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 (=Helicigoni-
nae, =Campylaecinae) (22 genera and subgenera), Murellinae (5), Thebinae (2) and Helicinae (47).

From anatomical and zoogeographical points of view, the subfamily Ariantinae is a compact taxono-
mical 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 sub-
genera 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 (Thiéss-
se, 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 monoto-
nous. However, a detailed study of the copulatory apparatus shows that the taxa often differ from each other in several important features (see be-
low). In recent years the molecular methods of re-
search in taxonomy and phylogeny of pulmonates, in particular, Ariantinae, have been gaining popula-
rity (for discussion, see, for example, Steinke et al., 2004; Groenenberg et al., 2011, 2012). These me-
thods 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 Chilotoma achates (Rossmässler, 1835) and Cochlopus obatus (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 situation: 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. fontenilli 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, Kosicia, and Faustina.

2. The walls are empty, i.e. contain a cavity. This group includes Cattania, Helicigona, Dinaria, Josephinella, Chilostoma, Liburnica, Arianta, and Cochlopusa.

Vidovicia 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 Vidovicia is a kind of exception because it has a peculiar shell.
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 (matting games), and thus serves as a pre-copulatory 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 Tyrrheibeatus), 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), 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.

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The diagnoses of taxa can be formulated as follows.

**Ariantinae** Mörch, 1864

Mörch, 1864: 284 (pro fam.).


– 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).
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


Type species – Helix holosericum Studer, 1820; OD.
Shell nearly flat, rather thin, of 6 narrow, rather convex whors. Body whorl deflected, rounded. Color light comeous to brown; peristome white. Embryonic whors 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.
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.


**Isognomostoma** Fitzinger, 1833

Fig. 4

Fitzinger, 1833: 97.

- *Plicostoma* Schlüter, 1838: 4 [t.-sp. *Plicostoma intestinalis* Schlüter, 1838; monotypy; nom. nud.]
- *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; 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-
**Ariantopsis** A. Wagner, 1928

Fig. 5


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

Distribution. SW and W Bulgaria.

**Drobacia** Brusina, 1904

Fig. 6


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


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.


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 superperipheral dark band. Embryonic whors smooth. Later whors lack regular sculpture. Aperture broadly ovate, well oblique, with reflected 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-
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.

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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.
– 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.
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.


**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 slightly 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.


Remark. Groenenberg et al. [2012] on the base
of molecular data consider *Wladislavia* together with *Ariantopsis* as subgenera of *Cattania*.

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

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

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

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


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 *Campylaenopsis* 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 suprapерipheral bands may be present. Aperture margins whitish. Embryonic whorls smooth, later whorls with very weak sculpture (nearly smooth). Aperture ovate, quite oblique, with reflected margins; peristome insertions approached and usually connected by parietal calulus. 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.


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, or with a dark suprapерipheral 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
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about middle of epiphallus or nearer to its distal end. Free oviduct and vagina subequal in length. Stylo-

phore 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 mm.

Mucus glands generally split half up to 2/3 of their length; rarely simple, or partly unindived, 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 su-

praperipheral band margined with light, diffuse zones. Sculpture of very fine granulation through-

out and extremely short setae. Aperture nearly en-

tire, 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.
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**

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 anastomozing.
1. **Family Helicidae: morphology, taxonomy, catalogue**

   **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 simple.

   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; OD Herrmannsen, 1847.

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


Flagellum a little longer then 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-Termoli [Groenenberg et al., 2012].

**Chilostoma** (Delphinatia Hesse, 1831)*

Hesse, 1831: 60 (Campylaee “Gruppe”).
Schileyko, 2006a: 1780, Fig. 2281 (Campylaee 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 whors. Last whorl evenly rounded to bluntly angulated at periphery, slightly descending in front. Color whitish to (dark) cornaceous, often somewhat spotted with dark and sometimes with weak dark suprapertipheral 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.


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

**Liburnica** Kobelt, 1904

Fig. 14

Kobelt, 1904 (October): 74, 131, 154, 185 (Campylaee subgen.).
Schileyko, 1971: 991; Subai, 2002: 1; Schileyko, 2006a: 1776, Fig. 2275 (Campylaee 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 whors. Last whorl strongly descending in front. Color whitish to (dark) cornaceous, often somewhat spotted with dark and sometimes with weak dark suprapertipheral band. Embryonic whorls almost smooth or very finely granulate. Postembryonic whors also with fine granulation; they 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.

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


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 suprapapillary 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 wrinkles 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 diverticule; 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** (*Altaria*nta) 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 *Altaria*nta it directed to penis (not to vagina) and 2. In *Altariantia* 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
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.
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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 spermovi duct 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. 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 па пиллы пениса *Arianta* s. str. (A) и *Arianta (Altarianta)* (B), схематизировано.

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,
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. praecoc., 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 whors smooth. Later whors 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 whors. 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


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 whors. 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 striate above; sometimes with whole ground-color deep chestnut, upon which there are white zigzag vermiculations and striations. Embryonic whors smooth. Postapical surface lightly obliquely striatulate. Aperture broadly
ovate, quite oblique, with almost straight or shortly reflected 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, Tyrrenian 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 wrinkles and extremely delicate radial striae. Aperture ovate, strongly oblique; margins not thickened, a little reflected. Umbilicus closed. Height 8.5-14.0, diam. 14-27 mm.

Jaw odontognathous.


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.


Schileyko, 2006a: 1773, Fig. 2270.
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.


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, diverticule 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* subg.).
Hesse, 1908: 109, Taf. 377, Fig. 3-9 (*Murella* subg.); Schileyko, 2006a: 1773, Fig. 2271.

Type species – *Helix sardonia* 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-rostre, 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 bi-ramous. 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 stylot-shaped, with a basal crown and 4 blades.

**Theba** Risso, 1826

Fig. 23


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 whors. Last whorl widely rounded, almost straight. Color whitish, mostly with many dark, irregular bands; peristome often pinkish. Embryonic whors 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 diverticule; 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-
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 Mabille 1867 (=muralis)
abromia Mabille 1867 (=muralis)
acarnanica Kobelt 1892 (conemenosi var.)
achates achates Rossmässler 1835 [Chilostoma (Chilostoma)]
acrotricha Bofill, Haas et Aguilar-Amat 1918 (=desmoulinisi)
acrotricha P. Fischer 1877 [Chilostoma (Corneola)]
acutangula Lowe 1861 (=subdentata helicella)
adami Kobelt 1873 (adelozone subsp.)
adami Pini 1876 (=cingulatum frigidum)
adelozone adelozone 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 appelii)
agarol Letourneux et Bourguignat 1887 (=pisana)
agnata Paulucci 1881 (=cingulata carrarensis)
alpha Moquin-Tandon 1855 (=pisana)
albica Jaeckel 1954 (stenomphala subsp.)
albica Kobelt 1899 (=pouzolzi montenegrina)
alanograeca Subai 1995 (Liburnica)
albellina Limnaeus 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 amplulacea)
alboranensis Odhner 1931 (non Beck 1837) (=arinagae)
albulana Bourguignat 1889 (=arbustorum)
alfaensis Paulucci 1881 (planospira subsp.)
alpestris Rossmässler 1837 (=arbustorum var.)
alpida Cotac 1819 (arbustorum subsp.)
alpina Michaud 1831 (fontinellii subsp.)
alpinum Fèrrussac 1821 [Chilostoma (Delphinatia)]
Altaria subg. nov. (Arianta)
alterutra Monterosato 1892 (muralis var.)
alicola Kobelt 1903 (fuscolabiata var.)
ditispira Paiva 1867 (=pisana)
adzonia K. Pfeiffer 1951 (=cingulatum hermsianum)
amathia Bourguignat in Locard 1882 (=cingulatum)
Ambigua Westerlund 1902
ambrosi Strobel 1851 (Kosicia)
amorgia amorgia Westerlund 1889 [Chilostoma (Thiessea)]
amulacea Pallary 1915 (pisana subsp.)
amacarica Bellini 1915 (=fuscolabiata)


clarinvalia Moquin-Tandon 1855 (=alpina)
claso-inflata Mousson 1857 (=geminata)
cocovellii Kobelt, 1904 (=fuscoliabata sapreensis)

**Cochloupia** Jan, 1830
coeulans C. Pfeiffer 1828 (Vidovicia)
colubrinum Cristofori et Jan 1832 (cingulatum subsp.)
comephora Bourguignat 1857 (Helicigona)
commoda Monterosato 1892 (=muralis)
compsopleura Bourguignat 1883 (=cingulatum gobanzi)
comythyphora Bourguignat 1857 (?Liburnica)
comemenosi O. Boettger 1885 (?Liburnica)
denella Benoist 1890 (macrostoma var.)
conexa Westerlund 1889 (platycheila var.)
conida Czait 1902 (=suburbana)
conidea Gallenstein 1840 (phalerata var.)
consiliana Kobelt 1904 (fuscoliabata var.)
conspicua Benoist 1857 (globularis var.)
contaminata Paulucci 1878 [Marmorata (Ambigu)]
conrea Draparnaud 1801 (Chilostoma)
Corneola Held 1838 (=Chilostoma)
corneoliformis Lessona 1880 (=arbusorum var.)
corrugata Rosssmässler 1836 (muralis var.)
corvina Kobelt 1903 (fuscoliabata var.)
cossuresenis Benoist 1857 (=muralis friwaldskyi)
costallata Kobelt 1902 (=serbica)
costulata Benoist 1857 (muralis var.)
costulata Brusina 1869 (insolita subsp.)
costulata Bourguignat 1884 (as var. alpestris costulata = arbusorum)
cricutula Low 1852 (nivosus subsp.)
criticola Mörch 1864 (arbusorum var.)
crinata Strobel 1854 (Liburnica)
crispata Benoist 1857 (=muralis)
crombezi Bourguignat 1882 [Chilostoma (Corneola)]
Cryptaxis Low 1852 (=Leptaxis)
epsiloniza Ziegler in Rosssmässler 1836 (=macrostoma var.)
cuttia Bourguignat 1889 (=pisana)
cyclolabe Deshayes 1839 [Chilostoma (Thiessea)]
Cylindruini Schileyko 2006
cylindrical Fitzinger 1833 (=Cochloupia)
danilo Bourguignat 1888 (=pouzolzi pouzolzi)
debettas Adami 1876 (=achates adelozoni)
debettas Pini 1876 (=cingulata frigida)
debils Westerlund 1889 (personatum var.)
decisa Brusina 1866 (=hoffmanni hoffmanni)
decristofori Pini 1876 (=cingulata frigida)
dehnei Rosssmässler 1846 (subdentata subsp.)

**Delphina** Hesse, 1931 (Helicigona subg.)
delpreti Monterosato 1892 (scabriuscula var.)
demissa Benoist 1857 (scabriuscula var.)
dentata Pini 1872 (non Wood 1828) (=pisana amplulacea)
demudata Brusina 1869 (=setosa inermis)
demudata Knipper 1939 (=kleiaplii var.)
demudata Reeve 1854 (=insolita insolita)
demulass Bourguignat 1836 (Liburnica)
depilata Paulucci 1880 (=setulosa)
depressa Czait 1910 (=niceniensis)
depressa Kobelt 1876 (platycheila var.)
depressa Pallary 1921 (=subdentata dehnei)
dermoi Servain in Bourguignat 1887 (=pisana)
desmoulinii desmoulinii Farines 1834 [Chilostoma (Corneola)]
despotii (=melintensis)
dinarica Bourguignat 1888 (=pouzolzi pouzolzi)
Dinarica Kobelt 1904
dioecetiana Bourguignat 1888 (=pouzolzi pouzolzi)
diodontostoma Bourguignat 1862 (=holosericea)
diseeae Kobelt 1904 (=lucana)
distans Martens 1876 (subzonata var.)
djerbanica Letourneux in Bourguignat 1887 (=pisana)
Dobracia Ehrmann, 1833 (=Drobacia)
dobruudoeae Clessin 1886 (=trizonal balsanica)
dochii Sturry 1907 (Liburnica)
donati Bourguignat 1860 (=pisana)
donelii Pallary 1904 (=pisana pisana)
doragelensis Maltzan 1886 (sardinius var.)
doriae Palucci 1878 (=picea)
dropanesira L. Pfeiffer 1856 (muralis var.)
Drobacia Brusina 1904
dunjana Knipper 1941 (Liburnica)
dupuyi Westerlund 1876 (niceniensis subsp.)
ediauxer Knipper 1941 [Chilostoma (Josephinella)]
efasiata Ehrmann 1910 (phalerata var.)
efasiata Kimakowicz 1890 (faustina var.)
eliaca Kobelt 1893 (Drobacia)
ereta Paulucci 1878 (=macrostoma)
erjeveci Clessin 1887 (illyricum subsp.)
erubescens Lowe 1831 (Leptaxis)
erycina Cristofori et Jan 1832 (scabriuscula)
erymnthia Kobelt 1893 (=argentellei)
erymphila Locardi 1894 (glacialis var.)
erythronixia Kobelt 1876 (=subdentata dehnei)
erythrostoma Beck 1837 (=subdentata helicella)
erythrostoma L. Pfeiffer 1850 (non Beck 1837) (=subdentata helicella)
etiamque Clessin 1887 (=faustina)
etrusca Kobelt 1876 (planospira var.)
euweber Frauenfeld 1867 [Chilostoma (Thiessea)]
examplelaxa L. Pfeiffer 1879 (=Campylaea)
eugenia L. Pfeiffer 1853 (globularis var.)
eurasia Westerlund 1889 (scabriuscula var.)
euparphy Hartmann 1840 (=Theba)
exelía Clessin 1886 (arbusorum var.)
exelía K. Pfeiffer 1931 (platycheila var.)
exiguia Kobelt 1876 (=inflata)
explanata Benoist 1857 (scabriuscula var.)
faogorum Kobelt 1906 (=serbica)
fagot Bourguignat 1882 (=xaritii)
fascella Greder 1856 (=cingulata colubrina)
aufau Sullioti 1883 (=niceniensis)
faudia Sullioti 1883 (=niceniensis)
faueri Subai 1990 [Chilostoma (Josephinella)]

**Faustina** Kobelt, 1904
faustina faustina Rosssmässler 1835 (Faustina)
flavorivenus Dumont et Mortillet 1852 (zonatum subsp.)
fiori Monterosato 1892 (platycheila subsp.)
fluctuosa Lowe 1852 (=christysomela subsp.)
foetens Studer 1820 (zonatum subsp.)
fontenillii fontenillii Michaud 1829 [Chilostoma (Delphina)]
forensis Wollaston 1878 (wollastoni subsp.)
forsthi Paulucci 1886 (=saxetana)
funtunata Bielz 1860 (=faustina)
franconica Büttner 1931 (achates var.)
frangipanii Kormos 1906 [Chilostoma (Arianta)]
frauenfeldi Zelebor 1867 (trizonal var.)
frigidecensus Del Prete 1879 (=cingulatum apuanum)
frigidecensus Adamani in Paulucci 1881 (cingulatum subsp.)
frigideosorus Cristofori et Jan 1832 (cingulatum subsp.)
frigidum Cristofori et Jan 1832 (cingulatum subsp.)
fridwal斯基 Calcar 1846 (muralis var.)
Lampadini Albers, 1854
Lampadini Schileyko, 2006
langi Parreys in Rossmässler 1857 (=phoeca)
lapicida lapicida Linnaeus 1758 [Chilostoma (Helicigona)]
laterbrosa Monterosato 1892 (scabriacula var.)
latilabris Westerlund 1876 (globularis var.)
Latomus Fitzinger, 1833 (=Helicigona)
lauriensis Kobelt 1906 (fungolabiata var.)
lautarentia Bourguignat 1882 (glacialis var.)
lecquii Moquin-Tandon 1855 (=lapicida)
lefeburianna Férussac 1821 [Chilostoma (Campylaea)]
legionarii Sacchi 1955 (subdentalia subsp.)
leovina Lowe 1852 (undata subsp.)
Lenticula Held 1837 (=Helicigona)

Lephtaxis Lowe, 1852
leucostoma Risso 1826 (=pisana)
Liburnica Kobelt, 1904
liguricum Kobelt 1876 (cingulatum subsp.)
linealaya Pallary 1921 (=pisana)
lithuana Möllendörff 1898 (faustina var.)
litoralis Brusina 1869 (=setosa setosa)
ljubetensis A. Wagner in Sturany et Wagner 1914 (trizona var.)

?Ljubotenia Groenengberg, 2012
lucana Westerlund 1889 [Marmorana (Ambigua)]
lucania Psalliucchi 1878 (=cingulata appella)
lucescens Brusina 1867 (=kleeiachi)
luiganensis Charpentier 1837 (=Cingulifera)
lutescens Linnaeus 1758 (arbustorum var.)
lychnaucha Locard 1894 (=lapicida)
lytopsoma Kobelt 1876 (=spheeriosoma)
amacadiana L. Pfeiffer 1853 [Thesa]
amacaran Mühlfeld in Martini et Chemnitz 1846 (=pouzolzi pouzolzi)
machairod Locard 1887 (=pisana)
macrostomum Rossmässler 1836 [Chilostoma (Campylaea)]

Macularia Albers, 1850
macorea Wenz 1926 (Drobacia)
magnesiæ O. Boettger 1886 (olympica subsp.)
magnetti Cantraine 1840 (=serpenitina hospitans)
magnifica Monterosato 1892 (=fungolabiata)
Magulus Monterosato 1892 (muralis subsp.)
major Westerlund 1886 (=pouzolzi pouzolzi)
maranagensis A. Wagner in Sturany et Wagner 1914 [Chilostoma (Cattania)]

Maratensis Kobelt 1904 (fungolabiata var.)
mariannae Kobelt 1879 (=fungolabiata)
Marmorana Hartmann, 1844
martinattiana De Betta 1852 (=ambrosii)
maruccina Tiberi 1878 (signata subsp.)
matrella Westerlund 1898 [Chilostoma (Thiessea)]
medoasense Adami 1886 (cingulatum subsp.)
melii Kobelt 1903 (=fungolabiata circiea)
melitensis Férussac 1821 [Marmorana (Murella)]
melpomene Subai 1996 (Thiessea)
membranacea Lowe 1852 (Leptaxis)
meridionalis Kobelt 1903 (=fungolabiata tiriolensis)
meridionalis Sacchi 1855 (subdentalia subsp.)
michaudia Moquin-Tandon 1855 (=alpina)
milettiana Psalliucchi 1881 (signata subsp.)
millieri Bourguignat 1880 [Chilostoma (Chilostoma)]
ingardi Kobelt 1904 (fungolabiata var.)
minor Brusina 1870 (=setosa var.)
minor Rossmässler 1839 (setosa var.)
minor Wohlberedt 1909 (=pouzolzi montenegrina)
minuta Ehrmann 1933 (arbustorum var.)

Mitra Albers 1850 (=Lampadia)
moellendorffii Kobelt 1871 (=Drobacia)
mollerati Morelet 1845 (=desmoulini)
moltensis Westerlund 1889 (strigata var.)
monozonata Pollonera 1886 (=zonatum)
monroi Letoutneux et Bourguignat 1887 (=pisana)
montanum Psalliucchi 1881 (=cingulatum apuanum)
montenegrina Rossmässler 1836 (pouzolzi subsp.)
moratschensis Kobelt 1898 (=pouzolzi montenegrina)
mormannensis Kobelt 1904 (=lucana tenetensis)
moulinsiana Fagot 1907 (=desmoulinis)
muneliana Sturany 1907 (=lochilis)
muralis Müller 1774 [Marmorana (Murella)]

Murella L. Pfeiffer 1877
Murellinae Hesse, 1918 (=Ariantinae)
nadoretta Westerlund 1889 (scabriacula var.)
narentana Knipper 1939 [huffmanni kleeiachi part.]
narentana Kobelt 1877 (=insolita insolita)
nepopolitana Psalliucchi 1880 (setulosa var.)
nebrodensis Pirajno 1842 [Marmorana (Murella)]
nebulosa Monterosato 1899 (globularis var.)
nicaensis Risso 1826 (=niciensis)
nicatis Costa 1836 (cingulatum subsp.)
nicisis Férussac 1821 [Marmorana (Macularia)]
nicis Férussac 1821 [Marmorana (Macularia)]
nicolai Kleéká 1880 (=setosa imberbis)
nicolisianum Adami 1886 (cingulatum subsp.)
nikitar Kobelt 1906 (=serbica)
nisoria Rossmässler 1836 (presli var.)
nivosara Sowerby 1824 (Leptaxis)
nominotipica Strobel 1857 (achates subsp.)
nobilis Kobelt 1876 (=cingulata colubrina)
nymph Paublai 1996 [Chilostoma (Thiessea)]
obliterata Férussac 1821 [Chilostoma (Helicigona)]
obtusa Draparnaud 1805 (Cochlopupa)
obtusangula Lowe 1861 (subdentata helicella)
occulatum Psalliucchi 1886 [Chilostoma (Campylaea)]
ochroleucum Babor et Koštal 1894 (achates subsp.)
oetae Martens 1889 (=argenterelli)
olivaresi Servain 1880 (=pisana)
olisiana Locard 1890 (=cornea)
olympica Roth 1855 (trizona subsp.)
Opica Kobelt 1904 (=Ambigu)
orba Kimakowicz 1890 (faustina subsp.)
orbis Hidalgo 1875 (=pisana)
organensis Germain 1829 (=muralis)
orites Westerlund 1889 (=serpenitina adjacens)
ornta Parreys 1885 (=phoeca var.)
orta Psalliucchi 1886 (=saxetana)
oxica O. Boettger 1885 (olympica subsp.)
paciniana philippi 1836 (scabriacula var.)
padanum Stabile 1864 (Fausitina)
pancici Kobelt 1872 (=serbica)
Partschia C. Boettger 1911 (=Drobacia)
parsula Mousson 1872 (non Rang 1831) (=eminenta)
paucetana Kobelt 1904 (signata subsp.)
eneta Hesse 1912 [Ariantopsis]
pellanica Bourguignat 1888 (=pouzolzi montenegro)
pevovsiana Bourguignat 1882 (glacialis var.)
pentheri Sturany 1908 (Murella) 1891?
perlatala Locard 1894 (alpina var.)
pereregrini Falkner 1998 (cingulatum subsp.)
perfecta Bourguignat 1883 (=cingulata gobanzi)
perforata Caziot 1910 (=niciensis)
peritricha O. Boettger 1885 (=subzonata subzonata)
Chilostoma (Ambigua)

personatum Lamark 1792 (=sognostomosmos)

petrolata Olivi 1792 (=pisana)

petrii Kimakowicz 1890 (aethiops subsp.)

petrovici A. Wagner 1914 [Chilostoma (Cattania)]

peucetana Kobelt 1879 (marianiae var.)

phalerata Rossmüller 1836 (non Webb et Berthelot 1833) (=chameleo chameleo)

philippii Kobelt 1905 (cingulatum subsp.)

phlebophora Lowe 1831 (Leptaxis)

phocaea phocaea Roth 1855 [Chilostoma (Josephinella)]

picaea Tiberi 1878 (=tetrazona)

picea Rossmüller 1837 (arbusorum subsp.)

picentina Kobelt 1903 (fuscobilabiata var.)

picta Monterosato 1892 (muralis var.)

pieperi Subai 1996 [Chilostoma (Thieseia)]

pilosa O. Boettger 1889 (=phaeriostoma)

pilosa Brusina 1867 (=setosa setosa)

pindica O. Boettger 1886 (subzonata var.)

pirinemis A. Wagner 1927 (polincki subsp.)

pisacanei Kobelt 1906 (=fuscobilabiata sapsensis)

pisana pisana Müller 1774 (Theba)

pisanela Servain in Bourguignat 1887 (=pisana)

pisanopsis Servain 1880 (=pisana)

planata Chemnitz 1795 (=subdentata helicella)

planata Lowe 1855 (nivosub var.)

planata Rossmüller 1854 (=pisana)

planicola Kobelt 1903 (fuscobilabiata var.)

planospira Lamark 1822 [Chilostoma (Campylaea)]

planulata Hidalgo 1866 (=pisana)

platychema Menke 1830 (=melitensis)

Plicostoma Schütter 1838 (=isognostomos)

pluridentatum Pollorena 1885 (holoscericae subsp.)

polinski A. Wagner 1927 [Chilostoma (Wladislavia)]

polla Paulucci 1878 (=strigata var.)

polydensis Kobelt 1905 (=vulgaris)

pollinennis Bacci 1951 (fuscobilabiata var.)

polyhymnia Subai 1996 [Chilostoma (Thieseia)]

portosanci Wollaston 1878 (Leptaxis)

posidonimensis Kobelt 1877 (=fuscobilabiata)

posthuma Knipper 1939 [Chilostoma (Thieseia)]

potentiae Kobelt 1903 (fuscobilabiata var.)

pouzolci Deshayes 1830 [Chilostoma (Dinarica)]

praesolida Monterosato 1892 (muralis var.)

praetexta Brusina 1874 (=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 (=fuscobilabiata var.)

preslii F. Schmidt in Rossmüller 1836 (cingulatum subsp.)

prokletijensis Knipper 1939 (=spaethbecki bindziensis)

propemuralis Monterosato 1892 (muralis var.)

provincialis Benoît 1842 (muralis var.)

pseudomphora Lowe 1852 (Leptaxis)

pseudocingulata A. Wagner 1914 (trizona subsp.)

pseudodochii Subai 2012 (Liburnica)

pseudohalmyris Caziot 1902 (=suburbaria)

pseudorusis Schlesch 1824 (arbusorum subsp.)

pseudospinans Caziot 1902 (=serpentina hospitals)

pterolakae Kobelt 1893 (=phocaea)

pubescens Paulucci 1880 (planospira subsp.)

pubescens Westerlund 1886 (=pouzolzi montenegrina)

pubiosa Paulucci 1882 (=serpentina isaraf)

querystamina Locard 1894 (cingulatum var.)

radesiana Mares in Bourguignat 1887 (=pisana)

recondita Westerlund 1876 (signata var.)

reischuetzi Subai 1990 (Liburnica)

reiher Branczik 1890 (=insolita insolita)

renschi Knipper 1939 [Chilostoma ("Cattania")]

repplini Reeve 1852 (arbusorum subsp.)

ressmanni Kobelt 1902 (=cingulata preslii)

reybodia Moquin-Tandon 1855 (=aolotina)

rhacticum Strobel 1857 (adolozona subsp.)

rhodopensis Kobelt 1906 (=trizona)

rhodostoma Drapnaud 1801 (=pisana)

ribbona Monterosato 1892 (muralis var.)

ridens Martens 1884 [Tyrrenherbus]

rissoi Trechmann 1838 (=melitensis)

rivellensis Kobelt 1904 (=fuscobilabiata laurieriensis)

rolois Malzahn 1886 (=muralis insularis)

romaniana Caziot et Maury 1906 (cingulatum var.)

rosalba Monterosato 1892 (=pisana)

rosaliae Benoît 1857 (platychema var.)

roschitzi Westerlund 1886 (serbica)

rossmaessleri L. Pfeiffer 1842 (Faustina)

rovellensis Kobelt 1906 (=fuscobilabiata laurieriensis)

ruberonota Monterosato 1892 (muralis var.)

rudis Rossmüller 1837 (=stenzi)

rufescens Pennant 1777 (=arbusorum)

rugosa Rossmüller 1835 (=muralis)

rumelica Ziegler in Rossmüller 1838 (trizona subsp.)

sabbieri Bourguignat 1886 (=pouzolzi pouzolzi)

sablaria Brusina 1904 (=Dinarica)

saccalina Letourneux 1886 (=pouzolzi)

sagittifer Gittenberger et Ripken 1887 (Theba)

sadleriana Rossmüller 1838 (=teufelburiana)

saintvesi Kobelt 1906 [Marmorana (Macularia)]

sapennis Kobelt 1904 (fuscobilabiata var.)

saracena Westerlund 1889 (=globularis ascherae)

sardica Caziot 1902 (=suburbaria)

sardoa Ziegler 1830 (=pisana)

sardonianus Martens 1884 [Tyrrenherbus]

sarmizegetusae Kimakowicz 1890 (faustina var.)

sativa Ziegler in Rossmüller 1835 (=faustina)

sattmanni Subai 1995 (Heliogonia)

saxetana Paulucci 1886 [Marmorana (Ambigua)]

scabriuscula Deshayes 1830 [Marmorana (Murella)]

scalariformis Benoît 1857 (=muralis drapnensis)

schmidtii Rossmüller 1836 [Arianta (Arianta)]

sciara Westerlund 1879 (olympica var.)

schlaerichroica Bourguignat 1870 (Campylaea)

sclerotricha Bourguignat 1879 (=schlaerichroica)

sebrianus Kobelt 1875 (=achates adolozona)

segestiana Filippi 1892 (scabriuscula var.)

selecta Bisacci 1929 (=planospira occultula)

selimuntina Filippi 1836 (scabriuscula var.)

sempitava Taylor 1912 (=subdentata dehnet)

sendmeri Clessin 1884 (arbusorum var.)

sentinense Piersanti 1933 (cingulatum subsp.)

serbica Kobelt 1872 [Chilostoma (Dinarica)]

serpentina Férrusac 1821 [Marmorana (Murella)]

serpentinarum Degner 1936 (fuscobilabiata var.)

sertum Monterosato 1892 (=pisana)

setigera setigera Rossmüller 1836 (Liburnica)

setipila Rossmüller, 1835 (=planospira setulosa var.)

setosa setosa Férrusac 1832 (Liburnica)

setulosa Branczik 1890 (planospira var.)

sicana Férrusac 1822 (platychema var.)

sicula Benoît 1857 (=serbica)

sigela Bourguignat 1883 (=cingulata gabanzi)

signata Férrusac 1821 [Marmorana (Murella)]
Family Helicidae: morphology, taxonomy, catalogue

tiurhina Martens 1899 (spp.)
tiesenhaueni Greldor 1889 (spp.)
tigrinum Cristofori et Dan 1832 (spp.)
tiphina Bourgiuguin 1860 (spp.)
tirilens Tagliani in Adam 1873 (spp.)
transalpina Stabile 1864 (spp.)
Transiberus Monterosato, 1892 (nom. nud. = Murella)
transiens Adam 1886 (spp.)
treccinensis Kobelt 1906 (spp.)
Triodopsis Martens 1860 (spp.)
trizona trizona Rossmann 1835 (Chilostoma (Cattania))
trochoilis Ruffiaen 1868 (arbustorum)
trichohora Benoit 1882 (spp.)
tchernagorica Bourgiuguin 1888 (spp.)
tubastoma Kimakowicz 1909 (spp.)
tullina Ehrmann 1910 (spp.)
tumidos Kobelt 1890 (spp.)
turgida Pallary 1915 (spp.)
turgidula Wood 1828 (arbustorum)

Tyrhenihibers Hesse et Kobelt, 1904
ulicis Kobelt 1890 (fuscolabiata ssp.)
ulleptischti Westerlund 1876 (illyrica)
Ulostoma Albers 1850 (fuscolabiata ssp.)
unbilicaris Brumati 1838 (illyrica)
umbrica Mabille 1867 (spp.)
undata undata Lowe 1831 (Leptaxis)
undulata Michaud 1831 (spp.)
unarmata Paulucci 1881 (Marmorana (Ambigua))
unfisciata Da Costa 1778 (arbustorum)
unitaeniata O. Bohettger 1885 (spp.)
ussiliana Paulucci 1878 (Marmorana (Ambigua))
ussilata Lowe 1852 (fuscolabiata ssp.)
ussiliana Paulucci 1887 (spp.)
vagiumn Pollonera 1890 (fuscolabiata ssp.)
valkanovi Urbański 1960 (Chilostoma (Thiessea))
vallicola Kobelt 1903 (fuscolabiata ssp.)
vareliensis Ripken et Falkner 2000 (arbustorum ssp.)
varronis Cantraire 1836 (spp.)
velanica Mabille 1881 (spp.)
velebitana Westerlund 1889 (spp.)
ventricosa A. Wagner 1914 (spp.)
verrucosa Kobelt 1890 (fuscolabiata var.)
vesulana Lessona 1886 (spp.)
Vidovicia Brusina, 1904
vibrayana Servain 1889 (arbustorum)
vieti Rossmann 1836 (fuscolabiata ssp.)
vikosensis Subai 1990 (? Chilostoma (Josephinella))
villicus Paulucci 1882 (Tyrhenihibers)
vilocania Lowe 1852 (undata ssp.)
wagneri Kimakowicz 1890 (spp.)
walleri O. Bohettger 1886 (spp.)
webbiana Lowe 1831 (Lampadina)
wiedemayri Kobelt 1903 (spp.)
wittmanni Zawadsky in Rossmann 1837 (arbustorum)

Wladislawia A. Wagner, 1927
wohlerediti Kobelt 1905 (spp.)
woollastonii wollaston Lowe 1852 (Leptaxis)
wullei Kobelt 1903 (fuscolabiata ssp.)
xatartii Farines 1834 (arbustorum ssp.)
xebiana Sturany 1907 (Chilostoma (Josephinella))
zieglers Rossmann 1836 (spp.)
zonaria Pennant 1777 (spp.)
zonaturn zonaturn Studer 1820 (Chilostoma (Thiessea))

...
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References


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 Ariantinae. Дан обзор существующих взглядов на систему подсемейств Helicidae, кроме номинативного подсемейства (Ariantinae, Murellinae и Thebinae). Сформулированы дифференциальные диагнозы таксонов. Особое внимание удалено морфологии папиллы пениса и атриального стимулятора, поскольку эти органы играют первостепенную роль в предотвращении интрогрессии (изолирующие механизмы).