
Family Helicidae excluding Helicinae (Gastropoda Pulmonata): morphology, taxonomy, and a catalogue of taxa

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ABSTRACT. The problem of generic and subgeneric rank in Ariantinae is briefly discussed. A review of existing views on the system of non-helicine Helicidae (Ariantinae, Murellinae, and Thebinae) and differential diagnoses of the taxa are presented. Special attention is paid to the morphology of the atrial stimulator and, especially, penial papilla, because these organs play an important role in evolution of helicoid groups, providing the functioning of a pre-copulatory isolating mechanism.

Introduction

The family Helicidae is a rather large group of snails having European and circummediterranean distribution. The family includes, as I estimate at present time, four subfamilies, which differ greatly in their number of genera: Ariantinae (=Helicigoniinae, =Campylaeinae) (22 genera and subgenera), Murellinae (5), Thebinae (2) and Helicinae (47).

From anatomical and zoogeographical points of view, the subfamily Ariantinae is a compact taxonomical and geographical unit. At the same time, views on the number of subfamilies in Helicidae and on the taxonomical structure of Ariantinae cannot be called settled [comp. Pilsbry, 1894; Boettger, Wenz, 1921; Hesse, 1931; Knipper, 1939; Zilch, 1960; Bank *et al.*, 2001; Schileyko, 2006a; Groenenberg *et al.*, 2012]. The discrepancies relate to the number, boundaries and classification of taxa.

More than 80 years ago, Paul Hesse [1931] attributed the main part of the Ariantinae to the genus *Helicigona*, within which he recognized 16 sections ("Sectio"). Eight years later Knipper [1939] distinguished in the same genus 25 "Gruppen" [in fact 23, because he included the genus *Elona* and an unnamed group for a single species *pyrenaica* Draparnaud (seemingly, current *Norelona*) which constitutes a separate family Elonidae Gittenberger, 1979].

According to common practice, the main diagnostic characters at the generic level in most of groups of Stylommatophora concern the peculiarities of the morphology of the reproductive organs.

Ariantinae constitute one of the few exceptions: generally accepted genera and subgenera (especially in the largest genus – *Chilostoma*) are primarily discriminated on the basis of conchological characters.

At the same time, it should be noted that the diversity of shells and especially of the reproductive tract of various Ariantinae is comparatively low. Thus, there is a problem of defining characters that can be used to distinguish taxa.

Some years ago, I wrote: "Subdivision of the genus *Helicigona* into subgenera at the present time is conditional and is based mainly on conchological features whereas anatomy of their type species is very similar. Nevertheless I represent the drawings of reproductive tracts of all type species except for the subgenus *Josephinella* whose anatomy is unknown." [Schileyko, 2006a: 1766]. Indeed, my main aim then was to show the diversity of the group; actually, I see that diagnoses of a number of subgenera do not virtually differ from one another. Unfortunately, I have overlooked the paper by Pintér and Subai [1979] containing a description of the reproductive tract of *Josephinella hemonica* (Thiéssé, 1884).

If (although it is not always possible) to write differential diagnoses for the majority of genera (subgenera) focusing only on the features of type species, then, while including of more and more number of species, these diagnoses are becoming increasingly blurred and lose their meaning.

Indeed, at the first glance, the structure of the reproductive tract of Ariantinae is very monotonous. However, a detailed study of the copulatory apparatus shows that the taxa often differ from each other in several important features (see below).

In recent years the molecular methods of research in taxonomy and phylogeny of pulmonates, in particular, Ariantinae, have been gaining popularity (for discussion, see, for example, Steinke *et al.*, 2004; Groenenberg *et al.*, 2011, 2012). These methods allow to establish a kinship between taxa, but they, like any other method, have certain limitations.

In particular, the results may depend on how long the samples under comparison were in alcohol [Groenenberg *et al.*, 2012].

The results of the morphological study presented here, not always coincide with results obtained by molecular methods. Perhaps, when the morphology of the copulatory apparatus of members of all genera (subgenera) is known, we will find some consensus in the understanding of the taxonomic structure of Ariantinae and the phylogenetic relationship among its (sub)genera.

Material and methods

The material for this work mainly consisted of the same specimens that I used in my book [Schileyko, 1978b]. The number of dissected specimens and localities are indicated in the same monograph. Besides, I had a chance to collect material of *Chilostoma achates* (Rossmässler, 1835) and *Cochlopus obtusa* (Draparnaud, 1805) in several localities in the Austrian Alps (Lower Austria, Styria). All the material was preserved in 70% ethanol. The anatomical study was performed by manual dissection in 70% ethanol under binocular microscope Olympus SZ51. Cross sections through penial papillae and stimulators were made by De Vekker iris-scissors.

Abbreviations in text: OD – original designation; SD – subsequent designation; t.-sp. – type species.

Abbreviations in figures: As – atrial stimulator; LF – longitudinal fold within penis; LT – lower tentacle; P – penis; PP – penial papilla; PS – penis sheath; PSt – papilla of stylophore; V – velum (a small lobe that covers penial pore); Va – vagina; ZMMU – Zoological museum of Moscow state university.

Problems of taxonomical structure of Ariantinae

First, we should briefly discuss the general problem – what is the genus (in particular, in Ariantinae)? Why do we refer a group of species to the category of genus, and the other group – to the category of subgenus? Groenenberg *et al.* [2012: 119] discussed this problem as follows:

«... the main difficulty with the classification of Ariantinae has been the delimitation of genera and subgenera in particular, because of their arbitrary use. In zoological taxonomy, the subgenus ... is the only rank between genus and species. It is a taxonomic rank, not a cladistic one. As such, there are no strict rules to consider a taxon either a genus or a subgenus. Already in 1942, Mayr said "... the subgenus is nearly always used in one of two situations: either when an author would like to make a new genus, but does not quite have the courage to do so ... or when an author wants to sink a genus

as unnecessary, but does not quite dare to do so because it is particularly old or well-known. The subgenus is a temporary stage in either case". ... we adhere to the following subgenus subdivision: "A subgenus is a distinct clade, thus characterized by autapomorphies that is nested within a larger monophyletic group which is ranked as a genus". Clearly, this definition (a clade within another clade) is imperfect from a cladistic perspective since virtually all phylogenies contain more clades than taxonomic ranks. At least it does provide a mean to tell which groups cannot be ranked as subgenera of a given genus».

Vinarsky [2013: 41] has given an analysis of a similar situation in Lymnaeidae and came to a conclusion that the decision depends on the theoretical approach to the problem: "... there are no grounds to delimit lymnaeid genera *objectively* as the solution critically depends on what taxonomic methodology (cladistic or 'evolutionary' taxonomy) is followed by a particular author. The 'evolutionary' taxonomic methodology (sensu Mayr) is favorable to the bigeneric approach, whereas the cladistic (Hennigian) methodology leads to the separation of a series of taxa of generic rank within Lymnaeidae. It is impossible to prefer one approach to another ultimately since the problem of acceptability of paraphyletic taxa is still not resolved. The co-existence of two different generic systems of the same family is therefore inevitable."

Since all evolutionary processes ultimately lead, as a rule, to the appearance and subsequent transformation of the morphological features of animals, I adhere to, in general, an "evolutionary" methodology. However, it should be added that to my mind, in nature a hierarchy of taxa objectively exists, and any taxonomist, sometimes unconsciously, takes into account this fact in his practice. In essence, any classification is based on a hierarchy of objects.

If within a group of organisms (in this case – in the family of Helicidae) there are, say, three hierarchical levels, we identify three Linnaean categories – family-genus-species. However, if we see that the number of such levels is more than three, we insert additional taxonomic categories – subfamily, tribe, subgenus etc. Thus, we have to try to subdivide Ariantinae into genera and the genera into subgenera, i.e. to understand, or to reflect a hierarchy.

Turning to the problem of taxonomy of Ariantinae, I must admit that the system of the subfamily, which I suggested in my Treatise [2006a] is erroneous. The point is that the name *Campylaeini* Kobelt, 1904 is a junior synonym of the name *Ariantini* Mörch, 1864. The reason of such a statement consists of the fact that these two taxa differ by a single character: in *Ariantini* sensu Schileyko [2006a] the mucus glands are simple (undivided) whereas in *Campylaeini* they are forked. Obviously, this taxo-

nomical decision was incorrect, since this character may vary within a single (sub)genus. Thus, in *Liburnica* there are species with simple as well as with forked mucus glands [Subai, 2002]. Moreover, Hesse [1931: 60, Taf. 11, Fig. 89 and Taf. 12, Fig. 103] has found that in the typical form of *Helicigona* [actually, *Delphinatia* – A. Sch.] *alpina* (Férussac, 1821) the mucus glands are simple, whereas in its var. *fontenillii* Michaud, 1829 they are forked.

In this context it should be noted that a strict adherence to certain character states may lead (and often leads) to an erroneous taxonomic conclusions. For example, the members of Camaenidae have no appendages of reproductive tract (except epiphallus and, rarely, an epiphallic caecum). Thus, under a formal approach the subgenus *Naegelea* (genus *Helix*) in which the stylophore and mucus glands are absent must be removed from the Helicidae and placed to Camaenidae. The fallacy of such a decision is obvious, and this example is not a single case.

The main problem of “deciphering” of the taxonomic structure of Ariantinae is, as already said, that it is a morphologically very compact group. An indirect confirmation of this is the comparison of the genus rank taxon diagnoses made by the various authors (see above): almost all the included features are more or less widely overlapping.

In fact, as correctly observed by Subai and Fehér [2006: 206], in analyzing of the system of Ariantinae at the generic level, we operate mainly with two characters connected to the copulatory apparatus: the structure of the penial papilla and the structure of the atrial stimulator. This is a very important statement, because what in fact is the function of the copulatory apparatus? – *This is the only morphological structure that prevents interspecific hybridization*, and the structure of penial papilla is species-specific. Thus, the morphological characteristics of the penial papilla and, to less degree, of the stimulator can help to understand the taxonomical structure of taxa and the phylogenetic relationship between them. By the way, such a situation with the copulatory apparatus among pulmonate molluscs is not unique: something like this takes place, for example, in Trochulinae (=Trichiinae) (Hygromiidae), where the structure of the penial papilla is one of characteristics of taxa of generic rank [Schileyko, 1978a,b]. Furthermore, the structural features of the copulatory apparatus have proven reliable and widely used in the taxonomy of other groups of animals, for example, in a number of groups of arthropods (some crustaceans, butterflies, spiders etc.).

Several authors [Hesse, 1931; Szigethy, 1976; Pintér, Subai, 1980; Subai, 1996, 1997, 2002, 2012] have studied and illustrated the external view of the

penial papillae of various Ariantinae. However, as will be shown below, the superficial, formal study of the papillae does not provide sufficient understanding of the complexity and diversity of the structure of this organ. Actually the papilla has rather complex inner organization, details of which allow to construct some hypotheses about possible genealogical connections between taxa.

Since the penial papilla and, to a lesser extent, the stimulator are very diverse morphologically (in contrast to other elements of the reproductive tract), and evidently play an important role in the systematics of the taxa under consideration, it is needed to look at them in more detail.

Penial papilla (verge) (Fig. 1)

The organ is an ovate or (rarely) conic tube, often with a narrow, more or less profound, longitudinal furrow on its surface that leads to the penial orifice (pore) and, as a rule, does not reach the top of the papilla. The pore of the papilla can be found in an apical or lateral position. The walls of the papilla are either solid (filled with a loose parenchyma) or contain a cavity filled with haemolymph.

Thus, there are three points for discussion: the wall structure of the penial papilla, the presence (or absence) of a superficial furrow on the surface of the papilla, and the position of the penial pore.

Concerning the wall structure of the penial papilla, one should bear in mind that with optical sagittal sections it is impossible to show longitudinal furrows on the surface of the papilla. For example, the papillae in *Ariantopsis* and *Helicigona*, as it appears in Fig. 1 differ only by the structure of their walls, but in fact they also differ by the presence of the above mentioned furrow on the papilla surface in *Helicigona* while in *Ariantopsis* the furrow is absent. Therefore, with that reservation, the one can recognize two principal groups as regards the wall structure of penial papilla (Fig. 1):

1. The walls of the papilla are filled with loose parenchyma. Such a structure is observed in *Causa*, *Isognomostoma*, *Ariantopsis*, *Drobacia*, *Koscicia*, and *Faustina*.

2. The walls are empty, i.e. contain a cavity. This group includes *Cattania*, *Helicigona*, *Dinari-ca*, *Josephinella*, *Chilostoma*, *Liburnica*, *Arianta*, and *Cochlopupa*.

Vidoviccia takes a somewhat isolated position, since the main part of the papilla walls are filled with parenchyma while the apical lobes and the most distal portion of the papilla proper contain cavities. I think, historically *Vidoviccia* is closer to the first group because its surface has no superficial furrow and the pore of the papilla occupies a terminal position. Besides, *Vidoviccia* is a kind of exception because it has a peculiar shell.

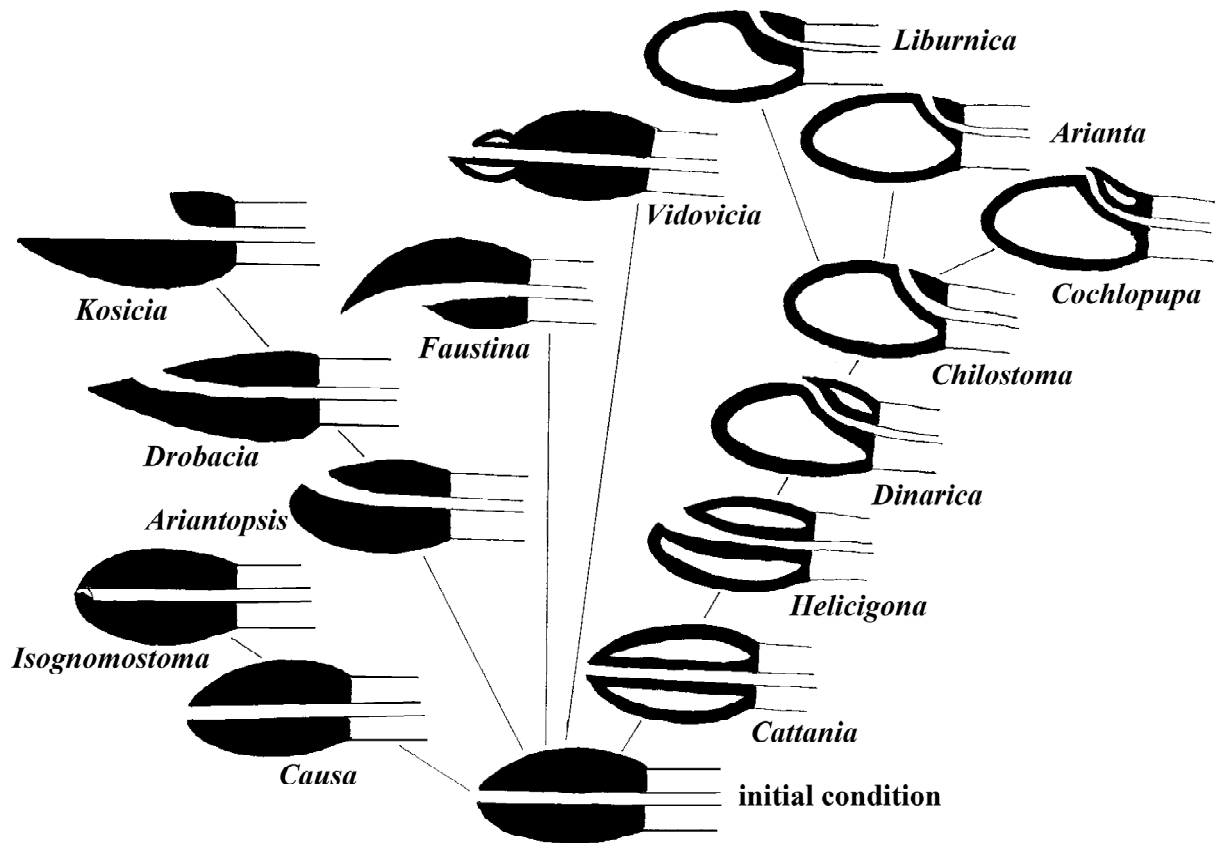


Fig. 1. Optical sagittal sections through penial papilla of various Ariantinae, schematized; longitudinal furrow not shown. Explanations in the text.

Рис. 1. Оптические сагиттальные срезы пениальной папиллы различных Ariantinae, схематизировано; продольная борозда не показана. Объяснения в тексте.

Evidently, the first variant is more archaic (plesiomorphic) than the second one. It follows from the very origin of papilla, since the organ arose by transformation of the circular thickening of tissue on the penis/epiphallus junction. This thickening consisted of connective and muscular tissue. Further evolution of the penial papilla was directed towards the disintegration of the parenchyma and its replacement by cavities.

At the same time it should be noted that the six taxa included in the first group are conchologically very different and united by only one formal character set – by the presence of parenchyma in the walls of papilla. So, one can suppose that they probably originated from common ancestor but drifted apart independently (or very early).

The other feature concerning the papilla – the position of the penial pore (outlet hole of the epiphallus cavity). The apical position of the pore in species of the second morphological group is probably plesiomorphic for the same reason (origin of the papilla). Within this group we see the gradual shifting of the pore position in the series *Cattania* (apical pore) – *Chilostoma* and closely related taxa (the

pore more or less shifted toward epiphallus) – *Liburnica*, *Arianta*, and *Cochlopupa* (the pore situated nearer to proximal end of the papilla).

At last, there is one more character, which is impossible (as stated above) to show on sagittal section (Fig. 1). This is the absence or degree of development of a longitudinal furrow on the papilla surface. Having traced the corresponding morphological series, one can see that in representatives of the first group (with parenchymatous walls of the papilla) the furrow is absent (*Causa*, *Isognomostoma*), very short (*Ariantopsis*, *Drobacia*), or long (*Kosicia*). This is connected with the position of the penial pore. The exception is the genus *Faustina*, where the very peculiar shape of the papilla excludes the presence of a furrow.

In parallel, in groups that make up the second group, the gradual formation of furrow can clearly be observed in the following series: *Cattania* (the furrow is absent) – *Helicigona* (the furrow is very short) – *Dinarica* (the furrow is well developed, occupies from 0.5 to 0.75 of the papilla length) – *Chilostoma* (the furrow occupies nearly entire length of the papilla). *Josephinella*, judging from Fig. 5b in

the paper by Pintér and Subai [1980], is close to *Dinarica*. Based on the papilla structure of *Chilostoma*-type the papillae of *Liburnica*, *Arianta*, and *Cochlopupa* arose independently. Other characters, conchological in particular, do not permit to unite them into one genus.

The degree of development of the furrow is associated with a shift of the penial pore in the direction to the epiphallus. Thus, it can be deduced that the species differ, among other characteristics, by ethological (courtship) and/or mechanical peculiarities of the copulation, which are almost unknown so far.

Fig. 1 shows the possible directions of historical development of the penial papilla. I would like to stress that *this is not a phylogenetic tree* of the Ariantinae; it is just one of the possible morphological series (rows) of the papilla structure. For example, it is quite probable that substitution of the parenchyma in the walls of the papilla by a cavity could occur more than once. In this case, the papilla of *Helicigona* could be derived from those of *Ariantopsis*, and the papilla of *Cattania* – from those of *Causa*.

In the root of the scheme (Fig. 1) the papilla in form of simple tube is shown with solid walls and a central canal. Among the Recent taxa, such a structure is found in *Causa*. The papilla of *Isognomostoma*, viewed in the optical sagittal section, has same structure, but an inner channel in *I. isognomostomos* has a semilunar shape due to the presence of a longitudinal fold. From the same initial state, the papilla of *Ariantopsis* could have arisen, where the penial pore is slightly shifted toward the lateral position.

The papilla of *Drobacia* has a similar structure, but here some special characters sets appear: a more conic shape, and numerous longitudinal grooves on the surface, one of which leads to penial pore. The continuation of this trend leads to the highly specialized papilla of *Kosicia ambrosi* (Strobel, 1851): here there are two very deep grooves, with penial pore disposed deep inside one of them.

The two-lobed papilla of *Faustina* is so specific that at the moment it is impossible to connect it with any other of the known variants, therefore I conditionally derive it directly from the initial papilla. The same holds true for the papilla of *Vidovicia*.

As for the morphological evolution of papillae in those taxa where the parenchyma is replaced by a cavity (2nd group), we see a trend to a change in the position of the penial pore from apical to lateral, followed by its gradual shift towards the epiphallus.

It is important to note, that this series is not always supported by other characters, in particular, by conchological traits. For example, shells of *Ariantopsis* and *Drobacia* markedly differ from each other, while shells of *Cattania* and *Faustina* are very similar.

Atrial stimulator

This organ, rarely reduced or modified, is present in all Ariantinae, except for *Kosicia* (at least, in the species *ambrosi* which has no stimulator), as well as in Thebinae and Murellinae. The shape of this organ varies from just thickening of a fold on the atrium inner surface (*Faustina*, *Dinarica*, *Cochlopupa*) to a large, well-developed triangular or clavate outgrowth (*Arianta* s. str.). Internally, the stimulator is always filled with loose parenchyma.

The diversity and species-specific shape of the stimulator suggest that this organ plays a role in courtship (mating games), and thus serves as a precopulatory isolating mechanism.

On the rank and position of *Theba*

To resolve the problem of the status of the genus *Theba* we should compare the anatomical differences between the subfamilies Ariantinae and Helicinae, since all conchological characters widely overlap.

Ariantinae: Stylophore sedentary or with vague neck. Dart lancet-shaped, with two longitudinal blades, without basal crown. Mucus glands tubular, simple or biramous. Diverticle of spermathecal stalk never reduced, thick, strongly developed; membrane between it and spermoviduct mostly well visible, intensively vascularized. A single penial papilla sometimes consisting of two lobes.

Reduction or disappearance of diverticle of spermathecal stalk is characteristic just for this subfamily.

Helicinae: Stylophore lacking narrowed neck. Dart in form of a stylet, with crown and four longitudinal blades. Mucus glands originally consisting of many branches, however, occasionally the number of branches can be reduced or the glands are completely absent (as, for example, in *Helix salomonica* Nägele, 1899 which also has no stylophore). Diverticle of spermathecal stalk initially and mostly present, slender; membrane between it and spermoviduct very thin, lacking visible vascularization. Sometimes the diverticle reduced or totally absent. Penis usually containing two papillae – proximal and distal (rarely there is only one papilla).

As can be seen from the above-said, the representatives of the genus *Theba* have characters of both subfamilies. Thus, the dart in species of *Theba* has the structure that is typical for Helicinae (with crown and four blades). However, the mucus glands in *Theba* are large and undivided – as in some species of the Ariantinae. An attention should be paid to three additional characters of *Theba pisana*: the peculiar alveolar structure of the mucus glands

and the rudimentary condition of the diverticle of spermathecal stalk. Both these features are not characteristic either for Helicinae, and for Ariantinae. The third, very important, character consists of the peculiar and unique structure of the penis (Fig. 23). Thus, it appears that *Theba* deserves a separation as a subfamily Thebinae Wenz, 1923.

On *Murella* and related taxa

Zilch [1960] placed the Recent *Murella* (with subgenera *Murella* s. str., *Ambigua*, *Marmorana*, and *Tyrrheiberus*), together with fossil (Upper Oligocene) *Praemurella* G. Pfeffer, 1929 in the subfamily Helicinae as a “Tribus Murelleae”.

Representatives of the genus *Murella* s. lat. as well as of the genus *Theba* have characters of both Ariantinae and Helicinae. However, in various *Murella* species the darts are different (Fig. 20) [Hesse, 1908] although they retain the basic structure typical for Helicinae (with crown and four blades). At the same time, the mucus glands in *Murella* are forked – as in some Ariantinae. Besides, the penial papilla is somewhat similar to those of *Drobacia banatica* (comp. Figs 6 and 21).

The systematic position and the rank of a group depend on the weight that we assign to a particular character. The fact that this group has features characteristic for Ariantinae (the structure of the mucus glands and the structure of the penial papilla) and for Helicinae (dart with a crown and four blades, the membrane between the diverticle of spermathecal stalk and the spermoviduct very thin, devoid of visible vascularization), gives arguments for the assumption that *Murella* and related taxa constitute a separate subfamily Murellinae Hesse, 1918.

On the subfamily Leptaxinae C. Boettger, 1909

Initially, the subfamily has been introduced (as Leptaxidinae) without formal diagnosis, for the genus *Leptaxis* (by default) [Boettger, 1909: 4, 7].

Some authors [Mandahl-Barth, 1950; Zilch, 1960] refer Leptaxinae to the family Helicidae. The subfamily Leptaxinae sensu Zilch [1960] includes two Recent genera (*Leptaxis* and *Lampadia*), inhabiting the islands of western Atlantic (Canary, Cabo Verde, Azores, and Madeira) and three fossil (*Fridolinia* and *Pseudoleptaxis* from the Oligocene of France and ?*Camaenopsis* from the lower Miocene of Morocco). The genus *Leptaxis* is also known from the Oligocene of Europe. Later, Backhuys [1975] described the monotypic genus *Helixena* inhabiting St. Maria Island (Azores) and assigned it to the Leptaxinae.

Without going into a discussion on the systematic position of the fossil forms, it should be noted that species of *Leptaxis* and *Lampadia webbiana* (Lowe,

1831) are very different anatomically, as was pointed out already by Mandahl-Barth [1950: 49].

Concerning *Leptaxis*, the position of this genus is not quite clear: the diverticle of spermathecal stalk is absent, the dart is lanceolate, but equipped with a crown [Mandahl-Barth, 1950]; besides, the structure of the mucus glands and penis in *Leptaxis* is characteristic for Hygromiidae, that is why I attributed the genus to this family and to subfamily Hygromiinae [Schileyko, 2006b]. To confirm the conclusion I am presenting the illustration of the reproductive tract of another species of *Leptaxis* – *L. nivosa* (Sowerby, 1824) (Fig. 2). Thus, the name Leptaxinae is a junior synonym of the name Hygromiinae.

The genus *Helixena*, having an unusual shell for helicoids, is anatomically a typical representative of the Hygromiinae [Schileyko, 2006b: 1974-1975, Fig. 2501].

The other genus of Leptaxinae sensu Zilch [1960] – *Lampadia* – is an aberrant representative of Helicidae. Some anatomical features of *Lampadia webbiana* prove the affiliation of this genus to the subfamily Helicinae: it has a well developed diverticle of spermathecal stalk, a dart typical for the subfamily having a crown and four blades, and the mucus glands consisting of 3-5 branches [Mandahl-Barth, 1950]. At the same time, judging from pl. 17, Fig. 3 [op. cit.], the inner structure of the penis is more characteristic for Ariantinae, because (1) it contains only one papilla, and (2) the papilla has a short longitudinal furrow and circular sculpture (comp., for example, with *Helicigona* – Fig. 11 B, or with *Dinarica* – Fig. 12 B, C). So I placed the genus *Lampadia* in the subfamily Ariantinae but singled it out as a separated tribe Lampadiini Schileyko [Schileyko, 2006a: 1786].

Based on the above facts and considerations, the diagnoses of taxa can be formulated as follows. The diagnoses are mainly based on Schileyko [2006a], but substantially revised and amended, for most of the taxa, including the change of their status in number cases. Genera and subgenera, which I have not studied, are marked with an asterisk (*).

Diagnoses of taxa

ARIANTINAE Mörch, 1864

Mörch, 1864: 284 (pro fam.).

– Helicigoninae Wenz, 1915: 65.

– Campylaeinae Kobelt, 1904: 71, 131.

Schileyko, 2006a: 1765.

Shell globose to flat (exception: *Cochlopupa* has cylindrical shell), usually of medium size, very diverse in all conchological characters. Aperture is toothless, except for two monotypic genera (*Causa* and *Isognomostoma*).

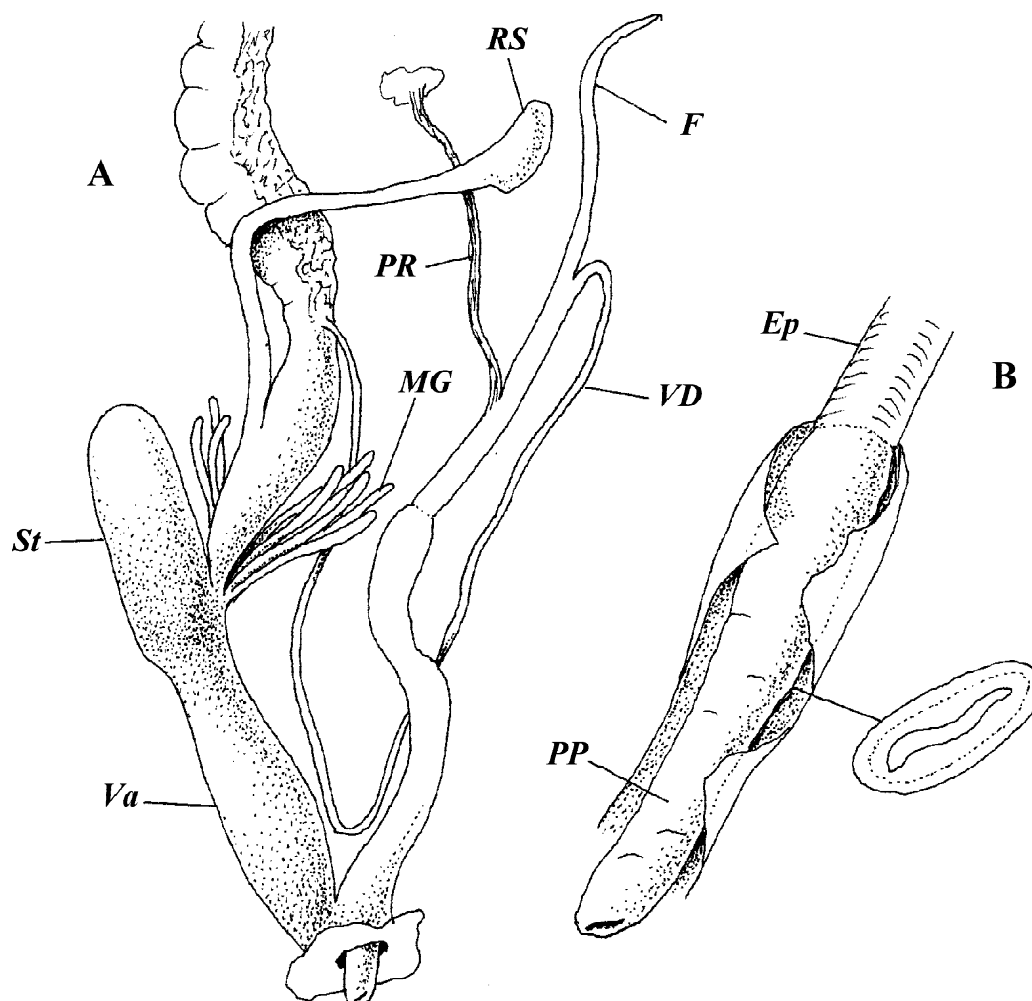


FIG. 2. *Leptaxis nivosa*. Madeira, W. Pico do Macarico, 11.07.1987. ZMMU No. Lc-39902. A – reproductive tract. B – inner structure of penis. Ep – epiphallus; F – flagellum; MG – mucus glands; PP – penial papilla; PR – penial retractor; RS – reservoir of spermatheca; St – stylophore; Va – vagina; VD – vas deferens.

РИС. 2. *Leptaxis nivosa*. Мадейра, 3. Пико до Макарико, 11.07.1987. ZMMU No. Lc-39902. А – репродуктивный тракт. В – внутреннее строение пениса. Ep – эпифаллус; F – флагеллум; MG – слизистые железы; PP – папилла пениса; PR – ретрактор пениса; RS – резервуар семеприемника; St – стилофор; Va – вагина; VD – семепровод.

Stylophore sessile or with very short neck. Mucus glands tubular, simple or biramous. Diverticle of spermathecal duct well developed; membrane between it and spermoviduct mostly strong, highly vascularized. There is a single penial papilla, sometimes consisting of two lobes.

Dart lanceolate, without crown, or (in Lampadini) stylet-shaped, with a basal crown.

Distribution. Europe, N Africa.

Ariantini Mörch, 1864

Shell globose to flat.

Penis sheath is present. Dart lanceolate, without crown.

Distribution. Europe, N Africa.

Causa Schileyko, 1971

Fig. 3

Schileyko, 1971: 997.

Schileyko, 1978b: 317; 2006a: 1773, Fig. 1833 (*Helicigona* subgen.); Groenenberg *et al.*, 2012: 148, Fig. 1(5), 2(7).

Type species – *Helix holosericum* Studer, 1820; OD.

Shell nearly flat, rather thin, of 6 narrow, rather convex whorls. Body whorl deflected, rounded. Color light corneous to brown; peristome white. Embryonic whorls practically glabrous. Postapical sculpture of thin and irregular radial striation and delicate granulation; fresh shells bear short, scattered hairs. Aperture not strongly oblique, with well-reflexed margins that supplied with 2-3 tubercular teeth: 1 palatal and 1-2 basal. Umbilicus moderately broad, subcylindrical, perspective. Height 5-6, diam. 9.0-10.5 mm.

Flagellum very short. Epiphallus long. Penis distinctly divided into two sections: globular proximal and slender cylindrical distal. Penial retractor attached to middle of epiphallus. Stylophore relatively small, mucus glands simple, of moderate length.

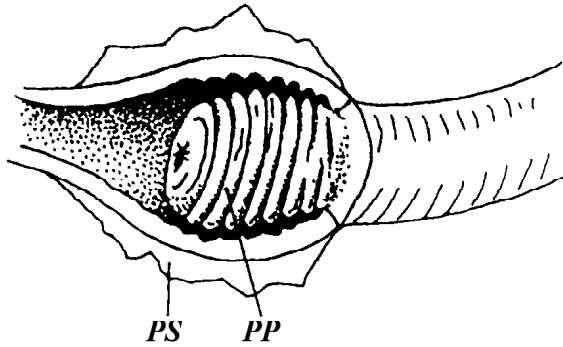


FIG. 3. *Causa holosericea*. Penial papilla. After Schileyko, 1978b.

РИС. 3. *Causa holosericea*. Папилла пениса. По Шилейко, 1978b.

Neck of spermathecal shaft short, diverticle stout, reservoir capacious, nearly reaching albumen gland.

Stimulator not large, tubercular, located at the very atrium.

Penial papilla contractile, with apical pore, occupies globular chamber of penis and covered with numerous circular folds; evidently, under smoothing of the folds the papilla may be considerably lengthened.

Distribution. Mountain regions of Central and E Europe (W Carpathians, Alps, Tatra, Sudetes, Franconian Jura in S Germany).

Isognomostoma Fitzinger, 1833

Fig. 4

Fitzinger, 1833: 97.

– *Plicostoma* Schlüter, 1838: 4 [t.-sp. *Plicostoma intestinalis* Schlüter, 1838; monotypy; nom. nud.).

– *Isognostoma* Hartmann, 1840 (1840-1844) (page without number, in “Systematische Übersicht ...”, after p. 227) (nom. err. pro *Isognomostoma* Fitzinger, 1833).

– *Isognomonostoma* Agassiz, 1847: 197 (nom. err. pro *Isognomostoma*).

– *Ulostoma* Albers, 1850: 95 (*Helix* subg.; part.).

– *Triodopsis* Martens in Albers, 1860: 97 (*Helix* subg.; part.).

Schileyko, 1978b: 315; 2006a: 1773, Fig. 1833; Groenenberg *et al.*, 2012: 157, Fig. 1(4), 2(8).

Type species – *Helix personata* Lamarck, 1792 (= *Helix isognostoma* Gmelin, 1780); monotypy.

Shell semiglobose, moderately thin, of 5 rather convex whorls. Last whorl evenly rounded, sharply deflected. Color reddish-corneous, brown or chestnut. Postapical sculpture of irregular radial striation and fine granulation; in fresh shells each granule bears minute triangular scale. Besides, there are numerous long, curved hairs. Aperture rounded triangular, with strongly reflexed, expanded margins. There is a strong lamellar palatal lamella; thick lip furnished with tubercular basal and palatal teeth. Umbilicus closed or slit-like. Height 5.5-6.5, diam. 7.8-11.5 mm.

Flagellum long, vermiform. Epiphallus rather short. Penis cylindrical or somewhat tapering. Pe-

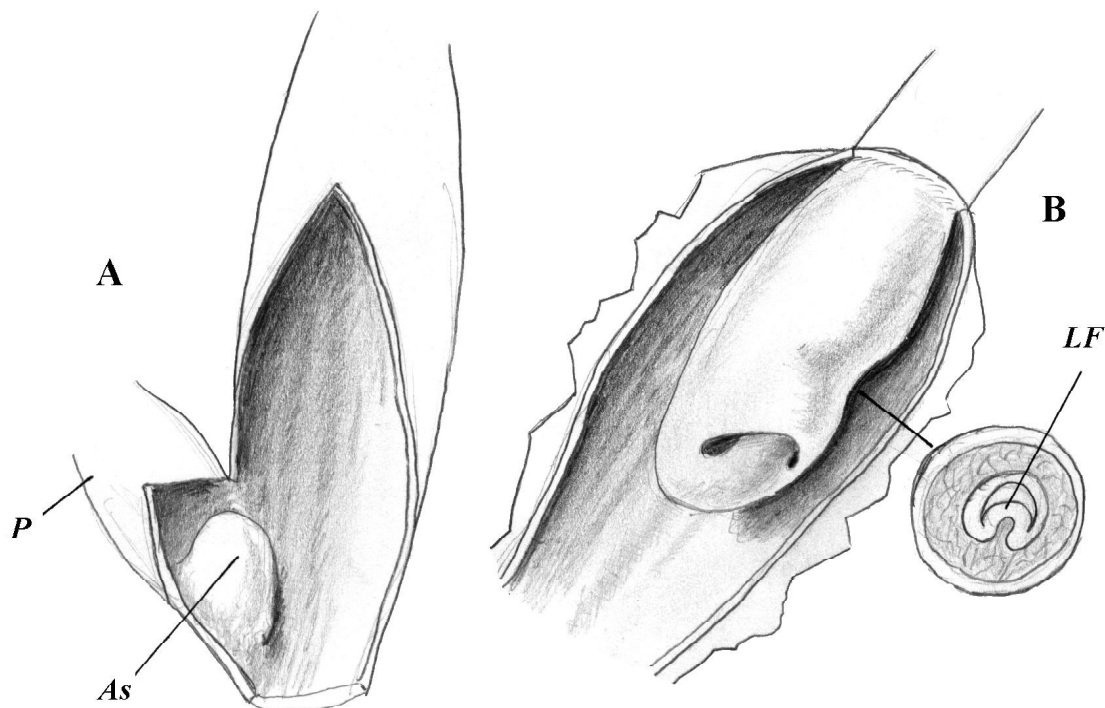


FIG. 4. *Isognomostoma isognomostomos*. Transcarpathian, Rakhov district, near Kvasy village, 10-22.09.1969. ZMMU No. Lc-19687. A – inner structure of atrium. B – penial papilla.

РИС. 4. *Isognomostoma isognomostomos*. Закарпатсье, Раховський р-н, близ с. Квасы, 10-22.09.1969. ZMMU No. Lc-19687. А – внутреннее строение атриума. В – пениальная папилла.

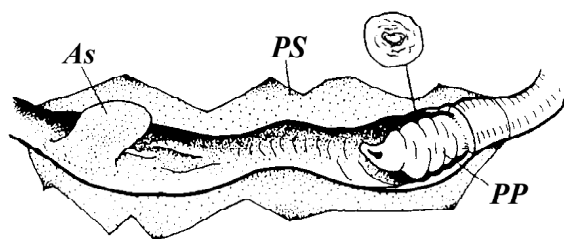


FIG. 5. *Ariantopsis pelia*. Penial dissected. After Damianov and Likharev, 1975.

РИС. 5. *Ariantopsis pelia*. Вскрытый пенис. По: Дамянов, Лихарев, 1975.

nial retractor attached to penis/epiphallus junction. Stylophore clavate. Mucus glands long, undivided. Neck of spermathecal stalk moderately short; diverticle stout.

Stimulator rather small, in form of ovate fleshy tubercle standing at penial side of atrium.

Penial papilla moderately long, thick-walled, with smooth surface, occupies most part of penis lumen. Pore of papilla subterminal in position; canal semilunar in cross-section due to presence of longitudinal fold. The walls of papilla filled with loose parenchyma.

Distribution. Mountain regions of Central and W Europe, to the south down to Slovenia, E France, Croatia, and N Italy.

***Ariantopsis* A. Wagner, 1928**

Fig. 5

Wagner A., 1928: 377.

Damianov, Likharev, 1975: 387, Fig. 317, 318; Schileyko, 2006a: 1781, Fig. 2282 (*Campylaea* subgen.); Groenenberg *et al.*, 2012: 153, Fig. 1(30), 2(29) (*Cattania* subgen.).

Type species – *Helicigona (Arianta) pelia* Hesse, 1912; monotypy.

Shell subglobular, somewhat translucent, shining, of 6-6.5 moderately convex whorls. Last whorl evenly rounded at periphery, only slightly descending in front. Color buff-yellow or ochraceous, without bands; irregularly spaced, darker radial streaks often present. Embryonic whorls smooth. Later whorls with irregular, fine radial wrinklets, delicate spiral striae and sometimes with fine granulation. Aperture shortly ovate, with little reflexed, thin margins and thin light lip. Umbilicus is narrow, partly covered. Height 7.5-13.0, diam. 11-22 mm.

Epiphallus 2-2.5 times shorter than flagellum. Mucus glands simple or forked. When forked, common ducts of the glands long, not shorter than branches.

Stimulator not large, rounded, located in the distalmost section of penis.

Penial papilla is comparatively small, with super-

ficial circular folds and subapical pore. Walls of the papilla filled with loose parenchyma.

Distribution. SW and W Bulgaria.

***Drobacia* Brusina, 1904**

Fig. 6

Brusina, 1904: 162 (*Campylaea*, "Gruppe" *Drobacia*).

– *Partschia* C. Boettger, 1911: 21 (*Campylaea* sect.; t.-sp. *Helix banatica* Rossmässler, 1838; OD).

– *Dobracia* Ehrmann, 1933: 138 (nom. err. pro *Drobacia* Brusina, 1904).

Schileyko, 1978b: 317; 2006a: 1771, Fig. 2266 (*Helicigona* subgen.); Groenenberg *et al.*, 2012: 154, Fig. 1(26), 2(9).

Type species – *Helix banatica* Rossmässler, 1838; OD.

Shell lenticular, moderately solid, slightly shining, of 6 strongly flattened whorls. Last whorl descending in front, with blunt but distinct peripheral angle. Color yellowish to brown, sometimes with darker zones above and below peripheral angle. Embryonic whorls smooth. Postapical sculpture of weak radial wrinklets and distinct spiral lines. Peristome insertions not approached. Height 14-18, diam. 25-30 mm.

Within atrium there is a U-shaped pilaster both arms of which run into vagina; in the middle part of bridge between arms there is a variously developed (but never large) stimulator in form of thin outgrowth.

Penial papilla very long, conic or slightly fusiform, with a short subterminal furrow and irregularly, coarsely rugose surface. The furrow has complex shape in cross-section. Walls of papilla filled with very loose parenchyma containing numerous sinuses and lacunae.

Distribution. Carpathians.

***Kosicia* Brusina, 1904**

Fig. 7

Brusina, 1904: 162 (*Campylaea*, "Gruppe" *Kosicia*).

Schileyko, 2006a: 1767, Fig. 2261 (*Helicigona* subgen.); Groenenberg *et al.*, 2012: 162, Fig. 1(15,16,17F), 2(13).

Type species – *Helix intermedia* C. Pfeiffer, 1828; OD.

Shell depressed, rather thin, lustrous, of about 5 moderately convex whorls. Last whorl rounded, strongly deflected. Color white or light grey, uniform or with 1-3 dark bands that sometimes consist of series of spots; besides, irregular indistinct radial dark streaks may be present. Embryonic whorls with very fine and vague spiral striae. Postapical sculpture of irregular delicate radial wrinklets or thin riblets and distinct wavy spiral striation. Aperture very oblique, with thin white lip. Peristome insertions somewhat approached. Umbilicus open, a little perspective. Height 6.5-8.5, diam. 14-16 mm.

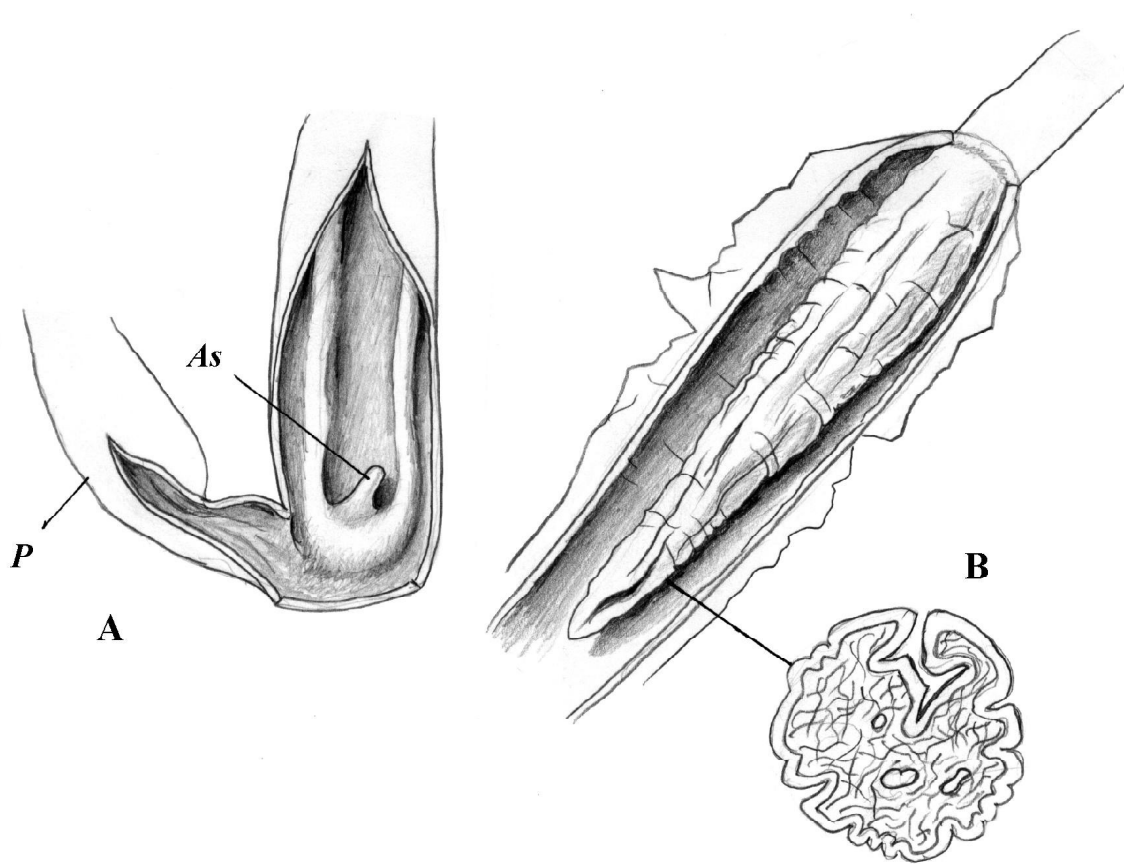


FIG. 6. *Drobacia banatica*. Transcarpathian, Khust, Ghoutinskije Mts., 13.09.1989. ZMMU No. Lc-19700. A – inner structure of atrium. B – penial papilla.

РИС. 6. *Drobacia banatica*. Закарпатье, Хуст, Гутинские горы, 13.09.1989. ZMMU No. Lc-19700. А – внутреннее строение атриума. В – папилла пениса.

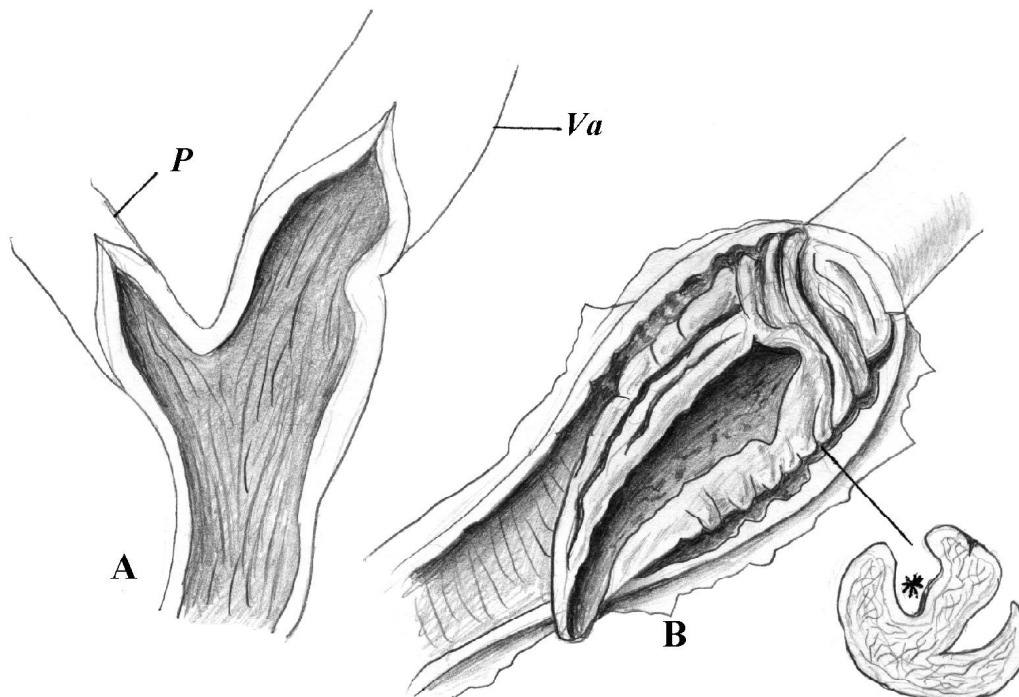


FIG. 7. *Kosicia ambrosi*. NO Italy, Mt. Canin, 2100 m, 7.07.2002. ZMMU No. Lc-39903. A – inner structure of atrium. B – penial papilla. Asterisk – principal groove, in which penial pore opens.

РИС. 7. *Kosicia ambrosi*. СВ Италия, гора Канин, 7.07.2002. ZMMU No. Lc-39903. А – внутреннее строение атриума. В – папилла пениса. Звёздочка – главная борозда, в которую открывается пениальная пора.

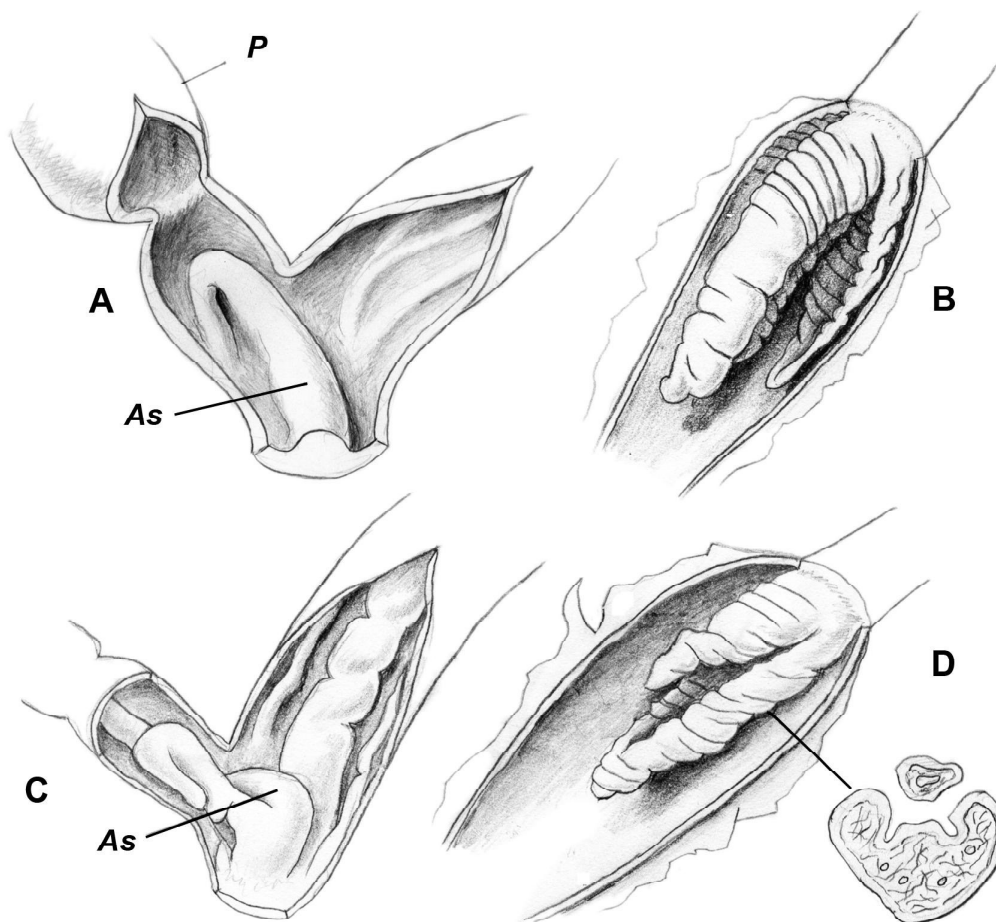


FIG. 8. *Faustina faustina*. A, B – Pred Bielym, Nizké Tatry, 13.07.1964. ZMMU No. Lc-19702. C, D – Transcarpathian, Rakhov district, above Kvasy village, 12-18.09.1969. ZMMU No. Lc-19692. A, C – inner structure of atrium. B, D – penial papilla.

РИС. 8. *Faustina faustina*. A, B – Низкие Татры, 13.07.1964. ZMMU No. Lc-19702. C, D – Закарпатье, Раховский р-н, над с. Квасы, 12-18.09.1969. ZMMU No. Lc-19692. A, C – внутреннее строение атриума. B, D – пениальная папилла.

Flagellum longer than penis+epiphallus. Penis consists of tubular distal and swollen proximal parts. Inner surface of penis, atrium, and vagina intensively pigmented with black. Mucus glands simple.

Stimulator absent. Inner surface of atrium, vagina, and distal part of penis with numerous, very thin, irregularly arranged folds.

Penial papilla conic, occupying proximal chamber of penis. Basal portion of the papilla bears strong circular folds; on the surface of the organ there are two very deep longitudinal furrows, one of them leads to penial pore.

Distribution. From the SE Alps in Austria to NE Italy, N Slovenia and NW Croatia.

Remark. The description is based not on the type species [*Kosicia ambrosi* (Strobel, 1851)]; therefore, there is no certainty that the text above corresponds to the genus.

Faustina Kobelt, 1904

Fig. 8

Kobelt, 1904: 131, 186 (*Campylaea* subgen.).

Schileyko, 1971: 992; 1978b: 308; 2006a: 1778, Fig. 2279 (*Campylaea* subgen.); Groenenberg *et al.*, 2012: 156, Fig. 1(12), 2(19).

Type species – *Helix faustina* Rossmässler, 1835; tautonymy.

Shell depressed to almost flat, glossy, of 4.5-6 slightly convex whorls. Last whorl markedly deflected. Color whitish to corneous, uniform or with one supraproperipheral dark band. Embryonic whorls smooth. Later whorls lack regular sculpture. Aperture broadly ovate, well oblique, with reflexed margins, peristome insertions somewhat approached. Umbilicus rather wide. Height 9-14, diam. 14.0-27.5 mm.

Epiphallus and flagellum of approximately equal length. Common ducts of mucus glands rather short (about 2 times shorter than branches). Inner surface of vagina bears a few smoothed axial folds.

Stimulator transformed into a strong V-shaped fold, bend of which directed into the lumen of the penis; ascending branch of stimulator begins from the genital opening, the descending branch is com-

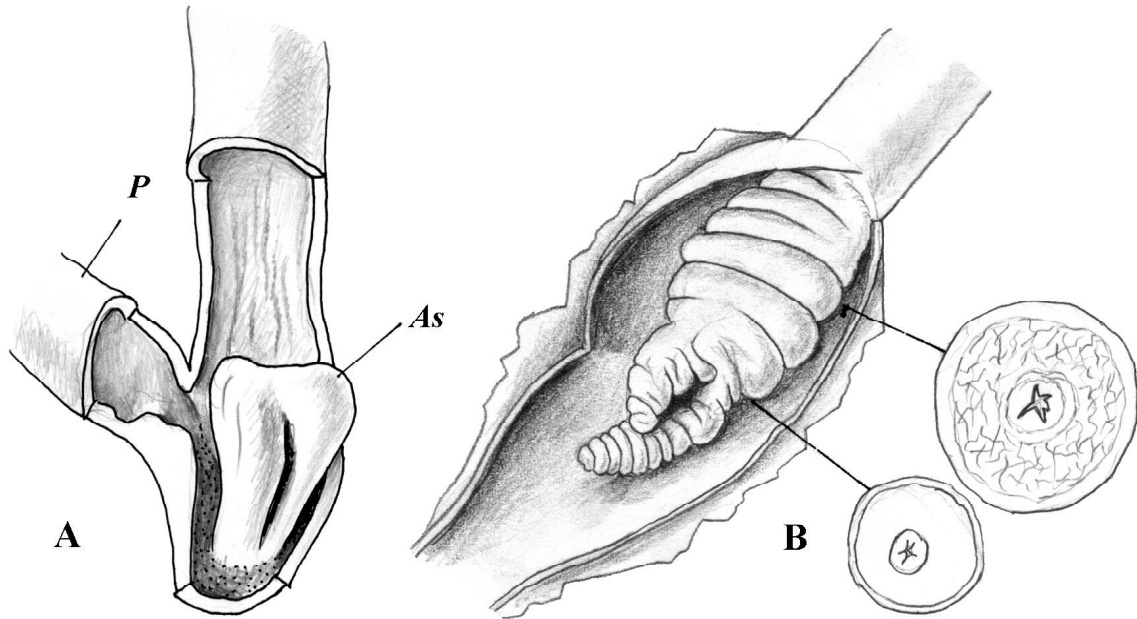


FIG. 9. *Vidovicia caerulans*. Ylija near Orebič, 1938. ZMMU No. Lc-28486. A – inner structure of atrium. B – penial papilla.
 РИС. 9. *Vidovicia caerulans*. Илия близ Оребиц, 1938. ZMMU No. Lc-28486. А – внутреннее строение атриума. В – папилла пениса.

ing to naught. Inner surface of vagina with a few variously developed axial folds.

Penial papilla consists of two large lobes, one of which is smaller than the other. Epiphallic pore situated on the bottom between the lobes. Larger lobes of papilla filled with parenchyma, containing small sinuses and lacunae, in smaller lobe there is a narrow cavity.

Distribution. Carpathian Mts. in Czech, Slovakia, Poland, Ukraine, and Romania; NE Hungary.

***Vidovicia* Brusina, 1904**
 Fig. 9

Brusina, 1904: 162 (*Campylaea*, “Gruppe” *Vidovicia*).
 – Hazaya Soós, 1909: 43 (t.-sp. *Helix caerulans* C. Pfeiffer, 1828; monotypy).
 Schileyko, 2006a: 1771, Fig. 2268; Groenenberg *et al.*, 2012: 165, Fig. 1(29), 2(11).

Type species – *Helix lacticina* Rossmässler, 1837; OD.

Shell low conic, rather thin but opaque, dull, of 4.5-5 quite convex whorls. Last whorl strongly descending in front, slightly, roundly angulated at periphery. Color whitish-grey, often with bluish tint; summit dark; peristome light brown to blackish; aperture internally whitish or dull-yellow. Embryonic whorls lack regular sculpture. Postapical sculpture of variously developed, sometimes rather coarse, smoothed, irregular radial wrinkles. Aperture subcircular, very oblique, nearly entire. Umbilicus minutely open, excentric. Height 9-12, diam. 14-20 mm.

Flagellum very long, slender, sinuous. Epiphallus moderately long, sharply bent in middle. Penis fusiform, thin-walled. Penial retractor attached to knee of epiphallus. Free oviduct short, vagina 2-3 times longer. Stylophore small. Mucus glands 2, enormously developed. Inner surface of vagina with many thin irregular folds. Neck of spermathecal stalk moderately long; diverticle stout.

Stimulator large, slightly clavate, with flattened tip, directed into vagina.

Penial papilla large, fleshy, inflated; its pore situated between 2 contractile apical lobes. The lobes contain cavities. Lumen (canal) of papilla is very narrow, in form of irregular many-rayed star in cross-section. Proximal portion of the papilla filled with loose parenchyma, in distal part, at the pore, the walls of papilla become thin, semitransparent, and canal here surrounded by a cavity.

Distribution. Croatia.

***Chilostoma* Fitzinger, 1833**

Fitzinger, 1833: 98.
 – *Eucampylaea* L. Pfeiffer, 1879 (1878-1881): 144 (t.-sp. *Helix planospira* Lamarck, 1822; SD Schileyko, 2006a).
 Schileyko, 2006a: 1769, Fig. 2264 (*Helicigona* subgen);
 Groenenberg *et al.*, 2012: 148, Fig. 1(3), 2(6,7).

Type species – *Glischrus foetens* Studer, 1820; SD J. Gray, 1847.

Shell more or less depressed – down to nearly flat.

Stimulator variously developed.

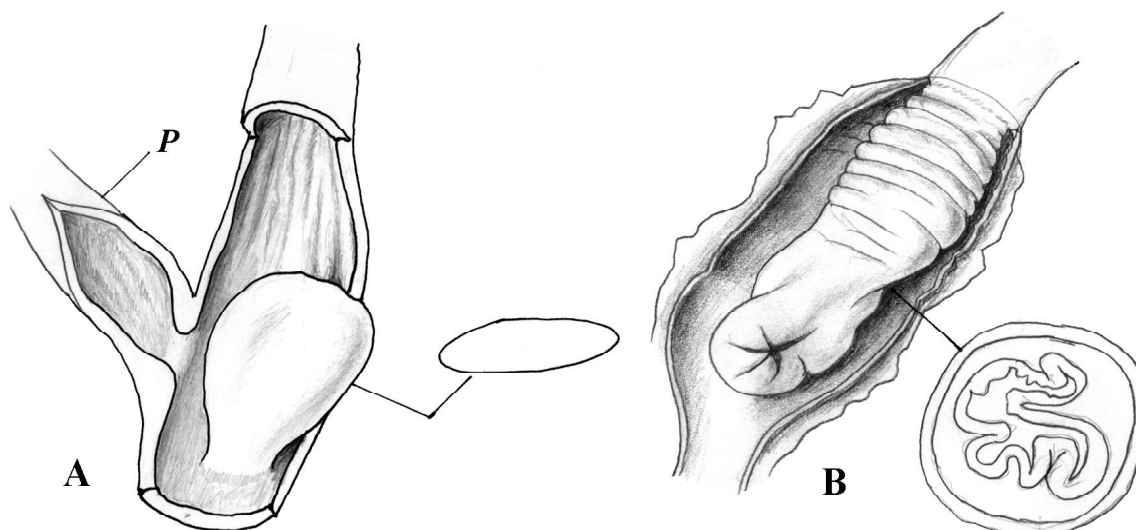


FIG. 10. *Chilostoma (Cattania) trizona balcanica* (Kobelt, 1876). Bulgaria, Tsarevets, Veliko Tynovo, 21.06.1966. ZMMU No. Lc-19703. A – inner structure of atrium. B – penial papilla.

РИС. 10. *Chilostoma (Cattania) trizona balcanica* (Kobelt, 1876). Болгария, Царевец, Велико Търново, 21.06.1966. ZMMU No. Lc-19703. А – внутреннее строение атриума. В – папилла пениса.

Walls of penial papilla contain a circular cavity. The initial position of the papillar pore is (sub)apical but the pore in the members of different subgenera more or less shifted laterally toward epiphallus.

Distribution. S and central Europe.

Remark. Groenenberg *et al.* [2012] separated some taxa related to *Chilostoma* as independent genera or subgenera. Since I have no material on these taxa, I follow the named authors.

Chilostoma (Cattania) Brusina, 1904

Fig. 10

Brusina, 1904: 162 (*Campylaea*, “Gruppe” *Cattania*).
Schileyko, 2006a: 1777, Fig. 2276 (*Campylaea* subgen.);
Groenenberg *et al.*, 2012: 144; Fig. 1(27,28), 2(27,28)
(pro gen.).

Type species – *Helix trizona* Rossmässler, 1834; OD.

Shell glossy, of about 5 moderately convex whorls. Last whorl strongly descending toward aperture, with rounded or angulated periphery. Color yellowish to corneous, usually with 3 dark bands. Embryonic whorls smooth. Postapical sculpture of fine, irregular radial wrinklets and spiral striae. Aperture widely ovate, quite oblique, with thin, slightly reflexed margins. Umbilicus moderately wide. Height 10-16, diam. 24.0-32.5 mm.

Epiphallus 1.5-2 times shorter than flagellum; diameters of these ducts subequal. Mucus glands divided from about a third up to over half of their length, but sometimes simple or trifurcate.

Stimulator is very large, in form of thick plate,

ovate in cross-section, sitting on a short, narrowed peduncle.

Penial papilla large, with very thin, semitransparent walls and (sub)terminal pore. Inner canal broad, very complex in cross-section. The canal surrounded by a cavity.

Distribution. S Europe (NE of Balkan peninsula, Carpathians, Serbia, Bulgaria, Macedonia, E Montenegro, N and E Albania, along northern boundary of Greece).

*Chilostoma (Wladislawia) A. Wagner, 1928**

Wagner A., 1928: 379 (*Campylaea* subgen.).
Schileyko, 2006a: 1778, Fig. 2278 (*Campylaea* subgen.);
Groenenberg *et al.*, 2012: 166, Fig. 1(31,32), 2(30) (*Cattania* subgen.).

Type species – *Campylaea polinskii* A. Wagner, 1928; monotypy.

Shell depressed-conic, dull to somewhat glossy, of 4.5-5 moderately convex whorls. Last whorl well deflected. Color opaque-whitish, usually with dark supraperipheral band. Embryonic whorls smooth. Later whorls with variously developed radial ribs and delicate spiral lines. Aperture subcircular, moderately or rather strongly oblique, with shortly reflexed margins and inner lip. Umbilicus moderately broad, profound. Height 5-10, diam. 7.8-16.2 mm.

Flagellum longer than penis+epiphallus. Mucus glands simple or biramous.

Distribution. Pirin Mts. (SW Bulgaria).

Remark. Groenenberg *et al.* [2012] on the base

of molecular data consider *Wladislawia* together with *Ariantopsis* as subgenera of *Cattania*.

?*Chilostoma* (*Campylaeopsis* Wagner, 1914)*

Wagner in Sturany, Wagner, 1914: 26, 93 (*Campylaea* subgen.).

Schileyko, 2006a: 1766, Fig. 2261 (*Helicigona* subgen.); Groenenberg *et al.*, 2012: 145, Fig. 1(18), 2(10) (pro gen.).

Type species – *Helix moellendorffi* Kobelt, 1871; SD Hesse, 1931

Shell depressed, thin, translucent, shining, of 5.5 rather convex whorls. Last whorl markedly deflected in front, with rounded periphery. Color corneous-brown, usually with darker supraperipheral band and (sometimes) with a few light varices. Embryonic whorls smooth. Later whorls delicately radially striated, with regularly arranged, widely spaced minute hairs. Aperture ovate, quite oblique, with thin lip. Peristome insertions somewhat approached. Umbilicus very narrow. Height 8-11, diam. 14-18 mm.

Flagellum somewhat longer than penis+epiphallus. Mucus glands simple.

Distribution. The mountains of Bosnia-Herzegovina and Montenegro.

Remark. Groenenberg *et al.* [2012] on the base of molecular data state that *Campylaeopsis* is a separate genus that forms a clade together with the genera *Delphinatia*, *Drobacia*, and *Vidovicia*.

Chilostoma* (*Campylaea* Beck, 1837)

Beck, 1837: 24 (*Helix* subgen.).

Schileyko, 2006a: 1776 (pro gen.), 1775, Fig. 2260 (*Campylaea* subgen.); Groenenberg *et al.*, 2012: 144, Fig. 1(13,14), 2(14) [*Campylaea* (*Campylaea*)].

Type species – *Helix hispana* Linnaeus, 1758; SD Gray, 1847.

Shell has no differential conchological diagnosis, similar to those of *Chilostoma* a. str.

Flagellum somewhat longer than penis+epiphallus. Mucus glands simple or divided up to half of their length and even both can occur within a single specimen.

Distribution. Mainland Italy, Sicily, S Austria, SW Hungary, SW Romania, Slovenia up to W and N Croatia, N Serbia; one species in E Algeria.

Remark. Groenenberg *et al.* [2012: 145] wrote that “The phylogenies based on concatenated dataset ... suggests a sister-group relation between *Isognomostoma* and *C.* (*Campylaea*), but without proper support”.

Chilostoma* (*Corneola* s. str.)

Held, 1837: 912.

Groenenberg *et al.*, 2012: 152, Fig. 1(24), 2(5) (pro gen.).

Type species – *Helix cornea* Draparnaud, 1801; SD Herrmannsen, 1847.

Shell flattened, moderately solid, of about 5 flattened whorls. Last whorl markedly descending in front, its periphery rounded or with variously developed angle. Color corneous; vague, light peripheral and indistinct, darker supraperipheral bands may be present. Aperture margins whitish. Embryonic whorls smooth, later whorls with very weak sculpture (nearly smooth). Aperture ovate, quite oblique, with reflexed margins; peristome insertions approached and usually connected by parietal callus. Umbilicus narrow to moderately wide. Height 5-8, diam. 12-15 mm.

Flagellum somewhat longer than penis+epiphallus. Mucus glands simple.

Distribution. Pyrenees; central and S France; along the Atlantic coast to Brittany; dept. of Alpes-Maritimes.

Remark. Groenenberg *et al.* (2012: 152) consider *Corneola* as a separate genus.

***Chilostoma* (*Helicigona* Férussac, 1821)**

Fig. 11

Férussac, 1821: 27, 40.

– *Chilotrema* Turton, 1831: 66 (t.-sp. *Helix lapicida* Linnaeus, 1758; monotypy).

– *Latomus* Fitzinger, 1833: 97 (t.-sp. *Helix lapicida* Linnaeus, 1758; monotypy).

– *Lenticula* Held, 1837: 913 (t.-sp. *Helix lapicida* Linnaeus, 1758; monotypy).

– *Lapidana* Caziot, 1910: 122 t.-sp. *Helix lapicida* Linnaeus, 1758; monotypy).

Schileyko, 1978b: 313 (pro gen.); 2006a: 1765 (pro gen.), 1771, Fig. 2267 (*Helicigona* s. str.); Groenenberg *et al.*, 2012: 157, Fig. 1(25), 2(8) (pro gen.).

Type species – *Helix lapicida* Linnaeus, 1758; SD Pilsbry, 1895 (1893-1895).

Shell depressed to nearly flat, sometimes lenticular, moderately to rather thin, opaque to slightly translucent, dull or somewhat glossy, of 5-6 slightly convex whorls. Last whorl well deflected, rounded to sharply angulate at periphery. Color light corneous to fulvous, uniform or with a dark supraperipheral band and lighter zones above and below this band; sometimes there are three bands. Embryonic whorls smooth, microgranulated or with vague spiral striae. Later whorls with delicate irregular radial striae and fine, crowded spiral lines; delicate hairs and light granulation may be present. Aperture ovate, well oblique, with thin, slightly reflexed margins; peristome insertions remote or more or less approached. Umbilicus open, moderately narrow, profound, perspective.

Flagellum long, sometimes twisted, epiphallus much shorter. Penis generally clavate, not large. Inner surface of penis lacking regular relief. Penis sheath thin, transparent. Penial retractor inserted on

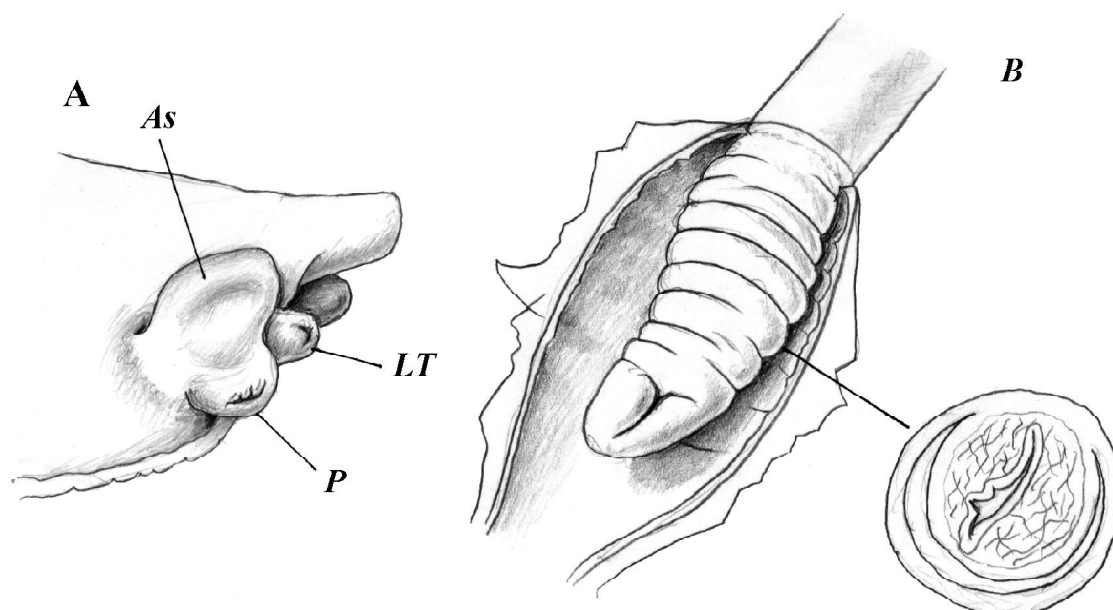


FIG. 11. *Chilostoma (Helicigona) lapicida*. France, valley between Bouter Villiers and St. Hilaire near Etampes, 7.05.1995. ZMMU No. Lc-22830. A – anterior part of animal, atrium everted to show distal part of penis and stimulator. B – penial papilla.

РИС. 11. *Chilostoma (Helicigona) lapicida*. Франция, долина между Бутер Вилье и Сент-Илер близ Этампа, 7.05.1995. ZMMU No. Lc-22830. А – передняя часть животного, атриум вывернут, видна дистальная часть пениса и стимулятор. В – папилла пениса.

about middle of epiphallus or nearer to its distal end. Free oviduct and vagina subequal in length. Stylophore rather small. Mucus glands simple.

Stimulator in form of subquadrangular fleshy plate.

Penial papilla conic, in inactive condition bears numerous circular folds; when it is active, its length may be much bigger. Walls of the organ contain semicircular cavity; inner canal of the papilla connected with inner surface of mentioned cavity by numerous fibers.

Distribution. N and W Europe, from S Scandinavia and England to the south up to S France; N Spain (Pyrenees).

*Chilostoma (Josephinella) Haas, 1936**

Haas, 1936: 130 (*Campylaea* subgen.).

Pintér, Subai, 1980: 173 (*Helicigona* subgen.); Schileyko, 2006a: 1769, Fig. 2265 (*Helicigona* subgen.); Groenenberg *et al.*, 2012: 161, Fig. 1(33,34), 2(18,22,26) (pro gen.).

Type species – *Helix hemonica* Thiésse, 1884; OD.

Shell depressed, very thin, fragile, much translucent, of 4.5-5 nearly flat whorls. Last whorl angled at periphery, gradually but markedly descending in front. Color light yellow to brown. Embryonic whorls finely granulate, same granulation retained on postnuclear whorls, where rather coarse radial wrinkles added; besides, there are numerous, small setae. Peristome insertions remote. Height 9-10, diam. 20-23 μ m.

Mucus glands generally split half up to 2/3 of

their length; rarely simple, or partly undivided, or even trifurcated.

Atrial stimulator weak, sometimes with two zig-zag-like processes; for the type species Pintér and Subai [1980: 174] indicate that “Atrium relativ kurz, innen einfach, ohne Reizkörper” (“Atrium relatively short, internally simple, without stimulator”).

Penial papilla oval, with a long longitudinal groove.

Distribution. S Albania, Macedonia, mainland Greece with Peloponnese, Ionian islands.

*Chilostoma (Thiessea) Kobelt, 1904**

Kobelt, 1904: 76, 131, 154, 187 (*Campylaea* subgen.).

Subai, 1996: 10 (*Helicigona* subgen.); Schileyko, 2006a: 1767, Fig. 2263 (*Helicigona* subgen.); Groenenberg *et al.*, 2012: 165, Fig. 1(35), 2(16) (pro gen.).

Type species – *Helix cyclolabris* Deshayes, 1839; SD C. Boettger and Wenz, 1921.

Shell much depressed to almost flat, moderately thin, of 4-4.5 slightly convex whorls. Last whorl strongly descending in front, rounded at periphery. Color whitish to corneous, with dark, narrow supraproperipheral band margined with light, diffuse zones. Sculpture of very fine granulation throughout and extremely short setae. Aperture nearly entire, subcircular. Height 9-12, diam. 15-25 mm.

Flagellum short to very long. Mucus glands undivided.

Stimulator weakly developed, in form of roughly triangular pad or light thickening of one of plicae within atrium.

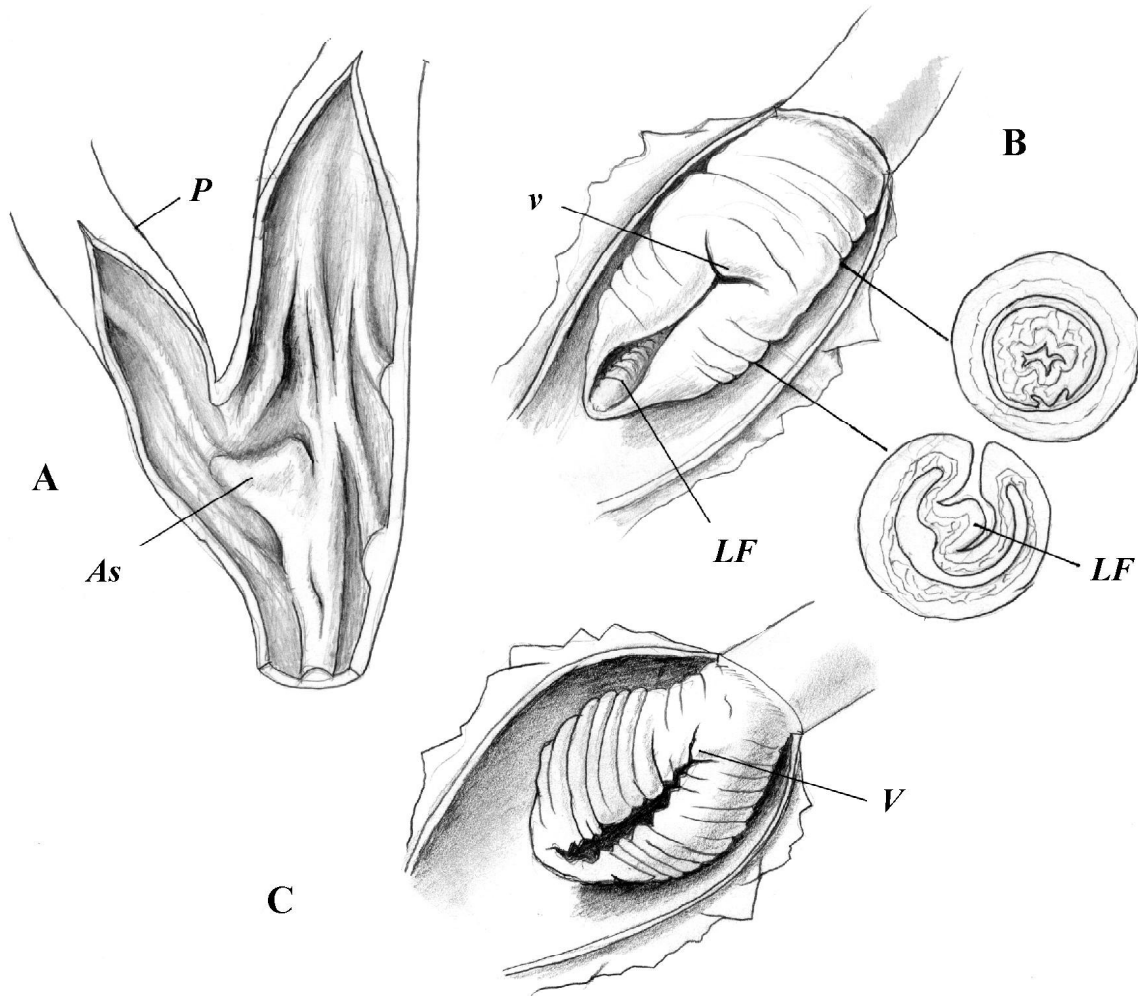


FIG. 12. *Chilostoma (Dinarica) pouzolzi*. A, B – Kotor, Montenegro, 04.1973. ZMMU No. Lc-19701. C – Kotor, 24.05.1974. ZMMU No. Lc-21820. A – inner structure of atrium. B, C – penial papilla.

РИС. 12. *Chilostoma (Dinarica) pouzolzi*. A, B – Котор, Черногория, 04.1973. ZMMU No. Lc-19701. C – Котор, 24.05.1974. ZMMU No. Lc-21820. A – внутреннее строение атриума. B, C – пениальная папилла.

Penial papilla is irregularly conic, with numerous longitudinal wrinkles. Position of penial pore is unknown.

Distribution. Mainland SE Greece, NE Peloponnese, Aegean Islands, SW Turkey.

Chilostoma (Dinarica) Kobelt, 1902

Fig. 12

Kobelt, 1902: 60, 61 [*Campylaea (Eucampylaea)*; sect.].

– *Joossia* Pfeffer, 1930: 96 (t.-sp. *Helix insignis* Zeiten, 1832; monotypy).

Schileyko, 2006a: 1780, Fig. 2280 (*Campylaea* subgen.); Groenenberg *et al.*, 2012: 153, Fig. 1(22), 2(23) (pro gen.).

Type species – *Helix dinarica* Bourguignat, 1888; tautonymy (syn. of *Helix pouzolzi* Deshayes, 1830)

Shell glossy, of about 6 rather convex whorls. Last whorl gradually deflected. Color mostly consisting of yellowish or light-corneous background and 3 chestnut bands, middle of them is the narrowest and the most distinct; above it there is a

wider band which is less distinct; the lowest is the widest (occupies nearly all basal surface of shell). Embryonic whorls smooth. Postnuclear sculpture of smoothed radial wrinkles and wavy spiral grooves. Aperture ovate, strongly oblique, with blunt margins; columellar and basal ones shortly reflexed, upper part nearly straight and flattened. Umbilicus moderately wide, profound. Height 14–27, diam. 25–50 mm.

Epiphallus at least 3 times shorter than flagellum. Mucus glands enormously developed, very long, glossy, with muscularized outer layers of walls; common ducts 1.5–2 times shorter than branches.

Stimulator as such is absent; in atrium there is a strong longitudinal pilaster having flattened lateral extension, which is, seemingly, a modified pilaster. From this extension branch off a narrow pilaster which runs to penis. In addition, in the vagina there are several thinner folds that can locally anastomosing.

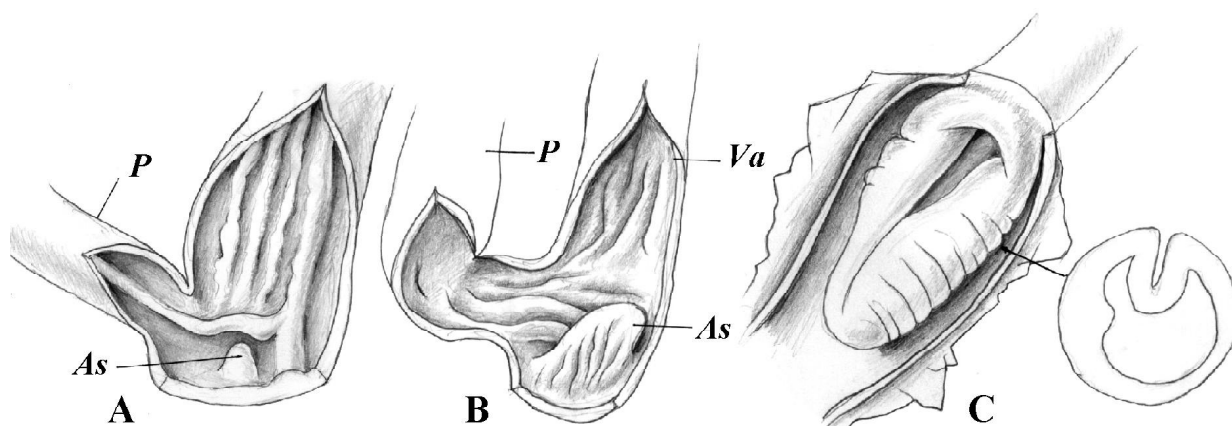


FIG. 13. *Chilostoma (Chilostoma) achates*. A – Italy, ca 18 km N of Cortina d’Ampezzo, Col Rosa Mt., 1700-1800 m, 27.04.1998. ZMMU No. Lc-28177. A, N – Austria, Ennstal, Grimming, Grimming Hütte, 14.05.2010. ZMMU No. Lc-39904. A, B – inner structure of atrium. C – penial papilla.

РИС. 13. *Chilostoma (Chilostoma) achates*. A – Италия, около 18 км к северу от Кортина д’Ампеццо, гора Коль Роза, 1700-1800 м, 27.04.1998. ZMMU No. Lc-28177. B, C – Австрия, долина р. Инн, Гримминг, Гримминг Хютте, 14.05.2010. ZMMU No. Lc-39904. A, B – внутреннее строение атриума. C – папилла пениса.

Penial papilla, when contracted, transversely folded, its proximal part thick-walled, contains a narrow canal in form of irregular many-rayed star. Canal has thick walls filled with loose parenchyma and surrounded by a narrow circular cavity. Distal part of the papilla bears a deep furrow, upper end of which covered with a small triangular velum. On the bottom of the furrow there is a longitudinal ridge.

Distribution. Eastern Adriatic coast from Croatia (N Dalmatia) to S Serbia.

?*Chilostoma (Sabljaria) Brusina, 1904**

Brusina, 1904: 162 (*Campylaea*, “Gruppe” *Sabljaria*).
Groenenberg *et al.*, 2012: 153, Fig. 1(21), 2(24) (*Dinarica* subgen.).

Type species – *Helix stenomphala* Menke, 1830; OD.

Shell depressed-conic, moderately thin-walled, of about 5 slightly convex whorls. Spire with nearly straight tangent-line. Coloration in typical case consists of pale-yellow background and 2 bands – supra- and subperipheral, the former is narrower, darker, and more distinct; basal surface below subperipheral band pale-brownish. Embryonic whorls smooth, sculpture of later whorls very weak. Aperture moderately oblique, with reflexed margins. Umbilicus narrow. Height 15-18, diam. 36-40 mm.

Flagellum considerably longer than penis+epiphallus. Mucus glands biramous.

Distribution. Velebit Mts. (Croatia).

Remark. Groenenberg *et al.* [2012] tentatively consider *Sabljaria* as a subgenus of the genus *Dinarica*.

Chilostoma (Chilostoma s. str.)

Fig. 13

Shell depressed to almost flat, thin, shining, of about 5.5 moderately convex whorls. Last whorl rounded to scarcely angulated, strongly but gradually deflected. Color yellowish-corneous, with dark supraproperipheral band. Embryonic whorls smooth. Postapical sculpture weak, of delicate, irregular radial lines. Peristome insertions more or less approached, connected by variously developed parietal callus. Height 9-12, diam. 18-27 mm.

Flagellum somewhat longer than penis+epiphallus. Mucus glands simple.

Stimulator small, rounded-triangular, located in the atrium near the very genital opening.

Penial papilla large, ovate-conic, with a deep longitudinal furrow. Along the bottom of the furrow runs a large longitudinal fold. Walls of the papilla contain a large cavity.

Distribution. Alps (Austria S of the Donau River, SE France, SE Switzerland, N Italy), SE Germany.

*Chilostoma (Cingulifera) Held, 1837**

Held, 1837: 911 (pro gen.).
Schileyko, 2006a: 1766, Fig. 2260 (*Helicigona* subgen.);
Groenenberg *et al.*, 2012: 149, Fig. 1(8,9,10), 2 (4).

Type species – *Glischrus cingulatus* Studer, 1820; SD Herrmannsen, 1847.

Shell is diverse in shape, coloration, and sculpture. Shape depressed to nearly flat, moderately solid, of about 5 flattened whorls. Last whorl evenly rounded at periphery, well deflected in front. Coloration is very various: white with a dark supra-

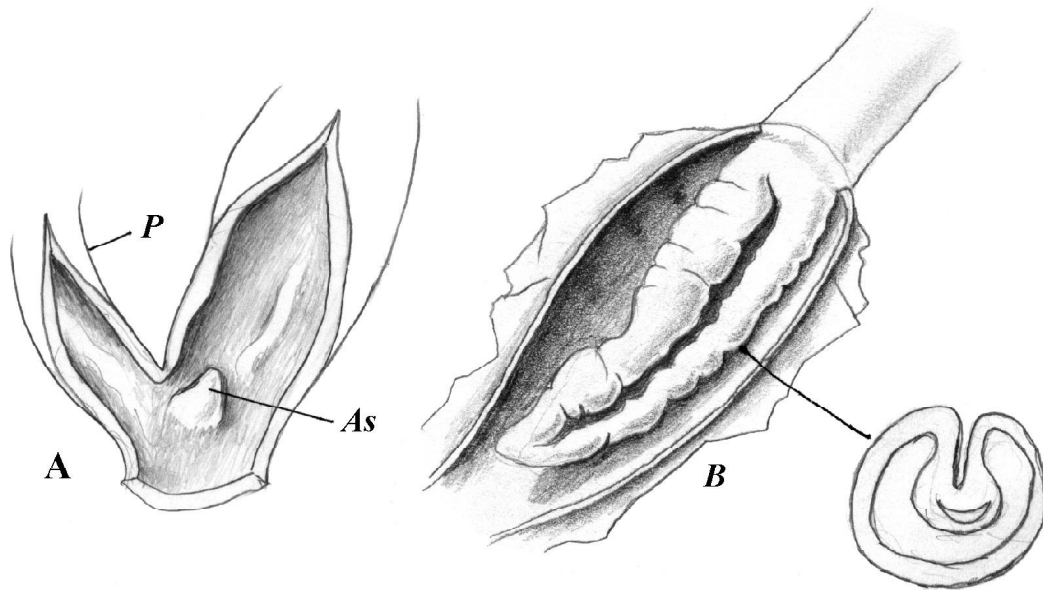


FIG. 14. *Liburnica setosa*. Makarska, Dalmatia, 25.07.1966. ZMMU No. Lc-19717. A – inner structure of atrium. B – penial papilla.

РИС. 14. *Liburnica setosa*. Макарска, Далмация, 25.07.1966. ZMMU No. Lc-19717. А – внутреннее строение атриума. В – пениальная папилла.

peripheral band, marbled, variegated. Embryonic whorls smooth. Postembryonic whorls from almost smooth to distinctly radially ribbed. Aperture ovate, very oblique, with shortly reflexed margins. Peristome insertions approached, connected by parietal callus. Umbilicus open, rather wide. Height 9-16, diam. 17-32 mm.

Flagellum a little longer than penis+epiphallus. Mucus glands simple.

Distribution. Alps of SE France, S Switzerland, S Germany, S and W Austria and Italy, north of the line Napoli-Termini [Groenenberg *et al.*, 2012].

?*Chilostoma (Delphinatia* Hesse, 1831)*

Hesse, 1831: 60 (*Campylaea* “Gruppe”).

Schileyko, 2006a: 1780, Fig. 2281 (*Campylaea* subgen); Groenenberg *et al.*, 2012: 153, Fig. 1(11), 2(12) (pro gen.).

Type species – *Helix alpina* Férussac, 1821; OD

Shell somewhat flattened, comparatively solid, of 5-6 moderately convex whorls. Last whorl evenly rounded to bluntly angulated at periphery, slightly descending in front. Color whitish to (dark) corneous, often somewhat spotted with dark and sometimes with weak dark supraperipheral band. Embryonic whorls smooth. Later whorls delicately, irregularly radially striated; locally traces of spiral striae may be present. Aperture rounded to widely ovate, with thin inner lip; margins shortly reflexed. Umbilicus moderately narrow, perspective. Height 7-16, diam. 13-30 mm.

Length of flagellum is approximately equal to length of penis+epiphallus. Mucus glands mostly

simple, but sometimes one of the glands can be partly divided.

Distribution. Alps in SE France and adjacent Italian Alps.

Remark. Groenenberg *et al.* [2012] believe that *Delphinatia* is a separate genus related to *Vidoviccia* and *Drobacia*.

***Liburnica* Kobelt, 1904**

Fig. 14

Kobelt, 1904 (October): 74, 131, 154, 185 (*Campylaea* subgen.).

– Botteria Brusina, 1904 (November): 162 (*Campylaea*, “Gruppe” Botteria, t.-sp. *Helix setosa* Rossmässler, 1836; OD).

– Superba Subai et Fehér, 2006: 206 (pro gen.; t.-sp. *Helicigona skipetarica* Subai, 1995; OD).

Schileyko, 1971: 991; Subai, 2002: 1; Schileyko, 2006a: 1776, Fig. 2275 (*Campylaea* subgen.); Subai, 2012: 35; Groenenberg *et al.*, 2012: 163, Fig. 1(20), 2(20).

Type species – *Helix setosa* Férussac, 1832; SD C. Boettger and Wenz, 1921.

Shell somewhat translucent, of about 5 slightly convex whorls. Last whorl strongly descending in front. Color mostly whitish-yellow, with 2 dark bands – above and below periphery. Embryonic whorls almost smooth or very finely granulate. Postembryonic whorls also with fine granulation; there are also fine radial wrinkles or even riblets and (often) golden hairs. Aperture strongly oblique, peristome insertions much approached and connected by thin but distinct callus. Aperture margins thin, shortly reflexed. Umbilicus deep, moderately broad. Height 7-15, diam. 15-35 mm.

Epiphallus thicker than flagellum and 3-5 times

shorter. Common ducts of mucus glands rather long; rarely glands simple. Inner surface of vagina with 1-3 smoothed folds.

Stimulator rather small, subtriangular.

Penial papilla is long, nearly conic, lacking additional lobe, with variously developed superficial longitudinal groove. Canal of the papilla is narrow, semicircular in cross-section. Walls of the papilla contain a vast circular cavity.

Distribution. Coastal territories of Adriatic Sea from Istria to S Montenegro, Albania down to Epirus Island (NW Greece).

Arianta Leach, 1831

Leach in Turton, 1831: 35.

– *Arianta* Martens in Albers, 1860: 127 (t.-sp. *Helix arbustorum* Linnaeus, 1758; OD)

Opinion 335 (1955): 47. Schileyko, 1978b: 310; 2006a: 1775, Fig. 2274; Groenenberg *et al.*, 2012: 141, Fig. 1(1,2), 2(1).

Type species – *Helix arbustorum* Linnaeus, 1758; by monotypy.

Shell somewhat depressed to globose, moderately thin, of 5-6 not very convex whorls. Body whorl markedly descending in front, evenly rounded. Color variable from white with a dark supraperipheral band to consisting of yellow, chestnut or brown background and light-yellow streaks and spots. Embryonic whorls smooth. Postembryonic sculpture generally of irregular fine radial wrinklets and dense spiral striae. Aperture ovate to rounded, oblique; margins reflexed, sharp, with a strong inner lip. Umbilicus narrow to almost closed. Height 10-24, diam. 15-24 mm.

Flagellum long, vermiform, epiphallus about 2 times shorter. Penis swollen, bulky, internally with numerous circular folds. Penial retractor attaching to epiphallus below its middle. Stylophore relatively small, elongate to subglobose. Mucus glands very long, always undivided. Spermathecal stalk with moderately long neck and very stout diverticle; reservoir attending albumen gland.

Stimulator enormously developed, bigger than in any other Ariantinae, lying in vagina (in this case it is rod-shaped) or in penis (in this case it is crest-like).

Structure of penial papilla is very similar to that of *Chilostoma (Dinarica) pouzolzi* (Fig. 12), but differs from it by the absence of triangular velum.

Distribution. N and Central Europe; southward to N Italy, Slovenia, Croatia, Serbia, and Bulgaria. Introduced to Moscow region (Russia).

Arianta (Arianta) s. str.)

Fig. 15, 16A

Shell somewhat depressed to globose, moderately thin, of 5-6 not very convex whorls. Body whorl markedly descending in front, evenly rounded.

Color variable from white with a dark supraperipheral band to consisting of yellow, chestnut or brown background and light-yellow streaks and spots. Embryonic whorls smooth. Postembryonic sculpture generally of irregular, fine radial wrinklets and dense spiral striae. Aperture ovate to rounded, moderately oblique; margins reflexed, sharp, with a strong inner lip. Umbilicus narrow to almost closed. Height 10-24, diam. 15-24 mm.

Flagellum long, vermiform, epiphallus about 2 times shorter. Penis swollen, bulky, internally with numerous circular folds. Penial retractor attaching to epiphallus below its middle. Stylophore relatively small, elongate to subglobose. Mucus glands very long, always undivided. Spermathecal stalk with moderately long neck and very stout diverticle; reservoir attending albumen gland.

Stimulator is rod-like, enormously developed, bigger than that of any other Ariantinae, attached to the atrium by its basal end, pointing into the vagina.

Structure of penial papilla very similar to that of *Chilostoma (Dinarica) pouzolzi* (Fig. 12), differs from it by absence of triangular velum.

Distribution. Central and N Europe. 4-5 spp.

Arianta (Altarianta) Schileyko, subgen. nov.)

Fig. 16B, 17

urn:lsid:zoobank.org:act:47675D7B-C712-4845-BAC8-5EFEEA6DA438

Type species – *Helix stenzii* Rossmässler, 1835

Etymology. The name comes from Latin *alt*[a] (high mountain) and *Arianta*.

The shell is different from *Arianta* s. str. by thinner walls, the more inflated and more rapid increase of the last whorl, as well as by a little coarser radial sculpture. Height 13-18, diam. 20-29 mm.

Stimulator differs from that of *Arianta* s. str. by two peculiarities: 1. In *Altarianta* it directed to penis (not to vagina) and 2. In *Altarianta* the stimulator is attached to the inner surface of the penis by lateral side (not by basal like in *Arianta* s. str.). Thus, stimulator is pectiniform.

Penial papilla differs from that of *Arianta* s. str. in absence of central longitudinal ridge (comp. Fig. 16A and 16B).

Distribution. S Austria, NE Italy. Probably, 1 sp.

Remark. I dissected three specimens of *A. stenzii* from one locality. Differences in the structure and topography of the stimulators and penial papilla between *A. stenzii* and two other species that I have studied (*A. arbustorum* and *A. styriaca*) are so obvious that I decided to segregate *A. stenzii* as a separate subgenus. Surprisingly, according to Groenenberg *et al.* (2012), *Arianta stenzii* very closely related to *A. arbustorum* by all used (four in

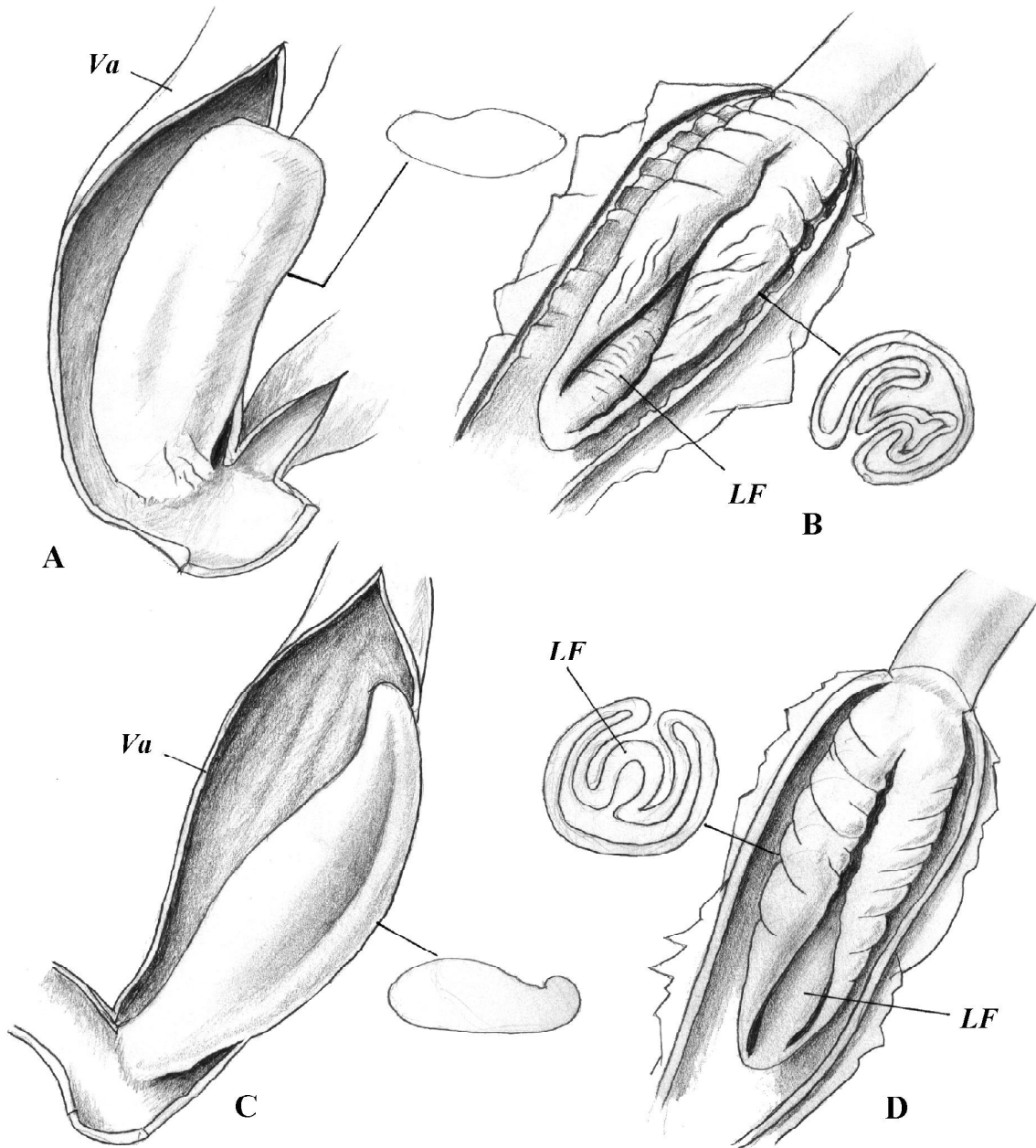


FIG. 15. Atrial stimulators and penial papillae of species of *Arianta* (*Arianta*). A, B – *Arianta arbustorum*. Plateau Minchul above Kvasy village, Rakhov district, Transcarpathians, 16.09.1969. ZMMU No. Lc-19711. C, D – *Arianta styriaca*. Austria, Styria, Hess-Hütte above Kummerbrücke, 1660-1690 m, 21.09.1996. ZMMU No. Lc-23416.

РИС. 15. Атриальные стимуляторы и пениальные папиллы видов *Arianta* (*Arianta*). А, В – *Arianta arbustorum*. Полонина Минчул над с. Квасы, Раховский р-н, Закарпатье, 16.09.1969. ZMMU No. Lc-19711. С, D – *Arianta styriaca*. Австрия, Штирия, Гесс-Хютте над Куммербрюке, 1660-1690 м, 21.09.1996. ZMMU No. Lc-23416.

number) molecular criteria. I cannot explain the reason of this strange fact.

Addition to Ariantini

Groenenberg *et al.* [2012] have introduced, based on molecular data, two new taxa, but the authors made a reservation that their work “is not issued for purposes of zoological nomenclature and is not published within the meaning of the International

Code of Zoological Nomenclature ...” (op. cit., p. 117). However, I find it appropriate to give, for completeness of picture, the characteristics of these taxa.

Kollarix Groenenberg *et al.*, 2012
[not available under Art. 8.2 of ICZN]

Groenenberg *et al.*, 2012: 162, Fig. 1(19), 2(15) (pro gen.).

Type species – *Helix kollari* Pfeiffer, 1856; OD.

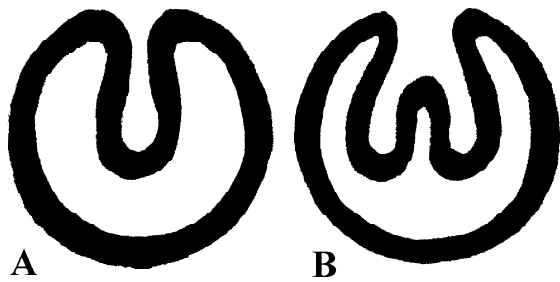


FIG. 16. Cross-sections through middle part of penial papilla of *Arianta* s. str. (A) and *Arianta* (*Altarianta*) (B), schematized.

РИС. 16. Поперечные срезы через срединную часть папиллы пениса *Arianta* s. str. (A) и *Arianta* (*Altarianta*) (B), схематизировано.

Shell clearly depressed, with hairs.
Mucus glands undivided.
Distribution. Serbia.

***Campylaea* (*Ljubotenia* Groenenberg *et al.*, 2012) [not available under Art. 8.2 of ICZN]**

Groenenberg *et al.*, 2012: 164, Fig. 2(25).

Type species – *Helicigona* (*Arianta*) *ljubetensis* Wagner, 1912; OD

Shell is similar to *Chilostoma* (*Cattania*).

Mucus glands forked.

“... the *Histone H3* sequence is identical to the sequences of *C. lefeburiana* and *C. illyrica* ...”

[Groenenberg *et al.*, 2012: 164], so *Helicigona ljubetensis* provisionally assigned to the genus *Campylaea*. The authors have not written what are morphological differences of the new subgenus from *Campylaea* s. str.

Distribution. Mount Ljuboten in the Šar mountain area, on the border between Kosovo and NW Macedonia.

Cylindruini Schileyko, 2006

Schileyko, 2006a: 1785

Shell cylindrical, pupiform.

Penis sheath is absent.

Flagellum long, slender. Penis contains one chamber. Stylophore fusiform, narrowed basally. Mucus glands simple, tubular, without alveolar inner structure; one of them or both may be more or less reduced. Diverticle of spermathecal stalk moderately developed, membrane between it and spermoviduct thin, weakly vascularized.

Dart lanceolate, without crown.

Distribution. Austrian Alps.

Cochlopupa Jan, 1830

Fig. 18, 19

Jan, 1830: 5 (pro subgen.; t.-sp. *Pupa obtusa* Draparnaud, 1805; monotypy).

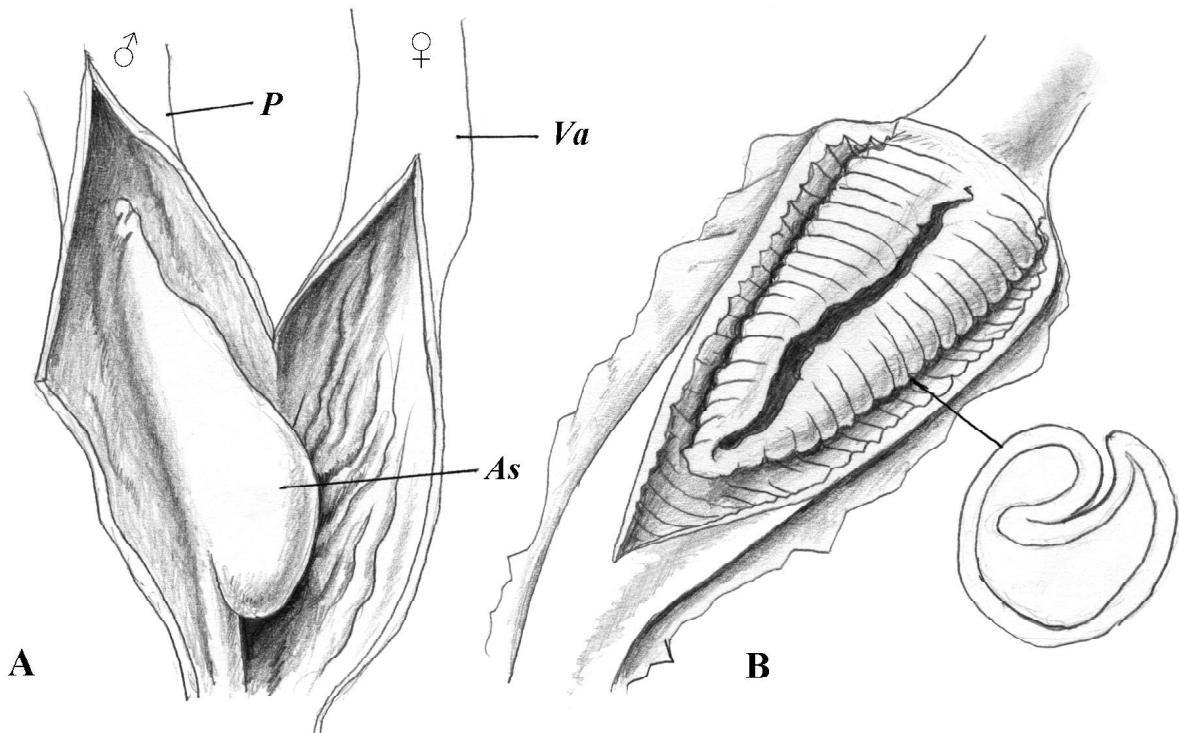


FIG. 17. *Arianta* (*Altarianta*) *stenzii*. NE Italy, Forcella Val Misera in 4-5 km E of Perarolo di Cadore, 2000 m above sea level, 10.08.1997. A – inner structure of atrium. B – penial papilla. ZMMU Lc-39905.

РИС. 17. *Arianta* (*Altarianta*) *stenzii*. СВ Италия, Форчелла Валь Мизера в 4-5 км восточнее Пералоло, 2000 м над уровнем моря, 10.08.1997. А – внутреннее строение атриума. В – папилла пениса. ZMMU Lc-39905.

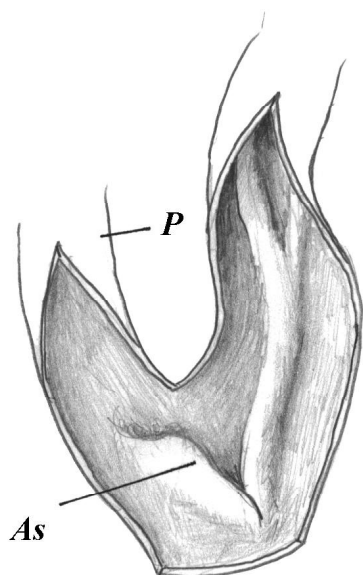


FIG. 18. *Cochlopupa obtusa*. Austria, Glockengruppe-Edelweißspitze-Edelweißwand, 27.07.2009. ZMMU No. Lc-39906. Inner structure of atrium.

РИС. 18. *Cochlopupa obtusa*. Австрия, Глокенгруппа-пик Эдельвейс-Эдельвейсwand, 27.07.2009. ZMMU No. Lc-39906. Внутреннее строение атриума.

– *Cylindrus* Fitzinger, 1833: 107 (t.-sp. *Pupa obtusa* Draparnaud, 1805; monotypy).

Schileyko, 1996a: 37 (*Cylindrus*); Schileyko *et al.*, 1997: 535 (*Cylindrus*); Schileyko, 2006a: 1785, Fig. 2286 (*Cylin-*

drus); 2012: 93; Groenenberg *et al.*, 2012: 152 (*Cylindrus*).

Type species – *Pupa obtusa* Draparnaud, 1805; monotypy.

Shell of 6.5-8.5 moderately convex, slightly compressed whorls. Embryonic whorls smooth. Later whorls finely, irregularly radially wrinkled. Aperture widely ovate, not strongly oblique. Height 9.5-17.0, diam. 4.0-5.3 mm.

Flagellum moderately long, slender. Epiphallus of approximately same length. Penis ovate, with thin, semitransparent walls. Penial retractor attached to lower half of epiphallus. Free oviduct moderately long, vagina somewhat longer. Stylophore relatively small, ovate. Mucus glands initially 2, mace-shaped, but in some eastern populations process of reduction of one of them down to complete disappearing has been observed. Inner surface of vagina with one smoothed axial pilaster. Spermathecal stalk very slender, diverticle thicker; neck moderately long; reservoir globular, attending albumen gland.

Stimulator is small, nearly triangular or in form of a short pectiniform fold, lying in atrium or in the distalmost section of penis.

Penial papilla comparatively large, thin-walled, with very broad lumen; epiphallic pore situated at base of papilla, covered by a small, more or less triangular velum; this velum variously developed,

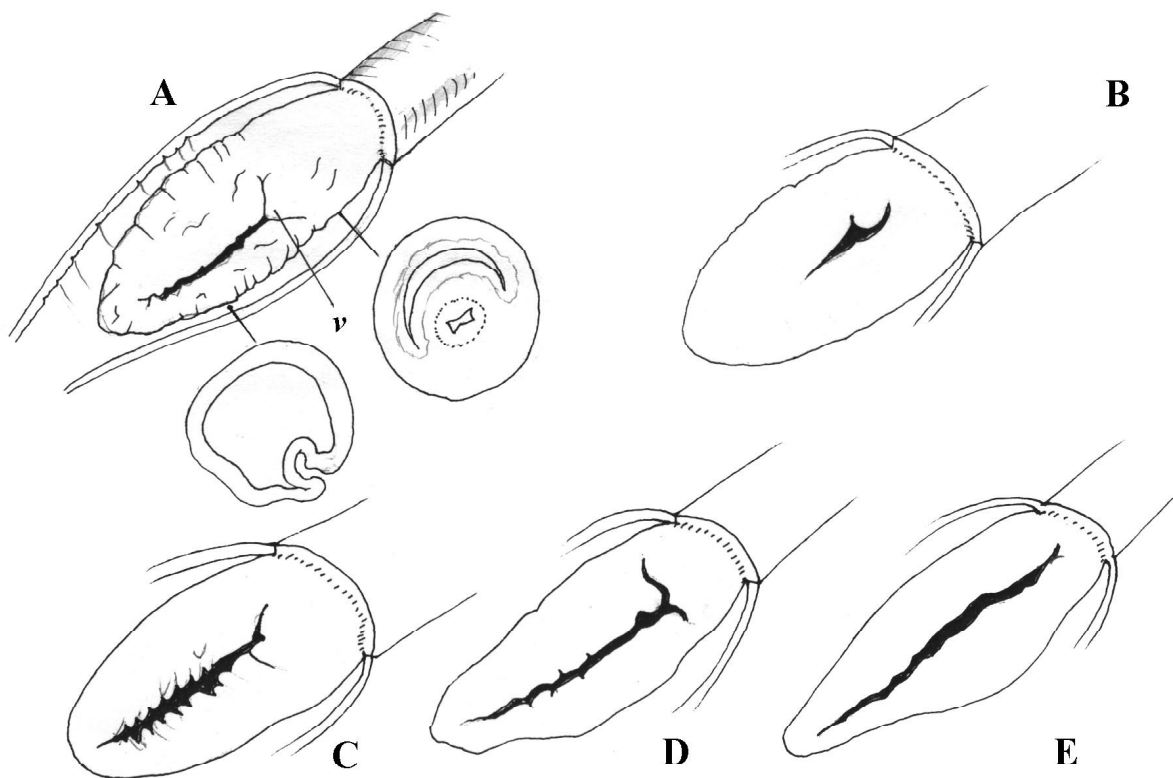


FIG. 19. Variability of penial papilla of *Cochlopupa obtusa*. A – Schneealpen, Rinnhofer Alm, Windberg, Osthang 1, 25.05.2009. ZMMU No. Lc-39907. B, C, D, E – Steiermark, Stadtfeldschneid, 17.08.2009. ZMMU No. Lc-39908.

РИС. 19. Изменчивость пениальной папиллы *Cochlopupa obtusa*. А – Шнееальпен, Ринхофер Альм, Виндберг, Восточный склон 1, 25.05.2009. ZMMU No. Lc-39907. В, С, Д, Е – Штирия, Штадфельдшнайнд, 17.08.2009. ZMMU No. Lc-39908.

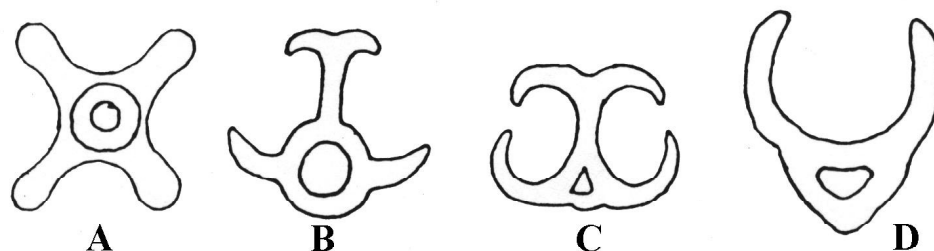


FIG. 20. Cross-sections through darts of Murellinae. A – *Murella muralis*. B – *Ambigua strigata*. C – *Marmorana serpentina*. D – *Tyrrheniberus sardonica*. After Hesse, 1908.

РИС. 20. Поперечные срезы через стрелы Муреллинае. А – *Murella muralis*. В – *Ambigua strigata*. С – *Marmorana serpentina*. D – *Tyrrheniberus sardonica*. По Hesse, 1908.

sometimes nearly absent. Narrow longitudinal superficial groove on the papilla leads to epiphallic pore. Distal part of the papilla contains a vast cavity, which in proximal part transformed in a narrow semicircular slit.

Distribution. Austrian Alps.

Lampadiini Schileyko, 2006

Schileyko, 2006a: 1786

Shell vitrinoid, with very large aperture.

Jaw nearly smooth, with delicate vertical and horizontal striae and weak median process.

Penis sheath present.

Dart stylet-shaped, with a crown and four blades.

Distribution. Madeira, Canary Islands.

Lampadia Albers, 1854

Albers, 1854: 53 (*Helix* subgen., nom nov. pro *Mitra* Albers, 1850, non Lamarck, 1798).

– *Mitra* Albers, 1850: 115 [nom. praeocc., non Lamarck, 1798 (*Pectinibranchia*); *Helix* subgen., t.-sp. *Helix webbiana* Lowe, 1831; monotypy].

Schileyko, 2006a: 1786, Fig. 2287.

Type species – *Helix webbiana* Lowe, 1831; by typification of replaced name.

Shell trochiform, thin, translucent, of 3-3.5 flattened to nearly flat whorls. Last whorl markedly descending in front, with a sharp peripheral angle or keel. Color corneous or dark-yellow, keel lighter. Embryonic whorls smooth. Later whorls with accurate granulation. Aperture broadly ovate, strongly oblique, with thin, reflexed and expanded margins. Peristome insertions approached. Height 4-11, diam. 7-20 mm.

Flagellum very long, vermiform. Epiphallus very short, sharply bent. Penis rather small, contains a longitudinal fold and short subglobular papilla. Penial retractor attached to the curvature of epiphallus. Stylophore comparatively very large. Each of

two mucus glands composed of 3-5 branches. Spermathecal stalk with a rather long neck, shorter stalk proper, small reservoir, and diverticle that is longer than stalk proper+reservoir.

Stimulator is a rather small thickening disposed in distal portion of penis.

Penial papilla short, subglobular, with a short furrow that occupies slightly lateral position; besides, there are circular grooves.

Distribution. Madeira.

Murellinae Hesse, 1918

Hesse, 1918: 35

Shell depressed to subglobular, rather solid, of 4-5 moderately convex whorls. Coloration mostly more or less variegated. Umbilicus narrow to nearly closed.

Dart with a crown; longitudinal blades on the dart surface have various shape and number. Membrane between diverticle of spermathecal stalk and the spermoviduct very thin, lacking visible vascularization.

Marmorana Hartmann, 1844* Fig. 20 C

Hartmann, 1844 (1840-1844): 210.

Schileyko, 2006a: 1783, Fig. 2282.

Type species – *Helix serpentina* Férussac, 1821; monotypy.

Shell depressed, (moderately) solid, somewhat shining, of about 4.5-5 slightly convex whorls. Last whorl rounded at periphery, rather abruptly descending in front. Color whitish or yellow tinged, with 5 more or less distinctly interrupted bands, or radially maculate and strigate above; sometimes with whole ground-color deep chestnut, upon which there are white zigzag vermiculations and strigations. Embryonic whorls smooth. Postapical surface lightly obliquely striatulate. Aperture broadly

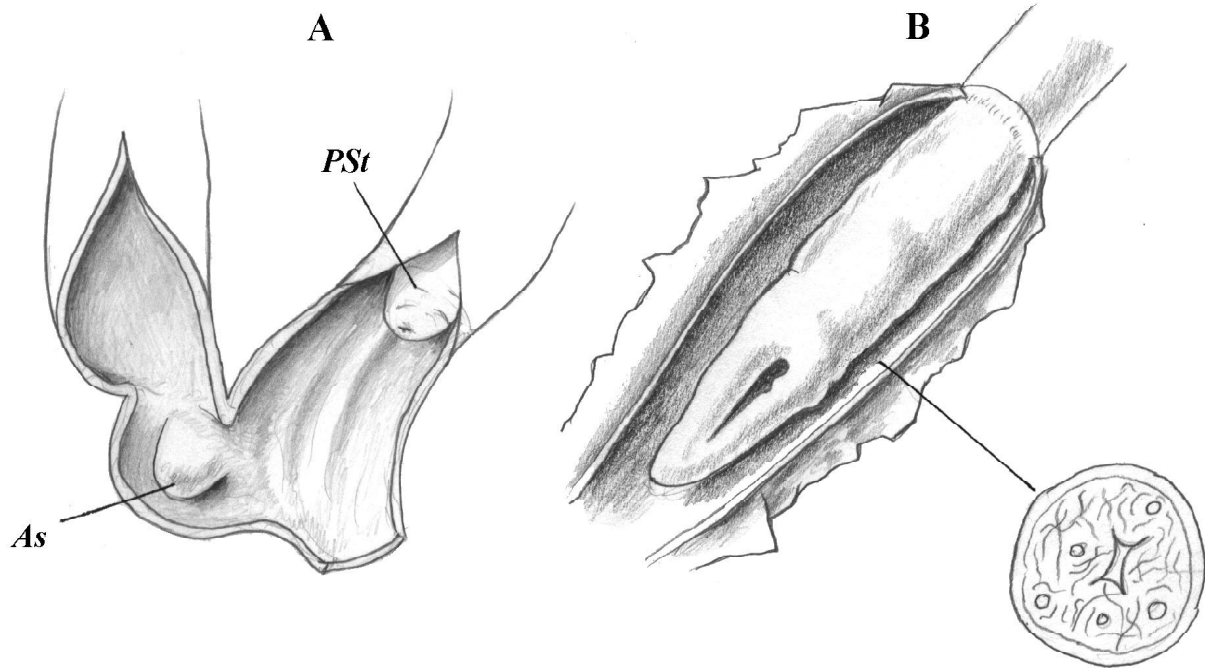


FIG. 21. *Murella muralis*. Rome, Coliseum, 1.11.1995. ZMMU No. Lc-28179. A – inner structure of atrium. B – penial papilla.

РИС. 21. *Murella muralis*. Рим, Колизей, 1.11.1995. ZMMU No. Lc-28179. А – внутреннее строение атриума. В – папилла пениса.

ovate, quite oblique, with almost straight or shortly reflexed margins. Umbilicus closed or slit-like. Height 8-16, diam. 15-28 mm.

Jaw odontognathous.

Flagellum of about same length as epiphallus+penis. Penis clavate. Penial retractor attached to epiphallus a little above penis/epiphallus junction. Each of mucus glands consists of 1 or 2 branches.

Dart in cross-section resembles a combination of the letter “C” and its mirror reflection, connected by their convex sides; internal canal of the dart is narrow, subtriangular, not central in position.

Distribution. Italy, Tyrrhenian Islands, Corsica, Sardinia.

Murella L. Pfeiffer, 1877

Figs. 20 A; 21

Pfeiffer L., 1877: 8 (*Helix*, sect. *Iberus*; subsect.).

Schileyko, 2006a: 1772, Fig. 2269; Giusti *et al.*, 1995: 472-479, Figs. 592-601 (*Marmorana* subgen.).

Type species – *Helix muralis* Müller, 1774; SD Kobelt, 1904.

Shell depressed, mostly comparatively thin, slightly translucent, of 4-4.5 moderately convex whorls. Last whorl rounded, strongly deflected at aperture. Outline of spire nearly conic. Coloration consisting of calcareous-white background, 4 variously developed bands, and dark marble pattern; light peripheral band may be present. Embryonic whorl smooth. Postapical surface with fine radial wrinklets and extremely delicate radial striae. Aperture ovate,

strongly oblique; margins not thickened, a little reflexed. Umbilicus closed. Height 8.5-14.0, diam. 14-27 mm.

Jaw odontognathous.

Vas deferens comparatively short. Flagellum either somewhat longer than penis+epiphallus or a little shorter. Penis fusiform, surrounded by very thin, transparent sheath. Penial retractor attached to middle of epiphallus. Free oviduct short, slender. Vagina long, stout. Stylophore situated very low, close to atrium. Mucus glands simple, rather short. Neck of spermathecal stalk not very short, more or less swollen basally. Diverticle thin.

Dart in cross-section in form of regular four-rayed star, with rather narrow central canal.

Stimulator, a rather small fleshy ovate plate, situated in widened distal portion (camera) of penis.

Penial papilla rather long, conic, with a short longitudinal furrow that starts at short distance from the tip of the papillae and ends at the boundary between two distal thirds of the organ. Walls of the papilla filled with very loose parenchyma containing numerous sinuses and lacunae.

Distribution. Sicily, Malta.

Ambigua Westerlund 1902*

Fig. 20 B

Westerlund, 1902: 96.

– *Opica* Kobelt, 1904: 132, 156, 198 (*Iberus* subgen.; t.-sp. *Helix strigata* Férussac, 1821; OD [evidently, *Helix signata* Férussac, 1821].

Schileyko, 2006a: 1773, Fig. 2270.

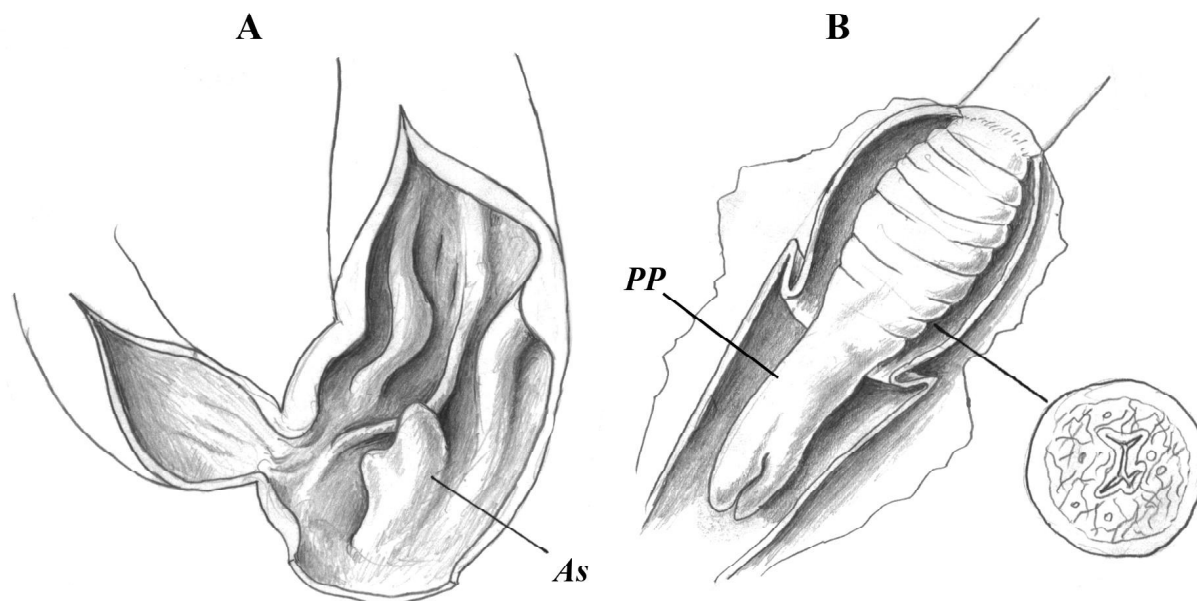


FIG. 22. *Macularia niciensis*. SE France, Carros, Alpes Maritime, 6.07.1982. ZMMU No. Lc-28187. A – inner structure of atrium. B – penial papilla.

РИС. 22. *Macularia niciensis*. ЮВ Франция, Карро, Приморские Альпы, 6.07.1982. ZMMU No. Lc-28187. А – внутреннее строение атриума. В – папилла пениса.

Type species – *Helix tetrazona* Cristofori et Jan, 1832 (= *Helix signata* Férussac, 1821); OD.

Shell depressed, solid, of 4-4.5 moderately convex whorls. Last whorl rounded or a little angulate, well descending in front. Color uniformly white or with 3-4 fulvous bands, uppermost often very weak or missing. Embryonic whorls smooth. Postnuclear whorls with very delicate radial wrinklets. Aperture widely ovate, strongly oblique, with slightly reflexed margins. Umbilicus cylindrical, moderately wide. Height 7-12, diam. 14-23 mm.

Jaw odontognathous.

Mucus glands, as a rule, forked, sometimes simple or with three branches.

Dart in cross-section with three blades; two of them are short, a little curved, sitting symmetrically on the main “trunk”. The third blade larger, forked at its upper end. Central canal wide. As a whole the dart in cross-section resembles an anchor.

Distribution. Middle and S Italy.

Macularia Albers, 1850

Fig. 22

Albers, 1850: 80 (*Helix* subgen.).

Schileyko, 2006a: 1782, Fig. 2283.

Type species – *Helix niciensis* Férussac, 1821; SD Lowe, 1854.

Shell depressed-conoid, moderately solid, somewhat glossy, of 4.5-6 slightly convex whorls. Body whorl rounded, markedly descending in front. Color whitish, normally with 5 brown bands broken into series of spots. Embryonic whorls smooth.

Postapical whorls with smoothed, irregular radial wrinkles and sometimes, locally, short spiral touches. Aperture ovate, moderately oblique, with thin or slightly thickened margins; baso-columellar margin with variously developed lip. Umbilicus very narrow, usually partly or completely covered. Height 11-17, diam. 15-27 mm.

Jaw odontognathous.

Flagellum extremely long. Epiphallus rather short. Penis with a long papilla; upper chamber of penis, containing basal part of papilla, invaginated into lower chamber. Free oviduct comparatively long, vagina 1.5-2 times shorter. Stylophore large, situated very low – just above atrium. Mucus glands attached to base of stylophore, common ducts of glands very short. Inner surface of vagina with 2-3 large axial pilasters. Neck of spermathecal stalk quite long, diverticle very long, strongly convoluted.

Stimulator rather small, of irregular shape.

Penial papilla with bilobed apex; lobes almost equal, pore situated between lobes. Lumen of papilla narrow, I-beam in cross-section. Walls of papilla filled with very loose parenchyma.

Distribution. Italy, Sardinia, Corsica.

?*Tyrrheniberus* Hesse et Kobelt, 1904*

Fig. 20 D

Hesse et Kobelt in Kobelt, 1904: 132, 157, 199 (*Iberus* subgen.). Hesse, 1908: 109, Taf. 377, Fig. 3-9 (*Murella* subgen.); Schileyko, 2006a: 1773, Fig. 2271.

Type species – *Helix sardonica* Martens, 1884; SD C. Boettger and Wenz, 1921.

Shell sublenticular, much flattened, moderately solid, of 4-4.5 almost flat whorls. Last whorl strongly deflected, with cord-like, uneven keel that is visible above suture on penultimate whorl. Color generally light corneous, usually there are 4 bands; upper surface somewhat variegated, with 1 band below keel, usually interrupted by light streaks. Embryonic whorls smooth. Later whorls coarsely, irregularly radially ribbed. Aperture ovate-rostrate, very oblique, with slightly reflexed margins. Umbilicus moderately narrow, usually a little covered. Height 7-13, diam. 15-27 mm.

Jaw smooth, without vertical riblets.

Flagellum thin, of about same length as epiphallus. Penis consists of bulky proximal and thinner distal parts. Penial retractor short, attached to about middle of epiphallus. Mucus glands simple or biramous. Basal part of spermathecal stalk considerably swollen. Diverticle of spermathecal stalk is absent or rudimentary.

Dart in cross-section with two blades, slightly resembles an upturned letter "A". Central canal of the dart is rounded-triangular.

Distribution. E Sardinia, Toscana (=Tuscany).

Remark. The genus *Tyrrheniberus* occupies somewhat isolated position since the species of this genus have smooth jaw (like those of *Lampadia*) and diverticle of spermathecal stalk in them is rudimentary or totally absent. Perhaps, it would be better to place the genus *Tyrrheniberus* in Helicinae, because reduction or total disappearance of diverticle of spermathecal stalk is characteristic just for this subfamily.

Thebinae Wenz, 1923

Wenz, 1923 (1923-1930): 381.

– Euparyphinae Perrot, 1939: 35.

Shell semiglobose to almost lens-shaped, of medium size.

Flagellum is from quite long to rudimentary. Penis contains two chambers: proximal chamber entering distal chamber through a broad papilla; another papilla protruded into atrial section of penis. Stylophore nearly sessile. Mucus glands simple, internally of alveolar structure. Diverticle of spermathecal stalk thin, somewhat rudimentary, membrane between it and spermoviduct exceptionally thin, without visible vascularization.

Dart stylet-shaped, with a basal crown and 4 blades.

Theba Risso, 1826

Fig. 23

Theba Risso, 1826: 73 (Opinion ICZN 431, 1956: 350).

– *Xerophila* Held, 1837: 913 (invalid name: Bull. ICZN, 1956, Opinion 431: 250).

– *Euparypha* Hartmann, 1843 (1840-1844): 204 [t.-sp. *Euparypha rhodostoma* Draparnaud, 1801 (= *Helix pisana* Müller, 1774); monotypy].

Gittenberger, Ripken, 1987 (revision of the genus); Schileyko, 2006a: 1784, Fig. 2285.

Type species – *Helix pisana* Müller, 1774; SD Gray, 1847 (Bull. ICZN, 1956, Opinion 431: 350).

Shell subglobose to sublenticular, (moderately) solid, glossy, of about 5 slightly to moderately convex whorls. Last whorl widely rounded, almost straight. Color whitish, mostly with many dark, irregular bands; peristome often pinkish. Embryonic whorls smooth, polished. Postapical sculpture of fine, irregular radial lines and spiral grooves. Aperture is large, subcircular to angulate, slightly oblique, with almost straight margins and smoothed lip. Umbilicus minutely open, often partly covered. Height 12-16, diam. 16-21 mm.

Talon large, exposed, hermaphroditic duct joins talon subapically. Vas deferens moderately long, entering epiphallus subapically, leaving rudimentary flagellum. Epiphallus is not long. Penis swollen, with proximal chamber having a vast lumen; walls of this chamber transversely folded. Proximal chamber entering distal one through a broad papilla that fills most of lumen of distal chamber; latter also with folded walls, enters narrow, distalmost section of penis through a short, sphincter-like papilla. Penial retractor inserted on lower half of epiphallus. Free oviduct long, more or less convoluted. Vagina is rather short. Stylophore ovate, without accented neck. Mucus glands look like alveolar in structure, attached to vagina a little above base of stylophore. Inner surface of vagina bears a few weak irregular folds. Spermathecal stalk slender, long, with very thin, somewhat rudimentary diverticle; neck long; reservoir globular, not large, attending albumen gland.

Stimulator represented by a strong longitudinal pilaster, located in the atrium and lower part of the vagina.

Penial papilla as such is very short, with small apical pore. Proximal part of penis thick-walled, its cavity contain numerous strong, irregular (sub)circular folds that fill most part of volume of the cavity.

Distribution. Circummediterranean.

Conclusion

I agree with Groenenberg *et al.* [2012] in the evaluation of the taxonomic situation in Ariantinae as contradictory. As can be seen from the material presented in this article, some morphological data support the molecular phylogeny, others do not. Therefore, the main aim of this paper is to show the morphological diversity of Ariantinae rather than presenting a final conclusion. Perhaps, when the structure of stimulators and, especially, penial papil-

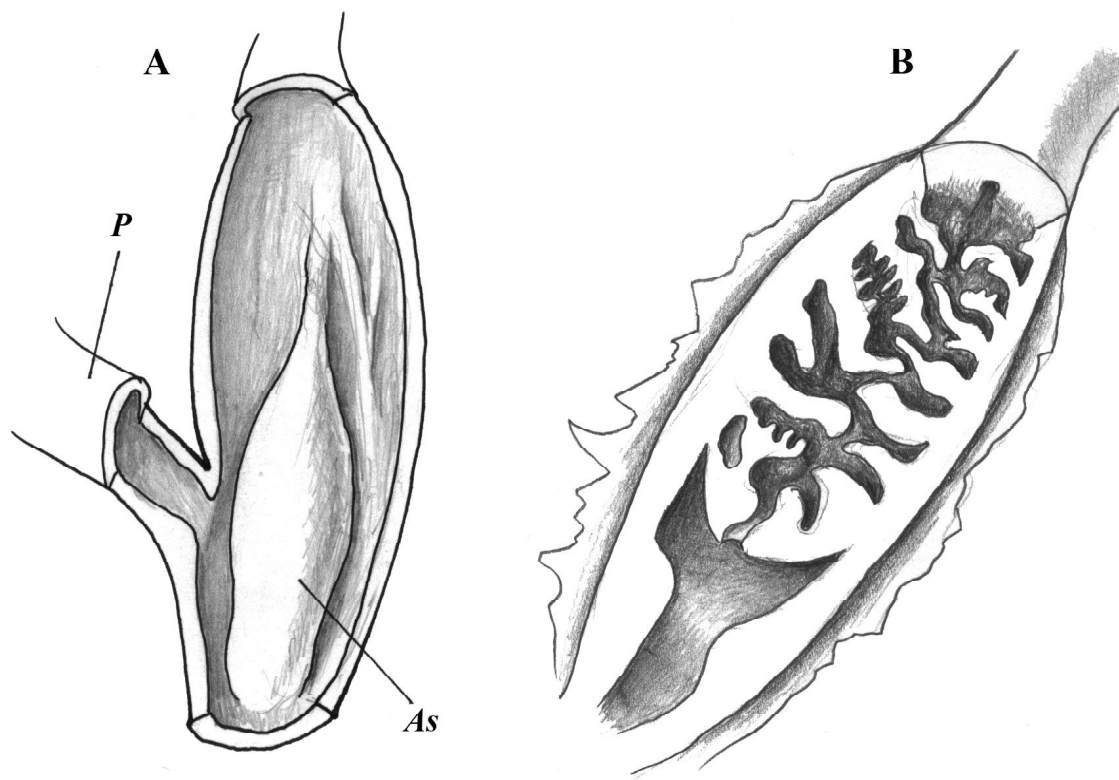


FIG. 23. *Theba pisana*. Cyprus, Larnaca, 20.02.1980. ZMMU No. Lc-28180. A – inner structure of atrium. B – longitudinal section of penis.

РИС. 23. *Theba pisana*. Кипр, Ларнака, 20.02.1980. ZMMU No. Lc-28180. А – внутреннее строение атриума. В – продольный срез пениса.

lae of type species of all (sub)genera is known, we have enough information to reconcile these two approaches.

Catalogue of Recent Helicidae excl. Helicinae

After the name of a taxon the name of the author and year follow; further in brackets – accepted generic (subgeneric) name (in **bold**). Notes «var.» and «subsp.» to some extent are conditional.

This list is preliminary and open to changes and clarifications.

abraea Mabilie 1867 (=muralis)
abromia Mabilie 1867 (=muralis)
acarnanica Kobelt 1892 (conemenosi var.)
achates achates Rossmässler 1835 [**Chilostoma (Chilostoma)**]
acrotricha Bofill, Haas et Aguilar-Amat 1918 (=desmoulinsi)
acrotricha P. Fischer 1877 [**Chilostoma (Corneola)**]
acutangula Lowe 1861 (=subdentata helicella)
adamii Kobelt 1873 (adelozona subsp.)
adamii Pini 1876 (=cingulatum frigidum)
adelozona adelozona Strobel 1857 [**Chilostoma (Chilostoma)**]
adjacensis Paulucci 1882 (serpentina var.)
adriatica Bourguignat 1888 (=pouzolzi pouzolzi)
advenoides Paiva, 1867 (erubescens subsp.)
aegusina Monterosato 1892 (=pisana)
aemula L. Pfeiffer 1852 (=ambrosi)

aethiops Bielz 1867 [**Arianta (Arianta)**]
affinis Paulucci 1878 (=cingulata appeli)
agaroi Letourneux et Bourguignat 1887 (=pisana)
agnata Paulucci 1881 (=cingulata carrarensis)
alba Moquin-Tandon 1855 (=pisana)
albanica Jaekel 1954 (stenomphala subsp.)
albanica Kobelt 1899 (=pouzolzi montenegrina)
albanograeca Subai 1995 (**Liburnica**)
albella Linnaeus 1758 (=pisana pisana)
albida Rossmässler 1839 (=setosa)
albina Brusina 1869 (=insolita insolita)
albinosa Monterosato 1892 (muralis var.)
alboranensis Beck 1837 (=pisana pisana)
alboranensis Lowe 1861 (=pisana ampullacea)
alboranensis Odhner 1931 (non Beck 1837) (=arinagae)
albulana Bourguignat 1889 (=arbustorum)
alifaensis Paulucci 1881 (planospira subsp.)
alpestris Rossmässler 1837 (=arbustorum var.)
alpicola Férussac 1819 (arbustorum subsp.)
alpina Michaud 1831 (fontinellii subsp.)
alpinum Férussac 1821 [**Chilostoma (Delphinatia)**]
Altarianta subg. nov. (**Arianta**)
alterutra Monterosato 1892 (muralis var.)
alticola Kobelt 1903 (fuscolabiata var.)
altispira Paiva 1867 (=pisana)
alzonai K. Pfeiffer 1951 (=cingulatum hermsianum)
amathia Bourguignat in Locard 1882 (=cingulatum)
Ambigua Westerlund 1902
ambrosi Strobel 1851 (**Kosicia**)
amorgia amorgia Westerlund 1889 [**Chilostoma (Thiessea)**]
ampullacea Pallary 1915 (pisana subsp.)
anacarpica Bellini 1915 (=fuscolabiata)

- anauniense* De Betta 1852 (*cingulatum* subsp.)
anconae Gentiluomo 1868 (*cingulatum* subsp.)
andalusica Gittenberger et Ripken 1987 (***Theba***)
andorrica Bourguignat 1876 (*lapicida* subsp.)
angistoma Férussac 1821 (*Helicigona*)
angusta Pollonera 1890 (*cingulata* var.)
angustata Férussac 1822 (*Helicigona*)
anonyma Westerlund 1889 (=pisana)
apfelbecki apfelbecki Sturany 1901 (?***Arianta***)
appellii Kobelt 1876 (=cingulatum apuanum)
apuanum Issel 1866 (*cingulatum* subsp.)
apula Kobelt 1880 (*mariannae* var.)
arbustorum Linnaeus, 1758 [***Arianta (Arianta)***]
arcadica Frauenfeld 1867 [***Chilostoma (Thiessea)***]
ardica Dedov et Subai 2006 (*Helicigona*)
argentarolae Paulucci 1886 (=saxetana)
argentellei Kobelt 1872 [***Chilostoma (?Josephinella)***]
argentellei Sattmann et Reischütz 1988 (non Kobelt, 1872; =sattmanni)
Arianta Leach in Turton 1831
 Ariantinae Mörch 1864
 Ariantini Mörch 1864
Ariantopsis Wagner 1927
arietina Rossmässler 1846 (*pisana* subsp.)
arinagae Gittenberger et Ripken 1987 (***Theba***)
Arionta Martens in Albers 1860 (=Arianta)
ascherae Kobelt 1880 (*globularis* var.)
ascoliensis Bourguignat 1879 (=tetrazona)
asketa Subai et Fehér 2006 (*skipetarica* subsp.)
asperulum Ehrmann 1910 (*cingulatum* subsp.)
aspidensis Tagliani 1942 (*fuscolabiata* var.)
associata Ziegler in Rossmässler 1837 (*faustina* subsp.)
athesina Paulucci 1881 (*Cingulifera*)
atricha Bofill 1915 (*desmoulinsi* subsp.)
bacchica Martens 1889 [***Chilostoma (Thiessea)***]
baileti Caziot et Maury 1906 (=cingulatum)
balcanica Kobelt 1876 (*trizona* subsp.)
baldense Rossmässler 1839 (*cingulatum* subsp.)
banatica Rossmässler 1838 (***Drobacia***)
barbozana Locard 1899 (=pisana)
barcensis Kimakowicz 1890 (***Faustina***)
basilicatae Kobelt 1903 (=fuscolabiata potentiae)
bechi Altimira 1959 (*desmoulinsi* subsp.)
benedictum Kobelt 1872 [***Chilostoma (Camylaea)***]
biagioi Bourguignat 1888 (=pouzolzi pouzolzi)
biguetia Moquin-Tandon 1855 (=alpina)
bindzaensis Sturany 1909 (*apfelbecki* subsp.)
bizona Rossmässler 1842 (*cingulatum* subsp.)
bocagei Locard 1899 (=pisana)
bocavallensis K. Pfeiffer 1951 (*cingulatum* subsp.)
boncevi Petrbock 1940 (*trizona* var.)
bonifaciensis Caziot 1902 (=serpentina jaspudea)
bosnica Bourguignat 1888 (=pouzolzi pouzolzi)
bosniensis Kobelt 1871 (=pouzolzi pouzolzi)
Botteria Brusina 1904 (=Liburnica)
braueri A. Wagner in Sturany et Wagner 1914 (=apfelbecki bindzaensis)
bredulense Pollonera 1890 (=cingulatum bizona)
brennoensis Mühlfeld in Martini et Chemnitz 1846 (=pouzolzi)
brenoica Bourguignat 1888 (=pouzolzi pouzolzi)
brenskii O. Boettger 1883 [***Chilostoma (Josephinella)***]
broemkei Kobelt in Rossmässler 1846 [***Chilostoma (Dinarica)***]
brunellae Sacchi 1956 (*fuscolabiata* var.)
brusinae Stossich 1876 (=setosa setosa)
buccariana Hirc 1880 (=setosa setosa)
bülowi Maltzan 1886 (*scabruscula* var.)
buressi A. Wagner 1928 (=balcanica)
byshekensis Knipper 1941 [***Chilostoma (Josephinella)***]
byzantina Roth 1839 (=pisana)
caerulans C. Pfeiffer 1828 (***Vidovicia***)
calabrica Kobelt 1879 (*setulosa* var.)
calcarea L. Pfeiffer 1849 (=pisana)
calcrea Högberg 1841 (*arbustorum* var.)
calliostoma Adams et Reeve 1848 (***Theba***)
caltabellottensis Kobelt 1890 (*globularis* var.)
calva Kobelt 1876 (*setulosa* var.)
camprodnica Kobelt 1877 (=xartatii)
Campylaea Beck, 1837 (=Helicigona)
Campylaeini Kobelt, 1904 (=Ariantini)
Campylaeopsis Sturany et Wagner, 1914
canigonensis Boubée 1833 (*arbustorum* subsp.)
canigonica Fagot 1879 (=xartatii)
canthensis Beyrich 1854 (*banatica* var.)
cantinensis Sacchi 1955 (*pisana* subsp.)
cantrainei Bourguignat 1888 (=pouzolzi pouzolzi)
Caracolla Lamarck 1822 (=Helicigona)
carae Cantraine 1841 (=serpentina var.)
carnica Ehrmann 1910 (*chameleon* subsp.)
carpiensis Bourguignat 1860 (=pisana)
carrarense Kobelt 1876 (=cingulatum apuanum)
carrarense Strobel 1852 (=cingulatum apuanum)
carseolana auct. (=carsoliana)
carsoliana Férussac 1801 (=signata)
caruanae Pilsbry 1889 (*melitensis* var.)
casertana Paulucci 1880 (*setulosa* var.)
cassinensis Paulucci 1880 (*planospira* var.)
cassinensis Tagliani 1942 (*fuscolabiata* var.)
castanea Rossmässler 1836 (=cornea)
castellana Monterosato 1892 (*nebrodensis* var.)
castellucensis Kobelt 1905 (*lucana* var.)
catocyphia Bourguignat 1860 (=pisana)
Cattania Brusina, 1904
Causa Schileyko, 1971
cenestinensis Crosse et Debeaux 1869 (=serpentina var.)
chambardi Bourguignat 1860 (=pisana)
chameleon chamaeleon L. Pfeiffer 1868 [***Arianta (Arianta)***]
charpentieri Scholtz 1843 (=faustina)
Chilostoma Fitzinger, 1833 (=an gen.?)
Chilotrema Turton 1831 (=Helicigona)
chiophila Bourguignat 1882 (*glacialis* var.)
choelotricha Benoit 1882 (=benedicta)
choristochila O. Boettger 1886 [***Chilostoma (?Josephinella)***]
chrysomela chrysomela L. Pfeiffer 1848 (***Leptaxis***)
chudeaui Germain 1908 (***Theba***)
cibiniensis Kimakowicz 1890 (*faustina* var.)
cinefacta Monterosato 1892 (*muralis* var.)
cingenda Montagu 1803 (=pisana)
cingulatum cingulatum Studer 1820 [***Chilostoma (Cingulifera)***]
Cingulifera Held, 1838
cingulella Rossmässler 1837 (***Faustina***)
cingulina Deshayes 1839 (*achates* subsp.)
cingulinum Strobel 1844 (*cingulatum* subsp.)
ciofaloi Cafici 1885 (*muralis* var.)
circeja Kobelt 1903 (*fuscolabiata* var.)
circumornata Férussac 1822 (=signata)
cisalpina Amstein 1890 (=achates rhaeticum)
cisalpina Stabile 1864 (=zonatum)
citrinula Ziegler in Rossmässler 1835 (=faustina)

- clarivalia* Moquin-Tandon 1855 (=alpina)
clauso-inflata Mousson 1857 (=geminata)
coccovelli Kobelt, 1904 (=fuscolabiata saprensis)
Cochlopupa Jan, 1830
coerulans C. Pfeiffer 1828 (**Vidovicia**)
colubrinum Cristofori et Jan 1832 (*cingulatum* subsp.)
comephora Bourguignat 1857 (*Helicigona*)
commoda Monterosato 1892 (=muralis)
compsopleura Bourguignat 1883 (=cingulatum gobanzi)
comythophora Bourguignat 1857 (?**Liburnica**)
conemenosi O. Boettger 1885 (?**Liburnica**)
confusa Benoit 1857 (*macrostoma* var.)
connexa Westerlund 1889 (*platychela* var.)
conoidea Caziot 1902 (=suburbana)
conoidea Gallenstein 1848 (*phalerata* var.)
consigliana Kobelt 1904 (*fuscolabiata* var.)
conspicua Benoit 1857 (*globularis* var.)
contaminata Paulucci 1878 [**Marmorana (Ambigua)**]
cornea Draparnaud 1801 (*Chilostoma*)
Corneola Held 1838 (=Chilostoma)
corneoliformis Lessona 1880 (=arbustorum)
corrugata Rossmässler 1836 (*muralis* var.)
corvina Kobelt 1903 (*fuscolabiata* var.)
cossurensis Benoit 1857 (=muralis friwaldskyi)
costellata Kobelt 1902 (=serbica)
costulata Benoit 1857 (*muralis* var.)
costulata Brusina 1869 (*insolita* subsp.)
costulata Kobelt 1884 (as var. *alpestris costulata* = *arbustorum*)
craticula Lowe 1852 (*nivosa* subsp.)
creticola Mörch 1864 (*arbustorum* var.)
crinita Strobel 1854 (**Liburnica**)
crispata Benoit 1857 (=muralis)
crobezi Bourguignat 1882 [**Chilostoma (Corneola)**]
Cryptaxis Lowe, 1852 (=Leptaxis)
cryptozona Ziegler in Rossmässler 1836 (=macrostoma var.)
cuttati Bourguignat 1889 (=pisana)
cyclolabre Deshayes 1839 [**Chilostoma (Thiessea)**]
Cylindruini Schileyko 2006
Cylindrus Fitzinger 1833 (=Cochlopupa)
danioli Bourguignat 1888 (=pouzolzi pouzolzi)
debettae Adami 1876 (=achates adelozona)
debettae Pini 1876 (=cingulata frigida)
debilis Westerlund 1889 (*personatum* var.)
decisa Brusina 1866 (=hoffmanni hoffmanni)
decrisofori Pini 1876 (=cingulata frigida)
dehnei Rossmässler 1846 (*subdentata* subsp.)
Delphinatia Hesse, 1931 (*Helicigona* subg.)
delpretei Monterosato 1892 (*scabriuscula* var.)
demissa Benoit 1857 (*scabriuscula* var.)
dentata Pollonera 1890 (*cingulata* var.)
dentata Taylor 1912 (non Wood 1828) (=pisana ampullacea)
denudata Brusina 1869 (=setosa imberbis)
denudata Knipper 1939 (=kleciachi part.)
denudata Reeve 1854 (=insolita insolita)
denudata Rossmässler 1836 (**Liburnica**)
depilata Paulucci 1880 (=setulosa)
depressa Caziot 1910 (=niciensis)
depressa Kobelt 1876 (*platychela* var.)
depressa Pallary 1921 (=subdentata dehnei)
dermoi Servain in Bourguignat 1887 (=pisana)
desmoulinsi desmoulinsi Farines 1834 [**Chilostoma (Corneola)**]
despottii (=melitensis)
dinarica Bourguignat 1888 (=pouzolzi pouzolzi)
Dinarica Kobelt 1904
diocletiana Bourguignat 1888 (=pouzolzi pouzolzi)
diodontostoma Bourguignat 1862 (=holosericea)
discesae Kobelt 1904 (=lucana)
distans Martens 1876 (*subzonata* var.)
djerbanica Letourneux in Bourguignat 1887 (=pisana)
Dobracia Ehrmann, 1833 (=Drobacia)
dobrudschae Clessin 1886 (=trizona balcanica)
dochii Sturany 1907 (**Liburnica**)
donatii Bourguignat 1860 (=pisana)
donelli Pallary 1904 (=pisana pisana)
dorgalensis Maltzan 1886 (*sardonius* var.)
doriae Paulucci 1878 (=picea)
drepanensis L. Pfeiffer 1856 (*muralis* var.)
Drobacia Brusina 1904
dunjana Knipper 1941 (**Liburnica**)
dupuyi Westerlund 1876 (*niciensis* subsp.)
edlaueri Knipper 1941 [**Chilostoma (Josephinella)**]
efasciata Ehrmann 1910 (*phalerata* var.)
efasciata Kimakowicz 1890 (*faustina* var.)
eliaca Kobelt 1893 (?**Drobacia**)
ereta Paulucci 1878 (=macrostoma)
erjaveci Clessin 1887 (*illyricum* subsp.)
erubescens Lowe 1831 (**Leptaxis**)
erycina Cristofori et Jan 1832 (=scabriuscula)
erymanthia Kobelt 1893 (=argentellei)
erymophila Locard 1894 (*glacialis* var.)
erythronixia Kobelt 1876 (=subdentata dehnei)
erythrostroma Beck 1837 (=subdentata helicella)
erythrostroma L. Pfeiffer 1850 (non Beck 1837) (=subdentata helicella)
etiamque Clessin 1887 (=faustina)
etrusca Kobelt 1876 (*planospira* var.)
euboea Frauenfeld 1867 [**Chilostoma (Thiessea)**]
Eucampylaea L. Pfeiffer 1879 (=Campylaea)
eugenia L. Pfeiffer 1853 (*globularis* var.)
eulasia Westerlund 1889 (*scabriuscula* var.)
Euparypha Hartmann 1840 (=Theba)
excelsa Clessin 1886 (*arbustorum* var.)
excelsa K. Pfeiffer 1931 (*platychela* var.)
exigua Kobelt 1876 (=inflata)
explanata Benoit 1857 (*scabriuscula* var.)
fagorum Kobelt 1906 (=serbica)
fagoti Bourguignat 1882 (=xatartii)
fascelina Gredler 1856 (=cingulata colubrina)
faudensis Sullioti 1883 (=niciensis)
faudina Sullioti 1883 (=niciensis)
faueri Subai 1990 [**Chilostoma (Josephinella)**]
Faustina Kobelt, 1904
faustina faustina Rossmässler 1835 (**Faustina**)
flavovirens Dumont et Mortillet 1852 (*zonatum* subsp.)
florioi Monterosato 1892 (*platychela* subsp.)
fluctuosa Lowe 1852 (=chrysomela subsp.)
foetens Studer 1820 (*zonatum* subsp.)
fontenillii fontenillii Michaud 1829 [**Chilostoma (Delphinatia)**]
forensis Wollaston 1878 (*wollastoni* subsp.)
forsythi Paulucci 1886 (=saxetana)
fortunata Bielz 1860 (=faustina)
francoica Büttner 1931 (*achates* var.)
frangepanii Kormos 1906 [**Chilostoma (Arianta)**]
frauenfeldi Zelebor 1867 (*trizona* var.)
frigidescens Del Prete 1879 (=cingulatum apuanum)
frigidissimum Adami in Paulucci 1881 (*cingulatum* subsp.)
frigidum Cristofori et Jan 1832 (*cingulatum* subsp.)
frigidum Cristofori et Jan 1832 (*cingulatum* subsp.)
friwaldskyi Calcara 1846 (*muralis* var.)

- fuchsi* Knipper 1939 [?*Chilostoma (Campylaea)*]
fuchsiana Knipper 1939 [*Chilostoma (Thiessea)*]
furia Subai 1996 (*amorgia* subsp.)
furva Lowe 1831 (**Leptaxis**)
fuscolabiata Rossmässler 1842 [*Chilostoma (Ambigua)*]
galdensis Kobelt 1904 (*lucana* var.)
gallica Bourguignat in Locard 1882 (*zonata* var.)
gasparinae Charpentier 1837 (=argentelei)
gauri Kobelt 1903 (*fuscolabiata* var.)
geminata Mousson 1857 (**Theba**)
gentilei Pollonera 1890 (*cingulata* var.)
ghibellinica Kobelt 1904 (*mariannae* var.)
glabrata A. Wagner 1912 (?=*denudata* Rossmässler)
glaciale Férussac 1832 [*Chilostoma (Delphinatia)*]
globularis Zelebor in Philippi 1836 [*Marmorana (Murella)*]
globuloidea Kobelt 1876 (nom. err. pro *globulosa* Brusina 1869)
globulosa Brusina 1869 (*setigera* subsp.)
gobanzi Frauenfeld 1867 (*cingulatum* subsp.)
gobanzi Gredler 1886 (=cingulatum *bocavallensis*)
Gonostoma Westerlund 1889 (=Isognomostoma)
gracilis Pallary 1915 (=pisana *ampullacea*)
grandis Cockerell 1921 (=pisan)
grasseti Mousson 1872 (**Theba**)
gravosaensis Mühlfeld in Menke 1828 (=pouzolzi)
grisea Subai et Feher 2006 (**Liburnica**)
grochmanni Philippi 1836 (*muralis* var.)
grossularia Martens 1900 [*Marmorana (Macularia)*]
grossulariae Voith 1838 (=lapicida var.)
guardiae Jaeckel 1952 (=pisana)
guebhardi Kobelt 1906 (*niciensis* subsp.)
haberhaueri Sturany 1897 (*trizona* var.)
harpya Subai 1995 (**Liburnica**)
Hazaya Soós 1909 (=Vidovicia)
hazayana Clessin 1887 [*Chilostoma (Campylaea)*]
heldreichi L. Pfeiffer 1846 [*Chilostoma (Thiessea)*]
helicella Wood 1828 (*subdentata* subsp.)
Helicigona Férussac, 1819
Helicigoninae Hesse 1931 (=Ariantinae)
heldreichi L. Pfeiffer 1846 (*Campylaea*)
hemonica Thiéssé 1884 [*Chilostoma (Josephinella)*]
hermesianum Pini 1874 (*cingulatum* subsp.)
hessei Kimakowicz 1883 (*schmidtii* var.)
hirsuta Brumati 1838 (=lefeburiiana)
hirta Menke 1830 (?**Liburnica**)
hispana Linnaeus 1758 [*Chilotrema (Campylaea)*]
hoffmani Walderdorff 1864 (nom. err. pro *hoffmanni* Rossmässler 1836)
hoffmanni hoffmanni Knipper 1939 [=insolita *costulata* part.]
hoffmanni hoffmanni Rossmässler 1836 (**Liburnica**)
hoffmanni Brusina 1866 (nom. err. pro *hoffmanni* Rossmässler 1836)
holosericea Studer 1820 [**Causa**]
holosericum Studer 1820 (=holosericea)
horatii Bourguignat 1888 (=pouzolzi *pouzolzi*)
hospes Caziot 1902 (=serpentina *hospitans*)
hospitans Rossmässler 1836 (*serpentina* var.)
huetiana Benoit 1857 (*globularis* var.)
hyaena Lowe 1852 (=erubescens)
hymetti Kobelt 1876 (*sphaeriosstoma* subsp.)
hymetti Mousson 1854 [*Chilostoma (Thiessea)*]
hymetti Knipper 1939 (nom. err. pro *hymetti* Mousson)
hynicola Mabile 1882 (=xatartii)
hyperplatea Servain 1880 (=pisana)
Iberus Montfort 1810 (=Murella part.)
ichthyomma Held 1857 (=achates)
illasiaca Adami 1885 (*illyricum* subsp.)
illusana Servain 1879 (=arbustorum)
illyrica *illyrica* Stabile 1864 (**Faustina**)
imberbis Brusina 1876 (*setosa* var.)
immaculata Tagliani 1942 (*signata* subsp.)
impervia Monterosato 1892 (*nebrodensis* var.)
improna Westerlund 1892 (=sphaeriosstoma)
impugnata Mousson 1857 (**Theba**)
incompta Kimakowicz 1890 (*faustina* var.)
indistincta Monterosato 1892 (*muralis* subsp.)
infernale Hesse 1931 (*cingulatum* subsp.)
inflata Bielz in Kobelt 1876 (*trizona* var.)
inflata Kobelt 1876 (**Faustina**)
ingloria Monterosato 1892 (*muralis* var.)
inornata Kimakowicz 1890 (*faustina* var.)
inornata Kobelt 1876 (=phocaea)
insignis Zeiten 1832 [*Chilostoma (Dinarica)*]
insoleta Kobelt 1889 (nom. err. pro *insolita* Rossmässler 1838)
insolida L. Pfeiffer 1846 (nom. err. pro *insolita* Rossmässler 1838)
insolita insolita Rossmässler 1838 (**Liburnica**)
insubricum Cristofori et Jan 1832 (*cingulatum* subsp.)
insularis Benoit 1857 (*muralis* subsp.)
intermedia Férussac 1832 (**Kosicia**)
intermedia Paulucci 1878 (=cingulatum *colubrina*)
intestinalis Schlüter 1838 (nom. nud.; evidently, syn. of *isognomostoma*)
iparia Benoit 1857 (*platychela* var.)
irpina Kobelt 1903 (*fuscolabiata* var.)
isarae Paulucci 1882 (*serpentina* var.)
isilensis Paulucci 1882 (*serpentina* var.)
Isognomonostoma Agassiz, 1847 (=Isognomostoma)
Isognomostoma Fitzinger, 1833
isognomostomos Schröter 1784 (**Isognomostoma**)
Isognomostoma Hartmann, 1840 (=Isognomostoma)
istriana Westerlund 1888 [?*Chilostoma (Campylaea)*]
italica Stabile 1864 (*planospira* var.)
jakupicae Urbanski 1979 (**Liburnica**)
jani Pini 1876 (=cingulata *frigida*)
jaspidea Moquin-Tandon 1855 (*serpentina* var.)
jetschini Uliëny 1885 (*arbustorum* var.)
joachimi Schröder 1911 (=arbustorum)
Josephinella Haas, 1936
Jossia C. Pfeiffer 1930 (=Dinarica)
kaeufeli Knipper 1939 (*Campylaea*, *Helicigona*)
kaeufeliana Knipper 1939 (=sphaeriosstoma)
Katostoma Lowe, 1854 (=Leptaxis)
kattingeri Knipper 1939 (*trizona* var.)
kiralikoeika Kimakowicz 1890 (**Faustina**)
kleciachi L. Pfeiffer 1870 (**Liburnica**)
knitteli Servain 1889 (=arbustorum)
kobeltiana Clessin 1887 (=illyrica *illyrica*)
kobeltiana Paulucci 1881 (=cingulata *carrarensis*)
kollari L. Pfeiffer 1856 (?**Liburnica**) (?**Kollarix**)
?Kollarix Groenenberg, 2012
komensis Kobelt 1899 (=pouzolzi *montenegrina*)
korabensis Subai 1997 (*Helicigona*)
kornisi Kimakowicz 1890 (*planospira* var.)
Kosicia Brusina, 1904
krueperi O. Boettger 1891 (?*Campylaea*)
kulmakana Subai et Fehér 2006 (**Liburnica**)
kuzmici Bourguignat 1888 (=pouzolzi *pouzolzi*)
labium Férussac 1832 (*Helicigona*)
lacticina Rossmässler, 1837 (=caerulans)
laghetensis Caziot 1910 (=pisana)
lagostana Sturany 1901 (=insolita *insolita*)

- Lampadia** Albers, 1854
Lampadiini Schilevko, 2006
langi Parreys in Rossmässler 1857 (=phocaea)
lapicida lapicida Linnaeus 1758 [**Chilostoma (Helicigona)**]
latebrosa Monterosato 1892 (*scabriuscula* var.)
latilabris Westerlund 1876 (*globularis* var.)
Latomus Fitzinger, 1833 (=Helicigona)
lauriensis Kobelt 1906 (*fuscolabiata* var.)
lautaretiana Bourguignat 1882 (*glacialis* var.)
lecoquii Moquin-Tandon 1855 (=lapicida)
lefeburiensis Férussac 1821 [**Chilostoma (Campylaea)**]
legionaria Sacchi 1955 (*subdentata* subsp.)
leonina Lowe 1852 (*undata* subsp.)
Lenticula Held 1837 (=Helicigona)
Leptaxis Lowe, 1852
leucostoma Risso 1826 (=pisana)
Liburnica Kobelt, 1904
liguricum Kobelt 1876 (*cingulatum* subsp.)
lineolata Pallary 1921 (=pisana)
lithuanica Möllendorff 1898 (*faustina* var.)
litoralis Brusina 1869 (=setosa setosa)
ljubetenensis A. Wagner in Sturany et Wagner 1914 (*trizona* var.)
 ?**Ljubotenica** Groenenberg, 2012
lucana Westerlund 1889 [**Marmorana (Ambigua)**]
lucensis Paulucci 1878 (=cingulata appeli)
lucescens Brusina 1876 (=kleciachi)
lujanensis Charpentier 1837 (=Cingulifera)
lutescens Linnaeus 1758 (*arborum* var.)
lychnucha Locard 1894 (=lapicida)
lysiostoma Kobelt 1876 (=sphaerostoma)
macandrewiana L. Pfeiffer 1853 (**Theba**)
macarana Mühlfeld in Martini et Chemnitz 1846 (=pouzolzi pouzolzi)
machadoi Locard 1887 (=pisana)
macrostomum Rossmässler 1836 [**Chilostoma (Campylaea)**]
Macularia Albers, 1850
maeotica Wenz 1926 (**Drobacia**)
magnesiae O. Boettger 1886 (*olympica* subsp.)
magnettii Cantraine 1840 (=serpentina hospitans)
magnifica Monterosato 1892 (=fuscolabiata)
magulus Monterosato 1892 (*muralis* subsp.)
major Westerlund 1886 (=pouzolzi pouzolzi)
maranajensis A. Wagner in Sturany et Wagner 1914 [**Chilostoma (Cattania)**]
marateensis Kobelt 1904 (*fuscolabiata* var.)
mariannae Kobelt 1879 (=fuscolabiata)
Marmorana Hartmann, 1844
martinatiana De Beta 1852 (=ambrosii)
maruccina Tiberi 1878 (*signata* subsp.)
matrella Westerlund 1898 [**Chilostoma (Thiessea)**]
medoacense Adami 1886 (*cingulatum* subsp.)
melii Kobelt 1903 (=fuscolabiata circeja)
melitensis Férussac 1821 [**Marmorana (Murella)**]
melpomene Subai 1996 (**Thiessea**)
membranacea Lowe 1852 (**Leptaxis**)
meridionalis Kobelt 1903 (=fuscolabiata tiriolensis)
meridionalis Sacchi 1955 (*subdentata* subsp.)
michaudia Moquin-Tandon 1855 (=alpina)
milettiana Paulucci 1881 (*signata* subsp.)
millieri Bourguignat 1880 [**Chilostoma (Chilostoma)**]
mingardi Kobelt 1904 (*fuscolabiata* var.)
minor Brusina 1870 (*setosa* var.)
minor Rossmässler 1839 (*setosa* var.)
minor Wohlberedt 1909 (=pouzolzi montenegrina)
minuta Ehrmann 1933 (*arborum* var.)
Mitra Albers 1850 (=Lampadia)
moellendorffii Kobelt 1871 (?**Drobacia**)
mollerati Morelet 1884 (=desmoulinsi)
moltenii Westerlund 1889 (*strigata* var.)
monozonata Pollonera 1886 (=zonatum)
monroi Letoutneux et Bourguignat 1887 (=pisana)
montanum Paulucci 1881 (=cingulatum apuanum)
montenegrina Rossmässler 1836 (*pouzolzi* subsp.)
moratschensis Kobelt 1898 (=pouzolzi montenegrina)
mormannensis Kobelt 1904 (=lucana tenetensis)
moulinsiana Fagot 1907 (=desmoulinsi)
munelana Sturany 1907 (=dochi)
muralis Müller 1774 [**Marmorana (Murella)**]
Murella L. Pfeiffer 1877
 Murellinae Hesse, 1918 (=Ariantinae)
nadorrica Westerlund 1889 (*scabriuscula* var.)
narentana Knipper 1939 [*hoffmanni kleciachi* part.]
narentana Kobelt 1877 (=insolita insolita)
neapolitana Paulucci 1880 (*setulosa* var.)
nebrodensis Pirajno 1842 [**Marmorana (Murella)**]
nebulosa Monterosato 1899 (*globularis* var.)
nicaeensis Risso 1826 (=niciensis)
nicatis Costa 1836 (*cingulatum* subsp.)
niciensis Férussac 1821 [**Marmorana (Macularia)**]
nicolai Klečák 1880 (=setosa imberbis)
nicolisianum Adami 1886 (*cingulatum* subsp.)
nikitai Kobelt 1906 (=serbica)
nisorica Rossmässler 1836 (*preslii* var.)
nivosa *nivosa* Sowerby 1824 (**Leptaxis**)
nomiotipica Strobel 1857 (*achates* subsp.)
nubila Kobelt 1876 (=cingulata colubrina)
nympha Subai 1996 [**Chilostoma (Thiessea)**]
obliterata Férussac 1821 [**Chilostoma (Helicigona)**]
obtusa Draparnaud 1805 (**Cochlopupa**)
obtusangula Lowe 1861 (=subdentata helicella)
occultatum Paulucci 1886 [**Chilostoma (Campylaea)**]
ochroleucum Babor et Košťál 1894 (*achates* subsp.)
oetaea Martens 1889 (=argentellei)
olivaresi Servain 1880 (=pisana)
oltisiana Locard 1890 (=cornea)
olympica Roth 1855 (*trizona* subsp.)
Opica Kobelt 1904 (=Ambigua)
orba Kimakowicz 1890 (*faustina* subsp.)
orbis Hidalgo 1875 (=pisana)
orgonensis Germain 1929 (=muralis)
orites Westerlund 1889 (=serpentina adjacensis)
ornata Parreys 1885 (?phocaea var.)
orta Paulucci 1886 (=saxetana)
ossica O. Boettger 1885 (*olympica* subsp.)
paciniana Philippi 1836 (*scabriuscula* var.)
padanum Stabile 1864 (**Faustina**)
pancici Kobelt 1872 (=serbica)
Partschia C. Boettger 1911 (=Drobacia)
parvula Mousson 1872 (non Rang 1831) (=geminata)
pauzetana Kobelt 1979 (=fuscolabiata)
paulucciana Monterosato 1892 (*scabriuscula* var.)
pedemontana Kobelt 1904 (*signata* subsp.)
pelia Hesse 1912 [**Ariantopsis**]
pellanica Bourguignat 1888 (=pouzolzi montenegrina)
pelvouxiana Bourguignat 1882 (*glacialis* var.)
penteri Sturani 1901 (**Liburnica**) 1891?
peraltata Locard 1894 (*alpina* var.)
peregrini Falkner 1998 (*cingulatum* subsp.)
perfecta Bourguignat 1883 (=cingulata gobanzi)
perforata Caziot 1910 (=niciensis)
peritricha O. Boettger 1885 (=subzonata subzonata)

- persianii* Tiberi 1878 [**Marmorana (Ambigua)**]
personatum Lamarck 1792 (=isognomostomos)
petholata Olivi 1792 (=pisana)
petrii Kimakowicz 1890 (*aethiops* subsp.)
petrovici A. Wagner 1914 [**Chilostoma (Cattania)**]
peucetana Kobelt 1879 (*mariannae* var.)
phalerata Rossmässler 1836 (non Webb et Berthelot 1833)
 (=chameleon chameleon)
philippii Kobelt 1905 (*cingulatum* subsp.)
phlebophora Lowe 1831 (**Leptaxis**)
phocaea phocaea Roth 1855 [**Chilostoma (Josephinella)**]
picaena Tiberi 1878 (=tetrazona)
picea Rossmässler 1837 (*arbustorum* subsp.)
picientina Kobelt 1903 (*fuscolabiata* var.)
picta Monterosato 1892 (*muralis* var.)
pieperi Subai 1996 [**Chilostoma (Thiessea)**]
pilosa O. Boettger 1892 (=sphaeriosstoma)
pilosa Brusina 1867 (=setosa setosa)
pindica O. Boettger 1886 (*subzonata* var.)
pirinensis A. Wagner 1927 (*polinskii* subsp.)
pisacanei Kobelt 1906 (=fuscolabiata *saprensis*)
pisana pisana Müller 1774 (**Theba**)
pisanelia Servain in Bourguignat 1887 (=pisana)
pisanoopsis Servain 1880 (=pisana)
planata Chemnitz 1795 (=subdentata *helicella*)
planata Lowe 1855 (*nivosa* subsp.)
planata Rossmässler 1854 (=pisana)
planicola Kobelt 1903 (*fuscolabiata* var.)
planospira Lamarck 1822 [**Chilostoma (Campylaea)**]
planulata Hidalgo 1866 (=pisana)
platychela Menke 1830 (=melitensis)
Plicostoma Schlüter 1838 (=Isognomostoma)
pluridentatum Pollonera 1885 (*holosericea* subsp.)
polinskii A. Wagner 1927 [**Chilostoma (Wladislawia)**]
polita Paulucci 1878 (*strigata* var.)
poljensis Kobelt 1905 (=vladica)
pollinensis Bacci 1951 (*fuscolabiata* var.)
polyhymnia Subai 1996 [**Chilostoma (Thiessea)**]
portosancti Wollaston 1878 (**Leptaxis**)
posidoniensis Kobelt 1877 (=fuscolabiata)
posthuma Knipper 1939 [**Chilostoma (Thiessea)**]
potentiae Kobelt 1903 (*fuscolabiata* var.)
pouzolzi Deshayes 1830 [**Chilostoma (Dinarica)**]
praesolida Monterosato 1892 (*muralis* var.)
praetexta Brusina 1876 (=insolita *costulata* part.)
praetexta Knipper 1939 (=hoffmanni *hoffmanni* part.)
praetexta L. Pfeiffer 1848 (=insolita *ventricosa*)
praetexta L. Pfeiffer 1870 (=hoffmanni)
praetextata Martens 1872 (laps. cal. pro *praetexta* Pfeiffer)
prausi Bacci 1951 (*fuscolabiata* var.)
preslii F. Schmidt in Rossmässler 1836 (*cingulatum* subsp.)
prokletijensis Knipper 1939 (=apfelbecki *bindzaensis*)
propemuralis Monterosato 1892 (*muralis* subsp.)
provincialis Benoit 1842 (*muralis* var.)
psammophora Lowe 1852 (**Leptaxis**)
pseudocingulata A. Wagner 1914 (*trizona* subsp.)
pseudodochii Subai 2012 (**Liburnica**)
pseudohalmyris Caziot 1902 (=suburbana)
pseudorudis Schlesch 1924 (*arbustorum* subsp.)
pseudospitans Caziot 1902 (=serpentina *hospitans*)
pterolakae Kobelt 1893 (=phocaea)
pubescens Paulucci 1880 (*planospira* subsp.)
pubescens Westerlund 1886 (=pouzolzi *montenegrina*)
pudiosa Paulucci 1882 (=serpentina *isarae*)
queyrasiana Locard 1894 (*cingulatum* var.)
radesiana Mares in Bourguignat 1887 (=pisana)
recondita Westerlund 1876 (*signata* var.)
reischuetzi Subai 1990 (**Liburnica**)
reiseri Branczik 1890 (=insolita *insolita*)
renschii Knipper 1939 [**Chilostoma (?Cattania)**]
repellini Reeve 1852 (*arbustorum* subsp.)
ressmanni Kobelt 1902 (=cingulata *preslii*)
reybaudia Moquin-Tandon 1855 (=alpina)
rhaeticum Strobel 1857 (*adelozona* subsp.)
rhodopensis Kobelt 1906 (=trizona)
rhodostoma Draparnaud 1801 (=pisana)
riberota Monterosato 1892 (*muralis* var.)
ridens Martens 1884 (**Tyrrheniberus**)
rissoi Trechmann 1938 (=melitensis)
rivellensis Kobelt 1904 (=fuscolabiata *lauriensis*)
rollei Maltzan 1886 (=muralis *insularis*)
romaniana Caziot et Maury 1906 (*cingulatum* var.)
rosalba Monterosato 1892 (=pisana)
rosaliae Benoit 1857 (*platychela* var.)
roschitzi Westerlund 1886 (=serbica)
rossmaessleri L. Pfeiffer 1842 (**Faustina**)
rovellensis Kobelt 1906 (=fuscolabiata *lauriensis*)
ruberota Monterosato 1892 (=muralis var.)
rudis Rossmässler 1837 (=stenzii)
rufescens Pennant 1777 (=arbustorum)
rugosa Rossmässler 1835 (=muralis)
rumelica Ziegler in Rossmässler 1838 (*trizona* subsp.)
sabljari Bourguignat 1888 (=pouzolzi *pouzolzi*)
Sabljaria Brusina 1904 (=Dinarica)
saccaliana Letourmeux 1886 (=pouzolzi)
sacchii Gittenberger et Ripken 1987 (**Theba**)
sadleriana Rossmässler 1838 (=lefeburiiana)
saintivesi Kobelt 1906 [**Marmorana (Macularia)**]
saprensis Kobelt 1904 (*fuscolabiata* var.)
saracena Westerlund 1889 (=globularis *ascherae*)
sardica Caziot 1902 (=suburbana)
sardoa Ziegler 1830 (=pisana)
sardonius Martens 1884 (**Tyrrheniberus**)
sarmizegethusae Kimakowicz 1890 (*faustina* var.)
sativa Ziegler in Rossmässler 1835 (=faustina)
sattmanni Subai 1995 (?*Helicigona*)
saxetana Paulucci 1886 [**Marmorana (Ambigua)**]
scabriuscula Deshayes 1830 [**Marmorana (Murella)**]
scalariformis Benoit 1857 (=muralis *drepanensis*)
schmidtii Rossmässler 1836 [**Arianta (Arianta)**]
sciara Westerlund 1879 (*olympica* var.)
schlaerotricha Bourguignat 1870 (?*Campylaea*)
sclerotricha Bourguignat 1879 (=schlaerotricha)
sebinensis Kobelt 1875 (=achates *adelozona*)
segestana Philippi 1892 (*scabriuscula* var.)
selecta Bisacci 1929 (=planospira *occultata*)
selinuntina Philippi 1836 (*scabriuscula* var.)
semifulva Taylor 1912 (=subdentata *dehnei*)
sendtneri Clessin 1884 (*arbustorum* var.)
sentinense Piersanti 1933 (*cingulatum* subsp.)
serbica Kobelt 1872 [**Chilostoma (Dinarica)**]
serpentina Férussac 1821 [**Marmorana (Marmorana)**]
serpentinorum Degner 1936 (*fuscolabiata* var.)
sertum Monterosato 1892 (=pisana)
setigera setigera Rossmässler 1836 (**Liburnica**)
setipila Rossmässler, 1835 (=planospira *setulosa* var.)
setosa setosa Férussac 1832 (**Liburnica**)
setulosum Briganti 1825 [**Chilostoma (Campylaea)**]
sicana Férussac 1822 (*platychela* var.)
sicula Benoit 1857 (?=signata)
sigela Bourguignat 1883 (=cingulata *gobanzi*)
signata Férussac 1821 [**Marmorana (Murella)**]

- silvestrii* Cafici 1885 (*nebrodensis* var.)
silvestris Westerlund 1886 (=pouzolzi montenegrina)
sirinensis Kobelt 1904 (*fuscolabiata* var.)
skipetarica skipetarica Subai 1995 (**Liburnica**)
soccaliana Letourneux 1886 (=pouzolzi pouzolzi)
solimae Sacchi 1955 (**Theba**)
soluta Rossmässler 1832 (=platychela sicana)
spelaea Kobelt 1906 (=planospira subsp.)
sphaeriosoma Bourguignat 1857 [**Chilostoma (Thiessea)**]
spinae Kobelt 1906 (=fuscolabiata lauriensis)
spirolineata Monterosato 1892 (=pisana)
splendens Maltzan 1886 (=ridens)
spoliata Monterosato 1892 (*globularis* var.)
spuria Westerlund 1876 (*platychela* var.)
squammatinum Rossmässler 1835 [**Chilostoma (Corneola)**]
squammatinum Dupuy 1848 [**Chilostoma (?Chilostoma)**]
stabilei Paulucci 1880 (=illyrica)
stenomphala stenomphala Menke 1830 [**Chilostoma (Sabljaria)**]
stenzii Rossmässler 1835 [**Arianta (Altarianta)**]
stiriae Forcart 1933 (*achates* subsp.)
strigata Férussac 1822 (non Müller 1774) (=signata)
strobili Lessona 1880 (*zonata* var.)
styriaca Kobelt 1876 [**Arianta (Arianta)**]
subaii Fauer 1991 [**Chilostoma (Cattania)**]
subcarinata Monterosato 1892 (*muralis* var.)
subconica Monterosato 1892 (=pisana)
subcostalis Kobelt 1876 (=insolita costulata)
subdeflexa O. Boettger 1885 (=argentellei)
subdentata subdentata Férussac 1821 (**Theba**)
subdepressa Caziot 1903 (=niciensis)
subflava Kimakowicz 1863 (*faustina* var.)
subgeminata Mousson 1852 (=impugnata)
subglobosa Ehrmann 1910 (*chameleon* subsp.)
subpisana Bourguignat 1887 (=pisana)
subsetosa Kobelt 1906? (=kleciachi)
substrigata Mabilille 1867 (=muralis)
suburbana Paulucci 1882 [**Marmorana (Ambigua)**]
subzonata subzonata Mousson 1859 (**Drobacia**)
sufflata Monterosato 1892 (=scabriuscula tayae)
superba Monterosato 1892 (*muralis* var.)
Superba Subai et Fehér 1906 (=Liburnica)
superbaformis Subai 2012 (**Liburnica**)
surrentina Martens 1858 (=fuscolabiata)
sybaritica Kobelt 1906 (*fuscolabiata* var.)
sztolcmani A. Wagner 1927 [**Chilostoma (Wladislawia)**]
tacheiformis Kobelt 1906 (*niciensis* var.)
talmacensis Kimakowicz 1890 (*faustina* var.)
talamonica Kobelt 1892 (=saxetana)
tayae Monterosato 1892 (*scabriuscula* var.)
taylori Cockerell 1922 (=pisana)
tchernagorica Bourguignat 1888 (=pouzolzi pouzolzi)
tegianica Degner 1936 (*fuscolabiata* var.)
templorum Monterosato 1892 (*muralis* subsp.)
tenetensis Kobelt 1904 (*lucana* var.)
tetrazona Cristofori et Jan 1832 (*signata* subsp.)
thamnivaga Mabilille 1883 (=arbustorum)
thateensis Subai 2012 [**Chilostoma (Wladislawia)**]
Theba Risso, 1826
themita Mabilille 1883 (=arbustorum)
Thiessea Kobelt, 1904
thlipsa Westerlund 1889 (=subdentata helicella)
thracica Kobelt 1906 (*trizona* var.)
tiberiana Benoit 1857 (*globularis* var.)
tiburtina Martens 1899 (*signata* subsp.)
tiesenhauseni Gredler 1889 (*illyricum* subsp.)
tigrinum Cristofori et Jan 1832 (*cingulatum* subsp.)
tinophila Bourguignat 1860 (=pisana)
tiriolensis Tagliani in Adami 1873 (*fuscolabiata* var.)
transalpina Stabile 1864 (=zonatum)
Transiberus Monterosato, 1892 [nom. nud. (=Murella)]
transiens Adami 1886 (=cingulata colubrina)
transiens K. Pfeiffer 1931 (*globularis* var.)
trecchinensis Kobelt 1906 (*fuscolabiata* var.)
Triodopsis Martens 1860 (=Isognomostoma part.)
trizona trizona Rossmässler 1835 [**Chilostoma (Cattania)**]
trochoidalis Roffiaen 1868 (=arbustorum)
trichothroa Benoit 1882 (=benedicta)
tchernagorica Bourguignat 1888 (=pouzolzi pouzolzi)
tubaestoma Kimakowicz 1890 (*faustina* var.)
tullina Ehrmann 1910 (*chameleon* subsp.)
tumidosa Kobelt 1890 (=scabriuscula nadorrnica)
turgida Pallary 1915 (=subdentata subdentata)
turgidula Wood 1828 (=arbustorum)
Tyrrheniberus Hesse et Kobelt, 1904
ulicis Kobelt 1906 (=fuscolabiata saprensis)
ullepitschi Westerlund 1876 (=illyrica illyrica)
Ulostoma Albers 1850 (=Isognomostoma)
umbilicaris Brumati 1838 (=illyrica illyrica)
umbrica Mabilille 1867 (=strigata)
undata undata Lowe 1831 (*Leptaxis*)
undulata Michaud 1831 (=muralis)
uniarmata Paulucci 1881 [**Marmorana (Ambigua)**]
unifasciata Da Costa 1778 (=arbustorum)
unitaeniata O. Boettger 1885 (=serbica)
usielliana Paulucci 1878 [**Marmorana (Ambigua)**]
ustulata Lowe 1852 (non Férussac 1823) (=macandrewiana)
uzielliana Paulucci 1878 (*signata* var.)
vagiennum Pollonera 1890 (=cingulatum bizona)
valkanovi Urbański 1960 [**Chilostoma (Thiessea)**]
vallicola Kobelt 1903 (*fuscolabiata* var.)
vareliensis Ripken et Falkner 2000 (*arbustorum* subsp.)
varronis Cantraine 1836 (=pouzolzi pouzolzi)
velanica Mabilille 1881 (=serpentina var.)
velebitana Westerlund 1889 (=setosa setosa)
ventricosa A. Wagner 1914 (*insolita* subsp.)
verrucosa Kobelt 1890 (*scabriuscula* var.)
vesulana Lessona 1886 (=glacialis)
Vidovicia Brusina, 1904
vibrayana Servain 1889 (=arbustorum)
vieta Rossmässler 1836 (=scabriuscula paciniana)
vikosensis Subai 1990 [?**Chilostoma (Josephinella)**]
villicus Paulucci 1882 (**Tyrrheniberus**)
vulcania Lowe 1852 (*undata* subsp.)
wagneri Kimakowicz 1890 (=faustina)
walteri O. Boettger 1886 (*hoffmanni* var.)
webbiana Lowe 1831 (**Lampadia**)
wiedemayri Kobelt 1903 (*chameleon* subsp.)
wittmanni Zawadsky in Rossmässler 1837 (=arbustorum)
Wladislawia A. Wagner, 1927
wohlberedi Kobelt 1905 (=pouzolzi montenegrina)
wollastoni wollastoni Lowe 1852 (*Leptaxis*)
wullei Kobelt 1903 (*fuscolabiata* var.)
xatartii Farines 1834 (*arbustorum* subsp.)
zebiana Sturany 1907 [**Chilostoma (Josephinella)**]
zieglerei Rossmässler 1836 (**Kosicia**)
zonaria Pennant 1777 (=pisana)
zonatum zonatum Studer 1820 [**Chilostoma (Chilostoma)**]

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Семейство Helicidae кроме Helicinae (Gastropoda Pulmonata): морфология, таксономия и каталог таксонов

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РЕЗЮМЕ. Кратко обсуждены проблемы ранга таксонов (рода и подрода) в подсемействе Argantinae. Дан обзор существующих взглядов на систему подсемейств Helicidae, кроме номинативного подсемейства (Argantinae, Murellinae и Thebinae). Сформулированы дифференциальные диагнозы таксонов. Особое внимание уделено морфологии папиллы пениса и атриального стимулятора, поскольку эти органы играют первостепенную роль в предотвращении интрогрессии (изолирующие механизмы).

