum* (Figs. 1F, 3), along with, to a lesser extent, other members of the family Peltospiridae (Fig. 2G). Peltospirids exhibit shell forms that lie on the borderline between beak shells and fully coiled “limpets.”

The main difference between a typical coiled snail shell and the shell of what is referred to here as a “coiled limpet” lies in the absence of the columellar muscle. Instead, head-foot retraction in these organisms is facilitated by a horseshoe-shaped shell muscle, similar to that found in ordinary limpets. This unique muscular arrangement, along with its internal anatomical structure and phylogenetic relationships, suggests that Chrysomallon is the product of secondary spiralization, derived from limpet-like ancestors.

Figure 4 illustrates the evolutionary progression of *Chrysomallon*, starting from the first gastropod lineage with a primary limpet shell (Fig. 4A). It then evolves into a coiled form (Fig. 4B), passing through the various stages of the limpetization process (Figs. 4C–E). The progression also includes an intermediate beak shell form (Fig. 4F), ultimately culminating in the coiled 'limpet' condition (Fig. 4G).



4. Table explaining main steps of re-coiling evolutionary process. **Line 1**: name of the process; **line 2**: examples of shells in each category (A, *Patinigera magellanica*, Nacellidae, 30 mm; B, *Littoraria angulifera*, Littorinidae, 25 mm; C, *Haliotis aurantium*, Haliotidae, 26 mm; D, *Gundlachia ticaga*, Planorbidae, 2 mm; E, *Fissurella mesoatlantica*, Fissurellidae, 20 mm; F, *Lepetodrilus fucensis*, Lepetodrillidae, 6 mm; G, *Chrysomallon squamiferum*, Peltospiridae, 35 mm); **line 3**: type of retractor muscle connecting head-foot to shell (schematic representation in dorsal view); **line 4**, subdesignation; **line 5**: name of type of retractor muscle connecting head-foot to shell. (Shells from MZSP collection.)

Discussion

A more detailed explanation, along with phylogenetic inferences on the limpetization process, was provided in Simone (2018). The present work serves as a complement, focusing on the further evolution of certain former limpet taxa that underwent a reversal toward a secondary coiled shell, passing through the beak shell phase (Figs. 1, 4). The shells themselves do not offer specific clues about this process, except possibly for muscular scars, when detectable. The primary evidence supporting the evolutionary pathway outlined here comes from morphological and anatomical analysis, as well as phylogenetic data.

In terms of morpho-anatomy, taxa with beak shells and coiled 'limpets' still retain a limpet-like internal organization, as described by Simone (2011, 2018). This includes a head-foot modified into a "cup" shape, with the shell muscle forming its boundaries (except in the head region), and the visceral mass enclosed within it, protruding perpendicularly toward the dorsal side. In the case of beak shells and coiled 'limpets,' the postero-dorsal end of the visceral mass coils further to the right.

In terms of phylogeny, all known beak shells and coiled 'limpets' are preceded by coiled forms in the phylogenetic cladograms. This is particularly well-supported in heterobranchs and caenogastropods (Figs. 2A–E). However, the phylogenetic placement of deepwater taxa, such as Lepetellida, Neomphalida (Figs. 1D–F, 2F–G), and Cocculinida, remains unclear. These taxa are currently classified as Vetigastropoda (MolluscaBase, 2025), but this classification is based primarily on molecular data (e.g., Aktipis & Giribet, 2010; Chen et al., 2025). Notably, they do not always exhibit the morphological synapomorphies characteristic of vetigastropods (Simone, 2011), and some molecular studies have placed representatives of these taxa outside the vetigastropod clade (e.g., Uribe et al., 2016). Given this uncertain scenario, it is possible that these three orders (Lepetellida, Neomphalida, and Cocculinida) represent independent gastropod lineages, potentially phylogenetically positioned between the Patellogastropoda (the earliest gastropod branch) and the remaining gastropods (Orthogastropoda). This remains an ongoing area of study.

Institutional abbreviations

Femorale, http://www.femorale.com/shellphotos/; FMNH, Field Museum of Natural History, Chicago, USA; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MZSP, Museu de Zoologia da Universidade de São Paulo, Brazil; NSMT, National Science Museum Tokyo, Japan.

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