
On the morphology of copulative apparatus of some Ariantinae (Pulmonata Helicidae)

A.A. SCHILEYKO

A.N. Severtzov Institute of Ecology and Evolution of Russian Academy of Sciences, Leninski prosp. 33, Moscow 119071, RUSSIA. E-mail: asch0829@gmail.com

ABSTRACT. The article contains additional data on the structure of the penial papillae and the atrial stimulators of the representatives of 13 species and subspecies of 8 (sub)genera of Ariantinae. The existence within the subfamily of five or six variants of structure of the copulative apparatus has been shown. Papilla of the penis or its elements can take on the role of stimulator; in such cases stimulator mostly is reduced down to full disappearance. Reproductive tract of some species has been re-described.

Abbreviations in figures: At – atrium; DSt – diverticle of spematheca; F – flagellum; FO – free oviduct; P – penis; Pil – pilaster; PP – penial papilla; RP – retractor of penis; PS – penis sheath; Sph – sphincter; Sti – stimulator; V – “velum”; Va – vagina.

Abbreviations of Museums:

HNHM – Hungarian Natural History Museum, Budapest, Hungary

NHMW – Naturhistorisches Museum Wien, Austria

RMNH – National Museum of Natural History, Leiden, The Netherlands

Introduction

When trying to understand the taxonomic structure of any group of organisms inevitably a problem arises of selection of characters on which we can rely. Obviously, for analysis only those characters are suitable which provide the basis for a comparison. One can distinguish only distinguishable things: if two objects have same color, then the inclusion of this feature to the analysis of the similarity/difference between objects does not make sense. In the given case (Ariantinae), if to use for identification of genera, for example, the structure of a jaw, or a kidney, or an external appearance of the reproductive tract, we do not get (or almost do not get) any material for analysis of relationship between taxa.

Earlier the author has published an article where considered, in particular, the variety of the structure of the penial papillae and stimulators of 15 species of Ariantinae [Schileyko, 2013]. Most of them are type species of genera or subgenera. Now I have got some material on the representatives of 8 genera (subgenera) which have been considered in the mentioned paper by only literature data. References to the original descriptions and other information for each taxon are given in my earlier article [Schileyko, 2013]. Here emphasis is placed on the structure of the penis papilla and stimulator.

Material and methods

List of the studied material follows the species names. Methods have been described in my previous article [Schileyko, 2013].

Results

Thiessa sphaeristoma sphaeristoma (Bourguignat, 1857) (Fig. 1)

Material: Greece, Thessalia, Magnissia, 4 km WSW of Marathia (32 km SE of Volos); 15 m alt. 28.V.1999. UTM F J 8232. Leg. et det. E. Gittenberger, D. Uit de Weerd. RMNH Mol. 62488, 43730-Helicidae. 1 specimen.

Vas deferens is rather long. Flagellum is about two times shorter than penis. Epiphallus very short (shorter than flagellum). Penis bulky. Penial retractor attached to the apex of a fleshy outgrowth located on the boundary between penis and epiphallus. Free oviduct somewhat longer than vagina. Mucus glands are simple.

Penis consists of two chambers: proximal one contains papilla and separated from distal chamber by a sphincter; distal chamber bears an axial pilaster. Penial papilla with almost smooth surface, thick walls, and narrow inner slit-like canal that opens on the tip of the papilla by a small pore. Walls of papilla filled with loose parenchyma.

Stimulator as such is absent, unless to believe that a strong longitudinal pilaster, located in the vagina and bearing the opening of stylophore, is its derivative. The other branch of the pilaster runs into penis.

Cingulifera cingulata (Studer, 1820) (Fig. 2)

Material: Strada ponale und Ponale-Fall bei Riva [Italy]. 1892. Leg. et det. R. Sturany. NHMW No. 19159. 1 specimen.

Penial papilla is thick-walled, with very strong, superficial semicircular folds of irregular shape. Inner surface of the penis has a relief corresponding to that of papilla. Inner canal of the papilla is slit-like, of irregular form in cross-section, opens on the tip of the organ. Walls of the papilla contain very loose parenchyma saturated with numerous lacunae and sinuses.

Stimulator is rather small, conical, located in vagina above atrium. Regular relief on the inner surface of the vagina is absent.

Wladislawia polinskii (A. Wagner, 1988)
(Fig. 3)

Material: Bulgaria, Blagoevgrad prov., Pirin Planina, Mt. Vikhren (30 km N of Melnik); alt. 2914 m, 8.IX.1967. Leg. et det. A.W. Janssen. RMNH, Mol. 336248, 43730-Helicidae. 2 specimens.

Vas deferens moderately long. Flagellum very long, about two times longer than penis+epiphallus. Epiphallus rather thin. Penis consists of 2 parts: narrowed, twisted distal part, the curves of this part are fixed by numerous thin muscle fibers (as in *Causa* – see below); proximal part is bulky, thin-walled, surrounded by semitransparent sheath. Penial retractor attached to epiphallus well above penis. Free oviduct and vagina are not long, of about equal length. Mucus glands forked.

Penial papilla is of irregular shape, thick-walled, with few superficial axial grooves and minute apical pore. Inner surface of penis with longitudinal, swollen, locally thickened pilasters; rounded fossae on the papilla surface correspond to these thickenings. Walls of the papilla contain loose parenchyma and small lacunae. Internal canal of the papilla narrow, in form of 3- or 4-rayed star.

Stimulator not large, ovate, occupies transverse position in the atrium. Inner surface of vagina supplied with one or two smoothed, broad longitudinal folds.

Cattania petrovici (A.J. Wagner, 1914)
(Fig. 4)

Material: Albania, 2010/55, Shkodër district, Prokletije Mts., Breg-Lumi, Shalë River in the village, 360 m, N 42°18.258' E 19°47.814', 23.05.2010. Leg. et det. Z. Fehér, D. Murányi, Zs. Újvári. HNHM. 1 specimen.

Penial papilla is large, with circular grooves in its basal part. On the proximal part of the papilla there is a vast, wide longitudinal slit; on the bottom of the slit lies a wide axial pilaster (similar to that in *Dinarica pouzolzi* or *Arianta arbustorum* – see Schileyko, 2013, Figs. 12 and 15). Orifice of epiphallus opens at the base of this pilaster. Walls of the papilla contain a loose parenchyma and large lacunae.

Stimulator large, fleshy, conic, directed to the

vagina. Inner surface of the vagina with strong, locally swollen, axial pilasters.

Remark. Taxonomic position of this species is not clear. The shape and size of the stimulator of *C. petrovici* is very similar to that of *C. trizona*, but structure of the penial papilla in these two species is different: in *C. petrovici*, as stated above, there is an axial pilaster whereas in *C. trizona* the pilaster is absent; in *C. petrovici* there is a slit on the surface of the papilla; in *C. trizona* such a slit is absent.

In the meanwhile I am refraining from solving the problem, since I dissected only one specimen of each species.

Causa holosericea (Studer, 1820)
(Fig. 5)

Material: Austria, Tirol, Stubaital, Neustift, Milders; alt. ca. 1000 m; on walls along road, 9/28.VIII.1957. Leg. et det. C.O. Regteren Altena van. RMNH, Mol. 6738 43730-Helicidae. 2 specimens.

Vas deferens is comparatively short, entering epiphallus subapically. Epiphallus long, thickened in its proximal section. Flagellum is short, rudimentary. Penis consists of two distinct parts: narrowed, twisted distal part, the curves of this part are fixed by numerous thin muscle fibers; proximal part is swollen, spherical, very thin-walled, surrounded by very thin, nearly transparent sheath. Penial retractor attached to middle section of epiphallus. Free oviduct long, curved; vagina somewhat shorter, its inner surface lacks regular relief (almost smooth). Mucus glands are simple.

Penial papilla short to very short, thick-walled, its walls filled with loose parenchyma. Papilla surface bears deep circular grooves; relief of inner surface of the penis corresponds to these grooves. Inner canal of the papilla is slit-like, roughly semilunar in cross-section, open terminally.

Stimulator is moderately large, lamellar, located obliquely-transversely in the atrium, directed toward the penis.

Kosicia intermedia (C. Pfeiffer, 1828)
(Fig. 6)

Material: Am Füâ des kleinen Tal am Plöken-Pass, Karnische Alpen [Austria], 16.7.1907. Leg. et det. R. Sturany. NHMW No 44.658. 1 specimen.

Austria, Karnische Alpen, Plöckenpass, 07.08.2008. NHMW No SpID#181, inID#2108. From project "Alpine landsnails". 1 specimen.

Vas deferens moderately long, entering epiphallus apically. Flagellum markedly longer than penis+epiphallus. Epiphallus short, thick, narrowed in proximal part. Penis is bulky, not long. Penial retractor attached to the middle of epiphallus. In one of dissected specimens there was an additional branch of the retractor that connects the main branch with the atrium, in the other specimen the

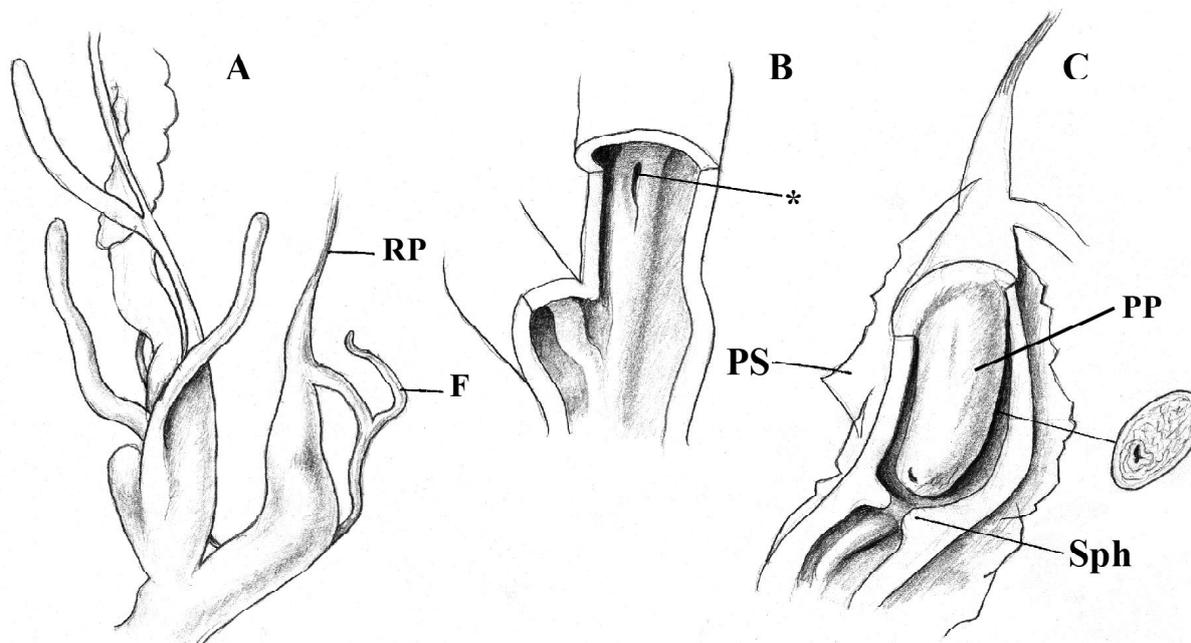


FIG. 1. *Thiessea sphaeristoma*. A – reproductive tract. B – inner structure of atrium and vagina. C – inner structure of penis. Asterisk – stylophore opening.

РИС. 1. *Thiessea sphaeristoma*. А – репродуктивный тракт. В – внутреннее строение атриума и вагины. С – внутреннее строение пениса. Звёздочка – отверстие стилофора.

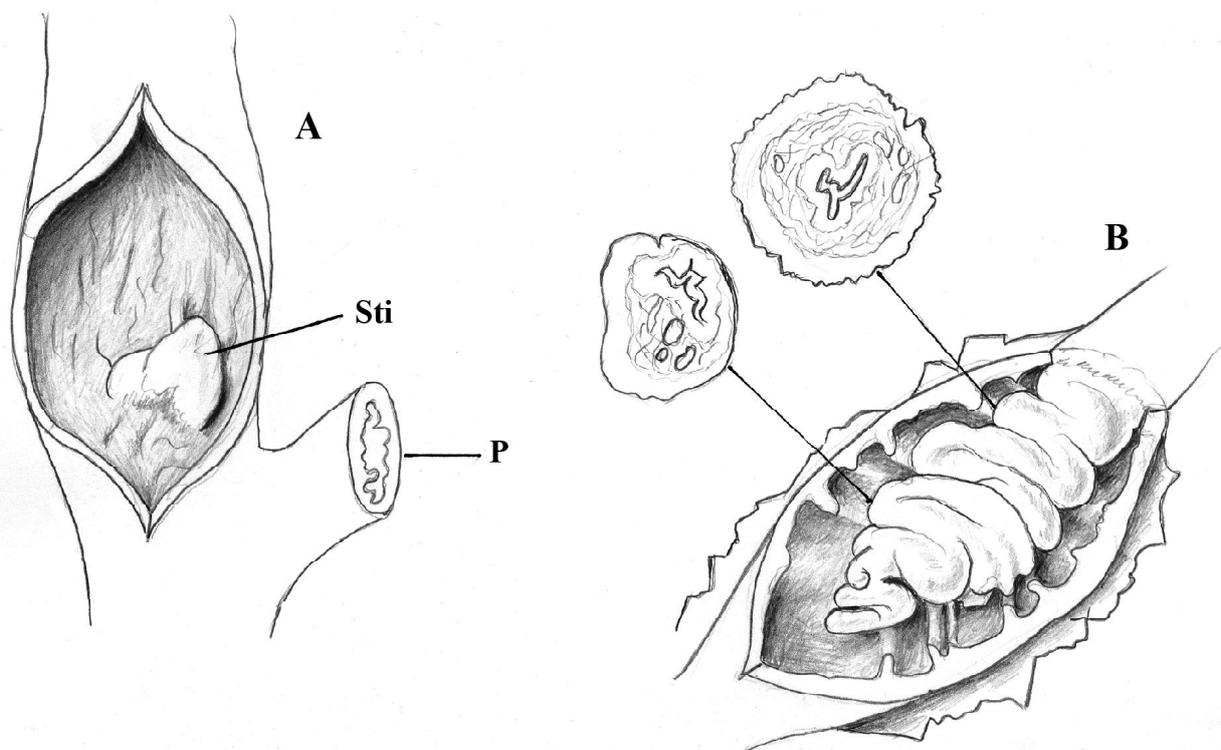


FIG. 2. *Cingulifera cingulata*. A – inner structure of vagina. B – inner structure of penis.

РИС. 2. *Cingulifera cingulata*. А – внутреннее строение вагины. В – внутреннее строение пениса.

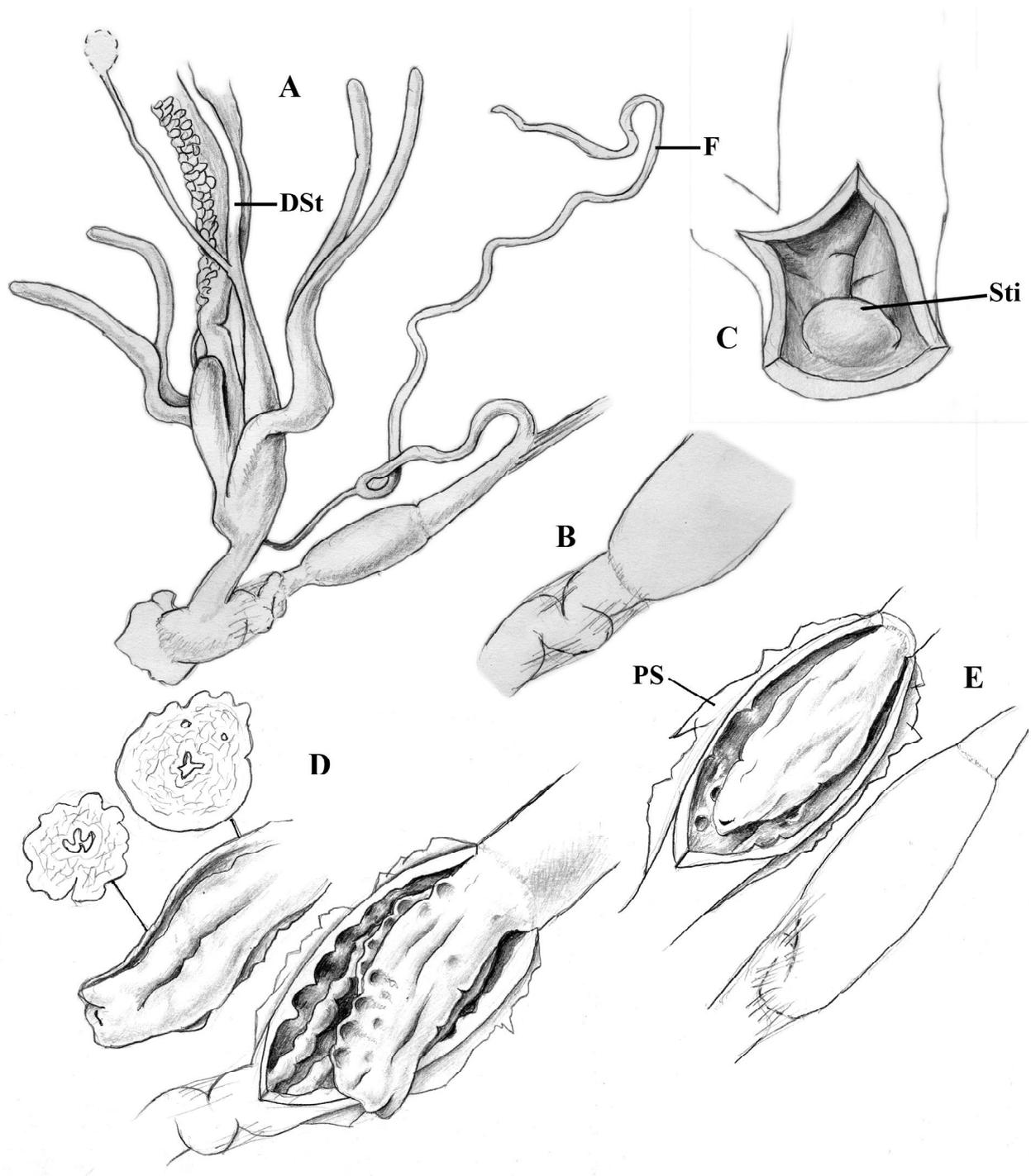


FIG. 3. *Wladislawia polinskii*. A – reproductive tract. B – distal part of penis. C – inner structure of vagina. D – inner structure of penis and papilla from other side. E – another specimen: distal part of penis and inner structure of proximal section of penis.

РИС. 3. *Wladislawia polinskii*. А – репродуктивный тракт. В – дистальная часть пениса. С – внутреннее строение вагины. D – внутреннее строение пениса и папилла с другой стороны. E – другой экземпляр: дистальная часть пениса и внутреннее строение проксимальной части пениса.

additional branch was absent. Free oviduct is not long, straight; vagina somewhat shorter. Mucus glands are simple.

Penial papilla is moderately long, thick-walled, with two very narrow, deep longitudinal grooves and several smaller ones. Besides, few transversal superficial grooves may be present. Inner canal of

the papilla is narrow, in form of irregular star with 3 or 4 rays. Pore of papilla slit-like, occupies subterminal position. Inner surface of penis lacks regular relief.

Stimulator is small, ovate, located obliquely-transversely in the atrium, directed into the penis. Vagina internally with narrow axial folds.

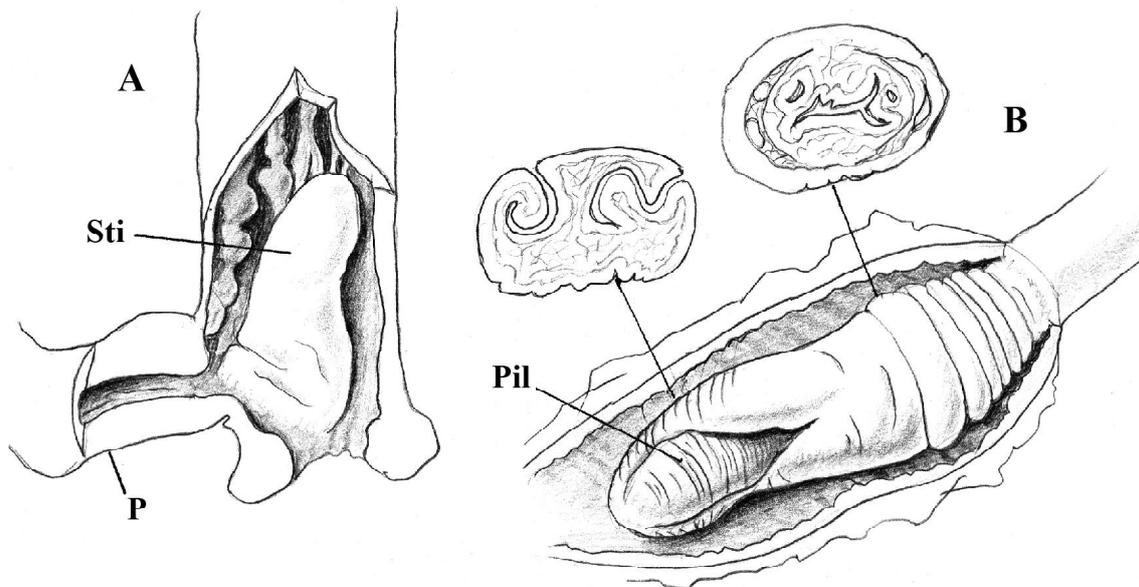


FIG. 4. *Cattania petrovici*. A – inner structure of atrium and vagina. B – inner structure of penis.

РИС. 4. *Cattania petrovici*. А – внутреннее строение атриума и вагины. В – внутреннее строение пениса.

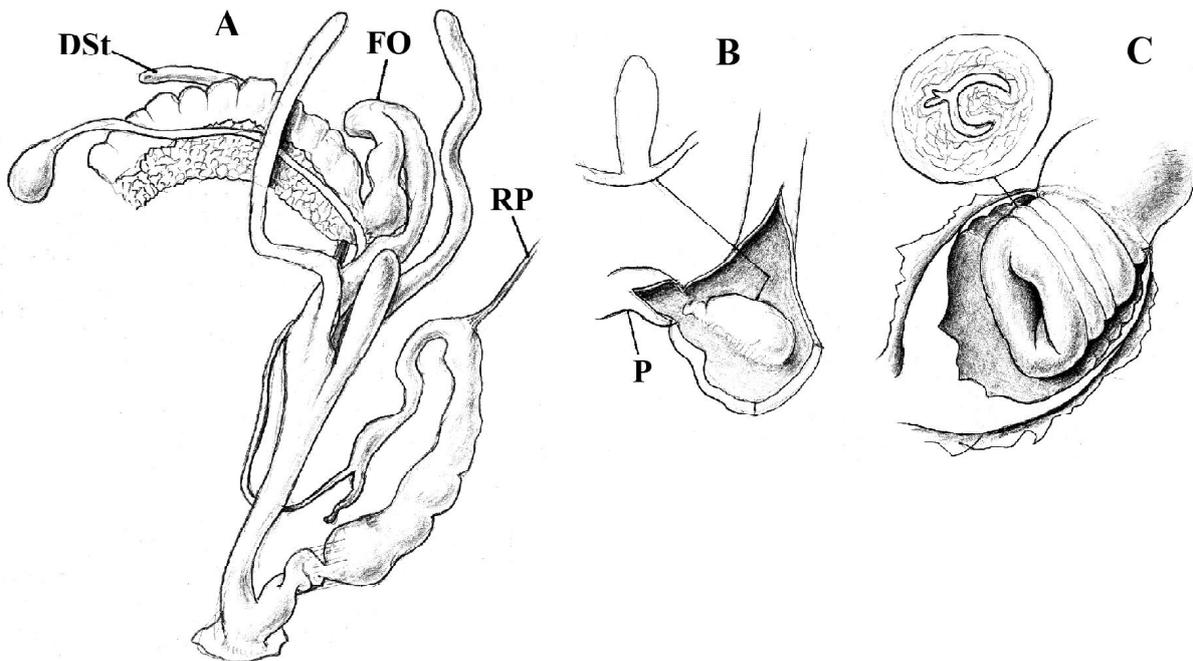


FIG. 5. *Causa holosericea*. A – reproductive tract. B – inner structure of atrium and cross section through stimulator. C – inner structure of penis.

РИС. 5. *Causa holosericea*. А – репродуктивный тракт. В – внутреннее строение атриума и поперечный срез через стимулятор. С – внутреннее строение пениса.

Kosicia ziegleri
(Schmidt in Rossmässler, 1836)
(Fig. 7)

Material: Slowenien, Steiner Alpen, Ceska Koca; Aufstieg, ca. 1440 m. 2-6.VII.1990. Leg. et det. H. Kothbauer, H. Sattmann, E. Wawra. NHMW No 90400. 2 specimens.

Vas deferens rather long. Flagellum a little longer

then penis+epiphallus. Epiphallus thin, longer than in *K. intermedia*. Penis is fusiform, not long. Penial retractor attached to the middle of epiphallus. Free oviduct rather short, straight; vagina somewhat shorter, internally with delicate axial folds. Mucus glands are simple. Atrium swollen, globular.

Penial papilla is voluminous, thick-walled, with several distinct, spirally directed furrows, one of

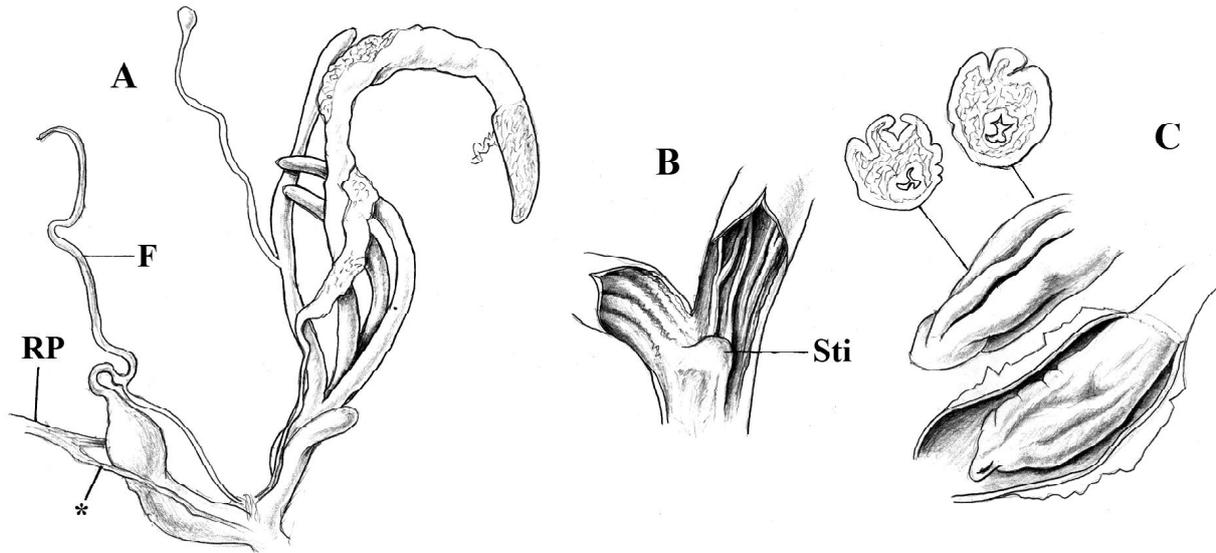


FIG. 6. *Koscicia intermedia*. A – reproductive tract. B – inner structure of atrium and vagina. C – inner structure of penis and papilla from other side. (Vienna 44.658). Asterisk – additional branch of penial retractor.

РИС. 6. *Koscicia intermedia*. A – репродуктивный тракт. B – внутреннее строение атриума и вагины. C – внутреннее строение пениса и папилла с другой стороны. (Vienna 44.658). Звёздочка – дополнительная ветвь пениального ретрактора.

them is deep, pore of epiphallus open in its depth. The remaining furrows are superficial. Inner canal of the papilla is narrow, in form of irregular star with 3 rays. Inner surface of penis more or less distinctly repeats the relief of the papilla.

Stimulator is moderately large, fleshy, occupies transverse position in the atrium.

Delphinatia alpina (Michaud, 1831) (Fig. 8)

Material: Frankrijk, Dép. Isere, Gorge de Guiers Mort [?Mont], Pic de l'Oeillette; 600 alt. 4.VIII.1970. Leg. et det. W.H. Neuteboom. RMNH, Mol. 48942, 43730-Helicidae. 2 specimens.

Vas deferens is moderately long. Flagellum is very long, twisted. Epiphallus 2-3 times shorter than flagellum, may be swollen in distal part. Penis consists of two sections: swollen proximal (containing papilla) and narrowed distal. Free oviduct and vagina rather short, of approximately equal length. Mucus glands forked.

Penial papilla is thick-walled, with a deep longitudinal and many circular grooves. On the other side of papilla these grooves joined under sharp angle. Orifice of epiphallus lies in the depth of longitudinal groove. Inner canal of the papillae in form of 3-beam star in cross section. Walls of papilla filled with a loose parenchyma containing lacunae.

Stimulator is not found (seemingly is absent). Inner surface of vagina with weak irregular axial furrows.

Josephinella hemonica (Thièsse, 1884) (Fig. 9)

Material: Ag. Antoniou, Veroia, Imathia, central Macedonia, Greece, 2011.03.15. Leg., det. - ? NHMW No spID#618, InLID3#6568, from the project "Alpine landsnails". 1 specimen.

Penial papilla is elongated, thick-walled, with distinct, deep longitudinal groove and numerous superficial circular furrows. In the middle part of the papilla the longitudinal groove is connected with inner canal of the papilla. The pore of the papilla occupies terminal position. Walls of the papilla filled with loose parenchyma. Inner surface of the penis corresponds to the circular furrows on the papilla surface.

Stimulator in form of fleshy elongated crest-like lamella that stands vertically in vagina. Inner surface of vagina with smoothed semicircular folds.

Josephinella byshekensis (Knipper, 1941) (Fig. 10)

Material: Pazori/Pacori, NW of Permet, Gjirokastra, Albania, 2012.04.12. Leg. et det. ?Reischütz. NHMW No spID#700, InLID#7015, from the project "Alpine landsnails". 1 subadult specimen.

Penial papilla of dissected subadult specimen differs from those of *J. hemonica* by the absence of circular furrows.

Stimulator similar in shape and position to those of *J. hemonica*, but differs in smaller size; besides,

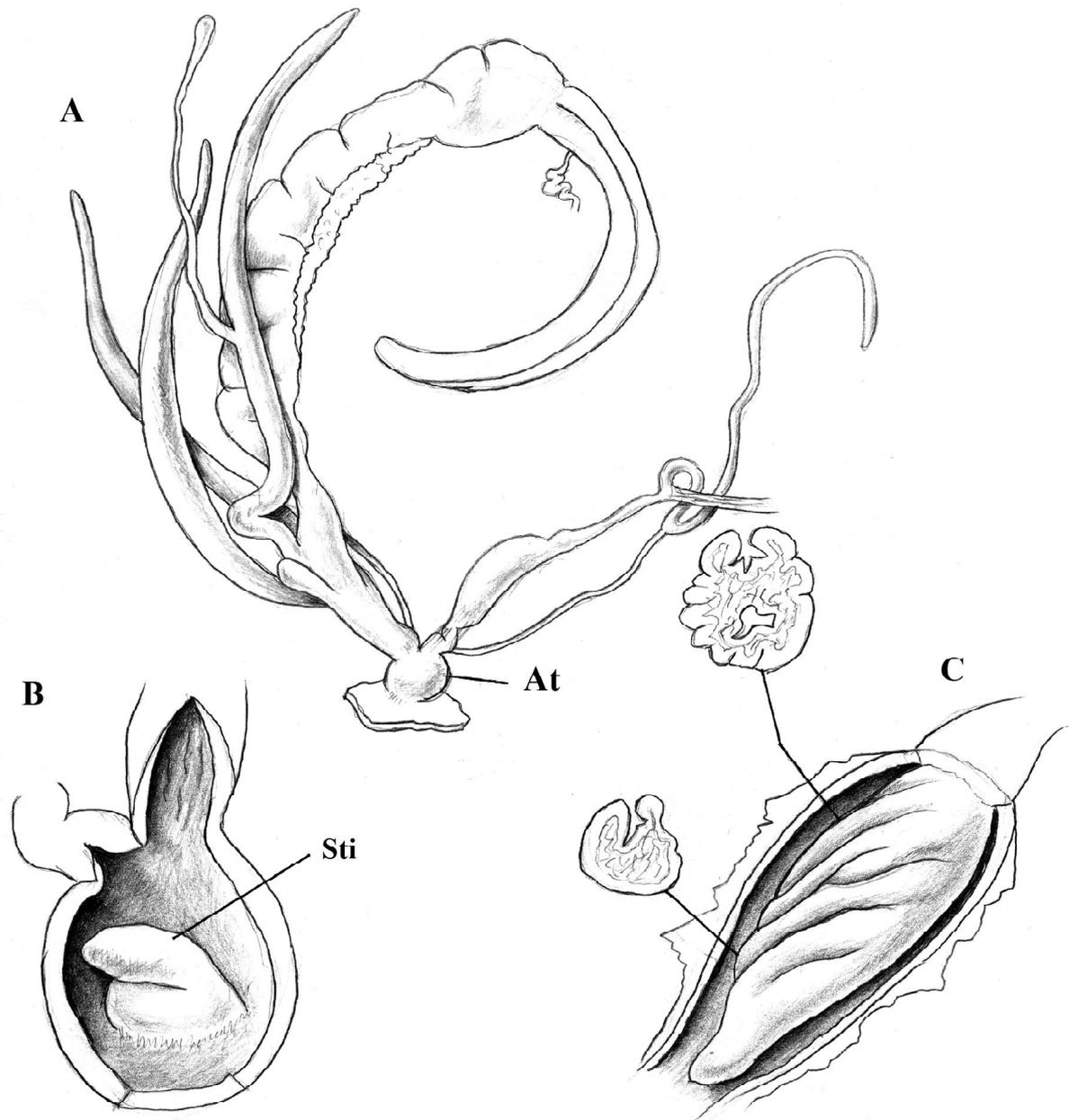


FIG. 7. *Koscicia ziegleri*. A – reproductive tract. B – inner structure of atrium. C – inner structure of penis.

РИС. 7. *Koscicia ziegleri*. А – репродуктивный тракт. В – внутреннее строение атриума. С – внутреннее строение пениса.

the inner surface of the vagina deprived of the semicircular folds.

Liburnica skipetarica skipetarica
(Subai, 1995)
(Fig. 11)

Subai, 1995: 88, Abb. 2, 13, 14, 22 (*Helicigona skipetaricus*).
(Type species of nominal genus *Superba* Subai et Fehér, 2006
[Subai, Fehér, 2006: 206]).

Material: 2006/155 Albania, Periferi Skrapar, Mali I Tomorrit, ca. 7 km NW of Terovë, NE of Çuka Partizan (1865-1950 m) [grassland, limestone rocks]. DL20 2006.08.25. Leg.

Fehér, Hunyadi, Huszár, Murányi, det. Z. Fehér. HMNH N40 42.983 E20 09.403. 1 specimen.

Penial papilla is generally in form of a wide trough or gutter, with a smoothed longitudinal pilaster on its bottom. Sides of the trough are more or less curved towards each other by their upper edges. Opening of the epiphallus is located in basal part of papilla. Inner surface of the penis lacks regular relief. A wall of the papilla contains loose parenchyma and lacunae.

Stimulator is small, somewhat rudimentary, rounded, standing in atrium between penis and vagina. Inner surface of vagina is almost smooth.

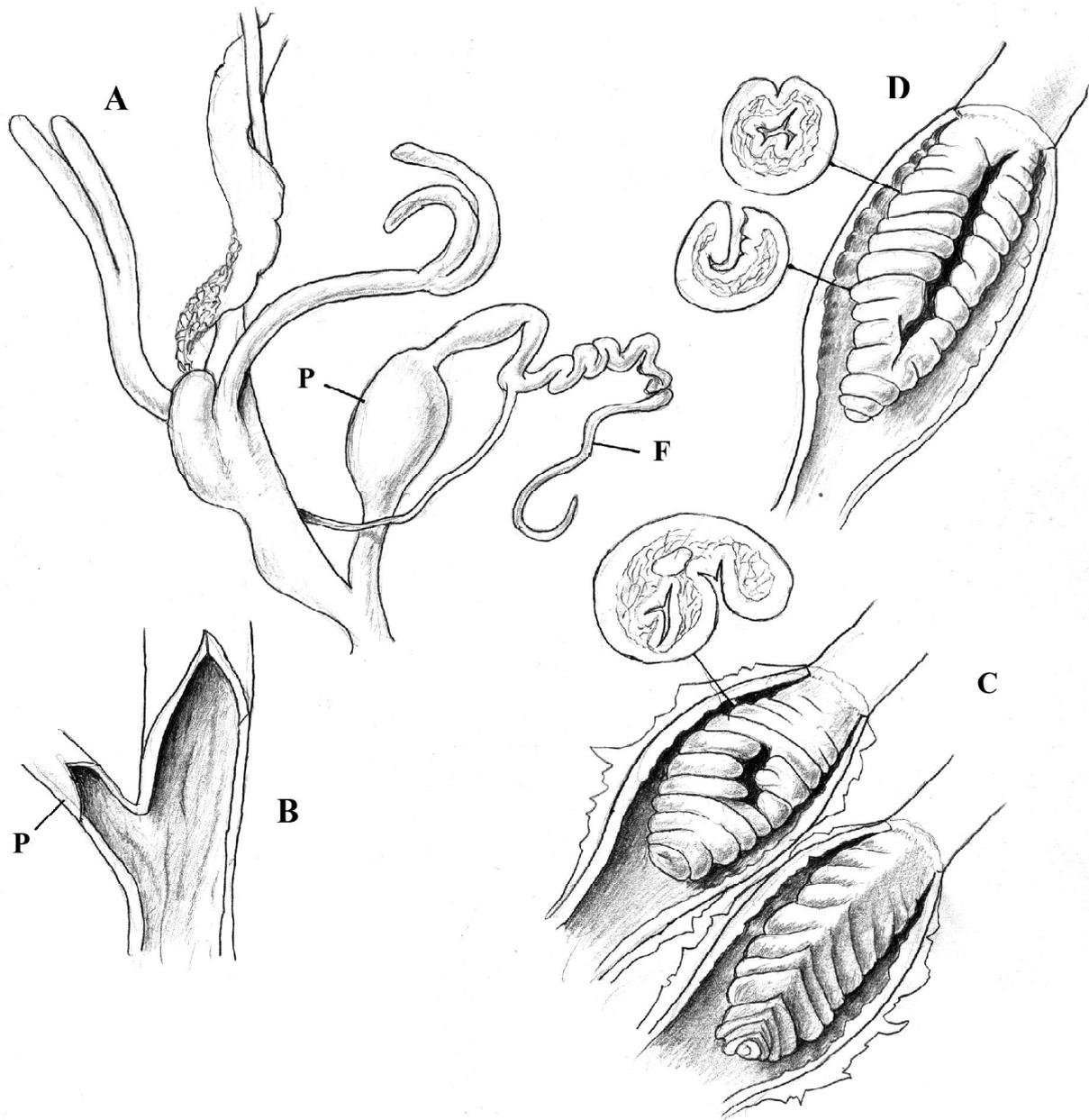


FIG. 8. *Delphinatia fontenillii alpinum*. A – reproductive tract. B – inner structure of atrium and vagina. C – inner structure of penis, view from two sides. D – other specimen: inner structure of penis.

РИС. 8. *Delphinatia fontenillii alpinum*. А – репродуктивный тракт. В – внутреннее строение атриума и вагины. С – внутреннее строение пениса, вид с двух сторон. D – другой экземпляр: внутреннее строение пениса.

Liburnica skipetarica asketa
Subai et Fehér, 2006
(Fig. 12)

Material: 2004/088 Albania, Periferi Berat, Mali I Tomorrit, 700 m N of Maja e Tomorrit, along the ridge (2375 m) [limestone rocks]. DK29 2004.08.10. Leg. et det. Z. Fehér. HNHM N40. 641560 E20.159300. 1 specimen (paratype).

From nominative subspecies this specimen differs mainly by the shape and position of stimulator: it has subquadrangular shape and located at the penial side of the atrium.

Campylaea ex gr. planospira
(Lamarck, 1822)
(Fig. 13)

Material: Sicilia, Borquetto [?Borghetto]: Sant. di Romitello, 1987.3.3. Leg. P. Kiss, L. Pintér, det. Z. Fehér et A. Schileyko. HNHM. 1 **subadult** specimen.

Mucus glands forked.

Inner surface of penis with few longitudinal branched pilasters; two of them in the proximal part sharply increasing and united by their edges, forming a sort of “velum” above the pore of the epiphal-

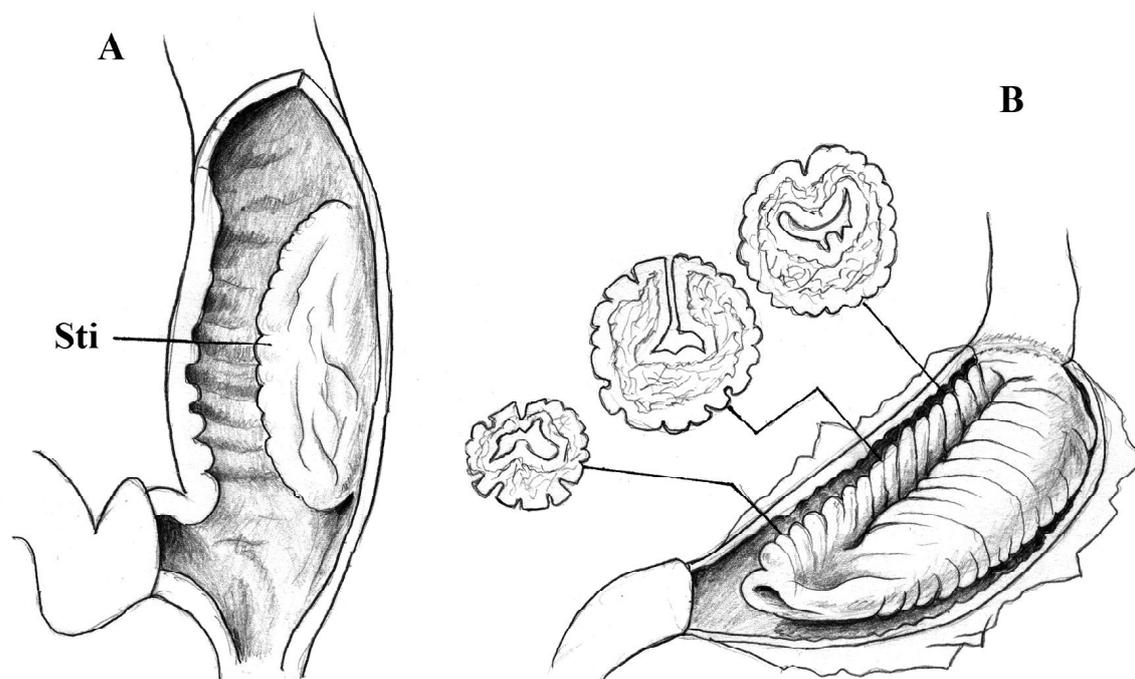


FIG. 9. *Josephinella hemonica*. A – inner structure of vagina. B – inner structure of penis.

РИС. 9. *Josephinella hemonica*. А – внутреннее строение вагины. В – внутреннее строение пениса.

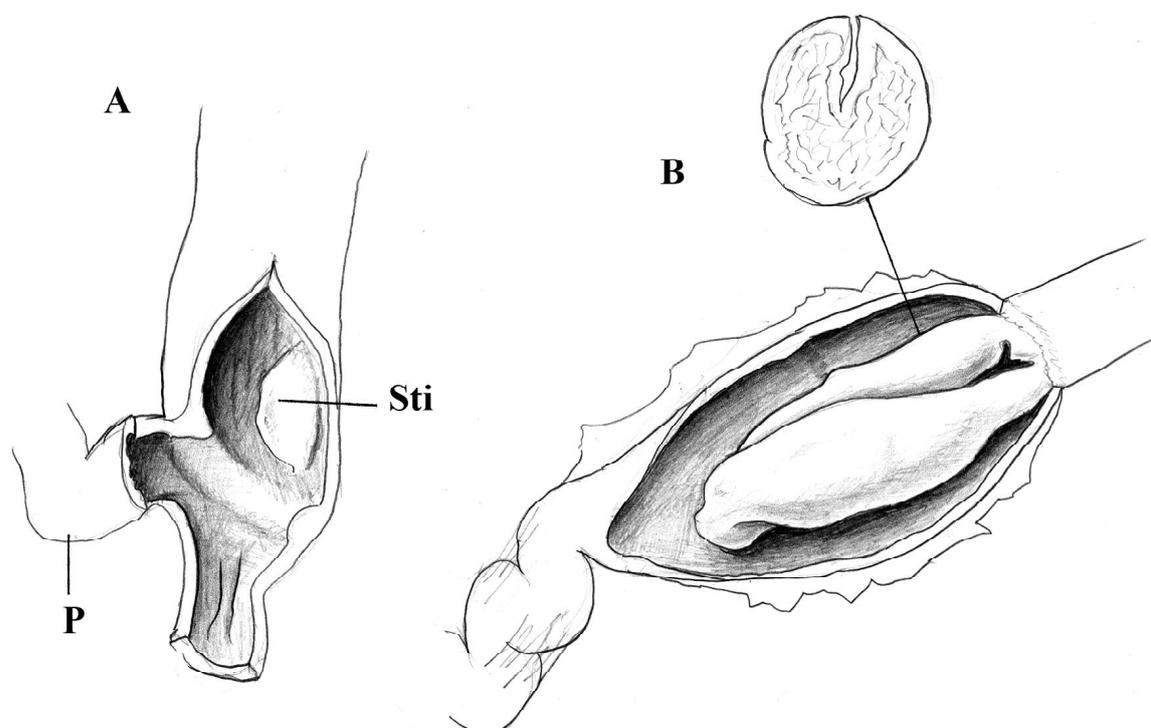


FIG. 10. *Josephinella byshekensis*. A – inner structure of vagina. B – inner structure of penis (subadult specimen).

РИС. 10. *Josephinella byshekensis*. А – внутреннее строение вагины. В – внутреннее строение пениса (не вполне взрослый экземпляр).

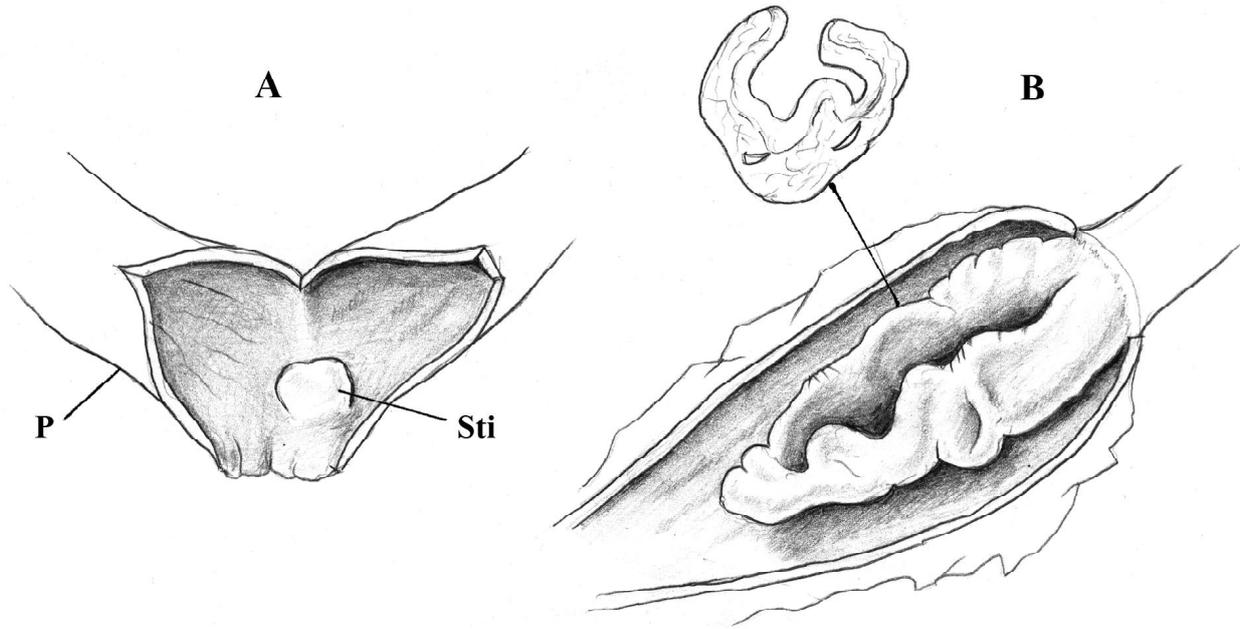


FIG. 11. *Liburnica skipetarica skipetarica*. A – inner structure of atrium and vagina. B – inner structure of penis.

РИС. 11. *Liburnica skipetarica skipetarica*. А – внутреннее строение атриума и вагины. В – внутреннее строение пениса.

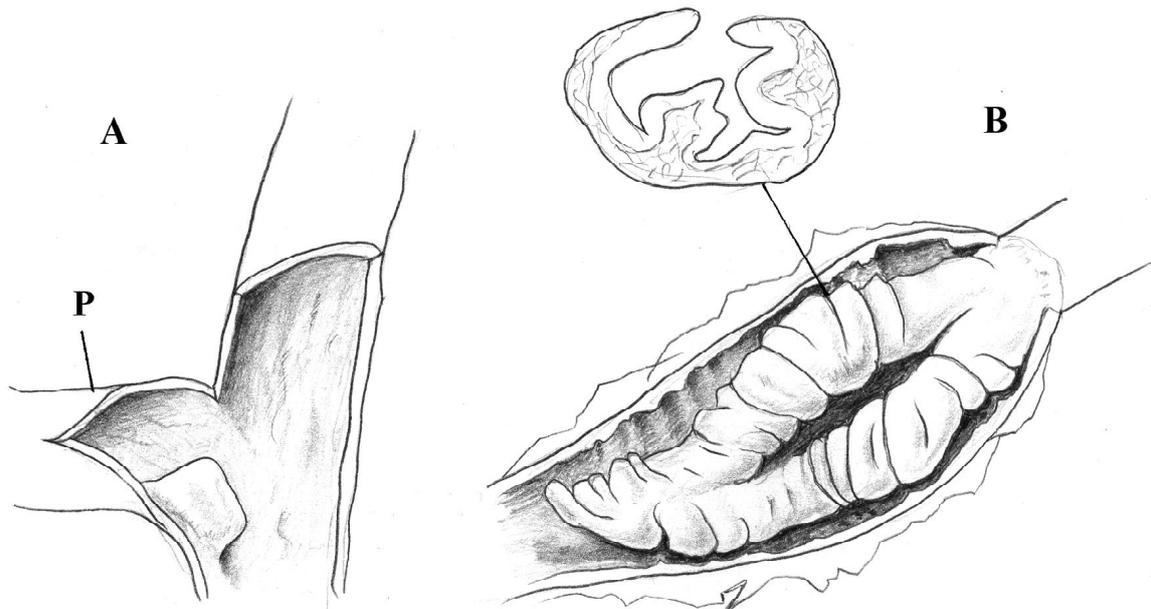


FIG. 12. *Liburnica skipetarica asketa*. A – inner structure of atrium and vagina. B – inner structure of penis.

РИС. 12. *Liburnica skipetarica asketa*. А – внутреннее строение атриума и вагины. В – внутреннее строение пениса.

lus [in general this structure reminds those observed in some *Pseudonapaeus* (Enidae); on Fig. 13 the “velum” has been bent up to show additional pilaster that runs into the cavity of epiphallus.

Stimulator not found. Inner surface of vagina is almost smooth, without regular relief.

Remark. It should be taken into consideration that the single specimen that I dissected was not fully adult.

Discussion

As stated earlier [Schileyko, 2013] penial papilla historically appeared as an excrescence of a sphincter that separates the cavities of epiphallus and penis. Consequently, the initial state of papilla is just a thick-walled muscular tube.

The main direction of evolutionary development of the papilla is morphological specialization and

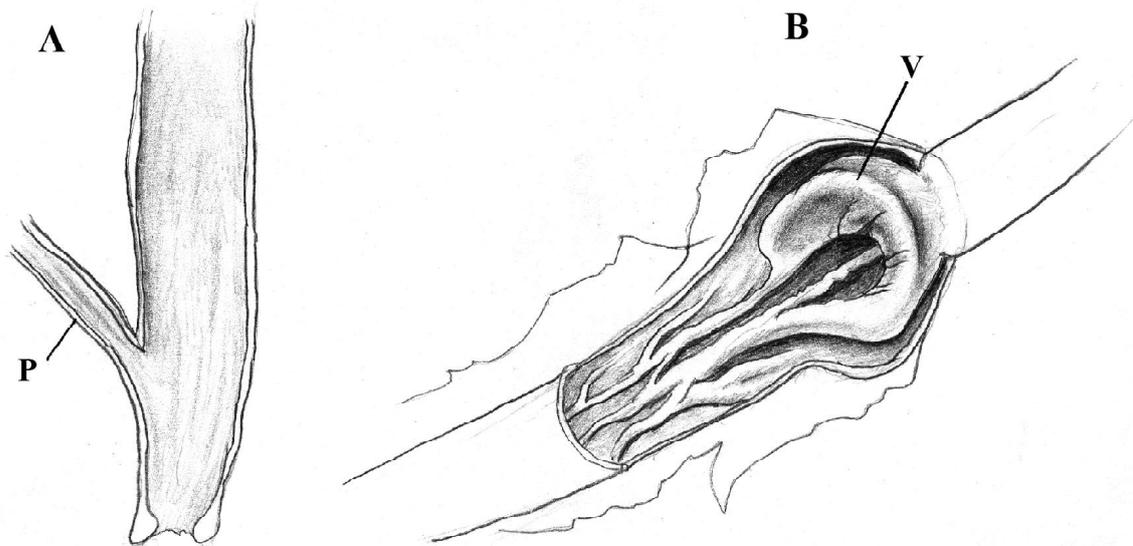


FIG. 13. *Campylaea* ex gr. *planospira*. A – inner structure of vagina. B – inner structure of penis. The protruding edge of papilla (“velum”) bent back.

РИС. 13. *Campylaea* ex gr. *planospira*. А – внутреннее строение атриума и вагины. В – внутреннее строение пениса. Выступающая кромка папиллы («велум») отогнута.

further disintegration of tissue in the walls of papilla: first muscle tissue in the walls was replaced by connective tissue. Next stage consists of further dissipation of the connective tissue due to, in particular, appearance of sinuses and lacunae. Final stage – forming a continuous cavity; seemingly, this condition could be realized more than one time.

Considering the ways of morphological specialization it is possible to recognize five or six types of papilla structure. Sometimes transformation of papilla is accompanied by peculiarities of stimulators (Fig. 14).

1. A simple tube with central or almost central canal; pore of the papilla occupies (sub)apical position; cavity of the canal in cross section varies from subcircular to many-rayed star. Stimulator small, very small, or absent: *Ariantopsis* – *Thiessea* – *Cingulifera* – *Wladislawia* (stimulator is absent) – *Cattania trizona* (parenchyma in walls of papilla replaced by a cavity) – ?*Cattania petrovici* – *Vidoviccia* (apical section of papilla is two-lobed).

2. Papilla consists of two lobes of different size. Stimulator transformed into a strong V-shaped fold [Schileyko, 2013, p. 137, Fig. 8]: *Faustina*.

3. Similar to “1”, differs by the presence of a longitudinal thickening in the inner canal, whereby the canal in cross-section has a crescent shape. Stimulator small but distinctly expressed: *Causa*, *Isognomostoma*.

4. Pilaster in the papilla cavity has differentiated into high, pectiniform distal and lower proximal parts; on the side of the papilla that located above pectiniform part, on the papilla walls a slit appears,

pore of the papilla opens at the depth of the papilla near the epiphallus. Stimulator small, sometimes rudimentary; in one genus (*Arianta*) very large: *Helicigona* – *Arianta* – *Chilostoma* – *Dinarica* – ?*Drobacia* – ?*Cochlopupa*.

5. Penial papilla gets the shape of the trough or gutter. Stimulator is very small (rudimentary) or totally absent: *Kosicia* – *Delphinatia* – *Josephinella* – *Liburnica*.

?6. Papilla forms a peculiar “velum” above the opening of the epiphallus. Stimulator is absent: *Campylaea*.

This list requires some explanations and morphofunctional interpretations.

First, it should be noted that the foregoing data are forcing to make some adjustments to the scheme of morphological transformations presented in my earlier article [Sñhileóko, 2013, p. 130, Fig. 1]. It should be born in mind that on the mentioned scheme, which shows sagittal sections, it was impossible to display the differences that are detected only in cross sections. As a result, the image of the papillae, for example of *Liburnica* and *Chilostoma*, have turned out identical, although the cross-sections of papillae in representatives of these genera differ markedly.

In the first group is in doubt the legitimacy of the placement of the two species studied by me, in same genus *Cattania*. In the type species of this genus (*C. trizona*) the penial papilla has no internal pilaster or slit in the wall while the papilla of the other species (*C. petrovici*) is similar to those of *Arianta* or *Dinarica*, i.e. has both named charac-

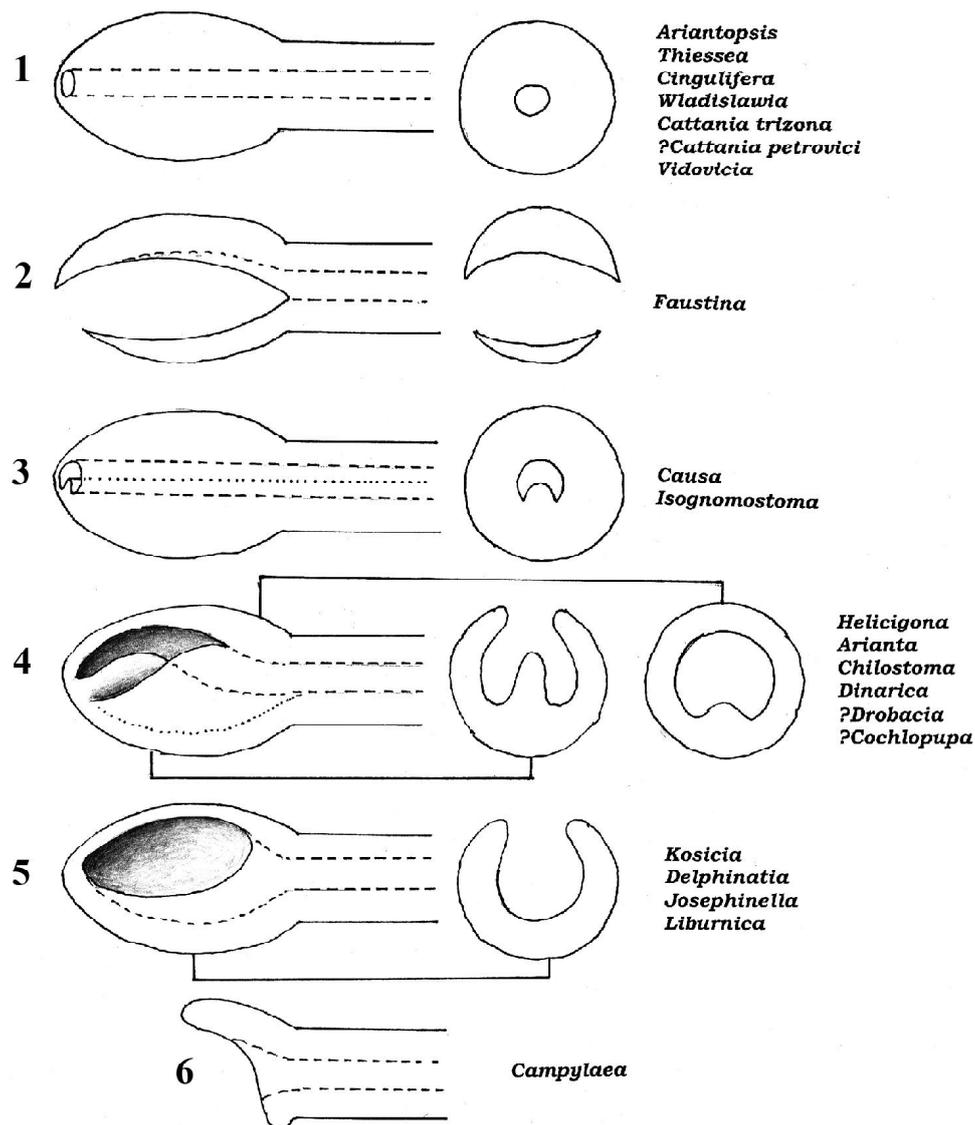


FIG. 14. Main variants of structure of penial papilla in Ariantinae.

РИС. 14. Основные варианты строения папиллы пениса у Ariantinae.

ters. On the other side, both species have unusually large stimulator (like in *Arianta*). To solve this problem it is necessary to revise the genus *Cattania* auct.

The monotypic genus *Vidovicia* is very peculiar from both conchological and anatomical points of views and occupies somewhat isolated position. Perhaps it makes sense to separate this species as an independent group. At the same time it should be noted that molecular data on *Vidovicia caerulans* presented by Groenenberg et al. [2012] are contradictory: according to phylogenetic tree based on the *Histon H3* dataset, this species is related to *Delphinatia*, according to *Cytochrome Oxidase subunit I* – to *Isognomostoma* and *Causa*, according to *Cytochrome B* – to *Kosicia*, according to *16S ribosomal subunit* – to *Corneola* [op. cit, p. 142, 146, 151,

and 155 correspondingly]. By the way, such contradictions take place for some other genera.

In general, the taxa that are placed in the first group, are distributed in the Balkan Peninsula and adjacent areas.

The position of *Faustina* (the second group) is doubtful. Formally, judging from the structure of the papilla (the presence of two lobes) [Schileyko, 1978, p. 309, Fig. 417, 418] this genus might be evaluated as cognates to *Vidovicia*, but this similarity, is most likely superficial, because the shells and the structure of the lobes themselves in the members of these two genera are quite different. Anyway, *Faustina* occupies somewhat isolated position among Ariantinae, as far as it concerns the structure of the papilla; similar conclusion may be done from the molecular data [Groenenberg et al., 2012].



FIG. 15. *Arianta arbustorum* in copuli. For explanations see the text. Photo courtesy of Mag. Katharina Jaksch.

РИС. 15. *Arianta arbustorum* in copuli. Объяснения в тексте. Фото публикуется с любезного разрешения маг. Катарины Якш.

The genus *Faustina* is distributed in Carpathians.

The third group is well delineated morphologically and has Central European distribution.

The fourth group is rather compact anatomically but includes two geographical subunits: most of genera is distributed in Central (partly in North) Europe (*Helicigona*, *Arianta*, *Chilostoma*, *Drobacia*, *Cochlopupa*), but one genus (*Dinarica*) – in Balkan Peninsula and nearby lands.

In this group two genera occupy somewhat isolated position: *Drobacia* and *Cochlopupa*.

Penial papilla of *Drobacia banatica* differs from those of all other members of the fourth group: it is unusually long and thin, and lacks axial pilaster, although has a slit on its surface; stimulator in this species is also peculiar [Schileyko, 2013, p. 136, Fig. 6].

As regards *Cochlopupa obtusa*, the structure of its papilla is more characteristic for the taxa of the fifth group (papilla has the appearance of a trough), although molecular data suggest its proximity to *Arianta-Chilostoma* complex [Groenenberg *et al.*, 2012; see also Schileyko, 2012].

The fifth group includes the genera distributed in Southern Alps and Balkan Peninsula.

The structure of the penial papilla of *Campylaea planospira* (sixth group), judging by a single, not fully adult specimen, is very peculiar, that is why I conventionally place the genus in a separate group. Such a structure might be evaluated either as primitive, or as advanced (secondary). However, another interpretation of this structure is possible: if to make the cut of the penis from the opposite side, the “velum” on the picture (see Fig. 13 and description above) will turn out to be from below, and will be

similar to the trough that is typical for members of the fifth group. For solution of this problem the dissection of adult specimens is needed.

Described morphological transformations are interconnected with peculiarities of functioning of the papillae in the representatives of different genera.

So, in the members of the first group the papilla during copulation just moves out. Parenchyma which fills the walls of the papilla, during copulation plays the role analogous to that of *corpora cavernosa* of mammals. The only exception being *Cattania trizona*, where parenchyma is completely replaced by a cavity that allows the papilla in time of copulation be turned out like the finger of a glove.

Atrial stimulator is also involved in the process of copulation, although it does not participate in transferring of spermatophore. Stimulators of various taxa differ by size and shape, sometimes it reduced down to full disappearance.

Therefore, to understand the mechanism of copulation it would be advisable to establish – whether the morphology of the papillae and stimulators depends on each other.

Direct observation on a pair of *Arianta arbustorum* (the third group) in copuli made in 20.08.2014 in Austria (environs of Sulzkarsee Lake, Styria, photo by Katharina Jaksch) showed that the stimulator works as a stimulator proper, i.e. it signalizes to the partner that the individual is ready to copulate (Fig. 15). In this species, similar to other species assigned to the same group, stimulator does not participate in the process of transferring of the spermatophore.

Although, strictly speaking, the single example

of *Arianta arbustorum* does not mean that in all other Ariantinae the stimulator is never involved in the transfer of spermatophore, I think that this is just so.

In the representatives of the first, second and third groups the papilla during copulation moves out and cannot be everted. In *Isognomostoma* and *Causa* (the third group) the presence of longitudinal pilaster in the inner canal of papilla could reflect the shape of the spermatophore in a cross section.

In species referred to the fourth group the papilla can be partly everted. The boundary, up to which the papilla is able to be everted, is determined by the length of the slit located on the surface of the papilla.

In the members of the fifth group the papilla cannot be everted because schematically it is a trough. Consequently, immediately before copulation the papilla moves out and functionally it is a stimulator. Perhaps, just for this reason the atrial stimulator in the members of the fifth group is rudimentary or absent.

If to admit that everted papilla is secondary in comparison to moving out one, it should be explained why the former is more progressive functionally. I suggest that this may be due to the fact that under everted papilla the way of spermatophore becomes shorter by a distance equal to an everted part of the organ; thus, the duration of pairing becomes shorter, too.

Reducing of the length of spermatophore path, and, consequently, decreasing the duration of the pairing independently observed in the series *Isognomostoma* - *Causa* (the third group), but here this result is achieved simply by shortening of the papilla.

The benefit of reducing of the pairing time is obvious, since the snails during this process are most vulnerable.

I suggest that one of the most perfect structure of papilla is observed in *Faustina faustina*, since during mating the lobes of the papilla is turning away, and the orifice of the epiphallus contacts directly with the atrium of a partner. At the same time the lobes of the papilla may play the role of stimulator. Most probably, the absence in *Faustina* the stimulator in traditional sense is connected just with functional substitution of the stimulator by the lobes of the papilla.

Similarly, in the members of fifth and sixth (*Campylaea*) groups the shortening of the way of the spermatophore is maximal because in this case the opening of the epiphallus contacts directly with the atrium of the partner.

Regarding the taxonomic interpretation of the presented data, perhaps, it may make sense to give to the listed groups the rank of tribe. However, at

the moment I refrain from such a step – until more full examination of species of different genera.

Summing up the data of this and earlier [Schileyko, 2013] articles, one can make the following preliminary conclusions on the possible ways of the evolution of copulative apparatus of Ariantinae.

1. Parenchyma which initially fills the walls of penial papilla, is replaced by a cavity through loosening of tissue and forming of sinuses and lacunae. This tendency has traced independently in several phylogenetic lineages.

2. Size and shape of a stimulator generally does not depend on the structure of papilla, unless some elements of papilla take on themselves the role of stimulator.

3. Papilla or its elements sometimes can play role of stimulator. In such cases stimulator is reduced down to full disappearance.

4. One of important directions of evolution of copulatory apparatus is shortening of path of the spermatophore to the vagina of a partner and reducing the time of mating. This is provided, in particular, by functional replacement of stimulator by elements of papilla or simply by shortening of papilla itself.

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Correction. In my article [Schileyko, 2013] on the Fig. 16 (p. 147), the letters “A” and “B” must be reversed: actually, the letter “A” refers to the *Arianta* (*Altarianta*) and “B” - to *Arianta* (*Arianta*).

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О морфологии копулятивного аппарата некоторых Ariantinae (Pulmonata Helicidae)

А.А. ШИЛЕЙКО

Институт проблем экологии и эволюции им. А.Н. Северцова РАН, 119071 Москва, Ленинский проспект, 33, РОССИЯ. E-mail: asch0829@gmail.com

РЕЗЮМЕ. Статья содержит дополнительные сведения о строении папиллы пениса и атриального стимулятора представителей 13 видов и подвидов из 8 (под)родов Ariantinae. Показано существование в пределах подсемейства пяти или шести вариантов строения копулятивного аппарата. Папилла пениса или её элементы могут принимать на себя роль стимулятора; в таких случаях стимулятор редуцируется вплоть до полного исчезновения.

