Ruthenica, 2017, vol. 27, No. 2: 65-79.
Published online April 11, 2017.

http: www.ruthenica.com

New anatomical data and taxonomical notes on Metafruticicolinae (Pulmonata, Hygromiidae)

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ABSTRACT. Based on the study of the reproductive tract of *Metafruticicola occidentalis* Subai, 1999, it is shown that the species belongs to a new subgenus (***Elbasania*** subgen. nov.). For comparison, the anatomy of seven species of the genus *Metafruticicola* (including type species) has been studied. It is shown that the species of this genus are clearly distinguished from one another by the structure of the copulative apparatus (mainly of penial papilla). Comparison of the genus *Metafruticicola* with the representatives of other genera of Hygromiidae that have no accessory organs on the vagina is conducted. We suggest that the genus *Cyrnotheba* Germain, 1929 may belong to the subfamily Metafruticicolinae while the genus *Caucasocressa* does not belong to this subfamily and might be included in the subfamily Monachainae. Problems of taxonomic structure of the genus *Metafruticicola* are briefly discussed.

Introduction

Bank *et al*. [2013] in the thorough revision of the genus *Metafruticicola* recognized four subgenera (*Metafruticicola* s. str., *Cretigena* Schileyko, 1972, *Rothifruticicola* Bank, Gittenberger et Neubert, 2013, and *Westerlundia* Kobelt, 1904). The subgenera, according to these authors, are characterized mainly by the peculiarities of the sculpture of postembryonic whorls (teleoconch). At the same time the authors claimed that "On the basis of only the morphology of the genitalia, a subdivision of *Metafruticicola* cannot be presented." [Bank *et al*., 2013: 69]. Nevertheless, they provided illustrated descriptions of some anatomical characters for 10 species and subspecies, although had not used these features in diagnoses of taxa. Unfortunately, the illustrations in the article by Bank *et al*. [2013] are not always comparable with drawings presented here, in particular, because of different style of drawings. Besides, Bank *et al*. sometimes gave insufficiently detailed descriptions and images of the structure of the penial papilla and had not presented cross-sections through this organ. Meanwhile, the peculiarities of anatomical details give a sufficient material for thoughts about taxonomy and phylogeny of some pulmonate taxa, in particular, of Metafruticicolinae.

Systematic position of *M. occidentalis* Subai, 1999 in the revision by Bank *et al*. remained unclear. By general shell morphology this species is somewhat similar to *M.* (*Rothifruticicola*) *redtenbacheri* (Pfeiffer, 1856); however, on the basis of microscopic pustulation of the shell surface, Bank *et al*. [2013] provisionally placed *M. occidentalis* into the subgenus *Westerlundia*.

It is worthy of note that *M. occidentalis* has a geographic range (from Central Albania to Epirus in Greece) northwest of and relatively far from the main range of the genus *Metafruticicola*. Distribution area of *Metafruticicola* sensu lato generally covers the north-eastern Mediterranean, the majority of its species inhabits Greece and the adjacent territories of Turkey; the easternmost findings are in Turkey (Vilayet Isparta) and in Cyprus island.

One of the authors (Z.F.) in the course of field work in Albania has collected one adult specimen of a snail which we determined as *Metafruticicola occidentalis* Subai, 1999. Since reproductive tract of this species clearly differs from all other species of *Metafruticicola* whose anatomy is known, we studied seven more species of this genus (including type species of the genus, *M. pellita*) to establish possible differences between species (or subgenera?) of the genus.

Because of lack of material, *we have not set ourselves the task of a new revision of* Metafruticicola. *The main aim of this work is to draw colleagues' attention to the anatomical characters* which are used here and to formulate some particular taxonomic hypotheses.

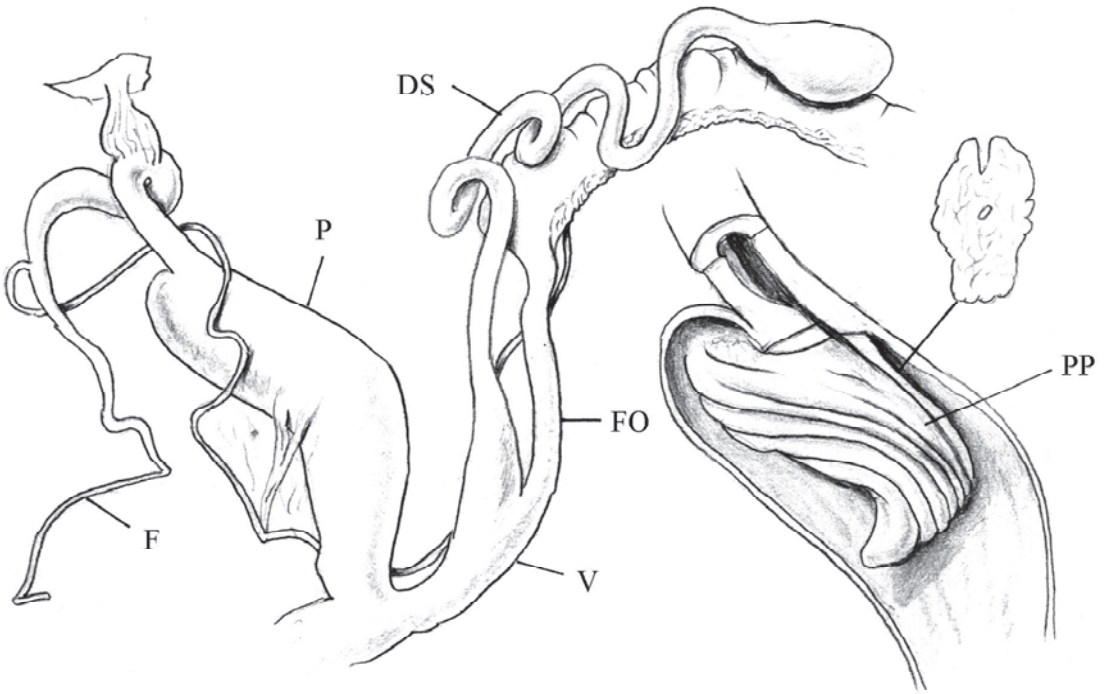

FIG. 1. *Metafruticicola* (*Metafruticicola*) *pellita*. Reproductive tract and inner structure of penis.

РИС. 1. *Metafruticicola* (*Metafruticicola*) *pellita*. Репродуктивный тракт и внутреннее строение пениса.

Material and methods

The list of used material is placed at the descriptions of each species, next to "locus typicus". Dissections were made manually under stereomicroscope Olympus SZ.

Abbreviations in the text and figures. HNC – Haus der Natur Cismar. HNHM – Hungarian Natural History Museum, Budapest. I.Z.PAN – Zoological Institute of Polish Academy of Sciences, Warsaw. NHMW – Natural History Museum, Vienna. ZMMU – Zoological Museum of Moscow State University. DS – duct of spermatheca; E – epiphallus; F – flagellum; FO – free oviduct; P – penis; Pd – "pad" in penis; PP – penial papilla; RP – retractor of penis; RS – reservoir of spermatheca; Sti – stimulator; V – vagina.

Systematic part

Bank *et al*. [2013] accepted 29 valid taxa (species and subspecies) within the genus *Metafruticicola*. Apart from the eight presented in this study, the structure, or at least the outlines of the penial papilla for seven more taxa are known.

Anatomical diagnoses of the subgenera based on their type species (except for the subgenus *Westerlundia*); the descriptions of the species are given below.

Metafruticicola Ihering, 1892

Ihering, 1892: 452; Hesse, 1931: 28; Schileyko, 2005: 2037; Bank *et al*., 2013: 68.

Type species – *Helix pellita* Férussac, 1832, by subsequent designation by Pilsbry, 1895 (1893-1895).

Reproductive tract simple, without additional organs except for long flagellum. Vagina short, comparatively thin-walled (exception: species of the subgenus *Elbasania* have a long, thick-walled vagina). Penial papilla of various structure. Stimulator absent, except for the subgenus *Elbasania* type species of which has small stimulator.

Metafruticicola (*Metafruticicola*) Ihering, 1892

Conchological diagnosis after Bank *et al*. [2013]: "Shell yellowish light-brown, with a white peripheral zone bordered by 1-2 distinctive reddish brown bands. Teleoconch with microscopically distinct, densely arranged spiral sculpture. The teleoconch has in addition long, straight hairs (leaving behind hair-scars when worn away)".

Penial papilla differs by curved tip, the presence of on its surface a series of deep, narrow, spirally directed furrows. Epiphallic pore opens into one of these furrows. Stimulator absent.

Metafruticicola (*Metafruticicola*) *pellita* (Férussac, 1832) (Fig. 1)

Helix (*Helicella*) *pellita* Férussac 1821: 42 (livr. 10, Folio edition), nom. nudum.

Helix pellita Férussac 1832 in Férussac et Deshayes, 1819-1851: iii, pl. 69.

Metafruticicola pellita – Hesse, 1884, Taf. 5, Fig. 13b; Hesse, 1931: 28, Taf. 5, Fig. 35; Taf. 16, Fig. 2; Schileyko, 1972: 13, fig. 1; Welter-Schultes, 2012: 550; Bank *et al*., 2013: 119, figs 96, 122-125, 134-136, 141, 150.

Locus typicus: "L'île de Rhodes, Olivier".

Material. Lemnos [Greece], 1927, leg. Werner, det. W. Adensamer. NHMW No. 55.943. 1 specimen.

Vas deferens very long, evenly slender. Flagellum long, gradually thickened towards epiphallus. Flagellum and epiphallus of about equal length. Penis much thicker (more than twice) than epiphallus. Inner penis surface lacks regular relief. Upper portion of penis occupied by voluminous, curved at tip, thick-walled papilla that bears on its surface a series of deep, narrow, spirally directed furrows. Epiphallic pore opens into one of these furrows. Penial retractor attached to epiphallus somewhat distal of its middle. Vagina and basal part of spermathecal duct slightly thickened. Free oviduct little longer than vagina. Duct of spermatheca very long, convoluted; reservoir bulky, lies on upper part of spermoviduct.

Metafruticicola (*Cretigena*) Schileyko, 1972

Schileyko, 1972: 18 (pro gen.); Bank *et al*., 2013: 76; Schileyko, 2005: 2038 (pro gen.).

Type species – *Helix sublecta* Maltzan, 1884, by original designation.

Conchological diagnosis, after Bank *et al*. [2013]: "Shell white to greyish-yellow, with three distinct reddish-brown bands. Teleoconch in most cases with clear, very characteristic spiral ridges; a spiral microsculpture is missing. Pustulation, when present, indistinct and variable in size".

Penial papilla tubular, thick-walled, transversely folded, with very narrow lumen and minute terminal pore. Walls of the papilla contain narrow circular cavity.

Metafruticicola (*Cretigena*) *sublecta* (Maltzan, 1884) (Fig. 2)

Helix lecta Férussac, 1832, in: Férussac and Deshayes: iii (Explication des planches des livraisons XXII-XXVII, pl. 69, fig. 2 (livraison 25). Nom. praeocc., non Fèrussac, 1827.

Helix sublecta Maltzan, 1884: 74.

Cretigena sublecta – Schileyko, 1972: 18, fig. 2; Schileyko, 2005: 2039, fig. 2575 B & C (under name *naxiana*, by mistake).

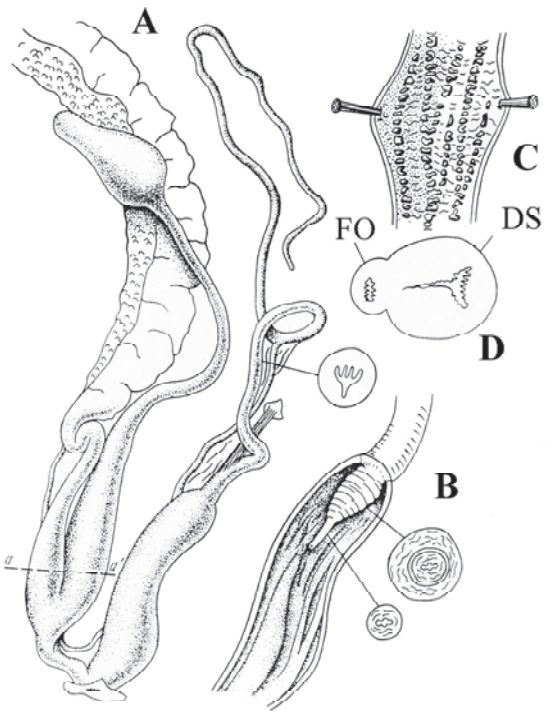

FIG. 2. *Metafruticicola* (*Cretigena*) *sublecta*. A – reproductive tract. B – inner structure of penis. C – inner structure of vagina. D – cross-section through female part of genitalia along the line a-a'. [after Schileyko, 1972].

РИС. 2. *Metafruticicola* (*Cretigena*) *sublecta*. A – репродуктивный тракт. B – внутреннее строение пениса. C – внутреннее строение вагины. D – поперечный срез через женский отдел по линии a-a'. [из Шилейко, 1972].

Metafruticicola sublecta – Welter-Schultes, 2012: 548; Bank *et al*., 2013: 76, figs 11-18, 24-27, 95.

Locus typicus: "fast überall auf der Insel Kreta".

Material. Crete, Knossos near Iraklion, 5.09.1959, leg. A. Riedel, det. I. Likharev and A. Schileyko. 2 specimens. I.Z.PAN.

Flagellum long, evenly thin, about two times longer than epiphallus. Penis generally subcylindrical, its inner surface with irregular axial folds. Penial papilla consists of thick-walled proximal and thin distal parts; proximal part contains narrow circular cavity, its surface bears a number of circular grooves. Penial retractor attached to the epiphallus just above penis/epiphallus junction. Vagina very short, free oviduct 2-2.5 times longer. Internally vagina with irregular longitudinal folds that may be broken into series of small tubercles. Spermathecal duct not convoluted, its basal part markedly swollen, thick-walled. Reservoir of spermatheca pear-shaped, adjoins to middle of spermoviduct.

Metafruticicola (*Rothifruticicola*) Bank, Gittenberger et Neubert, 2013

Bank *et al*., 2013: 82.

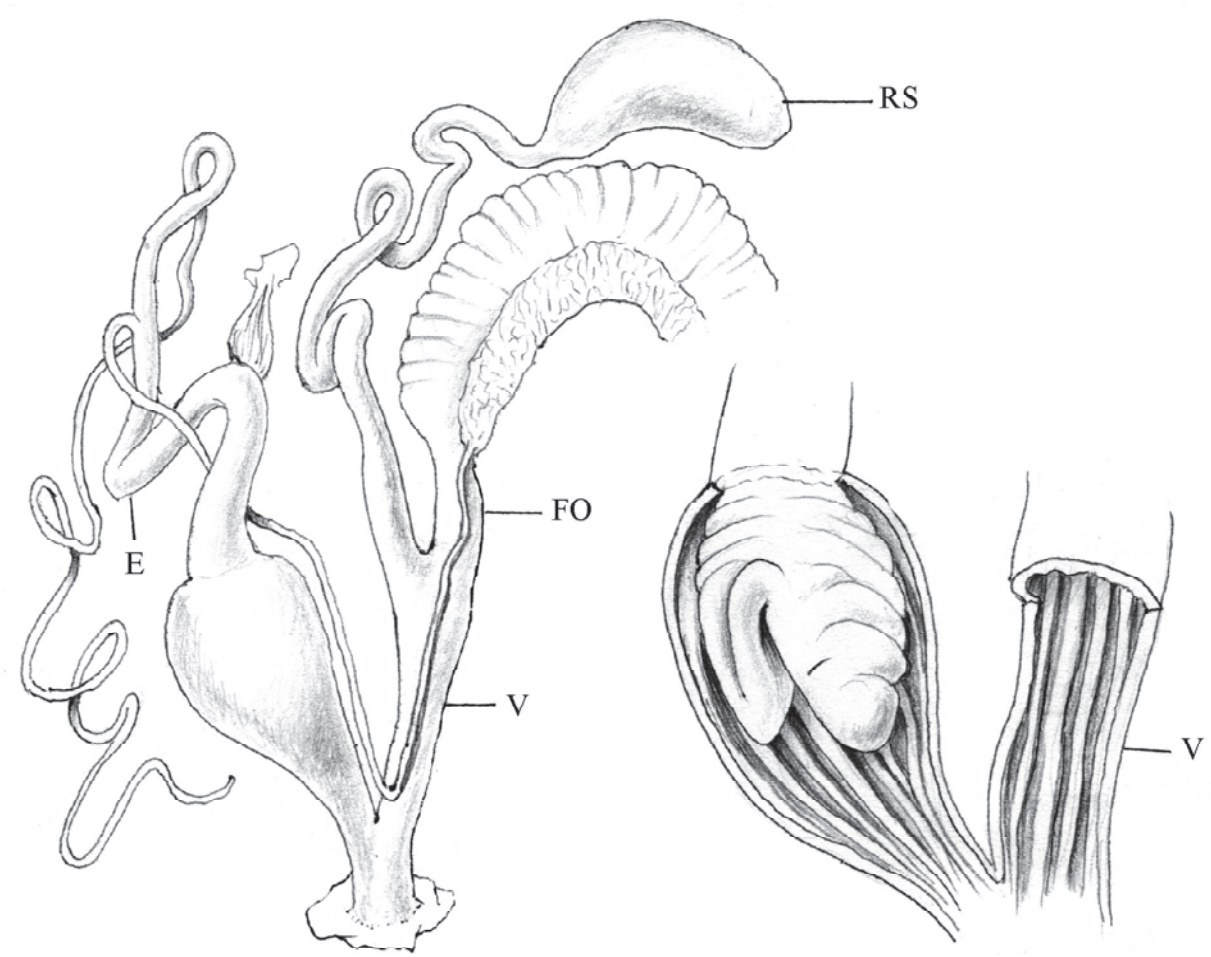

FIG. 3. *Metafruticicola* (*Rothifruticicola*) *redtenbacheri*. Reproductive tract and inner structure of penis and vagina.

FIG. 3. *Metafruticicola* (*Rothifruticicola*) *redtenbacheri*. Репродуктивный тракт и внутреннее строение пениса и вагины.

Type species – *Helix redtenbacheri* Pfeiffer, 1856; by original designation.

Original description: "Shell uniformly light corneous brown to brownish opaque/olive-green with a periphery that has a lighter colour; there are 0-1 coloured bands present. Teleoconch with microscopically weak to more distinct spiral sculpture. Hair-scars are present, although in some species weakly developed (*zonella*/*redtenbacheri*/*schuberti*); some taxa have short, slightly curved hairs (*nicosiana* and *dictaea*; only rarely seen in *redtenbacheri*)."

We can add some anatomical characteristics based mainly on the type species: penial papilla consists of two unequal lobes that bear sharp circular grooves. Pore of epiphallus situated in the depth of papilla between the lobes.

Metafruticicola (*Rothifruticicola*) *redtenbacheri* (L. Pfeiffer, 1856) (Fig. 3)

Helix redtenbacheri Pfeiffer L., 1856: 176, Taf. 2.
Metafruticicola redtenbacheri – Schütt, 1996: 419; Welter-Schultes, 2012: 550; Bank *et al*., 2013: 82, figs 28-37, 81-82.

Locus typicus: "insula Syra".

Material. Eastern Turkey, near Manisa, 06.1997, leg. A. Kuznetsov, det. A. Schileyko. ZMMU Lc-39309, 2 specimens.

Vas deferens thin, long. Flagellum enormously long (perhaps, longer than in any other species of *Metafruticicola*). Penis voluminous, pear-shaped, its inner surface with a number of thin longitudinal folds. Penial papilla consists of two unequal lobes, bearing sharp circular grooves. Pore of epiphallus situated in depth of papilla between lobes. Retractor of penis attached to boundary between first and second thirds of epiphallus. Vagina thin-walled, moderately long, its inner surface has relief similar to those of penis. Free oviduct about three times shorter than vagina. Spermathecal duct long, strongly sinuous. Reservoir of spermatheca large, bean-shaped, lies on upper part of spermoviduct.

Remark. Our data on the anatomy of *M. redtenbacheri* differ from those presented by Bank *et al*. [2013] by qualitative characteristics. In both of our

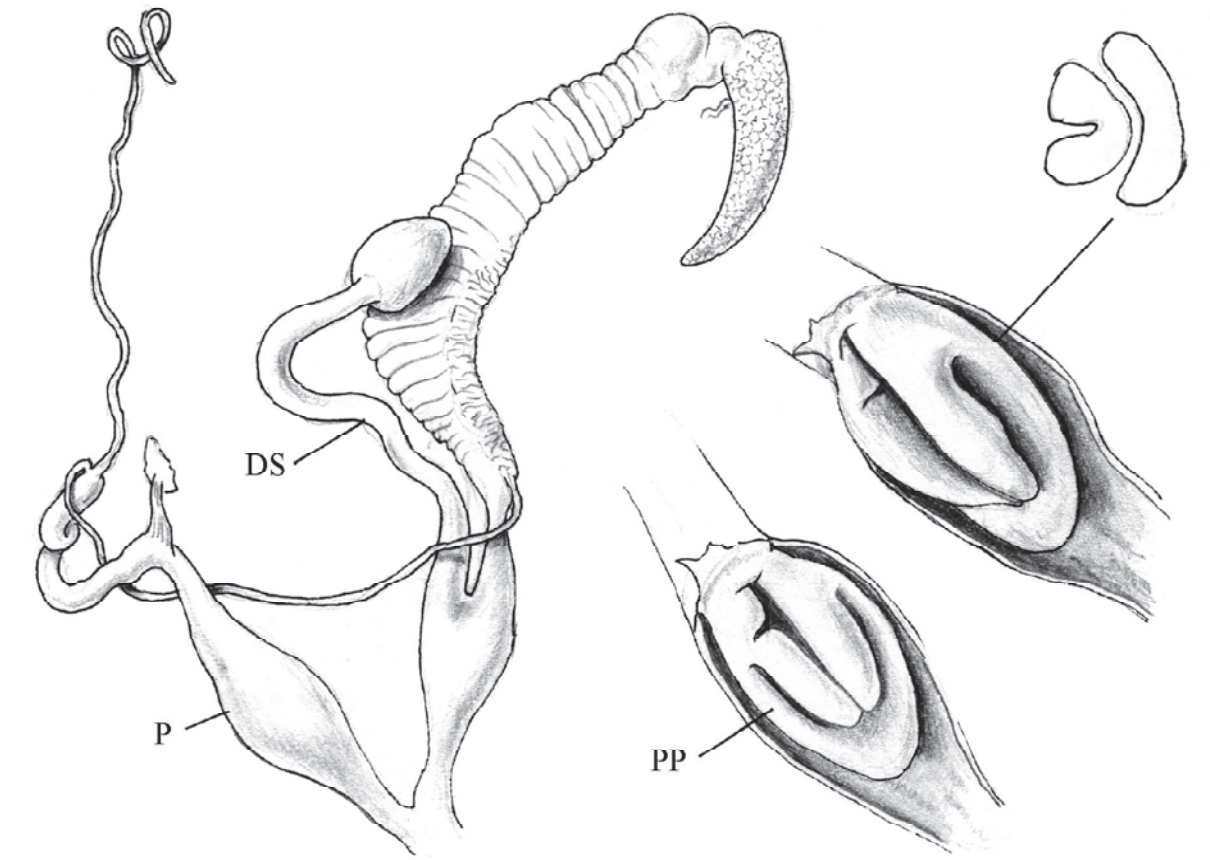

FIG. 4. *Metafruticicola* (?*Rothifruticicola*) *nicosiana soror*. Reproductive tract and inner structure of penis (penial papilla is shown in two positions).

РИС. 4. *Metafruticicola* (?*Rothifruticicola*) *nicosiana soror*. Репродуктивный тракт и внутреннее строение пениса (папилла пениса показана в двух положениях).

specimens the free oviduct is shorter than the vagina while in fig. 81 of Bank *et al*. [2013] the free oviduct is slightly shorter than the vagina. Furthermore, Bank *et al*. [2013] claimed that in this species there is a simple, conical papilla (op. cit., fig. 82) while in our individuals the papilla is clearly bilobed.

Metafruticicola (?*Rothifruticicola*) *nicosiana soror* Fuchs et Käufel, 1936
(Fig. 4)

Fuchs, Käufel, 1936: 640, fig. 70; Bank *et al*., 2013: 105, figs 61-62, 93, 101.

Locus typicus: “Insel Rhodos, Berg Prophet Elias“.

Material. “Griechenland, Rhodos, Mt. Attairo, 1200 m, 10.05.1971, leg. O. Paget, det. M. Mylonas”. NHMW No. 88038. 1 specimen.

Vas deferens thin, entering flagellum/epiphallus junction. Flagellum thin, markedly longer than epiphallus. Penis fusiform, without regular relief on inner surface. Penial papilla consists of two lobes: one of them is a fleshy, spoon-like plate slightly bent along the long axis; the other lobe (plate) is shorter, with a deep longitudinal groove; epiphallic pore opens at the base of this groove. Penial retractor attached to the lower section of epiphallus near penis/epiphallus junction. Vagina not long, free oviduct approximately two times shorter. Spermathecal duct somewhat sinuous, ovate reservoir lies on middle part of spermoviduct.

Remark. The structure of the penial papillae of *M. redtenbacheri* and *M. nicosiana soror* markedly differs (compare the descriptions above and Figs 3 and 4). Besides, these species differ from each other by the relative length of spermathecal duct. We refrain from a final taxonomic decision until anatomical data on other species are known.

Metafruticicola (*Westerlundia*) Kobelt, 1904

Kobelt, 1904: 131, 153 [nom. nov. pro *Latonia* Westerlund, 1889: 30, 68, t.-sp. *Helix berytensis* Pfeiffer, 1841, by subsequent designation of Westerlund, 1903: 91; nom. praeocc., non Meyer, 1843 (Reptilia)]; Bank *et al*., 2013: 110.

Type species – *Helix berytensis* Pfeiffer, 1841; by original designation.

Bank *et al*. [2013: 110] gave the following diag-

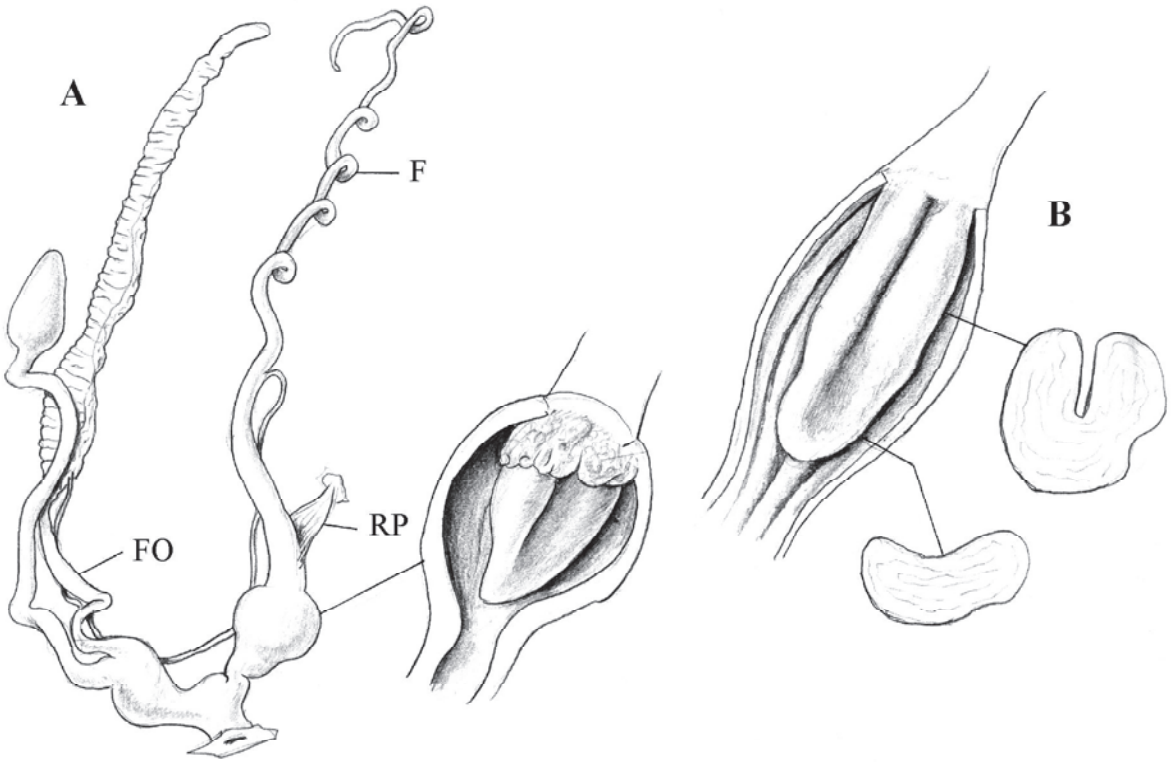

FIG. 5. *Metafruticicola* (*Westerlundia*) *coartata*. A – reproductive tract and inner structure of penis of specimen from Divounia island. B – inner structure of penis of specimen from Astipalea.

FIG. 5. *Metafruticicola* (*Westerlundia*) *coartata*. A – репродуктивный тракт и внутреннее строение пениса экземпляра из о-ва Дивоуния. B – внутреннее строение пениса экземпляра из о-ва Астипалеа.

nosis of the subgenus *Westerlundia*: "Shell greyish-white to reddish-brown, mostly with a pale periphery. There are 0-2 (rarely 3) coloured bands present. Teleoconch without a trace of hairs, but with dense pustulation, which is generally arranged in radial order; in addition, there is a very weak (hardly visible) spiral sculpture."

Inner surface of penis with few wide, smoothed axial folds. Penial papilla fleshy, with longitudinal furrow which at basal portion is narrower and deeper, but more distally becomes wider and more shallow. Epiphallic pore opens into the depth of this groove.

Metafruticicola (*Westerlundia*) *coartata coartata* (Fuchs et Käufel, 1936)
(Fig. 5)

Metafruticicola grelloisii coartata Fuchs et Käufel, 1936: 643, fig. XI, 33A-C, 72-73

Metafruticicola (*Westerlundia*) *coartata coartata* – Bank *et al*., 2013: 117, figs 129-132, 140, 152.

Locus typicus – Greece, "Insel Astropalia" (=Astypalea).

Material. Greece, Insel O-Unia [now Divounia, tiny island NE of Crete], 18.09.1971, leg. A. Pieper, HNHM No. 96480a/2, A1397 (body much contracted). 1 specimen; Greece, Astypalea, 09.07.1971, leg. A. Pieper. HNHM No. A1393, 96478/4. 1 specimen.

Vas deferens very long, convoluted, much longer than epiphallus. Boundary between epiphallus and penis is quite distinct. Penis ovate to subspherical, its inner surface with more or less developed, smoothed axial folds. Penial papilla conical to subcylindrical, with longitudinal groove. In the specimen from Divounia island basal part of papilla surrounded by tissue accrescence. Epiphallus pore situated in the very bottom of the mentioned groove. Penial retractor attached to epiphallus just above penis. Vagina not long, about 2 times shorter than free oviduct. Spermathecal duct long, sinuous; pear-shaped reservoir lies on middle part of spermoviduct.

Metafruticicola (?*Westerlundia*) *naxiana* (Férussac, 1832)
(Fig. 6)

Helix naxiana Férussac, 1832 in Férussac et Deshayes, 1819-1851: pl. 69.

Metafruticicola naxiana – Hesse, 1884: 240, Taf. 5, Fig. 13b; Hesse, 1931: 28, Taf. 5, Fig. 35, Taf. 16, Fig. 2; Welter-Schultes, 2012: 548; Bank *et al*., 2013: 119, figs 96, 122-125, 134-136, 141, 150.

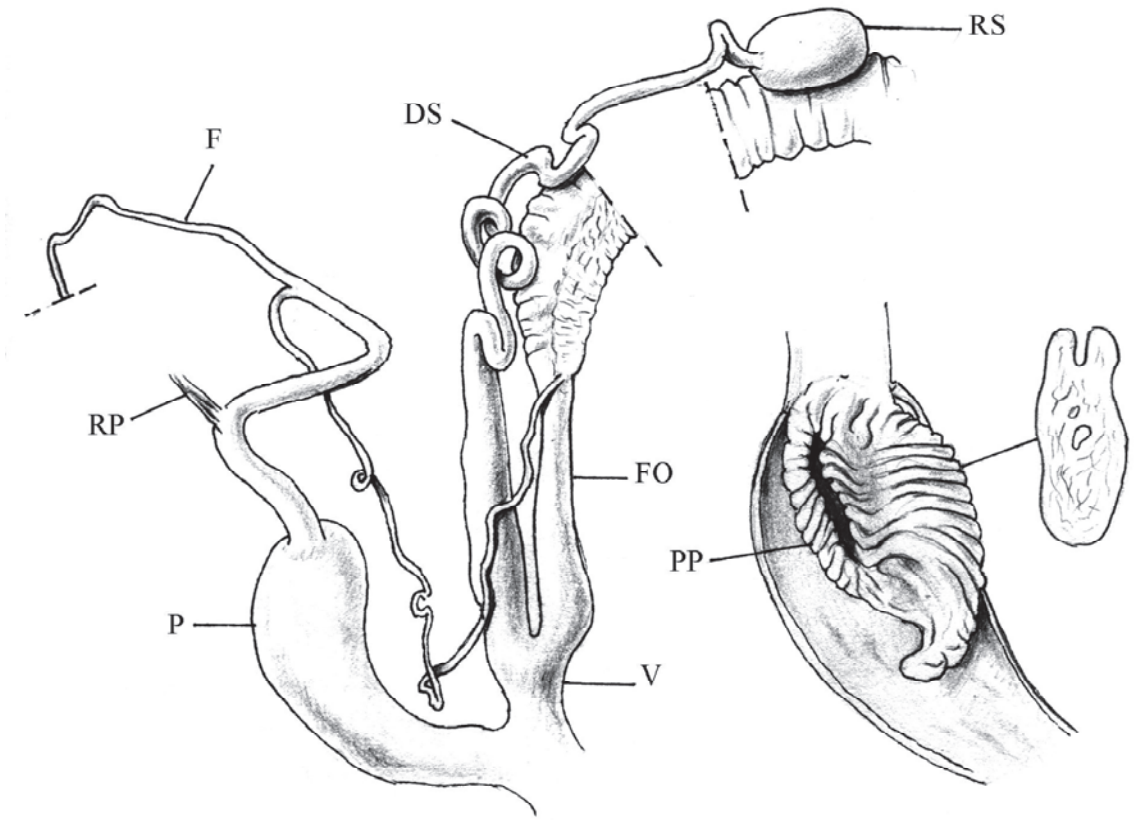

FIG. 6. *Metafruticicola* (?*Westerlundia*) *naxiana*. Reproductive tract and inner structure of penis.

FIG. 6. *Metafruticicola* (?*Westerlundia*) *naxiana*. Репродуктивный тракт и внутреннее строение пениса.

Locus typicus – not indicated (judging from the name, Naxos island; see Bank *et al*, 2013: 119).

Material. "Griechenland, Insel Kreta, Insel Janisada", 03.03.1979, leg. O. Paget, Schönmann, det. H. Sattmann. NHMW No. 85189. 1 specimen.

Vas deferens long, slender, in places convoluted. Length of flagellum and epiphallus almost equal (tail part of flagellum was amputated by an earlier examiner). Boundary between epiphallus and penis quite distinct. Penis bulky, clavate, without regular relief on its inner surface. Penial papilla with curved tip, numerous sharp circular furrows and one longitudinal groove on its surface. Epiphallus pore situated in the bottom of the named groove. Penial retractor attached to the epiphallus little lower of middle of this duct. Vagina very short, about 3 times shorter than free oviduct. Spermathecal duct very long, convoluted; ovate reservoir lies on upper portion of spermoviduct.

Metafruticicola (***Elbasania***) Schileyko et Fehér, subgen. nov.

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Type species – *Metafruticicola occidentalis* Subai, 1999.

Etymology. The name is derived from the name of the city of Elbasan (Albania).

Diagnosis. The subgenus differs from all other subgenera of the genus *Metafruticicola* by the unusually long vagina that has very thick, strongly muscularized walls, and very short free oviduct. Penial papilla is long, tubular. Stimulator is present.

[**Диагноз**. Подрод отличается от всех других подродов рода *Metafruticicola* необыкновенно длинной вагиной с сильно мускулизованными стенками и очень коротким овидуктом; папилла пениса длинная, трубчатая. Стимулятор имеется].

Remark. Our results show that the structure of some elements of reproductive tract of *M. occidentalis* and *M. andria* are different from those of other taxa, including type species of each of the currently accepted 4 subgenera. Therefore, it seems substantiated to move them into a new subgenus.

Metafruticicola (***Elbasania***) *occidentalis* Subai, 1999
(Figs 7, 8, 9)

Metafruticicola occidentalis Subai, 1999: 50, Taf. 10, Fig. 1a-d, Abb. 1-4.

Metafruticicola (?*Westerlundia*) *occidentalis* – Bank *et al*., 2013: 129, figs 145, 151.

FIG. 7. *Metafruticicola* (***Elbasania***) *occidentalis*. Shell. Scale bars 1 mm.

FIG. 7. *Metafruticicola* (***Elbasania***) *occidentalis*. Раковина. Масштаб 1 мм.

Locus typicus: “Griechenland, Epirus, 5 Km von der Landstraâe Filiates–Igoumenitsa in Richtung Mavroneri, oberhalb der Höhlenkapelle, im Fallaub, ca. 150-200 m ü.NN”.

Holotype and one paratype are deposited in the HNC (HNC 53144, HNC 53145)

Material: Albania, Elbasan district, 3 km E of Pashtresh (between Gjinar and Zavalinë), 1000 m a.s.l., rocks and rocky forest, 41°0.018’N, 20°14.844’E, 30.06.2014, leg. D. Angyal, Z. Fehér, J. Grego. The specimen is in NHMW, No. 110430/MN/0163.

Description of the shell of dissected specimen (Fig. 7). Shell depressed-conic, thin-walled, looking smooth, glossy, translucent, of 5 (in original description, 5-6) moderately convex whorls. Tangent-line straight (spire conic). Last whorl at first roundly angulate, toward aperture the angulation disappears. Apex blunt. Colour nearly uniform fulvous,. Embryonic whorls practically smooth, just with barely distinguishable dots. Sculpture of later whorls consists of irregular, smoothed, obliquely-radial wrinkles and, locally, microscopic dots. Aperture subcircular, well oblique, markedly descending in front, with shortly expanded margins. Insertions of margins approached, columellar margin expanded more than the rest ones. Umbilicus narrow, almost cylindrical, comma-like, only slightly covered (practically open). Dimensions: Shell height 8.4, diameter 15.0 mm (in original description: height 7.8-12.3, diameter 11.0-19.5 mm).

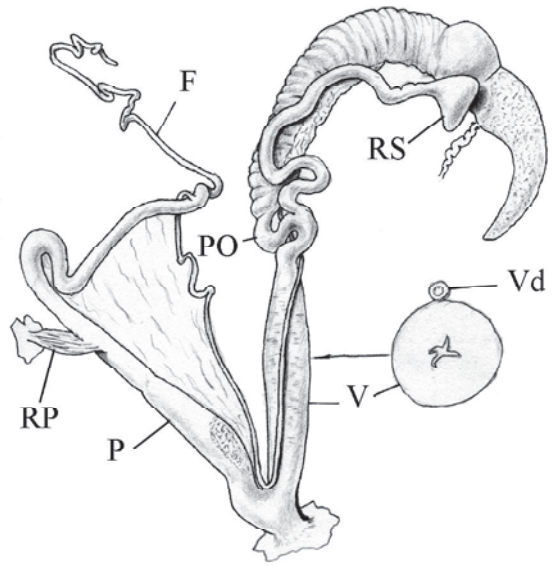

FIG. 8. *Metafruticicola* (***Elbasania***) *occidentalis*. Reproductive tract.

РИС. 8. *Metafruticicola* (***Elbasania***) *occidentalis*. Репродуктивный тракт.

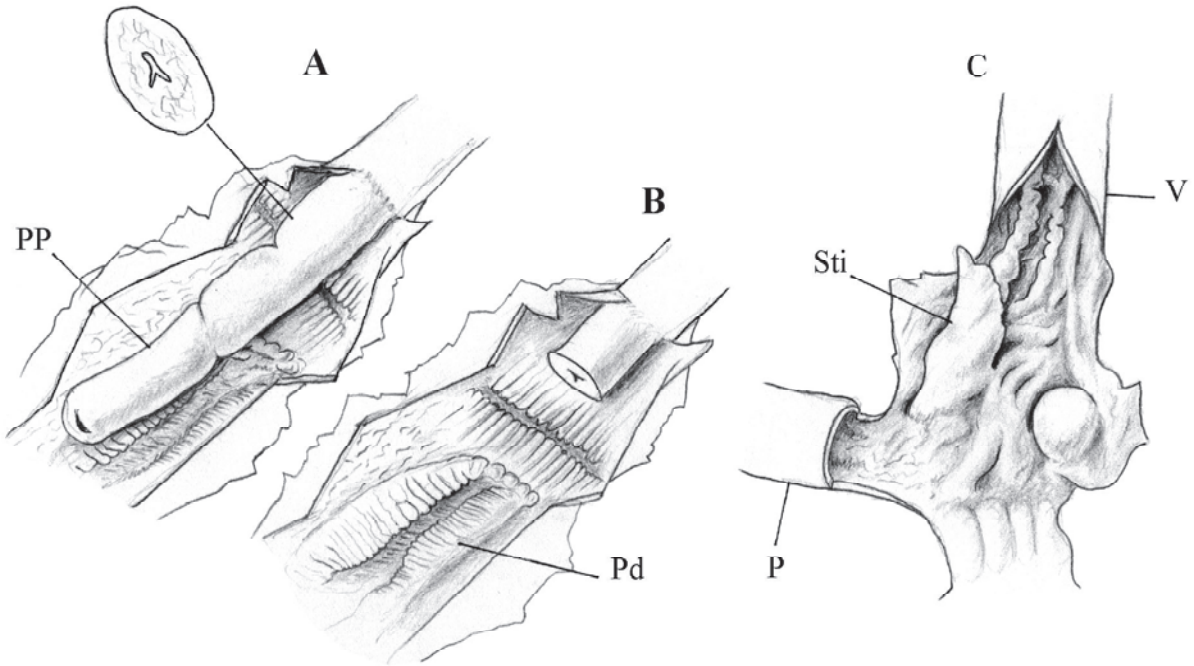

FIG. 9. *Metafruticicola* (***Elbasania***) *occidentalis*. A – inner structure of penis with intact papilla. B – the same, most part of papilla cut off. C – inner structure of atrium and vagina.

РИС. 9. *Metafruticicola* (***Elbasania***) *occidentalis*. A – внутреннее строение пениса с интактной папиллой. B – то же, большая часть папиллы ампутирована. C – внутреннее строение атриума и вагины.

Reproductive tract (Figs 8, 9). Vas deferens very thin, long, runs down to atrium, entering flagellum/epiphallus junction. Flagellum very long, slender, twisted. Epiphallus subcylindrical, about 3.5 times longer than penis; boundary between penis and epiphallus externally nearly absent. Penis slightly fusiform, somewhat thicker than epiphallus. Inner surface of penis bears a sort of a pad of two longitudinal pilasters connected by "bridge" of few rounded tubercles. Between pilasters there is shallow depression. One of pilasters covered with distinct transversal wrinkles some of which divided into 2-3 elongated tubercles. Second pilaster with similar but markedly weaker sculpture. Externally "pad" seen as ovate, light-ochreous, finely alveolar spot. Above "pad" there is an area covered by thin, rather regular longitudinal folds; not far from basis of penial papilla series of these folds cut by circular groove. Papilla of penis long, subcylindrical, with almost smooth surface and narrow semilunar apical pore. In intact penis distal part of papilla lies in depression between described pilasters. Between penis, epiphallus and vas deferens there is very thin, transparent membrane. Penial retractor attached to distal part of epiphallus. Vagina very long, with thick, enormously muscularized walls. Free oviduct very short (about 4.5 times shorter than vagina). Inner surface of vagina with complex system of short folds and small tongue-like stimulator. Spermathecal duct long, strongly sinuous, reservoir of spermatheca hummer-like, lies on boundary between spermoviduct and albumen gland.

Distribution. Westernmost Greece (Epirus) to Central Albania (Mirditë, Tiranë, Librazhd, Elbasan, Përmet and Sarandë districts) [Fehér, Erőss, 2009, Subai, 1999: 49, Abb. 1].

Remark. Bank *et al*. [2013] have placed *Metafruticicola occidentalis* in the subgenus *Westerlundia* with question mark. However, the species of this subgenus have a completely different structure of penial papilla; besides, there are some smaller differences (see Fig. 8, 9 and Bank *et al*., 2013, figs. 121, 123, 125, 127).

Metafruticicola (?***Elbasania***) *andria* (Martens, 1889)

(Fig. 10)

Helix andria Martens, 1889: 181, Taf. 10.
Metafruticicola andria – Welter-Schultes, 2012: 547.
Metafruticicola (*Westerlundia*) *andria* – Bank *et al*., 2013: 116, figs 128, 140.

Locus typicus: "Andros und Mykonos".

Material: Andros, Varithi [Greece], 8.10.1979, leg. et det. M. Mylonas. NHMW No. 82399, 2 specimens.

Vas deferens thin, slender. Flagellum comparatively short – 1.5-2 times shorter than epiphallus which is distinctly demarcated from penis. Latter

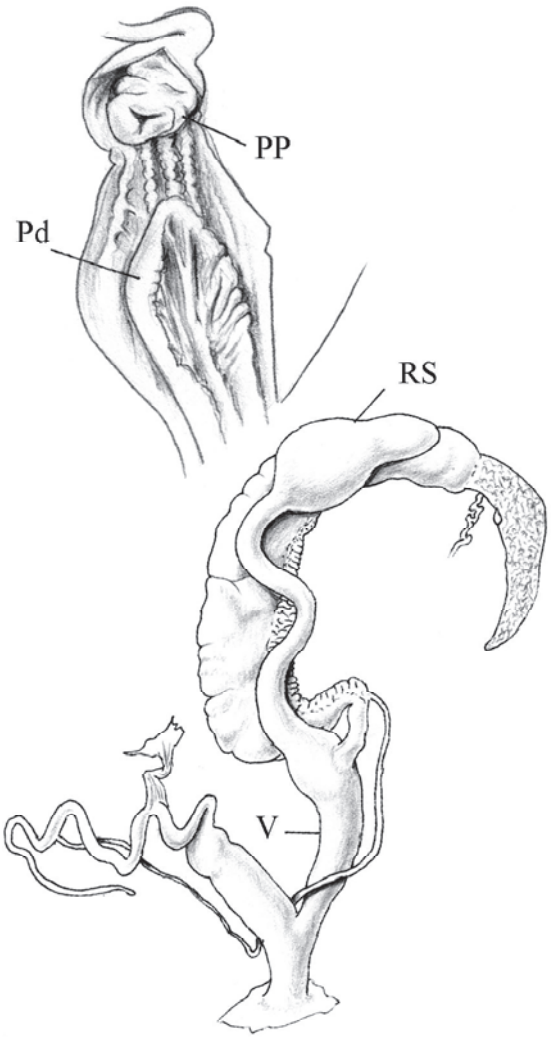

FIG. 10. *Metafruticicola* (?***Elbasania***) *andria*. Reproductive tract and inner structure of penis.

РИС. 10. *Metafruticicola* (?***Elbasania***) *andria*. Репродуктивный тракт и внутреннее строение пениса.

consists of two chambers: proximal (upper) one contains rather short, thin-walled papilla, lower chamber occupied by a sort of "pad" (somewhat similar to that of *Elbasania occidentalis* – see above) that consists of two longitudinal pilasters united by their upper ends. Pore of papilla terminal in shape of three-beam star. Besides, between "pad" and upper chamber there are 3-4 corrugated axial folds. Penial retractor attached to epiphallus somewhat lower of its middle. Vagina thick, long, about 3 times longer than free oviduct. Spermathecal duct thick, comparatively short, not convoluted. Reservoir of spermatheca is voluminous, pear-shaped, lies on uppermost section of spermoviduct.

Remark. Bank *et al*. [2013] attributed *M. andria* to the subgenus *Westerlundia*. However, this species, judging from the structure of penial papilla and the presence of conspicuous "pad" on the inner surface of penis, looks closer to *M. occidentalis* than to the type species of *Westerlundia* (*M. berytensis*) (in *M. occidentalis* and *M. andria* the papilla is tubular, although in *M. andria* it is much shorter). So, we provisionally include *M. andria* in the subgenus ***Elbasania*** because of similarity in the structure of copulatory apparatuses of *occidentalis* and *andria*.

Hiltrudia Nordsieck, 1993

Nordsieck, 1993: 14; Schileyko, 2005: 2006, fig. 2536.

Type species – *Helix mathildae* Westerlund, 1881, by original designation.

Shell diagnosis after Nordsieck [1993: 14]: "Teleoconch (except in the umbilicus) with relatively large radially arranged scales (corresponding to the course of the expansion lines, for example), which are usually abraded down to long elevations when the housing is empty."

Anatomically, from related genus *Metafruticicola*, genus *Hiltrudia* differs by the presence of îvidducal papilla. Atrial stimulator absent.

Hiltrudia kusmici (Clessin, 1887)
(Figs 11, 12)

Helix (*Trichia*) *Kusmici* Clessin, 1887: 51.
Hiltrudia kusmici – Nordsieck, 1993: 14; Maassen, 1995: 11, Abb. 1/3, 13, 15/17, 23/26.

Locus typicus: "… bei Cattaro in der Nähe des Fort Trinita, am Berge vis-à-vis der Stadt …".

Material: Croatia, Lokrum Island (east of Dubrovnik), near monastery, 26.07.1972, leg. P. Subai, L. Pintér, A. Szigethy. HNHM, Nr. A912, 16667a/1, 1 specimen; "Croatia, Sustjepan (north of Dubrovnik), Ombla Valley, in a cave, 31.07.1972, leg. P. Subai, L. Pintér, A. Szigethy". HNHM Nr. A911, 71416a/3, 1 specimen.

Flagellum somewhat longer than epiphallus. Penis generally ovate, its inner surface with very weak relief of circular folds. Penial papilla thick-walled, elongate, ovate-subcylindrical, with numerous circular furrows. Its cavity narrow, in form of three-beam star in cross-section; in apical view strong axial fold divided by narrow groove into two longitudinal parts is seen. Penial retractor attached to lower part of epiphallus. Vagina short, free oviduct two times longer, its basal portion markedly swollen, contains small conical papilla. Spermathecal duct straight, reservoir attends middle part of spermoviduct.

Remark. The genus *Hiltrudia* (2 species) inhabits the Adriatic coast in Croatia, Montenegro and Albania. It resembles *Metafruticicola* (*Elbasania*) in the presence of tubular papilla, although the flagellum in both species of *Hiltrudia* is markedly shorter [Maassen, 1995, figs 13-14]. The *Hiltrudia* species can be distinguished from *Metafruticicola occidentalis* by their peculiar shell sculpture, comparatively short flagellum, and the presence of oviducal papilla.

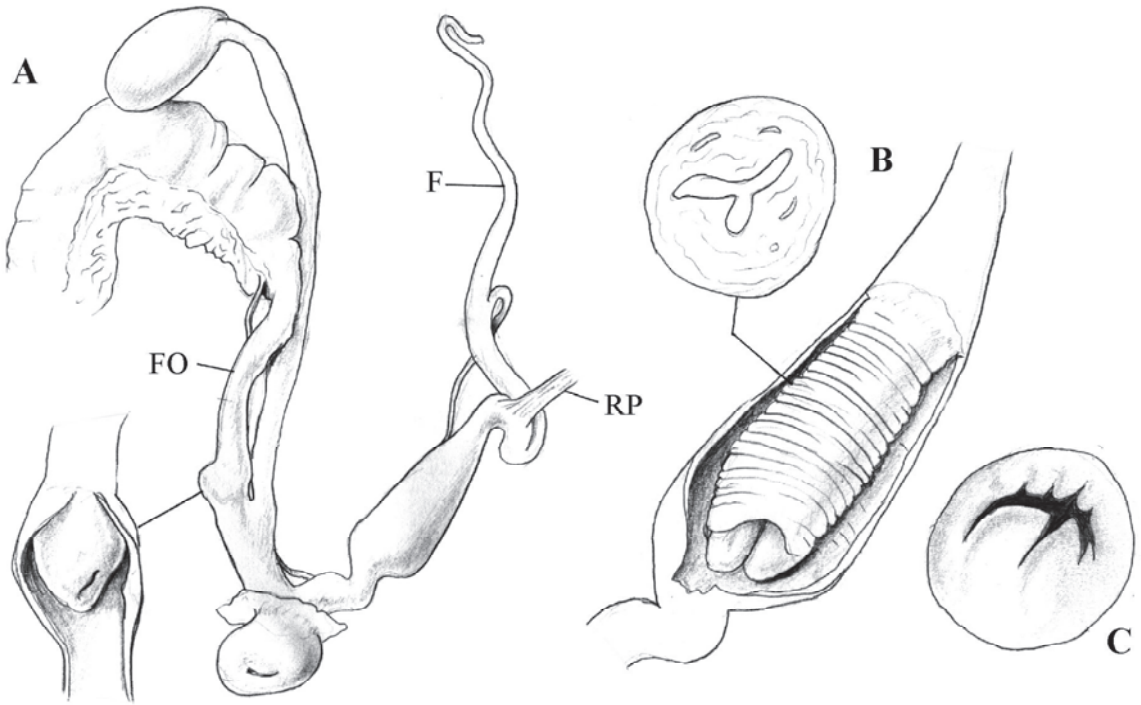

FIG. 11. *Hiltrudia kusmici*, specimen from Sustjepan. A – reproductive tract and inner structure of basal part of free oviduct to show oviducal papilla. B – inner structure of penis. C – penial papilla, apical view.

РИС. 11. *Hiltrudia kusmici*, экземпляр из Сустьепана. A – репродуктивный тракт и внутреннее строение базальной части овидукта, видна папилла овидукта. B – внутреннее строение пениса. C – папилла пениса, вид спереди.

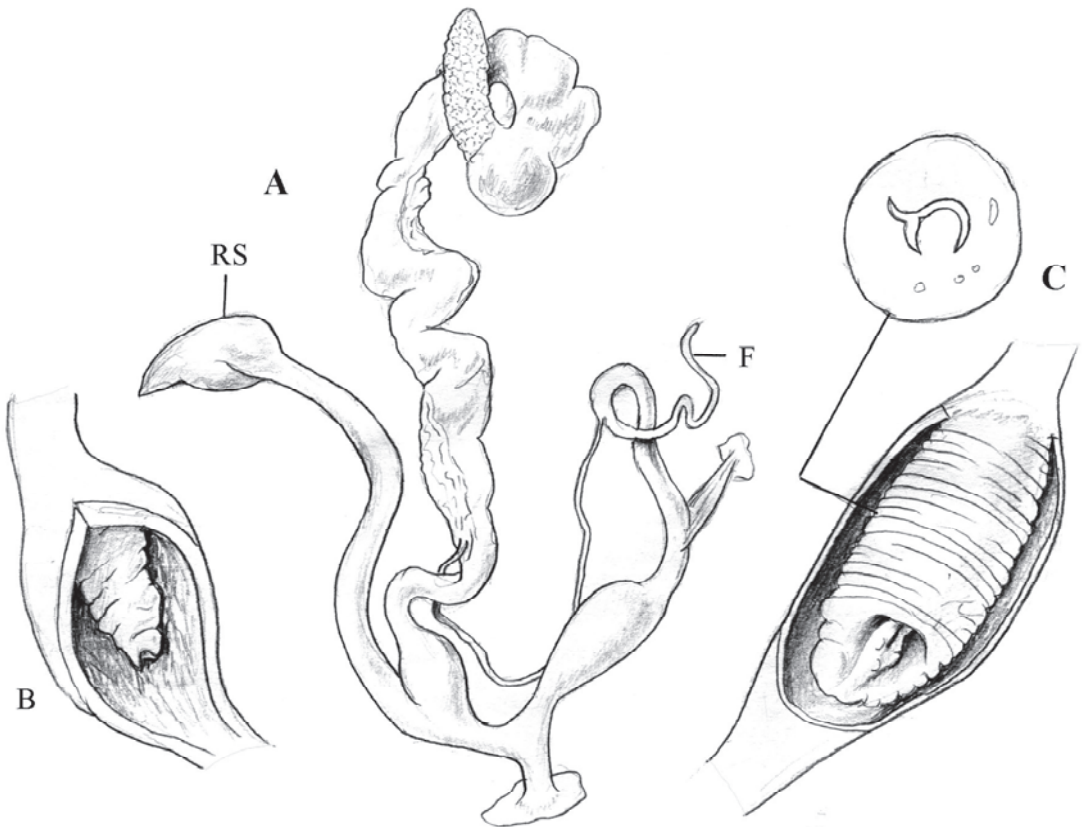

FIG. 12. *Hiltrudia kusmici*, specimen from Lokrum island. A – reproductive tract. B – basal part of free oviduct open to show oviducal papilla. C – inner structure of penis.

РИС. 12. *Hiltrudia kusmici*, экземпляр из о-ва Локрум. A – репродуктивный тракт. B – базальная часть свободного овидукта, вскрыта; видна папилла овидукта. C – внутреннее строение пениса.

Discussion

According to the revision of Bank *et al*. [2013], 29 valid species and subspecies of *Metafruticicola* are known [Bank *et al*., 2013; Boettger, 1907; Fuchs, Käufel, 1936; Gümüş, Neubert, 2012; Hausdorf *et al*., 2004; Martens, 1889; Reischütz, 1988; Subai, 1999; Welter-Schultes, 2012]. For 19 of them the external view of reproductive tract is studied; for 14 of them the structure of the penial papilla (or, at least, its outlines) is known. However, the genitalia in the representatives of the genus are simple and deprived of any additional organs (stylophores, mucous glands, atrial or vaginal appendages) that are used in taxonomy of other taxa of Hygromiidae. In fact, the species of *Metafruticicola* usually differ from one another, except conchological features, by *quantitative* characteristics (comparative length of flagellum, epiphallus, penis, vagina, free oviduct and spermathecal duct) only. Such uniformity obstructs the attempts of understanding of the system of the genus and its relations to other genera of the Hygromiidae family.

However, as it has been shown above, we have managed to find a structure on which is possible to lean in morphofunctional and taxonomic constructs. This structure is copulatory apparatus, mainly penial papilla. As shown above, the papilla has diverse structure, which indicates the existence of subtle differences in the mechanisms of copulation among the species. Interspecific differences in structure of the papillae are quite natural, since they evidently act as pre-copulatory isolating mechanisms. In eight species which we studied, the structure of this organ is distinctly different and sometimes correlates with the geographical distribution of species.

Thus conchologically similar species *Metafruticicola pellita* and *M. naxiana* have the papillae of similar structure: both have the curved tip and more or less deep longitudinal grooves, into one of which the epiphallic pore opens. At the same time the direction of the mentioned grooves in these two species is different. In both species the inner surface of the penis is deprived of permanent and regular relief. Above all, in both species the vagina is shorter than free oviduct. Bank *et al*. [2013] have placed *M. pellita* and *M. naxiana* in different subgenera (*Metafruticicola* s. str. and *Westerlundia* correspondingly). These subgenera, according to the named authors, differ mainly by the sculpture of teleoconch: in the species of *Metafruticicola* s. str. postembryonic whorls are with microscopical, densely arranged spiral sculpture; besides, the surface of teleoconch has long, straight hairs; in the species of the subgenus *Westerlundia* hairs or their traces are absent, but there is dense pustulation, which is generally arranged radially; besides, there is a hardly visible spiral sculpture.

Here we are facing with the problem of priority of characters: if to assume that the sculpture has a higher taxonomic weight, then the validity of the subgenus *Westerlundia* is justified. If to give the priority to anatomical features, then the species of this subgenus (at least some of them) should be placed in the nominative subgenus. We are inclined to the second variant because the structure of papillae amenable to interpretation from the functional point of view since differences in the structure of papillae suggest the existence of differences in the mechanism of copulation, whereas the role of differences in the sculpture in the mollusk's life is no more than an object of speculation (at least, at the given time).

These species occupy the southern part of the distribution area of the genus.

Cretan species *M. sublecta* with regard to the structure of papilla takes somewhat isolated position (Fig. 2), that is why at the present time it is hard to indicate its relatives.

Reproductive tract of *M. andria* somewhat resembles those of *M. occidentalis*: in both species the papilla is as a tube with apical position of the orifice (pore). The inner surface of the penis has a clear and complex relief (see the descriptions above). In both species the vagina is longer than free oviduct. These species occupy the central and western part of the distribution area of the genus.

Penial papilla of *M. nicosiana soror* differs clearly from all other species examined (see the description and Fig. 4): this organ consists of two lobes and the pore of the epiphallus is opened into the longitudinal groove extending along the surface of one of the lobes. Inner surface of the penis lacks a regular relief. Vagina is not long, free oviduct is about two times shorter. This taxon occupies central part of distribution area of the genus.

Formally, penial papilla of *M. redtenbacheri* is similar to that of *M. nicosiana soror* (in both species the papilla is two-lobed), but in latter the smaller lobe bears a deep longitudinal furrow (compare Figs 3 and 4). Bank *et al*. [2013: 83-84, fig. 82] wrote that this species (the specimen from island Antikythira) has "a simple, conical papilla"; they did not indicate where the pore of the papilla is situated. We find it difficult to explain the reason for this discrepancy. *M. redtenbacheri* widely distributed in eastern part of the genus area, mainly in coastal territories of southwestern Turkey [Bank *et al*., 2013, fig. 37; Schütt, 1996], while *M. nicosiana* occupies the islands Crete, Karpathos, Rhodes and Cyprus.

Diversity of characters connected with structure of the papilla indicates that it is possible to use them for decision of problems of taxonomic structure of the genus *Metafruticicola* and historical connections among the species. It is appropriate to

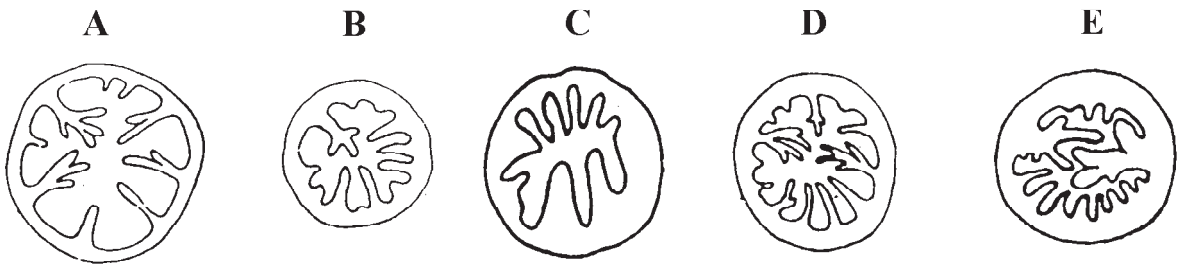

FIG. 13. Cross sections through penial papilla. A – *Caucasocressa delabris*, B – *Stenomphalia ravergiensis*, C – *Stenomphalia bactriana*, D – *Oscarboettgeria euages*, E – *Monacha fruticola* (from Schileyko, 1972, 2004).

РИС. 13. Поперечные срезы через пениальную папиллу. A – *Caucasocressa delabris*, B – *Stenomphalia ravergiensis*, C – *Stenomphalia bactriana*, D – *Oscarboettgeria euages*, E – *Monacha fruticola* (из Шилейко, 1972, 2004).

parallel the situation with Ariantinae (Helicidae), the structure of papillae of which allows to speculate about the historical links between taxa [Schileyko, 2013, 2014].

Generally, at the moment among *Metafruticicola* one can distinguish three principal variants of the papilla structure.

1. Simple tube with apical pore: in particular, *occidentalis*, *andria*, ?*berytensis*, ?*dictaea*, *sublecta*, ?*zonella*, *noverca*, *nicosiana freytagi*.

2. Conical papilla with longitudinal groove; pore of epiphallus situated on the bottom of this groove: *nicosiana claudia*, *nicosiana maasseni*, *pellita*, ?*naxiana*.

3. Bilobed papilla; epiphallic pore located in the depth between the lobes: *redtenbacheri*, *nicosiana nicosiana*.

These three groups are not quite coinciding with the subgenera which have been distinguished by Bank *et al*. [2013]. Moreover, the different subspecies of one of species (*nicosiana*) turned to be in different groups. These discrepancies are connected mainly with the scarcity of data, and we hope that further researches will help to remove the contradictions.

It should be added that comparison of the diagnoses of subgenera *Rothifruticicola* and *Metafruticicola* s. str. presented by Bank *et al*., shows that these subgenera, in essence, do not differ from one another, although type species of these subgenera differ by the structure of the papilla quite well. The solution of this problem should be postponed until anatomy of included species is investigated properly.

Finally, few words should be added about the volume of the Metafruticicolinae subfamily and its taxonomic borders.

In Hygromiidae, beside *Metafruticicola* sensu lato, there are five other genera with simple reproductive tract: *Cyrnotheba* Germain, 1929, *Hiltrudia* Nordsieck, 1993, *Aschfordia* Taylor, 1917, *Steenbergia* Mandahl-Barth, 1950, and *Caucasocressa* Hesse, 1921. Therefore, we should decide whether there are among them the taxa that are appropriate to include in the Metafruticicolinae.

Apparently, *Aschfordia* and *Steenbergia* lost vaginal appendages independently and do not related to *Metafruticicola*. This is evidenced by the distinct conchological differences and geographical distribution (*Aschfordia* lives in the Great Britain and Spain, *Steenbergia* – in Madeira and the Azores).

Corsican genus *Cyrnotheba* Germain, 1929 (2 species), perhaps, might be included in the Metafruticicolinae, since both shell and reproductive tract of *Cyrnotheba corsica* (Shuttleworth, 1843) somewhat resemble those of *Metafruticicola* (***Elbasania***) *occidentalis* (long flagellum, tubular papilla, long vagina and spermathecal duct) [Schileyko, 2005, p. 2004, 2006, fig. 2535].

Subfamily affiliation of the genus *Caucasocressa* is also not quite certain. Schileyko [1972, 1978, 2005] considers this genus in the subfamily Metafruticicolinae because the species of this genus have no vaginal appendages. Papilla in the species of *Caucasocressa* is tubular, thin-walled, with vast lumen, apical position of the pore and inner thin, high longitudinal folds; flagellum is comparatively short; vagina and free oviduct are very short. Distribution area of this genus embraces western Transcaucasia and adjacent territories of Turkey [Hausdorf, 2003; Hausdorf, Falkner, 2001; Schileyko, 2005].

We suggest that the simplicity of the reproductive tract of the species *Caucasocressa* arose independently and its ancestors can be found among some other Hygromiidae. We tend to assume that such ancestors could be some Monachainae, related to recent *Stenomphalia*, *Oscarboettgeria*, or some *Monacha*, which lost vaginal appendages. In the members of the listed genera within papilla there are numerous, high, longitudinal lamellae (Fig. 13).

If our assumption is correct, the genus *Caucasocressa* should be placed in Monachainae, while the subfamily Metafruticicolinae should be restricted by the genera *Metafruticicola* with subgenera, *Hiltrudia*, and, perhaps, *Cyrnotheba*.

Acknowledgements

This study was supported by the Austrian Science Fund (FWF P 26581-B25) (to Z.F.) and by the Society of Friends of the Natural History Museum in Vienna (Gesellschaft der Freunde der Naturhistorisches Museum Wien) (to A.Sch.). We are deeply grateful to Dr. Helmut Sattmann for his help in many ways. We are also indebted to Dorottya Angyal, Jozef and Maroš Grego who helped us in obtaining the specimen of *M. occidentalis* and to Anita Eschner and Elisabeth Belicic for valuable technical assistance. We are indebted to two anonymous reviewers of an earlier version of this paper. Although we do not fully agree with their opinions and believe that our findings provide useful new data, this version has benefited greatly from their critical comments.

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Новые данные по анатомии и заметки по таксономии Metafruticicolinae (Pulmonata, Hygromiidae)

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РЕЗЮМЕ. Показано, что виды рода довольно хорошо различаются строением копулятивного аппарата (в основном папиллы пениса). Проведено сравнение рода *Metafruticicola* с представителями других родов Hygromiidae, не имеющих дополнительных органов на вагине. Высказано предположение, что роды *Cyrnotheba* Germain, 1929 и *Hiltrudia* Nordsieck, 1993 могут принадлежать подсемейству Metafruticicolinae, тогда как род *Caucasocressa* принадлежит, вероятно, подсемейству Monachainae. На основании изучения репродуктивного тракта *Metafruticicola occidentalis* Subai, 1999 этот вид отнесён к новому подроду (***Elbasania*** subgen. nov.). Для сравнения исследовано ещё семь видов рода *Metafruticicola* (включая типовой вид рода) и один из двух известных видов рода *Hiltrudia*. Кратко обсуждаются проблемы таксономической структуры рода *Metafruticicola*.