

FUNCTIONAL INTERRELATIONS BETWEEN CONCHOLOGICAL AND ANATOMICAL CHARACTERS IN STYLOMMATOPHORA (MOLLUSCA, GASTROPODA)

Anatoly A. Schileyko

Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences; asch0829@gmail.com

Parameters of shells (shape, size) of stylommatophoran mollusks are determined by the history of the group, peculiarities of their food and conditions of life in different geological periods, as well as genetic nature.

The history of Stylommatophora since the Paleozoic is briefly discussed. It is assumed that one of the important factors determined the historical development of stylommatophorans were peculiarities of their food.

The aperture is the main channel of communication of a mollusk with the outside world and any elements of the apertural structure are related, directly or indirectly, with the adaptation of animals to their environment. Therefore, special attention is paid in the article to the morphofunctional analysis of apertural structures. The main results of this analysis may be summarized by six basic conclusions.

1. The teeth in the aperture are represented by two categories that are designated as superficial and immersed. Superficial teeth are local thickenings of the lip; immersed ones are natural result of narrowing of the last whorl at the final stages of the shell formation.

2. Superficial teeth and lip serve basically for squeezing mucus from the mantle collar and the epiphragm formation.

3. Superficial teeth there are mostly in mollusks, that dig themselves into the soil to survive of dry season.

4. The main function of immersed teeth is providing an optimal orientation of shell with visceral sack with respect to the cephalopodium and improvement of management of high shell.

5. With increase of aridity, amplification of the superficial teeth and weakening of immersed teeth is observed. This trend is clearly seen in the species that live openly and survive the drought by gluing to the substrate using the aperture.

6. Snails inhabiting steppe, desert and semi-desert areas often lack apertural teeth and well developed lip. In such species, a wide lapel of the aperture is often developed, contributing to tight contact of the aperture to the substrate.

In several families persisting in the current geological time, there is a clear trend toward shell reduction leading to the formation of a slug morphotype, with all reduction stages being observable over their members. Reduction of shell stimulates perfecting of the nervous system and improvement of physiological features of mollusks, as well as growing complexity of their behavior. From this a forecast follows that this trend will be intensified in the course of further evolution of Stylommatophora.

ФУНКЦИОНАЛЬНЫЕ ВЗАИМОСВЯЗИ КОНХОЛОГИЧЕСКИХ И АНАТОМИЧЕСКИХ ПРИЗНАКОВ У STYLOMMATORPHORA (MOLLUSCA, GASTROPODA)

Анатолий А. Шилейко

Институт проблем экологии и эволюции им. А.Н. Северцова РАН; asch0829@gmail.com

Параметры раковины (форма, размеры) стебельчатоглазых моллюсков (Stylommatophora) определяются историей развития группы, особенностями их питания и условиями существования в разные геологические периоды, а также эпигенетическими ограничениями.

Кратко анализируется история развития стиломматофор начиная с палеозоя. Предполагается, что одним из важных факторов, определивших развитие стебельчатоглазых моллюсков, были особенности их пищевых объектов.

Устье есть основной канал связи моллюска с внешним миром и любые элементы строения устья так или иначе связаны, прямо или опосредованно, с приспособлениями животных к условиям внешней среды. Поэтому особое внимание в статье уделено морфофункциональному анализу устьевых структур. Основные результаты этого анализа сводятся к шести базовым положениям.

1. Зубы в устье представлены двумя категориями, которые обозначаются как поверхностные и погружённые. Поверхностные зубы представляют собой местные утолщения губы; погружённые часто появляются как естественный результат более или менее ярко выраженного сужения последнего оборота на заключительных этапах онтогенетического формирования раковины.

2. Поверхностные зубы и губа служат в основном для выжимания слизи из края мантии и формирования эпифрагмы.

3. Поверхностные зубы имеются большей частью у моллюсков, зарывающихся в почву на сухой сезон.

4. Основная функция погружённых зубов — обеспечение оптимальной ориентации раковины с висцеральным мешком по отношению к цефалоподиуму и совершенствование управление высокой раковиной.

5. С возрастанием аридности условий наблюдается усиление поверхностных зубов и ослабление погружённых. Эта тенденция хорошо прослеживается у видов, живущих открыто и переживающих засуху, приклеиваясь устьем к субстрату.

6. Улитки, обитающие в степных, полупустынных и пустынных местностях, часто лишены устьевых зубов и хорошо развитой губы. У таких видов часто развит широкий отворот края устья, способствующий плотному прилеганию устья к поверхности субстрата.

В настоящее геологическое время в пределах нескольких семейств чётко прослеживается тенденция к редукции раковины, приводящая к становлению морфотипа слизней. В современной фауне прослеживаются все этапы утраты раковины. Редукция раковины стимулирует совершенствование нервного аппарата и физиологических характеристик моллюсков, а также усложнение их поведения. Из этого следует прогноз, согласно которому в ходе дальнейшей эволюции стебельчатоглазых эта тенденция будет усиливаться.

1. Introduction

Superorder Stylommatophora is a large (at least 25000 species) and diverse (about 90 families, 2600 genera and subgenera) group of terrestrial pulmonate mollusks spread all over the continents (absent in the Antarctic only, although present in sub-Antarctic islands). Although initially stylommatophorans are moisture-loving animals, many of them have mastered almost all types of biotopes and often form large aggregations.

Causes of prosperity (or, on the contrary, the oppressed state) of a group depend on external factors (climate, soil, topographic features, geologic history of the region, human activities) as well on the peculiarities of the organization of the animals themselves.

Although the "peculiarities of the organization" may include not only morphological, but also physiological, biochemical, and ethological properties of organisms, here are considered predominantly morphological characters, the adaptive significance of which is the subject of the present discussion.

Main and permanent danger threatening land mollusks living in conditions of dry climate (or in regions where the rainy periods are regularly replaced by dry seasons) is the danger of dehydration. Nevertheless, there is a large number of species living and even prospering in arid areas. Therefore, those

characters of molluscs should be considered first of all, which look like adaptations to the conditions existing in arid zones. Morpho-functional analysis often allows to advance a hypothesis on the adaptive significance of this or that character.

The systematic study of terrestrial pulmonate mollusks constituting superorder Stylommatophora began, naturally, from descriptions of their shells. Start of a broad study of the internal organization of terrestrial pulmonate mollusks was laid in 1855, when two fundamental publications have been issued by a German priest Adolf Schmidt and a French naturalist Alfred Moquin-Tandon. These studies have demonstrated the existence of a wide variety of characters, mainly those related to the structure of reproductive tract. Since that time, the anatomical method began to be widely used in studies on the systematics and phylogeny of pulmonate mollusks.

As a result, to date a vast array of information about the internal structure of stylommatophorans has been accumulated, first of all concerning reproductive tract and radula.

However, the functional significance of the structural features of these animals is rarely discussed. One of many examples of ignoring the functional role of certain characters is the division of Stylommatophora

into four large taxa of ordinal rank according to the structure of the excretory apparatus (Orthurethra, Sigmurethra, Mesurethra, and Heterurethra) proposed by Pilsbry (1900) and supplemented by Baker (1955). Actually, these four names describe, or characterize, the four states of the excretory system, and the most perfect condition (sigmurethria) can occur independently in different evolutionary branches of Stylommatophora (Schileyko, 1975, 1978a).

It should be noted that paleontologists, in contrast to zoologists, use very effectively the method of phylogenetic reconstructions based on the morphofunctional analysis of fossil material from which they “squeeze” all what is possible. One can point, as examples, to brilliant works by Bizikov (2008) on the evolution of cephalopod shells and by Parkhaev (2008) on minute Cambrian gastropods.

Correct analysis of functional relationships between anatomical and conchological features is impossible without taking into consideration the biological aspects, especially the behavior of snails during mating and feeding.

It is impossible to discuss the problems of functional morphology without touching the problems of phylogeny, because one of the most natural assumption of morphofunctional analysis is the assumption that some taxon has originated from some other taxon.

Nor less closely the morphofunctional analysis is related to the problems of systematics. For example, the understanding of the nature of such a feature as the topography of the retractor of right (in sinistral forms — left) ommatophore has permitted to suggest that xerophilic Hygromiidae do not constitute a separate taxon Helicellinae, but is a result of parallel evolution (Schileyko, 1978b).

Obviously, the conclusions based on morphofunctional analysis, are speculative to some extent and often give the reason to

reproach their author in anthropomorphism. However, any formulated and published hypothesis is a matter for further discussion, during which it will be either confirmed or improved, or rejected and replaced by a more correct interpretation of the known facts. In any case, nomination of a hypothesis serves as an impetus to further analysis and/or alternative interpretation of these facts and is targeted to the obtaining of new ones.

Abbreviations used in the figures throughout the article are as following: H – heart; K – kidney; LL – left lobe of mantle collar; MC – mantle collar; P – pneumostome; PL – pneumostomal lobe of mantle collar; R – rectum; RL – right lobe of mantle collar.

2. Shell and soft body

2.2. Shell shape and size

2.2.1. The shell shape

General analysis of the shell geometry has been presented by Raup (Raup, 1966; Raup, Stanley, 1971), who has selected four principal parameters:

1. The shape of the generating curve. This curve is a line of crossing the widening tube (cone) with the plane, in which lies the axis of coiling; in the majority of gastropods it coincides with the plane of aperture.

2. The whorl expansion rate. The rate of the widening of generating curve as it rotates around the axis (= rate of the whorl widening = step from the axis). This is a relation of any linear size (for example, of the diameter) of two generating curves separated by the entire whorl of the spire.

3. The position of the generating curve in relation to the axis. This parameter is important in some cases when the generating curve is not a circle.

4. The rate of whorl translation (= translation of the whorl, = step along the axis). It is expressed best of all by the relation of

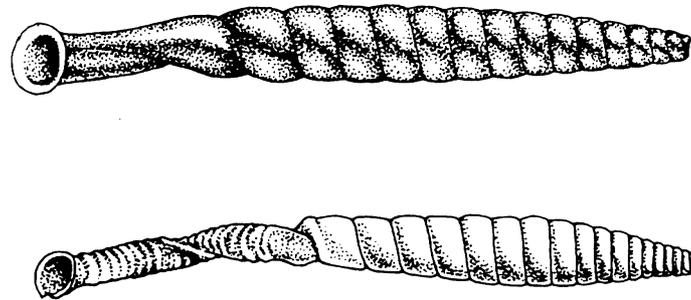


Fig. 1. Shells with partly uncoiled lower whorls. Above is *Tetrentodon barroi* Jaume et Torre, 1972, below is *Gyraxis brooksiana* (Pfeiffer, 1859). After Schileiko (1998–2007).

Рис. 1. Раковины с частично развёрнутыми последними оборотами. Вверху – *Tetrentodon barroi* Jaume et Torre, 1972, внизу – *Gyraxis brooksiana* (Pfeiffer, 1859). По Schileiko (1998–2007).

shifting along to the axis at any part of the whorl around the axis.

These four parameters usually do not change during growth, although exceptions are known. For example, in *Tetrentodon* and *Gyraxis* (Urocoptidae), all whorls form a tight spiral, except for 2–3 last whorls, which are not in contact with each other, forming a kind of corkscrew (Fig. 1).

In the context of our consideration, two parameters are most important: the second one (step from the axis) and the fourth one (step along the axis). An increase the step from the axis leads to formation of flattened shell, while that of the step along the axis leads to the arising of elongated shell.

The general habitus of the shell is mostly determined genetically, and many taxa of the family rank are characterized quite definitely by conchological characters. To such taxa one could attribute, for example, Vertiginidae, Gastrocoptidae, Pyramidulidae, Valloniinae (Valloniidae), Speleodiscidae, Strobilopsidae, majority of Enidae+Pachnodidae, Megaspiridae, Urocoptidae, Clausiliidae, Succineidae, where the external appearance

of shell usually allows a confident judging about the familial belonging of the species. However, the shell, for example, of helicoid appearance is characteristic for a number of families (Xanthonychidae, Epiphragmophoridae, Bradybaenidae, Camaenidae, Pleurodontidae, Helicidae, Hygromiidae), so it is impossible to reveal to which family belongs the species with such shell without prior knowledge of anatomy (before all, the structure of reproductive tract) of the given species.

A more or less swollen last whorl is characteristic for helicoid shells. This whorl is a container for withdrawal of cephalopodium: the larger relative volume it (cephalopodium) occupies, the more is the volume of a foot and hence the more muscular effort it can develop and more effectively the animal can burrow into the soil for aestivation or hibernation. At the same time, the presence of relatively bulky cephalopodium means that the animal is able to store a sufficiently large volume of water in its tissue, which is essential for the snails living in regions with a dry season. It is clear that much swollen last whorl is ob-

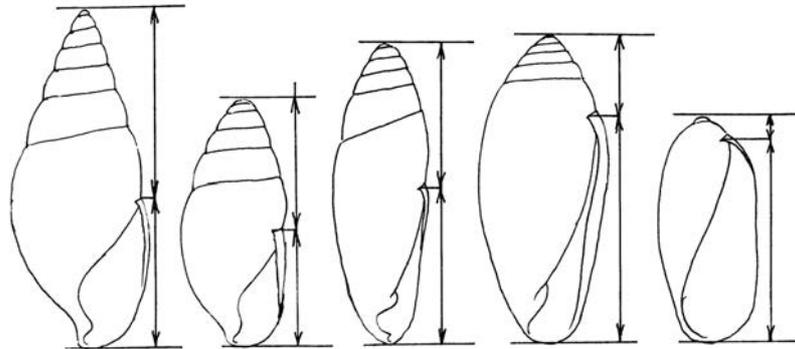


Fig. 2. Morphological series of Oleacinidae.

Рис. 2. Морфологический ряд Oleacinidae.

From left to right/Слева направо: *Varicella*, *Guillarmodia*, *Plicoleacina*, *Streptostyla*, *Strebelia*.

served, as a rule, in more or less depressed shells (from globular to flat). In such shells, there is often a peripheral angle or keel, the function of which will be discussed below.

Concerning high-spined shells, i. e. those having the height greater than the diameter, such a shape is usually achieved either by increasing the step along the axis, or by increasing the number of whorls.

Increasing of step of whorls along the axis is not always associated with a significant increase in the number of whorls, but such shells usually have relatively high aperture.

The results of evolution in this way can be seen on the example of Oleacinidae (Fig. 2). Now the question is, what such shells give to their owners? As the oleacinids are predators, they, to search of a prey (mainly oligochaetes, soil larvae of some insects and other snails), often must penetrate the soil holes. The depth of immersion of the molluscan head to the hole is mainly limited by the position of the breathing orifice. Evidently, if the angular region, where the pneumostome occurs, squeezes into a narrow passage, some difficulties with breathing may appear. The formation of a relatively high aperture, and

hence, the shift of the pneumostome upwards (i. e. towards the top) allows if not to avoid completely this problem, but at least to minimize it substantially. The same reason explains the fact that the anterior end of the cephalopodium in Oleacinidae is mostly strongly elongated, and this allows the snail to penetrate deep into the soil, leaving pneumostome above its surface. The tendency to increase relative height of aperture can be traced in the series of *Varicella* — *Guillarmodia* — *Plicoleacina* — *Streptostyla* — *Strebelia*; if a number of other representatives of oleacinids are included in this row, one can make it even smoother.

Another feature associated with the aperture is its orientation relative to vertical plane (i. e. the plane of the columella location). Aperture can be straight, i. e. its plane is parallel to the vertical plane, or can be located at an angle to it. In the latter case, the aperture is usually more or less descending in front, i. e. at a standard position the upper margin of the aperture is closer to the observer than the lower one. The stronger the last whorl descending, the more the plane of the aperture deviates from the vertical plane. In

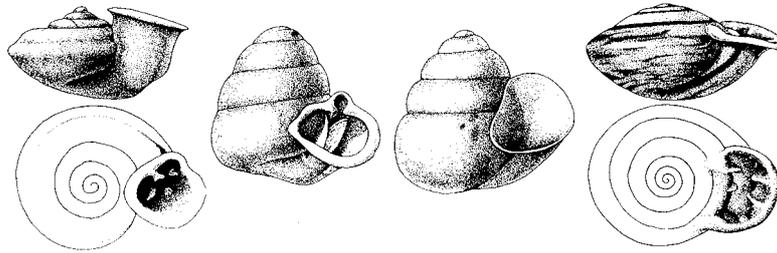


Fig. 3. Shells with aperture turned upward, after Schileyko (1998–2007).

Рис. 3. Раковины с обращённым вверх устьем, по Schileyko (1998–2007).

From left to right/Слева направо: *Hypselostoma roebeleni* (Moellendorff, 1890), *Campolaemus perexilis* (Smith, 1892), *Boysia boysii* (Pfeiffer, 1846), *Anostoma depressum* Lamarck, 1822.

flat lenticular shells the angle of inclination of the aperture can reach nearly 90° , i. e. in this case the aperture is almost horizontal. In very rare cases [*Hypselostoma*, *Campolaemus*, *Boysia* (Hypselostomatidae); *Anostoma* (Bulimulidae)] the aperture is also almost horizontal, but its plane turned upward, to the side of shell apex (Fig. 3).

The reasons causing the appearance of strongly descending aperture, are understandable from functional point of view: a snail with such aperture, when sitting, say, on the surface of a rock, can very tightly adjoin to the substrate and, is probably hardly noticeable for some natural enemies (mainly amphibians, birds, and some mammals). Besides, this orientation of the aperture created a more effective resistance to such effects as, e. g., strong gusts of wind or water flow in time of heavy shower. It should be added that strongly descended oblique aperture is often associated with the formation of an angle or even keel on the shell periphery, which further increases its “streamlining”. In this regard, an attention should be called to the fact that the angulated shell appears often in juvenile animals, whereas the angle may disappear in fully formed shells. This phenomenon is appropriate to connect with

the fact that definitive aperture, which often carries various structures (in particular, the lip which promotes to tight adjoining of the aperture to the substrate) that minimizes the adverse external effects, in juveniles have not yet been formed, and the presence of juvenile keel partly compensates the absence of “adult” structures.

It is more difficult to understand the reasons of appearance of the aperture, which plane is facing upward (like, for example, in *Anostoma*). For the correct interpretation of such a character, it is desirable to know the biology of the respective species, namely how they survive the unfavorable seasons, whether there is a difference in the conditions of life and behavior in young and adult individuals, in particular their behavior during copulation, the peculiarities of their diet and movement. One of possible suggestions is that such an aperture is associated with a specific behavior during mating, since juveniles have a normal position of aperture, and turning of the plane of the aperture upward begins just in subadult age, immediately before puberty.

Flattened shells (many Discidae, Trochomorphidae, Zonitidae and some others) are often characteristic for the mollusks living

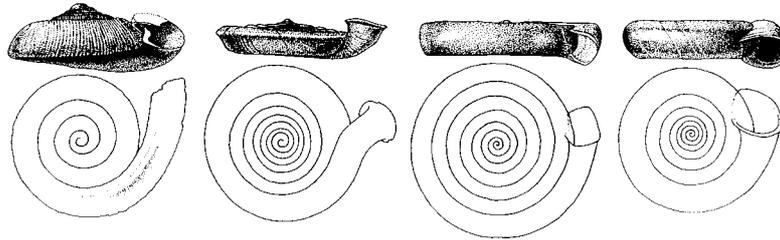


Fig. 4. Multi-whorled flat shells. After Schileyko (1998–2007).

Рис. 4. Многооборотные плоские раковины. По Schileyko (1998–2007).

From left to right/Слева направо: *Cupulella valley* Aguayo et Jaume, 1948, *Hendersoniella palmeri* (Dall, 1905), *Coxia macgregori* (Cox, 1870), *Polygyratia polygyrata* (Born, 1778).

under the bark of stumps, under stones and in similar places. Reasons for such a correlation are obvious. Increasing of the whorls number often also leads to formation of high shells [flat shells with a large number of whorls as *Cupulella* (Subulinidae), *Hendersoniella* (Urocoptidae), *Coxia* (Trochomorphidae), and *Polygyratia* (Camaenidae) are extremely rare (Fig. 4)]. In such shells the number of whorls can reach 30 or even more, and they are characteristic for the majority of Enidae, Clausiliidae, Megaspiridae, Bulimulidae, Urocoptidae. Snails with a similar elongated shell live mostly (though with many exceptions) on vertical surfaces — rocks, stems of grasses and shrubs, etc.). Freely hanging shell requires minimal effort to control it (more on this matter see below).

2.2.2. The shell size

The size of mollusks is determined by at least three factors: 1. Genetic nature of the species setting certain limits on their variability (for example, no one member of Vertiginidae can reach the size of the smallest species of Achatinidae); 2. Environmental conditions. This circumstance is often associated with the intraspecific variation: in general, more favorable conditions of life lead,

as a rule, to the increased size of individuals. 3. Biology of the species, i. e. peculiarities of nutrition, microhabitats, life cycles, and breeding peculiarities.

The first and second of the above factors do not require explanations. The third factor deserves a more detailed consideration, because it is closely linked to the evolution of terrestrial Pulmonata as a whole. This problem was discussed by the author (Schileyko, 2014), so I repeat here in brief the principal points only.

The most ancient findings of terrestrial pulmonate mollusks are dated by the Paleozoic (Carboniferous–Permian) (Solem, Yochelson, 1979) (Fig. 5). Noteworthy, all of them had a small size: the height of the bullet-shaped shells (*Dendropupa*, *Anthracopupa*) do not exceed 8 mm (*Dendropupa vetusta*), but usually they were even smaller, no more to 5 mm; the diameter of the flattened ones (*Protodiscus*) is no more than 2.5 mm.

Evidently, the very first steps of pulmonates moving from the sea onto the land were made through the littoral. At that time, the only source of their food was detritus — an organic material produced by the shallow-water inhabitants including content of bacterial and algal mats. Hence, for the earliest

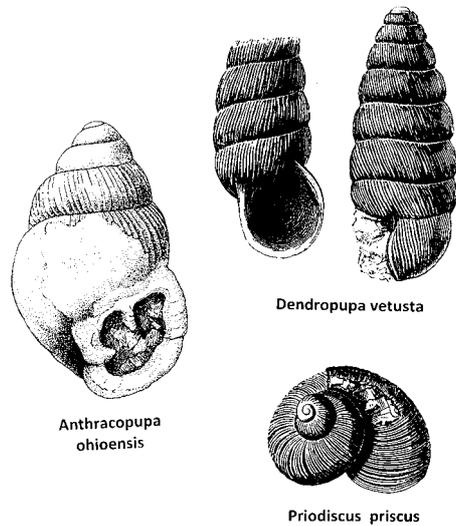


Fig. 5. Paleozoic Stylommatophora. After Solem, Jochelson (1979).

Рис. 5. Палеозойские стебельчатоглазые. По Solem, Jochelson (1979).

non-marine mollusks the initial type of their nutrition was detritophagy and probably bacteriophagy. If so, it is clear that with such a low-calorie food the mollusks could not reach large size.

Real heyday of the land pulmonates has started since the early Cretaceous simultaneously with widespread distribution of the angiosperm plants, which provided abundant and inexhaustible food resource. It should be underlined that the modern pulmonates do not eat either gymnosperms or ferns or mosses, which form the basis of the planet flora throughout most of the Mesozoic.

Starting from the upper Cretaceous, there appeared members of several Recent families as well as a number of groups extinct subsequently (Fig. 6): Filholiidae (middle Eocene to lower Oligocene of Europe), Anadromidae (upper Cretaceous to middle Eocene of Europe and north-western Africa), Grangerellidae (Paleocene of North America; though it is possible that they belonged to Bulimulidae, like Recent South American *Anostoma*) (Zilch, 1959–1960). Among Cretaceous and especially Tertiary pulmonates, there were, *inter alia*, shells of large size, for example, *Hodopoeus* (Lysinoeinae of Humboldtianidae, or perhaps Pleurodontidae) with shell diameter up to 60 mm (Eocene or Paleocene of the southern USA), or

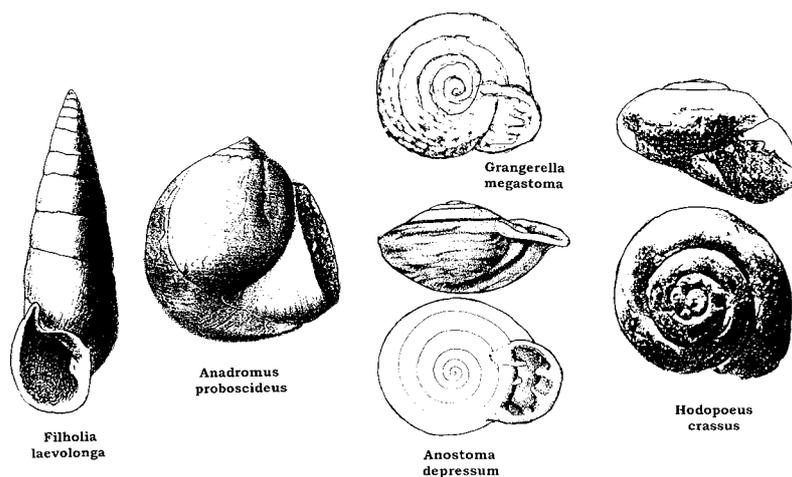


Fig. 6. Representatives of extinct families of terrestrial Pulmonata.

Рис. 6. Представители вымерших семейств наземных Pulmonata.

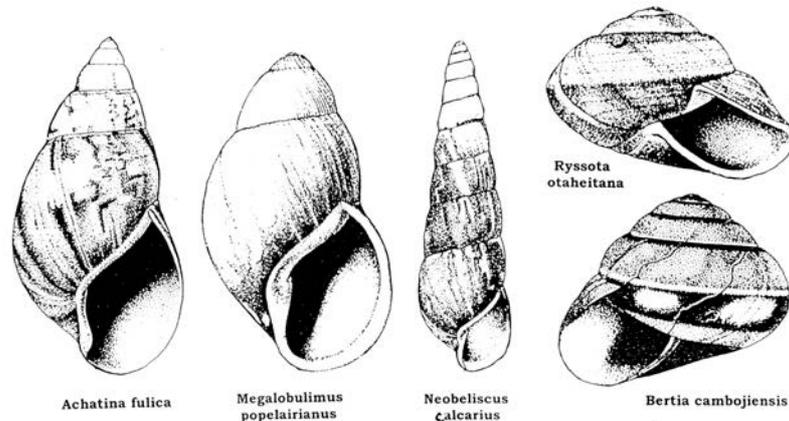


Fig. 7. The largest Recent Stylommatophora. After Schileyko (1998–2007).

Рис. 7. Самые крупные современные стебелчатоглазые. По Schileyko (1998–2007).

Achatina fulica Bowdich, 1822, *Megalobulimus popelairianus* (Nyst, 1845), *Neobeliscus calcarius* (Born, 1780), *Ryssota otaheitana ovum* (Valenciennes, 1827), *Bertia cambojiensis* (Reeve, 1860).

the above mentioned Filholiidae with shell height up to 100 mm.

Consequently, since the Cretaceous the limits for dimensional characteristics of the shell disappeared to an extent in which it (size) depended on the food peculiarities.

Recent stylommatophorans, according to their diet, can be divided into the following seven groups:

1. Detritophages/bacteriophages. Mollusks of small size.
2. Micromycophages. Feed on fungihyphae. Snails of small size.
3. Macromycophages. Eat fruit bodies of macromycetes. Dimensions not limited (slugs not considered).
4. Lichenophages. Feed on lichens. Mollusks of small or middle size.
5. Phytophages. Feed on living tissues of angiosperms. Dimensions not limited.
6. Predators. Feed on other mollusks (including cannibalism), soil oligochaete worms and insect larvae with soft coat. Dimensions not limited.

7. Polyphages. Eat everything, including the rotting parts of the angiosperms and organics of animal origin. Dimensions not limited.

Thus, the members of four groups of the above seven can reach a large size (Fig. 7). The largest snails are African Achatinidae (*Achatina*, shell height up to 200 mm), South American Megalobulimidae (*Megalobulimus*, height up to 160 mm), Subulinidae (*Neobeliscus*, height up to 120 mm), Philipianian Ryssotidae (*Ryssota*, diameter up to 120 mm) and south-eastern Asian Dyakiidae (*Bertia*, diameter up to 80 mm).

The snails of larger size usually live on the earth surface, often bury into the soil during the unfavorable for an active life, or (in the tropics) sometimes climb the trees.

The peculiarities of biology of the species upon which the size of mollusks depends also on the nature of preferred habitats. So, snails inhabiting forest litter have, as a rule, small or tiny size (typical examples are *Vertigo*, *Punctum*, *Euconulus*, *Pristiloma*, *Hawaiiia*).

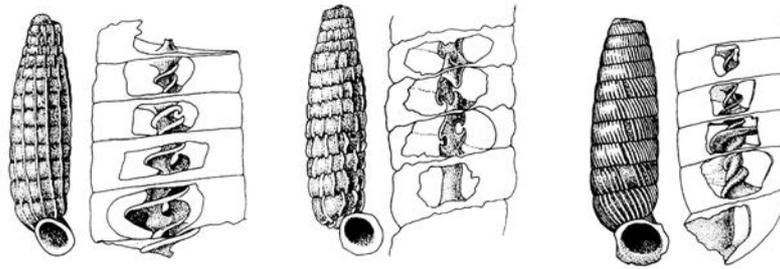


Fig. 8. Examples of complex columellae in Urocoptidae. After Schileyko (1998–2007).

Рис. 8. Примеры сложных столбиков у Urocoptidae. По Schileyko (1998–2007).

From left to right/Слева направо: *Amphistemma pilsbryana* (Ramsden, 1914), *Idiostemma uncatata* (Pfeiffer, 1859), *Ezochara strangulata* (Pfeiffer, 1856).

2.3. Aperture

The aperture is the main channel of communication of the mollusks with the outside world, so any elements of the apertural structure are related, directly or indirectly, with the adaptation of animals to any external factors. Therefore it is natural that the main emphasis here is given to the functional analysis of peculiarities of the apertural structures.

In a number of terrestrial pulmonates, juvenile shells differ from fully formed ones mainly by a number of whorls and, consequently, by their size (Achatinidae, many Subulinidae, Charopidae, Zonitidae, most of Helicarionidae, some Hygromiidae, Succineidae, etc.). More often, however, the fully mature individuals develop adult characters which testify puberty and cessation of growth of the mollusk (narrowing of the last whorl, the presence of lip and aperture armament). Such features are usually called definitive characters.

In the adaptive and evolutionary meanings the juvenile and definitive characters are equivalent and clear boundaries between them may be absent. But each of the age groups has its own, sometimes quite substantial, functional peculiarities, so there is a reason to consider them separately.

2.3.1. Juvenile characters

One can distinguish three types of apertural structures according to the time of their formation in the ontogenesis:

1. Those appearing in embryogenesis or early postembryogenesis and in the process of the shell growth but not undergoing significant qualitative changes (for example, columellar plates in Orculidae, Urocoptidae, Clausiliidae and some others).

2. Shell grows, without having the aperture armature, until reaching subadult state when the final portion of the shell is completed quickly together with the elements of armament of the aperture (numerous Pupillidae, Gastrocoptidae, Vertiginidae; a number of Bulimulidae; some Helicidae (Ariantinae), for example, *Causa*, *Isognomostoma*; some Hygromiidae, for example, *Chilanodon*, many Polygyridae and some others).

3. During the shell growth the elements of apertural armature are periodically formed but they are not related to the definitive aperture. Such elements may be called “pseudodefinitive” (palatal and/or basal folds in *Lauria* of Orculidae; Plectopylidae, some Streptaxidae, *Clappiella* of Zonitidae, *Paedhoplita* of Hygromiidae, the lips in many Hygromiidae).

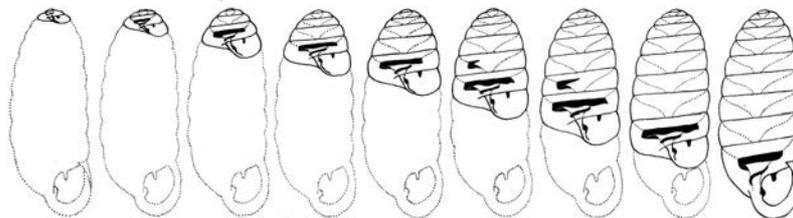


Fig. 9. Postembryonic development of *Sphyradium doliolum* shell. Apertural teeth in black. After Schileyko (1984).

Рис. 9. Постэмбриональное развитие раковины *Sphyradium doliolum*. Устьевые зубы зачернены. По Schileyko (1984).

The first type is associated with the history of the taxon, often has atavistic nature, and not in all cases amenable to functional analysis. Sometimes columellar plates exhibit a great variety and can reach a considerable complexity (the most striking example is Urocoptidae, Fig. 8), and in such cases they deserve a special consideration from the functional point of view. Unfortunately, I do not have enough material for such an analysis. At the moment I can only assume that such a complex structure linked to the thin differentiation of columellar muscle that facilitates the management of a high shell inherent to urocoptids.

As regards barriers located on the parietal wall of the aperture, they, in dependence on their origin, can be attributed either to the category of immersed or superficial.

So, the long parietal plate that appears at the end of embryogenesis, is homologous to columellar plate and belongs to the category of immersed. The point is that there is no clear boundary between parietal and columellar margins of the aperture and parietal plate is the columellar one that shifted to the parietal wall. Parietal plate of this type occurs, for example, in some Orculidae. Parietal teeth of superficial type are not connected with columella and can be formed either immediately before completion of

shell growth, or periodically with the shell growth: examples are *Triangustoma*, *Gemina*, *Chondrulopsina* (Enidae), *Paedhoplita* (Hygromiidae), *Isognomostoma* (Helicidae), many Polygyridae.

The second and third types are usually associated with the peculiarities of the biology and behavior of snails at different stages of their postembryogenesis (see below).

These types of apertural structures are convenient to consider on the example of the three species in Orculidae: *Sphyradium doliolum* (Bruguière, 1792), *Pagodulina lederi* (O. Boettger, 1886), and *Lauria cylindracea* (Da Costa, 1778) (Schileyko, 1967a, 1984). The following information is based on direct field observations, though not supported by strictly quantitative data.

The juveniles of *S. doliolum* live under conditions that are significantly different from those of the adults. These snails reproduce by laying 10–20 eggs in various shelters. Shell of newly hatched snails consists of one and a half whorls (Fig. 9), bearing spiral striation. These shells have already two apertural structures: tubercular parietal and thread-like columellar plates. By forming the first postembryonic whorl, the length of the parietal plate is about 3/4 of its length. By 2–3 shell whorls, this plate occupies almost the entire last whorl. When the shell has 3–4

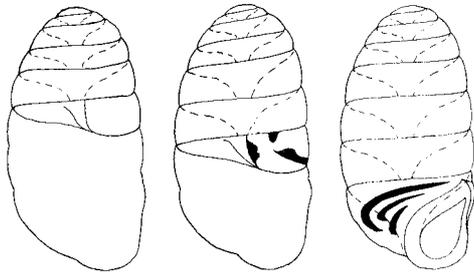


Fig. 10. Position of apertural teeth in *Pagodulina lederi*.

Рис. 10. Положение устьевых зубов у *Pagodulina lederi*.

definitive whorls, the appearance of the parietal plate changes: its lower edge becomes undulating. The plate reaches its maximum development at the stage of 5–8 definitive whorls. With the growth of the last whorl, the wave-like undulation of the plate edge disappears. At the early stages (1–4 whorls) the length of the plate is not more than one whorl; at 5–6 whorls the parietal plate length can reach two whorls, with further growth its length decreases again. Finally, in the fully formed shells the parietal plate usually extends up to 1–1.2 whorls (sometimes a little more).

Taking the above into consideration, let us consider the conditions under which the snails live at early stages of their postembryogenesis. Since the eggs are deposited in secluded and strongly shaded areas, the newly hatched snails turn out in the same conditions. With further growth the young snails crawl up to the middle and upper layers of the forest debris or litter, since for puberty these thermophilic animals require a certain minimal insolation. Aperture of the snail at that time is still relatively wide, and due to the growth of the shell, the role of the parietal plate as a means of protecting the aperture increases. At subdefinitive age the

snails live already alongside with adults and but they need intensification of protection of the aperture because the adult characters are not yet developed. In addition, at this time the snails eat particularly intensively, filled crop takes a significant volume, and parietal plate, serving as a partition between the crop and rectum, is a limiter which minimizes pressure on the rectum from the crop. Accordingly, just at this time parietal plate reaches the strongest degree of its development. More information about the role of the parietal plate can be found below in the section “definitive characters”.

Finally, the mature animals are associated mostly with the middle and especially with the upper layers of litter or rock slide, already having adult features: the aperture with lip and narrowed last whorl.

The shell of *P. lederi* that lives mainly in the litter of deciduous forests basically has same features of postembryonic morphogenesis as in *S. doliolum*, but, speaking figuratively, in a synoptic form.

Young pagodulinas, just hatched in the lower layers of the tree waste, lack any teeth in the aperture until they reach the subadult age (at 6–7.5 whorls) (Fig. 10). At this stage, a rather powerful aperture armament has formed: columellar and parietal lamellae and an elongate-tubercular palatal fold. At this time, these mollusks which have not yet reached puberty already live together with adults, but do not have the adult structure, the lip. Since the lip is absent, but the need to protect the aperture does exist, at this stage the provisional structures has formed, which perform, probably, the function of protection. Upon reaching full number of whorls (8–8.5) and with the formation of a lip, above mentioned teeth appear deep inside the last whorl and over the time undergo some reduction.

Thus, a provisional apparatus formed entirely at subadult stage of the shell formation

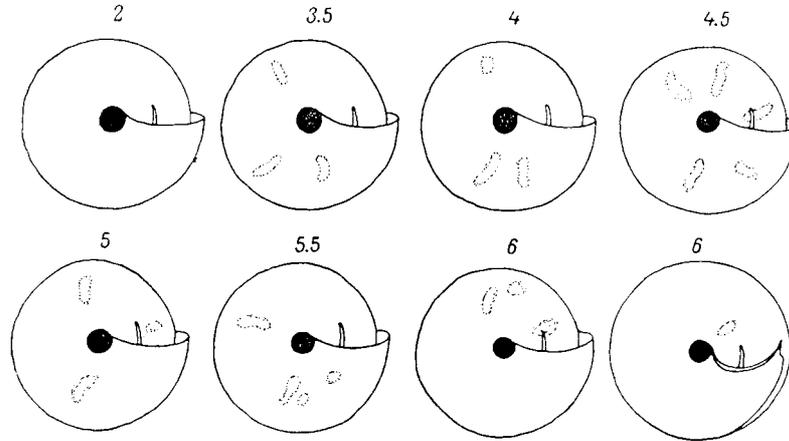


Fig. 11. Provisionary basal plicae in *Lauria cylindracea* transluceing through the shell wall at various stages of postembryogenesis. Numerals show the number of whorls. Figures are reduced to the same size. After Schileyko, 1984.

Рис. 11. Провизорные базальные складки у *Lauria cylindracea*, просвечивающие сквозь стенку раковины на разных стадиях постэмбриогенеза. Цифры показывают число оборотов. Изображения приведены к одному размеру. По Schileyko, 1984.

and, having fulfilled its function, becomes resorbed.

In *L. cylindracea*, unlike the previous two species, provisional structures arise several times during the shell growth (Fig. 11). It is an ovoviviparous species, with each individual producing from 4 to 12 young snails. The shell of a newly born snail has about two whorls and is equipped with one weakly developed parietal lamella. When the first postembryonic whorl is formed, there appears a radial fold on the basal edge of aperture, and at the stage of 3.5 whorls the number of folds achieves usually three. At the stage of 4 whorls the resorption of the first, i.e. posterior fold begins.

The maximal number of simultaneously present basal folds does not exceed 5, and such a situation is observed until 4.5–5 whorls of the shell. With further growth, the new basal folds begin to appear less regular-

ly, and at reaching of the full number (6–7 whorls) they are either completely absent (most often), or one of them is present at the beginning of the last whorl (eventually, totally resorbed).

Parietal lamella in *L. cylindracea* appears, as mentioned above, in late embryogenesis and lengthens with molluscan growth. In the course of further development the upper part of the plate disappears, remaining only a trace in form of a thin, light strip. Lamella as such is always present only in the last whorl, having almost constant height; when lip is formed, the lower end of the plate thickens, turning into tubercular tooth.

Based on the above description of the morphological transformations, let us consider some aspects of life of a juvenile snail after its birth.

Before the birth of young snails, the parental individual descends into lower layers

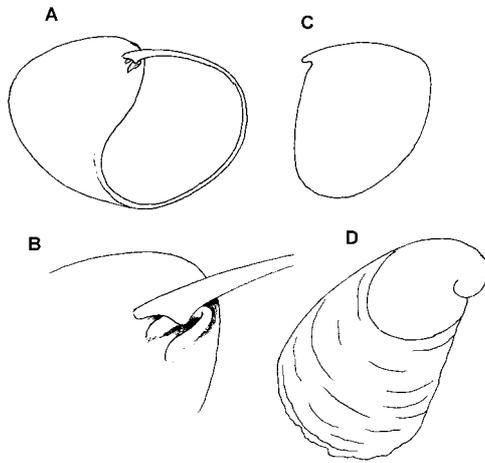


Fig. 12. *Parmacella ibera*. A – juvenile shell. B – region of juvenile shell, enlarged. C – “operculum”. D – shell of adult specimen.

Рис. 12. *Parmacella ibera*. А – ювенильная раковина. В – ангулярная область ювенильной раковины, увеличено. С – «крышечка». D – раковина взрослой особи.

of debris or litter (possibly newly born snails crawl downward). Consequently, young individuals find themselves in the conditions of constant and almost complete shade and high humidity. In such a situation, the weak development of aperture armament looks as a natural phenomenon. The growing snail still leads a secretive mode of life, but gradually rises to higher layers of the litter, where the problem of the water balance is somewhat exacerbated but yet not leading. In this regard, the appearance of basal folds is observed; these folds are functionally analogous to the definitive lip. Upon reaching of 4 whorls the snail lives already together with adult individuals, but needs additional protective devices, since its lumen of aperture is relatively larger than in adults, and the highest number of basal folds, as well as the degree of their development reach the maximum at this time. For all three cases

considered above (*Sphyradium*, *Pagodulina* and *Lauria*) it is characteristic that maximal development of provisional structures is reached at that stage of postembryogenesis when the juveniles occupy the same spatial niche as the mature animals, but have not yet the “adult” protecting structures.

The third type of apertural structures formed in postembryogenesis (periodic appearance of lips and provisory teeth) is not so rare. In addition to the mentioned species of the genera *Clappiella* and *Paedhoplita*, this phenomenon is observed, for example, in a number of species of *Varicella* (Oleacinidae), some Streptaxidae, *Aegopis verticillus* (Lamarck, 1822) (Zonitidae), *Kokotschashvilia phaeolaema* (O. Boettger, 1886) (Hygromiidae). In these cases, the young snails live together with the adults and are equally exposed to the same unfavorable life conditions.

It is appropriate to mention a very interesting way of survival of the dry season, which is observed in some juvenile slugs, in particular, in *Parmacella ibera* Eichwald, 1841 (Schileyko, 1967b). Here we see a combination of morphological and biological peculiarities of the species. Under conditions of the south-eastern Transcaucasia, the hatching takes place in late June to early July, i. e. at the peak of the dry season. Just hatched mollusk has a shell, consisting of approximately one and a half whorls, where it can entirely hide. This embryonic shell (nucleus) is provided with an “operculum” which is seemingly a modified epiphragm. In subangular region of the aperture there is a tiny horseshoe-like plica, both ends of which are directed outward (Fig. 12). Over the space between the branches of this plica, there is a beak-like outgrowth of the aperture margin.

When the “operculum” is closed, the notch on its upper left margin corresponds to the lower branch of horseshoe fold; the

stalk of the “operculum” which is placed over the notch enters the space between the upper branch of the horseshoe and the inner surface of the suture. In this place, the stalk grows together with the upper branch of the fold and, at a shorter distance with palatal margin of the aperture which is slightly bent down.

When the “operculum” is opened from inside under the pressure of the animal's body, the stalk is bent and the “operculum” rests against the beak-shaped outgrowth of the aperture, which limits the degree of opening of the “operculum”. When the animal hides in a shell, the stalk, by virtue of its elasticity, returns to its original state, tightly shutting the aperture. In time of coming the wet season the “operculum” falls off (because the stalk dries out, loses its elasticity and breaks down under the pressure of the snail body) and the horseshoe-like plica resorbs.

2.3.2. Adult characters

In most cases, the adult (definitive) characters are related, directly or indirectly, to the formation of apertural armature. The full set of aperture armature includes a lip having the form of radial folds, and a system of teeth of various size and shape, located inside the aperture. Topographically, the teeth are of two types, designated as superficial and immersed (Schileyko, 1984). Superficial teeth are arranged in the plane of the aperture margins and represent local thickening of the lip. Immersed teeth are mostly not connected with the lip and located in the aperture at some distance from its margin.

The differences between the superficial and the immersed elements of the aperture armament are very serious not only from the topographic but also from the functional point of view, that is why these categories deserve separate consideration.

2.3.2.1. Superficial teeth and adaptations to arid conditions

The lip is formed because at subdefinitive state, at the completion of the shell growth, the mantle margin (mantle collar) rapidly secretes calcium carbonate that is deposited on the entire free edge of the aperture in the form of a radial thickening, which is the lip. When there are zones of especially intensive secretion in the mantle collar, the local thickenings of the lip are generated, which are superficial teeth in such places (Edlauer, 1941).

One of the most important factors of life of the land snails is the water regime. As stated above, the main, and often the constant danger is the risk of dehydration. Water loss performs mainly through the aperture. Obviously, improving the mechanisms that slow down the evaporation is, perhaps, the most urgent problem, which strongly depends on the habitat conditions.

There are three methods to slow down the evaporation rate: (1) the narrowing of the last whorl toward the aperture; (2) the formation of a lip and superficial teeth; (3) the formation of a protective film (epiphragm) due to the intensification of mucus secretion by the mantle collar. The third method usually supplements the first two.

The snails usually survive dry seasons by one of two ways. The nature of morphological adaptations in representatives of these two ecological groups is considerably different.

1. Mollusks digging into the soil or hiding deep into crevices of rocks [for example, *Valtonia*, *Oligolimax*; *Cahillus greggi* (Miller, 1972) lives even in the extremal conditions of Death Valley (Johnson Canyon)]. These snails devoid of these features, but in reality they exist in the low horizons of rockslides or deeply in the cracks of the rocks, where the temperature is lower and humidity is always high enough.

2. Mollusks live openly, glued with the mucus to a stones, dry leafs or other flat surfaces. Such species often form aggregations (clusters) on grass or bush branches (for example, some Pachnodidae, a number of Bulimulidae, Sphincterochilidae and majority of xerophilic Hygromiidae, like *Xeropicta* or *Xerolenta*). They are characterized by three features: a toothless mouth, white shell color (usually with dark bands or radial stripes), as well as by a behavioral feature — they often form dense aggregations (clusters). All three features can be regarded as adaptations to life in arid conditions: lack of apertural teeth provides the fast retraction of the snail into the shell; white shell reflects the sun rays, reducing the risk of overheating; temperature within the cluster lower than the temperature of the ambient air (Fischer, 1971; Yom-Tov, 1971; Schmidt-Nielsen et al., 1972; Boss, 1974).

First, let us consider adaptations that are characteristic for the mollusks which bury themselves into the soil to survive the dry season. The close connection between the conditions of humidity and the degree of development of armament of the aperture in *Chondrula tridens* (Müller, 1774) (Enidae) has been shown by Matyokin (1950). According to this author, the drier are the conditions, the more intensive is the development of the apertural teeth. Thus, Matyokin has concluded that the teeth serve for squeezing of mucus from cephalopodium during withdrawal of the snail into the shell; the epiphragm is formed at the expense of this mucus. It is essential that in the mentioned species the elements of aperture armament are classified as superficial. Such a correlation occurs in other species that have superficial teeth, and not only at the population level, but also at the interspecific. For example, strongly developed lip of another representative of Enidae, *Chondrulopsina*

intimescens (Martens, 1874), bears only slight swelling, whereas in closely related species *Ch. fedtschenkoi* (Ancey, 1886), these swellings are transformed into strong tubercles, with the degree of their development varying, however, greatly depending on the conditions under which the given population lives. It should be clarified that the mucus, which is used for formation of the epiphragm, is actually taken not from cephalopodium, but from the mantle collar, since at the snail withdrawing into the shell, the cephalopodium does not contact with the aperture margin, and even more so with the lip. This can be seen if to fix the shell by a piece of plasticine, orienting it by the aperture toward the observer, and to direct to it a strong ray of light from an illuminator. In this case it is easy to notice that when the snail, irritated by light and heat flow is drawn into the shell, the inner margins of the aperture together with lip and teeth are immersed in the thick of mantle collar, and the mucus from the cephalopodium is wiped off not by teeth (with which cephalopodium, I am repeating, has no contact), but by the lobes of mantle collar (Fig. 13).

Only when cephalopodium is fully withdrawn, and the central hole of the mantle collar, where the cephalopodium was retracted, is covered by a thin film of transparent mucus, the withdrawing of the mantle collar begins. Just at this moment the mucus is removed from the surface of the mantle collar, using lip and teeth. The mucus is saturated with granules of calcium carbonate, and the epiphragm is formed due to just this mucus. Only the most central portion of the epiphragm includes that mucus, which had previously been removed by the lobes of the mantle collar from the surface of the cephalopodium (Schileyko, 1978).

I think, it is hard to disagree with the fact that in arid conditions an epiphragm satu-

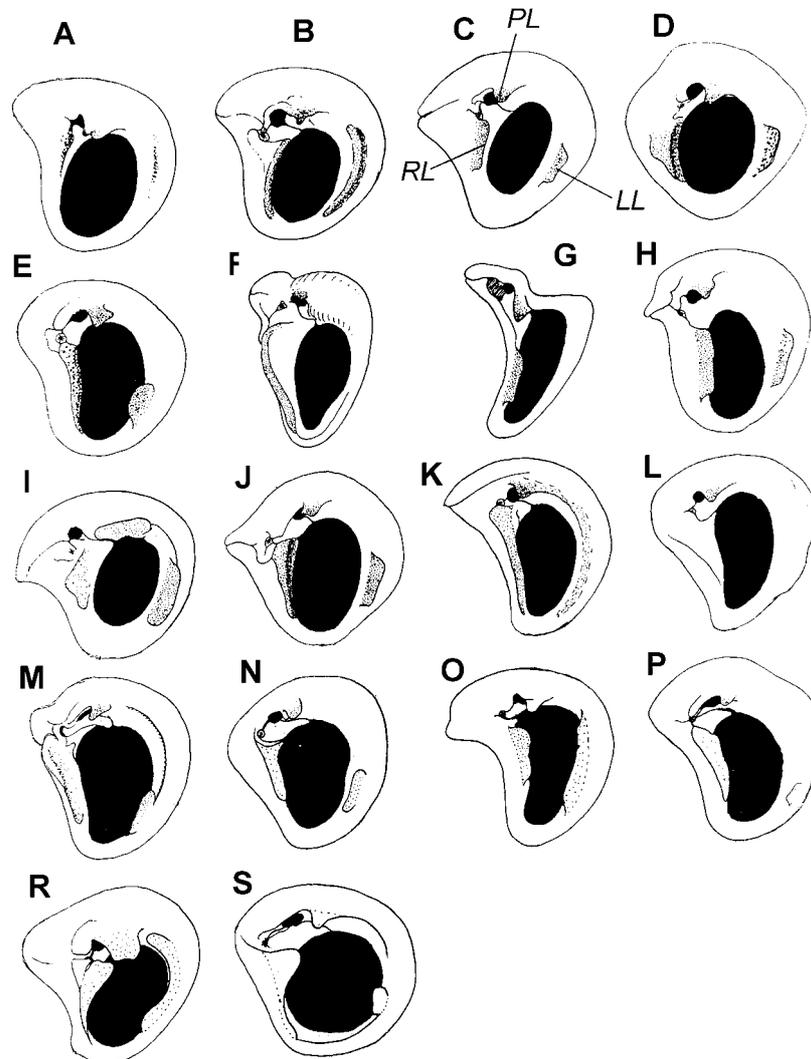


Fig. 13. Mantle collar in Stylommatophora.

Рис. 13. Мантийный валик у Stylommatophora.

A – *Sphincterochila candidissima* (Draparnaud, 1801); B – *Cerņuella cespitum* (Draparnaud, 1801); C – *Caucasigena abchastica* (Lindholm, 1927); D – *Arianta arbustorum* (Müller, 1774); E – *Fruticocampylaea narzanensis* (Krynicky, 1836); F – *Lindholmiola corcyrensis* (Férussac, 1839); G – *Helicodonta obvoluta* (Müller, 1774); H – *Metafruticicola pellita* (Férussac, 1832); I – *Helix pomatia* Linnaeus, 1758; J – *Euomphalia strigella* (Draparnaud, 1801); K – *Theba pisana* (Müller, 1774); L – *Ponsadenia semenovi* (Martens, 1864); M – *Angiomphalia caelestimontana* (Tzvetkov, 1940); N – *Leucozonella mesoleuca* (Martens, 1882); O – *Xeropicta derbentina* (Krynicky, 1836); P – *Lindholmomneme nordenskioldi* (Martens, 1876); R – *Cerņuella neglecta* (Draparnaud, 1805); S – *Karaftohelix middendorffi* (Gerstfeldt, 1859).

rated with granules of CaCO_3 more effectively retards evaporation than epiphragm, containing just a little of calcium carbonate. Consequently, one can assume that the more moisture deficit occurs in the given biotope, the more stringent are requirements for the properties of epiphragm and more intensely the zones of mucus secretion are working. As a result, two independent phenomena arise: strengthening of the superficial armament and intensification of saturation of epiphragm by calcium carbonate. Since the mucus from the foot surface is removed by the lobes of the mantle collar, the middle part of epiphragm is built due to this mucus whereas the peripheral part is formed at the expense of the secret released by the mantle collar, i.e. due to the same source as the superficial teeth (Campion, 1961).

Thus, it is reasonable to assume that the degree of development of apertural teeth really depends on parameters of the water balance at the given place, but this relationship is not direct, but "coupled" with the presence in the mantle collar the zones with intense secretion of mucus that is rich with CaCO_3 . This mucus is needed primarily to enhance the moisture loss resistance of the epiphragm; but the existence of the mentioned zones determines formation of the teeth on the aperture margins, contributing in turn, squeezing of the mucus from the mantle collar. In other words, a side effect of the development of the zones of enhanced secretion acquired an independent adaptive value.

In consideration of the snails attaching to the substrate by aperture in the dry season, as different from those burying in the soil, it is convenient to start with pronounced xerophilic mollusks living openly. Very significant is the fact that the vast majority of species belonging to this category lack not only the teeth of superficial type, but as well

as the lip (immersed teeth may be present). Therefore the relationship between degree of development of the elements of the aperture armament, properties of epiphragm, and parameters of the water regime, which was discussed above, seems to be typical for the burying forms only.

How, then, to minimize the water loss in the species living openly, i.e. under the most arid conditions? With onset of the dry season, adult or subadult snails rise up on stems of grass or branches of bushes. While the animal crawls, it keeps itself on a vertical surface due to sticky mucus secreted by the pedal gland located in the thickness of the foot and opening by a horizontal slit beneath the mouth opening. Then the snail stops and starts to withdraw itself into the shell, with its basal margin of aperture directed upward, while the shell apex downward (this is true for the snails with an elongated shell, in particular, for some Enidae). When the head and anterior part of the cephalopodium have withdrawn, the basal margin of aperture comes into contact with the substrate, and at this point the aperture sticks by the mucus secreted by the mantle collar. Now, when the aperture is fixed on the vertical surface, the rest parts of the cephalopodium retract gradually; as withdrawing the palatal and columellar margins are lowering onto the substrate; parietal margin contacts with the surface in the last turn. As a result, at the end of retraction of the snail, the aperture becomes glued along its entire perimeter — partly by the mucus, secreted by the mantle margin, partly by the mucus which has been removed from the foot by the lobes of the mantle collar. Description of these processes is based on the direct observation of the withdrawal of representatives of the Enidae, Crimean *Brephulopsis cylindrica* (Menke, 1828), and Transcaucasian *Georginapaeus hohenackeri* (Pfeiffer, 1848), and Hygromii-

dae — Central Asian *Xeropicta candaharica* (Pfeiffer, 1846).

2.3.2.2. Immersed teeth

Under the term “immersed teeth” I mean primarily the elements of the palatal margin, since the long, elongated along whorls parietal and columellar lamellae are not connected with definitive (adult) aperture, and have other origin and other functions.

Teeth located on the parietal and columellar margins of the definitive aperture, are not always connected with initial parietal and columellar lamellae. They can be formed independently and often belong to the category of superficial.

Sometimes the last whorl (in the high shells) narrows toward the aperture. In such cases, the perimeter of the subdefinitive aperture is reduced, but the perimeter of the mantle edge remains the same. As a result, the mantle edge crumples and the immersed teeth have formed in the emerged indentations. This has been shown for Clausiliidae (Edlauer, 1941) and is true, probably, for many other groups with “toothed” aperture.

A pertinent question concerns the correlations of emergence of the immersed palatal folds and narrowing of the last whorl. Obviously, this is common and natural, but not obligatory. For example, *Pseudonapaeus otostomus* (Westerlund, 1898) (Enidae) has a spindle-shaped shell, but the immersed teeth in this species are absent; on the contrary, a representative of the same genus, *P. entoptyx* (Lindholm, 1925), has a tower-shaped shell, but it has a longitudinal palatal fold inside the aperture. Immersed teeth may play a role in reducing evaporation (by reducing the area of the aperture), but this function is not primary. An elongated structure due to its shape is hardly effective for squeezing mucus from the mantle collar, since this purpose requires a structure, oriented perpendicular

to the axis of withdrawal and at longitudinal arrangement of folds the mantle slips on them, like on rails. Therefore, the main role of immersed folds is different — namely, to ensure the efficiency of gas exchange, protection of rectum and management of shell. This statement deserves a detailed consideration.

Aperture teeth, breathing, and excretion. If a shell has parietal teeth, there is usually also a small tooth in the upper part of the palatal margin. The crests of these teeth are directed towards one another. Together, these teeth form a kind of sinulus, which houses pneumostome, anus and the opening of the secondary ureter. Thus, the named teeth protect these organs (chiefly pneumostome) from the pressure of adjacent organs. This is important, because in time of intensive feeding, the crop that adjoins to mentioned organs, strongly swells and presses on them. It is clear that, at strong expansion of the crop, the rectum, secondary ureter and pneumostome are so strongly pressed against the outer wall of the shell that certain problems can arise with defecation, respiration and removal of excreta. This problem is particularly sharp when the last whorl is narrowed. The presence of rigid partition between the crop and pneumostome region eliminates (or, at least, attenuates) this problem and the parietal tooth participates in such partition.

If we take into account that the main pressure is made from one side, it becomes clear why the parietal tooth is more “necessary” than palatal; this explains the fact that the parietal tooth only (without palatal) is observed much more often than palatal only (without parietal).

Immersed teeth and management by shell. Shell and visceral sack with lung cavity can be likened to two cones inserted into one another. If the surface of these cones is smooth, the inner cone can be rotated relative to the outer and vice versa. But any

rigid structure protruding into the cavity of the aperture, will inevitably play the role of a stopper that limits an ability to rotate the visceral sac inside the shell, and the system of apertural teeth creates very effective coupling of shell with the body of the mollusk.

The parallel with two cones in this case is very conditional, because the visceral sack of a snail is curled into a spiral. Torque in this case can occur only in the region adjacent to the aperture, i. e. just where the complex of immersed teeth is located. Facilitating the management by the shell, the immersed teeth slow down the speed of retraction: it is possible that just with this fact it is linked to the absence of immersed teeth in a number of small snails, living in condition of strong temperature fluctuations. A palliative way out is observed, for example, in *Truncatellina*: a small palatal tooth, located deep inside the shell, increases the coupling between the body of the animal and shell without impeding at the same time the rapid retraction. Similar situation takes place in some Enidae: *Pseudonapaeus entoptyx* (Lindholm, 1925), *Siraphoroides moltschanovi* (Likharev et Rammelmeyer, 1952) (Schileyko, 1984).

In this connection a rare modification of columellar plate should be noted when it raises parallel to the columella, expanding at the same time into a blade. Such a structure of the columellar plate is observed in *Azeca* (Cochlicopidae), *Vertilla* (Vertiginidae), a few *Euxinolauria* (Orculidae) and in some Achatinellidae. Comparing position of the shell in respect to the foot in crawling *Azeca* and *Cochlicopa*, Paul (1974) drew attention to the fact that, in *Azeca*, the shell is oriented parallel to the foot, while in *Cochlicopa* (in which the columellar plate is absent) the shell is sideward deviated up to 20–30°.

Paul connects this difference to the fact that *Azeca* has the columellar plate of the described structure while *Cochlicopa* has not.

The assumption by Paul seems fair: when an animal is crawling, the extended vertical blade of columellar plate lies on the dorsal side of the cephalopodium, greatly limiting the possibility of deviation of the shell aside. Paul, however, overlooked that the same role is more effectively performed by the saddle-like system formed by parietal and subparietal plates interconnected by transverse thickenings: when a snail is crawling, this “saddle” covers the foot dorsal side from above and fixes the shell in certain position in relation to the cephalopodium. Such a rigid system is effective if the aim is to fix the shell in certain position relative to the foot with the minimal effort of the columellar muscle. However, this system greatly limits the mobility of the shell thus making difficult its management. Species of *Cochlicopa* that lost the apertural armature are more progressive in this regard, as they can actively manage the shell. Both *Azeca* and *Cochlicopa* live mainly among forest litter, small twigs, tangled grass, and their ability to manage the shell actively under such conditions is, to my mind, a valuable acquisition. Additionally, this is one of important circumstances that explain why *Azeca* has a relatively narrow area of a relic type and lives in a limited set of habitats, while species of *Cochlicopa* are common almost everywhere in Holarctic.

Maintaining of shell in certain position is a special case of its control, and an important role of immersed teeth often consists of keeping the shell in more or less constant orientation relative to the cephalopodium. In this regard shells of some Hypselostomatidae are remarkable: their aperture is sharply lifted, and its plane is almost horizontal. Therefore, when the animal is crawling, the summit of the shell is directed downwards and probably does not (or nearly does not) touch the substrate, i. e. the shell is a weigh. One can assume that, as a result, the problem of the

most advantageous position of the visceral sack with respect to the cephalopodium is exacerbated. So, there are four strong teeth with blunt tops in the aperture of the *Hypselostoma* species; I think that, leaning on the dorsolateral surfaces of the cephalopodium from right and left these teeth restrict the possibility of free movement of the shell and keeping it in the most favorable position. In parallel, the combination of parietal and upper palatal teeth creates a sinus, i.e. these teeth fulfill also the traditional function of protection of pneumostome and rectum.

As noted above, the appearance of the teeth of immersed type is often associated with the narrowing of the last whorl, which leads to the formation of fusiform shell. The role of this process and evolutionary consequences deserve a special consideration.

Narrowing of the last whorl is probably an ancient acquisition that repeatedly occurred during evolution of the stylomatophoran mollusks; indeed, species with fusiform shells are common among Chondrinidae, Enidae, Bulimulidae, Urocoptidae, Clausiliidae, and Streptaxidae. Therefore the assumption that this narrowing had occurred originally without any connection to some external conditions, but was acquired subsequently to facilitate the management of elongated shell, or for keeping it in the most favorable position relative to cephalopodium, looks quite plausible.

Reducing of the diameter of the last whorl provides a closer mutual adjoining of the internal organs, and, in particular, a more tight contact of the columellar muscle with the columella. Narrowing of the last whorl may be compared with taut corset: a gymnast or a dancer, with his clear and strictly coordinated movements, tightly tightens the belt that plays the role of an outer support during body turnings (Schileyko, 1984; Suvorov, 1993). It was shown above that long

columellar plate is an archaic character; the presence of this plate facilitates the management of the shell, and the latter is performed more successfully with the tighter contacts of the columellar muscle with the plate. In its turn, the tight adjoining of the columellar muscle is largely ensured by narrowing of the last whorl. Thus, in the groups targeted to increasing of the shell height, process of immersed armature formation is observed, some elements of which became more and more finely adapted to optimize the spatial orientation of the shell of moving animal.

Further development of the apertural armament of immersed type in this direction in a number of groups has reached an evolutionary dead end: a complex system of teeth blocked up the aperture to such a degree that the rate of withdrawal of the snail into the shell decreased significantly, and the amplification of the drought became fatal, especially for the animals with small size.

Snails with strongly toothed aperture spend more time than animals of same size and with same whorls number but with a simple aperture.

This difference is related to the fact, that if the aperture is devoid of teeth, just a simple contraction of the columellar muscle is enough for withdrawing the snail. If there are numerous hard projections in the lumen of the aperture, then withdrawal, in addition to retraction of the axial musculature, needs a complex redistribution of hemolymph in the body sinuses, which requires additional time.

The way out of this evolutionary dead end was found by snails, which had not time to reach an irreversible and critical specialization of complex aperture apparatus. It can be assumed that their development has gone toward a fine functional differentiation of the columellar muscle to maintain their ability for a quick withdrawal.

This hypothesis is based on the following facts.

1. Among Vertiginidae and Gastrocoptidae, the species with the strongest aperture armament were found in representatives having become extinct by middle of the Neogene (Steklov, 1967; Steklov, Tzytovich, 1967).

2. The most archaic and weakly variable species among Recent Vertiginidae is *Vertilla angustior* (Jeffreys, 1830) which has a complex aperture. On the contrary, the most evolutionarily advanced species, with a huge distributional area, a very wide amplitude of variability and often abundant, *Vertigo modesta* (Say, 1824) shows a tendency to reduction of teeth down to their complete disappearance.

3. Members of the genus *Euxinolauria* (Lauriinae, Orculidae), mostly inhabiting western regions of the Caucasian Isthmus, live only in forests, especially in relic forests, and are characterized by complex armature of the aperture. The representative of monotypic (perhaps, oligotypic) genus *Lauria cylindracea* (Da Costa, 1778), with vast area and wide spectrum of biotopes, from sparse deciduous forests to semi-deserts, has a relatively simple aperture equipped with a single small parietal tooth and (sometimes) a rudimentary columellar one.

I guess that the above explanation of these facts is related, ultimately, to the speed of retraction of the snail into the shell. The species of the genus *Euxinolauria* inhabit forests, under condition of permanent shade; they have not a risk of rapid drying out under straight sun rays. Sometimes periods happen in the western Caucasus when the forests dry out very much, but the drying is so slow process that it does not matter how long time the snail spends for withdrawing, a few seconds or a few minutes.

4. Species of *Euxinolauria* living in the most wet habitats, viz. in the moist shady

ravines, on the surface of the wet rocks, etc. [*E. rectidentata* Schileyko, 1975, *E. paulinae* (Lindholm, 1913)], have immersed elements of aperture armament only. *E. pulchra* (Retowski, 1883) lives in the driest places: this species inhabits deciduous forests in the northwest Caucasus, which dry out especially strongly. And it is this species that developed, in addition to the immersed teeth, the superficial tubercles and folds playing a role in protecting the body of the mollusk from the moisture loss.

On this conformity to natural laws the peculiarities of ecology of individual species may superimposed. So, judging from the structure of the aperture *E. tenuimarginata* (Pilsbry, 1922) is the most moisture-prefering species. It lacks the superficial teeth, but has a wide lapel of the aperture margin that provides a snug fit to the substrate. *E. sinangula* Schileyko, 1975, in contrast, has not only immersed, but also superficial teeth, this fact suggesting the greater resistance to drying out than *E. tenuimarginata*. *E. superstructa* (Mousson, 1876) occupies an intermediate position.

Quite a different situation exists in the conditions where *Lauria cylindracea* dwells. Scorching sun rays act as a hard instrument of selection for the speed of withdrawing. With the small size of this animal (the height of its shell is no more than 4.5 mm) the problem, as noted above, is so acute that even a slight slowdown in withdrawing threatens snail to die because of dehydration.

Note in passing that mollusks living in mesophitic conditions are subjected to thermal shock. For example, some slugs placed under direct sun rays, may die within a few minutes, although the body of the slug cannot lose so much water during such a short time to suggest the death due to dehydration.

Perhaps, it is because of almost complete absence of the teeth in the aperture that a

wide lapel of the aperture margin is developed in *Lauria cylindracea*, due to which the aperture is able to adjoin tightly to the substrate with a minimal clearance. Recall that provisional basal folds, periodically appearing in this species during shell growth (see above) are superficial at the time of their formation. Since a widely expanded margin of the aperture can appear only at the final stage of the shell growth, but the requirements to protect the aperture do exist already in young snails (although not in such sharp form), there is a need for some structures that are capable to temporarily replace functionally the definitive expansion of the aperture margin.

The main results of the analysis of aperture armament can be formulated as the following six basic statements.

1. The teeth in the aperture are represented by two categories that are designated here as superficial and immersed. Superficial teeth are local extension of the lip; during shell growth they may be formed more than once. Immersed teeth are the result of a more or less noticeable narrowing of the last whorl only at the final stage of the shell growth.

2. Superficial teeth and lip generally serve for squeezing mucus from the mantle collar and the formation of the epiphragm.

3. Superficial teeth are present mostly in those mollusks which bury themselves into the soil during the dry season.

4. The main function of the immersed teeth is providing orientation of the shell (with visceral sac) in respect to the cephalopodium and facilitation of the management of a high shell.

5. With increasing of aridity, a strengthening of the superficial teeth and weakening of the immersed ones is generally observed. This trend involves the openly-living species in which the snails survive the drought by gluing with their aperture to a substrate.

6. Species living openly in the arid steppe, semi-desert and desert landscapes mostly lack teeth and a well-developed lip. In such species a wide lapel of the aperture margin is often developed, which allows the snails to adjust tightly to the substrate.

All the above leads to an important general conclusion. If an organism, in the course of its evolution, can substitute rigid and permanent morphological structures for more plastic, more flexible and therefore more sophisticated physiological (or behavioral) acquisitions, such a replacement increases the chances of the respective species to gain an advantage in a competitive interactions with related taxa. Morphological simplification is one of the natural results of such replacement.

2.4. Axial musculature and aperture armament

Axial musculature consists of columellar muscle and its branches. In different groups of Stylommatophora one can observe a differentiation of columellar muscular trunk into several groups of branches to improve the shell management (Suvorov, 1993). As a high-spired shell requires a more sophisticated management than a depressed one, the variety of differentiation of the columellar trunk is especially noticed in members of Enidae, Clausiliidae and other groups with similar shell. Function of the shell management is provided by the columellar lamella in some Enidae, Chondrinidae, and some Streptaxidae, by columellar and supracolumellar lamellae and asymmetrical position of pedal branches in Orculidae, as well as by connective tissue partition which separates the left pedal retractor of the buccal mass from the right pedal retractor and from retractor of the mantle collar in Cochlicopidae and Enidae (Suvorov, 1993).

3. The shell in Stylommatophora: an evolutionary perspective

In connection with the above attempts of functional interpretation of some conchological characters, it is pertinent to discuss briefly the significance of the gastropod shell in a historical aspect.

One can say, with some reservations, that it is the shell that has created a mollusk, since a great number of unique morphological features characterizing the phylum Mollusca is associated with the shell origin. Shell provides relatively efficient protection to mollusk: 1) for most of the snails, this is protection predominately from predators, 2) for the terrestrial ones, it additionally provides protection against water loss (what sometimes is more important). However, the shell, as a means of *passive* protection, puts certain restrictions on the further progressive evolution of these animals. Therefore, the presence of shell can be considered, from a historical point of view, as passing phase in the evolution of the terrestrial pulmonates. In support of this suggestion, one can point to the fact that the tendency to shell reduction is observed almost wherever environmental conditions permit.

Among Recent taxa of Stylommatophora, all stages of the shell reduction can be found, from snails with well-developed shell to slugs, in which just conchiolin plate remains (sometimes inlaid with granules of lime) completely hidden under the mantle. The trend towards disappearance of the shell is absent or very weak in the ancient, mostly morphologically archaic groups only (all pupilloid taxa, Claisiliidae, Streptaxidae + Diapheridae, Megaspiridae, Urocoptidae, and some others). One can assume that the shell gradually becomes a brake of biological progress of the mollusks in course of their current evolution.

The shell, giving a rather effective protection, limits the diversity of snail's reactions to the whole broad spectrum of external irritations, in essence, their reaction is reduced only to the animal retraction into the shell. A slug lacking shell is forced to react more subtly, more diversely and more adequately to the external factors of various kinds.

In addition, the absence of an external shell facilitates penetration of mollusks into narrow chinks and other hiding places.

Another strong argument in favor of this hypothesis is the fact that the density of synaptic contacts in the cerebral ganglia of the slug *Limax cinereoniger* Wolf, 1803 is significantly higher than that of the snail *Helix pomatia* Linnaeus, 1758 (Zs.-Nagy, Sakharov, 1970). It follows from this comparison that the slugs, figuratively speaking, are "smarter" than snails, i. e. have a more perfect nervous organization and obviously more complex behavior.

Thus, I assume that the loss of benefits given by shell is compensated by a more complex behavior of mollusks. However, with the shell reduction the problem of gas exchange is exacerbated, as in this case the volume of lung is decreased and the respiratory surface — the ceiling of lung cavity — is reduced. This contradiction is largely eliminated by the fact that the skin breathing ability is significantly higher in slugs as compared to snails (Runham, Hunter, 1970; Likharev, Wiktor, 1980). Besides, additional respiratory surfaces are developed in some species, such as, for example, in Vitrinidae.

In the terrestrial pulmonates, their mantle collar is equipped initially with three lobes (some of them may be reduced): left, right and pneumostomal (= anal). The role of these lobes is double. First, in the time of withdrawal of the snail into the shell they (lobes) remove mucus from the surface of cephalopodium; at the expense of this mu-

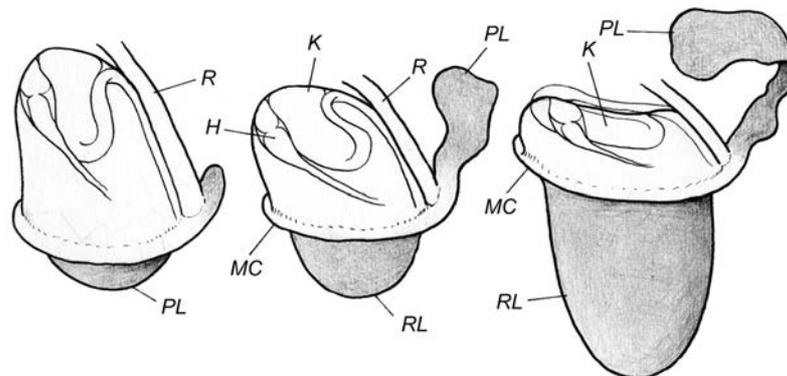


Fig. 14. Mantle lobes of Vitrinidae (from left to right): *Phenacolimax annularis*, *Vitrina pellucida*, *Semilimax kotulae*.

Рис. 14. Мантийные лопасти Vitrinidae (слева направо): *Phenacolimax annularis*, *Vitrina pellucida*, *Semilimax kotulae*.

cus the epiphragm is formed (see above). Second, at a gradual reduction of shell and formation of slug-like appearance (“limacization”) the respiratory surface is reduced, and the pneumostomal lobe is greatly expanding (often covers a significant part of the shell), creating additional respiratory surface and thus compensating the diminution of the lung volume. This dependence is illustrated by the morphological series in the family Vitrinidae: *Phenacolimax annularis* (Studer, 1820) (real snail with shell is well developed) — *Vitrina pellucida* (Müller, 1774) (shell is somewhat reduced) — *Semilimax kotulae* (Westerlund, 1883) (semislug with shell is much reduced) (Fig. 14).

In connection with the problem under discussion, a comparison of the fossil and contemporary cephalopods is indicative. The Paleozoic and Mesozoic cephalopods had an external shell, while it became lost in their Recent relatives (completely in octopuses, and partly in squids and cuttlefishes). The only exception is *Nautilus* retaining the outer shell. In this sense, the extant cephalopods could be regarded as analogs of the

terrestrial slugs; no doubt that they are more progressive than the extinct shelled groups. Moreover, it can be argued that biological progress is determined ultimately by more perfect organization of the nervous system, and this, in its turn, is connected with the disappearance of external shell. The analogy between cephalopod and gastropod mollusks, in the given context is, to my mind, justified and demonstrative.

Another striking example is Opisthobranchia. Their most biologically progressive representatives are so-called sea slugs (Nudibranchia) which are characterized by a complete loss of shell.

With regard to the superorder Stylommatophora, the process of reduction of the shell in them seems to fit the same general trend. As a matter of fact, in 21 of 52 taxa ranked as orders or families, there are genera containing slugs or semislugs, and evolutionary reduction of the shell within the entire superorder occurred (and is occurring currently) at least 18 times (Schileyko, 2003). In addition, two more circumstances should also be taken into consideration.

1. Presence of slugs and/or semislugs in some taxon does not always mean that the loss of shell in this group had taken place only once. For example, among Succineidae this process occurred independently at least twice, in South Asia and in South America (Tillier, 1981); in different branches of Helicarionoidea the loss of shell also occurred repeatedly. So the shell reduction took actually place not in 18, but in many more number of cases.

2. The table presented earlier by the author (Schileyko, 2003, p. 149) does not include the taxa experiencing initial stages of the shell reduction when it is still fully developed, but the first signs of the limacization can be seen. Thus, among Pachnodidae (infraorder Pupilloinei) where slugs and semislugs are absent, there are genera (*Amimopina*, *Rhachidina*, *Edouardia*, *Pachnodus*), in which all or many species are characterized by very thin walls of shell, with the number of whorls being reduced, and the last whorl being swollen and clearly prevails over the others. All this are the signs that can be interpreted as the very initial stages of the shell reduction. In any case, the reduction, as far as it can be seen in the factual material, begins with the appearance of just such symptoms. A similar situation is observed in Orthaliciidae (genus *Sultana*), Helicidae (genus *Cantareus*) and in some other families.

Within the suborder Succineiformes, representatives of only five genera and subgenera (of 28) can be allocated to the category of slugs or semislugs. But some signs of incipient reduction of the shell are marked in all genera constituting the suborder.

Same trend of gradual reduction of shell in Oleacinidae can be seen in Fig. 2.

The current ratio of the shelled (snails) and shell-less (slugs + semislugs) taxa of generic rank — 2316 against 209 (after Schileyko, 1998–2007) — indicates that,

at the geological time scale, the process of disappearing of the shell has just begun, although it is gradually taking the character of a general trend.

This trend is not evident in several either highly specialized or ancient and archaic taxa of the family rank, namely: all pupilloid taxa, Partulidae, Megaspiridae (1 species, extinct in historical time), Urocoptidae, Clausiliidae, Plectopiloidea, Strophocheiloidea, Cerionidae, Achatinoidea, Subulinoidea, Clausiliidae, Streptaxoidea, Endodontidae, Thyrophorellidae (1 species), Punctidae, Helicodiscidae, Discidae.

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